Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium — Part 3: Ophiuroids

with a chapter on: Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark) by Manfred Kutscher & John W.M. Jagt

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The present paper is divided into two parts. In the first, all Campanian, Maastrichtian and Danian ophiuroids known to date from the extended type area of the Maastrichtian Stage, are described and illustrated. The geographic and stratigraphic distribution of this diverse echinoderm group are documented. A total of twenty-one genera (one of them new) and thirty-seven species (seven of them new) are recorded from the Campanian-Danian of Liège-Limburg and the Aachen area (Germany). The following taxa are new: *Ophiocten*? *yvonnae* sp. nov., *Stegophiura*? *trispinosa* sp. nov., *Deckersamphiura inusitata* gen. et sp. nov., *Ophiarachna*? *martinblomi* sp. nov., *Ophiolepis*? *falsa* sp. nov., *Ophiomusium lux* sp. nov., and *Mesophiomusium decipiens* gen. et sp. nov. Additional species, recorded here in open nomenclature, may prove to be new as well, but limited material precludes their formal naming.
Many ophiuroid species from Liège-Limburg are also known from the Lower Maastrichtian of Rügen and Møn (Denmark). In general, material from those localities is much better preserved, which is why type specimens of additional new taxa have been selected from samples collected there. In the second part of the present paper a total of twenty-four new species and one new genus are described: *Ophiosmilax*? *alternatus* sp. nov., *Asteronyx*? *spinulosa* sp. nov., *Ophiomyxa*? *curvata* sp. nov., *Ophiomyxa*? *rhipidata* sp. nov., *Ophioscolex*? *clivulus* sp. nov., *Ophioscolex*? *cretaceus* sp. nov., *Ophiacantha*? *punctata* sp. nov., *Ophiacantha*? *rugosa* sp. nov., *Ophiacantha*? *striata* sp. nov., *Sinosura jasmundensis* sp. nov., *Hemieuryale*? *parva* sp. nov., *Amphiura*? *plana* sp. nov., *Ophiothrix*? *bongaertsi* sp. nov., *Ophiothrix*? *cristata* sp. nov., *Ophiothela*? *semirotunda* sp. nov., *Ophiactis*? *sulcata* sp. nov., *Ophiocoma*? *ishidai* sp. nov., *Ophioderma*? *radiatum* sp. nov., *Ophiolepis*? *granulata* sp. nov., *Ophiolepis*? *linea* sp. nov., *Ophiomusium biconcavum* sp. nov., *Ophiomusium sentum* sp. nov., *Ophiomusium sinuatum* sp. nov., and *Mesophiomusium moenense* gen. et sp. nov. Four additional species (*Trichaster*? sp., *Ophiacantha*? sp., *Sinosura* sp., and *S.* aff. *schneideri* Kutscher, 1987) are left in open nomenclature; these may prove to be new as well, but not enough material is currently available to erect new species upon.
Previously described ophiuroid species, some of which are here reassigned to other genera, in all of these faunas include: *Asteronyx*? *simplex* A.H. Müller, 1950, *Trichaster*? *ornatus* (Rasmussen, 1950), *Ophiomyxa*? *jekerica* (Berry, 1938), *Ophiacantha*? *danica* Rasmussen, 1952, *Stegophiura*? *hagenowi* (Rasmussen, 1950), *Felderophiura vanderhami* Jagt, 1991, *Ophioplinthaca*? *fuerstenbergii* (J. Müller, 1847), *Ophiocoma*? *senonensis* (Valette, 1915), *Ophiocoma*? *rasmusseni* Hess, 1960b, *Ophioderma*? *substriatum* (Rasmussen, 1950), *Ophiotitanos serrata* (Roemer, 1840), and *Ophiomusium granulosum* (Roemer, 1840). *Ophiomusium subcylindricum* (von Hagenow, 1840) and *O. danicum* Brünnich Nielsen, 1926 are considered to be junior synonyms of *O. granulosum*.
With very few exceptions, species assignment to extant genera is fraught with difficulties, even in those cases where more or less complete discs with arms attached are available. Most of our taxa are based on dissociated ossicles, or portions of arms at best, which are preferentially placed in the nomi-

nal genera of the various ophiuroid families. Despite this inordinate use of open nomenclature, the present paper demonstrates that Late Cretaceous-Early Palaeogene ophiuroid diversity greatly exceeds previous estimates, and that the white chalk facies of Rügen in particular was less hostile to benthic inhabitation than assumed by earlier authors.

Contents

Introduction

The observation (Jagt, 1999b) that Late Cretaceous and Early Palaeogene crinoids from the Maastrichtian type area received only scant attention in the literature, holds true for ophiuroids (brittlestars and basketstars) as well. Prior to the present study (inclusive of second part on material from northeast Germany and Denmark), only a handful of species were known from the area. In the present paper, part 3 in the current series (see Jagt, 1999a, b), the highly diverse ophiuroid faunas of Campanian, Maastrichtian and Danian age from this area are described and illustrated. For a discussion of the geographic-stratigraphic setting, general references as well as the aim of the current series, reference is made to Jagt (1999a, b).

In 1989, while co-operating with Manfred Kutscher (Sassnitz-Lancken, Rügen) in the study of a fine collection of ophiuroids from the upper Lower Maastrichtian of Rügen (NE Germany), it became apparent that this region and the Maastrichtian type area had many species in common. Since the Rügen material, although comprising mostly dissociated ossicles of arms and discs, generally was much better preserved and more diverse, it was decided to join forces and use this material for the description of new taxa. Most of these species have subsequently been collected from correlative strata in Møn (Denmark); they are here described in a separate section. Our material allows to document the presence in the Late Cretaceous of the (sub)families Ophiobyrsinae, Asteronychidae, Euryalidae, Ophiomyxidae, Ophiacanthidae, Hemieuryalidae, Ophiuridae, Amphiuridae, Ophiothricidae, Ophiocomidae, Ophiodermatidae, and Ophiolepididae.

Species not known from Rügen or Denmark, mostly of Early and early Late Campanian, early and late Late Maastrichtian and Early/Middle Danian age, are described in the first systematic section of the present paper. That part also includes references to previous papers, in which ophiuroids from the southeast Netherlands and northeast Belgium have been recorded. The Early Campanian *'Ophiura' fuerstenbergii* J. Müller, 1847 is revised and a neotype designated, while material from which Berry (1938) selected the types of his new taxa is illustrated photographically for the first time.

Material and methods

Most of the ophiuroid material from the extended Maastrichtian type area comes from the same samples which yielded the crinoids (see Jagt, 1999b for discussion). Included also are specimens from private collections, notably those of M.J. van Birgelen, Y. Coole, M.J.M. Deckers, R.W. Dortangs, and M.M.M. Kuypers; these have been transferred to the collections of the Natuurhistorisch Museum Maastricht and bear the prefix NHMM. Assistance received from these collectors over the past few years is gratefully acknowledged.

At a few localities (quarries Blom-Berg en Terblijt and ENCI-Maastricht BV in particular), ophiuroid discs preserving (portions of) arms have proved to be relatively common in obrution sediments. Such occurrences have naturally been given special attention, and allow analyses of population density to be made (compare e.g. Meyer, 1984, 1988). Specimens illustrated in the present paper are generally the best-preserved and/or most typical examples recognised in the various samples, on which the descriptions are based. In view of the small size of many ophiuroid ossicles, it was decided to illustrate these with photomicrographs, prepared by Mrs S.M. Kars (Vrije Universiteit, Amsterdam; JEOL JSM-6400 SEM).

Type material of the ophiuroid species discussed in the present paper (inclusive of the Rügen and Møn material) is housed at the Natuurhistorisch Museum Maastricht (prefix NHMM), the Ernst-Moritz-Arndt Universität, Greifswald (prefix FGWG), the Institut royal des Sciences naturelles de Belgique (Brussels, prefix IRScNB), the Geological Museum of Copenhagen University (prefix MGUH) and the Nationaal Natuurhistorisch Museum, Leiden (prefix RGM).

Previous work

J. Müller (1847-1859) appears to have been the first to record ophiuroids from the extended type area of the Maastrichtian. In part 1 (1847, pp. 5-6) of this work, he noted that at that time only very few ophiuroid species of Late Cretaceous age were known, and that, '... ein vollständiges Exemplar aus der Kreide wurde bis jetzt noch nicht bekannt gemacht, ein solches, und zwar in einer neuen Species aufzufinden, war uns daher ein höchst erfreulicher Fund.' From the 'Grünsand' near Vaals, a unit now known as the Vaals Formation of Early Campanian age (see Jagt, 1999a), he described and illustrated *'Ophiura' fuerstenbergii* Müller, noting that it was 'äusserst selten' there. Müller's original appears to have been destroyed during World War II air raids on the city of Aachen. However, in the C. Ubaghs Collection at Brussels (IRScNB), in the W.M. Felder Collection at Maastricht (NHMM) and in a number of private collections some twenty silicified discs and lots of arm fragments are present. These all come from the same locality and may thus be considered as topotypes. One of these specimens is designated neotype herein. Upon a closer examination it turned out that actually three species are involved. Only arm fragments are available of these other species, described below as *Ophiothrix*? *bongaertsi* Kutscher & Jagt, sp. nov., and *Ophiotitanos serrata* (Roemer, 1840).

From a number of localities in southern Limburg and contiguous German territory, Binkhorst van den Binkhorst (1859a) recorded the following ophiuroid species (in original spelling):

from the 'Coupe de Heunsberg près de Fauquemont' (pp. 41-42 = Valkenburg aan de Geul/Sibbe area), from a unit characterised by the large number of bryozoans: *Ophiura Furstenbergii* [sic], Muller and *O*. sp.

Unfortunately, the second species is not described.

On p. 109 in the same paper, Binkhorst noted, '... la troisième couche à bryozoaires renfermant, comme nous l'avons déjà dit, un si grand nombre d'espèces nouvelles pour notre craie et pour la science, une *Ophiura*, etc.'.

In another paper which came out the same year, Binkhorst van den Binkhorst (1859b, p. 407) recorded from what he named the 'dritte Bryozoen Schicht', 'zahlreiche Exemplare einer Ophiura, vielleicht Ophiura Fürstenbergii ....'. This record probably refers to the ophiolepidid *Ophiomusium granulosum*, which locally is common in the lower portion of the Maastricht Formation (Valkenburg, Gronsveld and Emael members).

Other local workers, and Bosquet (in Staring, 1860, p. 408) in particular, listed for 'Nederlandsch en Belgisch Limburg' the following ophiuroid (in original nomenclature):

863 *Palaeocoma Furstenbergi* Müll. sp.

but failed to indicate its stratigraphic provenance.

Later, Bosquet (in Dewalque, 1868, p. 29) recorded the same species [*Palæcoma Furstenbergi*, d'Orb., 1847 (*Ophiura Furstenbergi*, Mull., 1847] from the 'Hervien' (= Vaals Formation) and the 'Maestrichtien' (= Maastricht Formation). This record clearly shows that under the name '*Palæocoma Furstenbergi*' several species were lumped. It is very likely that, in view of their common occurrence in the Maastricht Formation, the collections of these local workers also comprised specimens of *Ophiomusium granulosum* and *Felderophiura vanderhami*.

Ubaghs (1879) recorded more than one species of ophiuroid. For the 'Partie supérieure du tuffeau de Maastricht', and the 'troisième niveau à Bryozoaires ou couche à Stellocavea ...' (p. 66), he listed (in original nomenclature):

Palæocoma Fustenbergi [sic] Muller sp.

From the 'craie blanche à silex noir', Ubaghs (1879, p. 129) recorded, under the name *Palæocoma* sp., '... un bras entièrement orné de petites tubercules et dont les articulations sont au moins quatre fois plus grandes que celles de l'espèce indiquée dans le Hervien, sables verts de Vaals, par Jos. Müller, l'Ouphiura Furstenbergi [sic]'. This record probably refers either to *Ophiomusium granulosum* or to *Stegophiura*? *hagenowi*. Both species are common in the Zeven Wegen Member of the Gulpen Formation (Late Campanian).

In a faunal list, Ubaghs (1879, p. 229) added the following stratigraphic data for these two species:

Palæocoma Furstenbergi, d'Orb., 1847 (*Ophiura Furstenbergi*, Mull., 1847)	h	M.M.
Palæocoma, sp.	s	

Abbreviations are as follows: h - 'Hervien' (= Vaals Formation), s - 'Senonien' (= Gulpen Formation, in part), M.M. - 'Maastrichtien Moyen' (= lower/middle part of Maastricht Formation).

Puzzling in the light of the above records is the fact that in the catalogue of his collection, Ubaghs (1885) did not list any ophiuroids.

In a listing of fossils contained in the collection of Ignaz Beissel, under the heading 'Crinoïden und Asterioidea', Ubaghs (1888) recorded from the 'Kreidemergel' (= Vijlen Member of the Gulpen Formation, in part) 'unbestimmte Palaeocomaglieder', and from the 'Grünsand von Vaals': *Palaeocoma Furstenbergi* (prachtvoll mit erhaltenen Aermchen).

Boehm (1889) discussed all records of fossil ophiuroids known at that time, and noted (p. 263 [32]) about '*Ophiura Fürstenbergii*, Müller' that, 'Letztere stammt aus dem Senon von Vaels und ist ganz ungenügend bekannt; vgl. Müller; Monographie der Petrefacten der Aachener Kreideformation. p. 6, T. I, F. 3.'

Klinghardt (1930, p. 716), who had ten specimens (Reuss Collection) of what he called *Ophiura fürstenbergii* Josef Weiss [sic!] at his disposal, noted that this species, 'Gehört zu den Ophiolepididen und steht *Ophiocten amitinum* sehr nahe.' He was able to examine Müller's type specimen (p. 717, footnote 6). In a subsequent paper, Klinghardt (1933, pp. 957-958, fig. 7; pl. 50, figs. 6-7) described the coiling reflex of the arms in '*Ophiura fürstenbergii* Josef Müller 1843'. His Fig. 7 presents a fair picture of the typical features of this species, and shows disc plating and granulation well (compare Pl. 7 here). Klinghardt referred to nine specimens and Müller's two originals, all apparently contained in the Beissel Collection, and noted the following (p. 958): 'Taf. 50, Fig. 6 zeigt die Bauchscheibe und darüber die Arme eingerollt. Hieraus folgt, daß diese Art zu den Streptophiuren J. Bell 1892 gehört. Die einzelnen Armglieder besitzen keine ausgebildeten Gelenkteile und haben darum die Fähigkeit, die Arme über die Bauchscheibe einzurollen.'

On a large material of dissociated ophiuroid ossicles (some 25,000 specimens) received from Dr J.H. Bonnema (Rijksuniversiteit Groningen) in 1935, Berry (1938) distinguished four species. The types of these are stated (p. 61) to have been deposited at the Johns Hopkins University (Baltimore). This material was collected at various localities (Bemelen, Jeker valley, Valkenburg, and Kunrade) and from various lithostratigraphic units. Berry noted the poor preservation of a portion of his material, notably specimens from the environs of Bemelen. Generic assignments were based on vertebrae; Berry's method has subsequently been rightly criticised by A.H. Müller (1950) and Rasmussen (1950, 1952). To make matters worse, Berry did not designate type specimens of his species, and application to the Johns Hopkins University, where he stated to have deposited the types, has so far not resulted in retracing the specimens (pers. comm. Jann W.M. Thompson, letter of February 2, 1996). Mrs Joan Grattan (letter of November 29, 1995) informed me that many specimens formerly held by the Geology Department of the Johns Hopkins University (Baltimore) were apparently handed over to the collections of the Smithsonian Institution (National Museum of Natural History, Washington DC). In the meantime, through the assistance of Professor L.M.J.U. van Straaten, I was able to locate Berry's material returned to Dr Bonnema, with small labels in his handwriting as well as typewritten ones. A number of ossicles from these samples have been selected for SEM photography (see Pl. 17, fig. 10; Pl. 18, figs. 1-9), to demonstrate the generally poor preservation of this material. Berry's taxa are here treated as nomina dubia, after Jagt (1991).

Rasmussen (1965) listed only a single species of ophiuroid from southern Limburg:

for the 'Tuffeau de Maastricht Mb': *Ophiomusium subcylindricum*.

In an unpublished report, Cupedo (1970) illustrated a variety of dissociated ophiuroid ossicles from the Upper Maastrichtian Kunrade Limestone facies, and applied Berry's (1938) names to a number of these. In a subsequent paper, Cupedo (1980) provided illustrations of ossicles of various extant species, in an attempt to stimulate local workers in the collection of fossil counterparts.

Zeleznik (1985) illustrated a number of dissociated ossicles of Late Campanian and early Late Maastrichtian age from the CPL SA quarry (Haccourt, Liège), but did not assign these to species.

In a number of short papers, Jagt (1985, 1986, 1987a, b) recorded from the Campanian, Maastrichtian and Danian of the Maastrichtian type area the species *Asteronyx*? *ornatus* (= *Trichaster*? *ornatus* herein), *Amphiura*? *senonensis* (= *Ophiocoma*? *senonensis* herein), and *Ophiomusium subcylindricum*.

Van Birgelen (1989) briefly reported on the discovery of topotype specimens of *'Ophiura' fuerstenbergii* in temporary outcrops at Vaals-Eschberg.

From the Upper Maastrichtian of Liège-Limburg, Jagt (1991) described a new genus and species of ophiurid, *Felderophiura vanderhami*, and commented on other species.

In faunal lists for the Lower Maastrichtian (Vijlen Member) of Liège-Limburg and the Aachen area, Keutgen (1996) recorded (in original nomenclature): *Amphiura*(?) *senonensis*, *Ophiacantha*(?) sp., *Ophiomusium danicum* Nielsen, 1926 and *Ophiura*(?) *hagenowi* Rasmussen, 1950. In material available for the present study, these species have all been recognised; however, *O. danicum* is here considered to be conspecific with *O. granulosum*.

Jagt (1998c) provided photographs of topotype specimens of *'Ophiura' fuerstenbergii* from the Ubaghs Collection (IRScNB, Brussels), one of which is designated neotype herein.

Wherever appropriate in the descriptions of species recognised in the material studied, comparisons are made with previously described ophiuroids of Cretaceous and Cenozoic age (e.g. W.B. Clark, 1893; Arnold, 1908; Alexander, 1931; Chapman, 1934; Berry, 1934, 1935, 1937, 1939, 1941a, b, 1942; Howe, 1942; D.L. Clark, 1959; Corgan, 1962; Skwarko, 1963; Binder & Steininger, 1967; Blake & Allison, 1970; Blake, 1975; Shone, 1986; Bignot et al., 1987; Cornell et al., 1991; Štorc, 1996, 1997; and Blake & Aronson, 1998).

Systematic palaeontology

Abbreviations — The following abbreviations are used to indicate the repository of specimens illustrated and/or referred to in the text:

BMNH	Natural History Museum, London (formerly British Museum of Natural History);
FGWG	Institut für geologische Wissenschaften, Ernst-Moritz-Arndt Universität Greifswald;
IRScNB	Institut royal des Sciences naturelles de Belgique, Brussels;
MGUH, GM	Geological Museum of Copenhagen University, type and reference collections, respectively;
NHMM	Natuurhistorisch Museum Maastricht, with individual collections bearing the following prefixes:

JJ - J.W.M. Jagt Colln
K - M.M.M. Kuypers Colln
MB - M.J. van Birgelen Colln
MD - M.J.M. Deckers Colln
RD - R.W. Dortangs Colln
YC - Y. Coole Colln;

RGM Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Geologie en Mineralogie);

RUG Rijksuniversiteit Groningen;

SGWG Sektion geologische Wissenschaften, Ernst-Moritz-Arndt-Universität, Greifswald.

Remarks — A number of species occurring in the Maastrichtian type area are also known from Rügen. For reasons outlined above, the various new species based on material from that locality are named and described in a separate section of the present paper, to which reference is made. Authorship of new taxa is best cited as Kutscher & Jagt, in Jagt (1999) for those from Rügen and Møn, and Jagt & Kutscher, in Jagt (1999) for those from the Maastrichtian type area.

Terminology — This follows Spencer & Wright (1966), Paterson (1985), Hendler et al. (1995) and Smith et al. (1995).

Taxonomic procedure — Since most material is preserved as dissociated ossicles only, and diagnostic features of ophiuroids are generally to be found in disc plating, oral frame structure and presence/absence of dental and oral papillae, generic attributions are provisional. For fossil material, lateral arm plates in particular have been shown to provide reliable criteria for species distinction by Hess (1962a, b, 1963, 1965, 1966, 1975a, b), Kutscher (1987) and Kutscher & Hary (1991). For those species of which discs and arms are known, attempts have been made to assign them to extant genera, using the keys provided by Fell (1960).

The fragmentary preservation of most of the species discussed in the present paper precludes cladistic analyses; Smith et al. (1995) are referred to for calibration against the stratigraphic record of a phylogenetic tree for ophiuroids. It is hoped to incorporate the various species from the Maastrichtian type area of which discs and arms are known into that phylogenetic scheme in future.

Class Ophiuroidea Gray, 1840
Subclass Ophiuridea Gray, 1840
incertae ordinis & familiae
Subfamily Ophiobyrsinae Matsumoto, 1915
Genus *Ophiosmilax* Matsumoto, 1915

Type species — *Ophiosmilax mirabilis* Matsumoto, 1915, by monotypy.

Ophiosmilax? *alternatus* Kutscher & Jagt, sp. nov.
Pl. 1, figs. 1-2.

Remarks — For synonymy, description and discussion see p. 47.

Material — Dissociated lateral arm plates only (NHMM JJ 3640, 3679, 10979, MB 1044-9a, 1175 (sample); RGM 428 057).

Occurrence — Known to date only from the Zeven Wegen and Vijlen members (Gulpen Formation) of the CBR-Lixhe and CPL SA quarries and of Snouwenberg (Voerstreek) (Figs. 2A, 8-9).

Order Euryalida Lamarck, 1816
Family Asteronychidae Verrill, 1899 (emend. Mortensen, 1933)
Genus *Asteronyx* Müller & Troschel, 1842

Type species — *Asteronyx loveni* Müller & Troschel, 1842, by monotypy.

Asteronyx? *spinulosa* Kutscher & Jagt, sp. nov.
Pl. 1, figs. 3-4.

Remarks — For synonymy, description and discussion see p. 50.

Material — Two ?dorsal arm plates, NHMM MB 1239-23a/b.

Occurrence — Known exclusively from the Vijlen Member (Gulpen Formation) at Mamelis-Selzerbeek (Fig. 2A).

Family Euryalidae Gray, 1840
Genus *Trichaster* L. Agassiz, 1836

Type species — *Euryale palmiferum* Lamarck, 1816, by monotypy.

Trichaster? *ornatus* (Rasmussen, 1950)
Pl. 1, figs. 5-6.

Remarks — For synonymy, description and discussion see p. 51.

Material — Numerous dissociated vertebrae in various collections, including NHMM JJ 2449/1-3, 2497, 3084, 3165, 3483, 3529, 9380, 9549, 10428, 10404, MB 1044-9b.

Occurrence — At present known from the Zeven Wegen to Meerssen members (Gulpen and Maastricht formations) of the CPL SA, CBR-Romontbos, ENCI-Maastricht BV and Blom quarries and of the temporary Albertkanaal sections near Vroenhoven-Riemst (Figs. 2A, 8, 11-12, 14).

Trichaster? sp.
Pl. 1, figs. 7-10.

Remarks — For synonymy, description and discussion see p. 52.

Material — Numerous dissociated vertebrae in a few collections, including NHMM JJ 3529, 7280k, 9473, 9623, 10509, 10600/5, 10601/3, MB 1044-9c.

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) of Haccourt (CPL SA quarry) and Heure-le-Romain and the Lanaye and Meerssen members (Gulpen Formation and Maastricht Formation, respectively) of the CBR-Romontbos and ENCI-Maastricht BV quarries (Figs. 2A, 8, 11-12).

Note — On poorly preserved material of Late Maastrichtian age collected at various localities in southern Limburg, Berry (1938, p. 65) erected *Asteronyx valkenburgensis*. Assignment to this genus was based on vertebral structure (Berry's pl. 16, figs. 13-16, 19). From the material returned by Berry to the Rijksuniversiteit Groningen (RUG X 525) a few typical vertebrae have been selected for SEM photography (see Pl. 18, figs. 5-7). The vertebra illustrated in Berry's pl. 16, figs. 13-16, 19, should be designated lectotype, if found. However, the state of preservation of this specimen is such (e.g. it lacks ornament) that the species is best treated as a nomen dubium. In addition, material here illustrated shows that it may be assigned both to *T.*? *ornatus* and to *T.*? sp. (Pl. 18, fig. 6 and figs. 5, 7, respectively).

Order Ophiurida Müller & Troschel, 1840
Suborder Ophiomyxina Fell, 1962
Family Ophiomyxidae Ljungman, 1867
Genus *Ophiomyxa* Müller & Troschel, 1842

Type species — *Ophiura pentagona* Lamarck, 1816, by monotypy.

Ophiomyxa? *rhipidata* Kutscher & Jagt, sp. nov.
Pl. 2, fig. 1.

Remarks — For synonymy, description and discussion see p. 56.

Material — A few dissociated lateral arm plates and a single spine (NHMM JJ 3921, 6458c, 10522a, 10526, MB 1175: sample).

Occurrence — Currently known from the Vijlen Member (Interval 6, Gulpen Formation) at the CPL SA quarry (Haccourt), from coeval strata at Snouwenberg (Voerstreek) and from the Meerssen Member (Maastricht Formation) at the ENCI-Maastricht BV and Blom quarries (Figs. 2A, 8, 12, 14).

Ophiomyxa? *jekerica* (Berry, 1938)
Pl. 2, fig. 4; Pl. 17, fig. 9; Pl. 18, fig. 4.

Remarks — For synonymy, description and discussion see p. 55.

Material — Several dozens of dissociated vertebrae, including NHMM MB 104b, 770-8a, K 1780, JJ 3759.

Occurrence — Recorded to date from the Zeven Wegen Member (Gulpen Formation) of Haccourt (CPL SA quarry) and the Nekum and Meerssen members (Maastricht Formation) at the quarries ENCI-Maastricht BV and Blom and at subterranean quarry de Schenk, Geulhem (Figs. 2A, 12, 14).

Note — The present species is the type of Berry's (1938, p. 68) genus *Platyarthra*. Although the generic name is best treated as a nomen dubium (see also Spencer & Wright, 1966), the type of vertebra, and thus also the species, appears to be highly distinctive. From sample RUG X 523, a single vertebra has been selected for SEM photography (Pl. 18, fig. 4). Awaiting the discovery of better-preserved material from the Maastrichtian type area, the species is here interpreted on the basis of well-preserved specimens from Rügen (see the separate section below).

Genus *Ophioscolex* Müller & Troschel, 1842

Type species — *Ophioscolex glacialis* Müller & Troschel, 1842, by monotypy.

Ophioscolex? *cretaceus* Kutscher & Jagt, sp. nov.
Pl. 2, figs. 2-3.

Remarks — For description and discussion see p. 59.

Material — A few dissociated lateral arm plates, including NHMM JJ 3168, 3557, 3700, 4100b, 8887, 10524, MB 1044; RGM 428 058.

Occurrence — Known to date from the Zeven Wegen and Vijlen members (Gulpen Formation) at Haccourt (CPL SA quarry), and from the Meerssen Member (Maastricht Formation) at the ENCI-Maastricht BV quarry (Figs. 2A, 8, 12).

Ophioscolex? *clivulus* Kutscher & Jagt, sp. nov.
Pl. 17, fig. 6.

Remarks — For description and discussion see p. 58.

Material — A single distal arm fragment (NHMM JJ 5054) and a few dissociated lateral arm plates (NHMM JJ 10600/7b, MB 387-10d).

Occurrence — Known from the Zeven Wegen Member (Gulpen Formation) at Haccourt (CPL SA quarry) and the Vijlen Member (Gulpen Formation) of Aachen (Hans-Böckler-Allee) (Figs. 2A, 8).

Suborder Ophiurina Müller & Troschel, 1840
Family Ophiacanthidae Perrier, 1891 s. lat.
Subfamily Ophiacanthinae sensu Paterson, 1985
Genus *Ophiacantha* Müller & Troschel, 1842

Type species — *Ophiacantha spinulosa* Müller & Troschel, 1842 = *Asterias bidentata* Retzius, 1805, by subsequent designation of H.L. Clark (1915).

Ophiacantha? *danica* Rasmussen, 1952
Pl. 2, figs. 5-7, 10.

Remarks — For synonymy, description and discussion see p. 61.

Material — A single, rather poorly preserved individual as well as a few fragmentary arms and numerous dissociated lateral arm plates, including NHMM JJ 5104, 9380-2, 9625, 10525, 10600/9, K 3387, MB 619-2a, 808-9a.

Note — A near-complete specimen (NHMM K 3387; Pl. 2, fig. 7), draped over the column of the bourgueticrinid crinoid *Dunnicrinus aequalis* (d'Orbigny, 1841) (see Jagt et al., 1998) preserves the disc and four arms, one of them regenerating. Unfortunately, disc plating is poorly preserved; it shows a jumble of small plates and scales and a large, elongate (?)radial shield; a few arm spines are also present. Although this is the first record of the disc of the present species, preservation is such that it cannot substantiate its generic assignment.

Occurrence — Currently known from the Zeven Wegen Member (Gulpen Formation) of Haccourt (CPL SA quarry), and the Lanaye, Gronsveld and Meerssen members (Gulpen and Maastricht formations) of the quarries CBR-Romontbos and ENCI-Maastricht BV (Figs. 2A, 8, 11-12).

Ophiacantha? *rugosa* Kutscher & Jagt, sp. nov.
Pl. 13, fig. 1.

Remarks — For description and discussion see p. 63.

Material — A single lateral arm plate (NHMM JJ 10600/12e).

Occurrence — Known exclusively from the Zeven Wegen Member (Gulpen Formation) at Haccourt (CPL SA quarry) (Figs. 2A, 8).

Ophiacantha? *striata* Kutscher & Jagt, sp. nov.
Pl. 13, figs. 2-3; Pl. 19, fig. 10; Pl. 20, figs. 1-3, 5.

Remarks — For description and discussion see p. 64.

Material — A few dissociated lateral arm plates (NHMM JJ 7280d, ? 2479, MB 387-10a, 734-12 sample).

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) of Haccourt (CPL SA quarry), the Vijlen Member (Gulpen Formation) at Aachen (Hans-Böckler-Allee), and from the Geulhem Member (Houthem Formation) of the temporary Albertkanaal sections (Figs. 2A, 8).

From the Beutenaken Member (Vaals Formation) of the Wingerd quarry (Welterberg, southern Limburg), remains of an indeterminate ophiacanthid(?) have been collected (Pl. 8, figs. 1-2). Although fairly well-preserved (with arm spines), this material cannot be properly placed at this time; it may even turn out to be referable to the Amphiuridae.

Subfamily Ophioplinthacinae Paterson, 1985
Genus *Ophioplinthaca* Verrill, 1899

Type species — *Ophiomitra dipsacos* Lyman, 1878, by monotypy.

Ophioplinthaca? *fuerstenbergii* (J. Müller, 1847)
Fig. 1; Pl. 7, figs. 6-12, ?13; Pl. 11, fig. 7?

* 1847 *Ophiura Fürstenbergii* Müller, p. 6, pl. 1, fig. 3.
non 1879 *Palaeocoma Furstenbergii*, Muller spec. — Ubaghs, p. 87.
pp 1879 *Palaeocoma Furstenbergi*, d'Orb., 1847 (*Ophiura Furstenbergi*, Mull., 1847) — Ubaghs, p. 229 (partim, probably includes *Felderophiura vanderhami* Jagt, 1991).
1889 *Palaeocoma Fürstenbergii* = *Ophiura Fürstenbergii*, Müller. — Boehm, p. 263 [32].
1930 *Ophiura fürstenbergii* Josef Weiss [sic]. — Klinghardt, p. 716.
1933 *Ophiolepis (Ophiura) fürstenbergii* Josef Müller, 1843 — Klinghardt, p. 957, fig. 7; pl. 50, figs. 6-7.
1989 *Ophiura fürstenbergii* Müller 1847 — van Birgelen, p. 17, figs.
1998 *'Ophiura' fuerstenbergii* Müller — Jagt, p. 79, fig. 4.

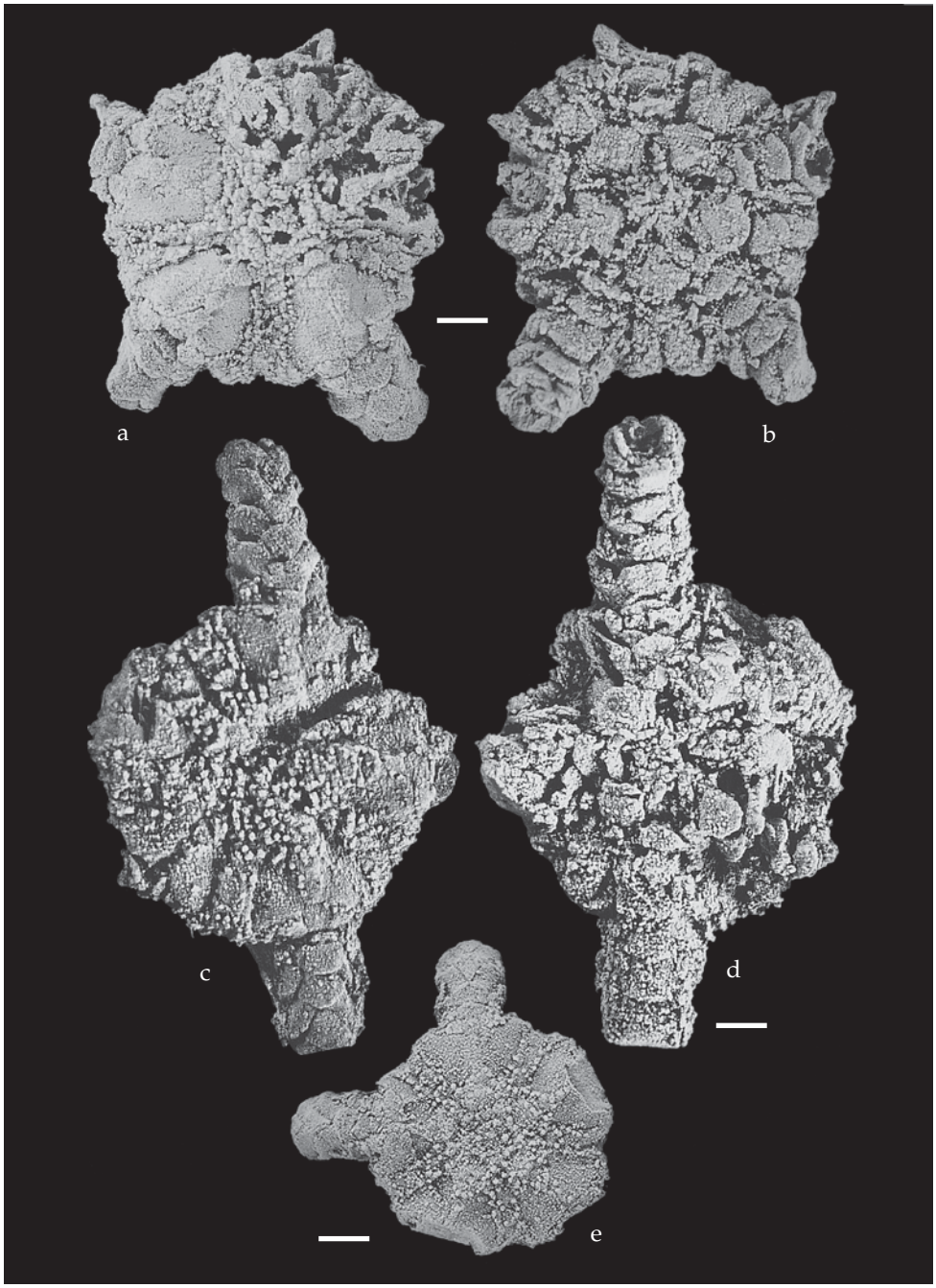

Fig. 1. *Ophioplinthaca*? *fuerstenbergii* (J. Müller, 1847) from the Vaals Formation at Vaals-Eschberg (southern Limburg); a-b: IRScNB IST 10756; c-d: IRScNB IST 10755 (**neotype**); e: IRScNB IST 10757; scale bars equal 10 mm.

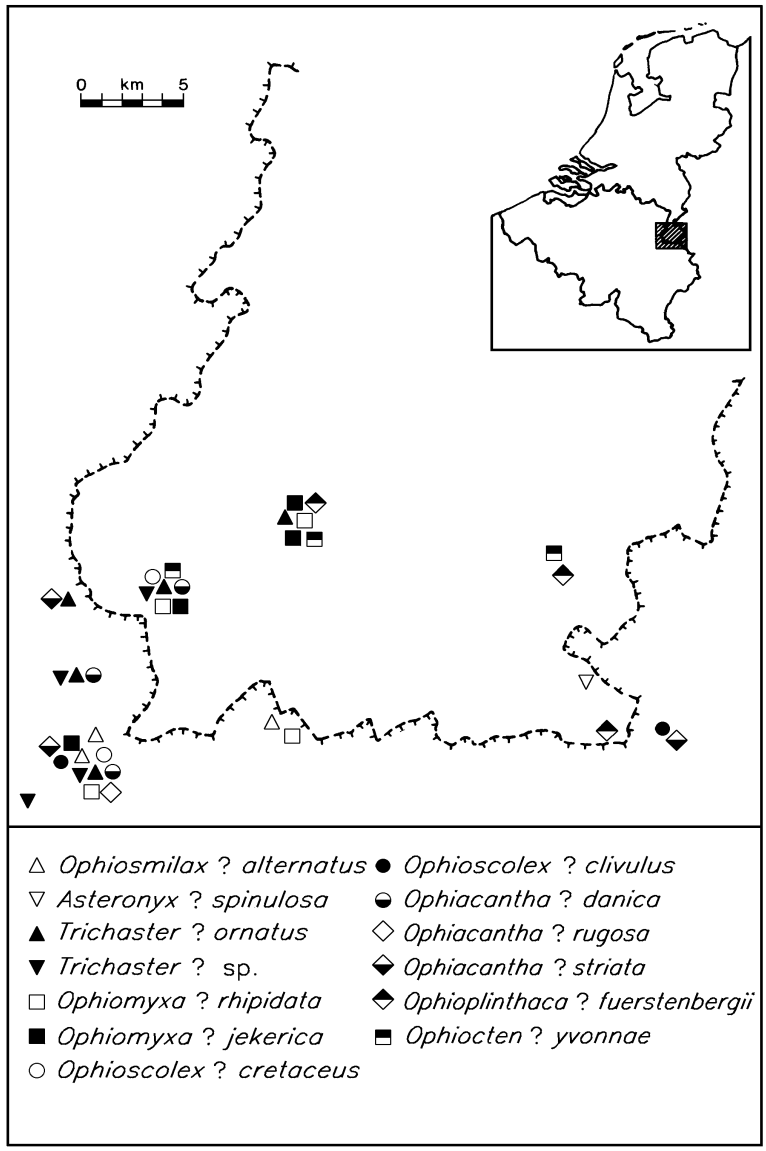

Fig. 2A. Geographic distribution of Late Cretaceous-Early Palaeogene ophiuroids in the type area of the Maastrichtian Stage.

Type — J. Müller's (1847) originals appear to have been destroyed during air raids in World War II. A neotype is selected from topotype material (Vaals Formation, Vaals-Eschberg, southern Limburg) in the Casimir Ubaghs Colln (IRScNB IST 10755-10760). The specimen illustrated in Fig. 1c-d is the neotype (IRScNB IST 10755).

Material — Several discs and numerous fragments of arms, including NHMM VG 3502 (W.M. Felder Colln); NHMM MB 661-2, 661-4a/b, 661-5, and 661-6. An arm frag-

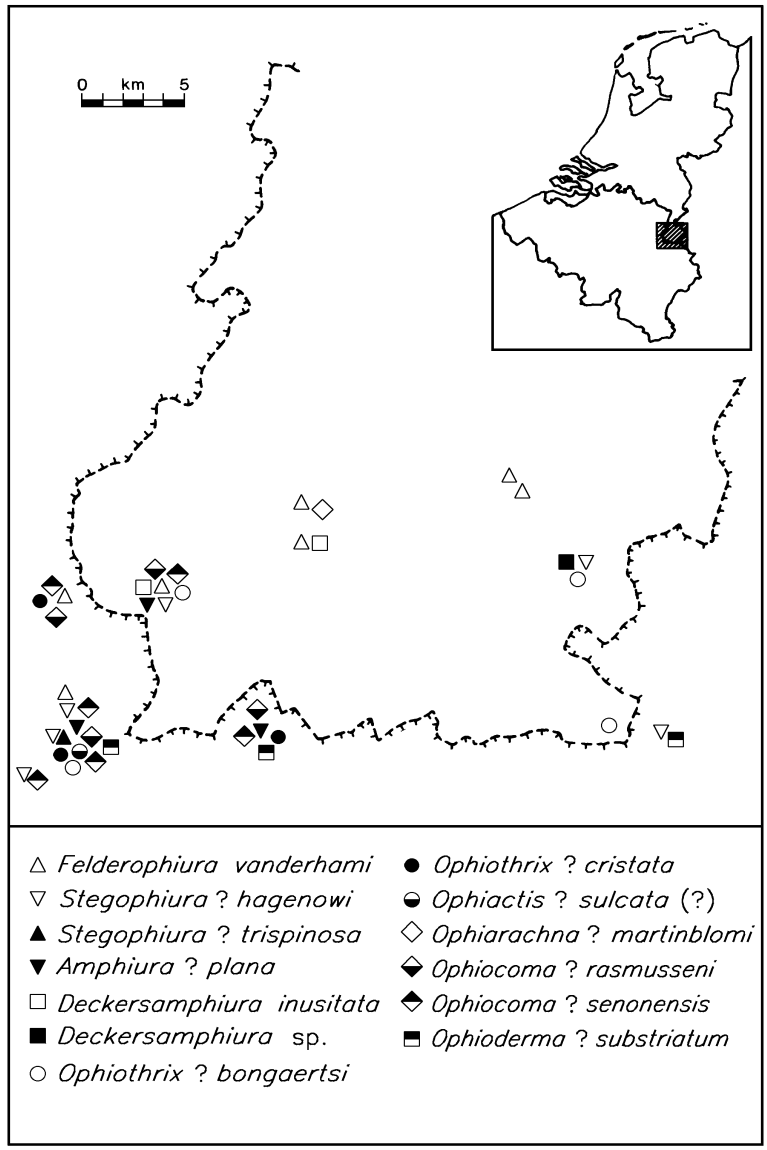

Fig. 2B. Geographic distribution of Late Cretaceous-Early Palaeogene ophiuroids in the type area of the Maastrichtian Stage.

ment (NHMM MB 865-25; Pl. 8, fig. 1-2) from de Wingerd quarry (Benzenrade Member, Vaals Formation) may also belong here, as may a single lateral arm plate (NHMM MB 784-3) from the Meerssen Member (Maastricht Formation) at Blom quarry (Pl. 11, fig. 7).

Description — From the original description (J. Müller, 1847, p. 6) it is clear that Müller had serious problems in unravelling the disc structure of this species, and the

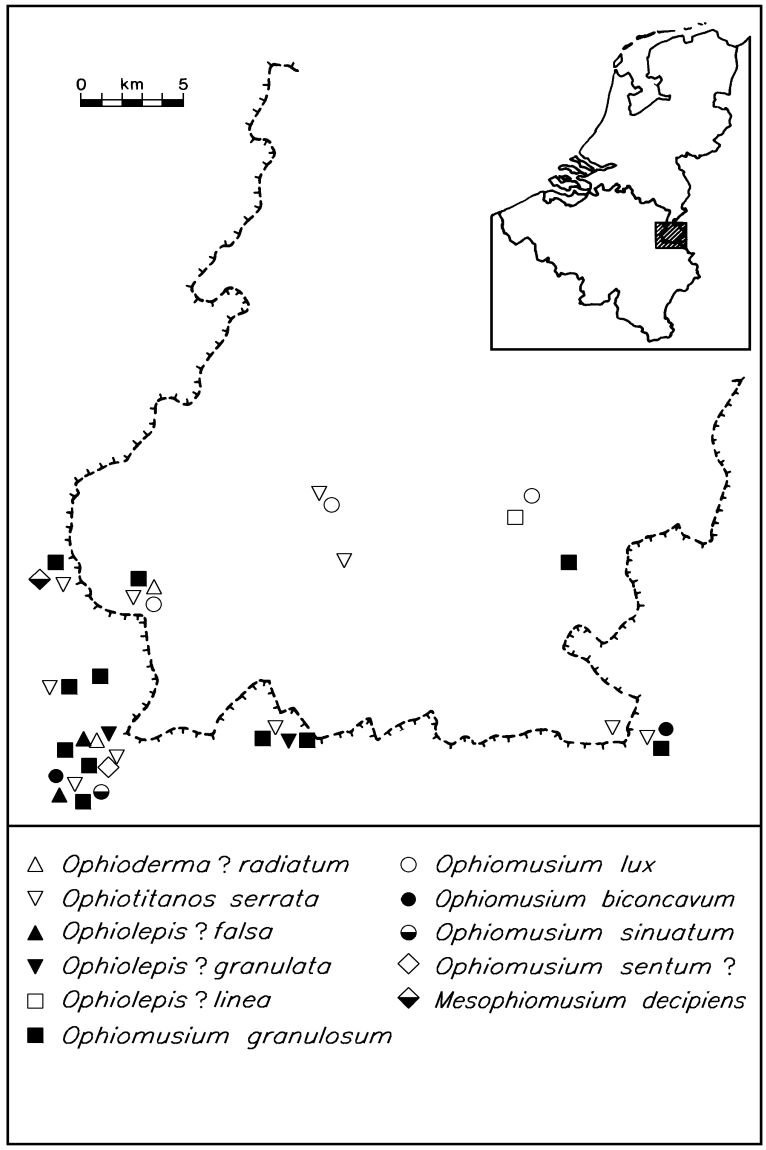

Fig. 2C. Geographic distribution of Late Cretaceous-Early Palaeogene ophiuroids in the type area of the Maastrichtian Stage.

ventral surface in particular ('Wir bemerken aber ausdrücklich hierbei, daß diese untere Seite nur nach Andeutungen des Originales conjecturirt ist'.). The following redescription of the structure of disc and arms is based mainly on the neotype, on specimen NHMM MB 661-5 (Pl. 7, fig. 6) and on a number of arm fragments, some of which preserve spines (Pl. 7, figs. 7-9, 11-12).

Disc low and flat, pentagonal with slightly concave interradial margins. Dorsal

disc surface covered in large radial shields, which abut over their entire length, but are covered proximally by many small, imbricating scales of variable size and shape (Pl. 7, fig. 6). Amongst these, a primary and secondary circlet may be recognised, the first consisting of a central plate, the second of radially arranged, similarly sized plates. Some specimens (Fig. 1c, e) preserve spine-like disc granules. Radial shields are more or less flat, with noticeably concave distal margin; they are separated interradially by one or more rows of elongate scales of variable size and shape.

Unfortunately, in all available specimens the ventral disc surface is poorly preserved, especially where details of the oral frame are concerned. Interradially, a large plate imbricating others left and right abuts the conspicuous arrow-shaped oral shield, with rounded distal margin, widest at midlength. Adoral shields are rectangular, with distal extension. Oral plates are apparently massive, and there are numerous oral papillae. Imbricating scales extend onto disc margin, and disappear beneath the radial shields.

Arms are fairly stout, tapering gradually. Dorsal arm plates apparently abut only in proximal arm portions, and are otherwise separated, of triangular shape with broadly or acutely rounded distal margin. Ventral arm plates are broadly pentagonal, separated (even in proximal arm segments), with pointed proximal margin, indented lateral margin and broadly rounded distal margin. Tentacle pore fairly large, at least in proximal segments; with a small, pointed inner and a larger, elongate outer scale. Lateral arm plates abut only ventrally, have a faint striation over most of their surface and up to 5 ring-shaped spine tubercles on the distal margin, increasing in size ventrally. The spines appear to be simple, pointed, striated/glassy, and reach up to two thirds the length of arm segment (Pl. 7, figs. 8-9). In life, they must have been slightly erect.

Discussion — Klinghardt (1930, p. 716) noted that this species should be placed in the Ophiolepididae and that it was very close to *Ophiocten amitinum* Lyman, 1878. Later, he (Klinghardt, 1933, fig. 7) illustrated for this species a single apical papilla and six oral papillae on each side of the oral slit. Unfortunately, the present material does not reveal such details of the oral frame. However, all other features of disc plating and arm structure suggest this form to belong to the Ophiacanthidae. Klinghardt's reconstruction of the apical and oral papillae would fit as well. In view of the fact that the radial shields are well developed and not bar-like, the disc is interradially indented, ventral and dorsal arm plates are separated and tentacle pores are not conspicuously large, a tentative assignment to *Ophioplinthaca* is favoured here (see Paterson, 1985, pp. 61-69).

Occurrence — Currently known with certainty from the Vaals Formation in the Vaals-Eschberg area (Fig. 2A). Material from the Benzenrade and Meerssen members (Vaals Formation and Maastricht Formation, respectively) differs in details, and appears closely related.

Infraorder Chilophiurina Matsumoto, 1915
Family Ophiuridae Lyman, 1865
Genus *Ophiocten* Lütken, 1855

Type species — *Ophiocten kröyeri* Lütken, 1855, by monotypy (= *Ophiura sericea* Forbes, 1852).

Ophiocten? *yvonnae* Jagt & Kutscher, sp. nov.
Pl. 6, figs. 1-2; Pl. 16, figs. 4-8.

Type — Holotype is NHMM K 2278a (Pl. 6, figs. 1-2); paratypes are NHMM K 979, 2278b, YC 1313.

Derivation of name — Named after Yvonne Coole (Stramproy), who has the knack of finding rare fossils such as the present one.

Diagnosis — Medium-sized ophiurid with low, flat disc apparently covered with many small, imbricating scales, well-developed radial shields and densely packed granules, large tentacle pores, evenly arched lateral arm plates with barely recognisable spine tubercles, a single apical papilla and at least three oral papillae in oral frame.

Material — A number of discs and arms, as well as many dissociated lateral arm plates in various collections, including NHMM K1639, and JJ 10609b.

Description — Disc low and flat (Pl. 16, fig. 6), pentagonal with straight to slightly convex interradial margins. Disc diameter varies between 4.5 and 8.9 mm (Fig. 3); arm width at the disc margin c. 2.5 mm in the holotype (D = 8.5 mm). Arm length at least four times the diameter of the disc (Pl. 16, fig. 7).

In most of the available specimens the dorsal disc surface is not sufficiently well preserved (see e.g. Pl. 16, figs. 4-5) to be described in detail. However, two fragmentary specimens in the van Birgelen Colln (no. 377-29) suggest the radial shields to have been fairly conspicuous, in length equalling up to a third of disc diameter, and abutting/partially overlapping over most of their length, except for a triangular notch in their joint distal margin. However, there is no sign of the peculiar wedge-shaped plates in between the radial shields that characterise *Felderophiura vanderhami*. Radial shields as well as all other disc plates show a fairly coarse stereom mesh, suggesting a dense cover of disc granules. Most specimens suggest the presence of at least three circlets of roundish plates of variable sizes, arranged both radially and interradially.

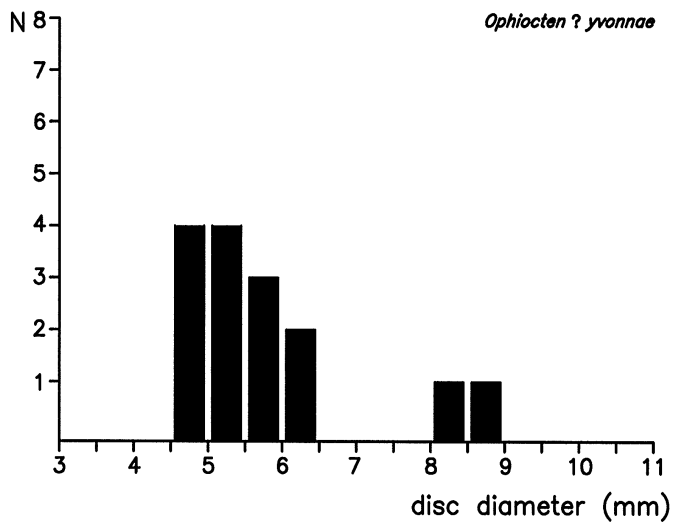

Fig. 3. Size frequency histogram for *Ophiocten*? *yvonnae* Jagt & Kutscher, sp. nov., from the Meerssen Member (Maastricht Formation) of the ENCI-Maastricht BV and Blom quarries.

The genital slit is fairly distinct, and there appears to be a small arm comb; however, no papillae are preserved.

The uncertainty over details of disc plating holds true for the margins and the interradii on the oral surface (Pl. 6, fig. 2) as well. The oral shield is narrowly rounded distally, longer than wide and has a pointed proximal end, the lateral margins being concave, the proximal margins straight. Adoral shields more or less rectangular, broadly in contact and with a distal extension which forms the margin of the second oral tentacle pore. Oral plates slightly larger than adoral shields, and with raised proximal end. A single, spatulate apical papillae at the end of each jaw and at least 3 oral papillae, the proximal two elongate and pointed, the third block like and rectangular. Second oral tentacle pore covered distally by a set of hook-shaped, pointed scales, abutting in their proximal half. A second, comparable set appears to lie below the first (Pl. 6, fig. 1).

The first ventral arm plate is broadly triangular (Pl. 6, fig. 2), with concave sides and a straight distal margin. Successive plates with straight or slightly concave distal margins, wider than long, with large tentacle indentations; a single large, elongate tentacle scale (Pl. 6, fig. 2). Lateral arm plates separated both ventrally and dorsally, evenly arched and smooth. Distal margin thin, with at least 4-6 shallow spine pits, barely recognisable. An arm fragment (NHMM JJ 10609b) preserves up to three thin, simple, appressed spines, of a length equalling slightly more than a third of the length of an arm segment. Arm cross section is triangular, with flattened ventral and tumid dorsal arm plates. Vertebrae are of the zygospondyline type.

In disc plating and arm structure, this form is reminiscent of extant representatives of the genus *Ophiocten* (see e.g. Paterson et al., 1982), to which it is referred for the time being. In many aspects, the present species is very close to *Felderophiura vanderhami*, in particular in the structure of the arms. However, it differs in details of the oral frame and in interradial, and, most importantly, in dorsal disc plating.

The specimen illustrated in Pl. 16, figs. 7-8 is of note in that one of its arms was regenerating.

Occurrence — Currently known from the Meerssen Member (Maastricht Formation) of the Blom and ENCI-Maastricht BV quarries, and the Kunrade Limestone facies in the Kunrade area (Figs. 2A, 12, 14).

Genus *Felderophiura* Jagt, 1991

Type species — Felderophiura vanderhami Jagt, 1991, by monotypy.

Felderophiura vanderhami Jagt, 1991

Pl. 6, figs. 4-6, 8-9; Pl. 7, figs. 1-3; Pl. 11, figs. 1-3; Pl. 18, fig. 1?

*1991 *Felderophiura vanderhami* Jagt, p. 200, figs. 2-3, pl. 1.
1998c *Felderophiura vanderhami* — Jagt, p. 77, fig. 1.

Type — Holotype is IRScNB IST 10507, paratypes are IRScNB IST 10508-10510.

Material — Numerous discs, arms and thousands of disssociated ossicles in various collections, including NHMM MD 3154, JJ 2668, 9547, 10603, 10609a, 10530, K 3024; RGM 428 038-043.

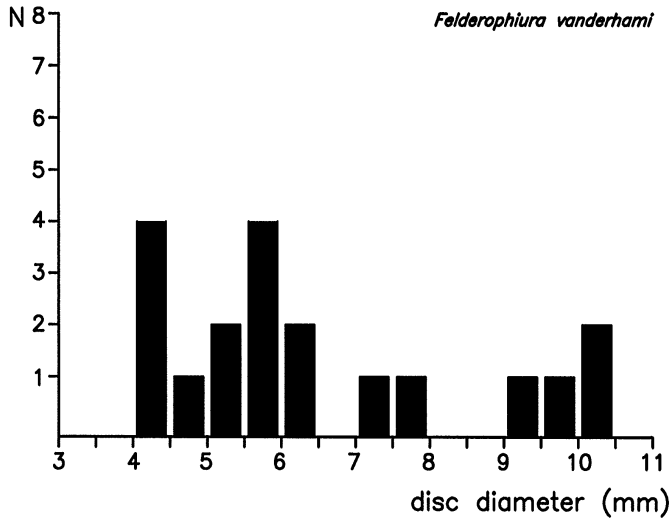

Fig. 4. Size frequency histogram for *Felderophiura vanderhami* Jagt, 1991 from the Meerssen Member (Maastricht Formation) of the ENCI-Maastricht BV, Blom, Ankerpoort-'t Rooth quarries and the Schunck outcrop.

Remarks — This species has turned out to be the commonest ophiuroid taxa in the type Maastrichtian, with many well-preserved discs (including juvenile ones; Fig. 4) currently known. With the possible exception of arm ossicles of *Ophiocten*? *yvonnae* sp. nov., described above, dissociated plates of the present species cannot be confused with any other ophiuroid. Especially typical is the set of triangular wedge-shaped between the radial shields.

Of particular interest is a specimen (NHMM K 3024; Pl. 7, figs. 1-2) from the Meerssen Member (IVf-4) at the ENCI-Maastricht BV quarry. With three (broken) arms lodged in the substrate, the disc in vertical position, and the remaining two arms curved above the sediment, this specimen may have been preserved in feeding position, or alternatively, while attempting to escape from being smothered by sediment.

Occurrence — This species first appears in the basal Schiepersberg Member, ranges through the Emael, Nekum and Meerssen members (CBR-Romontbos, Blom, ENCI-Maastricht BV and Ankerpoort-'t Rooth quarries), and occurs also in the Kunrade Limestone facies (Kunrade/Benzenrade area) (Figs. 2B, 11-15).

Genus *Stegophiura* Matsumoto, 1915

Type species — *Ophiura nodosa* Lütken, 1855, by original designation.

Stegophiura? *hagenowi* (Rasmussen, 1950)
Pl. 2, fig. 11; Pl. 3, figs. 1-2; Pl. 12, fig. 3.

Remarks — For synonymy, description and discussion see p. 69.

Material — Numerous arm fragments, as well as dissociated disc and arm ossicles, including NHMM JJ 2254a-e, 2981a-d, 6208, 7280i, 9520d, 9993a, 10600/1, 10601/1, 11119, K 2534, MB 761-6 and 1044-9i.

Note — In comparison with the common occurrence of well-preserved portions of arms, fragments of discs are rare and invariably compressed and distorted to varying degrees. This explains why details of oral frame and disc plating are still unknown for this common species. Isolated radial shields from the Kunrade Limestone facies at Kunrade (Pl. 16, fig. 9) and from the uppermost Meerssen Member at Geulhemmerberg (Geulhem; Pl. 16, fig. 10) are apparently close to this species.

Material from the Zeven Wegen Member generally is much more robust, has a more pronounced ornament and sturdier radial shields. We consider this material to fall within the range of variation; a recent re-examination of some of Rasmussen's (1950) originals (MGUH) has shown the above characters to be quite variable (see also Maryańska & Popiel-Barczyk, 1969). Although the species was first described from the Lower Maastrichtian, Rasmussen (1950, p. 116) also recorded material from the *mucronata* Zone (= Upper Campanian) of England (BMNH, C.W. Wright Colln).

Occurrence — Currently known from the Zeven Wegen and Vijlen members (Gulpen Formation) at the CPL SA and CBR-Lixhe quarries, the Benzenrade Member (Vaals Formation) at Welterberg (de Wingerd quarry), the Vijlen Member at Aachen (Hans-Böckler-Allee), and the Gronsveld Member (Maastricht Formation) at the ENCI-Maastricht BV quarry (Figs. 2B, 8-9, 12).

Stegophiura? *trispinosa* Jagt & Kutscher, sp. nov.
Pl. 3, figs. 3-9.

Type — Holotype is NHMM JJ 10604a (Pl. 3, fig. 4-5); paratypes are JJ 10604b, and NHMM MB 1044-9d/g.

Type locality and horizon — CPL SA quarry (Haccourt, Liège), Gulpen Formation, Zeven Wegen Member, basal 1-2 m, lower Upper Campanian.

Derivation of name — Lat. *tri*, three, and *spinosus*, bearing three spines.

Diagnosis — Strongly curved lateral arm plates with concave proximal and convex distal margin, three crater-like spine tubercles in a much constricted ventral portion of the plate, adjacent to the tentacle pore indentation. Outer surface, except proximal margin pitted, with pits aligned. Radial shields large, curved, smooth with bevelled margin; a pit-like depression for genital articulation on the inner surface.

Material — In addition to the types, a few lateral arm plates and radial shields (sample MB 1044-9).

Description — Of this apparently rare species, only the highly distinctive lateral arm plates and radial shields are currently known.

The strongly curved, large lateral arm plates are distinctly taller than long, with a concave proximal and convex distal margin, the ventral portion of the plate being particularly narrow. Between the proximal and distal margins the outer surface is strongly constricted, becoming wall like; this constriction effaces towards midheight. Distally of this 'wall', in a depression, are found three prominent, crater-like tubercles, the ventralmost of which is smaller than the other two (Pl. 3, figs. 4, 6). These tubercles are arranged in such a way that the third is furthest removed from the mar-

gin. The associated spines must have been erect. The remainder of the outer surface, with the exception of the proximal part covered by the abutting plate, shows a characteristic pattern of pits, in part arranged in lines. The tentacle pore notch is rather inconspicuous (Pl. 3, figs. 3-4, 6).

The inner surface (Pl. 3, fig. 3) shows only weakly developed articulation facets, a blunt low ridge extending from the dorsal to the ventral facets, parallel to the proximal margin. The distal margin lacks any distinctive articulation elements.

Radial shields (Pl. 3, figs. 8-9) are large, strongly curved and smooth, with beveled margins of variable width. On the distal margin of the inner surface a weakly developed elevation with a roundish depression just underneath for genital articulation can be made out.

Discussion — On account of details of outer surface ornament and the distinctive three spine tubercles, this species cannot possibly be confused with co-occurring *S.*? *hagenowi*, *Ophiotitanos serrata* and *Ophioderma*? *substriatum*. Although clearly different from *S.*? *hagenowi*, it is also referred to the genus *Stegophiura*, as based on a comparison with material of the extant species, *S. sladeni* (Duncan, 1879) and *S. brachyactis* (Clark, 1911). However, ultimate assignment has to rely on characters of disc plating and oral frame (see e.g. Ishida et al., 1996).

Occurrence — Apparently confined to the basal Zeven Wegen Member (Gulpen Formation) at Haccourt (CPL SA quarry) (Figs. 2B, 8).

Infraorder Gnathophiurina Matsumoto, 1915
Superfamily Gnathophiuridea Matsumoto, 1915
Family Amphiuridae Ljungman, 1867
Genus *Amphiura* Forbes, 1843b

Type species — *Amphiura chiajii* Forbes, 1843b, by subsequent designation of Verrill (1899).

Amphiura? *plana* Kutscher & Jagt, sp. nov.
Pl. 10, fig. 11; Pl. 11, fig. 1.

Remarks — For synonymy, description and discussion see p. 71.

Material — Several dozens of dissociated lateral arm plates and vertebrae as well as a few arm fragments, preserving spines and ventral arm plates, including NHMM JJ 2955, 3558, 3684, 3702, 10527, 10600/12b, MB 284-7, 1175 sample.

Occurrence — Currently known from the Zeven Wegen and Vijlen members (Gulpen Formation) at Haccourt (CPL SA quarry), the Vijlen Member at Snouwenberg (Voerstreek) and the Meerssen Member (Maastricht Formation) at the ENCI-Maastricht BV quarry (Figs. 2B, 8, 12).

Genus *Deckersamphiura* Jagt & Kutscher, gen. nov.

Type species — *Deckersamphiura inusitata* Jagt & Kutscher, sp. nov.
Other included species — *Deckersamphiura* sp. (? nov.; see below).
Derivation of name — Named after Mart J.M. Deckers (Tegelen), in recognition of

his much appreciated help during field work in recent years.

Diagnosis — An amphiurid with conspicuous dorsal disc plating, with a distinct central plate and up to two additional circlets, stout arms with dorsal and ventral arm plates abutting over the entire arm length, narrow, crescent-shaped lateral arm plates with up to 7 (or more ?) short, simple arm spines, arrow head shaped oral shields and paired, pointed infradental papillae.

Stratigraphic range — Late Campanian to latest Maastrichtian.

Deckersamphiura inusitata Jagt & Kutscher, sp. nov.
Pl. 8, figs. 7-11; Pl. 9, figs. 7-9.

Type — Holotype is NHMM RD 155 (Pl. 9, figs. 7-9); paratypes are NHMM MB 377-27, and MD 3061.

Type locality and horizon — ENCI-Maastricht BV quarry, Maastricht (southern Limburg); Maastricht Formation, Meerssen Member, IVf-4 (*Belemnella kazimiroviensis* Zone of authors).

Derivation of name — Lat. *inusitatus*, meaning unusual, in allusion to its highly distinctive disc plating.

Diagnosis — As for genus.

Material — A few discs and arm fragments, including NHMM K 2281 and MD 3059.

Description — Disc slightly elevated, with highest point centrally, gently sloping towards margins; pentagonal with indented interradial margins. Disc diameter in three specimens (NHMM MD 3059, MB 377-27, and RD 155, respectively): 7.3, 4.0 and 9.0 mm. Arm length estimated to have been at least 6-10 times the disc diameter, as based on associated arm fragments. Dorsal disc surface covered with smooth plates and scales, amongst which a distinct, pentagonal central plate (Pl. 8, fig. 7; Pl. 9, fig. 7), with straight margins, and a primary circlet of equal-sized or slightly larger plates, radially arranged with straight lateral margins and broadly convex distal, pointed margins. Plates of the second circlet are smaller than those of the first in small individuals (Pl. 8, fig. 7) but grow to the same size as those of the first in larger specimens (Pl. 9, fig. 7). The latter also have a small triangular plate resting on the proximal portion of the radial shields. Interradially, 2 or 3 plates occur of different size and shape, reaching halfway the radial shields in larger specimens. Radial shields fairly large, covered for the most part by other disc plates; distal margin abutting with two small rectangular plates above arm base (Pl. 9, fig. 7).

Ventral disc surface apparently with small irregularly sized scales interradially only. Oral shield arrow head shaped with straight proximal margins; adoral shields large, abutting over the oral shield, widest distally. Jaws stout with two block-like to pointed infradental papillae (Pl. 8, fig. 8); a single, pointed oral papilla distally and a smaller, pointed first oral tentacle scale proximally (Pl. 8, fig. 8).

First ventral arm plate small, wedged in between adoral shields (Pl. 8, fig. 8), successive plates more or less rectangular, with sloping lateral margins, wider than long, abutting over entire width, conspicuous to arm tip, and only slightly decreasing in width distally, and with weakly concave distal margin. Dorsal arm plates comparable but wider, occasionally divided into two along midline, thinning laterally, with

broadly convex distal margin (Pl. 8, fig. 10). Lateral arm plates crescent shaped with row of (?)circular spine tubercles on distal margin, apparently increasing in size dorsally, at least 7 in number; lateral arm plates separated by skin (Pl. 8, fig. 11), ventral process thick set. Lateral arm spines within disc fairly stout and pointed (Pl. 9, fig. 8). A single(?), pointed tentacle scale (Pl. 8, fig. 8). Vertebrae thin and of zygospondyline type.

Discussion — The occurrence of paired infradental papillae at the tip of the jaw shows the present species to be an amphiurid (see diagnoses in Fell, 1960, 1962; A.M. Clark, 1970 and Paterson, 1985). Within the Amphiuridae, genera are characterised mainly by the number and arrangement of oral papillae. The present fossil genus appears closely related to the extant *Amphiura*, but differs markedly in dorsal disc plating.

Fossil amphiurid ophiuroids are rare. Hess (1970, p. 1074, figs 3-6; pl. 1; pl. 2, fig. 7) described from the Upper Hauterivian of Neuchâtel (Switzerland) a new genus and species, *Xanthamphiura hauteriviensis*, which is easily distinguished from *Deckersamphiura* gen. nov. in having six contiguous oral papillae. Other fossil species referred to the Amphiuridae include:

Nullamphiura felli Skwarko, 1963 (p. 579, pl. 78, figs. 4-5; text-figs. 1-2) from the Cenomanian of Bathurst Island (northern Australia), referred here with a query, has poorly preserved jaws and teeth and cannot be compared in detail.

Amphiura cretacea Spencer, 1907 (p. 107) from the Cenomanian of England may not be an amphiurid after all; the species will be revised in the near future.

Amphiura? *senonensis* Valette, 1915, is here reassigned to *Ophiocoma* (see p. 27).

Amphiura sanctaecrucis Arnold, 1908 (p. 404, pl. 40) from the Upper Miocene of California has different dorsal disc plating, and longitudinally grooved ventral arm plates.

Amphioplus venezuelanus Berry, 1941b (p. 68, pl. 11, figs. 2, 9, 16) from the Eocene of Venezuela differs in disc plating and arm structure.

Amphiura? *kuehni* Binder & Steininger, 1967 (p. 21, pl. 1, figs. 1-2) from the Upper Miocene of Austria differs in having a densely plated disc.

Dissociated ossicles from the Miocene of Austria described by Küpper (1954, pp. 163-164, pl. 14, figs. 1-8; pl. 15, figs. 1-2) as *Amphiura*? *badensis* and *Amphiura*? *gigantiformis* probably represent ophiocomids rather than amphiurids.

The type of lateral arm plate in *D. inusitata* resembles that seen in various other species, such as *Amphiura*? *plana* Kutscher & Jagt, sp. nov. (see p. 71), *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov. (see p. 73), *Ophiocoma*? *ishidai* Kutscher & Jagt, sp. nov. (see p. 76), and *Ophiothrix*? *bongaertsi* Kutscher & Jagt, sp. nov. (see p. 72), all based on material from the Lower Maastrichtian of Rügen. Preservation of the present material is such that detailed comparisons are virtually impossible. However, in view of the fact that discs are associated, these specimens are considered to represent a new species. New, and better preserved material, is needed to substantiate our current views.

Occurrence — Known to date only from the Meerssen Member (Maastricht Formation) at the ENCI-Maastricht BV and Blom quarries (Figs. 2B, 12, 14).

Deckersamphiura sp. (? nov.)
Pl. 8, figs. 5-6; Pl. 9, figs. 2-4, 6.

Material — A single disc, a number of disc fragments and portions of arms (NHMM MB 619-2b, 865-15b/d, 865-16, 865-19).

Description — Disc slightly elevated, with highest point centrally, sloping gently towards margins, pentagonal with indented interradial margins. Disc diameter of the only complete disc is 5.3 mm. Arm length estimated (from associated arm fragments) to have been at least 6-10 times the disc diameter. Dorsal disc surface with smooth plates and scales, amongst which a primary circlet of radially arranged, large abutting plates with straight lateral margins and a broadly convex distal margin (Pl. 8, fig. 6). Plates of the second circlet are separated by smaller, irregularly shaped scales, are positioned interradially, slightly smaller than those of the primary circlet and quadrangular/rectangular with straight lateral and distal margins. In both laterodistal corners occur indentations for abutting scales. Two of these separate the proximal portion of the radial shields (Pl. 8, fig. 6; Pl. 9, fig. 4), the distal one with a pointed end, to about halfway. Radial shields are fairly large and abut except proximally (Pl. 8, fig. 5), but only their distal portion is free. Interradially, two larger plates are flanked by smaller scales which reach the indented margin (Pl. 8, fig. 6). Two small, rectangular plates abut the distal margin of the radial shields as well as the dorsal and lateral arm plates.

Ventral disc surface rather poorly preserved, showing four arm segments to occur within the disc, and many small scales interradially (Pl. 8, fig. 5). The oral frame shows stout oral plates, teeth (Pl. 9, fig. 6) and the first vertebrae with wing-like processes (Pl. 8, fig. 5). The size and shape of the oral and adoral shields, and the first ventral and lateral arm plates cannot be made out satisfactorily. However, the adoral shields appear to have been large and two infradental papillae block like. Arm spines with the disc are short, simple, rapidly tapering and pointed. The genital scale is sickle shaped(?). The genital plate (pl. 8, fig. 5) is thin and club shaped, with a widened, flattened distal end.

Arms are stout (Pl. 9, figs. 2-3) with a very slight taper; width and length of ventral arm plates almost equal, slightly sloping lateral margins, indented distal margin and pointed proximal margin, apparently abutting along entire arm length. Dorsal arm plates (Pl. 9, fig. 2) more or less tumid, broadly rounded triangular in outline, with proximal overlap and straight dorsal margin rounding into lateral margins; apparently also abutting along entire arm length. Lateral arm plates narrow, widest ventrally, dorsal portion partially covered by dorsal arm plates; distal margin with barely visible row of small spine tubercles (poorly preserved, number cannot be determined). Plates slope gently towards thin proximal margin, which was covered in skin during life (Pl. 9, fig. 3). Vertebrae of the zygospondyline type.

Discussion — The present species differs from its latest Maastrichtian congener (see above) in having more plates and scales covering the dorsal disc surface, slightly wider lateral arm plates, more tumid dorsal and ventral plates, with convex margins, and apparently also small scales on the interradial ventral disc surface. Both forms undoubtedly belong to the same lineage which appears to be characterised by the loss of certain disc plates in the younger species (paedomorphism). However, in the

absence of discs of larger specimens we refrain from formally naming this Late Campanian form. Should new material reveal that differences in disc plating, noted above, between these two forms are constant at all growth stages, a new species could be erected after all.

Occurrence — Apparently restricted to the Benzenrade Member (Vaals Formation) in the Ubachsberg-Heerlen/Benzenrade area (Fig. 2B).

Family Ophiothricidae Ljungman, 1867
Genus *Ophiothrix* Müller & Troschel, 1840

Type species — *Ophiura rosula* Fleming, 1828 = *Asterias pentaphylla* Pennant, 1777, by subsequent designation of Lyman (1865).

Ophiothrix? *bongaertsi* Kutscher & Jagt, sp. nov.
Pl. 9, fig. 1?; Pl. 11, figs. 2-5; Pl. 12, figs. 6-9.

Remarks — For description and discussion see p. 72.

Material — A few arm fragments preserving spines, vertebrae and lateral, ventral and dorsal arm plates, as well as many dissociated ossicles, including NHMM JJ 9380-8, 9395-5, MB 619-2c/d, 770-2, 1044-9h.

Discussion — Arm fragments and lateral arm plates are reminiscent of *Amphiura*? *plana* (see above), from which it differs in having even more clearly scythe-shaped lateral arm plates (thin dorsal portion), and more numerous and more close-set spine tubercles at the distal margin (9-11 in number). Spines (Pl. 11, fig. 3; Pl. 12, figs. 6, 9) are striated/glassy, pointed and increase in size ventrally. The two largest and (basally) broadest spines occur next to the tentacle pore indentation. Dorsal arm plates abut over entire arm length, and have a broadly rounded distal margin, the proximal margin being partially covered by the abutting plate (Pl. 12, figs. 6, 8); ventral arm plates broadly pentagonal, abutting over entire arm length; tentacle pore fairly large, with a single, large scale.

Occurrence — Recorded from the Zeven Wegen Member (Gulpen Formation) at the CPL SA quarry (Haccourt), the Benzenrade Member (Vaals Formation) in the Benzenrade area, the Vaals Formation at Vaals-Eschberg and the basal Gronsveld Member (Maastricht Formation) at the ENCI-Maastricht BV quarry (Figs. 2B, 8, 12).

Ophiothrix? *cristata* Kutscher & Jagt, sp. nov.
Pl. 11, fig. 11; Pl. 17, figs. 7-8?; Pl. 18, fig. 2?; Pl. 19, figs. 3-7; Pl. 20, fig. 4.

Remarks — For description and discussion see p. 73.

Material — A few dissociated lateral arm plates, including NHMM JJ 7280c, 10600/12c, MB 414-3f/g, 734-12 sample, 1175 sample.

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) at the CPL SA quarry (Haccourt), the Vijlen Member (Gulpen Formation) at Snouwenberg (Voerstreek) and the Geulhem Member (Houthem Formation) of the temporary Albertkanaal sections (Figs. 2B, 8).

Family Ophiactidae Matsumoto, 1915
Genus *Ophiactis* Lütken, 1855

Type species — *Ophiactis krebsii* Lütken, 1855 = *Ophiolepis savignyi* Müller & Troschel, 1842, by subsequent designation of H.L. Clark (1915).

Ophiactis? *sulcata* Kutscher & Jagt, sp. nov. (?)
Pl. 11, fig. 6?.

Remarks — For description and discussion see p. 75.

Material — A few dissociated lateral arm plates, including NHMM JJ 10600/12d, may belong here.

Occurrence — Currently known only from the Zeven Wegen Member (Gulpen Formation) at the CPL SA quarry (Figs. 2B, 8).

Superfamily Ophiocomidea Ljungman, 1867
Family Ophiocomidae Ljungman, 1867
Genus *Ophiarachna* Müller & Troschel, 1842

Type species — *Ophiura incrassata* Lamarck, 1816, by monotypy.

Ophiarachna? *martinblomi* Jagt & Kutscher, sp. nov.
Pl. 12, figs. 10-12.

Type — Holotype is NHMM MB 108-10a (Pl. 12, figs. 11-12); paratypes are NHMM MB 108-10b, and K 1400.

Type locality and horizon — Blom quarry (Berg en Terblijt, southern Limburg); Maastricht Formation, Meerssen Member (IVf-6/7), late Late Maastrichtian (*Belemnella kazimiroviensis* Zone of authors).

Derivation of name — Named after Martin Blom (Berg en Terblijt), who over the years allowed us access to his quarry and always took a keen interest in our palaeontological studies.

Diagnosis — Ophiocomid with robust lateral arm plates, four near equal-sized spine tubercles on distal margin, the dorsal one of which must have borne an erect spine. Articulatory bosses on proximal margin correspond to similar elements on inner surface of adjacent plate.

Material — Only the type specimens are available.

Description — The comparatively large lateral arm plates are weakly constricted and appear smooth. The proximal margin shows two wide articulation elements, the central one of which is larger (Pl. 12, figs. 11-12). These elements correspond to similar structures on the inner surface of abutting plates (Pl. 12, fig. 10). The four large, horseshoe-shaped tubercles are placed in circular-elongate 'pockets' directly on the distal plate margin. These tubercles are almost of the same size. The dorsal one faces upwards (Pl. 12, fig. 12) and can be seen from the inside (Pl. 12, fig. 10) and is not clearly separated from the others. Tentacle pore indentations are not very large (Pl. 12, fig. 10). On the inner surface there is also a narrow rim, running from the proximodistal corner to the tentacle pore.

Discussion — The present material was recognised amongst thick-set lateral arm plates of *Ophiotitanos serrata* (see below), with which they cannot be confused. There is a certain resemblance to median/distal lateral arm plates of *Ophiacantha*? *toarcensis* Hess, 1962b (p. 649, fig. 81) from the Toarcian of Solothurn (Switzerland). Even closer is Hess's 'Seewen Typ III B' (1962b, p. 652, figs. 110-115), which Kutscher (1996b, p. 16, pl. 4, figs. 1-4) described as *Ophiarachna*? *liasica* Kutscher, 1996b. The present form is assigned, albeit with a query, to *Ophiarachna* for the same reasons as outlined by Kutscher (1996b) for his form. The Cretaceous taxon differs in having even more massive lateral arm plates with 4 tubercles.

Occurrence — A rare species, known only from the upper Meerssen Member at Blom quarry (Figs. 2B, 14).

Genus *Ophiocoma* L. Agassiz, 1836

Type species — *Ophiura echinata* Lamarck, 1816, by subsequent designation of H.L. Clark (1915).

Ophiocoma? *rasmusseni* Hess, 1960b
Pl. 19, fig. 11.

Remarks — For synonymy, description and discussion see p. 77.

Material — A few dissociated lateral arm plates, including NHMM JJ 10523, and MB 432.GGGe.

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) at the CPL SA quarry (Haccourt), the Vijlen Member (Gulpen Formation) at Snouwenberg (Voerstreek), the Meerssen Member (Maastricht Formation) at the ENCI-Maastricht BV quarry and the Geulhem Member (Houthem Formation) of the temporary Albertkanaal sections (Figs. 2B, 8, 12).

Ophiocoma? *senonensis* (Valette, 1915)
Pl. 2, figs. 8-9; Pl. 11, figs. 8?, 9-10; Pl. 17, fig. 10?; Pl. 19, figs. 8-9.

Remarks — For synonymy, description and discussion see p. 78.

Material — A few arm fragments and numerous dissociated lateral, dorsal and ventral arm plates as well as vertebrae, including NHMM JJ 2481b/c, 2628, 6484, 7280g, 10521, 10600/10, MB 734-12e/l; RGM 428 044.

Occurrence — Currently known from the Zeven Wegen Member (Gulpen Formation) at the CPL SA and CBR-Lixhe quarries, the Vijlen Member (Gulpen Formation) at the CPL SA quarry and Snouwenberg (Voerstreek), the Meerssen Member (Maastricht Formation) at the ENCI-Maastricht BV quarry and the Geulhem Member (Houthem Formation) of the temporary Albertkanaal sections (Figs. 2B, 8-9, 12).

Infraorder Ophiodermatina Smith, Paterson & Lafay, 1995
Family Ophiodermatidae Ljungman, 1867
Genus *Ophioderma* Müller & Troschel, 1840

Type species — *Asterias longicauda* Retzius, 1805, by subsequent designation of H.L. Clark (1915).

Ophioderma? *radiatum* Kutscher & Jagt, sp. nov.
Pl. 12, figs. 1-2.

Remarks — For description and discussion see p. 80.

Material — A single arm fragment as well as a few dissociated lateral arm plates (NHMM JJ 5079, MB 808-9c).

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) of Haccourt (CPL SA quarry) and the Lanaye Member (Gulpen Formation) at Maastricht (ENCI-Maastricht BV quarry) (Figs. 2C, 8, 12).

Ophioderma? *substriatum* (Rasmussen, 1950)
Pl. 12, figs. 4-5.

Remarks — For synonymy, description and discussion see p. 81.

Material — A few dozens of dissociated lateral arm plates, including RGM 428 045 (ex Jagt Colln, no. 3914), NHMM JJ 10600/7a; and NHMM MB 1044-9.

Occurrence — Currently known from the Zeven Wegen and Lanaye members (both Gulpen Formation) at Haccourt (CPL SA quarry), the Vijlen Member (Gulpen Formation) at Aachen (Hans-Böckler-Allee) and at Snouwenberg (Voerstreek) (Figs. 2B, 8).

Genus *Ophiotitanos* Spencer, 1907

Type species — *Ophiotitanos tenuis* Spencer, 1907, by original designation.

Ophiotitanos serrata (Roemer, 1840)
Pl. 7, figs. 4-5?; Pl. 8, figs. 3-4; Pl. 15, figs. 9-12; Pl. 16, figs. 1-3; Pl. 17, figs. 2-3?; Pl. 19, figs. 1-2; Pl. 20, figs. 7-8; Pl. 21, figs. 1-4.

Remarks — For synonymy, description and discussion see p. 83.

Material — A few arm fragments preserving spines, jumbles of disc plates, and numerous dissociated lateral arm plates and vertebrae, including NHMM JJ 2804a/c, 3687, 3821a/i, 8008, 9370-3, 9380-9, 10491, 10600/6, 10601/4, MB 414-3d, 432.GGGa/b, 432.GGGc, 661-4c, 734-12r/s/v-y, 867-6b, 108-10c, NHMM 1998032; RGM 428 052 (ex Jagt Colln, no. 5952). Isolated radial shields of the type illustrated in Pl. 17, fig. 2, may also belong here.

Note — Specimens from the Meerssen and Geulhem members (Pl. 16, figs. 1-3; Pl. 19, figs. 1-2) are typically tumid and have well-developed articulation bosses at the proximal margin of the lateral arm plates. This may have been an adaptation to life in high-energy settings.

Occurrence — This species is long-ranging, with records from the Vaals Formation at Vaals-Eschberg, the Zeven Wegen Member (Gulpen Formation) at Heure-le-Romain and Haccourt (CPL SA quarry), the Vijlen Member (Gulpen Formation) at Aachen (Hans-Böckler-Allee), Haccourt (CPL SA quarry) and Snouwenberg (Voerstreek), the Lanaye, Gronsveld, Emael, Nekum and Meerssen members (Maastricht Formation) of the Ankerpoort-Marnebel, ENCI-Maastricht BV, CBR-Romontbos and

Blom quarries, as well as the Geulhem Member (Houthem Formation) of the temporary Albertkanaal sections (Figs. 2C, 8, 11-12).

Infraorder Ophiolepidina Ljungman, 1867
Family Ophiolepididae Ljungman, 1867
Genus *Ophiolepis* Müller & Troschel, 1840

Type species — *Ophiura annulosa* de Blainville, 1834, non Lamarck, 1816, by subsequent designation of Lyman (1865) (= *Ophiolepis superba* H.L. Clark, 1915).

Ophiolepis? *falsa* Jagt & Kutscher, sp. nov.
Fig. 5; Pl. 3, figs. 10-11; Pl. 4, figs. 1-4.

Types — Holotype is NHMM JJ 7551 (Fig. 5; leg. J. Reynders); paratypes are NHMM JJ 4989a/b and MB 761-9a/d.

Type locality and horizon — CPL SA quarry, Haccourt (Liège, B), Gulpen Formation, Zeven Wegen Member, top - c. 12 m, early Late Campanian.

Diagnosis — Small ophiolepidid with low, flat disc covered with tumid plates in two circlets, abutting radial shields partially covered by pentagonal and triangular plates, few interradial plates; only two proximalmost dorsal arm plates abut; lateral arm plates weakly constricted to tumid, robust, smooth, with excavated articulation

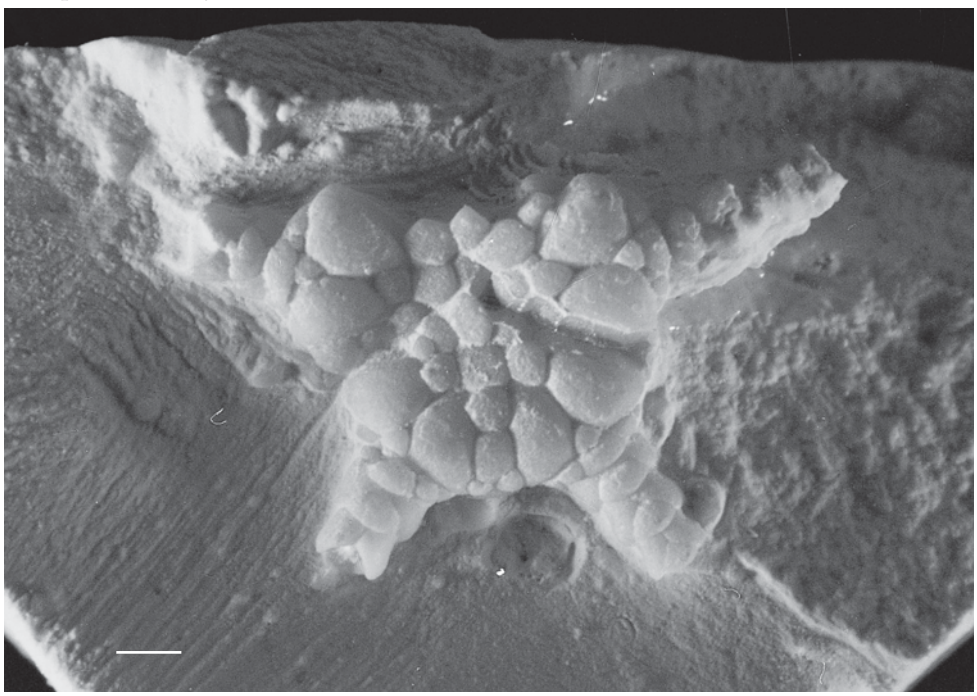

Fig. 5. *Ophiolepis*? *falsa* Jagt & Kutscher, sp. nov., **holotype** (NHMM JJ 7551), dorsal view of disc and proximal arm portions; CPL SA quarry, Haccourt (Liège); Zeven Wegen Member, top - c. 12 m; scale bar equals 1 mm.

bosses and four diminutive spine tubercles; large tentacle pore indentations over entire arm length; vertebrae of zygospondyline type.

Derivation of name — Lat. *falsus*, meaning deceitful, in allusion to the superficial similarity between this species and co-occurring juveniles of the ophiolepidid *Ophiomusium granulosum* (see below; Pl. 4, fig. 5), especially with regard to structure of the radial shields; lateral arm plates are very different.

Material — In addition to the type specimens, a few dissociated lateral arm plates (NHMM JJ 7280u(?), 10601/5).

Description — The low and flat disc, of which only the dorsal (adoral) surface is exposed in the holotype, has a diameter of 4.9 mm and is rounded pentagonal with near-straight interradial margins. Arm width at disc margin is 1.2 mm. Dorsal disc surface covered with smooth, slightly tumid plates and scales. No distinct central plate, but two rings of small scales of varying size and outline, which partially conceal the proximal ends of the radial shields. An arrow-shaped, pentagonal scale occurs in each radius, and appears wedged in between the radial shields. Radial shields abut over their entire length, are distinctly tumid, and bevelled, with dorsal margin straight; distally, a small triangular platelet (the first dorsal arm plate) appears similarly wedged in, and is followed by two abutting dorsal arm plates the width of which exceeds their length. The following tumid, triangular dorsal arm plates (of which two are preserved in the longest arm portion) are already separated.

Interradially, two plates (the distal one being the larger) are found, which at the margin, are joined by two much smaller triangular plates, and a larger marginal plate which apparently extends to the ventral (oral) surface. Abutting the distal margin of the radial shield and the second dorsal arm plate are two small ossicles, the outer one being the larger (? arm comb; papillae not preserved).

Lateral arm plates in the holotype appear slightly less tumid than the paratype ossicles (Pl. 3, figs. 10-11; Pl. 4, figs. 1-4), but are otherwise identical. These are small, robust, with the outer surface bearing ornament of fine granules, which may occasionally be arranged in rows. A few ossicles are weakly constricted, but most are tumid. The near-straight proximal margin bears two elongate, centrally excavated articulation bosses, the ventralmost one of which is larger. These correspond to similar bosses on the inner surface. The dorsal margin is convex, as is the ventral one, which shows a comparatively large tentacle pore indentation. The distal margin shows 4 excavations bordered by diminutive tubercles, the ventralmost one being the largest and close to the tentacle pore notch, the other three close together, almost at mid-plate height. Tubercles appear to consist of two small, parallel limbs; the associated spines must have been small and appressed. The distal articulation of the vertebra in one of the arms shows it to be of the zygospondyline type.

The ventral (oral) surface of disc and arms is concealed by matrix; because of the fragility of the present specimen we have refrained from further preparation. The dissociated lateral arm plates suggest the dorsal and ventral arm plates to have been separated over most of the arm (except for the two proximalmost arm segments, see above), and tentacle pores throughout the entire arm.

Discussion — To a certain extent, lateral arm plates of the present species resemble those of *Ophiolepis*? *granulata* Kutscher & Jagt, sp. nov. and *Ophiolepis*? *linea* Kutscher & Jagt, sp. nov., but differ in being more tumid (i.e. general lack of constriction), in

having even smaller spine tubercles and differently shaped articulation bosses. In addition, dorsal arm plates abut only in the two proximalmost arm segments in the present specimen, and tentacle pore notches are comparatively larger, but these may be juvenile features. Material from Rügen (see below) of the above-mentioned species comprises numerous ossicles of juvenile as well as (sub)adult specimens. Lateral arm plates of the latter certainly differ as outlined above, but to determine the exact relationship between the present species and the Rügen taxa larger sized individuals of *O.*? *falsa* are needed. Until such are found, the present form is treated as a distinct species.

Occurrence — Apparently confined to the Zeven Wegen Member (Gulpen Formation) at Heure-le-Romain and Haccourt (CPL SA quarry) (Figs. 2C, 8).

Ophiolepis? *granulata* Kutscher & Jagt, sp. nov.
Pl. 13, figs. 8-9.

Remarks — For description and discussion see p. 85.

Material — A poorly preserved arm fragment and a few dissociated lateral arm plates (NHMM JJ 8255 and MB 808-9e/f).

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) at Haccourt (CPL SA quarry) and the Vijlen Member (Gulpen Formation) at Snouwenberg (Voerstreek) (Figs. 2C, 8).

Ophiolepis? *linea* Kutscher & Jagt, sp. nov. ?
Pl. 17, figs. 4-5.

Remarks — For description and discussion see p. 86.

Material — A few dissociated lateral arm plates only (NHMM MB 414-3c/e).

Occurrence — Currently only known from the Kunrade Limestone facies (Maastricht Formation) in the Kunrade area (Fig. 2C).

Genus *Ophiomusium* Lyman, 1869

Type species — *Ophiomusium eburneum* Lyman, 1869, by original designation.

Ophiomusium granulosum (Roemer, 1840)
Pl. 4, fig. 5; Pl. 5, fig. 6; Pl. 13, fig. 5; Pl. 14; Pl. 15, figs. 1-4, 7-8; Pl. 20, figs. 6, 9.

Remarks — For synonymy and discussion see p. 88.

Material — Many thousands of dissociated disc and arm ossicles, as well as a few specimens preserving (portions of) discs and arms, including NHMM JJ 807a, 2719a-f, 4735a-c, 8604, 9577, 10600/2, 10600/12f, 10601/2, 10940, 11002, 11121, 11266, K 3385, MB 387-10c, 619-3, 734-12u/aa, 808-9b, RD 160; RGM 428 046-051.

Note — On the basis of the Rügen material (see p. 88), this species is considered to be highly variable, ranging from coarsely granulate outer surfaces of lateral arm plates and radial shields to almost smooth ones. The number of arm spines also varies.

Selected for illustration here from the copious material collected in Liège-Limburg

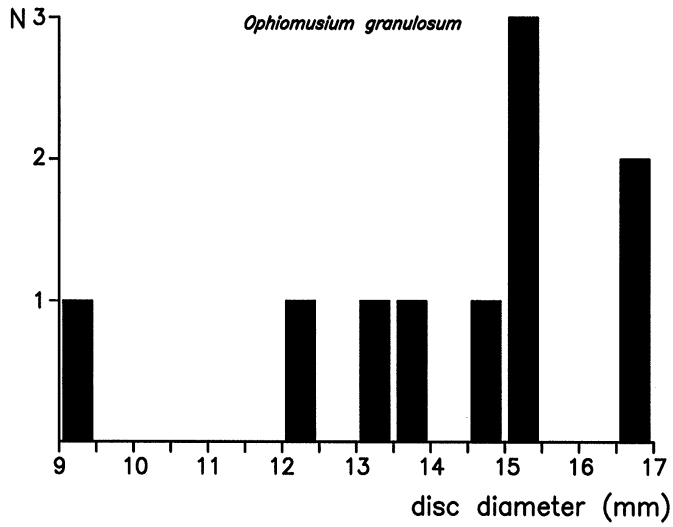

Fig. 6. Size frequency histogram for *Ophiomusium granulosum* (Roemer, 1840) from the basal Gronsveld Member (Maastricht Formation) of the ENCI-Maastricht BV quarry.

are various states of preservation, ranging from near-complete individuals (Pl. 15, figs. 1-2), portions of discs (Pl. 5, fig. 6) and arms (Pl. 14, figs. 4-5, 8-9; Pl. 15, figs. 3-4) to dissociated ossicles of disc and arms.

The best-preserved specimens are from the Zeven Wegen Member and basal Gronsveld Member, with the latter comprising the largest specimens known from the area (Fig. 6). These show tentacle pores to be confined to the heavy-plated disc, and arm length to be about four times the disc diameter. Spines, at least five or six, preserved in NHMM RD 78 (Pl. 14, figs. 8-9) are short, fairly stout, appressed and of variable length, not exceeding one third of arm segment length. A single arm fragment (NHMM MD 2731) shows regeneration.

Böhm's *Ophiurites trunensis* (1891, p. 100, pl. 4, fig. 14), from the Lower Maastrichtian Gerhardtsreiter Mergel (see Schmid & Schulz, 1979; Schulz & Schmid, 1983) of southern Germany may be a synonym as well, as may *Ophiomusium stephensoni* Berry, 1942 (p. 394, pl. 60, partim) from the Vincentown Sand of New Jersey. Gibson & Bybell (1995, fig. 1) showed this deposit to be of Late Palaeocene, rather than Eocene, age.

Ophiomusium rahbeki Brünnich Nielsen, 1941 (p. 66), which Rasmussen (1950) synonymised with *O. danicum*, is a different species, as a recent re-examination of the type specimen has shown; a redescription is in preparation.

Occurrence — Known to date from the Zeven Wegen, Vijlen, Lanaye, Valkenburg, Gronsveld and Emael members of Haccourt (CPL SA quarry), Lixhe (CBR-Lixhe quarry), Heure-le-Romain, Eben Emael (CBR-Romontbos and Ankerpoort-Marnebel quarries), Maastricht (ENCI-Maastricht BV quarry), Aachen (temporary outcrop Hans-Böckler-Allee), Welterberg (de Wingerd quarry), Snouwenberg (Voerstreek) and the temporary Albertkanaal sections (Figs. 2C, 8-12).

This species does not appear to range higher than the middle Emael Member

(Lava Horizon), but reappears in the Geulhem Member (Houthem Formation). Similar lateral arm plates from the Nekum and Meerssen members and the Kunrade Limestone facies belong to *Ophiomusium lux* (see below).

Ophiomusium lux Jagt & Kutscher, sp. nov.
Pl. 4, figs. 6-10; Pl. 5, figs. 1-4, 7; Pl. 6, figs. 3, 7; Pl. 9, fig. 5; Pl. 15, fig. 6; Pl. 18, fig. 8.

1995 Ophiuridae (n. gen. ?) n. sp. Jagt & Deckers, p. 273, fig. 1.

Types — Holotype is NHMM MD 3150 (Pl. 5, figs. 3-4), paratypes are NHMM 1994675, MD 3238, MB 487-4a, 655-1b, and RD 77-78.

Type locality and horizon — ENCI-Maastricht BV quarry, Maastricht (southern Limburg); Maastricht Formation, Meerssen Member, IVf-4), late Late Maastrichtian (*Belemnella kazimiroviensis* Zone of authors).

Derivation of name — Lat. *lux* for light, with reference to the Lichtenberg farm, situated directly above the type section of the Maastrichtian Stage.

Diagnosis — Medium-sized ophiolepidid with high disc, and prominent central plate and tumid plates of the radially arranged second series; radial shields large and separated by a series of small plates. Large oral and adoral shields, a single apical papilla, 2-3 dental papillae, and second oral tentacle pore with up to 3 papillae. Tentacle pores confined to disc, ventral and dorsal arm plates separated by lateral arm plates throughout arm; three diminutive, appressed arm spines.

Material — Several dozens of discs, many arm fragments and dissociated radial shields and lateral arm plates in the van Birgelen, Deckers, Dortangs, Jagt and Kuypers collections, including NHMM MD 3068-3069, 3072-3078, 3080, 3082, 3148, K 4140(11), and JJ 3872.

Description — Disc high, pentagonal with straight to slightly convex interradial margins. Disc diameter varies between 3.3 and 9.1 mm (Fig. 7); arm length must have been at least four times the disc diameter. Dorsal disc surface covered with smooth tumid plates and scales, amongst which a distinct, almost circular central plate (Pl. 5, fig. 4), a first (interradial) series of small triangular plates, and a conspicuous second series composed of interradially abutting, tumid ossicles, which constitute the highest point of the disc in lateral view (Pl. 5, fig. 3). The width of these plates, which have straight to slightly convex margins, decreases towards the disc margin. Similarly shaped, but increasingly smaller plates extend almost to the disc margin, abut with the first dorsal arm plate and separate the radial shields (Pl. 5, figs. 3-4, 7). Interradially, partially concealed by large radially arranged plates of the second series, are tumid rounded-triangular plates which abut with 2-4 smaller, rectangular, almost flat plates that extend to the interradial marginal plate (Pl. 5, fig. 4; Pl. 6, fig. 3). This marginal plate is rounded elliptical in outline and abuts the radial shields along their distal margin.

The distal interradial corner of the radial shield shows a characteristic incision (Pl. 4, fig. 10) for accommodation of the scythe-shaped genital plate and thin scale, the former partially covering the first free lateral arm plate (Pl. 5, fig. 7); arm comb papillae not preserved. Genital slit fairly distinct, no papillae preserved.

Oral disc surface (Pl. 5, figs. 1-2) covered by comparatively few, large plates, with one large, rounded interradial plate abutting the oral shield. Distal margin of oral

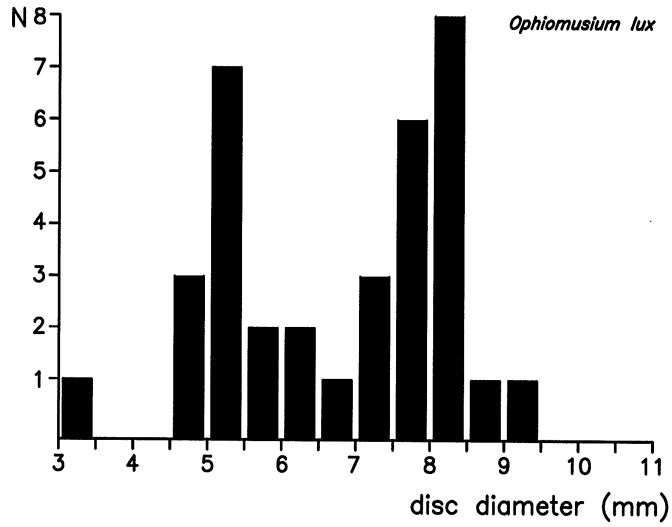

Fig. 7. Size frequency histogram for *Ophiomusium lux* Jagt & Kutscher, sp. nov., from the Meerssen Member (Maastricht Formation) of the ENCI-Maastricht BV and Blom quarries and the Schunck outcrop.

shield straight, width decreasing to pointed proximal end and indented sides. Adoral shields large, longer than wide, widest distally, broadly in contact, inner margin concave, outer margin slightly convex. Oral plates similar in outline and size to adoral shields (Pl. 5, fig. 1). A single large apical papilla at the end of each jaw, squarish, and up to 2 (3) oral papillae. Second tentacle pore opens still within mouth slit and has up to three squarish scales, the distal one being the largest. First ventral arm plate triangular, second broadly triangular (Pl. 5, fig. 2), separated by the lateral arm plates from the third arm segment onwards. Tentacle pores within disc large, with up to 5 squarish scales of near-equal size. A portion of a broken disc (Pl. 9, fig. 5) shows the genital plate and scale, the first two vertebrae, oral plates, teeth and disc plates.

Arms stout, conspicuously flattened ventrally and with gradual taper; dorsal arm plates triangular with convex distal margin (Pl. 4, figs. 6-7), ventral arm plates broadly triangular with (near)straight distal margin (Pl. 4, fig. 9). Lateral arm plates fairly tumid, with constricted proximal margin, smooth with distal margin slightly depressed (Pl. 4, fig. 8; Pl. 6, fig. 7). Close to distal margin three small spine tubercles, two of them close together (the ventralmost one closest to the margin), the third almost at midheight. Spines must have been short and appressed.

Discussion — Berry (1938, pl. 15, figs. 22, 25) illustrated poorly preserved lateral arm plates of *Ophiomusium* habit from the upper Maastricht Formation, under the name *Platyarthra jekerica*. A fairly well-preserved distal lateral arm plate (Pl. 30, fig. 3) from the collections of the Rijksuniversiteit Groningen (RUG X 523) is undoubtedly referable to the present species, as is another lateral arm plate from the uppermost Meerssen Member (Pl. 18, fig. 8). Superficially similar lateral arm plates are found in *Ophiomusium granulosum*, but this species does not seem to range higher than the middle Emael Member, to reappear in the Geulhem Member. On disc plating, radial shield

structure and the presence of dorsal and ventral arm plates beyond the proximalmost arm segments, the present species is easily distinguished from *O. granulosum*.

Occurrence — Apparently confined to the Nekum and Meerssen members in the Maastricht-Valkenburg area (ENCI-Maastricht and Blom quarries) and the upper part of the Kunrade Limestone facies in the Kunrade area (Figs. 2C, 12, 14).

Ophiomusium biconcavum Kutscher & Jagt, sp. nov.
Pl. 13, figs. 4, 10?

Remarks — For description and discussion see p. 87.

Material — A few dissociated lateral arm plates, including NHMM JJ 10600/12g, 10601/6, and MB 387-10b.

Note — Lateral arm plate MB 387-10b (Pl. 13, fig. 10), which is placed here with a query, differs in details of granulation, in lacking constrictions and in having a rather thin distal margin.

Occurrence — Known to date from the Zeven Wegen Member (Gulpen Formation) of Heure-le-Romain, and possibly from the Vijlen Member (Gulpen Formation) of Aachen (Hans-Böckler-Allee) (Fig. 2C).

Ophiomusium sentum Kutscher & Jagt, sp. nov. ?
Pl. 15, fig. 5.

Remarks — For description and discussion see p. 90.

Material — A small, rather poorly preserved disc with arms (NHMM MB 1044-9j) from the basal Zeven Wegen Member (Gulpen Formation) at the CPL SA quarry (Figs. 2C, 8), may belong here. The dorsal disc surface and lateral arm plates are coarsely granulate, but details of disc plating cannot be made out. The ventral surface has suffered considerably from recrystallisation.

Ophiomusium sinuatum Kutscher & Jagt, sp. nov. ?
Pl. 13, figs. 6-7.

Remarks — For description and discussion see p. 91.

Material — A few dissociated lateral arm plates, including NHMM JJ 2455a and MB 808-9d, may belong here; they differ from distal lateral arm plates of co-occurring *O. granulosum* in being constricted and in the position and structure of the spine tubercles, which, however, are not as prominent as in the material from Rügen. More material is needed to confirm the present assignment.

Occurrence — Currently known only from the Zeven Wegen Member (Gulpen Formation) at Haccourt (CPL SA quarry) (Figs. 2C, 8).

Genus *Mesophiomusium* Kutscher & Jagt, gen. nov.

Remark — For a diagnosis see p. 92.

Mesophiomusium decipiens Jagt & Kutscher, sp. nov.
Pl. 10, figs. 1-8, 9-10?; Pl. 21, figs. 5-6.

Type — Holotype is NHMM MB 734-12a (Pl. 16, figs. 1, 4); paratypes are NHMM JJ 4436 and MB 734-12b/d.

Type locality and horizon — Temporary Albertkanaal sections near Vroenhoven-Riemst (Limburg), Houthem Formation, Geulhem Member, lower part (*oedumi/abildgaardi* zone equivalents).

Material — The radial shields NHMM JJ 4452a/b and MB 734-12bb/cc may belong here.

Derivation of name — With reference to its being deceptively similar to species of the ophiolepidid *Ophiomusium*.

Diagnosis — Only dissociated lateral arm plates and arm fragments, possibly also radial shields, are known, which show this form to resemble *Ophiomusium* to a certain extent. Lateral arm plates robust, constricted in proximal portion, with dense granulation covering the entire outer surface, three widely spaced rather small spine tubercles near the broadly rounded distal margin, and well-developed tentacle pore indentations. Ventral arm plates small, medially constricted, pointed proximally and broadly rounded distally; two large (plus one ?) tentacle scales. Dorsal arm plates small, triangular, with straight margins; vertebrae of zygospondyline type. Radial shields rounded triangular, evenly arched and slightly bevelled, and with indented distal margin.

Description — Lateral arm plates are stout, squarish, have a (strongly) concave proximal and weakly convex distal margin; the central portion of the plate is constricted (Pl. 10, figs. 3-4, 6-8), the rim just proximally of the distal margin representing the highest point of the plate in lateral view. Spine tubercles are found in small depressions, apparently consist of two parallel limbs; inclination suggests the spines om these tubercles to have pointed in various directions. The inner surface (Pl. 10, fig. 2) shows two large articulation facets, the limited room for the vertebra, and no special articulation elements near the distal margin. Tentacle pore indentations are large, and apparently extended over the entire arm length. There are two spatulate, pointed tentacle scales and, possibly, a third much smaller, block-like one as well (Pl. 10, fig. 7). Ventral arm plates pointed proximally, partially concealed by adjacent plate, and with broadly rounded distal margin; sides constricted (Pl. 10, fig. 7). Dorsal arm plates small and triangular with straight margins, apparently also extending whole arm length, but not abutting.

Discussion — Awaiting the discovery of more complete material, preferably discs, features of the present form are such that it appears closely related to *Ophiomusium*. Although it is realised that inclusion in the new genus *Mesophiomusium*, with *M. moenense* as type species, cannot be but tentative at this time, this does emphasise the general *Ophiomusium* habit, but with extension of tentacle pores throughout the arms. In time, *Mesophiomusium* will no doubt prove to be a 'lump genus'. Of this, and other forms, discs are needed to determine their correct placement.

Occurrence — Apparently confined to the lower Geulhem Member (Houthem Formation), as formerly exposed in the Albertkanaal sections (Fig. 2C).

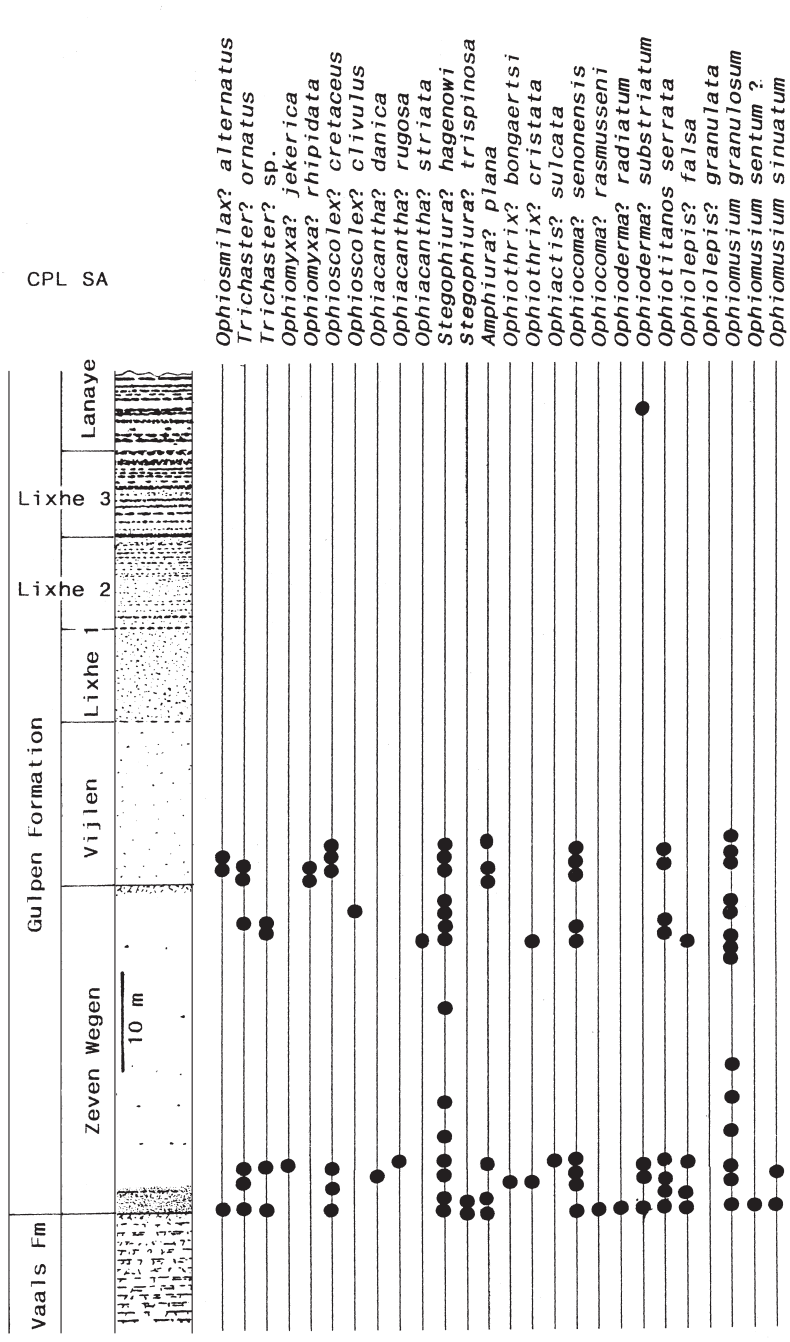

Fig. 8. Lithostratigraphy of section exposed at the Ciments Portland Liégeois SA quarry (Haccourt, Liège) and stratigraphic provenance of ophiuroid material studied herein.

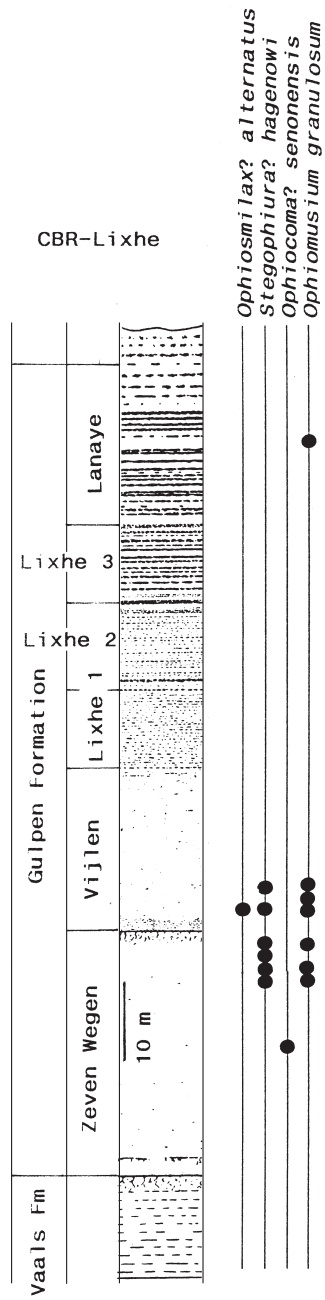

Fig. 9. Lithostratigraphy of section exposed at the Cimenterie Briqueterie Réunie quarry (Lixhe, Liège) and stratigraphic provenance of ophiuroid material studied herein.

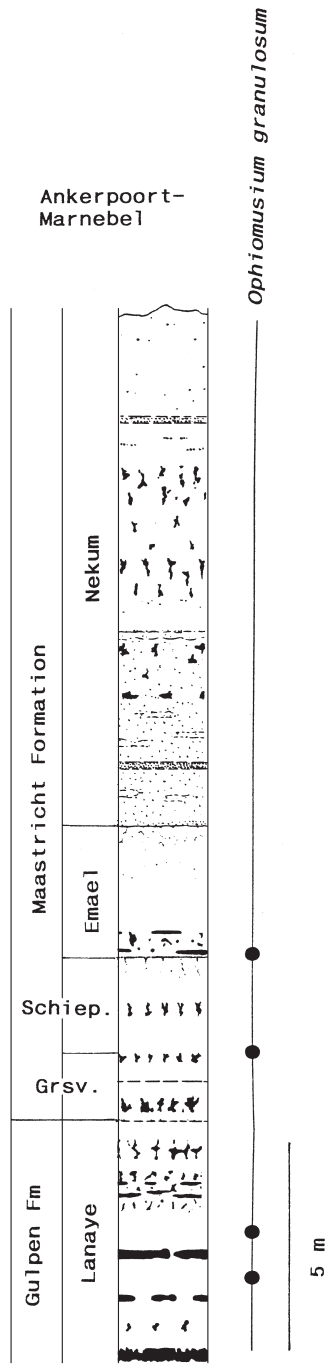

Fig. 10. Lithostratigraphy of section exposed at the Ankerpoort-Marnebel quarry complex (Eben Emael, Liège) and stratigraphic provenance of ophiuroid material studied herein.

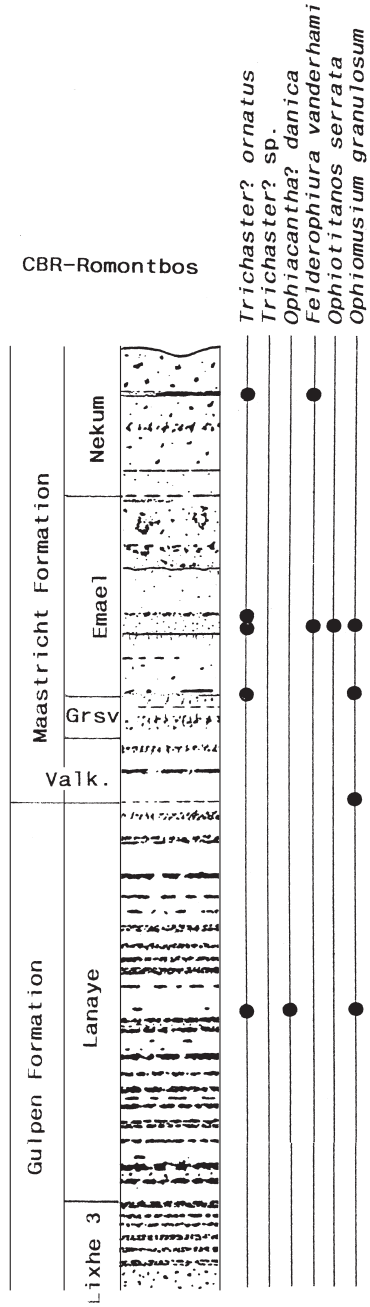

Fig. 11. Lithostratigraphy of section exposed at the Cimenterie Briqueterie Réunie-Romontbos quarry (Eben Emael, Liège) and stratigraphic provenance of ophiuroid material studied herein.

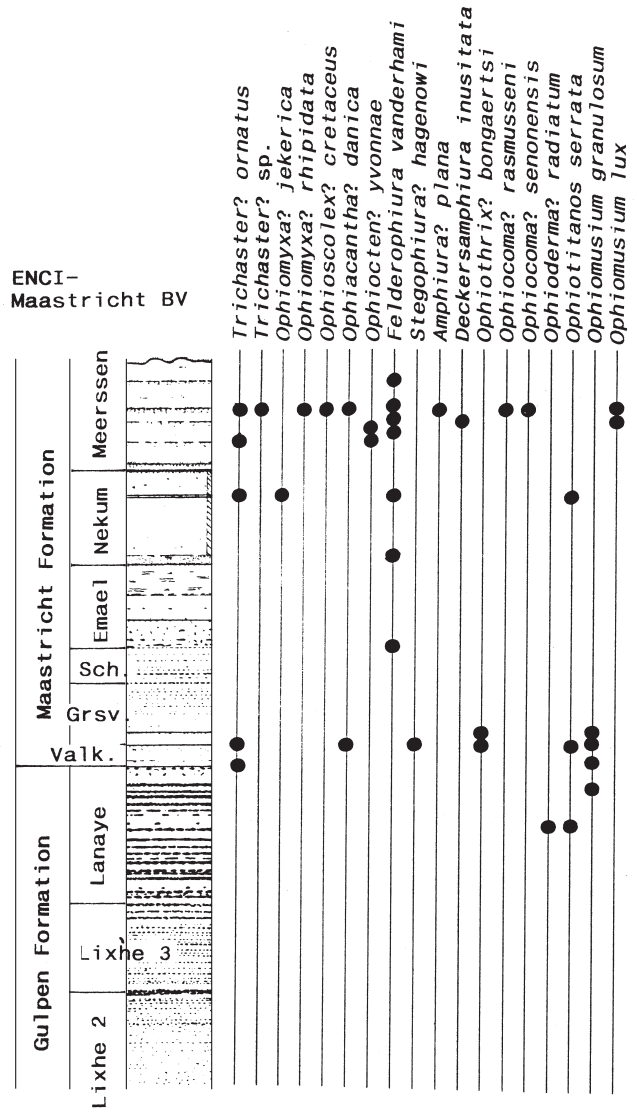

Fig. 12. Lithostratigraphy of section exposed at the ENCI-Maastricht BV quarry (Maastricht) and stratigraphic provenance of ophiuroid material studied herein.

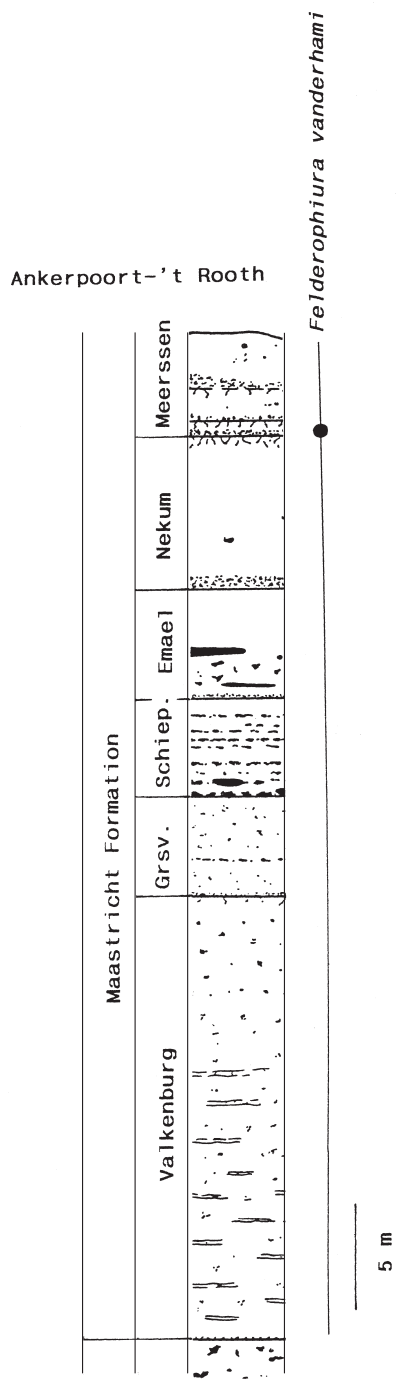

Fig. 13. Lithostratigraphy of section exposed at the Ankerpoort-'t Rooth (Nekami) quarry (Bemelen, southern Limburg) and stratigraphic provenance of ophiuroid material studied herein.

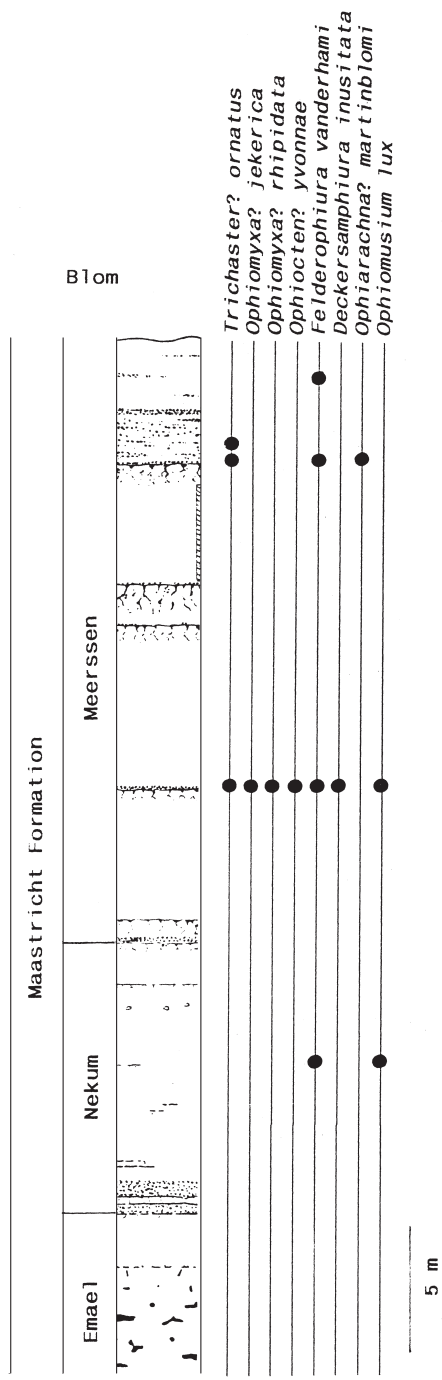

Fig. 14. Lithostratigraphy of section exposed at the Blom quarry (Berg en Terblijt, southern Limburg) and stratigraphic provenance of ophiuroid material studied herein.

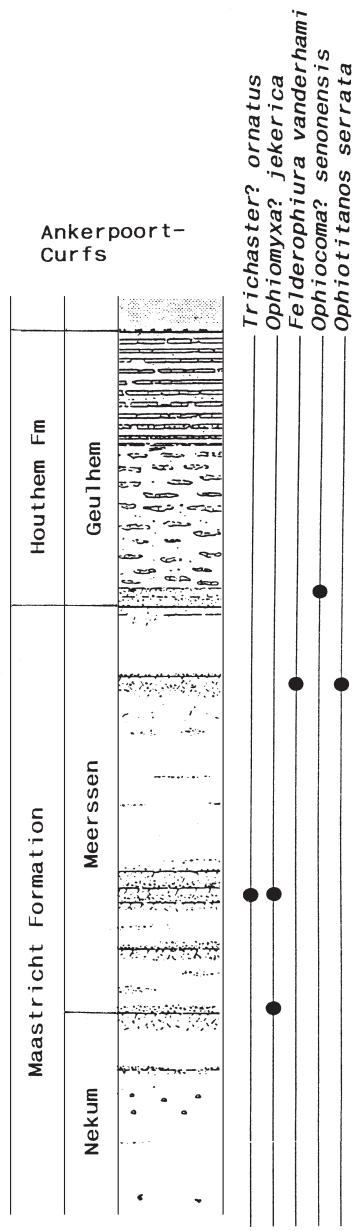

Fig. 15. Lithostratigraphy of section exposed at the Ankerpoort-Curfs quarry (Geulhem, southern Limburg) and stratigraphic provenance of ophiuroid material studied herein.

Acknowledgements

For full Acknowledgements see the final (sixth) part of this series at the end of this volume.

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Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark)

by Manfred Kutscher & John W.M. Jagt

Introduction

Although the study of Cretaceous faunas from Germany and Denmark was taken up well over a hundred years ago, so far only few authors have considered asterozoans in detail, or have referred to them in passing.

In his monograph on the Cretaceous fossils of Rügen, von Hagenow (1840, pl. 9, figs. 6-7) recorded two ophiuroid species, viz. *Ophiura (Aspidura) granulosa* and *Ophiura (Aspidura) subcylindrica*. Earlier that year, Roemer (1840) had described the first Cretaceous brittle stars ever, viz. *Ophiura serrata* and *Ophiura granulosa*.

Apart from critical assessments of fossil brittle stars by Lütken (1869) and Boehm (1889), it then took more than sixty years before Cretaceous ophiuroids from Europe were once again described and discussed by various authors, e.g. Spencer (1905-1908), Valette (1915), Brünnich Nielsen (1926, 1941) and Berry (1938). The last-named described exclusively dissociated ossicles, various types of which he interpreted to be conspecific.

Rasmussen (1950) described ophiuroid remains from Cretaceous strata in Denmark, and included data on German localities, while A.H. Müller (1950) wrote up material from Rügen, but failed to acknowledge von Hagenow's (1840) work. Comparable to Berry's, A.H. Müller's material comprised dissociated ossicles only. The method applied by A.H. Müller in assigning these ossicles to various species was subsequently criticised by Rasmussen (1952) and Hess (1962a), and rightly so, as will appear from the present paper. A.H. Müller erected a number of species, and even genera, on different types of vertebrae, to which he assigned all other ossicle types on the basis of morphological comparisons and sampling statistics.

Rasmussen (1952) attempted a revision of A.H. Müller's taxa, which, however, was only partially successful. Later, he (Rasmussen, 1972) recorded from the Early Palaeocene of northern Europe a number of ophiuroid species already known from the Cretaceous.

Kutscher (1996a) noted that the Rügen ophiuroid faunas contained many new forms, some of which were illustrated by Jagt & Kutscher (1998).

In the present contribution all ophiuroid species known to date from the Lower Maastrichtian of Rügen and Møn are described and named. Quite a number of these are also known from the Campanian-Maastrichtian of the extended Maastrichtian type area (see the separate section above). A total of thirty-eight species (twenty-four

of them new) in nineteen genera (one of them new) are described. Literature references may be found listed at the end of the main article in this issue.

Material and methods

Material available consists almost exclusively of dissociated ossicles, mostly lateral arm plates, from the upper Lower Maastrichtian of Rügen (see Herrig et al., 1996) and the lower/upper Lower Maastrichtian of Møn (see Schulz, 1979). Samples from which types and specimens illustrated have been selected are in the Kutscher Collection (nos 1941 and 1942, respectively).

In addition to A.H. Müller's (1950) originals (see list in Herrig & Nestler, 1989, p. 52), comparative material was available from the Lower Maastrichtian of Kronsmoor (NW Germany; Kutscher Colln, no. 1946), from the upper Upper Maastrichtian of Berg en Terblijt (southern Limburg; Kutscher Colln, no. 1943), and from the uppermost Lower Campanian (see Kennedy & Christensen, 1997) of Ivö Klack and Ignaberga (southern Sweden; Kutscher Colln, nos 1944 and 1945, respectively).

The Rügen and Møn material was collected from sieve residues of matrix samples as well as from macerated ophiuroid skeletons and echinoderm coprolites, provided that these had not suffered strong dissolution or recrystallisation. Of almost fifty percent of the species described below arm fragments are before us, which allow observations to be made on vertebral structure and, in a few cases, also on ventral and dorsal arm plates and arm spines. In general, echinoderm coprolites comprise skeletal remains of various echinoderm groups and several species. However, occasionally it is possible to combine isolated remains to species, not on the basis of vertebrae as A.H. Müller (1950) did, but lateral arm plates. It should be noted that, despite the fact that in some instances good results have been obtained, this method cannot be generally applied.

The holotypes of all species, with the exception of those of *Mesophiomusium moenense* gen. et sp. nov. and *Asteronyx*? *spinulosa* sp. nov. (both MGUH), have been transferred to the collections of the 'Institut für geologische Wissenschaften' of Greifswald University (registration number FGWG 112). Paratype material of most of the new species is deposited in the type collections of the Natuurhistorisch Museum Maastricht (NHMM) and the Nationaal Natuurhistorisch Museum, Leiden (RGM).

Photomicrographs of ossicles were prepared by A. Fischer and M. Reich (Greifswald) and Saskia M. Kars (Vrije Universiteit, Amsterdam; JEOL JSM-6400 SEM).

Systematic palaeontology

Taxonomic procedure — As outlined in the introduction, Rasmussen (1952) and Hess (1962a) criticised A.H. Müller's (1950) method of erecting species and even genera on the basis of isolated vertebrae. Hess (1962a) studied in detail which types of dissociated ophiuroid ossicles were suited for systematic descriptions. He demonstrated that in most instances vertebrae were wholly unsuitable, as similar vertebrae occurred in various genera, or even families. To make matters worse, distal and proximal vertebrae in an ophiuroid arm show considerable differences in morphology. Hess (1962a) even went so far as to assume that vertebrae of A.H. Müller's (1950) new species and genera, *Schizospondylus jasmundiana*, *Transspondylus bubnoffi* and *Ophiaxina intercarinata*, belonged to a single species. This, however, is not correct, but does

clearly show the nature of the problem. For example, the vertebra which A.H. Müller (1950, pl. 1, fig. B1-5) illustrated under the name *Ophiura tener* may be considered a standard type of ophiuroid vertebra, which occurs in virtually identical form in at least fifteen different species in the material before us, and which also is amongst the commonest of vertebral types in Recent ophiuroids.

Hess (1962a) came to the conclusion that of all skeletal elements only the lateral arm plates showed a sufficient number of features allowing species to be clearly differentiated.

Thickness and curvature of these ossicles, as well as structure of outer and inner surfaces, outer surface ornament, and structure, position and number of spine bases, allow conclusions to be drawn on the structure of vertebrae and arms, spine canopy, and even on the mode of life. In addition, they may be used for a broad systematic assignment. For instance, all lateral arm plates lacking outer surface ornament and clearly produced spine bases might well belong to those ophiuroids whose skeletons are skin covered, e.g. the order Euryalida and suborder Ophiomyxina (order Ophiurida).

Considered first and foremost in the descriptions below are thus lateral arm plates; only in those cases where we are sufficiently confident are other skeletal elements assigned to species. In view of the fact that generic diagnoses of ophiuroids normally comprise many features which in general are not readily seen in dissociated material, we had to consider extant taxa. Only rarely has it been possible to assign species to sufficiently well characterised fossil genera. In doing so, we follow Rasmussen (1952, 1972), Hess (1960a, d, 1962a, b, 1963, 1964, 1965, 1966, 1970, 1975a-c), Kutscher (1987, 1996b) and Kutscher & Hary (1991), who convincingly demonstrated that the use of open nomenclature in assigning dissociated ophiuroid ossicles works. We prefer to place species recognised in those extant genera which are the types of the various families. In comparison to the use of artificial entities or placement in 'lump genera', this method yields a much more reliable picture of ophiuroid diversity.

Class Ophiuroidea Gray, 1840
Subclass Ophiuridea Gray, 1840
incertae ordinis & familiae
Subfamily Ophiobyrsinae Matsumoto, 1915

Remark — Smith et al. (1995, p. 230) noted that their most parsimonious cladograms placed the Ophiobyrsinae within the clade Ophiurida, rather than the clade Euryalida, but that the evidence for this was weak.

Genus *Ophiosmilax* Matsumoto, 1915

Type species — *Ophiosmilax mirabilis* Matsumoto, 1915, by monotypy.

Ophiosmilax? *alternatus* Kutscher & Jagt, sp. nov.
Pl. 31, figs. 8-12; Pl. 33, figs. 9-11.

1950 *Transspondylus bubnoffi* A.H. Müller, p. 20, pl. 2, fig. E1-5.
1952 *Transspondylus bubnoffi* Müller — Rasmussen, p. 53.

Type — Holotype is FGWG 112/5 (Pl. 31, fig. 8), paratypes are RGM 428 024 and NHMM JJ 5393. Holotype of *T. bubnoffi* is SGWG 103/5.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *alternus*, in allusion to the variable number of arm spines.

Diagnosis — A species of *Ophiosmilax*(?) with medium-sized, stout lateral arm plates with long, sickle-shaped ventral portion and an alternate number of spine tubercles (3 or 4).

Material — In addition to the types, the Kutscher Collection (no. 1941/25) and GM 1999.24 comprise several dozens of vertebrae and lateral arm plates.

Description — Many lateral arm plates (e.g. Pl. 31, fig. 10) lack the broken-off ventral portion, which makes these ossicles appear almost symmetrical: domed with smooth outer surface, slightly curved distal margin and convex proximal margin which ventrally and dorsally extends into 'obtuse angles'. Well-preserved specimens show this ventral 'angle' to constitute the basal portion of a narrow, sickle-shaped, proximally directed process, the length and width of which correspond to the ossicle height and almost half the ossicle length, respectively. There are either 3 or 4, equally spaced spine tubercles. Undoubtedly, in the arms plates with 3 and 4 spines alternated. The structure of the spine tubercles does not differ from the remainder of the outer plate surface. The tubercles are relatively large and bear two pores; they had a more ventral position. Conspicuous on the inner surface of lateral arm plates (Pl. 31, figs. 10-11) is a central, granule- to wall-like element, running almost perpendicularly from the ventral to the dorsal side. Consequently, the associated vertebra should have a near-vertical lateral aspect.

The length of the ventral process also requires relatively wide vertebrae. For the same reason, the ventral arm plates, which are as yet unknown, will not have been in contact. The dorsal cover probably consisted of widely spaced, diminutive ossicles. The tentacle pore notches are large, but are not included conspicuously in the lateral arm plate.

The construction of the lateral arm plates and structural elements on the inner surface require relatively wide vertebrae (Pl. 33, figs. 9-11), which in lateral view would have been vertically placed. This may have increased the ability of arm coiling. In addition to vertebrae placed by A.H. Müller (1950) in *Asteronyx*, also his vertebral type E (= *Transspondylus bubnoffi*) meets these requirements. In fact, the present lateral arm plates have been found associated with these compact vertebrae, which dorsally are slightly saddle shaped.

Discussion — Matsumoto (1915, p. 50) noted that his subfamily Ophiobyrsinae differed from other ophiomyxids, in having, amongst other features, streptospondyline vertebrae. For his genus *Ophiosmilax*, Matsumoto (1917, p. 384) noted that the vertebrae might be saddle shaped. This holds also for specimens before us. Additionally, the type species, *Ophiosmilax mirabilis* Matsumoto, 1915, also has an alternate number of arm spines (see Matsumoto, 1917, fig. 5). On account of these similarities, the present Late Cretaceous form is tentatively assigned to this genus. The vertebrae of the present species are not fully streptospondyline, but are intermediate between this and the zygospondyline type.

Occurrence — Currently known from the Lower Maastrichtian of Rügen and Møn; for records from the Maastrichtian type area see p. 7.

Order Euryalida Lamarck, 1816
Family Asteronychidae Verrill, 1899 (emend. Mortensen, 1933)
Genus *Asteronyx* Müller & Troschel, 1842

Type species — *Asteronyx loveni* Müller & Troschel, 1842, by monotypy.

Asteronyx? *simplex* A.H. Müller, 1950
Pl. 32, figs. 8-9.

*1950 *Asteronyx simplex* A.H. Müller, p. 22, pl. 2, fig. G1-5.
1952 *Asteronyx*? *simplex* (A.H. Müller) — Rasmussen, p. 52.

Type — Holotype is SGWG 103/7.

Material — Fairly numerous dissociated vertebrae in the Kutscher Colln (no. 1941/36), GM 1999.32, and RGM 428 034.

Description — The medium-sized vertebrae (Pl. 32, figs. 8-9) are of the streptospondyline type. Dorsally and laterally they show saddle-shaped depressions. Conspicuous is the strong dorso-proximal inclination of all vertical elements. For instance, seen from the dorsal side, the distal articulation surface is hardly visible, while the proximal coiling is in full view. Such an inclination enables optimal coiling of the arms, typical of Recent *Asteronyx*. Special elements, as seen in *T.*? *ornatus* and *Trichaster*? sp., are lacking.

Discussion — Construction and type of articulation of these vertebrae suggest an ophiuroid with skin cover and considerable ability to coil arms. Amongst lateral arm plate types known to date from Rügen, none could be combined with these vertebrae. Vertebrae of the other species for which a skin cover may be assumed (e.g. *Ophiosmilax*? *alternatus*, *Ophiomyxa*? *rhipidata*, *Ophiomyxa*? *curvata*, *Ophioscolex*? *cretaceus* and *Ophioscolex*? *clivulus*) differ clearly from those of the present species.

Ornament on the dorsal and lateral sides immediately sets vertebrae of *T.*? *ornatus* and *Trichaster*? sp. apart, while differences between the present species and *A.*? *spinulosa* have been outlined above.

A.H. Müller (1950) did not justify his assignment of these vertebrae to the genus *Asteronyx*. Rasmussen (1952) was of the opinion that *Asteronyx*? *simplex* was identical to what he had earlier illustrated (1950, pl. 18, fig. 12) under the name *Asteronyx*? sp., assuming differences to fall within the range of variation. A direct comparison of these vertebral types, however, has shown these differences to be clear cut. Rasmussen discussed the possible placement of these vertebrae in the Trichasteridae (inclusive of *Asteronyx*) or the Gorgonocephalidae, excluding the latter since no vertebrae had been found to suggest that there were arm divisions.

In view of the fact that there are no lateral arm plates from the upper Lower Maastrichtian that might be considered conspecific with the vertebrae, it may be assumed that these were covered only by atypical platelets embedded in skin and that a conspicuous spine canopy did not exist. On account of the resemblance to those of the extant *A. loveni*, the present vertebrae are assigned to *Asteronyx*, albeit with a query.

Occurrence — Apparently confined to the Lower Maastrichtian of Rügen.

Asteronyx? *spinulosa* Kutscher & Jagt, sp. nov.
Pl. 30, figs. 1-4.

Type — Holotype is MGUH 24553 (Pl. 30, fig. 1), paratype is RGM 428 030.

Type locality and horizon — Møn (Maglevandspynt), Denmark; white chalk facies of early Early Maastrichtian age (? *obtusa* Zone).

Derivation of name — Lat. *spina*, with reference to the thorn-like spine tubercles.

Diagnosis — Crescentic lateral arm plates with thorn-like spine tubercles (in pristine examples) or trace-like impressions of spine bases, outer surface without ornament; zygospondyline vertebrae.

Material — Some forty ossicles in the Kutscher Colln (no. 1942/32), and GM 1999.29.

Description — The small but very stout lateral arm plates (Pl. 30, figs. 1-2) are especially thick set in median and distal arm portions, which also holds for the distal margin. This explains why the peculiar spine tubercles, 6 to 8 in number, are located directly on the distal margin. Depending on preservation, the structure of the spine tubercles varies. In pristine examples, the 'tubercles' consist of two thorn-like elevations interconnected at their base, of which the inner one is shorter than the outer. Seen from the inside, two pores are noted in front of both elevations, an inner diminutive and point like, and an outer more elongate to comma-shaped one.

In more abraded ossicles the thorn-like elevations are barely recognisable, but pores or impressions become more conspicuous. In structure, these impressions resemble what Hess (1962b, p. 627) referred to as 'Paarhuferfährte'. Between the unequal pores is a weakly developed wall; a similar elevation is seen in the area next to the outer, elongated pore. Both represent the remains of former thorny 'tubercles'. The outer surface of the lateral arm plates is smooth. Near the distal margin, the inner surface shows a wide thickening, which causes this margin to appear even more thick set.

A saddle-shaped element proximally of the thickening served the articulation with the vertebrae, the dorsal 'saddle portion' being elongate, wedge shaped.

The material from Møn comprises, apart from vertebrae assigned to the euryalids *Trichaster*? *ornatus* (Rasmussen, 1950) and *Trichaster*? sp. (see below), additional streptospondyline vertebrae which might belong to the present species. The lack of granules on the lateral surface clearly differentiates them from those of *T.*? *ornatus*; instead they are more closely similar to those of *Asteronyx*? *simplex* (see below). However, dorsally the present specimens are less excavated in a saddle-shaped manner; moreover, distally between the dorsal articulatory pegs runs a clear crest to the dorsal margin, and the dorsal articulatory pegs are wider apart on the proximal and distal sides, so that the pegs rejuvenate ventrally. The vertebrae also suggest a lesser tendency for the arms to coil; distal and proximal surfaces are nearly parallel. Vertebrae of this type are unknown from Rügen.

The shape of the dorsal arm plates is unknown, but may be assumed to have been relatively wide. In the material before us there are rod-like elements with convex dorsal and concave ventral sides. On both sides, these ossicles show two flats each, positioned under an obtuse angle, which differ in size and demonstrate the former presence of adjoining ossicles. Such specimens (Pl. 30, figs. 3-4) presumably are the dorsal arm plates themselves or adjoining arm plates.

Discussion — Hess (1962b, p. 627, figs. 29-33) was the first to describe from the

Pliensbachian of Seewen (Switzerland) lateral arm plates in which spine bases resembled what he referred to as 'Paarhuferfährten' (= artiodactyl traces), under the name *Hemieuryale*? *lunaris* Hess. However, in Hess's material the impressions appear to be more lateral than dorsal in position. Hess assigned these ossicles to the Hemieuryalidae, based on the close resemblance of lateral arm plates combined with streptospondyline vertebrae, to e.g. the extant *Sigsbeia murrhina* Lyman, 1878. Later, Hess (1964) recorded *H.*? *lunaris* from the Pliensbachian of Aston Magna (Worcestershire, GB). However, those specimens possess 'ausgeprägte Stachelansatzstellen' (well-developed spine bases), which are either positioned close to the distal margin, or closer to the centre of the outer surface.

Kutscher (1996b, p. 12, pl. 3, figs. 6-8; pl. 4, figs. 12-14) recorded lateral arm plates from the Lias of Quedlinburg and Mistelgau (Germany), which in part corresponded to the type described by Hess (1962b) as *H.*? *lunaris*, and described the structure of the impressions and the 'wall' that separates them. It thus became clear that they closely resembled the above-mentioned, more strongly abraded lateral arm plates. A new look at the Lias material has shown that here also tubercles are developed, which, if not so strongly pronounced, correspond to the structure described above. The inner surface also shows the thickening. Despite good preservation of this material, the above-mentioned, thorn-like spine tubercles cannot be seen. The number of spine bases is higher (10 or 11). Vertebrae held to be conspecific lack the crest towards the dorsal margin and the unequally shaped articulatory pegs.

Assignment of the present lateral arm plates, with similar inner surfaces, to the genus *Asteronyx* is based on the fact that these were presumably arranged along the lower regions of the arms, with similar spine tubercles, as in extant *A. loveni* (see Müller & Troschel, 1842).

Occurrence — Known to date from the Lower Maastrichtian of Møn and Rügen. For records from the Maastrichtian type area see p. 8.

Family Euryalidae Gray, 1840
Genus *Trichaster* L. Agassiz, 1836

Type species — *Euryale palmiferum* Lamarck, 1816, by monotypy.

Trichaster? *ornatus* (Rasmussen, 1950)
Pl. 32, figs. 1-3, 7.

*1950 *Asteronyx*? *ornatus* Rasmussen, p. 121, pl. 18, fig. 11.
1950 *Asteronyx granulosus* A.H. Müller, p. 33, pl. 2, fig. H1-5.
1952 *Asteronyx*? *ornatus* Rasmussen — Rasmussen, p. 52.
1969 *Asteronyx*? *ornatus* Rasmussen — Maryańska & Popiel-Barczyk, p. 136, pl. 1, fig. 4.
1972 *Asteronyx*? *ornatus* Rasmussen — Rasmussen, p. 78.
1985 ?*Asteronyx ornatus* Rasmussen — Jagt, p. 98, fig. 1.

Type — Holotype is MGUH 7564 (Rasmussen, 1950, pl. 18, fig. 11). Holotype of *A. granulosus* is SGWG 103/8.

Material — Numerous vertebrae in the Kutscher Colln (no. 1941/18), GM 1999.18, and RGM 428 017.

Description — The strong, but small vertebrae (H/W c. 4/4 mm; Pl. 32, figs. 1-3, 7) have a dumbbell-shaped, streptospondyline articulation. In lateral aspect, most vertebrae are shorter ventrally than dorsally, suggesting a high capacity for arm coiling. Laterally, a furrow occurs between the proximal and distal muscle insertion areas, on whose margins are found well-developed granules and/or wall-like elements, which, however, dorsally also leave the furrow free. The orientation of the granules is mostly dorsal. On the upper side the vertebra is slightly depressed in a saddle-shaped manner.

Furrow, wall-shaped elements and granules are of variable size and outline, but are invariably well developed and cover almost exclusively the furrow margins. Other arm plates are unknown.

Discussion — Rasmussen (1950) recorded these vertebrae from the Maastrichtian of Rügen and Møn, and very explicitly noted the coarse ornament and the absence of additional arm plates. So far no vertebrae have been found which would suggest arm divisions to have occurred. This allows us to conclude that these forms had either undivided arms or arms with very few (? distal) divisions.

On this basis, Rasmussen (1950) referred these vertebrae to *Asteronyx*, noting the dumbbell-shaped articulation and lack of proof of arm division. Streptospondyline vertebrae are found in representatives of the order Euryalida, but occur also in certain Ophiurida (see Smith et al., 1995). In none of these taxa is a comparable granulation of the vertebrae known. Amongst the Euryalina, the genera *Astroceras* and *Trichaster* have even more strongly developed rudimentary dorsal, lateral and ventral arm plates; Hertz (1927) considered these to be representatives of the more primitive group. Obviously the granulation is not just vertebral ornament; in fact, elements constitute the attachment sites of small, but strong arm platelets, embedded in a thin skin. In later stages of development a reduction of these arm platelets took place and arm tips divided, which ultimately led to the Gorgonocephalidae. It may well be that the vertebrae described here should be assigned to a species which predates this development. So long as other pieces of evidence are wanting, the vertebrae of the present species are assigned to the genus *Trichaster* with a query.

Matsumoto (1917, fig. 8) illustrated detailed views of arm segments, which as does the specimen in his pl. 2, fig. 8, suggest a comparable vertebral structure. The closest resemblance of the present species is to vertebrae described below as *Trichaster*? sp., which dorsally and laterally have less pronounced furrows, a more subtle granulation (especially in dorsal areas) which also covers the flat bottom of the furrow. Height exceeds width in these vertebrae, which suggests that these either represent a distinct species or come from more distal positions along the arms. Rasmussen (1950, pl. 18, fig. 12) figured as *Asteronyx*? sp. a streptospondyline vertebra, lacking ornament, which therefore cannot be assigned either to this or to the following form.

Occurrence — Known to date from the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen, Kronsmoor and Møn. For records from the Maastrichtian type area see p. 8.

Trichaster? sp.
Pl. 32, figs. 4-6.

1998 sp. 18 = *Trichaster*? sp. — Jagt & Kutscher, fig. 2c.

Material — Numerous vertebrae (Kutscher Colln, no. 1941/34; GM 1999.30, and RGM 428 032).

Description — In general, height exceeds width in these relatively small vertebrae (Pl. 32, figs. 4-6), whose distal and proximal aspects appear elliptical. Dorsally they are only slightly saddle shaped. Lateral furrows are only faintly developed or not at all. In lateral aspect, the dorsal portion is clearly longer than the ventral, which suggests a high ability of arm coiling.

Particularly conspicuous is the ornament. Dorsally and extending onto the lateral sides are small granules, which also cover the bottom of the lateral furrow and do not become larger in ventral direction until half height of the vertebra, where they are wall like and become concentrated on the furrow margins, without disappearing entirely from the bottom of the furrow.

Discussion — Generally, the small granules suggest an arm cover of numerous, small platelets in dorsal and dorso-lateral position, while in latero-ventral position presumably rudimentary lateral arm plates occurred. This would substantiate the developmental trend noted in *Trichaster*? *ornatus* (see above).

However, since we cannot rule out the fact that the numerous small granules are simply a reflection of an earlier developmental stage, with the granules fusing later on, these vertebrae could just as well be considered as distal or juvenile ones. In view of this uncertainty, we refrain from introducing a new name for this material.

Occurrence — Currently known from the upper Lower Campanian of southern Sweden as well as the Lower Maastrichtian of Rügen, Kronsmoor and Møn. For records from the Maastrichtian type area see p. 8.

Order Ophiurida Müller & Troschel, 1840
Suborder Ophiomyxina Fell, 1962
Family Ophiomyxidae Ljungman, 1867
Genus *Ophiomyxa* Müller & Troschel, 1842

Type species — *Ophiura pentagona* Lamarck, 1816, by monotypy.

Ophiomyxa? *curvata* Kutscher & Jagt, sp. nov.
Pl. 31, figs. 4-7.

1950 *Schizospondylus jasmundiana* A.H. Müller, p. 18, pl. 1, fig. D1-5.
1950 unbenanntes Lateralschild A.H. Müller, p. 29, pl. 3, fig. Q1-2.
1952 *Ophiacantha* ? *danica* Rasmussen, p. 52 (partim, reference to A.H. Müller, 1950).
1952 *Schizospondylus jasmundiana* Müller — Rasmussen, p. 53.
1998 sp. 17 = *Ophiomyxa*? n. sp. 1 — Jagt & Kutscher, fig. 1g.

Type — Holotype is FGWG 112/1 (Pl. 31, fig. 4), paratypes are RGM 428 016 and NHMM JJ 5398. Holotype of *S. jasmundiana* is SGWG 103/4.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *curvus*, in allusion to the curvature of the lateral arm plates.

Diagnosis — An ophiomyxid(?) with sickle-shaped, robust lateral arm plates, whose outer surface is very narrow, but broadens dorsally and bears up to 10 spine tubercles. Vertebrae wide with atypical streptospondyline articulation, dorsal cover of single platelets.

Material — The Kutscher Colln (no. 1941/17) contains several dozens of isolated lateral arm plates and vertebrae, as well as a fragmentary arm. GM 1999.17 comprises material from Møn.

Description — The sickle-shaped, narrow, but robust lateral arm plates (Pl. 31, figs. 4-7), which presumably were connected to adjoining plates by skin only, have a narrow outer surface, which widens slightly dorsally. In an almost central position, this shows well-developed, ring-shaped spine tubercles, of which there are 9-10 in proximal plates, 7-9 in median arm positions and 6-8 on distal plates. Tubercle size gradually increases dorsally; concomitantly the distance between them grows.

The height of the dorsal portion of each tubercle exceeds that of the ventral, which points to erect, slightly ventrally directed spines. Proximally of the tubercle row the outer surface ends in a sharp ridge and continues into the proximal margin, which is only slightly indented above the ventral portion, but lacks other notable features.

There are no tentacle pore indentations; however, a tentacle pore does occur distally of a dorso-proximally curved narrow crest (serving articulation with the vertebra). This crest ends dorsally in a knob, which highly restricts the height of the associated vertebra.

The lateral arm plates did not abut ventrally nor dorsally. However, the space between the paired lateral arm plates was larger dorsally. There was no single compact dorsal arm plate; instead a number of small, unequal ossicles may be assumed to have been present.

An arm portion before us (Kutscher Colln, no. 1941/17) shows the relatively large, stable vertebrae with widely separated articulatory pegs distally, which tend towards the streptospondyline type of articulation. Without any doubt, these vertebrae correspond to A.H. Müller's (1950) vertebral type D (*Schizospondylus jasmundiana*).

Discussion — A.H. Müller (1950, pl. 3, fig. Q1-2) illustrated the lateral arm plates described above, but did not name them or attempt to combine them with vertebrae. Under the name *S. jasmundiana* he also described and figured (pl. 1, fig. D1-5) a highly typical vertebra, but failed to recognise their relationship. Rasmussen (1952) attempted to revise A.H. Müller's species and assigned lateral arm plate type Q to *Ophiacantha*? *danica*, the lateral arm plates of which he had already illustrated in 1950 (pl. 18, fig. 10). However, these ossicles are clearly different. Rasmussen went on to discuss *S. jasmundiana* and remarked that associated plates were unknown, hinting at conspecificity with *Transspondylus bubnoffi*. These vertebral types, however, are easily distinguished. Rasmussen stressed the close resemblance of these vertebrae to those of the extant genus *Ophiocamax*, which we do not doubt.

However, ossicle design, absence of ornament and spine tubercle structure of the present species suggest a skin-covered species, which cannot be assigned to the ophiacanthid *Ophiocamax*. The fact that the Asteronychidae have different arm plates and clearly streptospondyline vertebrae, leaves only the Ophiomyxidae to be considered. In favour of such an assignment is also the dorsal arm cover of various platelets.

Occurrence — Known to date from the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen, Møn and Kronsmoor.

Ophiomyxa? *jekerica* (Berry, 1938)
Pl. 31, figs. 13-14.

*1938 *Platyarthra jekerica* Berry, p. 68, pl. 15, figs. 1, 4, 5, 7, 9.
1950 "*Platyarthra*"-like — Rasmussen, p. 98, fig. 8d.

Type — For a discussion see p. 9.

Material — Several dozens of dissociated vertebrae, including Kutscher Colln, no. 1941/35; GM 1999.31; RGM 428 033, and NHMM JJ 5401.

Description — The zygospondyline, low, short and comparatively wide vertebrae (Pl. 31, figs. 13-14) are easily recognised in all samples.

Obvious in dorsal aspect are the proximal indentation, the projection of the distal, dorsal articulatory pegs and the strongly proximally excavated ventral muscle scars. The lateral sides are characterised by three sharp ridges, two of which delimit the lateral side proximally and distally, while the third, central ridge served the attachment of muscles, which interconnected lateral and dorsal arm plates and vertebrae.

The ridges extend from the ventral side across the lateral side to far onto the dorsal side. In proximal aspect, the dorsal muscle scars are deeply excavated. The articulatory pegs are only poorly developed. Clearer, however, is a central, ventrally directed 'granule'. In distal view, the articulatory pegs constitute a dominant element, next to the four distal muscle scars.

Between the ventral articulatory pegs is an excavation for the reception of the granule-like element of the proximal side.

Measurements (in mm) of a few vertebrae before us are as follows (L - length, W - width, H - height):

arm position	L	W	H	H/W
proximal	1.1	3.9	3.0	0.76
middle	1.0	3.2	1.8	0.56
distal	1.0	2.0	1.0	0.50
juvenile	0.8	1.0	0.3	0.38

Lateral, dorsal and ventral arm plates are unknown.

Discussion — The proper assignment of these vertebrae is fraught with difficulties. This ophiuroid must have been a species which probably had:
- wide and flat arms with arm segments of near-equal length;
- limited mobility of arms, horizontal movement only;
- vertebrae covered by (presumably two) rows of platelets, embedded in thin skin, or covered by skin;
- abutting ventral arm plates.

Skin-covered brittle stars are found in the Ophiomyxidae, Asteronychidae and Asteroschematidae. We may exclude the Gorgonocephalidae, which have bifurcating

arms, since such vertebrae have so far not been recognised in our material. Moreover, like asteronychids and asteroschematids, gorgonocephalids have streptospondyline vertebrae.

It appears that even within the Ophiomyxidae there is no genus to which the present vertebrae could be referred with certainty. Awaiting the discovery of more complete material, these specimens are here assigned to the Ophiomyxidae, and the genus *Ophiomyxa*, with a query.

Berry (1938), who described these vertebrae under the name *Platyarthra jekerica*, was of the opinion that lateral arm plates of an ophiolepidid, dorsal and ventral arm plates and oral shields were conspecific. However, it is impossible to combine these ossicles in this way. Surprisingly, A.H. Müller (1950) did not record such vertebrae from Rügen, although they are not rare there. The dorsal side in Rasmussen's (1950) illustration shows almost all important features (with the exception of the median ridge). Although he recorded this vertebral type as coming from the 'Senonian' (= Maastrichtian) of Aalborg (Jylland, Denmark), he did not discuss it any further. He did, however, point out that Berry's method of combining dissociated ossicle types to species should be discarded.

From the St Cassian Beds (Triassic) of Milieres (near Cortina d'Ampezzo, Italy) comparable vertebrae are available to us (Kutscher Colln); however, these lack the median ridge. A developmental trend from compact lateral arm plates to rows of platelets may be indicated here.

Occurrence — Currently known from the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 9.

Ophiomyxa? *rhipidata* Kutscher & Jagt, sp. nov.
Pl. 30, figs. 12-17; Pl. 31, figs. 1-3; Pl. 33, figs. 6-7, 12.

1950 *Ophioderma arkonensis* A.H. Müller, p. 18, pl. 1, fig. C1-5 (non pl. 3, fig. P1-2).
1952 *Ophiura*? *hagenowi* Rasmussen — Rasmussen, p. 49 (vertebral type C of A.H. Müller, 1950).
1998 sp. 12 = *Ophiomyxa*? n. sp. 2 — Jagt & Kutscher, fig. 2d.

Type — Holotype is FGWG 112/1 (Pl. 30, fig. 12); paratypes are RGM 428 011 and NHMM JJ 5402a. Holotype of *Ophioderma arkonensis* is SGWG 103/3.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Gr. *rhipis*, *-idos*, meaning fan, in allusion to the fan-shaped spines.

Diagnosis — An ophiomyxid(?) with medium-sized, robust lateral arm plates, with three spine bases, the lower two of which bore horizontally placed spines and the upper one, the largest, which bore a vertically directed spine. Towards the top, spines are extended in a feather- or fan-like fashion.

Material — Several dozens of dissociated lateral arm plates, vertebrae and spines (Kutscher Colln, no. 1941/12, and GM 1999.12).

Description — The robust, medium-sized lateral arm plates (L/H proximally 1.2/2.0, distally 1.0/0.1) (Pl. 30, figs. 12-15, 17) are characterised by strongly developed tentacle pore indentations, which extended into the tips of the arms. The outer

surface of the semicircular plates shows no ornament of any kind, with the exception of three large, curious spine tubercles, which rise from the outer surface without transition. They do not correspond to typical spine bases, but rather resemble elongate-oval granules with a comma-shaped excavation.

Near the tentacle pore indentations, both ventral tubercles are relatively close together and suggest the associated spines to have been slightly erect in the direction of the tip of the arm. The position of the upper tubercle equals about half arm height. The conspicuously larger, dorsal tubercle is separated from the other two by a smooth area (in distal arm plates spacing between all three tubercles becomes more equal). Tubercle construction suggest they bore perpendicularly erect spines.

The inner surface of these plates (Pl. 30, fig. 14) is characterised by a knob-like element, in almost central position, which served the articulation with the vertebra. This was probably the strengthened end of a wall which ran dorso-distally in the direction of the tentacle pore.

The ventral portion of the plate extends to the middle of the arm, i.e. the lateral arm plates abutted ventrally and thus separated the ventral arm plates. The proximal margin of the laterals is concave. The lateral portion of these plates extends to almost two-thirds of the arm height.

Ventral arm plates may be assumed to have been broadly V-shaped, at least proximally, with concave distal margin and straight proximal margin and deep tentacle pore indentations.

Dorsal arm plates are unknown and, in fact, should not be expected, since this species would at best have had rudimentary platelets only.

The vertebrae (Pl. 30, fig. 16; Pl. 33, figs. 6-7, 12) are relatively long, in comparison to their height, and are of the zygospondyline type, in which the articulatory pegs are very extended distally and strongly excavated proximally. Laterally, the angle between the ventral and dorsal muscle insertion areas has a small protuberance proximally. In distal vertebrae a median furrow receives the knob-like element seen in the lateral arm plates.

The spines (Pl. 31, figs. 1-3) of this ophiuroid differ from those of all other fossil species known to date. At the margin, the irregular, strong spine base bears a groove for the reception of the tubercle margin and a 'nose' for articulation with the spine tubercle itself. Above the base, the spine widens in a fan-like fashion, with unequal ribs bifurcating further, resulting in extreme cases in widths and lengths four to five times the length of the base of the spine. This holds especially for those spines which articulated on the dorsal tubercles. In those of the other tubercles, four or five times the length of the base would equal only twice the width. The fan-like portions end in thorns and in part bear small lateral thorns as well.

Fan-like spines have been recorded for the Recent ophiurid *Ophiambix devaneyi* Paterson, 1985 (p. 142, figs. 54, 57a-d); in that species however, 3 or 4 tubercles occur, the lower one of which bears a hook-shaped spine and only the others are fan shaped. Moreover, the base of these spines is less clearly demarcated.

Discussion — Like all of his other illustrations, A.H. Müller's figure of a vertebra ('Wirbeltyp C') under the name *Ophioderma arkonensis* is very poor. A re-examination of the original specimens has now shown that what A.H. Müller had before him actually were vertebrae of the present species. In view of the fact that in our material the lateral arm plates are in a number of cases associated with the vertebrae, an assign-

ment of the latter to the genus *Ophioderma* can be ruled out.

Rasmussen (1952) revised A.H. Müller's species, and considered the vertebrae of *Ophioderma arkonensis* to belong to *Ophiura*? *hagenowi*. As demonstrated here, this interpretation is erroneous. Rasmussen failed to note that e.g. the inner surface of lateral arm plates of *O.*? *hagenowi* shows a long, wide ridge which cannot be combined with the lateral aspect of the present vertebral type. Whereas his fig. 1 does indeed represent a vertebra of *O.*? *hagenowi*, his fig. 2 corresponds to a distal vertebra of *Ophiomyxa*? *rhipidata*. Rasmussen (1952), however, was right in reassigning the lateral arm plates which A.H. Müller (1950) had referred to *Ophioderma arkonensis*.

The structure of the outer surface of the lateral arm plates and of the spine tubercles correspond to those of skin-covered ophiuroids, which are generally placed in the orders Euryalida and Ophiurida (suborder Ophiomyxina). Only those species that have traditionally been assigned to the family Ophiomyxidae have zygospondyline vertebrae. Our assignment of the present material to *Ophiomyxa* is based on a comparison with extant species of this genus, which show the close resemblance in arm construction, spine inclination and vertebral structure.

Ophiosmilax? *alternatus* (see above) differs in having 3 or 4 equally spaced spine tubercles, less conspicuous tentacle pore indentations and convex proximal margins.

Occurrence — Currently known from the Lower Maastrichtian of Rügen, Møn and Kronsmoor. For records from the Maastrichtian type area see p. 9.

Genus *Ophioscolex* Müller & Troschel, 1842

Type species — *Ophioscolex glacialis* Müller & Troschel, 1842, by monotypy.

Ophioscolex? *clivulus* Kutscher & Jagt, sp. nov.
Pl. 30, figs. 9-11.

Type — Holotype is FGWG 112/4 (Pl. 30, fig. 9), paratypes are RGM 428 027 and NHMM JJ 5402b.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *clivus* meaning hill, in reference to the structure of the dorsal spine tubercle.

Diagnosis — Robust lateral arm plates with granulate outer surface, two articulation bosses at the proximal margin and 2-3 spine tubercles, of which the dorsal one is very large and placed on an elevation.

Material — Several dozens of dissociated lateral arm plates and an arm fragment in the Kutscher Colln (no. 1941/28), and GM 1999.27.

Description — The lateral arm plates (Pl. 30, figs. 9-11), which are thick set especially in distal arm portions, have a weakly constricted to flat outer surface, which, in well-preserved specimens, shows a coarse granulation. At the proximal margin there are two strong articulation bosses, which correspond to two facets on the distal margin of the inner surface (Pl. 30, fig. 11).

Highly typical is the tuberculation. Proximal and median lateral arm plates have 3 (rarely 2) strong tubercles which are placed on 'mounds'. Two almost equal-sized tubercles are close together or (alternately ?) slightly more widely apart. Especially

conspicuous is the dorsal tubercle which lies on a mound, the diameter of which corresponds to half the length of the lateral arm plate. Whereas the lower spines must have been erect, but vertically arranged, the upper, presumably very large and differently shaped spine, was directed dorsally. Distal lateral arm plates also have 3 tubercles which, however, are of almost equal size. All plates (including the distal ones) have very large tentacle pore indentations. For articulation with the vertebra there is a broad 'wall'. In distal plates, hardly any room for the vertebrae is left.

A distal arm segment (Kutscher Colln, no. 1941/28) preserves large, triangular dorsal arm plates with slightly convex distal margin, and large ventral arm plates. Neither dorsal nor ventral plates abut, but they probably did in proximal arm portions. Vertebrae of this species resemble those of *Ophiomyxa*? *rhipidata*.

Discussion — There is a certain resemblance to *Ophiomyxa*? *rhipidata*; however, the present species differs in having a granulate outer surface, a different inner surface and articulation bosses at the proximal margin. Assignment to the Ophiomyxidae is based in particular on the structure of the lateral arm plates, spine tubercle construction (which would suggest skin cover), large tentacle pore indentations as well as vertebral structure. Rather than referring the material to *Ophiomyxa*, in which generally a skinny cleft separates adjoining lateral arm plates, it is placed in *Ophioscolex* since such a cleft can be ruled out for the present species. Furthermore, length of proximal plates exceeds height in *Ophioscolex* while those of *Ophiomyxa* are taller than long. Contradicting an assignment to the Ophiomyxidae is only the granulate outer surface of the lateral arm plates. The present species closely resembles the Early Oxfordian *Ophiopholis*? *trispinosa* Hess, 1965 (pp. 1067, 1075, figs. 16, 36-40), a fact already stressed by Kutscher (1996b, p. 19, pl. 4, fig. 6). Especially the holotype of this species from the Lower Oxfordian of Longecombe (France) (see Hess 1965, fig. 36) is reminiscent of the plates described here, especially with regard to constriction and granulation of the outer surface. Hess's figs. 39 and 40 are not conspecific with the plates in his figs. 36-38, but are probably best assigned to a species of the genus *Sinosura*.

Differences between the Jurassic and Cretaceous species become clear from Hess's description, who mentioned 'deutliche, ring- bis hufeisenförmige Stachelwarzen' (obvious ring- to horseshoe-shaped spine tubercles) as well as a totally different structure of vertebral articulation. Moreover, he noted that distal plates lacked tentacle pore indentations.

Kutscher (1996b) recorded *Ophiopholis*? *trispinosa* from the Toarcian-Aalenian of Quedlinburg and pointed out that the Hess's (1960c) and Kutscher's (1996b) descriptions and illustrations corresponded better with the Late Cretaceous form, but here too differences in tubercle structure and tentacle pores apply. In addition, part of the Jurassic material has 4 spine tubercles, none of which differs so extremely as does the dorsal one in *Ophioscolex*? *clivulus*.

Occurrence — At present, this species is known from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 10.

Ophioscolex? *cretaceus* Kutscher & Jagt, sp. nov.
Pl. 30, figs. 5-8.

Type — Holotype is FGWG 112/3 (Pl. 30, fig. 5), paratypes are RGM 428 015 and NHMM JJ 5397.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — In reference to the occurrence in the Late Cretaceous.

Diagnosis — Small species having curved lateral arm plates with smooth outer surface and generally 5 well-developed spine tubercles and a dorsally extended tongue-like process.

Material — The Kutscher Colln (no. 1941/16) contains numerous dissociated lateral arm plates and vertebrae. GM 1999.16 comprises material from Møn.

Description — The relatively small lateral arm plates (Pl. 30, figs. 5-8) have a smooth outer surface, which bears 4-5 (3 in distal plates) spine tubercles lying behind a well-developed distal tongue, and a weak articulation ridge on the ventral portion. Around this ridge the outer surface is weakly concave. The tubercles are well developed, but not conspicuous. The lower three are relatively close together, while the 4th or 4th and 5th, generally slightly better developed tubercles are more widely spaced. Whereas the lower tubercles bore spines which were directed towards the arm tip, the upper tubercles had dorsally directed spines. All lateral arm plates have tentacle pores (in distal plates) or tentacle pore indentations (in proximal plates).

Visible on the inner surface are a crest which runs dorso-proximally from the tentacle pore, and, distally of the tentacle pore, an articulation element which corresponds to the ridge on the proximal margin of the adjoining plate. The extension of the distal tongue is clearly dorsal. The smooth, dorsal margin of the lateral arm plates as well as the limited curvature around the vertebrae allow us to conclude that the dorsal and ventral arm plates abutted over almost the entire arm length. The vertebrae, which have not yet been found directly attached to the lateral arm plates, correspond to the standard type with zygospondyline articulation.

Discussion — This species can only be confused with distal lateral arm plates of *Ophiotitanos serrata* (see below); the latter, however, are more robust, tubercles are more numerous and arranged in 'pockets'. Moreover, the outer surface is gently striate and the distal tongue does not extend dorsally. It should be noted that the Rügen Cretaceous has yielded plates which differ from *Ophioscolex*? *cretaceus* in:
- having the outer surface finely granulate;
- having slightly larger and more pronounced spine tubercles;
- displaying in some specimens a second, almost centrally placed articulation ridge on the proximal margin.

Assignment to the genus *Ophioscolex* is based on similarities in lateral arm plate design. However, should these smooth plates turn out to be no more than less well-preserved analogues of the granulate plates (until now smooth plates predominate in our samples), an assignment to the Ophiomyxidae can no longer be upheld.

Occurrence — Known to date from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 10.

Suborder Ophiurina Müller & Troschel, 1840
Family Ophiacanthidae Perrier, 1891 s. lat.
Subfamily Ophiacanthinae sensu Paterson, 1985
Genus *Ophiacantha* Müller & Troschel, 1842

Type species — *Ophiacantha spinulosa* Müller & Troschel, 1842 = *Asterias bidentata* Retzius, 1805, by subsequent designation of H.L. Clark (1915).

Ophiacantha? *danica* Rasmussen, 1952
Pl. 24, figs. 7-10; Pl. 25, figs. 1-2.

1950 *Ophiacantha*? sp. — Rasmussen, p. 120, pl. 18, fig. 10.
*1952 *Ophiacantha*? *danica* Rasmussen, p. 52, fig. 6.
1972 *Ophiacantha*? *danica* Rasmussen, 1951 — Rasmussen, p. 60, pl. 6, fig. 2.
1998 sp. 3 = *Ophiacantha*? *danica* — Jagt & Kutscher, fig. 1b.
1998 *Ophiacantha*? *danica* — Kutscher, p. 41, fig. 4.

Type — Holotype is MGUH 7563 (Rasmussen, 1950, pl. 18, fig. 10; 1952, fig. 6).

Material — Numerous dissociated vertebrae and lateral arm plates (Kutscher Colln, no. 1941/3; GM 1999.3; NHMM JJ 5396, and RGM 428 002).

Description — The medium-sized lateral arm plates (Pl. 24, figs. 7-10; Pl. 25, figs. 1-2) are curved and considerably constricted centrally. The proximal margin has, depending on plate size, several articulation elements, of which only 1-3 are more pronounced and correspond to those of the inner surface at the distal margin. On the outer surface, a wall rises proximally of the distal margin, ending abruptly towards the free surface and bearing large, horseshoe-shaped spine tubercles, which indicate an erect spine canopy. Proximal lateral arm plates have 10-12 tubercles, median plates 7-9 and distal ones 4-6. The 'wall' broadens towards the dorsal side, so that the uppermost spine tubercle is also the largest. The constricted free surface shows a notched, finely granulate ornament.

On the inner surface, proximal and median lateral arm plates show well-developed tentacle pore indentations. For articulation with the vertebra there is an element which ventrally curves towards the tentacle pore indentation, to flex back and pass into a flat, broad 'wall'.

The paired lateral arm plates may have abutted dorsally and ventrally, thus separating the dorsal arm plates. Ventrally, the lateral arm plates show an attachment site which indicates that the ventral arm plates rested on the lateral arm plates and thus must have abutted, at least in proximal arm segments.

The vertebrae are of the standard type.

Discussion — Rasmussen (1952) provided a brief description of this species, the holotype of which (from the Maastrichtian of Aalborg, Jylland, Denmark) he had already (1950) illustrated as *Ophiacantha*? sp., noting 7 to 8 spine tubercles. Its size indicates the illustrated ossicle to be a median plate, which would explain the low number of tubercles. Other localities recorded by Rasmussen (1950) are Møn, and Fakse and Stevns Klint (Lower Palaeocene). In 1952, Rasmussen added the 'Senonian' of Rügen. This, however, is based on an error, since he listed in his synonymy also the lateral arm plate figured by A.H. Müller (1950, pl. 3, fig. Q1-2). This ossicle does not belong to the present species, but to *Ophiomyxa*? *curvata* (see above). Differences are obvious and refer to the absence of ornament, the very short proximal portion, the robustness of all plates, the absence of a constriction and the moderately developed tentacle pore indentations.

Ophiacantha? *danica* is closer to *O.*? *striata* (see below), whose lateral arm plates are, however, slightly smaller and more fragile. The transition from the 'wall' bearing tubercles to the constricted surface is not abrupt, but gradual from a 'collar'. The outer surface is more or less obliquely striated and the proximal margin does not bear

any obvious articulation bosses. Correspondingly, the inner surface does not reveal any articulatory elements, except for a weak ridge which runs parallel to the distal margin.

Ophiacantha? *punctata* (see below) is markedly smaller, has fewer tubercles and a conspicuous granulation on the outer surface and lacks articulation bosses on the proximal margin.

In comparison to Recent ophiacanthids, *O.*? *danica* resembles some species of the genus *Ophiomitra* Lyman, 1869, on account of the granulate outer surface, the presence of articulation bosses on the proximal margin and the abrupt transition of the tubercle row into the outer surface. For reasons outlined in the introduction above, we prefer to leave the present species in the genus *Ophiacantha*.

Occurrence — This species is now known to occur in the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 10.

Ophiacantha? *punctata* Kutscher & Jagt, sp. nov.
Pl. 25, figs. 3-5.

Type — Holotype is FGWG 112/14 (Pl. 25, fig. 3), paratypes are RGM 428 014 and NHMM JJ 5386.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *punctatus*, with reference to the ornament of numerous granules.

Diagnosis — A small ophiacanthid(?), whose lateral arm plates have up to 10 small, almost circular tubercles and an outer surface with small granules, in part arranged in rows.

Material — The Kutscher Colln (no. 1941/15) contains a fair number of dissociated arm ossicles; GM 1999.15 comprises additional material from Møn.

Description — The small lateral arm plates (Pl. 25, figs. 3-5), of which distal ones resemble those of the ophiolepidid genus *Ophiomusium*, have, proximally of a more or less obtuse distal tongue, 8-10 (proximal), 7-9 (median) or 4-6 (distal) small, near-circular tubercles. The equal-sized tubercles indicate the spines to have been erect. In the dorsal portion, the tubercles are more widely spaced than in the ventral portion. Proximally follows the faintly constricted outer surface, which starts with a weakly developed 'collar' and extends to the proximal margin, which does not show any articulation elements. The outer surface has fine and closely arranged granules, which may aligned; the portion of the plate closest to the tubercles may show a weak oblique corrugation. The proximal portion is conspicuously lower than the distal (Pl. 25, fig. 4). In proximal, median and, in part also distal plates, tentacle pore notches are present.

Ventral and dorsal arm plates probably abutted only in proximal arm segments, but were separated by lateral arm plates elsewhere. The small vertebrae are of the standard type.

Discussion — Amongst Cretaceous ophiuroids known to date, only the distal lateral arm plates of *Ophiacantha*? *danica* are to be considered in comparison to the pres-

ent species. All other species of *Ophiacantha*? and *S. jasmundensis* have wrinkled outer surfaces. *Ophiacantha*? *danica* differs in having spine tubercles which increase in size dorsally, a stronger constriction of the outer surface, articulation bosses on the proximal margin and a larger space for the vertebrae.

Ophiomusium-like distal lateral arm plates are also known in the ophiodermatid *Ophioderma*? *radiatum* (see below), but these lack the constriction, while the wide proximal margin does bear articulation bosses, the tubercles are not circular and the granulate ornament is radiate.

It should be noted that, when comparing the present species with Recent species of *Ophiacantha*, its generic assignment raises considerable doubts. Assignment is based solely on the presence of numerous spine bases (which bore erect spines) and of partial oblique corrugation.

Occurrence — Apparently confined to the Lower Maastrichtian of Rügen and Møn.

Ophiacantha? *rugosa* Kutscher & Jagt, sp. nov.
Pl. 25, fig. 7.

Type — Holotype is FGWG 112/13 (Pl. 25, fig. 7), paratype is RGM 428 025.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *rugosus*, in allusion to the wrinkled ornament.

Material — The Kutscher Colln (no. 1941/26) and GM 1999.25 contain a fair number of dissociated arm ossicles, including spines.

Diagnosis — Ophiacanthid(?) with small lateral arm plates, whose outer surface is only weakly constricted and shows a marked corrugation. Conspicuous features include a pronounced distal tongue and deep tentacle pore indentation.

Description — The rather small lateral arm plates (Pl. 25, fig. 7) have a conspicuous tongue forming the distal margin. Proximally occur 4 (in distal plates) to 7 (in proximal plates) equal-sized, distinct, horseshoe-shaped tubercles, which suggest the spines to have been erect. Joining this is the weakly constricted outer surface, which is covered by a distinct corrugation extending onto the ventral portion. The proximal margin does not show any significant articulation elements.

All plates, inclusive of distal ones, have a large and deep tentacle pore indentation. On the inner surface, the articulation with the vertebra consists of three separate elements, viz. a ventral, a ventro-lateral and a dorsal boss, which together describe the course noted for the other species of this genus described above.

The spines are slender and equal the length of an arm segment. Dorsal and ventral arm plates probably abutted in proximal arm segments, the latter plates having deep, lateral tentacle pore notches. They have a central excavation and a ridge each on both sides. Distal plates lack this excavation, and the lateral ridges coalesce into a single, central one. The vertebrae are of the standard type.

Discussion — The present species resembles *Ophiacantha*? *striata* (see below), which, however, has more fragile and more deeply constricted lateral arm plates, more numerous and unequal tubercles and a weaker corrugation, and lacks the distal tongue. There is a certain resemblance to *Sinosura jasmundensis* sp. nov. (see below) as

well, but the lateral arm plates of that species are more fragile, the corrugation is finer and the small spine tubercles are arranged in 'pockets'.

Ophiuroids with striated lateral and dorsal arm plates are found in the Recent ophiodermatid genera *Ophiuroconis* Matsumoto, 1915 and *Ophiurodon* Matsumoto, 1915. In the absence of discs of the Cretaceous forms, it cannot be decided whether these lateral arm plates should be assigned to ophiacanthids or to ophiodermatids. However, since species of *Ophiacantha* invariably have erect spines, our material is assigned to that genus, at least for the time being.

Occurrence — Lower Maastrichtian of Rügen and Møn; for records from the Maastrichtian type area see p. 11.

Ophiacantha? *striata* Kutscher & Jagt, sp. nov.
Pl. 25, figs. 8-10.

Type — Holotype is FGWG 112/12 (Pl. 25, fig. 8), paratype is RGM 428 022.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *striatus*, with reference to the striated outer surface.

Material — A number of dissociated lateral arm plates and vertebrae (Kutscher Colln, no. 1941/23; and GM 1999.22).

Diagnosis — Small species, with constricted lateral arm plates, proximal plates bearing up to 10 spine tubercles. The outer surface is striated or folded to close to the proximal margin.

Description — The small and fragile (especially proximal portions) lateral arm plates (Pl. 25, figs. 8-10) have 7-10 (proximal plates), 5-6 (median plates) or 3-4 (distal plates) well-developed, horseshoe-shaped tubercles, closely spaced and increasing in size dorsally.

The constricted outer surface starts proximally of the tubercles with a 'collar'. The constricted part shows a fine, but pronounced oblique striation or corrugation. The proximal margin does not show any articulation elements, and is rather thin. Correspondingly, there are no articulation elements on the distal margin on the inner surface. In well-preserved specimens, however, there is a crest running almost parallel to the distal margin. Up to this crest, the adjoining plate 'encroached' on the present ossicle. Serving the articulation with the vertebra is a similar structure as that seen in *Ophiacantha*? *danica*. However, in the present species the curved element is interrupted in the region of the tentacle pore indentation (which is almost invariably present), thus resulting in two elevations.

The vertebrae are of the standard type and resemble those illustrated by A.H. Müller (1950) under the name *Ophiura tener*.

Discussion — The present species differs from the previous in the striated outer surface of the generally smaller and more fragile lateral arm plates, and in the absence of articulation bosses at the proximal margin. *Ophiacantha*? *punctata* sp. nov. (see above) is more robust, has small tubercles and a granular outer surface which only occasionally develops into oblique corrugations. *Ophiacantha*? *rugosa* sp. nov. (see above) has fewer spine tubercles and the wrinkled outer surface is less clearly constricted.

Jurassic species assigned to *Ophiacantha*? (see e.g. Hess, 1962b, 1963, 1965, 1966, 1975c; Kutscher, 1987, 1996b; Kutscher & Hary, 1991) are generally more robust, have fewer tubercles and strong articulation elements at the proximal margin.

A wrinkled outer surface is also found in species of the genus *Sinosura*, previously held to be restricted to the Jurassic (see below). In these, however, the generally smaller tubercles mostly are arranged in 'pockets', with spines appressed.

Occurrence — Known to date from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 11.

Ophiacantha? sp.
Pl. 25, fig. 6.

Description — Eight lateral arm plates from the upper Lower Maastrichtian of Rügen (Kutscher Colln, no. 1941/19, and RGM 428 018) differ markedly from the previous species. These diminutive plates have 6-9 elongate, closely spaced, conspicuously oblique tubercles. The central tubercles are the largest, while the ventral and dorsal ones decrease in size. The obliquity is the result of the fact that the tubercles are placed perpendicular to the distal margin and the retracted 'collar', which recede distinctly dorsally-proximally.

The constricted and dorsally narrowed outer surface, on account of the retraction of the 'collar', is granulate. The granules tend to coalesce. The proximal margin is smooth and has on the transition between ventral and lateral portions a knob-like element. On the inner surface there are no additional elements, except for the vertebral articulation ridge and tentacle pore notch.

Discussion — The present species shows the closest resemblance to *Ophiacantha*? *striata* (see above), but differs in having a granulate outer surface, oblique tubercles and a retracted distal margin.

A similarly distinctly reflected distal margin is seen in *Sinosura wolburgi* (Hess, 1960c) of Liassic age (Hess, 1960c, p. 411, figs. 29-33; 1964, p. 779). In that species, however, the tubercles are very small and arranged in 'pockets', and the outer surface is wrinkled. The same holds true for *Sinosura* sp. (see below). Similarly obliquely placed tubercles are found in *Ophiothrix*? *cristata* (see below), but plates of this species lack a retracted distal margin, are stouter and have no 'collar'.

Although these specimens are clearly different, the limited number of available plates makes us refrain from introducing a new species at this time.

Occurrence — Apparently confined to the Lower Maastrichtian of Rügen.

Genus *Sinosura* Hess, 1964

Type species — *Acroura brodiei* Wright, 1866, by original designation (Hess, 1964, p. 779).

Remarks — This genus is particularly well known from Jurassic strata, from which a number of species have been described (Hess, 1960c, 1962b, 1964, 1975c; Kutscher, 1987, 1996b, 1997; Kutscher & Hary, 1991; Kutscher & Röper, 1995 and Delsate & Jagt, 1996). Smith et al. (1995, table 2) tentatively placed the genus *Sinosura* in the Ophioleucidae Matsumoto, 1915. The present records constitute the first documentation of this genus in strata of Late Cretaceous age.

Sinosura jasmundensis Kutscher & Jagt, sp. nov.
Pl. 27, fig. 14.

Type — Holotype is FGWG 112/15 (Pl. 27, fig. 14), paratype is RGM 428 028.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — In reference to the occurrence in the Jasmund peninsula (Rügen).

Diagnosis — Laterally strongly curved lateral arm plates with wrinkled outer surface and small spine bases arranged in 'pockets'.

Material — A number of dissociated lateral arm plates in the Kutscher Colln (no. 1941/29).

Description — In proximal or distal view, the small fragile lateral arm plates (Pl. 27, fig. 14) form a semicircle. Small tubercles, 6-8 in number, lie in pockets of the markedly corrugated outer surface. The width of these wrinkles decreases towards the proximal margin. The margin does not show any articulation elements. Tubercles are of equal size and suggest spines to have been appressed, relatively thin and short. Distally of the tubercles is a well developed tongue. Tentacle pore indentations are present in all available plates. Being filled with chalk matrix, the inner surface cannot be described. However, with the exception of the vertebral articulation no other elements are to be expected.

Discussion — Hess (1964) erected the genus *Sinosura* for dissociated lateral arm plates with corrugated surface. This genus is now well known, as a result of subsequent finds of completely preserved individuals. Most species [e.g. *S. wolburgi* (Hess, 1960c) and *S. brodiei*] have lateral arm plates with angular ventral/lateral sides and a constricted outer surface. In *S. wolburgi*, the tubercle row recedes dorsally, while in *S. brodiei* the tubercles are larger, and at the proximal margin distinct articulation bosses are developed. *Sinosura schneideri* Kutscher, 1987 (p. 59, pl. 1, fig. 6; pl. 4, figs. 4-5; pl. 6, fig. 1) also has larger tubercles.

From species of *Ophiacantha*? with corrugated outer surfaces described above, *S. jasmundensis* differs in having small tubercles, arranged in pockets and in having a rounded outer surface.

Occurrence — Definitely known from the upper Lower Maastrichtian of Rügen, and questionably, from the Lower Maastrichtian of Møn.

Sinosura aff. *schneideri* Kutscher, 1987
Pl. 27, figs. 11-13.

aff. 1987 *Sinosura schneideri* Kutscher, p. 59, pl. 1, fig. 6; pl. 4, figs. 4-5; pl. 6, fig. 1.

Description — Six lateral arm plates (Pl. 27, figs. 11-13; Kutscher Colln, no. 1941/33, and RGM 428 031) are currently available; at first glance they resemble those of *Ophioscolex*? *cretaceus*, but the following differences may be noted:

- the outer surface is finely pitted, with diminutive pits arranged in longitudinal rows;
- the tubercles (3-4 in number) are small, but distinct and horseshoe shaped. The two

lower ones are close together and directed along the arm axis. The (two) upper one(s) are more widely spaced and directed dorsally;
- the proximal margin shows a distinct articulation boss almost at mid-height.

In addition, all plates have a well-developed tongue and distinct tentacle pore notches as well as a narrow, curved crest for vertebral articulation on the inner surface.

Discussion — Kutscher (1987) erected *S. schneideri* for lateral arm plates from erratic boulders of Callovian age; these are closely comparable to the present Cretaceous material. Kutscher (1996b) recorded this species also from the Toarcian/Aalenian boundary; it corresponds to the plate illustrated by Hess (1965, fig. 39, as *Ophiopholis*? *trispinosa*). The Rügen specimens differ from those of *S. schneideri* only in having a well-developed articulation boss, and are thus here assigned to that species with a query.

Occurrence — Exclusively known from the upper Lower Maastrichtian of Rügen.

Sinosura sp.

Description — A few lateral arm plates (Kutscher Colln, no. 1941/30) from the upper Lower Maastrichtian of Rügen differ from *S. jasmundensis* in having even smaller tubercles, which decrease in size towards the dorsal side and also recede. The outer surface is not rounded, but, particularly so dorsally, slightly constricted. The proximal margin bears two weak articulation bosses. Tubercles, 5-6 in number, are arranged in pockets proximal of a fragile tongue. Tentacle pore notches are present. The outer surface is corrugated. On the inner surface, the vertebral articulation consists of two short crests, one proximal of the tentacle pore notch and one, comma-shaped, at the base of the lateral side.

Discussion — As pointed out above, this species differs from *S. jasmundensis* in having angular plates and even smaller tubercles. *Sinosura brodiei* has larger tubercles and a different structure of the inner surface. In *S. wolburgi*, the distal margin considerably recedes dorsally. In view of the limited number of available lateral arm plates we refrain from erecting a new species.

Occurrence — Apparently confined to the upper Lower Maastrichtian of Rügen.

Infraorder Hemieuryalina Verrill, 1899
Family Hemieuryalidae Verrill, 1899
Genus *Hemieuryale* von Martens, 1867

Type species — *Hemieuryale pustulata* von Martens, 1867, by monotypy.

Hemieuryale? *parva* Kutscher & Jagt, sp. nov.
Pl. 28, figs. 12-14.

Type — Holotype is FGWG 112/21 (Pl. 28, fig. 12), paratype is RGM 428 023.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *parvus* meaning small, in reference to small size of the

lateral arm plates.

Diagnosis — Diminutive lateral arm plates with granulate outer surface; distal margin curves into the dorsal margin. Generally with two small, but distinct spine tubercles; slight constriction near the proximal margin. Dorsal and ventral arm plates wide, separated by lateral arm plates over the entire arm length.

Material — Numerous dissociated arm plates and a distal arm fragment in the Kutscher Colln (no. 1941/24), and GM 1999.23.

Description — Most of the small lateral arm plates with granulate outer surface (Pl. 28, figs. 12-14) look as if they were distally pointed, on account of the fact that the short distal margin grades into the dorsal margin hyperbolically. Only proximal lateral arm plates have a broader distal margin. Therefore, the transition appears rather angular. The breadth of the distal margin also affects the number of small, but distinct tubercles. For instance, in proximal plates the distal margin shows 2-3, in median and distal ones 1-2 tubercles, which indicate the associated spines to have been more or less appressed. Tentacle pore notches are present in all plates. With the exception of the tentacle notch, the space for the slender vertebrae and the wide vertebral articulation surfaces, the inner surface does not show other elements.

Dorsal arm plates are triangular with faintly convex distal margins. They are very wide; in distal arm segments corresponding to arm width, and do not abut, being separated by lateral arm plates. Their outer surface is granulate. The ventral arm plates are also separated by the lateral arm plates, and almost equal arm width and are granulate. Laterally they have notches for tentacle pores.

Neither on a distal arm fragment (Kutscher Colln, no. 1941/24), nor on slender vertebrae associated with lateral arm plates of the type described here in an echinoderm coprolite, have we been able to determine beyond doubt whether the articulation is of the streptospondyline or zygospondyline type.

Discussion — Assignment to the Hemieuryalidae is based solely on the close resemblance of lateral arm plates to those of some extant species of the genus *Sigsbeia*, in which, however, the 'dorsal arm plates' are highly fragmented. Matsumoto (1917) subdivided the Hemieuryalidae into the Hemieuryalinae and Ophiochondrinae, the former having only three spines and 'dorsal arm plates' consisting of several platelets, and the latter having single dorsal arm plates, and 5-8 spines.

Hemieuryale? *parva* combines features of both subfamilies, in having entire dorsal arm plates but only 2-3 arm spines. We cannot consider vertebral structure (see above); hemieuryalids have streptospondyline vertebrae, which, however, also show certain zygospondyline features.

It has become apparent in several instances, that even in those cases where fossil ophiuroids preserve the disc, assignment to extant families or genera presents serious problems. In the present case, it appears probable that in the course of development, the compact dorsal arm plates of the Hemieuryalidae developed into separate platelets.

The present species cannot be confused with other Late Cretaceous ophiuroids; for differences from *Mesophiomusium moenense* see p. 92.

Occurrence — Known to date only from the Lower Maastrichtian of Rügen and Møn.

Infraorder Chilophiurina Matsumoto, 1915
Family Ophiuridae Lyman, 1865
Genus *Stegophiura* Matsumoto, 1915

Type species — *Ophiura nodosa* Lütken, 1855, by original designation.

Stegophiura? *hagenowi* (Rasmussen, 1950)
Pl. 24, figs. 1-6; Pl. 33, fig. 1.

1840 *Ophiura (Aspidura) granulosa* von Hagenow, p. 660, pl. 9, fig. 6 (non Roemer, 1840).
1889 *Ophiura (Aspidura) granulosa*, Hagenow — Boehm, p. 261[30].
*1950 *Ophiura*? *hagenowi* Rasmussen, p. 114, pl. 17, figs. 1-5.
1950 *Ophioderma rugensis* A.H. Müller, p. 16, pl. 1, fig. A1-5.
1950 *Asteronyx granulosus* A.H. Müller, p. 28, pl. 3, fig. N1-2.
1950 *Ophiura tener* A.H. Müller, p. 28, pl. 3, fig. 01-2.
1952 *Ophiura*? *hagenowi* W. Rasmussen — Rasmussen, p. 51, fig. 1.
1969 *Ophiura*? *hagenowi* Rasmussen, 1950 — Maryańska & Popiel-Barczyk, p. 133, pl. 1, figs. 1-2.
1972 *Ophiura*? *hagenowi* Rasmussen, 1950 — Rasmussen, p. 61.
1998 sp. 2 = *Stegophiura*? *hagenowi* — Jagt & Kutscher, fig. 1f.
1998 *Stegophiura*? *hagenowi* — Kutscher, p. 41, fig. 2.
1999 *Stegophiura*? *hagenowi* (Rasmussen, 1950) — Helm et al., pl. 1, figs. 1-2; pl. 3, fig. 6.

Type — Holotype is the specimen illustrated by Rasmussen (1950, pl. 17, fig. 1) in the collections of the Sedgwick Museum (Cambridge). Holotype of *Ophioderma rugensis* is SGWG 103/1, of *Ophiura tener* SGWG 103/2.

Material — Numerous dissociated arm ossicles, radial shields and other disc plates as well as a few arm fragments (Kutscher Colln, no. 1941/2; GM 1999.2, and RGM 428 001).

Description — Proximally, the height of the large and robust lateral arm plates (Pl. 24, figs. 1-6) exceeds their length; their outer surface bears an ornament, which, when well preserved, is seen to consist of granules amongst which occurs a finer granulation which ventrally grades into lines, while next to the relatively small tentacle pore notch, again granules occur. In distal plates, length exceeds height; they show the same ornament, but fainter.

The relatively wide proximal margin is not ornamented, but instead has a circular as well as an elongate-oval articulation element along the margin. The outer surface surrounding these elements is sunken, which is especially prominent in a distal direction in front of the circular element. The outer surface ornament is so typical that even distal lateral arm plates are immediately recognised by this indentation.

Spine tubercles of the present species also differ considerably from those of all other co-occurring ophiuroids. Depending on its arm position 2 to 5 well-developed tubercles are developed, which ventrally start directly above the tentacle pore notch and recede slightly from the distal margin. Articulating on these tubercles were primary spines, which were either appressed or slightly erect. The length of these obtusely clavate spines equalled only half the length of the lateral arm plate.

Above the primary tubercles are 4 (in distal plates) to 13 small secondary spine tubercles close to the margin, so that this appears denticulate. It is highly probable that only scale-like, appressed 'spines' articulated on these tubercles. Dorsally, the

distal margin recedes considerably.

On the inner surface are seen, in addition to the relatively broad crest for vertebral articulation, near the distal margin a circular as well as an elongate-oval element, which correspond to those seen on the outer surface. The tentacle pore notches are small, but probably extended along the entire arm length. In proximal and median arm segments the lateral arm plates abut ventrally only.

Dorsal arm plates abut and are triangular with rounded distal margin, bearing an ornament of granules and proximally on the outer surface a crest and two furrows, which are matched by two crests and a furrow distally on the inner surface.

Ventral arm plates are also near triangular with indentations for tube feet.

Vertebrae (Pl. 33, fig. 1) are slender and, in proximal arm segments, tall and in lateral view aspect show a broad and tall muscle scar. The articulation is of the zygospondyline type. The articulatory pegs are relatively small, the muscle pits deep. The distal vertebrae are *Ophiomusium*-like, but have large muscle scars.

Discussion — Rasmussen (1950) provided a lengthy discussion and good illustrations of this species of which he had arm portions available from the type locality (Trimingham, Norfolk, England); his pl. 17, fig. 3b, d-e shows a typical vertebra. A.H. Müller (1950) provided a poorly executed illustration of such a vertebra ('Wirbeltyp A', *Ophioderma rugensis*). Under the names *Asteronyx granulosus* and *Ophiura tener* he also described lateral arm plates which only differ as far as preservation is concerned (absence or presence of granulation) and belong to the present species.

Rasmussen (1952) recognised this error and referred these lateral arm plates to his *Ophiura*? *hagenowi*. However, he failed to note that A.H. Müller's 'Wirbeltyp A' also belonged there, and considered it '(invalid)'. Indeed, the preservation of A.H. Müller's holotype of *Ophioderma rugensis* has proved to be fair; Rasmussen's (1952) failure to note the conspecificity may be explained by him not having seen the original material. He had to rely on A.H. Müller's poor illustration.

Rasmussen's (1952, p. fig. 1) shows a vertebra in lateral aspect, which he considered to be 'possibly of *Ophiomusium*'. This specimen, however, undoubtedly belongs to the present species and is identical to the one Rasmussen himself had illustrated earlier (Rasmussen, 1950, pl. 17, fig. 3). Rasmussen noted (1950, p. 116) that assignment to the genus *Ophiura* was tentative at best, and that there was '... no sure evidence for affinity with the genus *Ophiura*.'

Matsumoto (1915, p. 78) erected the genus *Stegophiura* for extant ophiurids with numerous, often dimorphic spines arranged in two rows. Representatives of this genus have tall, relatively short, tapering arms. Such features may be assumed for the present species as well; awaiting the discovery of specimens preserving the disc, the present taxon is referred to this genus, mainly on account of similarities in spine arrangement to certain extant *Stegophiura* species.

In size of the lateral arm plates, *Stegophiura*? *hagenowi* differs markedly from all other co-occurring Maastrichtian ophiuroids, with the exception of *Ophiomusium granulosum* and *Ophioderma*? *substriatum* (see below), which have comparably sized lateral arm plates. For differences with these species reference is made to descriptions below.

Occurrence — Common in the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 19.

Infraorder Gnathophiurina Matsumoto, 1915
Superfamily Gnathophiuridea Matsumoto, 1915
Family Amphiuridae Ljungman, 1867
Genus *Amphiura* Forbes, 1843b

Type species — *Amphiura chiajii* Forbes, 1843b, by subsequent designation of Verrill (1899).

Amphiura? *plana* Kutscher & Jagt, sp. nov.
Pl. 29, figs. 1-5; Pl. 33, fig. 3.

1998 sp. 14 = *Amphiura*? n. sp. 1 — Jagt & Kutscher, fig. 2f.

Type — Holotype is FGWG 112/17 (Pl. 29, fig. 1), paratypes are RGM 428 013 and NHMM JJ 5395.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *planus*, in allusion to the near-flat outer surface.

Diagnosis — Amphiurid with small lateral arm plates, which have an almost flat, unornamented outer surface, up to seven spine tubercles and a dorsally receded distal margin.

Material — Numerous dissociated lateral arm plates and vertebrae (Kutscher Colln, no. 1941/14 and GM 1999.14).

Description — The small lateral arm plates (Pl. 29, figs. 1-5) are characterised by their smooth, slightly convex outer surface and a distal margin which recedes considerably dorsally. The rather small, horseshoe-shaped tubercles are of near-equal size, with the exception of the dorsal one, which is smaller. Proximal plates have 5-7, median ones 4-5 and distal ones 3-4 spine tubercles, which indicate the spines to have been erect. Tubercle interspace almost equals the width of a tubercle. The tubercles are placed directly on the distal margin, the ventral one directly besides the tentacle pore indentation, which is obvious in all plates.

Higher magnification reveals a fine granulation of the outer surface which, however, may be nothing more than a rather coarse stereom structure since the same structure is seen at the proximal margin and in the tubercles.

A faint flattening characterises the ventral side; the inner surface shows only a curved element for vertebral articulation and a crest on the margin of the tentacle pore notch, between which there is a narrow furrow.

The vertebrae resemble those of the ophiocomids described below, but do not have such pronounced excavations in the dorso-ventral region for the reception of the adjoining vertebra (Pl. 33, fig. 3).

The dorsal arm plates abut and are broad with concave to straight proximal and convex distal margins. The ventral arm plates abut as well, are broad and have lateral notches for tube feet and a convex distal margin.

The radial shields are relatively long with convex outer and near-straight inner margins. Of note is that the articulation with the genital does not occur on the inner surface but near the distal margin. The sides are bevelled, so that other platelets par-

tially covered the radial shield and made it appear smaller.

Whether or not the very long spines bore thorns or hooks is unknown; however, they do show a fine longitudinal striation.

Discussion — The present species is differentiated from all co-occurring ophiuroids by having smooth, faintly convex lateral arm plates, in which the distal margin recedes. Since distal plates have a faintly constricted outer surface, there is a certain resemblance to distal plates of *Ophiocoma*? *rasmusseni*. However, the smooth outer surface, widely separated spine tubercles and receding distal margin easily separate these species. *Ophiocoma*? *ishidai* (see below) is constricted, has narrower interspaces between tubercles and a granulate outer surface.

Assignment to the extant genus *Amphiura* is provisional at best and is based mainly on the structure of radial shields, vertebrae and presence of large tentacle pore indentations, as well as on lateral arm plate structure. There is a certain resemblance to e.g. *A. chiajii*.

Occurrence — Known to date from the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 21.

Family Ophiothricidae Ljungman, 1866
Genus *Ophiothrix* Müller & Troschel, 1840

Type species — *Ophiura rosula* Fleming, 1828 = *Asterias pentaphylla* Pennant, 1777, by subsequent designation of Lyman (1865).

Ophiothrix? *bongaertsi* Kutscher & Jagt, sp. nov.
Pl. 29, figs. 9-10.

Type — Holotype is FGWG 112/19 (Pl. 29, fig. 10), paratype is RGM 428 036.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Named after Hans L. Bongaerts (Posterholt, NL) in recognition of his much appreciated assistance over the years.

Diagnosis — Ophiothricid with small lateral arm plates, whose closely spaced spine tubercles are placed horizontally on the distal plate margin.

Material — Numerous dissociated arm ossicles in the Kutscher Colln (no. 1941/38).

Description — The small, constricted and granulate lateral arm plates (Pl. 29, figs. 9-10) have 10-12 (proximal), 8-9 (median) and 5-6 (distal) spine tubercles, of near-equal size and closely spaced. The dorsal and ventral limb of each tubercle are almost parallel and perpendicular to the generally almost straight distal margin.

Especially ventrally, the outer surface is slightly constricted. All plates have tentacle pore indentations. The proximal margin is slightly raised and has, apart from a weakly developed boss, no additional articulation elements. The inner surface shows a large tentacle pore indentation and a weakly developed ridge, which curves proximally.

The vertebrae would have been of the standard type; dorsal and ventral arm

plates would have abutted roughly to mid-arm length, with dorsal plates granulate.

Discussion — *Ophiothrix*? *bongaertsi* resembles *O.*? *cristata* (see below), but differs in having more numerous, slightly smaller tubercles, which are perpendicular to the partially straight distal margin. Lateral arm plates of the similarly ornamented *Ophiactis*? *sulcata* (see below) are larger, more strongly curved, bear fewer tubercles and have an obliquely striated proximal margin, while the up to 5 tubercles are more widely spaced.

Occurrence — Known to date from the upper Lower Maastrichtian of Rügen. For records from the Maastrichtian type area see p. 25.

Ophiothrix? *cristata* Kutscher & Jagt, sp. nov.
Pl. 29, figs. 6-8.

1998 sp. 10 = *Ophiothrix*? n. sp. 1 — Jagt & Kutscher, fig. 2a.

Type — Holotype is FGWG 112/18 (Pl. 29, fig. 8), paratypes are RGM 428 009 and NHMM JJ 5391.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *cristatus* meaning 'provided with a comb', in allusion to the placement and structure of the spine tubercles.

Diagnosis — Small ophiothricid with diminutive, markedly granulate lateral arm plates and obliquely placed tubercles whose inclination changes dorsally.

Material — Numerous dissociated arm ossicles (Kutscher Colln, no. 1941/10; and GM 1999.10).

Description — The small lateral arm plates (Pl. 29, figs. 6-8) have a slightly constricted and comparatively markedly granulate outer surface. Especially in median and proximal plates the proximal margin is distinctly concave and bears a very weakly developed articulation boss.

Highly typical are the comparatively large tubercles. Proximal plates have 5-7, median ones 4-5 and distal ones 3-4 spine tubercles, directly placed on the distal margin. They are not horseshoe shaped, but consist of paired, comma-shaped crests. As the distance between the paired crests is nearly equal to the next pair, this creates a certain comb-like appearance. It should be noted, however, that the inclination of all tubercles is different. Whereas the ventral tubercle is horizontal, the dorsal one must have borne an almost perpendicularly directed spine. The inclination of the other tubercles varies between the extremes. Especially in median and distal plates the dorsal portion may lack tubercles. The inner surface shows only the tentacle pore notch and a knob-shaped element in its direct vicinity.

The dorsal arm plates are broad, proximally rounded-triangular and distally with convex margin, and have the same granulation as the lateral arm plates. The granulated ventral arm plates are pentangular, with concave sides and convex distal margin. Both dorsal and ventral arm plates abut up to mid-arm length.

Radial shields are relatively broad, with a concave distal margin and a superficially similar granulation as in the lateral and dorsal arm plates. The zygospondyline vertebrae are of the standard type. Spines are simple and slightly longer than an arm segment.

Discussion — Near-equally sized plates of *Ophiactis*? *sulcata* (see below) have a comparably granulate outer surface, but are more strongly constricted. Being similar in structure, the tubercles of that species are not inclined, and the proximal margin bears a distinct oblique striation.

Ophiocoma? *rasmusseni* has a similar granulation as well, but differs in having slightly larger and more robust lateral arm plates with horseshoe-shaped tubercles, which are not inclined. Its granulation tends to be arranged in rows. The proximal margin is obliquely striated and flattened ventrally and dorsally.

Assignment to *Ophiothrix* is based mainly on the similarity of the radial shields. Ophiothricid-like are also the structure of dorsal, ventral and lateral arm shields and vertebrae. However, comparable structures are also known for various other genera and even families.

Occurrence — Currently known from the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 25.

Genus *Ophiothela* Verrill, 1867

Type species — *Ophiothrix (Ophiothela) mirabilis* Verrill, 1867, by original designation.

Ophiothela? *semirotunda* Kutscher & Jagt, sp. nov.
Pl. 29, figs. 11-13.

Type — Holotype is FGWG 112/22 (Pl. 29, fig. 11), paratype is RGM 428 021.

Type locality and horizon — Rügen (NE Germany); white chalk of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *rotundus*, round, and *semi*, half, in allusion to the semicircular outer view.

Diagnosis — Ophiothricid with diminutive, robust lateral arm plates with strongly convex distal margin and 5-7 small tubercles. Outer surface slightly constricted and weakly granulate. Inner surface simple, *Ophiomusium*-like.

Material — Fairly many dissociated arm ossicles in the Kutscher Colln (no. 1941/22), and GM 1999.21.

Description — The small, thick-set lateral arm plates (Pl. 29, figs. 11-13) have a rather weakly constricted outer surface (only in proximal plates is this character better developed), which, when well preserved, is finely granulate. Highly typical is the strongly convex distal margin which bears 5-7 small, but distinct tubercles; associated spines must have been slightly erect. The equally spaced tubercles are of identical size and recede slightly from the distal margin dorsally.

The proximal margin is smooth and shows an indentation ventrally. The inner surface is simple. All plates have a tentacle pore indentation. The space for the vertebra is narrow, and *Ophiomusium*-like. Dorsal and ventral arm plates would have been small and separated by lateral arm plates. The zygospondyline vertebrae are slender, with a broad lateral articulation scar for the lateral arm plate.

Discussion — Assignment to the genus *Ophiothela* is based on the similarity

between our lateral arm plates and those of *O. danae* Verrill, 1869 and is highly provisional. There is a certain resemblance to small-sized ophiacanthids as well. Although the present specimens are easily distinguished from those of other coeval Cretaceous species, there are similarities with certain fossil taxa assigned to the Hemieuryalidae. For instance, Hess (1964, p. 762, figs. 4-10) referred similar lateral arm plates from the Pliensbachian of Aston Magna (GB) to *Hemieuryale*? *lunaris* Hess, 1962b. This species was originally erected to contain dissociated plates from the Lias of Seewen (Solothurn), which showed similarities in the lateral arm plate/vertebrae relationship to hemieuryalids.

The material from Aston Magna differs especially in the absence of granulation on the outer surface, in having different tubercle structure and, since arm fragments are also available, in having streptospondyline vertebrae. Hess (1962b) also discussed possible relationships of this form with the Ophiacanthidae.

Kutscher & Hary (1991, p. 54, fig. 2/4a-c) recorded, as *Hemieuryale*? n. sp., lateral arm plates from the Lower Lias of Luxemburg; these specimens are granulate and have 4-6 tubercles. Features distinguishing them from *Ophiothela*? *semirotunda* include: tubercle position is different (not receding distally in the former), absence of a slight constriction, a structured proximal margin, and more room for the vertebra on the inner surface. In the tubercles, the raised limbs ('walls') in the present species are parallel to the arm axis, whereas in *H.*? n. sp. they are perpendicular to the axis.

Occurrence — Known from the Lower Maastrichtian of Rügen and Møn.

Family Ophiactidae Matsumoto, 1915
Genus *Ophiactis* Lütken, 1856

Type species — *Ophiactis krebsii* Lütken, 1856 = *Ophiolepis savignyi* Müller & Troschel, 1842, by subsequent designation of H.L. Clark (1915).

Ophiactis? *sulcata* Kutscher & Jagt, sp. nov.
Pl. 23, figs. 8-12.

Type — Holotype is FGWG 112/20 (Pl. 23, fig. 9), paratype is RGM 428 008.

Type locality and horizon — Rügen (NE Germany); white chalk of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *sulcus*, in reference to the distinctly striated proximal margin.

Diagnosis — Ophiactid(?) with lateral arm plates that appear bent, with a granulate outer surface, up to 5 spine tubercles and a fine, but distinct striation on the proximal margin.

Material — Fairly many dissociated arm ossicles (Kutscher Colln, no. 1941/9; and GM 1999.9).

Description — On account of their strongly concave outer surface, the rather elongate lateral arm plates (Pl. 23, figs. 8-12) appear bent. This is especially prominent in median and distal plates. The outer surface bears distinct granules, which dorsally and ventrally tend to coalesce and form crest-like rows. Highly typical is the proximal margin, which, instead of bosses or knobs, shows a closely spaced, fine, but distinct

striation, which proceeds from the granulate outer surface. Near the distal margin are 4-5 (proximal), 3-4 (median) or 2-3 (distal) tubercles; the associated spines must have been erect. With the exception of the dorsal one, tubercles are of near-equal size, not horseshoe-shaped, but demarcated by two perpendicular short limbs. The dorsal tubercle in proximal and median plates is the largest; it recedes slightly proximally.

Tentacle pore indentations are developed even in distal arm segments. The inner surface shows the vertebral articulation to be indistinct. Vertebral structure is of the standard type. The dorsal and ventral arm plates were large and abutted to mid-arm length; at least the dorsal plates must have been granulate.

Discussion — These plates are easily distinguished from other species on account of 'appearing bent' and of the striated proximal margin. A comparably granulate outer surface is seen in lateral arm plates of *Ophiothrix*? *cristata* (see above), but these are smaller, less constricted and the more numerous tubercles are inclined. A similar ornament is also known in lateral arm plates of *Ophiocoma*? *rasmusseni*, but these have horseshoe-shaped tubercles, while the plates are taller, more robust and less constricted and the striation on the proximal margin is only weakly developed.

Assignment of the present material to the Ophiactidae is based on:
- the outer surface ornament, as well as the number of spine tubercles and the constriction, are reminiscent of those in the genera *Ophiactis* and *Ophiopholis*;
- the striation of the proximal margin suggests this to have been a species in which the interspaces between the lateral arm plates were skin covered; this condition is found in the Ophiactidae.

From the Lower Oxfordian of Chapois and Longecombe (CH), Hess (1965, p. 1075, figs. 36-40) described lateral arm plates as *Ophiopholis*? *trispinosa*. At least median and distal plates bear a certain resemblance to the present species, but differ in having three horseshoe-shaped tubercles, distinct articulation bosses on the proximal margin and a different type of vertebral articulation.

Occurrence — At present known from the Lower Maastrichtian of Rügen and Møn. For possible records from the Maastrichtian type area see p. 26.

Superfamily Ophiocomidea Ljungman, 1867
Family Ophiocomidae Ljungman, 1867
Genus *Ophiocoma* L. Agassiz, 1835

Type species — *Ophiura echinata* Lamarck, 1816, by subsequent designation of H.L. Clark (1915).

Ophiocoma? *ishidai* Kutscher & Jagt, sp. nov.
Pl. 28, figs. 10-11.

Type — Holotype is FGWG 112/16 (Pl. 28, fig. 10), paratype is RGM 428 035.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Named after Yoshiaki Ishida (Chitosegaoka Senior High School, Tokyo), who provided extant ophiuroids for comparative purposes.

Diagnosis — Ophiocomid(?) with small, curved lateral arm plates which are sickle shaped in proximal arm segments. The receding distal margin bears up to 8 small, but distinct spine tubercles.

Material — A number of dissociated arm ossicles (Kutscher Colln, no. 1941/37; and GM 1999.33).

Description — The small lateral arm plates, which in proximal arm segments are short and sickle shaped (Pl. 28, figs. 10-11), have 6-8 (proximal), 4-5 (median) or 3-4 (distal) small, but distinct, horseshoe-shaped tubercles, of near-equal size, which extend to the dorsal margin. Between the tubercles is a narrow free space, which corresponds to half the width of the tubercle. The entire, slightly constricted outer surface is finely punctate, with impressions tending to coalesce into perpendicular striation. At mid-height of the proximal margin there is a larger, unornamented surface which corresponds to a similar one on the inner surface, lying between a rim which extends from the tentacle pore notch and running to the distal margin.

All plates have tentacle pore indentations. The ventral portion of the plates shows a relatively long extension, which prevents the ventral arm plates from abutting. Of note, in comparison with other related species, is the straight to slightly concave (in distal plates) dorsal margin and the dorsal tubercle which is partially visible from the inner surface as well.

The vertebrae are of the standard type. Ventral and dorsal arm plates are weakly ornamented and will only have abutted in proximal arm segments.

The spines are simple, their length equalling that of an arm segment.

Discussion — The present species most closely resembles *Ophiocoma*? *rasmusseni*, whose lateral arm plates are stouter, the distal margin does not recede, the less numerous (up to 6) tubercles are larger, and leave a free dorsal area. Moreover, the outer surface is granulate, the dorsal margin is in all plates convex and on the proximal margin an articulatory boss is developed, while the ventral portion is only weakly extended.

In being sickle shaped, slightly worn plates also resemble those of *Amphiura*? *plana* (see below), which, however, are near smooth, have a slightly convex outer surface, more widely spaced tubercles, and a more strongly receded distal margin also in distal plates.

Occurrence — Apparently confined to the upper Lower Maastrichtian of Rügen.

Ophiocoma? *rasmusseni* Hess, 1960b
Pl. 28, figs. 5-6, 8-9.

1952 *Ophiacantha*? sp. — Rasmussen, p. 51, fig. 8.
*1960b *Ophiocoma*? *rasmusseni* Hess, p. 753, figs. 5-7.
1998 sp. 13 = *Ophiocoma*? *rasmusseni* — Jagt & Kutscher, fig. 2e.

Type — Holotype is BMNH E.13734B (Lewis, 1993).

Material — Fairly many dissociated arm ossicles (Kutscher Colln, no. 1941/13; GM 1999.13; and RGM 428 012).

Description — The small, but solid lateral arm plates (Pl. 28, figs. 5-6, 8-9) are slightly constricted, their outer surface being covered in indistinct, closely spaced

granules, which, especially dorsally, may be arranged in rows or coalesce. At the distal margin in proximal plates 6 horseshoe-shaped tubercles are present (in median ones 4 and in distal ones 3), indicating the associated spines to have been erect. The tubercles are of near-equal size, the upper being slightly offset from the others and more dorsally directed; the associated spine was probably directed upwards. Ventrally and dorsally, the proximal margin is flattened (attachment sites for ventral and dorsal arm plates). Articulation bosses are only weakly developed and more clearly seen laterally of the middle of the margin. In well-preserved specimens, the proximal margin is very finely obliquely striated. All plates have tentacle pore notches.

On the inner surface the vertebral articulation shows a structure comparable to that seen in *O.*? *senonensis*. Consequently, the vertebrae of these two species are similar as well. However, the excavation for reception of the adjoining vertebra appears less deep. The length of the spines at most equals 1.5 times the length of an arm segment; they are simple in structure.

Dorsal and ventral arm plates correspond to those of the previous species, the latter being very thick set, studded with granules which may be arranged in longitudinal rows. The distal margin is convex, the proximal margin obtuse. A raised portion marks the spot up to which the ventral arm plate slipped underneath the distal portion of the abutting plate.

Discussion — The present species differs from *O.*? *senonensis* in having a granulate outer surface, more numerous spine tubercles and shorter spines. *Amphiura*? *plana* has similar lateral arm plates which, however, differ in lacking a constriction and granulation, and in having a more strongly dorsal recession of the distal margin and more widely spaced, slightly smaller tubercles. Differences between the present species and *Ophiocoma*? *ishidai* are outlined above.

Rasmussen (1952, fig. 8) illustrated a lateral arm plate from the Upper Palaeocene of New Jersey under the name *Ophiacantha*? sp., but did not provide a description. Size, shape and number of tubercles of this ossicle appear to correspond to those of *Ophiocoma*? *rasmusseni*.

Our material appears to resemble Hess's (1960b) species to such an extent that it is referred to that taxon. Hess (1960b, p. 756) compared Rasmussen's (1952) *Ophiacantha*? sp. with this species and assumed it to be conspecific; however, he was wrong in stating Rasmussen's specimen to be from Rügen.

Assignment to *Ophiocoma* is favoured on the same grounds as for *Ophiocoma*? *senonensis*.

Occurrence — This appears to be a long-ranging species with records from the Cenomanian of the United Kingdom, the upper Lower Campanian of southern Sweden, and the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 27.

Ophiocoma? *senonensis* (Valette, 1915)
Pl. 27, figs. 15-16; Pl. 28, figs. 1-4, 7; Pl. 33, figs. 4-5, 8.

*1915 *Amphiura senonensis* Valette, p. 140, fig. 6.
1950 *Amphiura* (?) *senonensis* (Valette) — Rasmussen, p. 118, pl. 15, figs. 6-10.
1952 *Amphiura*? *senonensis* (Valette) — Rasmussen, p. 50, figs. 4-5.
1960b *Amphiura*? *senonensis* (Valette 1915) — Hess, p. 755.

1972 *Amphiura*? *senonensis* Valette, 1915 — Rasmussen, p. 59, pl. 6, fig. 1.
1986 ?*Amphiura senonensis* Valette — Jagt, p. 92, figs. 1-4.
1987 ?*Amphiura senonensis* Valette — Jagt, p. 39, figs. 1-3.
1998 sp. 7 = *Ophiocoma*? *senonensis* — Jagt & Kutscher, fig. 2b.
1998 *Ophiocoma*? *senonensis* — Kutscher, p. 41, fig. 3.

Type — The specimen illustrated by Valette (1915, fig. 6/1) is holotype by monotypy; its present whereabouts are unknown.

Material — Numerous dissociated arm ossicles, and many arm fragments, some preserving spines (Kutscher Colln, no. 1941/7; GM 1999.7; and RGM 428 006).

Description — Rasmussen (1950) and Jagt (1987) provided lengthy discussions of the present species. Our abundant material allows us to expand upon these descriptions, which for a number of important characters need to be corrected as well. The Rügen material consists of dissociated ossicles as well as arm fragments preserving spines and tentacle scales.

The medium-sized, strong lateral arm plates (Pl. 27, figs. 15-16; Pl. 28, figs. 1, 4) have a slightly constricted, smooth (unornamented) outer surface. At the distal margin there generally are three large, horseshoe-shaped tubercles, which are notched in their curved portion and 'cut into' the outer surface. It should be noted that the number of spine tubercles varies between two and five, the latter being exceptional. Plates with 2 or 4 tubercles are fairly common. Valette (1915) was right in stating that, in ventral view, the second tubercle is the largest. However, the difference in size is not such that this can be seen as a specific character.

At the proximal margin, almost at mid-height, there is an almost circular depression, which corresponds to an element at the distal margin on the inner surface. Adjoining dorsally is a fine vertical striation at the proximal margin, which is only seen in well-preserved material. A similar depression occurs ventrally at the end of the proximal portion of the plate, which served as attachment site for the ventral arm plate.

Of note on the inner surface are, in addition to the element noted above, the tentacle pore notch and vertebral articulation, which runs from a curved ridge at the tentacle pore indentation to the proximal margin and there meets another ridge which extends from the middle of the proximal margin to the dorsal margin.

Tentacle pore notches extend right to the tip of the arms, with two scales, the inner one of which is small, the outer large and spatulate. The longest spines almost equal the length of two arm segments. Dorsal and ventral arm plates were described in detail by Rasmussen (1950) and Jagt (1987). The vertebrae were discussed and illustrated by Rasmussen (1950). They are of the standard type, which A.H. Müller (1950) figured as *Ophiura tener*, but differ from the holotype of that 'species' (which in fact is a vertebra of *Ophiotitanos serrata*), in being more triangular and in showing on the dorso-proximal side a paired indentation for the reception of the distal portion of the adjacent vertebra (Pl. 33, figs. 4-5, 8).

The oral and genital plates of this species are illustrated in Pl. 35, figs. 3-4 and Pl. 34, fig. 12, respectively.

Discussion — Rasmussen (1950, p. 119) discussed assignment of the present species to the genus *Amphiura*, noting that there was a certain resemblance to *Amphiura cretacea* Spencer, 1907 (p. 107, pl. 28, fig. 6) from the Cenomanian (*subglobosus* Zone)

of Folkestone (GB), but that the length of the spines contradicted such a placement. The present species was said to differ from *A. cretacea* in having lateral arm plates with 3 instead of 5 tubercles; Rasmussen (1950, p. 120) remarked that he could make out only 4 tubercles in the type. The collections of the Natural History Museum (London) comprise, in addition to the type of *A. cretacea* (BMNH E.5059; Lewis, 1993), an arm fragment preserved on slab BMNH E.5058 which appears to be conspecific. This specimen preserves arm spines and tentacle scales and contributes substantially to our knowledge of this taxon; a revision is under way.

As outlined above, the number of tubercles varies between 2 and 5, being dependent not of age of the individual, but of arm position. Rasmussen (1950, 1972) and Jagt (1987) noted that assignment to *Amphiura* was questionable; generally, the Amphiuridae is characterised by short, erect spines and mostly but a single tentacle scale (except for *A. chiajii*, which has two small scales) or no scales at all. We may thus exclude this family from consideration.

Within the order Ophiurida the present species is most similar to representatives of the Ophiocomidae and Ophiothricidae. Members of the latter family have thorny, partially transformed spines, while those of *Ophiocoma*? *senonensis* are long, but simple in structure. Awaiting the discovery of specimens preserving the disc, which could yield important taxonomic features, the present species is tentatively assigned to *Ophiocoma*.

Similar is only *Ophiocoma*? *rasmusseni* (see above), which differs in having a granulate outer surface, more numerous tubercles, generally smaller lateral arm plates and differently shaped proximal and distal margins.

Occurrence — Known from the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen, Møn and Kronsmoor. For records from the Maastrichtian type area see p. 27.

Infraorder Ophiodermatina Smith, Paterson & Lafay, 1995
Family Ophiodermatidae Ljungman, 1867
Genus *Ophioderma* Müller & Troschel, 1840

Type species — *Asterias longicauda* Retzius, 1805, by subsequent designation of H.L. Clark (1915).

Ophioderma? *radiatum* Kutscher & Jagt, sp. nov.
Pl. 27, figs. 7-10.

Type — Holotype is FGWG 112/11 (Pl. 27, fig. 7), paratype is RGM 428 010.

Type locality and horizon — Rügen (NE Germany); white chalk of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *radiatus*, in allusion to the radiate ornament.

Diagnosis — Small ophiodermatid(?) with roundish lateral arm plates, numerous spine tubercles and fine granules on the outer surface between which radiating ridges interconnect adjoining granules.

Material — Fairly numerous dissociated arm ossicles (Kutscher Colln, no. 1941/11; and GM 1999.11).

Description — The small, roundish lateral arm plates (Pl. 27, figs. 7-10) are not constricted and have a convex distal margin with 5 (distal) to 12 (proximal) small tubercles consisting of two limbs each. The larger ventral tubercles are further removed from the distal margin than the smaller, dorsal ones. At the proximal margin, two articulation elements are conspicuous, of which the centrally placed one is circular, the ventral one being more elongate and closer to the margin. In poorly preserved material generally only the rounded element further away from the margin, is obvious.

Highly typical is the ornament of the outer surface, which consists of small granules interconnected by fine ridges, giving the impression of a radiating system of 'lines and knobs'.

On the inner surface, the weakly developed articulation elements on the distal margin and an equally weakly developed surface for vertebral articulation are noted. Especially in distal arm segments, the vertebrae were very narrow to fit the limited room left by the lateral arm plates.

Proximal and median plates show tentacle pores, distal ones corresponding pores. Ventral and dorsal arm plates abutted up to mid-arm length. The dorsal arm plates in proximal arm portions were broad, distally triangular with convex distal margin and bore the same ornament as the lateral arm plates. The small vertebrae correspond to those of the previous species.

Discussion — Amongst the ophiuroids from Rügen and Møn there is no other species with which *Ophioderma*? *radiatum* could be confused. There is a certain resemblance to *Ophiomusium vermiculatum* Valette, 1915 (p. 142, fig. 8) from the Lower Campanian of Yonne (France). However, this species, which undoubtedly should be removed from the genus *Ophiomusium*, has a different ornament on the outer surface.

Distal plates resemble lateral arm plates of certain species of *Ophiomusium*, e.g. *O.*? *sinemurense* Kutscher & Hary, 1991 (p. 50, fig. 2/3a-b) from the Sinemurian of Luxemburg. These, however, have fewer and smaller tubercles, a slight constriction and an inner surface typical of species of *Ophiomusium*.

Assignment to *Ophioderma* is based solely on the large number of tubercles and a comparable structure of vertebrae and tubercles to representatives of that genus and is highly provisional.

Occurrence — Known from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 28.

Ophioderma? *substriatum* (Rasmussen, 1950)
Pl. 27, figs. 1-6; Pl. 33, fig. 2.

*1950 *Ophiura*? *substriata* Rasmussen, p. 116, pl. 18, figs. 1-9.
1950 *Ophiaxina intercarinata* A.H. Müller, p. 21, pl. 2, figs. 1-5.
1952 *Ophiura*? *substriata* W. Rasmussen — Rasmussen, p. 52, fig. 3.
1998 sp. 6 = *Ophioderma*? *substriata* [sic] — Jagt & Kutscher, fig. 1h.
1998 *Ophioderma*? *substriata* [sic] — Kutscher, p. 41, fig. 5.
1999 *Ophioderma*? *substriatum* (Rasmussen, 1950) — Helm et al., pl. 2, figs. 1-2.

Type — Holotype is BMNH E.13116 (Lewis, 1993); holotype of *Ophiaxina intercarinata* is SGWG 103/6.

Material — Numerous dissociated arm ossicles (Kutscher Colln, no. 1941/6; GM 1999.6; NHMM JJ 5387; and RGM 428 005).

Description — The comparatively large and stout lateral arm plates (Pl. 27, figs. 1-6) resemble those of *Stegophiura*? *hagenowi* (see above) in size and robustness. Behind a distal tongue are 10-12 (proximal) or 7-9 (distal) spine tubercles. Of these the dorsal 1-3 tubercles are markedly smaller, while the others are of near-equal size and bore spines whose length equalled almost half the length of an arm segment. The tubercles are dumbbell-shaped, ventro-dorsally oriented, with a pore each in the narrow region. Granules of varying sizes cover the lateral arm plates up to the centre of these plates, the proximal half being unornamented, but with two weakly developed articulation elements at the proximal margin.

Proximal and median lateral plates have distinct tentacle pore indentations, distal ones a corresponding pore. The inner surface of these plates, which leave ample room for the vertebrae, shows a broad vertebral articulation and near the distal margin, only weakly developed, the equivalent of the elements on the proximal margin of the outer surface.

The spines are pointed conical; their length equals 1/2-3/4 the length of an arm segment.

Dorsal arm plates abut in proximal and median arm segments; these are broad with a rounded distal margin and granulate outer surface. Rasmussen (1952, fig. 3) referred a ventral arm plate to the present species; the thick-set plate with tentacle pore indentations has a granulate outer surface, with granules arranged in rows. However, assignment of this ossicle to *Ophioderma*? *substriatum* is doubtful, as its size does not correspond to that of the lateral arm plates. Of note is that similar ventral arm plates occur in *Ophiocoma*? *rasmusseni* (see above).

The vertebrae (Pl. 33, fig. 2) are broad, the distal articulatory pegs widely jutting out distally, and considerably extending ventro-distally. In lateral view, a small articulation surface is developed above the ventral muscle scar for the lateral arm plate. Distal vertebrae are compact, barrel-shaped. Rasmussen (1950, pl. 18, fig. 6a-e) illustrated a vertebra from a median arm segment.

Discussion — Rasmussen (1950) described *Ophiura*? *substriata* from the 'Lower Senonian' of Kent (GB) and from the 'Upper Senonian' of Rügen and Aalborg (DK), mentioning only 8 spine tubercles. This low number may be explained by the fact that he missed the smaller dorsal tubercles. He noted that *O.*? *substriata* recalled *O.*? *hagenowi*, but listed the following distinguishing features: the present species differs from *Stegophiura*? *hagenowi* in having equal-sized tubercles, a distal tongue, another type of outer surface ornament, a barely receding distal margin, poorly developed articulation bosses on the proximal margin, broader vertebrae with less well-developed muscle scars for lateral arm plate articulation and large dorsal and ventral arm plates.

A re-examination of the holotype has shown that the vertebra which A.H. Müller (1950) illustrated under the name *Ophiaxina intercarinata* corresponds to the vertebral type described above. However, he did not combine this vertebra with lateral arm plates.

Rasmussen (1952), in his revision of A.H. Müller's taxa, failed to note that the *Ophiaxina intercarinata* vertebra exactly matched those he himself had illustrated

(1950, pl. 18, fig. 6a-e) for *Ophiura*? *substriata*. Consequently, he did not synonymise *Ophiaxina intercarinata* with that species, but did recognise the same vertebral type amongst Danish material and hinted at a similarity of these to Recent *Ophiomyxa*. In recording *Ophiura*? *substriata*, Rasmussen (1952) again mentioned Rügen as locality and wondered why A.H. Müller had not described the lateral arm plates which are not rare at that locality. To explain this, he assumed that A.H. Müller had confused these lateral arm plates with those of *Ophiura*? *hagenowi* and the vertebrae with those of *Ophiura*? *serrata*. While the first argument may apply, the second assumption is wrong, since A.H. Müller had described the vertebra belonging to '*Ophiura*'? *serrata* as *Ophiura tener*, a conclusion which Rasmussen (1952) himself also arrived at. Vertebrae of these species, however, are utterly different.

Rasmussen (1950, p. 117) noted that, 'There is no basis for a certain generic determination.' Representatives of the extant genus *Ophiura* have fewer spines, and ventral arm plates do not abut, not even in proximal arm segments. The Ophiodermatidae on the other hand comprise many species with numerous, appressed spines and abutting ventral arm plates, e.g. members of the genera *Ophioderma* and *Pectinura*. Based on the close resemblance between the arm structure of the present species and extant ophiodermatids, it is tentatively placed here.

Occurrence — Known from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 28.

Genus *Ophiotitanos* Spencer, 1907

Type species — *Ophiotitanos tenuis* Spencer, 1907, by original designation.

Ophiotitanos serrata (Roemer, 1840)
Pl. 26, figs. 8-11; Pl. 32, figs. 10-11.

*1840 *Ophiura serrata* Roemer, p. 28, pl. 6, fig. 23.
1843a *Ophiura serrata*, Roemer — Forbes, p. 234, fig. 2.
1846 *Ophiura serrata* Roemer — Reuss, p. 58, pl. 20, fig. 26.
1850 *Ophiura serrata* Roemer — Forbes, in Dixon, p. 337, pl. 23, figs. 2-3.
1869 *Ophioglypha serrata* Roemer — Lütken, p. 73.
1887 *Ophioglypha* af. *serrata*, Roemer — Peron, p. 214, pl. 3, figs. 40-42.
1907 *Ophiura serrata*, Roemer — Spencer, p. 102, pl. 27, fig. 3.
*1907 *Ophiura parvisentum* Spencer, p. 103, pl. 27, fig. 4.
1908 *Ophiura parvisentis* Spencer, p. 135.
1915 *Ophioglypha parvisentis* (Spencer) — Valette, p. 131, fig. 2.
?1915 *Ophioglypha gracilis* Valette, p. 135, fig. 3.
1950 *Ophiura serrata* Roemer — Rasmussen, p. 111, pl. 16, figs. 1-8.
*1950 *Ophiura tener* A.H. Müller, p. 16, pl. 1, fig. B1-5 (non Pl. 3, fig. O1-2).
*1950 *Ophioderma arkonensis* A.H. Müller, p. 29, pl. 3, fig. P1-2 (non Pl. 1, fig. C1-5).
1952 *Ophiura* ? *serrata* (Roemer) — Rasmussen, p. 50, fig. 7.
1960b *Ophiotitanos serrata* Roemer — Hess, p. 751.
1969 *Ophiura serrata* Roemer — Maryańska & Popiel-Barczyk, p. 137.
1972 *Ophiura serrata* Roemer, 1840 — Rasmussen, p. 60.
1998 sp. 4 = *Ophiotitanos serrata* — Jagt & Kutscher, fig. 1c.
1999 *Ophiotitanos serrata* (Roemer, 1840) — Helm et al., pl. 1, figs. 12-17; pl. 2, figs. 3-5; pl. 3, fig. 4.

Types — Holotype, by monotypy, of *O. serrata* is the specimen illustrated by Roemer (1840), whose present whereabouts are unknown; holotype, by monotypy, of *O. parvisentis* is BMNH E.5052; holotype, by monotypy, of *O. gracilis* is the specimen figured by Valette (1915), whose current whereabouts are unknown.

Material — Numerous dissociated arm and disc ossicles as well as an arm fragment (Kutscher Colln, no. 1941/4; GM 1999.4; NHMM JJ 5383, and RGM 428 003).

Description — Height exceeds length in these medium-sized, moderately thick lateral arm plates (Pl. 26, figs. 8-11) in proximal and median arm segments. Distal and proximal margins are virtually parallel. Behind a distal tongue lie 9-11 (proximal), 5-9 (median) and 3-5 (distal) small, but distinct tubercles arranged in 'pockets', suggesting spines to have been appressed. The outer surface is not constricted and shows, when well preserved, a fine, close-set longitudinal striation.

At the proximal margin there are two narrow, proximally pointed articulation bosses, the upper one at mid-height, the lower one in the lower third. Ventrally, a narrow ridge extends in a slight curve from the proximal margin inwards. It delimits the attachment site of the ventral arm plates. Tentacle pore indentations are well developed; in distal plates pores occur.

Ventral arm plates are pentagonal with convex distal margin and lateral indentations for tube feet, and abut up to almost mid-arm length. Dorsal arm plates in proximal arm segments are markedly broader than long with largest width across the distal margin, distal plates being triangular with convex distal margin, and acutely pointed proximal end. Dorsal plates still abut well beyond mid-arm length.

Vertebrae (Pl. 32, figs. 10-11) are of the standard type and resemble those of *Ophiocoma*? *senonensis*, but differ from those in having a nearly closed dorso-proximal edge and relatively long, slender articulatory pegs distally.

A single arm fragment (Kutscher Colln, no. 1941/4) preserves simple, pointed conical, roundish to flattened spines, whose length equalled c. half the length of an arm segment.

Discussion — As the extended list of synonyms shows, this is a widely distributed and comparatively well-known species. Extensive descriptions were provided by Spencer (1907), who also had fragmentary disks available, Valette (1915), Rasmussen (1950) and Hess (1960b), who restudied Spencer's original material. Rasmussen (1950) failed to note the close resemblance between *Ophiura*? *serrata* and the English species of *Ophiotitanos*; Hess (1960b), on the other hand, favoured assignment of the present species to that genus.

Since assignment of the present species to *Ophiura* could be ruled out on differences in lateral arm plate structure alone, Hess (1960b) assigned *O. serrata* to *Ophiotitanos*. However, Hess's assumption that Rasmussen's (1952, fig. 1) vertebra could belong to *O. serrata* misses the mark. This large specimen belongs to *Stegophiura*? *hagenowi* (see above). Hess (1960b) also discussed placement of the genus *Ophiotitanos* in the subfamily Ophiolepidinae and concluded that it could not be compared with any of the Recent genera. However, when comparing lateral arm plate construction of the present species with that of other extant genera, the similarity to the Ophiodermatidae becomes immediately apparent. Lateral arm plates of Recent species of the genera *Ophioderma* and *Pectinura* have comparably numerous small tubercles arranged in 'pockets' and broad dorsal arm plates, short spines and conspicuous

articulatory bosses at the proximal margin (see e.g. *Ophiarachnella megalaspis* H.L. Clark, 1911, p. 25, fig. 2). In those species too the radial shields are relatively small and widely spaced. Their vertebrae correspond to those of the present species as well. Based on these data, we prefer to reassign the genus *Ophiotitanos* to the Ophiodermatidae.

A.H. Müller (1950) described lateral arm plates of *O. serrata* as *Ophioderma arkonensis* and vertebrae as *Ophiura tener*. He did not compare these ossicles to previous records in the literature. In addition, the line drawings (as a re-examination of the types has shown) often differ considerably from the original specimens. Spencer (1907, pl. 27, fig. 3) provided fairly detailed representations of the vertebrae of *O. serrata*, which match those in Rasmussen (1950).

Occurrence — This species is long ranging, with records from the Cenomanian of the United Kingdom, the upper Lower Campanian of southern Sweden and the Lower Maastrichtian of Rügen, Møn and Kronsmoor. For records from the Maastrichtian type area see p. 28.

Infraorder Ophiolepidina Ljungman, 1867
Family Ophiolepididae Ljungman, 1867
Genus *Ophiolepis* Müller & Troschel, 1842

Type species — *Ophiura annulosa* de Blainville, 1834, non Lamarck, 1816, by subsequent designation of Lyman (1865) (= *Ophiolepis superba* H.L. Clark, 1915).

Ophiolepis? *granulata* Kutscher & Jagt, sp. nov.
Pl. 25, figs. 11-12; Pl. 26, figs. 1-2, 7.

Type — Holotype is FGWG 112/6 (Pl. 25, fig. 11), paratype is RGM 428 004.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *granum*, in reference to the granulate outer surface.

Diagnosis — Ophiolepidid with small, robust lateral arm plates which, when well preserved, show a coarsely granulate outer surface. The proximal margin shows three articulation bosses, 2 (or 3) spine tubercles are small and placed directly at the distal margin.

Material — Fairly many dissociated arm ossicles and a few arm fragments in the Kutscher Colln (no. 1941/5), and GM 1999.5.

Description — The small, relatively robust lateral arm plates (Pl. 25, figs. 11-12; Pl. 26, figs. 1-2, 7) are very slightly constricted and, when well preserved, show a coarsely granulate outer surface. At the proximal margin occur, oriented ventrally, three bar-like articulation bosses, which correspond to three such elements at the distal margin on the inner surface.

Near the distal margin occur 2 (in proximal lateral arm plates rarely 3) small spine tubercles, indicating the associated spines to have been appressed; their length would have equalled only 1/5 the length of an arm segment.

The tubercles are so close to the margin, that the plates appear indented. Outer and inner surfaces meet distally under an acute angle, so that these plates appear

sharpened. All plates have well-developed tentacle pore notches. There were one (or two) tentacle scale(s). The dorsal margin of the lateral arm plates is convex, which immediately distinguishes these from those of the following species. Of the 2 (3) tubercles the ventral one is the larger (largest). On the inner surface, a proximally directed 'ridge' serves vertebral articulation.

It should be noted that on many plates the granulation is missing, which, however, does not hamper proper assignment to the present species.

Dorsal arm plates are triangular with concave distal margin; they abut up to mid-arm length. The same holds for the ventral arm plates, which are pentagonal, have a convex distal margin and lateral indentations for tube feet.

With a few arm fragments available, we have been able to determine that the zygospondyline vertebrae are of the standard type.

Discussion — From its Rügen congener, *Ophiolepis*? *linea* (see below), the present species differs in being less strongly constricted, coarsely granulate and in not having a straight to slightly concave dorsal margin. Valette (1915, p. 137, fig. 4) described from the Turonian of Yonne (France) a similar species under the name *Ophioglypha pulchra* Valette, but did not refer to any granules. In this small arm fragment three spines are recorded, whereas *Ophiolepis*? *granulata* generally has but two.

A close resemblance exists also between the present species and *Ophiura*? *astonensis* Hess, 1964 (p. 767, figs. 15-17) from the Pliensbachian of Aston Magna (GB), the Sinemurian of Luxemburg (Kutscher & Hary, 1991, p. 51, fig. 2/2a-c) and the Toarcian of Quedlinburg (Kutscher, 1996b, p. 15, pl. 3, figs. 13-16). Even in pristine specimens, there is no granulation. Such lateral arm plates generally have three spine tubercles, all either closely spaced, or with the the dorsal one further apart from the other two (Kutscher, 1996b), in which case the associated spine was directed dorsally. Specimens of *O.*? *astonensis* recorded by Kutscher & Hary (1991) have no granules on the outer surface of the lateral arm plates either. Hess (1964), however, in the original description described a 'feine Körnelung' (= fine granulation) for proximal plates; this distinctly differs from the granulation of the present species.

Assignment of the present material to the genus *Ophiolepis* is based on the close resemblance it bears in particular to median and distal arm plates of the extant *Ophiolepis cincta* Müller & Troschel, 1842.

Occurrence — Currently known from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 31.

Ophiolepis? *linea* Kutscher & Jagt, sp. nov.
Pl. 26, figs. 3-6.

Type — Holotype is FGWG 112/7 (Pl. 26, fig. 3), paratype is RGM 428 026.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *linea*, in allusion to the straight dorsal margin of lateral arm plates.

Diagnosis — Ophiolepidid with small lateral arm plates, smooth, slightly constricted outer surface, straight or slightly concave dorsal margin, 3 (2) spine tubercles and 2-3 articulation ridges on the distal margin.

Material — Fairly many dissociated arm ossicles (Kutscher Colln, no. 1941/27; and GM 1999.26).

Description — The small, fairly robust lateral arm plates (Pl. 26, figs. 3-6) have a smooth (under higher magnification weakly granulate), slightly constricted outer surface; no granulation developed. At the distal margin are 3 (in distal plates 2) small spine tubercles arranged in 'pockets' and thus causing the distal margin to occasionally appear indented.

Whenever 3 tubercles are present, the distance between them is equal, or the ventral tubercle (invariably slightly larger) is further removed from the central one. This may be a feature of alternation. At the proximal margin are 3 articulation ridges, two of which are fairly well developed and correspond to two elements on the distal margin of the inner surface. The dorsal margin is straight or slightly concave. Tentacle pore notches also occur in distal arm plates. The lateral arm plates abutted dorsally and ventrally for at least 2/3 of total arm length, thus separating dorsal and ventral arm plates.

Dorsal and ventral arm plates and vertebrae correspond to those of *Ophiolepis*? *granulata* (see above).

Discussion — For differences between the present and previous species see above. In addition, *O.* ? *linea* much more often has 3 tubercles, whereas specimens with two dominate our samples of *O.*? *granulata*. A direct comparison of the two shows the lateral arm plates of *O.*? *linea* to be more elongate, while those of the other species appear more hemispherical and robust.

There is a certain resemblance to lateral arm plates of the Early Oxfordian *Ophiopetra*? *oertlii* Hess, 1965 (p. 1076, figs. 41-42), but this differs in having more and larger spine tubercles (up to 5 in proximal plates), in being less constricted and in being generally slightly smaller (Kutscher, 1996b, p. 14, pl. 3, figs. 9-12).

Occurrence — Known to date from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 31.

Genus *Ophiomusium* Lyman, 1869

Type species — *Ophiomusium eburneum* Lyman, 1869, by original designation.

Ophiomusium biconcavum Kutscher & Jagt, sp. nov.
Pl. 22, figs. 7-11.

1998 sp. 20 = *Ophiomusium* n. sp. 2 — Jagt & Kutscher, fig. 1e.

Type — Holotype is FGWG 112/9 (Pl. 22, fig. 8), paratypes are RGM 428 019 and NHMM JJ 5382b.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *biconcavus*, in allusion to the biconcave lateral arm plates.

Diagnosis — Small species of *Ophiomusium* with equally granulate lateral arm plates, which are concave ventrally and dorsally, the dorsal area being more strongly

constricted, and with 2-4 diminutive tubercles.

Material — Fairly many dissociated lateral arm plates in the Kutscher Colln (no. 1941/20). GM 1999.19 comprises material from Møn.

Description — The small lateral arm plates (Pl. 22, figs. 7-11) are laterally, dorsally and ventrally constricted, so that in lateral view they are biconcave, the constriction of the dorsal region being more pronounced.

Considering plate size, the outer surface is equally coarsely granulate, with the exception of the proximal margin only. This margin, which may occupy up to c. 1/3 of the entire plate length in proximal ossicles, bears, in well-preserved specimens, flatter articulation elements, which correspond to three similar structures on the distal margin of the inner surface. As the granulation extends to the distal margin and includes the tubercles, these can hardly be made out. Generally there are 2 to 3, more rarely a single one in distal and 4 in proximal ossicles. They are either closely or more widely spaced.

Tentacle pore indentations are restricted to proximal lateral arm plates. In most other ossicles, on the inner surface, a small pore is seen next to the vertebral articulation muscle scars.

Radial shields (Pl. 34, fig. 2) of this species resemble those of *O. sentum* (see below), are granulate and bear rows of knobs, which in part may be arranged in a star-like fashion.

Discussion — Its lateral profile and the type of granulation distinguishes the lateral arm plates of the present species from all other Late Cretaceous congeners. The closest resemblance exists to juvenile, distal ossicles of *O. granulosum* which, however, are straight ventrally, dorsally much more weakly concave, and bear only a fine, closely spaced granulation and generally are more symmetrical.

Occurrence — Known from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 35.

Ophiomusium granulosum (Roemer, 1840)
Pl. 22, figs. 1-6; Pl. 32, figs. 12-13.

*1840 *Ophiura granulosa* Roemer, p. 28, pl. 6, fig. 22.
*1840 *Ophiura (Aspidura) subcylindrica* von Hagenow, p. 661, pl. 9, fig. 7.
1889 *Ophiura (Aspidura) subcylindrica*, Hagenow — Boehm, p. 265[34].
*1926 *Ophiomusium danicum* Brünnich Nielsen, p. 11, figs. 2-4.
1950 *Ophiomusium danicum* Br. Nielsen — Rasmussen, p. 102, pl. 12, figs. 1-6.
1950 *Ophiomusium granulosum* (Roemer) — Rasmussen, p. 105, pl. 13, figs. 1-4; pl. 14, figs. 1-3.
1950 *Ophiomusium subcylindricum* (Hagenow) — Rasmussen, p. 108, pl. 14, figs. 4-6.
1969 *Ophiomusium subcylindricum* (Hagenow), 1840 — Maryańska & Popiel-Barczyk, p. 135, pl. 2, fig. 3.
1969 *Ophiomusium danicum* Nielsen, 1926 — Maryańska & Popiel-Barczyk, p. 135, pl. 2, fig. 2.
1972 *Ophiomusium danicum* Nielsen, 1926 — Rasmussen, p. 59.
1972 *Ophiomusium subcylindricum* (Hagenow, 1840) — Rasmussen, p. 60.
1987a *Ophiomusium subcylindricum* (von Hagenow) sensu Rasmussen 1950 — Jagt, p. 20, figs. 1-3.
1987 *Ophiomusium subcylindricum* (Hagenow) — Wright & Smith, p. 217, pl. 47, fig. 5.
1998 sp. 1 = *Ophiomusium subcylindricum* — Jagt & Kutscher, fig. 1a.
1999 *Ophiomusium subcylindricum* (von Hagenow, 1840) — Helm et al., pl. 1, figs. 3-11; pl. 3, figs. 1-3, 5, 7.

Types — The holotype by monotypy of *O. granulosum* is the specimen figured by Roemer (1840), whose present whereabouts are unknown; the holotype, by monotypy, of *O. subcylindricum* is the specimen illustrated by von Hagenow (1840), which must be presumed lost, and the holotype of *O. danicum* is MGUH 7574.

Material — Numerous dissociated arm and disc ossicles, as well as a few arm fragments, and remains of discs (Kutscher Colln, no. 1941/1; GM 1999.1, and RGM 428 000).

Description — Rasmussen (1950), Maryańska & Popiel-Barczyk (1969) and Jagt (1987a) provided detailed descriptions and illustrations of lateral arm plates. However, these descriptions are in part inadequate or even erroneous, which may be explained by preservational differences. The Rügen material, which is well preserved, allows us to expand upon these earlier records.

Adult specimens of the robust, almost semicircular lateral arm plates of this species are markedly constricted in proximal arm segments. This constriction gradually becomes less marked towards the arm tip and in juvenile individuals, so that distal or juvenile lateral arm plates show almost no constriction. In general, increase of the ratio L/H means decrease of proximal constriction. Similarly variable are the granulation and the number of articulation elements.

When well preserved, all plates are granulate. Adult, proximal plates have a very coarse granulation, while distal plates have a finer and denser granulation. However, many ossicles have no (a matter of preservation ?), or very weak granulation only, and then in particular ventrally and dorsally.

Also dependent of preservation is the presence of very small arm spine tubercles. All well-preserved lateral arm plates bear tubercles, their number varying between 2 and 4. The higher number of tubercles does not appear to characterise proximal lateral arm plates; rather this feature seems to vary between adjoining ossicles. In most cases the point-like tubercles are closely spaced. However, we have also many ossicles to which this observation does not apply.

The articulation elements on the proximal margin, to which scars on the inner surface correspond, constitute an important feature. Rasmussen (1950) recorded 5, Maryańska & Popiel-Barczyk (1969) 5-8 such elements. Indeed, there is a wide range of variation: distal plates have one, proximal adult lateral arm plates have up to 8. It should be stressed, however, that in addition to these 1-8 narrow, ridge-like elements on each ossicle further, wide articulation scars are developed both ventrally and dorsally, so that the total number of elements is between 3 and 10.

Of special note is the fact that, although only proximal ossicles have tentacle pore indentations, all other lateral arm plates display a small pore close to the wall-like ridge on the inner surface.

Dorsal and ventral arm plates are developed only in proximal arm segments; even there they are very small and do not abut. Dorsally, they are triangular with convex distal margin and ventrally broadly triangular, the distal margin showing a V-shaped indentation.

The vertebrae (Pl. 22, fig. 5; Pl. 32, figs. 12-13) are typical of the genus and correspond to the type illustrated by Rasmussen (1952, fig. 9).

A subadult specimen in the Kutscher Colln (no. 1941/1) preserves not only lateral arm plates and vertebrae, but also radial shields, genital plates, oral plates and shields

and interradial marginal disc plates. With the exception of the oral and adoral shields, all outer surfaces are granulate. The adoral shields join above the oral plate, which is relatively long. The interradial disc plates resemble those illustrated by Rasmussen (1950, pl. 12, fig. 5; pl. 14, fig. 5). Oral plate and adoral shield resemble ossicles illustrated by Kutscher (1992, pl. 1, figs. 3-4).

Genital scales are elongate-triangular and have also a granulate outer surface; the genital plates bear an articulation boss, to which corresponds a furrow on the radial shields.

Discussion — Jagt's (1987) assessment of previous descriptions is detailed, and not much can be added. Remarkable is that neither Rasmussen (1950) nor Jagt (1987) compared *O. subcylindricum* with *O. granulosum* (Roemer, 1840) and *O. danicum* Brünnich Nielsen, 1926, although Rasmussen provided detailed descriptions of these two taxa. In view of the range of variation of *O. granulosum* documented here, which is dependent of size as well as of preservation, it does not seem warranted to separate these species. As shown above, the presence/absence of granulation, spine tubercles and constriction is not a reliable character on which to distinguish species.

However, our material does include a number of congeners which differ markedly from *O. granulosum* in size, structure of lateral arm plates and ornament.

Occurrence — At present, this species is known to range from the Lower Campanian of the United Kingdom and Germany to the Lower Palaeocene of Denmark, including records from the Lower Maastrichtian of Rügen, Møn and Kronsmoor. For records from the Maastrichtian type area see p. 31.

Ophiomusium sentum Kutscher & Jagt, sp. nov.
Pl. 23, figs. 4-7.

1998 sp. 8 = *Ophiomusium* n. sp. 1 — Jagt & Kutscher, fig. 1d.

Type — Holotype is FGWG 112/8 (Pl. 23, fig. 6), paratype is RGM 428 007.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *sentus* meaning thorny, in allusion to the outer surface ornament.

Diagnosis — Small ophiolepidid with constricted, strongly granulate lateral arm plates, with granules transforming into thorns between spine tubercles and distal margin, 2-4 tubercles being placed on a ridge.

Material — Fairly many dissociated arm ossicles and radial shields possibly belonging here, in the Kutscher Colln (no. 1941/8), and GM 1999.8.

Description — The small lateral arm plates (Pl. 23, figs. 4-7) are constricted almost centrally and bear a conspicuous granulation on the outer surface, which distinguishes them immediately in all samples. This granulation extends over the entire outer surface and leaves only the proximal margin free, which does not show any other element. Three (maximum: 4) spine tubercles are positioned on a ridge, which recedes dorsally and concomitantly increases in width, and consists of the tubercles themselves. Thus the dorsal tubercle is the largest. Tubercle arrangement points to erect spines.

The tubercles themselves are included in the granulation to such an extent that

they hardly stand out. In front of the tubercle-covered ridge and up to the distal margin, the granules transform into obtuse thorns, which are directed distally as well as laterally. In lateral view, the ventral side forms a straight line, while the dorsal side is curved sinuously. On the inner surface, next to the ridge for vertebral articulation, are seen only pores or tentacle pore indentations.

In samples contained in the Kutscher Colln there are small radial shields which bear granules and thorns (Pl. 34, fig. 6); judging by size and outer surface ornament these could well belong to the present species.

Discussion — Amongst the Late Cretaceous ophiuroids known to date, there is none that is likely to be confused with *O. sentum*. From the Toarcian of Seewen (Hess, 1962b) and the Toarcian-Aalenian of Quedlinburg and Mistelgau (Kutscher, 1996b), however, there are lateral arm plates of a species of *Ophiomusium* which is very close to *O. sentum*. This species, *Ophiomusium scabrum* Hess, 1962b, differs from its Early Maastrichtian congener in having a broader proximal margin lacking granules and extending in some specimens to the middle of the plate and in lacking thorns on the distal margin. That only granules are visible is not a matter of preservation, since the Quedlinburg material is even better preserved than that from the Rügen Cretaceous.

Of note is that in material assigned to *O. scabrum* there are many more plates, also median and distal ones, that have tentacle pore indentations. It is possible that the comparison of these two species reveals a tendency for tentacle pore reduction. In the Recent genus *Ophiomusium* tentacle pore notches are restricted to the 2-5 proximalmost arm segments. Hertz (1927) coined the name *Ophiomusa* for species with only 2 tentacle pore notches and considered forms with 3-5 indentations to be the more primitive. Hess (1960b) already pointed out this development and proposed to modify the genus. Comparable is the tendency to decrease the number of spine tubercles and arm spine length. *Ophiomusium scabrum* is thus best assigned to a new genus, *Mesophiomusium* gen. nov. (see below).

Occurrence — Apparently confined to the Lower Maastrichtian of Rügen and Møn. For a possible record from the Maastrichtian type area see p. 35.

Ophiomusium sinuatum Kutscher & Jagt, sp. nov.
Pl. 23, figs. 1-3.

Type — Holotype is FGWG 112/10 (Pl. 23, fig. 1), paratype is RGM 428 020.

Type locality and horizon — Rügen (NE Germany); white chalk facies of late Early Maastrichtian age (*sumensis*, *cimbrica* and *fastigata* zones).

Derivation of name — Lat. *sinuare*, alluding to the constriction of the lateral arm plates.

Diagnosis — Small species of *Ophiomusium* with constrictions at the end of the proximal margin as well as in the middle of lateral arm plates and generally with 2 tubercles, relatively widely separated from the distal border and on elevations.

Material — Fairly many dissociated arm ossicles in the Kutscher Colln (no. 1941/21) and GM 1999.20.

Description — The lateral arm plates of this rather small species (Pl. 23, figs. 1-3) are easily distinguished on the structure of the outer surface, which (in ventral and dorsal view) gives these ossicles a sinuous profile. The smooth proximal margin, which only bears 3-5 articulation elements, proceeds distally into a conspicuous

curved ridge. Behind that, the outer surface is constricted, to rise again towards the tubercles. This rise appears even stronger since the tubercles are closely spaced and placed on elevations. From there the outer surface slopes to the distal border. Only in well-preserved material can the outer surface be seen to be finely granulate.

The tubercles, mostly two in number, are situated relatively far back, the small ventral one being closer to the distal border, the dorsal one being the larger. Tubercle structure suggests the associated spines to have been erect. In addition to a marked asymmetry, median and distal lateral arm plates are conspicuous in having a clearly more raised proximal region, which suggests the arms to have been short. Tentacle pore indentations were confined to proximal lateral arm plates. The inner surface corresponds to that of congeners, leaving little room for vertebrae, and with a broad ridge and articulation surfaces at the distal margin.

Discussion — Rasmussen (1950, pl. 15, figs. 1-2, 4) illustrated, under the name *Ophiomusium* sp., lateral arm plates from the 'Upper Senonian' of Aalborg (Jylland, DK). His fig. 2a-e in particular is reminiscent of the plates before us. Rasmussen, however, made mention of 3-4 spine tubercles between the distal margin and the large granules. In addition, the proximal portion is reported not to be sharply demarcated from the remainder of the outer surface. These features are not seen in the present species. Distal ossicles of *O. granulosum* differ immediately in being symmetrical, in lacking constrictions and in having inconspicuous tubercles close to the margin.

Occurrence — Known from the Lower Maastrichtian of Rügen and Møn. For records from the Maastrichtian type area see p. 35.

Genus *Mesophiomusium* Kutscher & Jagt, gen. nov.

Type species — *Mesophiomusium moenense* sp. nov., by monotypy.

Derivation of name — In allusion to the occurrence in the Mesozoic.

Diagnosis — Ophiolepidid similar to *Ophiomusium* with compact lateral arm plates which abut dorsally and ventrally over almost the entire arm length; room for vertebrae very limited. Over ten arm segments had tentacle pore indentations. Dorsal and ventral arm plates very small, not abutting. Spine tubercles weakly developed. Spine canopy comprised but few, mostly appressed, short to moderately long (up to one arm segment) spines. Vertebrae *Ophiomusium* like.

Included species — In addition to the type species, *M. moenense*, the Jurassic *Ophiomusium scabrum* Hess, 1962b and the Early Palaeocene *M. decipiens* Jagt & Kutscher, sp. nov., are referred here.

Mesophiomusium moenense Kutscher & Jagt, sp. nov.
Pl. 26, figs. 12-14.

Type — Holotype is MGUH 24552 (Pl. 26, fig. 12), paratype is RGM 428 029.

Type locality and horizon — Møn (Maglevandspynt, Denmark); white chalk facies of early Early Maastrichtian age (? *obtusa* Zone).

Derivation of name — Named after the type locality, Møn.

Diagnosis — Pear-shaped lateral arm plates with slight proximal constriction and pitted outer surface, 1-2 point-like spine tubercles at the distal margin. Tentacle pore indentations in all lateral arm plates. Room for vertebrae hardly larger than the tenta-

cle notch. Large surfaces for articulation to paired plate.

Material — A number of dissociated lateral arm plates (Kutscher Colln, no. 1942/31; and GM 1999.28).

Description — The small, robust, pear-shaped lateral arm plates are slightly constricted proximally and, when well preserved, regularly pitted on the outer surface. In distal plates the outer surface is only slightly curved, in proximal plates however very strongly so. Pitting extends from the proximal to the distal margin. The greatest height of the plate, in distal direction, is right behind the constriction. The proximal margin is almost straight and does not show any distinctive elements. The distal margin is either straight for a short stretch or slightly convex; however, it curves backwards dorsally in both cases.

On the pitted outer surface there are one or two weak indentations near the distal margin, in which the barely visible tubercles are lodged. The spines were probably very small and appressed. The inner surface shows a narrow ridge for the articulation with the vertebrae and the entirely even dorsal and ventral surface for articulation with the paired plate, with which it abuts over almost its entire length and height. All lateral arm plates have tentacle pore notches. This notch almost equals the room left for the vertebra. In relation to the total plate height the ratios ventral surface/vertebral furrow/dorsal surface roughly is 2/1/3 in proximal plates and 1/1/1 in distal ones. Proximal lateral arm plates resemble diminutive coffee beans. Abutting lateral arm plates leave but little room for the diminutive ventral and dorsal arm plates. The dorsal arm plates were triangular with straight to convex distal margin, the ventral arm plates probably had very large tentacle pore indentations laterally.

Discussion — From all Cretaceous ophiuroids known to date, *M. moenense* differs in external aspect, the limited number of barely visible tubercles and inner surface structure. Distal plates are somewhat similar to those of the much smaller *Hemieuryale*? *parva* (see above), whose outer surface is not pitted but granulate, while the tubercles (mostly two) are distinct; moreover, on the inner surface there was much more room for the vertebrae. With regard to tubercle structure, constriction and inner surface there are similarities to representatives of *Ophiomusium*. However, this genus comprises members in which only the first 2-5 arm segments have tentacle pore indentations. Hertz (1927), who erected the genus *Ophiomusa* for those forms with only two pairs of tentacle pores, considered the genus *Ophiomusium* to represent the most primitive, on account of the higher number of tentacle pore notches. Although the genus *Ophiomusa* has not been generally accepted and is mostly synonymised with *Ophiomusium*, the observation that *Ophiomusium* originated from a fossil genus, whose representatives had *Ophiomusium*-like lateral arm plates but a higher number of tentacle pores, appears legitimate. Especially from strata of Jurassic age species of *Ophiomusium* have been described that show tentacle pore indentations over longer portions along the arm. In view of this Hess (1960b) suggested to broaden the concept of *Ophiomusium* to allow inclusion of fossil species. Kutscher (1992) also noted that many fossil species assigned to this genus had a markedly higher number of arm segments with tentacle pore notches, longer spines and better developed tubercles, and thus did not fit the generic diagnosis. Generally, there is a reduction in number of tentacle pore indentations and in spine length. For instance, *O. geisingense* Kutscher, 1992 from the Lias has tentacle pores along a considerable stretch of the

arms and spines that equal an arm segment in length, while *O. weymouthiense* (Damon, 1880) from the Lower Oxfordian (see Hess, 1964) has only c. 10 arm segments with tentacle pore notches and considerably shorter arm spines.

The Late Cretaceous species *O. granulosum*, *O. biconcavum* and *O. sinuatum*, on the other hand, represent typical examples of the genus *Ophiomusium*. Hess's suggestion to broaden the generic concept, does not seem to be very effective since the generic assignment of most fossil species relies solely on dissociated material, and lateral arm plates in particular. Thus is not certain whether or not these species would still be considered to be species of *Ophiomusium* if all details were known. For that reason we prefer here to erect the genus *Mesophiomusium* to contain fossil ophiuroid species of *Ophiomusium* type, but higher number of tentacle pore notches and mostly longer spines. Of course, it cannot be ruled out that this genus in future will turn out to be a 'lump genus'. After all, fossil ophiuroids are generally not preserved entire, which means that quite a number of diagnostically important morphological features are not available.

Occurrence — Apparently confined to the lower Lower Maastrichtian of Møn.

Table 1. Revision of ophiuroid taxa described by A.H. Müller (1950) and Rasmussen (1950, 1952); only lateral arm plates and vertebrae have been considered.

A.H. Müller (1950)	Rasmussen (1950, 1952)	this paper
vertebrae		
Ophioderma rugensis	invalid	*Stegophiura? hagenowi*
Ophiura tener	*Ophiura? serrata*	*Ophiotitanos serrata*
Ophioderma arkonensis	*Ophiura? hagenowi*	*Ophiomyxa? rhipidata*
Schizospondylus jasmundiana	*Schizospondylus jasmundiana*	*Ophiomyxa? curvata*
Transspondylus bubnoffi	*Transspondylus bubnoffi*	*Ophiosmilax? alternatus*
Ophiaxina intercarinata	*Ophiaxina intercarinata*	*Ophioderma? substriatum*
Asteronyx simplex	*Asteronyx? simplex*	*Asteronyx? simplex*
Asteronyx granulosus	*Asteronyx? ornatus*	*Trichaster? ornatus*
lateral arm plates		
Asteronyx granulosus	*Ophiura? hagenowi*	*Stegophiura? hagenowi*
Ophiura tener	*Ophiura? hagenowi*	*Stegophiura? hagenowi*
Ophioderma arkonensis	*Ophiura? serrata*	*Ophiotitanos serrata*
Transspondylus bubnoffi	*Ophiomusium subcylindricum*	*Ophiomusium granulosum*
Q 12 unbenannt	*Ophiacantha? danica*	*Ophiomyxa? curvata*
	Ophiomusium danicum	*Ophiomusium granulosum*
	Ophiomusium subcylindricum	*Ophiomusium granulosum*
	Ophiomusium subcylindricum	*Ophiomusium granulosum*
	Ophiura serrata	*Ophiotitanos serrata*
	Ophiura? hagenowi	*Stegophiura? hagenowi*
	Ophiura? substriata	*Ophioderma? substriatum*
	Amphiura? senonensis	*Ophiocoma? senonensis*
	Ophiacantha? sp.	*Ophiacantha? danica*
	Asteronyx? ornatus	*Trichaster? ornatus*
	Asteronyx? sp.	*Asteronyx? spinulosa*
	Ophiacantha? sp.	*Ophiocoma? rasmusseni*

Specifically indeterminate ophiuroid ossicles

In our material from Rügen and Møn there are numerous dissociated ossicles such as radial shields, ventral and dorsal arm plates, genital plates, oral plates and spines, which generally cannot be referred to species, but are conspicuous on account of abundance and/or peculiar shapes and size. A few are here discussed briefly.

Radial shields

In part, the assignment of isolated radial shields poses serious problems since size and outer surface ornament may differ utterly from those of lateral arm plates. For instance, the radial shields may be smooth, have an ornament resembling that of the lateral arm plates or one that differs markedly from that of those plates. From Rügen, nineteen types of radial shields are currently known:

Type 1: Large, thick-set ossicles with weakly convex outer surface, which bears a coarse, dense granulation; granules may distally coalesce into longer 'ridges'. Amongst the granules are found point-like impressions. At the distal margin, on the inner surface, are two short elevations and between these a shallow depression. Directly in front of this is a roundish depression for the articulation with the genital plate. On account of size, thickness and, in particular, ornament these ossicles appear to be assignable to *Ophioderma*? *substriatum*.

Type 2: Comparably large, but less stout, ossicles (Pl. 34, fig. 3), the central portion being flattened to slightly concave and granulate. The rim is bevelled and bears grooves. On the distal margin an oblique ridge is conspicuous. On the inner surface (seen in distal direction) a large, round groove may be noted, in front of which is a fine pore and a furrow on the distal margin, demarcated by two weak elevations. In front of the raised area on the adradial side are an elongated depression and the oblique ridge. These ossicles probably belong to *Stegophiura*? *hagenowi*.

Type 3: Thick-set ossicles, distally broader than those of Type 1 (Pl. 34, fig. 1); outer surface with coarse, but not closely spaced granules. The rim is broad, bevelled and shows grooves. In comparison to Type 1 the elevations on the inner surface are longer, so that the roundish depression is displaced closer to the centre of the plate. A.H. Müller (1950) described four types of radial shields. A re-examination of his material has shown the specimens to be poorly preserved, allowing definite separation of his Type J and Type M only. Those of his Type K and Type L resemble J, but are entirely smooth. Such ossicles do not exist; they are either strongly abraded or suffered from acid treatment of samples. It is these ossicles that he assigned to his *Ophiura tener* and *Transspondylus bubnoffi*. Bearing the absence of ornament in mind, A.H. Müller's type J, K and L could belong to the same type of radial shield and match our Type 3. A macerated individual of *Ophiomusium granulosum* in the Kutscher Colln shows these radial shields to belong to that species.

Type 4: This type resembles Type 2 in outer aspect (Pl. 34, fig. 4), but the granulation is finer, the rim more evenly bevelled, especially with regard to the distal margin. The oblique ridge is also missing. On the inner surface the articulation is closer to that of Type 1, with a rather weak groove and elevations closely spaced. When well preserved at the distal margin (only visible from the inside) an oblique furrow is developed, as in Type 2. These radial shields correspond to A.H. Müller's (1950) Type M and most probably belong to *Ophiotitanos serrata*.

Type 5: The small, broad and relatively short ossicles have a small, coarsely granulate outer surface (Pl. 34, fig. 7). The margins (except dorsal margin) are bevelled and bear conspicuously elongated grooves. On the inner surface two elongate elevations demarcate a broad furrow, which ends in a weak, roundish depression. The adradial elevation is extended into a granule at the distal margin and surrounded by a furrow. Fragmentary discs demonstrate these ossicles to belong to *Ophiocoma*? *senonensis*.

Type 6: The outer surface of these elongate-oval ossicles is finely granulate (Pl. 34, fig. 9); the lateral and anterior margins are bevelled and in part covered in grooves. On the inner surface a well-developed elevation is seen near the distal margin, which, when well preserved, shows it to consist of two unequally long elevations, of which the distinctly longer one extends to the distal margin. Assigning these ossicles to species presented problems. Similarly granulate lateral arm plates are known in e.g. *Ophioderma*? *radiatum*, *Ophiacantha*? *punctata* and *Ophiothrix*? *bongaertsi*. Of other species which might be considered the radial shields are known. Representatives of the Ophiomyxidae and Asteronychidae need not be considered as the marginal grooves indicate the presence of additional disc plates. This type of radial shield cannot be assigned to any species with confidence.

Type 7: These radial shields, which belong either to *Amphiura*? *plana* or *Ophiocoma*? *rasmusseni*, are elongate with straight radial and convex adradial sides. The free outer surface does not show any ornament. From the centre to the sides these ossicles are slightly convex, the margins being bevelled. The inner surface is depressed and surrounded by a 'rim'. At the radial side/distal side junction there is a granule-like element surrounded by a furrow, which served the articulation with the genital plate.

Type 8: The convex outer surface is evenly finely granulate (Pl. 34, fig. 8). The radial margin is almost straight, the adradial one strongly curved, the largest breadth being in the first third. The ossicles constitute a rounded, scalene triangle. Particularly conspicuous is the articulation with the genital plate, which is distinctly displaced beyond the distal margin in the direction of the arm and in structure resembles Type 7. Such shields with displaced articulation, even granulation and margins which provide no evidence of abutting disc plates are known in the Ophiothricidae amongst extant ophiuroids. These radial shields are therefore tentatively assigned to *Ophiothrix*? *cristata*.

Type 9: These ossicles are relatively thick set. Their length equals no more than 1.3 times the breadth. The free outer surface is relatively small, and covered in coarse granules. The adradial margin is wide, bevelled and bears grooves. The distal one is adradially displaced in the direction of the arm. The type of articulation is comparable to that of the previous species and consists of an articulatory boss and a furrow. Both are visible only from the inside. On the outer surface, at the juncture between distal and radial margins, 2-3 obtuse 'thorns' are seen in a few ossicles. Similar, slightly irregularly shaped radial shields are seen in the Recent ophiolepidid *Ophiozonella longispina* (Clark, 1908). The outer surface ornament of these ossicles corresponds to that of the lateral arm plates of *Ophiolepis*? *granulata*, so that they are referred to that species.

Type 10: These ossicles (Pl. 34, fig. 5), which appear cut off, are very strongly

granulate, so that granule-free spots resemble impressions. The straight radial margin is bevelled and coarsely pitted, the adradial margin only faintly bevelled and strongly curved. On the inner surface the articulation occurred in the middle of both margins by means of two elevations, of which the adradial one resembles a boss. In a jumble of lateral arm plates of *Ophioderma*? *radiatum* (Kutscher Colln, no. 1941/11) there also are disc plates with the above-mentioned outer surface ornament, so that these radial shields are tentatively assigned to this species.

Type 11: These ossicles, which undoubtedly belong to *Ophiomusium biconcavum* are easily distinguished on account of the depressed outer surfaces, their fine granulation and especially the radiating or star-like arrangement of rows of spine-like elongate granules (Pl. 34, fig. 2).

Type 12: Small, very thick-set radial shields with small outer surface without any ornament. The articulation with the genital plates resembles that of Types 10 and 11, in which the latter has a distinct articulation group, which cannot be recognised beyond doubt in Type 12. The disc to which these ossicles belonged must have been very compact; this in turn suggests the presence of stout lateral arm plates. In view of this, an assignment to *Ophiomusium sinuatum* appears possible.

Type 13: The small ossicles have a coarsely granulate outer surface. The margins are bevelled and also granulate. Especially typical on the outer surface are numerous, thorn-like granules in bundles, some of which even develop lateral thorns. On the inner surface there are two ridge-like elements in the distal portion for the articulation with the genital plate, of which the adradial one is the larger. Articulation depressions cannot be demonstrated. The overall structure — and the type of articulation in particular — suggests an assignment to the order Ophiurida. The outer surface ornament corresponds to that seen in the lateral arm plates of *Ophiomusium sentum*, so that this assignment appears certain.

Type 14: These ossicles resemble Type 13 in overall shape, size and structure of functional elements on the inner surface. Obvious differences, however, exist in the outer surface ornament, which is characterised by fine granulation and absence of thorn-like granules. A similar granulation is seen in the lateral arm plates of *Ophiactis*? *sulcata*, *Ophiothela*? *semirotunda* and *Hemieuryale*? *parva*. However, the radial shields of Recent representatives of the genera *Ophiactis* and *Ophiothela* have a different type of articulation with the genital plates. A specific assignment at this time is thus impossible.

Type 15: This is a relatively large radial shield with smooth, curved outer surface and bevelled margins. The inner surface is also bent perpendicularly to the length axis. Two widely spaced elevations, on both sides of a V-shaped depression, served the articulation with the genital plate. An assignment to the Ophiothricidae appears likely.

Type 16: These ossicles resemble those of Type 8 with regard to overall outline, but lack the distally displaced articulation and outer surface ornament. An assignment to the Ophiothricidae seems probable.

Type 17: Resembling Types 7 and 16, these ossicles are less triangular and have their greatest breadth immediately above the distal margin. In one case the corresponding genital plate is preserved (Kutscher Colln); the distal end forms a dorsal depression and a slightly curved ridge, which falls into the furrow in the radial shield. An assignment is currently not possible.

Type 18: Very thick-set radial shields with strongly curved, unornamented outer surface and concave inner surface, in which no distinct articulation with the genital plate can be made out. Most probably such ossicles belonged to the Ophiomyxidae or Asteronychidae.

Type 19: Elongated, very thin radial shields, weakly convex in length and breadth and without outer surface ornament. On the inner surface there are two elevations distally. Of note is a small ridge which is visible over almost the entire length of the shield. An assignment is not possible.

Spines

Assigning spines to species is extremely difficult, unless they are found directly associated with lateral arm plates. Only in exceptional cases is spine shape such that they differ from the standard type. This standard type, roundish to slightly flattened, more or less acutely conical and smooth, occurs in c. 50% of all species described above, in several adaptations (length, inclination, structure of tip). Other types of spines, however, supplied the bearers with special properties or supported peculiar modes of life. To this group undoubtedly belong the spines of *Ophiomyxa*? *rhipidata* (Pl. 31, figs. 1-3). The construction of these spines appear to indicate an epibenthic habit and suggest a restricted swimming ability.

Koehler (1922, pls 92-103) illustrated numerous spines, most of which however belong to species of the genus *Ophiothrix*. Whereas Clark (1911) provided only general data on the spines of Recent Pacific ophiuroids and Mortensen (1927) only in some cases made reference to spines, Paterson (1985) ascribed specific characteristics to some species.

In our material there are, in addition to those of *Ophiomyxa*? *rhipidata*, various types which differ from the standard type:

Type 1: These acutely conical spines are characterised by a coarse ornament all around, which grades into thorns (Pl. 34, figs. 18-19), but these are not arranged. Koehler (1922, pl. 92, fig. 2; pl. 94, fig. 1) illustrated similar spines for *Ophiomyxa irregularis* Koehler, 1905 and *Ophientrema leucostictum* (H.L. Clark, 1911). Spines of *Amphioplus legatus* Koehler, 1922 (pl. 96, fig. 9) show a similar structure. An assignment seems impossible. We may assume that these must be combined with hook-like ventral spines, such as occurring in many ophiuroids. Such spines, which generally are diminutive, have not yet been found in our material.

Type 2: This cylindrical spine type bears widely spaced thorns on a few distinct ribs (Pl. 34, fig. 14). Comparable spines are known in the ophiomyxid *Ophiophryxus confinis* Koehler, 1922. The Rügen material could therefore belong to *Ophiomyxa*? *curvata*. However, similar spines are also seen in certain ophiacanthids (e.g. *Ophiocamax rugosa* Koehler, 1904).

Type 3: This type, most closely comparable to the standard type, differs in having a knob-like tip. Comparable spines are known in some Recent ophiocomids. Of representatives of *Ophiocoma*? described above, however, the spines are known, and these correspond to the standard type. However, it should be stressed that not all spines of one and the same individual need be similarly shaped. For instance, the Recent *Ophiocoma scolopendrina* (Lamarck, 1806) dorsally has rounded-conical spines, while the ventral ones are club shaped.

Type 4: These spines have numerous ribs, which in part are indistinct, and bear fine thorns (Pl. 34, figs. 16, 21). The bearers of these spines would best be sought amongst the Ophiacanthidae or Ophiothricidae.

Type 5: These coarsely ribbed spines, the tip of which is unknown, are characterised by the 'webs' between the ribs and in particular, by characters of the base (Pl. 34, fig. 24). This has a process which lodges into the tubercle. The process bears a distinct, pore-like depression for muscle attachment. The process on both sides of the base, divided by a furrow underneath, probably served attachment of additional muscles. All this suggests an ophiuroid with generally appressed spines, possibly also used for active burrowing. Koehler (1922) illustrated comparable spines of the ophiothricid genera *Ophiogymna* and *Ophioteron*.

Type 6: While the shaft is comparable to that of Type 5, it differs in the structure of the base (Pl. 34, fig. 20). On a weakly convex base follows a lateral ridge, with a large muscle attachment area directly opposite, along the axis. This shows 2 (3) depressed muscle scars. The spines were appressed and probably belong to representatives of the Ophiomyxidae or Asteronychidae.

Type 7: In their flattened structure, these spines (Pl. 34, figs. 22-23), which have numerous ribs, in part bifurcating several times, closely resemble those described by Paterson (1985) for his new ophiurid *Ophiambix devaneyi*. Members of the genera *Ophiolepis*?, *Ophiomusium* and *Stegophiura*?, as described above, can be excluded; the type of tubercles alone would not allow such type of spine. More likely candidates are members of the Ophiomyxidae or Asteronychidae, particularly as these spines resemble those of *Ophiomyxa*? *rhipidata*.

Type 8: In an echinoderm coprolite this type of spine (Pl. 34, fig. 17) co-occurred with lateral arm plates of *Ophiomyxa*? *curvata* and *Ophiosmilax*? *alternatus*. The figured spine probably represents a shortened version, the larger ones of similar structure would have been more cylindrical, under identical spine base articulation. The ornament of the shaft consists of an alternation of fine, irregular longitudinal pits and ridges. A comparison with the lateral arm plate tubercles of the above-mentioned species shows that, if these spines do indeed belong to one of these species, they must be referred to *Ophiosmilax*? *alternatus*. The ridge between both tubercles fits the furrow of the spine base well.

Oral plates

Matsumoto (1917) opined that the ambulacral portion of oral plates (Fig. 16) was of considerable taxonomic importance. No doubt this holds true for Recent species. But, in fossil material combining oral plates with lateral arm plates or vertebrae is rarely possible, which causes this type of ossicle to be of limited value. To make matters worse, also amongst oral plates a certain morphology predominates which is not subject to considerable variation. This explains why in many unrelated ophiuroid taxa similarly shaped oral plates occur.

A.H. Müller (1950) provided poor illustrations of four types of oral plates; the original ossicles show these figures to diverge considerably. An assignment to the species based on vertebrae should thus not even be attempted. In our material six types predominate:

Type 1: Conspicuous in these plates, which may grow to a large size (Pl. 35, figs.

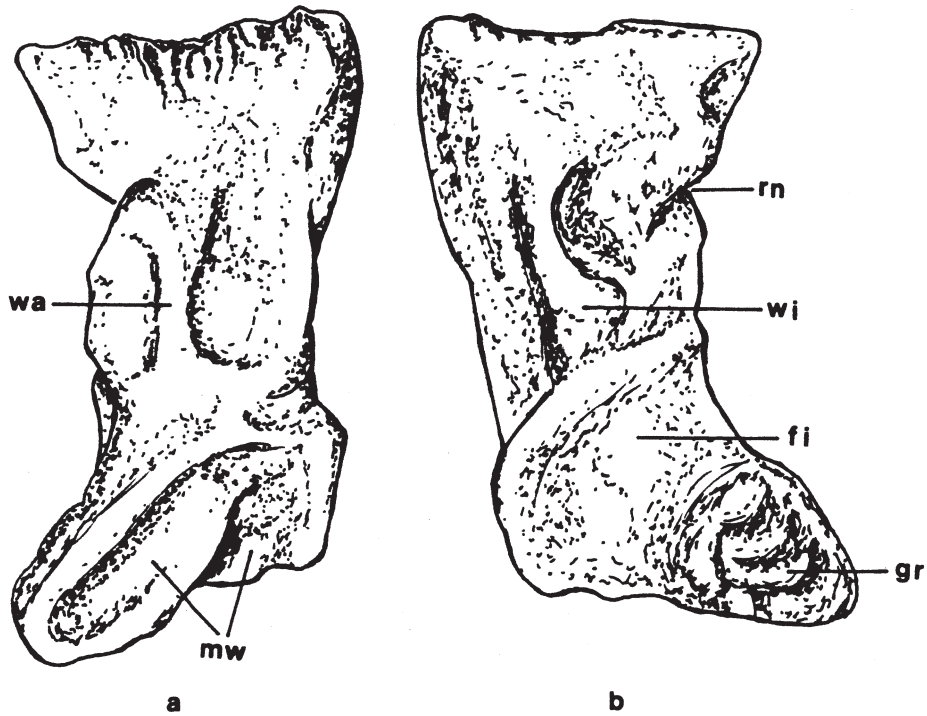

Fig. 16. Morphological terms applied to oral plates; a-b: abradial and adradial views, respectively. Abbreviations: wa = abradial (outer) ridge, mw = muscle scars for articulation with first vertebra, rn = furrow of ring nerve, wi = adradial (inner) ridge, fi = free area, gr = articulation facet for adjoining oral plate.

1-2), is the long ridge between the muscle scars (mw) for articulation with the first vertebra and the small articulation surface for the adjoining oral plate (gr). In view of their size, these plates could well have belonged to *Stegophiura*? *hagenowi*, *Ophioderma*? *substriatum*, *Ophiomyxa*? *rhipidata*, or *O.*? *curvata*. In a single specimen (Kutscher Colln) the first vertebra (juvenile) is associated, which favours an assignment to *O.*? *curvata* or *Ophioderma*? *radiatum*. A.H. Müller (1950, pl. 3, fig. T1-2) illustrated this type and referred it to *Asteronyx granulosus*; indeed, an assignment to the Asteronychidae cannot be ruled out.

Type 2: These ossicles (Pl. 35, figs. 3-4) are the commonest by far. Apart from representing a kind of standard type, these are probably best assigned to the very common *Ophiocoma*? *senonensis*. However, *Ophiacantha*? *rugosa* appears to have had similar plates. They differ from the similar Type 6 in having longer elements and the ridge wi on the inner surface (Pl. 35, fig. 4) is distinctly narrower. Whether A.H. Müller (1950) illustrated this type in pl. 3, fig. S1-2 or in pl. 3, fig. V1-2 cannot be decided.

Type 3: Types 3 and 4 are very similar, the former (Pl. 35, fig. 5) being distally less constricted, the furrow rn for the nerve ring less elongate and the ridge wa displaced to the exterior. This type of oral plate has been seen in small *Ophiomusium granulosum*.

Type 4: These small plates have been observed in co-occurrence with lateral arm plates of *Ophiothrix*? *bongaertsi* (Pl. 35, fig. 6).

Type 5: These plates resemble those of Type 1, but the ridge wi is distally elongated, thus making the free area fi smaller. They cannot be assigned to species.

Type 6: This type resembles Type 2, but is squatter and the ridge wmi is distinctly wider. These common ossicles cannot be assigned to species.

Ventral arm plates

The assignment of ventral arm plates (Pl. 35, figs. 7-17) also presents problems. Even when they are associated with vertebrae and lateral arm plates and are thus easily assigned to species, similar plates cannot be referred to species with certainty, for obvious reasons:

- comparable construction and limited number of distinguishing features;
- even within a single arm there is considerable variation;
- post-mortem corrosion may efface or obliterate ornament.

Ossicles illustrated in Pl. 35, figs. 7-17 are either those which are commonest or are noted for their special habit. The ones in figs. 7, 17 and 8 are assignable to *Ophiocoma*? *rasmusseni* (see *Ophioderma*? *substriatum*), *Ophiotitanos serrata* and *Ophiocoma*? *senonensis*, respectively. The ossicles in figs. 9, 10, 12 and 14 probably belong also to the latter species and document the range of variation. Of note in these ossicles is the depression of the plate centre, which does not become flush again until the tip of the arm (fig. 8).

A small, but very thick-set plate is illustrated in Pl. 35, fig. 16; in all probability this is referable to *Ophiomusium granulosum*, not only on account of the size/thickness relationship but also because of the weakly developed tentacle pore indentations and the extreme rarity of such ossicles. Ossicles illustrated in figs. 11, 13, and 15 cannot be assigned to species as yet; the one in fig. 11 is very thick distally on account of the proximally-distally running ridge. It cannot be determined whether this represents the inner or outer surface; an assignment is not possible. Despite the regular structure the ossicle in Fig. 15 could rather represent an intermediate ossicle of an undescribed asteroid than a ventral arm plate of an ophiuroid. The peculiar inner surface makes this much more likely.

Dorsal arm plates

Of the dorsal arm plates (Pl. 36, figs. 1-9, 12) a certain number can be combined with lateral arm plates and are identifiable to species:

figs. 3, 6: *Ophiotitanos serrata*
fig. 4: *Ophioderma*? *substriatum*
fig. 5: *Stegophiura*? *hagenowi*
fig. 7: *Ophiocoma*? *rasmusseni*
fig. 9: *Ophiolepis*? *granulata*
fig. 12: *Ophiocoma*? *Senonensis.*

A symmetrical, curved roof-shaped ossicle which is not rare, cannot be assigned yet to any of the described species, despite the fact that we are fairly certain that it has to be an ophiuroid ossicle (figs. 1-2) from the arm. Conspicuous at the margin of the inner surface are two short limbs, which probably served articulation with the verte-

brae. The outer surface is coarsely granulate.

Fig. 8 shows a slightly damaged ?dorsal arm plate with oblique striation; whether this really is a dorsal arm plate of one of the species of *Sinosura* or an intermediate plate of an asteroid, remains to be determined.

Of genital plates (Pl. 34, figs. 10-13) recognised in our material four types are illustrated here. Assignment to species is possible only when they can be combined beyond doubt with known ossicle types, or co-occur with these. This holds true only for the genital plate illustrated in fig. 12; this ossicle was observed with radial shield type 5 which is referred to *Ophiocoma*? *senonensis*. However, this is not to say that similar types of genital plates do not occur in other ophiuroid species. The type of genital plate in fig. 10 could belong to *Ophiomusium biconcavum*; the types illustrated in figs. 11 and 13 are not easily assigned. Kutscher (1996, pl. 5, fig. 4) illustrated a radial genital plate from the Upper Toarcian of Quedlinburg, which closely corresponds to that in fig. 13. As at both these localities representatives of the genera *Sinosura* and *Ophiacantha*? occur, these ossicles are possibly assignable to either one of these genera.

Other ophiuroid ossicles (Pl. 36, figs. 10-11, 13-15)

While fig. 15 illustrates an adoral shield which possibly belongs to *Ophiomusium granulosum*, the assignment of the other ossicles presents more problems. The one in fig. 13 is either an oral shield or a disc plate of *Ophiomusium biconcavum*. Fig. 10 (inner surface) shows an ossicle with an outwardly curved extension, of the type known in oral plates of the Ophiothricidae, where they serve the attachment of skin. The illustrated ossicle is relatively common in our material, despite the fact that it is not very stout. More thick set is the ossicle illustrated in fig. 11 with two distally (? proximally) directed processes, but not outwardly. This may represent a ventral arm plate, of the type found in the Recent *Ophiarachnella incrassata* (Lamarck, 1816). The ossicle in fig. 14 is most likely comparable to that in Pl. 35, fig. 15, but occupied a more distal position.

Ophiuroid palaeoecology

The considerable number of ophiuroid species now known from Rügen should not be surprising (c. 30 species have been recorded from the Mediterranean), unless one adheres to the view held prior to 1978 that sediment composition in Cretaceous seas was hostile to burrowing and crawling organisms.

Voigt (1929) noted the virtual absence of gastropods, burrowing bivalves, echinoids and decapod crustaceans. Nestler (1965) more or less adopted this view, but did record the 'spreiten' of endobenthic organisms and the occurrence of endopelitic ostracods. Kutscher (1979) was the first to point out that the soft subtrate fauna of the Cretaceous seas was not as impoverished as previous authors had assumed it to have been. He recorded burrowing decapod crustaceans, gastropods and especially small, rapidly burrowing echinoids (Kutscher, 1978a, b). Nestler (1980) accepted this revised interpretation.

Following Kutscher's (1984) first description of a species- and specimen-rich gastropod fauna, adapted to life on indurated strata and soft bottoms alike, the Cretaceous sea floor can no longer be considered to be an unfavourable environment. This

view is substantiated by the present work on ophiuroids. We may safely assume these to have lived on secondary hardgrounds such as inoceramid and oyster shells, echinoid tests, sponges and bryozoans, as well as on and in soft substrates. In this respect, forms with few and/or appressed spines may be seen as burrowing species, e.g. representatives of the genera *Ophiolepis*?, *Sinosura* and *Amphiura*? *plana*. Diminutive forms often crawl about through sessile benthos in search of food; to this group *Ophiothela*? *semirotunda*, *Ophiacantha*? *punctata* and *Ophiomusium sentum* could well have belonged. Mass occurrences can probably only be expected in *Ophiocoma*? *senonensis*, *O.*? *rasmusseni* and *Ophiotitanos serrata*. Numerous lateral arm plates of *Ophiomusium granulosum*, and *Stegophiura*? *hagenowi* available should be viewed with caution; these are large ossicles of long-armed species.

Representatives of the Ophiomyxidae would have hidden under secondary hardgrounds or burrowed. *Ophiomyxa*? *rhipidata* could well have changed position by swimming, using its fan-like spines. A few Recent species of the genera *Ophiacantha* and *Amphiodia* are known to swim.

A direct comparison between the modes of life of fossil and Recent species is virtually impossible, since:
- the generic assignment of fossil species is provisional at best,
- in descriptions of extant ophiuroids, generally only depth of collection is recorded.

Clark (1911) is one of the few authors working with extant ophiuroids who provided details of sediment.

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[For additional references see also Parts 1 and 2 of the current series (see Jagt, 1999a, b).]

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Plate 1

Figs. 1-2. *Ophiosmilax*? *alternatus* Kutscher & Jagt, sp. nov.
1: NHMM JJ 3679, lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Vijlen Member, base + 0-2 m.
2: NHMM MB 1044-9a, lateral arm plate, same locality, Gulpen Formation, base Zeven Wegen Member.

Figs. 3-4. *Asteronyx*? *spinulosa* Kutscher & Jagt, sp. nov.; NHMM MB 1239-23a/b, outer and inner surface of ?dorsal arm plates, Mamelis-Selzerbeek, Gulpen Formation, lower Vijlen Member.

Figs. 5-6. *Trichaster*? *ornatus* (Rasmussen, 1950)
5: NHMM MB 1044-9b, distal view of vertebra, CPL SA quarry, Haccourt (Liège), Gulpen Formation, base Zeven Wegen Member.
6: NHMM JJ 3165, oblique distal view of vertebra, same locality, Gulpen Formation, Vijlen Member, base + 2.15 m.

Figs. 7-10. *Trichaster*? sp.
7, 8: NHMM MB 1044-9c; lateral and distal views of vertebra, CPL SA quarry, Haccourt (Liège), Gulpen Formation, base Zeven Wegen Member.
9: NHMM JJ 10509, lateral view of vertebra, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).
10: NHMM JJ 9473, lateral view of vertebra, same locality, Gulpen Formation, Zeven Wegen Member, base sponge level + 1.5-2 m.

Scale bars equal 100 µm, except in figs. 5-6, where they represent 1 mm.

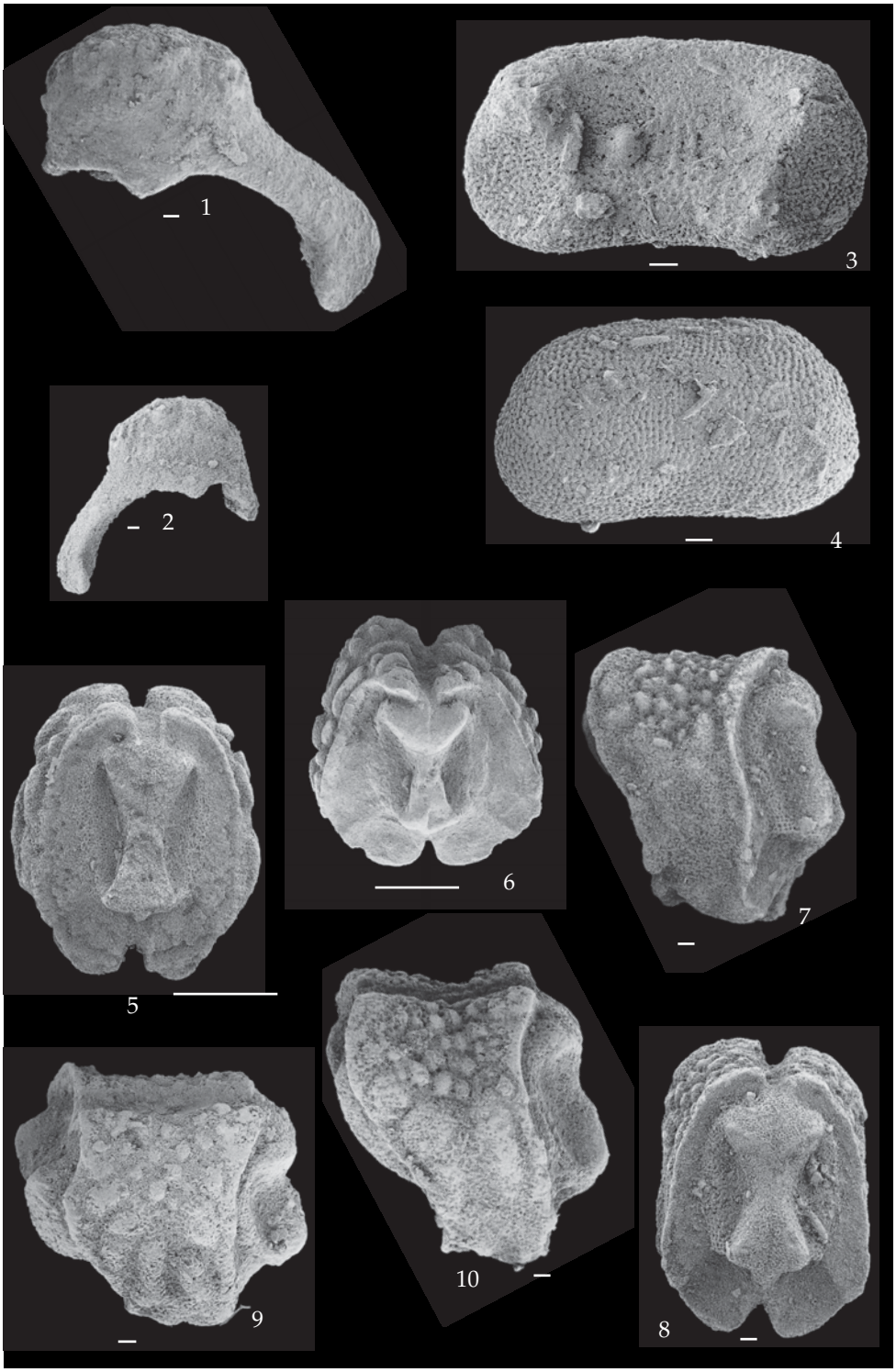
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Plate 2

Fig. 1. *Ophiomyxa*? *rhipidata* Kutscher & Jagt, sp. nov.; NHMM MB 1175, fan-shaped spine, Snouwenberg (Voerstreek), Gulpen Formation, Vijlen Member.

Figs. 2-3. *Ophioscolex*? *cretaceus* Kutscher & Jagt, sp. nov.
2: RGM 428 037 (ex Jagt Colln, no. 10600/12a), lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 3-4 m.
3: NHMM JJ 3700, lateral arm plate, CPL SA quarry, Hacccourt (Liège), Gulpen Formation, Vijlen Member, base + 0-2 m.

Fig. 4. *Ophiomyxa*? *jekerica* (Berry, 1938); NHMM MB 770-8a, dorsal view of vertebra, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.

Figs. 5-7, 10. *Ophiacantha*? *danica* Rasmussen, 1952
5-6: NHMM MB 619-2a, median/distal arm fragment, Benzenrade ('kapelletje'), Vaals Formation, Benzenrade Member.
7: NHMM K 3387, individual with one arm resting on column of the bourgueticrinid crinoid *Dunnicrinus aequalis* (d'Orbigny, 1841), ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, base Gronsveld Member.
10: NHMM MB 808-9a, distal arm fragment, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.

Figs. 8-9. *Ophiocoma*? *senonensis* (Valette, 1915); NHMM K 1707a, lateral and oblique dorsal view of arm fragment, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 2 m.

Fig. 11. *Stegophiura*? *hagenowi* (Rasmussen, 1950); NHMM K 2534, individual preserving portions of three arms, CBR-Lixhe quarry, Lixhe (Liège), Gulpen Formation, Zeven Wegen Member, top - c. 5 m.

Scale bars equal 100 µm, except in figs. 5-9 and 11, where they represent 1 mm.

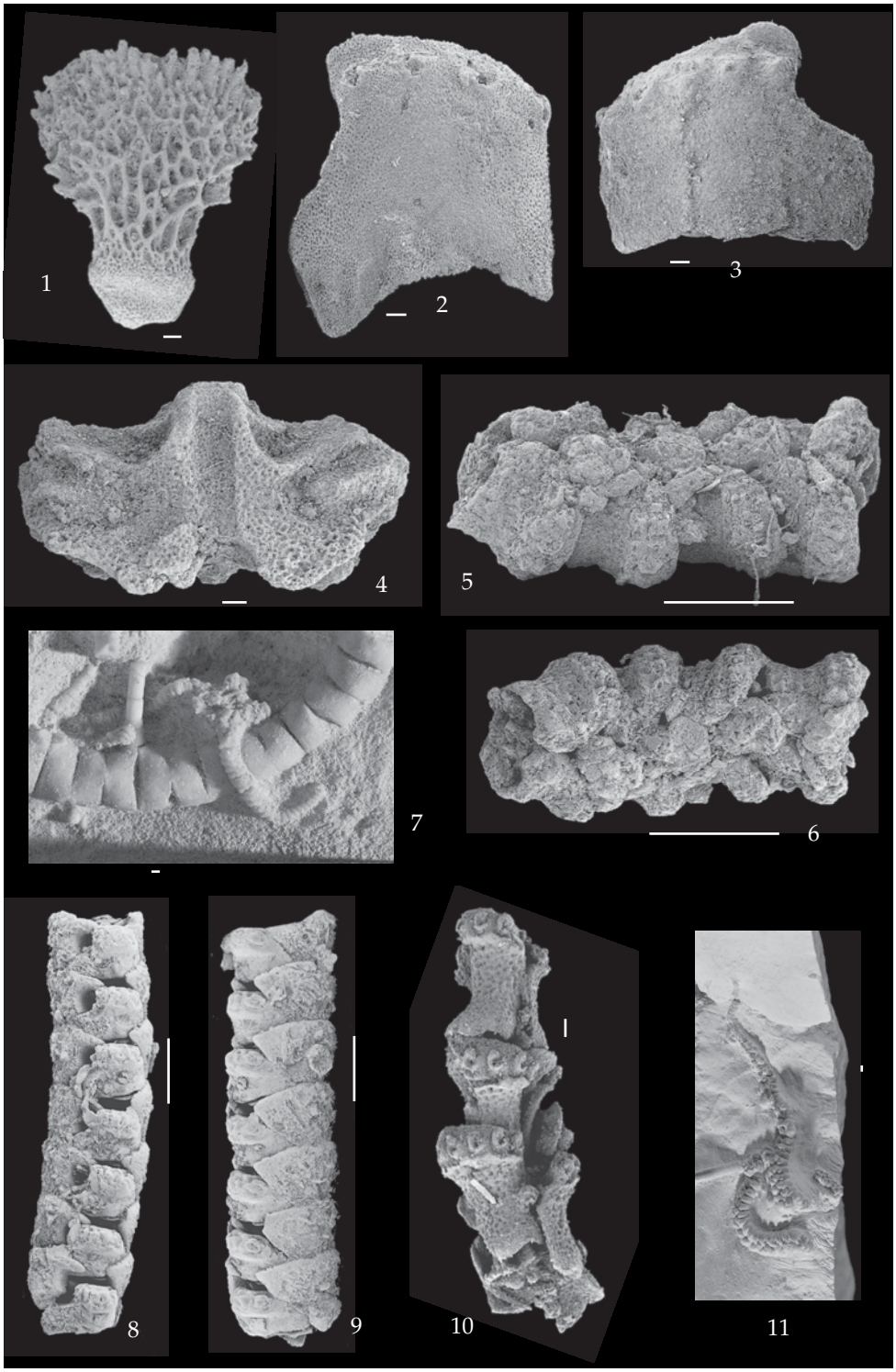
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Plate 3

Figs. 1-2. *Stegophiura*? *hagenowi* (Rasmussen, 1950); NHMM MB 761-6, lateral and oblique dorsal views of arm median arm segment, Heure-le-Romain (Liège), Gulpen Formation, Zeven Wegen Member, top - c. 8 m.

Figs. 3-9. *Stegophiura*? *trispinosa* Jagt & Kutscher, sp. nov.
3: NHMM MB 1044-9d (**paratype**), inner surface of lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, base Zeven Wegen Member.
4-5: NHMM JJ 10604a (**holotype**), oblique ventral view and outer surface of lateral arm plate, same locality and stratigraphy (base + c. 3.5 m).
6: NHMM MB 1044-9e (**paratype**), oblique ventral view of lateral arm plate, same locality and stratigraphy.
7: NHMM MB 1044-9f (**paratype**), outer surface of lateral arm plate, same locality and stratigraphy.
8: NHMM 1044-9g (**paratype**), inner surface of radial shield, same locality and stratigraphy.
9: NHMM JJ 10604b (**paratype**), outer surface of radial shield, same locality, Zeven Wegen Member, base + c. 3.5 m.

Figs. 10-11: *Ophiolepis*? *falsa* Jagt & Kutscher, sp. nov.; NHMM JJ 4989a/b (**paratypes**), lateral arm plates, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 9-10 m.

Scale bars equal 1 mm, except in figs. 6, 10-11, where they represent 100 μm.

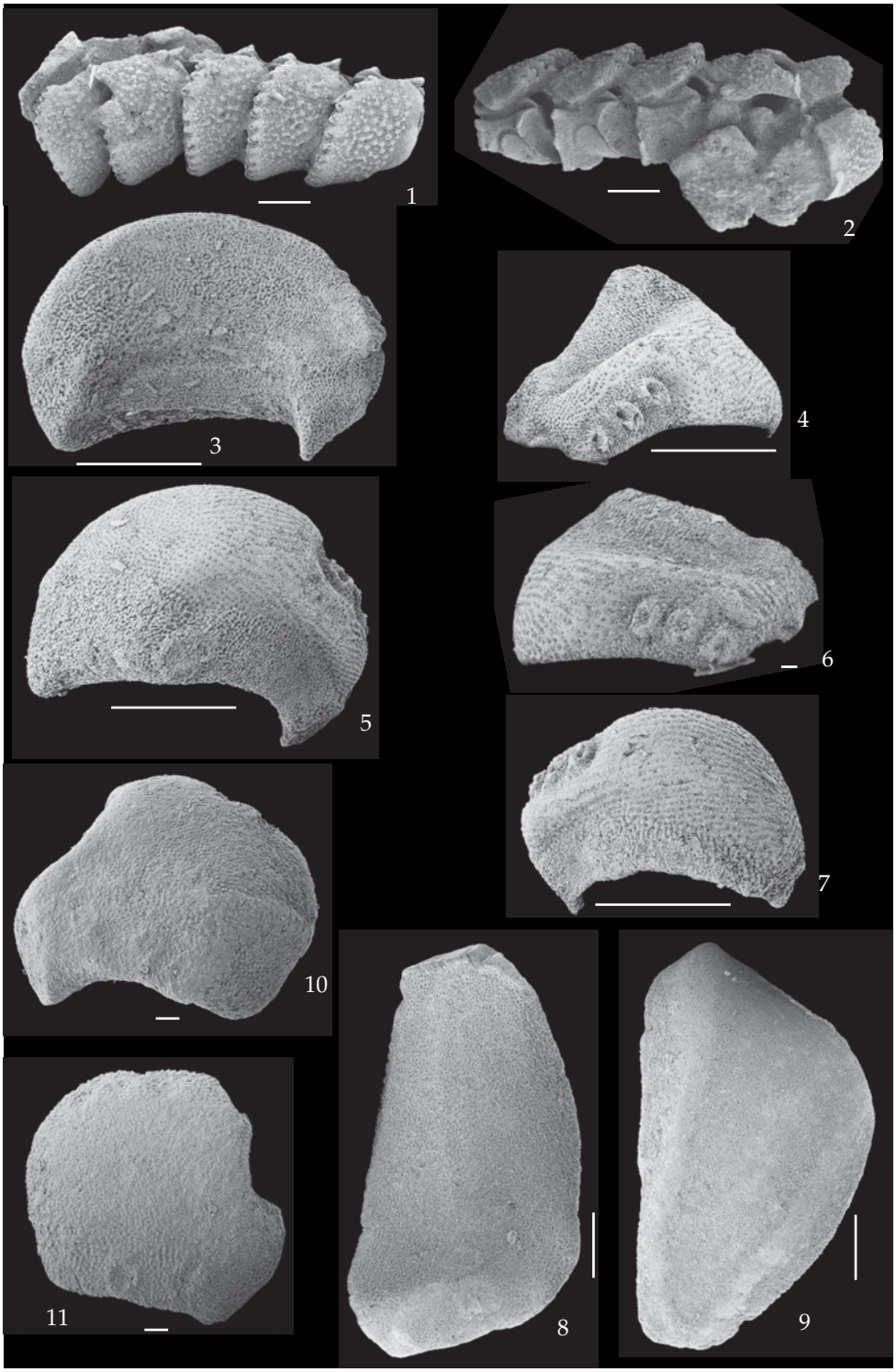
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Plate 4

Figs. 1-4. *Ophiolepis*? *falsa* Jagt & Kutscher, sp. nov.
1-2: NHMM MB 761-9a/b (**paratypes**), lateral arm plates, outer and inner surface, respectively, Heure-le-Romain (Liège), Gulpen Formation, Zeven Wegen Member, top - c. 8 m.
3-4: NHMM MB 761-9c/d (**paratypes**), lateral arm plates, proximal view and outer surface, respectively, same locality and stratigraphy.

Fig. 5. *Ophiomusium granulosum* (Roemer, 1840); NHMM MB 808-9b, portion of juvenile disc and proximal arms, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.

Figs. 6-10. *Ophiomusium lux* Jagt & Kutscher, sp. nov.
6: NHMM RD 77 (**paratype**), dorsal view of arm segment, outcrop southwest of Schunck quarry, Kunrade, Maastricht Formation, Kunrade Limestone facies.
7-8: NHMM RD 78 (**paratype**), ventral and oblique lateral views of arm segment, same locality and stratigraphy.
9: NHMM MB 655-1a, ventral view of arm segment, same locality and stratigraphy.
10: NHMM MB 487-4a (**paratype**), inner surface of radial shield, disused Ransdaal (Karstraat) quarry, Limburg, Maastricht Formation, Kunrade Limestone facies.

Scale bars equal 1 mm, except in figs. 1-4, where they represent 100 µm.


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Plate 5

Figs. 1-4, 7. *Ophiomusium lux* Jagt & Kutscher, sp. nov.
1-2: NHMM MD 3238 (**paratype**), ventral view of disc and close-up of proximal tentacle scales, respectively, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).
3-4: NHMM MD 3150 (**holotype**), oblique lateral and dorsal views of disc, respectively, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).
7: NHMM MB 655-1b (**paratype**), dorsal view of disc segment with proximal arm portion, outcrop southwest of Schunck quarry, Kunrade, Maastricht Formation, Kunrade Limestone facies.

Fig. 5. *Felderophiura vanderhami* Jagt, 1991; NHMM MD 3154, ventral view of fragmentary disc with proximal arm portion, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).

Fig. 6. *Ophiomusium granulosum* (Roemer, 1840); NHMM MD 3166, portion of disc preserving oral plates, proximalmost vertebrae, radial shields and genital scale, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, base Gronsveld Member.

Scale bars equal 1 mm.

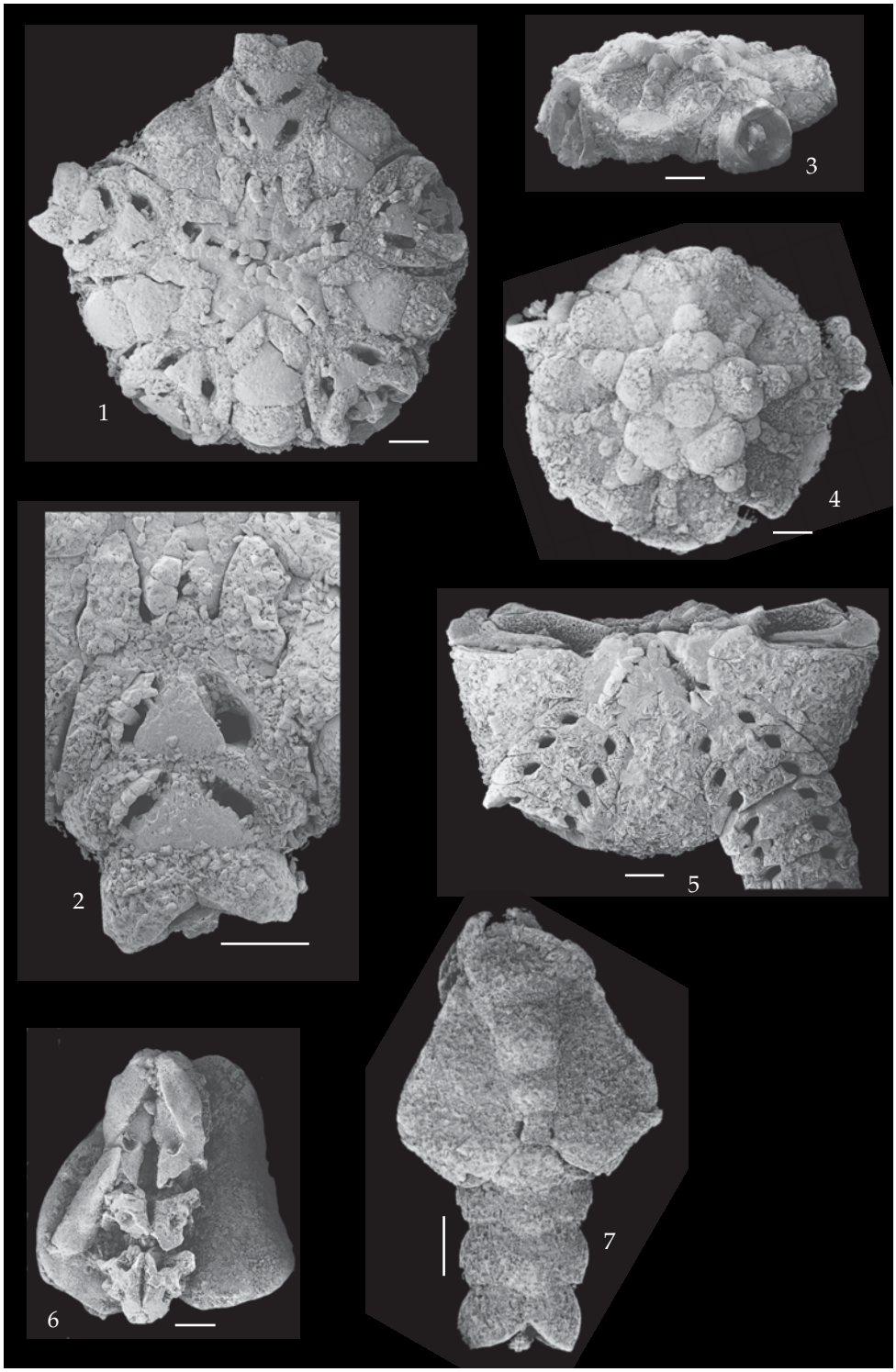
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Plate 6

Figs. 1-2. *Ophiocten*? *yvonnae* Jagt & Kutscher, sp. nov.; NHMM K 2278a (**holotype**), close-up of oral frame and ventral view of disc, respectively, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).

Figs. 3, 7. *Ophiomusium lux* Jagt & Kutscher, sp. nov.
3: NHMM MD 3238 (**paratype**), oblique lateral view of disc, same as Pl. 5, figs. 1-2.
7: NHMM MB 487-4b, lateral arm plate, disused Ransdaal (Karstraat) quarry, Limburg, Maastricht Formation, Kunrade Limestone facies.

Figs. 4-6, 8-9. *Felderophiura vanderhami* Jagt, 1991; all from CBR-Romontbos quarry, Eben Emael (Liège), Maastricht Formation, Emael Member (Lava Horizon).
4-5: RGM 428 040-041, outer surface of radial shields.
6: RGM 428 038, inner surface of radial shield.
8: RGM 428 039, outer surface of wedge-shaped ossicle associated with radial shield.
9: RGM 428 042, as Fig. 8, but inner surface.

Scale bars equal 1 mm, except in figs. 7-9, where they represent 100 µm.

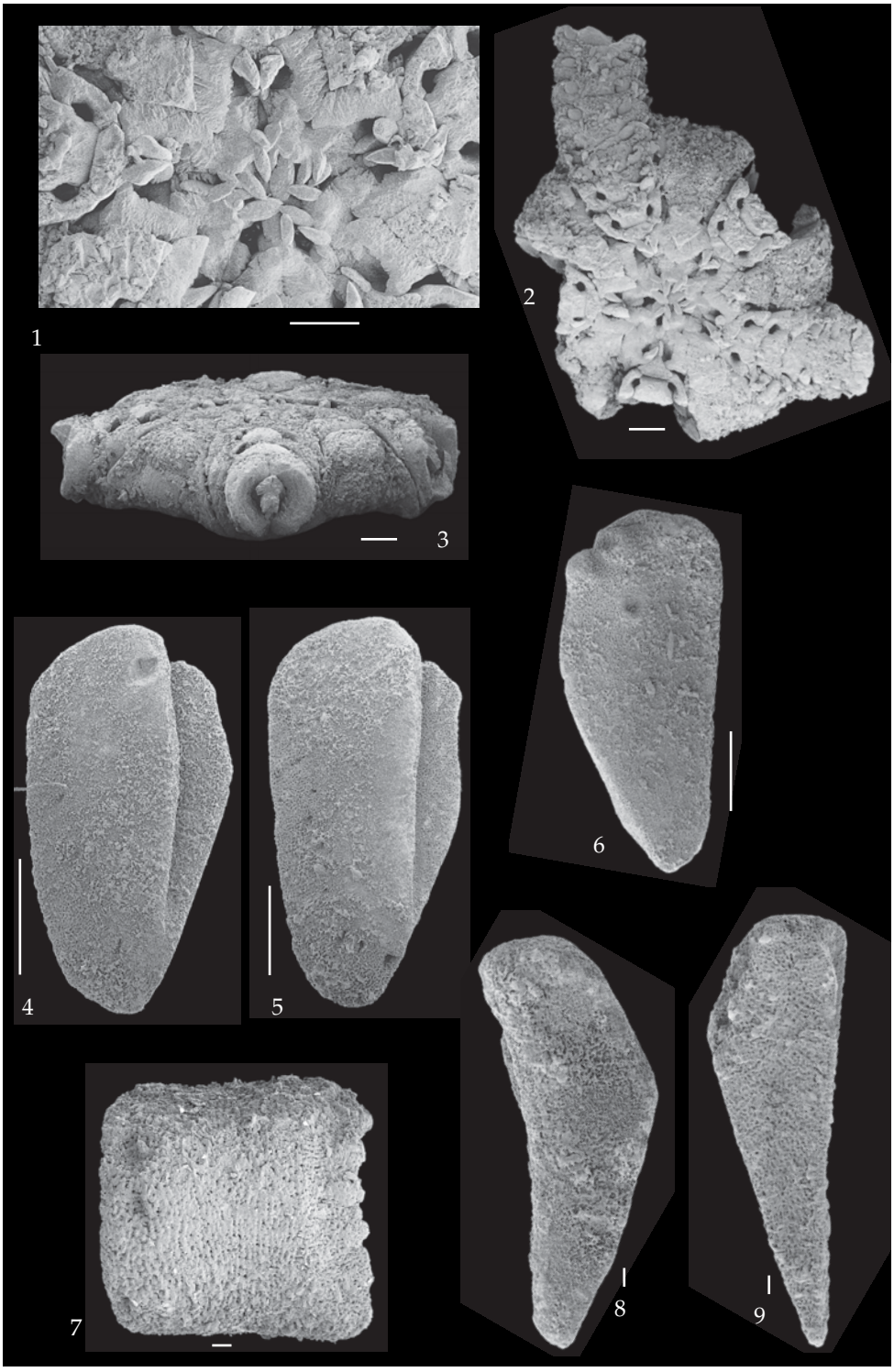
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Plate 7

Figs. 1-3. *Felderophiura vanderhami* Jagt, 1991
1-2: NHMM K 3024, individual apparently preserved in situ (? feeding position), ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).
3: RGM 428 043, inner surface of lateral arm plate, CBR-Romontbos quarry, Eben Emael (Liège), Maastricht Formation, Emael Member (Lava Horizon).

Figs. 4-5. *Ophiotitanos serrata* (Roemer, 1840)?; NHMM MB 432.GGGa/b, proximal and distal views of vertebrae, respectively, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, uppermost Geulhem Member.

Figs. 6-12. *Ophioplinthaca*? *fuerstenbergii* (J. Müller, 1847)
6: NHMM MB 661-5, disc, temporary outcrop at Vaals-Eschberg, Vaals Formation.
7, 11: IRScNB IST 10756b (Ubaghs Colln), oblique lateral view of arm segment preserving spines, Vaals area, Vaals Formation.
8: IRScNB IST 10758 (Ubaghs Colln), oblique lateral view of arm segment preserving spines, same locality and stratigraphy.
9-10: IRScNB IST 10759 (Ubaghs Colln), dorsal and oblique lateral views of arm fragment preserving spines, same locality and stratigraphy.
12: NHMM MB 661-4b, median arm segment, temporary outcrop at Vaals-Eschberg, Vaals Formation.

Fig. 13. *Ophioplinthaca*? *fuerstenbergii* (J. Müller, 1847)?; NHMM 865-25, dorsal view of arm segment preserving spines, de Wingerd quarry, Vaals Formation, Benzenrade Member.

Scale bars equal 1 mm, except in figs. 3-5, where they represent 100 μm.

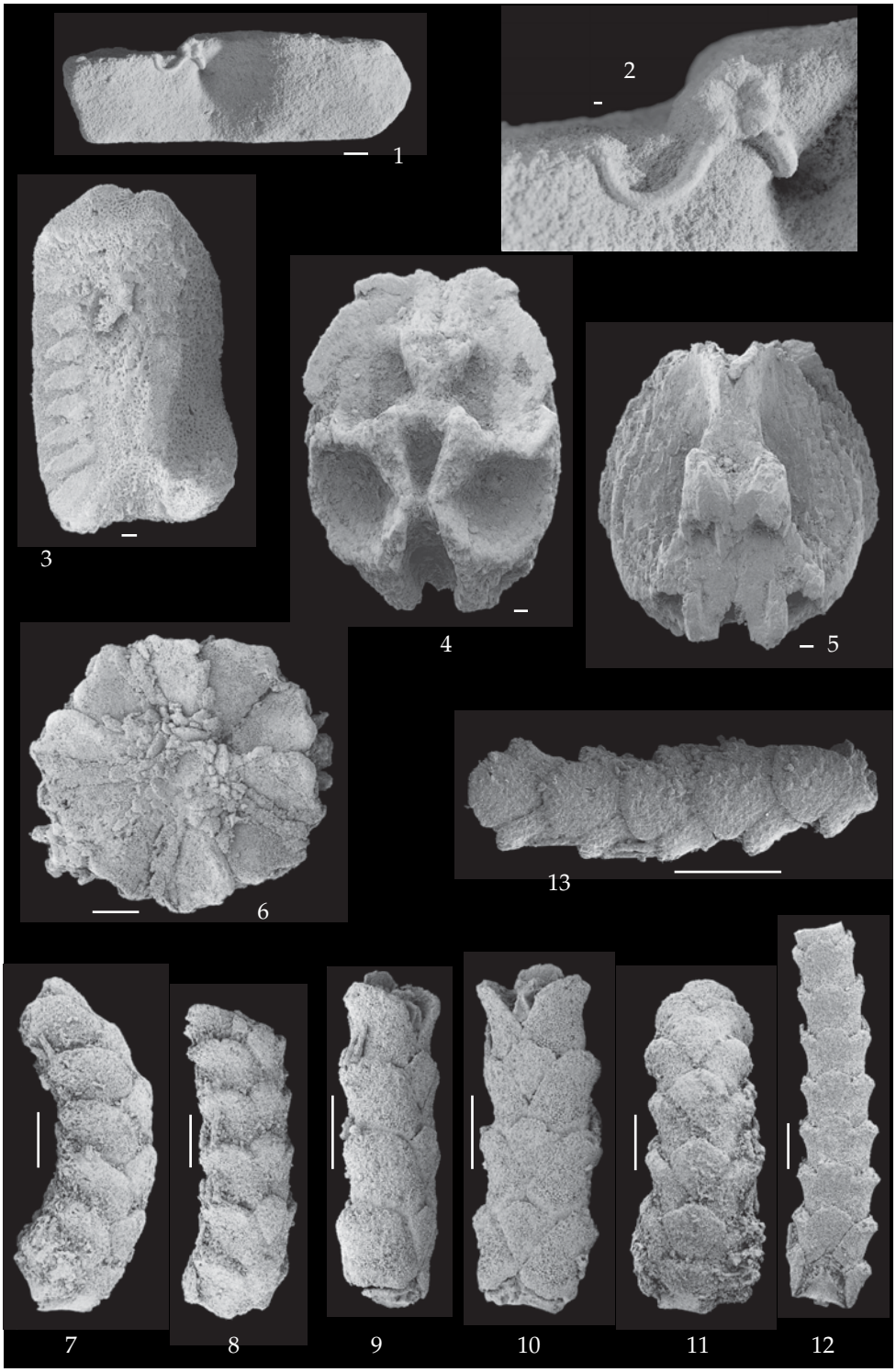
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Plate 8

Figs. 1-2. ?Ophiacanthidae indet.; NHMM MB 865-15a, ventral and lateral views of arm segment preserving spines, de Wingerd quarry, Vaals Formation, Benzenrade Member.

Figs. 3-4. *Ophiotitanos serrata* (Roemer, 1840); NHMM MB 661-4c, ventral and lateral views of arm segment preserving spines, temporary outcrop at Vaals-Eschberg, Vaals Formation.

Figs. 5-6. *Deckersamphiura* sp. (? nov.)
5: NHMM MB 865-15b, oral frame and portions of disc, de Wingerd quarry, Vaals Formation, Benzenrade Member.
6: NHMM MB 865-16, dorsal view of disc, same locality and stratigraphy.

Figs. 7-11. *Deckersamphiura inusitata* Jagt & Kutscher, gen. et sp. nov.
7: NHMM MB 377-27 (**paratype**), juvenile disc with proximal arm portion, Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (base IVf-3).
8-11: NHMM MD 3061 (**paratype**), disc preserving proximal arm portion and dorsal and lateral views of arm fragment preserving spines, respectively, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).

Scale bars equal 1 mm, except in fig. 6, where it represents 100 µm.

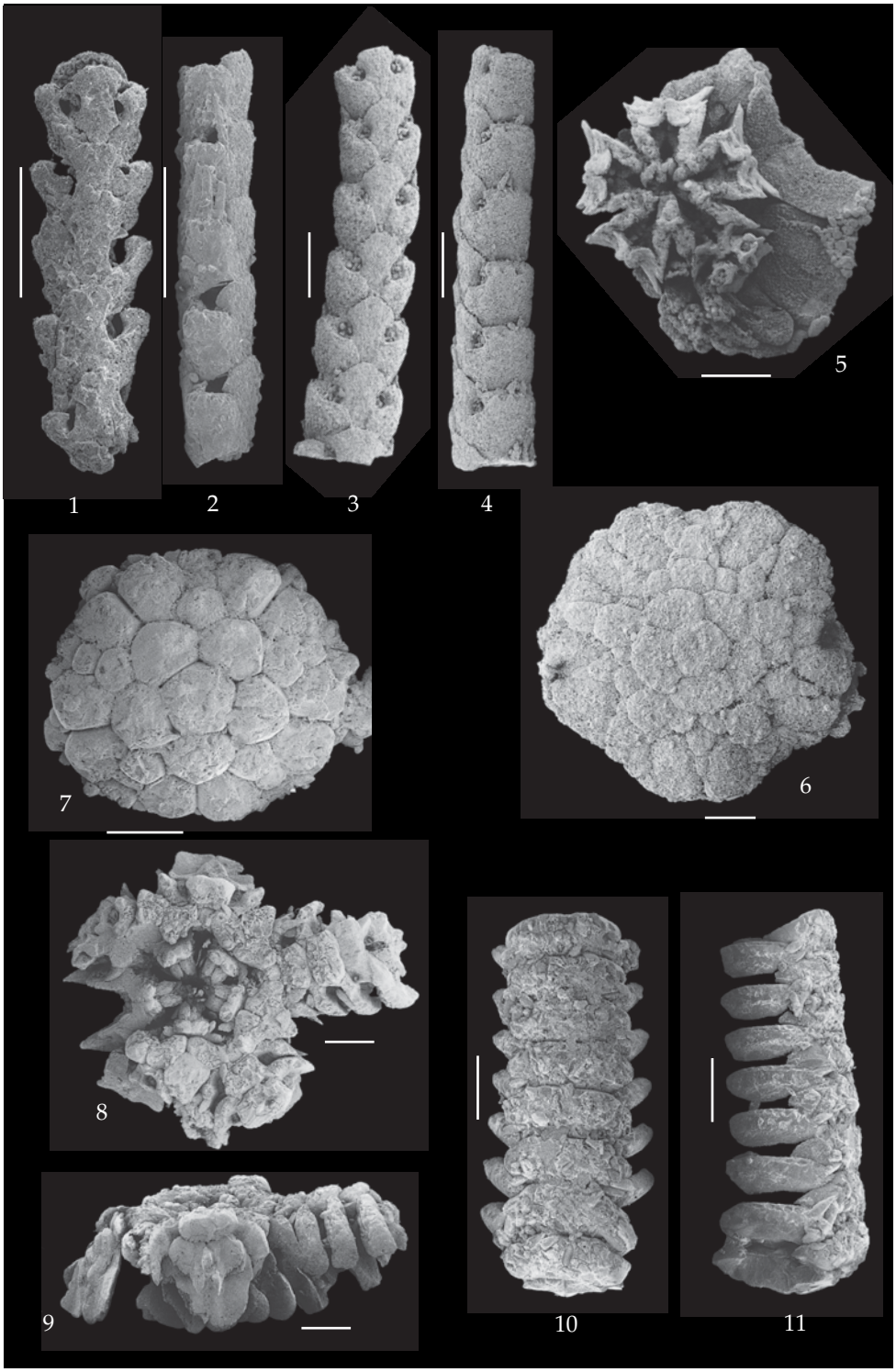
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Plate 9

Fig. 1. *Ophiothrix*? *bongaertsi* Kutscher & Jagt, sp. nov.?; NHMM MB 619-2b, arm fragment preserving disc plates(?), Benzenrade ('kapelletje'), Vaals Formation, Benzenrade Member.

Figs. 2-4, 6. *Deckersamphiura* sp. (? nov.).
2-3: NHMM 865-19, dorsal and oblique lateral views of arm segment, de Wingerd quarry, Vaals Formation, Benzenrade Member.
4: NHMM MB 865-15c, portion of disc, same locality and stratigraphy.
6: NHMM MB 865-15d, portion of oral frame preserving teeth in situ, same locality and stratigraphy.

Fig. 5. *Ophiomusium lux* Jagt & Kutscher, sp. nov.; NHMM MD 3148, portion of disc preserving oral plates, proximal vertebrae and genital plate/scale, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).

Figs. 7-9: *Deckersamphiura inusitata* Jagt & Kutscher, gen. et sp. nov.; NHMM RD 155 (**holotype**), dorsal, ventral and lateral views of portions of disc, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).

Scale bars equal 1 mm.

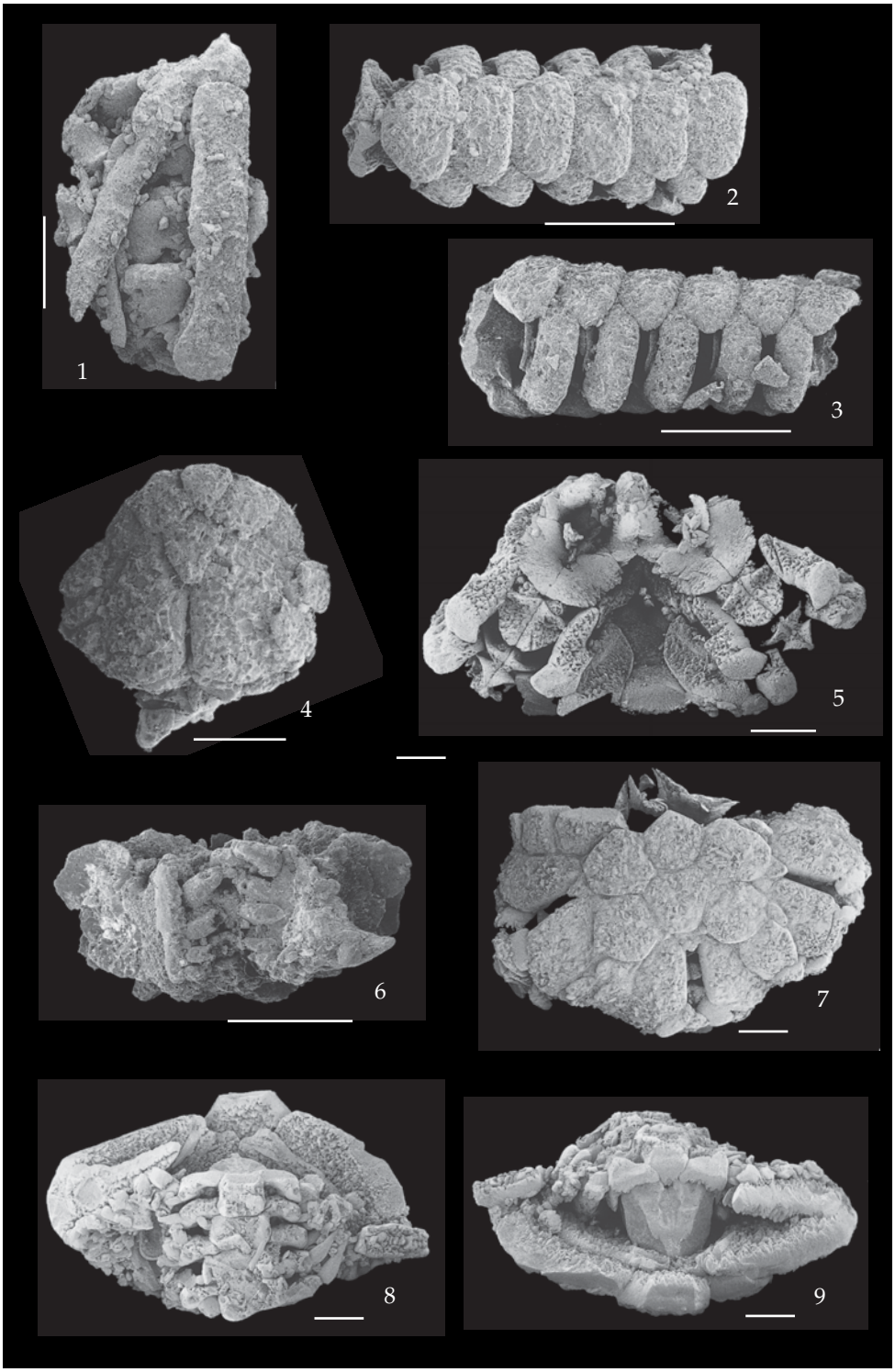
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Plate 10

Figs. 1-8, 9-10?. *Mesophiomusium decipiens* Jagt & Kutscher, sp. nov.
1, 4: NHMM MB 734-12a (**holotype**), outer surface and ventral views of lateral arm plate, respectively, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 1.5-2 m.
2: NHMM MB 734-12b (**paratype**), inner surface of lateral arm plate, same locality and stratigraphy.
3, 5: NHMM MB 734-12c (**paratype**), dorsal view and outer surface of lateral arm plate, respectively, same locality and stratigraphy.
6: NHMM MB 734-12d (**paratype**), outer surface of lateral arm plate, same locality and stratigraphy.
7-8: NHMM JJ 4436 (**paratype**), ventral and oblique lateral views of arm segment preserving tentacle scales, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 2-4 m.
9-10. NHMM JJ 4452a/b, outer and inner surface of radial shields, respectively, same locality and stratigraphy.

Fig. 11. *Amphiura*? *plana* Kutscher & Jagt, sp. nov.; NHMM MB 284-7, portion of arm preserving vertebra, lateral arm plates and spines, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Lixhe 1 Member, top - 3 m.

Scale bars equal 100 µm, except in figs. 7-10, where they represent 1 mm.

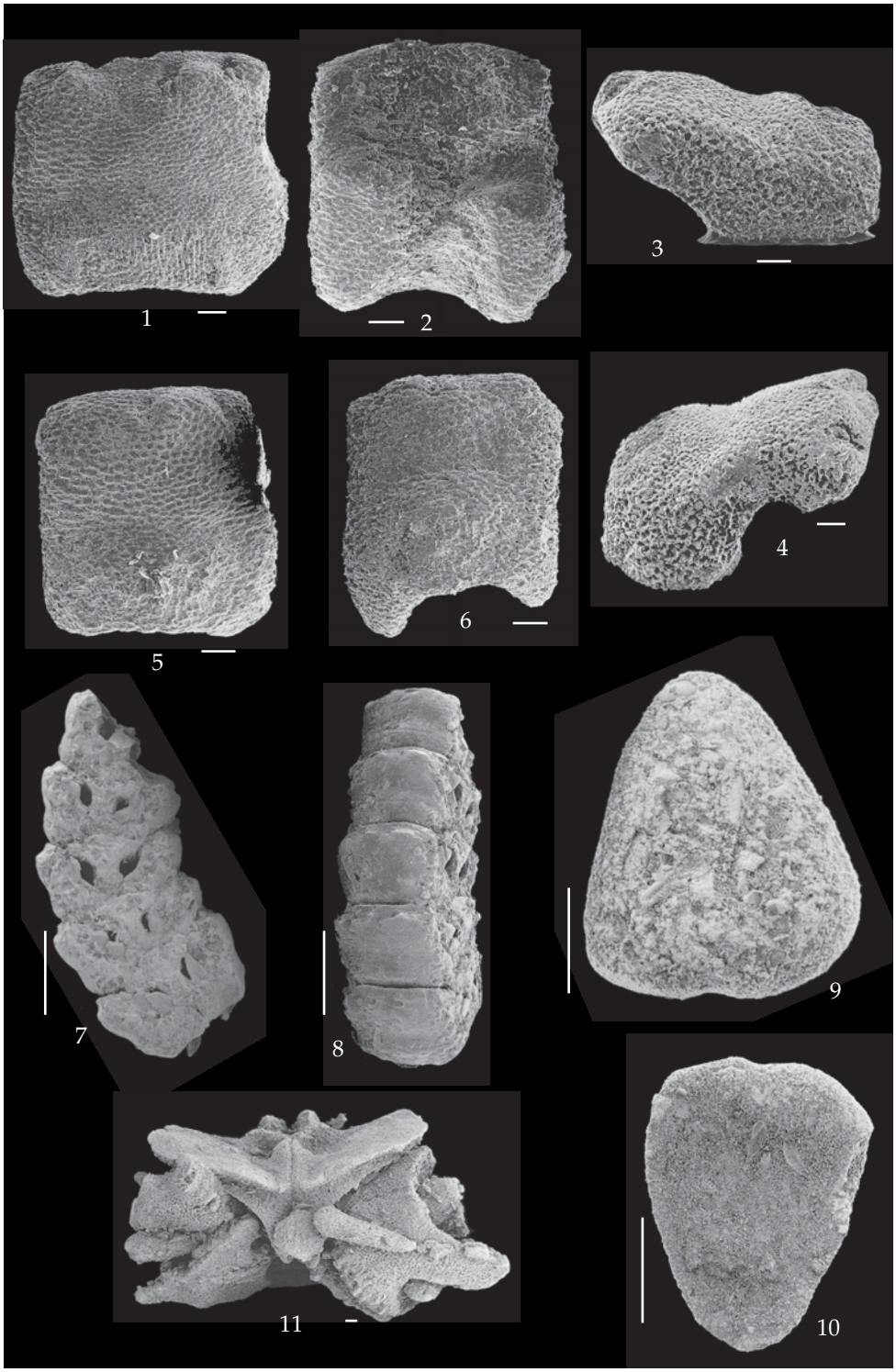
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Plate 11

Fig. 1. *Amphiura*? *plana* Kutscher & Jagt, sp. nov.; NHMM JJ 10600/12b, lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 3-4 m.

Figs. 2-5. *Ophiothrix*? *bongaertsi* Kutscher & Jagt, sp. nov.
2: NHMM MB 619-2c, lateral view of arm segment, Benzenrade ('kapelletje'), Vaals Formation, Benzenrade Member.
3: NHMM MB 619-2d, arm fragment preserving lateral and ventral arm plates, vertebrae and spines, same locality and stratigraphy.
4: NHMM MB 770-2, portion of arm preserving lateral arm plates and vertebrae, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.
5: NHMM MB 1044-9h, lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, base Zeven Wegen Member.

Fig. 6. *Ophiactis*? *sulcata* Kutscher & Jagt, sp. nov.?; NHMM JJ 10600/12d, median lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 3-4 m (specimen inadvertently destroyed).

Fig. 7. *Ophioplinthaca*? *fuerstenbergii* (J. Müller, 1847)?; NHMM MB 784-3, lateral arm plate, Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (IVf-6/7).

Figs. 8?, 9-10. *Ophiocoma*? *senonensis* (Valette, 1915); RGM 428 044 (ex Jagt Colln, no. 2481b), lateral arm plates, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, base Geulhem Member.

Fig. 11. *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.; NHMM JJ 10600/12c, proximal lateral arm plate, same locality and stratigraphy (specimen inadvertently destroyed).

Scale bars equal 100 µm, except in figs. 2-3 and 5, where they represent 1 mm.

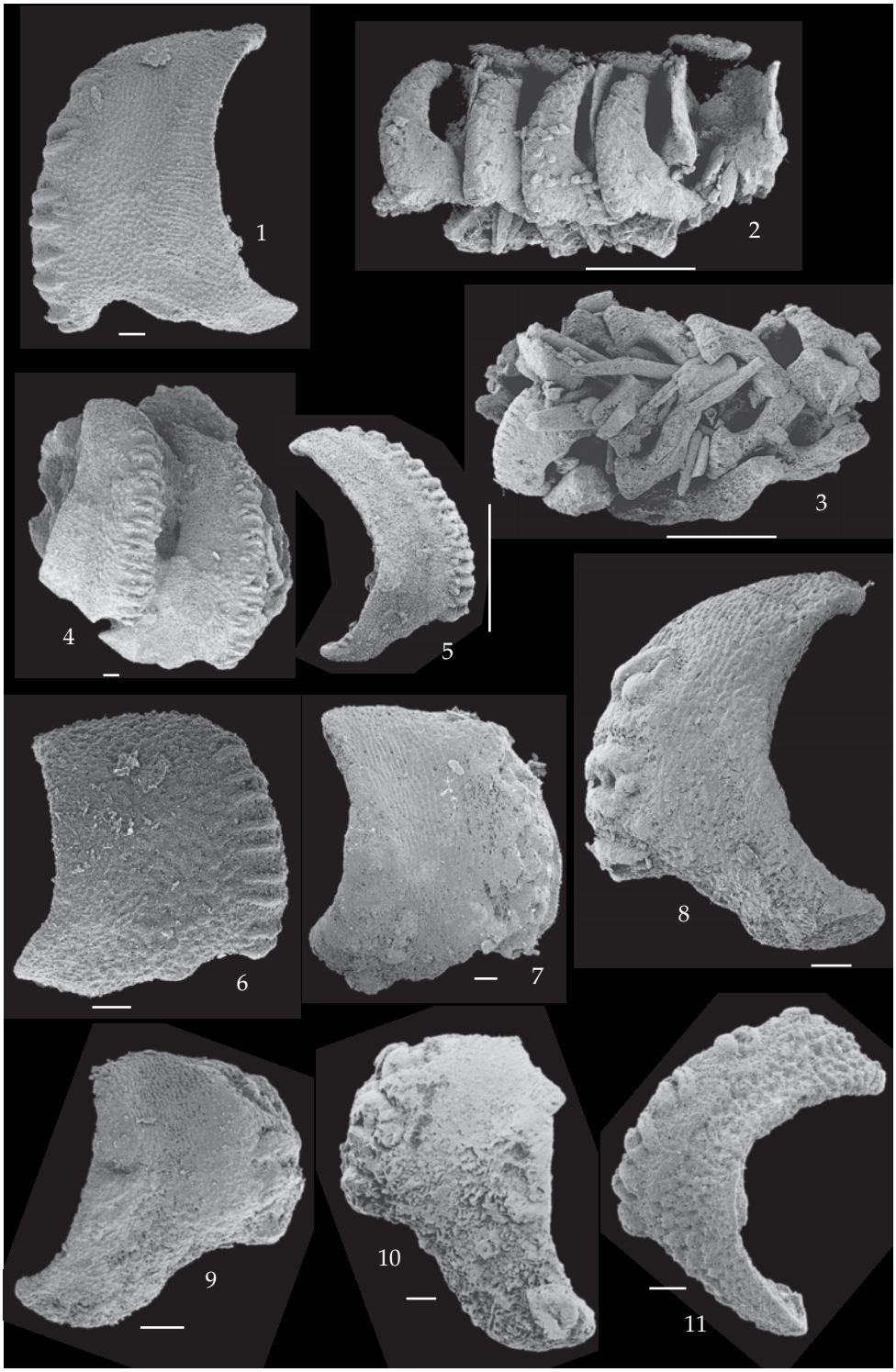
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Plate 12

Figs. 1-2. *Ophiocoma*? *radiatum* Kutscher & Jagt, sp. nov.; NHMM MB 808-9c, ventral and lateral views of arm segment, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.

Fig. 3. *Stegophiura*? *hagenowi* (Rasmussen, 1950); NHMM MB 1044-9i, outer surface of radial shield, CPL SA quarry, Haccourt (Liège), Gulpen Formation, base Zeven Wegen Member.

Figs. 4-5. *Ophioderma*? *substriatum* (Rasmussen, 1950); RGM 428 045 (ex Jagt Colln, no. 3914), outer surface and oblique proximal view of lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Lanaye Member (6/7).

Figs. 6-9. *Ophiothrix*? *bongaertsi* Kutscher & Jagt, sp. nov.
6-7: IRScNB IST 10760a (Ubaghs Colln), dorsal and lateral views of arm segment preserving spines, Vaals area, Vaals Formation.
8-9: IRScNB IST 10760b (Ubaghs Colln), dorsal and lateral views of arm segment preserving spines, same locality and stratigraphy.

Figs. 10-12. *Ophiarachna*? *martinblomi* Jagt & Kutscher, sp. nov.
10: NHMM MB 108-10b (**paratype**), inner surface of lateral arm plate, Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (IVf-6/7).
11-12: NHMM MB 108-10a (**holotype**), outer surface and proximal view of lateral arm plate, same locality and stratigraphy.

Scale bars equal 1 mm.

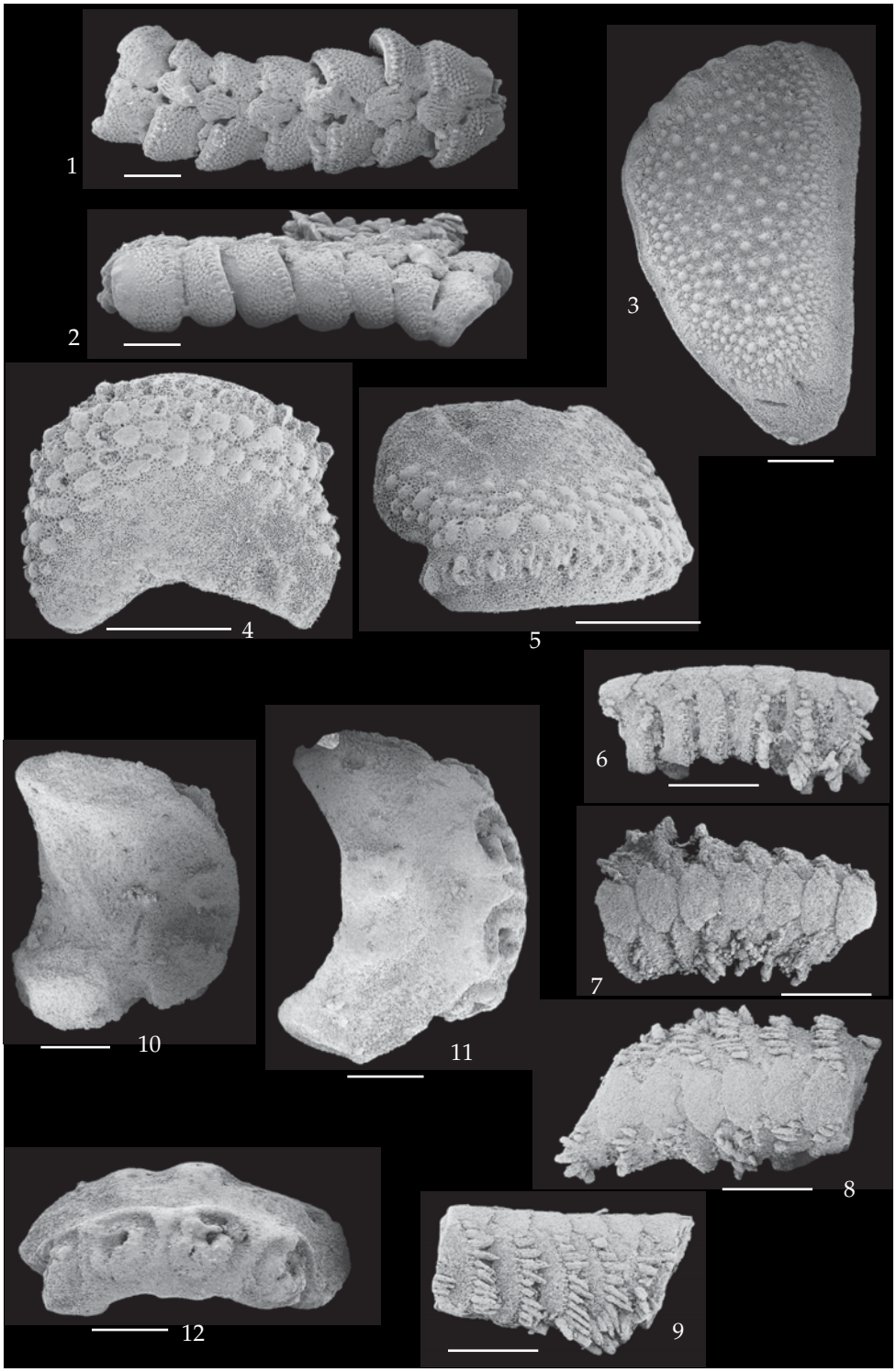
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Plate 13

Fig. 1: *Ophiothrix*? *rugosa* Kutscher & Jagt, sp. nov.; NHMM JJ 10600/12e, lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 3-4 m.

Figs. 2-3. *Ophiacantha*? *striata* Kutscher & Jagt, sp. nov.
2: NHMM MB 387-10a, lateral arm plate, temporary outcrop Hans-Böckler-Allee (Aachen), Gulpen Formation, Vijlen Member.
3: NHMM JJ 2479, lateral arm plate, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, base Geulhem Member.

Fig. 4. *Ophiomusium biconcavum* Kutscher & Jagt, sp. nov.; NHMM JJ 10600/12g, outer surface of lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 3-4 m.

Fig. 5. *Ophiomusium granulosum* (Roemer, 1840); NHMM JJ 10600/12f, outer surface of lateral arm plate, same locality and stratigraphy.

Figs. 6-7. *Ophiomusium sinuatum* Kutscher & Jagt, sp. nov.?; NHMM MB 808-9d, outer surface and lateral view of lateral arm plate, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.

Figs. 8-9. *Ophiolepis*? *granulata* Kutscher & Jagt, sp. nov.
8: NHMM MB 808-9f, arm fragment preserving lateral and dorsal arm plates, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + c. 6-7 m.
9: NHMM MB 808-9e, outer surface of lateral arm plate, same locality and stratigraphy.

Fig. 10. *Ophiomusium biconcavum* Kutscher & Jagt, sp. nov.?; NHMM MB 387-10b, outer surface of lateral arm plate, temporary outcrop Hans-Böckler-Allee (Aachen), Gulpen Formation, Vijlen Member.

Scale bars equal 100 µm, except in fig. 8, where it represents 1 mm.

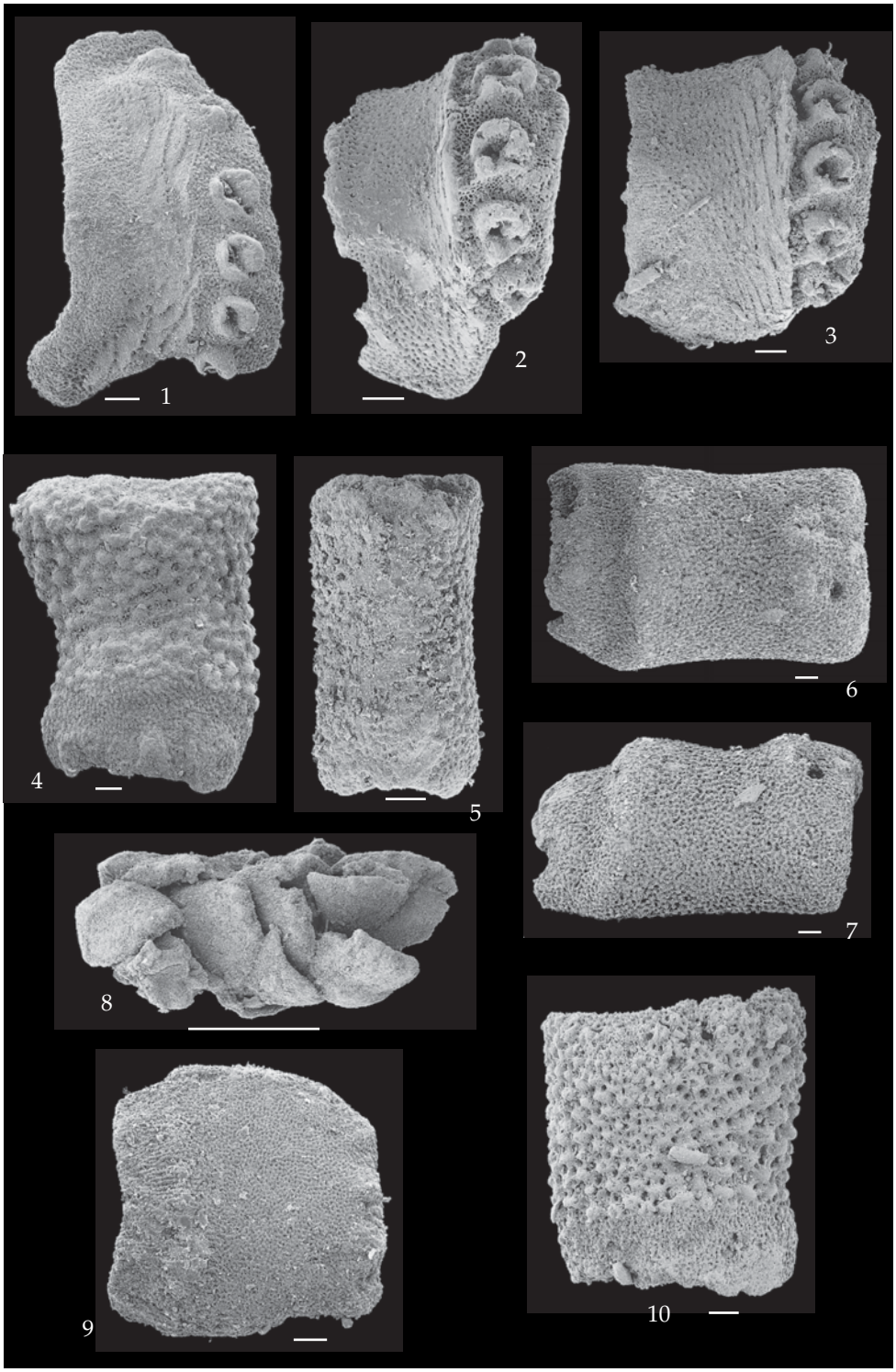
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Plate 14

Figs. 1-11. *Ophiomusium granulosum* (Roemer, 1840)
1-2, 11: RGM 428 047-049 (ex Jagt Colln, no. 2455), outer surface of lateral arm plates, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 3-4 m.
3: RGM 428 046 (ex Jagt Colln, no. 2455), outer surface of radial shield, same locality and stratigraphy.
4-5: NHMM JJ 2719, dorsal and lateral views of proximal arm segment, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Zeven Wegen Member, base + 1.8 m.
6: NHMM MB 387-10c, outer surface of lateral arm plate, temporary outcrop Hans-Böckler-Allee (Aachen), Gulpen Formation, Vijlen Member.
7: NHMM MB 542-8, outer surface of lateral arm plate, CBR-Romontbos quarry, Eben Emael (Liège), Maastricht Formation, Emael Member (Lava Horizon); 10: NHMM JJ 9577, outer surface of lateral arm plate, same locality and stratigraphy.
8-9: NHMM RD 160, dorsal and lateral views of arm segment preserving spines, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, base Gronsveld Member.

Scale bars equal 1 mm, except in figs. 2 and 11, where they represent 100 µm.


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Plate 15

Figs. 1-4, 7-8. *Ophiomusium granulosum* (Roemer, 1840)
1-2: NHMM K 3385, ventral view of nearly complete individual, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, base Gronsveld Member.
3-4: RGM 428 050 (ex Jagt Colln, no. 3615), dorsal and lateral views of arm segment, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Vijlen Member, base + c. 2 m.
7: RGM 428 051 (ex Jagt Colln, no. 9577), outer surface of lateral arm plate, CBR-Romontbos quarry, Eben Emael (Liège), Maastricht Formation, Emael Member (Lava Horizon).
8: NHMM MB 619-3, outer surface of lateral arm plate, Benzenrade ('kapelletje'), Vaals Formation, Benzenrade Member.

Fig. 5. *Ophiomusium sentum* Kutscher & Jagt, sp. nov.?; NHMM MB 1044-9j, CPL SA quarry, Haccourt (Liège), Gulpen Formation, base Zeven Wegen Member.

Fig. 6. *Ophiomusium lux* Jagt & Kutscher, sp. nov.; NHMM JJ 3872, outer surface of lateral arm plate, temporary Albertkanaal sections, Vroenhoven-Riemst, Maastricht Formation, Meerssen Member (IVf-6).

Figs. 9-12. *Ophiotitanos serrata* (Roemer, 1840)
9-10: NHMM MB 867-6b, lateral and dorsal views of arm segment preserving spines, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Vijlen Member, top - c. 4 m.
11: RGM 428 052 (ex Jagt Colln, no. 5952), lateral view of arm fragment preserving spines, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Vijlen Member, base + 5-7 m.
12: NHMM 1998032 (ex van der Ham Colln, no. 285), dorsal view of arm segment, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, upper Geulhem Member.

Scale bars equal 1 mm, except in figs. 6 and 8, where they represent 100 µm.

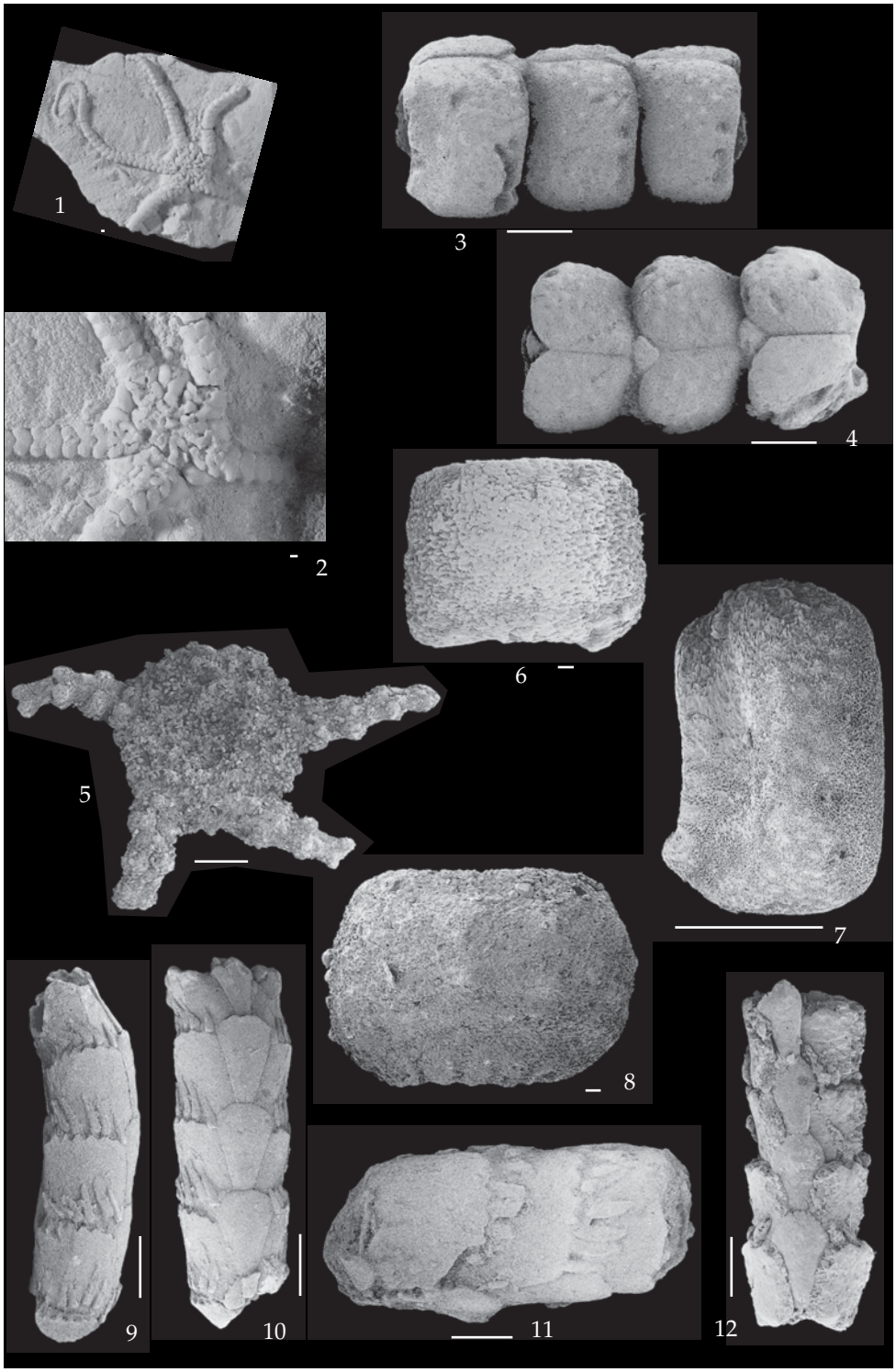
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Plate 16

Figs. 1-3. *Ophiotitanos serrata* (Roemer, 1840)
1-2: NHMM MB 108-10c, outer surface and proximal view of lateral arm plate, Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (IVf-6/7).
3: NHMM MB 432.GGGc, inner surface of lateral arm plate, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, upper Geulhem Member.

Figs. 4-8. *Ophiocten*? *yvonnae* Jagt & Kutscher, sp. nov.
4: NHMM K 2278 (**paratype**), dorsal view of disc, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).
5-6: NHMM K 979 (**paratype**), dorsal and lateral view of disc, Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (base IVf-3).
7-8: NHMM YC 1313 (**paratype**), near-complete individual with one arm regenerating, ENCI-Maastricht BV quarry, Maastricht, Maastricht Formation, Meerssen Member (IVf-4).

Figs. 9-10. Indeterminate radial shield
9: NHMM MB 414-3b, outer surface, field east of Kunderberg quarry, Kunrade, Maastricht Formation, Kunrade Limestone facies.
10: NHMM MB 1299-16, outer surface, Geulhemmerberg section, Geulhem, Maastricht Formation, Meerssen Member, Berg en Terblijt Horizon + c. 1.5 m.

Scale bars equal 1 mm.

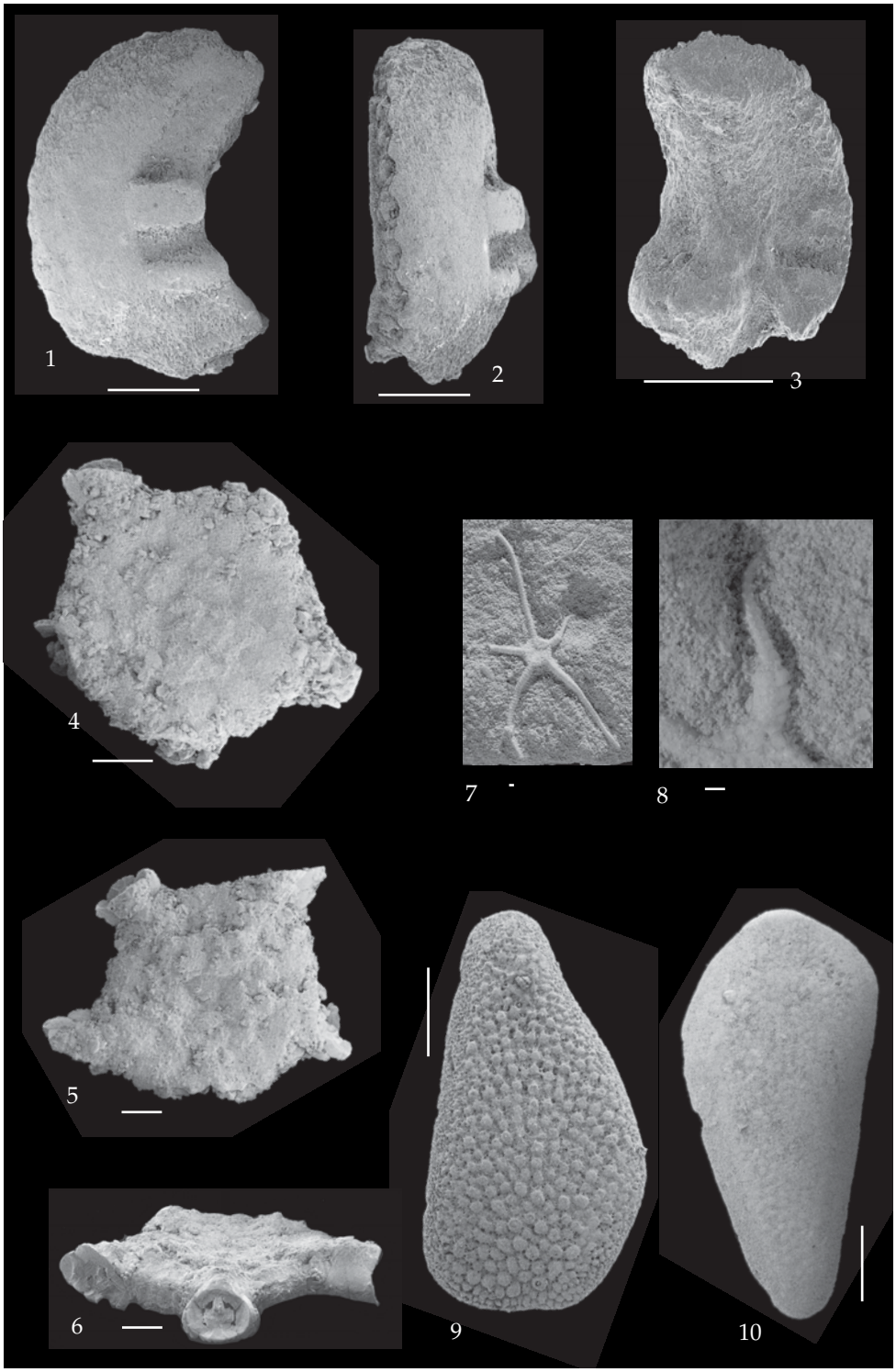
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Plate 17

Fig. 1. Indeterminate radial shield, NHMM JJ 4437, inner surface, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 2-4 m.

Figs. 2-3. *Ophiotitanos serrata* (Roemer, 1840)?
2: NHMM JJ 3687, outer surface of radial shield, CPL SA quarry, Haccourt (Liège), Gulpen Formation, Vijlen Member, base + 0-2 m.
3: NHMM MB 414-3d, outer surface of lateral arm plate, same locality and stratigraphy as figs. 4-5.

Figs. 4-5. *Ophiolepis*? *linea* Kutscher & Jagt, sp. nov.?; NHMM MB 414-3c/e, outer surface of lateral arm plates, field east of Kunderberg quarry, Kunrade, Maastricht Formation, Kunrade Limestone facies.

Fig. 6. *Ophioscolex*? *clivulus* Kutscher & Jagt, sp. nov.; NHMM MB 387-10d, outer surface of lateral arm plate, temporary outcrop Hans-Böckler-Allee (Aachen), Gulpen Formation, Vijlen Member.

Figs. 7-8. *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.?; NHMM MB 414-3f/g; outer surface of lateral arm plates, locality and stratigraphy as figs. 3-5.

Fig. 9. *Ophiomyxa*? *jekerica* (Berry, 1938); NHMM MB 104b, proximal view, de Schenk subterranean quarry, Geulhem, Maastricht Formation, base Meerssen Member.

Fig. 10. Berry's (1938) lateral arm plate N (*Asteronyx valkenburgensis* Berry, 1938), here assigned to *Ophiocoma*? *senonensis* (Valette, 1915)?, outer surface of lateral arm plate (see also Pl. 18).

Scale bars equal 100 µm, except in figs. 1-2 and 9, where they represent 1 mm.

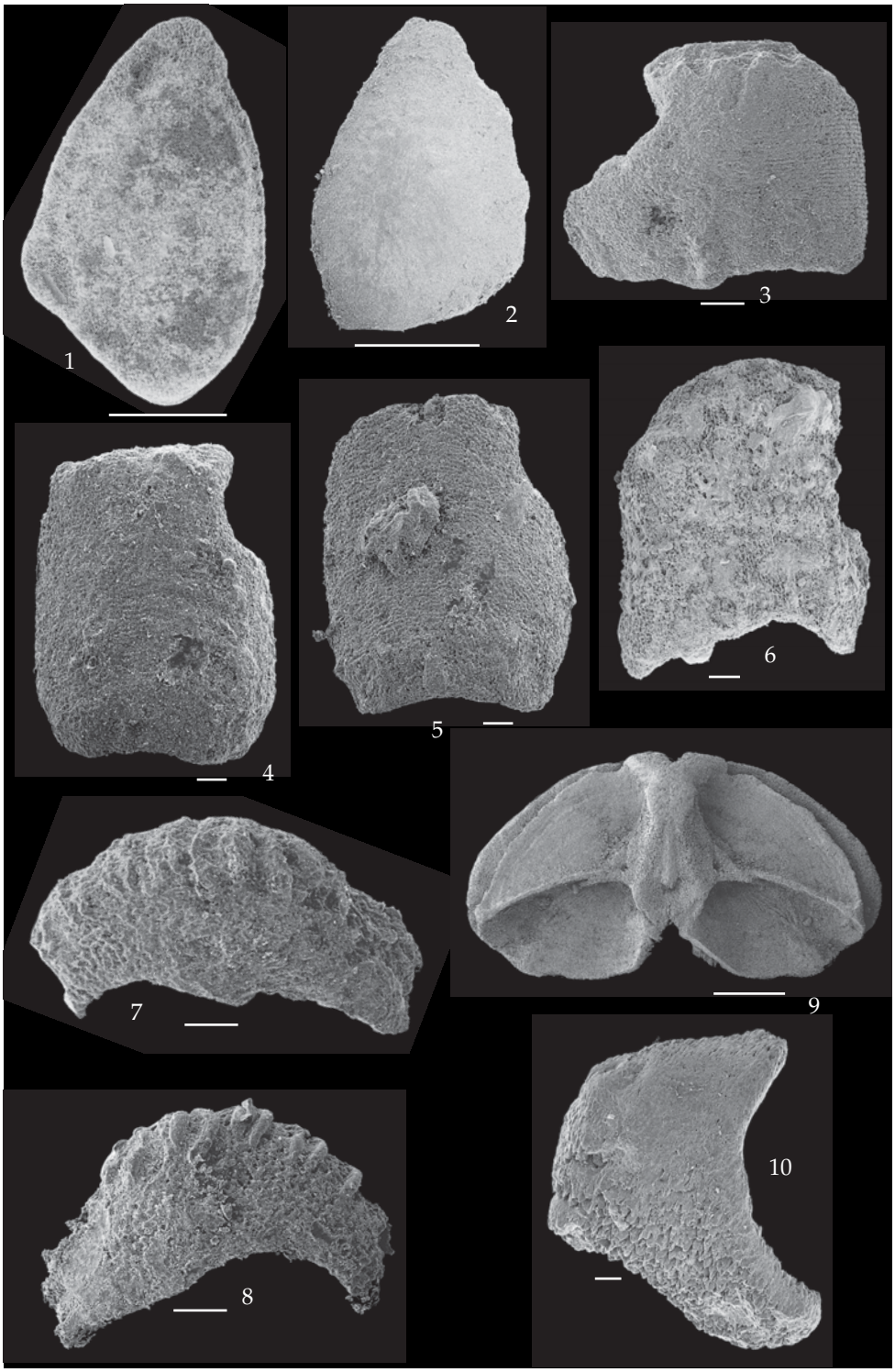
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Plate 18

All specimens from the Bonnema Colln (Rijksuniversiteit Groningen), studied and labelled by Berry and returned to Groningen. All material from Maastricht Formation, as exposed at various localities in southern Limburg (The Netherlands).

Figs. 1-2. Lateral arm plates reminiscent of Berry's (1938) lateral arm plate N, here referred with a query to *Felderophiura vanderhami* Jagt, 1991 (fig. 1) and *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.? (fig. 2), outer surface of lateral arm plates.

Fig. 3. Berry's (1938) vertebral ossicle D (*Dolichoarthra belemnica* Berry, 1938), ventral view of vertebra.

Fig. 4. Berry's (1938) vertebral ossicle A (*Platyarthra jekerica* Berry, 1938), here referred to as *Ophiomyxa*? *jekerica*, dorsal view of vertebra.

Figs. 5-7. Berry's (1938) vertebral ossicle C (*Asteronyx valkenburgensis* Berry, 1938, here assigned to *Trichaster*? *ornatus* (Rasmussen, 1950) and *Trichaster*? sp.; 5: dorso-distal view of vertebra, 6: proximal view of vertebra, 7: distal view of vertebra.

Fig. 8. Berry's (1938) lateral arm plate M (*Platyarthra jekerica* Berry, 1938), here referred to *Ophiomusium lux* Jagt & Kutscher, sp. nov., outer surface of distal lateral arm plate.

Fig. 9. Berry's (1938) ventral plate I (*Ophiura kunradeca* Berry, 1938), here tentatively referred to *Ophiocten*? *yvonnae* Jagt & Kutscher, sp. nov.

Scale bars equal 100 µm.

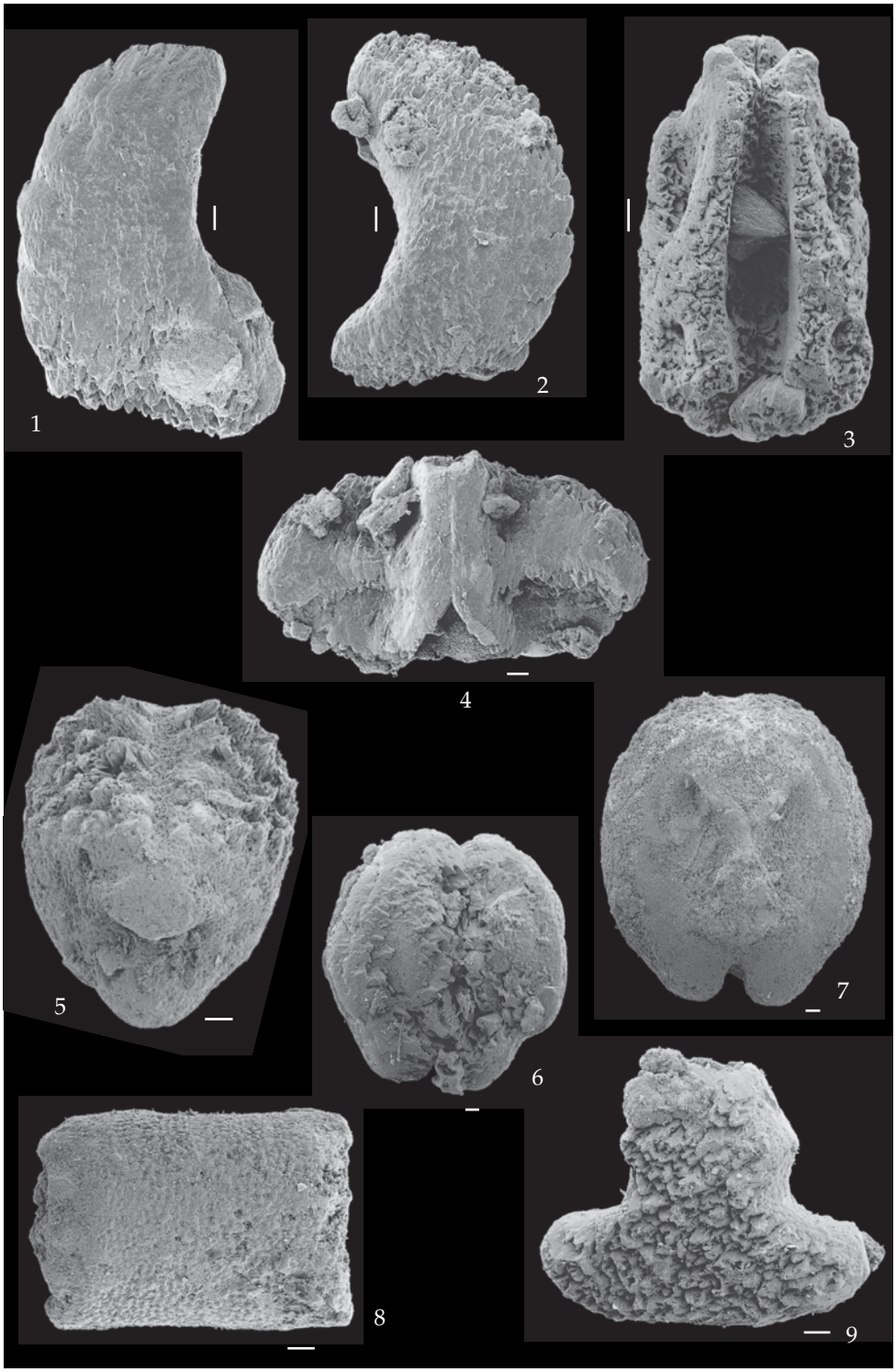
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Plate 19

Figs. 1-2. *Ophiotitanos serrata* (Roemer, 1840); NHMM MB 432.GGGd, outer surface and proximal view of lateral arm plate, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, uppermost Geulhem Member.

Figs. 3-7. *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.; outer surface of lateral arm plates, temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 1.5-2 m.
3: NHMM MB 734-12f.
4: NHMM MB 734-12j.
5: NHMM MB 734-12i.
6: NHMM MB 734-12h.
7: NHMM MB 734-12g.

Figs. 8-9. *Ophiocoma*? *senonensis* (Valette, 1915); same locality and stratigraphy as figs. 3-7.
8: NHMM MB 734-12l.
9: NHMM MB 734-12e.

Fig. 10. *Ophiacantha*? *striata* Kutscher & Jagt, sp. nov.; NHMM MB 734-12k, lateral arm plate, same locality and stratigraphy as figs. 3-9.

Fig. 11. *Ophiocoma*? *rasmusseni* Hess, 1960b; NHMM MB 432.GGGe, same locality and stratigraphy as figs. 1-2.

Scale bars equal 100 µm, except in figs. 1-2, where they represent 1 mm.

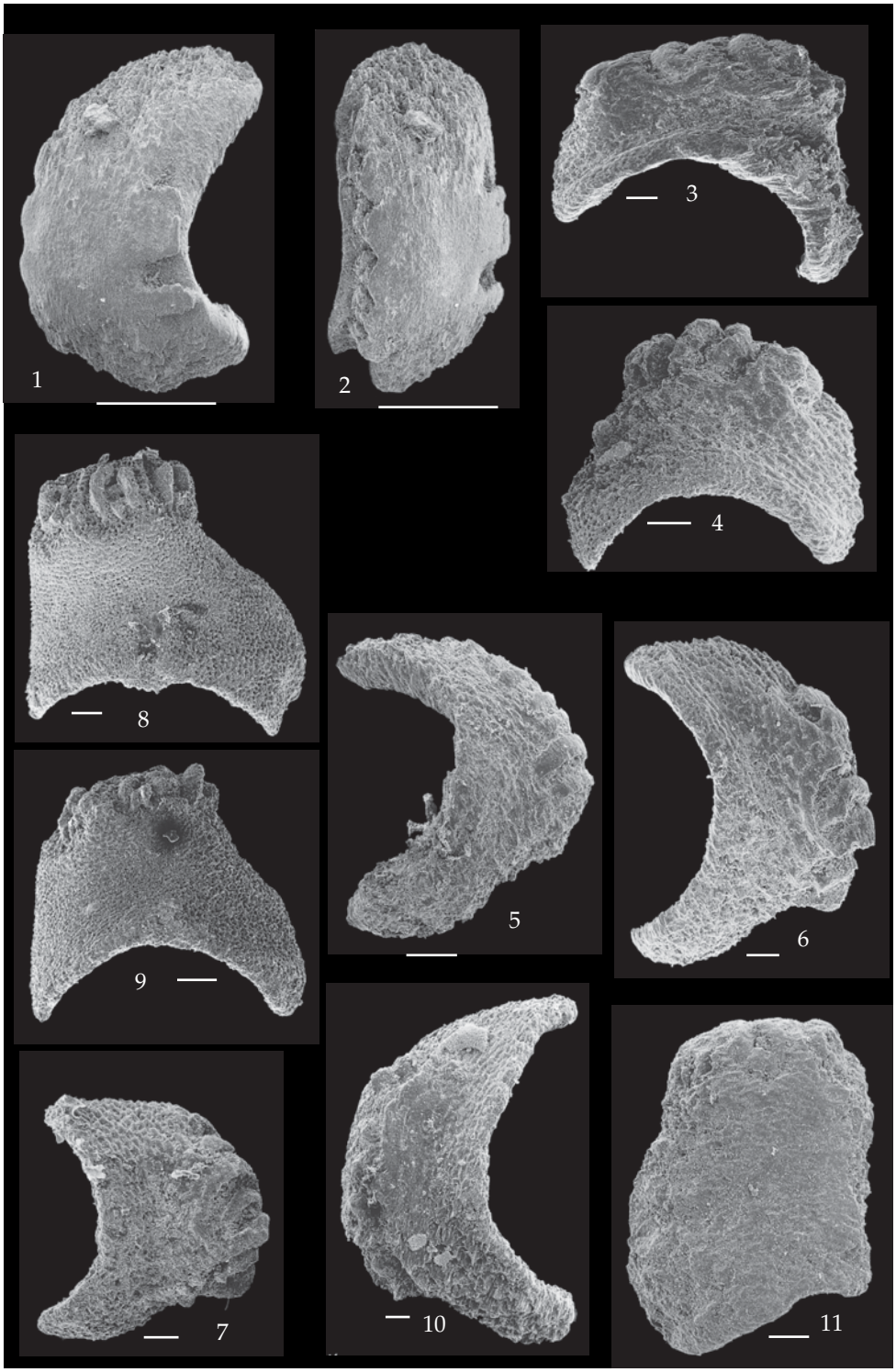
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Plate 20

All specimens from temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 1.5-2 m.

Figs. 1-3, 5. *Ophiacantha*? *striata* Kutscher & Jagt, sp. nov.; lateral arm plates.
1: NHMM MB 734-12o.
2: NHMM MB 734-12q.
3: NHMM MB 734-12p.
5: NHMM MB 734-12m.

Fig. 4. *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.; NHMM MB 734-12n, outer surface of lateral arm plate, same locality and stratigraphy.

Figs. 6, 9. *Ophiomusium granulosum* (Roemer, 1840)
6: NHMM MB 734-12u, outer surface of lateral arm plate.
9: NHMM MB 734-12aa, outer surface of radial shield.

Figs. 7-8. *Ophiotitanos serrata* (Roemer, 1840)
7: NHMM MB 734-12r, inner surface of lateral arm plate.
8: NHMM MB 734-12s, distal view of vertebra.

Scale bars equal 100 µm, except in fig. 9, where it represents 1 mm.

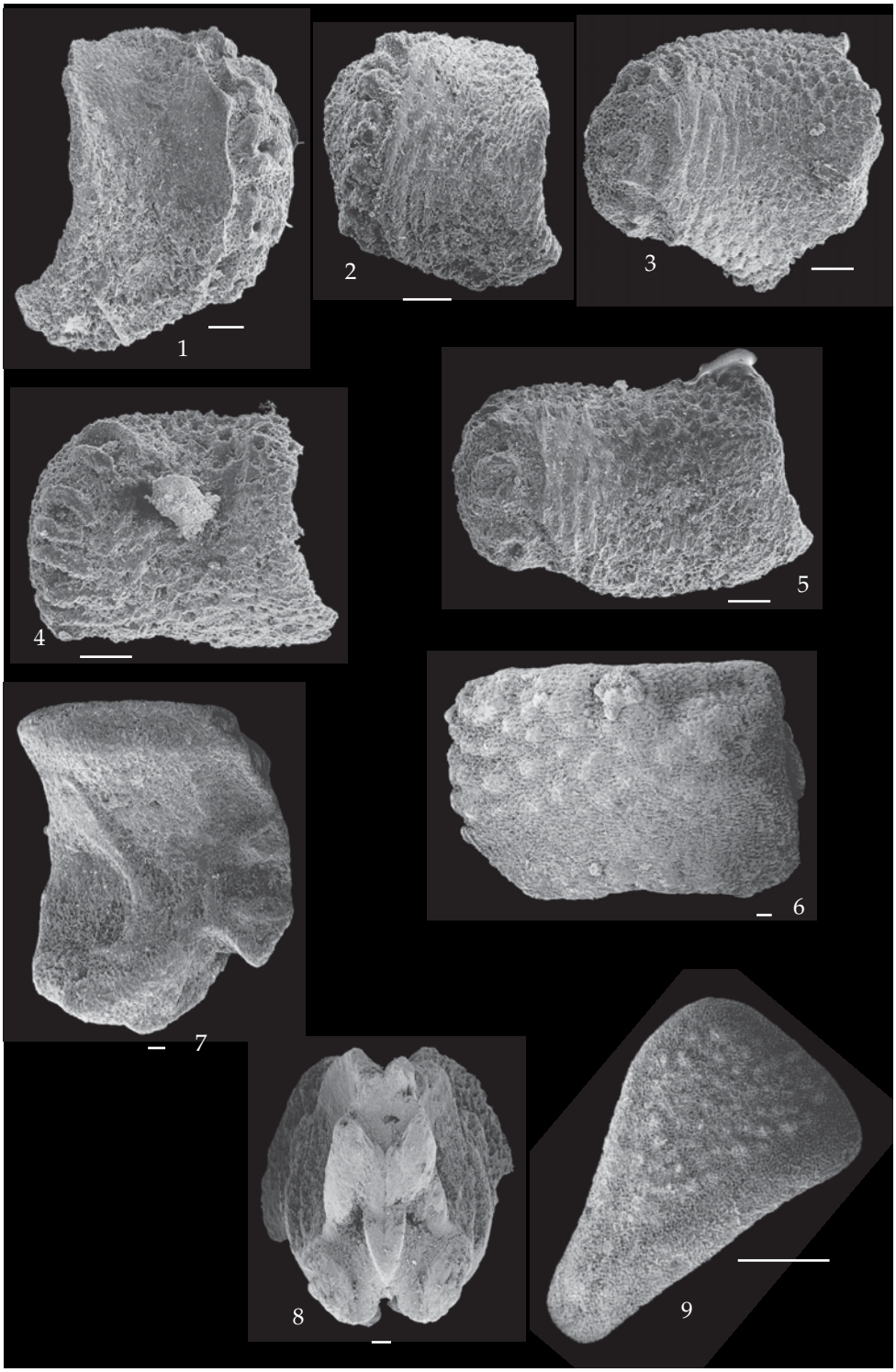
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Plate 21

All specimens from temporary Albertkanaal sections, Vroenhoven-Riemst, Houthem Formation, Geulhem Member, base + 1.5-2 m.

Figs. 1-4. *Ophiotitanos serrata* (Roemer, 1840), lateral arm plates.
1: NHMM MB 734-12v.
2: NHMM MB 734-12x.
3: NHMM MB 734-12y.
4: NHMM MB 734-12z.

Figs. 5-6. *Mesophiomusium decipiens* Jagt & Kutscher, sp. nov.?; NHMM MB 734-12bb/cc, outer and inner surface of radial shields, respectively (compare Pl. 10, figs. 9-10).

Scale bars equal 100 µm.

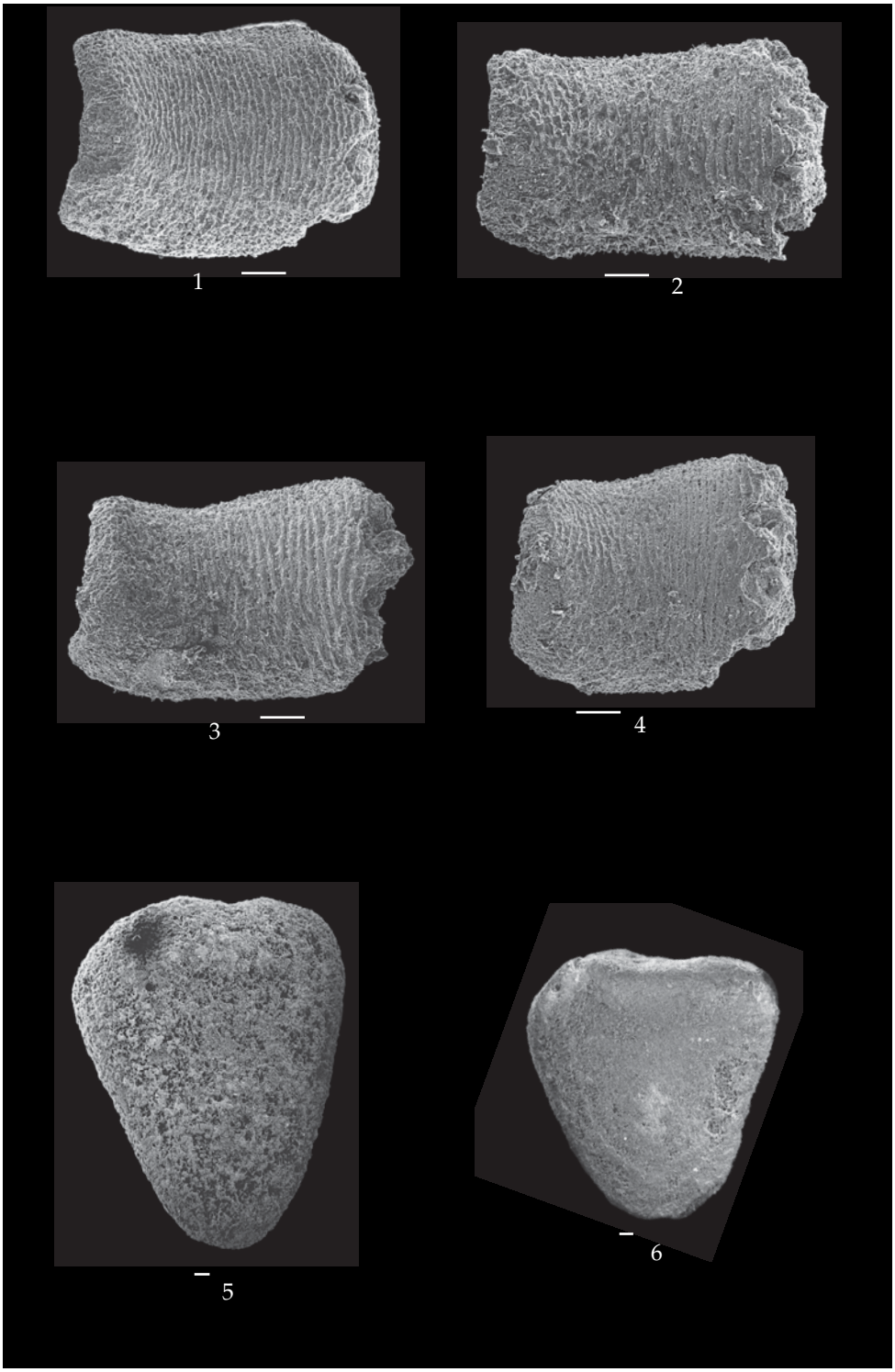
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Plate 22

Figs. 1-6. *Ophiomusium granulosum* (Roemer, 1840); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/1b, proximal lateral arm plate, outer surface.
2: Kutscher Colln, no. 1941/1d, proximal lateral arm plate, inner surface.
3: Kutscher Colln, no. 1941/1c, median lateral arm plate, outer surface.
4: Kutscher Colln, no. 1941/1e, median lateral arm plate, outer surface.
5: Kutscher Colln, no. 1941/1g, lateral view of proximal vertebra.
6: Kutscher Colln, no. 1941/1f, distal lateral arm plate, outer surface.

Figs. 7-11. *Ophiomusium biconcavum* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
7: Kutscher Colln, no. 1941/20b, proximal lateral arm plate, outer surface.
8: FGWG 112/9 (**holotype**), proximal lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/20c, median lateral arm plate, inner surface.
10: Kutscher Colln, no. 1941/20d, median lateral arm plate, outer surface.
11: Kutscher Colln, no. 1941/20e, distal lateral arm plate, outer surface.

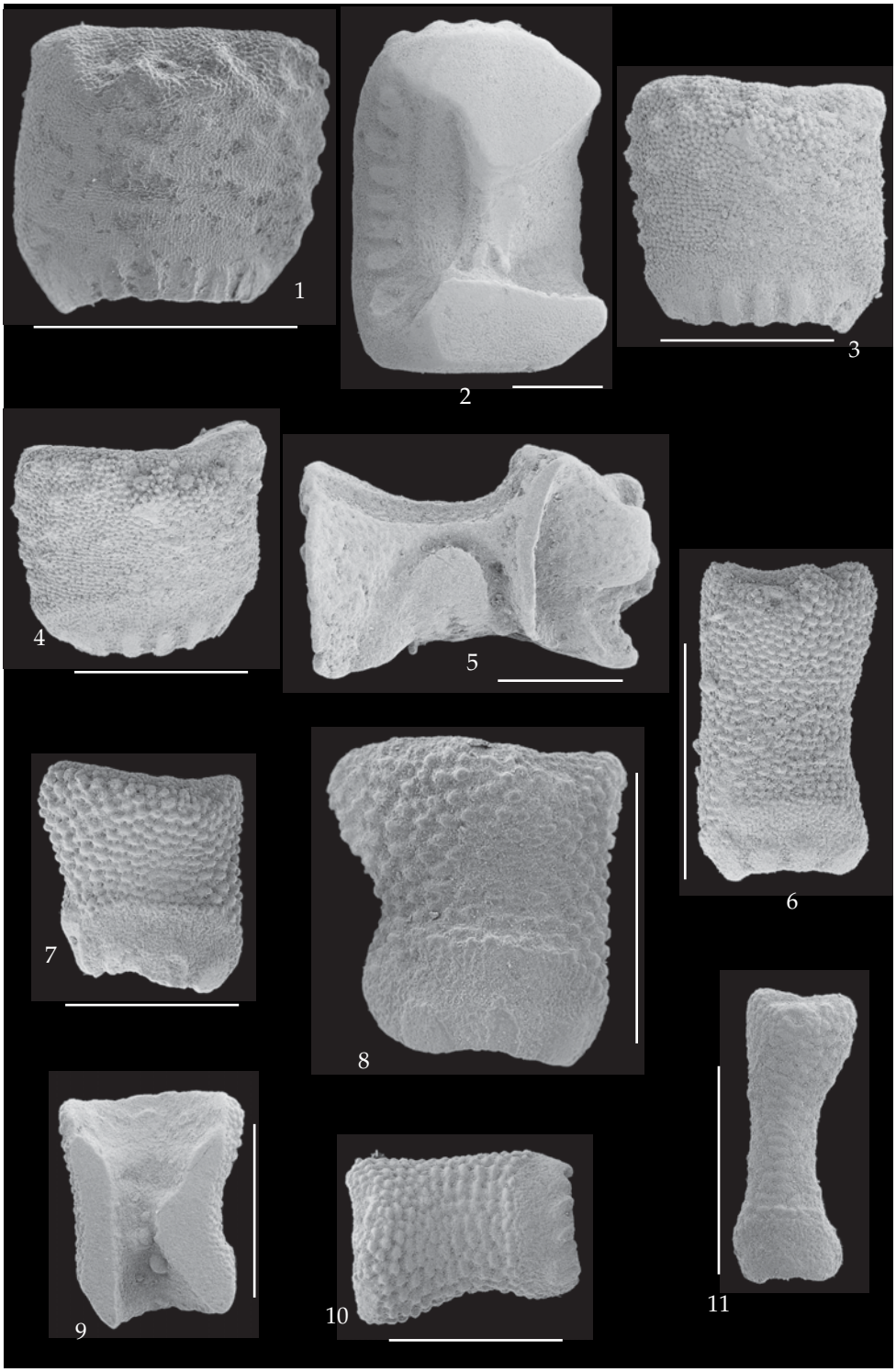
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Plate 23

Figs. 1-3. *Ophiomusium sinuatum* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: FGWG 112/10 (**holotype**), proximal lateral arm plate, outer surface.
2: Kutscher Colln, no. 1941/21b, median lateral arm plate, inner surface.
3: Kutscher Colln, no. 1941/21c, distal lateral arm plate, outer surface.

Figs. 4-7. *Ophiomusium sentum* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
4: Kutscher Colln, no. 1941/8c, distal lateral arm plate, outer surface.
5: Kutscher Colln, no. 1941/8d, median lateral arm plate, inner surface.
6: FGWG 112/8 (**holotype**), proximal lateral arm plate, outer surface.
7: Kutscher Colln, no. 1941/8b, median lateral arm plate, outer surface.

Figs. 8-12. *Ophiactis*? *sulcata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
8: Kutscher Colln, no. 1941/9d, proximal lateral arm plate, inner surface.
9, 11: FGWG 112/20 (**holotype**), proximal lateral arm plate, outer surface and lateral view.
10: Kutscher Colln, no. 1941/9b, proximal lateral arm plate, outer surface.
12: Kutscher Colln, no. 1941/9c, median lateral arm plate, outer surface.

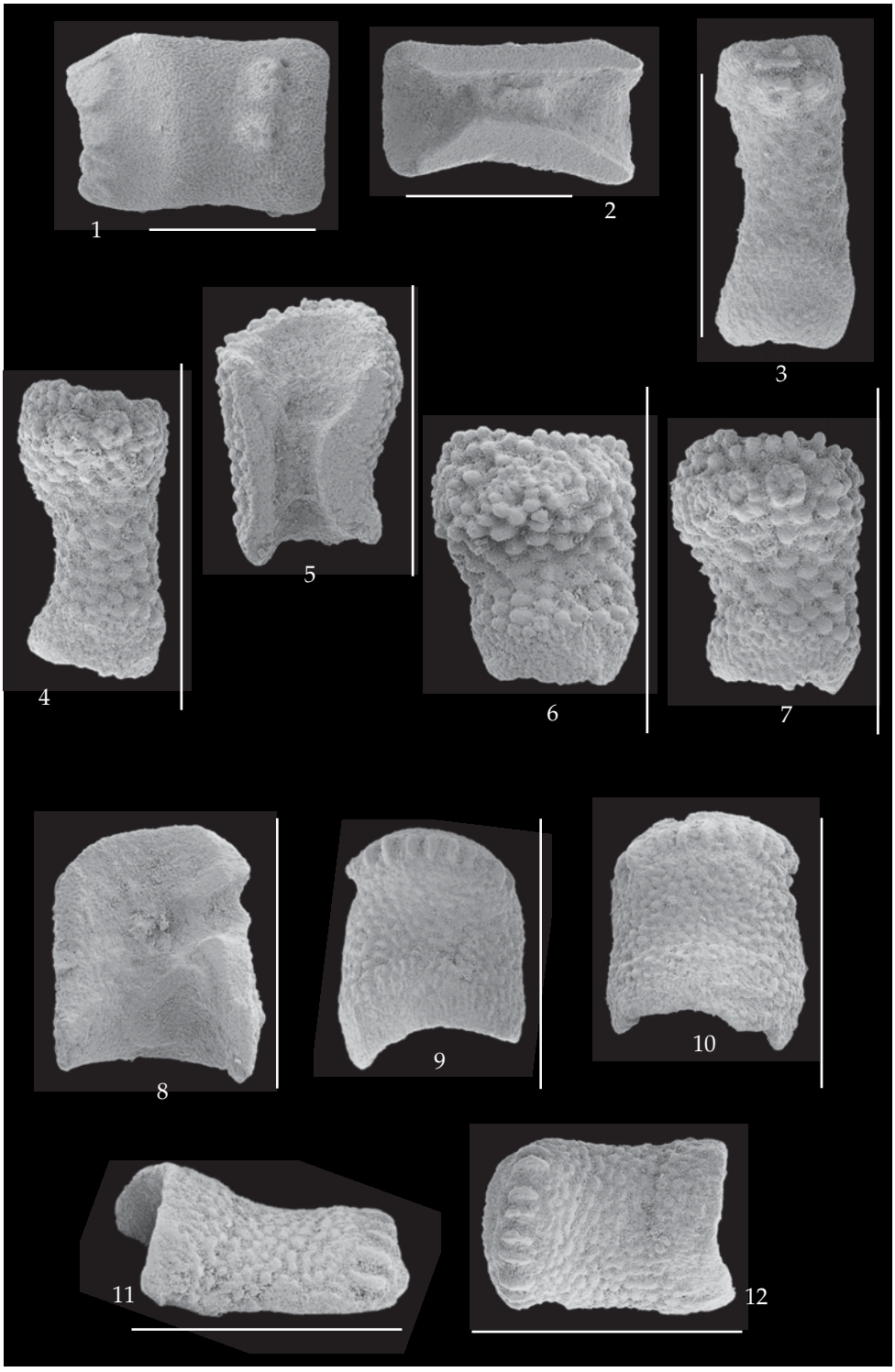
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Plate 24

Figs. 1-6. *Stegophiura*? *hagenowi* (Rasmussen, 1950); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/2b, proximal lateral arm plate, outer surface.
2: Kutscher Colln, no. 1941/2c, distal lateral arm plate, outer surface.
3-4: Kutscher Colln, no. 1941/2e, proximal lateral arm plate, distal and lateral views.
5: Kutscher Colln, no. 1941/2f, proximal lateral arm plate, inner surface.
6: Kutscher Colln, no. 1941/2d, distal arm fragment, ventral view.

Figs. 7-10. *Ophiacantha*? *danica* Rasmussen, 1952; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
7: Kutscher Colln, no. 1941/3b, median lateral arm plate, outer surface.
8: Kutscher Colln, no. 1941/3g, distal lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/3e, proximal lateral arm plate, outer surface.
10: Kutscher Colln, no. 1941/3f, median lateral arm plate, outer surface.

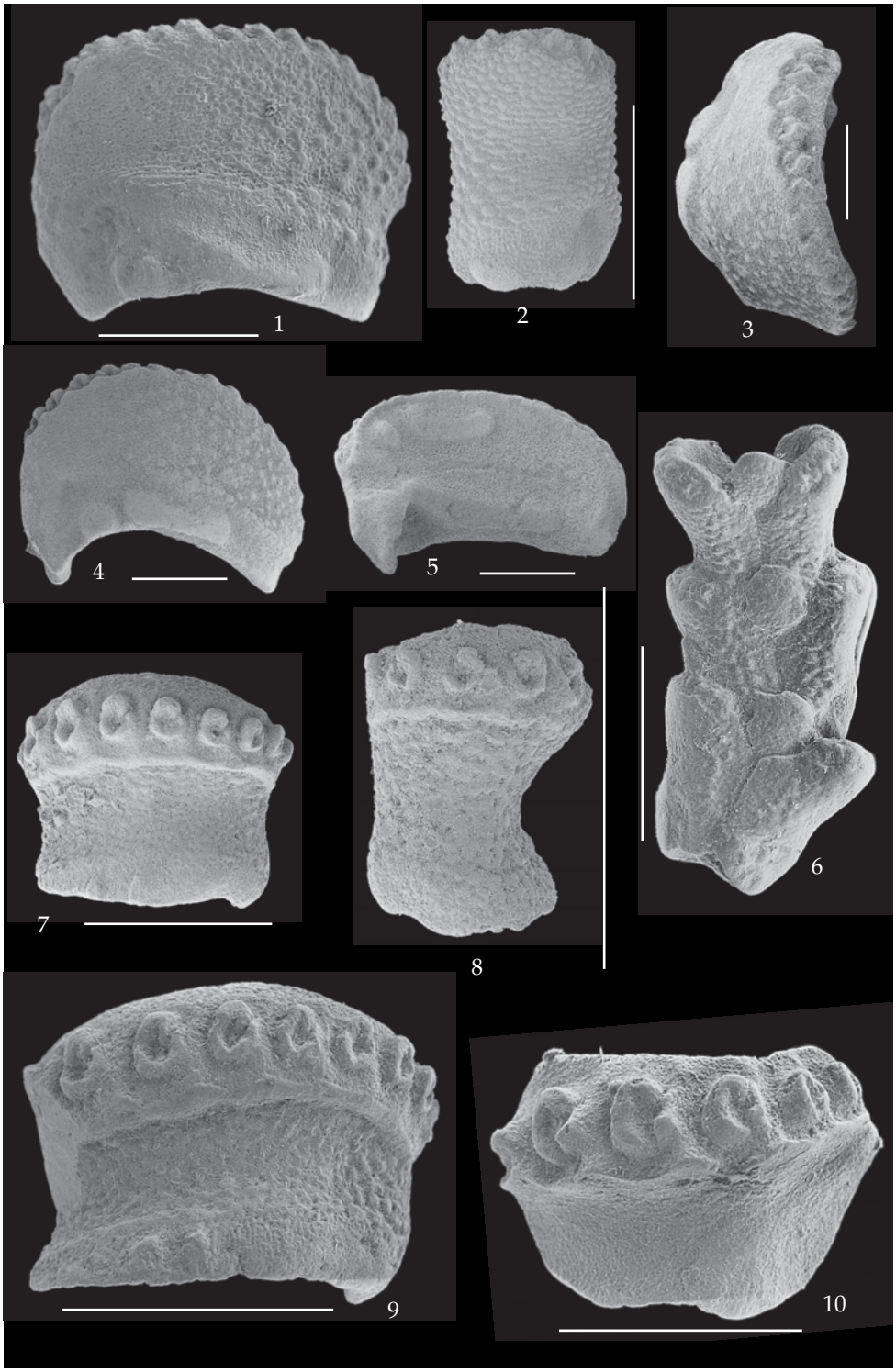
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Plate 25

Figs. 1-2. *Ophiacantha*? *danica* Rasmussen, 1952; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/3c, proximal lateral arm plate, proximal view.
2: Kutscher Colln, no. 1941/3d, proximal lateral arm plate, distal view.

Figs. 3-5. *Ophiacantha*? *punctata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
3: FGWG 112/14 (**holotype**), proximal lateral arm plate, outer surface.
4: Kutscher Colln, no. 1941/15c, proximal lateral arm plate, ventral view.
5: Kutscher Colln, no. 1941/15b, proximal lateral arm plate, inner surface.

Fig. 6. *Ophiacantha*? sp.; upper Lower Maastrichtian of Rügen (NE Germany), Kutscher Colln, no. 1941/19b, lateral arm plate, outer surface. Scale bar equals 1 mm.

Fig. 7. *Ophiacantha*? *rugosa* Kutscher & Jagt, sp. nov.; FGWG 112/13 (**holotype**), proximal lateral arm plate, outer surface, upper Lower Maastrichtian of Rügen (NE Germany). Scale bar equals 1 mm.

Figs. 8-10. *Ophiacantha*? *striata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
8: FGWG 112/12 (**holotype**); proximal lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/23b, proximal lateral arm plate, inner surface.
10: Kutscher Colln, no. 1941/23c, median lateral arm plate, outer surface.

Figs. 11-12. *Ophiolepis*? *granulata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
11: FGWG 112/6 (**holotype**), proximal lateral arm plate, outer surface.
12: Kutscher Colln, no. 1941/5b, proximal lateral arm plate, outer surface.

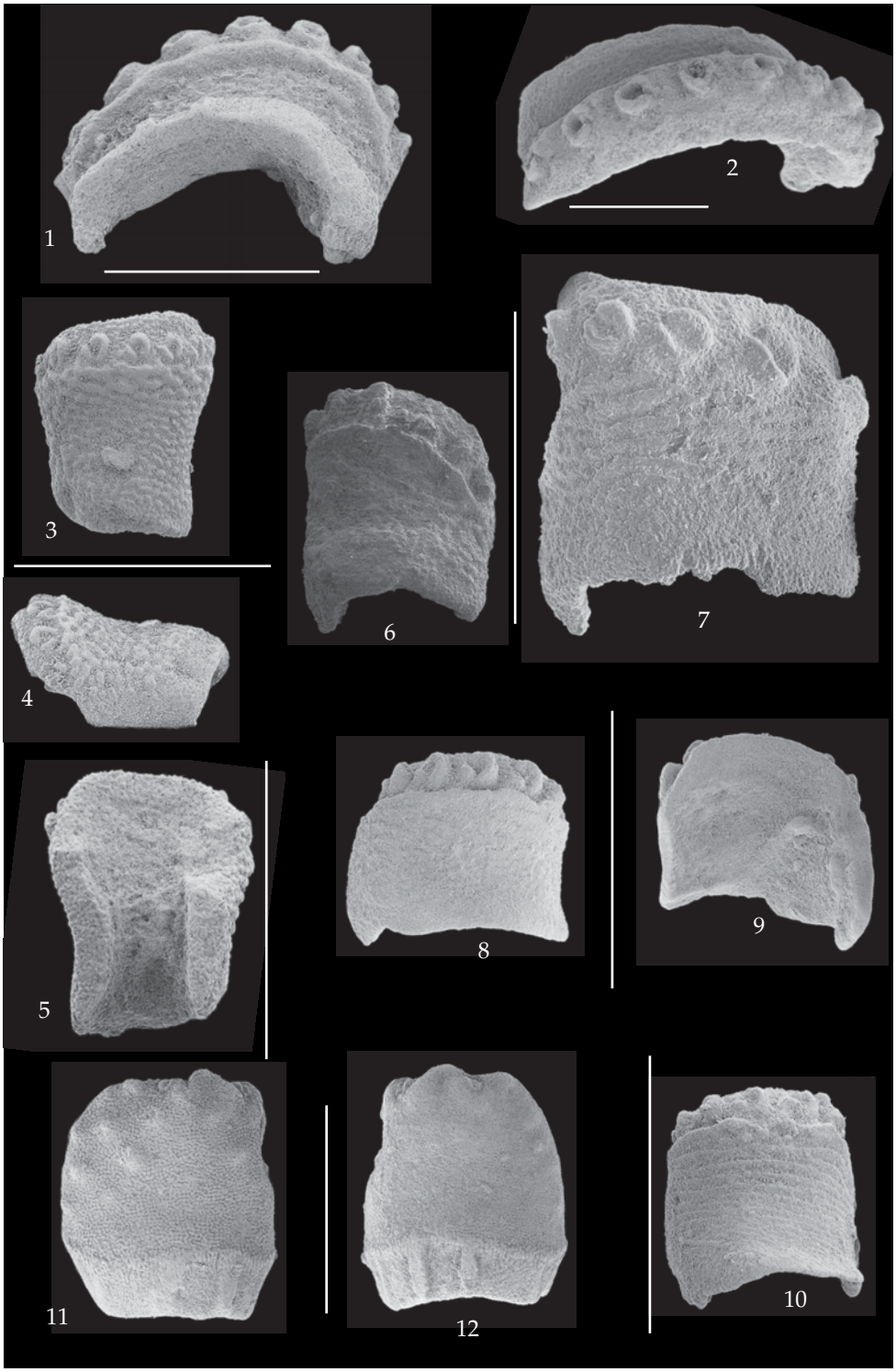
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Plate 26

Figs. 1-2, 7. *Ophiolepis*? *granulata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/5c, proximal lateral arm plate, inner surface.
2: Kutscher Colln, no. 1941/5e, proximal lateral arm plate, dorsal view.
7: Kutscher Colln, no. 1941/5d, median lateral arm plate, outer surface.

Figs. 3-6. *Ophiolepis*? *linea* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
3: FGWG 112/7 (**holotype**), proximal lateral arm plate, outer surface.
4: Kutscher Colln, no. 1941/27d, distal lateral arm plate, outer surface.
5: Kutscher Colln, no. 1941/27b, median lateral arm plate, outer surface.
6: Kutscher Colln, no. 1941/27c, proximal lateral arm plate, inner surface.

Figs. 8-11. *Ophiotitanos serrata* (Roemer, 1840); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
8: Kutscher Colln, no. 1941/4b, proximal lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/4e, distal lateral arm plate, outer surface.
10: Kutscher Colln, no. 1941/4d, proximal lateral arm plate, outer surface.
11: Kutscher Colln, no. 1941/4c, median lateral arm plate, outer surface.

Figs. 12-14. *Mesophiomusium moenense* Kutscher & Jagt, gen. et sp. nov.; lower Lower Maastrichtian of Møn (Denmark). Scale bars equal 1 mm.
12: MGUH 24552 (**holotype**), proximal lateral arm plate, outer surface.
13: Kutscher Colln, no. 1942/31b, proximal lateral arm plate, inner surface.
14: Kutscher Colln, no. 1942/31c, median lateral arm plate, outer surface.

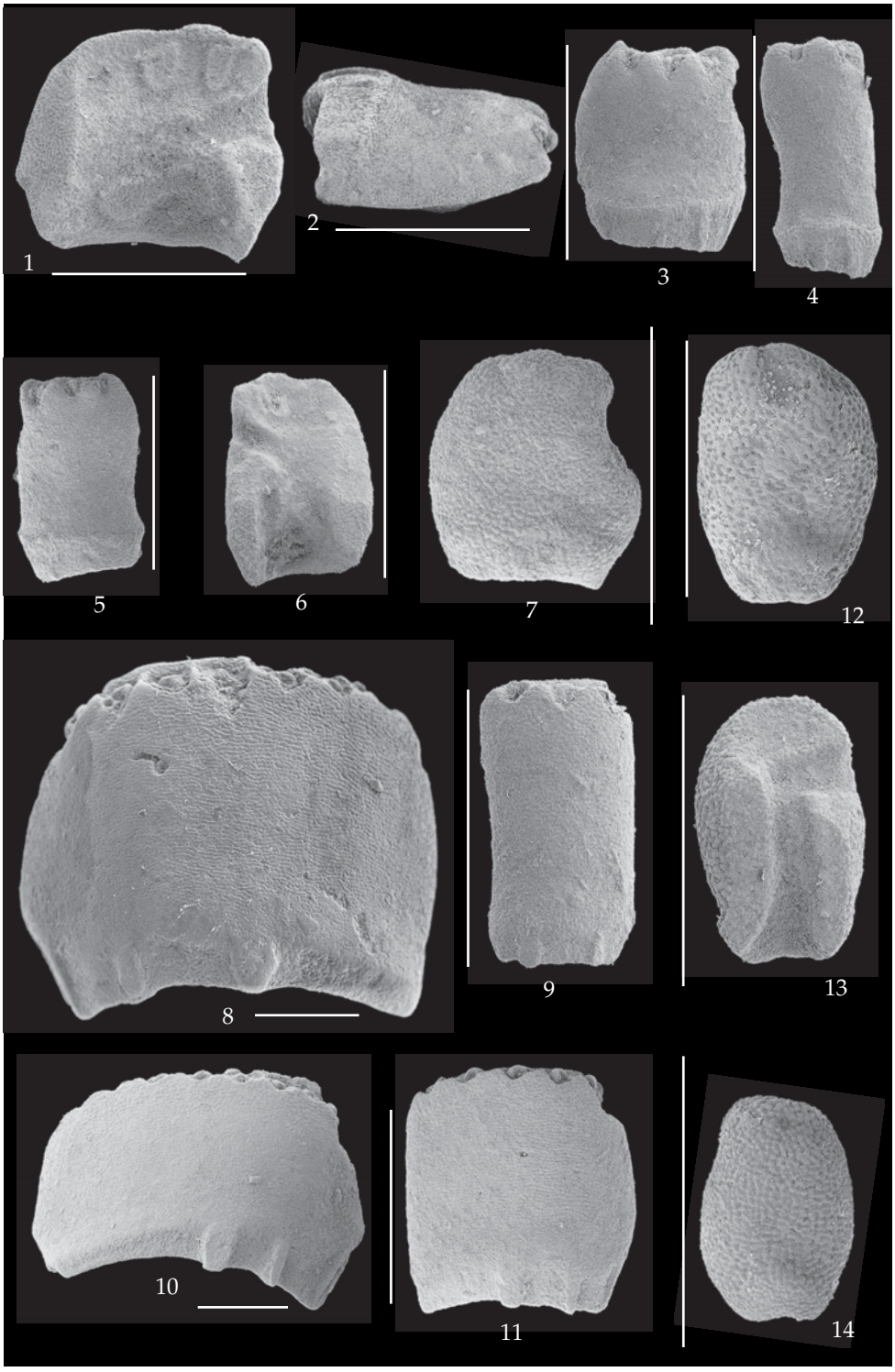
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Plate 27

Figs. 1-6. *Ophioderma*? *substriatum* (Rasmussen, 1950); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/6b, proximal lateral arm plate, outer surface.
2: Kutscher Colln, no. 1941/6c, proximal lateral arm plate, outer surface.
3: Kutscher Colln, no. 1941/6d, proximal lateral arm plate, inner surface.
4: Kutscher Colln, no. 1941/6e, proximal lateral arm plate, distal view.
5: Kutscher Colln, no. 1941/6f, median lateral arm plate, outer surface.
6: Kutscher Colln, no. 1941/6g, distal lateral arm plate, outer surface.

Figs. 7-10. *Ophioderma*? *radiatum* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
7: FGWG 112/11 (**holotype**), proximal lateral arm plate, outer surface.
8: Kutscher Colln, no. 1941/11b, median lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/11c, proximal lateral arm plate, inner surface.
10: Kutscher Colln, no. 1941/11d, proximal lateral arm plate, distal view.

Figs. 11-13. *Sinosura* aff. *schneideri* Kutscher, 1987; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
11: Kutscher Colln, no. 1941/33b, proximal lateral arm plate, outer surface.
12: Kutscher Colln, no. 1941/33c, distal lateral arm plate, outer surface.
13: Kutscher Colln, no. 1941/33d, median lateral arm plate, outer surface.

Fig. 14. *Sinosura jasmundensis* Kutscher & Jagt, sp. nov.; FGWG 112/15 (**holotype**), lateral arm plate, upper Lower Maastrichtian of Rügen (NE Germany). Scale bar equals 1 mm.

Figs. 15-16. *Ophiocoma*? *senonensis* (Valette, 1915); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
15: Kutscher Colln, no. 1941/7d, median lateral arm plate, outer surface.
16: Kutscher Colln, no. 1941/7b, proximal lateral arm plate, outer surface.

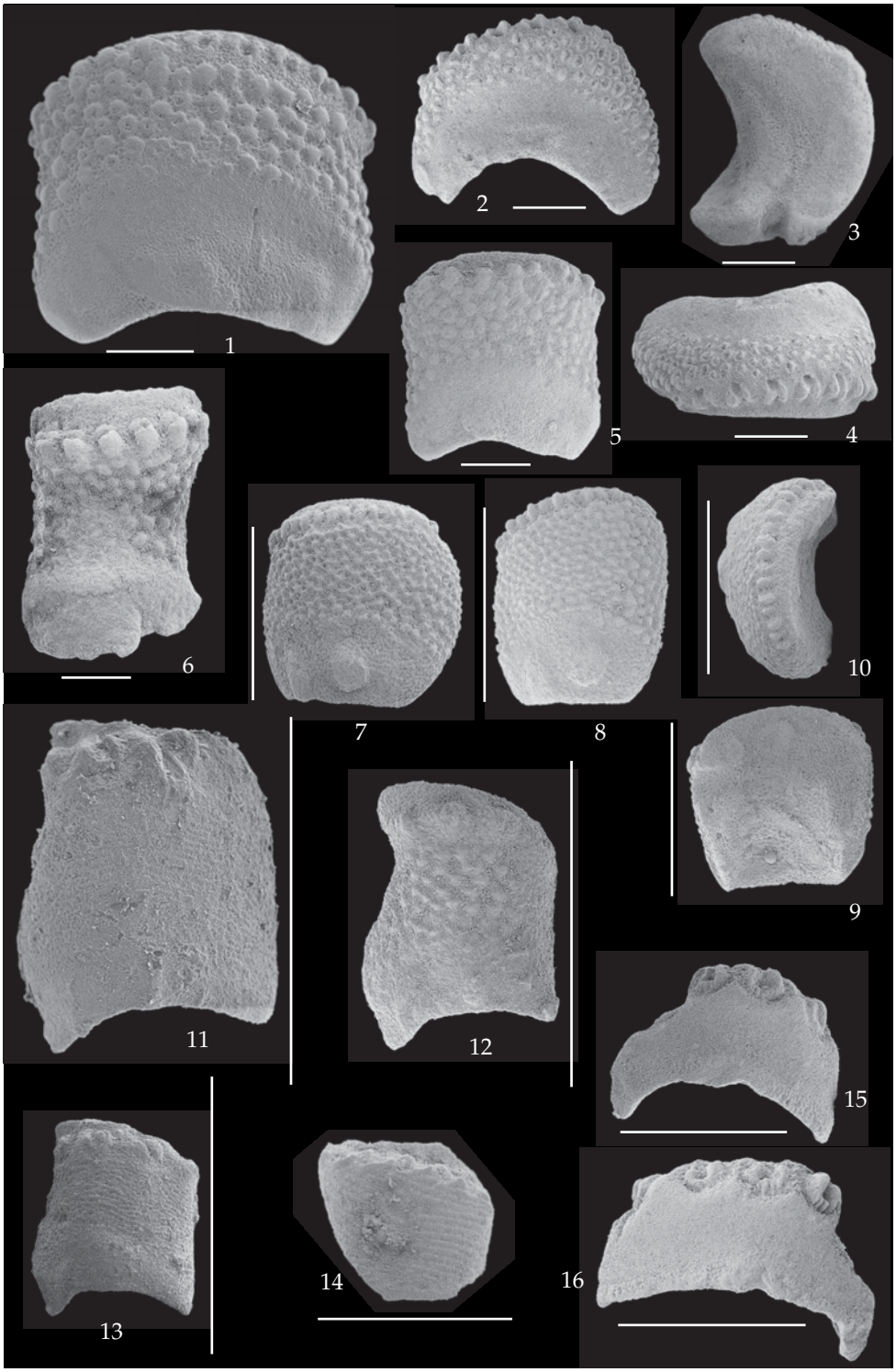
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Plate 28

Figs. 1-4, 7. *Ophiocoma*? *senonensis* (Valette, 1915); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/7f, proximal lateral arm plate, outer surface.
2-3: Kutscher Colln, no. 1941/7e, arm segment, dorsal and lateral view, respectively.
4: Kutscher Colln, no. 1941/7c, distal lateral arm plate, outer surface.
7: Kutscher Colln, no. 1941/7g, median lateral arm plate, inner surface.

Figs. 5-6, 8-9. *Ophiocoma*? *rasmusseni* Hess, 1960b; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
5: Kutscher Colln, no. 1941/13b, proximal lateral arm plate, outer surface.
6: Kutscher Colln, no. 1941/13c, proximal lateral arm plate, outer surface.
8: Kutscher Colln, no. 1941/13d, distal lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/13e, median lateral arm plate, outer surface.

Figs. 10-11. *Ophiocoma*? *ishidai* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
10: FGWG 112/16 (**holotype**), proximal lateral arm plate, outer surface.
11: Kutscher Colln, no. 1941/37b, lateral arm plate, inner surface.

Figs. 12-14. *Hemieuryale*? *parva* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
12: FGWG 112/21 (**holotype**), lateral arm plate, outer surface.
13: Kutscher Colln, no. 1941/24b, lateral arm plate, inner surface.
14: Kutscher Colln, no. 1941/24c, lateral arm plate, outer surface.

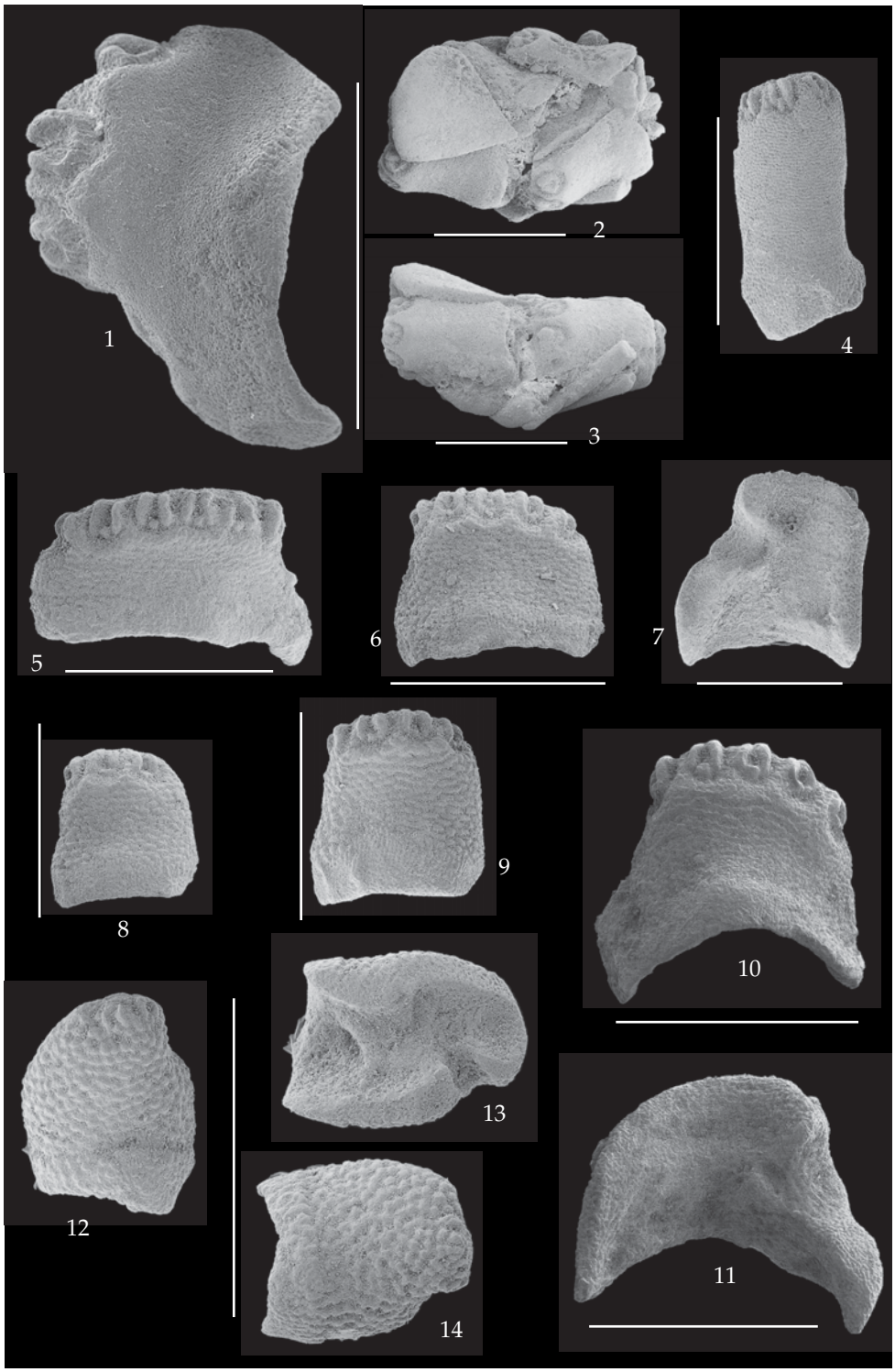
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Plate 29

Figs. 1-5. *Amphiura*? *plana* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1, 5: Kutscher Colln, no. 1941/14b, proximal lateral arm plate, outer surface and distal view.
2: FGWG 112/17 (**holotype**), proximal lateral arm plate, outer surface.
3: Kutscher Colln, no. 1941/14c, proximal lateral arm plate, inner surface.
4: Kutscher Colln, no. 1941/14d, median lateral arm plate, outer surface.

Figs. 6-8. *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
6: Kutscher Colln, no. 1941/10c, median lateral arm plate, outer surface.
7: Kutscher Colln, no. 1941/10b, distal lateral arm plate, outer surface.
8: FGWG 112/18 (**holotype**), proximal lateral arm plate, outer surface.

Figs. 9-10. *Ophiothrix*? *bongaertsi* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
9: Kutscher Colln, no. 1941/38b, median lateral arm plate, outer surface.
10: FGWG 112/19 (**holotype**), proximal lateral arm plate, outer surface.

Figs. 11-13. *Ophiothela*? *semirotunda* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
11: FGWG 112/22 (**holotype**), proximal lateral arm plate, outer surface.
12: Kutscher Colln, no. 1941/22b, proximal lateral arm plate, inner surface.
13: Kutscher Colln, no. 1941/22c, proximal lateral arm plate, outer surface.

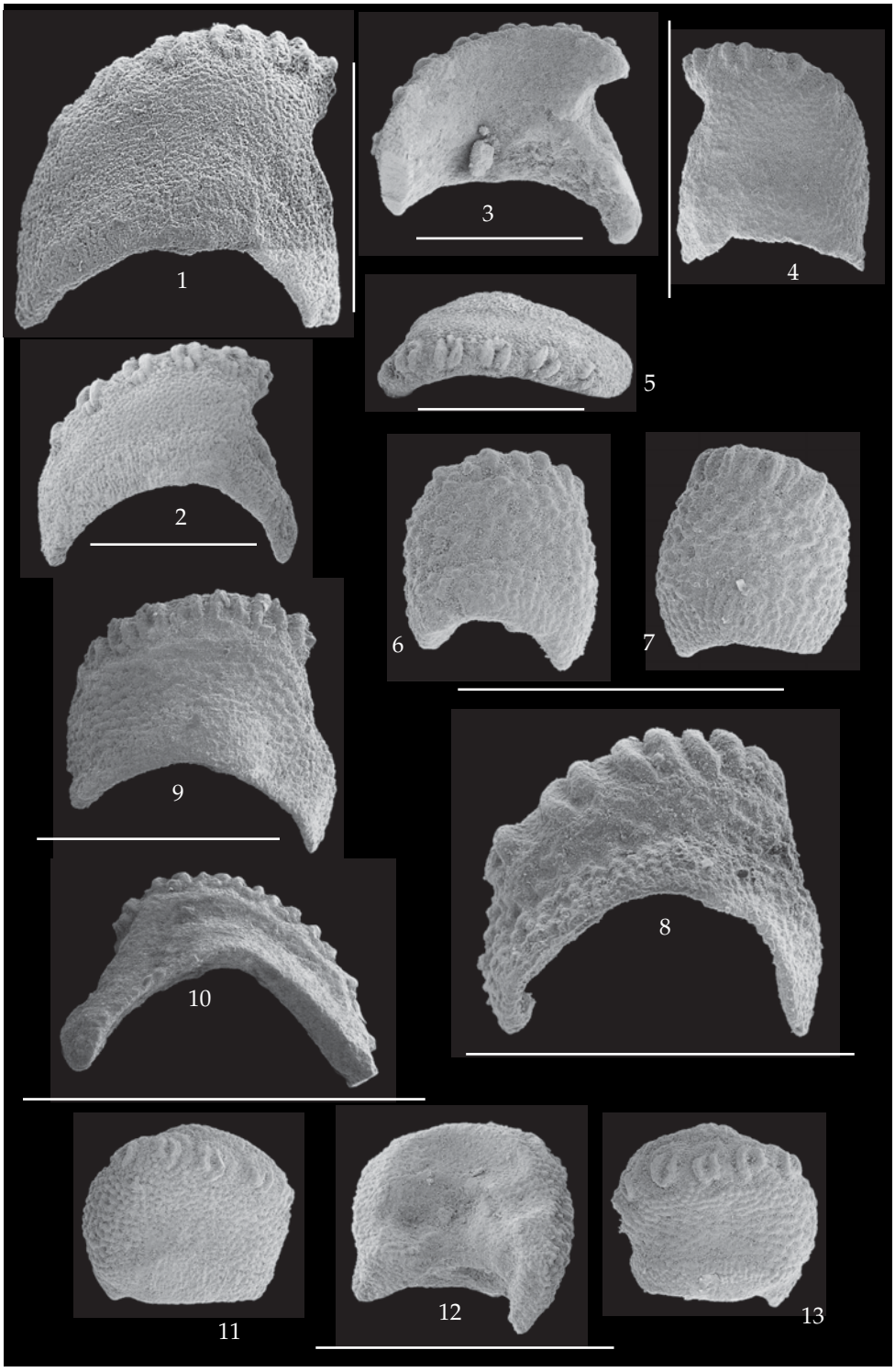
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Plate 30

Figs. 1-4. *Asteronyx*? *spinulosa* Kutscher & Jagt, sp. nov.; lower Lower Maastrichtian of Møn (Denmark). Scale bars equal 1 mm.
1: MGUH 24553 (**holotype**), lateral arm plate, outer surface.
2: Kutscher Colln, no. 1941/32b, lateral arm plate, inner surface.
3: Kutscher Colln, no. 1941/32c, ?dorsal arm plate, inner surface.
4: Kutscher Colln, no. 1941/32d, ?dorsal arm plate, outer surface.

Figs. 5-8. *Ophioscolex*? *cretaceus* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
5: FGWG 112/3 (**holotype**), proximal lateral arm plate, outer surface.
6: Kutscher Colln, no. 1941/16c, median lateral arm plate, inner surface.
7-8: Kutscher Colln, no. 1941/16b, median lateral arm plate, outer surface and oblique distal view.

Figs. 9-11. *Ophioscolex*? *clivulus* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
9: FGWG 112/4 (**holotype**), median lateral arm plate, outer surface.
10: Kutscher Colln, no. 1941/28c, distal lateral arm plate, outer surface.
11: Kutscher Colln, no. 1941/28b, proximal lateral arm plate, inner surface.

Figs. 12-17. *Ophiomyxa*? *rhipidata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
12: FGWG 112/1 (**holotype**), proximal lateral arm plate, outer surface.
13: Kutscher Colln, no. 1941/12b, proximal lateral arm plate, outer surface.
14: Kutscher Colln, no. 1941/12d, median lateral arm plate, inner surface.
15: Kutscher Colln, no. 1941/12c, median lateral arm plate, outer surface.
16: Kutscher Colln, no. 1941/12f, vertebra, dorsal view.
17: Kutscher Colln, no. 1941/12e, distal lateral arm plate, outer surface.

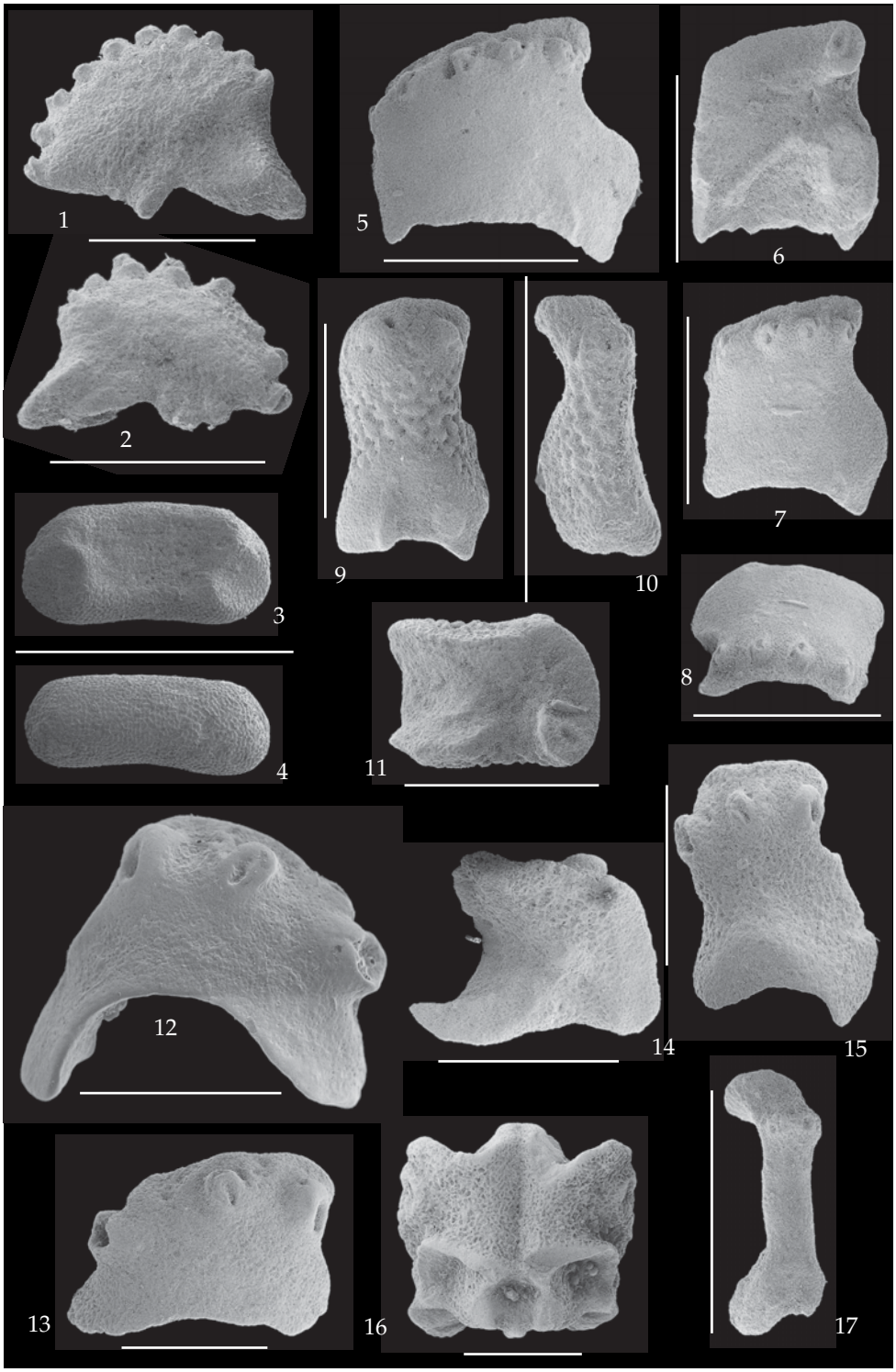
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Plate 31

Figs. 1-3. *Ophiomyxa*? *rhipidata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/12h, spine of dorsal tubercle.
2: Kutscher Colln, no. 1941/12g, spine of dorsal tubercle.
3: Kutscher Colln, no. 1941/12i, spine of ventral tubercle.

Figs. 4-7. *Ophiomyxa*? *curvata* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
4: FGWG 112/2 (**holotype**), proximal lateral arm plate, outer surface.
5: Kutscher Colln, no. 1941/17b, proximal lateral arm plate, inner surface.
6-7: Kutscher Colln, no. 1941/17c, median lateral arm plate, distal margin and outer surface.

Figs. 8-12. *Ophiosmilax*? *alternatus* Kutscher & Jagt, sp. nov.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
8: FGWG 112/5 (**holotype**), proximal lateral arm plate, outer surface.
9: Kutscher Colln, no. 1941/25b, distal lateral arm plate, outer surface.
10: Kutscher Colln, no. 1941/25d, median lateral arm plate, inner surface.
11: Kutscher Colln, no. 1941/25c, proximal lateral arm plate, inner surface.
12: Kutscher Colln, no. 1941/25e, spine.

Figs. 13-14. *Ophiomyxa*? *jekerica* (Berry, 1938); Kutscher Colln, no. 1941/35b, vertebra, upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.

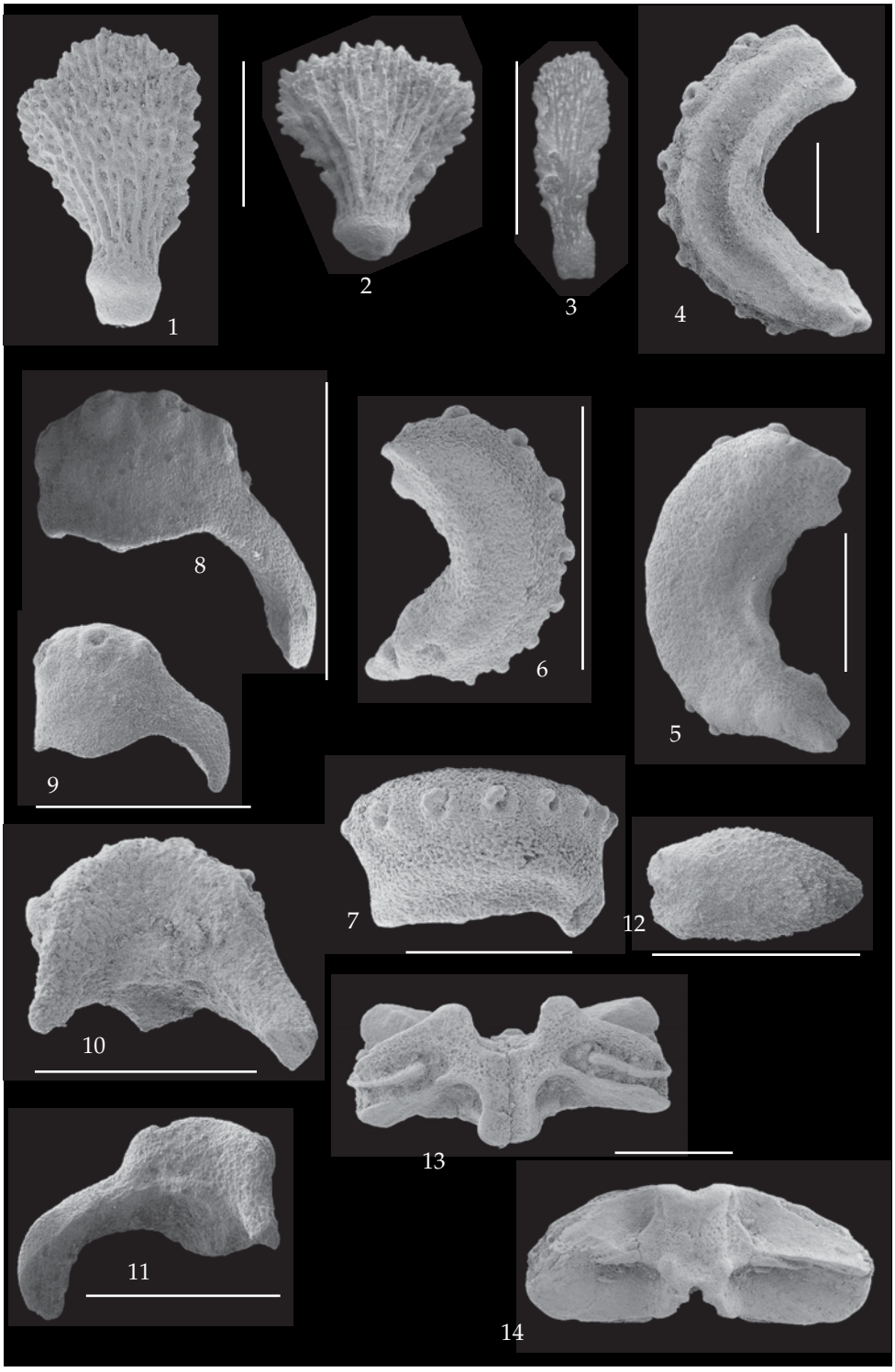
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Plate 32

Figs 1-3, 7. *Trichaster*? *ornatus* (Rasmussen, 1950); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
1: Kutscher Colln, no. 1941/18b, proximal vertebra, distal view.
2, 3: Kutscher Colln, no. 1941/18c, proximal vertebra, lateral and proximal views.
7: Kutscher Colln, no. 1941/18d, distal vertebra, distal view.

Figs. 4-6. *Trichaster*? sp.; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
4, 6: Kutscher Colln, no. 1941/34b, vertebra, dorso-distal and lateral views.
5: Kutscher Colln, no. 1941/34c, vertebra, dorso-distal view.

Figs. 8-9. *Asteronyx*? *simplex* A.H. Müller, 1950; upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.
8: Kutscher Colln, no. 1941/36b, vertebra, dorso-distal view.
9: Kutscher Colln, no. 1941/36c, vertebra, ventral view.

Figs. 10-11. *Ophiotitanos serrata* (Roemer, 1840); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm, distal and proximal views, respectively, Kutscher Colln, no. 1941/4f/g.

Figs. 12-13. *Ophiomusium granulosum* (Roemer, 1840); upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm, dorsal and distal views, respectively, Kutscher Colln, no. 1941/1g.

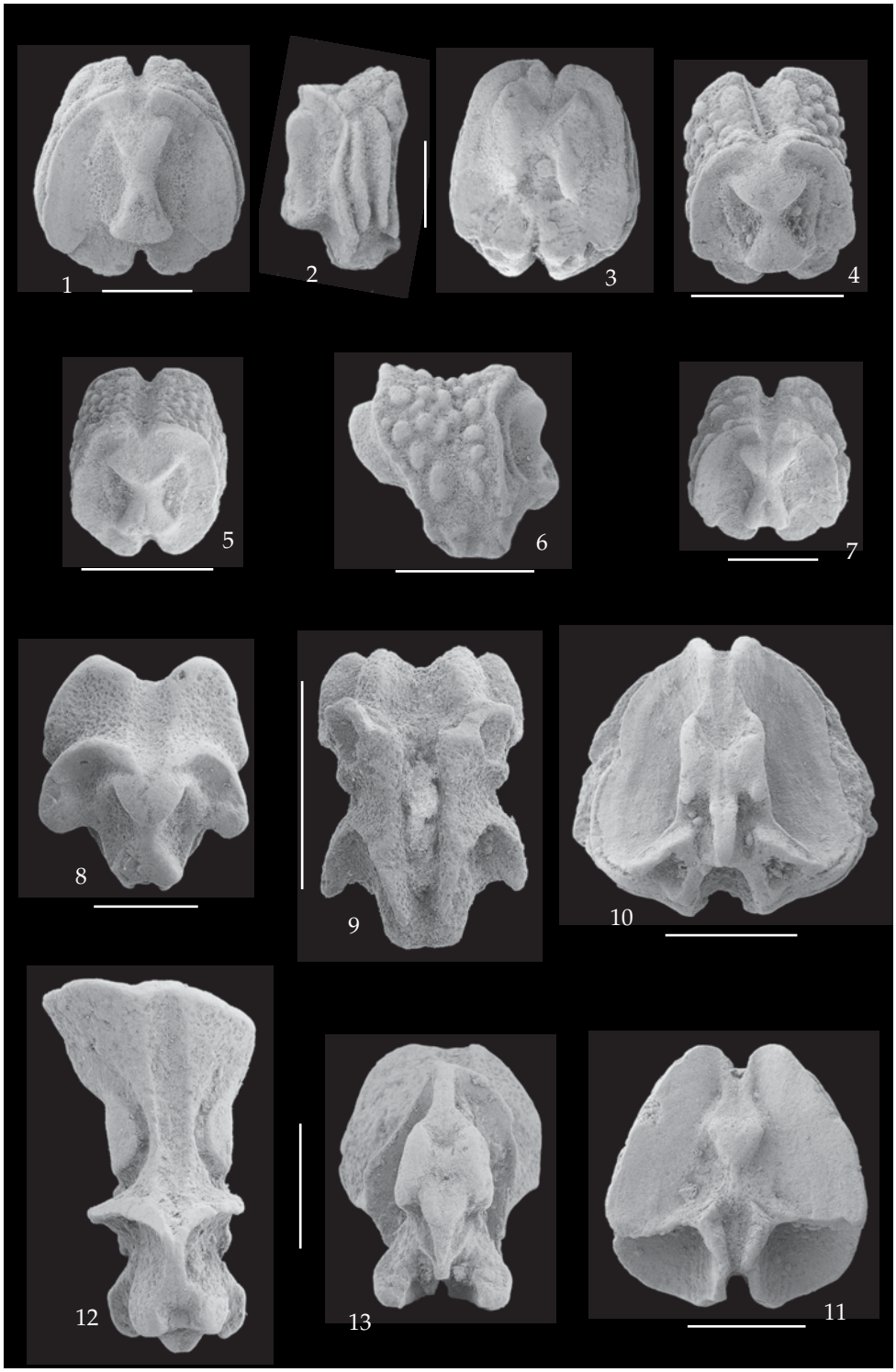
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Plate 33

Ophiuroid vertebrae from the upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.

Fig. 1. *Stegophiura*? *hagenowi* (Rasmussen, 1950); distal view, Kutscher Colln, no. 1941/2g.

Fig. 2. *Ophioderma*? *substriatum* (Rasmussen, 1950); dorsal view, Kutscher Colln, no. 1941/6h.

Fig. 3. *Amphiura*? *plana* Kutscher & Jagt, sp. nov.; dorso-distal view, Kutscher Colln, no. 1941/14e.

Figs. 4-5, 8. *Ophiocoma*? *senonensis* (Valette, 1915); proximal, dorsal and distal views, respectively, Kutscher Colln, no. 1941/7h/i.

Figs. 9-11. *Ophiosmilax*? *alternatus* Kutscher & Jagt, sp. nov.; proximal, dorsal and ventral views, respectively, Kutscher Colln, no. 1941/25f/g.

Figs. 6-7, 12. *Ophiomyxa*? *rhipidata* Kutscher & Jagt, sp. nov.; distal, proximal and ventral views, respectively, Kutscher Colln, no. 1941/j-l.

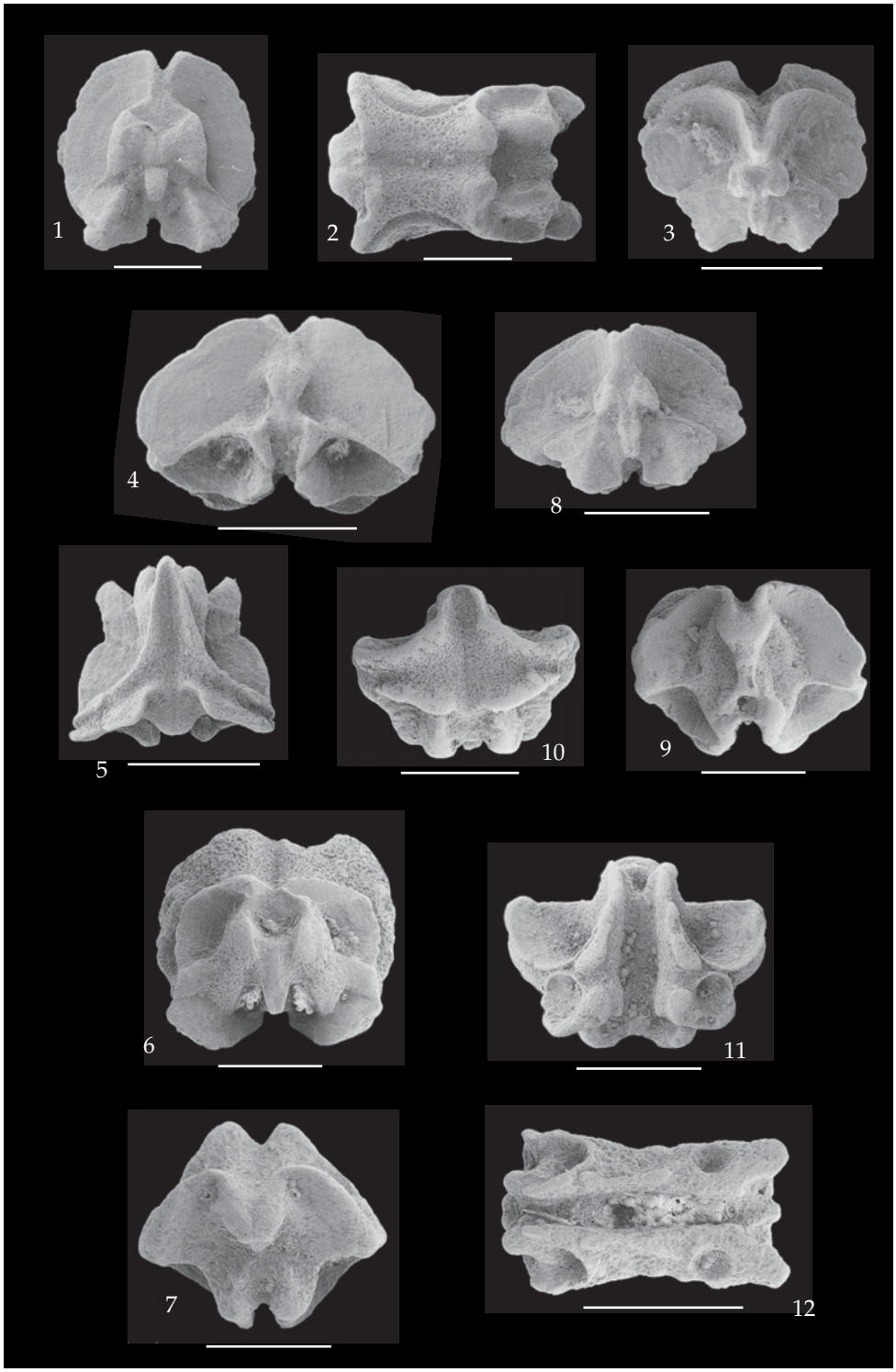
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Plate 34

Ophiuroid radial shields (1-9), genital scales (10-13) and spines (14-24) from the upper Lower Maastrichtian of Rügen (NE Germany). Scale bars equal 1 mm.

Fig. 1. Type 3, *Ophiomusium granulosum* (Roemer, 1840); Kutscher Colln, no. 1941/1h.

Fig. 2. Type 11, *Ophiomusium biconcavum* Kutscher & Jagt, sp. nov.; Kutscher Colln, no. 1941/20f.

Fig. 3. Type 2, *Stegophiura*? *hagenowi* (Rasmussen, 1950); Kutscher Colln, no. 1941/2h.

Fig. 4. Type 4, *Ophiotitanos serrata* (Roemer, 1840); Kutscher Colln, no. 1941/4h.

Fig. 5. Type 10; Kutscher Colln, no. 1941.

Fig. 6. Type 13, *Ophiomusium sentum* Kutscher & Jagt, sp. nov.; Kutscher Colln, no. 1941/8e.

Fig. 7. Type 5, *Ophiocoma*? *senonensis* (Valette, 1915); Kutscher Colln, no. 1941/7j.

Fig. 8. Type 8, *Ophiothrix*? *cristata* Kutscher & Jagt, sp. nov.; Kutscher Colln, no. 1941/10d.

Fig. 9. Type 6; Kutscher Colln, no. 1941.

Figs. 10-13. Incertae sedis; Kutscher Colln, no. 1941.

Fig. 14. Type 2.

Fig. 15. Type 3.

Figs. 16, 21. Type 4.

Fig. 17. Type 8, *Ophiosmilax*? *alternatus* Kutscher & Jagt, sp. nov.; Kutscher Colln, no. 1941/25h.

Figs. 18-19. Type 1.

Fig. 20. Type 6.

Figs. 22-23. Type 7.

Fig. 24. Type 5.


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Plate 35

Ophiuroid oral and ventral arm plates from the upper Lower Maastrichtian of Rügen (NE Germany); all Kutscher Colln, no. 1941. Scale bars equal 1 mm.

Figs. 1-2. Type 1.

Figs. 3-4. Type 2.

Fig. 5. Type 3.

Fig. 6. Type 4.

Fig. 7. *Ophiocoma*? *rasmusseni* Hess, 1960b.

Figs. 8-9, 10, 12, 14. *Ophiocoma*? *senonensis* (Valette, 1915).

Figs. 11, 13, 15. Incertae sedis.

Fig. 16. *Ophiomusium granulosum* (Roemer, 1840).

Fig. 17. *Ophiotitanos serrata* (Roemer, 1840).

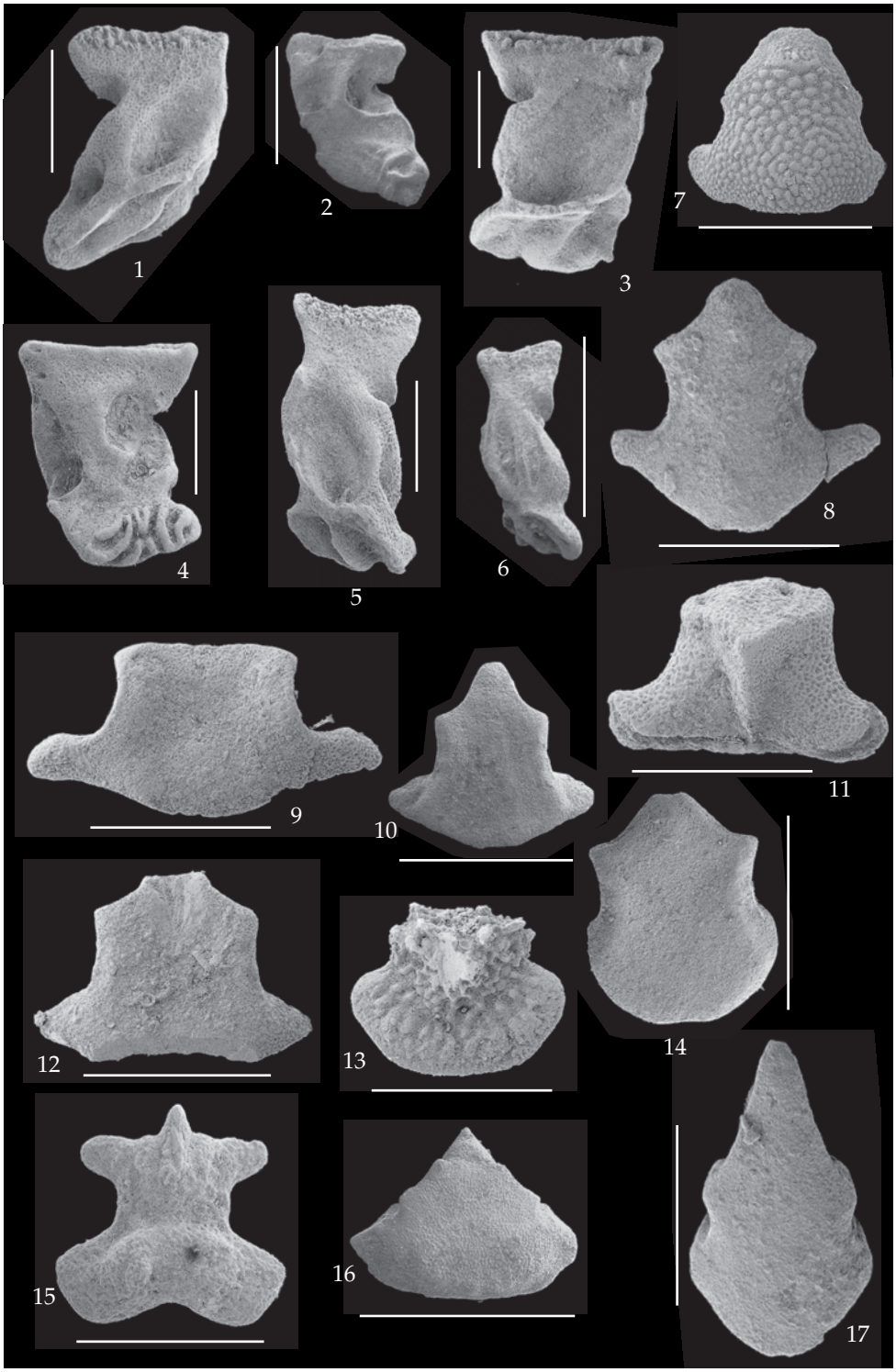
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Plate 36

Ophiuroid dorsal arm plates (figs. 1-11) and additional unidentified ossicles from the upper Lower Maastrichtian of Rügen (NE Germany); all Kutscher Colln, no. 1941. Scale bars equal 1 mm.

Figs. 1-2, 8, 10-11, 14. Incertae sedis.

Figs. 3, 6. *Ophiotitanos serrata* (Roemer, 1840).

Fig. 4. *Ophioderma*? *substriatum* (Rasmussen, 1950).

Fig. 5. *Stegophiura*? *hagenowi* (Rasmussen, 1950).

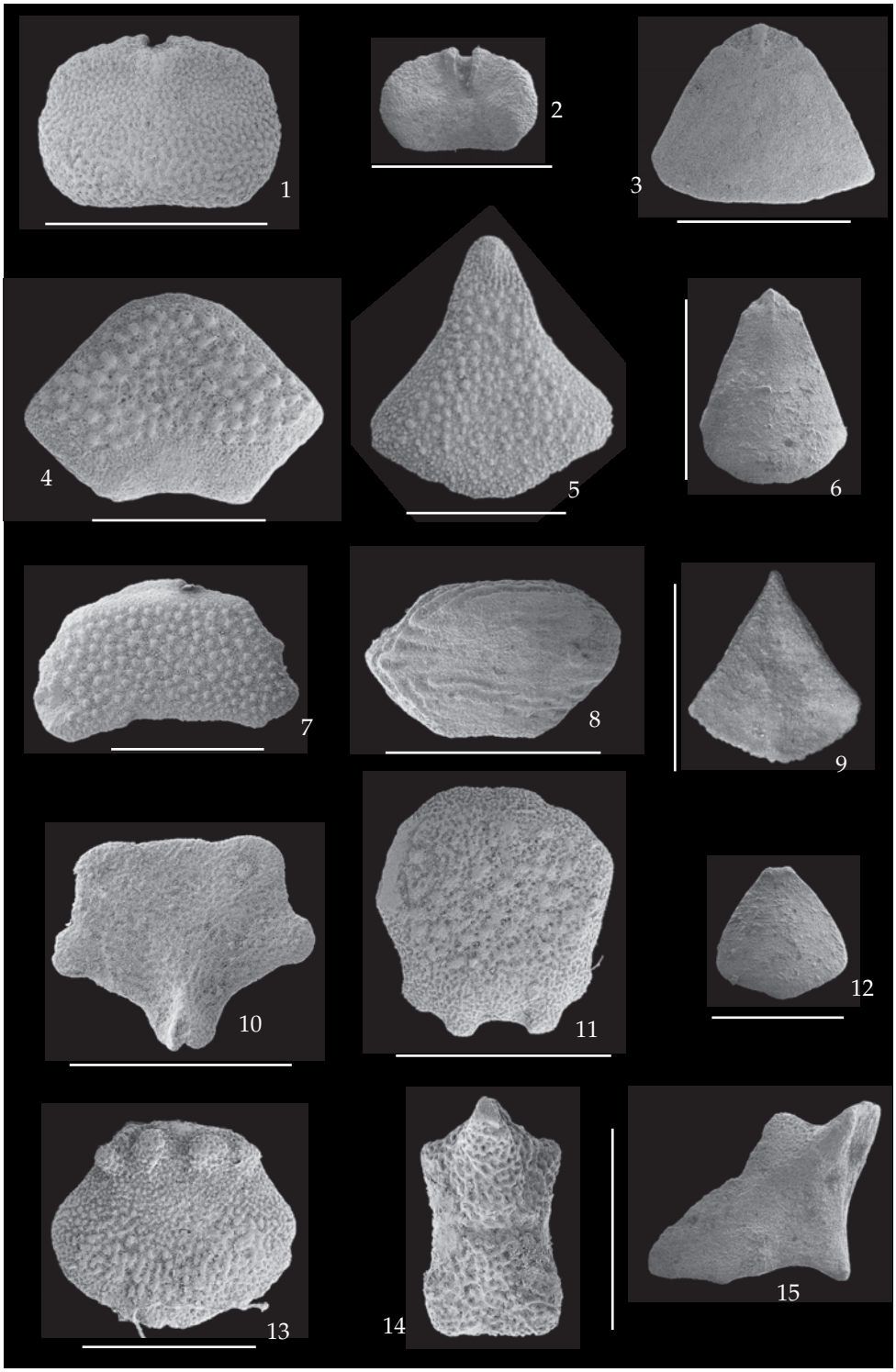
Fig. 7. *Ophiocoma*? *rasmusseni* Hess, 1960b.

Fig. 9. *Ophiolepis*? *granulata* Kutscher & Jagt, sp. nov.

Fig. 12. *Ophiocoma*? *senonensis* (Valette, 1915).

Fig. 13. ? *Ophiomusium biconcavum* Kutscher & Jagt, sp. nov.

Fig. 15. Adoral plate of ? *Ophiomusium granulosum* (Roemer, 1840).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