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Ophiuroid diversity in the type area of the Maastrichtian Stage

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Abstract

With the exception of holothurians, all Late Cretaceous (Campanian–Maastrichtian) and Early Palaeogene (Danian) echinoderms from the extended type area of the Maastrichtian Stage are currently being revised. In addition to a handful of taxa described previously in the literature, many new genera and species of brittle star and basket star (Ophiuroidea) have been recognised in recent years. In fact, the study area is one of the very few regions in the world that have yielded diverse ophiuroid faunas of latest Cretaceous age. Of note also is the fact that many of the new taxa are based on more or less complete specimens, i.e., discs preserving (portions of) arms, making generic assignment much more reliable. The various ophiuroid groups recognised are briefly discussed and selected specimens are illustrated in order to document the diversity. Formal descriptions will be published elsewhere. Ophiuroid taxa described by Berry (1938), as based on poorly preserved material from the Late Maastrichtian of the area, are briefly commented upon.

Introduction

Echinoderms from the type area of the Maastrichtian Stage (Figure 1) have figured prominently in the palaeontological literature since the late 18th century, but this has mostly concerned echinoids. Other echinoderm groups have been virtually neglected. Amongst these are the brittle stars and basket stars, or ophiuroids (Jagt 1998, Kutscher & Jagt in press).

The above observation also holds true for other regions in NW Europe. To make matters worse, the few studies of Late Cretaceous ophiuroids that have appeared (by, among others, Müller 1950, Rasmussen 1950, 1952) suffer from a certain collection bias. Only a portion of the former ophiuroid faunas is represented, generally comprising the more robust and commoner taxa. Material of fragile and/or diminutive species, such as ophiothricids, hemieuryalids and amphiurids, is mostly absent.

In recent years, numerous new forms have been collected from the Maastrichtian type area, with good stratigraphic control (Figure 2). Many of these species had been recognised in the meantime by co-worker Manfred Kutscher in the Early Maastrichtian of Rügen (NE Germany) and Møn (Denmark). In view of the fact that material from those localities is generally disarticulated but much better preserved, it was decided to base the revision of Late Cretaceous ophiuroids primarily on those faunas (Jagt & Kutscher 1998, Kutscher & Jagt in press). This revision will considerably improve our knowledge of fossil ophiuroids (see Simms et al. 1993, Smith et al. 1995), and of Late Cretaceous ones in particular.

Smith et al. (1995) published a phylogenetic tree for ophiuroids, calibrated against the stratigraphic record. The classification proposed by those authors, which differs in many respects from that of Matsumoto (1915, 1917), is followed here. Neontological studies of ophiuroids focus mainly on features of disc plating and oral frame. Only rarely are details of arm plating (ornament, spines) noted. This is especially unfortunate since various studies of fossil forms have now demonstrated the value of dissociated arm ossicles. Lateral arm plates in particular (Hess 1962, 1975 and references therein) are a good basis for the

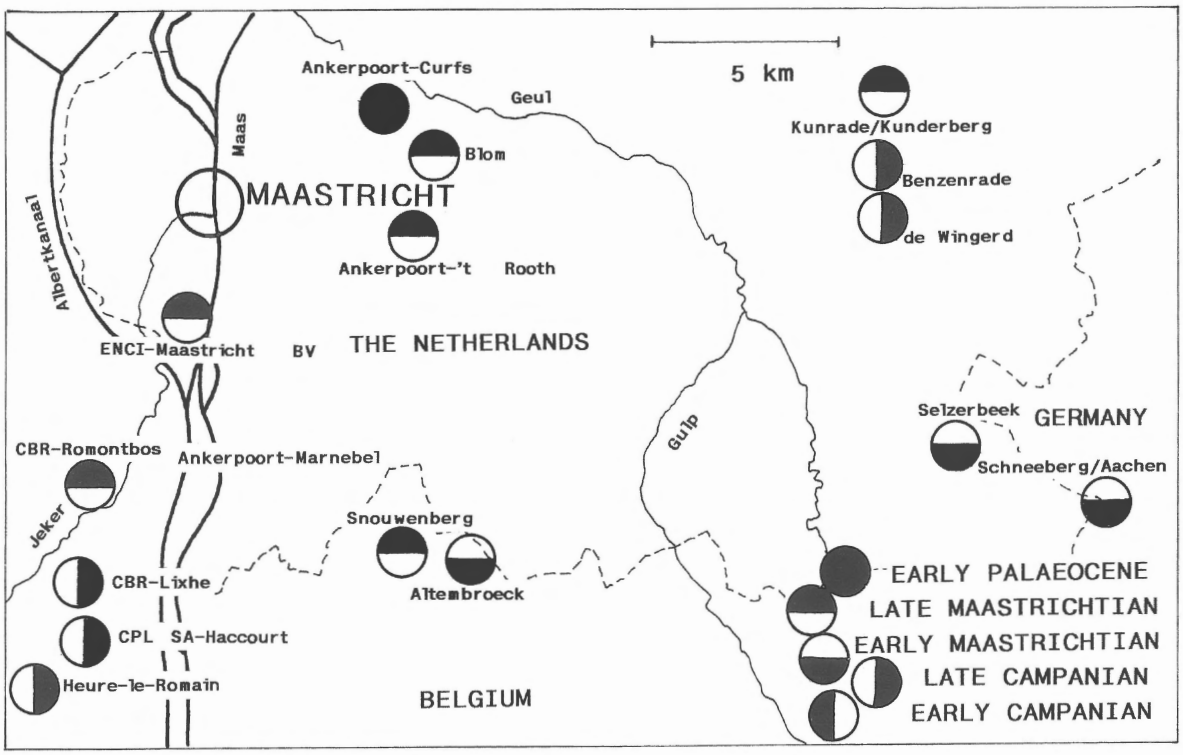

Figure 1. Southern Limburg (The Netherlands) and contiguous areas showing main localities, and their stratigraphy.

identification of fossil species and occasionally even genera.

Most fossil ophiuroids are known from fragmentary remains; more or less complete discs preserving (portions of) arms are comparatively rare and represent exceptional preservation by obrution. Rapid burial by storm activity often led to the pristine preservation of echinoderm communities (e.g. Donovan 1991; Lawrence 1996). The type Maastrichtian includes a number of such echinoderm 'Lagerstätten', two of them involving ophiuroids (Maastricht Formation: Gronsveld and Meerssen Members).

The various ophiuroid groups of which representatives are now known from the Late Cretaceous and Early Palaeogene of the Maastrichtian type area are briefly discussed below. Formal descriptions of new taxa may be found in Kutscher & Jagt (in press). The main objective of the present paper is to document the good preservation of these rich faunas, and to make broadbrush palaeobiological inferences, based on a comparison with extant ophiuroids (Mortensen 1927, Hyman 1955, Hendler et al. 1995). For details concerning stratigraphic provenance and repositories of

Houthem Formation	Geleen Member Bunde Member Geulhem Member
Maastricht Formation	Meerssen Member Nekum Member Emael Member Schiepersberg Member Gronsveld Member Valkenburg Member
Gulpen Formation	Lanaye Member Lixhe 3 Member Lixhe 2 Member Lixhe 1 Member Vijlen Member Beutenaken Member Zeven Wegen Member
Vaals Formation	Benzenrade Member Terstraten Member Beusdal Member Vaalsbroek Member Gemmenich Member Cottessen Member Raren Member

Figure 2. Lithostratigraphy of the Upper Cretaceous and Lower Palaeogene of the extended type area of the Maastrichtian Stage (after Felder & Bosch in press).

specimens illustrated, reference is made to Kutscher & Jagt (in press).

Ophiobyrsinae

Similar to ophiomyxids (see below), members of this group have thick skin covering disc and arms. The type genus, *Ophiosmilax* Matsumoto 1915, has short and stout vertebrae of the streptospondyline kind, and few arm spines converted into compound hooks.

The only representative of this group recorded so far is *Ophiosmilax*? n. sp. (Plate I, specimens 1–2), from the Zeven Wegen and Vijlen Members (Late Campanian – Late Maastrichtian). Of this species, dissociated lateral arm plates and vertebrae were collected, generally in small numbers.

Euryalida

In this group of ophiuroids the disc and arms are covered by naked skin or by closely set granules; occasionally even distinct scales may occur. Ventral and dorsal arm plates are lacking or rudimentary at best, and are also covered by thick skin. Lateral arm plates are small and occur only on the lower side of the arms. These forms are mostly found attached to corals and other coelenterates; coiling of the arms is made possible by the streptospondyline type of vertebral articulation, with hourglass-shaped articulation pegs (see, as an example, Plate I, specimen 4).

Asteronychids have long and slender, unbranched arms with a thick skin cover. At least one species, *Asteronyx*? n. sp. (Plate I, specimen 3), known from the Vijlen Member, may be placed here. This appears to be an extremely rare taxon, with only very few dissociated lateral and dorsal(?) arm plates collected. Like extant *Asteronyx loveni* Müller & Troschel 1842, this form may have clung to pennatulids or gorgonids, feeding mainly on copepod crustaceans. Juvenile specimens of the extant species live on the sea floor and eat benthos.

Of the Euryalidae, which have moderately large discs and stout, simple or branched arms, two species are known: *Trichaster*? *ornatus* (Rasmussen 1950) (Plate I, specimen 4) and *Trichaster*? sp. (Plate I, specimen 5). Most conspicuous in these forms are the coarse granules on the lateral surfaces of the vertebrae, which constitute the attachment sites of small platelets, embedded in thick skin. Only dissociated vertebrae are known of these forms, which may prove to be conspecific. The subtler granulation of *Trichaster*? sp. may be a 'juvenile' trait, i.e. one occurring in young individuals or in the dorsal arm portion of adult specimens.

Ophiomyxina

Ophiomyxids have thick, naked skin covering both arms and disc, and concealing scales and plates, which are exceedingly brittle and poorly developed. Arm spines are stout and erect.

The extant *Ophiomyxa flaccida* (Say 1825) is found in reef habitats as well as in seagrass beds, but may be associated with many substrate types. Recorded stomach contents include sponges, algae and detritus. *Ophioscolex glacialis* Müller & Troschel 1842, another extant species, lives on muddy bottoms, in arctic and boreal waters, down to depths of 500–1100 m.

Of this group, at least four species from the Campanian and Maastrichtian are known in the study area. Of *Ophiomyxa*? *jekerica* (Plate I, specimen 6; Plate IV, specimen 13) only dissociated vertebrae are known. Of its congener, *Ophiomyxa*? n. sp., a fair number of lateral arm plates and the highly typical, fan-shaped arm spines, were collected. Similarly limited material is available of *Ophioscolex*? n. sp. 1 (Plate I, specimen 9) and *O.*? n. sp. 2, both comprising mainly dissociated arm ossicles.

Ophiurina

Ophiacanthidae

Discs in ophiacanthids have a close-set cover of small scales, with spines, stumps or granules; arm spines are erect, slender and often long. The Ophiacanthidae form one of the largest ophiuroid families. Its representatives are often found clinging to corals and other coelenterates and sponges, with arms being able to coil ventrally. Most probably these are rather sluggish detritus feeders.

Of *Ophiacantha*? *danica* (Plate I, specimen 8), a number of more or less complete individuals from the basal Gronsveld Member at the ENCI-Maastricht BV quarry are now known, the best preserved of which is the individual illustrated in Jagt et al. (1998, their plate 7, figure 4). This specimen preserves the disc and four arms, one of which was regenerating. However, the

state of preservation of the disc is such that it cannot substantiate the generic assignment.

Of two other species (Plate I, specimens 7, 10–11; Plate II, specimen 5) only dissociated lateral arm plates are known, from the Zeven Wegen and Vijlen Members, and possibly from the Geulhem Member (Early Palaeogene).

Ophiuridae

Ophiurids have scale-covered discs that are mostly naked, with arms short or of medium length with closely appressed, small, more or less rudimentary arm spines. Extant species of the genus *Ophiura* Lamarck 1816 are found both on hard (sandy) and soft, muddy bottoms, moving about freely and do not bury themselves. They acquire food either by placing themselves over it or by grabbing it by extending their arms. All sorts of animals, such as worms, crustaceans, molluscs, other echinoderms are eaten, but also detritus.

At least five species in the study area may be assigned to the Ophiuridae, of which *Felderophiura vanderhami* Jagt 1991 (Plate II, specimens 1–2) is the commonest and most easily recognised ophiuroid from the area. Many complete specimens have been collected lately, especially from storm-dominated portions of the succession (i.e. middle Meerssen Member). Found associated is a new species (Plate II, specimen 3), the generic assignment of which has not yet been established. It is characterised by a disc cover of several small platelets, arranged in fairly regular circlets, and a triangular cross-section of the arms. Of *Stegophiura? hagenowi* (Plate I, specimens 12–13), numerous arm fragments and partial discs are known; of its congener, *S.*? n. sp. (Plate I, specimens 15–18), only dissociated lateral arm plates and radial shields are available, from a single locality (CPL SA quarry, Haccourt).

The first ophiuroid ever described from the study area is *'Ophiura' fuerstenbergii* J. Müller 1847 (Plate II, specimens 18–20), which is here provisionally assigned to the ophiacanthid genus *Ophioplinthaca* Verrill 1899. Road works near Vaals–Eschberg during the late 1980s resulted in the discovery of quite a number of topotype specimens from a single level within the Early Campanian Vaals Formation.

Amphiuridae

As a rule, amphiurids have distinctly scaled discs, which may occasionally bear spines. Arms are long, slender and flexible, and spines short and erect. Amphiurids usually live buried at depths of about 10 cm, with only the arm tips protruding. These catch detritus, but also small animals such as worms and juvenile molluscs. Sometimes many individuals form webs across the seafloor. Most extant species live on muddy bottoms, but some occur under stones in shallow waters. Unlike other ophiuroids, amphiurids do not move about freely.

Despite their preferred mode of life, amphiurids are rare fossils. At least three species are known from the study area. Of *Amphiura*? n. sp. (Plate II, specimen 4), only arm ossicles were found. A few arm fragments preserve arm spines and ventral arm plates. Of the other two species, discs and arms are available. Paired infradental papillae in both of these show that they are assignable to the Amphiuridae. On the basis of the highly distinctive disc plating, a new genus will be established (Kutscher & Jagt, in press). This comprises two forms; one restricted to the early Late Campanian Benzenrade Member (Plate III, specimens 12, 17, 18), the other to the latest Maastrichtian Meerssen Member (Plate III, specimen 15). These forms may be members of a single lineage in which the younger is characterised by the loss of certain disc plates. This may be a paedomorphic trait.

Ophiothricidae

This family comprises brittle stars whose discs have well-developed scales, but this may be concealed by small spines or thorny stumps. Arms bear many long, erect spines, generally distinctly thorny and of a glassy appearance. Most species live in the tropics, often attached to sponges, gorgonians, comatulid crinoids, etc.

The Recent species *Ophiothrix fragilis* (Abildgaard 1789) occurs on hard bottoms, in empty shells, amongst serpulids, and also under stones on the shore. It may hide in small cavities, and feeds on worms and crustaceans, but also on small shells, other echinoderms, foraminifera and ascidians. Detritus is occasionally caught as well. This and related species occur in shallow waters close to the shore.

At least two species in the study area are assignable to the Ophiothricidae. Only fragmentary arms and dissociated arm ossicles were found (Plate II, specimens 10, 11, 14–17; Plate III, specimen 14). In the absence of discs, generic assignment is difficult. Representatives of this group are amongst the most fragile of

ophiuroids. This may explain why they have rarely been recorded as fossils.

Ophiocomidae

Ophiocomids include relatively large and conspicuously coloured forms, which have discs covered in granules concealing both scales and radial shields. Ventral and dorsal arm plates are well developed. Spines are solid and erect. The extant genus *Ophiocoma* Agassiz 1836 is highly typical of littoral settings in tropical seas.

At least two species of this group are known from the study area. The commoner is the widely distributed *Ophiocoma*? *senonensis* (Valette 1915) (Plate III, specimens 13, ?16), which has long, simple spines. Many arm fragments were found, but the generic assignment cannot be substantiated in the absence of discs. The species used to be classified with the Amphiuridae.

Ophiodermatidae

Ophiodermatids have close-set granules concealing the fine scales of both sides of the disc. The arms appear smooth, with small and closely appressed spines.

Fossils assignable to this family are amongst the best known Cretaceous ophiuroids: many specimens of the long-ranging *Ophiotitanos serrata* (Roemer 1840) (Plate II, specimens 6, 7, 12, 13) have been recorded from various European localities. Abundant material of *Ophioderma*? *substriatum* (Rasmussen 1950) and its congener *Ophioderma*? n. sp. (Plate I, specimen 14) was collected from the Late Campanian of the region.

Only few sturdy lateral arm plates are known of a new, latest Maastrichtian species (Plate II, specimens 8, 9); this form is provisionally referred to the genus *Ophiarachna* Müller & Troschel 1842.

Ophiolepididae

Like ophiodermatids (see above), ophiolepidids are well known from the fossil record. Discs and arms are commonly heavily plated, and, in species referred to the genus *Ophiomusium* Lyman 1869, arms are stiff and lack ventral and dorsal arm plates for most of their length. Tentacle pores are restricted to the proximalmost arm joints (e.g. Plate III, specimen 4), and arm spines generally are small or rudimentary. The best known species is *Ophiomusium granulosum* (Roemer 1840) (= *O. subcylindricum* (von Hagenow 1840); Plate IV, specimens 1–4), which is highly variable in ornament and number of spine tubercles. This species is especially common in the entire Zeven Wegen Member and at the base of the Gronsveld and Emael Members. Comparatively many, more or less complete discs with arms attached, are known from the basal 0.5 m of the Gronsveld Member at the ENCI-Maastricht BV quarry. These specimens allow a fuller characterisation of the species, since they also display internal features of oral frame and genital/radial shield articulation.

Also known from well-preserved discs is a new species of *Ophiomusium* (Plate III, specimens 1–4), which is particularly common in the Meerssen Member (latest Maastrichtian).

Much smaller is another, yet undescribed species of the same genus (Plate IV, specimen 5), which occurs in the Zeven Wegen and Vijlen Members. This has medially constricted, closely granulate lateral arm plates. Associated are remains of a generally small species, tentatively referred to the genus *Ophiolepis* Müller & Troschel 1842 (Plate III, specimens 9–11; Plate IV, specimen 6).

In the Geulhem Member (Early Palaeogene), another ophiolepidid is found; this represents a new species (Plate III, specimens 5–8), of which only a single arm fragment and dissociated lateral arm plates and radial shields are known so far.

Conclusions

The present overview shows the Late Cretaceous–Early Palaeogene ophiuroid faunas from the type area of the Maastrichtian Stage to be generally well-preserved and remarkably diverse. All the modes of life displayed by extant forms appear to be represented: forms clinging to coelenterates and thus occurring well above the substrate, those resting and moving about freely on the sediment surface, and those burying themselves to variable depths within the sediment. A single form, with fan-shaped spines (*Ophiomyxa*? n. sp.), may even have been able to swim over short distances, possibly to escape attacks by predators.

Instances of predation, manifested in the form of regenerating arms, were observed in at least four species, i.e., *Ophiacantha*? *danica*, *Felderophiura vanderhami*, *Ophiocten*? n. sp. and *Ophiomusium granulosum*. In fossil ophiuroid 'populations', the number of regenerating arms may be a measure of

predation pressure on those populations (see, among others, Aronson 1987).

Remarks on Berry's (1938) ophiuroid taxa

In samples taken at various localities in southern Limburg (the Netherlands) and received from Dr J. Bonnema, Berry (1938) distinguished four new species of ophiuroids. This material was collected from various lithostratigraphic units and is mostly poorly preserved. In earlier studies (by, among others, Rasmussen 1950, 1952, Jagt 1991) it has been suggested that Berry's taxa are best treated as *nomina dubia*, since it could be shown that several of his taxa consisted of a mixture of ossicles of distinct species. The recent discovery in the type Maastrichtian of more or less complete discs with arms attached has enabled us to assign most dissociated arm and disc ossicles to species confidently.

Although Berry indicated that the types of his species would be transferred to the Johns Hopkins University collections (Baltimore, U.S.A.), the material cannot be traced there at present. However, the collections at Groningen (Netherlands) State University contain material identified and labelled by Berry and returned to Bonnema. Through the courtesy of Professor van Straaten, I could select a number of ossicles for SEM photography (Plate IV, specimens 7–14). These pictures illustrate the poor preservation.

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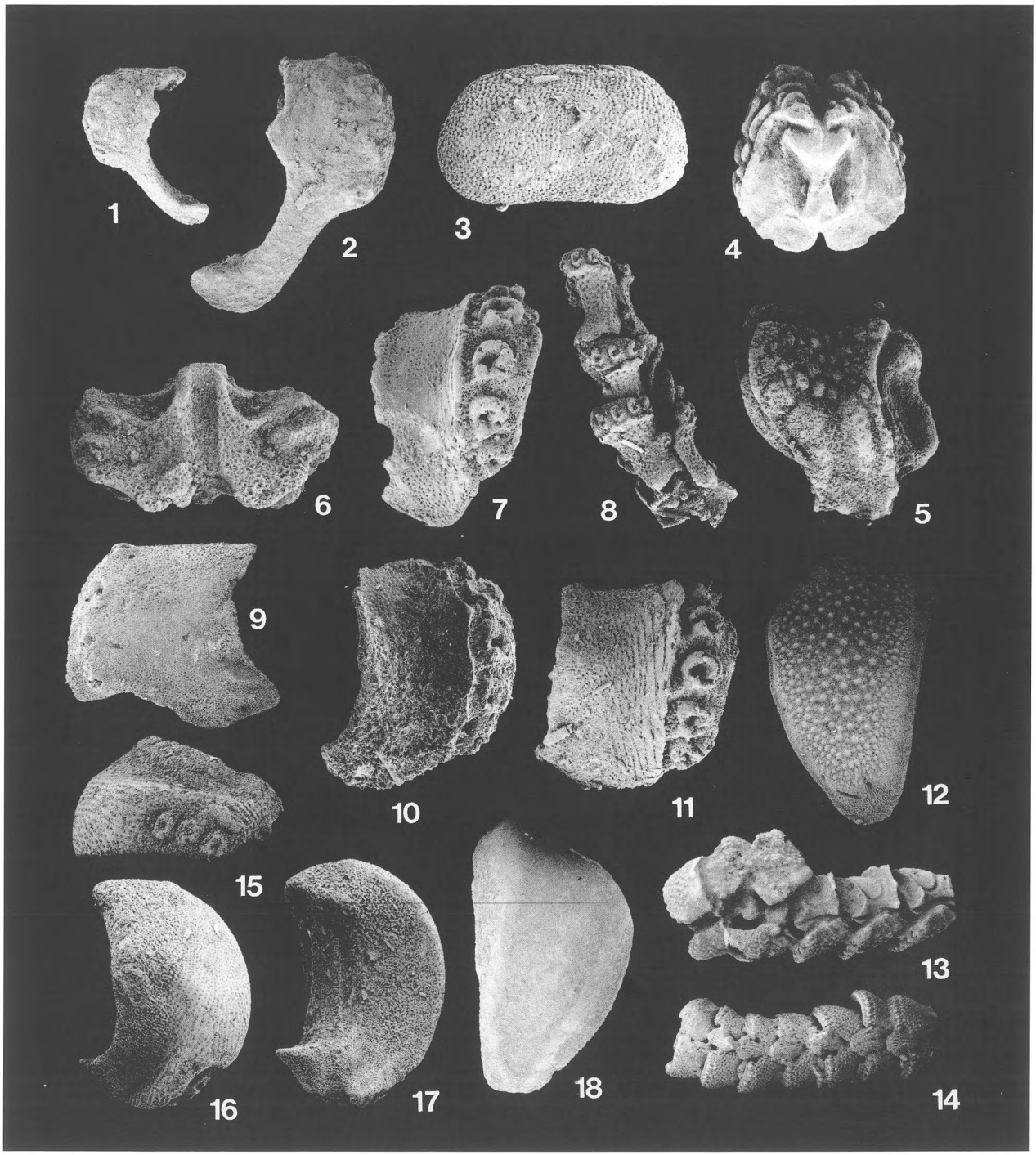

Plate I. Late Cretaceous and Early Palaeogene ophiuroids. 1–2: *Ophiosmilax*? n. sp., lateral arm plates, both × 13. 3: *Asteronyx*? n. sp., dorsal(?) arm plate, × 32. 4: *Trichaster*? *ornatus*, vertebra, × 14. 5: *Trichaster*? sp., vertebra, × 28. 6: *Ophiomyxa*? *jekerica* (Berry 1938), vertebra, × 40. 7, 10–11: *Ophiacantha*? n. sp., lateral arm plates, × 42, × 55 and × 50, respectively. 8: *Ophiacantha*? *danica* (Rasmussen 1952), distal arm fragment, × 40. 9: *Ophioscolex*? n. sp., lateral arm plate, × 40. 12–13: *Stegophiura*? *hagenowi* (Rasmussen 1950), radial shield and arm fragment, × 5.3 and × 8, respectively. 14: *Ophioderma*? n. sp., arm fragment, × 16. 15–18: *Stegophiura*? n. sp., lateral arm plates and radial shield, × 18 and × 5.4, respectively.

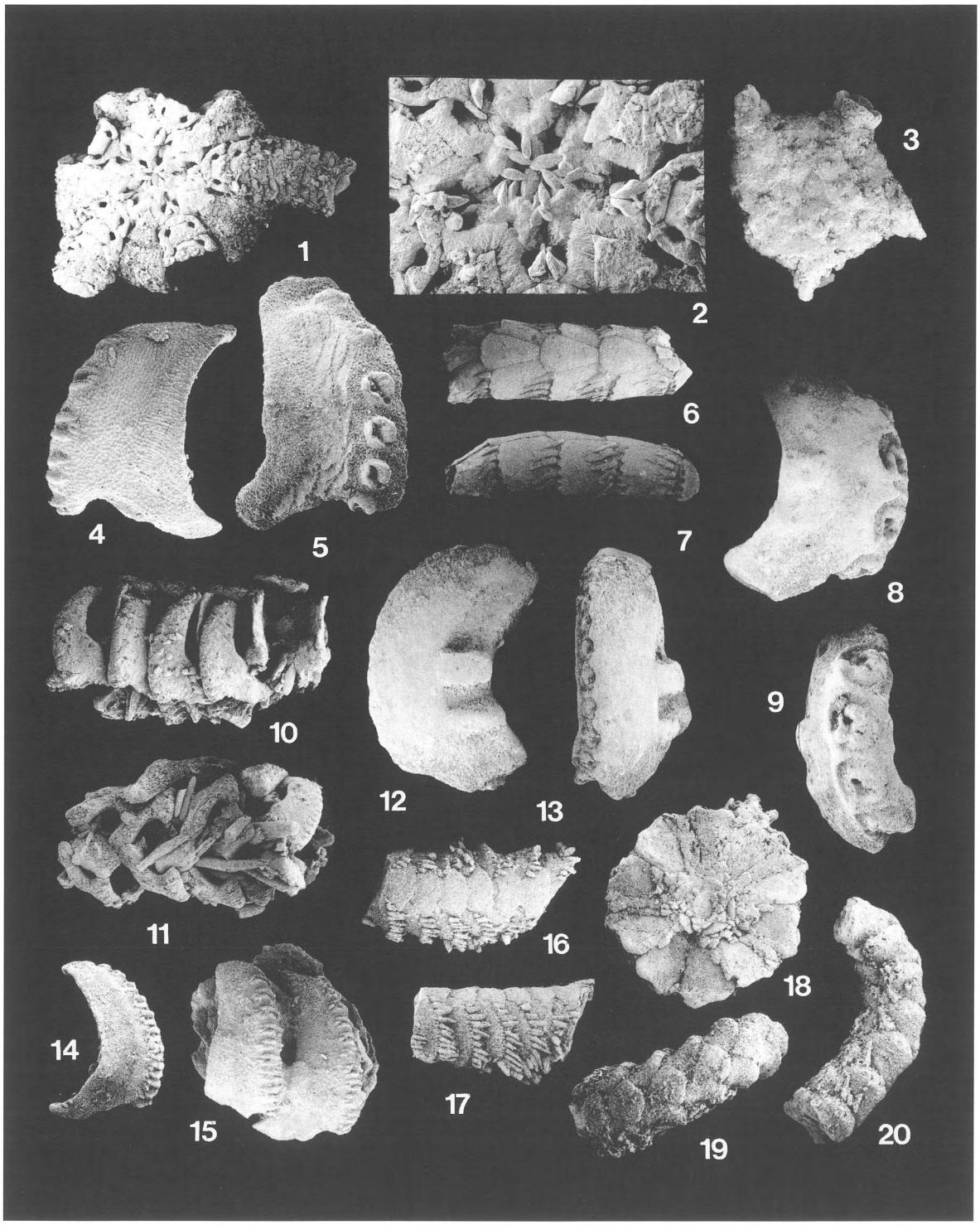

Plate II. Late Cretaceous and Early Palaeogene ophiuroids. 1–2: *Felderophiura vanderhami* Jagt 1991, ventral view of disc and close-up of oral frame, × 10 and × 30, respectively. 3: *Ophiocten*? n. sp., dorsal view of disc, × 5.7. 4: *Amphiura*? n. sp., lateral arm plate, × 52. 5: *Ophiacantha*? n. sp., lateral arm plate, × 52. 6–7, 12–13: *Ophiotitanos serrata* (Roemer 1840), arm fragments preserving spines and lateral arm plate, × 12 and × 15, respectively. 8–9: *Ophiarachna*? n. sp., lateral arm plate, × 12. 10–11, 14–17: *Ophiothrix*? n. sp. 1, arm fragments [preserving spines] and lateral arm plates, × 16 (10, 11), × 60 (14), × 30 (15) and × 8 (16, 17). 18–20: *Ophioplinthaca*? *fuerstenbergii* (J. Müller 1847), dorsal aspect of disc and arm fragments, × 8 and × 10, respectively.

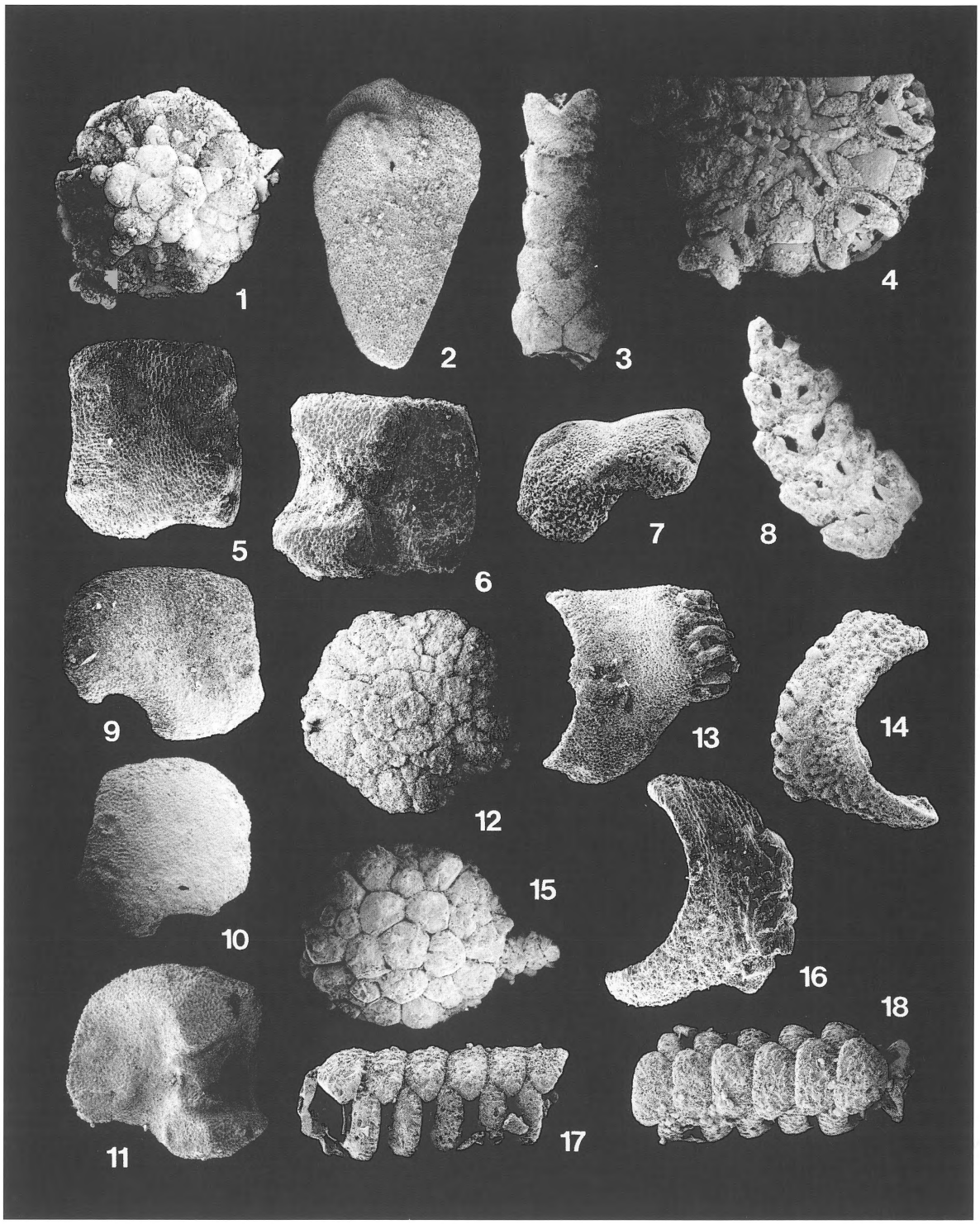

Plate III. Late Cretaceous and Early Palaeogene ophiuroids: 1–4: *Ophiomusium* n. sp. 1, ventral and dorsal views of disc, radial shield and arm fragment, × 6 (1), × 14 (2), × 11 (3) and × 12 (4). 5–8: Ophiolepididae n. sp., lateral arm plates and arm fragment, × 50 (5–7) and × 13. 9–11: *Ophiolepis*(?) n. sp. 2, lateral arm plates, all × 50. 12, 17–18: Amphiuridae n. gen. (? n. sp.), dorsal aspect of disc and arm fragments, × 9 (12) and × 20 (17, 18). 13, 16(?): *Ophiocoma*? *senonensis* (Valette 1915), lateral arm plates, × 35 and × 40, respectively. 14: *Ophiothrix*? n. sp. 2, lateral arm plate, × 40. 15: Amphiuridae n. gen., n. sp., dorsal aspect of disc, × 11.

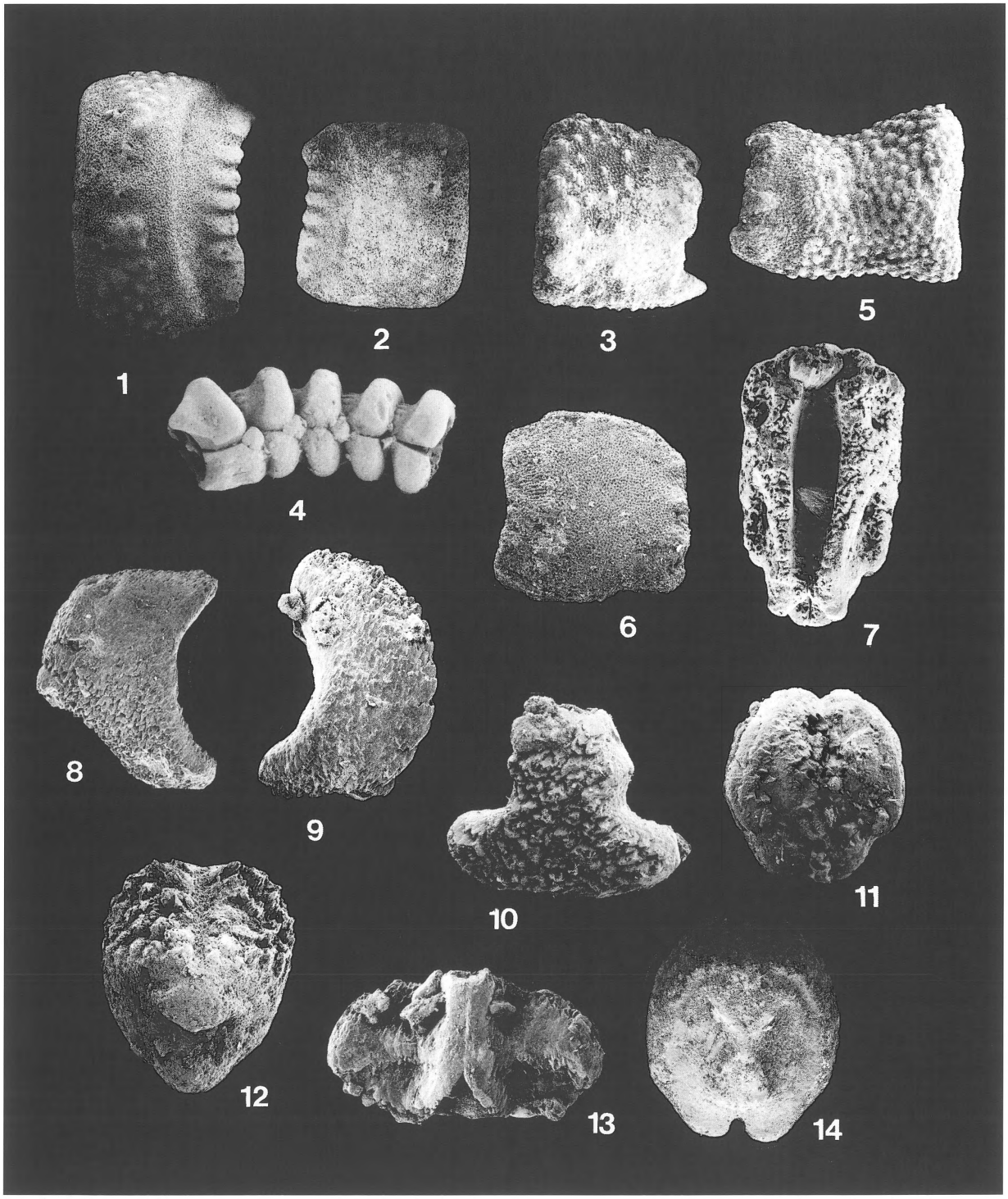

Plate IV. Late Cretaceous and Early Palaeogene ophiuroids: 1–4 : *Ophiomusium granulosum* (Roemer 1840), lateral arm plates and proximal arm fragment, × 16 (1), × 19 (2), × 30 (3) and × 7 (4). 5: *Ophiomusium* n. sp. 2, lateral arm plate, × 45. 6: *Ophiolepis*? n. sp. 1, lateral arm plate, × 50. 7: indeterminate (= *Dolichoarthra bemelenica* Berry 1938), vertebra, × 60. 8: lateral arm plate, possibly belonging to *Ophiocoma*? *senonensis* Valette 1915, × 50. 9–10: lateral and ventral arm plates, possibly belonging to *Felderophiura vanderhami* Jagt 1991, × 30 and × 40, respectively. 11–12, 14: *Asteronyx valkenburgensis* Berry 1938 [= *Trichaster*? sp. and *T.*? *ornatus* (Rasmussen 1950)], vertebrae, × 35 (11), and × 40 (12, 14). 13: *Platyarthra jekerica* Berry 1938 (= *Ophiomyxa*? *jekerica*), vertebra, × 45.