BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN

SCIENCES DE LA TERRE, 75: 183-200, 2005
AARDWETENSCHAPPEN, 75: 183-200, 2005

New latest Cretaceous and earliest Paleogene asteroids (Echinodermata) from The Netherlands and Denmark and their palaeobiological significance

by Daniel B. BLAKE & John W.M. JAGT

BLAKE, D.B & JAGT, J.W.M., 2005. — New latest Cretaceous and earliest Paleogene asteroids (Echinodermata) from The Netherlands and Denmark and their palaeobiological significance. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **75**: 183-200, 5 pls; Bruxelles-Brussel, March 31, 2005 – ISSN 0374-6291.

Abstract

Three new starfish (*Skiaster vikingr* n. gen., n. sp., *Betelgeusia exposita* n. sp., and *Aldebarania taberna* n. sp.), and the first fossil occurrence of *Cheiraster*? sp., are recorded from Maastrichtian (Late Cretaceous) and Danian (Early Paleogene) rocks of The Netherlands and Denmark. *Skiaster vikingr*, a member of the goniasterid subfamily Pseudarchasterinae, adds to the known diversity and apparent significance of that subfamily. *Betelgeusia exposita* is the second Cretaceous species of the Radiasteridae to be described; together, the two species suggest that this now infrequently encountered deep-water family was of greater significance in the past. Morphology and occurrences of *Betelgeusia* suggest niches similar to those now occupied by *Astropecten*. *Aldebarania taberna* (Astropectinidae) is similar to *A. arenitea* from eastern North America, suggesting communication across a narrower North Atlantic. *Cheiraster*? sp. (Benthopectinidae) provides added support for shelf occurrence during the Cretaceous of this now deep-water family; it is a member of the Neobenthopectininae, indicating Mesozoic presence of derived benthopectinids. Reflecting earlier work, the present study suggests gradual emergence of the modern asteroid fauna during the Mesozoic and Cenozoic without major terminal Cretaceous extinction.

Key-words: Asteroidea, Cretaceous, Paleogene, The Netherlands, Denmark, taxonomy.

Résumé

Trois nouvelles astéries (*Skiaster vikingr* n. gen., n. sp., *Betelgeusia exposita* n. sp., et *Aldebarania taberna* n. sp.) et la première présence fossile de *Cheiraster*? sp. ont été reconnues sur la marge continentale dans des dépôts d'âge Maastrichtien (Crétacé supérieur) et Danien (Paléocène) des Pays-Bas et du Danemark. *Skiaster vikingr* de la sous-famille goniastéride Pseudarchasterinae étend la diversité connue et la signification apparente de cette sous-famille. *Betelgeusia exposita* est le second taxon crétacé des Radiasteridae à être décrit. A eux deux ces deux espèces laissent supposer que cette famille typique, pour les dépôts profonds, mais rare aujourd'hui, fût plus importante dans le passé. La morphologie et les occurrences de *Betelgeusia* suggèrent des niches similaires à celles occupées par *Astropecten*. *Aldebarania taberna* (Astropectinidae) est proche de *A. arenitea* de l'Est de l'Amérique du Nord – probablement grâce à un Océan Atlantique nord plus étroit. *Cheiraster*? sp. (Benthopectinidae) ajoute un argument en faveur de la présence de cette famille sur le shelf pendant le Crétacé de cette famille alors qu'aujourd'hui elle est limitée aux mers profondes. Elle appartient aux Neobenthopectininae, ce qui démontre la présence au Mésozoïque de benthopectinidés dérivés.

Mots-clefs: Asteroidea, Crétacé, Paléogène, Pays-Bas, Danemark, taxionomie.

Introduction

Although the Asteroidea includes many heavily skeletonized species, specimens are rare among marine invertebrate fossils, and as a result overall history of the class and its phylogeny are poorly understood. The Cretaceous and Paleogene chalks of northwest and central Europe have provided one of the more extensive ancient asteroid faunas, and one that has been studied by generations of dedicated palaeontologists. Nevertheless, fossils are infrequently encountered, and most occurrences consist of disarticulated marginals, which, although important, provide only an incomplete history. Mesozoic and Cenozoic events leading to the emergence of the contemporary fauna have received only limited attention.

Four recently discovered chalk specimens representing all three orders of valvatacean asteroids (*sensu* BLAKE, 1987) document a bit of the status of this important group near the end of the Mesozoic and beginning of the Cenozoic eras. These fossils, in conjunction with others previously described (*e.g.*, BLAKE & REID, 1998; VILLIER *et al.*, 2004), suggest a gradual emergence of familial groups established in the Mesozoic and absence of abrupt faunal change at the end of the Cretaceous.

Geographic and stratigraphic setting

Of the four taxa here described, three have been collected from units assigned to the Maastricht Formation [late Maastrichtian, *Belemnitella junior* and *Belemnella (Neobelemnella) kazimiroviensis* zones], as exposed in the type area of the Maastrichtian Stage (SE Netherlands, NE Belgium). In recent years, the basal portion of the Gronsveld Member at the ENCI-Maastricht bv quarry (St Pietersberg, Maastricht) has yielded numerous well-pre-

served bourgueticrinine crinoids (JAGT, 1999b), with associated, albeit rarer, comatulids, as well as ophiuroids (JAGT, 2000a) and dissociated asteroid ossicles (JAGT, 2000b). This assemblage, which includes *Cheiraster*? sp., accumulated under storm conditions followed by near-absence of bioturbation. LIEBAU (1978) typified this part of the Maastricht Formation as a mid-sublittoral setting, with subtropical temperatures and characterised by the occurrence of seagrass communities.

Aldebarania taberna n. sp. is from the upper portion of the Nekum Member, which at the CBR-Romontbos quarry (Eben Emael, Liège), comprises a discontinuous tabular flint level from which numerous echinoids and ammonoids have been collected recently. This level is close to the Kanne Horizon, an undulating erosion surface overlain by very coarse bioclastic sand. The type of *Betelgeusia exposita* n. sp. was collected from the overlying unit, the Meerssen Member, at the ENCI-Maastricht bv quarry, from a level that has yielded numerous ophiuroids (JAGT, 2000a) and decapod crustacean remains. According to LIEBAU (1978), the Nekum and Meerssen members are high-energy deposits, being characterised by a high production of carbonate detritus that led to the establishment of a broad, shallow, well-lit and warm carbonate platform with a rich phytal association. There is a continuous shallowing trend with the Meerssen Member, but deposition of the highest unit (IVf-6) must have occurred in deeper water.

Skiaster vikingr n. gen., n. sp., is from Stevns Klint, north of Højerup Kirke, having been collected from the early Paleocene (Danian) *Tylocidaris abildgaardi* Zone bioherms (GRAVESEN, 1993). The matrix is bryozoan limestone, which BROMLEY (1979) considered to have been deposited in shallow water, below wave base. Associated goniasterid asteroids include the key index taxa *Metopaster spencerii* BRÜNNICH NIELSEN, 1943, *M. kagstrupensis* BRÜNNICH NIELSEN, 1943, and *Crateraster anchylus* (BRÜNNICH NIELSEN, 1943).

Palaeobiological significance

Fossils described here document a small part of status of crown-group asteroid occurrence near the Mesozoic-Cenozoic transition. The fossil record of asteroids is poor and provides only limited information on the post-Palaeozoic history of the class (VILLIER & KUTSCHER, 1999). These authors nevertheless were able to recognise two stages in crown-group diversification, consisting of a Jurassic radiation followed by a long period of comparative quiescence. The crown group is first known from the Triassic (ZARDINI, 1973; BLAKE & HAGDORN, 2003) but the fossil record from this interval is extremely sketchy, even by the standards of asteroids. Significant asteroid diversification has been documented from Jurassic strata [*e.g.*, WRIGHT, 1863-1880; SCHÖNDORF, 1910; HESS, 1972, 1975; BLAKE, 1984, 1990a] including representation of many surviving families. Other families, some of fragile construction, have a Cretaceous earliest-known occurrence (*e.g.*, BLAKE, 1988; VILLIER *et al.*, 2004). The poor fossil record of asteroids has not demonstrated significant extinction within the group at the end of the Cretaceous; instead, implications such as those discussed below suggest more subtle change in faunal make-up through the Mesozoic and Cenozoic.

Discussion below treats the Pseudarchasterinae as basal within the Goniasteridae; this approach follows the phylogeny of extant families of BLAKE (1987, 1990b), which in turn was based on publications of many systematists, including VERRILL (1899), discussed below. *Pseudarchaster* is known from the Portlandian (Upper Jurassic; see BLAKE, 1986), which is fairly close to but somewhat younger than the age of the oldest-known goniasterids. This chronological inconsistency might result from the poor fossil record (VILLIER & KUTSCHER, 1999), or pseudarchasterines might remain unrecognised among known Jurassic fossils, or phylogenetic inference based on the morphology of extant taxa might be incorrect; these are hypotheses to be tested by future research.

No phylogenetic analysis is attempted here. A pseudarchasterine-like morphology was selected as a basal configuration for crown-group asteroid morphology (BLAKE, 1990b) and discussions here do not affect that interpretation. Efforts have been made to isolate a stem-group branch basal to the crown group (BLAKE & HAGDORN, 2003; BLAKE & HOTCHKISS, 2004), but candidate genera do not appear close enough to pseudarchasterines to provide a reliable outgroup for phylogenetic reconstruction of the Pseudarchasterinae. Discussions below, *e.g.* on the position of *Skiaster* n. gen., therefore use a traditional descriptive notion of morphological intermediacy.

Skiaster vikingr n. gen., n. sp. (Valvatida) is a member of the Pseudarchasterinae SLADEN, 1889. VERRILL (1899) found this subfamily to be morphologically intermediate between more typical goniasterids and certain astropectinids; he specifically cited *Plutonaster* SLADEN, 1889 but *Tethyaster* SLADEN, 1889 and other genera could be listed as well. The fossil record includes examples of seemingly intermediate morphology; for instance, the Jurassic astropectinid *Pentasteria* VALETTE, 1929 is suggestive of astropectinids such as *Plutonaster* as well as of goniasterids (*e.g.*, HESS, 1960, 1973, 1987; HESS & BLAKE, 1995; KUTSCHER & RÖPER, 1999).

VERRILL (1899) carried evaluation of inferred transitional types a step further in noting that *e.g.*, *Mediaster* is intermediate between pseudarchasterines and more characteristic goniasterids. The more characteristic goniasterids typically have non-fasciolate, more equidimensional (rather than tabular) marginals. In addition, abactinals are tabular, closely abutted, and both marginals and abactinals are incompletely granulate in some taxa. Apparent dominance of goniasterid assemblages by varied non-pseudarchasterines in the Cretaceous chalk faunas (*e.g.*, SLADEN, 1891, 1893; SPENCER, 1905, 1907, 1908, 1913; SCHULZ & WEITSCHAT, 1971, 1975, 1981; BRETON, 1979, 1992; GALE, 1987a, b; JAGT, 2000b) documents significant diversification of goniasterids during Cretaceous time.

Pseudarchaster and *Skiaster* n. gen. are joined by another Mesozoic pseudarchasterine, *Formalhautia* BLAKE & REID, 1998, which exhibits a third, distinctive pseudarchasterine morphology (in *Formalhautia*, a comparatively small disk and long, slender arms reminiscent of those of certain species of *Astropecten*). The morphological differences among the three suggest a diversity of pseudarchasterines during the Mesozoic and perhaps the early Cenozoic, as well as significant convergence between pseudarchasterines and other goniasterids.

Betelgeusia exposita (Paxillosida; Radiasteridae) is only the second member of its family to be described, joining the mid-Cretaceous *B. reidi* BLAKE & REID, 1998. *Betelgeusia* is similar to extant *Radiaster*, which is known from a comparatively few widely separated deep-water settings, whereas *Betelgeusia* in contrast is now known from Cretaceous shallow-water, perhaps turbulent sediments from both sides of the North Atlantic. *Betelgeusia* is suggestive of *Astropecten* in marginal and fasciolar development as well as in the arrangement of ambulacral-adambulacral muscle flanges, which were interpreted (BLAKE, 1981) as suited for twisting of arms, useful in predation or righting behaviour. Given the limited fossil record, *Betelgeusia* distribution in time and space suggests past success in shallow-water niches similar to those occupied by *Astropecten* and *Luidia* today. BLAKE (1987) assigned *Radiaster* to a basal position within the Paxillosida, and its Cretaceous occurrence is consistent with this interpretation.

Aldebarania taberna (Paxillosida; Astropectinidae) is similar to the type species, *A. arenitea* BLAKE & STURGEON, 1995 from eastern North America, demonstrating occurrence on both sides of the then-smaller North Atlantic. Both *Aldebarania* species are of low profile and constructed of stout primary ossicles with sturdy granules, and share an overall form similar to those of certain modern and Cretaceous species found in shallow, turbulent sedimentary settings (BLAKE & KUES, 2002) that are at least similar to the *Aldebarania* occurrences.

Cheiraster? sp. (Notomyotida) represents the family Benthopectinidae, which is today a largely deep-water family. In contrast, *Cheiraster*? sp. and other fossil benthopectinids have been collected from shallow-water sediments (*e.g.*, BLAKE, 1984; BLAKE & REID, 1998; JAGT, 2000b) and thus the Benthopectinidae is among families once but no longer common in shallow-water settings (BOTTJER & JABLONSKI, 1988). BLAKE (1984) recognised the Paleobenthopectininae for certain Jurassic species; *Cheiraster*? sp., a member of the living Neobenthopectininae, helps to constrain the divergence of crown-group benthopectinids.

Taxonomy

Terminological usage follows SPENCER & WRIGHT (1966) and BLAKE & HAGDORN (2003). The following abbreviations are used to denote the repository of material referred to in the text: CAS - California Academy of Sciences, San Francisco; NHMM - Natuurhistorisch Museum Maastricht (K - M.M.M. Kuypers Colln; MD - M.J.M. Deckers Colln); RGM - Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Geologie en Mineralogie); USNM - United States National Museum, Washington DC.

Class Asteroidea DE BLAINVILLE, 1830
Order Valvatida PERRIER, 1884
Family Goniasteridae FORBES, 1841
Subfamily Pseudarchasterinae SLADEN, 1889

REMARKS

Skiaster n. gen. exhibits robust, tabular, closely appressed marginals that lack significantly enlarged spines, and stout, paxilliform abactinal ossicles. These characters indicate the subfamily Pseudarchasterinae within the family Goniasteridae. Further, superomarginals abutted at the dorsal arm midline are only known in goniasterids. Ossicular form is also broadly suggestive of certain members of the Astropectinidae although abactinals are more gracile in this family and marginals less uniform and tabulate.

Genera included in this subfamily are *Pseudarchaster* SLADEN, 1889, and *Paragonaster* SLADEN, 1889, reported from both fossil and Recent occurrences; *Gephyreaster* FISHER, 1910, and *Perissogonaster* FISHER, 1913, reported only from Recent occurrences; and *Formalhautia* BLAKE & REID, 1998, and *Skiaster* n. gen., known exclusively from fossil occurrences.

DESCRIPTION

Abactinal ossicles robust, paxilliform, more or less columnar. Crowns convex, rounded or elliptical; in larger ossicles, re-entrant present below crown, column distinct. Base enlarged, lobate, providing passageway for papulae. Arrangement such that about six abactinals cluster about another abactinal, all aligned in rows. Carinal series enlarged.

Marginals tabular, moderately large, wide compared to length, closely appressed, deeply fasciolated, paired. Other than in *Skiaster* n. gen., superomarginals rarely abutted across arm midline, and then only close to arm tips. Outer surfaces of marginals arched; however, not strongly so as to yield a bulbous appearance; outer surfaces not flattened. Lateral shoulders of marginals rounded rather than angular, re-entrants beneath shoulders (above shoulders in inferomarginals) at most weakly developed. Superomarginals closely granulated; inferomarginals of some species with several somewhat enlarged spines whereas in other species, inferomarginals evenly granulated.

Adambulacrals robust, furrow margins angular, in life providing partial separation between subsequent tube feet; angular margins serving to narrow furrow, especially distally. Furrow spines curved or divergent, subambulacral spines either in longitudinal rows or clustered. Actinal series numerous in many species; ossicles angular, arranged in columns parallel to the ambulacral furrows. Specialized spinules but not true pedicellariae can be adjacent to ambulacrals; pedicellariae found only rarely on actinal, marginal ossicles of *Paragonaster*.

Mouth angle ossicles large, prominent, with elongate spinules both on ventral surfaces and at ossicular margins. In some species or individuals, an enlarged, unpaired median spine is present at proximal end of ossicles.

DISCUSSION

SLADEN (1889) assigned both *Pseudarchaster* and *Aphroditaster* SLADEN, 1889, to the then-new Pseudarchasterinae, but he provided no diagnosis. Since that time, the concept has received scattered recognition in the literature but little discussion. The most comprehensive available treatment of the subfamily is that of VERRILL (1899). VERRILL (1899) did not formally list assigned genera but he included species of *Pseudarchaster*, *Aphroditaster*, *Paragonaster*, and *Rosaster* PERRIER, 1894, and he included the type species for all but *Paragonaster*, which was only subsequently designated by FISHER (1919). Presumably VERRILL's approach was intended to encompass genera rather than only the cited species.

The above description was largely rephrased from VERRILL (1899), although it has not been comprehensively checked against component species, and it might need to be altered further. Marginal and abactinal form are given greater emphasis here than that accorded by VERRILL. Because pseudarchasterine ancestry and a comprehensive phylogeny are not available, apomorphic characters cannot now be recognised.

SPENCER & WRIGHT (1966) also recognised the subfamily, and they included *Paragonaster*, *Perissogonaster*, *Pseudarchaster* and *Aphroditaster*. *Aphroditaster* was considered to be a synonym of *Pseudarchaster* by MORTENSEN (1927), an interpretation subsequently embraced by A.M. CLARK (1993) and followed here. *Gephyreaster* also is included here.

Marginal and abactinal form indicate alignment of *Skiaster* n. gen. with *Pseudarchaster* whereas the superomarginals, abutted across the midline of the arm, might suggest affinities with any of the numerous non-pseudarchasterine goniasterids similarly developed. Non-pseudarchasterine goniasterid genera with abutted superomarginals were surveyed here, and their marginal and abactinal form found to be distinct from that of the Pseudarchasterinae. In the pseudarchasterines, marginals are tabular (their width, or dimension normal to the arm margin, is significantly greater than their length) whereas in the other genera, marginals are proportionately narrower, even becoming square in dorsal (or ventral, for inferomarginals) outline. The outer face of the marginal is approximately parallel to the overall dorsal (or ventral) surface near the abactinals (or actinals), and it curves to perpendicular to the body plane at the ambitus, where the surface joins that of the paired marginal. In pseudarchasterines, curvature is approximately even, typically yielding a rounded shoulder, whereas in the other genera, the shoulder tends to be quite abrupt, in many genera with a re-entrant at the juncture of the superomarginals and inferomarginals. Fascioles between subsequent inferomarginals are present in pseudarchasterines but absent from the other genera. Narrow, sharp grooves bordered by small granules occur between abactinals, marginals, and actinals of many goniasterids; these grooves typically are quite large and well defined in pseudarchasterines and smaller in other goniasterids. Accessories consist of closely spaced granules in pseudarchasterines, and spines can occur on inferomarginals. Among other genera, ossicular surfaces bare of granules and even raised relative to the granulate area are present, and spines are lacking.

Abactinals are paxilliform in pseudarchasterines whereas in other goniasterids they are more nearly tabular, broader, and less uniform, although in some (*e.g.*, *Mediaster*), tabulae approach a paxilliform condition. The paxilliform dorsals of the pseudarchasterines are separated by passageways near their dorsal ends whereas abactinals of the other genera tend to be closely fitted and hence of polygonal outline.

VERRILL (1899) found pseudarchasterine abactinals and marginals and their accessories to be similar to those of the goniasterid *Mediaster* and its allies but differing in the angular furrow margins of the adambulacrals, the lack of bivalved pedicellariae, and the divergent furrow spinules. He noted the presence of fascioles, spines on the actinals and inferomarginals, and the unpaired oral spine provide further distinguishing characters.

The recommended synonymy of *Aphroditaster* with *Pseudarchaster* (MORTENSEN, 1927) is accepted here, and *Rosaster* is not included because its marginal and abactinal morphology are not pseudarchasterine. *Paragonaster* and *Perissogonaster* are similar to *Pseudarchaster*, and the difference between *Perissogonaster* and *Paragonaster* is limited to presence of an odd interbrachial marginal in *Perissogonaster*. *Formalhautia* BLAKE & REID, 1998, shares the essential marginal and abactinal form of *Pseudarchaster*, as does *Skiaster* n. gen., insofar as can be determined.

Genus ***Skiaster*** n. gen.

TYPE SPECIES

Skiaster vikingr n. sp., by monotypy.

DERIVATION OF NAME

From Gr. *skia*, meaning shadow. Superomarginals abutted across the midline of the arms shadows development in typical goniasterid genera, but presence in a pseudarchasterine indicates a separate lineage and thereby a shadowing of the pattern evolved in other goniasterids.

DIAGNOSIS

Monospecific, see below.

Skiaster vikingr n. gen., n. sp.
(Pl. 1, Figs. 1, 2; Pl. 2, Figs. 1-8)

TYPE

Holotype and only known specimen is NHMM K 2086, from the Lower Danian Bryozoan Limestone (*Tylocidaris abildgaardi* Zone), north of Højerup Kirke, Stevns Klint

(Sjælland, Denmark). Specimen incomplete, exposed in dorsal view, consisting of the disc and one incomplete arm. Radius of the arm remnant approximately 17 mm, interbrachia 10 and 11 mm. The marginal frame is partially collapsed and ossicles are displaced; the dorsal surface is collapsed into the disk displacing abactinal ossicles. Recrystallization partially obscures ossicular detail, and dorsal ossicles are further obscured by remnants of accessory ossicles.

DERIVATION OF NAME

From Old Norse vikingr, or Norseman, in allusion to its geographic provenance; grammar: noun, gender: masculine.

DIAGNOSIS

Pseudarchasterine with pentagonal disc and superomarginals abutted at dorsal arm midlines, the abutted arrangement extending from the proximal end of the arm. Abactinals paxilliform, slender and columnar to robust with a flaring base and short re-entrant below crown.

DESCRIPTION

Five-armed asteroid, disc proportionately large, pentagonal. Arms slender, robust, length unknown.

Abactinals paxilliform, up to approximately 1 mm in height, 1 mm in diameter at base. Crown hemispherical, column short, stout, situated medially on base; base conical, circular or equidimensional and polygonal in outline with facets for papulae on some ossicles. Enlarged abactinals (*e.g.*, primary circlet, carinal series) not detected on largely disrupted and debris-obscured surface.

Inferomarginals incompletely exposed, but marginals of two series generally similar insofar as can be ascertained. Marginals tabular, width of interbrachial superomarginal about 2 mm, length about 1 mm, height about 1.5 mm; superomarginals at arm base of width about 3 mm, length 1.5 mm. Dorsally directed portion of superomarginals quite wide, then evenly rounded approaching lateral side faces (*i.e.*, ossicular transverse section not angular). Longitudinal profile of adradial part of interbrachial superomarginals rounded. Adjacent superomarginals sharing very regular, straight-sided boundary furrow approximately 0.2 mm wide. Outer face finely and evenly pitted, pits clearly separated, some ossicular debris suggests an even covering of granules; no indication of differential sizes of pits to indicate differentiation of accessories. Interossicular grooves smooth. Side faces comparatively large, bordered by a low, rounded ridge, remainder of surfaces slightly sunken, flattened medially. Marginals from adjacent sides of arm abutted at arm midline beginning at disc. Adradial-ventral corner of superomarginal and adradial-dorsal corner of inferomarginal bearing a rounded notch that would have formed a broad interior groove in the living individual. Intermarginal face of superomarginal apparently concave, that of inferomarginal flattened. Inferomarginals probably fasciolate, ossicular debris suggests presence of enlarged spinelets.

No other ossicular type clearly exposed.

REMARKS

Body shape, including the pentagonal disc and apparently elongate arms with marginals abutted along the arm midline, is indicative of the Goniasteridae. Both arm shape and the conformable fit of the marginals along the arm midline indicate that the ossicles were abutted in life rather than collapsed together taphonomically. Abactinals are similar to those of *Pseudarchaster* or perhaps *Mediaster* (Goniasteridae) but not greatly unlike those of *e.g.*, *Tethyaster*, *Blakiaster* PERRIER, 1881, and *Patigaster* FISHER, 1906 (Astropectinidae).

Skiaster n. gen. is the only pseudarchasterine with marginals abutted at the dorsal arm midline. Among goniasterids with marginals abutted at the midline, it is suggestive of *Nymphaster* SLADEN, 1889 (see Pl. 1, Figs. 4, 6 here), from which it differs in shape of both marginals and abactinals. Probably for both taphonomic and taxonomic reasons, abactinal ossicles have not been well illustrated in the literature, but among the examples available to the authors, the abactinal morphology of the Cretaceous (late Campanian) species *Nymphaster studlandensis* (SCHULZ & WEITSCHAT, 1975) is most suggestive of that of the pseudarchasterines in that these ossicles are both tall and slender and thereby suggestive of paxillae (see Pl. 1, Figs. 9-11). In *N. studlandensis*, however, abactinals are closely fitted and columnar, with subdued papular pores and deep lateral depressions (for connective tissues?), which are characteristic of non-pseudarchasterine goniasterid abactinals in spite of their paxillae-like height. Among non-pseudarchasterines, *Skiaster* n. gen. and other pseudarchasterines are quite similar in marginal and abactinal shape to such genera as *Mediaster* (see Pl. 1, Figs. 5, 8), from which they differ in a number of characters as outline by VERRILL (1899; see above). Specifically, *Mediaster* lacks abutted superomarginals.

Attempts to further expose the ventral skeleton were unsuccessful due to preservational constraints.

Order Paxillosida PERRIER, 1884
Family Radiasteridae FISHER, 1916
Genus *Betelgeusia* BLAKE & REID, 1998

TYPE SPECIES

Betelgeusia reidi BLAKE & REID, 1998, by original designation.

Betelgeusia exposita n. sp.
(Pl. 3, Figs. 1-5)

v. 2000b astropectinid sp. nov. JAGT, p. 387 (*partim*), pl. 5, figs. 1-5.

TYPE

Holotype and only known specimen is NHMM K 3364, from the higher Meerssen Member (Maastricht Forma-

tion), upper Upper Maastrichtian [*Belemnella (Neobelemnella) kazimiroviensis* Zone], ENCI-Maastricht BV quarry, Maastricht. The incomplete specimen is exposed in ventral view. It consists of about one-half of the disc, one complete arm, and part of a second. Arm radii approximately 15 mm, interbrachial radius about 8 mm. A fragment from the proximal right side of the incomplete arm is separate from the remainder of the specimen. The fragment is about 6 mm in length and includes 7 marginal pairs; both dorsal and ventral surfaces are exposed. The specimen was preserved largely undistorted; however, recrystallization and some accessories partially obscure detail.

DERIVATION OF NAME

From Latin *expositus, -a*, because the specimen was found on the moss-covered bedding plane of a well-exposed slab of rock at the ENCI-Maastricht bv quarry.

DIAGNOSIS

Betelgeusia with a rounded body margin that largely results from a rounded margin to the superomarginals. Actinal and inferomarginal series not corresponding; mouth angle pair robust, forming a keel-shaped, broad, angular surface. Prominent ventral spines not recognised.

DESCRIPTION

Arm spacing indicating a five-armed asteroid; disc of moderate size; interbrachia rounded but not broad; arms triangular, broad at base, straight-sided, tapering evenly.

Abactinals paxilliform, delicate, with a low, expanded base; column slender, grading evenly into an expanded crown; crown not differentiated from column by distinct re-entrant. Paxillae small, about four in one mm in transverse series on proximal arm fragment. Paxillae aligned in transverse and probably inclined longitudinal series. Crown bearing cluster of small, cylindrical spinelets. No differentiation of abactinals recognised on available very small fragment of dorsal surface, which does not include either mid-arm interval (that would reveal possible carinals) nor central disc (that would reveal a differentiated primary circlet). Madreporite not exposed. Terminal robust, square, prominent.

Marginals paired, approximately 16 between midline of interbrachia and terminal; more proximal marginals radially arranged, more distally becoming inclined to arm axis. Marginals of two series similar but inferomarginals larger than superomarginals; proximal inferomarginal approximately 1.25 mm in width, corresponding superomarginal approximately 0.75 mm, superomarginal set back from arm margin such that a portion of inferomarginal is visible in dorsal view. Marginals uniformly tabular but with prominent lateral articular ridges (or perhaps disjunct articular facets); fasciolar groove large. Articular ridges set back from abradial margin of both marginal series forming a well-defined fasciolar abradial notch on margins of arms. Fascioles parallel sided, aligned or slightly offset from corresponding grooves separating adjacent actinal and abactinal series on ventral and dorsal surfaces. Ventral surface of inferomarginals and dorsal surfaces of inferomarginals and superomarginals bearing apparently uniform, closely spaced cylindrical spinelets about 0.3 mm in length, similar to but perhaps a bit more robust than paxillary spinelets. Inferomarginals with a dense, marginal, laterally directed fringe of somewhat more robust spinelets approximately 0.5 mm in length. Spinelets circular or perhaps somewhat flattened in cross section.

Actinals arranged in distinct radial series separated by well-developed fasciolar grooves; 19 to 22 series of actinals correspond to about 12 proximalmost inferomarginals; beyond that interval, inferomarginals abut adambulacrals. Actinals poorly exposed; ossicles probably massive, nearly 15 ossicles present in longer series near interbrachia, becoming reduced to a single ossicle at series termination.

Ambulacral-adambulacral series approximately 33 to 35 between mouth angle ossicle and terminal; distalmost 3 or 4 ossicular pair extremely tiny, partially enclosed by the much-enlarged terminal. Ambulacrals very similar to those of *Astropecten*, with a nearly square adradial interval bearing robust cross-furrow articular structures. Ossicles robust, with lateral (rather than overlapping) longitudinal articular surfaces. Podial pores large. Ambulacral-adambulacral articulation flanges asymmetrical, the proximal offset adradially and hook-shaped; distal flange J-shaped and prolonged abradially.

Adambulacrals incompletely exposed, upright, rectangular in outline, transversely elongate with long axes inclined to the arm axis. Like inferomarginals, abradial ends of ossicles inclined distally. Proximalmost adambulacral somewhat enlarged relative to subsequent ossicles, its adradial side abutting mouth angle ossicles. No differentiation of furrow series spine bases from subambulacral bases can be recognised; any differentiation must have been comparatively minor. Remaining spines few, essentially similar to other ventral-surface spines: short, cylindrical, simple.

Mouth angle ossicles robust, broad, keel-like, outline of pair rounded rectangular to broadly elliptical, adjacent pairs not closely abutted in life. Furrow sides bearing uniform pustules extending well up sides of ossicle. Dorsal articular flange apparently large, broad, blade-like, extended strongly towards oral-aboral axis. Circumoral (*i.e.*, first ambulacral) similar to ambulacrals in ventral view, but more robust. Odontophore partially visible between mouth angle ossicles; ossicle robust, closely fitted between MAO.

REMARKS

Recrystallization and the sandy carbonate sediment render determination of detail under about 1 mm difficult. The new species is similar to the type species, *Betelgeusia reidi*, in all essential aspects, differing only in comparatively minor details. The margin of the body was more angular in *B. reidi*, with the superomarginal cuneate in outline (BLAKE & REID, 1998, figs. 8.6, 8.7, 8.15), whereas the margin of *B. expositа* n. sp. is more rounded.

Actinal series approximately correspond in number with inferomarginals in the type species, but series are more numerous in the new species. The mouth angle pair is more robust, rounded, and keel-like in the new species. The ventral surface of the single specimen of the new species has been almost entirely denuded of spines, but those remaining do not suggest presence of the elongate spines of the type, and the dorsal ossicles appear to be more delicate in the new species. The proportionately greater width of the marginals of the type species might be a function of specimen size.

Betelgeusia exposita n. sp. appears similar in form to *Dipsacaster jadeti* BRETON *et al.*, 1995, from the Maastrichtian of Petites-Pyrénées (France). The latter species is also known from a single specimen, unfortunately (for comparison purposes) with the dorsal rather than the ventral surface exposed. *Dipsacaster* (Astropectinidae) is similar to *Betelgeusia* in overall form but the two species of concern here differ in some details. The marginal ossicles of *D. jadeti* (the inferomarginals only incompletely exposed) appear robust in comparison with those of *Betelgeusia exposita* n. sp. The somewhat delicate ambulacral ossicles (largely obscured by abactinals) and the delicate, aligned series of apparently paxilliform abactinals both appear similar to those of *Betelgeusia*, and reflect the difficulty of taxonomic assessment of scanty and incompletely exposed asteroid material. Unfortunately, many asteroid taxa are known only from such material.

Family Astropectinidae GRAY, 1840
Genus *Aldebarania* BLAKE & STURGEON, 1995

TYPE SPECIES
Aldebarania arenitea BLAKE & STURGEON, 1995, by original designation.

Aldebarania taberna n. sp.
(Pl. 4, Figs. 1-6)

v. 2000b *Aldebarania* sp. nov. JAGT, p. 392, pl. 4, figs. 8-10; pl. 5, figs. 6-12 (?pl. 7, figs. 5, 6).

TYPES
The five specimens included in the hypodigm are all from the Nekum Member (Maastricht Formation); the holotype (NHMM 1999015-1) and paratypes (NHMM 1999015-2, -3, NHMM JJ 2787) come from the CBR-Romontbos quarry. All three NHMM 1999015 specimens are external moulds in flint preserving both surfaces and all were buried nearly intact with only limited ossicular disruption, although arm tips have been lost. In NHMM 1999015-1, R of most complete arm is 22 mm with a few mm missing; r = 13 mm; in NHMM 1999015-2, R = 14 mm, r = 6 mm, and in NHMM 1999015-3, R = 6 mm, r = 4 mm. NHMM JJ 2787 is a single well-preserved distal superomarginal and paratype RGM 428 072 (from the ENCI-Maastricht BV quarry) is a well-preserved medial superomarginal.

Two disc fragments, NHMM MB 377-23/a, b, both from the Meerssen Member (base IVf-3; Maastricht Formation) at Blom quarry (Berg en Terblijt), might belong to the new species, but granular preservation does not allow unequivocal assessment. Although the fragments are included here they are not considered a part of the hypodigm on which the species is based and they are not specifically encompassed in the description below, although they are not known to be inconsistent with this description.

DERIVATION OF NAME
From Latin *taberna, -a*, hut, inn (grammar: noun, gender: feminine); the species name, a play on words, is in honour of Mr Ludo Indeherberge of Zonhoven, Belgium, who collected these (and other) important fossils and has made them available for study.

GENERIC AND FAMILIAL ASSIGNMENT
The new species shares all of the diagnostic characters of *Aldebarania* BLAKE & STURGEON, 1995, including stellate overall shape and rectangular marginals with deep fascioles. BLAKE & STURGEON (1995) discussed ordinal and familial assignment of the genus, which is not repeated here.

DIAGNOSIS
Paxillae low, stout, with a subpolygonal crown; paxillae arranged in regular series. Accessories consist of closely fitted short spinelets. Superomarginals weakly inset from edge of inferomarginals. Medial, raised ridge on inferomarginals lacking.

DESCRIPTION
Similar to the type and only other known species, *A. arenitea* BLAKE & STURGEON, 1995, in form and paxillary arrangement. Paxillae uniform over surface except those adjacent to interbrachial superomarginals and distally on arm are progressively reduced in size; no indication of enlarged carinals nor primary circlet in limited available material. Paxillae stout, low, some at least with papulary facets; crowns subpolygonal forming tightly fitted dorsal surface. Ossicles arranged in intersecting radial, longitudinal series with one or two series reaching terminal. Madreporite not located. Terminal enlarged relative to adjacent ossicles, elongate, outline polygonal with distal tip somewhat rounded, surface rounded, covered by short spinelets.

Marginals similar to those of *A. arenitea* in form and arrangement. Superomarginals weakly inset from edge of superomarginals, no raised ridges present on inferomarginals. Inferomarginal fringe spinelets elongate, spinelets of ventral surface uniform.

Actinal fields collapsed and obscured taphonomically, but similar to those of *A. arenitea* insofar as can be ascertained except actinal ossicle articular flanges relatively subdued. Mouth angle ossicular pair prominent,

broadly rounded. MAO accessories including scattered spinelets but preservation incomplete; other mouth frame characters unavailable. Ambulacrals, adambulacrals very incompletely exposed, form typical of astropectinids and similar to those of *A. arenitea*. Ambulacrals nearly bilateral with robust cross-furrow articular structures; adambulacrals upright, strongly overlapping, with furrow series of curved, flattened spines; subambulacrals straight, conical, pointed, similar to those of the furrow series.

REMARKS

Differentiation of the two known species is subtle in part because of similarities, in part because of limited material available for each, and in part due to taphonomic disruption. The two species differ in the form of the inferomarginals, and more subtly, in the nature of the abactinals.

Order Notomyotida LUDWIG, 1910
Family Benthopectinidae VERRILL, 1899
Subfamily Neobenthopectininae BLAKE, 1984

REMARKS

The rectangular to subelliptical form of the marginals, with a bulbous outer face and a single spine base, the small, conical abactinals, and the rectangular form of ambulacral ossicles are typical of modern benthopectinids (BLAKE, 1984), indicating affinities with the Neobenthopectininae of the Benthopectinidae.

Genus ***Cheiraster*** STUDER, 1883

REMARKS

Characterisation of modern benthopectinid genera (CLARK & DOWNEY, 1992) stresses characters not readily available in fossil material in general and in the present specimen in particular. The fossil has robust, blocky marginals; among modern benthopectinid genera, CLARK & DOWNEY (1992) identified three with similar enlarged marginals, *Cheiraster*, *Acontiaster* DÖDERLEIN, 1921 and *Pectinaster* PERRIER, 1885. Unfortunately, blocky marginals perhaps are plesiomorphic at the familial level because they are suggestive of marginals of other valvatacean families and unlike the distinctive flatter marginals with prominent spine bases that typify most benthopectinid genera.

Species assignments among *Pontaster*, *Pectinaster* and *Cheiraster* have been uncertain (see CLARK, 1989), testifying to the uncertainty of the generic concepts. Presence of prominent spines serve to separate *Acontiaster*. Similtarities between the fossil and *Cheiraster echinulatus* (PERRIER, 1875) suggest affinities (see below) with that genus, and *C. echinulatus* is the type species of the subgenus *Barbadosaster* CLARK, 1981, indicating correct assignment of *C. echinulatus* at the generic level. Final taxonomic assessment of the present specimen, however, must await re-evaluation of modern species with more comprehensive treatment of their ossicular morphology.

***Cheiraster*? sp.**
(Pl. 5, Figs. 1-7)

MATERIAL

The sole known specimen is NHMM MD 4105 from the basal Gronsveld Member (Maastricht Formation), Upper Maastrichtian, ENCI-Maastricht bv quarry. The specimen, exposed in dorsal view, consists of most of the ventral portion of the disc and proximal intervals of three arms. Arm remnant radii approximately 18, 17 and 15 mm, interbrachia 4 and 5 mm. Dorsal disc ossicles have been nearly lost, and ossicles of the arms have suffered some displacement, although overall arm form is retained. Recrystallization and some accessories partially obscure ossicular detail.

DESCRIPTION

Arm spacing indicating a five-armed asteroid; disc small; arms slender, columnar; length unknown. A few small (approx. 0.5 mm), conical abactinals remain on the disc and proximal intervals of the arms; these are too few to determine original numbers or arrangement. Madreporite not recognised.

Marginals in a double series; probably slightly offset, elliptical in outline, elongate parallel to arm axis, outer face bulbous (arched), inferomarginals overlapping, superomarginals abutting, intermarginal faces flat. Outer face bearing one(?) enlarged, circular spine base, remainder of face bearing small, separated pustules.

Ambulacrals preserved in approximate life positions, with dorsal and adradial portions exposed but ventral and abradial portions largely obscured. Ambulacrals robust, length of proximal ossicles approximately 1 mm, width approximately 2 mm. Dorsal outline hourglass shaped, with large ampullar basins. Ossicles approximately bilateral (although incompletely exposed and some apparently truncated taphonomically). Adambulacral articular flanges large, broad. Adradial part of ossicle large, robust, lateral ambulacral-ambulacral articular surfaces robust, abutted laterally (rather than overlapping), cross-furrow articular structures robust. Dorsal ridge well defined medially but both adradial and abradial ends of ossicle flattened. Other ossicular types not clearly exposed.

REMARKS

The enlarged marginals of this specimen are similar to those of *Cheiraster echinulatus* (see Pl. 5, Fig. 8), which, like the fossil, has comparatively small marginal spine bases; debris associated with the fossil also suggests small spines.

Ambulacral ossicles in the fossil are typical of neobenthopectinids in general; unfortunately, these ossicles are not well enough known among benthopectinid genera to be used in identification.

Acknowledgements

We thank M.J.M. Deckers, L. Indeherberge and M.M.M. Kuypers for donation of material, D.L. Pawson, Cynthia Ahern and authorities of

the U.S. National Museum (Washington DC) who made facilities fully available and allowed access to collections in their care, L. Villier for commenting on an earlier version of the typescript, and the managements of CBR and ENCI-Maastricht bv (Heidelberg Cementgroup) for permission to do fieldwork at their quarries over recent years.

References

BLAINVILLE, H.M. DE, 1830. Zoophytes. *Dictionnaire des Sciences Naturelles*, F.G. Levrault, Strasbourg, 60 p.

BLAKE, D.B., 1981. The new Jurassic sea star *Eokainaster* and comments on life habits and the origins of the modern Asteroidea. *Journal of Paleontology*, **55**: 33-46.

BLAKE, D.B., 1984. The Benthopectinidae (Asteroidea: Echinodermata) of the Jurassic of Switzerland. *Eclogae geologicae Helvetiae*, **77**: 631-647.

BLAKE, D.B., 1986. Some new post-Paleozoic sea stars (Asteroidea: Echinodermata) and comments on taxon endurance. *Journal of Paleontology*, **60**: 1103-1119.

BLAKE, D.B., 1987. A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata). *Journal of Natural History*, **21**: 481-528.

BLAKE, D.B., 1988. A first fossil member of the Ctenodiscidae (Asteroidea; Echinodermata). *Journal of Paleontology*, **62**: 626-631.

BLAKE, D.B., 1990a. Hettangian Asteriidae (Echinodermata: Asteroidea) from southern Germany: taxonomy, phylogeny and life habits. *Paläontologische Zeitschrift*, **64**: 103-123.

BLAKE, D.B., 1990b. Adaptive Zones of the Class Asteroidea (Echinodermata). *Bulletin of Marine Science*, **46**: 701-718.

BLAKE, D.B. & HAGDORN, H., 2003. The Asteroidea (Echinodermata) of the Muschelkalk (Triassic of Germany). *Paläontologische Zeitschrift*, **77**: 23-58.

BLAKE, D.B. & HOTCHKISS, F.R.C., 2004. Recognition of the asteroid (Echinodermata) crown group: implications of the ventral skeleton. *Journal of Paleontology*, **78**: 359-370.

BLAKE, D.B. & KUES, B.S., 2002. Homeomorphy in the Asteroidea (Echinodermata); a new Late Cretaceous genus and species from Colorado. *Journal of Paleontology*, **76**: 1007-1013.

BLAKE, D.B. & REID, R., III., 1998. Some Albian (Cretaceous) asteroids (Echinodermata) from Texas and their paleobiological Implications. *Journal of Paleontology*, **72**: 512-532.

BLAKE, D.B. & STURGEON, K., 1995. *Aldebarania arenitea*, a new genus and species of Astropectinidae (Asteroidea; Echinodermata) from the Maastrichtian (Upper Cretaceous) Peedee Formation of North Carolina. *Journal of Paleontology*, **69**: 376-380.

BOTTJER, D.J. & JABLONSKI, D., 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios*, **3**: 540-560.

BRETON, G., 1979. Les astéries du Crétacé de Normandie. *Bulletin trimestriel de la Société géologique de Normandie et Amis du Muséum du Havre*, **65**: 5-85.

BRETON, G., 1992. Les Goniasteridae (Asteroidea, Echinodermata) jurassiques et crétacés de France: taphonomie, systématique, biostratigraphie, paléobiogéographie, évolution. *Bulletin trimestriel de la Société géologique de Normandie et Amis du Muséum du Havre*, Hors-série, Supplément **78**: 1-590.

BRETON, G., BILOTTE, M. & SIGRO, G., 1995. *Dipsacaster jadeti* sp. nov., Astropectinidae (Asteroidea, Echinodermata) du Maastrichtien des Petites-Pyrénées (France). *Bulletin trimestriel de la Société géologique du Normandie et Amis du Muséum du Havre*, **82**: 35-42.

BROMLEY, R.G., 1979. Chalk and bryozoan limestone: facies, sediments and depositional environments. *In*: BIRKELUND, T. & BROMLEY, R.G. (Editors), Cretaceous-Tertiary Boundary Events Symposium, I. The Maastrichtian and Danian of Denmark. University of Copenhagen, pp. 16-32.

BRÜNNICH NIELSEN, K., 1943. The asteroids of the Senonian and Danian deposits of Denmark. *Biologiske Skrifter fra det danske Videnskabernes Selskab*, **(2)**5: 3-68.

CLARK, A.M., 1989. Notes on Atlantic and other Asteroidea, 1. Family Benthopectinidae. *Bulletin of the British Museum of Natural History (Zoology)*, **41**: 91-135.

CLARK, A.M., 1989. An index of names of Recent Asteroidea – Part 1: Paxillosida and Notomyotida. *In*: JANGOUX, M. & LAWRENCE, J.M. (Editors), Echinoderm Studies 3. A.A. Balkema, Rotterdam, pp. 225-349.

CLARK, A.M., 1993. An index of names of Recent Asteroidea - Part 2: Valvatida. *In*: JANGOUX, M. & LAWRENCE, J.M. (Editors), Echinoderm Studies 4. A.A. Balkema, Rotterdam, pp. 187-366.

CLARK, A.M. & DOWNEY, M.E.D., 1992. Starfishes of the Atlantic. Chapman & Hall, London, 794 pp.

DÖDERLEIN, L., 1921. Die Asteriden der Siboga-Expedition i: Porcellanasteridae, Astropectinidae, Benthopectinidae. *Siboga-Expeditie Monograph*, **46**(1): 1-47.

DÜBEN, M.W. & KOREN, J., 1846. Öfversigt af Skandinaviens Echinodermer. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **1844**: 229-238.

FISHER, W.K., 1906. The starfishes of the Hawaiian Islands. *Bulletin of the United States Fish Commission*, **23**: 987-1130.

FISHER, W.K., 1910. New genera of starfishes. *Annals and Magazine of Natural History*, **5**: 171-173.

FISHER, W.K., 1913. Four new genera and fifty-eight new species of starfishes from the Philippine Islands, Celebes and the Moluccas. *Proceedings of the United States National Museum*, **46**: 599-648.

FISHER, W.K., 1916. Notes on the systematic position of certain genera and higher groups of starfishes. *Proceedings of the Biological Society of Washington*, **29**: 1-6.

FISHER, W.K., 1919. Starfishes of the Philippine Seas and adjacent waters. *Bulletin of the United States National Museum*, **100**: 1-712.

FORBES, E., 1841. A history of British starfish and other animals of the class Echinodermata. John Van Voorst, London, 162 pp.

GALE, A.S., 1987a. Goniasteridae (Asteroidea, Echinodermata) from the Late Cretaceous of north-west Europe. Part 1. Introduction. The genera *Metopaster* and *Recurvaster*. *Mesozoic Research*, **1**: 1-69.

GALE, A.S., 1987b. Goniasteridae (Asteroidea, Echinodermata) from the Late Cretaceous of north-west Europe. 2. The genera *Calliderma*, *Crateraster*, *Nymphaster* and *Chomataster*. *Mesozoic Research*, **1**: 151-186.

GRAVESEN, P., 1993 Early Danian species of the echinoid genus *Tylocidaris* (Cidaridae, Psychocidarinae) from eastern Denmark. *Contributions to Tertiary and Quaternary Geology*, **30**: 41-73.

GRAY, J.E., 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias* Linnaeus). *Annals and Magazine of Natural History*, **20**: 193-204.

HESS, H., 1960. *Pentasteria* (*Archastropecten*) *procera* n. sp. (Asteroidea, Astropectinidae) aus dem Bajocien von Cheltenham (England). *Eclogae geologicae Helvetiae*, **53**: 331-334.

HESS, H., 1972. Eine Echinodermen-Fauna aus dem mittleren Dogger des Aargauer Juras. *Schweizerische Paläontologische Abhandlungen*, **92**: 1-87.

HESS, H., 1973. Neue Echinodermenfunde aus dem mittleren Dogger des Aargauer Juras. *Eclogae geologicae Helvetiae*, **66**: 625-656.

HESS, H., 1975. Die fossilen Echinodermen des Schweizer Juras. *Veröffentlichungen aus dem Naturhistorischen Museum Basel,* **8**, 1-130.

HESS, H., 1987. Neue Seesternfunde aus dem Dogger des Schweizer Juras. *Eclogae geologicae Helvetiae*, **80**: 907-918.

HESS, H. & BLAKE, D.B., 1995. *Coulonia platyspina* n. sp., a new astropectinid sea star from the Lower Cretaceous of Morocco. *Eclogae geologicae Helvetiae*, **88**: 777-788.

JAGT, J.W.M., 1999a. Late Cretaceous-Early Paleogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 1: Introduction and stratigraphy. *Scripta Geologica*, **116**: 1-57.

JAGT, J.W.M., 1999b. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 2: Crinoids. *Scripta Geologica*, **116**: 59-255.

JAGT, J.W.M., 2000a. 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 and John W.M. Jagt. *Scripta Geologica*, **121**: 1-179.

JAGT, J.W.M., 2000b. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 5: Asteroids. *Scripta Geologica*, **121**: 181-375.

KUTSCHER, M. & RÖPER, M., 1999. Die Asteroidea (Seesterne) aus den ''Papierschiefern'' von Hienheim und Ried (Malm Zeta 3, Untertithonium). *Archaeopteryx*, **17**: 1-13.

LIEBAU, A., 1978. Paläobathymetrische und paläoklimatische Veränderungen im Mikrofaunenbild der Maastrichter Tuffkreide. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **157**: 233-237.

LUDWIG, H., 1910. Notomyota, eine neue Ordnung der Seesterne. *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften*, **23**: 435-466.

MORTENSEN, T., 1927. Echinoderms of the British Isles. Oxford University Press, Oxford, 269 pp.

PERRIER, E., 1875-1876. Révision de la collection de stellérides du Muséum d'Histoire Naturelle de Paris. *Archives de Zoologie expérimentale et générale,* **4**(1875): 265-540; **5**(1876): 1-104, 209-309.

PERRIER, E., 1881. Description sommaire des espèces nouvelles d'astéries. *Bulletin of the Museum of Comparative Zoology*, **9**: 1-31.

PERRIER, E., 1884. Mémoire sur les étoiles de mer recueillis dans la Mer des Antilles et le Golfe de Mexique. *Nouvelles Archives du Muséum d'Histoire Naturelle Paris*, **6**: 127-276.

PERRIER, E., 1885. Première note préliminaire sur les échinodermes recueillis durant les campagnes de dragages sous-marins du Travailleur et du Talisman. *Annales des Sciences naturelles*, **(6)19**: 1-72.

PERRIER, E., 1894. Expéditions scientifiques du Travailleur et du Talisman: échinodermes. G. Masson, Paris, 431 pp.

SCHÖNDORF, F., 1910. Die Asteriden der deutschen Trias. *Jahresbericht des Niedersächsischen Geologischen Vereins*, **1910**: 90-115.

SCHULZ, M.-G. & WEITSCHAT, W., 1971. Asteroideen aus der Schreibkreide von Lägerdorf (Holstein) und Hemmoor (Nord-Niedersachsen). *Mitteilungen aus dem geologisch-paläontologischen Institut der Universität Hamburg*, **40**: 107-130.

SCHULZ, M.-G. & WEITSCHAT, W., 1975. Phylogenie und Stratigraphie der Asteroideen der nordwestdeutschen Schreibkreide. Teil I: *Metopaster/Recurvaster*- und *Calliderma/Chomataster*-Gruppe. *Mitteilungen aus dem geologisch-paläontologischen Institut der Universität Hamburg*, **44**: 249-284.

SCHULZ, M.-G. & WEITSCHAT, W., 1981. Phylogenie und Stratigraphie der Asteroideen der nordwestdeutschen Schreibkreide. Teil II: *Crateraster/Teichaster*-Gruppe und Gattung *Ophryaster. Mitteilungen aus dem geologisch-paläontologischen Institut der Universität Hamburg*, **51**: 27-42.

SLADEN, W.P., 1885. Asteroidea. *In*: WYVILLE THOMSON, C. & MURRAY, J., Report on the Scientific Results of the voyage of H.M.S. Challenger during the years 1873-76, Narrative **1**(2): 607-617.

SLADEN, W.P., 1889. The Asteroidea. *Report of the Scientific Results, Voyage of the Challenger (Zoology)*, **30**: 1-935.

SLADEN, W.P., 1891. A monograph on the British fossil Echinodermata from the Cretaceous formations, Volume second. The Asteroidea, Part First. *Monograph of the Palaeontographical Society of London*, **1891**: ii + 1-28.

SLADEN, W.P., 1893. A monograph on the British fossil Echinodermata from the Cretaceous formations, Volume Second. The Asteroidea, Part Second. *Monograph of the Palaeontographical Society of London*, **1893**: 29-66.

SPENCER, W.K., 1905. A monograph on the British fossil Echinodermata from the Cretaceous formations, Volume second. The Asteroidea, Part Third. *Monograph of the palaeontographical Society of London*, **1905**: 67-90.

SPENCER, W.K., 1907. A monograph on the British fossil Echinodermata from the Cretaceous formations, Volume second. The Asteroidea and Ophiuroidea, Part Fourth. *Monograph of the Palaeontographical Society of London*, **1907**: 91-132.

SPENCER, W.K., 1908. A monograph on the British fossil Echinodermata from the Cretaceous formations, Volume second. The Asteroidea and Ophiuroidea, Part Fifth. *Monograph of the Palaeontographical Society of London*, **1908**: 133-138.

SPENCER, W.K., 1913. The evolution of the Cretaceous Asteroidea. *Philosophical Transactions of the Royal Society of London,* **B214**: 99-177.

SPENCER, W.K. & WRIGHT, C.W., 1966. Asterozoans. *In:* MOORE, R.C. (Editor), Treatise on Invertebrate Paleontology, Part U, Echinodermata 3. Geological Society of America and University of Kansas Press, Boulder and Lawrence, pp. U4-U107.

STIMPSON, W., 1857. On the Crustacea and Echinodermata of

the Pacific shores of North America. *Boston Journal of natural History,* **6**: 444-532.

STUDER, T., 1883. Bericht über die Asteriden welche während der Reise SMS 'Gazelle' um die Erde gesammelt wurden. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, **1883**: 128-132.

STUDER, T., 1884. Verzeichniss der während der Reise SMS 'Gazelle' um die Erde 1874-76 gesammelten Asteriden und Euryaliden. *Physikalische Abhandlungen der Königlich-Preussichen Akademie der Wissenschaften zu Berlin*, **1884**(3): 1-64.

VALETTE, A., 1929. Note sur quelques stellérides jurassiques du Laboratoire de Géologie de la Faculté des Sciences de Lyon. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon,* **16**: 1-39.

VERRILL, A., 1899. Revision of certain genera and species of starfishes with description of new forms. *Transactions of the Connecticut Academy*, **10**: 145-234.

VILLIER, L., BLAKE, D.B, JAGT, J.W.M. & KUTSCHER, M., 2004. A preliminary phylogeny of the Pterasteridae (Echinodermata, Asteroidea) and the first fossil record: Late Cretaceous of Germany and Belgium. *Paläontologische Zeitschrift*, **78**: 281-300.

VILLIER, L. & KUTSCHER, M., 1999. How dissociated ossicles can further our understanding of the origins of the Neoasteroidea. An example from the Toarcian of Western Europe. *In*: CANDIA CARNEVALI, M.D. & BONASORO, F. (Editors), Echinoderm Research 1998, Proceedings of the Fifth European Conference on Echinoderms, Milan/Italy/7-12 September 1998. A.A. Balkema, Rotterdam/Brookfield, pp. 417-422.

WRIGHT, T., 1863-1880. British Fossil Echinodermata of the Oolitic formations: vol. 2, Asteroidea and Ophiuroidea. *Monograph of the Palaeontographical Society of London,* **1861**(1863): 1-130; **1864**(1866): 131-154; **1880**(1880): 155-203.

ZARDINI, R., 1973. Fossili di Cortina; atlante degli echinodermi cassiani. Trias Medio Superiore della Regione Dolomitica Attorno a Cortina d'Ampezzo. Foto Ghedina, Cortina d'Ampezzo, 29 pp.

Daniel B. BLAKE
Department of Geology,
Room 245 Natural History Building
University of Illinois
1301 West Green Street
Urbana, IL 61820
USA
E-mail: dblake@uiuc.edu

John W.M. JAGT
Natuurhistorisch Museum Maastricht
de Bosquetplein 6
NL-6211 KJ Maastricht
The Netherlands
E-mail: john.jagt@maastricht.nl

Typescript submitted: July 1, 2004
Revised typescript received: October 15, 2004

Explanation of Plates

PLATE 1

Comparative morphology of Pseudarchasterinae (Figs. 1, 2) and non-pseudarchasterine goniasterids (Figs. 3-11). Scale bar equals 5 mm in 1-5, 1 mm in 6-11.

Figs. 1, 2 — *Skiaster vikingr* n. gen., n. sp., holotype (NHMM K 2086) in inclined dorsal and full dorsal views, respectively; marginals are abutted across the midline of the arm.

Figs. 3, 7 — *Pseudarchaster parelli* DÜBEN & KOREN, 1846; inclined dorsal view (CAS 137908; Recent, Aleutian Islands, Alaska) and lateral view of abactinal ossicles (CAS 117915; Recent, off Oregon); tabular marginals and paxilliform abactinals such as those of *Pseudarchaster* indicate pseudarchasterinae affinities of *Skiaster vikingr* n. gen., n. sp.

Figs. 4, 6 — *Nymphaster moebii* (STUDER, 1884); Muséum national d'Histoire naturelle collections, Paris (unnumbered); Recent, 12^0 55' S, 44^0 57' E; inclined dorsal view and lateral view of abactinals. Species is similar to *S. vikingr* but marginals are too angular with an intermarginal re-entrant and abactinals are not paxilliform; compare with Figs. 9-11.

Figs. 5, 8 — *Mediaster aequalis* STIMPSON, 1857; University of Illinois collections, unnumbered specimen; Recent, off California. VERRILL (1899) recognised *Mediaster* as intermediate between pseudarchasterines and other goniasterids (see text). Abactinals are superficially similar to those of *Pseudarchaster*, but they are not paxilliform. Marginals are more rounded, although differences are subtle.

Figs. 9-11 — *Nymphaster studlandensis* (SCHULZ & WEITSCHAT, 1975); 9, NHMM 1994640b, ambulacrals and lower surfaces of abactinals to right; 10, 11, NHMM 1994640a. This fossil is close to the pseudarchasterines but the abactinals, although tall, are facetted and closely fitted rather than paxilliform (see Pl. 2, Figs. 2, 5-8).

PLATE 2

Skiaster vikingr n. gen., n. sp., holotype (NHMM K 2086). Scale bar equals 1 mm.

Fig. 1 — Marginals at base of arm are closely fitted, indicating that they abutted at the arm midline in life.

Fig. 2 — Central disc, marginal series encloses paxillae.

Fig. 3 — Superomarginals in slightly inclined dorsal view.

Fig. 4 — Superomarginal in lateral view.

Fig. 5 — Interbrachial superomarginals with paxillae to right.

Fig. 6 — Superomarginals (centre), inferomarginal (lower left), and abactinals (right), with smaller abactinals below.

Figs. 7, 8 — Paxilliform abactinal with re-entrant below crown; papular facets to left of right photograph; compare Pl. 1, Figs. 6-11.

PLATE 3

Betelgeusia exposita n. sp., holotype and only known specimen (NHMM K 3364). Scale bar in 1-3 equals 3 mm, and 1 mm in 4, 5.

Fig. 1 — Ventral view showing general configuration.

Fig. 2 — Alignment of actinals between marginals and adambulacrals, with distinct fasciolar grooves between series of ossicles. Fasciolar grooves are not precisely aligned between ossicular types. Two mouth angle pair to right.

Fig. 3 — Arrangement of actinals, adambulacrals; ambulacrals as seen to left are similar to those of *B. reidi* as well as those of *Astropecten* (see BLAKE & REID, 1998) suggesting functional parallels.

Fig. 4 — Ventral view of terminal to right partially enclosing distalmost adambulacrals; small distal marginals border adambulacrals.

Fig. 5 — Delicate dorsals bordered by marginal series. Slots between the marginals are fascioles.

PLATE 4

Aldebarania taberna n. sp. Scale bar equals 5 mm.

Figs. 1, 2, 4 — Holotype (NHMM 199901-1); 1, 2, dorsal and ventral views, respectively, showing general configuration; 4, ventral view of distal arm showing simple spinelets on inferomarginals, lacking raised areas of *A. arenitea*, the type species.

Figs. 3, 6 — Paratype (NHMM 199901-3); 3, dorsal view with uniform, small paxillae (collapsed towards centre), terminals on upper arms, form of marginals; 6, ventral view, inferomarginals similar to superomarginals, central disc is disrupted, showing ambulacrals, actinal arrangement.

Fig. 5 — Paratype (NHMM 199901-2); ventral view, inferomarginals, mouth angle pair preserved in interbrachium to left, actinals disrupted but partially exposed in all interbrachia; ventral surfaces of paxillae visible to right of mouth angle pair.

PLATE 5

Figs. 1-7 *Cheiraster*? sp., (NHMM MD 4105). Scale bar equals 3 mm in 1, 8, and 1 mm in 2-7.

Fig. 1 — Overall dorsal view of specimen.

Fig. 2 — Lateral view of four medial ambulacrals from the left side of the lower arm (see Fig. 1).

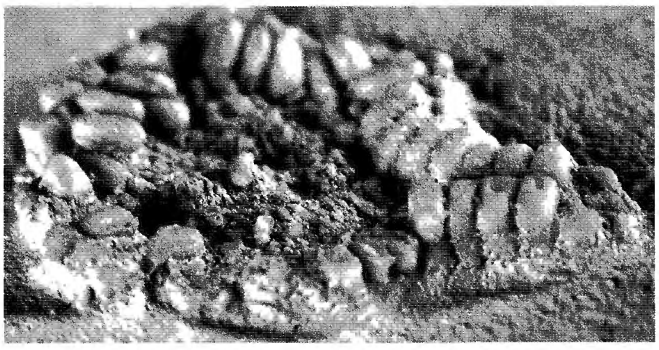
Fig. 3 — Dorsal-lateral view of four ambulacrals, the two distal partially obscured by bulbous marginals, from proximal right side of the upper arm (see Fig. 1).

Fig. 4 — Dorsal view of ambulacrals with one marginal to upper right and several below, right proximal side of medial arm (see Fig. 1).

Fig. 5 — Dorsal view of ambulacral series bordered by marginals, upper arm (see Fig. 1).

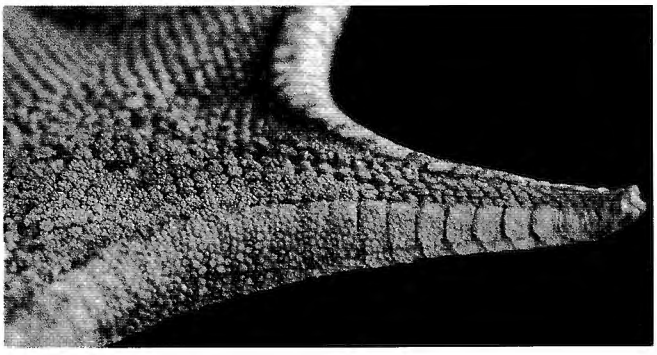
Figs. 6, 7 — Two inclined views of right side of upper left arm showing form and arrangement of ambulacrals along midline of arm, and marginals.

Fig. 8 — *Cheiraster echinulatus* (PERRIER, 1875), USNM E23500, Recent, off Venezuela. Inclined dorsal view of arm; abactinal, marginal form and spine development are similar to those of NHMM MD 4105 but similarities are too generalized to finalise fossil assignment (see text).

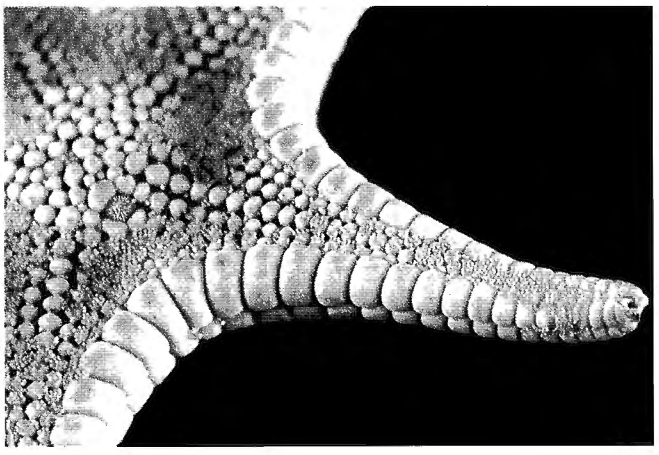


1 —

2 —

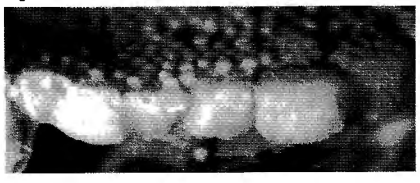


3 —

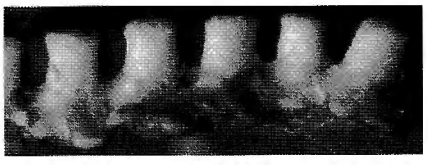


5 —

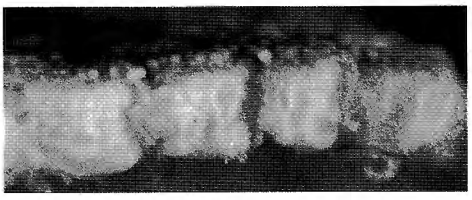
4 —



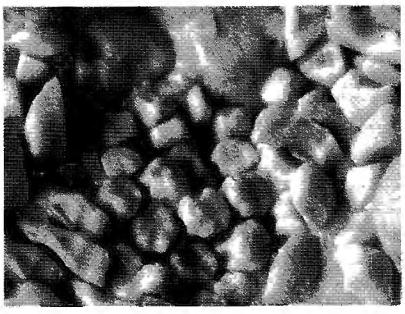
6 —



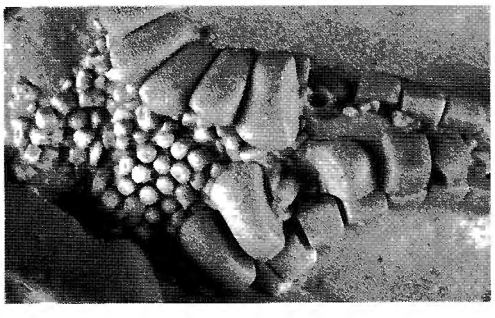
7 —



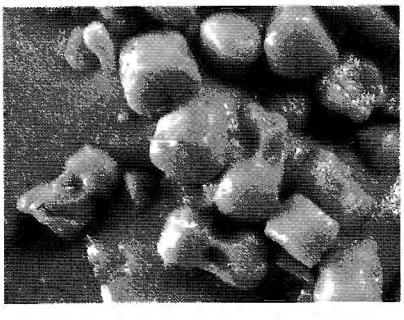
8 —



9 —

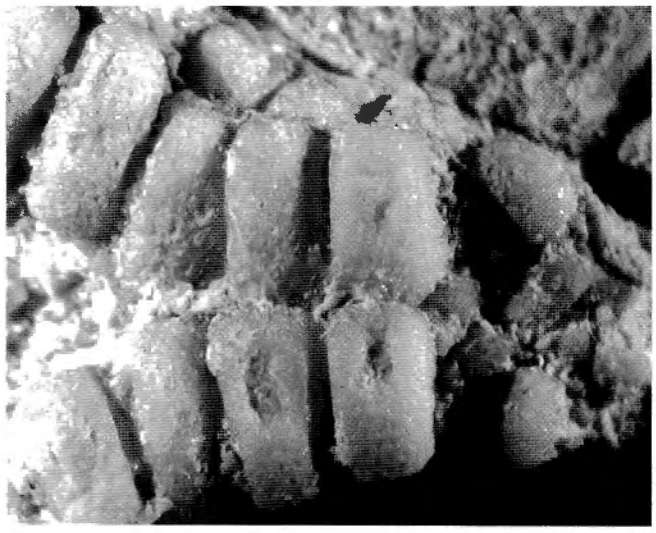


10 —



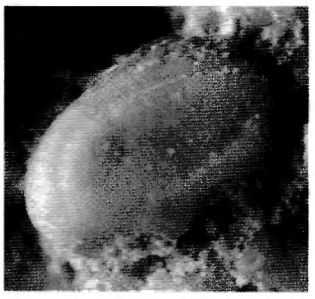
11 —

PLATE 1



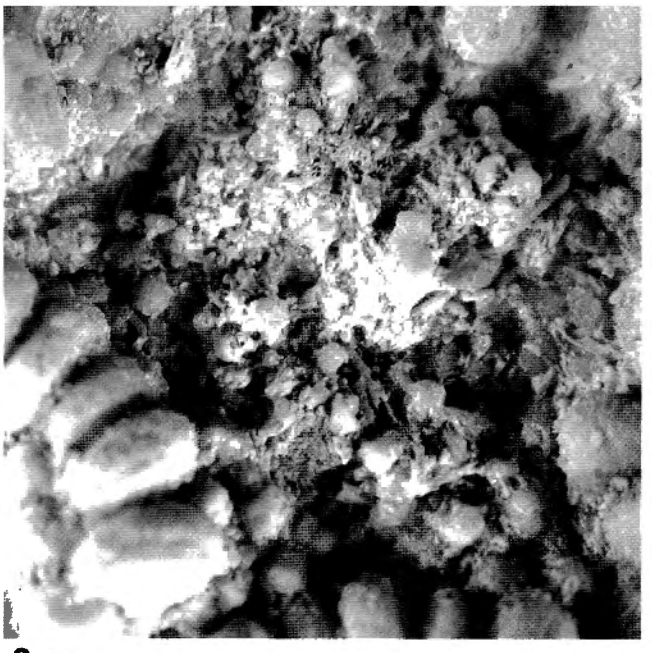
1

3

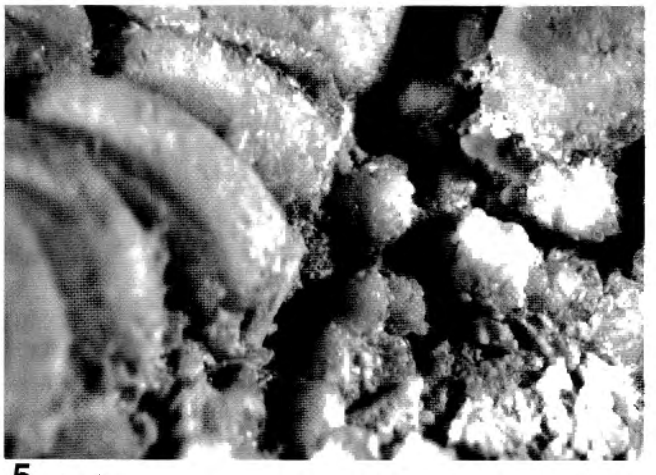


4

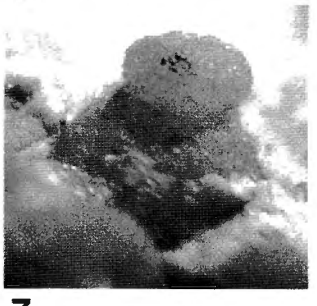
6



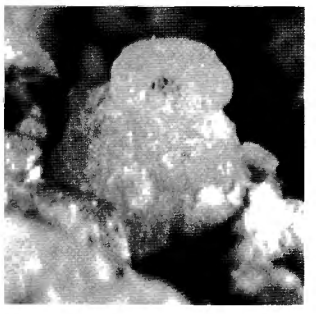
2



5

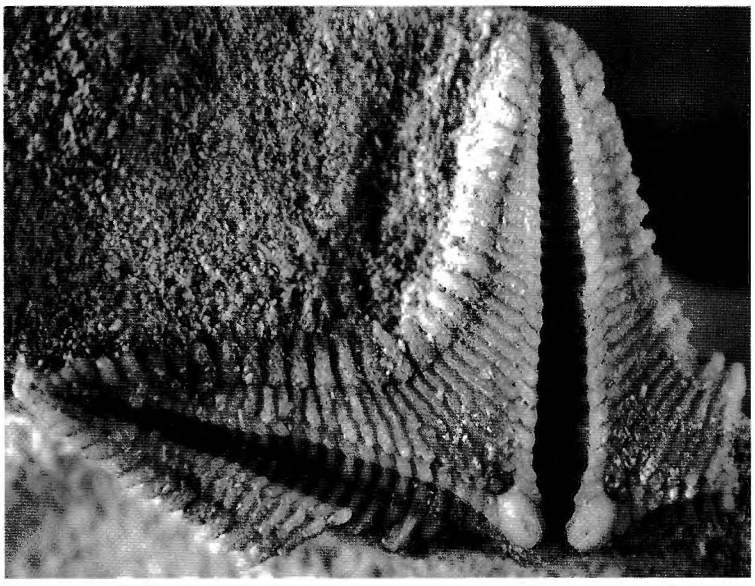


7



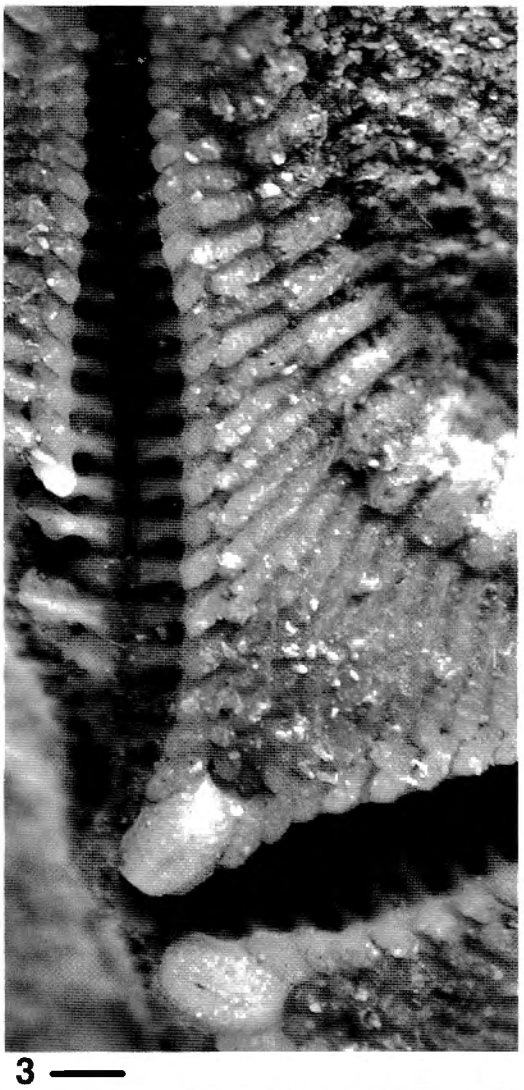
8

PLATE 2

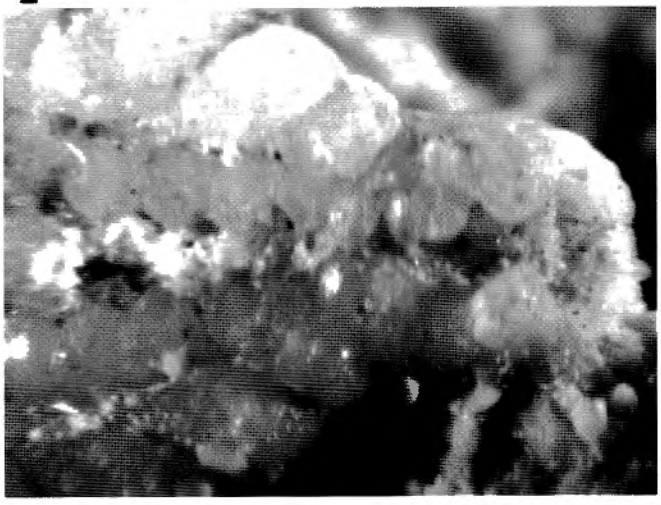


1

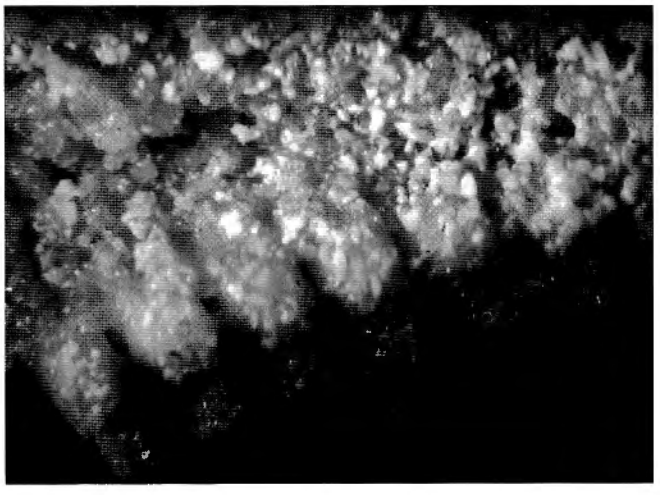
2



3



4

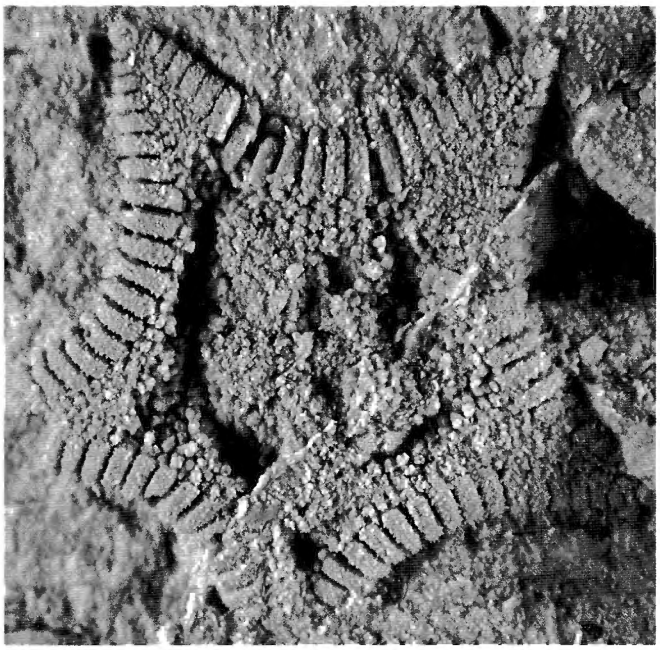


5

PLATE 3

1

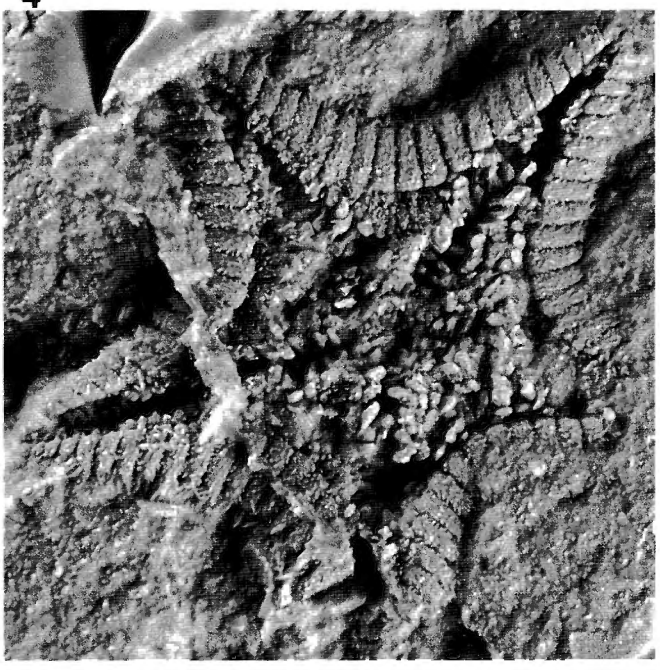
2



3

4

5



6

PLATE 4

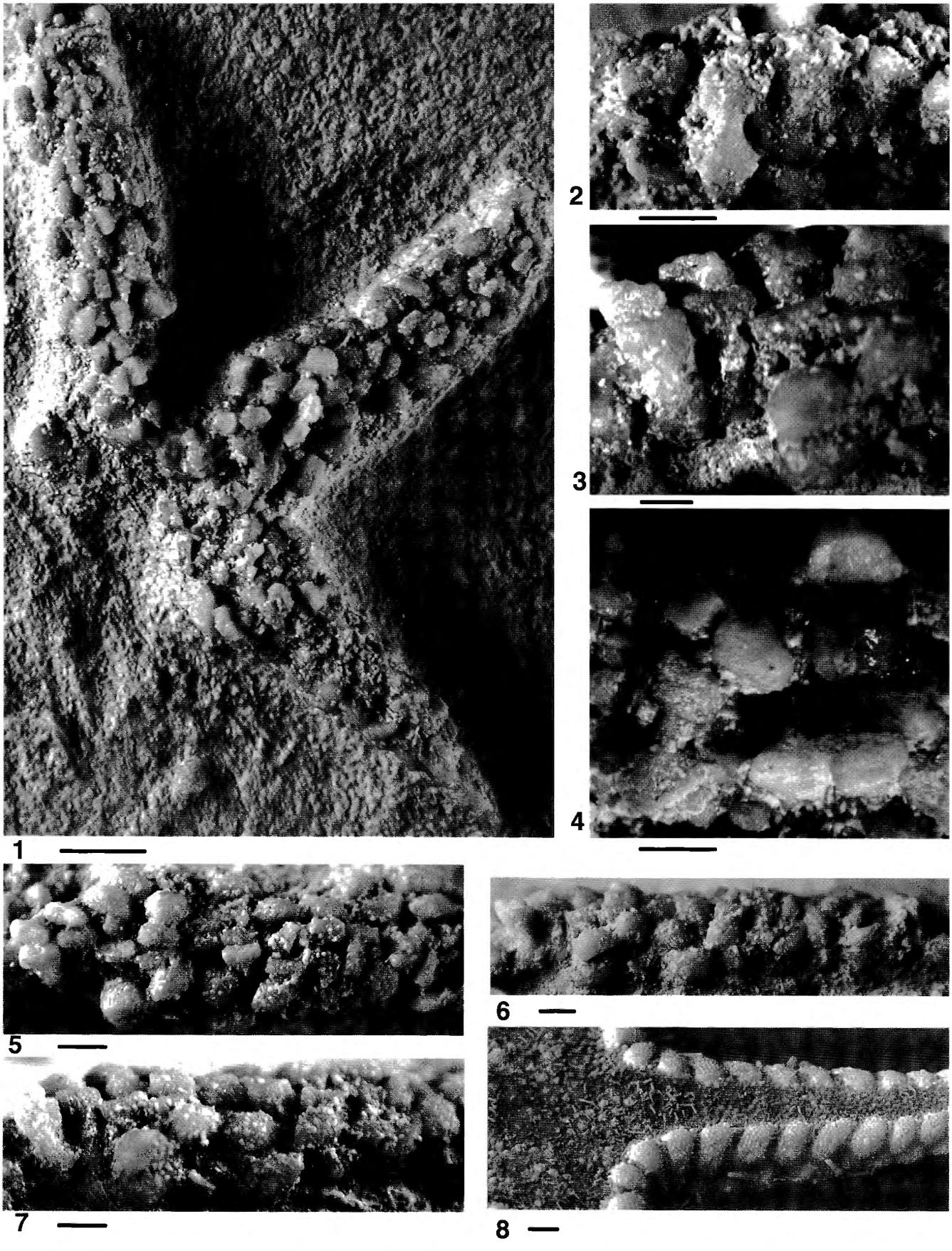


PLATE 5