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Starfish (Asteroidea, Echinodermata) from the Cretaceous of southern England (UK) and Western Australia, including a revision of the goniasterid genus *Tomidaster* Sladen, 1891

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ABSTRACT:

Gale, A.S. and McNamara, K.J. 2026. Starfish (Asteroidea, Echinodermata) from the Cretaceous of southern England (UK) and Western Australia, including a revision of the goniasterid genus *Tomidaster* Sladen, 1891. *Acta Geologica Polonica*, **76** (3), e88.

Two new asteroid species are described from the Santonian–Campanian Toolonga Calcilutite of Western Australia, the first Cretaceous starfish recorded from Australia. These are the goniasterid *Tomidaster timothyi* sp. nov. and the goniopectinid *Chrispaulia australis* sp. nov. The taxonomy of *Tomidaster* Sladen, 1891 is revised on the basis of material from southern England; it is concluded that *Comptoniaster* Breton, 1984 is a junior synonym. To date, species of *Tomidaster* are known from the UK, Belgium, France, Egypt, Australia, and the USA (Texas). *Chrispaulia australis* sp. nov. is a deposit-feeding mudstar and the first record of the genus from outside southern England.

Key words: Asteroids; Goniasteridae; Goniopectinidae; Cretaceous.

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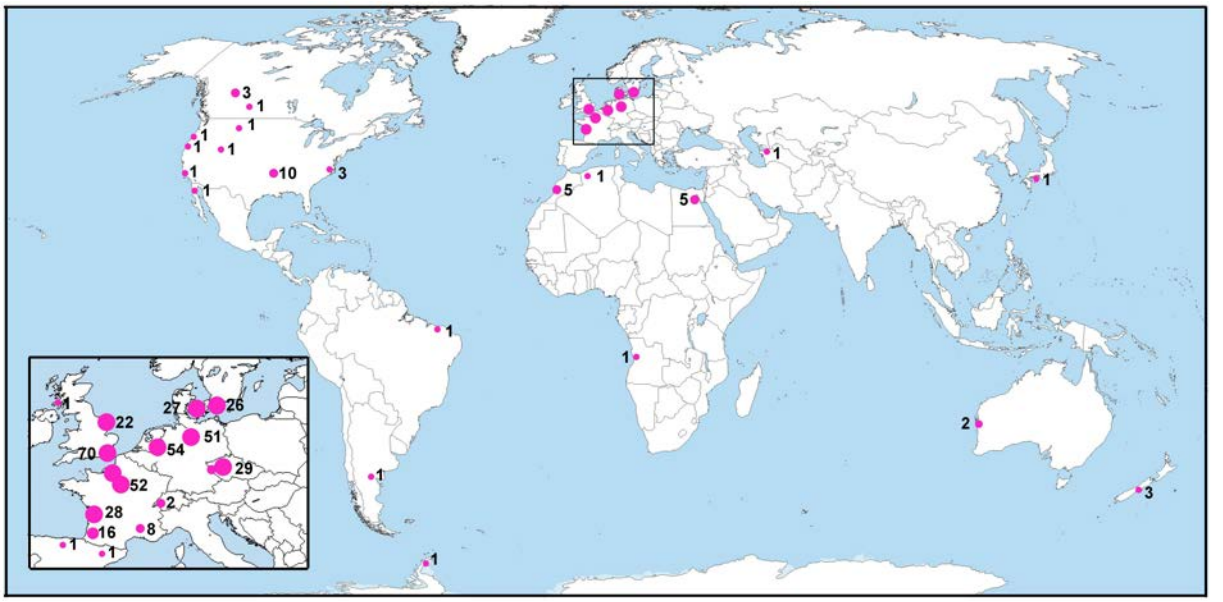
INTRODUCTION

Cretaceous asteroid faunas are highly diverse, including representatives of extant families belonging to the orders Valvatida (Goniasteridae, Ophidiasteridae, Asterinidae, Odontasteridae, Sphaerasteridae and possible Chaetasteridae), Paxillosida (Astropectinidae, Goniopectinidae, Benthopectinidae and Pseudarchasteridae), Forcipulatida (Asteriidae and Zoroasteridae) and Velatida (Pterasteridae and Korethrasteridae). In addition, extinct families present in the Cretaceous, but lost in the Paleogene or Neogene, include the valvatidan families Stauranderasteridae and Pycinasteridae.

However, all of the most diverse faunas come from north-west Europe (Text-fig. 1), from both deeper-water chalks and their marginal equivalents, in the United Kingdom (81 species; Sladen 1891, 1893; Spencer 1905, 1907, 1908, 1914; Gale 1987a, b, 1989, 2005, 2020a, b, 2021, 2022, 2023; Gale and Jagt 2025), France (80 species; Valette 1902, 1915; Mercier 1935, 1936; Breton 1979, 1981, 1984, 1986, 1987a, b, 1988, 1992; Néreaudeau and Breton 1993; Villier *et al*. 1997, 2004a, 2026; Villier 2001, 2010; Gale and Cottard 2025), Germany (51 species; Geinitz 1872; Müller 1953, 1956; Schulz and Weitschat 1971, 1975, 1981; Niebuhr and Seibertz 2016; Neumann and Girod 2018; Neumann *et al*. 2023), Belgium and



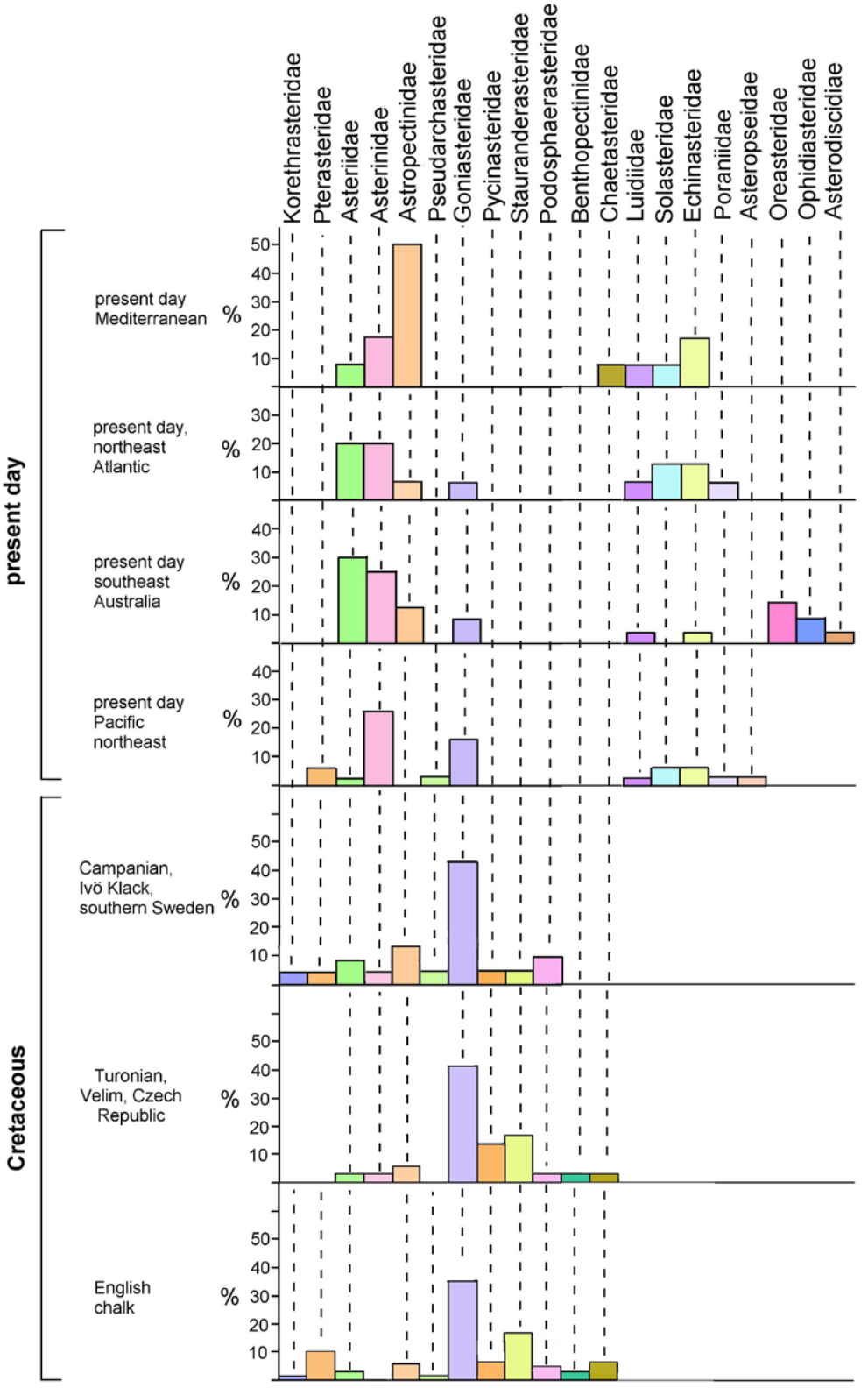
Text-fig. 1. Worldwide distribution of Cretaceous asteroids; numbers refer to taxa present at each locality (see Appendix). Note the much greater diversity in north-west Europe (inset map).

the Netherlands (54 species; Jagt 2000; Blake and Jagt 2005; Gale and Jagt 2021, 2025), Denmark (27 species; Nielsen 1943; Rasmussen 1950; Blake and Jagt 2005), Sweden (26 species; Gale 1987a, 2025), Switzerland (4 species; de Loriol 1874; Hess 1970), Spain (1 species; Neumann and Hess 2001), and the Czech Republic (29 species; Žitt *et al.* 1997; Žitt 2004, 2005a, b). In the rest of the world, Cretaceous asteroids are largely known from isolated finds of single taxa (see Appendix), with the exception of the moderately diverse Albian–Cenomanian faunas from Texas, USA (7 species; Blake and Reid 1998), the Barremian of Morocco (5 species; Blake and Reboul 2011; Ewin and Gale 2020), and the Santonian of Egypt (5 species; de Loriol 1888, 1904, 1909; Fourteau 1914; Jux 1957).

The question this pattern poses are the reasons for these discrepancies. Articulated asteroids are rare fossils, as they disintegrate rapidly after death into their constituent ossicles which are small, inconspicuous fossils. Articulated specimens, on the other hand, are rare and prized discoveries which frequently end up in museums and are often described. Can the isolated ossicles of these have been so widely overlooked? Unfortunately, this is impossible to test, but of the extra-European records (Text-fig. 1; Appendix) of which we are aware, only one (Wade 1926, from Tennessee) is based on isolated plates. However, it is also possible that a component of the discrepancy is that asteroids were not abundant or important components of marine benthos, in some regions at least. One of us (ASG) spent approximately 3 months collecting fossils in the Albian–Turonian deposits of the Cauvery Basin, south-east India, and did not find any asteroid material.

Although many Cretaceous asteroids belong to extant families, the relative abundance and diversity of these differs significantly between the Cretaceous and the present day. Cretaceous starfish faunas from both near- and offshore settings are dominated by members of the family Goniasteridae, a distinctive group with large, block-like marginal ossicles, with pycinasterids and stauranderasterids as significant components of faunas (Text-fig. 2). In contrast, at the present, relatively shallow-water asteroid assemblages (<200 m) are largely made up of asterinids, asteriids, and astropectinids which are present in some Cretaceous assemblages, but there are of relatively low diversity. Other significant present-day families, such as the luidiids, echinasterids, asteropseids, and oreasterids do not seem to have evolved by the Cretaceous (Gale 2011).

In terms of diversity outside of north-west Europe, astropectinids (42%) and goniasterids (30%) are dominant. In the highly diverse fauna from the United Kingdom, in which extensive processing has yielded ossicles of smaller taxa, goniasterids are dominant (44%), but astropectinids (5%) are much



Text-fig. 2. Relative abundance of asteroid families in the Cretaceous and at the present day, in relatively shallow waters (<200 m). Cretaceous faunas are dominated by goniasterids, with a smaller but significant component of stauranderasterids and pycinasterids (modified after Gale 2025, fig. 5).

less so. This poses the question as to whether the apparent dominance of astropectinids and goniasterids on a worldwide scale is really a result of the fact that the marginal frames of these families are more robust (i.e., there is a greater potential for preservation of articulated specimens) or an original abundance.

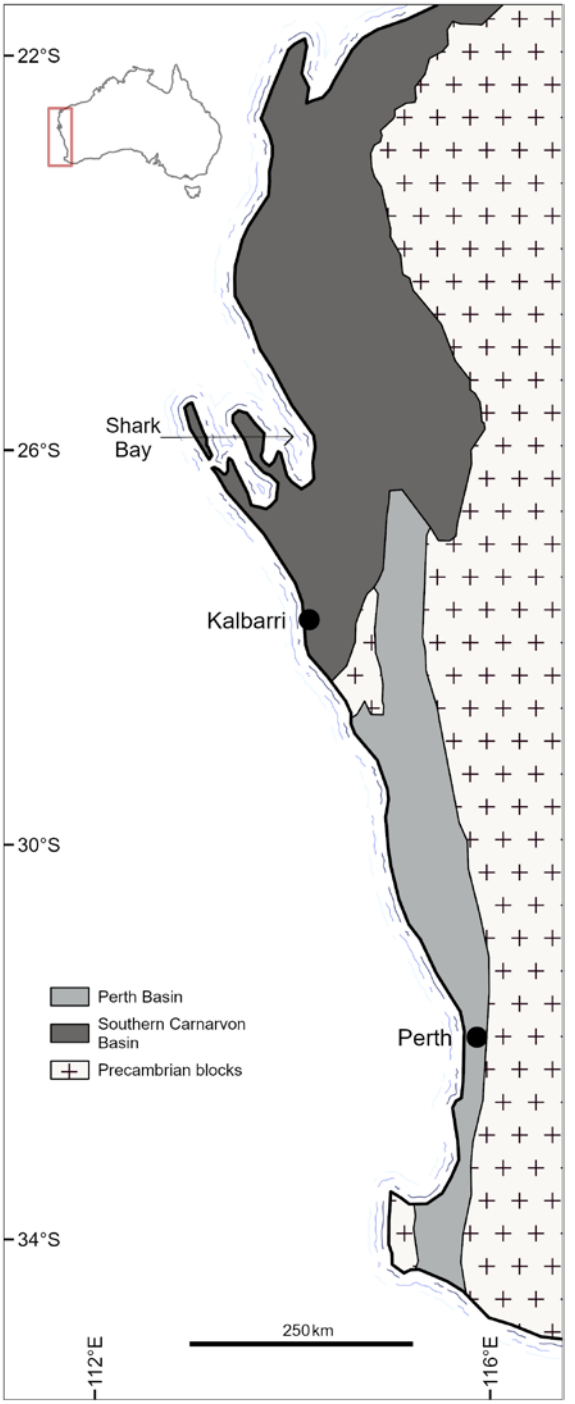
In the present paper, we describe the first finds of asteroids in the Cretaceous of Australia, from Kalbarri and Shark Bay (Western Australia). Interestingly, one of these belongs to the genus *Tomidaster* Sladen, 1891, which is found widely in north-west Europe and is also known from Egypt and Texas, USA. The other, *Chrispaulia* Gale, 2005, was previously known only from the UK.

LOCALITIES AND STRATIGRAPHY

The Toolonga Calcilutite is an extensive sequence of Upper Cretaceous carbonates that occurs along the western margin of the southern Carnarvon Basin in Western Australia (Text-fig. 3). The unit crops out sporadically from near Kalbarri in the south to the Giralia Range, some 600 km to the north. It ranges in age from mid-Coniacian to early Campanian (Lynch 1991; Haig 2002). As Gale *et al.* (1995) have pointed out, the Toolonga Calcilutite is a true chalk, being composed mainly of calcareous nannofossils and foraminifera.

The type section is in the south of the basin on the north side of the Murchison River, near Kalbarri. Here it is 26 m thick (Johnstone *et al.* 1958). Both crinoid species, *Uintacrinus socialis* Grinnell, 1876 and *Marsupites testudinarius* (von Schlotheim, 1820), are present in the lower part of the unit, indicating a late Santonian age for this part of the section in the Kalbarri region (Gale 2024, text-fig. 27, column 9). Young (2016) recorded *Uintacrinus socialis* over a thickness of almost 4 m, overlain by 2 m with *Marsupites testudinarius*. The invertebrate fauna in this lower part of the Toolonga Calcilutite is dominated by large species of *Inoceramus* spp. and the ostreid *Pycnodonte vesicularis* (Lamarck, 1806) (Darragh and Kendrick 1991), along with crinoids, brachiopods (Craig 1999), the serpulid *Rotulispira* sp. (McNamara 2023) and occasional cirripedes and echinoids.

The upper part of the section, from immediately above the *Marsupites testudinarius* Zone, shows a marked lithological change, with the development of a more marly chalk and the appearance of chert nodules, which increase in concentration up the section. With this lithological change there is also a faunal change, with the formerly abundant *Inoceramus* spp. disappearing and ostreids becoming rarer. Cirripedes, which are rare in the lower part of the section, increase in abundance. *Rotulispira* sp. is still present, but species abundances change mark-



Text-fig. 3. Map of Western Australia to show localities.

edly (McNamara 2023). The lower 5 m of the unit is characterised by the presence of the ammonite aptychus form genus *Spinaptychus* Trauth, 1927, not hitherto recognised in the Cretaceous of Australia. The disappearance of *Marsupites testudinarius* below this level, and the occurrence of the calcareous nannofossil *Broinsonia parca* (Stradner, 1963) in the upper part of the Toolonga Calcilutite, indicates an early Campanian age for this upper part of the section (Lynch 1991; Gale *et al.* 1995). Howe *et al.* (2000) suggested that the Toolonga Calcilutite was deposited in water depths in excess of 100 m during the Santonian and early Campanian.

Of the two asteroid species present in the Toolonga Calcilutite, *Tomidaster timothyi* sp. nov. occurs in the upper Santonian part of the section, where it was found in the most southerly known outcrop of the Toolonga Calcilutite at Meanarra Hill, 5 km east of the township of Kalbarri (27.69º S, 114.21º E). The material of *Chrispaulia australis* sp. nov. was collected from an extensive outcrop on Yaringa Station, 5 km east of Shark Bay (25.97º S, 114.30º E) (Text-fig. 3). The beds here occur in the higher, more marly part of the unit, where *Inoceramus* spp. is absent, and is therefore likely to be early Campanian in age.

Institutional abbreviations

BGS – British Geological Survey, Keyworth, Nottinghamshire, UK;
Nds LH – Niedersächsisches Landesmuseum, Hannover, Germany;
NHMM – Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands;
NHMUK – Natural History Museum, London, UK;
RGM – Naturalis Biodiversity Center (formerly Rijksmuseum van Geologie en Mineralogie), Leiden, the Netherlands;
TMM – Texas Memorial Museum, Austin, Texas, USA;
WAM – Western Australian Museum, Perth, Australia.

SYSTEMATIC PALAEONTOLOGY

Order Valvatida Perrier, 1884
Family Goniasteridae Forbes, 1841

DIAGNOSIS: Body flat, distal arms sometimes raised abactinally. Disc proportionately broad, large, opposing supero- and inferomarginals. Abactinal surface formed of tessellation of tabular to low paxilliform ossicles (Gale 1987a).

REMARKS: Goniasteridae is a highly diverse asteroid family, including 112 extant genera (https://www.marinespecies.org/aphia.php?p=taxdetails&id=123135), and has a long fossil record, extending back to the Lower Jurassic (Gale 2011). In the present paper, we revise Cretaceous forms which possess elongated, bivalved, slit-like pedicellariae.

Genus *Tomidaster* Sladen, 1891

DIAGNOSIS: Disc broad, arms relatively short (R2:r1 R/r 2:1), interradial margins evenly concave. Approximately 20 marginal pairs in each radius of fully-grown individuals. Breadth of interradial marginals twice length, breadth decreasing distally. Marginals with dense cover of rounded-polygonal granule pits, absent on adradial abactinal borders of distal superomarginals. Elongated, bivalved slit pedicellariae present on some marginals, actinals and abactinals, variably present on actinal surface of inferomarginals.

SYNONYM: *Comptoniaster* Breton, 1984.

TYPE SPECIES: *Tomidaster sulcatus* Sladen, 1891, by designation herein.

INCLUDED SPECIES: In addition to the type species, *Goniaster* (*Stellaster*) *comptoni* Forbes, 1848, the following: *Comptonia schlumbergeri* de Loriol, 1888; *Comptoniaster adamsi* Blake, 2010; *Comptoniaster godeti* Breton, 1992; *Comptoniaster peetersorum* Jagt, 2000, and *Tomidaster timothyi* sp. nov.

REMARKS: In 1890, W. Percy Sladen took over the task of continuing Thomas Wright's Cretaceous Echinodermata Palaeontographical Society monograph series. Sladen was an expert on living asteroids and had published the remarkable *Challenger* report on extant species collected across the globe by the HMS Challenger (Sladen 1885). The first 8 plates and 28 pages on Cretaceous asteroids and ophiuroids were published in 1891, shortly after the time Sladen became very ill (Nichols 2002, 2003) and he never completed the work.

On plate 5, figure 1, Sladen (1891) figured the actinal surface of a goniasterid asteroid from the 'Grey Chalk' of Dover (Kent, UK), under the name of *Tomidaster sulcatus* Sladen, 1891, but never described the species or the specimen, which is in the Natural History Museum, London. It is remarkable in its possession of numerous, elongated, bivalved

pedicellariae on the marginal, actinal and abactinal ossicles. William Kingdon Spencer, who took over from Sladen to complete the monograph (Spencer 1905, 1907, 1908), viewed the specimen as an individual of *Calliderma smithiae* (Forbes, 1848) which happened to possess pedicellariae, a result of the "... somewhat freakish way in which pedicellariae occur in starfishes …" (Spencer 1907, p. 124).

Gale (1988) retained Sladen's species *sulcatus*, but placed it in the genus *Ophryaster* Spencer, 1914, on account of the similar pedicellariae. Breton (1992, p. 304) resurrected *Tomidaster*, providing the first diagnosis of the genus and stated, in agreement with Spencer (1907), that the only difference between *Calliderma* and *Tomidaster* lay in the presence of elongated pedicellariae of the latter genus. However, Gale (1987b, p. 170) had demonstrated that the pedicellariae of *Calliderma* are very distinct, and quite different to those of other goniasterids in their possession of an oval, raised central rim (Text-fig. 4C, D).

Breton (1984) erected the genus *Comptoniaster* [type species: *Goniaster* (*Stellaster*) *comptoni* Forbes, 1848], to which he ascribed numerous Jurassic and Cretaceous forms. *Goniaster* (*Stellaster*) *comptoni* was based on two complete, but silicified individuals, both from the upper Albian Blackdown Greensand of Devon, UK (Text-fig. 5C, D). These both possess abundant, elongated bivalved pedicellariae, on the marginals, actinals and abactinals, similar in form and arrangement to those of *Tomidaster sulcatus*. The genus *Comptoniaster* is therefore treated here as a subjective junior synonym of *Tomidaster*. The early Hauterivian species *Comptoniaster godeti* Breton, 1992, from Isère (France) is certainly a member of *Tomidaster*, although the terminals referred to this species (Breton 1992, pl. 25, figs 3, 12) originate in the forcipulatid *Terminaster*.

The Jurassic species of *Comptoniaster* described by Breton (1992) lack pedicellariae and certainly cannot be referred to *Tomidaster*; they include very diverse goniasterid morphologies. '*Comptoniaster*' *jangouxi* Breton, 1992, from the Oxfordian of Calvados (France), has long arms, a broad disc and inferomarginals which broaden from the interradii into the arms. '*Comptoniaster*' *basseti* (de Loriol, 1887), from the Kimmeridgian of Aquitaine (France), has very short arms, angled interradii and wedge-shaped interradial inferomarginals which slope strongly to the lateral margin. '*Comptoniaster*' *sharpei* (Wright, 1880), from the Bajocian of the United Kingdom, has narrow inferomarginals which taper very slowly into the arms. '*Comptoniaster*' *vrinensis* Villier, Kutscher and Mah, 2004 is based on isolated marginals from the Toarcian (Lower Jurassic) of western France, which have a goniasterid morphology. Villier *et al*. (2004b), following Breton (1992), suggested that *Comptoniaster* may be paraphyletic, forming sister taxa for multiple stellate Mesozoic goniasterid lineages. Blake (2010, fig. 1) undertook a cladistic analysis of selected Mesozoic goniasterids and Paxillosida which provided some weak support for the monophyly of Cretaceous *Comptoniaster*.

Comptonia schlumbergeri de Loriol, 1888 (see illustration in de Loriol 1909, pl. 10, fig. 2) and *Forbesiaster wrighti* de Loriol, 1909 (pl. 3, fig. 2) from the Santonian of Egypt appear to be conspecific and possess elongated, bivalve pedicellariae on marginals and actinals. The species is here referred to *Tomidaster*.

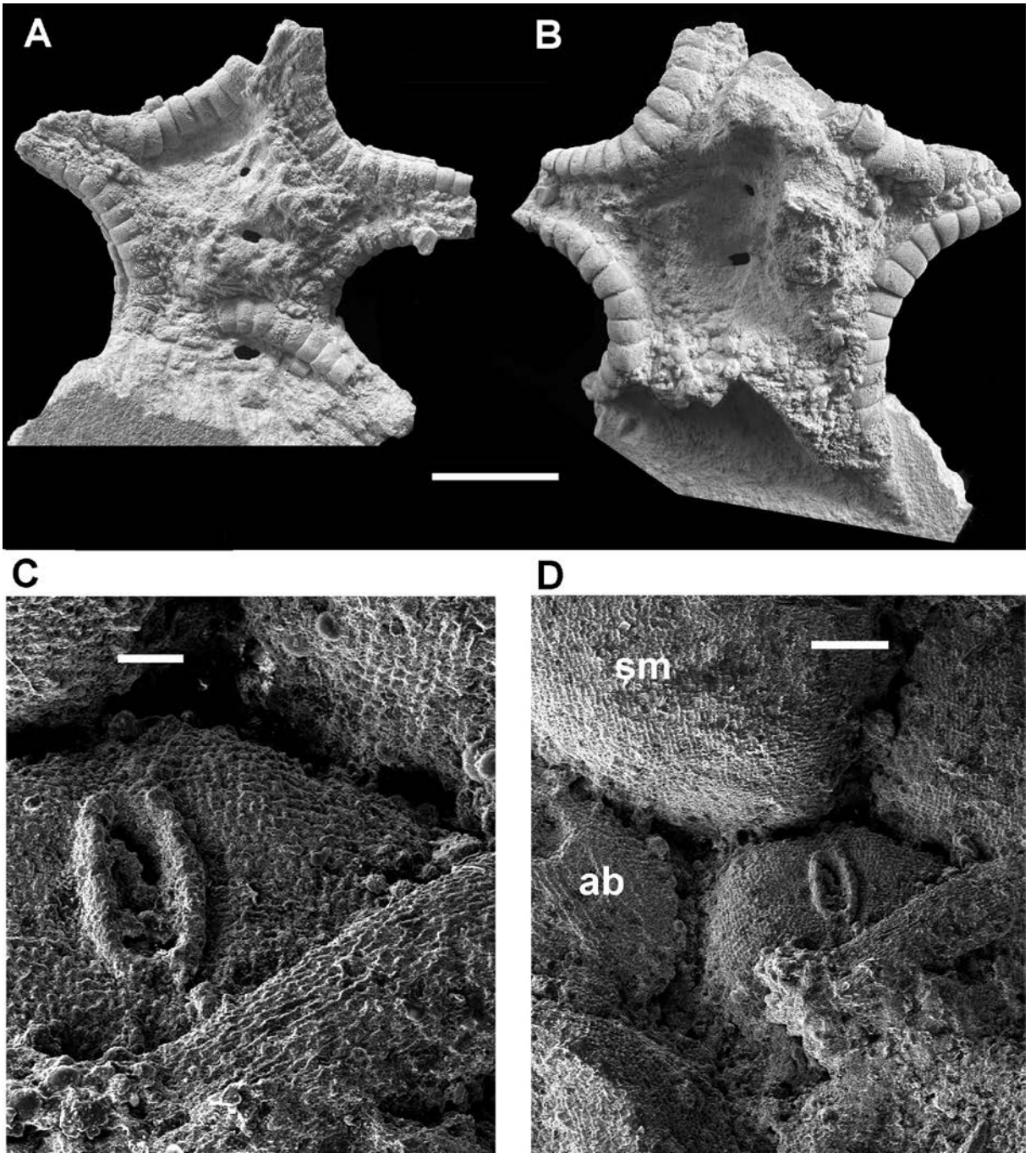
Tomidaster sulcatus Sladen, 1891
(Text-figs 4A, B, 5A, B, 6, 7E, 8K, N)

*1891. *Tomidaster sulcatus* Sladen, pl. 5, fig. 1.
1907. *Calliderma smithiae* (Forbes); Spencer, pp. 123, 124.
1988. *Comptoniaster comptoni* (Forbes); Gale in Smith *et al*., p. 200, pl. 42, fig. 1.
1988. *Ophryaster sulcatus* (Sladen); Gale in Smith *et al*., p. 202, pl. 41, fig. 5.
1988. *Comptoniaster weitschati* Breton, p. 14, figs 6–8.
1992. *Tomidaster sulcatus* Sladen; Breton, p. 304.
1992. *Tomidaster* sp.; Breton, p. 305, pl. 37, figs 5–8.
p1992. *Comptoniaster comptoni* (Forbes); Breton, p. 218, pl. 23, figs 1, 2 only.
1992. *Comptoniaster weitschati* Breton; Breton, p. 241, pl. 26, fig. 6.

DIAGNOSIS: *Tomidaster* in which the interradial marginals possess well-demarcated actinal/abactinal surfaces and are relatively narrow and short. Marginals carry an even, dense cover of impressed granule pits.

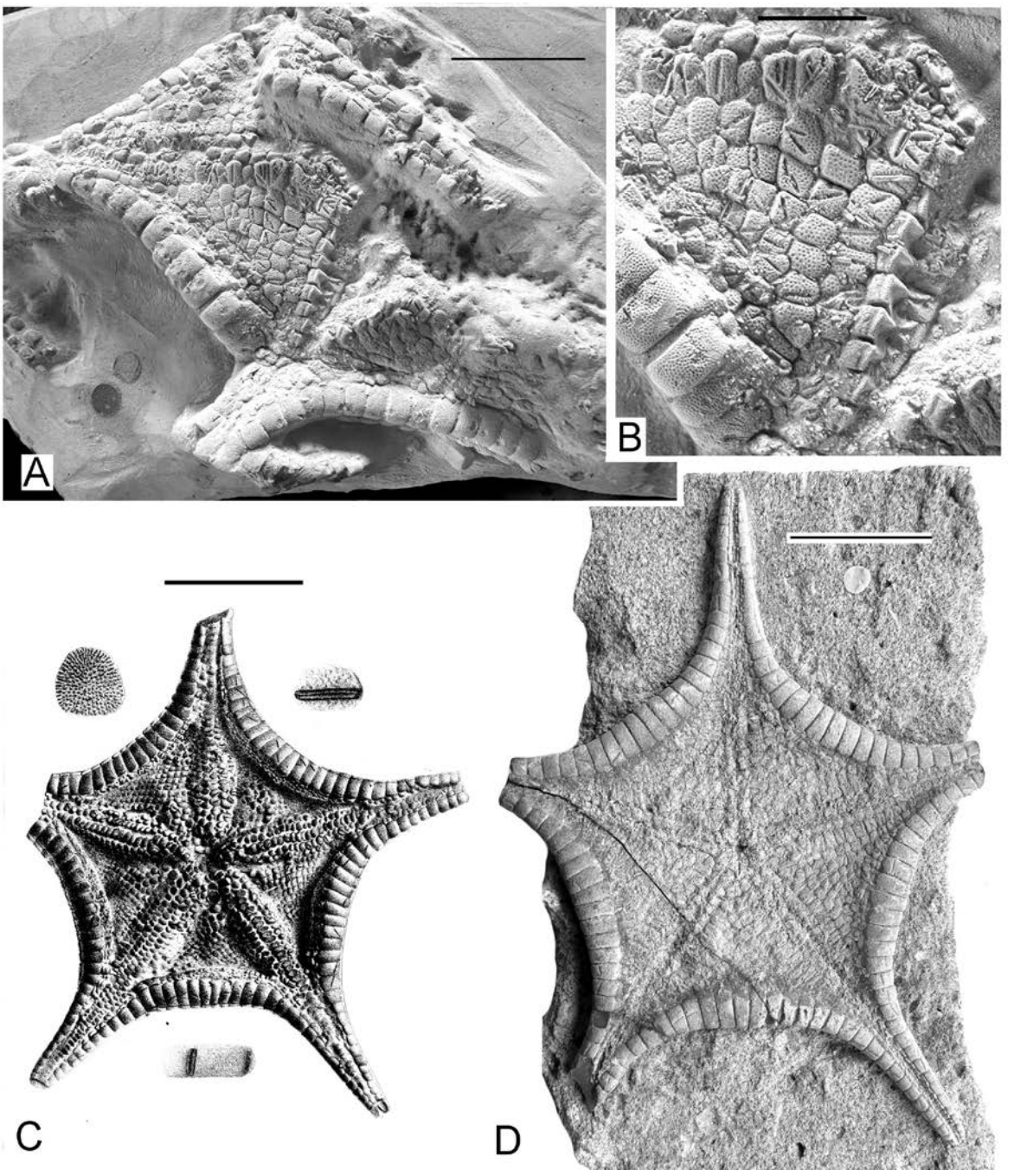
TYPE: The specimen showing the actinal surface, figured by Sladen (1891, pl. 5, fig. 1) is here designated lectotype (NHMUK E.5063), from the 'Grey Chalk of Dover, Kent'; Cenomanian Grey Chalk Subgroup on the shore between Dover and Folkestone (Kent, UK).

MATERIAL: In addition to the type, there are four further specimens in the NHMUK (E.1116, E.13048, 75515, PI EE 18380) and two in BGS (BGS GSM108645, BGS unregistered), all from the Cenomanian Grey Chalk Subgroup between Dover and Folkestone.



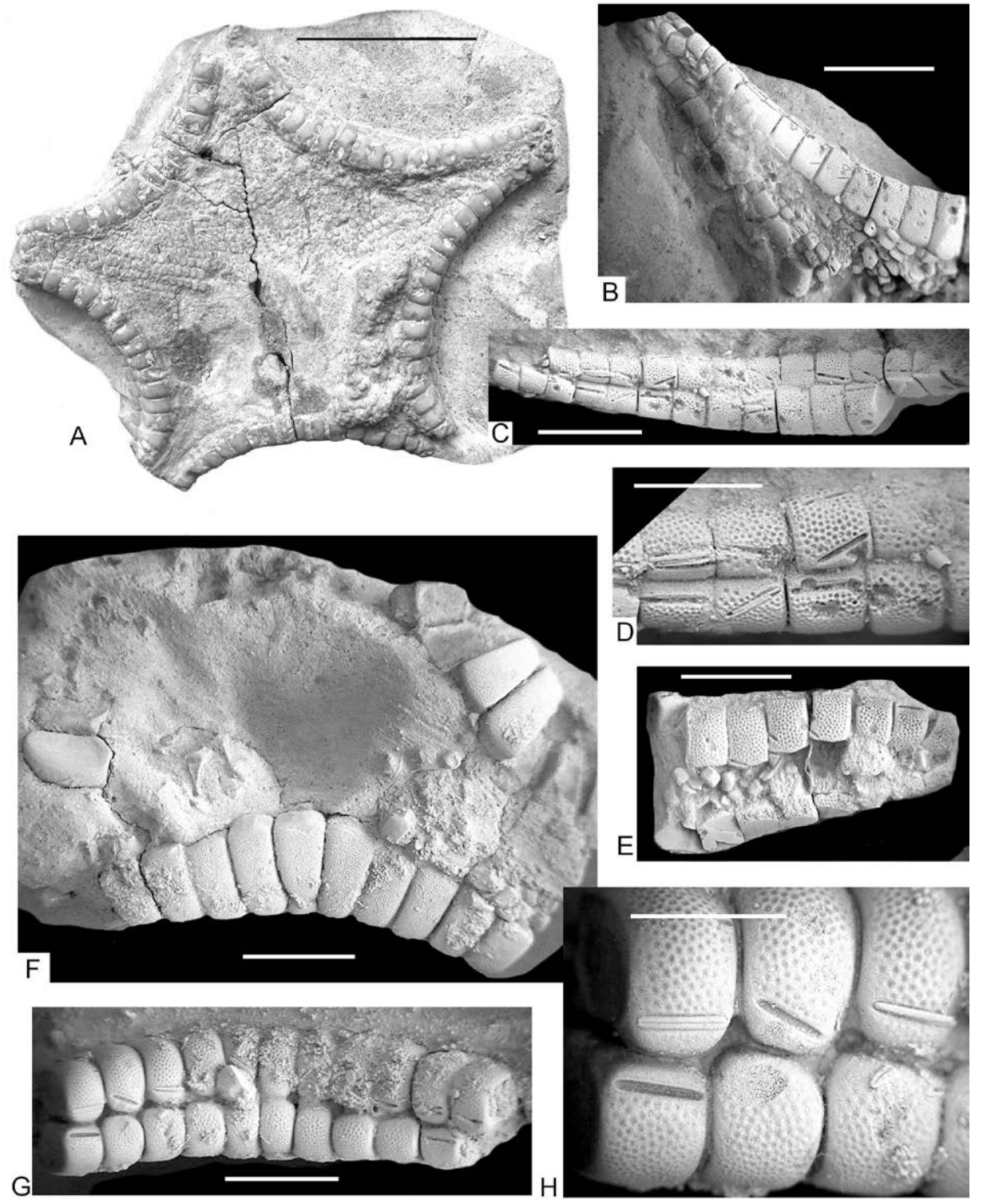
Text-fig. 4. Cretaceous goniasterid asteroids. A, B – *Tomidaster sulcatus* Sladen, 1891; abactinal (A) and actinal (B) surfaces of specimen NHMUK E 374, figured by Breton (1992, pl. 37, figs 5–8). C, D – *Calliderma smithiae* (Forbes, 1848), views of pedicellariae on abactinal surface, specimen BGSYd 5420. Provenance: A, B are from an unknown locality in southern England, probably lower Turonian; C, D are from the Grey Chalk Subgroup, Zig Zag Formation, middle Cenomanian, *Turrilites costatus* ammonite Subzone, Lydden Spout, Kent (UK). Scale bars equal 5 cm (A, B) and 0.3 mm (C, D). Abbreviations: ab – abactinal ossicle; sm – superomarginal ossicle.

DESCRIPTION: Disc broad, interradial arcs evenly concave. Marginal frame relatively narrow (Text-figs 5A, 6A), composed of ossicles with a breadth:length ratio of ratio <2:1; 12–14 marginal pairs in each interradius. Superomarginals do not meet over mid-radial line and are separated by a broad zone of abactinal plates. External surfaces of marginals with even, dense cover of impressed granule pits (Text-fig. 6G, H).

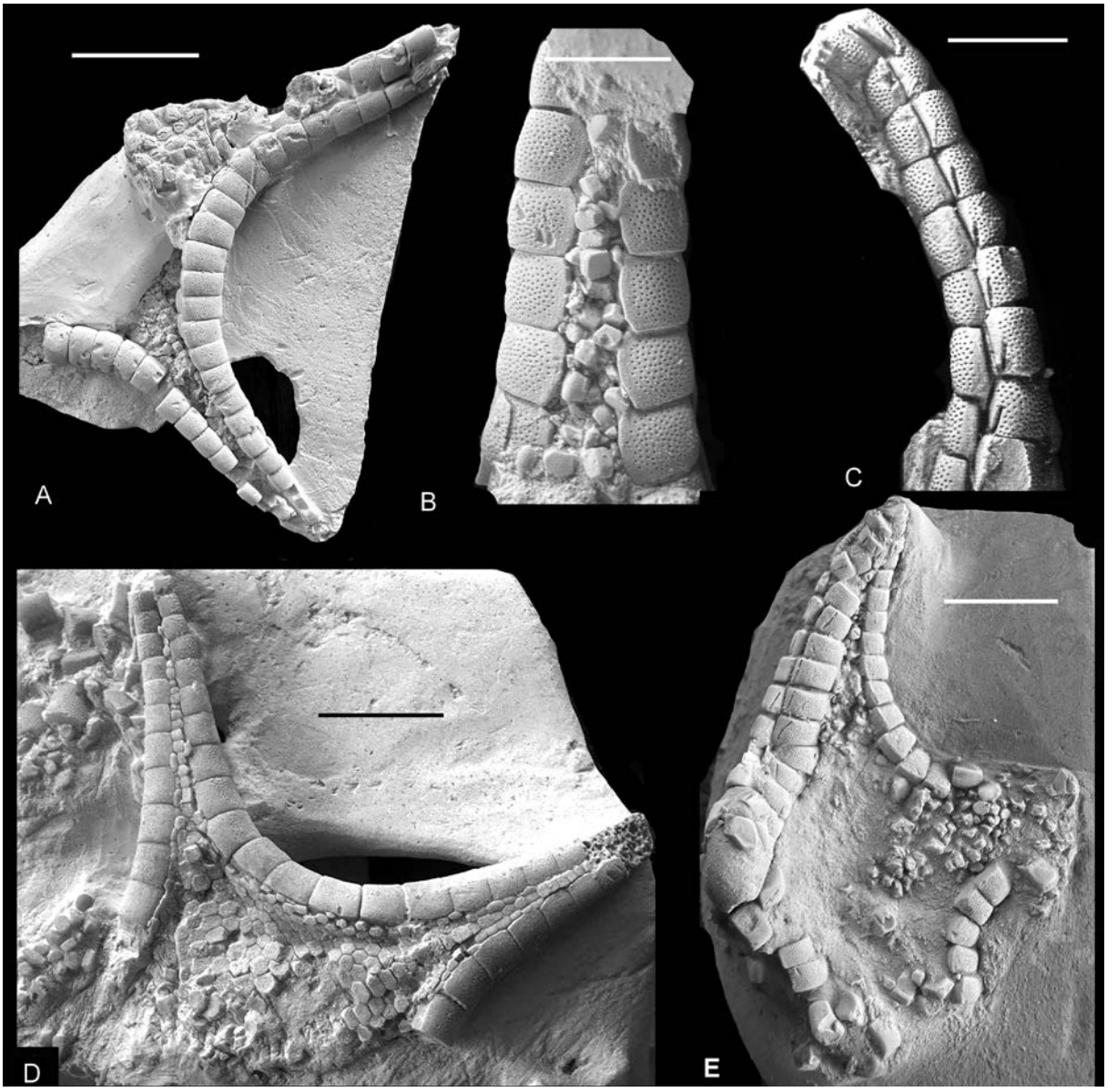


Text-fig. 5. Cretaceous goniasterid asteroids. A, B – Actinal surface of the lectotype of *Tomidaster sulcatus* Sladen, 1891 (A), enlarged (B) to show details of pedicellariae; NHMUK E.5063, the original of Sladen (1891, pl. 5, fig. 1). C, D – *Tomidaster comptoni* (Forbes, 1848); C – Abactinal surface of specimen formerly in the Northampton Museum, the original of Forbes (in Dixon 1850, pl. 22, fig. 8) and Spencer (1905, pl. 18, fig. 2); D – Actinal surface of NHMUK 34311, specimen figured by Spencer (1905, pl. 17, fig. 3). Provenance: A, B are from the Grey Chalk Subgroup, Cenomanian, between Dover and Folkestone, Kent (UK); C, D are from the Upper Greensand Formation, *Pervinquieria* (*Pervinquieria*) *pricei* ammonite Zone, Blackdown, Devon (UK). Scale bar equals 5 cm.

External faces of interradial marginals strongly convex, lateral and actinal/abactinal surfaces of marginals set at 90º (Text-fig. 8K, N). Interradial inferomarginals broader than superomarginals. Arms rapidly tapering (Text-fig. 6A, B), marginals progressively decreasing in breadth towards arm tip. Elongated slit-like bivalved



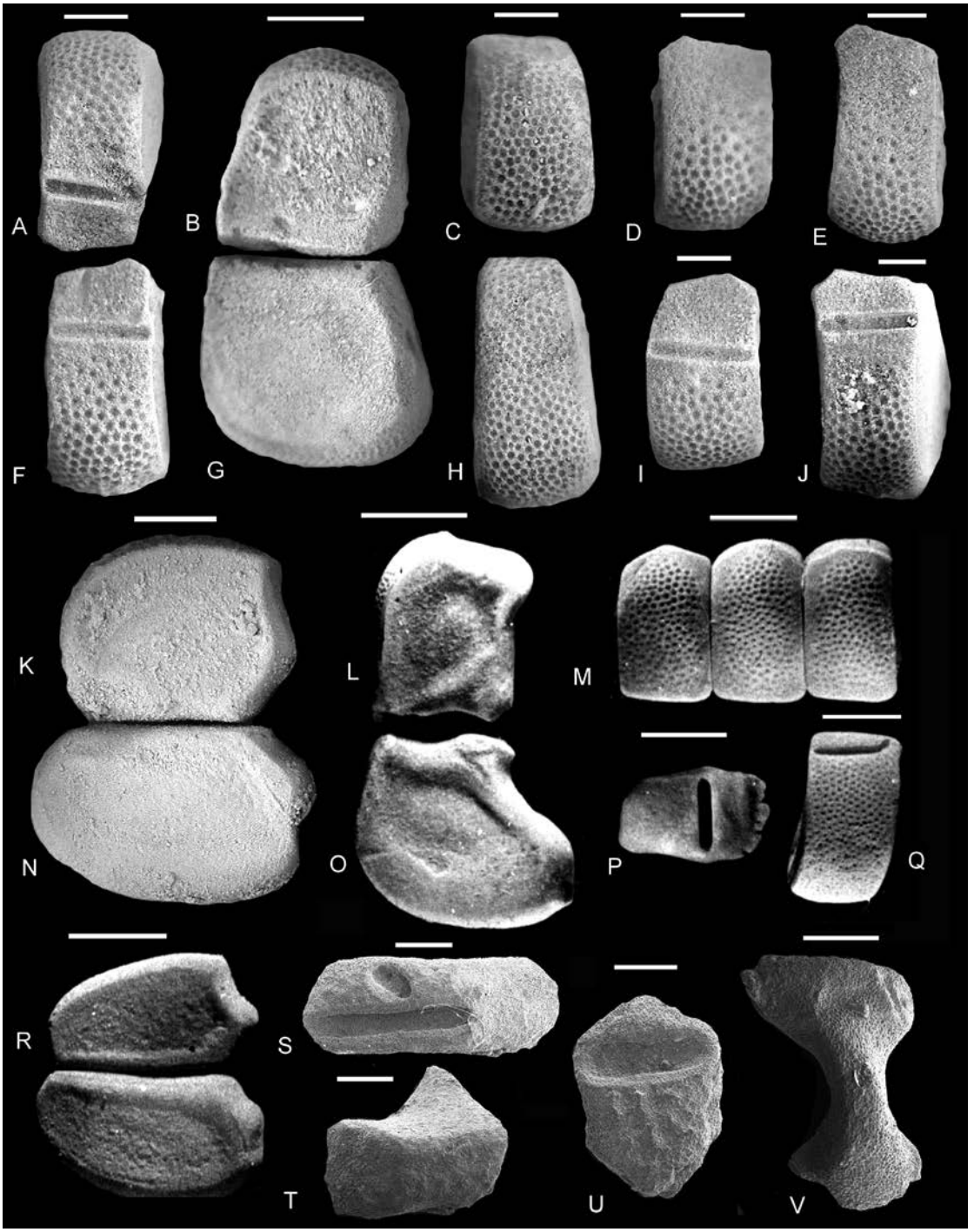
Text-fig. 6. *Tomidaster sulcatus* Sladen, 1891 from the Cenomanian of Kent (UK). A – Actinal surface of specimen showing predation-related gouges on superomarginals (NHMUK E 1116); B–E – Well-preserved arm, in actinal (B), lateral (C, D) and abactinal (E) views (NHMUK PI EE 18380); F–H – Partial individual (BGS GSM108645), in actinal (F), lateral (G) and enlarged lateral views, to show pedicellariae (H). Provenance: A, F–H are from the Grey Chalk Subgroup, Cenomanian, between Dover and Folkestone, Kent (UK); B–E are from the Grey Chalk Subgroup, Zig Zag Formation, middle Cenomanian, *Turrilites costatus* ammonite Subzone, Lydden Spout, Kent (UK). Scale bars equal 5 cm (A), 10 mm (B, C, F, G) and 5 mm (D, H).



Text-fig. 7. Cretaceous goniasterid asteroids. A–C – *Ophryaster oligoplax* (Sladen, 1891); A, B – actinal (A) and abactinal (B) views of specimen BGS GSM 118350; C – lateral view of arm, figured after Schulz and Weitschat (1981, pl. 7, fig. 2). D – *Ophryaster dorsolaevis* Schulz and Weitschat, 1981, abactinal view of holotype (NHMUK E 13945), the original of Schulz and Weitschat (1981, pl. 6, fig. 1). E – *Tomidaster sulcatus* Sladen, 1891, abactinal view of incomplete specimen (BGS unregistered). Provenance: A, B are from the Santonian chalk, southern United Kingdom, locality unknown; C is from the lower Campanian, *Offaster pilula* echinoid Zone, Lägerdorf, northern Germany; D is from the lower Campanian, *Offaster pilula* echinoid Zone or *Gonioteuthis quadrata* belemnite Zone, East Harnham, Wiltshire (UK); E is from the Grey Chalk Subgroup, Cenomanian, between Dover and Folkestone, Kent (UK). Scale bars equal 5 mm (A, C–E) and 2 mm (B).

pedicellariae variably developed on marginals. In some individuals, these are restricted to the lateral surfaces of the marginals (Text-fig. 6F–H), whereas in others (e.g., Text-fig. 6B–D) slightly shorter pedicellariae occur irregularly on the actinal and abactinal surfaces of marginals.

Abactinal ossicles small, polygonal, forming 3–4 columns of hexagonal plates over mid-radial line, extending from centre of disc to arm tips. Approximately 50% of actinals carry short, bivalved pedicellariae. Actinals (Text-fig. 5A, B) flat, subrectangular, arranged in nested chevrons parallel with ambulacral



Text-fig. 8. Cretaceous goniasterid asteroids. A–J, S–V – *Tomidaster timothyi* sp. nov., ossicles from holotype (WAM 2026.3); A, B, C – superomarginals, in lateral (A), proximal/distal (B) and abactinal (C) views; D–J – inferomarginals, in lateral (D–F, I, J), proximal/distal (G) and actinal (H) views; S, U – actinal or abactinal ossicles, in external views; T – adambulacral ossicle, in external view; V – ambulacral ossicle, in abactinal view. K, N – *Tomidaster sulcatus* (Sladen, 1891), proximal/distal views of marginal pair (BGS GSM 108645). L, M, O–Q – *Tomidaster peetersorum* (Jagt, 2000), ossicles originating in one individual (BGS unregistered); L, O – proximal/distal views of marginal pair; M – lateral view of articulated superomarginals; P – actinal ossicle; Q – lateral view of inferomarginal. R – *Ophryaster oligoplax* (Sladen, 1891), proximal/distal views of marginal pair (BGS unregistered). Provenance: A–J, S–V are from the Toolonga Calcilutite Formation, upper Santonian, Miannara Hill, Western Australia; K, N are from the Grey Chalk Subgroup, Cenomanian, between Dover and Folkestone, Kent (UK); L, M, O–Q are from the Portsdown Chalk Formation, upper Campanian, *Belemnitella mucronata* belemnite Zone, Studland, Dorset (UK); R is from the Seaford Chalk Formation, *Micraster coranguinum* echinoid Zone, Broadstairs, Kent (UK). Scale bars equal 5 mm (A–R) and 0.5 mm (S–V).

groove, with even, dense cover of impressed granule pits. Actinals with irregularly distributed bivalved pedicellariae. Some lack any, others bear 2–3, angled or subparallel in arrangement.

Adambulacral ossicles (Text-fig. 5B) carry 8–10 small subambulacral spine bases, and 6–7 adambulacral spines, some of which are present *in situ*. These are short and blunt.

The marginal ossicles of many specimens bear oval to circular depressions of variable dimensions (e.g., Text-figs 5A, 6A–D), which have in some cases significantly denuded the plates (Text-fig. 6A). These are also present on *Calliderma smithiae*, also from the Grey Chalk Subgroup and are possibly grazing traces left by eulimid gastropods.

REMARKS: This species can be distinguished from the closely related *T. comptoni* in the profile (strongly convex, well-demarcated actinal/abactinal surfaces) and shape (relatively narrow) of the marginal ossicles.

OCCURRENCE: *Tomidaster sulcatus* is best known from the Cenomanian Grey Chalk Subgroup between Dover and Folkestone, Kent. Isolated marginals of the species also occur in the same levels in Sussex. A single specimen is known from the Cenomanian of Le Havre, Seine-Maritime, France (Breton 1992, pl. 23, figs 1, 2).

Tomidaster comptoni (Forbes, 1848)
(Text-fig. 5C, D)

*1848. *Goniaster* (*Stellaster*) *comptoni* Forbes, p. 476.
1850. *Goniaster* (*Stellaster*) *comptoni* Forbes; Forbes in Dixon, p. 335, pl. 22, fig. 8.
1905. *Comptonia comptoni* Forbes; Spencer, p. 69, pl. 17, fig. 3; pl. 18, fig. 2.
1914. *Comptonia comptoni* Forbes; Spencer, p. 131.
1984. *Comptoniaster comptoni* (Forbes); Breton, p. 244.
non 1988. *Comptoniaster comptoni* (Forbes); Gale in Smith *et al*., p. 202, pl. 41, fig. 5.
non 1992. *Comptoniaster comptoni* (Forbes); Breton, p. 218, pl. 23, figs 1, 2.

DIAGNOSIS: Disc broad, arms short, rapidly tapering. Interradial marginals broad, short, external surfaces gently convex, lacking discrete actinal/abactinal-lateral surfaces.

TYPE: Two individuals are known, which Spencer (1905) considered to be cotypes. The present whereabouts of the individual showing the abactinal surface (Spencer 1905, pl. 18, fig. 2), stated to be in the collection of the Northampton Museum, are unknown. The specimen showing the actinal surface (Spencer 1905, pl. 17, fig. 3) is in the NHMUK (34311) and is here designated lectotype.

DESCRIPTION: Disc very broad, arms short, rapidly tapering (R2:r1 R/r 2:1), interradii gently concave. Interradial inferomarginals broad, short, with a breadth:length ratio of 2.5:1. Inferomarginals narrowing rapidly into the arm; each half radius includes 18–20 marginal pairs. Superomarginals slightly narrower than inferomarginals. External surfaces of inferomarginals evenly convex, lacking discrete actinal/abactinal-lateral surfaces. Slit-like bivalved pedicellariae abundant on lateral surfaces of marginals and variably present on actinal and abactinal surfaces of marginals. Spine pits obscured by preservational mode. Abactinal ossicles small, polygonal, plates in radial areas arranged in rows extending from centre of disc towards arm tips; some plates carry short bivalved pedicellariae. Actinal ossicles (Text-fig. 5D) flat, subrectangular, arranged in nested chevrons parallel with ambulacral groove. Larger rows of rectangular ossicles present on either side of adambulcrals. Actinals bear irregularly distributed bivalved pedicellariae.

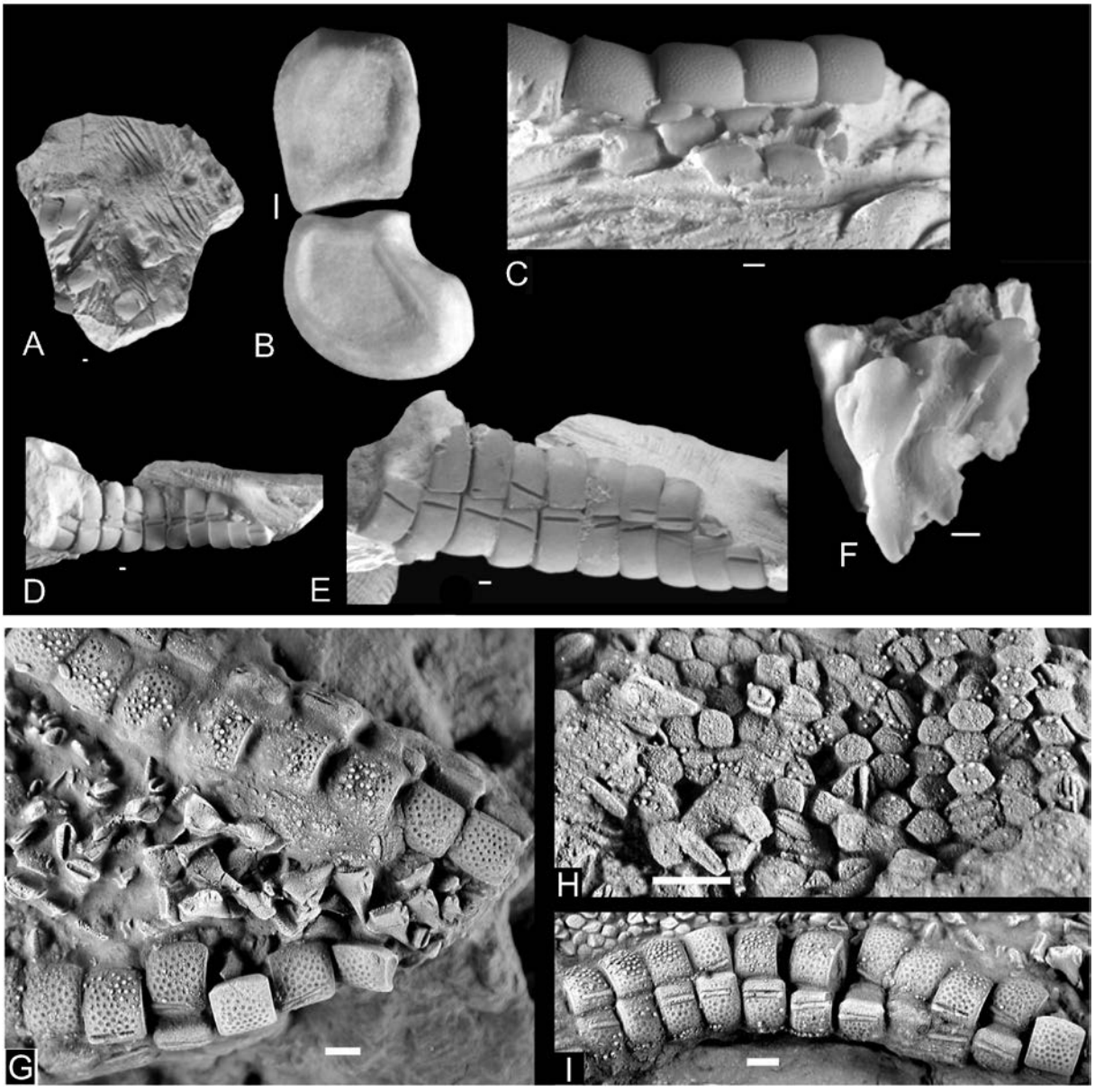
REMARKS: This species differs from all other congeners in its broad, short interradial marginal ossicles which have a breadth:length ratio of 2.5:1 (Text-fig. 5C, D). In contrast, the interradial marginals of *T. sulcatus* have a ratio <2:1. Additionally, the external surfaces of the interradial marginals are evenly convex, whereas in *T. sulcatus* they have demarcated lateral and actinal/abactinal surfaces (Text-fig. 8K, N).

OCCURRENCE: *Tomidaster comptoni* is known exclusively from the upper Albian *Pervinquieria* (*Pervinquieria*) *pricei* ammonite Zone of Blackdown, Devon (UK).

Tomidaster peetersorum (Jagt, 2000)
(Text-figs 8L, M, O–Q, 9A–F)

*2000. *Comptoniaster peetersorum* Jagt, p. 421, pl. 16, figs 1–6.

DIAGNOSIS: Medium- to large-sized species, with straight to weakly concave interbrachial disc margin; marginals numerous, short and tall, with outer face of superomarginals gently curved and slightly swollen aborally, and with markedly sloping inner margin (covered by adjoining abactinals). Ornament of close-



Text-fig. 9. Cretaceous goniasterid asteroids. A–F – *Tomidaster peetersorum* (Jagt, 2000); A, C–F – portions of holotype (NHMM JJ 11438), showing dissociated marginals (A), ambulacrals (F), margin in lateral view (D, E), and margin in actinal view (C); B – proximal/distal profile of marginals (RGM 428 074); copied from Jagt (2000, pl. 16, figs 1–6). G–I – *Tomidaster adamsi* (Blake, 2010), holotype (TMM NPL 31736), actinal view of base of arm (G); abactinal surface (H), lateral view of interradial marginals (I); figured after Blake (2010, fig. 5). Provenance: A–F are from the upper Campanian, Gulpen Formation, Zeven Wegen Member, Haccourt, Belgium; G–I are from the Britton Formation (probably Cenomanian), Coppell, Dallas County, Texas, USA. Scale bars equal 1 mm (A–F) and 2 mm (G–I).

set, fine granule pits, more numerous on inferomarginals; pedicellariae large, elongate and numerous on both supero- and inferomarginals (after Jagt 2000, p. 421).

TYPES: NHMM JJ 7649/a–b, Gulpen Formation, Zeven Wegen Member, upper Campanian, CPL SA quarry, Haccourt, north-east Belgium.

MATERIAL: In addition to the type material, a large group of associated ossicles from the upper Campanian *Belemnitella mucronata* Zone of Studland, Dorset, UK (BGS unregistered).

REMARKS: This species is distinguished by the erect superomarginals, in which the lateral face is

tall and vertical, the abactinal face very short, and a broad abactinal surface for articulation with the abactinal ossicles (Text-figs 8L, O, 9B). The inferomarginals are broad and tall, with a strongly convex external surface, and lateral and actinal surfaces are set at 90º. Slit-like pedicellariae are variably present on supero- and inferomarginals and on the actinal ossicles (Text-figs 8P, Q, 9E). *Tomidaster peetersorum* is closest to *T. timothyi* sp. nov. in the erect superomarginals, but in the latter species there is a broad external, spine-bearing surface (Text-fig. 8B, C). Additionally, in *T. timothyi* sp. nov., the interradial inferomarginals are very robust and broad (Text-fig. 8G).

Tomidaster timothyi sp. nov.
(Text-fig. 8A–J, S–V)

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DIAGNOSIS: *Tomidaster* in which both supero- and inferomarginals are very broad in proximal/distal view, and have sharply demarcated lateral, abactinal and actinal surfaces set at 90º.

TYPE: Approximately 100 associated ossicles, including marginals, actinals, abactinals, ambulacrals and adambulacrals. Toolonga Calcilutite, upper Santonian, Meanarra Hill, Kalbarri, Western Australia (WAM 2026.3).

DERIVATION OF NAME: After Timothy McNamara who found the only known specimen.

DESCRIPTION: Marginals block-like, interradial marginals almost square in proximal/distal profile and with discrete, subequal actinal-abactinal surfaces set at 90º. Interradial marginals very broad (Text-fig. 8B, G). External surfaces with dense, even cover of rounded-polygonal, deeply impressed granule pits which are absent close to ambitus. Slit-like pits for bivalved pedicellariae present immediately above (superomarginals) or below (inferomarginals) ambitus; granule pits fade adjacent to these pits. Slight offset between supero- and inferomarginals indicated by double ambital articulations (Text-fig. 8A, F, I, J). Actinal and abactinal ossicles of variable outlines (elongated – Text-fig. 8S; short, hexagonal – Text-fig. 8U) and approximately 50% bearing elongated pits for pedicellariae similar to those present on marginals. Adambulacals (Text-fig. 8T) with adradial prominence and deeply concave margin to accommodate podia. Ambulacrals (Text-fig. 8V) waisted, heads elongated in arm.

REMARKS: *Tomidaster timothyi* sp. nov. differs from its congeners principally in possessing very broad, nearly square interradial marginals with sharply demarcated lateral surfaces. In *T. sulcatus* (Text-fig. 8K, N) the external surfaces of marginals are convex; in *T. peetersorum* (Text-fig. 8L) an external abactinal margin is absent. *T. timothyi* sp. nov. differs from *T. adamsi* (Text-fig. 9G, I) in its larger, more robust marginals.

Genus *Ophryaster* Spencer, 1914

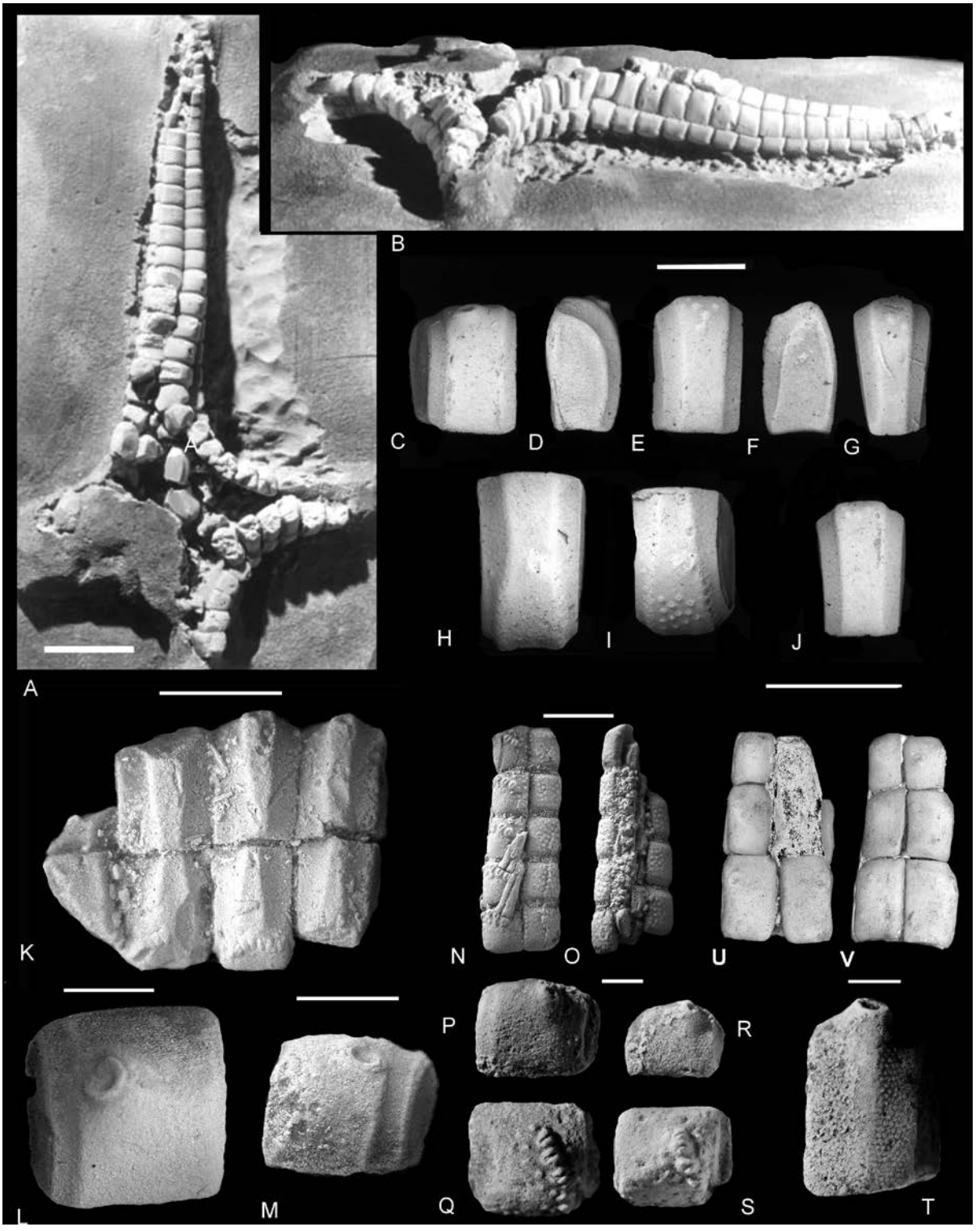
DIAGNOSIS: Interradius evenly concave, arms poorly demarcated from disc. Supero- and inferomarginals low, external surfaces evenly convex, sloping, lateral surfaces absent or poorly demarcated. Spine pits tend to be absent on inner abactinal surfaces of superomarginals. A single, slightly obliquely oriented, slit-like bivalved pedicellaria is present on lateral surfaces of every inferomarginal, and these are irregularly distributed on the actinal and adambulacral ossicles, but never on abactinals. Actinal and abactinal ossicles finely rugose.

TYPE SPECIES: *Nymphaster oligoplax* Sladen, 1891, by original designation.

INCLUDED SPECIES: *Ophryaster magnus* Spencer, 1914 and *Ophryaster dorsolaevis* Schulz and Weitschat, 1981.

REMARKS: *Ophryaster* is included here in order to discuss the differences with and similarities to *Tomidaster*. Both have a comparable overall construction (broad disc, poorly demarcated arms, evenly

Text-fig. 10. Jurassic and Cretaceous goniopectinid asteroids. A–J – *Chrispaulia radiatus* (Spencer, 1905); A, B – holotype (NHMUK E 375), in abactinal (A) and lateral (B) views, the original of Spencer (1905, pl. 25, fig. 1) and Gale (2005, figs 4–7, 8e–j, 9); C–G, J – superomarginal ossicles in lateral (C, E, G, J) and proximal/distal views (NHMUK EE 5782); H, I – inferomarginals in lateral views (NHMUK EE 5781). K–M – *Chrispaulia australis* sp. nov.; K – articulated interradial marginals, in lateral view (WAM 2026.4); L, M – superomarginals from proximal arm, in lateral view (WAM 2026.5, 6). N–T – *Borszczia spinosa* (Gale and Jagt, 2021); N, O – holotype arm fragment (Nds LH 105.107), in lateral (N) and actinal (O) views; P, R, T – superomarginals in lateral views (NHMUK PI EE 17999–18000); Q, S – distal marginals in lateral views (NHMUK PI EE 18001, 18002). U, V – *Chrispaulia wrightorum* Gale and Jagt, 2021, holotype arm fragment (NHMUK PI EE 17997), →



in abactinal (U) and lateral (V) views. Provenance: A, B are from the Grey Chalk Subgroup, Cenomanian, between Dover and Folkestone, Kent (UK); C–J are from the Grey Chalk Subgroup, Middle Cenomanian, *Turrilites acutus* ammonite Subzone, west of Dover, Kent (UK); K–M are from the Toolonga Calcilutite Formation, upper Santonian, Shark Bay, Western Australia; N, O are from the lower Hauterivian, *Endemoceras amblygonium* ammonite Zone, Engelbostel, Hannover, Germany; P–T are from the upper 3 m of Tealby Clay (Hauterivian) at Nettleton, Lincolnshire (UK); U, V are from the Hunstanton Formation, upper Albian, Speeton, Yorkshire (UK). Scale bars equal: 10 mm (A, B), 5 mm (K, N, O, U, V) and 1 mm (C–J, L, M, P–T).

curved interradii, abactinals separate superomarginals in the arms) and both possess elongated slit-like bivalved pedicellariae. However, the marginal frame is less robust in *Ophryaster* (Text-fig. 7A–D) and the marginals have a lower profile (Text-fig. 8R). Additionally, the distribution of pedicellariae is different. On *Ophryaster* marginals, a single one is found on the lateral surfaces of every inferomarginal (Text-fig. 7C) and never on the superomarginals. In *Tomidaster* they occur, albeit irregularly, on all surfaces of all marginals and are abundant on the actinal and abactinal ossicles (Text-fig. 5A, B) and never occur on the adambulacrals. In *Ophryaster*, they occur abundantly on the actinal ossicles and adambulacrals (Text-fig. 7A) but never on the abactinals, which are finely rugose. The two genera are certainly closely related and probably shared a common ancestor.

Order Paxillosida Perrier, 1884
Suborder Cribellina Fisher, 1911
Family Goniopectinidae Verrill, 1899

DIAGNOSIS: Cribriform organs consist of discrete spinelets not joined vertically into comb-like structures, protected by cover lamellae; fasciolar channels run from inferomarginals across actinal interareas.

INCLUDED GENERA: *Goniopecten* Perrier, 1881, *Prionaster* Verrill, 1899, *Pectinidiscus* Ludwig, 1907 and *Chrispaulia* Gale, 2005.

Genus *Chrispaulia* Gale, 2005

DIAGNOSIS: Arms long, narrow, disc small with gently rounded interbrachial arcs; superomarginals meeting adradially over entire length of arm; distal marginals imbricated and carrying rounded or elongated areas of smooth, dense stereom; some interbrachial marginals bearing enlarged spines attached to conical abactinal or distal spine pit.

TYPE SPECIES: *Nymphaster radiatus* Spencer, 1905, by original designation.

INCLUDED SPECIES: In addition to the type species, *Chrispaulia wrightorum* Gale and Jagt, 2021. *Chrispaulia jurassica* Gale, 2011 and *C. spinosus* Gale and Jagt, 2021 were transferred to *Borszczia* Pauly and Villier, 2025 by Pauly and Villier (2025). This genus differs in the presence of elongated, distally directed spines on the inferomarginals, attached to a column of horseshoe-shaped bases on the inferomarginals (Text-fig. 10N–T).

Chrispaulia australis sp. nov.
(Text-fig. 10K–M)

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DIAGNOSIS: *Chrispaulia* in which the interradial inferomarginals bear a crescentic arc of pustules on the lower part of the lateral surface, and the interradial marginals each carrying an abactinally directed, crater-like spine base.

TYPES: The articulated radius, incorporating 4 partial supero- and inferomarginals is the holotype (WAM 2026.4). The two superomarginals from the arm are paratypes (WAM 2026.5, 2026.6), from the Toolonga Calcilutite, early Campanian at Yaringa Station, near Shark Bay, Western Australia.

DERIVATION OF NAME**:** From Latin *australis*, meaning southern, on account of the occurrence in Australia.

DESCRIPTION: Interradial marginals tall, rectangular (height 1.5 times greater than breadth), flat. A raised central area occupies one-third of the breadth, tapering towards the ambitus, flanked by broad, depressed fasciolar surfaces. The abactinal crest of each superomarginal bears a single, raised circular pit, which bore an abactinally directed spine. The lower, actinal surface of the inferomarginals carries a transverse, actinally concave, cluster of pustules which may have borne spines. The superomarginals from the proximal arm (Text-fig. 10L, M) are square in lateral view with a narrow abactinal surface, and each carries a distally directed, oval, rimmed spine base at the distal summit of the lateral surface. The distal fasciolar surface is broader than the proximal one.

REMARKS: *Chrispaulia australis* sp. nov. differs from *C. radiatus* (Text-fig. 10A–J) in the presence of large, abactinally directed spine pits on the interradial superomarginals, absent in the latter species (Text-fig. 10E, G, J) and in the presence of pustules on the interradial inferomarginal. Additionally, the marginals of *C. australis* sp. nov. entirely lack rugosities. It differs from *C. wrightorum* (Text-fig. 10U, V) in the shorter distal superomarginals. This is the first *Chrispaulia* from outside the United Kingdom.

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APPENDIX

Occurrences of extra-European Cretaceous asteroids. Some familial assignments are new in the present paper.

Country/state or region	Reference	Age	Name	Family
Canada British Columbia	McLearn (1944)	?	*Lophidiaster silentensis* McLearn, 1944	Astropectinidae
		?	*Coulonia stelcki* McLearn, 1944	Goniasteridae?
Canada Alberta	Hall and Moore (1990)	Turonian	?*Tethyaster albertensis* Hall and Moore, 1990	Astropectinidae
USA California	Durham and Roberts (1948)	?Campanian	*Astropecten matilijaensis* Durham and Roberts, 1948	Astropectinidae
	Blake and Petersen (1993)		*Pegaster stichos* Blake and Petersen, 1993	?Forcipulatida
	Blake (1971)	Late Cretaceous	*Sucia suavis* Blake, 1971	Pseudarchasteridae
	Blake (1986)	Campanian?	*Mediaster hayi* Blake, 1986	Goniasteridae
USA Colorado	Blake and Kues (2002)	Turonian	*Codellaster keepersae* Blake and Kues, 2002	Goniasteridae
USA South Dakota	Blake *et al.* (2018)	Campanian	*Betelgeusia brezini* Blake, Halligan and Larson, 2018	Astropectinidae
USA Wyoming	Weller (2005)	?	*Pentagonaster browni* Weller, 2005	?
USA North Carolina	Blake and Sturgeon (1995)	Maastrichtian	*Aldebarania arenitea* Blake and Sturgeon, 1995	?
	Mah (2022)		*Peedeeaster sandersoni* Mah, 2022	Goniasteridae
			Sclerasterias sp.	Asteriidae
USA Texas	Blake and Reid (1998)	Albian–Cenomanian	*Craterаster texensis* (Adkins, 1920)	Goniasteridae
			Craterаster mccarteri (Adkins, 1928)	Goniasteridae
			Fomalhautia hortensae (Adkins and Winton, 1920)	Goniasteridae
			Capellia mauricei Blake and Reid, 1998	Astropectinidae
			Betelgeusia reidi Blake and Reid, 1998	Astropectinidae
			Alkaidia sumralli Blake and Reid, 1998	Zoroasteridae
			Denebia americana (Adkins, 1920)	Ophidiasteridae
			Altiaria wintoni (Adkins, 1920)	Ophidiasteridae
	Blake and Sprinkle (1996)	Campanian	*Astrocratis acutispina* Blake and Sprinkle, 1998	Astropectinidae
	Blake (2010)		*Tomidaster adamsi* Blake, 2010	Astropectinidae
USA Tennessee	Wade (1926)		*Metopaster tennesseensis* Wade, 1926	Goniasteridae
Mexico	Blake (1988)	?Campanian	*Paleoctenodiscus campaniurnis* Blake, 1988	Porcellanasteridae
Brazil	Manso (2006)	Turonian	not named	Goniasteridae
Argentina	Fernández *et al.* (2014)	Valanginian	*Tethyaster antares* Fernández, Péres, Luci and Carizzo, 2014	Astropectinidae
Angola	Blake *et al.* (1996)	Coniacian	*Afraster scalariformis* Blake, Breton and Gofas, 1996	Forcipulatida
Morocco Agadir, Taba	Hess and Blake (1995)	Barremian	*Coulonia platyspina* Hess and Blake, 1995	Astropectinidae
Morocco Agadir	Blake and Reboul (2011)		*Marocaster coronatus* Blake and Reboul, 2011	Goniasteridae
	Ewin and Gale (2020)		*Alkaidia megaungula* Ewin and Gale, 2020	Zoroasteridae
			Odontaster tabaensis Ewin and Gale, 2020	Odontasteridae
			indet.	Asteriidae
Morocco Middle Atlas, Bakrit	Gale and Villier (2013)	Maastrichtian	*Cretasterias reticulatus* Gale and Villier, 2013	Asteriidae
Algeria	Villier *et al.* (2007)	Berriasian	*Protothrissacanthias africanus* Villier, Breton and Atrops, 2007	Astropectinidae
Egypt Abou Roach	de Loriol (1888)	Santonian	*Tomidaster schlumbergeri* (de Loriol, 1888)	Goniasteridae
	de Loriol (1909)		*Tomidaster fourteaui* (de Loriol, 1909)	Goniasteridae
			Metopaster teilhardi de Loriol, 1909	Goniasteridae
			Sladenia fourteaui de Loriol, 1909	Ophidiasteridae
			Chariaster elegans de Loriol, 1909	Ophidiasteridae
	Jux (1957)		*Recurvaster lorioli* Jux, 1957	Goniasteridae
			Forbesiaster gaensis Jux, 1957	Goniasteridae
Iran Kopet Dagh	Ghaderi and Villier (2013)	Coniacian–Santonian	*Metopaster parkinsoni* (Forbes, 1848)	Goniasteridae
Japan	Gale *et al.* (2024)	Albian	*Coulonia hokahira* Gale, Ishida, Jagt, Thuy and Komatsu, 2024	Astropectinidae
New Zealand	Fell (1952)	'Senonian'	*Ophryaster novaezelandiae* Fell, 1952	Goniasteridae
	Fell (1956)		*Hippasteria antiqua* Fell, 1956	Goniasteridae
	Stevens (2020)	Lower Cretaceous	*Paragonaster felli* Stevens, 2020	Pseudarchasteridae
Australia Western Australia	this paper	Campanian	*Chrispaulia australis* sp. nov.	Goniopectinidae
		Santonian	*Tomidaster timothyi* sp. nov.	Goniasteridae
Antarctica	Medina and Del-Valle (1983)	?	*Cladaster carrioni* Medina and Del-Valle, 1983	Goniasteridae