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Crinoids (Echinodermata, Articulata) from the Campanian (Upper Cretaceous) rocky shore at Ivö Klack, southern Sweden

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ABSTRACT:

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Ten species of crinoids are recorded from a rocky shoreline deposit of upper lower Campanian age at Ivö Klack in southern Sweden. These include three comatulids, i.e., *Semiometra annulata* Rasmussen, 1961, *S. impressa* (Carpenter, 1881), and *Loriolometra retzii* (Lundgren, 1875), three isocrinids, i.e., *Nielsenicrinus* cf. *carinatus* (Roemer, 1840), and isocrinid sp. 1 and sp. 2, as well as four pelagic roveacrinids, i.e., *Stellacrinus lineatus* Gale, 2018, *Crassicoma suedica* sp. nov., *Applinocrinus cretaceus* forma *spinifer* Gale, 2018 and *Cultellacrinus labyrinthus* Gale, 2016. The comatulids and isocrinids coexisted in shallow (<30 m), high-energy coastal environments, whereas the roveacrinids were Chalk Sea dwellers in the upper water column that were washed into the shallows by currents. The presence of isocrinids in such shallow habitats is remarkable given that these environments are characterised by high biodiversity, intense predation pressure, strong currents and wave-agitated waters – conditions typically considered unsuitable for these slow-moving stalked crinoids, and the reason they are thought to be confined to depths in excess of 100 m in present-day oceans. The Ivö Klack specimens presented herein represent the only known occurrence of isocrinids in a rocky shoreline deposit, marking a notable shift in isocrinid ecology and habitat association. The limited stratigraphical ranges of the roveacrinids in expanded chalk successions elsewhere corroborates other age assignments of the succession at Ivö Klack.

Key words: Crinoids; Campanian; Rocky shoreline; Ivö Klack; Sweden.

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INTRODUCTION

Exposures at Ivö Klack in Skåne, southern Sweden (Text-fig. 1), provide a profile through a rocky shoreline of late early Campanian age, where boulders of Proterozoic gneiss were eroded by wave action, encrusted by zoned epifauna (Surlyk and Christensen 1974; Surlyk and Sørensen 2010), then buried beneath

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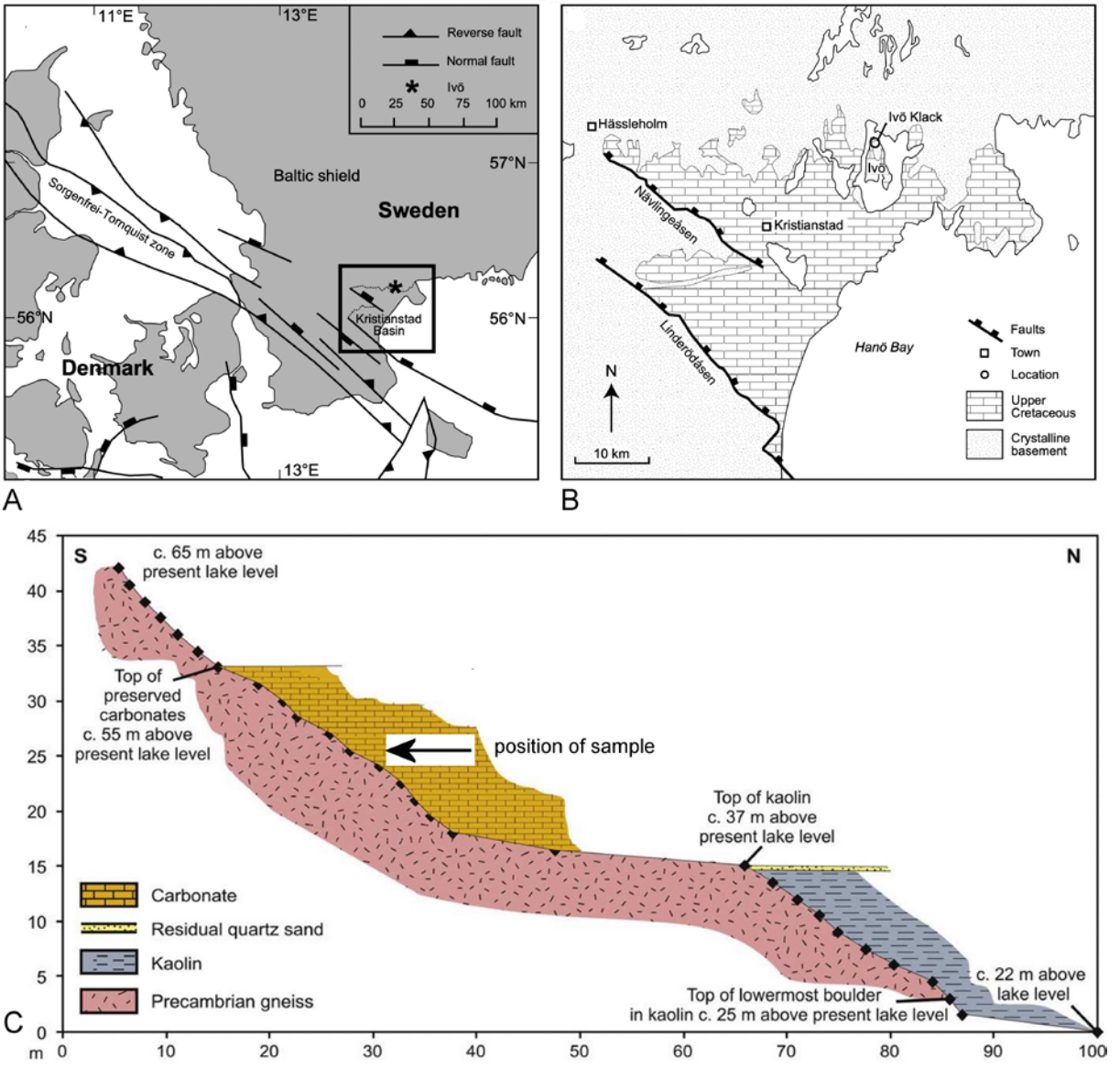


Text-fig. 1. Location of Ivö Klack. A – Map showing the position of the Kristianstad Basin in south-east Sweden; B – Kristianstad Basin with the position of Ivö Klack; C – Schematic cross-section through the Ivö Klack region to illustrate sedimentary facies and location of the bulk sample used for this study (after Sørensen and Surlyk 2010, figs 2 and 6).

bioclastic shell sands and gravels composed of the calcitic remains of invertebrates, some of which lived on the boulders, and others in the surrounding carbonate sands and gravels. This locality probably represents a maximum water depth of 30 m, and among the diverse and abundant faunas (comprising over 200 species), bryozoans, bivalves, echinoderms, serpulids and brachiopods were particularly abundant (Sørensen and Surlyk 2010, 2011; Sørensen *et al*. 2011, 2012; Schrøder *et al*. 2018), as were cirripedes (Gale and Sørensen 2014, 2015). This community included known predators of extant comatulids, such as decapod crustaceans and regular echinoids (Stevenson *et al*. 2017; Einarsson 2018). In a monograph on Cretaceous Crinoidea, Rasmussen (1961) recorded two crinoids (comatulids) from Ivö Klack, i.e., *Semiometra impressa* and *S. annulata* Rasmussen, 1961. He also described an isocrinid, *Isocrinus*? *brotzeni* Rasmussen, 1961, from the locality of Båstad on the south-west coast of Sweden, probably of late Campanian age. More recently, Gale (2016) described and illustrated three species of pelagic microcrinoids from Ivö Klack.

The kaolinite quarry at Ivö Klack ceased to be worked in the 1960s. It exposes a remarkably well preserved late early Campanian steep gneissic rocky shoreline (Surlyk and Sørensen 2010). The gneisses are overlain and draped by Cretaceous bioclastic limestones which have been overgrown progressively ever since. However, a pocket of soft, unconsolidated material set between large gneiss boulders, on the wooded slope representing the old back wall of the quarry, approximately 10 m beneath the highest Cretaceous sediments was discovered in the 1990s (Text-fig. 1C). The preservation of material in this lens is exceptionally good; there is little calcite overgrowth, and many of the smaller fossils are perfectly preserved. It probably represents very little time and thus provides a snapshot of biodiversity.

METHODS

The present study is based on material picked from washed residues from a site at Ivö Klack which is stratigraphically about 10 m beneath the highest preserved carbonate sediments (Text-fig. 1C). Approximately 500 kg of soft sediment were collected, washed and separated into fractions. All of the >3 mm fraction and approximately 1.5 kg of the 0.5–3 mm material was handpicked. In addition, a small portion of the 0.2–0.5 mm residue was picked. This represents about 200 hours of picking and yielded a total of 350 crinoid ossicles, including three articulated comatulid cups. The figured material has been deposited in the collections of the Natural History Museum, Department of Palaeontology, London (prefix NHMUK).

SYSTEMATIC PALAEONTOLOGY

Class Crinoidea Miller, 1821
Order Isocrinida Sieverts-Doreck, 1952
Suborder Isocrinina Sieverts-Doreck, 1952
Family Balanocrinidae Roux, 1981
Subfamily Diplocrininae Roux, 1981

Genus *Nielsenicrinus* Rasmussen, 1961

DIAGNOSIS: A cryptosyzygy is present between secundibrachials 3 and 4 and there is no symmorphy (Hess and Messing 2011, p. *T*61). The higher classification of Isocrinida follows that of Amézaine *et al*. (2023).

TYPE SPECIES: *Pentacrinus obsoletus* Nielsen, 1913, by original designation.

REMARKS: Rasmussen (1961) did not assign *Isocrinus*? *carinatus* to a genus but Jagt (1999) provided a detailed description of extensive material from north-east Belgium and the south-east Netherlands and placed it in *Nielsenicrinus* (see also Roux *et al*. 2008, p. 36).

Nielsenicrinus cf. *carinatus* (Roemer, 1840)
(Text-fig. 2A–F)

*1840. *Pentacrinites carinatus* Roemer, p. 26, pl. 6, fig. 1.
1961. *Isocrinus*? *carinatus* (Roemer, 1840); Rasmussen, p. 115, pl. 20, figs 3–8.
1999. *Nielsenicrinus carinatus* (Roemer, 1840); Jagt, p. 81, pl. 5, figs 4–7, 9, 10; pls 6, 7; pl. 8, figs 1–9; pls 9–11; pl. 12, figs 1–6, 8.

TYPE: The pluricolumnal illustrated by Roemer (1840, pl. 6, fig. 1) is the lectotype by designation of Rasmussen (1961) but has not been traced.

MATERIAL: 25 isolated columnals from Ivö Klack, upper lower Campanian (NHMUK collections).

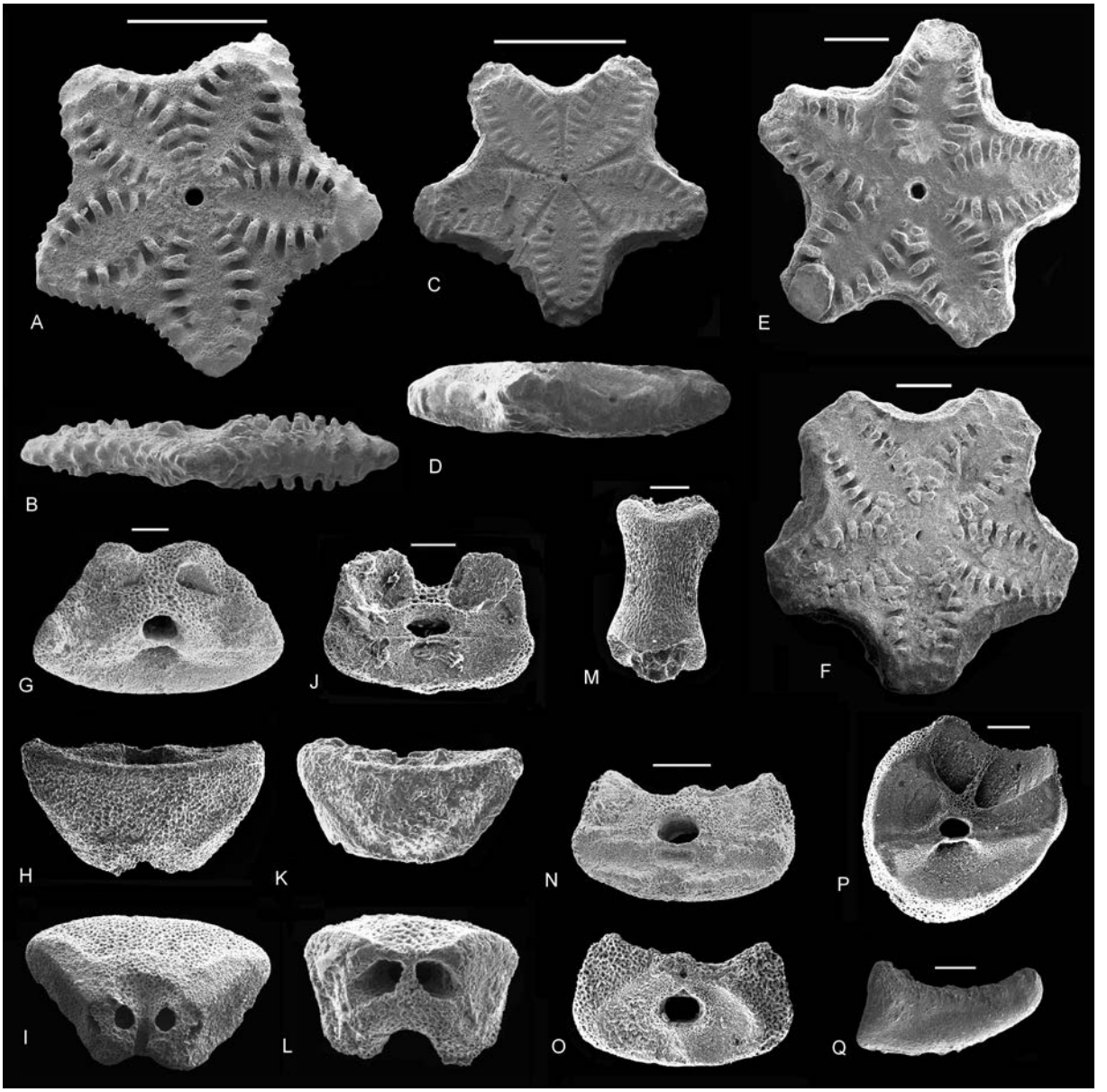
DESCRIPTION: Columnals from the proxistele are low, with a symplectical articulum and the lateral sculpture comprises irregularly positioned blunt, thorn-like processes which project on the radial margins (Text-fig. 2A, B). The culmina are tall and project proximally and distally, and the corresponding crenellae are deep. The ossicles compare well with proxistele internodals figured by Jagt (1999, pl. 7, figs 7, 8), although the column section is more nearly pentagonal. Nodals (Text-fig. 2C–F) are pentastellate, and the proximal articulum is cryptosymplectical. The cirral sockets occupy the entire height of the nodals and carry broad articular ridges.

REMARKS: The Ivö Klack specimens compare well with the extensive material of this species illustrated by Jagt (1999, pls 5–8) from the Zeven Wegen Member (Gulpen Formation; lower upper Campanian) of Haccourt and Lixhe, north-east Belgium. This appears to be the first record of Isocrinida from a rocky shoreline deposit.

Isocrinid sp. 1
(Text-fig. 2G–I)

MATERIAL: A single radial plate, NHMUK PI EE 18228.

DESCRIPTION: The radial is 1.4 mm wide, low and triangular in lateral view and notched aborally for



Text-fig. 2. Isocrinids (A–L) and comatulids (M–Q) from the upper lower Campanian of Ivö Klack, southern Sweden. A–F – *Nielsenicrinus* cf. *carinatus* (Roemer, 1840); A, B – articular and lateral views, respectively, of internodal from proxistele, showing symplectical articulum (NHMUK PI EE 18226); C, D – nodal columnal, in articular view showing cryptosymplectial articulation and lateral view with cirrus sockets, respectively (NHMUK PI EE 18227); E, F – nodal columnals (NHMUK PI EE 18252). G–I – Isocrinid sp. 1, radial, in adoral, lateral and basal views, respectively (NHMUK PI EE 18228). J–L – Isocrinid sp. 2, radial, in adoral, lateral and basal views, respectively (NHMUK PI EE 18252). M – comatulid cirral ossicle (NHMUK PI EE 18253). N, O – IBr1, in proximal and distal views, respectively (NHMUK PI EE 18229). P – distal comatulid brachial (NHMUK PI EE 18230). Q – terminal element of comatulid cirral (NHMUK PI EE 18231). Scale bars equal 1 mm (A–F) and 0.2 mm (all others).

contact with the basals. The adoral margin is long and gently concave, the radial facet triangular and the axial canal large and transversely oval. The adoral muscle facets are unusually small. The paired nerve canals to the basals are large and round.

REMARKS: This radial differs significantly from those assigned to *Nielsenicrinus carinatus* by Jagt (1999, pl. 9, figs 1, 3, 9, 10) in the absence of rugosities on the lateral surface which characterise that species, and the very small articular facets for the basals;

which are broad in *N. carinatus* and in life articulated with relatively large basals.

Isocrinid sp. 2
(Text-fig. 2J–L, N, O)

MATERIAL: A single radial plate and one proximal brachial (IBr1), NHMUK PI EE 18229a, b.

DESCRIPTION: The radial is 1.2 mm wide, subrectangular in adoral view, the breadth being greater than the height. The radial facet bears a large, oval axial canal, a weak fulcral ridge and large adoral muscle facets separated by a U-shaped groove. The external surface is trapezoidal in outline and slightly convex. The paired nerve canals to the basals are large and closely spaced. A single IBr1 has an adoral surface which corresponds in morphological details with the radial facet, but the adoral muscle fossae are broken away.

REMARKS: In overall form, this radial corresponds well with those of *Isselicrinus*, as figured by Rasmussen (1961, pl. 5, figs 5, 10) in the trapezoidal form of the radial plate in lateral aspect, the tiny basals and the rectangular adoral outline of the radial facet in which the interradial margins converge slightly towards the lumen. However, this generic assignment cannot be confirmed in the absence of material from the column. The radial is quite different to that of isocrinid sp. 1 in both its lateral profile and nature of the radial facet.

Order Comatulida A.H. Clark, 1908
Superfamily Notocrinoidea Mortensen, 1918
Family Notocrinidae Mortensen, 1918

Genus *Semiometra* Gislén, 1924

DIAGNOSIS: Centrodorsal low, disc shaped with a distinct dorsal star; cirrus sockets small and crowded, not forming columns; centrodorsal cavity 20–30% of centrodorsal diameter, and surrounded by small, shallow radial pits (modified after Hess and Messing 2011, p. 128).

TYPE SPECIES: *Antedon impressa* Carpenter, 1881, by original designation.

Semiometra impressa (Carpenter, 1881)
(Text-fig. 3A–C, G, L, N)

*1881. *Antedon impressa* Carpenter, p. 135, pl. 6, figs 8, 9.

1924. *Semiometra impressa* (Carpenter); Gislén, p. 172, figs 237, 238.

part 1961. *Semiometra impressa* (Carpenter); Rasmussen, p. 309, pl. 45, fig. 1 only.

1995. *Semiometra impressa* (Carpenter); Jagt, p. 189, figs 4, 7.

1999. *Semiometra impressa* (Carpenter); Jagt, p. 100, pl. 25, figs 1, 2; text-fig. 51a–c.

DIAGNOSIS: A *Semiometra* in which the centrodorsal is rounded-subpentagonal in outline and has a low conical form; the aboral surface has a smooth central region, in which the dorsal star comprises five, short oval slots. Cirrus sockets are numerous and arranged in alternating columns.

TYPE: The lectotype, designated by Rasmussen (1961, p. 309), is the specimen figured by Carpenter (1881, pl. 6, fig. 9) from the Campanian of Balsberg, southern Sweden. It is lost.

MATERIAL: Five centrodorsals and three cups from Ivö Klack (NHMUK collections).

REMARKS: The present material compares moderately well with the specimen from Båstad in Sweden illustrated by Rasmussen (1961, pl. 45, fig. 1), but the smooth aboral region of the centrodorsal is much broader in the new Ivö Klack material. Jagt (1999, p. 102) restricted the usage of this species to material from the Campanian of Sweden and Belgium and considered that the cup figured by Rasmussen (1961, pl. 45, fig. 2), from the upper Maastrichtian of north-east Belgium belonged to a separate species, *Semiometra saskiae* Jagt, 1999.

Semiometra annulata Rasmussen, 1961
(Text-fig. 3D–F, H–K, Q–S)

*1961. *Semiometra annulata* Rasmussen, p. 305, pl. 44, figs 4, 7.

DIAGNOSIS: *Semiometra* in which the centrodorsal is truncated aborally with a flat aboral surface. The dorsal star is depressed and forms a deep, pentagonal dorsal pit. The cirrus sockets are large and arranged in two slightly irregular tiers.

TYPE: Statens Naturhistorisk Museum, Copenhagen, MGUH 8982, from Ivö Klack, upper lower Campanian.

MATERIAL: 13 centrodorsals from the type locality (NHMUK collections).

REMARKS: The new material is closely similar to the specimen described and illustrated by Rasmussen (1961) but is better preserved and provides details of the centrodorsal cavity, cirrus sockets and ontogeny. The centrodorsal cavity is deep, and its breadth is 20% of the centrodorsal diameter. Keyhole-shaped, oval or circular interradial slots are present immediately lateral to the cavity. The basals are rod-shaped (Text-fig. 3H) and the end adjacent to the cavity is expanded.

The new material includes two juvenile specimens. The smaller (Text-fig. 3Q–S) is 0.6 mm in diameter and has ten alternately inset cirrus sockets (Text-fig. 3Q), which in lateral view (Text-fig. 3R) form two tiers. The centrodorsal cavity is one third of the breadth of the ossicle (Text-fig. 3R). A larger centrodorsal (Text-fig. 3I–K), with a diameter of 3.5 mm, has a narrow, deep dorsal pit surrounded by a zone that lacks cirrus sockets. In lateral view (Text-fig. 3J) the cirrus sockets are arranged in two slightly irregular tiers, the lower of which is variably inset. The largest specimen (Text-fig. 3D–F) is 6 mm in diameter. Ontogeny involves a progressive increase in cirrus socket numbers, a broadening of the dorsal pit and surrounding cirrus-free zone, development of a broader and lower lateral profile and narrowing of the centrodorsal cavity. *Semiometra annulata* differs from congeners in its truncated aboral surface and the broad, deep dorsal pit.

Genus *Loriolometra* Gislén, 1924

DIAGNOSIS: Centrodorsal large, high, columnar or slightly conical, with rounded aboral apex bearing an aboral pit or dorsal star. Cirrus sockets large, with a wide axial canal, lateral articular tubercles and marginal crenulae (after Hess and Messing 2011, p. 128).

TYPE SPECIES: *Comaster retzii* Lundgren, 1875, by original designation.

Loriolometra retzii (Lundgren, 1875)
(Text-fig. 3O, P)

*1875. *Comaster retzii* Lundgren, p. 66, pl. 3, figs 1–13.

1961. *Loriolometra retzii* (Lundgren, 1875); Rasmussen, p. 302, pl. 43, figs 1–3.

1999. *Loriolometra retzii* (Lundgren, 1875); Jagt, p. 108, text-fig. 51D–L; pl. 25, fig. 3.

DIAGNOSIS: As for genus.

TYPE: The lectotype, designated by Rasmussen (1961, p. 302), is from Köpinge in southern Sweden, and the probable age is late Campanian (Christensen 1975). It is in the collections of Lund University.

MATERIAL: Two centrodorsals from Ivö Klack (NHMUK collections).

REMARKS: The two Ivö Klack specimens are not well preserved but the shape of the centrodorsals and arrangement of the cirrus sockets resembles material figured by Rasmussen (1961, pl. 43, figs 1–3) and Jagt (1999, text-fig. 51D–L). In addition to the material from Köpinge, Båstad and Ignaberga in southern Sweden, cited by Rasmussen (1961, p. 302), Jagt (1999, p. 109) recorded the species from the lower upper Campanian portion (Benzenrade Member) of the Vaals Formation in the south-east Netherlands.

Order Roveacrinida Sieverts-Doreck in Ubaghs, 1953
Family Saccocomidae d'Orbigny, 1852
Subfamily Saccocominae d'Orbigny, 1852

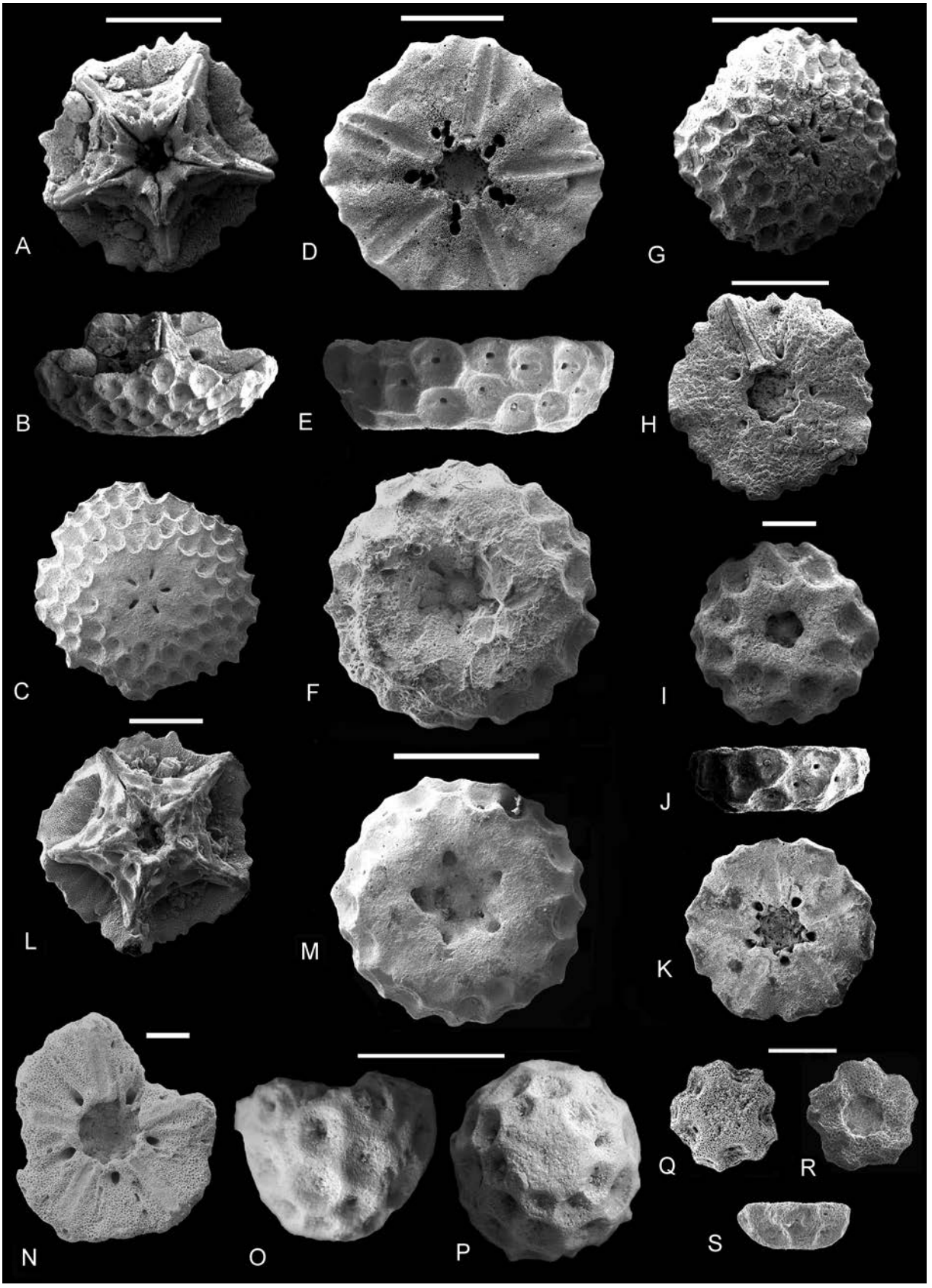
Genus *Crassicoma* Hess and Sieverts-Doreck, 2002

TYPE SPECIES: *Crassicoma schattenbergi* Hess and Sieverts-Doreck, 2002, by original designation.

DIAGNOSIS: Cup low, composed of thick-walled radials. Small basals fused with centrale, inset, or forming low aboral projection.

REMARKS: *Crassicoma* is predominantly a Late Jurassic genus, best known from the Oxfordian and lower Kimmeridgian of southern Germany (Hess and Sieverts-Doreck 2002). The discovery, in the upper Turonian–Santonian of the Anglo-Paris Basin of a

Text-fig. 3. Comatulids from the upper lower Campanian of Ivö Klack, southern Sweden. A–C, G, L, N – *Semiometra impressa* (Carpenter, 1881); A–C – aboral cup, in adoral, lateral and aboral views, respectively (NHMUK PI EE 18232); G – aboral view of centrodorsal (NHMUK PI EE 18233); L – adoral view of aboral cup (NHMUK PI EE 18234); N – adoral view of centrodorsal (NHMUK PI EE 18235). D–F, H–K, M, Q–S – *Semiometra annulata* Rasmussen, 1961; D–F – centrodorsal, in adoral, lateral and aboral views, respectively (NHMUK PI EE 18236); H – centrodorsal, in adoral view (NHMUK PI EE 18237); I–K – small centrodorsal in aboral, lateral and adoral views, respectively (NHMUK PI EE 18238); M – centrodorsal in aboral view (NHMUK PI EE 18239); Q–S – very small controdorsal, in aboral, adoral and lateral views, respectively (NHMUK PI EE 18240). O, P – *Loriolometra retzii* (Lundgren, 1875), large centrodorsal, in lateral and aboral views, respectively (NHMUK PI EE 18241). Scale bars equal 5 mm (O, P), 2 mm (A–G, L, M), 1 mm (H–K), 0.5 mm (Q–S) and 0.3 mm (N). →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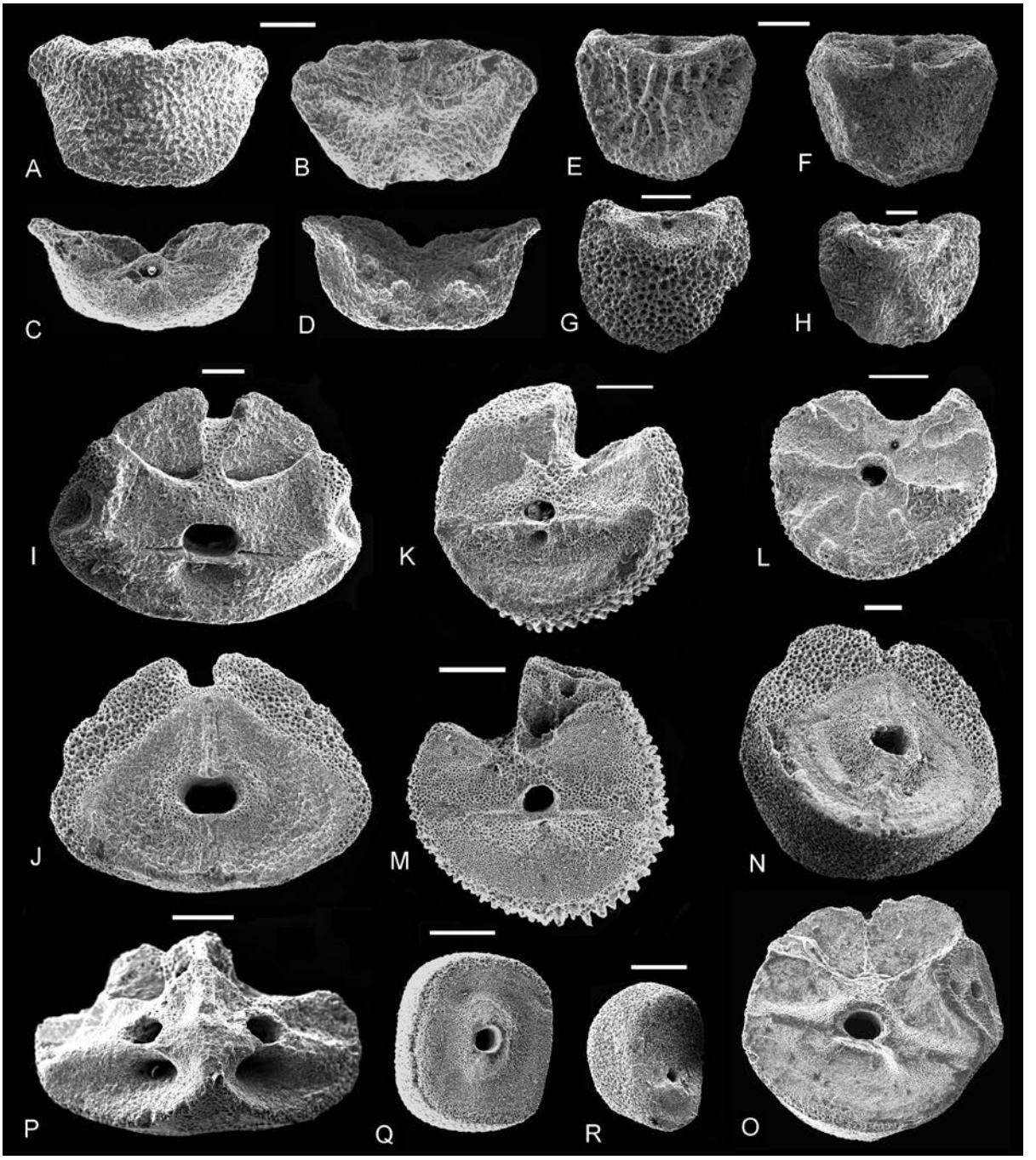


Text-fig. 4. Selected saccocomids and comatulids from Sweden, France and the United Kingdom. A–D – *Crassicoma suedica* sp. nov., radial (holotype), in external lateral, internal, adoral and aboral views, respectively (NHMUK PI EE 18225). E, F – *Crassicoma veulesensis* Gale, 2019, radial (holotype), the original of Gale (2019, pl. 3, fig. 1), in external lateral and internal views, respectively (NHMUK PI EE 16198). G, H – *Crassicoma cretacea* Gale, 2019, radials (paratypes), the originals of Gale (2019, pl. 3, figs 2, 12), in external lateral views (NHMUK PI EE 16699, 16707). I–P – isolated brachials, probably belonging to the comatulid *Semiometra*; I, J – proximal brachial IBr1 in distal and proximal views, respectively (NHMUK PI EE 18242); K–M – distal brachials, showing muscular (K, M) and syzygial (L) articulations (NHMUK PI EE 18243–18245); N, O – IIBr1, showing synarthrial proximal articulation and distal muscular articulation, with pinnule facet, respectively (NHMUK PI EE 18246); P – axillary IBr2, distal view (NHMUK PI EE 18247). O, R – distal/proximal views of pinnulars (NHMUK PI EE 18248, 18249). Provenance: A–D, I–O are from the upper lower Campanian of Ivö Klack, southern Sweden; E, F are from the upper Santonian, *Marsupites laevigatus* crinoid Zone, Veules-les-Roses, Seine-Maritime, France; G is from the upper Turonian, Lewes Marl, Lewes Nodular Chalk Formation, *Plesiocorys plana* echinoid Zone, Bridgwick, Lewes, East Sussex, UK; H is from the upper Turonian, Lewes Marl, Puys, near Dieppe, Seine-Maritime, France. Scale bars equal 0.2 mm.

species that appears to be closely related to Jurassic forms, was therefore unexpected and remarkable (Gale 2019), as was the discovery of a further species in the upper lower Campanian at Ivö Klack.

Crassicoma suedica sp. nov.
(Text-fig. 4A–D)

DIAGNOSIS: *Crassicoma* in which the radials are broad, low and the external surface is strongly convex.

TYPE: The unique radial plate from the upper lower Campanian at Ivö Klack is the holotype (NHMUK PI EE 18225).

DERIVATION: Latin *suedica*, meaning from Sweden.

DESCRIPTION: The radial plate has a breadth of 0.85 mm and a height of 0.55 mm and is trapezoidal in lateral aspect (Text-fig. 4A). The exterior is convex and the upturned lateral margins of the plate narrow towards the contacts with adjacent plates; the basal margin being gently convex. The exterior is composed of finely rugose stereom. Details of the articular facet are not clear on account of damage, but the axial canal is large and the muscle fossae are broad. The external ligament depression is shallow, and the nerve canal openings are basal in position (compare with Hess and Sieverts-Doreck 2002, pl. 1).

REMARKS: *Crassicoma suedica* sp. nov. differs from *C. cretacea* Gale, 2019, described from the Turonian of the Anglo-Paris Basin (Text-fig. 4G, H), in its broader and lower radial plate in which the articular facet does not protrude from the margin of the plate. In the Santonian species *C. veulesensis* Gale, 2019 (Text-fig. 4E, F), the radial is pentagonal and its external face is slightly concave and constructed of anastomosing subvertical trabeculae.

Subfamily Applinocrininae Peck, 1973

DIAGNOSIS: Theca conical to fusiform, delicately constructed, consisting of a basal circlet, usually fused, made up of five basals and a small centrale; five convex, trapezoidal radials; arms reduced to a single, highly modified, brachial in each radius.

Genus *Applinocrinus* Peck, 1973

DIAGNOSIS: Applinocrininae in which brachials are equilaterally triangular, imbricated and form a precisely articulated low, conical cap above the theca. The double articular structure comprises a larger, adoral, oval flange which imbricates a corresponding facet on the adjacent plate, and a lower small, low process which fits into a notch close to the base of the adjacent plate.

Applinocrinus cretaceus (Bather, 1924) forma *spinifer* Gale, 2018
(Text-fig. 5A–E, J)

part 2016. *Applinocrinus cretaceus* (Bather); Gale, p. 12, figs 5A–D, 7A, I, J only.
*2018. *Applinocrinus cretaceus* forma *spinifer* Gale, p. 30, fig. 3V, W.

DIAGNOSIS: *Applinocrinus cretaceus* in which an elongated, adorally curved, laterally compressed, tapering spine is present on the radial plate. The base of the cup is drawn out into an elongated shaft constructed of fused aboral radials.

TYPES: The elongated spine with a preserved radial facet (Gale 2018, fig. 3W) is the holotype (NHMUK PI EE 16228), from Paulsgrove pit, Hampshire, UK. The other figured spine is paratype (NHMUK PI EE 16229), from sample WF8, Warren Farm, Hampshire, UK. Both are from the lower Campanian *Gonioteuthis quadrata* belemnite Zone.

MATERIAL: Eleven partial radial plates bearing elongated spines on the adoral border; three basal cups with elongated aboral processes from Ivö Klack (NHMUK collections).

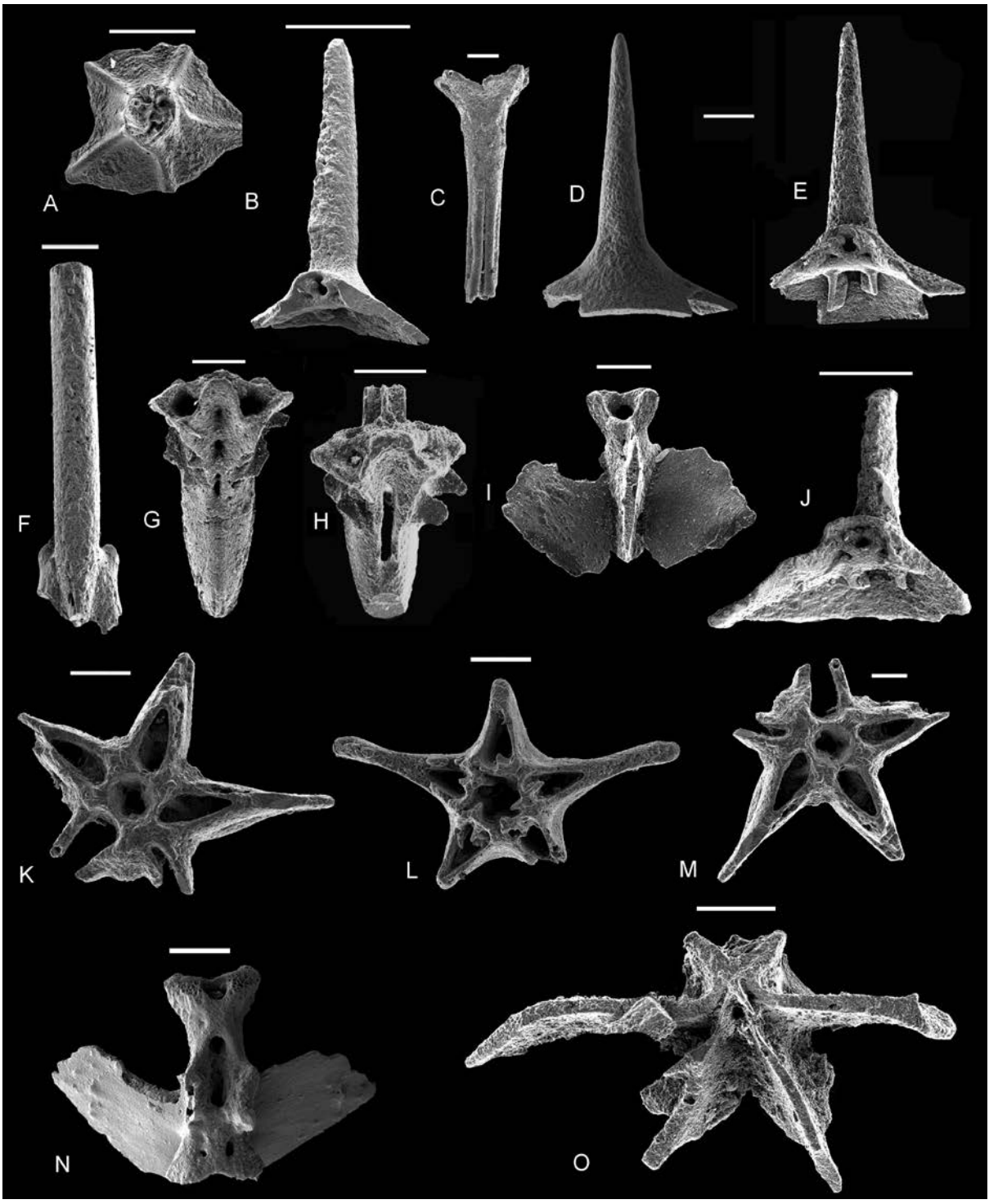
REMARKS: The elongated radial spines are characteristic of this forma (compare Gale 2018, fig. 3W), as are the aboral spikes composed of fused aboral radials. The forma is typical of the upper part of the lower Campanian, extending from crinoid zones CaR6 to the lower part of CaR11 (Gale 2018, 2021).

Family Roveacrinidae Peck, 1943
Subfamily Hessicrininae Gale, 2016

DIAGNOSIS: Roveacrinids which possess a cup with a basal web separating radial and basal cavities.

Genus *Stellacrinus* Gale, 2016

DIAGNOSIS: Hessicrinine in which radials bear a centrally placed, elongated and sigmoidally recurved spine; radials are weakly articulated, with one aboral



Text-fig. 5. Roveacrinids from the upper lower Campanian of Ivö Klack, southern Sweden. A–E, J – *Applinocrinus cretaceus* (Bather, 1924) forma *spinifer* Gale, 2018; A – aboral view of broken cup, the original of Gale (2016, fig. 8P; NHMUK PI EE 16072); B, J – internal (oblique adoral) view of radial spines and radial articulation (NHMUK PI EE 18228, 18229); D, E – lateral and internal views of radial spine, the original of Gale (2016, fig. 8I, J; NHMUK PI EE 16071). F, G – *Stellacrinus lineatus* Gale, 2018; F – external view of radial, the original of Gale (2016, fig. 17J; NHMUK PI EE 16190); G – external view of IBr2 (NHMUK PI EE 18250). H, M – *Stellacrinus* sp., distal brachials, in internal and external views, the originals of Gale (2016, fig. 17F, H; NHMUK PI EE 16185, 16186). J–L – *Cultellacrinus labyrinthus* Gale, 2016, basal circlets; J, K – the originals of Gale (2016, fig. 17K, L; NHMUK PI EE 16188, 16189). N – Indeterminate distal brachial (NHMUK PI EE 18251). Scale bars equal 0.4 mm (A, N, O), 0.3 mm (B), 0.2 mm (C–E, I, J) and 0.1 mm (F, G, H, K–M).

and one adoral fenestra between abutting articular struts, and small central fenestrae adjacent to the radial spine; basals form a fused ring which carries aborally deflected elongated blades and tall, adorally expanding processes for articulation with radials.

TYPE SPECIES: *Stellacrinus hughesae* Gale, 2016, by original designation.

Stellacrinus lineatus Gale, 2018
(Text-fig. 5F–H)

part 2016. *Stellacrinus hughesae* Gale, fig. 15B only.
*2018. *Stellacrinus hughesae* forma *lineatus* Gale, p. 32, fig. 5I.
2020. *Stellacrinus lineatus* Gale; Gale *et al*., p. 455, fig. 11A–F.

DIAGNOSIS: *Stellacrinus* which possesses extremely elongated, bladed basal spines with a median ridge.

TYPE: The basal figured by Gale (2018, fig. 5I) is the holotype (NHMUK PI EE 16240), from the lower Campanian *Gonioteuthis quadrata* belemnite Zone at Paulsgrove, Hampshire, UK.

MATERIAL: A single radial plate (Text-fig. 5F), several axillary primibrachials (IBr2; Text-fig. 5H) and nine brachials (Text-fig. 5I, N, O) from Ivö Klack (NHMUK collections).

REMARKS: The radial plate (Text-fig. 5F) with a very robust, erect radial spine can be referred to this species by comparison with material from the UK (Text-fig 5G; Gale 2021, fig. 11J, M). The IBr2 (Text-fig. 5H) are also closely comparable to the UK specimens (Text-fig. 5G) and to those from Texas (Gale *et al*. 2020, fig. 11F). The distal brachials (Text-fig. 5I, N, O) with broad lateral flanges also probably belong to *Stellacrinus* (Gale 2019). In southern England, the species ranges from crinoid zones CaR6 to CaR10 (Gale 2018, 2021).

Genus *Cultellacrinus* Gale, 2016

DIAGNOSIS: Derived Hessicrininae, in which the weakly articulated radials carry a long, laterally compressed and adorally recurved, blade-like central spine. There is a single large interradial fenestra, a large radial:basal fenestra and a small, pore-like foramen adjacent to the radial process. The basals are fused into a robust central ring which carries long, aborally deflected bladed processes. The basal ring is perforated by one central and five interradial, vertically oriented pores. There are apparently no arms, but the modified radial articulation occasionally forms a concave facet extending along the upper surface of the radial process.

TYPE SPECIES: *Cultellacrinus gladius* Gale, 2016, by original designation.

Cultellacrinus labyrinthus Gale, 2016
(Text-fig. 5K–M)

*2016. *Cultellacrinus labyrinthus* Gale, p. 38, fig. 17I, K, L.
2018. *Cultellacrinus labyrinthus* Gale; Gale, fig. 5M.
2021. *Cultellacrinus labyrinthus* Gale; Gale, p. 5.

DIAGNOSIS: Basal ring fused, in which five deep, arrowhead-shaped slots extend into the basal spines. Irregular vertical flanges are developed on the walls of the central cavity.

TYPE: A basal ring is the holotype, from Warren Farm, Hampshire, UK, at a level 7 m beneath the Portsdown Marl (NHMUK PI EE 16187). Paratypes are from the lower upper Campanian of Ivö Klack, southern Sweden (NHMUK PI EE 16188, 16189).

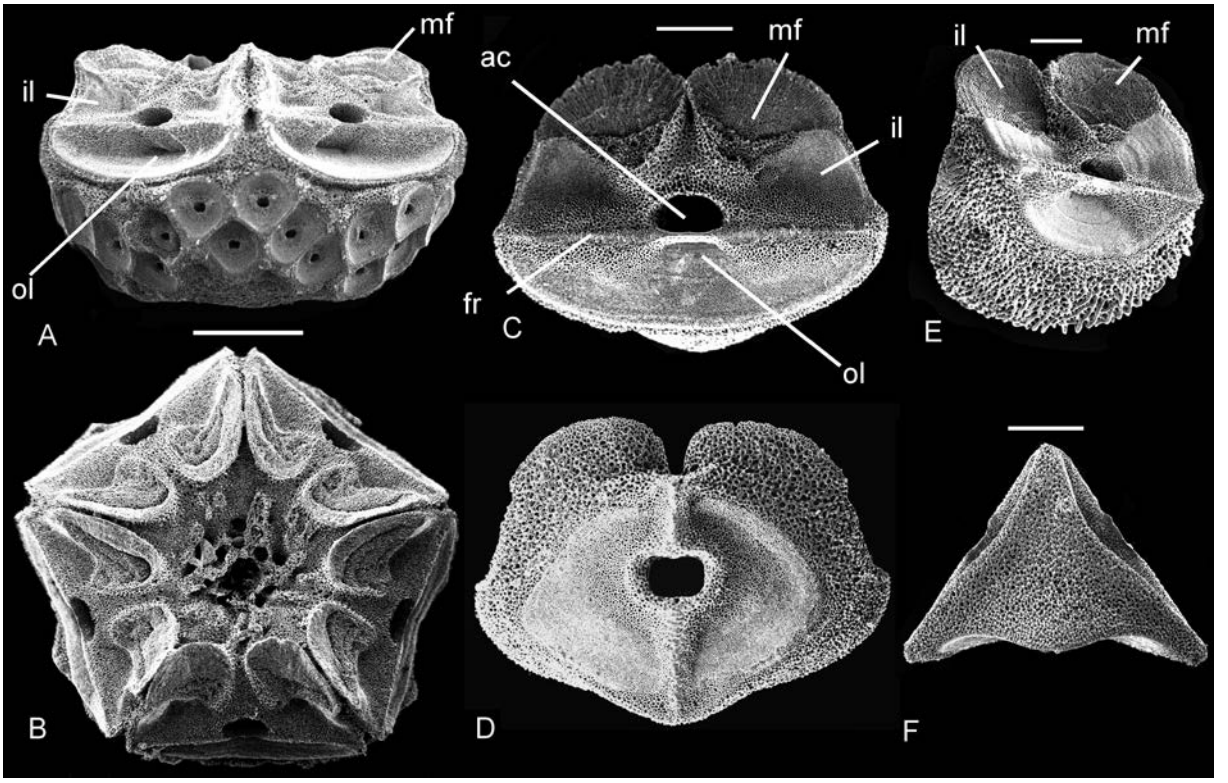
MATERIAL: Twelve basal rings from Ivö Klack (NHMUK collections).

REMARKS: The basal rings from Ivö Klack are identical to specimens from the lower Campanian chalks of southern England, where the species ranges from crinoid zones CaR10 to CaR13 (Gale 2018, 2021).

DISCUSSION

Composition and palaeoecology of the Ivö Klack crinoid fauna

The comatulids and isocrinids are very well preserved (Text-figs 2–4); these were part of the indigenous fauna at Ivö Klack. The presence of isocrinids in such shallow habitats is remarkable given that these environments are characterised by high biodiversity, intense predation pressure, strong currents and wave-agitated waters – conditions typically considered unsuitable for these slow-moving stalked crinoids, and the reason they are now thought to be confined to depths in excess of 100 m in present-day oceans (Oji 1989).



Text-fig. 6. The extant *Antedon bifida* (Pennant, 1777) from Plymouth, Devon, United Kingdom. A, B – cup in lateral and adoral views, respectively; C, D – IBr1, in proximal and distal views, respectively; E – distal brachial; F – axillary IBr2, in lateral view. Abbreviations: ac – axial canal; fr – fulcral ridge; il – inner ligament; ol – outer ligament; mf – muscle fossa. Scale bars equal 0.3 mm (A, B) and 0.2 mm (C–F).

The Ivö Klack specimens presented herein represent the first confirmed occurrence of isocrinids in a rocky shoreline deposit, marking a notable shift in isocrinid ecology and habitat association. The new records align more closely with the ecological characteristics of modern isocrinid communities than those of other fossil isocrinids. For instance, modern isocrinids typically inhabit hard or coarse-grained substrates (García-Penas *et al*. 2024), while many extinct forms thrived in markedly different conditions, including soft, muddy substrates. Did environmental pressures, such as competition or changing oceanographic conditions, necessitate adaptations to new substrate types? Alternatively, could the differences reflect localised niche specialisation rather than a broader trend? Investigating these dynamics may provide insights into the resilience and ecological plasticity of isocrinids throughout their long evolutionary history.

The crinoid community at Ivö Klack exhibits a remarkable range of morphologies, reflecting the diverse adaptations of these organisms to their environment. This diversity likely contributed to their ecological success in this setting. One particularly intriguing example is the small Isocrinid sp. 1, which may have had limited motility due to its unusually small adoral muscle facets. In contrast, the similarly small Isocrinid sp. 2 possessed larger adoral muscle facets, suggesting a greater capacity for movement, perhaps even the ability to crawl. In living forms, the size of the muscle fossae and their distance to the transverse ridge can be a good predictor of swimming ability (Janevski and Baumiller 2010).

The Ivö Klack comatulid species *Semiometra impressa* (superfamily Notocrinoidea, family Notocrinidae) is most noteworthy because its centrodorsal closely resembles that of the extant swimming genus *Antedon*, despite *A. bifida* (Text-fig. 6) belonging to a different superfamily of Comatulida (superfamily Antedonoidea Norman, 1865). The similarities in muscle fossa size and shape suggest that *S. impressa* may also have had some capacity for swimming, although further investigation would be needed to confirm this. Interestingly, *S. impressa* had more numerous cirri sockets than *A. bifida*, which might have allowed it to grasp substrates more firmly in the relatively strong currents and turbulent environments that it inhabited.

In contrast, the larger comatulid species *S. annulata* had approximately half as many cirri sockets as *S. impressa*. *Semiometra annulata* differs from *S. impressa* and other species of the genus in having a truncated aboral surface and a broad, deep dorsal pit.

The ecological success of these different benthonic crinoid species at Ivö Klack may be reflected in their relative abundances. *Semiometra annulata* was the most abundant of the three comatulid species, with thirteen centrodorsals found, outnumbering *S. impressa* and *Loriolometra retzii* by three to seven times, respectively. It is unclear what made *S. annulata* more successful than the other two taxa.

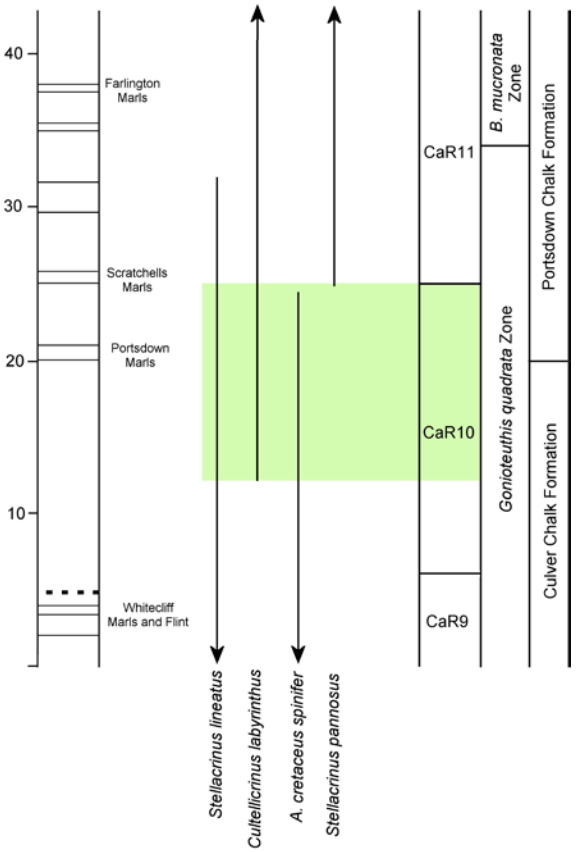
The pelagic microcrinoids are scarce, and they were evidently allochthonous, having been derived from the open waters of the Chalk Sea by currents which washed them into a coastal habitat. Roveacrinids were probably vertical migrators and part of the zooplankton community (Gale 2016), but it is unclear whether this vertical migration was passive or active, with evidence suggesting several possible mobility strategies. For instance, in *Crassicoma suedica* sp. nov., the presence of broad muscle fossae coupled with a shallow ligament depression suggests some capacity for active movement. However, it is difficult to envision efficient swimming in forms such as *Applinocrinus cretaceus*, characterised by a cup extended into an elongated shaft, or *Stellacrinus lineatus*, with its radial spines and broad lateral flanges. These morphological features are more reminiscent of passive structures akin to sails and rudders, potentially optimised for stability or slow, passive drift rather than active locomotion.

Comparison with other Cretaceous rocky shoreline crinoid faunas

There are rather few described Cretaceous rocky shorelines which have yielded crinoids. The best known are associated with the Cenomanian–Turonian transgression onto the Bohemian Massif in the Czech Republic, for example, at Velim (Žítt *et al*. 1997; Tomás Kočí, pers. comm., September 2024). The Velim fauna includes three isocrinids, three comatulids, four roveacrinids (Žitt *et al*. 2019) and a species of the holopodid *Cyathidium* (Žítt 1996; Žítt *et al*. 2014). Cenomanian and Turonian shallow-water deposits unconformably overlie Carboniferous sandstones at Kassenberg (Westphalia, Germany) and have yielded six roveacrinids (Gale and Thiel 2023), three comatulids, an isocrinid (Weidert 1995) and a species of *Cyathidium* (Sieverts 1931; Rasmussen 1961). The diverse faunas of roveacrinids, comatulids and isocrinids are comparable with that at Ivö Klack. However, both the Czech and Kassenberg deposits are highly condensed and represent a succession of superimposed palaeoenvironments that probably included both shallower and deeper facies. In contrast, the Ivö Klack deposits appear to be the product of a single transgressive pulse of short duration. *Cyathidium* is present in the Czech and German deposits yet absent from Ivö Klack; it appears to be likely that this genus preferred somewhat deeper water habitats (Gale and Jagt 2024).

Implications for the age of the Ivö Klack locality and its faunas (Text-fig. 7)

Pelagic microcrinoids of the order Roveacrinida are of considerable biostratigraphical value in Cretaceous (Albian to Maastrichtian) successions, and Gale



Text-fig. 7. Distribution of microcrinoids in the lower Campanian Culver and Portsdown chalk formations of Portsdown, Hampshire, United Kingdom. The stratigraphical ranges of four species also present at Ivö Klack, southern Sweden, are shown. The overlapping ranges can be taken to indicate that the Ivö Klack locality falls within the upper part of the CaR10 microcrinoid Zone (green; see Gale 2018, 2021 for original data) in the upper part of the lower Campanian (*Gonioteuthis quadrata* Zone), supporting the age given by belemnites (Christensen 1975).

(2018, 2021) established a zonation for the Campanian Stage based on material from the white chalk facies of southern England. Part of this has proved to be applicable to the succession in the Gulf Coast, USA (Gale *et al*. 2020); it was used to demonstrate the presence of a Santonian–Campanian hiatus in central Texas. The discovery of pelagic microcrinoids at Ivö Klack (Gale 2016) is remarkable and unexpected, as these crinoids are open sea dwellers which washed up onto the Campanian shorelines of southern Sweden. Of the four species present at Ivö Klack, one is new (*Crassicoma suedica* sp. nov.) but the other three are short-ranged taxa which indicate that the Ivö Klack succession falls within the lower Campanian microcrinoid zone CaR10 as defined in Hampshire, southern England. This supports the evidence from belemnites (Christensen 1975) that the Ivö Klack succession is approximately equivalent to the *Gonioteuthis quadrata gracilis* belemnite Zone (uppermost lower Campanian) of the northern German chalk facies. The typical Ivö Klack belemnite, *Belemnellocamax mammillatus* (Nilsson, 1826), has been found at this level in limestone quarries of the Hannover district, northern Germany (Girod and Rösner 2011).

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