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Echinoids (Echinodermata) from the Campanian (Upper Cretaceous) rocky coast at Ivö Klack, southern Sweden

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ABSTRACT:

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The echinoid fauna from the Campanian rocky shoreline at Ivö Klack in Sweden is described taxonomically; it includes 16 taxa, comprising three cidaroids, one diadematoid, two phymosomatoids, four saleniids, two holectypoids, three cassiduloids, and a single holasteroid. Of these, *Tylocidaris* (*Tylocidaris*) *imbricata, Hirudocidaris botryoformis, H. zeamays, Trochalosoma ivoensis, Globator schroederi* and *Scaniosoma* (n. gen.) *surlyki* are new. These taxa are interpreted to represent three distinct ecological groups; of these, one was adapted to living epifaunally on boulders, one epifaunally in crevices and the third shallowly buried in shell sands and gravels. The present study is based on material picked from residues of a large (500 kg) bulk sample from the upper part of the succession, and examination of historical collections.

Key words: Echinoids; Upper lower Campanian; Rocky coastline; Northern Europe.

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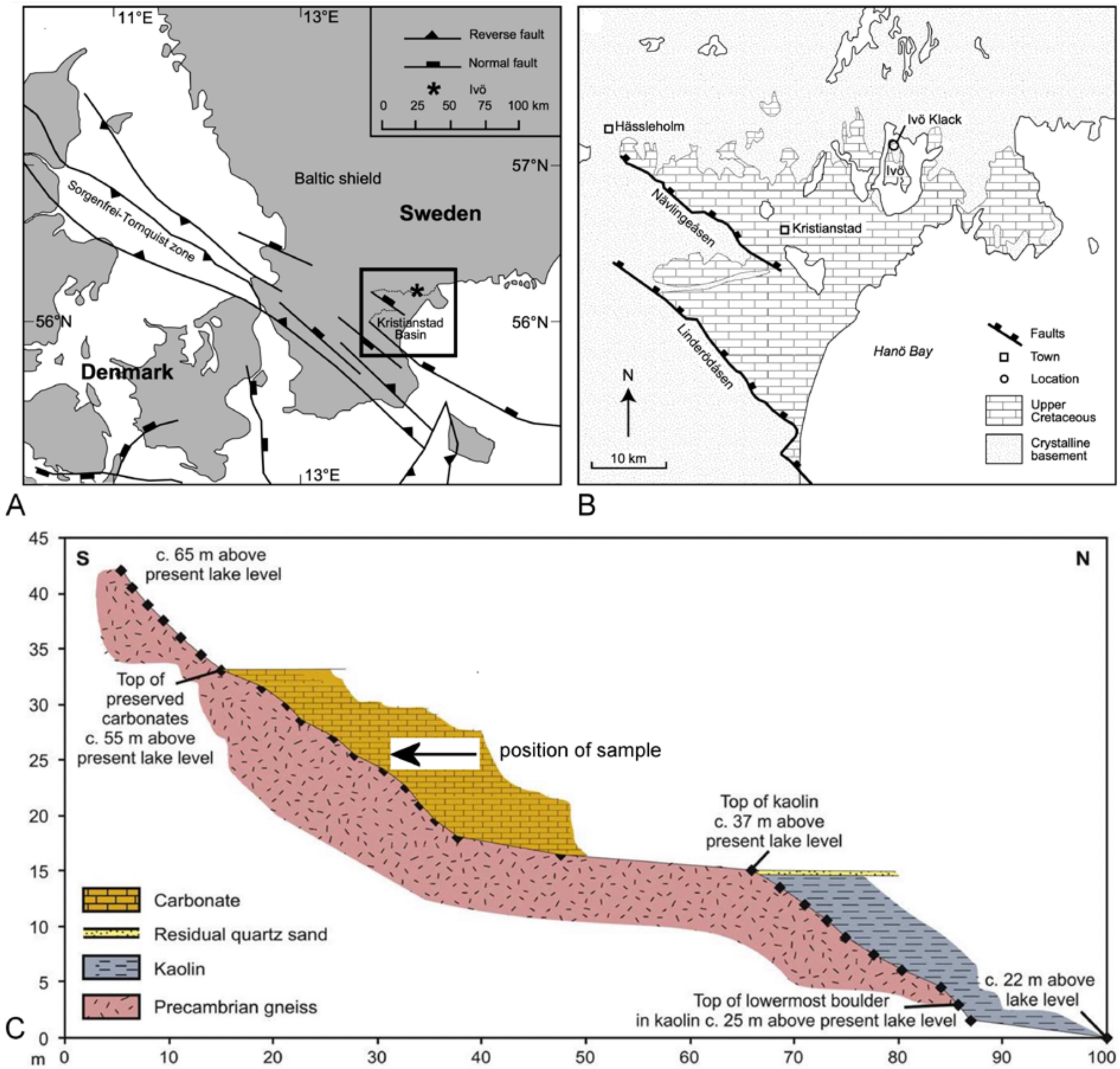
INTRODUCTION

The exposures at Ivö Klack in Skåne, southern Sweden (Text-fig. 1), provide a profile through a rocky shoreline of late early Campanian age, set within a protected archipelago on the northern side of the present-day Kristianstad Basin (Sørensen and Surlyk 2011, fig. 3). Here, boulders of Proterozoic gneiss were eroded by wave action, encrusted by zoned epifauna (Surlyk and Christensen, 1974; Surlyk and Sørensen 2010), then buried by bioclastic shell sands and gravels composed of calcitic remains of invertebrates, some of which lived on the boulders, and others in the surrounding carbonate sands and gravels. The locality probably represents a maximum water depth of 30 m, and among the diverse and abundant faunas (over 200 species recorded to date), bryozoans, bivalves, echinoderms, serpulids and brachiopods were particularly abundant (Sørensen and Surlyk 2010, 2011; Surlyk and Sørensen 2010; Sørensen *et al*. 2011, 2012;



Text-fig. 1. Location of Ivö Klack. A – Map showing the position of the Kristianstad Basin in southeast Sweden; B – Kristianstad Basin, to show the position of Ivö Klack; C – Cross-section through the Ivö Klack region to show sedimentary facies and location of large bulk sample (after Sørensen and Surlyk 2010, figs 2, 6).

Schrøeder *et al.* 2019), as were cirripedes (Gale and Sørensen 2014, 2015). The crinoids were described by Gale and Stevenson (2025) and the asteroids by Gale (2025).

Mortensen (1932) described representatives of the echinoid family Saleniidae Agassiz, 1838 from southern Sweden and recorded four species from Ivö Klack, namely *Trisalenia loveni* (Cotteau, 1888), *Salenia areolata* (Wahlenberg, 1821), *Polysalenia notabilis* Mortensen, 1932, and *Polysalenia cottaldi* Mortensen, 1932. Since then, the only illustrations of echinoid specimens from Ivö Klack are those by Sørensen and Surlyk (2011, figs 12, 17, 18), who figured *T. loveni*, a cidaroid spine and a specimen identified as the irregular genus *Catopygus* Agassiz, 1836.

MATERIAL AND METHODS

The present study is based largely on material picked from washed residues from a site at Ivö Klack which is stratigraphically about 10 m beneath the highest preserved carbonate sedimentary rocks (Text-fig. 1C). Approximately 500 kg of soft sediment were collected, washed and separated into fractions. All of the >3 mm fraction was picked, and approximately 1.5 kg of the 0.5–3 mm material. In addition, a small portion of the 0.2–0.5 mm residue was screened. This represents about 200 h of picking, yielding abundant echinoid material, albeit mostly fragmentary. The material has been deposited in the collections of the Natural History Museum, Copenhagen, Denmark (MGUH). The present paper discusses the taxonomy of the echinoids, and their palaeoecological significance. The historical collections at Copenhagen, Uppsala and Stockholm were also visited and studied.

TAPHONOMY AND PRESERVATION

The calcarenites and calcirudites exposed at Ivö Klack are composed largely of calcite bioclastic debris, including abundant oysters, echinoderm ossicles, brachiopods, bryozoans and cirripedes (Sørensen and Surlyk 2010). The majority of the skeletal grains are angular, and probably formed by the crushing effects of storm waves on the coast. Echinoids are largely represented by broken test fragments and isolated radioles, common in residues and surface-picked material. Complete tests are rare, and only juvenile *Trisalenia* and *Echinogalerus* were found in the residues. The fragile larger irregular echinoids are all broken into pieces smaller than 1 cm^2. Larger complete tests of saleniids, phymosomatids and 1/5 test segments of cidarids were collected quarrying activity in the early 20th century but there is no information as to the precise levels of occurrence of these.

Institutional abbreviations:

BGS – British Geological Survey, Keyworth, Nottingham, United Kingdom.
MGUH – Natural History Museum, Copenhagen, Denmark.
NHMM – Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands.
NHMUK – The Natural History Museum, London, United Kingdom.
PMU – Museum of Evolution, Uppsala University, Uppsala, Sweden.
SMNH – Swedish Museum of Natural History, Stockholm, Sweden.

SYSTEMATIC PALAEONTOLOGY

Order Cidaroida Claus, 1880
Family Psychocidaridae Ikeda, 1936
Genus and subgenus *Tylocidaris* Pomel, 1883

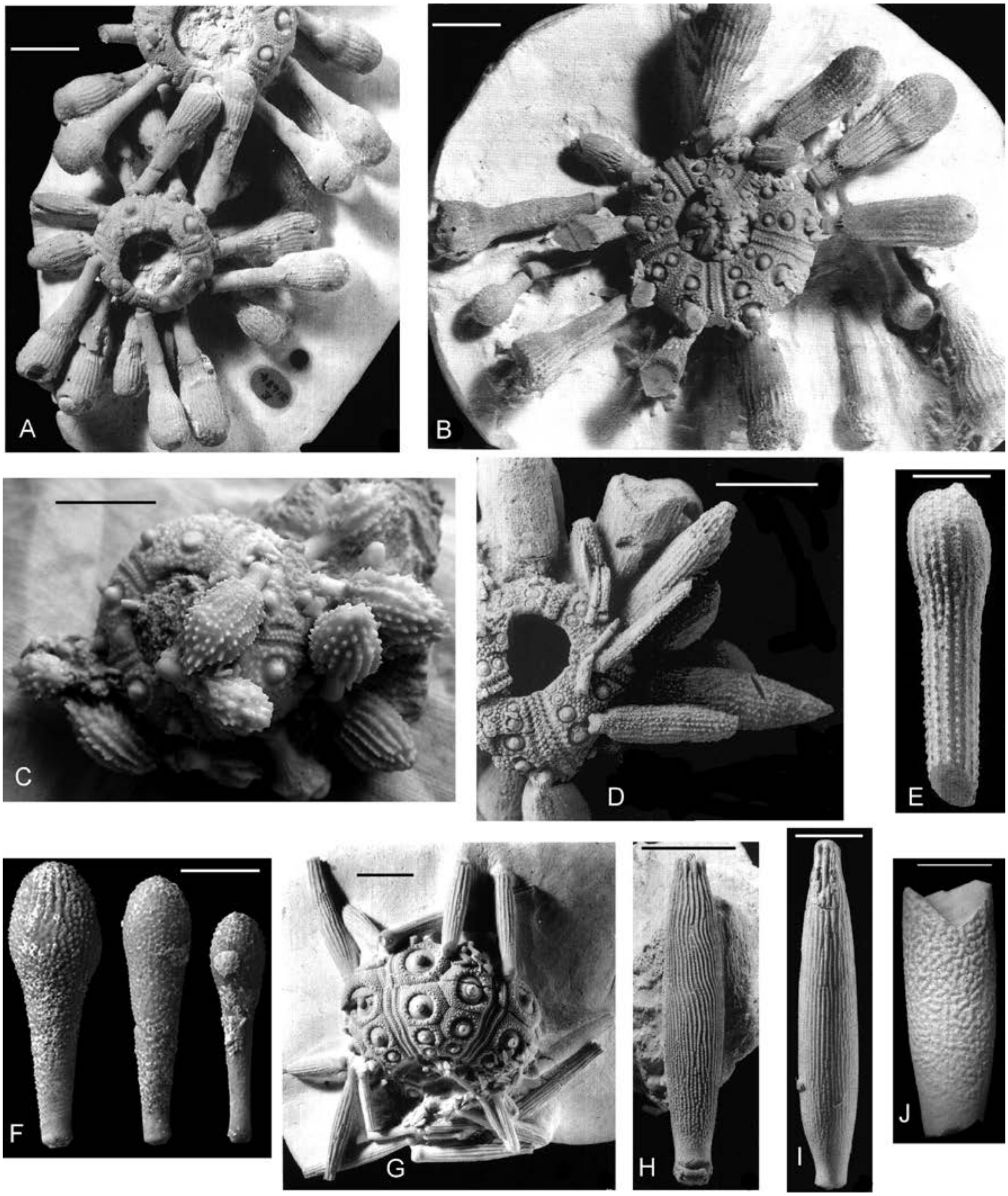
TYPE SPECIES: *Cidaris clavigera* Mantell, 1822, under plenary powers, ICZN Opinion 1459.

DIAGNOSIS: Spines claviform to glandiform, shaft with dense beaded ribs or thorns.

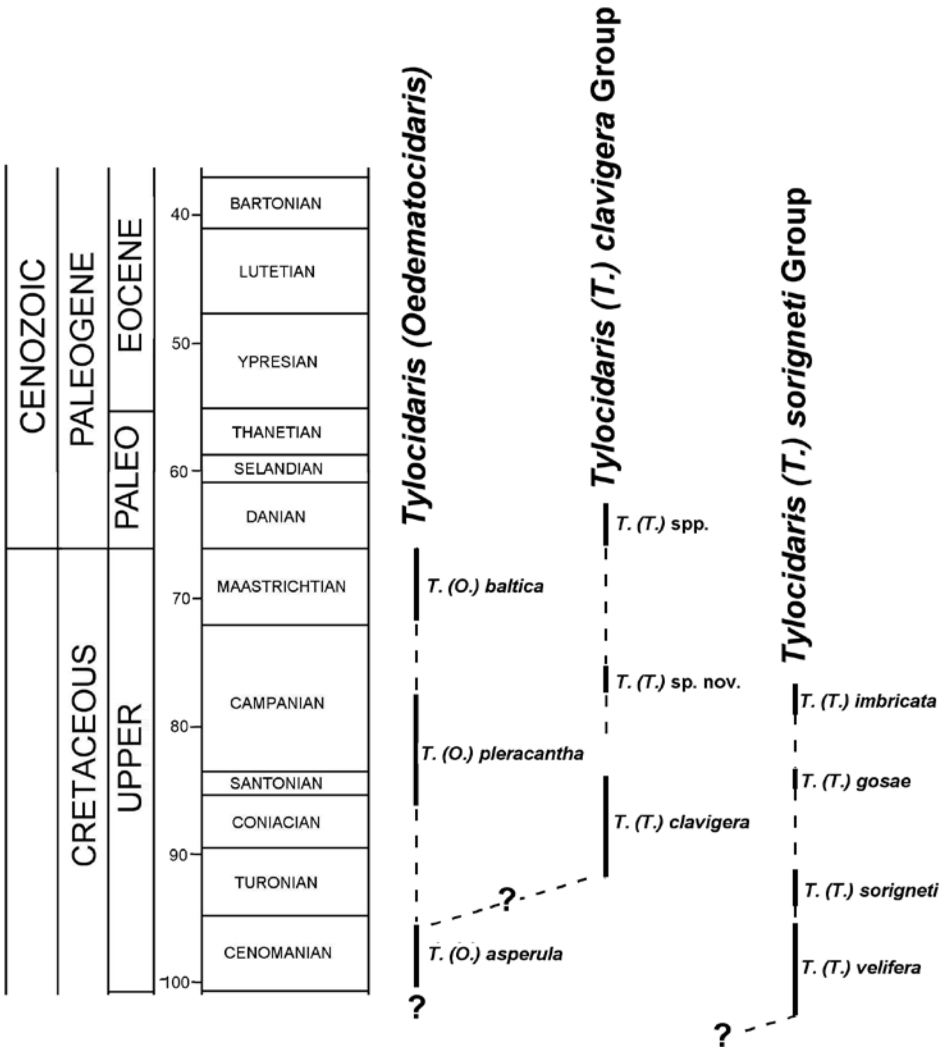
REMARKS: Smith and Wright (1989, text-fig. 6) provided a phylogeny of species of *Tylocidaris* and proposed a lineage leading from the Albian–Cenomanian *T.* (*T.*) *velifera* (Agassiz and Desor, 1846), through the Turonian *T.* (*T.*) *sorigneti* (Desor, 1856) to the Coniacian–Santonian *T.* (*T.*) *clavigera*. The last-named species was then inferred to have given rise to *T.* (*T.*) *gosae* (C. Schlüter, 1892), which subsequently led to *T.* (*T.*) *hardouini* (Desor, 1855) in the Campanian. *Tylocidaris* (*T.*) *vexilifera* (Schlüter, 1892) was also shown as being derived from *T.* (*T.*) *clavigera* during the Campanian and extending into the Paleogene.

There are a number of problems with this scenario, particularly the transition between Late Cretaceous and Paleogene species of *Tylocidaris* (*Tylocidaris*) as noted by Jagt (2000). On reappraisal, these appear to fall into two groups, as follows:

Tylocidaris (*T.*) *clavigera* Group: forms in which the neck of the shaft is elongated, and tapers slowly towards the base, as typified by the adapical spines of *T.* (*T.*) *clavigera* (Text-fig. 2A, B). Those of the early Danian species *T.* (*T.*) *oedumi* Brünnich Nielsen, 1938 (Text-fig. 2F) and *T.* (*T.*) *abilgaardi* Ravn, 1928 are similar in shape, but not in sculpture to those of *T.* (*T.*) *clavigera* (see Gravesen 1993, pls 1–3). The early Danian *Tylocdidaris* (*T.*) *hardouini* (Desor, 1855) (see Jagt 2000, pl. 1, figs 16–31) also belongs here. The spine figured as *T.* (*T.*) *gosae* by Smith and Wright (1989, pl. 5, fig. 9; Text-fig. 2E herein), from the upper Campanian of Norfolk (UK), is similar in shape, but not in sculpture, to those of *T.* (*T.*) *oedumi* from the lower Danian (see Gravesen 1993, pl. 1) and belongs to an undescribed species. The group is also characterised by ambital spines of which the length equals or exceeds the test diameter (Text-fig. 2A, B). Additionally, the spines on the adoral part of the test of *Tylocidaris* (*Oedematocidaris*) *asperula* (Roemer, 1841) are quite similar in sculpture (rows of fine thorns) and shape (parallel sides) to those of *T.* (*T.*) *clavigera* (Text-fig. 2D) and this Cenomanian species



Text-fig. 2. Comparative morphology of Cretaceous–Paleocene cidaroids. A, B – *Tylocidaris* (*T.*) *clavigera* (Mantell, 1822), tests with spines, apical surface; A – original of Smith and Wright (1989, pl. 6, fig. 1), Santonian, Woolwich, Kent, UK (NHMUK E31684); B – original of Smith and Wright (1989, pl. 6, fig. 5), Santonian, Gravesend, Kent, UK (NHMUK 39998). C – *Tylocidaris* (*T.*) *sorigneti* (Desor, 1856), test with spines, apical view, lower Turonian, Branscombe, Devon, UK (private collection of Rob Beard, with permission). D – *Tylocidaris* (*Oedematocidaris*) *asperula* (Roemer, 1841), test with spines, oral view, original of Smith and Wright (1989, pl. 9, fig. 4), Cenomanian, Southerham, Sussex, UK. E – *Tylocidaris* (*T.*) sp. nov., primary spine, original of Smith and Wright (1989, pl. 5, fig. 9), upper Campanian, Bridgeham, Norfolk, UK. F – *Tylocidaris* (*T.*) *oedumi* Nielsen, 1938, primary spines, lower Danian, Denmark (Søren Bo Andersen Collection). G–I – *Hirudocidaris hirudo* (Sorignet, 1850); G – test with spines, original of Smith and Wright (1989, pl. 27, fig. 2), horizon unknown, probably Santonian, Bromley, Kent, UK (NHMUK E75342); H – primary spine, original of Smith and Wright (1989, pl. 32, fig. 5), Cenomanian, Hitchin, Hertfordshire, UK (BGS 118185); I – primary spine, original of Smith and Wright (1989, pl. 25, fig. 3), lower Campanian, Fareham, Hampshire, UK (BGS Yc 4000). J – *Hirudocidaris botryoformis* sp. nov., primary spine (paratype), upper lower Campanian, Ivö Klack, southern Sweden (MGUH 35045). Scale bars equal: 10 mm (A–D, G) and 5 mm (E, F, H–J).



Text-fig. 3. Proposed possible phylogeny of Late Cretaceous–early Paleocene *Tylocidaris*.

is here provisionally placed at the base of the *T.* (*T.*) *clavigera* Group (Text-fig. 3).

Tylocidaris (*T.*) *sorigneti* Group: forms in which the neck is proportionately short and nearly parallel-sided, including *T.* (*T.*) *velifera* (Text-fig. 4P), *T.* (*T.*) *sorigneti* (Text-figs 2C, 4M, N), *T.* (*T.*) *gosae* (Text-fig. 4O) and *T.* (*T.*) *imbricata* sp. nov. (Text-fig. 4A–F). The thorns are larger and denser in this group. In addition, the largest primary spines are approximately half the maximum test diameter (Text-fig. 2C).

We therefore propose that the groups described above represent separate lineages, of which only the former crossed the Cretaceous–Paleogene (K/Pg) boundary (Text-fig. 3). There is a gap between the latest occurrence of *T.* (*T.*) *clavigera* in the upper Santonian, and the first representatives of *T.* (*T.*) *oedumi* in the lower Danian, infilled only by a single spine from the upper Campanian of the United Kingdom (Text-fig. 2E).

Tylocidaris (*Tylocidaris*) *imbricata* sp. nov.
(Text-fig. 4A–F)

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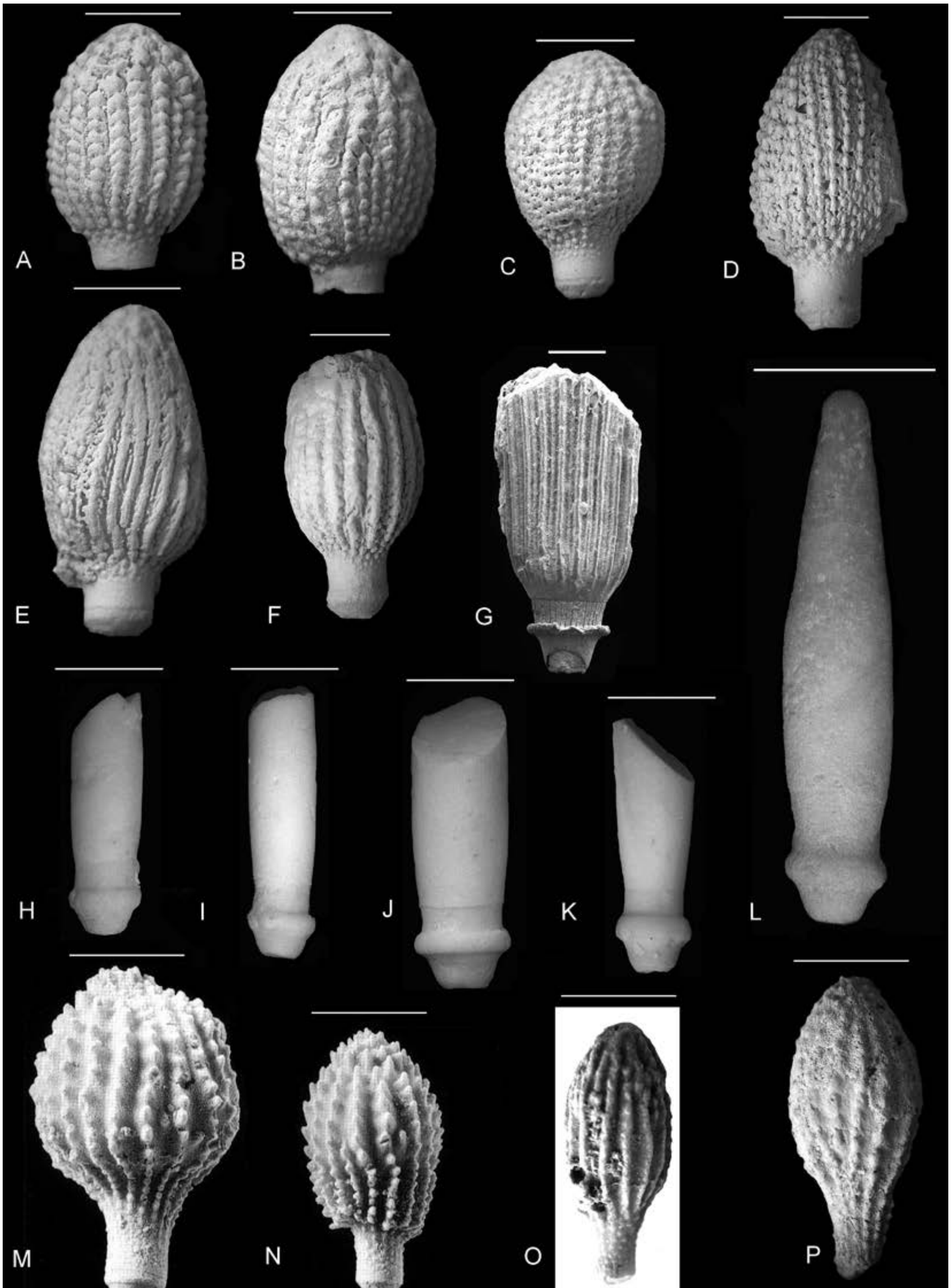
DIAGNOSIS: Primary spines clavate; neck short, shaft with distally imbricating, adpressed, triangular thorns set in well-defined rows.

TYPES: The spine figured (Text-fig. 4A) is the holotype (MGUH 35035); the other spines illustrated are



Text-fig. 4. Selected psychocidarids (A–F and M–P), saleniids (H–L) and phymosomatids (G) from Ivö Klack, southern Sweden. A–F – *Tylocidaris* (*T.*) *imbricata* sp. nov., primary spines; A is the holotype (MGUH 35035), B–F are paratypes (MGUH 35036–35040). G – *Trochalosoma ivoensis* sp. nov., primary spine (MGUH 35093). H–L – primary spines, probably belonging to *Trisalenia loveni* (MGUH 35056–35060). M, N – *Tylocidaris* (*T.*) *sorigneti* (Desor, 1856), primary spines (NHMUK E39571, E39572), originals of Smith and Wright (1989, pl. 5, figs 5, 6). O – *Tylocidaris* (*T.*) *gosae* (Schlüter, 1892), primary spine, copied from Schneider and Neumann (2006, fig. 3). P – *Tylocidaris* (*T.*) *velifera* (Agassiz and Desor, 1846), primary spine (NHMUK PI EE 18377). Provenance: A–L are from the upper lower Campanian, Ivö Klack, southern Sweden; M, N are from the Holywell Chalk Formation, lower Turonian, Branscombe, Devon, UK; O is from the middle Santonian, Lengede, northern Germany; P is from the Zig Zag Chalk Formation, upper Cenomanian, *Calycoceras guerangeri* ammonite Zone, Eastbourne, East Sussex, UK. All scale bars equal 5 mm.

paratypes (Text-fig. 4B–F; MGUH 35036–35040), all from the upper lower Campanian of Ivö Klack, southern Sweden.

MATERIAL: Approximately 50 primary spines (MGUH collections).

DERIVATION OF NAME: From the imbricating thorns on the primary spines.

DESCRIPTION: Spines very robust with a very short, parallel sided neck representing 10–25% of total length. The neck is smooth, but distally bears a scatter of fine rugosities at the transition to the shaft. Shaft clavate, oval to fusiform, tapering abruptly to a bluntly rounded or low conical tip. The shaft bears 15–20 raised columns, composed of distally imbricated, adpressed chevrons (Text-fig. 4A) which may conjoin laterally by short struts (Text-fig. 4C, D). In some specimens, one side of the shaft is flattened and abraded, probably from wear on a hard substrate (Text-fig. 4E).

REMARKS: *Tylocidaris* (*T.*) *imbricata* sp. nov. differs from all congeners in the possession of sharply defined rows of distally imbricating, triangular thorns. The primary spines with a worn, flattened undersurface (Text-fig. 4E) probably indicate that this species lived on hard substrata.

Family Cidaridae Gray, 1825
Genus *Hirudocidaris* Smith and Wright, 1989

DIAGNOSIS: Four to six adambulacral plates in each column, one or both periapical plates in a zone with rudimentary tubercles. Ambulacral tuberculation very uniform, organised into horizontal and vertical rows, and ambulacral pores nonconjugate. Spines stout and subfusiform, with fine sculpture (after Smith and Wright 1989, p. 78).

TYPE SPECIES: *Cidaris hirudo* Sorignet, 1850, by original designation.

Hirudocidaris botryoformis sp. nov.
(Text-figs 2J, 5A–D, F–J, 6A)

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DIAGNOSIS: *Hirudocidaris* with very coarse, closely packed interambulacral miliaries and fusiform primary spines with dense sculpture of irregular, short, fine rugosities which form poorly defined rows on proximal shaft.

TYPES: The primary spine illustrated in Text-fig. 5C is the holotype (MGUH 35043); the other spines and test fragments are paratypes (MGUH 35041, 35042, 35044–35048), all from the upper lower Campanian of Ivö Klack, southern Sweden.

MATERIAL: Over 200 spines and test fragments from the same locality (MGUH collections).

DERIVATION OF NAME: From Latin *botryo* meaning a bunch of grapes, in allusion to the form of the interambulacral miliaries.

DESCRIPTION: Test low, broad, with 4–5 interambulacral plates in each column (Text-figs 5A, B, 6A); 4 or 5 interambulacrals carry fully-formed tubercles, the most adapical in one column of a pair has a rudimentary tubercle only. Scrobicular ring comprises 10–13 rather widely separated tubercles. Miliaries large, round to oval, densely clustered, and becoming finer towards weakly impressed plate sutures. Areole broad, margins deep, mamelons perforate. Ambulacra sinuous, relatively broad, each plate carrying three tubercles, of which the adradial is smallest (Text-fig. 5H). Spines (Text-fig. 5C, D, G, I, J) robust, fusiform, with a short neck and swollen shaft, termination conical, simple. Spine sculpture comprises dense cover of low, rounded rugosities, which form irregular networks; sculpture on proximal shaft forming poorly defined ridges (Text-fig. 5C).

REMARKS: This species differs from *H. hirudo* (Text-fig. 2G–I) in the lower, broader test, the very coarse, dense miliaries on the interambulacrals and the fine, irregular rugosities on the more robust primary spines.

Hirudocidaris zeamays sp. nov.
(Text-figs 5L–Q, 6B)

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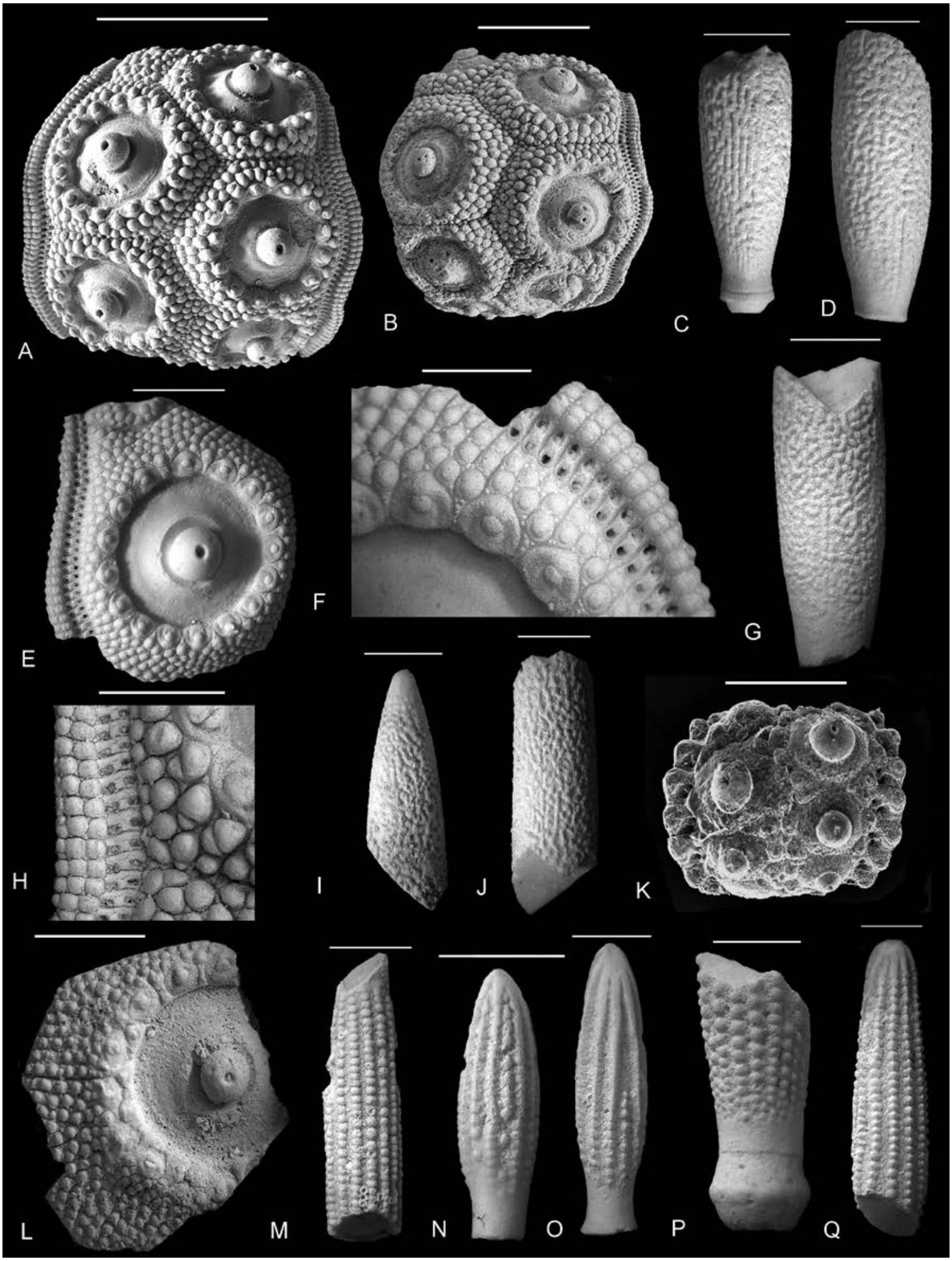
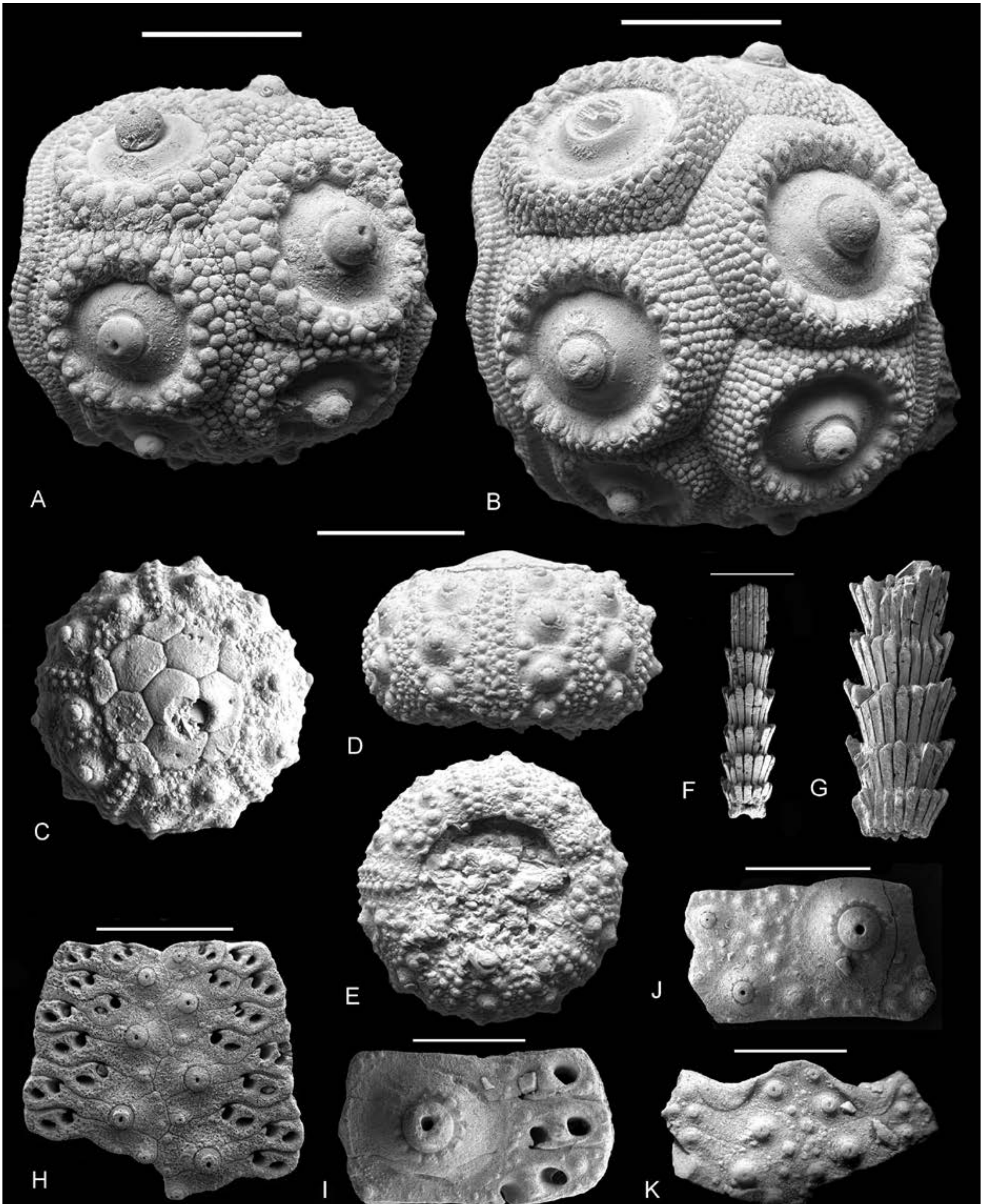
DIAGNOSIS: Spines bearing 12–14 sharply defined, widely separated, columns of oval to rectangular low, rounded rugosities which become thorn-like and imbricate distally on upper shaft.

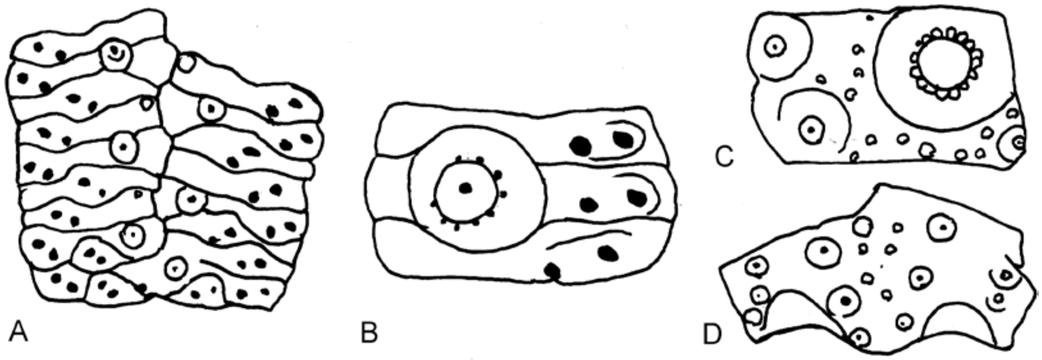
TYPES: The spine figured here (Text-fig. 5Q) is the



Text-fig. 5. Selected cidarids from Ivö Klack, southern Sweden. A–D, F–J – *Hirudocidaris botryoformis* sp. nov. A, B – sections of test in lateral aspect (MGUH 35041, 35042), with enlarged ambulacrum of A in H, and enlargement of B in F; C, D, G, I, J – primary spines (MGUH 35043–35047); C is the holotype, D, G, I, J are paratypes. E, L–Q – *Hirudocidaris zeamays* sp. nov. E – interambulacral plate with attached ambulacrals (MGUH 35049); L – interambulacral plate (MGUH 35050); M–Q – primary spines (Q is the holotype, M–P are paratypes, MGUH 35051–35055). K – Juvenile cidarid, 1/5 portion of test in lateral view (MGUH 35059). Provenance: upper lower Campanian, Ivö Klack, southern Sweden. Scale bars equal: 10 mm (A, B), 5 mm (C–E, G, I, J, L–Q), 2 mm (F, H), and 1 mm (K).



Text-fig. 6. Selected cidarids (A, B), saleniids (C–E) and diadematids (F–K) from southern Sweden. A – *Hirudocidaris botryoformis* sp. nov., section of test in lateral aspect (MGUH 35048). B – *Hirudocidaris zeamays* sp. nov., section of test in lateral view (SHMNS Ec0001350). C–E – *Salenia areolata* (Wahlenberg, 1821), test in apical (C), lateral (D), and oral (E) views (MGUH 35061). F–K – *Centrostephanus* sp. F, G – primary spines (MGUH 35062, 35063); H – adoral ambulacrum (MGUH 35064); I – ambital ambulacral plate (MGUH 35065); J – interambulacral plate (MGUH 35066); K – interambulacral fragment, showing margin of peristome (MGUH 35067). Provenance: A, B, F–K are from the upper lower Campanian, Ivö Klack, southern Sweden; C–E are from the upper lower Campanian, Barnakälla, southern Sweden. Scale bars equal: 10 mm (A–E), 4 mm (G, H, K), 1 mm (F, G) and 0.5 mm (I, J).



Text-fig. 7. Interpretative drawings of plating in *Centrostephanus* sp. A – adoral portion of ambulacrum; B – ambital ambulacral plate; C – interambulacral plate; D – adoral portion of an interambulacrum, showing buccal notches. Compare with photographs of the same specimens (Text-fig. 6I–K).

holotype (MGUH 35055). The other figured spines and test segments are paratypes (MGUH 35049–35054, SMNH Ec0001350), all from the upper lower Campanian of Ivö Klack, southern Sweden.

MATERIAL: Fifty-six primary spines, three interambulacral plates and a 1/5 segment of test, with interambulacrals and ambulacrals, all from the same locality (Text-fig. 6B) (MGUH collections).

DERIVATION OF NAME: From the maize plant, *Zea mays*, in allusion to the fact that the more actinal primary spines closely resemble corn-on-the cob.

DESCRIPTION: Interambulacral plates belonging to this species (Text-figs 5L, 6B) possess a broad, shallow areole and a proportionately small, perforate mamelon. The scrobicular ring is narrow, and the miliaries rather small and of even size, formed into poorly defined rows by shallow grooves. The highly distinctive spines (Text-fig. 5M–Q) are fusiform, with a relatively long, smooth neck. Ambital to adapical spines (Text-fig. 5M, P, Q) are relatively short, fusiform and robust; each with 12–14 sharply defined, rather widely separated columns of even-sized rounded-rectangular low rugosities on the proximal shaft. On the distal shaft (Text-fig. 5Q) these become triangular, with a sharp margin, and imbricate towards the tip. The tip is bluntly rounded and simple. Spines from the oral surface (Text-fig. 5N, O) are proportionately short and fusiform, the sculpture comprising columns of rugosities which fuse into raised ridges distally.

REMARKS: The distinctive spine sculpture separates this species from all congeners.

Order Diadematoida Duncan, 1889
Family Diadematidae Peters, 1855
Genus *Centrostephanus* Peters, 1855

DIAGNOSIS: Diadematid in which only a single enlarged tubercle is present on each interambulacral plate and in which there is no naked adapical interradial zone. Ambulacral tubercles large, occupying full plate width adorally (after Smith and Wright 1990, p. 113).

TYPE SPECIES: *Diadema longispina* Philippi, 1845, by original designation.

REMARKS: There are 10 living species of *Centrostephanus* (Pawson and Miller 1983) which inhabit temperate and subtropical regions of the world's oceans (Byrne and Andrew 2020). All are nocturnal crevice dwellers on rocky substrates, down to a depth of about 100 m, and omnivorous grazers.

Centrostephanus sp.
(Text-figs 6F–K, 7A–D)

MATERIAL: Thirty-two test fragments and 15 primary spines from Ivö Klack, Sweden (MGUH 35062–35067).

REMARKS: This fragmentary material can be referred to the Diadematidae on account of numerous features, including the diadematid compounding of ambulacrals in triads (Text-fig. 6H), the form of the buccal notches and the distinctive verticillate spines (Text-fig. 6F, G, K). The presence of a single large tubercle on each interambulacral plate confirms the identification as *Centrostephanus*. The adoral ambulacral plating (Text-fig. 6H) shows bi-triserial pore pairs. The material is comparable to that of *Centrostephanus fragilis* (Wiltshire in Wright, 1882) from the Santonian and lower Campanian of southern England, figured by Smith and Wright (1990, text-fig. 25, pl. 2, figs 1–10). However, there are differences in the adoral interambulacral tuberculation immediately adjacent to the peristome. In the Ivö Klack material, the primary tubercles of adjacent interambulacral columns are widely spaced and separated by a zone of secondary tubercles and miliaries on the three most adoral plates (Text-fig. 6H, J). These are absent in *C. fragilis* (Smith and Wright 1990, text-fig. 25B) in which the primary tubercles on the most adoral interambulacrals nearly abut interradially. Also, the lips of the buccal notches are much larger in the Ivö Klack material than in the UK Chalk individual.

Order Calycina Gregory, 1900
Family Saleniidae Agassiz, 1838
Subfamily Saleniinae Agassiz, 1838
Genus *Salenia* Gray, 1835

DIAGNOSIS: Saleniinae with relatively broad ambulacra, with primary, secondary and miliary tubercules differentiated, plating bigeminate or unigeminate. Disc circular or pentagonal, smooth or granular, with sutural pits at triple suture junctions and midway between.

TYPE SPECIES: *Cidarites scutigera* Goldfuss, 1829, by monotypy.

Salenia areolata (Wahlenberg, 1821)
(Text-figs 6C–E, 8E, F, 9F–H)

1820. *Echinus areolatus* König, p. 4, pl. 8, fig. 100.
*1821. *Echinites areolatus* Wahlenberg, p. 46, pl. 3, figs 3, 4–5.
1847. *Salenia areolata* Wahlenberg; Agassiz and Desor, p. 37.
1888. *Salenia areolata* Wahlenberg; Cotteau, p. 105, pl. 13, figs 1–4.
1932. *Salenia areolata* (Wahlenberg); Mortensen, p. 476, pl. 5, figs 6–12.

DIAGNOSIS: Small (<20 mm diameter), low hemispherical test, oral surface flat. Ambulacra straight, adapically uniserial, biserial around peristome. Primary interambulacral tubercles small, crenulate. Apical disc 50–60% of test diameter, smooth, flat, lacking sutural pits.

TYPE: According to Mortensen (1932, p. 480), the type specimen should be in the collections of the PMU, but there it could not be traced during a recent visit by ASG (March 2025).

REMARKS: This species is perhaps closest to the Maastrichtian–Paleocene *Salenia belgica* Lambert, 1898, known from Belgium (Jagt 2000) and Kazakhstan (Jeffery 1997) from which it differs principally in the smaller apical disc, lacking sutural pits along plate boundaries (Text-figs 6C, 8E). However, Text-fig. 9F does show sutural pits, albeit small ones. The species was not found during the 2011–2012 study; it has always been rare at Ivö Klack (Mortensen 1932). We have seen only two individuals from Ivö Klack (SMNH Ec0001233). However, it was abundant at Barnakälla in southern Sweden (Christensen 1975), where specimens are very well preserved (Text-fig. 6C–E). There are numerous tests from this locality in the SMNH collections and a few in those at MGUH.

Genus *Trisalenia* Lambert, 1895

DIAGNOSIS: Saleniinae in which the adoral pore zones are broad, the mamelons are coarse and the apical disc is flat.

TYPE SPECIES: *Salenia loveni* Cotteau, 1888, by original designation.

Trisalenia loveni (Cotteau, 1888)
(Text-figs 8D, G, H, 9C, 10A–C, E–G, I–K)

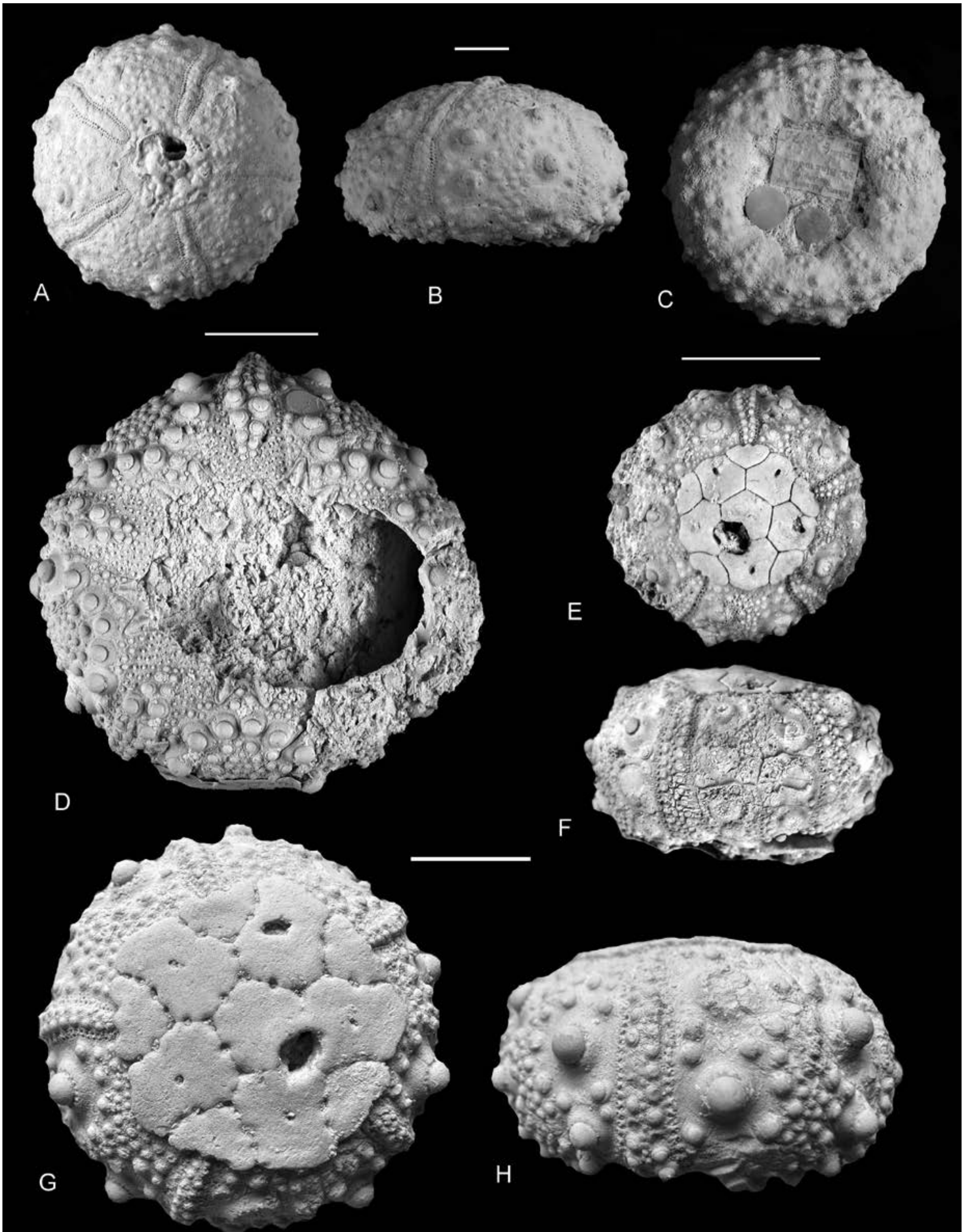
*1888. *Salenia Loveni* Cotteau, p. 107, pl. 13, figs 5–9.
1910. *Salenia loveni* Cotteau; Lambert and Thiéry, p. 211.
1932. *Trisalenia loveni* (Cotteau); Mortensen, p. 485, pl. 4, figs 4–10; pl. 5, figs 13–24.

DIAGNOSIS: As for genus.

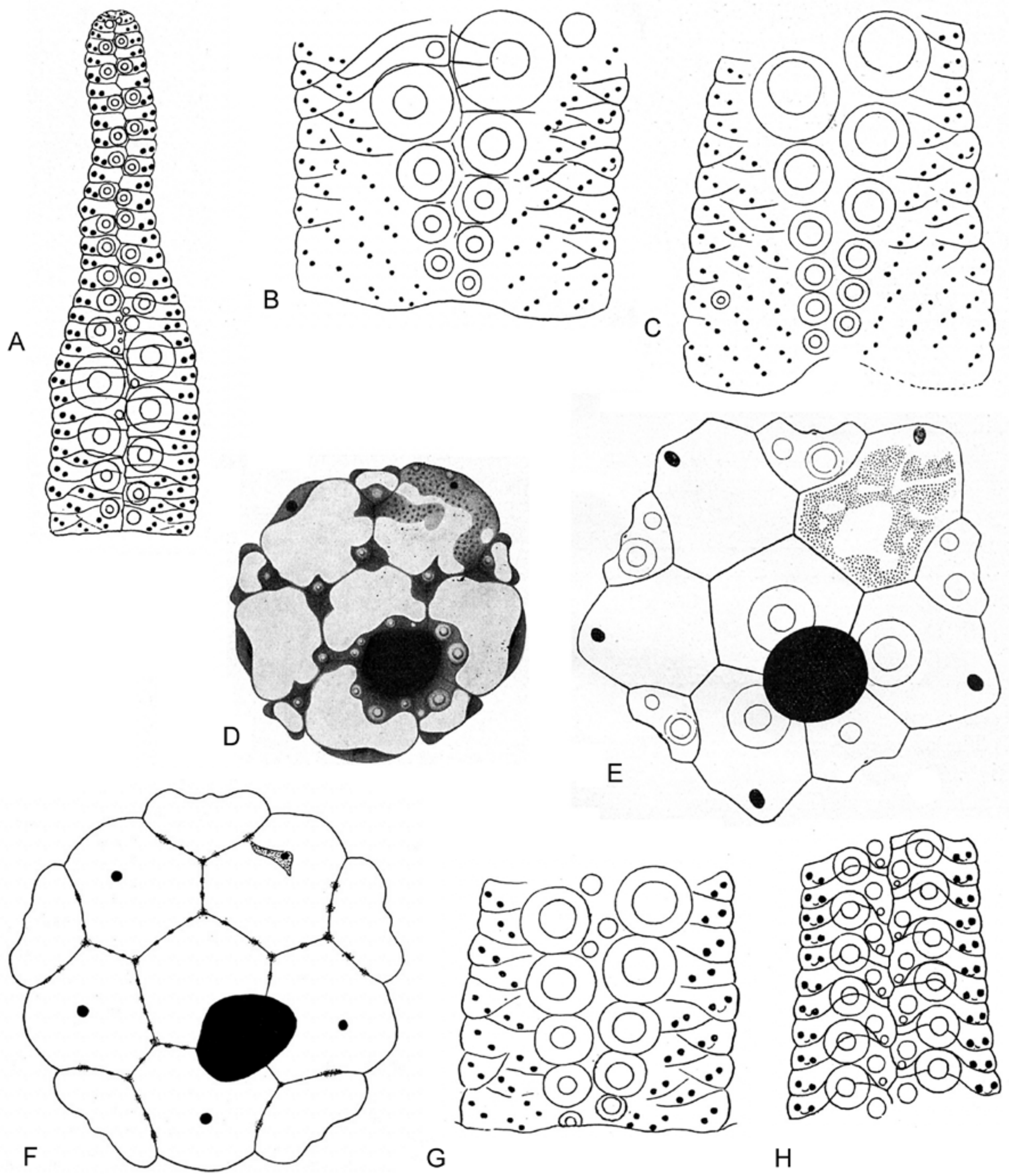
TYPE: According to Mortensen (1932, p. 472) the types should be in the SMNH collections but were not available in March 2025.

MATERIAL: Over 100 small tests, fragments of larger tests and spines probably belonging to this species from Ivö Klack, and numerous tests in the SMNH and PMU collections, plus two specimens in the NHMUK collections.

REMARKS: This distinctive species was described

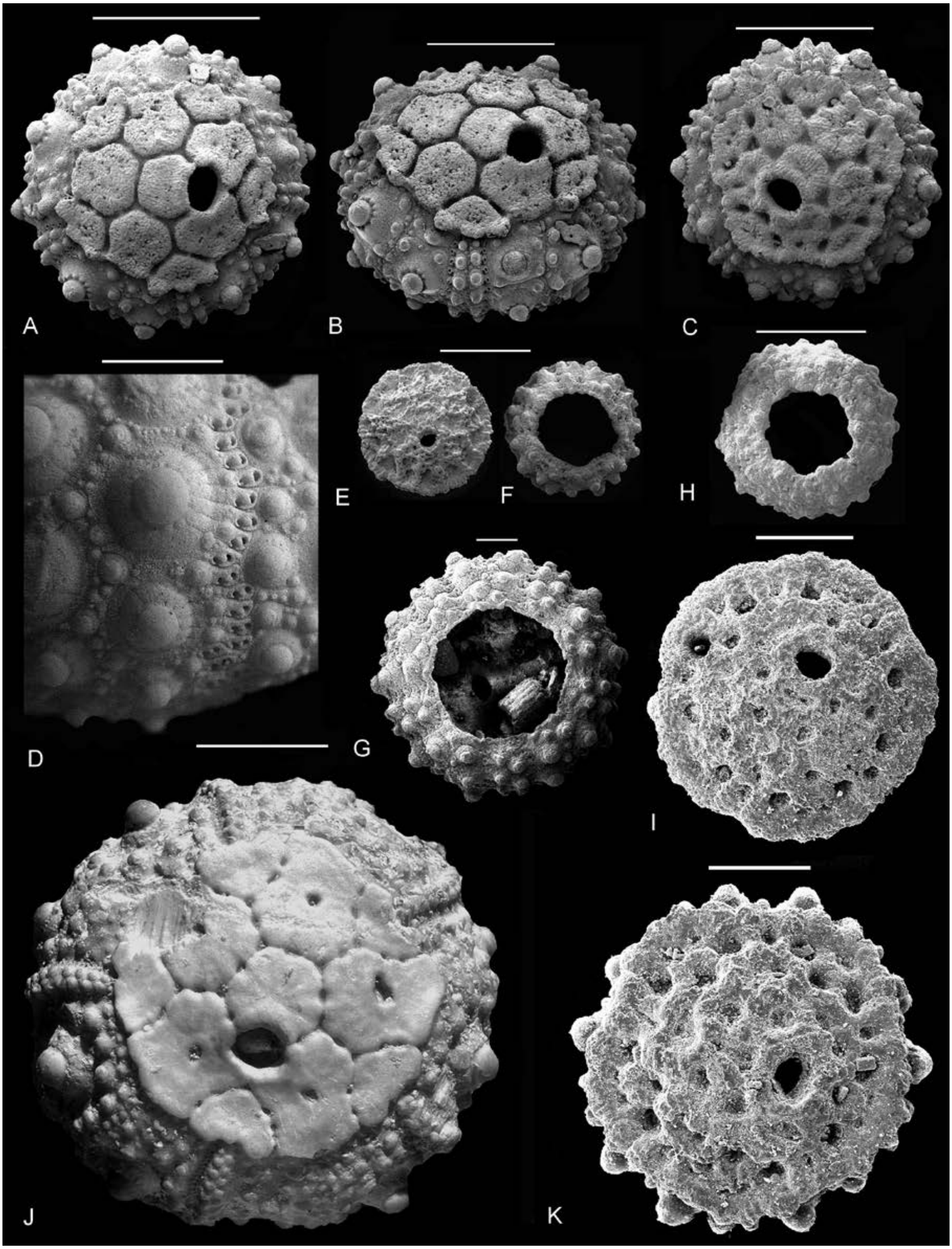


Text-fig. 8. Selected saleniids from Ivö Klack, southern Sweden. A–C – *Polysalenia notabilis* Mortensen, 1932, test in apical (A), lateral (B) and oral (C) views, original of Mortensen (1932, pl. 4, figs 1–3; SMNH Ec0000175). D, G, H – *Trisalenia loveni* (Cotteau, 1888); D – oral view of large test (SMNH Ec0008370); G, H – test (NHMUK E83003) in apical (G) and lateral (H) views. E, F – *Salenia areolata* (Wahlenberg, 1821), test (SMNH Ec0001233) in apical (E) and lateral (F) views. All from the upper lower Campanian at Ivö Klack, southern Sweden. All scale bars equal 10 mm.



Text-fig. 9. Selected saleniids from southern Sweden. A, D – *Polysalenia cottaldi* Mortensen, 1932; A – ambulacral plating, D – apical disc, figured after Mortensen (1932, figs 23, 24). B, E – *Polysalenia notabilis* Mortensen, 1932; B – adoral ambulacral plating, E – apical disc, figured after Mortensen (1932, figs 18, 22). C – *Trisalenia loveni* (Cotteau, 1888), adoral ambulacral plating, figured after Mortensen (1932, fig. 11). F–H – *Salenia areolata* (Wahlenberg, 1821); F – apical disc, G – adoral ambulacral plating, H – ambital ambulacral plating, figured after Mortensen (1932, figs 5, 3, 2, respectively).

in detail by Mortensen (1932) and there is little to add to his study. The new material includes numerous very small juvenile tests of the species, down to a diameter of 0.7 mm (Text-fig. 10E, F). At this size, the apical disc covers the entire apical test surface, and the margins protrude slightly. At a diameter close to 1 mm (Text-fig. 10I, K) the apical disc is conspicuously pitted although it is not pos-



Text-fig. 10. Selected saleniids (A–C, E–G, I–K) and phymosomatids (D, H) from Ivö Klack, southern Sweden. A–C, E–G, I–K – *Trisalenia loveni* (Cotteau, 1888). A, B – small test (MGUH 35068) in apical (A) and oblique lateral (B) views; small test (MGUH 35069) in apical view; E, F – very small test (MGUH 35071) in apical (E) and oral (F) views; G – small test (MGUH 35072) in oral view; J – very large test (NHMUK E44375) in apical view; I, K – small tests (MGUH 35073–35074) in apical views. D, H – *Trochalosoma ivoensis* sp. nov. D – test fragment (MGUH 35070) in lateral view, to show ambulacral plating; H – small test (MGUH 35075) in apical view. All from the upper lower Campanian, Ivö Klack, southern Sweden. Scale bars equal: 10 mm (J), 2 mm (A–D), 0.5 mm (E–G) and 0.3 mm (I, K).

sible to resolve the relationship between the pitting and plate boundaries. At test diameter of 3 mm the positions of the sutural pits are visible in some specimens (Text-fig. 10C), but absent in others (Text-fig. 10A, B). At this diameter (Text-fig. 10A–C), the disc occupies 2/3 of the apical surface of the test and the form closely resembles that of fully-grown individuals with a test diameter of 40 mm (Text-fig. 10J). The adoral pore zones are very broad in larger specimens (Text-fig. 8D) and the pores are arranged tri- or quadriserially.

Mortensen (1932, p. 479, pl. 5, figs 18–24) attributed isolated, smooth, parallel-sided to weakly fusiform primary spines (Text-fig. 4H–L) from Ivö Klack to *Trisalenia loveni*, on the argument that this species is the only possible source of such spines. However, some of these might be adoral spines of the phymosomatid genus *Trochalosoma* which is also common at Ivö Klack or to other species of saleniid.

Genus *Polysalenia* Mortensen, 1932

DIAGNOSIS: Apical disc small and weakly raised above corona, with indented sutures and prominent sutural pits. Periproct displaced towards ambulacrum 1; single suranal plate present. Ring of small tubercles along inner margin of genital plates surrounding periproct. Ambulacral plating trigeminate aborally and polygeminate adorally, with distinct phyllodes.

TYPE SPECIES: *Polysalenia notabilis* Mortensen, 1932, by monotypy.

Polysalenia notabilis Mortensen, 1932
(Text-figs 8A–C, 9B, E)

*1932. *Polysalenia notabilis* Mortensen, p. 491, pl. 4, figs 1–3.

DIAGNOSIS: Large species, attaining maximum diameter of 51 mm. Apical disc small, 35% of test diameter, plates bearing large tubercles. Peristome broad, 50% of test diameter. Pores uniserial above ambitus, becoming progressively more polyserial towards peristome; quadriserially there and forming broad phyllodes.

TYPE: The specimen figured by Mortensen (1932, pl. 4, figs 1–3) is the holotype (SMNH Ec0000175; Text-fig. 8A–C herein), from the upper lower Campanian of Ivö Klack, southern Sweden.

MATERIAL: Mortensen (1932, p. 494) stated that he had seen seven specimens, collected by S. Holm and R. Hägg, all from Ivö Klack.

REMARKS: This highly distinctive, very large species is characterised particularly by the small, tuberculate apical disc (Text-figs 8A, 9E), the wide peristome (Text-fig. 8C) and the polyserial adoral pore pairs. The species is not present in the new collection of material; it was evidently very rare at Ivö Klack, the only known locality for *Polysalenia*. We have examined four specimens of this species (SMNH Ec0000171, Ec0000172, Ec0000174 and Ec0000175).

Polysalenia cottaldi Mortensen, 1932
(Text-fig. 9A, D)

*1932. *Polysalenia cottaldi* Mortensen, p. 494, pl. 4, figs 11–13.

DIAGNOSIS: Apical disc small (43% of test diameter), with depressed margin around periproct and between plates in which small tubercles are present. Adoral pore zones narrow.

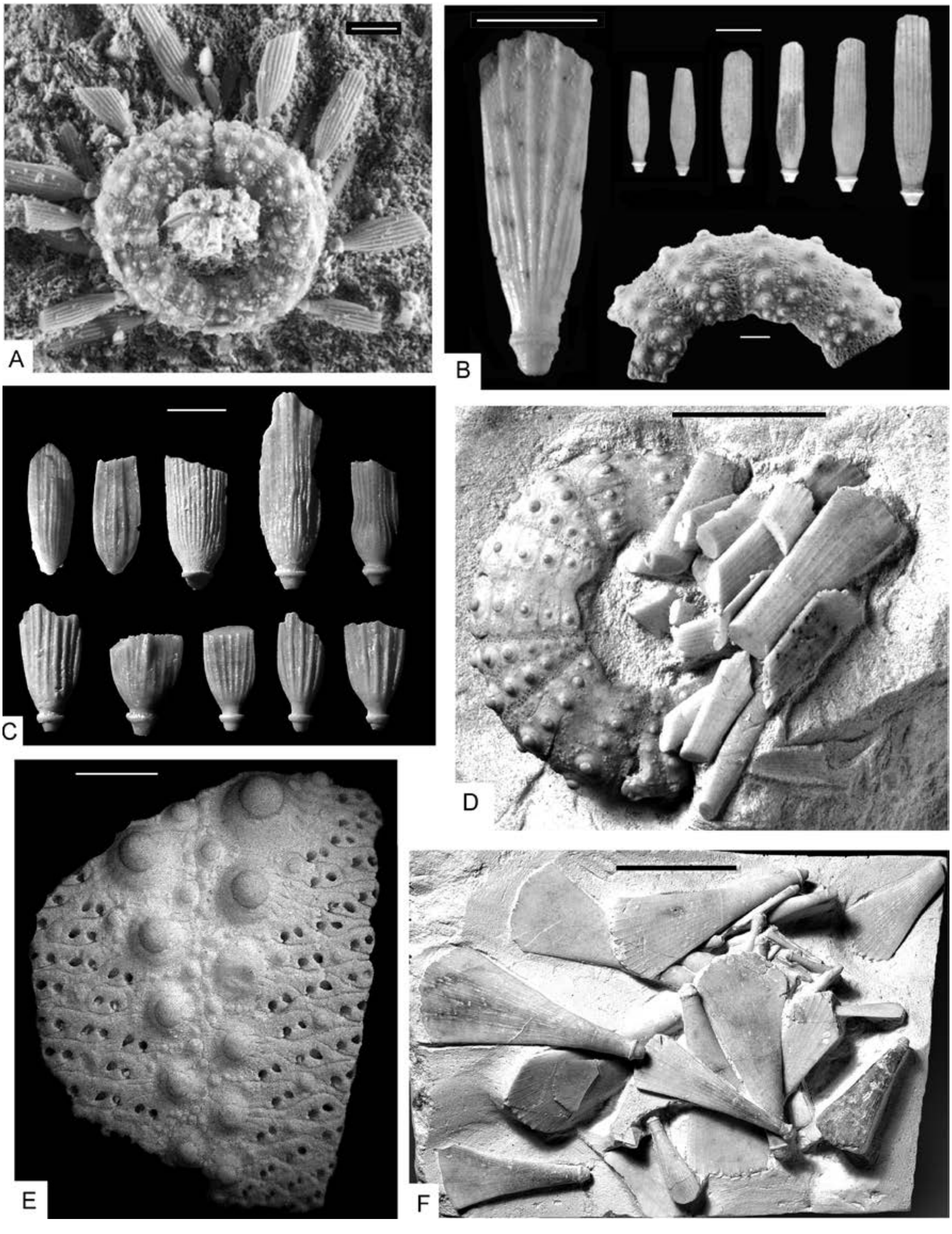
TYPE: The specimen figured by Mortensen (1932, pl. 4, figs 11–13) is the holotype and only known specimen, thought to have come from Ivö Klack. It was not found in the SMNH collections during a visit by ASG (March 2025).

REMARKS: No material of this species was seen in the new collections, and as the type specimen was not available, there is nothing to currently add to Mortensen's (1932) description.

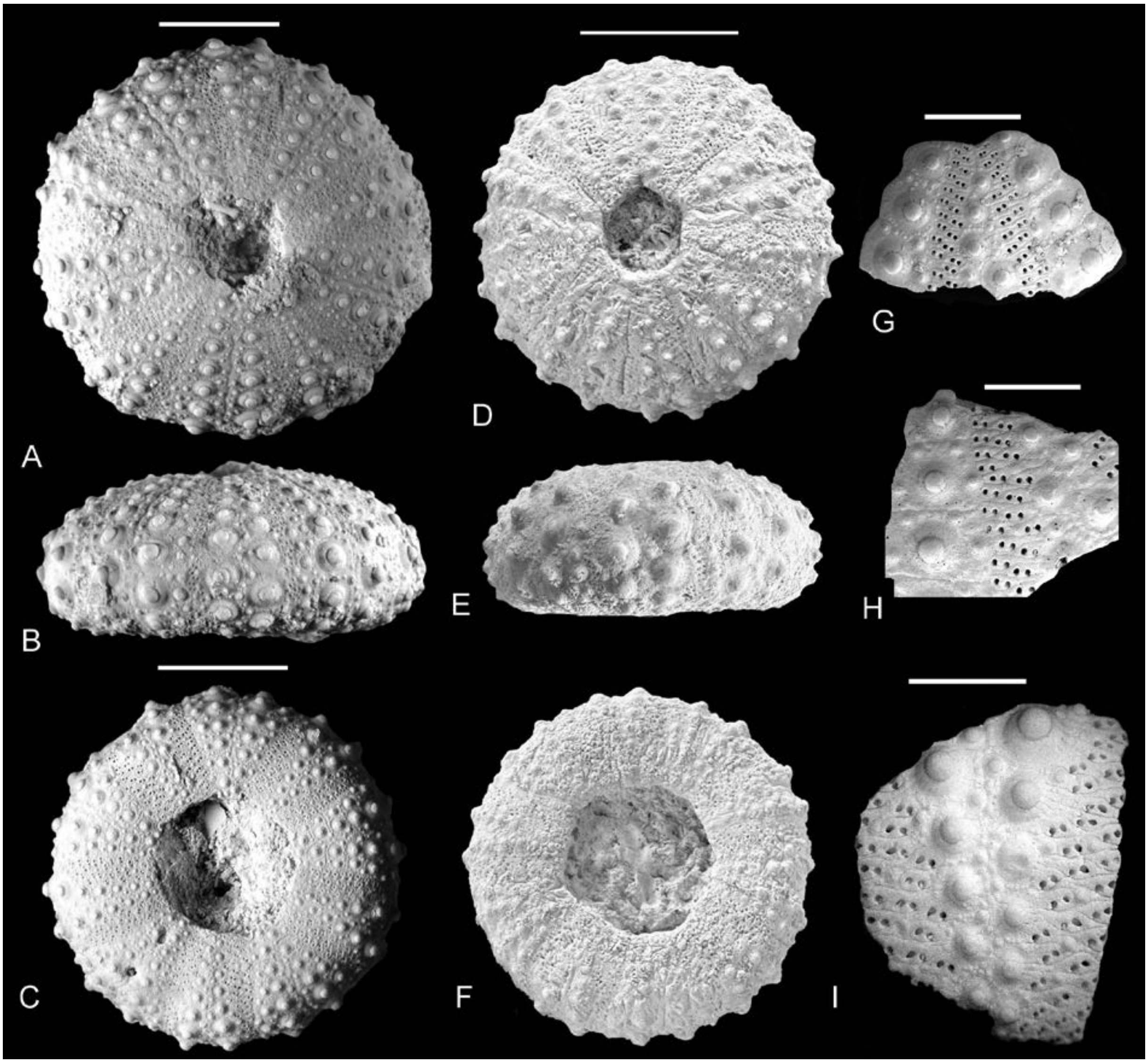
Superorder Stirodonta Jackson, 1912
Family Phymosomatidae Pomel, 1883
Genus *Trochalosoma* Lambert, 1898

DIAGNOSIS: Test flattened, ambitus rounded, subpentagonal in outline; ambulacra trigeminate on oral surface, polygeminate at ambitus and above, plate compounding phymosomatid. Pore pairs biserial above ambitus, expanded orally into phyllodes. Ambulacrals with single large primary tubercle, largest at ambitus, reducing sharply in size above. Ambulacral and adambulacral tubercles of similar size. Primary tubercles non-crenulate, or weakly crenulate, imperforate.

TYPE SPECIES: *Cyphosoma rugosum* Agassiz in Agassiz and Desor, 1846, by monotypy.



Text-fig. 11. Representatives of *Trochalosoma* spp. A, B – *Trochalosoma corneti* (Cotteau, 1875); A – test with spines (NHMM AC M-100) in oral view, original of Jagt (2000, pl. 13, fig. 16), top Nekum Member, Maastricht Formation, ENCI-Maastricht BV Quarry, Maastricht, the Netherlands; B – primary spines, originals of Jagt (2000, pl. 13, figs 9–15), specimen on the left is from the Nekum Member, Maastricht Formation, CBR-Romontbos quarry, Eben Emael, Maastricht, the Netherlands (NHMM K 4152/6), specimens on the right are from the Meerssen Member, Maastricht Formation, ENCI-Maastricht BV quarry, Maastricht, the Netherlands (NHMM BL 0123). C, E – *Trochalosoma ivoensis* sp. nov.; C – primary spines (collection of Søren Bo Andersen, Denmark); E – view of adoral ambulacrum (MGUH 35094). D, F – *Trochalosoma taeniatum* (von Hagenow, 1840); D – test with spines and primary spines (MGUH collections) in apical view, upper Maastrichtian, Stevns Klint, Denmark. Scale bars equal: 10 mm (D, F) and 5 mm (A–C, E).



Text-fig. 12. *Trochalosoma ivoensis* sp. nov. A, B – large test (PMU 17870), in apical (A) and lateral (B) views; C – paratype test (SMNH Ec0031416) in oral view; D–F – paratype test (MGUH 35076) in apical (D), lateral (E) and oral (F) views; G–I – SEM images of test fragments; G – apical ambulacrulum and interambulacral (MGUH 35077); H – ambital structure (MGUH 35078); I – ambulacrum, adjacent to peristome (MGUH 35079). All from the upper lower Campanian, Ivö Klack, southern Sweden. Scale bars equal: 10 mm (A–F) and 4 mm (G–I).

REMARKS: There has been considerable discussion on *Trochalosoma*, partly because the type species is poorly known, and no material of it is currently available. Smith and Jeffery (2000) placed a number of species in this genus largely on account of the non- or weakly crenulate primary tubercles. Jagt (2000) identified *Cyphosoma corneti* Cotteau, 1875 as belonging to the genus with some doubt, and illustrated a test with primary spines attached, the oral surface of an incomplete test, and numerous primary spines (reproduced here, Text-fig. 11A, B). Ambital spines are spatulate, splay distally and bear narrow ridges (Text-fig. 11A, B). *Trochalosoma taeniatum* (von Hagenow, 1840) is a distinctive and well-known species from the Maastrichtian chalk of Denmark, northern Germany and Poland (Ravn 1928; Kutscher 2003; Jagt and Kin 2010); this has very flat, broadly spatulate ambital spines which are finely striate or nearly smooth (Text-fig. 11D, F). In spite of the uncertainties surrounding the type species, there is a consensus that *Trochalosoma* includes phymosomatids in which the ambulacrals are biserial above the ambitus, expand into phyllodes adorally, have weakly crenulate primary tubercles and possess at least some spatulate primary spines.

In the Ivö Klack echinoid fauna collected during 2011–2012, there are numerous fragments, and several complete tests of a distinctive species of phymosomatid with weakly crenulate tubercles, in which the pore pairs are biserial above the ambitus. In the same assemblage are spatulate primary spines found; these bear close similarities to those of *T. corneti*. It appears highly probable that these belong to the same taxon, which is described below.

Trochalosoma ivoensis sp. nov.
(Text-figs 4G, 10D, H, 11C, E, 12A–I, 13A–C)

urn:lsid:zoobank.org:act:55A087F4-EA84-416A-8677-8610D4441380

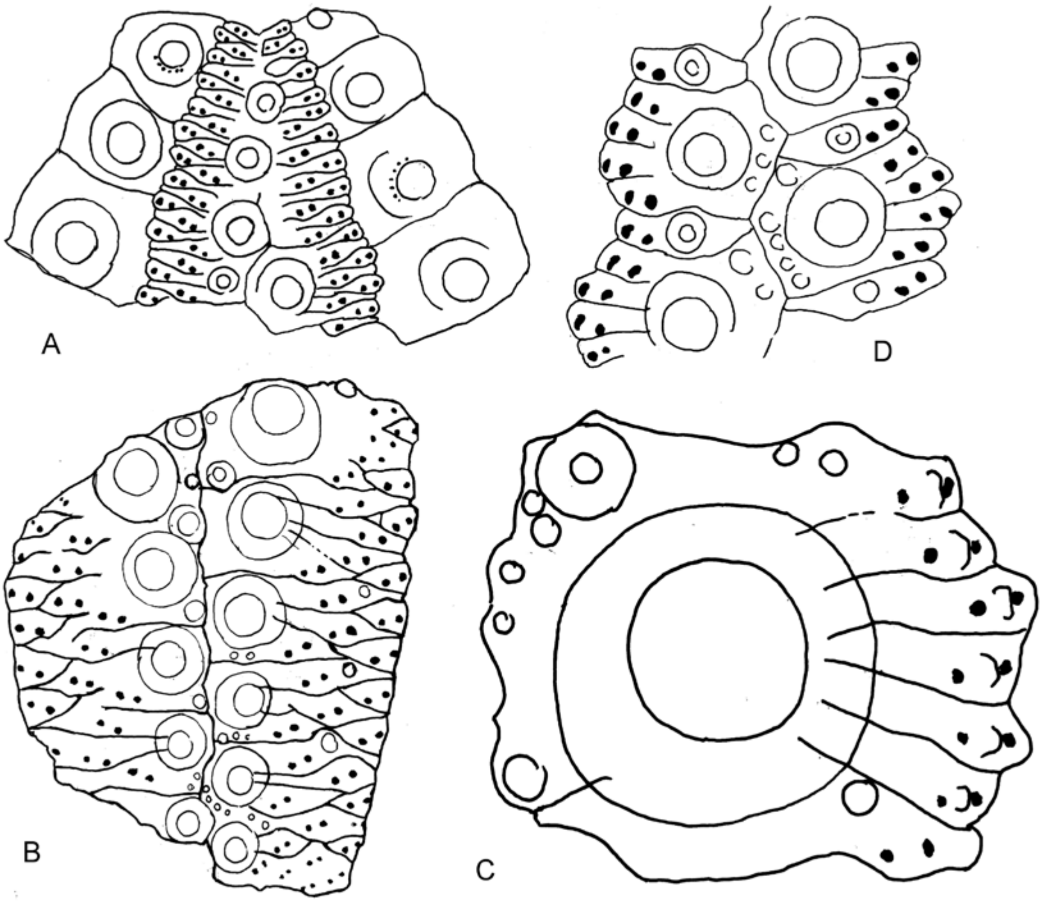
DIAGNOSIS: *Trochalosoma* with very broad and trigeminate adoral pore zones; ambital ambulacrals uniserial and sinuous and adapical pore zones broad and biserial. Adapical interambulacrals narrow. Primary ambital spines robust, parallel-sided or flared distally, with broad milled ring.

TYPES: The test illustrated in Text-fig. 12A, B is the holotype (PMU 17870). The other two figured tests are paratypes (Text-fig. 12C, SMNH Ec0031416; Text-fig. 12D–F, MGUH 35076).

MATERIAL: Four tests, numerous fragmentary tests and 10 primary spines from the type locality.

DERIVATION OF NAME: After Ivö Klack, the type locality.

DESCRIPTION: The test (Text-fig. 12A–F) is circular in outline and the small periproct occupies 25% of the diameter. In lateral profile, the height is half the diameter, the oral face is flat, and the apical margin gently domed. The peristome is slightly inset, subpentagonal and occupies less than 50% of the test diameter. The ambulacral tubercles are slightly smaller than those

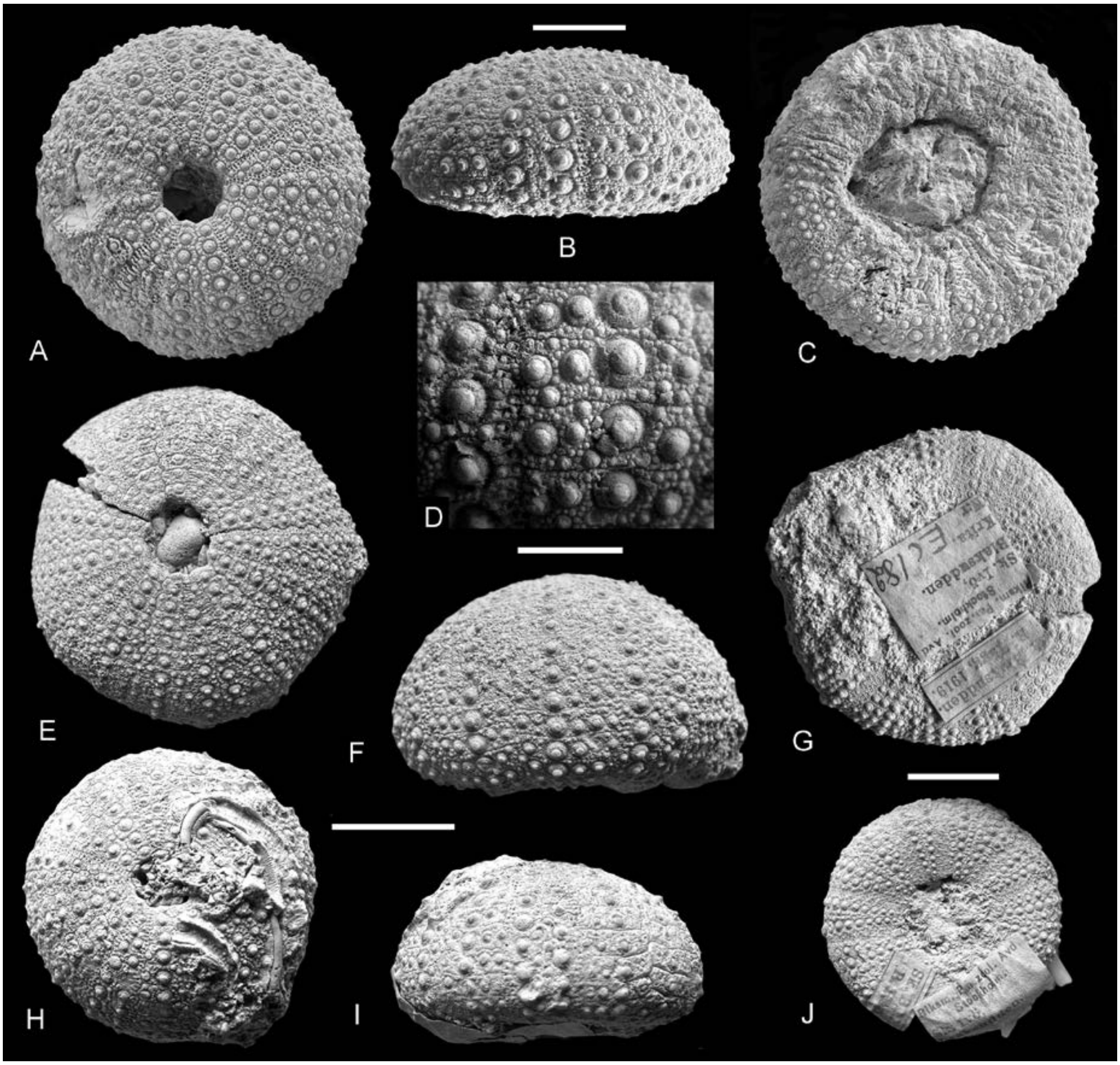


Text-fig. 13. Interpretative drawings of echinoid plating. A–C – *Trochalosoma ivoensis* sp. nov., apical plating of test fragment, adoral plating of ambulacrum and ambital ambulacral plate, respectively; D – ambital ambulacral plating of *Scaniasoma surlyki* gen. et sp. nov.

on the interambulacrals, and all are imperforate. All except the most adapical interambulacral tubercles are non-crenulate and the most apical two or three interambulacral tubercles are weakly crenulate. Secondary tubercles are present on the perradial, adapical and adoral margins of ambital ambulacrals (Text-fig. 12H).

Plate compounding is of phymosomatid type (Text-figs 10D, 13A–C) with a large adoral and an adapical element which reach the perradius, and five shorter central elements which do not. Adorally, the ambulacrals are polygeminate, and the broad pore zones are triserial, then quadriserial adjacent to the peristome (Text-figs 12C, I, 13B). The ambital ambulacra are uniserial and straight (Text-fig. 12A, D), the adapical ambulacral zones are broad and bi- to triserial (Text-figs 12G, 13A). The adapical interambulacrals are narrow (Text-fig. 13A).

The primary spines (Text-figs 4G, 11C), probably coming from around the ambitus by comparison with an articulated specimen of *Trochalosoma corneti* (Text-fig. 11A), are robust, flattened and parallel-sided to slightly flared distally. The shaft bears a sculpture of 3–15 raised ridges with intervening grooves; these can have lower, secondary ridges between the grooves. The milled ring (Text-fig. 4G) is short and very broad.



Text-fig. 14. *Scaniosoma surlyki* gen. et sp. nov. A–D – holotype test (MGUH 35080) in apical (A), lateral (B) and oral (C) views, and enlargement of interambulacrum (D); E–G – paratype test (SMNH Ec182) in apical (E), lateral (F), and oral (G) views; H, I – paratype test (SMNH Ec81) in apical (H) and lateral (I) views; J – paratype test (SMNH Ec194) in oral view. All from the upper lower Campanian, Ivö Klack, southern Sweden. All scale bars equal 10 mm.

REMARKS: *Trochalosoma ivoensis* sp. nov. is most closely related to *T. corneti* from the upper Maastrichtian of the southeast Netherlands and northeast Belgium (Text-fig. 11A, B), but differs in its much broader, polygeminate adoral ambulacral pore zones and the broader, more strongly ridged primary ambital spines.

Order Stomopneustoidea Kroh and Smith, 2010
Family Stomechinidae Pomel, 1883
Genus *Scaniasoma* nov.

urn:lsid:zoobank.org:act:E8CEC2A0-F482-4E81-BA21-31140C14AB13

DIAGNOSIS: Test circular; small subpentagonal disc occupying 17% of test diameter. Apical surface evenly domed, peristome 30% of test diameter. Tubercles small, all imperforate, non-crenulate, ambulacral and interambulacral tubercles of equal size. Transversely broad interambulacrals carrying four to six tubercles of subequal size. Ambulacral compounding comprising four adoral elements, not extending perradially beyond tubercle, and one adapical element reaching perradius and bearing a secondary tubercle. Spines unknown.

TYPE SPECIES: *Scaniasoma surlyki* gen. et sp. nov.

REMARKS: *Scaniasoma* gen. nov. superficially resembles *Echinotiara* Pomel, 1883 in test profile, wide interambulacral zones and relatively small primary tubercles. However, it differs in its very small periproct, the distinctive tuberculation of the interambulacrals, the uniserial pores on the adapical ambulacrals, and the distinctive ambulacral plate compounding. In *Echinotiara*, the ambulacral plates are compounded into triads, and the interambulacrals carry a single enlarged tubercle (Smith 1995, fig. 41).

Scaniasoma surlyki gen. et sp. nov.
(Text-figs 13D, 14A–J)

urn:lsid:zoobank.org:act:730228B7-A803-43E9-987B-7D42C992DA47

DIAGNOSIS: As for genus.

TYPES: The well-preserved test figured here (Text-fig. 14A–D) is the holotype (MGUH 35080). The other figured tests are paratypes (Text-fig. 14E–G; SMNH Ec182; Text-fig. 14H, I, SMNH Ec81; Text-fig. 14J, SMNH Ec194). There are further specimens in the PMU and SMNH collections.

DERIVATION OF NAME: For Finn Surlyk, Copenhagen, in honour of his work on the Ivö Klack faunas.

DESCRIPTION: Test circular to subpentagonal, adapical profile evenly convex in lateral view, base flat to weakly convex. Height of test 50–65% of the diameter, variably more (Text-fig. 14F) and less (Text-fig. 14B) domed adapically. Apical disc subpentagonal, not preserved, representing 15–20% of test diameter. Peristome wide, representing 25–30% of test diameter, with short buccal notches. Conspicuously larger tubercles forming two columns on ambulacra and two on interambulacral, adjacent to perradius. Interambulacral plates low and broad (Text-fig. 14D). The tuberculation comprises five to six transversely arranged tubercles which increase in size towards the perradius; the 3rd or 4th tubercles are largest and form well-defined columns (Text-fig. 14D). The 5th and 6th tubercles, adjacent to the perradius, are small. Ambulacral plates (Text-fig. 13D) with distinctive compounding, comprising four adoral elements which do not extend perradially beyond the tubercle, and an adapical element which reaches the perradius and bears a secondary tubercle. Ambulacra uniserial above ambitus, pore pairs weakly sinuous. Ambulacral plating of oral surface not clearly exposed, but bi- to trigeminal around peristome with rather narrow phyllodes.

Cohort Irregularia Latreille, 1825
Suborder Holectypina Duncan, 1889
Family Holectypidae Lambert, 1900
Subfamily Coenholectypinae Smith and Wright, 1999
Genus *Coenholectypus* Pomel, 1883

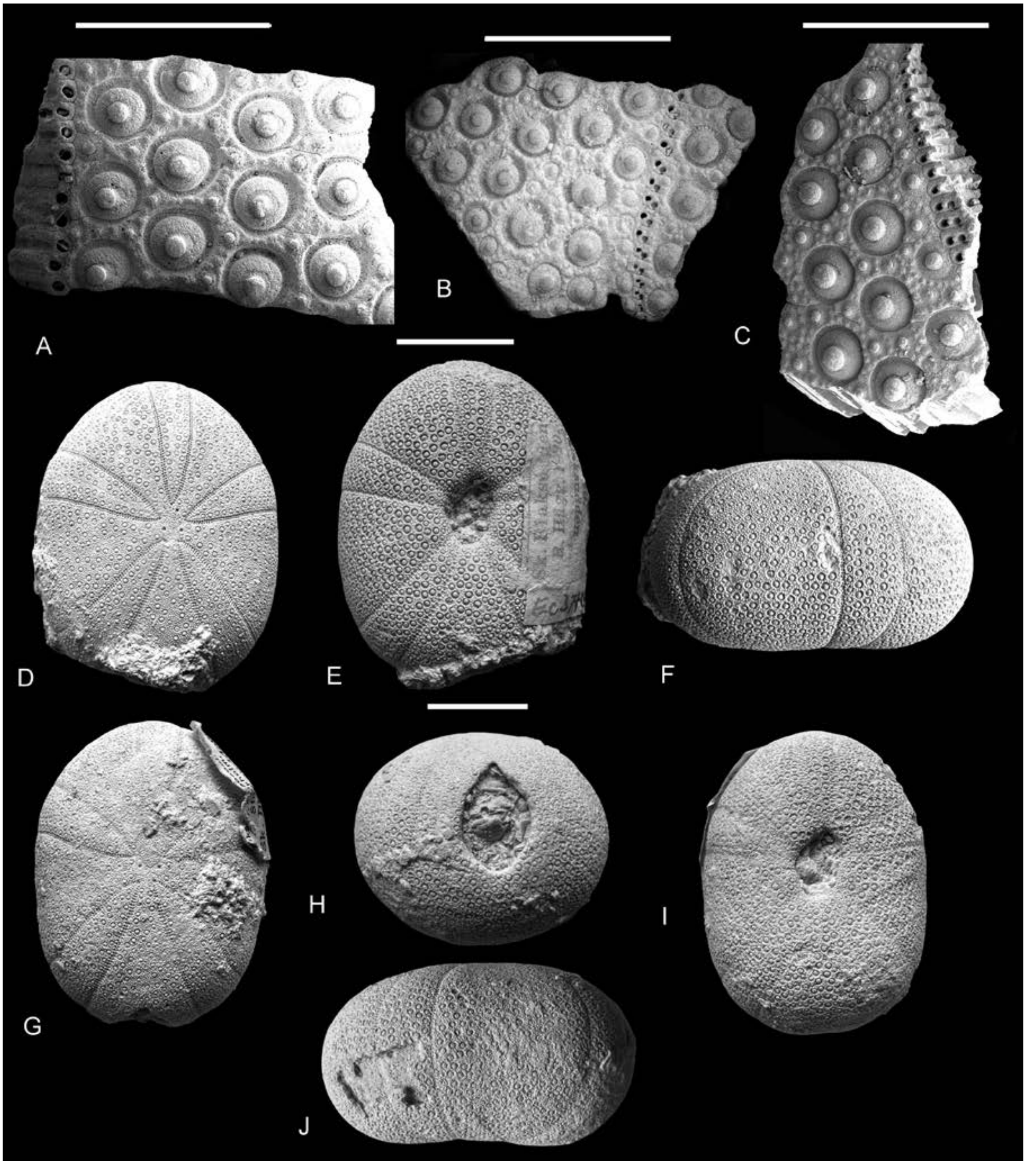
DIAGNOSIS: Holectypids with domed to low subconical profile and plating without sutural pits. Periproct on oral surface. Aboral ambulacral plating simple.

TYPE SPECIES: *Holectypus macropygus* Desor, 1842, by the subsequent designation of Hawkins (1912).

Coenholectypus sp.
(Text-fig. 15A–C)

MATERIAL: Twenty-five test fragments (MGUH collections).

REMARKS: The fragmentary material can be assigned to *Coenholectypus* with some confidence on account of the narrow, uniserial adoral pore pairs, the tuberculation and the presence of buccal notches around the peristome [compare with the Texan Albian species *Coenholectypus ramatus* (Roemer, 1852), as illustrated by Smith and Rader 2009, fig. 18A–F]. However, the adoral interambulacral tubercles are much more numerous than in the Texas species and have more deeply embayed areoles. The material is also comparable with *Coenholectypus subcrassus* Peron and Gauthier, 1881, from the Coniacian of Algeria (N. Schlüter *et al*. 2025, figs 24, 25), but differs in the much denser concentration of adoral interadambulacral tubercles.



Text-fig. 15. Selected holectypids (A–C) and conulids (D–J) from Ivö Klack, southern Sweden. A–C – *Coenholectypus* sp., test fragments from oral surface (MGUH 35081–35083). D–J – *Globator schroederi* sp. nov.; D–F – paratype test (SMNH Ec37704) in apical (D), oral (E), and lateral (F) views; G–J – holotype test (SMNH Ec8550) in apical (G), oral (I), lateral (J) and posterior (H) views. All from the upper lower Campanian, Ivö Klack, southern Sweden. Scale bars equal: 10 mm (D–J) and 4 mm (A–C).

Family Conulidae Lambert, 1911
Genus *Globator* Agassiz, 1840

DIAGNOSIS: Ovate to subglobular Conulidae, with rounded ambitus. Apical disc with posterior genital plates broadly in contact. Aboral interambulacral plates with dense epistroma; lacking sunken pits and secondary spinelets. Periproct posterior, marginal to supramarginal (Smith and Wright 1999, p. 367).

TYPE SPECIES: *Globator nucleus* Agassiz, 1840, by original designation.

Globator schroederi sp. nov.
(Text-fig. 15D–J)

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DIAGNOSIS: *Globator* with elongated test; maximum width level with apical disc. Periproct very large, ambulacral pores of adapical surface set in shallow grooves.

TYPES: The specimen illustrated in Text-fig. 15G–J is the holotype (SMNH Ec8550), and the other illustrated specimen is paratype (SMNH Ec37704).

DERIVATION OF NAME: After Ane Elise Schrøder, in recognition of her work on Ivö Klack brachiopods.

MATERIAL: There are approximately 30 specimens in the SMNH collections.

DESCRIPTION: Test oval, length slightly greater than height. Oral surface strongly convex, apical surface weakly convex, summit flat. Rounded ambitus at or slightly above mid-point of height, maximum width level with apical disc. Ambulacra uniserial with undifferentiated pore pairs, uniserial above ambitus, weakly arcuate below. Large, teardrop-shaped periproct situated vertically on posterior margin. Peristome oblique, oval. Tuberculation very even, with slightly sunken primary tubercles surrounded by dense miliaries. Pore pairs of adapical surface set in narrow grooves

REMARKS: Material of this species has been labelled as *G. bleicheri* (Gauthier, 1889) in museum collections, a form from the undefined Upper Cretaceous of southern Iran, the Campanian of Tunisia and the Maastrichtian of Oman (see Smith 1995, pp. 186–188, for discussion and synonymy). *Globator schroederi* sp. nov. differs from *G. bleicheri* in its more elongated test, the maximum width of which is slightly more posterior. Additionally, the periproct is larger and the ambulacral pores are set in narrow grooves that are not visible on *G. bleicheri*.

Cohort Neognathostomata Smith, 1981
Order Cassiduloidea Claus, 1880
Family Nucleolitidae Agassiz and Desor, 1847
Genus *Phyllobrissus* Cotteau in Cotteau and Triger, 1859

DIAGNOSIS: Test small, subquadrate, with rounded anterior and truncate posterior margin. Lower surface concave, peristome anterior of centre, pentagonal, without bourrelets. Petals parallel and open distally, usually poorly developed. Periproct supramarginal, closer to posterior margin than apex, opening into a distinct sulcus (modified after Smith and Wright 2000, p. 398).

TYPE SPECIES: *Catopygus gresslyi* L. Agassiz, 1839, by subsequent designation of Cotteau and Triger (1860).

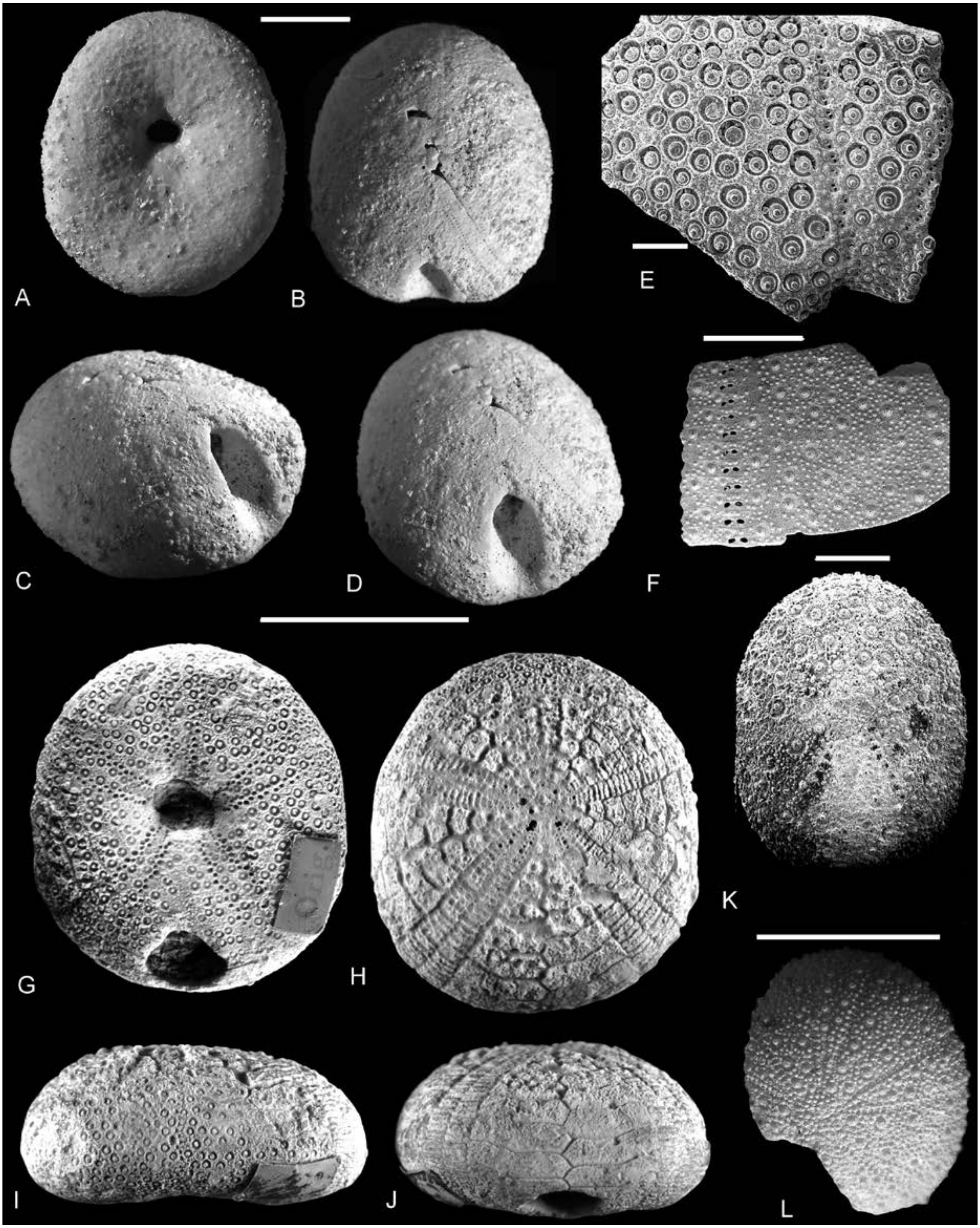
Phyllobrissus sp.
(Text-fig. 16A–E)

MATERIAL: A single test in the collection of Søren Bo Andersen, Aarhus, Denmark. Ten test fragments, upper lower Campanian, Ivö Klack (MGUH collections).

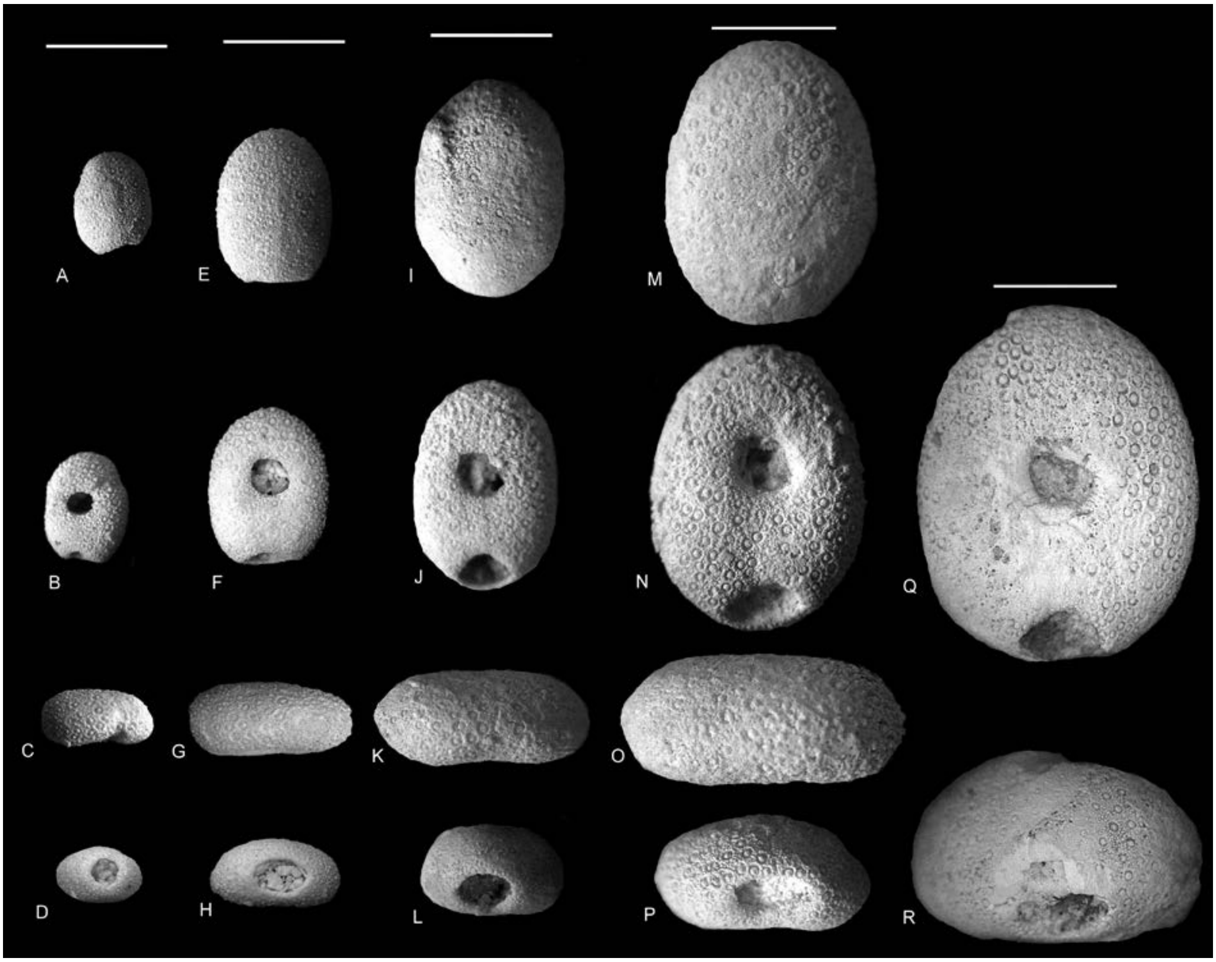
REMARKS: The single available entire test (Text-fig. 16A–D) has a rounded anterior margin and a truncate posterior margin. The oral surface is concave, and the peristome slightly anterior to the centre and pentagonal. A moderately deep anal sulcus is present. An adoral test fragment, probably belonging to the same species (Text-fig. 16E) does not possess buccal pores and has an angular peristomal margin. This is the only post-Cenomanian record of the genus.

Genus *Echinogalerus* König, 1825

DIAGNOSIS: Ovate pygaulids, rounded anteriorly and slightly pointed posteriorly, depressed in profile. Petals weakly developed, phyllodes composed of a



Text-fig. 16. Selected nucleolitids (A–E, G–K) and probable cardiasterids (F) from southern Sweden. A–E – *Phyllobrissus* sp. ; A–D – test in oral (A), apical (B), and oblique (C, D) views (collection of Søren Bo Andersen, Aarhus, Denmark); E – fragment of test adjacent to peristome (MGUH 35084). F – ?Cardiasteridae gen. et sp. indet., test fragment from lateral apical surface (MGUH 35085). G–K – *Echinogalerus peltiformis* (Wahlenberg, 1821); G–J – lectotype test (PMU Sk4), original of Wahlenberg (1821, pl. 3, figs 1–3), in oral (G), apical (H), lateral (I) and posterior (J) views; K – small test (MGUH 35086) in apical view. L – *Echinogalerus* sp., small test (MGUH 35092) in apical view. Provenance: A–F, K, L are from the upper lower Campanian, Ivö Klack, southern Sweden; G–J are from an unknown locality, probably upper lower Campanian, southern Sweden. Scale bars equal: 10 mm (A–D, G–J), 5 mm (L), 3 mm (E, F) and 2 mm (K).



Text-fig. 17. Ontogenetic series of tests (MGUH 35087–35091) of *Echinogalerus peltiformis* (Wahlenberg, 1821), in apical (A, E, I, M), oral (B, F, J, N, Q), lateral (C, G, K, O), and posterior (D, H, L, P, R) views. All specimens from the upper lower Campanian, Ivö Klack, southern Sweden. All scale bar equals 5 mm.

single series of pore pairs in each half ambulacrum. Periproct oval to subtrigonal, inframarginal.

TYPE SPECIES: *Echinites peltiformis* Wahlenberg, 1821, by subsequent designation of Lambert (1987).

Echinogalerus peltiformis (Wahlenberg, 1821
(Text-figs 16G–K, 17A–R)

*1821. *Echinites peltiformis* Wahlenberg, p. 50, pl. 3, fig. 1.
1976. *Echinogalerus peltiformis* (Wahlenberg); Reyment, p. 5, fig. 15.
1995. *Echinogalerus* sp.; Frerichs, p. 14, fig. 10.
2002. *Echinogalerus peltiformis* (Wahlenberg); Neumann *et al.*, p. 126, pl. 2.1–3, fig. 2C.
2023. *Echinogalerus peltiformis* (Wahlenberg); N. Schlüter and Schneider, p. 598, fig. 88.

DIAGNOSIS: *Echinogalerus* in which maximum test height is close to mid-length of test (Neumann *et al.* 2002, p. 127).

TYPE: The lectotype specimen, figured by Wahlenberg (1821), is in the Palaeontological Institute, Uppsala (PMU Sk4); it is refigured here (Text-fig. 16G–J).

MATERIAL: Ten tests and 25 test fragments from Ivö Klack. The PMU and SMNH collections contain very numerous specimens from across Skåne.

DESCRIPTION: The ontogeny of *Echinogalerus peltiformis* is illustrated in Text-fig. 17. The smallest individual (Text-fig. 17A–D) is 3.5 mm in length. The peristome and periproct are proportionately large, and the periproct is situated vertically on the posterior margin. With size increase (Text-fig. 17E–L), both peristome and periproct decrease in proportional size, and the periproct moves to a sub-ambital position on the posterior margin (Text-fig. 17J, N). Up to a length of 11 to 12 mm, the apical test surface is flat and parallel with the oral margin (Text-fig. 17C, G, K, O). At larger sizes, >14 to 15 mm (Text-figs 16K, 17Q, R), the apical surface is convex. The lectotype specimen is much more rounded in outline than the other individuals figured in this paper.

REMARKS: *Echinogalerus peltiformis* differs subtly from *E. bueltenensis* (Schlüter, 1902) from the Santonian of northern Germany in the position of the apex, which is at mid-length or slightly anterior to this in *E. peltiformis*, but anterior to mid-length in *E. bueltenensis* (Neumann *et al*. 2002).

Echinogalerus sp.
(Text-fig. 16L)

MATERIAL: A single incomplete test from Ivö Klack, southern Sweden (MGUH 35092).

DESCRIPTION: The single incomplete test is oval in apical outline and evenly convex adapically, its original length estimated at approximately 8 mm. The ambulacral and interambulacral tubercles are small, the areoles narrow and shallow and each is surrounded by two rings of miliaries, which sparsely cover the interradial and perradial surfaces. The adapical pores are small and do not form petals.

REMARKS: This form differs from *E. peltiformis* (Text-figs 16G–K, 17A–R) in which the adapical tubercles are fewer, larger and the areoles are wider and deeper.

Order Holasteroida Durham and Melville, 1957
?Family Cardiasteridae Lambert, 1917
Gen. et sp. indet.
(Text-fig. 16F)

MATERIAL: Three test fragments, from the 2011–2012 sampling at Ivö Klack, southern Sweden.

REMARKS: Thin-tested fragments from the lateral, apical surface of a large echinoid have evenly spaced, small, perforate, crenulate tubercles, surrounded by dense miliaries. On the ambulacral plates, pore pairs are oval and conjugate. This structure is typical of holasteroids and compares with material of *Cardiaster* spp. figured by Smith and Wright (2003, pl. 155).

DISCUSSION

Relative abundance of echinoid taxa

Because almost all the echinoid material is fragmentary, it is difficult to provide meaningful values of relative abundance. However, the commonest taxon in the residues is *Hirudocidaris botryoformis* sp. nov. (70%), followed by *Trochalosoma ivoensis* sp. nov. (15%) and *Trisalenia loveni* (5%); the other taxa each represent a few percent of the total. It is interesting that Mortensen (1932) viewed *Trisalenia loveni* as the commonest echinoid at Ivö Klack, presumably because he only saw complete tests.

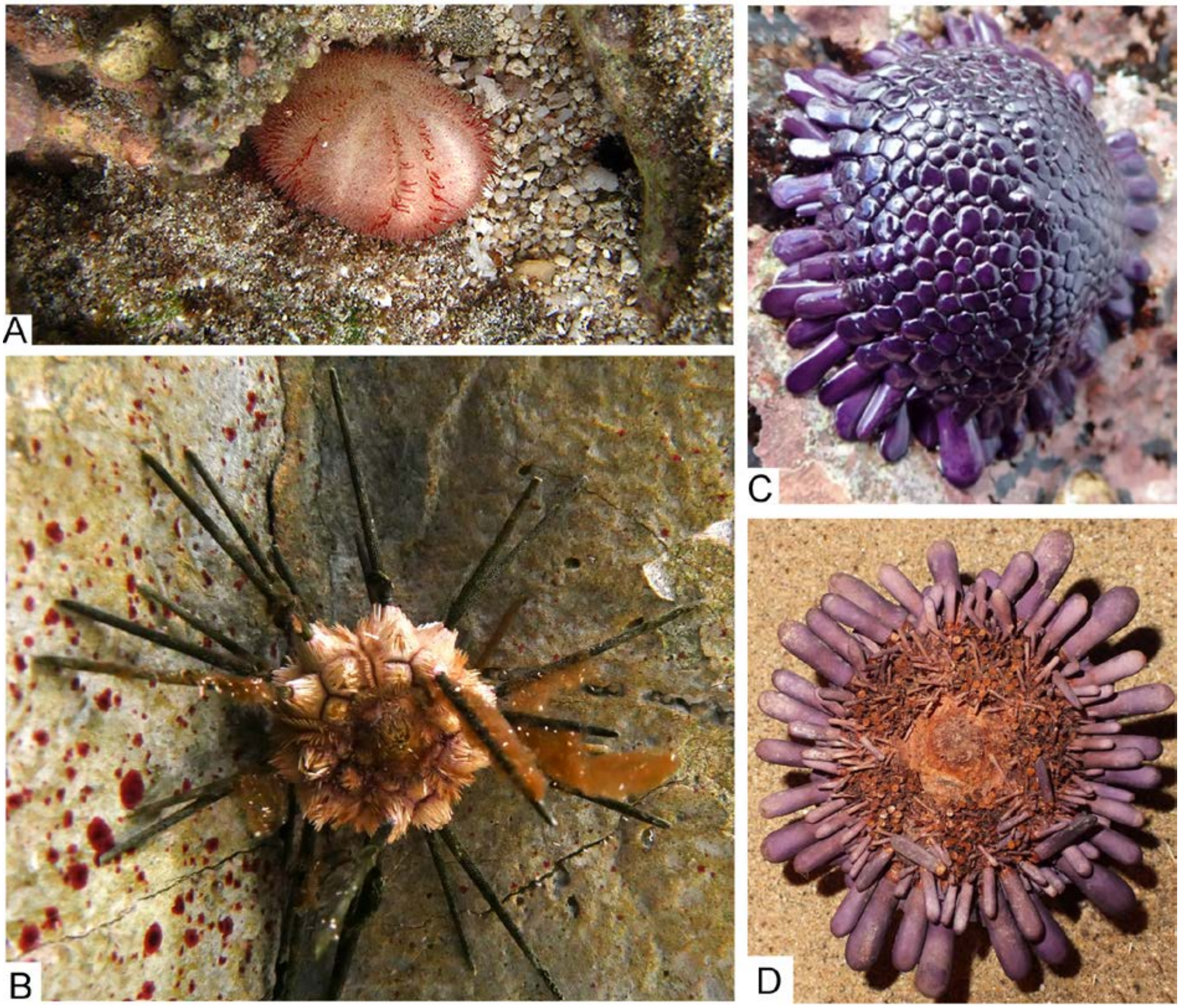
Modes of life and habitats of Ivö Klack echinoids

Cidaroids
[*Tylocidaris* (*T.*) *imbricata* sp. nov., *Hirudocidaris zeamays* sp. nov. and *H. botryoformis* sp. nov.]

Cidarids are not highly adapted to high-energy conditions, because their ambulacra have uniserial tube feet and they are unable to generate broad adoral regions bearing multiple tube feet for firm attachment to hard substrates. Additionally, the tube feet are small and have small discs which limit their capacity for both locomotion and attachment (Lawrence and Jangoux 2020). They are active predators and scavengers on diverse invertebrates and tend to occupy sheltered interstital habitats which afford protection from currents and predators. At Ivö Klack, they probably lived in crevices between boulders.

Diadematoids
(*Centrostephanus* sp.)

At the present day, *Centrostephanus* spp. are omnivorous nocturnal crevice-dwellers on rocky substrates down to about 100 m (Byrne and Andrew 2020). However, during the Cretaceous, morphologically similar forms are also found in soft-bottomed, deep-water chalk environments (Smith and Wright 1990; Jagt 2000; N. Schlüter and Schneider 2023). The Ivö Klack species is likely to have been an omnivorous, nocturnal crevice-dweller.



Text-fig. 18. Extant echinoids. A – *Echinoneus cyclostomus* (Linnæus, 1758), living individual on coarse sandy substrate. B – *Cidaris cidaris* (Linnæus, 1758), living individual wedged in crevice, attached by oral tube feet and braced by spines. Photo by Klaus Rudloff, Berlin, with permission. C, D – *Colobocentrus* (*Podophora*) *atratus* (Linnæus, 1758), living individuals, in apical (C) and oral (D) views, respectively; in C, attached to rocky substrate in intertidal zone, by numerous, powerful tube feet.

Saleniidae
(*Trisalenia loveni*, *Polysalenia* and *Salenia*)

At the present day, saleniids exclusively live in the deep sea, but in the Cretaceous they extended into shallow-marine habitats. The very broad adoral ambulacra of the Ivö Klack saleniids *Trisalenia* and *Polysalenia*, bearing numerous tube feet (Text-fig. 8C, D), were adapted for attachment to hard substrates, gripping with the tube feet (Mortensen 1932). They probably possessed P4 isopores, which are specialised for hard substrate attachment (Smith 1978). At Ivö Klack, they would have attached to gneiss boulders and fed on encrusting algae and epizoans. The smaller *Salenia areolata* (Text-figs 6C–E, 8E, F) has much narrower adoral ambulacra and was less highly specialised for high-energy settings.

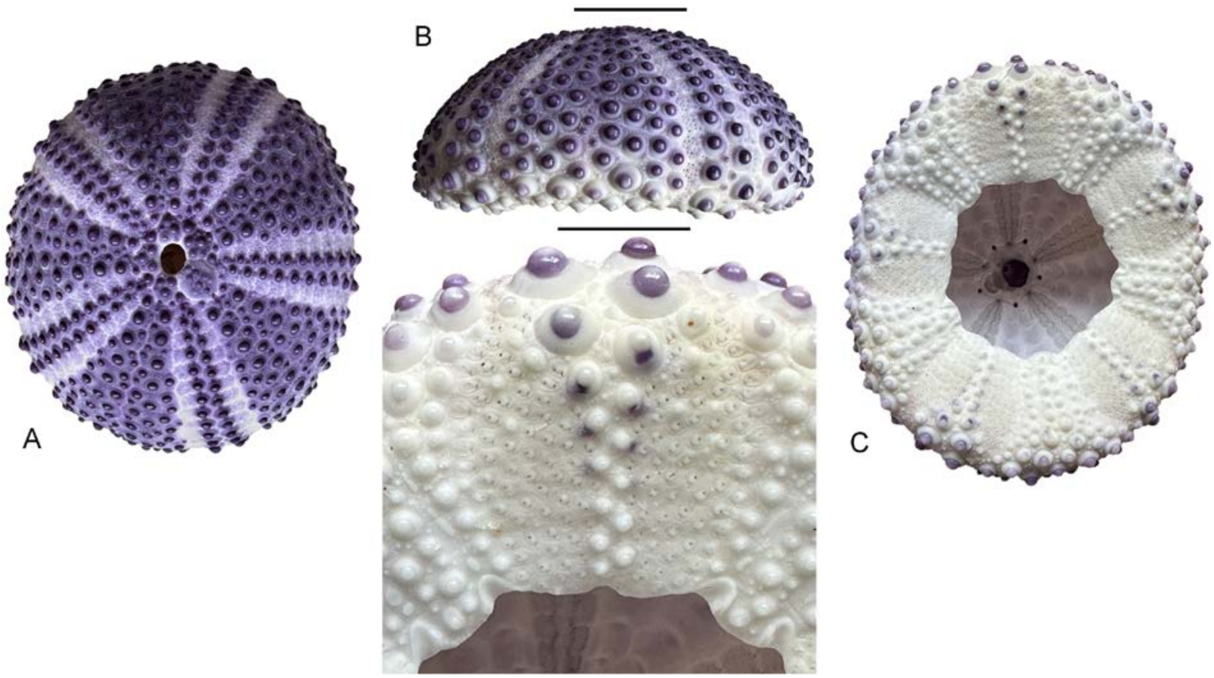
Phymosomatids
(*Trochalosoma ivoensis* sp. nov. and *Scaniosoma surlyki* gen. et sp. nov.)

The phymosomatids are extinct, but in the Cretaceous were widespread globally in a diversity of habitats. *Trochalosoma ivoensis* sp. nov. has very broad, triserial adoral ambulacra which carried numerous tube feet (Text-figs 12C, I, 13B), and flat, robust, spatulate primary spines (Text-fig. 11C). A similar species. *T. corneti*, which lived in slightly deeper water, had similar spines but only biserial adoral ambulacrals (Text-fig. 11B). Thus, *T. ivoensis* sp. nov. was probably able to attach very firmly to boulders. The spatulate spines, however, are generally interpreted as an adaptation to soft substrates as these are seen in species inhabiting the Chalk Sea, such as *T. taeniatum* (Text-fig. 11D, F). However, the ambital spines of *Trochalosoma ivoensis* sp. nov. are broadly similar (flattened, flanged) to the marginal spines of the living echinometrid *Colobocentrus* (*Podophora*) *atratus* (Linnæus, 1758) which is a specialist rock-dweller in very high-energy tropical environments (Santos and Flammang 2007; see below). The apical spines of *C.* (*P.*) *atratus* are short, very stout, and form an apical mosaic covering the upper surface (Text-fig. 18C, D). The apical spines of *Trochalosoma ivoensis* sp. nov. are unknown, but those present on *Trochalosoma corneti* (Text-fig. 11A) are short and fusiform. Flattened marginal spines also have the effect of streamlining the profile of the urchin, thus reducing the impact of wave action. It is therefore interesting that the flattened, spatulate spines which were used as “snowshoes” on soft, fine substrata like that of the Chalk Sea, were probably also ex-adapted for the completely different function of streamlining body profile on high-energy rocky coastlines.

Another feature of the spines of *Trochalosoma ivoensis* sp. nov. is the presence of a very broad milled ring on the spatulate primary spines (Text-figs 4G, 11C). The proximal surface of the milled ring is where the muscles controlling spine movement are inserted (Perricone *et al.* 2020), so this feature may well have served to improve the bracing ability of the spines.

Holectypoids (*Coenoholectypus* sp. and *Globator schroederi* sp. nov.)

Holectypoids are extinct, but their mode of life has been inferred in some detail from the construction of the test (Smith 1978, 1984), who used the Jurassic species *Holectypus depressus* as a case study. As *Coenholectypus* is very similar to *Holectypus*, comparable inferences can be drawn. The round, low-domed, flat-based test served to aid shallow burrowing, and prevented overturning in currents. The large periproct is suggestive of an unselective deposit feeder (bulky faeces), using its lantern to gather bulk sediment. At Ivö Klack, *Coenholectypus* would have inhabited shell sands



Text-fig. 19. Denuded test of *Colobocentrus* (*Podophora*) *atratus* (Linnæus, 1758) from Roches Noires, Mauritius, an intertidal species living in a very high-energy environment on basalt outcrops, in aboral (A), lateral (B) and adoral (C) views; D – enlargement of a single adoral ambulacrum. Note the broad adoral phyllodes bearing numerous pore pairs which provide high tenacity. Compare with Ivö Klack regular echinoids with similar adaptations to living in high-energy conditions on a rocky shoreline (Text-figs 8D, 9C, 14J). Scale bars equal: 10 mm (A–C) and 5 mm (D).

and gravels between exposed boulders, shallowly buried for part of the time.

Cassiduloids (*Phyllobrissus* sp. and *Echinogalerus peltiformis*)

Cassiduloids are shallow burrowers in coarser sand and gravel, ingesting the surrounding sediment and utilising the interstitial microfauna and organic matter found in it (De Ridder and Lawrence 1982). At Ivö Klack, these lived as shallow infauna in shell gravel.

Habitat reconstruction

The information provided above permits a reconstruction of echinoid habitats on the coast at Ivö Klack. These fall into three groups, as follows:

1. Species living epifaunally on gneiss boulders, by virtue of the development of numerous adoral phyllode tube feet which permitted secure attachment in a very high-energy environment (*Trisalenia loveni*, *Trochalosoma ivoensis* sp. nov., *Scaniasoma surlyki* gen. et sp. nov.). Although more highly specialised than the echinoids at Ivö Klack (flattened tessellation of aboral spines; Text-fig. 18C) comparisons can be made with the extant Indian Ocean species *Colobocentrotus* (*Podophora*) *atratus* (Text-figs 18C, D, 19) which lives attached to boulders in the high-energy intertidal zone (Santos and Flammeng 2008). This species has exceptional tenacity, enabled by the very broad phyllodes (quinquegeminate) which bear a total of approximately 600 tube feet (Text-fig. 19, Table 1). In contrast, *Trisalenia loveni* and *Trochalosoma ivoensis* sp. nov. each possess about 300 adoral tube feet (tri- and quadrigeminate) in their broad phyllodes (see Text-figs 8D and 12C), more than the number recorded for any extant regular echinoids other than *C.* (*P.*) *atrata*. The ratio of the breadths of the adoral interambulacra and ambulacra adjacent to the peristome may provide a useful proxy for the tenacity of fossil echinoids (Table 1). In *Trisalenia loveni*, *Trochalosoma ivoensis* sp. nov. and *Scaniasoma surlyki* gen. et sp. nov. this ratio exceeds a value of 2 (i.e., they have broad adoral ambulacra and narrow interambulacra), as compared with 3.2 in *C.* (*P.*) *atratus*. In contrast, saleniids and phymosomatids from low-energy deeper-water Cretaceous chalks have ratios of 0.8–1.15 (Table 1).

2. Epifaunal species with low tenacity living interstitially in rather more protected habitats, between boulders, in crevices (cidarids, *Centrostephanus* sp.). The living *Cidaris cidaris* (Text-fig. 18B) is shown wedged into a crevice, attached by tube feet and possibly braced by the long spines.

3. Infaunal, shallow burrowers in shell sands and gravels (*Coenholectypus*, *Globator*, *Phyllobrissus* and *Echinogalerus*). These are comparable with the extant *Echinoneus cyclostomus* (Text-fig. 18A), a living member of the Echinonoida, which burrows in shell gravel.

Comparisons with contemporaneous chalk faunas

The most striking difference between the Ivö Klack echinoid fauna and that found in deeper-water chalks is the virtually complete absence of holasteroids and spatangoids. There are probably two reasons for their absence; firstly, the high-energy environment, which would continually re-expose and break up thin-tested burrowers, and secondly, the very coarse substrates. Holasteroids and spatangoids were able to colonise shallow-water sandy facies successfully during the Cretaceous, as in the Cenomanian at Wilmington, Devon (Smith *et al.* 1988), but are not present in coarser sediments.

Taxon	Interambulacral-ambulacral oral ratio	Number of oral tubefeet/pore pairs	Number of adoral pore rows	Age/location
Colobocentrotus (*Podophora*) *atratus*	3.2	600	5	present day, Indian Ocean
Gauthieria princeps	0.8	c. 150	2	Maastrichtian, chalk, UK
Gauthieria spatulifera	1.15	c. 150	2	Santonian chalk, UK
Phymosoma granulosum	0.9	c. 150	2	Campanian chalk, UK
Polysalenia notabilis	1.4	?	?	Campanian, Ivö Klack, Sweden
Salenia petalifera	1.0	c. 100	2	Cenomanian chalk, UK
Scaniosoma surlyki	2.55	300	3–4	Campanian, Ivö Klack, Sweden
Trisalenia loveni	2.15	300	3–4	Campanian, Ivö Klack, Sweden
Trochalosoma ivoensis	2.09	c. 250	3	Campanian, Ivö Klack, Sweden

Table 1. Characteristics of adoral test construction of present day and Cretaceous regular echinoids. Taxa from high-energy environments possess broader adoral ambulacrals, greater numbers of adoral pore pairs and fewer columns of these than those living in lower-energy, deeper water palaeoenvironments.

Of the genera present at Ivö Klack, four are very closely related to species living in deeper-water (200 m+), penecontemporaneous chalk environments. The two species of *Hirudocidaris* at Ivö Klack are closely related to, and probably descendants of, the long-ranged (Cenomanian–Campanian) species, *H. hirudo*. *Tylocidaris imbricata* sp. nov. is also a possible descendant of a chalk-dwelling species. The *Centrosephanus* sp. is similar to *C. fragilis*, a Coniacian–Campanian species found in the chalk facies of the Anglo-Paris Basin. Finally, *Trochalosoma ivoensis* sp. nov. belongs to a genus which is present in Campanian and Maastrichtian chalks, siliceous chalks and biocalcarenitic limestones in Germany, Denmark, Poland, Belgium and the Netherlands.

However, it is not really possible to comment usefully about onshore-offshore migration patterns, because the Ivö Klack fauna is really a single snapshot of echinoid diversity in an environment which is not usually preserved. Broadly comparable rockground facies, as found in the Cenomanian–Turonian interval in the Czech Republic (Žítt *et al*. 2006) yield only a limited echinoid fauna, dominated by cidarids.

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