

# Cirripedia (Crustacea) from the Upper Cretaceous (Campanian) of the Kristianstad Basin and Vomb Trough, southern Sweden

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## ABSTRACT:

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The cirripede faunas from the Cretaceous (Campanian) of Skåne, southern Sweden, are reviewed and a total number of 31 species are recorded, the majority of which come from the upper lower Campanian (*Belemnelloamax mammillatus* Zone) of Ivö Klack, in the Kristianstad Basin. A number of new taxa are described, including the family Angulalepadidae and genus *Angulalepas* (type species *Pollicipes nilssoni* Steenstrup, 1839), as are *Zeugmatolepas alifera* sp. nov., *Arcuatoscalpellum carlssoni* sp. nov., *Regioscalpellum ahlbergi* sp. nov., and *Epibrachylepas lineatum* sp. nov. *Pollicipes angelini* Darwin, 1851, is placed in the genus *Solidoscalpellum* Gale, 2025, and *Pollicipes undulatus* Steenstrup, 1839 in the genus *Arcuatoscalpellum* Gale, 2015. The palaeoecology of the rocky shoreline cirripede fauna from Ivö Klack is discussed, and taxa are assigned to 6 microniche habitats, determined largely by the degree of turbulence and the nature of the substrates.

**Key words:** Cirripedes; Cretaceous; taxonomy; palaeoecology; southern Sweden.

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## INTRODUCTION

The Cretaceous deposits of Skåne, southern Sweden were deposited along the north-eastern margin of the Chalk Sea in a region of NW-SE trending horsts on the southern margin of the Baltic Shield (Text-fig. 1A). An upper lower Campanian transgression resulted in the formation of rocky shorelines which were buried by bioclastic calcarenites, calcirudites and basement-derived debris. Locally, in the Kristianstad Basin, these sediments have yielded highly diverse shallow marine vertebrate and invertebrate faunas, best known from Ivö Klack, which were

reviewed by Surlyk and Sørensen (2010), Sørensen and Surlyk (2015), and Surlyk and Sørensen (unpublished manuscript). Campanian deposits in both the Kristianstad Basin and the Vomb Trough (Text-fig. 1) have yielded cirripedes (Steenstrup 1839; Withers 1935; Carlsson 1953; Gale and Sørensen 2014, 2015) which represent the best known and most diverse shallow water Cretaceous assemblages known from anywhere in the world.

In 1839, Johannes Japetus Steenstrup described 4 new species of cirripedes from the Campanian of Skåne – *Pollicipes undulatus* (from Ivö Klack), *Pollicipes nilssoni* (from Ignaberga), *Pollicipes solidulus* (from



Kjuge) and *Pollicipes validus* (from unknown localities). Darwin (1851) recorded 4 species as coming from Skåne, and synonymised Steenstrup's *P. undulatus* with his *P. solidulus*. Darwin also erected *Pollicipes Angelini* partly on the basis of a scutum from Kjuge, in the Kristianstad Basin, collected by N.P. Angelin, a professor in Lund University, and erected *Scalpellum semiporcatum* on the basis of a scutum from Köpinge.

In 1932, Brünnich Nielsen (Copenhagen) presented a large collection of Campanian cirripedes from Ivö Klack and Ignaberga in Skåne to the British Museum (Natural History) (Withers 1935, p. 6). These were described by Withers in 1935, who erected 4 species of *Calantica* (*Scillaelepas*): *C. (S.) scanica*, *C. (S.) caelata*, *C. (S.) ifoensis*, *C. (S.) angulata* and an early balanomorph, *Catomerus* (*Pachydiadema*) *cretacea* from Ivö Klack. Gale and Sørensen (2015) provided an exhaustive account of the taxonomy of a diverse cirripede fauna from the upper lower Campanian (*Belemnellocamax mammillatus* Zone) of Ivö Klack, in the Kristianstad Basin, based on residues from large samples from one horizon. They recorded a total of 28 species, of which 7 were new, and assigned species referred by Withers (1935) to *Calantica* (*Scillaelepas*) to different genera. However, they did not include a number of taxa previously described from various localities in the Cretaceous of Skåne, because these were not present in the Ivö Klack samples, including *Pollicipes nilsoni*, *Pollicipes undulatus* and *Pycnolepas ignabergensis* Carlsson, 1953. The author visited collections in the SMNH (Stockholm) and PMU (Uppsala) in March 2025, and the Zoological Collections in Lund in November 2025, and photographed or borrowed material in these collections. This included a number of new taxa, described here, together with a review of all the Campanian cirripedes from Skåne. Unfortunately, some of the material recorded and figured by Carlsson (1953) could not be found.

## STRATIGRAPHY AND LOCALITIES

The stratigraphy of the Upper Cretaceous deposits of the Kristianstad Basin, southern Sweden (Text-figs 1B, 2), were reviewed and described by Christensen (1975) and dated using belemnite faunas. The localities yielding cirripedes mostly fall within the upper lower Campanian *Belemnellocamax mammillatus* Zone. The most important locality is Ivö Klack, where calcarenites and calcirudites of the *B. mammillatus* Zone age were deposited on a rocky shoreline of Precambrian crystalline basement. These have yielded abundant

and diverse cirripedes (Gale and Sørensen 2014, 2015). The locality of Ignaberga includes coarse calcarenites deposited along the Nävlinge Åsen horst limiting the Kristianstad Basin towards the south-west, represents a slightly offshore setting of the same age as Ivö Klack, and has provided a more limited cirripede assemblage. Historical localities mentioned in the text but no longer accessible include: Söndraby (Text-fig. 1B) which showed fine quartz sand overlain by 2 m of coarse calcarenite including clasts of basement rocks (Christensen 1975, p. 15); Tullstorp formerly exposing calcarenites containing scattered clasts of basement rocks (Finn Surlyk, pers comm 2025); and Kjuge, which has yielded historical material, and exposing both upper lower and lower upper Campanian age calcarenites (Christensen 1975, p. 14). A few of the species listed by Carlsson (1953) come from localities identified by Christensen (1975) as being of lower upper Campanian age (*Belemnellocamax balsvikenensis* Zone); these include Barnakälla, Ballingslöv, and Hanaskog.

The Vomb Trough, situated to the south of the Kristianstad Basin in the Fennoscandian Border Zone (Text-fig. 1C), has yielded less cirripede material. The most important locality is Köpinge (Text-fig. 1) from which Carlsson (1953) listed 5 species. Christensen (1986, p. 9) reviewed the locality, and dated most of the Köpinge sandstone to the middle upper Campanian on the basis of belemnite and ammonite faunas (see also Kennedy and Christensen 1997). Carlsson (1953) also suggested that material coming from Ystad actually referred to the Köpinge localities.

## NATURE AND PALAEOECOLOGY OF THE CIRRIPEDE ASSEMBLAGES

### The marginal marine Kristianstad Basin fauna

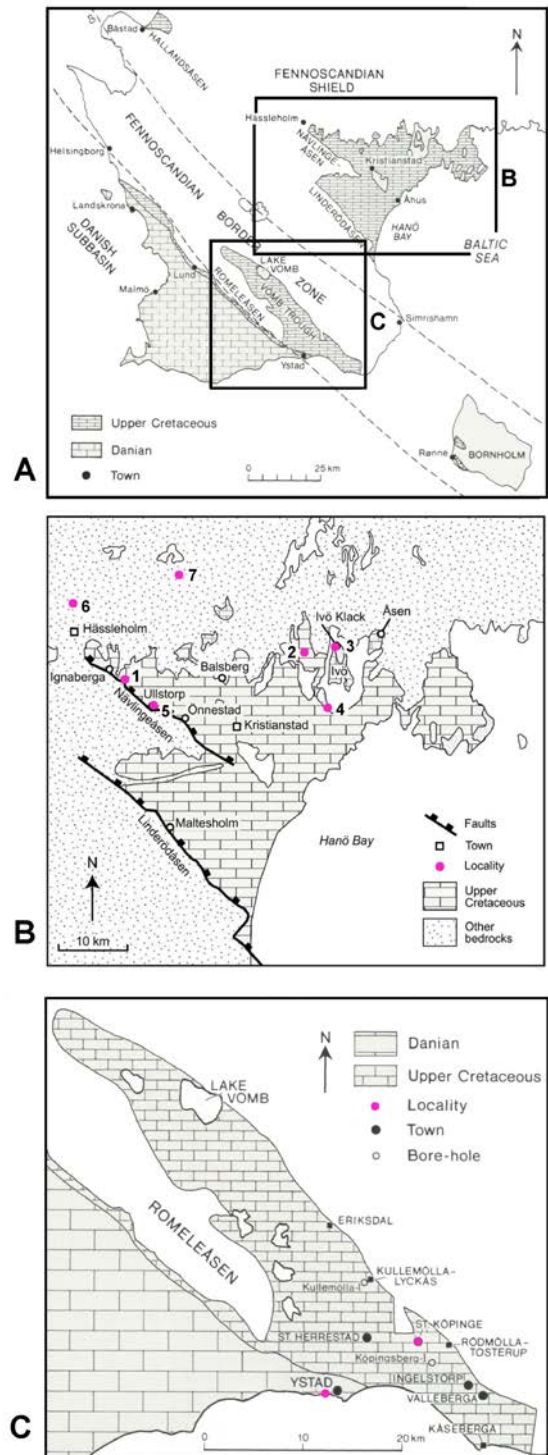
The cirripede fauna from the early Campanian rocky coast at Ivö Klack is remarkable in both its diversity and composition (Gale and Sørensen 2014, 2015). There are relatively few Cretaceous cirripede assemblages known from rocky shoreline deposits, and these are all dominated by a single species. Zullo *et al.* (1987) described a shallow marine assemblage from the Campanian of Arkansas, USA, yielding over 3,000 valves of a single species (*Brachylepas americana* Zullo, Russell and Mellen, 1987) and 9 valves of a scalpellid (*Virgiscalpellum* sp.). From the marginal lower Turonian of Kank, in the Czech Republic, Koči *et al.* (2016) recorded 1,300 valves

of a single species (*Myolepas reussi* Koči, Kočova Veleská, Buckeridge and Jagt, 2016). Kočova Veleská *et al.* (2015) recovered 95 valves of a single taxon (*Capitulum sklenari* Kočova Veleská, Koči, Collins and Gale, 2015) from lower Turonian rocky shore deposits at Velim, Czech Republic. There are additional records of cirripedes from these localities, including abundant valves of *Cretiscalpellum glabrum* (Roemer, 1841), *Jagtscaepellum striatum* (Darwin, 1851) and *Diotascaepellum angustatum* (Geinitz, 1843) (see Koči and Kočová Veselská 2012a, b, 2013a–c; Kočová Veselská *et al.* 2014). However, the faunas are not very diverse.

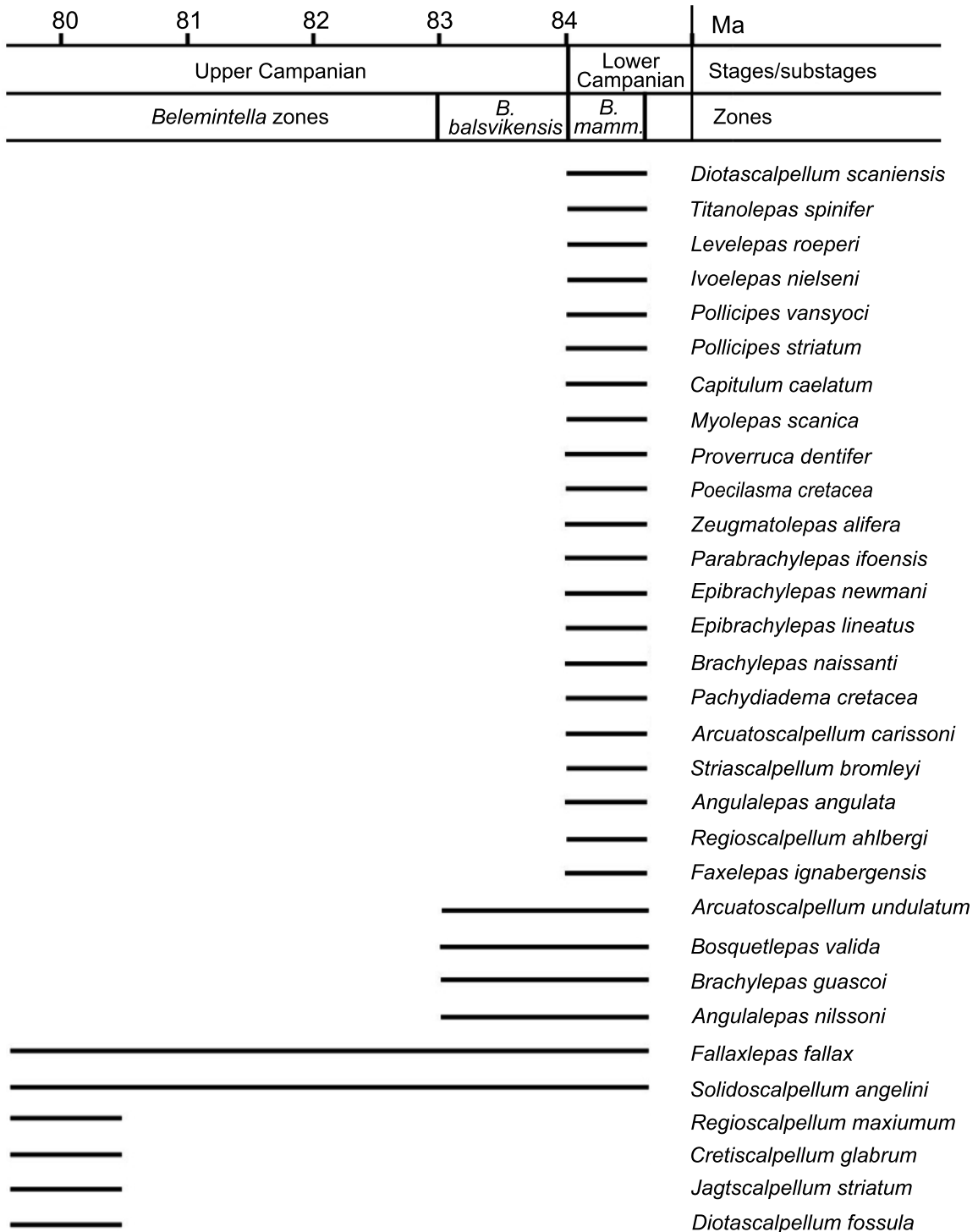
In striking contrast, a single Swedish lower Campanian locality, Ivö Klack, has yielded a total of 24 species of cirripedes, of which ten can be described as common to abundant (Gale and Sørensen 2015). There are a number of factors which can partly explain this. Firstly, the diversity of microhabitats at Ivö Klack was remarkable, as described by Schröder *et al.* (2019) for brachiopods, including: 1) protected dysphotic environments between and beneath boulders; 2) relatively low-energy shell gravel substrates between boulders; 3) semi-exposed surfaces of boulders; and 4) fully exposed surfaces of boulders with high water turbulence. Secondly, the preservation of the material is remarkably good, with rapid burial and little diagenesis which permits ready identification to species level.

It is impossible to meaningfully compare the Ivö Klack cirripede fauna with that from other Skåne localities, because most no longer exist and sampling for smaller taxa from them is therefore not possible. However, the presence of 4 larger Ivö Klack species in collections from localities of both the *B. mammillatus* and *B. balsvikensis* zones in the Kristianstad Basin (Text-fig. 2; data from Carlsson 1953) makes it likely that the diverse Ivö Klack cirripede fauna had a greater geographical and stratigraphic distribution. It is not known how long the diverse Ivö Klack-type fauna survived in Skåne. However, the presence of diverse myolepadids (*Bosquetlepas* spp.) and brachylepadids [*Brachylepas guascoi* (Bosquet, 1857), *Epibrachylepas smeetsi* (Bosquet, 1857)] in the shallow-water facies of the Maastrichtian of the Maastricht district, the Netherlands (Withers 1935) indicates that a number of these forms survived elsewhere until the end of the Cretaceous.

Cirripedes are mostly sessile, benthonic, extension-feeding planktivores, preying on small to moderate size plankton, mainly crustaceans. Analysis of the Ivö Klack fauna indicates the presence of a number of distinct elements in the fauna:



Text-fig. 1. Maps of southern Sweden to show Cretaceous localities. A – General geological map, to show positions of Kristianstad Basin and Vomb Trough. B – Kristianstad Basin, with localities after Christensen (1975). Explanations: 1 – Ignaberga; 2 – Söndrabý; 3 – Ivö Klack; 4 – Kjúge; 5 – Ullstorp; 6 – Tullstorp; 7 – Västra Olinge. C – Vomb Trough, after Christensen (1975). The localities of Köpinge and Ystad have yielded cirripede material.



Text-fig. 2. Stratigraphic distribution of Cretaceous cirripedes from Skåne, based on records from Carlsson (1953), Gale and Sørensen (2014, 2015) and examination of museum collections. Timescale from Gale *et al.* (2020). The majority of species are only known from the upper lower Campanian (*Belemnellocamax mammillatus* Zone) rocky shoreline of Ivö Klack, which is the only locality from which smaller taxa have been picked from residues. Some of the larger species range up into the lower upper Campanian (*Belemnellocamax balsvikensis* Zone), also probably representing a rocky coastal habitat. The middle upper Campanian (*Belemnitella* zones) fauna is known only from the Köpings Sandstone at Köpings in the Vomb Trough represents a deeper water environment and is very similar to contemporaneous cirripede faunas from the chalk facies in Germany and England.

Group A: The large (maximum dimensions 50–60 mm), very robust sessile taxon *Pachydiadema cretacea* (Text-fig. 3A, B) had a low, conical profile (Text-fig. 3B) was adapted to living attached to boulders in exposed high-energy conditions (habitat 4, above; Gale and Sørensen 2014, 2015). This can be directly compared with the living primitive balanomorph *Catomerus polymerus* (Darwin, 1854) which lives below mid-tide level on rocky shorelines of SE Australia (Anderson 1983), which has a similar morphology (Text-fig. 3C), although the plates are thinner than those of *P. cretacea*.

Group B: Includes species adapted to high-energy conditions, including strong surf, which colonise cracks and depressions in rocky intertidal environments. At Ivö Klack, these include species of the extant genera *Pollicipes* Leach, 1817 and *Capitulum* Gray, 1825 (Text-fig. 3D, F); the ecology of the living species of *Pollicipes* was described in detail by Barnes (1996). *Pollicipes pollicipes* Gmelin, 1789 is shown crowded in a rocky depression (Text-fig. 3E) and *Capitulum mitella* (Linnæus, 1858) wedged into a crack. These probably represent habitat 3 (above). Additionally, there are robustly constructed pedunculate genera present in the Campanian of Skåne which became extinct by the end of the Cretaceous, including the Myolepadidae (*Myolepas* Gale in Gale and Sørensen, 2015; *Bosquetlepas* Gale in Gale and Sørensen, 2015). *Myolepas* was a specialist high-energy dweller with unique retractor muscles, which enabled shortening of the peduncle and rapid closure of the occludent aperture (Gale and Sørensen 2015) and this probably occupied a habitat similar to those of *Pollicipes* and *Capitulum*.

Group C: small (<10 mm maximum dimension) to medium-sized sessile forms (the extinct brachylepadids), moderately robust (Text-fig. 3H) to weakly constructed (Text-fig. 3I, J), which lived attached to shells and pebbles in lower-energy environments (habitats 1, 2). The more robust *Brachylepas guascoi* (Text-fig. 3H) was probably able to live in higher energy conditions.

Group D: small, sessile, asymmetrical cirripedes in which the moveable tergum and scutum form an opercular lid, represented at Ivö Klack by *Proverruca dentifer* Gale in Gale and Sørensen, 2015; see Text-fig. 4A). *Proverruca* Withers, 1914 is extinct, but the morphologically convergent Cretaceous to present day *Verruca* Schumacher, 1817 (Text-fig. 4B; Gale 2015) uses its cirri to capture small benthos (habitats 1, 2, above).

Group E: Pedunculate, delicately constructed taxa which lived in lower energy environments (between

boulders, on shell gravels, attached to pebbles, algae, colonial benthos, shells), including scalpellids (Text-fig. 4E) and the extinct titanolepadids (Text-fig. 4C, D). Ecologically equivalent extant scalpellids (Text-fig. 4F) mostly live in deeper water, but *Scalpellum scalpellum* (Linnæus, 1758) extends up to low water from 400 m (habitats 1, 2, above).

Group F: Small lepadids which live attached to the surfaces of decapod crustaceans (Text-fig. 4H; Chan *et al.* 2009). Very rare, but represented at Ivö Klack by *Poecilasma cretacea* Gale, 2025 (Text-fig. 4G).

### The Köpinge (Vomb Trough) fauna

The only known middle upper Campanian fauna from Skåne comes from Köpinge in the Vomb Trough (Text-fig. 1C), where the glauconitic, calcareous Köpinge Sandstone (Christensen 1986) has yielded a diverse cirripede fauna typical of contemporaneous mid-upper Campanian basinal chalks (Text-fig. 2), including *Fallaxlepas fallax* (Darwin, 1851), *Diotascalpellum fossula* (Darwin, 1851), *Regioscalpellum maximum* (J. de C. Sowerby, 1829), *Cretiscalpellum glabrum* and *Jagtscalpellum striatum*. *Solidoscalpellum angelini* comes close to *S. cylindraceum* (Darwin, 1851) from the UK Chalk. It is likely that this represents a significantly deeper water facies than that represented by the *Belemnellocomax mammillatus* and *B. balsvikensis* zones in the Kristianstad Basin.

### Institutional abbreviations

MGUH – Natural History Museum, Copenhagen, Denmark.

MZLU – Lund Biological Museum, Zoological Collections, Lund, Sweden.

NHMUK – The Natural History Museum, London, UK.

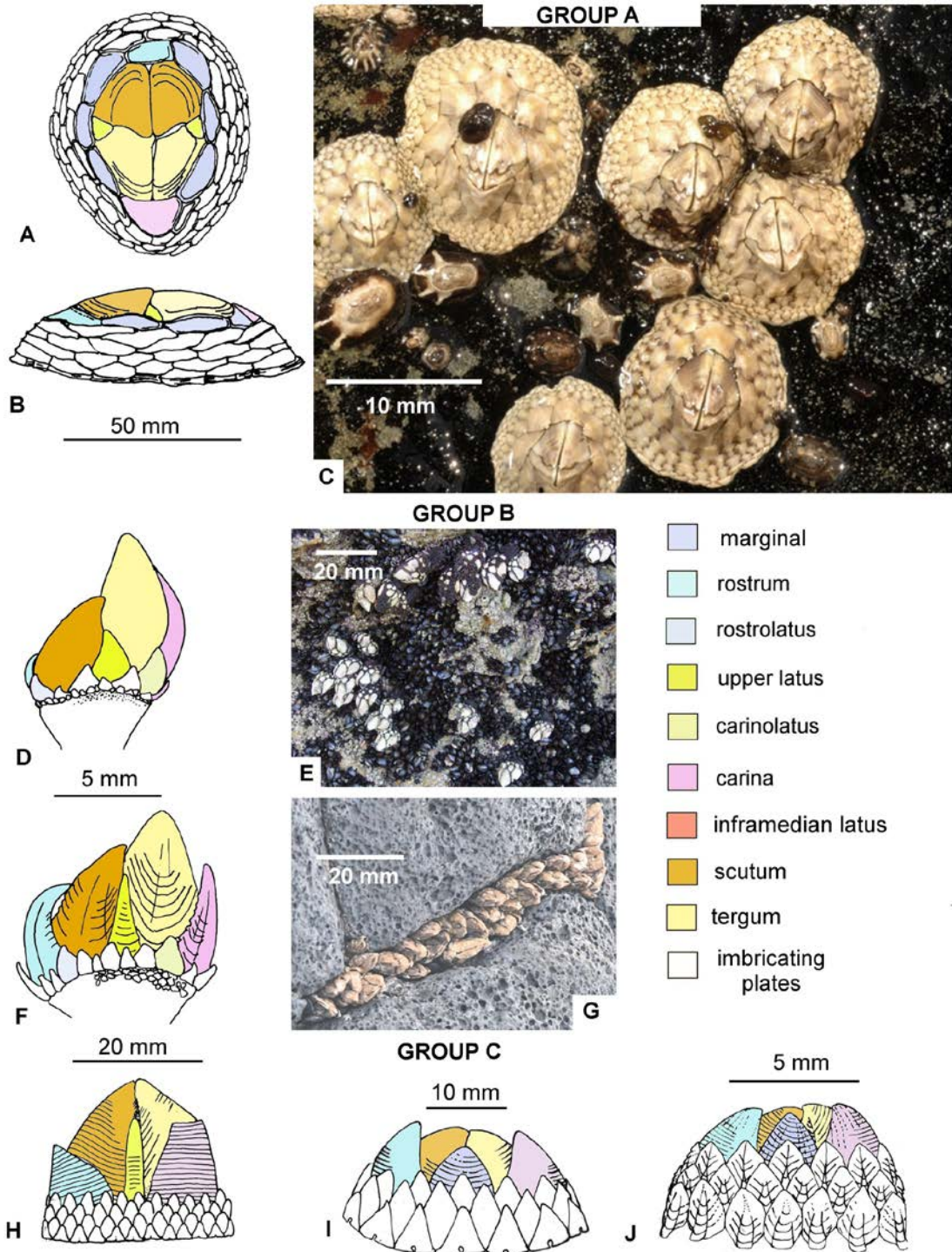
PMU – Uppsala University, Uppsala, Sweden.

SMNH – Swedish Museum of Natural History, Stockholm, Sweden.

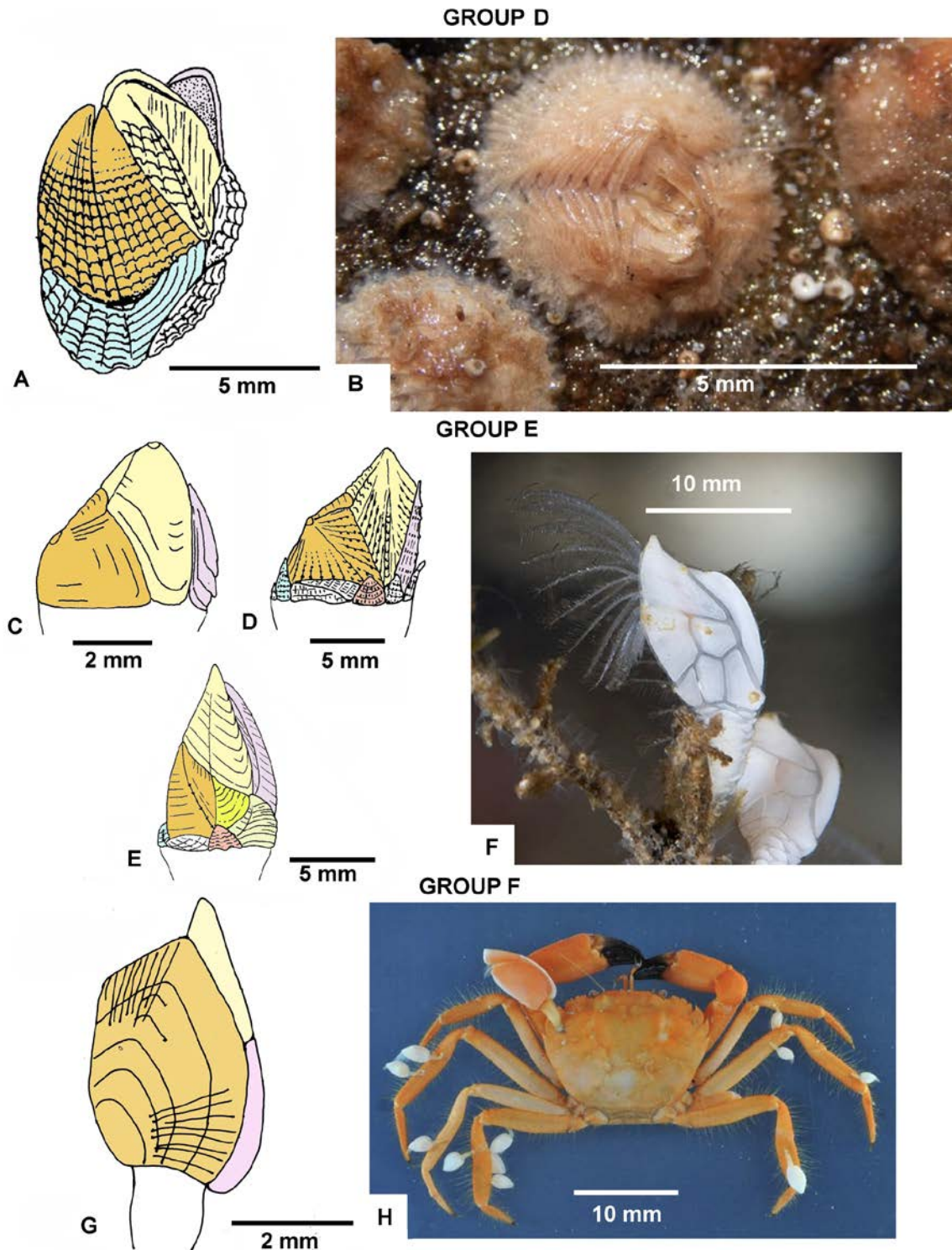
### SYSTEMATIC PALAEOLOGY

Order Archaeolepadoromorpha Chan, Dreyer, Gale, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall and Høeg, 2021

DIAGNOSIS: Robust forms, in which the capitulum is formed of 6–10 plates; the peduncle is typically armoured with eight to ten columns of broad, strongly imbricating plates.



Text-fig. 3. Ecological groups from the upper lower Campanian of Ivö Klack and their extant equivalents. A–C – Group A, large balanomorphs living in highly exposed, high-energy conditions, attached to rocks; A, B – *Pachydiadema cretacea* (Withers, 1935), Ivö Klack, in apical (A) and lateral (B) views; C – *Catomerus polymerus* Darwin, 1855, present day, SE Australia. D–G – Group B, forms adapted to high-energy rocky coasts, but tending to inhabit crevices or depressions; D – *Pollicipes vansyoci* Gale in Gale and Sørensen, 2015, Ivö Klack; E – *Pollicipes pollicipes* Gmelin, 1789, present day, west coast of Morocco, north of Agadir; F – *Capitulum caelatum* (Withers, 1935), Ivö Klack; G – *Capitulum mitella* (Linnaeus, 1758), present day, Hong Kong, China. H–J – Group C, small to very small sessile brachylepadids, no modern equivalents; H – *Brachylepas guascoi* (Bosquet, 1857), Ivö Klack; I – *Parabrachylepas ifoensis* (Withers, 1935), Ivö Klack; J – *Epibrachylepas newmani* Gale in Gale and Sørensen, 2014, Ivö Klack.



Text-fig. 4. Ecological groups from the upper lower Campanian of Ivö Klack and their extant equivalents. A, B – Group D, small, sessile asymmetrical taxa living subtidally attached to pebbles, shells or algae; A – *Proverruca dentifer* Gale in Gale and Sørensen, 2015, Ivö Klack; B – *Verruca* sp., present day, Bangladesh. C–F – Group E, small, delicate pedunculate species living in sheltered habitats; C – *Levelepas roeperi* Gale in Gale and Sørensen, 2015, Ivö Klack; D – *Titanolepas spinifer* Gale in Gale and Sørensen, 2015, Ivö Klack; E – *Diotascalpellum scaniensis* (Gale in Gale and Sørensen, 2015), Ivö Klack; F – *Weltnerium nymphocola* (Hoek, 1883), present day, Norway. G, H – Group F, species occurring as ectoparasites on crustaceans; G – *Poecilasma cretacea* Gale, 2025, Ivö Klack; H – *Poecilasma kaempferi* (Darwin, 1852), present day, Japan.

REMARKS: The Archaeolepadomorpha is a diverse assemblage of Jurassic and Cretaceous cirripedes which includes the families Archaeolepadidae, Myolepadidae, Stramentidae and Angulalepadidae nov. They are characterised by the small number (6–10) of robust capitular plates, typically including paired terga, scuta, a carina and a rostrum. However, secondary loss of capitular lateral plates occurred in numerous lineages (e.g., the Virgiscalpellinae Gale, 2020), so there is always a degree of uncertainty as to whether any 6-plated cirripede is either plesiomorphic or derived paedomorphically from a multi-plated ancestor.

#### Family Angulalepadidae nov.

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DIAGNOSIS: Six-plated, robust cirripedes in which the beak-like carina is broad, curved ventrally, and bears a central ridge; lateral surfaces angled; rostrum similar in morphology to carina; scutum low, triangular, tergum sub-rhombic, with long, straight carinal margin, low, rounded apex and convex occludent margin. External sculpture of weak, discontinuous apicobasal ridges.

INCLUDED GENERA: *Angulalepas* gen. nov.

REMARKS: The robust, 6-plated capitular structure places these forms in the Archaeolepadomorpha, but the distinctive shapes of the scuta, terga and carinae are very different to taxa placed within the Stramentidae, Archaeolepadidae, and Myolepadidae.

#### Genus *Angulalepas* nov.

urn:lsid:zoobank.org:act:178D5477-D1BC-4764-A1A1-F1AF438B51F2

DIAGNOSIS: As for family.

TYPE SPECIES: *Pollicipes nilssoni* Steenstrup, 1839.

DERIVATION OF NAME: With reference to the strongly angled lateral surfaces of the carinae.

INCLUDED SPECIES: *Calantica (Scillaelepas) angulata* Withers, 1935.

*Angulalepas nilssoni* (Steenstrup, 1839)  
(Text-figs 5A–C, 6A–I, O–Q, 7C, 8N, O)

part 1839. *Pollicipes nilssoni* Steenstrup, p. 401, pl. 4, figs 20, 20\* only.

part 1851. *Pollicipes nilssoni* Steenstrup; Darwin, p. 52, pl. 11b, c only.

1854. *Pollicipes nilssoni* Steenstrup; Darwin, p. 635.

1935. *Calantica (Scillaelepas) nilssoni* (Steenstrup); Withers, p. 111, pl. 4, fig. 13.

1942. *Calantica (Scillaelepas) nilssoni* (Steenstrup); Carlsson, p. 4, pl. 1, fig. 3.

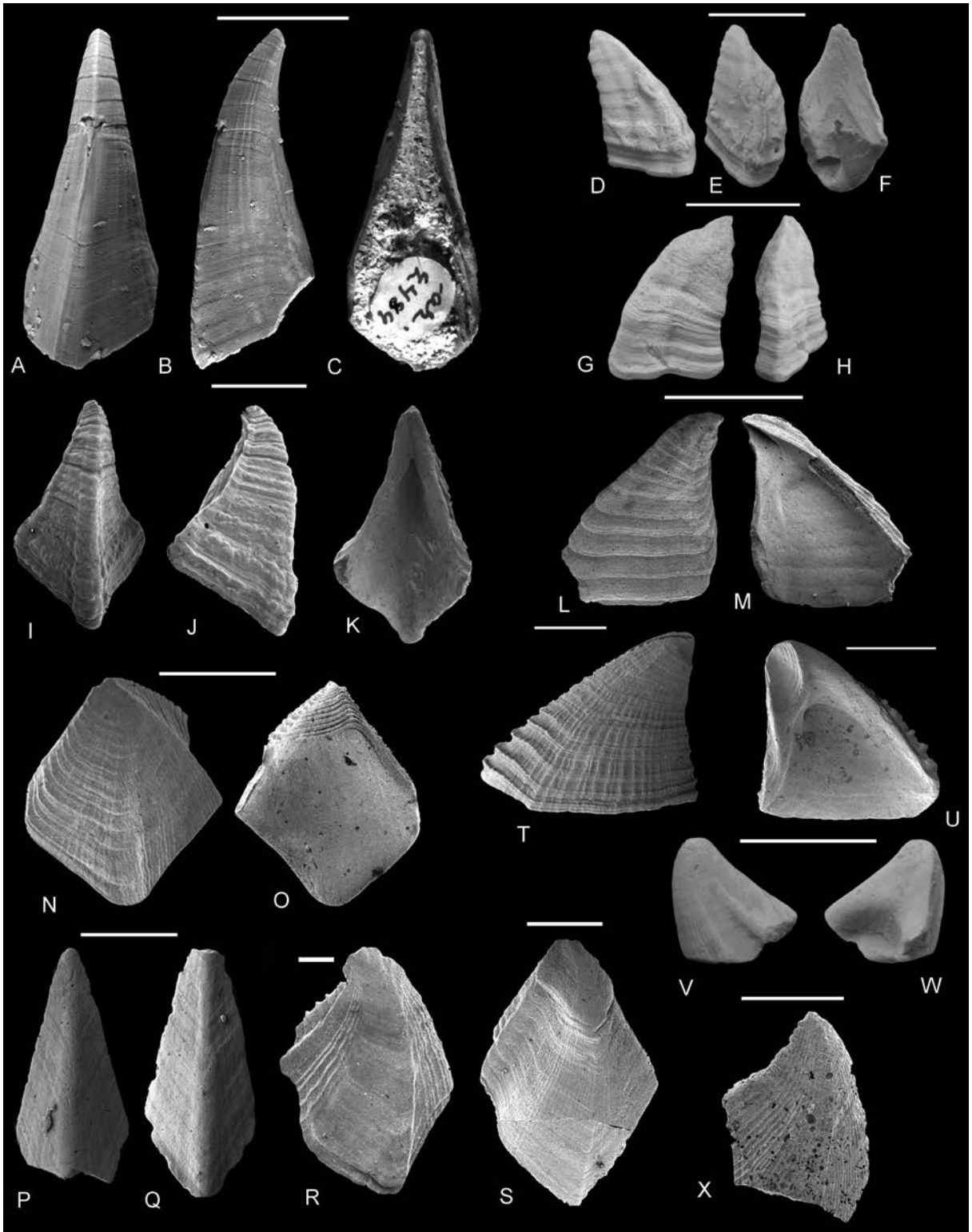
1953. *Calantica (Scillaelepas) nilssoni* (Steenstrup); Carlsson, p. 10, pl. 1, figs 7–10.

DIAGNOSIS: A large to very large form (carina up to 30 mm in height); sculpture comprises apicobasal ribs which tend to weaken basally; carina very broad. A sharp median ridge weakens basally to become broad and rounded.

TYPE: The carina figured by Steenstrup (1839, pl. 4, figs 20, 20\*) was selected as lectotype by Withers (1935, p. 111). This is from the upper Lower Campanian at Ignaberga, Skåne, Sweden (MGUH 986).

MATERIAL: Carlsson (1953, p.10) recorded numerous (over 100 specimens) of this species in Swedish collections from 12 localities (upper lower and lower upper Campanian) in the Kristianstad Basin, including mostly carinae, but also a few scuta and terga. On a recent visit to the SMNH and PMU collections, I was able to locate a large carina, in the latter collection (PMU 17875), which lacked locality details. In the

Text-fig. 5. Ecological groups from the upper lower Campanian of Text-fig. 5. Cirripedes from the Campanian of the Kristianstad Basin. A–C →  
– *Angulalepas nilssoni* (Steenstrup, 1839), PMU 17875, large carina in dorsal (A), lateral (B) and internal (C) views. D–K – *Angulalepas angulata* (Withers, 1935); D–F – NHMUK In.29419, rostrum in lateral (D), ventral (E) and internal (F), original of Withers (1935, pl. 10, fig. 9); G, H – NHMUK In.29418, holotype carina, in lateral (G) and dorsal (H) views, original of Withers (1935, pl. 10, fig. 10); I–K – NHMUK IC 1010, carina in dorsal (I), lateral (J) and internal (K) views. L, M – *Epibrachylepas lineatus* sp. nov., NHMUK IC 1017, holotype scutum in external (L) and internal (M) views, original of Gale in Gale and Sørensen (2015, fig. 19P, Q). N–Q – *Zeugmatolepas alifera* sp. nov.; N, O – NHMUK IC 1008, holotype tergum in external (N) and internal (O) views, original of Gale in Gale and Sørensen (2015, fig. 19A, B); P, Q – NHMUK IC 1014 and 1015, paratype rostra in external views, originals of Gale in Gale and Sørensen (2015, fig. 19M, N, respectively). R – *Zeugmatolepas mockleri* forma *ornata* Gale, 2024, NHMUK Pi In 65142, tergum in external view, original of Gale (2024, pl. 18, fig. 24). S – *Icenilepas collinsi* Gale, 2014a, NHMUK IC 1128, tergum in external view, original of Gale (2014, fig. 10a). T, U – *Epibrachylepas newmani* Gale in Gale and Sørensen, 2015, NHMUK IC 855 and 876, scuta in external (T) and internal (U) views, originals of Gale in Gale and Sørensen (2015, fig. 16A, B). V, W – *Bosquetlepas valida* (Steenstrup, 1839), NHMUK In.29417, apical portion of scutum, original of Withers (1935, pl. 10, fig. 7, figured as



*Calantica (Scillaelepas) angulata* Withers, 1935). X – *Arcuatoscappellum carlssoni* sp. nov., NHMUK IC 959, holotype tergum in external view, original of Gale in Gale and Sørensen (2015, fig. 10H). Provenance: A–C are from the upper lower Campanian of the Kristianstad Basin, Sweden, locality unknown; D–Q, T–X are from the upper lower Campanian, Ivö Klack, Skåne, southern Sweden; S is from the upper Cenomanian, Zig Zag Chalk Formation, Dover, Kent, UK; T is from the Santonian chalk, *Uintacrinus socialis* Zone, Wattisfield, Suffolk, UK. Scale bars equal: 10 mm (A–C); 5 mm (D–H, V, W); 1 mm (I–U).

Lund University Museum collections there are numerous carinae from Hanaskog, Ullstorp, Ignaberga, and Stafordsvad. However, Carlsson's (1953) material of scuta and terga of the species were not found and his illustrations are refigured here (Text-fig. 6F–I).

**DESCRIPTION:** Carinae large, beak-like, broad basally, inclined ventrally, with acuminate apex; rostral-basal angle 45°. Sculpture variable, comprising apicobasal ridges and intervening grooves, which weaken basally on some specimens (Text-fig. 5A, B) but persist on the tergal margin in others (Text-fig. 5D). Sharp median apicobasal ridge in early growth, which weakens and becomes broadly rounded in later stages. Lateral surfaces of carina gently convex. Scutum (Text-fig. 6A, B) triangular, flat, slightly inclined ventrally, bearing a low median apicobasal ridge and a broader, rounded ridge defining the boundary of the narrow tergal surface. Basal margin nearly straight; interior shows large subapical scar for scutal adductor. Tergum (Text-fig. 6C, D) subrhombic, height greater than maximum breadth, carinal margin single, long and straight. Apical margin low, convex, occludent surface bears a low ridge which broadens basally; scutal margin short, straight, basal angle acute. Curved apicobasal ridge present. The reconstruction (Text-fig. 7C) has a broad capitulum and shows the carina projecting above the tergum, with a long, convex occludent margin. Rostrum not known.

**REMARKS:** The carinae, according to Carlsson (1953, p. 10) were represented by over 100 carinae in the Swedish collections, whereas scuta and terga were few (4 scuta, 5 terga). The species was recorded from numerous localities in the Kristianstad Basin, including Ignaberga, Ivö, Barnakälla, Båstad-Malen, Hanaskog, Hörrod, Mörby, Västra Olinge, Balsberg, Bjärnum, Ballingslöv, and Norra Ströö. These localities are of upper lower and lower upper Campanian age according to Christensen (1975).

*Angulalepas angulata* (Withers, 1935)  
(Text-fig. 5D–K)

part 1935. *Calantica (Scillaelepas) angulata* Withers, p. 129, pl. 10, figs 8, 9 only.

part 1953. *Calantica (Scillaelepas) angulata* Withers; Carlsson, p. 13, pl. 3, figs 2, 4 only.

2015. '*Calantica (Scillaelepas) angulata* Withers; Gale in Gale and Sørensen, p. 228, fig. 19E–G.

**DIAGNOSIS:** Small *Angulalepas* gen. nov., in which the lateral surfaces of the carina are very broad and bear a sculpture of pustulose ridges parallel with the basal margins.

**TYPE:** The carina figured by Withers (1935, pl. 10, fig. 8) is the holotype (NHMUK In.29418). Ivö Klack, Sweden.

**MATERIAL:** A carina (NHMUK IC 1010), figured by Gale in Gale and Sørensen (2015, fig. 19E–G). A rostrum (NHMUK In.29419), figured by Withers (1935, pl. 10, fig. 9), both from Ivö Klack. The supposed scutum figured by Withers (refigured here, Text-fig. 5V, W) is probably the apex of a scutum of *Bosquetlepas valida* (Steenstrup, 1839).

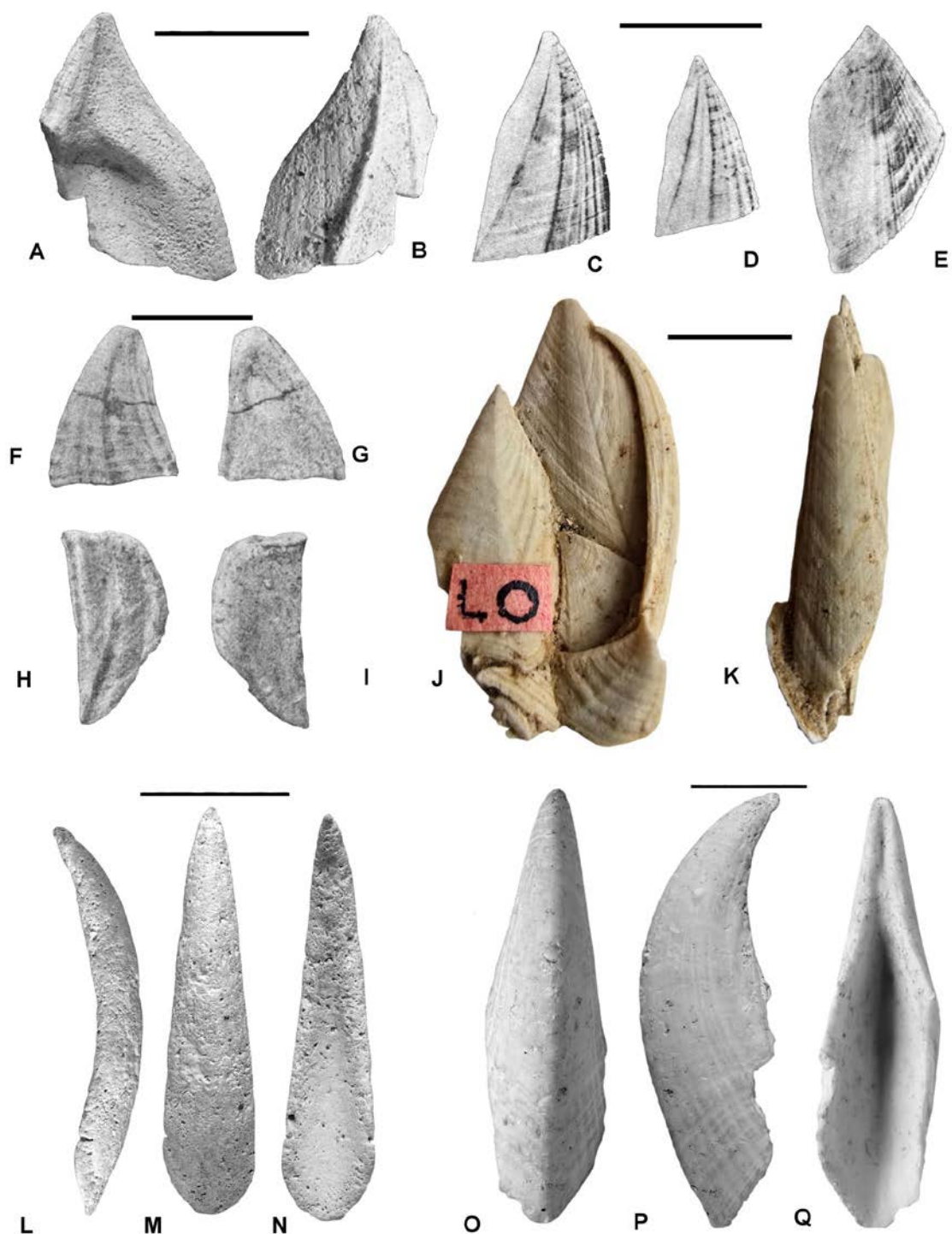
**DESCRIPTION:** Carina asymmetrically rhombic in dorsal view (Text-fig. 5H), basal margins strongly angled, shorter than carinal margins. Triangular in lateral aspect (Text-fig. 5G), broad, with flat to slightly concave sides; a rounded, elevated median ridge runs from the apex to the mid-line of the basal margin. Sculpture comprises ridges, parallel with basal margins, which display irregular pustulose swellings. Rostrum (Text-fig. 5D–F) similar in morphology to carina, but the interior has a raised apical region, bearing growth lines and has a V-shaped basal margin.

**REMARKS:** The carina of *A. angulata* differs from that of *A. nilssoni* in its smaller size, the very broad lateral surfaces, and the presence of pustulose ridges parallel with the basal margin. At an equivalent size, the carina of *A. nilssoni* (Text-fig. 5A, B) bears weak apicobasal ridges and transverse constrictions. The species is only known from Ivö Klack.

Family Myolepadidae Gale in Gale and Sørensen,  
2015

**INCLUDED GENERA:** *Bosquetlepas* Gale in Gale and Sørensen, 2015; *Myolepas* Gale in Gale and Sørensen, 2015.

Text-fig. 6. Cirripedes from the Campanian of the Kristianstad Basin. A–E – *Jagtscalpellum striatum* (Darwin, 1851); A, B – MGUH 992a, lectotype scutum of *Scalpellum semiporcatum* Darwin, 1851, in internal (A) and external (B) views, original of Darwin (1851, pl. 1, fig. 6) and Withers (1935, pl. 20, fig. 6); C, D – external views of scuta, figured after Carlsson (1953, pl. 3, figs 9, 10); E – external view of tergum, figured after Carlsson (1953, pl. 3, fig. 12). F–I, O–Q – *Angulalepas nilssoni* (Steenstrup, 1839); F, G – scutum in external (F) and internal (G) views, figured after Carlsson (1953, pl. 1, fig. 9); H, I – tergum in external (H) and internal (I) views, figured after Carlsson (1953, pl. 1, fig. 10);



O–Q – MGUH 986, lectotype carina in dorsal (O), lateral (P), and internal (Q) views, original of Steenstrup (1839, pl. 4, fig. 20) and Withers (1935, pl. 4, fig. 13). J, K – *Regioscalpellum maximum* (J. de C. Sowerby, 1829), MZLU LO3531t, capitulum in lateral (J) and dorsal (K) views, original of Carlsson (1953, pl. 4, fig. 5). L–N – MGUH 981, indeterminate calantid or scalpellid carina, type of *Pollicipes solidulus* Steenstrup, 1839, in lateral (L), dorsal (M), and internal (N) views, original of Steenstrup (1839, pl. 5, figs 14, 14\*) and Withers (1935, pl. 33, fig. 6). Provenance: A–E, J, K are from the upper Campanian of Köpinge, Sweden; F–I are from the upper lower Campanian of Västra Olinge, Kristianstad Basin, Sweden; L–N are from the Campanian of Kjöge, Skåne, Sweden; O–Q are from the upper lower Campanian of Ignaberga, Skåne, Sweden. Scale bars equal: 10 mm (A–I, L–Q) and 5 mm (J, K).

**DIAGNOSIS:** The capitulum is robust, constructed of two scuta, two terga, carina and rostrum; lateral plates are absent. A short internal spur at the rostral angle of the scutum carries ridges and grooves for the insertion of a large rostro-scutal muscle. The exterior of the scutum has a shallow groove running from the apex to the basal margin, which forms an inflexion on the basal margin adjacent to the spur.

**REMARKS:** Myolepadidae are a distinct group of robust Late Cretaceous cirripedes which evolved from the archaeolepadid *Loriolepas* Gale in Gale and Sørensen, 2015, distinguished by possession of a grooved rostro-scutal spur which served as an insertion site for rostro-scutal depressor muscles. In *Bosquetlepas* the spur is narrow, but in the descendant *Myolepas* it is enlarged and has complex ridging. This genus additionally possesses a tergal spur and the scutum and tergum have an interpenetrant articulation (Gale and Sørensen 2015). These features broadly parallel those developed in balanomorph cirripedes. Myolepadids were inhabitants of shallow, high-energy environments, and are virtually unknown in chalks (compare Jagt *et al.* 2023).

Genus *Bosquetlepas* Gale in Gale and Sørensen, 2015

**DIAGNOSIS:** The interior of the scutum has a short, grooved spur adjacent to the rostral angle for the insertion of depressor muscles. A shallow apicobasal groove extends parallel to the curved occludent margin on the scutum. There is no tergal spur and the scutal-tergal articulation is simple.

**TYPE SPECIES:** *Mitella darwiniana* Bosquet, 1854, by original designation.

**INCLUDED SPECIES:** *Pollicipes valida* Steenstrup, 1839; *Pollicipes gracilis* Roemer, 1841; *Pollicipes zeidleri* Reuss, 1864; *Calantica (Scillaelepas) brydonei* Withers, 1935; *Calantica (S.) subplena* Collins, 1983; *C. (S.) contigua* Collins, 1983 from the Late Cretaceous of the Vendée, western France; *Bosquetlepas* (Jagt *et al.* 2023).

**REMARKS:** *Bosquetlepas* is only known from isolated valves. Following Gale (2024) the species of the genus fall into two distinct groups:

1. The *B. valida* group, including *B. valida*, *B. subplena*, *B. contigua*, and *B. brydonei*, in which the scutum is tall, not inclined dorsally and the tergum is narrow and subrhomboidal. These forms are comparable

in valve shape with *Loriolepas subjurensis* (de Loriol and Pallat, 1867) from which the genus *Bosquetlepas* probably evolved (Gale and Sørensen 2015).

2. The *B. darwiniana* group, including *B. darwiniana*, *B. gracilis*, and *B. zeidleri*, in which the scuta are low and slanted dorsally and the terga are broad with very elongated occludent margins. This group is dominantly found in the upper Maastrichtian and appears to be more derived than the *B. valida* group.

*Bosquetlepas valida* (Steenstrup, 1839)  
(Text-fig. 9A–U)

part 1839. *Pollicipes validus* Steenstrup, p. 412, pl. 5, figs 28, 29, 31 only.

1851. *Pollicipes validus* Steenstrup; Darwin, p. 68, pl. 4, fig. 2e–f.

1935. *Calantica (Scillaelepas) valida* (Steenstrup); Withers, p. 196, pl. 6, figs 1, 2.

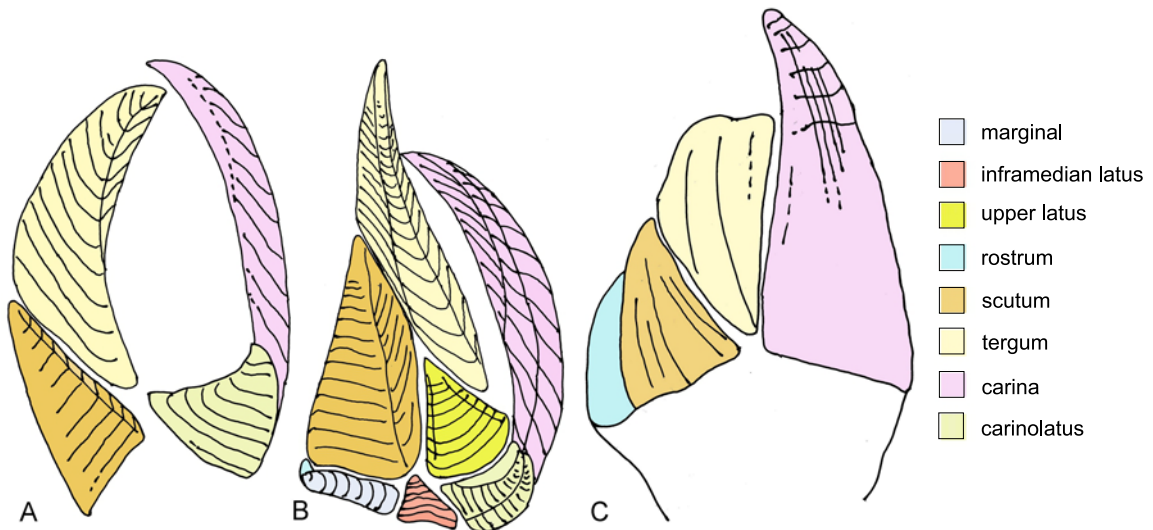
1942. *Calantica (Scillaelepas) valida* (Steenstrup); Carlsson, p. 3, pl. 1, fig. 2.

1953. *Calantica (Scillaelepas) valida* (Steenstrup); Carlsson, p. 8, pl. 1, figs 1–6.

2015. *Bosquetlepas valida* (Steenstrup); Gale in Gale and Sørensen, p. 217, figs 3E–I, 4A, B, 5B.

**TYPE:** Steenstrup's (1839) original figures of specimens assigned to this species are shown in Text-fig. 10. The lectotype, designated by Withers (1914), is the scutum illustrated by Steenstrup (1839, pl. 5, fig. 32) and supposedly refigured by Darwin (1851, pl. 4, fig. 2e, f). Its current whereabouts are unknown, although Withers (1935, p. 110) states that the specimens are in the collections of the Zoological and Mineralogical museums in Copenhagen. This was an unfortunate choice, because this specimen does not resemble any of the several hundred scuta of the species which I have examined; it shows four strong apicobasal ridges, never developed on *B. valida*, and rather closely resembles the scutum of *Proverruca laurae* Withers, 1923 (Withers 1935, pl. 44, fig. 1). I also do not think that the scutum figured by Darwin (1851, pl. 4, figs 2e, f), from Skåne, is the same specimen as shown in Steenstrup's (1839) pl. 5, fig. 32. As Withers (1935) pointed out, the scutum in Steenstrup's (1839) pl. 4, fig. 30 should correctly be referred to the Danian calanticid species *Scillaelepas dorsata* (Steenstrup, 1839).

**MATERIAL:** The species is uncommon at Ivö Klack, where it is represented by small specimens, but numerous, very large, thickened valves are present in the Lund and Uppsala collections from various



Text-fig. 7. Reconstructions of cirripedes from the Campanian of southern Sweden. A – *Solidoscalpellum angelini* (Darwin, 1851). B – *Regioscalpellum maximum* (J. de C. Sowerby, 1829). C – *Angulalepas nilssoni* (Steenstrup, 1839).

localities in Skåne, including Ignaberga, Västra Olinge, Mörby, Oppmana, and Karstad. Carlsson (1953, p. 9) lists the species from additional localities.

**DESCRIPTION:** The carina (Text-fig. 9K–M) are tall, triangular, inclined ventrally and the external surface is evenly convex with irregularly developed commarginal growth lines and ridges. Larger specimens are similar but more strongly incurved. The rostrum (Text-fig. 9N, O) is equilaterally triangular, concavo-convex, and inclined dorsally.

The scuta (Text-fig. 9A–J) display remarkable ontogenetic changes. The smallest specimen (Text-fig. 9A, B; height 7 mm) is triangular, weakly inclined dorsally and a raised rim runs along the occludent margin. An apicobasal ridge separates the slightly depressed occludent surface from the tergal surface, and, on the interior, the scutal adductor muscle scar is not clearly marked. In larger specimens (Text-fig. 9C, D; height 15 mm), the occludent surface has formed an incised groove, rimmed by the raised occludent rim; on the interior, the scutal adductor scar has deepened. At this size, the scutum of the species is comparable to those of other *Bosquetlepas* species (see Gale 2024, text-fig. 46A, B, F, G), such as *B. subplena* and *B. brydonei*. At larger sizes (20–35 mm maximum height) the scuta have become greatly thickened, the scutal adductor scar has become a deep depression (Text-fig. 9E–J) and the occludent groove is lost.

The smallest terga (Text-fig. 9P, Q; height 15 mm) are subrhombic in outline, relatively thin, inclined

dorsally and have a raised, flat-topped apicobasal ridge. At larger sizes (Text-fig. 9R–U; 16–25 mm), the terga become very robust and thickened, especially in the apical region.

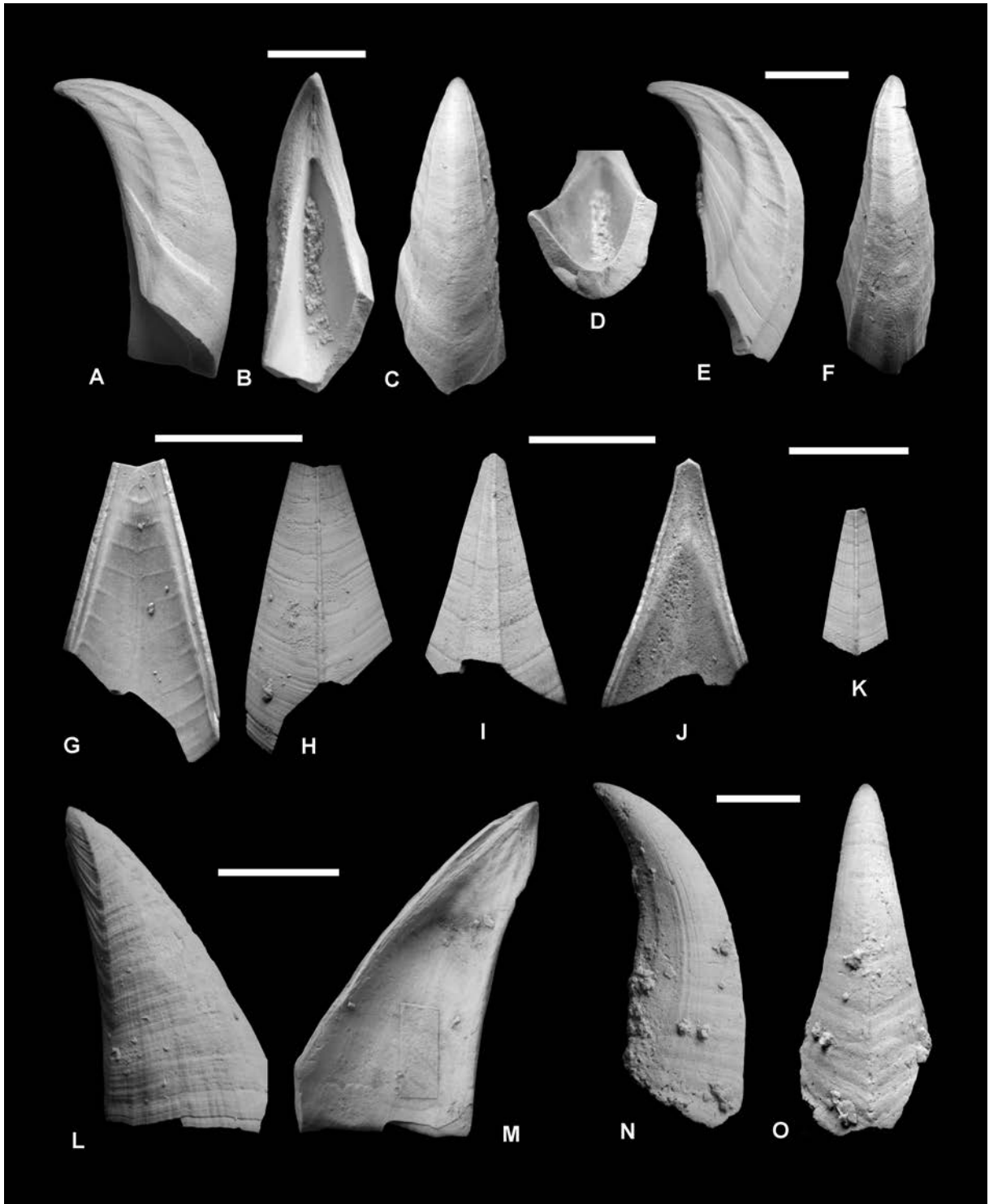
**REMARKS:** Larger valves of *Bosquetlepas valida* are greatly thickened and are probably the most heavily calcified valves known of any pedunculate cirripede. This was perhaps an adaptation to living in a very high-energy environment, and possibly a deterrent to predatory drilling gastropods. Extant *Pollicipes* and *Capitulum* species which live in comparable situations, whilst robust, do not develop such thickened scuta and terga.

Order Pollicipedomorpha Chan, Dreyer, Gale,  
Glennner, Ewers-Saucedo, Pérez-Losada, Kolbasov,  
Crandall and Høeg, 2021

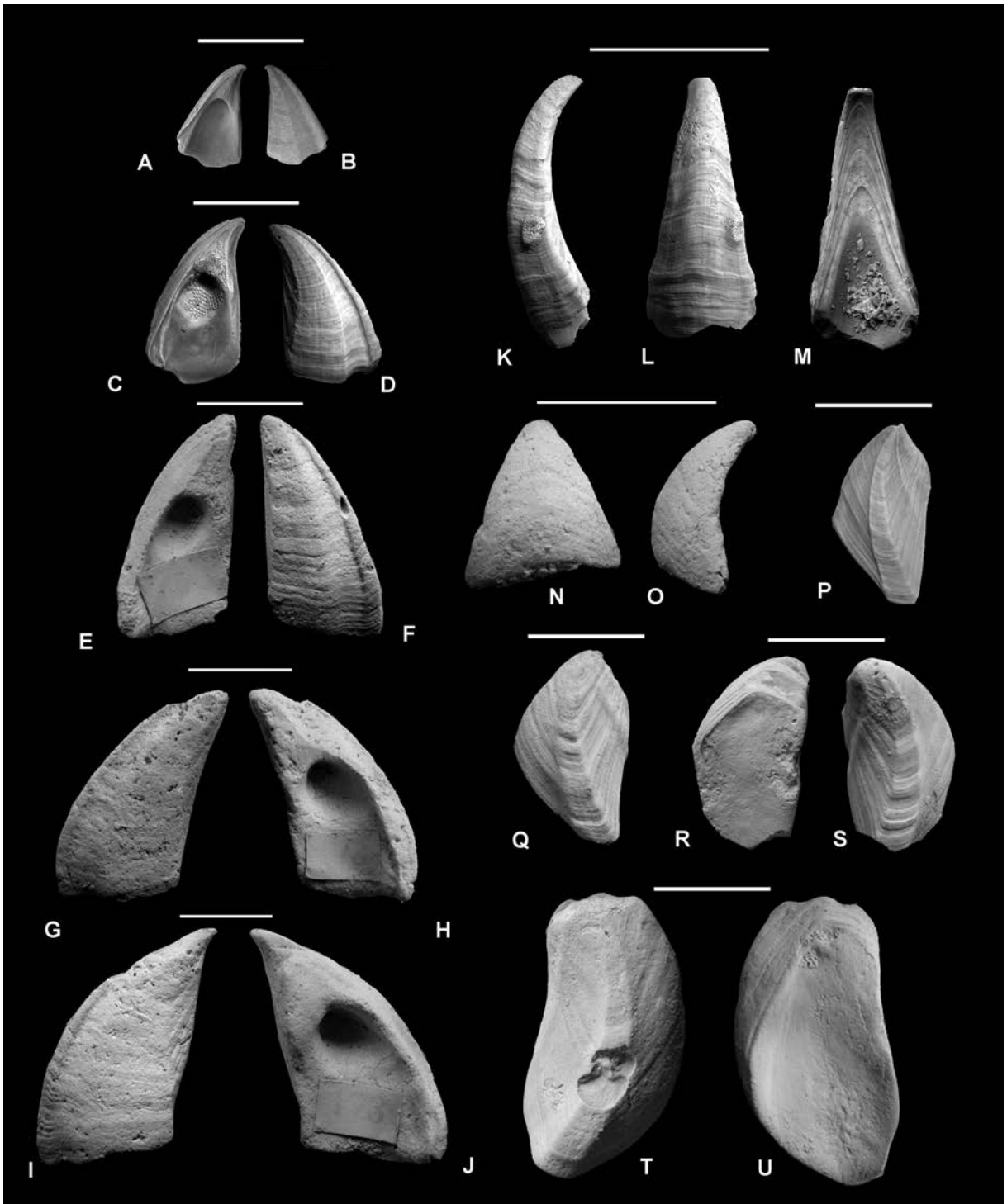
**INCLUDED FAMILIES:** Pollicipedidae Leach, 1817; Zeugmatolepadidae Newman, 1996, emend. Newman, 2004.

**DIAGNOSIS:** The capitulum includes numerous, basally imbricating lateral plates which decrease in size towards the peduncle; these include subrostra and subcarinae (modified from Chan *et al.* 2021).

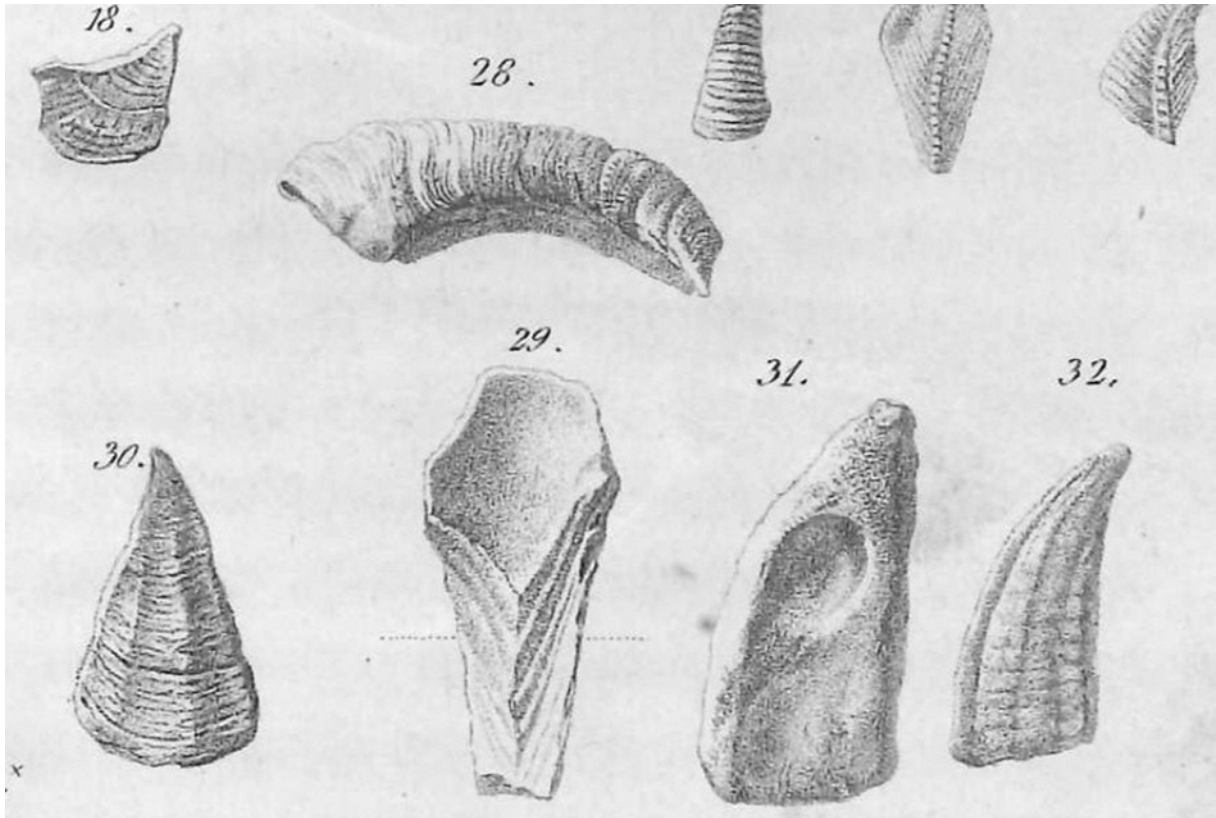
Family Zeugmatolepadidae Newman, 1996 emend.  
Newman, 2004



Text-fig. 8. Cirripedes from the Campanian of southern Sweden. A–F – *Regioscalpellum ahlbergi* sp. nov.; A–D – MZLU LO12538T, holotype carina in lateral (A), internal (B), dorsal (C), and cross-sectional (D) views; E, F – MZLU LO12539t, paratype carina in lateral (E) and dorsal (F) views. G–K – *Cretiscalpellum glabrum* (Roemer, 1841), MZLU LO12548t–12550t, carinae in internal (G, H) and dorsal (H, I, K) views. L, M – *Solidoscalpellum angelini* (Darwin, 1851), MZLU LO12551t, large scutum in external (L) and internal (M) views. N, O – *Angulalepas nilssoni* (Steenstrup, 1839), MZLU LO12540t, large carina in lateral (N) and dorsal (O) views. Provenance: A–F are from the upper lower Campanian of Västra Olinge, Kristianstad Basin, Sweden; G–K are from the upper Campanian of Köpinge, Skåne, Sweden. L, M are from the upper Campanian of Oppmanna, Skåne, Sweden; N, O are from the Campanian, locality unknown, Skåne, Sweden. Scale bars equal 10 mm.



Text-fig. 9. *Bosquetlepas valida* (Steenstrup, 1839) from the Campanian southern Sweden. A–J – external (B, D, F, G, I) and internal (A, C, E, H, J) views of scuta: A, B – NHMUK IC 919, original of Gale in Gale and Sørensen (2015, fig. 3H, I); C, D – NHMUK IC 920, original of Gale in Gale and Sørensen (2015, fig. 4A, B); E–J – MZLU LO12541t–LO12543t, large scuta in internal (E, H, J) and external (F, G, I) views; K–M – NHMUK IC 917, carina in lateral (K), dorsal (L), and internal (M) views, original of Gale in Gale and Sørensen (2015, fig. 3E, F, K); N, O – MZLU LO12544t, rostrum; P–U – NHMUK IC 918, terga in external (P, Q, S, T) and internal (R, U) views, original of Gale in Gale and Sørensen (2015, fig. 3G); Q–U – MZLU LO12545t–12547t, terga in external (Q, S, T) and internal (R, U) views. Provenience: A–D, K–M and P are from the upper lower Campanian of Ivö Klack, Skåne, southern Sweden; E–J, N, O, Q–U are from the upper lower Campanian of Västra Olinge, Kristianstad Basin, Sweden. Scale bars equal 10 mm.



Text-fig. 10. Steenstrup's original material of *Pollicipes validus* Steenstrup, 1839 (pl. 3), refigured; he assigned figures 28–32 to this species. Withers (1935, pp. 109, 110) selected the scutum illustrated in fig. 32 as lectotype and noted that the scutum in fig. 30 should correctly be referred to the Danian species *Scillaelepas dorsata* (Steenstrup, 1839).

INCLUDED SUBFAMILIES: Martillepadinae Gale, 2014a; Zeugmatolepadinae Newman, 1996 emend. Newman, 2004.

DIAGNOSIS: Pollicipedomorphs with tall, laterally compressed capitula of delicate construction which include three, or often more, alternating series of lower lateral plates that decrease progressively in size towards the peduncle and include at least one sub-rostrum and a subcarina. There is not always a clear demarcation between the lower latera of the capitulum and peduncular plates.

Genus *Zeugmatolepas* Withers, 1913

TYPE SPECIES: *Zeugmatolepas mockleri* Withers, 1913.

OTHER SPECIES: *Pollicipes cretae* Steenstrup, 1839; *Zeugmatolepas gaultinum* Gale, 2024; *Zeugmatolepas capelensis* Gale, 2024; *Zeug-*

*matolepas vectensis* Gale, 2024; *Zeugmatolepas eo-cenica* Gale, 2024.

DIAGNOSIS: The capitulum is tall. A line from the apex of the carina to the base of the rostrum is obliquely angled ( $45^\circ$ ) to the median axis of the capitulum. The upper latus is inclined ventrally; the lower laterals have acute apices and are not arranged in tiers.

*Zeugmatolepas alifera* sp. nov.

(Text-fig. 5N–Q)

urn:lsid:zoobank.org:act:92D92F1A-02E8-421E-8F95-DE863AC81748

2015. Scalpelliform tergum, unknown affinities; Gale in Gale and Sørensen, p. 228, fig. 19A, B.

2015. *Zeugmatolepas* sp. Gale in Gale and Sørensen, p. 237, fig. 19A, B.

DIAGNOSIS: *Zeugmatolepas* in which the tergum is symmetrically rhombic, bearing a blunt cingulum

on the upper carinal surface, and the external face is nearly flat, with weak apicobasal ribbing.

TYPE: The well-preserved, very small tergum illustrated here (Text-fig. 5O, P) is the holotype (NHMUK IC 1008), and the 2 rostra (Text-fig. 5Q, R) are paratypes (NHMUK IC 1014, 1015). All from the upper lower Campanian at Ivö Klack.

DERIVATION OF NAME: Latin, *alifera*, meaning wing-bearer, in illusion to the wing-like process on the tergum.

DESCRIPTION: The body of the tergum (Text-fig. 5O, P) is nearly square in outline; the occludent margin is gently convex, the other margins are straight. The basal and lower-upper carinal angles are rounded, and the carinal surface bears prominent growth lines which inflect apically on the upper carinal margin. The occludent:scutal margin is slightly depressed, and has faint ribbing, which extends from the apex to the scutal margin. A wing-like process, called a cingulum by Gale (2024), extends over the apical half of the occludent margin.

The rostra (Text-fig. 5Q, R) are kite-shaped and the basal margin is V-shaped. The height is approximately twice the breadth, and a raised, broadly rounded apicobasal ridge is present. Growth lines are weak and parallel the basal margins.

REMARKS: The tergum of this species shows some resemblance to those of *Zeugmatolepas mockleri* forma *ornata* Gale, 2024 (Text-fig. 5S) and *Icenilepas collinsi* Gale, 2014a (Text-fig. 5T) in the presence of a noded cingulum on the upper carinal margin (compare with Gale 2024, text-fig. 47), but differs from these species in the absence of a depressed occludent surface, separated from the carinal surface by a ridge. Indeed, the external surface is almost flat, bearing only weak apicobasal ribbing. The rostra (Text-fig. 5Q, R) are typical of *Zeugmatolepas* (compare with Gale 2024, pl. 18, figs 29, 30; note that these were incorrectly labelled as carinae).

Order Calanticomorpha Chan, Dreyer, Gale, Glenner, Ewers-Saucedo, Pérez-Losada, Kolbasov, Crandall and Høeg, 2021

INCLUDED FAMILIES: Calanticidae Zevina, 1978; Cretiscalpellidae Buckeridge, 1983; Titanolepadidae Gale in Gale and Sørensen, 2015.

DIAGNOSIS: The capitular plate numbers are highly variable, usually with three pairs of larger laterals (rostrolatus, upper latus and carinolatus) and often with a subrostrum and a subcarina; the inframedian latus is commonly absent.

Family Cretiscalpellidae Buckeridge, 1983

INCLUDED GENERA: *Cretiscalpellum* Withers, 1922; *Striascalpellum* Gale, 2020; *Witherscalpellum* Gale, 2020; *Jagtscalpellum* Gale, 2020.

DIAGNOSIS: Pedunculate thoracicans which possess 17 plates in the capitulum (paired scuta, terga, upper latera, inframedian latera, rostrolatera, upper carinolatera (C11), lower carinolatera (C12), carina, rostrum and subcarina). The upper carinolatus is rectangular to rhomboidal in outline, the lower is triangular. The peduncular plates relatively large, in eight to twelve columns, with an inwardly directed basal ledge.

Genus *Cretiscalpellum* Withers, 1922

TYPE SPECIES: *Pollicipes unguis* J. de C. Sowerby, 1836.

OTHER SPECIES: In addition to the type species, *Pollicipes unguis* J de C. Sowerby, 1836: *Scalpellum glabrum* Roemer, 1841; *Scalpellum bronni* Roemer, 1841; *Scalpellum simplex* Darwin, 1851; *Scalpellum longissimum* Withers, 1911; *Scalpellum paucistriatum* Woodward, 1906; *Cretiscalpellum obtusum* Jagt and Collins, 1989.

DIAGNOSIS: Smooth to weakly sculptured, large cretiscalpellids, in which the tergum is asymmetrically rhomboidal with a low, straight apicobasal ridge. The carinolatera, inframedian latus and rostrolatus are convex, bearing an oblique transverse ridge.

*Cretiscalpellum glabrum* (Roemer, 1841)  
(Text-fig. 8G–K)

1841. *Pollicipes glaber* Roemer, p. 104, pl. 16, fig. 11a–c.  
1845. *Pollicipes glaber* Roemer; Reuss, p. 17, pl. 5, figs 45–49; pl. 13, figs 86–91.  
1851. *Pollicipes glaber* Reuss [sic]; Darwin, p. 61, pl. 3, figs 10a–l.  
part 1906. *Pollicipes glaber* Roemer; Woodward, p. 346, text-figs 26, 27 only.  
1923. *Scalpellum* (*Cretiscalpellum*) *glabrum* (Roemer); Withers, p. 11, pl. 1, figs 3–14.

1935. *Cretiscalpellum glabrum* (Roemer); Withers, p. 161, pl. 15, figs 8–17; pl. 16, figs 1–20; pl. 18, figs 1–5; pl. 19, figs 1–6.
1953. *Cretiscalpellum glabrum* (Roemer); Carlsson, p. 13, pl. 3, figs 5–8.
2025. *Cretiscalpellum glabrum* (Roemer); Gale, p. 106, pl. 27, figs 1–9, pl. 29, figs 8–14, pl. 33, figs 1, 2.

TYPES: Roemer (1841, pl. 16, fig 11a–c) founded the species on three valves, a carina (a), a scutum (b) and a tergum (c), of which Withers (1935, p. 164) selected the carina as lectotype. The specimens are from the ‘Unterer Kreidemergel’ (Cenomanian) of Lindener Berg, near Hannover, northern Germany, and cannot be traced.

DIAGNOSIS: *Cretiscalpellum* in which the tergum is symmetrically rhombic, with a relatively broad carinal surface and straight margins of subequal length. The carina is elongated and bears a sharp apicobasal ridge.

MATERIAL: Carlsson (1953, p.14) records numerous specimens of this species from Köpinge (upper Campanian) in the SMNH and the Palaeontological Institute in Lund which could not be located on my visits to these collections. However, a number of moderately well preserved carinae from the same locality, evidently different to the material recorded by Carlsson, are present in Lund (MZLU LO12548t-2550t).

REMARKS: The carinae (Text-fig. 8G–K) mostly fall within the morphological range of the species (smooth, with periodical evenly spaced growth increments and a sharp apicobasal ridge), but one specimen (Text-fig. 8I, J) possesses a flat, raised apicobasal ridge which is not typical for this species. This is perhaps pathological.

#### Genus *Jagtscalpellum* Gale, 2020

TYPE SPECIES: *Pollicipes striatus* Darwin, 1851, by original designation.

OTHER SPECIES: *Scalpellum filiosum* Withers, 1911; *Jagtscalpellum spinosum* Gale, 2020; *Jagtscalpellum africanum* Gale, 2020; *Arcoscalpellum gaultinum* Withers, 1935; *Cretiscalpellum striatum* var. *dissimile* Withers, 1935; *Cretiscalpellum niadini* Alekseev, 2009.

DIAGNOSIS: Ornate cretiscalpellids, characterised by striate or spinose sculpture. The upper carinolatus

is large and rectangular and the lower carinolatus small and triangular.

#### *Jagtscalpellum striatum* (Darwin, 1851) (Text-fig. 6A–E)

1851. *Pollicipes striatus* Darwin, p. 70, pl. 4, fig. 4a–c.
1851. *Scalpellum semiporcatum* Darwin, p. 70, pl. 1, fig. 6.
1906. *Scalpellum attenuatum* Woodward, p. 352, fig. 37.
1912. *Pollicipes striatus* Darwin; Withers, p. 311.
1935. *Cretiscalpellum striatum* (Darwin); Withers, p. 183, pl. 20, figs 1–5, 15–21; pls 21, 22.
1935. *Cretiscalpellum semiporcatum* (Darwin); Withers, p. 196, pl. 20, fig. 6.
1953. *Cretiscalpellum striatum* (Darwin); Carlsson, p. 15, pl. 3, figs 1.1, 1.12.
1953. *Cretiscalpellum semiporcatum* (Darwin); Carlsson, p. 14, pl. 3, figs 9, 10.
2015. *Cretiscalpellum striatum* (Darwin); Gale, p. 8, fig. 4B–K.
2020. *Jagtscalpellum striatum* (Darwin); Gale, p. 254, fig. 6a–j.
2025. *Jagtscalpellum striatum* (Darwin); Gale, p. 114, pl. 32, figs 1–32.

TYPE: The scutum figured by Darwin (1851, pl. 4, fig. 5c) was designated lectotype by Withers (1912). It is in the Fitch Collection of the NCM (no. 2154) and came from the upper Campanian Norwich Chalk.

DIAGNOSIS: *Jagtscalpellum* in which the sculpture of the valves comprises strong, fine apicobasal ridges. The terga have a flat occludent margin.

MATERIAL: Carlsson (1953, p. 16) recorded 64 valves of this species in the SMNH collections, and three in the Palaeontological Institute in Lund, all from the upper Campanian of Köpinge, Skåne; Carlsson also records two scuta he attributed to *Cretiscalpellum semiporcatum* (here considered to be a synonym of *J. striatum*) in the SMNH collections. None of these were located during my visits to these institutes, so I have copied Carlsson’s (1953) illustrations of scuta and a tergum (Text-fig. 6C–E). Darwin’s type specimen of *Scalpellum semiporcatum* is in the Copenhagen collection (MGUH 992a) and is refigured here (Text-fig. 6A, B).

REMARKS: The type specimen of *Scalpellum semiporcatum* Darwin, 1851, is a large incomplete scutum (Text-fig. 6A, B) from Köpinge. It shows the upper part of the flat, raised apicobasal ridge, which extends from the apex to the basitergal angle and the middle

of the basal margin which is typical of *J. striatum*. The other scuta figured by Carlsson (Text-fig. 6C, D) are closely comparable with the *J. striatum* scutum illustrated by Gale (2025, pl. 32, fig. 9). *Jagtscalpellum striatum* is a morphologically variable species, and in my view *Scalpellum semiporcatum* belongs to this species. In Skåne, the species is only known from the upper Campanian of Kjöpinge.

Order Scalpellomorpha Buckeridge and Newman,  
2006

Suborder Scalpelloidea Chan, Dreyer, Gale, Ewers  
Saucedo, Pérez-Losada, Kolbasov, Crandall and  
Høeg, 2021.

Family Scalpellidae Pilsbry, 1907

DIAGNOSIS: Scalpellomorphs which possess a maximum of fourteen plates (carina, rostrum, paired scuta, terga, upper latera, carinolatera, rostromedial latera), rarely thirteen, by secondary loss of the rostrum.

Genus *Arcuatoscypellum* Gale, 2015.

TYPE SPECIES: *Scalpellum arcuatum* Darwin, 1851, by original designation.

DIAGNOSIS: Strongly ribbed scalpelline in which the carinolatus is upright and slightly inclined ventrally. The rostromedial narrows towards its dorsal margin. The carina possesses a sharp apicobasal ridge.

REFERRED SPECIES: *Scalpellum trilineatum* Darwin, 1851; *Scalpellum accumulatum* Withers, 1910; *Pollicipes undulatus* Steenstrup, 1839; *Arcuatoscypellum carlssoni* sp. nov.

*Arcuatoscypellum undulatum* (Steenstrup, 1839).  
(Text-fig. 11A–J)

1839. *Pollicipes undulatus* Steenstrup, p. 403, pl. 4, fig. 6. part 1851. *Scalpellum solidulum* Steenstrup; Darwin, p. 42, pl. 1, fig. 8a only.

1935. *Scalpellum (Arcoscalpellum) undulatum* (Steenstrup); Withers, p. 268, pl. 35, fig. 3.

1953. *Scalpellum (Arcoscalpellum) undulatum* (Steenstrup); Carlsson, p. 22, pl. 5, figs 7–9.

DIAGNOSIS: *Arcuatoscypellum* in which the occludent surface of the tergum is very narrow and the occludent margin nearly straight. The carina is

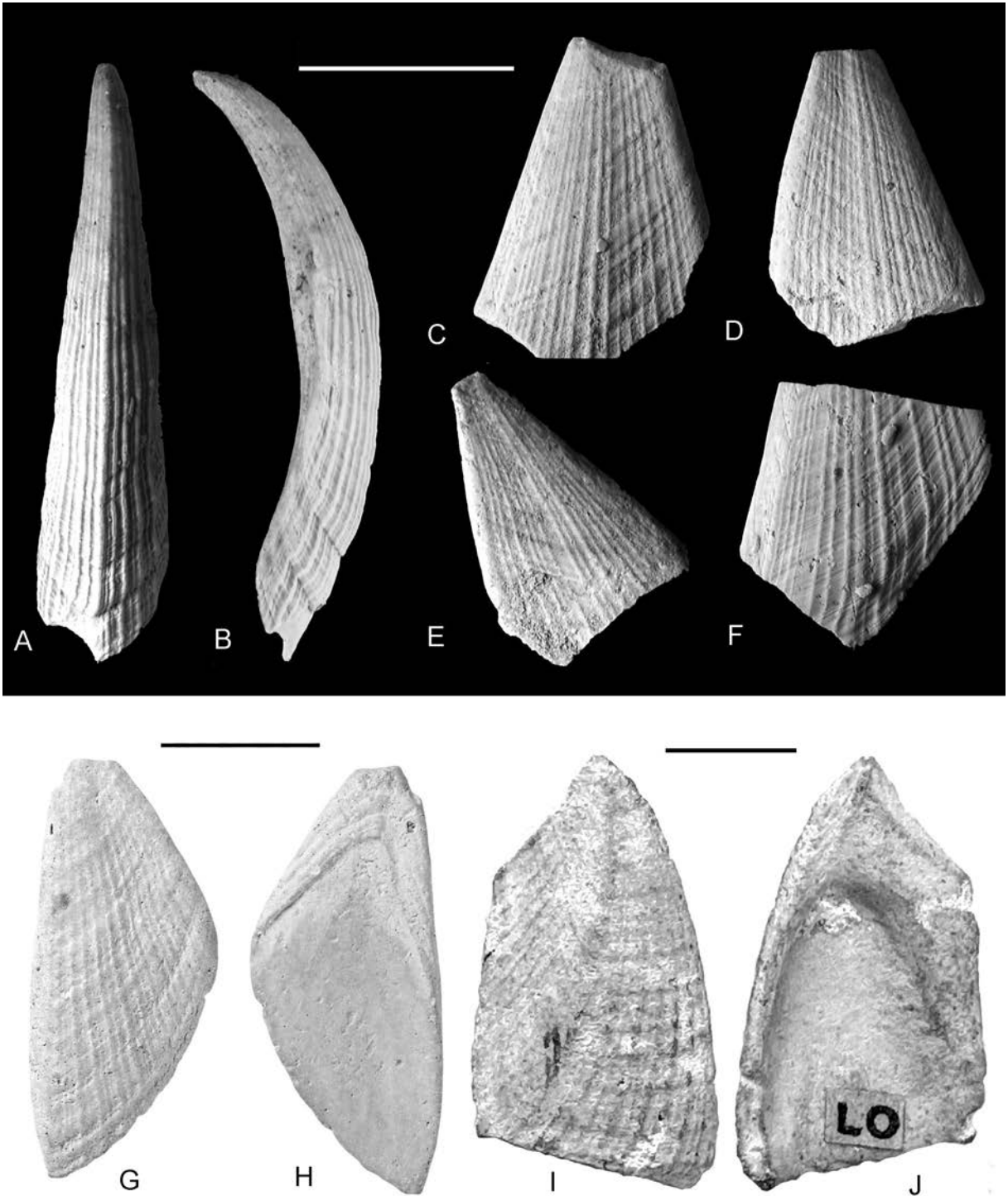
coarsely striate, and strongly incurved towards the ventral margin.

TYPE: The tergum figured by Steenstrup (1839, pl. 4, fig. 6) from Ivö Klack is the lectotype (MGUH 977), selected by Withers (1935, p. 268).

MATERIAL: In the SMNH collection, there is a carina from Tullstorp (SMNH Ar0009057a) and 4 broken terga from Söndraby (SMNH Ar0008713). In the PMU collections there is a tergum from Tullstorp. A scutum in the MZLU collection is from Staversvad (LO3533t). Carlsson (1953) also recorded the species from Roalöv and Kjøge, Skåne.

DESCRIPTION: The height of the carina (Text-fig. 11A, B) is four times the breadth of the base, and in dorsal view tapers evenly from the base to the apex. In lateral view, the external margin is strongly and evenly convex, the inner margin concave. The external surface bears a sharp median ridge and on the lateral surfaces 12 strong, evenly spaced apicobasal ridges which fade towards the inner margin. Indistinct, fine transverse striations are present, and towards the base there are growth interruptions which form constrictions. The terga (Text-fig. 11C–H) are flat, robust, triangular in outline and the height is approximately two times the breadth. The occludent margin is elongated and straight to slightly sinusoidal; the upper and lower carinal margins are gently convex and subequal in length. The apex, although broken off all specimens, was acuminate. The occludent surface is very narrow and forms a slightly depressed slip adjacent to the occludent margin. The sculpture comprises strong, evenly spaced apicobasal ribs, fine striations and growth interruptions parallel to the lower carinal margin. There is no apicobasal ridge, but few more prominent ribs separate the slightly depressed occludent side of the plate.

The scutum (Text-fig. 11I, J) is subtrapezoidal in outline, and the height is one and a half times greater than the basal breadth. The occludent margin is long and gently convex, the tergal margin straight and short and the lateral margin is straight and subparallel with the occludent margin. A strong, curved apicobasal ridge separates a depressed tergal:lateral surface from the occludent surface. Apicobasal ribs are present on the occludent surface; on the tergal:lateral surface, ribs run from the apex to the lateral margin. On the interior of the valve, the occludent margin carries a ridge which extends down to the basal margin, and a very broad tergal notch is present.



Text-fig. 11. *Arcuatoscypellum undulatum* (Steenstrup, 1839). A, B – SMNH Ar0009057a, carina in dorsal (A) and lateral (B) views; C–F – SMNH Ar0008713, fragmentary terna in external view; G, H – MGUH 977, lectotype tergum in external (G) and internal (H) views, original of Steenstrup (1839, pl. 4, fig. 6) and Withers (1935, pl. 35, fig. 3); I, J – MZLU LO3533t, scutum in external (I) and internal (J) views, original of Carlsson (1953, pl. 5, fig. 8). Provenance: A, B are from the upper lower Campanian of Tullstorp, Skåne, Sweden; C–F are from the upper lower Campanian of Söndraby, Skåne, Sweden; G, H are from the upper lower Campanian of Ivö Klack, Skåne, Sweden; I, J are from the Campanian of Staversvad, Skåne, Sweden. Scale bars equal 10 mm.

REMARKS: The species is referred to *Arcuatoscappelum* on account of the strong apicobasal ribbing, the median ridge on the carina and the shapes of the terga and scuta. *Arcuatoscappelum undulatum* differs from the Albian species *A. arcuatum* (Darwin, 1851) and the Cenomanian species *A. trilineatum* (Darwin, 1851) particularly in its very narrow occludent surface, differences in the shapes of the terga, and the very coarsely striate carina.

*Arcuatoscappelum carlssoni* sp. nov.  
(Text-fig. 5X)

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1953. *Cretiscappelum striatum* var. *dissimile* Withers; Carlsson, p. 16, pl. 4, fig. 1.

2015. *Arcoscappelum* sp.; Gale in Gale and Sørensen, p. 228, fig. 10H.

DIAGNOSIS: Finely striate *Arcuatoscappelum* in which the tergum carries a broad, flat-topped apicobasal ridge. Ribbing is coarser on the ventral side of the valve.

TYPE: The incomplete tergum from the upper lower Campanian at Ivö Klack is the holotype (NHMUK IC 959).

MATERIAL: A well-preserved tergum was illustrated by Carlsson (1953, pl. 4, fig. 1), from the upper lower or lower upper Campanian of north-east Skåne which probably belongs to the same species.

DERIVATION OF NAME: After J.G. Carlsson, in recognition of his work on Cretaceous cirripedes from Sweden.

DESCRIPTION: Although incomplete, the tergum is moderately well-preserved. The inferred height is approximately twice the breadth, and the lower and upper carinal margins are subequal in length. The occludent margin is slightly concave, the scutal margin straight. A basally broadening, flat ridge runs from the apex to the lower scutal margin and the basal angle, and the carinal and upper scutal surfaces are slightly depressed. Strong, rounded apicobasal ridges are present; those on the upper scutal and occludent surfaces are relatively coarse and extend from the apex to the scutal margin. The ridges on the carinal surface are very fine and extend from the apex to the

lower carinal margin. Ridges on the apicobasal shelf are indistinct, probably on account of damage.

REMARKS: In the shape of the tergum, and the presence of strong apicobasal ribbing, *A. carlssoni* sp. nov. is typical of *Arcuatoscappelum*. It differs from all congeners in its possession of a flat, broad apicobasal ridge, and the differences in coarseness of ribbing on the ventral and dorsal surfaces of the valve.

Genus *Regioscappelum* Gale, 2015

DIAGNOSIS: Scalpellines in which a concave, internal upper latus surface and short carinal margin is present on the carinolatus, covered by epidermis; carinolatus umbones incurved, lateral margin of carinolatus strongly convex.

TYPE SPECIES: *Scalpellum regium* Thomson, 1873, by original designation.

INCLUDED SPECIES: *Scalpellum darwini* Hoek, 1883; *S. moluccanum* Hoek, 1883; *Pollicipes maximus* J. de C. Sowerby, 1829; *Regioscappelum ahlbergi* sp. nov.; *Arcoscappelum sanchezae* Withers, 1953.

*Regioscappelum maximum* (J. de C. Sowerby, 1829)  
(Text-figs 6J, K, 12M–O, R–X, 13M–T)

part 1829. *Pollicipes maximus* J. de C. Sowerby, p. 222, pl. 606, figs 4, 6 only.

1851. *Scalpellum maximum* (Sowerby); Darwin, p. 26, pl. 2, figs 1, 4–10.

1851. *Scalpellum hastatum* Darwin, p. 37, pl. 2, figs 13a–d. part 1906. *Brachylepas fallax* (Darwin); Woodward, p. 340, text-fig. 20 only.

1906. *Scalpellum maximum* (Darwin); Woodward, p. 350, text-figs 33a, b, 34, 35.

1923. *Scalpellum (Arcoscappelum) maximum* Sowerby; Withers, p. 20, pl. 1, figs 35–41, pl. 2, figs 1–12.

1935. *Scalpellum (Arcoscappelum) maximum* (J. de C. Sowerby); Withers, p. 239, pl. 29, figs 2–10, pl. 30, figs 1–12; pl. 31, figs 1–19.

part 1953. *Scalpellum (Arcoscappelum) maximum* (J. de C. Sowerby); Carlsson, p. 18, pl. 4, figs 5–7, 10 only.

2015. *Regioscappelum maximum* (J. de C. Sowerby); Gale, p. 33, fig. 18N, O, P, S.

2025. *Regioscappelum maximum* (J. de C. Sowerby); Gale, p. 162, pl. 46, figs 1–8.

DIAGNOSIS: A large species with sharply demarcated parietes and intraparietes, in which the valves are entirely devoid of apicobasal ribs or striations.

TYPE: A carina figured by J. de C. Sowerby (1829, p. 606, fig. 4) was selected as lectotype by Withers (1923). The specimen (NHMUK In.13658) came from the *M. coranguinum* Zone (Coniacian or lower Santonian) of Northfleet, Kent.

MATERIAL: Carlsson (1953, p. 18) recorded hundreds of valves of this species, from localities both the Kristianstad Basin and the Vomb Trough, in the SMNH and the Palaeontological Institute in Lund. The material in the SMNH which I have seen is all from Söndraby, and is here assigned to *Solidoscalpellum angelini* (Darwin, 1851). The capitulum figured by Carlsson from Köpings (Text-fig. 6J, K) is preserved in the MZLU (LO3534t). The carina from Västra Olinge assigned to *Scalpellum* (*Arcoscalpellum*) *maximum* var. *sulcatum* (J. de C. Sowerby, 1829) by Carlsson (1953, pl. 5, fig. 1) is in the same collection (LO 3532t) and is here referred to *Regioscalpellum ahlbergi* sp. nov.

REMARKS: Typical material of this species from the Campanian chalks of Germany and the UK are illustrated in Text figs 12M–O, R–X and 13M–T. The capitulum from Köpings (Text-fig. 6J, K) differs from these principally in its rhombic rather than crescentic tergum but falls within the range of variation of the species. Carinae figured by Carlsson (1953, pl. 4, figs 7–10) also belong to this species.

*Regioscalpellum ahlbergi* sp. nov.  
(Text-fig. 8A–F)

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1953. *Scalpellum* (*Arcoscalpellum*) *maximum* (J. de C. Sowerby) var. *sulcatum* J. de C. Sowerby; Carlsson, p. 20, pl. 5, fig. 1.

DIAGNOSIS: *Regioscalpellum* in which the carina is very robust and thick-shelled, the basal part of the tectum is finely striated.

TYPE: The carina figured in Text-fig. 8A–D is the holotype (MZLU LO12538T). The other figured carina is the paratype (MZLU LO12539t), as is the carina figured by Carlsson (MZLU LO3525t). All are from the upper lower Campanian of Västra Olinge, Skane.

MATERIAL: Two further carinae from the type locality (MZLU LO, unregistered).

DERIVATION OF NAME: For Prof. Per Ahlberg, University of Lund, who has helped greatly with this project.

DESCRIPTION: Only carinae are known. These are very robust and thick-shelled, and the apex is strongly inclined ventrally. The tectum is convex, and sharply demarcated from the parietes by narrow lateral ridges; in some specimens (e.g., Text-fig. 8E, F) there is a poorly defined apicobasal ridge, but in others (e.g., Text-fig. 8A–C), the tectum is evenly convex. The basal part of the tectum is weakly and finely striated. The parietes are slightly concave apically, broaden basally, and are separated from the concave intraparietes by a rounded ridge.

REMARKS: The carina of *Regioscalpellum ahlbergi* sp. nov. is similar in shape to specimens of *R. maximum* in which the parietes and intraparietes are sharply demarcated (e.g., Text-fig. 13R–T) – the var. *sulcatum* of previous authors from Campanian chalks. However, it is far more robust and the valves of all five specimens are two to three times thicker than those of *R. maximum*. Additionally, the basal part of the tectum is finely striated. The species probably evolved from *R. maximum*, adapting to a high-energy coastal environment by developing a robust form.

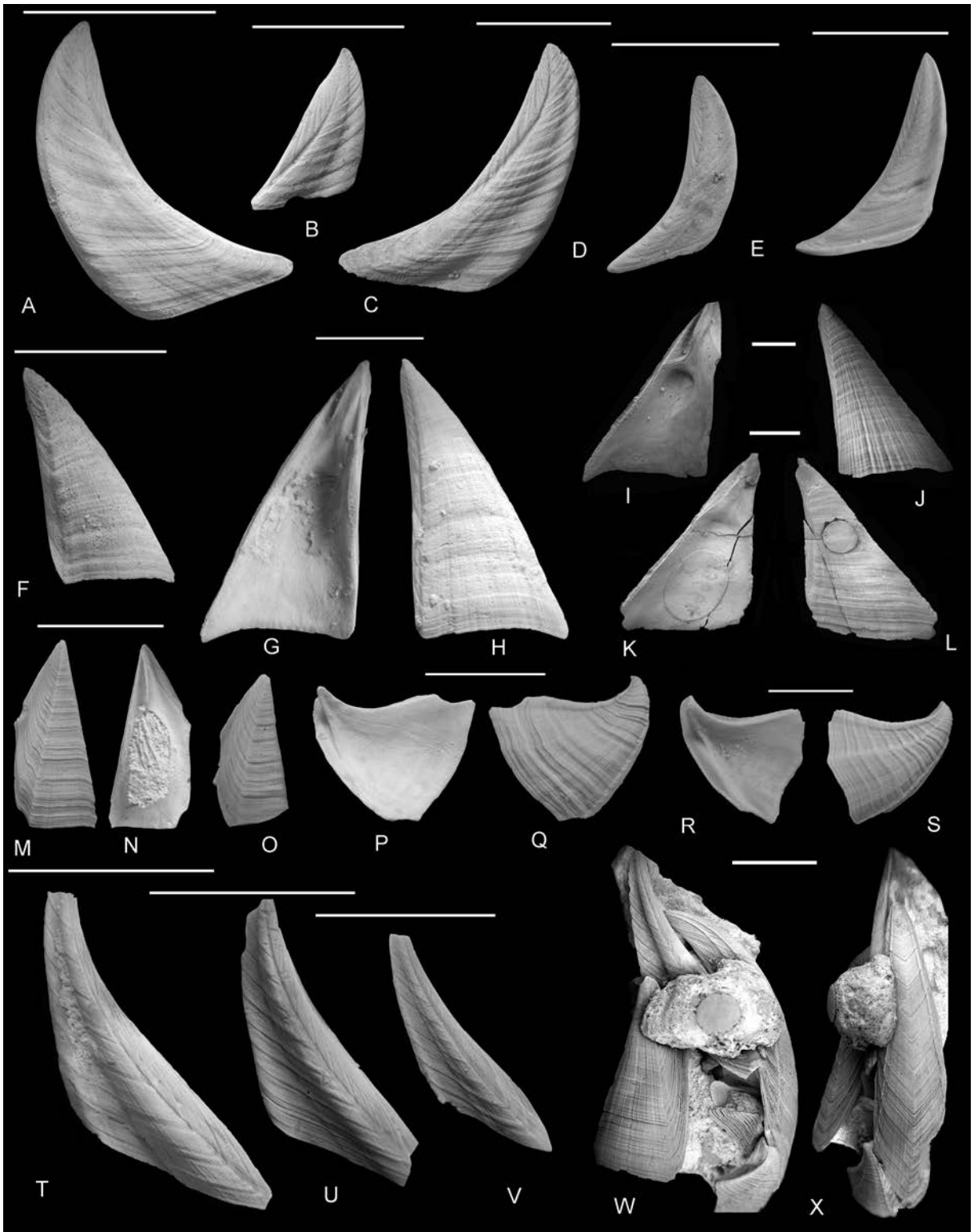
Genus *Diotascalpellum* Gale, 2015

TYPE SPECIES: *Scalpellum diota* Hoek, 1907, by original designation.

OTHER SPECIES: *Scalpellum rubrum* Hoek, 1883; *Scalpellum gigas* Hoek, 1883; *Scalpellum indicum* Hoek, 1883; *Pollicipes angustatus* Geinitz, 1843; *Arcoscalpellum scaniensis* Gale in Gale and Sørensen, 2015; *Scalpellum gracile* Bosquet, 1854; *Scalpellum fossula* Darwin, 1851.

DIAGNOSIS: Scalpelline in which there is no specialised contact between the carina and carinolatus, merely a crescentic concavity on the interior of the plate which forms a rim slightly overlapping the upper latus. The umbo of the carinolatus is upright, only slightly incurved, the dorsal margin gently convex;

Text-fig. 12. Cirripedes from the Campanian of southern Sweden. A–H, P, Q – *Solidoscalpellum angelini* (Darwin, 1851); A–E – SMNH Ar0008780a–e, terga in external views; F–H – SMNH Ar0008723a–c, scuta in external (F, H) and internal (G) views; P, Q – SMNH Ar0008784, carinolatus in internal (P) and external (Q) views. I–L – *Solidoscalpellum cylindraceum* (Darwin, 1851), scuta in internal (I, K) and external (K, L) views; I, J – NHMUK In.26347; K, L – NHMUK I.13664. M–O, R, S–X – *Regioscalpellum maximum* (J. de C. Sowerby, 1829);



M–O – NHMUK Pi In 66711 (M, N), 66712 (O), scuta in external (M, O) and internal (N) views; R, S – NHMUK Pi In 66713, *carinolatus* in internal (R) and external (S) views; T–V – NHMUK Pi In 66714–66716, terga in external views; W, X – NHMUK I.750, capitulum in lateral (W) and dorsal (X) views, original of Smith (1816, pl. 3, fig. 4), Withers (1935, pl. 30, fig. 1), and Gale (2025, pl. 46, fig. 1). Provenance: A–H, P, Q are from the upper lower Campanian of Sönderby, Skåne, Sweden; I–L, W, X are from the upper Campanian of Norwich, Norfolk, UK; M–O, R–V are from the lower Campanian of Misburg, Hannover, Germany. Scale bars equal 5 mm.

inframedian surface of carinolatus well demarcated and slightly inset (after Gale 2015).

*Diotascalpellum fossula* (Darwin, 1851)

1851. *Scalpellum fossula* Darwin, p. 24, pl. 1, figs 4a–h.  
 1906. *Scalpellum fossula* Darwin; Woodward, p. 352, fig. 36.  
 1922. *Scalpellum (Arcoscalpellum) fossula* Darwin; Withers, p. 656, pl. 10, fig. 6.  
 1923. *Scalpellum (Arcoscalpellum) fossula* Darwin; Withers, p. 16, pl. 1, figs 15–29.  
 1935. *Scalpellum (Arcoscalpellum) fossula* Darwin; Withers, p. 223, pl. 26, figs 2–10; pl. 27, figs 2–6.  
 1953. *Scalpellum (Arcoscalpellum) fossula* (Darwin); Carlsson, p. 17, pl. 4, figs 1–4.  
 2015. *Diotascalpellum fossula* (Darwin); Gale, p. 33, fig. 18A–C.  
 2025. *Diotascalpellum fossula* (Darwin); Gale, p. 161, pl. 47, figs 1–11.

DIAGNOSIS: A *Diotascalpellum* in which the tectum of the carina bears two broad lateral ridges and the tergum lacks an apicobasal groove.

TYPES: A partial capitulum in the collection of the NCM (no. 2136) was chosen by Withers (1912, p. 311) as lectotype. It was formerly in the collection of Robert Fitch and studied and figured by Darwin (1851).

MATERIAL: Carlsson (1953, p. 18) records extensive material of this species, probably all from the upper Campanian of Köpinge, in the SMNH, the Geological Survey of Sweden and the Palaeontological Institute in Lund. I have been unable to trace any of these specimens.

REMARKS: The illustrations and description of this species by Carlsson (1953, pl. 4, figs 2–4) conform well with specimens from the UK (Gale 2025, pl. 47, figs 1, 8, 11) particularly in the raised ridges on the lateral margins of the tectum.

Genus *Solidoscalpellum* Gale, 2025

DIAGNOSIS: A scalpellid in which the apical part of the carina is greatly thickened and the scuta are

strongly inclined dorsally. The terga are crescentic, and upper latera, inframedian latera and rostrilatera were probably not present.

TYPE SPECIES: *Scalpellum maximum* var. *cylindraceum* Darwin, 1851.

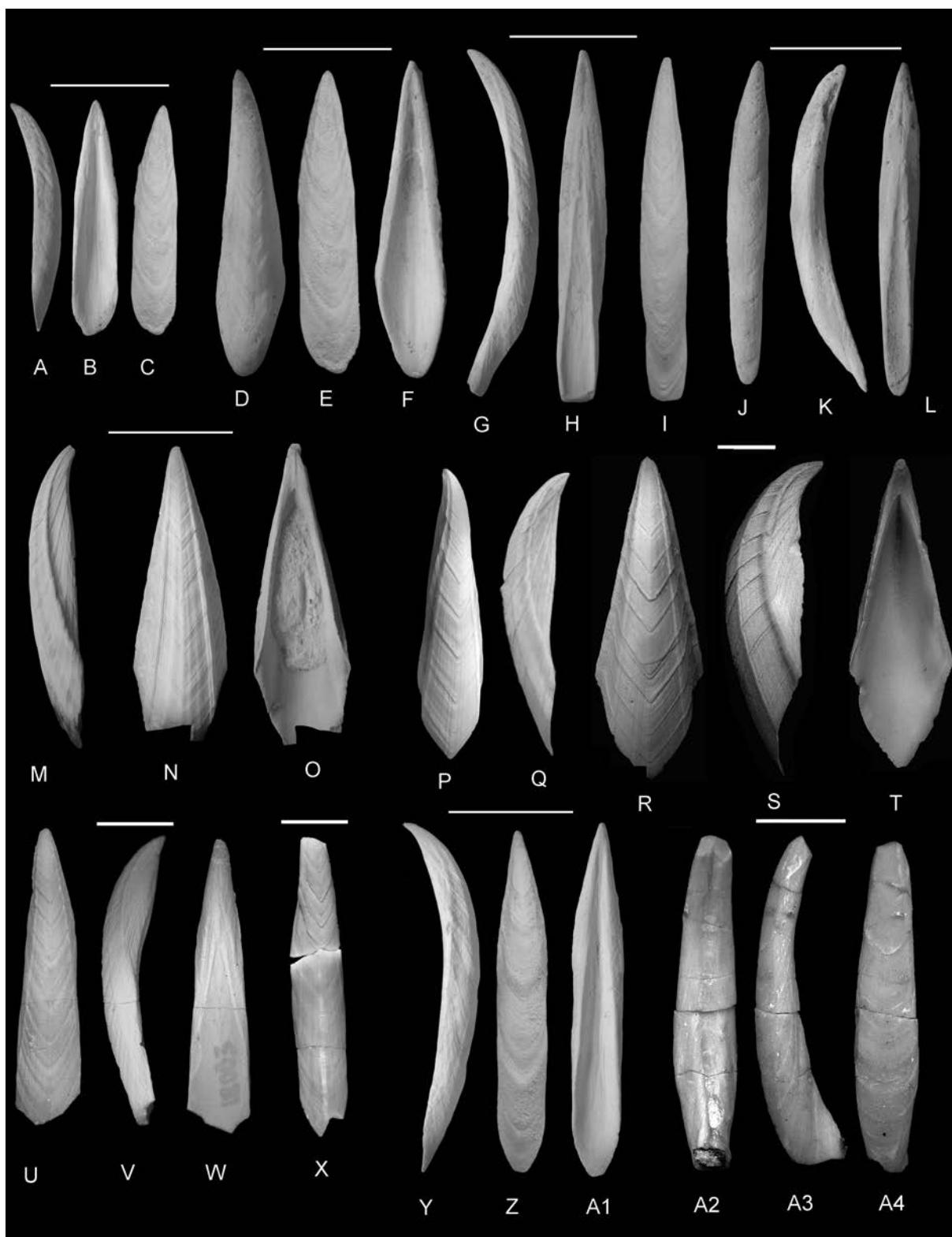
INCLUDED SPECIES: *Arcoscalpellum maximum* var. *triminghamensis* Withers, 1935; *Cretiscalpellum sharapovi* Alekseev, 2009; *Pollicipes angelini* Darwin, 1851.

REMARKS: *Solidoscalpellum* was established on the basis of robust carinae and triangular, ventrally inclined scuta from the upper Campanian chalk of Norwich, Norfolk, UK (Gale 2025) and assigned to *Solidoscalpellum cylindraceum* (Darwin, 1851). The carinae were previously referred to *Arcoscalpellum maximum* var. *solidulum* (Steenstrup, 1839) by Withers (1935, p. 256), but Gale (2025) argued that the type specimen (Text-fig. 6L–N) is too poorly preserved to be determinable. Both carinae and scuta displayed remarkable similarities with *Pachyscalpellum* Buckeridge, 1991 (dorsally inclined scuta, robust, thickened basally narrowing carinae – see Gale *et al.* 2020), but the presence of internal grooves on the apical interior of the occludent margin for the accommodation of dwarf males indicated scalpellid affinities.

The discovery in the SMNH of a large suite of over 150 valves from the upper lower Campanian of Söndraby, morphologically similar to the type species of *Solidoscalpellum*, permits the genus to be described in more detail, and comparisons to be made with *Regioscalpellum maximum* (J. de C. Sowerby, 1829) with which the taxon has been confused (Darwin 1851; Withers 1935). The Swedish material is referred to *Solidoscalpellum angelini*. Interestingly, the extensive material of *S. angelini* from Sönderby includes only terga, scuta, carinolatera and carinae, and a complete absence of other lateral plates, which were probably not present in this genus (Text-fig. 7A), but present in *Regioscalpellum maximum* (Text-fig. 7B).

The carinae of *Solidoscalpellum* (Text-fig. 13A–L, U–A4) are narrow and variable in morphology, ranging from forms in which the apical portion of the valve is not thickened and the interior of the valve is strongly concave (Text-fig. 13D–F), to forms in which

Text-fig. 13. Comparative morphology of scalpellid carinae. A–L, Y–A1 – *Solidoscalpellum angelini* (Darwin, 1851); SMNH Ar0008784a–e, carinae in lateral (A, D, G, K, Y), dorsal (C, E, J, Z), and internal (B, F, H, L, A1) views. M–T – *Regioscalpellum maximum* (J. de C. Sowerby, 1829), carinae in lateral (M, Q, S), dorsal (N, P, R), and internal (O, T) views; M–O – NHMUK Pi In 66717; P, Q – NHMUK Pi In 66718; R–T – NHMUK I.13663, original of Withers (1935, pl. 32, fig. 6). U–X – *Solidoscalpellum cylindricum* (Darwin, 1851), carinae in lateral (V), dorsal (U, X), and internal (W) views; U–W – NHMUK In.63520, original of Gale (2025, pl. 40, fig. 4); X – NHMUK I.13661, lectotype, original of Darwin →



(1851, pl. 2, fig. 2). A2–A4 – *Solidoscalpellum triminghamensis* (Withers, 1935), NHMUK In.30165, carina in internal (A2), lateral (A3), and dorsal (A4) views., original of Withers (1935, pl. 32, fig. 4). Provenance: A–L, Y–A1 are from the upper lower Campanian of Sönderby, Skåne, Sweden; M–Q are from the lower Campanian of Höver, Hannover, Germany; R–X are from the upper Campanian of Norwich, Norfolk, UK; A2–4 are from the lower Maastrichtian, probably *Belemnella sumensis* Zone of Trimingham, Norfolk, UK. Scale bars equal 5 mm.

the apical portion is robust, and the interior concavity of the valves is restricted to a shallow, apically narrowing groove occupying the basal part only (Text-fig. 13G–L). The tectum is convex, with V-shape growth increments towards basal margin; the boundary of the tectum and the parietes are poorly defined. When present, the intraparietes are short and restricted to the apical part of the carina (Text-fig. 13G, Y). In contrast, the carinae of *Regioscalpellum maximum* (Text-fig. 13M–T) are relatively short, broad basally, and the limit of the tectum and intraparietes is sharply defined (Text-figs 12W, X, 13M, N, P, R, S). The intraparietes are also well defined and occupy about 75% of the total height of the valves.

The terga of *Solidoscalpellum* (Text-fig. 12A–E) have a crescentic, asymmetrical boomerang-shaped outline; the occludent margin is strongly and evenly convex, the scutal margin short and straight and the carinal margin strongly concave. The carinal surface is separated from the scutal surface by a groove, is very narrow and is only present on the apical half of the valve; it tapers slowly towards the base. In contrast, the terga of *Regioscalpellum maximum* (Text-fig. 12T–X) are elongated, triangular, with a sinusoidal, long carinal margin, a gently convex occludent margin and a narrow carinal surface which broadens basally.

The scuta of *Solidoscalpellum* (Text-fig. 12F–L) are twice as high as broad, inclined ventrally, and the occludent margin is weakly convex. The tergal surface is very narrow, and there is a short rostral-basal process. The scuta of *Regioscalpellum maximum* (Text-fig. 12M–O, W) are upright, the occludent surface forms a flat isosceles triangle, and the tergal surface is broad with undulose growth lines. The carinolatera (Text-fig. 12P–S) of both species are similar in shape, but those of *R. maximum* carry better defined ridges running from the apex to the inframedian latus margin. In conclusion, *Solidoscalpellum* probably evolved from *Regioscalpellum* in the Campanian by developing a very robust carina with a shallow interior groove, shape changes in the scuta and terga and loss of some latera.

*Solidoscalpellum angelini* (Darwin, 1851)

(Text-figs 7A, 8L, M, 11A–H, P, Q,  
12L, M, 13A–L, Y–A1)

part 1839. *Pollicipes maximus* Sowerby; Steenstrup, pl. 4, fig. 17 only.

part 1851. *Pollicipes Angelini* Darwin, 1851, p. 56, pl. 3 figs 7a, b only.

non 1906. *Pollicipes angelini* Darwin; Woodward, p. 346, text-figs 25, 26.

non 1912 *Pollicipes angelini* Darwin; Withers, p. 320.

part 1953. *Scalpellum (Arcoscalpellum) maximum* (J. de C. Sowerby); Carlsson, p. 18, pl. 9, figs 11–14 only.

2015. *Arcoscalpellum* cf. *maximum* (J. de C. Sowerby); Gale in Gale and Sørensen, p. 226, fig. 11C.

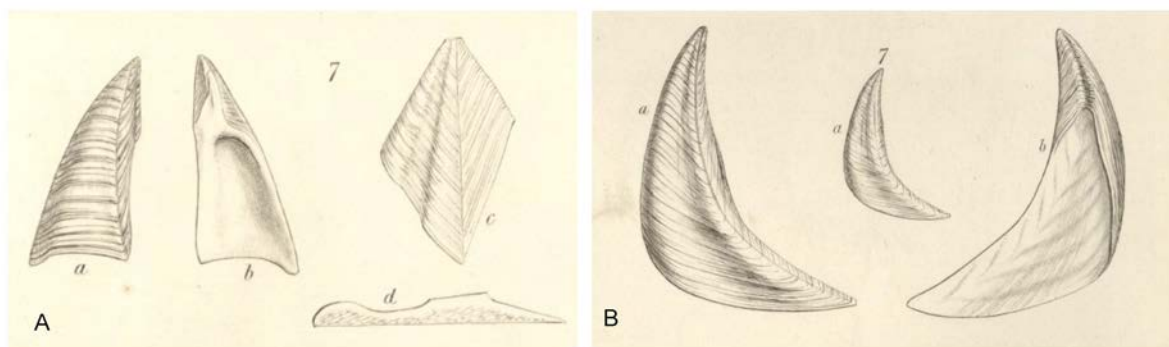
DIAGNOSIS: *Solidoscalpellum* in which the upright, triangular scutum is only slightly inclined ventrally, the occludent margin is evenly and gently convex, and the tergal surface is very narrow and of even breadth from the apex to the base.

TYPE: The well-preserved scutum figured by Darwin (1851, pl. 3, fig. 7a, b) is selected as lectotype. This is probably the specimen from Kjøge, Skåne, which was sent to him by J. Steenstrup, collected by N.P. Angelin. According to Christensen (1975) there were 2 former localities at Kjøge, one in the *Belemnellocomax mammillatus* Zone, the other in the *B. balsvikensis* Zone. The present whereabouts of the specimen are unknown.

MATERIAL: Over 150 valves, including scuta, terga, carinae and carinolatera from the *B. mammillatus* Zone of Söndraby, Skåne (SMNH Ar0008723, Ar0008782a, Ar0008780, Ar0008784). Carlsson (1953, pl. 4, figs 11–14) figured material from the same locality. A large scutum from Oppmana is present in the MZLU collection (MZLU LO12551t).

DESCRIPTION: Terga crescentic, shaped like a slightly asymmetric boomerang (Text-fig. 12A–E); occludent margin long and strongly convex, scutal margin short and straight, carinal margin evenly concave. Basal angle acute. A short, basally narrowing carinal surface is separated from the broad occludent surface by a shallow groove; the occludent surface bears a shallow, central apicobasal depression. Scuta triangular, height approximately twice breadth of basal margin, slightly inclined ventrally (Text-fig. 12F–H). Occludent surface smooth, convex; tergal surface narrow, of even breadth from apex to base. Interior of scutum with deeply impressed, subapical scutal adductor scar. A groove for the accommodation of dwarf males is present on the apical interior of the occludent margin (Text-fig. 12G). Very large scuta (Text-fig. 8L, M) reach a height of 25 mm. Carinolatera (Text-fig. 12P, Q) equilaterally triangular, concavo-convex, carinal margin gently convex, acute umbo reflexed.

Carinae (Text-fig. 13A–L, Y–A1) narrow, evenly convex dorsally, concave ventrally; tectum convex,



Text-fig. 14. Original figures of Darwin (1851, pls 2, 3). A – Darwin’s material of *Pollicipes Angelini*. The scutum figured in A (a, external, b, internal) is here selected as lectotype (Darwin 1851, pl. 3, fig. 7). This probably came from the Campanian of Kjøge in Sweden; c, d are a tergum of *Cretiscalpellum glabrum* (Roemer, 1841), probably from the upper Campanian of Norwich, UK. B – Tergum of *Solidoscalpellum cylindraceum* (Darwin, 1851) in external (a, a) and internal (b) views. Figured after Darwin (1851, pl. 2, fig. 7) as *Scalpellum maximum*, Var. 3, probably from the upper Campanian of Norwich, UK. All specimens lost. Scale bar equals 10 mm.

poorly and variably differentiated from parietes. Intraparietes short, poorly demarcated. External growth lines with U-V-shape towards basal margin. Carinae of rather variable morphology. Some (e.g., Text-fig. 13D–F, Y–Z) are concavo-convex in cross-section with a deep interior cavity, others (e.g., Text-fig. 13G–L) greatly thickened, with inner cavity forming a shallow sulcus on the basal two thirds of the valve.

The reconstruction (Text-fig. 7A) shows a biconvex capitulum, with a very long, strongly convex occludent margin. The reconstruction is based on the fact that scalpellids with full (i.e., unreduced) terga always have a straight contact between the scutum and tergum (Gale 2025, text-fig. 79). There is thus a large, oval gap between the tergum and the inner margin of the carina. With this reconstruction, there is no space for inframedian or rostrilatera, although an upper latus could be present. The fact that all latera, except the carinolatus, are absent in the Söndraby material tends to support this reconstruction. This compares strikingly with the reconstruction of *Regioscalpellum maximum* (Text-fig. 7B) in which a full complement of plates is present.

REMARKS: Following Withers (1935), this species has been viewed as a synonym of *Regioscalpellum maximum*. Darwin’s original figure (refigured here as Text-fig. 14A) illustrated a well-preserved scutum, probably the specimen from Kjøge (Skåne), sent to him by Steenstrup (Darwin 1851, pl. 3, fig. 7a, b) and a tergum belonging to *Cretiscalpellum glabrum* (Darwin 1851, pl. 3, fig. 7c, d), probably from the Campanian chalk of Norwich, Norfolk, UK. The

scutum (Text-fig. 14A, B) is identical in all details with material figured here (Text-fig. 12F–H) from Söndraby, which is about 9 km from Kjøge and is probably of the same age (Text-fig. 1B). This species differs from *Solidoscalpellum cylindraceum*, from the upper Campanian chalk of Norfolk, UK, in a number of features. Firstly, the terga (Text-fig. 12A–E) have a short, straight scutal margin, as compared with the longer, more convex scutal margin of *S. cylindraceum* (Text-fig. 14B). Secondly, the scuta of *S. angelini* (Text-fig. 12F, H) are more upright than those of *S. cylindraceum* (Text-fig. 12I–L) and have a tergal surface of even breadth which extends from the apex to the base.

#### Family Pycnolepadidae Gale and Vidovic, 2023

DIAGNOSIS: Capitulum symmetrical, laterally compressed, upright, comprising paired scuta, terga, upper latera, carina, rostrum. Exterior of valves with regular, terraced sculpture. Noded apicobasal ridges on scuta and terga.

INCLUDED GENERA: *Pycnolepas* Withers, 1914; *Faxelepas* Gale, 2014b; *Pedupycnolepas* Gale, 2014b.

#### Genus *Faxelepas* Gale, 2014b

DIAGNOSIS: Pycnolepadids which display variable asymmetry in slanting of rostra and carinae and breadth of apicobasal ridges on scuta and terga; tergal notch on scuta deep, elongated; broad, flat occludent surface on interior of scuta extends to basal margin.

TYPE SPECIES: *Pycnolepas bruennichi* Withers, 1914.

INCLUDED SPECIES: *Pollicipes paronai* De Alessandri, 1895; *Pycnolepas landenica* Withers, 1953; *Pycnolepas ignabergensis* Carlsson, 1953.

*Faxelepas ignabergensis* (Carlsson, 1953)  
(Text-fig. 15A–D)

1953. *Pycnolepas ignabergensis*, Carlsson; p. 23, pl. 5, fig. 10, pl. 6, figs 1, 2.

2007. *Pycnolepas ignabergensis*, Carlsson; Jagt *et al.*, p. 39.

2023. *Faxelepas ignabergensis* (Carlsson); Gale and Vidovic, p. 28.

DIAGNOSIS: *Faxelepas* in which the terracing on scutum comprises commarginal raised ridges and the intervening grooves bear fine apicobasal striations.

TYPE: The scutum figured by Carlsson (1953, pl. 6, fig. 2) is holotype (SMNH Ar.0008742). Upper lower Campanian, Ignaberga, Skåne, Sweden (Text-fig. 15B).

MATERIAL: A further broken scutum from the type locality (SMNH Ar.0008731), and a partial scutum from the upper lower Campanian of Västra Olinge (MZLU LO12552t).

DESCRIPTION: The scuta (Text-fig. 15A–D) are flat, triangular and strongly inclined dorsally. The occludent margin is very convex, and the apicobasal ridge is variable in breadth. In the type specimen (Text-fig. 15B) it is narrow but is broad on the specimen from Västra Olinge (Text-fig. 15C). The tergal surface is narrow (1/3 of that of the occludent surface) and depressed. The sculpture on the holotype comprises sharp, closely and evenly spaced ridges which parallel the basal margin on the occludent surface but deflect obliquely towards the tergal margin on the tergal surface. Between the transverse ridges, there is a very fine, closely spaced apicobasal striation. On the specimen from Västra Olinge, the commarginal ridges are fewer and more widely separated (Text-fig. 15C). The interior of the scutum (Text-fig. 15D) shows a deep tergal notch and a very broad occludent surface.

REMARKS: This species differs from its congeners (Text-fig. 15E, F, I–K) in the very strongly convex lower part of the occludent margin, and the nature of the apically deflected ribbing on the tergal surface. In

*F. paronai* (Text-fig. 15E, F) and *F. bruennichi* (Text-fig. 15I, J) these run transversely to the tergal margin, but in *F. ignabergensis* they are deflected apically.

Order Balanomorpha Pilsbry, 1916

DIAGNOSIS: Symmetrical sessile cirripedes in which the rostrum and carina are of similar size, and the terga and scuta form an operculum positioned in an orifice. There is a strong articulation between the terga and scuta.

REMARKS: The definition of the order was modified to include the Brachylepadidae.

Family Brachylepadidae Woodward, 1901

DIAGNOSIS: Capitulum low, carina and rostrum short, hemiconical; primary wall surrounded by imbricating plates conjoined by peg-and socket articulations. Rostro- and carinomarginals absent.

INCLUDED GENERA: *Brachylepas* Woodward, 1901; *Epibrachylepas* Gale in Gale and Sørensen, 2014; *Fallaxlepas* Gale, 2020; *Parabrachylepas* Gale in Gale and Sørensen, 2014.

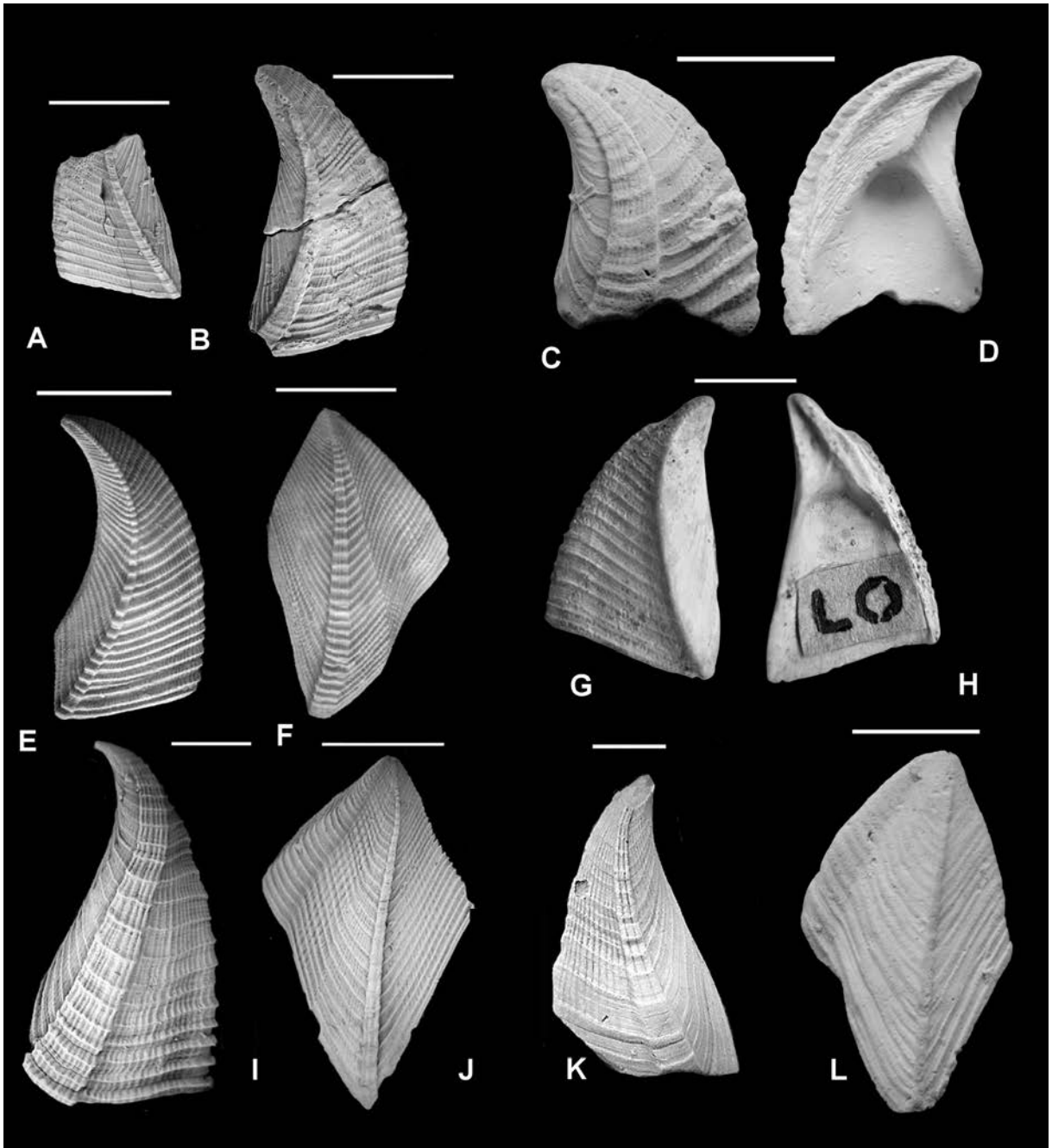
Genus *Fallaxlepas* Gale, 2020

DIAGNOSIS: Rostrum and carina tall, cylindrical, tapering apically, often with slight lateral slanting; rostrum, carina and imbricating plates smooth or with weakly defined commarginal growth lines; scuta, terga and upper latera with sharply defined, closely spaced terracing.

TYPE SPECIES: *Pollicipes fallax* Darwin, 1851.

INCLUDED SPECIES: *Brachylepas nervosa* Alekseev, 2009.

REMARKS: The tall, subcylindrical carinae (dorsally reclined) and rostra distinguish this genus from *Brachylepas* in which the rostra and carinae are low and blunt apically. However, in its possession of tall rostra and carinae, the shape of the scuta and terga, and the strong, even terracing on the scuta and terga, *Fallaxlepas* appears to be closer to the pycnolepadids than do other brachylepadids. Indeed, Withers (1914, 1923) originally placed *Pollicipes fallax* in the genus *Pycnolepas* (see Withers 1935, p. 372).



Text-fig. 15. Cirripedes from the Campanian of southern Sweden. A–D – *Faxelepas ignabergensis* (Carlsson, 1953); A – SMNH Ar0008742z, partial paratype scutum, original of Carlsson (1953, pl. 6, fig. 1); B – SMNH Ar0008742, external view of holotype scutum, original of Carlsson (1953, pl. 6, fig. 2); C, D – MZLU LO12552t, external (C) and internal (D) views of scutum. E, F – *Faxelepas paronai* (De Alessandri, 1895); E – NHMUK IC 1823, external view of scutum, original of Gale and Vidovic (2023, fig. 15C); F – NHMUK IC 1827, external view of tergum, original of Gale and Vidovic (2023, fig. 15). G, H, L – *Fallaxlepas fallax* (Darwin, 1851); G, H – MZLU LO3534t, scutum in external (J) and internal (K) views, original of Carlsson (1953, pl. 6, fig. 4); L – MZLU LO12553t, tergum in external view. I, J – *Faxelepas bruenichi* (Withers, 1914); I – NHMUK Pi In 64875, scutum in external view, original of Gale and Vidovic (2023, fig. 15R); J – NHMUK Pi In 64878, tergum in external view, original of Gale and Vidovic (2023, fig. 15T). K – *Faxelepas landenica* (Withers, 1953), NHMUK In.38043, scutum in external view, original of Gale and Vidovic (2023, fig. 15Y). Provenance: A, B are from the upper lower Campanian of Ignaberga, Skåne, Sweden; C, D are from the upper lower Campanian of Västra Olinge, Kristianstad Basin, Sweden; E, F are from the Plio-Pleistocene of Rodrigues Ridge, Indian Ocean; G, H are from the upper Campanian of Köpinge, Skåne, Sweden; I, J are from the middle Danian of Faxe, Denmark; K is from the Selandian, Heers Formation of Wansin, NE of Namur, Belgium; L is from the upper lower Campanian of Karlshamn, Skåne, Sweden. Scale bars equal 10 mm (A–H); 5 mm (I–L).

*Fallaxlepas fallax* (Darwin, 1851)  
(Text-fig. 15G, H, L)

- 1851a. *Pollicipes fallax* Darwin, p.75, pl. 4, fig. 8a, b.  
 1857. *Mitella fallax* (Darwin); Bosquet, p. 17, pl. 2, figs 1–12, pl. 3, figs 1, 2.  
 1878. *Pollicipes fallax* Darwin; Kafka, p. 19, pl. 3, figs 2r, 3a, b only.  
 1887. *Pollicipes fallax* Darwin; Fritsch and Kafka, p. 10, fig. 17.  
 1906. *Brachylepas (Pollicipes) fallax* (Darwin); Woodward, p. 340, figs 5–18, 21–24.  
 1914. *Pynolepas fallax* (Darwin); Withers, p. 175, pl. 7, figs 10–14, pl. 8, fig. 5.  
 1923. *Pynolepas fallax* (Darwin); Withers, p. 35, pl. 2, fig. 27.  
 1935. *Brachylepas fallax* (Darwin); Withers, p. 367, pl. 48, figs 1–24.  
 2014. *Brachylepas fallax* (Darwin); Koči *et al.*, p. 227, pl. 3, figs 1, 2, pl. 4, figs 1–8.  
 2020. *Fallaxlepas fallax* (Darwin); Gale, p. 277, fig. 15J, K.  
 2023. *Fallaxlepas fallax* (Darwin); Gale and Vidovic, p. 46, fig. 26A–U.  
 2026. *Fallaxlepas fallax* (Darwin); Gale, pl. 62, figs 1–17.

DIAGNOSIS: *Fallaxlepas* in which the rostrum and carina are smooth or bear only weak growth lines; secondary ridge on tergum weakly developed or absent.

TYPE: A scutum figured by Darwin (1851, pl. 1, fig. 8a) was selected as lectotype by Withers (1912). The specimen is from the upper Campanian chalk of Norwich, Norfolk, UK (NCM 2153).

MATERIAL: I have seen three terga from the upper lower Campanian of Tullstorp in Skåne (PMU 17872–17874) and a tergum from Karlshamn (MZLU LO12553t). Carlsson (1953, pl. 6, figs 3–6) illustrated specimens from the upper lower Campanian of Västra Ölinge in the Kristianstad Basin. The scutum figured by Carlsson (1953, pl. 6, fig. 4) from the upper Campanian of Köpings in the Vomb Trough is in the MZLU collection (LO3534t) and is refigured here (Text-fig. 15G, H).

REMARKS: The terga and scuta conform with material of the species from England and Germany (Gale and Vidovic 2023, fig. 26; Jagt *et al.* 2023, fig. 15A–K) in all details.

OCCURRENCE: Turonian to Maastrichtian in the UK; Campanian and Maastrichtian of southern Sweden, Denmark, Germany, Netherlands, Belgium

(Jagt and Collins 1989); Turonian to Campanian, Czech Republic (Kafka 1878; Fritsch and Kafka 1887; Koči *et al.* 2014).

Genus *Epibrachylepas* Gale in Gale and Sørensen, 2014

DIAGNOSIS: Scutum low, triangular, tergal notch deep, articular ridge present. Tergum kite-shaped, bearing large scutal auricle, tergal depressor scars on interior of lower carinal margin; reticulate sculpture on all plate exteriors. Marginal plate triangular, robust.

TYPE SPECIES: *Epibrachylepas newmani* Gale in Gale and Sørensen, 2014,

INCLUDED SPECIES: *Mitella smeetsi* Bosquet, 1857; *Epibrachylepas lineatus* sp. nov.

REMARKS: *Epibrachylepas* is a derived brachylepadid; the shape of the scutum, the interpenetrant articulation between the scutum and tergum and the presence of discrete tergal retractor scars on the lower carinal margin of the tergum approach the condition in seen in balanomorphs. A pair of marginal plates are present.

*Epibrachylepas lineatus* sp. nov.  
(Text-fig. 5L, M)

urn:lsid:zoobank.org:act:41B955BF-EF27-45D0-9661-AA6D64C54FCC

2015. Scutum (type B) of unknown scalpelliform; Gale and Sørensen, p. 228, fig. 19P, Q.

DIAGNOSIS: *Epibrachylepas* in which the sculpture comprises broad, and evenly separated growth elements separated by constrictions, parallel with the basal margin.

TYPE: The holotype is the well-preserved scutum (NHMUK IC 1017) figured by Gale and Sørensen (2015, fig. 19P, Q). Upper lower Campanian, Ivö Klack, Skåne.

DERIVATION OF NAME: Latin *lineatus*, *-a*, *-um*, with reference to the broadly and evenly spaced growth increments.

DESCRIPTION: The specimen is very small, with a height of 1.3 mm. Scutum triangular, height slightly greater than maximum breadth, weakly inclined

dorsally, apex acuminate. Occludent margin long, slightly undulose, tergal margin depressed. External sculpture comprises broadly and evenly separated growth elements separated by constrictions, parallel with basal margin, but deflected apically close to occludent and tergal margins. Interior of valve shows very large, subapical scutal adductor scar and deep, apical tergal notch.

REMARKS: The specimen agrees in shape (almost equilaterally triangular, slightly inclined ventrally) with scuta of *Epibrachylepas newmani* (Text-fig. 5U, V). Additionally, it bears a deep tergal notch, and a large, subapical scutal adductor scar typical for the genus. It differs from *E. newmani* in the steeper occludent margin, and in the external sculpture, which comprises broad, evenly spaced growth increments. In *E. newmani*, the sculpture is cancellate.

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