

Roveacrinida (Crinoidea, Articulata) from the Late Maastrichtian Peedee Formation (Upper Cretaceous) of North Carolina, USA – the last pelagic microcrinoids.

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Abstract. Microcrinoids belonging to the Order Roveacrinida are described from the Late Maastrichtian Peedee Formation of North Carolina. Five species are present, *Applinocrinus texanus* Peck, 1973, *Lucernacrinus multispinosus* Gale, sp. nov., *Birgenelocrinus degraafi* Jagt, 1999, *B. jagti* Gale, sp. nov. and *Peedeecrinus sadorfi* Gale, gen et sp. nov. Two of these species (*A. texanus*, *B. degraafi*) and close relatives of two others (*Lucernacrinus*, *Birgenelocrinus jagti*) are present in the Late Maastrichtian of the Netherlands and indicate that the Roveacrinida were flourishing and widespread up to the end of the Cretaceous. It is concluded that Paleogene and Neogene records of Roveacrinidae represent contamination of samples by Cretaceous (Turonian) material.

Introduction.

Pelagic microcrinoids of the Order Roveacrinida were abundant and diverse in open marine settings through parts of the Triassic, Jurassic and much of the Cretaceous (Hess and Messing 2011; Hess et al. 2016; Gale 2016), and were locally rock-forming in Cretaceous pelagic limestones of the Tethyan region (e.g. Berthou and Bengston 1988). The order underwent major evolutionary radiations in the Albian-Cenomanian (Hess 2015) and the Early Campanian (Gale 2016, 2017), and representatives of this last radiation are known from the Late Maastrichtian of Europe (Jagt 1999, 2005).

Here we describe a new fauna of Roveacrinida, recovered from clays of the Late Maastrichtian Peedee Formation at Wilmington, on the Brunswick River in North Carolina. The material is abundant and very well preserved, and includes four species, three of which are new. Importantly, it also provides new information about the widespread Maastrichtian species *Applinocrinus*

texanus Jeck, 1972, particularly concerning its ontogeny. The Wilmington fauna shows marked similarities with contemporaneous assemblages described from the Maastrichtian of the Netherlands (Jagt 1999), and provides a valuable insight into North American microcrinoids from the latest Cretaceous.

The roveacrinid material from the Late Maastrichtian of Wilmington, NC, represents the last certainly known representatives of the order Roveacrinida. We discuss the supposed Paleocene and Neogene records of the group from Poland (Salamon et al. 2010; Gorzelak et al. 2011), and conclude that they are contaminants of Turonian roveacrinid species.

Locality and Geology

The geographical location of the locality is shown in Fig. 1 The Late Maastrichtian Peedee Formation is a marine sequence composed of dark greenish to gray muddy sands with some mica and glauconite (Landman et al., 2004, Sohl and Owens, 1991). It rests unconformably on top of the Donoho Creek Formation and is unconformably overlain by Paleogene and younger sediments. The study area is on a structural high known as the Cape Fear Arch. Cretaceous sediments are exposed along much of the axis of the arch while Paleogene and younger rocks are exposed along the flanks (Harris et al. 1986; Harris and Self-Trail 2006; Soller 1988).

At the study area, the Peedee Formation is fine grained muddy sand with irregular calcareous cemented concretions. There are areas where the Pleistocene Waccamaw Formation unconformably rests on the Peedee Formation. The base of the Peedee Formation is not visible at the site. The exposed outcrop where samples were collected is weathered to a greenish yellow colour. The Peedee Formation in North Carolina probably belongs to the *Discoscaphites conradi* Zone (Landman et al. 2004) which is of Upper Maastrichtian (but not uppermost) in age.

Methods

Bulk samples were collected from the outcrop and later thoroughly dried. Once dried, the bulk samples were soaked in water to break the matrix down enough to wet sieve using a 0.6 mm brass sieve retaining the fraction that was larger than 0.6 mm. The drying and sieving process was repeated to remove as much of the remaining silt and clay as possible. The residue was dried and then dry sieved using a 0.6 mm brass screen and a 1.0 mm brass screen. The larger fraction material was picked under magnification (reading glasses) while the 0.6 to 1.0 mm fraction was picked under a binocular microscope.

Fauna.

The abundant microcrinoid material from the Late Maastrichtian of Wilmington, NC contains several hundred cups and thousands of brachials of Roveacrinida. It includes five taxa; two Applinocrininae, *Applinocrinus texanus* Peck, 1972 and *Peedeecrinus sadorfi* Gale, gen. et sp. nov., and three Hessicrininae; *Lucernacrinus spinosus* Gale, sp. nov., *Birgenelocrinus degraafi* Jagt, 1999 and *B. jagti* Gale, sp. nov. Of these, *A. texanus* is known from the Upper Campanian and Maastrichtian of the US Gulf Coast (Texas, Florida, Mississippi; Peck, 1972; Gale 2016), the Maastrichtian of the Netherlands and Germany (Jagt 1999) and the Upper Campanian or Maastrichtian of south-east India (). *Birgenelocrinus degraafi* occurs in the Upper Maastrichtian of Maastricht, Netherlands, and *Lucernacrinus multispinosus* sp. nov. bears comparisons with some individuals of *Veugeliersia diana* Jagt, 1999 (e.g. Pl. 45 figs 1-3). Gale (2016) treated *V. diana* as an heterogeneous assemblage of poorly preserved Hessicrininae.

It therefore appears that an abundant and widespread fauna of Roveacrinida, subfamilies Applinocrininae and Hessicrininae, was present on both sides of the Atlantic in the Late Maastrichtian.

Cenozoic roveacrinids?

Although roveacrinids have long been considered to become extinct at the K-Pg boundary (see refs in Jagt 1999), Salomon et al. (2010) described finds of roveacrinid ossicles from the Danian P1b zone of the Vistula valley, eastern Poland. Subsequently, Gorzelak et al. (2011) documented material from the Middle Miocene (NN5-6) of Korytnicka, Poland. Here, we review this material in the context of our own studies.

Salomon et al. (2010 Fig. 2) illustrated two roveacrinid proximal brachials from the Danian P1b zone of the Vistula. Fig. 2D (refigured here as Fig. 13) is a damaged IIBr2 (not a radial as stated) of a *Roveacrinus* sp., group of *R. alatus* Douglas, 1908. This has a narrow median ridge and weakly reticulate lateral surfaces, a form typical of and common in the Lower and Middle Turonian of the Anglo-Paris Basin, but not known from other levels. A comparable ossicle from the mid- Turonian of Eastbourne is figured here for comparison (Fig. 2). Fig. 2E of Salomon et al. (2010) is a IBr2 of a *Roveacrinus* sp. nov. aff. *communis* Douglas, 1908; this morphology is highly distinctive, with strong, rounded, bifid, median ridges separated by a weakly reticulate central concavity. Additionally, the aboral part of the ossicle is ridged and reticulate. This IBr2 morphology is characteristic of and restricted to the early Upper Turonian and occurs widely in the Anglo-Paris Basin (Fig. 2). The succession of Turonian-Coniacian forms of *Roveacrinus* IBr2 is shown in Fig. 2. The other 3 ossicles are indeterminate crinoid distal brachials. The Neogene material includes a single IIBr2 (Gorzelak et al. 2011, Fig. 2a,b; figured as a radial) which also has a Turonian morphology.

The genus *Roveacrinus* ranges from the Late Albian to the mid-Coniacian; records from the Santonian (Rasmussen 1961, pp 366-7) are mis-horizoned. The record of *Roveacrinus* cf. *communis* from the lower Campanian of Sussex (Gale 2016, fig. 90) is actually an undescribed species of *Birgenelocrinus*. In residues from over 1,000 samples of Santonian, Campanian and Maastrichtian chalk from northwest Europe, not a single cup, radial, or distinctive proximal brachial of the genus *Roveacrinus* has been observed amongst over 5,000 roveacrinid plates

seen, whereas hessicrinine, saccocone and applinocrinine forms are often abundant.

In view of these facts, we believe that the material figured by Salomon et al. (2010) actually originated in the Turonian, and represents either reworking into the Danian (unlikely) or (more likely) contamination from Turonian samples. The very high abundance of *Roveacrinus* material in some Turonian residues makes contamination a real problem.

In conclusion, a moderately diverse and very abundant (four genera, four species) fauna of Roveacrinida existed in the Late Maastrichtian of North Carolina, and represent the youngest roveacrinids known. The order became extinct at the K-Pg boundary.

Systematic Palaeontology (ASG)

Roveacrinida Sieverts-Doreck, in Ubaghs, 1953.

Applinocrininae Hess, 2011

Diagnosis. (modified after Gale 2016). Theca conical to fusiform, delicately constructed, consisting of a basal circlet, usually fused, made up of five basals and a small centrale; five convex, trapezoidal radials; arms reduced to a single brachial, flattened, highly modified, triangular, imbricating; the five brachials form a cap over the cup.

Phylogeny. The new material described herein, in conjunction with the studies of Gale (2016, 2017), permits the reconstruction of a phylogenetic tree of this highly derived group of Roveacrinida (Fig.3). The subfamily evolved from a saccocone ancestor, by the (probably pedomorphic) development of a single brachial in each radius. *Sagittacrinus* Gale, 2016, an applinocrinine known only from brachials, is basal to the subfamily, because the brachials do

not form a closely articulated adoral cap. *Applinoecrinus cretaceus* forma *cretaceus*, with a tight brachial cap, appears in the Late Santonian, and survived to the late Campanian, when it is replaced by *A. texanus* (possibly late Campanian, Maastrichtian). *A. cretaceus* forma *spinifer* evolved by the development of a conical radial spine in the early Campanian, and subsequently gave rise to the Maastrichtian *Peedeecrinus* gen. nov. by the development of vertical, trifoliate lateral bars on the radial spines.

Genus *Applinoecrinus* Peck, 1973

Applinoecrinus texanus Peck, 1973

Fig. 3A-L, Fig. 4A-H, J,K, Fig. 5A

1973 *Applinoecrinus texanus* Peck, p. 98, text-fig. 1a, b; pl. 1, figs. 4, 5.

1973 *Applinoecrinus cretacea* (Bather), Peck, text-fig. 1c, d; pl. 1, figs. 1, 2, 7-12.

p1999 *Applinoecrinus cretaceus* (Bather), Jagt, pl. 39, fig. 9; pl. 40, figs. 1-4, 7, 8.

p1996 *Applinoecrinus cretacea* (Bather), Donovan et al., fig. 2.2 only.

1996 *Applinoecrinus ramaraoi* Jain and Mallikarjuna 1996, pp.189-192, pl. 1, figs. 1-5.

2016 *Applinoecrinus texanus* Peck, Gale, p. 15, Fig. 6D,E; Fig. 7D,E, H-K.

Types. The theca figured by Peck (1973, pl. 1, figs. 4, 5) is holotype; it is from well cuttings, from close to the Taylor-Navarro contact, Hemingway and Bartell no. 1, 5.5 miles north-northeast of Caldwell, Burleson County, Texas. USNM 179139. The other two figured thecae are paratypes (Peck 1973, text-fig. 1b; pl. 1, fig. 5), from the Navarro Group, Corsicana Marl, two feet above the top of the Taylor on the south bank of the San Gabriel River, south of San Gabriel, Texas. USNM 179140. Another paratype (Peck 1973, text-fig. 1a), from the Upper Taylor, E.R. Martz no. 1 Patton well, 1 mile southeast of new Webberville, Bastrop County, Texas. USNM 179141. These localities all fall in upper Campanian or Maastrichtian sediments.

Diagnosis. *Applinocrinus* in which the radials carry vertical ridges or aligned linear rugosities, also found on the brachials; sutural contacts between radials and between radials and basals within raised double ridge; the lower flange overlapping the adjacent brachial is large and rectangular and contacts the adjacent radial. In large specimens, a lateral - adoral directed blade is present on the adoral part of the brachials.

Material. Peck's 1973 material of *A. texanus* (including all his specimens figured as *A. cretacea*, which are juvenile *A. texanus*) came from the upper Campanian and/or Maastrichtian of Texas, Florida and Mississippi. The theca illustrated by Jain and Mallikarjuna (1996, pl. 1) from the Campanian or Maastrichtian Ariyalur Group of the Ariyalur district, southeast India, also belongs to this species. The whereabouts of this material is unknown. The material figured by Jagt (1999) comes from the upper lower Maastrichtian of Rügen, northeast Germany (NHMM JJ 10849; RGM 396 326–396 331). The new material from the Peedee Formation comprises over 150 cups, many with in situ brachials, and isolated brachials, radials and fused basal rings.

Description. The new material described here permits detailed study of the morphology and ontogeny of *A. texanus* for the first time. The smallest individuals (Fig. 4A,B,E,F,H-L) are subspherical, with a height (Fig. 4A,B) of 0.7mm and a diameter of 0.6mm; the brachial cap forms approximately one third of the total height. There is considerable variation in the sculpture of the small individuals, from virtually smooth (Fig. 4E,H,L) through forms with weak ribs on the upper part of the radials, to highly ornate individuals (Fig. 4F,J) with strongly ribbed radials, and a complex sculpture on the brachials, which comprises a central region with discontinuous vertical ribs, and a roll-like raised ridge on the overlapping margin of each brachial, which extends from the radial contact to the apex. This carries very fine, twisted ridges. The brachials articulate very closely, and the adoral tips are twisted slightly (Fig. 4H). On some individuals (Fig. 4H, I), the base of each brachial bears a transversely arranged pair of tiny oval foramina, each about 0.25u in diameter.

In the smallest individuals (Fig. 4A,B,K,L) the basals form a low, flat-based structure raised aborally from the radials, which occupies approximately 15% of the base of the cup. Each basal is triangular, and the margin contacting the radials has a double concavity (Fig. 4K,L). There is a round foramen, about 20u in diameter on each basal, positioned two thirds of the distance from the radial margin. A centrale is not present.

With increased size, a number of significant ontogenetic changes take place, illustrated by the sequence B-D in Fig. 4. At a maximum cup diameter of 1mm, the basals form an aborally directed, short, conical projection, and each basal bears a rounded interradiar ridge, which extends to the base of the structure. The foramina are not apparent, and have evidently closed. With increased size (1.5mm diameter), the projection becomes proportionately longer, and the ridges only occupy the adoral part of the structure, and the aboral portion is smooth and rounded. The largest basal spikes, not found articulated (Fig. 5B-D) are very elongated, and strong rounded ridges run adorally-aborally along the line of the basal contacts, sometimes slightly twisted.

The radials plates undergo relatively little ontogenetic change; the small centrally placed adoral extension at the brachial margin becomes somewhat narrower, and sculpture is evidently lost, as all the large individuals are smooth. However, sculpture is retained on some fully grown individuals from other localities (Gale 2016). The brachials, however, are dramatically transformed during ontogeny; from rather low, triangular structures (Fig. 4A,B,J), they become taller, and develop a short, centrally positioned, laterally flattened blade, flanked by two grooves (Fig. 4D). In the largest, disarticulated, brachials (Fig. 5F,G) the blade has elongated and developed a triangular adoral process, extending obliquely from the apex. The interbrachial contact is highly modified for articulation with adjacent plates. A sharply demarcated depressed region (Fig. 5F, left hand side) is overlapped by a flange on the adjacent plate (Fig. 5G, right hand side). Secondly, a short rectangular

process, adjacent to the radial plate (Fig. 5F, bottom left) fits into a notch on the adjacent brachial (Fig. 5F,G).

Remarks. *A. texanus* has a complex ontogeny, and the juveniles display a number of enigmatic structures, particularly the paired foramina on the brachials, and the central foramen on each basal, the functional significance of which is puzzling. It is now clear, from the Peedee material, that the specimens figured as *A. cretaceus* by Peck (1973, Text-fig. 1c,d; Pl. 1 figs 1-3, 6-12) actually are of juvenile stages of *A. texanus*. *A. texanus* is well demarcated from *A. russelli* Gale, 2016 and *A. cretaceus* (Bather, 1924) by the presence of a crest-like extension on each brachial in the adult form.

Reconstruction. The new material permits reconstruction of the form of fully grown *Applincrinus texanus* for the first time (Fig. 7A). The cup with brachials has an elongated, fusiform appearance in lateral aspect, brought about by the tall, flange-bearing brachials, and the aborally tapering basal ring. The triangular flanges on the brachials form a bladed adoral crest.

Genus *Peedeecrinus* Gale, nov.

Diagnosis. Applincrininae in which each of the five stout radial spines are terminated by an elongated, vertically oriented bar which is triradiate in cross section, with a laterally positioned groove.

Derivation of name. After the Maastrichtian Peedee Formation of North Carolina.

Remarks. The form of the interior of the adoral radials in *Peedeecrinus* is closely similar to that of *Applincrinus*, in the presence of a pair of flattened processes which are directed obliquely and adorally into the cup, and presumably carried ligaments or muscles for the purpose of adducting the brachials (Gale 2016). Additionally, the smoothly convex aboral surfaces of the radial adjacent to the spine are similar to those in *A. cretaceus* forma *spinifer* Gale, 2017. Presumed brachials are also like those of *A. cretaceus*, in

their equilaterally triangular outlines and centrally positioned grooves, but are more symmetrical than those of *A. cretaceus*, and have a central groove. However, the vertically oriented, triradiate bars on the ends of the radial spines closely resemble those of the Campanian *Assericrinus portusadernensis* Gale, 2017 (see below).

Peedeecrinus sadorfi Gale *sp. nov.*

Fig. 5M; Fig. 6A-E, G, J-O; Fig. 7B.

Diagnosis. As for genus.

Derivation of name. For Eric Sadorf, who found the material figured herein.

Type specimens. The radial plate figured herein (Fig. 6A-D) is holotype, the other figured specimens (radial spines, Fig. 6E, G, J, K-O) are paratypes.

Material. Over 100 radials spines, radial fragments and three brachials, all from the locality.

Description. Only the robust adoral portions of the radials, and the radial spines, are preserved. In the most complete specimens (Fig. 6A-D, N, O), the thickened adoral rim of the radials and the articular structure for the brachial are seen; the delicate aboral portion of the radial is invariably broken away. The radial articular facet (Fig. 6A,C) is crescentic in outline, and carries a transverse articular ridge, which separates two deep cavities. These represent the aboral ligament pit (outer) and the nerve canal (inner). Aboral to these, a pair of flattened, bladed processes project obliquely into the radial cavity (Fig. 6C,O). These are similar to structures developed in *Applinocrinus* (Fig. 6F, I), which were interpreted by Gale (2016) as possible sites for attachment of adductor muscles which closed the brachial lid.

The robust radial spines are directed obliquely (laterally and adorally) from the body of the radials, and form a seamless extension of the outer surface of the

radial plate (E.g. Fig. 6B,N). The spines consist of a distally tapering shaft, rounded in cross-section, terminated by a trifoliate, vertically oriented bar, set at right angles to the shaft (Fig. 6A,B,D,E,G,K,L,M). The bar is variable in size (Fig. 6J) and is not always well developed (Fig. 6N). The lateral margins of the bars bear two rounded rims, separated by a concave groove (Fig. 6L). The bars are invariably broken, and their ab- and adoral terminations cannot be seen. Some individuals (Fig. 6A,D,E,G) additionally possess a short adorally directed process on the shaft adjacent to the articular facet.

Three poorly preserved brachials tentatively identified as belonging to *Peedeocrinus* are present in the material (Fig. 5M). These are almost equilaterally triangular in outline, and bear a centrally placed deep groove adorally which deepens towards the apex of the plate.

Reconstruction. The form of the cup with articulated brachials (Fig. 7B) is based upon the abundant, but fragmentary, material available. The conical cup has low, symmetrical brachials, and bears five highly distinctive radial spines, which consist of a short lateral process, often with a short adoral spur, and a tall, vertically oriented, trifoliate bar at the lateral margin. The length of these bars is inferential, because no complete examples are preserved, but the absence of significant taper or curvature on the longest fragments available (Fig. 6K,M) can be taken as evidence that they extended aborally beneath the cup and adorally above it and were essentially vertical. Although it is possible that *Peedeocrinus* gen nov. had an extended, conical aboral process at the base of the cup, no examples which cannot be referred to *A. texanus*, in which this feature was present, are found in the material. In the convergent taxon *Assericrinus* (Gale 2017), the vertical bars on the radial spines extend approximately equal distances above and below the lateral process. The chances of finding complete specimens of the very fragile *Peedeocrinus* gen nov. appear to be slight.

Remarks. *Peedeocrinus sadorfi* gen. et sp. nov. shares a number of features with the genus *Applinocrinus*, most particularly with *Applinocrinus cretaceus* forma *spinifer* Gale, 2017 (Fig. 4 H-J). These include:

- the overall shape of the radial plate, and the robust radial spine which is an extension of the outer aboral surface of the plate (Fig. 6; compare H, N).
- The presence of obliquely directed, paired internal processes aboral to the articular facet (Fig. 6; compare C,F,O).
- The shape of the inferred brachial plates (Fig. 5M) is similar to that of *A. cretaceus* (Fig. 5L).

Some individuals of *P. sadorfi* have a robust radial spine, with poorly developed vertical structures (Fig. 6N), and these are morphologically close to *A. cretaceus* forma *spinifer* (E.g. Fig. 6H,I). *Peedeocrinus* gen. nov. probably evolved from *Applinocrinus cretaceus* forma *spinifer* by the development of vertically oriented, trifoliate bars on the radial spines, as shown in a proposed phylogeny of the Applinocrininae (Fig. 3).

The reconstruction of *P. sadorfi* gen et sp. nov. (Fig. 7B; 9D) shows some striking similarities with that of the saccocomine *A. portusadernensis* Gale, 2017, in the development of tall, vertically oriented trifoliate bars on the terminations of the radial spines (compare Figs 6 and 9). *A. portusadernensis* was originally based upon numerous fragmentary radial spines from the Lower Campanian chalk of Hampshire, southern England (Gale 2017 Fig. 4A-E,I; Fig. 8J-O herein), which only occur commonly within a 10 m level at Paulsgrove pit, near Portsmouth, Hampshire, UK. Subsequently, numerous near-complete, but crushed, individuals bearing identical spines were collected in the Lower Campanian Ozan Formation of the Waxahachie dam spillway section in Ellis County, central Texas (Fig. 8A,B,D). These demonstrate that the cup of *A. portusadernensis* is of a construction closer to that of the saccocomine *Costatocrinus* Gale, 2016 in the presence of tall, narrow radials with marked interradian processes (Gale 2017; Fig. 2 herein) and well-developed radial articulation facets. Additionally, the lateral bars of

the radial spines of *Assericrinus* are found approximately half way up the radials, rather than on the adoral margins of the plates, and the lateral bars are strongly compressed and thin (Fig. 9B,C), in comparison to the robust, oval lateral processes of *Peedeecrinus* (Fig. 9E,F). It is concluded that, remarkably, the development of the distinctive triradiate terminal processes on the radial spines evolved convergently in the two genera, presumably as either stabilization devices or possibly to slow down vertical movement through the water column.

Hessicrininae Gale, 2016

Diagnosis (amended from Gale 2016). Roveacrinidae in which the basals are enlarged, external, and form the aboral portion of the theca. The basals are triangular, often fused, and possess adoral processes which contact the radials. The basal cavity is separated from the radial cavity by a basal web comprising a complex pentagonal structure made up of fine calcite struts, the corners of which are situated interradially. Large, radially positioned fenestrae are present between the basal/radial contacts, and interbasal fenestrae are often present. The lateral parts of the radials are perforated by small fenestrae and foramina, and from the interior; the cup has a reticulate appearance. The proximal brachials possess sheet-like lateral flanges.

Genus *Lucernacrinus* Gale, 2016

Diagnosis. Hessicrininae in which the radials and basals are of approximately equal height and carry centrally placed, bladed spines. A single, large, oval radial/basal fenestra is present, and the deeply inset lateral surfaces of the radials and the adjoining parts of the basals are perforated by numerous foramina. The adoral processes of the basals, and the lower parts of the radials form a fused ring which bears aborally directed spines.

Lucernacrinus multispiniferus sp. nov.

Fig. 10A-J

Diagnosis. Delicately constructed *Lucernacrinus* in which a large, oval radial:basal fenestra is present; both radials and basals carry moderately elongated spines

Types. The cup figured in Fig. 10B is holotype. The other figured specimens (Fig. 10A, C-J) are paratypes. NHMUK EE.

Material. Over 50 cups and fragmentary cups from the Peedee Formation.

Derivation of name. *multispiniferus*, Latin, meaning with numerous spines.

Description. The cup is conical in lateral profile, tapering aborally, and is 20% taller than broad. The radials form 60% of the total height of the cup, and are trapezoidal in lateral aspect (Fig. 10H). The interradiial processes are tall, and are perforated by a single column of foramina (Fig. 10B,H). The lateral, aboral parts of the radials are deeply inset and each bear a pair of foramina; the abradial column of these is contiguous with the foramina on the interradiial processes (Fig. 10B). The triangular radial facet slopes steeply aborally, at 50-60° to the axis of the cup, and the axial canal is broad and deep. Tall, triangular muscle fossae (Fig. 10F,I,J), and a deep ligament pit are present. Two conical radial spines, directed obliquely aborally, extend from the radial plate aboral to the radial facet.

The basal plates are Y-shaped in lateral aspect (Fig. 7G), and lateral processes articulate adorally with the radials. Large, oval radial/basal fenestrae are present (Fig. 10A-D), and the basals are fused aborally; the aboral part of the cup thus forms a cage-like structure, in which the

Discussion. *L. multispiniferus* sp. nov. can be readily referred to *Lucernacrinus* on account of the large, single radial/basal fenestrae, and the deeply inset, perforate aboral-lateral regions of the radials. The species differs from the type species of the genus, *L. woodi*, in its possession of larger, oval, radial/basal fenestrae, the larger foramina on the radials, and the presence of

aborally directed paired spines on each radial and basal. In *L. woodi*, a single bladed spine is present on each plate.

Genus *Birgelenocrinus* Jagt, 1999.

Type species. *B. degraafi* Jagt, 1999 by original designation.

Diagnosis. Cup conical, tall, broad adorally; radials with large, laterally facing radial facets, subparallel to axis of cup; basals tall triangular, separated by radially positioned elongated r:b fenestrae; single small interradiial r:b fenestrae present.

Remarks. In my 2016 paper (Gale 2016) I provisionally assigned *Birgenelocrinus* to the Roveacrininae, because of its overall fusiform construction and aborally sloping radial facets are reminiscent of *Roveacrinus* and other related genera. The new material demonstrates the presence of large external basals, and radial/basal fenestrae, which indicate its affinity with Hessicrininae. It differs from all other hessicrinine genera in the presence of elongated triangular basals separated by radial:basal fenestrae (Fig. 7E).

Birgenelocrinus degraafi Jagt, 1999

Fig. 11A,E,G,J

1992. Roveacrinidae n. gen. (?) n. sp. Jagt, p. 159, fig. 2g-i.

1995. roveacrinid n. gen. 2. Jagt, p. 192, figs 6-7.

1999. *Birgenelocrinus degraafi* Jagt, p. 148, Pl. 42, figs 3,5-10; Pls 43, 44.

2005. *Birgenelocrinus degraafi* Jagt, p. 134, fig. 2A-E.

Diagnosis. *Birgenelocrinus* in which the cup is relatively low and broad adorally, lacks spines on the radials, and has low basals.

Types. Holotype NHMM MB 506-15i; paratypes NHMM MB 506-15g/15h/15j/15k; NHMM JJ 5152a,b, 9543/a,b; RGM 396, 336. Kunrade Limestone, Late Maastrichtian, Benzenrade, Netherlands.

Remarks. The species has been described and figured in detail by Jagt (1999). The material from the Peedee Formation of North Carolina is virtually identical to that from the type area, the most important features of specific identity being:

- the presence of a radial foramen set within a bulbous swelling, immediately aboral to the radial facet (Fig. 10A, E, G,J)
- the proportionately low, relatively small basals, which contact two narrow processes at the aboral margin of the radials (Fig. 10G)
- absence of a laterally-aborally directed spine on each radial (Fig. 10A,E,G,J).

Brachials tentatively referable to *B. degraafi* are present. A IBr1 (Fig. 12B,C) possesses a radial articulation with a rounded lateral margin, and relatively low muscle fossae, comparable with the radial morphology (Fig.11A,E,G). The distal surface is synarthrial (Fig. 12C).

Birgenelocrinus jagti sp. nov.

Fig. 11B,C,D,H-M

Diagnosis. *Birgenelocrinus* with tall basals making up over 50% of the height of the cup; the aboral portion of the cup is elongated and twisted. A single, aborally-laterally directed spine projects from the margin of each radial facet. Irregularly shaped, deeply inset foramina are present in the radial plates.

Types. The cup illustrated here (Fig. 11C) from the Peedee Formation of Wilmington, N.C. is holotype (NHMUK EE), the other cups from the same locality figured are paratypes (Fig. 11B,C,F,H-M).

Derivation of name. In honour of John Jagt's contribution to the study of Cretaceous crinoids.

Description. The cups are tall and conical, with the height 2-3 times that of the maximum breadth. The radial plates possess tall, broad interrarial processes which are perforated by large foramina in a single column on each side of the plate (Fig. 11B,C). The radial facet is triangular, and an aborally-laterally directed spine extends from the lateral margin of the radial facet (Fig. 11B-D, F, H-M). The spines are short and blunt in some individuals (Fig. 11B,C,D) and long and sharp in others (Fig. 11F,I). Foramina are variably developed on the aboral part of the radial plates. In some individuals, a single foramen is present (Fig. 11D), whereas in others (Fig. 11B,C) 2 or 3 irregular spaces are present. The radial:basal contact lies a short distance aboral to the radial spine, well seen in some individuals (Fig. 11D, L,M), and the radials and basals share two small fenestrae, one positioned radially, the other interradially (Fig. 7C, Fig. 11D,L,M). The radially positioned fenestra is elongated, the interrarial one short and rounded (Figs 7C, 11D). The contacts between the radials and basals are well shown by fragmentary cups in which the basals are broken away (Fig. 11M). The bifid aboral processes of the radials contact an adoral process from a basal on each side (compare Fig. 11D). The basals are elongated, triangular and Y-shaped, and make up over 50% of the total height of the cup. Each arm of the Y contacts an aboral process from an adjacent radial (Fig. 7E, 11D). The basals are variably twisted, and this appears to be more pronounced in larger individuals (see Fig. 11B-D). Basal foramina are variably present, as elongated spaces in basals (e.g. Fig. 11B), and in some individuals inter-basal fenestrae are present (Fig. 11L). Neither are shown on the diagrammatic representation of a basal (Fig. 7E).

Proximal brachials referable to *Birgenelocrinus jagti* sp. nov. are present in the material. The IBr1 (Fig. 12E) has a lateral spine, corresponding with the spine on the radial plate, and very elongated processes which contacted the tall interrarial processes on the radials. IBr2 is axillary, and is rhombic in

outline (Fig. 12A), the articulation surfaces for IIBr1 have deep ligament pits and triangular muscle fossae. Three adorally directed processes are present. Distal brachials are referable to *Birgenelocrinus* sp. possess an elongated, dumb-bell shaped central shaft (Fig. 12H-L) with inwardly-directed paired processes at each end (Fig. 12J-L). On some, a dagger-shaped, flattened process extends out from the proximal (?) margin of the brachial (Fig. 12J,K). Contacts between successive distal brachials (Fig. 12 I,L) or synarthrial (Fig. 12H).

Remarks. *B. jagti* sp. nov. differs from *B. degraafi* Jagt, 1999 in its more elongated cup, taller basals, elongated cup with a twisted aboral region, and the presence of a spine on the radial margin.

Acknowledgements.

ASG would like to thank Christine Hughes of the School of Biological Sciences, University of Portsmouth, for her help with SEM work. E. S. thanks Kevin R. Shannon (the first person to find *Applinocrinus* in North Carolina) who showed E.S. what they look like which encouraged him to look for them, and Don Clements, who told E.S. about the Peedee outcrops at the boat ramp area near Wilmington.

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Figure captions.

Fig. 1. A, map of North Carolina to show position of detailed map of outcrop locality C. B, Photograph of Leyland Ramp outcrop of Peedee Formation on the Brunswick River, Wilmington, North Carolina. Scale of tape measure 1m.

Fig. 2. Comparison between supposedly Cenozoic roveacrinid ossicles from the Paleogene (Danian - Gorzelak et al. 2010) and Neogene of Poland (Salamon et al. 2011), marked by asterisk, and comparative material from the Turonian of the Anglo-Paris Basin. A-D, stratigraphical succession of *Roveacrinus* IBr2 morphologies from the Turonian-Coniacian chalk of southern England. A, undescribed species from the Middle and basal Upper Turonian, level of Glynde Marls, East Cliff Dover, Kent. B, undescribed species from the Upper Turonian, Southerham Marl 1, East Cliff, Dover, Kent. C, undescribed form from the Upper Turonian, 1m beneath the Navigation Hardground, Langdon Stairs, Dover, Kent. D, *Roveacrinus communis* Douglas, 1908, from the Lower Coniacian, 2m above Hope Gap Hardground, Seaford, Sussex. E, *R. communis*, smooth, broad morphotype typical of Middle Coniacian, level of Shoreham Marl 2, Beachy Head, Sussex. This is the youngest *Roveacrinus* form known; the genus becomes extinct beneath the Seven Sisters Flint at this locality and elsewhere. F, original of Gorzelak et al. (2010 Fig.2E, figured as *R. communis*), supposedly from the Danian of Nasilow Quarry, Vistula Valley, Poland. Note the close morphological similarity with E, including the strongly developed, paired, rounded median ridges, the large pores arranged in irregular vertical rows between these and on the lateral surfaces, and the large, sloping articular facets. G,I,J, *Roveacrinus* sp. nov. from the Middle Turonian, 6m above the Lulworth Marl, Holywell, Sussex, UK. G, radial plate in lateral aspect; I,J IBr2 secundibrachials, external aspect. H, IBr2, original of Gorzelak et al. 2010 Fig. 2D, as radial plate, from the Danian of Nasilow Quarry, Vistula Valley, Poland. Close similarities with the Turonian form include the narrow, sharp median ridge and the irregularly developed pores on the lateral surfaces. K, lateral aspect of cup of *Roveacrinus* sp. from the Middle Turonian, Lydden Spout path, Dover, Kent. L,M, broken radial, original of Salamon et al. 2011, Fig. 2B, supposedly from the Miocene Korytnica Clay, Korytnica, Poland. Similarities with K include the strong median ridge and large articular region. The genus *Roveacrinus* is unknown worldwide from Cretaceous sediments younger than the Middle Coniacian, and evidently became extinct then. We suggest that the Polish Paleogene and Neogene material represents Turonian contamination. Scale bars 200 microns.

Fig. 3. Postulated phylogeny of late Cretaceous Saccocomidae, based on information provided by Gale (2016, 2017) and this paper. The most basal group, which shares a number of characters with a plesiomorphic *Saccocoma*-like ancestor, includes *Costatocrinus* Gale, 2016 and *Assericrinus* Gale, 2017. These characters include the presence of arms constructed of numerous brachials, and an axillary 1Br2. The more derived group, the Applinocrininae Hess, 2011, are characterized by the presence of a single large primibrachial, which has a highly specialized interior surface (Gale 2016). In *Sagittacrinus* Gale, 2016, these imbricate and diverge from the cup adorally, whereas in *Applinocrinus* and *Peedeecrinus* gen nov. they form a tight-fitting cap over the oral surface of the crinoid. Note the striking convergence between *Assericrinus* and *Peedeecrinus*, in the development of vertical bars extending ab- and adorally from a lateral process on the radial.

Fig. 4. *Applinocrinus texanus* Peck, 1972 from the Maastrichtian Peedee Formation at Leyland, North Carolina. Cups with articulated brachials (A,B D-F, H-L), and lacking brachials (C, G). The succession of forms B-C-D-G are published at the same scale, and represent ontogenetic progression; note the progressive elongation of an aboral spike made up of fused basals, and the elevation of the adoral tips of the brachials. The surface sculpture of ridges is also lost with increased size. The continued ontogeny is represented in Fig. 3, figs B-D and F,G. Distinctive features of the juvenile cups include the presence of a central pore on each brachial (Figs K,L), and a pair of pores on each brachial immediately adoral to the articulation with the radials (H,I). A,B, small cup with articulated brachials in lateral aspect (NHMUK EE). C, cup lacking brachials, lateral view (NHMUK EE). D, large cup with brachials, lateral aspect. NHMUK EE. E,F, small cups with attached brachials, in (E) adoral and (F) lateral views. Note the variation in sculpture. G, large cup, with elongated aboral spike. H,I, cup in adoral aspect, to show pair of pores on brachials immediately adoral to radial articulation. NHMUK EE. J, small, strongly ornate cup in oblique adoral view. NHMUK EE. K,L, aboral view of small individual to show flat basals with central pores. NHMUK EE. Scale bars

I,K, 50 microns. A, B, E,F,L, 100 microns. H,J, 200 microns. C,D,G, 500 microns.

Fig. 5. A-H, J, K, *Applinocrinus texanus* Peck, 1973. A, large cup with brachials, oblique adoral view. NHMUK EE. B,C,D, aboral spikes, constructed of basals. Note twisted form in B,C. E, interior view of radial plate. NHMUK EE. F,G, large brachial, in external (F) and oblique internal views (G). Note the flattened adoral process. NHMUK EE. H, cup with brachials, lateral view, original of Peck 1973 fig. 1a, paratype, USNM 17941, and Gale 2016 fig. 7H. from the (late Campanian) Upper Taylor, E.R. Martz no. 1 Patton well, 1 mile SE of New Webberville, Bastrop County, Texas. J,K, small cups with brachials, adoral view, to show complex sculpture of brachials and apparent incomplete closure of aboral extremity. I, L. *Applinocrinus cretaceus* Bather, 1924. I, cup with brachials in oblique adoral aspect. Original of Gale 2016 Fig. 7A. NHMUK EE 16056. L. isolated brachial, external view. Original of Gale 2016 Fig. 7R, NHMUK EE 16057. Lower Campanian, *G. quadrata* Zone, Charmandean Lane, Worthing, Sussex, UK. M, *Peedecrinus sadorfi* gen. et sp. nov. Brachial, external view, probably belonging to this species. Maastrichtian, Peedee Formation, Leyland, North Carolina. N, *Applinocrinus russelli* Gale, 2016. Cup in lateral aspect. Paratype, original of Gale 2016 fig. 7B, NHMUK EE 16059. Prairie Bluff Chalk, Starkville, Mississippi. Scale bars A-G, J,K, 200 microns. H,I, L-N 500 microns.

Fig. 6. A-E, G, J-O, *Peedecrinus sadorfi* gen et sp. nov. Radial plates. A-D, holotype, in adoral (A), aboral (B), oblique internal (C) and lateral (D) aspects. Note internal paired processes in C, to compare with F. NUMUK EE. E, Paratype, radial in lateral view. NHMUK EE. G, paratype radial in lateral view showing vertical three-sided vertical process on radial spine. NHMUK EE. J, paratype radial with smaller vertical process. NHMUK EE. K,L,M, paratypes, elongated three-sided vertical bars of radial spines in lateral, distal and internal aspects. NHMUK EE. N, paratype, aboral view of radial with small vertical process, lacking trifoliate form. NHMUK EE. O, internal view of paratype radial, showing aboral internal processes (p) aboral to radial facet

(r). NHMUK EE. F, H,I, radial of *Applinocrinus cretaceus* forma *spinifer* Gale, 2017, original of Gale 2016 fig. 7I,J. NHMUK EE 16071, lower upper Campanian, Ivö Klack, Sweden. Note the internal paired processes, projecting obliquely and aborally, as developed in *P. sadorfi* shown in Figs C and O. Also compare the aboral view H, with that of the *P. sadorfi* specimen which has a weakly developed vertical radial bar (N). Late Maastrichtian, Peedee Formation, Leyland Ramp, Wilmington, North Carolina. Scale bars 200 microns.

Fig. 7. Reconstructions and homologies of Roveacrinida. A, fully grown *Applinocrinus texanus* Peck, 1973, based on material illustrated here (Figs 3,4). B, *Peedeocrinus sadorfi* gen et sp.nov., based on material in fig. 5. C, *Applinocrinus cretaceus* forma *spinifer* Gale, 2017; this is the probable ancestor of *Peedeocrinus* gen nov. D-homologies in the fenestrae and foramina of the aboral cup in hessicrinines. D, *Hessicrinus filigree* Gale, 2016. E, *Birgenelocrinus jagti* sp nov. F, *Lucernocrinus woodi* Gale, 2016. G, *Lucernocrinus multispinus* sp. nov. Basal plates green.

Fig. 8. *Assericrinus portusadernensis* Gale, 2017, illustrated for comparison with the convergent *Peedeocrinus sadorfi* gen et sp. nov. A,B, D, crushed cups of *A. portusadernensis* in lateral aspect, to show the elongated aboral spike, and the vertical trifoliate processes on the radial spines. NHMUK EE -. The adoral part of the radials is very thin, and preserved only as an internal mould. C,I,O, portions of the aboral spike, probably originating from a single individual NHMUK EE. E-G, isolated portions of the vertical radial spines to show trifoliate form, and for comparison with the material from the UK (J-O). H, adoral portion of spike, NHM EE XXXXX. J-N are originals of Gale 2017 fig. 3, J, NHMUK EE.16224, holotype. K, NHMUK 16228, paratype. L, NHMUK EE 16227. M,N, NHMUK EE 16225. A-G, Ozan Formation, Lower Campanian, *Globotruncanita elevata* Zone, Waxahachie dam spillway, Ellis Co. Texas. H, J-O, from the Lower Campanian Culver Chalk, *Goniot euthis quadrata* Zone, Paulsgrove pit, Hampshire, UK. Scale bars 200 microns.

Fig. 9. Comparison of the morphology of *Assericrinus portusadernensis* Gale, 2017 (A-C), with that of *Peedeecrinus sadorfi* gen et sp.nov. (D-F). A, reconstruction of cup of *A. portusadernensis*, based on material illustrated in Fig. 7A,B,D. B,C, radial process, to show laterally flattened blade leading to lateral trifoliate process. Also illustrated in fig. 7M,N.NHMUK EE16225. D, reconstruction of the cup of *Peedeecrinus sadorfi* gen et sp.nov.; regions coloured green are known from material. E,F, lateral and aboral aspects of holotype radial, figured in Fig. 4A-D. NHMUK EE. Although the trifoliate vertical part of the radial spines is remarkably similar in morphology in both taxa, the lateral processes are delicate and laterally compressed in *A. portusadernensis*, but rounded and robust in *P. sadorfi*. Additionally, the radial spines originate from the middle portion of the radial plates in *A. portusadernensis*, but the adoral margin in *P. sadorfi*.

Fig. 10. A-J, *Lucernacrinus multispiniferus* sp. nov. Cups. A, paratype cup in lateral radial view with nearly complete spines. NHMUK EE. B, holotype cup in lateral interradial view. NHMUK EE. C, paratype cup in lateral view to show large cavity internal to radial/basal fenestrae. NHMUK EE. D, lateral view of paratype cup. NHMUK EE. E, aboral view of paratype cup, NHMUK EE. F, oblique view to show radial facet and subjacent spine. Paratype, NHMUK EE. G, adoral view of broken paratype cup to show basal web. NHMUK EE. H, Well preserved adoral portion of cup, to show concave interradial regions with numerous foramina. NHMUK EE. I,J, adoral views of paratype cups, to show internal features, and radial facets. NHMUK EE-EE. All specimens from the Maastrichtian Peedee Formation, Leyland, North Carolina. K,L, *Lucernacrinus woodi* Gale, 2016. K, lateral radial view of holotype cup, for comparison with *L. multispiniferus* sp .nov. Original of Gale 2016, fig. 9A,B, NHMUK EE 16084. *Goniotectis quadrata* Zone, Lower Campanian, North Lancing, Sussex, UK. L, paratype cup, original of Gale 2016 fig. 9I, NHMUK EE 16089. Lower Campanian, *Offaster pillula* Zone, 2m above Peacehaven Marl, Peacehaven, Sussex, UK. Scale bars all 200 microns, except K which is 500 microns.

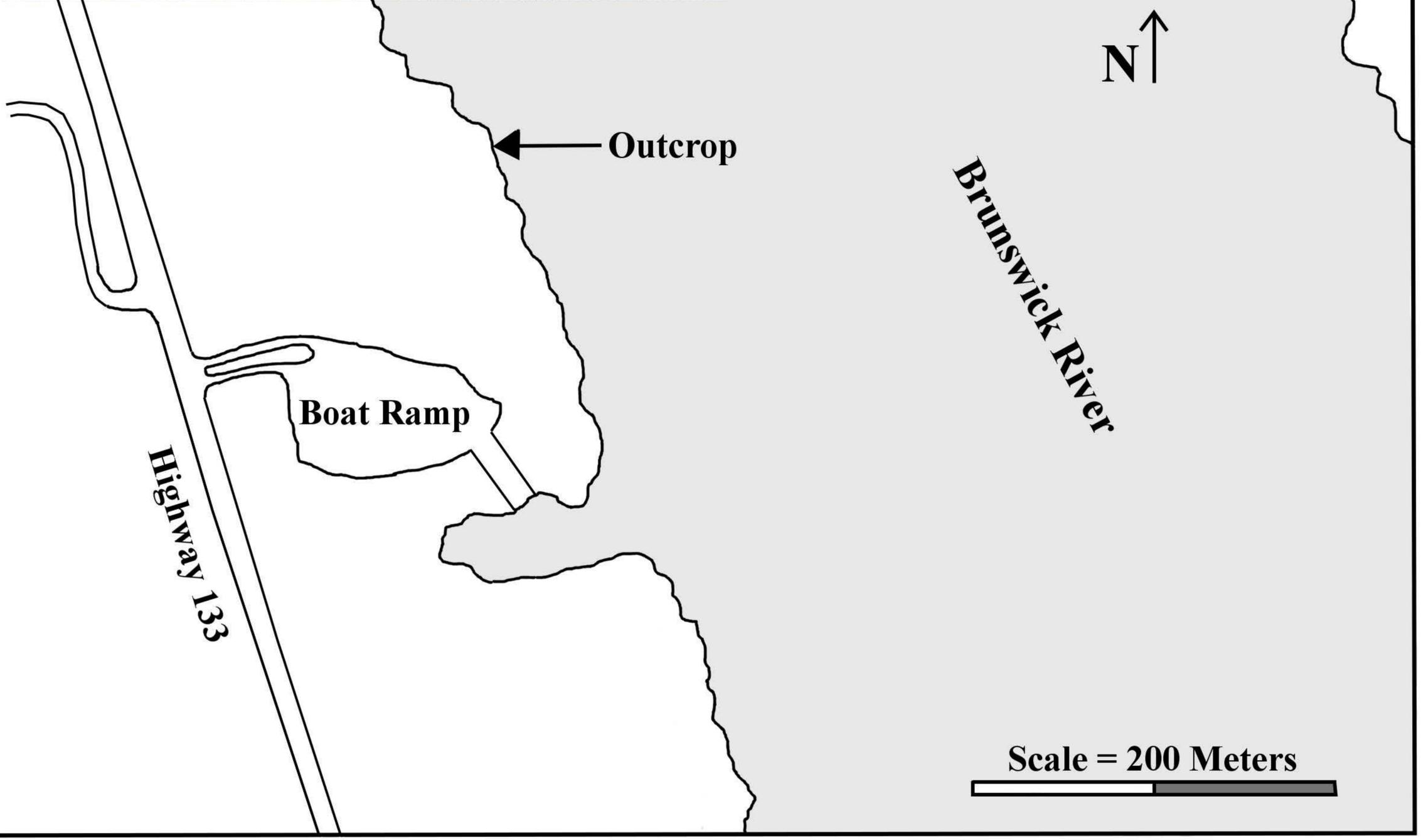
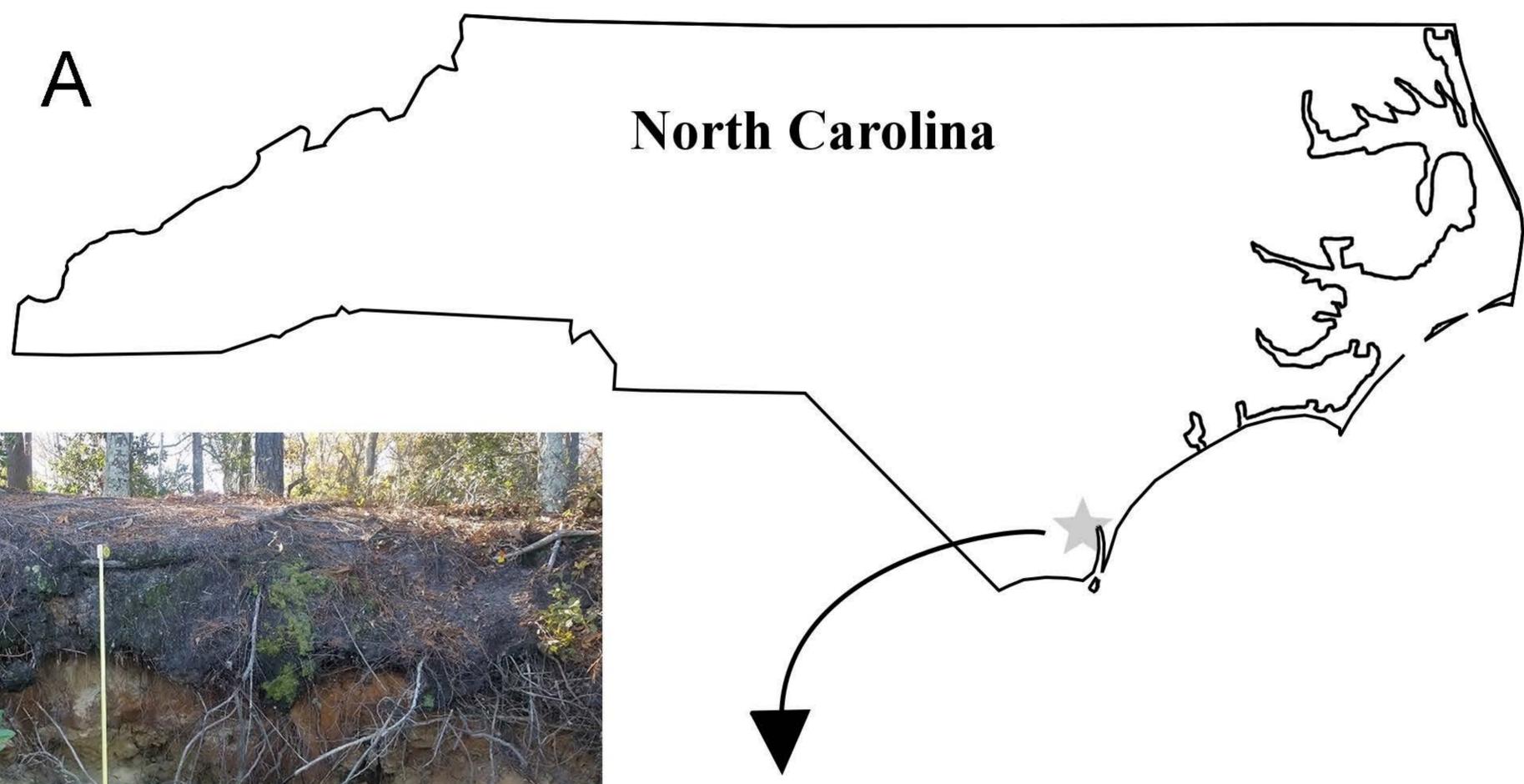
Fig. 11. A, E, G, J. *Birgenelocrinus degraafi* Jagt, 1999. A, E, cups in lateral aspect, A interradial, B, radial. NHMUK EE, EE. G, radial (adoral) portion of

cup, showing paired processes from aboral margins of radials for basal contact. NHMUK EE. J, original of Jagt 1999, pl. 43 fig. 1 (NHMM MB 506-15j), ENCI-Maastricht BV quarry, basal Emael Formation. Paratype.

Birgenelocrinus jagti sp. nov. B-D, ontogenetic sequence of cups in lateral aspect. Note the irregular shapes of the fenestrae, variable development of foramina, and progressive elongation and torsion of the aboral part of the cup. C, is holotype, B, D paratypes. NHMUK EE-EE.. F, incomplete specimen showing complete spines beneath radial facets. NHMUK EE. H, I, slender cups with well developed radial spines. NHMUK EE, EE. K,L, aboral views of cups. Note clear radial:basal contacts in L, and aboral inter-basal fenestrae. NHMUK EE, EE. M, partial cup, missing basals, in aboral aspect. Note paired processes on radials for basal contact. NHMUK EE.

All specimens except J from the Late Maastrichtian, Peedee Formation, Leyland Ramp, Wilmington, North Carolina. Scale bars, C,D,H,I,J, 500 microns; A,B, E,F,G,K-M, 200 microns.

Fig. 12. Brachials of Roveacrinidae. A, IBr2, distal aspect, probably belonging to *Birgenelocrinus jagti* sp. nov. B,C, IBr1, possibly *B. degraafi* Jagt, 1999. B, proximal view, C, distal view. D, IBr1, unknown affinity. Proximal surface. E, IBr1, probably belonging to *Birgenelocrinus jagti* sp. nov. F,G, IBr1 of unknown affinity. F, distal and G, proximal aspects. H-L, distal brachials, probably belonging to *Birgenelocrinus* spp. Late Maastrichtian, Peedee Formation, Leyland Ramp, Wilmington, North Carolina. Scale bar 200 microns.



TURONIAN

CONIACIAN

MIDDLE

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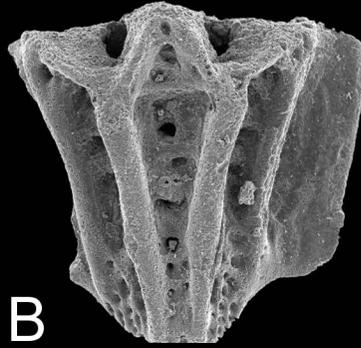
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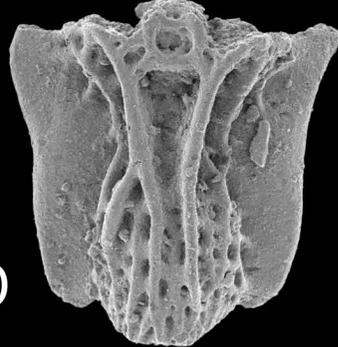
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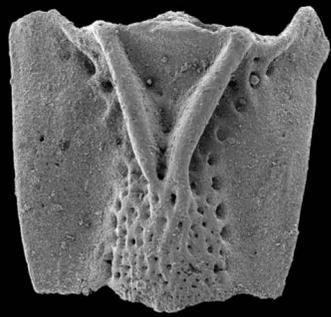
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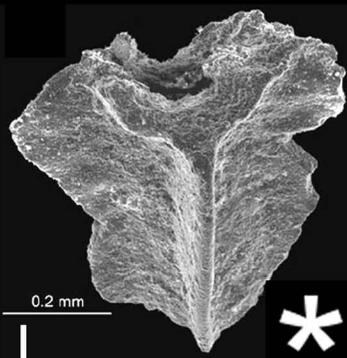
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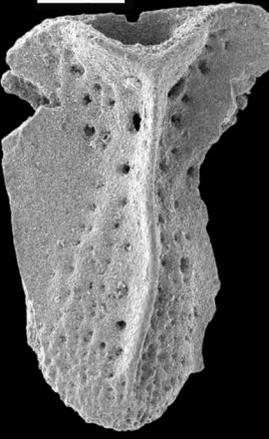
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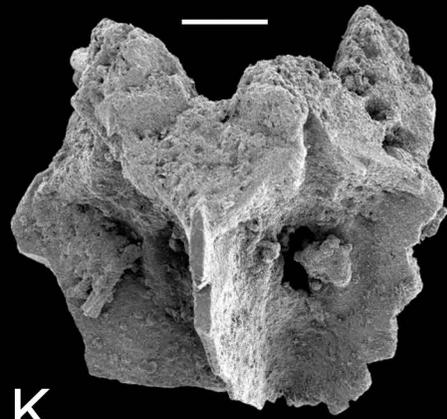
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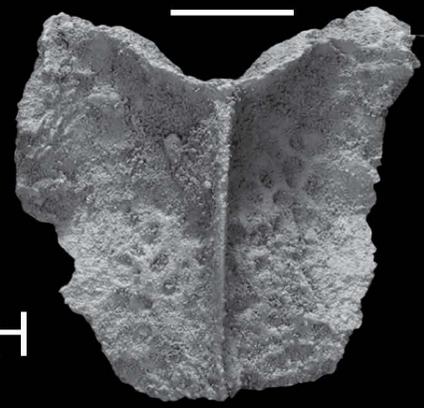
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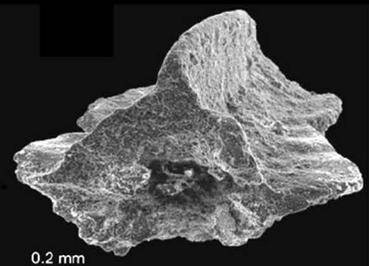
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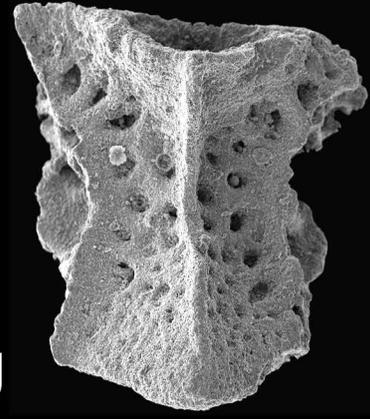
H



M



J



*

Saccocomidae

Applinocrininae

Saccocominae

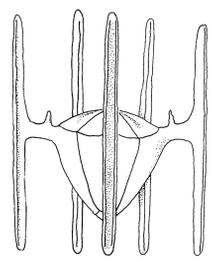
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MAASTRICHTIAN

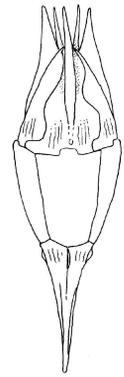
U. CAMPANIAN

L. CAMPANIAN

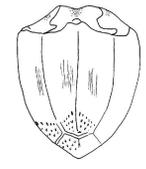
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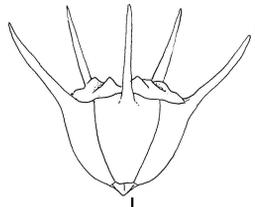
Peedeocrinus sadorfi



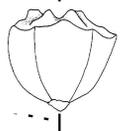
Applinocrinus texanus



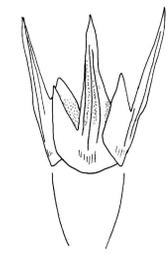
Applinocrinus russelli



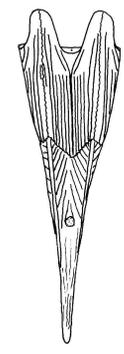
Applinocrinus cretaceus spinifer



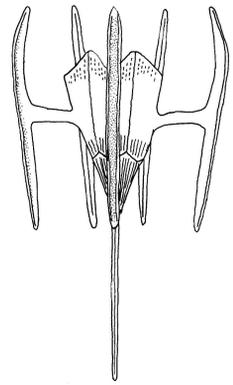
Applinocrinus cretaceus cretaceus



Sagittacrinus spp.



Costatocrinus spp.



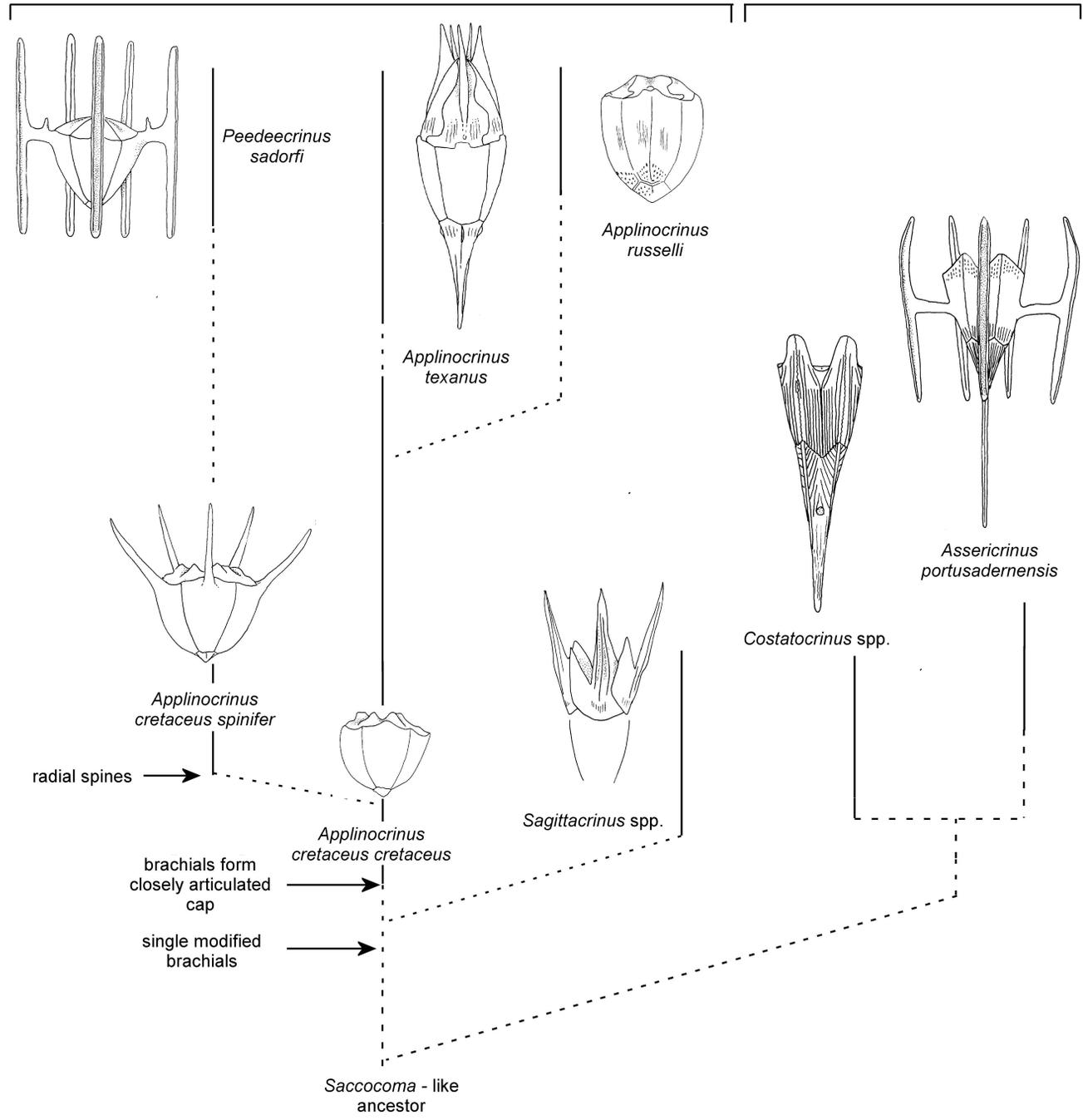
Assericrinus portusadernensis

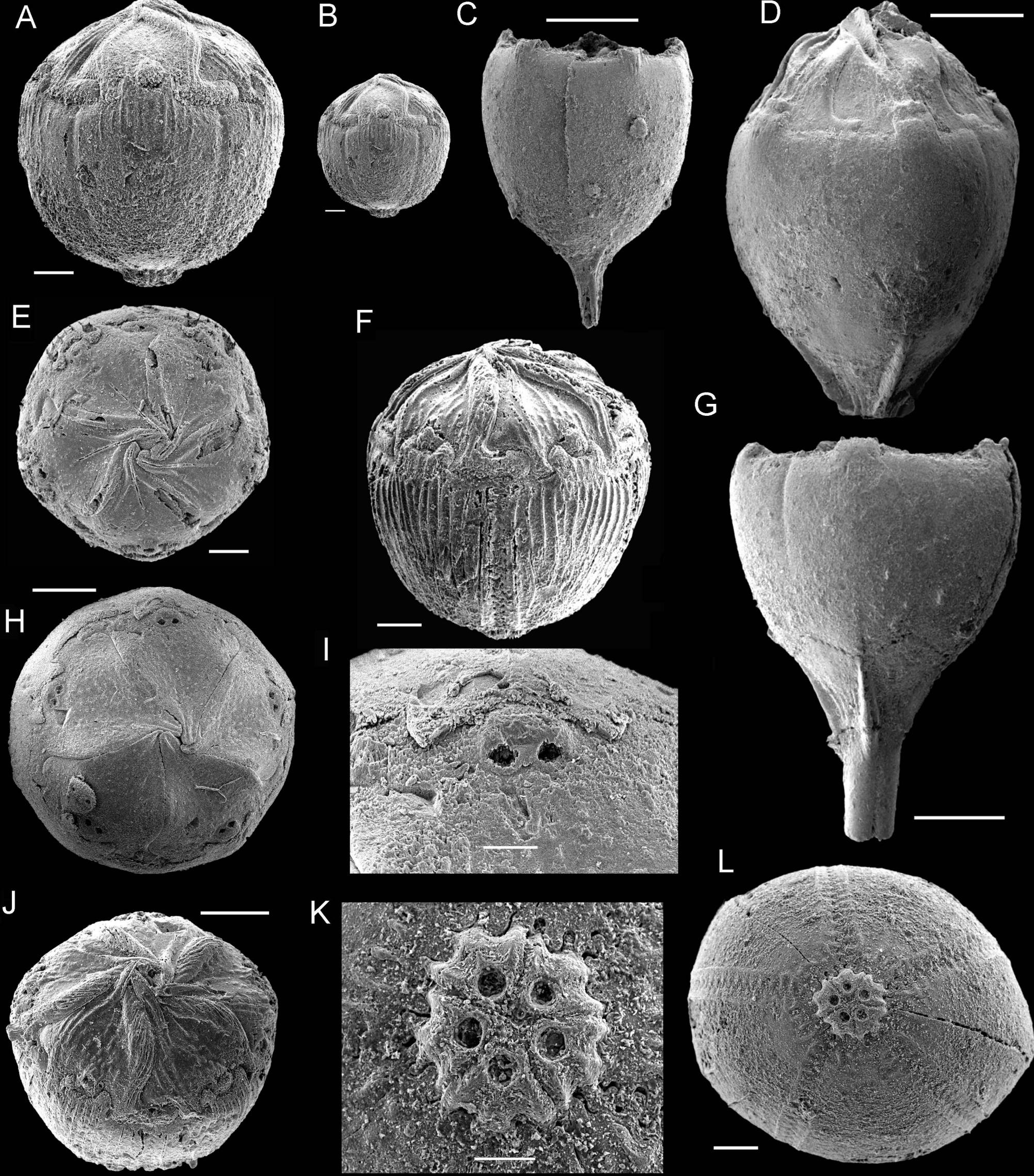
radial spines →

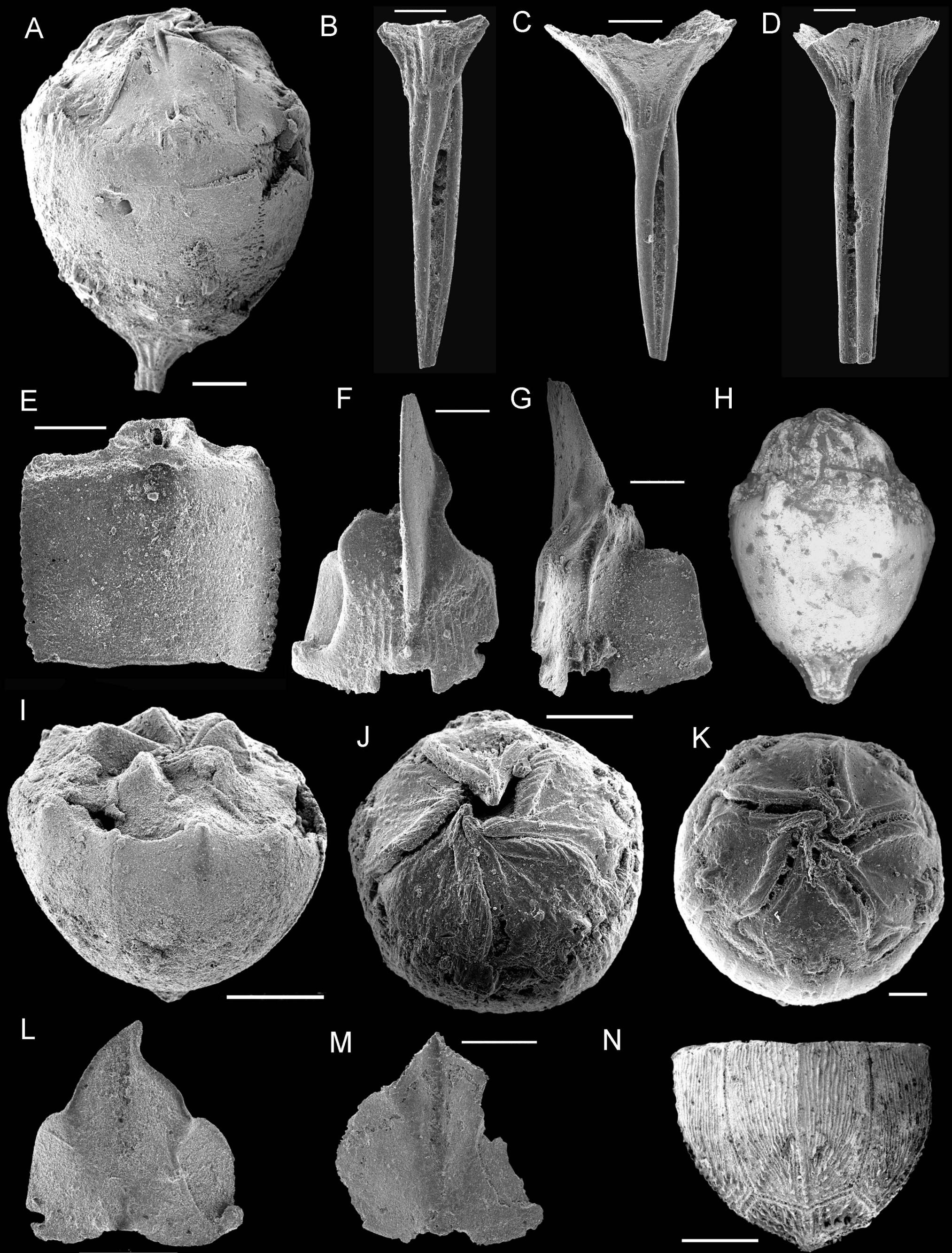
brachials form closely articulated cap →

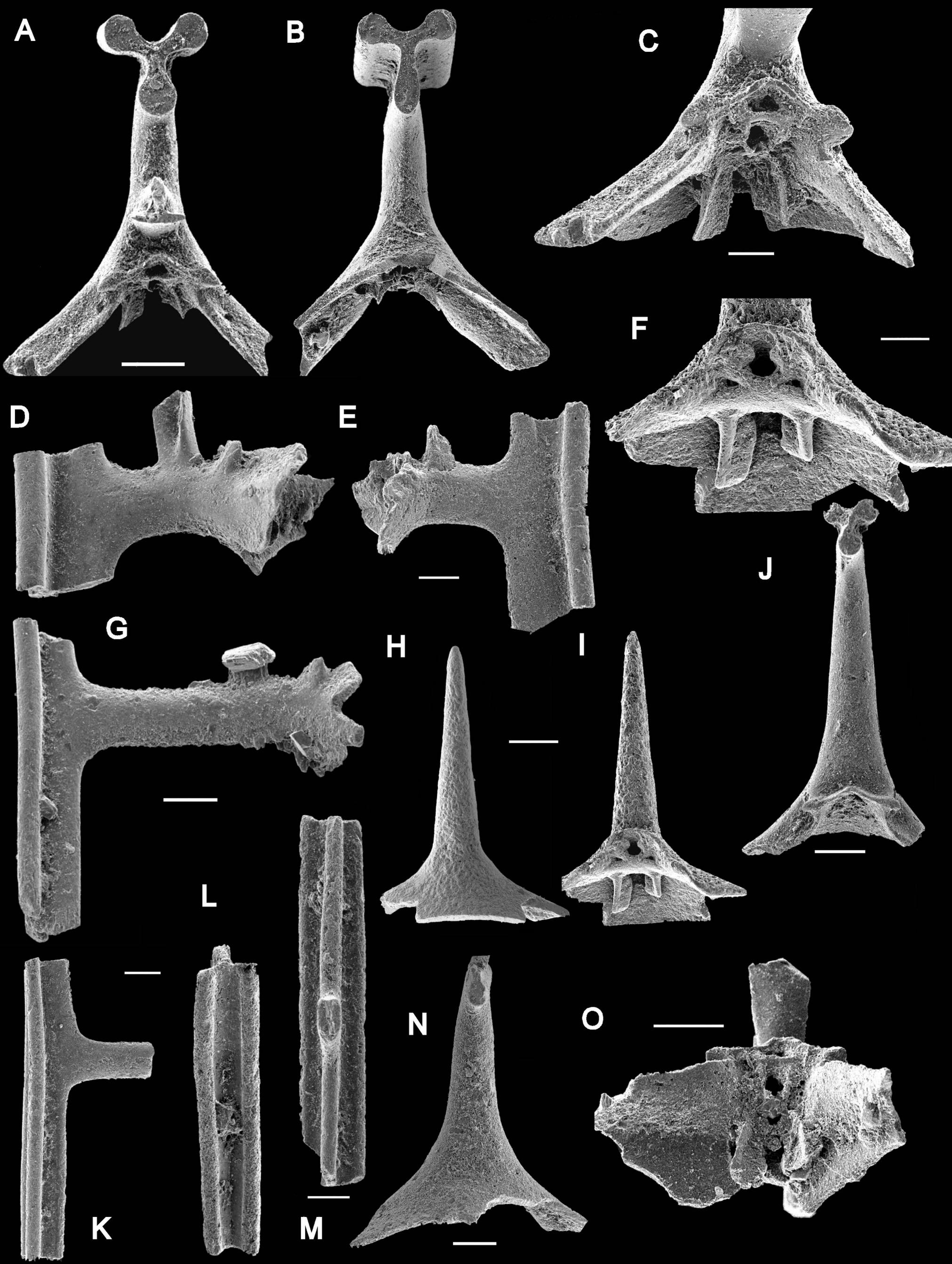
single modified brachials →

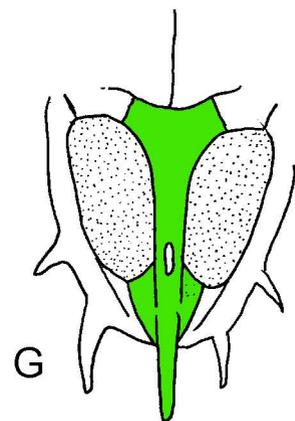
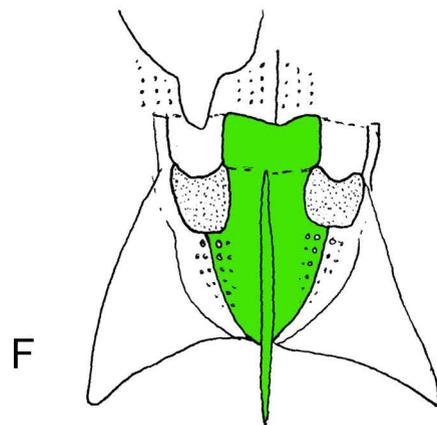
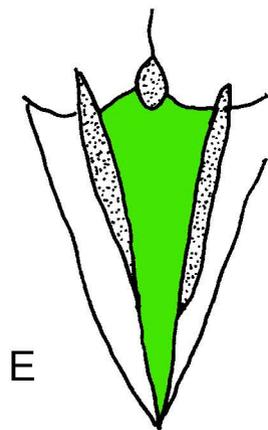
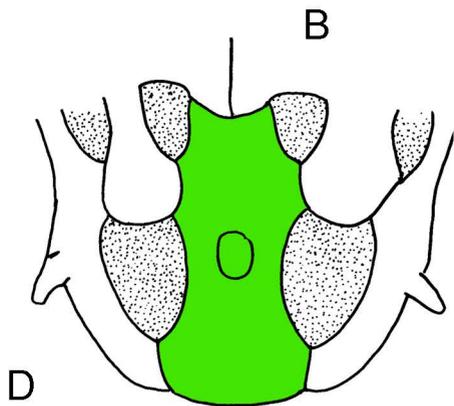
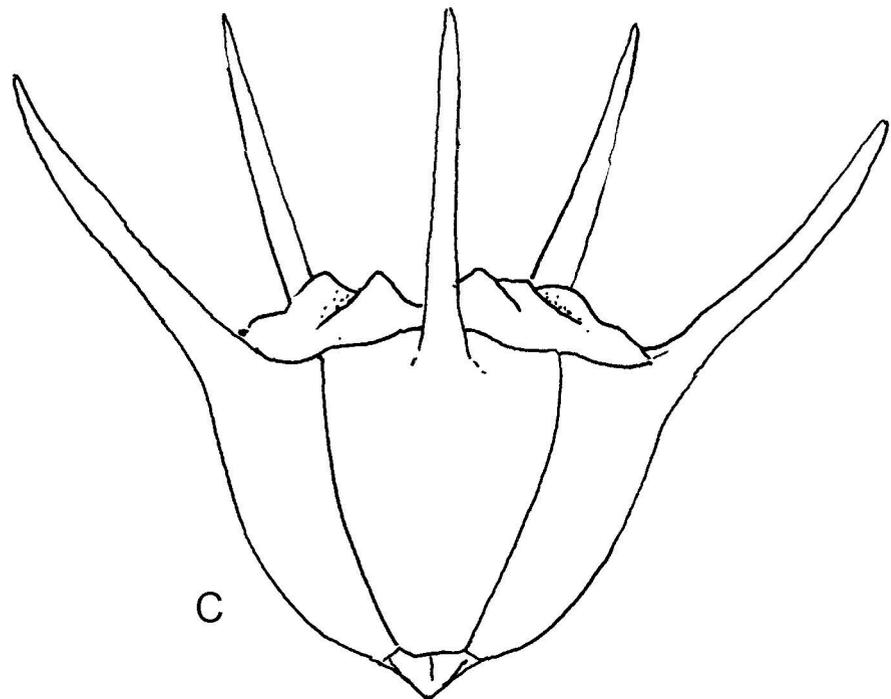
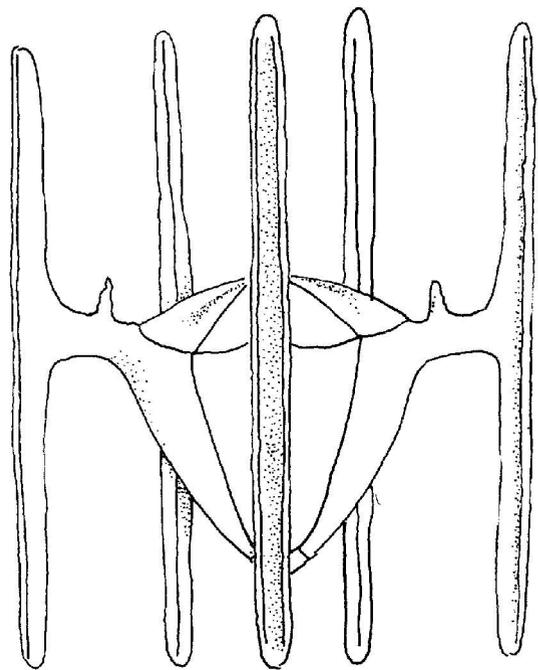
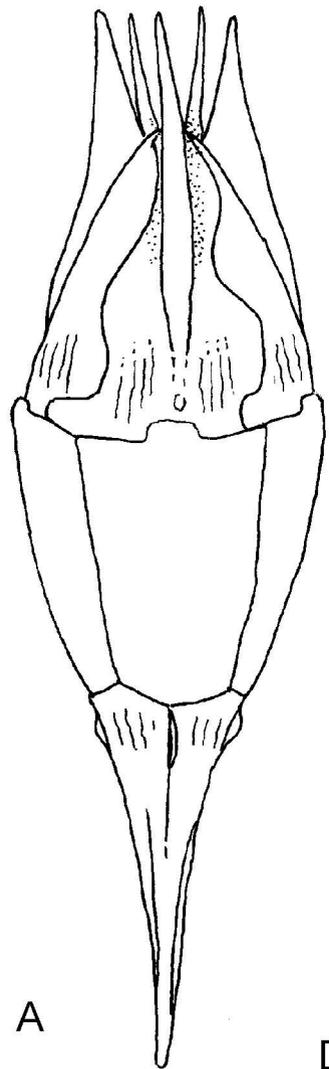
Saccocoma - like ancestor











A

B

C

D

E

F

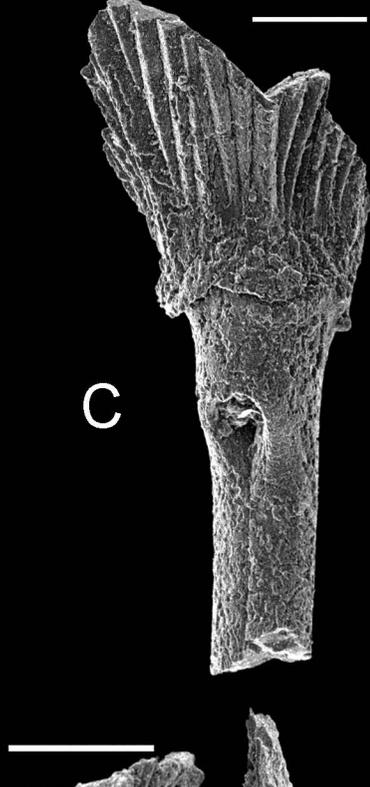
G



A



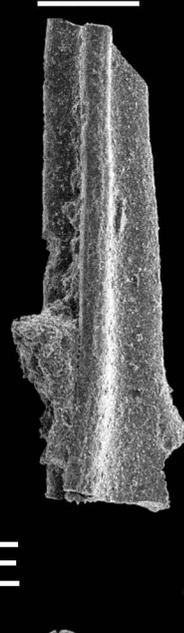
B



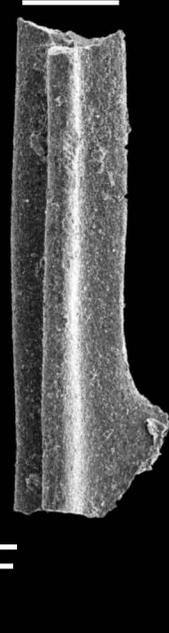
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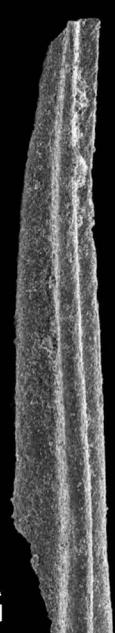
D



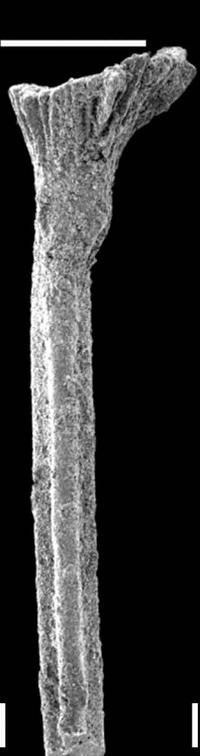
E



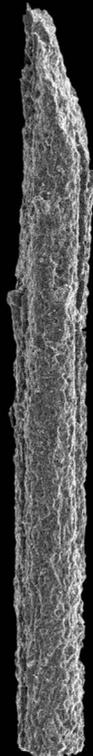
F



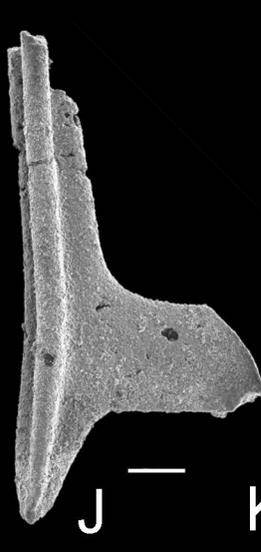
G



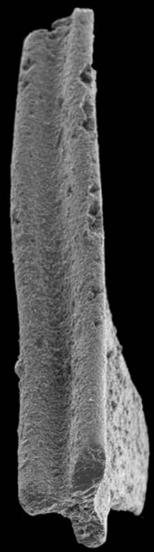
H



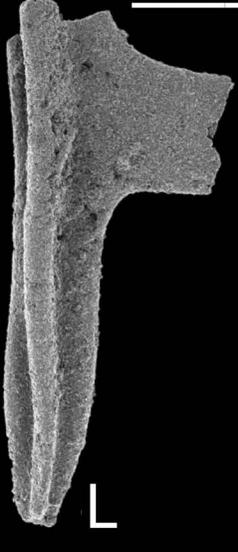
I



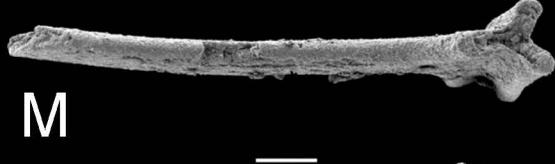
J



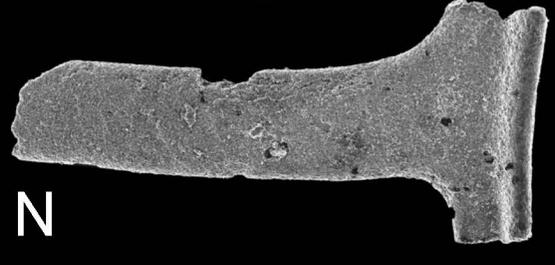
K



L



M



N



O

Assericrinus portusadernensis

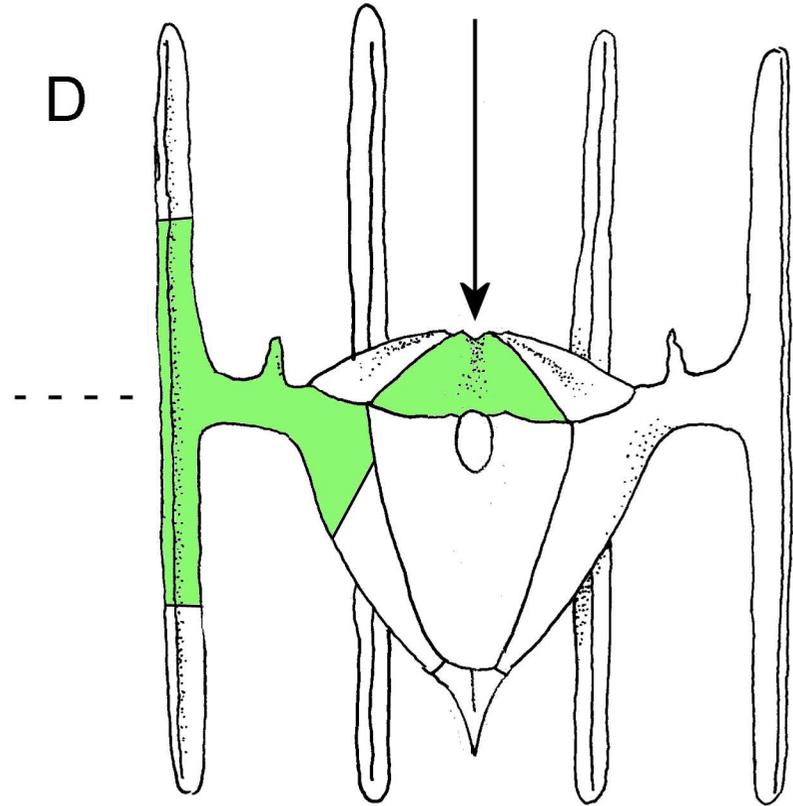
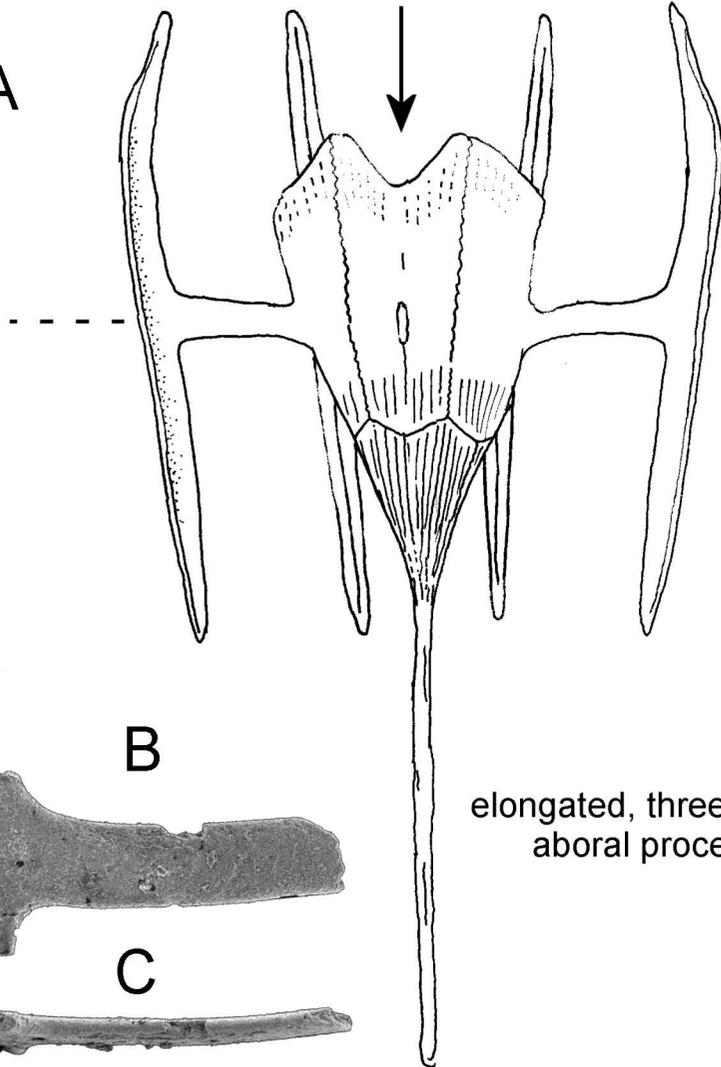
Peedeocrinus sadorfi

radial facet
large, external

radial facet internal

A

D



B

E

F

elongated, three-lobed
aboral process

lateral process
robust, rounded
adoral spur present

C

lateral process
compressed, delicate

