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Microcrinoids (Roveacrinidae) from the Middle–Upper Cenomanian Grey Chalk Subgroup, Dover (Kent, United Kingdom): biostratigraphy and re-evaluation of cup structure in roveacrinids

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ABSTRACT:

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New material of Roveacrinidae from the Middle–Upper Cenomanian Grey Chalk Group of the Kent coast (Folkestone-Dover) is described. The fauna includes 10 taxa, including a new genus and species (*Dubrisicrinus minutus*) and three new species (*Styracocrinus shakespearensis*, *Roveacrinus aboudaensis* and *Dentatocrinus serratus*). The biostratigraphical significance of roveacrinid faunas is placed in a global context, and it is demonstrated that the roveacrinid zone CeR5, previously recorded only from Morocco, is approximately equivalent to the upper Middle Cenomanian *Acanthoceras jukesbrownei* ammonite Zone, and zone CeR6 – to the *Calycoceras guerangeri* ammonite Zone. The new material also provides novel information on the cup structure of roveacrinids, which is reviewed and placed in a phylogenetic context.

Key words: Cenomanian; Chalk; UK; Microcrinoids.

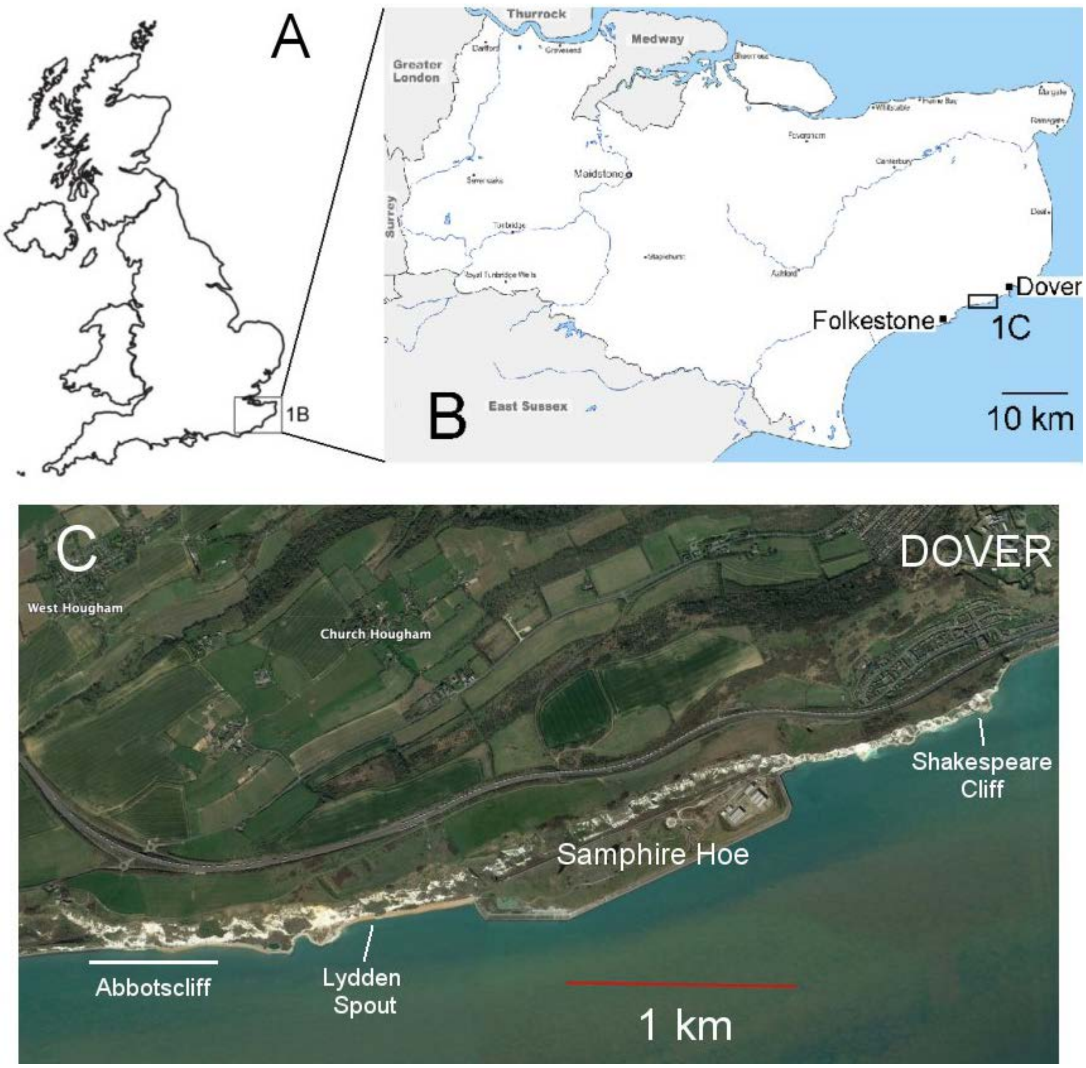
INTRODUCTION

Pelagic microcrinoids form an important component of the mesofauna of Turonian to Campanian chalks in the Anglo-Paris Basin (southern England and northern France), are highly diverse and of considerable value in biostratigraphy (Gale 2016, 2018, 2019). Only few microcrinoids have been recorded from the Cenomanian marly chalks of the region, and almost all came from the basal few metres of the Cenomanian succession near Cambridge in East Anglia (Peck 1955; Wienberg Rasmussen 1961; Gale 2019). In North Africa, and the Gulf region of the USA (Texas, Oklahoma), microcrinoids are abundant in Cenomanian claystones (Peck 1943; Gale 2020; Gale in Gale *et al.* 2021a, b), and a succession of zones (CeR1–7) have been identified, some of which can be correlated in detail across the Cretaceous Tethyan Atlantic.

For this reason, I resolved to study the Cenomanian chalk microcrinoids from the UK, choosing the well-exposed sea cliff succession between Folkestone and Dover in east Kent (Text-figs 1, 2). The lithostratigraphy and ammonite biostratigraphy of this region have been researched extensively (Kennedy 1969; Jenkyns *et al.* 1994, appendix; Gale *et al.* 1999; Kennedy and Gale 2006; Wright and Kennedy 2017) and the foraminiferal biostratigraphy has also been studied (Hart *et al.* 1989; Petrizzo and Gale 2022). Additionally, the east Kent chalks have undergone relatively little diagenetic hardening, making processing significantly easier. The present paper reports on the results of this study.

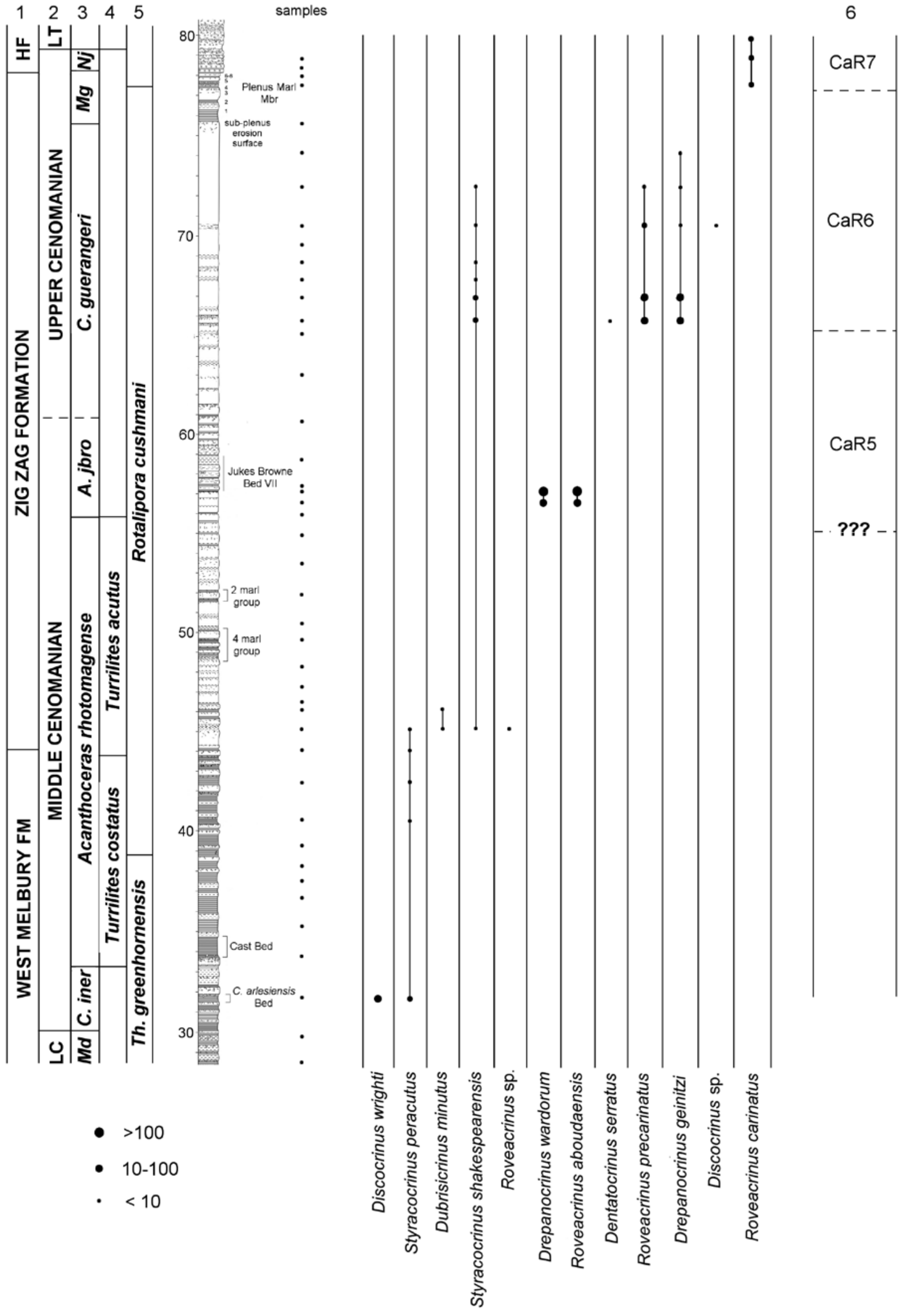
STRATIGRAPHY AND LOCATION

The Middle–Upper Cenomanian succession exposed in cliffs to the west of Dover (Kent, UK) was illustrated by Jenkyns *et al.* (1994, appendix a) and Kennedy and Gale (2006, fig. 2). It comprises approximately 48 m of marly chalk assigned to the Grey Chalk Subgroup, and the basal 2 m of the Holywell Formation of the overlying White Chalk Subgroup (Rawson *et al.* 2001). The Grey Chalk Subgroup is divided into two formations; a lower, more clay-rich West Melbury Formation and an upper Zig Zag Formation which correspond to the Chalk Marl and Grey Chalk of older publications, respectively. The boundary between the two is transitional and its position is disputed (Gale and Hancock 1999). The Grey Chalk Subgroup comprises chalks which are conspicuously rhythmic on a scale of several decimetres (Gale *et al.* 1999) with a clay content of between 5 and 30%. The biostratigraphy of the Grey Chalk



Text-fig. 1. Map of the United Kingdom (A), Kent (B) and Google Earth image (C) of the coast immediately west of Dover (Kent), to show localities mentioned in the text.

Text-fig. 2. Stratigraphy of the Middle–Upper Cenomanian chalk succession exposed in cliffs between Dover and Folkestone (Kent, UK), to show occurrences of microcrinoids. The stratigraphy and metre scaling are taken from Jenkyns *et al.* (1994, appendix a) and Kennedy and Gale (2006). Columns: 1 – lithostratigraphy; 2 – substages; 3 – ammonite zones; 4 – ammonite subzones; 5 – planktonic foraminiferan zones; 6 – microcrinoid zones. Abbreviations: LC – Lower Cenomanian; LT – Lower Turonian; *Md – Mantelliceras dixoni*; *C. iner – Cunningtoniceras inerme*; *Ajbro – Acanthoceras jukesbrownei*; *C. guerangeri – Calycoceras guerangeri*; *Mg – Metoicoceras geslinianum*; *Nj – Neocardioceras juddii*; *Th. – Thalmaninella.* Ammonite zones are from Kennedy and Gale (2006) and Wright and Kennedy (2017); planktonic foraminiferan zones after Petrizzo and Gale (2022). →


1 2 3 4 5
HF
LT
WEST MELBURY FM
ZIG ZAG FORMATION
LC
MIDDLE CENOMANIAN
UPPER CENOMANIAN
Md
C. iner
Acanthoceras rhotomagense
A. jbro
C. guerangeri
Mg
Nj
Turrilites costatus
Turrilites acutus
Th. greenhornensis
Rotalipora cushmani
samples
80
70
60
50
40
30
Plenus Marl Mbr
sub-plenus erosion surface
Jukes Browne Bed VII
2 marl group
4 marl group
Cast Bed
C. arlesiensis Bed
Discocrinus wrighti
Styracocrinus peracutus
Dubrisicrinus minutus
Styracocrinus shakespearensis
Roveacrinus sp.
Drepanocrinus wardorum
Roveacrinus aboudaensis
Dentatocrinus serratus
Roveacrinus precarinatus
Drepanocrinus geinitzi
Discocrinus sp.
Roveacrinus carinatus
6
CaR7
CaR6
CaR5
???
>100
10-100
< 10

Subgroup is based on ammonites which are common in the Lower and Middle Cenomanian (Kennedy 1969; Kennedy and Gale 2006) and on foraminifera (Hart *et al.* 1989; Petrizzo and Gale 2022). Ammonites of the *Cunningtoniceras inerme*, *Acanthoceras rhotomagense* and *Acanthoceras jukesbrownei* zones are recorded from the cliffs west of Dover (Wright and Kennedy 2017), and the position of the *Calycoceras guerangeri, Metoicoceras geslinianum* and *Neocardioceras juddii* zones can be inferred from their occurrences at Eastbourne, 85 km to the west (Gale *et al.* 2005).

A gentle northern dip (2–3º) means that successively younger beds are present in the cliff in an easterly direction towards Dover. Exposures at Abbotscliff and Lydden Spout (Text-fig. 1) provide access to the lower part of the succession (29–61 m in Text-fig. 2), and those at Shakespeare Cliff to the upper part (62–81 m).

METHODS

Forty-two samples of chalk of approximately 7 kg weight were dried, then broken into smaller pieces, and covered with 96% acetic acid. When the chalk had disintegrated, it was sieved in water, and the +0.5 mm residue reserved and dried. This was picked with a binocular microscope, and selected specimens were placed on stubs for SEM imaging.

CENOMANIAN ROVEACRINID STRATIGRAPHY

Cenomanian microcrinoid zones (CeR1–6) were established by Gale (2020) in the Aït Lamine Formation near Taghazout, north of Agadir in the Agadir Basin (western Morocco). Parts of the Agadir succession yielded abundant roveacrinid material, particularly from the Lower and Upper Cenomanian substages, but the virtual absence of ammonites from all but the lowermost Cenomanian made the precise determination of ages very difficult. The planktonic foraminiferan biostratigraphy provided by Gertsch *et al.* (2010), Jati *et al.* (2010) and Essafroui *et al.* (2015) has demonstrated the presence of the *Thalmaninella globotruncoides* and *Rotalipora cushmani* zones, but these are of considerable duration and provide little aid for precise dating. However, Gertsch *et al.* (2010; a paper overlooked by Gale 2020) had identified the Middle Cenomanian carbon isotope excursion (MCE) in the road section at Taghazout, which provides evidence for the position of the Lower–Middle Cenomanian boundary. The zonation of the Lower Cenomanian was modified on the basis of material from Texas (Gale in Gale *et al.* 2021a). The zonal succession (Text-fig. 3) comprises:

CeR1. Base marked by the first occurrence (FO) of *Euglyphocrinus euglypheus* Peck, 1943 and *Poecilocrinus signatus* (Peck, 1943), the top by the FO of *Roveacrinus spinosus* Peck, 1943. Co-occurrence with *Graysonites adkinsi* ammonite zone (Texas, Morocco) and the lower part of the *Graysonites wacoense* ammonite zone (Texas). Unknown from Europe.

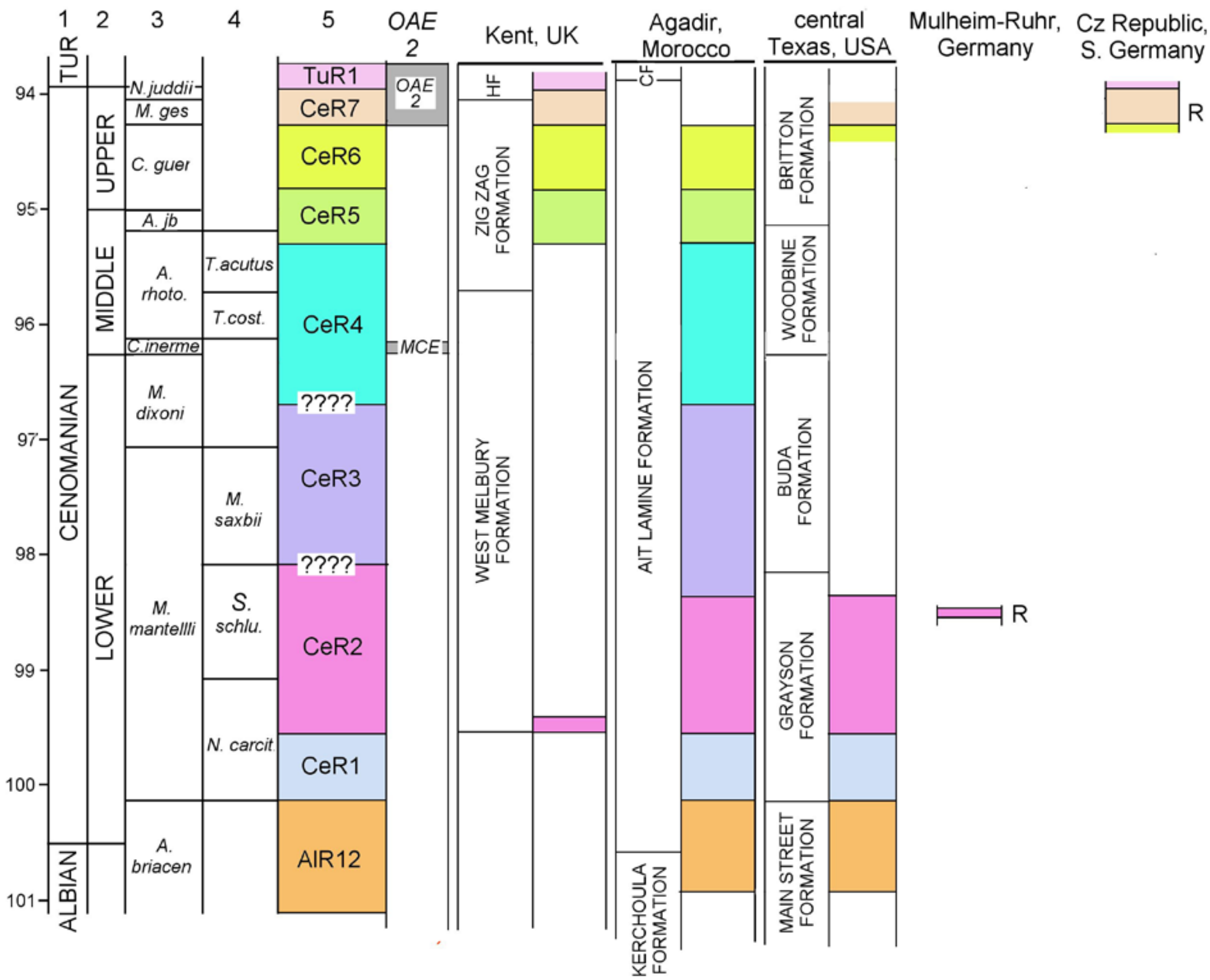
CeR2. Base marked by the FO of *Roveacrinus spinosus*, the top by the FO of *Roveacrinus gladius* Gale, 2020. Zone well known from Texas and the Agadir Basin, Morocco. In the UK, zone CeR2a is present in the lower part of the West Melbury Formation near Cambridge (see below). In Texas, the upper part of the zone is separated as CeR2b, characterised by the species *Roveacrinus pentagonus* Peck, 1943 and *R. multisinuatus* Peck, 1943 (Gale in Gale *et al.* 2021a), which in north Texas is erosionally truncated by the unconformity at the base of the Woodbine Formation (Gale *et al.* 2021a). The CeR2b fauna is present in Germany in the *Neostlingoceras carcitanense* Subzone (see below).

CeR3. Base marked by the LO of *Poecilocrinus signatus*, the top by the FO of *Euglyphocrinus jacobsae* Gale, 2020 in the Abouda road cutting near Agadir, Morocco (Gale 2020). Only known from the Agadir Basin. Upper Lower Cenomanian, precise age uncertain.

CeR4. Base defined by the FO of *Euglyphocrinus jacobsae,* the top by the FO of *Euglyphocrinus truncatus* Gale, 2020 in the Abouda road cutting near Agadir, Morocco (Gale 2020). This zone spans the Lower–Middle Cenomanian boundary, as the MCE is present within the zone (see below).

CeR5. Characterised by the co-occurrence of *Drepanocrinus wardorum* Gale, 2020, *Roveacrinus aboudaensis* sp. nov. and *Euglyphocrinus truncatus*, established in the Abouda road cutting near Agadir in Morocco. Now also recorded from the lower part of the *Acanthoceras jukesbrownei* ammonite zone at Dover (see below).

CeR6. Total range zone of *Drepanocrinus geintizi* (Schneider, 1989), established on Taghazout Plage, Agadir Basin, Morocco (Gale 2020). The zone is present in the *Calycoceras guerangeri* ammonite zone at Dover (see below) and in condensed deposits in the Czech Republic and at Dresden, Germany (see below). It is also present in the Eagle Ford Group im-



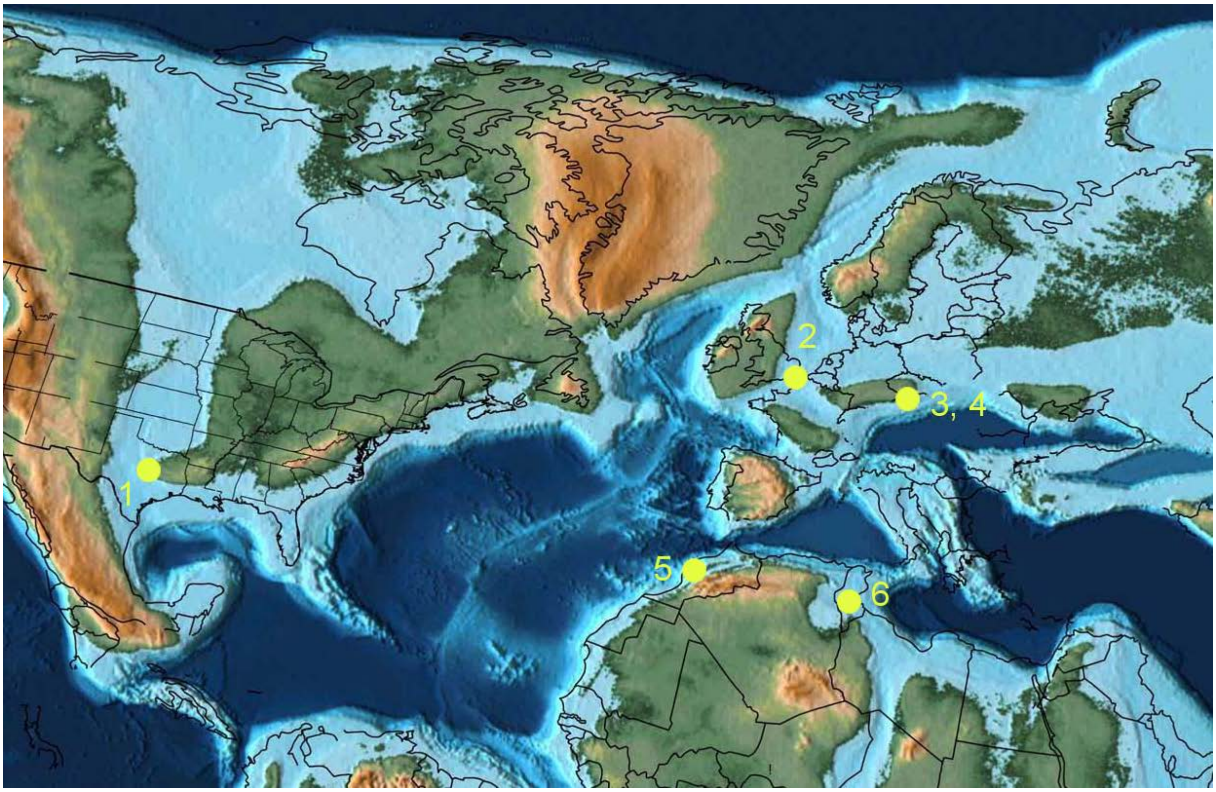
Text-fig. 3. Distribution of Cenomanian roveacrinid zones, showing Kent (herein), Agadir, Morocco (Gale 2020), central Texas (Gale *et al.* 2021a), Mülheim-Ruhr, Germany (Hess and Thiel 2014; Gale and Thiel in press) and Dresden/Předboj (Žítt *et al*. 2019). Note the uncertainty of the precise ages of CeR3 and CeR4, from which ammonites are not known. Columns: 1 – stages; 2 – substages; 3 – ammonite zones; 4 – ammonite subzones; 5 – microcrinoid zones; 6 – carbon isotope excursions. Abbreviations: MCE – Middle Cenomanian carbon isotope excursion; OAE2 – Oceanic Anoxic Event 2, both recorded from the UK, Morocco and Texas, USA; TUR – Turonian; *A. briac* – *Arraphoceras briacensis*; *Ajb* – *Acanthoceras jukesbrownei*; *A. rhoto* – *Acanthoceras rhotomagense*; *C. guer* – *Calycoceras guerangeri*; *C. inerme* – *Cunningtoniceras inerme*; *M. dixoni* – *Mantellicers dixoni*; *M. ges.* – *Metoicoceras geslinianum*; *M. mantelli* –*Mantelliceras mantelli*; *M. saxbii* – *Mantelliceras saxbii*; *N. carcit* – *Neostlingoceras carcitanense*; *N. juddii* – *Neocardioceras juddii*; *S. schlu* – *Sharpeiceras schlueteri*; *T. acutus* – *Turrilites acutus*; *T. cost* – *Turrilites costatus*; CF – Casbah Formation; HF – Holywell Formation; R – condensed, remanié faunas.

mediately beneath the *Sciponoceras gracile* Zone at Dallas, Texas (Nestell and Gale in preparation).

CeR7. Total range zone of *Roveacrinus carinatus* Nekvasilová and Prokop, 1963. Established at Eastbourne, East Sussex, UK (Gale 2019) and equivalent to the *Metoicoceras geslinianum* and *Neocardioceras juddii* ammonite zones. The zone is present in condensed facies in the Czech Republic and at Dresden, Germany (see below) and also occurs in the basal *Sciponoceras gracile* (= *Metoicoceras geslinianum*) ammonite zone in the Eagle Ford Group near Dallas, Texas, USA (Nestell and Gale 2022).

BIOSTRATIGRAPHICAL RESULTS FROM THE CENOMANIAN CHALK OF THE UNITED KINGDOM

The microcrinoid fauna recorded from the Lower Cenomanian, basal West Melbury Formation near Cambridge, of inferred *Neostlingoceras carcitanense* Subzone age (Gale 2019), includes long-ranging taxa such as *Styracocrinus peracutus* (Peck, 1943) and *Discocrinus wrighti* Peck, 1955, but also some specimens of *Roveacrinus spinosus*, which characterises zone CeR2 at Agadir and in Texas (Gale in



Text-fig. 4. Localities and regions which have yielded Cenomanian roveacrinids: 1 – central Texas; 2 – south-east England, UK; 3, 4 – Dresden, Germany and Předboj, Czech Republic; 5 – Agadir, Morocco; 6 – central Tunisia. Map courtesy of Dr. Chris Scotese.

Gale *et al.* 2021a and b). *Roveacrinus bifidus* Gale, 2019, from Cambridge, is also recorded from central Texas and both species are found in the upper part of the *Graysonites wacoense* ammonite zone there. The presence of this ammonite species in remanié preservation, with other elements of the *N. carcitanense* fauna at Stour Bank, Dorset, UK (Wright and Kennedy 2015), plus the roveacrinid occurrences at Cambridge, supports the interpretation that the lowermost Cenomanian is not preserved in the UK, having been lost within the Albian–Cenomanian disconformity (Gale *et al.* 1996).

A notable feature of the UK (and northern European) Early Cenomanian roveacrinid faunas is the total absence of the genera *Euglyphocrinus* and *Poecilocrinus*, which are abundant in the Tethyan regions of the Gulf coast (Texas, Oklahoma) and in North Africa (Text-fig. 4).

Samples from the Lower Cenomanian at Dover studied have yielded only rare, indeterminable brachials. The earliest significant occurrences are in the Middle Cenomanian *C. arlesiensis* Bed, of *C. inerme* Zone age, which yields common *Discocrinus wrighti* and *Styracocrinus peracutus*, both long-ranging species. The overlying *A. rhotomagense* Zone, *T. acutus* Subzone has provided *Dubrisicrinus minutus* gen. et sp. nov., *Roveacrinus* sp. and *Styracocrinus* spp., plus indeterminable brachials. None of these permit wider correlation.

In the lower part of the Middle Cenomanian *A. jukesbrownei* Zone a 0.5-m-thick level yields roveacrinid radials and brachials, with an abundance level in a thin marl at the base of Jukes Browne Bed VII (Text-fig. 2). These are identified as *Roveacrinus aboudaensis* sp. nov. and *Drepanocrinus wardorum,* which occur in comparable abundance (but in better preservation) in the Aït Lamine Formation north of Agadir, between 418 and 425 m (Gale 2020, text-fig. 8), and indicate that roveacrinid zone CeR5 is correlative, at least in part, with the Middle Cenomanian *A. jukesbrownei* Zone.

Roveacrinids reappear in abundance in the Dover section in a burrowed marl bed (66 m in Text-fig. 2) and continue upwards, in decreasing abundance, to 74 m, within the Upper Cenomanian *C. guerangeri* Zone of the Zig Zag Formation. Although ammonites of this zone are not preserved at Dover (Kennedy 1969), they are present in correlative levels

85 m to the west at Eastbourne (Gale *et al.* 2005). The roveacrinid fauna includes, most significantly, *Drepanocrinus geinitzi* (marker species of roveacrinid zone CeR6), accompanied by *Dentatocrinus serratus* sp. nov. and *Roveacrinus precarinatus* sp. nov., plus common *Styracocrinus shakespearensis* sp. nov. Thus, the *C. guerangeri* Zone can be broadly correlated with roveacrinid zone CeR6. The occurrence of *R. precarinatus* sp. nov. is particularly interesting, because its descendant species, *R. carinatus*, is locally abundant in the overlying Plenus Marl Member and basal Holywell Formation of *M. geslinianum* and *N. juddii* zone age at Eastbourne, UK (Gale 2019) which are included within CeR7.

In conclusion, for almost all of the Lower and Middle Cenomanian chalk of the UK, roveacrinids are rare components of the mesofauna, being represented mostly by infrequent occurrences of long-ranging species. In contrast, the upper part of the Middle Cenomanian (lower *A. jukesbrownei* Zone) and Upper Cenomanian (middle *C. guerangeri* Zone, upper *M. geslinianum* Zone) are characterised by brief floods of abundant, short-ranged, yet geographically widespread taxa which represent northerly extensions of the ranges of predominantly Tethyan species. From the *M. geslinianum* Zone upwards, through the Turonian, roveacrinids are ubiquitously present and often abundant in UK chalks (Gale 2019).

This pattern of distribution can perhaps be related to progressive warming of sea surface water through the Cenomanian, documented in the oxygen isotope record from Dover (Jenkyns *et al.* 1994, fig. 4). This probably permitted the predominantly warmer-water Tethyan roveacrinids to migrate northwards periodically into the mid-latitudes. Concentrations of microcrinoids also tend to occur in transgressive levels, as in the basal Middle Cenomanian *C. inerme* Zone, *C. arlesiensis* Bed (Text-fig. 2), the basal part of the *A. jukesbrownei* Zone and the upper part of the Plenus Member, Upper Cenomanian, *M. geslinianum* Zone. These levels all correspond to transgressive system tracts identified by Robaszynski *et al.* (1998).

THE AGE OF MICROCRINOID FAUNAS FROM CONDENSED SECTIONS IN CENTRAL EUROPE

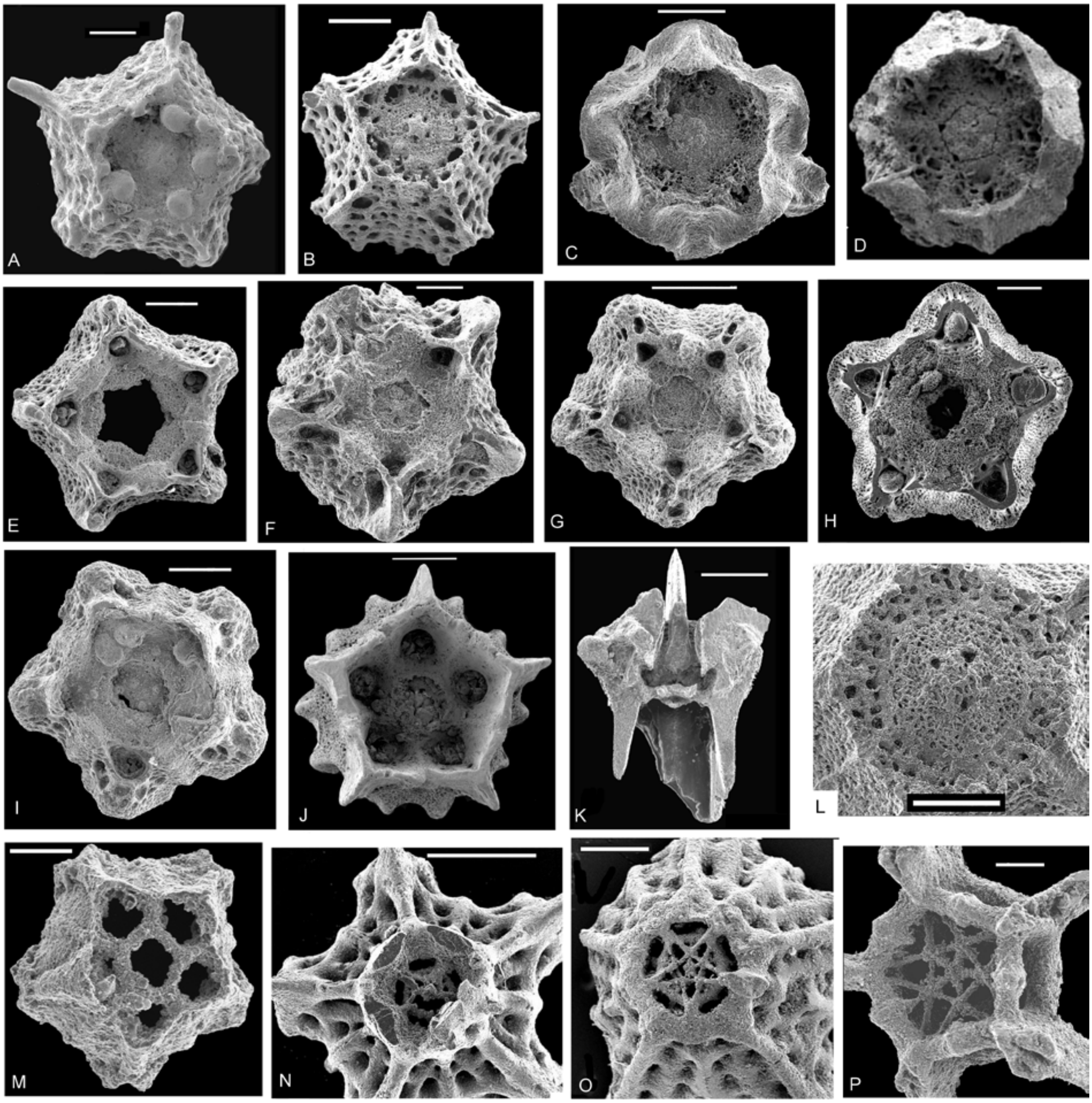
The best known, and exceptionally well-preserved, Cenomanian microcrinoid faunas from continental Europe come from thin, highly condensed deposits overlying basement rocks of Carboniferous age which formed parts of the Mid-European Island. These are from transgressive lags preserved within cavities ('surf pockets') in the surface of the unconformity (Text-figs 3 and 4).

The highly condensed Cenomanian deposits occurring locally at Kassenberg, Mülheim-Ruhr (Germany) have yielded abundant roveacrinids of Early Cenomanian age (Hess and Thiel 2015). The deposit yielding this material can be dated to the Early Cenomanian *N. carcitanense* Subzone on the basis of the ammonite fauna (Kaplan *et al.* 1998). The fauna, redescribed by Gale and Thiel (*in press*) includes abundant *Roveacrinus pentagonus*, indicative of roveacrinid zone CeR2b, which is otherwise known only from the upper part of the Grayson Formation in central Texas (Gale in Gale *et al.* 2021a).

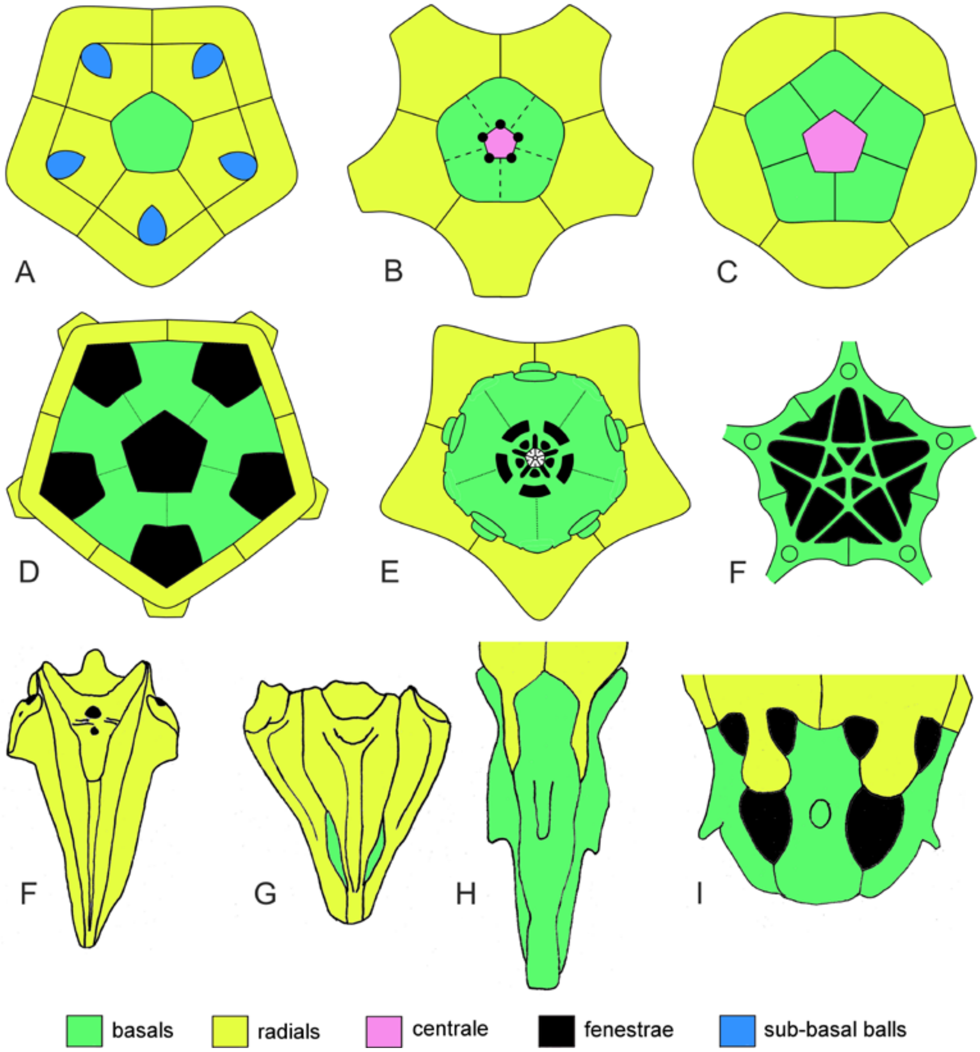
The extensive and exceptionally preserved roveacrinid material from the Hoher Stein (Dresden, Germany) and Předboj (Czech Republic) described by Žítt *et al.* (2019) can now be dated more precisely by comparison with the expanded chalk succession from Dover. The fauna includes species characteristic of zones CeR6 (*Drepanocrinus geinitzi*), CeR7 (*Roveacrinus carinatus*) and TuR1 (*Drepanocrinus sessilis* Jækel, 1918, *Lebenharticrinus canaliculatus* Žítt, Löser, Nekvasilová, Hradecká and Švábenická, 2019) and thus represents a condensation of the upper *C. guerangeri, M. geslinianum, N. juddii* and *W. devonense* zones, spanning the Cenomanian–Turonian boundary. The fauna of the Dresden surf pocket has previously been attributed entirely to the *M. geslinianum* Zone (Tröger 1956; Voigt *et al.* 2006) on the basis of the occurrence of the belemnite *Praeactinocamax plenus* (Blainville, 1827), but evidently the infilling sediment represents a considerably longer time interval.

EVOLUTION OF CUP STRUCTURE IN THE ROVEACRINIDAE

In most roveacrinids the basals are internal and form a partition separating an aboral basal cavity from an adoral radial cavity in the fully grown adult (Schneider 1987; Hess and Messing 2011; Gale 2020). In early ontogeny, external basals and a centrale are present in *Poecilocrinus*, but these are progressively overgrown and covered by aboral extensions of the radials (Gale in Gale *et al.* 2021a, pl. 19). Specimens which show the internal structure of roveacrinids are very rare, as specimens need to be naturally broken transversely and lack attached sediment and diagenetic overgrowth. Renewed interest in their evolution was stimulated by the discovery of a new structural



Text-fig. 5. Cups of roveacrinids, in aboral view in which the basal cavity is broken transversely (A–J, M–P); in K, the cup is split longitudinally. **A** – *Euglyphocrinus pyramidalis* (Peck, 1943), the original of Gale in Gale *et al.* (2021a, pl. 6, fig. 9; NMB M 11594). **B** – *Euglyphocrinus cristagalli* Gale, 2020, the original of Gale (2020, pl. 4, fig. 3; NHMUK PI EE 17387). **C** – *Calvaticrinus monocarinatus* (Destombes, 1984), the original of Gale and Matrion (2021, fig. 7.6; MHNH 2011.2.5456c). **D** – *Calvaticrinus integer* (Hess, 2011), the original of Hess and Gale (2010, fig.7D; NHMUK EE 13740). **E**–**G**, **I** – *Styracocrinus peracutus* (Peck, 1943); E, I – the originals of Gale in Gale *et al.* (2021a, pl. 4, figs 14, 15; NHMUK PI EE 17742, 17743); F, G – the originals of Gale (2020, pl. 5, figs 5, 7; NHMUK PI EE 17405, 17406). **H** – *Hyalocrinus magnezi* Destombes, 1984, the original of Gale (2019, pl. 38, fig. 3c; NHMUK PI EE 16063). **J**, **K** – *Orthogonocrinus apertus* (Peck, 1943), the originals of Gale in Gale *et al.* (2021a, pl. 2, figs 7, 13; NHMUK PI EE 17727, NMB M 11607, respectively). **L** – *Roveacrinus gladius* Gale, 2020, the original of Gale (2020, pl. 12, fig. 11; NHMUK PI EE 17476). **M** – *Dubrisicrinus minutus* gen. et sp. nov. (NHMUK PI EE 18094). **N**, **O** – *Hessicrinus filigree* Gale, 2016; N – the original of Gale (2016, fig. 10A; NHMUK PI EE 16098); O – the original of Gale (2019, pl. 44, fig. 7; NHMUK PI EE 16923). **P** – *Stellacrinus hughesae* Gale, 2016, the original of Gale (2016, fig. 14E; NHMUK PI EE 16202). A, J, K are from the Duck Creek Formation, Upper Albian, Fort Worth, Texas, USA. B is from the Main Street Formation, Upper Albian, Fort Worth, Texas, USA. C is from the Middle Albian, Bully, Normandy, France. D is from the Shenley Limestone, Lower Albian, Shenley, UK. E, I are from the Duck Creek Formation, Upper Albian, Horseshoe Bend, Love County, Oklahoma, USA. F, G, L are from the Aït Lamine Formation, Abouda road cutting, Agadir, Morocco. H is from the Gault Clay Formation, Middle Albian, Bed 3, Folkestone, Kent, UK. M is from the Zig Zag Formation, Middle Cenomanian, *T. acutus* Subzone, Dover, Kent, UK. N, P are from the Seaford Chalk Formation, Lower Campanian, Sussex, UK. O is from the Upper Santonian, Veules-les-Roses, Normandy, France. Scale bars equal 0.5 mm (F, J, N), 0.1 mm (L, M, P) and 0.2 mm (all others).



Text-fig. 6. Diagrammatic illustration of cup structure in roveacrinids. A, F – Cup type A1, with sub-basal balls. D – Cup type A2, large radially positioned fenestrae, central fenestra. B – Cup type A3, sub-basal balls absent. C, G – Cup type B, with basals extending aborally, forming slips between radials. H – Cup type C1, basals forming solid aboral cone. E – Cup type C2, basals forming transverse web, aboral cone with fenestrae. A, F – *Styracocrinus peracutus* (Peck, 1943). B – *Roveacrinus gladius* Gale, 2020. C – *Drepanocrinus sessilis* (Jækel, 1918). D – *Dubrisicrinus minutus* gen. et sp. nov. E, I – *Hessicrinus filigree* Gale, 2016. F – *Stellacrinus hughesae* Gale, 2016. G – *Drepanocrinus communis* (Douglas, 1908). H – *Dentatocrinus dentatus* Gale, 2019.

type in *Dubrisicrinus* gen. nov., and a selection of SEM images of the best examples is here presented in Text-fig. 5, and interpretative drawings in Text-fig. 6. Roveacrinids can be divided into a number of cup types, as follows:

Cup type A

In orthogonocrinines (*Styracocrinus* spp., Text-figs 5E–G, I, 6A; *Orthogonocrinus* spp., Text-fig. 5J, K) the basals form a well-defined, centrally positioned, rounded to pentagonal region which occupies 20–25% of the cup diameter (aboral view). The basal plates appear to be fused, and it is not apparent whether or not a centrale is present; examples such as that illustrated in Text-fig. 5F hint at the presence of a centrale separated from the basals by tiny foramina. Other specimens of the same species from the same sample, such as that in Text-fig. 5G, evidently lack these structures. In longitudinally broken specimens, the basals form a thin transverse partition separating the basal and radial cavities (Text-fig. 5K). In **Cup type A1**, including all orthogonocrinines (except *Discocrinus* spp.) enigmatic subspherical structures called sub-basal balls are present, lodged in radially positioned, rounded depressions, especially well shown by *Hyalocrinus* spp. (Text-fig. 5H; Gale 2019; Gale and Matrion 2021). Additionally, paired openings on each radial plate, lateral to the radial facet (paired radial tubes) are restricted to the Orthogonocrininae, as are elongated primibrachials Ibr_2 (Gale 2019; Gale and Matrion 2021). In **Cup type A2**, known only in *Dubrisicrinus minutus* gen. et sp. nov. (Text-figs 5M, 6D) the basals form a broad, pentagonal region internal to the radials, perforated by five pentagonal, radially positioned fenestrae and one large, central foramen.

A similar cup construction, **Cup type A3**, but lacking sub-basal balls, comprises a central rounded to pentagonal region made up of basals, sometimes with a centrale and tiny fenestrae, is found in *Roveacrinus gladius* (Text-figs 5L, 6B), *Calvaticrinus* spp. (Text-fig. 5C, D) and some species of *Euglyphocrinus* Gale, 2019 [*E. pyramidalis* (Peck, 1943), Text-fig. 5A; *E. cristagalli* Gale, 2020, Text-fig. 5B]. *Euglyphocrinus euglypheus* has large, well-defined external basals and a centrale, but the internal structure is unknown.

Cup type B

In many roveacrinines, including *Drepanocrinus*, the basals and centrale form a concave floor to the radial cavity (Schneider 1987) which occupies approximately 60% of the diameter of the cup (Text-fig. 6C). Aboral extensions of the basals may be present, visible externally as narrow slips between the radials [e.g., *D. striatulus* Gale, 2019; *D. communis* (Douglas, 1908); Schneider 1987; Text-fig. 6G]. As far as *Caveacrinus* Gale, 2019 is concerned, new, exceptionally preserved material shows that basals are present, forming the roof of a basal cavity which possesses large interradial fenestrae, some of which have a grill of fine, vertically arranged struts (Text-fig. 7).

Cup type C

In *Dentatocrinus* Gale, 2019, the aboral portion of the cup forms a tall, aborally tapering cone composed entirely of basals; short processes from the radials overlap the adoral part of the cup. The radial and basal cavities are separated by a solid, concave roof formed by the basals (Text-fig. 6H).

Cup type D

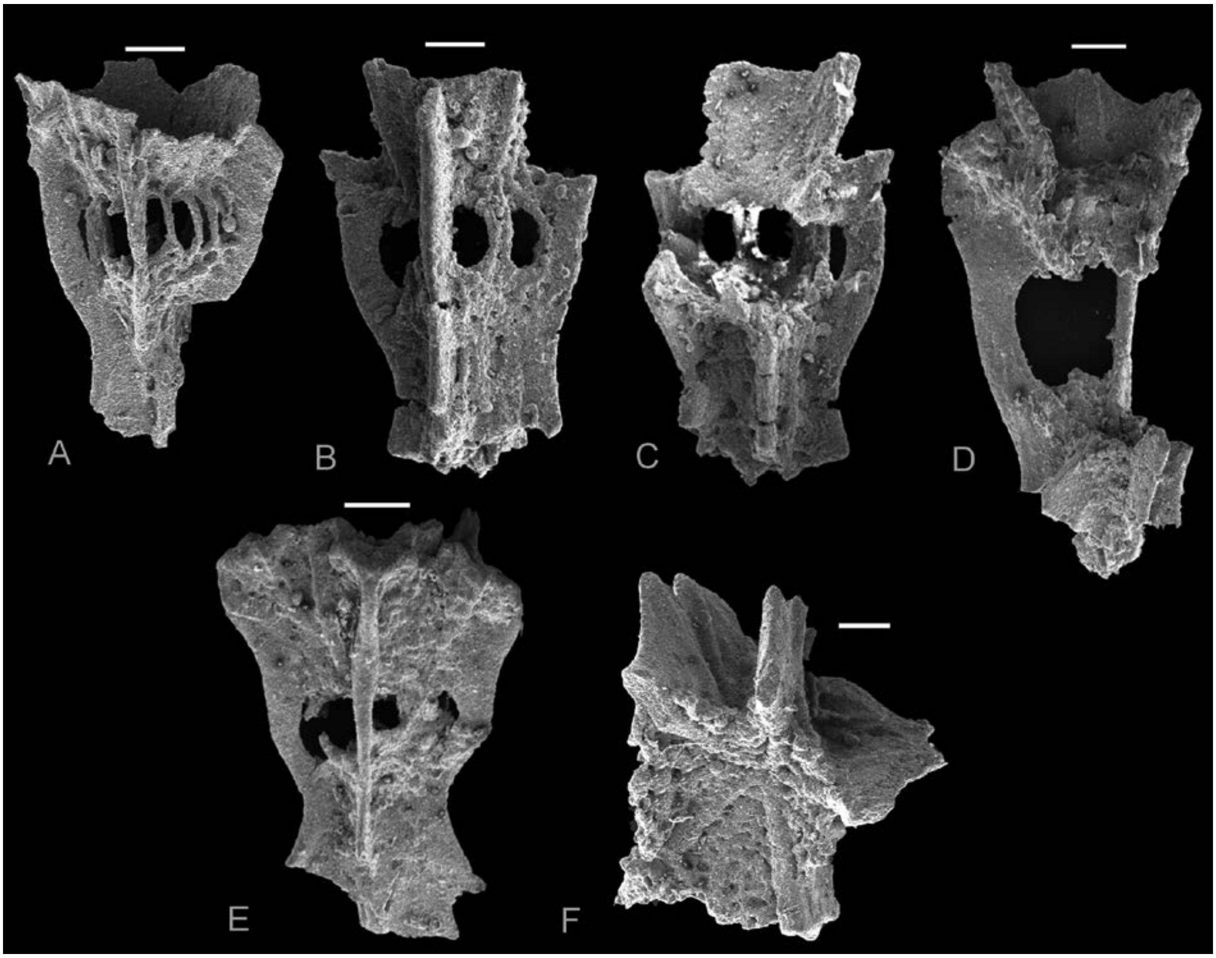
In the hessicrinines *Hessicrinus filigree* Gale, 2016 and *Stellacrinus hughesae* Gale, 2016 external basals form an aboral circlet perforated by interbasal and radial/basal fenestrae (Gale 2016; Text-fig. 6E, F, I herein). A pentagonally arranged web of struts and intervening fenestrae separates the basal and radial cavities (Text-figs 5N–P, 6E, F).

Phylogeny

Mapping the distribution of cup types A–D onto the updated phylogeny of Gale and Matrion (2021, fig. 9; Text-fig. 8 herein), with *Dubrisicrinus* gen. nov. and *Sergipecrinus* Gale in Poatskievick Pierezan *et al.*, in press, provides an interesting perspective on phylogeny of the family. It appears that Cup type A construction is basal to the Roveacrinidae, occurring in most orthogonocrinines, plotocrinines and basal roveacrinines (*Roveacrinus* spp.). *Euglyphocrinus* appears in some features to be transitional between orthogonocrinines and plotocrinines, as one species (*E. pyramidalis*) retains sub-basal balls. Thus, the plesiomorphic condition in roveacrininds is with entirely internal basals (with or without centrale) forming an essentially imperforate plug between the radial and basal cavities. However, early ontogenetic stages of roveacrinids possess large external basals and a centrale (Gale 2020) and paedomorphic retention of these probably led to adult forms such as *Euglyphocrinus euglypheus*. External basal faces are incompletely developed in some species of *Drepanocrinus* (Cup type B) appearing as slips between the radials in the surface of the aboral cup (Text-fig. 6; Schneider 1987; Gale 2019). In *Dentatocrinus* (Cup type C1), the basal circlet forms an elongated cone containing the basal cavity (Text-fig. 5B) separated from the radial cavity by transverse processes from the basals. *Dentatocrinus* is basal to the Hessicrininae (Cup type C2; Text-fig. 6C, D) in which a well-developed basal circlet, perforated by interbasal and radial basal fenestrae, is present. In *Stellacrinus* and *Hessicrinus*, the radial and basal cavities are separated by a pentagonally structured web (Text-figs 5N–P, 6E, F).

Functional significance

The functional significance of roveacrinid cup structure has previously been discussed by Schneider (1987, 1995), Hess (2015) and Gale (2016). The function of a discrete, enclosed basal cavity was interpreted by Schneider (1987, 1995) as storage of gas or low-density fluids which functioned as a hydrostatic organ, enabling vertical movements, possibly by transfer of gas or liquid from one chamber to the other. Transfer of gas or liquid across the solid stereom which forms the base of the radial cavity seems



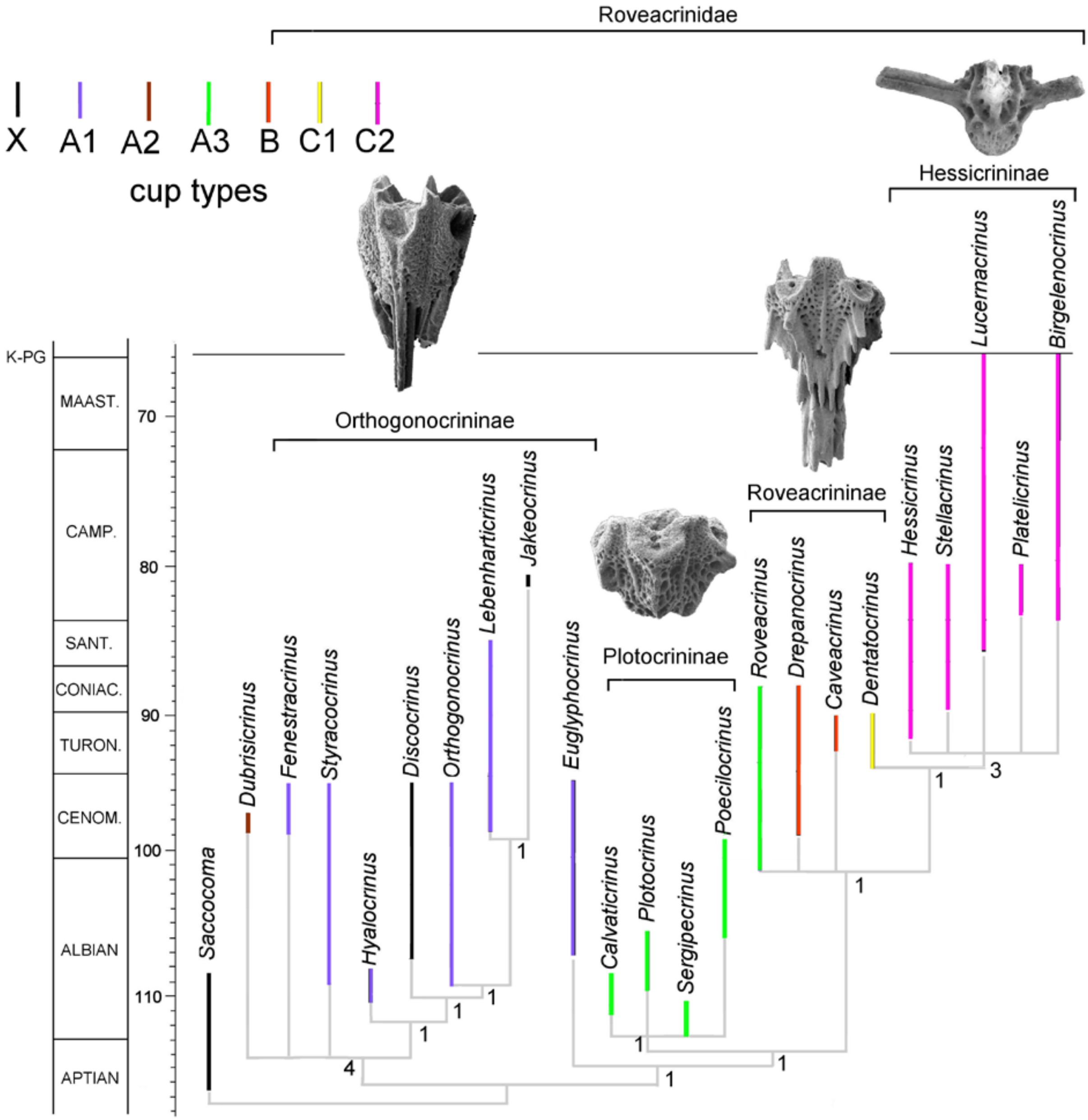
Text-fig. 7. Cup structure of *Caveacrinus asymmetricus* Gale, 2019. A – cup in lateral view to show grill-like structure within fenestrae on basal cavity (NHMUK PI EE 18137). B, C – internal and external views of broken cup, respectively (NHMUK PI EE 18138). D – fragmentary cup to show bar-like form of radials surrounding basal cavity (NHMUK PI EE 18139). E – cup to show structure of radials (NHMUK PI EE 18140). F – adoral view, to show base of basal cavity (NHMUK PI EE 18141). All specimens are from the New Pit Formation, Turonian, 6 m above base of formation, Ashwell, Hertfordshire, UK. Scale bars equal 0.2 mm.

improbable, and as Hess (2015) has pointed out, lightening the aboral part of the cup by infilling the basal cavity with gas/liquid would result in inversion of the crinoid to a mouth-downwards posture, and the hypothesis therefore appears to be speculative and improbable. The morphology of the proximal brachials indicates active swimming in an oral-upwards posture (Hess 2015). The streamlined, aborally tapering cup morphology, together with the presence of stabilising devices in some forms supports the idea that most Roveacrinida were vertical migrators in the zooplankton, perhaps swimming actively upwards and descending passively. The evolution of an external basal cone, interpenetrant with the radials (Text-fig. 6H, I) in Cup type C probably provided structural integrity to the aboral region of the cup.

In the Hessicrininae, extensive development of perforations of the cup wall – fenestrae (between plates) and foramina (within plates) – served mainly to reduce the weight of the skeleton. The evolution of a perforate web, rather than a solid partition between the radial and basal cavities, also decreased weight.

Repositories of specimens

MHNH, Musée d’histoire naturelle du Havre, Seine-Maritime, France; MMG SAK, Senckenberg Naturhistorische Sammlung, Dresden, Germany; NHMUK, Natural History Museum, London, UK; NMB, Naturhistorisches Museum Basel, Switzerland; USNM, United States National Museum, Washington DC, USA.



Text-fig. 8. Cladogram of roveacrinid relationships, modified after Gale and Matrion (2021, fig. 9), to show genera in which cup construction is known. Colours refer to cup types described in text. Cup type A is basal to the family Roveacrinidae and is modified in more derived forms (*Drepanocrinus*, *Caveacrinus* and *Dentatocrinus*). X types are not presently classified.

SYSTEMATIC PALAEONTOLOGY

Family Roveacrinidae Peck, 1943

DIAGNOSIS: Roveacrinida in which a double thecal cavity is present, the lower of which is enclosed by basals, or basals and radials; the basals form a transverse structure, either solid or perforated, separating the two cavities.

Subfamily Orthogonocrininae Gale, 2019

DIAGNOSIS: Cup pyriform or conical, elongated aborally; aboral surface bearing high, bladed, interradial processes; radial cavity shallow, narrow, base formed by small basals, not visible on exterior of cup; basal cavity elongated, the adoral surface of the cavity bearing five radially placed pits that each housed a ball-shaped structure; brachials highly modified,

Ibr_1 very short, Ibr_2 elongated, distal secundibrachials elongated, bearing pinnules.

INCLUDED GENERA: *Orthogonocrinus* Peck, 1943 (Albian–Cenomanian); *Hyalocrinus* Destombes, 1984; *Styracocrinus* Peck, 1955 (Albian–Cenomanian); *Lebenharticrinus* Žítt, Löser, Nekvasilová, Hradecká and Švábenická, 2019 (Cenomanian–Santonian) and *Jakeocrinus* Gale, 2016 (Campanian).

Genus *Discocrinus* Peck, 1943

TYPE SPECIES: *Discocrinus catastomus* Peck, 1943, OD.

INCLUDED SPECIES: *Discocrinus wrighti* Peck, 1955 and *D. africanus* Gale, 2020.

DIAGNOSIS: Cup low, broad, with tall muscle fossae on radials; radial cavity floored by thin perforated sheet; aboral cover of cup very fragile or non-mineralised.

Discocrinus wrighti Peck, 1955
(Pl. 1, Figs 1–15, 17, 18; Text-fig. 9J–M)

1955. *Discocrinus wrighti* Peck, p. 1028, pl. 106, fig. 13.
1961. *Discocrinus wrighti* Peck; Wienberg Rasmussen, p. 388, pl. 56, fig. 8.
2019. *Discocrinus wrighti* Peck; Gale, p. 476, pl. 35, figs 1, 3.

DIAGNOSIS: *Discocrinus* in which the cup tapers ad- and aborally; radial facets flush with surface of cup and not extending to aboral margin.

TYPES: The holotype (NHMUK E 15512; Pl. 1, Figs 13–15) and paratype cups (NHMUK E 15517; Pl. 1, Figs 17, 18) are from the Lower Cenomanian ‘Chalk Marl’ (West Melbury Formation), 3 m above the base, near Cambridge, UK, lower *Mantelliceras mantelli* ammonite Zone.

MATERIAL: The species has proved to occur commonly in the *C. arlesiensis* Bed (Middle Cenomanian, *Cunningtoniceras inerme* Zone; 31.7 m in Text-fig. 2) at Dover, from which 2 cups and numerous (>50) brachials have been recovered.

REMARKS: The new larger cup is similar in size and structure to the holotype and paratype cups (Text-fig. 9J–M). Brachials of *Discocrinus* are highly distinctive as they are waisted and composed of coarsely reticulate stereom (Pl. 1, Figs 4–12). Distal brachials carry large pinnular facets (Pl. 1, Fig. 8).

Differentiating between the three described species of *Discocrinus* (*D. catastomus* Peck, 1943, Upper Albian of Texas and Oklahoma; *D. wrighti* Peck, 1955, Lower Cenomanian of Cambridge, UK, and *D. africanus* Gale, 2020, Lower Cenomanian of Agadir, Morocco) is currently poorly resolved. Therefore, I here illustrate material of all species (Text-fig. 9) for comparison. The genus displays strongly allometric growth, with increased proportional height of the cup with greater size (e.g., *D. catastomus*, Text-fig. 9A–D), but there is also significant variation in proportionate height between individuals of similar diameter (compare Text-fig. 9A, B and C). Additionally, size of the radial facets increases in proportion to diameter with growth. Diagnoses can be summarised as follows:

D. catastomus: small species, never exceeding 1.5 mm in diameter. Cup cylindrical. Radial facets standing out from cup, lower portions triangular. Broad concave region between facets; base of radial facets flush with cup.

D. wrighti: cup slightly fusiform, tapering ad- and aborally. Radial facets flush with cup, not extending to base of cup. Raised interradial seam.

D. africanus: cup tapering adorally in smaller individuals, with aborally rounded radial facets. Transition to specimens of exceptional size (2.5 mm diameter) unknown.

Discocrinus sp.

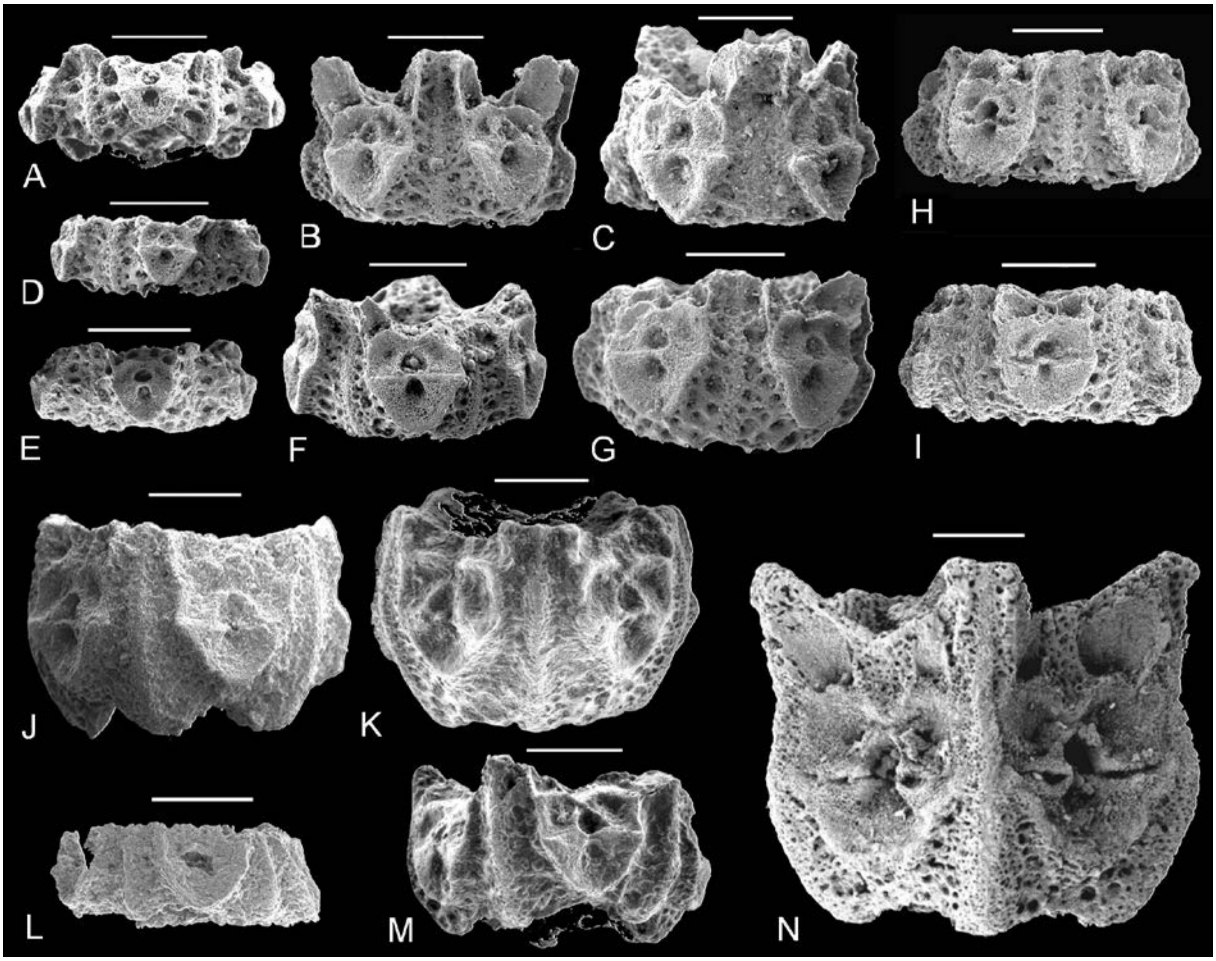
MATERIAL: Five worn brachials, Zig Zag Chalk (70.5 m), *C. guerangeri* Zone, Dover, Kent, UK.

REMARKS: Brachials are not diagnostic of species but indicate that the range of *Discocrinus* continued up into the Upper Cenomanian *C. guerangeri* Zone. They are also present at an approximately equivalent level in the Agadir Basin, Morocco (Gale 2020).

Genus *Styracocrinus* Peck, 1955

DIAGNOSIS: Cup tall, conical, extended aborally to an acute point. Interradial processes tall, pointed. IBr_2 elongated, flattened, bearing narrow rounded central ridge and lateral flanges.

TYPE SPECIES: *Drepanocrinus peracutus* Peck, 1943, OD.



Text-fig. 9. *Discocrinus* spp. cups in lateral view. **A**–**G** – *Discocrinus catastomus* Peck, 1943, NHMUK PI EE 18141-18147. **H**, **I**, **N** – *Discocrinus africanus* Gale, 2020, NHMUK PI EE 18148-18150. **J**–**M** – *Discocrinus wrighti* Peck, 1955. M – holotype cup, the original of Peck (1955, pl. 106, fig. 13; NHMUK E 15512); K – the original of Wienberg Rasmussen (1961, pl. 56, fig. 8; NHMUK E 21807). A–G are from the Weno Formation, Upper Albian, *Pervinquieria* (*Submortoniceras*) *rostrata* ammonite Zone, Cleburn, Johnson Co., Texas, USA. H, I, N, are from the Aït Lamine Formation, Lower Cenomanian, Abouda road cutting, Agadir, Morocco. J, L are from the West Melbury Formation, Middle Cenomanian, *Cunningtoniceras inerme* Zone, Dover, Kent. K, M are from the West Melbury Formation, 3 m above base, near Cambridge, UK. Scale bars all equal 0.5 mm.

Styracocrinus peracutus (Peck, 1943)
(Pl. 2, Figs 5–9, 16, 17)

1943. *Drepanocrinus peracutus* Peck, p. 463, pl. 76, figs 9–22, 26, 28, 33.
1955. *Styracocrinus peracutus* Peck, p. 1022, pl. 106, figs 10–12.
1961. *Styracocrinus peracutus* (Peck); Wienberg Rasmussen, p. 383, pl. 56, figs 1–3.
2015. *Roveacrinus peracutus* (Peck); Hess, fig. 17a–f.
2019. *Styracocrinus peracutus* (Peck), Gale, p. 476, pl. 37 figs 1–6.
2020. *Styracocrinus peracutus* (Peck), Gale, p. 290, pl. 1, fig. 6; pl. 2, figs 1, 2; pl. 5, figs 1–11.
2021a. *Styracocrinus peracutus* (Peck), Gale in Gale *et al*., p. 25, pl. 4, figs 1–17.

DIAGNOSIS: *Styracocrinus* in which the aboral portion of the cup is fully mineralised, the surface of which is non-reticulate and sparsely rugose; no swelling beneath radial facets.

TYPE: The holotype is the theca figured by Peck (1943, pl. 76, fig. 21) from the Grayson Formation of central Texas; collections of the University of Missouri (E-23-3), but not found.

MATERIAL: 10 cups and several primibrachials

(IBr_2) were collected from the Middle Cenomanian upper West Melbury and lower Zig Zag formations, from the *C. inerme* Zone (*C. arlesiensis* Bed, 31.7 m, Text-fig. 2) to the *T. acutus* Subzone (44 m, Text-fig. 2).

REMARKS: The cups (Pl. 2, Figs 6–9) are typical of the species (e.g., Gale in Gale *et al.* 2021a, pl. 4, figs 1–5, 10, 11, 13), the aboral part of the cup tapering evenly from beneath the radial facets and lacking rounded swellings immediately beneath the facets that are present in *S. shakespearensis* sp. nov. (see below). The $IIBr_1$ (Pl. 2, Figs 5, 16, 17) are elongated, parallel sided with a central ridge.

OCCURRENCE: This is a long-ranging species, which existed from the Late Albian to the Middle Cenomanian, with records from North Africa (Morocco, Tunisia), the USA (Texas, Oklahoma), Germany (Schmid 1971) and the UK.

Styracocrinus shakespearensis sp. nov.
(Pl. 2, Figs 1–4)

DIAGNOSIS: *Styracocrinus* in which each radial plate possesses a smooth, oval swelling immediately aboral to the radial facet.

TYPES: The holotype (Pl. 2, Fig. 1; NHMUK PI EE 18088) is a cup from the Upper Cenomanian Zig Zag Formation (67 m in Text-fig. 2), and a paratype (Pl. 2, Fig. 2) is a broken cup from the same level. Both are from Shakespeare Cliff, west of Dover, Kent, UK (Text-fig. 1).

MATERIAL: 25 cups from the Zig Zag Formation (Middle and Upper Cenomanian), between Samphire Hoe and Shakespeare Cliff, west of Dover, Kent, UK.

DERIVATION OF NAME: After Shakespeare Cliff, west of Dover (Text-fig. 1), where most specimens were collected.

DESCRIPTION: Cup tall, conical aboral pole acute. Radials smooth, tapering aborally, bearing rounded central ridge, expanded into oval, globose swelling immediately aboral to articular facet. Articular facets triangular, vertical, parallel with axis of cup. Depressed interradial region between facets, surmounted by transverse ridge which co-joins lateral surfaces of facets. Interradial processes short, triangular.

REMARKS: Cups of which the aboral portion is broken away are very similar to those of *Hyalocrinus magnezii* Destombes, 1984, with which they share the swollen regions aboral to the radial facets. However, hundreds of cups of *H. magnezii* are known, and none of these possess any aboral cup extensions, which are thought to have been uncalcified (Gale 2019). Additionally, in *H. magnezii* the interradial regions between the radial facets are concave (e.g., Gale and Matrion 2021, fig. 5.1–5), whereas in *S. shakespearensis* sp. nov. a transverse bar is present (Pl. 2, Figs 1, 2).

Dubrisicrinus gen. nov.

DIAGNOSIS: Cup very small (0.5–0.6 mm maximum diameter), conical, tapering evenly aborally; radial cavity broad, deep, radial wall thin, radial articular facets widely separated, small. Interradial processes short, small. Floor of radial cavity with five large, radially positioned foramina and a central foramen.

DERIVATION OF NAME: From the Roman name for Dover, Dubris, near which the specimens were found.

TYPE SPECIES: *Dubrisicrinus minutus* sp. nov.

REMARKS: The genus superficially resembles the orthogonocrinine genera *Styracocrinus* and *Hyalocrinus* in the high, aborally conical form of the cup and the aborally tapering radials which are variably swollen aboral to the articular facets. However, in *Dubrisicrinus* gen. nov. the radial cavity is broad and deep, and the wall of the adoral cup is thin, in contrast with orthogonocrinine genera, in which the wall of the adoral cup is thick and the radial cavity narrow (compare Pl. 2, Fig. 9 with Pl. 2, Fig. 10). The radial facets are widely separated in *Dubrisicrinus* gen. nov., but confluent in *Styracocrinus* and *Hyalocrinus*. Additionally, and importantly, the floor of the radial cavity is broad in *Dubrisicrinus* gen. nov. and perforated by one central and five radially positioned large foramina. In contrast, the base of the radial cavity in *Styracocrinus* contains a centrally placed, narrow pentagonal ring occupied by five fused basals and possibly a centrale (Gale 2020, pl. 5, figs 6, 8). A similar development is present in many roveacrinids, including *Roveacrinus* (Gale 2020, pl. 12, fig. 12; pl. 14, fig. 1), but here the fused basal circlet has five tiny foramina. Amongst roveacrinids, only genera of the Hessicrininae possess a perforated basal floor to the radial cavity, but in these this is a complex, geometric reticular structure (Gale 2019). Cladistic analysis places *Dubrisicrinus* gen. nov. within the Orthogonocrininae (see below).

Dubrisicrinus minutus sp. nov.
(Pl. 2, Figs 10–15)

DIAGNOSIS: As for genus.

TYPES: The cup illustrated in Pl. 2, Figs 10–12 is the holotype (NHMUK PI EE 18094); the other two figured cups (Pl. 2, Figs 13, 14; NHMUK PI EE 18095; Pl. 2, Fig. 15; NHMUK PI EE 18096) are paratypes. The holotype and second paratype come from the Zig Zag Formation, Middle Cenomanian *T. acutus* Subzone, 45 m in Text-fig. 2, and the first paratype from slightly higher, 46 m. All from the eastern end of Samphire Hoe, west of Dover, Kent, UK (Text-fig. 1).

DERIVATION OF NAME: Latin *minutus*, after the tiny size of the cups, 0.5–0.7 mm in diameter.

DESCRIPTION: Cup tiny (0.5–0.7 mm maximum diameter) pentagonal in adoral view, corners formed by radial facets. Cup height twice that of maximum breadth, tapering evenly aborally from radial facets to aboral pole. Radial cavity broad and deep, walls thin, radial facets small, widely separated, protruding from corners of cup. Interradial seam slightly swollen at level of radial facets, interradial processes narrow, short. Cup surface smooth, radials slightly swollen immediately aboral to radial facets. Floor of radial cavity with large radially placed foramina and a single central foramen.

Genus *Roveacrinus* Douglas, 1908

DIAGNOSIS: Roveacrininae characterised by delicately constructed, adorally broad cups which bear elongated, aborally flanged, alar extensions from each lateral radial margin, and possess a globular basal cavity clearly visible on the exterior of the cup. IBr_2 and $IIBr_1$ triangular, possessing lateral spines and flanges. Basals completely internal.

REMARKS: As defined here, the genus comprises roveacrinines in which alar extensions are developed on the radial mid-line, aboral to the radial facets; these usually have a thickened adoral margin. The external expression of the radial cavity is slightly to very bulbous, and sometimes finely perforated. The primibrachials are variable in morphology at successive stratigraphical levels and, in conjunction with cup morphology, are used to define species. The rather delicate cups did not survive well on the chalk sea floor and are usually fragmentary.

TYPE SPECIES: *R. alatus* Douglas, 1908, OD.

Roveacrinus aboudensis sp. nov.
(Pl. 3, Figs 1–4, 6–13)

part 2020. *Roveacrinus gladius* Gale, p. 298, pl. 13, fig. 6 only.

DIAGNOSIS: *Roveacrinus* with a very broad radial cavity; radials bear short, blunt, irregularly distributed processes. IBr_2 triangular, with deep median groove flanked by short flanges.

TYPES: Cup figured by Gale (2020, pl. 13, fig. 6), NHMUK PI EE 17486, sample TAN25, Cenomanian, Aït Lamine Formation, Abouda, west Morocco.

MATERIAL: Cups, isolated radials and primibrachials from the Abouda road cutting, north of Agadir, Morocco. Over 50 isolated radials and proximal brachials from the Zig Zag Formation, Middle Cenomanian *A. jukesbrownei* Zone (56.5–57.1 m in Text-fig. 2) at Abbotscliff, Dover, Kent, UK.

DERIVATION OF NAME: After Abouda Plage, near Taghazout, Morocco, where the type material was collected.

DESCRIPTION: Cup as broad as high, radial cavity broad, open, aboral pole acute (Pl. 3, Fig. 11). Radials constructed of medium- to coarse-meshed stereom with low median ridge; ridge bearing short, irregularly distributed processes. IBr_1 (Pl. 3, Figs 6, 7) rectangular, constructed of coarse stereom; distal surface with oval synarthrial surface for articulation with IBr_2. IBr_2 (Pl. 3, Figs 9, 10, 12, 13) triangular, slightly elongated, deep central groove flanked by two flanges, variably striated. $IIBr_2$ (Pl. 3, Fig. 8) oval, elongated, bearing irregular smooth flanges.

REMARKS: *Roveacrinus aboudaensis* sp. nov. was included within my concept of *R. gladius* in Gale (2020), but re-examination of the original material plus the new specimens from Dover indicates that is a distinct, slightly later species. In *R. gladius*, the radials carry flat, bladed processes which bear coarse striations close to the cup (Pl. 3, Figs 14–16), whereas in *R. aboudaensis* sp. nov. the blades are weakly developed as short processes, or entirely absent (e.g., Pl. 3, Fig. 11). The primibrachials IBr_2 also differ significantly; in *R. gladius* (Pl. 3, Fig. 17) these are rectangular in outline and carry a short median process on the distal portion. In contrast, those of *R.*

aboudaensis sp. nov. are triangular and have a deep median groove lacking a median blade (Pl. 3, Figs 9, 10, 12, 13).

OCCURRENCE: This species occurs commonly in the Aït Lamine Formation of the Abouda road cutting, Agadir Basin, between 407 and 420 m (Gale 2020, text-fig. 8), where it is associated with abundant *Drepanocrinus wardorum*. Both species occur commonly in 0.5 m of the lower *A. jukesbrownei* Zone (56.5–57.1 m in Text-fig. 2) at Dover, Kent, UK.

Roveacrinus precarinatus sp. nov.
(Pl. 5, Figs 1–3, 5, 9–13)

DIAGNOSIS: *Roveacrinus* bearing horizontal, slightly aborally recurved radial spines, attached to the mid-radials by a thin flange; cup surrounding basal cavity weakly swollen. IBr_2 bearing strong proximal-distal ridges and a central groove.

TYPES: The well-preserved cup (Pl. 5, Fig. 1) is the holotype (NHMUK PI EE 18124); the other figured cups (Pl. 5, Figs 2, 3) and isolated radials (Pl. 5, Figs 5, 6) are paratypes (NHMUK PI EE 18125, 18126, 18132-18136). All are from the upper Zig Zag Formation, *C. guerangeri* Zone (66–68 m in Text-fig. 2), at Shakespeare Cliff, west of Dover, Kent, UK (Text-fig. 1).

DERIVATION OF NAME: Occurring at a lower level, and probably ancestral to, *R. carinatus*.

MATERIAL: Thirty cups and fragmentary cups, plus numerous brachials. All from the upper Zig Zag Formation, *C. guerangeri* Zone (66–68 m in Text-fig. 2), at Shakespeare Cliff, west of Dover, Kent, UK.

DESCRIPTION: Cup conical, breadth equal to height. Radials bearing laterally flattened spine projecting from beneath the radial facet, robust adorally, conjoined to mid-line of radials by thin flange. Spine horizontal to weakly recurved. Cup surrounding basal cavity slightly swollen, bearing five low radial flanges in larger individuals (Pl. 5, Fig. 2). IBr_2 (Pl. 5, Figs 9, 11–13) triangular, bearing strong proximal-distal ridges separated by median groove.

REMARKS: *Roveacrinus precarinatus* sp. nov. differs from the later (presumably descendant) species *R. carinatus* in the absence of a very large, strongly swollen basal cavity with a single, aboral spine (Pl. 6, Figs 1, 2), in the much shorter radial spines (compare Pl. 5, Figs 1, 3 with Pl. 6, Figs 5, 6), and in the strongly ridged IBr_2 (Pl. 5, Figs 9, 11–13). In *R. carinatus*, IBr_2 are weakly ridged and possess a pair of elongated spines (Pl. 6, Figs 3, 4, 7, 8).

OCCURRENCE: Upper Cenomanian *C. guerangeri* Zone of Dover, Kent, UK.

Roveacrinus carinatus Nekvasilová and Prokop, 1963
(Pl. 6, Figs 1–8)

part 1932. *Drepanocrinus sessilis* Jækel; Sieverts, figs 1, 6, 6a.
1963. *Roveacrinus carinatus* Nekvasilová and Prokop, p. 49, pl. 1, figs 1–4.
part 1961. *Roveacrinus alatus*; Wienberg Rasmussen, pl. 54, fig. 2a, b only.
2019. *Roveacrinus alatus*; Žítt *et al*., p. 89, fig. 5A–S.
2019. *Roveacrinus carinatus* Nekvasilová and Prokop; Gale, p. 442, pl. 8, figs 1–12.

DIAGNOSIS: Cup with globose aboral swelling, finely punctate, around basal cavity, terminating in adoral point; radials possessing thin triangular flange, thickened at aboral margin, barely extending aborally onto basal cavity swelling; IBr_s concave, triangular, carrying two laterally directed spines.

TYPE: The holotype is the specimen figured by Nekvasilová and Prokop (1963, pl. 1, fig. 1) in the collections of the Comenius University at Prague (Czech Republic), number NP73-8, and is from Předboj near Prague; Upper Cenomanian, *Praeactinocamax plenus* belemnite Zone.

OCCURRENCE: Abundant in the upper 0.3 m of Bed 8 of the Plenus Marl, *Metoicoceras geslinianum* Zone at Holywell, Eastbourne, Sussex, from which 50 cups have been collected, extending up through the basal Holywell Chalk to Meads Marl 4. Present, but less abundant, at the same level at Dover, Kent, UK (Text-fig. 2), other UK localities, and at Penly, near Dieppe (France).

REMARKS: *Roveacrinus carinatus* is a highly distinctive form, characterised by the globular aboral swelling around the basal cavity, the greatly elongated, triangular spines on the radials and the triangular, concave IBr_2 which possesses elongated, laterally directed spines. It evolved from the earlier Cenomanian *R. precarinatus* sp. nov. by development of a swollen region surrounding the basal cavity and elongated radial spines. This species is restricted to the Aït Lamine Formation, sample AGN3 (458.5 m in Gale 2020, fig. 4), Taghazout Plage, north of Agadir, Morocco, and the *Metoicoceras geslinianum* and *Neocardioceras juddii* ammonite zones of the uppermost Cenomanian (Plenus Marl and Melbourne Rock up to Meads Marl 4) of the Anglo-Paris Basin. The types are from the Czech Republic, and the species also occurs at Dresden in Germany, having been figured as *R. alatus* by Žítt *et al.* (2019).

Genus *Drepanocrinus* Jækel, 1918

TYPE SPECIES: *Drepanocrinus sessilis* Jækel, 1918, OD.

DIAGNOSIS: Cups conical, robust, with radial buttresses lacking alar extensions or flanges. Basal cavity inconspicuous on cup exterior. Basals highly variable, internal or with small external surfaces. IBr_1 and IBr_2 triangular to trapezoidal, flat, sculpture ridged or reticulate, lacking spines or flanges.

STRATIGRAPHICAL RANGE: Cenomanian to Middle Coniacian.

REFERRED SPECIES: *Drepanocrinus westphalicus* (Sieverts, 1932); *D. communis* (Douglas, 1908); *D. geinitzi* (Schneider, 1989); *D. striatulus* Gale, 2019 and *D. marocensis* Gale, 2019.

Drepanocrinus wardorum Gale, 2020
(Pl. 4, Figs 1–19)

2020. *Drepanocrinus wardorum* Gale, p. 300, pl. 14, figs 4, 6, 7, 11, 12; pl. 12, figs 1–9.

DIAGNOSIS: Cup conical, height equal to breadth, with broad, rounded, irregularly striate radial ridges which carry smaller lateral swellings; IBr_2 trapezoidal, with irregular striations, double central ridge bifid, flattened.

TYPE: Cup (NHMUK PI EE 17501) from the Middle Cenomanian Aït Lamine Formation, Abouda, western Morocco, sample TAN 25 (Gale 2020).

MATERIAL: Over 500 isolated radial plates and brachials from the *Acanthoceras jukesbrownei* ammonite Zone, Abbotscliff, Kent, UK.

REMARKS: The material from Abbotscliff includes several hundred isolated radials and basals, many broken. The radials (Pl. 4, Figs 1–3) possess a robust median flange which bears vertical ridges, as in specimens from Morocco (Pl. 4, Fig. 19). The IBr_2 (Pl. 4, Figs 2, 6–8, 10, 11, 13) are highly variable in form. They are rounded-trapezoidal in outline, and many bear a symmetrical pair of distally diverging short flanges or nodes. About 10% have inconspicuous, flattened nodes and are strongly striated (Pl. 4, Fig. 10) and compare closely with specimens from Morocco (e.g., Pl. 4, Fig. 17), but the majority are entirely smooth (e.g., Pl. 4, Figs 4, 7, 11). $IIBr_2$ (Pl. 4, Figs 5, 6, 12) are distinctly asymmetrical, and the sculpture varies in parallel with that on the IBr_2. There is considerable variation in the brachial sculpture of *D. wardorum* and *D. geinitzi,* and in the Moroccan assemblages the latter species infrequently has smooth IBr_2 (Pl. 4, Fig. 20). The Dover material is referred to *D. wardorum* on account of the absence of lateral flanges on the radials, and the absence of paired deep pits on the IBr_2 (see Pl. 6, Figs 17–20). Brachial sculpture may vary regionally.

Drepanocrinus geinitzi (Schneider, 1989)
(Pl. 5, Figs 4, 7, 8; Pl. 6, Figs 12–14)

*1989. *Roveacrinus geinitzi* Schneider, p. 171, figs 3.1–3.4, 5a, b.
2019. *Roveacrinus geinitzi* Schneider; Žítt *et al.*, p. 91, figs 8A–H, K–S, 12A–H.
2016. *Roveacrinus geinitzi* Schneider; Niebuhr and Ferré, fig. 1q, r.
2020. *Drepanocrinus geinitzi* (Schneider); Gale, p. 301, pl. 14, fig. 8; pl. 15, figs 10–19; pl. 16, figs 9–11, 14, 15.

DIAGNOSIS: *Drepanocrinus* in which the radial flanges bear a number of delicate lateral wings, usually imbricated; IBr_2 with rather few ridges, and a pair of tall central flanges, lateral to which are broad concavities.

NEOTYPE: In view of the fact that Schneider's original material cannot be located, the specimen originally figured by Geinitz (1871) from the Upper Cenomanian of Hoher Stein, Dresden, was designated neotype by Niebuhr and Ferré (2016). It is housed in the Senckenberg Naturhistorische Sammlung, Dresden, no. SAK 883.

MATERIAL: Four fragmentary cups and ten isolated radials from the Zig Zag Formation, Upper Cenomanian, *C. guerangeri* Zone (Shakespeare Cliff, west of Dover, Kent, UK).

REMARKS: The new material from Dover, although not very well preserved, displays the lateral flanges on the radial blades typical of the species (Pl. 5, Figs 4, 7, 8). Illustrations from Žítt *et al.* (2019) of superbly preserved cups from the Hoher Stein, Dresden (Germany) are provided for comparison (Pl. 6, Figs 12–14).

OCCURRENCE: The new material demonstrates that this species occurs in the *C. guerangeri* Zone, as correlative levels at Eastbourne, 85 km to the west of Dover, yield ammonites typical of that zone (Gale *et al.* 2005).

Dentatocrinus Gale, 2019

DIAGNOSIS: A roveacrinine in which spinose basals form the elongated aboral portion of the cup and are overlapped radially by narrow aboral extensions of the radials.

TYPE SPECIES: *Dentatocrinus dentatus* Gale, 2019.

REFERRED SPECIES: In addition to the type species, *D. minutus* Gale, 2019, *D. compactus* Gale, 2019, *D. hoyezi* Gale, 2019 and *D. serratus* sp. nov.

Dentatocrinus serratus sp. nov.
(Pl. 5, Fig. 6)

DIAGNOSIS: *Dentatocrinus* in which a single, short spine is present on each radial immediately aboral to the radial facet; a narrow-mid radial blade bearing evenly sized blunt serrations.

TYPES: The broken cup illustrated in Pl. 5, Fig. 6 is the holotype (NHMUK PI EE 18129); from the upper Zig Zag Formation, *C. guerangeri* Zone (66 m in Text-fig. 2).

DERIVATION OF NAME: Latin *serratus*, meaning serrated, after the sawblade-like form of the mid-radials.

MATERIAL: Only the type material is known.

DESCRIPTION: Cup conical, fragile, height slightly greater than breadth, tapering evenly up from narrow aboral pole. Radials smooth, bearing a central crest on which are evenly spaced, low serrations, and immediately aboral to the radial facet, a short, rounded spine which projects laterally. Basals form a low, parallel-sided narrow cone making up the aboral pole of the cup.

REMARKS: Although the material is limited and not very well preserved, it does show a number of comparable features to the Turonian *D. dentatus*, notably the serrations on the mid-radials (e.g., Gale 2020, pl. 32, fig. 5) and the presence of a short, conical aboral cone. It differs from *D. dentatus* in the shorter aboral cone, the regular serration and the delicate radial spine. This is the only known species of *Dentatocrinus* from the Cenomanian.

OCCURRENCE: Only known from the upper Zig Zag Formation, *C. guerangeri* Zone, 66 m, Shakespeare Cliff, Dover, Kent, UK.

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PLATE 1

1–**15**, **17**, **18** – *Discocrinus wrighti* Peck, 1955. 1 – large cup in lateral aspect (NHMUK PI EE 18077); 2, 3 – small cup in lateral and aboral aspect, respectively (NHMUK PI EE 18078); 4, 5 – IBr_2 in lateral and external views, respectively (NHMUK PI EE 18079, 18080); 6–8 – mid-arm to distal secundibrachials (NHMUK PI EE 18081–18083); 9–12 – proximal secundibrachials (NHMUK PI EE 18084–18087); 13–15 – holotype cup, the original of Peck (1955, pl. 106, fig. 13), in adoral, lateral and aboral views, respectively (NHMUK E 15512); 17, 18 – paratype cup, in lateral and adoral views, respectively, the original of Wienberg Rasmussen (1961, pl. 56, fig. 8; NHMUK E 21807).

16 – *Discocrinus catastomus* Peck, 1943, aboral view of cup, the original of Gale (2019, pl. 35, fig. 2; NHMUK PI EE 16138).

Figures 1–12 are from the Middle Cenomanian, *Cunningtoniceras inerme* ammonite Zone, *C. arlesiensis* Bed (31.8 m in Text-fig. 2), Lydden Spout, west of Dover, Kent, UK (Text-fig. 1). Figures 13–15, 17, 18 are from the Lower Cenomanian, *Neostlingoceras carcitanense* Subzone, West Melbury Formation, 3 m above base, near Cambridge, UK. Figure 16 is from the Duck Creek Formation, Horseshoe Bend, Red River, Bryan County, Oklahoma, USA.

Scale bars equal 0.5 mm (13–15, 17, 18), 0.3 mm (1) and 0.2 mm (all others).

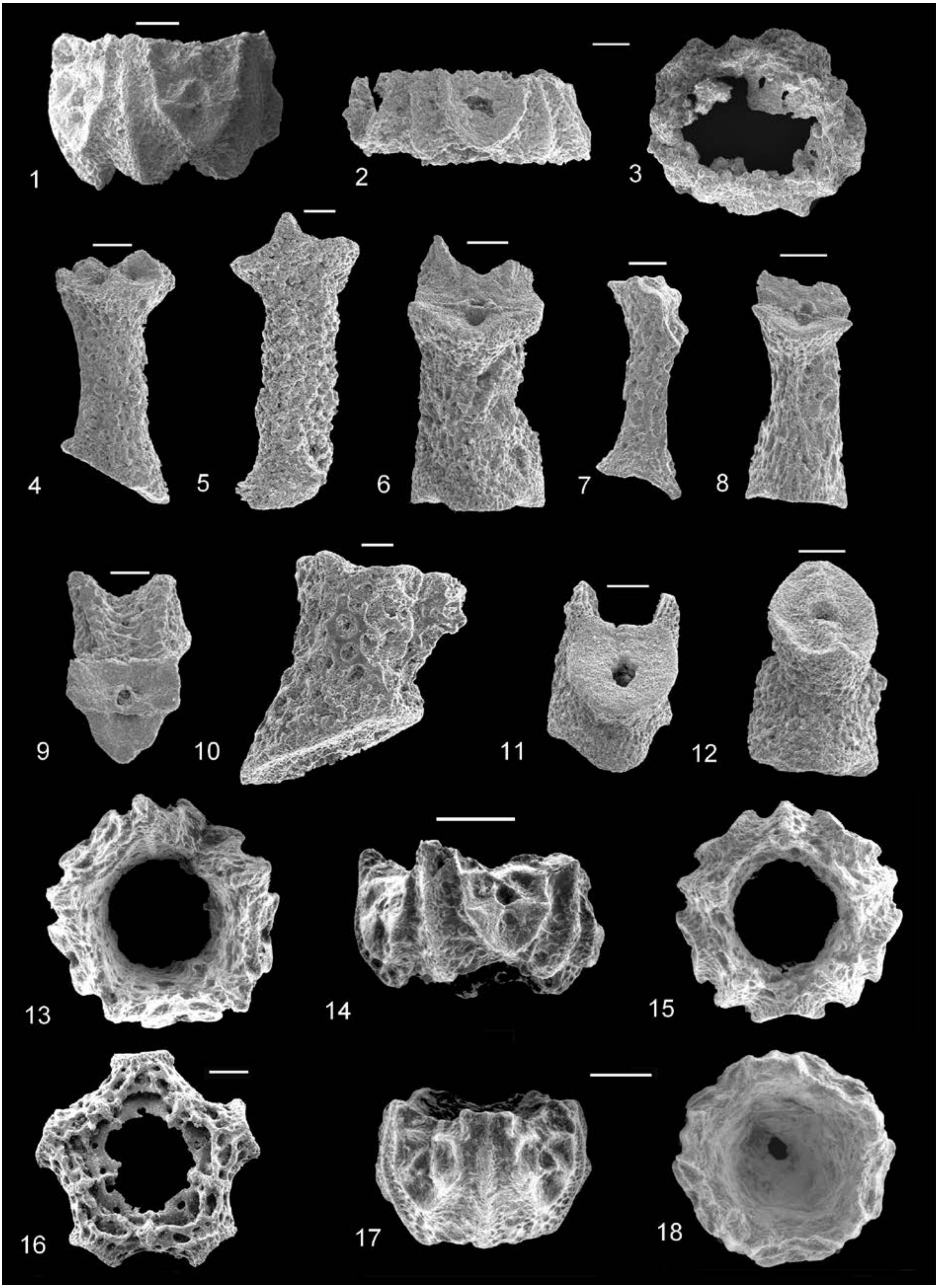
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PLATE 2

1–**4** – *Styracocrinus shakespearensis* sp. nov. 1 – holotype cup, in lateral view (NHMUK PI EE 18088); 2, 3 – paratype cup, in lateral and adoral views, respectively (NHMUK PI EE 18089); 4 – paratype cup, in lateral view (NHMUK PI EE 18090).

5–**9**, **16**, **17** – *Styracocrinus peracutus* (Peck, 1943). 5 – IBr2, external view (NHMUK PI EE 18091); 6, 7 – cup in lateral and adoral view, respectively (NHMUK PI EE 18092); 8, 9 – cup in lateral and adoral view (NHMUK PI EE 18093); 16, 17 – external and oblique internal views of brachial IBr2 (NHMUK PI EE 18097).

10–**15** – *Dubrisicrinus minutus* gen. et sp. nov. 10–12 – holotype cup in adoral, oblique lateral and aboral views, respectively (NHMUK PI EE 18094); 13, 14 – paratype cup, in adoral and lateral views, respectively (NHMUK PI EE 18095); 15 – paratype cup, in lateral view (NHMUK PI EE 18096).

Figures 1–3 are from the Zig Zag Formation, Upper Cenomanian, *C. guerangeri* Zone (66 m in Text-fig. 2), Shakespeare Cliff, Dover, Kent, UK (Text-fig. 1). Figures 4, 10–12, 15 are from the Zig Zag Formation, Middle Cenomanian, *Turrilites acutus* Subzone (46.3 m in Text-fig. 2), eastern end of Samphire Hoe, Dover, Kent, UK. Figures 5, 8, 9 are from the West Melbury Formation, Middle Cenomanian, *Cunningtoniceras inerme* ammonite Zone, *C. arlesiensis* Bed (31.8 m in Text-fig. 2), Lydden Spout, west of Dover, Kent, UK (Text-fig. 1). Figures 6, 7 are from the Zig Zag Formation, Middle Cenomanian, *Turrilites acutus* Subzone (44 m in Text-fig. 2), Dover, UK. Figures 13, 14 are from the Zig Zag Formation, Middle Cenomanian, *Turrilites acutus* Subzone (42.7 m in Text-fig. 2), Dover, UK. Figures 16, 17 are from the Cambridge Greensand, Lower Cenomanian, *Neostlingoceras carcitanense* ammonite Subzone, Barrington, near Cambridge, UK.

Scale bars equal 0.2 mm (6–9, 16, 17) and 0.1 mm (all others).

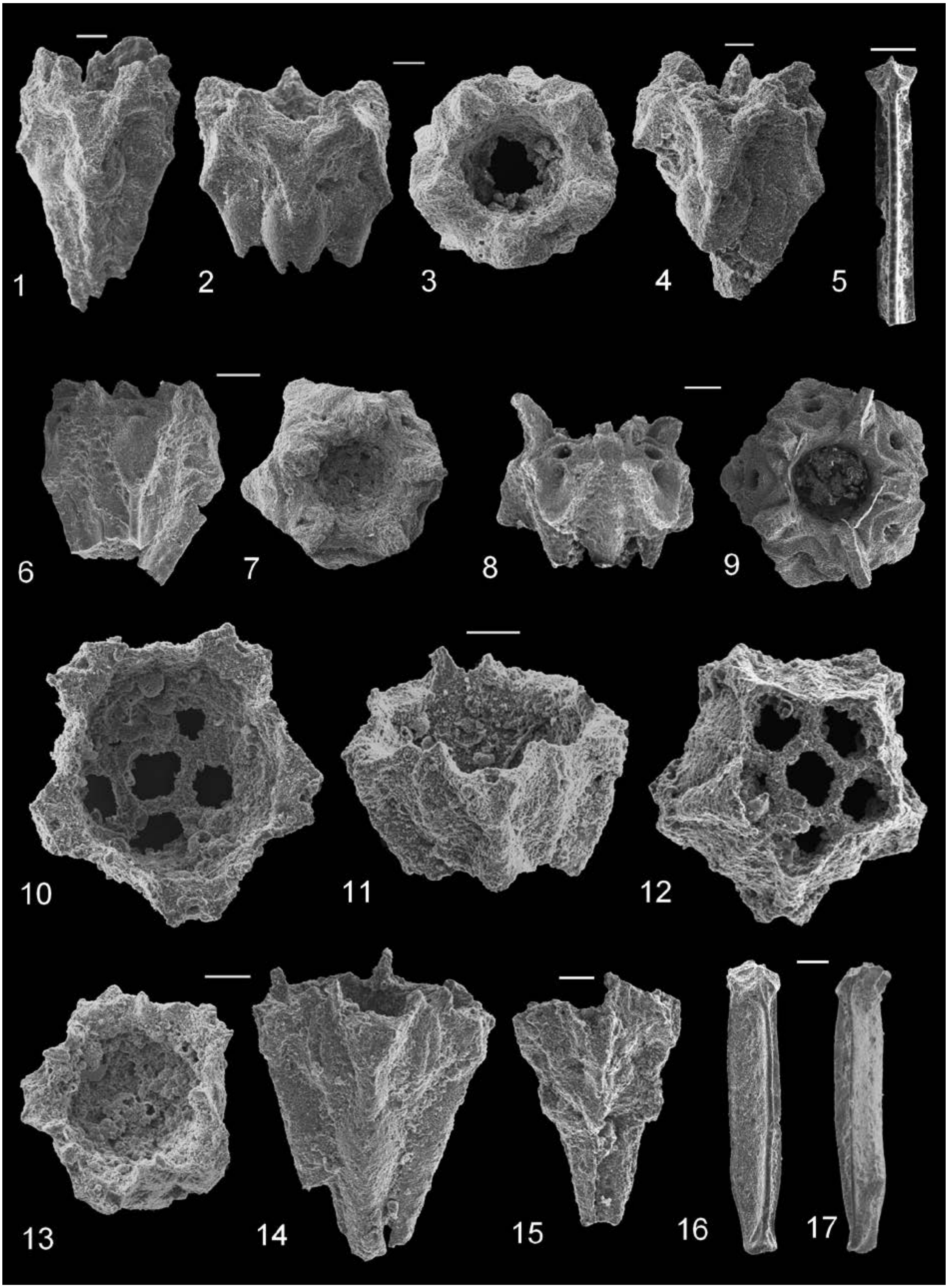
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PLATE 3

1–**4**, **6**–**13** – *Roveacrinus aboudaensis* sp. nov. 1–4 – isolated radial plates (NHMUK PI EE 18098–18101); 6, 7 – IBr_1 (NHMUK PI EE 18103, 18104); 8 – $IIBr_2$ (NHMUK PI EE 18105); 9, 10 – IBr_2, external view (NHMUK PI EE 18106, 18107); 11 – holotype cup, in lateral view, the original of Gale (2020, pl. 13, fig. 6; NHMUK PI EE 17486).

5 – *Roveacrinus* sp., isolated radial plate (NHMUK PI EE 18102).

14–**17** – *Roveacrinus gladius* Gale, 2020. 14 – holotype cup, in lateral view, the original of Gale (2020, pl. 12, fig. 1; NHMUK PI EE 17465); 15, 16 – isolated radial plates; 15 – original of Gale (2020, pl. 12, fig. 9; NHMUK PI EE 17474), 16 – NHMUK PI EE 18110; 17 – external view of IBr_2, the original of Gale (2020, pl. 13, fig. 2; NHMUK PI EE 17478).

Figures 1–4, 6-10 are from the Zig Zag Formation, Middle Cenomanian, *Acanthoceras jukes-brownei* Zone, basal marl of Jukes-Browne Bed VII (57.1 m in Text-fig. 2), Abbotscliff, Dover, Kent, UK (Text-fig. 1). Figure 5 is from the Zig Zag Formation, Middle Cenomanian, *Turrilites acutus* Subzone (46.3 m in Text-fig. 2), eastern end of Samphire Hoe, Dover, Kent, UK. Figures 11–13 are from the Aït Lamine Formation, Middle Cenomanian, sample TAN25 (420.5 m; see Gale 2020, fig. 4), Abouda road cutting, north of Agadir, Morocco. Figures 14–17 are from the Aït Lamine Formation, Lower Cenomanian, sample TA0 (310 m, see Gale 2020, fig. 4), Abouda road cutting, north of Agadir, Morocco.

Scale bars equal 0.1 mm (3, 5–7, 10), 0.5 mm (14, 17) and 0.2 mm (all others).

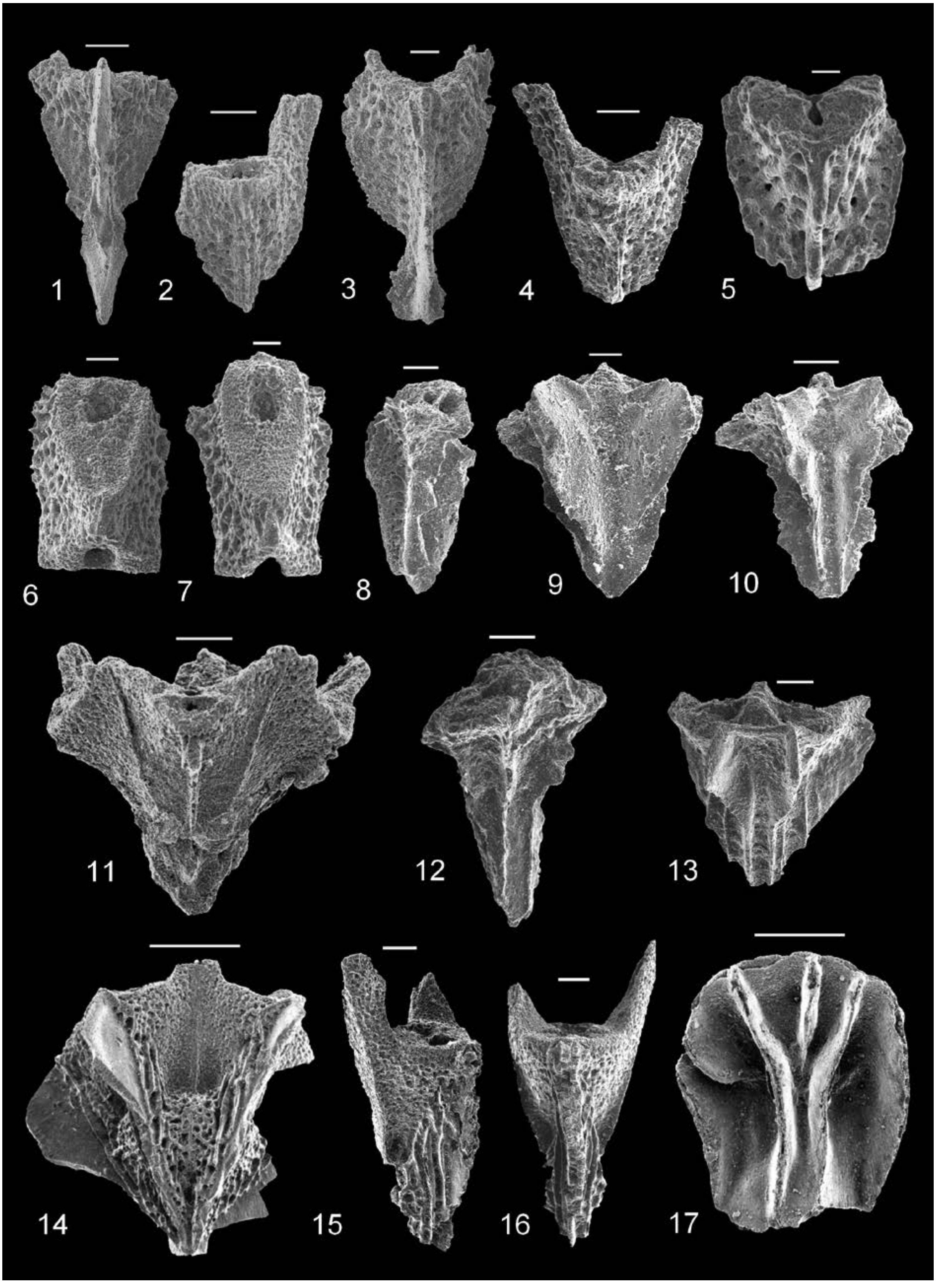
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PLATE 4

1–19 – *Drepanocrinus wardorum* Gale, 2020. 1–3 – isolated radial plates (NHMUK PI EE 18111–18113); 4, 6–8, 11, 13 – IBr_2 (NHMUK PI EE 18114, 18116–18118, 18121, 18123); 5, 9, 12 – $IIBr_2$ (NHMUK PI EE 18115, 18122); 5, 9, 10, 12, IIBr2; 14 – lateral view of holotype cup, the original of Gale (2020, pl. 15, fig. 1; NHMUK PI EE 17501); 15 – IBr_2, the original of Gale (2020, pl. 16, fig. 16; NHMUK PI EE 17530); 16 – $IIBr_2$, the original of Gale (2020, pl. 15, fig. 6; NHMUK PI EE 17506); 17 – IBr_2, the original of Gale (2020, pl. 15, fig. 4; NHMUK PI EE 17503); 18 – IBr_2, the original of Gale (2020, pl. 15, fig. 8; NHMUK PI EE 17504); 19 – isolated radial plate, the original of Gale (2020, pl. 15, fig. 3; NHMUK PI EE 17505).

20 – *Drepanocrinus geinitzi* (Schneider, 1989), IBr_2, the original of Gale (2020, pl. 15, fig. 17; NHMUK PI EE 17513).

Figures 1–13 are from the Zig Zag Formation, Middle Cenomanian, *Acanthoceras jukesbrownei* Zone, basal marl of Jukes-Browne Bed VII (57.1 m in Text-fig. 2), Abbotscliff, Dover, Kent, UK (Text-fig. 1). Figures 14–19 are from the Aït Lamine Formation, Middle Cenomanian, sample TAN 25 (420.5 m on log; see Gale 2020, fig. 4), Abouda Plage road cutting, north of Agadir, Morocco. Figure 20 is from the Aït Lamine Formation, sample AGN3 (458.5 m, see Gale 2020, fig. 4), Taghazout Plage, north of Agadir, Morocco.

Scale bars equal 0.5 mm (14), 0.1 mm (2, 5, 7, 9, 13) and 0.2 mm (all others).

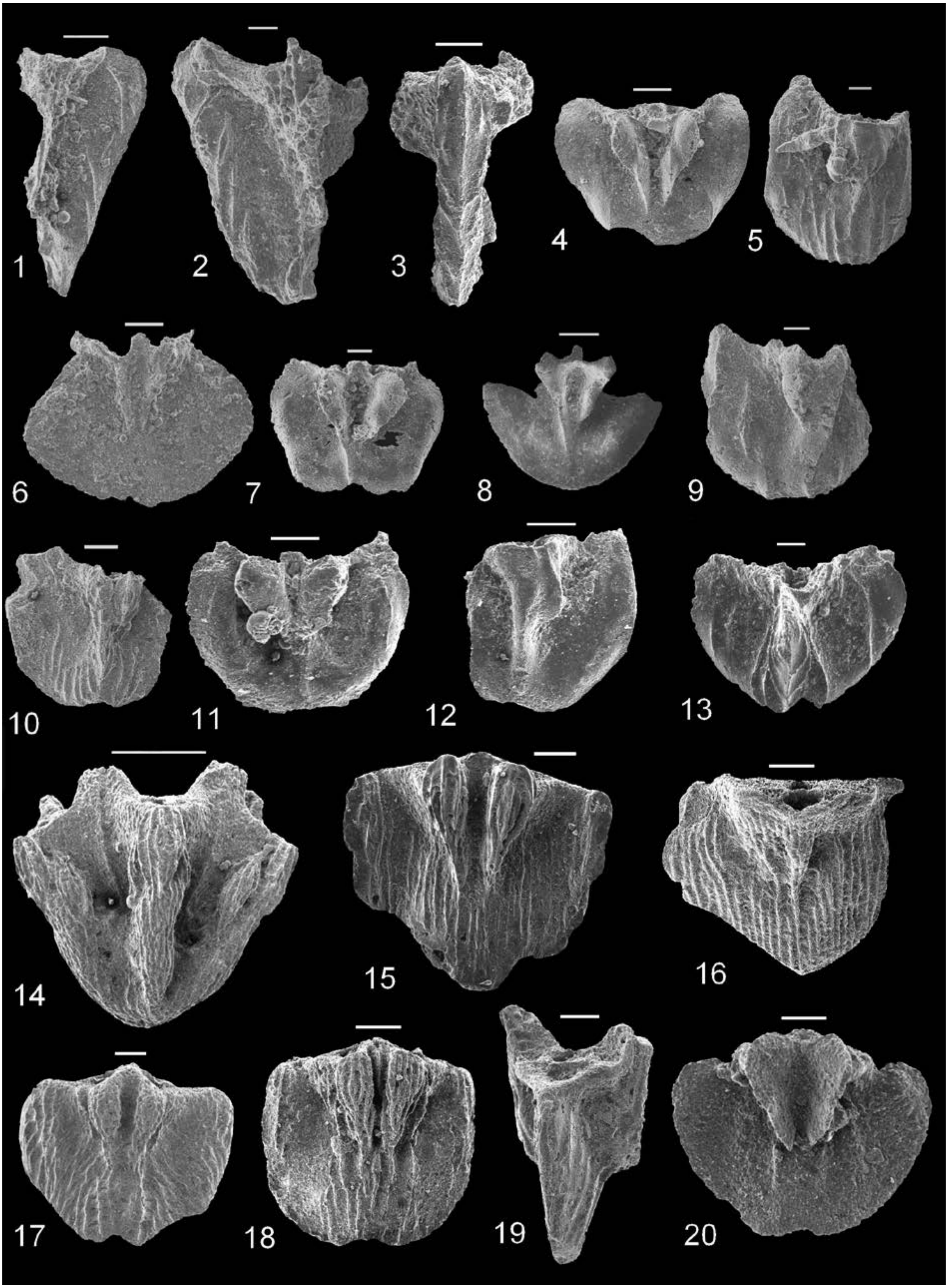
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PLATE 5

1–**3**, **5**, **9**–**13** – *Roveacrinus precarinatus* sp. nov. 1 – holotype cup, in lateral view (NHMUK PI EE 18124); 2 – paratype cup, in lateral view (NHMUK PI EE 18125); 3 – paratype cup, in oblique lateral view (NHMUK PI EE 18126); 5, 10 – paratype isolated radials, in lateral view (NHMUK PI EE 18128, 18133); 9, 11–13 – paratypes, isolated IBr_2, in external view (NHMUK PI EE 18132, 18134–18136).

4, **7**, **8** – *Drepanocrinus geinitzi* (Schneider, 1989). 4 – cup in lateral view (NHMUK PI EE 18127); 7, 8 – isolated radials (NHMUK PI EE 18130, 18131).

6 – *Dentatocrinus serratus* sp. nov., holotype cup in lateral view (NHMUK PI EE 18129).

All specimens are from the Zig Zag Formation, Upper Cenomanian *Calycoceras guerangeri* Zone (66–68 m in Text-fig. 2), Shakespeare Cliff, west of Dover, Kent, UK (Text-fig. 1).

Scale bars equal 0.4 mm (3), 0.3 mm (4), 0.1 mm (7, 9, 10) and 0.2 mm (all others).

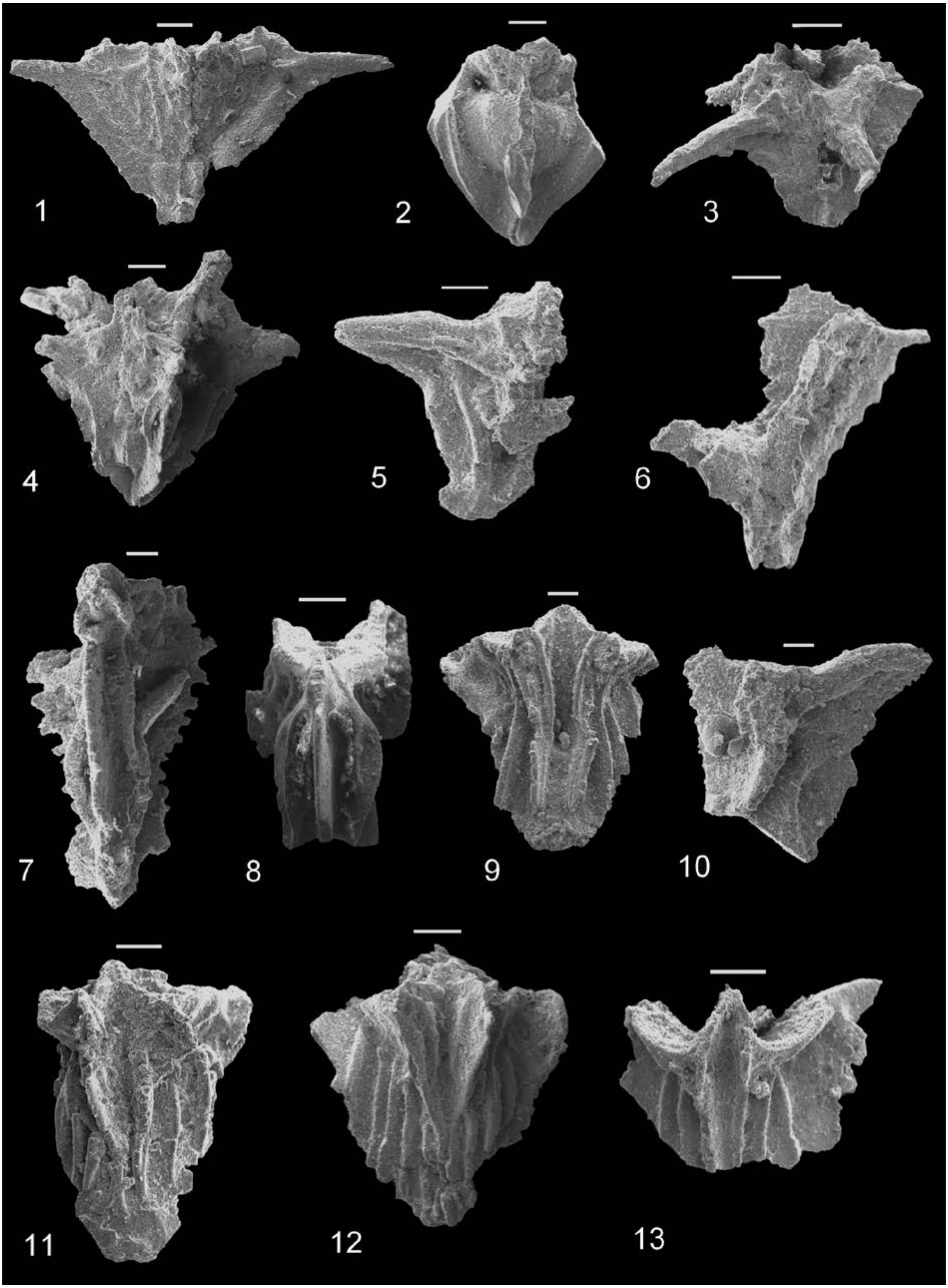
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PLATE 6

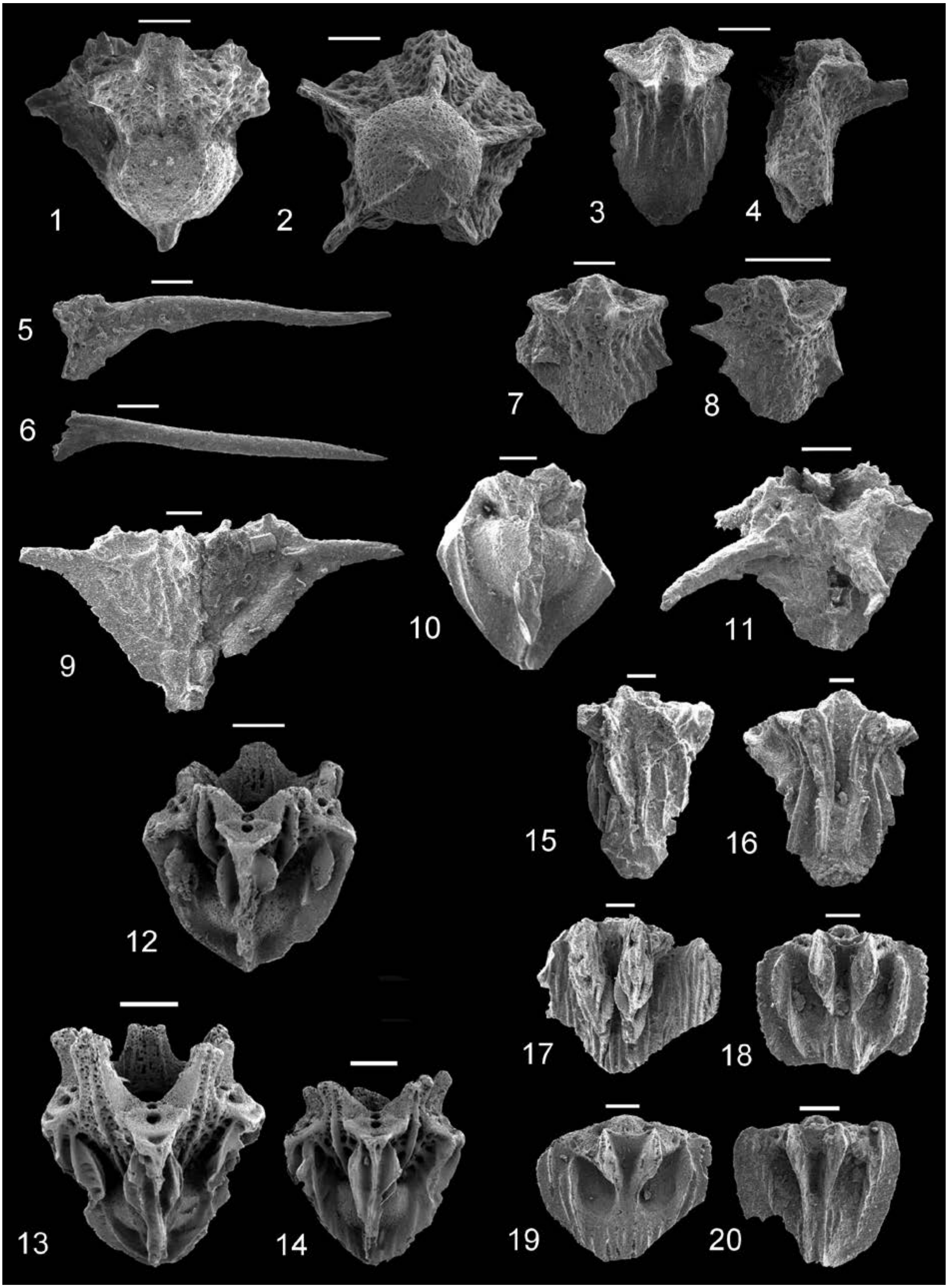
1–**8** – *Roveacrinus carinatus* Nekvasilová and Prokop, 1963. 1, 2 – cups in lateral and aboral views, respectively, the originals of Gale (2019, pl. 8, figs 1, 4; NHMUK PI EE 16729, 16732); 3, 4 – IBr_2, the original of Gale (2019, pl. 8, fig. 5; NHMUK PI EE 16733); 5, 6 – radial spines, the originals of Gale (2019, pl. 8, figs 7, 13; NHMUK PI EE 16735, 16739); 7 – IBr_2, the original of Gale (2019, pl. 8, fig. 8; NHMUK PI EE 16736); 8 – $IIBr_2$, the original of Gale (2019, pl. 8, fig. 9; NHMUK PI EE 16737).

9–**11**, **15**, **16** – *Roveacrinus precarinatus* sp. nov. 9 – holotype cup in lateral view (NHMUK PI EE 18124); 10, 11 – paratype cups (NHMUK PI EE 18125, 18126); 15, 16 – paratype IBr_2 (NHMUK PI EE 18134, 18132).

12–**14**, **17**–**20** – *Drepanocrinus geinitzi* (Schneider, 1989). 12–14 – cups in lateral view, the originals of Žítt *et al.* (2019, fig. 8C, A, B; MMG SAK 15829–15831); 17–20 – IBr_2, the originals of Gale (2020, pl. 16, figs 9, 10, 11, 15; NHMUK PI EE 17523–17526).

Figures 1–8 are from the Zig Zag Formation, Plenus Marl Member, Bed VIII, Holywell, Eastbourne, East Sussex, UK. Figures 9–11, 15, 16 are from the Zig Zag Formation, Upper Cenomanian *Calycoceras guerangeri* Zone (66–68 m in Text-fig. 2), Shakespeare Cliff, west of Dover, Kent, UK (Text-fig. 1). Figures 12–14 are from the Upper Cenomanian, Hoher Stein, Dresden, Germany. Figures 17–20 are from the Aït Lamine Formation, sample AGN3 (458.5 m, see Gale 2020, fig. 4), Taghazout Plage, north of Agadir, Morocco.

Scale bars equal 0.5 mm (1–8, 12–14), 0.4 mm (11), 0.1 mm (16) and 0.2 mm (all others).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