

New starfish (Asteroidea, Echinodermata) from the Upper Triassic (Lower Carnian) of northern Italy

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ABSTRACT:

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Abundant well-preserved isolated asteroid ossicles are described from the Carnian Stage (Julian Substage) Cassian Formation of South Tyrol, northeast Italy. Detailed study of articulation surfaces and external sculpture, aided by comparison with articulated specimens of related taxa from the German Muschelkalk (Anisian–Ladinian) indicates that three species are present, here assigned to *Cortinaster papillifera* gen. et sp. nov. (type species), *Cortinaster zardini* gen. et sp. nov., and *Soleaaster thuyi* gen. et sp. nov. It is concluded that all belong to the Triassic asteroid order Trichasteropsida Blake, 1987, but they display remarkable variation in the morphology of the adambulacral ossicles which, in two of the species, possess characters comparable to those of some Late Palaeozoic asteroids. The third species has adambulacral structure essentially similar to taxa of the post-Triassic order Valvatida Perrier, 1884. The diversity of Triassic asteroids is reviewed, and a new genus, *Hagdornaster* gen. nov. with the type species *H. bieletorum* (Blake and Hagdorn, 2003), is described from the German Muschelkalk.

Key words: Triassic; Carnian; Asteroids.

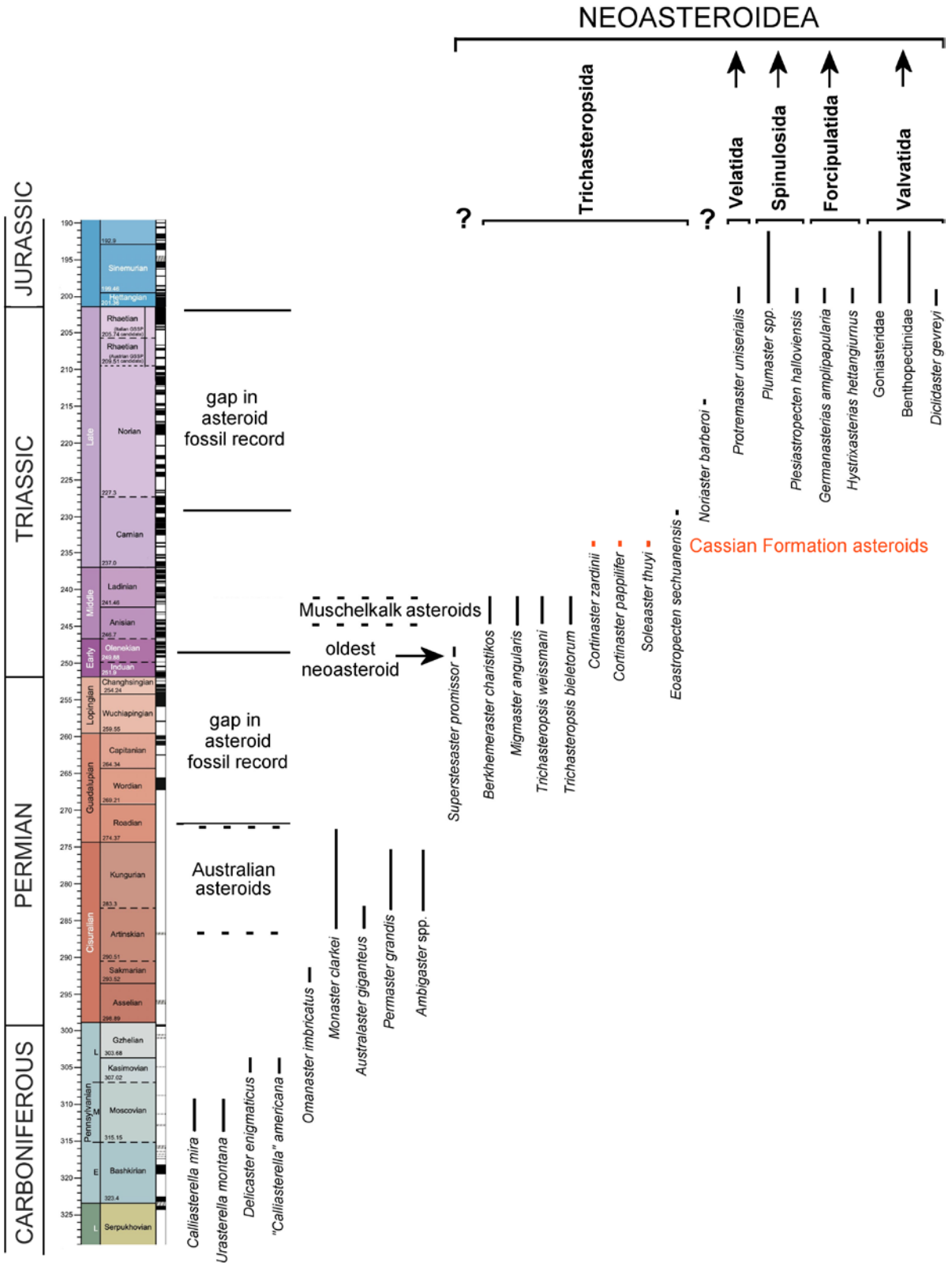
INTRODUCTION

The Late Palaeozoic–Early Mesozoic was a critical interval for asteroids, because it was marked by the disappearance of all known Palaeozoic families, genera and species, apparently before the end of the Permian, and their replacement by a new group, the Neoasteroidea Gale, 1987. This group (Early Triassic to present day) possessed more complex musculo-skeletal systems in the arms which permitted complex movements, and a more flexible mouth frame which probably enabled wider dilation (Gale 2011, 2012, 2015). However, details of the transition between Palaeozoic and Mesozoic asteroids are poorly known.

The fossil record of Permian asteroids is very limited and known mostly from endemic taxa from

the Artinskian to Rhodian stages in Australia (Text-fig. 1; Gale and McNamara 2024). Triassic asteroids are also poorly known and their affinities are controversial. Villier *et al.* (2018) described *Superstesaster* from the Early Triassic (Smithian) of Utah, USA as the earliest neoasteroid, but the material is very poorly preserved and its ordinal affinities are uncertain. Most Triassic asteroid material comes from the Middle Triassic (Anisian) Muschelkalk of Germany and northern Italy (Blake and Hagdorn 2003; Blake *et al.* 2006, 2017) and is best known from the genus *Trichasteropsis* Eck, 1879 which was placed in a separate order, the Trichasteropsida Blake, 1987, and considered to be closely related to the extant order Forcipulatida Perrier, 1884 (Blake 1987; Blake and Hagdorn 2003). *Noriaster* Blake, Tintori and Hagdorn, 2000, based on a single specimen from the





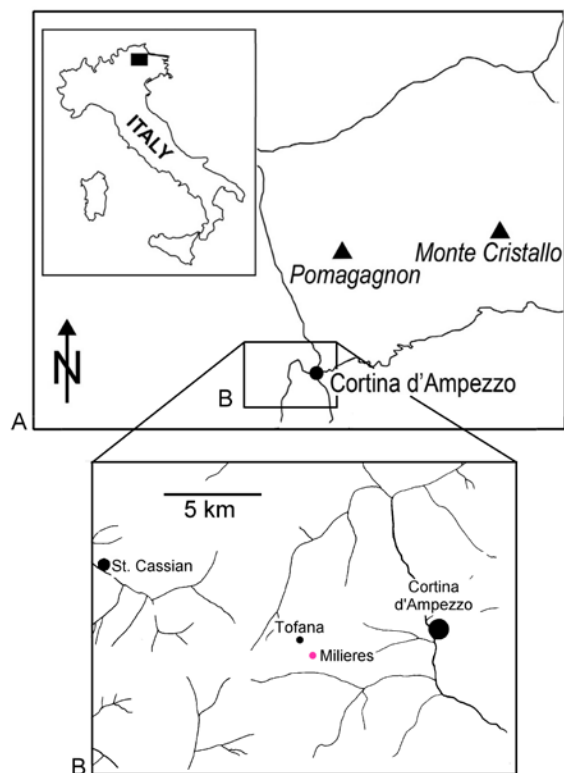
Text-fig. 1. The distribution of Late Palaeozoic and Early Mesozoic asteroids. Note the large gaps in the fossil record across critical intervals (late Permian–earliest Triassic, 22 myr; Late Triassic 31 myr). The earliest Jurassic (Hettangian) is marked by the appearance of new groups, many of which persist to the present day. Ranges of new material described in this paper in red.

Late Triassic (Norian) of northern Italy was assigned to the extant family Poraniidae Perrier, 1875 (Blake *et al.* 2000), which was doubted by Gale (2011). *Carniaster* Blake and Zonneveld, 2004, from the Late Triassic (Carnian) of British Columbia, Canada, is of unknown affinity. *Eoastropecten* Gale, 2020, based on isolated marginal ossicles from the Late Triassic (Carnian) of Sechuan, China, was placed in the extant family Astropectinidae Gray, 1840 by Gale (2020). Asteroid ossicles from the Late Triassic (Carnian) of the Cassian Formation of northern Italy were assigned to the Order Valvatida by Gale (2011). The earliest Jurassic (Text-fig. 1) saw the nearly simultaneous appearance of numerous asteroid families, some of which survive to the present day (Blake 1990; Gale 2011). The detailed affinities of some Jurassic forcipulate asteroids are currently being reassessed (Fau *et al.* in press).

Gale (2011) expressed doubts as to the affinities of the asteroids from the German Muschelkalk and Triassic of northern Italy, and Thuy *et al.* (2017) argued that one taxon, *Migmaster* Blake, Bielert and Bielert, 2006, was a possible Palaeozoic survivor. The discussion and detailed cladistic analysis of Villier *et al.* (2018) included only a single species of the group Trichasteropsida, *Trichasteropsis weissmanni* (Münster, 1843). Most of the described Triassic material comprises partial or complete articulated specimens, which give a clear impression of external morphology but provide little or no evidence of the phylogenetically important ambulacral groove and mouth frame ossicles (Gale 1987, 2011). However, the basal facies of the Cassian Formation (Lower Carnian) of the Italian dolomites yields well preserved asteroid ossicles (Zardini 1973; Gale 2011) which were transported from nearby carbonate platforms into deeper water clays (Fürsich and Wendt 1977; Bizzarini and Laghi 2005; Bizzarini *et al.* 1989). New material from the Cassian Formation is described in this paper and the affinities of the taxa represented are discussed.

LOCALITY AND STRATIGRAPHY

The material was collected from the Cassian Formation section at Milières, 1 km SE of the peak called Tofana, and 6 km WSW of Cortina d'Ampezzo, Belluno Province, northeast Italy (Text-fig. 2; Bizzarini *et al.* 1989; Urlichs 2017). This falls within the Upper Triassic, Lower Carnian, Julian Substage, *Austrotrachyceras austriacum* Zone, dating to approximately 234 Ma (Ogg and Chen 2020).



Text-fig. 2. Locality map. A – position of the region between St. Cassian and Cortina d'Ampezzo; B – to show location of the Milières section. After Urlichs (2017, fig. 1).

METHODS

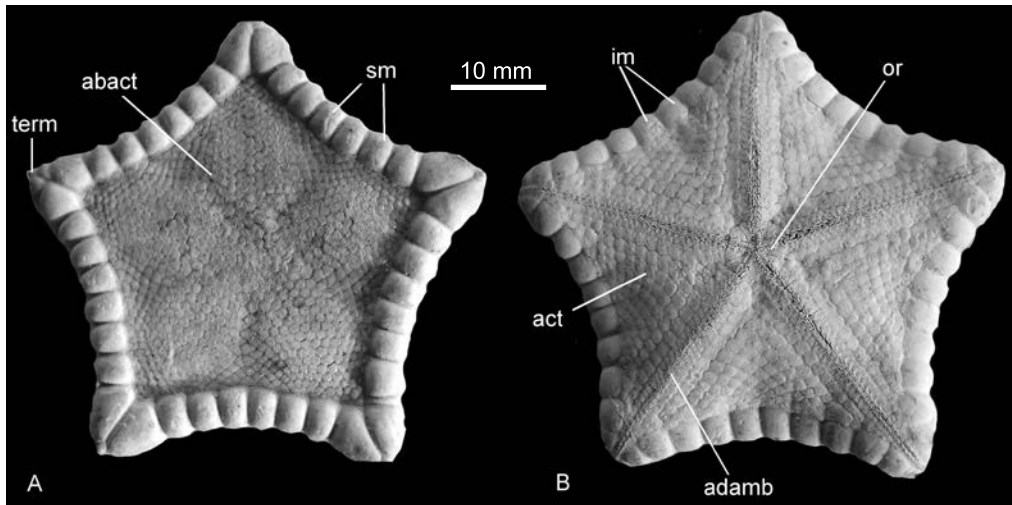
Approximately 200 kg of clay were collected from the Milières section and washed using a clay machine (Ward 1981). The residues were graded and completely picked down to 0.5 mm. Approximately 450 asteroid ossicles were recovered. Selected specimens were mounted on stubs and studied using an SEM.

TERMINOLOGY OF THE ASTEROID SKELETON

The main skeletal structures of the asteroid skeleton are shown in Text-fig. 3. The abactinal (dorsal) side (Text-fig. 3A) is made up of a polygonal tessellation of abactinal ossicles, framed by large superomarginal ossicles. The tip of the arm bears a small terminal ossicle. The actinal (ventral surface; Text-fig. 3B) is framed by inferomarginal ossicles, and the ambulacral grooves are protected by block-like adambulacrals. The peristome (mouth) is surrounded by five pairs of oral ossicles. The actinal interareas between

ab	abactinal ossicle	df	distal flange (pterasterid and korethrasterid amb)
abr	abactinal ridge (on amb)	doda	distal odontophore articulation (on oral, odontophore)
abtam	abactinal transverse amb muscle	exab	external abductor (pedicellariae)
abiim	abactinal interrarial interoral muscle (oral)	exod	external face of odontophore
aciim	actinal interrarial interoral muscle	fs	attachment of furrow spine
act	actinal ossicle	ico	interrarial chevron ossicles
actam	actinal transverse amb muscle	ig	interrarial groove
actf	actinal face (of oral)	ilad	internal longitudinal adductor (pedicellariae)
actin	actinostome	im	inferomarginal
actr	actinal ridge (on amb)	ima	inferomarginal articulation on axillary/odontophore
ad	adambulacral ossicle	int	intermarginal
ada1	single distal amb-adamb articulation	iioa	interrarial interoral articulation (on oral)
ada1a	distal adradial amb-adamb articulation	is	interrarial septum
ada1b	distal abradial amb-adamb articulation	itad	internal transverse adductor (pedicellariae)
ada2	proximal adradial amb-adamb articulation	k	keel (on odontophore)
ada3	proximal abradial adamb-amb or adamb-adamb articulation	ka	keel articulation on axillary/oral in <i>C. mira</i>
adada	adamb-adamb articulation	lia	longitudinal interambulacral articulation
adadm	interadambulacral muscle	lim	longitudinal interambulacral muscle
adca	adoral carina	ln	lateral notch (on odontophore)
adex	adambulacral extension	ls	lateral surface of keel (on odontophore)
adexa	adambulacral extension articulation	mad	madreporite
adexm	adambulacral extension muscle	od	odontophore
adpm	adamb prominence (on adamb)	od/ax	odontophore/axillary
adr	adradial ossicles	odc	odontophore muscle capsule (on oral)
ads	adambulacral spine	odom	oral-odontophore muscle
adsm	adambulacral spine membrane (pterasterids)	or	oral ossicle
al	alveolus (pedicellariae)	orada	adambulacral articulation (on oral)
alm	actinolateral membrane (pterasterids)	oradm	oral adambulacral muscle
als	actinolateral spine base (pterasterids, korethrasterids)	osp	attachment of oral spine
amb	ambulacral ossicle	pab	proximal abductor (pedicellariae)
ambb	base of ambulacral ossicle	padam	proximal adamb-amb muscle
ambg	ambulacral groove	pb	proximal blade (oral ossicle)
ambh	head of ambulacral ossicle	pcoa	proximal oral-circumoral articulation
ambsh	shaft of ambulacral ossicle	pcp	proximal circumoral process (on circumoral)
amn	ampullar notch (on amb)	pe	peristome
amp	ampulla	ped	pedicellaria
ap	aperture in pterasterid actinolateral membrane	pedu	peduncle (on pedicellariae)
apo	apophyse on oral	pir	primary interrarial ossicle
aps	apertural spine in pterasterids	pn	podial notch (on adamb)
art	articulation surface on base of ped valves	poda	proximal odontophore articulation (on oral and odontophore)
bp	basal piece (pedicellariae)	pr	primary radial
ca	articulation on odontophore of chevron ossicles	ra	radial
can	abactinal canopy in Pterasteridae	rart	radial articulation of proximal blade (on oral)
ce	centrale	riom	radial interoral muscle
cha	chevron ossicles artic with odontophore of Pterasteridae	rng	ring nerve groove on oral
coh	circumoral head	rvg	ring vessel groove on oral
co	circumoral ossicle	sa	superambulacral articulation on amb base
crib	cribriform organ	samb	superambulacral
cup	cupule (pedicellariae)	sm	superomarginal ossicle
dab	distal abductor (crossed peds)	sos	attachment of suboral spine
dad	distal adductor (crossed peds)	t	terminal ossicle
dadam	distal amb-adamb muscle	tb	transverse bar of odontophore
dcoa	distal circumoral articulation on oral	tf	tube foot
dep	distal circumoral process on circumoral	1st tf	space occupied by first tube foot between oral/circumoral
de	dentition (orals, amb, peds)	va	valves of pedicellaria

Table 1. Abbreviations.



Text-fig. 3. Asteroid morphology illustrated by a present day goniasterid, *Metopaster* sp. Philippines. A – abactinal surface; B – actinal surface. Abbreviations; abact – abactinal ossicles; act – actinal ossicles; adamb – adambulacral ossicles; im – inferomarginal ossicles; or – oral ossicles; sm – superomarginal ossicles; term – terminal ossicle.

the ambulacral grooves are covered by rows of actinal ossicles. The relative sizes and shapes of these ossicle types are highly variable between different groups.

The detailed morphology of the ossicles of the ambulacral groove and mouth frame are important in the understanding of asteroid phylogeny (Gale 1987, 2011). Ambulacral and adambulacral ossicles alternate in all post-Palaeozoic starfish and are united by a series of muscles and articulation structures (Text-fig. 4A–C, F–H). Successive adambulacrals have an articular contact (adad) and a muscle (adadm), and the adambulacral–ambulacral contact is united by two muscles (padam, dadam) and has four articular surfaces (adala, 1b, ada2, ada3). The oral ossicles (Text-fig. 4D, E) articulate distally with an adambulacral, with a specialised articulation (orada) and a muscle (oradm). The two orals of a pair are united to the odontophore by muscles (odom) and share articular surfaces (iioa).

Museum abbreviations

GPIT – Tübingen University Museum, Tübingen, Germany;
 ISGS – Illinois State Geological Survey, Illinois, USA;
 MHI – Muschelkalk Museum, Ingelfingen, Germany;
 MnhnL – Musée National d’Histoire Naturelle, Luxembourg;
 NHMUK – Natural History Museum, London, UK;
 TCD – Trinity College Dublin, geological collections, Dublin, Republic of Ireland;

ZMCA – Zardini collection, Museo Cortina d’Ampezzo, Italy.

SYSTEMATIC PALAEOLOGY

Subclass Neoasteroidea Gale, 1987

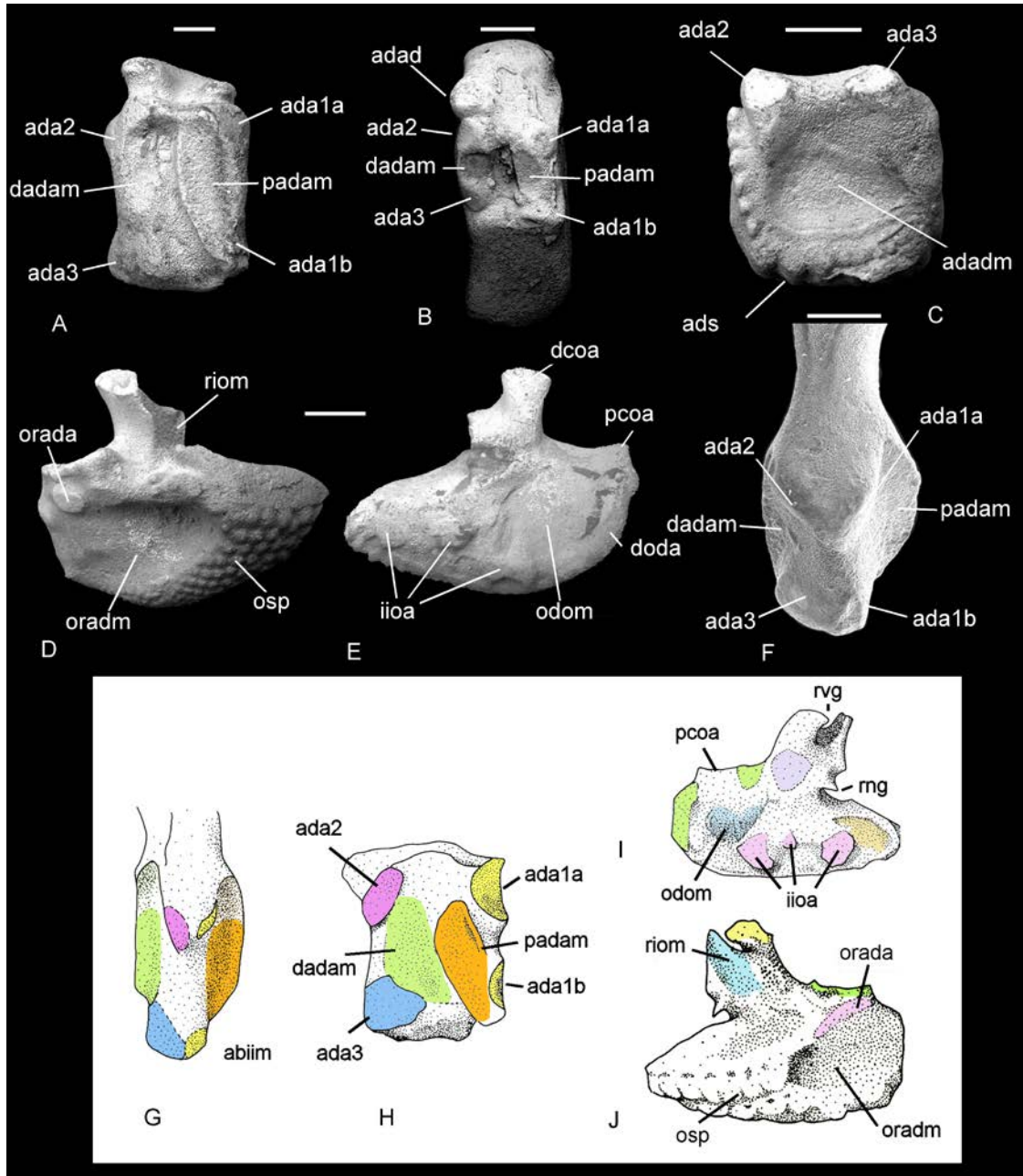
DIAGNOSIS: Asteroids in which actinal ossicles are present and in which there is a complex and consistent pattern of articulation and muscularisation between the alternating ambulacral and adambulacral ossicles. An internal odontophore is present between the oral ossicles and these are conjoined by specialised articulations and muscles.

REMARKS: Details of the features of the ambulacral groove and mouth frame of neoasteroids are shown in Text-fig. 4. Further details were described by Gale (2011). The group is exclusively post-Palaeozoic.

Order Trichasteropsida Blake, 1987

DIAGNOSIS: Neoasteroids which possess a single row of marginals, sometimes with intercalated intermarginals, broad, short adambulacrals and an interradial row of actinal ossicles which extends from the distal margin of the oral ossicles to the marginal frame.

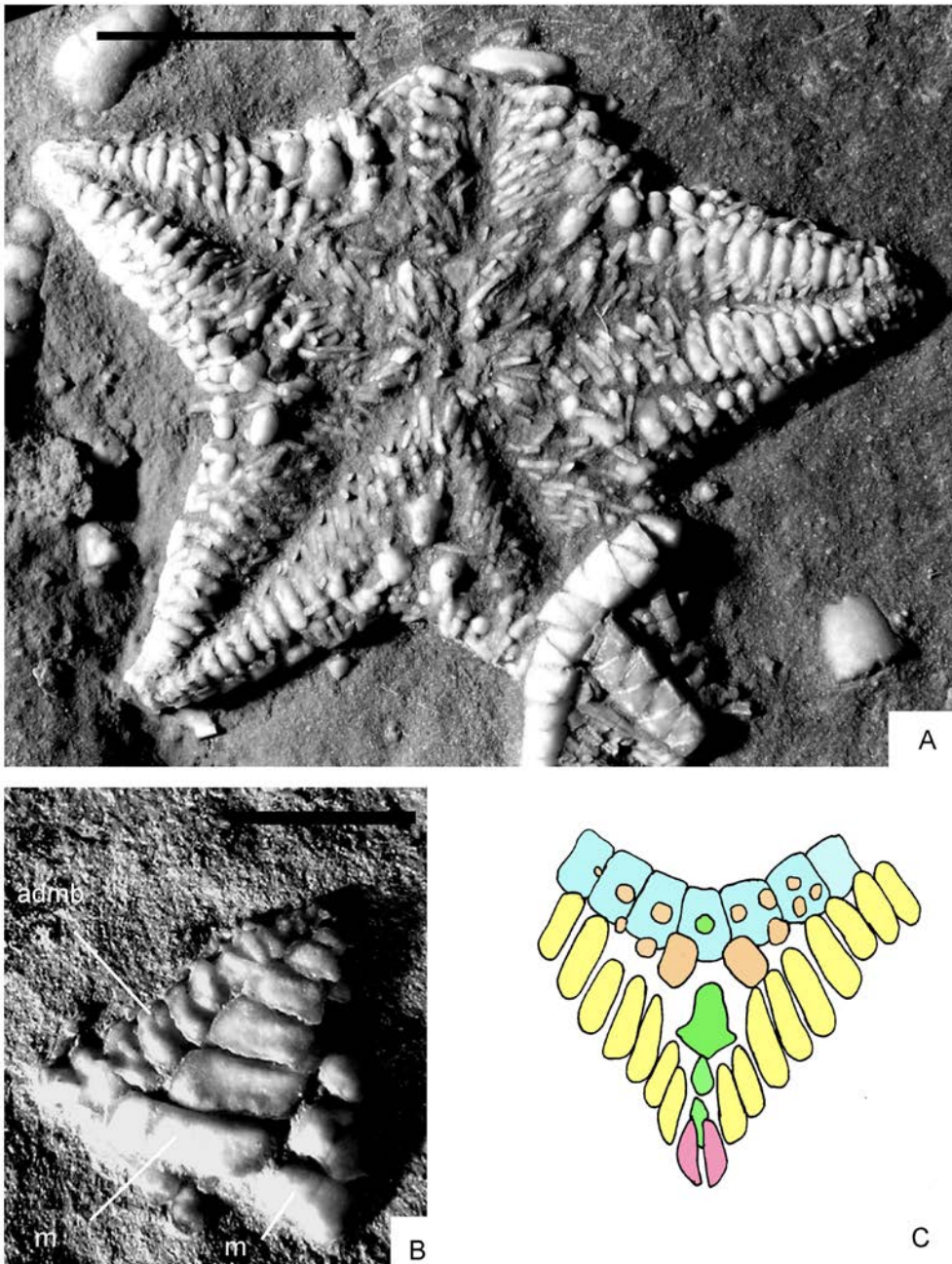
INCLUDED FAMILIES: Trichasteropsidae Blake and Hagdorn, 2003; Migmasteridae Gale, 2011.



Text-fig. 4. Morphological terminology for asteroid ambulacral groove ossicles (A–C, F–H) and oral ossicles (D, E, I, J). A–F – *Cortinaster* spp., images of adambulacral ossicles (A–C) in abactinal (A, B) and distal (C) views; D, E – oral ossicle in radial (D) and interradial (E) views; F – adradial view of base of ambulacral ossicle. G–J – present day ophiasterid *Nardoia* sp. G – adradial view of ambulacral base; H – abactinal view of adambulacral; I – interradial; J – radial views of oral ossicle. In terms of overall construction, the Triassic and present day taxa have similar morphological features. See Table 1 for abbreviations.

REMARKS: Articulated specimens of Trichasteropsida are illustrated in Text-figs 5–8. The group is characterised by the single marginal row (Text-figs 5A, 6–8) and the presence of a row of interradial ossicles which extend between the oral ossicles

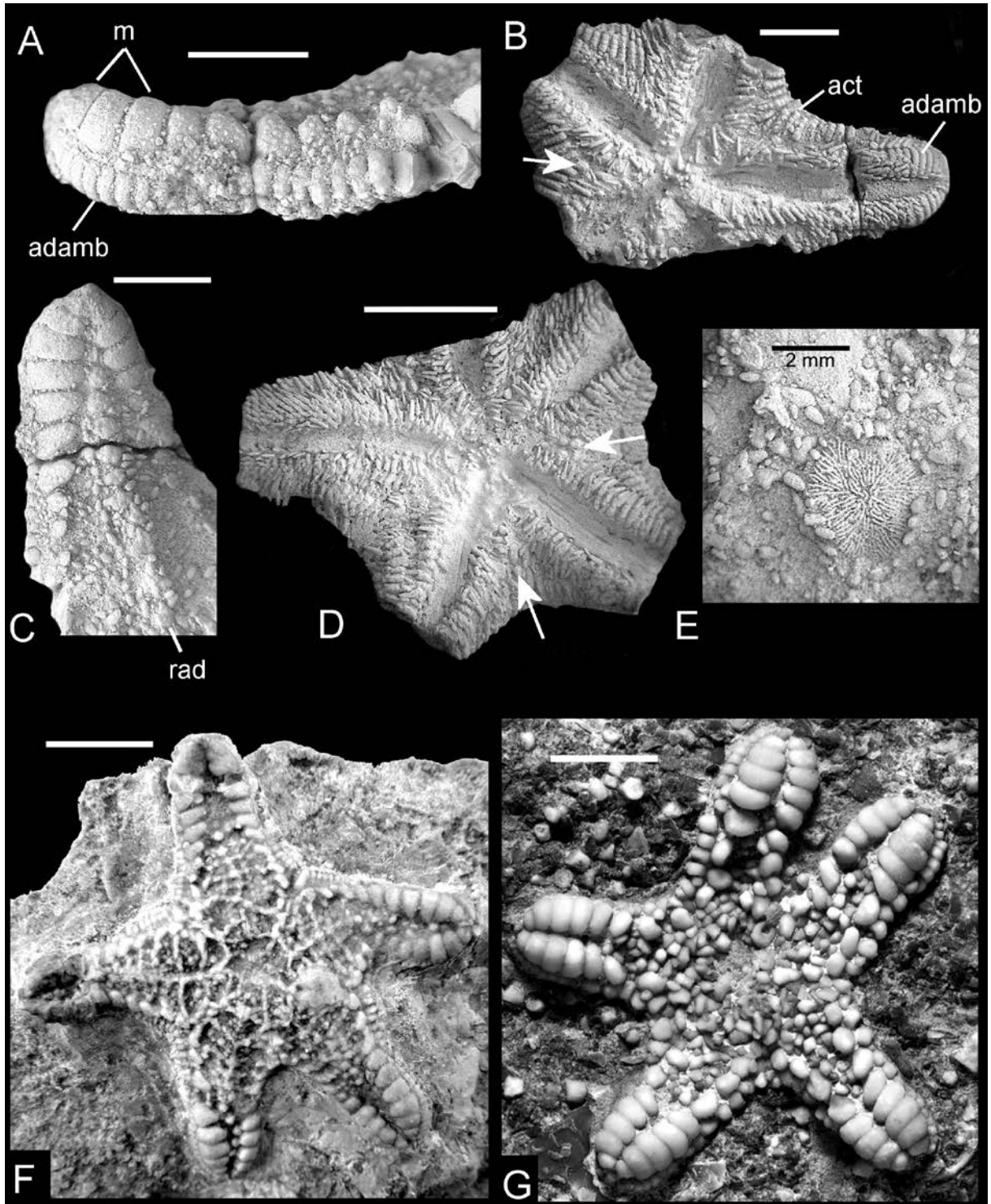
and the margin (Text-figs 5A, C, 6B, D, 7, 9F, G). In *Migmaster* (Text-figs 5, 9G) one of these ossicles is enlarged (Thuy *et al.* 2017). Interradial actinal ossicles of this type are found in the Permian asteroid *Monaster* Etheridge, 1892 (Text-fig. 9E)



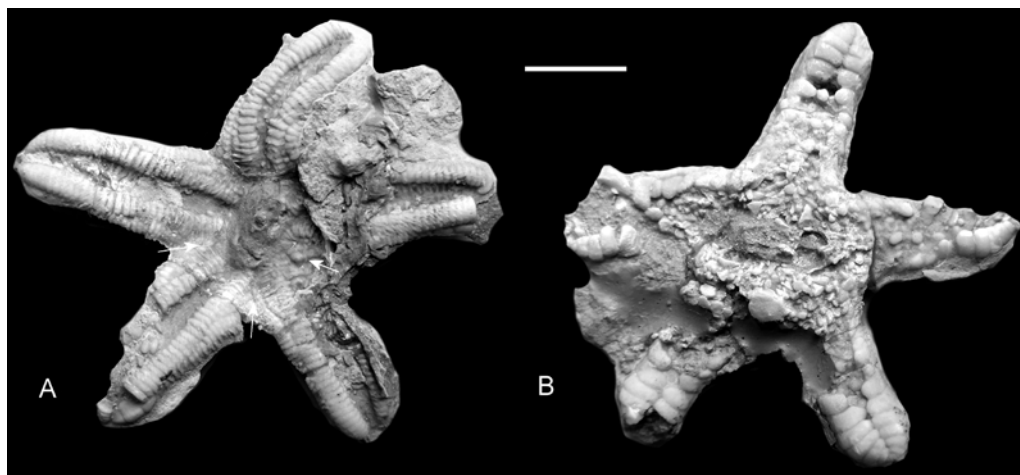
Text-fig. 5. *Migmaster angularis* Blake, Bielert and Bielert, 2006 from the Lower Muschelkalk, Anisian (Pelsonian), Herberhausen, near Göttingen, Germany. A – actinal view of unique holotype specimen (MHI 1809); B – associated arm tip from the same individual; C – interpretation of the construction of actinal surface. Note the relatively few actinal ossicles which were probably set in a membrane, and the large arrowhead shaped interradial actinal. Scale bar = 10 mm. Colour key as in Text-fig. 9.

but are never present in post-Triassic asteroids (Gale 2015; Gale and McNamara 2024), even in taxa in which a single interradial marginal pair is present (e.g., *Odontasteridae* Verrill, 1899, Text-fig. 9I; see Ewin and Gale 2020, fig. 8; *Prionaster* Verrill, 1899,

see Fisher 1919, pl. 3). The interradial ossicles are a vestige of the link between the axillary ossicle, an interradial marginal which articulated with the orals in Palaeozoic starfish and its homologue, the internal odontophore, in neoasteroids (Text-fig. 9; Gale 2011,



Text-fig. 6. A–F – *Trichasteropsis weissmanni* (Münster, 1843). A–C, E – GPIT PST/AS/53-1, individual in lateral (A), actinal (B) and abactinal (C) views, and enlargement of madreporite (E); D – GPIT PST/AS/53-1, actinal surface of larger individual; F – MHI 843/1, abactinal view of well-preserved specimen, original of Blake and Hagdorn (2003, fig. 1B); G – *Hagdornaster bieletorum* (Blake and Hagdorn, 2003), MHI 1755, holotype, abactinal surface, original of Blake and Hagdorn (2003, fig. 4E). A–E are from the Muschelkalk, Crailsheim, Baden Württemberg, Germany; D is from Germany; F is from the Muschelkalk *nodosus* biozone, mo3, Leyh Quarry, Bölgental, Germany; G is from the Muschelkalk, Herberhausen Quarry, near Göttingen, Germany. Arrows on B and D point to actinal interradial ossicles; m – marginals; adamb – adambulacral; rad – radials. Scale bars: 5 mm for A–D and G; 2 mm for E; 10 mm for F. See Table 1 for abbreviations.



Text-fig. 7. *Hagdornaster bieletorum* (Blake and Hagdorn, 2003), MHI 495, from the Muschelkalk; A – actinal and B – abactinal surface. Arrows mark position of interradial ossicles. Scale bar = 10 mm.

2015). Their presence can therefore be taken as evidence of the basal position of the Trichasteropsida within the neoasteroids.

Almost all post-Triassic asteroids possess two rows of marginals, the supero- and inferomarginals (Text-fig. 3); the exceptions are a zoroasterid (*Zoroaster* Thomson, 1873; see Blake and Elliot 2003; Ewin and Gale 2020) and the paxilloSIDAN *Luidia* Forbes, 1839 (Blake 1987; Gale 2011). It is considered that these represent secondary losses of the supero-marginals. Palaeozoic asteroids and the Triassic Trichasteropsida possess only a single marginal row (Text-figs 5–9; Blake and Elliot 2003; Blake and Hagdorn 2003; Blake 2018).

Blake and Hagdorn (2003) placed the Forcipulatida and the Trichasteropsida within a superorder, the Forcipulatacea Blake, 1987, on the basis of a number of supposed shared morphological characters. These included the presence of adoral carinae (adambulacra distal to the oral ossicles which abut interradially), quadriserial tube feet, the alternately carinate and non-carinate nature of the proximal adambulacra (seen in the forcipulate family Zoroasteridae Viguiet, 1878) and the reticulate construction of the abactinal skeleton. These characters were discussed in some detail by Gale (2011) and Villier *et al.* (2018). The presence of adoral carinae in *T. weissmanni* is not clear (Villier *et al.* 2018, p. 411), and a reticulate abactinal skeleton and (disputed) quadriserial tube feet are also found in other, distantly related asteroids (Gale 2011). Although the tree of Villier *et al.* (2018, fig. 7) placed *T. weissmanni* and Jurassic forcipulates within the same clade, the relationship is not well

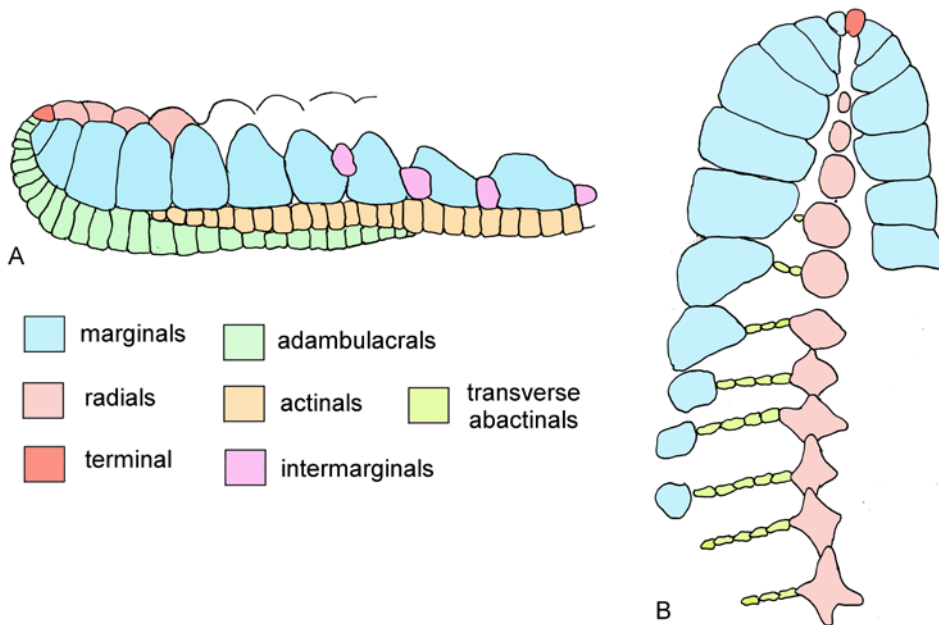
supported. I prefer to identify the Trichasteropsida as a basal neoasteroid group which retains some pleiomorphic characters inherited from Palaeozoic ancestors and which, presumably, gave rise to all later neoasteroids during a Late Triassic radiation about which we have little fossil evidence (Text-fig. 1). The question arises as to whether the post-Triassic neoasteroids are monophyletic (i.e., derived from a single, ancestral trichasteropsid) or whether the Jurassic to present day groups evolved from various Triassic forms by the independent acquisition of a second marginal row and loss of the interradial actinal ossicles.

Migmasteridae Gale, 2011

DIAGNOSIS: Short, rapidly tapering arms, interradial margin angled, marginals block-like; a large interradial actinal is present, actinal interareas with few ossicles, probably mostly membranous; oval, transversely broad adambulacra that carry four or five blade-like spines adradially; abradially, they each bear a single large, blade-like spine on the distal margin.

INCLUDED GENERA: *Migmaster* Blake, Bielert and Bielert, 2006.

REMARKS: The single marginal row and unpaired interradial actinal ossicles place it in the Trichasteropsida. *Migmaster angularis* Blake, Bielert and Bielert, 2006 is only known from a single specimen



Text-fig. 8. Interpretative drawings of arm structure in *Trichasteropsis weissmanni* (Münster, 1843). A – lateral view of arm, to show shape changes in marginal ossicles and intermarginal ossicles; based on SMNS 9394, original of Blake and Hagdorn (2003, fig. 1D–F) from the Muschelkalk, *nodosus* biozone, Grosslingersheim, Germany; B – abactinal view of arm, based on GPIT PST/AS/53-1 (see Text-fig. 6C) from the Muschelkalk, Crailsheim, Baden Württemberg, Germany. Not to scale.

(Text-figs 5, 9G), the holotype; the paratypes belong to a separate taxon which possesses two marginal rows (Gale 2011; Villier *et al.* 2018).

Trichasteropsidae Blake and Hagdorn, 2003

DIAGNOSIS: Marginals of interradius and mid-radius low, imbricating interradially, distal marginals tall, broad, forming a swollen arm tip with flat intermarginal contacts. Actinal ossicles form crescentic series.

INCLUDED GENERA: *Trichasteropsis* Eck, 1879, *Hagdornaster* gen. nov., *Cortinaster* gen. nov.

REMARKS: The main unifying feature of this group is the morphology of the marginal ossicles, which are smaller and imbricated in the interradius/mid-arm but enlarged distally to form a swollen arm tip. Both actinals and abactinals are variable in morphology between genera. In *Trichasteropsis*, the abactinals form an open reticulate structure (Text-figs 6A, C, F; 7). The proximal radials are cruciform, and the distal radials are broad and transversely oval. The radials are linked to the marginals by rows of small ossi-

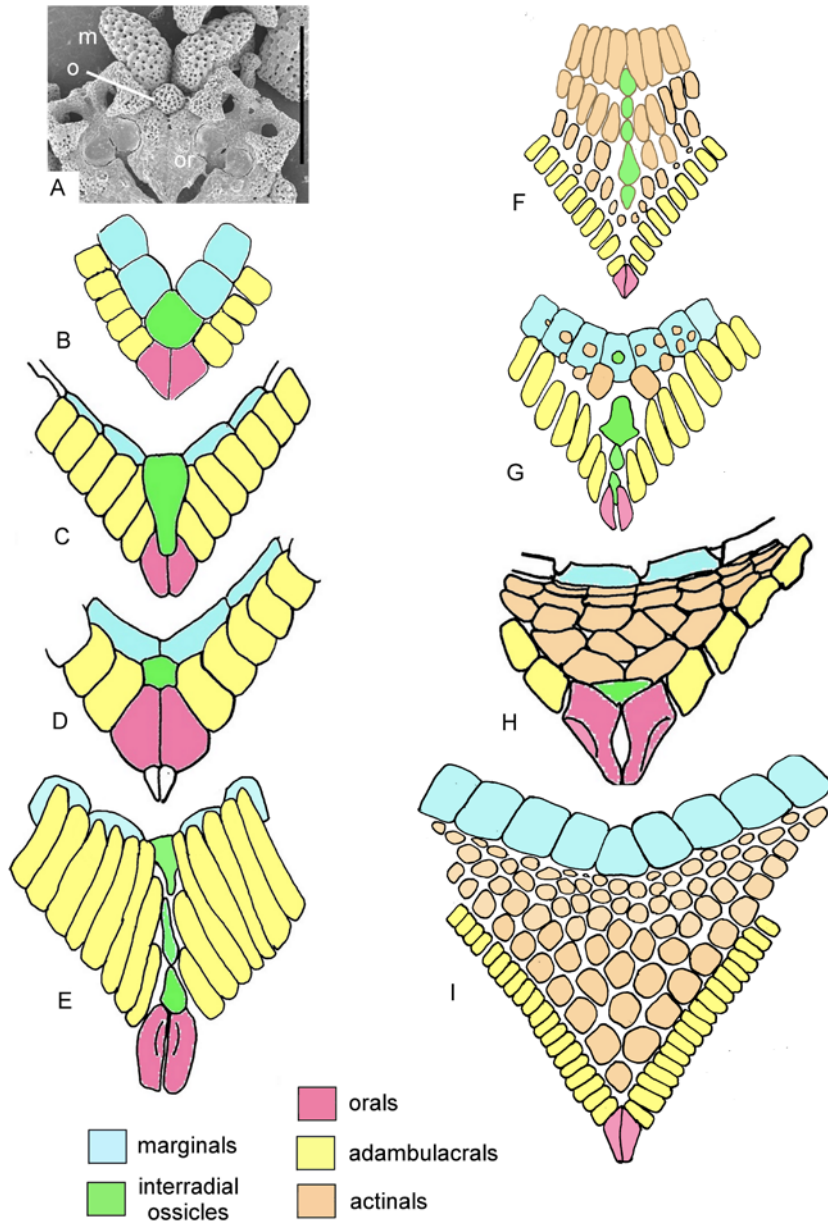
cles. In *Hagdornaster* gen. nov., the abactinals are small, rounded-polygonal and form a tessellation. In *Cortinaster papillifera* gen. et sp. nov., the abactinals are conical with a small abactinal surface, and the intervening spaces were probably infilled with soft tissue or smaller ossicles. The actinals in *Trichasteropsis* are broad and narrow and set in well-defined crescentic rows between the adambulacrals and the margin (Text-fig. 6B, D). In *Cortinaster* gen. nov., the actinals are small and block-like and probably formed rows parallel with the adambulacrals.

Hagdornaster gen. nov.

DIAGNOSIS: Small, robust asteroids in which the distal arms are swollen and formed by enlarged marginals. Abactinal ossicles form a tessellation of small rounded-polygonal ossicles.

TYPE SPECIES: *Trichasteropsis bieletorum* Blake and Hagdorn, 2003.

DERIVATION OF NAME: In honour of the extensive work on Triassic echinoderms by Hans Hagdorn, Ingelfingen.



Text-fig. 9. Actinal interradial structure of asteroids, all actinal views. A – juvenile *Echinaster* sp. (present day, Brazil), to show odontophore (o) between the first formed inferomarginal pair (im) and the oral ossicles (or). This arrangement is very similar to that in some Palaeozoic asteroids (e.g., B). B – *Siluraster* sp., Ordovician. C – *Ambigaster* sp., Permian. D – *Permaster* sp., Permian. E – *Monaster* sp., Permian. F – *Trichasteropsis* sp., Triassic. G – *Migmaster* sp., Triassic. H – *Porcellanaster* sp., present day. I – *Odontaster* sp., present day. Unpaired interradial marginals called the axillary (green, B–D) articulated with the oral ossicles in many Palaeozoic asteroids. In the Permian *Monaster* sp. (E) a series of interradial ossicles (green) links the marginal frame to the orals. In neozooids (Triassic to present day, F–I) the homologue of the axillary, the odontophore, has become internal, although it has a small external face in some taxa (e.g., H). In the Triassic *Trichasteropsida* (F, G) the series of interradial ossicles is retained from Palaeozoic ancestors but are lost in all post-Triassic taxa.

REMARKS: There are significant differences between the skeletal structure of *H. bieletorum* and that of the type species of *Trichasteropsis*, *T. weissmanni* which justify separate generic status. The abactinal

skeleton in *H. bieletorum* is a tessellation of small, rectangular ossicles (Text-figs 6G, 7B), very different to the open reticular network of *T. weissmanni* (Text-figs 6C, E, F, 8B). On the actinal surface of *H.*

bieletorum (Text-fig. 7A) the interareas are narrow and V-shaped, and oval interradiial ossicles are present (arrowed in Text-fig. 7A).

Cortinaster gen. nov.

DIAGNOSIS: Trichasteropsids in which the abactinal ossicles are broad based and conical with a small, sculptured external surface. The concave spaces between the abactinals were probably infilled with soft tissues or small secondary ossicles. The actinal ossicles are rectangular and probably formed rows parallel with adambulacrals.

TYPE SPECIES: *Cortinaster papillifera* gen. et sp. nov.

DERIVATION OF NAME: After the town of Cortina d'Ampezzo, Tyrol, northeast Italy.

REMARKS: It is always difficult to reconstruct a starfish from isolated plates, because of uncertainties as to which ossicles belong to the same taxon. In this instance, however, the task is rendered possible by the highly distinctive external sculpture of the marginals, orals, adambulacrals, actinals and abactinal ossicles. These indicate that two species, with contrasting sculptures, were present in the Cassian fauna at Milières. Similarities of the shapes of the marginal ossicles of *Cortinaster* gen. nov. to those of *Trichasteropsis* (compare Text-fig 6A, C with Text-fig. 10A–L) include comparable progressive changes in morphology from the interradius to the distal arm. Additionally, the articular surfaces of the marginals indicate that a single row was present. The actinals (Text-fig. 10M–P) are square to rectangular in outline and suggest that these formed actinal interareas with rows of plates running parallel, or subparallel to the adambulacrals, rather like the arrangement shown in Text-fig. 9I. The abactinals, however, are so diverse in form (Text-figs 10Q–U, 11A–F, Q) as to render accurate reconstruction impossible. Ossicles which lack an external surface, such as ambulacrals, cannot be assigned to a species.

The presence of a single marginal row, with 3 distinct morphological groups along the radius, is similar to the marginal development in *Trichasteropsis weissmani* (Text-fig. 6A–F; see also Blake and Hagdorn 2003, fig. 1E, F) and it is also likely that *Cortinaster* gen. nov. possessed small intermarginals like those present in *T. weissmani*. However, the abactinal ossicles are very different to those of

Trichasteropsis, being conical with a small exposed abactinal surface. The actinal ossicles are block-like and rectangular, and the oral ossicles have a well-developed proximal blade (Text-fig. 13M–P) unlike the short, small orals of *Trichasteropsis*.

Cortinaster papillifera gen. et sp. nov.
(Text-figs 10A–U, 11A–Q, 13Q, R, 14B)

2011. Spinulosida incertae sedis; Gale, p. 68, pl. 16, figs 4, 5.

DIAGNOSIS: *Cortinaster* gen. nov. in which the external surfaces of the marginals, abactinals, actinals, adambulacrals and orals possess a sculpture of rounded papillae, set within a rugose, raised central area. The adambulacrals are broad and the articular surface with the ambulacrals is restricted to the abradial part of the abactinal surface.

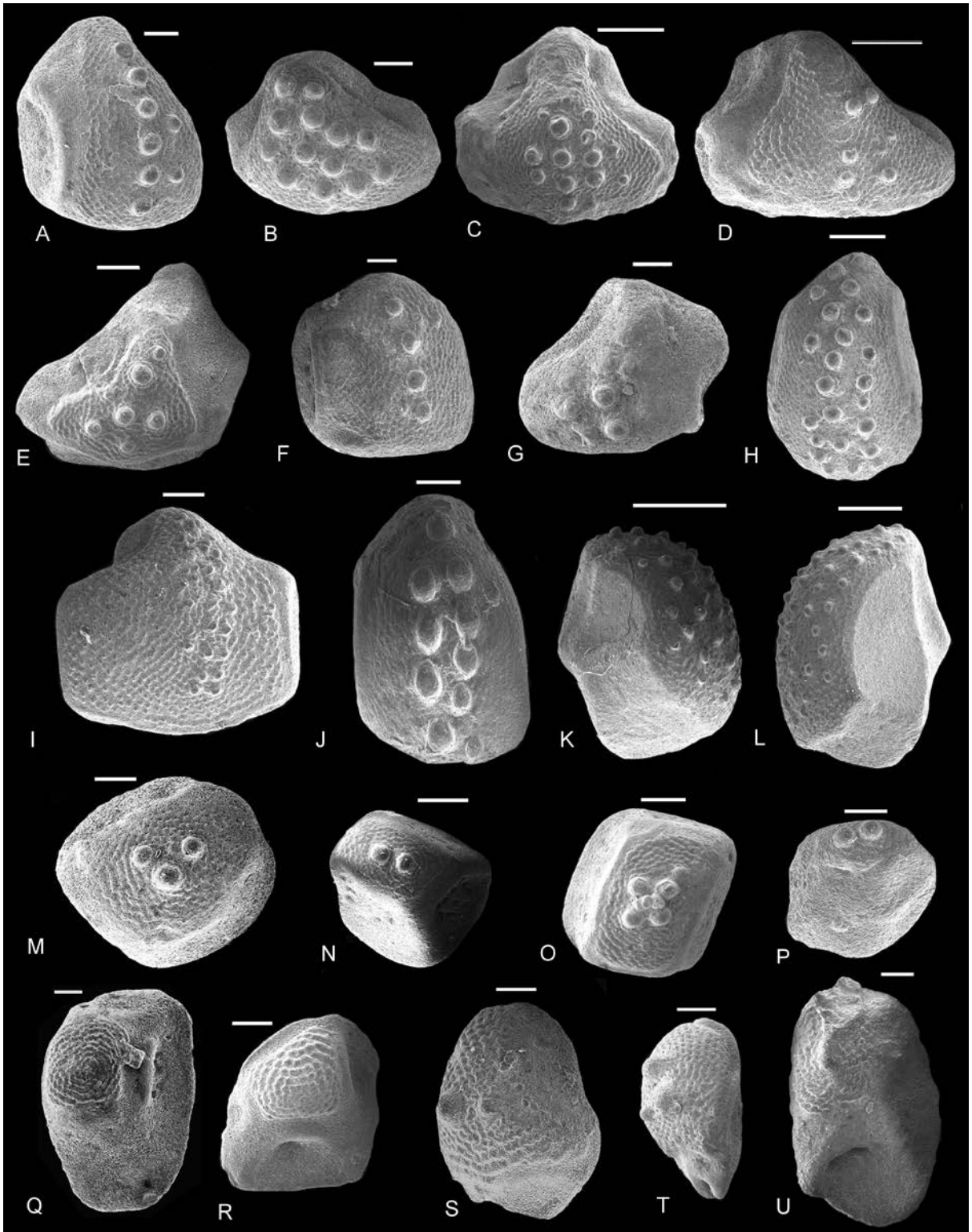
TYPES: A marginal (Text-fig. 10A) is the holotype (MnhnL OPH221), all other figured ossicles are paratypes (MnhnL OPH222–256). Lower Carnian, Julian, *Austrotrachyceras austriacum* Zone, Milières, Cortina d'Ampezzo, South Tyrol, Italy.

DERIVATION OF NAME: *Papilla*, -ae, Latin for nipple, and *ferre*, Latin for to carry, in allusion to the distinctive sculpture of the external ossicles.

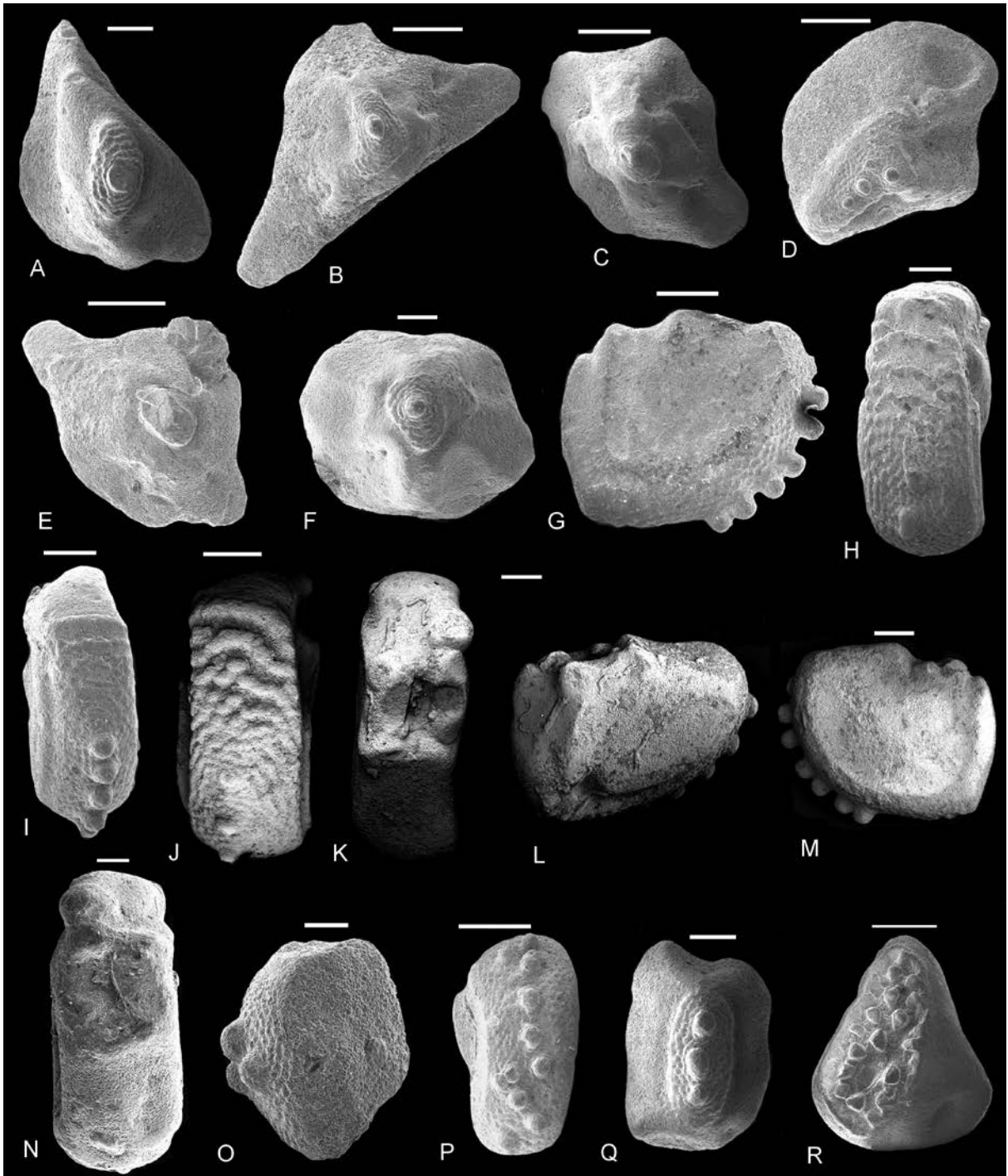
MATERIAL: 245 ossicles, including abactinals, marginals, actinals, adambulacrals and orals. Same locality and horizon as the type.

DESCRIPTION: All external ossicles possess a well-defined, slightly raised central area with a finely rugose sculpture which has a weakly concentric arrangement. In the central area a variable number of prominent papillae are present, circular to oval in shape, which have a rounded termination. The interradiial marginals (Text-fig. 10C) are symmetrically triangular with a swollen external surface. Those from the mid radius are asymmetrical, slightly elongated proximally and imbricated towards the interradius (Text-fig. 10B, D, E, G, I). They are tumid and also have a sharply defined central area. Distally, the marginals increase in height and become nearly symmetrical (Text-fig. 10A, H, J–L). The definition of the central area is poor, and the papillae are smaller and more evenly distributed. The articular surfaces between these distal marginals are large and concavo-convex. The size of the distal facet decreases towards the extreme arm tip (Text-fig. 10K, L).

The actinal ossicles (Text-fig. 10M–P) are rect-



Text-fig. 10. *Cortinaster papillifera* gen. et sp. nov. A–L – MnhnL OPH221–232, marginal ossicles in lateral aspect; A is the holotype (MnhnL OPH221), all others are paratypes; C is an interradial marginal (symmetrical); B, D, E, G are from the mid-arm (asymmetrical), and A, H, J–L, Q are from the swollen distal arm. M–P – MnhnL OPH233–236, actinal ossicles. Q–U – MnhnL OPH237–241, abactinal ossicles, situated close to marginals. All specimens are from the Cassian Formation, Lower Carnian (Julian), *Austrotachyceras austriacum* Zone, Milières, west of Cortina d’Ampezzo, Tyrol, Italy. Scale bars: 1 mm for C, D, H, K, L; 0.5 mm for A, B, E, G, I, J, N, O, R, S; and 0.3 mm for all others.



Text-fig. 11. A–Q – *Cortinaster papillifera* gen. et sp. nov. A–F, O–Q – MnhnL OPH242–250, abactinal ossicles. G–N – MnhnL OPH251–255, adambulacral ossicles in actinal (H–J), internal (K, N), and proximal/distal views (G, L, M); see Text-fig. 4B for identification of structures. R – *Cortinaster* sp., MnhnL OPH256, marginal ossicle. All specimens are from the Cassian Formation, Lower Carnian (Julian), *Austrotrachyceras austriacum* Zone, Milières, west of Cortina d’Ampezzo, Tyrol, Italy. Scale bars: 1 mm for B, C, E, R; 0.5 mm for G, H; 0.3 mm for O; and 0.4 mm for all others.

angular, block-like and have a well-defined rugose central area bearing 2 to 4 papillae. Small wedge shaped actinals (Text-fig. 11O) would have infilled

spaces adjacent to the marginal plates. The abactinal ossicles (Text-figs 10Q–U, 11A–F, Q) fall into 2 broad categories. One group (Text-fig. 10Q–U) have

an oval to triangular outline, a relatively large raised, rugose central area and a depressed concave region which was overlapped by an adjacent ossicle. It appears likely that these were positioned close to the marginal frame. A second group (Text-fig. 11A–F, Q) are highly variable in outline, from elongated triangular, rectangular to having irregular outlines. All are conical with a broad base, smooth, concave sides and a small, raised central to subcentral prominence which has a finely rugose sculpture and carries one to several papillae. The original arrangement of these cannot be deduced.

The adambulacrals (Text-figs 4B, 11G–N) are proportionately short, broad, with parallel proximal and distal faces. In proximal and distal view (Text-fig. 11G, L, M) they are triangular, with straight abactinal and abradial surfaces and an evenly convex external surface which bears papillae, and, abradially, transverse ridges and rugae for the articulation of adambulacrals spines (Text-fig. 11H–J). On the abactinal surface, the articulation surfaces *adala*, *b*, *ada2*, *3* and muscle facets *padam* and *dadam* (Text-figs 4B, 11K, L, N) and the interadambulacrals articular structure (*adad*) are clearly demarcated, but narrow, occupying less than 30% of the abactinal surface of the ossicle. The body of the oral ossicle (Text-fig. 13Q, R) is triangular and the actinal margin is convex. The apophyse is robust and vertical, and the adambulacrals surface has a small muscle insertion site for the *oradm*. The actinal surface carries 5 rounded bases for oral spines (*osp*), and 6 large bases for suboral spines (*sosp*). The interradsial surface (Text-fig. 13R) has a large surface for insertion of the *odom*.

REMARKS: The structure of the adambulacrals is most unusual. In almost all neoasteroids, the articular surfaces and muscle insertion sites extend over the entire breadth of the abactinal surface of the adambulacrals (Text-fig. 4A, C, H; see Gale 2011, text-fig. 10). In *C. papillifera* gen. et sp. nov., in contrast, these sites are restricted to the abradial part of the abactinal surface, and a broad, smooth, non-articular abradial surface is present. A reconstruction of the cross-section of the arm of *C. papillifera* gen. et sp. nov. is provided (Text-fig. 14B). Although speculative in the absence of articulated material, this takes into account the detailed morphology of all the ossicle types present in the available material. The main uncertainty is the infilling of the spaces between the abactinal ossicles. The external sculpture of *C. papillifera* gen. et sp. nov. differs from that of *C. zardini* gen. et sp. nov. in the presence of coarse, rounded rugosities on the marginal, abactinal, actinal, adam-

bulacrals and oral ossicles. In *C. zardini* gen. et sp. nov., these are smaller and much more dense.

Cortinaster zardini gen. et sp. nov.
(Text-figs 12A–S, 13A–P)

1973. Asteroid ossicle; Zardini, pl. 20, fig. 14.

2011. Asteroid close to Ophidiasteridae; Gale 2011, pl. 16, figs 1–3, 7, 8, 15C.

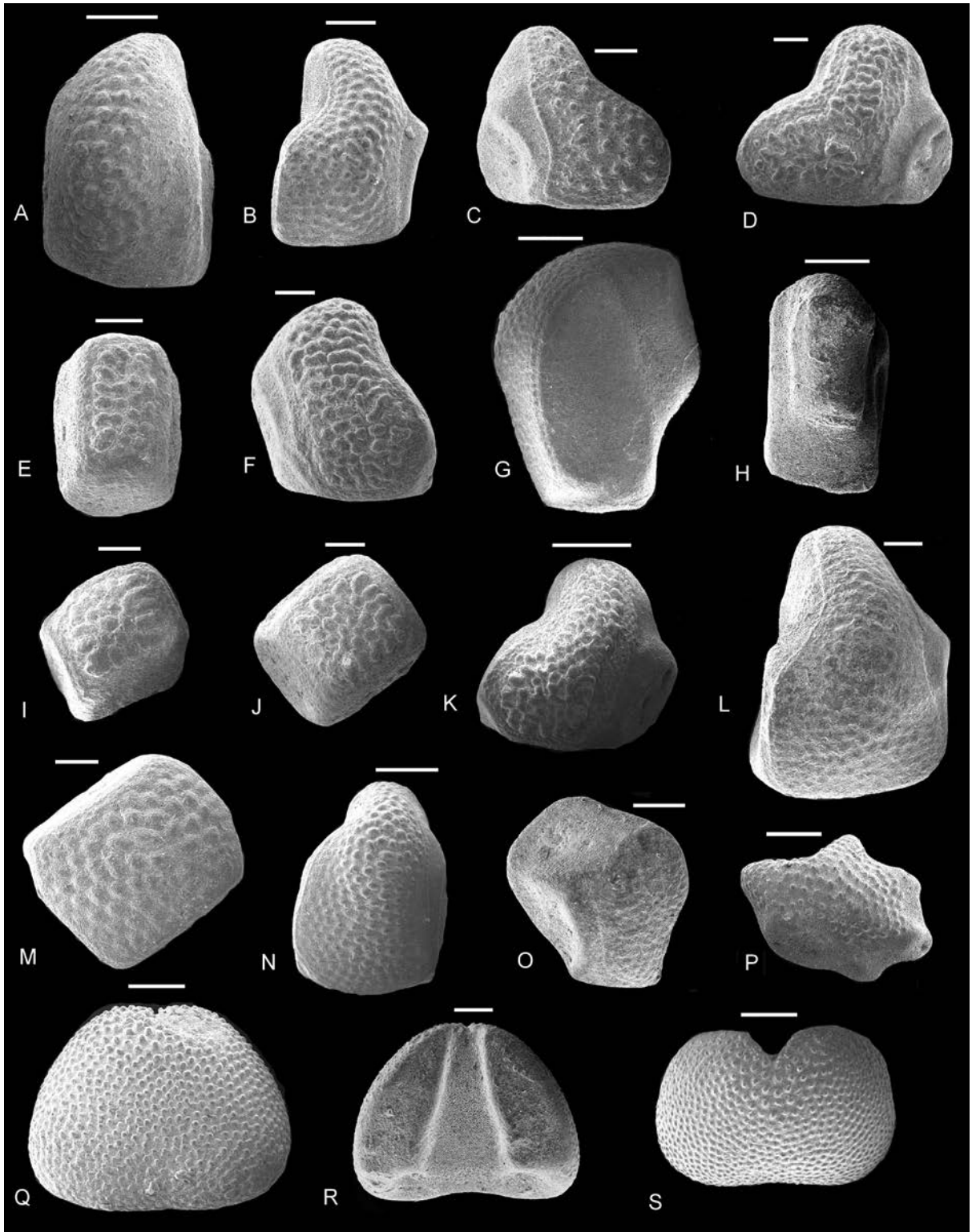
DIAGNOSIS: External sculpture comprises a central area bearing coarse rugae which coalesce in an irregular linear pattern on the proximal marginals and actinals. The sculpture becomes finely rugose on the distal marginals and terminals. Adambulacrals block-like, rectangular, with well-defined rows of bases for adambulacrals spines. Orals with prominent, triangular proximal blade bearing dense suboral spine bases.

TYPES: The marginal ossicle figured here (Text-fig. 12F) is the holotype (MnhnL OPH260). All other figured ossicles are paratypes (MnhnL OPH261–279). Lower Carnian, Julian, *Austrotrachyceras austriacum* Zone, Milières, Cortina d'Ampezzo, South Tyrol, Italy.

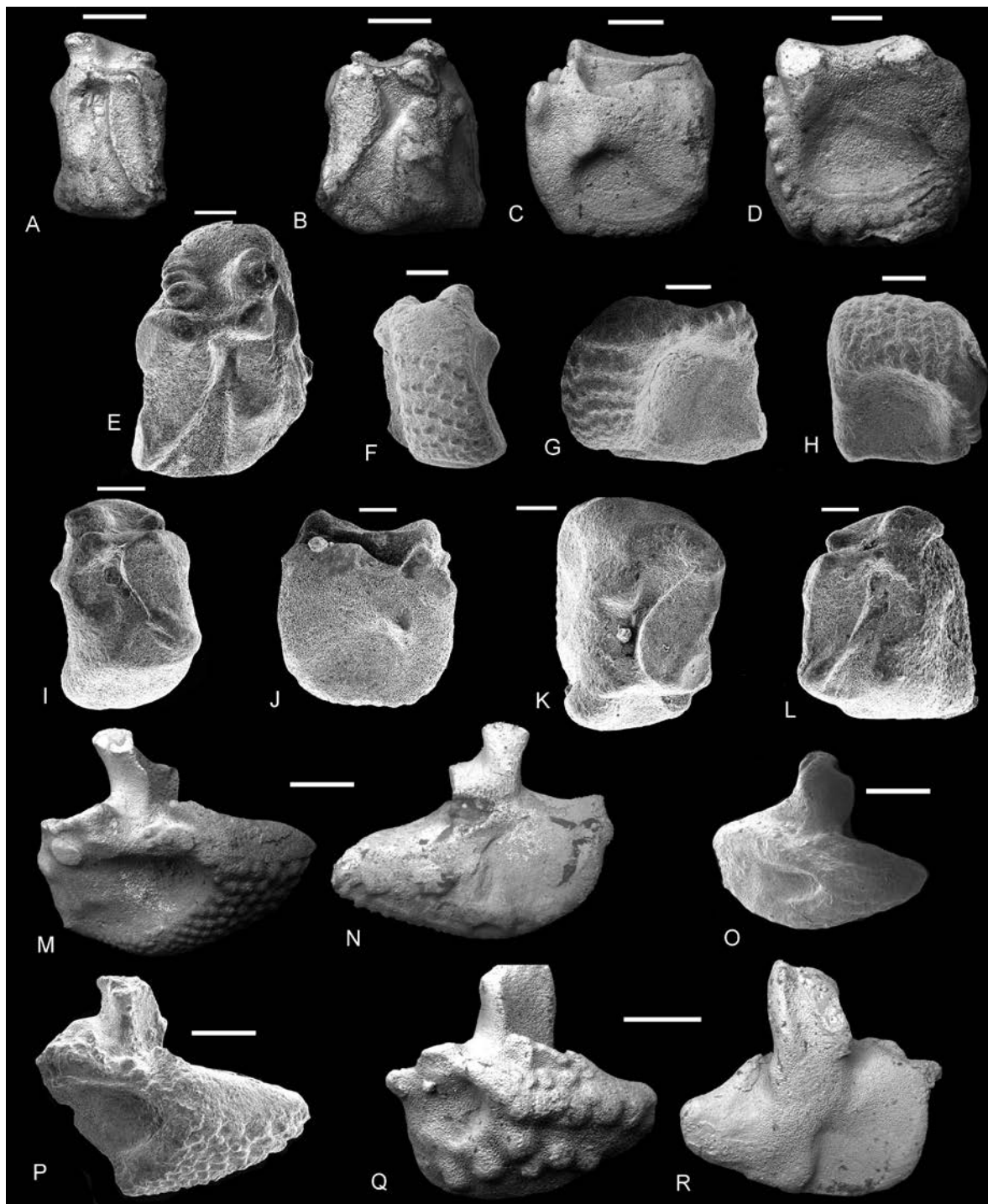
DERIVATION OF NAME: In honour of the work of Rinaldo Zardini on the faunas of the Cassian Formation.

MATERIAL: 158 ossicles including adambulacrals, orals, actinals, marginals, terminals and abactinals. Same locality and horizon as the type.

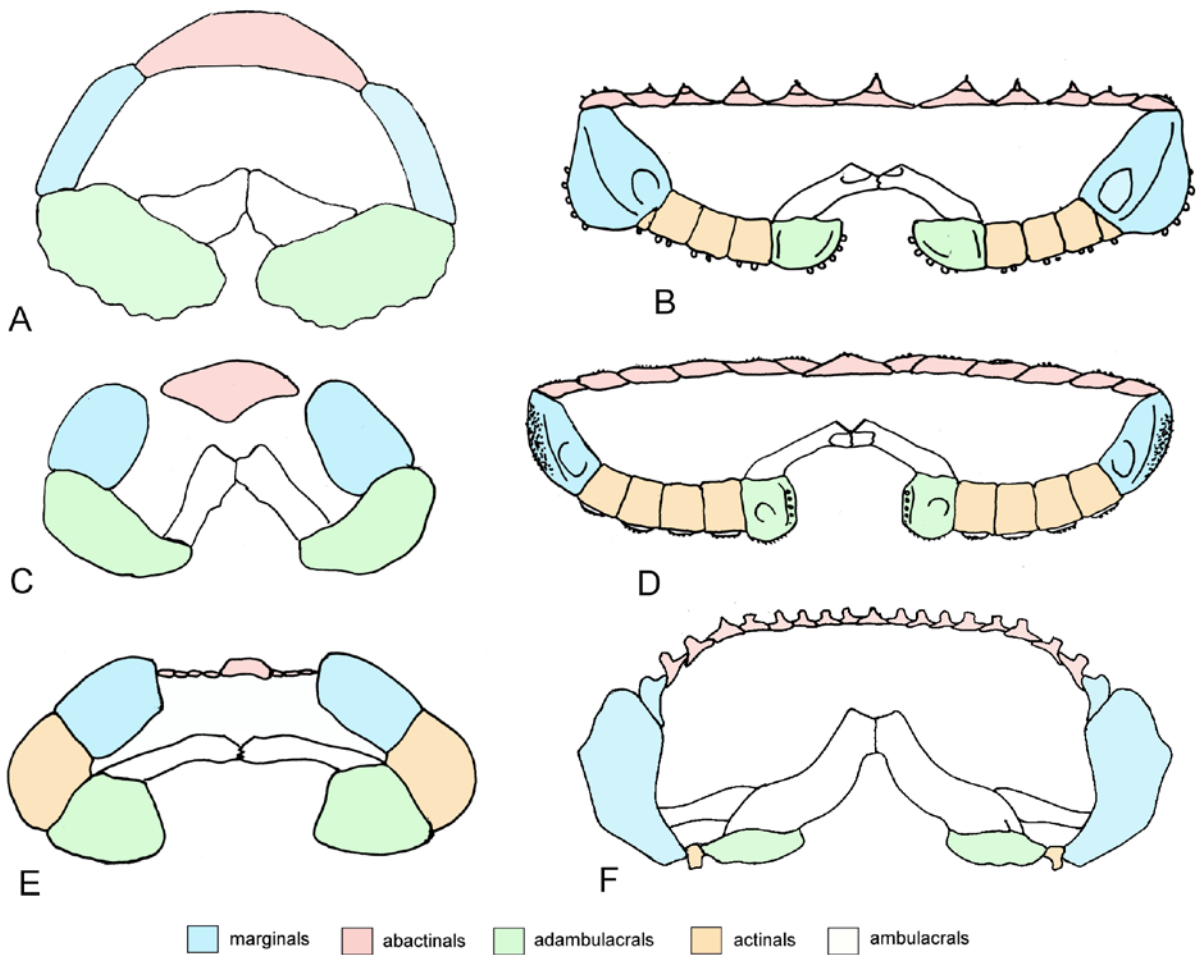
DESCRIPTION: Marginals, actinals, terminals and abactinal ossicles all bear a raised central area with sculpture comprising coarse, densely spaced rugosities which tend to conjoin to form short ridges (Text-fig. 12B–F). In the distal arm, the rugosities become finer and more evenly sized (Text-fig. 12A, L, N) and a similar sculpture is present on the abactinals (Text-fig. 12P) and terminals (Text-fig. 12Q–S). The marginals from the mid radius (Text-fig. 12B–D, F, K) are triangular, asymmetrical with an elongated proximal part and are slightly imbricated. The distal marginals (Text-fig. 12A, G, H, L, N) are proportionately taller, tumid and nearly symmetrical. The actinals (Text-fig. 12E, I, J, M) are robust, quadrangular and have slightly raised central areas with a sculpture which is identical to that of the marginals. The abactinals (Text-fig. 12P) are stellate, flat, and bear fine rugosities. The short lateral processes under- and overlapped those on adjacent ossicles. The



Text-fig. 12. *Cortinaster zardini* gen. et sp. nov. A–D, F–H, K, L, N, O – MnhnL OPH257–266, marginal ossicles in lateral (A–D, F, K, L, N, O), internal (H), and proximal (G) views; D is the holotype (MnhnL OPH260), all others are paratypes. E, I, J, N – MnhnL OPH267–270, actinal ossicles in actinal view. P – MnhnL OPH271, abactinal ossicle. Q–S – terminal ossicles (MnhnL OPH294–296) in abactinal (Q), actinal (R) and distal (S) views. All specimens are from the Cassian Formation, Lower Carnian (Julian), *Austrotrachyceras austriacum* Zone, Milières, west of Cortina d’Ampezzo, Tyrol, Italy. Scale bars: 1 mm for A, G, H, K, N, P, S; 0.5 mm for B, C, J, L, R; and 0.4 mm for all others.



Text-fig. 13. A–P – *Cortinaster zardini* gen. et sp. nov. A–L – adambulacral ossicles; A, C – NHMUK EE 13579, original of Gale (2011, pl. 16, figs 2, 12), in abactinal (A) and proximal views (C); B – NHMUK EE 13578, original of Gale (2011, pl. 16, fig. 1) in abactinal view; D – NHMUK EE 13580, original of Gale (2011, pl. 16, fig. 3) in distal view; E, I, K, L – MnhnL OPH272–275 in abactinal views; F–H – MnhnL OPH276–279, in oblique actinal views; G is a proximal adambulacral, F, H are more distal in position. M–P – oral ossicles, unregistered, Zardini coll., Museo Cortina; M, N show the holotype, original of Zardini (1973, pl. 20, fig. 14) and Gale (2016, pl. 16, figs 7, 8) in radial view (M) and interradial view (N). O, P – MnhnL OPH280–281, orals in radial views. Q, R – *Cortinaster papillifera* gen. et sp. nov., NHMUK EE 13581, holotype, oral ossicle in radial (Q) and interradial (R) views, original of Gale (2016, pl. 16, figs 4, 5). All specimens are from the Cassian Formation, Lower Carnian (Julian), *Austrotrachyceras austriacum* Zone, Milieres, 500 m west of Campo di Sotto, Cortina d’Ampezzo, Tyrol, Italy. Scale bars: 1 mm for M–R; 0.5 mm for F, G; and 0.4 mm for all others.



Text-fig. 14. Cross sections of arms of asteroids. A – *Calliasterella mira* (Trautschold, 1879), Carboniferous, Moscovian, after Gale (2011). B – *Cortinaster papillifera* gen. et sp. nov., Triassic, Carnian. Reconstruction of cross section of mid-arm. C – *Superstesaster promissor* Villier et al., 2018, after Villier et al. (2018, fig. 4B). D – *Cortinaster zardinii* gen. et sp. nov., Triassic, Carnian. Reconstruction of cross section of mid-arm. E – *Trichasteropsis weissmanni* (Münster, 1843), Triassic, Anisian, cross section of mid arm drawn from specimen GPIT PST/AS/53-1. F – present day *Luidia* sp. Not to scale.

terminal ossicles (Text-fig. 12Q–S) are abactinally convex, triangular, with a sculpture of fine, evenly sized rugosities. The actinal surface (Text-fig. 12R) has a central notch and flat surfaces for articulation of the most distal pair of marginals.

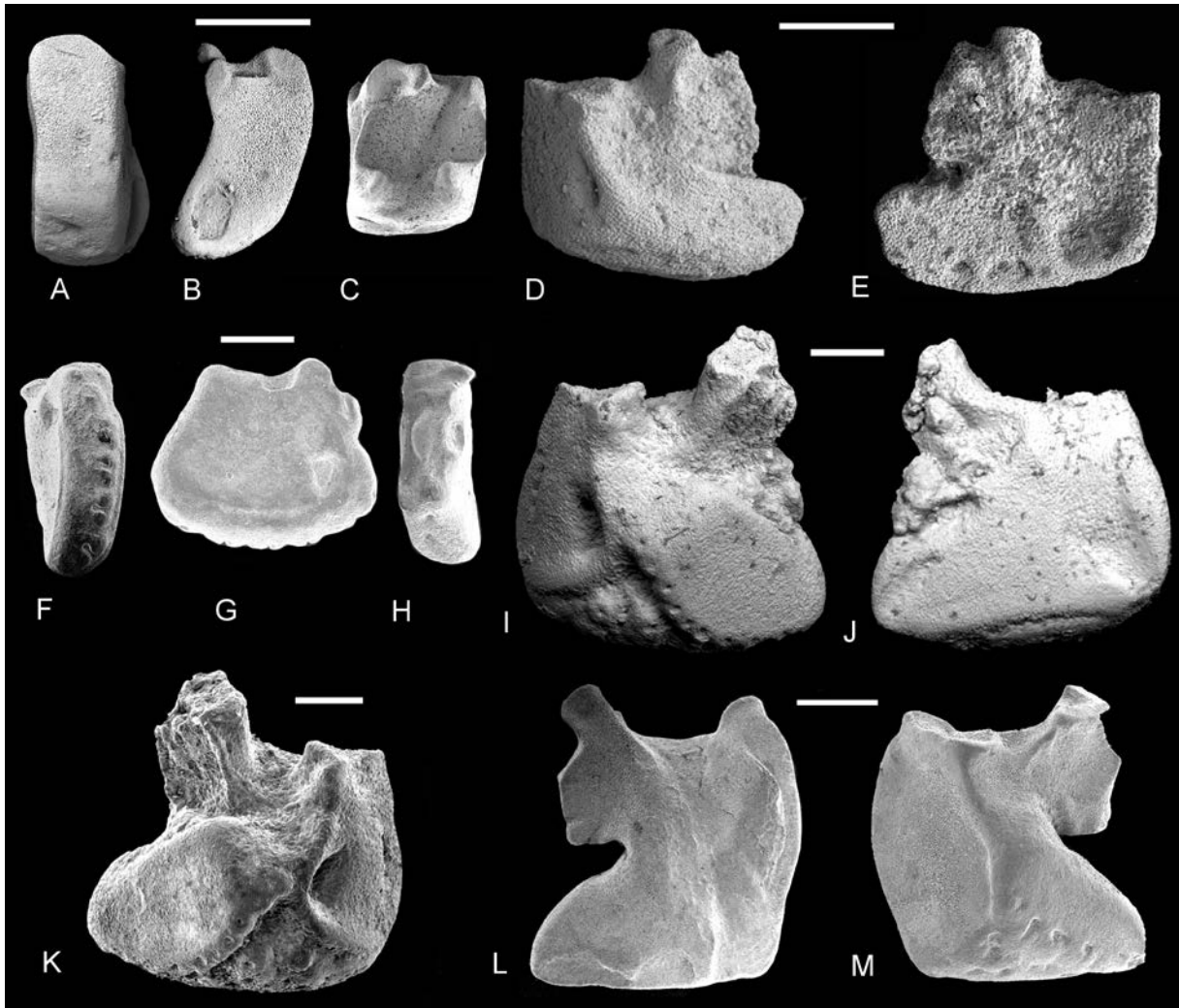
The adambulacrals (Text-figs 4A, C, 13A–L) are nearly square in proximal/distal aspect, and more proximal adambulacrals possess an extended distal flange and imbricated strongly (Text-fig. 13G). Distal adambulacrals are shorter and proximal and distal faces are parallel (Text-fig. 13A, C, D, F, I–L). The actinal surface carries rows of rugosities parallel with the ambulacral groove which bore a dense cover of subadambulacral spines, and the distal, adradial margin of each plate has a column of 5–6 short, rounded

processes (Text-fig. 13D, G). The abactinal surface of the adambulacral (Text-figs 4A, D, 13A–E, I–L) is occupied by oval muscle facets (padam, dadam) and articular structures (ada1a, b, ada2, ada3). Proximal and distal surfaces bore the interadambulacral (adadm) muscles and articulation surfaces (adad).

The body of the oral ossicles (Text-figs 4D, E, 13M–P) is rhombic in outline, and the apophyse is low. A broad triangular proximal blade bears dense rows of rugosities which carried oral and suboral spines (sosp). The surface for articulation with the adambulacral is long and oval and has a large area for insertion of a muscle (oradm) and a small oval articulation surface (orada). The interrarial surface (Text-figs 4E, 13N) is flat, and bears articular surfaces (iioa)



Text-fig. 15. A–E – *Cortinaster zardinii* gen. et sp. nov. A–D – MnhnL OPH 282–285, primary interradial ossicles in abactinal view; E – MnhnL OPH286, primary radial in abactinal view. I–N – *Cortinaster* sp. I–L – MnhnL OPH288–291, ambulacral ossicles in ventral view; M – MnhnL OPH292, circumoral ossicle in actinal view; N – MnhnL OPH293, abactinal ossicle in abactinal view. F–H, O–Q – *Soleaaster thuyi* gen. et sp. nov. F–H – MnhnL OPH287, adambulacral in distal (F), abactinal (G) and actinal (H) views. O–Q, oral ossicles; O – MnhnL OPH293 in radial view, original of Gale (2021, fig. 8G); P, Q – NHMUK EE 13584, original of Gale (2011, pl. 16, figs 10, 11) in radial (P) and interradial (Q) views. All specimens are from the Cassian Formation, Lower Carnian (Julian), *Austrotrachyceras austriacum* Zone, Milières, west of Cortina d’Ampezzo, Tyrol, Italy. Scale bars: 1 mm for J, K, 0.5 mm for D, F–I, L–P, and 0.4 mm for all others.



Text-fig. 16. A–E – *Sphaeraster tabulatus* (Goldfuss, 1833). A–C – NHMUK EE 176231, original of Gale (2021, fig. 7F–H), adambulacral ossicle in external (A), proximal (B) and actinal views (C). D, E – NHMUK EE 17644, original of Gale (2021, fig. 8A, D), oral ossicle in radial (D) and interradial views (E). F–K – *Soleaster thuyi* gen. et sp. nov. F, G, H – MnhnL OPH 287, adambulacral ossicle in actinal (F), distal (G) and actinal (H) views. I, J – NHMUK EE 13584, originals of Gale (2011, pl. 16, figs 10, 11), oral ossicle in radial (I) and interradial (J) views. K – MnhnL OPH 293view, oral ossicle in radial view. L, M – *Manfredaster bulbiferus* (Forbes, 1848), NHMUK EE 17647, original of Gale (2021, fig. 8N), oral ossicle in interradial (L) and radial (M) views. Scale bars: 0.5 mm for D, E, L, M; and 0.2 mm for all others.

and muscle insertion sites (odom). The circumoral ossicle articulated with the apophyse (pcoa) and the distal margin (dcoa). A smaller specimen (Text-fig. 13O) with a maximum dimension (proximal:distal) of 3 mm is of similar shape and structure to the larger (5 mm) holotype (Text-fig. 13M, N) and indicates that there was no ontogenetic variation in form.

Primary interradials (Text-fig. 15A–D) and a primary radial (Text-fig. 15E) are assigned to this species on the basis of the similarity of sculpture to that of the marginals. These are polygonal-oval in outline and bilaterally symmetrical, bearing a raised

oval central crest with irregular rugosities. 6 broadly rounded ridges extend from the crest to the margins. The forms with concave proximal and distal margins are primary interradials, and the ossicle with a pointed distal margin is a primary radial (compare with Ewin and Gale 2020, fig. 13.1).

REMARKS: The adambulacrals and orals are remarkably similar in detailed morphology to those of valvatidans such as ophiasterids (Text-fig. 4G–J; see Gale 2011 and discussion below). However, there are differences, such as the column of 4–6 nodes

on the adradial, distal surface (Text-fig. 4C) which are not found on any other asteroids. However, the single row of marginals, which display comparable shape changes from the interradius to the arm tip as found in *Trichasteropsis* (Text-figs 6A, C, 8A, B) support its inclusion in the Trichasteropseridae. A reconstruction of the cross-section of the mid-radius is provided in Text-fig. 14D.

Cortinaster gen. nov. sp. indet.
(Text-fig. 15I–N)

MATERIAL: Ossicles unassigned to species fall into several groups. Ambulacrals (Text-fig 15I–L) are common in the Cassian assemblage and are presumed to belong to either of the two species of *Cortinaster* gen. nov. The ambulacrals are dumbbell shaped with a central narrow waist and clear head and base regions. Articulations on the actinal surface of the base for contact with the adjacent adambulacrals (Text-fig. 4F) and muscle facets are clearly marked. The dentition on the head (for articulation of a pair of ossicles across the ambulacral groove) is coarse and irregular. The circumoral (Text-fig. 15M) has two processes for contact with the apophyse of the oral ossicle, a short proximal one and an elongated distal process. The shape of the circumoral is perhaps closest to that of ophiasterids (Gale 2011, text-fig. 19K).

Soleaaster gen. nov.

DIAGNOSIS: Adambulacrals short, broad, trapezoidal in proximal/distal view, bearing single transverse row of 4 horseshoe shaped spine bases; orals with actinal and distal margins of equal length set at right angles; external face with single row of oral spines, suboral spine bases crater-like.

TYPE SPECIES: *Soleaaster thuyi* gen. et sp. nov.

DERIVATION OF NAME: *Solea*, Latin for horseshoe, and *aster*, Latin for star, in allusion to the shape of the adambulacral spine bases.

REMARKS: Both the oral ossicles and the adambulacrals share lipped spine pits (horseshoe, crater morphologies) and for this reason are considered to belong to the same taxon. As noted previously (Gale 2011, 2021) the shape of the oral ossicles is similar to that of Jurassic and Cretaceous sphaerasterids and stauranderasterids, but the nature of the spine bases and adambulacrals is quite different.

Soleaaster thuyi gen. et sp. nov.
(Text-fig. 15F–H, O–Q)

2011. Undescribed taxon, possible stauranderasterid; Gale, p. 66, pl. 16, figs 10, 11.

2021. Stauranderasteridae; Gale, p. 12, fig. 8G.

DIAGNOSIS: As for genus.

TYPES: The oral ossicle (Text-fig. 15O) is the holotype (MnhnL OPH173), and the other oral ossicle (NHMUK EE 13584) is a paratype. The adambulacral ossicle (Text-fig. 15F–H) is also a paratype (MnhnL OPH287). Lower Carnian, Julian, *Austrotrachyceras austriacum* Zone, Milieres, Cortina d'Ampezzo, South Tyrol, Italy.

MATERIAL: Only the type specimens are available.

DERIVATION OF NAME: In honour of the work of Ben Thuy on ophiuroids.

DESCRIPTION: The two well-preserved oral ossicles (Text-fig. 15O–Q) possess convex actinal and distal margins of equal length, set at right angles. The external actinal surface bears a proximal row of fine os attachments, and five larger, crater-like, lipped, suboral spine bases (sosp) are present. The distal surface for contact with the adamb (orada, oradm) is large and well developed and there is a deep pit for insertion of the oradm (Text-fig. 15O, P). The apophyse (apo) is short and blunt. The adambulacral is short and broad (Text-fig. 15F–H) and trapezoidal in proximal/distal view (Text-fig. 15F) and the proximal and distal surfaces are parallel. The actinal surface bears 5 large, horseshoe-shaped spine bases set in a single ad-abradial row. The abactinal surface of the adambulacral bears clear structures for articulation with the ambulacrals, including a single, narrow ada1, ada2 and ada3, and small insertion sites for the muscles dadam and padam.

REMARKS: As in the case of *Cortinaster papillifera* gen. et sp. nov. (see above), the adambulacrals are unusual in that the articular structures for the ambulacrals are small (<40% of the abactinal surface) and the muscle insertion sites padam and dadam are very small (see discussion below). The oral ossicles are similar in shape to those of *Sphaeraster* Quenstedt, 1875 (Text-fig. 16D, E) and the stauranderasterid *Manfredaster bulbiferus* (Forbes, 1848) (Text-fig. 16L, M) in that the tall proximal margin is set at right angles to the actinal margin and the sur-

face for contact with the first adambulacral is short and tall. However, the adambulacrals are very different from those of both sphaerasterids and stauranderasterids. In *Sphaeraster* (Text-fig. 16A–C) the adambulacrals are narrow and tall and the abactinal surface (Text-fig. 16C) is square and entirely occupied by articular and muscle insertion sites. In contrast, the adambulacrals of *Soleaster thuyi* gen. et sp. nov. (Text-fig. 16F–H) are broad, short and the area occupied by ambulacral articular structures is small.

DISCUSSION

The evolution of ambulacral groove ossicles in the Palaeozoic–Mesozoic transition

It is generally agreed that some of the fundamental morphological changes in the evolution of the neoasteroids across the Palaeozoic–Mesozoic transition involved ossicles of the ambulacral groove – specifically, how the ambulacrals and adambulacrals articulate, and the nature of the musculature and articulation surfaces which unite them (Blake 1987; Gale 1987, 2011; Villier *et al.* 2018). A major problem here is the great scarcity of specimens which display these features, as articulated specimens seldom provide much information about the internal skeleton, and isolated ossicles are rarely collected and difficult to attribute to taxa.

The Carboniferous and Permian have yielded a small number of specimens which show the details of these ossicles. The type specimen of *Calliasterella mira* (Trautschold, 1879; Pennsylvanian, Moscovian) provides details of ambulacral and adambulacral structure (Text-fig. 17E–H; Gale 2011) and some features of the ambulacrals are visible in *C. americana* Kesling and Strimple, 1966 (Text-fig. 17J; Pennsylvanian, Kasimovian). Details of the ambulacral groove are visible on a specimen of the Permian *Australaster giganteus* Etheridge, 1892 (Permian, Artinskian; Gale and McNamara 2024, fig. 9) and isolated well preserved ambulacral and adambulacral ossicles from the Mississippian (Asbian) of Gleniff, Ireland (Text-fig. 17A–D, I) were illustrated by Gale (1987), and Gale and McNamara (2024, fig. 15).

In summary, the few Carboniferous and Permian asteroids for which ambulacral and adambulacral ossicle morphology is known indicate the presence of two fundamentally different morphological groups:

Type A, including *Calliasterella mira* (Text-figs 17E–H, 18A3) and *C. americana* (Text-fig. 17J) in which the adambulacrals are broad and short, the

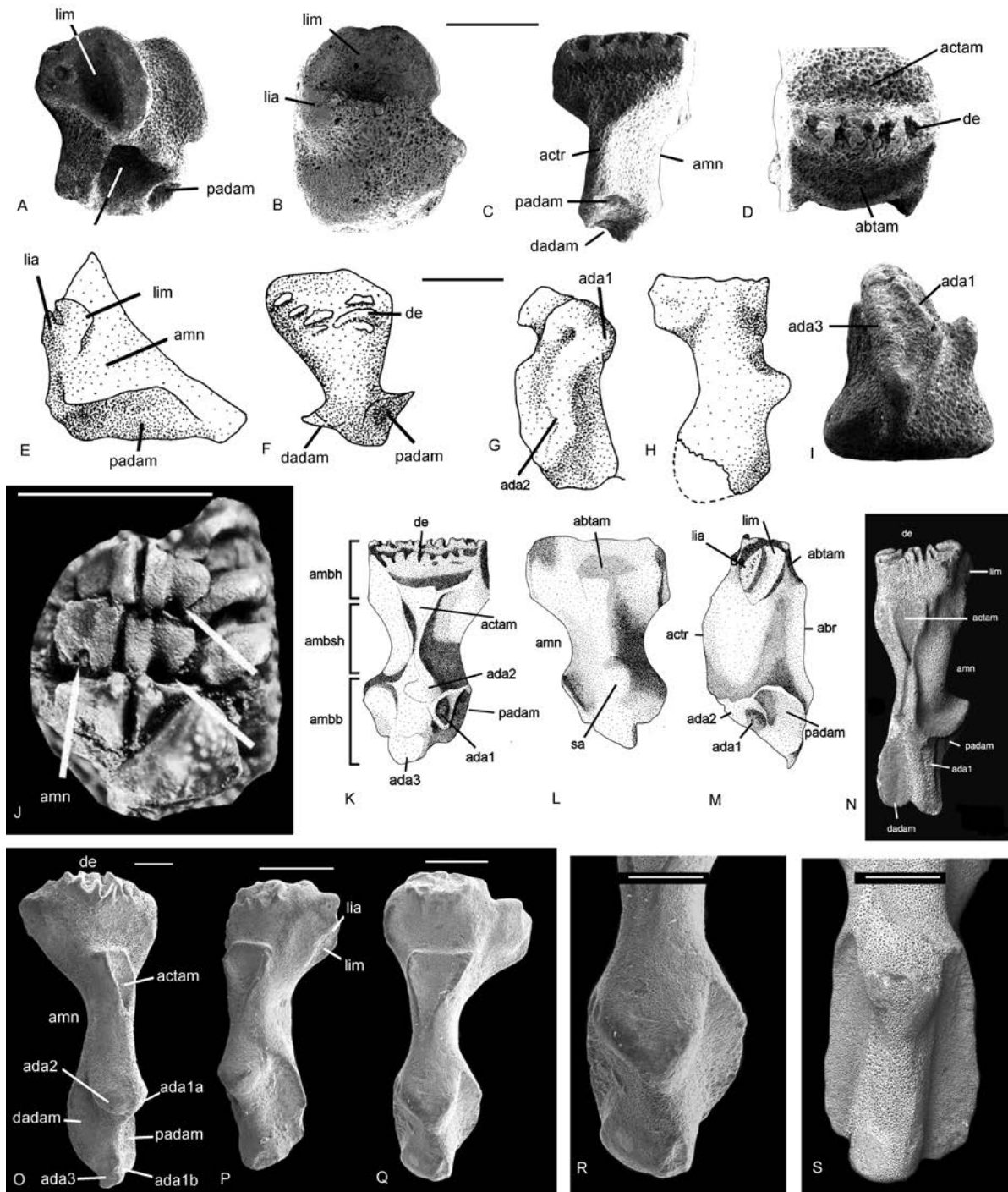
ambulacrals are small and triangular, but a poorly defined ambulacral base is present which possessed lateral flanges for the insertion of the padam and dadam. However, this type lacks musculature between opposing adambulacral pairs (actam, abtam).

Type B, including *Australaster giganteus* and the Gleniff asteroid (Text-fig. 17A–D, I) in which there is no ambulacral base and the ambulacral simply abuts two adambulacral ossicles onto which padam and dadam insert. In this form, there are large muscle sites (actam, abtam) which serve to open and close the ambulacral groove, and large longitudinal muscle sites and articulations between successive ambulacrals (lim, lia).

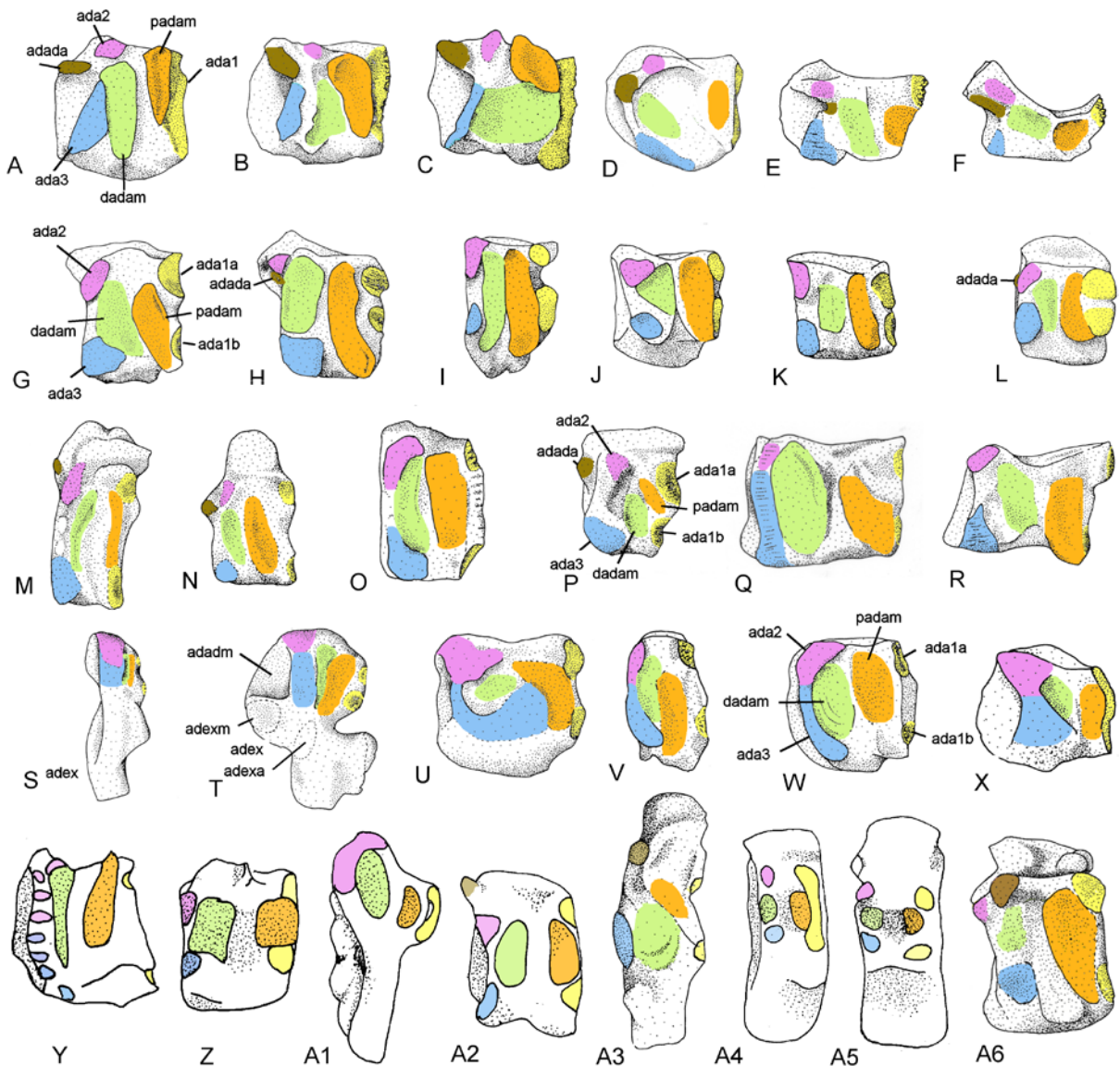
This presents an enigma, because the neoasteroid ambulacrals combine modified morphological features of both type A and B. In neoasteroids, the ambulacral base is flanged proximally and distally to accommodate the insertion sites of muscles (padam, dadam) which attach to the abactinal surface of the adambulacrals (Text-fig. 17N–S) and the articulation surfaces (ada1a, b, ada2, 3) are positioned on the sides of a ridge on the actinal side of the ambulacral base. This is essentially similar to the situation in Type A (Text-fig. 17E–G), although the articulation surfaces are poorly defined in this group. However, the features of the ambulacral head, most significantly the muscles (actam, abtam) which serve to open and close the ambulacral groove (the dentition acting as a fulcrum) are absent (Text-fig. 17F, H, J). In contrast, these are exceptionally well developed, and large in Type B (Text-fig. 17B–D), but here the articulation between the ambulacrals and adambulacrals is quite different. There is no ambulacral base, and the actinal surface of the ambulacral simply abuts the adambulacrals (see also Gale and McNamara 2024, fig. 9A, B which shows the articulation *in situ*).

The oldest neoasteroid known, *Superstesaster promissor* Villier, Brayard, Bylund, Jenks, Escarguel, Olivier, Stephen, Vennin and Fara, 2018, from the Lower Triassic (Scythian) of Utah, USA, shows the presence of an ambulacral base of a similar morphology to that of many neoasteroids (Villier *et al.* 2018, fig. 5) but the preservation is not adequate to see articulation surfaces or muscle facets. The cross section of the arm in *Superstesaster* (Text-fig. 14C) is remarkably similar to that of the Carboniferous *Calliasterella mira* (Text-fig. 14A) in the presence of very broad adambulacrals and the single row of abactinals.

The oldest well preserved neoasteroid ambulacrals and adambulacrals are illustrated here, from the Carnian (Julian) of the Cassian Formation (Text-



Text-fig. 17. A–D, I – undescribed asteroid ambulacrals, originals of Gale (1987, fig. 9Ai, Aii, Bi, Bii), and Gale and McNamara (in press, fig. 15) from the Meenymore Formation, Mississippian, Asbian, Gleniff, Slievemore, County Sligo, Republic of Ireland; A, I – TCD 25681, ambulacral in oblique distal (A) and abradial (I) views; B – TCD 25683, ambulacral in proximal view; C, D – TCD 25680, ambulacral in actinal (C) and adaradial (D) views. E–H – PIN, unregistered specimens from the Mississippian (Moscovian) of Moscow, Russia, ambulacrals of *Calliasterella mira* (Trautschold, 1879) in proximal (E), actinal (F), basal (G) and lateral (H) views. J – *Calliasterella americana* Kesling and Strimple, 1966, ISGS 42P2, *in situ* ambulacrals from the Pennsylvanian (Kasimovian) of Illinois, USA; original of Blake (2018, pl. 15, fig. 11) in abactinal view. K–M – features of neoasteroid ambulacrals, present day *Goniopecten* sp. in (K) actinal, proximal (L) and abactinal (M) views. N – ambulacral of extant *Astropecten* sp. in actinal view (ASG coll.). O–R – *Cortinaster* gen. et sp. nov. from the Carnian of Cortina d’Ampezzo, Italy, ambulacrals in actinal views. S – actinal view of base of living ophiasterid *Nardoa* sp. Scale bars: 5 mm for J; and 0.5 mm for A–I and O–S. See Table 1 for abbreviations.



Text-fig. 18. Abactinal views of adambulacrals of selected asteroids. Colour key indicated. A–Y – present day asteroids. A–F – Order Paxillosida: A – *Luidia* sp.; B – *Radiaster* sp.; C – *Astropecten* sp.; D – *Benthopecten* sp.; E – *Ctenodiscus* sp.; F – *Syracaster* sp. G–L – Order Valvatida: G – *Nardoa* sp.; H – *Archaster* sp.; I – *Protoreaster* sp.; J – *Acanthaster* sp.; K – *Mediaster* sp.; L – *Asteropsis* sp. M–N, P–R – Order Forcipulatida: M – *Asterias* sp.; N – *Zoroaster* sp.; P – *Heliaster* sp.; Q – *Brisinga* sp.; R – *Freyella* sp. S, T – Order Velatida: S – *Remaster* sp.; T – *Pteraster* sp. O, U–X – Order Spinulosida: O – *Echinaster* sp.; U – *Porania* sp.; V – *Asterina* sp.; W – *Crossaster* sp.; X – *Odontaster* sp. Y–A6 – fossil taxa: Y – *Plumaster* sp. (Jurassic); Z – *Sphaeraster* sp. (Jurassic); A1 – *Tropidaster* sp. (Jurassic); A2 – *Stauraster* sp. (Jurassic); A3 – *Calliasterella mira* (Trautschold, 1879) (Carboniferous); A4 – *Soleaster thuyi* gen. et sp. nov.; A5 – *Cortinaster papillifera* gen. et sp. nov.; A6 – *Cortinaster zardini* gen. et sp. nov. See Table 1 for abbreviations.

figs 11H–N, 13A–L, 15F–M). The ambulacrals ascribed to *Cortinaster* sp. (Text-fig. 17O–R) are very similar to those of valvatidan neoasteroids such as the ophiasterid *Nardoa* sp. (Text-fig. 17S) in terms of the positions of articulation surfaces and muscle facets, although there are minor differences in the

precise arrangement of the surfaces. The adambulacrals, here assigned to *Cortinaster zardini* gen. et sp. nov. (Text-figs 13A–L, 18A6) are also remarkably similar to those of valvatidans, and Gale (2011) made the presumptuous conclusion that these belonged to an ophiasterid.

However, other adambulacrals from the Cassian Formation are very different. In almost all post-Triassic asteroids, the actinal (upper) surface of the adambulacrals which articulates with the actinal surface of the ambulacral base is narrow and entirely occupied by articulation structures and facets for contact with the actinal (lower) surface of the ambulacral base (Text-fig. 18A–R, U–Z, A2, A6). The muscle facets *dadam* and *padam* (green and orange) are relatively large and occupy up to 50% of the surface. The only exceptions are the velatidans (Text-fig. 18S, T) and tropidasterids (Text-fig. 18A1) in which there is a narrow abradial extension. In some Carnian taxa, here referred to *Cortinaster papillifera* gen. et sp. nov. (Text-fig. 18A5) and *Soleaaster thuyi* gen. et sp. nov. (Text-fig. 18A4), the adambulacrals are broad, short, and the areas occupied by muscle facets and articulation structures are limited to approximately 30% of the abactinal surface. In particular, the muscle facets *padam* and *dadam* are very small, and cannot have generated sufficient force to allow much movement. The adambulacrals of these taxa are comparable with those of the Carboniferous *Calliasterella mira* (Text-fig. 18A3) in terms of proportions. Other Triassic asteroids, of which the detailed internal ambulacral and adambulacral structure is unknown include *Superstesaster promissor* (Text-fig. 14C) and *Migmaster angularis* (Text-fig. 5) also have very broad, short adambulacrals.

Phylogenetic placement of Triassic asteroids

New well preserved asteroid ossicles from the Carnian of Cortina d'Ampezzo, dating to approximately 234 Ma, demonstrate for the first time that some Triassic asteroids assigned to the order Trichasteropsida had ambulacral groove and mouth frame ossicles which were very similar in detail to those of Jurassic to present day neoasteroids. The specialised neoasteroid ambulacral groove articulation structures and musculature are present in *Cortinaster zardinii* gen. et sp. nov., and the morphology of the oral ossicles is very similar to those of post-Triassic asteroids (Text-figs 4, 17). However, the adambulacral ossicles of the other two Cassian Formation species, *Cortinaster papillifera* gen. et sp. nov. and *Soleaaster thuyi* gen. et sp. nov. have more in common with those of some Late Palaeozoic taxa.

Articulated material of Trichasteropsida from the Middle Triassic (Anisian) German Muschelkalk, shows that there were important differences in skeletal construction from later (post-Triassic) neoasteroids, most particularly in the presence of only a single

marginal row and the possession of a row of ossicles between the mouth frame and margin in each actinal interradius. Both of these features are interpreted as plesiomorphic retentions from Palaeozoic ancestors (Gale 2015; Gale and McNamara 2024). In post-Triassic neoasteroids, the interradiial actinal row is lost and almost all possess two rows of marginals.

The presence of marginal ossicles of *Eoastrapecten sechuanensis* Gale, 2020, in the Carnian of Sechuan China is important, because these are virtually identical to those of the Jurassic to present day family Astropectinidae. *Eoastrapecten sechuanensis* marginals possess distinctive grooves for intermarginal fascioles which are only known in the Order Paxillosida Perrier, 1884 and indicate that a significant part of the radiation of the Neoasteroidea had taken place by the Carnian. However, the almost complete absence of fossil asteroids from 30 myr of the Late Triassic (Text-fig. 1) leaves a very significant gap in knowledge, as by the Early Jurassic (Hettangian) a number of extant groups are present. It therefore appears that neoasteroid morphological features appeared successively through the early Mesozoic. In order, these were:

- the presence of an internal odontophore and basic neoasteroid ambulacral–adambulacral articulation (*Superstesaster*, Scythian; Villier *et al.* 2018);
- actinal ossicles and triangular actinal interareas set between the adambulacrals and the marginals (*Trichasteropsis*, Anisian; Blake and Hagdorn 2003);
- the evolution of short adambulacrals of which most of the abactinal surface is occupied by muscle facets and articulation structures (*Cortinaster zardinii* gen. et sp. nov. herein), early Carnian (Julian);
- the evolution of a second marginal row (superomarginals) in *Eoastrapecten* from the late Carnian (Tuvalian).

The timing of the loss of an interradiial ossicle axis is unknown, but this feature is unknown from Jurassic asteroids. It is also interesting that the two species, *Cortinaster zardinii* gen. et sp. nov. and *Cortinaster papillifera* gen. et sp. nov., share similar marginal morphology but have very different adambulacrals. There was evidently greater diversity of adambulacral structure in Triassic asteroids than in post-Triassic ones (Text-fig. 18).

Palaeoecology

The Cassian Formation contains fossil derived by transport from a tropical, shallow marine carbonate platform where a diverse fauna of echinoids includ-

ing cidaroids and basal euechinoids (Kroh 2011), ophiuroids, sponges, corals, brachiopods, gastropods and bivalves were living (Fürsich and Wendt 1977; Neutzel 2019). The robust ossicle morphology, and the strongly and distinctively sculptured external ossicles of *Cortinaster* gen. nov. are broadly comparable with those of present day ophiasterid and oreasterid starfishes found in modern carbonate platform environments. Many of these feed on encrusting organisms, surface films and can also scavenge (Jangoux 1982).

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