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Superstesaster promissor gen. et sp. nov., a new starfish (Echinodermata, Asteroidea) from the Early Triassic of Utah, USA, filling a major gap in the phylogeny of asteroids

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We describe *Superstesaster promissor* gen. et sp. nov., a starfish from the Smithian (Early Triassic) of Utah (USA) that fills a major gap in the fossil record of the Asteroidea. The post-Palaeozoic crown group Asteroidea are distinct from any of the diverse Palaeozoic forms. However, current understanding of the Palaeozoic–Mesozoic transition is blurred by a large gap in the fossil record between the Early Permian and the Middle Triassic. Building on the newly described taxon, a phylogenetic analysis investigates the relationships between Palaeozoic and Mesozoic Asteroidea. Including 30 species and 70 morphological characters, it is the most comprehensive phylogeny produced for fossil starfishes so far. Relationships among Palaeozoic forms remain poorly resolved, but their position in the tree is grossly consistent with stratigraphy. The tree topology implies the appearance of a wide range of morphologies during the Ordovician, a bottleneck during the end-Devonian events, and a second diversification during the Carboniferous, before a diversity decline at the end of the Permian. *Superstesaster promissor* nests above Palaeozoic taxa and appears as the sister group to the post-Palaeozoic Asteroidea. It represents the first record of a member of the stem group in the Mesozoic, and it likely reflects the ancestral morphology of the crown group. *S. promissor* shares with the crown group typical ambulacral and adambulacral plate shape and articulation. Phylogenetic relationships within the crown group remain poorly resolved, although three clades are consistent with molecular and morphological phylogenies available for extant forms: Valvatacea (*Comptoniaster*, *Pentasteria*, *Advenaster*, *Noviaster*), Forcipulatacea (*Germanasterias*, *Argoviaster*) and Velatida (*Tropidaster*, *Protremaster*). A Triassic and Jurassic radiation of the crown group is confirmed. Most Triassic and Jurassic forms do not share all synapomorphies with extant clades and usually represent separate clades or stem members of modern clades rather than true members of modern families.

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Keywords: Triassic; Asteroidea; phylogeny; new taxon

Introduction

About 1900 living and 600 fossil species contribute to the high diversity of starfishes (Mah & Blake 2012). Our under- standing of their systematics at high ranks has been consid- erably modifi during the past few decades with the emergence of phylogenetic studies. However, relationships are still under intense debate. Comparisons of the currently available phylogenies within the crown group, based on either morphological or molecular data, have not allowed for a consensus to be reached (Gale 2011a, 2013; Blake & Mah 2014). Nonetheless, results based on molecular data tend to converge with morphology-based analyses, which suggests that a signifi ant phylogenetic signal is present (Mah & Foltz 2011a, b; Mah & Blake 2012; Feuda & Smith 2015). The monophyly of several major groups of living starfi es is strongly supported (e.g. orders Paxillosida, Velatida and Forcipulatida including Brisingida). Valvatida and Spinulosida are understood differently among different authors, and may be either monophyletic or paraphyletic, or even polyphyletic. The most prominent points of conflict concern the position of Paxillosida and Forcipulatida (Fig. 1). On the one hand, Gale (1987, 2011a, 2013) sug- gested a basal position for Paxillosida, and placement of the Forcipulatida within a large clade characterized by the occurrence of three-part pedicellariae. On the other hand, Blake (1987) and Blake & Mah (2014) supported the idea of a basal dichotomy of two main clades, namely Forcipulatacea (including Forcipulatida and Brisingida) and Valvata- cea (including Spinulosida, Valvatida, Paxillosida and Velatida). These inconsistencies in phylogenetic interpreta- tions may result from the evolutionary history of starfishes, and fossils may help to achieve a better understanding.

The seminal papers of Blake (1987) and Gale (1987) recognized independently that all post-Palaeozoic fossil and living forms share characters of the ambulacral column that are found only in very few Palaeozoic forms. The name Neoasteroidea was given to the crown group (Gale 1987), and the name Ambuloasteroidea to the more inclusive clade of living and fossil forms sharing modern ambulacral shape and ambulacral-adambulacral articula- tion processes (Fig. 1). Ambuloasteroidea include the crown group and the Palaeozoic Calliasterellidae, Neo-paelasteridae and Compsasteridae (Blake & Hagdorn 2003). Several authors have interpreted the monophyly of post-Palaeozoic starfishes as the consequence of a strong bottleneck effect on biodiversity at the Permian–Triassic transition, followed by an evolutionary radiation during the Triassic and Jurassic that gave birth to all orders and most families of the crown group (Blake & Hagdorn 2003; Villier *et al*. 2004; Twitchett & Oji 2005; Gale 2011a). All post-Palaeozoic taxa are currently assigned to the crown group, even though some may represent extinct clades (Mah & Blake 2012).

If the crown-group clades emerged early in the Meso- zoic from a single or a few lineages that survived the end- Permian bottleneck, then they have a very brief common history, and will likely share a limited number of synapo- morphies. Character evolution in the critical Permian–Triassic interval is central to the phylogenetic reconstruc- tion of the crown group (Blake 2000; Blake *et al*. 2000b; Blake & Hagdorn 2003; Blake & Hotchkiss 2004; Gale 2011a, 2015). Unfortunately, the starfish fossil record is particularly sparse at this time. Late Palaeozoic taxa have been described only from the Carboniferous of the USA (mostly Mississippian), from two Late Carboniferous localities (Russia and Ireland), and from a few localities in the Early Permian of Australia (Blake & Elliott 2003). So far, no starfish taxon is known from the Middle to Late Permian and Early Triassic. This implies a »30 myr gap in the fossil record of the group. Triassic taxa are restricted to the Middle Triassic of France and Germany, and to a few localities in the Middle/Late Triassic of Europe and Canada (Twitchett & Oji 2005). A more diverse and wide- spread distribution of starfi h fossils emerged in the Early Jurassic (Villier *et al*. 2004; Gale 2011a).

It remains unclear whether any Palaeozoic group except the ancestral lineage(s) of the crown group survived the end-Permian extinction, and if the clade(s) of the crown group differentiated

during the Jurassic, the Triassic, or even the late Palaeozoic. The description of a new Early Triassic taxon from Utah is thus of paramount importance to test current hypotheses on the effects of the end-Permian bottleneck and to discuss the evolutionary origins of the crown group. The phylogenetic position of the new taxon and its consequences for evolutionary scenarios are investigated here with a new fossil-based phylogenetic analysis. Taxon sampling was designed to cover the widest range of morphologies known for late Palaeozoic and early Mesozoic starfihes in order to trace the ancestry of the crown group and to consider the earliest members of modern orders.

Geological setting

The new starfish specimens studied here come from two sections of the Sinbad Formation in the Torrey area near Capitol Reef National Park, south-central Utah (Fig. 2B). Lower Triassic rocks are well exposed in the Torrey area and are represented by interfingered siliciclastic andcarbonate deposits (Fig. 2C; Blakey 1974; Dean 1981; Goodspeed & Lucas 2007; Olivier et al. 2016) belonging to the Thaynes and Moenkopi groups (*sensu* Lucas *et al*. 2007). The two studied specimens are preserved in an intensely bioturbated bioclastic grainstone together with abundant bivalves, gastropods and ammonoids as well as serpulids. Stratigraphically, one specimen comes from the top of a bioclastic unit just below beds containing *Guo- dunites* and *Churkites* (*Owenites* beds; FFA2 in Brayard *et al*. 2013), and the other from just below a late Smithian bioclastic limestone unit (*Anasibirites kingianus* beds; FFA3 in Brayard *et al*. 2013).
Marine deposits of the Smithian Sinbad Formation yield abundant fossils such as ammonoids, bivalves and gastropods (e.g. Fraiser & Bottjer 2004; Nützel & Schulbert 2005; Brayard *et al*. 2013, 2015; Olivier *et al*. 2016). Sponges and an ophiuroid specimen have also been reported from the Sinbad Formation in this area (Hofmann *et al*. 2014; Olivier *et al*. 2016). Brayard *et al*. (2013, 2015) and Olivier *et al*. (2016) recently detailed the Smi- thian environments and biostratigraphy of the studied sec- tions. The sedimentary system in which the starfish specimens occur corresponds to a mid/inner shelf passing laterally into a tide-dominated shoal complex.
During the Early Triassic, the site was located on the southeastern margin of the near-equatorial western USA basin extending from British Columbia to southern Utah (Fig. 2A). In Utah, Lower Triassic sedimentary deposits mainly record environments corresponding to a shallow epicontinental sea (Blakey 1974; Goodspeed & Lucas 2007; Olivier *et al*. 2014, 2016; Vennin *et al*. 2015).

Terminology

Description of starfish body and skeleton usually follows the *Treatise on invertebrate paleontology* (Spencer & Wright 1966). The body of a starfish is typically stellate, with five (or more) arms radiating around a central disc. The size of a starfish body is traditionally measured using a large radius ‘R’ (taken from the centre of the disc to the arm tip) and a minor radius ‘r’ (between the centre of the disc and the interradial margin). The addition of R plus r defines the diameter, and the ratio R/r relates to the relative elongation of the arms.
The anus opens near the centre of the upper face, and the mouth in the centre of the lower face. A groove that hosts the ambulacra runs along the lower side of the arms and converges to the mouth. The lower and upper sides of the body are designated in the literature as adoral, ventral or actinal, and aboral, dorsal or abactinal, respectively. The position along the arms is also used as a reference axis for description (the radial axis), with ‘proximal’ referring to the mouth and ‘distal’ to the arm tip directions. The abradial/adradial axis is horizontal and perpen- dicular to the arm axis. Adradial means towards, and abradial means outwards from the radial symmetry plane that separates an arm into two lateral parts.
The starfish skeleton is composed of numerous ele- ments attached by connective tissues and muscles. All skeletal elements of the primary skeleton are described as ossicles or plates. The use of both the words ossicle and plate can be justified, and we hereafter consistently use plate. Usually, new plates are added at or near the tip of the arm. Any plate of a row can be numbered

(1, 2, 3 etc.) from those appearing first during ontogeny to the most recent. The disc and the arm are bordered by morphologically differentiated rows of marginal plates. All plates of the dorsal side of the body (i.e. above the marginal frame) are abactinals. When a row of morphologically differenti- ated abactinal plates is found in the arm axis, they are called carinals. Among abactinal plates of the disc can be found a centrodorsal plate, five primary radial plates (in the arm axis), five primary interradial plates, and a madreporite plate (the sieve plate) that allows filling of the water vascular system with seawater. An unpaired terminal plate is found at the distal extremity of every arm. The ambulacral groove is supported by two rows of ambula- cral plates and bordered by a row of adambulacral plates on each side. The mouth frame is maintained by the first ambulacral plates and 10 oral plates (also known as mouth angle plates) that are attached in pairs in the interradius. The odontophores are unpaired plates attached in the interradius between the oral and the first ambulacral plates. The plates filing the space between the adambulacral and the marginal plates on the oral side are called actinolaterals. The accessory skeleton includes all small elements attached to large primary elements of the skeleton, and facing the external side. Spines, spinelets, granules and pedicellariae are typical elements of the accessory skeleton. Dermal sclerites and granules are common in some groups, and an interradial septum can be partially calcified.

Several references are available for the description of individual plate types and articulations (Spencer & Wright 1966; Turner & Dearborn 1972; Blake 1973, 1976; Breton 1992; Gale 2011a). Pending terminological revision, we have tried to use unambiguous terms in the descriptions; otherwise, the meaning of specific terms can be found in the Supplemental data.

The length of a plate is measured in the direction paral- lel to the arm axis (proximal/distal axis) or parallel to the disc margin. The width of any particular body element is measured along the abradial/adradial axis, perpendicular to the length. Height is the vertical dimension. The descriptive terms tall, low, wide, narrow, long and short refer to the three reference axes of the body.

Systematic palaeontology

Repositories of figured specimens are abbreviated UBGD, signifying Université de Bourgogne, Géologie, Dijon, France.

Class Asteroidea de Blainville 1830 Subclass Ambuloasteroidea Blake & Hagdorn 2003
Genus *Superstesaster* gen. nov.

Type species. *Superstesaster promissor* sp. nov., the only known species.

Diagnosis. As for the species.

Derivation of name. From the Latin name *superstes*, which means survivor, and *aster* for star. The new genus is the earliest and only post-Palaeozoic starfish known so far from the Early Triassic. Its morphology combines derived characters unambiguously related to the Mesozoic Neoasteroidea and many characters inherited from its Palaeozoic relatives. It represents the single, or one of the few, starfish lineage survivors of the end-Permian extinction.

Occurrence. Sinbad Formation, late middle Smithian (Early Triassic); southern Utah, USA.

Superstesaster promissor sp. nov. (Figs 3–6)

Material. Holotype: UBGD 30578, site 1 of Figure 2B, referred to as ‘French Fork’ in Olivier *et al*. (2016), 4 km south of Torrey, Utah, bioclastic unit below *Owenites* beds, Sinbad Formation. Paratype: UBGD 30579, gravel pit, site 2 of Figure 2B, 4 km south of Torrey, Utah, bio- clastic unit below *Anasibirites kingianus* beds, Sinbad Formation.

Diagnosis. Disc small, interbrachial arcs angular, five long slender arms with pointed tips. Arm structure with one central row of carinal plates and one row of marginal plates, no actinolateral plates, and two rows of adambu- lacral plates that join the marginal plates along the body

margin. Additional abactinal plates unknown. Ambulacral plates typical of those of the crown-group Asteroidea, with an ambulacral body that develops a keel for articula- tion with two adambulacral plates and lateral processes for attachment of muscles, with a central constriction on both sides to manage space for an internal ampulla, and with a squared ambulacral head, slightly offset distally. Adambulacral plates twice as wide as long, with well- developed proximal and distal concavities for insertion of muscles with the adjoining plates, with ornament of a few short conical spines aligned perpendicularly to the ambulacral furrow. A large unpaired interradial plate in contact with the oral (axillary/odontophore), the first adambulacral and the marginal plates. Oral plates relatively large and triangular in cross-section. Marginal plates block-like, rounded, grossly alternating with the adambulacral plates along the arm.

Derivation of name. From the Latin name *promissor*, meaning promising. The hypothetical ancestor of all modern Neoasteroidea taxa is currently thought to be phylogenetically close to, and morphologically similar to, the new species. The name highlights the future evolutionary success of the group.

Description. The holotype was discovered while breaking a large slab. The fracture plane passed through the body plane. The specimen thus offers a cross section in the mid plane of the starfish body (Fig. 3A, B). The initial microstructure of the skeleton was lost due to a complete recrystallization of the initial calcite meshwork of all skeletal elements into a homogeneous, compact, white calcite crystal. The varied orientations of cleavage planes across the arms allow the recognition of sections of each individual plate type in varied views. Their overall morphology and a clear depiction of the plate contacts can thus be reconstructed. However, none of the skeletal elements shows its external face.

The paratype is an arm fragment lying at the surface of a weathered limestone slab (Fig. 3C). The structure of the arm can be described in three dimensions, but all individual skeletal plates show a dissolved surface, preventing a description of the details of the ornament.

The body is stellate with five long, slender, parallel- sided arms and angular interbrachial arcs (Fig. 3A, B). The arm tips are missing and the body shape is slightly distorted, which prevents an accurate measurement of the dimensions. The longest preserved arm portion reaches 22 mm in length, which approximates R, and r is about 5 mm. The R/r ratio is surely greater than 5. The peristome is widely opened, representing 30–50% of the lower surface of the disc.

One side of the slab shows an arm cut perpendicularly (upper right arm inn Fig. 3A, B). The arm is flattened and the ambulacral furrow is opened by compression of the flexible body during burial (Fig. 4). In living conditions, the arm was likely arched. Wide adambulacral plates form a flattened base to the arm, and their rounded abradial margin marks the margin of the body. There is a single row of blocky marginal plates lying on the adambulacrals. A single row of abactinal plates is recognized in the mid-arm plane (carinal plates). Although preservation is poor and exposure of the abactinal side limited, it can be assumed that no other abactinal rows of plates were present while alive (Fig. 4). There are no actinolateral plates, even in the disc area. Super-ambulacral plates cannot be recognized on any of the available sections. All the plates visible in the central area of the disc likely belong to the mouth frame. The dorsal side of the disc cannot be described from the available specimens.

The ambulacral plates are elongate, a shaft clearly separating an ambulacral head from an ambulacral base (Figs 5, 6A, B). The ambulacral base develops one distal and one proximal blade for insertion of the muscles that attach the ambulacral to the adambulacral (Fig. 6C, D). The central projection that articulates with the adambulacral plates is triangular wedge-shaped. The ambulacral shaft is constricted, with symmetrical gentle concavities. In cross section, the base of the ambulacral head varies from a triangular shape on the furrow side to rectangular, parallel-sided on the dorsal side. This indicates a differentiated face for insertion of an actinal transverse ambulacral muscle (Fig. 5). The ambulacral head is squared on the dorsal side. A strong dentition marks the articulation of the median plane with the facing ambulacral (Fig. 5). There is a slight projection of the distal part for the ambulacral head (Figs 5, 6A, B), which implies a limited over- lapping of the adjoining ambulacrals, but allows the attachment of inter-ambulacral muscles. The upper edge of the ambulacral head is slightly indented at the distal corner (Fig. 6A, C), which could mark the position of an abactinal transverse muscle.

The adambulacral plates are robust, block-like elements, grossly twice wider than long and high (Fig. 6A, B). The abactinal part does not project distally, nor overlap the next adambulacral plate. Thus, the adambulacral and ambulacral plates alternate along the arm. The abactinal side of the adambulacral plates makes a symmetrical edge, with the two faces for articulation with the ambulacral plates. The proximal and distal articulations with the other adambulacral plates of the row develop into large slightly concave faces on which insert strong inter-adambulacral muscles (see the large contact surfaces between close adambulacral plates in Fig. 6A–D). The outer face of the adambulacral plates is oriented towards the adoral and abradial sides; the cross section appears either rounded or angular when it crosses a spine base (Fig. 6A, B). The cross sections of the adambulacral spines suggest a few large, robust, conical spines aligned on the adambulacral plate edge, perpendicular to the fur- row. There is no evidence of shape differentiation of the adambulacrals along the arm, nor of alternation of carinate and non-carinate plates on the groove side.

An unpaired plate inserts between the pairs of mouth angle plates abutting in each interradius (Fig. 6E). The plate is positioned dorsally to the mouth angle plates and its proximal extremity extends between the dorsal blades of the mouth angle plates. It also seems to be in contact with the first adambulacral, first ambulacral, and maybe also the marginal series, but this cannot be observed. Position and contacts are similar to those found in the odontophore of all members of the crown group and the axillary of some Palaeozoic taxa (at least the Neopalaeasteridae and *Calliasterella mira*; Gale 2011a).

The shape and arrangement of the marginal plates is difficult to describe from the available specimens that mostly show sections in the ambulacral and adambulacral plates. Marginal plates are robust, block-like elements with rounded angles (Fig. 6B). They are relatively small and numerous, and alternate with the adambulacral plates. Ornament is unknown. The marginal rows abut the adambulacral in the arm and the axillary in the interradius.

The mouth angle (or oral) plates are triangular in cross section and of moderate size (Fig. 6E). The side facing the mouth opening forms a relatively sharp angle of greater than 60° along the mouth opening, grading rapidly towards the ambulacral furrow. No abactinal shaft can be clearly recognized in the cross sections. The first ambulacral plate (circumoral) has a wide, squared head with a differentiated proximal circumoral process. Long robust cylindrical spines are attached to the mouth angle plates, but their number remains unknown.

Remarks. The arm construction with large adambulacral plates forming part of the body margin, a single row of marginal plates, a limited development of the abactinal plates, the occurrence of an odontophore, and the lack of an actinolateral field are all widespread characters among late Palaeozoic starfishes (Blake & Elliot 2003). These represent plesiomorphic characters for the crown group, some of which are associated with only a few post-Palaeozoic forms (several Zoroasteridae and *Terminaster*) (Blake & Hagdorn 2003; Villier *et al*. 2009; Gale 2011a, b). However, the combination of a mouth frame with fairly large triangular oral plates, the ambulacral that is well differentiated into three parts with a constricted shaft, and the robust adambulacral design is distinct from any of these taxa, and these characters justify the erection of *Superstesaster promissor* gen. et sp. nov.

By comparison, the Carboniferous *Calliasteralla mira* has proportionally broader and more compressed adambu- lacral plates. The external blades that support the spine bases have no equivalent in *Superstesaster promissor*, in which spines seem to insert on large bosses. In *C. mira*, the articulation between consecutive adambulac- ral plates does not exhibit a large surface for insertion of muscles; instead, the articulation is made of distinct processes (Gale 2011a). In comparison to those of *S. promissor*, the ambulacral plates of *C. mira* are proportionally low, the ambulacral base enlarges regularly towards the head, and the dorsal side of the ambulacral head extends as a blade. The marginal plates look taller in *C. mira*.

Calliasterella americana, also a Carboniferous taxon, is mostly known from its dorsal side that shows relatively few, large abactinal plates on the disc, the occurrence of a long, robust spine on some plates, and more robust mar- ginal plates (Kesling & Strimple 1966), similar to those of *Superstesaster promissor*. Limited information is avail- able for the ambulacral groove and the oral area of *C. americana* (Kesling & Strimple 1966; Blake 2000; Gale 2011a). However, significant anatomical differences of the ambulacral and adambulacral plates separate *C.*

americana from *S. promissor*. The ambulacral plates are low, robust elements in *C. americana*, whereas they are tall and thin elements in *S. promissor* and the crown-group Asteroidea. The ambulacral heads of *C. americana*, being square in cross section and slightly overlapping distally, are fairly similar to those found in *S. promissor*. The adambulacral plates of *C. americana* are characterized by a strong deflexion of the internal blade for articulation between the ambulacral plates (Kesling & Strimple 1966, pl. 143, figs 3, 4). There is a strong gap between adambulacral plates, suggestive of a kind of fasciolar groove or the occurrence of strong inter-adambulacral muscles. By comparison, the adambulacral plates are closely arranged in *S. promissor*, without a differentiated deflected internal blade. The spines inserted on the adambulacral plates are organized in a tuft of a few long and robust spines in *C. americana*.
The Jurassic *Terminaster* differs mostly from *Superstesaster promissor* in the occurrence of two rows of plates along the body margin (distinct from the adambulacral plates), the better developed abactinal plates, proportionally larger marginal compared to adambulacral plates, narrower adambulacral plates that appear squared in cross section, and the much shorter mouth angle plates that appear approximately the same size as the first adambulacral plates in adoral view.
Although similar to *Superstesaster promissor* in overall shape and arm structure, extant Zoroasteridae are clearly distinct in developing a greater number of plate rows in the body wall (in particular, the actinolateral plates), the compressed shape of the adambulacral plates that are often differentiated into an alternating pattern of carinate and non-carinate plates, and the development of four rows of tube feet in many species.

Phylogenetic analysis

Few authors have produced character matrices to address the phylogeny of the starfish crown group from morpho- logical data (Blake 1987, 2010; Gale 1987, 2011a; Blake & Hagdorn 2003; Blake & Portell 2011). Current under- standing of the crown-group phylogeny is based strongly on the opinions of Andy Gale and Dan Blake, who differ in their approach and have contrasting views (Gale 2011a, 2013; Blake & Mah 2014). Gale selected a small number of extant taxa and rooted his phylogenetic analyses using Palaeozoic fossils. The position of the post-Palaeozoic fossils and the history of modern taxa were discussed in a second step, following phylogenetic results from living forms (Gale 1987, 2011a). Blake employed a more com- prehensive taxon sampling in his phylogenetic analyses, including both living and fossil taxa (Blake 1987; Blake & Hagdorn 2003; Mah & Blake 2012). Almost all post-Palaeozoic fossils were assigned to a modern group, either directly from the obtained phylogenies or by subsequent comparisons. Both authors interpreted Triassic trichasteropsids as a distinct clade, basal among the forcipulataceans in the case of Blake & Hagdorn (2003) but as *incertae sedis* Neoasteroidea by Gale (2011a). Another obvious difference between the approaches of Gale and Blake was in the way that the morphological characters were coded. Gale (2011a) derived numerous characters from the comparative anatomy of isolated skeletal elements, and he strongly favoured characters of the axial skeleton and the mouth frame. The matrices presented by Blake (1987) and Blake & Hagdorn (2003) were more conservative. The characters of the axial skeleton were favoured, with characters traditionally used in the description of extant forms contributing a higher proportion, including body shape, plate arrangement and ornament. Obvious divergences also appear in some character interpretations. In an effort to avoid favouring one of these historical views, we propose here a new phylogenetic analysis grounded on an independent strategy of character coding and taxon sampling. This approach: (1) samples a wide range of Palaeozoic taxa to increase the chances of approaching the origins of the crown group; (2) samples numerous late Palaeozoic and early Mesozoic forms to document the Permian–Triassic transition and the radiation of the crown group; and (3) reduces the potential bias caused by long branches by not considering extant taxa.

Outgroup selection and tree rooting

It is usually recommended to select outgroups from within a sister clade or among the phylogenetically closest forms to the ingroup. Among extant echinoderms, the Asteroidea could be

sister to either Ophiuroidea (asterozoan model) or to a clade containing Ophiuroidea and Echinoidea plus Holothuroidea (cryptosyringid model) (Telford *et al*. 2014). In both asterozoan and cryptosyringid models the fossil Somasteroida are placed just stem-ward of Asteroidea. This group shares numerous character states with the earliest Asteroidea (Blake 2008, 2013) and was therefore selected as outgroup.

Selection of taxa

The Palaeozoic asteroid taxa are diverse and display a wide range of morphologies, often comparable to extant forms. Recognition of the origin of the crown group therefore remains difficult (Blake & Guensburg 1989, 2005; Blake 2002; Blake & Rozhnov 2007; Blake & Ettensohn 2009). As a consequence, inclusion of vari- ous Palaeozoic taxa is required to address the relation- ships between Palaeozoic and post-Palaeozoic forms, as well as to test the position of new species. Taxa considered as belonging to the ingroup include 16 Palaeozoic species, covering the Ordovician–Permian interval, and 15 species representing most of the genera described to date from the Triassic and the Early/Middle Jurassic (Supplemental Table 1). Only those taxa sufficiently documented to allow a full comparison and to minimize unavailable data in the character matrix were selected. Our selection maximizes the variety of character combinations expressed in fossil forms. It potentially minimizes the phylogenetic distance between the earliest elements of the crown group and their stem groups, which in theory increases the chance of capturing a robust phylogenetic signal. Thus, it becomes possible to test for the monophyly of post-Palaeozoic forms, and to resolve the phylogenetic position of the new Early Triassic taxon.

Character coding strategy

The derivation of a phylogeny from morphological data has become the usual approach for starfishes, whether fossil, living or the two combined (Blake *et al*. 2000a). The morphological characters coded for the parsimony analysis were primarily selected to describe the transition between Palaeozoic and post-Palaeozoic forms, following a critical reappraisal of formerly published phylogenies (Blake 1987; Gale 1987; Blake & Hagdorn 2003; Gale 2011a), a broad survey of the literature (see Supplemental Table 1), and a survey of major fossil collections (Natural History Museum, London; Muséum National d'Histoire Naturelle, Paris).

The homologies remain intensely debated for some morphological features (e.g. marginal plates, axillary of the Palaeozoic forms vs the odontophore of post-Palaeozoic taxa, single or multiple evolutions of the pedicellariae). Characters with ambiguous definitions were avoided as often as possible. A review of character concepts and of our character interpretation is available in the Supplementary material.

The difficulties encountered in delineating homologies result from the high frequency of homeomorphism in star- fish evolution (Blake & Guensburg 1989; Breton 1997; Blake & Kues 2002), and from the limited understanding of basal states. No attempt was made here to order the character states prior to the parsimony analysis. Ontogenetic sequences of the skeletons remain poorly described and were not considered in character definition; all coded specimens were adults. The poor quality of the starfish fossil record limits the significance of the chronology of appearances for character ordination (Gale 2011a).

Data processing

A data matrix of 70 characters coded *de novo* for 30 taxa (Supplemental Appendix 1) was analysed with the soft- ware PAUP 4.0 (Swofford 2002). Characters are all binary and considered unordered. The features expressed in the outgroup *Archegonaster pentagonus* determine the basal condition for the ingroup Asteroidea that is assumed to be monophyletic. The most parsimonious trees were calculated with the heuristic algorithm and the ACCTRAN option, which favours reversions. When several trees wereobtained, a strict consensus tree was computed. The robustness of the results was measured using bootstrap analysis. Additional analyses were performed with sub- sampling of taxa and characters to test for analytical biases.

Results

Optimal trees. Analysis of the entire data matrix yielded five equal, most parsimonious trees with lengths of 235 steps. The strict consensus tree (Fig. 7) shows several interesting patterns:

1.The species pool is strongly segregated according to stratigraphical position. Species known from the Ordovician to the Devonian all branch in a basically pectinate pattern in the lower part of the tree. Carboniferous and Permian taxa are clustered in the middle part of the tree. All Mesozoic forms occupy the upper part of the tree.
2.The tree retains a clade Ambuloasteroidea, characterized by the opening of internal ampulae between the ambulacral, including all post-Devonian taxa coded here.
3.*Supersteaster promissor* is found to be a sister taxon of the crown group Neoasteroidea, constituted by all post-Palaeozoic taxa with the possible exception of *Terminaster cancriformis*.
4.The relationships among Mesozoic taxa are consistent with an early separation of the main modern clades. The clade formed by *Tropiaster pectinatus* and *Protremaster universalis* may represent the Velatida. A forcipulatacean group would include *Trichasteropsis weissmanni*, *Germanasterias ampli- papularia*, *Argoviaster occultus* and maybe *Plesiosolaster moretonis*. The Forcipulatacea appear as a sister clade to a large valvatacean clade.
5.*Compsaster formosus* is a Palaeozoic taxon that unexpectedly branches within the crown group.

Boostrap analysis. The topology of the tree is unstable (Supplemental Fig. 1): bootstrap values are low for each clade of the tree due to a high level of homoplasy in the matrix. However, the few nodes supported by more than 50% bootstrap values are of high evolutionary significance and show:

1.A valvatidan clade including Goniasteridae and Astropectinidae.
2.A forcipulatacean clade including *Trichasteropsis weissmanni* at its base (trichasteropsid) and a pair of species assigned in the literature to the Asteriidae.
3.The position of *Supersteaster promissor* as sister to the crown group Neoasteroidea.
4.The calliasterellids being the Palaeozoic taxa closest to the post-Palaeozoic species.
5.The association of *Delicaster enigmaticus* and *Emphereaster missouriensis*, two members of the family Neopalaeasteridae.

Taxon subsampling. Subsampling of taxa from the crown group modifies tree topology. Only the valvatacean and forcipulatacaean clades are retained in all tested com- binations of taxa, as in the bootstrap test. The position of *Terminaster cancriformis* switches either to become sister group to the crown-group or to be positioned at the base of the Forcipulatacea. The position of *Compsaster formosus* is highly unstable, but its exclusion from the analysis does not clearly improve the overall robustness of the trees.
The position of *Supersteaster promissor* and the two *Calliasterella* species just stem-ward of the crown-group is a robust feature. However, the topology within Neoasteroidea is modified regardless of whether one, two or three of these taxa are considered in the taxon set. For example, the tree obtained with deletion of C. mira is con- sistent with a basal separation of the clade 'Astropectinidae C Goniasteridae', with Forcipulatacea nesting high in the tree, which is a hypothesis roughly similar to that assumed by Gale (1987, 2011a, 2013). When *S. promissor* is considered alone, the obtained tree suggests an early dichotomy of Forcipulatacea on the one hand and a large Valvatacean clade on the other, which rather matches the hypotheses of Blake & Hagdorn (2003).

Taxonomic and phylogenetic discussion

Tree shape and the long-term evolutionary history of the Asteroidea
The obtained tree is fairly congruent with the stratigraphical occurrences of the fossils. All Ordovician, Silurian and Devonian taxa are grouped in the lower part of the tree (Fig. 8).

Starfishes appear in the Early Ordovician, at the same time as other asterozoans and somasteroids (Shackleton 2005). Starfishes attained a high morphological diversity early in their history (Blake & Guensburg 1993, 2005; Blake 1994, 2007, 2008, 2013; Blake *et al*. 2007; Blake & Rozhnov 2007), potentially allowing Palaeozoic taxa to explore many adaptive strategies recognized in the crown group that evolved much later in starfish history (Mah & Blake 2012). The association of Ordovician, Silurian and Devonian taxa in the lower part of the tree may illustrate the coexistence of various line- ages during that time interval. Starfishes, like other echinoderms, thrived through the end-Ordovician extinction events with numerous surviving lineages (Sheehan 2001). The maximum parsimony strict consensus tree shows segregation between the Ordovician–Devonian and the Carboniferous–Permian taxa (Fig. 8). This does not necessarily mean that all late Palaeozoic taxa and the crown- group taxa belong to a single clade. There are additional Carboniferous surviving lineages that were not sampled in this analysis. Seventeen species (from 13 genera and 10 families) have been described from Carboniferous and Permian fossil localities (Supplemental Table 2), a sample that is substantially smaller than the one from the Silurian–Devonian interval. Thus, a decrease in diversity can be suspected at the end of the Devonian. The majority of the Carboniferous–Permian species belong to the Ambuloasteroidea, including the crown group. The recovery of starfish diversity can be linked to the radiation of this group (Mah & Blake 2012). The end-Devonian mass extinction strongly shaped the evolutionary history of echinoderms (Foote 1992; Ausich *et al*. 1994; Dornbos 2008; Waters & Webster 2009), and this also seems to be the case for starfishes specifically. The phylogeny of Palaeozoic taxa, as a whole, requires reappraisal, but it can be helpful to understand the effects of the successive Palaeozoic mass extinctions. Our preliminary results suggest that Ambuloasteroidea root within some robust, arm- oured earlier forms characterized by a developed axillary, reduced or no actinolateral fields, reduced abactinal plate rows, a well-developed primary circlet, and blocky adambulacral plates with restriction of the podial basin to the ambulacral column.

Crown-group origins

Blake (1987) and Gale (1987) both recognized post-Palae- ozoic starfishes as a clade. Gale (1987, 2005, 2011a, 2013) defined the crown group as Neoasteroidea and ranked it as a subclass within the class Asteroidea. From that point of view, all known post-Palaeozoic taxa are assumed to belong to the Neoasteroidea, and no crown-group member is recorded in the Palaeozoic, which implies the survival of a limited number of starfish lineages (at least one) during the Permian–Triassic mass extinction (Twitchett & Oji 2005). Several synapomorphies of the ambulacral column, the mouth frame, and the ambulacral/adambulacral articulation agree with the Neoasteroidea crown group concept (Blake 1987; Gale 1987, 2011a, 2013). Our phylogenetic results fully support the post-Palaeozoic neoasteroid radiation. *Superstesaster promissor* is basal to all included members of the crown group and is thus the first documented stem-group Neoasteroidea that survived the Permian–Triassic mass extinction. The hypothesis that the crown group likely emerged and radiated during the Triassic and the Jurassic from a single ancestor (Blake 1987; Blake & Hagdorn 2003; Villier *et al*. 2004; Mah & Blake 2012; Gale 1987, 2011a, 2013) is therefore strongly reinforced by the Early Triassic age of *S. promissor*.

Blake & Hagdorn (2003) erected a subclass clade Ambuloasteroidea, including the crown group plus the stem-ward Palaeozoic taxa that share the following characters of the axial skeleton with post-Palaeozoic taxa: internal ampulae passing through rounded constrictions of the ambulacral base, and offset of ambulacral-adambulacral articulation. *Fandasterias* is found as a sister group to Ambuloasteroidea. Ambuloasteroidea include Calliasterellidae, Compsasteridae, Neopalaesteridae, Monasteridae, *Superstesaster promissor* and Neoasteroidea (Blake 2000; Blake & Elliott 2003; Mah & Blake 2012). However, Neopalaesteridae and Calliasterellidae appear paraphyletic in our tree. The Palaeozoic ambuloasteroid taxa clos- est to the crown group share various morphological characters that should represent the ancestral conditions for the crown group: a small disc, slender arms, a single row of marginal plates, an enlarged axillary ossicle homologous to the odontophore of the crown group,

reduced actinolateral fields, and adambulacral plates bear- ing a row of conical spines perpendicular to the ambulacral furrow. Almost all these characters are expressed as plesiomorphies in *Superstesaster promissor* together with synapomorphies of the crown group (true odontophore, development of the ambulacral plates). Thus, based on these criteria *Superstesaster promissor* reflects the ancestral morphology of the crown group.

Relationships within the crown group

The Jurassic *Terminaster cancriformis* is difficult to classify. Authors do not consistently homologize the two lat- eral rows of plates on each side of the arms: they are interpreted either as one row of inferomarginal and one row of actinolateral plates (Hess 1974; Mah 2007), or as two rows of marginal plates (Villier *et al*. 2009; Gale 2011b). With a single row of marginal plates, *Terminaster* is close to Zoroasteridae, and could even nest within this family as sister group to an abyssal clade (Mah 2007). Villier *et al*. (2009) suggested several options for the phylo- genetic position of *Terminaster*: basal to Forcipulatacea, Forcipulatida, or Zorasteridae. Gale (2011a, b) recognized the uncommon morphology of *Terminaster*. He erected a new family for this taxon, Terminasteridae, assuming a phylogenetic position basal to Forcipulatida. The similarity of body construction between *Superstesaster promissor* and *T. cancriformis* has major phylogenetic consequences. Indeed, *T. cancriformis* appears basal to all other post-Palaeozoic forms in the phylogenetic tree, dif- fering mostly from *S. promissor* in the occurrence of two rows of marginal plates, most other characters expressed in *Terminaster* being plesiomorphic. So far, it has always been considered a crown-group member, likely nesting within Forcipulatacea. Its plesiomorphic morphology in our phylogenetic analysis may lead to exclusion of *Terminaster* from the crown group (Villier *et al*. 2009).

Tropiaster pectinatus is assigned to its own family, Tropidasteridae, classified within Velatida by Blake (1996), or within Spinulosida, a group that includes the Velatida *sensu* Gale (2011a). *Protremaster universalis*, initially described as an asterinid (Smith & Tranter 1985), may represent a stem-group Spinulosida and/or Velatida (Gale 2011a, 2013). The definition and phylogenetic posi- tion of Velatida and Spinulosida have been intensively debated. Conservatively, we consider the clade associated with *T. pectinatus* and *P. universalis* to represent the stem-group Velatida. There is no crown-group Velatida in our phylogenetic analysis, and the oldest unambiguous fossil occurrence of the crown group is recorded by the Late Jurassic *Savignaster wardi* (Gale 2011a, b).

Plesiosolaster moretonis is a multiarmed starfish char- acterized by strongly developed and keeled oral plates. Despite a higher number of arms, typically bulbous spine bases, and a lack of typical paxillar marginal and abactinal plates, Blake (1993) classified *P. moretonis* within the extant Solasteridae, a hypothesis followed by Gale (2011a). Blake (1993) recognized some similarities with the multiarmed Heliasteridae in the reticulated skeleton within the disc, the shape of the adambulacral plates, and the high number of arms. However, Heliasteridae belongs to Forcipulatacea and has distinct ambulacral and oral plates. The phylogenetic position of *P. moretonis* thus remains unclear. It likely represents a distinct clade of multiarmed starfishes emerging during the Mesozoic radi- ation that has no modern allies (Gale 2013).

Germanasterias amplipapularia and *Argoviaster occultus* are two species assigned to the extant family Asteriidae. They support a clade Forcipulatacea (Hess 1972; Blake 1990). However, *G. amplipapularia* together with several other Early Jurassic taxa displays distinctive pedicellariae and plate arrangement in the arms (Gale & Villier 2013). Further research is needed to determine whether they represent stem-group Asteriidae or a distinct clade of Asteriidae restricted to the Jurassic. The position of *Trichasteropsis weismanni* as a sister taxon to the Asteriidae is consistent with its interpretation as basal within Forcipulatacea (Blake & Hagdorn 2003). The interpretation of other Triassic species assigned to *Trichasteropsis* or to Trichasteropsiidae has been debated as they may not belong to a single clade (Gale 2011a; Blake & Mah 2014).

Advenaster inermis, *Pentasteria kelleri*, *Noviaster poly- plax* and *Comptoniaster basseti* are traditionally assigned to Astropectinidae and Goniasteridae. Proximity between the two families within the Valvatacea is assumed by some morphological and molecular phylogenies (Blake &

Hagdorn 2003; Blake 2010; Mah & Foltz 2011a). A basal position for Paxillosida, as favoured by Gale (1987, 2011a), is not seen in our results (Fig. 7). Most described Mesozoic species belong to Astropectinidae and Goniasteridae, some with very distinct character combinations. A dedicated phylogenetic analysis would be necessary to test for their relationships and their link with extant taxa.

The large sister clade to the Forcipulatacea includes only species considered to be Valvatacea, with the exception of the Palaeozoic *Compsaster formosus*. *Carniaster orchardi* has been assigned to Valvatacea (Blake & Zon- neveld 2004), but the poor preservation of the single avail- able fossil precludes a more precise taxonomic assignment. *Noriaster barberoi* may be a poraniid (Blake *et al*. 2000b), although it does not share all apomorphies with modern taxa of this family.

Our phylogenetic results for the crown group suggest an early separation of the main modern clades during the Triassic and the Jurassic, which was predicted by the phylogenetic analyses of living taxa. The Velatida, Valvatacea and Forcipulatacea are here recognized, although none of the Triassic or Jurassic taxa possesses all of the synapomorphies characterizing their living relatives. Many early Mesozoic taxa assigned to modern families may represent at best stem groups. Consequently, the post-Palaeozoic diversification of the crown group provides evidence of clades that did not survive to the Recent.

Incidentally, we note that the most parsimonious topology (Velatida (Forcipulatida C Valvatacea)) recovered here for Neoasteroidea from fossil-based morphological data, while incongruent with those proposed by Blake (1987) and Gale (1987, 2011a), closely matches the molecular phylogenetic hypothesis most recently pro- posed by Janies *et al*. (2011) and Feuda & Smith (2015), both consistently pointing towards the scenario (Velatida (Forcipulatida (Spinulosida C Valvatida C Paxillosida))). Even if not conclusive, such congruence is all the more remarkable in that it results from totally different data sets without any terminal taxon in common. It suggests that, based on available morphological and molecular evidence, the integration of *Superstesaster promissor* in our morphological data set may allow for the correct interpre- tation of the primitive morphological conditions for Neo-asteroidea, ultimately resulting in a stable identification of cladistic relationships between the main neoasteroidean clades.

Phylogenetic position of *Compsaster formosus*

The consistent nesting of *Compsaster formosus* within the crown group is an unexpected result, because it does not share all synapomorphies of the ambulacral plates of the crown group. Ambulacral plates of *C. formosus* look much more robust and bar-like, and lack differentia- tion of the ambulacral base (Blake 2002). Its position in the tree is supported by similarities of the external aspect of the adambulacral plates, and highly homoplastic characters of the body shape and arrangement of the abac- tinal skeleton. All of these characters were recognized by Blake (2002) as adaptive convergences with living Forcipulatacea.

Blake *et al*. (2000a) explored the possibility that *Compsaster formosus* represented a good outgroup for rooting the crown group, but settled on the use of a theo- retical ancestor and *Devonaster* as outgroups. A later phy- logenetic analysis (Blake & Hagdorn 2003) indicated that *C. formosus* is the sister clade to the crown group, branching just above *Calliasterella americana*. The unstable position of *C. formosus* after all attempts to determine its phylogenetic position illustrates the difficulty of properly recognizing homologies in the complex morphology of the taxon. For example, the Middle Jurassic *Uraster spiniger* Wright, 1880 was assigned by Spencer & Wright (1966) to *Compsaster*, despite an axial skeleton typical of the Forcipulatida (Blake 2002). The position of *C. formosus* within the crown group would totally challenge our understanding of character evolution through the fossil record, otherwise fully consistent with a post-Palaeozoic radiation of the crown group. The position of *C. formosus* is thus interpreted to be a consequence of the inadequacy of our character set to recover its true place within Palaeozoic taxa.

Status of Calliasterellidae

Several taxa have been assigned historically to Calliasterellidae, most of which assume very different definitions for this family. Spencer & Wright (1966) considered the body construction to offer the most relevant characters: a small disc with enlarged primary radials, long slender arms, and a prominent transverse ridge on the adambulacral plates, the other plates of the arm also bearing a median ridge. Following this definition, the Calliasterellidae include:

Arthraster Spencer, 1918, which is a very distinctive Cretaceous member of the crown group, with small tall, adambulacral plates, and hourglass-shaped ambulacral plates;

Protarthraster Spencer, 1918, similar to *Arthraster* in arm construction but clearly distinct in the plating of the cen- tral disc, and, more importantly, in the development of the adambulacral (wide and compressed) and ambulacral plates (block-like and facing the adambulacral plates) that are typical of the Palaeozoic aspect;

Calliasterella Schuchert, 1915 which defines the family and is characterized by arm enrolment towards the oral side (Spencer & Wright 1966);

Silicaster Kesling, 1969, which is a Devonian genus assigned to Calliasterellidae based on the arm structure limited to adambulacrals, one row of marginal and one row of carinal plates. The shapes of the ambulacral plates remain unknown, but are necessary to discuss its relationships with *Calliasterella* (Blake & Elliott 2003). It is, however, distinguished by cross-shaped carinal and club-shaped marginal plates, leaving wide spaces between the arm plates.

Calliasterella shares several characters with Neopalaeasteridae (Blake & Elliott 2003), including the small disk, elongate arms, a single row of marginal plates contributing to the body margin, the development of an axillary, and a reduced number of plate rows contributing to the arm structure. Following the obtained tree topology (Fig. 7), all of these characters represent plesiomorphies of the Calliasterellidae, and no longer support its monophyly.
Both *Athraster* and *Protarthraster* are easily distinguished from *Calliasterella* and can be excluded from the Calliasterellidae (Blake & Elliott 2003). Although *Silicaster* has the same number of plate rows in the arms, it clearly differs from *Calliasterella* in the shape of all described arm plate types. Its delicate dorsal plates and the shape of its adambulacral plates look rather similar to those of *Delicaster*, a stem-ward taxon.

The two species usually assigned to *Calliasterella* are not associated in a clade (Fig. 7), but they are arranged in a pectinate way. The genus is thus paraphyletic and requires a taxonomic reappraisal, as already stressed by Blake & Elliot (2003) and Gale (2011a). The name *Calliasterella* was given by Schuchert (1915) as a replacement for *Calliaster* Trautschold, 1879, a homonym of a very distinct living starfish (*Calliaster* Gray, 1840). *Calliaster mirus* Trautschold, 1879 was designated as the type species and must retain the name *Calliasterella mira*. The name *Calliasterella* was extended by Kesling & Strimple (1966) to include *Calliasterella americana*, a species from the Pennsylvanian of Illinois. *Calliasterella americana* belongs to a single genus of Asteroidea together with the nominal *Onychaster confragosus* Miller, 1891, *O. demissus* Miller, 1891, *Calyptactis spenceri* Chestnut & Ettensohn, 1988, and potentially *Protaster perarmatus* Whidborne, 1896 (Chesnutt & Ettensohn 1988; Jell 1997; Blake & Elliot 2003). The names *Calliasterella* and *Onychaster* are not available because they are associated with distinct clades (the type species of *Onychaster* is an ophiuroid). The type species of *Calyptactis*, *C. spinosus* Spencer, 1930, was alternatively considered an asteroid (Jell 1997) or an ophiuroid (Blake 2002; Blake & Elliot 2003). Pending a thorough revision and reassessment of *C. spinosus*, it remains unclear whether the erection of a new genus name is required for *C. americana*.

Status of Trichasteropsida

Several starfish species from the Middle Triassic (Muschelkalk) formations of Germany were grouped in the family Trichasteropsidae by Blake (1987). Three gen- era have been described as trichasteropsid sea stars: *Trichasteropsis*, *Berckhemeraster* and *Migmaster* (Blake & Hagdorn 2003; Blake *et al*. 2006). Trichasteropsidae are assumed to be a monophyletic group rooted

within basal forcipulataceans (Blake & Mah 2014). Gale (2011a) highlighted the diversity of morphological features expressed by the three genera and challenged the validity of Trichasteropsidae as a natural group, without offering an alternative hypothesis.

Trichasteropsis is understood to be a basal member of the forcipulataceans (Blake 1987; Blake & Hagdorn 2003). This assignment is grounded on the characters shown primarily by *Trichasteropsis weismanni*: a reticulate dorsal skeleton, including rod-like elements, a so-called adoral carina, and the structure of the ambulacral grooves with alternating carinate and non-carinate adambulacral plates.

With the exception of *Neomorphaster* and several Zoroasteridae, all forcipulataceans have a reticulate dorsal skeleton. The rod-like elements of the dorsal skeleton are shared by most Asteriidae, Pedicellasteridae and Brisingida; they could be considered a valuable character to infer relationships. However, many other groups of liv- ing starfishes have a reticulate skeleton, and Gale (2011a) suggested that it may not be a good character to support a phylogenetic assignment to the forcipulataceans. Only two trichasteropsid species have been described with a reticulate dorsal skeleton: *Trichasteropsis weissmanni* and *T. senfti*.

Although assumed to be present by Blake & Hagdorn (2003), the occurrence of an adoral carina remains unclear in trichasteropsids. Only the first adambulacral plates potentially abut interradially in *Trichasteropsis weiss- manni*, *T. senfti* and *T. bielertorum*, the other adambulacral plates being clearly separated by actinolateral plates (Blake & Hagdorn 2003, figs 1G, 3C; Blake *et al*. 2006, fig. 5F). Adambulacral plates are all separated by actinolateral plates in *Berckhemeraster charistikos* and the holotype of *Migmaster angularis*. All observed patterns fail to fit with the definition of an adoral carina used in our character coding.

The alternating pattern of carinate and non-carinate adambulacral plates is described only for *Trichasteropsis weissmanni*, in which it is restricted to the proximal half of the arm, the distal adambulacral plates becoming enlarged and losing their pattern of alternation. By comparison with the living Zoroasteridae, Blake & Hagdorn (2003) suggested four rows of tube feet to be present in *T. weissmanni*, despite the lack of a clear ambulacral differentiation. The other taxa assigned to the trichasteropsids have a more robust construction of the ambulacral column.

The lack of strict synapomorphies in the Forcipulatacea challenges the attribution of the trichasteropsid genera to this family (Gale 2011a). In our tree, *Trichasteropsis weissmanni* branches as a sister group to the asteriids; a position at the base of Forcipulatacea is likely. The morphology of *Berckhemeraster* is not sufficiently understood for a definitive statement, but it lacks some of the usual forcipulatacean characters. *Migmaster angularis* was defined from a holotype of 'large size' and three smaller paratypes. Differences in the development of the marginal plates – uniform and tabular in the paratypes and enlarged distally and developing an abradial tip in the holotype – are assumed to be related to ontogenetic changes (Blake *et al*. 2006). Gale (2011a) recognized additional morpho- logical differences between the holotype and the para- types and suggested their segregation into two distinct taxa. Gale (2011a) even proposed a new family name to accommodate the original character combination of *Migmaster*. Blake & Mah (2014) reiterated the initial descrip- tion and taxonomic interpretation of Blake *et al*. (2006). Our understanding of *Migmaster* is closer to that of Gale (2011a). The paratypes range from 6 to 16 mm in diameter and develop short triangular arms. They have two rows of plates on the body margin that face each other, from the interradius to the terminal plate (Fig. 9). Such a configura- tion is illustrative of two rows of marginal plates rather than one row of marginal and one row of actinolateral plates. The adambulacral plates are relatively narrow (as wide as long) and more numerous than the marginal plates. The actinolateral field is limited to the disc and includes only a few plates. An enlarged plate is located in the interradius, close to or associated with the inferomar- ginal frame. It is described as an 'axillary-like ossicle' in Blake *et al*. (2006); potential homology with the axillary of Palaeozoic forms and the unpaired interradial plates occurring in Poraniidae remains unclear. The holotype reaches 43 mm in diameter, with triangular arms. The number of marginal plate rows remains uncertain as only the oral side is exposed. The inferomarginal plates are small and block-like in the interradius, becoming larger, wider, lower, and diamond shaped in the mid-part of the arm. The inferomarginal plates are smaller and more block-like near the arm tip. The adambulacral plates are compressed, about two times wider than long, especially near the arm base. The actinolateral

field is limited to the disc and the proximal half of the arm. Occurrence of an unpaired enlarged 'axillary-like ossicle' in the interradius is assumed, but it does not seem connected to the marginal frame. Of the character set available for the paratypes and the holotype, very few can be directly assumed to be similar. In the absence of intermediate ontogenetic stages, the discrimination between one taxon for the holotype and a second for the paratypes may be the most pragmatic interpretation.

The problem with recognition of ancestral conditions

Selection of taxa and rooting of the tree are key issues for resolving phylogenies (Philippe *et al*. 2011). These issues are all the more critical for starfishes because the phylogeny of the group is highly influenced by outgroup choice. When working with molecular data, the only available taxa for identification of the basal conditions are ophiuroids, echinoids and holothuroids. These later groups have been separated from starfishes at least since the early Ordovician (Blake 2013). Therefore, a minimum of 960 million years of independent evolution between the living ingroup and outgroup taxa must result in spurious long-branch attractions leading to difficulty in properly resolving the trees. Echinoderms were severely affected during the Permian–Triassic mass extinction (Twitchett & Oji 2005), whereas the ancestor of the crown-group star- fishes is expected to have arisen in the Permian or Early Triassic (Gale 2011a; Mah & Blake 2012). Several groups of echinoids, ophiuroids and asteroids are restricted to the Triassic, which also suggests a significant depletion of their taxonomic richness at the Triassic–Jurassic transition. Modern clades thus arose during the Late Triassic and/or Early Jurassic times. This relatively brief interval of clade differentiation and successive bottlenecks would imply a limited phylogenetic signal for resolution of the internal nodes of the tree. This is consistent with the short branches or unresolved basal nodes reported in the molec- ular trees of starfishes (Mah & Folz 2011a, b; Mah & Blake 2012).

Similar sampling and rooting issues likely explain most of the inconsistency of morphology-based phylogenies of the Neoasteroidea. Considering their close relationships to the crown group, *Calliasterella mira*, *C. americana* and *C. formosus* have been alternatively used to root phyloge- netic analyses of the crown group (Gale 1987, 2011a; Blake & Hagdorn 2003). Blake (1987) even tentatively assigned *C. americana* to the crown group, before definitively rejecting this hypothesis (Blake & Hagdorn 2003). Our newly proposed phylogenetic scheme, including all Late Palaeozoic candidates for sister taxa to the crown group, is consistent with morphological and molecular-based phylogenies proposed in the literature. However, the tree topologies supported by the works of Blake (1987), Blake & Hagdorn (2003) and Gale (1987, 2011a) can be generated from our data set by simply modifying the sampling of stem groups. These unstable topologies clearly call for extended character sets, and the disentangling of unclear homologies. The comparative anatomy of skeletal plate types (Blake 1973, 1976; Gale 2011a) also generates a significant increase in the number of characters.

Conclusions

The new Early Triassic starfish *Superstesaster promissor* gen. et sp. nov. (Utah, USA) morphologically resembles Carboniferous species traditionally assigned to Neopalaeasteridae and Calliasterellidae. However, the ambulacral and adambulacral plates are typical of post-Palaeozoic starfishes. Phylogenetic analysis places *S. promissor* as the sister group of the crown-group Neoasteroidea. Thus, it represents the first report of a stem-group member of Neoasteroidea from the Mesozoic. Available data suggest that *S. promissor* is morphologically close to the hypothetical ancestor of the crown group, and that Palaeozoic relatives are rooted near the calliasterelids. The Early Triassic age of *S. promissor* supports a strong bottleneck in starfish diversity at the end of the Permian, followed by a rapid Mesozoic radiation of the crown group.

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Supplemental material

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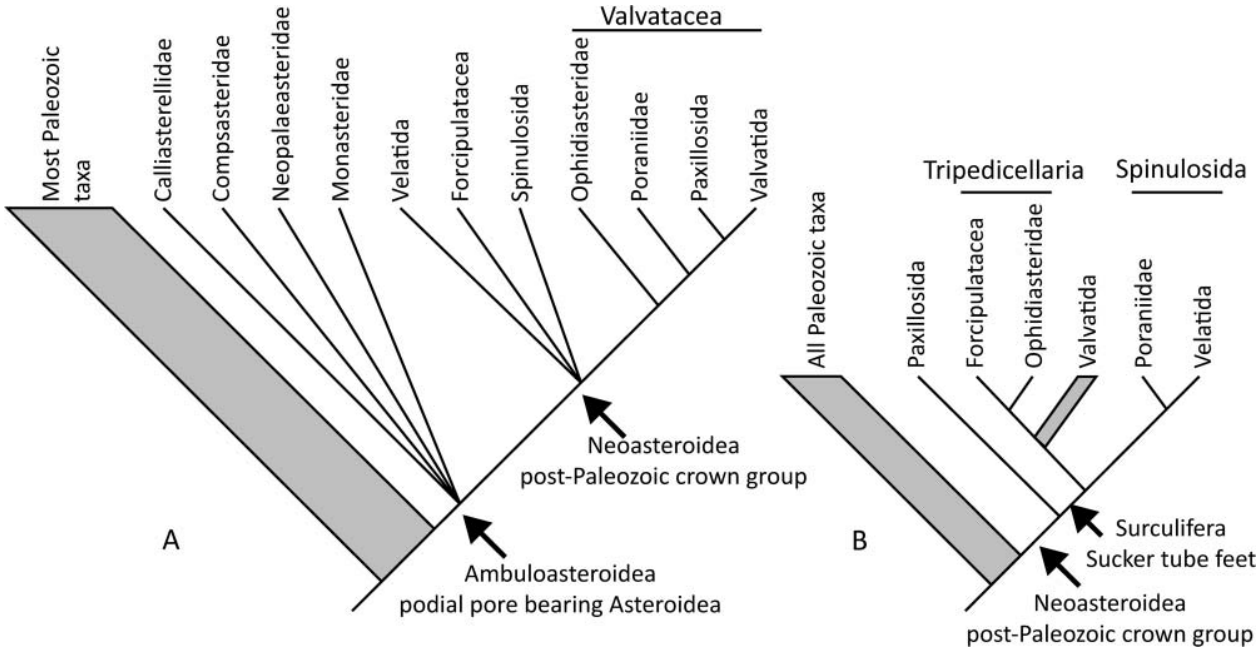


Figure 1. Example of conflicting phylogenies of the Asteroidea. A, tree redrawn from Mah & Blake (2012), with the addition of some relevant Palaeozoic taxa and deletion of some extant groups lacking a fossil record; B, alternative hypothesis for the relationships within the crown group, redrawn and simplified from Gale (2011a). Note that the two alternative hypotheses interpret Valvatida and Spinulo- sida with very different definitions and inclusiveness. Paraphyletic groups are shown as grey bars.

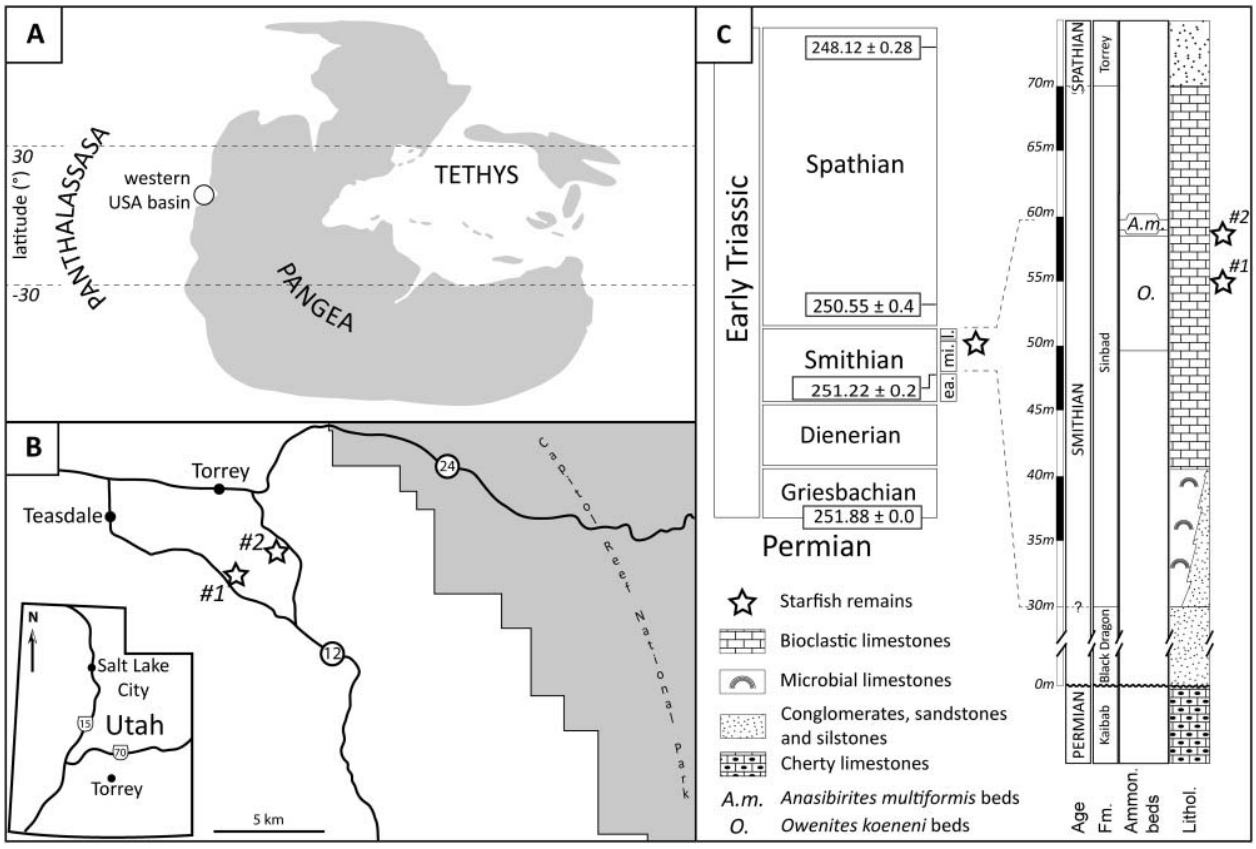


Figure 2. Geological setting. A, palaeogeographical location of the western USA basin during the Early Triassic; B, present-day loca- tion of the studied sections in the Torrey area; C, synthetic lithological succession of the Torrey area (see Olivier *et al*. 2016 for details), with position of the starfish remains. Ammonoid zonation after Brayard *et al*. (2013) and Jattiot *et al*. (2016). Abbreviations: ea., early; mi., middle; l., late.

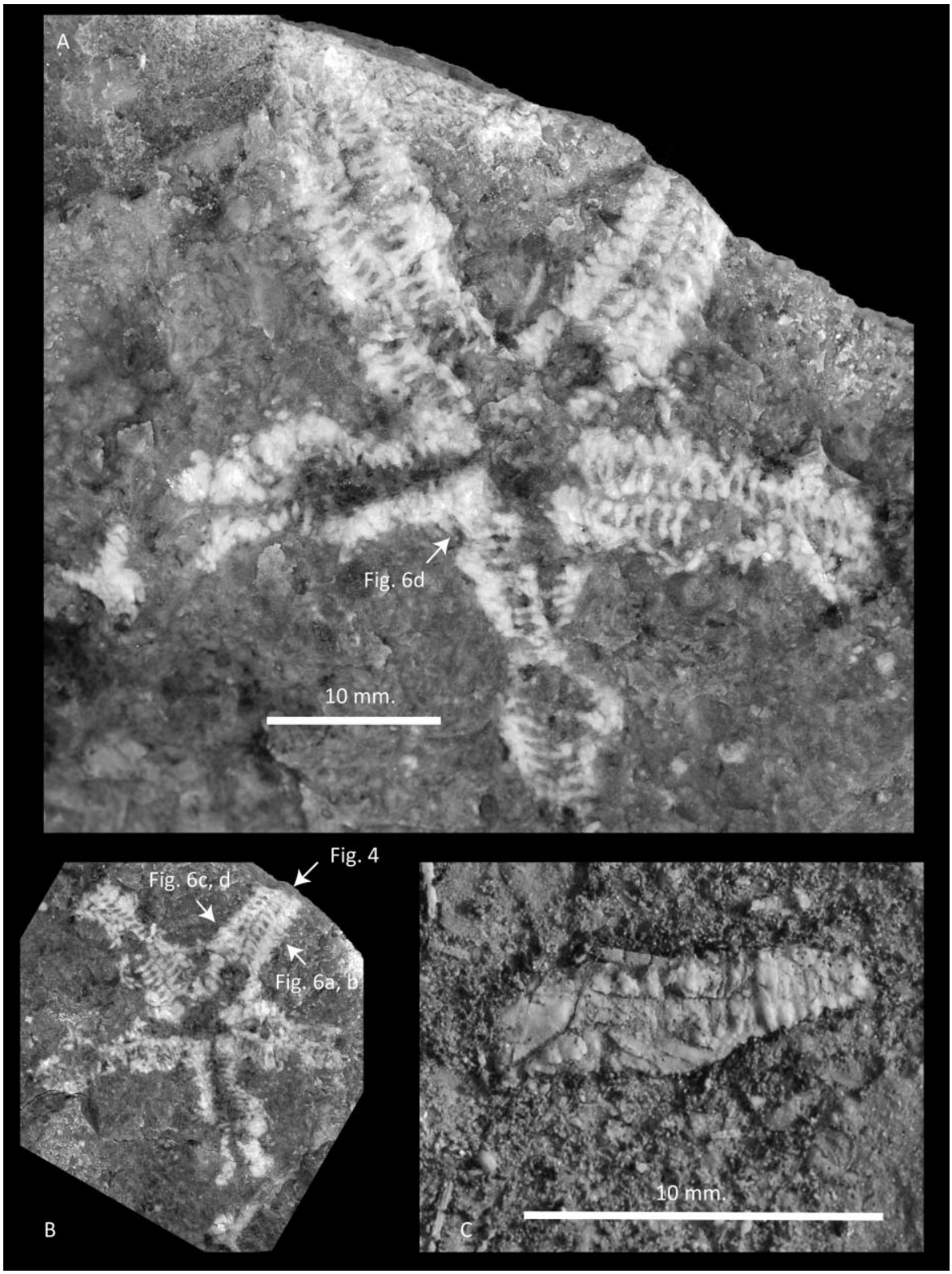


Figure 3. *Superstesaster promissor* gen. et sp. nov., Sinbad Formation, late middle Smithian (Early Triassic) of Torrey area, Utah, USA. Overall views of the three available specimens. A, B, holotype, UBGD 30578, Site 1, both sides of the slab that cleaved within the plane of the starfish body; A, section with an aboral view; B, section with an adoral view. C, paratype, UBGD 30579, Site 2, arm tip fragment, partially recrystallized. Arrows indicate the location of the close-ups shown in Figures 4 and 6.

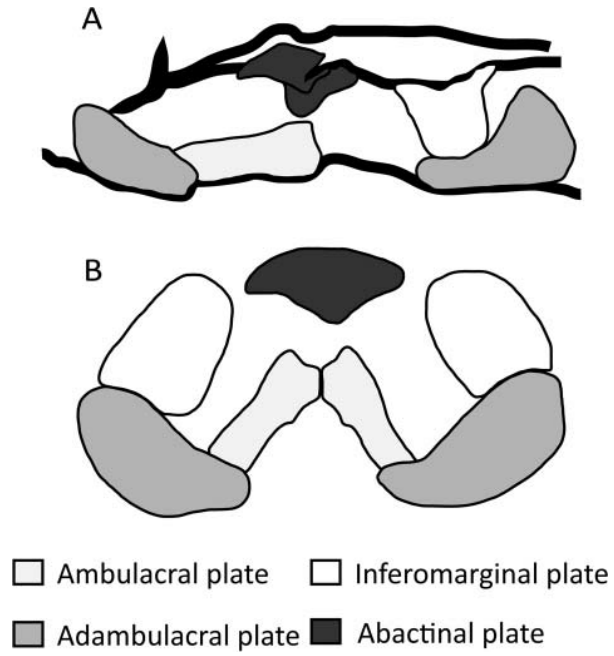


Figure 4. *Superstesaster promissor* gen. et sp. nov., structure of the arm in cross section. A, line drawing and interpretation of the cross section of the arm as it appears at the slab border of the holotype, UBGD 30578; B, reconstruction of the arm cross section.

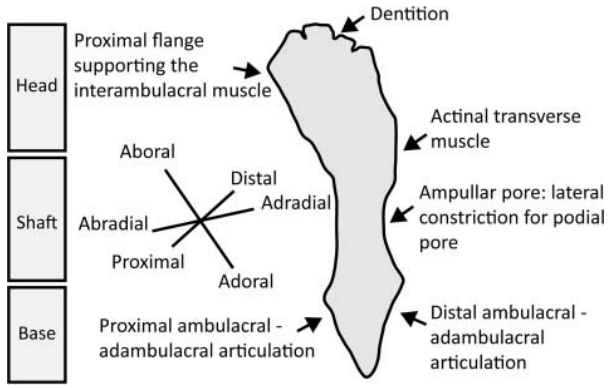


Figure 5. *Superstesaster promissor* gen. et sp. nov., line draw- ing and anatomical interpretation of one of the better preserved ambulacral plates. Note that the oblical section plane allows rec- ognition of most articulation processes. The three anatomical axes are sketched to illustrate the initial orientation of the cross section.

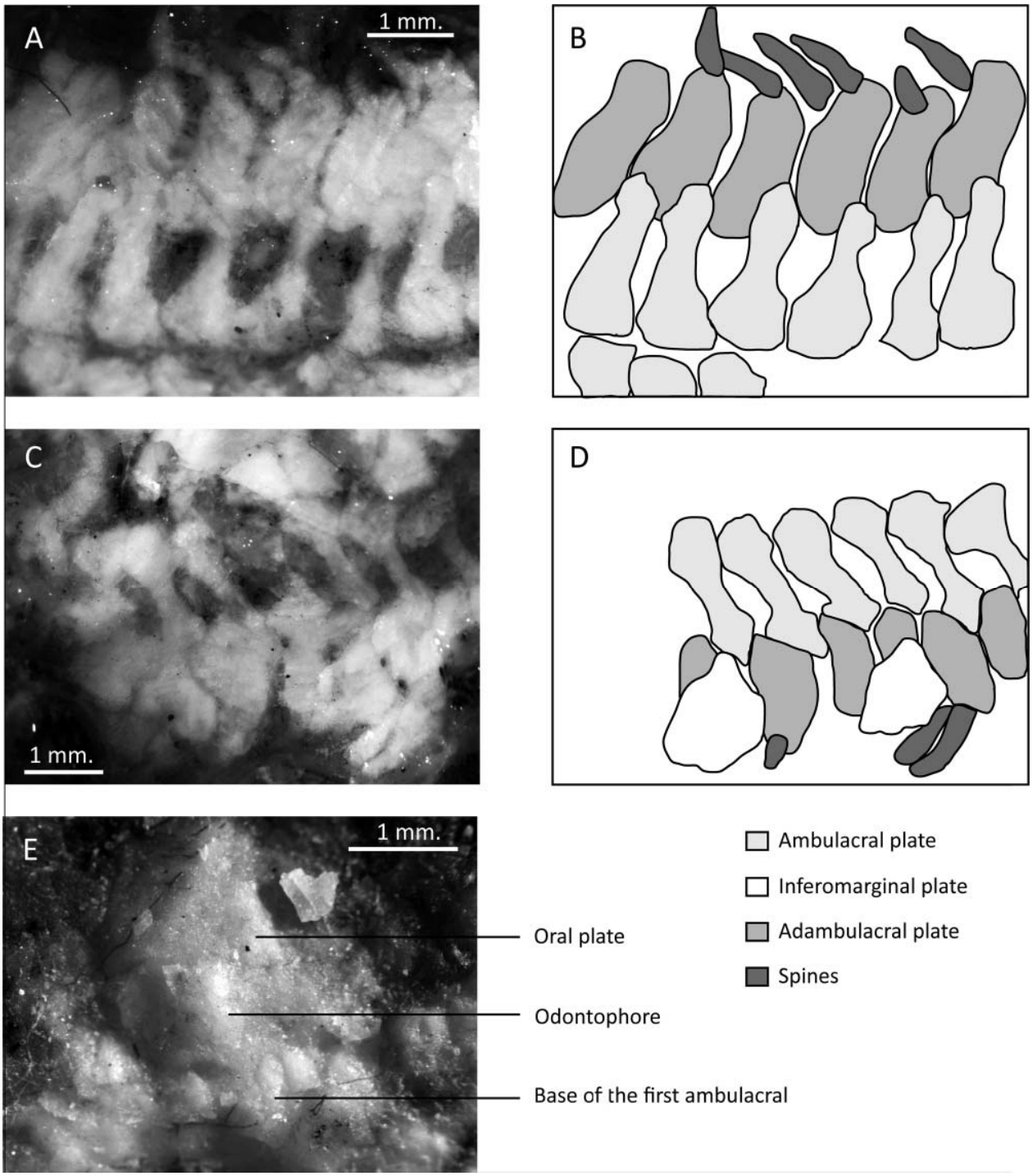


Figure 6. *Superstesaster promissor* gen. et sp. nov., details of the anatomy of the holotype, UBGD 30578, with photographs on the left side and partial interpretations on the right. A, B, details of an arm showing the articulation of the ambulacral plates along the radius, ambulacral/adambulacral plate articulations and the orientation of adambulacral spines; C, D, details of an arm showing the ambulacral/ adambulacral plate articulations and the relationship between adambulacral and inferomarginal plate rows; E, details of the oral frame showing the proximal contact on adambulacral, ambulacral and oral plates, and the insertion of odontophore between the adjoining oral plates. The calcite recrystallization and fracture planes prevent a clear delineation of individual skeletal plates from being drawn.

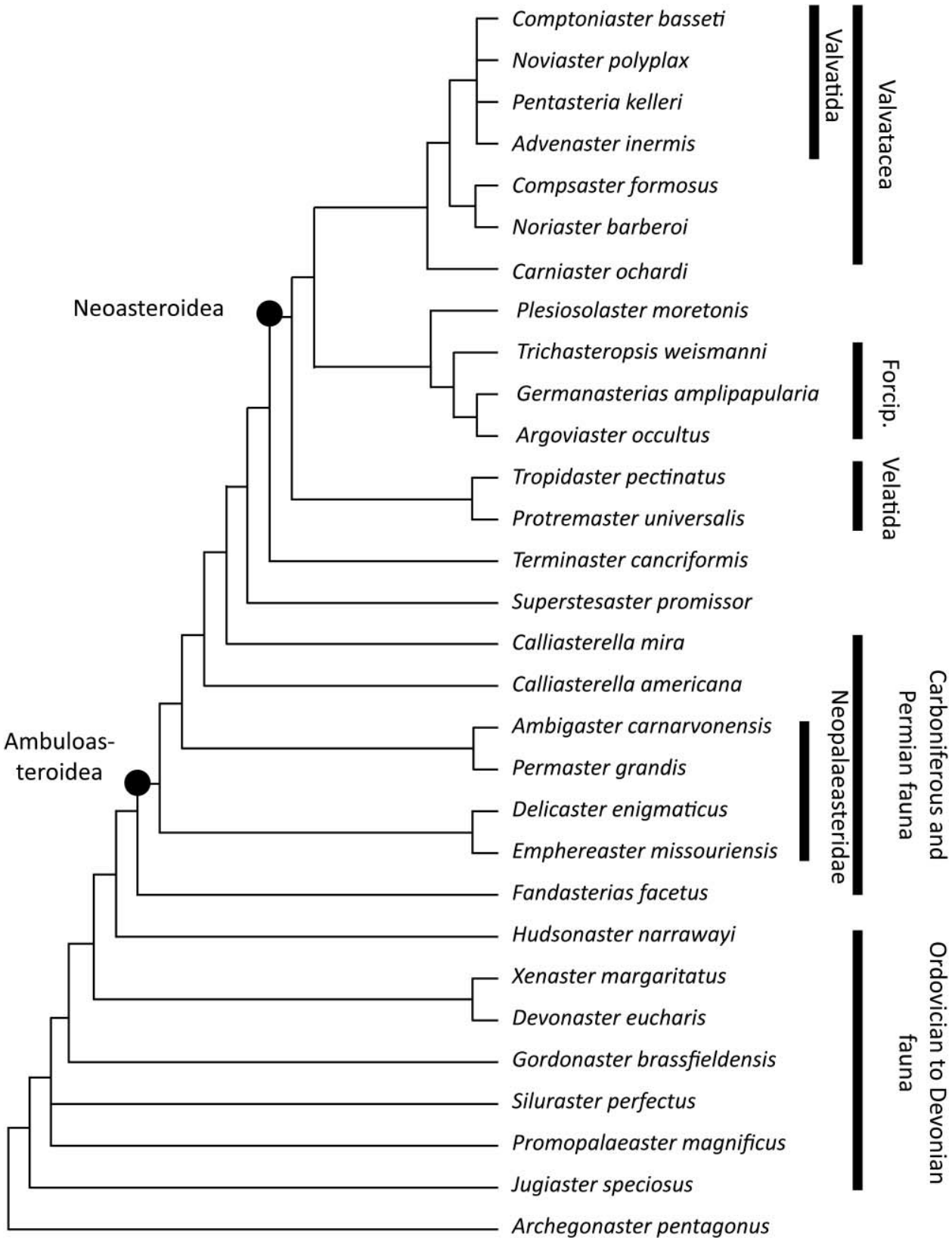


Figure 7. Strict consensus tree of the five most parsimonious trees (235 steps length, retention index (RI) D 0.658) obtained after a heuristic search with PAUP.

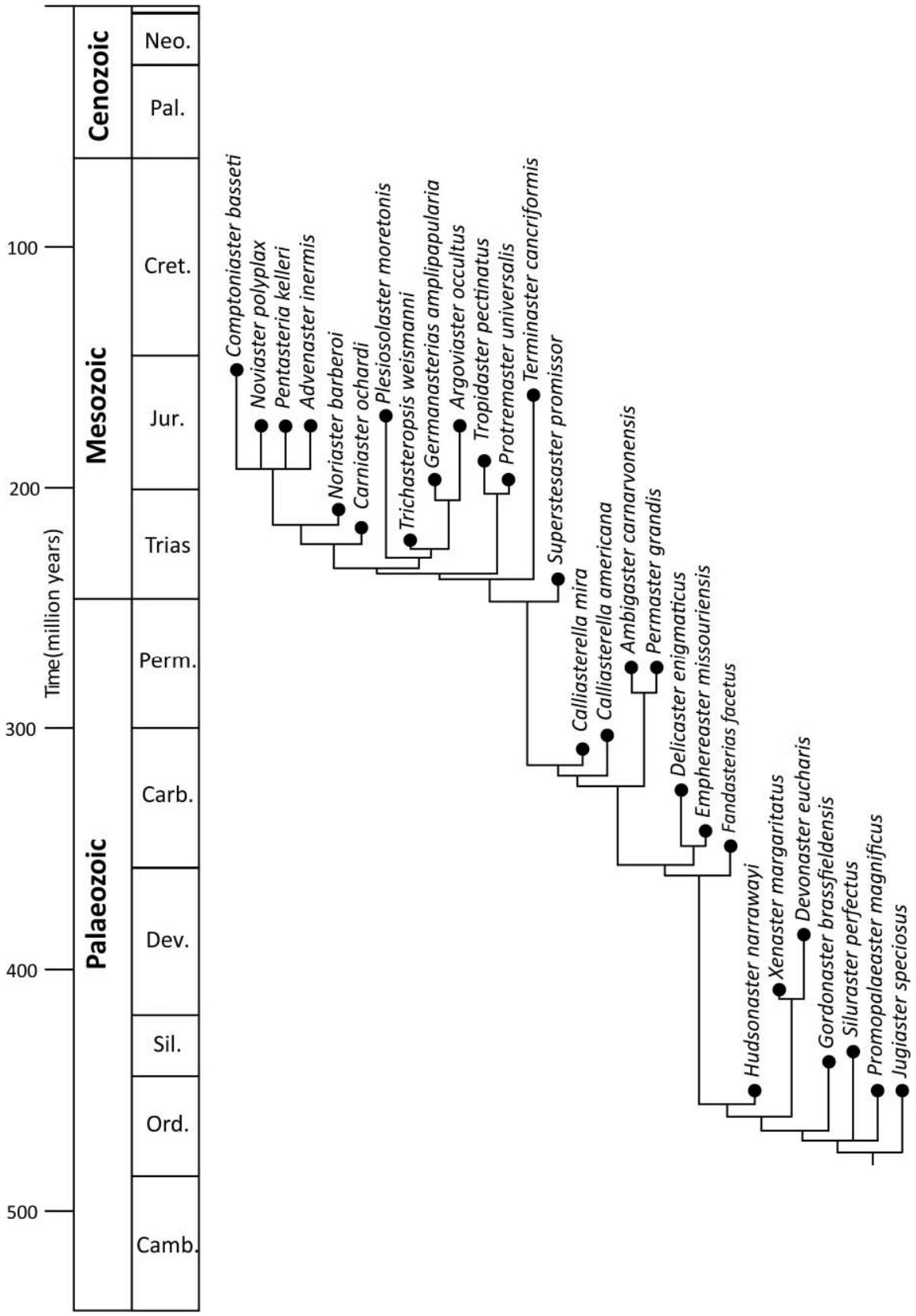


Figure 8. Phylogenetic tree calibrated according to fossil ages. *Compsaster formosus* is excluded due to its inaccurate position in the tree which would significantly increase the length of ghost lineages.

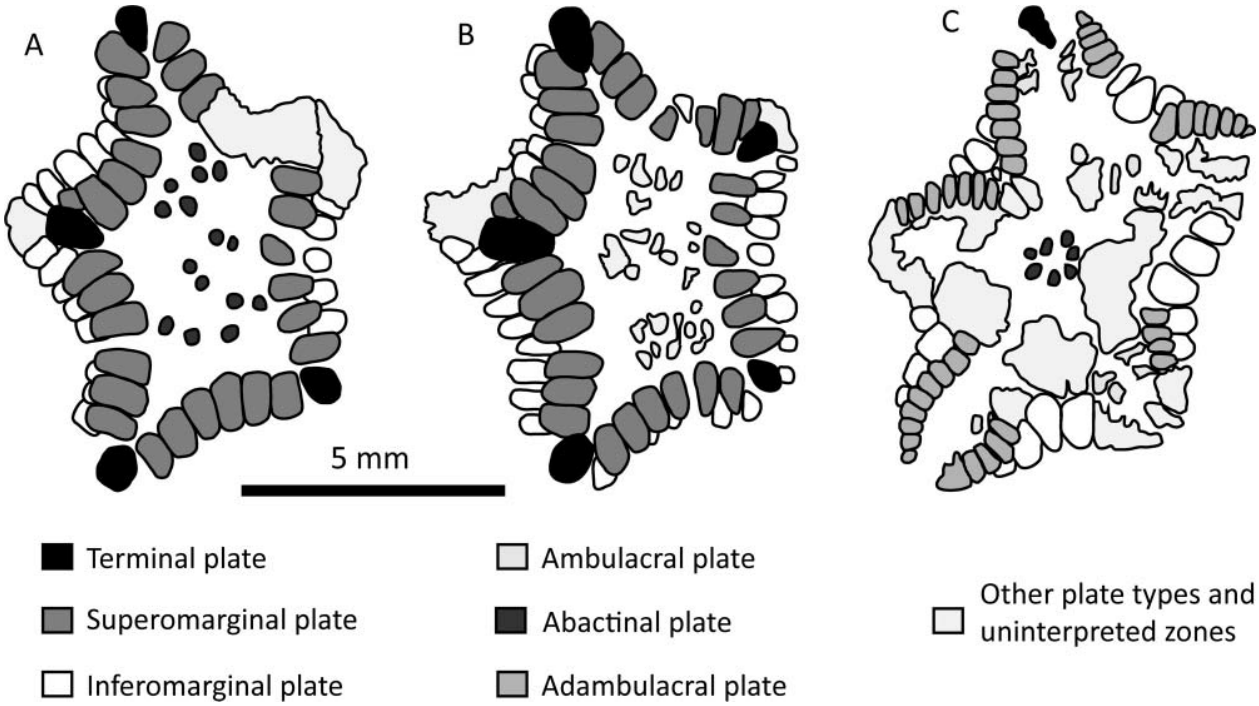


Figure 9. Interpretation of plate homologies in the paratypes of *Migmaster angularis*, MHI 1808 (Muschelkalkmuseum Ingelfingen), Herberhausen Quarry, Anisian, Middle Triassic. A, actinal view in reflected light (based on Blake *et al*. 2006, fig. 3C); B, abactinal view (based on Blake *et al*. 2006, fig. 3F); C, abactinal view in reflected light (based on Blake *et al*. 2006, fig. 3D).