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The Cambrian Substrate Revolution and the early evolution of attachment in suspension-feeding echinoderms

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ABSTRACT

The Cambrian, characterized by the global appearance of diverse biomineralized metazoans in the fossil record for the first time, represents a pivotal point in the history of life. This period also documents a major change in the nature of the sea floor: Neoproterozoic-type substrates stabilized by microbial mats were replaced by unconsolidated soft substrates with a well-developed mixed layer. The effect of this transition on the ecology and evolution of benthic metazoans is termed the Cambrian Substrate Revolution (CSR), and this is thought to have impacted greatly on early suspension-feeding echinoderms in particular. According to this paradigm, most echinoderms rested directly on non-bioturbated soft substrates as sediment attachers and stickers during the Cambrian Epoch 2. As the substrates became increasingly disturbed by burrowing, forming a progressively thickening mixed layer, echinoderms developed new strategies for attaching to firm and hard substrates. To test this model, we evaluated the mode of attachment of 83 Cambrian suspension-feeding echinoderm species; attachment mode was inferred based on direct evidence in fossil specimens and interpretations of functional morphology. These data were analyzed quantitatively to explore trends in attachment throughout the Cambrian. In contrast to previous studies, the majority of Cambrian clades (eocrinoids, helicoplacoids, helicocystoids, isorophid edrioasteroids, and solutes) are now interpreted as hard (shelly) substrate attachers. Only early edrioasteroids attached directly to firm substrates stabilized by microbially induced sedimentary structures. Contrary to the predictions of the CSR paradigm, our study demonstrates that Cambrian echinoderms were morphologically pre-adapted to the substrate changes that occurred during the Cambrian, allowing them to fully exploit the appearance of hardgrounds in the Furongian. We find no support for the claim that the CSR explains the peak in echinoderm diversity during Cambrian Epochs 2–3, or that it caused the extinction of helicoplacoids.

Keywords: palaeoecology, evolution, seafloor, attachment

1. Introduction

The Cambrian fossil record documents a time span of profound change, epitomized by the appearance of abundant remains of biomineralized metazoans for the first time in Earth’s history: the Cambrian ‘Explosion’. Additionally, a diversification of ichnofossils is preserved in sedimentary rocks from the latest Ediacaran times, as a result of which a major shift in mat preservation occurred with the evolution of metazoan grazers in the Cambrian. Thus, extensive sediment colonisation with a potential for preservation in the rock record was severely curtailed (Schieber et al., 2007).

It has been suggested that the increase in bioturbation depth and intensity led to a shift from Proterozoic-style soft substrates stabilized by microbial mat encrustation to Phanerozoic-style unconsolidated soft substrates with a well-developed mixed layer (Droser and Bottjer, 1988; Droser et al., 1999; Seilacher, 1999). This transition is widely thought to have had a major impact on the ecology and evolution of many non-burrowing benthic metazoans, an event which is referred to as the Cambrian Substrate Revolution (CSR) (Bottjer et al., 2000; Bottjer, 2010).

Echinoderms are one of the metazoan groups that have been most strongly associated with the CSR. Previous work has hypothesized that the majority of early suspension-feeding echinoderms (during Cambrian Epochs 2–3) lived as sediment attachers or shallow sediment stickers in largely unburrowed substrates stabilized by microbial mats, whereas later forms (during Furongian to Carboniferous times) were restricted to attachment on hard substrates (Dornbos, 2006). Building on this idea, the CSR has been proposed as an explanation for the diversification of morphological structures associated with substrate attachment in echinoderms (Bottjer, et al., 2000; Dornbos, 2006; Domke and Dornbos, 2010), the relatively high diversity of echinoderms during Cambrian Epochs 2–3 (Nardin and Lefebvre, 2010), and the extinction of certain groups (e.g., helicoplacoids) by the end of this period (Dornbos and Bottjer, 2000, 2001).

However, recent reviews of the global distribution of microbially induced sedimentary structures (MISS) demonstrate that microbial mats and biofilms had a fairly continuous and widespread record across the Ediacaran–Cambrian transition (Schieber et al., 2007; Álvaro et al., 2013; Davies et al., 2016), arguing against the claim (e.g., Bottjer et al., 2000) that they were more common in the Precambrian. Another criticism arises from recent studies on sedimentary structures formed close to the sediment/water interface and ichnofossil assemblages across the Ediacaran–Cambrian transition, which suggest that infaunal mixing remained suppressed throughout this interval (Droser et al., 2004; Tarhan and Droser, 2014) and limited until at least the late Silurian (Tarhan et al., 2015). There was an increase in ichnofossil diversity throughout the Terreneuvian and Cambrian Epoch 2, and the majority of ichnogenera had appeared by the latter, coinciding with the appearance of trilobites, one of the main taxa that disturbed the sediment. In the Terreneuvian, nearly all of the ichnofossils were emplaced in firmgrounds. Cohesive sediment close to the sediment/water interface may explain the rich Cambrian record of well-preserved marine ichnofossils.

These arguments raise the question as to whether there is a close association between attachment strategy in early suspension-feeding echinoderms and the prevalence of microbial mats, as previously hypothesized (Dornbos and Bottjer, 2000; Dornbos, 2006). In order to test if early echinoderms exhibited an evolutionary response to changes in substrates during the Cambrian, we have revised the interpretation of the mode of attachment for all known Cambrian suspension-feeding echinoderms based on an updated version of the dataset from Zamora et al. (2013a). We have incorporated new direct evidence of echinoderms attached to the substrate, as well as rigorous interpretations of attachment structures. The results provide a clear picture of how echinoderms interacted with the substrate during this critical time span in their early evolutionary history.

2. Material and methods

A total of 83 species belonging to six major groups of Cambrian suspension-feeding echinoderms were analyzed (Appendix A). These include edrioasteroids (Fig. 1A), eocrinoids (Fig. 1D), helicocystoids (Fig. 1C), helicoplacoids, and some early rhombiferans. We also included solutes or homoiosteleans (Fig. 1B), an enigmatic group of asymmetrical echinoderms, in the analysis, although their feeding mode is debated, because some Cambrian taxa were clearly attached to the substrate in life and are thus important for our study. Taxa were studied through direct observation of articulated museum specimens, supplemented with published images. Specimens figured herein are housed in the collections of the following institutions: United States National Museum of Natural History, USA (USNM); Natural History Museum, London, UK (NHMUK); Museo de Ciencias Naturales, Zaragoza University, Spain (MPZ); Paleontological collection, University of West Bohemia (PCZCU); Paleontology Museum of Guizhou University, China (GM and GTBM); Museum of Comparative Zoology, Harvard University, USA (MCZ); Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China (NIGPAS); National Museum of Prague, Czech Republic (L); Museo Nacional de Ciencias Naturales, Madrid, Spain (MCNM); Muséum national d'histoire naturelle, Paris, France (MNHN).

Species were placed in one of the attachment categories established by Thayer (1975, 1983) and adapted by Dornbos (2006) for echinoderms, with a few modifications as explained below. These categories include: holdfast strategist (hf), hard substrate attacher (hs), iceberg strategist (is), sediment attacher (sa), sediment rester (sr), shallow sediment sticker (sss), and snowshoe strategist (sn). For the purposes of our study, which is restricted to Cambrian suspension feeders, only the categories 'hf', 'hs', 'sa', 'sss', and 'sn' were applicable. Holdfast strategists introduced part of the stem into the sediment. Hard substrate attachers fixed directly to hard substrates such as carbonate hardgrounds, shelly pavements, and isolated skeletal debris. Sediment attachers fixed directly to stabilized clayey substrates. Shallow sediment stickers partially introduced the distal part of the body into the sediment in stabilized substrates. Snowshoe strategists broadly distributed their body mass over the sediment surface in order to maintain stability (e.g., on soft substrates). All the genera included in our analysis and their modes of attachment are discussed in detail below. Out of all studied species, only 33.7% (28 taxa) provided direct evidence of attachment (i.e., individuals preserved attached to a substrate). When direct evidence was not available, interpretations based on the morphology of the attachment structure and comparisons with similar species, for which direct evidence of attachment is available, were used to assign species to a category. In this manner, 43.4% of studied species (36 taxa) were indirectly assigned a mode of attachment. Attachment was listed as unknown for the remaining 22.9% of species (19 taxa), which were excluded in subsequent analyses. Details of species and their mode of attachment are provided in Appendix A.

In addition to qualitative observations, trends in the proportion of suspension-feeding echinoderms that attached to hard substrates and the diversity of attachment strategies were examined throughout the Cambrian. This analysis included all 64 species for which a mode of attachment could be confidently assigned (Appendix A). Taxa were placed into series-level bins and (i) the proportion of the species in each bin that directly attached to hard substrates and (ii) the number of distinctive modes of attachment were calculated. For each calculation, error bars were based on 1000 bootstrap replicates. The resulting trends were examined for biases related to the taxonomic scale of study. Because variation in species definitions (i.e., lumping vs. splitting) could be particularly significant, given the inclusion of different groups of echinoderms, analyses were repeated at the genus-level. In all but one case (the Cambrian Epoch 3 edrioasteroid *Totiglobus*), the mode of attachment was consistent within genera, such that the attachment mode of a genus was simply that of its constituent species; the two species of *Totiglobus*, *T. nimius* and *T.*? *lloydi*, were left separate in the genus-level analysis based on the provisional placement of *T.*? *lloydi* into the genus by Sprinkle (1985). To further examine the robustness of the pattern and determine if a shift in group (i.e., ‘class’) diversity was influencing perceived trends, the patterns in attachment were also normalized by group. In each bin, 1000 subsamples were conducted by first randomly choosing with replacement one of the groups in the bin, then randomly selecting one of the species within that group. This method normalizes the weight of the different groups while retaining the different modes of attachment represented within them. All analyses were run using R version 3.0.3 (R Core Team, 2014).

3. Attachment strategies of Cambrian suspension-feeding echinoderms

In the following section, we discuss the mode of attachment of all the Cambrian echinoderms included in our analysis. We refer to publications that describe key specimens, as well as material housed in museum collections preserving direct evidence of the mode of attachment. This includes cases where specimens are clearly attached to a substrate; for example, some species of *Gogia* (e.g., *G. spiralis*) are found attached to trilobite sclerites (Sprinkle, 1973: plate 12, figs. 1, 2). In cases where direct evidence of attachment is not available, the mode of attachment is inferred based on secondary evidence, chiefly palaeobiological interpretations. For example, the edrioasteroid *Cambraster cannati* has never been found attached, but specimens of *Cambraster* sp. are preserved directly attached to the substrate; because both forms possess nearly identical aboral attachment surfaces, this suggests that all species of *Cambraster* were probably attached to the sediment as sediment attachers. This is also supported by environmental and morphological data suggesting that *Cambraster* attached to firm substrates in relatively high-energy environments (Zamora et al., 2013b). The modes of attachment for all taxa are summarized in Appendix A.

3.1. Helicoplacoids

Helicoplacoids have a spirally-plated, spindle- to bulb-shaped theca constructed with multiple rows of polygonal interambulacral plates and three recumbent ambulacra (Fig. 2A). The ambulacra, which form part of the body wall, consist of paired floor plates, with alternating pits for the tube feet podia, and multiple sheets of cover plates. The mouth is thought to be located on the lateral margin of the theca where the three ambulacra converge, with the anus situated at the upper pole (Durham and Caster, 1963; Paul and Smith, 1984; Sprinkle and Wilbur, 2005; Smith, 2008).

3.1.1. *Helicoplacus*, *Polyplacus*, and *Waucobella*

There are three known genera of helicoplacoids: *Helicoplacus, Polyplacus,* and *Waucobella*. Several authors have suggested that helicoplacoids attached to the substrate with their lower pole, but there is disagreement as to whether they attached to single shell fragments (Wilbur, 2004; Sprinkle and Wilbur, 2005) or directly to firm stabilized substrates (Dornbos and Bottjer, 2000, 2001; Dornbos, 2006). Sprinkle and Wilbur (2005) based their hypothesis on a single specimen of *Helicoplacus giberti* found attached to a trilobite glabella (Wilbur, 2004) (Fig. 2C). We report a second specimen of *Helicoplacus* that is preserved attached to a trilobite sclerite (Fig. 2B), which strongly suggests that helicoplacoids were attached to shell fragments in life. This is also supported by morphological arguments: helicoplacoids possess a lower pole constructed of multiple small plates that form a holdfast-type structure (Fig. 2D), which is morphologically very similar to the aboral attachment structures found in some gogiid eocrinoids that preserve direct evidence of attachment to shelly substrates (Fig. 2H). Of all known helicoplacoid genera, only *Helicoplacus* has been described in detail based on a relatively large number of specimens; *Polyplacus* and *Waucobella* are rare and incompletely understood. We believe that attachment to shelly substrates represents the most likely strategy for all helicoplacoids, but we prefer to treat the attachment mode of *Polyplacus* and *Waucobella* as uncertain for the purposes of our study.

3.2. Helicocystoids

Helicocystoids have a spindle-like, spirally-plated body, a cup of tessellated plates, and a short polyplated stem (Figs. 1C, 2E–G). The large spiral region consists of rows of polygonal interambulacral plates (some of which are spine like) and five recumbent ambulacra. The latter are composed of paired floor plates and several series of cover plates, and lead to the mouth, which is situated on the upper pole and surrounded by a frame of oral plates. The anus is a conical structure located at mid-height on the lateral side of the body. The lower part of the spiral region abruptly becomes a cup, which is composed of irregular circlets of large polygonal plates. The stem consists of unorganized small circular plates (Smith and Zamora, 2013).

3.2.1. *Helicocystis*

Helicocystoids are represented by a single genus, *Helicocystis* (Fig. 1C). None of the specimens originally described in Smith and Zamora (2013) were attached to any type of substrate. However, as the holdfast of *Helicocystis* (Fig. 2F, G) is almost identical to that of gogiids (Fig. 2H), we interpret it as a hard substrate attacher.

3.3. Eocrinoids

Eocrinoids have a sack-like theca, multiple erect feeding appendages (brachioles; Fig. 1D), and usually an aboral stalk or stem. The theca is composed of numerous polygonal plates, which are either irregularly arranged, or organized into discrete circlets or zones. In many cases, the theca is covered with sutural pores (epispires), which are thought to have been involved in respiration (Sprinkle, 1973). The brachioles are long and slender, consisting of floor (brachiolar) plates and cover plates; they arise from five ambulacra (arranged in a 2–1–2 pattern) situated on the upper surface of the theca. Brachioles are exothecal structures, meaning that they lack a direct connection to the interior of the thecal cavity (David et al., 2000). The aboral appendage takes the form of an elongated hollow stalk with irregularly arranged plates (e.g., *Gogia*) or a stem with cylindrical columnals (e.g., *Ubaghsicystis*), sometimes with a distal attachment structure; it is absent or highly reduced in a handful of taxa (e.g., *Lichenoides*) (Sprinkle, 1973).

3.3.1. *Acanthocystites* and *Akadocrinus*

These two eocrinoid genera are endemic to the Prague Basin. *Acanthocystites* is incompletely known and there is no evidence of its mode of attachment because available specimens do not preserve the stem and attachment structure. It was interpreted as a shallow sediment sticker by Dornbos (2006), but its poor preservation precludes any confident interpretation of its attachment mode. *Akadocrinus* was recently reviewed by Nohejlová and Fatka (2016), who described specimens preserving the holdfast. The attachment disk is composed of large polygonal plates surrounded by smaller elements (Fig. 2I). Its morphology is suggestive of attachment to hard substrates, although direct evidence of this is absent and hence the attachment mode is treated as uncertain.

3.3.2. *Alanisicystis*

Alanisicystis is a gogiid from the Cambrian Epoch 2 of southern Spain and was first described by Ubaghs and Vizcaïno (1990). There is no direct evidence of attachment, but the morphology of its holdfast is very similar to that of *Gogia*, and it is therefore interpreted as a hard substrate attacher.

3.3.3. *Balangicystis* and *Lyracystis*

Balangicystis from China (East Gondwana) and *Lyracystis* from North America (Laurentia) are two poorly known genera characterized by long polyplated stems (Parsley and Zhao, 2006; Sprinkle and Collins, 2006; Sprinkle et al., 2011). None of the reported specimens are preserved attached to the substrate, nor do they preserve a complete distal attachment structure. For these reasons, their mode of attachment is herein considered uncertain.

3.3.4. *Cigara*

Cigara is an enigmatic echinoderm originally described from Bohemia (Barrande, 1887); its eocrinoid affinities are problematic (Sprinkle, 1973). Poor preservation of all available specimens means that interpretations of its mode of attachment are highly speculative. Dornbos (2006) interpreted *Cigara* as a shallow sediment sticker, but based on the lack of clear evidence it is better to treat the attachment mode as uncertain.

3.3.5. *Eustypocystis*

Eustypocystis is a small eocrinoid with columnals that is endemic to Laurentia. Its stem is short and is never found complete; consequently, the mode of attachment is uncertain (Sprinkle, 1973).

3.3.6. *Gogia*

Gogia (Fig. 1D) is by far the most abundant, diverse, and widespread eocrinoid known from Cambrian Epoch 3 (Zamora et al., 2009). There are several species of *Gogia,* but all have similar distal structures for attachment, which comprise an expanded polyplated holdfast. *Gogia* is commonly preserved attached to skeletal fragments (Fig. 2H) and is therefore best interpreted as a hard substrate attacher, as suggested by Sprinkle (1973), Dornbos (2006), Zamora et al. (2009), and Álvaro et al. (2013), among others.

3.3.7. *Globoeocrinus*

Globoeocrinus is a gogiid with a short holdfast reported in China (East Gondwana). Numerous specimens have been described that are preserved attached to hard shells. For instance, Lin et al. (2008) described a total of 79 specimens, of which 67 are attached to linguliform brachiopods, eight to trilobite sclerites, three to a single hyolithid, and one probably to *Scenella*. This clearly demonstrates that *Globoeocrinus* was a hard substrate attacher.

3.3.8. *Guizhoueocrinus*

No direct evidence of attachment was reported by Zhao et al. (2007) for this genus, but comparison with other gogiids displaying similar attachment structures suggests it was most probably a hard substrate attacher.

3.3.9. *Lepidocystis* and *Kinzercystis*

Dornbos (2006) suggested that *Lepidocystis* was a shallow sediment sticker and that *Kincercystis* was a sediment attacher. However, based on specimens of *Lepidocystis* cf. *wanneri* figured in Sprinkle (1973, plate 3 fig. 4), there is direct evidence that this taxon was attached to shell fragments (Fig. 3F, G, H), most likely to the cephalons of small trilobites. *Kinzercystis* has a very similar stem and holdfast to *Lepidocystis* (Fig. 3A, B), suggesting that it shared the same mode of attachment. Thus, both *Lepidocystis* and *Kinzercystis* are herein treated as hard substrate attachers.

3.3.10. *Lichenoides*

Lichenoides is a stemless eocrinoid from Gondwana that has been interpreted as a shallow sediment sticker (Dornbos, 2006). *Lichenoides priscus*, the type species, comes from Bohemia and lacks a clear holdfast; instead, it has small plates in the aboral part of the theca that probably functioned as an attachment structure (Fig. 2L). This interpretation is confirmed by more primitive species from Morocco reported by Smith et al. (2013), which clearly show a holdfast similar to that present in some gogiids (Fig. 2J). This is also supported by one specimen from Spain described by Álvaro et al. (2013), which is attached to a trilobite sclerite (Fig. 2K). Therefore, *Lichenoides* is herein considered as a hard substrate attacher.

3.3.11. *Luhocrinus*

Luhocrinus is a poorly known eocrinoid from Bohemia that has a columnal-bearing stem with an unknown attachment structure (Prokop and Fatka, 1985). The attachment mode of this genus is uncertain.

3.3.12. *Llanocystis*

Llanocystis is an eocrinoid with a long columnal-bearing stem, described from the Furongian of Texas (Laurentia). The three available specimens lack the distal attachment structure (Zamora et al., 2015a), and thus its mode of attachment is uncertain.

3.3.13. *Marjumicystis*

Marjumicystis is a gogiid that lacks epispires and has a short holdfast. Ubaghs and Robison (1985) described several specimens with the holdfast preserved, one of which is attached to a fragment of a solute; this provides direct evidence that *Marjumicystis* was a hard substrate attacher, and not a shallow sediment sticker, as was suggested by Dornbos (2006).

3.3.14. *Nolichuckia*

This genus was described based on only a few specimens in which the distal part of the stem is incomplete, and thus its mode of attachment is uncertain (Sprinkle, 1973).

3.3.15. *Pareocrinus*

This is a poorly known genus from the Cambrian of Siberia. Dornbos (2006) interpreted it as a hard substrate attacher, but none of the specimens described by Yakovlev (1956) were found attached to any type of substrate, so the attachment mode is treated herein as uncertain.

3.3.16. *Sinoeocrinus*

Lin et al. (2008) analyzed the mode of attachment of *Sinoeocrinus* and found that 37% of 30 specimens of *Sinoeocrinus lui* were attached to shell fragments, with the remaining specimens apparently transported post-mortem. This suggests that *Sinoeocrinus* attached to hard substrates in life.

3.3.17. *Trachelocrinus* and *Tatonkacystis*

The trachelocrinids *Trachelocrinus* and *Tatonkacystis* have long columnal-bearing stems and the strata where they appear are rife with discoidal holdfasts attached to hardgrounds. Unfortunately, none of the described specimens appear with the distal stem and attachment structure preserved (Sprinkle, 1973; Sumrall et al., 1997). They are tentatively considered as hard substrate attachers based on their co-existence with discoidal holdfasts and appearance in relatively proximal high-energy environments. Further specimens will serve to test this interpretation.

3.3.18. *Turbanicystis*

Parsley and Zhao (2010) described this genus based on a few specimens from the Cambrian of China (East Gondwana). It has a wide attachment structure composed of tiny plates that closely resembles the attachment structures of certain gogiids, but is somewhat more expanded. Therefore, we treat it as a hard substrate attacher, like other eocrinoids.

3.3.19. *Ubaghsicystis*

This genus was originally described from the Cantabrian Mountains in North Spain (Gil Cid and Domínguez Alonso, 2002) and later found in North America, Morocco, and Bohemia (Zamora et al., 2013a; Smith et al., 2013; Sumrall and Zamora, 2015). It has a columnal-bearing stem with a distal discoidal holdfast (Fig. 3I, J). Some specimens from Bohemia appear attached to trilobite sclerites (SZ, personal observation), strongly suggesting it was a hard substrate attacher. Discoidal holdfast from Bohemia similar to that observed in *Ubaghsicystis* have recently been described

(Nolčova and Mergl, 2016) attached to brachiopod shells (Fig. 3D, E). Lastly, similar holdfast are herein reported from the Iberian Chains (NE Spain) attached to trilobite sclerites (Fig. 3C).

3.3.20. *Vyscystis*

This is a poorly known imbricate eocrinoid from Bohemia described based on only a few poorly preserved specimens. Its attachment mode is uncertain (Fatka and Kordule, 1990).

3.3.21. *Wudingeocrinus*

This is a long-stemmed eocrinoid from China (East Gondwana) for which only limited information is available. The distal attachment structure is not preserved in any published specimens (Hu et al., 2007), and hence the mode of attachment is uncertain.

3.4. Edrioasteroids

Edrioasteroids have a discoidal to globular theca and lack erect feeding appendages (Fig. 1A). They possess five ambulacra, which are composed of floor and cover plates, and are arranged around a central mouth in a 2–1–2 pattern (shared DE, unpaired A, shared BC ambulacra). The anus is located on the upper surface between the C and D ambulacra. A border of plates surrounds the mouth and is constructed from modified uniserial floor plates (e.g., *Protorophus*), interradial oral plates (e.g., stromatocystitids), or both oral plates and interradial oral plates (e.g., *Kailidiscus*) (Zamora and Smith, 2010; Zhao et al., 2010; Kammer et al., 2013; Zamora et al., 2013b).

3.4.1. *Aragocystites*

The genus is characterized by an attachment disc on the lower surface (aboral part) that is composed of a central plate surrounded by seven to eight large fused plates (Fig. 4H). This morphology is similar to some species of *Stromatocystites* that have been interpreted as sediment attachers (Zamora et al., 2015b and references therein); therefore, *Aragocystites* is herein interpreted as a sediment attacher.

3.4.2. *Cambraster*

This edrioasteroid is known from the Cambrian of Spain, France, and Australia (Gondwana). It has an aboral plated part and a marginal ring on the dorsal surface (Fig. 4C). Based on morphological and paleoenvironmental arguments, Zamora et al. (2013b) proposed that the genus inhabited high-energy environments. Dornbos (2006) interpreted *Cambraster* as a sediment attacher, but all reported specimens known at that time were transported, and hence the mode of attachment could not be confidently established. A new life assemblage of *Cambraster* from Spain, first reported herein, preserves 20 complete specimens attached on the sediment a few millimeters above (so disconnected from) microbial mats (see below). This confirms that *Cambraster* was a sediment attacher.

3.4.3. *Cambroblastus*

The original specimens of this genus described by Smith and Jell (1990) were all transported and lack direct evidence of attachment. However, new material from China, recently described by Zhu et al. (2014), provides direct evidence that *Cambroblastus* attached to trilobite sclerites (Fig. 4D, E), as was predicted by Dornbos (2006), indicating that it was a hard substrate attacher.

3.4.4. *Camptostroma*

This is one of the most enigmatic edrioasteroids. Interpretation of this form is difficult, but some examined specimens appear to be preserved *in situ* (Fig. 4G). These specimens probably attached to the sediment, but information from cross-sections is not available to confirm this. The lateral surface consists of a circle of vertical rows composed of multiple plates, which is not present in any other edrioasteroids. It appears that this part of the body functioned to regulate the animal's depth within the sediment, and thus we agree with Dornbos (2006) that *Camptostroma* was likely a shallow sediment sticker.

3.4.5. *Chatsworthia*, *Hadrodiscus*, *Protorophus*, and an indeterminate isorophid

These genera belong to the isorophid edrioasteroids and all have unplated aboral surfaces and marginal rings. Although *Chatsworthia* and *Hadrodiscus* lack evidence of attachment (Smith and Jell, 1990), *Protorophus* has been found attached to trilobite fragments (Fig. 4B) and is thus a hard substrate attacher (Zamora and Smith, 2010). An indeterminate isorophid found in the same locality as *Protorophus* also attached to trilobite sclerites (Fig. 4A). Based on their close morphological similarity, this strongly suggests that all Cambrian isorophids were hard substrate attachers.

3.4.6. *Edriodiscus*

This is a poorly known form from Australia in which the mode of attachment is currently uncertain (Henderson and Shergold, 1971; Jell et al., 1985; Smith and Jell, 1990).

3.4.7. *Kailidiscus* and *Walcottidiscus*

These two closely related genera have an unplated aboral part (Zhao et al., 2010). *Walcottidiscus* was interpreted as a sediment attacher and Zhao et al. (2010) also suggested that *Kailidiscus* probably attached directly to stabilized substrates. Thus, we consider both genera as sediment attachers.

3.4.8. *Persiadiskos*

This is an isorophid edrioasteroid that was recently described attached to a hard-ground (Guensburg and Rozhnov, 2014), and thus it is interpreted as a hard substrate attacher.

3.4.9. *Stromatocystites*

This is the most diverse and widespread edrioasteroid known from the Cambrian (Zamora et al., 2015b). It is closely related to *Cambraster*, but the thecal shape differs between these forms in several ways that are probably related to their differing ecological requirements (Zamora et al., 2013b). *Stromatocystites* (Fig. 1A) has a plated aboral surface for attachment that consists of a central pad of fused plates (Fig. 4I). It was considered as a sediment attacher by Dornbos (2006) and we follow this interpretation in our analysis.

3.4.10. *Totiglobus*

The type species *T. nimius* has an attachment structure that consists of a basal disk (Fig. 4F). It was interpreted as a sediment attacher by Bell and Sprinkle (1978), a hypothesis followed by Dornbos (2006) and confirmed based on taphonomic arguments by Domke and Dornbos (2010). We agree with this interpretation. *T.*? *lloydi*, in contrast, has a basal part composed of tiny plates similar to the attachment structures found in many gogiids (Sprinkle, 1985). A single unpublished specimen from the Spence Shale (Idaho, USA) is attached to a trilobite fragment (Guensburg and Sprinkle, 2000; Robison et al. 2015), suggesting that this species was a hard substrate attacher.

3.5. Early glyptocystitid rhombiferans

The glyptocystitids are a clade of rhombiferans that diversified during the Palaeozoic. They originated at the end of the Cambrian and ranged through to the Devonian. Cambrian forms are morphologically intermediate between eocrinoids and ‘true’ glyptocystitids (Zamora et al., 2016); all taxa possess a similar bipartite stem (Fig. 5B) that tapers distally.

The distal end of early rhombiferans is in most cases incompletely preserved (i.e., *Cambrocrinus* and *Vizcainoia*), and thus the mode of attachment can only be inferred indirectly. Distal holdfasts have never been found and these echinoderms are common in soft siliciclastic substrates from Gondwana. This strongly suggests that they were not hard substrate attachers. Another possibility is that they rested on the sediment surface, maintaining the theca above the substrate by means of the flexible proximal stem, but it seems highly likely that this mode of life would have resulted in instability on the seafloor. Alternatively, they could have introduced the distal part of the large stem into the sediment (i.e., holdfast strategist), but without development of any complex root-like holdfast (as seen in many Palaeozoic crinoids). This was the category assigned to these forms by Dornbos (2006) and the one we consider most likely herein.

3.6. Solutes

Solutes (Fig. 1B) have an asymmetrical, polyplated theca with an appendage at either end. The short flexible appendage at the anterior part is typically composed of two rows of floor plates that are opposed by two rows of smaller cover plates. The mouth is located at the base of this appendage, which is taken to be a feeding ambulacrum; it is debated whether this represents an arm (e.g., Smith, 2005) or a brachiole (e.g., David et al., 2000). Hydropore and gonopore openings are situated near the base of the anterior appendage in many taxa. The longer appendage (stele) at the posterior is either made up of numerous unorganized platelets (i.e., *Coleicarpus*) or differentiated into a highly flexible proximal region and a rigid distal part (other solutes). The anus is a large opening surrounded by specialized plates, and is located close to the stele insertion (Jefferies, 1990; David et al., 2000; Smith, 2005; Noailles et al., 2014).

The only solute reported from the Furongian was a free-living form (Zamora et al., 2013c), but genera from Cambrian Epoch 3 (i.e., *Castericystis* and *Coleicarpus*) were attached to shell fragments during at least some stage of their ontogeny and are thus interpreted as hard substrate attachers. *Coleicarpus* is always found attached to trilobite sclerites (Daley, 1996) (Fig. 5A). Moreover, Ubaghs and Robison (1985) and Daley (1995) reported several juvenile specimens of *Castericystis* attached to adult specimens (although all adult specimens are thought to have been free-living). This suggests that *Castericystis* was a hard substrate attacher as a juvenile, but switched to a vagile snowshoe strategy as an adult.

4. Temporal trends in attachment strategy

Trends in the mode of attachment for the early echinoderms described above were analyzed quantitatively through the Cambrian (Fig. 6). Results show a high and consistent proportion of echinoderms attached to hard substrates from Cambrian Epochs 2 to 3 followed by a drop in proportion during the Furongian (Fig. 6A, C, E). This drop is likely the result of a dramatic decrease in eocrinoid diversity (Fig. 6G), the majority of which attached to hard substrates. During the same interval, echinoderms showed a slight increase in the number of attachment strategies (Fig. 6B, D, F). The rise in attachment diversity (Fig. 6H) is caused by the appearance of holdfast strategists (rhombiferans) and snowshoe strategists (solutes), offsetting the loss of shallow sediment stickers (*Camptostroma*).

The results of the species- genus-, and group-level analyses are very similar (Fig. 6A–F). Only Cambrian Epoch 3 had a higher number of species per genus (1.95 compared to 1.1 in Epoch 2 and 1.2 in the Furongian), largely the result of the ubiquitous eocrinoid *Gogia* and the edrioasteroid *Stromatocystites*. However, this change in the taxonomic level of analysis does not alter our results. Normalizing by group only slightly changed the resulting patterns, appearing to make the change in proportion in hard substrate attachment more gradual through the Cambrian, which is likely the result of de-emphasizing the influence of eocrinoids in the analysis. The results still indicate high levels of hard substrate attachment and diverse modes of attachment prior to the CSR, regardless of the taxonomic scale of study.

The large number of species (22.9%) with uncertain modes of attachment could potentially alter the result, although this proportion is expected, given the taphomically sensitive nature of Early Palaeozoic echinoderms (Brett et al., 1997). However, the recognition of the attachment strategy for the uncertain case studies is unlikely to alter the observed trends. In fact, given that the majority of the unknown taxa (15 out of 19) are helicoplacoids and eocrinoids (largely interpreted as hard substrate attachers) from Cambrian Epochs 2 and 3, the current trend would likely be more pronounced with additional morphological data.

5. Microbial stabilization of substrates and echinoderm attachment

It has been suggested that suspension-feeding echinoderms from Cambrian Epochs 2–3 were able to fix themselves to the substrate as shallow sediment stickers or sediment attachers because the seafloor was relatively firm and stabilized by microbial mats (Dornbos and Bottjer, 2000; Lefebvre and Fatka, 2003). The absence of intense bioturbation and a well-developed mixed layer were also thought to be important factors promoting shallow sediment sticking and/or sediment attachment (Dornbos and Bottjer, 2001). Under this paradigm, the presence of microbial mats stabilizing the substrate is currently assumed to have been of key significance, but direct evidence of microbial mats, biofilms and MISS on the fossiliferous slabs is lacking in most cases (Davies et al., 2016). Furthermore, it is even rarer to find echinoderms preserved directly attached to the substrate stabilized by microbial mats, and so there is little empirical data supporting the hypothesized association between prevalence of microbial mats and a sediment sticking/attachment mode of life (as suggested by Dornbos and Bottjer, 2000; Lefebvre and Fatka, 2003). Echinoderms are also absent in microbially encrusted reef cores from Cambrian Epochs 2–3, but common in microbially-free (hydrodynamically controlled) reef flanks, so an antagonistic relationship between microbial mats and echinoderms was documented by Álvaro et al. (2013) for Cambrian times. Some Cambrian echinoderms are locally associated with sedimentary structures and burrowing that needed firm substrates to be preserved (Droser et al., 2004).

Herein, we report a new life assemblage of *Cambraster* from the Furongian Valtorres Formation of Northeast Spain that provides unique insights into how some edrioasteroids associated with microbial mats in the Cambrian (Fig. 7). The material was collected in the vicinity of Ateca village (see geological and stratigraphic setting in Álvaro et al., 2007) and is associated with other echinoderms including stylophorans and early rhombiferans. The assemblage consists of at least 20 *Cambraster* specimens (21–26 mm in diameter). All specimens (with the exception of one) are oriented with the upper pole facing upwards. Some of them are in contact with one another at their thecal margins, which are flattened (Fig. 7C), similar to other specimens that inhabited an environment with limited available space for growth (Sumrall et al., 2006; Sumrall and Zamora, 2011).

The edrioasteroids lie on millimeter- to centimeter-scale clayey/silty alternations (Fig. 7D). Background sedimentation (homogeneous claystone) was deposited from suspension and episodically disturbed by fodinichnia traces (e.g., *Gordia*, *Helminthopsis*, and *Phycodes*) and scratch marks (e.g., *Cruziana*, *Diplichnites*, and *Monomorphichnus*), presumably reflecting both available organic detritus and sufficient oxygenation of the surface. Silty interlayers were deposited as episodic distal tempestites and preserve burrows made by suspension feeders (e.g., *Arenicolites*, *Diplocraterion*, and *Skolithos*). In both cases, collapsed and lined traces are rare to absent, suggesting stable substrates. The presence of contorted and slumped episodes punctuating background sedimentation points to shifting substrate conditions, which ranged from soupground to softground (Álvaro et al., 2007). Edrioasteroids occur on burrowed beds (reflecting background sedimentation subsequently affected by storm-induced processes and burrowing) and are sandwiched between surfaces with microbially induced sedimentary structures (MISS) (Fig. 7D–F). On the bed surface, MISS occur as wrinkle structures with sinus-shaped loops. On slab and in thin-section, these are identified by millimeter-thick, wavy-crinkled, carbonaceous laminae (Fig. 7E, F). Diagenetic features related to biofilm decay provided favorable conditions for the precipitation of “anoxic” minerals (*sensu* Schieber et al., 2007), which occur as both scattered pyritic grains and strongly pyritic laminae mimicking the original, wavy and anastomosing, microbial textures. Despite the episodic presence of mat interlayers, the aboral surfaces of edrioasteroids do not attach directly on them. Instead, they lie on the above-reported clayey substrates (Fig. 7D), so the echinoderms were not in contact with MISS surfaces but colonized soft-firmground clayey substrates.

6. Morphological adaptations for attachment and the evolution of suspension-feeding echinoderms

As explained above, it has been argued that early suspension-feeding echinoderms contributed to the CSR, with taxa evolving new morphological structures to exploit alternative attachment strategies coincident with a change in the dominant substrate type (Bottjer et al., 2000; Dornbos, 2006; Domke and Dornbos, 2010). However, this is not supported by our observations of fossil specimens, which demonstrate that echinoderms were already diverse in terms of their morphological adaptations for hard substrate (mainly shelly) attachment by Cambrian Epochs 2–3 (Fig. 6). For example, basal attachment structures indicative of attachment to hard substrates are found in several early forms from Cambrian Epoch 2, including helicoplacoids, gogiids (e.g., *Gogia* and *Globoeocrinus*), and imbricate eocrinoids (Figs. 2, 3). Moreover, two of the major groups that switched from offshore to shoreface conditions across the Cambrian–Ordovician boundary interval (isorophids and columnal-bearing eocrinoids) were already present in offshore siliciclastic and unconsolidated substrates by Cambrian Epoch 3. These echinoderms lived attached to skeletal fragments, and were thus able to later colonize energetic shoreface environments where carbonate hardgrounds became common from the Furongian onwards (Brett et al., 1983; Wilson et al., 1992; Sprinkle and Guensburg, 1995).The analysis presented herein suggests that most Cambrian suspension-feeding echinoderms attached directly to hard substrates, generally skeletal debris, throughout the Cambrian (Figs. 2–6; Appendix A). This agrees with previous suggestions for pelmatozoan communities from Laurentia (Guensburg and Sprinkle, 1992), but also seems to be the rule for helicoplacoids, helicocystoids, and some edrioasteroids and solutes. The same pattern is replicated in Gondwana. Stromatocystitid edrioasteroids (*Cambraster*, *Stromatocystites*) are an exception because they were apparently attached to fine-grained siliciclastic substrates (Figs. 4, 7). Direct evidence suggests they used pre-existing firmground conditions, likely stabilized by microbial mats, to attach a few millimeters above the mat, in organic-rich and non-bioturbated sediments (Fig. 7). In extant stalked crinoids, larvae attach to the substrate early in ontogeny (Nakano et al., 2003; Amemiya et al., 2016), and a similar phase of larval attachment has been inferred for Cambrian suspension-feeding echinoderms (Smith, 2008). In many taxa (e.g., helicoplacoids and gogiid eocrinoids), attachment was apparently obligate and persisted into adulthood, as demonstrated by the presence of complex, clearly differentiated attachment structures (e.g., large holdfasts composed of multiple small plates; Fig. 2D, H) in adult specimens. However, in the solute *Castericystis*, attachment seems to have varied during ontogeny: juveniles have been described attached to adult individuals (Ubaghs and Robison, 1985; Daley, 1995), whereas adults are thought to have been free-living snowshoe strategists.

The relative proportion of different attachment strategies through the Cambrian is in part controlled by the diversity of certain echinoderm groups. For example, rhombiferans originated in Cambrian Epoch 3 and diversified in the Furongian, resulting in an increase in the relative proportion of holdfast attachers towards the end of the Cambrian. There is also a reduction in the total number of eocrinoids in the Furongian (compared to Cambrian Epochs 2–3). This is probably the product of taphonomic biases related to the poor Furongian rock record and the diversification of suspension-feeding echinoderms associated with proximal highly energetic environments (Smith, 1988; Sumrall et al., 1997). Furthermore, the proportion of sediment attachers and shallow sediment stickers remains low and decreases throughout the Cambrian, reflecting the replacement of stromatocystitid edrioasteroids adapted for these modes of attachments by isorophid edrioasteroids, which first appeared in Cambrian Epoch 3 and subsequently colonized hard substrates (either shell fragments or carbonate hard-grounds).

Nardin and Lefebvre (2010) suggested that the Cambrian Substrate Revolution might partly explain the global increase in echinoderm diversity from Cambrian Epochs 2–3, as the associated change in dominant substrate type allowed early echinoderms to radiate into and fill new ecological niches. However, our analysis demonstrates that the number of attachment modes did not change appreciably from Cambrian Epochs 2–3 (Fig. 6), indicating that early echinoderms already occupied most of the niches that were filled during the Cambrian by Epoch 2.

It has been proposed (Dornbos and Bottjer, 2000, 2001) that helicoplacoids went extinct in the Cambrian because, unlike edrioasteroids and eocrinoids, they were unable to adapt to the presumed switch from mat-stabilized sediments to unconsolidated soft substrates that occurred during this period. However, we have shown that helicoplacoids were in fact hard substrate attachers from their earliest appearance and were therefore potentially pre-adapted to any changes in substrate type through the Cambrian. Consequently, there is no reason to believe they would have been impacted by substrate changes more than any other sessile suspension-feeding echinoderms that persisted beyond the Cambrian. The extinction of helicoplacoids is probably mainly related to their restricted palaeogeographic distribution compared to that of more successful early suspension feeders (i.e., eocrinoids).

Attachment structures became more diverse and complex in post-Cambrian times (Brett, 1981), but all their basic morphologies were already present from near the beginning of the Cambrian. While some groups (such as the pelmatozoans) developed diverse anchoring strategies later in the Palaeozoic (i.e., emerging complex roots), other groups, such as isorophid edrioasteroids, were more conservative and their attachment structures (i.e., peripheral rim) experienced little change.

7. Conclusions

A revision of the attachment strategies of Cambrian echinoderms demonstrates that most of them attached directly to skeletal debris and did not interact with clayey substrates, either microbially encrusted or not, as sediment attachers or sediment stickers. The interpretation of the modes of attachment of some taxa are revised, such as for the helicoplacoids, which are interpreted as hard substrate attachers, based on direct evidence of attachment to trilobite sclerites. Close morphological similarities are highlighted between the lower pole of helicoplacoids and the holdfast of some gogiid eocrinoids (which are found attached to shell fragments). Helicocystoids are also considered as hard substrate attachers because they possess a distal polyplated holdfast similar to that of certain gogiids. Although some eocrinoids were previously considered as shallow sediment stickers, our re-evaluation suggests that all articulated taxa with direct evidence of attachment were hard substrate attachers. This includes gogiids, imbricates and columnal-bearing forms (*Ubaghsicystis*). Early rhombiferans were most likely holdfast strategists. Edrioasteroids were the most varied in terms of attachment strategy: early forms (e.g., *Camptostroma* and stromatocystitids) were shallow sediment stickers or sediment attachers, but later forms attached to trilobite sclerites (isorophids and edrioblastoids); they are the only group that fits with the predictions of the CSR paradigm. Solutes were attached to shell fragments, either as adults (*Coleicarpus*) or at earlier ontogenetic stages (*Castericystis*), with the exception of one taxon (new form D) that is interpreted as a free-living snowshoe strategist, similar to adults of *Castericystis*. Overall, our study confirms that the proportion of echinoderms attaching to hard substrates was high throughout the entire Cambrian, which undermines the previously hypothesized close link between early echinoderms and the CSR paradigm.

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Appendix A. Taxa included in the analysis

Supplementary data for this article can be found online at XXXXXXX.

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Figure captions

Fig. 1. Morphology of some Cambrian echinoderms considered in this work with indication of most important terminological information. A. Edrioasteroid *Stromatocystites pentangularis* (after Zhao et al. 2010). B. Solutan *Coleicarpus sprinklei* (after Noailles et al. 2014). C. Helicocystoid *Helicocystis moroccoensis* (after Smith and Zamora, 2013). D. Eocrinoid *Gogia parsleyi* (after Zamora et al. 2009).

Fig. 2. Attachment structures in helicoplacoids (A, B, C, D), helicocystoids (E–G), and eocrinoids (H–L). A. *Helicoplacus* showing basal structure for attachment (D), USNM PAL642413. B, C. *Helicoplacus* attached to a trilobite fragment. The specimen shown in B corresponds to USNM PAL642414 and the specimen shown in C is courtesy of Bryan Wilbur. E, F. *Helicocystis* showing general body organization and distal attachment structure (G) (NHM UK EE14847, NHM UK EE15375, NHM UK EE15374). H. *Gogia gondi* attached to a trilobite fragment, MNHN.F.A48949. I. *Akadocrinus* showing distal attachment structure, L42227a. J–L. Different species of *Lichenoides* showing large holdfast structure, NHM UK EE 29346 (J), small holdfast attached to a trilobite fragment, MPZ 2013/9 (K), and tiny basal plates for attachment,

NHM UK EE 15353 (L). All specimens are latex casts whitened with NH_4Cl. Arrows indicate the contact between the attachment structure and skeletal fragments.

Fig. 3. Attachment structures in imbricate eocrinoids (A, B, F, G, H) and columnal-bearing eocrinoids (?C, ?D, ?E, I, J). A. *Kinzercystis* showing basal structure for attachment, MCZ 581. B. Detail of distal holdfast of *Kinzercystis*. C. Two small discoidal holdfasts attached to a trilobite fragment, MPZ 2017/569, 570. D, E. Discoidal holdfast showing pentaradial articulation facet attached to a brachiopod shell, PCZCU 2073. F. *Lepidocystis* specimen attached to a trilobite fragment, MCZ 628. G, H. Detail of distal holdfast of *Lepidocystis*. I, J. *Ubaghsicystis* showing a columnal-bearing stem and a distal discoidal holdfast for attachment, MCNM 30849. All specimens are latex casts whitened with NH_4Cl.

Fig. 4. Attachment structures in Cambrian edrioasteroids. A. Indeterminate isorophid attached to a trilobite fragment, MPZ2010/857. B. *Protorophus*, the earliest isorophid edrioasteroid, attached to a trilobite fragment by means of a peripheral rim, MPZ2009/1233a. C. Aboral view of *Cambraster cannati* showing the side in contact with the substrate during attachment, MNHN.F.A45786B. D, E. Edrioasterid *Cambroblastus* attached to a trilobite fragment, NIGPAS156159. F. Attachment structure of *Totiglobus nimius* viewed from interior, MCZ 990. G. Aboral view of *Camptostroma*; both specimens lie in life position with the aboral pole inserted in the sediment, MCZ 116394. H. *Aragocystites,* stromatocystitid edrioasteroid showing a clear pad of fused plates for attachment, MPZ2007／1890. I. *Stromatocystites* showing the aboral surface for attachment directly to the substrate, NHMUK EE 15897. All

specimens are latex casts whitened with NH_4Cl. Arrows indicate the contact between the attachment structure and skeletal fragments.

Fig. 5. A. The solute *Coleicarpus* attached to a trilobite fragment, NHMUK EE 4971. B. The early rhombiferan *Sanducystis* showing the construction of the stem, NIGPAS163198. Specimen B is a latex cast whitened with NH_4Cl. Arrow indicates the contact between the attachment structure and skeletal fragment.

Fig. 6. Trends in attachment mode in Cambrian suspension-feeding echinoderms at the species (A, B), genus (C, D), and class-levels (E, F), and attachment modes of suspension-feeding echinoderms through the Cambrian (G, H). Values are given as sample means with error bars calculated as the standard error of 1000 bootstrap replicates. A. Proportion of species directly attached to hard substrates. B. The number of modes of attachment seen in Cambrian species. C. Proportion of genera that attached directly to hard surfaces. D. The number of modes of attachment seen in Cambrian genera. E. Proportion of classes that attached directly to hard surfaces. F. The number of modes of attachment seen in Cambrian genera. G. Sample sizes of different groups included in the analyses. H. Proportion of different attachment types. Abbreviations: Ea, Edrioasteroidea; Ec, Eocrinoidea; Hc, Helicocystoidea; hf, holdfast strategist; Hp, Helicoplacoidea; hs, hard substrate attacher; Rh, Rhombifera; So, Soluta; sa, sediment attacher; sn, snowshoe strategist; sss, shallow sediment sticker.

Fig. 7. Cambrian edrioasteroids and microbially induced sedimentary structures (MISS). A. General view of the slab showing seven specimens of *Cambraster* (MPZ

2017/549–568). B. Counterpart of the slab showing the attachment surface (s_1) and the underlying level containing MISS (s_0). Note that the aboral surfaces of edrioasteroids are directly attached to the s_1 sedimentary layer. C. Two specimens of *Cambraster* with arrow indicating modified morphology due to limited available space. D. Cross-section of one specimen showing attachment to an unconsolidated clayey substrate previously stabilized by underlying MISS. E. Photomicrograph of a limonitized *Cambraster* “floating” on a clayey sediment underlain by wavy anastomosing, carbonaceous siltstone/claystone alternations (MISS). F. Close-up showing confinement of scattered pyrite grains, commonly weathered to iron oxy-hydroxides. Abbreviations: i, integument; mr, marginal ring; s_0, sedimentary layer which contains MISS; s_1, sedimentary layer where edrioasteroid attaches.

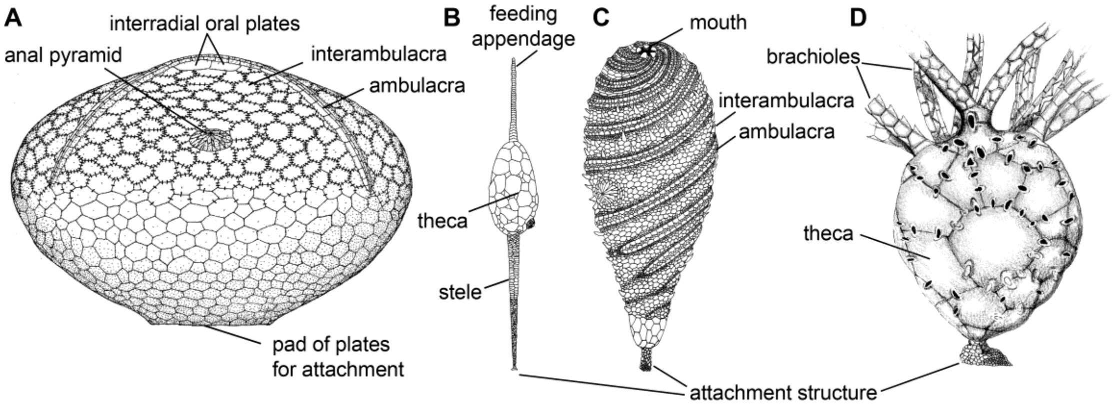
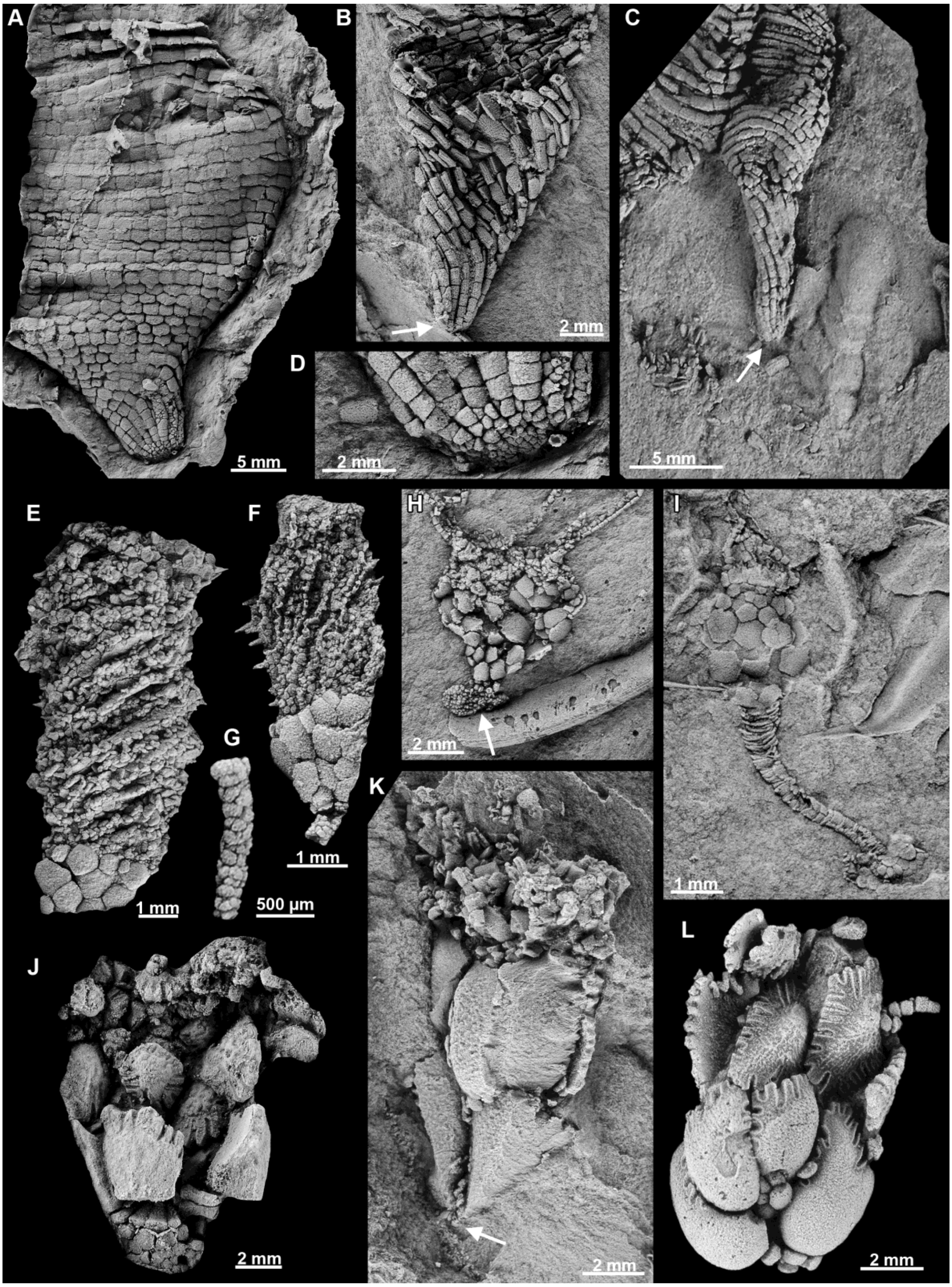

A
interradial oral plates
anal pyramid
interambulacra
ambulacra
pad of plates
for attachment
B
feeding
appendage
theca
stele
C
mouth
interambulacra
ambulacra
D
brachioles
theca
attachment structure

Fig. 1


A
B
C
2 mm
D
5 mm
2 mm
5 mm
E
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I
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K
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Fig. 2

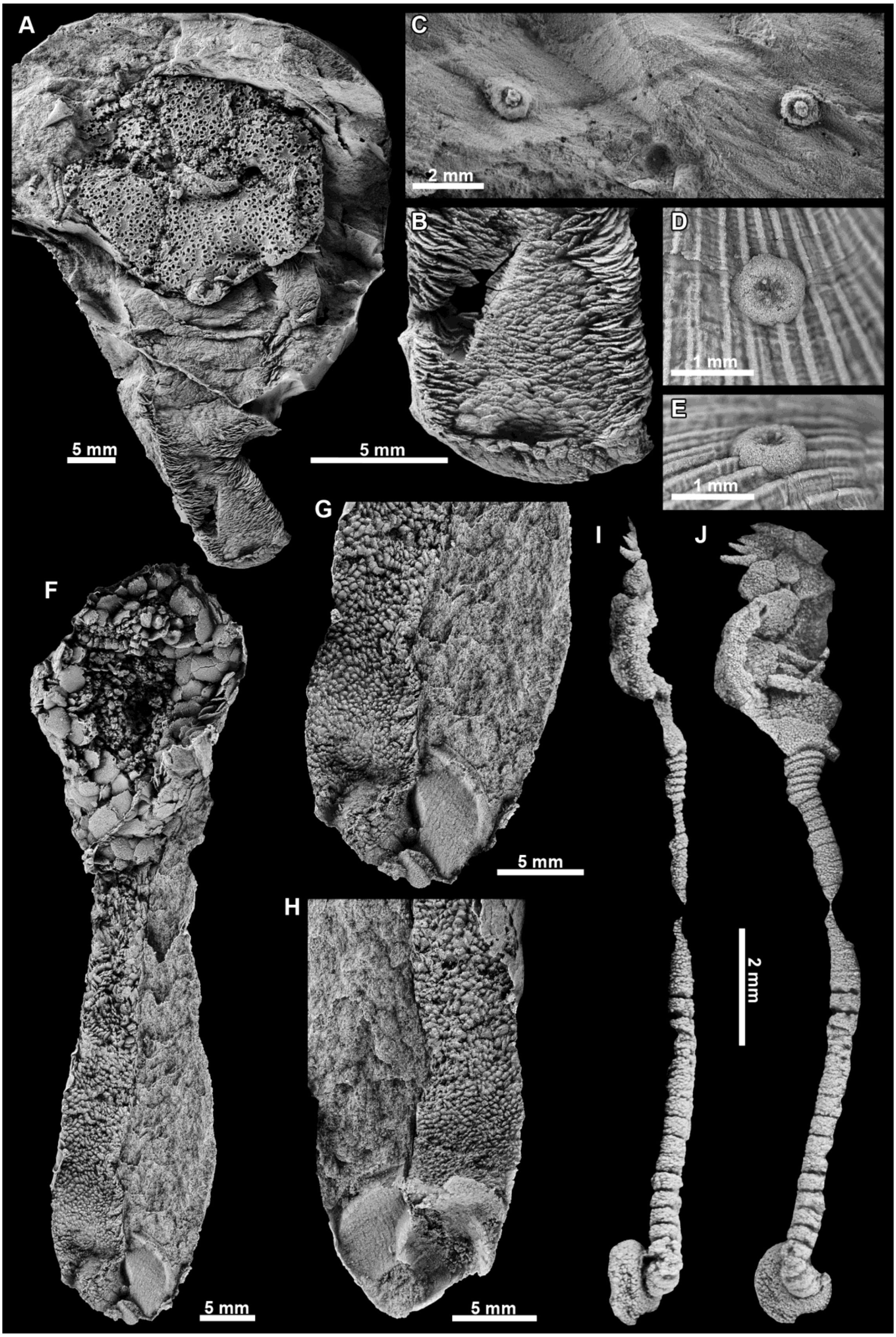


Fig. 3

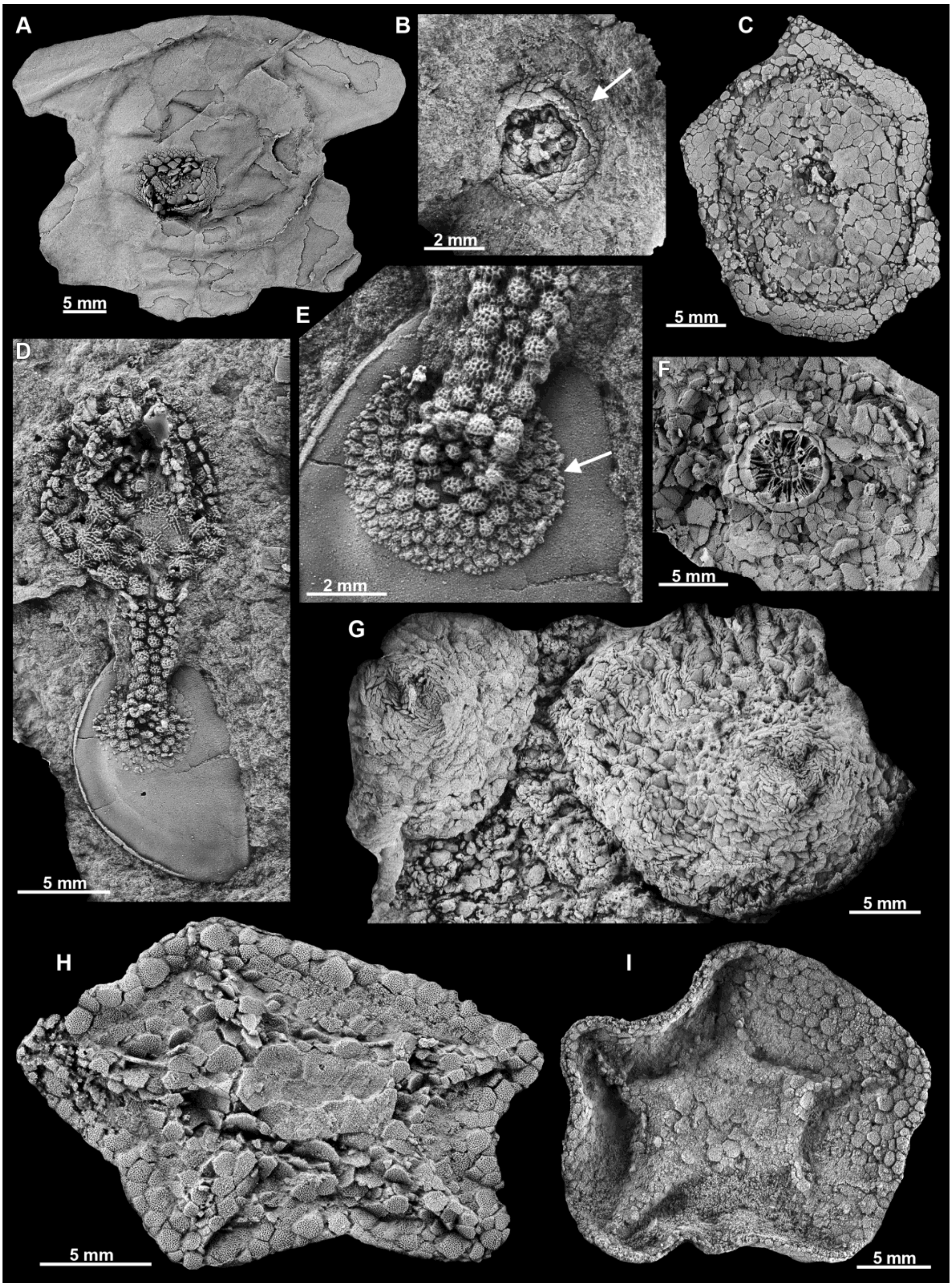


Fig. 4

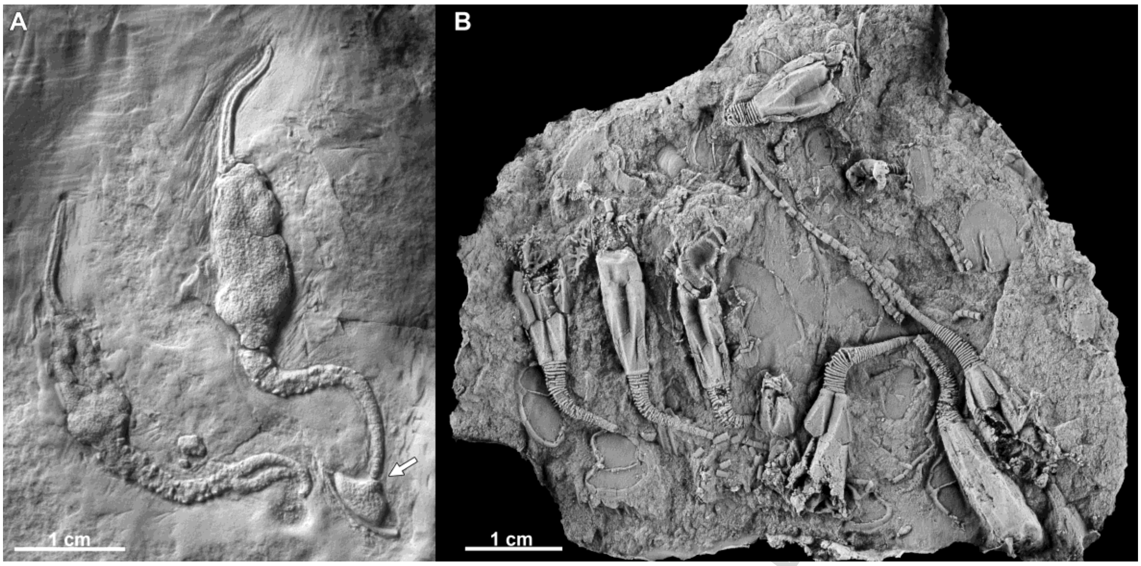
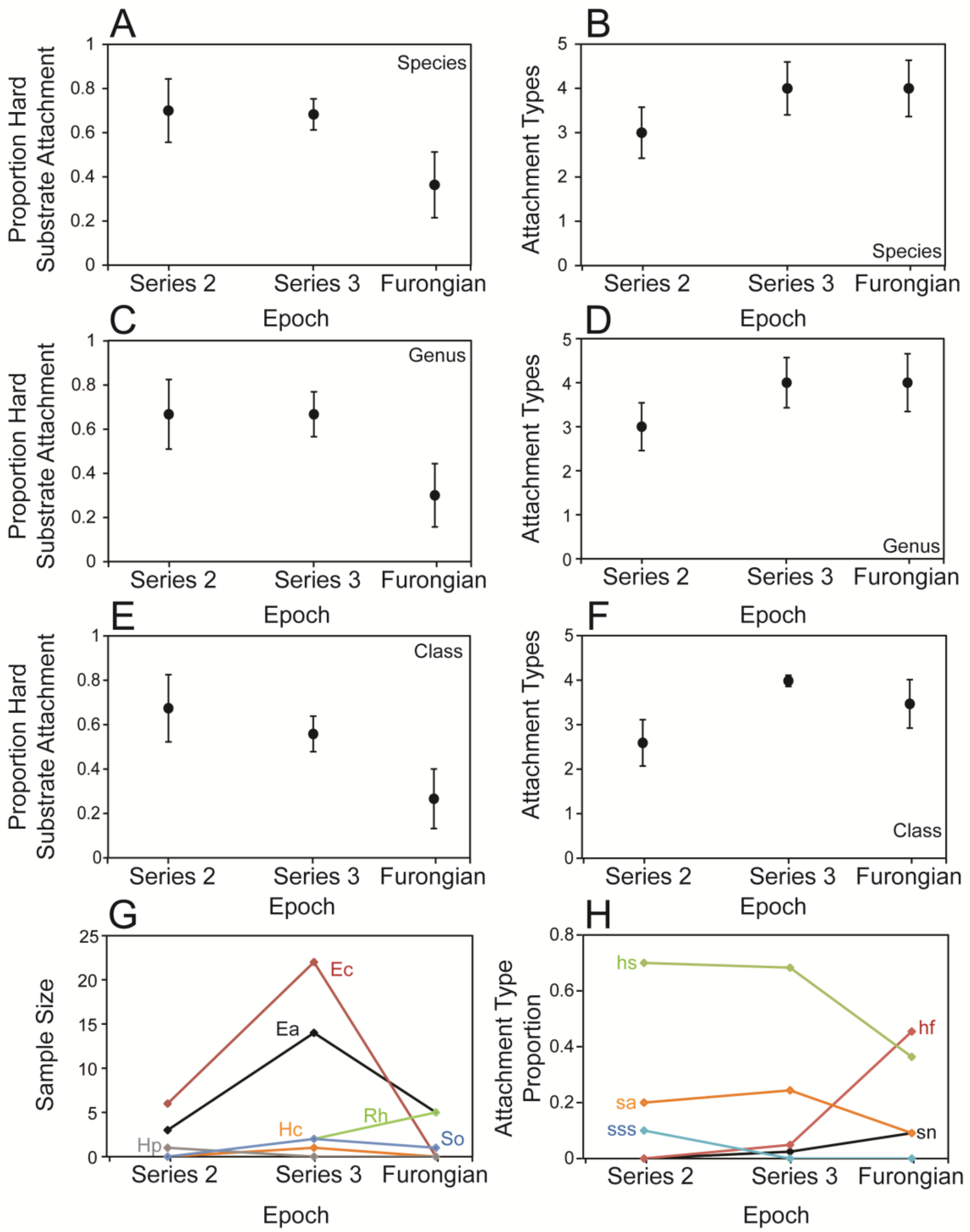


Fig. 5


A
Species
Proportion Hard Substrate Attachment
1
0.8
0.6
0.4
0.2
0
Series 2
Series 3
Furongian
Epoch
B
Species
Attachment Types
5
4
3
2
1
0
Series 2
Series 3
Furongian
Epoch
C
Genus
Proportion Hard Substrate Attachment
Series 2
Series 3
Furongian
Epoch
D
Genus
Attachment Types
Series 2
Series 3
Furongian
Epoch
E
Class
Proportion Hard Substrate Attachment
Series 2
Series 3
Furongian
Epoch
F
Class
Attachment Types
Series 2
Series 3
Furongian
Epoch
G
Sample Size
25
20
15
10
5
0
Ec
Ea
Hp
Hc
Rh
So
Series 2
Series 3
Furongian
Epoch
H
Attachment Type Proportion
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0.2
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hf
sa
sss
sn
Series 2
Series 3
Furongian
Epoch

Fig. 6

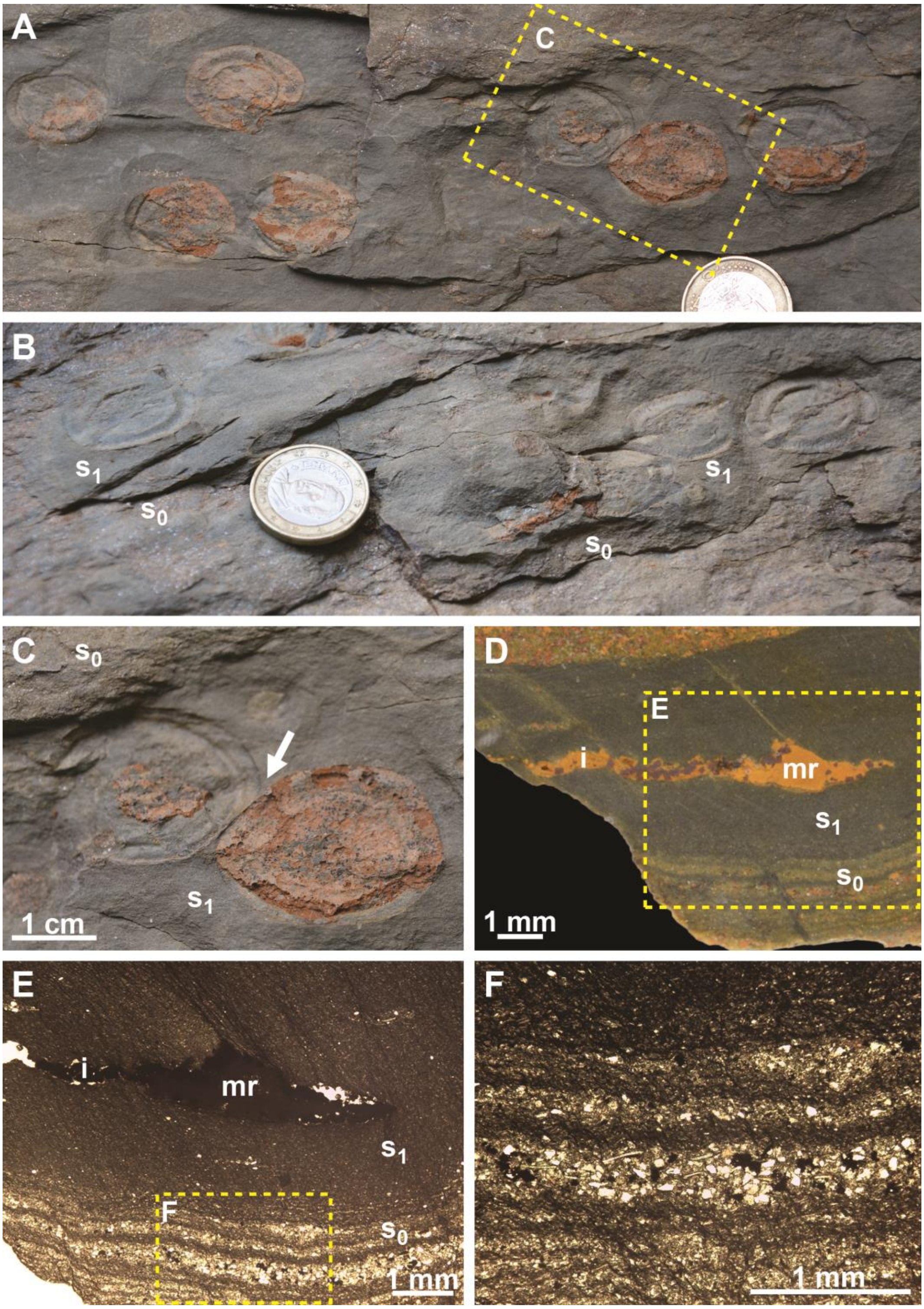

Fig. 7