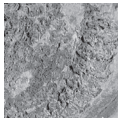


New edrioasteroid (Echinodermata) from the Spence Shale (Cambrian), Idaho, USA: further evidence of attachment in the early evolutionary history of edrioasteroids

RONGQIN WEN, LOREN E. BABCOCK, JIN PENG & RICHARD A. ROBISON



A new species of *Totiglobus*, *T. spencensis* (class Edrioasteroidea, order Edrioasterida), is reported from the Spence Shale (Cambrian: Miaolingian Series, Wuliuan Stage) of eastern Idaho. The holotype, which was evidently buried at the base of a tempestite bed, is attached by a basal disk to a hyolithid conch. In contrast to the closely related species *T. nimius*, which attached to mat-stabilized sediment by means of a suction disk on the aboral surface, *T. spencensis* attached to hard substrates by means of an attachment disk on the aboral surface. Edrioasteroids first evolved mechanisms for attaching to hard substrates in the Wuliuan Age, and *T. spencensis* is thus among the earliest-known edrioasteroids to show this habit. By the Drumian Age, attachment to hard substrates had become the dominant post-larval life habit of edrioasteroids. • Key words: Edrioasteroid, Cambrian, Spence Shale, Idaho, Cambrian Substrate Revolution.

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The Cambrian Period was a time of sweeping reorganization in marine ecosystems. A series of diversification events resulted in the introduction of varied taxa, and evolutionary radiation was accompanied by fundamental changes in substrate consistency leading, ultimately to more fluidized sediment surfaces. For echinoderms and suspension-feeders in general, the Cambrian was a time of evolutionary experimentation (e.g., Domke & Dornbos 2010, Zamora & Smith 2010, Zamora *et al.* 2017, Lefebvre & Leroosey-Aubril 2018). One interesting aspect of the paleoecology of the early to mid-Cambrian (late Epoch 2 to Miaolingian Epoch) was the widespread presence of mat-stabilized sediment surfaces in shallow marine ecosystems (e.g., Seilacher & Pflüger 1994, Bottjer *et al.* 2000). Prior to the widespread fluidization of substrates by burrowing animals (referred to as the Cambrian Substrate Revolution; Bottjer *et al.* 2000), some early echinoderms, including taxa assigned as helicoplacoids (Bottjer *et al.* 2000), edrioasteroids (Sumrall & Sprinkle 1992, Domke & Dornbos 2010), eocrinoids, and hom-

oiostelians (Zamora *et al.* 2017), evidently attached to or stuck to mat-stabilized surfaces in post-larval phases of life. Twelve named genera of edrioasteroids, plus some undetermined forms, have been recorded from Cambrian deposits worldwide (Pompeckj 1896; Jaekel 1899, 1921; Schuchert 1919; Bassler 1935, 1936; Bell & Sprinkle 1978; Jell *et al.* 1985; Smith 1985; Sprinkle 1985; Smith & Jell 1990; Ubahgs 1998; Fatka *et al.* 2004; Parsley & Prokop 2004; Zamora *et al.* 2007, 2013, 2015; Domke & Dornbos 2010; Lefebvre *et al.* 2010; Zamora & Smith 2010; Zhao *et al.* 2010; Zamora 2013; Guensburg & Rozhnov 2014; Robison *et al.* 2015; Lefebvre & Leroosey-Aubril 2018). Of these, nearly all show evidence of attachment (Tab. 1). In this paper, we discuss attachment in a new species of the Cambrian edrioasteroid *Totiglobus*. This example presents an interesting addition to the life habit information previously documented for the genus (Bell & Sprinkle 1978, Domke & Dornbos 2010, Zamora *et al.* 2017).

The new species was collected from the Spence Shale (Cambrian: Miaolingian Series, Wuliuan Stage) in

southeastern Idaho. Wuliuan shales of the Great Basin, especially the Spence Shale in Idaho and Utah, and the equivalent Chisholm Shale in Nevada and Utah, have yielded a moderately diverse fauna of echinoderms, principally from layers at the bases of tempestites (e.g., Bell & Sprinkle 1978, Robison 1991, Domke & Dornbos 2010, Robison *et al.* 2015). Overall, Laurentian deposits have yielded four genera and at least seven species (Tab. 1). As discussed by Zamora *et al.* (2017) most of these taxa were probably attached suspension-feeders. Domke & Dornbos (2010) studied numerous specimens of *Totiglobus nimius* from the Chisholm Shale of Nevada and concluded that the species attached by suction, possibly with the addition of a biogluce, to mat-stabilized sediment surfaces. The Spence and Chisholm formations represent predominantly fine-grained siliciclastic or mixed siliciclastic-carbonate sedimentation, including some organic-rich black shale intervals, on a storm-influenced continental shelf. As sessile, and commonly attached, metazoans, intact echinoderms were preserved after rapid *in situ* burial and entombment resulting from storm-related sediment disturbance and deposition (see Sprinkle 1973, LoDuca *et al.* 1997, Robison *et al.* 2015). The interpretation of echinoderms attaching to mat-stabilized surfaces (Domke & Dornbos 2010) adds an important detail that helps to explain occurrences of extensive echinoderm-bearing obrution beds in the Cambrian.

The new *Totiglobus* documented here is attached by means of a basal attachment disk to a hard, shelly substrate. Its attachment mechanism differs from the better-known suction-style of attachment documented in *T. nimius* (Domke & Dornbos 2010; also see Bell & Sprinkle 1978, pl. 6, fig. 9). This specimen, plus another that has been illustrated (Robison *et al.* 2015, fig. 188) but not described, confirm that *Totiglobus* was attached in post-larval life, but had varied means of attachment and species-level preferences for types of stabilized surfaces. Available evidence suggests that edrioasteroids first evolved the capacity for attachment to hard substrates in the Wuliuan Age of the Cambrian, and thus edrioasteroids from the Spence Shale are among the earliest species to show this habit.

Locations and stratigraphy

The holotype of *Totiglobus spencensis* sp. nov. is from the type locality of the Spence Shale in Spence Gulch, Idaho (Fig. 1). The specimen was collected by the Gunther family in 1992. The Spence Shale is rich in fossils and includes a diverse polymerid and agnostoid trilobite fauna (e.g., Walcott 1908, Resser 1939, Sprinkle 1973, Campbell 1974, Gunther & Gunther 1981, Robison 1991, Liddell *et al.* 1997, Bonino & Kier 2010, Robison &

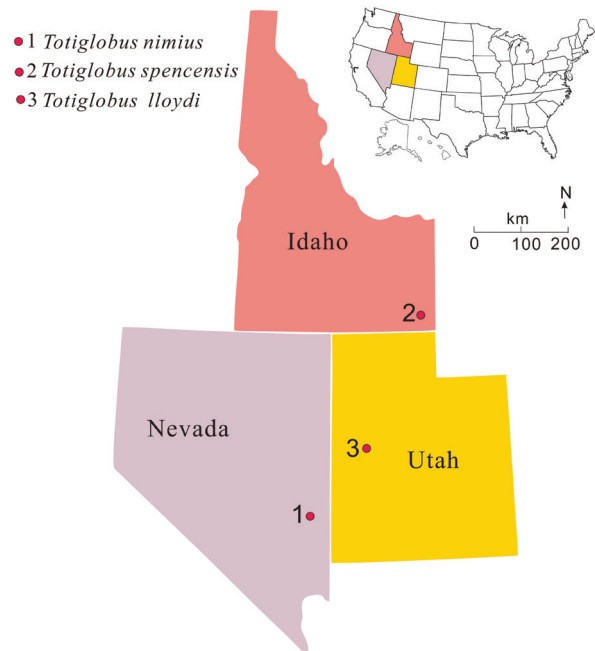


Figure 1. Geographic occurrences of named species of *Totiglobus* in the Great Basin, USA. • 1 – *Totiglobus nimius* Bell & Sprinkle, 1978 from the Chisholm Shale. • 2 – *Totiglobus spencensis* sp. nov. from the Spence Shale. • 3 – *Totiglobus lloydi* Sprinkle, 1985 from the Marjum Formation.

Babcock 2011, Garson *et al.* 2012, Robison *et al.* 2015). The polymerid trilobite fauna includes representatives of open-shelf and restricted-shelf Laurentian environments. Restricted-shelf polymerid trilobites present are indicative of the *Glossopleura* Zone, open-shelf polymerid trilobites present are indicative of the *Oryctocephalus* Zone, and agnostoids present are indicative of the *Ptychagnostus praecurrens* Zone (e.g., Robison & Babcock 2011, Robison *et al.* 2015). Strata of the Spence Formation are correlated with the Miaolingian Series, Wuliuan Stage, which were formerly referred to in literature as provisional Series 3 and provisional Stage 5 (see Cohen *et al.* 2018, Zhao *et al.* in press).

Various authors have discussed the lithostratigraphy, sequence stratigraphy, or paleoenvironmental setting of the Spence Shale (e.g., Walcott 1908, Resser 1939, Sprinkle 1973, Campbell 1974, Gunther & Gunther 1981, Robison 1991, Liddell *et al.* 1997, Bonino & Kier 2010, Robison & Babcock 2011, Garson *et al.* 2012, Robison *et al.* 2015). The formation is dominated by shale, with thin silty shale or siltstone interbeds in places. The lower portion of the formation tends to show dark, organic-rich shale, including black shale, beds, and the upper portion of the formation tends to be rich in tan to olive-green shales. Liddell *et al.* (1997) and Garson *et al.* (2012) suggested that the extraordinary preservation of nonbiomineralized tissue in fossils of the Spence Shale was favored

during times of low or depleted levels of bottom-water oxygenation. Robison (1991) showed that echinoderms were often preserved in articulated condition at the bases of tempestite beds.

Paleoecology and Taphonomy

Cambrian edrioasteroids from North America are rather infrequently reported (Tab. 1). Indeed, articulated remains of echinoderms in general are relatively rare in Cambrian strata. It is likely that this is largely related to the relatively unusual condition in which live animals were buried episodically under rapidly deposited sediment layers such as tempestites (see Robison 1991, Parsley & Zhao 2006, Zhao *et al.* 2010, Robison & Babcock 2011, Robison *et al.* 2015) or sediment gravity flows (see Conway Morris & Whittington 1985, Conway Morris 1986). This relationship between episodic burial and preservation of intact echinoderms also applies through much of the post-Cambrian Phanerozoic. Brett & Eckert (1982) and LoDuca *et al.* (1997), for example, emphasized the importance of episodic burial under smothering muds for the preservation of fully articulated echinoderms in some post-Cambrian deposits. Meyer & Meyer (1986) and Baumiller & Ausich (1992) demonstrated empirically that echinoderms normally begin disarticulating within hours of death, which emphasizes the speed with which bodily remains must be buried if they are to be preserved intact. Overall, disarticulated echinoderm ossicles are far more common in Cambrian deposits than are articulated remains (see Babcock 1994, Hollingsworth & Babcock 2011), but with rare exception (*e.g.*, the distinctive ossicles of helicoplacoids; Wilbur 2006, English & Babcock 2010, Hollingsworth & Babcock 2011) cannot easily be associated with a particular echinoderm group.

The specimen reported here (Fig. 2) appears to have buried in an obrution deposit, and as such, presumably preserves the animal's remains in place, and in paleoecological context. The specimen is attached by means of a basal disk to the dorsal surface of a hyolithid conch (Fig. 2A, B, E) identified as *Haplophrentis reesei* Babcock & Robison, 1988. A hyolithid operculum of matching size is present near the aperture of the conch, and probably belongs to the same individual. This suggests that the edrioasteroid attached to the conch of a living hyolithid animal, and grew to large size upon it. The presence of an operculum in association with the conch suggests that the hyolithid was alive shortly before burial. We did not find helens associated with the hyolithid. They may not have preserved well, or perhaps were lost shortly before final burial. As preserved, the edrioasteroid, and some of the hyolithid, is coated with a yellowish-brown iron oxide, probably a pseudomorph after pyrite (compare

Lin *et al.* 2008). The Idaho edrioasteroid, preserved attached to a hyolithid, is inferred to have been toppled and buried rapidly by sediment smothering during a storm event (compare Robison 1991, Lin *et al.* 2008, Robison *et al.* 2015). It may have undergone a small amount of current transport moments before burial but is unlikely to have been transported very far. Extensive current transport would have likely resulted in detachment of the edrioasteroid from the hyolithid shell.

A number of fossil echinoderms have been shown to have attached to hyolithids or other hard, shelly substrates. Robison *et al.* (2015, fig. 188), for example, previously illustrated a specimen of the edrioasteroid *Totiglobus* attached to a trilobite sclerite. Bell & Sprinkle (1978, pl. 6, fig. 9) illustrated a specimen of *T. nimius* “pressed against a fragment of another invertebrate”; this possibly represents attachment of the edrioasteroid to a trilobite sclerite. Zamora *et al.* (2017) illustrated a helicoplacoid and some eocrinoids attached to trilobite sclerites. Lin *et al.* (2008), Zhao *et al.* (2008), Yan *et al.* (2010), Parsley (2012), and Sun *et al.* (2016) discussed the attachment of eocrinoids to hyolithid conchs or other calcareous biotritus in the Cambrian of Guizhou, China. During the Paleozoic, hyolithid conchs were commonly used as substrates for the attachment of epibiont macroorganisms including echinoderms (Lin *et al.* 2008, Yan *et al.* 2010, Robison *et al.* 2015, Sun *et al.* 2016) and conulariids (Babcock *et al.* 1987).

In addition to a hyolithid, the new edrioasteroid from Idaho is also associated on the same bedding plane with disarticulated trilobite sclerites (fragmentary thoracic segments, a free cheek, and a cranidium; Fig. 2B). Whereas the edrioasteroid-hyolithid ensemble was most likely buried *in situ* (autochthonously) and alive under a sediment cloud, the broken and disarticulated trilobite sclerites could have been either autochthonous or parautochthonous, but were more likely parautochthonous. Babcock & Speyer (1987) showed that vagile trilobites preserved by being buried alive under storm-deposited sediment probably dug into the sediment and became fully enrolled as a means of survival. Normally, the animals would unroll and dig out of the sediment after passage of the storm (see Stitt 1983, Velbel 1985, Babcock 2003). This implies that remains of articulated trilobite exoskeletons in such event beds are normally moults or carcasses. Disarticulated sclerites and broken sclerites of trilobites are common in mid-Cambrian event beds of the Great Basin (Robison & Babcock 2011). Disarticulated sclerites and broken sclerites from subtidal settings such as these have been attributed to the action of carnivores, both as the result of predation and scavenging (*e.g.*, Babcock 2003, Robison *et al.* 2015). Mechanical breakage of sclerites may be a possibility, but it seems more likely to have occurred in marginal-marine environments (see Hughes 1993, Babcock *et al.* 2014),

Table 1. Occurrences of edrioasteroids in Cambrian strata, including information about attachment structures. For some species, evidence of attachment is unknown at present, and if so, is indicated as such. Abbreviations: [*] – *nomen dubium* according to Smith (1958); [**] – revised as junior synonym of *S. pentangularis*; Fm. – Formation.

Species reported	Geographic occurrence	Stratigraphic occurrence	Attachment structures	Other references
<i>Kailidiscus chinensis</i> Zhao <i>et al.</i> , 2010	Guizhou, China	Kaili Fm. (<i>Oryctocephalus indicus</i> Zone; Wuliuan Stage)	Suction disk for attachment to mat-stabilized surface.	Zhao <i>et al.</i> (2017)
<i>Walcottidiscus typicalis</i> Bassler, 1935	British Columbia, Canada	Burgess Shale (<i>Ptychagnostus praecurrens</i> Zone; Wuliuan Stage)	Unplated aboral surface; possibly attached to mat-stabilized surface.	Zamora <i>et al.</i> (2017)
<i>Walcottidiscus magister</i> Bassler, 1936	British Columbia, Canada	Burgess Shale (<i>Ptychagnostus praecurrens</i> Zone; Wuliuan Stage)	As for <i>W. typicalis</i> .	Zamora <i>et al.</i> (2017)
<i>Totiglobus nimius</i> Bell & Sprinkle, 1978	Nevada, USA	Chisholm Shale (<i>Glossopleura</i> Zone; Wuliuan Stage)	Suction disk for attaching to mat-stabilized surface or hard substrate.	Domke & Dornbos (2010), Zamora <i>et al.</i> (2017)
New totiglobid edrioasteroid	Utah, USA	Spence Shale (<i>Glossopleura</i> Zone/ <i>Oryctocephalus</i> Zone; Wuliuan Stage)	As for <i>T. spencensis</i> .	Robison <i>et al.</i> (2015)
<i>Totiglobus spencensis</i> sp. nov.	Idaho, USA	Spence Shale (<i>Glossopleura</i> Zone/ <i>Oryctocephalus</i> Zone/ <i>Ptychagnostus praecurrens</i> Zone; Wuliuan Stage)	Basal disk for attaching to hard substrate.	This paper
<i>Totiglobus lloydi</i> Sprinkle, 1985	Utah, USA	Marjum Fm. (<i>Bolaspidea</i> Zone/ <i>Ptychagnostus punctuosus</i> Zone; Drumian Stage)	As for <i>T. spencensis</i> .	Robison <i>et al.</i> (2015)
<i>Edriodiscus primiticus</i> Henderson & Shergold, 1971	Queensland, Australia	Beetle Creek Fm., Yelvertoft Member (Wuliuan Stage)	Unplated aboral surface and marginal ring for attachment.	Smith & Jell (1990), Zamora (2013), Zamora <i>et al.</i> (2017)
<i>Hadriodiscus parma</i> Smith & Jell, 1990	Queensland, Australia	Chatsworth Limestone (<i>Peichiasiania secunda-Prochuangia glabella</i> Ass. Zone; Paibian Stage)	As for <i>E. primiticus</i> .	Zamora (2013), Zamora <i>et al.</i> (2017)
<i>Chatsworthia spinoda</i> Smith & Jell, 1990	Queensland, Australia	Chatsworth Limestone (<i>Peichiasiania secunda-Prochuangia glabella</i> Ass. Zone; Paibian Stage)	As for <i>E. primiticus</i> .	Zamora (2013), Zamora <i>et al.</i> (2017)
<i>Protophorus hispanicus</i> Zamora & Smith, 2010	NE Spain	Uppermost Murero Fm. (<i>Solenopleuropsis thoralis</i> age; Wuliuan Stage)	Unplated aboral surface and marginal ring for attachment to hard substrate for attachment.	Zamora <i>et al.</i> (2017)
<i>Persiadiskos zhuravlevi</i> Guensburg & Rozhnov, 2014	Northern Iran	Mila Fm., Member 2 (Paibian Stage)	Marginal rim; attached to hardground (hard substrate).	Zamora <i>et al.</i> (2017)
<i>Isorophida</i> sp.	NE Spain	Murero Fm. (<i>Eccaparadoxides brachyrachis</i> beds; Wuliuan Stage)	Unplated aboral surface and marginal ring for attachment to hard substrate.	Zamora & Smith (2010), Zamora <i>et al.</i> (2017)
<i>Cambraster tastudorum</i> Jell <i>et al.</i> , 1985	Tasmania, Australia	Cateena Group (Drumian Stage)	Plated aboral surface and marginal ring for attachment, possibly to sediment.	Zamora <i>et al.</i> (2007, 2012, 2017)
<i>Cambraster</i> cf. <i>tastudorum</i> Jell <i>et al.</i> , 1985	NE Spain	Upper Murero Fm. (<i>Solenopleuropsis verdiagana</i> + <i>S. riberoi</i> Biozone; Drumian Stage)	As for <i>C. tastudorum</i> .	Zamora <i>et al.</i> (2007)
<i>Cambraster cannati</i> Miquel, 1894	South France	Coulouma Fm. (<i>Paradoxides mediterraneus</i> Zone; Wuliuan Stage)	As for <i>C. tastudorum</i> .	Zamora <i>et al.</i> (2007, 2012, 2017)
<i>Cambroblastus enubilatus</i> Smith & Jell, 1990	Queensland, Australia	Chatsworth Limestone (<i>Peichiasiania secunda-Prochuangia glabella</i> Assemblage-Zone, Paibian Stage)	Plated aboral surface and marginal ring for attachment to hard substrate.	Zhu <i>et al.</i> (2014), Zamora <i>et al.</i> (2017)
<i>Aragocystites belli</i> Zamora, 2013	Spain	Middle-upper Murero Fm. (Wuliuan Stage)	Basal disk for attachment to sediment.	Zamora <i>et al.</i> (2017)
<i>Stromatocystites</i> sp.	Northern Spain	Oville Fm. (Wuliuan Stage)	Plated aboral surface with central pad for attachment to sediment.	Zamora <i>et al.</i> (2015, 2017)
<i>Stromatocystites</i> cf. <i>pentangularis</i> Pompeckj, 1896	Southeastern Turkey	Koruk Fm. (Drumian Stage)	As for <i>Stromatocystites</i> sp.	Lefebvre <i>et al.</i> (2010), Zamora <i>et al.</i> (2015)
<i>Stromatocystites walcotti</i> Schuchert, 1919; <i>S. pentangularis</i> Pompeckj, 1896	Newfoundland	Forteau Fm. (<i>Olenellus</i> Zone; Stage 4)	As for <i>Stromatocystites</i> sp.	Smith (1985), Zamora <i>et al.</i> (2015)
<i>Stromatocystites pentangularis</i> Pompeckj, 1896	Sweden	Alum Shale (<i>Eccaparadoxides pinus</i> Zone; lower Wuliuan Stage)	As for <i>Stromatocystites</i> sp.	Lefebvre <i>et al.</i> (2010), Zamora <i>et al.</i> (2015)
<i>Stromatocystites balticus</i> Jaekel, 1899 [*]	Northern Germany	Glacial erratic blocks (<i>Paradoxides paradoxissimus</i> Zone; Wuliuan Stage)	As for <i>Stromatocystites</i> sp.	Jaekel (1921)
<i>Stromatocystites reduncus</i> Smith & Jell, 1990	Queensland, Australia	Beetle Creek Fm., Yelvertoft Member (Stage 4)	As for <i>Stromatocystites</i> sp.	Jell <i>et al.</i> (1985), Zamora <i>et al.</i> (2015)
<i>Stromatocystites</i> cf. <i>pentangularis</i> Pompeckj, 1896	Northern Germany	Glacial erratic blocks (<i>Paradoxides paradoxissimus</i> Zone; Wuliuan Stage)	As for <i>Stromatocystites</i> sp.	Zamora <i>et al.</i> (2015)
<i>Stromatocystites</i> sp.	Poland	Usarzów Fm. (<i>Eccaparadoxides insularis</i> Zone and <i>Paradoxides pinus</i> Zone; Wuliuan Stage)	As for <i>Stromatocystites</i> sp.	Zamora <i>et al.</i> (2015)
<i>Stromatocystites pentangularis</i> Pompeckj, 1896	Czech Republic	Buchava Fm., Slapnice Member (<i>Eccaparadoxides pusillus</i> Zone; Wuliuan to Drumian Stage)	As for <i>Stromatocystites</i> sp.	Zamora <i>et al.</i> (2015)
<i>Stromatocystites flexibilis</i> Parsley & Prokop, 2004	Czech Republic	Jince Fm. (lower part of the <i>Paradoxides gracilis</i> Zone; Wuliuan Stage)	As for <i>Stromatocystites</i> sp.	Fatka <i>et al.</i> (2004)
? <i>Stromatocystites</i> sp. [**]	France	<i>Velieucystis</i> level (upper Paibian Stage)	Uncertain.	Ubahgs (1998)
<i>Stromatocystites</i> sp.	Morocco	Wawrmast Fm., Tarhoucht Member (<i>Morocconus notabilis</i> Zone; Wuliuan to Drumian Stage)	As for <i>Stromatocystites</i> sp.	Zamora (2013), Zamora <i>et al.</i> (2015)

where exoskeletal remains could have been washed ashore (see Babcock *et al.* 2014), desiccated, and become brittle, making them more susceptible to breakage.

All known species of *Totiglobus* evidently lived attached in post-larval life (Sprinkle *et al.* 2009, Robison *et al.* 2015, Zamora *et al.* 2017), although most previously documented specimens became detached prior to final burial. The mode of attachment, however, is variable, and appears to be species-specific. Originally, *T. nimius* Bell & Sprinkle, 1978, the type species of the genus from

the Chisholm Formation (Cambrian: Wuliuan) of Nevada (Fig. 1), was interpreted as a sediment attacher, although one basal disk (Bell & Sprinkle 1978, p1. 6, fig. 9) was found attached to an arthropod fragment. Domke & Dornbos (2010) argued that, the attachment structure of *T. nimius* was an invaginated basal disk that created suction for adhesion to a mat-stabilized sediment surface and also hypothesized that a bioglue may have further stabilized the attachment. Species ?*Totiglobus lloydi* Sprinkle, 1985, from the Marjum Formation (Cambrian:

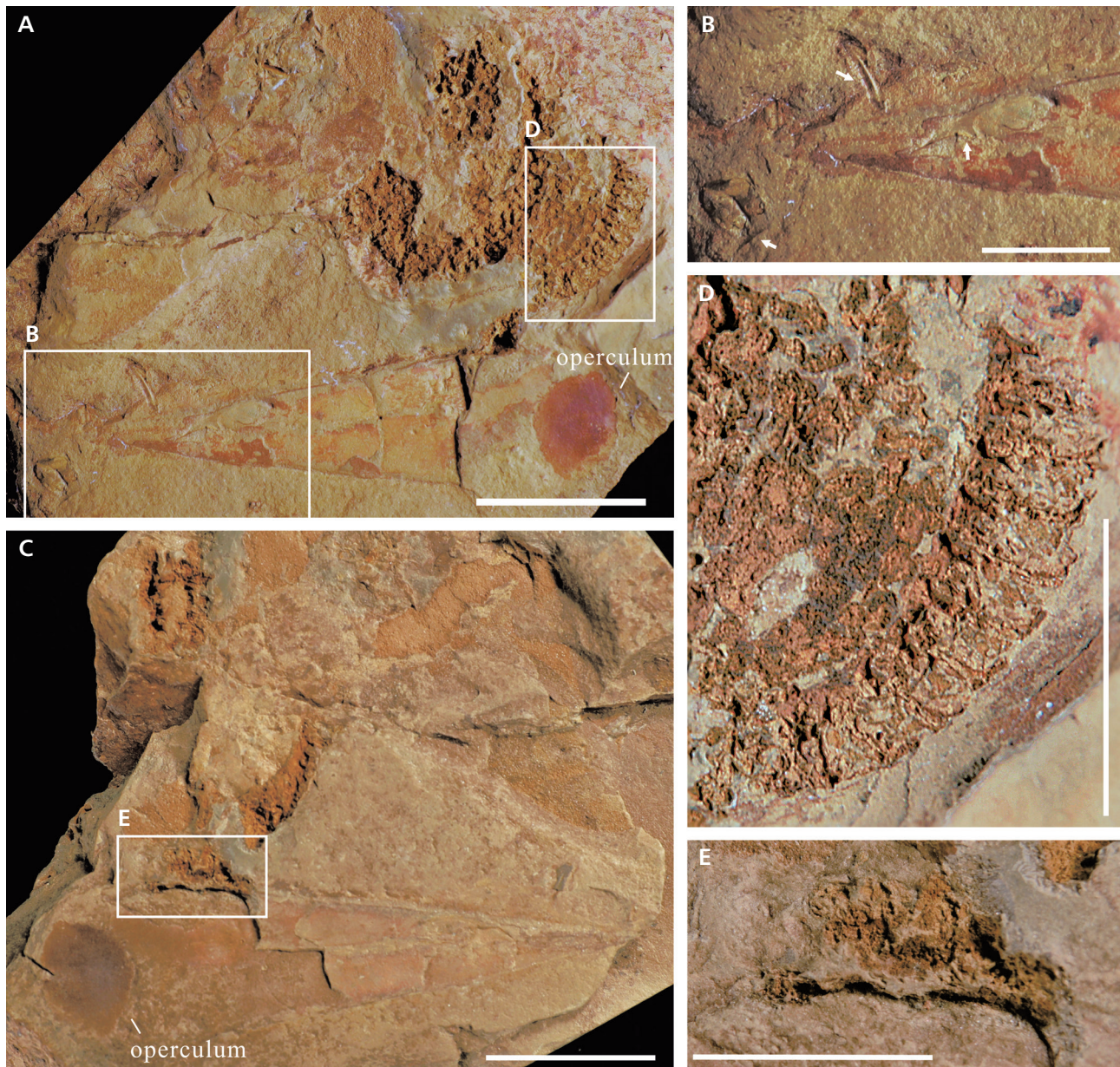


Figure 2. *Totiglobus spencensis* sp. nov., holotype, from the Spence Shale (Cambrian: Wuliuan Stage), Spence Gulch, Idaho; A – (part, KUMIP 49294A) and C – (counterpart, KUMIP 49294B); B – enlargement of part (see A), white arrows indicate trilobite sclerites; D – enlargement of part (see A) showing ambulacra and interambulacral plates; E – enlargement of counterpart (see C) showing attachment structure. Scale bar = 10 mm for (A, C); 5 mm for (B, D, E).

Drumian) of Utah has a conical aboral theca tapering down to a slightly concave basal surface (?disk). The aboral area is composed of tiny plates similar to the attachment structures found in many gogiids (Sprinkle 1985). The holotype of *T. spencensis*, reported here, has a conical aboral theca terminating in a basal attachment disk, and it is attached to a hyolithid conch (Fig. 2). We infer that *T. spencensis* and ?*T. lloydi*, both attached to hard substrates, and adhesion was made possible or enhanced by means of a biogluce.

Temporal occurrences of Cambrian edrioasteroids and attachment mechanisms

As summarized in Tab. 1, edrioasteroid occurrences cluster into fairly discrete time intervals of the Cambrian. This may be related more to depositional environments and favorable taphonomic conditions than to aspects of the evolutionary history of the clade. All recorded occurrences are in strata of provisional Stage 4, the Wuliuan Stage, the Drumian Stage, or the Paibian Stage. The early parts of each of these stages/ages represent time intervals of inferred eustatic sea level rise or highstand, when continental shelves were widely inundated with shallow marine water (Peng *et al.* 2012, Babcock *et al.* 2015). The edrioasteroid specimens discussed here are from the Wuliuan Stage, at a time when *Laurentia* was located in the tropics and covered with broad, epeiric seas. The shelf area that now forms the Great Basin region is inferred to have been subjected to episodic storms that have commonly resulted in the preservation of fully articulated echinoderms (see Sprinkle 1973, Robison 1991, Robison *et al.* 2015).

Numerous Cambrian edrioasteroids are known to have attachment structures, and Tab. 1 summarizes what we currently know of those structures, as well as whether these echinoderms were attached to sediment, including mat-stabilized sediment, or hard substrates. The earliest edrioasteroids (e.g., *Stromatocystites*, beginning in provisional Age 4; and *Totiglobus*, beginning in the Wuliuan Age) attached either to sediments (commonly mat-stabilized) or hard substrates. Available information shows that edrioasteroids first evolved mechanisms for attaching to hard substrates in the Wuliuan Age. By the Drumian, attachment to hard substrates had become the dominant post-larval life habit in edrioasteroids. This change in attachment seems to correlate with a reduction in mat-stabilized sediment in shallow marine ecosystems as sediment became increasingly fluidized through the action of benthic burrowers such as trilobites, other arthropods, and varied worms (e.g., Seilacher & Pflüger 1994, Bottjer *et al.* 2000, Babcock 2003, Domke & Dornbos 2010, Buatois *et al.* 2014, Mángano & Buatois 2014).

Systematic paleontology

Class Edrioasteroidea Billings, 1858
Order Edrioasterida Bell, 1976
Family Totiglobidae Bell & Sprinkle, 1978

Genus *Totiglobus* Bell & Sprinkle, 1978

Type species. – *Totiglobus nimius* Bell & Sprinkle, 1978.

Diagnosis. – The emended diagnosis of Sprinkle (1985) is followed herein.

Occurrence. – *Totiglobus* has been reported from Cambrian strata of the Great Basin of the western United States (Utah, Nevada, and Idaho). It ranges from the Wuliuan Stage through Drumian Stage (Miaolingian Series).

Totiglobus spencensis sp. nov.

Figure 2

Holotype. – University of Kansas Museum of Invertebrate Paleontology, part (KUMIP 49294A) and counterpart (KUMIP 492941B).

Type horizon and locality. – Spence Shale of Spence Gulch, Bear River Range, southeastern Idaho (Cambrian: Miaolingian Series, Wuliuan Stage).

Material. – Holotype only.

Etymology. – Name derived from Spence Gulch, the location of the holotype, and type section of the Spence Shale.

Diagnosis. – Species of *Totiglobus* having hemispherical adoral area, ambulacra slightly curved counterclockwise, extending to the aboral area, relatively small interambulacral plates, and a relatively short, conical aboral theca terminating in a basal attachment disk.

Description. – Only one incomplete specimen is known (Fig. 2). Theca preserved in oblique side view with parts of four ambulacra visible. Theca as preserved 28 mm long, 26 mm wide, maximum width just below mid-length. Adoral theca hemispherical; ambulacra slightly curved anticlockwise, tapering, and extending to area of contact with aboral area; two or three pairs of ambulacral cover plates present. Interambulacra relatively wide, slightly concave, with relatively small interambulacral plates, apparently lacking pores. Aboral theca conical, relatively short, slightly tapering, and terminating in a small basal attachment disk. Mouth, anal plates, and the hydropore not observed.

Remarks. – This new species brings to three the number assigned to *Totiglobus*. Previously, *Totiglobus nimius* Bell & Sprinkle, 1978, the type species of the genus, was reported from numerous specimens collected from the Chisholm Formation in the Pioche mining district of Nevada (Bell & Sprinkle 1978, Domke & Dornbos 2010), and ?*Totiglobus lloydi* Sprinkle, 1985 (later referred to as *T. lloydi*; Robison et al. 2015) was described from a single specimen collected from the Marjum Formation of western Utah (Sprinkle 1985). *Totiglobus spencensis* resembles *T. nimius* principally in the general shape of the adoral area, but differs in having less curvature in the ambulacra, and in having a conical aboral region terminating in an attachment disk. As preserved in the holotype, the attachment disk is 6 mm in diameter. *Totiglobus spencensis* differs from *T. lloydi* most notably in having a different overall shape, including a shorter aboral area, in having slightly curved, rather than straight, ambulacra, and in lacking pustular or rugose ornament on the thecal plates of the aboral area. It is conceivable that curvature of the ambulacra has been enhanced somewhat through compaction in sediment, but likely that much of the apparent curvature was present in life. Spiraling of the ambulacra is a common trait in edrioasteroids, and indeed other echinoderms; spiral or helical asymmetry has been interpreted as a fundamental aspect of the biology of many extant and ancient organisms (Galloway 1991, Babcock 2005).

Robison et al. (2015) illustrated a “new totiglobid edrioasteroid” from the Spence Shale of western Utah that was attached to a trilobite free cheek. This specimen evidently represents a new species of *Totiglobus*, one that appears to differ from *T. spencensis* in having nearly straight ambulacra, and probably a longer theca. Its attachment structure is obscured.

Occurrence. – Spence Shale of Spence Gulch, Bear River Range, southeastern Idaho (Cambrian: Miaolingian Series, Wuliuan Stage).

Conclusion

The Cambrian edrioasteroid *Totiglobus* shows two styles of attachment in post-larval life. In the type species, *T. nimius*, attachment was by means of a suction disk on the aboral surface. The suction disk allowed adhesion to mat-stabilized surfaces. Species ?*Totiglobus lloydi* and *T. spencensis* sp. nov. were both attached to hard substrates by means of a more elongate, conical aboral surface. Attachment by means of a suction-type device was more common among the earliest edrioasteroids such as *T. nimius* and *Stromatocystites*. With increasing fluidization of sediments by benthic burrowers in the Cambrian,

suction-type attachment became less common and devices for attaching to hard substrates, such as those exemplified in *T. lloydi* and *T. spencensis*, became more prevalent. Attachment to hard substrates dominated the life mode of edrioasteroids from about the Drumian Age through the post-Cambrian.

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References

- BABCOCK, L.E. 1994. Biostratigraphic significance and paleogeographic implications of Cambrian fossils from a deep core, Warren County, Ohio. *Journal of Paleontology* 68(1), 24–30. DOI 10.1017/S0022336000025579
- BABCOCK, L.E. 2003. Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems, 55–92. In KELLEY, P., KOWALEWSKI, M. & HANSEN, T.A. (eds) *Predator-prey interactions in the fossil record*. Springer, Boston.
- BABCOCK, L.E. 2005. Asymmetry in the fossil record. *European Review* 13(Suppl. 2), 135–143. DOI 10.1017/S1062798705000712
- BABCOCK, L.E., FELDMANN, R.M., WILSON, M.T. & SUÁREZ-RIGLOS, M. 1987. Devonian conulariids of Bolivia. *National Geographic Research* 3, 210–231.
- BABCOCK, L.E. & ROBISON, R.A. 1988. Taxonomy and paleobiology of some Middle Cambrian *Scenella* (Cnidaria) and hyolithids (Mollusca) from western North America. *University of Kansas Paleontological Contributions* 121, 1–22.
- BABCOCK, L.E. & SPEYER, S.E. 1987. Enrolled trilobites from the Alden Pyrite Bed, Ledyard Shale (Middle Devonian) of western New York. *Journal of Paleontology* 61(3), 539–548. DOI 10.1017/S0022336000028699
- BABCOCK, L.E., BARANOSKI, M.T. & COOK, A.E. 2014. Cambrian

- (Guzhangian Stage) trilobites from Ohio, USA, and modification of the *Cedaria* Zone as used in Laurentia. *Geologiska Föreningens i Stockholm Förhandlingar* 136(1), 6–15. DOI 10.1080/11035897.2013.879736
- BABCOCK, L.E., PENG, S.C., CARLTON, E.B., ZHU, M.Y., AHLBERG, P., BEVIS, M. & ROBISON, R.A. 2015. Global climate, sea level cycles, and biotic events in the Cambrian Period. *Palaeoworld* 24, 5–15. DOI 10.1016/j.palwor.2015.03.005
- BASSLER, R.S. 1935. The classification of the Edrioasteroidea. *Smithsonian Miscellaneous Collections* 93, 1–11.
- BASSLER, R.S. 1936. New species of American Edrioasteroidea. *Smithsonian Miscellaneous Collections* 95, 1–33.
- BAUMILLER, T.K. & AUSICH, W.I. 1992. The broken-stick model as a null hypothesis for crinoid stalk taphonomy and as a guide to the distribution of connective tissue in fossils. *Paleobiology* 18(3), 288–298. DOI 10.1017/S009483730001085X
- BELL, B.M. 1976. Phylogenetic implications of ontogenetic development in the class Edrioasteroidea (Echinodermata). *Journal of Paleontology* 50(6), 1001–1019.
- BELL, B.M. & SPRINKLE, J. 1978. *Totiglobus*, an unusual new edrioasteroid from the Middle Cambrian of Nevada. *Journal of Paleontology* 52(2), 243–266.
- BILLINGS, E. 1858. On the Asteriadae of the Lower Silurian rocks of Canada, 75–85. In LOGAN, W.E. (ed.) *Figures and descriptions of Canadian organic remains, Decade 3, Geological Survey of Canada Separate Report* 425.
- BONINO, E. & KIER, C. 2010. *The Back to the Past Museum Guide to Trilobites*. 495 pp. Casa Editrice Marna, Lecco.
- BOTTJER, D.J., HAGADORN, J.W. & DORNBOS, S.Q. 2000. The Cambrian substrate revolution. *GSA Today* 10(9), 1–7.
- BRETT, C.E. & ECKERT, J.D. 1982. Palaeoecology of a well-preserved crinoid colony from the Silurian Rochester Shale in Ontario. *Royal Ontario Museum Life Sciences Contribution* 131, 1–20. DOI 10.5962/bhl.title.52074
- BUATOIS, L.A., NARBONNE, G.M., MANGANO, M.G., CARMONA, N.B., & MYROW, P. 2014. Ediacaran matground ecology persisted into the earliest Cambrian. *Nature Communications* 5, 3544. DOI 10.1038/ncomms4544
- CAMPBELL, D.P. 1974. *Biostratigraphy of the Albertella and Glossopleura zones (lower Middle Cambrian) of northern Utah and southern Idaho*. 295 pp. Master thesis, University of Utah, Salt Lake City, USA.
- COHEN, K.M., HARPER, D.A.T., GIBBARD, P.M. & FAN, J.X. 2018. *International chronostratigraphic chart, v 2018/08*. International Commission on Stratigraphy. www.stratigraphy.org
- CONWAY MORRIS, S. 1986. The community structure of the Middle Cambrian phyllopod bed (Burgess Shale). *Palaeontology* 29(3), 423–467.
- CONWAY MORRIS, S. & WHITTINGTON, H.B. 1985. Fossils of the Burgess Shale: a National Treasure in Yoho National Park, British Columbia. *Geological Survey of Canada, Miscellaneous Report* 43, 1–31.
- DOMKE, K.L. & DORNBOS, S.Q. 2010. Paleoeecology of the middle Cambrian edrioasteroid echinoderm *Totiglobus*: implications for unusual Cambrian morphologies. *Palaios* 25(3), 209–214. DOI 10.2110/palo.2009.p09-111r
- ENGLISH, A.M. & BABCOCK, L.E. 2010. Census of the Indian Springs Lagerstätte, Poleta Formation (Cambrian), western Nevada, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295, 236–244. DOI 10.1016/j.palaeo.2010.05.041
- FATKA, O., KORDULE, V. & SZABAD, M. 2004. Stratigraphical distribution of Cambrian fossils in the Příbram-Jince Basin (Barrandian area, Czech Republic). *Senckenbergiana lethaea* 84(1), 367–381.
- GALLOWAY, J.W. 1991. Macromolecular asymmetry, 16–35. In BOCK, G.R. & MARSH, J. (eds) *Biological asymmetry and handedness*. Wiley, Chichester.
- GARSON, D.E., GAINES, R.R., DROSER, M.L., LIDDELL, W.D. & SAPPENFIELD, A. 2012. Dynamic palaeoredox and exceptional preservation in the Cambrian Spence Shale of Utah. *Lethaia* 45(2), 164–177. DOI 10.1111/j.1502-3931.2011.00266.x
- GUENSBURG, T.E. & ROZHNOV, S.V. 2014. A unique edrioasteroid from the upper Middle Cambrian of Iran, its phylogenetic implications and paleoecology. *Paleontological Journal* 48(4), 401–406. DOI 10.1134/S0031030114040078
- GUNTHER, L.F. & GUNTHER, V.G. 1981. Some Middle Cambrian fossils of Utah. *Brigham Young University Geology Studies* 28(1), 1–81.
- HENDERSON, R.A. & SHERGOLD, J.H. 1971. Cyclocystoides from early Middle Cambrian rocks of northwestern Queensland, Australia. *Palaeontology* 14(4), 704–710.
- HOLLINGSWORTH, J.S. & BABCOCK, L.E. 2011. Base of Dyeran Stage (Cambrian Stage 4) in the middle member of the Poleta Formation, Indian Springs Canyon, Montezuma Range, Nevada. *Museum of Northern Arizona Bulletin* 67, 256–262.
- HUGHES, N.C. 1993. Distribution, taphonomy and functional morphology of the Upper Cambrian trilobite *Dikelocephalus*. *Milwaukee Public Museum Contributions in Biology and Geology* 84, 1–47.
- JAEKEL, O. 1899. *Stammesgeschichte der Pelmatozoen: Thecoidea und Cystoidea*. 442 pp. Julius Springer, Berlin. DOI 10.5962/bhl.title.8521
- JAEKEL, O. 1921. Phylogenie und system der Pelmatozoen. *Paläontologische Zeitschrift* 3(1), 1–128. DOI 10.1007/BF03190413
- JELL, P.A., BURRETT, C.F. & BANKS, M.R. 1985. Cambrian and Ordovician echinoderms from eastern Australia. *Alcheringa* 9(3), 183–208. DOI 10.1080/03115518508618967
- LEFEBVRE, B. & LEROSEY-AUBRIL, R. 2018. Laurentian origin of solutan echinoderms: new evidence from the Guzhangian (Cambrian Series 3) Weeks Formation of Utah, USA. *Geological Magazine* 155(5), 1190–1204. DOI 10.1017/S0016756817000152
- LEFEBVRE, B., HÖSGOR, I., NARDIN, E., FATKA, O. & GÖNCÜOĞLU, M.C. 2010. First report of Stromatocystites (Echinodermata) from the Middle Cambrian of Turkey: Palaeobiogeographic implications. *Department of Geology Science Yearbook* 39, 227–228.
- LIDDELL, W.D., WRIGHT, S.H. & BRETT, C.E. 1997. Sequence stratigraphy and paleoecology of the Middle Cambrian Spence Shale in northern Utah and southern Idaho. *Brigham Young University Geology Studies* 42, 59–78.
- LIN, J.P., AUSICH, W.I., ZHAO, Y.L. & PENG, J. 2008. Taphonomy,

- palaeoecological implications, and colouration of Cambrian gogiid echinoderms from Guizhou Province, China. *Geological Magazine* 145(1), 17–36.
DOI 10.1017/S0016756807003901
- LODICA, S.T., BRETT, C.E. & BAIRD, G.C. 1997. The Medusaegraptus epibole and lower Ludlovian Konservat-Lagerstätten of eastern North America, 369–405. In BRETT, C.E. & BAIRD, G.C. (eds) *Paleontological Events: Stratigraphic, Ecological, and Evolutionary Implications*.
- MÁNGANO, M.G. & BUATOIS, L.A. 2014. Decoupling of body-plan diversification and ecological structuring during the Ediacaran-Cambrian transition: evolutionary and geobiological feedbacks. *Proceedings in Biological Science* 281, 1–9. DOI 10.1098/rspb.2014.0038
- MEYER, D.L. & MEYER, K.B. 1986. Biostratigraphy of Recent crinoids (Echinodermata) at Lizard Island, Great Barrier Reef, Australia. *Palaios* 3(3), 294–302. DOI 10.2307/3514692
- MIQUEL, J. 1894. Note sur la géologie des terrains primaires du département de l'Hérault: Le Cambrien et l'Arenig. *Bulletin de la Société d'étude des sciences naturelles de Béziers* 17, 5–36.
- PARSLEY, R.L. 2012. Ontogeny, functional morphology, and comparative morphology of lower (Stage 4) and basal middle (Stage 5) Cambrian gogiids, Guizhou Province, China. *Journal of Paleontology* 86(4), 569–583.
DOI 10.1666/10-153R2.1
- PARSLEY, R.L. & PROKOP, R.J. 2004. Functional morphology and paleoecology of some sessile Middle Cambrian echinoderms from the Barrandian region of Bohemia. *Bulletin of Geosciences* 79(3), 147–156.
- PARSLEY, R.L. & ZHAO, Y.L. 2006. Long stalked eocrinoids in the basal Middle Cambrian Kaili Biota, Taijiang County, Guizhou Province, China. *Journal of Paleontology* 80(6), 1058–1071.
DOI 10.1666/0022-3360(2006)80[1058:LSEITB]2.0.CO;2
- PENG, S.C., BABCOCK, L.E. & COOPER, R.A. 2012. The Cambrian Period, 437–488. In GRADSTEIN, F.M., OGG, J.G., SCHMITZ, M.D. & OGG, G.M. (eds) *The Geologic Time Scale 2012*. Elsevier BV, Amsterdam.
- POMPECKJ, J.F. 1896. Die Fauna des Kambrium von Tejšovic und Skrej in Böhmen. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 45, 495–615.
- RESSER, C.E. 1939. The Spence Shale and its fauna. *Smithsonian Miscellaneous Collections* 97(12), 1–29.
- ROBISON, R.A. 1991. Middle Cambrian biotic diversity: examples from four Utah Lagerstätten, 77–98. In SIMONETTA, A. & CONWAY MORRIS, S. (eds) *The Early Evolution of Metazoa and the Significance of Problematic Taxa*. Cambridge University Press, Cambridge.
- ROBISON, R.A. & BABCOCK, L.E. 2011. Systematics, paleobiology, and taphonomy of some exceptionally preserved trilobites from Cambrian Lagerstätten of Utah. *University of Kansas Paleontological Contributions* 5, 1–47.
- ROBISON, R.A., BABCOCK, L.E. & GUNTHER, V.G. 2015. Exceptional Cambrian fossils from Utah: a Window into the Age of Trilobites. *Utah Geological Survey Miscellaneous Publication 15-1*, 1–97.
- SCHUCHERT, C. 1919. A Lower Cambrian edrioasteroid, *Stromatocystites walcotti*. *Smithsonian Miscellaneous Collections* 70, 1–7.
- SEILACHER, A. & PFLÜGER, F. 1994. From biomats to benthic agriculture: A biohistoric revolution, 97–105. In KRUMBEIN, W.E. et al. (eds) *Biostabilization of sediments: Oldenburg, Germany. Bibliotheks und Information system der Carl von Ossietzky Universität Oldenburg (BIS)*.
- SMITH, A.B. 1985. Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids. *Palaeontology* 28(4), 715–756.
- SMITH, A.B. & JELL, P.A. 1990. Cambrian edrioasteroids from Australia and the origin of starfishes. *Memoirs of the Queensland Museum* 28, 715–778.
- SPRINKLE, J. 1973. *Morphology and Evolution of Blastozoan Echinoderms*. 283 pp. Special Publication, Museum of Comparative Zoology, Harvard University, Cambridge.
- SPRINKLE, J. 1985. New edrioasteroid from the Middle Cambrian of western Utah. *University of Kansas Paleontological Contributions, Paper 116*, 1–4.
- SPRINKLE, J., GUENSBURG, T.E. & JAMISON, P. 2009. New Middle Cambrian edrioasteroid from the Spence Shale of northern Utah. *Geological Society of America Abstracts with Programs* 41(6), 14.
- STITT, J.H. 1983. Enrolled late Cambrian trilobites from the Davis formation, southeast Missouri. *Journal of Paleontology* 57(1), 93–105.
- SUMRALL, C.D. & SPRINKLE, J. 1992. Could edrioasteroids move? *The Paleontological Society Special Publication* 6, 284.
DOI 10.1017/S2475262200008443
- SUN, H.J., BABCOCK, L.E., PENG, J. & KASTIGAR, J.M. 2016. Systematics and palaeobiology of some Cambrian hyoliths from Guizhou, China, and Nevada, USA. *Alcheringa* 41(1), 79–100. DOI 10.1080/03115518.2016.1184426
- UBAGHS, G. 1998. Échinodermes nouveaux du Cambrien supérieur de la Montagne Noire (France méridionale). *Geobios* 31(6), 809–829. DOI 10.1016/S0016-6995(98)80111-3
- VELBEL, D.B. 1985. Ichnologic, taphonomic, and sedimentologic clues to the deposition of Cincinnati shales (Upper Ordovician), Ohio, U.S.A., 299–301. In CURRAN, H.A. (ed.) *Biogenic Structures: Their use in Interpreting Depositional Environments*. Society of Economic Paleontologists and Mineralogists Special Publication 35. DOI 10.2110/pec.85.35.0299
- WALCOTT, C.D. 1908. Cambrian Geology and Paleontology I, Nomenclature of some Cambrian Cordilleran formations. *Smithsonian Miscellaneous Collections* 53(1), 1–12.
- WILBUR, B.C. 2006. Reduction in the number of early Cambrian helicoplacoid species. *Palaeoworld* 15(3-4), 283–293.
DOI 10.1016/j.palwor.2006.10.009
- YAN, X., MAO, Y.Q., ZHAO, Y.L., PENG, J. & WU, M.Y. 2010. The holdfasts of eocrinoids in Cambrian, Guizhou Province. *Acta Palaeontologica Sinica* 49, 380–388. [in Chinese with English abstract]
- ZAMORA, S. 2013. Morphology and phylogenetic interpretation of a new Cambrian edrioasteroid (Echinodermata) from Spain. *Palaeontology* 56(2), 421–431.
DOI 10.1111/j.1475-4983.2012.01209.x
- ZAMORA, S. & SMITH, A.B. 2010. The oldest isorophid edrio-

- asteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids. *Acta Palaeontologica Polonica* 55(3), 487–494. DOI 10.4202/app.2010.0012
- ZAMORA, S., SUMRALL, C.D. & VIZCAÍNO, D. 2012. Morphology and ontogeny of the Cambrian edrioasteroid echinoderm *Cambraster cannati* from western Gondwana. *Acta Palaeontologica Polonica* 58(3), 545–559. DOI 10.4202/app.2011.0152
- ZAMORA, S., DELINE, B., ÁLVARO, J.J. & RAHMAN, I.A. 2017. The Cambrian substrate revolution and the early evolution of attachment in suspension-feeding echinoderms. *Earth-Science Reviews* 171, 478–491. DOI 10.1016/j.earscirev.2017.06.018
- ZAMORA, S., LEFEBVRE, B., ÁLVARO, J.J., CLAUSEN, S., ELICKI, O., FATKA, O., JELL, P., KOUCHINSKY, A., LIN, J.P., NARDIN, E., PARSLEY, R., ROZHN OV, S., SPRINKLE, J., SUMRALL, C., VIZCAÍNO, D. & SMITH, A.B. 2013. Cambrian echinoderm diversity and palaeobiogeography, 151–164. In HARPER, D.A.T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography. Geological Society of London, Memoir* 38. DOI 10.1144/M38.13
- ZAMORA, S., LEFEBVRE, B., HOSGÖR, I., FRANZEN, C., NARDIN, E., FATKA, O. & ÁLVARO, J.J. 2015. The Cambrian edrioasteroid *Stromatocystites* (Echinodermata): Systematics, palaeogeography, and palaeoecology. *Geobios* 48(5), 417–426. DOI 10.1016/j.geobios.2015.07.004
- ZAMORA, S., LINÁN, E., ALONSO, P.D., GOZALO, R. & VINTANED, J.A.G. 2007. A Middle Cambrian edrioasteroid from the Murero biota (NE Spain) with Australian affinities. *Annales de Paléontologie* 93(4), 249–260. DOI 10.1016/j.annpal.2007.09.003
- ZHAO, Y.L., PARSLEY, R.L. & PENG, J. 2008. Basal Middle Cambrian short-stalked eocrinoids from the Kaili biota: Guizhou province, China. *Journal of Paleontology* 82(2), 415–422. DOI 10.1666/06-041.
- ZHAO, Y.L., PARSLEY, R.L., PENG, J., BABCOCK, L.E., GUO, Q.J., YIN, L.M., YANG, X.L., WANG, C.J., GAINES, R.R., ESTEVE, J., YANG, R.D., YANG, Y.N., SUN, H.J., TAI, T.S. in press. Global Stratotype Standard Stratotype-Section and Point for the base of the Miaolingian Series and Wuliuan Stage ratified. *Episodes*.
- ZHAO, Y.L., SUMRALL, C.D., PARSLEY, R.L. & PENG, J. 2010. *Kailidiscus*, a new plesiomorphic edrioasteroid from the basal middle Cambrian Kaili Biota of Guizhou Province, China. *Journal of Paleontology* 84(4), 668–680. DOI 10.1666/09-159.1
- ZHU, X.J., ZAMORA, S. & LEFEBVRE, B. 2014. Morphology and palaeoecology of a new edrioblastoid from the Furongian of China. *Acta Palaeontologica Polonica* 59(4), 921–926. DOI 10.4202/app.2012.0116