

Eldonioids with associated trace fossils from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia

Natalie I. Schroeder,¹ John R. Paterson,¹ and Glenn A. Brock²

¹Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia (nschroed@myune.edu.au), (jpater20@une.edu.au)

²Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia (glenn.brock@mq.edu.au)

Abstract.—Rare specimens of eldonioids recovered from the lower Cambrian (Series 2, Stage 4) Emu Bay Shale (EBS) Konservat-Lagerstätte represent the first record of the group for the Cambrian of East Gondwana. The disc-shaped body of the EBS taxon bears fine concentric corrugations on the dorsal surface and, ventrally, a series of internal lobes that have primary and secondary bifurcations, as well as a coiled sac. It appears to be most similar to *Rotadiscus* and *Pararotadiscus* of the Cambrian Chengjiang and Kaili biotas of South China, respectively. While the structure of the internal lobes would indicate that this occurrence in the EBS represents a new taxon within the Rotadiscidae, lack of detail regarding the precise number of internal lobes and the condition of the circumoral tentacles warrants a more conservative approach in leaving the genus and species under open nomenclature. The EBS specimens also host trace fossils, including the remains of a burrow, which are generally lacking in the body-fossil-bearing layers of the Konservat-Lagerstätte interval. These traces appear to have been made by small organisms and are similar to traces associated with the discs of *Pararotadiscus guizhouensis* (Zhao and Zhu, 1994) from the Kaili Biota. The available taphonomic, paleoenvironmental, and ichnological evidence indicates that the EBS eldonioids are most likely vagrants that were transported or settled into the ‘preservational trap’ and subsequently exposed on the substrate for a brief period before burial, thereby allowing organisms to exploit their carcasses for nutrients or other purposes.

Introduction

Recent intensive excavation of the lower Cambrian (Series 2, Stage 4) Emu Bay Shale (EBS) at Buck Quarry on the northeast coast of Kangaroo Island has significantly increased the known diversity of this Konservat-Lagerstätte to over 50 species (Paterson et al., 2016). Like most Cambrian Konservat-Lagerstätten, the fauna is dominated by arthropods, both in diversity and, especially, abundance of individual animals (Ivantsov et al., 2005; Zhao et al., 2014; Paterson et al., 2016). Ongoing work at Buck Quarry continues to reveal new taxa; the diversity of nonarthropod fauna is also becoming better known (García-Bellido et al., 2013, 2014; Paterson et al., 2016). Many of these newly discovered taxa are enigmatic, and are often only represented by one or two specimens. One such group is the Eldonioidea Dzik, 1991, which includes disc-shaped organisms whose complex internal structure belies their superficially medusoid appearance. Anatomical features observed across the group include dorsal and ventral discs enclosing a distinctive coiled digestive system, with a ventrally located mouth and anus, two circumoral tentacles, and a suite of variously observed and interpreted radial structures and concentric rings. Only two eldonioid specimens are known from more than 5,500 specimens collected from Buck Quarry and registered in the South Australian Museum paleontology collection.

The affinity of eldonioids remains problematic, with suggestions ranging across the major metazoan groups, including cnidarians and lophophorate protostomes (Dzik, 1991; Zhao and Zhu, 1994; Chen et al., 1995; Dzik et al., 1997; Zhu et al., 2002), as well as deuterostomes (Conway Morris, 1993a, 1993b, figs. 2, 4; Chen et al., 1995; Chen, 2012; Zhang et al., 2013), such as holothurian echinoderms (Durham, 1974; Chen, 2009) and other ambulacrarians (as part of the informal, unranked stem-group called the ‘cambroernids’ sensu Caron et al., 2010b; Conway Morris et al., 2015). A taxonomic review of the group is long overdue, but two families that include Cambrian taxa are recognized, the Eldoniidae Walcott, 1911a and the Rotadiscidae Dzik, 1991, with a third post-Cambrian group informally referred to as the paropsonemids.

A summary of the geographic and stratigraphic distributions of eldonioids, along with some of their key morphological characteristics, is provided in Table 1.

Here we document a rare eldonioid from the EBS that displays similarities to *Pararotadiscus guizhouensis* from the middle Cambrian (Series 3, Stage 5) Kaili Biota of South China, including the presence of associated trace fossils on the discs of both forms. This adds support for close faunal affinities between the Konservat-Lagerstätten of South Australia and those of South China (Paterson et al., 2016) and extends the known geographical range of Cambrian eldonioids to East Gondwana.

Table 1. Geographic and stratigraphic distribution of Paleozoic eldonioids and their key morphological characteristics.

| Family | Genus and species | Previous names | Age | Formation and locality | No. of specimens | Ornament | Disc rigidity | No. internal lobes | No. bifurcations | Tentacle form | Diameter (mm) | Main references |
|-----------------|---|---|---|---|---------------------------------|--------------------------|---------------|--------------------|------------------|---------------------------|-----------------------------|---|
| Eldoniidae | <i>Eldonia ludwigi</i> Walcott, 1911a | | middle Cambrian | Burgess Shale Fmn, ?Duchesnay Fmn, British Columbia, Canada | >1,000 | Simple radial | Flexible | ~30 | 1 | Dendritic, short & stubby | ~120 (max) | Walcott (1911a) |
| | | | middle Cambrian | Spence Shale, Utah, USA | 1 | Simple radial | Flexible | ? | ? | ? | ~40 | Conway Morris and Robison (1988) |
| | | | middle Cambrian | Marjum Fmn, Utah, USA | 2 | Simple radial | Flexible | ? | ? | ? | ~80 | Conway Morris and Robison (1988); Conway Morris et al. (2015) |
| | | | middle Cambrian | Siligir Fmn, Siberia, Russia | 1 | Simple radial | Flexible | ~30 | 1 | ? | 38 | Friend et al. (2002) |
| | | <i>Eldonia eumorpha</i> (Sun and Hou, 1987) | <i>Stellostomites eumorphus</i> Sun and Hou, 1987; <i>Yunnanomedusa elegans</i> Sun and Hou, 1987 | early Cambrian | Chiungchussu Fmn, Yunnan, China | >2,000 | Simple radial | Flexible | 44 | 1 | Dendritic, long & slender | ~45–80 |
| Rotadiscidae | <i>Eldonia berbera</i> Alessandrello and Bracchi, 2003 | | Ordovician | Lower Ktaoua Fmn & First Bani Gp, Tafilalt, Morocco | 71 | Radial | Flexible | ~40–50 | 1 | ? | 85–195 | Alessandrello and Bracchi (2003) |
| | <i>Rotadiscus grandis</i> Sun and Hou, 1987 | | early Cambrian | Chiungchussu Fmn, Yunnan, China | >50 | Fine concentric | Rigid | ~90 | 1 | Digitate | ~150 (ave) | Zhu et al. (2002) |
| | <i>Rotadiscus</i> sp. | <i>Brzechowia</i> sp. Dzik, 1991; <i>Rotadiscus</i> sp. Masiak and Zylińska, 1994 | early - middle Cambrian | Ociesęki & Stowiec Sandstone Fmns, Holy Cross Mountains, Poland | 5 | Radial & fine concentric | Rigid | ? | ? | ? | 40–180 | Stasińska, 1960; Masiak and Zylińska, 1994 |
| | <i>Pararotadiscus guizhouensis</i> (Zhao and Zhu, 1994) | <i>Rotadiscus guizhouensis</i> Zhao and Zhu, 1994 | middle Cambrian | Kaili Fmn, Guizhou, China | >100 | Radial & fine concentric | Stiffened | ~40 | 1 | Dendritic | 15–105, most ~50–60 | Zhao and Zhu (1994); Zhu et al. (2002) |
| | Emu Bay Shale taxon | | early Cambrian | Emu Bay Shale, Kangaroo Island, Australia | 2 | Fine concentric | Stiffened | ~30–35 | 2 | ? | ~21 | Paterson et al. (2016); herein |
| Rotadiscidae? | <i>Velumbrella czarnockii</i> Stasińska, 1960 | | early - middle Cambrian | Ociesęki & Stowiec Sandstone Fmns, Holy Cross Mountains, Poland | >100 | Radial & concentric | Stiffened | ~28 | ? | ? | 19–86 | Stasińska (1960); Masiak and Zylińska (1994) |
| | <i>Seputus pomeroyi</i> MacGabhann and Murray, 2010 | | Ordovician | Bardahessiagh Fmn, Co. Tyrone, Ireland | 4 | Radial & ?concentric | Stiffened | up to 120 | 0 | ? | up to 70 | MacGabhann and Murray (2010) |
| 'Paropsonemids' | <i>Paropsonema cryptophya</i> Clarke, 1900 | | Devonian | Grimes Siltstone Fmn, ?Nunda Sandstone Fmn, Genesee Gp, New York, USA | >11 | Complex | Flexible | ~25–30 | 2 | ? | 71–195 | Clarke (1900) |
| | <i>Paropsonema mirabile</i> (Chapman, 1926) | <i>Discophyllum mirabile</i> Chapman, 1926 | Silurian | Dargile Fmn, Melbourne, Australia | 5 | Complex | Flexible | ~22–30 | 1 | ? | 80x130; 75x105 (elliptical) | Chapman (1926); Conway Morris (1993a) |
| | <i>Discophyllum peltatum</i> Hall, 1847 | | Ordovician | Troy Frontal Zone, Troy, New York, USA | 2 | Complex | Flexible | 22–26 | 1 | ? | 80–100 | Hall (1847); MacGabhann and Murray (2010) |

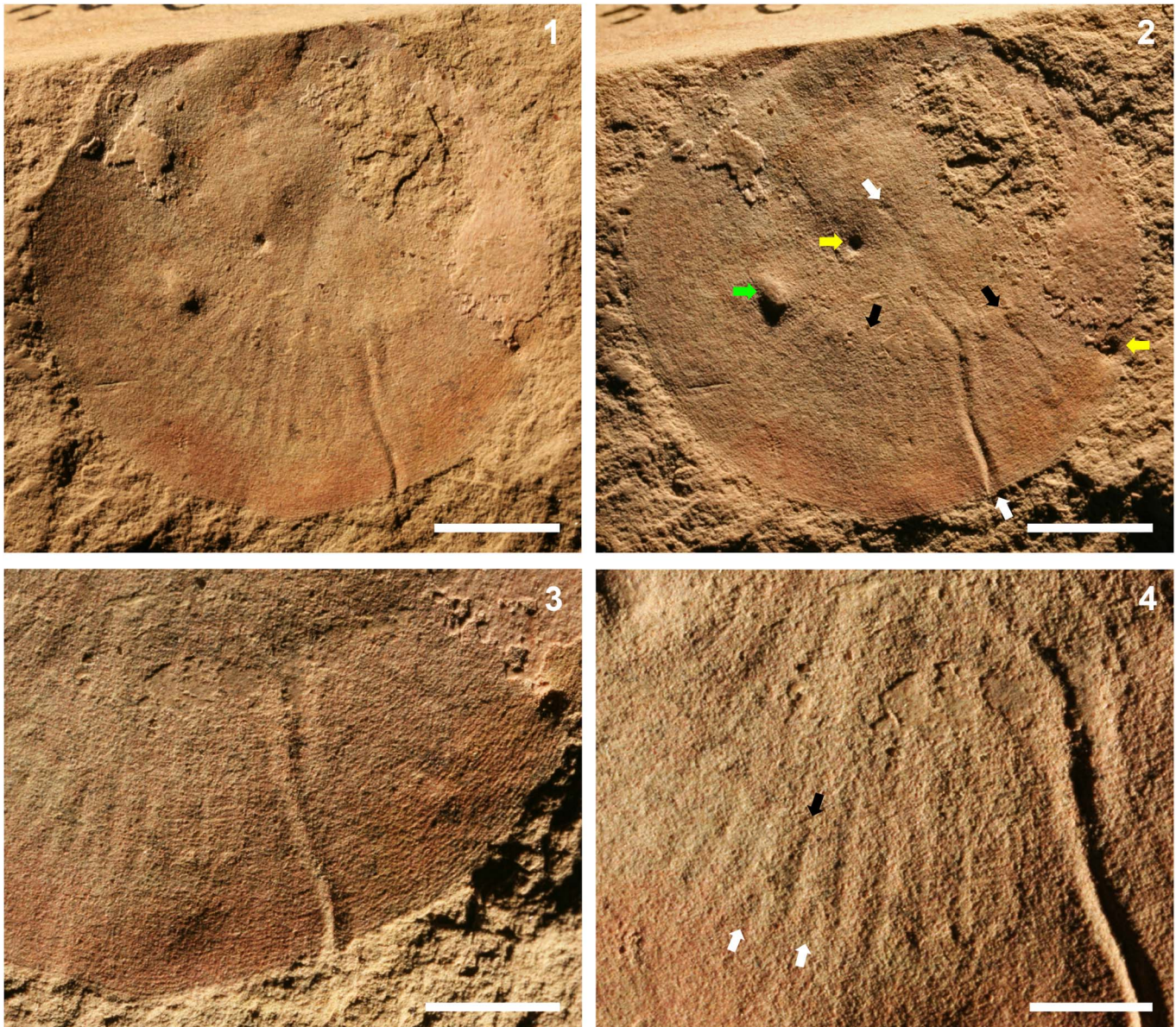


Figure 1. Eldonioid from the early Cambrian Emu Bay Shale, Kangaroo Island, South Australia, SAM P45196; previously illustrated by Paterson et al. (2016, fig. 6g). (1) Near complete specimen; lighting from top left. (2) Image taken with very low-angled light from top right to show surface relief and other features such as the associated traces (burrow [white arrows]; circular indentations [yellow arrows]; tubercular protuberance [green arrow]) and the bulge of the coiled sac near the center (black arrows). (3) Close-up showing detail of concentric corrugations; lighting from bottom right. (4) Close-up showing detail of internal lobes, including primary bifurcation (black arrow) and secondary bifurcations (white arrows); lighting from bottom right. (1, 2) Scale bar = 5 mm; (3) scale bar = 3 mm; (4) scale bar = 2 mm.

Materials and methods

Specimens were collected from the lower Cambrian (Series 2, Stage 4) Emu Bay Shale Konservat-Lagerstätte at Buck Quarry, Big Gully, Kangaroo Island, South Australia (for detailed locality information, see Gehling et al., 2011; Paterson et al., 2016).

Photographs were taken with a Canon EOS 5D digital SLR camera with a Canon MP-E 65 mm 1–5x macro lens, using low-angled light from different directions to enhance the morphological detail of the fossils.

Repository and institutional abbreviation.—Two specimens, SAM P45196 and P46361, are deposited in the South Australian

Museum paleontology (SAM P) collection in Adelaide, South Australia.

Description

The specimens represent two incomplete, but clearly subcircular, nonbiomineralized discs. SAM P45196 (Fig. 1) has a diameter of 20.9 mm; SAM P46361 (Fig. 2) is too incomplete to be measured, but is of a similar size. Neither specimen shows evidence of a mouth, tentacles, or anus, which are located on the interpreted ventral side of other eldonioids. Consequently, we interpret the exposed surface of the EBS specimens as representing the dorsal disc, though its orientation in life is not certain.

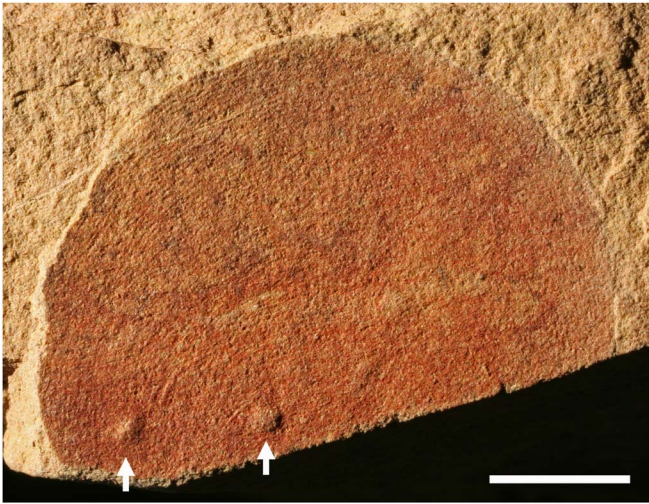


Figure 2. Eldonioid from the early Cambrian Emu Bay Shale, Kangaroo Island, South Australia, SAM P46361. Lighting from top left. White arrows indicate tubercular protuberances. Scale bar = 4 mm.

SAM P45196 is almost complete and provides the most morphological information for this description. About one-seventh of the disc margin is missing (Fig. 1.1, 1.2, top of specimen). SAM P46361 comprises about two-thirds of a disc (Fig. 2). Where preserved, the margins of both discs are sharply delineated, with no evidence of any structures protruding beyond the margins.

Eldonioids are characterized by a series of internal radial lobes, which extend in all directions from near the center of the disc toward its margin. In SAM P45196, the internal lobes appear as raised ridges on approximately one-quarter of the disc, imprinting through the integument (Fig. 1). They are indistinct near the center of the disc and terminate about 3 mm from the margin. Each lobe bifurcates twice, with the primary bifurcation situated near the marginal side of the coiled sac, and the secondary bifurcations occurring close to the distal end (Fig. 1.4). It is estimated that the whole disc bore approximately 30–35 lobes.

Another distinctive feature of eldonioids is the ‘coiled sac’ (sensu Zhu et al., 2002, fig. 1) or stomach (sensu Caron et al., 2010b), generally considered to be the digestive organ overlying the internal lobes. This structure may be represented on SAM P45196 by a slightly convex ridge (shown by black arrows in Fig. 1.2) that is in a similar position to the ‘coiled sac’ in some eldonioid specimens from China (e.g., Chen et al., 1995, fig. 4; Zhu et al., 2002, fig. 4a), which also exhibit convex relief.

The external surface in both specimens consists of very fine, evenly and closely spaced concentric corrugations. This ornament is well preserved around the outer portion of the disc (Figs. 1.3, 2) but becomes gradually more indistinct toward the center. In SAM P45196, the concentric ornament clearly drapes over the ridges and valleys of the internal lobes without interruption (Fig. 1.3, 1.4). The internal lobes seem to have been resistant to compression, so the integument must have had some degree of flexibility.

Associated trace fossils.—The EBS eldonioids also host distinctive trace fossils. SAM P45196 has a narrow,

sinuous burrow running between the margin of the disc and its center (Fig. 1.2). It does not extend beyond the disc margin into the surrounding matrix. Near the disc margin, the trace on SAM P45196 is a clear, shallow groove about 1 mm across, flanked with low levees, but it becomes less distinct nearer the disc center. The fine concentric ornament on the disc surface also crosses the contours of the groove and levees of the trace without disruption, which indicates it was caused by activity just below, rather than at or above, the disc surface.

In situ orientation of the EBS specimens was not recorded, but most eldonioids and rotadiscids from China (Chen et al., 1995; Zhu et al., 2002) are found with the dorsal surface facing upward relative to the bedding plane. Such an orientation in the EBS specimens is supported by the lack of ventral structures (e.g., circumoral tentacles) and the presence of more robust structures visible through the disc, such as the internal lobes and probable coiled sac. Assuming this is the correct orientation for SAM P45196, burrowing activity beneath the disc is preserved in negative epirelief.

SAM P45196 also bears two circular indentations and a small, protruding, tubercle-like feature (Fig. 1.2), while SAM P46361 has two tubercles (Fig. 2). Similar protuberances (e.g., Wang et al., 2009, figs. 2E, 3D, 6A) and circular indentations (e.g., Wang et al., 2009, figs. 2A, 3C, 5B) can be seen on discs of *Pararotadiscus guizhouensis*.

Discussion

Taxonomic considerations.—Despite there being only two EBS specimens, with imperfect preservation, the size of the discs, the number and structure of radial internal lobes, and the fine concentric dorsal ornament strongly support an eldonioid affinity. While the EBS discs have some superficial similarities to features of the brachiopod *Heliomedusa orientalis* Sun and Hou, 1987 from the Chengjiang Biota (see Jin and Wang, 1992; Chen et al., 2007; Zhang et al., 2009), an affinity can be easily dismissed. Apart from the EBS discs and valves of *H. orientalis* being similar in size and possessing a fine concentric ornament, the EBS discs do not exhibit radial striae like *H. orientalis* (e.g., Chen et al., 2007, fig. 4.5). The radial lobes of the EBS discs bear a faint resemblance to the lophophore of *H. orientalis*, but the lophophore tentacles in *H. orientalis* do not bifurcate (e.g., Zhang et al., 2009, figs. 2, 3, 6). Other important features of *H. orientalis* (that are absent in the EBS discs) include mantle setae that extend beyond the margins of both valves, a pseudointerarea, and a well-developed visceral cavity (Jin and Wang, 1992; Chen et al., 2007; Zhang et al., 2009).

At about 21 mm in diameter, the EBS specimens are among the smallest eldonioids known (Table 1). In their redescription of *Pararotadiscus*, Zhu et al. (2002) measured the diameter of 75 specimens, which ranged from ~12 to ~105 mm. They concluded that the disc becomes larger and increasingly sclerotized throughout ontogeny. In their smallest specimens, the disc margin is unclear and the disc easily deformed. Specimens greater than 20 mm in diameter, with a relatively stiff disc and clear disc margins, are considered to be adults. Using these criteria, the EBS specimens would appear to be adult animals, but whether they represent two young (similar-sized)

individuals that could potentially have grown larger, or members of a miniature species, cannot yet be ascertained.

The number of internal lobes is fairly consistent for each of the well-known Cambrian eldonioid species (Table 1). *Eldonia ludwigi* Walcott, 1911a has a maximum of 30, *E. eumorpha* (Sun and Hou, 1987) has ~44, *Rotadiscus grandis* Sun and Hou, 1987 has up to 88, and *Pararotadiscus guizhouensis* has ~40. The EBS specimens are estimated to have ~30–35 lobes, thus falling within the range observed in both eldoniids and rotadiscids. However, internal lobes that have primary and secondary bifurcations, as observed in SAM P45196, have not been documented in other Cambrian eldonioids.

The three families of eldonioids can be distinguished by the ornament on their dorsal surface. Simple concentric corrugations, as found on the EBS specimens, are characteristic of the Rotadiscidae. The post-Cambrian paropsonemids are also ornamented, but they have a far more complex pattern, and the ornament of the Eldoniidae is radial, not concentric (MacGabhann and Murray, 2010). The concentric corrugations observed in rotadiscids have been interpreted as lines of accretionary growth at the disc margin (Dzik, 1991; Chen et al., 1995; Dzik et al., 1997; Chen, 2012). An alternative interpretation is that, at least in some instances, the concentric corrugations are taphonomic artefacts, due to compression of a dome- or bell-shaped (and variably sclerotized) body (Zhu et al., 2002; Caron et al., 2010b). Given the small size of the EBS specimens, and the regularity and spacing of the fine concentric corrugations, it seems unlikely that the taphonomic interpretation applies in this instance.

Zhu et al. (2002) compared the degree of sclerotization of the dorsal disc in the three Chinese eldonioid taxa, using the frequency of specimens represented by folded or deformed discs as a proxy for disc stiffness or rigidity. Specimens of *Eldonia eumorpha* were most often folded or distorted, so were interpreted as being the most lightly sclerotized. Specimens referred to *Pararotadiscus* and *Rotadiscus* showed progressively lesser degrees of folding. Deformation of the dorsal disc to reveal the form of the underlying internal lobes is typical of *Pararotadiscus*, but does not occur in *Rotadiscus* (Zhu et al., 2002). The EBS specimens show no sign of folding, but the internal lobes in SAM P45196 imprint through part of the dorsal surface, suggesting a stiff, but not completely rigid, disc, most similar to that of *Pararotadiscus*.

At present, lack of important morphological detail in the two EBS specimens precludes assignment to a new or existing genus and species. While their concentric ornament and stiffened dorsal disc would suggest placement of the EBS eldonioids within the family Rotadiscidae, the unknown condition of their circumoral tentacles prevents an assignment to either of the included genera. On comparison with other characteristics, *Pararotadiscus* seems the most similar, as both it and the EBS specimens have a stiff but not completely rigid disc and a similar number of internal lobes. However, internal lobes that show secondary bifurcations (as in the EBS specimens) would warrant designation to a separate species. Until further information regarding the precise number of internal lobes, the condition of the circumoral tentacles, and perhaps their size range becomes available, we consider the EBS specimens as being representative of the Rotadiscidae, but leave the genus and species under open nomenclature.

The eldonioid–trace fossil association.—Examples of body and trace fossil associations can be found in the major Cambrian Konservat-Lagerstätten. For example, in the Burgess Shale, Chengjiang, Kaili, Sirius Passet, and Stanley Glacier assemblages, traces can be found on, or immediately below, body fossils, in the sediment surrounding them, or crossing between sediment and body fossil. These burrows and trails meander, intersect, or branch and occur on a variety of hosts (e.g., Zhang et al., 2007, Wang et al., 2009; Caron et al., 2010a; Lin et al., 2010; Mángano, 2011; Mángano et al., 2012). In the Burgess Shale and Stanley Glacier assemblages, traces are found on and around various arthropod exoskeletons (such as *Hurdia* Walcott, 1912 and *Tuzoia* Walcott, 1912), and the vetulicolian *Banffia* Walcott, 1911b (Caron, 2006; Caron et al., 2010a; Mángano, 2011). In the Sirius Passet Lagerstätte, exoskeletons of the large, trilobite-like arthropod *Arthroaspis* Stein et al., 2013 (see Mángano et al., 2012), and rarely the trilobite *Buenellus* Blaker, 1988 (see Babcock and Peel, 2007), host trace fossils. The Chengjiang Biota hosts include vetulicolians, the bivalved arthropods *Isoxys* Walcott, 1890 and *Branchiocaris* Resser, 1929, and other nonbiomineralized arthropods (Zhang et al., 2007). In the Kaili Biota, typical hosts include arthropods such as *Canadaspis* Novozhilov, 1960, *Naraoia* Walcott, 1912, *Skania* Walcott, 1931, *Tuzoia*, and *Waptia* Walcott, 1912. One of the most common Kaili fossils, the rotadiscid *Pararotadiscus*, is also the most common trace fossil host (Wang et al., 2009; Lin et al., 2010).

Aside from large coprolites containing trilobite fragments (Nedin, 1999; Daley et al., 2013), trilobite exoskeletons showing injuries (Conway Morris and Jenkins, 1985), and perhaps the ‘epibionts’ seen in some specimens of the EBS vetulicolian *Nesonektris* (cf. García-Bellido et al., 2014, figs. 1B, C, 4A), trace fossils are notably scarce from the body-fossil-bearing layers of the EBS Lagerstätte interval (Paterson et al., 2016). The near-complete absence of traces associated with EBS body fossils is clearly not due to a lack of suitable hosts—similar taxa to those listed, including *Nesonektris* García-Bellido et al., 2014 and the bivalved arthropods *Tuzoia* and *Isoxys* (García-Bellido et al., 2009), are common to very abundant in the EBS. Therefore, the scarcity of EBS body–trace fossil associations most likely relates to specific (probably restrictive) paleoenvironmental conditions, particularly at the sediment–water interface (Paterson et al., 2016).

The discovery of eldonioids with associated traces in the EBS is important, not only for expanding the ichnological diversity of this fossil deposit, but also for providing new paleoecological information on the biota. For example, the simple, sinuous burrow on one of the discs (SAM P45196; Fig. 1.2) may represent a feeding trace. The form of the trace, a groove with flanking levees, is typical of a burrow produced by sediment displacement (Carbone and Narbonne, 2014). Smooth, curved, unbranched burrows such as this suggest a single-use, nonselective feeding strategy (Mikuláš et al., 2012). Burrowing seems to have occurred just below the disc, perhaps to feed on bacteria or other nutrients situated beneath it (Mángano et al., 2012), with the disc subsequently draping over the burrow during (or possibly before) burial of the eldonioid. The simplicity and short length of the burrow may be due, in part, to the small size of the disc, but the presence of additional traces

on SAM P45196 suggests a more complex situation than the form of the burrow implies (discussed in the following).

Tubercule-like features preserved on both EBS specimens have also been observed on eldonioid discs and arthropod exoskeletons from the Kaili Biota and from Cambrian sites in the Czech Republic. These have been interpreted as attempts at upward movement by the trace-maker, which was unable to pierce the sclerotized disc or exoskeleton (Wang et al., 2009; Mikuláš et al., 2012). Priapulids are proposed as possible contenders for the trace-makers at Kaili and other Lagerstätten (Wang et al., 2009). Interestingly, small palaeoscolecid worms with a body width (or diameter) similar to the observed burrow have been described from the EBS (García-Bellido et al., 2013), implicating them as suspected trace-makers.

The circular indentations on SAM P45196 (Fig. 1.2) are similar to those appearing with *Gordia*-like traces on some of the Kaili specimens illustrated, but not discussed, by Wang et al. (2009, figs. 2A, D, 3C, 5). These may represent sites of epibiont attachment, or perhaps, contrary to Wang et al. (2009), are the result of successful perforations of the disc surface by the trace-maker.

The presence of different trace forms on a single specimen (e.g., Fig. 1.2) suggests that either multiple trace-makers were present in the immediate vicinity of the individual and converged on it, or one trace-maker was able to produce several trace forms.

Mode of life and taphonomic considerations.—Previous studies have suggested that eldonioids were either pelagic (Walcott, 1911a; Durham, 1974; Sun and Hou, 1987; Zhu et al., 2002; Hu et al., 2007; Chen, 2009, 2012), nektobenthic (Caron et al., 2010b), or benthic (Dzik et al., 1997; MacGabhann and Murray, 2010). Taxa envisaged as living at or near the seafloor have been portrayed as vagile, oriented with the disc facing convex side upward and the tentacles combing the substrate (Caron et al., 2010b), or sessile, with tentacles facing upward and the convex side of the disc lying passively on or within the sediment (Dzik et al., 1997). Eldonioids were also a common, and occasionally abundant, element of the early to middle Paleozoic fauna, with some taxa known from hundreds or thousands of specimens (see Table 1).

The two EBS eldonioid specimens represent isolated individuals, found in different stratigraphic levels within Buck Quarry, separated by about 1.5 m. Both specimens are undistorted, with the discs preserved parallel to laminations within mudstone beds. This suggests that these individuals were buried under relatively calm conditions, as opposed to being swept up by the intermittent sediment gravity flows that captured other faunal elements (including benthic and nektobenthic taxa) of the EBS biota prior to rapid burial (Gehling et al., 2011; García-Bellido et al., 2014; Paterson et al., 2016).

Unfortunately, there is limited taphonomic (and certainly no morphologic) evidence to elucidate the lifestyle of the EBS eldonioid. The paucity of specimens in the EBS—coupled with the otherwise depauperate diversity of the autochthonous benthic fauna in the exaerobic zone (see Paterson et al., 2016)—would indicate that a sessile life mode is unlikely, unless individuals were infrequently relocated from their original habitat. Moreover, the style of preservation of the EBS specimens neither supports

nor contradicts a mobile benthic, nektic, or pelagic habit, but their rarity suggests that these individuals either were transported or settled into the ‘preservational trap,’ as represented by the Konservat-Lagerstätte interval. Irrespective of lifestyle, the associated trace fossil evidence suggests that the EBS eldonioids were exposed on the substrate for a short period before burial, allowing organisms to exploit these particular carcasses before the entombing sediment became truly anoxic (Hall et al., 2011; McKirdy et al., 2011; Mángano et al., 2012; Gaines, 2014; Paterson et al., 2016).

Acknowledgments

This research was supported by grants from the Australian Research Council (FT120100770 to JRP) and National Geographic (#8991-11), with additional financial assistance from Beach Energy Ltd. and the South Australian Museum, and logistical support from SeaLink. We are grateful to the Buck family for access to the field area, and to our regular EBS collaborators G. Edgecombe, D. García-Bellido, J. Gehling, J. Jago, and M. Lee. We thank R. Atkinson, M.-A. Binnie, A. Camens, A. Daley, R. Gaines, M. Gemmell, J. Holmes, K. Kenny, P. Kruse, J. Laurie, B. McHenry, M. Mills, L. Reid, D. Rice, E. Thomson, and members of the South Australian Museum Waterhouse Club for assistance in the field and lab, and for discussions. Thanks also to the two anonymous referees for their helpful reviews of the manuscript.

References

- Alessandro, A., and Bracchi, G., 2003, *Eldonia berbera* n. sp., a new species of the enigmatic genus *Eldonia* Walcott, 1911 from the Rawtheyan (Upper Ordovician) of Anti-Atlas (Erfoud, Tafilalet, Morocco): *Atti della Società italiana di scienze naturali e del museo civico di storia natural di Milano*, v. 144, p. 337–358.
- Babcock, L.E., and Peel, J.S., 2007, Palaeobiology, taphonomy and stratigraphic significance of the trilobite *Buenellus* from the Sirius Passet Biota, Cambrian of North Greenland: *Memoirs of the Association of Australasian Palaeontologists*, v. 34, p. 401–418.
- Blaker, M.R., 1988, A new genus of nevadiid trilobite from the Buen Formation (early Cambrian) of Peary Land, central North Greenland: *Grønlands Geologiske Undersøgelse Rapport*, v. 137, p. 33–41.
- Carbone, C., and Narbonne, G.M., 2014, When life got smart: The evolution of behavioral complexity through the Ediacaran and early Cambrian of NW Canada: *Journal of Paleontology*, v. 88, p. 309–330. doi: 10.1666/13-066.
- Caron, J.-B., 2006, *Banffia constricta*, a putative vetulicolid from the middle Cambrian Burgess Shale: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 96, p. 95–111.
- Caron, J.-B., Gaines, R.R., Mángano, M.G., Streng, M., and Daley, A.C., 2010a, A new Burgess Shale-type assemblage from the “thin” Stephen Formation of the southern Canadian Rockies: *Geology*, v. 38, p. 811–814.
- Caron, J.-B., Conway Morris, S., and Shu, D., 2010b, Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive deuterostomes: *PLoS ONE*, v. 5, e9586.
- Chapman, F., 1926, New or little-known fossils in the National Museum. Part 30: A Silurian jelly-fish: *Proceedings of the Royal Society of Victoria*, v. 39, p. 13–17.
- Chen, J.-Y., 2009, The sudden appearance of diverse animal body plans during the Cambrian explosion: *The International Journal of Developmental Biology*, v. 53, p. 733–751.
- Chen, J.-Y., 2012, Evolutionary scenario of the early history of the animal kingdom: Evidence from Precambrian (Ediacaran) Weng’an and early Cambrian Maotianshan biotas, China, in Talent, J.A., ed., *Earth and Life: Dordrecht, Netherlands, Springer*, p. 239–379.
- Chen, J.-Y., Zhu, M.Y., and Zhou, G.Q., 1995, The early Cambrian medusiform metazoan *Eldonia* from Chengjiang Lagerstätte: *Acta Palaeontologica Polonica*, v. 40, p. 213–244.

- Chen, J.-Y., Huang, D.Y., and Chuang, S.H., 2007, Reinterpretation of the lower Cambrian brachiopod *Heliomedusa orientalis* Sun and Hou, 1987a as a discinid: *Journal of Paleontology*, v. 81, p. 38–47.
- Clarke, J.M., 1900, *Paropsonema cryptophya*—A peculiar echinoderm from the *Intumescens*-zone (Portage beds) of western New York: *Bulletin of the New York State Museum*, v. 39, p. 172–178.
- Conway Morris, S., 1993a, Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America: *Paleontology*, v. 36, p. 593–635.
- Conway Morris, S., 1993b, The fossil record and the early evolution of the Metazoa: *Nature*, v. 361, p. 219–225.
- Conway Morris, S., and Jenkins, R.J.F., 1985, Healed injuries in early Cambrian trilobites from South Australia: *Alcheringa*, v. 9, p. 167–177.
- Conway Morris, S., and Robison, R.A., 1988, More soft-bodied animals and algae from the middle Cambrian of Utah and British Columbia: *University of Kansas Paleontological Contributions*, v. 122, p. 1–48.
- Conway Morris, S., Selden, P.A., Gunther, G., Jamison, P.G., and Robison, R.A., 2015, New records of Burgess Shale-type taxa from the middle Cambrian of Utah: *Journal of Paleontology*, v. 89, p. 411–423.
- Daley, A.C., Paterson, J.R., Edgecombe, G.D., García-Bellido, D.C., and Jago, J.B., 2013, New anatomical information on *Anomalocaris* from the Cambrian Emu Bay Shale of South Australia and a reassessment of its inferred predatory habits: *Paleontology*, v. 56, p. 971–990.
- Durham, J.W., 1974, Systematic position of *Eldonia ludwigi* Walcott: *Journal of Paleontology*, v. 48, p. 750–755.
- Dzik, J., 1991, Is fossil evidence consistent with traditional views of the early metazoan phylogeny? in Simonetta, A.M., and Conway Morris, S., eds., *The Early Evolution of Metazoa and the Significance of Problematic Taxa*: Cambridge, UK, Cambridge University Press, p. 47–56.
- Dzik, J., Zhao, Y.L., and Zhu, M.Y., 1997, Mode of life of the middle Cambrian eldoniid lophophorate *Rotadiscus*: *Paleontology*, v. 40, p. 385–396.
- Friend, D., Zhuravlev, A.Y., and Solov'ev, I.A., 2002, Middle Cambrian *Eldonia* from the Siberian Platform: *Paleontological Journal*, v. 36, no. 1, p. 20–24.
- Gaines, R.R., 2014, Burgess Shale-type preservation and its distribution in space and time: *The Paleontological Society Papers*, v. 20, p. 123–146.
- García-Bellido, D.C., Paterson, J.R., Edgecombe, G.D., Jago, J.B., Gehling, J.G., and Lee, M.S.Y., 2009, The bivalved arthropods *Isoxys* and *Tuzoia* with soft-part preservation from the lower Cambrian Emu Bay Shale Lagerstätte (Kangaroo Island, Australia): *Paleontology*, v. 52, p. 1221–1241.
- García-Bellido, D.C., Paterson, J.R., and Edgecombe, G.D., 2013, Cambrian palaeoscolecid (Cycloneuralia) from Gondwana and reappraisal of species assigned to *Palaeoscolex*: *Gondwana Research*, v. 24, p. 780–795.
- García-Bellido, D.C., Lee, M.S.Y., Edgecombe, G.D., Jago, J.B., Gehling, J.G., and Paterson, J.R., 2014, A new vetulicolian from Australia and its bearing on the chordate affinities of an enigmatic Cambrian group: *BMC Evolutionary Biology*, v. 14, p. 214.
- Gehling, J.G., Jago, J.B., Paterson, J.R., García-Bellido, D.C., and Edgecombe, G.D., 2011, The geological context of the lower Cambrian (Series 2) Emu Bay Shale Lagerstätte and adjacent stratigraphic units, Kangaroo Island, South Australia: *Australian Journal of Earth Sciences*, v. 58, p. 243–257.
- Hall, A.P., McKirdy, D.M., Halverson, G.P., Jago, J.B., and Gehling, J.G., 2011, Biomarker and isotopic signatures of an early Cambrian Lagerstätte in the Stansbury Basin, South Australia: *Organic Geochemistry*, v. 42, p. 1324–1330.
- Hall, J., 1847, *Paleontology of New York*, Volume I: Albany, New York, C. Van Benthuysen.
- Hu, S., Steiner, M., Zhu, M., Erdtmann, B.D., Luo, H., Chen, L., and Weber, B., 2007, Diverse pelagic predators from the Chengjiang Lagerstätte and the establishment of modern-style pelagic ecosystems in the early Cambrian: *Paleogeography, Palaeoclimatology, Palaeoecology*, v. 254, p. 307–316.
- Ivantsov, A.Y., Zhuravlev, A.Y., Leguta, A.V., Krassilov, V.A., Melnikova, L.M., and Ushatinskaya, G.T., 2005, Palaeoecology of the early Cambrian Sinsk biota from the Siberian platform: *Paleogeography, Palaeoclimatology, Palaeoecology*, v. 220, p. 69–88.
- Jin, Y., and Wang, H., 1992, Revision of the lower Cambrian brachiopod *Heliomedusa* Sun & Hou, 1987: *Lethaia*, v. 25, p. 35–49.
- Lin, J.P., Zhao, Y.L., Rahman, I.A., Xiao, S., and Wang, Y., 2010, Bioturbation in Burgess Shale-type Lagerstätten—Case study of trace fossil–body fossil association from the Kaili Biota (Cambrian Series 3), Guizhou, China: *Paleogeography, Palaeoclimatology, Palaeoecology*, v. 292, p. 245–256.
- MacGabhann, B.A., and Murray, J., 2010, Non-mineralised discoidal fossils from the Ordovician Bardahessiagh Formation, Co. Tyrone, Ireland: *Irish Journal of Earth Sciences*, v. 28, p. 1–12.
- Mángano, M.G., 2011, Trace-fossil assemblages in a Burgess Shale-type deposit from the Stephen Formation at Stanley Glacier, Canadian Rocky Mountains: Unraveling ecologic and evolutionary controls, in Johnston, P.A., and Johnston, K.J., eds., *Proceedings of the International Conference on the Cambrian Explosion: Palaeontographica Canadiana*, v. 31, p. 89–107.
- Mángano, M.G., Bromley, R.G., Harper, D.A.T., Nielsen, A.T., Smith, M.P., and Vinther, J., 2012, Nonbiomineralized carapaces in Cambrian seafloor landscapes (Sirius Passet, Greenland): Opening a new window into early Phanerozoic benthic ecology: *Geology*, v. 40, p. 519–522.
- Masiak, M., and Żylińska, A., 1994, Burgess Shale-type fossils in Cambrian sandstones of the Holy Cross Mountains: *Acta Paleontologica Polonica*, v. 39, p. 329–340.
- McKirdy, D.M., Hall, P.A., Nedin, C., Halverson, G.P., Michaelsen, B.H., Jago, J.B., Gehling, J.G., and Jenkins, R.J.F., 2011, Paleoredox status and thermal alteration of the lower Cambrian (Series 2) Emu Bay Shale Lagerstätte, South Australia: *Australian Journal of Earth Sciences*, v. 58, p. 259–272.
- Mikuláš, R., Fatka, O., and Szabad, M., 2012, Paleocologic implications of ichnofossils associated with slightly skeletonized body fossils, middle Cambrian of the Barrandian area, Czech Republic: *Ichnos*, v. 19, p. 199–210.
- Nedin, C., 1999, *Anomalocaris* predation on nonmineralized and mineralized trilobites: *Geology*, v. 27, p. 987–990.
- Novozhilov, N.I., 1960, in Orlov, Yu. A. (ed.), *Osnovy Paleontologii, Arthropoda, Trilobitomorpha and Crustacea*: Moscow, Nedra, p. 515.
- Paterson, J.R., García-Bellido, D.C., Jago, J.B., Gehling, J.G., Lee, M.S.Y., and Edgecombe, G.D., 2016, The Emu Bay Shale Konservat-Lagerstätte: A view of Cambrian life from East Gondwana: *Journal of the Geological Society*, v. 173, p. 1–11.
- Resser, C.E., 1929, New lower and middle Cambrian Crustacea: *Proceedings of the US National Museum*, v. 76, p. 1–18.
- Stasińska, A., 1960, *Velumbrella czarnockii* n. gen., n. sp.—medusa du Cambrien inférieur des Monts de Sainte-Croix: *Acta Paleontologica Polonica*, v. 5, p. 337–344.
- Stein, M., Budd, G.E., Peel, J.S., and Harper, D.A.T., 2013, *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry: *BMC Evolutionary Biology*, v. 13, p. 99.
- Sun, W.G., and Hou, X.G., 1987, Early Cambrian medusae from Chengjiang, Yunnan, China: *Acta Paleontologica Sinica*, v. 26, p. 257–271.
- Walcott, C.D., 1890, The fauna of the lower Cambrian or *Olenellus* Zone: *Reports of the U.S. Geological Survey*, v. 10, p. 509–763.
- Walcott, C.D., 1911a, Middle Cambrian holothurians and medusa: *Smithsonian Miscellaneous Collections*, v. 57, p. 41–68.
- Walcott, C.D., 1911b, Cambrian Geology and Paleontology 2. No. 5. Middle Cambrian annelids: *Smithsonian Miscellaneous Collections*, v. 57, p. 109–145.
- Walcott, C.D., 1912, Cambrian Geology and Paleontology 2. No. 6. Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata: *Smithsonian Miscellaneous Collections*, v. 57, p. 145–228.
- Walcott, C.D., 1931, Addenda to descriptions of Burgess Shale fossils: *Smithsonian Miscellaneous Collections*, v. 85, p. 1–46.
- Wang, Y., Lin, J.P., Zhao, Y.L., and Orr, P.J., 2009, Palaeoecology of the trace fossil *Gordia* and its interaction with nonmineralizing taxa from the early middle Cambrian Kaili Biota, Guizhou Province, South China: *Paleogeography, Palaeoclimatology, Palaeoecology*, v. 277, p. 141–148.
- Zhang, X.G., Bergström, J., Bromley, R.G., and Hou, X.G., 2007, Diminutive trace fossils in the Chengjiang Lagerstätte: *Terra Nova*, v. 19, p. 407–412.
- Zhang, Z., Li, G., Emig, C.C., Han, J., Holmer, L.E., and Shu, D., 2009, Architecture and function of the lophophore in the problematic brachiopod *Heliomedusa orientalis* (early Cambrian, South China): *Geobios*, v. 42, p. 649–661.
- Zhang, Z., et al., 2013, A sclerite-bearing stem group entoproct from the early Cambrian and its implications: *Scientific Reports*, v. 3, p. 1066.
- Zhao, F., Caron, J.-B., Bottjer, D.J., Hu, S., Yin, Z., and Zhu, M., 2014, Diversity and species abundance patterns of the early Cambrian (Series 2, Stage 3) Chengjiang Biota from China: *Paleobiology*, v. 40, p. 50–69.
- Zhao, Y.L., and Zhu, M.Y., 1994, Medusiform fossils of Kaili fauna from Taijiang, Guizhou: *Acta Paleontologica Sinica*, v. 33, p. 272–280.
- Zhu, M.-Y., Zhao, Y.-L., and Chen, J.-Y., 2002, Revision of the Cambrian discoidal animals *Stellostomites eumorphus* and *Pararotadiscus guizhouensis* from South China: *Geobios*, v. 35, p. 165–185.

Accepted 13 August 2017