NEW ANATOMICAL INFORMATION ON ANOMALOCARIS FROM THE CAMBRIAN EMU BAY SHALE OF SOUTH AUSTRALIA AND A REASSESSMENT OF ITS INFERRED PREDATORY HABITS

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Abstract: Two species of Anomalocaris co-occur in the Emu Bay Shale (Cambrian Series 2, Stage 4) at Big Gully, Kangaroo Island. Frontal appendages of Anomalocaris briggsi Nedin, 1995, are more common than those of Anomalocaris cf. canadensis Whiteaves, 1892, at a quarry inland of the wave-cut platform site from which these species were originally described. An oral cone has the three large, node-bearing plates recently documented for Anomalocaris canadensis, confirming that Anomalocaris lacks a tetraradial ‘Peytoia’ oral cone and strengthening the case for the identity of the Australian specimens as Anomalocaris. Disarticulated anomalocaridid body flaps are more numerous in the Emu Bay Shale than in other localities, and they preserve anatomical details not recognized elsewhere. Transverse lines on the anterior part of the flaps, interpreted as strengthening rays or veins in previous descriptions of anomalocaridids, are associated with internal structures consisting of a series of well-bounded, striated blocks or bars. Their structure is consistent with a structural function imparting strength to the body flaps. Setal structures consisting of a series of lanceolate blades are similar to those of other anomalocaridids and are found in isolation or associated with body flaps. A single specimen also preserves putative gut diverticula. The morphology of the appendages, oral cone, gut diverticula and compound eyes of Anomalocaris, along with its large size, suggests that it was an active predator, and specimens of coprolites containing trilobite fragments and trilobites with prominent injuries have been cited as evidence of anomalocaridid predation on trilobites. Based on frontal appendage morphology, Anomalocaris briggsi is inferred to have been a predator of soft-bodied animals exclusively and only Anomalocaris cf. canadensis may have been capable of durophagous predation on trilobites, although predation (including possible cannibalism) by Redlichia could also explain the coprolites and damage to trilobite exoskeletons found in the Emu Bay Shale.

Key words: Radiodonta, Anomalocaris briggsi, coprolites, bite marks, predation.

The first Australian record of anomalocaridids was based on a few frontal appendages and a putative oral cone attributed to Anomalocaris by McHenry and Yates (1993), found in the lower Cambrian (Series 2, Stage 4) Emu Bay Shale on the north coast of Kangaroo Island, South Australia. Drawing on a sample of 30 frontal appendages, Nedin (1995) identified two different Anomalocaris species from the Emu Bay Shale, one newly named as Anomalocaris briggsi and another left under open nomenclature as Anomalocaris sp. Subsequently, Nedin (1999) attributed damage to trilobites and the nektaspid Eumcaris (referred to as Naraoia, but see Paterson et al. 2010) and a coprolite containing fragments of the trilobite Redlichia takooensis to predation by Anomalocaris; the coprolite was subsequently re-illustrated and discussed by Vannier and Chen (2005). Working on material from Buck Quarry, Paterson et al. (2011) identified large compound eyes as those of Anomalocaris and illustrated associated frontal appendages and the first body flap documented from the Emu Bay Shale.
As a result of an ongoing programme of excavation at Buck Quarry, material that includes additional body parts of anomalocaridids is available for study. We evaluate the new collections in the light of the previously documented material, emend the descriptions of the two known species and strengthen the case for assignment to Anomalocaris (rather than another anomalocaridid genus) by confirming the identification of the oral cone figured by McHenry and Yates (1993). Body flaps and setal blades are described, with emphasis on structures that have not been recognized previously or that have not received much attention. A single specimen with a partially preserved axial region has putative gut diverticula similar to those seen in other anomalocaridids and stem lineage arthropods.

LOCALITY AND MATERIAL

The Emu Bay Shale Konservat-Lagerstätte is restricted to the Big Gully locality (including Buck Quarry), situated 3 km east of Emu Bay on the north-east coast of Kangaroo Island; for detailed information about the stratigraphy of the Emu Bay Shale and the overall geology of the area, refer to Gehling et al. (2011). Prior to the excavations at Buck Quarry that commenced in September 2007, all previously documented fossils from the Emu Bay Shale at Big Gully, including those of anomalocaridids (McHenry and Yates 1993; Nedin 1995), were sourced from outcrops along the wave-cut platform and adjacent cliffs to the east of the mouth of Big Gully. New anomalocaridid material from Buck Quarry, located approximately 500 m inland (south) of the original wave-cut platform site, includes specimens of both Anomalocaris species recognized by Nedin (1995). Other arthropods described from Buck Quarry thus far are the bivalved taxa Isoxys and Tuzoia (García-Bellido et al. 2009), nектаспids (Paterson et al. 2010), the leańcholliid Oestokerkus (Edgecombe et al. 2011), the arthropodans Squamacula and Australimicola (Paterson et al. 2012) and large compound eyes of an unidentified taxon (Lee et al. 2011).

Anomalocaridid material from the Emu Bay Shale consists of isolated appendages, body flaps, setal structures (= ‘gills’ of Whittington and Briggs 1985) and a single oral cone, all preserved as part and counterpart in buff-weathering mudstones. These structures show consistent orientation with the plane of each fossil being parallel to bedding. The existence of two species of Anomalocaris in the Emu Bay Shale was demonstrated by two distinct morphs of frontal appendages and readily distinguished by the presence (A. briggsi) or absence (Anomalocaris sp.; here referred to Anomalocaris cf. canadensis) of spinules along the proximal and distal margins of the ventral spines (Nedin 1995). The wave-cut platform exposure is the source of the type material of A. briggsi and well-preserved material of Anomalocaris cf. canadensis, but frontal appendages of both species are also present in the collections from Buck Quarry. Anomalocaris briggsi is much more common at Buck Quarry, and thus circumstantially, it is likely that most of the additional body parts, including the large compound eyes (Paterson et al. 2011), belong to that species. There are no distinct morphs of body flaps or setose blades from Buck Quarry, so they have not been attributed to either species.

SYSTEMATIC PALAEONTOLOGY

STEM EUARTHROPODA
Order RADIODONTA Collins, 1996

Genus ANOMALOCARIS Whiteaves, 1892

Type species. Anomalocaris canadensis Whiteaves, 1892; from the Stephen Formation (Cambrian Series 3, Stage 5) of British Columbia, Canada.

Anomalocaris briggsi Nedin, 1995

Figures 1, 2

1995 Anomalocaris briggsi Nedin, pp. 31–35, figs 1, 3A.
1999 Anomalocaris briggsi Nedin, p. 989.
2002 Anomalocaris briggsi Hagadorn, p. 98.
2006 Anomalocaris briggsi Van Roy and Tetlie, pp. 240, 244, fig. 1A.
2006 Anomalocaris briggsi Paterson and Jago, p. 43.
2008 Anomalocaris briggsi Hendricks et al., table 1.
2008 Anomalocaris briggsi Paterson et al., p. 320.
2009 Anomalocaris briggsi García-Bellido et al., p. 1221.
2010 Anomalocaris briggsi Daley and Peel, p. 354.
2011 Anomalocaris briggsi Jago and Cooper, p. 239.
2011 Anomalocaris briggsi Paterson et al., p. 239, SI fig. 2.
2012 Anomalocaris briggsi Jago et al., p. 252.

Holotype. SAM P40180 (Fig. 1A, B), originally referred to as AUGC 1046-630 (Nedin 1995).

Paratype. SAM P40763, originally referred to as AUGC 1046-335 (Nedin 1995).

Other material. Fifty-six additional specimens of isolated frontal appendages, of which 26 come from the wave-cut platform and adjacent cliff exposure, 27 come from Buck Quarry and three from an exposure on the road south of Buck Quarry (see
Supplementary Information for catalogue numbers). Three specimens with multiple appendages come from the wave-cut platform and adjacent cliffs (see Supplementary Information). All material is housed in the palaeontological collections at the South Australian Museum (prefix SAM P), Adelaide, Australia.

Emended diagnosis. *Anomalocaris* with long, distally tapering frontal appendages consisting of 14 podomeres separated by triangular regions of flexible cuticle; podomeres 2–12 bearing a pair of proximally curving ventral spines that are longer than the height of the associated podomere and originate from the distal margin of the ventral surface of the podomere; proximal base and entire distal length of the ventral spines with prominent spinules; ventral spines terminate in a point with a pair of short spines flanking it; podomeres 1 and 13 with pair of short, spikelike ventral spines; podomere 14 with forked terminal end; elongated dorsal spines projecting forward medially from the distal margins of podomeres 12–14.

Description. Complete frontal appendages 87–175 mm long (mean = 119 mm, SD = 30 mm, n = 7), as measured along the outwardly convex dorsal margin. Podomeres are tall and narrow in the proximal region, but shorter and more elongated towards the distal end. Boundaries between podomeres are often preserved as simple lines (Fig. 1C–D), but occasionally, the boundaries are preserved as elongated triangular regions that extend from half to almost the full height of the podomeres (Fig. 1A–B). The triangular regions are interpreted as more flexible cuticle, based on their pockmarked and mottled preservation (Fig. 1A; McHenry and Yates 1993, figs 6–7). The most proximal podomere appears to be as long as at least four or five of the immediately succeeding podomeres (Fig. 1C–D), is much taller (Fig. 1A–B) and has an irregular attachment margin that may be concave in outline (Fig. 1).

A pair of spines extends from the distal margin of the ventral surface of podomeres 1–13 (vs in Figs 1B, D, 2). SAM P44851, P40180, P42037 and possibly P44859) from the wave-cut platform (see Supplementary Information). All specimens come from the wave-cut platform (see Supplementary Information). All specimens with multiple appendages come from the wave-cut platform and adjacent cliffs (see Supplementary Information). All material is housed in the palaeontological collections at the South Australian Museum (prefix SAM P), Adelaide, Australia.

The distal end of the appendage is narrow and elongated, with a pronounced ventral curvature (Fig. 1A–B). SAM P43724, P14681 and P40180 (ts in Fig. 1B) show that podomere 14 tapers to a pair of simple spines, giving the terminal end of the appendage a forked appearance (Fig. 2). Single dorsal spines (ds in Figs 1B, 2) extend from the medial distal region of the dorsal margin on podomeres 12 and 13 at an oblique angle to the appendage. SAM P43724 shows that the dorsal spine on podomere 12 is only 3–4 mm long, but that on podomere 13 is much longer and arches over nearly the full length of the terminal podomere (ds in Fig. 2). Podomere 14 has a relatively long dorsal spine that protrudes from just above the forked terminal end of the appendage (Fig. 2).

Remarks. The original description of *Anomalocaris briggsi* (Nedin 1995, p. 33) is largely confirmed. We amended the diagnosis to include mention of the origination of the ventral spines from the distal region of the ventral surface of the podomere, as this is a unique characteristic of *A. briggsi* that readily allows identification of incomplete specimens. Nedin (1995) described spinules on the ventral spines of podomere 13 and a bifurcation of the dorsal spine on podomere 14; however, these features were not evident in the more complete, newly collected specimens. The other difference from Nedin’s (1995) reconstruction is the presence in some specimens of spinules along the proximal margin of the ventral spines (Fig. 2). Whilst four specimens show this feature clearly, many more specimens with well-preserved proximal margins to their ventral spines show no evidence of the presence of spinules. Owing to its inconsistency, these proximal spinules were not included in the diagnosis.

*Anomalocaris* cf. *canadensis* Whiteaves, 1892

Figure 3

1995 *Anomalocaris* sp. Nedin, pp. 31, 33–36, figs 2, 3B.
2006 *Anomalocaris* sp. Paterson and Jago, p. 43.
2011 *Anomalocaris* sp. nov. Paterson et al., p. 239.

Material. Eleven specimens, with six from Buck Quarry (SAM P14985, P15374, P43616, P45749, 48158, 48164) adding to the two previously described specimens (SAM P40807, originally referred to as AUGD 1046-600, and P40822, originally referred to as AUGD 1046-346; Nedin 1995) and an additional three specimens (P44851, P42037 and possibly P44859) from the wave-cut platform (see Supplementary Information).
Description. *Anomalocaris* frontal appendages with 14 podomeres, ranging from 70 to 183 mm long (mean = 136 mm, SD = 47 mm, n = 4) measured along the dorsal margin. Podomeres appear roughly rectangular in compacted lateral view with dorsal margins wider than ventral margins, imparting a convex profile along the dorsal length of the appendage with the distal end being curled under (Fig. 3A–B, G–H). The size of the podomeres decreases distally. Podomere boundaries are preserved as straight or slightly curved lines, with no evidence of arthrodial membrane or flexible cuticle between them, likely due to the tightly coiled nature of the specimens.

Podomeres 1 to at least 11 each show paired ventral spines protruding from the centre of their ventral margins (vs in Fig. 3B, H). Podomeres 12 and 13 lack complete ventral margins in all specimens, so the presence of ventral spines is unknown. Podomere 14 does not show ventral spines (po14 of left appendage in Fig. 3B). The ventral spine of podomere 1 is preserved only in SAM P15374, where it is nearly as long as the height of the associated podomere and tapers to a point flanked by two thin auxiliary spines less than 1 mm long. Podomeres 2 to at least 11 have ventral spines that alternate in length, with those on the even-numbered podomeres being longest. The ventral spines on podomere 2 are as long as the podomere is high. The rest of the ventral spines decrease in size distally, those near the distal end of the appendage no more than one-fourth the height of the associated podomere. Most of these ventral spines terminate in a point flanked by two auxiliary spines protruding at an oblique angle and 1–3 mm long (as in Fig. 3B, H). However, in SAM P40807, the right appendage shows a ventral spine with two pairs of auxiliary spines on podomere 4 (1–4 in Fig. 3D). These spines seem to be clearly attached to the ventral spine with no articulations or boundaries at their bases. The left appendage of SAM P40807 shows at least three, and possibly four, auxiliary spines (1–4? in Fig. 3C) on the ventral spine of podomere 2/4 (podomeres cannot be counted to the proximal portion of the appendage). In this case, a clear boundary separates auxiliary spine 2 from the ventral spine, so it could be an overlap of one of the auxiliary spines from the other ventral spine of the pair from that podomere. In SAM P15374, the second ventral spine from the proximal end shows two pairs of auxiliary spines, and possible one more on the right side from a third pair (1–5? in Fig. 3E). A similar morphology is evident in SAM P42037, where the ventral spine on podomere 2 shows three auxiliary spines on the left side and two on the right (1–5 in Fig. 3F).

The most proximal podomere is not completely preserved in any specimen, but SAM P40822 shows it to be elongated to a length equivalent to the following three podomeres with a rounded, outwardly convex proximal margin. The most distal margin of podomere 14 is preserved in only one specimen (po14 of the left appendage in Fig. 3B) where it appears rounded with a small terminal spine (ts in Fig. 3B). Simple, elongated dorsal spines on podomeres 10–14 are located medially on the sagittal axis of the most distal region of the dorsal margin of the podomere and arch forward over the full length of the podomere distal to it (ds in Fig. 3B, H).

Remarks. Nedin (1995) described some of this material as *Anomalocaris* sp. and not *A. canadensis* because the Emu Bay Shale material was interpreted as having the longest ventral spines on the odd-numbered podomeres, but *A. canadensis* has the longest ventral spines on the even-numbered podomeres (Whiteaves 1892; Briggs 1979; Whittington and Briggs 1985). This was based largely on SAM P40807 (Nedin 1995, fig. 2A, B) and SAM P40822. SAM P40822 has an incomplete distal end, and the proximal region does not preserve podomere boundaries, so it

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**FIG. 1.** *Anomalocaris briggsi* Nedin, 1995. Frontal appendages in lateral aspect. A–B, holotype, SAM P40180, previously illustrated by Nedin (1995, fig. 1A). C–D, SAM P47020a, previously illustrated by Paterson et al. (2011, SI fig. 2a, b). Abbreviations: as, auxiliary spine; bs, basal spines; ds, dorsal spine; fc, flexible cuticle (arthrodial membrane); po, podomere; sp, spinules; ts, terminal spine; vs, ventral spine. Scale bars represent 1 cm.

**FIG. 2.** Reconstruction of *Anomalocaris briggsi* frontal appendage in lateral view. Podomeres had a pair of ventral spines but, for clarity, only one ventral spine is shown per podomere. Abbreviations as in Figure 1.
cannot be determined whether the longest ventral spines are on the even or odd podomeres. In SAM P40807, the situation is clearer. We consider the number of podomeres in SAM P40807 to be one more than originally counted; a line of articulation is visible between podomeres 1 and 2 (right appendage in Fig. 3A–B), but this boundary was not included in a previous camera lucida drawing of this specimen (Nedin 1995, fig. 2B). With that boundary identified, the longest ventral spines of these appendages are on the even-numbered podomeres, making it indistinguishable from *A. canadensis* in this respect.

The sole difference between the Emu Bay Shale frontal appendages and those of *A. canadensis* is a newly described feature, the presence of extra pairs of auxiliary spines on some of the ventral spines. The left and right frontal appendages of SAM P40807 each show a ventral spine with two pairs of auxiliary spines (Fig. 3B–D) instead of the one pair observed in *A. canadensis* (Whiteaves 1892; Briggs 1979; Whittington and Briggs 1985). The presence of two pairs of auxiliary spines is also seen in the appendages of *A. saron* (Hou et al. 1995, figs 2B–F, 3). Other *A. cf. canadensis* appendages show single ventral spines with three pairs of auxiliary spines (SAM P15374, P42037), which bears some resemblance to the shorter ventral spines of *A. brigssi* (e.g. the ventral spine of po12 in fig. 1B). Owing to this inconsistent ventral spine morphology, we have left these Emu Bay Shale specimens under open nomenclature.

Nedin (1995) also compared this material to specimens from the Chinese Chengjiang biota that were formerly attributed to *Anomalocaris canadensis* by Hou and Bergström (1991). The Chengjiang specimens were, however, subsequently reassigned by Hou *et al.* (1995) to *A. saron* (frontal appendages in Hou and Bergström 1991, pl. 2, fig. 2; Chen *et al.* 1994, figs 1–2) and *Anomalocaris* sp. (frontal appendages in Hou and Bergström 1991, pl. 2, fig. 3).

**ANATOMICAL DESCRIPTION OF ISOLATED ANOMALOCARIS ELEMENTS**

**Oral cone**

A single specimen of an *Anomalocaris* oral cone from the Emu Bay Shale (SAM P31956) is derived from the wave-cut platform and was figured as a ‘possible mouth of *Anomalocaris*’ by McHenry and Yates (1993, p. 82). Restudy of the specimen (Fig. 4) after removal of a calcite crust by acid dissolution shows that it conforms to the morphology of the oral cone of *A. canadensis* described by Daley and Bergström (2012, especially fig. 2a–d therein) in all respects. The specimen exhibits triradial symmetry with three large plates (L in Fig. 4B) arranged with the largest separated from the other two by about 125 degrees and the two slightly smaller plates separated...
by about 110 degrees (compared with angles of 130–140 and 90–100 degrees in Daley and Bergström 2012). In between the three large plates are small and medium plates with an irregular number and arrangement (11 on left side, 7 on right side, 4 posteriorly). Scale-like nodes are preserved on the large and medium plates, some with an asymmetrical profile and most with the peaks broken off. Daley and Bergström (2012) described subdivisions at the outer margins of the large and medium plates as consisting of up to five folds extending no more than one-fourth the total length of the plate. In the Emu Bay Shale specimen, two individual plates show one and two subdivisions that extend to about half the length of the plate (left side of Fig. 4B). In the series of four plates just to the left of the anterior large plate, three shorter plates appear to be subdivisions of an adjacent longer plate that extends all the way into the central region, despite the presence of clear divisions and boundaries.

The outline of the oral cone is irregular, but is roughly rounded rather than diamond-shaped or rectangular, a distinction that was formerly thought to separate the Anomalocaris oral cone from that of Peytoia (Collins 1996). Daley and Bergström (2012) showed that the Burgess Shale Anomalocaris oral cone is round. The central region of the Emu Bay Shale oral cone does not consist of an opening, but instead, the three large plates extend into it, similar to the small and irregular central gap described for A. canadensis. One of the large plates has four rounded teeth-like projections (t in Fig. 4B). Daley and Bergström (2012, fig. 2f) also reported four teeth on one of the larger plates in A. canadensis (ROM 61669).

This oral cone confirms the identity of the anomalocaridid appendages from the Emu Bay Shale as being from Anomalocaris. The specimen comes from the wave-cut platform, as do both species of Anomalocaris, so it is not possible to determine its specific assignment.

Body flaps

Emu Bay Shale Anomalocaris body flaps (Figs 5–6) have been found almost exclusively at Buck Quarry. Fifty-five specimens consisting of single flaps and 15 assemblages consisting of two or more flaps, or flaps with setal structures, have been sourced from Buck Quarry, whereas only four specimens of single flaps have been collected from the wave-cut platform and adjacent cliffs (see Supplementary Information for catalogue numbers). Flaps range in size up to 73 mm in width (SAM P48153), as measured from the tip of the flap directly across to the attachment area. Body flaps from the Emu Bay Shale are found isolated or closely associated with two or three flaps of similar size and preservation (Fig. 6F). SAM P47203, SAM P46354 and P45441 consist of single flaps with closely associated setal structures (Fig. 5C, E), and SAM P44236 shows setal blades (Fig. 5I) and a partially preserved axial region (Fig. 5H) in close association with the flap (described below).

Flaps are subtriangular in outline, with a longer, broadly convex margin towards the anterior (based on comparison with full-body specimens of Anomalocaris) and a shorter margin, usually straight (Figs 5D–E, H, 6A, C) or broadly concave (Figs 5A–C, 6F), directed towards the posterior. The margin of attachment is straight (Figs 5A, 6A–C) in specimens where it is not obscured by or continuous with irregular organic material, presumably parts of the rest of the body (Figs 5B–C, E, H, 6F). The most conspicuous structures on the surface of the flaps are evenly spaced, subparallel lines oriented transversely on the anterior half of the flaps (Figs 5A, D, 6C). There are up to twelve of these transverse lines, which originate at the anterior margin of the flap and extend about halfway into the flap at an angle of 35–45°. The lines end along a straight line in the centre of the flap, but no solid feature defines this boundary (Fig. 5A–D), nor is there any evidence of a boundary line along the margin of the flap. The transverse lines typically run parallel to one another, but SAM P15133 shows them branching and pinching off (arrows in Fig. 5B). In addition to the transverse lines, one specimen (SAM P43656) preserves fine, faint striations in the posterior region of the flap (black arrow in Fig. 5D).

Emu Bay Shale flaps preserve internal microstructures of the transverse lines (Fig. 6). In most specimens, the external, surficial morphology of the transverse lines is as simple, slightly curved lines preserved as thin impressions or raised ridges on the flap (Fig. 5A–C, E, H). A few specimens show that below these simple external lines, the internal structure consists of distinct boundary lines delimiting a series of tiny raised blocks or bars between them (Fig. 6C–D, F–H). The boundary lines are simple and slightly curved upward and outward in the anterior
region of the flap, with the distance between them decreasing gradually towards the outer margin of the flap (Fig. 6D, G). Between the boundary lines is a series of thin raised bars, often perpendicular to the boundary lines (Fig. 6D), but sometimes in an imbricated arrangement (Fig. 6G). The raised bars are spaced about as far apart as they are wide (Fig. 6D) or are very closely spaced (Fig. 6H). In one specimen, each bar shows striations (Fig. 6G). In fainter, possibly more decomposed or decayed specimens, the boundary lines are not visible, and the inner structure appears as a series of small bars and/or indentations with indistinct margins (Fig. 6E). The raised bars are regarded as being internal because some specimens show them together with the simple lines of the external surface of the flap, as a series of raised swellings beneath or near them (white arrows in Fig. 5D). In SAM P47153, simple external lines are visible on the dorsal surface at the distal end of the flap (bottom half of Fig. 6B), and the convex swellings of the upper surface of the internal bars are visible beneath the external lines further towards the medial region of the flap (top of Fig. 6B). The more proximal region of the flap preserves concave depressions into the underlying impression of the ventral surface of the flap on the sediment, representing the lower surface of the internal bars (right side of Fig. 6A) and demonstrating the internal nature of the structures. Less well-preserved specimens show partial decay preferentially located along the transverse lines (black arrows in Fig. 6E). Two specimens also show regularly spaced raised bars running between the transverse lines, perpendicular to and bounded by them (black arrows in Fig. 5F and white arrows in Fig. 6E).

Setal blades (‘gills’)

Material collected from Buck Quarry includes 36 specimens interpreted as possible isolated setal structures belonging to *Anomalocaris*, the ‘gills’ of Whittington and Briggs (1985). The most well-preserved, isolated setal structures are small (blades less than 1 cm long) and consist of a series of lanceolate blades attached at one end and free-hanging at the other (Fig. 5G). Isolated specimen SAM P45525 (Fig. 5G) preserves a curved line to which the lanceolate blades are attached. Some specimens, such as SAM P45599, show several larger setal structures that overlap and setae that are preserved as a series of parallel-sided blades.

Setal blades are found in association with both frontal appendages and body flaps. The slab with the holotype of *Anomalocaris briggsi* (SAM P40180) preserves a mass of fibrous, thin filaments, which may be setal blades, about 2 cm from the dorsal margin of the appendage. Four specimens of anomalocaridid body flaps are preserved with nearby setal structures. In SAM P47203, these consist of a mass of roughly parallel blades (thin lines) that are situated anterior and central to the preserved flap, near its base (black arrow in Fig. 5C). SAM P44236 preserves a small setal structure that consists of a central ramus with eight small blades branching from it (Fig. 5I). In SAM P45441, the setal structure consists of a mass of highly textured, tangled threads or thin blades (Fig. 5E). SAM P46354 shows a faint impression of a lamellar structure near its flap.

**Possible axial region**

Although flaps are common in the collections from Buck Quarry, they are nearly all detached from the rest of the body, apart from the association with detached setal blades noted above. A single specimen, SAM P44236 (Fig. 5H), preserves a fragment of the axial region of the *Anomalocaris* body. It consists of a body flap attached to a large fragment of distorted cuticle that extends the full length of the flap. Near the attachment of the body flap to this cuticle are four, high-relief oval swellings in a paired arrangement, lined up approximately 2 mm apart, and a further two swellings situated anterior and posterior to the pairs, in line with those on the left side (white arrows in Fig. 5H). These swellings are approximately 4–5 mm in diameter and have gradual margins that are continuous with the cuticle surrounding it, as though the body cuticle is draped over internal high-relief structures. Preparation of one of the swellings yielded an internal structure consisting of densely packed spheres. This specimen is also associated with the clear setal structure (Fig. 5I) described in the previous section (white box in Fig. 5H). The rest of the cuticular material is indistinct with no recognizable features.

**Figure 6.** *Anomalocaris* body flaps, showing detail of the transverse lines. A–B, SAM P47153; A, flap showing both the external and internal morphology of the transverse lines; B, enlargement of boxed area in A, showing external morphology of simple transverse lines (lower half) and the seriated blocks as internal structure underneath them. C–D, SAM P14822a, previously illustrated by Paterson et al. (2011, SI fig. 1f); C, flap with seriated blocks for transverse lines; D, enlargement of boxed area in C. E, SAM P46963a, flaps showing vertical bars between seriated transverse lines (white arrows) and preferential decay occurring along transverse lines (black arrows). F–G, SAM P47142; F, pair of body flaps with seriated transverse lines; G, enlargement of boxed area in F, showing striations on the seriated blocks of the transverse lines. H, SAM P45672, flap with highly striated transverse lines. Scale bars represent 5 mm in A, C, E–F, H and 3 mm in B, D, G.
DISCUSSION

Anomalocaridid material from the Emu Bay Shale includes a diverse collection of specimens showing isolated body parts. Although whole bodies have yet to be found, the disarticulated material is informative owing to the novel preservation at the Emu Bay Shale locality. This locality not only has yielded a species of *Anomalocaris* unique to this site, but also brings to light structures in the body flaps that are not evident in anomalocaridids from Chengjiang, the Burgess Shale or Fezouata. This parallels the preservation of ommatidial lenses on the surface of the eyes of Emu Bay Shale *Anomalocaris* (Paterson et al. 2011), the corresponding surface being smooth and devoid of structure in anomalocaridid eyes from Chengjiang and the Burgess Shale. The unique taphonomic pathway of the Emu Bay Shale ensures preservation of detailed microstructures not preserved in other Cambrian fossil Lagerstätten, but the overall morphology and size of the specimens are similar enough to other Cambro–Ordovician anomalocaridids that their identity is assured, despite their disarticulated nature and novel preservation. The Emu Bay Shale is also the main locality yielding alleged evidence for the inferred predatory lifestyle of *Anomalocaris*, particularly in regards to trilobites (Conway Morris and Jenkins 1985; Nedin 1999; Vannier and Chen 2005).

Morphology of anomalocaridid body flaps

The identity of the structures described herein as *Anomalocaris* body flaps was established by comparison with the most morphologically similar articulated specimens, those of *Anomalocaris saron* and *Amplectobelua symbrachiata* from the Chengjiang biota in China, a comparison enhanced by similarities in style of preservation. The spacing and orientation of the transverse lines are similar in Emu Bay Shale and Chengjiang body flaps, with *Anomalocaris saron* specimens showing as many as 18 transverse lines on a single flap (Hou et al. 1995, figs 4–5). The transverse lines of both *Amplectobelua* and *Anomalocaris* from Chengjiang show bifurcations and anastomoses similar to those seen in some Emu Bay Shale specimens (Chen et al. 1994, figs 3B, 4D; Hou et al. 1995, figs 4–6), and one specimen is described as showing a series of faint, fine striations along the posterior margin (Chen et al. 1994, fig. 3B). Associated setal blades are also observed near the attachment area of the flaps in the Chengjiang anomalocaridids (Chen et al. 1994, figs 1B, 2–3; Hou et al. 1995, figs 4–6), as are present in the Emu Bay Shale material. However, unlike the Emu Bay Shale specimens, *Amplectobelua* and *Anomalocaris saron* have a pronounced boundary line that cuts through the middle of the flap, dividing an anterior region with transverse lines from a posterior region without lines (Chen et al. 1994, figs 1D, 2, 3A; Hou et al. 1995, figs 4A, 5). Chengjiang specimens of *Amplectobelua* also preserve a structure of the same nature as the transverse lines running along the margin of the flap (Chen et al. 1994, fig. 4B), which has not been observed in the Emu Bay Shale material. Despite these differences, the similarities between the Emu Bay Shale specimens and *Anomalocaris saron* and *Amplectobelua symbrachiata* are strong enough to confirm the identity of these specimens as anomalocaridid body flaps.

The Burgess Shale has the greatest anomalocaridid diversity of any Cambrian Konservat-Lagerstätte (Whittington and Briggs 1985; Daley et al. 2009; Daley and Budd 2010), and many whole-body specimens have well-preserved body flaps. However, transverse lines are typically poorly preserved and are only present in about half of the whole-body specimens of *Peytoia* (USNM 274143/47, USNM 274164, USNM 274144/48, USNM 247145/62 and USNM 274146) and three of the ten *Hurdia* specimens (ROM 59320, ROM 60010, ROM 60029) with visible flaps. The transverse lines are most obvious in *Peytoia nathorsti* (Whittington and Briggs 1985, figs 20, 28, 30, 42–43, 50–51, 59), where they are described as evenly spaced and highly reflective, with negligible relief such that they are barely visible in low-angle lighting (Whittington and Briggs 1985, p. 584). They are preserved in a similar fashion in *Amiella ornata* (Whittington and Briggs 1985, figs 91, 94; Daley et al. 2013, fig. 14F) and an unidentified anomalocaridid USNM 274154 (and counterparts 274156 and 274161) (Whittington and Briggs 1985, figs 81–88, 100; Daley et al. 2013, fig. 14D). The transverse lines of the flaps of these Burgess Shale taxa typically extend from the anterior margin to at least halfway into the flap (Whittington and Briggs 1985, figs 20, 59, 91, 94), but sometimes extending the full length (Whittington and Briggs 1985, figs 28, 30, 42–43, 51–52, 81–88, 100). *Hurdia victoria* has diminutive flaps, but some specimens show clear transverse lines that also cover almost the entire surface of the flap (Daley et al. 2013, figs 18A–B, 20D–F, 21A–B). A unique feature to Burgess Shale taxa is that specimens of *Peytoia* (Whittington and Briggs 1985, fig. 30), *Hurdia* (Daley et al. 2013, fig. 20D–F) and the unidentified anomalocaridid USNM 274154 (Whittington and Briggs 1985, figs 82–88) show partially decomposed body flaps with the transverse lines extending outward beyond the margin of the flap, suggesting that the transverse lines were more decay resistant than the flap itself. The only anomalocaridid from the Burgess Shale that does not preserve clear transverse lines is *Anomalocaris canadensis*. ROM 51212 (Collins 1996, fig. 4.2) may preserve faint transverse lines on its body flaps, but both ROM 51212 and ROM 51211 (Collins 1996, fig. 4.1) preserve very fine striations along through the anterior half.
of their body flaps, bounded by a clear line that bisects the flap. These striations are described in most to what is evident on the posterior margin of the Emu Bay Shale specimen SAM P43656 (black arrow in fig. 5D) and in Chengjiang material (Chen et al. 1994, fig. 3B).

Anomalocaridid body flaps are also preserved in the lower and middle Cambrian of Nevada and Utah and the Lower Ordovician Fezouata Formation of Morocco. A specimen interpreted to be the posterior body region of Peytoia nathorsti from the middle Cambrian Marjum Formation of Utah shows a series of parallel lines passing through the anterior region of most of the body flaps, beginning along the anterior margin and extending into the body flap at an angle of approximately 45 degrees (Briggs and Robison 1984). These are similar in orientation, spacing and location to the transverse lines of anomalocaridids from the Emu Bay Shale, Chengjiang and Burgess Shale. Cambrian specimens from the Poche Formation of Nevada consist of three partial putative bodies with flaps and a single isolated flap (Lieberman 2003). The three body specimens do not have transverse lines visible on their flaps, but the single isolated flap (with length of only 15 mm) is described as having five transverse lines that extend through the whole flap in a wide arc from the proximal anterior margin to the distal posterior margin (Lieberman 2003, pp. 683–684, fig. 6.5). A much larger partial body of an anomalocaridid described from the Spence Shale Member in Utah consists of several body flaps bearing transverse lines that parallel the anterior margin of the flap and extend for most of its length (Briggs et al. 2008, fig. 1). The putative transverse lines in both these specimens are orthogonal to the transverse lines in other anomalocaridid material from the Emu Bay Shale, Chengjiang and Burgess Shale, which run from the distal anterior margin towards the centre of the flap, rarely reaching the posterior margin. Ordovician material includes two incomplete anomalocaridid bodies. In one specimen (YPM 226437, called YPM 226637 in the Supplementary Information of Van Roy and Briggs 2011), two flaps preserve transverse lines (Van Roy and Briggs 2011, figs 1a, c, S2a, b) that are subparallel and present only in the anterior region of the flap (for the more posterior flap) or along the more proximal region of the second, partially preserved flap. The transverse lines have little to no relief and are visible as black lines that are either highly reflective or dark stained (Van Roy and Briggs 2011, fig. 1c). YPM 266339 also has a preserved flap, with pronounced transverse lines (Van Roy and Briggs 2011, fig. S3a, b) that are preserved as robust structures with relief. The structure is a relatively thick line with a rim along either side (as seen in Emu Bay Shale specimens), but the inner region does not have the raised ridges or bars evident in the Australian material.

Interpretation of the transverse lines. The transverse lines on the anterior part of the body flaps have been described under two alternative nomenclatures that imply different functions – they are variously described as veins (Chen et al. 1994; Hou et al. 1995) or as strengthening rays (Whittington and Briggs 1985). In Chengjiang anomalocaridids, Chen et al. (1994) referred to these lines as ‘canals’ and ‘veins’ and drew support for this interpretation from the ‘wrinkled, three-dimensionally preserved structure in one specimen’ of Amplectobelua (Chen et al. 1994, p. 1306). They also called these structures ‘canal systems’ (p. 1305) for Anomalocaris, based on comparison with Amplectobelua. Unlike species of Anomalocaris and Amplectobelua from Chengjiang, a well-defined central ‘vein’ along the middle of the flap is lacking in Emu Bay Shale Anomalocaris. The indistinct nature of a marginal line (‘vein’) in the Emu Bay Shale material, if it were originally present (as is the case in Chengjiang Amplectobelua), could be attributed to comparatively poor preservation of the anterior margin of the flaps in most specimens, whereas the absence of a central line/vein is harder to attribute to it not being preserved. The apparently blind termination of the lines at their posterior ends is inconsistent with a network of veins, but is not inconsistent with a mechanical role for these structures. It is also difficult to reconcile the apparently rigid internal structures associated with the transverse lines in Emu Bay Shale Anomalocaris with an originally tubular structure as would be expected for veins or canals. Whittington and Briggs (1985) discussed the swimming motion of anomalocaridids and interpreted the transverse lines as likely being strengthening rays that would also have assisted with movements in a function similar to fin rays in fishes. They quote Webb (1975, p. 47), who said that ‘individual segments are capable of fairly extensive independent movement because muscular forces are transmitted to stiff fin rays supporting a thin, highly flexible finweb’. The former also suggested that the strengthening rays would have been most prominent in the anterolateral region of the flap because they would have assisted in maintaining the most hydrodynamic shape to the lobe during the downward stroke of the swimming motion (Whittington and Briggs 1985, fig. 103b). This position of the transverse lines is well documented in anomalocaridids from the Emu Bay Shale, Chengjiang and the Burgess Shale. Several Burgess Shale specimens also show the transverse lines protruding from the ragged margins of partially decayed Peytoia and Hurdia body flaps, providing further evidence of the robust nature of the transverse lines and their function as structural elements.

The structure of the transverse lines in the anomalocaridids essentially consists of a pair of distinct boundary lines sandwiching an area of raised blocks or bars.
Functionally analogous microstructures are also seen in the stiffening rods of fin-like structures that a variety of other animals use to propel themselves through fluid, be it water or air. For example, the fin rays of the median and paired fins of many Actinopterygii (ray-finned fishes) consist of two semilunate half rays (hemitrichs) that are joined together by thin fibres of collagen and elastin (Lanzing 1976; Geerlink and Videler 1987; Lauder et al. 2006). Differential movement of the two hemitrichs imparts flexibility to the fin, allowing it a small degree of bending whilst still retaining a stiff and strong overall structure that can withstand the forces generated along the distal margin of the fin during forward propulsion. In several batoid (stingrays and skates) families (Dasyatidae, Potamotrygonidae, Rajidae, Urotrygonidae), fin rays of the pectoral wings consist of a pair of catenate calcified chains, which imparts flexibility and strength to the wing, and oscillatory swimmers also exhibit cross-bracing consisting of cartilaginous extensions that join adjacent fin rays (Schaefer and Summers 2005), similar to the branching seen in the transverse lines of Anomalocaris body flaps from Emu Bay Shale. Even the wing veins of some insects, like dragonflies, consist of two layers of chitin with a mass of protein and muscle fibrils in between, albeit arranged into the tubular form of the vein (Wang et al. 2008). A general morphology of two boundary structures enclosing an inner region of densely packed fibres imparts flexibility and strength to the propulsive fins and flaps of a variety of animals and may be comparable in function to the microstructure of the transverse lines of body flaps in specimens of Anomalocaris from the Emu Bay Shale.

Setal structures and possible axial region structures in anomalocaridids

The setal structures described for Anomalocaris from the Emu Bay Shale have a morphology comparable to those seen in the Burgess Shale taxa Hurdia (Daley et al. 2009, figs 2E, S2C, H), Peytoia (Daley et al. 2009, fig. S2A–B, D–F, I) and Opabinia (Bergström 1986, fig. 1F; Budd 1996, fig. 1A–B; Budd and Daley 2012, fig. 4C–D), but are generally much smaller in size. Hurdia has large setal structures on the body, but in the anterior region just behind the head, there are three or four pairs of smaller setal structures comparable in size to the isolated structures from the Emu Bay Shale (Fig. 5G, I). The isolated setal structure of SAM P45525, with its scalloped margin of attachment (Fig. 5G) is particularly similar to isolated Hurdia setal structures (Daley et al. 2009, fig. 2E; Daley et al. 2013, fig. 15), which have been compared with the ‘transverse rods’ of Peytoia (Whittington and Briggs 1985), suggesting that these mineralized, nodular rods are the attachment points for the setal blades (Bergström 1987; Daley et al. 2009). Setal structures are poorly preserved in other anomalocaridids, but are described as lamellar structures in Anomalocaris canadenisis (Whittington and Briggs 1985, p. 579, fig. 3; Collins 1996), Anomalocaris saron (Chen et al. 1994, p. 1305, fig. 2; Hou et al. 1995, pp. 165, 167, figs 4–6) and Amplectobelua symbrachiata (Chen et al. 1994, fig. 3a).

The only known specimen from the Emu Bay Shale with a putative axial region of the body has paired high-relief structures that are arranged serially amidst a large area of indistinct body cuticle (Fig. 5H). The closely allied taxon Opabinia from the Burgess Shale has three-dimensional diverticula preserved in a paired arrangement on either side of the gut in the axial region of the body, with an elliptical shape and a smooth or laminated surface (Budd and Daley 2012, p. 90, fig. 7A–F). Other Cambrian taxa such as the armoured lobopodians Kerygmachela (Budd 1999) and Pambdelurion (Budd 1998) and the euarthropod Leacholita (Butterfield 2002) have gut diverticula with a similar shape and position, and these are either phosphatized or preserved in darker material than the rest of the specimen. Based on similarities in structure, position and preservation, the swellings observed in the Emu Bay Shale Anomalocaris specimen may also represent diverticula of the gut, which are recognized as well in the co-occurring bivalved arthropod Isoxys (García-Bellido et al. 2009), the leanchoiliid Oestokerkus (Edgecombe et al. 2011) and the arthropodans Squamaculata and Australimicola (Paterson et al. 2012). Paired patches of nodular mineralization are also associated with the gut in the anomalocaridids Peytoia nathorsti (Whittington and Briggs 1985, p. 584, figs 20, 30, 50) and Anomalocaris canadenisis (Whittington and Briggs 1985, p. 579, figs 3–6; personal observation of unpublished material) from the Burgess Shale, and in Peytoia nathorsti from the Marjum Formation (Briggs and Robison 1984, p. 5, figs 3, 4). Anomalocaris saron from Chengjiang also has paired, serially repeated structures in close association with the gut (Chen et al. 1994, p. 1305, figs 1–2) that appear nodular and are preserved in darker material than the rest of the body and have been interpreted as digestive glands (Vannier and Chen 2005, fig. 11A; Vannier 2009, fig. 5E). Similar structures have also been observed in Amplectobelua symbrachiata (Chen et al. 1994, 2x to 4x in fig. 3A) and have been equated to the paired nodular patches in Peytoia nathorsti from the Burgess Shale.

Reassessing the evidence for predatory habits of Anomalocaris

Emu Bay Shale fossils have played a key role in establishing the idea that Anomalocaris was a top visual predator...
in Cambrian ecosystems. Cited evidence includes damage to trilobites and allegedly to nektaspids (Conway Morris and Jenkins 1985; Nedin 1999), large coprolites containing trilobite fragments (Nedin 1999; Vannier and Chen 2005) and the discovery of large, high-resolution compound eyes attributed to Anomalocaris (Paterson et al. 2011). However, durophagy in anomalocaridids, particularly feeding on trilobites, has been recently brought into question (Hagadorn 2009a; Hagadorn et al. 2010; Daley and Bergström 2012), and the functional inability for the oral cone to produce certain injuries to trilobite exoskeletons has been noted previously (e.g. Whittington and Briggs 1985; Hou et al. 1995).

Nedin (1999) documented an elongate (43 × 28 mm) coprolite from the Emu Bay Shale containing identifiable fragments of the trilobite Redlichia takooensis, including a genal spine, thoracic pleurae and parts of the cephalon with distinctive terrace line ornamentation (Nedin 1999, fig. 4; Vannier and Chen 2005, fig. 9). Nedin attributed this coprolite to Anomalocaris based not only on its size, but also his proposed model on how Anomalocaris could fragment trilobite cuticle by repeated flexure of the exoskeleton using its frontal appendages (Nedin 1999, fig. 3). A number of other trilobite-dominated aggregates have been sourced from Buck Quarry (Fig. 7A–H) and appear to represent bone fide coprolites (sensu Hagadorn 2009b), as opposed to ecological or environmental (e.g. current) accumulations (sensu Vannier and Chen 2005). These isolated aggregates are mainly elongate, contain fragmented sclerites of the trilobites Redlichia takooensis and/or Estaingia bilobata and are commonly enveloped by a coating of iron oxide. SAM P45413 (Fig. 7A–B) is elongate (preserved length and width: 31 and 12 mm, respectively), tapers at one end and contains sclerites of Redlichia, including a relatively complete right thoracic pleura from an individual that would have been around 50 mm long; this estimate is supported by the fact that thoracic pleurae in Redlichia have a fairly consistent width (tr.) along most of the trunk. Elongated specimens such as SAM P45413 (Fig. 7A–B) and SAM P47144 (Fig. 7H) may represent coprolites excreted whilst the animal was in motion, whereas rounded specimens such as SAM P47146 (Fig. 7C–D) and P15255 were possibly deposited when the animal was stationary. In SAM P45413, the iron oxide coating is largely restricted to the sclerite aggregate (Fig. 7A–B) and could represent the solid component of the faeces, whereas many other specimens (e.g. P47146, sclerite-bearing portion 25 mm long, 14 mm wide) show aggregates fringed by more extensive iron oxide haloes (Fig. 7C–D), which has been interpreted to represent diffusion of the fluidized component into the surrounding sediment (cf. Nedin 1999; Vannier and Chen 2005). Some coprolites contain concentrated Estaingia fragments, for example, SAM P15470a, b (length 23 mm, width 7 mm) and SAM P47144a, b (incomplete length 28 mm long, width 8 mm; Fig. 7H), whereas P45433 (length 50 mm, width 20 mm; Fig. 7E–G) contains Estaingia sclerites, including a librigena (Fig. 7F) and a complete thoracic segment with its long axis oriented parallel to the long axis of the coprolite (Fig. 7G), together with fragments of Redlichia. Currently twelve coprolites are known from the Emu Bay Shale Konservat-Lagerstätte; eight contain fragments of Redlichia takooensis, three contain fragments of Estaingia bilobata and one contains fragments of both species. Estaingia is much more abundant in the Lagerstätte than Redlichia, so the higher number of coprolites containing fragments of Redlichia suggests that Anomalocaris preferentially preyed on this less common taxon.

Unequivocal evidence of predation damage to trilobite exoskeletons is relatively rare in the Emu Bay Shale. Previously documented specimens of Redlichia show injuries to both sides of the thorax (Conway Morris and Jenkins 1985, figs 1, 2; Nedin 1999, fig. 2B; Daley and Paterson 2012, p. 19), with individuals ranging from 50 to 210 mm in estimated length. However, the injury reported by Nedin (1999, fig. 2A) to the right lateral posterior shield of the nektaspid Emuca rus (referred to as Nara oia) continues well into the surrounding sediment, indicating that this is not an injury but rather represents the uneven edge where a fragment has broken off of the rock sample (Paterson et al. 2010, pl. 2, fig. 2). Some injuries to Emu Bay Shale trilobites appear to have been fatal (contra Conway Morris and Jenkins 1985) because there is no evidence of healing or repair around the affected areas, as has been seen in other injured trilobites from the middle Cambrian of the Northern Territory, Australia (Jago and Haines 2002) and British Columbia, Canada (Rudkin 1979). A large specimen (P48149) from the coast with a scattering of Redlichia fragments is possibly not a coprolite, but may represent the remains of an attack that shattered this relatively large Redlichia specimen (Fig. 7I). Anomalocaridids are often suspected to have inflicted such injuries on Cambrian trilobites (Rudkin 1979, 2009; Briggs and Mount 1982; Babcock and Robison 1989; Pratt 1998; Babcock 1993, 2003; Nedin 1999; Jago and Haines 2002; Babcock and Peel 2007), but recent arguments (Hagadorn 2009a; Hagadorn et al. 2010; Daley and Bergström 2012) suggest that the oral cone of Anomalocaris – which is prone to wrinkling, folding and tearing – would have been too soft and pliable to break the mineralized exoskeleton of a trilobite. The oral cone of anomalocaridids could not occlude (Whittington and Briggs 1985; Hagadorn 2009a; Hagadorn et al. 2010) and the irregular shape and small size of the central opening in Anomalocaris made it unsuitable for strong biting motions (Daley and Bergström 2012), but the oral cone may have been capable of breaking weakly mineralized trilobites (Hagadorn 2009a). This supports the
suggestion of Conway Morris and Jenkins (1985) that healed injuries in *Redlichia* resulted from attacks that occurred during the unmineralized stage immediately following moulting. Some modern aquatic predators (including cannibals) that feed on freshly moulted arthropods are able to detect specific moulting hormones (e.g. ecdysone) released by their prey (Marshall et al. 2005; Jackrel and Reinert 2011). It is possible that some anomalocaridids could use chemoreception to detect freshly moulted trilobites and other arthropods, which would complement their visual acuity (Plotnick et al. 2010; Paterson et al. 2011). Nevertheless, the scenario of *Anomalocaris* feeding upon postecdysial, 'soft-shelled' trilobites, whilst plausible, cannot account for the mineralized trilobite fragments present in coprolites, unless Nedin’s (1999) model is warranted. This model, which involves

**FIG. 7.** Trilobite-dominated aggregates from the Emu Bay Shale interpreted as coprolites (A–H) and remnants of an attack (I). A–B, SAM P45413; A, part, coprolite with *Redlichia* fragments; B, counterpart. C–D, SAM P47146; C, aggregate fringed with extensive iron oxide halo; D, enlargement of sclerite-bearing central portion of aggregate. E–G, SAM P45433; E, part of aggregate containing both *Estaingia* and *Redlichia* fragments; F, enlargement of boxed area in E, showing librigena of *Estaingia bilobata*; G, enlargement from the counterpart of *Estaingia* thoracic segment indicated on part by arrow in E. H, SAM P47144a, aggregate containing concentrated *Estaingia* fragments. I, SAM P48149, loose aggregate of *Redlichia* fragments possibly representing the remnants of an attack. Scale bars represent 5 mm in A–E, H, 2 mm in F, G and 10 mm in I.
Anomalocaris lodging a trilobite in its oral cone and using its appendages to break the trilobite exoskeleton by repeated flexure, would undoubtedly cause damage to the oral cone and appendages in the form of broken spines or scarring; however, no damage of this type has been observed.

The considerable diversity of anomalocaridid frontal appendages and oral cones (Whittington and Briggs 1985; Chen et al. 1994; Hou et al. 1995; Nedin 1995; Collins 1996; Lieberman 2003; Briggs et al. 2008; Daley et al. 2009; Caron et al. 2010; Daley and Budd 2010; Daley and Peel 2010; Daley and Bergström 2012) indicates that these stem-group arthropods had a varied diet and range of feeding strategies. The functional morphology of the frontal appendages suggests that some anomalocaridid taxa may have been durophagous predators, whilst others fed exclusively on soft-bodied organisms (Briggs 1979; Whittington and Briggs 1985; Collins 1996; Nedin 1999; Daley and Budd 2010), which represent up to 98 per cent of individuals in some Cambrian deposits (Caron and Rudkin 2009). Whilst the presence of more than one anomalocaridid taxon in a single Cambrian Konservat-Lagerstätte is not unique (Daley and Budd 2010), the co-occurrence of two similar-sized Anomalocaris species from the Emu Bay Shale implies that different feeding mechanisms might have been employed to exploit disparate prey resources and alleviate interspecific competition. Anomalocaris cf. canadensis, with its short, stout ventral spines, was likely a durophagous predator or scavenger, whereas the frontal appendages of A. briggsi were too fragile for such a feeding mode (Nedin 1999). Anomalocaris briggsi likely fed in a way comparable to that described for Hurdia and Peytoia (= Laggania) (Whittington and Briggs 1985; Nedin 1995; Daley and Budd 2010), with the appendages functioning like a net apparatus to trap small prey items in their long spine ventral spines as they moved through the water column or through the substrate.

If anomalocaridids were not strictly durophagous predators, few other organisms in the Emu Bay Shale can be identified as candidates for inflicting damage to trilobites and producing large coprolites. Given the size of coprolites, prey fragments within some coprolites (individuals of Redlichia >40 mm) and injured Redlichia (up to 210 mm in length), at least some of the predators may have had a body size greater than 20 cm in length. A very large, as yet unnamed species of Tuzoia (García-Bellido et al. 2009) may have approached this length, but the known appendages in another species of this genus (see Caron et al. 2010, fig. DR4A–C) seem ill equipped to handle trilobites, especially as Tuzoia is interpreted to be free-swimming (Vannier et al. 2007). The only other arthropod taxon of that size from the Emu Bay Shale (other than the anomalocaridids) is Redlichia takoonensis, with a length of up to 25 cm (Paterson and Jago 2006). Conway Morris and Jenkins (1985) suggested that the injuries in Redlichia from the Emu Bay Shale may be the result of cannibalism. In modern arthropod populations, cannibalism is common, especially when other food resources are limited (for reviews, see Fox 1975; Richardson et al. 2010). It is morphologically feasible that Redlichia was capable of durophagy, as redlichiids are known to possess gnathobasic appendages (Shu et al. 1995; Ramsköld and Edgecombe 1996; Fortey and Owens 1999; Hou et al. 2009). In some modern arthropods such as Limulus, the nonmineralized (chitinous) gnathobases are capable of crushing clam shells (Botton 1984; Shuster et al. 2003), and Sidneyia from the Burgess Shale, which has unmineralized gnathobasic limbs, has been found with trilobite fragments in its alimentary tract (Bruton 1981), as have Utahcaris from the Spence Shale and an undescribed fuxianhuiid from the Kaili biota, but the trunk appendages of these latter two taxa are poorly known (Conway Morris and Robison 1988; Zhu et al. 2004; Vannier and Chen 2005). The width of the alimentary tract in Eoredlichia (Hou et al. 2009) and other Cambrian trilobites (Chatterton et al. 1994; Lin 2007; Lerosey-Aubril et al. 2012) is relatively consistent and occupies approximately one-quarter of the axis, indicating an alimentary tract up to 12 mm wide in the largest known specimens of Redlichia. This would allow excretion of solid faeces of the sizes represented by the sclerite-dense portion of the coprolites from the Emu Bay Shale.

Regardless of durophagous tendencies, Anomalocaris was undoubtedly a highly mobile visual predator, given its large body size, spinose frontal appendages, triradial mouth with a dentate inner margin, high-resolution compound eyes and streamlined body with flexible body flaps and a large tripartite tail fan. Whilst A. cf. canadensis from the Emu Bay Shale cannot be completely ruled out as a durophagous predator, it is likely that A. briggsi at least was restricted to unmineralized prey items.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Anomalocaridid material from the Emu Bay Shale, South Australian Museum collections.

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