

Original Article

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Author for correspondence:

Russell DC Bicknell,
Email: rdcbicknell@gmail.com

Malformed individuals of the trilobite *Estaingia bilobata* from the Cambrian Emu Bay Shale and their palaeobiological implications

Russell DC Bicknell¹ , James D Holmes² , Diego C García-Bellido^{3,4}  and John R Paterson¹ 

¹Palaeoscience Research Centre, School of Environmental & Rural Science, University of New England, Armidale, NSW 2351, Australia; ²Department of Earth Sciences, Palaeobiology, Uppsala University, Villavägen 16, Uppsala 752 36, Sweden; ³School of Biological Sciences, University of Adelaide, North Terrace, Adelaide, South Australia 5005, Australia and ⁴South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia

Abstract

Malformed trilobite specimens present important insight into understanding how this extinct arthropod group recovered from developmental or moulting malfunctions, pathologies, and injuries. Previously documented examples of malformed trilobite specimens are often considered in isolation, with few studies reporting on multiple malformations in the same species. Here we report malformed specimens of the ellipsocephaloid trilobite *Estaingia bilobata* from the Emu Bay Shale *Konservat-Lagerstätte* (Cambrian *Series 2, Stage 4*) on Kangaroo Island, South Australia. Ten malformed specimens exhibiting injuries, pathologies, and a range of teratologies are documented. Furthermore, five examples of mangled exoskeletons are presented, indicative of predation on *E. bilobata*. Considering the position of malformed and normal specimens of *E. bilobata* in bivariate space, we demonstrate that the majority of malformed specimens cluster among the larger individuals. Such specimens may exemplify larger forms successfully escaping predation attempts, but could equally represent individuals exhibiting old injuries that were made during earlier (smaller) growth stages that have healed through subsequent moulting events. The available evidence from the Emu Bay Shale suggests that this small, extremely abundant trilobite likely played an important role in the structure of the local ecosystem, occupying a low trophic level and being preyed upon by multiple durophagous arthropods. Furthermore, the scarcity of malformed *E. bilobata* specimens demonstrates how rarely injuries, developmental malfunctions, and pathological infestations occurred within the species.

1. Introduction

Malformed fossils present insight into how extinct forms responded to developmental, parasitic, and injury-related complications (Owen, 1985; Babcock, 1993; Klompmaker *et al.* 2019; De Baets *et al.* 2022). Such specimens have been particularly useful for understanding facets of extinct arthropod groups (Babcock, 2003), including chelicerates, crustaceans, and trilobites (Owen, 1985; Klompmaker *et al.* 2013; Bicknell *et al.* 2018c, 2022b; Mitov *et al.* 2021; De Baets *et al.* 2022). The most commonly documented malformed arthropod fossils are trilobites – a record that reflects their biomineralized exoskeleton (Babcock, 2003, 2007; Fatka *et al.* 2015; Bicknell *et al.* 2022d). This exoskeleton increases the preservational potential of individuals, and, by extension, improves the possibility of identifying malformed specimens.

Trilobites with malformations are often documented as stand-alone records, with examples ranging from the Cambrian through to the Carboniferous (Owen, 1985; Babcock, 2007; Bicknell *et al.* 2022a). As such, few publications have presented a thorough record of malformations from the same deposit, especially considering the ratio of malformed individuals in the context of non-malformed specimens of the same species. However, over the last five years, there has been a transition to presenting detailed records of malformed specimens from the same deposit and contextualizing these specimens within a larger population (see Pates *et al.* 2017; Bicknell *et al.* 2019, 2022a; Pates & Bicknell, 2019; Bicknell & Smith, 2022). To extend this line of enquiry, we considered *Estaingia bilobata* Pocock, 1964 from the Emu Bay Shale (Cambrian *Series 2, Stage 4*) of South Australia. This species is exceptionally abundant within the Emu Bay Shale *Konservat-Lagerstätte*, with the vast majority of specimens preserved as articulated exoskeletons (Paterson *et al.* 2016; Holmes *et al.* 2021a, b; Bicknell *et al.* 2022a). The sheer abundance of specimens increases the likelihood of identifying malformed trilobites. Furthermore, injuries and pathologies are already known in other trilobites from the Emu Bay Shale and adjacent strata (Pocock, 1974; Conway Morris & Jenkins, 1985; Nedin, 1999; Paterson & Edgecombe, 2006; Holmes *et al.* 2020; Bicknell *et al.* 2022a). Here we document specimens of *E. bilobata* that exhibit injuries,

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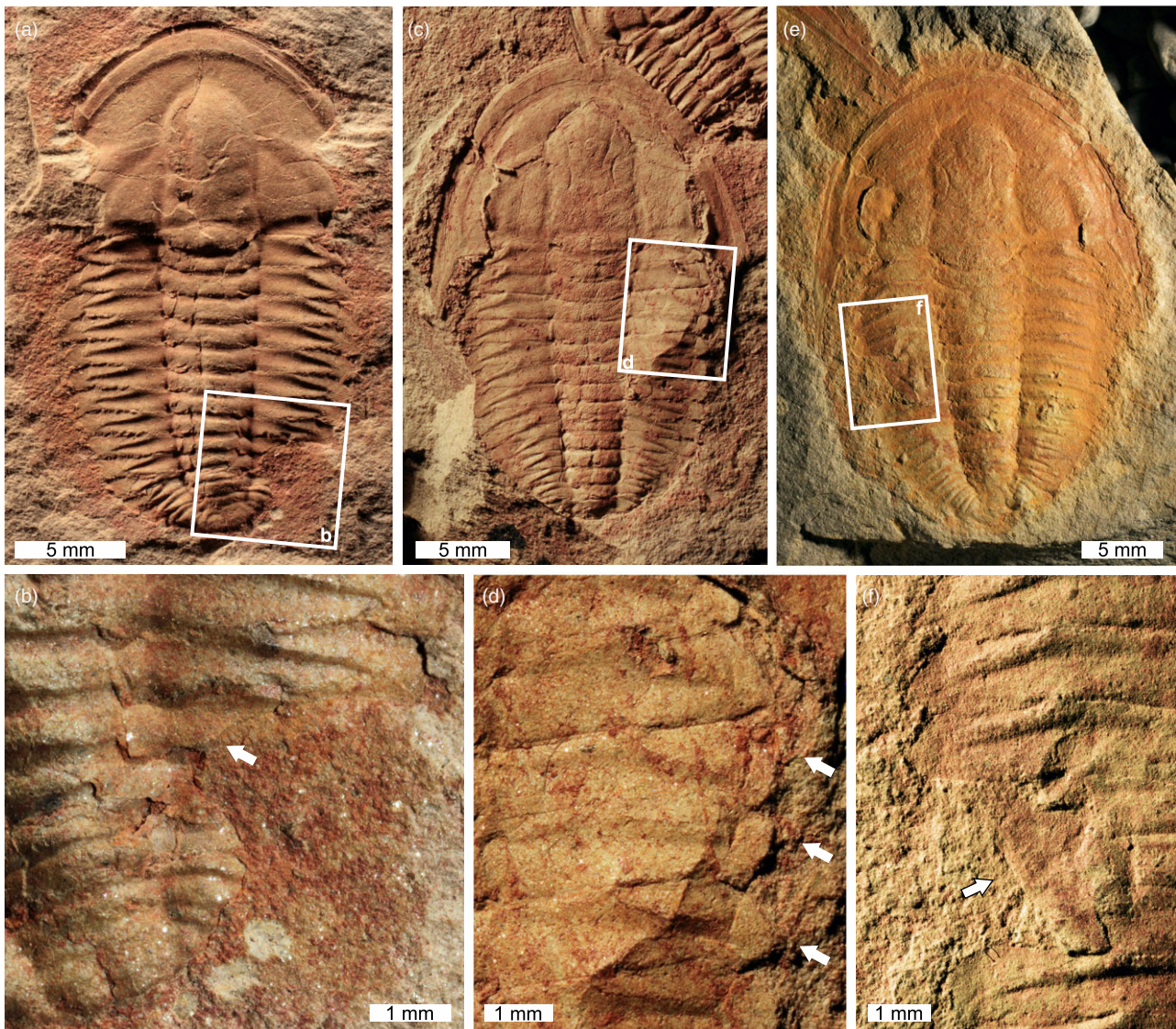


Fig. 1. (Colour online) *Estaingia bilobata* with L-, U- and W-shaped injuries. (a, b) SAMA P46113. U-shaped injury to right side of thorax. (a) Complete specimen. (b) Close-up of injury (white arrow). (c, d) SAMA P45360. L-shaped injury to right side of thorax. (c) Complete specimen. (d) L-shaped injury showing recovering pleural spines (white arrows). (e, f) SAMA P52886. W-shaped injury to left side of thorax. (e) Complete specimen. (f) Close-up of injury (white arrow).

pathologies, and teratologies, as well as evidence of possible durophagy (Figs 1–5). Furthermore, given the detailed information available on *E. bilobata* ontogeny (Holmes *et al.* 2021a, b), we compare these specimens to a population of non-malformed individuals to illustrate at which size class malformed specimens occur, presenting unique insights into the palaeoecology of this abundant Emu Bay Shale trilobite.

2. Geological and palaeoenvironmental context

The Emu Bay Shale forms part of the Kangaroo Island Group in the Stansbury Basin, which crops out on the north coast of Kangaroo Island (South Australia), and is interpreted as a nearshore delta complex (Gehling *et al.* 2011; Jago *et al.* 2021). The Emu Bay Shale is considered to be *c.* 512 Ma (*Pararaia janeae* Zone; Cambrian Series 2, Stage 4) in age (Bengtson *et al.* 1990; Paterson & Jago, 2006; Paterson & Brock, 2007; Jago *et al.* 2020), based primarily on the co-occurrence of the emuellid trilobite *Balcoracania dailyi* Pocock, 1970 and an associated radiometric

date of 511.87 ± 0.14 Ma in the Billy Creek Formation of the Arrowie Basin (Paterson & Edgecombe, 2006; Paterson *et al.* 2007; Betts *et al.* 2018).

In the Big Gully area of Kangaroo Island, the Emu Bay Shale is 78 m thick at the shoreline and *c.* 61 m thick near Buck and Daily quarries, where the material considered here was sourced (*c.* 400 m inland; see García-Bellido *et al.* 2009 for a detailed locality map). Here, the formation commences with a thin (up to 2 m) interval of polymict conglomerate, the base of which is interpreted as a sequence boundary separating it from the underlying Marsden Sandstone. Above this, the conglomerate transitions sharply into a package of dark grey, laminated mudstone with siltstone and fine sandstone event beds that become thicker and more common towards the contact with the sandstones of the overlying Boxing Bay Formation (Gehling *et al.* 2011). The mudstone interval of the lower Emu Bay Shale is interpreted as representing a relatively deep-water prodelta environment, and hosts the *Konservat-Lagerstätte* that contains a diverse biota (50+ species, mainly within the basal *c.* 15 m of the formation), with many taxa considered to

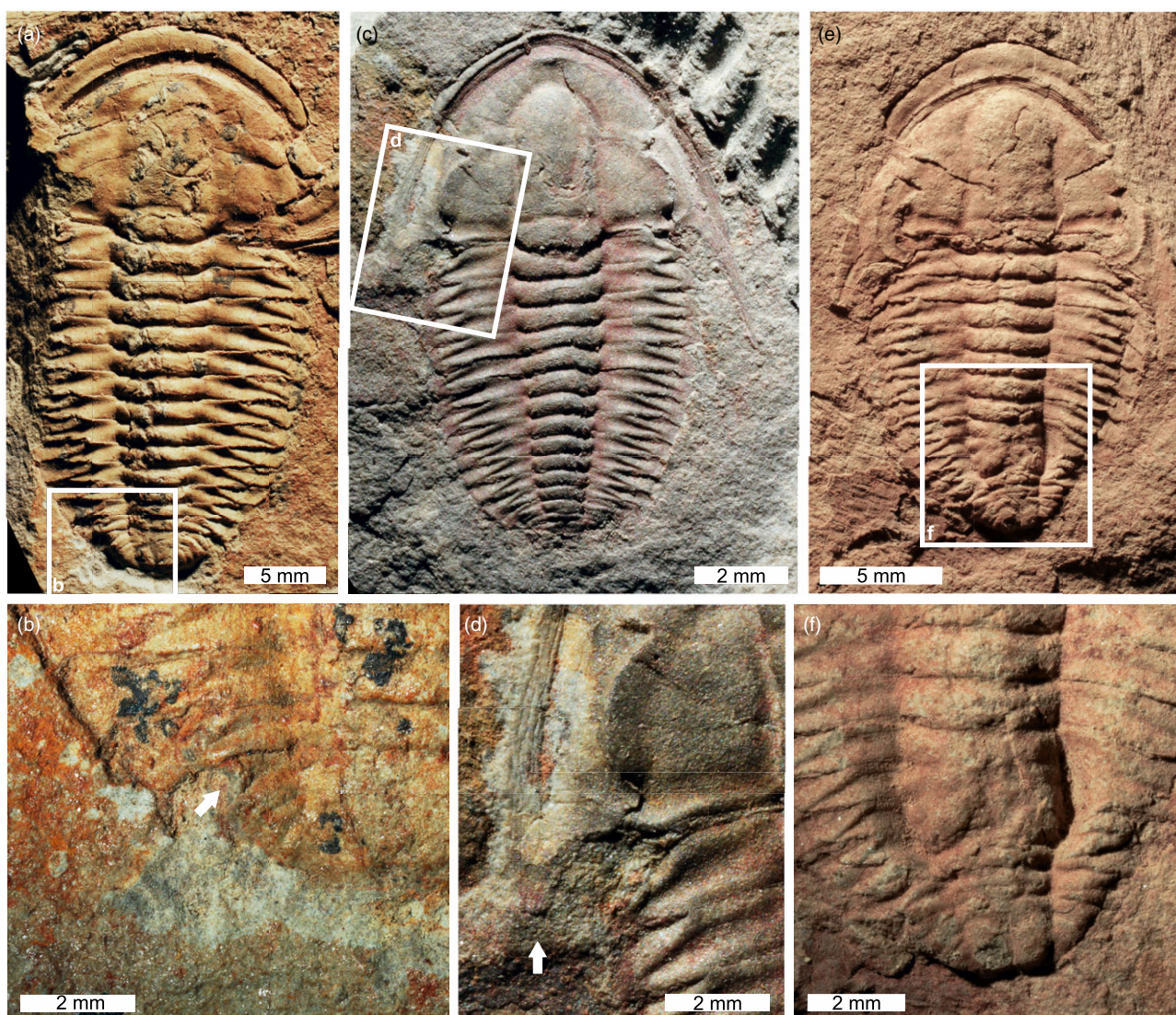


Fig. 2. (Colour online) *Estaingia bilobata* with cephalic and trunk injuries. (a, b) SAMA P46113. U-shaped injury to left side of pygidium. (a) Complete specimen. (b) Close-up of injury showing cicatrization (white arrow). (c, d) SAMA P52817. Stunted and rounded left genal spine. (c) Complete specimen. (d) Close-up of injury (white arrow). (e, f) SAMA P52892. Malformed and fused posterior thorax. (e) Complete specimen. (f) Close-up of injury.

have been transported from shallower settings upslope, or having settled out of the water column (Paterson *et al.* 2016). Exceptions include certain trilobite species, particularly the extraordinarily abundant *Estaingia bilobata* (with up to 600 individuals per square metre; JRP, unpublished data), as well as the redlichoids *Redlichia takooensis* Lu, 1950 and *R. rex* Holmes, Paterson & García-Bellido, 2019 (Holmes *et al.* 2020). Intact moult configurations of these species suggest that they lived in or close to the low-oxygen environment of the prodelta setting, although were likely subject to occasional 'mass kill' events resulting from fluctuations of the oxycline (Paterson *et al.* 2016). The prevalence of dorsum-down trilobite specimens in the deposit (up to 90% for *E. bilobata*; Drage *et al.* 2018) may indicate a physiological response to oxygen stress.

3. Methods

All *Estaingia bilobata* specimens housed in the South Australian Museum (Adelaide, South Australia) palaeontological collection (SAMA P) were examined for evidence of malformations.

Identified specimens were photographed under normal (fibre optic) lighting conditions using a Canon EOS 5D digital camera with a Canon MP-E 65 mm 1–5× macro lens.

The linear measurement dataset published by Holmes *et al.* (2021a) was used to determine where malformed *Estaingia bilobata* specimens were located in bivariate space compared to non-malformed specimens. The cephalic and trunk (thorax + pygidium) lengths in the dataset were used (Fig. 6a). Where possible, measurements from malformed specimens were added (Supplemental Information 1). Not all specimens documented here could be included due to partial preservation. Data were natural-log (ln) normalized and plotted. Data points were coded for malformation presence or absence.

4. Terminology

4.a. Cicatrization

Exoskeletal thickening in a region where damage has occurred. This indicates an individual was alive and subsequently healed

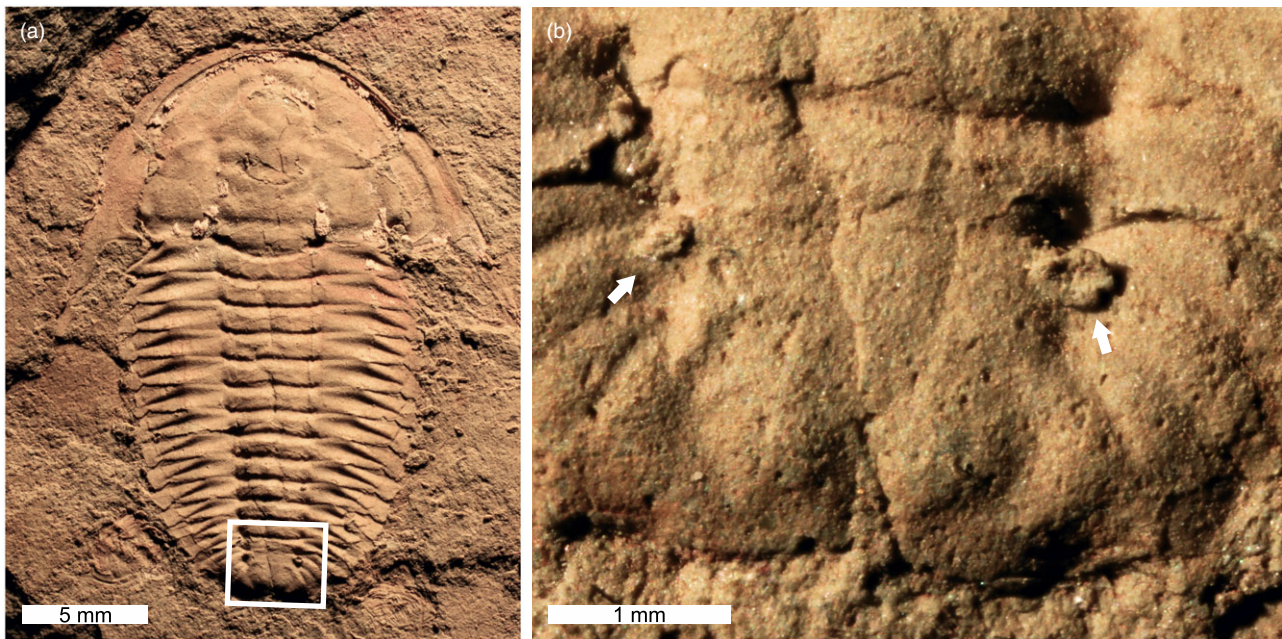


Fig. 3. (Colour online) *Estaingia bilobata* with two pathologies. (a, b) SAMA P59491. (a) Complete specimen. (b) Close-up of region with pathological neoplasms (white arrows).

from the incurred injury (Rudkin, 1979, 1985; Babcock & Robison, 1989; Babcock, 1993, 2003).

4.b. Injury

Exoskeletal breakage through accidental injury, attack or moulting complications (*sensu* Bicknell *et al.* 2022a). Injuries are usually L-, U-, V-, or W-shaped indentations across the exoskeleton (Babcock, 1993; Bicknell & Pates, 2019; Bicknell *et al.* 2022a). They can also be expressed as the reduction and rounding of exoskeletal sections, or as a 'single segment injury' (Bicknell *et al.* 2022a, d). These features generally show cicatrization and/or segment repair and regeneration. Occasionally, injured exoskeletal areas recover abnormally, resulting in the fusion of exoskeletal sections and a lack of segment expression (Owen, 1985; Bicknell *et al.* 2022a). Injuries do not extend across the entire specimen – such breaks likely reflect post-mortem, taphonomic processes (Leighton, 2011).

4.c. Malformation

Evidence for injuries, teratologies, or pathologies (Owen, 1985).

4.d. Pathology

Malformed exoskeletal sections resulting from parasitic activity or infections. These structures are often expressed as circular to ovate swellings (Šnajdr, 1978; Owen, 1985; De Baets *et al.* 2022).

4.e. Teratology

External expressions of developmental, embryological, or genetic malfunctions (Owen, 1985). These morphologies include addition or removal of nodes, segments, and spines, as well as abnormally developed morphologies (Owen, 1985; Bicknell & Smith, 2021).

5. Results

Examination of *Estaingia bilobata* specimens uncovered several examples of injuries, pathologies, and teratologies. We also found evidence for possible durophagous predation or post-mortem scavenging in the form of mangled exoskeletons.

5.a. Injuries

Six injured *Estaingia bilobata* are identified. Most injuries are unilateral, show L-, U-, W-shaped morphologies (Figs. 1, 2; Table 1) and are located on the trunk, showing evidence for pleural spine regeneration and rounding (Fig. 1c, d) and cicatrization (Figs 1e, f, 2a, b). However, there is a single specimen with a highly deformed posterior trunk showing fused thoracic segments (Fig. 2e, f). There is only one specimen that displays a cephalic injury, represented by a broken genal spine that has partially regenerated (Fig. 2c, d).

5.b. Pathologies

Only one specimen shows evidence for pathological growths on the pygidium in the form of two ovate neoplasms (Fig. 3). Pathological growth on the right side of the pygidium is twice the size of the left neoplasm.

5.c. Teratologies

Three examples of teratologies are observed. The first shows abnormally developed posterior segments on the right side of the thorax, including the apparent fusion of certain axial rings (e.g. T5 and T6) and pleurae, some of which bifurcate distally (Fig. 4a, b). The second specimen displays very minor, partial fusion of distal sections of two anterior pleurae on the left side of the thorax (Fig. 4c, d). The third specimen has an additional 'half-segment' immediately behind T3 on the right side of the thorax. This additional segment begins at the sagittal line and rapidly expands to form the right half of an axial ring and a normal

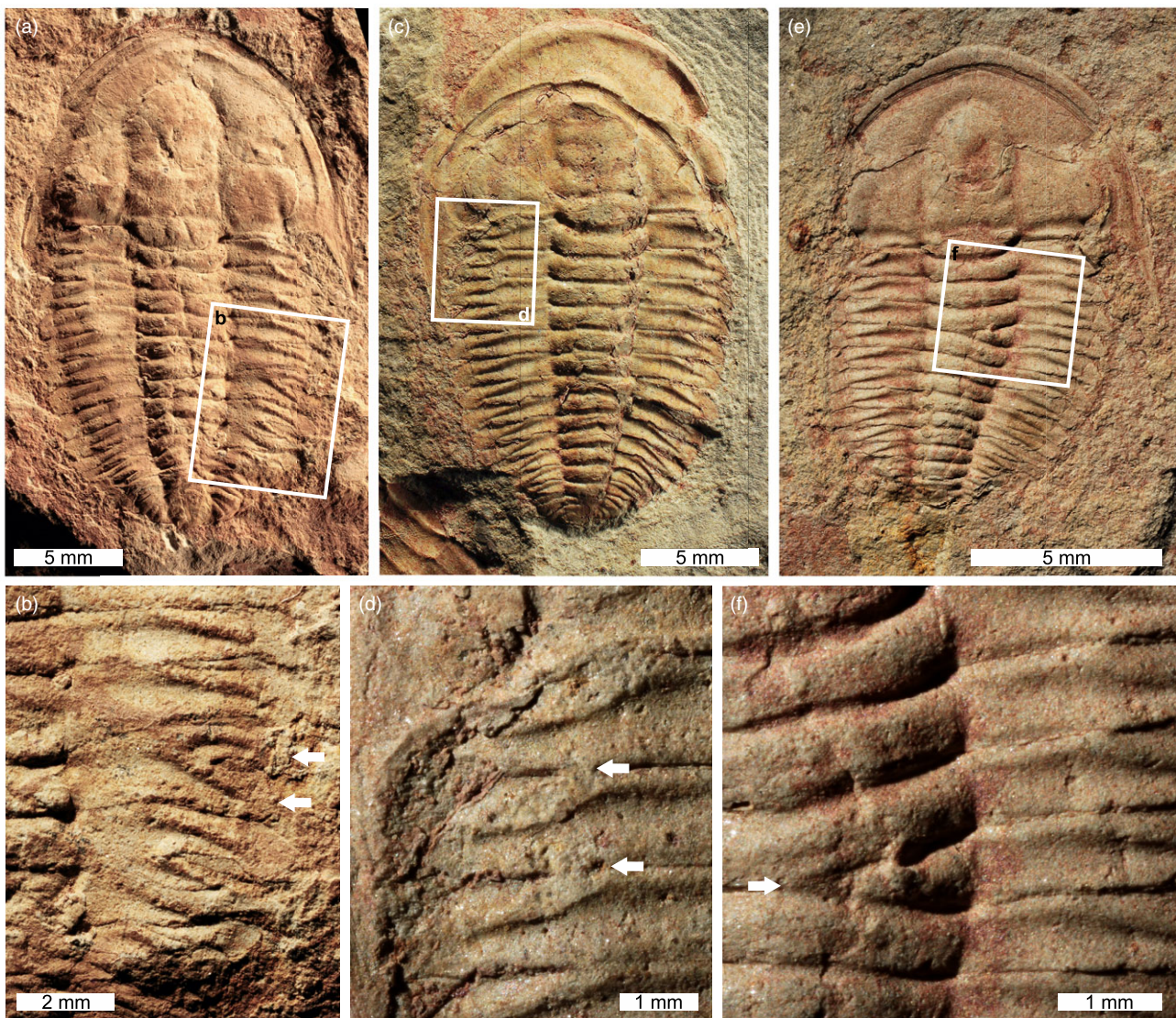


Fig. 4. (Colour online) *Estaingia bilobata* with teratologies. (a, b) SAMA P54957. Fusion of axial rings (T5 and T6) and pleurae, some of which bifurcate distally. (a) Complete specimen. (b) Close-up of pleural bifurcations (white arrows). (c, d) SAMA P59487. Partial fusion of distal pleural sections. (c) Complete specimen. (d) Close-up of teratology (white arrows). (e, f) SAMA P59490. Additional 'half-segment'. (e) Complete specimen showing asymmetrical trunk. (f) Close-up of teratology (white arrow).

pleura (Fig. 4e, f). This has resulted in a highly asymmetrical trunk morphology, with the additional 'half-segment' also causing the posteriorly adjacent segment to bend.

5.d. Mangled exoskeletons

Five specimens with substantial exoskeletal breakage or ripping are noted (Fig. 5). The fully biomineralized specimens show extensive breakage over major exoskeletal regions (Fig. 5c, f). Specimens preserved in very low relief – interpreted as newly moulted, soft-shelled individuals (Drage & Daley, 2016) – appear shredded or torn (Fig. 5a, b, e) and, in one case, shows complete removal of the cephalon and posterior trunk regions (Fig. 5d).

5.e. Bivariate space

The distribution of malformed *Estaingia bilobata* in bivariate space illustrates a clear overall size pattern (Fig. 6). The majority of malformed individuals cluster among the largest holaspis stages (Fig. 6b). The exceptions are two smaller specimens that are

separate from other malformed individuals. There is no marked distinction between where injured, pathological, and teratological specimens are located in shape space.

6. Discussion

The specimens of *Estaingia bilobata* documented here show evidence for the three major groups of trilobite malformations (Owen, 1985). This is rare among Cambrian trilobites, as the vast majority of malformed specimens record injuries, with limited evidence for teratologies and pathologies (Bergström & Levi-Setti, 1978; Bicknell & Paterson, 2018; De Baets *et al.* 2022). As such, *E. bilobata* presents a unique opportunity to study the palaeobiological significance of malformation types in one trilobite species from a single deposit.

The majority of observed *Estaingia bilobata* injuries (Figs. 1, 2a, b, e, f) are comparable to other documented examples of injured Cambrian trilobites (Rudkin, 1979; Babcock, 1993; Bicknell & Pates, 2020; Zong, 2021a, b). Indeed, select *E. bilobata* injuries

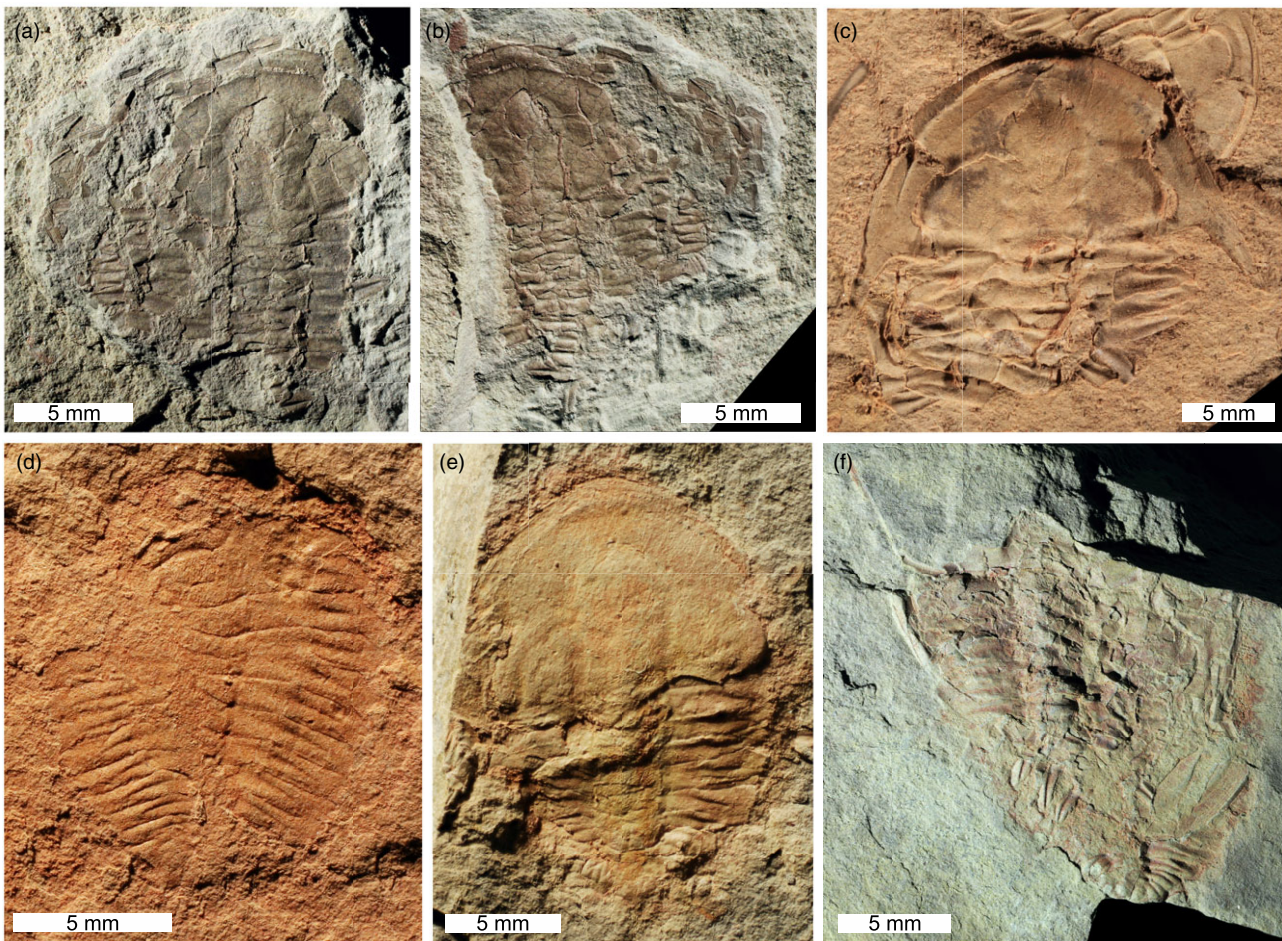


Fig. 5. (Colour online) Examples of mangled *Eostaingia bilobata* exoskeletons. (a, b) SAMA P46939. Shredded soft-shelled individual. (a) Part. (b) Counterpart. (c) SAMA P54820. Individual with severely broken and partially missing trunk. (d) SAMA P47975. Partial soft-shelled exoskeleton with torn thorax. (e) SAMA P54276. Soft-shelled individual with broken and partially missing trunk. (f) SAMA P 52867. Severely crushed exoskeleton with folded cephalon.

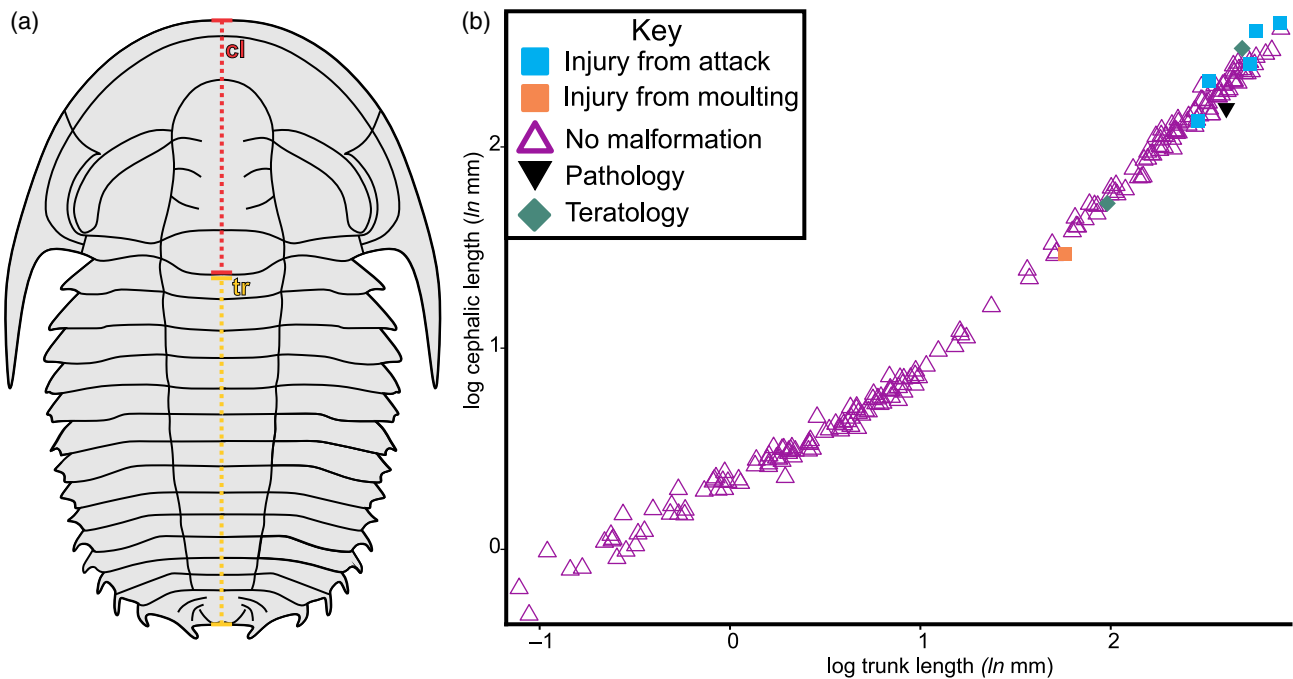


Fig. 6. (Colour online) Measurements of *Eostaingia bilobata* and bivariate plot showing distributions of malformations. (a) Reconstruction of *E. bilobata* showing measurements used in (b). (b) Bivariate space of *E. bilobata*. Most malformed specimens cluster with the largest specimens. Data found in Supplemental Data 1. Data were natural log normalized for plotting. Abbreviations: cl: cephalic length; tr: trunk (thorax + pygidium) length.

Table 1. Summary of injured *Estaingia bilobata*

Specimen	Injury location	Side	Injury morphology and evidence for recovery	Figure
SAMA P46113	Thorax, pleural lobe, segments 9–13 and anterior pygidium	Right	U-shaped, sharp edge along indentation	1a, b
SAMA P45360	Thorax, pleural lobe, segments 3–5	Right	L-shaped, rounded pleural tips	1c, d
SAMA P52886	Thorax, pleural lobe, segments 5–7	Left	W-shaped, fusion of segments, cicatrized edge	1e, f
SAMA P46113	Pygidium	Left	U-shaped, cicatrized edge	2a, b
SAMA P52817	Genal spine	Left	Reduced, rounded spine	2c, d
SAMA P52892	Thoracic segments 8–11	Midline and right	Malformed, fused thoracic region, possible cicatrization along midline	2e, f

are very similar to those observed on the co-occurring *Redlichia takooensis* and *R. rex* that have been attributed to failed predation (Conway Morris & Jenkins, 1985; Bicknell *et al.* 2022a). It is highly likely that these injuries in *E. bilobata* also reflect failed predation. Evidence for cicatrization (Figs 1a, b, e, f, 2a, b) and regeneration (Fig. 1c, d) at injury sites indicates that these individuals survived and continued to moult after attacks. Other evidence for predation on, or post-mortem mastication of, *E. bilobata* is represented by the mangled exoskeletons (Fig. 5). Similar examples of *R. takooensis* have been interpreted as rare evidence of possible durophagy (e.g. Bicknell *et al.* 2022a, fig. 1C–E). Such evidence of durophagy, combined with examples of failed predation, further bolsters the idea that *E. bilobata* was a key prey item within the Emu Bay Shale biota. This smaller trilobite species likely occupied a relatively low trophic level within the ecosystem (Jago *et al.* 2016), especially given its extreme abundance (>80% of individuals across all known species), and yet injured specimens of *E. bilobata* are exceedingly rare. Further, most injured specimens cluster among the larger individuals in bivariate space. This may suggest that only larger individuals were capable of escaping and recovering from attacks, preserving records of failed predation. Alternatively, these specimens may preserve evidence of older injuries that recovered through subsequent moulting events. In either case, this pattern indicates a possible record of survivorship bias within the trilobite fossil record.

One injured specimen of *Estaingia bilobata* shows a substantially disrupted posterior thorax (Fig. 2e, f). This malformation is comparable to rare specimens of other Cambrian trilobite species with highly disrupted and wrinkled pleurae adjacent to the injury (Conway Morris & Jenkins, 1985; Bicknell *et al.* 2022a). This condition is more commonly observed in the trunk of younger iso- and macropygous trilobites (Ormiston *et al.* 1967; Šnajdr, 1981; Owen, 1985; Rudkin, 1985). Disruption of pleurae indicates that the individual may have been attacked during the soft-shelled stage (shortly after moulting), resulting in a highly deformed exoskeleton that became fixed in subsequent moults (Conway Morris & Jenkins, 1985; Rudkin, 1985).

Trilobite genal spine malformations are particularly rare (Owen, 1985). Most malformed genal spines are represented by disrupted borders (e.g. Chatterton, 1971; Cowie & McNamara, 1978; Owen, 1985; Babcock, 1993; Bicknell *et al.* 2018c), abnormal cephalic fringes (Owen, 1983), or bifurcating genal spines (Owen, 1985). Complete removal (Kay, 1937) and recovery (Sinclair, 1947; Hessin, 1988; Bicknell *et al.* 2022c) of genal spines is exceedingly rare, as reflected by the single *Estaingia bilobata* specimen documented here. The documentation of only one genal spine injury (Fig. 2c, d) is noteworthy. Given the constrained anatomical

region, a predator would unlikely have limited an attack to the genal area. As such, we can exclude failed predation as the most plausible explanation. Instead, the injury could reflect a complication during moulting or mechanical (non-predatory) damage that resulted in spine breakage (Owen, 1983).

Teratological trilobite specimens with an additional ‘half-segment’ are almost completely unknown. To our knowledge, the only other example of an additional ‘half-segment’ within the thoracic region is a malformed *Emuella polymera* Pocock, 1970 that has multiple ‘half-segments’ (Pocock, 1974; Owen, 1985; Paterson & Edgecombe, 2006). One further record of this ‘half-segment’ condition is known from a *Toxochasmops* McNamara, 1979 pygidium from the Upper Ordovician (Katian) of Norway (Nielsen & Nielsen, 2017). These rare teratologies likely record damage to a generative zone and the resultant propagation of additional, unaligned segments (Pocock, 1974; Owen, 1985). It is noteworthy that two of the three examples represent early Cambrian forms, one of which (*E. polymera*) belongs to the family Emuellidae, which is characterized by unusually large numbers of trunk segments (Paterson & Edgecombe, 2006). Emuellids in particular may have been more prone to teratologies as they added new segments through euanamorphosis (Paterson & Edgecombe, 2006). These trilobites certainly had unusual patterns of trunk segment development compared with other forms (Holmes *et al.* 2021a). This may have increased the likelihood of developmental malformations, indicating possible evidence for increased developmental plasticity within Cambrian trilobites compared to younger forms (Webster, 2007). However, the rarity of these exceptional specimens suggests that these malfunctions seldom occurred.

Fused exoskeletal sections are rarely observed in thoracic pleurae (see Öpik, 1975, pl. 17), but more commonly recognized in pygidial regions (Strusz, 1980; Owen, 1985; Babcock, 1993; Nielsen & Nielsen, 2017; Bicknell & Smith, 2021). Such teratologies have been attributed to genetic malfunctions (Nielsen & Nielsen, 2017) and/or moulting complications producing a malformation that propagated in subsequent moults (Bicknell & Smith, 2021). As the teratological thoracic segments (Fig. 4c, d) lack any evidence of an injury, this rare malformation was likely caused by a developmental abnormality that impacted a limited exoskeletal region. This may record segments failing to separate or articulate correctly when they budded off from the pygidium.

The morphologies of exceptionally preserved appendages in two Emu Bay Shale arthropod species have been linked to durophagy, potentially on *Estaingia bilobata*. Firstly, the short, stout gnathobasic spines on the biramous appendages of the very large trilobite *Redlichia rex* (Fig. 7e, f) have been shown to be comparable with other known durophages, such as the

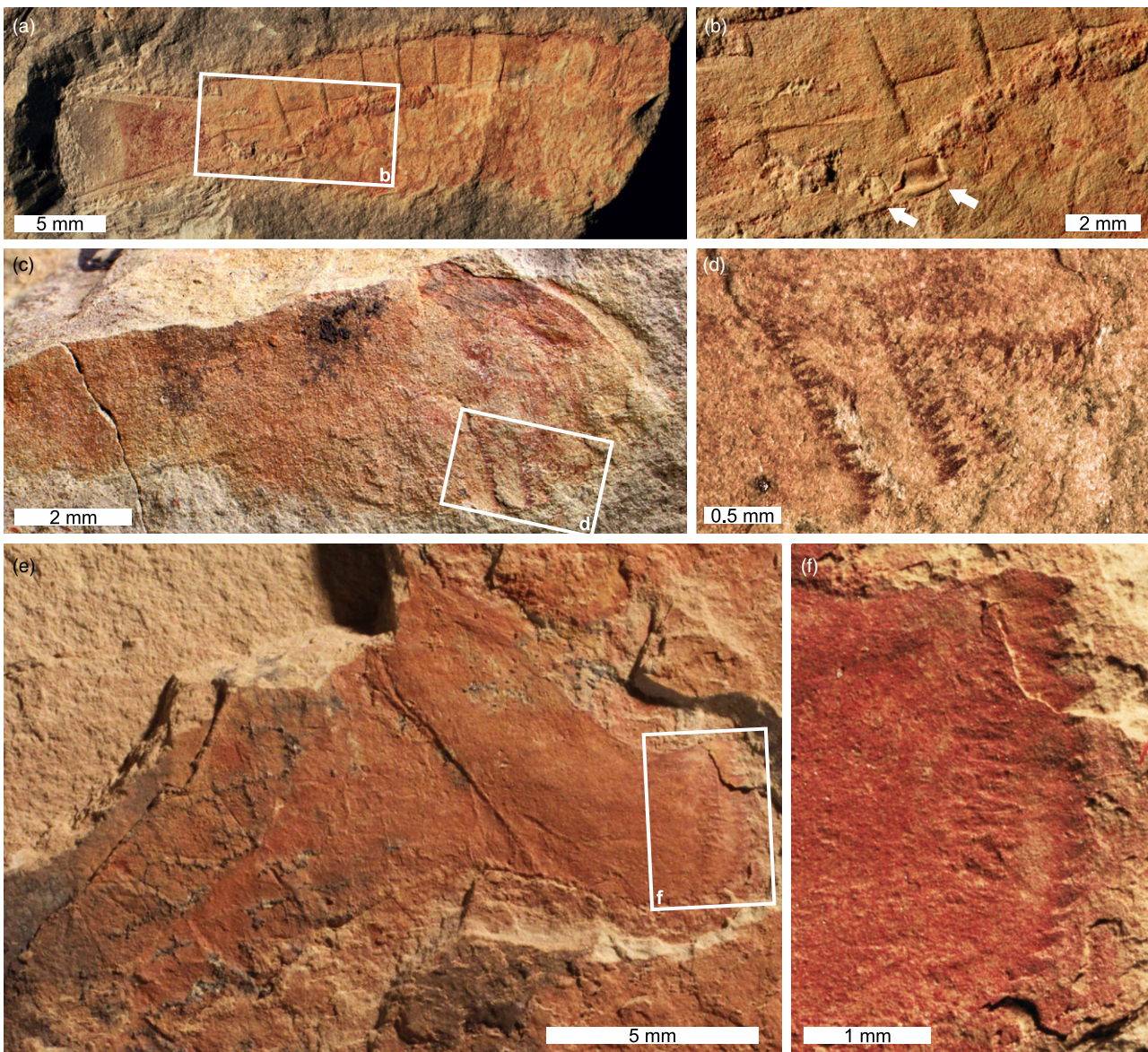


Fig. 7. (Colour online) Examples of possible predators of *Eostaingia bilobata*. (a–d) *Wisangocaris barbarahardyae*. (a, b) SAMA P55603a. Specimen showing shelly cololite containing *E. bilobata* fragments. (a) Near-complete specimen. (b) Close-up of cololite with sclerite fragments (white arrows). (c, d) SAMA P45629. Specimen showing series of gnathobases possibly used in durophagy of *E. bilobata*. (c) Near-complete specimen. (d) Close-up showing rows of gnathobasic spines. (e, f) SAMA P54942. Biramous appendage of *Redlichia rex* showing stout gnathobasic spines. (e) Complete specimen. (f) Close-up of stout gnathobasic spines.

Cambrian Burgess Shale arthropod *Sidneyia inexpectans* Walcott, 1911 and the extant horseshoe crab *Limulus polyphemus* (Linnaeus, 1758) (Botton, 1984; Bicknell *et al.* 2018a, b, 2021, 2022a; Holmes *et al.* 2020). This has permitted the linking of injuries identified on *R. takoensis* specimens with failed predation by the larger *R. rex*, and injuries to *R. rex* as possible instances of attempted cannibalism (Bicknell *et al.* 2022a). Individuals of *R. rex* (and potentially *R. takoensis*, although morphological details of the appendages are unknown) may have also consumed *E. bilobata*, as supported by centimetre-scale coprolites containing *E. bilobata* remains (Daley *et al.* 2013, fig. 7E–H) that have been attributed to *R. rex* (Daley *et al.* 2013; Bicknell *et al.* 2022a). The gnathobasic spines of the Emu Bay Shale chelicerate *Wisangocaris barbarahardyae* Jago *et al.*, 2016 (Fig. 7c, d) show similar morphologies to those of *R. rex* and other known

durophages, and were likely also adapted for crushing biomineralized material (Jago *et al.* 2016). This is supported by the presence of shelly cololites in certain specimens of *W. barbarahardyae*, some containing fragments of *E. bilobata* (Fig. 7a, b; Jago *et al.* 2016, fig. 5c–g). Given the maximum reported size of *W. barbarahardyae* is c. 60 mm, this arthropod may have targeted and consumed *E. bilobata* meraspides. Juveniles of *E. bilobata* are abundant in the *Lagerstätte* interval and range from c. 1 to 5 mm in length (Holmes *et al.* 2021a, b). This is consistent with the size of *E. bilobata* pleurae preserved within a *W. barbarahardyae* cololite (Fig. 7b). The size range and sheer abundance of *E. bilobata* within the Emu Bay Shale suggest that this small trilobite occupied an important position within the lower trophic levels of the local ecosystem, and was an important prey item for multiple species of predator.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0016756822001261>

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