An exceptional record of Cambrian trilobite moulting behaviour

preserved in the Emu Bay Shale, South Australia

Running header: Diverse trilobite moulting from the Emu Bay Shale

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Trilobites dominate the Emu Bay Shale (EBS) assemblage (Cambrian Series 2, Stage 4, South Australia) in terms of numbers, with *Estaingia bilobata* Pocock 1964 being extremely abundant, and the larger *Redlichia takooensis* Lu 1950 being common. Many specimens within the EBS represent complete moulted exoskeletons, which is unusual for Cambrian fossil deposits. The abundance of complete moults provides an excellent record that has allowed the recognition of various recurrent moult configurations for both species, enabling the inference of movement sequences required to produce such arrangements. Moult configurations of *E. bilobata* are characterised by slight displacement of the joined rostral plate and librigenae, often accompanied by detachment of the cranidium, suggesting ecdysis was achieved by anterior withdrawal via opening of the cephalic sutures. Moulting in *R. takooensis* often followed the same method, but configurations show greater displacement of cephalic sclerites, suggesting more vigorous movement by the animal during moulting. Both species also show rare examples of Salter's configuration, with the entire cephalon anteriorly inverted, and several other unusual configurations. These results indicate that moulting in trilobites was a more variable process than originally thought. In contrast, other Cambrian Konservat-Lagerstätten with an abundance of trilobites (e.g., Wheeler Shale, USA, and Mount Stephen Trilobite Beds, Canada)

show larger numbers of 'axial shields' and isolated sclerites, often interpreted as disarticulated exuviae. This points to a higher level of disturbance from factors such as animal activity, depositional processes, or water movement, compared to that of the EBS, where quiescent conditions and intermittent seafloor anoxia contributed to an unparalleled trilobite moulting record.

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Trilobite exoskeleton moulting behaviour is highly variable in comparison to what has been observed for other Cambrian arthropods, and for modern groups (Daley & Drage 2016). Trilobites moulted throughout their lifetime to develop, grow, and repair, and in doing so left various 'moult configurations' preserved in the fossil record. Data suggest that trilobite moulting behaviour and the resulting configurations were both inter- and intraspecifically variable (Daley & Drage 2016), and this variability appears to be consistent amongst trilobites with less derived morphologies (unlike more specialised groups such as the Phacopina, Daley & Drage 2016). Other Cambrian arthropods (although with less heavily calcified exoskeletons) moulted using more consistent standardised behaviours, producing a uniform location for the 'exuvial gape' (where the animal exits the old exoskeleton). For example, the anterior exuvial gape can be observed in an exceptional specimen of *Marrella splendens* Walcott 1909 from the Burgess Shale preserved midway through moulting (García-Bellido & Collins 2004). More recent arthropods also show consistent moulting behaviour, such as in many decapod crustaceans where moults can be identified by their characteristic Open Moult Position with dorsal carapace displaced from the abdomen (see Daley & Drage 2016). In comparison, studies of trilobite moulting have demonstrated the significant variability of the exuvial gape location (e.g. McNamara & Rudkin 1984; McNamara 1986; Brandt 2002; Budil & Bruthansova 2005; Paterson *et al.* 2007; Daley & Drage 2016). The evolutionary function of this variability is mostly untested, and the lack of moulting behaviour specialisation in trilobites has been suggested as responsible for their eventual progressive extinction (Brandt 2002), or contrastingly their geological longevity (Hughes 2003; Daley & Drage 2016).

In a comprehensive attempt to standardise and better enable research into trilobite moulting, Henningsmoen (1975) described and named a number of these behaviours and their resulting configurations. However, these do not represent the full variability of trilobite moult configurations. Due to the susceptibility of arthropod exoskeletons to disarticulation from decay and physical processes (e.g. water currents), only under conditions of exceptional *in situ* preservation would the intraspecific variability of moult configurations be preserved. This means that a greater flexibility in moulting behaviour cannot be observed at most trilobite-bearing localities. However, the Cambrian Series 2 Emu Bay Shale (EBS) Konservat-Lagerstätte, with soft-body preserving beds containing abundant complete *in situ* trilobite moult configurations, presents a rare opportunity to document the full variability in these behaviours and the fossils they produce.

At Big Gully, on the north coast of Kangaroo Island, South Australia, the EBS houses a diverse Konservat-Lagerstätte assemblage containing over 50 taxa, including sponges, brachiopods, hyoliths, polychaetes, priapulids, lobopodians, radiodontans, other non-mineralised arthropods (e.g. nektaspids and other artiopodans, as well as megacheirans), trilobites, vetulicolians, and several problematic forms (Paterson *et al*. 2008, 2016; García-Bellido *et al*. 2009). Like the majority of Cambrian Lagerstätten, the assemblage is dominated by arthropods, however the EBS is unusual in that trilobites, and in particular *Estaingia bilobate* Pocock 1964, overwhelmingly dominate in numerical abundance. *E. bilobata* approaches densities of up to 300 individuals per square metre within the EBS (comprising up to 80% of individuals on each slab), and it has been suggested that this species was an exaerobic specialist, occupying a niche between oxic and anoxic

areas of the seafloor (Paterson *et al*. 2016). Specimens of the larger trilobite *Redlichia takooensis* Lu 1950 are also very common. In contrast, the three other known species of trilobite from the EBS, *Balcoracania dailyi* Pocock 1970, *Megapharanaspis nedini* Paterson & Jago 2006, and *Holyoakia simpsoni* Paterson & Jago 2006, are all extremely rare (Paterson & Jago 2006; Paterson *et al*. 2007).

The majority of trilobite specimens (>90%; Gehling *et al*. 2011) from the EBS Lagerstätte probably represent carcasses showing a high degree of articulation, with the remainder being moulted exoskeletons. Many of these moults experienced little-to-no disturbance prior to burial, providing a unique opportunity to infer moulting behaviours (exuviation) by reconstructing sequences of movement and disarticulation. This is unlike the majority of Cambrian fossil deposits, where even minor amounts of disturbance have resulted in the movement and separation of disarticulated sclerites, making moult configurations difficult to interpret (Daley & Drage 2016). The EBS provides the perfect opportunity to study moulting behaviour in Cambrian trilobites, which we reconstruct here using detailed descriptions of moult configurations of *E. bilobata* and *R. takooensis*. These are compared with specimens from two other exceptionally preserved Cambrian assemblages, namely *Ogygopsis klotzi* (Rominger 1887) from the Burgess Shale (British Columbia, Canada) and *Elrathia kingii* (Meek 1870) from the Wheeler Shale (Utah, USA), covering three different Cambrian trilobite orders (Redlichiida, Ptychopariida, and Corynexochida). This study is intended to describe the variable configurations resulting from trilobite moulting, rather than as a quantitative case study, such that it can be used as a tool for future studies identifying preserved moulting behaviours.

Geological Setting

The EBS outcrops at the shoreline northwest of the Emu Bay jetty (Paterson *et al*. 2008; Jago & Cooper 2011) and at Big Gully, which is situated approximately 7 km east of the Emu Bay township, and 1.5 km west of White Point (see Paterson *et al*. 2016, fig. 1). Early collections from this second locality were sourced from the wave-cut platform and cliff exposures immediately to the East of the mouth of Big Gully, however, since 2007 excavations at 'Buck Quarry' approximately 400 m inland have yielded a richer assemblage and better quality preservation than previously encountered (García-Bellido *et al*. 2009). More recently, 'Daily Quarry' has been opened slightly closer to shore and is also yielding high-quality material.

The EBS forms part of the early Cambrian (Series 2) Kangaroo Island Group, a largely clastic shelf succession that outcrops on the central northern coast of the island. Conglomerate facies within the EBS, as well as within the older White Point Conglomerate (that thin towards the south), suggest that the sequence was deposited adjacent to an active tectonic margin, with the source area immediately to the North of the present coastline (Daily *et al*. 1980; Gehling *et al*. 2011). Syndepositional faulting South of this margin may have resulted in the formation of isolated oxic-to-anoxic sections of the seafloor within which the Lagerstätte was rapidly deposited (Gehling *et al*. 2011). This near-shore depositional environment is very different from that observed for other Cambrian Konservat-Lagerstätten, which are generally deposited in outer shelf settings (Gaines 2014). This seems to be reflected in the unusual mode of preservation, which differs from that of other

Burgess Shale-type (BST) localities. Preservation of non-mineralised material within Cambrian Konservat-Lagerstätten is usually represented by two-dimensional compression fossils composed of primary carbonaceous remains, a pathway termed 'Burgess Shale-type preservation' (Gaines 2014). In contrast, preservation within the EBS seems to be somewhat different, with fossils exhibiting some three-dimensionality due to early-stage diagenetic mineralisation, including the phosphatisation of certain soft tissues (e.g. muscle and gut), as well as phosphatisation and pyritisation of cuticular structures such as eyes, and late diagenetic casting of fossils by fibrous calcite (see Paterson *et al*. 2016 and references therein).

Soft-bodied preservation occurs predominantly in the lowest 10–12 m of the EBS at Big Gully, within dark grey, micaceous, finely-laminated mudstone, interspersed with siltstone and fine sandstone horizons interpreted as gravity flow or storm deposits (Gehling *et al*. 2011). The majority of material collected from the EBS since 2007 (including the material discussed herein) originates from a c. 2 m thick section exposed in Buck Quarry, approximately 10 m above the base of the EBS. Material from Daily Quarry, approximately 50 m north of Buck Quarry along strike, was sourced from the same beds. A prominent sandstone bed c. 20 cm thick exposed in both quarries allows correlation between the two. The Konservat-Lagerstätte bearing mudstones are highly fossiliferous throughout this interval, with fossils preserved in millimetre-scale discontinuous laminate beds. Mudstone bedding planes do not appear to represent single events; rather, these are interpreted as background accumulations of fine sediment, with benthic taxa presumably tolerant of low oxygen conditions preserved *in situ,* and other elements being transported in

or settling out of the water column (Paterson *et al*. 2016). Preservation of moult configurations appears to be consistent throughout this interval and between the two quarries.

Based on the presence of *E. bilobata*, *R. takooensis* and *B. dailyi* the EBS has been correlated with the *Pararaia janeae* trilobite zone of mainland South Australia (Jell in Bengtson *et al*. 1990; Jago *et al*. 2006; Paterson & Brock 2007), which is equivalent to the mid-late Botoman Stage of Siberia, the upper Nangaoan/lower Duyunian of South China, and the Dyeran of North America (Paterson & Brock 2007; Peng *et al*. 2012). Absolute age is estimated at *c*. 514 Ma based on correlation with the Cambrian timescale presented in Figure 19.3 of Peng *et al*. (2012). The comparative localities of the North American Burgess and Wheeler Shales are both middle Cambrian (Series 3) in age. The former is late Stage 5, corresponding to *c.* 505 Ma, with the latter being early Drumian, *c.* 504 Ma (Collom *et al*. 2009; Robison & Babcock 2011; Peng *et al*. 2012).

Sedimentology and taphonomy of moult configurations

Context must be considered when examining trilobite moult assemblages, with a focus on understanding how taphonomic processes could have affected the relative arrangement of sclerites. Data on the sedimentology and taphonomy for the EBS are detailed (Gehling *et al.* 2011; McKirdy *et al.* 2011) and demonstrate its particular suitability for a study of *in situ* trilobite moult assemblages. All specimens of *E. bilobata* and *R. takooensis* used for this study originate from the same mudstone beds as the soft-bodied preservation at the EBS (e.g. Paterson *et al.* 2016).

Geochemical analyses conducted by McKirdy *et al*. (2011) suggest that the fossiliferous EBS mudstones were consistently deposited beneath a largely oxic water column, as is also suggested by the diverse free-swimming elements of the biota (Paterson *et al*. 2016). The original presence of pyrite within the sediment, impoverished representation of fixosessile taxa, and absence of trace fossils (which become abundant subsequent to the zone of exceptional preservation) suggest that the pore water below the sediment-water interface was anoxic, with low-oxygen conditions also occurring at least occasionally above the seafloor (Gehling *et al*. 2011; McKirdy *et al*. 2011). Geochemical content is relatively homogenous throughout the exceptional-preservation mudstones (McKirdy *et al.* 2011, fig. 4). The EBS study beds, and the trilobite moult configurations described herein, therefore show a consistent preservation style as part-counterpart internal-external moulds, which, although compressed, exhibit some three-dimensionality. This suggests no preservational bias is influencing the results from this study.

Further, the fossiliferous section of the EBS preserves soft tissue and *in situ* trilobite moult assemblages in part due to its almost complete lack of bioturbation, predation, or scavenging (Gehling *et al.* 2011; McKirdy *et al.* 2011), presumably as a consequence of the periodic low-oxygen conditions. This is consistent across all soft-bodied fossil-bearing mudstones, which retain their finely laminated texture, and in contrast to the silty, less fossiliferous intervening beds (McKirdy *et al.* 2011, fig. 2). There is rare evidence of predation or scavenging on *E. bilobata* by the chelicerate *Wisangocaris*, as well as injuries inflicted upon specimens of *R. takooensis* (Conway Morris & Jenkins 1985) and the nektaspid *Emucaris* (Nedin 1999), suggesting that at times the seafloor was at least partially oxygenated. However, most trilobite

carcasses and moult configurations show a high degree of articulation. This may have resulted from depth fluctuations of the oxycline, causing mass asphyxiation of individuals, with the prevailing low-oxygen conditions helping to facilitate preservation by preventing scavenging and bioturbation prior to burial (Paterson *et al*. 2016). Mat-forming cyanobacteria may have helped maintain a sharp redox boundary between water column and sediment, and inhibited decay and disruption of soft tissues and articulated cuticle (McKirdy *et al.* 2011). The EBS also shows less evidence of weathering or thermal metamorphism than comparable early Cambrian Konservat-Lagerstätten (McKirdy *et al.* 2011).

In addition, Gehling *et al.* (2011) found no sedimentological evidence for water movement at the EBS. Large surfaces are not often recovered due to persistent cleavage and the lenticular nature of the bedding planes, however the trilobite moult configurations and intact carcasses show no consistent orientation. These factors, combined with the high degree of fossil articulation, suggest that within the exceptional-preservation mudstones certain taxa are found not only *in situ*, but with essentially no disturbance prior to burial. Due to these combined sedimentological and taphonomic aspects producing the observed high fossil articulation and exceptional preservation, and the abundance of two trilobite species, the EBS is an ideal locality with which to explore trilobite moulting variability and behaviour.

Material and Methods

All figured material from the Emu Bay Shale was collected from Buck and Daily Quarries and is housed in the palaeontological collections of the South Australian Museum, Adelaide (prefix SAM). The Mount Stephen Trilobite Beds (Burgess Shale), British Columbia, and the Wheeler Shale, Utah, were chosen for comparison to the EBS due to their vast numbers of singular trilobite species (*Ogygopsis klotzi* and *Elrathia kingii,* respectively) and similar exceptional preservation conditions. Figured material from these localities is housed in the Natural History Museum, London (prefix NHMUK), Oxford University Museum of Natural History (prefix OUMNH), and Smithsonian National Museum of Natural History (prefix NMNH).

The problem of distinguishing between arthropod moults and carcasses has been discussed by a number of authors and a range of criteria for this proposed (e.g. Henningsmoen 1975; Whittington 1990; Daley & Drage 2016). In their review of the fossil record of moulting, Daley & Drage (2016) considered that the major requirements for the recognition of trilobite moults were, (1) evidence for the opening of exoskeletal sutures, and (2) repeated configurations of displaced exoskeletal units, coupled with consideration of the preservational environment. These criteria were applied when identifying the moult configurations from the SAM, NHMUK, OUMNH, and NMNH. There are approximately 5000 specimens of *E. bilobata* and 300 of *R. takooensis* within the collections of the SAM, of which perhaps 10% represent moulted exoskeletons. Figured specimens were chosen as clear examples of the various configurations described herein due to their completeness and quality of preservation. 78 moult configurations of *O. klotzi* and 35 of *El. kingii* were compared to the selected EBS specimens, and appropriate

representatives figured. In order to explore the relationship between trilobite orientation and moult configuration, a field sample of 100 randomly selected *E. bilobata* specimens taken from adjacent mudstone beds were examined.

Most specimens were photographed dry using Canon EOS 500D or 50D Digital SLR cameras, with a Canon EF-S 60 mm 1:2.8 Macro Lens under incident lighting from the standard NE direction. Particularly small specimens were photographed using a Canon MP-E 65 mm 1:2.8 1-5x Macro Lens. The camera was remotely controlled using the Canon EOS Utility 2.8.1.0 program. Additional specimens were photographed dry using a Canon SX60HS PowerShot digital camera with the above light settings. Photographs were adjusted and edited, and figures produced in Adobe Photoshop and Illustrator CS3 and CS6.

Results

Descriptions of recognised moult configurations

Minor variations on seven general types of moult configuration were recognised for the EBS specimens, three of which have been described in the literature for other trilobite species (Henningsmoen 1975). The existing configurations are presented here for clarity, and the four new configurations described and named. Individual moult configurations may vary slightly within this classification, such as in the specific placement of the separated sclerites. This will aid future studies of trilobite moulting in Cambrian Konservat-Lagerstätte, and be of

value as generalised descriptions for describing trilobite moults throughout their

evolutionary history (Fig. 1).

Trilobite moult configurations identified in the fossil record of the EBS (see Fig. 1):

1. *Axial shield* (named in Henningsmoen 1957). The cranidium, thorax, and

    pygidium are joined as a single unit (i.e. entire dorsal exoskeleton minus the

    librigenae). This is not a moulting configuration *per se*, but rather the product

    of displacement of sclerites (rostral plate, hypostome and librigenae)

    separated during moulting. As such, it can originate from Harrington's,

    Somersault, McNamara's or Nutcracker configurations described below.

2. *Harrington's configuration* (named in Henningsmoen 1975). Moult

    configuration comprising axial shield and displaced 'lower cephalic unit' (LCU;

    all parts of the cephalon except the cranidium, joined by integument or

    partially fused facial sutures, *sensu* Henningsmoen 1975). The joined LCU

    (comprising the librigenae and rostral plate, but usually lacking the

    hypostome) is often displaced posteriorly below the axial shield, or singular

    parts of the LCU may be disrupted presumably by decay of the integument or

    suture decalcification. The cranidium remains attached to the thorax.

3. *Henningsmoen's configuration* (named here). Similar to Harrington's

    configuration, although usually with minor displacement of the LCU, and

    showing displacement of the cranidium with respect to the trunk (joined

    thorax and pygidium). Named such because Henningsmoen (1975) notes the

    possible occurrence of this in addition to his Harrington's configuration (p.

    194).

4. *Nutcracker configuration* (named here). Librigenae, and usually the rostral plate, separated and generally displaced outwards from the axial shield. The hypostome is usually displaced but may remain close to life position. Named for the postulated relatively simultaneous outwards displacement of most cephalic sclerites.

5. *Somersault configuration* (named here). Moult configuration with one or both librigenae disarticulated from the cranidium and anteriorly inverted, leaving the genal spine pointing forwards. The rostral plate may or may not be visibly displaced, and in some cases may be joined to the librigenae as an intact LCU. Named for the similar direction of movement in the acrobatic action.

6. *McNamara's configuration* (named here). Similar to the above configuration, but with one or both librigenae disarticulated and laterally inverted. Suggested by McNamara & Rudkin (1984, fig. 5) and McNamara (1986) to occur in *Batocara mitchelli, Asaphiscus wheeleri, Redlichia forresti,* and *Redlichia micrograpta*.

7. *Salter's configuration* (also called *Salterian configuration*, named in Richter 1937; Richter *et al.* 1959; Henningsmoen 1975). Cephalon is disarticulated from the trunk and anteriorly inverted, usually resulting in the anterior margin of the cephalon facing posteriorly and often underlapping the trunk.

All of these configurations (with the exception of Salter's) likely result from Henningsmoen's (1975) 'Sutural Gape' mode of moulting. This involved moulting through an anterior exuvial gape (opening in the old exoskeleton) produced by

opening of the cephalic exoskeleton sutures (comprised of the facial, rostral, connective, and hypostomal sutures), with the cranidium and the LCU forming the dorsal and ventral exuvial elements, respectively. Different movements of the individual during this mode of moulting result in the above configurations preserved at the EBS. The exception, Salter's configuration, is produced through the 'Salterian' mode of moulting, which utilises an exuvial gape produced at the cephalothoracic joint. Other rarer modes of moulting, resulting in more unusual configurations, were also described by Henningsmoen (1975), such as the *Harpes* mode using the marginal-interlamellar cephalic suture (ibid. p. 189), or the *Ductina* mode using a marginal cephalic suture and sometimes resulting in 'Maksimova's configuration' (ibid. p. 190), or 'Hupe's configuration' with a displaced rostral plate (ibid. p. 192). However, these are linked to derived morphologies (e.g. fusion of the facial sutures), and are therefore not observed for *E. bilobata* or *R. takooensis*. The outlined configuration definitions are used below to describe the preserved moults of *E. bilobata* and *R. takooensis*, and thus to interpret their moulting behaviours and movements.

Description of moulting in Estaingia bilobata *Pocock, 1964*

Estaingia bilobata is a small trilobite (up to *c.* 30 mm in length) with 13 thoracic segments, narrow librigenae bearing long genal spines, and a small pygidium. The opisthoparian facial and rostral sutures are operative, with the detached rostral plate slightly shorter than the anterior border of the cranidium (Pocock 1964). *Estaingia* is restricted to early Cambrian sediments of Australia,

Antarctica and South China (Jell in Bengston *et al*. 1990; Palmer & Rowell 1995; Paterson 2005; Paterson & Brock 2007; Dai & Zhang 2012).

Pocock (1964, p. 461) noted that 'many specimens of *Estaingia* show that the cephalon has rolled forward over the detached rostral plate, and that the librigenae are free, but only slightly displaced; this appears to have been the characteristic mode of moulting in this trilobite'. Our observations support this interpretation, although moult configurations of *E. bilobata* within the EBS exhibit considerable variation. As discussed, the majority can be explained by the Sutural Gape mode of moulting, with the opening of the facial and rostral sutures, and common dislocation of the cephalothoracic joint, resulting in a range of configurations due to the movements of the moulting trilobite. The vast majority of *E. bilobata* moults exhibit either Henningsmoen's (Figs 1–2) or Harrington's configurations (Figs 1, 3; around 35 and 55% of specimens respectively). Specimens in Harrington's configuration exhibit disarticulation and posterior displacement of the LCU (which may not always comprise both librigenae) relative to the cranidium. The positioning of the LCU relative to the axial shield varies, and occasionally displays slight disassociation or rotation of its components. Henningsmoen's configuration is similar, but with the cranidium displaced in addition to the LCU. Inversions of the librigenae (Somersault and McNamara's configurations) were very rare, as was Salter's configuration and instances of thoracic disarticulation.

SAM-P 43837 (Fig. 2A) shows an example of Henningsmoen's configuration in *E. bilobata*. The librigenae are slightly displaced, the rostral plate has moved 2–3 mm posteriorly relative to the cranidium, and the cranidium shows minor displacement from the thorax. SAM-P 43974 (Fig. 2B), 43402 (Fig. 2C), and 46933

(Fig. 2E) also display variations of Henningsmoen's configuration. Figure 2B displays anterior movement (*c.* 2 mm) and minor anti-clockwise rotation of the cranidium, lateral and anterior displacement of the left librigena, and the right librigena joined with the rostral plate. In Figure 2C the cranidium is only slightly anteriorly displaced, and the rostral plate and left librigena have been pushed backwards to underlie the occipital ring and anterior of the trunk. The right facial suture is open. In Figure 2E the rostral plate and left librigena appear connected and are slightly displaced outwards and rotated. The cranidium and poorly preserved right librigena are anteriorly displaced, with some anti-clockwise rotation. SAM-P 45519 and 46362 (Fig. 2D, F) show Henningsmoen's configuration, but differ from the regular pattern as their cranidia are anteriorly displaced (so that in Fig. 2D the middle of the glabella overlaps the rostral plate) but the joined LCU remains largely *in situ* with negligible displacement. However, the rostral plate may have remained in place for Figure 2F based on the unusually deep anterior cephalic border furrow.

SAM-P 46956 (Fig. 2G) consists of a moult pair of *E. bilobata*. The right-hand specimen shows a variant of Henningsmoen's configuration, with the left librigena remaining joined to the trunk, the joined right librigena and rostral plate carried *c.* 3 mm forwards, and the cranidium deposited a further 2 mm in front. Unusually, the left specimen shows disarticulation between the first and second thoracic segments, rather than at the cephalothoracic joint. The cephalic region with associated first thoracic segment is displaced forwards *c.* 6 mm and laterally offset. The rostral plate and joined right librigena are displaced to the right and rotated anti-clockwise. Other specimens, e.g. SAM-P 45697 (Fig. 2H), show similar moult configurations to this paired example.

SAM-P 15339 (Fig. 3A) exemplifies Harrington's configuration in *E. bilobata.* This specimen shows left-lateral displacement and minor anti-clockwise rotation of the LCU. The axial shield is otherwise preserved intact. Moult configurations similar to this are very common for *E. bilobata*. Moults showing inversions of the librigenae were generally much rarer than Henningsmoen's or Harrington's configuration (representing around 6% of specimens, combined), with two specimens clearly exhibiting the Somersault configuration (e.g. SAM-P 54204, Fig. 3D) and a further four showing variations of McNamara's configuration (e.g. SAM-P 54207, Fig. 3B).

SAM-P 54206 and 15459 (Fig. 3C, E) show *E. bilobata* moults in modified versions of Salter's configuration (representing around 4% of specimens), the former with the trunk resting on the inverted cephalon, and the latter with the cephalon inverted anteriorly but lying directly adjacent to the trunk. In the first specimen, both librigenae are displaced forwards relative to the cranidium (but towards the posterior of the specimen), and rotated outwards. Another, smaller specimen in the SAM collections shows an almost identical arrangement. In the second specimen, the left librigena remains in place relative to the cranidium and the right is detached and missing. Interestingly, one specimen (SAM-P 54205, Fig. 3F) has the final five thoracic segments and pygidium rotated 180°, the rostral plate displaced backwards, and is possibly missing the left librigena. This appears to be a very unusual moult configuration for *E. bilobata*.

The moult configurations above were described from previously collected specimens in museum collections, and this was complemented by a field study that examined the orientation of *E. bilobata* carcasses and moults. Of the 100 specimens of *E. bilobata* examined, 90 were oriented dorsum-down (overturned), six were

upright, and four were small and/or partial specimens that were either enrolled, or potentially representing moulted exoskeletons in Salter's configuration. Of the six upright specimens, at least two likely represent moults and the remaining four were difficult to analyse owing to poor and/or partial preservation.

Description of moulting in Redlichia takooensis *Lu, 1950*

Redlichia takooensis is a large redlichiid trilobite known from lower Cambrian (late Botoman) sediments in Australia and South China (Zhang *et al*. 1980; Jell in Bengtson *et al*. 1990). The cephalic shield is semi-circular, with large librigenae bearing long genal spines that form a continuous curved border with the anterior of the cranidium, which in turn bears a long occipital spine. As in *E. bilobata*, the (opisthoparian) facial and rostral sutures are operative, with the rostral plate slightly narrower than the anterior of the cranidium (Jell in Bengtson *et al*. 1990). The thorax has 15 segments, each bearing a medial spine that is elongated on the 6th and particularly the 11th, and is relatively narrow compared to the width of the cephalon, especially in smaller specimens (Paterson & Jago 2006). The pygidium is small. Articulated specimens up to 25 cm long are known from Big Gully (Paterson *et al*. 2016), although most specimens from the Buck and Daily Quarries are 5–7 cm in length.

As with *E. bilobata*, specimens considered to be moults of *R. takooensis* exhibit considerable variation. *R. takooensis* also usually employed a Sutural Gape mode of moulting, but in general this produced different moult configurations to *E. bilobata*. Outwards displacement (away from the axial shield) of individual cephalic

sclerites (e.g. the Nutcracker configuration, Fig. 1), rather than a joined LCU (this was not observed), is common, as is thoracic disarticulation. The latter is often associated with segments 6 and 11. The hypostome appears to have been shed during moulting, although displaced little and therefore often remained close to life position within the moult configuration.

SAM-P 48085 (Fig. 4A), 44214 (Fig. 4B), and 44544 (Fig. 4D) illustrate the Nutcracker configuration for *R. takooensis* (representing around 90% of specimens). In these moult configurations the librigenae are displaced outwards from the cranidium (by *c*. 1–10 mm), and show some rotation. Figure 4A and D have the rostral plate displaced forwards, although the anterior of the fossil is broken for Figure 4B. In Figure 4A the thorax is disarticulated between segments 11 and 12, with the posterior part of the trunk disrupted and rotated slightly clockwise. Figure 4D displays disarticulation between segments 3 and 4 (*c*. 2 mm), and 9 and 10 (*c*. 5 mm), and displacement of the hypostome to lie beneath the anterior cephalic border. SAM-P 45440 (Fig. 4C) is a small specimen of *R. takooensis* that also shows disarticulated librigenae, slight posterior displacement of the hypostome, and thoracic dislocation. The trunk posterior to segment 8 is missing, and segments 4–6 are heavily imbricated. The hypostome is much more visibly displaced and inverted in SAM-P 46207 (Fig. 4E), its anterior wings being adjacent to the right of segment 4. This specimen may also represent the Nutcracker configuration, as the librigenae are absent, although much of the specimen has been truncated by rock fracture.

Moult configuration SAM-P 48062 (Fig. 4F) shows the left librigena displaced outwards (*c*. 5 mm), however the right is laterally inverted so that the medial edge is facing away from the axial shield in the uncommon McNamara's configuration (<5%

specimens). The cranidium is also slightly disrupted, and the rostral plate is not preserved due to truncation. SAM-P 46047 (Fig. 4G) also displays McNamara's configuration, with the right librigena laterally inverted, the cranidium and left librigena rotated anti-clockwise, and the rostral plate displaced.

SAM-P 45368, 43593, and 45875 (Fig. 4H–J) show Salter's configuration (representing around 5% of specimens). Figure 4H is incomplete posterior to the 11th segment, revealing the long medial thoracic spine. The occipital spine extending from the cranidial base is also preserved, confirming that the cephalon must have been inverted anteriorly during moulting, and that these are internal moulds (causing the underlapping cephalon to be impressed upon the overlying trunk). This is also the case for the more complete specimens in Figure 4I and J. SAM-P 45875 (Fig. 4J) also shows dislocation between segments 4 and 5, and 11 and 12; there also appears to be extensional damage to the joint between the axial rings of segments 10 and 11, likely a result of pressure on the 11th segment's extended medial spine.

As seen from these examples, almost all associations at the EBS are relatively complete, although occasionally the posterior-most of the axial shield is missing. As such they are generally easily recognisable as moults or carcasses. Configurations consisting of entirely disarticulated sclerites, such that they are not behaviourally informative, are very unusual. In *R. takooensis* these usually consist of the rostral plate with attached hypostome and the individual librigenae, presumably from the same individual (they are size-compatible), but without a proximal axial shield. The corresponding axial shield may however have been preserved close by, but broken from the specimen during collecting. Isolated axial shields (e.g. Fig. 4E if it were not truncated) are also extremely rare for both *E. bilobata* and *R. takooensis*.

Description of trilobite moulting at other Cambrian Konservat-Lagerstätten

Mount Stephen Trilobite Beds, British Columbia, Canada.- The middle Cambrian Mount Stephen Trilobite Beds (Burgess Shale Formation, British Columbia) preserve trilobite fossils in great abundance (Fletcher & Collins 2003). In particular, specimens of *Ogygopsis klotzi* (Order Corynexochida), including moults, are extremely numerous, the locality often being referred to as the *'Ogygopsis* Shales' (Rudkin 2009). The majority of *O. klotzi* moults observed for this study (62 specimens at the NHMUK, OUMNH, and NMNH) comprise only axial shields (e.g. Fig. 5C), confirming the taxon usually moulted by the Sutural Gape mode (Henningsmoen 1975). For these specimens no further details about moulting behaviour can be inferred as they lack associated disarticulated sclerites. Disarticulated associations seem more common than for the EBS (from more than 30 individual larger slabs with preserved trilobite material in background matrix housed at the NHMUK and NMNH), showing disarticulation and accumulation of individual sclerites such that they are indeterminable as moults or carcasses (e.g. Fig. 5F). Almost every observed larger slab displayed fragmentary *O. klotzi* material, usually alongside axial shields or complete trilobites.

In some cases where complete moult configurations are preserved, probable exuvial movements can be inferred in the same manner as for EBS trilobites. NHMUK I.4751(1) (Fig. 5A) is missing the librigenae, but also shows very slight displacement and rotation of the cranidium (akin to an incomplete Henningsmoen's configuration). Several configurations appear to represent more 'difficult' moulting

events, as the full anterior exuvial gape failed to open (potentially damaging the individual moulting through this smaller gape). For example, NHMUK I.4741 (Fig. 5D) shows disruption to the left librigena and distortion of thoracic segments. NHMUK I.4751(2) (Fig. 5B) shows a relatively complete *O. klotzi* moult. The right librigena is missing, the left is displaced under the axial shield, and the middle thoracic segments have been displaced, leaving some remnants nearby. Two specimens from the NMNH represent similar moult configurations, with singular librigena rotated laterally (right) away from the axial shield, with one also showing thoracic disarticulation between segments 7 and 8. Pygidium disarticulation was also observed in two NMNH axial shield moult configurations.

Isolated thoracopyga were also observed (e.g. NHMUK In.19410, Fig. 5E), although not as complete moult assemblages as the disarticulated cephalic structures are not generally found in association. A single trunk (complete thorax and pygidium) from the NMNH was associated with the right librigena and potentially the fragmented hypostome, both displaced slightly to the left. Librigenal inversions (Somersault or McNamara's configurations) were not observed for *O. klotzi,* although one specimen showing anterior librigenal inversion was described by McNamara & Rudkin (1984, fig. 9), and one in McNamara's configuration figured by Rudkin (2009, fig. 1C). The cephalothoracic joint was not usually involved in moulting, nor was Salter's configuration observed. The rostral plate was rarely preserved, with the exception of one axial shield specimen with the fused rostral plate-hypostome complex found anterior to the cranidium.

Wheeler Shale, Utah, USA.- As at Mount Stephen, the exceptional Burgess Shale-type

preservation at the middle Cambrian Wheeler Shale (House Range, Utah, USA) has

produced well-preserved soft-bodied fossils. The Wheeler Shale seems to represent

very similar exaerobic conditions to the EBS, with a single trilobite dominating, in this

case *Elrathia kingii* (Order Ptychopariida) rather than *Estaingia bilobata* (Gaines &

Droser 2003). This may also be the case within the Mount Stephen Trilobite Beds,

where *O. klotzi* is found in great abundance (Rudkin 2009, 2011), although

Bathyuriscus rotundatus may be similarly numerous. Specimens of *El. kingii*

dominate at the Wheeler Shale, with up to 500 individuals per square metre, while

other trilobite species are generally rare (Gaines & Droser 2003).

Unlike at the EBS, biomineralised *El. kingii* exoskeletons, owing to their

nodular preservation from dolomite precipitation, are commonly found weathered

out of their background matrix (Fig. 5G–J). This reduces identifiable moult

assemblages in most museum collections to just axial shields (25 specimens at the

OUMNH and NHMUK; e.g. NHMUK It.21001, Fig. 5G). This is also often the case for

rarer Wheeler Shale trilobites (e.g. *Asaphiscus wheeleri*; McNamara & Rudkin 1984,

fig. 6). A larger sample of specimens preserved within original slabs (i.e. through field

rather than museum study) would likely provide more detailed information about *El.*

kingii moulting, although figured slabs (e.g. Brett *et al.* 2009, figs 13–14) also appear

to consist mostly of carcasses and isolated axial shields. These specimens indicate

that, like for *O. klotzi, E. bilobata,* and *R. takooensis*, moulting through opening of

the facial sutures (Sutural Gape; Henningsmoen 1975) was the normal mode. When

identified *in situ*, moulted *El. kingii* axial shields are occasionally preserved in

association with their disarticulated sclerites, although seemingly not with the

frequency of those from the EBS. Several specimens show both librigenae displaced

backwards similar to Harrington's configuration, but with the rostral plate not visible

presumably because it is hidden beneath the dorsal cuticle (e.g. NHMUK It.21003,

Fig. 5I). However, due to their minor displacement, this may also have resulted from

decay and disturbance of the specimen. Some *El. kingii* moults show greater

displacement of associated librigenae (e.g. Gaines & Droser 2003, fig. 1A), but their

unusual positioning (both to the posterior-left of the axial shield) seem a product of

transportation, rather than the movements of the exuviating trilobite.

Moult configurations from the Wheeler Shale, however, do regularly display

thoracic disarticulation, or between the thorax and pygidium, and lateral

displacement or rotation of this section (e.g. NHMUK It.20999, Fig. 5H), although

individuals otherwise appearing as carcasses may also display thoracic

disarticulations (such as NHMUK It.5937, Fig. 5J). Very rarely, moults of *El. kingii*

display cephalo-thoracic disarticulations, with the cranidium displaced. Librigenal or

cephalic inversions (i.e. the Somersault, McNamara's, or Salter's configurations)

were not observed. The rostral plate was also rarely observed.

Discussion

Inferred moulting behaviour of Estaingia bilobata

The prevalence of librigenal and rostral plate displacement in moult

configurations of *E. bilobata* suggests that the operation of the facial and rostral

sutures, producing an anterior exuvial gape in the manner described by

Henningsmoen (1975), was the standard mode of ecdysis in this trilobite. This,

coupled with the high proportion of specimens exhibiting anterior displacement of

the cranidium, suggests that *E. bilobata* moulted similarly to a number of other

Cambrian trilobite genera, e.g. *Ogygopsis*, *Paradoxides* (McNamara & Rudkin 1984;

Whittington 1990), *Redlichia* (McNamara 1986), and *Balcoracania* (Paterson *et al.*

2007). This method involved an initial downward (towards the sediment) angling of

the cephalon and upwards flexure of the dorsal thorax (producing a partial

enrolment referred to as 'downwards flexure of the cephalon' in McNamara &

Rudkin 1984, and termed 'dorsal flexure' here). This was followed by the opening of

the cephalic sutures, allowing anterior egression of the trilobite from the old

exoskeleton through the resulting exuvial gape. This may have been aided by

relaxation and extension of the moulting trilobite from the partially enrolled exuviae

(Whittington 1990). For *E. bilobata*, the LCU (forming the ventral section of the

exuvial gape) was usually preserved intact, while the cranidium (the dorsal section)

often became detached from the trunk. Anterior inversions of the librigenae

(Somersault configuration), and Salter's configuration where the entire cephalon is

anteriorly inverted (Richter 1937), were rare (<10% of specimens, combined). Moult

configurations showing these anterior inversions would require a relatively severe

degree of dorsal flexure, with the cephalon at a high angle to the sediment. The

forward movement of the moulting animal may then have resulted in the trunk

being dragged over the librigenae or cephalon, causing them to become inverted

(see McNamara & Rudkin 1984, fig. 11; Whittington 1990, fig. 6). However, the rarity

of these configurations compared to the prevalence of Henningsmoen's and

Harrington's configurations (around 90% of specimens) suggests that this was an unusual occurrence. This in turn indicates the degree of flexure in this species was perhaps less than for some other Cambrian trilobites, usually prohibiting anterior inversions.

The opening of the facial and rostral sutures in *E. bilobata* and the resulting exuvial gape was generally sufficient for moulting, with variations of Harrington's configuration (e.g. Fig. 3A) being very common (around 55% of specimens). Subsequently, the LCU would have been free of the cranidium, but seems to have generally remained articulated and connected to the thorax by integument. This explains why the LCU usually remained *in situ* or only slightly displaced relative to the trunk in Harrington's and Henningsmoen's configurations (e.g. Fig. 2A–B, D). Millimeter-scale displacements may have resulted from some degree of flexibility in the unmineralised cuticle connecting these sclerites, disturbance produced by the moulting animal, and/or subsequent decay of the connective integument. The LCU was often posteriorly displaced, presumably having been pushed backwards by the forwards movement of the individual during moulting (e.g. Fig 2D). The total absence of the Nutcracker configuration suggests that disarticulation of cephalic sclerites owing to the decay or breakage of unmineralised integument prior to burial was rare in *E. bilobata* compared to the larger *R. takooensis*. Despite this, it does not seem that disarticulation of the LCU from the cranidium as a complete unit always occurred, or was necessary for successful moulting, with a number of specimens exhibiting rostral plates with one associated librigena, and the other remaining joined to the displaced cranidium (Fig. 2C, E, possibly B). Some moulting events may have involved multiple progressive breakages of the integument. For example, SAM-

P 46956 (Fig. 2G) where the trunk and left librigena were initially shed. The trilobite then moved forward and discarded the rostral plate and right librigena, before leaving behind the cranidium.

Henningsmoen's configuration (Fig. 1) was also very common for *E. bilobata* (around 35% of specimens), suggesting that the cranidium easily became disarticulated during moulting, and in doing so presumably enlarging the exuvial gape. Whittington (1990), however, noted that the weakest part of a moult would have been the flexible membranes attaching the cranidium to the thorax, decay of which could easily result in disarticulation and transport. He therefore suggested caution in interpreting cranidium detachment as an aid in moulting. Nevertheless, the frequency of occurrence within the EBS and rarity of disarticulations in other joints suggest this is a legitimate biological pattern. Cranidial displacement was usually to the anterior, presumably having been carried forward by the post-ecdysial trilobite. The apparent weakness in the cephalothoracic joint may also explain the rare examples of Salter's configuration preserved for this species (Fig. 3C, E). This may have provided an alternative method of moulting following a failed opening of the facial and/or rostral sutures, with the trilobite extracting itself through the resulting exuvial gape. Given the displacement of cephalic elements in both figured specimens it is unlikely that complete failure of the sutures occurred in either of these cases.

Inferred moulting behaviour of Redlichia takooensis

In general, *Redlichia takooensis* also used the Sutural Gape mode of moulting via opening of the cephalic sutures. In contrast to *E. bilobata*, however, *R. takooensis* moults tend to show greater displacement of the cephalic sclerites in variations of the Nutcracker configuration (90% of moults), with the librigenae, rostral plate, and hypostome independent rather than joined in the LCU. This implies that breakage of the connective integument between sclerites prior to burial was common in the larger *R. takooensis* but rare in *E. bilobata*. This may indicate that exuvial movements in *R. takooensis* were more vigorous, resulting in more dispersed moult configurations. It is also possible that the connective integument was less robust in the larger species, and that this displacement may be a result of decay and subsequent disarticulation and movement (although we consider this less likely as there is no other evidence of decay). Assuming disarticulation occurred during moulting, the cephalic sclerites would then have fallen back down to the sediment and been displaced by any sideways and forward movements of the moulting animal, pushing them away from the axial shield (e.g. Fig 4A–B). The apparent breakage of integument and greater outwards displacement of the cephalic sclerites (producing the Nutcracker configuration, rather than Harrington's configuration) may indicate more extreme body movements during moulting for *R. takooensis* compared to *E. bilobata*, causing the sclerites to be pushed or carried further from the axial shield.

As has been suggested for other species of *Redlichia* (figs 2-5, McNamara 1986), it is probable that dorsal flexure played an important role in the standard mode of moulting in *R. takooensis*. The absence of anterior librigenal inversion (Somersault configuration, Fig. 1), however, suggests that enrolment may have been

less acute prior to opening of the facial sutures, causing the librigenae to settle back down to the sediment following moulting in their relatively normal orientations. This may also imply less pressure on the cephalothoracic joint, possibly explaining the relative rarity of cranidial displacement in moult configurations of *R. takooensis*. However, as Salter's configuration was slightly more common for *R. takooensis* than *E. bilobata* (although still relatively rare; around 5% of moults), the facial sutures may have failed to open more frequently. It also seems that in *R. takooensis* the facial sutures were likely to fail completely, rather than partially as in *E. bilobata*. In these scenarios, the individual may have employed a particularly high angle of dorsal flexure to enable the cephalothoracic joint to break. McNamara (1986, figs 1–2) observed pygidial inversion for *Redlichia forresti*, which he inferred to have resulted due to posterior movement during moulting to allow extraction from the cephalic region following failure of the sutures, increasing the angle of dorsal flexure at the pygidium. He also noted thoracic segment inversions for both *R. forresti* and *R. idonea* that he interpreted to have resulted from dorsal flexure, as well as a specimen of each with an inverted right librigena in variations of McNamara's configuration supposedly resulting from a zone of low pressure beneath the cephalon caused by rapid movement away from the sediment (McNamara 1986, figs 1B, C, E, 3). Whittington (1990) rejected the idea of posterior movement in this instance, and suggested such patterns of displacement and movement may simply be a result of transport and disturbance of partially decayed exuviae, or even carcasses (a possibility given the lack of evidence for the opening of facial sutures in certain specimens). We agree that specimens showing no evidence of opened cephalic sutures, other than full cephalon disarticulations (e.g. Salter's

configuration), are unlikely to be moults. However, because multiple specimens of *R. takooensis* within the EBS collections also exhibit McNamara's configuration (around 5% of moult specimens), this arrangement likely represents a true biological signal. We consider that McNamara's configuration results simply from the librigenae occasionally becoming laterally inverted due to the presumably spasmodic movement of the moulting trilobite, although a pressure gradient caused by this movement as suggested by McNamara & Rudkin (1984, fig. 5) is a possibility. Inversions, other than of cephalic structures, were not observed for *R. takooensis* or *E. bilobata*.

It is possible that the posterior-most pleural spines of *R. takooensis* were pushed into the sediment as an anchor for dorsal flexure, as suggested by Whittington (1990) for *Paradoxides*. Assuming the *Redlichia* specimens exhibiting pygidial inversion figured by McNamara (1986, figs 1–2) do represent moults, the pygidium may have been used in a similar way during moulting. The rotated pygidium and posterior-most thoracic segments observed in *E. bilobata* (Fig. 4F) can also be explained by its use as an anchor for dorsal flexure, particularly given the spinose nature of the pygidium in this species (Pocock 1964). Recurring presence of thoracic disarticulation in putative *R. takooensis* moult configurations immediately below segments 6 and 11, both of which supported extended dorsal spines (Paterson & Jago 2006), may have occurred during moulting. However, because of their orientation this is more likely the result of physical processes acting on the larger surface area of these segments prior to or during burial.

The normal sequence of moulting in *R. takooensis* therefore likely began with dorsal flexure away from the sediment, followed by opening of the cephalic sutures,

with the animal exiting the exoskeleton through the resulting anterior exuvial gape.

This likely involved more vigorous movements of the individual, causing the

disarticulated librigenae to be displaced sideways and outwards from their usual

position or, very occasionally, to become laterally inverted (Fig. 4F, G). Salter's

configuration, although rare, is more common than for *E. bilobata*, suggesting that

this was an important alternative strategy following the failure of the cephalic

sutures to open.

Comparison with trilobite moulting at the Mount Stephen Trilobite Beds and Wheeler

Shale

The favourable depositional conditions at the EBS have preserved essentially

undisturbed moult configurations exhibiting high levels of variation in the

positioning of moulted sclerites, allowing detailed reconstructions of exuvial

movements (comparable to but more numerous than those illustrated in McNamara

& Rudkin 1984 figs 5, 11; McNamara 1984, figs 2-5; Whittington 1990, figs 2-6). The

Mount Stephen Trilobite Beds and the Wheeler Shale reveal that for *Ogygopsis klotzi*

and *Elrathia kingii* respectively the standard mode of moulting is the same as for the

EBS species, suggesting a common behaviour for Cambrian trilobites in the similar

environmental and ecological settings of the Trilobite Beds and Wheeler Shale.

However, even these exceptionally preserved deposits with very high trilobite

abundances seemingly do not preserve such a complete and diverse record of

moulting as the EBS, or are intensely impacted by historical sampling bias. The

greater prevalence of isolated axial shields (e.g. Fig 5A, C, G), as well as aggregations

of disarticulated specimens and fragmentary sclerites seen in the larger slabs (e.g. Fig 5F), may indicate slight transportation and disturbance of moult configurations prior to emplacement as even very minor currents may have been sufficient to transport disarticulated sclerites. It is also extremely difficult to determine orientations of specimens from the Trilobite Beds because they originate from non-*in situ* talus (Rudkin 2011). This makes it difficult to interpret aspects of movement such as dorsal flexure, because complete moult configurations are less frequently observed. However, the lack of associated sclerites may itself indicate a style of moulting involving greater displacement of sclerites than for *E. bilobata* and *R. takooensis*, for example if the librigenae of *O. klotzi* were carried further away by the post-ecdysial trilobite as suggested by McNamara & Rudkin (1984). This may be supported by the moult configurations with librigenae displaced laterally. The presence of intact moult configurations within these deposits (Fig. 5, but see also McNamara & Rudkin 1984, figs 9, 10, 13A; Gaines & Droser 2003, fig. 1A; Rudkin 2009, fig. 1C), however, suggests a range of conditions. These deposits likely represent a combination of census and time-averaged assemblages as proposed by Caron and Jackson (2006) for the Greater Phyllopod Bed (Burgess Shale). While this is likely true for the EBS as well, conditions in general indicate extremely low levels of disturbance, with isolated axial shields and accumulations of disarticulated sclerites being extremely rare. It has been suggested that a fluctuating oxycline may have resulted in episodic mass kill events that excluded scavengers and inhibited decay at the EBS (Paterson *et al*. 2016), with carcasses (and moults) then smothered in a steady accumulation of fine sediment under extremely quiescent conditions.

This could explain how such an exceptional *in situ* record of moulting was preserved at the EBS.

The intact moult configurations presented here for *O. klotzi* from the Mount Stephen Trilobite Beds show separation of the librigenae, and occasionally strong movements of the body to imbricate and displace the middle thoracic segments (Fig. 5B). Isolated axial shields seem generally more common than for *El. kingii* at the Wheeler Shale (and more common at both than at the EBS), but all of these Cambrian trilobite species still demonstrate a relatively high level of flexibility in their moulting behaviour. McNamara & Rudkin (1984) described two moults of *O. klotzi* (also from Mount Stephen), as well as a specimen of *Paradoxides davidis* Salter 1863, all in a modified version of the Somersault configuration, possibly with the entire LCU inverted to lie beneath the cranidium, and used this to argue for a sharp (greater than 90°) dorsal flexure to dislocate the cranidium from the thorax (McNamara & Rudkin 1984, fig. 11). Whittington (1990) considered this unlikely, based on the prevalence of complete axial shields, as well as the fact that the facial sutures had operated in these specimens and therefore cranidium removal was not necessary. He argued that such a sharp angle would have dislocated all joints between the cephalon and the first three thoracic segments and instead advocated a more continuous enrolment for moulting, such that *O. klotzi* moulted in a manner similar to that described for *Paradoxides* (i.e. via the Sutural Gape mode with dorsal flexure facilitated by posterior thoracic pleural spines). Isolated thoracopyga of *O. klotzi* (e.g. Fig. 5E) may indicate instances of moulting through disarticulation at the cephalothoracic joint, as in the manner described for the EBS trilobites, although without the associated cephalon preserved this is difficult to confirm. It is also

possible that these isolated fragments are the result of disarticulation resulting from decay and subsequent transport.

El. kingii moult specimens from the Wheeler Shale (Fig. 5G–J) indicate moulting was also accomplished via the Sutural Gape mode, but many provide no information on what additional behaviours may have been involved. This is because the location of disarticulated sclerites relative to the axial shield does not as often seem to reflect their moulted position (e.g. Gaines & Droser 2003, fig. 1A), suggesting higher levels of disturbance than at the EBS. The apparent scarcity of individual cephala or thoracopyga of *El. kingii* suggest that, as for *E. bilobata* and *R. takooensis*, moulting through other means (such as disarticulation of the entire cephalon) was very rare. The lack of inversions for *El. kingii* and *O. klotzi* potentially imply less dorsal flexure during moulting than for the EBS trilobites, although the *El. kingii* moult configurations may indicate greater angling of the pygidium due to their higher degree of posterior disarticulation and displacement.

Exploration of detailed moulting variation is made possible by access to the abundant trilobite collections at the SAM. This is not so readily accessible for *O. klotzi* and *El. kingii*, meaning results may also be more affected by collecting bias, and as such the smaller sample sizes here represent a generalised rather than direct comparison of the three localities. This allows us to discern similarities like the shared preference for the Sutural Gape mode of moulting, and differences such as the greater prevalence of isolated axial shields within the two localities in comparison to the EBS. However, the limited sample size represented for *O. klotzi* and *El. kingii* likely has constrained the observed variation in their moulting

configurations, and so the specimens presented here are not presumed to display their full moulting variation.

Recognising moult configurations

As for other arthropod groups, the sedimentological context and depositional environment must be considered when distinguishing moults and carcasses in the fossil record (Daley & Drage 2016). Determining the significance of thoracic segment disarticulation for exoskeleton moulting is particularly problematic, as thoracic breakages could be produced either during moulting or during decay of the integument articulating the segments in carcasses or moults. Specimens with systematic thoracic breaks may represent moult configurations, although as discussed above, the recurring dislocation below segments 6 and 11 in *R. takooensis* may have occurred after moulting due to physical processes acting on the enlarged spines of these segments. Specimens of *R. takooensis* with relatively minor cephalic displacement and thoracic breaks (e.g. Fig. 4D), or of *E. bilobata* with multiple thoracic dislocations are difficult to distinguish as moults or carcasses. SAM-P 54209 (Fig. 4K) shows a thoracic break in a specimen considered a carcass due to the closed cephalic sutures. Whittington (1990) explored this problem when reviewing some of the putative *Redlichia* moults figured by McNamara (1986), suggesting these could easily represent carcasses following decay and disturbance. We argue that the presence of thoracic dislocation alone (i.e. without the disruption of the cephalic sutures to indicate an exuvial gape) is likely to represent decay rather than evidence of moulting, although some uncertainty remains. This is also true of specimens that

show very minor disarticulation of cephalic sutures, and can make the identification of trilobite moults problematic.

Certain features, when more fully understood, may become useful tools in distinguishing trilobite carcasses and moults. In some cases, the presence/absence and positioning of ventral cephalic structures may be important for identifying moult configurations in trilobites with hypostomal and rostral sutures. The EBS trilobite moult configurations show that disarticulation of the rostral plate was integral to the opening of the anterior exuvial gape (separately for *R. takooensis,* and as part of the LCU for *E. bilobata*; e.g. Figs 2D, 3A, 4A), except perhaps for Salter's configuration. The hypostome was also frequently displaced for *R. takooensis* (e.g. Fig 4E), however several specimens otherwise considered moults due to their obvious anterior exuvial gapes seem to have the hypostome (Fig. 4B) and occasionally rostral plate (Fig. 4C) close to life position, possibly held in place via integument. It is therefore likely that specimens showing any evidence for opening of an anterior exuvial gape represent moults, regardless of the degree of hypostomal movement. Further, many global trilobite-bearing localities do not appear to preserve clear hypostomes, or they are obscured by the dorsal exoskeleton (HBD, pers. obs. 2016). At the EBS, ventral structures are easily observed due to the moldic preservation, without the calcitic exoskeleton. Delicate moulted parts, such as the antennae and legs, are rarely observed for this reason. Ventral structures can therefore aid in determining moulting if easily identifiable, but their absence or lack of movement does not conclusively define a carcass.

In complete carcasses of *E. bilobata*, the pygidium and final few thoracic segments are often curled under the thorax (e.g. Fig. 3G), presumably due to muscle

contraction during death and/or decay. However, preserved moult configurations of *E. bilobata* do not seem to show pygidial enrolment, presumably due to the lack of required musculature. This may assist in moult identification for specimens of *E. bilobata* with only slight displacement of sclerites, and has the potential to be of broader use if identified in other trilobite species.

A large proportion of trilobite specimens within the EBS are preserved dorsum-down with previous sampling of a number of different surfaces indicating that greater than 75% of specimens are orientated in this manner (Gehling *et al*. 2011). In our field study, 90% of specimens were oriented dorsum-down, while at least two of the six specimens oriented upright were moults. Gehling *et al.* (2011) suggested that carcasses may be flipped dorsum-down due to the escape of gases from decay of internal soft tissues (discussed also by other authors, such as Speyer & Brett 1985; Speyer 1987; Ebbestad *et al.* 2013; etc.). It is therefore possible that the majority of upright specimens in this sample represent moults, as they would not have had much internal tissue to create enough decay gas to cause the exoskeleton to turn over. If this is indeed the case, it may provide additional evidence in identifying moults from carcasses at EBS, and potentially at other sites as well. However, Ebbestad *et al.* (2013) found an approximately equal number of dorsum-up and down moult specimens in their paradoxidid mass moult assemblage, and therefore suggested the represented species may have been equally able to moult in either orientation. Speyer (1987) also noted that moults preserved inverted may for some species represent a behavioural adaptation in moulting. This needs further quantitative examination on a larger scale at the EBS to determine whether there is a statistical bias towards moulting in one body orientation.

Collection bias

Several factors must be considered regarding the taphonomy, collection, and interpretation of preserved moult configurations. For example, the preservation of the unmineralised integument between exoskeleton sclerites may impact the moulting configurations seen, as is clear from the EBS material. The integument would likely have decayed rapidly post-moulting, resulting in disarticulation and displacement of configurations except under low hydrodynamic energy conditions (Whittington 1990), such as at the EBS. In localities with decay and disturbance prior to burial, configurations such as Henningsmoen's and Harrington's defined by the joined LCU would therefore not be observed. This would affect interpretations of the individual's movements during moulting.

Collecting bias for 'display-quality' specimens may also affect interpretations of moulting behaviour variability for trilobites, although it is difficult to predict whether complete moult configurations or articulated body fossils would be preferentially collected. For moult configurations, the more unusual behaviours may be chosen over those displaying subtler patterns (e.g. McNamara & Rudkin 1984). This may affect observations for species such as *E. bilobata*, as most *in situ* putative moults show only minor displacement of the LCU (Pocock 1964). Collection bias is likely also a problem for sampling of the Trilobite Beds and Wheeler Shale. It is likely that EBS trilobite moults are not significantly under or over-represented due to their frequent collection on samples containing other taxa of interest, and abundance in the SAM collections. Regardless, this study is a qualitative exploration to represent

the range of observed moulting behaviours at the EBS, and we have only indicated relative proportions broadly estimated from the existing museum collections. A quantitative study of the numbers of these moulting configurations (from a field sample), and how these differ between the two species, is beyond the scope of the present study, but would be extremely useful for furthering our understanding of trilobite exuvial variability.

Variation in trilobite moulting behaviour

The large, exceptionally preserved sample from the EBS revealed a broader range of intraspecific moulting behaviours and configurations than previously described for trilobites (e.g. in Henningsmoen 1975; Brandt 2002). Both discussed moulting methods (Sutural Gape and Salterian) have demonstrably occurred within a single species before (see Daley & Drage 2016), but without the number of configurations these have produced at the EBS (Fig. 1). The quiescent environmental conditions at the EBS were responsible for the preservation of this range in trilobite movement during moulting. Many localities with greater disturbance prior to burial therefore did not preserve the full variation in moulting behaviour and movement. Trilobite moulting was therefore a potentially more flexible behaviour than previously hypothesised, and much more variable than for other arthropods (for example decapod crustaceans, and chelicerates like eurypterids and scorpions; see Daley & Drage 2016). Brandt (2002), in one of few evolutionary studies of trilobite moulting, determined this flexibility was broadly detrimental to Trilobita, by their moult habit being unspecialised and therefore inefficient. However, the data from

the EBS indicates this is a useful behavioural flexibility, in which rarer 'emergency behaviours' could increase individual survival chances during difficult moulting events to broaden the exuvial gape, or when the usual gape failed to open. This may have happened more frequently for trilobites than for other arthropods, due to their highly reinforced exoskeleton. On an individual and population level, this would have increased survival rates, and therefore this variability may have contributed to their extremely long geological record (Hughes 2003).

Conclusions

Descriptions of the moulting behaviour for two abundant trilobite species from the early Cambrian Emu Bay Shale Konservat-Lagerstätte, *Estaingia bilobata* and *Redlichia takooensis*, have allowed for detailed interpretations of individual moulting movements (similar to those illustrated in McNamara & Rudkin 1984, fig. 11; Whittington 1990, figs 2-6). The moult configurations figured suggest that Cambrian trilobites, as observed from localities showing exceptional preservation, generally use a Sutural Gape mode of moulting (Henningsmoen 1975), involving opening of the cephalic sutures to create an anterior exuvial gape. However, the two species exhibit differing patterns of behavioural variation within this mode. For example, *E. bilobata* usually produces configurations in Harrington's or Henningsmoen's configuration with a joined Lower Cephalic Unit (*sensu* Henningsmoen 1975), whereas *R. takooensis* usually disarticulates the same sclerites but disconnected and displaced laterally outwards from the axial shield in the

Nutcracker configuration. Both species preserve a range of moulting configurations including Salter's configuration through the alternative Salterian mode of moulting.

Minor enrolment, or 'dorsal flexure' of the exoskeleton away from the sediment, seems necessary to produce most of the configurations described here, which is consistent with the moulting methods determined in earlier literature (McNamara & Rudkin 1984; McNamara 1986; Whittington 1990; Paterson *et al.* 2007). More extreme movement, not just in an anterior direction, is inferred for many specimens, as rotation and lateral displacement of sclerites is common. There is an absence of inverted thoracic segments or pygidia, possibly associated with the presence of elongated thoracic medial spines in *R. takooensis*.

The Wheeler Shale and Mount Stephen Trilobite Beds, both of which exhibit Burgess Shale-type preservation, contain a higher proportion of axial shields, which provide less information on trilobite movement during moulting than derived from the EBS. It is likely, therefore, that these sites reflect conditions of slightly higher hydrodynamic energy and/or slower burial, resulting in disarticulation of moults due to decay and transport (although it is possible this may also reflect greater movements of the exuviating trilobites). At the EBS, the lack of evidence for water movement, rapid burial, and detailed behavioural record, however, seem to confirm a difference in environment, as suggested by its unique depositional setting. It is this differing environment that appears responsible for highlighting the inherent biological flexibility in moulting for *E. bilobata* and *R. takooensis*. This variability appears widespread in trilobites not least due to its occurrence across the three Orders represented here (Corynexochida, Ptychopariida, Redlichiida), and may have been integral to their extremely long-lived and successful evolutionary history.

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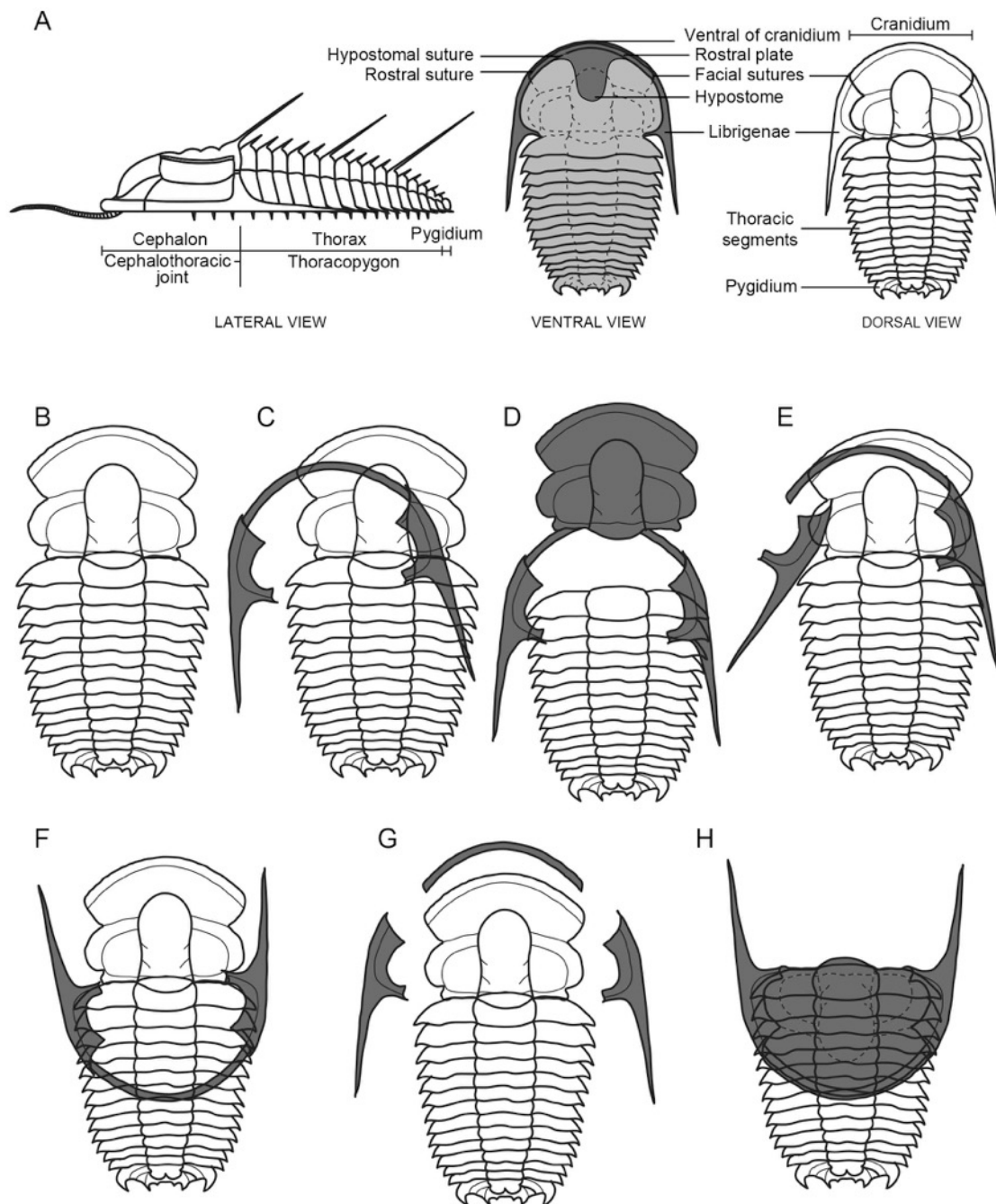*Palaeontologia Sinica, new series B (no. 16) 159*, 1–497.

Figure legends

Figure 1: Trilobite anatomy (A) and moult configurations (B-H) described from the Emu Bay Shale and represented on the body of *Estaingia bilobata*. Ventral structures (rostral plate, hypostome), and structures that in some instances underlap the ventral exoskeleton due to moulting (librigenae, cephalon) are shaded grey. B, axial shield; C, Harrington's configuration (e.g. SAM-P 15339, see Fig. 3A); D,

Henningsmoen's configuration (e.g. SAM-P 45519, see Fig. 2D); E, McNamara's

configuration (e.g. SAM-P 48062 and 54207, see Figs. 4F and 3B respectively); F,

Somersault configuration (e.g. SAM-P 54204, see Fig. 3D); G, Nutcracker

configuration (e.g. SAM-P 48085, see Fig. 4A); H, Salter's configuration (e.g. SAM-P

43593 and 15459, see Figs. 4I and 3E). Axial shields are incomplete moult

configurations, Salter's configuration results from a 'Salterian' mode of moulting,

and the remaining five complete configurations result from a 'Sutural Gape' (*sensu*

Henningsmoen 1975) mode of moulting. Configurations C, D, and F are found at the

EBS for only *Estaingia bilobata*; G for only *Redlichia takooensis*; and B, E, and H for
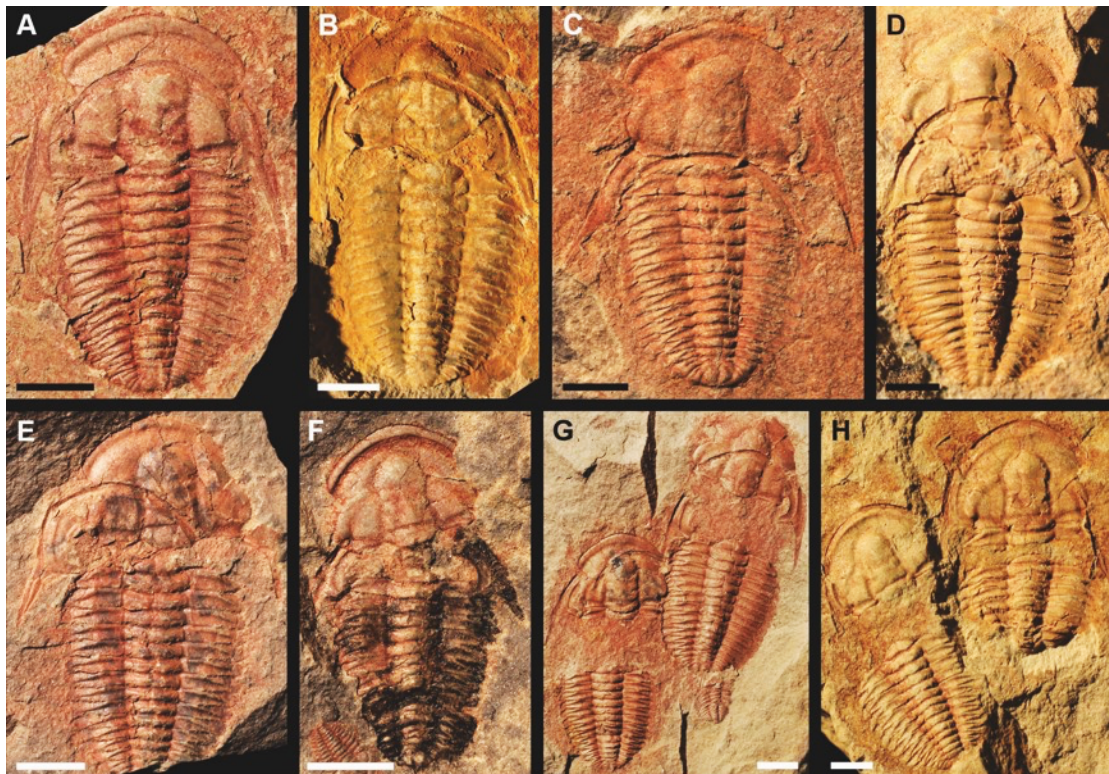
both species.

Figure 2: Example moult configurations of *Estaingia bilobata* from the Emu Bay Shale

collections of the South Australian Museum, referred to in the text. A, SAM-P 43837;

B, SAM-P 43974; C, SAM-P 43402; D, SAM-P 45519; E, SAM-P 46933; F, SAM-P 46362; G, SAM-P 46956; H, SAM-P 45697. A-H display Henningsmoen's configuration; G (left individual) and H (right individual) Harrington's configuration. Scale bars 5 mm, D and H scale bars 2.5 mm.
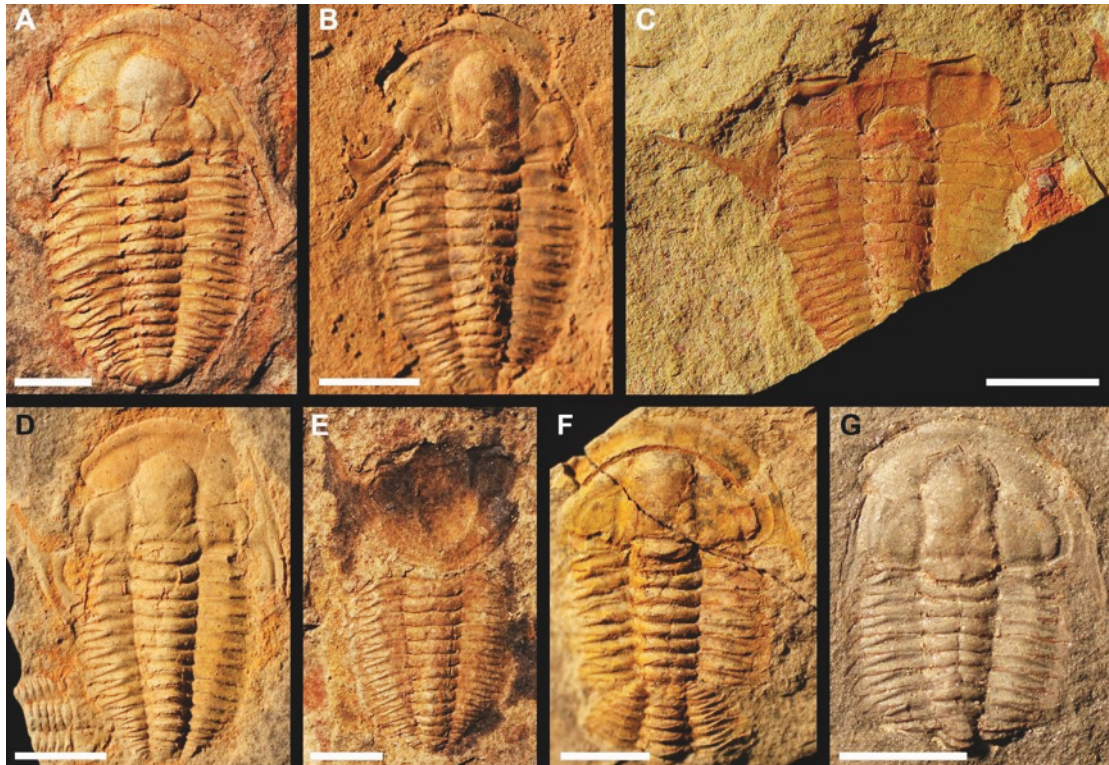

Figure 3: Example moult configurations of *Estaingia bilobata* from the Emu Bay Shale collections of the South Australian Museum, referred to in the text. A, SAM-P 15339; B, SAM-P 54207; C, SAM-P 54206; D, SAM-P 54204; E, SAM-P 15459; F, SAM-P 54205; G, SAM-P 54208. A and likely F display Harrington's configuration; B McNamara's configuration; C and E Salter's configuration; D the Somersault configuration. F is a complete carcass. Scale bars 5 mm.

Figure 4: Example moult configurations of *Redlichia takooensis* from the Emu Bay Shale collections of the South Australian Museum, referred to in the text. A, SAM-P 48085; B, SAM-P 44214; C, SAM-P 45440; D, SAM-P 44544; E, SAM-P 46207; F, SAM-P 48062; G, SAM-P 46047; H, SAM-P 45368; I, SAM-P 43593; J, SAM-P 45875; K, SAM-P 54209. A-E display the Nutcracker configuration; F and G McNamara's configuration; H-J Salter's configuration. J is a complete carcass. Scale bars 10 mm.
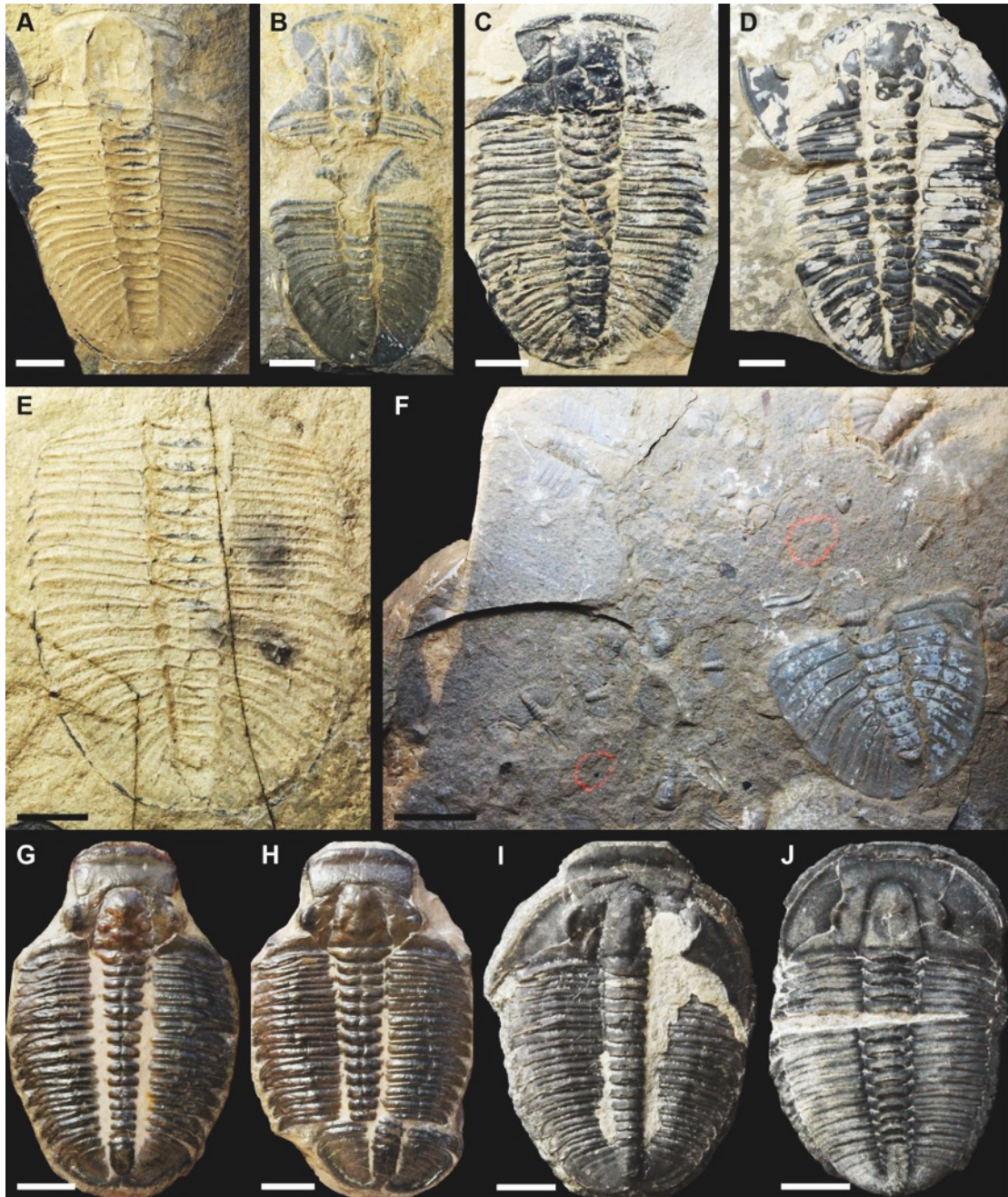
Figure 5: Example moult configurations of *Ogygopsis klotzi* from Mount Stephen Trilobite Beds, Burgess Shale, British Columbia (A–F), and *Elrathia kingii* from the Wheeler Shale, Utah (G–J), photographed from the Natural History Museum, London, collections. A, NHMUK I.4751(1); B, NHMUK I.4751(2); C, NHMUK I.4746; D, NHMUK I.4741; E, NHMUK In.19410; F, NHMUK I.4753; G, NHMUK It.21001; H, NHMUK It.20999; I, NHMUK It.21003; J, NHMUK It.5937. A, C, G and H are axial shields; B and D variants of the Nutcracker configuration; I Harrington's

configuration. E shows an isolated trunk, and J is a complete carcass. A–E scale bars

10 mm, F scale bar 20 mm, G, H, J scale bars 5 mm, I scale bar 2.5 mm.