The fossil record of ecdysis, and trends in the moulting behaviour of trilobites

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ABSTRACT: Ecdysis, the process of moulting an exoskeleton, is one of the key characters uniting arthropods, nematodes and a number of smaller phyla into Ecdysozoa. The arthropod fossil record, particularly trilobites, eurypterids and decapod crustaceans, yields information on moulting, although the current focus is predominantly descriptive and lacks a broader evolutionary perspective. We here review literature on the fossil record of ecdysis, synthesizing research on the behaviour, evolutionary trends, and phylogenetic significance of moulting throughout the Phanerozoic. Approaches vary widely between taxonomic groups, but an overall theme uniting these works suggests that identifying moults in the palaeontological record must take into account the morphology, taphonomy and depositional environment of fossils. We also quantitatively analyse trends in trilobite ecdysis based on a newly generated database of published incidences of moulting behaviour. This preliminary work reveals significant taxonomic and temporal signal in the trilobite moulting fossil record, with free cheek moulting being prevalent across all orders and throughout the Phanerozoic, and peaks of cephalic moulting in Phacopida during the Ordovician and rostral plate moulting in Redlichiida during the Cambrian. This study and a review of the literature suggest that it is feasible to extract large-scale evolutionary information from the fossil record of moulting.

Keywords: Ecdysis, Moulting, Arthropoda, Trilobita, Evolution, Fossil record

1. Introduction

Ecdysis, the process of moulting an exoskeleton, is one of the key characters uniting arthropods, nematodes and a number of smaller phyla in the aptly named group Ecdysozoa (Fig. 1) (Telford et al., 2008). Ecdysozoans include both the most abundant and the most diverse animal groups on the planet today, representing over 80% of total biodiversity. They have been key components of ecosystems since the early Cambrian when trilobites and various soft-bodied Burgess Shale-type ecdysozoans including arthropods, lobopodians, priapulids and palaeoscolecids dominated marine animal communities (Budd and Jensen, 2000), and have remained important throughout the whole of the Phanerozoic. Understanding the processes and behaviour of ecdysis in the fossil record is important because this life history strategy would have imparted constraints on morphology throughout the evolution of modern animal groups. In addition, it allows us to access information on growth and development in deep time, which can help resolve the affinity of enigmatic taxa early in the evolution of animals. This is particularly important because many of these Cambrian fossils are early diverging stem lineage taxa that are critically important for breaking up long branches, helping us to resolve current ambiguous relationships in modern taxa (e.g. Legg et al., 2012). Additionally, studying ecdysis in the fossil record can provide insight into understanding ecology as one of the only examples of direct evidence of behaviour preserved in the fossil record.

For both extant and extinct taxa, moulting is best known for the arthropods. The arthropod external cuticle is a chitinous exoskeleton that provides protection from mechanical injury and dessication, while also giving strong structural support for muscle attachment and locomotion (Moussian, 2013). This rigid exoskeleton is moulted during normal growth and development, at which time regeneration and repair of damage may also occur. In extant taxa, moulting of the exoskeleton is a relatively rapid process, with actual exuviation and subsequent hardening of the new exoskeleton taking only a brief period of time (minutes to hours generally, but highly variable between taxa). The brevity of this physical process is reflected in the fossil record by the rarity of specimens that are preserved mid-moult (e.g. García-Bellido and Collins, 2004; Peel et al., 2013) or during the immediate post-exuviation stage when the exoskeleton is not yet fully hardened (e.g. Whittington, 1990). During this process the arthropod is unable to move to escape threats and is vulnerable to desiccation, leading to an evolutionary constraint for exuviation to occur as rapidly as possible and behavioural adaptations that minimise risk (e.g. mass moulting behaviour and seeking shelter during moulting).

The full process of moulting begins with a complex series of biological interactions long before the actual act of exuviation takes place. The exoskeleton consists of cuticle that was secreted by underlying epidermal cells, to which it remains attached during its functional lifetime (Moussian, 2013). The process of moulting starts with the separation of the cuticle from the epidermis, referred to as apolysis, after which the epidermal cells undergo a round of cell division to increase surface area, followed by the secretion a new layer of cuticle, which remains soft until the old cuticle is shed (Nijhout, 2013). A moulting fluid is secreted between the old and new cuticles, and in some taxa is involved with digestion and reabsorption of the old exoskeleton. At some point, all structures associated with the old cuticle (e.g. muscle attachment, sensory neurons, circulatory system, etc.) must be transferred to the new cuticle (Ewer, 2005). The old cuticle is then split open along specific lines of weakness, usually by movement of the body or through an increase in internal pressure, so that the arthropod can emerge and the new cuticle can begin to harden. This process is controlled by the hormone ecdysone in all arthropods (Krishnakumaran and Schneiderman, 1970; Nijhout, 2013), although there is great variation in the number of moulting episodes within the phylum, with some taxa requiring many moults to reach adult size, while others can reach the same size in fewer moults by growing in larger increments at each moult (Nijhout, 2013).

Most palaeontological data that exist for arthropod moulting are derived from the trilobites, eurypterids and crustaceans. Research on moulting tends to be descriptive and focused on particular specimens or assemblages, with only a few studies examining the fossil record of ecdysis as a whole. Henningsmoen (1975) describes in detail the characteristic modes of moulting observed in different groups of trilobites, but does not examine the evolutionary significance of these trends. A broader look at such evolutionary trends is taken by Brandt (2002), who examines the link between trilobite moulting method and geological survivorship of taxa. A brief treatment of the fossil record of moulting is used by Valentine and Collins (2000) in conjunction with molecular phylogenetic information to make broad inferences on the process of evolution within Ecdysozoa, but this focuses mostly on developmental data in modern taxa and does not succinctly summarise or integrate the broad record known from fossils. A more fossil-based perspective is provided by Speyer (1990), who evaluates the reliability of the fossil record for understanding moulting behaviour in a wide variety of moulting groups, including trilobites (based heavily on Henningsmoen, 1975), decapod crustaceans, insects, and spiders. An informative and substantial body of research focused specifically on evidence of moulting in the fossil record, particularly for the arthropods, has been accumulating since these reviews. Here, we bring together this information into a large-scale literature review examining the prevalence and pattern of moulting in fossil ecdysozoans, with the aim of reviewing the current knowledge on this major morphological innovation. This literature review comprises the first half of our paper, with the second half focused on a quantitative evaluation of the patterns in ecdysial behaviour in trilobites in relation to taxonomic and temporal signal.

1.1 Criteria for distinguishing moults from carcasses in the fossil record

Describing patterns of ecdysis in the fossil record necessitates the ability to distinguish preserved exoskeleton moults from carcasses. Only in rare cases have specimens been preserved mid-moult (e.g. García-Bellido and Collins, 2004; Peel et al., 2013) with both the empty moult and the exiting animal in close association. In the vast majority of cases, individual specimens must be examined to determine if they are empty moults or full carcasses. Important aspects to consider when identifying moults include the locations of 'gape sutures', planes of weakness where the exoskeleton splits to produce an opening through which the individual exits; movements of the animal to facilitate opening of the exoskeleton 'gape sutures'; the direction of exuviation (anteriorly or posteriorly); the orientation during exuviation (dorsal- or ventral-up); and the final configuration of exuviae segments that may be recorded in the fossil record. Interpretations of moulting behaviour can only be made from definite exuviae, so as not to introduce misleading signals on, for example, the locations of 'gape sutures' identified from fragmented carcasses. Physical disturbance of carcasses (e.g. from scavenging, decay, currents, reworking, or compaction) can lead to preservation of disarticulated assemblages, and distinguishing these from true empty moults requires consideration of the morphology, taphonomic and depositional environment of the fossil. The procedure for identifying moults depends on the taxonomic group, owing to the broad morphological and behavioural variation within Ecdysozoa. This is more difficult for some groups, particularly those with suture lines that close following exuviation (e.g. modern *Limulus*; Vrazo and Braddy, 2011), but may be aided by consideration of the taphonomic aspects detailed below.

Numerous criteria have been suggested for identifying fossil moults, based on observations from fossil material in previous studies (Henningsmoen, 1975; Whittington, 1990; Braddy, 2001; Tetlie et al., 2008; Ebbestad et al., 2013). We suggest that at least Criteria 1 and/or 2 below are crucial for identifying a moulted exuvia. Criterion 3 may provide additional evidence for identifying moults, but only if Criteria 1 and/or 2 have been met and the depositional environment and preservational processes considered (Criterion 4). Criteria 4-6 provide further support and are dependent on the preservation type (soft-part; mineralised).

Criteria for identifying moults in the fossil record:

(1) Presence of suture lines showing evidence of having been opened. Criteria 1 and/or 2 are crucial for identification of a fossil moult specimen.

(2) Repeated configurations of specific exoskeletal parts (for examples see Figs. 2 to 6). Criteria 1 and/or 2 are crucial for identification of a fossil moult specimen.

(3) Disturbance of mineralised exoskeletal features in a systematic, repeated and characteristic way. This may include flattening or distortion of elements (Braddy, 2001); superimposition of dorsal and ventral surfaces; telescoping of segments (Braddy, 2001); and possibly crushing of the glabella (Figs. 2C, 4B) (Ebbestad et al., 2013). The exact nature of the disturbance may vary between different assemblages and types of fossils. Identification of these types of features may assist with recognising fossil moults in taxa where suture lines close after exuviation, for example with the scorpions where the relative positioning of anatomical features allows for identification of fossil moults even without suture lines (McCoy and Brandt, 2009). Generally, Criterion 3 would not be enough on its own to conclusively identify a moult assemblage, but may provide additional evidence if Criteria 1 and/or 2 are met and if Criterion 4 has been considered.

(4) Consideration of contextual information, including biostratinomic data, palaeoenvironmental conditions, and preservational processes. Evidence indicating a quiet depositional environment with low energy conditions and a low degree of transportation is preferred for moulting assemblages, as it would preclude post-depositional disarticulation that could cause carcasses to look like empty moults. Avoiding heavily reworked and/or time averaged deposits also reduces the chance of incorrectly identifying carcasses as moults. This type of information is not enough on its own to identify a moult, but would provide supporting evidence for moults identified using Criteria 1, 2 and/or 3.

(5) Lack of clear internal carcass features, including: the midgut and/or gut contents (as some arthropods moult part of the gut with the exuviae); musculature; and the nervous or circulatory system. This criterion is only applicable at localities known to have soft-part preservation, so is not diagnostic on its own for the arthropod taxa that comprise the vast majority of the fossil record of ecdysis, including trilobites, eurypterids and crustaceans. Only rarely are these taxa found with soft-part preservation (e.g. Whittington, 1990) and so a lack of internal organs in arthropod taxa does not necessarily indicate a moult unless minimally Criteria 1 and/or 2 are also met. Criterion 5 is more relevant when discussing the ecdysis fossil record of lobopodians, loriciferans, priapulids and stem-lineage arthropods without a hardened exoskeleton.

(6) Lack of evidence of behaviours associated with body fossils, such as predation and scavenging. For eurypterids and crustaceans at least, moult assemblages are thought to be better preserved than carcasses, because they would not be a target for scavenging and predatory activities (Clarke and Ruedemann, 1912; Feldmann and Tshudy, 1987; Braddy, 2001). Again, this criterion is not enough on its own to identify a moult assemblage, but provides supporting evidence for specimens that minimally meet Criteria 1 and/or 2.

Preservation potential must also be considered when investigating the moult fossil record. Moults in animals with thickened exoskeletons, such as Trilobita, may have increased preservation potential as compared to carcasses. This could result in a bias to moults in the fossil record of these groups, exacerbating inflation already present from the fact that one individual produces numerous moults during its lifetime (but only one carcass). This bias is also dependent on additional moulting behaviours. Specifically, some taxa consume their moults entirely, while others reabsorb exoskeletal material for energy conservation (Brandt, 2002). Consequently, moults of some clades may be more fragile (for example eurypterids; Vrazo et al., 2014), with decreased preservation potential compared to their respective carcasses. Further, body sections in segmented ecdysozoans are more likely to become disarticulated in the moult as connective tissue may be lacking. However, the opposite could also be true; preserved carcasses could appear to be moults (based on criterion 3 above) due to the presence of exoskeletal distortion following the rapid decay of soft connective tissue (Hegna, 2012). Factors such as these may decrease the likelihood of moult preservation, but the lack of published experimental taphonomic (decay) data comparing moults and carcasses compounds this knowledge gap (although see Hegna, 2012, for preliminary data on crustacean decay experiments). A number of criteria must therefore be considered when attempting to justify a moult identification, and decisions must be rooted within specific contextual knowledge of the clade and depositional environment.

2. Literature review of the fossil record of moulting

The fossil record of moulting consists mainly of specimens belonging to the phylum Arthropoda, or falling on the stem lineage to this phylum (e.g. lobopodians), however the smaller ecdysozoan phyla Priapulida, Tardigrada and Loricifera, and the vermiform cycloneuralian group Palaeoscolecida, also have preserved evidence of moulting. The ecdysozoan phyla Nematoda, Nematomorpha, and Kinorhyncha have poor or absent fossil records and no fossil moulting assemblages have yet been found. In taxonomic studies, individual trilobites are often distinguished as an empty moult or an unmoulted carcass, providing information on the ecdysial mode for that group and on growth and development. The ecdysial fossil record also provides insight into unique behaviours, such as mass moulting and reabsorption/retention of previous moults.

2.1. Trilobite ecdysis

The majority of literature published on ecdysis in the fossil record concerns patterns of moulting in Class Trilobita. This group was extremely long-lived and diverse, living from the Early Cambrian until their disappearance in the fossil record at the end-Permian mass extinction, following a drawn-out decline (Brandt, 2002). In addition to being geologically successful and geographically diverse, trilobites filled numerous niches, including as predators, scavengers and filter-feeders. Trilobites have been variously interpreted as related to the mandibulates, chelicerates and as stem lineage arthropods (see Budd and Telford, 2009; Edgecombe, 2010 for a review), but regardless of their exact phylogenetic affinity, they are important as early arthropods owing to their abundance in Palaeozoic marine environments. Their thick cuticles had a high preservation potential; providing researchers with extensive collections of material with which to investigate biostratigraphy, biogeography, and their morphology, development and ecology. Trilobites were a key component of ancient marine ecosystems, with a complex evolutionary history shaped by their ability to ecdyse. Understanding their ecdysial behaviours is central to the study of the early evolution of Arthropoda and its evolution for the next 540 million years (Henningsmoen, 1975).

Trilobite moult configurations (Figs. 2, 3), the repeated patterns of fragmented exuviae preserved in the fossil record, demonstrate that the ecdysial behaviours employed by trilobites were highly varied. These behaviours have been reconstructed using the consistent patterns observed in empty moult configurations, because no specimens have yet been found that preserve a trilobite midway through the act of moulting. The most common methods of ecdysis across Trilobita are the opening of the facial sutures (Figs. 2-4) (sometimes including the rostral suture, figs. 4G-J), usually followed by the release and/or inversion of the librigenae (free cheeks), and a disarticulation between the cephalon and the thoracopygon (the rest of the body, including thorax and pygidium). Other behaviours have also been described in the literature (Henningsmoen, 1975), including: breaks at other points along the thorax (Figs. 2B, C, 3K, L); displacement of the pygidium (Fig. 3J); removal of the rostral plate and ventral exuviation of the animal; and release of the librigenae followed by dislocation of the cranidium from the thorax (Fig. 2F). These modes have been dissected into the resulting 'characteristic' configurations that are preserved in the fossil record (Budil and Bruthansová, 2005, fig. 3). For example, Salterian moulting (Henningsmoen, 1975) consists of a break at the joint between the cephalon and the thorax during ecdysis, and the subsequent inversion of the cephalon to rest with the anterior edge towards the thoracopygon (Fig.

3I), resulting in Salter's Configuration (Richter, 1937). The trilobite would arch its body during ecdysis, angling the dorsal cephalon towards the substrate. This mode of moulting may also have produced different exuviae configurations, if the cephalic angle was too small for inversion (for example, in *Trimerus stelmophorus*, Busch and Swartz, 1985).

Many adult trilobite taxa were not restricted to a single method of ecdysis. The mode employed by the individual likely depended on a number of factors, including developmental stage and size, and ease of moulting in a particular environment (and associated risk). Some taxa seem to have the ability to account for failure of the usual moulting mode by employing an unusual method if needed (McNamara, 1986; Budil and Bruthansová, 2005; Paterson et al., 2007; Tortello and Clarkson, 2008). Additionally, there may have been morphological constraints, and some ecdysial characteristics may be constant for this reason. For example, the Salterian mode of moulting likely occurred more frequently in species with apparently inactive facial sutures, as in some phacopids (Henningsmoen, 1975). Other methods may have been key for species with more complex morphologies. We may also see trends in ecdysis through geological time, possibly in response to a phylogenetic signal. For example, Budil and Bruthansová (2005) found Middle Ordovician taxa displayed more variation in modes of moulting.

Trilobites may have been as likely to moult dorsal-up as ventral-up. This may be common across the Class; a close to equal ratio between the two moult positions has been noted in trilobites such as olenids and paradoxidids (Clarkson et al., 2003; Ebbestad et al., 2013). However, other species show a bias towards one orientation (Karim and Westrop, 2002). For example, inverted *Phacops* moults have been suggested to result from dorsum-down exuviation, this orientation being beneficial for opening of the ecdysial gape between cephalon and thorax (Speyer, 1985, 1987). Whereas exuvia of *Greenops* are rarely found in this position, possibly indicating only dorsum-up exuviation (Speyer, 1985, 1987). Morphology may be key for determining moult orientation, although this is difficult to determine without preserved mass moult assemblages. Further, singular ventral-up specimens could result from taphonomic effects, such as inversion via transport following ecdysis, rather than being informative for moulting behaviour. For orientation to inform exuvial behaviour, rapid burial and preservation would be required (Speyer, 1987).

The general characteristics of trilobite moulting do not seem to specifically align them to any modern arthropod group. The facial sutures of trilobites represent a system of ecydsial suture that is unique in its complexity, with no known equivalent amongst modern arthropods or other ecdysozoans (Ax, 1987; Paterson and Edgecombe, 2006). Trilobites show continuous, or indeterminate, growth, meaning that they continued to grow in size and moult after reaching their adult morphology (Hughes, 2007). Of extant arthropods, myriapods and crustaceans also continue to grow and moult as adults, whereas insects and arachnids show determinate growth, meaning they do not continue to grow and moult after reaching sexual maturity (Nijhout, 2013). Trilobites differ from extant arthropods in that there is no evidence for reabsorption of the old cuticle prior to moulting, as is seen in extant groups (Ewer, 2005; Nijhout, 2013). All preserved material also suggests trilobites exited their exuviae anteriorly, as is seen in modern xiphosurans and scorpions, but which is unlike other arthropods, such as spiders and crabs, which exit their exuviae posteriorly (Henningsmoen, 1975). Few ecdysial characteristics have been included in phylogenetic analyses of trilobite relationships beyond those associated with the morphology of facial sutures. Moulting behaviours for each trilobite Order are discussed below and summarised in Table 1.

2.1.1. Ecdysis in Redlichiida

Descriptions of ecdysial behaviour are more common in the literature for the speciose Orders Phacopida and Redlichiida (Fig. 3). Most *Redlichia* individuals would moult by opening of both the facial sutures (Fig. 3B) (Öpik, 1958; McNamara, 1986) and the rostral sutures, the latter of which was necessary to release the “stitched rostral shield” (Öpik, 1958, pg. 28) that interlocks with the cranidium by a series of small nodes. The cranidium also detaches (Fig. 3E), leaving the thoracic segments and pygidium as a cohesive unit that is often found preserved (Öpik, 1958, 1970; McNamara, 1986). A moulted, but admittedly malformed, specimen of *R. hupehensis* shows only the detachment of the librigenae, i.e. a complete axial shield (cranidium, thorax and pygidium) (Han and Zhang, 1991). Specimens of *R. forresti* individually show inversion of the pygidium (McNamara, 1986, figs. 1A, D, H, I), thoracic segments (Öpik, 1958, pl. 2, figs. 2, 3) and librigenae (McNamara, 1986, fig. 1B), whereas *R. idonea* (McNamara, 1986, fig. 1E) and *R. micrograpta* (McNamara, 1986, fig. 1C) each only show inversion of thoracic segments or librigenae respectively.

McNamara (1986) highlights the unusual occurrence of inversion of part of the body (free cheeks, thoracic segments, and/or pygidium) during moulting. He focuses on three species of *Redlichia* with inverted elements and describes scenarios for each specimen that require partial enrolment of the specimen during ecdysis. This link between ecdysial moult configurations and enrolment behaviour was in contrast to previous suggestions that Cambrian micropygous trilobites were rigid and unable to enrol (Harrington, 1959; Bergström, 1973), although later studies have shown that at least flexing, if not entire enrolment, was possible in these trilobites (Esteve et al., 2011, 2013; Ortega-Hernández et al., 2013). McNamara (1986) stresses that inversions in *Redlichia* were "the exception, rather than the rule" (pg. 412), and should be considered in the context of the individual specimen (rather than generalised as behavioural differences between taxa). To account for the inverted body elements, McNamara (1986) invokes an ecdysial scenario that begins with a posterior movement of the trilobite in the early stages of exuviation, and suggests that this may have been used to separate the cephalon from the thorax in cases where the rostral suture failed to open. This implies a flexibility of ecdysial behaviour in *Redlichia* individuals and response to situations where the usual modes of moulting were unsuccessful.

Ebbestad et al. (2013) described redlichiid moults of two paradoxidid species, including one *Eccaparadoxides*, which also moulted using the cephalic sutures (Fig. 4). They particularly emphasise the open position of the facial sutures in all specimens (Ebbestad et al., 2013, figs. 3D-F), even where the librigenae are somewhat in place, and a total absence of *in-situ* hypostomes. Other paradoxidids, like *Paradoxides davidis,* also opened the cephalic sutures for moulting, displacing the librigenae and rostral-hypostomal plate as in the first step for ecdysis in *Redlichia* (Whittington, 1990).

Particular redlichiid trilobite taxa demonstrate the variability in ecdysial behaviour seen within species of other trilobite Orders, employing multiple methods for moulting. *Olenellus gilberti* and *Nephrolenellus geniculatus* (Webster, 2007) seem to have moulted the hypostome and rostral plate before emergence ventrally through the resulting gap, but occasionally specimens of the former also show a dislocation and displacement of the thoracopygon beneath the cephalon (Webster, 2015, fig.10). This mode of ecdysis differs from other redlichiids, such as *Eccaparadoxides* and *Redlichia*, because olenelloids lack facial sutures around the librigenae (Webster, 2015). *Balcoracania dailyi* appeared to have employed the usual redlichiid style of ecdysis; strongly flexing the exoskeleton, pushing the spines into the sediment and allowing for opening of the cephalic sutures. The animal would emerge anteriorly, leading to the librigenae, rostral plate, hypostome and/or cranidium becoming dislodged (Paterson et al., 2007, figs. 8A, B, E, H). However, at least one moult of *B. dailyi* displays fragmentation between the first and second thoracic segments (Paterson et al., 2007, fig. 8C), prior to opening of the facial sutures. As in *Redlichia*, this may well reflect flexibility in behaviour to overcome a particularly difficult moulting period (McNamara, 1986), reinforcing the plasticity that some trilobite species can show during ecdysis.

2.1.2 Ecdysis in Phacopida

Budil and Bruthansová (2005) presented an initial exploration of the complicated nature of phacopid trilobite ecdysis, extoling the need for a more thorough analysis. In particular, there is great variability in ecdysial behaviours of dalmanitoid and acastoid phacopid trilobite taxa. The most common behaviour across all species described (and most other phacopid taxa) was complete disarticulation of the cephalon from the rest of the body (Fig. 3H), without the cephalon inversion involved in producing Salter's configuration (Fig. 3I) (Budil and Bruthansová, 2005, fig. 4).

However, particularly in *Ormathops,* as well as *Zeliszkella, Dalmanitina* and *Kloucekia,* the break releasing the cephalon during ecdysis occurred several segments into the thorax (Fig. 3K). Thoraces broken into multiple segments in *Baniaspis (?) quadrata* (Budil and Bruthansová, 2005, figs. 6C, E, F) and *Zeliszkella cf. oriens* (Budil and Bruthansová, 2005, fig. 7E), representing multiple gape sutures, may indicate instances of problematic moulting as in some described redlichiids.

Demonstrating the apparent versatility of dalmanitoid trilobite moulting habit, separation of the librigenae from the remainder of the axial shield via opening of the facial sutures was common in young individuals of *Dalmanitina proaeva elfrida, Dalmanitina proaeva proaeva,* and *Ormathops (Ormathops) atavus* (Budil and Bruthansová, 2005, figs. 7B, C). Some specimens of *Ormathops (Ormathops) atavus* also show the librigenae disconnected from the separated cranidium (Budil and Bruthansová, 2005, figs. 4E, 5C). However, Budil and Bruthansová (2005) state that free-cheek moulting (by opening of the facial sutures) was replaced by more 'advanced modes' (Budil and Bruthansová, 2005, pg. 376), with a loss of facial suture functionality into adulthood of these phacopid trilobites and ecdysis using the cephalic or thoracic disarticulations.

Cephalic sutures of *Trimerus stelmophorus* (Homalonotidae), like most phacopids, were non-functional during ecdysis. Phacopids instead utilised the common behaviour of separating the cephalon and thorax (Busch and Swartz, 1985, fig. 1.8; Speyer, 1985). This often resulted in preservation of moults in Salter's Configuration, suggesting arching of the body with the dorsal cephalon towards the substratum. *Plagiolaria poothai* (Cronier and Fortey 2006) and *Paciphacops sp.* (Rustán et al., 2011, fig. 2) also moulted in this way, although the last is interpreted differently. The species of *Paciphacops* figured by Rustán et al., (2011) may have utilised a gape suture between the cephalon and thorax for ecdysis while infaunal. *Phacops rana* and *Greenops boothi* both moulted by removing the cephalon, as determined by the prevalence of thoracopygidia, although Salterian configurations were rare or absent in these species (Speyer, 1985).

From a single, complete inferred exuvia, McNamara and Tuura (2011) suggest a total moulting sequence for *Greenops widderensis.* This begins with the familiar break of the join between cephalon and thorax, and leads to the disarticulation of the pygidium (McNamara and Tuura, 2011, fig. 1). This is also the case for *Plagiolaria nandanensis* (Wang and Han, 1997). As with most other phacopids described, the facial sutures were not employed, although *G. widderensis* ecdysis has only been interpreted from the one specimen.

However, *Flexicalymene retrorsa* (Calymenidae) exuviae indicate the functionality of facial sutures, and the release of the librigenae, for ecdysis in some phacopid taxa (Hunda et al. 2006, fig. 9L). The subsequent rotation of the cranidium, they suggest, may reflect post-ecdysial disturbances (Hunda et al., 2006, fig. 9M). Some specimens of *F. retrorsa* showing an articulated thoracopygon without a cephalon have been interpreted as moults, suggesting they may have occasionally utilised a gape suture behind the cephalon, as most phacopid trilobites did (Hunda et al., 2006, fig. 9N).

2.1.3 Ecdysis in Ptychopariida

Like redlichiid taxa, ptychopariid trilobite exuviae emphasise the importance of cephalic sutures for ecdysis across the Order, often leading to the displacement of the hypostome and rostrum (Cederström et al., 2011, figs. 11C-F). This is certainly the case for moults of *Strenuaeva inflata,* although Cederström et al. (2011) consider the opened facial sutures and displaced librigenae to result from taphonomic processes, with the other cephalic sutures being more important for emergence.

Ctenopyge (Eoctenopyge) angusta utilised the facial sutures during moulting, as indicated by the preservation of separated yoked librigenae and hypostomes, with the cranidium also detached in some exuviae (Clarkson et al., 2003, pl. 8.1). Other olenids may have moulted similarly, releasing the librigenae with the axial shield remaining intact, including: *Acerocare ecorne* (Henningsmoen, 1957); *Parabolina frequens argentina* (Tortello and Clarkson, 2008, fig.

9.1); *Wujiajiania sutherlandi* (Chatterton and Ludvigsen, 1998, fig. 10); and *Aciculolenus palmeri* (Chatterton and Ludvigsen, 1998).

These Olenidae trilobite exuviae are often considered as preserved in 'Harrington's Configuration' (Henningsmoen, 1975), with the shed librigenae found below the axial shield (Tortello and Clarkson, 2008). Ptychopariids may also show within-taxon variation in ecdysial pattern. For example, some moulted specimens of *Parabolina frequens argentina* have missing cranidia with the librigenae close to normal position (Tortello and Clarkson, 2008, figs. 8.7, 8.10, 9.3, 9.10), as do those of the olenid *Cloacaspis dejecta* (Fortey, 1974, pl. 12.1). *Parabolina frequens argentina* also displays signs of employing alternative ecdysial behaviours such as disarticulated thoraces and displaced pygidia (Tortello and Clarkson, 2008, figs. 8-10) during difficult moulting periods, much like *Balcoracania dailyi* (Paterson et al., 2007) and *Redlichia* (McNamara, 1986). Unlike all other ptychopariids described, a lone *Burnetiella leechi* exuvia displays a Salterian mode of moulting (Chatterton and Ludvigsen, 1998. fig. 22.6).

2.1.4. Ecdysis in Odontopleurida

Descriptions of ecdysial behaviour are sparse for the remaining trilobite Orders. *Odontopleura (Odontopleura) arctica* and *Odontopleura (Odontopleura) brevigena* opened the facial sutures for ecdysis, releasing the librigenae and hypostome (Adrain and Chatterton, 1990, fig. 7.5). Edgecombe and Sherwin (2001) also note the librigenae, hypostome and rostral plate of *Odontopleura (Sinespinaspis) markhami* detached during ecdysis (Edgecombe and Sherwin, 2001, figs. 3D, 4A).

2.1.5. Ecdysis in Asaphida

Exoskeleton moulting in the Ordovician *Homotelus bromidensis* took place through disarticulation of the cranidium, with the librigenae yoked anteriorly (Karim and Westrop, 2002). Conversely, preserved moulting configurations of *Labiostria westropi,* and occasionally *Pterocephalia norfordi,* usually consist of complete axial shields with the librigenae nearby, in a range of different positions (rotated, inverted, displaced), although some individuals may also have moulted the cranidium or cephalon (Chatterton and Ludvigsen, 1998, figs. 19, 29).

2.1.6. Ecdysis in Corynexochida and Proetida

Chen et al. (2008) describe a similar scenario of moulting to *Balcoracania dailyi* (Paterson et al., 2007) for the corynexochid trilobite *Oryctocephalus indicus*, including a downwards flexing to produce a break between the cephalon and thorax, with the librigenae also becoming disarticulated during this process. The remaining cranidium then became inverted during full exuviation of the animal from the old exoskeleton. The moulting of *Telephina (Telephus) spiniferus* has been described as a very similar process to *O. indicus* (Fischer, 1946, fig. 1), involving shifting of the librigena and horizontal inversion of the cranidium (free cheeks "slightly shifted" with the glabella "overturned and carried forward", Fischer, 1946, p. 566). Glaessner (1948) notes that this moult configuration seems to span several trilobite Families, but that preservation of all disarticulated moulted sclerites in position is extremely rare. A single moult of *Aulacopleura pogsoni* demonstrates that proetid trilobites could undergo ecdysis through disarticulation of the entire cephalon (Edgecombe and Sherwin, 2001).

2.1.7. Ecdysis in Agnostida

Descriptions of ecdysial modes in the literature are also rare for Agnostida, considered by some research to be the earliest diverging trilobite Order (Cotton and Fortey, 2005) or as stem lineage mandibulates (Legg et al., 2013). *Pagetia significans* exuviae from the Cambrian Kaili Formation, China, suggest ecdysis only through opening of the facial sutures, and disarticulation of the librigenae (Lin and Yuan, 2009). Although entire cephala seem common in the agnostoid fossil record. Whether Agnostida are trilobites, or close relatives of the Trilobita, greater knowledge of their moulting methods would allow better tracing of trends in arthropods with similar morphologies, and the origins of the patterns and variability in trilobite ecdysis.

2.1.8. Summary of trilobite ecdysis

Ecdysis utilising gapes created through opening of the facial (and often anterior and rostral) sutures is commonly observed across trilobite Orders (Table 1) and through geological time (see Section 3.2). This is to the exception of most phacopid trilobites, which had inactive facial sutures; phacopid taxa typically exploit a gape suture created through the disarticulation of the cephalon from the thorax (Figs. 3G-L). As a generalisation, Redlichiida, Ptychopariida, Odontopleurida, Asaphida, and Agnostida all exhibit a high occurrence of facial suture moulting. Whereas some Redlichiida (*Redlichia),* Asaphida, and Corynexochida combine this with disarticulation of the cranidium. However, these are all very broad trends, and in reality those Orders with ample exuviae descriptive literature (Redlichiida, Phacopida, Ptychopariida) show considerable flexibility in which ecdysial method they employed. Whether the ecdysial methods discussed for Odontopleurida, Asaphida, Corynexochida, Proetida and Agnostida are representative of most taxa within their Orders is unclear, as these are based on few species descriptions. More detailed results from a preliminary quantitative analysis of these trends is presented in Section 3.2 of this work.

In a rare exploration of ecdysis and its broader evolutionary trends, Brandt (2002) analysed the interplay between trilobite moulting and geological survivorship. Brandt (2002) contrasted the extensive variation in trilobite ecdysial behaviour to the often-stereotyped moult styles characterising other arthropod groups. In this way, trilobites were described as having an "inefficient moult habit" (Brandt, 2002, pg. 399), which, when coupled with the apparent need to from a new calcitic exoskeleton after each moult without the benefit of reabsorption of old cuticle material, may have been evolutionary disadvantageous and contributed to their ultimate decline. Further, the taxonomic survivorship analyses of Brandt (2002) support an association between morphology and ecdysis; taxa with simpler morphologies (particularly fewer thoracic segments) and therefore easier ecdysis had longer chronological ranges. Our quantitative analysis (Section 3) builds on the works of Brandt (2002) by investigating more specific ecdysial behaviours and considering the possible evolutionary advantage of flexibility in ecdysis. Öpik (1970) alternatively suggested a decline in the efficiency of ecdysial hormones and moulting success factored into the extinction of *Redlichia* species. Ultimately, we know very little about the broader evolutionary impacts of moulting behaviour in trilobites, but there is huge potential to explore these implications thanks to their extensive fossil record. Elucidating such trends may be a challenge given that higher-level trilobite phylogenetic relationships are currently in a state of flux, with essentially no resolution despite numerous analyses (Adrain, 2011). However, further research along the lines of the preliminary analyses described in Section 3 could also help to resolve phylogenetic uncertainty within the group.

2.2. Eurypterids

The other main group of fossils from which ecdysis is relatively well known is the eurypterids (Figs. 1, 5). There has been much debate on whether various eurypterid fossils represent exuviae or carcasses, much of which has focused on the abundant and well-preserved specimens of the Bertie Waterlime in New York State. For example, Andrews et al. (1974) consider the Bertie eurypterids to be carcasses, whereas Braddy (2001) and Tetlie et al. (2008) thought they were exuviae. Tetlie et al. (2008) considered the presence of musculature and the midgut as the only internal structures that would indicate a carcass (as opposed to an empty moult), owing to the tendency for other structures (i.e. fore- and hindgut; book lungs) to be shed with the exoskeleton. The only definitive carcasses that meet his criteria are specimens from the Devonian Gogo Formation (Tetlie et al., 2004) and the Ordovician Soom Shale (Braddy et al., 1995, 1999), but he also suggested that generally most specimens preserving any part of the gut are quite likely to be carcasses rather than exuviae. Preservation of these internal structures is still very rare, and so the majority of eurypterid assemblages are considered to be exuviae rather than carcasses (e.g. Selden, 1981; Tetlie et al., 2008; Vrazo et al., 2014). In the Bertie Waterlime, the lack of evidence for scavenging is taken as further evidence for these specimens being exuviae (Clarke and Ruedemann, 1912), as is the presence of crumpling, flattening or distortions of the exoskeleton, superimposition of dorsal and ventral surfaces, and telescoping or other disturbance of disarticulated body elements (as in Selden, 1981).

As such, in eurypterid studies, the assumption seems to be that a specimen is a moulted exuviae unless it can be shown to be a carcass by the presence of very specific internal structures (i.e. midguts and musculature; Tetlie et al., 2008). As discussed in sections 1.1 and 4, these structures have a much lower preservation potential than the external exoskeleton, and so on their absence alone may not be enough to discriminate moults from carcasses. This assumption is built on the idea that because every eurypterid individual produces multiple exuviae during its lifetime but only one carcass upon death, so there is a much higher probability of finding an exuvium rather than a carcass (Braddy, 2001). This is coupled with a higher preservation potential because of a lower probability of scavengers disrupting the exuviae after deposition (Clarke and Ruedemann, 1912; Braddy, 2001). This underlying assumption has important consequences for the understanding of eurypterid ecdysial processes. Tetlie et al. (2008), who take a quantitative approach to studying moulting patterns in a large sample of eurypterids from the Bertie Waterlime, began with the assumption that all specimens are empty exuviae and that the large number of complete and intact specimens must be indicating that eurypterids exuviae "behaved like horseshoe crab exuviae" (Tetlie et al., 2008, pg. 188) with ecdysial sutures closing after egress, leaving little evidence that moulting has taken place. An alternative, possibly simpler, hypothesis could be that the Bertie eurypterids represent a mix of carcasses and moulted exuviae.

The quantitative study of Eurypterid assemblages from the Bertie Waterlime was based on completeness estimates and counts of specimens showing characteristic combinations of body segments (Tetlie et al., 2008), making it possible to describe the moulting process in *Eurypterus*. This begins with the opening of suture joints between the ventral plates and the marginal carapace suture, followed by the separation of the head and first opisthomal segment as a single unit, after which the animal egressed anteriorly (Fig. 5) (Tetlie et al., 2008, fig. 10). This was based on an abundance of *Eurypterus remipes* assemblages that showed the cephalic carapace and first opisthomal segment together (228 specimens), however many specimens also showed the carapace in isolation (172 specimens), with the first 2 opisthomal segments (34 specimens), or rarely with breaks elsewhere along the opisthoma, indicating that there was variation in where this suture opening formed, even within one species. Variation must also exist in moulting behaviour between species, as indicated by comparison with adelopthalmid eurypterids from the Dinas estate in Brecon, Wales in the collections at the OUMNH (Figs. 5D-F). Moult ensembles of these eurypterids show a break between the cephalic carapace and the rest of the opisthomal segments during moulting (Fig. 5D), with many carapaces found in isolated without attached opisthomal segments (Figs. 5E-F).

The novel analytical approach employed by Tetlie et al. (2008) allowed for comparison with the moulting modes in aquatic chelicerates and scorpions, in line with a chelicerate affinity for the eurypterids. Further study is needed to identify if ecdysial mode provides insight into the phylogenetic uncertainty for the position of eurypterids within Chelicerata, namely whether they are most closely related to arachnids (Weygoldt and Paulus, 1979; Shultz, 1990, 2007; Kamenz et al., 2011; Lamsdell, 2013), and the scorpions in particular (Kjellesvig-Waering, 1986; Dunlop and Webster, 1999) or the more traditional view of being sister taxa with the xiphosurans (Woodward, 1867, 1872; Strømer, 1944, 1955) in Merostomata, which has also received recent support (Garwood and Dunlop, 2014). *Eurypterus* shares in common with modern *Limulus* the ventral anterior location of the prosomal suture and the tendency of the ecdysial suture to close after egress (Loveland, 2002; Shuster and Sekiguchi, 2004; Tetlie et al., 2008), but also shows similarity to scorpion ecdysis in that the more anterior opisthomal segments remain attached to the cephalic carapace during formation of the anterior ecdysial opening (Tetlie et al., 2008). Further documentation of ecdysial characters for eurypterids, and their inclusion in phylogenetic analyses may help resolve affinity disputes related to the position of these fossil chelicerates.

Tetlie et al. (2008) also attempted to determine if the eurypterids were moulting prose or supine (as seen in modern scorpions). Although evidence for supine ecdysis in the prevalence of ventral-up specimens in other collections had been reported (Tollerton, 1997), Tetlie et al. (2008) did not identify a statistically significant difference in the number of ventral-up versus dorsal-up specimens, and interpreted this to mean that *Eurypterus* could moult in either position. It seems particularly difficult to identify eurypterid moulting orientation given the possibility that exuviae could have been reoriented by currents or other post-depositional processes (Tollerton, 1997; Tetlie et al., 2008). Given the conserved moulting behaviour within closely related modern scorpions, with different taxa consistently moulting either prone or supine (Rosin and Shulov, 1962; De Armas, 1986; Gaban and Farley, 2002), it seems unlikely that the eurypterids had an "absence of preferred dorsal or ventral moulting posture" (Tetlie et al., 2008, pg. 189). Rather, it could be that the data currently available do not allow us to determine this quantitatively. Some scorpion taxa begin moulting in the prone position, but flip over onto the dorsal surface once the legs are freed to continue moulting in the supine position (Gaban and Farley, 2002). Given that the majority of the ventral-up specimens are relatively incompletely preserved, and so were more likely to have been affected by post-depositional reorientation, the data of Tetlie et al. (2008) seem to suggest that moulting in the supine position may not have occurred in *Eurypterus*, or at most was only occupied only very briefly during ecdysis.

Eurypterids form an exemplary case study for examining the evolutionary demands exerted on morphology by the ecdysial process. In eurypterids, mode of moulting may have imparted constraints on the size ratio of morphological features, owing to the necessity of large morphological features to pass through narrow spaces during egress (Tetlie et al., 2008). This is at odds with the ecological or functional morphological pressures to enlarge features such as the swimming paddles and telson (for greater lift, thrust and manoeuvrability during swimming) and the chelicerae (for increased predatory capability).

2.3 Other Chelicerata

Non-eurypterid chelicerates generally have a poor fossil record of moulting, and this is particulary true for the marine groups. In pycnogonids, moulting changes with instars during development owing to substantial change in morphology, and they exhibit determinate growth such that they cease moulting after reaching adulthood (Nakamura, 1981; Tetlie et al., 2008). The thin cuticle and tendency to fragment means that all pycnogonid fossils have been interpreted as carcasses, not moults (Siveter et al., 2004; Tetlie et al., 2008). Horseshoe crabs (Fig. 1) also stop moulting at adulthood (Tetlie et al., 2008), so any moult of a horseshoe crab in the fossil record would have to represent a juvenile individual. Given that xiphosurans moult by exiting anteriorly through a wide suture along the prosoma that immediately closes after egress, the probability of distinguishing a xiphosuran exuvium is low (Babcock et al., 2000; Tetlie et al., 2008). It is also difficult to determine if fragmentary assemblages represent moults or carcasses that have disarticulated, particularly given the tendency for horseshoe crabs to moult in shallow, marginal marine environments with low preservation potential and high energy (Babcock et al., 2000; Rudkin and Young, 2009).

Of the terrestrial chelicerates, the scorpions have the best fossil record of moulting, partly because they possess an extra proteinaceous hyaline layer to their cuticle not present in other arthropods, which is thought to increase fossilisation potential (Selden and Jeram, 1989; Jeram, 2001; Gaban and Farley, 2002). Kjellesvig-Waering (1986) concluded that most scorpion fossils are moulted exuviae rather than carcasses, based on highly detailed examinations of numerous scorpion fossils. These exuvial fossils typically include booklung lamellae, pectines with sensory pegs, and bristles, hairs and sensilla on other parts. Taphonomic experiments conducted on modern scorpions moults and carcasses have established a set of criteria for distinguishing between them (McCoy and Brandt, 2009), and when applied to a collection of Late Silurian and Middle Pennsylvanian scorpions, approximately 89% met the criteria of being fossil moults. This supports the qualitative observation of Kjellesvig-Waering (1986) on the abundance of moults in the scorpion fossil record. The four main criteria for identifying fossil scorpion moults are (1) splayed walking leg posture; (2) distinctive position of the pedipalps with chelae angled inwards toward each other; (3) a curved body line; and (4) extended chelicerae (McCoy and Brandt, 2009). More fragmentary scorpion material was also thought to be derived from exuviae because they are delicate and easy to disperse (Wills, 1959; Jeram, 2001), however the taphonomic experiments of McCoy and Brandt (2009) showed that there is no significant difference in the time required for moults to disarticulate as compared to carcasses. For fossil scorpions, anatomical features related to the positioning of body elements during ecdysis are more useful for identifying moults than examination of the degree of exoskeleton disarticulation. Other examples of moulting in the scorpion fossil record include a specimen of *Compsoscorpius buthiformis* with distortion of the carapace thought to have occurred during ecdysis (Kjellesvig-Waering, 1986), and a tritonyph of a Cheliferoidea pseudoscorpion from the Lower Cretaceous amber of Archingeay, France, which was found partly enclosed in a layer of silk and is thought to represent the first fossil record of a moulting nest (Judson, 2009).

Other arachnid fossil evidence of moulting is scarce, perhaps owing to the relatively poor terrestrial record of arthropods in general. The preservation of spider exuviae in amber suggest that they may have moulted in a similar manner to modern spiders, whilst hanging from silk threads, leaving the exuvia hanging in the web, as was seen for the fossil taxon *Amaurobius succinic* (Petrunkevitch, 1942). Exuviae of this taxon were identified as such based on the presence of broken appendages and general disarticulation. The Devonian *Palaeocteniza crassipes* from the Rhynie Chert is thought to represent a moulted specimen, owing to its general condition of being crumpled and folded, the presence of a detached carapace in close proximity to the rest of the specimen, and the absence of the distal portions of the palps (Selden et al., 1991). The Permian spider *Permarachne novokshonovi* from the Ural Mountains, Russia, is also thought to represent a moulted exuviae owing to general displacement of the specimen and lateral orientation of the collapse chelicerae on top of one another (Eskov and Selden, 2005).

2.4. Crustaceans

The crustacean (Fig. 1) fossil record provides much insight for understanding ecdysis in this group of arthropods. The decapod crustacean moulting fossil record is best known and is described in detail in section 2.4.2. However, even the earliest fossil record of the crustaceans contains information on moulting. Three-dimensionally preserved phosphatised fossils from the Upper Cambrian Orsten fauna of Sweden largely represent individual carcasses of larvae and adult arthropods <2mm in size (e.g. Waloszek 1993, 2003; Waloszek and Maas, 2005; Hughes et al., 2008), and the occasional specimen found with a wrinkled and shrivelled appearance may represent an individual that died during ecdysis or shortly afterwards during the phase when the freshly moulting cuticle has not yet hardened (Müller, 1979; Müller and Waloszek, 1985). Additionally, the presence and position of moulting sutures in the Orsten fossils has proved useful for deciphering the affinity of enigmatic taxa, as in the identification of head shield sutures as one of the synapomorphic characteristics placing *Cambropycnogon kalusmuelleri* with Pycnogonida (Waloszek and Dunlop, 2002). The ontogenetic patterns and number of moulting stages in the Orsten bradoriid *Rehbachiella* were used to help identify its affinity within Branchiopoda (Waloszek, 1995).

The Bradoriids are another group of Early Palaeozoic taxa for which information is known about their moult stages. These small marine arthropods are characterised by a bivalve carapace, and were abundant in the fossil record in the Cambrian to early Ordovician (Shu et al., 1999; Duan et al., 2013). Their affinity has been debated, but they probably represent either stem or crown group crustaceans (e.g. Hou et al., 2010). The abundance of bradoriid bivalved carapaces in the fossil record, and the lack of obvious suture lines anywhere on the body, suggest that bradoriids may have moulted by directly shedding the old valves. The moulting behaviour and ontogeny of two supposed bradoriids from Australia was examined and found to be taxonomically informative (Zhang, 1987). A quantitative analysis of the size of *Phaseolella dimorpha* carapaces showed that these fossils do not segregate into well-defined size categories, as would be expected for a periodically moulting individual, suggesting that this taxon could actually belong to another group of bivalved arthropods, Phosphatocopida, which also produced moults continuously and at short intervals during their lives (Müller, 1979). *Phaseolella dimorpha* has since been synonymised with

Dabashanella hemicyclica and placed withing the Order Phosphatocopida (Hou et al., 2001). On the other hand, *Houlongdongella xichuanensis* shows at least nine distinct moulting stages (Zhang, 1987), in a manner that seems typical for the bradoriids, with other fossil taxa such as *Kunmingella douvillei* reported to have at least five distinct moulting stages (Zhang, 2007; Duan et al., 2013).

Ostracods are the most abundant arthropod in the fossil record and thousands of species have been identified from their characteristic bivalved carapaces, the valves of which populate the fossil record from the Ordovician onwards (Siveter et al., 2003). Soft parts are extremely rare (Siveter et al., 2003, 2014) and it is difficult to distinguish fossil moults from decayed carcasses. Ostracods show determinate growth and moult up to nine times in total during their life (Turpen and Angell, 1971). Given the abundance of ostracod valves in the fossil record, it is possible to reconstruct the ontogeny and development of fossil taxa using their different moult stages (e.g. Shaver, 1953; Tinn and Meidla, 2003). Removal of the valves during ostacod moulting is usually complete (Turpen and Angell, 1971), however an enigmatic group probably belonging to Ostracoda, the Eridostracina, show an unusual moulting physiology and valve morphology (Olempska, 2012). These Middle Ordovician to Middle Carboniferous aged crustaceans produce a multi-layered calcified carapace by retaining unshed moults during growth and development. Successive newly deposited cuticles are larger than the previous carapace, such that they are visible on the external surface as growth bands. Retention of moults is thought to strengthen the carapace, while the characteristic number and arrangement of retained moults has useful taxonomic relevance (Olempska, 2012). Other arthropods exhibiting retention of moults include the spinicaudatan (conchostracan) branchiopod crustaceans, which are found in the fossil record from sites such as the Upper Carboniferous deposits of France and Ireland (e.g. Orr and Briggs, 1999; Vannier et al., 2003; Orr et al., 2008) and the Lower Devonian Willwerath Lagerstätte of Germany (Gross, 1934).

Early Devonian branchiopods such as *Lepidocaris rhyniensis* and *Castracollis wilsonae* from Rhynie Chert likely represent exuviae, whereas the oldest notostracan from the Upper

Devonian Strud Locality, *Strudops goldenbergi*, likely represent whole body carcasses (Lagebro et al., 2015). This was determined based on the presence of a gut and its content, and owing to the intact nature of the body parts in most specimens. The preservation potential of notostracans have been studied using experiments where both carcasses and empty moults of modern notostracans were observed during decay under controlled conditions (Hegna, 2012). It was concluded that a carcass does come to resemble a moulted exoskeleton if decay is allowed to proceed to a certain point. These experiments confirmed that the presence of a gut can be used as evidence of a carcass, as can an undisturbed position for the thoracic appendage, abdominal segments and telson (Hegna, 2012).

2.4.1. Isopod crustaceans

The rest of the crustacean fossil record of moulting is focused on Mesozoic specimens, with little input from the fossil record of the later Palaeozoic. Decapods form the bulk of the crustacean ecdysis fossil record during the Mesozoic (Section 2.4.2), but it is also important to consider moulting when examining the fossil record of isopods. Living isopod crustaceans exhibit biphasic moulting, with the posterior part being moulted as an intact unit several days before the fragmentary moulting of the anterior carapace. Given that the majority of fossil isopods are of the posterior region of the body only, it is thought that they represent empty moults (Wieder and Feldmann, 1989; Feldmann, 2009). The near absence of anterior sclerites is likely owing to the fragmentation of these structures during moulting, such that the head, various limbs and the thoracic segments are disarticulated from each other. This fragmentation may be contributing to the poor fossil record of this group as a whole, leading to taxonomic confusion, as the posterior regions tend to be similar between separate species and it is likely that many species named only from posterior parts could be incorrectly included in the same fossil genus (Wieder and Feldmann, 1989). Only unusually are isopods found with anterior and posterior sections intact, such as in a single specimen of *Palaega goedertorum* from the late Oligocene Pysht Formation in Washington State (Wieder and Feldmann, 1989), some Early Cretaceous specimens including *Archaeoniscus* *aranguthyorum* from the Tlayúa Formation in Mexico (Feldmann et al., 1998), and a scavenging assemblage of complete *Brunnaega tomhurleyi* from the Toolebuc Formation of Queensland, Australia (Wilson et al., 2011). Another single specimen of the criolanid isopod *Cirolana garassinoi* is thought to have been preserved in the pre-moult condition owing to the presence of three pairs of dermoliths (sites of calcium and phosphorous storage during the pre-moult condition of modern isopods) and a thin, apparently transparent cuticle (Feldmann, 2009). This shows a highly specific moulting behaviour in a fossil that had previously only been known from living taxa.

2.4.2. Decapod crustaceans

The decapod fossil record is particularly good owing to their heavily calcified skeletons, with lobsters and crabs having a greater abundance of fossilised moulted exuviae as compared to crayfish/shrimp, owing to the tendency of the latter to eat their own exuviae after moulting (Bishop, 1986). Moulted exuviae are so readily identifiable and abundant at many localities that it is generally thought that they may be biasing the fossil record of decapod crustaceans by inflating their overall numbers (Schäfer, 1972). Sure moults in the fossil record could outnumber carcasses by about five to one for decapod crustaceans (Mertin, 1941).

Many decapod exuviae fossils are preserved in a characteristic assemblage known as 'Open Moult Position' (or Salterian Position, or Salter's Position), which varies slightly for crabs and lobsters. In extant lobsters, moulting begins with the separation from the first abdominal segment, followed by a dorsal splitting of the carapace along the median line, through which the animal emerges, leaving a characteristic exuvial arrangement with the carapace displaced nearly 90° to the abdomen (Glaessner, 1969). The Lobster Open Moult Position refers to exuviae preserved on the side, with the carapace split medially and raised posteriorly relative to the abdomen (Figs. 6A-D), as is seen in moults of *Oncoparia, Linuparus* and *Hoploparia* from the Late Cretaceous Carlile fauna (Bishop and Williams, 1986) and *Oosterinkia neerlandica* from Middle Triassic Anisian sediments of the Winterswijk quarry in the Netherlands (Klompmaker and Fraaije, 2011). A specimen of the fossil lobster *Meyeria pueblaensis* from the Aptian deposits of the San Juan Raya Formation in Mexico is preserved in the Lobster Open Moult Position with its walking legs displaced; its identification as a moult is reinforced by its fully compressed preservation, and the fact that it exhibits less morphological detail on the carapace than carcass specimens from the same site (Feldmann et al., 1995). Another species of this genus, *Meyeria magna,* is also preserved in the characteristic Lobster Open Moult Position (González-León et al., 2014) (Figs. 6A-D). Other taxa preserved in this position include *Palaeohomarus* from the Upper Cretaceous, and *Glyphea* and *Protaxius* from the Jurassic (Glaessner, 1969).

When a crab moults, the carapace splits open along the posterior and sides (the pleural sutures), hinging near the mouth such that the carapace is pushed upwards and forward as the animal exits posteriorly. This Open Moult Position can be recognised in the fossil record by the carapace making an angle of approximately 90° to the sternum, and the splitting of the carapace along the pleural sutures such that parts of the carapace outside the pleural sutures remain attached to the sternal plastron (Fig. 6E, F). The crab *Carcineretes planetarius* is found abundantly as moults with articulated appendages in the Maastrichtian deposits of the Ocozocoautla Formation in Chiapas, southeastern Mexico (Vega et al., 2005). Other crab taxa showing Open Moult Position include *Ranina, Notopocorystes, Coeloma, Potamon* and *Macrophthalmus* (Glaessner, 1969; Bishop, 1972, 1986).

Given that the articulation between the cephalothorax and the abdomen tends to be a particularly weak joint, it had also been suggested that the arrangement of fossil lobsters in Open Moult Position alone was not enough to definitively identify the specimen as a moult (Bishop, 1986), particularly as it had long been thought that fossil crustacean cuticles did not preserve structures distinguishing between exuviae and unmoulted carapace (Glaesser, 1969; Schäfer, 1972). However, detailed examination of the cuticular ultrastructure of fossil specimens of *Hoploparia stokes* from the Maastrichtian of the Lopez de Bertodano Formation on Seymour

Island, Antarctica, showed that moults can be distinguished from carcasses (Feldmann and Tshudy, 1987). Owing to reabsorption of the cuticle prior to moulting, exuviae are characterised by deterioration or complete loss of lamination in the inner endocuticle only (as compared to loss of laminations in other regions of the cuticle reflecting diagenetic alteration). These fossil moults tend to be extremely well preserved as compared to carcasses, probably owing to a higher rate of disturbance to the carcasses from post-mortem scavenging. Based on this ultrastructure, Feldmann and Tshudy (1987) were able to conclude that specimens found in the Salterian position were indeed moults, as were many of the more fragmented specimens. Other specimens from Antarctica have been identified as moults, such as *Metanephrops jenkinsi* from the Cretaceous and Paleocene of Seymour Island, which is preserved in the Salterian position (Feldmann, 1989), and a single specimen of *Antarctidromia infalta* from the early Miocene of Cape Melville, in which the abdominal structures are articulated but rotated out of their life-plane and remain attached to the cephalothorax only in a small region (Feldmann and Gaździcki, 1998).

Another characteristic moult assemblage for decapod crustaceans consists of the carapace preserved upside-down and rotated on the sternum, known as the Overturned-Carapace Moult Position (Bishop, 1972, 1986). Fossils found in this Position include specimens of the crab *Dakotiocancer overanus* from the Upper Cretaceous Pierre Shale in South Dakota (Bishop, 1972). Specimens of the fossil lobsters *Pseudoglyphea* cf. *P. spinosa* and *Clytiopsis argentoratensis* from Middle Triassic Anisian sediments of the Winterswijk quarry in the Netherlands preserve the cephalothorax upside down and separated from the abdomen, with occasional splitting of the cephalothorax along the median line (Klompmaker and Fraaije, 2011).

Decapod moults do not always take the form of one of the three Moult Positions described above. Specimens of *Carcineretes woolacotti* from the Maastrichtian Ocozocuautla Formation in Mexico were identified as moults based on the thickness of the carapace and displacement of the sternal plastron. This collection also includes six pairs of specimen found in close association, consisting of a smaller moult and a larger carcass, interpreted as a freshly moulted individual preserved with its recent exuvia (Vega et al., 2001). In all three pairs, the carcass was approximately 16% larger than the exuvia. Several specimens of the crab *Dakoticancer australia* from the Maastrichtian Difunta Group in Mexico are thought to represent moults owing to a lack of carapace material and preserved appendages, and displacement of the sternal plate (Vega and Feldmann, 1991). Similar sternal plate dislocation was used to determine that *D. australis* specimens found articulated in burrows at a nearby locality also represent moults, perhaps indicating a behaviour for these crabs of moulting in their burrows (Vega and Feldmann, 1991). The crab *Longusorbis cuniculosus* from the Upper Cretaceous Spray Formation of Vancouver Island, British Columbia, was found associated with filled burrows and encased in burrow-fill lithology, from which it was suggested that the specimens may have dug these burrows and moulted in enlarged terminal chambers (Richards, 1975). A specimen of carcineretid crab from the Late Cretaceous Point Loma Formation of San Diego, California has also been described in the terminal chamber of an burrow, but it is unknown if this specimen represents a moult or a carcass (Bishop, 1972). Additionally, specimens of the mud lobster *Thalassina* from Pleistocene deposits in northern Australia, New Guinea and Japan (Förster and Barthel, 1978; Murray and Hanley, 1986; Bishop and Williams, 2005) preserved in Lobster Open Moult Position have been found in the ends of tunnels, suggesting they may also moult in their burrows.

Polz (1995) reported the discovery of a fossil phyllosoma (lobster larval stage) being caught in the act of moulting, based on the presence of larval and "post-larval" features in the same specimen. Haug et al. (2009) alternatively suggest that this specimen, and another possible scyllarid larva, could actually be very late larval stages that already exhibit some "post-larval" characters. These specimens therefore need not represent crustaceans preserved mid-moult.

2.5 Hexapods

Moulted exuviae have been found in the hexapod fossil record. These empty moults may have a shrivelled appearance indicating partial desiccation, or deformations in the head or thorax.

The exuvial fissure is usually located dorsally in the anterior region of the body (Rasnitsyn, 2002). These may also have a "composite nature" (Kukalova, 1968, pg. 311) owing to the dorsal and ventral surfaces pressing together during preservation such that impressions of structures from both surfaces are superimposed onto both part and counterpart. Moulted cuticles identified in the literature include specimens of the mayfly nymph *Protereisma* from the Lower Permian of Oklahoma, USA, and Moravia, Czech Republic (Kukalova, 1968); a single specimen of the palaeodictyopteran *Lycocerus goldenbergi* from the Upper Carboniferous shales of Commentary, France (Kukalova, 1969; Kukalova-Peck, 1975); as well as numerous specimens of the mayfly *Ephemeropsis melanurus*, the beetle *Coptoclava longipoda* and the dragonfly *Hemeroscopus baissicus* in the Early Cretaceous of Baissa in Siberia (Rasnitsyn, 2002). A *Coptoclava* beetle specimen from the last locality has even been preserved mid-moult (Rasnitsyn, 2002, fig. 24). These published occurrences of fossil insect moults are preserved as compressions and impressions on fine-grained sediment, rather than preserved in amber.

The preservation of abundant moults in the insect fossil record could be effecting the ecological interpretation of assemblages by biasing the size and frequency distributions. In the lacustrine assemblage of the Early Cretaceous locality at Baissa, Siberia, where moults are abundant, dragonfly fossils are found two to ten times (and occasionally over 100 times) more frequently than beetles. Given that the assemblage is dominated by moulted exuviae, this discordance in abundance is likely reflecting the fact that dragonflies moult several more times during their lifetime than do beetles, rather than indicating that dragonflies were actually more abundant (Zherikhin, 1997; Rasnitsyn, 2002). Taphonomic experiments on extant decapod crustacean assemblages have suggested that a large abundance of empty moults in an assemblage can greatly affect the the size-frequency distributions of samples in comparison with living populations, with moults outnumbering carcasses by 15:1 under some mortality regimes (Hartnoll and Bryant, 1990).

2.6. Other arthropods

The Cambrian record of soft-bodied taxa preserved in fossil lagerstätten such as the Burgess Shale have yielded abundant arthropod fossils, some of which help illuminate the early fossil record of ecdysis. The best example of a fossil preserved mid-moult is seen in a single specimen of the extremely abundant arthropod *Marrella splendens* (García-Bellido and Collins, 2004). An ecdysial suture is present at the anterior end of the head shield, through which the individual can be seen emerging (Fig. 7C). The wide lateral spines are folded inwards and backwards, indicating it was softer than usual during egress. Given the placement of this taxon in the stem lineage to mandibulata (Legg et al., 2013), its ecdysial behaviour can help identify the plesiomorphic condition for crustaceans and hexapods.

Other examples of arthropod moulting in the Cambrian fossil record are more circumstantial. For the trilobite-like arthropod *Naraoia* from the Chengjiang biota in China, the presence of isolated appendages, head shields, and pygidium elements are thought to indicate post-depositional disarticulation, possibly in connection with moulting (Hou et al., 1991). A single incomplete and partially degraded specimen of the stem lineage chelicerate *Sidneyia* from the Burgess Shale is preserved surrounded by numerous specimens of the scavenging priapulid-like worm *Ottoia* (Bruton, 2001). It was suggested that this assemblage could represent a dead, freshly moulted individual of *Sidneyia* that was providing a food source for the *Ottoia* worms (Bruton, 2001), although upon re-examination Vannier (2012) pointed out that the carcass appears quite decayed, making it difficult to ascertain if it really was a freshly moulted individual. *Sidneyia* specimens typically preserve guts, digestive glands and abdominal pockets in phosphate, indicating that specimens are carcasses rather than empty moults (Zacaï et al., this volume). A third example of possible moults from the Burgess Shale includes the highly disarticulated assemblages of the cephalic structures of the anomalocaridid *Hurdia*. This possible predator has a head bearing numerous partially sclerotized structures, including an oral cone with many plates, a pair of segmented appendages, a triangular central head shield element, and two lateral head shield elements (Daley et al., 2009, 2013). Disarticulated assemblages of these sclerotised head structures are found in consistent orientation in many specimens, suggesting that they may represent moult ensembles (Daley et al., 2013, pg. 749).

Large fossils surfaces covered in numerous empty moults of the stem-lineage arthropods *Canadaspis* and *Alalcomenaeus* from the Burgess Shale are thought to be indicative of mass moulting behaviour (Fig. 8A, B, F). This synchronized moulting is similar to that seen in a wide variety of modern crustaceans, insects and arachnids (Haug et al., 2013). The reasons for synchronized moulting are discussed in Section 2.7. A notable Cambrian mass moulting locality is the Mount Stephen Trilobite Beds of the Burgess Shale, where abundant trilobite exuviae (Fig. 8D) are found associated with numerous frontal appendages of the Cambrian apex predator *Anomalocaris canadensis* (Fig. 8C). It has been suggested that this predator was taking the opportunity of the mass moulting event to feast on the freshly moulted trilobites before their exoskeletons had the chance to completely harden after moulting (Rudkin, 1979, 2009).

2.6. Other ecdysozoans

The moulting fossil record of other ecdysozoans (Fig. 1) is mostly confined to the Cambrian, with specimens of lobopodians, Loricifera, palaeoscolecids and Priapulida providing insight into moulting behaviour in non-arthropod ecdysozoans. Sub-fossil Holocene moults from tardigrades have also been described (Gibson et al., 2007). The other ecdysozoan phyla Kinochyncha, Nematoda, and Nematomorpha have a very poor (or non-existent) fossil record generally, such that the odds of finding moults are low.

2.6.1. Loriciferans

As one of the most recently discovered metazoan phyla (Kristensen, 1983), it is not surprising that the fossil record of Loricifera is sparse and poorly known. These tiny marine animals live in the sediment inside a protective outer case called a lorica. The only plausible palaeontological record of loriciferans consists of the macrofossils *Sirilorica carlsbergi* and *Sirilorica pustulosa* from the early Cambrian Sirius Passet biota of Greenland (Peel, 2010).

Although it is the less common of the two species, a single specimen of *S. pustulosa* has been preserved in the process of moulting (Peel et al., 2013). A nearly complete animal, including its anterior thorax with denticles, the loricate abdomen, and part of the anal field, is seen emerging from an opening between the anterior and posterior plate circlets of the lorica of the exuvia (Fig. 7A). This is exactly the same moulting behaviour observed in the modern loriciferan taxon *Rugiloricus* (Higgins and Kristensen, 1986; Peel et al., 2013). The fossil specimen is thought to represent a moult not only because of this orientation, but also because of the distorted and ruptured exuvial lorica, and the lack of an introvert in the exuvia.

2.6.2. Lobopodians

Lobopodians are soft-bodied Cambrian animals with an annulated body bearing paired limbs, distinguished by a variety of specialised appendages anteriorly and dermal sclerites along the body (Chen et al., 1995; Liu and Dunlop, 2014; Ma et al., 2014). As an abundant fossil of the Cambrian, studies of their phylogenetic affinities are revealing them to be early steam lineage members of both Arthropoda and Onychophora (Smith and Ortega-Hernández, 2014). Their fossil record consists of both full-body preservation in Cambrian lagerstätten such as the Chengijang Biota in China and the Burgess Shale in Canada, and of sclerotized dermal sclerites that make up a large proportion of the mineralised microfossil record. A single body specimen of the xenusiid lobopodian *Hadranax* from the Sirius Passet biota of North Greenland was suggested to be a moulted exuvia because of its distorted preservation, and it has been suggested that xenuxian lobopodians in general shed their cuticle through a mid-ventral split in the body (Dzik and Krumbiegel, 1989; Bergström and Hou, 2001). However, Zhang and Aldridge (2007) considered these specimens as inconclusive evidence of ecdysis.

The dermal sclerites of lobopodians provide much more information on ecdysis in this group. These help illustrate lobopodian ontogeny, with the identification of discrete instars showing characteristic changes in morphology during growth, suggesting that lobopodians moulted as they grew, rather than having incremental growth (Zhang and Aldridge, 2007). The lobopodian sclerite fossil record also reveals specimens thought to have been preserved just prior to moulting, before the old sclerite was shed from the body. These conjoined specimens consist of a larger plate attached to the underside of a smaller plate, with the larger being in the range of 13-20% for *Microdictyon sinicum* from the Chengjiang Biota (Chen et al., 1995), and 24% in *Onychodictyon* sp. from North Greenland (Fig. 7B) (Topper et al., 2013). In the *Microdictyon*, at least five full body specimens show multiple conjoined plates along the body of the lobopodian (Chen et al., 1995). Rare conjoined plates have also been found in large collections of isolated sclerites of *Microdictyon jinshaense*, *Microdictyon chinense* and *Quadratopora zhenbaensis*, showing that this type of ecdysis behaviour, with the new plate growing in underneath the old plate, is widespread in lobopodians. No indication of reabsorption was found in these conjoined sclerite specimens, with the old one showing no sign of deformation or wrinkling as compared to the new one (Zhang and Aldridge, 2007).

A different mode of moulting has been described for the Cambrian lobopodian *Hallucigenia* from the Burgess Shale, which has sclerites in the form of appendicular claws and dorsal spines. These sclerites have a unique “cone-in-cone construction” (Caron et al., 2013, pg. 5), which consists of a stack of three to five elements that are separated from each other along a logarithmic curve and grow from a basal accretional zone (Smith and Ortega-Hernández, 2014). These have been shown to have fundamentally the same construction as the claws in the extant onychophoran *Euperipatoides* (Caron et al., 2013; Smith and Ortega-Hernández, 2014). In both *Euperipatoides* and *Hallucigenia*, internal constituent elements are future replacements of the outermost elements, which are discarded during ecdysis. After the outermost element is discarded, a new innermost element is secreted and the bases of all existing elements are extended. This represents an ecdysial behaviour that is distinct from other ecdysozoans, being quite different from the direct replacement seen in some lobpodians (Zhang and Aldridge, 2007) and from the retained exuviae in Eridostracina ostracods (Olempska, 2012) where overlying moults are retained during ontogeny and accumulate as the organisms grows, without removal by ecdysis. Owing to this shared moulting behaviour, Smith and Ortega-Hernández (2014) suggest an onychophoran affinity for the enigmatic Cambrian taxon *Hallucigenia*.

2.6.3. Palaeoscolecids

Palaeoscolecids are a lower Palaeozoic group of vermiform animals that have a widely debated affinity, but are generally aligned with Cycloneuralia (ie. non-Panarthropoda ecdysozoans), and specifically either with Priapulida or Nematomorpha (García-Bellido et al., 2013). Their cuticle was annulated and covered in rows of sclerites, fragments or elements which are often found as 3-dimensionally preserved phosphatic small shelly fossils (SSF). Complete body fossils may also show soft-bodied preservation in fine-grained shales (e.g. Burgess Shale-type localities), and one such specimen of *Wronascolex antiguus* from the Emu Bay Shale in South Australia (Cambrian Series 2, Stage 4) is thought to represent an empty moult. It is distinctive in possessing a break through its middle and a pronounced wrinkle across its width, while also being strongly compressed with weakly expressed annulations and lacking surficial relief (García-Bellido et al., 2013, fig. 3D , E). The authors thought it unlikely that the tear through the trunk represented the position of the exuvial opening, based on comparison to the location of the rupture at the base of the introvert, and not in the middle of the trunk, in the extant *Priapulus caudatus*. Palaeoscolecid material from the middle Cambrian Georgina Basin of Queensland, Australia, is preserved as 3-dimensional Orsten-type fossils, two of which show a double-layer structure of the phosphatised cuticle with sclerites (Müller and Hinz-Schallreuter, 1993, text-figs. 12B, 14C). This has been interpreted to represent individuals preserved shortly before moulting (Müller and Hinz-Schallreuter, 1993; García-Bellido et al., 2013), in a manner similar to that described in section 2.6.2 for lobopodian dermal sclerites.

2.6.4. Priapulida

Stem lineage priapulid body fossils are relatively abundant in some Cambrian Burgess Shale-type localities, while isolated microfossils of the spines lining the pharynx and introvert are widespread in Cambrian deposits. A detailed study of body fossils of *Ottoia prolifica* from the Burgess Shale revealed that the majority of published specimens were carcasses rather than moults, as indicated by the presence of gut structures and other internal organs (Conway Morris, 1977). Moulting capability in *Ottoia prolifica* is indicated by the frequent detachment of the body wall and cuticle, visible in the fossil as a contracted area of highly reflective body wall that has pulled away from the outer cuticle, which is left in place as an unreflective area that still maintains the original body outline (Conway Morris, 1977). One specimen in particular was described as "on the threshold of moulting" (Conway Morris, 1977, pg. 11) because its anterior end appears to have withdrawn, leaving behind a dark area. The cuticle seems to have been more resistant to decay than the internal structures, and some specimens consist of a collapsed and folded outer cuticle with an absence of nearly all internal organs, except for traces of the gut, which indicate that these fossils are decayed remnants of carcasses rather than moults (e.g. Conway Morris, 1977, text-figs. 49, 52, 64). Some specimens that are exceptionally well preserved seem not to have been affected by decay at all, and these have the body wall preserved as a highly reflective film that obscures details of the internal anatomy (Conway Morris, 1977, text-fig. 67). The lack of visible internal anatomy in these specimens could lead to them being interpreted as empty moults, however consideration of contextural information such as their completeness, lack of distortion and presence of some traces of internal anatomy should prevent them from being misidentified as moults. The only specimens suggested to actually represent moults of *Ottoia prolifica* are a few specimens consisting of the anterior proboscis only (e.g. Conway Morris, 1977, pg. 31, text-figs. 47, 48), based on comparisons to the moulted cuticle of the modern taxon *Priapulus*, where the anterior proboscis is everted and detached from the specimen during moulting (Lang, 1948).

The only other published description of moulting in the fossil record of Priapulida is a specimen of *Eximipriapulus globocaudatus* from the Chengjiang biota that has been interpreted as an empty moulted cuticle, based on the complete absence of internal anatomical features and its contracted and wrinkled appearance (Ma et al., 2014, figs. 1.5a, 1.5b , 2.7). This is inconsistent with the type of specimens described as moults by Conway Morris (1977), highlighting the need for more detailed study on moulting in Cambrian priapulid worms.

2.7. Mass moulting behaviour

Ecdysis may constitute a significant social behaviour in fossil ecdysozoans. Synchronised mass moulting events have been observed in many modern crustaceans, insects and arachnids. These are variously triggered abiotically (for example circadian rhythms in aphids; Johnson et al., 1957) or through active communication (pheromones) (Haug et al., 2013). These mass moultings were succinctly reviewed in Haug et al. (2013) for extinct arthropod groups. Mass moulting assemblages include trilobites from the Cambrian (Fig. 8E) (Paterson et al., 2007; Ebbestad et al., 2013), Ordovician (Karim and Westrop, 2002) and Devonian (Speyer and Brett, 1985); the soft-bodied arthropods *Canadaspis* and *Alalcomenaeus* from the Cambrian Burgess Shale (Fig. 8A, B, F) (Haug et al., 2013); eurypterids from the Silurian (Braddy, 2001; Vrazo and Braddy, 2011); and shrimps from the Jurassic (Polz and Tischlinger, 2000), all of which consist of large numbers of empty exuviae in close proximity. These assemblages show no evidence for abiotic transport, reworking or time-averaging, and so are generally accepted to represent actual biological mass moulting events. Another example of a supposed mass moult of mantis shrimps from the Carboniferous (Schöllmann, 2004) has been shown to co-occur with complete carcasses (Haug et al., 2013) and so may not represent a mass moult assemblage.

Haug et al., (2013) also discuss the possible evolutionary functions of coordinated moulting. In extant arthropods, mating is often synchronised with moulting, particularly at the moult stage when the organism reaches sexual maturity (e.g. Kamio et al., 2014), as the associated gregarious behaviour of many individuals in close proximity would decrease the predation pressure on any one individual (Haug et al., 2013). Synchronised moulting, mating and spawning in adults would also lead to synchronised development in offspring, which would then benefit from a similar reduction of predation pressure in crowded nursery habitats. This may explain trilobite (Speyer and Brett, 1985; Karim and Westrop, 2002; Paterson et al., 2007) and eurypterid (Braddy, 2001; Vrazo and Braddy, 2011) mass moult assemblages. However, Haug et al. (2013) and other researchers (for example Tetlie et al., 2008) reject this idea, although note that it may explain clusters of *Canadaspis perfecta* exuviae. The 'mass-mate-moult' hypothesis suggested for eurypterids (Speyer and Brett, 1985; Braddy, 2001), where females remain in shallow water post-mating and deposit their eggs prior to moulting, is dependent on the system of gender recognition. As pointed out by Haug et al. (2013), this hypothesis is influenced by comparisons to the extant horseshoe crab *Limulus*, which generally does not couple moulting with mating (Loveland, 2002; Shuster and Sekiguchi, 2004) even if large numbers of individuals aggregate during mating. Despite uncertainties about the motivation behind it, the repeated occurrence of mass moulting within trilobites and other Palaeozoic arthropods suggests that this behaviour may have been common within early ecdysozoans, and even ancestral to Trilobita.

3. Quantitative analysis of the trilobite fossil record of moulting

Our review of the literature indicates that an abundance of information on moulting has been accumulating in publications on fossil ecdysozoans, with a particular focus on moulting methods within trilobites. Many of these publications are isolated reports on the taxonomy or systematics of particular groups, where identification of moult assemblages is included as part of the descriptive work, or they examine moulting behaviour within a particular trilobite group or geological time period (e.g. Whittington, 1990). Reviews examining patterns in moulting behaviour amongst all trilobites are rare (Henningsmoen, 1975; Speyer, 1990) but highly informative for examining large-scale trends in the evolution of trilobite ecdysis (Brandt, 2002). Enough published work has now accumulated that quantitative analyses are possible, and the prevalence of different moulting behaviours can be identified within trilobite Orders (Table 1) and traced throughout geological time. We amassed all published information on trilobite moulting behaviour into a database (Appendix 1) and subjected it to a series of statistical analyses designed to reveal the evolutionary patterns of this important behaviour and validate trends described qualitatively in previous publications (Henningsmoen, 1975; Speyer, 1990).

3.1. Methods

To facilitate visualisation and statistical analysis of the trends in trilobite moulting, a summary data set was produced from the literature (see Appendix 1). This scored the presence of six ecdysial behaviours preserved for a range of trilobite taxa across eight Orders from the Early Cambrian to Late Carboniferous. This included: opening of the facial sutures; removal of the rostral plate; removal of the cephalon; removal of the cranidium; displacement of the pygidium; and disarticulation along the thorax. We used Brandt (2002, table 2) as a starting point, adding omitted descriptive literature and work published post-2002 with information about trilobite moulting. Only adult specimens specifically described as exuviae were included. A single taxon could display multiple ecdysial behaviours between or within specimens (e.g. opening of the facial sutures followed by disarticulation of the cranidium); this has been indicated when noted in the literature (Appendix 1). This produced a larger sample size of total occurrences (of ecdysial behaviours) than the total number of trilobite taxa sampled. For each entry in the database, the geological age of the specimen was determined from the publication where moulting was described, if this was easily translated to the most recent International Chronostratigraphic Chart (ICS) (Gradstein et al., 2012). For specimens where the given locality date did not correspond directly with the current Stages/Epochs of the ICS (e.g. Middle Cambrian), more recent literature or occurrence data (in the Palaeobiology Database) were consulted to place the localities in the current ICS framework and gather them into time bins corresponding to geological Periods (Fig. 10) and Series (Fig. 11).

Graphs created in R (R Development Core Team 2008) display the variation in occurrence of the six different ecdysial behaviours between trilobite Orders and through geological time (Figs. 9-11). Chi^2 analyses were performed in PAST3 (Hammer et al., 2001) for each behaviour using the observed data paired with expected numbers of observations. Uneven sample sizes were corrected for in calculating the expected observations. Agnostida (n=1) was removed for analyses testing the differences in mode of ecdysis between trilobite Orders. We tested H_0 = no significant difference in ecdysial behaviour across geological Periods or Series, or between the trilobite Orders.

Specimens were photographed by a Canon EOS 500D digital SLR under incident and polarised lighting. The camera was fitted with a Canon EF-S 60 mm Macro Lens, and remotely operated by the EOS Utility 2.8.1.0 program. Adobe Photoshop and Illustrator CS6 were used to make minor adjustments to the exposure of the images and removed unwanted background, and to make figures.

3.2. Results

Figure 9 shows clear differences in ecdysial behaviour between and within the different trilobite Orders (summarised in Table 1), providing initial support for a link between phylogeny and moulting in Trilobita. Phacopid taxa show a significantly higher occurrence of cephalon removal during ecdysis ($p=5.8x10^{-7}$, Table 2) as compared to other moulting methods, although facial suture utilisation is also prevalent. Opening of the facial sutures during ecdysis, usually accompanied by removal of the librigenae, was the prevalent behaviour in all Orders excepting Phacopida (Fig. 9A). This produced an insignificant result when applying the Chi^2 test (p=0.378) because there is no clear difference between which Orders display the behaviour. Redlichiida also show a tendency towards removal of the rostral plate (possibly followed by ventral exuviation of the moult; p=0.00234, Table 2) (Fig. 9A). The Chi^2 test applied to all Orders with sample sizes >5 also determined a significant difference in which Orders employed disarticulation of the cranidium (following detachment of the librigenae) during ecdysis (p=0.0418, Table 2). Odontopleurida and

Phacopida rarely, if ever, show this behaviour (Fig. 9A). Overall, Redlichiida and Ptychopariida display the greatest variation in ecdysial behaviour. This may be an artefact of their larger sample sizes, however it could also be reflecting the greater morphological plasticity of these trilobites during the Cambrian as compared to later trilobite groups (Webster, 2007).

Family-level variation in ecdysial behaviour for Phacopida indicates the secondary utilisation of facial sutures during moult exuviation is owing to the high prevalence of this moulting method in Calymenidae, Dalmanitidae and Encrinuridae (Fig. 9B). The other five Families show removal of the cephalon in 100% of the taxa sampled. Family-level data for Redlichiida reveals extensive variation in ecdysial habit within the Order (Fig. 9C). Four of the Families show removal of the rostral plate in 100% of taxa (Fallotaspididae, Olenellidae, Wanneriidae, Xystriduridae), and four employment of the facial sutures in 100% of taxa (Emuellidae, Gigantopygidae, Redlichiidae, and Xystriduridae) (Fig. 9C).

The results also suggest patterns in ecdysis varied through geological time. As expected, cephalic disarticulation and opening of the facial sutures were the most common methods of ecdysis throughout the majority of the Early Cambrian to Late Carboniferous (Fig. 10, 11). These show an opposing pattern due to being mutually exclusive behaviours. The continued utilisation of the facial sutures resulted in an insignificant Chi^2 result ($p=0.051$ and 0.7) (Fig. 10, 11). Cephalon removal for ecdysis was at its peak during the Devonian (92% of taxa), resulting in only 8% of trilobite taxa displaying opened facial sutures (Fig. 10). This behaviour was also common during the Ordovician (48% of taxa, 71% in Late Ordovician) (Fig. 10). This temporal variation in a cephalon-thorax fracture during moulting is considered statistically significant ($p=2.18\text{x}10^{-6}$, Table 2).

Removal of the cranidium (necessitating release of the librigenae) for ecdysis is widespread (present in >25% of taxa) during the Cambrian, Ordovician and Carboniferous As expected this somewhat tracks trends in utilisation of the facial sutures (Fig. 10, 11), although this was not significant. Loss of the rostral plate for ecdysis is common in the Cambrian (39% of taxa, >70% during the first half), but declines in frequency until its absence in the Devonian and Carboniferous (Fig. 10, 11). This trend is statistically significant (p=0.0084, Table 2). The other two ecdysial behaviours are less common. Pygidium displacement is present in 50% of taxa during the Middle Devonian (Fig. 10, 11), but is otherwise rare or absent. Thoracic dislocation is very rare from the Middle Ordovician (present in 17% of taxa at this time).

3.3. Discussion:

The preliminary results presenting variation in trilobite ecdysial behaviour suggest some chronological and taxonomic signal resides in the moult fossil record. Generally, modes of ecdysis that vary significantly across trilobite Orders (disarticulation of the cephalon, and of the cranidium, Table 2) agreed with those qualitatively summarised in the literature review (Section 2.1.). Further, the lack of significant taxonomic variation in facial suture moulting was expected from the prevalence of this behaviour across all Orders (Fig. 9A). The Family-level variation in phacopids and redlichiids described in the literature is also captured in Figure 9B and 9C. Overall the results clearly support the well-known inter- and intraspecific variability in trilobite moulting. This high variability in the moulting method used by different trilobite individuals belonging to the same Family, Genus or even Species is in opposition to the “canalised ecdysial habit” of other arthropods (Brandt, 2002, pg. 399), where moulting method is robust and consistent for all members of a Genus, Family or higher taxonomic classification (e.g. the “Open Moult Position” of decapod crustaceans such as lobsters and crabs (Glaessner, 1969; Bishop, 1972, 1986). In these extant arthropods, taxa with a similar overall morphology will moult using the same method, whereas trilobite taxa sharing similar overall morphology may moult using many different methods. This lack of consistency in moulting behaviour within trilobites may have affected the evolutionary success and survivorship of the clade (Brandt 2002), although these links are far from straightforward. Our results suggest that a quantitative approach to studying large-scale evolutionary trends of trilobite ecdysis is feasible and warrants further investigation.

However, low sample sizes for several of the Orders (particularly Agnostida, Corynexochida, Odontopleurida, and Proetida) and during the Carboniferous indicate the need for more extensive sampling of trilobite moulting patterns before more rigorous statistical analysis. Perhaps fewer significant trends would be observed if all Order sample sizes were greater, and the full range of within-Order variation in ecdysis could be observed. Significant trends in variation of ecdysial behaviours through geological time may also be attributable to fluctuations in biodiversity and abundance of certain trilobite clades. For example, Phacopida trilobites moult by cephalon removal, and so a peak in this method of moulting is seen during the Ordovician coincidental with the origin and radiation of the Order.

The analysis presented exploring trends in trilobite moulting should be extended to encompass a much larger sample size, but also similar ventures made into detailing and quantifying the ecdysial patterns preserved in the fossil records of other arthropods. Following from the work of Brandt (2002), many other lines of inquiry may prove associations between ecdysial mode in different ecdysozoan groups to broader-scale macroevolutionary processes, such as development and body size, particular environmental cues, or phylogeny.

4. Conclusions:

The focus on trilobite ecdysis in this paper reflects the bias to this group in the moult fossil record descriptive literature. However, we have detailed what information does exist for ecdysis in other marine arthropods (particularly Eurypterida and Crustacea), as well as for non-arthropod ecdysozoans. Work focusing on moulting in these groups is sparse, and in most cases limited to very few specimens of loriciferans, palaeoscolecids, priapulids, and lobopodians from the early Palaeozoic. Even rarer glimpses of exuviation preserved mid-moult (e.g. García-Bellido and Collins, 2004) have the potential to identify the taxonomic affinity of enigmatic fossils (Peel et al., 2013; Smith and Ortega-Hernández, 2014).

Methods of studying moulting in the fossil record are highly dependent on the group under examinationm, and no canonised set of rules or assumptions exists across Ecdysozoa generally. In some sclerotised taxa, such as eurypterids (Tetlie et al., 2008; Vrazo and Braddy, 2011; Vrazo et al., 2014) and decapods (Mertin, 1941; Schäfer, 1972), moults are thought to be more prevalent than carcasses in the fossil record, and specimens are assumed to be moults unless proven otherwise. Fossils of carcasses in these taxonomic groups are relatively rare. In Eurypterids, this is influenced by comparisons to modern taxa, such as *Limulus*, where the exuvial suture closes up after moulting, although this may not be the most appropriate analogue given the uncertain affinity of eurypterids (Tetlie et al., 2008) and the great expanse of geological time separating them. On the other hand, Mesozoic crustacean fossils benefit from having direct modern analogues, and so detailed information on their ultrastructure can provide more confidence in identifying moults in the fossil record.

A different tact is employed when studying the trilobite fossil record of moulting – more debate exists on deciding whether a specimen is a moult or not, with a tendency to assume complete trilobites are carcasses. Debate here focuses on whether disarticulated materials represent moult assemblages, or post-depositional disruption, meaning that more emphasis is placed on understanding the depositional environment (Henningsmoen, 1975). In contrast to eurypterids and even decapods, there is no published suggestion that trilobite ecdysial sutures could close after moulting, giving the false appearance of a complete carcass. For example, once the facial sutures opened in a trilobite, there is little chance they will close up again immediately afterwards. This is partly due to the mineralised nature of the trilobite exoskeleton, as compared to the sclerotized cuticles of other ecdysozoan taxa. As such, the trilobite fossil record of moulting contains important signal on temporal and taxonomic variation of this major morphological innovation.

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References

Adrain, J.M., 2011. Class Trilobita Walch, 1711. In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148, 104-109.

Adrain, J.M. and Chatterton, B.D.E., 1990. *Odontopleura* (Trilobita, Silurian), and a method of constrained congruency analysis. J. Paleo. 64, 600-614.

Andrews, H.E., Brower, J.C., Gould, S.J. and Reyment, R.A., 1974. Growth and variation in *Eurypterus remipes* Dekay. B. Geol. Inst. Uni. Uppsala, New Series 4, 81-114.

Ax, P., 1987. The Phylogenetic System. John Wiley & Sons, New York, pp. 340.

Babcock, L.E., Merriam, D.F. and West, R.R., 2000. *Paleolimulus*, an early limuline (Xiphosurida), from Pennsylvanian-Permian Lagerstatten of Kansas and taphonomic comparison with modern *Limulus*. Lethaia 33, 129-141.

Bergström, J., 1973. Organization, life, and systematics of trilobites. Fossils Strata 2, 69 pp.

Bergström, J. and Hou, X.-G., 2001. Cambrian Onychophra or Xenusians. Zool. Anz. 240, 237-245.

Bishop, G.A., 1972. Moults of *Dakoticancer overanus*, an Upper Createceous crab from the Pierre Shale of South Dakota. Palaeontology 15, 122-123.

Bishop, G.A., 1986. Taphonomy of the North American decapods. J. Crustacean Biol. 6, 326-355.

Bishop, G.A. and Williams, A.B., 1986. The fossil lobster *Linuparus canadensis*, Carlile Shale (Cretaceous), Black Hills. Nat. Geogr. Res. 2, 372-387.

Bishop, G.A. and Williams, A.B., 2005. Taphonomy and preservation of burrowing thalassinidean shrimps. P. Biol. Soc. Wash. 118, 218-236.

Braddy, S.J., 2001. Eurypterid palaeoecology: palaeobiological, ichnological and comparative evidence for a 'mass-moult-mate' hypothesis. Palaeogeogr. Palaeocl.172, 115-132.

Braddy, S.J., Aldridge, R.J. and Theron, J.N., 1995. A new eurypterid from the Late Ordovician Table Mountain Group, South Africa. Palaeontology 38, 563-581.

Braddy, S.J., Aldridge, R.J., Gabbott, S.E. and Theron, J.N., 1999. Lamellate book-gills in a late Ordovician eurypterid from the Soom Shale, South Africa: support for a eurypterid-scorpion clade. Lethaia 32, 72-74.

Brandt, D.S., 2002. Ecdysial efficiency and evolutionary efficacy among marine arthropods: implications for trilobite survivorship. Alcheringa 26, 399-421.

Bruton, D.L., 2001. A death assemblage of priapulid worms from the Middle Cambrian Burgess Shale. Lethaia 34, 163-167.

Budd, G.E. and Jensen, S., 2000. A critical reappraisal of the fossil record of the bilaterian phyla. Biol. Rev. 75, 253–295.

Budd, G.E. and Telford, M.J., 2009. The origin and evolution of arthropods. Nature 457, 812-817.

Budil, P. and Bruthansová, J., 2005. Moulting in Ordovician dalmanitoid and acastoid trilobites of the Prague Basin. Preliminary Observation. Geol. Acta 3, 373-383.

Busch, R.M. and Swartz, F.M., 1985. Molting and description of a new homalonotid trilobite from Pennsylvania. J. Paleo. 59, 1062-1074.

Caron, J.-B., Smith, M.R. and Harvey, T.H.P., 2013. Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. P. Roy. Soc. B 280, 20131613.

Cederström, P., Ahlberg, P., Nilsson, C.H., Ahlgren, J. and Eriksson, M.E., 2011. Moulting, ontogeny and sexual dimorphism in the Cambrian ptychopariid trilobite *Strenuaeva inflata* from the Northern Swedish Caledonides. Palaeontology 54, 685-703.

Chatterton, B.D.E. and Ludvigsen, R., 1998. Upper Steptoean (Upper Cambrian) trilobites from the McKay Group of Southeastern British Columbia, Canada. Mem. Pal. Soc. 49, 1-43.

Chen, J.-Y., Zhou, G.-Q. and Ramsköld, L., 1995. The Cambrian lobopodian *Microdictyon sinicum*. Bull. Nat. Mus. Nat. Sci. 5, 1-93.

Chen, G.-Y., Han, N.-R. and Zhao, Y.-L., 2008. Moulting of the Cambrian trilobite *Oryctocephalus indicus* (Reed, 1910). Earth Sci. J. China Uni. Geosci. 6, 783-792.

Clarke, J.M. and Ruedemann, R., 1912. The Eurypterida of New York. Mem. New York State Mus. Nat. Hist. 14, 1-439.

Clarkson, E.N.K., Ahlgren, J. and Taylor, C.M., 2003. Structure, ontogeny, and moulting of the olenid trilobite *Ctenopyge (Eoctenopyge) angusta* Westergård, 1922 from the Upper Cambrian of Västergötland, Sweden. Palaeontology 46, 1-27.

Conway Morris, S., 1977. Fossil priapulid worms. SP Palaeont. 20, 1-155.

Cotton, T.J. and Fortey, R.A., 2005. Comparative morphology and relationships of the Agnostida. In: Koenemann, S. and Jenner, R.A. (Eds.) Crustacea and arthropod relationships. Taylor & Francis, Florida, pp. 95-136.

Cronier, C. and Fortey, R.A., 2006. Morphology and ontogeny of an Early Devonian phacopid trilobite with reduced sight from Southern Thailand. J. Paleo. 80, 529-536.

Daley, A.C., Budd, G.E., Caron, J.-B., Edgecombe, G.D. and Collins, D., 2009. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. Science 323, 1597-1600.

Daley, A.C., Budd, G.E. and Caron, J.-B., 2013. The morphology and systematics of the anomalocaridid *Hurdia* from the Middle Cambrian of British Columbia and Utah. J. Syst. Palaeontol. 11, 743–787.

De Armas, L.F., 1986. Biologia y morfometria de *Rhopalurus garridoi* Armas (Scorpiones, Buthidae). Poeyana 333, 1-27.

Duan, Y., Han, J., Fu, D., Zhang, X., Yang, X., Komiya, T., and Shu, D., 2013. Reproductive strategy of the bradoriid arthropod *Kunmingella douvillei* from the Lower Cambrian Chengjiang Lagerstätte, South China. Gond. Res. 25, 983-990.

Dunlop, J.A. and Webster, M., 1999. Fossil evidence, terrestrialization and arachnid phylogeny. J. Arachnol. 27, 86-93.

Dunn, C.W., Giribet, G., Edgecombe, G.D. and Hejnol, A., 2014. Animal phylogeny and its Evolutionary Implications. Annu. Rev. Ecol. Evol. Syst. 45, 371-395.

Dzik, J. and Krumbiegel, G., 1989. The oldest 'onychophoran' *Xenusian*: a link connecting phyla? Lethaia 22, 169-181.

Ebbestad, J.O.R., Rushton, A.W.A., Stein, M. and Weidner, T., 2013. A paradoxidid moult ensemble from the Cambrian of Sweden. GFF 135, 18-29.

Edgecombe, G.D., 2010. Arthropod phylogeny: an overview from the perspectives of morphology, molecular data and the fossil record. Arthropod Struct. Dev. 39, 74-87.

Edgecombe, G.D. and Sherwin, L., 2001. Early Silurian (Llandovery) trilobites from the Cotton Formation, near Forbes, New South Wales, Australia. Alcheringa 25, 87-105.

Eskov, K.Y. and Selden, P.A., 2005. First record of spiders form the Permian period (Araneae: Mesothelae). Bull. Br. Arachnol. Soc. 13, 111-116.

Esteve, J., Hughes, N.C. and Zamora, S., 2011. Purujosa trilobite assemblage and the evolution of trilobite enrollment. Geology 39, 575-578.

Esteve, J., Hughes, N.C. and Zamora, S., 2013. Thoracic structure and enrolment style in middle Cambrian *Eccaparadoxides pradoanus* presages caudalization of the derived trilobite trunk. Palaeontology 56, 589-601.

Ewer, J., 2005. How the ecdysozoan changed its coat. PLoS Biol. 3, e349.

Feldmann, R.M., 1989. *Metanephrops jenkinsi* n. sp. (Decapoda: Nephropidae) from the Cretaceous and Paleocene of Seymour Island, Antartica. J. Palaeontol. 63, 64-69.

Feldmann, R.M., 2009. A new cirolanid isopod (Crustacea) from the Cretaceous of Lebanon: Dermoliths document the pre-molt condition. J. Crustacean Biol. 29, 373-378.

Feldmann, R.M. and Gaździcki, A., 1998. Cuticular ultrastructure of fossil and living homolodromiid crabs (Decapoda: Brachyura). Acta Palaeontol. Pol. 43, 1-19.

Feldmann, R.M. and Tshudy, D., 1987. Ultrastructure in Cuticle from Hoploparia stokes (Decapoda: Nephropidae) from the Lopez de Bertodano Formation (Late Cretaceous – Paleocene) of Seymour Island, Antarctica. J. Paleontol. 61, 1194-1203.

Feldmann, R.M., Vega, F.J., García-Barrera, P., Rico-Montiel, R. and Martínez Lopez, L., 1995. A New Species of *Meyeria* (Decapoda: Mecochiridae) from the San Juan Raya Formation (Aptian: Cretaceous), Puebal State, Mexico. J. Palaeontol. 69, 402-406.

Feldmann, R.M., Vega, F.J. Applegate, S.P. and Bishop, G.A., 1998. Early Cretaceous Arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebal, México. J. Paleontol. 72, 79-90.

Fischer, A.G., 1946. A carapace of the Ordovician trilobite *Telephus.* J. Paleontol. 20, 566-569.

Förster, R. and Barthel, K.W., 1978. On Recent and fossil *Thalassina* (Decapoda, Crustacea) and their burrows. Neues Jahrb. Geol. P. M. 5, 291-306.

Fortey, R.A., 1974. The Ordovician trilobites of Spitsbergen. I. Olenidae. Norsk Polarinstitutt Skrifter 160, 81 pp.

Gaban, R.D. and Farley, R.D., 2002. Ecdysis in scorpions: supine behavior and exuvial ultrastructure. Invertebr. Biol. 121, 136-147.

García-Bellido, D. and Collins, D.H., 2004. Moulting arthropod caught in the act. Nature 429, 40.

García-Bellido, D. C., Paterson, J.R. and Edgecombe, G.D., 2013. Cambrian palaeoscolecids (Cycloneuralia) from Gondwana and reappraisal of species assigned to *Palaeoscolex*. Gond. Res. 24, 780-795.

Garwood, R.J. and Dunlop, J., 2014. Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. PeerJ Nov 13, e641.

Gibson, J.A.E., Cromer, L., Agius, J.T., McInnes, S.J. and Marley, N.J., 2007. Tardigrade eggs and exuviae in Antarctic lake sediments: insights into Holocene dynamics and origins of the fauna. J. Limnol. 66, 65-71.

Glaessner, M.F., 1948. An Ordovician trilobite and some later Paleozoic Crustacea in moulting positions. J. Paleontol. 22, 531-532.

Glaessner, M.F., 1969. Decapoda. In: Moore, R.C. (Ed.) Treatise on Invertebrate Paleontology, Pt. R 4(2), Arthropoda. Geological Society of America and University of Kansas Press, Lawrence, pp. R400- R533.

González-León, O., Moreno-Bedmar, J.A. and Vega, F.J., 2014. Morphology and ontogeny of the fossil lobster *Meyeria magna* M'Coy, 1849 (Astacidae, Mecochiridae) from the Lower Cretaceous (Lower Aptian) of Mexico, United Kingdom and Spain. N. Jb. Geol. Paläont. Abh. 271, 49-68.

Gradstein, F. M., Ogg, J. G., Schmitz, M.D. and Ogg, G. M., 2012. The geologic timescale 2012. Elsevier, Oxford, UK.

Gross, W., 1934. Eine *Estheria* aus dem rheinischen Unterdevon. Senckenbergiana 16, 309-313.

Hammer, Ø., Harper, D.A.T. and Ryan, P.D., 2001. PAST: Palaeontological Statistics Software Package for education and data analysis. Palaeontol. Electron. 4, 9 pp.

Han, N.R. and Zhang, J.L., 1991. Malformed thoracic pleurae of *Redlichia* (*Redlichia*) *hupehensis* Hsu. Acta Palaenotol Sinica 30, 126-128.

Harrington, H.J., 1959. General description of Trilobita. In: Moore, R.C. (Ed.) Treatise of Invertebrate Palaeontology, Part O, Arthropoda. Geological Society of American and University of Kansas Press, Lawrence, Kansas, pp. O38-O117.

Hartnoll, R.G. and Bryant, A.D., 1990. Size-frequency distributions in decapod Crustacea – the quick, the dead and the cast-offs. J. Crustacean Biol. 10, 14-19.

Haug, J.T., Caron, J.-B. and Haug, C., 2013. Demecology in the Cambrian: synchronized molting in arthropods from the Burgess Shale. BMC Biol. 11, 1-10.

Haug, J.T., Haug, C., Waloszek, D., Maas, A., Wulf, M. and Schweigert, G., 2009. Development in Mesozoic scyllaris and implications for the evolution of Achelata (Reptantia, Decapoda, Crustacea). Palaeodiversity 2, 97-110.

Hegna, T.A., 2012. Phylogeny and fossil record of branchipod crustaceans: an integrative approach. Unpublished PhD Thesis, Yale University, 262 pp.

Henningsmoen, G., 1957. The trilobite family Olenidae. Skr. ut. Norske Vid. Acad. Oslo I Mat.-Naturv. Klasse 1, 303 pp.

Henningsmoen, G., 1975. Moulting in trilobites. Fossils Strata 4, 179-200.

Higgins, R.P. and Kristensen, R.M., 1986. New Loricifera from Southeastern United States coastal waters. Smitson. Contr. Zool. 438, 1-70.

Hou, X., Ramsköld, L. and Bergström, J., 1991. Composition and preservation of the Chengjiang fauna – a Lower Cambrian soft-bodied biota. Zool. Scr. 20, 395-411.

Hou, X., Siveter, D.J., Williams, M., and Feng, X., 2001. A monograph of the Bradoriid arthropods from the Lower Cambrian of SW China. T. Roy. Soc. Edin. Earth 92, 347-409.

Hou, X., Williams, M., Siveter, D.J., Siveter, D.J., Aldridge, R.J., and Sansom, R.S., 2010. Soft-part anatomy of the Early Cambrian bivalved arthropods *Kunyangella* and *Kunmingella*: significance for the phylogenetic relationships of Bradoriida. Proc. R. Soc. B 377, 1689.

Hughes, N.C., 2007. The Evolution of Trilobite Body Patterning. Annu. Rev. Earth Planet Sci. 35, 401-434.

Hughes, N.C., Haug, J.T. and Waloszek, D., 2008. Basal euarthropods development: a fossil-based perspective. In: Minelli, A. and Fusco, G. (Eds.) Key Themes in Evolutionary Developmental Biology. Cambridge University Press, Cambridge, pp. 279-296.

Hunda, B.R., Hughes, N.C. and Flessa, K.W., 2006. Trilobite taphonomy and temporal resolution in the Mt. Orab shale bed (Upper Ordovician, Ohio, U.S.A.). Palaios 21, 26-45.

Jeram, A.J., 2001. Paleontology. In: Brownell P.H. and Polis, G.A. (Eds.) Scorpion Biology and Research. University Press, Oxford/New York, pp. 370-392.

Johnson, C.G., Haine, E., Cockbain, A.J. and Taylor, L.R., 1957. Moulting rhythm in the alienicolae of *Aphis fabae* Scop. (Hemiptera: Aphididae) in the field. Ann. Appl. Biol. 45, 702-708.

Judson M.L.I., 2009. Cheliferoid pseudoscorpions (Arachnida, Chelonethi) from the Lower Cretaceous of France. Geodiversitas 31, 61-71.

Kamenz, C., Staude, A. and Dunlop, J.A., 2011. Sperm carriers in Silurian sea scorpions. Naturwissenschaften 98, 889-896.

Kamio, M., Schmidt, M., Germann, M.W., Kubanek, J., and Derby, C.D., 2014. The smell of moulting: *N*-acetylglucosamino-1,5-lactone is a premoult biomarker and candidate component of the courtship pheromone in the urine of the blue crab, *Callinectes sapidus*. J. Exp. Biol. 217, 1286-1296.

Karim, T. and Westrop, S.R., 2002. Taphonomy and palaeoecology of Ordovician trilobite clusters, Bromide Formation. Palaios 17, 394-402.

Kjellesvig-Waering, E.N., 1986. A restudy of the fossil Scorpionida of the world. Palaeont. Americana 55, 1-287.

Klompmaker, A.A. and Fraaije, R.H.B., 2011. The oldest (Middle Triassic, Anisian) lobsters from the Netherlands: taxonomy, taphonomy, paleoenvironment, and paleoecology. Palaeontol. Electron. 14, 1A:15p, http://palaeo-electronica.org/2011_1/220/index.html

Krishnakumaran, A. and Schneiderman, H.A., 1970. Control of molting in mandiculate and chelicerate arthropods by ecdysones. Biol. Bull. 139, 520-538.

Kristensen, R.M., 1983. Loricifera, a new phylum with Aschelminthes chraacters from meiobenthos. Zeitschr. Zool. Syst. Evolutionsforsch. 21, 163-180.

Kukalova, J., 1968. Permian Mayfly Nymphs. Psyche 75, 310-327.

Kukalova, J., 1969. Revisional study of the Order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France Part II. Psyche 76, 439-486.

Kukalova-Peck, J., 1975. Megasecoptera from the Lower Permian of Moravia. Psyche 82, 1-19.

Lagebro, L., Gueriau, P., Hegna, T.A., Rabet, N., Butler, A.D and Budd, G.E., 2015. The oldest notostracan (Upper Devonian Strud Locality, Belgium). Palaeontology 58, 497-509.

Lamsdell, J.C., 2013. Revised systematics of Palaeozoic 'horseshoe crabs' and the myth of monophyletic Xiphosura. Zool. J. Linn. Soc.-Lond. 167, 1-27.

Lang, K., 1948. Contribution to the ecology of *Priapulus caudatus* Lam. Zool. Verh. Leiden 112, 1-118.

Legg, D.A., Garwood, R.J., Dunlop, J.A. and Sutton, M.D., 2012. A taxonomic revision of orthosternous scorpions from the English Coal-measures aided by X-ray Micro-Tomography (XMT). Palaeontol. Electron. 15.2.14A.

Legg, D.A., Sutton, M.D. and Edgecombe, G.D., 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. Nat. Comm. 4, 2485.

Lin, J.-P. and Yuan, J.-L., 2009. Reassessment of the mode of life of *Pagetia* Walcott, 1916 (Trilobita, Eodiscidae) based on a cluster of intact exuviae from the Kaili Formation (Cambrian) of Guizhou, China. Lethaia 42, 67-73.

Liu, J. and Dunlop, J.A., 2014. Cambrian lobopodians: A review of recent progress in our understanding of their morphology and evolution. Palaeogeogr. Palaeocl. 398, 4-15.

Loveland, R.E., 2002. The Life History of Horseshoe Crabs. In: Tanacredi, J.T. (Ed), *Limulus* in the Limelight. Kluwer Academic Publishers, New York, pp. 93-102.

Ma, X., Edgecombe, G.D., Legg, D.A. and Hou, X., 2014. The morphology and phylogenetic position of the Cambrian lobopodian *Diania cactiformis*. J. Syst. Palaeontol. 12, 445-457.

McCoy, V.E. and Brandt, D.S., 2009. Scorpion taphonomy: criteria for distinguishing fossil scorpion molts and carcasses. J. Arachnol. 37, 312-320.

McNamara, K.J., 1986. Techniques of exuviation in Australian species of the Cambrian trilobite *Redlichia*. Alcheringa 10, 403-412.

McNamara, K.J. and Tuura, M.E., 2011. Evidence for segment polarity during regeneration in the Devonian asteropygine trilobite *Greenops widderensis.* J. Paleontol. 85, 106-110.

Mertin, H., 1941. Decapode Krebse aus dem Subhercynen und Braunschweiger Emscher und Untersenon. Nova Acta Leopoldina, Neue Folde, 10, 149-263.

Moussian, B., 2013. The Arthropod Cuticle. In: Minelli, A., Boxshall, G. and Fusco, G. (Eds), Arthropod Biology and Evolution: Molecules, Development, Morphology. Springer-Verlag Berlin Heidelberg, pp. 171-196.

Müller, K.J., 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. Lethaia 12, 1-27.

Müller, K.J. and Hinz-Schallreuter, I., 1993. Palaeoscolecid worms from the Middle Cambrian of Australia. Palaentology 36, 549-592.

Müller, K.J. and Waloszek, D., 1985. A remarkable arthropod fauna from the Upper Cambrian "Orsten" of Sweden. Earth Env. Sci. T. R. So. 76, 2-3.

Murray, P.F. and Hanley, J.R., 1986. Unmuddling the mudlobster, observations on the age and taphonomy of fossil *Thalassina*. Beagle: Rec. Mus. Art Gall. Northern Terr. 3, 59-70.

Nakamura, K., 1981. Post embryonic development of a pycnogonid, *Propallene logiceps*. J. Nat. Hist. 15, 49-62.

Nijhout, H.F., 2013. Arthropod Developmental Endocrinology. In: Minelli, A., Boxshall, G. and Fusco, G. (Eds), Arthropod Biology and Evolution: Molecules, Development, Morphology. Springer-Verlag Berlin Heidelberg, pp. 123-148.

Olempska, E., 2012. Morphology and affinities of Eridostracina: Palaeozoic ostracods with moult retention. Hydrobiologia 688, 139–165.

Öpik, A.A., 1958. The Cambrian trilobite *Redlichia*: organization and generic concept. Bureau Min. Res. Geolog. Geophys. (Australia) Bull. 42, 38 pp.

Öpik, A.A., 1970. *Redlichia* of the Ordian (Cambrian) of Northern Australia and New South Wales. Bureau Min. Res. Geolog. Geophys. (Australia) Bull. 114, 67 pp.

Orr, P.J. and Briggs, D.E.G., 1999. Exceptionally preserved conchostracanas and other crustaceans from the Upper Carboniferous of Ireland. SP Palaeontol. 62, 1-68.

Orr, P.J., Briggs, D.E.G. and Kearns, S.L., 2008. Taphonomy of exceptionally preserved crustaceans from the Upper Carboniferous of southeastern Ireland. Palaios 23, 298-312.

Ortega-Hernández, J., Esteve, J., and Butterfield, N.J., 2013. Humble origins for a successful strategy: Complete enrolment in early Cambrian olenellid trilobites. Biol. Lett. 9, 20130679.

Paterson, J.R. and Edgecombe, G.D., 2006. The Early Cambrian Trilobite Family Emuellidae Pocock, 1970: Systematic Position and Revision of Australia Species. J. Paleontol. 80, 496-513.

Paterson, J.R., Jago, J.B., Brock, G.A. and Gehling, J.G., 2007. Taphonomy and palaeoecology of the emuellid trilobite *Balcoracania dailyi* (early Cambrian, South Australia). Palaeogeogr. Palaeocl. 249, 302-321.

Peel, J.S., 2010. A corset-like fossil from the Cambrian Sirius Passet Lagerstätte of North Greenland and its implications for cycloneuralian evolution. J. Paleontol. 84, 332-340.

Peel, J.S., Stein, M. and Kristensen, R.M., 2013. Life Cycle and Morphology of a Cambrian Stem-Lineage Loriciferan. PLoS ONE 8, e73583.

Petrunkevitch, A.I., 1942. A study of amber spiders. Trans. Connectic. Acad. Arts Sci. 34, 119-464.

Polz, H., 1995. Ein außergewöhnliches Jugendstadium eines palinuriden Krebses aus den Solnhofener Plattenkalken. Archaeopteryx 13, 67–74.

Polz, H. and Tischlinger, H., 2000. *Anthonema* – Der 'Blütenfaden' aus dem Altmühljura. Fossilien 5, 289-296.

Rasnitsyn, A.P., 2002. Introduction to palaeoentomology. In: Rasnitsyn, A.P. and Quicke, D.L.J. (Eds), History of Insects. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 19-20

R Development Core Team., 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.

Richards, B.C., 1975. *Longusorbis cuniculosus*: A New Genus and Species of Upper Cretaceous Crab; with Comments on Spray Formation at Shelter Point, Vancouver Island, British Columbia. Can. J. Earth Sci. 12, 1850-1863.

Richter, R., 1937. Von bau und leben der trilobiten, 8. Die “Salter’sche Einbettung” als folge und kennzeichen des häuntungs-vorgangs. Senckenbergiana 19, 413-431.

Rosin, R. and Shulov, A., 1962. Studies on the scorpion *Nebohierochonticus*. Proc. Zool. Soc. Lond. 140, 547-575.

Rota-Stabelli, O., Daley, A.C. and Pisani, D., 2013. Multiple timetrees reveal a Cambrian colonisation of land and a new scenario for ecdysozoan evolution. Curr. Biol. 23, 392-398.

Rudkin, D.M., 1979. Healed injuries in *Ogygosis klotzi* (Trilobita) from the Middle Cambrian of British Columbia. ROM Life Sci. Occasional Paper 32, 1-8.

Rudkin, D.M., 2009. The Mount Stephen Trilobite Beds. In: Caron, J.-B. and Rudkin, D. (Eds.) A Burgess Shale Primer – History, Geology, and Research Highlights. The Burgess Shale Consortium, Toronto, pp. 90-102.

Rudkin, D.M. and Young, G.A., 2009. Horseshoe Crabs – An Ancient Ancestry Revealed. In: Tancredi, J.T., Botton, M.L. and Smith, D.R. (Eds), Biology and Conservation of Horseshoe Crabs. Springer Dordrecht Heidelberg London New York, pp. 25-44.

Rustán, J.J., Balseiro, D., Waisfeld, B., Foglia, R.D. and Vaccari, N.E., 2011. Infaunal molting in Trilobita and escalatory responses against predation. Geology 39, 495-498.

Schäfer, W., 1972. Ecology and Palaeoecology of Marine Environments. University of Chicago Press, Chicago.

Schöllmann, L., 2004. Archaeostomatopodea (Malacostraca, Hoplocarida) aus dem Namur B (höheres Mardenium, Kabon) von Hagen-Vorhalle (NRW, Deutschland) und eine Neudefinition einiger Arten der Familie Tyrannophontidae. Geol. Paläontol. Westf. 62, 111-141.

Selden, P.A., 1981. Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). T. Roy. Soc. Edin.-Earth 72, 9-48.

Selden, P.A. and Jeram, A.J., 1989. Palaeophysiology of terrestrialiation in the Chelicerata. T. Roy. Soc. Edin. Earth 80, 303-310.

Selden, P.A., Shear, W.A. and Bonamo, P.M., 1991. A spider and other arachnids from the Devonian of New York, and reinterpretation of Devonian Araneae. Palaeontology 34, 241-281.

Shaver, R.H., 1953. Ontogeny and sexual dimorphism in *Cytherella bullata*. J. Paleontol. 27, 471-480.

Shu, D., Vannier, J., Luo, H., Chen, L., Zhang, X., and Hu, S., 1999. Anatomy and lifestyle of *Kunmingella* (Arthropoda, Bradoriida) from the Chengiang fossil Lagerstätte (lower Cambrian; Southwest China). Lethaia 32, 279-298.

Shultz, J.W., 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6, 1-38.

Shultz J.W., 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. Zool. J. Linn. Soc.-Lond. 150, 221-265.

Shuster, C.N., Jr. and Sekiguchi, K., 2004. Growing Up Takes About Ten Years and Eighteen Stages. In: Shuster, C.N., Jr, Brockman, H.J. and Barlow, R.B. (Eds), The American Horseshoe Crab. Harvard University Press, Cambridge, pp. 103-131.

Siveter, D.J., Sutton, M.D., Briggs, D.E.G. and Siveter, D.J., 2003. An Ostracode Crustacean with Soft Parts from the Lower Silurian. Science 302, 1749-1751.

Siveter, D.J., Sutton, M.D, Briggs, D.E.G. and Siveter, D.J., 2004. A Silurian sea spider. Nature 432, 978-980.

Siveter, D.J., Tanaka, G., Farrell, U.C., Martin, M.J., Siveter, D.J., and Briggs, D.E.G., 2014. Exceptionally Preserved 450-Milllion-Year-Old Ordovician Ostracods with Brood Care. Curr. Biol. 24, 801-806.

Smith, M.R. and Ortega-Hernández, J., 2014. *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. Nature 514, 363-366.

Speyer, S.E., 1985. Moulting in phacopid trilobites. T. Roy. Soc. Edin. Earth Sci. 76:2-3, 239-253.

Speyer, S.E., 1987. Comparative taphonomy and palaeoecology of trilobite lagerstatten. Alcheringa 11, 205-232.

Speyer, S.E., 1990. In: Boucot, A.J. (Ed.) Evolutionary paleobiology of behavior and coevolution. Elsevier, New York, pp. 491-499.

Speyer, S.E. and Brett, C.E., 1985. Clustered trilobite assemblages in the Middle Devonian Hamilton Group. Lethaia 18, 85-103.

Strømer, L., 1944. On the relationships and phylogeny of fossil and Recent Arachnomorpha. Skr. ut. Norske Vid. Acad. Oslo I Mat.-Naturvidens. Klasse 1944 I 5, 1-158.

Strømer, L., 1955. Merostomata. In: Moore, R.C. (Ed.) Treatise on Invertebrate Paleontology, Part P, Arthropoda 2. Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp. 4-41.

Telford, M.J., Bourlat, S.J., Economou, A., Papillon, D. and Rota–Stabelli, O., 2008. The evolution of the Ecdysozoa. Philos. Trans. R. Soc. Lond. B Biol. Sci. 363, 1529–1537.

Tetlie, O.E., Braddy, S.J., Butler, P.D. and Briggs, D.E.G., 2004. A new eurypterid (Chelicerata: Eurypterida) from the Upper Devonian Gogo Formation of Western Australia, with a review of the Rhenopteridae. Palaeontology 47, 801-809.

Tetlie, O.E., Brandt, D.S. and Briggs, D.E.G., 2008. Ecdysis in sea scorpions (Chelicerata: Eurypterida). Palaeogeogr. Palaeocl. 265, 182-194.

Tinn, O. and Meidla, T., 2003. Ontogeny and thanatocoenosis of early Middle Ordovician ostracode species *Brezelina palmata* (Krause, 1889) and *Ogmoopsis bocki* (Sarva, 1959). J Palentol 77, 64-72.

Tollerton Jr., V.P., 1997. Eurypterids and associated fauna at Litchfield, a classic locality in Herkimer County. 69th Annual Meeting and Guidebook New York State Geological Association, pp. 253-264.

Topper T.P., Skovsted C.B., Peel J.S. and Harper D.A.T., 2013: Moulting in the lobopodian *Onychodictyon* from the lower Cambrian of Greenland. Lethaia 46, 490–495.

Tortello, M.F. and Clarkson, E.N.K., 2008. Ontogeny, structure, and moulting of *Parabolina frequens argentina* (Kayser) (Trilobita, Olenidae) from the Furongian of Northwestern Argentina. Ameghiniana 45, 13-31.

Turpen, J.B. and Angell, R.W., 1971. Aspects of molting and calcification in the ostracod *Heterocypris*. Biol. Bull. 140, 331-338.

Valentine, J.W. and Collins, A.G., 2000. The significance of moulting in Ecdysozoan evolution. Evol. Dev. 2, 152-156.

Vannier, J., 2012. Gut Contents as Direct Indicators for Trophic Relationships in the Cambrian Marine Ecosystem. PLoS ONE 7, e52200.

Vannier, J., Thiéry, A., and Racheboeuf, P.R., 2003. Spinicaudatans and ostracods (Crustacea) from the Montceau Lagerstätte (Late Carboniferous, France): morphology and palaeoenvironmental significance. Palaeontology 46, 99-1030.

Vega, F.J. and Feldmann, R.M., 1991. Fossil crabs (Crustacea, Decapoda) from the Maastrichtian Difunta Group, Northeastern Mexico. Ann. Carnegie Mus. 60, 163-177.

Vega, F.J., Feldmann, R.M., García-Barrera, P., Filkorn, H., Pimentel, F. and Avendaño, J., 2001. Maastrichtian Crustacea (Brachyura: Decapoda) from the Ocozocuautla Formation in Chiapas, Southeast Mexico. J. Paleontol. 75, 319-329.

Vega, F.J., Dávila-Alcocer, V.M. and Filkorn, H.F., 2005. Characterization of cuticle structure in Late Cretaceous and Early Tertiary decapod Crustacea from Mexico. Bull. Mizunami Fossil Museum 32, 37-43.

Vrazo, M.B. and Braddy, S.J., 2011. Testing the 'mass-moult-mate' hypothesis of eurypterid palaeoecology. Palaeogeogr. Palaeocl. 311, 63-73.

Vrazo, M.B., Trop, J.M. and Brett, C.E., 2014. A new eurypterid lagerstätte from the Upper Silurian of Pennsylvania. Palaios 29, 431-448.

Waloszek, D., 1993. The Upper Cambrian *Rehbachiella kinnekullensis* and the phylogeny of Branchiopoda and Crustacea. Fossils Strata 32, 1-202.

Waloszek, D., 1995. The Upper Cambrian *Rehbachiella,* its larval development, morphology and significance for the phylogeny of Branchiopoda and Crustacea. Hydrobiologia 298, 1-13.

Waloszek, D., 2003. The 'Orsten' window – a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda. Paleontol. Res. 7, 71-88.

Waloszek, D. and Dunlop, J.A., 2002. A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian 'Orsten' of Sweden, and the phylogenetic position of pycnogonids. Palaeontology 45, 421-446.

Waloszek, D. and Maas, A., 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. Evol. Dev. 7, 515-527.

Wang, J.-L. and Han, N.-R., 1997. Moulting in *Plagiolaria* (Trilobita) from the Lower Devonian of China. Geobios 30, 831-834.

Webster, M., 2007. A Cambrian peak in morphological variation within trilobite species. Science 317, 499-502.

Webster, M., 2015. Ontogeny and intraspecific variation of the Early Cambrian trilobite *Olenellus gilberti,* with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization. J. Syst. Palaeontol. 13, 1-74.

Weygoldt, P. and Paulus, H.F., 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata1 II. Cladogramme und die Entfaltung der Chelicerata. J. Zool. Syst. Evol. Res. 7, 177-200.

Whittington, H.B., 1990. Articulation and exuviation in Cambrian trilobites. Philos. Trans. R. Soc. Lond. B. 329B, 27-46.

Wieder, R.W. and Feldmann, R.M., 1989. *Palaega goedertorum*, a Fossil Isopod (Crustacea) from the Late Eocene to Early Miocene Rocks of Washington State. J. Paleontol. 63, 73-80.

Wills, L.J., 1959. The external anatomy of some Carboniferous scorpions, Part 1. Palaeontology 3, 276-332.

Wilson, G.D.E., Paterson, J.R. and Kear, B.P., 2011. Fossil isopods associated with a fish skeleton from the Lower Cretaceous of Queensland, Australia – Direct evidence of a scavenging lifestyle in Mesozoic Cymothoida. Palaeontology 54, 1053-1068.

Woodward, H., 1867. On some points in the structure of the Xiphosura, having reference to their relationship with the Eurypterida. Ann. Mag. Nat. Hist. Ser. 3 110, 144-145.

Woodward, H., 1872. Further Remarks on the Relationship of the Xiphosura to the Eurypterida and to the Trilobita and Arachnida. Q. J. Geol. Soc. 23, 28-63.

Zacaï, A., Vannier, J., and Lerosey-Aubril, R., 2016. Reconstructing the diet of a 505-million-year-old arthropod: *Sidneyia inexpectans* from the Burgess Shale fauna. Arthropod Struct. Dev. this volume.

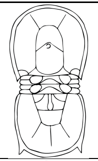
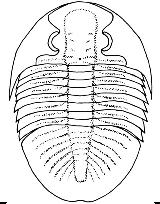
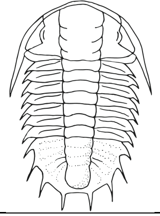
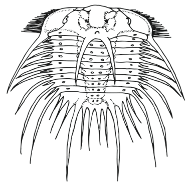
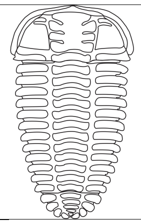
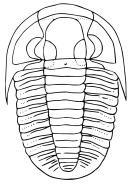
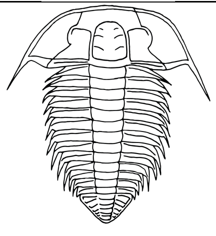
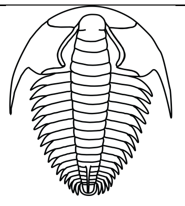
Zhang, X.-G., 1987. Moult stages and dimorphism of Early Cambrian bradoriids from Xichuan, Henan, China. Alcheringa 11, 1-19.

Zhang, X.-G., 2007. Phosphatized bradoriids (Arthropoda) from the Cambrian of China. Palaeont. Abteil. A 281, 93-173.

Zhang, X.-G. and Aldridge, R.J., 2007. Development and diversification of trunk plates of the lower Cambrian lobopodians. Palaeontology 50, 401-415.

Zherikhin, V.V., 1997. Taphonomical characters of insects. In: Ochev V.G. and Tverokhlebova G.I. (Eds), Tafonomiya nazemnykh organizmov (Taphonomy of Terrestrial Organisms), Izdatel'stvo Saratov Univ, Saratov, pp. 34-46 (in Russian).

Table 1: Summary table of published descriptions of moulting behaviour in trilobite Orders

Order	**Morphology**	**Moulting behaviour**[1]	**# of sp.**[2]	**Age range**	**Key References**[3]
Agnostida e.g. *Girvanagnostus*		1. Facial sutures opened	1	Cambrian-Ordovician	Lin and Yuan (2009)
Asaphida e.g. *Ogygiocaris*		1. Facial sutures opened 2. Cranidium removed 3. Cephalon removed	9	Cambrian-Silurian	Chatterton and Ludvigsen (1998); Karim and Westrop (2002)
Corynexochida e.g. *Olenoides*		1. Facial sutures opened 2. Rostral plate removed 2. Cephalon removed 2. Cranidium removed	3	Cambrian-Devonian	Chen et al. (2008)
Odontopleurida e.g. *Odontopleura*		1. Facial sutures opened 2. Rostral plate removed 2. Pygidium displaced	4	Cambrian-Devonian	Adrain and Chatterton (1990); Edgecombe and Sherwin (2001)
Phacopida e.g. *Placoparia*		1. Cephalon removed 2. Facial sutures opened 3. Pygidium displaced 4. Thoracic dislocation 5. Cranidium removed	32	Ordovician-Devonian	Budil and Bruthansová (2005); Hunda et al. (2006); Rustán et al. (2011)
Proetida e.g. *Cyphoproetus*		1. Facial sutures opened 2. Cranidium removed 3. Cephalon removed	7	Cambrian-Permian	Edgecombe and Sherwin (2001)
Ptychopariida e.g. *Olenus*		1. Facial sutures opened 2. Cranidium removed 3. Thoracic dislocation 4. Pygidium displaced 5. Rostral plate removed 5. Cephalon removed	21	Cambrian-Ordovician	Chatterton and Ludvigsen (1998); Clarkson et al. (2003); Tortello and Clarkson (2008)
Redlichiida e.g. *Redlichia*		1 Facial sutures opened 2. Rostral plate removed 3. Cranidium removed 4. Thoracic dislocation 5. Pygidium displaced 6. Cephalon removed	24	Cambrian	McNamara (1986); Öpik (1958); Paterson et al. (2007)

[1] In order of most common moulting behaviour (1) amongst individuals of species within that Order, to least common.

[2] Number of species from the Order in data set.

[3] A selection of references that specifically describe ecdysis for species of each Order.

Table 2: Chi^2 and p-values testing for variation in the six trilobite ecydsial behaviours, with significant results shaded in grey.

	Rostral plate removed	**Facial sutures opening**	**Cephalon removed**	**Dislocation along thorax**	**Pygidium displaced**	**Cranidium removed**
Geological Periods (Cambrian-Devonian)	[1]χ^2=12.8	χ^2=7.77	χ^2=29.1	χ^2=2.1	χ^2=5.35	χ^2=3.11
	p=0.0084	p=0.051	p=2.18E-06	p=0.552	p=0.148	p=0.375
	[2]n=19	n=56	n=33	n=13	n=13	n=22
Geological Series (Terreneuvian-Late Ordovician)	χ^2=23.4	χ^2=3.83	χ^2=25.1	χ^2=5.4	χ^2=1.07	χ^2=2.89
	p=0.00061	p=0.7	p=0.000328	p=0.494	p=0.983	p=0.823
	n=21	n=49	n=21	n=12	n=9	n=21
Orders (without Agnostida)	χ^2=25.9	χ^2=6.42	χ^2=39.5	χ^2=4.02	χ^2=3.47	χ^2=10.9
	p=0.000234	p=0.378	p=5.8E-07	p=0.674	p=0.748	p=0.0919
	n=19	n=57	n=32	n=13	n=13	n=22
[3]Orders (without Agnostida, Corynexochida, Odontopleurida)	χ^2=25.5	χ^2=4.91	χ^2=38.2	χ^2=3.1	χ^2=2.55	χ^2=9.92
	p=3.94E-05	p=0.296	p=1E-07	p=0.54	p=0.635	p=0.0418
	n=19	n=57	n=32	n=13	n=13	n=22

1: Chi^2 value calculated in PAST3 (Hammer et al. 2001) for the observed versus expected observations of trilobite ecdysial behaviour. H_0 = no significant difference in ecdysial behaviour across geological Periods or Series, or between the trilobite Orders (see left-most column).

2: Sample size (n) represents the number of occurrences of each ecdysial behaviour; this is greater than the number of taxa included because some specimens exhibit more than one behaviour.

3: Chi^2 analyses run while excluding all trilobite Orders with a sample size of n=<5.

Figure captions:

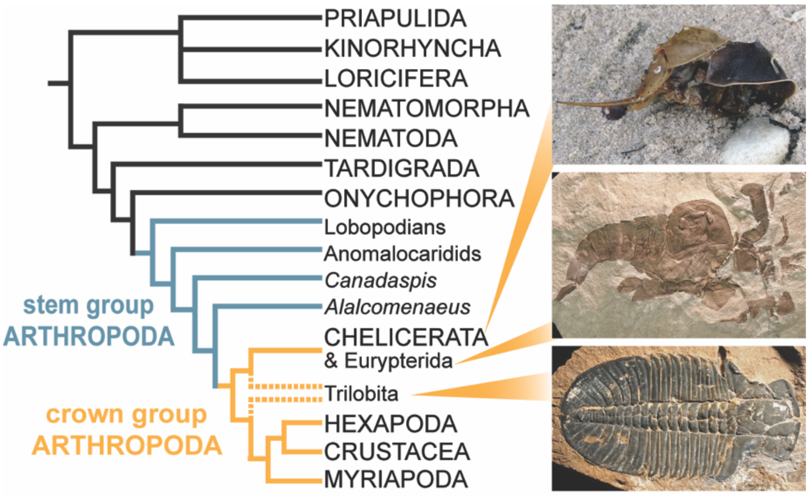


Fig. 1. Generalised phylogeny of ecdysozoans, with extant phyla in ALLCAPS and fossil groups/taxa in lowercase lettering. Phylogeny based on Dunn et al. (2014), Rota-Stabelli et al. (2013) and Legg et al. (2013). Images from top: Horseshoe crab in the process of moulting (Image credit: Wikimedia Commons); Eurypterid moult ensemble, YPM 208303 (Image credit: J. Utrup); Trilobite moulted exuvia, OUMNH AT.205 (Image credit: H. Drage).

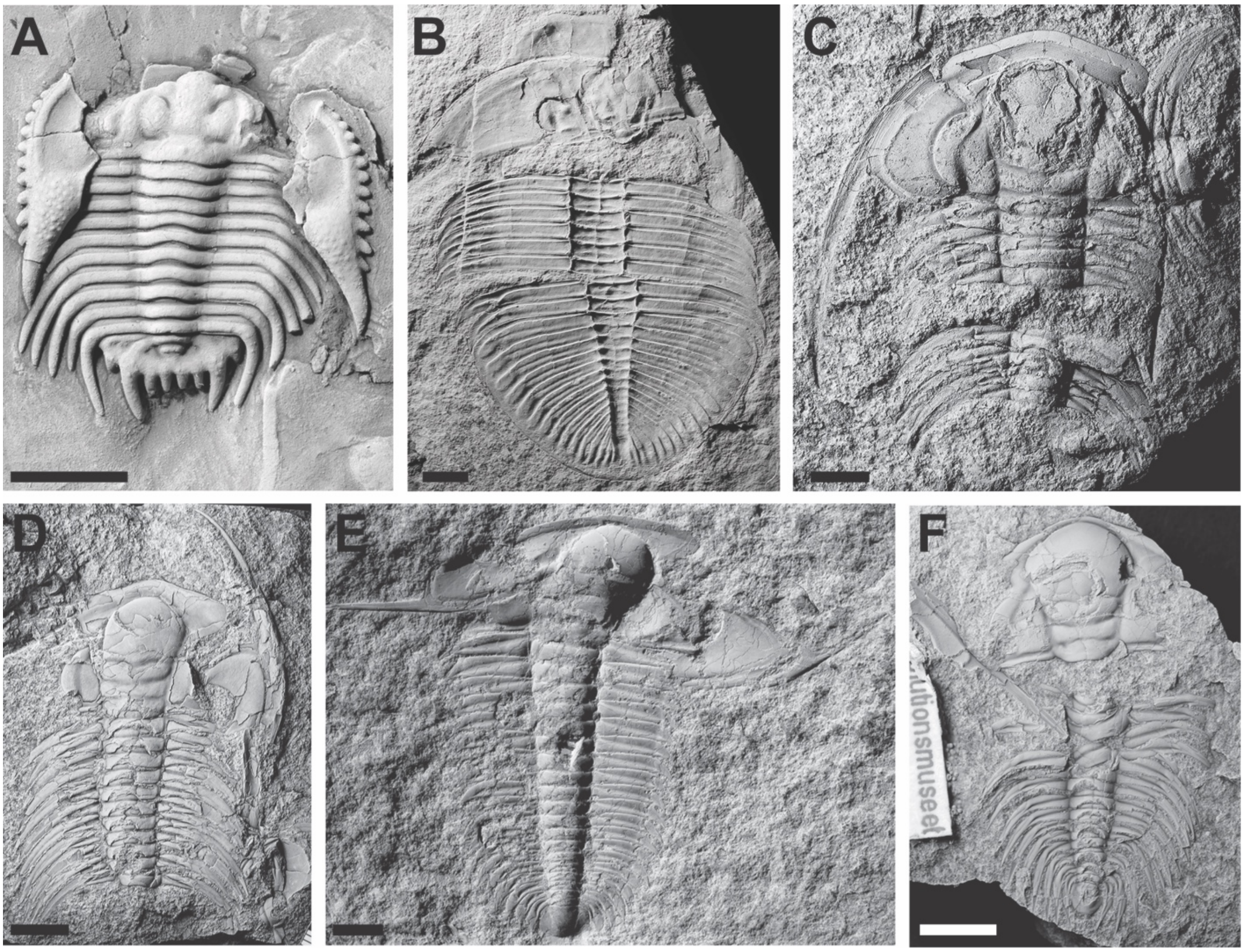


Fig. 2. Different moulting behaviours preserved as exuviae of trilobites. A: *Acidaspis coronata* from the Silurian Wenlock Shale in Malvern, UK, facial sutures opened and displaced slightly backwards. OUMNH C.17494. B: *Ogygiocarella debuchii* from the Ordovician Llandeilo Series in Meadowtown, Shropshire, with cephalon displaced and break through the thorax. OUMNH B.263. C-F: Cambrian trilobites from Jämtland, Sweden. C: *Acadoparadoxides* with left facial suture opened, crushed glabella, and middle thoracic segments displaced and rotated 90° over the right side of the cephalon. PMU 28736. D: *Acadoparadoxides* with left free cheek missing and right free cheek inverted. PMU 25995. E: *Eccaparadoxides* showing both free cheek inverted. PMU 25636. F: *Accadoparadoxides* with right free cheek missing, left free cheek flipped, cephalon removed, and disrupted thoracic segments. PMU 25690. Scale bars 5 mm in A, C, E-F and 10 mm in B, D.

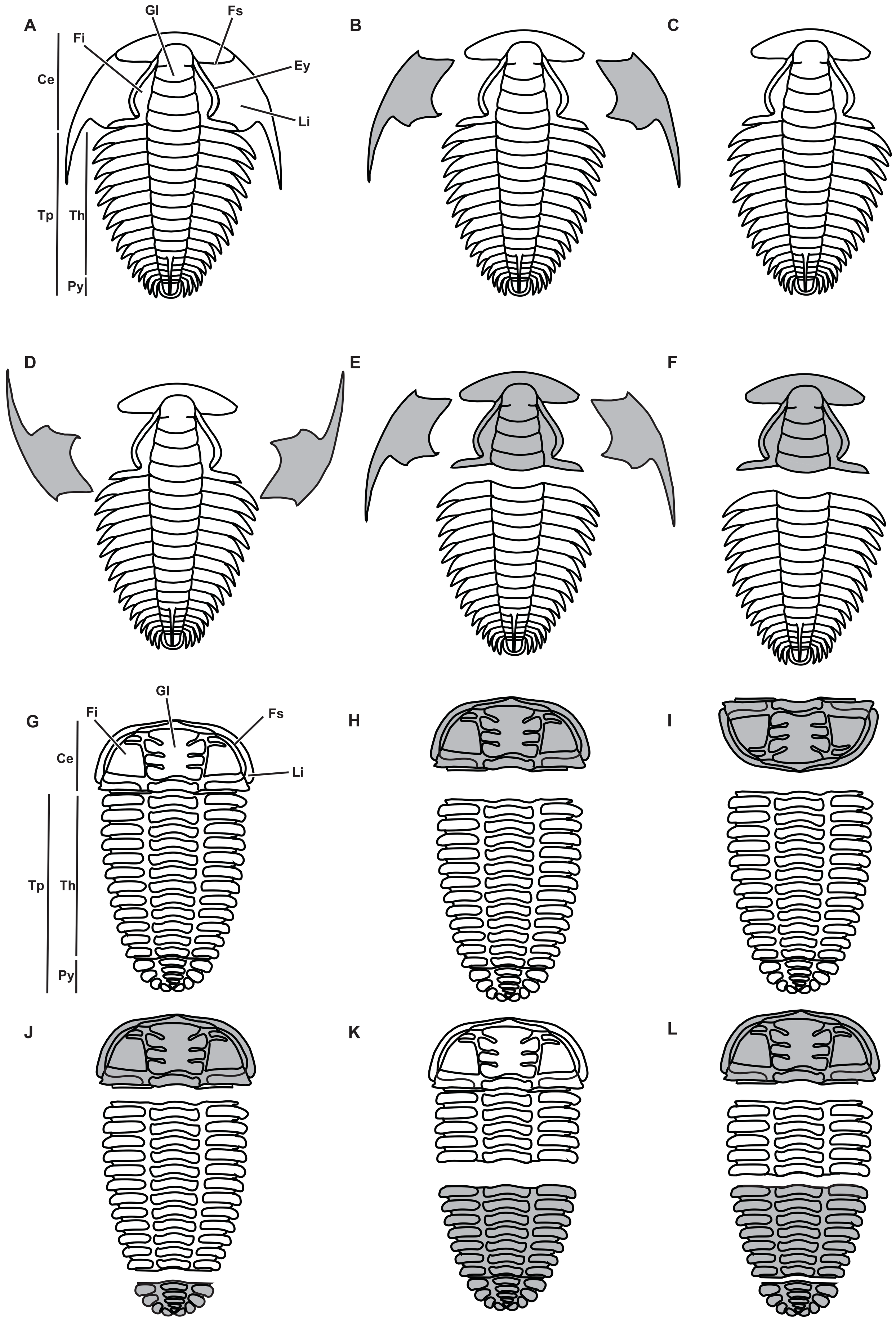

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Fig. 3. Summary of the most common trilobite moult configurations preserved in the fossil record, illustrated by *Redlichia* (A-F, usually moulted via the facial sutures and librigena) and *Placoparia* (G-L, usually moulted via disarticulation of the entire cephalon). Exoskeleton sections disarticulated during the moulting process shaded grey. A: Complete labeled dorsal exoskeleton of *Redlichia*. B: Facial sutures opened and librigena displaced outwards. C: Facial sutures opened and librigena missing. D: Facial sutures opened and librigena horizontally flipped (possible if the individual arched during exuviation). E: Facial sutures and cephalothoracic join opened, causing disarticulation of the librigena and cranidium. F: As in E, but librigena missing. G: Complete labeled dorsal exoskeleton of *Placoparia.* H: Cephalon disarticulated, leaving exuvial gape between cephalon and thorax. I: Cephalon disarticulated and flipped horizontally (Salter's configuration). J: Cephalon and pygidium disarticulated. K: Disarticulation along the thorax (unspecific location). L: Cephalon, thorax and pygidium disarticulated in the same exuvia. Other combinations of these moult configurations can be found preserved in the fossil record, for example disarticulation of the thorax with release of the librigena. Abbreviations: Ar, axial ring; Ce, cephalon; Ey, eye; Fi, fixigena (fixed cheeks); Fs, facial suture; Gl, glabella; Gs, genal spine; Li, librigena (free cheeks); Pl, pleura; Py, pygidium; Th, thorax; Tp, thoracopygon. Cranidium is the cephalon minus the librigenae; axial shield is the cranidium plus the thoracopygon.

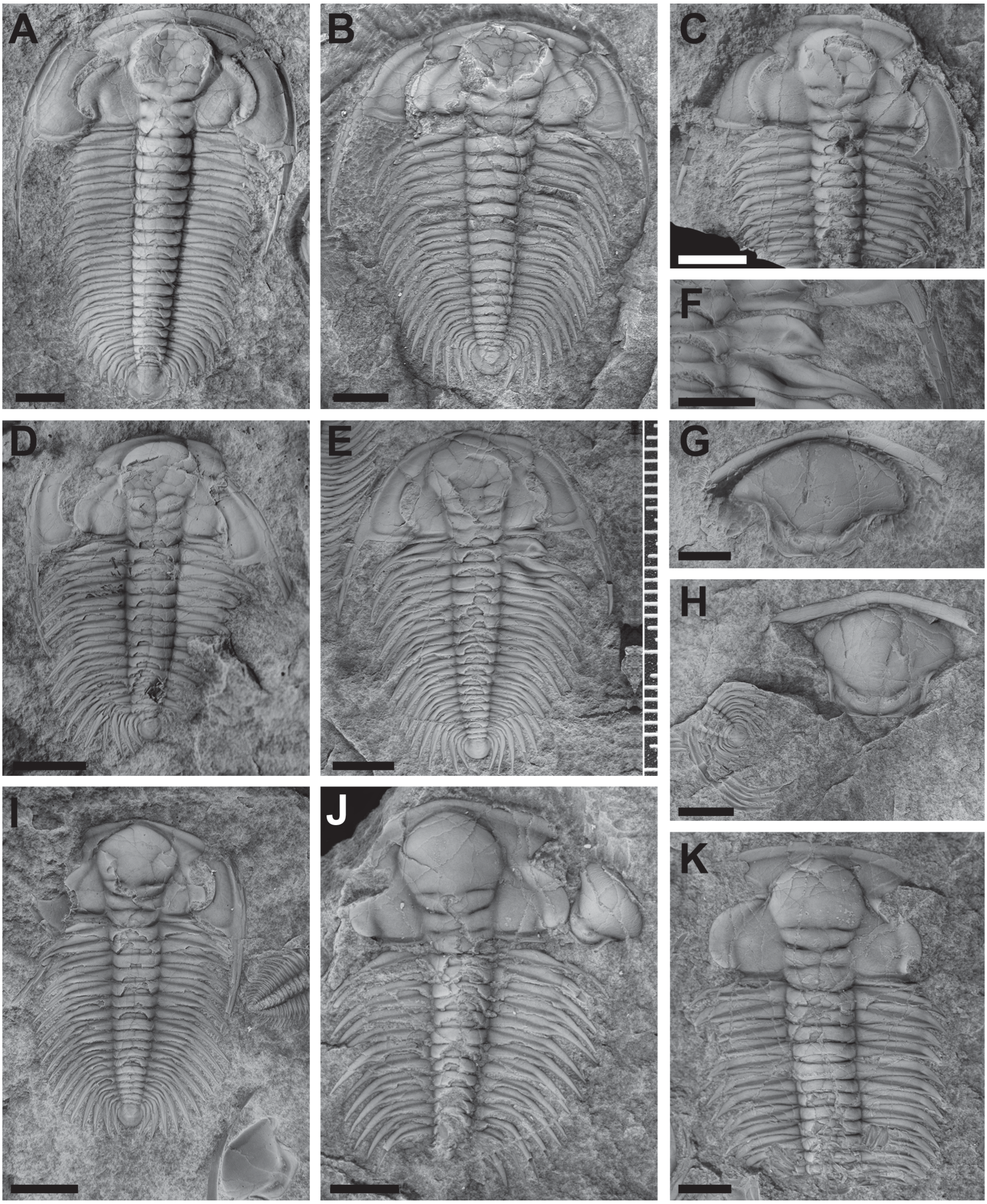

Fig. 4. Moulted exuviae of paradoxidid trilobites from a mass moulting surface from the Cambrian of Jämtland, Sweden. A-B: Trilobites with facial sutures opened. A: PMU 25711/29. B: PMU 25711/09b. C-D: Trilobites with facial sutures opened and free cheeks slightly displaced. C: PMU 25711/59. D: PMU 25711/66. E-F: Specimen with facial sutures opened and damage to first thoracic segment on right side, probably caused by problems during moulting. PMU 25711/61. E:

Whole specimen. F: Closeup of damaged thoracic segment. G-H: Moulted hypostome and rostral plate complexes. G: PMU 25711/45. H: PMU 25711/14. I: Facial sutures opened, left free cheek flipped and right free cheek displaced. PMU 25711/67. J: Free cheeks absent and hypostome displaced next to cephalon. PMU 25711/46. K: Free cheeks absent and break through thoracic segments. PMU 25711/25. Scale bars 5 mm in A-B, D-E, G-I; 3 mm in C, F, J-K. All specimens are latex casts except for A-B, H and K, which are rock. Photo credit for all images: J. Ebbestad (Ebbestad et al., 2013).

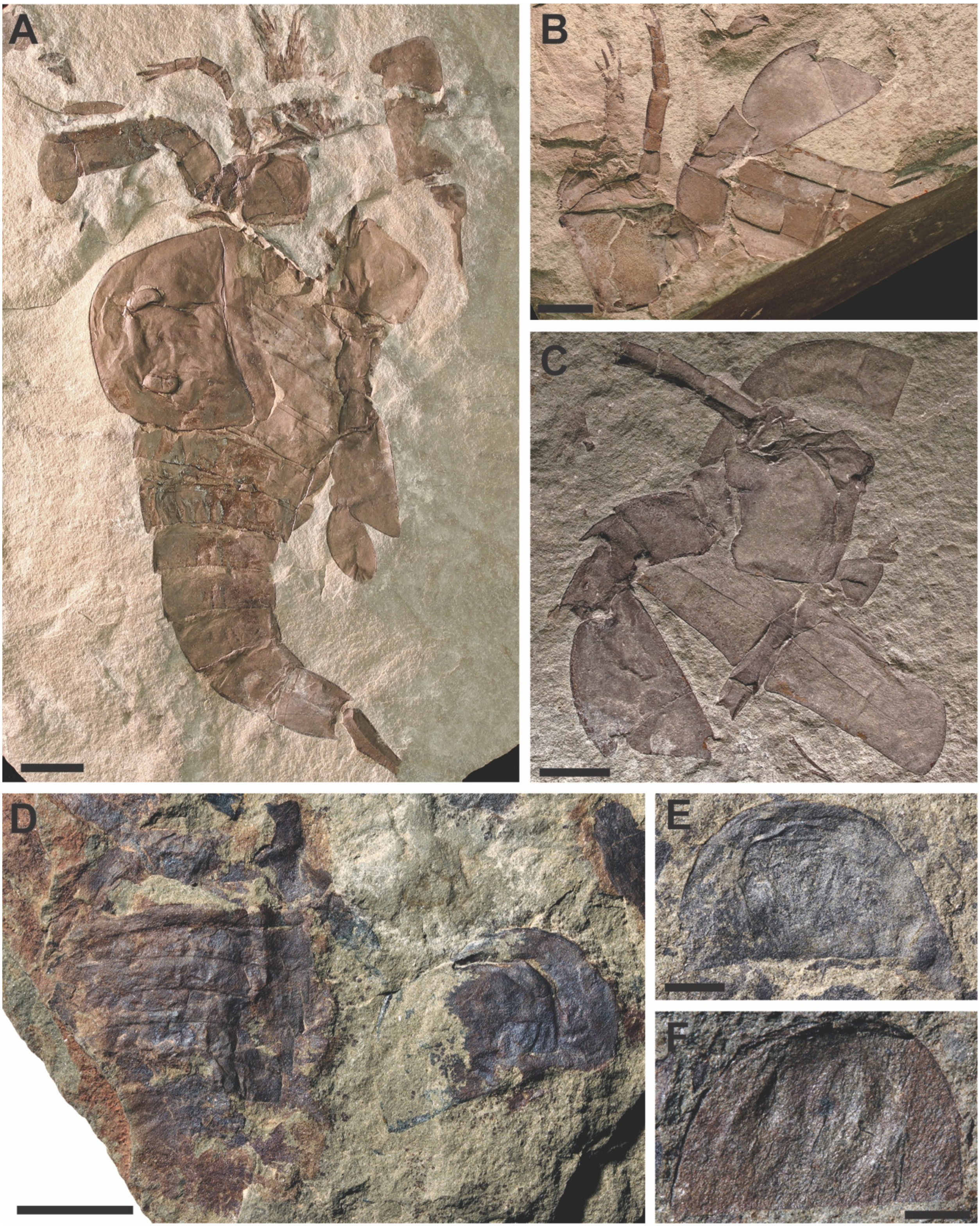

Fig. 5. Eurypterid moult assemblages. A-C: *Eurypterus lactustris* from the Williamsville Formation in Ridgemount Quarry, Ontario. Photo credit: J. Utrup. A: Mostly complete mouth ensemble with cephalic carapace and one opisthosomal segment dislocated and superimposed on the abdomen. YPM 208303. Scale bar 10 mm. B: Dissociated ventral plates with prosomal appendage attached. YPM 208456. Scale bar 10 mm. C: Ventral plate and swimming leg in moult

ensemble. YPM 209023. Scale bar 10 mm. D-F: Adelopthalmid eurypterid from the Devonian Lower Old Red Sandstone of the Dinas Estate in Brecon, Powys, Wales. D: Moult ensemble with cephalic carapace (right) dislocated from all opisthomal segments of the abdomen (left). OUMNH D.2184. Scale bar 10 mm. E-F: Dislocated cephalic carapaces preserved in isolation, without the first opisthomal segment. E: OUMNH D.2178. Scale bar 5 mm. F: OUMNH D.2173. Scale bar 3 mm.

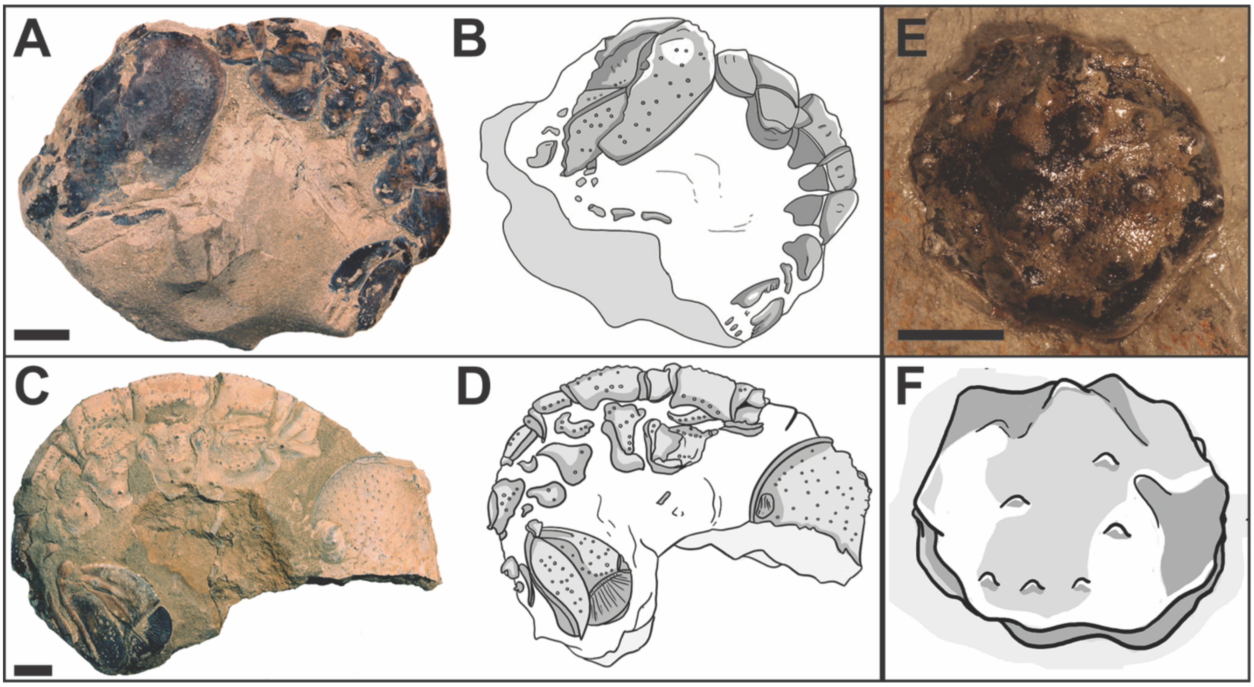

Fig. 6. Moulting in decapod crustaceans. A-D: Photographs and sketches of *Meyeria magna* from the Lower Greensand of Atherfield Clay, Isle of Wight, showing typical "Lobster Open Moult" position, with carapace displaced from the abdomen. A-B: OUMNH K.756. C-D: OUMNH K.755. E-F: Photograph and sketch of *Necrocarcinus labeschii* from the Cretaceous Gault Clay, Folkestone, UK, with disarticulated carapace broken along the pleural sutures. OUMNH K.64003. Scale bars 5 mm.

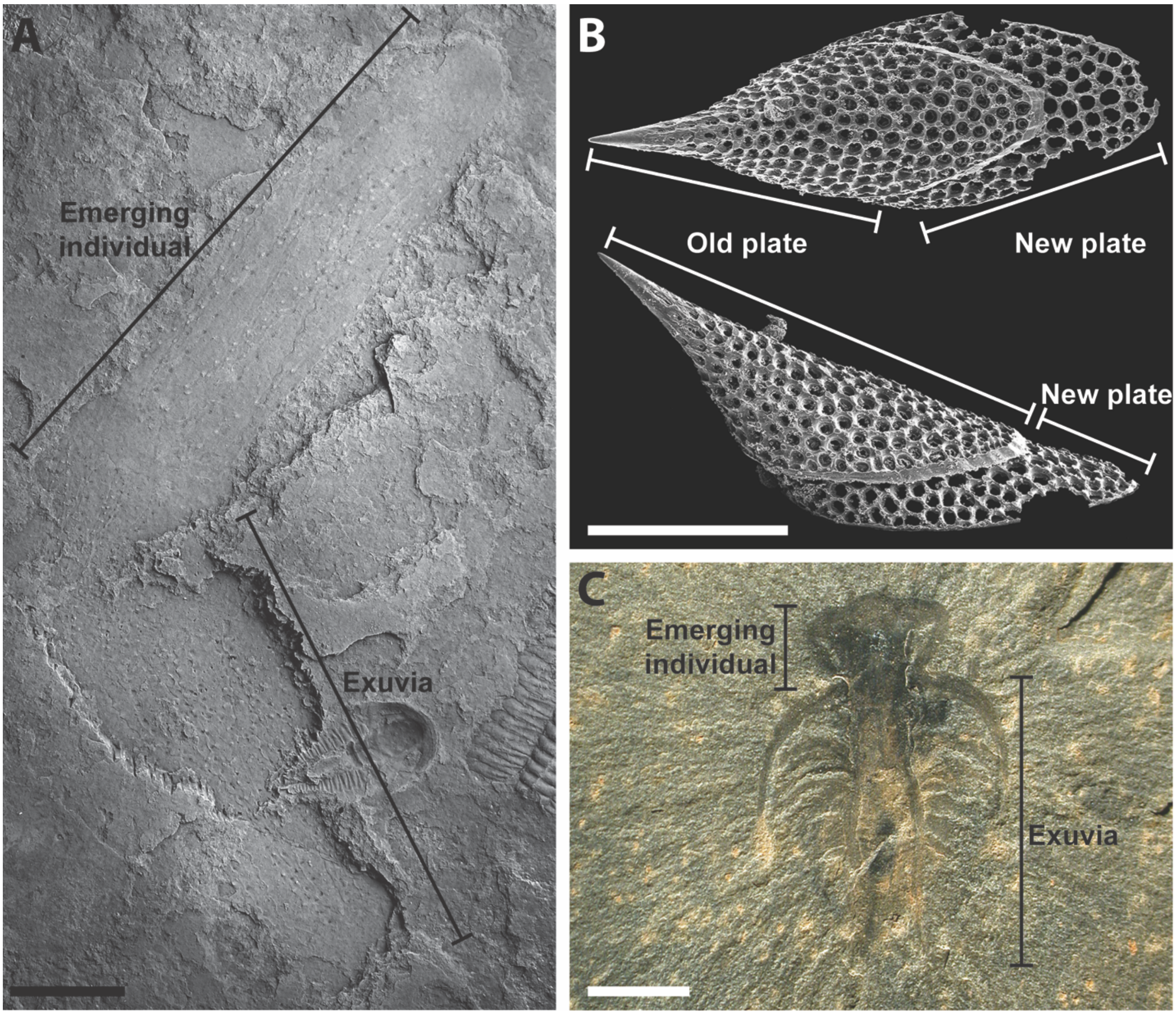

Fig. 7. Rare examples of Cambrian fossil preservation during ecdysis. A: The stem-lineage loriciferan *Sirilorica pustulosa* from the lower Cambrian Sirius Passet fauna of North Greenland, with a compressed specimen emerging from an exuvia. Scale bar 10 mm. Photo credit: J. Peel (Peel et al., 2013). B: Conjoined plates of the lobopodian *Onychodictyon* sp. from the lower Cambrian of North Greenland in plan (top image) and lateral (bottom image) view. The new, larger plate underlies the smaller, older plate. Scale bar 500 μm. Photo credit: T. Topper (Topper et al., 2013). C: The arthropod *Marrella splendens* from the middle Cambrian Burgess Shale. Scale bar 5 mm. Photo credit: D. García-Bellido (García-Bellido and Collins, 2004).

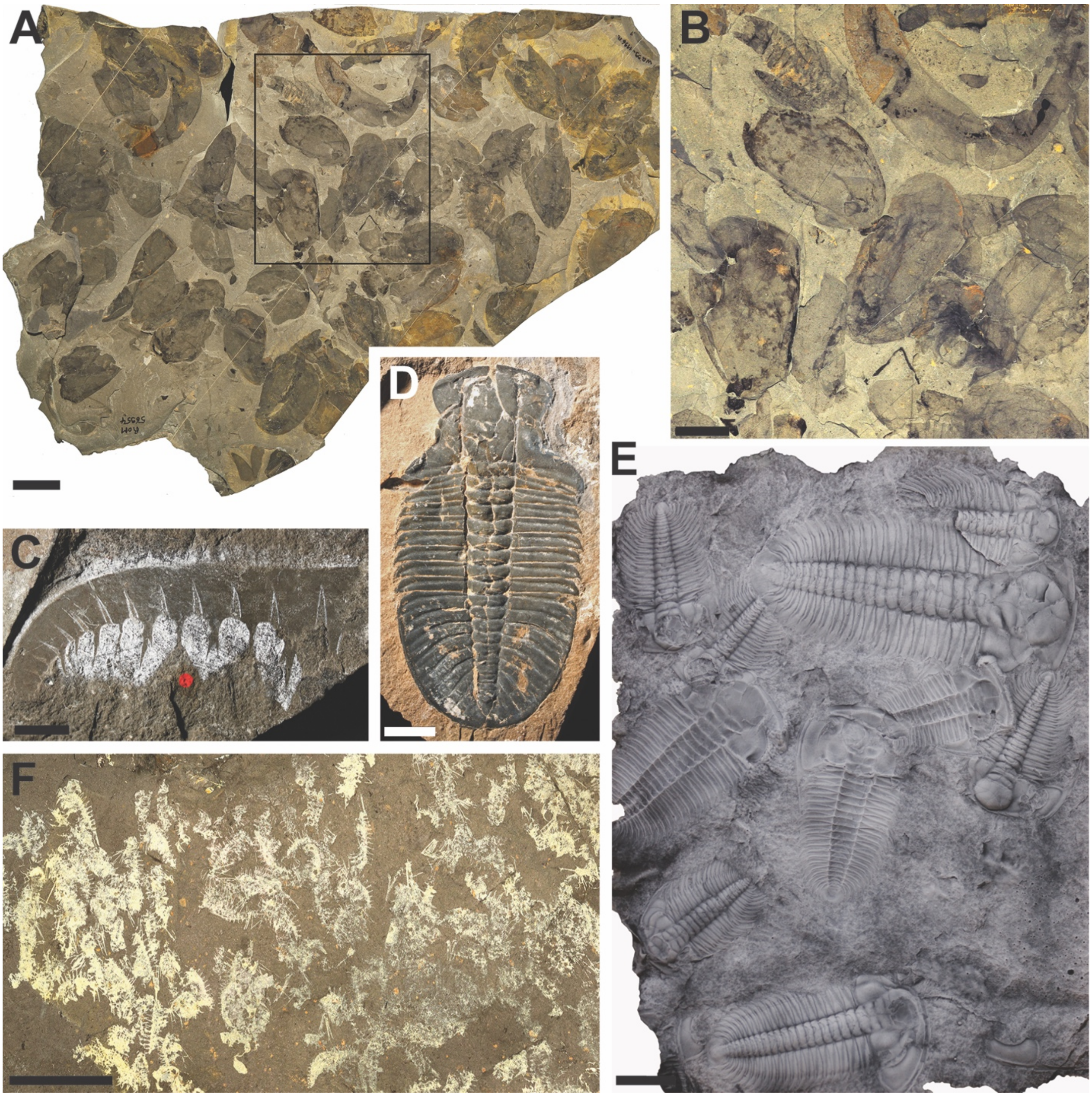

Fig. 8. Mass moulting in the Cambrian fossil record. A: Complete slab showing synchronized moulting in *Canadaspis* from the Burgess Shale. ROM 62274. Scale bar 10 mm. Photo credit: J. Haug (Haug et al., 2013). Black box indicates closeup in B. C: Frontal appendage of *Anomalocaris canadensis* found with supposed trilobite mass moulting event in the Mount Stephen trilobite beds. GSC 3418a. Scale bar 10 mm. D: Exuvia of *Ogygopsis klotzi* from mass moulting event at the Mount Stephen trilobite beds. OUMNH AT205. Scale bar 5 mm. E: Cluster of paradoxidid trilobites preserved on a mass moulting surface from Jämtland, Sweden. PMU 25711/4-6, 74-79. Scale bar 10 mm. Photo credit: J. Ebbestad (Ebbestad et al., 2013). F: Synchronized moulting slab

of megacheiran specimens from the Burgess Shale. ROM 62275. Scale bar 5 mm. Photo credit: J. Haug (Haug et al., 2013).

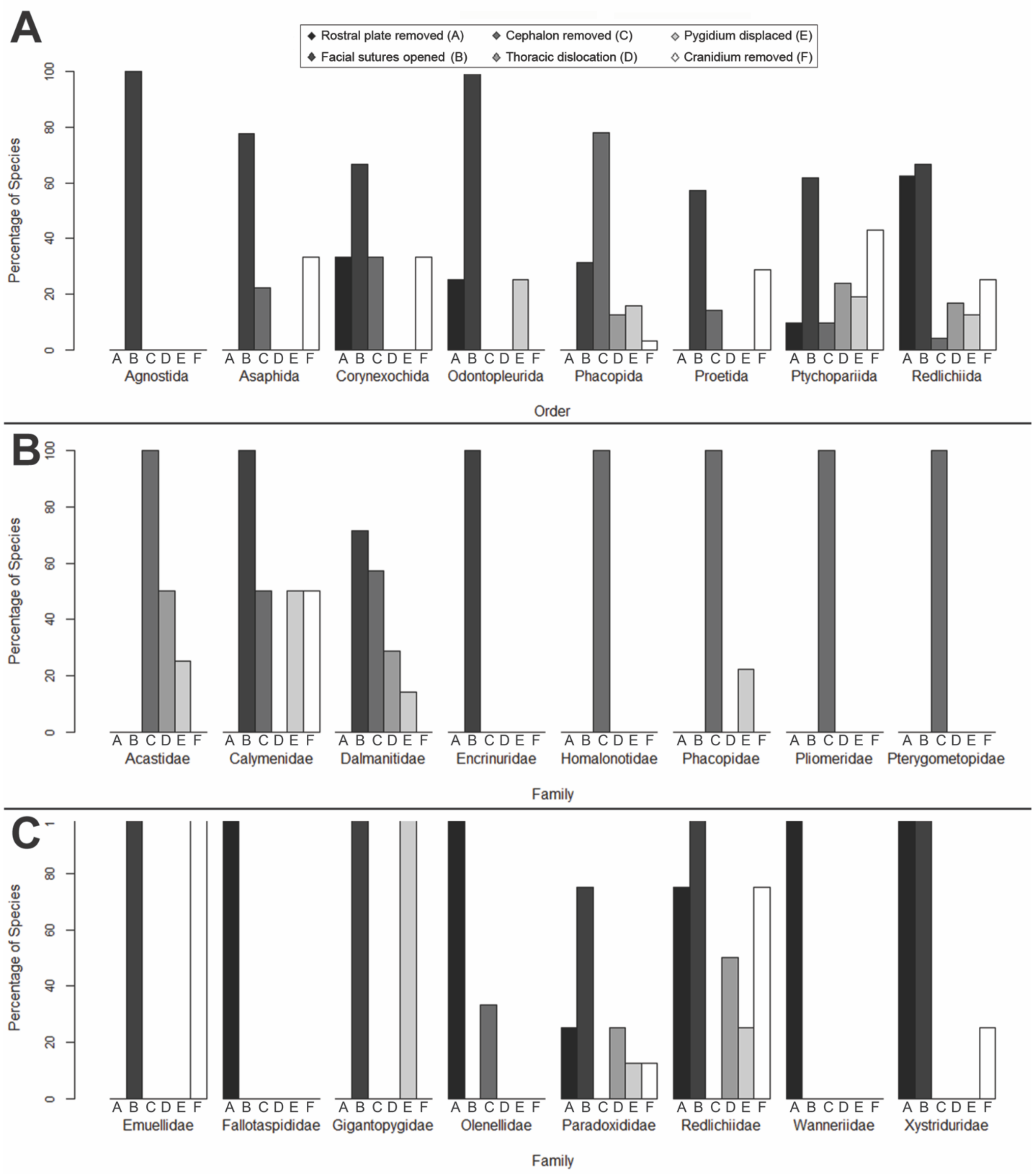

Fig. 9. Ecdysial behaviour displayed by trilobite Orders and Families. A: The percentage of trilobite species within different Orders displaying each of the six ecdysial behaviours. However, n=<5 for Agnostida, Corynexochida and Odontopleurida. B: The percentage of phacopid trilobite species within different Families displaying each of the six ecdysial behaviours. However, n=<5

for all Families but Dalmanitidae and Phacopidae. C: The percentage of redlichiid trilobite species within different Families displaying each of the six ecdysial behaviours. However, n=<5 for all Families but Paradoxididae. These behaviours are not mutually exclusive (ie. one species may show two or three ecdysial behaviours), and so totals may add up to more than 100% for each Order.

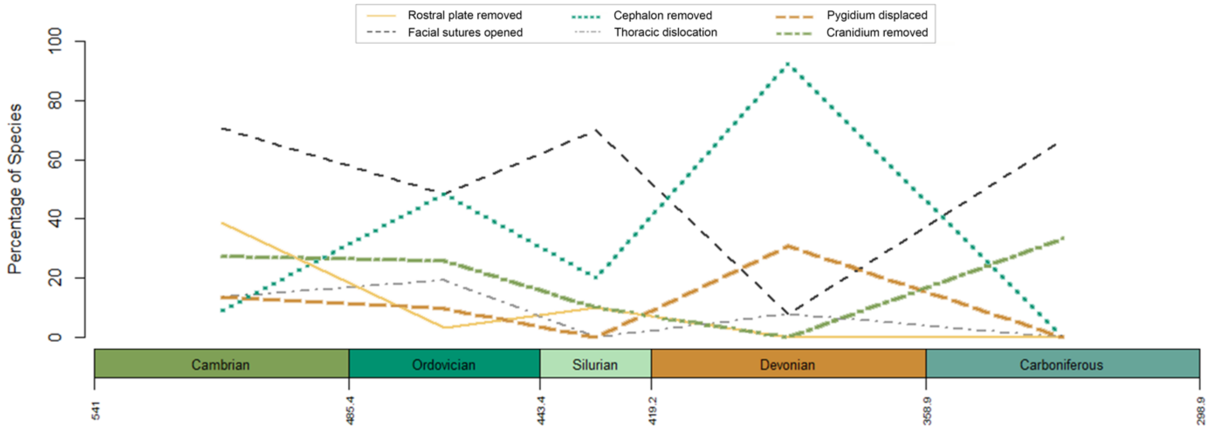

Fig. 10. The percentage of trilobite species across all eight Orders displaying each of the six ecdysial behaviours, through geological Periods from the Cambrian to Carboniferous. These behaviours are not mutually exclusive (ie. one species may show two or three ecdysial behaviours), and so totals may add up to more than 100% for each time Period. Time scale after Gradstein et al. (2012). Abbreviations: Terre., Terreneuvian; Miss., Mississippian; Pennsyl., Pennsylvanian.

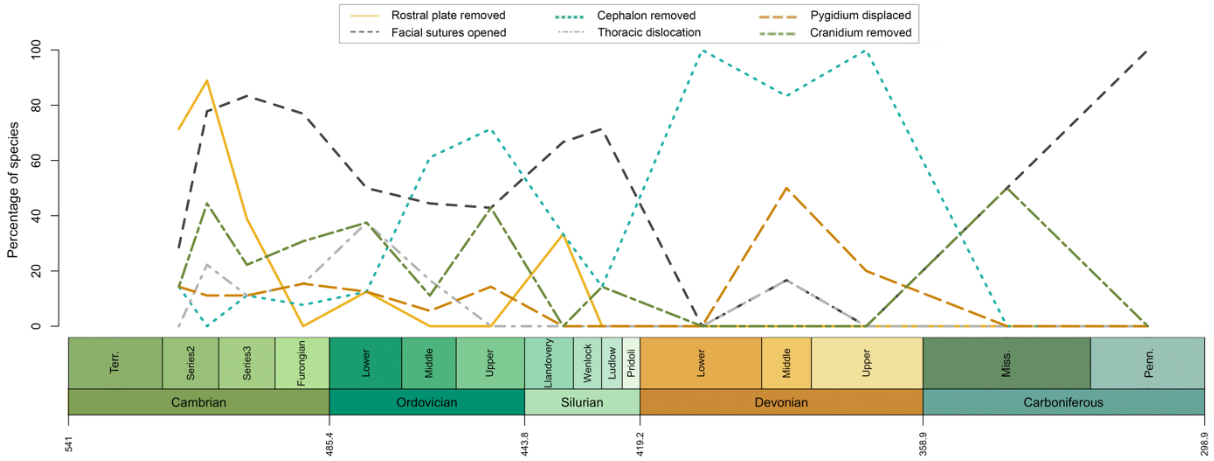

Fig. 11. The percentage of trilobite species across all eight Orders displaying each of the six ecdysial behaviours, through geological Series, from the Terreneuvian (Early Cambrian) to Pennsylvanian (Late Carboniferous). These behaviours are not mutually exclusive (ie. one

species may show two or three ecdysial behaviours), and so totals may add up to more than 100% for each geological Series. Time scale after Gradstein et al. (2012). Abbreviations: Terre., Terreneuvian; Miss., Mississippian; Pennsyl., Pennsylvanian.