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

Allison C. Daley [a, b, *], Harriet B. Drage [a, b]

[a] Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom
[b] Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PZ, United Kingdom

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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, synthesising 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.

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

* Corresponding author. Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom.
E-mail address: Allison.Daley@zoo.ox.ac.uk (A.C. Daley).

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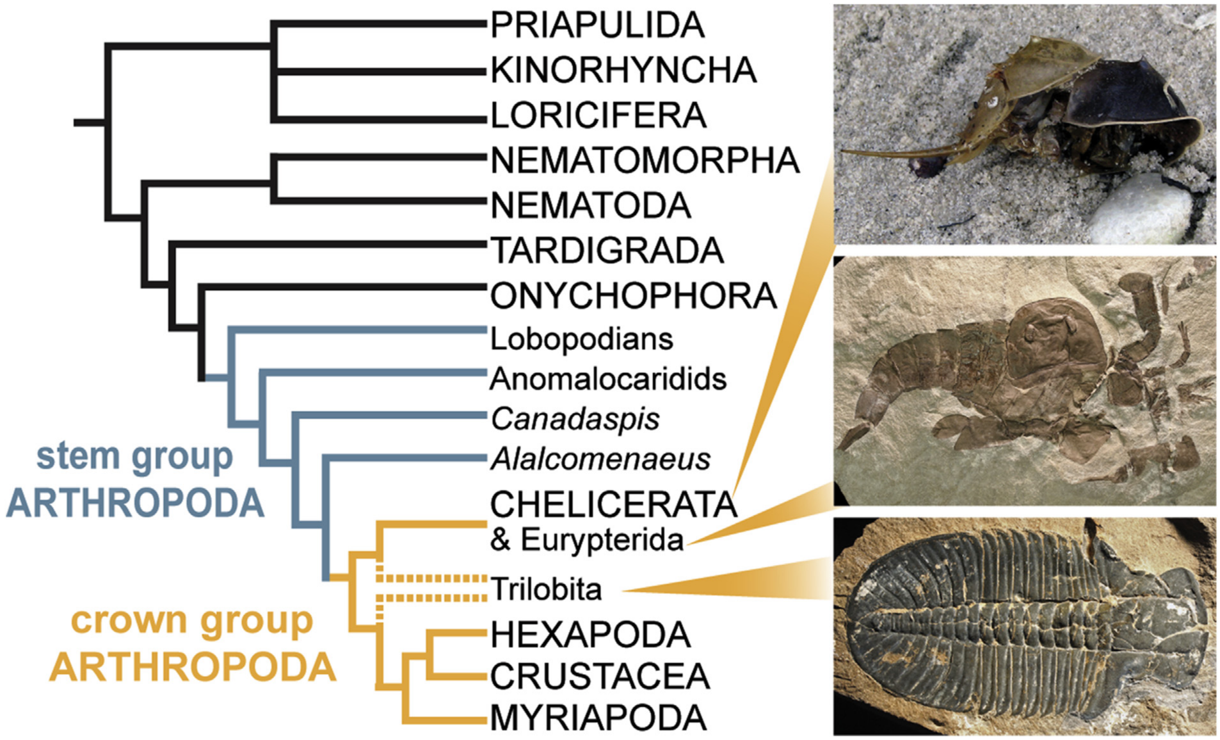

Fig. 1. Generalised phylogeny of ecdysozoans, with extant phyla in ALLCAPS and fossil groups/taxa in lowercase lettering. Phylogeny based on Dunn et al. (2014), Rota-Stabelli et al. (2013) and Legg et al. (2013). Images from top: Horseshoe crab in the process of moulting (Image credit: Wikimedia Commons);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

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.