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Tracing the trilobite tree from the root to the tips: A model marriage of fossils and phylogeny

Bruce S. Lieberman [a,b,*], Talia S. Karim [b]

[a] Department of Geology, 1475 Jayhawk Boulevard, 120 Lindley Hall, University of Kansas, Lawrence, KS 66045, USA
[b] Division of Invertebrate Paleontology, Natural History Museum/Biodiversity Research Center, University of Kansas, Lawrence, KS 66045, USA

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ABSTRACT

Trilobites are a highly diverse group of extinct arthropods that persisted for nearly 300 million years. During that time, there was a profusion of morphological form, and they occupied a plethora of marine habitats. Their diversity, relative abundance, and complex morphology make them excellent candidates for phylogenetic analysis, and partly as a consequence they have been the subject of many cladistic studies. Although phylogenetic knowledge is certainly incomplete, our understanding of evolutionary patterns within the group has dramatically increased over the last 30 years. Moreover, trilobites have formed an important component of various studies of macroevolutionary processes. Here, we summarize the phylogenetic breadth of knowledge on the Trilobita, and present various hypotheses about phylogenetic patterns within the group, from the highest to the lowest taxonomic levels. Key topics we consider include the question of trilobite monophyly, the phylogenetic position of trilobites vis à vis extant arthropod groups, and inter- and intra-ordinal relationships.

1. Introduction

The Trilobita are an impressively diverse extinct clade, familiar to schoolchildren and scientists alike, that captures the imagination for both aesthetic and scientific reasons. Their 300 million year history, deployed across perhaps 10,000 species, combined with a complex anatomy (Fig. 1) that can be coded for a broad array of quantitative and qualitative characters, has made them model citizens for applying phylogenetic methods to fossil organisms. Indeed, trilobites figured prominently in some of the earliest forays into cladistic analysis on American shores (e.g., Eldredge, 1972, 1973; Schaeffer et al., 1972; Eldredge and Cracraft, 1980). Given the early adoption of cladistic approaches by some trilobite workers, it is only fitting to consider how phylogenetic approaches have broadened our understanding of evolution. The principle focus of this paper will be on the phylogenetic position of trilobites within the Arthropoda and phylogenetic patterns nested within the Trilobita at several hierarchical levels. However, one noteworthy aspect of phylogenetic studies incorporating trilobites is that they have not only been used to adduce questions about the nature of evolutionary patterns. They have also figured in studies about the processes that may have motivated these patterns. For instance, punctuated equilibria (Eldredge, 1971a; Eldredge and Gould, 1972), the notion that species are stable throughout much of their history and new species evolve via allopatric speciation, was developed based on information from trilobite phylogenies. Trilobite phylogenies have been used to explore how rates of evolution, especially rates of speciation, vary throughout the history of life (e.g., Lieberman, 2001a), and consider the meaning of disparity and how it varies over evolutionary time and during the Cambrian radiation (e.g., Smith and Lieberman, 1999). They have also served as the basis for studies of the mechanisms of evolutionary radiations (e.g., Eldredge and Cracraft, 1980; Eldredge, 1982; Abe and Lieberman, 2009) and mass extinctions (Congreve and Lieberman, 2008). In addition, phylogenetic analyses of trilobites have served as the essential component data of various paleobiogeographic studies (e.g., Lieberman and Eldredge, 1996; Lieberman, 1997, 2000; Turvey, 2002, 2005; Lee et al., 2008). Finally, they have even played a role in testing hypotheses in the burgeoning new field of evo-devo (e.g., Hughes et al., 1999; Scholtz and Edgecombe, 2005, 2006).

Here we present a survey of phylogenetic research on trilobites. We present the phylogenies herein not as the final word on evolutionary relationships, and readers are of course referred to the cited references for greater details on analytical protocols, character data, stratigraphic distributions, and other pertinent information. Instead, they are offered as a framework to build on for future

* Corresponding author at: Department of Geology, 1475 Jayhawk Boulevard, 120 Lindley Hall, University of Kansas, Lawrence, KS 66045, USA. Tel.: +1 785 864 2741; fax: +1 785 864 5276.
E-mail address: blieber@ku.edu (B.S. Lieberman).

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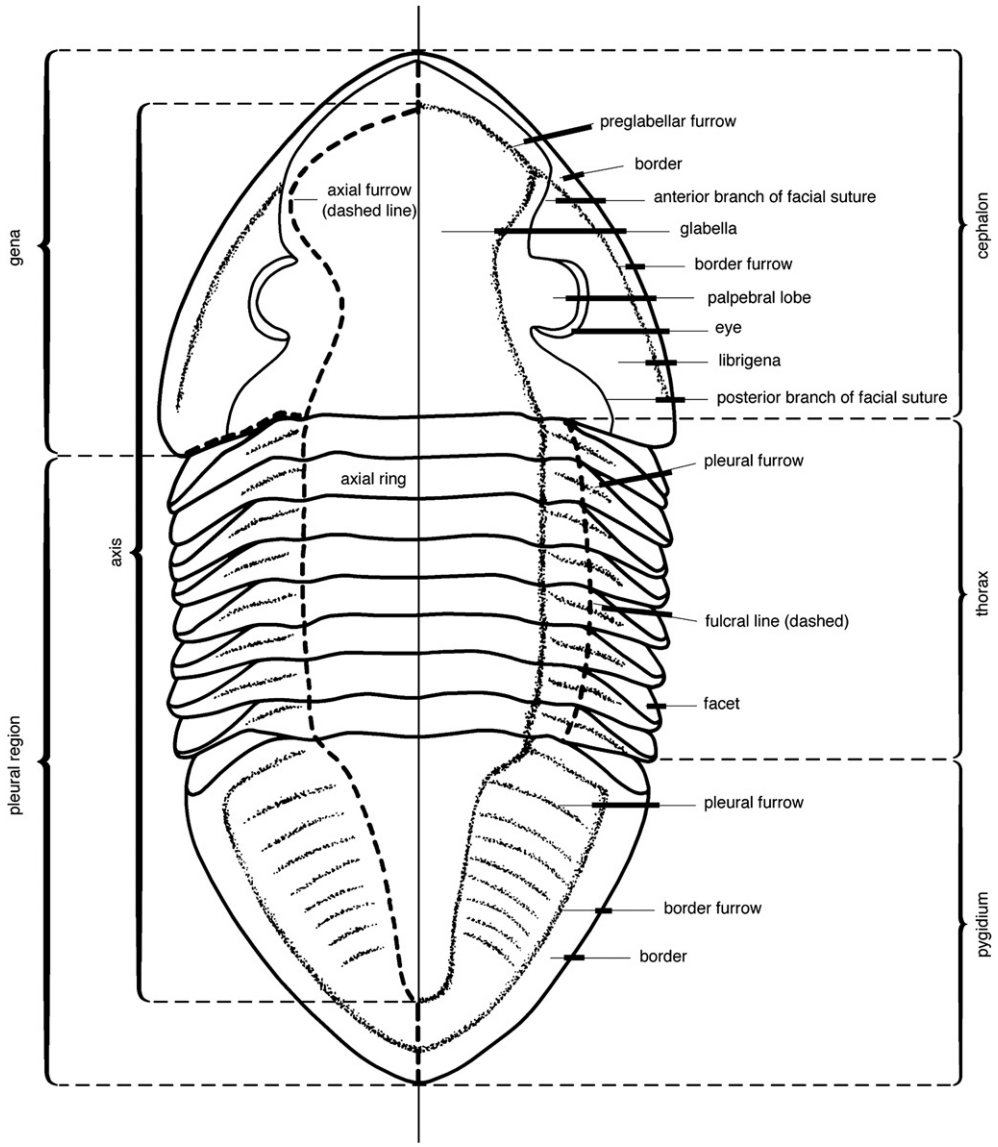

Fig. 1. Trilobite (*Isotelus*, from the Ordovician period) exoskeleton showing major anatomical features, from Whittington et al. (1997), used with permission of the Paleontological Institute, University of Kansas.

studies. There is of course an extensive literature on trilobites that does not include an analytical phylogenetic component. Much of this literature also contains many important insights into trilobite evolution, but for the purposes of brevity and clarity it will not be considered herein. Further, our survey itself can serve as a unified resource and synthesis of what is available regarding cladistic studies of trilobites. This will of course point out to those who may not be familiar with it the breadth of phylogenetic research conducted on trilobites thus far. However, it will perhaps also allow additional hypotheses about survival during mass extinctions, the tempo and mode of evolution, and paleobioeography to be framed and tested.

2. Stratigraphic history of the Trilobita

The oldest trilobites are found in Lower Cambrian rocks roughly 525–530 million years old. The first records may be in Baltica (present day Scandinavia and the eastern European platform); however, shortly on the heels of these occurrence records, trilobites also appear in Lower Cambrian rocks from Siberia and China and then Antarctica, North America, and Australia (in no particular order). One interesting aspect of the early history of trilobites is that straightaway trilobites show a prominent pattern of biogeographic differentiation (Fortey et al., 1996; Fortey and Owens, 1997; Lieberman, 1999a). Fortey et al. (1996) were the first to argue in detail that this early pattern of biogeographic differentiation implied a potentially long, hidden history of trilobites that might indicate the group's origins extend well back into the Proterozoic. Lieberman (2003) and Meert and Lieberman (2004) used phylogenetic analysis, phylogenetic biogeography, and information from tectonics to constrain the earliest origins of trilobites to Siberia, which was once a separate continental bloc. Further, results suggested that the origins of Trilobita could be constrained somewhere within the interval 550–600 Ma and occurred during the breakup of the supercontinent Pannotia (Lieberman, 2003; Meert and Lieberman, 2004): that is to say, anywhere from 20 to 70 million years before the group first appeared in the fossil record. This pattern of an early, hidden history with subsequent proliferation may be