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

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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.

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## 1. Introduction

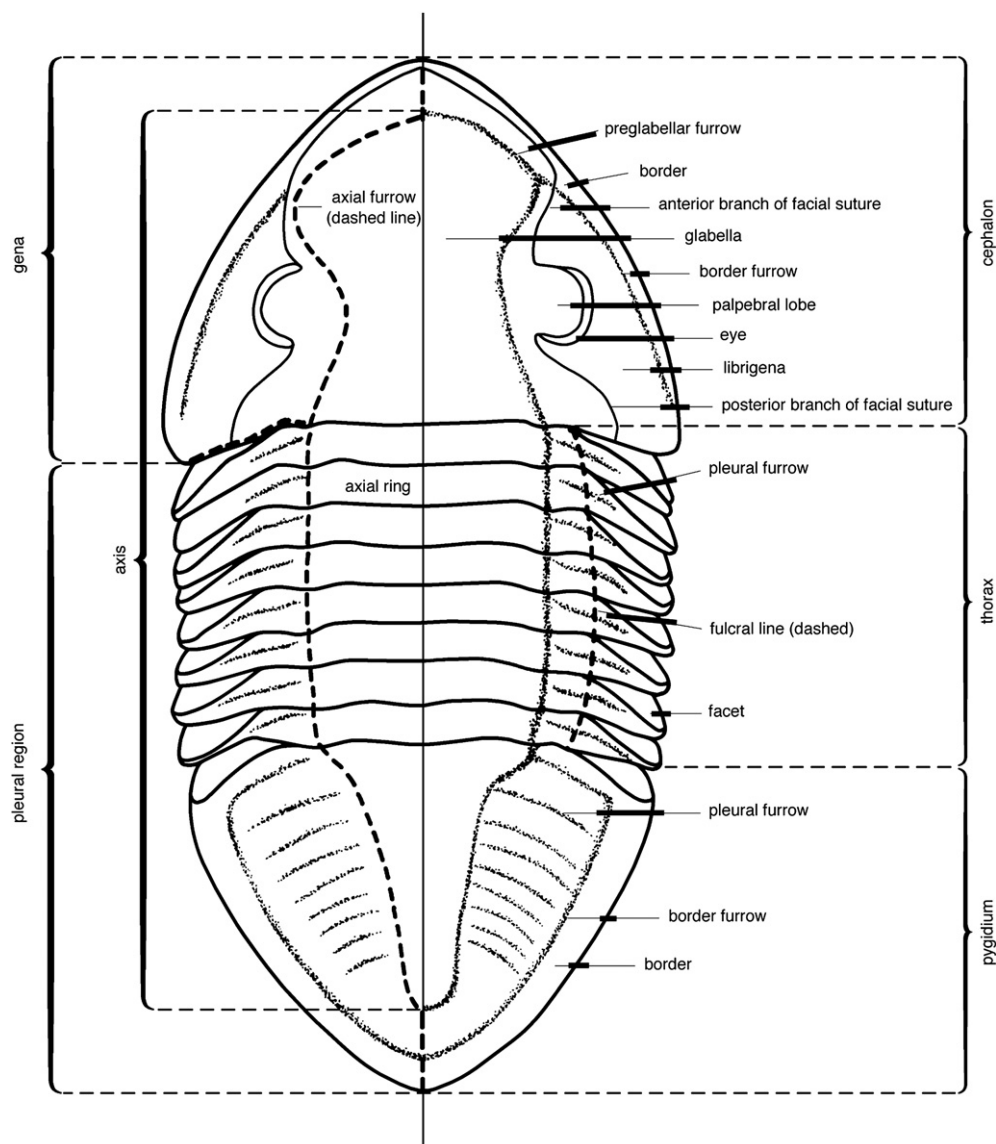
The Trilobita are an impressively diverse extinct clade, familiar to schoolchildren and scientists alike, that captures the imagination for both aesthetic and scientific reasons. Their 300 million year history, deployed across perhaps 10,000 species, combined with a complex anatomy (Fig. 1) that can 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

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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 paleobiogeography 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

a more general phenomenon that perhaps has relevance for our understanding of how large scale evolution typically transpires (Lieberman et al., 2007). Regarding the initial diversification of trilobites, it is likely that the breakup of the supercontinent Pannotia at the end of the Proterozoic may have provided fuel for the evolution of trilobites, and other taxa, during the Cambrian radiation by amplifying opportunities for allopatric speciation.

Trilobites may well represent the exemplar animal of the Cambrian, and continued to radiate throughout the Ordovician (Droser et al., 1996; Adrain et al., 1998, 2000, 2004), but they were particularly hard hit during the end Ordovician mass extinction (Chatterton and Speyer, 1989; Fortey and Owens, 1990, 1997; Melott et al., 2004). This was one of five great debacles in the history of life when a large percentage of animal life was eliminated in a geologically short period of time. Although their diversity rebounded somewhat, again they were hard hit during the next so-called mass extinction, the Late Devonian biodiversity crisis (McGhee, 1996; Rode and Lieberman, 2004). They stayed at relatively low diversity levels after that (Brezinski, 1999), succumbing at the end of the Permian during the largest mass extinction in the history of life (Fortey and Owens, 1990, 1997).

One especially poignant pattern in trilobite evolution is that they basically appear to thrive, except during times of mass extinction. The precise reasons for the trilobite's ultimate demise is one of those age old questions whose answer will likely never be known, but it appears tied up, paradoxically, with their proclivity to have high rates of speciation. The reasons this matters is that groups that have high speciation rates also tend to have high rates of extinction (Eldredge, 1979; Stanley, 1979; Vrba, 1980). Trilobites are in this respect a highly volatile animal group, as were the ammonoids (Gilinsky and Bambach, 1987; Gilinsky, 1994). The typically high rates of extinction in trilobites conspired with the inordinately high rates of extinction during a mass extinction to push the group to, and over, the proverbial edge.

### 3. The question of trilobite monophyly and the phylogenetic position of Trilobita within the Arthropoda

Two of the major topics in trilobite phylogenetics have been the question of trilobite monophyly and addressing their place within the broader arthropod clade. Lauterbach (1980, 1983) was the first to challenge the age old assumption of trilobite monophyly. However, both Fortey and Whittington (1989) and Ramsköld and Edgecombe (1991) reconsidered Lauterbach's proposal in greater detail and concluded that the trilobites were indeed monophyletic and several synapomorphies could be used to define the group. The principle divergence between Ramsköld and Edgecombe's (1991) analysis and Fortey and Whittington's (1989) concerns the position of the agnostoids, an appropriately named 'trilobite-like' group consisting of diminutive, blind, presumed pelagic forms that lack dorsal sutures (used for molting) on the exoskeleton and also lack a trilobite style hypostome. Ramsköld and Edgecombe (1991) treated these as outside of the trilobite ingroup whereas Fortey and Whittington (1989) and Fortey and Theron (1995) viewed them as ingroup trilobites (see also Fortey, 2001) (Fig. 2). Fortey (2001), by contrast, grouped the agnostoids and eodiscoids with the Olenellina. (Even though the agnostoids are enigmatic, this has not made them completely recalcitrant to phylogenetic analysis, as Westrop et al. (1996) presented a phylogenetic analysis of one of the important families of these, the Ptychagnostidae.)

Part and parcel with the issue of trilobite monophyly, phylogenetic approaches made it possible to consider the issue of trilobite relationships with other arthropods in greater detail. Until relatively recently, the consensus view was that among the major extant clades of arthropods the chelicerates were the group

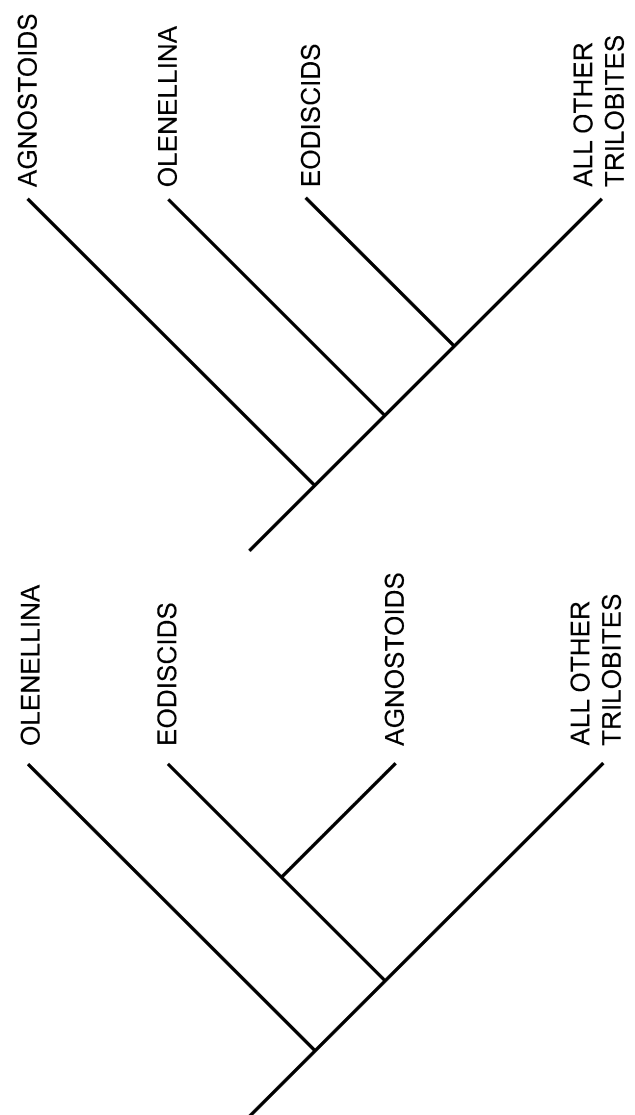


Fig. 2. Competing hypotheses for the positions of Trilobita relative to agnostoids from Ramsköld and Edgecombe (1991) (top) and Fortey and Whittington (1989) (bottom).

trilobites shared closest affinity with. For instance, Edgecombe and Ramsköld (1999) viewed trilobites as arachnates, nested within several clades of arachnomorph arthropods from such Cambrian soft-bodied faunas as the Burgess Shale and the Chengjiang biota. (A monophyletic Arachnomorpha would include these taxa plus chelicerates; further, many arachnomorphs would be part of a paraphyletic grade broadly resembling chelicerates yet lacking the defining features of that clade, including chelicerae. Such "arachnomorphs" were presumed to share a common ancestor with chelicerates to the exclusion of other arthropod groups on the basis of their shared possession of certain developmental commonalities and also the shape of the cephalic shield.) Hendricks and Lieberman (2008) reiterated their conclusions. Wills et al. (1998), building on the analyses of Briggs and Fortey (1989) and Briggs et al. (1992), incorporated a broad range of Cambrian soft-bodied arthropods into a phylogenetic analysis that also included trilobites and several extant representatives of chelicerates, crustaceans, and uniramiens, as well as onychophorans. They recovered Schizoramia, with the crustacea sister to the arachnomorphs (Fig. 3). The results from Cotton and Braddy (2003) largely reiterated this phylogenetic topology.



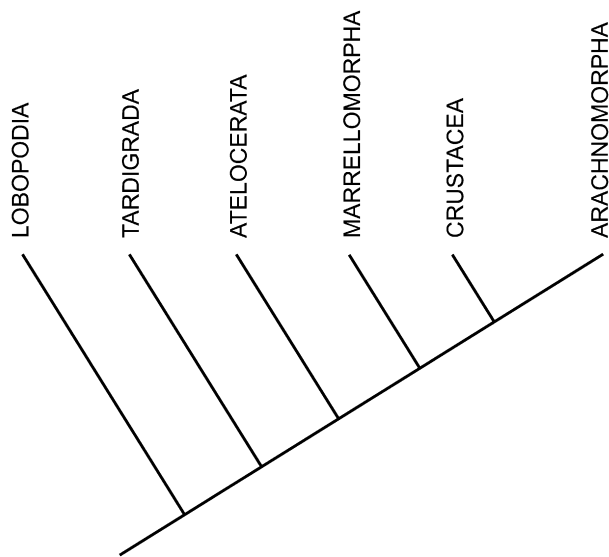


Fig. 3. Hypothesis of relationships derived from analysis presented in Wills et al. (1998).

Dunlop (2005) and Scholtz and Edgecombe (2005, 2006), however, have presented an interesting discussion of the potential problems with the Schizoramia grouping, and the association of trilobites with some arachnomorphs and with the chelicerates. In particular, the studies endorsing trilobite affinities with chelicerates were not able to consider the relationships of relevant taxa like the arachnids and pycnogonids (Dunlop, 2005). Including arachnids and especially pycnogonids in such studies, while maintaining the same tree topology, would result in many character reversals and losses (Scholtz and Edgecombe, 2005).

Studies that concentrate on extant taxa and combine molecular and morphological data tend to retrieve the group Mandibulata (crustaceans and uniramians), which is in turn sister to the Chelicerata (Edgecombe et al., 2000; Giribet et al., 2001; Dunlop, 2005). Scholtz and Edgecombe (2005) argued against the notion that there even was an “arachnomorph” clade and, of greatest relevance here, suggested that trilobites did not group with the chelicerates. Instead, they are part of the stem-lineage of Mandibulata, sharing

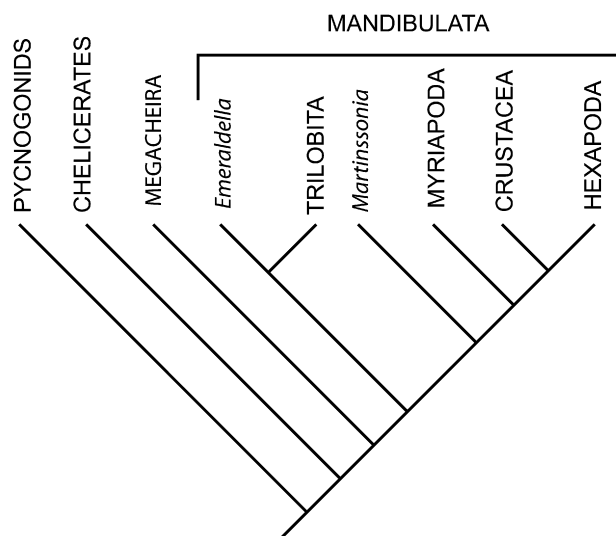


Fig. 4. Hypothesis of relationships derived from analysis presented in Scholtz and Edgecombe (2006).

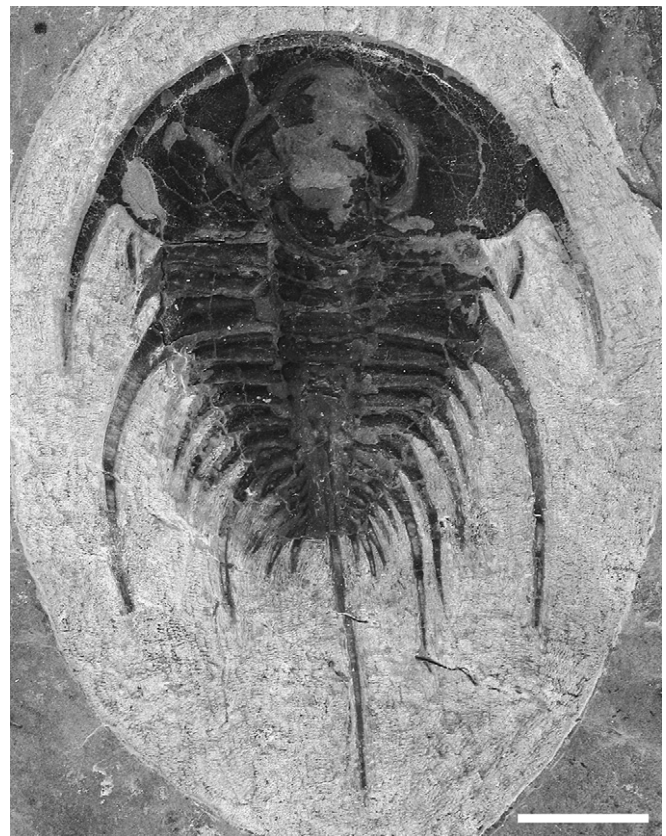


Fig. 5. *Bristolina* sp., University of Kansas Museum of Invert. Paleo. (KUMIP) 314495, from the Lower Cambrian, Northwest Territories, Canada. Scale bar = 1.0 cm.

among other traits a sensorial antenna. In a sense, this was a return to what was the more traditional, pre-cladistic view of trilobites, that treated them as most closely related to crustaceans on account of their common biramous appendages (these were held to be of especial significance before it was recognized how many different fossil arthropods also had biramous appendages) and their aforementioned antennae, although Arachnomorpha including trilobites is also an old concept (Scholtz and Edgecombe, 2005).

Clearly the results of Wills et al. (1998) are distinctly at odds with the discussion of Scholtz and Edgecombe (2005). Notably the latter authors did consider in great detail the homology of various character complexes, and this culminated in a new analysis by Scholtz and Edgecombe (2006) that retrieved the topology in Fig. 4. Thus, sadly at this time consensus about the higher-level position of trilobites within Arthropoda is lacking. Interestingly, the monophyly of trilobites was originally considered within the context of chelicerate affinity, although even among those workers endorsing mandibulate affinity monophyly for the group still is favored (e.g., Dunlop, 2005; Scholtz and Edgecombe, 2005, 2006).

#### 4. The basal split within the Trilobita

There is ample phylogenetic evidence for a basal phylogenetic split within the Trilobita. Indeed, it was this basal phylogenetic split that largely relates to the aforementioned pattern of biogeographic differentiation in the earliest known trilobites (Lieberman, 1999a). On one side of this dichotomy are the wholly Early Cambrian *Olenellina*, with a diversity of ~100 species that includes several large trilobites, some of which serve as the veritable poster children of Early Cambrian life (Fig. 5). These trilobites had traditionally been

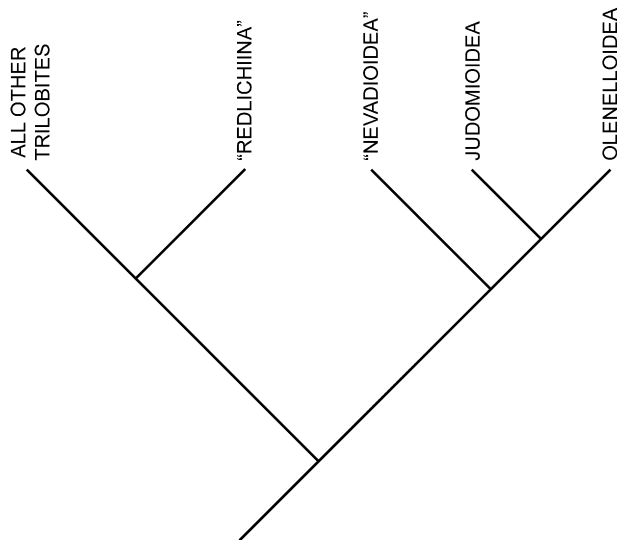


Fig. 6. Hypothesis of relationships based on results presented in Lieberman (2002).

grouped by their shared possession of several primitive characters, including their absent dorsal sutures and a highly reduced pygidium, but phylogenetic studies have also revealed support for this clade (Lieberman, 1998, 1999b, 2001b). This group includes one diverse superfamily, the Olenelloidea (containing ~80 species), along with the Judomioidea, and what is presently a paraphyletic superfamily, the “Nevadioidea”, on the branch leading to these. Juxtaposed against these are all the other trilobites, including a paraphyletic grade of Cambrian trilobites, the “Redlichiina”, that leads to the post-Cambrian stock of trilobites (Lieberman, 1998, 2001b, 2002) (Fig. 6). A detailed species-level supertree for the Olenelloidea was published in Lieberman (1999b); a species-level

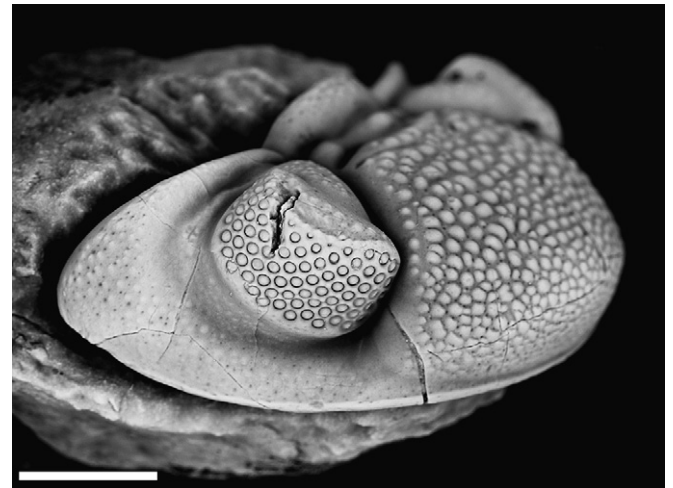


Fig. 8. *Phacops rana*, KUMIP 240296, from the Middle Devonian, Lucas County, Ohio, loc. RHR88-2. Scale bar = 0.5 cm.

supertree for the Olenelloidea plus “Nevadioidea” plus basal “Redlichiina” was presented in Lieberman (2002). (Because these have been recently published they are not provided herein.)

## 5. Discerning broad structure in the trilobite tree

Since many of the major groups of trilobites were defined in a pre-cladistic context, it is perhaps not surprising that several of these groups are paraphyletic, e.g., “Redlichiina.” This has partly served as an impediment to large scale phylogenetic studies aimed at working out ordinal relationships. Throughout, Richard Fortey has led the charge in this area as the veritable doyen of trilobite research (e.g., Fortey and Owens, 1975, 1990, 1997; Fortey, 1983, 1990, 2001, 2003). One pattern manifestly apparent in a consideration of trilobite relationships is not only is “Redlichiina” paraphyletic but “Corynexochida” and also “Ptychopariida” are as well. The latter particularly is a pivotal group that gives rise to the great majority of post-Cambrian trilobites (Eldredge, 1977; Fortey and Chatterton, 1988; Edgecombe, 1992; Fortey and Owens, 1990, 1997; Fortey, 2001; Jell and Adrain, 2003). At this time “Ptychopariida” largely comprise a waste basket taxon of small Middle and Upper

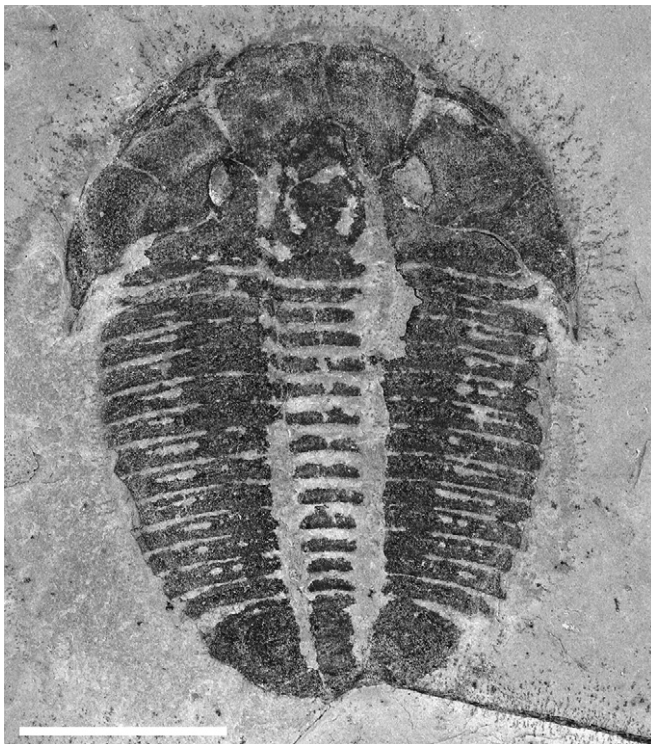


Fig. 7. *Elrathia kingii*, KUMIP 195429, from the Upper Cambrian, Millard County, Utah, loc. GRV80-21/5. Scale bar = 1.0 cm.

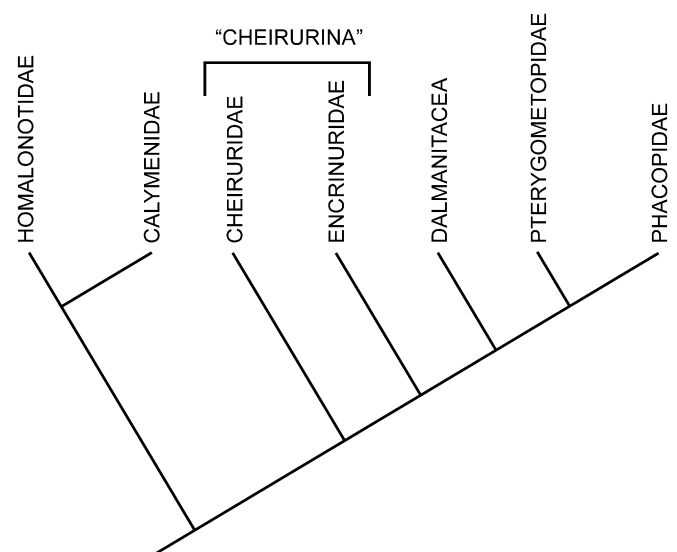


Fig. 9. Hypothesis of relationships based on results presented in Edgecombe (1992).

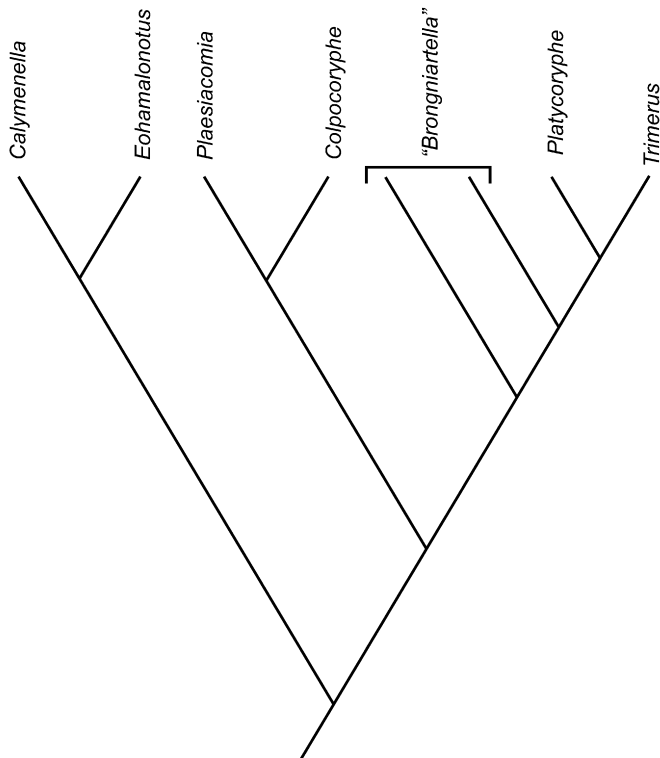


Fig. 10. Hypothesis of relationships based on results presented in Congreve and Lieberman (2008).

Cambrian trilobites, often disarticulated, that includes the most common trilobite, and among the most prolific of all fossils, *Elrathia kingii* (Fig. 7).

Understanding the relationships of the dominant post-Cambrian groups of trilobite to their older Cambrian sister-taxa remains a major unresolved question in trilobite evolution. This problem was termed “cryptogenesis” by Stubblefield (1959) and Whittington (1981). At present this question has been largely unexamined due in part to poor sampling across the critical time of

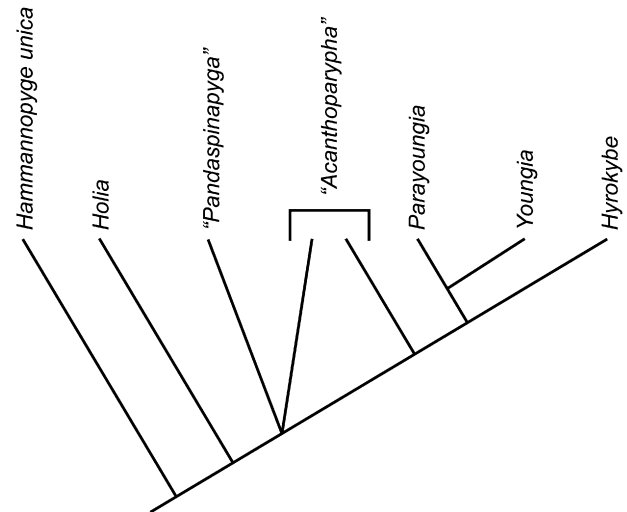


Fig. 12. Hypothesis of relationships based on results presented in Adrain (1998).

diversification. Worker bias (i.e., specialists working only on Cambrian or only on Ordovician trilobites) has also hampered our understanding of the origins of the dominant post-Cambrian groups (Edgecombe, 1992; Fortey, 2001).

Edgecombe (1992) commented in detail on “cryptogenesis” and ptychopariid paraphyly. In particular, its existence exaggerates the perceived amount of taxonomic turnover at the Cambrian–Ordovician boundary because a number of *de novo* Ordovician trilobite orders have been established without considering the context of their origins; further, the “Ptychopariida” was presumed to disappear at the end of the Cambrian (Edgecombe, 1992).

There have been some attempts to unravel phylogenetic structure within the group. In particular, the paper by Fortey and Chatterton (1988) appears to represent the first published study on trilobites using computer analysis of character data. Their results were expanded on and presented as evolutionary trees in Fortey and Owens (1997) and Fortey (2001). “Ptychopariida” is posited to emerge out of the paraphyletic mass of “Redlichiina” with the set of relationships suggested by Fortey (2001). Fortey and Chatterton (1988) and Edgecombe (1992) discussed in greater detail some of the specific families of “Ptychopariida” that might be most closely

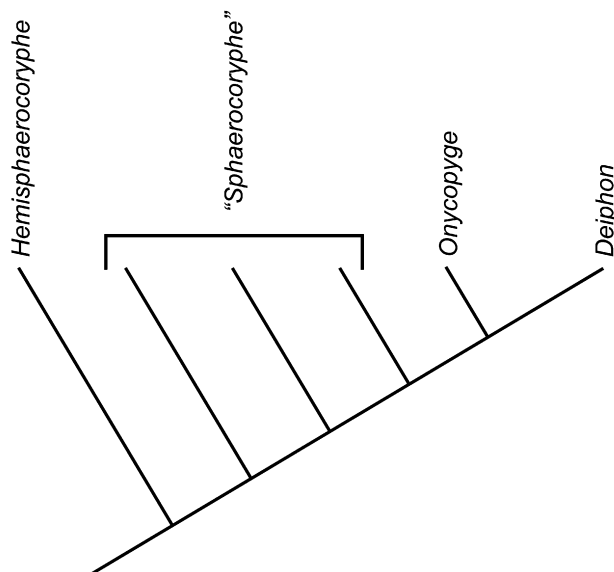


Fig. 11. Hypothesis of relationships based on results presented in Congreve and Lieberman (2010).

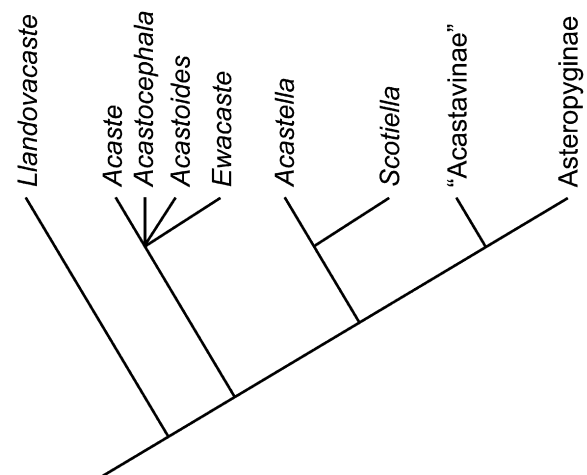


Fig. 13. Hypothesis of relationships based on results presented in Ramsköld and Edgecombe (1993). The Calmoniidae are presumed to be nested within the Acastidae (Edgecombe, pers. comm., 2009).



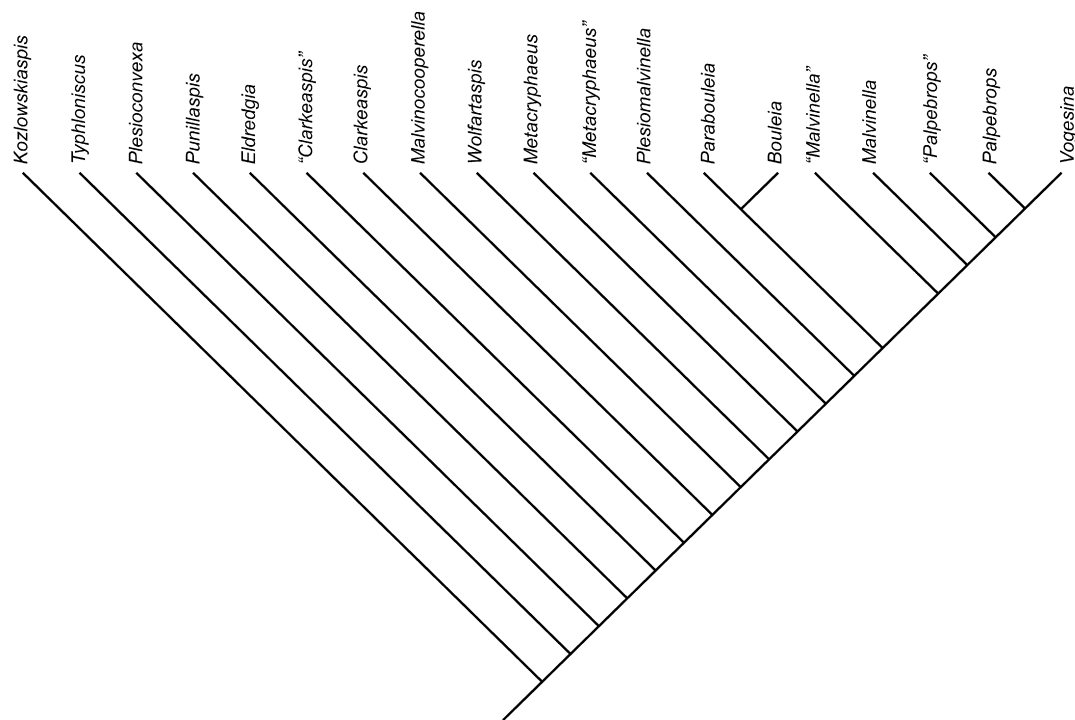


Fig. 14. Hypothesis of relationships based on results presented in Lieberman et al. (1991) and Lieberman (1993).

related to the Asaphida. Although phylogenetic analyses of trilobites within this paraphyletic grade have proven challenging, some of the structure of the individual groups has been examined in cladistic studies (see discussion below).

## 6. Intra-ordinal relationships

### 6.1. Phacopida

The Phacopida comprises one of the most diverse and charismatic components of trilobite diversity: certain representatives display particularly intricate form including spinose projections, head ornaments, etc. For this reason it is not surprising that the greatest number of phylogenetic studies of trilobites have concentrated on this order. Phacopids were originally presumed to originate in the Ordovician, although their roots clearly extend back into the paraphyletic mass of “Ptychopariida” in the Cambrian (Jell and Adrain, 2003). They vanished during the Late Devonian mass extinction (biodiversity crisis). Members of the Phacopida are united by, among other traits, their shared possession of a schizochroal, large lensed eye (Fig. 8). (Note that it was the evolution of those lenses that figured so prominently in the development of punctuated equilibria by Eldredge, 1971a and Eldredge and Gould, 1972.)

Edgecombe (1992) used parsimony analysis to consider the phylogenetic relationships of the major groups within the Phacopida, and he recognized that some of these groups as presently defined may be paraphyletic (Fig. 9). The close relationship between Homalonotidae and Calymenidae was also supported by a phylogenetic analysis based on larval characters conducted by Chatterton et al. (1990).

#### 6.1.1. Homalonotidae and Calymenidae

Further structure can be discerned within many of the major clades in Fig. 9. For instance, focusing on genera within the Homalonotidae, Congreve and Lieberman (2008) recovered the patterns of generic relatedness shown in Fig. 10.

There is less detailed knowledge of generic relationships within the Calymenidae. However, Ramsköld et al. (1994) generated a phylogeny for species of *Alcymene* and Turvey (2002) generated a phylogeny for species of *Neseuretus* and closely related genera.

#### 6.1.2. Cheiruridae

The Cheiruridae have been the subject of several recent phylogenetic analyses. For instance, unpublished work by J. Adrain and BSL revealed that species formerly assigned to the genus *Heliomera* in fact comprise a paraphyletic grade leading to *Heliomeroides*. Work by Congreve and Lieberman (2010) on one of the subfamilies (the Deiphoninae) within the Cheiruridae indicated the pattern of relationship in Fig. 11. Further, Adrain (1998) analyzed patterns within the Acanthoparyphinae (Fig. 12). However, the relationships among the different subfamilies within Cheiruridae have not as yet been rigorously examined in a phylogenetic context.

#### 6.1.3. Encrinuridae

A series of comprehensive phylogenetic analyses have been conducted on the Encrinuridae. This includes some of the earliest work applying computer based methods to phylogenetic analysis of trilobites (e.g., Edgecombe and Chatterton, 1990a). In a series of studies, Edgecombe et al. (1988) and Edgecombe and Chatterton (1990a, b) examined generic relationships within Encrinurinae (see also Edgecombe, 1994a). Lespérance and Desbiens (1995) conducted a phylogenetic analysis of species previously assigned to *Encrinuroides*; their results were subsequently reevaluated by Edgecombe et al. (1998). The results of this work highlight the need for the monophyly of many trilobite genera to be tested in a phylogenetic context. Additional species-level phylogenies for encrinurid genera have been presented by Edgecombe and Chatterton (1992, *Distyrax*) and Ramsköld and Edgecombe (1994, *Wallacia*).

#### 6.1.4. Acastoidea

Eldredge (1971b) was the first to consider evolutionary patterns within the Acastoidea using aspects of a phylogenetic perspective



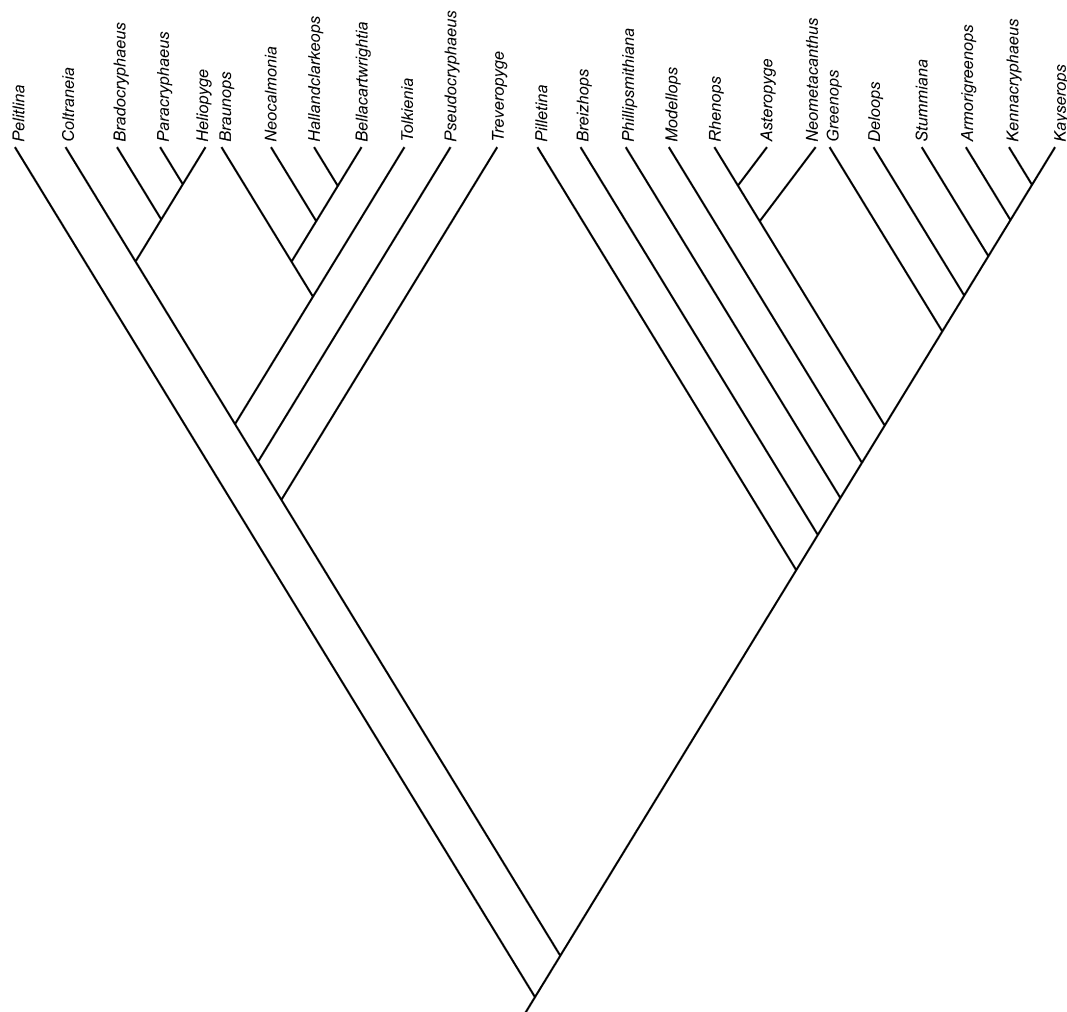


Fig. 15. Hypothesis of relationships based on results presented in Lieberman and Kloc (1997).

and this pioneering work ushered in a series of efforts aimed at unraveling relationships within this clade. [Ramsköld and Edgecombe \(1993\)](#) also paved the way for our understanding of patterns within this group ([Fig. 13](#)) (see also [Edgecombe, 1993](#)).

Additional detailed studies of the Calmoniidae were presented in [Eldredge and Branisa \(1980\)](#) and [Eldredge and Cracraft \(1980\)](#). This group was confined to Gondwana and underwent a prolific radiation during the Devonian, shortly before the demise of the entire Phacopida. Our current understanding of phylogenetic patterns within this family is growing thanks to work by [Edgecombe](#), and the relationships of some of the genera within the calmoniid tree have been considered ([Lieberman et al., 1991](#); [Lieberman, 1993](#)) ([Fig. 14](#)). A supertree filling in the tips of the cladogram in [Fig. 14](#) is given in [Abe and Lieberman \(2009\)](#). [Edgecombe \(1994b\)](#) also presented a species-level phylogeny for another genus (*Bainella*) within the Calmoniidae.

Also relevant here, the phylogenetic relationships of the Asteropyginae have been examined by [Lieberman and Kloc \(1997\)](#) ([Fig. 15](#)). This study used *Pelitina*, a member of the expressly paraphyletic “Acastavinae” (see [Fig. 13](#)) as the outgroup.

#### 6.1.5. Phacopidae

Finally, regarding Phacopida, [Ramsköld and Werdelin \(1991\)](#) analyzed phylogenetic patterns at the species-level within part of the eponymous Phacopidae and a composite tree based on their work is shown in [Fig. 16](#). They noted that aspects of their results disagree

with those of [Eldredge \(1972, 1973\)](#). More recently, [Crônier \(2003\)](#) examined species-level patterns within the genus *Trimeroccephalus*.

#### 6.2. Proetida

The proetids are made up of what might be referred to as garden variety trilobites: nothing too fancy or spectacular. Yet when it

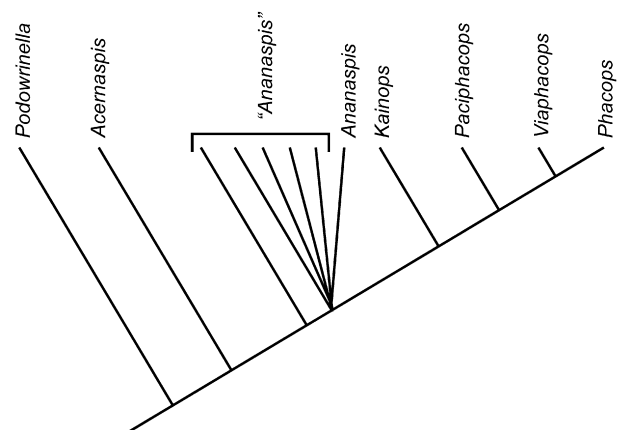


Fig. 16. Hypothesis of relationships based on results presented in [Ramsköld and Werdelin \(1991\)](#).

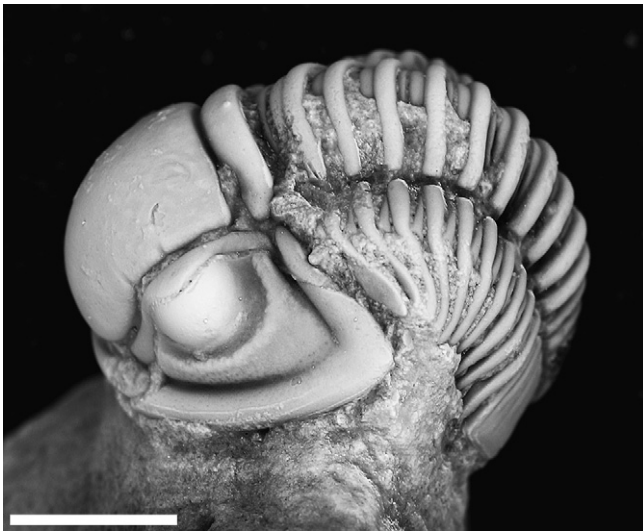


Fig. 17. *Gerastos cuvieri*, KUMIP 314478, from the Middle Devonian, near Gees, Germany, loc. BM-1. Scale bar = 0.5 cm.

comes to longevity they were one of the real success stories of the Trilobita. They were typically assumed to have first appeared in the Ordovician, although their roots clearly extend back into the Cambrian (Jell and Adrain, 2003). They then embarked on a long and successful evolutionary history during which they survived not only the end Ordovician mass extinction but also the Late Devonian biodiversity crisis (they were the only trilobite order to survive the latter). Indeed, they underwent a moderate, if not spectacular, radiation in the Carboniferous (Brezinski, 1999), before they at last succumbed at the end Permian mass extinction.

#### 6.2.1. Proetidae and Tropidocoryphidae

One set of phylogenetic studies of this order focused on the Proetidae (Fig. 17). Lieberman (1994) identified five major divisions

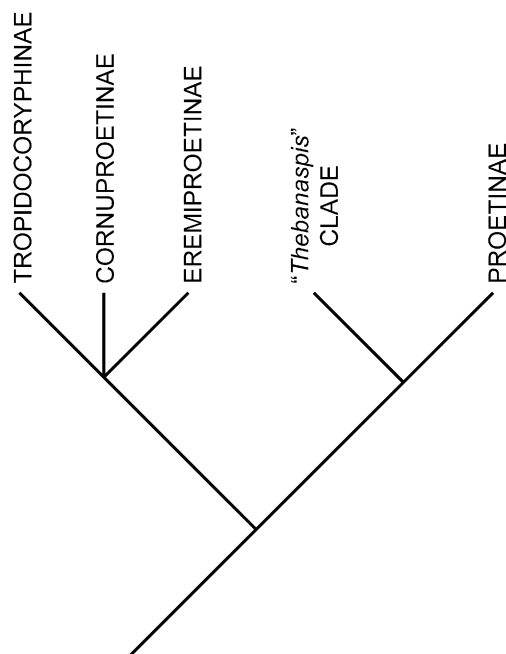


Fig. 18. Hypothesis of relationships based on results presented in Lieberman (1994).

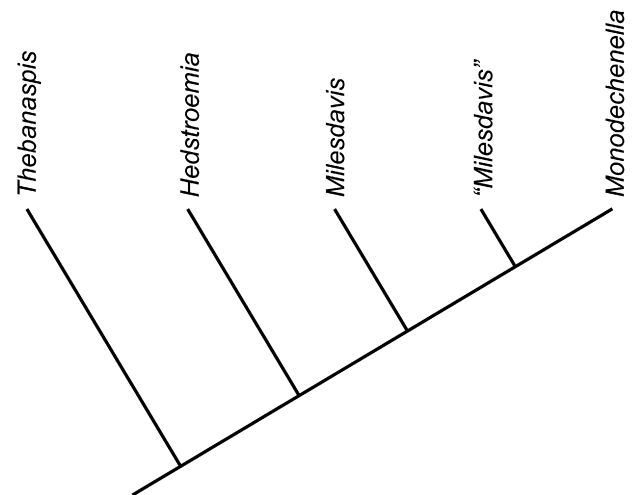


Fig. 19. Hypothesis of relationships based on results presented in Lieberman (1994).

within the Proetidae (Fig. 18); he also presented phylogenetic analyses of genera within the “*Thebanaspis*” clade and the Proetinae (Figs. 19 and 20). Finally, Lieberman (1994) presented species-level phylogenies for the genera *Basidechenella*, *Crassiproetus*, and *Dechenella*. Edgecombe et al. (1997) presented a phylogenetic analysis for species of the tropidocoryphid *Stenoblepharum*.

#### 6.2.2. Aulacopleuroidea

Aulacopleuroidea have been another focus of phylogenetic research within the Proetida. For instance, Adrain and Chatterton (1993) identified the pattern of relationship shown in Fig. 21 and they discerned additional phylogenetic structure within the Aulacopleuroidea (Fig. 22). Adrain and Chatterton (1993) also recognized some additional phylogenetic structure within the Brachymetopidae, Rorringtoniidae, and Scharyiidae. Species-level phylogenies have been presented by Ebach and Edgecombe (1999, *Cordania*) and Adrain and Chatterton (1994, *Otarion*).

Chatterton et al. (1998) examined patterns among the Toernquistidae, Dimeropygidae, and Hystricidae. Following on this study, Adrain et al. (2001) analyzed genera within the Dimeropygidae and recognized several monophyletic groups based on their results. Adrain and Westrop (2007) presented a species-level phylogeny for the dimeropygid genus *Bearriverops*.

#### 6.3. “Ptychopariida”

Phylogenetic analyses of trilobites within this paraphyletic grade have proven challenging and are thus somewhat sparse (Lieberman, 2004), but work at the genus and species-levels has been conducted. Waisfeld et al. (2001) presented a large species-level phylogeny of shumardiid genera including many poorly defined taxa such as *Shumardia* and *Conophrys*. Westrop and Ludvigsen (2000) examined relationships among species of the menomoniid genus *Hysteropleura*. An analysis of the Conocoryphidae was presented by Cotton (2001).

The Olenidae, a highly diverse, but likely monophyletic ptychopariid family (Fortey, 2001) has until recently been completely unexamined in a phylogenetic context. Much of the current classification for the group has been largely based on stratigraphic distribution of genera, as olenids have been frequently used for biostratigraphic purposes (see e.g., Henningsmoen, 1957). This naturally casts doubt on the monophyly of some previously recognized clades within the group. An analysis examining several

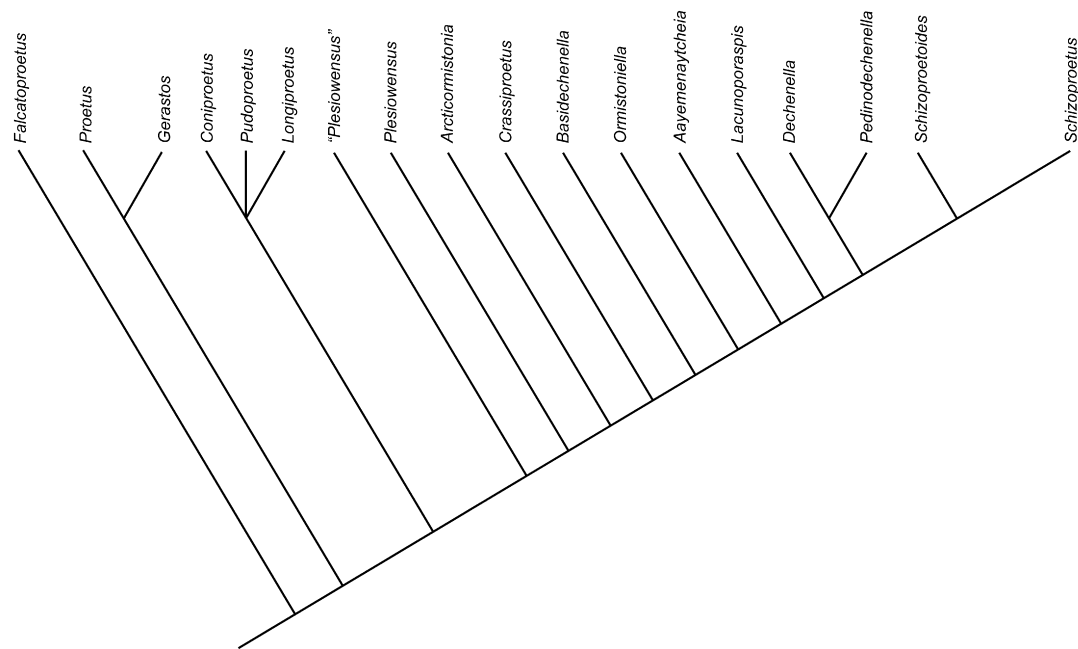


Fig. 20. Hypothesis of relationships based on results presented in Lieberman (1994).

olenid genera spanning the Cambrian–Ordovician boundary interval by Karim (2008) is the first step toward a phylogenetic based classification for the group.

One additional “ptychopariid” family that has been subjected to phylogenetic analysis is the Harpetidae. Ebach and McNamara (2002) presented separate species-level phylogenetic analyses for seven harpetid genera. More recently, Adrain and Westrop (2006) examined the phylogenetic relationships among species of the harpetid genus *Notchpekia*. They also proposed that the Harpididae and Harpetidae might not be as closely related as suggested by Ebach and McNamara (2002); however, this statement has yet to be tested in a phylogenetic context.

#### 6.4. Other orders

Phylogenetic treatments of other orders of trilobites are somewhat variable. Pollitt et al.'s (2005) analysis of lichids using both parsimony and Bayesian methods represents the only attempt thus far at examining higher-level relationships among the order Lichida using phylogenetic techniques. Species-level analyses focusing on relationships within a single lichid genus or sub-genus have been published by Ebach and Ahyong (2001, *Acanthopyge* (*Lobopyge*)) and Adrain (2003, *Borealarges*).

Regarding the order Odontopleurida, Ramsköld's (1991) analysis of Odontopleuridae is an important study that examined higher-level relationships of the group in a phylogenetic context. A portion of this analysis was revised by Adrain et al. (2008), who analyzed members of the Koneprusiinae. Species-level studies within Odontopleuridae include Adrain and Chatterton's (1990) phylogenetic analysis of *Odontopleura*, Chatterton et al.'s (1997) analysis of *Ceratocara*, and Adrian and Ramsköld's (1997) analysis of *Edgcombeaspis*.

Phylogenetic analysis of illaenid trilobites has proven difficult due to their typically highly effaced nature. Amati and Westrop's (2004) analysis of species assigned to *Thaleops* and *Illaenus* was a first attempt at examining the monophyly of genera within this group. Their study demonstrated that commonly known “trash can” genera such as *Illaenus* are not monophyletic and are in need

of revision before the higher-level relationships of the group can be explored.

Lee et al. (2008) conducted an analysis of missisquoiid trilobites, a group that has been historically important in biostratigraphic studies. The results of their analysis were also used to explore biogeographic patterns of the clade.

Forrey and Chatterton (1988) remains the only higher-level analysis of asaphids thus far, but none of the clades used in their analysis have been subjected to examination in a phylogenetic context.

Finally, Ebbestad and Budd (2003) presented a cladistic analysis of the enigmatic Middle and Upper Cambrian burlingiid trilobites,

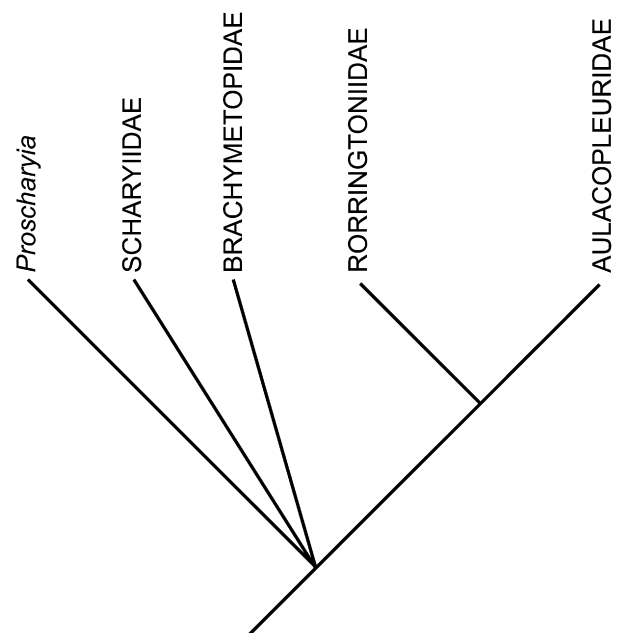


Fig. 21. Hypothesis of relationships for Aulacopleuroidea based on results presented in Adrain and Chatterton (1993).



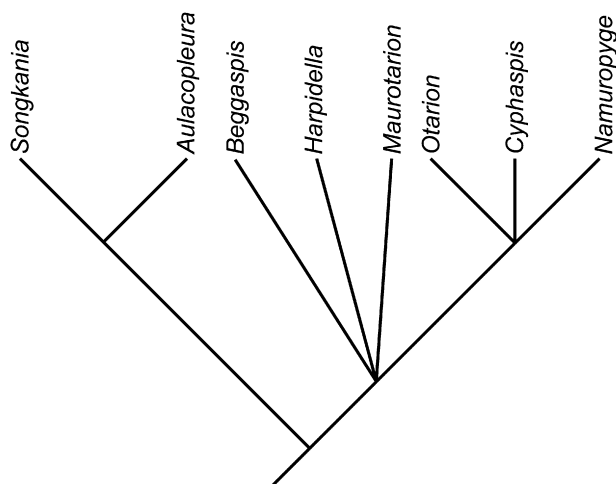


Fig. 22. Hypothesis of relationships for Aulacopleuridae based on results presented in Adrain and Chatterton (1993).

but noted that the group's relationship to other Cambrian sister-taxa is still unclear.

## 7. Conclusions

During the last 20 years trilobite workers have made major strides towards reconstructing the trilobite "tree of life". Prominent questions certainly still exist, paraphyletic groups like "Ptychopariida" continue to be a messy problem, and some orders are basically unknown from a phylogenetic perspective, yet significant progress has been made. Eldredge (1977) represented the first call to arms to reconstruct trilobite evolution using cladistic methods, and it is clear that that call to arms was effective in stimulating additional research. We suspect that phylogenetic analyses of trilobites will continue apace. Some of these will take the form of studies that try to tease apart in greater detail ordinal and familial relationships. Others will focus on species-level phylogenies to gain insight not only into the nature of evolutionary patterns but also the processes that may generate these patterns. Moreover, detailed phylogenetic work at the species-level will be critical for unraveling the higher-level relationships among trilobites as many genera are undoubtedly not monophyletic. We find it encouraging and also salutary that such long extinct organisms can continue to capture the public's imagination and spur scientific research. Once an evolutionary success story, they now serve as a potential model of how to integrate fossils and phylogeny in the service of shedding light on evolutionary patterns and processes.

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