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The trouble with trilobites: classification, phylogeny and the cryptogenesis problem

John R. Paterson

Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale NSW 2351, Australia

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Author for correspondence: John R. Paterson, Email: jpater20@une.edu.au

Abstract

Trilobites are an iconic group of extinct arthropods that lived in Palaeozoic oceans for *c.* 270 Ma, before their demise at the end of the Permian Period. Despite their considerable diversity (> 22 000 species) and abundance, particularly in Cambrian and Ordovician rocks, as well as intensive study for well over 200 years, trilobite systematics remains in a state of flux. In this contribution, the complex history of trilobite classification over the last century is briefly reviewed, including the seminal scheme published by Henry Swinnerton in 1915. The cryptogenesis problem, which relates to the supposedly obscure phylogenetic links between major post-Cambrian trilobite clades and their Cambrian sister taxa, is also discussed. Previous studies have suggested that the cryptogenesis problem is largely a taxonomic artefact, but the Cambrian origins of some post-Cambrian groups, such as the orders Proetida and Odontopleurida, are still unclear. Future directions for research on trilobite systematics are outlined, from taxonomic studies involving comprehensive documentation and extensive illustration of morphology at the species level, through to broad-scale phylogenetic analyses that initiate or test hypotheses about relationships across the major groups. Other ongoing issues to be addressed include identifying the sister group of Trilobita, and determining whether certain taxa, such as the suborder Agnostina and Cambrian family Burlingiidae, represent trilobites.

1. Introduction

Over the past 155 years, *Geological Magazine* has published myriad articles on trilobites, an extinct group of marine arthropods that inhabited Palaeozoic oceans for *c.* 270 Ma (during *c.* 521–252 Ma). In fact, the first original article to appear in Volume 1, Number 1 was by Salter (1864), who reported on Palaeozoic fossils (including trilobites) from the Budleigh Salterton Pebble Bed in Devonshire, United Kingdom. Since that time, many important trilobite studies have been published in this journal, particularly those focused on systematics. These include seminal classification schemes (e.g. Reed, 1898, 1905, 1927, 1928; Swinnerton, 1915, 1919), extensive taxonomic works (e.g. Woodward, 1883, 1884*b*; Thomas & Narbonne, 1979; McNamara, 1980; Rushton & Hughes, 1981; Fortey & Owens, 1991; Edgecombe *et al.* 1994; Adrain & Westrop, 2005; Feist & McNamara, 2007; Żylińska & Masiak, 2007; Feist *et al.* 2009; Lerosey-Aubril, 2012; Crônier *et al.* 2018), and key papers that have attempted to reveal, support or dispute the relationships between groups (e.g. Temple, 1956; Lane & Thomas, 1978; Ludvigsen & Chatterton, 1980; Fortey, 1981; Tripp & Evitt, 1981; Whittington, 1981; Park & Choi, 2011*a*; Park, 2018), as well as the affinities of trilobites with other arthropods (e.g. Woodward, 1871, 1884*a*; Mickleborough, 1884; Walcott, 1894; Zeng *et al.* 2017). The aim of this review is to focus on some of these studies and how they have influenced our understanding of trilobite evolution, as well as to highlight some of the perpetual problems that plague the systematics of this iconic invertebrate group.

2. An abridged history of trilobite classification

Since the naming of Trilobita by Walch in 1771 (Walch, 1771; see Kihm & St John, 2007 for a translation of this pioneering work), the classification of the group has had a complicated history. This not only relates to the disparate schemes (e.g. Harrington *et al.* 1959; Bergström, 1973; Fortey, 1990, 1997, 2001; Adrain, 2011) and disputes (e.g. Fortey & Owens, 1975, 1979; Bergström, 1977; Lamsdell & Selden, 2015) relating to higher-level groupings such as orders, suborders and superfamilies, but also debate over the monophyly of Class Trilobita (see Lauterbach, 1980, 1983, 1989; Fortey & Whittington, 1989; Hahn, 1989; Ramsköld & Edgecombe, 1991; Edgecombe & Ramsköld, 1999; Paterson & Edgecombe, 2006).

In what could be considered one of the first comprehensive and authoritative tomes on trilobite systematics – the 1959 trilobite *Treatise* (Harrington *et al.* 1959) – Harrington provided a

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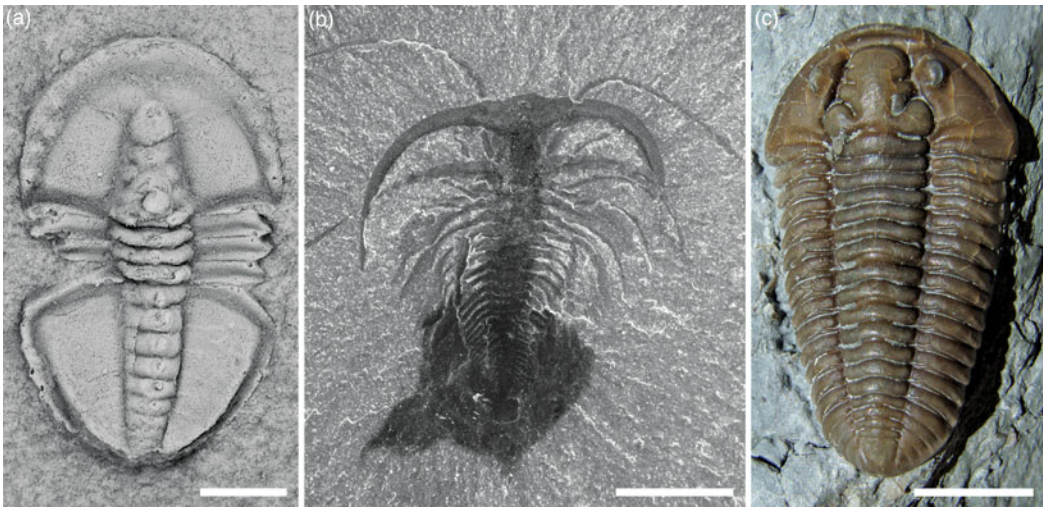


Fig. 1. Exemplar species that represent some of the higher-level groups established by Beecher (1897) and Swinnerton (1915) in their trilobite classification schemes. (a) *Serrodiscus gravestocki* (order Eodiscida) from the lower Cambrian (Series 2, Stage 4) Mernmerna Formation, Elder Range, South Australia; such taxa were classified in Beecher's (1897) 'Hypoparia'; South Australian Museum, SAM P40229; photograph, J. Paterson. (b) *Marrella splendens* from the middle Cambrian (Miaolingian, Wuliuan) Burgess Shale, British Columbia, Canada; although no longer considered a trilobite, this species formed a part of Swinnerton's (1915) 'Protoparia'; Smithsonian Institution, USNM 57674; photograph, D. García-Bellido. (c) *Flexicalymene retrorsa* from the Upper Ordovician (Katian) Dillsboro Formation, Cincinnati Arch region, USA; a classic example of Swinnerton's (1915) suborder Calymenina (order Phacopida); photograph, E. Bonino. Scale bars: (a) 2 mm; (b) 5 mm; and (c) 10 mm.

history of the various major classification schemes that had been erected since the early 1800s. Among these schemes was Pierre Hupé's extensive works (Hupé, 1953*a*, *b*, 1955), as well as Swinnerton's (1915) pivotal study published in *Geological Magazine*.

Swinnerton's (1915) classification was largely focused on using cephalic (facial) suture patterns to diagnose orders and their subdivisions, building on the seminal work of Beecher (1897). Although Swinnerton rejected Beecher's (1897) concept of the order Hypoparia – trilobites that allegedly have ventral librigenae, and lack dorsal sutures and dorsal compound eyes (e.g. Fig. 1a) – he adopted the orders Opisthoparia and Proparia (discussed below). Swinnerton (1915, p. 493) also erected a new order, the Protoparia, for "trilobites and trilobite-like organisms in which the absence of facial sutures is primary". At the time, membership of the Protoparia was limited to supposedly non-biomineralized euarthropods from the mid-Cambrian Burgess Shale of Canada, namely *Marrella splendens* (Fig. 1b) and *Nathorstia transitans*. However, as correctly pointed out by Stubblefield (1936) and Harrington (in Harrington *et al.* 1959), *Marrella* is no longer considered a trilobite (see García-Bellido & Collins, 2006; Legg *et al.* 2013; Aria & Caron, 2017; Vannier *et al.* 2018) and *Nathorstia* is a soft-shelled moult stage of the (opisthoparian) trilobite *Olenoides serratus* (see Whittington, 1980). This polyphyletic grouping of disparate arthropods is therefore redundant.

Swinnerton's (1915) main contribution to trilobite classification was the subdivision of the Opisthoparia, taxa with cephalic sutures that cut the posterior margin of the cephalon adaxial to the genal angle. His concept of the Opisthoparia included groupings of families into suborders and sections (Table 1). Importantly, Swinnerton erected some groups that have endured subsequent classification schemes and held up to phylogenetic scrutiny (Harrington *et al.* 1959; Fortey, 1997, 2001; Lieberman & Karim, 2010), none more so than Calymenina (Fig. 1c; Henry, 1980; Chatterton *et al.* 1990; Fortey, 1990; Edgecombe, 1992; Adrain, 2011, 2013). However, in a modern context, Calymenina is now a suborder within the order Phacopida (Fortey, 1997; Adrain, 2011), other members of which (e.g. Phacopidae, Encrinuridae and Cheiruridae) were placed in Proparia by Swinnerton (1915) (Table 1).

The first trilobite *Treatise* (Harrington *et al.* 1959) remained the primary classification scheme for almost 40 years, until the revised edition appeared in the late 1990s (Whittington *et al.* 1997). Unlike its predecessor, the 1997 *Treatise* did not include all known trilobite genera and their suprageneric ranks, but it did provide comprehensive treatment of the orders Agnostida and Redlichiida (as Volume 1); additional volumes on the remaining orders are still in preparation (Adrain, 2008, 2013). Fortey (1997), in a similar vein to Harrington (in Harrington *et al.* 1959), masterfully summarized the current state of trilobite classification, and presented a revised scheme that did not differ substantially from the 1959 *Treatise* (Table 1). His main changes included: an expanded Corynexochida, including the suborders Illaenina and Leiostegiina; raising Asaphida to ordinal level (based on the study by Fortey & Chatterton, 1988); demoting the Odontopleurida to a superfamily within the Lichida; a reshuffling of the Ptychopariida; and relegating the Bathynotidae to an Order Uncertain category, thereby disbanding the suborder Bathynotina (*sensu* Harrington *et al.* 1959). Notably, this scheme did not formally adopt the subclass Libristoma (*sensu* Fortey, 1990) – trilobites having a natant hypostomal condition (i.e. the hypostome is detached from the cephalic doublure; Fig. 2a) or secondarily derived conterminant condition (i.e. the hypostome is attached to the cephalic doublure; Fig. 2b) – because a broad-scale phylogenetic analysis necessary to determine all constituent clades had not yet been conducted. Nonetheless, Fortey (1997) still recognized the Libristoma as being composed of the orders Asaphida, Proetida and Ptychopariida.

In the intervening years since the 1997 *Treatise*, other key publications have provided updates, overviews or new ideas on broad-scale trilobite systematics (e.g. Fortey, 2001; Jell & Adrain, 2003; Whittington, 2007; Lieberman & Karim, 2010; Adrain, 2011, 2013). Fortey (2001), Whittington (2007) and Lieberman & Karim (2010) have provided excellent reviews on trilobite classification and phylogenetics. One of the repeated and perhaps

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Table 1. Trilobite classification schemes of Swinnerton (1915), Harrington *et al.* (1959), Fortey (1997), and Adrain (2011)

Swinnerton (1915)	Harrington *et al.* (1959)	Fortey (1997)	Adrain (2011)
Order Protoparia	Order Agnostida	Order Agnostida	Order Eodiscida
Marrellidae	Suborder Agnostina	Suborder Agnostina	Order Redlichiida
Nathorstia [= *Olenoides*]	Suborder Eodiscina	Suborder Eodiscina	Suborder Olenellina
Order Opisthoparia	Order Redlichiida	Order Redlichiida	Suborder Redlichiina
Suborder Mesonacida	Suborder Olenellina	Suborder Olenellina	Order Corynexochida
Suborder Conocoryphida	Suborder Redlichiina	Suborder Redlichiina	Suborder Corynexochina
Section Olenina	Suborder Bathynotina	Order Corynexochida	Suborder Illaenina
Section Conocoryphina	Order Corynexochida	Suborder Corynexochina	Suborder Leiostegiina
Section Ptychoparina	Order Ptychopariida	Suborder Illaenina	Order Lichida
Section Calymenina	Suborder Ptychopariina	Suborder Leiostegiina	Order Odontopleurida
Suborder Trinucleida	Suborder Asaphina	Order Lichida	Order Phacopida
Suborder Odontopleurida	Suborder Illaenina	Order Phacopida	Suborder Phacopina
Order Proparia	Suborder Harpina	Suborder Calymenina	Suborder Cheirurina
Encrinuridae	Suborder Trinucleina	Suborder Phacopina	Suborder Calymenina
Cheiruridae	Order Phacopida	Suborder Cheirurina	Order Proetida
Phacopidae	Suborder Cheirurina	Order Proetida	Order Aulacopleurida
Burlingiidae	Suborder Calymenina	Order Asaphida	Order Asaphida
?Agnostidae	Suborder Phacopina	Order Ptychopariida	Order Olenida
	Order Lichida	Suborder Ptychopariina	Order Harpida
	Order Odontopleurida	Suborder Olenina	
		Suborder Harpina	[Order Uncertain (58 families)]
	[Order Uncertain (5 families)]		
		[Order Uncertain (4 families)]	

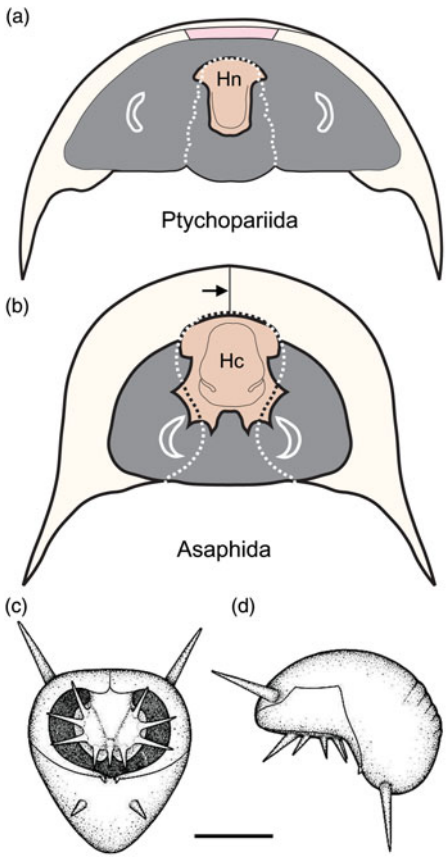


Fig. 2. Key morphological features of the Libristoma (*sensu* Fortey, 1990), including the order Asaphida (*sensu* Fortey & Chatterton, 1988; Fortey, 1990). (a) Ventral view of the cephalon of *Ptychoparia* (Ptychopariida) showing the natant hypostomal (Hn) condition; drawing by Sam Gon III. (b) Ventral view of the cephalon of *Lachnostoma* (Asaphida) showing the conterminant hypostomal (Hc) condition and the ventral median suture (arrowed); drawing by Sam Gon III. (c, d) Ventral and lateral views of a bulbous 'commutavi' (or 'asaphoid-type') protaspis (*Isotelus* sp. (Asaphida: Asaphidae), Middle Ordovician, Virginia, USA); modified from Evitt (1961, text-fig. 3); 0.5 mm scale bar applies to (c) and (d) only.

concerning messages throughout these papers is that we still know very little about the relationships between, and indeed the validity of, the major groups (especially orders and suborders), which also compounds the issue of finding the as-yet unknown 'roots' of several post-Cambrian trilobite clades, known as the cryptogenesis problem (see Section 3). This critical knowledge gap is perhaps best illustrated in Fortey's (2001, fig. 1) hypothetical phylogenetic tree, which is riddled with broken branches and question marks.

The most recent efforts in dealing with trilobite classification on a grand scale are those of Jonathan Adrain and Peter Jell (Jell & Adrain, 2003; Adrain, 2011). In a monumental piece of work, Jell & Adrain (2003) compiled lists of all known genera (including their synonyms) and families into what has been nicknamed 'the trilobite phonebook'. This publication has become invaluable for taxonomists wanting to know the authorship, validity or availability of generic names, plus details about type species or familial classifications. It has also provided the raw data for quantitative studies (e.g. Tarver *et al.* 2007; Álvaro *et al.* 2013).

In the latest trilobite classification scheme to be published, Adrain (2011) made considerable modifications to Fortey's (1997) scheme, particularly with regard to the number of orders recognized (Table 1), as well as their constituent superfamilies and families. Notable changes include: the abandonment of Ptychopariida in favour of reassigning the majority of its families to either an Order Uncertain list, or the new orders Aulacopleurida and Olenida; the resurrection of the Odontopleurida; and the exclusion of Agnostina from Trilobita altogether, thus elevating the suborder Eodiscina to ordinal rank and considering it to be monophyletic. Although Adrain (2011) did not explicitly state why he rejected the Agnostina, there is a substantial body of evidence that supports this view (see Müller & Walossek, 1987; Walossek & Müller, 1990; Ramsköld & Edgecombe, 1991; Shergold, 1991; Bergström & Hou, 2005; Haug *et al.* 2010; Ortega-Hernández & Brena, 2012; Legg *et al.* 2013); see Section 4 for further discussion. Moreover, in a recent large-scale phylogenetic analysis of Cambrian trilobites, Paterson *et al.* (2019) have shown that the Eodiscida is indeed monophyletic, but their position is highly labile

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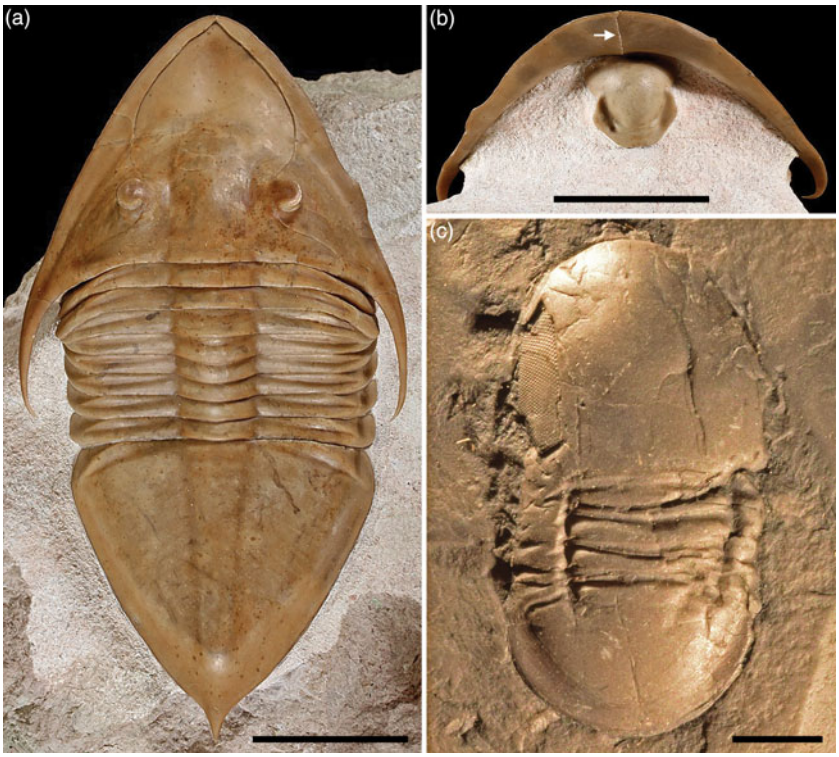


Fig. 3. Examples of the order Asaphida. (a, b) *Megistaspidella triangularis* (Asaphoidea: Asaphidae) from Middle Ordovician strata of the St Petersburg region, Russia; (a) entire exoskeleton in dorsal view and (b) oblique ventral view of anterior of cephalon showing the ventral median suture (arrowed) and *in situ* conterminant hypostome; photographs, A. Evdokimov. (c) *Microparia speciosa* (Cyclopygoidea: Cyclopygidae) from the Upper Ordovician (Katian) Králův Dvůr Formation, Prague Basin, Czech Republic; Museum of Comparative Zoology, Harvard University, MCZ 3354; photograph, R. Bicknell. Scale bars: (a, b) 20 mm; (c) 5 mm.

across different tree topologies produced by Bayesian and parsimony analyses.

In a major review of Ordovician trilobite diversity and distribution, Adrain (2013) took the opportunity to provide a more detailed commentary on his 2011 classification scheme. While much of the discussion was focused on families, Adrain (2013) also presented his views on various orders, particularly for Asaphida, Harpida, Lichida, Odontopleurida, Olenida, and Proetida. Importantly, Adrain (2013) provided critical information on the stratigraphic ranges of many families, several of which extend down into Cambrian strata, thus having important implications for the cryptogenesis problem (see Section 3 below).

3. The cryptogenesis problem: trilobite evolution across the Cambro-Ordovician boundary

In 1981, *Geological Magazine* published a special issue dedicated to one of the doyens of trilobite research, Sir James Stubblefield (Calver, 1981). In this issue, an article by Whittington (1981) highlighted two of Stubblefield's key papers on trilobite classification and evolution (Stubblefield, 1936, 1959). The latter is of particular relevance here, as it focused on what is now referred to as cryptogenesis: our poor understanding of the phylogenetic relationships between major post-Cambrian trilobite groups and their Cambrian sister taxa (Stubblefield, 1959; Whittington, 1981; Edgecombe, 1992; Lieberman & Karim, 2010). In short, Stubblefield (1959) considered the majority of post-Cambrian superfamilies – and by extension, many orders and suborders – to be cryptogenetic (i.e. of unknown Cambrian origin or appearing *de novo* in the Ordovician), based on the higher-level classification of trilobites at that time (Harrington *et al.* 1959).

Whittington (1981) provided an update on the cryptogenesis problem, with particular reference to the orders Phacopida, Odontopleurida and Lichida. He also hypothesized that trilobites were undergoing elevated rates of extinction and origination throughout late Cambrian – Early Ordovician time, with origination rates taking over in the latter part of this interval. However, despite over 20 years of trilobite research since Stubblefield's (1959) seminal essay, Whittington (1981, p. 594) concluded with: "How the major taxa of post-Cambrian trilobites arose, and their relationship to each other or to older groups, is still unknown."

In what is now considered one of the classic papers on trilobite systematics, Fortey & Chatterton (1988) conducted a large-scale study on the order Asaphida (Fig. 3), which included cladistic (parsimony) analyses. While their main aim was to present a new phylogenetic classification of a major trilobite group, they had essentially tackled a part of the cryptogenesis problem. They demonstrated that, with the exception of the superfamily Cyclopygoidea (Fig. 3c), the evolutionary history of most ingroup clades is reasonably complete from the middle–late Cambrian Period and extending well into the Ordovician Period, as supported by their stratigraphic records. The two key synapomorphies that Fortey & Chatterton (1988) considered to unite members of the Asaphida have been subsequently criticized, with both the ventral median cephalic suture (Figs 2b, 3b; Whittington, 2003; Zhu *et al.* 2007, 2010; Park & Choi, 2009, 2010, 2011*a*; Park *et al.* 2014) and the bulbous 'commutavi' (or 'asaphoid-type') protaspis (Fig. 2c, d; Park & Kihm, 2015; Park *et al.* 2016; Park, 2018) thought to have evolved independently across disparate groups. Even so, this does not render these characters as inoperative for diagnosing Asaphida. Fortey & Chatterton's (1988) paper

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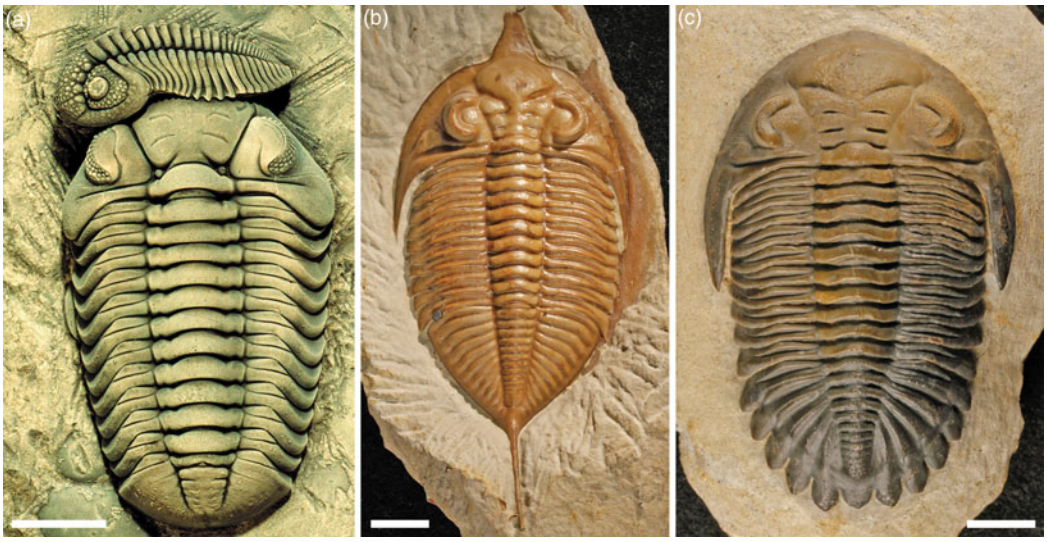


Fig. 4. Examples of the suborder Phacopina, a classic 'cryptogenetic' clade. (a) *Acernaspis copperi* (Phacopoidea: Phacopidae) associated with a small exoskeleton of *Rielaspis elegantula* (Cheirurina: Encrinuridae) from the lower Silurian (Llandovery) Jupiter Formation, Anticosti Island, Québec, Canada (previously illustrated by Chatterton & Ludvigsen, 2004, pl. 37, figs 2–6); photograph, B. Chatterton. (b) *Huntoniatonia oklahomae* (Dalmanitoidea: Dalmanitidae) from the Lower Devonian Haragan Formation, Oklahoma, USA; Smithsonian Institution, USNM 376737; photograph, R. Bicknell. (c) *Hollardops mesocristata* (Acastoidea: Acastidae) from the Lower Devonian (Emsian) Timrhanrhart Formation, south of Foum Zguid, Morocco; Smithsonian Institution, RMH2002-256; photograph, R. Bicknell. Scale bars: (a) 5 mm; (b, c) 10 mm.

therefore remains an important study on the evolutionary relationships between Cambrian and post-Cambrian trilobites, and their concept of the Asaphida is still partly followed in the latest classification scheme of Adrain (2011, 2013).

Edgecombe (1992) took a novel cladistic approach to investigate the cryptogenesis problem. He slightly modified and reanalysed the dataset of Fortey & Chatterton (1988) and calibrated the cladogram with stratigraphic first appearances for each lineage. Importantly, Edgecombe (1992) applied the 'ghost lineage' concept – range extensions inferred from the earlier appearance of a sister group – to show that clades can be older than the fossil record suggests (see his fig. 5.5). While Edgecombe's results were essentially the same as those of Fortey & Chatterton (1988), the consideration of ghost lineages had filled any perceived stratigraphic gaps across clades, for example, allowing the long range extension of the Cyclopygoidea to the middle–late Cambrian Period; with the exception of some latest Cambrian species of Nileidae, all other cyclopygoids are Ordovician in age (Adrain, 2013).

Edgecombe (1992) applied the same methodology to the order Phacopida, a classic example of a supposedly cryptogenetic clade (Stubblefield, 1959; Whittington, 1981). Interestingly, the results of one of his parsimony analyses using holaspid characters permit considerable disparity of the order already within the Cambrian Period, provided the Pilekiinae (Cheirurina: Cheiruridae) are of late Cambrian age (Edgecombe, 1992, fig. 5.12A); recent stratigraphic data for this subfamily would support this view (see Adrain, 2013). However, some derived subclades, such as the suborder Phacopina (Fig. 4; Edgecombe, 1992, fig. 5.11), are consistent with traditional notions of cryptogenesis during the Ordovician Period, again supported by current stratigraphic data (Adrain, 2013).

Other aspects of the cryptogenesis problem have apparently been solved by reclassifying some of the major groups. For example, Fortey (1990, 1997) expanded the scope of the order Corynexochida to also include the suborders Illaenina and Leiostegiina. The Illaenina (Fig. 5a) was considered to be exclusively post-Cambrian in age in the 1959 *Treatise* (where it was classified under Ptychopariida; Harrington *et al.* 1959), and was one of Stubblefield's (1959) cryptogenetic groups. Fortey's reclassification implied that the sister group of Illaenina must lie with Cambrian members of the Corynexochina or Leiostegiina; it is also important to note that Fortey (1997) included the Cambrian family Tsinaniidae in the Illaenina, and the family Styginidae is now known to extend down into Cambrian strata (Adrain, 2013). An affinity between all three suborders of the Corynexochida is supported by several ontogenetic (Chatterton & Speyer, 1997; Lee & Chatterton, 2003) and holaspid characters (Fortey, 1990), but how these suborders are related to one another, and to other orders, remains an open question (Fortey, 2001; Adrain, 2011).

While many studies published since Stubblefield's (1959) paper have partially alleviated the cryptogenesis problem, there are certain major post-Cambrian clades that remain cryptogenetic in a modern context. For example, the oldest unequivocal representatives of the distinctive orders Odontopleurida (Fig. 5b) and Proetida (Fig. 5c) (*sensu* Adrain, 2011) are Early Ordovician (Floian) in age (see Adrain, 2013). It has been previously suggested that the Odontopleurida and Lichida (Fig. 5d) are sister taxa (e.g. Thomas & Holloway, 1988; Fortey, 1997, 2001), the latter extending back to the middle Cambrian Period (Guzhangian) (see Adrain, 2013). However, Adrain (2013) presented a compelling argument that refutes a close relationship between these two orders; the Cambrian roots of Odontopleurida therefore remain unclear. The Cambrian sister group of Proetida also remains obscure (Edgecombe, 1992; Fortey, 2001; Lamsdell & Selden, 2015). Although Adrain (2013) stated that the Proetida and Aulacopleurida may prove to be related – the latter having an extensive Cambrian record – he also noted that there is currently little evidence to support this relationship. Future work on older Ordovician (Tremadocian) and Cambrian (especially Furongian) trilobite assemblages may push back the first appearance of these groups, and broad-scale phylogenetic analyses may help to reveal their Cambrian sister taxa.

The cryptogenesis problem has largely existed because trilobite workers have struggled to detect distinctive morphological traits

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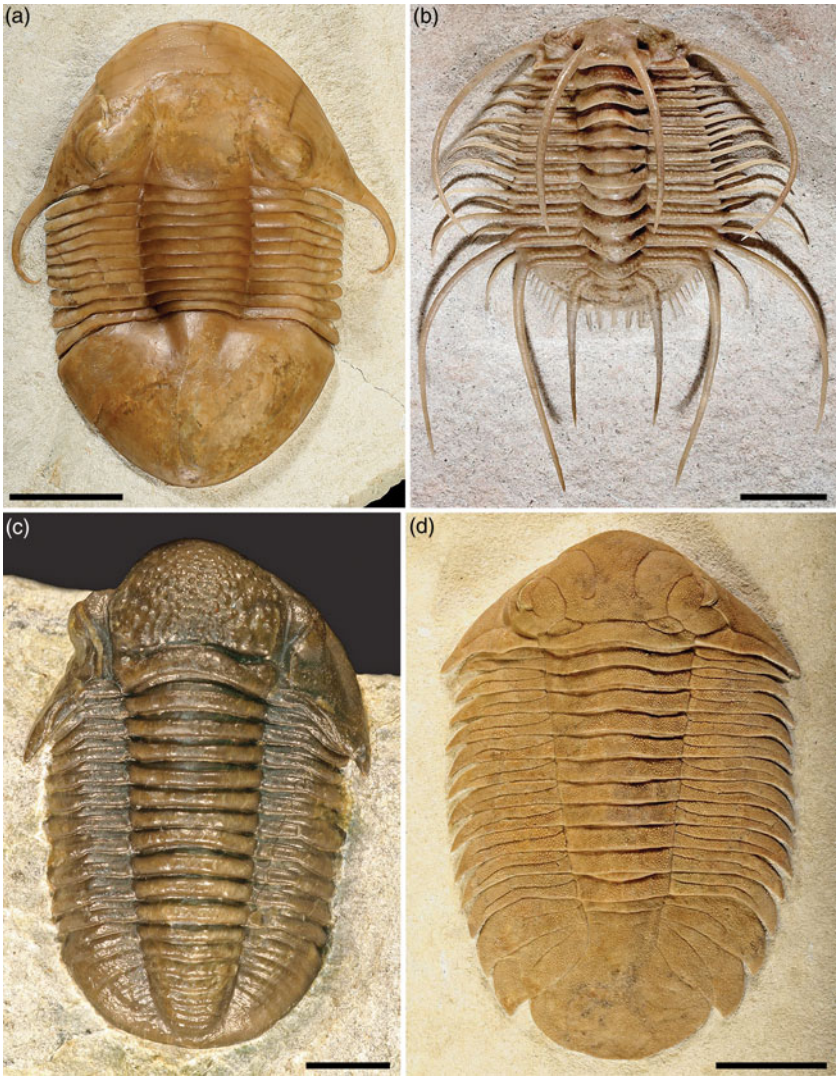


Fig. 5. Examples of other trilobite orders, including the 'cryptogenetic' Odontopleurida and Proetida. (a) *Illaenus tauricornis* (Corynexochida: Illaenina) and (b) *Boedaspis ensifer* (Odontopleurida) from Middle Ordovician strata of the St Petersburg region, Russia; photographs, A. Evdokimov. (c) *Gerastos cultrijugati* (Proetida) from the Middle Devonian (Eifelian) Lauch Formation, Eifel, Germany; photograph, H. Prescher. (d) *Metopolichas huebneri* (Lichida) from the Middle Ordovician of the St Petersburg region, Russia; photograph, A. Evdokimov. Scale bars: (a, d) 20 mm; (b) 10 mm; (c) 5 mm.

that link Cambrian and post-Cambrian taxa. Given that trilobites are indeed monophyletic, all major post-Cambrian clades must have Cambrian roots, but unique synapomorphies have been (and in many cases remain) elusive. Also, lack of a robust phylogenetic framework across the entire Trilobita has been a long-term issue, with previous attempts to show relationships between major groups being largely hypothetical and often ambiguous (e.g. Swinnerton, 1915, p. 542; Henningsmoen, 1951, fig. 2; Bergström, 1973, fig. 12; Hahn & Hahn, 1975, fig. 1; Eldredge, 1977, fig. 8; Fortey, 1990, text-fig. 19; Fortey, 2001, fig. 1; Jell, 2003, fig. 1). Edgecombe (1992) and Fortey (2001) outlined many reasons why there have been such contrasting approaches to trilobite classification and phylogeny, which can amplify or dampen the cryptogenesis effect around the Cambro-Ordovician boundary depending on the view followed. One purported reason is that trilobite workers typically specialize in either Cambrian or post-Cambrian taxa but rarely both, and therefore do not often recognize the phylogenetic links. This also has implications regarding pseudoextinctions of paraphyletic groups around the Cambro-Ordovician boundary (see Fortey, 1989).

Fortey's (1983, p. 181) statement that "the Cambrian-Ordovician boundary marks a watershed in trilobite evolution" is still correct, given the substantial evidence for the origination and proliferation of families, genera and species during the Great Ordovician Biodiversification Event (Adrain *et al.* 1998, 2004; Servais *et al.* 2010; Adrain, 2013; Servais & Harper, 2018). However, resolving the ongoing issues related to the cryptogenesis problem, such as identifying the Cambrian sister taxa of Proetida and Odontopleurida, will require more comprehensive and detailed morphological studies across a range of groups in an attempt to reveal key synapomorphies.

4. The future of trilobite systematics

A recurring theme in reviews on trilobite systematics is to announce that it is still in an unsatisfactory state, at least concerning higher-level classification and phylogeny (Fortey, 2001). In the first trilobite *Treatise*, Harrington (in Harrington *et al.* 1959, p. O145) stated "A wholly satisfactory, natural classification of trilobites is beyond possibility at the present moment." Over 50 years

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later, it seems little progress had been made in this regard with Adrain (2011, p. 104) asserting that "Higher trilobite phylogeny remains essentially unresolved."

Fortey (1997) noted that the perennial instability of trilobite classification is not only the result of changing taxonomic methods and ongoing discoveries, but also relates to the issue of dealing with such a large, diverse group. Indeed, 6 years ago, Jonathan Adrain's trilobite database contained 21 161 valid species (Adrain, 2013), with a multitude of new species published since that time; this number is now over 22 000 (J. Adrain, pers. comm., Feb. 2019). This huge diversity is one of the reasons why trilobite taxonomists tend to specialize in particular groups and/or time periods (as mentioned above), and is perhaps also a disincentive to tackle higher-level classification and phylogenetic analyses.

From a Linnean perspective, future research on trilobite systematics could benefit from a combined bottom-up and top-down approach. The former starts with rigorous, high-quality taxonomic work at the species level. Where possible, trilobite workers should be collecting large numbers of specimens and extensively illustrating them to get a better sense of overall morphology and inter- and intraspecific (including ontogenetic) variability, which can be supplemented with the application of morphometric techniques if preservational quality allows; see Webster's (2015) study on *Olenellus gilberti* as a great example. Obtaining large collections is not always practical, however, as some species can be very rare and others are available only as crack-out specimens that are time-consuming to collect and prepare. Conversely, secondarily silicified specimens can be easily recovered in vast numbers by careful acid digestion of limestones. The work by Jonathan Adrain and colleagues on Cambrian and Ordovician silicified faunas from the USA (especially Utah) provide excellent case studies (e.g. Adrain & Westrop, 2004, 2005, 2007; McAdams & Adrain, 2009, 2010, 2011*a*, *b*, *c*; Adrain *et al.* 2011*a*, *b*, 2012, 2014; Adrain & McAdams, 2012), showing that comprehensive documentation can lead to a much better understanding of morphological variation and species diversity. In turn, such vigilant taxonomic work underpins all other aspects of trilobite research, such as studies on biostratigraphy, palaeoecology, biogeography and phylogeny (see Adrain & Westrop, 2005, p. 379–380; Westrop & Adrain, 2016, p. 397).

Ideally, the bottom-up approach – beginning with a detailed knowledge of species, followed by comprehensive systematic studies (including phylogenetic analyses) of genera, families and so on – would be the best way of constructing a robust natural classification of trilobites, or indeed any organismal group. The reality, however, is that this is not necessarily practical for a clade with over 22 000 species. A compromise might entail an associated top-down approach of conducting broad-scale phylogenetic analyses at higher taxonomic levels (e.g. Edgecombe, 1992; Fortey & Chatterton, 1988; Paterson & Edgecombe, 2006; see Lieberman & Karim, 2010 for other examples), at least to provide testable hypotheses regarding trilobite relationships, with the possibility of using monophyletic groupings for classification purposes. Also, the clades produced by such analyses can assist in the pursuit of new synapomorphies by providing distinct search areas in tree space. Trilobite workers should attempt more ambitious phylogenetic analyses of large datasets using both parsimony and Bayesian methods (e.g. Pollitt *et al.* 2005; Paterson *et al.* 2019). Considered character formulations are also important, not only with discrete traits that comprise most of the characters in existing phylogenetic matrices, but also concerning the use of meristic and continuous traits (see Paterson *et al.* 2019). Of course, ontogenetic characters have long been considered important for revealing trilobite relationships (see Chatterton & Speyer, 1997; Fortey, 2001; Park & Choi, 2011*b*), and will no doubt continue to be a critical component of phylogenetic datasets and used in the diagnoses of higher-level clades.

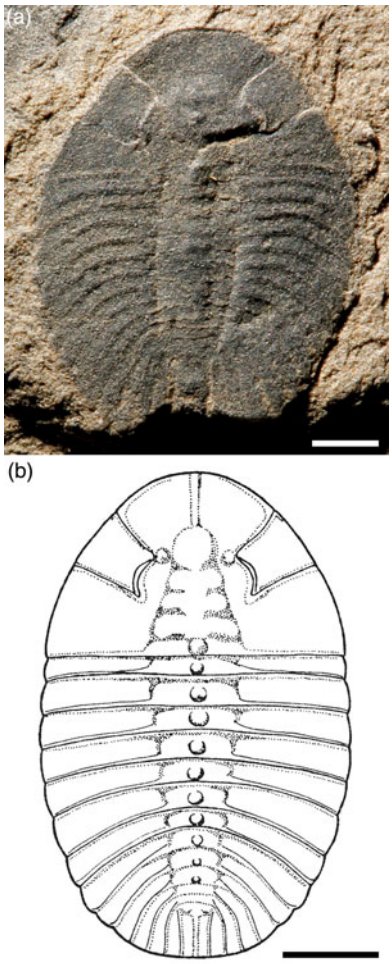


Fig. 6. Type species of the Cambrian family Burlingiidae. (a) Lectotype of *Burlingia hectori* from the middle Cambrian (Miaolingian, Wuliuan) Stephen Formation, British Columbia, Canada (previously illustrated by Walcott, 1908, pl. 1, fig. 8 and Whittington, 1994, pl. 1, fig. 1); photograph, R. Bicknell. (b) Reconstruction of *Schmalenseeia amphionura* by Whittington (1981, fig. 1). Both scale bars are 1 mm.

Other ongoing issues in trilobite systematics include: identifying the sister group of Trilobita; continued use of antiquated groupings; and whether certain groups, such as the suborder Agnostina (*sensu* Fortey, 1997) and Cambrian family Burlingiidae (Fig. 6), represent trilobites. The phylogenetic relationship between trilobites and their artiopodan relatives has received considerable attention over the past 20 years (e.g. Edgecombe & Ramsköld, 1999; Caron *et al.* 2004; Cotton & Braddy, 2004; Hendricks & Lieberman, 2008; Paterson *et al.* 2010, 2012; Budd, 2011; Stein & Selden, 2012; Ortega-Hernández *et al.* 2013; Stein *et al.* 2013; Edgecombe *et al.* 2017; Hou *et al.* 2017, 2018; Lerosey-Aubril *et al.* 2017b; Zeng *et al.* 2017; Du *et al.* 2018; Mayers *et al.* 2019). Unfortunately, the results of these analyses are ambiguous, in that trilobites are resolved either in a polytomy with other artiopodan clades, or their position jumps around depending on taxon sampling, character selection and coding, and the analytical methods used.

Many suprafamilial names and concepts have come and gone over the decades (see Harrington *et al.* 1959; Fortey, 1997), but

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one of the most enduring is the order Ptychopariida. While Fortey (1997, 2001) recognized this group as being problematic, it has undergone so many different iterations (e.g. Table 1) that the Ptychopariida has essentially become a 'wastebasket taxon' (Lieberman & Karim, 2010), mainly for a plethora of Cambrian families. As noted in Section 2, Adrain (2011, p. 107) abandoned the idea of the group altogether, stating that "it serves no scientific purpose". Previous claims for the Ptychopariida representing a plesiomorphic grade and being ancestral to typical post-Cambrian groups, such as the Asaphida, Phacopida and Proetida (Swinnerton, 1915; Henningsmoen, 1951; Hahn & Hahn, 1975; Fortey, 2001; Cotton, 2001), are therefore now meaningless.

The phylogenetic affinity of the suborder Agnostina (*sensu* Fortey, 1997) remains a challenge. Ever since the discovery of appendages in small (larval) specimens of *Agnostus pisiformis* (Müller & Walossek, 1987), many have questioned the systematic placement of Agnostina in the Trilobita (see Bergström & Hou, 2005), and therefore the monophyly of order Agnostida (Agnostina + Eodiscina) (see Adrain, 2011). Previous phylogenetic studies have argued that the Agnostina are trilobites, representing a monophyletic group nested within a paraphyletic Eodiscina (Fortey & Theron, 1994; Jell, 1997, 2003; Cotton & Fortey, 2005). However, results from more recent phylogenetic analyses with broader taxonomic and character sampling across many arthropod groups show that the Agnostina (using *A. pisiformis* as the exemplar taxon) falls outside the Trilobita (Legg *et al.* 2013, fig. 4; Aria & Caron, 2017, extended data fig. 10; Vannier *et al.* 2018, supplementary material S22).

Fortey (2001) predicted that the discovery of appendages in Eodiscina, the larvae of other trilobites, or indeed adult Agnostina, should cast further light on the agnostid problem. Moysiuk & Caron (2019) recently documented soft tissues (including appendages) in adult specimens of the agnostines *Peronopsis* cf. *columbiensis* and *Ptychagnostus praecurrens* from the Burgess Shale. Interestingly, the appendicular morphology of these taxa differ considerably from what is known in 'polymerid' trilobites (see Zeng *et al.* 2017). Notably, they seem to possess a cephalon with six appendage pairs (antennae + five post-antennal), which contrasts with the four (antennae + three post-antennal) observed in trilobites (Scholtz & Edgecombe, 2005, 2006; Park & Kihm, 2017; Zeng *et al.* 2017). Also, while the finer details of the post-antennal cephalic appendages in the Burgess Shale agnostines are somewhat obscure, they do not seem to show the typical homonomous biramous morphology, including the lamellipedian exopods, seen in polymerid trilobites (Zeng *et al.* 2017). Further differences can be found in the cephalic digestive structures, which in the Burgess Shale agnostines are more like those seen in naraoiids (cf. Zhang *et al.* 2007; Mayers *et al.* 2019) as opposed to trilobites (cf. Lerosey-Aubril *et al.* 2012, 2017*a*; Gutiérrez-Marco *et al.* 2017; Hopkins *et al.* 2017; Wang *et al.* 2018). The results of the phylogenetic analysis conducted by Moysiuk & Caron (2019) show that Agnostina (*Agnostus* + *Peronopsis*) is sister to the polymerid trilobites, which is mainly supported by shared features such as the calcified tergites, style of tergal articulation, and a dorsally segmented cephalon (including the occipital lobe). In summary, although the combined soft-tissue and biomineralized morphology of agnostines may now suggest an affinity closer to artiopodans (even as sister to polymerid trilobites; Moysiuk & Caron, 2019) than to pancrustaceans (Walossek & Müller, 1990; Bergström & Hou, 2005), further analyses are needed to test whether they are trilobites *sensu stricto*. This will require a new, more holistic dataset that contains an expanded sampling of trilobite taxa, especially members of the Eodiscina, plus many more tergal characters, given their importance in this debate (see Shergold, 1991 versus Cotton & Fortey, 2005, for example). Fortey's (2001) hope that the discovery of eodiscine or larval polymerid appendages will resolve this issue, of course, still stands.

The Burlingiidae (Fig. 6) is an unusual Cambrian family that were assigned to the Proparia by Swinnerton (1915) (Table 1) and later elevated to their own monotypic superfamily (within the Ptychopariida) in the 1959 *Treatise* (Harrington *et al.* 1959). Their unique combination of features – including a small (< 15 mm long), thin-cuticle exoskeleton, proparian facial sutures, plus a strange non-fulcrate trunk that lacks well-developed tergite articulations (see Whittington, 1994; Hughes *et al.* 2006; Hughes, 2007; Ebbestad & Weidner, 2017) – is perhaps why Fortey (1997) relegated them to Order Uncertain (but still considered them trilobites), and Adrain (2011) excluded them from the Trilobita. Several studies on the family have been published over the past 50 years, including two in *Geological Magazine* (Whittington, 1981; Yuan & Esteve, 2015), but none have attempted a large-scale phylogenetic analysis to place them among trilobites or non-trilobite arthropods (Jago, 1972; Rushton, 1978; Ahlberg, 1989; Whittington, 1994; Jell & Hughes, 1997; Yuan *et al.* 2002; Ebbestad & Budd, 2003; Peng *et al.* 2004; Robison & Babcock, 2011; Geyer & Corbacho, 2015; Ebbestad & Weidner, 2017). It is indeed possible that burlingiids have a closer affinity to other artiopodans than to trilobites – for example, *Kleptothule rasmusseni* (see Budd, 1995; Ebbestad & Budd, 2003) or even the 'Protosutura' (*sensu* Du *et al.* 2018) – but the suggestion that they are a trilobite lineage that arose via paedomorphosis (Stubblefield, 1936; Whittington, 1981) cannot be ruled out either. Future discovery of burlingiid appendages may answer this question of relationship, but a phylogenetic analysis including the better-known burlingiid taxa (including those with ontogenetic data), various non-trilobite artiopodans and a range of relevant trilobite groups (see Whittington, 1994; Ebbestad & Budd, 2003; Ebbestad & Weidner, 2017) should be conducted in the interim.

Until the suggested bottom-up and top-down approaches are adopted by trilobite workers *en masse*, and many of the above-mentioned issues are resolved, trilobite systematics will continue to be riddled with problems, particularly at the suprafamilial level. With the high-resolution digital imaging capabilities, computing power, analytical methods and software now available, trilobite systematics has the potential to enter a revolutionary new age of research.

Author ORCID. John R. Paterson, 0000-0003-2947-3912

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References

Adrain JM (2008) A global species database of Trilobita: progress, results, and revision of the *Treatise*. In *Advances in Trilobite Research* (eds I Rábano, R Gozalo and DC García-Bellido), pp. 27–8. Cuadernos del Museo Geominero 9, Madrid: Instituto Geológico y Minero de España.

Adrain JM (2011) Class Trilobita Walch, 1771. In *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness* (ed. Z-Q Zhang). *Zootaxa* 3148, 104–9.

https://doi.org/10.1017/S0016756819000426 Published online by Cambridge University Press

Adrain JM (2013) A synopsis of Ordovician trilobite distribution and diversity. In *Early Palaeozoic Biogeography and Palaeogeography* (eds DAT Harper and T Servais), pp. 297–336. Geological Society of London, Memoir no. 38.

Adrain JM, Edgecombe GD, Fortey RA, Hammer Ø, Laurie JR, McCormick T, Owen AW, Waisfeld BG, Webby BD, Westrop SR and Zhou Z-Y (2004) Trilobites. In *The Great Ordovician Biodiversification Event* (eds BD Webby, ML Droser and F Paris), pp. 231–54. New York: Columbia University Press.

Adrain JM, Fortey RA and Westrop SR (1998) Post-Cambrian trilobite diversity and evolutionary faunas. *Science* **280**, 1922–5.

Adrain JM, Karim TS and Westrop SR (2014) The Early Ordovician (Floian) bathyurid trilobite genera *Jeffersonia*, *Cullisonia* and *Bathyurina*. *Memoirs of the Association of Australasian Palaeontologists* **45**, 305–47.

Adrain JM and McAdams NEB (2012) The Lower Ordovician (upper Floian) bathyurid trilobite *Aponileus* Hu, with species from Utah, Texas, and Greenland. *Zootaxa* **3293**, 1–67.

Adrain JM, McAdams NEB and Karim TS (2012) The Middle Ordovician bathyurid trilobite *Pseudoolenoides*, with a revised trilobite biostratigraphy of the Dapingian and lower Darriwilian of western Laurentia. *Zootaxa* **3467**, 1–97.

Adrain JM, McAdams NEB and Westrop SR (2011a) Affinities of the Lower Ordovician (Tulean; lower Floian) trilobite *Gladiatoria*, with species from the Great Basin, western United States. *Memoirs of the Association of Australasian Palaeontologists* **42**, 321–67.

Adrain JM, McAdams NEB, Westrop SR and Karim TS (2011b) Systematics and affinity of the Lower Ordovician (Tulean; lower Floian) trilobite *Psalikilopsis*. *Memoirs of the Association of Australasian Palaeontologists* **42**, 369–416.

Adrain JM and Westrop SR (2004) A late Cambrian (Sunwaptan) silicified trilobite fauna from Nevada. *Bulletins of American Paleontology* **365**, 1–56.

Adrain JM and Westrop SR (2005) Late Cambrian ptychaspidid trilobites from western Utah: implications for trilobite systematics and biostratigraphy. *Geological Magazine* **142**, 377–98.

Adrain JM and Westrop SR (2007) *Bearriverops*, a new Lower Ordovician trilobite genus from the Great Basin, western USA, and classification of the family Dimeropygidae. *Canadian Journal of Earth Sciences* **44**, 337–66.

Ahlberg P (1989) Cambrian stratigraphy of the När 1 deep well, Gotland. *GFF* **111**, 137–48.

Álvaro JJ, Ahlberg P, Babcock LE, Bordonaro OL, Choi DK, Cooper RA, Ergaliev GKH, Gapp IW, Ghobadi Pour M, Hughes NC, Jago JB, Korovnikov I, Laurie JR, Lieberman BS, Paterson JR, Pegel TV, Popov LE, Rushton AWA, Sukhov SS, Tortello MF, Zhou Z and Żylińska A (2013) Global Cambrian trilobite palaeobiogeography assessed using parsimony analysis of endemicity. In *Early Palaeozoic Biogeography and Palaeogeography* (eds DAT Harper and T Servais), pp. 273–96. Geological Society of London, Memoir no. 38.

Aria C and Caron J-B (2017) Burgess Shale fossils illustrate the origin of the mandibulate body plan. *Nature* **545**, 89–92.

Beecher CE (1897) Outline of a natural classification of the trilobites. *American Journal of Science* **3**, 89–106, 181–207.

Bergström J (1973) Organization, life, and systematics of trilobites. *Fossils and Strata* **2**, 1–69.

Bergström J (1977) Proetida – a disorderly order of trilobites. *Lethaia* **10**, 95–105.

Bergström J and Hou X-G (2005) Early Palaeozoic non-lamellipedian arthropods. In *Crustacea and Arthropod Relationships* (eds S Koenemann and RA Jenner), pp. 73–93. Boca Raton: Taylor & Francis.

Budd GE (1995) *Kleptothule rasmusseni* gen. et sp. nov.: an ?olenellinid-like trilobite from the Sirius Passet fauna (Buen Formation, Lower Cambrian, North Greenland). *Transactions of the Royal Society of Edinburgh: Earth Sciences* **86**, 1–12.

Budd GE (2011) *Campanamuta mantonae* gen. et sp. nov., an exceptionally preserved arthropod from the Sirius Passet fauna (Buen Formation, lower Cambrian, North Greenland). *Journal of Systematic Palaeontology* **9**, 217–60.

Calver MA (1981) Palaeozoic studies in honour of Sir James Stubblefield. *Geological Magazine* **118**, 581–9.

Caron J-B, Rudkin DM and Milliken S (2004) A new late Silurian (Pridolian) naraoiid (Euarthropoda: Nektaspida) from the Bertie Formation of southern Ontario, Canada—delayed fallout from the Cambrian explosion. *Journal of Paleontology* **78**, 1138–45.

Chatterton BDE and Ludvigsen R (2004) Early Silurian trilobites of Anticosti Island, Québec, Canada. *Palaeontographica Canadiana* **22**, 1–264.

Chatterton BDE, Siveter DJ, Edgecombe GD and Hunt AS (1990) Larvae and relationships of the Calymenina (Trilobita). *Journal of Paleontology* **64**, 255–77.

Chatterton BDE and Speyer SE (1997) Ontogeny. In *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita (Revised)* (ed. RL Kaesler), pp. 173–247. Geological Society of America, Boulder and University of Kansas Press, Lawrence.

Cotton TJ (2001) The phylogeny and systematics of blind Cambrian ptychoparioid trilobites. *Palaeontology* **44**, 167–207.

Cotton TJ and Braddy S (2004) The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**, 169–93.

Cotton TJ and Fortey RA (2005) Comparative morphology and relationships of the Agnostida. In *Crustacea and Arthropod Relationships* (eds S Koenemann and RA Jenner), pp. 95–136. Boca Raton: Taylor & Francis.

Crônier C, Abbache A, Khaldi AY, Oudot M, Maillet S and Ouali Mehadji A (2018) Middle Devonian trilobites of the Saoura Valley, Algeria: insights into their biodiversity and Moroccan affinities. *Geological Magazine* **155**, 811–40.

Du K-S, Ortega-Hernández J, Yang J and Zhang X-G (2018) A soft-bodied euarthropod from the early Cambrian Xiaoshiba Lagerstätte of China supports a new clade of basal artiopodans with dorsal ecdysial sutures. *Cladistics*, published online 2 July 2018, doi: 10.1111/cla.12344.

Ebbestad JOR and Budd GE (2003) Burlingiid trilobites from Norway, with a discussion of their affinities and relationships. *Palaeontology* **45**, 1171–95.

Ebbestad JOR and Weidner T (2017) Extreme protomeric development in a burlingiid trilobite from Cambrian glacial erratics of Denmark. *Palaeontology* **60**, 233–53.

Edgecombe GD (1992) Trilobite phylogeny and the Cambrian–Ordovician "Event": cladistic reappraisal. In *Extinction and Phylogeny* (eds MJ Novacek and QD Wheeler), pp. 144–77. New York: Columbia University Press.

Edgecombe GD, Paterson JR and García-Bellido DC (2017) A new aglaspidid-like euarthropod from the early Cambrian Emu Bay Shale of South Australia. *Geological Magazine* **154**, 87–95.

Edgecombe GD and Ramsköld L (1999) Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology* **73**, 263–87.

Edgecombe GD, Vaccari NE and Waisfeld BG (1994) Lower Devonian calmoniid trilobites from the Argentine Precordillera: new taxa of the *Bouleia* Group, and remarks on the tempo of calmoniid radiation. *Geological Magazine* **131**, 449–64.

Eldredge N (1977) Trilobites and evolutionary patterns. In *Patterns of Evolution as Illustrated by the Fossil Record* (ed. A Hallam), pp. 305–32. Amsterdam: Elsevier.

Evitt WR (1961) Early ontogeny in the trilobite family Asaphidae. *Journal of Paleontology* **35**, 986–95.

Feist R and McNamara KJ (2007) Biodiversity, distribution and patterns of extinction of the last odontopleuroid trilobites during the Devonian (Givetian, Frasnian). *Geological Magazine* **144**, 777–96.

Feist R, McNamara KJ, Crônier C and Lerosey-Aubril R (2009) Patterns of extinction and recovery of phacopid trilobites during the Frasnian–Famennian (Late Devonian) mass extinction event, Canning Basin, Western Australia. *Geological Magazine* **146**, 12–33.

Fortey RA (1981) *Prospectatrix genatenta* (Stubblefield) and the trilobite superfamily Cyclopygacea. *Geological Magazine* **118**, 603–14.

Fortey RA (1983) Cambrian–Ordovician trilobites from the boundary beds in western Newfoundland and their phylogenetic significance. *Special Papers in Palaeontology* **30**, 179–211.

Fortey RA (1989) There are extinctions and extinctions: examples from the Lower Palaeozoic. *Philosophical Transactions of the Royal Society of London B* **325**, 327–55.

Fortey RA (1990) Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* **33**, 529–76.

Fortey RA (1997) Classification. In *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita (Revised)* (ed. RL Kaesler), pp. 289–302.

https://doi.org/10.1017/S0016756819000426 Published online by Cambridge University Press

Geological Society of America, Boulder and University of Kansas Press, Lawrence.
Fortey RA (2001) Trilobite systematics: the last 75 years. *Journal of Paleontology* **75**, 1141–51.
Fortey RA and Chatterton BDE (1988) Classification of the trilobite suborder Asaphina. *Palaeontology* **31**, 165–222.
Fortey RA and Owens RM (1975) Proetida – a new order of trilobites. *Fossils and Strata* **4**, 227–39.
Fortey RA and Owens RM (1979) Enrollment in the classification of trilobites. *Lethaia* **12**, 219–26.
Fortey RA and Owens RM (1991) A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine* **128**, 437–64.
Fortey RA and Theron JN (1994) A new Ordovician arthropod, *Soomaspis*, and the agnostid problem. *Palaeontology* **37**, 841–61.
Fortey RA and Whittington HB (1989) The Trilobita as a natural group. *Historical Biology* **2**, 125–38.
García-Bellido DC and Collins DH (2006) A new study of *Marrella splendens* (Arthropoda, Marrellomorpha) from the Middle Cambrian Burgess Shale, British Columbia, Canada. *Canadian Journal of Earth Sciences* **43**, 721–42.
Geyer G and Corbacho J (2015) The Burlingiidae (Trilobita): revised generic composition, stratigraphy, and the first species from the early Middle Cambrian of West Gondwana. *GFF* **137**, 212–25.
Gutiérrez-Marco JC, García-Bellido DC, Rábano I and Sá AA (2017) Digestive and appendicular soft-parts, with behavioural implications, in a large Ordovician trilobite from the Fezouata Lagerstätte, Morocco. *Scientific Reports* **7**, 39728. doi: 10.1038/srep39728.
Hahn G (1989) Reconstruction of the phylogenetic relationships among the higher taxa of trilobites. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* **28**, 187–99.
Hahn G and Hahn R (1975) Forschungsbericht über Trilobitomorpha. *Paläontologische Zeitschrift* **49**, 432–60.
Harrington HJ, Henningsmoen G, Howell BF, Jaanusson V, Lochman-Balk C, Moore RC, Poulsen C, Rasetti F, Richter E, Richter R, Schmidt H, Sdzuy K, Struve W, Størmer L, Stubblefield CJ, Tripp R, Weller JM and Whittington HB (1959) *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1*. Geological Society of America, New York and University of Kansas Press, Lawrence, 560 p.
Haug JT, Maas A and Waloszek D (2010) †*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* gen. et sp. nov. and heterochronic events in early crustacean evolution. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **100**, 311–50.
Hendricks JR and Lieberman BS (2008) New phylogenetic insights into the Cambrian radiation of arachnomorph arthropods. *Journal of Paleontology* **82**, 585–94.
Henningsmoen G (1951) Remarks on the classification of trilobites. *Norsk Geologisk Tidsskrift* **29**, 174–217.
Henry J-L (1980) Evolution and classification of some Ordovician Calymenina (Trilobita). *Geological Magazine* **117**, 351–62.
Hopkins MJ, Chen F, Hu S and Zhang Z (2017) The oldest known digestive system consisting of both paired digestive glands and a crop from exceptionally preserved trilobites of the Guanshan Biota (early Cambrian, China). *PLoS ONE* **12**, e0184982. doi: 10.1371/journal.pone.0184982.
Hou X, Williams M, Gabbott S, Siveter DJ, Siveter DJ, Cong P, Ma X and Sansom R (2017) A new species of the artiopodan arthropod *Acanthomeridion* from the lower Cambrian Chengjiang Lagerstätte, China, and the phylogenetic significance of the genus. *Journal of Systematic Palaeontology* **15**, 733–40.
Hou X, Williams M, Sansom R, Siveter DJ, Siveter DJ, Gabbott S, Harvey THP, Cong P and Liu Y (2018) A new xandarellid euarthropod from the Cambrian Chengjiang biota, Yunnan Province, China. *Geological Magazine*, published online 3 December 2018, doi: 10.1017/S0016756818000730.
Hughes NC (2007) The evolution of trilobite body patterning. *Annual Review of Earth and Planetary Sciences* **35**, 401–34.
Hughes NC, Minelli A and Fusco G (2006) The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology* **32**, 602–27.
Hupé P (1953a) Classification des Trilobites. *Annales de Paléontologie* **39**, 61–168.
Hupé P (1953b) Classe des Trilobites. In *Traité de Paléontologie. Tome 3. Les Formes Ultimes d'Invertébrés. Morphologie et Évolution. Onycophores. Arthropodes. Échinoderms. Stomocordés* (ed. J Piveteau), pp. 44–246. Paris: Masson et Cie.
Hupé P (1955) Classification des Trilobites. *Annales de Paléontologie* **41**, 91–325.
Jago JB (1972) Two new Cambrian trilobites from Tasmania. *Palaeontology* **15**, 226–37.
Jell PA (1997) Introduction to suborder Eodiscina. In *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita (Revised)* (ed. RL Kaesler), pp. 384–6. Geological Society of America, Boulder and University of Kansas Press, Lawrence.
Jell PA (2003) Phylogeny of early Cambrian trilobites. *Special Papers in Palaeontology* **70**, 45–57.
Jell PA and Adrain JM (2003) Available generic names for trilobites. *Memoirs of the Queensland Museum* **48**, 331–553.
Jell PA and Hughes NC (1997) Himalayan Cambrian trilobites. *Special Papers in Palaeontology* **58**, 1–113.
Kihm R and St. John J (2007) Walch's trilobite research – a translation of his 1771 trilobite chapter. In *Fabulous Fossils, 300 Years of Worldwide Research on Trilobites* (eds DG Mikulic, E Landing and J Kluessendorf), pp. 115–40. *New York State Museum Bulletin* 507.
Lamsdell JC and Selden PA (2015) Phylogenetic support for the monophyly of proetide trilobites. *Lethaia* **48**, 375–86.
Lane PD and Thomas AT (1978) Silurian trilobites from NE Queensland and the classification of effaced trilobites. *Geological Magazine* **115**, 351–8.
Lauterbach K-E (1980) Schlüsselereignisse in der Évolution. des Grundplans der Arachnata (Arthropoda). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* **23**, 163–327.
Lauterbach K-E (1983) Synapomorphien zwischen Trilobiten- und Cheliceratenzweig der Arachnata. *Zoologischer Anzeiger* **210**, 213–18.
Lauterbach K-E (1989) Trilobites and phylogenetic systematics: A reply to G. Hahn. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* **28**, 201–11.
Lee D-C and Chatterton BDE (2003) Protaspides of *Leiostegium* and their implications for membership of the order Corynexochida. *Palaeontology* **46**, 431–45.
Legg DA, Sutton MD and Edgecombe GD (2013) Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications* **4**, 2485. doi: 10.1038/ncomms3485.
Lerosey-Aubril R (2012) The late Palaeozoic trilobites of Iran and Armenia and their palaeogeographical significance. *Geological Magazine* **149**, 1023–45.
Lerosey-Aubril R, Hegna TA, Kier C, Bonino E, Habersetzer J and Carré M (2012) Controls on gut phosphatisation: the trilobites from the Weeks Formation Lagerstätte (Cambrian; Utah). *PLoS ONE* **7**, e32934. doi: 10.1371/journal.pone.0032934.
Lerosey-Aubril R, Paterson JR, Gibb S and Chatterton BDE (2017a) Exceptionally-preserved late Cambrian fossils from the McKay Group (British Columbia, Canada) and the evolution of tagmosis in aglaspidid arthropods. *Gondwana Research* **42**, 264–79.
Lerosey-Aubril R, Zhu X and Ortega-Hernández J (2017b) The Vicissicaudata revisited – insights from a new aglaspidid arthropod with caudal appendages from the Furongian of China. *Scientific Reports* **7**, 11117. doi: 10.1038/s41598-017-11610-5.
Lieberman BS and Karim TS (2010) Tracing the trilobite tree from the root to the tips: A model marriage of fossils and phylogeny. *Arthropod Structure & Development* **39**, 111–23.
Ludvigsen R and Chatterton BDE (1980) The ontogeny of *Failleana* and the origin of the Bumastinae (Trilobita). *Geological Magazine* **117**, 471–8.
Mayers B, Aria C and Caron J-B (2019) Three new naraoiid species from the Burgess Shale, with a morphometric and phylogenetic reinvestigation of Naraoiidae. *Palaeontology* **62**, 19–50.
McAdams NEB and Adrain JM (2009) *Heckethornia*, a new genus of dimeropygid trilobites from the Lower Ordovician (Ibexian; Tulean and Blackhillsian) of the Great Basin, western Utah. *Canadian Journal of Earth Sciences* **46**, 875–914.

https://doi.org/10.1017/S0016756819000426 Published online by Cambridge University Press

McAdams NEB and Adrain JM (2010) A new species of the Lower Ordovician pliomerid trilobite *Pseudocybele* and its biostratigraphic significance. *Zootaxa* **2550**, 21–38.

McAdams NEB and Adrain JM (2011a) Systematics of the Lower Ordovician pliomerid trilobite *Hintzeia*, with species from the Great Basin, western USA. *Zootaxa* **2910**, 1–45.

McAdams NEB and Adrain JM (2011b) *Panisaspis*, a new genus of pliomerid trilobites from the Lower Ordovician (Ibexian; Tulean and Blackhillsian) of the Great Basin, western USA. *Zootaxa* **2969**, 1–68.

McAdams NEB and Adrain JM (2011c) Revision of the Lower Ordovician (lower Floian; Tulean) pliomerid trilobite *Protopliomerella*, with new species from the Great Basin, western USA. *Zootaxa* **3144**, 1–113.

McNamara KJ (1980) Taxonomy and distribution of chasmopine trilobites. *Geological Magazine* **117**, 65–80.

Mickleborough J (1884) Locomotory appendages of trilobites. *Geological Magazine (new series, decade III)* **1**, 80–4.

Moysiuk J and Caron J-B (2019) Burgess Shale fossils shed light on the agnostid problem. *Proceedings of the Royal Society B* **286**, 20182314. doi: 10.1098/rspb.2018.2314.

Müller KJ and Walossek D (1987) Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. *Fossils and Strata* **19**, 1–124.

Ortega-Hernández J and Brena C (2012) Ancestral patterning of tergite formation in a centipede suggests derived mode of trunk segmentation in trilobites. *PLoS ONE* **7**, e52623. doi: 10.1371/journal.pone.0052623.

Ortega-Hernández J, Legg DA and Braddy SJ (2013) The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics* **29**, 15–45.

Park T-Y (2018) Ontogeny of the two co-occurring middle Furongian (late Cambrian) shumardiid trilobites and the protaspid morphology of shumardiids. *Geological Magazine* **155**, 1247–62.

Park T-Y and Choi DK (2009) Post-embryonic development of the Furongian (late Cambrian) trilobite *Tsinania canens*: implications for life mode and phylogeny. *Evolution & Development* **11**, 441–55.

Park T-Y and Choi DK (2010) Ontogeny and ventral median suture of the ptychaspidid trilobite *Asioptychaspis subglobosa* (Sun, 1924) from the Furongian (Upper Cambrian) Hwajeol Formation, Korea. *Journal of Paleontology* **84**, 309–20.

Park T-Y and Choi DK (2011a) Ontogeny of the Furongian (late Cambrian) remopleuridioid trilobite *Haniwa quadrata* Kobayashi, 1933 from Korea: implications for trilobite taxonomy. *Geological Magazine* **148**, 288–303.

Park T-Y and Choi DK (2011b) Constraints on using ontogenetic data for trilobite phylogeny. *Lethaia* **44**, 250–4.

Park T-Y and Kihm J-H (2015) Post-embryonic development of the Early Ordovician (ca. 480 Ma) trilobite *Apatokephalus latilimbatus* Peng, 1990 and the evolution of metamorphosis. *Evolution & Development* **17**, 289–301.

Park T-Y and Kihm J-H (2017) Head segmentation of trilobites. *Lethaia* **50**, 1–6.

Park T, Kihm JH, Kang I and Choi DK (2014) Ontogeny of a new species of the Cambrian Series 3 (middle Cambrian) trilobite genus *Liostracina* Monke, 1903 from North China and the taxonomic position of the superfamily Trinucleoidea. *Journal of Paleontology* **88**, 395–402.

Park T-Y, Kihm J-H, Woo J, Kim Y-H and Lee JI (2016) Ontogeny of the Furongian (late Cambrian) trilobite *Proceratopyge* cf. *P. lata* Whitehouse from Northern Victoria Land, Antarctica, and the evolution of metamorphosis in trilobites. *Palaeontology* **59**, 657–70.

Paterson JR and Edgecombe GD (2006) The Early Cambrian trilobite family Emuellidae Pocock, 1970: systematic position and revision of Australian species. *Journal of Paleontology* **80**, 496–513.

Paterson JR, Edgecombe GD, García-Bellido DC, Jago JB and Gehling JG (2010) Nektaspid arthropods from the lower Cambrian Emu Bay Shale Lagerstätte, South Australia, with a reassessment of lamellipedian relationships. *Palaeontology* **53**, 377–402.

Paterson JR, Edgecombe GD and Lee MSY (2019) Trilobite evolutionary rates constrain the duration of the Cambrian explosion. *Proceedings of the National Academy of Sciences (USA)* **116**, 4394–9.

Paterson JR, García-Bellido DC and Edgecombe GD (2012) New artiopodan arthropods from the early Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia. *Journal of Paleontology* **86**, 340–57.

Peng S-C, Babcock LE and Lin H-L (2004) *Polymerid Trilobites from the Cambrian of Northwestern Hunan, China - Volume 2: Ptychopariida, Eodiscida, and Undetermined Forms*. Beijing: Science Press, 355 p.

Pollitt JR, Fortey RA and Wills MA (2005) Systematics of the trilobite families Lichidae Hawle & Corda, 1847 and Lichakephalidae Tripp, 1957: the application of Bayesian inference to morphological data. *Journal of Systematic Palaeontology* **3**, 225–41.

Ramsköld L and Edgecombe GD (1991) Trilobite monophyly revisited. *Historical Biology* **4**, 267–83.

Reed FRC (1898) Blind trilobites. *Geological Magazine (new series, decade IV)* **5**, 439–47, 493–506, 552–9.

Reed FRC (1905) The classification of the Phacopidae. *Geological Magazine (new series, decade V)* **2**, 172–8, 224-8.

Reed FRC (1927) Recent work on the Phacopidae. *Geological Magazine* **64**, 308–22, 337–53.

Reed FRC (1928) Notes on the family Encrinuridae. *Geological Magazine* **65**, 51–77.

Robison RA and Babcock LE (2011) Systematics, paleobiology, and taphonomy of some exceptionally preserved trilobites from Cambrian Lagerstätten of Utah. *Paleontological Contributions* **5**, 1–47.

Rushton AWA (1978) Fossils from the Middle-Upper Cambrian transition in the Nuneaton district. *Palaeontology* **21**, 245–83.

Rushton AWA and Hughes CP (1981) The Ordovician trilobite fauna of the Great Paxton Borehole, Cambridgeshire. *Geological Magazine* **118**, 623–46.

Salter JW (1864) On some points in ancient physical geography, illustrated by fossils from a pebble-bed at Budleigh Salterton, Devonshire. *Geological Magazine* **1**, 5–12.

Scholtz G and Edgecombe GD (2005) Heads, hox and the phylogenetic position of trilobites. In *Crustacea and Arthropod Relationships* (eds S Koenemann and RA Jenner), pp. 139–65. Boca Raton: Taylor & Francis.

Scholtz G and Edgecombe GD (2006) The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Development Genes and Evolution* **216**, 395–415.

Servais T and Harper DAT (2018) The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration. *Lethaia* **51**, 151–64.

Servais T, Owen AW, Harper DAT, Kröger B and Munnecke A (2010) The Great Ordovician Biodiversification Event (GOBE): The palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology* **294**, 99–119.

Shergold JH (1991) Protaspid and early meraspid growth stages of the eodiscoid trilobite *Pagetia ocellata* Jell, and their implications for classification. *Alcheringa* **15**, 65–86.

Stein M, Budd GE, Peel JS and Harper DAT (2013) *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry. *BMC Evolutionary Biology* **13**, 99. doi: 10.1186/1471-2148-13-99.

Stein M and Selden PA (2012) A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and reassessment of its affinities. *Journal of Systematic Palaeontology* **10**, 361–83.

Stubblefield CJ (1936) Cephalic sutures and their bearing on current classifications of trilobites. *Biological Reviews* **11**, 407–40.

Stubblefield CJ (1959) Evolution in trilobites. *Quarterly Journal of the Geological Society of London* **115**, 145–62.

Swinnerton HH (1915) Suggestions for a revised classification of trilobites. *Geological Magazine (new series, decade VI)* **2**, 487–96, 538–45.

Swinnerton HH (1919) The facial suture of trilobites. *Geological Magazine (new series, decade VI)* **4**, 103–10.

Tarver JE, Braddy SJ and Benton MJ (2007) The effects of sampling bias on Palaeozoic faunas and implications for macroevolutionary studies. *Palaeontology* **50**, 177–84.

Temple JT (1956) Notes on the Cheiruracea and Phacopacea. *Geological Magazine* **93**, 418–30.

Thomas AT and Holloway DJ (1988) Classification and phylogeny of the trilobite order Lichida. *Philosophical Transactions of the Royal Society of London B* **321**, 179–262.

Thomas AT and Narbonne GM (1979) Silurian trilobites from arctic Canada. *Geological Magazine* **116**, 1–19.

Tripp RP and Evitt WR (1981) Silicified Lichidae (Trilobita) from the Middle Ordovician of Virginia. *Geological Magazine* **118**, 665–77.

https://doi.org/10.1017/S0016756819000426 Published online by Cambridge University Press

Vannier J, Aria C, Taylor RS and Caron J-B (2018) *Waptia fieldensis* Walcott, a mandibulate arthropod from the middle Cambrian Burgess Shale. *Royal Society Open Science* **5**, 172206. doi: 10.1098/rsos.172206.

Walch JEI (1771) *Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur*. Nürnberg: Paul Jonathan Felstecker, 235 p.

Walcott CD (1894) Note on some appendages of the trilobites. *Geological Magazine (new series, decade IV)* **1**, 246–51.

Walcott CD (1908) Cambrian trilobites. *Smithsonian Miscellaneous Collections* **53**, 13–52.

Walossek D and Müller KJ (1990) Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia* **23**, 409–27.

Wang P, Fatka O, Sun Z, Budil P and Gao J (2018) Fossilized gut of the trilobite *Lioparia bassleri* and the distribution of exceptional preservation in the Cambrian Stage 4–Drumian Manto Formation of North China. *Bulletin of Geosciences* **93**, 491–8.

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. *Journal of Systematic Palaeontology* **13**, 1–74.

Westrop SR and Adrain JM (2016) Revision of *Irvingella tropica* Öpik 1963 from Australia and related species from North America: implications for correlation of the base of the Jiangshanian Stage (Cambrian, Furongian). *Australasian Palaeontological Memoirs* **49**, 395–432.

Whittington HB (1980) Exoskeleton, moult stage, appendage morphology, and habits of the middle Cambrian trilobite *Olenoides serratus*. *Palaeontology* **23**, 171–204.

Whittington HB (1981) Paedomorphosis and cryptogenesis in trilobites. *Geological Magazine* **118**, 591–602.

Whittington HB (1994) Burlingiids: small proparian Cambrian trilobites of enigmatic origin. *Palaeontology* **37**, 1–16.

Whittington HB (2003) The upper Cambrian trilobites *Plethopeltis* and *Leiocoryphe*: morphology, paedomorphism, classification. *Journal of Paleontology* **77**, 698–705.

Whittington HB (2007) Reflections on the classification of the Trilobita. In *Fabulous Fossils, 300 Years of Worldwide Research on Trilobites* (eds DG Mikulic, E Landing and J Kluessendorf), 225–30. *New York State Museum Bulletin* 507.

Whittington HB, Chatterton BDE, Speyer SE, Fortey RA, Owens RM, Chang WT, Dean WT, Fortey RA, Jell PA, Laurie JR, Palmer AR, Repina LN, Rushton AWA, Shergold JH, Clarkson ENK, Wilmot NV and Kelly SRA (1997) *Treatise on Invertebrate Paleontology, Part O, Revised. Arthropoda 1, Trilobita 1 (Introduction, Order Agnostida, Order Redlichiida)*, 530 p. The Geological Society of America, Boulder and The University of Kansas, Lawrence.

Woodward H (1871) On the structure of trilobites. *Geological Magazine* **8**, 289–94.

Woodward H (1883) Synopsis of the genera and species of Carboniferous limestone trilobites. *Geological Magazine (new series, decade II)* **10**, 445–54, 481–7, 534–42.

Woodward H (1884a) On the structure of trilobites. *Geological Magazine (new series, decade III)* **1**, 78–9.

Woodward H (1884b) Synopsis of the genera and species of Carboniferous limestone trilobites. *Geological Magazine (new series, decade III)* **1**, 484–9.

Yuan J-L and Esteve J (2015) The earliest species of *Burlingia* Walcott, 1908 (Trilobita) from South China: biostratigraphical and palaeogeographical significance. *Geological Magazine* **152**, 358–66.

Yuan J-L, Zhao Y-L, Li Y and Huang Y-Z (2002) *Trilobite Fauna of the Kaili Formation (uppermost Lower Cambrian–lower Middle Cambrian) from southeastern Guizhou, South China*. Shanghai: Shanghai Science and Technology Publishing House, 423 p.

Zeng H, Zhao F, Yin Z and Zhu M (2017) Appendages of an early Cambrian metadoxidid trilobite from Yunnan, SW China support mandibulate affinities of trilobites and artiopods. *Geological Magazine* **154**, 1306–28.

Zhang X-L, Shu D-G and Erwin DH (2007) Cambrian naraoiids (Arthropoda): morphology, ontogeny, systematics, and evolutionary relationships. *Paleontological Society Memoir* **68**, 1–52.

Zhu X, Hughes NC and Peng S (2007) On a new species of *Shergoldia* Zhang & Jell, 1987 (Trilobita), the family Tsinaniidae and the order Asaphida. *Memoirs of the Association of Australasian Palaeontologists* **34**, 243–53.

Zhu X, Hughes NC and Peng S (2010) Ventral structure and ontogeny of the late Furongian (Cambrian) trilobite *Guangxiaspis guangxiensis* Zhou, 1977 and the diphyletic origin of the median suture. *Journal of Paleontology* **84**, 493–504.

Żylińska A and Masiak M (2007) Cambrian trilobites from Brzechów, Holy Cross Mountains (Poland) and their significance in stratigraphic correlation and biogeographic reconstructions. *Geological Magazine* **144**, 661–86.

https://doi.org/10.1017/S0016756819000426 Published online by Cambridge University Press