



Phylogenetic support for the monophyly of proetide trilobites

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The monophyly of the order Proetida, the only trilobite group to survive the end-Devonian mass extinction, has been regularly questioned since its erection almost three decades ago. Through analysis of a novel phylogenetic data set comprising 114 characters coded for 55 taxa, including both traditional members of the Proetida along with a number of other trilobite groups, the monophyly of proetide trilobites is rigorously tested for the first time. Proetida is shown to be monophyletic, united by the initial compound eye formation in early protaspids occurring at the lateral margin rather than the anterior margin, and the form of the protaspid glabella being tapering with a pre-glabellar field. A number of adult characters, including the possession of a quadrate or shield-shaped hypostome with angular posterior margins, the hypostome median body being divided by a deep groove that entirely traverses the median body, the presence of an enlarged thoracic spine on the sixth tergite and a tergite count of between 7 and 10, also define the basal node. Hystricurid and dimeropygoid trilobites are shown to resolve at the base of the group, while the remaining proetide taxa are divided between large proetoid and aulacopleuroid clades. Some taxa previously allied with Aulacopleuroidea, such as rorringtoniids and scharyiids, are retrieved as basal members of the Proetoidea. □ *Cladistics, monophyly, ontogeny, Palaeozoic, Proetida, pygidium, Trilobita.*

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Trilobites are a monophyletic group of arthropods (Ramsköld & Edgecombe 1991) and are some of the most iconic Palaeozoic organisms, with some 10,000 species and an evolutionary history stretching some 300 million years from the Cambrian to the Permian (Lieberman & Karim 2010). Trilobite diversity was adversely affected by a number of mass-extinction events, including the end-Ordovician (Chatterton & Speyer 1989; Adrain *et al.* 1998), from which trilobite diversity recovered (Adrain *et al.* 2000; Congreve 2013), and the end-Devonian (Feist 1991; McNamara & Feist 2006; Feist & McNamara 2007; McNamara *et al.* 2009) which marked the beginning to the terminal decline of the trilobites until their eventual extinction at the end-Permian (Owens 2003).

The youngest known trilobites, and the only group to persist through the Devonian into the Carboniferous, belong to the order Proetida. Proetides were one of the last major trilobite groups to be formally recognized and were raised to ordinal status by Fortey & Owens (1975), removing them from the Illaenidae with which they had been allied in the *Treatise on Invertebrate Paleontology* (Moore 1959).

The group has had a checkered taxonomic history, however, with its monophyly challenged a number of times (Bergström 1977; Adrain 2011) resulting in a polyphyletic Proetida being implicitly considered in a number of studies (e.g. Lerosey-Aubril & Feist 2005). Therefore, ascertaining the monophyly or otherwise of proetide trilobites is a key question in trilobite systematics, especially given their distinction of being the only trilobite group to weather the Late Devonian biodiversity crisis.

The application of paraphyletic or polyphyletic groups in biodiversity studies can have drastic effects on our understanding of mass-extinction events, with erroneous patterns of pseudo-extinction retrieved when monophyly is not recognized while incorrect assumptions of monophyly can dampen the observed loss of biodiversity, especially when studies are conducted at higher taxonomic levels (Patterson & Smith 1989). Given that the Late Devonian may be potentially unique among the Big Five mass extinctions in being driven primarily by a decrease in endemism and a drop in speciation rate rather than a marked increase in extinction rate (Rode & Lieberman 2004; Stigall 2012) and that

accurate phylogenetic hypotheses are required to assess the mechanisms behind changes in speciation, extinction and biogeography (Rode & Lieberman 2005; Stigall 2010), uncertainty of the monophyly of major groups such as proetides can have serious negative implications for our understanding of the patterns and processes underlying the biotic turnover occurring during this period. Proetides have already been the subject of a number of biodiversity studies focusing on the Late Devonian (Lerosey-Aubril & Feist 2012; Feist & McNamara 2013) and beyond (Owens 2003), with a number of pseudo-extinctions amongst Late Devonian proetides having already been hypothesized (Owens 1994). Uncertainty over the order's status serves to only further muddy the waters, and until the issue is resolved the results of such biodiversity studies must be treated with caution.

Taxonomic history of the Proetida

As with many of the major trilobite groups, proetides have had a complicated taxonomic history. The superfamily Proetacea was first diagnosed by Hawley & Corda (1847). For many years, trilobite classification hinged on whether authors considered cephalic suture morphology (Beecher 1897) or pygidium size (Gürich 1907) to be of greater importance for defining groups; however, following Swinnerton (1915), a more nuanced hierarchy began to emerge. At this time, proetids comprised part of the Olenina, while bathyurids were included along with illaenids in Ptychopariina; however, Richter (1933) removed illaenids to Bathyuriscidea within Redlichiina, and placed proetids and otarionids together as part of Ellipsocephalidea within Ptychopariina. By the 1950s, a more modern approach to trilobite systematics began to prevail, encapsulated by Henningsmoen (1951) and Hupé (1955), which discarded the use of single characteristics as the sole criterion for assigning relationships. In the scheme of Hupé (1955), the groups that later became the order Proetida fell broadly into two superfamilies: Holotrachelidae, Proetidae, Tropidocoryphidae, Cyrtosymbolidae, Dechenellidae, Phillipsiidae and Brachymetopidae comprised the Proetoidea, while Hystricuridae, Toernquistiidae, Dimeropygidae, Bathyuridae and Otariionidae were included among the Solenopleuroidea. This classification was heavily revised for the *Treatise on Invertebrate Paleontology* (Moore 1959), in which Proetacea was included with the superfamily Illaenacea in the suborder Illaenina within the Ptychopariida (Harrington *et al.* 1959), based on the general lack of glabella furrows, a general lack of eye

ridges and a usual thoracic segment count of between 6 and 10. At the time of the *Treatise*, Proetacea comprised the families Proetidae, Phillipsiidae, Otariionidae, Aulacopleuridae, Brachymetopidae, Phillipsinellidae, Celmidae, Plethopeltidae and Dimeropygidae, with Holotrachelacea and Bathyuracea being included within Illaenina. Bergström (1973) later transferred the Holotrachelidae and Lecanopygidae (from Bathyuracea) into Proetacea, retaining the superfamily within Illaenida, but moving the group out of the ptychopariids. Bathyurids and proetoids, therefore, were considered to be derived independently from illaenids, while hystricurids remained part of the Solenopleuroidea.

Fortey & Owens (1975) raised Proetida to ordinal status, including within it the families Aulacopleuridae, Bathyuridae, Celmidae, Dimeropygidae, Glaphuridae, Otariionidae, Proetidae and the subfamily Hystricurinae. This new grouping was considered to exhibit a common larval morphology and was further defined based on twelve adult characteristics (although these comprised a mixture of both apomorphic and plesiomorphic characters): (1) a medially transversely narrow rostral plate that generally tapers backwards; (2) a well-defined vaulted glabella; (3) poorly expressed anterior glabellar furrows; (4) a well-defined occipital ring; (5) well-developed (often blade-like) genal spines; (6) semicircular holochroal eyes medially or backwardly positioned; (7) posterior sections of the facial suture diverging at a moderate-to-high angle, anterior branches usually divergent; (8) doublure of convex species usually recurved steeply beneath the border of the free cheek to form a lateral cephalic 'tube'; (9) thorax usually with 8–10 segments (maybe as few as 6 or as many as 22), width of pleurae equal to or exceeding in width that of the axis, thoracic segments in contact along their length, pleural furrows diagonal; (10) pygidium with strong pleural furrows and margin usually entire, doublure with strong terrace lines; (11) hypostome longer than wide with elongate, oval middle body and one pair of relatively posteriorly situated middle furrows, borders narrow; and (12) preglabellar field variously developed, species with shorter pre-glabellar field tending to have a granular surface sculpture, those with a longer pre-glabellar field tending to have a surface sculpture of fine terrace lines. As well as explicitly stating that these taxa formed a natural group – a monophylum – Fortey & Owens (1975) considered there to be no compelling link between Proetida and Illaenida. Bergström (1977) contested that Proetida was an unnatural group, citing the occurrence of two different types of enrolment, and split proetides among three groups: one consisting of the Bathyuridae, Proetidae and

Brachymetopidae, another comprising the Hystricurinae, Dimeropygidae and Aulacopleuridae, with Glaphuridae and Celmidae forming the third group. Bergström (1977) considered each of these groups to be independently derived and not closely related to one another, with the hystericurine group forming part of the Solenopleuracea and the glaphurid group being included within the Odontopleurida. Fortey & Owens (1979) refuted Bergström's (1977) contention that enrolment type defined specific groups and maintained the validity of the order. Lütke (1980) provided an in-depth revision of the proetides, which were considered to be a monophyletic suborder of ptychopariid trilobites derived from the Hystricurinae, which had once again been placed within the Solenopleuracea. The group was split into two superfamilies: the Proetacea, incorporating the Proetidae (which included cornuproetids, phillipsiids, cyphoproetids and others as sub-families) and Tropidocoryphidae, and the Aulacopleuracea, comprising the Aulacopleuridae (including brachymetopids, scharyiids and rorringtoniids), Dimeropygidae and Cyphaspididae. Glaphuridae and Celmidae were retained within proetides, but were considered of uncertain affinity. At the same time, Chatterton (1980) recognized Telephinidae as being members of the proetide clade. Finally, Fortey (1990) revisited the Proetida as part of a broad revision of trilobite systematics in the light of hypostomal characters. Fortey (1990) identified the possession of a fusiform, anteriorly rounded or pointed glabella with a preglabellar field in protaspides as a derived character that unites the group, potentially further supported by the natant hypostomal condition being attained early in ontogeny and the larval hypostome margin lacking spines. This classification became widely adopted (e.g. Owens & Hammann 1990), and in the revision of the *Treatise* was refined to divide Proetida into three superfamilies, with Proetoidea including Proetidae and Phillipsiidae, Aulacopleuroidea comprising Aulacopleuridae, Brachymetopidae and Rorringtoniidae, and Bathyroidea consisting of Bathyuridae, Dimeropygidae, Celmidae, Lecanopgiidae, Glaphuridae, Holotrachelidae and Telephinidae (Fortey 1997).

Recently, however, it has again been suggested that Proetida comprises at least two independently derived groups. Adrain (2011) presented a revised trilobite classification that split aulacopleuroids off into their own order, reducing Proetida to Proetidae and Tropidocoryphidae. Aulacopleurida was also greatly expanded beyond Aulacopleuridae, Brachymetopidae, Dimeropygidae, Rorringtoniidae and Scharyiidae to include the traditional proetide groups Bathyuridae and Telephinidae, along with

Holotrachelidae and Hystricuridae, and the ptychopariid families Alokistocaridae, Crepicephalidae, Ehmaniellidae, Marjumiidae (including Coosellidae), Solenopleuridae and Tricrepicephalidae. The rationale for this split hinges upon morphological differences among the larval stages in each group, with Proetida possessing a non-adult-like globular form while Aulacopleurida have adult-like larvae featuring paired spines or tubercles (see Chatterton (1980) for the original definition of adult- and non-adult-like protaspids and Chatterton *et al.* (1990) for further discussion). There are a number of potential flaws with the classification, however, not least that it is presented as a simple list with no clear justification for sweeping taxonomic changes beyond the few lines that appear in footnotes. Furthermore, the apparent separation of 'proetoid' and 'aulacopleuroid' larval type is not as clear-cut as the classification suggests; a globular protaspis is known from both dimeropygids (Chatterton 1994) and aulacopleuroids (Yuan *et al.* 2001), while the pattern of paired tubercles considered diagnostic of aulacopleuroids by Adrain (2011) is absent in ehmaniellids (Hu 1998), coosellids (Hu 1978) and crepicephalids (Hu 1971) at least. The supposedly diagnostic paired spines on the posterior of the aulacopleuroid larva are common in trilobites, including redlichiids (Dai & Zhang 2012), olenellids (Webster 2014), olenids (Månsson & Clarkson 2012) and cheirurids (Lee & Chatterton 1997a), among others. The assertion that there is no clear sister relationship between proetoids and aulacopleuroids also ignores certain characters known to be present in both groups, such as the development of the pre-glabellar field in the meraspid stage. Given the sudden expansion of the aulacopleuroids with the inclusion of a number of disparate ptychopariid families under the vague characteristic of the possession of a 'flattened, adult-like larvae', there is the possibility that, in Adrain's (2011) classification, the group has become something of a wastebasket taxon for various Cambrian taxa of uncertain affinity, much like Ptychopariida itself had been. Even if the revised concepts of Proetida and Aulacopleurida are maintained, there is still the potential that the two clades remain sister taxa, a possibility which Adrain (2013) has since considered.

Here, we present a novel phylogenetic analysis comprising both traditional members of the Proetida along with a number of other trilobite groups to test the monophyly of proetide trilobites and ascertain the limits of the Aulacopleuroidea. While this issue has been considered in the light of phylogenetic methodology previously, this is the first time that proetide monophyly has been tested using

computational phylogenetics, and represents the first rigorous analysis to test the balance of the various criteria used to argue for and against the validity of the order.

Methods

Terminology

Trilobite terminology largely follows Whittington & Kelly (1997); however, an attempt has been made to quantify more accurately the distinctions between the standard pygidial size classifications. The current divisions between the micropygous, isopygous and macropygous classifications are unclear at best, especially when such mid-tier classifications as sub-isopygous are included. A new method is set out here that compares the size of the pygidium to the cephalon by overlaying rectangular boxes over the cephalon and pygidium, from which their areas are calculated and compared, giving the size of the pygidium relative to the cephalon as a percentage. Distinctions between micropygous, isopygous and macropygous size ranges were made at major discontinuities of pygidial sizes: micropygous pygidia occupy <23% the area of the cephalon, isopygous pygidia occupy 25–110% the area of the cephalon, and macropygous pygidia occupy greater than 150% the area of the cephalon. Furthermore, micropygous and isopygous pygidia can be further subdivided, with the degree of micropygosity varying from micropygous (10–23%) and extremely micropygous (0.5–5%) and the degree of isopygosity ranging from isopygous (90–105%), sub-isopygous (35–90%) and extremely sub-isopygous (25–32%). While these divisions hold true for the taxa included in this analysis, further work is needed to expand the method across the other trilobite groups.

Phylogenetic analysis

For the phylogenetic analysis, a matrix of 114 characters and 55 taxa was compiled. Species were coded from figures in the literature, supplemented with observations of specimens where possible. The redlichiid trilobite *Eoredlichia intermedia* (Lu 1940) (see also Hou *et al.* 2009; Dai & Zhang 2013) was specified as the out-group, as it represents a well-known member of the potentially paraphyletic group from which ptychopariids likely originated (Fortey 1990), and from which both ventral morphological characteristics and earlier ontogenetic stages are known.

In-group taxa were selected based on morphological completeness and, where possible, the existence of earlier ontogenetic stages assigned to the species. A number of higher level trilobite groups were included alongside proetide taxa in the analysis, each represented by multiple exemplars where possible, as these more accurately represent the character states and transitions of a group than a single exemplar such as a token species or composite taxon would (see Brusatte 2010), as well as allowing for the potential of para- or polyphyly. In a number of cases (such as for *Aulacopleura*), multiple species of a single genus were included. These cases arose for a variety of reasons. Including species for which protaspid and meraspid data are well known occasionally resulted in incorporating species with a poor holaspid record, and in these cases a second species represented by more complete holaspid specimens was included. Some genera also show a degree of variability among the characters for which they are coded in the analysis; multiple species are therefore coded to ascertain the polarity of these characters within the genus (resolving the ground pattern) and to test whether the genus is truly monophyletic. Both scenarios apply to *Aulacopleura*, while *Ceraurina* and *Remopleurides* have multiple species coded due to the first scenario.

A number of ptychopariid groups considered by Adrain (2011) to comprise part of his revised Aulacopleuroidea were included, specifically Alokistocaridae/Ehmaniellidae (represented by *Altioculus harrisi* (Robison 1971), *Elrathia kingii* (Meek 1870) (see also Bright 1959; Hu 1998), *Ehmaniella apolabella* Hu 1998), Crepicephalidae (*Coosella prolifica* Lochman 1936 (see also Hu 1978; Stitt & Perfetta 2000); *Crepicephalus buttsi montanaensis* Lochman *in* Lochman & Duncan 1944 (see also Lochman 1950; Hu 1971; Stitt & Perfetta 2000)), Holotrachelidae (*Holotrachelus punctillosus* (Törnquist 1884) (see also Suzuki 2001)), Marjumiidae (*Marjumiella typa* Walcott 1916 (see also Robison 1964); *Modocia kohli* Robison & Babcock 2011), Solenopleuridae (*Solenopleura canaliculata* (Angelin 1851) (see also Westergård 1954); *Parasolenopleura gregaria* (Billings 1865) (see also Fletcher 2005)) and Tricrepicephalidae (*Tricrepicephalus texanus* (Shumard 1861) (see also Lochman 1936)). Alongside these members of the Aphelaspidae (*Aphelaspis brachyphasis* Palmer 1962) (see also Lee & Chatterton 2005), Olenidae (*Olenus wahlenbergi* (Westergård 1922) (see also Clarkson & Taylor 1995a,b); *Parabolina spinulosa* (Wahlenburg 1818) (see also Clarkson & Taylor 1995b; Clarkson *et al.* 1997; Ahlberg *et al.* 2006); *Leptoplastus crassicornis* (Westergård 1944) (see also Whitworth 1970; Clarkson & Taylor 1995b)) and

Ellipsocephalidae (*Lermontovia dzevanovskii* (Lermontova 1951) (see also Suvorova 1956)) were included as ptychopariids that have not been considered to be allied to the aulacopleuroids. Representatives of the other major trilobite groups hypothesized to be derived from the ptychopariids (Fortey 2001) were included to test whether the ptychopariid taxa included in the analysis resolve either: (1) as in-group or stem proetides; (2) as part of a monophyletic Ptychopariida; or (3) as stem taxa to any of the other included trilobite orders. Asaphida was represented by *Asaphus expansus* (Wahlenburg 1818) (see also Bergström *et al.* 2003), *Isotelus parvirugosus* Chatterton & Ludvigsen 1976; *Proceratopyge rectispicatus* (Troedsson 1937) (see also Choi *et al.* 2008), *Proceratopyge promisca* Choi *et al.* 2008; *Remopleurides caelatus* Whittington 1959; and *Remopleurides eximius* Whittington 1959, representing asaphids, ceratopygids and remopleuridids, while Phacopida was represented by *Flexicalymene senaria* (Conrad 1841) (see also Chatterton *et al.* 1990), *Calyptaulax annulata* (Raymond 1905) (see also Shaw 1968), *Ceraurinel-la nahanniensis* Chatterton & Ludvigsen 1976; *Ceraurinel-la typa* Cooper 1953 (see also Demott 1987), *Parapilekia olesnaensis* (Růžicka 1935) (see also Mergl 1984), *Anacheirurus frederici* (Salter 1864) (see also Whittard 1967) and *Kawina arnoldi* Whittington 1963, comprising members of Calymenina, Phacopina and Cheirurina. Harpetida were represented by *Eskoharpes palanusus* McNamara *et al.* 2009; *Entomaspis radiatus* Ulrich in Bridge 1930 (see also Rasetti 1952), *Eoharpes benignensis* (Barrande 1872) (see also Whittington 1948) and *Harpes macrocephalus* (Goldfuss 1839) (see also Basse 1997), with *Harpides atlanticus* Billings 1865 (see also Whittington 1965) also being included.

Finally, 20 proetide trilobites were included in the analysis so as to test the monophyly of the group. Hystricurids were represented by *Hintzecurus paragenalatus* (Ross 1951) (see also Lee & Chatterton 1997b; Adrain *et al.* 2003) and *Politicurus politus* (Ross 1951) (see also Adrain *et al.* 2003), while dimeropygids and toernquistiids were represented by *Dimeropyge speyeri* (Chatterton 1994) and *Toernquistia sanchezae* (Chatterton *et al.* 1998), respectively. *Tropidocoryphe bassei* (Van Viersen *et al.* 2009), *Scharyia micropyga* (Hawle & Corda 1847) (see also Owens 1974; Šnajdr 1978) and *Rorringtonia kennedyi* (Owens 1981) represented Tropidocoryphidae, Scharyiidae and Rorringtonidae. *Bathyrurus ulu* (Ludvigsen 1979) and *Bathyurellus nitidus* (Billings 1865) (see also Whittington 1963) were included for bathyurids while *Proetus talenti* (Chatterton 1971),

Phillipsia belgica (Osmólska 1970) and *Gerastos tuberculatus macrocensis* Chatterton *et al.* 2006 (see also Gibb & Chatterton 2010) were included for proetids. Among the aulacopleurids, *Aulacopleura wulongensis* (Wang 1989) (see also Yuan *et al.* 2001), *Aulacopleura longecornuta* (Roemer 1854) (see also Alberti 1969), *Aulacopleura konincki* (Barrande 1846) (see also Prantl & Přibyl 1950; Hughes & Chapman 1995), *Cyphaspis dabrowni* (Chatterton 1971), *Maurotarion struszi* (Chatterton 1971), *Maurotarion periergum* (Haas 1969) (see also Adrain 2009), *Brachymetopus germanicus* (Hahn 1964) (see also Hahn & Hahn 1996), and *Otarion huddyi* (Adrain & Chatterton 1994) were selected for inclusion.

The 114 characters and data matrix are included in the supplementary online information. Characters 1–96 are coded for holaspids only, 97–107 are coded for protaspids only, and 108–114 are coded for meraspids only.

Of the 114 characters included in the analysis, 59 codes for features of the cephalon, 13 for the thorax, 23 for the pygidium, 16 for cuticular sculpture and 19 applies only to juvenile instars. It has long been noted that some trilobite groups, including proetides, may only be united by characteristics evident during juvenile stages (Fortey & Owens 1975; Adrain & Chatterton 1993; Fortey & Chatterton 1998). There has recently been increased discussion surrounding the treatment of ontogenetic characteristics in phylogenetic analyses; while ontogenetic data do improve the accuracy of phylogenetic analyses (Laurin & Germain 2011), it has been shown that incorrect handling of ontogenetic data can negatively impact tree resolution (Lamsdell & Selden 2013) in a manner similar to pedomorphic species (Weins *et al.* 2005). Most analyses to include ontogenetic data do so as discrete characters as part of a broader morphological matrix (Weins *et al.* 2005; Olesen 2009; Haug *et al.* 2010), and this method has been applied in some previous trilobite analyses (e.g. Fortey & Chatterton 1998), while others have been performed utilizing only larval characters (e.g. Chatterton *et al.* 1990) or performed multiple tree searches using separate larval and adult character data sets (e.g. Edgecombe 1992). These latter analyses paralleled an alternative method that seeks to assess the phylogenetic signal of different ontogenetic stages through the use of ontotrees (i.e. performing a number of analyses with the same taxa where each analysis includes data from only a single ontogenetic stage). Such a method has been utilized both phenetically (Michener 1977) and phylogenetically (Steyer 2000); however, while absolute

congruence between all the ontotrees would allow a definitive hypothesis of relationships between the included taxa, it is impossible to resolve any incongruence between the different ontotree topologies. A new method was recently proposed by Wolfe & Hegna (2014) that, in a number of ways, represents a progression beyond the ontotree concept; this method also codes individual instars as separate taxonomic units, but includes all instars in a single analysis. This method, however, is primarily intended for testing the affinities of larval stages of uncertain taxonomic affinity, a situation most likely to arise where species undergo metamorphic development. Coding ontogenetic data as separate characters is also problematic, however, as heterochronic perturbations in the timing of development and maturities can make the recognition of homologous developmental stages difficult. Recent studies on trilobites have shown that the protaspid larval phase does not encompass the same developmental stages in all trilobites (Park & Choi 2011a), casting doubt on the validity of the standard direct comparison between final stage protaspides.

To account for these issues, it has been suggested that comparisons be made only when the entire ontogenetic series is taken into account (Park & Choi 2011a), and recent work has attempted to characterize this both descriptively (Lerosey-Aubril & Feist 2006) and quantitatively (Crônier 2013) in a number of trilobite species. In many cases, however, the entire ontogenetic series will not be available for study, and although instars can be recognized as in the current study it is impossible to correlate these stages with certainty between species. Another concern, as noted by Wolfe & Hegna (2014), is that characters that describe the same structure in different ontogenetic stages result in an increased weighting of that characteristic in the phylogenetic analysis. A number of steps have been taken in this analysis to circumvent these issues: first, rather than being coded for specific instars, juvenile characters are applied to the relative stages of development (e.g. protaspid, meraspid) rather than the supposed instar; therefore, coding equivalent stages in development rather than focusing on the exact timing of these stages; second, the coding of a morphological characteristic's presence or absence at a juvenile stage was used to define the presence or absence of the characteristic in the species as a whole. In this manner, specific morphological characteristics were not weighted disproportionately in the analysis through being included as multiple characters. For the majority of characteristics used in this analysis,

such as the presence of posterior spines on the posterior of the protaspid stage, this treatment is logically consistent with the occurrence of the character during species development as these spines are universally lost after the protaspid stage.

The situation is more complicated when a trait is secondarily lost in only some species, or when seemingly homologous structures occasionally develop later in ontogeny in species lacking them during earlier stages. While neither situation occurs in any of the characters utilized for this study, they can conceivably be resolved in the future by having the first case occur as a dependent character (such as spines lost in adult instars) that is coded as inapplicable if spines are not present on the juveniles. If the primary character on which the dependent character relies is unknown, then the dependent character will also be coded as unknown. For the second scenario, the development of homologous structures at a different point in ontogeny could be coded as a second state within the existing character; in this case, when the earlier ontogenetic stages are unknown, the character will have to be coded as unknown. Alternatively, the presence or absence of the structures in the species could be coded as a single character and the timing of their development being a separate dependent character. While these protocols should serve to remove the problems of unduly weighting certain morphological traits in the analysis, further work is needed to ascertain how best to implement them across other data sets.

The analysis was performed using TNT (Goloboff *et al.* 2008; made available with the sponsorship of the Willi Hennig Society) employing random addition sequences followed by tree bisection–reconnection (TBR) branch swapping (the *mult* command in TNT) with 100,000 repetitions with all characters unordered and of equal weight. Jackknife (Farris *et al.* 1996) and Bremer support (Bremer 1994) values were calculated in TNT and the Consistency, Retention, and Rescaled Consistency indices were calculated in Mesquite 2.73 (Maddison & Maddison 2010). Nonparametric bootstrapping is often difficult with morphological data due to the limited size of the data set (Zander 2003), and so was not performed for this analysis. Jackknifing was performed using simple addition sequence and tree bisection–reconnection (TBR) branch swapping, with 100,000 repetitions and 33% character deletion. The matrix and character listing has been deposited in the online MorphoBank database (O'Leary & Kaufman 2012) under the project code p540 and can be accessed from <http://morphobank.org/permalink/?P540>.

Results

Analysis of the phylogenetic matrix as detailed in the methods section yielded twelve most parsimonious trees with a tree length of 444 steps, an ensemble Consistency Index of 0.319, ensemble Retention Index of 0.671 and Rescaled Consistency Index of 0.214, the strict consensus of which is presented here (Fig. 1). A traditional proetide clade is retrieved, comprising Hystricuridae, Dimeropygidae, Toernquistidae, Rorringtoniidae, Tropicocoryphidae, Scharyiidae, a paraphyletic Bathyridae, Proetidae (including Phillipsiidae; see Adrain 2013), Aulacopleuridae, Brachymetopidae and Otarionidae. Aulacopleurida as defined by Adrain (2011) is shown to be paraphyletic in regard to Proetida, with hystricurids resolving as sister group to all other proetides and dimeropygids and toernquistiids forming a dimeropygoid clade as sister group to the remaining proetides. These form two clades, one consisting of proetids and proetid-like aulacopleuroids while the other comprises Aulacopleuroidea *sensu stricto*. This first clade, comprising Bathyridae, Proetidae, Tropicocoryphidae, Rorringtoniidae and Scharyiidae, is herein considered to represent the superfamily Proetoidea. There is no logical reason to ascribe ordinal status to the second clade of remaining aulacopleuroids, and so they are also reduced to superfamilial status. As defined herein, the superfamily Aulacopleuroidea therefore consists of the families Aulacopleuridae, Brachymetopidae and Otarionidae (including at present the Cyphaspidae).

The sister group to Proetida comprises a large clade including various ptychopariids and representatives of two of the other traditional trilobite orders: Phacopida and Asaphida. Phacopida, comprising Phacopina, Cheirurina and Calymenina, is monophyletic, with the relationships of Cheirurina agreeing with other recent phylogenetic analyses (Congreve 2012). Asaphides, however, are revealed to be polyphyletic, forming part of a paraphyletic grade including olenids leading to Phacopida. Remopleurids and aphelaspids, forming Remopleuroidea, resolve as the sister group to Phacopida, while Asaphida *sensu stricto* (here represented by asaphids and ceratopygids – Asaphoidea) are positioned at the base of the clade, separated from the remopleuroids by the olenids. Evidence of asaphide polyphyly, and some form of relationships with olenids, has been mounting in recent years, with supposed asaphide synapomorphies being shown to have non-homologous developmental origins in asaphoids and remopleuroids (Adrain *et al.* 2009; Park & Choi

2011b). The topology herein, therefore, corroborates these findings.

The remaining ptychopariids in the analysis resolve as polyphyletic, with ellipsocephalids, sole-nopleurids and marjumiids (in part) forming a grade of taxa at the base of the tree, while ehmaniellids form the sister group to the asaphide/phacopide and proetide clades. Harpetids resolve between ehmaniellids and the other ptychopariids, with tricrepicephalids, crepicephalids, coosellids and some majumiids resolving at the base of the harpetid group. A non-monophyletic Ptychopariida is unsurprising and agrees with previous phylogenetic analyses (Edgecombe 1992). Further work, however, along with a more comprehensive taxonomic sampling, is needed to fully unravel the relationships of the various ptychopariid groups.

Discussion

The recovery of proetide monophyly through phylogenetic analysis confirms that only one major clade of trilobites survived through the Late Devonian into the Carboniferous, as has been assumed in recent studies of trilobite biodiversity over the Late Palaeozoic (Owens 2003; Lerosey-Aubril & Feist 2012; Feist & McNamara 2013). Two ontogenetic characteristics define a monophyletic Proetida: the initial compound eye formation in early protaspids occurring at the lateral margin rather than the anterior margin, and the form of the protaspid glabella – tapering, with a pre-glabellar field, a result remarkably similar to the scenario suggested by Fortey (1990). A number of adult characters also define the base of the clade, although most are subsequently lost or modified in some proetide groups; these include the possession of a quadrate or shield-shaped hypostome with angular posterior margins, the hypostome median body being divided by a deep groove that entirely transverses the median body, the presence of an enlarged thoracic spine on the sixth tergite and a tergite count of between 7 and 10. The two major proetide clades, the Aulacopleuroidea and Proetoidea, are further united by the later protaspid stages having a tubercular swelling on the occipital ring. Aulacopleuroids are united by the occurrence of a tubercle on the eye ridge in the meraspid stage, an extension of the cephalic sculpture onto the genal spines, L1 being detached from the glabella (a condition which is achieved convergently in proetids and phillipsiids), and S2 being effaced. Proetoids are defined by the compound eye being scimitar-shaped and expanding beyond the palpebral lobe, with a number of reversals; the compound eyes diverge

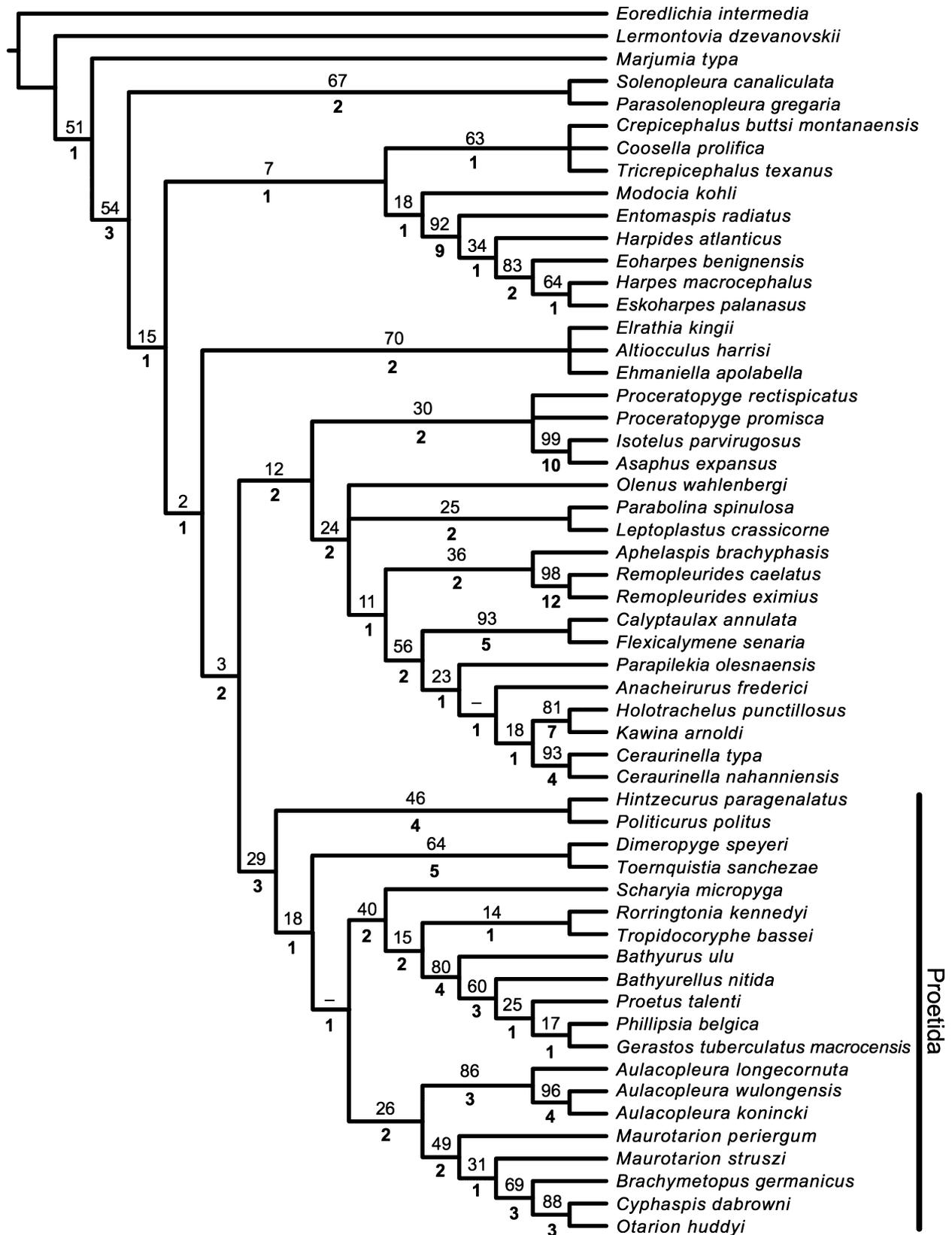


Fig. 1. Strict consensus of twelve most parsimonious trees. Numbers above the nodes are jackknife values with 33% deletion, and numbers beneath the nodes in bold are Bremer support values.

posteriorly as opposed to being equilateral and occupy at least 30% of the cephalon length, while the meraspid stages lack a row of tubercles on the fixed cheek either side of the glabella. The division of taxa between the proetoids and aulacopleuroids is different to previous classifications, with bathyurids, rorringtoniids and scharyiids being aligned with tropidocoryphids and proetids under Proetoidea. The relationship of rorringtoniids and scharyiids with aulacopleurids and brachymetopids has always been in flux; rorringtoniids were considered sister group to aulacopleurids by Adrain & Chatterton (1993), with scharyiids and brachymetopids positioned at the base of the clade, while Owens & Hammann (1990) included scharyiids within brachymetopids, and placed rorringtoniids at the base of the group. Both scharyiids and rorringtoniids, however, possess the proetoid scimitar-shaped eyes and as well as broad, blade-like genal spines, which they share with both proetids and tropidocoryphids. Scharyiids and tropidocoryphids also share the expression of a sudden constriction of the anterior third of the glabella. The enigmatic genus *Holotrachelus*, meanwhile, resolves within the cheirurids, an assignment suggested previously by Suzuki (2001).

The rearrangement of the proetide familial groups serves to alter the patterns of proetide evolution throughout the Palaeozoic, with a number of proetoid groups going extinct prior to the Carboniferous. The current topology suggests a Cambrian origin for each of the major proetide clades; however, it is possible that both aulacopleuroids and proetoids originated from a paraphyletic Hystricuridae (as originally posited by Fortey & Owens (1975)), or some currently unsampled ptychopariid groups, in the Ordovician. Either way, it is clear that both aulacopleuroids and proetoids independently survived the end-Devonian mass extinction and persisted into the Carboniferous and Permian. This begs the question as to whether there was some inherent property of the group that permitted two of its clades to weather this biotic crisis that resulted in the extinction of all other trilobite groups; however, further studies are needed to ascertain whether such a consideration bears any merit or if proetides were simply fortuitous benefactors of contingency (*sensu* Gould 1989). The phylogenetic framework presented here, with its support of proetide monophyly, is a crucial first step towards resolving this issue.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Comprising the morphological character list and character matrix used in the phylogenetic analysis.