

THE PHYLOGENY AND SYSTEMATICS OF BLIND CAMBRIAN PTYCHOPARIOID TRILOBITES

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ABSTRACT. The paraphyletic trilobite suborder Ptychopariina includes a large proportion of Cambrian trilobite diversity and is probably ancestral to most groups of post-Cambrian trilobites. Resolution of the phylogenetic relationships within the group is therefore crucial to a better understanding of the initial radiation of trilobites. The recognition of approaches that can successfully resolve the relationships of ptychoparioid taxa is an important first step towards this aim. Cladistic analysis was used to determine relationships within the Cambrian ptychoparioid trilobite family Conocoryphidae, and to test claims that the family is polyphyletic. Ninety-seven characters were coded for 40 conocoryphid species and nine non-conocoryphids. The results indicate that the family consists of four distantly related clades. Three are recognized here as distinct families, including an extensively revised Conocoryphidae, and the families Holocephalidae and Atopidae. The fourth clade is referred to the subfamily Acontheinae (Corynexochida) as the new Tribe Hartshillini. Analysis of the disparity of these four clades shows that they are significantly less morphologically variable than the original polyphyletic taxon, demonstrating the possible effects of taxonomic error on macroevolutionary studies of morphological disparity.

KEY WORDS: trilobites, Conocoryphidae, Ptychopariina, blindness, Cambrian, phylogeny, systematics.

THE ptychoparioid trilobites (suborder Ptychopariina Swinnerton, 1915) have been described as one of the biggest taxonomic wastebaskets in palaeontology (Palmer 1958; Geyer and Malinky 1997). As currently recognized the group is explicitly paraphyletic, consisting of the primitive members of the trilobite subclass Libristoma which lack the synapomorphies of more derived groups (Fortey 1990). Whilst the scope of the group is reasonably well established, in that widely accepted and clear criteria for membership have been proposed, the relationships between constituent groups are extremely problematic. This difficulty has long been recognized (e.g. Rasetti 1951) and authors have often resorted to completely abandoning suprageneric classification within the group, and arranging genera alphabetically (Palmer 1954; Palmer, *in* Palmer and Halley 1979; Rasetti 1963).

The most recent classification recognized 31 families within the Ptychopariina (Fortey 1997), but many, if not most, of these families are unlikely to be monophyletic (Fortey 1990). Diagnoses of higher taxa within the group are typically vague and extensively refer to structures as 'usually' or 'sometimes' being present, and to 'trends' and 'tendencies' towards certain states (e.g. Harrington *et al.* 1959). Most of the families and superfamilies have been extensively criticized (e.g. Ptychoparioidea and Solenopleuroidea: Rasetti 1954; Öpik 1967; Ahlberg and Bergström 1978) but none of the currently proposed alternative classifications has any clear phylogenetic justification. Geyer and Malinky's (1997, p. 633) recent diagnosis of the family Antagmidae, for example, explicitly 'does not include single characters that permit a direct identification of antagmids, and the concept of the family has largely to base [*sic*] on recognition of 'outgroups'. Despite the plesiomorphic nature of the character set, the group appears to represent a natural group'. However, the authors present no arguments or evidence that this is the case. Regional differences in taxonomy may also have had a profound effect on the profusion of poorly founded familial and suprafamilial taxa within the group. Many geographically highly restricted, but morphologically undistinguished, families have been erected (e.g. Zhang, 1963; Zhang and Jell 1987), and there are major geographical differences in the use of family names that have subsequently been considered synonymous (e.g. Öpik 1967, p. 184; Geyer 1998).

The phylogeny of the ptychoparioids is of particular importance because they are thought to be ancestral

to the majority of post-Cambrian trilobites (see Fortey 1990; Fortey and Owens 1997), and therefore occupy a crucial position in the phylogeny and radiation of the trilobites as a whole. Secondly, they are the most diverse Cambrian trilobite group and as such have great potential for revealing patterns of evolution during the trilobite radiation. The whole of the Ptychopariina is in need of detailed phylogenetic attention, but this is an enormous task due to the huge diversity of the taxon. One alternative approach would be to identify a small number of potentially useful characters and carefully analyse their distributions across the group, as has proved fruitful in a number of recent discussions of high-level trilobite phylogeny (e.g. Fortey and Chatterton 1988; Fortey 1990; Chatterton *et al.* 1994a). This kind of method is impractical in the case of the Ptychopariina, however, because few of the constituent taxa (families) are satisfactory and few useful characters have previously been identified. The numerous suggestions of extensive iterative evolution within the ptychoparioids (e.g. Palmer 1965; Sundberg 1994) would perhaps lead to this 'key characters' approach being poorly received, since, in the absence of a formal cladistic hypothesis, the selected characters could be interpreted as prone to convergence. Another possible approach, taken here, is to undertake a detailed analysis of a subset of the group with the aim of identifying characters and methods which can be used in a comprehensive analysis of ptychoparioid phylogeny. The application of cladistic methods to trilobites as a whole is still relatively rare (Adrain and Westrop 1999) and, in particular, there have been few such studies of Cambrian trilobites (Hughes and Rushton, 1990; Babcock 1994a; Westrop *et al.* 1996; Sundberg and McCollum 1997; Lieberman 1998, 1999). This study represents only the second application of formal cladistic methods to ptychopariid trilobites (following Sundberg, 1999).

One of the very few families within the group that is presently diagnosed by a plausible monophyletic synapomorphy is the Conocoryphidae (e.g. Foote 1991, p. 476), which are united by loss of the eyes. However, many other instances of eye loss within the trilobites have been shown to be the result of convergence (e.g. Jell 1975; Fortey and Owens 1990; Clarkson 1997), and many authors have suggested that the Conocoryphidae may be polyphyletic, without proposing formal subdivisions. If the Conocoryphidae were to constitute a polyphyletic assemblage of blind ptychoparioids then detailed phylogenetic revision of the group should provide a useful illustration of characters and approaches capable of resolving other aspects of the ptychoparioid problem.

PREVIOUS STUDIES OF THE CONOCORYPHIDAE

Taxonomic history

The taxonomic history of the conocoryphids dates back to the earliest years of scientific trilobite study. The type species of the nominal genus of the family was assigned to *Trilobites sulzeri* by Schlotheim in 1823, but material attributed to this species was described over fifty years before this (see Šnajdr 1958). The family Conocoryphidae was erected in the middle of the nineteenth century (Angelin 1854), and a superfamily, then called Conocoryphidea, early in the twentieth century (Swinerton 1915). Both of these taxa have been used to include all the current Ptychopariida or Ptychoparioidea (e.g. Swinerton 1915; Richter and Richter 1941; Henningsmoen 1951), regardless of the presence or absence of eyes. More usually, they have been confined specifically to blind generalized ptychoparioids (after Stubblefield and Bulman 1927; Resser 1936) following the widely used classification of Harrington *et al.* (1959). Many authors have subsequently suggested that the family is polyphyletic. Lake (1940, p. 247), for example, commenting on the previous classification of Resser (1936), expressed some doubt that the genera *Dasometopus* and *Hartshillia* should be included within the family, and Westergård (1950) regarded only the genera *Conocoryphe*, *Bailiella*, *Bailiaspis* and *Ctenocephalus* as true conocoryphids.

The classification of Hupé (1953, 1954, 1955) represents the most extensive subdivision of the family to date. Hupé proposed the subfamily Hartshilliinae for the genera *Hartshillia* and *Hartshillina*, which he assigned to the Protolenidae (1952, 1953, 1954), and the new family Atopsidae (1954, 1955) for *Atops* and *Pseudatops*. He divided the remaining genera into four subfamilies of a reduced Conocoryphidae, which he still considered to be polyphyletic (1954, 1955). Most subsequent authors also regarded the group as polyphyletic, but without suggesting alternative relationships (Hutchinson 1962; Rasetti 1967; Fortey 1990). Jenkins and Hasenohr (1989) suggested that the position of the facial suture on the brim is a key character defining 'true' conocoryphids, which on this basis would include *Atops*, *Conocoryphe* and

Hartshillia (amongst others), but exclude *Bailiella* and *Bailiaspis*, implying a very different taxonomy to most other authors. Jell *et al.* (1992) distinguished between Lower Cambrian forms with a wide rounded glabella reaching the border furrow and Middle Cambrian forms with a 'ptychoparioid' glabella and pleural tips.

In contrast, very few authors have explicitly argued for the monophyly of the Conocoryphidae. In the most complete review of the family, Korobov (1973) did not discuss the polyphyly issue, but his discussion of evolution within the group (*op. cit.*, chapter 7) implies that he accepted the Conocoryphidae as monophyletic. A number of other authors have assigned taxa to the family without comment (e.g. Babcock 1994a).

The family Shumardiidae has previously been aligned (with doubt) with the Conocoryphidae to form the blind superfamily Conocoryphacea (Poulsen, *in* Harrington *et al.* 1959), but this Ordovician group shows no particular similarities to the conocoryphids and is not considered further here. The genus *Hospes* Stubblefield, *in* Stubblefield and Bulman 1927 has been included in the Conocoryphidae by some authors (Poulsen *op. cit.*), but has more recently been consistently assigned to the Shumardiidae (following Sdzuy 1955), and a large number of features support this assignment (Peng 1984, 1990; Zhou 1981).

Conocoryphid distribution

The Conocoryphidae ranges from the late Early Cambrian through much of the Middle Cambrian (Korobov 1973). The family has a worldwide distribution in the Cambrian, and has been recorded from all of the major Cambrian continents. This wide geographic range is consistent with suggestions that the family was adapted to outer- or off-shelf environments (Lochman-Balk and Wilson 1958; Fortey 1990; Babcock 1994b; St. John and Babcock 1997). Blind trilobites were often associated with deeper-water conditions (Fortey and Owens, 1990, 1997). The absence of eyes in conocoryphids, along with some morphological features, such as a thin cuticle (Jenkins and Hasenohr 1989; Fortey and Wilmot 1991), of olenimorph (Fortey and Owens *op. cit.*) trilobites, which were also adapted to deep-water environments, supports the evidence from biofacies analysis. Cambrian polymeroid trilobites in general show strong facies dependence and geographic endemism (e.g. see Whittington, 1997b; Zhang, 1998; Palmer, 1998). If the family is shown to have an unusually wide geographic distribution, probably due to the potential for dispersal beneath a thermocline (Cook and Taylor 1975; Taylor, 1977; Babcock 1994b; St. John and Babcock 1997), then it may be useful in biostratigraphic studies.

PHYLOGENETIC ANALYSIS

Taxonomic scope

A phylogenetic analysis of 49 taxa was undertaken to determine relationships between taxa assigned to the Conocoryphidae, to test suggestions that the family is polyphyletic, and to assess possible relationships with non-conocoryphid taxa. Forty of the 49 taxa considered are currently assigned to the Conocoryphidae. These were selected to represent the morphological diversity present within the family, and include all of the validly described genera and subgenera. Where possible the type species of each genus was included, but where better material and/or descriptions of similar species were available, these were coded instead. Species that are morphologically distinct from the type species were also coded and, in most polytypic genera, more than one species was used so that potential generic synapomorphies could be determined from the analysis.

Abundant missing data in cladistic matrices can lead to poorly resolved trees and to large numbers of equally most parsimonious trees (MPTs). It has therefore become common practice to exclude poorly known fossil taxa, with abundant missing data, from cladistic analyses (e.g. Sundberg and McCollum 1997; Lieberman 1998). However, such poorly known taxa may preserve unique character state combinations, and their *a priori* exclusion can result in incorrect hypotheses about the relationships of better known taxa (Wilkinson 1995a, b; Wilkinson and Benton 1996). Quality of preservation or description was therefore not used as a major criterion for omitting terminals in this study, unless superior data were available for very similar taxa.

Nine non-conocoryphid taxa were included in the analysis, selected according to previous hypotheses of relationships between conocoryphid taxa and non-conocoryphids. *Agraulos ceticephalus* (Barrande, 1846) was coded following the suggestion of a relationship (Sdzuy 1961, 1966) between the Agraulidae and the conocoryphid genus *Holocephalina* Salter, 1864. The conocoryphid genera *Conocoryphe* and *Bailiella* closely resemble the 'generalized' ptychoparioids of the families Ptychopariidae, Solenopleuridae and Marjumiidae (Westergård 1950; Ahlberg and Bergström 1978; Fortey 1990; Geyer 1998) which were represented by *Elrathia kingii* (Meek, 1870) and *Ptychoparia striata* (Emmrich, 1839). The recognition of a fused rostral-hypostomal plate in the conocoryphid *Hartshillia* (Hutchinson 1962; Lewis 1988), along with the anteriorly expanding glabella, makes a relationship with the Corynexochida possible. This was investigated by including *Olenoides serratus* (Rominger), and two blind corynexochids: *Clavigellus annulus* Geyer, 1994, and an undescribed new species of *Acontheus* from the Middle Cambrian of south-west Wales (described in an unpublished thesis by Lewis 1988, and to be formally described elsewhere). Relationships between the ellipsocephaloid ptychopariids and two conocoryphid groups: the Lower Cambrian conocoryphid *Atops* (Hupé 1955; Ahlberg and Bergström 1978), and the genera *Hartshillia* and *Hartshillina* (Hupé 1953, 1954; Sdzuy 1961), have been proposed. A generalized member of the Protolenidae (following Geyer 1990) was coded to assess these suggestions. This was coded with morphometric characters corresponding to the most frequent state within the family; other characters that vary within the family were coded as polymorphic. The advantages and disadvantages of representing higher taxa as terminals by using polymorphic coding compared to other methods of representing higher taxa (Bininda-Emonds *et al.* 1998) has not been assessed, and this is beyond the scope of this paper. In this case, however, few of the characters were variable within the Protolenidae, and this method of coding is therefore unlikely to have caused any major bias.

Two additional taxa were used as outgroups to determine character polarity: *Eoredlichia intermedia* (Lu) and *Olenellus* (*Olenellus*) *thompsoni* (Hall). These taxa are both widely accepted as outgroups to all the other taxa considered here. The Olenelloidea are considered to be the sister group to all other trilobites, and the Redlichiida a paraphyletic assemblage ancestral to all trilobites other than the Olenellina (Lieberman 1998; Fortey 1997). These outgroups were rooted at an internal node with a basal polytomy. Brief taxonomic details and some important references for the taxa included in this study are given in Table 1. Taxa are referred to by their current taxonomic assignment throughout the main body of this work. Where taxonomic changes are proposed, these are discussed in the Systematic Palaeontology section.

Characters and coding

Ninety-seven exoskeletal characters were coded. Descriptions of all the characters and character states are given in the Appendix, and coding for each taxon is shown in the data matrix in Table 2. Some characters are discussed in more detail below. All characters that were polymorphic within a taxon were treated identically to multistate coding representing uncertainty. This has no effect except on terminal branch lengths.

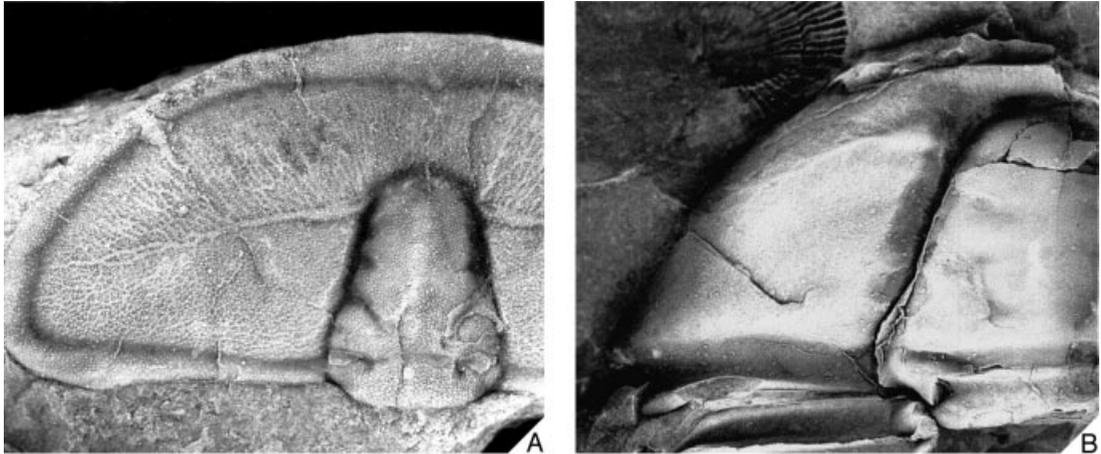
The coding of inapplicable characters in phylogenetic analysis is a difficult problem (Maddison and Maddison 1997; Wagoner 1996). Two methods have been used. Firstly, inapplicable character states can be coded as missing data. A complex structure may comprise characters: 'absent/present' and 'state1/state2', with taxa lacking the structure coded as absent for the first character and as missing for the second. Some authors have regarded this method as problematic because it may lead to reconstruction of impossible ancestral states, and hence unjustified trees (Platnick *et al.* 1991). The alternative is to code the second character as a third 'not applicable' state in taxa that lack the structure. This can also be problematic, however, as it reduces character independence and effectively weights the inapplicable character. Wagoner (1996) accepted that using a separate inapplicable character state introduces unjustified weighting of the absence of complex characters, but he also suggested that coding as missing data is tantamount to discarding data. These views are inconsistent: coding a taxon as absent for one character codes all of the information about the complex character that is available, coding other states as inapplicable clearly codes this state again, and does not include any distinct information. In this study, inapplicable characters are treated as missing data for most analyses because, due to the large number of

TABLE 1. Authorship and important references for taxa included in the cladistic analyses.

Atopina antiqua Korobov, 1966; Korobov 1973.
Atops rupertensis Jell *et al.*, 1992.
A. trilineatus (Emmons, 1844); Walcott 1886; Lake 1940; Howell and Stubblefield 1950.
Bailliaspis bobrovi Korobov, 1973.
B. dalmani (Angelin, 1854); Westergård 1950.
B. glabrata (Angelin, 1854); Westergård 1950; Sdzuy 1966.
B. venusta Resser, 1937; Hutchinson 1962.
Bailliella aequalis (Linnarsson, 1883); Westergård 1950.
B. baileyi (Hartt, *in* Dawson, 1868); Matthew 1885.
B. emarginata (Linnarsson, 1883); Westergård 1950.
B. lantenoisi (Mansuy, 1916); Zhang and Jell 1987; Jell and Hughes 1997.
B. levyi (Munier-Chalmas and Bergeron, *in* Bergeron, 1889); Thoral 1946; Courtessole 1973.
Conocoryphe caecigena Dean, 1982.
C. sulzeri (Schlothheim, 1823); Šnajdr 1958; Šnajdr 1982.
Comucoryphe schirmi Sdzuy and Liñan, 1996.
Couloumania heberti (Munier-Chalmas and Bergeron, *in* Bergeron, 1889); Sdzuy 1961; Courtessole 1973.
Ctenocephalus (*C.*) *bergeroni* Thoral, 1946; Courtessole 1973.
C. (C.) coronatus (Barrande, 1846); Šnajdr 1958.
C. (Hartella) antiquus Thoral, 1946; Courtessole 1973.
C. (H.) exsulans (Linnarsson, 1883); Westergård 1950.
C. (H.) matthewi (Hartt, *in* Dawson, 1868); Matthew 1885.
C. (H.) terranovicus Resser, 1937; Hutchinson 1962.
Dasometopus breviceps (Angelin, 1854); Linnarsson 1883; Westergård 1950; Korobov 1973.
D. granulatus Korobov, 1973.
D. maensis Korobov, 1973.
Elyx laticeps (Angelin, 1851); Westergård 1950.
E. matthewi Hutchinson, 1962.
Hartshillia clivosa Lazarenko, 1965; St. John and Babcock 1997.
H. inflata (Hicks, 1872); Lake 1938; Lewis 1988 [unpublished].
Hartshillina spinata (Illing, 1916); Lake 1938; Lewis 1988 [unpublished].
Holocephalina leve Gozalo and Liñan, 1996.
H. primordialis Salter, 1864; Lake 1938; Hutchinson 1962; Lewis 1988 [unpublished].
Holocephalites incertus (Illing, 1916); Lake 1938; Zhou, *in* Zhou *et al.* 1982.
Meneviella venulosa (Hicks, 1872); Lake 1938, 1940; Hutchinson 1962.
M. viatrix Shergold, 1973.
Parabailiella languedocensis Thoral, 1946; Courtessole 1973.
Pseudatops reticulatus (Walcott, 1890); Lake 1940; Howell and Stubblefield 1950.
Sdzuyella stremina Hajrullina, *in* Repina *et al.*, 1975.
Tchaispis szdzyi Korobov, 1966; Korobov 1973.
Tchaispis sp. nov. St. John and Babcock 1997.
Acontheus sp. nov. Lewis 1988 [unpublished].
Agraulos ceticcephalus (Barrande, 1846); Šnajdr 1958.
Clavigellus annulus Geyer, 1994.
Elrathia kingii (Meek, 1870); Palmer 1954.
Eoredlichia intermedia (Lu); Zhang *et al.* 1980; Shu *et al.* 1995.
Olenellus thompsoni (Hall); Whittington 1989; Lieberman 1998.
Olenoides serratus (Rominger); Whittington 1980; Sundberg 1994.
 Protolenidae Richter and Richter, 1948; Geyer 1990.
Ptychoparia striata (Emmrich, 1839); Šnajdr 1958.

such characters in the matrix, coding them as a distinct character state (and therefore heavily weighting them) could result in them dominating the analysis. However, the effects of this assumption were investigated by using a distinct character state in some analyses (see Results below), and they are shown as distinct to 'true' missing data (using the symbol 'N') in the matrix (Table 2). Unless otherwise stated, a coding of 'N' was treated as missing data, and identical to a coding of '?'. These methods are equivalent to Pleijel's (1995) coding methods C and B, respectively.

Considerable debate has also surrounded the use of quantitative characters in phylogenetic analysis (e.g. Chappill 1989; Rae 1998). The general case for the use of such characters is well established (Thiele 1993; Rae 1998), but a number of methods for coding them have been proposed, and there is no consensus as to which is most appropriate (see Thiele 1993, for a review). For this study, quantitative characters were coded informally. Large discontinuities in the distribution of a state between species were identified and used to form distinct character states. The number of character states for quantitative characters is therefore determined by the degree of discontinuity between



TEXT-FIG. 1. A, *Meneviella venulosa* (Hicks, 1872), BMNH It.13575; Middle Cambrian, *Paradoxides davidis* Zone, Manuel's Brook Formation, Manuel's Brook, Newfoundland; dorsal view of left side of cephalon; $\times 6.5$. B, *Bailiella baileyi* (Hartt, in Dawson, 1868), BMNH It.3951; Middle Cambrian, Fossil Brook Formation, Fossil Brook, St. Martins, New Brunswick; dorsal view of left side of cephalon; $\times 3.2$.

species. This approach is intended to be similar to that used in coding discrete characters. Less conservative coding of quantitative characters, using a formal gap coding method (e.g. Mickevich and Johnson 1976), may have improved the resolution of the results, but would require a detailed consideration of levels of intraspecific variation.

Preservational control of character states is unlikely to have had a significant effect on the results of this study. Most of the taxa considered are known from undistorted material. The coding was conservative, resulting in a large amount of missing and multistate character coding (21.3 per cent of all observations) in the data matrix. Many of the characters that are most susceptible to taphonomically induced variation (see Hughes, 1995) were found to have lower than average character consistency indices (see Appendix), and therefore little influence on topology.

Terminology for all characters described in the Appendix and below follows Whittington (1997a), unless otherwise stated. A number of characters warrant extended discussion:

Genal caeca and eye ridges. The presence of a system of radiating, anastomosing ridges on the frontal area and anterior genae of many trilobites has long been recognized (Öpik 1959, 1961; Jell 1978), but the relationship between this system and the eye ridge and eye lobe has received relatively little attention. In sighted trilobites with a prominent caecal system (e.g. *Harpides atlanticus* Billings; Whittington 1997a, fig. 17), a single ridge (the genal ridge) continues the line of the eye ridge beyond the eye lobe. It has been suggested that the thread-like eye ridge of blind trilobites (including conocoryphids) is homologous with this genal ridge, rather than the eye ridge of sighted forms (Whittington 1997a, p. 15). However conocoryphids have two distinct ridges across the genae, one usually lying over the other (Jell and Hughes, 1997, p. 62). In *Meneviella*, the putative eye ridge bifurcates adaxially, one branch running around the front of the glabella and the other inserting under the axial furrows, and abaxially, where two ridges follow separate paths across the posterolateral genae (Text-fig. 1A). In other taxa, such as *Bailiella baileyi*, the two ridges separate just outside the axial furrow, forming a low node (Text-fig. 1B). In other species, only a single ridge is visible. In *Bailiella emarginata*, this ridge terminates in the middle of the genae, and the caecal system is not evident. This suggests that the ridge in *B. emarginata* represents the eye ridge, and that the longer of the two ridges in other conocoryphids, which is associated with the caecal system, is absent in this species and is the homologue of the genal ridge of trilobites with normal ocular structures. The close correspondence between the prominence of the genal ridge and caecal system, which

is lacking between the eye ridge and the caecal system, makes it likely that the genal ridge is part of the caecal system whereas the eye ridge is a separate structure. These two structures usually lie on top of one another and it is not always possible to distinguish between them. It may therefore prove useful to refer to them collectively as the genal ridges (as in the Appendix). The function of the various caecal structures has been the subject of some debate (e.g. Öpik 1961; Bergström 1973; Fortey 1974; Jell 1978; Chatterton *et al.* 1994b). The interpretation of these structures argued here supports theories that two distinct organs are represented.

A number of characters of the eye ridge, genal ridge and caecal system are coded in this study. The presence of the (ventral with respect to the dorsal cuticle) caecal system on the external surface probably reflects a thinning of the cuticle. Its absence from internal moulds may indicate either a reduction of the caecal system itself or a change in the relationship between the caecal system and the cuticle. The insertion of the eye ridges into the glabella is variable (Korobov 1973). In some taxa raised ridges cross the axial furrows, and initially run anterolaterally (e.g. *Pseudatops reticulatus*, Pl. 2, figs 1–3). In other taxa the ridges do not interrupt the axial furrows and run directly laterally or posterolaterally (e.g. *Conocoryphe sulzeri*, Pl. 3, figs 9–10). The interruption of the axial furrows by the eye ridges may be of importance in separating the advanced ellipsocephaloids and ptychoparioids from more primitive ellipsocephaloids such as the Antatlasidae and Protolenidae (Ahlberg and Bergström 1978). Finally, the caecal system is usually much weaker posterior to the eye ridge (e.g. *Papyriaspis lanceola* Whitehouse; Jell 1978, fig. 1A), but there are exceptions (e.g. *Meneviella venulosa*, Pl. 3, figs 1–2, 4).

Preglabellar boss. Conocoryphids show a number of unusual specializations of the anterior genae and prelabellar field. An inflated boss occurs on the prelabellar field of *Ctenocephalus* and *Elyx* within the Conocoryphidae, and is widely distributed within ptychopariids (Fortey and Hughes 1998). Fortey and Hughes (1998) suggested that the boss represents the brood pouch of a female dimorph. However, they failed to identify possible male dimorphs for the majority of *Ctenocephalus* species. Secondly, the geographical distribution of the dimorphic pair they postulated, *Ctenocephalus* (*Hartella*) *exsulans* and *Bailiaspis dalmani*, may be different; *Bailiaspis dalmani* occurs with a *Ctenocephalus* (*Ctenocephalus*) species in Britain in the absence of any species referable to *Hartella*. Furthermore, the stratigraphical ranges of the genera *Ctenocephalus* and *Bailiaspis*, as currently understood, are not closely congruent (Korobov 1973, figs 2–10). Finally, the boss in some species of *Elyx* (e.g. *Elyx palmeri* Korobov, 1973, pl. 6, figs 1–1A) takes the form of a narrow, raised ridge which is unlikely to have functioned as a brood pouch. The hypothesis of Fortey and Hughes (*op. cit.*) warrants further attention, but the evidence for a brood pouch in the conocoryphids is, at best, equivocal. The presence of the prelabellar boss was not treated as sexually dimorphic in this analysis.

Preglabellar furrows. Diverging prelabellar furrows, which can be considered as a distinct, novel structure or as anterior extensions of the axial glabellar furrows, are present in a range of conocoryphid species, including the type species of the nominal genus *Conocoryphe sulzeri* (Pl. 3, figs 9–10). In these taxa, the prelabellar furrows run from the anterolateral margins of the glabella to the continuous anterior border furrow. Furrows are also present in a similar position in some *Bailiaspis* species (e.g. *Bailiaspis menneri* Korobov, 1973, pl. 9, fig. 4) and *Tchaispis szuyi* Korobov, 1966 (Pl. 4, fig. 9). These are not considered to be homologous to the arrangement in *Conocoryphe* or *Ctenocephalus*, but instead to represent an extreme development of the inward curving of the border furrow present in other *Bailiaspis* species. This is shown by the absence of a border furrow between the anteriormost points of the furrows, and the smooth connection of these furrows with the lateral border furrow. The arrangement of prelabellar furrows in *Elyx* (e.g. *Elyx trapezoidalis* Babcock, 1994a, fig. 8; *Elyx laticeps*, Pl. 4, fig. 6) is considered to be homologous with that in *Ctenocephalus*. A very faint border furrow divides the boss from the border, at least in some species, and the junction between the prelabellar furrows and the lateral border furrow is angular.

Anterior genal ridges. Posterolaterally directed ridges are present on the anterior genae of members of the

subgenus *Ctenocephalus* (*Ctenocephalus*) (Pl. 4, figs 5, 8). These have been treated as homologous to the eye ridge (e.g. Hutchinson 1962), but most authors (Lake 1940; Courtessole 1973) have recognized them as distinct structures, since they usually consist of a ridge and a furrow, and do not meet the anterolateral corners of the glabella. The form of these structures, and their often extreme elevation above the ventral margin of the cephalon, also indicates that they are distinct from the paradoublural line present in some species of *Dasometopus* (e.g. *Dasometopus maensis* Korobov, 1973, pl. 5, figs 1–4).

Hypostomes. The ventral morphology is known in very few conocoryphid taxa. Hypostome condition is coded following the terminology of Fortey and Chatterton (1988) and Fortey (1990). The form of the hypostome is not coded in detail, but a number of taxa share the conservative natant morphology ('generalised ptychoparioid form' in Appendix, character 71) identified by Fortey (1990, p. 551, text-fig. 11).

Prosopon. It has been a widespread assumption in trilobite systematics that the pattern of sculpture or prosopon (following Gill 1949) is of 'low taxonomic value' and can be used, at best, to distinguish species, but not higher taxa. Prosopon is coded here alongside other characters, since its taxonomic value, at least in the group in question, has not been tested phylogenetically, and ignoring prosopon would amount to *a priori* weighting of characters.

Methods

Two distinct sets of analyses were performed. The initial analyses included only taxa that have been assigned to the Conocoryphidae. The matrix used in these analyses excluded the last 9 taxa, and characters 89–97, shown in Table 2. The second set of analyses used all the taxa and characters shown in Table 2. Analyses were carried out using PAUP* version 4.0b2a (Swofford 1999). Unless otherwise stated, all analyses used heuristic searches with 50 random addition sequence replicates. The software package MacClade version 3.07 (Maddison and Maddison 1997) was used for comparing tree topologies and investigating patterns of character evolution. Tree statistics were calculated by PAUP* and checked with MacClade.

Quantitative characters, and those dimensions that were coded as discrete characters (i.e. those that could have been coded as quantitative characters), were treated as ordered in the main analyses. The effects of this decision were investigated by re-analysing the data using different sets of character ordering assumptions. These sets were: (1) all characters unordered; (2) quantitative characters (as above) and those coding the degree of effacement of various structures treated as ordered; and (3) as above with characters coding other shape changes where intermediate states are plausible (Wilkinson 1992) added to the set of ordered characters. These sets of characters are shown in the Appendix.

A number of authors (e.g. Sundberg and McCollum 1997; Sundberg, 1999) have advocated the reweighting of multistate characters so that the total weight of each character is equal, rather than the weight of each transition equal. The latter is more appropriate since multistate characters can be coded as an equivalent number of binary characters (e.g. Pleijel 1995). When coded in this way, each transition of a multistate character becomes a distinct binary character and is, hence, accorded equal weight. In most analyses all characters were treated as of equal weight, but the effects of this assumption were tested in some analyses by reweighting continuous multistate characters (those ordered in the first, or 'quantitative', character set described above and in the Appendix). In these analyses multistate characters were reweighted so that the range of states had the same total weight in each case, e.g. characters with four states were downweighted to a third of the weight of binary characters, those with five states to a quarter. The weight of binary characters was maintained as one throughout.

Support for individual nodes was assessed by bootstrap analysis (Felsenstein 1985) and by calculating Bremer support indices (Bremer 1988, 1994). These methods measure two distinct aspects of support for phylogenetic hypotheses. Trees or nodes may be considered well supported (1) to the extent to which alternative topologies are much less parsimonious, as measured by the support index (Wilkinson 1996), or (2) where they are consistent with a large proportion of characters, so that character sampling is unlikely to

have had much influence on topology, as assessed by bootstrapping (Page 1996). Bootstrapping was performed with 100 bootstrap replicates, each of ten addition sequence replicates. Support indices are also based on heuristic searches with ten addition sequence replicates.

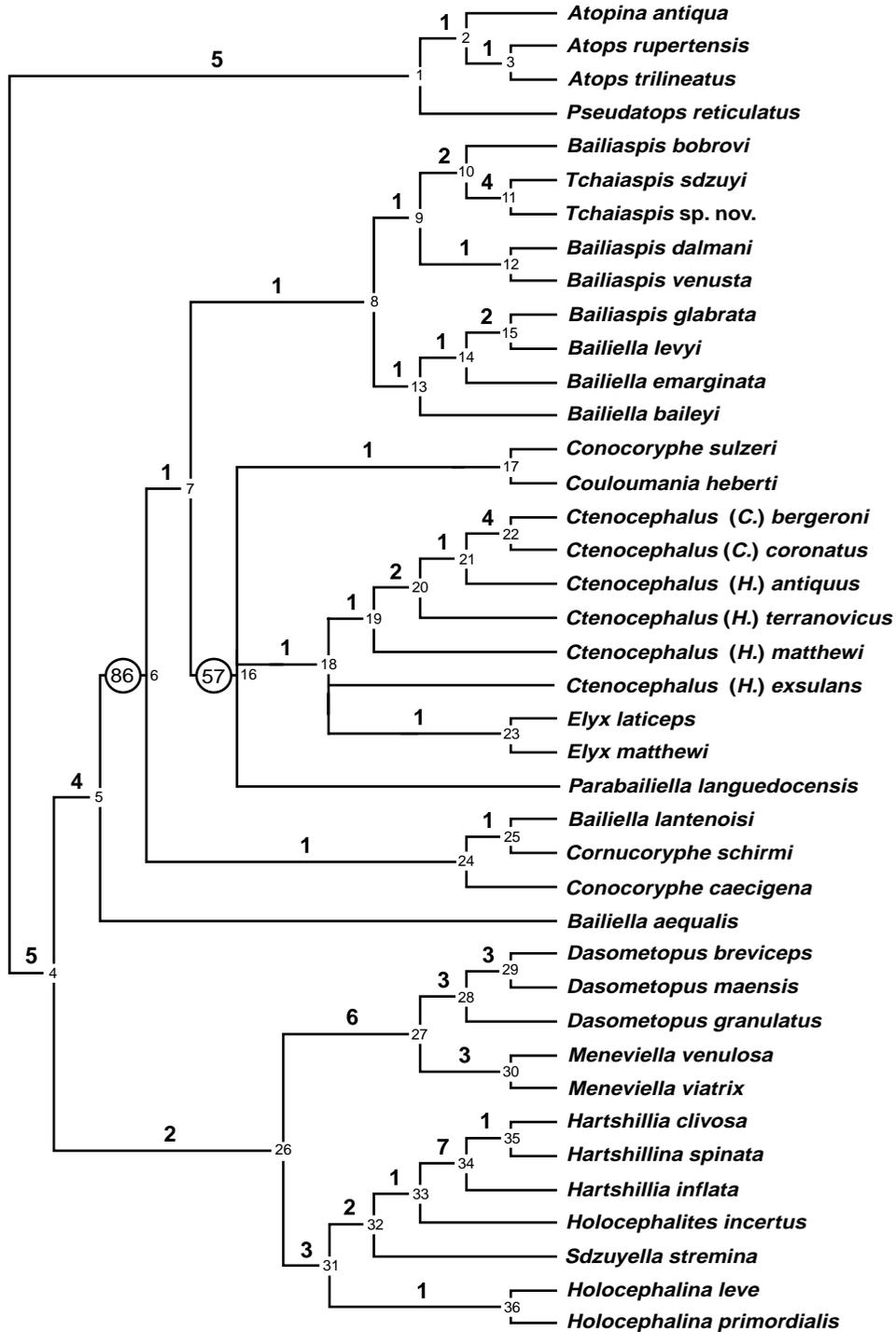
Results

Analysis of taxa assigned to the Conocoryphidae. Initial analysis of the conocoryphid-only dataset (40 taxa and 88 informative characters) recovered 14 equally most parsimonious trees (MPTs), 301 steps in length. The midpoint rooted majority-rule consensus tree is shown in Text-figure 2. This midpoint rooting is also the most stratigraphically consistent (*Atops*, *Atopina* and *Pseudatops* are Lower Cambrian, whilst other conocoryphid taxa are Middle Cambrian, Korobov 1973), and results from outgroup rooting with *Eoredlichia intermedia*. The consistency index (CI) of these trees is 0.442, and the retention index (RI) is 0.712. Three major clades within the Conocoryphidae are easily recognized on the basis of this analysis, in that they are well supported, and subtended by long branches. The first (subtended by node 1 on Text-fig. 2) consists of the genera *Atopina*, *Atops*, and *Pseudatops*, the second (node 26) of *Dasometopus*, *Hartshellia*, *Hartshellina*, *Holocephalina*, *Holocephalites*, *Meneviella*, and *Sdzuyella*, and the third (node 5) of the remaining taxa.

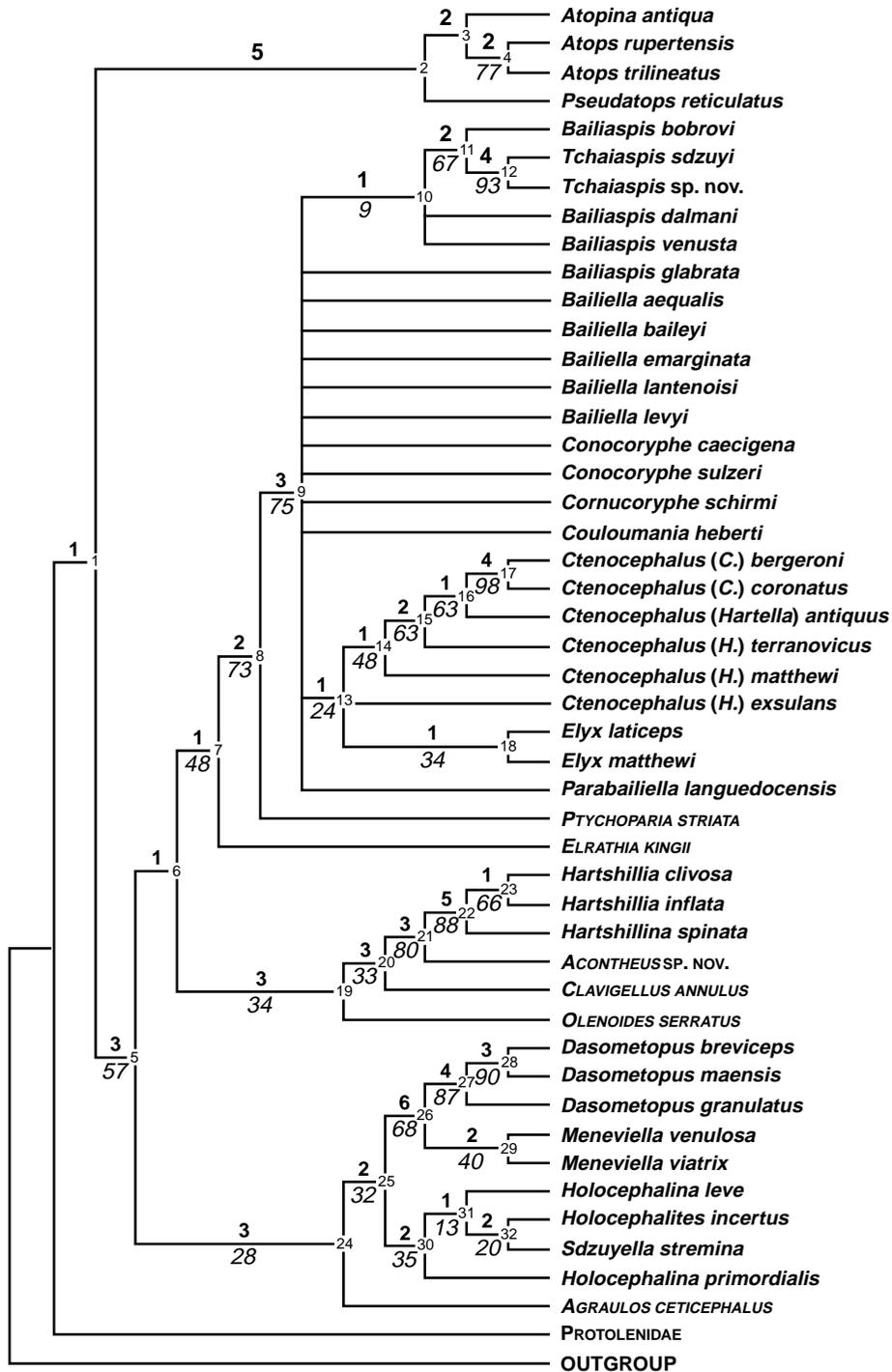
Changes in the levels of resolution and support (as measured by the support index) when various taxa are excluded from the analysis can be used to identify problematic clades or terminals of uncertain phylogenetic position. The exclusion of *Hartshellia* (two taxa) and *Hartshellina* from the analysis resulted in a set of 131 MPTs of length 266 (with uninformative characters excluded). The shortest trees not showing the second major clade (node 26, without *Hartshellia* and *Hartshellina* in this case) in this analysis were 269 steps long. This gives a support index of three for this node compared to the index of two in the analysis including all taxa. Similarly the support index for node 31 increases from three to five when *Hartshellia* and *Hartshellina* are excluded. The reduced support for these clades when all taxa are included shows that the position of *Hartshellia* and *Hartshellina* is less certain than that of the other members of this clade.

Similarly, both the lack of resolution in the strict consensus tree, and the low support indices within the third major clade (including *Conocoryphe*, *Bailiella*, *Bailiaspis* and *Ctenocephalus*, node five), may be a result of uncertainty about the correct position of a small number of terminals. This possibility was investigated by re-analysing the data without some terminals. Exclusion of *Parabailiella languedocensis* resulted in two trees of length 299, compared to the 14 equally parsimonious trees obtained when it was included. Exclusion of *Ctenocephalus* (*Hartella*) *exsulans* and *Parabailiella languedocensis* results in a single most parsimonious tree 294 steps long. The robustness of these results was also assessed by exploring the effects of different weighting and assumptions. The data were re-analysed separately treating each of the three sets of characters discussed above (see Appendix) as ordered, and all characters as unordered. These analyses gave similar (although generally less well resolved) results, indicating that the tree shown in Text-figure 2 is highly robust with respect to character ordering assumptions.

Analysis of larger sample of taxa. The second stage of analysis included all of the data shown in Table 2 (49 taxa, 97 characters). Thirty-eight equally most parsimonious trees were recovered, each 432 steps long. The strict consensus of these trees is shown in Text-figure 3. Four unrelated clades are included in the Conocoryphidae, at nodes 2, 9, 22, and 25 on Text-figure 3. These clades are more closely related to non-conocoryphid taxa than they are to each other, necessitating the division of the Conocoryphidae. They are recognized below as the families Atopidae (node 2), Holocephalidae (node 25), an emended Conocoryphidae (node 9; note that the name 'Conocoryphidae' in this paper refers to the old, polyphyletic, use of the name, except in the Systematic Palaeontology section), and the tribe Hartshellini (node 22). Character state changes on this tree were reconstructed using the accelerated transformation optimization criterion (the ACCTRAN option of PAUP*), and are listed in the Appendix. Accelerated transformation was preferred to other optimization criteria because it maximizes the interpretation of homoplasy as reversals, rather than as parallelisms, and hence minimizes rejection of the initial hypotheses of homology made during coding (Pinna 1991). The hypothesis of conocoryphid polyphyly is well supported by this analysis;



TEXT-FIG. 2. Majority rule consensus tree from analysis of conocoryphid-only matrix (see text). Numbers over branches in circles indicate the percentage of the MPTs in which the node occurs, for nodes not present in all trees. Numbers in small type over nodes are node numbers, referred to in the text. Support indices are shown in bold type above branches.



TEXT-FIG. 3. Strict consensus tree from analysis of complete matrix. Numbers in small type over nodes are node numbers, referred to in the text and Appendix. Support indices are shown in bold type above branches. Bootstrap percentages are shown in italic type below branches, for all nodes with relative frequencies greater than 5 per cent.

Separate analyses including only the 24 taxa (coded for 39 informative characters) belonging to this clade (the emended Conocoryphidae, node 9 on Text-fig. 3) confirmed the importance of rooting. Fifty-five MPTs, 120 steps long, were found. The unrooted consensus of these trees supports only the *Bailiaspis-Tchaispis* (node 9 of Text-fig. 2, node 10 of Text-fig. 3), *Bailiella emarginata-Bailiaspis glabrata* (node 14 of Text-fig. 2) and *Ctenocephalus-Elyx* (node 18 of Text-fig. 2, node 13 of Text-fig. 3) clades. The topology of this group is therefore strongly dependent upon the position of the ancestral root. Analyses including the same set of 24 taxa and one of the two related non-conocoryphids for rooting (*Ptychoparia striata* and *Elrathia kingii*), produced very different topologies, as shown in Text-fig. 4. In view of these difficulties, systematic revision of the genera included in this clade (the emended family Conocoryphidae) is limited to those taxa that were supported by all of the analyses presented here. Further knowledge of the phylogeny of the 'generalised' ptychoparioids to which the restricted Conocoryphidae clade is related is required before its phylogeny can be established.

TAXONOMIC RANK AND MORPHOLOGICAL DISPARITY

Introduction and methods

The Ptychopariida is the most diverse Cambrian trilobite taxon and, as such, biases and errors in the systematics of the group may have had a profound effect on interpretations of patterns of evolution in trilobites during the early Palaeozoic radiation. The diversity of higher taxa, such as families, has regularly been used as a proxy for other evolutionary metrics in palaeobiology (see e.g. Kemp 1999, pp. 157–158). There has been much recent discussion of the relationship between morphological diversity (hereafter referred to as disparity, see Wills *et al.* 1994) and taxonomic diversity during the Palaeozoic radiation. On the basis that disparity reached a maximum early in the Palaeozoic, it has been claimed that the rate of morphological diversification peaked earlier in the history of taxa than that of taxonomic diversification (Gould 1991; Foote 1993, 1999; Wagner 1995, 1997). Other studies have shown that disparity of arthropods may not have been significantly higher in the Cambrian than in the Recent (Briggs *et al.* 1992, 1993), a result which may still suggest a rapid early increase in disparity. A number of possible explanations for such patterns have been suggested (e.g. Valentine 1986, 1995; Wagner 1996; Foote 1999).

Despite much interest in these problems, comparatively few studies have used morphometric approaches to study disparity; rather they have relied (in particular those with a wide taxonomic scope) on the use of higher taxonomic diversity as a proxy for disparity (Foote 1996). Such an approach would be valid if these taxa had some biological reality in terms of morphology beyond that of the constituent species, or if taxa of a particular rank had (1) a similar disparity, and (2) were evenly distributed in morphospace (i.e. represent morphotypes; Foote 1991). The former view has been advocated by some authors, who argue that high rank taxa, such as phyla and classes, represent distinct bodyplans (Gould 1991; Hall 1996, provided a thorough review of such concepts). These theories remain somewhat vague, but, in any case, have generally been restricted to the highest taxonomic ranks, so it is the second justification that is likely to be relevant at the taxonomic levels employed in most studies. Many, if not most, higher taxa in most groups are unlikely to be monophyletic (e.g. trilobite higher taxa analysed by Foote 1991; see Fortey 1990, 1997). Whilst this has no direct implications for their use as proxies for disparity, provided that the conditions outlined above are met, phylogenetic revision obviously leads to changes in taxonomy that may profoundly alter patterns based on such data. Interpretation of the results of studies in which probable non-monophyletic taxa are used may also be problematic (e.g. Foote 1991; Eble 1999).

The effect of using higher taxa as proxies for disparity, and the impact of subsequent taxonomic revision, were investigated by comparing the four blind trilobite clades identified herein with the polyphyletic Conocoryphidae previously recognized. Firstly, disparity was crudely measured as the mean number of character state differences between taxa, based on the matrix used for the cladistic analyses. Secondly, the taxa were ordinated onto principal coordinate (PCO) axes based on a matrix of intertaxon euclidean distances (Wills *et al.* 1994). The matrix of intertaxon distances was derived from the cladistic character matrix (Table 2) following the method of Wills *et al.* (*op. cit.*) for avoiding problems

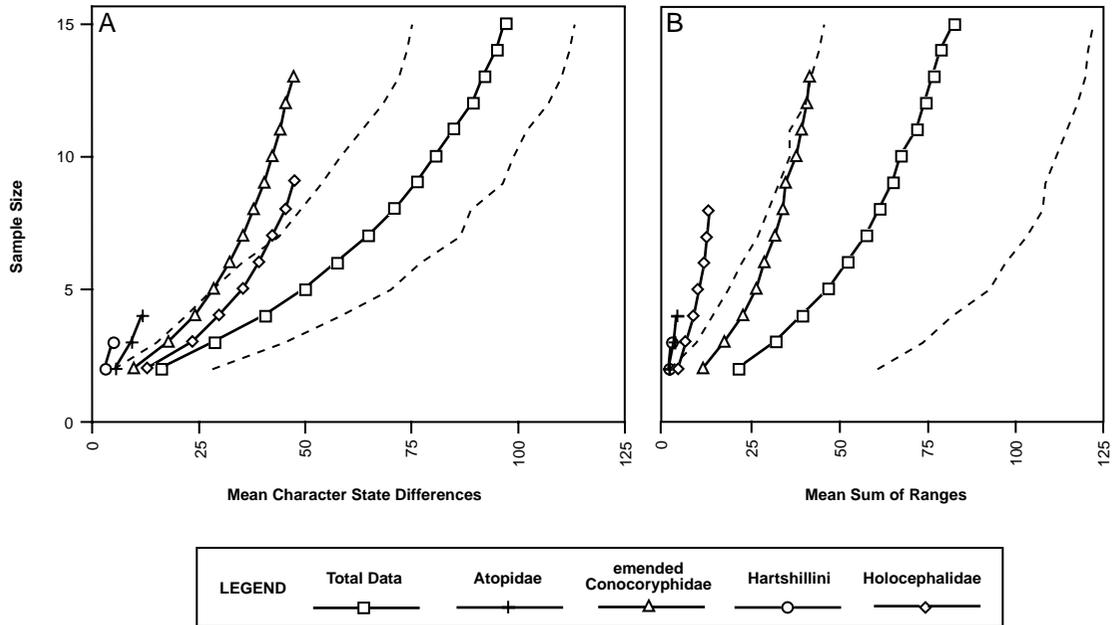
with negative eigenvalues. This allowed morphological disparity to be measured as ranges and variances for each of the samples, and the distance between the samples to be investigated. The relative merits of the many different possible disparity metrics have been discussed extensively (Foote 1999; Wills *et al.* 1994). Rarefaction analysis was used to compare the expected disparity at different sample sizes, following the method of Foote (1992), and using the computer application RARE 1.2 (Wills 1998), with 1000 bootstrap replicates at each sample size.

The use of cladistic character distribution matrices in studies of disparity has been somewhat controversial (Gould 1991; Erwin 1992; Wagner 1995). These criticisms have focussed on two points: (1) the inclusion of autapomorphic characters, and (2) assessment of the magnitude of morphological differences. Autapomorphic characters or character states need not be omitted from a cladistic matrix, and many published matrices include some autapomorphies, which do not affect the cladistic analysis. There is no logical reason why autapomorphic features cannot be coded in the same way as informative characters. However, since morphometric techniques require homologous structures to be recognized in all forms being compared (see e.g. Bookstein 1991, chapter 3, for discussion), such methods can hardly take into account truly unique features of individual taxa without abandoning homology altogether. An example of this is the coding of the cephalon of olenellids as homologous to the cranidia of other trilobites (Foote 1991), when in reality there is no homologue of the cranidium in olenellids since facial sutures had not yet evolved (Fortey and Whittington 1989; Lieberman 1998). Homologous structures or points are progressively more difficult to recognise, and novel or missing features more frequent, at higher taxonomic levels. In such broad studies, landmark or outline methods have little chance of coding representative character variation. Assessment of morphological differences between specimens using morphometric techniques can include more information about the magnitude of difference than cladistic coding of the same feature. Most morphometric studies, however, are necessarily limited to considering a single, easily recognized homologous feature (e.g. outline of the trilobite cranidium; Foote 1989, 1991), whereas cladistic matrices can include a wider range of the morphology of the organism. Cladistic techniques using step-matrices (implemented in PAUP* 4.0b2a; Swofford 1999) allow cladistic analysis of quantitative characters without extensive loss of information about the magnitude of character state differences. Matrices developed for cladistic analyses are therefore eminently suited to the analysis of disparity, and may represent a more comprehensive basis for abstracting morphological information than those used in conventional morphometric techniques, particularly when distantly related organisms are compared.

Results

The results of the rarefaction analysis (Text-fig. 5, Tables 3–4) indicate that the polyphyletic Conocoryphidae comprises considerably more disparity at the family level than the four clades identified herein. This does not depend upon the higher diversity of the total sample (40 taxa) than the sub-samples (3, 4, 9 and 24 taxa). In other words, the new taxa are far more cohesive morphologically than the polyphyletic Conocoryphidae. All four samples fall well below the 95 per cent confidence interval for disparity of the combined data, even at low sample sizes, as measured by either the mean number of differing character states (Table 3) or by the sum of ranges on the PCO axes (Table 4). Similarly, morphological disparity appears to vary between the newly recognized clades. This result is, however, somewhat equivocal since it is sensitive to the method of assessing disparity. The Holocephalidae has the highest disparity of the four, in terms of character state differences, but a lower disparity than the emended Conocoryphidae when range on the PCO axes is used. The significance of differences in disparity between the four taxa is difficult to assess because of the very low sample sizes of two of these taxa. The taxa considered clearly do not have a similar disparity. The first of the conditions outlined above for the use of taxa as proxies for disparity is therefore not met for suprageneric taxa of blind Cambrian trilobites, and is highly sensitive to phylogenetic revision of their taxonomy.

The distribution of the species in the first three dimensions of the PCO morphospace is shown in Text-figure 6. These dimensions represent 64 per cent of the variance in the data. The four emended taxa clearly occupy different regions of morphospace, and do not appear to be evenly distributed within it. For example, the hartshillinid samples are closer to all of the atopids than they are to any of the conocoryphids.



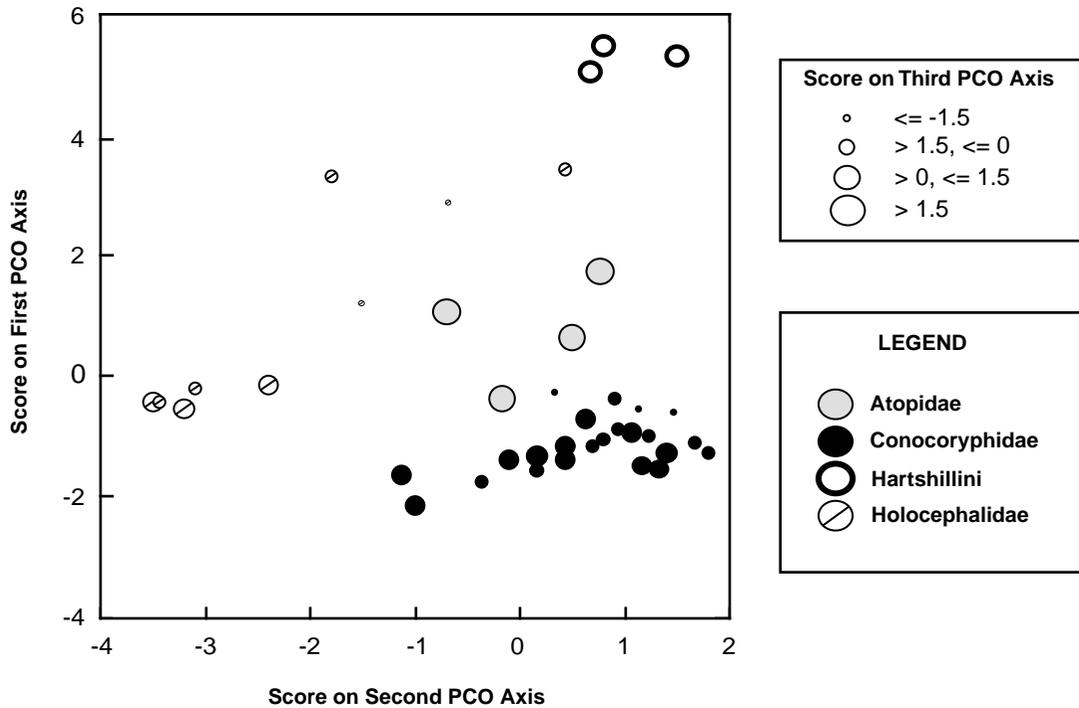
TEXT-FIG. 5. Results of rarefaction analysis of morphological disparity for all conocoryphids and the four monophyletic subgroups. Disparity is measured as the mean number of character state differences (A) and the mean sum of ranges on 40 PCO axes (B). Dotted lines show the 95 per cent confidence intervals for the disparity of the total data.

The distribution of the samples in morphospace was quantified by calculating the mean pairwise distance between members of the four taxa. As shown in Table 5, there are large differences in the distances between the taxa. Thus the second condition required to allow taxonomic diversity to make a good proxy for disparity, that taxa are evenly distributed in morphospace, is also not met by these taxa.

If trilobite taxa in general are not a good proxy for disparity, the conclusions of any studies based on the trilobite taxonomic hierarchy may, at least in part, be an artefact of the recognition of non-monophyletic higher taxa. How closely taxa fit the requirements for their diversity to be an accurate estimate of disparity is likely to be extremely sensitive to their phylogenetic status, since more extensive taxonomic revision will be required in groups whose taxonomy poorly reflects phylogeny. The use of taxonomic proxies for morphological disparity is likely to be unsafe when the phylogenetic status of the taxa used is uncertain.

DISCUSSION

Whilst the polyphyly of the Conocoryphidae has previously been suggested, it has not been convincingly demonstrated, and authors have differed widely in their hypotheses of relationships between the included genera. The cladistic analyses presented here clearly demonstrate the polyphyletic nature of the family Conocoryphidae Angelin, 1854, and suggest that four distantly related clades should be recognized in its place. Three of these clades are distributed amongst the basal ptychopariids, and the fourth consists of two genera assigned to the subfamily Acontheinae of the Corynexochida. These conclusions are robust to character sampling and assumptions about character evolution. The newly recognised families have wide geographic distributions, indicating their potential biostratigraphic utility. The Conocoryphacea have been characterized as one of the most secure of the superfamilies of the Ptychopariida. The wide taxonomic distribution of the clades previously included in the Conocoryphidae illustrates the potential degree of error inherent in traditional taxonomies, at least within the Trilobita. If this example were representative of the state of family level taxonomy in Cambrian trilobites as a whole, then any attempt to characterize



TEXT-FIG. 6. Distribution of conocoryphid taxa on the first three axes of the PCO morphospace. The first two PCO axes are shown as the axes of the graph and scores on the third axis are indicated by the size of the circles.

Recognition of the repeated evolution of blindness in ptychopariids provides further evidence of the convergent nature of eye loss in trilobites (Fortey and Owens 1990; Clarkson 1997). The clades recognized here are all examples of the atheloptic morphotype, since their close relatives had normal eyes (Fortey and Owens 1987, 1990, 1997). It has previously been suggested that the mechanism of eye loss varied between members of one of the clades recognized here (the emended Conocoryphidae): ‘*Bailiella* has short, ‘marooned’ eye ridges and comparatively wide fixed cheeks, while *Conocoryphe* and *Meneviella* have long genal ridges and marginal sutures’ (Fortey 1990, p. 563). Most species of *Bailiella*, however, have long eye ridges, with a very similar morphology to those of *Conocoryphe*. It is only in species such as *Bailiella emarginata*, where the caecal system is not developed and only a single short ridge is present rather than the two ridges (see above) of *Conocoryphe*, that the morphology differs (see Jell and Hughes, 1997, p. 62). There is, therefore, no evidence that the mechanism of eye loss in these genera was different, and following the cladistic results, blindness is considered here to be a valid synapomorphy of this clade.

A number of authors have suggested that levels of morphological variation in Cambrian trilobites were unusually high, and that this makes suprageneric classification difficult (McNamara 1986; Hughes 1991; Rushton and Hughes 1996). However, the suggested pervasive iterative evolution in Cambrian trilobites,

TABLE 5. Mean intertaxon euclidean distances for the four monophyletic suprageneric taxa recognised herein.

	Conocoryphidae	Hartshillini	Holocephalidae
Atopidae	4.8776	6.0700	5.4940
Conocoryphidae	-	7.0262	5.2583
Hartshillini	-	-	6.3189

and in ptychopariids in particular, has not been convincingly demonstrated. The level of homoplasy implied by a cladistic analysis of Cambrian trilobites has previously been suggested as evidence against this view (Lieberman 1998). The amount of homoplasy found in the analyses presented here (CI = 0.442 for the first analysis, CI = 0.342 for the second analysis) is slightly below average compared to other data sets of similar sizes (Archie 1989; Sanderson and Donoghue 1989), and far lower than that expected from random data (Klassen *et al.* 1991). Similarly, a recent cladistic analysis of alokistocarid phylogeny (Sundberg, 1999) found only moderate levels of homoplasy (19 taxa, 50 characters, CI = 0.592). There is therefore no evidence that levels of homoplasy are unusually high in the Ptychopariida (*contra* Sundberg 1994), and no need to rely on a combination of stratigraphic data and overall similarity to form hypotheses about ptychopariid relationships. Resolution of ptychopariid phylogeny is likely to centre on the relationships of basal, generalized forms rather than more derived forms. Two of the groups recognised herein, the Holocephalidae and emended Conocoryphidae, consist of 'generalized' ptychoparioids. The recovery of highly resolved and well-supported cladograms for such groups, both here and by Sundberg (1999), shows that cladistic methods have potential for resolving the problem of ptychopariid phylogeny, and that homoplasy is not so prevalent that such methods are of little use.

Many of the characters employed herein have not previously been regarded as phylogenetically significant, and are likely to be of more general use. A number of characters were of above average consistency (see Appendix for a list of character consistency indices). These characters fall into easily recognized categories: nature of the cephalic borders and shape of the cephalon, the form of the glabella, glabellar furrows and axial furrows, thoracic characters and gross morphology of the pygidium. Ptychoparioid trilobites show complex patterns of, often subtle, variation but there is no evidence that this variation is such that valid synapomorphies cannot be recognised, or that different sclerites show very different patterns of variation. Cladistic analysis provides a consistent approach to assessing the importance of variation in a wide range of characters, that other methods of phylogenetic reconstruction lack. Coding of detailed differences in morphology, and particularly in shape, should permit the resolution of the 'ptychoparioid problem' using cladistic methods.

SYSTEMATIC PALAEOLOGY

The taxonomy of suprafamilial taxa and previously recognized families follows the recent revision of the trilobite Treatise (Fortey 1997). Paraphyletic taxa are indicated using the quotes convention of Wiley (1979). Detailed systematic revision and redescriptions will be presented elsewhere.

Class TRILOBITA *sensu* Ramsköld and Edgecombe, 1991

[see Edgecombe and Ramsköld 1999]

Subclass LIBRISTOMA Fortey, 1990

Order 'PTYCHOPARIIDA' Swinnerton, 1915

Suborder 'PTYCHOPARIINA' Richter, 1932

[see Kaesler 1997, p. 510, regarding authorship]

Superfamily 'ELLIPSOCEPHALOIDEA' Matthew, 1888

[see Nikolaisen and Henningsmoen 1990, p. 64, regarding authorship of this superfamily and of the 'Ptychoparioidea', below]

Family ATOPIDAE Hupé, 1954 emend.

Plate 1, figures 1–4, 8–9; Plate 2, figures 1–3.

Emended diagnosis. Blind ellipsocephaloid trilobites with thin 'threadlike' eye ridges that interrupt the axial furrows. Length of cephalon (sag.) less than 50 per cent of cephalic width. Facial sutures only on cephalic border, librigenae consist only of a thin strip of the posterolateral border and genal spines on the dorsal surface. Anterior arch absent. Genal convexity moderate. Eye lobe absent. Threadlike genal ridges on external surface of anterior genae interrupt axial furrows adaxially, then run obliquely forwards before turning laterally and closely following the cephalic border furrow. Anterolateral cephalic border of even

width, downslowing or weakly convex. Border furrow continuous across genal angles, posterior border furrow of even width or slightly expanding (exsag.) laterally. Caecal network present anterior to the genal ridges. Genal spines long (greater than 65 per cent of sag. cephalic length) and directed backwards parallel to axis. Glabella prominent and convex (trans.), reaching or crossing anterior border furrow, at least 70 per cent of cephalic length. Glabella sides approximately parallel to converging slightly forwards, especially anteriorly. Frontal lobe of glabella broadly rounded. Four pairs of straight or slightly curved lateral glabellar furrows usually visible, posteriormost pair may be transglabellar. Thorax consists of 17 or more segments. Pleurae with spinose terminations, macropleural spines may be present on some segments. Pleural furrows wide (exsag.), straight and transverse. Pygidium semicircular. Number of axial rings uncertain. Axis wide (trans.), reaching posterior border. Pleural furrows oblique, curved.

Included genera. *Atops* Emmons, 1844 (Pl. 1, figs 1–4) (= *Ivshiniellus* Korobov, 1966; Pl. 1, fig. 8); *Atopina* Korobov, 1966 (Pl. 1, fig. 9); *Pseudatops* Lake, 1940 (Pl. 2, figs 1–3).

Discussion. The members of this family show a number of similarities to the primitive libristomates, or advanced redlichiids, of the paraphyletic (see e.g. Forzey 1997) superfamily Ellipsocephaloidea. In particular, a number of features indicate a relationship with the Protolenidae (Protoleninae in the taxonomy of Geyer 1990): (1) the convexity of the cephalon and the definition of the furrows are distinct from the effacement of the Agraulidae and Ellipsocephalidae; (2) the glabella of the protolenids is long and approximately parallel-sided, compared to the shorter, tapering glabella of the ellipsocephalids. None of the ellipsocephaloids shows the distinctive form of the eye ridge, but some protolenids have eye ridges that are highly curved, positioned relatively far anteriorly, and directed relatively transversely, rather than obliquely posterolaterally (e.g. *Orodes schmitti* Geyer, 1990, pl. 51, figs 1–6; *Protolenus (Protolenus) elegans* Matthew, 1892; Pl. 1, figs 5, 7). In his emended diagnosis of the Protoleninae, Geyer (1990, p. 336) highlighted a number of characters that are also found in the Atopidae, such as the long, convex glabella which is parallel-sided posteriorly.

A few sighted Early Cambrian ptychoparioids show some resemblance to the atopids, and may be closely related. The genus *Rimouskia* has previously been compared to *Atops* (Richter and Richter 1941; Sdzuy 1961; Rasetti 1967) and is similar in the width of the fixigenae, the long, simple, subparallel lateral glabellar furrows, the shape of the glabella, and the form of the cephalic borders, but differs in the presence of eyes and the form of the eye ridge. A number of other Early Cambrian species share the long glabella and wide fixigenae. The three species of *Alacephalus*, *A. contortus* Repina, 1960 (Pl. 1, fig. 6), *A. latus* Repina and Romanenko, 1978, and *A? davisii* (see Lane and Rushton 1992, pl. 1; Blaker and Peel 1997, fig. 81), have a glabellar structure very similar to some species of atopid and to *Rimouskia*. *Gelasene acanthinos* Palmer (1968, pl. 2, figs 1–3, 5–6), from the Lower Cambrian of Alaska shares unusual double pleural spines with *Alacephalus? davisii*, but its long glabella is strongly tapered, the facial suture is complex and the genae relatively narrow (trans.). Fritz's conocoryphid sp. 1 (1973, pl. 6, figs 28–31), from

EXPLANATION OF PLATE 1

Fig. 1. *Atops trilineatus* (Emmons, 1844). BMNH I.1587; Lower Cambrian, Washington County, New York; dorsal view; $\times 2.2$.

Figs 2–4. *Atops* sp., BMNH In.19186; Lower Cambrian, entrance to Saltwater Pond, Canada Bay, Newfoundland. 2, anterior view; 3, lateral view; 4, dorsal view; $\times 2.5$.

Figs 5, 7. *Protolenus (Protolenus) elegans* Matthew, 1892, ROM 7795, syntype; Lower Cambrian, Hanford Brook, New Brunswick. 5, lateral view; 7, dorsal view; $\times 4.5$.

Fig. 6. *Alacephalus contortus* Repina, 1960, CSGM 134/351; Lower Cambrian, Kuznetsky-Alatau, Russia; dorsal view; $\times 1.7$.

Fig. 8. *Ivshiniellus nikolaii* Korobov, 1966, cast of holotype GIN 91/3583; Lower Cambrian, Ezhim River, north Tuva, Russia; dorsal view; $\times 2$.

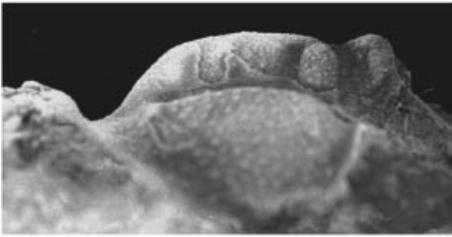
Fig. 9. *Atopina antiqua* Korobov, 1966, GIN 89/3583, holotype; Lower Cambrian, Ezhim River, north Tuva, Russia; dorsal view; $\times 1.5$.



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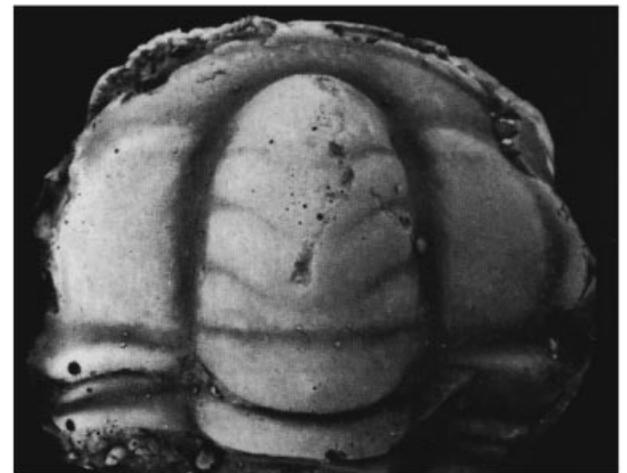
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the Lower Cambrian of the Mackenzie Mountains of northwestern Canada, is particularly interesting in this respect, showing a combination of features that are typical of the Atopidae, including blindness, the form of the genal ridges, and the position of the suture, with a tapering glabella similar to that of *Gelasene*, *Nehanniaspis* Fritz, 1972 and *Keeleaspis* Fritz, 1972. In this species, the anterior pairs of lateral glabellar furrows are highly reduced compared to those in most other atopids and the posteriormost pair is transglabellar, both features shared with the unusual atopid *Atopina antiqua* Korobov, 1966. Fritz's species also shares a number of features with *Atops? calanus* Richter and Richter, 1941 (also discussed by Sdzuy 1962), which, as previously argued (Orłowski 1985; Jell *et al.* 1992), should be excluded from the genus. Finally, these two species share some features with *Atops korobovi* Romaneko (*in Repina et al.*, 1999) and an undescribed species from Canada Bay, north-west Newfoundland (Pl. 1, figs 2–4), preliminarily assigned to *Atops*. Following the reasoning of Fortey (1990, p. 548), the absence of a preglabellar field in atopids and these other genera suggests that their affinities may lie with the conterminant ellipsocephaloids rather than the libristomate (= ptychopariid) ellipsocephaloids. This can only be confirmed when the ventral features are known. These unusual Lower Cambrian ptychoparioids are rather poorly documented, and a complete review is needed.

The interruption of the axial furrows by the eye ridges in atopids is likely to be homologous to the state in primitive ellipsocephaloids with eyes (Ahlberg and Bergström 1978). This character may be of diagnostic importance because, unlike the condition of hypostomal attachment, it is visible in the majority of material. If Fortey (1990) is correct, and the natant hypostomal condition originated somewhere within the Protolenidae, then the condition of the eye ridge at the axial furrows may define a clade within the Libristomata, excluding the protolenids and antatlasids. The broad form of the pygidium in the Ellipsocephaloidea varies from typically redlichoid [e.g. *Palaeolenus antiquus* (Chernysheva), Rushton and Powell 1998, fig. 33] to ptychoparioid [e.g. *Kingaspis campbelli* (King), Rushton and Powell 1998, figs 22, 26], and pygidial morphology may provide a suite of useful characters, especially amongst effaced forms.

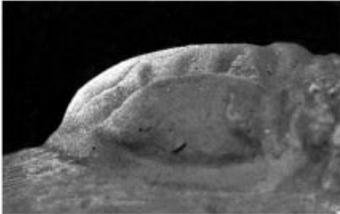
The type material of the genus *Ivshiniellus* Korobov, 1966, is very poorly preserved. It should not have been the basis of a new genus (Jell *et al.* 1992). The material is indistinguishable from *Atops*, and most of the features listed in Korobov's diagnosis are shared with that genus. Computer aided retrodeformation (see Jell and Hughes, 1997, pp. 17–18) of Korobov's (1966, 1973) illustrations of *Ivshiniellus* suggests that the greater forward tapering of the glabella is a preservational artefact. At least one of the species originally assigned to the genus, *I. nikolaii* (Korobov, 1966, pl. 6, figs 3–4), represents an atopid, on the basis of the form of the eye-ridges, the length of the glabella and the marginal position of the facial suture. Korobov's other species, *I. patulus*, is even more poorly preserved, and cannot be assigned to the family with confidence. Both species should be considered doubtful. The Australian species *Ivshiniellus briandailyi* Jenkins and Hasenohr, 1989, is referred to *Atops* herein. The tapering of the glabella in

EXPLANATION OF PLATE 2

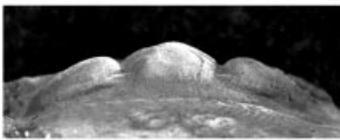
- Figs 1–3. *Pseudatops reticulatus* (Walcott, 1890), BUGM 5961; Lower Cambrian, south of Comley Quarry, Church Stretton, Shropshire, east of British Geological Survey Museum 53515. 1, dorsal view; $\times 1.4$; 2, lateral view; $\times 2$; 3, anterior view; $\times 1.4$.
- Figs 4–5. *Agraulos cetecephalus* (Barrande, 1846), Middle Cambrian, *Eccaparadoxides pusillus* Zone, Skryje, Bohemia. 4, BMNH I.3434; dorsal view of almost complete exoskeleton; $\times 3.5$. 5, BMNH 42368; dorsal view of cranium; $\times 5$.
- Figs 6, 9–10. *Holocephalina primordialis* Salter, 1864. 6, BMNH 42648, holotype; Middle Cambrian, *Paradoxides davidis* Zone, Porth-y-rhaw, St Davids, Dyfed, Wales; dorsal view; $\times 6.5$. 9–10 (ex *Holocephalina americana*), Middle Cambrian, Manuel's Brook Formation, Manuel's Brook, Newfoundland. 9, BMNH It.13584; $\times 4.3$. 10, BMNH It.13585; $\times 3.5$.
- Figs 7–8. *Sdzuyella stremina* Hajrullina, *in Repina et al.*, 1975, holotype MMG 219/483; Turkestan Ridge, Uzbekistan. 7, dorsal view; $\times 3.8$; 8, lateral view; $\times 4.5$.
- Fig. 11. *Holocephalites incertus* (Illing, 1916), latex cast of NMW 80.34G.852; Middle Cambrian, *Tomagnostus fissus* Zone, Menevian beds, Penepheidia, Caerfai Bay, St Davids, Dyfed, Wales; dorsal view of almost complete exoskeleton; $\times 8.75$.



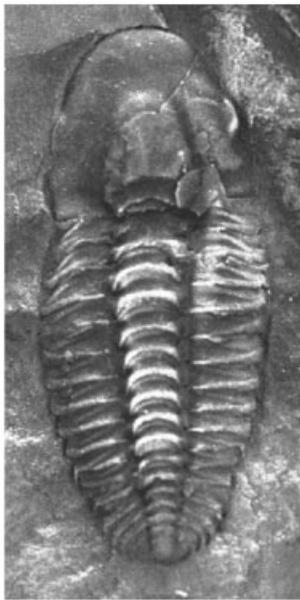
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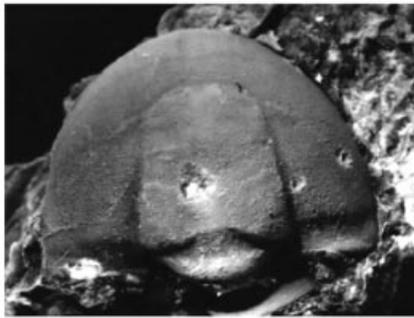
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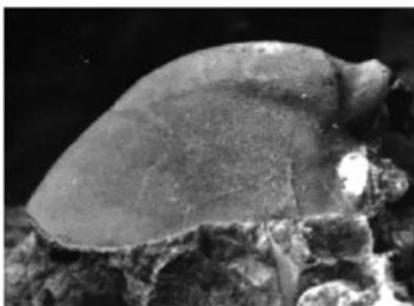
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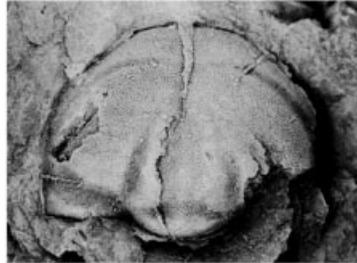
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their reconstruction (fig. 4) is not matched by that of the specimens, and the species closely resembles the other Australian atopid, *Atops rupertensis* Jell *et al.*, 1992, in other respects.

Family HOLOCEPHALIDAE Hupé, 1953 emend.

nom. transl. ex HOLOCEPHALINAE Hupé, 1953

[= HOLOCEPHALINAE Hupé, 1953; MENEVIELLINAE Hupé, 1955; HOLOCEPHALINIDA Hupé, 1952,

Egorova *et al.*, 1982]

Text-fig. 1A; Plate 2, figures 6–11; Plate 3, figures 1–4.

Emended diagnosis. Blind agrauloid trilobites with short glabellae, dorsal librigenae consisting only of the genal spines, and downsloping genae. Cephalon wide in proportion to length, fixigenae very wide (facial sutures remain on cephalic border), consisting of thin strip of the border and the genal spine on dorsal surface. Palpebral lobes and eyes (visual surfaces) entirely absent. Preglabellar field wide (sag.), confluent with anterior genae, or slightly depressed relative to them. Prominent caecal network and genal ridges present, at least on internal moulds. Genal ridges very narrow (sag.), more or less straight and directed posterolaterally. Axial furrows not interrupted by eye ridge, which divides adaxially; anterior branches join around the front of the glabella, resulting in preglabellar furrow weaker than axial furrows. Prominent reticulate caeca posterior to the eye ridge. Anterolateral cephalic border moderately to entirely effaced or defined by broad, weak furrows, flat and sloping upwards or horizontal. Anterior border slightly wider axially than laterally. Posterior cephalic border furrow of even width or gradually expanding laterally, may arch forwards well inside genal angles, or become effaced at genal angles. Genal spines long and directed obliquely posterolaterally.

Glabella short to very short (sag., less than 0.6 cephalic length), tapering forwards. Three pairs of glabella furrows, variably defined. Thorax of 18 or more segments, terminating in short spines. Thoracic pleural furrows narrow, oblique and straight. Pygidium with short axis of three to four rings (excluding terminal piece). Wide postaxial field bearing furrows, pleural and interpleural furrows oblique and curved abaxially. Pygidium small, less than five per cent of length of entire exoskeleton.

Included genera. *Holocephalina* Salter, 1864 (Pl. 2, figs 6, 9–10); *Dasometopus* Resser, 1936 (Pl. 3, fig. 5); *Holocephalites* Zhou, in Zhou *et al.*, 1982 (Pl. 2, fig. 11); *Meneviella* Stubblefield, 1951 (Text-fig. 1A; Pl. 3, figs 1–4); *Sdzuyella* Hajrullina, in Repina *et al.*, 1975 (Pl. 2, figs 7–8).

EXPLANATION OF PLATE 3

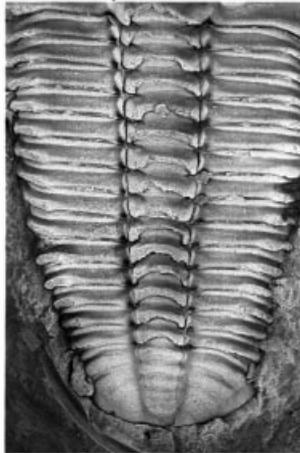
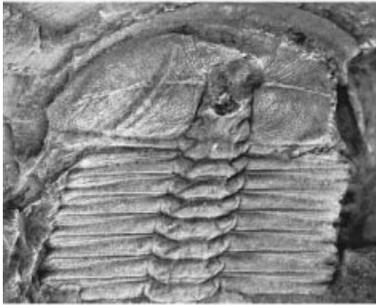
- Figs 1–4. *Meneviella venulosa* (Hicks, 1872). 1, BMNH It.13575; Middle Cambrian, *Paradoxides davidis* Zone, Manuel's Brook Formation, Manuel's Brook, Newfoundland; dorsal view of cranidium; $\times 4$. 2, BMNH 59319; Middle Cambrian, Menevian beds, Porth-y-Rhaw, St Davids, Dyfed; dorsal view of cephalon and anterior thoracic segments; $\times 2.25$. 3, latex cast of BMNH I.7734; Middle Cambrian, near Dolgellau, Wales; pygidium; $\times 6$. 4, BMNH I.7733, Middle Cambrian, near Dolgellau, Wales; dorsal view of cranidium and anterior thoracic segments; $\times 3$.
- Fig. 5. *Dasometopus* sp., latex cast of NMW 80.34G.850; Middle Cambrian, *Hypagnostus parvifrons* Zone, Menevian beds, St Davids series, Porth-y-rhaw, St Davids, Dyfed; distorted cranidium; $\times 6.5$.
- Figs 6, 9–10. *Conocoryphe sulzeri* (Schlothheim, 1823). 6, 9, BMNH 59826; Middle Cambrian, *Eccaparadoxides pusillus* Zone, Jince, Bohemia. 6, posterior thorax and pygidium; $\times 1.5$; 9, cranidium and anterior thorax; $\times 1.8$. 10, BMNH 42375, Middle Cambrian, *Eccaparadoxides pusillus* Zone, Ginetz, Bohemia, cranidium and anterior thorax; $\times 1.6$.
- Fig. 7. *Elrathia kingii* (Meek, 1870), BMNH It.20992; Middle Cambrian, Wheeler Shale, House Range, Utah; entire exoskeleton; $\times 2.75$.
- Figs 8, 11–12. *Ptychoparia striata* (Emmrich, 1839). 8, 11, BMNH 42374; Middle Cambrian, Ginetz, Bohemia. 8, posterior thorax and pygidium; 11, cranidium; $\times 1.8$. 12, BMNH I.3737; Middle Cambrian, Jince, Bohemia; cranidium; $\times 2$.



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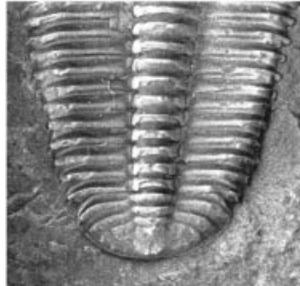
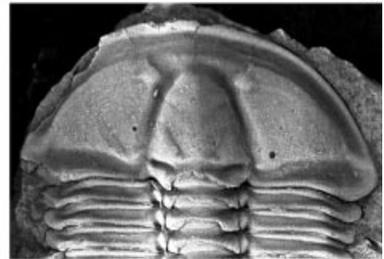
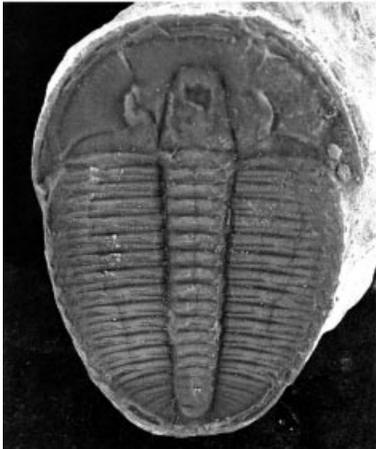
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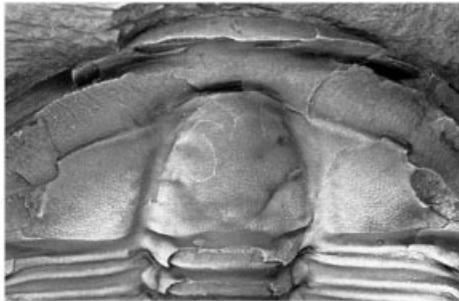


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Discussion. Two major groups of genera can be recognized within this family: (1) *Meneviella* and *Dasometopus*; (2) *Holocephalina*, *Holocephalites* and *Sdzuyella*. These groups may merit formal status when the phylogeny of basal ptychopariids becomes better known. Whilst superficially highly distinct, members of the two groups share a number of characters (diagnosis above), and a close relationship is strongly supported by the phylogenetic analysis presented herein. *Meneviella* and *Dasometopus* show no great similarities to any other group, but the second group shares a number of characters with the Agraulidae. These include the short tapering glabella, flat genae, effaced anterior border furrow, and a long thorax. The pygidium is unknown from this second group, but that of *Meneviella* (Pl. 3, fig. 3) is similar in size and form to that of *Agraulos* (Pl. 2, fig. 4). The suprageneric classification of the Agraulidae and their putative relatives is unresolved; there is a great profusion of families and genera (see e.g. Zhang *et al.* 1980; Zhang and Jell 1987). As with many effaced trilobite groups, few characters are available to determine relationships between many of these taxa. Ahlberg and Bergström (1978) proposed that the agraulids are closely related to the ellipsocephaloids, and a number of authors have subsequently included them in the Ellipsocephaloidea (e.g. Geyer 1990; Fortey 1997). This approach is followed here.

Holocephalina incerta Illing, 1916 was referred to the new genus *Holocephalites* Zhou, in Zhou *et al.*, 1982 (type species *H. punctatus* Zhou *op. cit.*). The specimens of *Holocephalina* described by Egorova *et al.* (1982) as *Holocephalina* aff. *incerta* and *Holocephalina* sp. also belong within this genus. The species of the genus *Holocephalina*: *H. primordialis* Salter, 1864, *H. agrauloides* Sdzuy, 1966, *H. americana* Resser, 1937, *H. leve* Gozalo and Liñan, 1996, *H. menevensis* (Hicks, 1872) and *H. teres* (Grönwall, 1902), show a considerable variety, and are in need of revision. *Holocephalina agrauloides* resembles *Holocephalites* in the extremely rounded shape of the glabella, the complete effacement of the anterolateral border, the broad-based occipital spine, and the form of the posterior cephalic border, but more closely resembles *H. primordialis* in the shape of the cephalon and the length of the glabella. The species *H. americana* (Pl. 2, figs 9–10) and *H. menevensis* are subjective junior synonyms of *H. primordialis* (see Lewis 1988). *Holocephalina teres* and *H. leve* are very similar, and may be synonyms, but the former has been illustrated only by a drawing of a single cranidium (Grönwall 1902, pl. 2, fig. 2; redrawn in Harrington *et al.* 1959, fig. 181.5).

Meneviella is unusually wide-ranging geographically for Cambrian ptychoparioids; this may be because its distinctive morphology has enabled it to be consistently recognized throughout its range, in contrast to more generalized taxa (e.g. four generic synonyms of *Ptychoparella* Poulsen have been identified from Laurentia alone; Blaker and Peel 1997). Of the two described species, *M. venulosa* (Hicks, 1872) (see Morris 1988 for a discussion of the authorship of this species) has been described from Newfoundland, New York, England and Wales, Bornholm, Kazakhstan and eastern Siberia (reviewed by Lewis 1988), and *M. viatrix* Shergold, 1973, is known only from Australia. Unidentified species of *Meneviella* have been reported from Lodochny on the Sisim River in eastern Sayan (Repina 1960, p. 222, pl. 17, fig. 11), and from the Olenek River, North Siberian Platform (Pokrovskaya 1965, p. 341).

Superfamily 'PTYCHOPARIOIDEA' Matthew, 1888
Family CONOCORYPHIDAE Angelin, 1854 emend.

Text-fig. 1B; Plate 3, figures 6, 9–10; Plate 4, figures 1–11.

Emended diagnosis. Blind generalized ptychoparioids with anteriorly tapering glabella and convex genae. Fixigenae wide, position of facial suture variable. Anterior arch usually present. Cranidium approximately half as long (sag.) as wide (trans.), or slightly narrower (length between 0.45 and 0.65 of width). Preglabellar field may be separated from the genae by diverging preglabellar furrows, lowered relative to the anterior genae, or confluent with the cheeks. Genal spines directed backwards. Palpebral lobes usually absent. Threadlike genal ridges present, at least on internal moulds, rarely present on external surface, interrupted by axial furrows medially, run directly posterolaterally. Caecal network present on anterior genae on internal moulds only. Reticulate sculpture absent posterior to eye ridges. Threadlike ridges diverge to form a flattened subcircular boss just abaxial to the axial furrows. Cephalic border highly convex

laterally, convex anteriorly but somewhat flattened where the border is expanded (sag.) anteromedially. Border defined by strong furrows both anteriorly and posteriorly, continuous across genal angles. Posterior border furrows of approximately even width along length, or widening halfway across genae, giving arched appearance.

Glabella tapering evenly over most of its length, anterior termination moderately rounded to blunt, usually of medium length (0.5–0.6 cephalic length) and narrow (0.25–0.31 cephalic width). Preglabellar furrow of similar definition to axial furrows. S1 lateral glabellar furrow simple (not bifurcating), may be recurved or simply curved. S2 furrows shorter than S1, longer than S3, oblique backwards. S3 furrows very short slits or indentations. Occipital ring of medium length. Paired prominent pits posterior to occipital furrow.

Thorax of 14 or 15 segments, with short, roundly pointed terminations with articulating facets. Thoracic pleural furrows wide, straight, and perpendicular to the axis. Axis of medium width (26–33 per cent of thorax width). Pygidium of intermediate or large size, at least 6 per cent of length of exoskeleton. Axis of four rings (excluding terminal piece), narrow postaxial field of approximately same width as pygidial border. Interpleural furrows absent, pleural furrows more or less straight, curving slightly posteriorly abaxially. Hypostome natant and of typical ptychoparioid morphology.

Included genera. *Conocoryphe* Hawle and Corda, 1847 (Pl. 3, figs 6, 9–10) (= *Couloumania* Thoral, 1946; Pl. 4, fig. 4); *Bailiaspis* ('*Bailiaspis*') Resser, 1936 (Pl. 4, fig. 7); *Bailiaspis* (*Tchaispis*) Korobov, 1966 (Pl. 4, fig. 9); *Bailiella* Matthew, 1885 (Text-fig. 1b; Pl. 4, figs 2–3); *Cainatops* Matthew, 1899 (= *Cornucoryphe* Sdzuy and Liñan, 1996, figs 1–9); *Ctenocephalus* ('*Hartella*') Mathew; 1885 (Pl. 4, figs 10–11); *Ctenocephalus* (*Ctenocephalus*) Hawle and Corda, 1847 (Pl. 4, figs 5, 8); *Elyx* Angelin, 1854 (Pl. 4, fig. 6); *Parabailiella* Thoral, 1946 (Pl. 4, fig. 1).

Discussion. The Conocoryphidae, as emended here, is a clade of blind ptychopariids of otherwise 'generalized' (but nonetheless derived compared to the earliest ellipsocephaloid trilobites; see Geyer 1990) appearance. The sister group of the conocoryphids could lie amongst any of the sighted generalized ptychoparioids, a large number of family-level taxa have been proposed for such forms, based on very few diagnostic differences. Such groups include the Antagmidae (Geyer and Malinky 1997), Dokimocephalidae, Ehmaniellidae (Sundberg 1994), Marjumiidae, Ptychopariidae, and Solenopleuridae, amongst others. These can hardly be differentially diagnosed, and the synonymy of many of these families has frequently been suggested (e.g. Öpik 1967; Ahlberg and Bergström 1978; Fortey 1990; Blaker and Peel 1997), but rarely adopted. The use of another family name is defensible because the Conocoryphidae share the synapomorphy of blindness compared to these other generalized taxa, and can be readily distinguished from other blind trilobites by the characters described above.

The cladistic analyses presented herein provide little evidence for the monophyly of the largest conocoryphid genera, *Conocoryphe* Hawle and Corda, 1847 and *Bailiella* Matthew, 1885. The problem of defining these genera and the similar genera *Couloumania* Thoral, 1946 and *Parabailiella* Thoral, 1946 remains. Distinction between these four taxa currently rests on two features (Westergård 1950; Courtessole 1973; Jell and Hughes 1997): (1) the position of the facial suture with respect to the border furrow (on the border in *Conocoryphe* and *Couloumania*, crossing it in *Bailiella* and *Parabailiella*), and (2) the possession of diverging preglabellar furrows (present in *Conocoryphe* and *Parabailiella*, absent in *Bailiella* and *Couloumania*). The analyses presented here indicate that the first is the more important; it has a higher character consistency index on all the cladograms. This is supported by the phylogenetic position of the species *Bailiella lantenoisi* (Mansuy, 1916), in which the preglabellar furrows are absent, but the sutures remain on the border (see Jell and Hughes 1997). This species and *B. aequalis* consistently fall outside the *Bailiella* clade in the cladistic analyses presented here, but are tentatively retained in the genus, pending further study. The analyses provide strong evidence that *Bailiaspis glabrata* (Angelin 1854) should be assigned to the genus *Bailiella*, as tentatively suggested by Sdzuy (1966); it was included in a clade of *Bailiella* species in all analyses.

The species *Conocoryphe caecigena* Dean, 1982, is representative of a group of six very similar species (reviewed by Dean *op. cit.*) in the cladistic analyses, all previously assigned to *Conocoryphe*. They do not share the essential features of *Conocoryphe*, being more similar to *Couloumania* in that the suture remains

on the border and the diverging preglabellar furrows are absent. They also have the unique (within the Conocoryphidae clade) synapomorphy of pseudoculate (see Courtessolle 1973; Dean 1982) protuberances on the genae, which are likely to represent non-functional homologues of the palpebral lobes. They do not appear to be closely related to *Conocoryphe*, and a new genus, or subgenus, should be erected to accommodate them. The type species of *Couloumania*, *C. heberti*, appears to be closely related to *Conocoryphe sulzeri*, and *Couloumania* is therefore considered to be a subjective junior synonym of *Conocoryphe*.

Order CORYNEXOCHIDA Kobayashi, 1935

Suborder CORYNEXOCHINA Kobayashi, 1935

Family CORYNEXOCHIDAE Angelin, 1854

Subfamily ACOTHEINAE Westergård, 1950, emend. Geyer, 1994

[= TRINIIDAE Poletaeva, 1956, p. 17; TRINIINAE Suvorova, 1964, p. 227;

CORYNEXOCHELLINAE Suvorova, 1964, p. 229; ABAKANIINAE Romanenko, *in Repina et al.*, 1999, p. 17]

Discussion. Geyer (1994) extensively discussed this subfamily, and his concept of the subfamily is adopted here. Repina *et al.* (1999) rejected Geyer's revision and based their classification on the presence or absence of eyes and facial sutures, uniting sighted forms in the family Milaspidae. As demonstrated here, and discussed above, blindness is of little phylogenetic significance in trilobites, and Geyer's arguments for a close phylogenetic relationship between proparian and blind corynexochoids is accepted.

Three subfamilies, Abakaniinae, Milaspidae and Triniinae, were included in the Milaspidae by Repina *et al.* (1999). The Triniinae was included in the Acontheinae by Geyer (1994). The subfamily Abakaniinae Romanenko (*in Repina et al.* 1999) also fits Geyer's concept, and is synonymized with the Acontheinae herein. *Milaspis* (see Repina *et al.* 1999, pp. 17–19, pl. 2, figs 2–9), the only genus in the Milaspidae, differs from the other trilobites discussed here in a number of respects, including its relatively wide and flat fixigenae and wide and spinose thoracic pleurae, and is excluded from the Acontheinae.

Tribe HARTSHILLINI nov.

Diagnosis. Blind and strongly effaced corynexochids with anteriorly expanding glabella and distinctive

EXPLANATION OF PLATE 4

Fig. 1. *Parabailiella languedocensis* Thoral, 1946, BMNH It.3964; Middle Cambrian, Coulouma, Hérault, France; cranidium; ×2.

Figs 2–3. *Bailiella baileyi* (Hartt, *in Dawson*, 1868). Middle Cambrian, Fossil Brook Formation, Fossil Brook, St Martins, New Brunswick; distorted cranidia. 2, BMNH It.3952; ×3. 3, BMNH It.3953; ×4.

Fig. 4. *Couloumania heberti* (Munier-Chalmas and Bergeron, *in Bergeron*, 1889), BMNH 41892; Middle Cambrian, Coulouma, Hérault, France; cranidium; ×3.

Fig. 5. *Ctenocephalus (Ctenocephalus)* sp., BMNH I.2763; Middle Cambrian, Coulouma, Hérault, France; distorted cranidium; ×2.4.

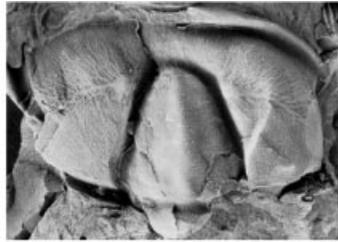
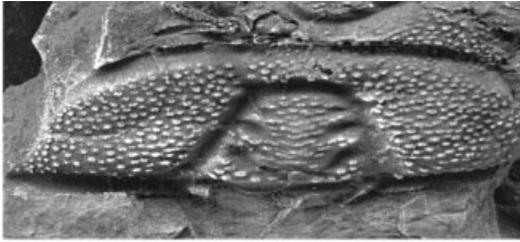
Fig. 6. *Elyx laticeps* (Angelin, 1851), BMNH It.2640; Middle Cambrian, *Paradoxides forschammeri* Zone, Andrarum Limestone, Andrarum, Scania; partly exfoliated ?cranidium; ×2.4.

Fig. 7. *Bailiaspis venusta* Resser, 1937, NMW 88.55G.144; Middle Cambrian, *Paradoxides hicksi* Zone, Manuels River Formation, St Davids Series, Manuels River, Avalon Peninsula, Newfoundland; cranidium; ×3.

Fig. 8. *Ctenocephalus coronatus* (Barrande, 1846), BMNH It.532; Middle Cambrian, Skryje, Bohemia; cranidium; ×3.

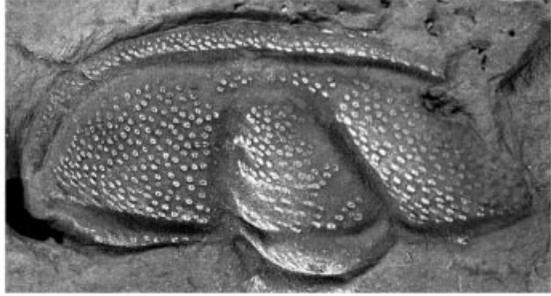
Fig. 9. *Tchiaspis szuyi* Korobov, 1966, latex cast of holotype GIN 88/3583; Middle Cambrian, southern Siberian platform, Maya River, Chayskaya Hill, Siberia, Russia; ?cranidium; ×4.

Figs 10–11. *Ctenocephalus (Hartella) matthewi* (Hartt, *in Dawson*, 1868), BMNH It.3930, Middle Cambrian, Fossil Brook Formation, Fossil Brook, St Martins, New Brunswick. 10, cast of counterpart; 11, internal mould; ×4.



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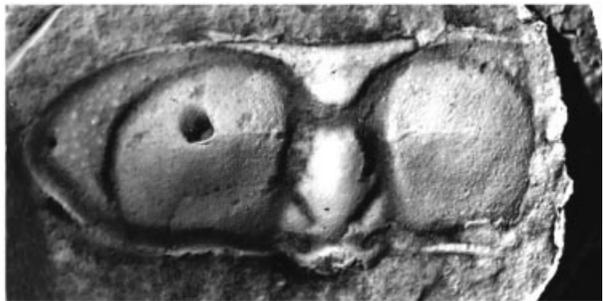
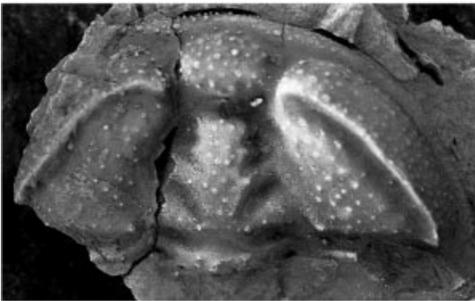
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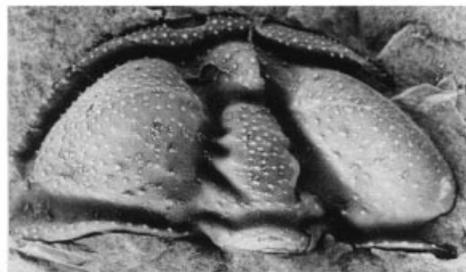
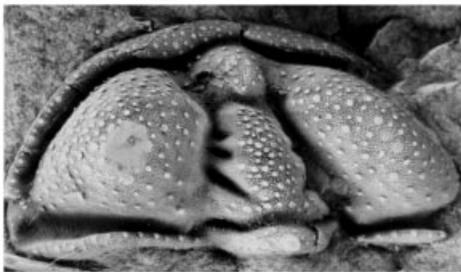
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punctate sculpture. Cephalon very narrow compared to length (length greater than 75 per cent of cephalic width), long in proportion to entire exoskeleton (greater than 40 per cent of total length). Facial suture entirely absent on dorsal surface. Blind; palpebral lobes, visual surfaces and genal ridges all absent. Lateral glabellar furrows and anterolateral cephalic border entirely effaced. Posterior cephalic border entirely effaced or indicated by lack of punctate sculpture on exterior surface, becomes entirely effaced at genal angles. Prominent, punctate cephalic sculpture (granulose on internal casts) may be missing from posterior cephalic furrows.

Anterior glabella, genae and border confluent. Glabella long and expanding (trans.) anteriorly, clavate, may be slightly raised above genae or confluent with them (especially in holaspids). Axial furrows weakly expressed near occipital furrow, completely effaced, or represented by impunctate bands. Occipital furrow entirely effaced or indicated by smooth bands. Occipital ring extended into long spine or short rounded protuberance.

Thorax of eight segments, with blunt, faceted terminations, and a wide axis (greater than one-third of total thoracic width). Thoracic pleural furrows narrow, oblique and highly curved. Pygidium at least 10 per cent of length of entire exoskeleton. Axis of two rings and terminal piece, width at least 35 per cent of maximum pygidial width (both trans.), without postaxial field. Hypostome conterminant and fused to rostral plate.

Included genera. *Hartshillia* Illing, 1916; *Hartshillina* Lake, 1940.

Discussion. The tribe Hartshillini is erected within the Acontheinae to accommodate the highly derived genera *Hartshillia* and *Hartshillina*. These genera are most similar to blind *Acontheus* species, such as *Acontheus acutangulus* Angelin (Westergård 1950, p. 9, pl. 18, figs 4–6) and *Acontheus burkeanus* Öpik, 1961, sharing a similar shape of the glabella, the position of the facial suture and a distinctive punctate sculpture. *Hartshillina* shares some distinctive characteristics of the pygidium with other members of the Acontheinae (see Geyer 1994) and is generally less effaced than *Hartshillia*, so is likely to be the sister taxon to *Hartshillia*. Considering the degree of variation, particularly in characters relating to effacement amongst specimens assigned to *Hartshillia inflata* (Hicks 1872) from Britain (Lake 1938) and Greenland (Babcock 1994a), the validity of the other species assigned to the genus (*H. clivosa*, *H. pusilla* and *H. taimyrica*, all Lazarenko, 1965, and *H. terranovica* Hutchinson, 1962) is in need of reassessment. The Hartshillini will be discussed in more detail elsewhere.

Acknowledgements. This work was improved by discussion with J. M. St. John, A. W. A. Rushton, D. E. G. Briggs and R. A. Fortey. The morphometric analysis benefited from the advice of M. A. Wills. D. Coultas and E. Hill helped with the translation of Chinese and Spanish references respectively, and L. E. Babcock provided a translation of an important Russian reference. R. M. Owens and S. R. Howe provided access to the Lewis Collection of the National Museum and Galleries of Wales. S. Powell and D. C. Lees assisted in producing the plates and photographic figures. I am grateful to D. E. G. Briggs, J. A. Cotton, R. A. Fortey, N. C. Hughes, A. W. A. Rushton and J. H. Shergold for their comments and suggestions on various drafts of this paper. This work was supported by The Geological Society of London Curry Research Studentship.

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APPENDIX

Characters and character states used in phylogenetic analyses

Character state distributions are shown in Table 2. Some characters are discussed further in the text. The three sets of characters used to investigate the effects of alternative assumptions on the results of phylogenetic analysis were: (1) quantitative characters, numbers 1, 18, 19, 22–24, 26–27, 39, 56, 59, 63, 72–73, 79 and 82–85; (2) effacement characters, 8–9, 30, 32 and 54; and (3) other characters, 43 and 48. The conditions for characters to be coded as 'not applicable' (see text) are shown in square brackets after the character description. For example, character 2 could only be coded for taxa with a backwardly convex anterior border, coded as state 2 of character 1 (1:2), and is coded as 'not applicable' for taxa with other states of character 1.

1. Adaxial expansion (sag.) of anterior cephalic border. 0: border of even width or border expands gradually without change in the curvature of the border furrow, 1: border expands such that posterior edge of border becomes truncated in front of the glabella, 2: border expands such that a transverse line cuts the posterior edge of the border in more than two places.
2. Degree of backward convexity of the anterior cephalic border, in dorsal view [1: 2]. 0: border weakly convex, 1: border strongly convex.

3. Anterior cephalic border constricted adaxially. 0: absent, 1: present.
4. Cephalic border furrow partially effaced in front of the glabella. 0: absent, 1: present.
5. Shape of the anterior cephalic border, in sagittal cross-section. 0: convex, 1: flattened.
6. Degree of convexity of convex anterior cephalic borders, in sagittal cross-section [5:0]. 0: strongly convex, 1: more weakly convex.
7. Slope of flattened anterior cephalic borders [5:1]. 0: sloping downwards anteriorly, 1: sloping upwards anteriorly, 2: more or less horizontal.
8. Definition of the anterior cephalic border. 0: defined by strong border furrow, 1: defined by faint furrow and/or change in convexity, 2: border completely confluent with genae.
9. Effacement of the posterior cephalic border furrow on external surface. 0: not effaced, 1: posterior border faintly discernible, defined by a wide and shallow furrow or by a change in convexity, 2: effaced entirely or represented only by lack of sculpture on external surface.
10. Cephalic border furrow continuous across genal angles. 0: present, 1: absent, furrows become effaced at or near genal angles.
11. Posterior cephalic border furrow turns forwards before becoming effaced [10:1]. 0: absent, effacement occurs well before genal angle, 1: present.
12. Posterior cephalic border furrow arches forwards well inside the genal angles [10:0]. 0: absent, cephalic border furrow closely follows the posterolateral margin of the cephalon, 1: present.
13. Shape of the posterior cephalic border furrow. 0: furrow of approximately even width along entire length, 1: furrow gradually expands laterally, 2: furrow expands laterally then contracts, resulting in an ovate appearance.
14. Anterior margin of cephalon transverse axially. 0: absent, 1: present.
15. Shape of the anterolateral corners of cephalon. 0: evenly rounded, 1: angular.
16. Expansion of the lateral margins of cephalon. 0: absent, maximum cephalic width at posterior margin, 1: present, maximum cephalic width anterior to the posterior margin.
17. Anterior arch of the cephalon, in anterior view. 0: absent, 1: present.
18. Length of cephalon (sag.) as proportion of maximum width of cephalon (trans.). 0: shorter (0.35–0.45), 1: approximately half as long as wide (0.45–0.55), 2: slightly longer (0.55–0.65), 3: moderately longer (0.65–0.75), 4: much longer (>0.75).
19. Position of facial sutures on dorsal surface. 0: marginal or sutures absent, 1: sutures remain on cephalic border, 2: sutures reach border furrow but do not cross it, 3: sutures cross border furrow onto cheek.
20. Facial sutures sinuous. 0: absent, 1: present.
21. Position of facial sutures at the genal angles result in posteriorly projecting posterolateral corners of the cranium. 0: absent, 1: present.
22. Length of glabella (sag., excluding occipital ring) as proportion of length of cephalon (sag.). 0: very short (≤ 0.49), 1: short (0.5–0.6), 2: long (0.61–0.71), 3: very long (≥ 0.72).
23. Width of glabella (trans.) at base as proportion of maximum width of cephalon (trans.). 0: very narrow (≤ 0.25), 1: narrow (0.251–0.34), 2: wide (0.341–0.43), 3: very wide (≥ 0.431).
24. Width of glabella (trans.) at base as proportion of length of glabella (sag., excluding occipital ring). 0: narrow (≤ 0.94), 1: medium (0.95–1.09), 2: wide (≥ 1.1).
25. Shape of glabella. 0: strongly tapers forward, 1: approximately parallel-sided, 2: expands anteriorly.
26. Shape of anterior termination of glabella. 0: rounded, 1: somewhat blunt, 2: square.
27. Number of visible pairs of lateral glabellar furrows. 0: 0, 1: 1, 2: 2, 3: 3, 4: 4.
28. Strength of posterior lateral glabellar furrows [27: 1–4]. 0: strongly defined, 1: weakly defined.
29. Lateral glabellar furrows defined by lack of sculpture only [27: 1–4]. 0: absent, 1: present.
30. Condition of the preglabellar furrow. 0: present, 1: less firmly incised than axial furrows, 2: completely effaced.
31. Glabella defined anteriorly by change in convexity from preglabellar field. 0: absent, 1: present.
32. Condition of axial furrows. 0: present, 1: effaced anteriorly, 2: entirely effaced.
33. Lateral glabellar furrows indicated on internal moulds by shallow rounded depressions. 0: absent, 1: present.
34. S1 furrows bifurcate adaxially on external surface. 0: absent, 1: present.
35. Shape of S1 furrows. 0: straight or simply curved, 1: recurved backwards and then inwards.
36. Length of S2 furrows. 0: short (shorter than sagittal length of L4), 1: longer.
37. Shape of S2 furrows. 0: transverse, 1: oblique backwards.
38. Length of S3 furrows. 0: pits or very short slits, 1: long and deep furrows.
39. Length of occipital ring (sag., from midpoint of SO) as a proportion of the length of the glabella (sag., excl. occipital ring). 0: short (≤ 0.2), 1: medium (0.21–0.37), 2: long (≥ 0.38).
40. Broad-based posteriorly directed occipital spine. 0: absent, 1: present.
41. Occipital node. 0: absent, 1: present.

42. Pair of pits along posterior edge of occipital furrow. 0: absent (e.g. Pl. 1, figs 1, 7), 1: present (e.g. Text-fig. 1A; Pl. 4, fig. 9).
43. Eye ridges. 0: absent, 1: present only on internal moulds, 2: present on external surface.
44. Form of eye ridges [43: 1–2]. 0: highly curved, 1: more or less straight.
45. Direction of eye ridges [43: 1–2]. 0: eye-ridges run backwards and outwards obliquely, 1: eye-ridges run transversely or anteriorly and transversely.
46. Eye ridges project anteriorly before turning backwards [43: 1–2]. 0: absent, 1: present.
47. Nature of insertion of eye ridges adaxially [43: 1–2]. 0: into glabella, interrupting axial furrows with prominent raised ridges, 1: into axial furrows, axial furrows not interrupted by eye ridges.
48. Caecal network present on anterior genae. 0: absent, 1: present only on internal moulds, 2: present on external surface.
49. Prominent (compared to caecal network) reticulate sculpture present on genae. 0: absent, 1: present.
50. Genal node, caused by thickened eye ridge just abaxial to anterior axial furrows [43: 1–2]. 0: absent, 1: present.
51. Anterior branch of eye ridge runs around front of glabella (parafrenal band) [43: 1–2]. 0: absent, 1: present.
52. Presence of anterior genal ridges, other than eye ridges. 0: absent, 1: present.
53. Elevation of preglabellar field [55:1]. 0: confluent with cheeks, 1: depressed relative to cheeks, in anterior view, 2: raised to form preglabellar boss.
54. Preglabellar field crossed by furrow, other than border furrows [55:1]. 0: absent, 1: weak furrows present, 2: clear furrows present.
55. Preglabellar field. 0: absent, 1: present.
56. Length of preglabellar field (sag.) as proportion of length of preglabellar area (sag.) [55:1]. 0: very narrow (≤ 0.3), 1: narrow (0.31–0.45), 2: approximately equal (0.46–0.6), 3: wide (0.61–0.75), 4: very wide (≥ 0.76).
57. Nature of preglabellar boss [53: 2]. 0: confluent with anterior border, 1: separated from border by border furrow.
58. Tuberculate or spinose sculpture on cephalon. 0: absent, 1: present.
59. Density of tubercles [58: 1]. 0: sparse, 1: medium, 2: dense.
60. Pustulose sculpture on cephalon. 0: absent, 1: present.
61. Punctate sculpture on cephalon. 0: absent, 1: present.
62. Convexity of genae. 0: downsloping laterally (maximum height of genae at axial furrows), 1: independently convex (maximum height of genae abaxial to axial furrows).
63. Degree of genal convexity [62:1]. 0: weakly convex, 1: elevated more or less to the level of glabella, 2: elevated clearly above the level of the glabella.
64. Genal spines. 0: absent, 1: present.
65. Angle of insertion of genal spines [64:1]. 0: Genal spines directed backwards approximately parallel to the axis, 1: Genal spines directed obliquely outwards and backwards.
66. Length of genal spines as proportion of length of cephalon [64:1]. 0: short (≤ 0.45), 1: medium (0.46–0.65), 2: long (≥ 0.65).
67. Genal spines gently sinuous in shape [64:1]. 0: absent, 1: present.
68. Paradoxal line. 0: absent, 1: present.
69. Shape of paradoxal line [68:1]. 0: extends evenly beyond border, 1: extends posteromedially to form plectrum.
70. Hypostomal condition. 0: conterminant, 1: natant.
71. Shape of hypostome (see Fortey 1990). 0: primitive shape, 1: fused to rostral plate, 2: generalized ptychoparioid form.
72. Length of cephalon (sag.) as a proportion of length of entire exoskeleton (sag.). 0: cephalon proportionately small (≤ 0.3), 1: cephalon of intermediate proportional size (0.31–0.4), 2: cephalon proportionately large (≥ 0.41).
73. Number of thoracic segments. 0: less than 8, 1: 8, 2: 13, 3: 14, 4: 15, 5: 17, 6: 18, 7: 20 or greater,
74. Nature of thoracic pleural terminations. 0: blunt, faceted terminations, 1: oblique falcate points, 2: extended to form spines.
75. Length of thoracic pleural spines [74:2]. 0: short, 1: long.
76. Width of thoracic pleural furrows (exsag.). 0: wide (approx. half sag. pleural length or greater), 1: narrow (less than half pleural length). Note: pleural-furrow width is very difficult to measure, because the boundaries of the furrows are often indistinct. This character was therefore coded conservatively, and the two states used are highly distinct in the taxa under consideration.
77. Direction of thoracic pleural furrows. 0: transverse, 1: oblique.
78. Shape of thoracic pleural furrows. 0: straight, 1: highly curved.
79. Width of thoracic axis (trans.) compared to width of whole segment (trans., excluding pleural spines) on anterior segments. 0: narrow (≤ 0.25), 1: medium (0.26–0.33), 2: wide (0.34–0.43), 3: very wide (≥ 0.44).
80. Macropleural spines on thoracic segments. 0: absent, 1: present.

81. Nature of pleural geniculations. 0: smoothly rounded, 1: prominently raised, with tubercles.
82. Length of pygidium (sag.) as a proportion of length of entire exoskeleton (sag.). 0: pygidium proportionately small (≤ 0.05), 1: pygidium of intermediate proportional size (0.06–0.1), 2: pygidium proportionately large (≥ 0.11).
83. Length of pygidial post-axial field. 0: post-axial field absent, 1: short (approx. equal to border width) post-axial field, 2: longer.
84. Width of pygidial axis (trans., anteriorly) as proportion of maximum width of pygidium (trans.). 0: axis narrow (≤ 0.34), 1: axis of intermediate relative width (0.35–0.49), 2: axis broad (≥ 0.5).
85. Number of segments (excluding terminal piece) in pygidial axis. 0: 2, 1: 3, 2: 4, 3: 5, 4: 6.
86. Interpleural furrows on pygidium. 0: absent, 1: present.
87. Furrows on postaxial field of pygidium. 0: absent, 1: present.
88. Form of pygidial pleural furrows. 0: highly curved and very oblique backwards, 1: much less curved and run more directly transversely.
89. Anterior border constricted due to encroachment of the glabella. 0: absent, 1: present.
90. S1 lateral glabellar furrows transglabellar. 0: absent, 1: present.
91. Presence of palpebral lobes on genae. 0: absent, 1: present.
93. Palpebral lobes wider (trans.) than and elevated above eye ridges. 0: absent, 1: present.
93. Eye ridges divided from palpebral lobes. 0: absent, 1: present.
94. Width (sag.) of eye ridges. 0: thread-like, 1: wider.
95. Thoracic axial furrows zig-zag in shape. 0: absent, 1: present.
96. Pygidial border zonate. 0: absent, 1: present.
97. Broad form of pygidium. 0: semicircular fused plate, 1: tiny pauci-segmented elongate or circular plate.

Synapomorphy scheme for ingroup nodes of the cladogram shown in Text-figure 3

Character numbers, reconstructed changes, number of steps and character consistency indices are shown for each apomorphy. Characters and character states numbered as in the previous section and Table 2.

Node 1. 20: 1>0 (1,0.167), 22: 3>2 (1,0.273), 75: 0>1 (1,0.200), 84: 2>1 (1,0.286), 85: 0>1 (1,0.444), 93: 0>1 (1,1.000), 94: 1>0 (1,1.000).

Node 2 (Atopidae). 19: 3>1 (2,0.158), 45: 0>1 (1,0.250), 46: 0>1 (1,1.000), 48: 0>2 (1,0.286), 49: 0>1 (1,0.250), 55: 1>0 (1,0.250), 62: 0>1 (1,0.250), 80: 0>1 (1,0.333), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).

Node 3. 5: 1>0 (1,0.333), 14: 0>1 (1,0.200), 22: 2>3 (1,0.273).

Node 4 (*Atops*). 6: 0>1 (1,0.111), 13: 0>1 (1,0.200), 60: 0>1 (1,0.091).

Node 5. 22: 2>1 (1,0.273), 24: 0>1 (1,0.167), 25: 1>0 (1,0.667), 28: 0>1 (1,0.125), 38: 1>0 (1,1.000), 47: 0>1 (1,1.000), 66: 2>0 (1,0.222), 77: 0>1 (1,0.333), 83: 0>1 (1,0.667), 84: 1>0 (1,0.286).

Node 6. 2: 0>1 (1,1.000), 5: 1>0 (1,0.333), 20: 0>1 (1,0.167), 39: 1>0 (1,0.400), 51: 1>0 (1,0.500), 69: 0>1 (1,0.500), 73: 5>2 (3,0.538), 82: 1>2 (1,0.400), 85: 1>2 (1,0.444).

Node 7. 48: 0>2 (1,0.286), 74: 2>1 (1,0.667), 85: 2>3 (1,0.444), 88: 0>1 (1,0.500).

Node 8. 13: 0>2 (1,0.200), 39: 0>1 (1,0.400), 42: 0>1 (1,0.250), 60: 0>1 (1,0.091), 66: 0>1 (1,0.222), 73: 2>3 (1,0.538), 77: 1>0 (1,0.333), 86: 1>0 (1,0.500).

Node 9 (Conocoryphidae). 17: 0>1 (1,0.500), 19: 3>2 (1,0.158), 20: 1>0 (1,0.167), 27: 4>3 (1,0.250), 43: 2>1 (1,0.200), 48: 2>1 (1,0.286), 50: 0>1 (1,0.333), 53: 0>1 (1,0.333), 58: 0>1 (1,0.111), 62: 0>1 (1,0.250), 85: 3>2 (1,0.444), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).

Node 10 (*Bailiaspis*). 1: 0>2 (2,0.200), 13: 2>0 (1,0.200), 14: 0>1 (1,0.200), 18: 1>2 (1,0.190), 20: 0>1 (1,0.167), 28: 1>0 (1,0.125), 50: 1>0 (1,0.333), 56: 2>1 (1,0.308).

Node 11. 5: 0>1 (1,0.111), 15: 0>1 (1,0.500), 18: 2>1 (1,0.190), 19: 2>1 (1,0.158), 20: 1>0 (1,0.167), 25: 0>1 (1,0.167), 44: 0>1 (1,0.250), 45: 0>1 (1,0.250).

Node 12 (*Tchaispis*). 23: 1>0 (1,0.231), 24: 1>0 (1,0.167), 36: 1>0 (1,0.333), 53: 0>2 (2,0.333), 58: 0>1 (1,0.333).

Node 13. 3: 0>1 (1,0.500), 13: 2>0 (1,0.200), 19: 2>1 (1,0.158), 26: 0>1 (1,0.167), 28: 1>0 (1,0.125), 53: 1>2 (1,0.333), 54: 0>2 (1,0.333), 56: 2>3 (1,0.308), 59: 2>1 (1,0.250), 63: 0>1 (1,0.333), 66: 1>2 (1,0.222), 82: 2>1 (1,0.400).

Node 14. 26: 1>2 (1,0.167), 59: 1>2 (1,0.250), 63: 1>2 (1,0.333).

Node 15. 6: 0>1 (1,0.111), 18: 1> (1,0.190), 43: 1>0 (1,0.200).

Node 16. 21: 0>1 (1,1.000), 24: 1>2 (1,0.167).

Node 17. 13: 0>2 (1,0.200), 52: 0>1 (1,1.000), 56: 3>4 (1,0.308), 73: 3>4 (1,0.538).

Node 18 (*Elyx*). 3: 1>0 (1,0.500), 4: 0>1 (1,0.250), 14: 0>1 (1,0.200), 44: 0>1 (1,0.250), 50: 1>0 (1,0.333), 57: 1>0 (1,1.000).

- Node 19. 22: 1>3 (2,0.273), 25: 0>2 (1,0.667), 27: 4>2 (2,0.250), 55: 1>0 (1,0.250), 70: 1>0 (1,0.500), 71: 2>1 (1,1.000), 73: 2>0 (2,0.538), 76: 0>1 (1,0.333), 79: 1>2 (1,0.429), 96: 0>1 (1,0.500).
- Node 20 (*Acontheinae*). 5: 0>1 (1,0.333), 18: 1>3 (2,0.190), 20: 1>0 (1,0.167), 24: 1>0 (1,0.167), 27: 2>1 (1,0.250), 36: 1>0 (1,0.333), 72: 1>2 (1,0.667), 74: 2>0 (1,0.667), 89: 0>1 (1,0.500), 95: 0>1 (1,0.500).
- Node 21. 18: 3>4 (1,0.190), 19: 3>0 (3,0.158), 23: 1>0 (1,0.231), 30: 0>2 (1,0.667), 41: 1>0 (1,0.143), 43: 2>0 (1,0.200), 61: 0>1 (1,0.333), 64: 1>0 (1,0.500), 65: 0>1 (1,0.250), 83: 1>0 (1,0.667), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).
- Node 22 (*Hartshillini*). 8: 0>2 (1,0.333), 9: 0>2 (1,0.500), 10: 0>1 (1,0.333), 27: 1>0 (1,0.250), 31: 1>0 (1,1.000), 32: 0>2 (1,0.500), 73: 0>1 (1,0.538), 78: 0>1 (1,1.000), 84: 0>1 (1,0.286), 85: 2>0 (2,0.444).
- Node 23 (*Hartshillia*). 40: 0>1 (1,0.500), 88: 0>1 (1,0.500), 95: 1>0 (1,0.500), 96: 1>0 (1,0.500).
- Node 24. 1: 0>2 (2,0.200), 8: 0>1 (1,0.333), 9: 0>1 (1,0.500), 12: 0>1 (1,0.500), 13: 0>1 (1,0.200), 18: 1>2 (1,0.190), 30: 0>1 (1,0.667), 33: 0>1 (1,0.333), 37: 1>0 (1,1.000), 44: 0>1 (1,0.250), 65: 0>1 (1,0.250), 82: 1>0 (1,0.400), 83: 1>2 (1,0.667), 87: 0>1 (1,1.000).
- Node 25 (*Holocephalidae*). 11: 1>0 (1,0.500), 19: 3>1 (2,0.168), 27: 4>3 (1,0.250), 49: 0>1 (1,0.250), 73: 5>6 (1,0.333), 76: 0>1 (1,0.333), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).
- Node 26. 7: 0>1 (1,1.00), 9: 1>0 (1,0.500), 13: 1>0 (1,0.200), 18: 2>1 (1,0.190), 22: 1>0 (1,0.273), 23: 1>0 (1,0.231), 28: 1>0 (1,0.125), 33: 1>0 (1,0.333), 42: 0>1 (1,0.250), 48: 0>2 (1,0.286), 53: 0>1 (1,0.333), 56: 2>3 (1,0.308), 81: 0>1 (1,1.000).
- Node 27 (*Dasometopus*). 1: 2>0 (2,0.200), 12: 1>0 (1,0.500), 34: 0>1 (1,1.000), 39: 1>2 (1,0.400), 56: 3>4 (1,0.308), 58: 0>1 (1,0.111), 80: 0>1 (1,0.333), 84: 0>1 (1,0.286), 85: 1>0 (1,0.444).
- Node 28. 18: 1>0 (1,0.190), 59: 2>0 (2,0.250), 60: 0>1 (1,0.091), 68: 0>1 (1,0.333).
- Node 29 (*Meneviella*). 8: 1>0 (1,0.333), 72: 1>0 (1,0.667), 73: 6>7 (1,0.538).
- Node 30. 26: 0>1 (1,0.167), 29: 0>1 (1,0.333), 32: 0>1 (1,0.500), 39: 1>0 (1,0.400), 41: 1>0 (1,0.143), 43: 2>0 (1,0.200), 67: 0>1 (1,0.500), 75: 1>0 (1,0.200).
- Node 31. 8: 1>2 (1,0.333), 10: 0>1 (1,0.333), 18: 2>3 (1,0.190), 23: 1>2 (1,0.231), 61: 0>1 (1,0.333), 79: 1>0 (1,0.429).
- Node 32. 13: 1>0 (1,0.200), 24: 1>0 (1,0.167), 27: 3>0 (3,0.250), 32: 1>0 (1,0.500), 33: 1>0 (1,0.333), 66: 0>2 (1,0.222).

Institutional abbreviations

BMNH, Department of Palaeontology, The Natural History Museum, London, UK.

BUGM, Department of Earth Sciences, University of Bristol, UK.

CSGM, Central Siberian Geological Museum, Novosibirsk, Russia.

GIN, Museum of the Geological Institute, Russian Academy of Sciences, Moscow, Russia.

MMG, Museum of the Ministry of Geology, Tashkent, Uzbekistan.

NMW, National Museum of Wales, Geology Department, Cardiff, UK.

ROM, Department of Invertebrate Paleontology, Royal Ontario Museum, Toronto, Canada.