

Chapter 20

A synopsis of Ordovician trilobite distribution and diversity

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Abstract: Ordovician trilobites are reviewed based on a new species-level relational database. The stratigraphical ranges of all 56 families with occurrences in the Ordovician are documented and the content, phylogenetic status, diversity and Ordovician distribution by major palaeocontinent/terrane are discussed. Aspects of higher classification are also dealt with. Global sampling is heavily biased towards a small number of highly sampled areas. Much of the world has a very limited record of formally named trilobite species. Even within heavily sampled units, sampling is patchy by environment and time. Genus endemism was at a peak in Laurentia, Baltic, and Avalonia in the Floian and declined more-or-less steadily through the remainder of the Ordovician.

Ordovician trilobite distribution was addressed in a classic paper by Whittington & Hughes (1972). This work featured one of the earliest applications of nonmetric multidimensional scaling in palaeontology. The faunal provinces they discriminated – the Laurentian Bathyrurid province, the Baltic Asaphid province and the Gondwanan *Selenopeltis* and *Asaphopsis* provinces – remain valid today. A follow-up work on the Tremadoc (Whittington & Hughes 1974) was marred by the global miscorrelation with the upper Cambrian prevalent at the time. Since this work, there have been a number of excellent continental- or regional-scale synthetic studies (e.g. Fortey & Barnes 1977; Shaw & Fortey 1977; Fortey & Cocks 1988; Zhou *et al.* 2007, 2009; Zhou & Zhen 2008; Benedetto *et al.* 2009; Harper *et al.* 2009). Trilobites provided some of the Ordovician data for a magisterial series of papers by Cocks & Torsvik (2002, 2005, 2007, 2011); Torsvik & Cocks (2004, 2009; also Cocks & Fortey 2009). Probably the most important recent paper on Ordovician trilobite distributions is the excellent global review by Fortey & Cocks (2003). Despite these advances, the paper by Whittington & Hughes (1972) remains the only attempt ever published at a global numerical synthesis of Ordovician trilobite biogeography.

Serious progress in resolving Ordovician biogeographical problems will require the application of component-based cladistic biogeography (see, e.g. Ebach & Edgecombe (2001) for a review using trilobites). For example, there has been a great deal of debate over the derivation and position through time of the Argentine Precordillera Terrane (see Benedetto *et al.* (2009) for a review). Trilobite data have been applied to the problem, but thus far only in a phenetic way based on the presence of higher taxa (genera and subfamilies). There is a clear influx of Gondwanan taxa in the Darriwilian and Sandbian, while the bulk of the fauna remains of Laurentian aspect. Much more information could be gleaned if more species-level phylogenetic analyses were available (see Chatterton *et al.* (1997) and Edgecombe *et al.* (1997, 1998) for those that have been carried out). Separate undescribed species from the Darriwilian Table Cove Formation of western Newfoundland (Edgecombe *et al.* 1999, p. 1144) have been identified as putative sister species of the cheirurid *Macrogrammus rafi* Edgecombe, Chatterton, Vaccari & Waisfeld, 1999, and the telephiniid *Telephina problematica* Chatterton, Edgecombe, Vaccari & Waisfeld, 1999, from the Darriwilian and Sandbian of the Precordillera. If these and similar relationships were confirmed in a modern analytical framework, the resulting phylogenies could formally test hypotheses of isolation v. faunal exchange between the terrane and Laurentia. There is excellent potential for multiple tests and corroboration as many separate Darriwilian–Sandbian groups have been described from the Precordillera on the basis of rich silicified faunas. Similar work

could contribute much to unravelling the histories of other complex areas (e.g. the Kazakh terranes) beyond simple occurrence data.

That said, perusal of the family-level summaries presented below will demonstrate that modern phylogenetic work is not widely available for Ordovician trilobites. Many large and important families have received no analysis whatsoever, and even those taxa (such as encrinurids and dimeropygids) for which multiple studies have appeared still lack anything approaching a phylogenetic hypothesis of their overall structure. There is much work to be done.

Given that, it seems there may be value in a fresh look at global distributional data, taking into account the advances in understanding of the last 40 years. I have completed a hierarchical taxonomic database of all trilobite species, which can form the foundation for new analyses. The database at time of writing includes 21,161 valid trilobite species, of which 5460 are Ordovician. Initially (in collaboration with A. W. Owen and R. A. Fortey), I attempted ordination and clustering analyses similar in scope to those of Whittington & Hughes (1972). It soon became apparent, however, that sampling problems (see below) made analyses using only formally named species less than satisfactory. The record from many parts of the world and various times during the Ordovician is much sparser than one might expect. Much of the diversity in these cases tends to be reported in open nomenclature, or sometimes (usually incorrectly) as established species from other regions or continents. I have added functionality to the database to incorporate these data, but have only begun to compile the necessary information for the Ordovician.

In anticipation of such analyses, here I survey what is known of the diversity and distribution of Ordovician trilobites, mostly on the basis of their formally named species. The goals of the work are to present the first species-level assessments of global and continental/terrane-level taxonomic richness and endemism, and to document the diversity history, phylogenetic status and distribution of each family present in the Ordovician. I also take the opportunity to expand on several phylogenetic questions, mainly stemming from a recently published revised classification of trilobites (Adrain 2011) and in anticipation of preparation of further revised volumes of the *Treatise on Invertebrate Paleontology, Part O (Trilobita, Revised)*.

Summed diversity, sampling and endemism

As classified below, there are 56 families of Ordovician trilobites, and the stratigraphical range of each is shown in Figure 20.1. Total global species richness is plotted in Figure 20.2, and divided by palaeocontinent/terrane. No attempt was made to account for

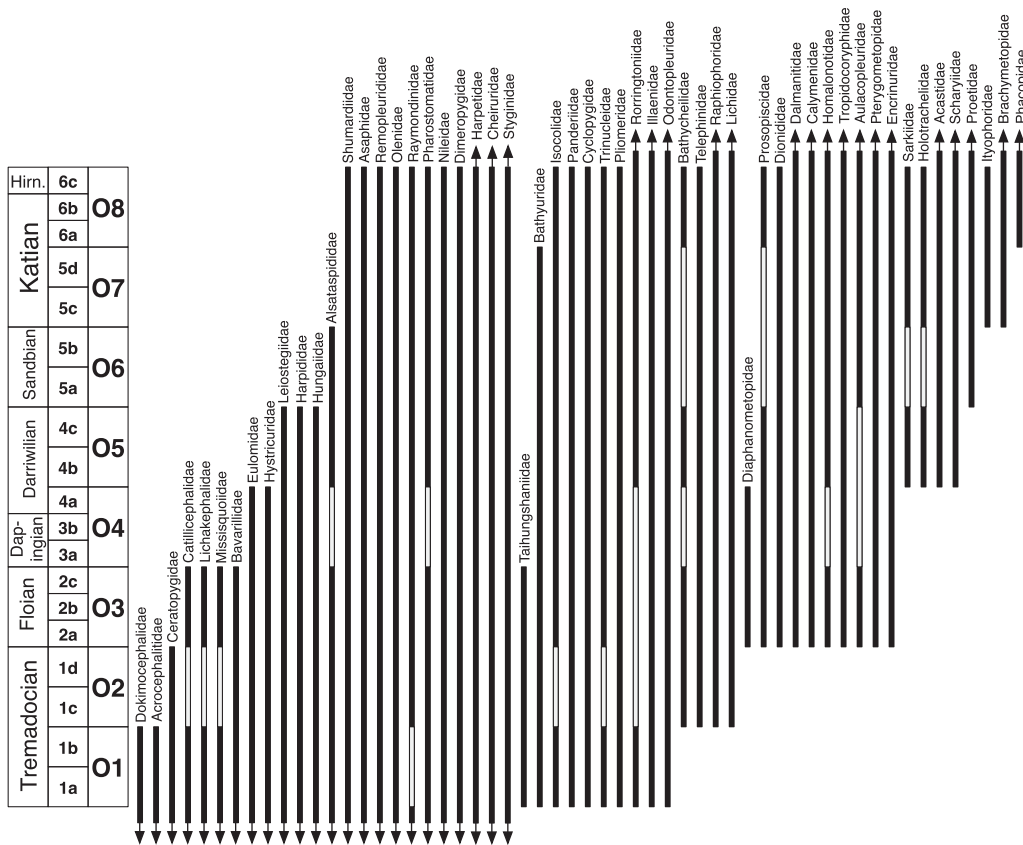


Fig. 20.1. Stratigraphical ranges of all Ordovician trilobite families as classified herein. Arrows indicate range continuations. White segments are sampling gaps. Trilobite species age was recorded using time slices O1–O8 (right column on left). The middle column shows the time slices of Webby *et al.* (2004) and the left column the global stages of the Ordovician ('Hirn', Hirnantian). Note that the Hirnantian (slice 6c of Webby *et al.* 2004) was not discriminated in this compilation and also that the time slices differ slightly from the nine used by Adrain & Westrop (2000) and Adrain *et al.* (2004) in that O7–O9 in those works are replaced by only two intervals, O7 and O8 herein, owing to lack of global sampling resolution, and a desire to make the intervals more broadly time equivalent. O1–O6 are identical to those used in the previous works.

large-scale sampling effects – the time slices are not of even duration, for example, nor is the rock record available for sampling evenly distributed among them. Hence the summed trajectory must be interpreted cautiously. The most striking feature of Figure 20.2 is the gross disparity in sampling levels between different palaeocontinents. While there are 5460 valid species of Ordovician trilobites, they are heavily concentrated in only a few well-sampled parts of the world (North America, western Europe, and to a certain extent China). Some large palaeocontinents with abundant Ordovician outcrop (e.g. Siberia) have an incredibly sparse record of formally named species. However,

the fourth largest source of data is Avalonia, which was geographically tiny. Much of our foundational knowledge of Ordovician trilobite systematics is based on study of Avalonian faunas. This is comparable to gaining an understanding of the modern world through focus on the South Island of New Zealand. On one hand, Perunica, which is mostly the record from the Prague Basin, is similarly thoroughly documented. On the other hand, almost nothing is known of, for example, Middle and Upper Ordovician South American faunas – there are only two species of trilobites described from the South American Katian! Disparities like these emphasize the need to take account of open nomenclature reports and at least initially to use presence/absence datasets in global analyses.

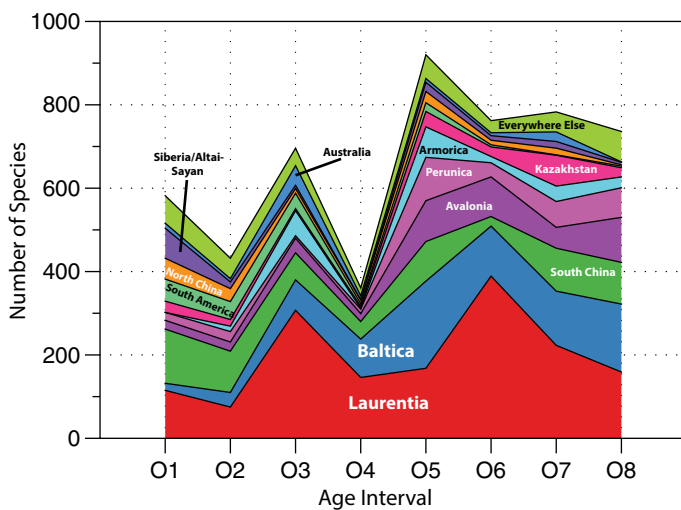


Fig. 20.2. Trilobite species richness (y axis) by major time slice and palaeocontinent or region. 'Kazakhstan' is all of the Kazakh terranes summed. 'South America' is South American Gondwana. 'Australia' is Australian Gondwana. Time slices are as defined in Figure 20.1.

Even in data-rich palaeocontinents, there is often extreme patchiness in sampling across an environmental gradient. Floian Laurentian species, for example, comprise the second largest single amount in Figure 20.2, yet they are overwhelmingly dominated by relatively shallow water bathyrurid biofacies taxa. Virtually the only exception is the deeper-water autochthonous biofacies from the East Svalbard Terrane documented by Fortey (1974b, 1975, 1980). The same is true of the Dapingian and lower Darriwilian, augmented only by some illaenid–cheirurid associations from East Svalbard and the monographic spike of Whittington (1963), who described a diverse marginal build-up fauna from western Newfoundland.

It is now possible to calculate endemism with some precision, and this is less affected by sampling disparities as it depends only upon presence/absence. Proportional genus endemism by time slice and palaeocontinent is shown in Figure 20.3. Definition of sampling units will, however, affect the result. Perunica and Armorica were nearby regions of core high-latitude Gondwana, for example, and so separating them will reduce their endemism because they share a high proportion of their genera. Nevertheless, the plot shows a fairly strong and interpretable pattern, particularly for those units that were isolated for much of the Ordovician. In Laurentia, Baltica and Avalonia, there is a clear Floian peak in

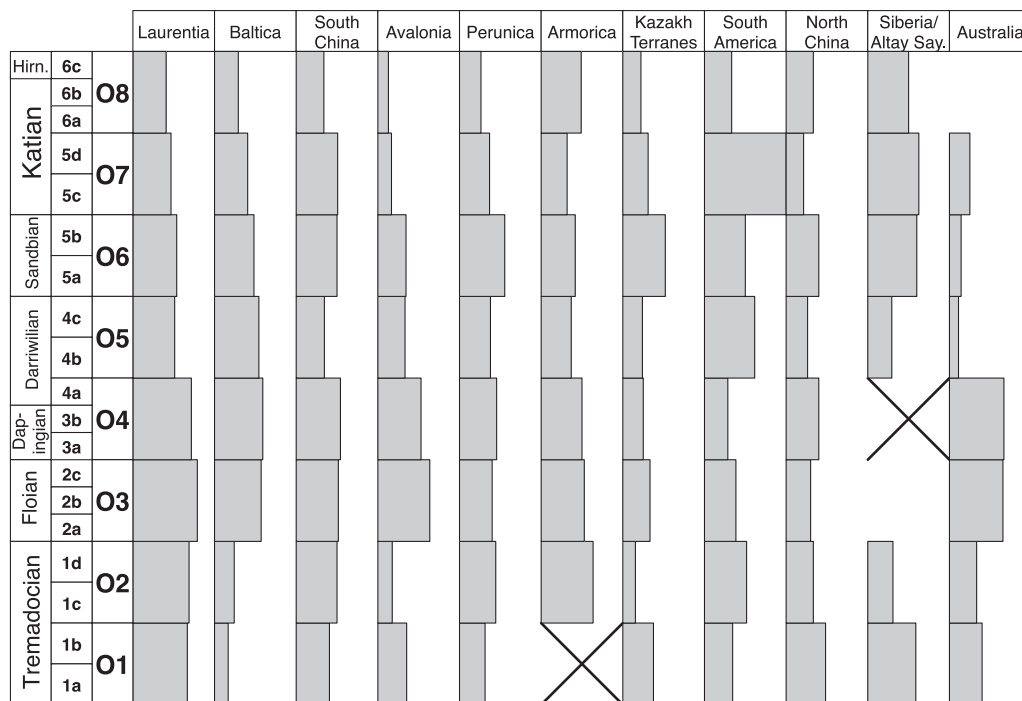


Fig. 20.3. Proportional genus endemism by time slice for major palaeocontinents, regions and terranes through the Ordovician. The width of each column represents 100%. The proportion of the width filled with grey indicates the proportion of genera occurring in that geographical unit during that time slice that is restricted to that unit in that time slice, based on the distribution of formally named species. Cells with a large X entirely lack data, whereas those that are blank indicate a complete lack of endemics. Left-hand columns are as in Figure 20.1.

endemism, which is gradually eroded through the remainder of the Ordovician with the closure of Iapetus.

Family-level histories

Assignment to orders follows Adrain (2011). Each history attempts to summarize the genus and species diversity of the taxon during the Ordovician, its diversity history, and its distribution through the major time slices and across major palaeocontinents (represented graphically). An attempt is also made to summarize the current subfamily-level classification, to assess the phylogenetic status of major subgroups and, where relevant, the family itself, and to cite any modern phylogenetic work that has been published. By 'modern' I refer to quantitative analyses based on explicit data. Within trilobites, almost all such studies employ parsimony, although there is at least one published work using Bayesian analysis (Pollitt *et al.* 2005). The pace of quantitative phylogenetic work is accelerating, but the overwhelming majority of trilobite taxonomy remains premodern, with taxa either explicitly conceived of as paraphyletic or whose phylogenetic status has never been addressed or tested.

Order Corynexochida Kobayashi, 1935a

Family Illaenidae Hawle & Corda, 1847

Illaenidae includes 24 valid genera with occurrence during the Ordovician, and 223 currently accepted Ordovician species (Fig. 20.4). Its monophyly is generally agreed, with the exception of the question of the status and affinity of Panderiidae (see below). The lower Tremadocian record of the family is dubious, as *Illaeus? berkutensis* Lisogor, 1977, from the Malvi Karatau, and particularly *Illaeus? priscus* Rozova in Rozova *et al.*, 1985, from Salair, are very poorly known and may not belong to the family. However, the upper Tremadocian *I. hinomotoensis* Kobayashi, 1934, from North China (South Korea and China; see Zhou & Fortey 1986) is definitely a member of the family. The earliest Laurentian species is *I. weaveri* (Reed in Gardiner & Reynolds 1909) from probably latest Floian rocks in western Ireland (see Adrain & Fortey 1997). The earliest records are tropical, but by

the Darrivilian the family is known from southern Gondwana and thereafter had a global distribution until the end of the Ordovician, although with a considerable degree of generic endemism.

There are no modern hypotheses of the overall phylogenetic structure of the family, but Amati & Westrop (2004) have presented a detailed cladistic analysis of *Thaleops* Conrad, 1843 and (Carlucci *et al.* 2012) of *Bumastoides* Whittington, 1954. There have been few attempts to recognize major natural groupings even in narrative terms (but see, for example, important work such as Jaanusson 1954) and no subfamilies have been recognized, with the exception of those workers who have included Panderiidae within Illaenidae, grouping the traditional illaenids in a nominal subfamily (see below).

Illaenidae survived the end-Ordovician with *Stenopareia* Holm in Schmidt, 1886 crossing the boundary, but was a minor component of Silurian faunas, with three genera and 26 species recognized. The youngest known species is the Prídolían *Quadra-tillaenus tewoensis* Wu, 1987, from North China.

Family Panderiidae Bruton, 1968a

Bruton (1968a) erected Panderiinae (Fig. 20.5) as a subfamily of Illaenidae, and it has been treated as such by some subsequent workers (e.g. Lane & Thomas 1983) but as a separate family by others (e.g. Fortey 1997a; Ebbestad 1999). Bruton (1968a) included only *Panderia* Volborth, 1863, but he also erected *Ottenbyaspis*, which he considered of uncertain affinities. This taxon has subsequently been assigned to Panderiidae (Ebbestad 1999; Mergl 2006). Mergl (1994) considered that *Hemibarrandia* Prantl & Přibyl, 1949 was related to *Ottenbyaspis*. Finally, the somewhat obscure *Pogrebovites* Balašova, 1976, which has *Niobe volborthi* Schmidt, 1907, as its type, seems possibly to belong. *Panderia* itself is mostly Baltic, but occurs also in Sibumasu, South China, Taurides, Kazakhstan, Armorica and Avalonia. The group (if it is a group as thus conceived) disappeared at the end-Ordovician. No phylogenetic analyses have been published.

Family Styginidae Vogdes, 1890

Opinion on the classification of Styginidae (Fig. 20.6) has long varied. The history of classification was thoroughly reviewed by

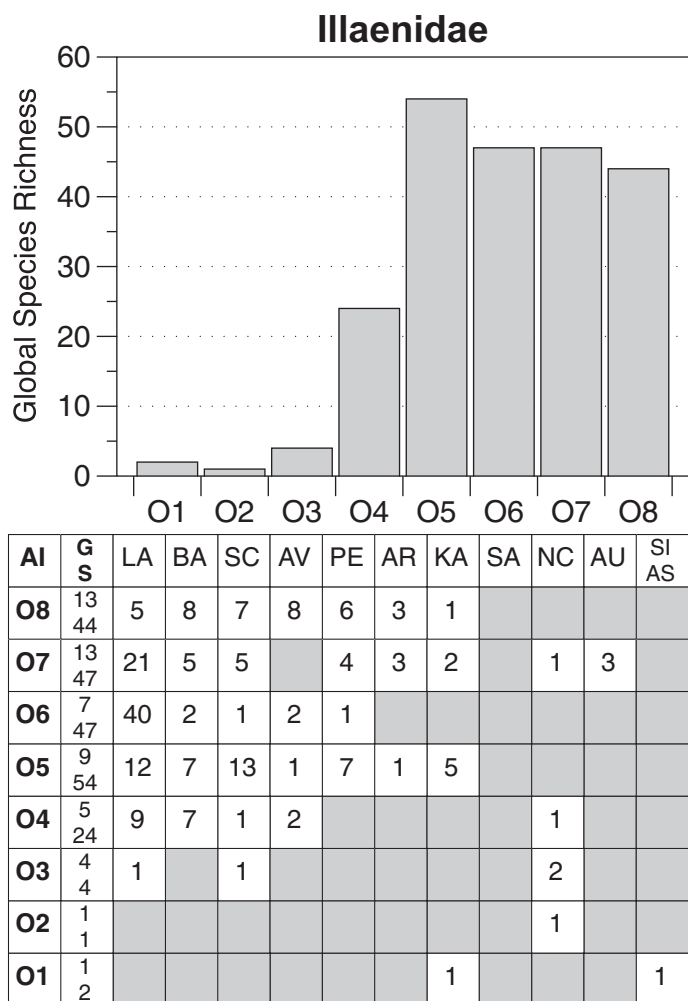


Fig. 20.4. Global taxonomic richness of the Family Illaenidae during the Ordovician. Top panel: summed global species richness by major time slice (AI, age interval). Bottom panel: genus (top numbers) and species (bottom numbers) richness (left column) and species richness by time slice and major palaeocontinent, region, or terrane. Time slices are as defined in Figure 20.1. Listed species do not necessarily sum to the global total for each time slice as many small terranes and areas are not depicted. LA, Laurentia; BA, Baltica; SC, South China; AV, Avalonia; PE, Perunica; AR, Armorica and Iberica; KA, Kazakh terranes; SA, South America; NC, North China; AU, Australia; SI, Siberia; AS, Altai-Sayan.

Lane & Thomas (1983). Many workers have and continue to recognize a Family Scutelluidae, which includes mainly species with well-impressed furrows and often prominent sculpture. In this view, Styginidae is restricted to mostly effaced Ordovician taxa, as explicitly advocated by Holloway (2007). The problem with this is that it seems highly unlikely that such a restricted Styginidae is monophyletic, and almost certain that the 'Scutelluidae' nest within its structure and create paraphyly. Holloway (2007, p. 2) did not discuss the phylogenetic status of his restricted Styginidae, and the only justification of separation of Scutelluidae was: 'I regard the Scutelluidae as an independent family because it encompasses a rather wide range of morphological diversity, suggesting that it includes several phylogenetic lineages that could in the future be recognized as subfamilies'. Styginidae is an unusual taxon in that its history proceeds from plesiomorphic effaced taxa to incised and sculptured taxa, and (possibly iteratively) to secondarily effaced forms. Broadly speaking, these are 'styginids', 'scutelluids' and 'bumastines', respectively, but separating them as separate family-group taxa risks recognizing two paraphyletic and one possibly polyphyletic group. For these reasons (which are similar to those of Lane & Thomas 1983), in the present

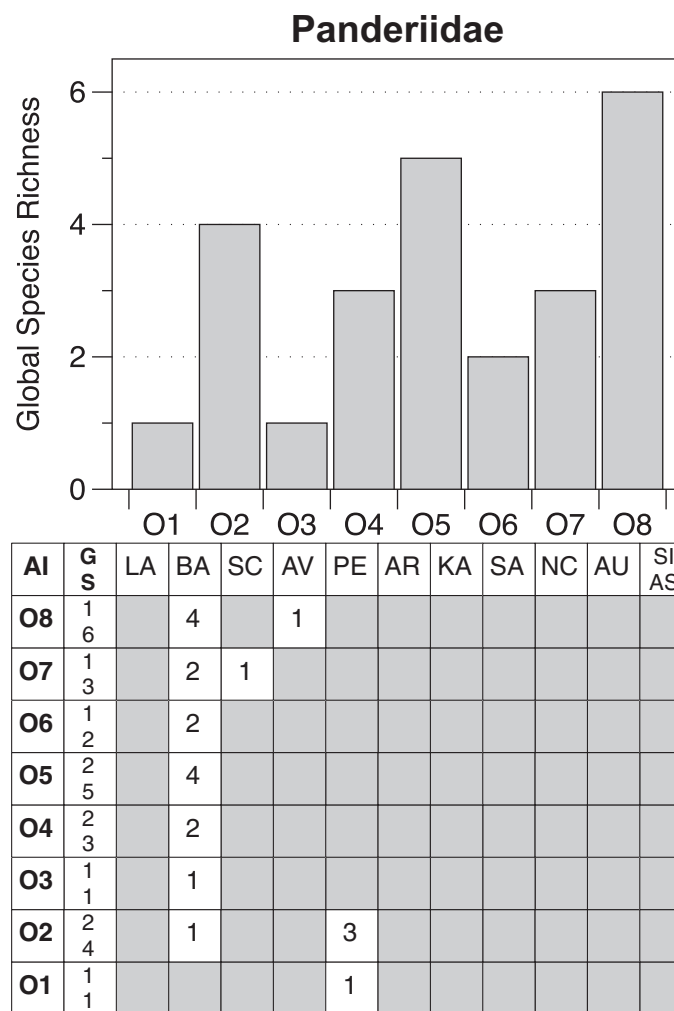


Fig. 20.5. Global taxonomic richness of the Family Panderiidae during the Ordovician. See Figure 20.4 for explanation.

state of knowledge, I recognize a single family. Phillipsinellidae (Whittington 1950a), has been considered a separate family since its proposal. Work in progress suggests that the phillipsinellines are either in-group Styginidae or the styginid sister taxon, and I consider them a subfamily of Styginidae. Progress with this difficult taxon will require modern phylogenetic analysis.

The earliest (sparse) history of the group is Baltic–Gondwanan, but much of the diversity is Laurentian–Baltic from the Floian on. By the Sandbian an essentially global distribution was achieved, and this continued until the end of the Ordovician. The group survived the end-Ordovician to become one of the main constituents of Siluro–Devonian trilobite faunas. It persisted until the Frasnian. There are 34 genera with Ordovician occurrence and 164 valid Ordovician species. No modern phylogenetic analyses of any part of the group have been published.

Family Leiosteigiidae Bradley, 1925

Although *Leiostegium* Raymond, 1913b, itself has a Darriwilian type species, most of the 79 genera and 350 species of leiosteigiids are Cambrian, with only 22 genera and 93 species occurring in the Ordovician (Fig. 20.7). There are several exclusively Cambrian subfamilies (Chelidonocephalinae Wittke, 1984, Ordosiinae Lu, 1954, Pagodiinae Kobayashi, 1935a), but Ordovician species are assigned to either Leiosteigiinae (19 genera and 50 species with Ordovician occurrence) or the exclusively Ordovician Eucalymeninae Lu, 1975 (two genera; 43 species). Neither of the

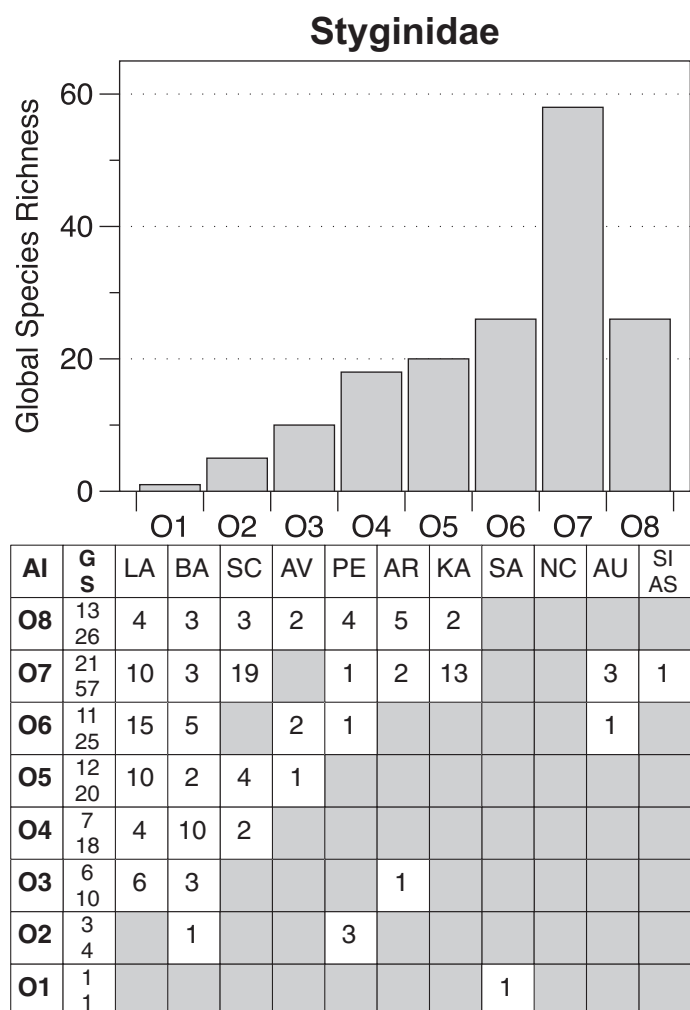


Fig. 20.6. Global taxonomic richness of the Family Styginidae during the Ordovician. See Figure 20.4 for explanation.

Ordovician groups have ever been subject to phylogenetic analysis. Eight of the Ordovician lelostegiine genera are monotypic and few species of Ordovician lelostegiines are adequately described. The group has a range from the Cambrian to Darriwilian and is known mainly from low latitudes (Laurentia, North and South China, Taurides). The Tremadocian–Darriwilian eucalymines include eight genera now considered junior subjective synonyms, but are generally better described. *Annamitella* Mansuy, 1920, is broadly distributed at low latitudes, whereas *Pseudocalymene* Pillet, 1973, is known mainly from South China and the Alborz Terrane of Iran.

Family Missisquoiidae Hupé, 1953

Missisquoiids (Fig. 20.8) were broadly distributed at low latitudes during the latest Cambrian, but only six species assigned to four genera are known from the Early Ordovician. The only species younger than early Tremadocian is the Floian *Tasmanocephalus stephensi* Etheridge, 1883; (see Jell & Stait 1985a), the affinities of which are not entirely straightforward. It has obvious similarity to taxa classified in Styginidae and Jell & Stait's classification of it in Missisquoiidae reflected a gradistic outlook in which the latter was cast as an explicitly paraphyletic group. Shergold *et al.* (1988) assigned *Tasmanocephalus* to Styginidae. Lee *et al.* (2008) carried out an extended cladistic analysis of Missisquoiidae, but did not attempt to address the issue of the putative styginid sister group and root position.

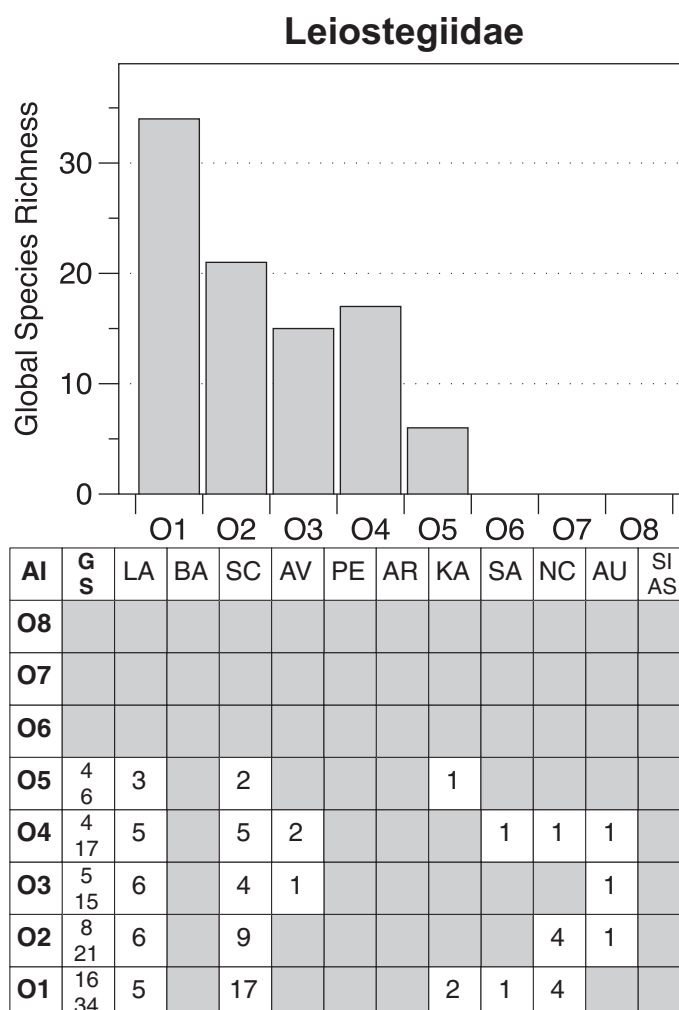


Fig. 20.7. Global taxonomic richness of the Family Lelostegiidae during the Ordovician. See Figure 20.4 for explanation.

Order Lichida Moore, 1959

The status and content of Lichida hinge on the question of its relationship or lack thereof with Odontopleurida. Many workers, including Chatterton & Speyer (1997) and Fortey (1997b, 2001) have considered that the families are closely related and have united them in a single Order Lichida. The evidence for this is the presence in either group of complex glabellar lobation, and the possession of larvae with similar spinose morphology. Fortey (1990) explicitly classified the Cambrian damesellids in Odontopleurida, but maintained Lichida as a separate order. However, Fortey (1997b) classified damesellids, lichids and odontopleurids each as a superfamily of a single Order Lichida. Adrain (2011) considered that a relationship between odontopleurids and lichids on the one hand was not well established, and that one between odontopleurids and damesellids had not been supported with very much detailed evidence on the other. Hence I retained separate orders Lichida and Odontopleurida and considered Damesellidae to be of uncertain affinity.

It is clear that Fortey (2001, p. 1147) regarded what were considered Cambrian lichakephalids by Thomas & Holloway (1988) as odontopleurids, following Bruton (1983). As explained at length below, it seems beyond doubt that these taxa are lichids, and not odontopleurids. Some of the points listed by Fortey (1990) perfectly describe similarity between damesellids and lichakephalids. In any event, as explained below, I think there is strong evidence for a damesellid–lichid relationship and I would now include Damesellidae within the Order Lichida. The points

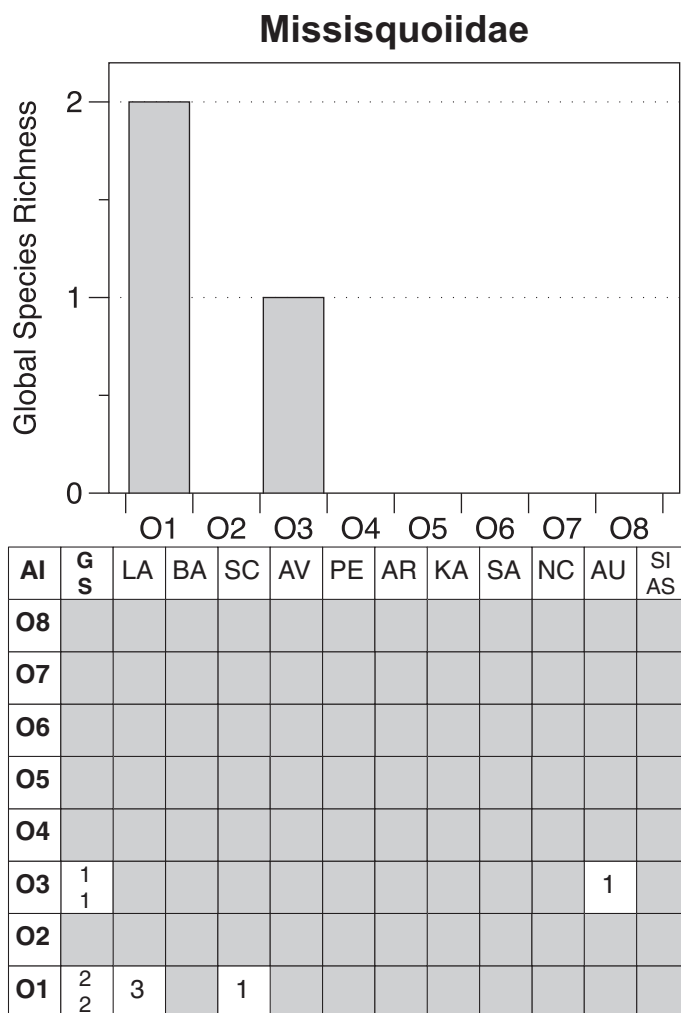


Fig. 20.8. Global taxonomic richness of the Family Missisquoiidae during the Ordovician. See Figure 20.4 for explanation.

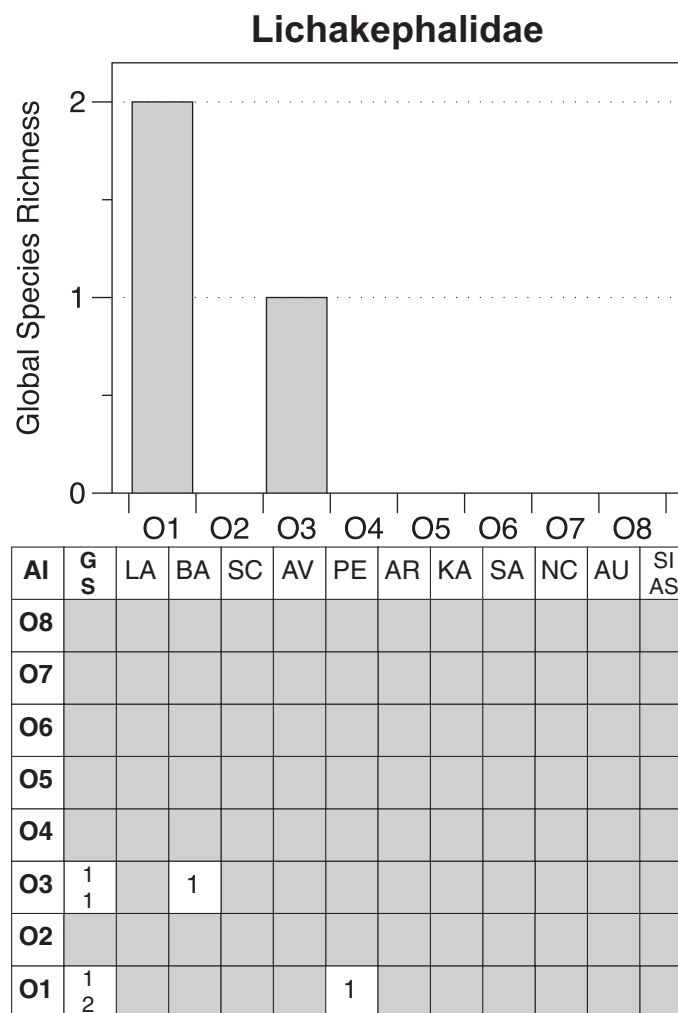


Fig. 20.9. Global taxonomic richness of the Family Lichakephalidae during the Ordovician. See Figure 20.4 for explanation.

of similarity are striking, there is no stratigraphical sampling gap (the bulk of Damesellidae is Guzhangian and so are the earliest lichakephalids), and Lichidae probably roots within (a therefore presently paraphyletic) Damesellidae.

I remain unconvinced that odontopleurids are related to lichids + damesellids. It is true that odontopleurid glabellar lobation can be complex, but it is not at all evident that this complexity, which can be matched within Odontopleuridae (see Ramsköld 1991a, fig. 6, for an interpretation of complex homologies across several odontopleurid clades), relates in any way to the very different complex subdivisions seen in lichakephalids and lichids. While larvae of the groups are indeed broadly similar as they are tuberculate and share a similar pattern of proto-cranial paired spines, this basic pattern (usually three or four paired fixigenal spines and typically three prominently expressed pairs of glabellar spines) is also seen in many different spinose/tuberculate trilobite groups, including Aulacopleurida, Phacopida and the Family Styginidae. Fortey (1990) has suggested that a relationship with Styginidae is an alternative hypothesis for lichid affinities. I am by no means arguing in favour of that hypothesis, but lichid larvae (Chatterton & Speyer 1997, fig. 183) seem considerably more similar to those of styginids (Chatterton & Speyer 1997, fig. 171.4–6) than to those of odontopleurids (Chatterton & Speyer 1997, figs 185.1, 2, 10, 11). All share the basic paired tubercle pattern, but odontopleurids have fringing cephalic spines which lichids and styginids lack, and they have tiny, spinose protopygidia whereas lichids and styginids have larger protopygidia composed of clear segments with small

pleural spines. Again, my point is not to advocate for a lichid–styginid relationship, but to emphasize that there seems to be little in the way of specific putative synapomorphies uniting lichids and odontopleurids on the basis of protaspis morphology.

I regard the question of odontopleurid affinity as open, and they may yet prove to be related to lichids. The first unequivocally dated odontopleurids are Floian (but see discussion of *Archaeopleura* below) and at present they remain a classically ‘cryptogenetic’ (Stubblefield 1959) taxon.

Family Lichakephalidae Tripp, 1957

When he erected Lichakephalidae (Fig. 20.9), Tripp (1957) included only the nominate genus which was at that point monotypic. Thomas & Holloway (1988) recognized the Cambrian Family Eoacidaspidae Poletaeva, 1957, which had been proposed as and revised by Bruton (1983) as an odontopleuroid taxon, as a junior synonym of Lichakephalidae. They excluded from it only the genus *Acidaspides* Lermontova, 1951, which they agreed represented an odontopleurid. The history of taxonomy from that point forwards is somewhat complex and classification is not agreed upon. Most authors, including Bruton (1983) and Thomas & Holloway (1988) queried the association of the cranidia and single known pygidium (reillustrated by Thomas & Holloway 1988, plate 16, fig. 352) assigned to *A. precurrens* Lermontova, 1951, the type species from northeastern Kazakhstan. Bruton (1983) selected one of the cranidia as a lectotype. Ramsköld

(1991a) agreed with Thomas & Holloway's (1988) synonymy of Lichakephalidae and Eoacidaspidae, but pointed out that Lermontova (1951) had both designated the pygidium of *A. precurrens* as the holotype in her plate caption and also queried the identity of the cranidia herself, which in any case would have made the pygidium the holotype by monotypy. Hence Bruton's selection of a cranidium as a lectotype was invalid. The pygidium resembles those of neither lichakephalids nor odontopleurids, with its large, tubular but not denticulate spines and well-impressed axial and pleural furrows. It strongly resembles a typical damesellid pygidium with the front portion broken off (compare, e.g. with the pygidium of *Taihangshania wangcunensis* Peng, Babcock & Lin, 2004, plate 37, fig. 14), but is apparently considerably younger than any damesellids. For the present its affinities must be considered uncertain, but there is no reason to include it in either Lichakephalidae or Odontopleuridae. Ramsköld (1991a) restricted *A. precurrens* to the holotype pygidium and named a new odontopleurid genus and species, *Archaeopleura kazakhstanensis*, for the cranidia. The age of the species is uncertain – Lermontova (1951) reported it as of uncertain position around the Cambrian–Ordovician boundary. Ramsköld (1991a) noted that, at the time Lermontova was writing, the Tremadocian was considered part of the Cambrian. On this basis he suggested that *Archaeopleura* might actually be Arenig (Floian), which would put it around the same age as the oldest securely dated odontopleurids. All of the other trilobites described by Lermontova (1951), however, are either clearly upper Furongian or possibly lower Tremadocian.

Following Thomas & Holloway's (1988) synonymy of Lichakephalidae and Eoacidaspidae, Zhang (1990, p. 177, postscript) rejected the idea, although his arguments did not address phylogeny and appealed to negative evidence ('because more skeletal parts of both families are needed'). Shergold *et al.* (2000) also contested the synonymy of the families, apparently on gradistic grounds. They accepted Lichakephalidae as outlined by Thomas & Holloway (1988) except that they transferred *Eoacidaspis* Poletaeva in Černyševa *et al.*, 1956, back to Eoacidaspidae, in which they included also *Paraacidaspis* Poletaeva, 1963, *Usoviana* Poletaeva, 1977, and *Archikainella* Liu, 1982, none of which were mentioned by Thomas & Holloway (1988). Shergold *et al.* (2000) did not say whether they accepted a phylogenetic relationship between the families as thus conceived (i.e. with Eoacidaspidae considered a paraphyletic grade) or whether they simply considered them unrelated. Peng *et al.* (2004) endorsed the views of Shergold *et al.* (2000), but again gave no indication of their view of the relationship (if any) between the families as thus conceived.

Comparing the morphology of, for example, *Paraacidaspis* (classified as Eoacidaspidae by Zhang (1990), Shergold *et al.* (2000) and Peng *et al.* (2004)) with that of *Acidaspina plana* Lazarenko, 1960 (see Thomas & Holloway 1988, plate 16, figs 353, 354, 356, 357), which they apparently accept as Lichakephalidae, reveals no substantive differences. They share complex glabellar lobation which is comparable in exact detail across all lichakephalids and 'eoacidaspids' together with fan-shaped pygidia with well-impressed pleural furrows which differ only in minor detail among the taxa. For these reasons one must assume that the classification endorsed by Shergold *et al.* (2000) and Peng *et al.* (2004) is gradistic. In any case, the notion that the two sets of genera are not directly phylogenetically related to each other is contrary to their considerable similarity and Thomas & Holloway's (1988) recognition of Eoacidaspidae as a synonym of Lichakephalidae is well supported.

That said, it is important to emphasize that Lichakephalidae *sensu* Thomas & Holloway (1988) was explicitly conceived of by those authors as a paraphyletic grade from which Lichidae was derived. As pointed out by Fortey (2011a), it seems unlikely that lichakephalids will survive as an independent family in light of phylogenetic analysis, as they appear to consist of a grouping of plesiomorphic basal lichids.

Lichids hence have a stratigraphical range extending back to the Guzhangian (upper Cambrian Series 3) and their oldest known representatives are contemporaries of the damesellids. As noted above, there are striking similarities between Cambrian 'lichakephalids' and damesellids. Shergold *et al.* (2000, plate 6, fig. 10) illustrated the hypostome of their new *Paraacidaspis ultima*. It is clearly of damesellid morphology, with a narrower anterior region, an inflated, posteriorly tapering middle body, enlarged, posteriorly extended and lobate posterolateral regions with basal depressions, and prominent swollen maculae at the inner edge of the posterolateral lobes. It is virtually identical to the hypostome of species such as *Palaeadotes hunanensis* (Yang in Zhou *et al.*, 1977; see Peng *et al.* 2004, plate 39, figs 3–5), yet not remotely similar to those of odontopleurids. Further, damesellids such as *Palaeadotes*, Öpik, 1967, developed complex glabellar lobes which can be matched in exact, point-for-point detail with the similar complex lobes of species such as *Acidaspina plana* (cf. Peng *et al.* 2004, plate 38, fig. 10, with Thomas & Holloway 1988, plate 16, fig. 353). The taxa also share a similar short anterior border against which the glabella terminates, and narrow fixigenae crossed by obliquely set, prominently inflated eye ridges which are posteriorly contiguous with the inflated rim of the palpebral lobe. 'Lichakephalid' pygidia are broad and fan-shaped, with prominent, long axes with deep ring furrows and seven or eight rings, often with a faint post-axial ridge, and with the pleurae crossed by deeply impressed pleural furrows. They are strikingly similar to those of species of *Palaeadotes*, with the exceptions that they lack a macropleural first segment and pleural spines.

In light of these synapomorphies, I suggest that lichids root within damesellids and the families should be classified together in an Order Lichida. None of these synapomorphies are shared with the much younger Odontopleurida.

As presently classified, Ordovician 'lichakephalids' include three species assigned to two genera. *Lichakephalus* Sdzuy, 1955, is known from two lower Tremadocian Gondwanan species, and *Lichakephalina* Ancygin, 1973, is known from a single Floian species from Baltica (Urals). No phylogenetic analyses of basal lichids have been published.

Family Lichidae Hawle & Corda, 1847

Lichidae (Fig. 20.10) has been thoroughly reviewed by Thomas & Holloway (1988) and this work serves as the basis for a modern understanding of the group. Thomas & Holloway recognized five subfamilies, one of which (Lichinae) they regarded as expressly paraphyletic. The scheme was expanded to six subfamilies by Holloway & Thomas (2002). The oldest species presently assigned is the lichine *Holoubkovia klouceki* (Růžička, 1926) from the upper Tremadocian of the Czech Republic. However, given the discussion above, this is semantic, as *Lichakephalus* occurs in the lower Tremadocian and the group extends far back into the Cambrian. The six currently recognized subfamilies are Lichinae (upper Tremadocian to Lochkovian, 10 genera, 99 species), Echinolichinae Phleger, 1936 (Pragian to Givetian, four genera, eight species), Homolichinae Phleger, 1936 (Darriwilian to upper Katian, six genera, 27 species), Platylichinae Phleger, 1936; (Darriwilian to Homeric, four genera, 38 species), Tetralichinae Phleger, 1936 (Dapingian to upper Katian, four genera, 54 species), and Trochurinae Phleger, 1936 (Darriwilian to Givetian, 21 genera, 175 species). Lichids are very rare in Lower Ordovician rocks, but are fairly common and cosmopolitan in the Middle Ordovician. Prior to the late Katian, lichines were mainly distributed in Gondwana, Avalonia, and Baltica, platyllichines were mainly Baltic, whereas tetralichines and trochurines were mainly Laurentian. The family maintained a broad distribution through the Late Ordovician. The tetralichines and homolichines disappeared at the end-Ordovician extinction, but platyllichines survived until the Homeric and lichines until the Ludlow; trochurines

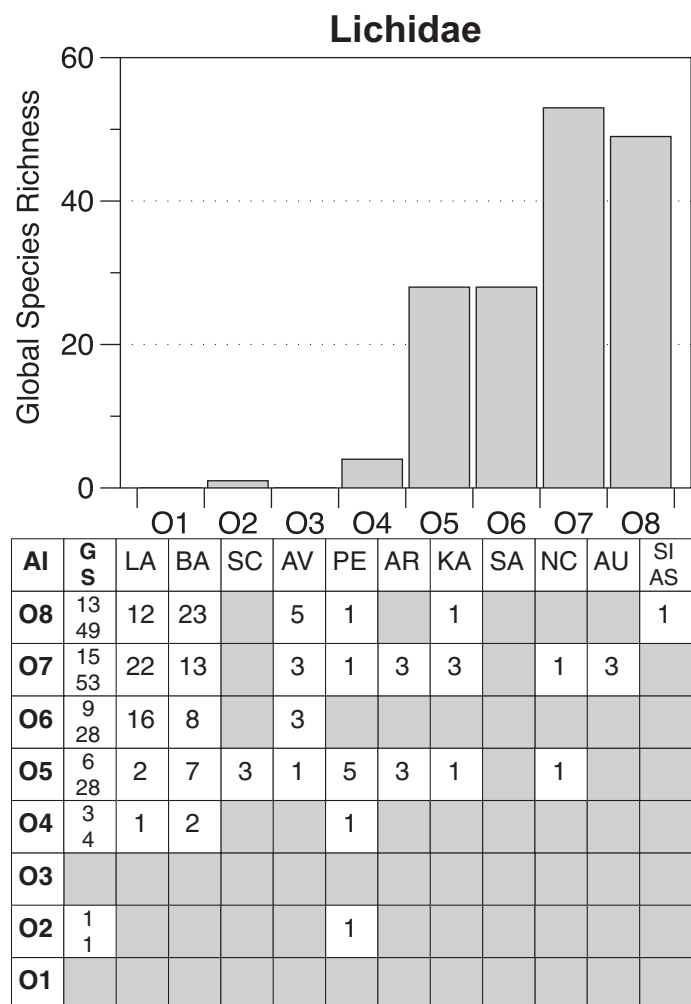


Fig. 20.10. Global taxonomic richness of the Family Lichidae during the Ordovician. See Figure 20.4 for explanation.

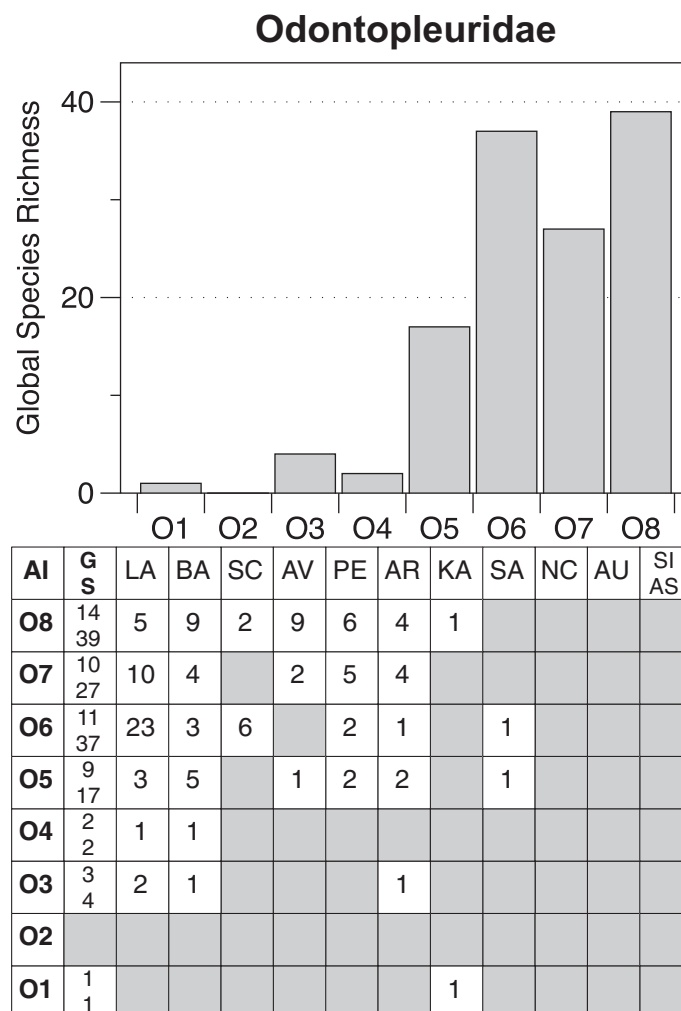


Fig. 20.11. Global taxonomic richness of the Family Odontopleuridae during the Ordovician. See Figure 20.4 for explanation.

underwent much post-Ordovician diversification, persisting until the Givetian. There are 24 valid genera with occurrence in the Ordovician and 166 Ordovician species.

There has been a relatively large amount of phylogenetic work on lichids. Pollitt *et al.* (2005) analysed the entire group, although instead of using species as in-group taxa they used composite codings of genera which implicitly assumed genus monophyly. Species-level analyses of particular taxa have been published by Ebach & Ayong (2001), Adrain (2003), Campbell & Chatterton (2009), and Carlucci *et al.* (2010).

Order Odontopleurida Whittington in Moore, 1959

Family Odontopleuridae Burmeister, 1843

The question of a relationship between odontopleurids and lichids was addressed under discussion of the latter group above. Odontopleurids (Fig. 20.11) are highly distinctive, spinose trilobites which have attracted considerable study. The earliest securely dated species are Floian (see a review of Floian taxa by Ramsköld (1991a, pp. 162–164), but see discussion of the genus *Archaeopleura* above). Much of the foundation for a modern understanding of the family stems from the early work of Bruton (e.g. 1965, 1966, 1968b). The scheme adopted herein is that derived from the pioneering phylogenetic work of Ramsköld (1991a, b; Ramsköld & Chatterton 1991), in which six putatively monophyletic

subfamilies are recognized. They are Odontopleurinae (Darriwilian to Givetian, 13 genera, 177 species), Acidaspinae Salter, 1864 (Darriwilian to Frasnian, 13 genera, 102 species), Apianurinae Whittington, 1956 (Dapingian to upper Katian, three genera, 17 species), Ceratocephalinae Richter & Richter, 1925 (Dapingian to Emsian, two genera, 37 species), Koneprusiinae Vaněk & Pek, 1987 (upper Katian to Givetian, four genera, 42 species), and Selenopeltinae Hawle & Corda, 1847 (Floian to Emsian, 10 genera, 72 species). Odontopleurids became both fairly common and globally distributed beginning in the Darriwilian. They survived the end-Ordovician and ranged to the Frasnian. There are 22 genera with Ordovician occurrence and 128 valid Ordovician species. Parts of the family have been the subject of cladistic analyses. Those including Ordovician species are by Chatterton *et al.* (1997) and Adrain *et al.* (2008).

Order Phacopida Salter, 1864

Suborder Phacopina Salter, 1864

Family Acastidae Delo, 1935. Acastidae (Fig. 20.12) is a major clade of post-Ordovician trilobites, including nearly 400 Silurian and Devonian species. All of the Ordovician species are assigned to a Subfamily Kloucekiinae Destombes, 1972, which includes 24 valid Ordovician species assigned to four genera. Kloucekiinae is almost certainly paraphyletic, and probably comprises

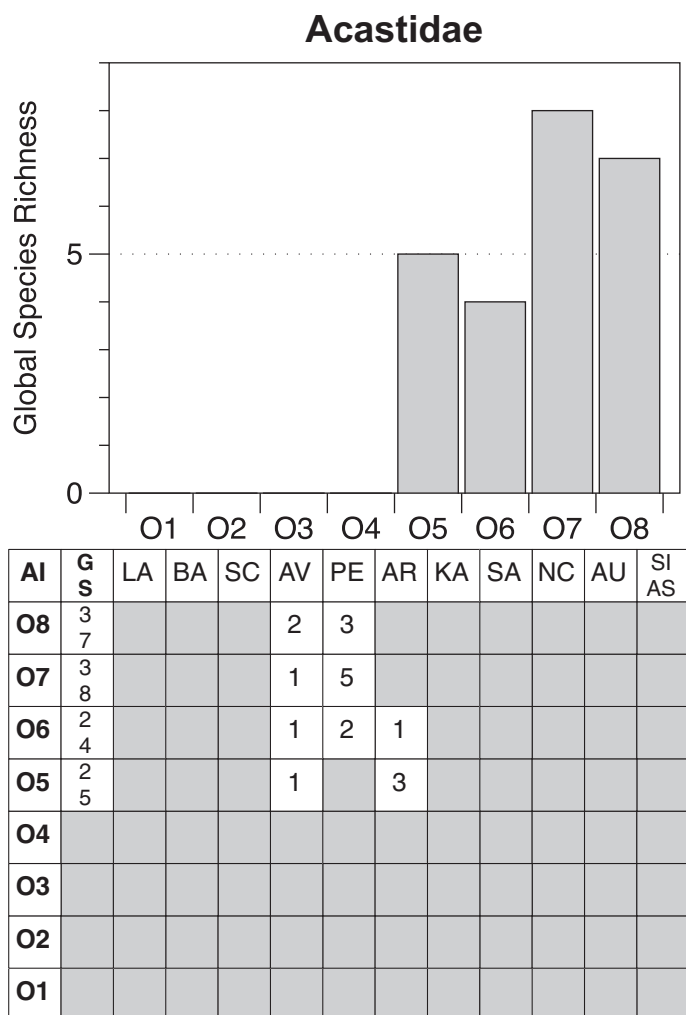


Fig. 20.12. Global taxonomic richness of the Family Acastidae during the Ordovician. See Figure 20.4 for explanation.

the plesiomorphic sister taxa of the remainder of Acastoidea (Acastidae + Calmoniidae Delo, 1935). It is exclusively Avalonian–Gondwanan, and has not been subjected to phylogenetic analysis.

Family Dalmanitidae Vogdes, 1890. All Ordovician species assigned to Dalmanitidae (Fig. 20.13) are assigned to the almost entirely Ordovician Zeliszkellinae Delo, 1935 (the only exceptions are Rhuddanian species), which like Kloucekiinae (above) is probably paraphyletic. The group was exclusively Avalonian–Gondwanan from its first appearance in the Floian until the late Katian, when like many taxa it became cosmopolitan. It had considerable diversity and is a major component of many Gondwanan trilobite faunas. There are 113 valid Ordovician species assigned to 21 genera. The group has not been subject to phylogenetic analysis.

Family Phacopidae Hawle & Corda, 1847. Phacopids (Fig. 20.14) became an important group during the Silurian and achieved enormous diversity (in terms of species richness and taxa, if not morphology) during the Devonian. Only a single species, *Sambreusaspis fossesensis* Lespérance in Lespérance & Sheehan, 1988, is known from the Ordovician (upper Katian, and definitely pre-Hirnantian). This is to some extent a semantic distinction, as the phacopids are widely considered to root within the presumptively paraphyletic Pterygomtopidae.

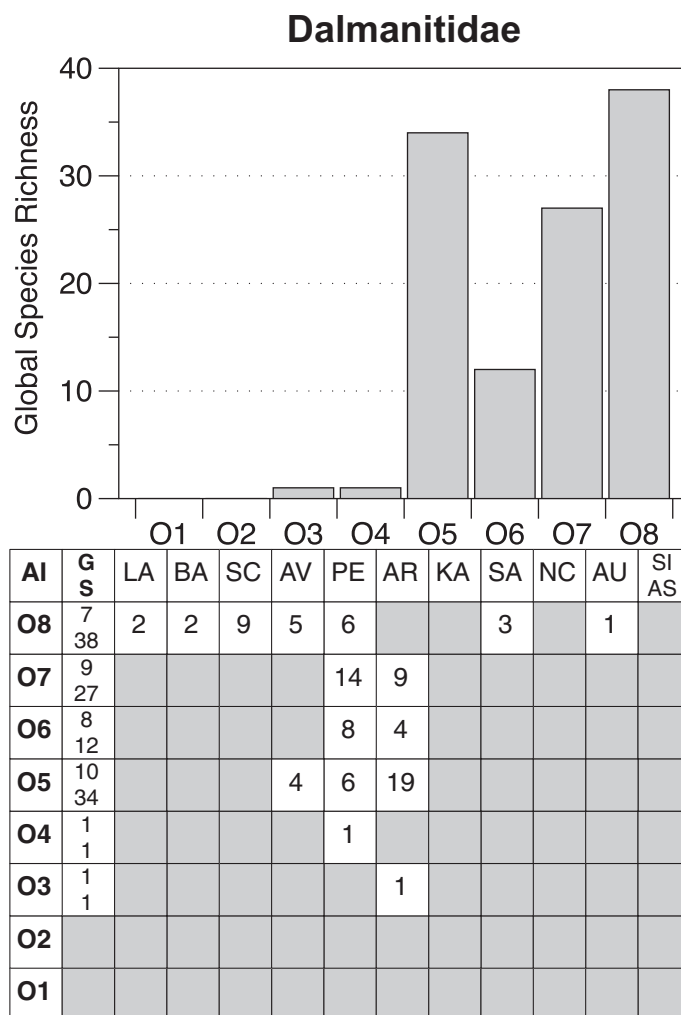


Fig. 20.13. Global taxonomic richness of the Family Dalmanitidae during the Ordovician. See Figure 20.4 for explanation.

Family Pterygomtopidae Reed, 1905. Pterygomtopidae (Fig. 20.15) includes 36 genera with Ordovician occurrence containing 202 valid Ordovician species. Four subfamilies are recognized, each with a strong biogeographical signal. Pterygomtopinae (14 genera, 49 species) ranges from the Floian to upper Katian and is largely Baltic; some assignments of species from elsewhere need to be examined in light of a phylogenetic hypothesis for the overall group. Chasmopinae Pillet, 1954 (eight genera, 50 species), with a range from Darrivilian to upper Katian, is exclusively Baltic until the Katian, from which it is known also from Avalonia and Laurentia. The Upper Ordovician (Sandbian to upper Katian) Monorakinae Kramarenko, 1952 (six genera, 32 species), was reviewed by Holloway (2004) and is mostly Siberian, with the only exceptions from the Omulevka Terrane and other terranes in far northeastern Russian and Alaska. Finally, Eomonorachinae Pillet, 1954 (eight genera, 71 species), with a range from Floian to upper Katian, is largely Laurentian. Eomonorachinae is generally considered paraphyletic. It includes the only Silurian pterygomtopid, *Podowrinella* Clarkson, Eldredge & Henry, 1977, which may represent the sister taxon of Phacopidae (e.g. Ludvigsen & Chatterton 1982, p. 2188). The other subfamilies require detailed analysis, but Chasmopinae and Monorakinae seem likely to be monophyletic. No phylogenetic analyses of any part of the family have been published.

Family Diaphanometopidae Jaanusson in Moore, 1959. The monotypic genera *Diaphanometopus* Schmidt, 1881 (Dapingian;

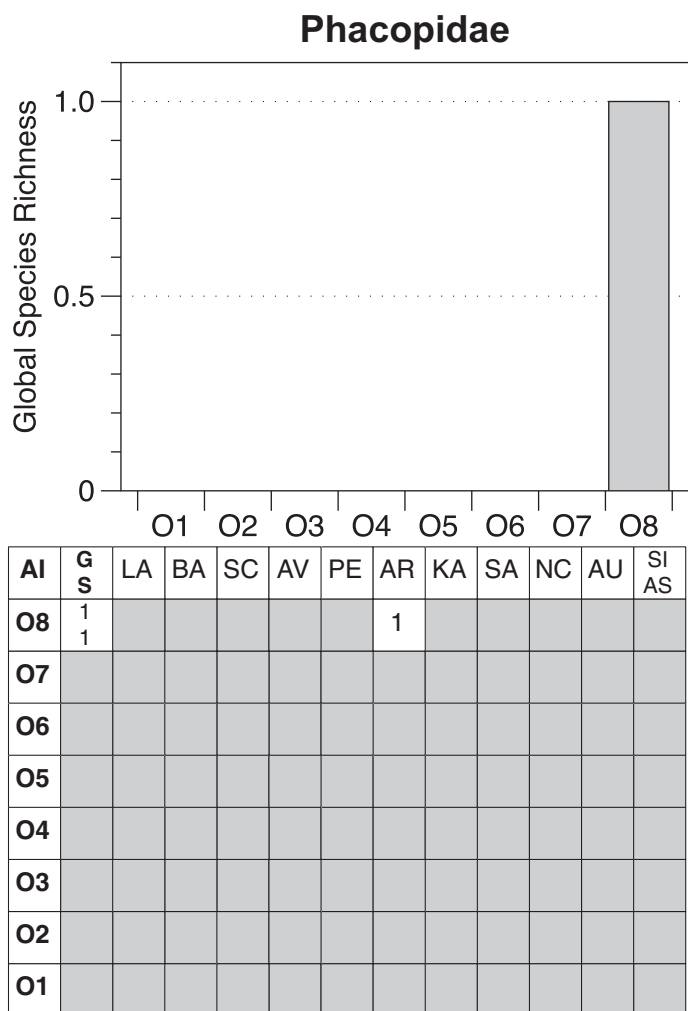


Fig. 20.14. Global taxonomic richness of the Family Phacopidae during the Ordovician. See Figure 20.4 for explanation.

Baltica), *Gyrometopus* Jaanusson, 1975 (Floian; Baltica) and *Prodalmanitina* (Cugaeva 1968; Floian; Omulevka Terrane, Kolyma) were grouped in Diaphanometopidae (Fig. 20.16) by Adrain (in Jell & Adrain 2003). However, each represents an apparently very plesiomorphic member of Phacopina. Jaanusson (1975) considered that *Gyrometopus* and *Diaphanometopus* were related, but they did not form a clade in Edgecombe's (1992, fig. 5.9) cladistic analysis. It is unlikely that together the three genera form a clade and unlikely that a family rank will survive for any of them once the basal structure of Phacopina is better understood.

Family Prosopiscidae Fortey & Shergold, 1984. Prosopiscidae (Fig. 20.17) is a monotypic family of blind trilobites whose affinity was variously thought to lie with encrinurids, pliomerids or cheirurids. Fortey & Shergold (1984) argued convincingly that *Prosopiscus* Salter in Salter & Blanford, 1865, was an early member of Phacopina, and this was reinforced with evidence from early life history by Edgecombe *et al.* (1999). The genus had a distinctive tropical Gondwanan distribution throughout its history, with occurrences in Australia, South China, North China and the Himalaya, and its palaeobiogeography was reviewed by Paterson (2004). The only exception is a Darriwilian occurrence in the Argentine Precordillera Terrane (Edgecombe *et al.* 1999), which at that time was still strongly dominated by Laurentian taxa, mixed with a few Gondwanan endemics such as *Prosopiscus*. Eleven species have been named, the earliest known from the Floian of Australia. The genus

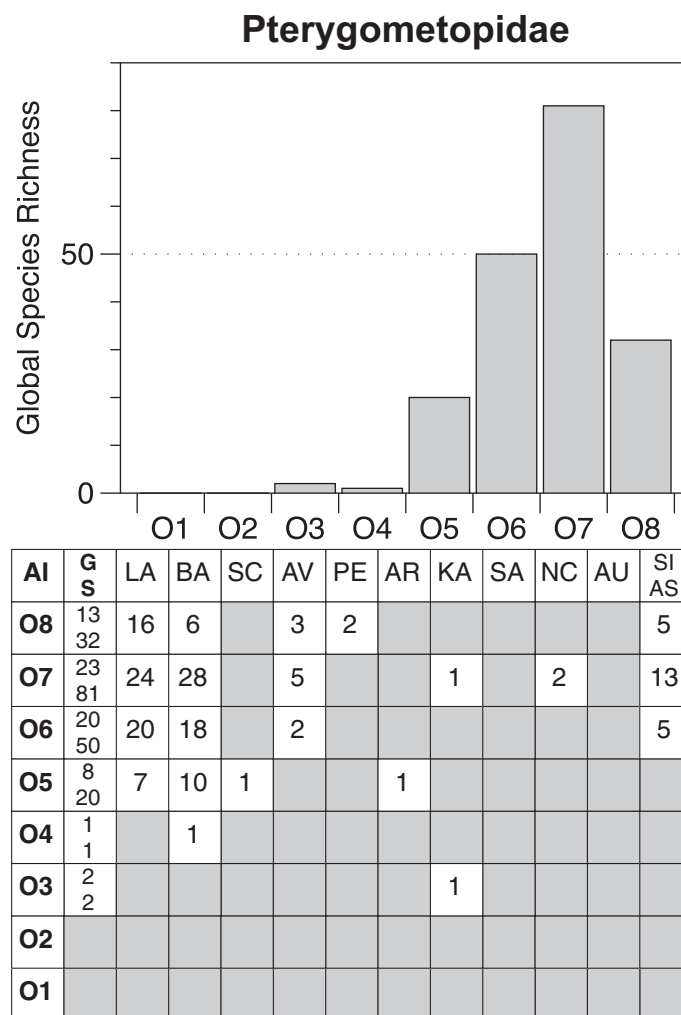


Fig. 20.15. Global taxonomic richness of the Family Pterygommetopidae during the Ordovician. See Figure 20.4 for explanation.

persisted until the late Katian. No phylogenetic analyses have been carried out.

Suborder Cheirurina Harrington & Leanza, 1957

Family Cheiruridae Hawle & Corda, 1847. Cheirurids (Fig. 20.18) are a major trilobite group which ranged from the uppermost Cambrian to the Givetian, with a total of 657 valid species assigned to 99 genera. There are eight presently recognized subfamilies, although it is clear that not all are monophyletic. They are Cheirurinae (probably monophyletic, Floian to Givetian, 38 genera, 269 species), Acanthoparyphinae Whittington & Evitt, 1954 (probably monophyletic, Floian to Ludfordian, 15 genera, 109 species), Cyrtometopinae Öpik, 1937 (phylogenetic status uncertain, Floian to upper Katian, five genera, 22 species), Deiphoninae Raymond, 1913a (probably monophyletic, Dapingian to Gorstian, six genera, 71 species), Eccoptochilinae Lane, 1971 (possibly paraphyletic, Floian to upper Katian, 13 genera, 67 species), Heliomerinae Evitt, 1951 (monophyletic, two genera, 13 species), Pilekiinae Sdzuy, 1955 (certainly paraphyletic, upper Furongian to Darriwilian, 19 genera, 56 species) and Sphaerexochinae Öpik, 1937 (monotypic, Floian to Přídolí, one genus, 50 species). The most important modern treatment of the family is Lane (1971), although Přibyl *et al.* (1985) also comprehensively reviewed the group. I am in the midst of a species-level review of the family, and defer extended commentary for publication elsewhere. There are 440 valid Ordovician species assigned to 76 genera. Phylogenetic work includes Adrain (1998) and Congreve & Lieberman (2010, 2011).

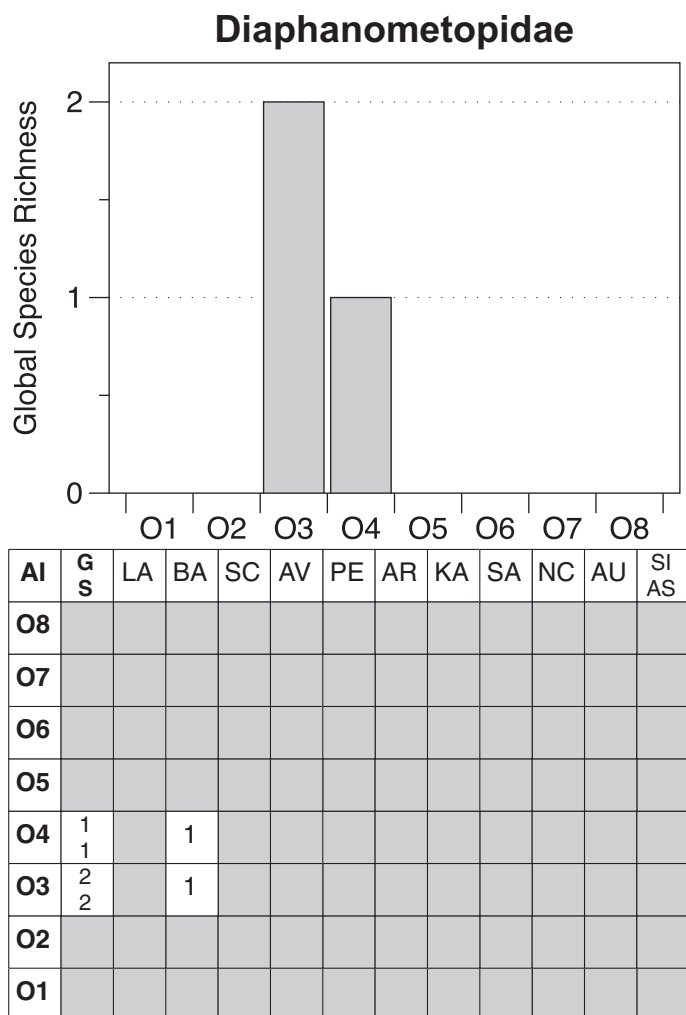


Fig. 20.16. Global taxonomic richness of the Family Diaphanometopidae during the Ordovician. See Figure 20.4 for explanation.

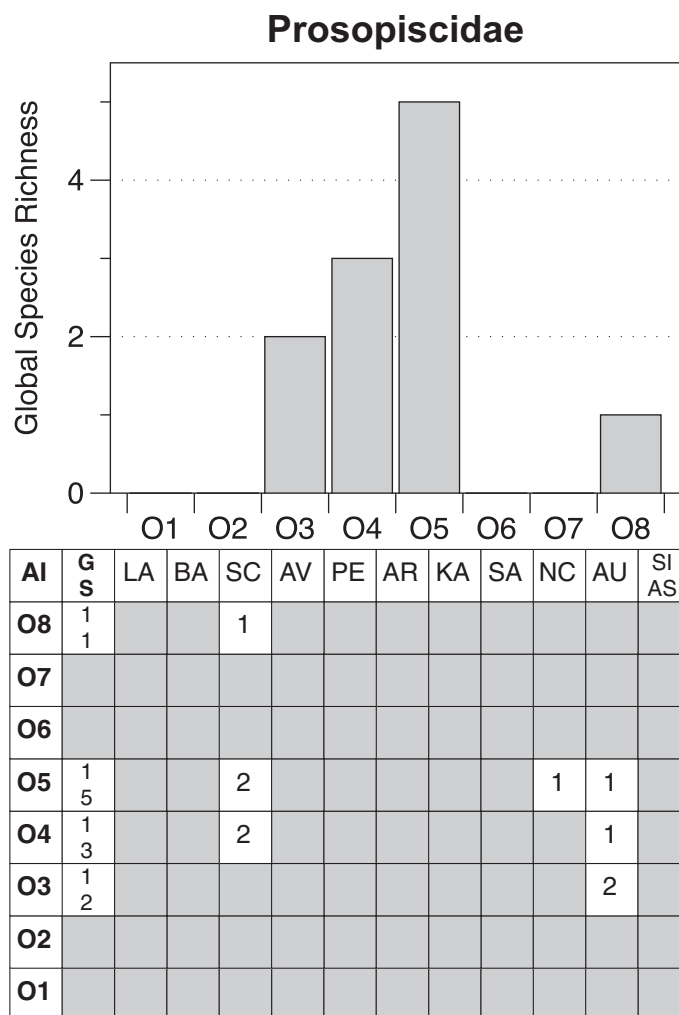


Fig. 20.17. Global taxonomic richness of the Family Prosopiscidae during the Ordovician. See Figure 20.4 for explanation.

Family Encrinuridae Angelin, 1854. Encrinurids (Fig. 20.19) include 29 valid genera with occurrence in the Ordovician to which 186 Ordovician species have been assigned. The group first appeared during the Floian, and probably roots amongst the cybelopsine pliomerids (Adrain *et al.*, work in progress). Only a few species are known from the Floian. Although Cybelinae is thought to be rendered paraphyletic by the other subfamilies, Cybelinae and Encrinurinae appear essentially simultaneously, cybelines in the form of Laurentian species of *Lyrapyge* Fortey, 1980, along with '*Cybele*' *rotundata* Ancygin, 1978, from Mayachnaya Mountain, Kazakhstan. The earliest encrinurine and only Floian species is '*Encrinuroides*' *regularis* Pärnaste, 2006, from Baltica. Encrinurines (nine total Ordovician genera and 64 species) remain rare during the Dapingian (one species, Laurentia) and Darriwilian (four species, all Laurentia) and the handful of Floian through Darriwilian species are presently all assigned to the 'rubbish-bin' taxon *Encrinuroides* Reed, 1931. Encrinurines proliferated in the Sandbian, where six genera and 18 species are recognized, but the group remained almost exclusively Laurentian, with the only exception being the Avalonian Irish '*Encrinuroides*' *fallax* (Reed 1899). Six genera and 21 species are known from the lower Katian, with a much wider distribution including Laurentia, Baltica, Kazakhstan, Australia, South China and Tarim. Three genera and 19 species are recognized in the upper Katian, from Laurentia, Baltica, Avalonia, and South China. Encrinurinae survived the end-Ordovician mass extinction and radiated dramatically during the Llandovery, becoming one of the emblematic Silurian trilobite taxa. A mainly South China Subfamily

Coronocephalinae Zhang, 1983, if recognized, creates paraphyly in Encrinurinae. The encrinurines (and coronocephalines) became extinct around the Silurian–Devonian boundary. Encrinurinae has probably been subject to more modern phylogenetic analyses than any other family-group taxon, although many of these studies have concerned Silurian taxa (e.g. Edgecombe & Ramsköld 1996). Notable analyses of Ordovician encrinurines include Edgecombe *et al.* (1998) and Lespérance & Desbiens (1995).

Cybelinae (12 genera and 92 species) is known from only two Laurentian and one Kazakh species in the Dapingian. By the Darriwilian the group was widely distributed in low latitudes (Laurentia, Baltica, South China, etc.) but generally absent from high-latitude Gondwana. This pattern continued until the group's disappearance at the end of the Ordovician. In contrast with the much-studied Encrinurinae, there have been no phylogenetic analyses of Cybelinae which might address their internal structure and putative paraphyly.

Two minor encrinurid subfamilies are Dindymeninae Henningsmoen in Moore, 1959, and Staurocephalinae Prantl & Püßyl, 1948. Staurocephalinae (four valid Ordovician genera and 11 species) has often been treated at family rank (e.g. Kielan 1957; Evitt & Tripp 1977; Holloway 1980), but this seems based mainly on the phenetic dissimilarity of its more derived, 'bubble-headed' taxa, especially *Staurocephalus* Barrande, 1846, itself. The morphology and ontogeny of earlier, less derived species such as *Libertella corona* Hu, 1971, leave no doubt that the staurocephalines are in-group Encrinuridae (see Edgecombe *et al.* 1988, pp. 791–792). The Laurentian *L. corona* is the only definite

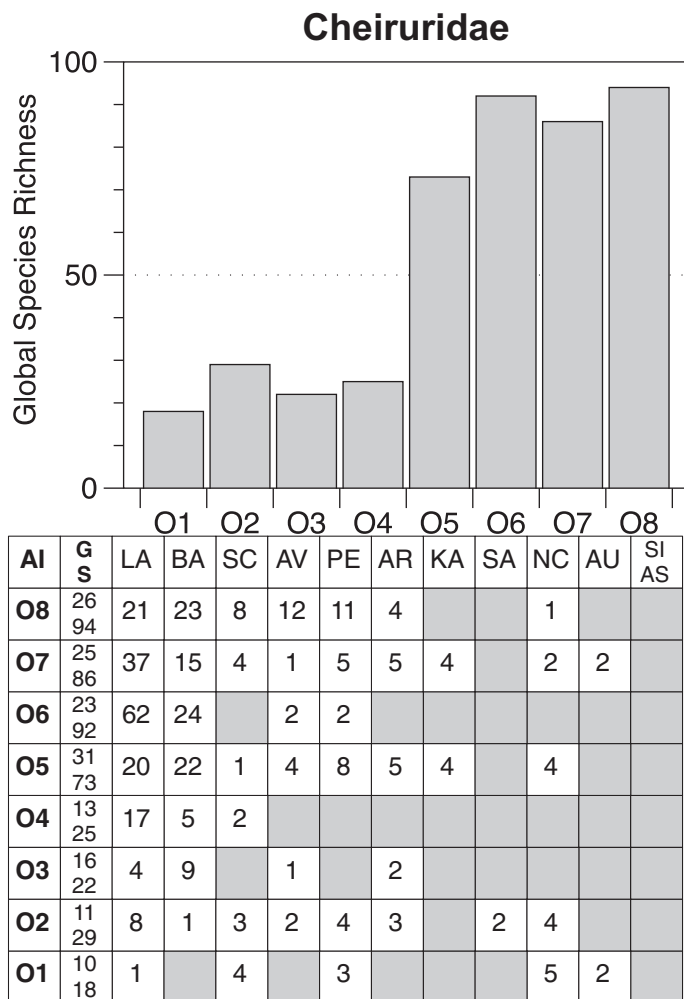


Fig. 20.18. Global taxonomic richness of the Family Cheiruridae during the Ordovician. See Figure 20.4 for explanation.

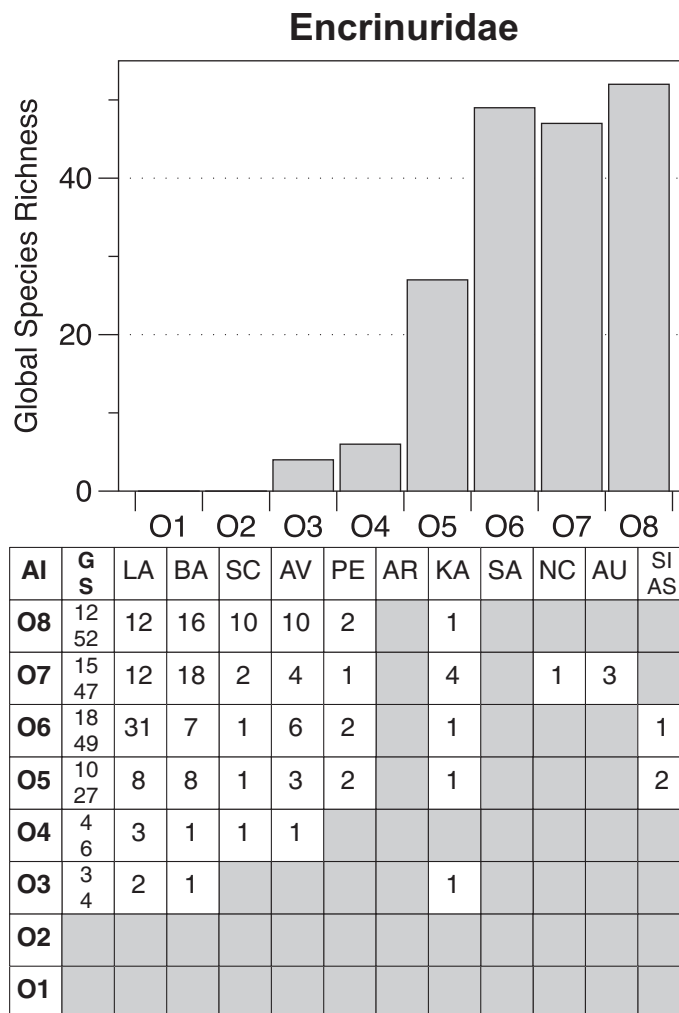


Fig. 20.19. Global taxonomic richness of the Family Encrinuridae during the Ordovician. See Figure 20.4 for explanation.

Sandbian member of the subfamily. During the Katian the group occurred in Baltica, Avalonia, South China, Sibumasu and Kazakhstan. A single genus, *Staurocephalus*, survived the end-Ordovician extinction. Ten Silurian species have been assigned, with the youngest known from the upper Ludlow. The Ordovician genus *Alwynulus* Tripp, 1967, was placed in Staurocephalidae by Tripp (1993, p. 99), but when he erected it (Tripp, 1967, p. 75), he noted similarity with *Josephulus* Warburg, 1925. *Josephulus* was assigned by Fortey (1997a, p. 436) to Hammatocnemidae Kielan, 1960 (considered a subfamily of Pliomeridae by Chen & Zhou (2002) and herein), and *Alwynulus* should also be assigned to that taxon. No modern phylogenetic analyses of Staurocephalinae have been published.

The exclusively Ordovician Dindymeninae (three genera; 18 species) has its earliest occurrence in the Dapingian of Avalonia. In the Darriwilian it is known only from Avalonia and 'Perunica', joined in the Sandbian by Kazakhstan. By the late Katian the group was cosmopolitan, with species known also from Laurentia, Baltica and South China. No modern phylogenetic analyses have been published.

Family Pliomeridae Raymond, 1913a. The content and definition of Pliomeridae (Fig. 20.20) have never been particularly clear. A central problem is recognition of the basal node of Cheiruridae. Several Tremadocian genera which have regularly been assigned to Pliomeridae (e.g. *Rossaspis* Harrington, 1957; *Tesselacauda* Ross, 1951) appear to be basal cheirurids. Of the six genera presently recognized in the lower Tremadocian, five are monotypic

and so poorly known that their affinity is uncertain. Three main groups emerged in the Floian, concentrated in Laurentia. The base of one major clade is currently classified as *Pseudomera* Holliday, 1942 (and *Kanoshia* Harrington, 1957, which is probably a junior synonym). This group diversified throughout the remainder of the Ordovician, and includes *Pliomera* Angelin, 1854, itself. As Pliomeridae s.s., this group is probably monophyletic. A second group, also apparently monophyletic but whose sister taxon remains uncertain, includes genera such as *Protopliomerella* Harrington, 1957, *Pseudocybele* Ross, 1951 and *Lemureops* McAdams & Adrain, 2009a. A third group, 'Cybelopsinae' Fortey, 1979, is more broadly distributed, with many Floian Australian representatives, and seems likely to be paraphyletic and include Encrinuridae within its present structure. Of the other pliomerid subfamilies that have been used in the literature, Placopariinae Hupé, 1953, lies within the structure of Pliomeridae s.s. Hammatocneminae Kielan, 1960, is definitely related but is highly derived and no firm ideas about its sister taxon have emerged. Protopliomeropinae Hupé, 1953, is at present more or less a taxon of convenience containing a mish-mash of early taxa. Quinquecostinae Edgecombe & Chatterton, 1992, may fall within the structure of Encrinuridae. Pliomeridae s.s. (including Placopariinae) and Hammatocneminae ranged from the Floian until the upper Katian. As understood herein, the family includes 42 valid genera and 181 species, all from the Ordovician. It is unusual in that it had a more-or-less cosmopolitan distribution throughout the Ordovician, but problems of identifying the basal node, tenuous knowledge of phylogenetic

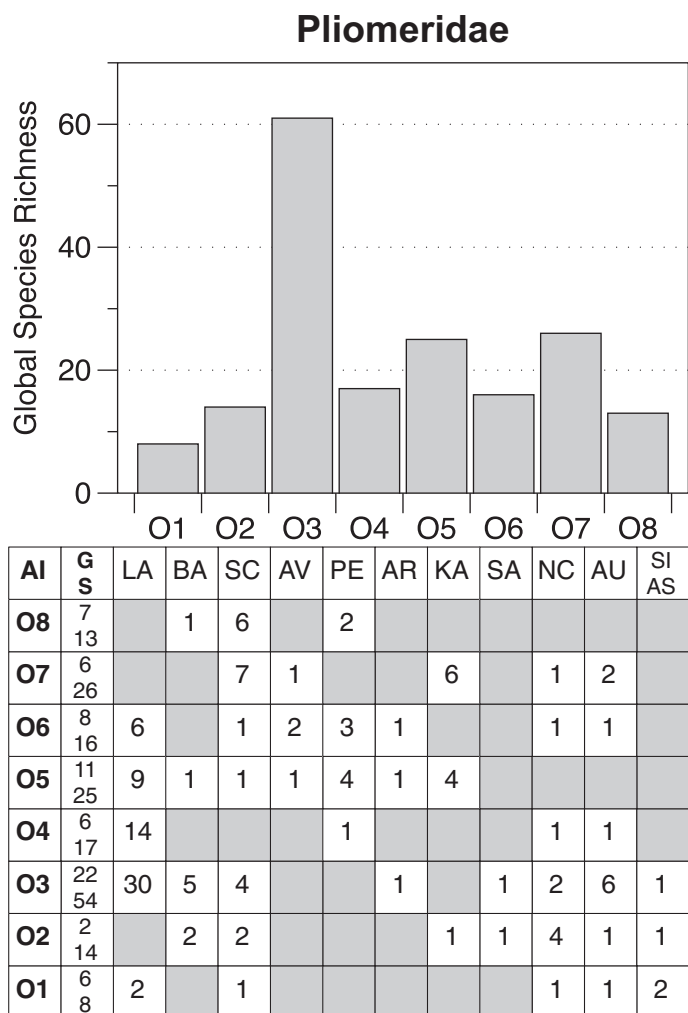


Fig. 20.20. Global taxonomic richness of the Family Pliomeridae during the Ordovician. See Figure 20.4 for explanation.

structure and potential parphyly all make discussion of patterns of distribution difficult at present. Work on the general phylogenetic structure of the family is in progress. Thus far, an analysis of *Paniaspis* McAdams & Adrain, 2011, has been published. Zhou *et al.* (2010) analysed the hammatocnemine *Ovalocephalus* Koroleva, 1959.

Suborder Calymenina Swinnerton, 1915

Family Bathycheilidae Přibyl, 1953. Bathycheilidae (Fig. 20.21) is a small group comprising only four genera and eight species with a mainly Gondwanan distribution in the Lower and Middle Ordovician. Only a few species are reasonably well known on the basis of distorted internal and external moulds (e.g. Hammann 1983; Mergl 2006). Members of the family have broadly calymenid-like glabellar morphology and the group has almost universally been classified as Calymenina, and on occasion regarded as a subfamily of Calymenidae (e.g. Henry 1980a). Often Pharostomatidae has been included in Bathycheilidae as a subfamily. Some aspects of bathycheilid morphology are not seen elsewhere within Calymenina. They tend to have their posterior fixigena greatly extended posteriorly and where known have 12 thoracic segments in contrast with the nearly universal 13 of Calymenina. Bathycheilids have not been subject to phylogenetic analysis.

Family Bavarillidae Sdzuy, 1957. Bavarillidae (Fig. 20.22) is a tiny clade comprising only three species assigned to a single genus (*Holoubkocheilus* Mergl, 1994, was assigned by Jell & Adrain

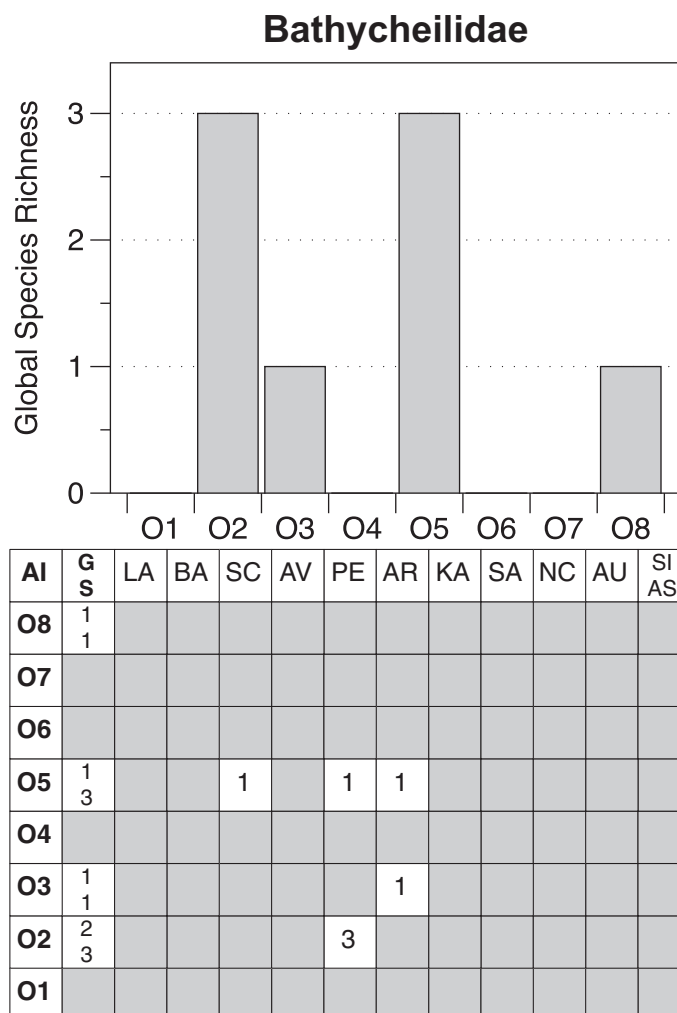


Fig. 20.21. Global taxonomic richness of the Family Bathycheilidae during the Ordovician. See Figure 20.4 for explanation.

(2003) but regarded as Pharostomatidae by Mergl (1994, 2006); Mergl's opinion is followed herein). The oldest assigned species is uppermost Cambrian (*Bavarilla tchoica* Petrunina, 1990, from the Gorny Altay) and the remainder are Lower Ordovician. None of the species are very well known, but the status of the taxon as Calymenina is very tenuous. *Bavarilla zemmourensis* Destombes In Destombes *et al.*, 1970, appears to have a median plectrum and pits in its anterior border furrow. *Bavarilla* may represent Olenida Adrain, 2011, and may possibly have affinities with Eulomidae. Bavarillids have not been subject to phylogenetic analysis.

Family Calymenidae Swinnerton, 1915. Calymenids (Fig. 20.23) first appear during the Floian, and the group persisted until the Middle Devonian (the last known species are Eifelian). Altogether, 316 valid species assigned to 33 genera are presently recognized, of which 168 and 21, respectively, occur in the Ordovician. There are two main subclades. The Subfamily Reedocalymeninae Hupé, 1955 (eight genera; 62 species), is restricted to the Ordovician with a range from Floian to upper Katian. It appeared nearly simultaneously during the Floian with Calymeninae, which has considerably lower Ordovician diversity but accounts for all post-Ordovician calymenid diversity. Reedocalymenines were widely distributed in Gondwana and South China during the Floian, and while very diverse, never achieved a wider distribution. The subfamily has been subject to detailed phylogenetic analysis by Turvey (2002). The earliest calymenines are Floian species from the Montagne Noire, France, described by Courtessole *et al.*

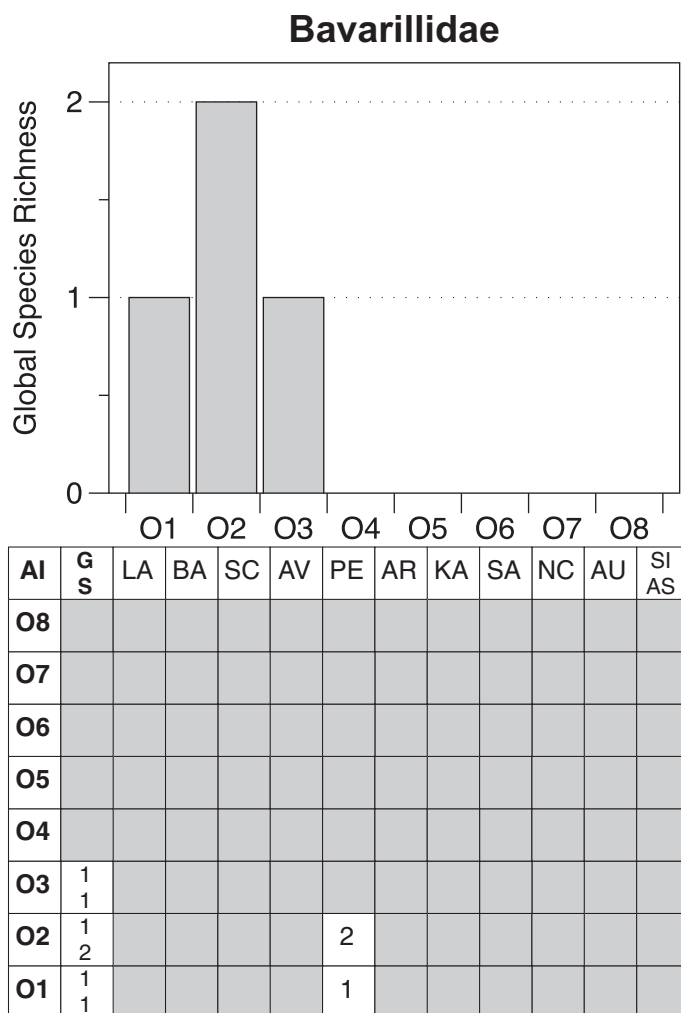


Fig. 20.22. Global taxonomic richness of the Family Bavarillidae during the Ordovician. See Figure 20.4 for explanation.

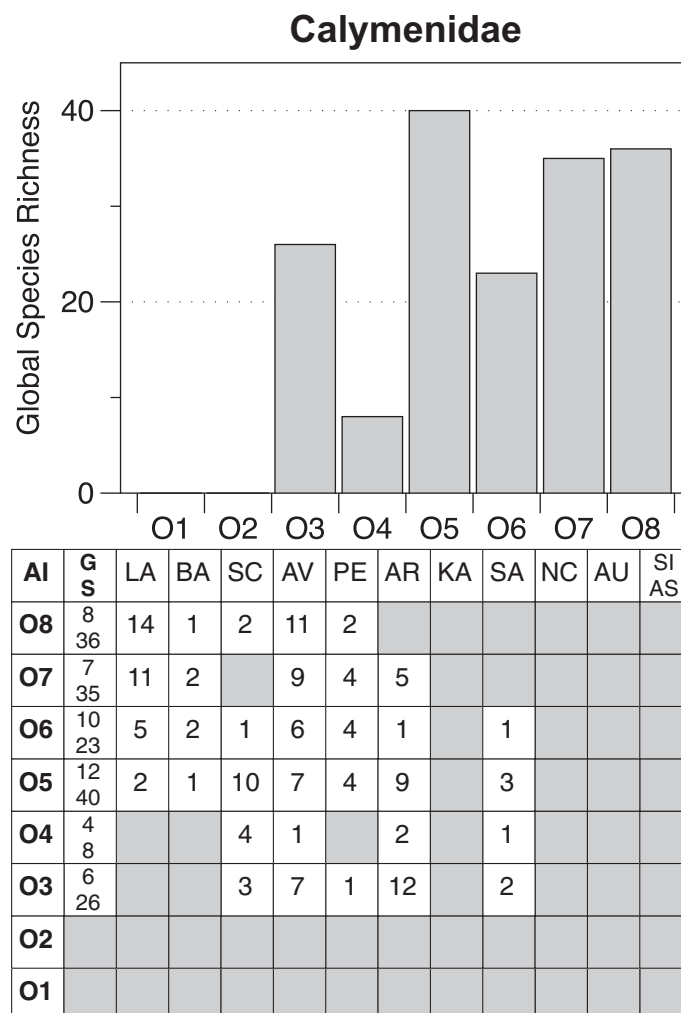


Fig. 20.23. Global taxonomic richness of the Family Calymenidae during the Ordovician. See Figure 20.4 for explanation.

(1983). The group appeared in Laurentia during the Dapingian (unnamed species described as '*Protocalymene* n. sp. A' by Fortey & Droser (1999)) and soon thereafter achieved an essentially global distribution. The calymenines were further split by Siveter (1977), who separated a new Subfamily Flexicalymeninae primarily on the absence of fixigenal buttresses to the glabellar lobes. This subfamily has been used by many authors, but it is clearly rendered paraphyletic by the thus restricted Calymeninae, and for this reason it is of dubious value. Calymenines include 11 genera and 81 species with occurrence in the Ordovician, and a still greater number of Siluro–Devonian species. A third small group is the exclusively Gondwanan Colpocoryphinae Hupé, 1955, which ranges from the Floian to Sandbian (two genera; 25 species). Colpocoryphinae was historically assigned to Homalonotidae, but Henry (1980b) demonstrated convincingly that it is in-group Calymenidae. Ordovician calymenines and colpocoryphines have not been subjected to phylogenetic analysis.

Family Homalonotidae Chapman, 1890. Homalonotids (Fig. 20.24) are the effaced sister group of Calymenidae. They appear during the Floian and, as with Calymeninae, the earliest known species are from Armorican Gondwana. The group persisted until the Middle Devonian (the youngest species are Givetian). Of a total of 171 valid species classified in 22 genera, 57 and eight, respectively, occur in the Ordovician. Most genera are assigned to the nominate subfamily, but two small Ordovician groups (comprising two genera each) are recognized as the subfamilies

Eohomalonotinae Hupé, 1953, and Kerfornellinae Henry, 1980b. Through much of the Ordovician, Homalonotidae was restricted in its distribution to Gondwana, but became essentially globally distributed during the Katian. While the group has been the subject of a cladistic analysis by Congreve & Lieberman (2008), the validity of this work is questionable, as among other issues only 15 species (less than 10% of the total) were included. Two of the species belong to *Colpocoryphe* Novák in Perner, 1918, which is a calymenid (Henry 1980b), and hence Congreve & Lieberman (2008) 'analysed' a polyphyletic in-group.

Family Pharostomatidae Hupé, 1953. Pharostomatidae (Fig. 20.25) is undoubtedly monophyletic and includes 49 species among eight genera with a distribution spanning the Ordovician, at the end of which the group became extinct. Most of the diversity is assigned to two genera: *Prionocheilus* Rouault, 1847 (24 species), and *Pharostomina* Sdzuy, 1955 (14 species). Although pharostomatids have an unusual morphology of ventrally spinose cephalic margins, their status as in-group Calymenina seems clear, as they have 13 segments and their general morphology is strikingly calymenid-like in most respects. They have often been classified as a subfamily of Bathycheilidae (e.g. Hammann 1983; Mergl 2006), but the status of Bathycheilidae as Calymenina is far less obvious and there are few obvious putative synapomorphies that would unite the groups. It is more likely that the pharostomatids are in-group Calymenidae (Adrain 2011). Pharostomatids have not been subject to phylogenetic analysis.

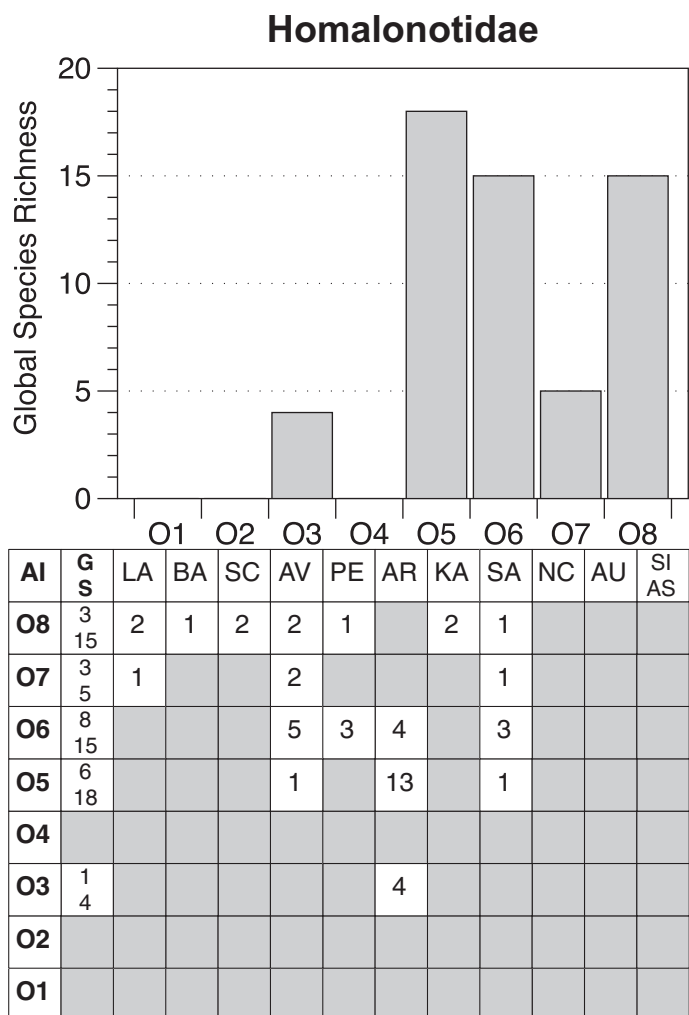


Fig. 20.24. Global taxonomic richness of the Family Homalonotidae during the Ordovician. See Figure 20.4 for explanation.

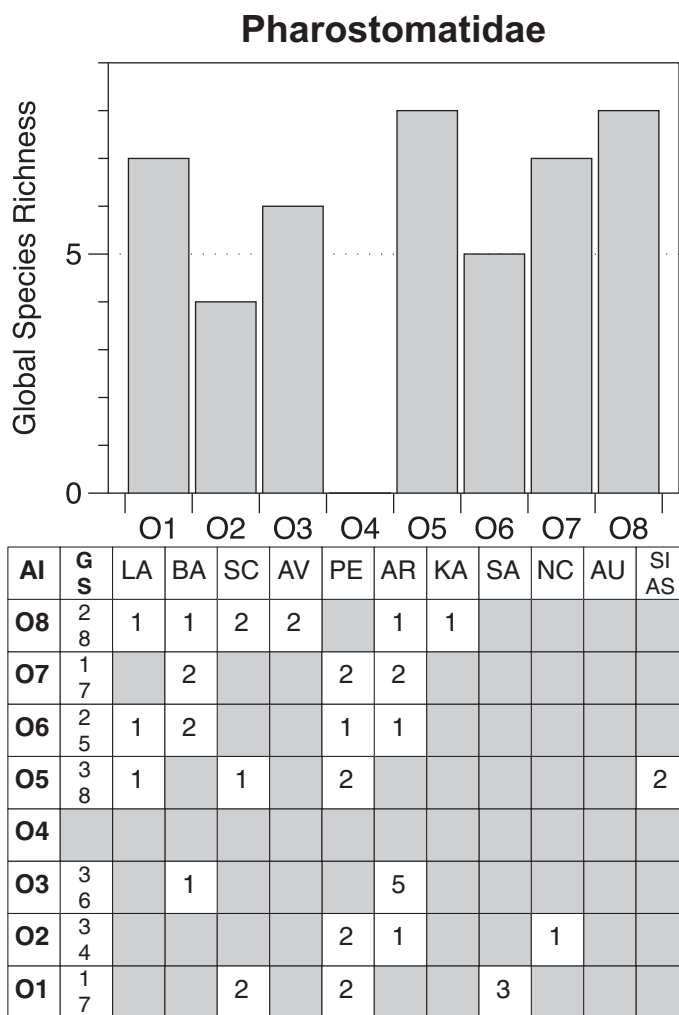


Fig. 20.25. Global taxonomic richness of the Family Pharostomatidae during the Ordovician. See Figure 20.4 for explanation.

Order Proetida Fortey & Owens, 1975

Adrain (2011) transferred many families previously classified in Proetida to a new Order Aulacopleurida (see below). The basis for this was the presence in all known examples of proetoidean ontogenies of only a single adult-like larval stage which lacks paired primary tubercles, preceded where known by a single, tiny and globular non-adult-like stage. The adult-like stage of proetoideans is most broadly similar to those of species of Aulacopleurida. While it remains conceivable that Proetida and Aulacopleurida will prove related, there is little or no positive evidence in the present state of knowledge. Aulacopleurida (with the taxa assigned to it by Adrain (2011)) has an extensive Cambrian history whereas Proetida as now restricted remains classically ‘cryptogenetic’ with a first appearance probably in the uppermost Floian (Adrain & Fortey 1997).

Proetida as a whole is the most diverse clearly monophyletic major clade of trilobites and also the longest ranging, as it occurs from near the beginning of the Middle Ordovician until the end of the Permian. At present there are a total of 314 genera and 1948 species referred to Proetidae and 74 genera and 513 species referred to Tropicoryphidae. Unfortunately, perhaps because of the very high diversity, systematics of the group are in serious disrepair. Even classification at family level lacks general agreement. Ordovician through Devonian taxa have often been classified in two families, Proetidae Salter, 1864 and Tropicoryphidae Přibyl, 1946, with the basic distinction

between them first outlined by Owens (1973a). Many workers, however, have not accepted this distinction and have treated Tropicoryphidae as a synonym of Proetidae. Despite this, established practice is to refer many post-Devonian proetoideans to a third family, Phillipsiidae (Oehlert 1886). This is one of the most absurd gradistic name-changes in palaeontology, in which a long-established and diverse taxon simply acquires a different name at a geological boundary. Whatever the chaos of familial classification, subfamilial classification is much worse, with different workers proposing radically different and irreconcilable schemes, and the assignment of (greatly oversplit) genus-group taxa changing from year to year and paper to paper. Virtually no significant phylogenetic work has been carried out on the detailed structure of the group, and a large-scale effort using modern systematic concepts and phylogenetic methods will probably be required before any substantial progress can be made.

Family Proetidae Salter, 1864

Despite the problems outlined above, classification of Ordovician through Devonian proetids and tropidocoryphids, while as gradistic as that of most other trilobite groups, is at the same time in no worse a state, with widely agreed and reasonably stable subfamilial classification (Fig. 20.26). Proetids are the less diverse of the two families in the Ordovician. The earliest assigned

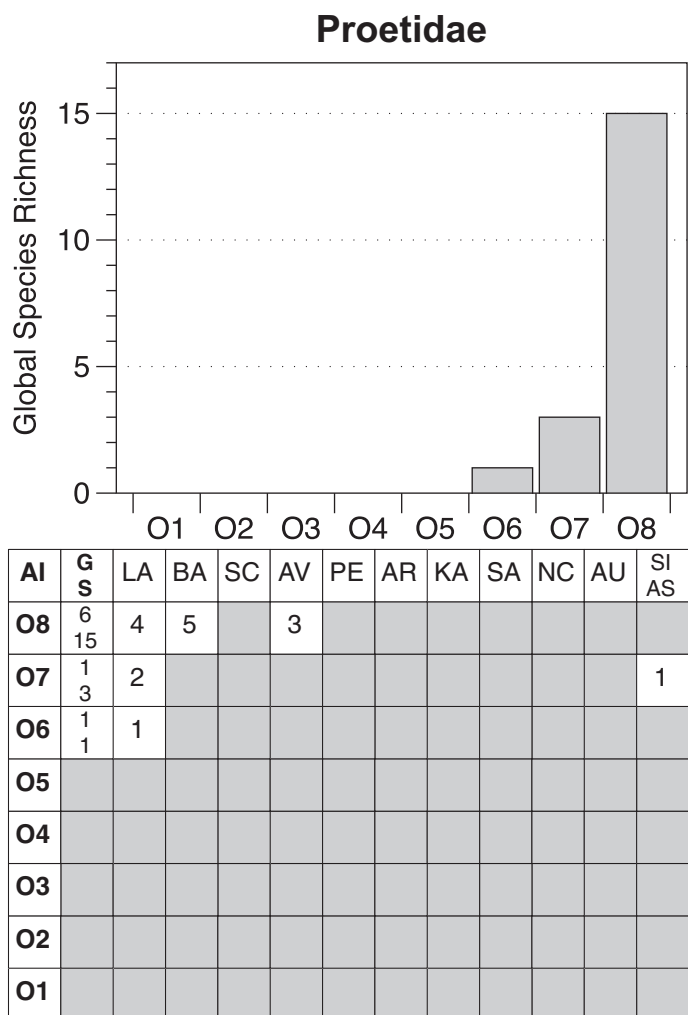


Fig. 20.26. Global taxonomic richness of the Family Proetidae during the Ordovician. See Figure 20.4 for explanation.

species is the crassiproetine *Astroproetus owensi* (Tripp, 1980), from the Sandbian of Laurentian Scotland, although *Mezzaluna? xeelee* Budil, Fatka, Zwanzig, and Rak, 2010, from the Darriwilian of Perunica, may belong. In total there are five genera with occurrence in the Ordovician and 19 valid Ordovician species. Ordovician diversity is strongly concentrated in Laurentia, but it is known also from the Katian of Baltica, Avalonia and Siberia. There has been a certain amount of phylogenetic work on Proetidae, but to date none which has investigated the relationships of Ordovician species.

Family Tropicocoryphidae Přibyl, 1946

Tropicocoryphidae (Fig. 20.27) appeared earlier and had more Ordovician diversity than Proetidae. The earliest known species is *Phaseolops ceryx* Adrain & Fortey, 1997, from a Laurentian-affiliated terrane in western Ireland. Adrain & Fortey (1997) considered that the age of the fauna was Dapingian (early White-rockian), but accumulating evidence suggests that it is probably upper Floian. A small handful of Darriwilian species are known, and I am presently describing collections containing several new tropicocoryphid genera from the Darriwilian Table Cove Formation of western Newfoundland, Canada. The family radiated in the Upper Ordovician and continued into the Silurian and beyond. By the Darriwilian it had appeared in Baltica, Avalonia and Gondwana and by the late Katian it was widely distributed. There is a significant species richness spike in the upper Katian

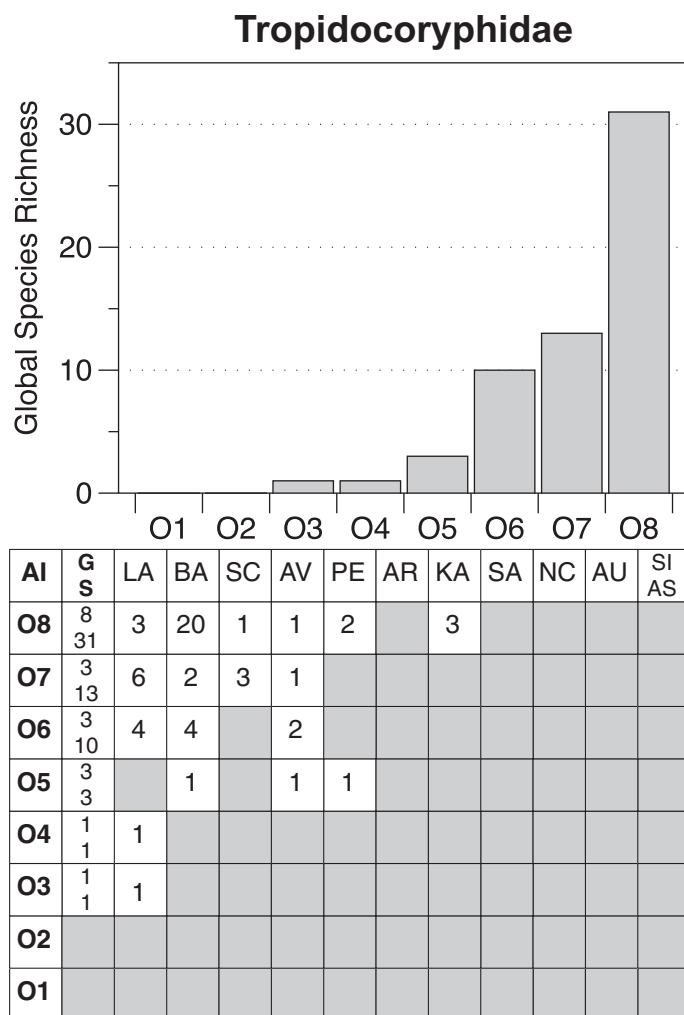


Fig. 20.27. Global taxonomic richness of the Family Tropicocoryphidae during the Ordovician. See Figure 20.4 for explanation.

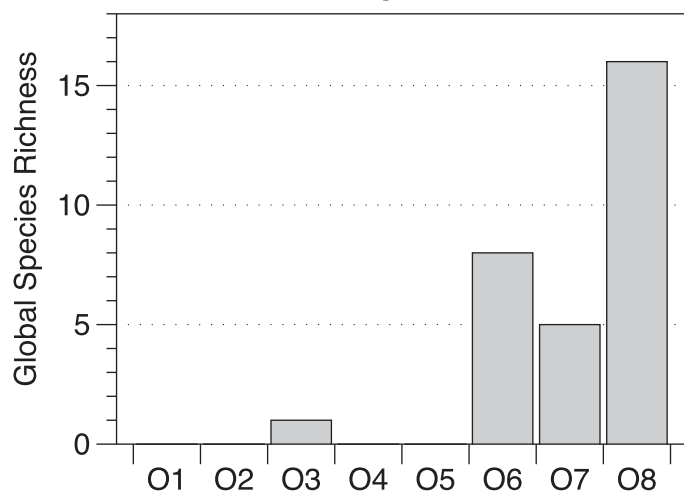
of Baltica (e.g. Pärnaste *et al.* 2009), but this is probably a monographic effect from the work of Owens (1973b). There are 10 genera with Ordovician occurrence and 59 valid Ordovician species. There has been some phylogenetic work, as Edgecombe *et al.* (1997) have analysed species of *Stenoblepharum* Owens, 1973b.

Order Aulacopleurida Adrain, 2011

Family Aulacopleuridae Angelin, 1854

The earliest aulacopleurid species is a matter of some dispute (Fig. 20.28). *Aulacopleura (Paraaulacopleura) szechuanica* Lu, 1975, was described as from the lower Tremadocian of the Panho Formation, Sichuan, South China. As noted by Adrain & Chatterton (1995, p. 327), the single specimen (a fairly well preserved complete dorsal exoskeleton) seems to be a genuine species of *Aulacopleura*. However, if that is so, the next oldest known species is Lower Silurian and the genus must have a history spanning the Ordovician without ever having been sampled. If Lu's specimen really is from the Tremadocian it is highly significant. The fact that no other specimens of aulacopleurids have ever been reported from rocks of this age, together with the close resemblance of the specimen to Silurian species of *Aulacopleura*, still invites strong doubt about the provenance of the species. It is so strikingly aberrant that I consider it best queried

Aulacopleuridae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	5 16	7	1		3	1		2				
O7	2 5	5										
O6	4 9	7	1									
O5												
O4												
O3	1 1			1								
O2												
O1												

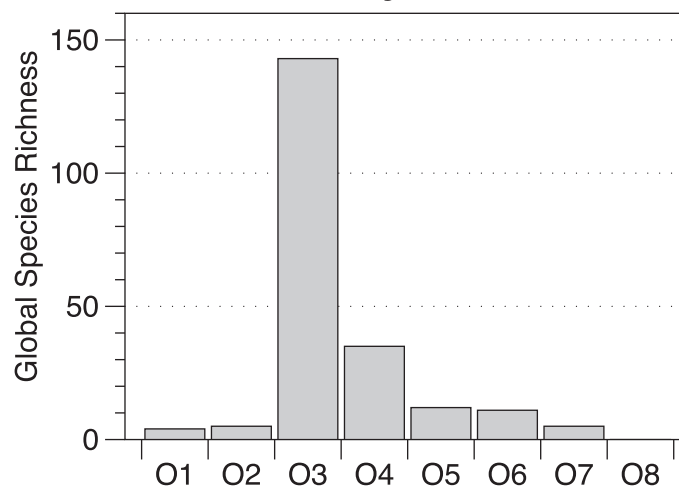
Fig. 20.28. Global taxonomic richness of the Family Aulacopleuridae during the Ordovician. See Figure 20.4 for explanation.

and ignored until its provenance can be corroborated with well-documented new material.

Setting *A. szechuanica* aside, the earliest potential aulacopleurid species is '*Otarion*' *insolitum* Dean, 1966, from the Landeyran Formation (upper Floian) of the Montagne Noire, France. Unfortunately, Dean based this species on a single incomplete and poorly preserved cranidium. Its isolated L1 means that it is probably, although not definitively, an aulacopleurid. In its general dimensions, it is broadly similar to the Sandbian species *Strasburgaspis cona* (Hu, 1971) (see Adrain 2005). However, it could also represent a scharyiid such as *Panarchaeogonus* Öpik, 1937, although the earliest known scharyiid is Darriwilian. Another early species is '*Aulacopleura* (*Paraaulacopleura*)' *dawanensis* Lu, 1975, from the upper Floian or Dapingian of the Dawan Formation, Hubei, South China. This species is known from several specimens and its aulacopleurid affinity seems more certain. Nevertheless, it is not well described (partial cranidia and part of an articulated thorax) and at present difficult to assess in detail, but it should not be assigned to *Aulacopleura* Hawle & Corda, 1847. No other Floian or Dapingian species have been described, nor have any Darriwilian, but I have abundant material of an undescribed Laurentian Darriwilian species from the Table Cove Formation of Newfoundland, Canada. Aulacopleurids are fairly common in the Sandbian (mostly Laurentia, but one species from Baltica) and lower Katian. Like many other groups they are widely distributed in the upper Katian.

Adrain & Chatterton (1995) proposed a classification into a Subfamily Otariioninae Richter & Richter, 1926 (Darriwilian

Bathyuridae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8												
O7	2 5	5										
O6	3 11	11										
O5	5 14	13										1
O4	12 33	32		1								
O3	29 143	133		1						1		5
O2	2 5	4		1								
O1	2 4	1		1						2		

Fig. 20.29. Global taxonomic richness of the Family Bathyuridae during the Ordovician. See Figure 20.4 for explanation.

to Carboniferous, 10 genera, 217 species), and a Subfamily Aulacopleurinae (Silurian to Middle Devonian, two genera, 34 species). The low-diversity Subfamily Cyphaspidinae Přibyl, 1947 (upper Katian to Eifelian, although no Silurian species are known, two genera, 12 species) is difficult to interpret as no species are well known and the group has highly derived morphology, but it is provisionally accepted as Aulacopleuridae. Ordovician aulacopleurids include 31 species assigned to seven valid genera. All but one of the Ordovician species is presently assigned to Otariioninae. Cyphaspidinae is represented by a single upper Katian pygidium (*Protocyphaspidites deani* Lütke, 1980). Although there are several phylogenetic studies of Silurian and Devonian species (e.g. Adrain & Chatterton 1994; Yuan *et al.* 2001; Rustán & Vaccari 2010), as yet no analyses have examined the phylogenetic structure of Ordovician taxa.

Family Bathyuridae Walcott, 1886

The exclusively Ordovician Bathyuridae (Fig. 20.29; 38 genera; 222 species) is a predominantly Laurentian taxon, although it had minor distributions in other low-latitude palaeocontinents (North and South China, peri-Siberia, Omulevka Terrane) through much of its history. Tremadocian taxa are generally rare and not well understood. The family proliferated in shallow-water environments during the Floian and Dapingian. Diversity was severely curtailed during the Darriwilian, but the group persisted until the early Katian.

Following a proposal by Fortey & Owens (1975) the sub-families Bathyrinae and Bathyrellinae Hupé, 1953, have been in use (see also Fortey 1979). Adrain *et al.* (2003, 2011a), however, have argued that these groups are not monophyletic and have not used them. Work on a comprehensive revision of the family is underway (e.g. McAdams & Adrain 2007; Adrain *et al.* 2011a, b; Adrain & McAdams 2012) with species-level phylogenetic analyses in progress for all genera.

Family Brachymetopidae Prantl & Přibyl, 1951

Brachymetopids (Fig. 20.30) have been considered by Owens & Thomas (1975) to include the protoidean Subfamily Warburgellinae Owens, 1973a, and by Owens (in Owens & Hammann 1990) to include a Subfamily Scharyiinae Osmólska, 1957. Adrain & Kloc (1997) restricted the family to what these previous authors had termed Brachymetopinae, and considered Scharyiidae to be a separate family (see below). Brachymetopids first appear in the lower Katian. They have limited Ordovician and Silurian diversity, all of which is presently assigned to *Radnorina* Thomas & Owens, 1975. The group diversified during the Devonian and survived until the end of the Permian. As presently classified there are 12 post-Devonian genus-group taxa, but as is typical of Upper Palaeozoic trilobites, the species involved are often very poorly illustrated and the genus-group taxonomy is very finely parsed. There are six named Katian species, from Armorica, South China and the Kazakh terranes.

Family Dimeropygidae Hupé, 1953

Classification of the exclusively Ordovician Dimeropygidae (Fig. 20.31; 15 genera; 86 species), like that of several aulacopleuroidean families, has been in flux. The history, main problems of classification and current taxonomic arrangements were reviewed by Adrain & Westrop (2007a) and are not repeated here. The early history of the family is concentrated in Laurentia and the handful of Tremadocian and Dapingian species from elsewhere are not well known and of questionable affinity. Beginning in the Sandbian, the group became cosmopolitan at low latitudes. A relatively large amount of phylogenetic work has been carried out. Chatterton (1994) analysed *Dimeropyge* Öpik, 1937, along with some species of *Ischyrotoma* Raymond, 1925. Chatterton *et al.* (1998) analysed most of the group, although aspects of the taxon sampling, character analysis and results were not accepted by Adrain & Westrop (2007a). Adrain *et al.* (2001) analysed *Ischyrotoma* and *Dimeropygiella* Ross, 1951, Adrain & Westrop (2007a) analysed their new *Bearriverops*, and McAdams & Adrain (2009b) their new *Heckethornia*. Yuan *et al.* (2006) analysed *Pseudopetigurus* Prantl & Přibyl, 1949.

Family Holotrachelidae Warburg, 1925

This family includes only *Holotrachelus* Holm, 1898, which is known from four formally named Katian species (Fig. 20.32). The affinity of the genus is difficult to determine. The cephalon

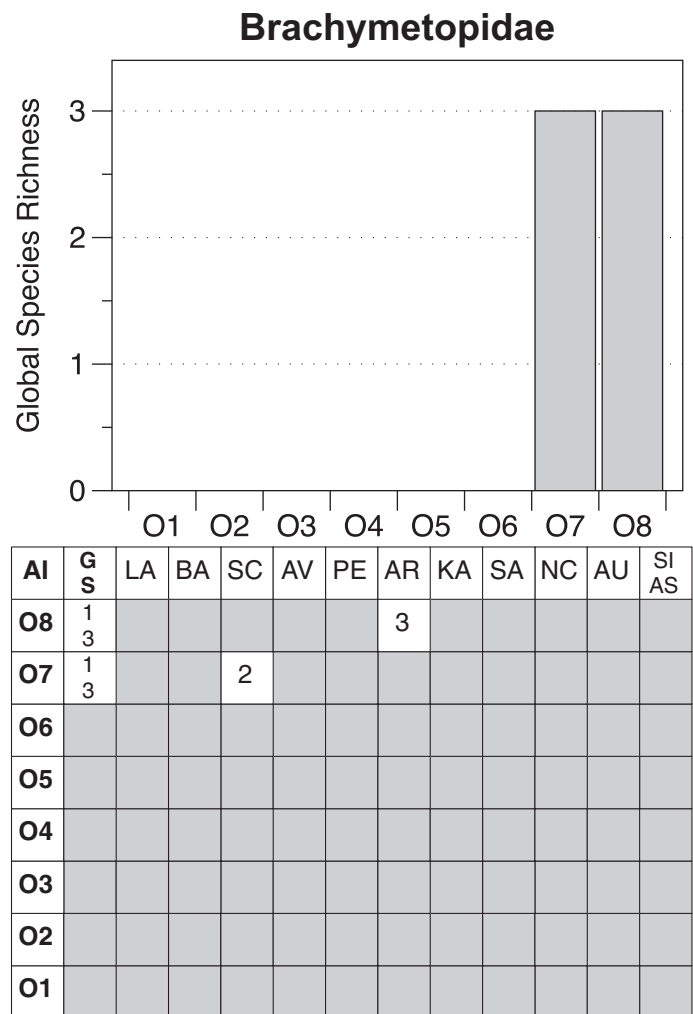


Fig. 20.30. Global taxonomic richness of the Family Brachymetopidae during the Ordovician. See Figure 20.4 for explanation.

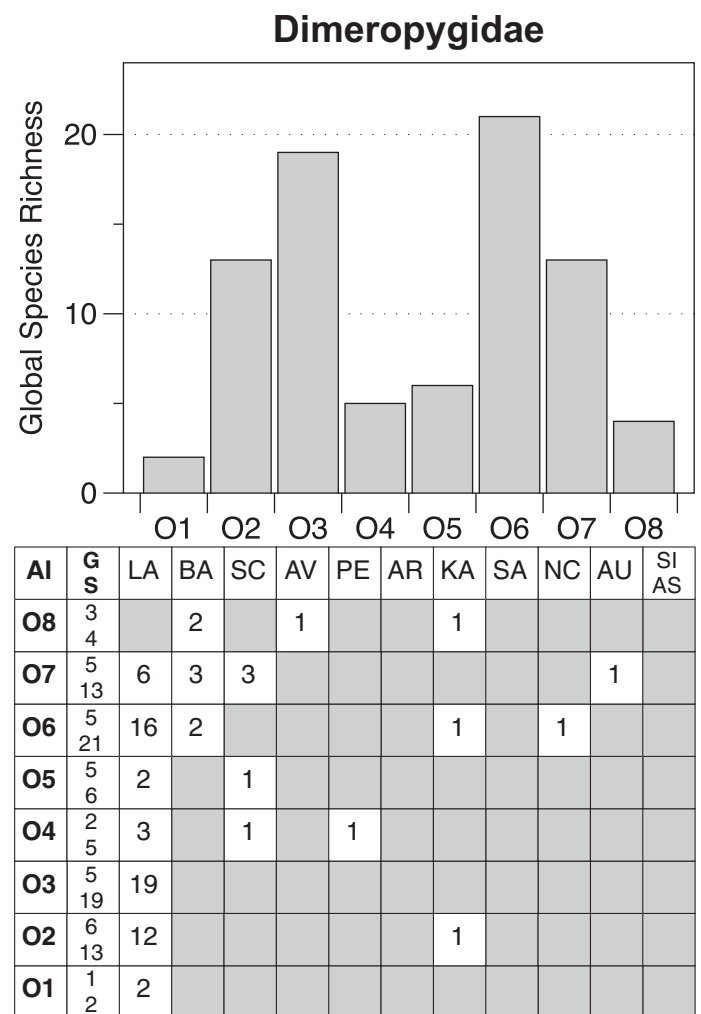
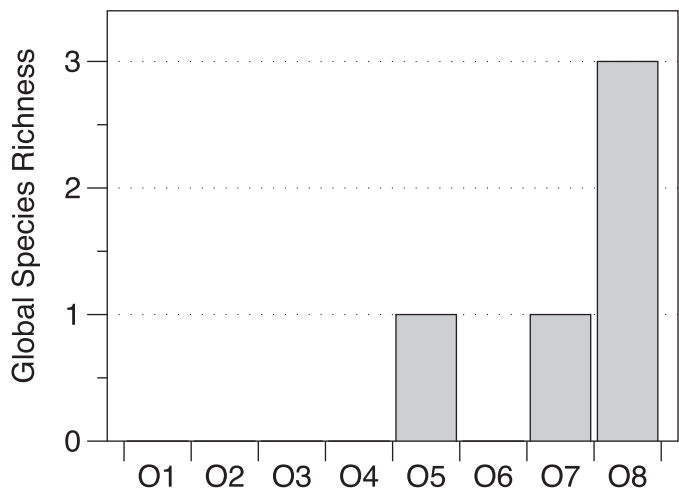


Fig. 20.31. Global taxonomic richness of the Family Dimeropygidae during the Ordovician. See Figure 20.4 for explanation.

Holotrachelidae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	1 3	1	1	1								
O7	1 1							1				
O6												
O5												
O4												
O3												
O2												
O1												

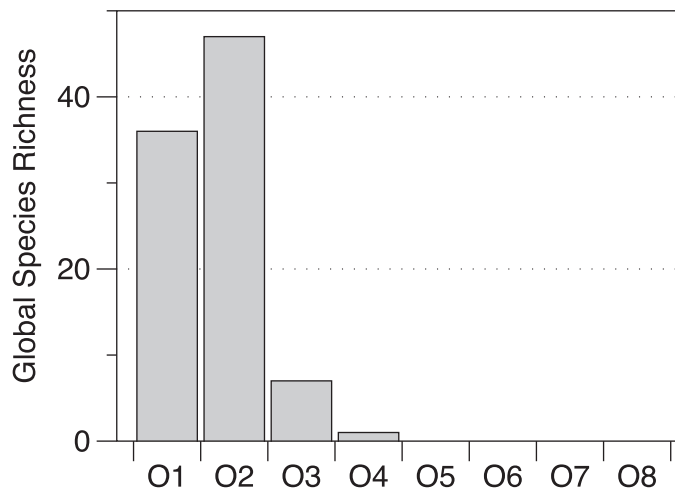
Fig. 20.32. Global taxonomic richness of the Family Holotrachelidae during the Ordovician. See Figure 20.4 for explanation.

is effaced and the pygidium has an unusual morphology, with broad, nearly flat, featureless segments. There is a general resemblance to both Bathyruridae and (effaced) Dimeropygidae. It seems unlikely that a ‘family’ will ultimately be retained for the genus, as it is presumably a highly derived in-group species nested within the phylogenetic structure of some other established Ordovician family. *Kinderlania* Ancygin, 1977, from the Darriwilian of Baltica (Urals) was assigned to the family by its author and listed as such by Jell & Adrain (2003). However, *Kinderlania* lacks the unusual pygidium of *Holotrachelus*, and instead has a large, normally segmented tail similar to that of some Bathyruridae, to which it may belong. Xiang & Ji (1988) assigned their new *Qijiangia* to a new monotypic Family Qijiangiidae, but considered that it was most closely related to *Holotrachelus*. Cranidia of *Qijiangia szechuanensis* Xiang and Ji, 1988, bear a prominent glabellar tubercle and the taxon appears to represent Nileidae, of which Qijiangiidae should be considered a junior synonym. Despite its low number of species, *Holotrachelus* was widely distributed.

Family Hystricuridae Hupé, 1953

The phylogenetic status of Hystricuridae (Fig. 20.33) was reviewed by Adrain *et al.* (2003), who began the process of recognizing putatively monophyletic components of the group. Much work remains to be done, as particular groups currently included in the taxon may prove to be the sister taxa of other families (e.g. Dimeropygidae, Aulacopleuridae). At present, the

Hystricuridae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8												
O7												
O6												
O5												
O4	1 1	1										
O3	4 7	2		1				1			1	2
O2	15 47	35				1				4	2	2
O1	13 36	24								2		6

Fig. 20.33. Global taxonomic richness of the Family Hystricuridae during the Ordovician. See Figure 20.4 for explanation.

subfamilies Hystricurinae, Hintzeturinae Adrain, Lee, Westrop, Chatterton & Landing, 2003 and Hillyardininae Adrain & Westrop, 2007a have been discriminated, although together they do not include all genera possibly belonging to the family (e.g. *Millardicurus* Adrain & Westrop, 2006a, does not belong to any of them). *Millardicurus* includes the oldest presently assigned species, some of which have been listed by Loch in Miller *et al.* (2003) as having ranges in the uppermost Cambrian, although no material of these has yet been illustrated. Certainly species of the genus occur only a few metres above the Cambrian–Ordovician boundary in western Utah.

The main potentially monophyletic groups of Hystricuridae and most of the total taxa are restricted to the Tremadocian. The few Floian and Dapingian genera presently assigned to the family are mostly not well known and their affinities not well established. Hystricurids were widely distributed at low latitudes during the Tremadocian, although their numbers are overwhelmingly concentrated in Laurentia. This is surely driven to some extent by global sampling bias. At present, the family includes 91 Ordovician species assigned to 30 valid genera. Although considerable work is in progress, no detailed phylogenetic analyses have yet been published, although some hystricurids were included in the analysis of Chatterton *et al.* (1998).

Family Rorringtoniidae Owens in Owens & Hammann, 1990

The erection of Rorringtoniidae (Fig. 20.34) was an important step in clarifying monophyletic groups within Aulacopleuroidea, and

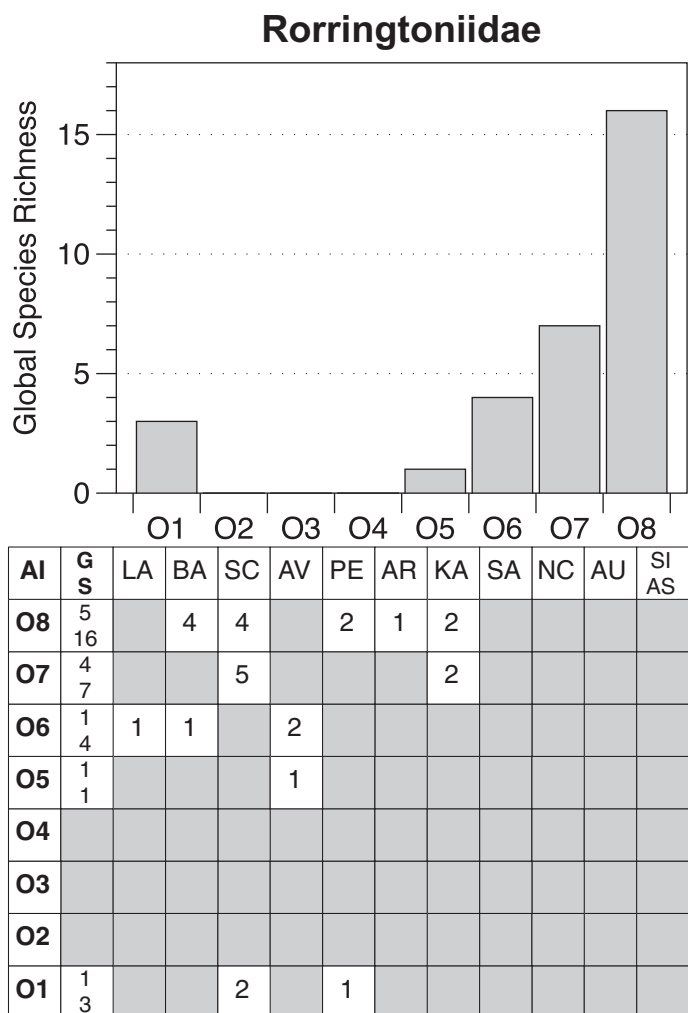


Fig. 20.34. Global taxonomic richness of the Family Rorringtoniidae during the Ordovician. See Figure 20.4 for explanation.

knowledge of its members is due largely to the meticulous work of Owens (e.g. 1970, 1979, 1981, 2004). The picture was muddled by Adrain & Chatterton (1993), who misassigned their new *Goodsiraspis* to the family. Adrain & Edgecombe (1996) re-assigned the genus to Aulacopleuridae and considered it a junior subjective synonym of *Malimanaspis* Baldis & Longobucco, 1977. The family is mainly Ordovician, although Owens (2004) demonstrated that *Pseudobirmanites* Li, 1978 (the available name for the preoccupied but not replaced *Madygenia* Petrunina in Repina *et al.*, 1975; see Adrain in Jell & Adrain (2003, p. 433) and Özdikmen (2009, p. 161)) ranges to the Aeronian. The earliest species presently assigned are those from the early Tremadocian of Bavaria and South China assigned to *Protarchaeogonus* Sdzuy, 1955. These are not well known and their affinity does not seem established beyond doubt. The next oldest species is the Darriwilian *Rorringtonia kennedyi* Owens, 1981, so if *Protarchaeogonus* is a rorringtoniid then there is a substantial sampling gap. There are seven genera containing 31 Ordovician species, and no subfamilies are recognized. There have been no phylogenetic analyses of any members of the family.

Family Scharyiidae Osmólska, 1957

Scharyiidae (Fig. 20.35) has had an unsettled modern taxonomic history, as both its family-group affinity and genus content have been in flux. It has been considered a subfamily of Aulacopleuridae

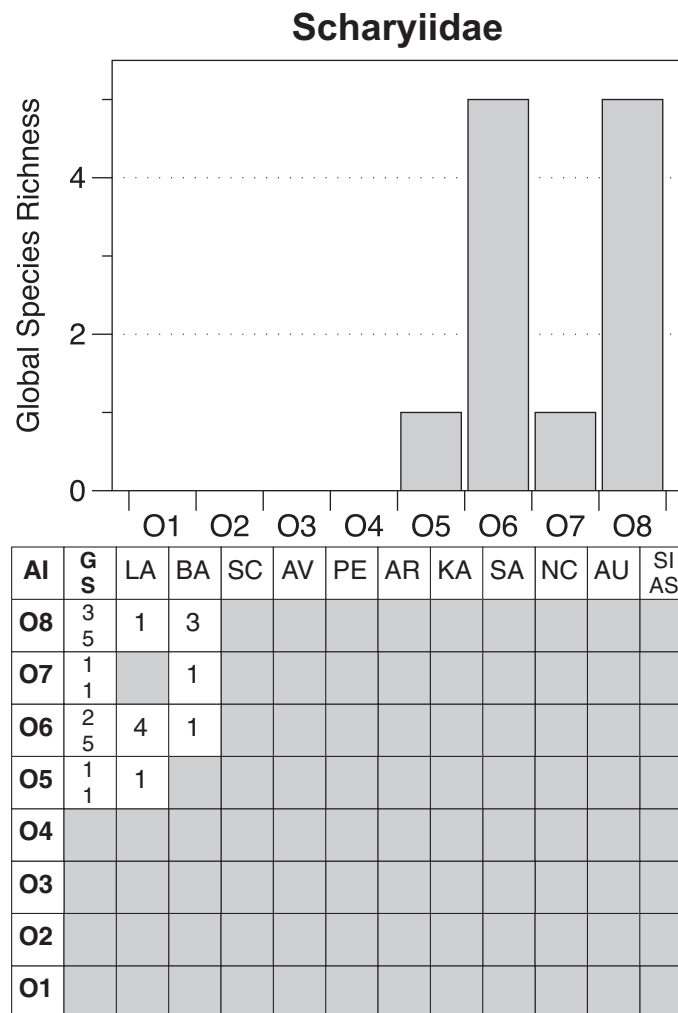


Fig. 20.35. Global taxonomic richness of the Family Scharyiidae during the Ordovician. See Figure 20.4 for explanation.

following Owens (1974) and Thomas & Owens (1978), a subfamily of Brachymetopidae following Owens & Hammann (1990), and an independent aulacopleuroidean family following Adrain & Chatterton (1993) and Adrain & Kloc (1997). It has been construed as including only *Scharyia* Přibyl, 1946 (e.g. Thomas & Owens 1978), as including *Panarchaeogonus* Öpik, 1937, *Isbergia* Warburg, 1925 and *Cyamella* Owens in Owens & Hammann, 1990 (e.g. Owens 1979), as including *Oenonella* Fortey, 1980, and as including *Proscharyia* Peng, 1990a (e.g. Adrain & Kloc 1997). The current classification is as outlined by Adrain in Jell & Adrain (2003) and accepted and diagnosed by Owens & Fortey (2009): Scharyiidae is an apparent clade consisting of *Scharyia*, *Panarchaeogonus*, *Niuchangella* Zhang, 1974 and *Lasarchopyge* Chatterton, Edgecombe, Waisfeld & Vaccari, 1998. No subfamilies are recognized.

All of the genera have Ordovician species assigned. *Niuchangella* ranges into the lower Llandovery, whereas *Scharyia* ranges to the Eifelian. A total of 12 Ordovician species have been described. The earliest is *Lasarchopyge correae* Chatterton, Edgecombe, Waisfeld & Vaccari, 1998, from the Darriwilian Las Aguaditas Formation of the Precordillera Terrane, Argentina. No phylogenetic analyses have been published.

Family Telephinidae Marek, 1952

The exclusively Ordovician (Fig. 20.36; eight genera; 127 species) telephinids are an important group because they include many

species which had an epipelagic life habit. As a result, nearly alone among Ordovician trilobites, they achieved genuine intercontinental distributions (e.g. McCormick & Fortey 1999) and are exceptionally useful for biostratigraphical correlation. No sub-families are presently recognized, although there has been historical confusion, with the synonymous taxon *Opipeuteridae* Fortey, 1974a, having been repeatedly assigned to Remopleuridoidea. Dean (1971) named Carrickiinae, which if recognized would include only the genus *Phorocephala* Lu in Lu *et al.*, 1965. The relationship of this taxon to the remainder of the family is at present uncertain and it is conceivable it does not belong. Work in progress suggests that the family roots among taxa historically assigned to Hystricuridae. The telephinids originated in the late Tremadocian and *Carolinites* Kobayashi, 1940 and *Opipeuterella* Fortey, 2005, became very common with a global distribution at low latitudes (as well as some high-latitude occurrences) by the end of the Floian. Although *Carolinites* persisted into the Darriwilian, a second major clade, including *Telephina* Marek, 1952 and *Telephops* Nikolaisen, 1963, radiated dramatically during the Darriwilian and persisted until the end-Ordovician. Thus far no phylogenetic analyses have been published, although McCormick & Fortey (2002, text, fig. 1) presented a phylogeny for *Carolinites*, which was said to be based on an unpublished cladistic analysis. Work is in progress on comprehensive analyses of *Carolinites*, *Opipeuterella* and *Goniophrys* Ross, 1951 (Adrain, Karim and McAdams, unpublished data).

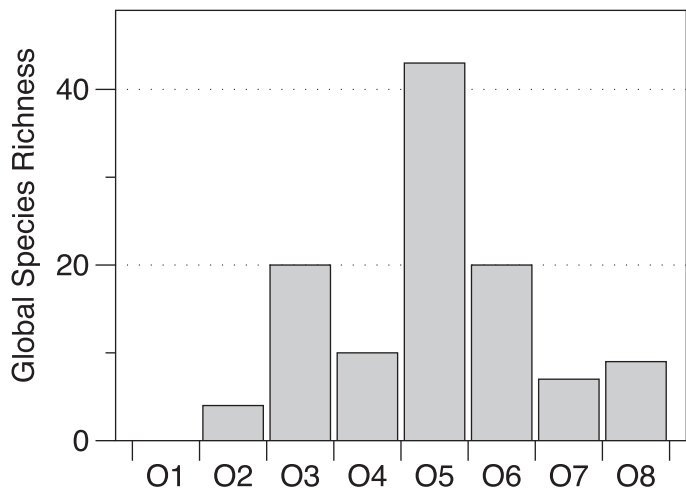
Order Asaphida Salter, 1864

This taxon was thoroughly reviewed by Fortey & Chatterton (1988). Although I regard Remopleurididae as Order Olenida, and some of the other families assigned or tentatively assigned by Fortey & Chatterton as of less certain affinity, their paper was a major milestone in a modern understanding of higher trilobite phylogenetic structure, and it included one of the first large-scale cladistic analyses of these problems. My discussions of asaphide taxa below are brief, as all of the remarks made by Fortey & Chatterton (1988) still apply.

Superfamily Asaphoidea Burmeister, 1843

Family Asaphidae Burmeister, 1843. The most widely distributed, most species-rich, and most important of Ordovician trilobite families is also one of the least well understood from a phylogenetic perspective (Fig. 20.37). Ordovician asaphids include 146 genera containing 754 species. Part of the problem is morphological – asaphids tend to be effaced and major groups had conservative body plans with a limited range of morphological variation. A major part is historical – works such as Balašova (1976) introduced a great number of finely divided genus-group and family-group taxa whose phylogenetic coherency is not always evident. In this respect the asaphids are quite similar to the taxonomic quagmire that is Mid and Upper Palaeozoic Proetida (see comments above).

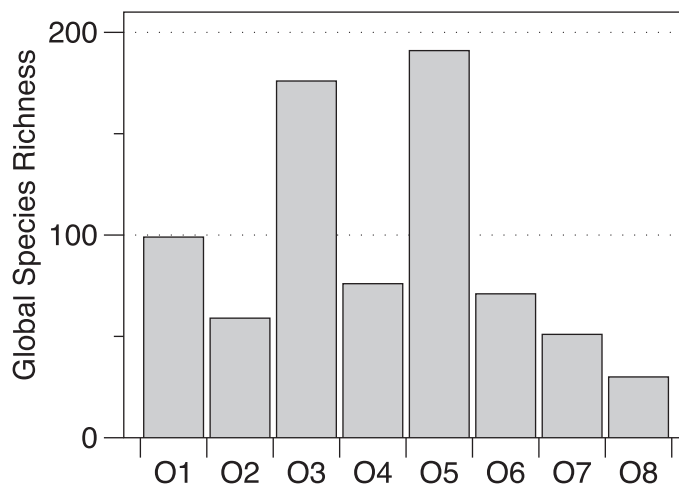
Telephinidae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	2 9		1	4	1	1		1				
O7	2 7	1		2				1		1		
O6	3 20	6	1	2				1			1	
O5	4 43	12	11	8						1	2	1
O4	3 10	7		3								
O3	4 20	6	1	3			1		1		7	
O2	2 4	2		2								
O1												

Fig. 20.36. Global taxonomic richness of the Family Telephinidae during the Ordovician. See Figure 20.4 for explanation.

Asaphidae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	10 30	12	3	3	1	1		1				
O7	15 51	21	5	4		3		5		3		1
O6	21 71	30	14	6	7	1		2		3	2	
O5	54 191	8	102	17	10	6	8	4	7	11	2	6
O4	31 76	1	19	3	1	2		1	3	4	5	
O3	62 176	44	27	22	7	1	12	2	20	2	24	
O2	20 59	3	7	18	2		1	2	12	4	1	
O1	22 99	47		14	4			1	3	4		18

Fig. 20.37. Global taxonomic richness of the Family Asaphidae during the Ordovician. See Figure 20.4 for explanation.

Despite the taxonomic problems, it is clear that there is considerable geographical signal among the generally recognized subfamilies. Major components of Asaphinae are characteristic of Baltica. Isotelinae Angelin, 1854, is strongly concentrated in Laurentia. Nobiliasaphinae Balašova, 1971, has a tropical Gondwana–South China distribution (Turvey 2007) and Ogygiocaridinae Raymond, 1937, is characteristically Avalonian–Gondwanan–Baltic. Asaphids were fairly common in the late Cambrian, with 14 genera concentrated in Australia and North and South China. They became extinct at the end-Ordovician.

No phylogenetic perspective has ever truly been applied to Asaphidae, and no modern analyses have been published. Carrying out a comprehensive analysis would be a huge task, but in its absence, even disregarding the taxonomic difficulties referenced above, there are few firm ideas about the inclusivity or monophyly of major asaphid subgroups. It is hence difficult to carry out even a phenetic biogeographical analysis, and probably the single largest source of family-level data on the distribution of Ordovician trilobites cannot fully be exploited.

Family Ceratopygidae Linnarsson, 1869

Ceratopygidae (Fig. 20.38) is a mainly Cambrian family. Four subfamilies are recognized, of which two, the nominal subfamily (13 genera, 37 species) and Macropyginae Kobayashi, 1937 (10 genera, 118 species), occur in the Ordovician. There is a total of 12 genera with Ordovician occurrence and 56 valid Ordovician

species. The group is found in most palaeocontinents save Laurentia during the Tremadocian. A Floian Laurentian genus, *Gladiatoria* Hupé, 1955, has generally been considered to be a macropygine ceratopygid. However Adrain *et al.* (2011a) have shown that it is a bathyurid. Hence ceratopygids became extinct, as far as is known, at the end of the Tremadocian. No modern phylogenetic analyses of the group have been published.

Superfamily Cyclopygoidea Raymond, 1925

Family Cyclopygidae Raymond, 1925. Cyclopygidae (Fig. 20.39) includes deep-water trilobites with large, sometimes hypertrophied eyes. They are interpreted as mesopelagic swimmers (see Fortey 1985, pp. 222–223), but their occurrence is tied closely to the deep-water ‘atheloptic assemblage’ of often blind benthic trilobites recognized by Fortey & Owens (1987, p. 105). In this respect they are unlike the other main Ordovician pelagic group, Telephinae, whose species are found in a much broader range of generally shallower environments. Despite this, cyclopygids achieved very wide distributions, although it has not been clearly established that individual species had intercontinental distributions, as seems certainly to have been the case with some telephinae. The single most important taxonomic work on the group, following the early review of Czech taxa by Marek (1961), is the revision by Fortey & Owens (1987). There have been three subfamilies recognized. They are the nominal subfamily (15 genera, 114 species), Ellipsotaphrinae Kobayashi &

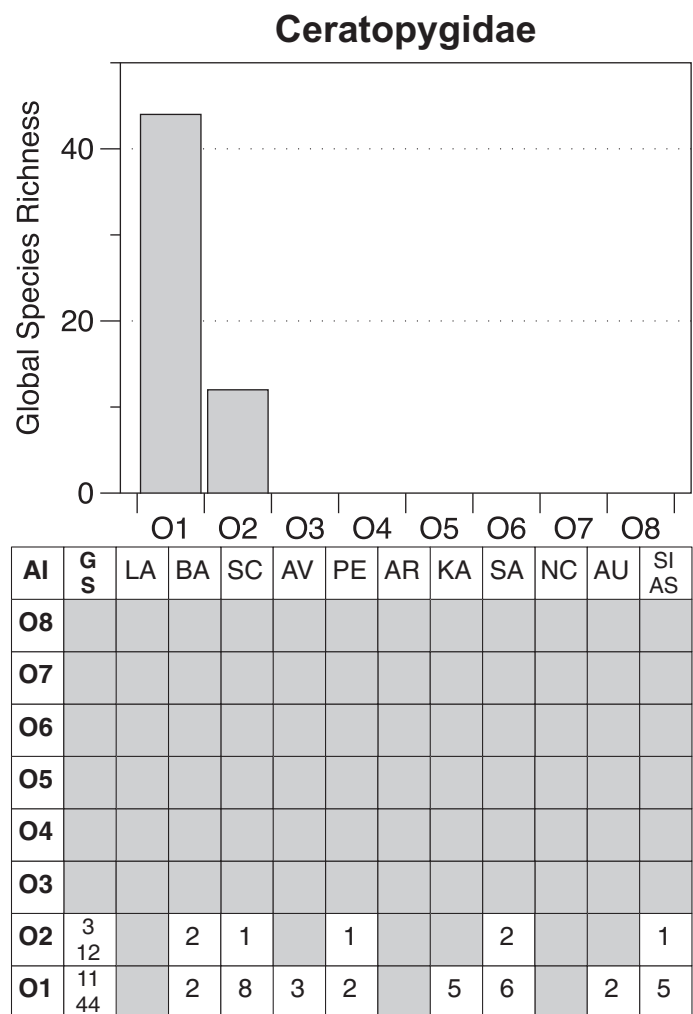


Fig. 20.38. Global taxonomic richness of the Family Ceratopygidae during the Ordovician. See Figure 20.4 for explanation.

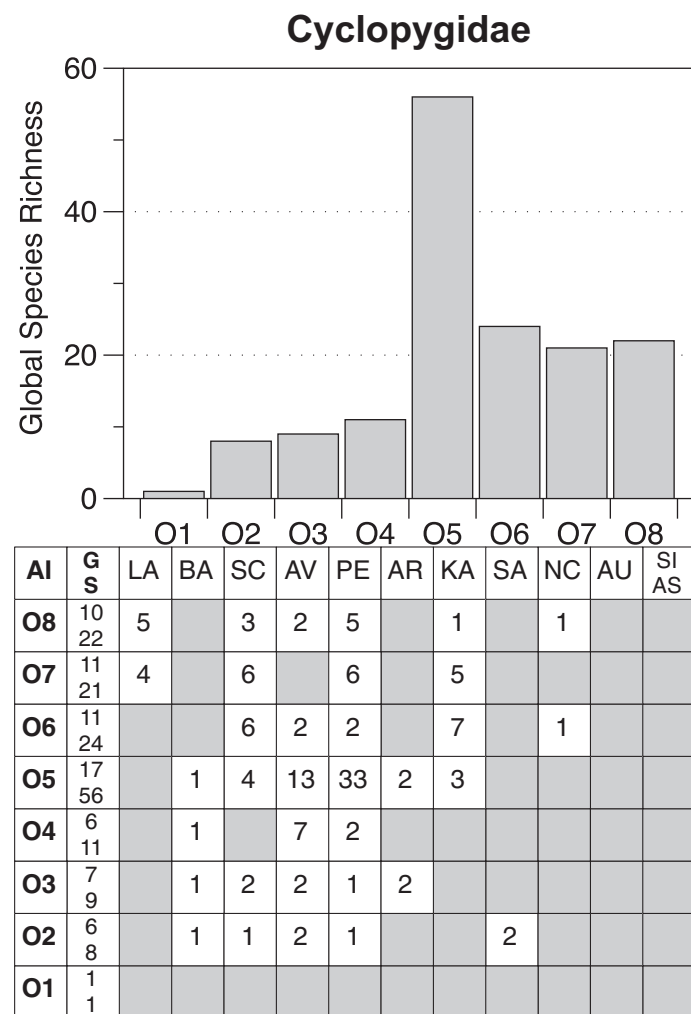


Fig. 20.39. Global taxonomic richness of the Family Cyclopygidae during the Ordovician. See Figure 20.4 for explanation.

Hamada, 1971*b* (three genera, 11 species) and Pricyclopyginae Fortey & Owens, 1987 (four genera, 29 species). A family Boehmilleridae Barrande, 1872 (two genera, seven species), was considered remopleuridoidean by Fortey & Owens (1987). I regard it as most probably in-group Cyclopygidae and treat it as a fourth subfamily. *Girvanopyge* Kobayashi, 1960, was assigned to Remopleuridae by Fortey (1981) and Fortey & Owens (1987); I regard it as a cyclopygid in keeping with the opinion of most previous workers. The earliest known cyclopygid species is the early Tremadocian *Prospectatrix exquisita* Zhou, McNamara, Yuan & Zhang, 1994, from Tarim. Cyclopygids have a strongly Gondwanan signal through most of their history, but appeared in Laurentia in the Katian. The exclusively Ordovician family ranged until the end-Ordovician extinction. It includes 24 genera and 161 valid species. No modern phylogenetic analyses have been published.

Family Nileidae Angelin, 1854. The earliest recognized nileids are a handful of latest Cambrian species assigned to three genera, but the bulk of the family is Ordovician (Fig. 20.40). There are 27 genera with Ordovician occurrence and 146 valid Ordovician species. The family became extinct at the end-Ordovician. No subfamilies are recognized. The only significant taxonomic controversies are the affinities of some genera such as *Symphysurina* Ulrich in Walcott, 1924 (see, e.g. Fortey & Chatterton 1988, p. 200, v. Whittington 2003, p. 642). Nileids had a cosmopolitan distribution for nearly their entire history, but their diversity was greatly reduced in the Upper Ordovician following a Darriwilian peak. No modern phylogenetic studies have been published.

Family Taihungshaniidae Sun, 1931. Taihungshaniidae (Fig. 20.41) is a small, exclusively Ordovician family to which six genera and 41 species are assigned and within which no subfamilies are recognized. It increased in diversity through the Lower Ordovician to a Floian peak, but abruptly became extinct at that point. The taxon has a distinctively Gondwanan distribution. No modern phylogenetic analyses have been published.

Superfamily Trinucleoidea Hawle & Corda, 1847

Family Alsataspididae Turner, 1940. Grouped together here are taxa which have been assigned separately to Hapalopleuridae Harrington & Leanza, 1957 and Orometopidae Hupé, 1955 (Fig. 20.42). There is more general agreement that Alsataspididae and Hapalopleuridae are synonyms (e.g. Fortey & Shergold 1984; Fortey & Owens 1991). It appears, however, that the family is paraphyletic, and is based on plesiomorphic trinucleoid morphology. Vaccari *et al.* (2006) argued for the separation and recognition of Orometopidae, which had also been considered a synonym of Alsataspididae by Jell & Adrain (2003). The characters they cited in support of this (reduction in the number of thoracic segments and development of a trinucleid-like pygidium) certainly serve to separate the orometopids from the alsataspidids. They do not, however, separate Orometopidae from the remainder of Trinucleoidea. Vaccari *et al.* (2006) cited the characters as 'synapomorphies that link Orometopidae, Raphiophoridae, Trinucleidae and Dionididae'. They are hence symplesiomorphies in the

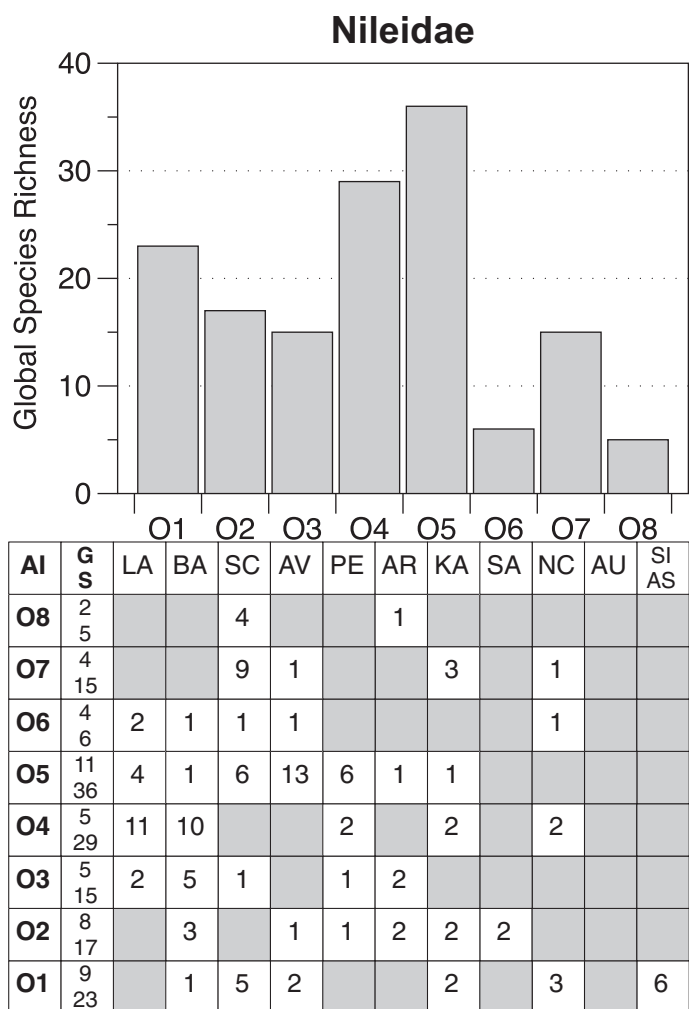


Fig. 20.40. Global taxonomic richness of the Family Nileidae during the Ordovician. See Figure 20.4 for explanation.

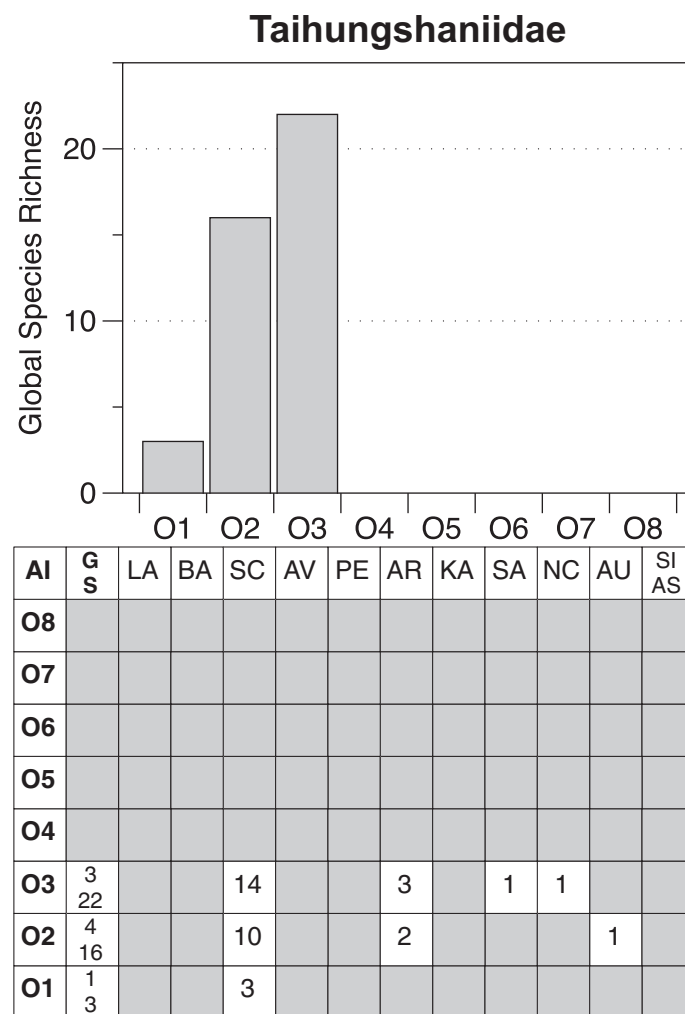


Fig. 20.41. Global taxonomic richness of the Family Taihungshaniidae during the Ordovician. See Figure 20.4 for explanation.

Alsataspididae

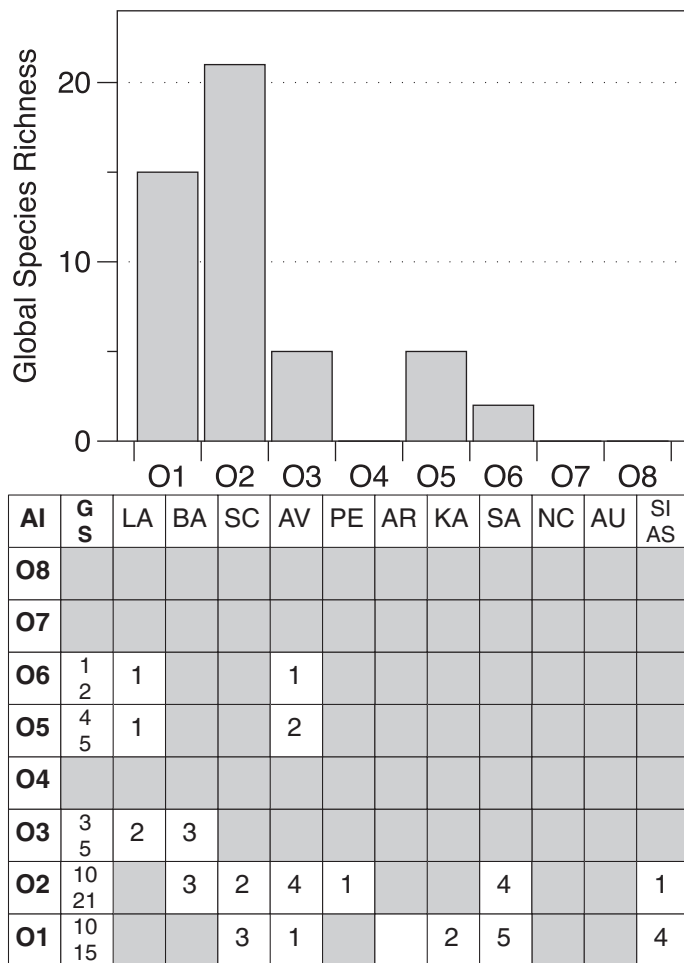


Fig. 20.42. Global taxonomic richness of the Family Alsataspididae during the Ordovician. See Figure 20.4 for explanation.

Dionididae

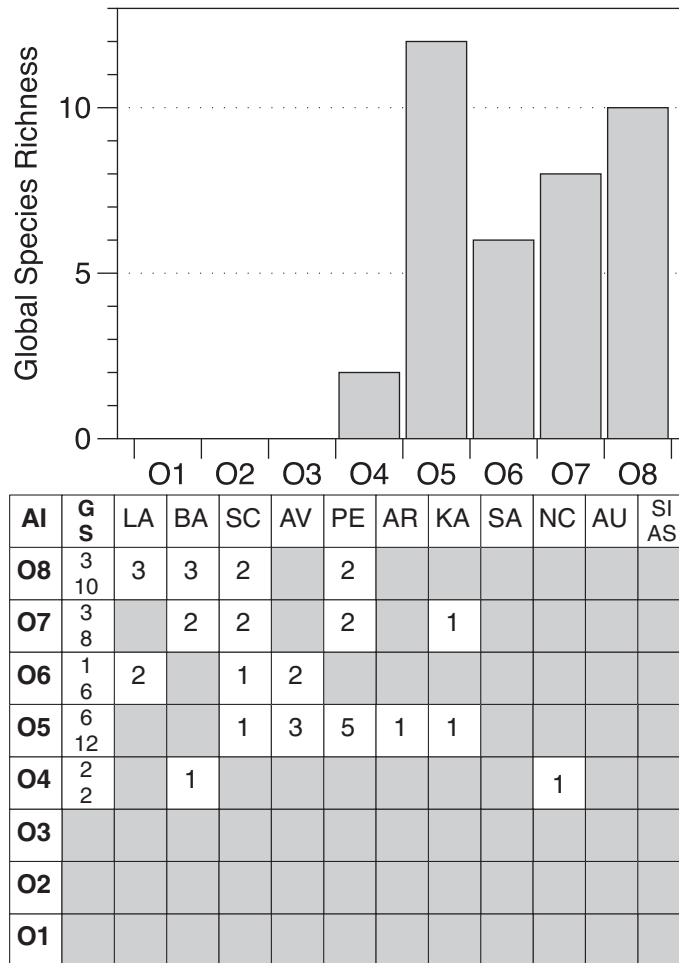


Fig. 20.43. Global taxonomic richness of the Family Dionididae during the Ordovician. See Figure 20.4 for explanation.

context of Orometopidae. They cited no potential synapomorphies of that family, and the strong suspicion must remain that it is composed of the basal components of post-‘alsataspidid’ trinucleoideans. Its recognition apart from Alsataspididae in effect creates two (putatively) paraphyletic grade groups at the base of Trinucleoidea instead of one. While there is some value in this (it permits recognition of the node subtending Trinucleoidea s.s. to the exclusion of the very basal ‘alsataspidids’), I regard proliferating paraphyletic ‘families’ at the base of the same clade as not very informative, and this is why I recognize only one grade group.

This paraphyletic grouping of basal trinucleoideans contains 21 genera with Ordovician occurrence and 48 valid Ordovician species. Its Tremadocian peak in taxonomic richness and sharp decline thereafter are artefacts of its non-natural phylogenetic status. No modern phylogenetic studies have been published, but they are essential in order to classify this fairly large group of taxa (including Cambrian occurrences, over 30 genera and over 100 species in total) using modern systematic concepts. It is possible that significant components of both ‘Alsataspididae’ and ‘Orometopidae’ may prove monophyletic, but this remains to be demonstrated.

Family Dionididae *Gürich, 1907.* Dionididae (Fig. 20.43) is a relatively small, exclusively Ordovician family with a range from the Dapingian to the upper Katian. Nine genera and 43 valid species are recognized, and no subfamilies are recognized. The oldest known species are *Tongxinaspis polymorpha* Z.-Q. Zhou, 1981, from the North China margin, the Baltic *Trinucleoides*

praecursor Poulsen, 1965, and Avalonian species questionably assigned to *Dionidella* Prantl & Přibyl, 1949, by Fortey & Owens (1987). The family maintained a cosmopolitan distribution until the end of the Ordovician. It is widely regarded as monophyletic, but no modern phylogenetic analyses have been published.

Family Raphiophoridae *Angelin, 1854.* Raphiophoridae (Fig. 20.44) includes two subfamilies, the nominal subfamily (26 genera, 217 species) which ranges from the upper Tremadocian to the lower Ludlow, and Endymioniinae Raymond, 1920 (13 genera, 36 species), which ranges possibly from the lower Tremadocian, but definitely from the Floian, to the upper Katian. At issue for the latter is the monotypic lower Tremadocian Laurentian genus *Typhlokorynetes* Shaw, 1966, which may belong but is inadequately known (it is not included on Fig. 20.44). Raphiophorids tend to be found in deep-water settings, and they occur globally from the Floian to the end of the Ordovician with a peak diversity in the Darriwilian and Sandbian. Three genera have been recorded from the Silurian, although the validity of the monotypic *Metalonchodomas* Kobayashi & Hamada, 1971a, and *Sinoluia* Li, 1988, needs to be further investigated. Most Silurian species are assigned to *Raphiophorus* Angelin, 1854. There are 37 genera with Ordovician occurrence and 226 valid Ordovician species. There have been no modern phylogenetic studies of any part of the family.

Family Trinucleidae *Hawle & Corda, 1847.* The exclusively Ordovician Trinucleidae (Fig. 20.45) ranges throughout the period, with 51 genera and 227 valid species. The earliest taxa are the

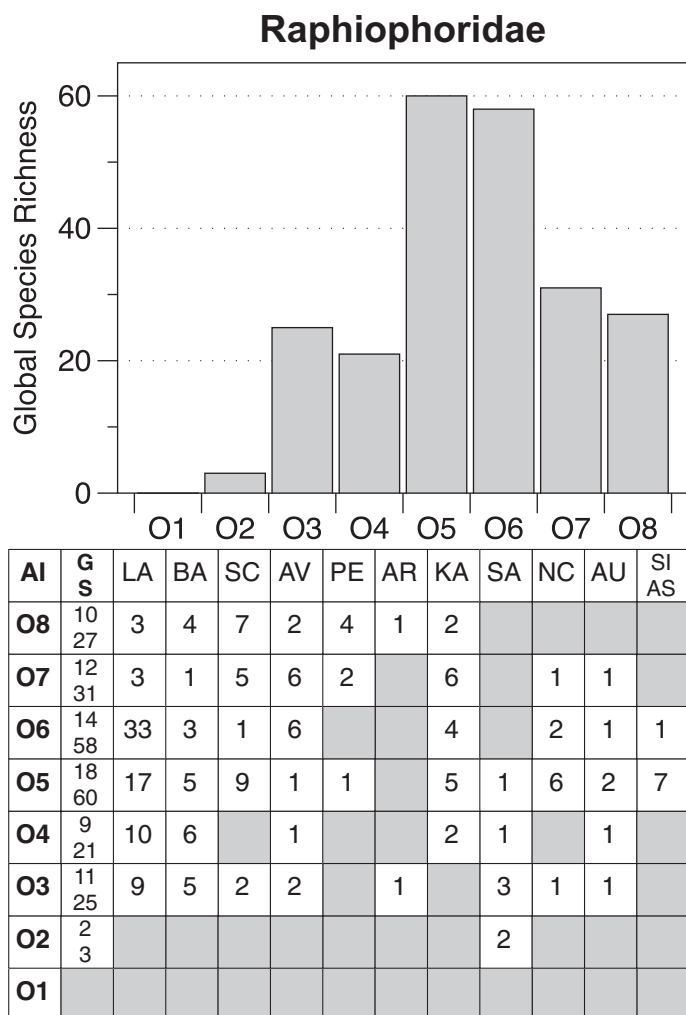


Fig. 20.44. Global taxonomic richness of the Family Raphiophoridae during the Ordovician. See Figure 20.4 for explanation.

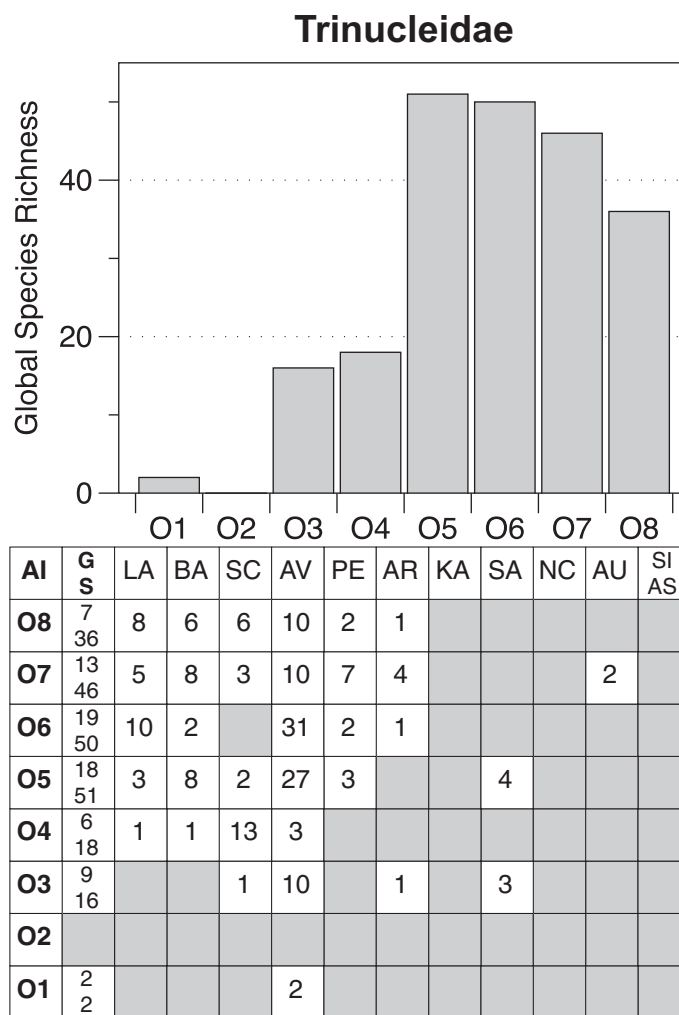


Fig. 20.45. Global taxonomic richness of the Family Trinucleidae during the Ordovician. See Figure 20.4 for explanation.

lower Tremadocian Avalonian *Myinda* Stubblefield in Stubblefield & Bulman, 1927, and *Myindella* Hutchison & Ingham, 1967, but the group did not begin to diversify until the Floian. It experienced a major burst in diversity during the Darriwilian and remained an important group until its end-Ordovician demise. The Lower Ordovician history of the group is restricted to Gondwana and affiliated blocks; a wider distribution to Baltica and Laurentia was achieved by the Dapingian and the family remained essentially cosmopolitan until its disappearance. The major work on trinucleid taxonomy is by Hughes *et al.* (1975), who reviewed all genera and proposed a five-fold subfamilial classification that has been followed by most subsequent workers. Nevertheless, there has been no modern phylogenetic work on any aspect of the group, and the monophyly of the subfamilies has never been tested. They are the nominal subfamily (29 genera, 115 species), Cryptolithinae Angelin, 1854 (five genera, 27 species), Hanchungolithinae Lu, 1963 (two genera, 18 species), Marrolithinae Hughes, 1971 (10 genera, 58 species) and Reedolithinae Hughes, Ingham & Addison, 1975 (five genera, nine species). The group has attracted a certain amount of phenetic study (e.g. Hughes 1970; Bowdler-Hicks *et al.* 2002), as the patterns of fringing pits lend themselves to statistical analysis.

Order Olenida Adrain, 2011

This order was proposed on the basis of a previously undetected complex synapomorphy involving the articulation of the inner

edge of the doublure underlying the cranidium (i.e. the librigenal anterior projections) with the ventral aspect of the cranidium. The detailed evidence for this will be presented elsewhere. The feature is difficult to observe except when preserved via silicification, but it is present in every single species of every single family assigned in which it has been possible to check, and it has not been found on any species not assigned to the order. The taxa thus grouped have additional putative synapomorphies which, again, will be discussed in detail elsewhere.

Family Olenidae Burmeister, 1843

Olenidae (Fig. 20.46) is a large and important taxon containing a total of nearly 70 genera and over 400 species, with a stratigraphical range from the Guzhangian to the end of the Ordovician. Although it is another major group that has seen very little modern phylogenetic analysis, it has received considerable taxonomic attention, with major works such as Henningsmoen (1957) and Fortey (1974b). Eight subfamilies are recognized (five with occurrence in the Ordovician), although some of these have very low diversity. Oleninae (Guzhangian to upper Tremadocian; 20 genera, 122 species) is probably paraphyletic. Balnibarbiinae Fortey, 1974b (Floian to Dapingian, two genera, 11 species), is probably monophyletic, as are the similarly small Hunanoleninae Liu, 1977 (entirely Furongian, two genera, six species) and Hypermecaspidinae Harrington & Leanza, 1957 (two genera, 20 species). The phylogenetic status of Leptoplastinae Angelin,

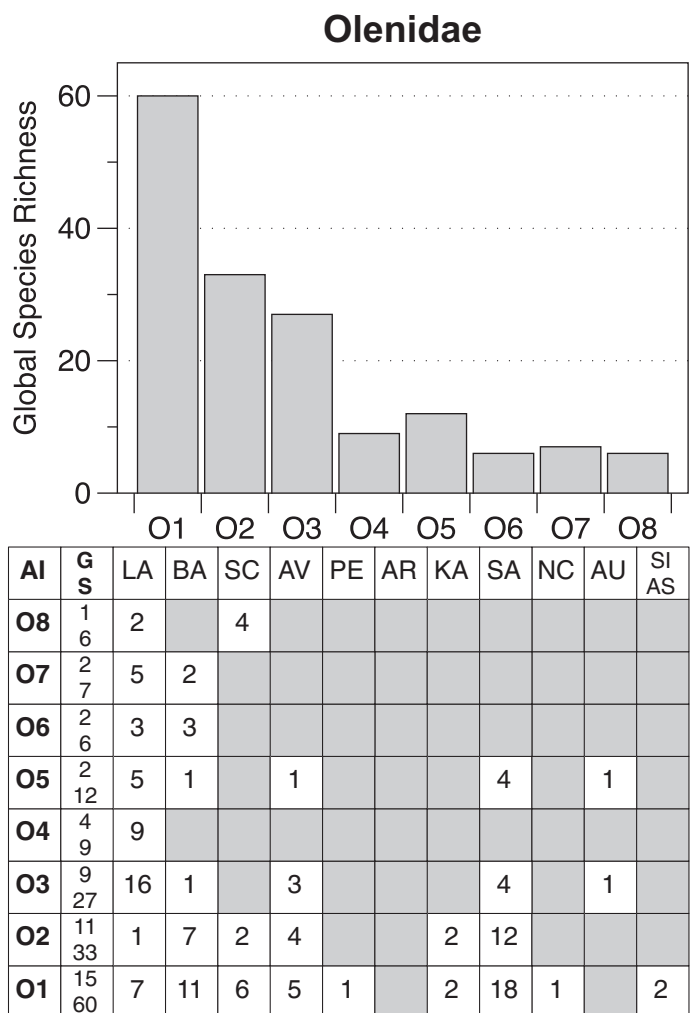


Fig. 20.46. Global taxonomic richness of the Family Olenidae during the Ordovician. See Figure 20.4 for explanation.

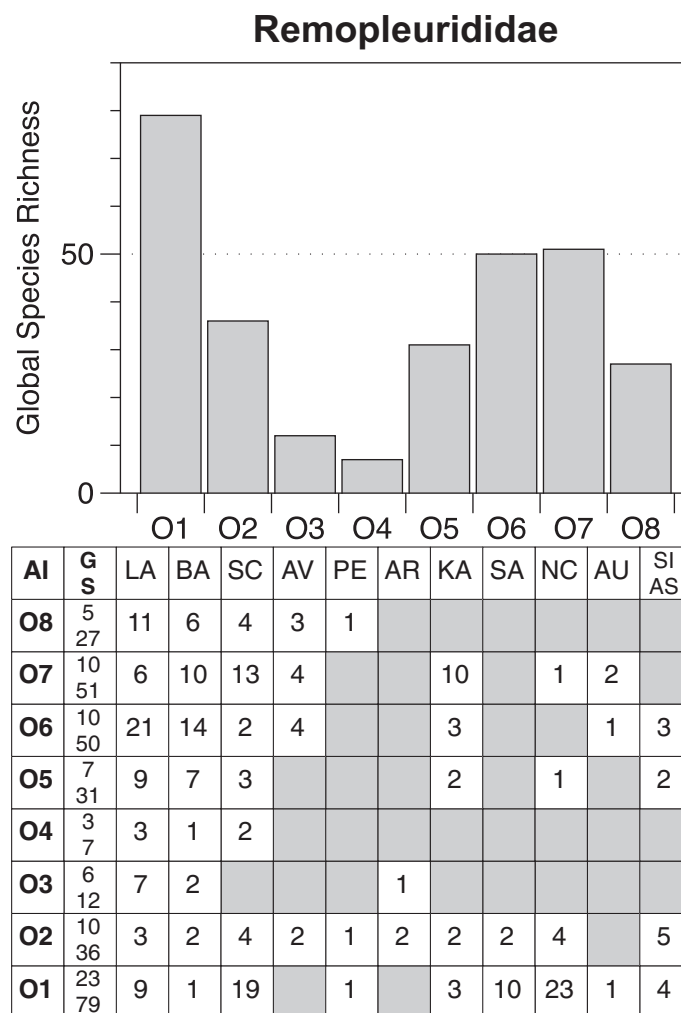


Fig. 20.47. Global taxonomic richness of the Family Remopleurididae during the Ordovician. See Figure 20.4 for explanation.

1854 (exclusively upper Furongian, six genera, 48 species), Pelturinae Hawle & Corda, 1847 (mid-Furongian to Floian, 19 genera, 95 species) and Plicatolininae Robison & Pantoja-Alor, 1968 (mid-Furongian to Floian, five genera, 24 species) has not been evaluated. Triarthrinae Ulrich in Bridge, 1931 (upper Furongian to upper Katian, six genera, 59 species) is probably monophyletic. Olenidae reached its peak global species richness in the upper Furongian. It remained diverse during the lower Tremadocian, but rapidly declined in diversity from that point onwards. Only Triarthrinae remained by the Dapingian, and it ranged until the end-Ordovician. Olenids were globally distributed during the Lower Ordovician, but were largely restricted to Laurentia and Baltica by the Upper Ordovician. In total, there are 28 genera with Ordovician occurrence and 161 valid Ordovician species. The only modern phylogenetic analysis of any part of Olenidae was a study by Karim (2008) of several genera of Pelturinae.

Family Remopleurididae Hawle & Corda, 1847

Classification of Remopleurididae (Fig. 20.47) is one of the larger departures from the classification of Fortey & Chatterton (1988) and Fortey (1997b), who considered it had affinity to Asaphida. It unambiguously possesses the key synapomorphy of Olenida, but again the evidence for this will be presented elsewhere. Adrain *et al.* (2009) argued in favour of a phylogenetic link with the Guzhangian *Cedarina* Lochman, 1940, and the Family

Cedariidae Raymond, 1937 (which was also included in Olenida by Adrain (2011)).

Park & Choi (2011) independently contested the inclusion of Remopleurididae in Asaphida. This work, however, was in reference to the morphology of species of *Haniwa* Kobayashi, 1933, which they considered a 'remopleuridoidean'. Although some authors had suggested or made a remopleuridoidean assignment (e.g. Shergold 1975; Zhu & Wei 1991; Sohn & Choi 2007), others had previously classified *Haniwa* either as Family Uncertain (e.g. Zhou & Zhang 1985; Duan *et al.* 1986) or as Anomocaridae Poulsen, 1927 (e.g. Luo 1983; Zhang & Wang 1985; Shah *et al.* 1991). While the genus has general similarities to remopleuridids in its cephalic morphology, it lacks all of the putative synapomorphies of the group and almost certainly does not belong to it. Remopleurididae has a plesiomorphic thoracic morphology of 12 segments with an axial spine on the eighth. Derived Ordovician species reduce the number to 11 or 10, but there is invariably a spine on the eighth. *Haniwa* has an 11 segment thorax completely lacking an axial spine. In addition, *Haniwa* unquestionably lacks the specialized ventral articulation of the inner edge of the cephalic doublure that is the cardinal synapomorphy of Olenida. Further, every single known Cambrian remopleuridid has a ventral median suture (one of the features which led Fortey & Chatterton (1988) to argue for a relationship with Asaphida). *Haniwa* lacks a suture entirely, and has medially yoked librigenae. Finally, the pygidial morphology of *Haniwa* involves a fairly robust, highly tagmatized sclerite with a prominently raised axis and no pleural

spines in the holaspid. This does not resemble pygidia typical of remopleuridids, which have flattened pleurae with pleural spines on each segment, and which are at most weakly tagmatized, with clearly defined segmentation. In sum, there seems no serious question that *Haniwa* is neither a remopleuridid nor a member of Olenida. It is irrelevant to the question of ‘remopleuridoidean’ affinity.

Classification of Remopleurididae was discussed at length by Adrain *et al.* (2009, pp. 38–42). Briefly, although Cambrian and some Ordovician species have generally been assigned to a Family Richardsonellidae Raymond, 1924, and the more derived Ordovician taxa to Remopleurididae, the latter certainly creates pointless paraphyly in the former. For this reason, Jell & Adrain (2003), Adrain *et al.* (2009), and Adrain (2011) recognized the group as a single family. If one maintains the paraphyletic Richardsonellinae at subfamilial rank, it ranges with certainty from the upper Furongian to Darriwilian and has 46 genera and 209 species assigned. The monophyletic Remopleuridinae ranges from lower Tremadocian to upper Katian, with 19 genera and 180 species. A minor monophyletic component of the family is exclusively upper Furongian Atratebiinae Shergold, 1980 (four genera, 11 species).

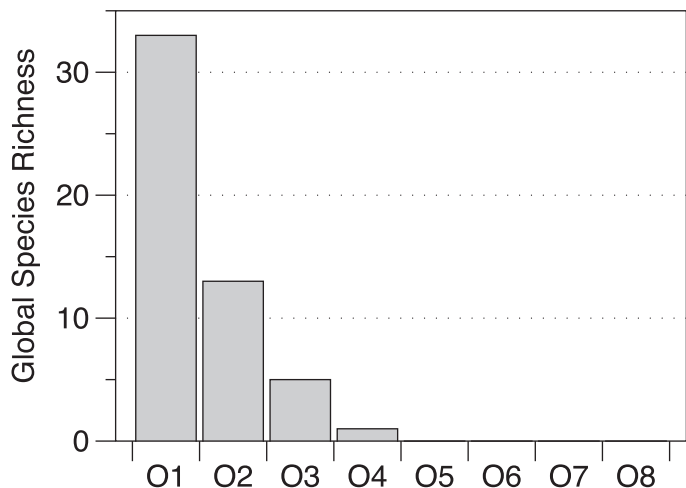
Remopleuridid distribution during the Ordovician follows an evolutionary pattern. During the Tremadocian the family was entirely cosmopolitan, with occurrence on virtually every continent or terrane with a trilobite record. Most of these forms were plesiomorphs (‘richardsonellines’), which then disappeared from much of the world at the end of the Tremadocian. Floian diversity

was strongly concentrated in Laurentia and Baltica. The earliest occurrence of the more derived group (‘remopleuridines’) was concentrated in the lower Tremadocian of Laurentia (*Remopleuridiella* Ross, 1951, but species of this genus also occurred in North and South China). The derived group remained concentrated in Laurentia and Baltica, but by the Darriwilian had spread, and remopleuridids became globally distributed for a second time. The family became extinct at the end-Ordovician. In total, there are 48 genera with Ordovician occurrence, and 294 valid Ordovician species. Despite its rich diversity and wide distribution, no part of the family has ever been subject to modern phylogenetic analysis.

Family Eulomidae Kobayashi, 1935a

Eulomidae (Fig. 20.48) first appeared in the Guzhangian, but was of very low diversity until the upper Furongian, where it reached its peak genus and species richness. It remained an important group into the Tremadocian, but its diversity rapidly declined and it had disappeared by the Darriwilian. The youngest known species is *Lateuloma latigena* (Dean, 1973), from the Dapingian of the Taurides Terrane. Most species are included in the nominal subfamily, but also assigned is the small Subfamily Triplacephalinae Lu & Qian in Zhou *et al.*, 1977 (=Amzasskiellinae, Rozova in Rozova *et al.*, 1985), to which one Ordovician taxon, the Tremadocian Australian *Natmus* Jell, 1985, is assigned. Overall, there are 10 genera with Ordovician

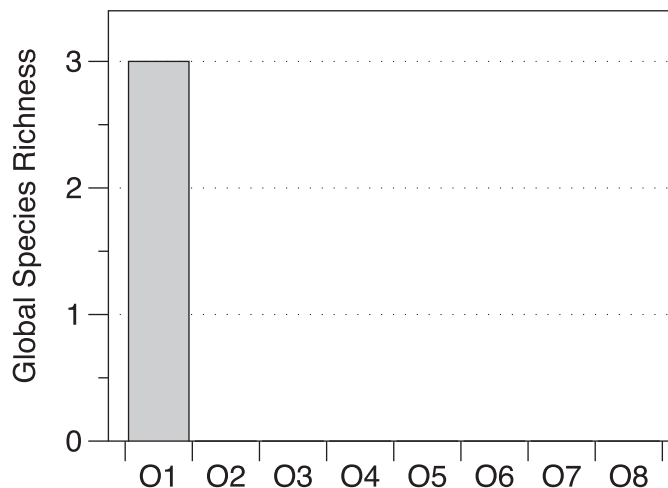
Eulomidae



AI	G _S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI _{AS}
O8												
O7												
O6												
O5												
O4	1 1											
O3	2 5		1			2	1					
O2	5 13		1	1	2	1	2	4				1
O1	7 33			15	1	1		4			2	8

Fig. 20.48. Global taxonomic richness of the Family Eulomidae during the Ordovician. See Figure 20.4 for explanation.

Dokimocephalidae



AI	G _S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI _{AS}
O8												
O7												
O6												
O5												
O4												
O3												
O2												
O1	1 3			3								

Fig. 20.49. Global taxonomic richness of the Family Dokimocephalidae during the Ordovician. See Figure 20.4 for explanation.

occurrence and 53 valid Ordovician species. The group was concentrated in Gondwana and affiliated blocks, but occurred also in Baltica and Siberia/peri-Siberia. The family has never been subject to modern phylogenetic analysis.

Family Dokimocephalidae Kobayashi, 1935a

As presently conceived, Dokimocephalidae (Fig. 20.49) is a sprawling taxon comprising 57 valid genera and 205 species, most of Cambrian age. Its monophyly is dubious, although Laurentian taxa including *Dokimocephalus* Walcott, 1924, clearly represent a group of Olenida (see Westrop *et al.* 2010). A single genus, *Acrocephalina* Troedsson, 1937, has lower Tremadocian species from South China assigned. Westrop *et al.* (2010) undertook cladistic analysis of the core Laurentian group.

Family Sarkiidae Hupé, 1953

Like Holotrachelidae and Ityophoridae (below), Sarkiidae (Fig. 20.50) is a 'family' consisting of a very small number of species, in this case the Darriwilian-type species of *Sarkia* Klouček, 1916, from Perunica, and two Katian species from South China. Opinion has varied on its affinity, with Snajdr (1981) considering it a trinucleoidean and Z.-Y. Zhou (1981) assigning it to the otherwise Cambrian Conocoryphidae Angelin, 1854 (which Cotton (2001) subsequently argued was a polyphyletic group).

I will present the detailed arguments elsewhere, but species of *Sarkia* display the key synapomorphy uniting Olenida and, while more work will be needed to determine the exact affinity of the genus, it seems possible that it will prove to be highly derived in-group Eulomidae.

Order Harpida Whittington, 1959

Whittington (in Moore, 1959) erected Harpina as a suborder of Ptychopariida to include the families Harpetidae, Harpididae (which he considered a senior synonym of Loganopeltidae Hupé, 1955) and Entomaspididae, all of which have broad cephalic fringes and, at least in derived taxa, marginal cephalic sutures and lower lamellae. Adrain & Westrop (2006b) considered Harpetidae to be a senior synonym of Entomaspididae. While species of Harpetidae and Harpididae each display a broad cephalic fringe, their morphology is otherwise not very comparable. In particular, the marginal suture was developed in completely different ways in either group. In the harpidids, presumably plesiomorphic forms have a narrow strip of librigenae that extends posteromedially from an anterolateral point on the margin. The genal angle is intact and the sutures are far forward from it. In harpetids, the Cambrian taxa which retain a facial suture are clearly opisthoparian, with the genal spine on the librigena and the suture cutting the posterior border adaxial to the spine. A narrow strip of librigena is retained, but it runs forwards from

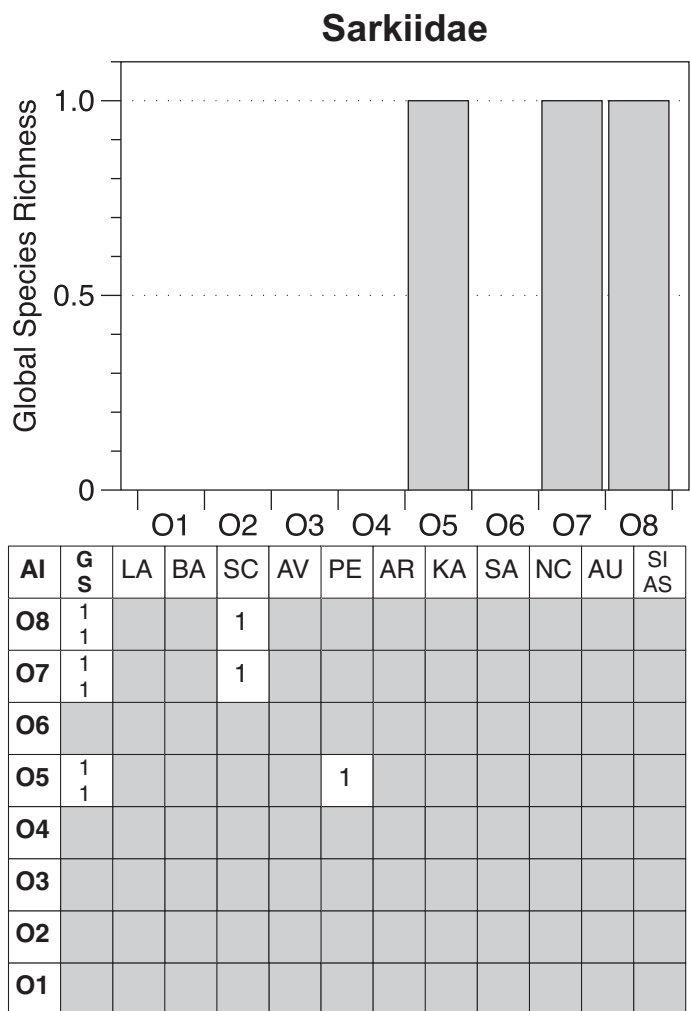


Fig. 20.50. Global taxonomic richness of the Family Sarkiidae during the Ordovician. See Figure 20.4 for explanation.

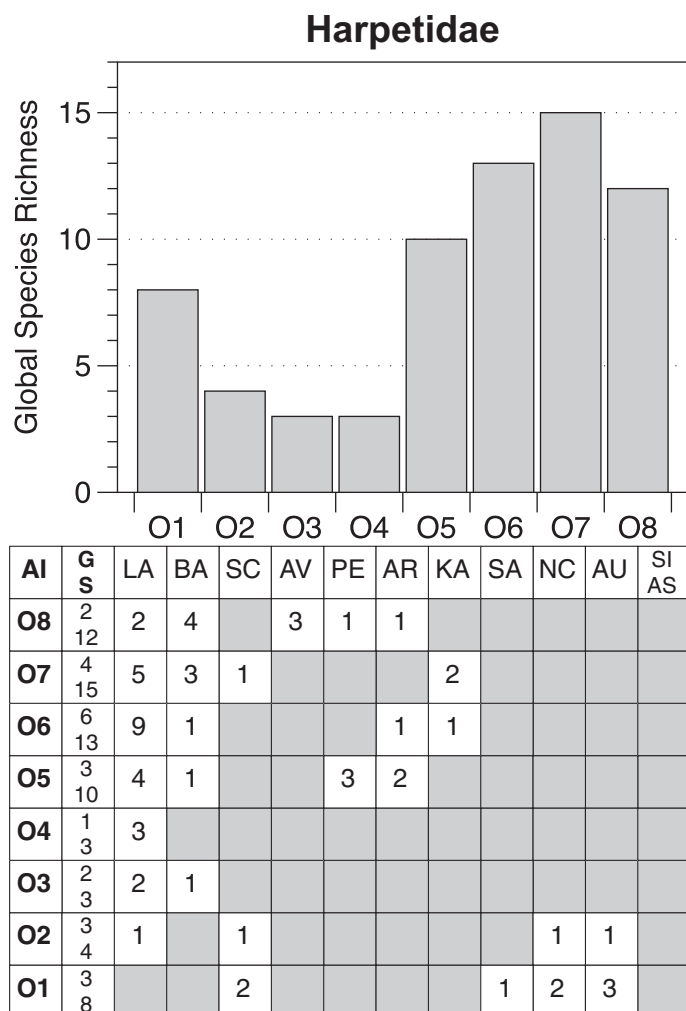


Fig. 20.51. Global taxonomic richness of the Family Harpetidae during the Ordovician. See Figure 20.4 for explanation.

just in front of the genal spine (Rasetti 1952). Pygidia of the groups are also not comparable, as those of harpetids are broad and short (exsag.), with a trend in reduction in length from less derived upper Furongian (Sunwaptan) forms to *Entomaspis* Ulrich in Bridge, 1931, to derived Ordovician species. The plesiomorphic condition in harpidids, in contrast, is a completely different elongate morphology with a relatively short axis and long, dorsally concave, posteriorly dropped pleural regions which form a pair of posteriorly directed triangular spines (e.g. Ludvigsen & Westrop in Ludvigsen *et al.* 1989, plate 38, figs 6 & 11). Hence I consider that there is scant evidence for a relationship between the families, and consider their respective sister taxa as unknown. Since an ordinal taxon already exists for Harpetidae it is employed here; Harpididae is considered of uncertain ordinal affinity.

Ebach & McNamara (2002, pp. 237–238) changed the name of the taxon to Harpetida Whittington, 1959. The basis for this was ICZN Opinion 1436 (1987), which emended the family name Harpida Hawle & Corda, 1847 to Harpetidae owing to homonymy of the former. Names above family-group rank, however, are not governed by the Code. McNamara *et al.* (2009, p. 14) cited the name as Order Harpetida Ebach & McNamara, 2002, despite authorship actually having been attributed to Whittington in that work. As the concept of the taxon remains attributable to Whittington, and there is no requirement to alter its name in light of the ICZN, I see no reason not to maintain Whittington's original spelling and authorship, following Fortey (1997b) and Adrain (2011).

Family Harpetidae Hawle & Corda, 1847

The Cambrian origin of Harpetidae (Fig. 20.51) was recognized by Adrain & Westrop (2006b), who considered Entomaspidae Ulrich in Bridge, 1931, to be a junior subjective synonym. Members of the family have a very distinctive morphology, but in similar fashion to the phacopids it is also quite conservative. The group persisted from the Furongian to the Frasnian and *Scotoharpes* Lamont 1948 has an apparently genuine range from the upper Tremadocian to the Ludfordian, one of the longest for a non-'rubbish-bin' trilobite genus. Harpetids were distributed at low latitudes during the Tremadocian, but appeared in Gondwana in the Darriwilian. There are nine genera with Ordovician occurrence, and 68 Ordovician species. The family has been the subject of a series of phylogenetic analyses by Ebach & McNamara (2002). An analysis examining the basal structure of the group and including all Cambrian species is in progress (Adrain & S. R. Westrop, unpublished data).

Order uncertain

Family Acrocephalitidae Hupé, 1953

Acrocephalitidae (Fig. 20.52) have a rich Cambrian history, but three lower Tremadocian genera have been assigned. The monotypic *Afghancephalites* Wolfart, 1970, is from Gondwanan-affiliated central Afghanistan. *Dolgedola* Ancygin, 2001, includes

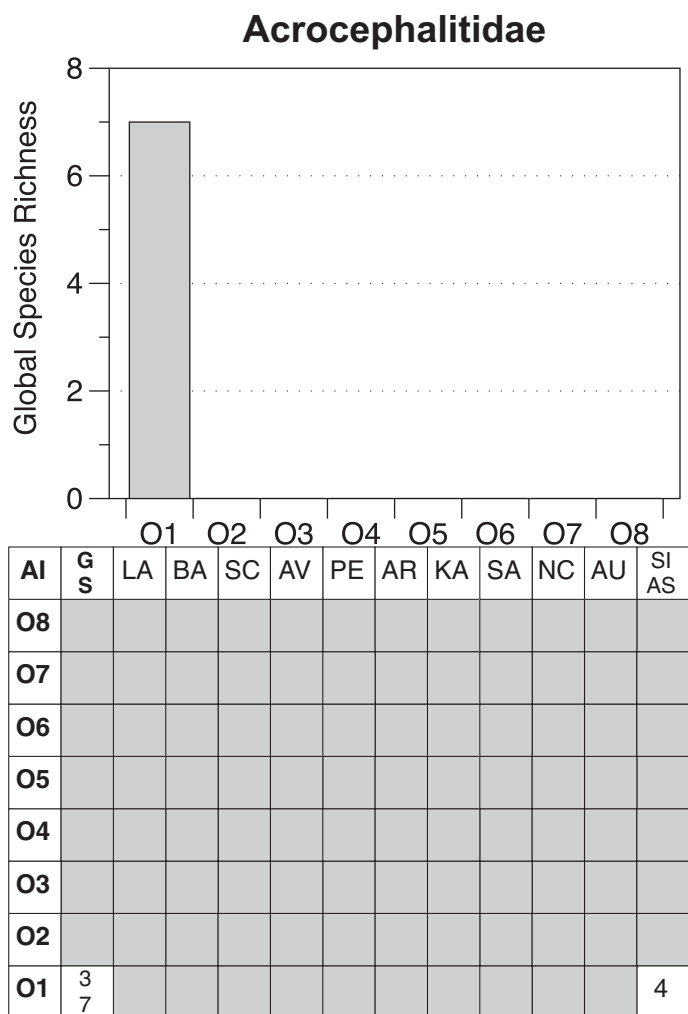


Fig. 20.52. Global taxonomic richness of the Family Acrocephalitidae during the Ordovician. See Figure 20.4 for explanation.

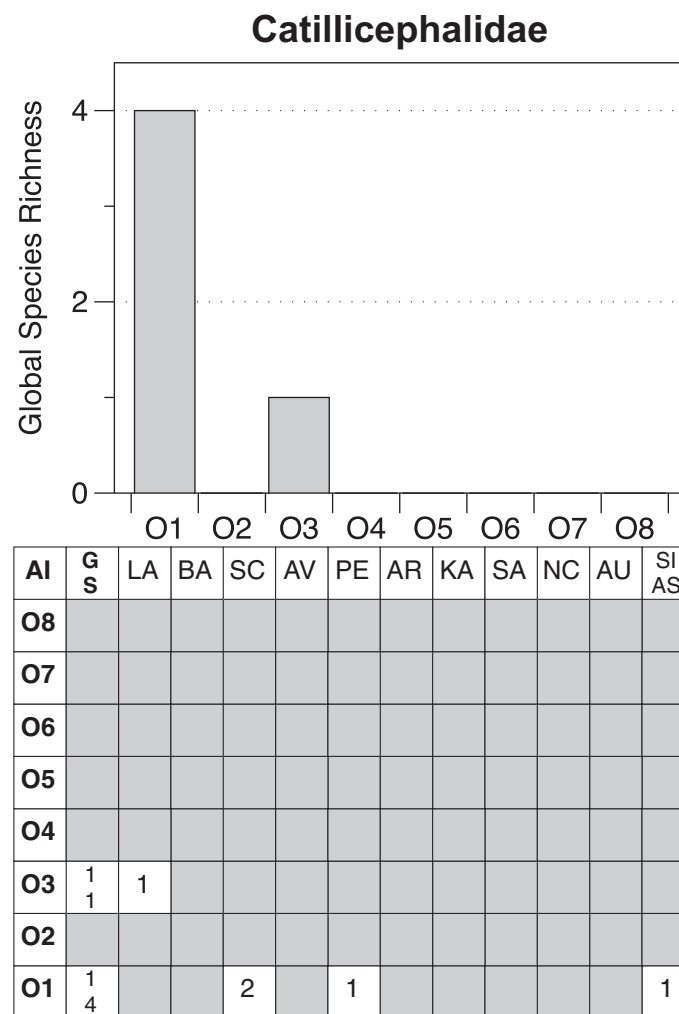


Fig. 20.53. Global taxonomic richness of the Family Catillicephalidae during the Ordovician. See Figure 20.4 for explanation.

two named species from the Uralian margin of Baltica. *Ijacephalus* Ogienko, 1974, includes four species from the Siberian Platform. The group as a whole has never been subjected to phylogenetic analysis.

Family Catillicephalidae Raymond, 1938

Catillicephalidae (Fig. 20.53) is a large Cambrian group of dubious monophyly (Fortey & Chatterton 1988; Ludvigsen & Westrop in Ludvigsen *et al.* 1989) which includes taxa both with a rostral plate and with a ventral median cephalic suture. Taxa assigned share an often effaced and strongly vaulted cephalic morphology, typically with small librigenae. The only named genus with Ordovician occurrence is *Onchonotellus* Lermontova, 1951, to which several species from the lower Tremadocian of South China, Gondwana (Bavaria) and the Altai-Sayan have been assigned. *Onchonotellus* has a middle Cambrian-type species and contains some 27 species distributed through the remainder of the Cambrian and lower Tremadocian. Many are poorly known and the monophyly of the genus is suspect. Other ‘catillicephalids’ do occur in the Ordovician, but their genus assignments have been queried or else they have been reported in open nomenclature. Ingham (in Ingham *et al.* 1986) described *Diztazeris adoceta* from the Floian of Scotland, but Pratt (1992) rejected inclusion of the species in the otherwise Guzhangian genus; it presently lacks a genus assignment. Adrain & Fortey (1997) described

a distinctive species in open nomenclature from the probable uppermost Floian of western Ireland. However, *Buttsia inexpectata* Fortey, 1980, from the Floian of the Laurentian East Svalbard Terrane, does not appear to belong to *Buttsia* Wilson, 1951, which has a Furongian (Steptoean) type species. Rather, work in progress strongly indicates that it is a telephinid related to (mainly undescribed) plesiomorphic species of *Carolinites* Kobayashi, 1940, and *Opipeuterella* Fortey, 2005 (Adrain *et al.*, unpublished data). No subfamilies are recognized. Catillicephalids have never been subject to phylogenetic analysis.

Family Harpididae Whittington, 1950b

Harpididae (Fig. 20.54) was regarded as a senior synonym of the mainly upper Cambrian Loganopeltidae Hupé, 1955, by Whittington (in Moore, 1959). Ludvigsen & Westrop (in Ludvigsen *et al.* 1989) argued that the families were distinct and their morphological similarities convergent, on the basis of the enlarged L1 of Ordovician species and their broader lower lamella. There are certainly significant morphological differences between the taxa but, pending further analysis, I regard loss of the facial suture which closed anteriorly (in derived taxa) combined with the development of a fringe and lower lamella as likely to be synapomorphic, and I follow Whittington (and Jell & Adrain 2003) in considering the families to be synonyms. The family

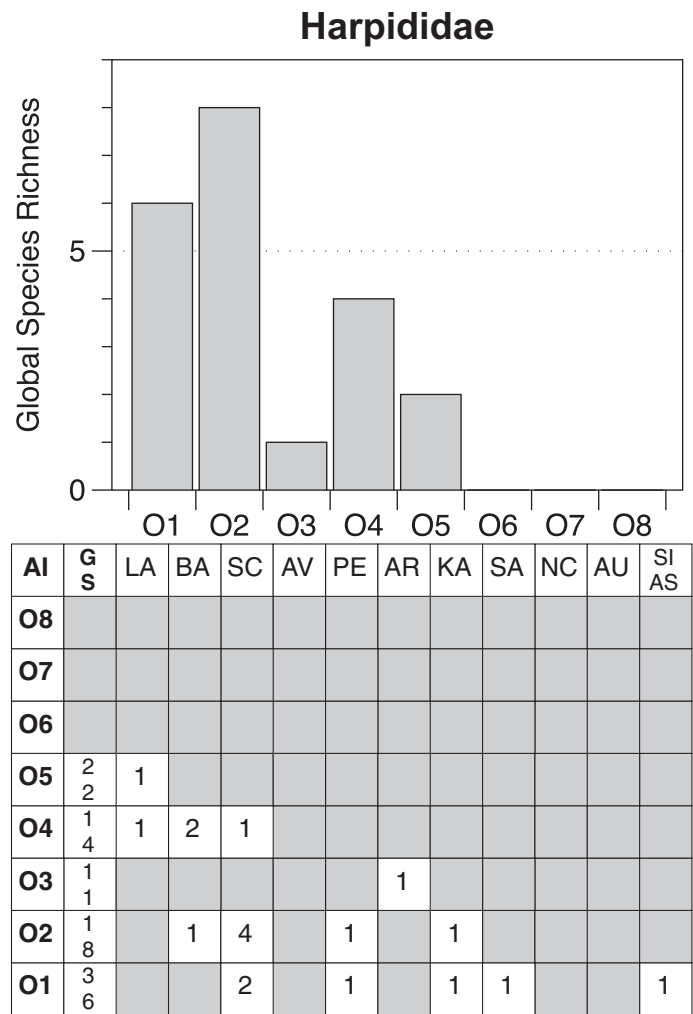


Fig. 20.54. Global taxonomic richness of the Family Harpididae during the Ordovician. See Figure 20.4 for explanation.

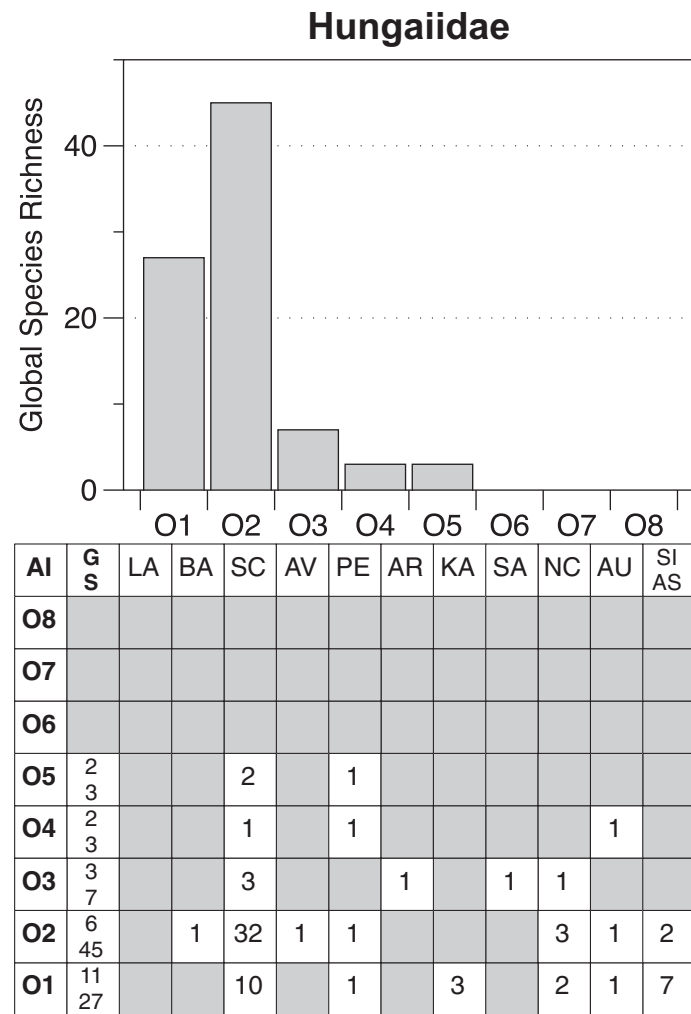


Fig. 20.55. Global taxonomic richness of the Family Hungaiidae during the Ordovician. See Figure 20.4 for explanation.

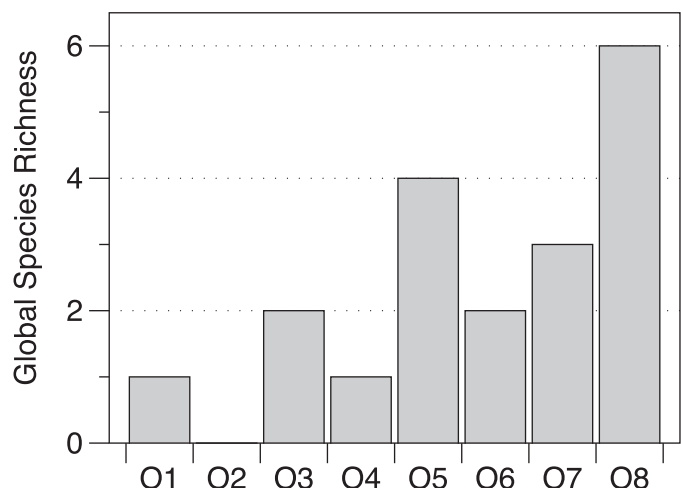
does not seem to be closely related to Harpetidae (see comments above under Order Harpida) and its sister taxon is at present uncertain. No subfamilies are recognized, although recognition of a paraphyletic Loganopeltinae and a monophyletic Harpidinae would match common practice in other families (while serving no purpose). There are six Ordovician genera which contain 21 Ordovician species, although opinion on the validity of all of the genera has varied. The group was essentially globally distributed in the upper Cambrian and Tremadocian, but by the Dapingian it was restricted to low latitudes and by the Darriwilian to only Laurentia. No phylogenetic analyses have been carried out.

Family Hungaiidae Raymond, 1924

Ludvigsen & Westrop in Ludvigsen *et al.* (1989) proposed synonymy of Hungaiidae with Dikelokephalinidae Kobayashi, 1934 (Fig. 20.55). This has been followed by some workers (e.g. Jell & Adrain 2003; Zhou & Zhen 2008; Zhou *et al.* 2011), but when dealing with Ordovician taxa many have continued to use Dikelokephalinidae, usually without mention of Ludvigsen & Westrop's ideas (e.g. Ebbestad 1999; Bruton *et al.* 2004; Ghobadi Pour 2006; Mergl 2006; Turvey 2007). Only Fortey (2011*b*) explicitly discussed any reasons for rejecting the synonymy. Fortey's (2011*b*, pp. 406–407) arguments were primarily geographical, as he considered that a family distributed in the upper Furongian of Laurentia but restricted to Gondwana and affiliated terranes in the Lower Ordovician (with one Baltic exception) would be 'rather unusual'.

Of course, allowing geographical distribution to dictate ideas about phylogenetic relationship has no place in modern systematics, but Fortey also focused on several morphological differences between species of *Hungaia* Walcott, 1914, and those of *Dikelokephalina* Brögger, 1896. The most important points are: (1) the pygidia of species of *Hungaia* are short, with a posteriorly blunt axis with only four rings, and with pleural spines developed on each segment, whereas those of species of 'Dikelokephalinidae' are long, with a tapering axis of at least seven segments, a generally intact margin, and often two lobate triangular spines associated with the pleurae of the fourth segment; (2) the cranidium of species of *Hungaia* has inflated bacculae opposite the rear of the glabella and such structures are unknown in 'Dikelokephalinidae'; and (3) the structure of the eye ridge is very different, with that of species of *Hungaia* contacting the glabella in a more posterior position than in *Dikelokephalina*. The last mentioned does not seem entirely relevant, as the very anteriorly positioned contact seems to be a synapomorphy of *Dikelokephalina*. In other 'dikelokephalinid' taxa (e.g. *Asaphopsoides* Hupé, 1955, see Jell & Stait (1985*b*, plate 9, figs 2, 7, 9–11); *Songtaoia* Yin in Yin & Li, 1978, see Peng (1990*b*, fig. 4.1–4.3); *Hungioides* Kobayashi, 1936, see Fortey & Shergold (1984, plate 44, fig. 2)) the eye ridge contacts the glabella in the same posterior position as in *Hungaia*. Fortey (2011*b*, p. 407) also drew attention to the fact that the eyes are very close to the glabella in species of *Hungaia*. However, the cranidia of the Laurentian Furongian (Sunwaptan) '*Dikelokephalina*' *tripunctata* (Kobayashi, 1935*b*) from Alaska, reillustrated by Palmer (1968, plate 14, figs 14, 15), and which

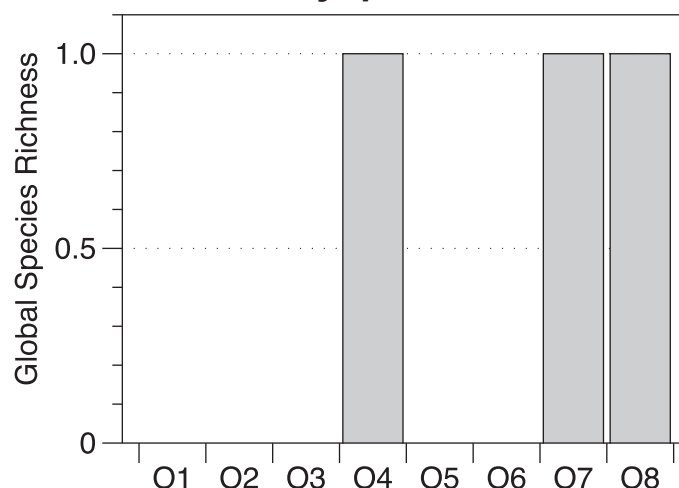
Isocolidae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	4 6		1		3							
O7	2 3			3								
O6	2 2	2										
O5	3 4											
O4	1 1	1										
O3	2 2						2					
O2												
O1	1 1	1										

Fig. 20.56. Global taxonomic richness of the Family Isocolidae during the Ordovician. See Figure 20.4 for explanation.

Ityophoridae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	1 1		1									
O7	1 1		1									
O6												
O5												
O4	1 1											
O3												
O2												
O1												

Fig. 20.57. Global taxonomic richness of the Family Ityophoridae during the Ordovician. See Figure 20.4 for explanation.

Fortey (2011b) considered related to *Hungaia*, clearly have fairly wide interocular fixigena, again no different from those of many Ordovician ‘dikelokephalinids’. The other differences are inarguable, but modern systematics works on the basis of shared derived similarity, not phenetic difference, and the list of putative synapomorphies (nearly identical glabellar structure, wide cephalic doublure with prominent paradoublural line, etc.; see Ludvigsen & Westrop in Ludvigsen *et al.* (1989, p. 28)) seems at least as compelling. I would agree with Fortey that the question of affinity must remain open, but I tentatively accept the synonymy based on positive morphological information.

Hungaiidae was most common in South China during the Tremadocian, with a distribution also in North China and both low- and high-latitude Gondwana, a pattern which was to remain fixed, albeit with dwindling diversity, until the group’s disappearance by the end of the Darriwilian. There are 14 genera containing 85 valid Ordovician species. No subfamilies are recognized. No phylogenetic work has been carried out, although the family was coded as a terminal taxon in Fortey & Chatterton’s (1988) early cladistic analysis of ‘Asaphina’.

Family Isocolidae Angelin, 1854

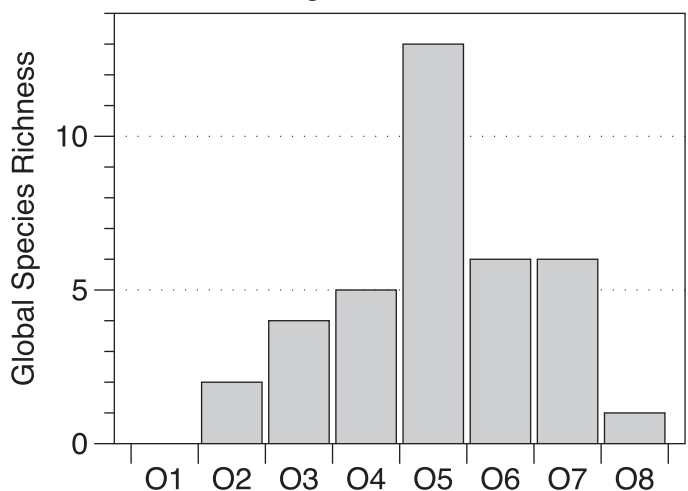
Isocolids are depicted in Figure 20.56 as having occurrence in the Tremadocian, but the basis for this is the very tentative assignment of the monotypic *Triarthroides* Raymond, 1937, by Jell & Adrain (2003). The unique holotype of *T. cyclas* Raymond,

reillustrated by Shaw (1966, plate 162, fig. 6) is a juvenile, and while it is broadly isocolid-like, it could also represent an ontogenetic stage of an olenid. Definite isocolids appear simultaneously in the Floian in Armorica and Laurentia (see Adrain & Fortey 1997, for the latter). The family has a spotty distribution owing probably to strong facies control, as most species are found associated with carbonate buildups. The group ranged to the upper Katian, but disappeared at the end-Ordovician. There are 10 genera and 19 valid species. No phylogenetic work has been published.

Family Ityophoridae Warburg, 1925

This family (Fig. 20.57) includes two fairly well-known monotypic genera from the Katian of Baltica, *Frognaspis* Nikolaisen, 1965, and *Ityophorus* Warburg, 1925. Zhou & Zhou (2008) have also assigned *Xinertaiella* Zhang, 1988, from the Dapingian of the Tien Shan terranes, Xinjiang, China. The Baltic taxa were discussed by Suzuki (2002), who concluded that they belonged to the otherwise Cambrian (Furongian) and Laurentian Family Loganellidae, although she referenced no specific loganellid in making the case. A more likely affinity is that suggested by Owens (2004), that the taxa may be related to rorringtoniids, in which case the ityophorids should be assigned to Aulacopleurida. Given that they comprise only two or three species of uncertain affinity, more information will probably be necessary before any formal phylogenetic work can be undertaken.

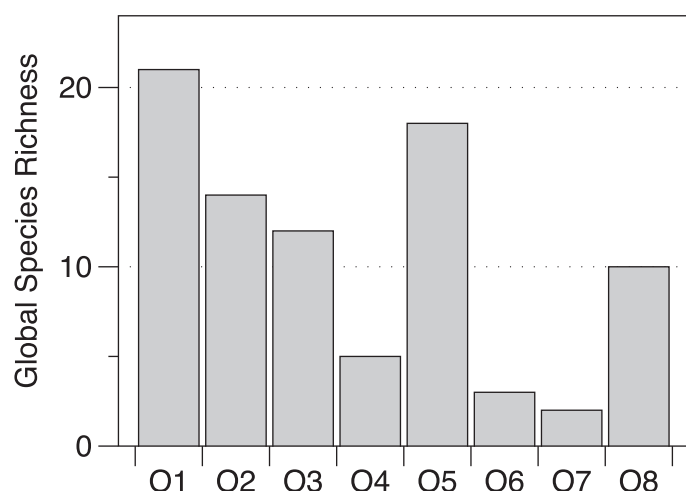
Raymondinidae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	1 1				1							
O7	3 6							4		1		
O6	2 6	5										1
O5	3 13	2	3					1		2		
O4	2 5	3	2									
O3	3 4	2	2									
O2	3 2							1				1
O1												

Fig. 20.58. Global taxonomic richness of the Family Raymondinidae during the Ordovician. See Figure 20.4 for explanation.

Shumardiidae



AI	G S	LA	BA	SC	AV	PE	AR	KA	SA	NC	AU	SI AS
O8	4 10	1		4	2	1				1		
O7	1 2			1							1	
O6	2 3	2										
O5	6 18	9			1			4				1
O4	5 5	3			1							
O3	6 12	4	2		1							2
O2	2 14		1	5	2				2	1		2
O1	4 21		2	9	2				3			2

Fig. 20.59. Global taxonomic richness of the Family Shumardiidae during the Ordovician. See Figure 20.4 for explanation.

Family Raymondinidae Clark, 1924

Raymondinidae (Fig. 20.58) contained only the Laurentian Furongian (Sunwaptan) *Raymondina* Clark, 1924, which was reviewed by Ludvigsen & Westrop in Ludvigsen *et al.* (1989). Adrain & Fortey (1997) pointed out that the Cambrian species had synapomorphies with Ordovician Glaphuridae Hupé, 1953, including modifications of the glabellar lobes and yoked librigenae, and considered Glaphuridae a junior subjective synonym of Raymondinidae. Raymondinids have a fossil record spanning the Ordovician and comprising five Ordovician genera containing 39 valid species. They were widely distributed at low latitudes for most of their history, and reached peak diversity in the Darriwilian. No phylogenetic work has been published, but a comprehensive analysis is in progress (Adrain & Karim, unpublished data).

Family Shumardiidae Lake, 1907

Shumardiids (Fig. 20.59) have a well-established upper Cambrian history, which was extended back to the Guzhangian with the description of species of *Oculishumardia* Peng, Babcock, Hughes & Lin, 2003, and *Limbishumardia* Peng, Babcock & Lin, 2004). As pointed out by Park & Choi (2012), the Cambro-Ordovician genus *Clelandia* Cossman, 1902, which was misclassified as Kingstoniidae by Jell & Adrain (2003, p. 359), may be a plesiomorphic shumardiid. Shumardiids crossed the Cambrian–Ordovician boundary with no disruption to their diversity, and although their numbers were generally winnowed through the Ordovician, they maintained a cosmopolitan distribution until their end-Ordovician disappearance. There are 13 genera with Ordovician occurrence and 95 valid Ordovician species. The group has been the subject of a detailed, species-level phylogenetic analysis by Waisfeld *et al.* (2001).

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