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Spontaneous Article

Early Palaeozoic radiolarian macroevolutionary dynamics and possible relation to global change

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ABSTRACT: A factor analysis of an exhaustive sample-based dataset of Cambrian (Miaolingian) to Silurian radiolarian species occurrences allows the detection of three evolutionary faunas composed of specific radiolarian families, which record simultaneous increases and decreases in radiolarian species richness over geological time. The oldest evolutionary fauna is composed of Cambrian to Early Ordovician archaeospicularians, assigned to the families Echidninidae and Palaeospiculidae, and of the entactinarian family Protoentactiniidae. This evolutionary fauna is complemented in the Early Ordovician by the oldest spumellarian family Antygoporidae, as well as by the order *incertae sedis* families Aspiculidae and Proventocitidae. Next, a new evolutionary fauna emerged during the Darriwilian and persisted during the Sandbian; it is dominated by the spumellarian family Inaniguttidae and to a lesser extent by the entactinarian families Haplentactiniidae, Entactiniidae and Pylentonemidae. Last, a third evolutionary fauna emerged since the Katian (Late Ordovician) and continued during the entire Silurian; it is dominated by the archaeospicularian family Secuicollactidae, the entactinarian family Paleoscenidiidae and the spumellarian family Haplotaeniatidae. These three early Palaeozoic radiolarian evolutionary faunas seem to correlate with major climatic and biotic changes known in the Ordovician: (i) the transition between the first and second evolutionary faunas is sharp and underlined by profound changes in taxonomic composition and turnover during the Middle Ordovician; it is correlated with the sudden early Darriwilian climate shift, global cooling and the main phase of the Great Ordovician Biodiversification Event (GOBE); (ii) the transition between the second and third evolutionary faunas is correlated with the Late Ordovician mass extinction (LOME; Katian–Hirnantian) and associated climate cooling.

KEYWORDS: evolutionary faunas, macroevolution, plankton, polycystine radiolarians; GOBE

Polycystine radiolarians are marine pelagic heterotrophic unicellular microorganisms secreting an aesthetically pleasing siliceous skeleton, made initially of amorphous silica (De Wever *et al.* 2001). Living at different depths of the oceanic water column, including the deep-sea realm, they are present today in all modern oceans, with a diversity estimated at ca. 400–500 different living species (Lazarus 2005). Polycystine radiolarians constitute one of the oldest lineages of the rhizarian supergroup of eukaryotes, which comprises ecologically diverse amoeboid protists, including foraminifers and cercozoans (Sierra *et al.* 2013). Molecular dating estimates place the origin of skeleton-less radiolarians in the Neoproterozoic (ca. 760 Ma; Sandin *et al.* 2025), but the earliest fossil record of polycystine radiolarians can be traced with confidence back to the Cambrian Series 2 (Obut & Iwata 2000; Pouille *et al.* 2011; Korovnikov *et al.* 2013; Aitchison *et al.* 2017; Sennikov *et al.* 2017; Obut 2023), slightly later than the earliest record of hexactinellid sponges (Terreneuvian; Chang *et al.* 2017). Thus, the emergence of silica biomineralisation in these two eukaryotic, but phylogenetically distinct, lineages (Danelian & Moreira 2004) had profound implications since the early Cambrian, on the oceanic silica cycle and chert accumulation in early Palaeozoic oceans (Tolmacheva *et al.* 2001; Zhang *et al.* 2013; Chang *et al.* 2020).

Polycystine radiolarians have long been proven to be useful in numerous geological and palaeoenvironmental studies (i.e., Danelian *et al.* 2012; Matsuzaki & Itaki 2017) and more recently to decipher plankton palaeobiodiversity dynamics in relation to past palaeoceanographic/palaeoclimatic events (i.e., Danelian & Johnson 2001; Kiessling & Danelian 2011; Renaudie & Lazarus, 2013). Renewed interest in Palaeozoic radiolarians since the early 1980s and the extensive use of the scanning electron microscope allowed substantial progress in their taxonomic and biostratigraphic understanding (see Danelian *et al.* 2017 for a historical overview). Regarding the early Palaeozoic, interest has focused on understanding radiolarian palaeobiodiversity dynamics in relation to the Great Ordovician Biodiversification Event (GOBE; Noble & Danelian 2004) or Silurian palaeoceanography (Tetard *et al.* 2017), or to explore patterns in their biogeographic distribution (Danelian *et al.* 2013). Finally, Danelian & Monnet (2021) analysed an exhaustive sample-based dataset of middle Cambrian to Silurian radiolarian occurrences to document changes in taxonomic diversity over a 90-million-years' time interval, and more importantly to evaluate, with modern quantitative techniques, possible biases (i.e., sampling effort) that may affect the observed patterns in diversity changes. We here continue further the previous palaeobiological effort and

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present results of a factor analysis that was applied to an updated version of the above-mentioned dataset. Our results establish the presence of three evolutionary radiolarian faunas within early Palaeozoic radiolarians that are composed of radiolarian families with simultaneous dominance through their increases and decreases in their species richness over geological time.

1. Material and methods

1.1. Occurrence data

The analyses presented in this study are based on an exhaustive global dataset of all known Cambrian to Silurian radiolarian occurrences in temporally well-dated samples (at the stage resolution) and for which the age is based on evidence independent to radiolarians (i.e., conodonts, graptolites or radiometric ages; see supplementary material available at https://doi.org/10.1017/S1755691025100947; Appendix A). The compilation constitutes an update (both in terms of radiolarian samples/occurrences and taxonomy) of the dataset used by Danelian & Monnet (2021); it includes 55 publications, six of which concern the Cambrian (Dong *et al.* 1997; Won & Below 1999; Won & Iams 2002; Won *et al.* 2005; Pouille *et al.* 2014a; Sheng *et al.* 2020), nine the Early Ordovician (Kozur *et al.* 1996; Aitchison 1998; Won *et al.* 2005, 2007; Maletz & Bruton 2007; Won & Iams 2011, 2013, 2015; Pouille *et al.* 2014a), 12 the Middle Ordovician (Nazarov & Popov 1980; Maletz & Bruton 2007, 2008; Maletz *et al.* 2009; Pouille *et al.* 2013, 2014b; Yi *et al.* 2018; Kachovich & Aitchison 2020, 2021; Perera *et al.* 2020; Wu *et al.* 2024, 2025), seven the Late Ordovician (Nazarov & Popov 1980; Renz 1990; Wang 1993; Noble & Webby 2009; Perera & Aitchison 2022, 2023; Obut 2023), and 21 the Silurian (Goodbody 1986; Renz 1988; Furutani 1990; Noble 1994; Amon *et al.* 1995; MacDonald 1998, 2004, 2006a, 2006b; Noble *et al.* 1998; Kurihara & Sashida 2000a; Noble & Maletz 2000; Umeda & Suzuki 2005; Jones & Noble 2006; Kurihara 2007; Noble & Lenz 2007; Siveter *et al.* 2007; Nuramkhaan *et al.* 2013; Tetard *et al.* 2014a, 2014b, 2015). Radiolarian assemblages that were not accurately dated to the stage level were not included in the analysis (e.g., Nazarov 1975; Goto *et al.* 1992; Li 1995; Aitchison *et al.* 1998; Danelian & Clarkson 1998; Danelian 1999; Kurihara & Sashida 2000b; Buckman & Aitchison 2001; Danelian & Floyd 2001; Won *et al.* 2002; Danelian & Popov 2003; Danelian *et al.* 2011; Yan *et al.* 2025). The constructed dataset contains 16 families, 89 genera and 446 species through the 21 time-bins covering the Miaolingian (Cambrian) to Pridoli (Silurian) interval (ca. 509 to 419 Ma). Some of the analysed species are left in open nomenclature (i.e., 'sp. A') or are of doubtful species identification (i.e., 'cf'). The taxonomy of the dataset follows essentially the recent updates by Caridroit *et al.* (2017) and Noble *et al.* (2017).

1.2. Palaeobiodiversity

The global biodiversity through time of the studied radiolarians is estimated primarily at the species taxonomic rank by using two traditional incidence-based binning approaches and two modern occurrence-based resampling methods (Fig. 1). First, species richness is calculated as total diversity, defined as face-value range-through diversity, including single-interval taxa (for details see Alroy 2010; Foote 2000); it corresponds to the count of all documented taxa per time-bin, in addition to interpolated discontinuous taxon ranges. Total diversity is here complemented with the diversity of boundary-crossers, which counts the number of common taxa between two successive time-bins. Second, to overcome uneven sampling and preservation among the considered time intervals (Close *et al.* 2018), species richness is calculated by shareholder quorum subsampling (SQS; Alroy 2010; here, results are illustrated at a quorum/coverage of 50) and by corrected first-order jackknife (cJ1; Alroy 2020). Each of these methods reduces the effect of sample size on diversity estimates relative to using simple counts of species (Kerr & Alroy 2021).

Furthermore, the fossil record completeness of each geological stage considered is evaluated by means of a classical size-based rarefaction analysis (supplementary Fig. 1; Gotelli & Colwell 2001; Chao *et al.* 2014). Also, insufficient sampling is highlighted by comparing the actual coverage to the maximum observed within-stage total diversity (see Marcot *et al.* 2016). Early Palaeozoic radiolarian diversity is further investigated by evaluating taxonomic changes through time (i.e., origination and extinction components) with a poly-cohort analysis (supplementary Fig. 2), which enables to graphically investigate and compare survivorship and prenascence of taxonomic assemblages through time (Raup 1978; Van Valen 1979; Foote 2001; Monnet *et al.* 2003). By measuring the remaining percentage of taxa through time within each cohort separately (i.e., the pool of species present in a given stratigraphic interval), this analysis allows to localise potential time breakpoints in the dynamics of origination or extinction: typically, in the interpolated contour graph of survivorship and prenascence log values, contour lines are expected to be parallel to the diagonal only if the extinction and origination rates are constant through time (for further details see Monnet *et al.* 2003; Brayard *et al.* 2009).

1.3. Evolutionary faunas

To further investigate diversity dynamics of early Palaeozoic radiolarians, the total diversity (species richness) within families (Fig. 2) is processed to evaluate the possible presence of so-called 'evolutionary faunas' (Sepkoski 1981; see also Adrain *et al.* 1998; Figueirido *et al.* 2012; Cleal & Cascales-Miñana 2014; Bault *et al.* 2022; Rojas 2022; Allaire *et al.* 2025). These evolutionary faunas correspond here to radiolarian families that record simultaneously high species richness through successive stages. The presence of such long-term shifts in taxonomic composition holds the potential to highlight periods of consistent functional and biotic/environmental conditions or of differential responses to their changes. Like Sepkoski (1981), radiolarian evolutionary faunas are here identified by a factor analysis (FA). Resulting factors (supplementary Fig. 3) define the evolutionary faunas, the historical diversity of which is rescaled to the global total diversity (Fig. 3) according to their proportion of explained variance in the FA model. Furthermore, the pervasiveness of the FA-based evolutionary faunas is evaluated by a hierarchical cluster analysis (HCA with Pearson's correlation and complete agglomeration method; Legendre & Legendre 2012) of the within-family total species richness through the successive analysed time-bins (supplementary Fig. 4).

Interestingly, despite relying on species richness, evolutionary faunas enable to highlight large-scale turnovers in taxonomic composition (rather than fluctuations in global diversity) because they focus on the concomitant and relative dominance of subclades through their richness. These two aspects of biodiversity are relatively independent, and changes in evolutionary faunas (taxonomic composition) may occur without changes in global taxonomic richness. Furthermore, the recognition of evolutionary faunas appears to be hardly sensitive to low sampling. Indeed, time intervals with low diversity due to insufficient data (e.g., the Dapingian; see Danelian & Monnet 2021) contribute to the residuals of the

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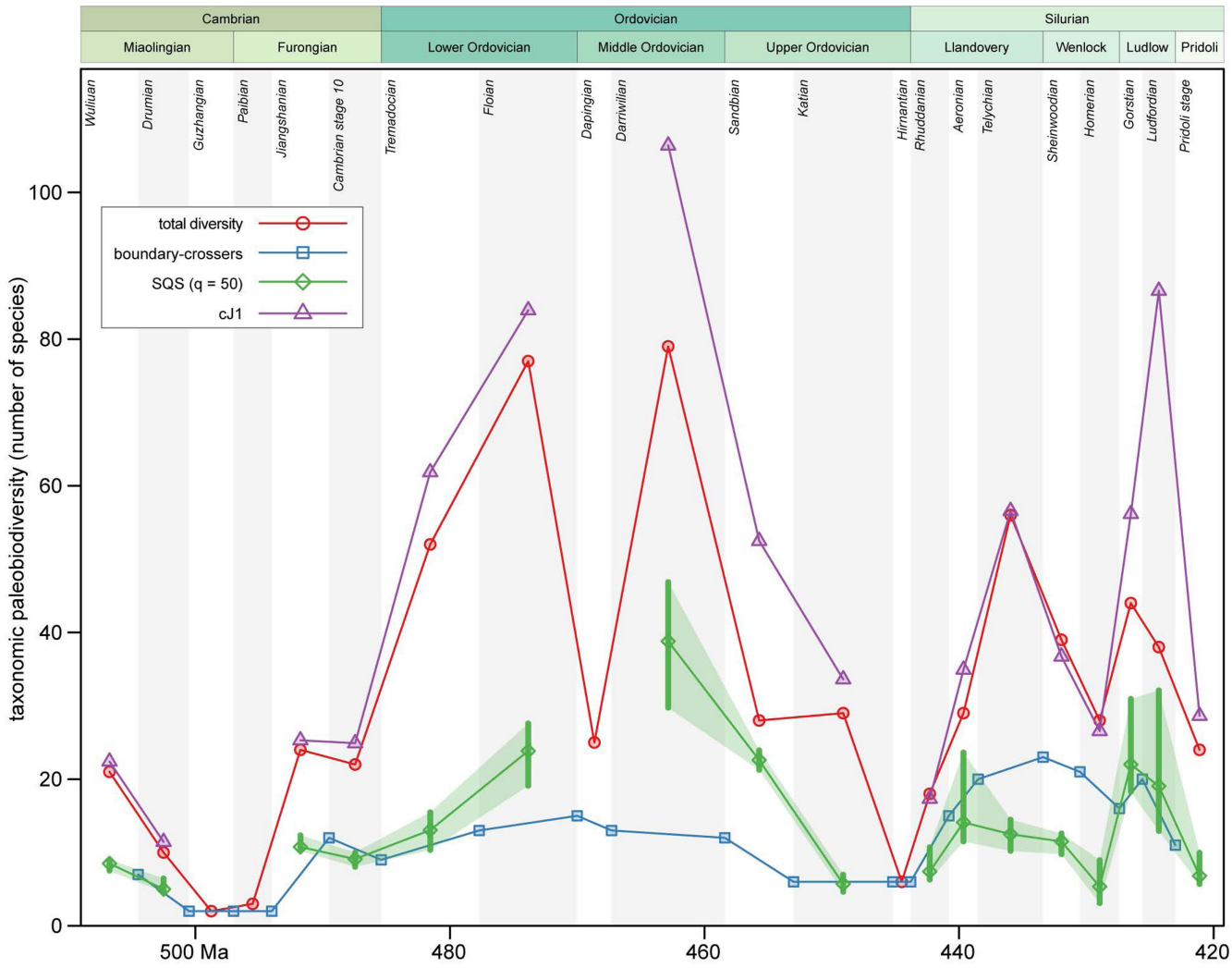


Figure 1 Palaeobiodiversity (species richness) of early to mid-Palaeozoic radiolarians according to face-value counting (total diversity and boundary-crosser diversity) and sample-standardised estimates (coverage-based rarefaction with a quorum of 50, SQS; and corrected first-order jackknife, cJ1).

factor analysis, and thus they do not contribute to the reconstructed evolutionary faunas (see supplementary Fig. 3). Although insufficient sampling may impact the global diversity, it does not necessarily create turnovers in the relative within-family richness through time: insufficient sampling does not prevent macroevolutionary adaptive innovations in some families leading them to diversify and dominate over other families through time (see supplementary Fig. 4).

2. Results

2.1. Changes in palaeobiodiversity

Early Palaeozoic radiolarian diversity trajectories at the species level and at the stage resolution are presented in Figure 1, both at face-value and sample-standardised taxonomic richness metrics. In general, they confirm the trends recognised by Danelian & Monnet (2021). More specifically, the curves of the sample-standardised taxonomic richness (SQS50) and of the corrected first-order jackknife (cJ1) establish that the obtained diversity patterns are robust, except for the Guzhangian, the Paibian, the Dapingian and the Hirnantian, which still remain undersampled in terms of radiolarian occurrences in the studied samples (see also supplementary Fig. 1).

In short, the analysed data point to: (i) a substantial and protracted diversity increase during the late Cambrian–Early Ordovician interval, peaking in the Darriwilian (Middle Ordovician); the Dapingian drop in total diversity values is due to the paucity of data for this stage; (ii) a continuous diversity decrease after the Darriwilian up to the end of the Ordovician, although no data exist for the Hirnantian; and (iii) a rapid recovery and increase in diversity during the Llandovery (early Silurian), followed by two diversity highs expressed in the Aeronian–Telychian and Gorstian–Ludfordian intervals.

2.2. Evolutionary faunas within early Palaeozoic radiolarians

Factor analysis on species richness within the 16 radiolarian families encountered over the 21 time-bins (geological stages) considered for the Cambrian–Silurian interval (ca. 509 to 419 Ma) produced six major eigenvectors, which explain almost 90 % of the original variance (supplementary Fig. 3). These factors clearly aggregate in clusters of adjacent time units and, therefore, constitute three major radiolarian evolutionary faunas, which follow one another over time (Fig. 3): (i) a Cambrian–Early Ordovician fauna (EF1); (ii) a Darriwilian–Sandbian fauna (EF2); and finally (iii) a Katian to Silurian fauna (EF3). It is noteworthy that these three evolutionary faunas are clearly reflected in their origination/extinction rates, which also cluster in three distinct successive intervals as highlighted by the polycohort analysis (supplementary Fig. 2).

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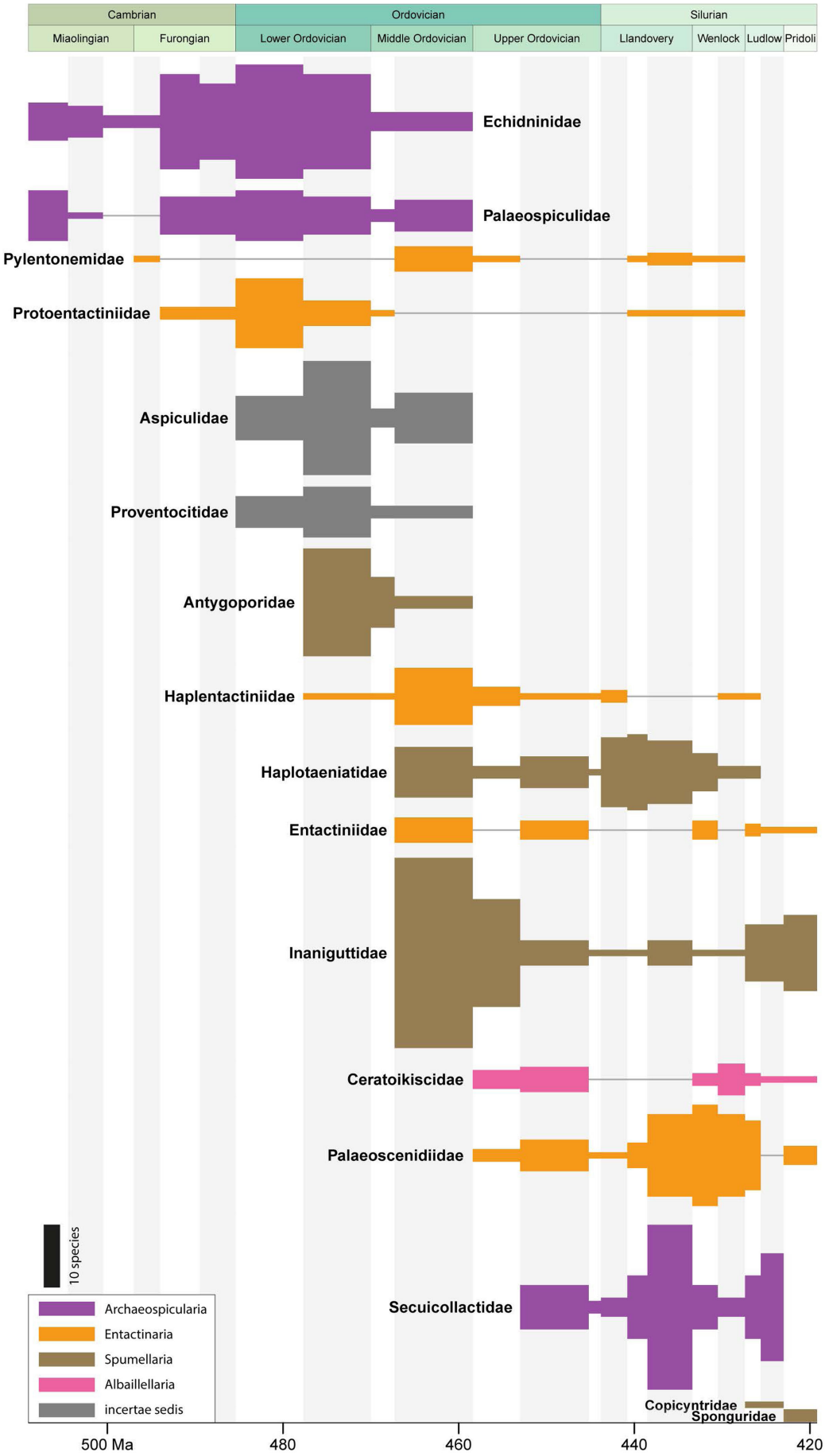


Figure 2 Spindle diagram illustrating the variations in within-family radiolarian total diversity (species richness) across the mid-Cambrian to Silurian interval. Colours refer to the different radiolarian taxonomic orders: purple = Archaeospicularia; orange = Entactinaria; brown = Spumellaria; pink = Albaillelaria; grey = *incertae sedis*.

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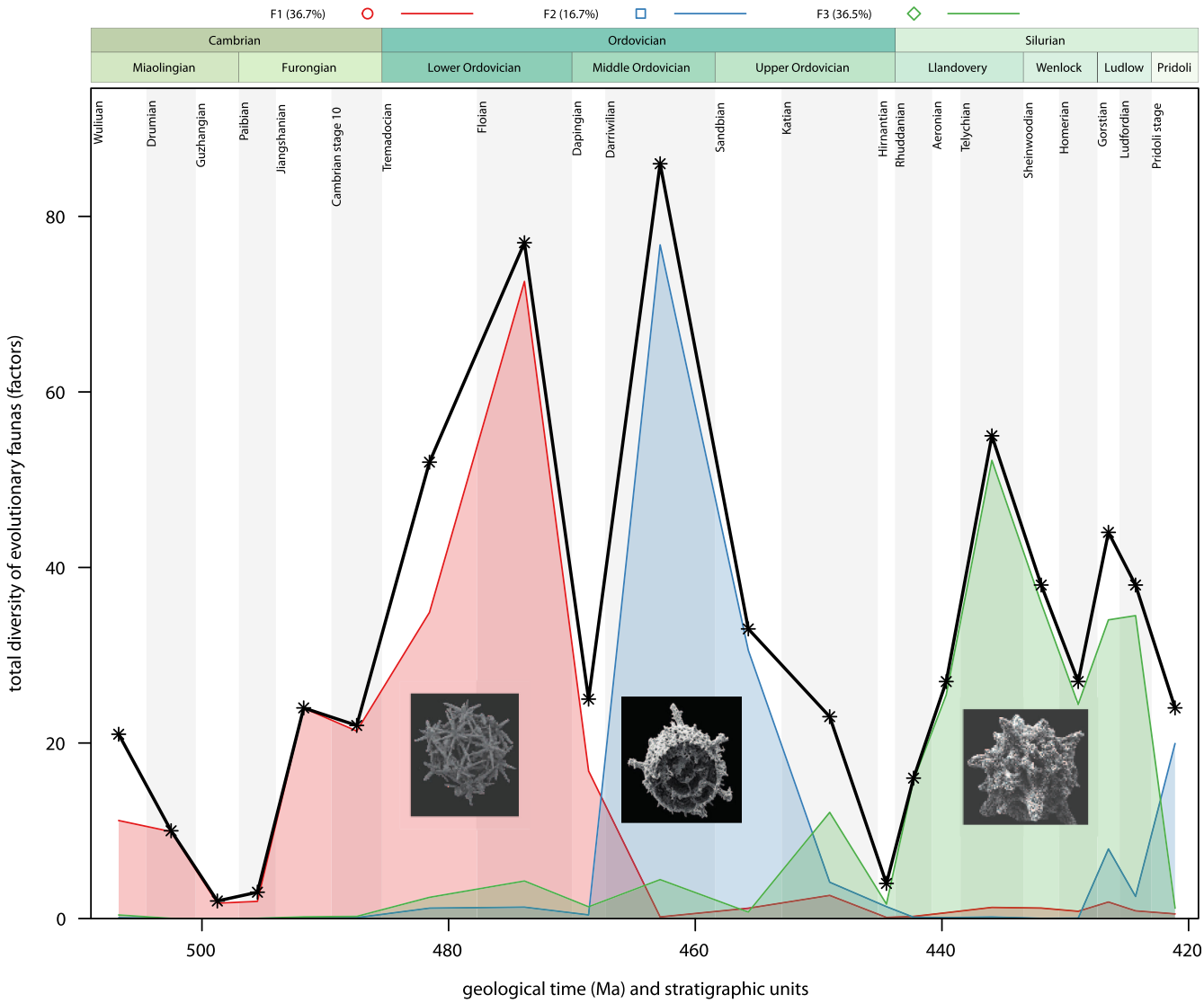


Figure 3 Palaeobiodiversity of the three early to mid-Palaeozoic radiolarian evolutionary faunas (pink: Cambrian–Early Ordovician fauna; blue = Darriwilian–Sandbian fauna; green = Katian-Silurian fauna) extracted from the factor analysis of the within-family species richness through geological stages. Palaeobiodiversity of the faunas is rescaled to the total diversity (thick black line) based on the relative proportion of explained variance of their factors.

Finally, these three evolutionary faunas are also recovered by the cluster analysis on within-family species richness, both among families and among stages (supplementary Fig. 4).

The oldest evolutionary fauna EF1 is composed of Cambrian to Early Ordovician radiolarians assigned to the families Echidninidae and Palaeospiculidae (order Archaeospicularia) and the family Protoentactiniidae (order Entactinaria). This evolutionary fauna is complemented in the Early Ordovician by radiolarians assigned to the family Antygoporidae, which includes the oldest representatives of the order Spumellaria, as well as radiolarians assigned to the families Aspiculidae and Proventocitidae (order *incertae sedis*). Nearly all these families appear to be still present in the Middle Ordovician, although with a much-reduced diversity.

A new evolutionary fauna EF2 emerged during the Darriwilian (Middle Ordovician) and lasted clearly during the Sandbian (Late Ordovician); it is dominated by the spumellarian family Inaniguttidae, and to a lesser extent by the entactinarian families Haplentactiniidae, Entactiniidae and Pylentonemidae. The spumellarian family Haplotaeniatidae is well present in this fauna (EF2), but it contributes more to the next one (EF3).

The Late Ordovician Katian stage records clearly the dominance of the third evolutionary fauna EF3, which emerged timidly in the Early Ordovician and continued throughout the entire Silurian. Although the EF3 evolutionary fauna is composed taxonomically overall by the same families as EF2, it is mostly characterised by the archaeospicularian family Secuicollactidae, the entactinarian family Paleoscenidiidae, the spumellarian family Haplotaeniatidae and the deep-dwelling albaillellarian family Ceratoiciscidae.

It is worth noting that some families may be present beyond the time interval of the evolutionary fauna that they characterise. For example, the family Protoentactiniidae is characteristic of the Cambrian–Early Ordovician EF1, but some of its representatives persisted until the mid-Silurian. Likewise, the family Ceratoikiscidae (order Albaillellaria), although it probably first appeared in the latest Darriwilian (i.e., *Protoceratoikiscum clarksoni* Buckman & Aitchison 2001; Danelian & Floyd 2001), is a main biotic component of the youngest evolutionary fauna EF3, since it is more diverse during the Silurian. A third example is the spumellarian family Haplotaeniatidae, which although it first appeared in the

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Darriwilian and contributes to the diversity of this interval, is a characteristic component of the EF3 fauna.

3. Discussion

The publication of putative lower Cambrian radiolarians has been recently discussed by Maletz (2017) who commented on early reports by Braun *et al.* (2005, 2007) and Cao *et al.* (2014) and has rightfully considered them as being contaminations with younger radiolarian material. Maletz stressed on the fact that well-preserved middle Cambrian radiolarian fauna establish that the skeleton of Cambrian radiolarians was formed by a spicular skeleton that was not necessarily spherical in shape. A number of recent reports documenting poorly preserved spherical or ellipsoidal microfossils from China, most of them displaying lattice shells, are equally problematic, and may be considered as contaminations from younger material (Chang *et al.* 2018; Ma *et al.* 2019; Zhang & Feng 2019; Zhang *et al.* 2021; Huang *et al.* 2025).

Analysis of the updated radiolarian occurrence dataset confirms overall the previously observed trends in radiolarian palaeobiodiversity (Danelian & Monnet 2021). However, the contrast thought to exist between the Late Ordovician and Silurian evolutionary history and dynamics is not confirmed here (see discussion below).

Regarding the Ordovician, the sample-standardised curves suggest a protracted rise in species diversity throughout the late Cambrian Stage 10 up to the Darriwilian, if the Dapingian drop in apparent total radiolarian diversity is due to the paucity of data for this stage. Indeed, radiolarian data for this stage come from a single study (Maletz & Bruton 2007) and the rarefaction curve suggests a huge potential to increase the radiolarian diversity for this stage by adding new samples.

Radiolarian assemblages participating in the Cambrian Stage 10 _ Dapingian phase of this radiolarian diversity increase are all part of the evolutionary fauna EF1, which is dominated essentially by the archaeospicularian families Echidninidae and Palaeospiculidae and the entactinarian family Protoentactinidae. Archaeospicularians are characterised by hollow shells made of spicular elements, while Entactinarians initiate their test development from a small initial spicule made of a bar and rays trifurcating from each end of this median bar. These are the radiolarian groups that participated in the 'Ordovician plankton revolution' (*sensu* Servais *et al.* 2016). The subsequent participation in the EF1 evolutionary fauna of the Order *incertae sedis* families Aspiculidae and Proventocitidae (since the Tremadocian) and of the spumellarian family Antygoporidae (since the Floian) contributed to the sharp continuous diversity increase recorded during the Tremadocian and the Floian.

Our new analysis confirms and further supports the 'game-changing' character of the Darriwilian for the evolutionary history of polycystine radiolarians. Indeed, the performed factor analysis highlights the uniqueness of the Darriwilian–Sandbian evolutionary fauna (EF2), which stands out clearly, with sharp transitions, compared to the other two evolutionary faunas (see Fig. 3). Our analysis highlights also the profound significance of the Darriwilian diversification of the spumellarian family Inaniguttidae, made of large porous spherical shells bearing rod-like spines initiated from an internal microsphere, but also of the diverse entactinarians assigned to the families Haplentactiniidae, Entactiniidae and Pylentonemidae. As representatives of the EF1 are still present in the Darriwilian, this stage records the highest sample-standardised diversity for the entire analytical interval. As mentioned already by Danelian & Monnet (2021), it is likely that a major faunal turnover took place within the Darriwilian, with as a result an accumulated species richness at the level of this stage, an inevitable consequence of our analytical level, which is performed at the stage level. It is now clear to us that the Darriwilian evolutionary fauna EF2 emerged in relation to the global cooling and associated oceanographic changes that took place during this stage. Indeed, Rasmussen *et al.* (2016) established that a sudden greenhouse to icehouse climatic shift took place during the early Darriwilian, which would have initiated an oceanic 'conveyor belt' and polar front shifts (Vandenbroucke *et al.* 2010) in the global ocean, a global climatic context that coincides with the main phase of the GOBE (Rasmussen *et al.* 2016; Kröger *et al.* 2019; Stigall *et al.* 2019).

Thanks to the additional recent data obtained from Perrera & Aitchison (2022, 2023) and Obut (2023) from the Sandbian and the Katian stages, our updated dataset confirms the continuous and rather sharp decline in radiolarian diversity that is recorded in the sample-standardised curves of species richness (SQS, cJ1; Fig. 1) between the Darriwilian and the Katian; regrettably there are still no radiolarian data available for the Hirnantian. This is especially true since the Sandbian has still a great potential to reveal a higher diversity with the addition of new samples (see supplementary Fig. 1).

Although it appeared timidly since the Early Ordovician, the third evolutionary fauna (EF3) became prominent since the Katian, with a clear separation from the previous EF2 fauna. This was an unexpected result of our analysis, which suggests an evolutionary affinity of the Katian fauna with the Silurian one. This new perception contrasts with the one reached a few years earlier (Danelian & Monnet 2021), suggesting that the evolutionary dynamics of Silurian radiolarian was distinct compared to the Late Ordovician ones. The emergence in the Katian of the EF3 coincides with the climate cooling recorded since this stage, ahead of the Hirnantian glaciation, and the initiation of the Late Ordovician Mass Extinction (LOME; Rasmussen *et al.* 2023).

As previously concluded by Danelian & Monnet (2021), the analysed dataset points to a rapid recovery and increase in diversity during the Llandovery (early Silurian), followed by two diversity highs expressed in the Aeronian–Telychian and Gorstian–Ludfordian intervals.

4. Conclusions

Analysis of the updated early Palaeozoic radiolarian occurrence dataset confirms the previously observed trends in radiolarian palaeobiodiversity dynamics: a protracted rise in species richness throughout the late Cambrian Stage 10 to the Darriwilian, followed by a progressive, protracted drop during the entire Late Ordovician and a post-extinction rebound since the earliest Silurian.

Factor analysis of the dataset allows to establish the presence of three radiolarian evolutionary faunas reflecting the concomitant dominance of some families, and provide complementary insights to early Palaeozoic radiolarian macroevolution:

- It confirms the evolutionary affinity of the Early Ordovician radiolarian fauna with the one present in the late Cambrian oceans; however, although the oldest evolutionary fauna EF1 is dominated by spicular radiolarians (Archaeospicularia), it also includes entactinarian families (since the Cambrian Stage 10) and the oldest spumellarians (since the Floian).
- It highlights the uniqueness of the Darriwilian–Sandbian evolutionary fauna (EF2), the origination of which coincides with the early Darriwilian climate shift and the main phase of

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the GOBE; the EF2 is clearly characterised by the spumellarian family Inaniguttidae and to a lesser extent by the entactinarian families Haplentactiniidae, Entactiniidae and Pylentonemidae.

- The third evolutionary fauna (EF3), although composed taxonomically of the same families as EF2, is characterised more specifically by representatives of the archaeospicularian family Secuicollactidae, the entactinarian family Paleoscenidiidae, the spumellarian family Haplotaeniatidae and the deep-dwelling albaillellarian family Ceratoiciscidae. It is the first time that existing data point to a rather sharp shift in radiolarian assemblage composition during the Late Ordovician (Sanbian to Katian transition) and an evolutionary affinity of the Katian fauna with the Silurian one. This faunal change coincides with the Katian climate cooling and initiation of the Late Ordovician mass extinction.

5. Supplementary material

Supplementary material is available online at https://doi.org/10.1017/S1755691025100947.

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7. Competing interests

The authors declare none.

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