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Taniel Danelian, Claude Monnet

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1 **Early Paleozoic radiolarian plankton diversity and the Great Ordovician**

2 **Biodiversification Event**

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5 Taniel Danelian ^{1,*}, and Claude Monnet ¹

6

7 ¹ Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France

8 * Corresponding author. Email: taniel.danelian@univ-lille.fr

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10

11

12 **ORCID**

13 Taniel Danelian <https://orcid.org/0000-0001-9496-2363>

14 Claude Monnet <https://orcid.org/0000-0002-0899-8392>

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17 **ABSTRACT**

18 Based on a new and exhaustive sample-based dataset of middle Cambrian to Silurian radiolarian
19 occurrences we investigate the diversity patterns of all radiolarian species to find out trends in their
20 taxonomic evolution and to evaluate possible biases influencing these patterns. We also review and discuss
21 the long term radiolarian biotic changes in the context of the Great Ordovician Biodiversification Event
22 (GOBE) and associated global changes that affected the Earth system at the time. The Cambrian stage 10 –
23 Middle Ordovician interval is characterized by a protracted diversification trend peaking in the Darriwilian.
24 The rising trend is initially produced during the Tremadocian by Archaeospicularian radiolarians and it may
25 be partly correlated with the basal Ordovician “plankton revolution”. Subsequently, the radiolarian diversity
26 increase is mainly due to Spumellarian and Entactinarian radiolarians; the Darriwilian peak is the highest for
27 the entire studied interval; it reflects a profound turnover in Ordovician radiolarian plankton assemblages.
28 The Darriwilian appears to be a “game changing” interval for radiolarians and it is likely due to the profound
29 oceanographic changes that followed the early Darriwilian cooling trend of Earth’s climate. The transition
30 with the Silurian is separated and highlighted by a Late Ordovician large drop in diversity, which records the
31 lowest taxonomic richness of the studied interval. Next, the Silurian is first characterized by a rapid
32 protracted recovery culminating in the Aeronian, and, secondly, by another peak in richness recorded in the
33 Gorstian. Our results suggest that radiolarian microzooplankton have responded during all the major diversity
34 events recognized in the early Paleozoic evolution of the marine biosphere. However, although the long-term
35 trends in radiolarian biodiversity are robust, the documented patterns remain partly and locally biased by
36 uneven sampling through space and time.

37

38 **KEYWORDS**

39 Radiolaria, Plankton, Paleozoic, Paleobiodiversity, Macroevolution, GOBE

40 1. Introduction

41

42 The Great Ordovician Biodiversification Event (GOBE; Webby et al., 2004) is a unique and major event
43 in the evolutionary history of the marine biosphere that corresponds to an exceptionally rapid diversity
44 increase at lower taxonomic levels (e.g., genus). It records a burst of adaptive radiations in all the
45 components of the marine ecosystem, from benthos to plankton, as well as reefs (Servais and Harper, 2018).
46 Although the macroevolutionary importance of this Ordovician biodiversification is established since the
47 pioneering analysis of Sepkoski (1995), the coordinated effort of the successive International Geological
48 Correlation Programmes on the Ordovician (IGCPs 410, 503, 653) allowed to achieve an enormous progress in
49 understanding its temporal and spatial details, possible biases, as well as clade-by-clade dynamics. It also
50 became apparent that the GOBE represents a unique case in Earth System studies, as changes in Ordovician
51 climate, oceanic circulation and oxygenation appear to have played an important role for the development of
52 the GOBE (Stigall et al., 2019). However, recent debates showed that the concept of the GOBE and its
53 duration needed to be clarified.

54 Servais and Harper (2018) argue that the GOBE sums all the numerous and discrete biodiversification
55 events that took place during the Ordovician, well after the early “Cambrian Explosion” (Zhuravlev and
56 Riding, 2000). The earliest of these events concerns the “Ordovician plankton revolution” (Servais et al.,
57 2008), a unique macroecological event, which may have started since the late Cambrian with the
58 diversification of acritarchs (Servais et al., 2016). The “revolutionary” character of this event is best illustrated
59 by the sudden colonization of the water column, at the beginning of the Ordovician. A number of metazoan
60 lineages with Cambrian benthic ancestors, such as the graptolites (Maletz, 2019) and the planktotrophic
61 gastropods (Nützel and Frýda, 2003), “suddenly” adopted a planktic mode of life, at least for part of their life
62 cycle. Two other major diversification events are considered to be part of the GOBE *sensu* Servais and Harper
63 (2018). They concern the diversification of a great number of bottom-dwelling clades around the
64 Early/Middle Ordovician boundary and the diversification of reef-builders during the Middle/Late Ordovician
65 transition. Finally, Harper et al. (2020) reviewed recently the pattern of changes that took place in the marine
66 biosphere based on genus-level data extracted from the Paleobiology Database. They argue that the GOBE
67 appears to be part of a very long standing interval of continuous diversifications that started in the late
68 Precambrian and ended in the Devonian.

69 Some recent studies have highlighted the critical changes that took place during the Darriwilian and
70 suggested restricting the GOBE to this shorter, Mid Ordovician time interval. More specifically, Kröger and
71 Lintulaakso (2017) established that Ordovician diversification rates increased at statistically higher levels
72 during the Darriwilian, while Rasmussen et al. (2019) concluded that the GOBE took place during the
73 Darriwilian–early Katian, with a very steep rising trend starting in the early Darriwilian. This was also

74 confirmed by Kröger et al. (2019). Using the same analytical framework as Rasmussen et al. (2019) they
75 evaluated the genus level rates of origination and extinction, as well as trends in survivorship of the early
76 Paleozoic marine biosphere. Finally, Stigall et al. (2019) reviewed global, clade by clade and regional diversity
77 dynamics to also conclude that the GOBE should be restricted to the rapid Darriwilian diversification. They
78 suggested that the term “Ordovician Radiation” should be used to describe the broader pattern of
79 diversifications that took place throughout the Ordovician.

80 Interestingly, most inferences regarding the early Paleozoic evolution of the marine biosphere lack a
81 microzooplankton perspective, in spite of its importance for the development of marine food webs, nutrient
82 recycling and the maintenance of fragile equilibria in global biogeochemical cycles (Sieburth et al., 1978;
83 Calbet and Landry, 2004; Castellani and Edwards, 2017). Radiolaria are an important component of today’s
84 oceanic microzooplankton (Lazarus, 2005) and as such they are dependent on the physical properties of the
85 water mass (e.g., temperature and chemistry) and on phytoplankton and bacterial availability. They are thus
86 sensitive indicators of current and past oceanic circulation, nutrient flux and global climate change (Hays et
87 al., 2005).

88 Polycystine radiolarians are one of the oldest lineages amongst Rhizarians (Sierra et al., 2013) with a
89 good fossil record stretching back to the early Cambrian (Obut and Iwata, 2000; Korovnikov et al., 2013;
90 Sennikov et al., 2017; Aitchison et al., 2017a). They may provide important insights to the initiation of
91 siliceous biomineralization in eukaryotic lineages (Danelian and Moreira, 2004), as well as to the evolution,
92 since the Cambrian, of the oceanic silica cycle (Zhang et al., 2013; Tolmacheva et al., 2001).

93 After having survived repeated periods of major extinctions (De Wever et al., 2003), polycystine
94 radiolarians have always recovered to become abundant and diverse, with several hundred of species living
95 in modern oceans (Lazarus, 2005). However, the patterns of their changes in diversity through geological
96 time still remain poorly documented and are often only studied at large temporal and taxonomic scales (e.g.,
97 Vishnevskaya and Kostyuchenko, 2000; Umeda, 2002; De Wever et al., 2003). Moreover, few studies have
98 attempted to evaluate the various biases possibly impacting radiolarian diversity curves (such as the sampling
99 effort; see case studies by Danelian and Johnson, 2001; Kiessling and Danelian, 2011; Renaudie and Lazarus,
100 2013).

101 Regarding the early Paleozoic, a first attempt to estimate Ordovician radiolarian biodiversity patterns
102 was produced by Noble and Danelian (2004), as a preliminary contribution to IGCP 410 (Webby et al., 2004).
103 Normalized species diversity showed a sudden peak in the middle Darriwilian (time slice 4b of Webby et al.,
104 2004), with high values persisting in the late Darriwilian and early Sandbian (time slices 4c and 5a). However,
105 data on Ordovician radiolarians were rather sparse at the time and additional studies were required to
106 confirm these patterns. In spite of these limitations, a new paleobiodiversity analysis with the application of
107 modern standardized techniques is timely. Many new and valuable Ordovician radiolarian data have been

108 published during the last twenty years (see Danelian et al., 2017 for a historic account). This includes the
109 Tremadocian (Won et al., 2005, 2007; Pouille et al., 2014a), the Floian (Maletz and Bruton, 2007; Won and
110 Iams, 2011), the Dapingian (Maletz and Bruton, 2007), the Darriwilian (Maletz and Bruton, 2008, Pouille et
111 al., 2013, 2014b; Kachovich and Aitchison, 2020, 2021) and the Katian (Noble and Webby, 2009). Regarding
112 the Silurian, Tetard et al. (2017) recently explored the diversity patterns of radiolarians and compared them
113 with the graptoloid record. They revealed an early Silurian diversity increase, suggesting a diversification
114 recovery following the end Ordovician mass extinction. However, the robustness of their results remains to
115 be evaluated by applying modern resampling diversity metrics.

116 By using a new, exhaustive dataset of all well-preserved early Paleozoic radiolarian assemblages within
117 a revised taxonomic and temporal framework, together with traditional range-based and modern
118 occurrence-based resampling paleobiodiversity metrics, we aim to address and evaluate in this study the
119 following questions:

120 1) What are the radiolarian diversity patterns during the various phases of the GOBE *sensu* Servais and
121 Harper (2018)?

122 2) How do Ordovician levels and patterns of radiolarian diversity compare with the Silurian ones?

123 3) How do radiolarian diversity trends and events compare with global and per-clade diversity patterns
124 and environmental/oceanographic/climatic events known from the early Paleozoic?

125 Although our main questions concern the Ordovician, our analysis also covers the middle-late
126 Cambrian and the entire Silurian in order to place the documented patterns of Ordovician radiolarian
127 diversity in a wider temporal framework and to acknowledge the relative significance of changes in early
128 Paleozoic radiolarian diversity with respect to the unique and impressive Great Ordovician Biodiversification
129 Event (GOBE).

130

131 **2. Material and methods**

132

133 *2.1. Sample-based data*

134 A global dataset of early Paleozoic radiolarian occurrences was compiled based on the available literature
135 (Appendix A). The compilation is exhaustive and is based on 51 publications, but only includes studies for
136 which radiolarian assemblages were dated independently of radiolarians and at least at the temporal
137 resolution of the chronostratigraphic stage. In other words, were considered only occurrences that were
138 able to be assigned to a single geological stage. Thus, a number of radiolarian assemblages for which the age
139 was assigned, even marginally, to more than one single stage they were not included in the analysed dataset
140 (e.g. Bengtson, 1986; Buckman & Aitchison, 2001; Danelian & Clarkson, 1998; Danelian, 1999; Danelian &
141 Floyd, 2001; Goto et al., 1992; Kurihara & Sashida, 2000b; Li, 1995; Nazarov, 1975; Won et al., 2002). The

142 constructed dataset is sample/collection-based. It provides a list of all taxa identified at the species rank and
143 in each individual sample or bed described within a given reference. The dataset consists of incidence
144 (presence) data, because abundance data for radiolarians are rarely available, inconsistent, and were only
145 present in a handful of the surveyed publications. The ages of samples reported in these references were
146 either constrained by fossils other than radiolarians or by radiometric age dating and correlation to the
147 international chronostratigraphic chart (see Cohen et al. 2013). The ages of some samples have been revised
148 from the original work when relevant information has later become available (e.g Tetard et al., 2017). The
149 duration of early Paleozoic stages varies between 1.4 Myr (Hirnantian) to 8.9 Myr (Darriwilian) with a mean
150 at about 4.3 Myr (see Cohen et al., 2013, update v.2016/10). To create a taxonomic framework that reflects
151 the current state of research with as much consistency as possible, taxonomic assignments of species were
152 reviewed in the original publications and species names were revised and updated to remove nomenclatural
153 artifacts that might impede accurate measures of radiolarian diversity. This revision also relies on the
154 recently updated taxonomic and biostratigraphic framework of Paleozoic radiolarians (Caridroit et al., 2017;
155 Noble et al., 2017; Aitchison et al., 2017a, b). The taxa counted herein include also reports of species
156 assigned under open nomenclature (such as 'sp. A') or with an uncertain specific identification (such as 'cf.').

157 The constructed dataset contains 19 families, 83 genera and 405 species. It is based on 51 publications
158 covering the 21 stages of the studied interval (Appendix B). Figure 1 illustrates the paleogeographic
159 distribution of the analyzed radiolarian occurrences; it shows that most of the analyzed radiolarian localities
160 were situated at the time at low latitudes; this is particularly true for the middle Cambrian–Early Ordovician
161 (Won and Iams, 2002, 2011; Won et al., 2005, 2007; Pouille et al., 2014a; Maletz and Bruton 2007, 2008;
162 Renz, 1990a, b). This dataset can be also expressed as a synthetic occurrence range chart (Appendix C) in
163 which each species is ordered by genus, family and order membership and then by appearance.

164

165 2.2. Biodiversity metrics

166 Evaluation of paleobiodiversity and its variation through geological time is a major issue in
167 macroevolution. Although major biases (rock/fossil preservation, facies/ecology, sampling, etc.) may affect
168 taxonomic richness estimation (Raup, 1972; Foote, 2000; Smith, 2001; Benton, 2009; Hunt, 2010), substantial
169 progress was achieved in the past few decades in our knowledge of changes in Phanerozoic biodiversity
170 (Sepkoski et al., 1981; Benton, 1993; Alroy et al., 2008; Fan et al., 2020), notably because of the use of
171 resampling methods (Alroy, 2010a; Chao et al., 2012, 2014; Close et al., 2018). As a component of
172 biodiversity, taxonomic richness (count of the distinct names of a specific taxonomic rank, such as species,
173 irrespective of their phylogenetic relationships or morphological distinctness) is here estimated based on
174 both traditional, range-based and modern, sample-based biodiversity approaches against the succession of
175 time-ordered chronostratigraphic intervals (i.e. stages). Although this study focuses on taxonomic richness

176 measured at the species rank, genus and family level patterns of changes in diversity are also discussed as
177 they provide important insights when comparisons are made with global environmental changes. Biodiversity
178 analysis was computed at the chronostratigraphic rank of the middle Cambrian–Silurian stages (Cohen et al.,
179 2013). Various paleobiodiversity indices were assessed by using the scientific environment R version 3.6.2 (R
180 Core Team 2019) and with the use of the ‘epaleo’ package, version 0.8.39 (Monnet C, unpublished, University
181 of Lille; for applications using this package, see e.g., Nowak et al., 2015; Tetard et al., 2017; Bault et al., 2021).

182 Although taxonomic richness is an intuitive measure of biodiversity, it is an elusive quantity to measure
183 properly because as more individuals are sampled more species will be recorded. This corresponds to the so-
184 called “sampling bias” (Simpson, 1949; Raup, 1972; Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001;
185 Chao et al., 2014). Recently, the reconstruction of paleobiodiversity trajectories has emphasized the need to
186 use sample-based over range-based data. The former enable using resampling techniques to correct the
187 possible effects of the “sampling bias”, which may be sometimes overwhelming. Techniques such as size-
188 based rarefaction (CR), coverage-based rarefaction (SQS), and richness estimated using a Poisson sampling
189 model (TRiPS) have been applied here. The conventional size-based rarefaction (Sanders, 1968; Hurlbert,
190 1971; Foote, 1992; Shimadzu, 2018) estimates taxonomic richness by repeated random subsampling of the
191 data to a user-defined sample size, enabling thus comparison of the time intervals considered at equal
192 sampling effort. Coverage-based rarefaction (or shareholder quorum subsampling, SQS; Alroy 2010a, b, c)
193 repeatedly draws randomly selected taxa from compiled in-bin occurrence lists until a summed proportion of
194 relative occurrence frequency for these taxa reaches a certain ‘quorum’ to finally sum the taxa sampled.
195 TRiPS (Starrfelt and Liow, 2016) aims to estimate true richness by modeling per-interval sampling rates
196 (inferred by maximum likelihood using observed taxon occurrence frequencies and interval durations) as a
197 homogeneous Poisson process. Coverage-based rarefaction has been shown by both simulation studies and
198 empirical data to be a robust method for correcting preservation and sampling heterogeneity (Alroy, 2010a,
199 b; Chao and Jost, 2012; Close et al., 2018). In this study, these resampling diversity approaches were applied
200 by including dominant and single-interval taxa.

201 For comparison, traditional range-based indices such as sampled-in-bin diversity (SIB), range-through
202 (or total) diversity (RT) including or excluding single-interval taxa (RTinS and RTexS, respectively), normalized
203 diversity (NORM), and boundary-crosser diversity (BC), are reconstructed. All these traditional metrics may
204 be biased by various effects such as heterogeneous sampling, but they are still useful in highlighting
205 peculiarities in the dataset (such as uneven amounts of inferred ranges or single-interval taxa). For additional
206 details and discussion on these approaches, see Foote (2000), Cooper (2004), and Alroy (2010b), among
207 others. Additionally, the recent stochastic uniform-time-bin diversity (UTB) of Gibert and Escarguel (2017)
208 was applied. This approach is a back-transformation into a virtually continuous-time averaged time series of
209 the time-discretized dataset constructed from the fossil record. The period of time under study here was split

210 into 2 Myr time bins, and each specimen was assigned multiple times at random to one of the bins between
211 its maximum and minimum age brackets. This method has been shown to provide more accurate estimates
212 of standing diversity than traditional range-based binning approaches (Gibert and Escarguel, 2017).

213 Finally, origination and extinction rates are calculated based on range-through diversity excluding
214 single-interval taxa. The more precise and accurate methods of calculating origination/extinction rates such
215 as the gap filler methods (Alroy, 2014, 2015) could not be applied to our dataset because of the high
216 proportion of taxa documented in less than four time intervals.

217

218 **3. Results**

219

220 *3.1. Paleobiodiversity patterns at the species level*

221

222 Species level radiolarian paleobiodiversity curves were obtained after analysis of the entire dataset and
223 all 21 stages covering the middle Cambrian–Silurian interval (Figures 2–3 and Appendices D–E). Because
224 taxonomic richness is a function of sample size (diversity increases with the number of collected specimens;
225 Bunge and Fitzpatrick, 1993), a rarefaction analysis (Hurlbert, 1971; Gotelli and Colwell, 2001) was
226 performed to evaluate the sampling effort within each stage (Fig. 4).

227 The pattern of sample-standardized taxonomic richness (SQS) throughout our study interval (Fig. 2)
228 establishes that the obtained diversity patterns are robust for the entire studied interval, with the exception
229 of the Guzhangian, the Paibian, the Dapingian and the Hirnantian for which there are either very little or no
230 data available. It shows: 1) protracted and substantial rise of radiolarian diversity throughout the Cambrian
231 stage 10 to the Darriwilian, 2) then a drastic drop of diversity until the latest Ordovician, 3) followed by a
232 quick recovery during the entire Llandovery (early Silurian), 5) a gently decreasing plateau until the Homerician
233 low, 6) a sharp diversity increase during the Gorstian recording the highest Silurian radiolarian richness, and
234 7) a decreasing trend till the Pridoli (latest Silurian). The documented Lower–Middle Ordovician protracted
235 radiolarian diversification trend peaks in the Darriwilian and in that stage records the highest taxonomic
236 richness of the entire studied time interval. Regrettably, the data are not abundant enough during the
237 Dapingian to assess whether there is a continuous diversity rise between the Floian and the Darriwilian. Also,
238 there are not enough data in the Sandbian and Hirnantian to evaluate the shape of the Late Ordovician
239 diversity decrease. Nevertheless, this interval records the lowest diversity for the entire studied interval.

240 Comparison of the SQS curves with two other resampling techniques (CR = size-based rarefaction; and
241 TRiPS = Poisson sampling model estimate) show similar patterns (Appendix D). Comparison with major
242 range-based metrics (BC, RT, and SIB) are reported on Figure 3. These approaches illustrate three different
243 diversity estimates according to the relative weight given to the species occurrence in and around a

244 stratigraphic interval. For our dataset these traditional estimators show similar results to the sample-
245 standardized estimators (e.g., SQS, Fig. 2), but some marked discrepancies occur. The sampled-in-bin (SIB)
246 diversity accounts for all species that are actually documented from a given stratigraphic interval. Similar to
247 the SQS, the highest SIB taxonomic richness is recorded in the Darriwilian (Middle Ordovician). However, it
248 already displays an impressive increase in the Tremadocian and Floian. This seemingly earlier quicker
249 diversification of radiolarians in the Early Ordovician results from both higher sample sizes (Fig. 4) and the
250 large number of single-interval taxa (Fig. 3 and Appendix E). The Dapingian also shows a sudden diversity
251 drop, but this may just reflect a very small sample size (Fig. 4). The Hirnantian is devoid of detailed
252 descriptions of radiolarian occurrences highlighting a lack of data for this stage. Finally, the Telychian (latest
253 Llandovery) also stands in contrast by showing a SIB peak, again caused by a high sample size and a large
254 number of single-interval taxa (Figs 3–5).

255 The range-through (RT) diversity (excluding single-interval taxa, RTexS) displays fluctuations in
256 species richness (Fig. 3) that follow the general pattern of the SIB diversity (although with much less
257 important values of diversity). Finally, the boundary-crosser (BC) diversity (Fig. 3) focuses on stage
258 boundaries and accounts for all species recorded in two successive intervals. This curve fluctuates gently and
259 appears as a long-term smoothed variant of the RT diversity curve. This diversity estimate corroborates
260 the hypothesis that the Dapingian SIB decrease and the Telychian SIB peak are artifacts; the first is related to
261 a very low sample size, and the second to a large amount of single-interval taxa. It is noteworthy that the
262 comparison between SIB and BC curves suggests that most peaks of diversity result from large numbers of
263 single-interval taxa of radiolarians; also, some of these peaks could be artifacts as shown by the sample-
264 standardized SQS diversity (Fig. 3).

265 The taxonomic turnover of radiolarians is given in Figure 5, which illustrates the per stage number of
266 first (origination) and last (extinction) occurrences (O_{RTexS} and E_{RTexS} , respectively). These curves establish that
267 the previously discussed peaks in diversity recorded during the Floian, Darriwilian and Gorstian correspond
268 to intervals of major faunal turnover, as they are all characterized by peaks in both origination and
269 extinction. It is also interesting to note that the Tremadocian is equally characterized by a significant
270 turnover, although first occurrences are more numerous than last occurrences, in contrast to the Cambrian
271 stage 10 for which we observe the opposite. It is also worth noting that very few new species are recorded in
272 the Katian, although a moderate peak in extinction is recorded within this stage; on the other hand, the early
273 Silurian diversity increase encountered during the Llandovery is mainly due to persistent higher origination.

274 These patterns of origination and extinction are also corroborated by the poly-cohort analysis
275 (Appendix F). Indeed, the poly-cohorts established for the study interval highlight the complete turnover
276 that took place during the Darriwilian, the Rhuddanian, and the Gorstian, as underlined by the poly-cohorts
277 which do not cross these stages and cluster in four groups. Therefore, these three stages (Darriwilian,

278 Rhuddanian, and Gorstian) document abrupt turnover events compared to other studied stages. Within
279 these groups of poly-cohorts, survivorship and pre-nascence curves have equal slopes suggesting rather
280 constant rates of extinction and origination. Interestingly, Early–Middle Ordovician poly-cohorts have lower
281 slopes compared to early–middle Silurian poly-cohorts, suggesting lower rates of origination and extinction
282 on average, but this may be biased by the longer, on average, duration of the Ordovician stages as compared
283 to the Silurian ones.

284

285 *3.2. Paleobiodiversity patterns among taxonomic ranks and within orders*

286 The pattern of changes in radiolarian diversity at the species, genus, and family ranks assessed by
287 means of the SQS metric (for the RT metric, see Appendix G) is displayed in Figure 6. The sample-
288 standardized family richness (SQS, Fig. 6) shows a slight increase until the Dapingian (early Middle
289 Ordovician), then fluctuates until the end-Ordovician (Hirnantian). It reaches low values in the early Silurian,
290 to finally recover with high values in the Sheinwoodian and the Gorstian. Despite uneven sampling during the
291 Late Ordovician, the Katian still records a high diversity compared to the species pattern. It is noteworthy that
292 the diversities at the family and species levels are somewhat decoupled. The range-through (RT) diversity of
293 families results (Appendix G) appear more stable with a gently protracted increase during the late Cambrian–
294 Middle Ordovician to reach a plateau of about ten families per stage for most of the rest of the Ordovician
295 and Silurian. A Darriwilian (late Middle Ordovician) peak of 15 families emerges above this “diversity plateau”
296 that corresponds to a profound faunal turnover, as five new families emerged and six families went extinct
297 during this stage. Interestingly, no radiolarian family went extinct before the Darriwilian (Middle Ordovician).
298 Family level diversity increased during the late Cambrian–Floian by accumulation of new families emerging at
299 each stage. The family level diversity dropped progressively during and after the Gorstian. It is also worth
300 noting that with the exception of the spumellarian family Copicyntridae, which first occurred during the
301 Pridoli, no other new family is known to have originated during the Silurian. Differences between the SQS
302 and RT diversities of radiolarian families appear to result from the discontinuous record of several families,
303 especially during the poorly documented intervals such as the Sandbian.

304 The genus level diversity curve is very similar to the one displayed by the family patterns (Fig. 6;
305 Appendix G) and confirms most trends seen at the family and species levels. It appears as a warped
306 intermediate between these two taxonomic ranks. Indeed, the genus level richness was stable during the late
307 Cambrian, then increased during the Early and Middle Ordovician, with a first peak recorded in the Floian
308 and a second even more prominent peak in the Darriwilian. The latter represents the highest genus level
309 diversity recorded for the entire studied interval. Like the diversity peak recorded for radiolarian species, the
310 genus level diversity peak of the Darriwilian corresponds to a complete faunal turnover, with most genera
311 first recorded or last recorded during this stage. Genus level richness erratically decreased after the

312 Darriwilian to reach its lowest value during the Hirnantian (latest Ordovician). Although this lowest genus
313 level richness may be partly due to the absence of data from the Hirnantian, the continuously increasing
314 trend during the early Silurian is noteworthy and suggests that diversity drop during the Late Ordovician
315 corresponds to a genuine signal. The early Silurian shows a continuous diversity increase reaching two peaks
316 in the Sheinwoodian and Gorstian, separated by a drastic decrease in the Homerian. As for the Darriwilian,
317 the Gorstian peak is characterized by a major faunal turnover. Interestingly, a major discrepancy between the
318 genus and species diversity occurs during the early–middle Silurian, with a gentle and protracted increase at
319 the genus rank compared to a large and quick diversification at the species rank.

320 The species level pattern of changes in radiolarian taxonomic richness (SIB) with the pattern of changes
321 within each one of the four radiolarian orders taken individually (Archaeospicularia, Entactinaria, Spumellaria
322 and Albaillellaria) is compared in Figure 7.

323 Archaeospicularia are considered as the most primitive order among polycystine radiolarians (De
324 Wever et al., 2001), with their fossil record going back to the early Cambrian (Obut and Iwata, 2000;
325 Aitchison et al., 2017a). They are characterized by a spicular shell made of a variable number of spicules,
326 which are either free, interlocked, or coalescent in order to form a shell (Dumitrica et al., 1999; Noble et al.,
327 2017). Archaeospicularian diversity was high during the late Cambrian and the Early Ordovician.
328 Representatives of this order nourished the full diversity of radiolarians at that time. Their diversity
329 decreased rapidly during the Middle Ordovician to be nearly zero during the Late Ordovician. The
330 contribution of this order to the radiolarian diversity became important again during the Silurian, with two
331 diversity peaks recorded during the Telychian and the Ludfordian. It is worth noting that the Darriwilian
332 (Middle Ordovician) has clearly marked the evolution of archaeospicularians. Nearly all Cambrian–Ordovician
333 archaeospicularian genera and families (such as the major families Archeoentactiniidae, Echidninidae and
334 Palaeospiculidae) went extinct during or before the Darriwilian. It is also worth noting that nearly all Silurian
335 archaeospicularians belong to the family Secuicollactidae. The latter originated in the Darriwilian. They are
336 characterized by an empty spherical shell made of spicules that are well fused to each other.

337 Early Paleozoic Spumellaria are characterized by a spherical body plan and by the presence of an initial
338 microsphere situated at the innermost part of their skeleton (De Wever et al., 2001). With their earliest
339 record known since the late Floian (Lower Ordovician), spumellarians appear to have taken rapidly an
340 important place in nourishing the radiolarian diversity for the rest of the Ordovician. Indeed, they contribute
341 approximately to half of the radiolarian diversity of the Darriwilian. Similar to the archaeospicularians, the
342 Darriwilian is a key interval for the evolutionary history of spumellarians. Their diversity decreased drastically
343 during the Late Ordovician, but it recovered rapidly during the Rhuddanian to reach a moderate plateau
344 during the rest of the Silurian that is punctuated by a Homerian diversity drop.

345 Another order that contributes significantly to the radiolarian taxonomic richness since the Darriwilian

346 is the Entactinaria. Although rather similar in their external appearance to spumellarians, these radiolarians
347 are characterized by a very specific initial spicular system that is situated at the innermost part of their
348 spherical shell (De Wever et al., 2001; Nakamura et al., 2020). This order probably emerged during the late
349 Cambrian (Dong et al., 1997) but has a firm record only since the Dapingian (Middle Ordovician).
350 Entactinarian species diversity is overall rather low, with the exception of a peak in the Darriwilian and a
351 moderate plateau during the Telychian to Gorstian interval.

352 The fourth radiolarian order, Albaillellaria, is characterized during the early Paleozoic by a small
353 number of radiating rod-like spines (Goto et al., 1992). Its earliest record dates back to the mid-late
354 Darriwilian (Renz, 1990); however, it contributes only a minor proportion to the diversity of radiolarians
355 during the studied interval.

356

357 **4. Discussion**

358

359 *4.1. Adequacy of the record*

360 Well-constrained early Paleozoic radiolarian assemblages are not evenly distributed in space and
361 time. Indeed, the analyzed dataset is largely represented by data coming from low latitudinal/tropical
362 regions and this is especially true for the middle Cambrian – Middle Ordovician interval (Fig. 1). More
363 importantly, as this was also pointed out by Danelian et al. (2013) in their preliminary paleobiogeographic
364 contribution to the IGCP 591, most Ordovician well-preserved radiolarian assemblages are known from
365 limited geographical areas around Laurentia. Some intervals are clearly much better documented than
366 others (Appendix B). For example, there are few existing data for the Dapingian and none are currently
367 available for the Hirnantian. Because taxonomic richness is a function of sample size (diversity increases with
368 the number of collected specimens; Bunge and Fitzpatrick, 1993), a rarefaction analysis (Hurlbert, 1971;
369 Gotelli and Colwell, 2001) was performed to evaluate the sampling effort within each stage (Fig. 4). This
370 analysis is of particular interest as it shows that the Floian, Telychian, Sheinwoodian and Katian stages,
371 among others, are well sampled, as indicated by their asymptotic curve. In contrast, the Sandbian,
372 Rhuddanian and Dapingian are very poorly documented. It is worth noting that the Darriwilian is one of the
373 richest stage despite having a moderate sample size. Therefore, it is expected that future studies will even
374 further increase the radiolarian taxonomic richness that may have existed during the Darriwilian.

375 Another potential bias affecting the radiolarian record is all the taphonomic processes involved in the
376 preservation of biogenic silica (for an overview, see De Wever et al., 2001). Most of the assemblages analyzed
377 in our dataset come from pelagic carbonate rocks, in which radiolarians are relatively well-preserved.
378 Therefore, the influence of taphonomic bias and preservation linked to lithology may be regarded as
379 homogeneous throughout our dataset. Moreover, radiolarian assemblages extracted from limestones

380 commonly have the advantage of having a rather precise time constraint thanks to the co-occurrence of
381 conodonts, graptolites or even trilobites.

382 Other potential biases may be related to insufficient taxonomic understanding and differences in the
383 opinions of various authors. However, recent syntheses (Caridroit et al., 2017; Noble et al., 2017) diminish
384 this bias to some extent for Paleozoic radiolarians. We are fully aware that it is unlikely that all first and last
385 occurrences recorded in our dataset represent true originations (cladogenetic events) and extinctions.
386 However, there is no stable phylogeny yet available for early Paleozoic radiolarians. Therefore, in spite of all
387 the above mentioned potential biases, we believe that it is important to synthesize the entire data available
388 today because they provide important insights into the major evolutionary trends experienced by
389 radiolarians. Finally, modern resampling techniques enable us to produce and highlight the rather robust
390 paleobiodiversity trajectories, overcoming some of these biases.

391

392 *4.2. Early Paleozoic radiolarian diversity trends and global biotic and environmental change*

393 The oldest radiolarian record recognized to date is composed of few archaeospicularians recognized in
394 the Botoman strata (Cambrian stage 4) of the Altaï mountains in southern Siberia (Obut and Iwata, 2000;
395 Pouille et al., 2011). Nevertheless, the oldest well preserved and diverse radiolarian assemblages come from
396 the middle Cambrian strata of the Georgina Basin in Australia (Won and Below, 1999). Some trends and a
397 number of events stand out in the pattern of taxonomic evolution we obtained from our analysis and they
398 are discussed below.

399

400 *4.2.1 The Cambrian–Ordovician transition and the Early Ordovician*

401 The increase in taxonomic richness observed in the SQS curve for the Cambrian stage 10 and the
402 Tremadocian bears a particular paleobiological significance in the context of the GOBE (*sensu* Servais and
403 Harper, 2018) and may be correlated with the “Ordovician plankton revolution” (Servais et al., 2016). Pouille
404 et al. (2014a) analyzed qualitatively the radiolarian faunal changes during the Cambrian-Ordovician boundary
405 interval and found a complex and differential pattern in their biotic response, specific to each genus. Some
406 genera suffered total extinction at the end of the Cambrian, others experienced a species faunal turnover. Yet
407 others not only survived through the boundary but also experienced a strong species diversification at the
408 beginning of the Tremadocian.

409 The curves of taxonomic turnover produced in Figure 5 show that the number of first occurrences
410 (FO) of species recorded in the Cambrian stage 10 is half the number of last occurrences (LO), while the
411 opposite is observed for the Tremadocian. This is an important result, which implies that the Tremadocian
412 records a net accumulation of radiolarian species with respect to the Cambrian stage 10.

413 Insights into radiolarian assemblages available today for this interval are based exclusively on well

414 preserved assemblages that come from pelagic slope carbonates preserved in western Newfoundland (Won
415 and Iams, 2002; Won et al., 2005, 2007; Pouille et al., 2014a), which were at that time part of a Laurentian
416 margin situated in tropical paleolatitudes (Fig. 1). The Cambrian stage 10–Tremadocian radiolarian diversity
417 increase coincides with a similarly rapid increase in diversity during the early Tremadocian recorded in the
418 curve of Rasmussen et al. (2019) and to the interval IV of Kröger et al. (2019).

419 Consequently, it is the archaeospicularian radiolarians that took part to the “Ordovician plankton
420 revolution”, which was initiated following the latest Cambrian and intensified during the Tremadocian
421 (Servais et al., 2016). However, the Tremadocian high in taxonomic richness appears to reflect a faunal
422 change that took place within archaeospicularians during the ca. 8 Myr lapsed during this stage as the study
423 of Won et al. (2007) establishes a radiolarian faunal turnover between the early and the late Tremadocian.

424 As discussed above, the Floian and the Darriwilian stages record high levels of species richness, with
425 the highest SQS values recorded for the Darriwilian. Radiolarian diversity of this interval still has the potential
426 to increase even further. The Floian to Darriwilian interval also records a number of important faunal changes
427 discussed above as well as the introduction of new bodyplans (orders).

428

429 4.2.2. *Darriwilian (Middle Ordovician): a game changing interval*

430 It should be emphasized that the Darriwillian peak in diversity recorded in our dataset is mainly due to
431 spumellarians. Genus and family level diversity analysis reveals that the Darriwilian records the highest
432 values. It corresponds in reality to a major faunal change that took place during this stage, with the last
433 occurrence of four families and the first occurrence of seven others.

434 Important climatic and environmental changes took place during the Darriwillian Stage. According to
435 Rasmussen et al. (2016) the early Darriwilian experienced a sudden shift from greenhouse to icehouse
436 climate state, which was accompanied by significant global cooling. This is testified by the shift recorded on
437 the $\delta^{18}\text{O}$ curve established on the basis of brachiopod shells. This climate cooling would have also initiated an
438 early Paleozoic “Great Conveyor Belt”. In addition to the above mentioned radiolarian turnover, recorded at
439 all analyzed taxonomic levels (species, genus and family), during the Darriwilian are also recorded the
440 currently known oldest representatives of the Alballellaria radiolarian order, considered as deep dwelling
441 radiolarians (Xiao et al., 2017).

442 We may reasonably assume that the climate-driven oceanographic changes that took place during the
443 early Darriwilian allowed the development of a wider spectrum of horizontal and vertical environmental
444 gradients. These favored radiolarian speciations within spumellarians and entactinarians (with a preference
445 for very shallow water habitats; Xiao et al., 2017) and the origin of the deep dwelling Alballellaria.

446 The Darriwilian peak in radiolarian species richness and dramatic faunal turnover that took place
447 during this stage is coeval with the highest pulse in diversification of bottom dwelling organisms observed in

448 the study of Rasmussen et al. (2019), interpreted by these authors to be the expression of the GOBE. The
449 latter took place during the Darriwilian–early Katian interval, with a very steep rising trend during the early
450 Darriwilian, followed by a gentler and downsloping trend in diversification over the following 15 Myr.

451

452 *4.2.3. The Late Ordovician diversity drop*

453 Radiolarian species richness collapsed during the Sandbian and the Katian (Fig. 3). This is also reflected
454 in the genus level diversity. The asymptotic rarefaction curve of the Katian (Fig. 4) shows that the diversity
455 sampled at this stage is sufficient, thus supporting this diversity drop. The Katian saw very few new species
456 originating while the stage records a fairly high rate of extinctions (Fig. 5). The lack of new appearances of
457 species explains the drop in species diversity, which correlates well with the Katian drop in diversity recorded
458 in the generic diversity curve produced by Rasmussen et al. (2019) and be partly correlated with the dramatic
459 episode of extinction recorded in graptoloid plankton during the Late Ordovician Mass Extinction (Crampton
460 et al. 2016).

461

462 *4.2.4. The Silurian diversity trends revisited*

463 The diversity increase of radiolarians during the first 10–12 Myr of the Silurian, following the end
464 Ordovician mass extinction is another interesting similarity with the curve produced by Rasmussen et al.
465 (2019). Tetard et al. (2017) analysed the pattern of changes in the diversity of Silurian radiolarians and found
466 that taxonomic richness was lowest during the Rhuddanian and reached rapidly a plateau of moderate values
467 until the Gorstian, when a sudden peak occurred due to a pulse in origination. The range-based trends
468 discussed by Tetard et al. (2017) are here confirmed by the sample-standardized analyses. Indeed, they are
469 devoid of any sampling bias, as the SQS curve produced in our analysis confirms the major trends; it displays
470 a diversity increase during the Rhuddanian–Aeronian. A plateau occurred until the Shenwoodian followed by
471 a substantial diversity drop in the Homerian, which preceded an impressive rebound during the Gorstian and
472 the Ludfordian.

473 A Homerian low in diversity followed by a Gorstian rebound is also recognized in the graptoloid
474 diversity curve produced by Cooper et al. (2014). The Homerian low has been correlated with the Mulde
475 event, a $\delta^{13}\text{C}$ event that corresponded to an anoxic event, which affected several other planktic (acritarchs)
476 and nekctic (conodonts) groups. It is noteworthy that Kröger et al. (2019) found that extinction rates peaked at
477 the Homerian/Gorstian boundary and they considered it as the reflexion of the Mulde event.

478

479 **5. Conclusions**

480 There is a contrast between the Cambrian–Ordovician and Silurian intervals in terms of major
481 evolutionary innovations, with an absence of any new body plans emerging during the Silurian. The

482 reconstructed paleobiodiversity trajectories of early Paleozoic radiolarians are consistent and highlight the
483 presence of the following trends. The Cambrian stage 10–Floian diversity increase correlates well with the
484 “Early Ordovician Plankton revolution” (Servais et al. 2016). However, it should be stressed that this
485 corresponds mainly to a faunal turnover within each stage and concerns essentially the archaeospicularian
486 radiolarians. However, since our dataset is heavily loaded with data coming from western Newfoundland, it is
487 not clear at this stage whether the documented trends reflect global vs regional changes.

488 The Darriwilian appears to be a “game changing” interval for radiolarian evolution, with the nearly
489 complete extinction of Early Ordovician genera and the origination of many new spumellarian and
490 entactinarian ones. In addition, a Darriwilian peak of diversity is recorded both at the radiolarian genus and
491 species levels (coupled with a major turnover at all taxonomic ranks) that coincides with the initial phase of
492 the GOBE *sensu* Rasmussen et al. (2019). As the Darriwilian was a critical interval in Earth’s climate state and
493 oceanic circulation, it is likely that these major changes in the global structure of oceanic water masses were
494 at the origin of the profound changes recorded during the Darriwilian in radiolarian diversity and community
495 structure. Although our dataset is marked by an absence of data for the Hirnantian, the low diversity values
496 recorded with confidence for the Katian may be put in parallel with the Late Ordovician mass extinction
497 (LOME) suggested by Rasmussen et al. (2019).

498 The main result highlighted by the various biodiversity indices is a clear, important and protracted
499 Silurian diversification recovery phase following the Hirnantian glaciation and peaking in the Telychian.
500 Overall, a bias in focus (sampling and/or geographic) cannot be discarded for some intervals (such as the
501 Dapingian, Katian, and Hirnantian). Nonetheless, the biodiversity curves produced in this study reflect the
502 current knowledge of early Paleozoic radiolarians and highlight the need for additional taxonomic and
503 biostratigraphic studies to further evaluate these biodiversity patterns.

504

505 **Author contribution**

506 T.D. prepared the radiolarian dataset and provided the taxonomic expertise. C.M analyzed the data. Both
507 authors conceived the study and wrote the manuscript.

508

509 **Declaration of Competing Interest**

510 The authors declare that they have no known competing financial interests or personal relationships that
511 could have appeared to influence the work reported in this paper.

512

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523

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850

851 **Captions**

852

853 **Figure 1. A)** Paleogeographic distribution of Late Ordovician–Silurian radiolarian assemblages plotted on a
854 440 Ma (Ordovician–Silurian boundary interval) reconstruction (after Torsvik & Cocks, 2014). (1) Noble et al.
855 (1998); (2) Noble (1994); (3) Goodbody (1986), Jones and Noble (2006), MacDonald (1998, 2004, 2006a, b),
856 Noble and Lenz (2007), Renz (1988), Tetard et al. (2015); (4) Siveter et al. (2007); (5) Noble and Maletz
857 (2000); Umeda and Suzuki (2005); (6) Amon et al. (1995); (7) Tetard et al. (2014a, b); (8) Nazarov and Popov
858 (1980); (9) Wang (1993); (10) Furutani (1990), Kurihara and Sashida (2000a), Kurihara (2007), Nuramkhaan et
859 al. (2013); (11) Noble and Webby (2009).

860 **Figure 1. B)** Paleogeographic distribution of middle Cambrian–Middle Ordovician radiolarian assemblages
861 plotted on a 490 Ma (Cambrian – Ordovician boundary interval) reconstruction (after Torsvik & Cocks,
862 2014). (12) Renz (1990a, b), Kozur et al. (1996) ; (13) Won and Iams (2011), Won et al. (2005, 2007), Pouille
863 et al. (2014b), Kachovich and Aitchison (2020, 2021), Won and Iams (2002, 2013, 2015a); (14) Perera et al.
864 (2020); (15) Maletz and Bruton (2007, 2008); (16) Pouille et al. (2013, 2014a); (17) Yi et al. (2018) ; (18) Dong
865 et al. (1997); (19) Won and Below (1999) (20) Maletz et al. (2009).

866

867 **Figure 2.** Sample-standardized paleobiodiversity of early Paleozoic radiolarians estimated by coverage-based
868 rarefaction (SQS) with quorums of 30, 40, 50, 60 and 70.

869

870 **Figure 3.** Paleobiodiversity trajectories (taxonomic richness) of early Paleozoic radiolarians. SIB = sampled-in-
871 bin diversity; BC = boundary-crosser diversity; RTexS = range-through diversity excluding single-interval taxa;
872 and SQS50 = coverage-based rarefaction with a quorum of 50.

873

874 **Figure 4.** Size-based rarefaction curves with 95% confidence interval for each studied stage.

875

876 **Figure 5.** Bin-based taxonomic origination (O_{RTexS}) and extinction (E_{RTexS}); comparison with the single interval
877 diversity (SGL).

878
879 **Figure 6.** Coverage-based rarefaction (SQS) of early Paleozoic radiolarians at the family, genus and species
880 ranks with a quorum of 50.

881
882 **Figure 7.** Comparison of the total diversity (TRinS) of all early Paleozoic radiolarians with the ones calculated
883 for each individual radiolarian order. Archaeospicularia: a) *Subechidnina florea*, from Pouille et al., 2014a; b)
884 *Secuicollacta hexactinia*, from Tetard et al., 2014; Spumellaria: c) *Triplococcus aksuranensis*, Pouille et al.,
885 2013; Entactinaria: d-e) *Polyentactinia spinulenta*, Pouille et al., 2014b; Albaillellaria: f) *Protoceratoikiscum*
886 *clarksoni*. Danelian & Floyd, 2001.

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