

1 **Title**

2 Sampling biases obscure the early diversification of the largest living vertebrate
3 group

4 **Authors**

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12

13 **Abstract**

14 Extant ray-finned fishes (Actinopterygii) dominate marine and freshwater
15 environments, yet their spatiotemporal diversity dynamics following their origin in the
16 Palaeozoic are poorly understood. Previous studies investigate face-value patterns of
17 richness, with only qualitative assessment of potential biases acting on the Palaeozoic
18 actinopterygian fossil record. Here, we investigate palaeogeographic trends and apply
19 richness estimation techniques to a recently-assembled occurrence database for Palaeozoic
20 ray-finned fishes. We reconstruct patterns of local richness of Palaeozoic actinopterygians,
21 alongside sampling standardised estimates of 'global' diversity. We identify substantial fossil
22 record biases, such as geographic bias in the sampling of actinopterygian occurrences centred
23 around Europe and North America. Similarly, estimates of diversity are skewed by extreme

24 unevenness in the abundance distributions of occurrences, reflecting past taxonomic practices
25 and historical biases in sampling. Increasing sampling of poorly represented regions and
26 expanding sampling beyond the literature to include museum collection data will be critical in
27 obtaining accurate estimates of Palaeozoic actinopterygian diversity. In conjunction, applying
28 diversity estimation techniques to well-sampled regional subsets of the 'global' dataset may
29 identify accurate local diversity trends.

30 **Keywords**

31 diversity; sampling standardisation; Actinopterygii; fossil record bias; Palaeozoic.

32 **Introduction**

33 There are around 32,000 species of living ray-finned fishes (actinopterygians),
34 amounting to over half of extant vertebrate diversity, and split roughly evenly between marine
35 and freshwater environments (1). Ray-finned fishes originated in the Palaeozoic, which saw
36 major evolutionary events and changes in the vertebrate fauna, such as the emergence of
37 jaws (2), the rise of actinopterygians (3), and the move onto land (4). Despite these pivotal
38 changes, and a long history of research on actinopterygians, there are relatively few
39 macroevolutionary studies investigating diversity trends in their early evolution, and all
40 examine face-value patterns of taxonomic richness (3,5–9).

41 Few studies investigate the suitability of the Palaeozoic ray-fin record for investigating
42 diversity patterns, or potential biases. Notably, biases may impact the marine and freshwater
43 record differently – late Palaeozoic Lagerstätten influence freshwater osteichthyan diversity
44 more than marine (5). Low taxonomic diversity in the Devonian followed by an explosive
45 increase in the early Carboniferous is generally interpreted as representing a genuine
46 biological signal (3,10). Some authors qualitatively suggest that low Permian diversity is linked
47 to the rarity of suitable deposits (11), or attribute the decline in richness among freshwater
48 taxa to the loss of extensive Euramerican freshwater habitats (5). Other authors propose that
49 the consistent ecomorphologies in typical Palaeozoic actinopterygians hint at constraints on

50 diversification into new ecologies and habitats and thus low richness (10). To date, previous
51 studies only present face-value counts of actinopterygians through time without employing
52 recent advances in methodologies to estimate diversity trends. An exception to this (5)
53 performed coverage-based rarefaction to compare the Permian and Triassic as a whole, rather
54 than to estimate diversity trends through time.

55 Assessing the degree to which fossil record biases affect interpretations of richness is
56 critical to obtaining an accurate estimate of diversity trends (12–14). These biases can be
57 geological (15,16), geographic (17–19), or anthropogenic (20,21) in nature, and recent
58 analyses show that ‘global’ fossil records are intimately linked to the spatial extent of that
59 record (17,18). Various statistical methods attempt to tease apart bias from genuine changes
60 (e.g. classical rarefaction and residual modelling), though not without complications (e.g.
61 classical rarefaction can flatten diversity patterns (22–25). Recent years have seen the
62 application of Shareholder Quorum Subsampling (SQS), also termed coverage-based
63 rarefaction (25,26), to palaeobiological occurrence databases (17–19,27–31) as a means of
64 deducing trends in palaeodiversity through time. As SQS subsamples intervals to equal levels
65 of completeness it returns more accurate relative richness estimates between sampled
66 intervals than size-based rarefaction (23), although is still susceptible to some biases (21,24).
67 Principally, SQS estimates can have a significant evenness signal (21,24,32), which may be
68 particularly important for datasets that are biased in ways that skew the evenness of frequency
69 distributions within sampled intervals. A new richness estimator, squares (33), estimates
70 higher richness when there are numerous rare taxa (i.e. singletons) and when common taxa
71 are especially abundant. Squares is more robust to uneven distributions than SQS, though
72 falls short when the ratio of richness counts to total number of taxa within intervals is very high
73 (24).

74 Until recently, no comprehensive through-Palaeozoic occurrence database existed (9),
75 with previously-published databases limited in scope or not updated (3,5). Here, we apply
76 coverage-based sampling standardisation to a newly-assembled occurrence database of

77 Palaeozoic actinopterygians to examine patterns of diversity, the suitability of the dataset, and
78 the likely extent and impact of sampling biases.

79 **Methods**

80 ***Data preparation***

81 Global occurrences of Palaeozoic Actinopterygii (9) were screened for taxonomically
82 indeterminate occurrences and scale- and teeth-based occurrences. After removal, this
83 resulted in a dataset of 1,611 occurrences of 468 species (belonging to 225 genera), from 507
84 unique geographic localities. All occurrences were assigned to intervals of roughly equal
85 length (~9 Ma), determined by either combining shorter intervals (e.g. Kasimovian [3.3 Ma]
86 and Gzhelian [4.8 Ma] = Kasimovian and Gzhelian [8.1 Ma]), or splitting longer intervals (e.g.
87 Visean [15.8 Ma] = early Visean [Chadian-Holkerian; 8.7 Ma] and late Visean [Asbian-
88 Brigantian; 7.1 Ma]; boundary based on the age of the Dunsapie basalt, see (34)). The cleaned
89 dataset was used for local richness and diversity estimation. All analyses were conducted
90 within R 4.1.0 (35).

91 ***Alpha diversity (local richness)***

92 Species per locality were counted as a measure of alpha diversity (local richness (36)).
93 Modern coordinates for these localities were translated into palaeocoordinates using the R
94 'chronosphere' package (37). Local richness was then subset by marine and freshwater
95 environment (brackish environments were included in marine counts) and plotted against
96 palaeolatitude. Additionally, palaeogeographic maps showing local richness were produced in
97 'chronosphere' (37) for each interval. It is uncertain whether some Permian localities (Pastos
98 Bons – Brazil; Deep Red Run, Dundee, McCann Quarry, Pond Creek, South Dakota State
99 Cement Plant Quarry – USA; Sobernheim – Germany) are Artinskian or Kungurian in age, and
100 these localities are therefore plotted in both palaeogeographic maps.

101 ***Sampling standardisation and diversity estimation***

102 Coverage-based sampling standardisation (22,26,38,39) was used to estimate global
103 diversity patterns via the R package iNEXT (version 2.0.19 (40)), following the procedure
104 outlined in Dunne *et al.* (28). The data were rarefied by geographic locality by analysing
105 incidence-frequency matrices of the occurrence data. Extrapolated estimates were limited to
106 no more than twice the observed sample size (40). Coverage-standardised richness was
107 computed at genus level using roughly equal length bins, at quorum levels 0.3, 0.4, 0.5 for
108 genus-level analysis and up to 0.6 quorum for species-level analysis; higher quorums were
109 unattainable. Devonian bins were excluded due to the very small sample-sizes and low levels
110 of coverage. Rank abundance distributions and size- and coverage-based rarefaction curves
111 were generated for each interval to investigate the reliability of coverage-based rarefaction
112 estimates.

113 Squares extrapolated estimates of genus and species richness were conducted in R
114 by applying Alroy's equation (33), following the same procedure as Allen *et al.* (30).

115 **Results**

116 ***Alpha diversity (local richness)***

117 Local richness is generally low in the Devonian (figure 1), with only one locality
118 containing more than three genera (Paddy's Valley, Gogo Formation, Frasnian, Australia).
119 Levels of local richness are highest in the Carboniferous, particularly around the
120 Serpukhovian-Moscovian boundary (figure 1), before declining steadily in the latest
121 Carboniferous (Kasimovian and Gzhelian) and early Permian (Cisuralian). Notable localities
122 contributing to the mid-Carboniferous peak include Glencartholm (Scotland, late Viséan,
123 marine), Ardenrigg (Scotland, Bashkirian, freshwater), Longton (England, Bashkirian, marine)
124 and the Bear Gulch localities (USA, Serpukhovian, marine) (figure 1a). Sampling of marine
125 and brackish palaeoenvironments in the latest Carboniferous (Kasimovian and Gzhelian) and
126 earliest Permian (Asselian and Sakmarian) is very poor. Freshwater localities are also poorly
127 sampled in the Artinskian and Kungurian, yielding very low richness, while richness and

128 sampling also remains low in marine deposits. In the latest Permian (Wuchiapingian and
129 Changhsingian), marine localities generally have much higher genus counts than freshwater
130 localities.

131 ***Palaeomaps and geographic spread***

132 Devonian

133 Despite their earliest occurrence being just north of the palaeoequator (*Meemannia*,
134 Lochkovian, South China), actinopterygians are known almost exclusively from southern
135 palaeolatitudes in the Devonian (figure 1b; figure 2a). Only two other northern hemisphere
136 occurrences are reported (*Cheirolepis*, Givetian, Svalbard (41); *Krasnoyarichthys*,
137 Famennian, Russia (42)). The majority of taxa occur at low palaeolatitudes (0° to -30°), with a
138 small number just crossing into the mid-palaeolatitudinal band (-30° to -60°). A clear outlier,
139 near the southern palaeopole (-83.81°), is the recently-reported *Austelliscus ferox* from Brazil
140 (43).

141 Devonian actinopterygian occurrences mirror both continental configurations—the
142 majority of landmasses and shallow seas were palaeoequatorial and in the southern
143 hemisphere (44)—and the broader Devonian fossil record (18,45,46). Givetian and Eifelian
144 occurrences are dominated by European (especially Scottish) deposits, with limited
145 contributions from the USA, Australia, the Antarctic and Brazil (figure 2a). In contrast, Frasnian
146 occurrences (figure 2b) are dominated by the Australian Gogo Formation, with fewer
147 occurrences from Europe and North America, and a single occurrence from Iran. The USA
148 dominates Famennian occurrences (figure 2c), with additional occurrences from Russia,
149 Greenland and Belgium.

150 Carboniferous

151 In general, Carboniferous localities have both higher local richness and a broader
152 palaeolatitudinal spread than in the Devonian, although are generally still restricted to low and
153 southern palaeolatitudes (figure 1b). Most Tournaisian localities are clustered at low

154 palaeolatitudes around the southern edge of Euramerica in regions that correspond to present-
155 day Canada, USA, UK, and European Russia. Localities with lower local richness are found
156 in Australia, Turkey, and Siberia. In contrast, early Visean (Chadian-Holkerian) low- to mid-
157 palaeolatitudes are depauperate (figure 2e), although the Waaipoort Formation in South Africa
158 (-78°) represents the richest high-palaeolatitude locality of the entire Palaeozoic.

159 For much of the rest of the Carboniferous, local richness greatly increases while
160 palaeolatitudinal spread decreases. Other than single occurrences from Australia and the
161 USA, all late Visean actinopterygians are clustered in the UK and Ireland, including the highly
162 diverse Glencartholm locality (figures 1b and 2f). Similarly, in the Serpukhovian (figure 2g),
163 only a single occurrence is found outside a 20° palaeolatitudinal band centred around the
164 palaeoequator encompassing UK localities, a single Belgian locality, and the speciose Bear
165 Gulch localities. Geographic spread continues to decline in the Bashkirian (figure 2h) and
166 Moscovian (figure 2i), with all occurrences within 10° of latitude of the palaeoequator. Again,
167 localities only are only known in Europe (Belgium, Czechia, France, Ireland, UK) and North
168 America (Canada, USA). The only latest Carboniferous (Kasimovian and Gzhelian; figure 2j)
169 locality outside of this band is the -60° Gzhelian Ganigobis Shale, which outcrops in South
170 Africa and Namibia, albeit with low local richness. Broadly, Carboniferous actinopterygian
171 palaeolatitudinal distribution matched other contemporaneous groups (18,46).

172 Permian

173 Compared to the Carboniferous and Devonian, Permian occurrences generally display
174 a broader geographic spread (reflecting increases in the broader fossil record (18,46)) but
175 lower local richness. The extent of palaeogeographic sampling in the Asselian and Sakmarian
176 (figure 2k) is greater than the Kasimovian and Gzhelian, with more occurrences at higher
177 palaeolatitudes, including the diverse Uruguayan fauna from Rio Negro (-53°). The Artinskian
178 (figure 2l) is the most depauperate interval of the Palaeozoic outside of the Devonian, despite
179 a comparatively high palaeogeographic spread: the locality with the highest local richness,

180 Loeriesfontein, contains only four genera. Contrary to most other Palaeozoic intervals, there
181 are very few European Artinskian localities.

182 From the Kungurian (figure 2m) onwards, localities occur across the broadest
183 palaeolatitudinal spread of the entire Palaeozoic. This includes the first sampling of northern
184 mid-palaeolatitudes since the Tournaisian. Wordian and Roadian localities (figure 2n) with the
185 highest local richness are found in Russia, centred around 30° palaeolatitude, although less
186 diverse occurrences are seen at high southern palaeolatitudes in Brazil, India, and Zimbabwe.
187 In contrast to most other intervals, only two depauperate localities occur near the
188 palaeoequator. This trend continues into the Capitanian (figure 2o), where localities yielding
189 few genera are found across a wide range of palaeolatitudes, with very few at equatorial
190 latitudes, and most diversity stems from Russia.

191 The Wuchiapingian and Changhsingian interval (figure 2p) has the broadest
192 geographic spread in sampling of the Palaeozoic, possibly due to intensive research focus on
193 the Permo-Triassic mass extinction event (47,48). Numerous localities are spread from
194 southern mid- to high-palaeolatitudes, including opposing sides of the palaeopole (present-
195 day South Africa and Australia). Notably, this interval contains the first Palaeozoic
196 actinopterygians from the eastern Palaeotethys (present-day China) aside from a single
197 Lochkovian occurrence. Northern low- to mid-palaeolatitudes have the highest local richness,
198 stemming from assemblages in the UK and Germany, Russia, and Greenland.

199 ***Palaeodiversity estimates***

200 Coverage-based rarefaction

201 Estimates of relative genus richness using coverage-based rarefaction (figure 3a)
202 suggest a gradual overall decline in diversity through the Carboniferous, with a sharp rise then
203 subsequent fall in the Permian. Richness levels decrease from the Tournaisian through to the
204 late Viséan (the most intensely sampled interval of the Carboniferous), before peaking in the
205 Serpukhovian. The remainder of the Carboniferous is marked by a decline, with the lowest

206 observed values in the Kasimovian and Gzhelian, another intensely sampled interval.
207 Richness estimates rise slightly across the Carboniferous-Permian boundary, followed by a
208 precipitous rise in the Kungurian, where the highest levels in the Palaeozoic are reached. A
209 steady decline marks the remainder of the Permian.

210 Coverage-rarefied estimates of species richness differ notably from genus estimates
211 (figure 3b). Overall, estimates of species diversity generally increase, albeit irregularly, across
212 the Carboniferous until a crash in the Kasimovian and Gzhelian, followed by two distinct peaks
213 and declines in the Permian. Species richness initially decreases through the Tournaisian and
214 Visean and increases in the Serpukhovian, with a drop into the Bashkirian and subsequent
215 rise into the Moscovian, which represents the highest richness levels of the Carboniferous.
216 This peak is immediately followed by a Kasimovian and Gzhelian trough. Levels rise steeply
217 in the Asselian and Sakmarian followed by another abrupt drop in the Artinskian. There is only
218 a modest rise into the Kungurian, with the major peak in species-level estimates seen in the
219 Roadian and Wordian. A relative decrease in the Capitanian is followed by a minor decline
220 through the Wuchiapingian and Changhsingian.

221 Squares

222 Squares diversity estimates contrast starkly with coverage-based rarefaction
223 estimates: where coverage-based rarefaction returns low estimates, squares estimates are
224 generally high. Squares-extrapolated genus richness estimates (figure 4a) gradually increase
225 throughout the Devonian and into the Tournaisian. Early Visean estimates drop back to
226 Famennian levels, before gradually rising in the late Visean to Serpukhovian. A slight decrease
227 into the Bashkirian is followed by a steeper decline in the Moscovian. The highest estimates
228 thus far are seen in the latest Carboniferous with a further increase into the Asselian and
229 Sakmarian, followed by a precipitous drop in the Artinskian. Richness estimates rise in the
230 Kungurian and marginally in the Roadian and Wordian before dropping in the Capitanian. The
231 latest Permian (Wuchiapingian and Changhsingian) is the most diverse interval of the
232 Palaeozoic.

233 Squares-extrapolated species richness trends (figure 4b) differ again from genus
234 richness estimates. The pattern in the Devonian is in direct contrast, with estimates decreasing
235 from the mid- through to late-Devonian in the Givetian and Eifelian, although a rise is observed
236 across the Devonian-Carboniferous. As with genus estimates, the early Visean has lower
237 richness than the Tournaisian. Species richness estimates rise significantly in the late Visean,
238 quadrupling relative to the early Visean. The Serpukhovian sees a moderate decrease in
239 richness, and this trend continues throughout the Bashkirian and Moscovian. Richness rises
240 sharply in the Kasimovian and Gzhelian to the highest level of the entire Palaeozoic. A slight
241 decrease across the Carboniferous-Permian boundary is followed by a precipitous drop in the
242 Artinskian. Richness increases slightly in the Kungurian, recovers further in the Roadian and
243 Wordian, declines again in the Capitanian, and finally increases in the latest Permian.

244

245 **Discussion**

246 ***Biogeographic trends and biases***

247 Palaeozoic actinopterygian occurrences are overwhelmingly geographically biased
248 towards the northern hemisphere: fewer than 9% of known localities (52/586) are from the
249 southern hemisphere (9). Certain regions are notably underrepresented throughout the
250 Palaeozoic, such as the northern, eastern and southern Palaeotethys (present-day Middle
251 East, south and east Asia, north Africa) and the northern coastline of Laurussia (present-day
252 Siberia, Kazakhstan and interior of Asia). Sampling through much of the Devonian and
253 Carboniferous is limited to a narrow band around the palaeoequator, largely corresponding to
254 present-day Europe and North America (figure 2), which also contain localities with the highest
255 local richness (9). The most diverse localities trend from low- to mid-palaeolatitudes through
256 the Palaeozoic, essentially tracking the migration of North America and Europe (figure 1b).
257 Reporting new taxa from underrepresented regions (41,43) will have major implications for
258 palaeogeographical spread, patterns of diversity, and interpretations of ray-finned fish

259 evolution, especially in the face of taxonomic revisions invalidating many existing generic
260 referrals (49,50).

261 Ideally, rarefaction curves for sampled intervals should be close to asymptote before
262 performing diversity estimation techniques to ensure that future sampling will not drastically
263 alter face-value counts of richness. Inspection of the Palaeozoic ray-finned fish record
264 suggests this condition has not yet been reached (figure S1). In the short term, increased
265 sampling of the most under sampled intervals will improve comparability. However, research
266 focus on taxa from well-sampled regions that are languishing undescribed in museum
267 collections (51,52) is also vital for attaining accurate estimates of actinopterygian diversity in
268 the Palaeozoic, particularly at local scales.

269 Both marine and freshwater deposits are recorded throughout the Palaeozoic, with the
270 number of sampled marine and freshwater deposits roughly tracking each other through much
271 of the Carboniferous. However, marine palaeoenvironments are scarce in the later
272 Palaeozoic. This long-recognised Permian imbalance (10,11,53) also extends back into the
273 late Carboniferous (figure 1a). The near-complete lack of marine deposits suggests that low
274 marine diversity in this period is linked to a geological bias and relative absence of these rocks
275 rather than a true biological signal. There is certainly a change in the sampling of terrestrial
276 vertebrates from aquatic to dryland terrestrial environments across the Carboniferous-
277 Permian (54), and a similar change may explain the drop in sampling of Permian
278 actinopterygians. Concurrent with this environmental shift is a noticeable palaeogeographical
279 expansion: rather than being restricted to palaeoequatorial regions, Permian occurrences are
280 reported from much higher and lower palaeolatitudes. It is unclear to what extent this
281 represents a shift in sampling regime rather than an ecological expansion.

282

283 ***Palaeozoic actinopterygian diversity patterns***

284 Changes in local richness largely track changes in 'global' (gamma) raw diversity (9),
285 with the exception of the latest Carboniferous and earliest Permian (figure 1). In the late
286 Carboniferous and early Permian, high levels of sampling (localities and equal-area grid cells
287 (9)) of isolated localities with low alpha diversity drives high 'global' diversity, with few
288 contributions from diverse assemblages. These richness patterns are drastically different to
289 those reported for Palaeozoic tetrapods (28), and the overall decrease from the Carboniferous
290 to Permian contrasts the biodiversification of invertebrates over the same period (55).

291 In contrast to coverage-rarefied diversity estimates, extrapolated estimates from
292 squares analysis return very similar trends to face-value counts of richness (3,5,9). These
293 differences persist regardless of whether sampling is via equal length intervals or geological
294 stages and are likely due to taxonomic biases (see below). This recalls recent work on
295 Palaeozoic tetrapods, which found that diversity patterns among reptiles and synapsids
296 changed significantly depending on the quorum levels or use of squares (56). For example,
297 coverage-rarefied actinopterygian diversity decreases from the Tournaisian to the late Viséan
298 in contrast with previous hypotheses (3,6,9), yet both the face-value counts and squares
299 estimates increase significantly from the early to late Viséan. There is consensus however, in
300 the high diversity of the Serpukhovian (3,9), indicating genuine diversity, though the vast
301 majority of this is driven by the highly-diverse Bear Gulch fauna.

302 Trends into the Pennsylvanian also differ, with the greatest difference in the
303 diametrically opposed estimates for the Kasimovian and Gzhelian, which is attributable to the
304 ways in which the methods estimate diversity. The same is also true for the Asselian and
305 Sakmarian and late Permian. Coverage-rarefied diversity estimates depend on the attainable
306 level of coverage, and examination of abundance distributions (figure S2) and rarefaction
307 curves (figure S3) reveals that at higher coverage, the Kasimovian and Gzhelian would most
308 likely represent one of the most diverse intervals. Squares, however, estimates higher
309 richness when there are many singletons and when common taxa are especially common

310 (24), and these intervals fulfil both of these criteria. The combined presence of superabundant
311 taxa and numerous singletons results in these conflicting estimations.

312 Taxonomy also plays a key role. The observed rise in early Permian species-level
313 diversity estimates in both analyses and face value readings (9) reflects the presence of
314 numerous species of few genera (namely *Amblypterus* and *Paramblypterus*). The problem of
315 superabundant genera is not unique to actinopterygians; such genera are known to bias other
316 osteichthyan groups (57). In contrast, Kungurian estimates are based on very few occurrences
317 of monospecific genera, and sampling of a high number of genera at low quorums results in
318 high—yet unreliable—genus-level coverage-rarefied diversity estimates. The extremely high
319 Roadian and Wordian species-level estimates in both analyses, not reflected at genus-level,
320 can also be explained by high numbers of singletons and relative absence of common genera.

321

322 ***Unevenness in the actinopterygian fossil record***

323 Coverage-based rarefaction techniques produce the most reliable richness estimates
324 when rank abundance does not differ considerably between samples, even when samples
325 have comparable face-value richness (22–26,32,38). Unevenness in abundance distributions
326 can therefore heavily influence the reliability of diversity estimates. Rank abundance
327 distribution plots for Palaeozoic actinopterygian genera and species indicate extreme
328 unevenness within intervals and variation in evenness between intervals (figure S2). Some
329 intervals (e.g. Kasimovian and Gzhelian) contain one or two taxa with more than 60
330 occurrences, a handful with between 30 and ten occurrences, and a long tail of singletons or
331 doubletons; others (e.g. Frasnian) have a more even distribution. Differences can even arise
332 between the genus- and species-level abundance distributions in the same interval: in the
333 Asselian and Sakmarian most species-level diversity stems from multiple species of two
334 genera (*Amblypterus* and *Paramblypterus*), resulting in low genus estimates at lower

335 quorums, but higher species-level estimates due to the more even abundance distributions
336 (compare figures S2a and S2b; S3f and S3i).

337 Much of this imbalance is driven by ‘waste-basket’ genera erected by monographic
338 descriptions (58–61), despite a wide range of varied morphologies and extensive temporal
339 and geographic ranges within genera (9,62,63). These ‘waste-baskets’ serve to concentrate
340 frequency counts of the most common genera, contributing to unevenness in the abundance
341 distribution and distortion of coverage-based rarefaction estimates (22,23). The intervals most
342 heavily biased towards superabundant taxa are the late Visean (*Elonichthys*: 54/266
343 occurrences; *Rhadinichthys*: 54/266 occurrences), Kasimovian and Gzhelian (*Elonichthys*:
344 65/230; *Sphaerolepis*: 60/230), Asselian and Sakmarian (*Paramblypterus*: 53/154
345 occurrences; *Amblypterus*: 30/154 occurrences), and Wuchiapingian and Changhsingian
346 (*Palaeoniscum*: 66/225 occurrences; *Platysomus*: 26/225 occurrences). As coverage-based
347 rarefaction produces lower estimates when evenness is low (23), highly uneven intervals have
348 low richness estimates at lower quorum levels (figure 3; figure S3). In contrast, at high
349 quorums, where more taxa in the abundance distribution can be sampled, uneven intervals
350 receive much higher richness estimates (see exponential rise in the rarefaction curves of
351 uneven intervals at high coverage; figure S3).

352 ‘Waste-basket’ taxa may also mask true diversity: the dominance of highly abundant
353 taxa means that a high proportion of sampled taxa consists of these few taxa, likely
354 contributing to lower diversity estimates. Revisionary taxonomic work, such as recognising
355 new genera among previously congeneric actinopterygians (49), and restriction of *Elonichthys*
356 to just three species (50) rather than its previous 57, will alleviate this issue and mitigate the
357 dominance of superabundant forms. These revisions, however, have the potential to increase
358 unevenness in the other direction, as new taxa may end up as singletons or doubletons.
359 Concurrently, the biostratigraphic significance of actinopterygians in deposits from the
360 Permian of Russia (64–66) may contribute to oversplitting of taxa, echoing problems prevalent
361 in the marine invertebrate fossil record (23).

362 Major variation in evenness between intervals is highlighted in the different trajectories
363 of coverage-based rarefaction curves (figure S3). Taxonomic and geographic biases are
364 exacerbated by small sample sizes and low coverage, with rarefaction curves crossing
365 multiple times. Higher (more reliable) quorum levels are unobtainable for Palaeozoic
366 actinopterygians due to the high number of singleton taxa (figure S3) controlling Good's u (67).
367 As a result, coverage is generally low (figure S2) and only low quorums—at which evenness
368 signals are more pronounced (24)—can be used. When evenness varies at low levels of
369 sampling, size-based rarefaction can in fact be less biased than coverage-based rarefaction,
370 especially at low levels of coverage (23). Trends between coverage- and size-based
371 rarefaction estimates generally agree (figure S4), although size-based rarefaction estimates
372 higher diversity in some highly uneven intervals (e.g. late Viséan; Wuchiapingian and
373 Changhsingian). Small sample sizes (<200 occurrences) also have an effect on the accuracy
374 of coverage estimates using Good's u (23): only four of the sampled Palaeozoic intervals have
375 more than 200 occurrences (late Viséan: 266; Serpukhovian: 204; Kasimovian and Gzhelian:
376 230; Wuchiapingian and Changhsingian: 232). Coverage-based rarefaction curves (figure S3)
377 show these intervals to have among the highest coverage, along with the Bashkirian and
378 Moscovian, highlighting the greater sampling of the Carboniferous than the Permian.
379 Consequently, variation in evenness between intervals is having an overriding effect on
380 sampling-standardised diversity estimates through time, with diversity estimates mostly
381 tracking evenness and reflecting biases in the underlying data (23,68).

382

383 **Conclusions and future directions**

384 We present here the first local richness and palaeogeographic trends in Palaeozoic
385 ray-finned fishes. Sampling of the Palaeozoic actinopterygian fossil record is heavily biased
386 towards western Europe (especially the UK) and North America, which translates to a very
387 restricted palaeogeographic spread for most of the Palaeozoic. A suite of compounding
388 problems plagues the actinopterygian fossil record and results in bias towards occurrences of

389 both superabundant and singleton taxa, variation and unevenness in and between sampled
390 intervals, and distortion of relative richness estimates. A combination of flawed taxonomic
391 practices, differential researcher effort, and geographic sampling biases confounds attempts
392 to accurately estimate relative richness between intervals. Meanwhile, sampling is poor for
393 regions other than Europe and North America for all but a few Carboniferous and Permian
394 intervals. The result of this poor sampling is the inability to reach the high levels of coverage
395 that allow statistical methods of sampling standardisation to generate meaningful diversity
396 estimates.

397 Identifying the underlying issues with Palaeozoic actinopterygian data and the
398 interweaving biases that are impacting the fossil record is crucial, and improving sample sizes
399 and coverage will help to mitigate the sensitivity to evenness (25). Documenting and including
400 existing 'dark data' (51,52) in museum collections, as well as focus on new material from under
401 sampled regions, represent key first steps. As a result, size-based rarefaction curves for
402 Palaeozoic intervals will likely not reach asymptote soon (figure S1). More complete sampling
403 of well-known regions (69) may facilitate deduction of accurate local richness patterns (36).
404 This strategy also goes some way towards accounting for the significant spatial structuring of
405 'global' fossil records (17–19,27).

406 Other recently proposed methods, such as coverage-rarefaction of extrapolated
407 richness estimates (instead of face-value counts) (23), represent prospective avenues of
408 research, both at local and global scales. However, existing global occurrence data for
409 Palaeozoic actinopterygians is as yet inadequate for extrapolation in this way: sample sizes
410 vary widely between intervals, which may result in inaccurate extrapolated richness trends
411 (23,70,71); sample sizes in all intervals are too low for size-based rarefaction curves to
412 asymptote (figure S1), meaning sample size has an overwhelming effect on diversity estimates
413 (23); and abundance distributions are also highly uneven, which biases extrapolators (though
414 to a lesser extent than coverage-based rarefaction; 17).

415 Overall, the occurrence data recorded in the literature is heavily impacted by sampling
416 and likely results in inaccurate estimated diversity trends at present. Localised diversity
417 estimates for well-sampled regions presents a feasible avenue of research for reconstructing
418 regional diversity. In addition, research efforts to fix problematic taxonomy of ‘waste-basket’
419 taxa, in hand with a general increase in sampling, open the possibility of estimating diversity
420 in a spatially-standardised framework, so that we can truly begin to understand the origin, rise
421 and establishment of the largest vertebrate clade.

422

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622 **Figures**

623 Figure 1 – Local richness (number of species per fossil locality) of actinopterygians through
624 the Palaeozoic. (a) Local richness plotted by environment, separated by freshwater (red) and
625 marine (blue; incorporates brackish occurrences). Colour saturation (transparency) indicates
626 density of localities, and the most genus-rich localities are labelled. Note that purple
627 indicates contemporary localities with similar diversity of marine and freshwater
628 actinopterygians. (b) Palaeolatitude of localities through time, with local richness indicated by
629 colour (yellow localities have low richness, progressing through green to the most diverse
630 localities in indigo).

631 Figure 2 – Palaeomaps showing palaeogeographic spread and local richness of individual
632 localities through time plotted in roughly even-length intervals. Colour scales correspond to
633 the richness of localities, ranging from low (light blue) to high (pink) richness.

634 Figure 3 – Coverage-based rarefaction estimates of Carboniferous and Permian
635 actinopterygian diversity at (a) genus- and (b) species-level, showing estimates for different
636 quorum levels in different colours from low quorums (0.3) in light blue to higher quorums
637 (0.6) in darker blue. The shaded areas for each quorum are confidence intervals of
638 estimates. Devonian intervals removed (see Methods). Estimates were either interpolated
639 (circles) or extrapolated (squares) up to twice the reference sample size (40).

640 Figure 4 – Squares diversity estimates of Devonian to Permian (a) genus (circles) and (b)
641 species (triangles) richness, plotted at the midpoints of equal-length intervals.

642 Figure S1 – Size-based rarefaction curves for (a) Carboniferous genus-level occurrences,
643 (b) Permian genus-level occurrences, (c) Carboniferous species-level occurrences, (d)
644 Permian genus-level occurrences.

645 Figure S2 – Rank order abundance distributions of the sampled equal-length intervals
646 (coloured correspond with the International Commission on Stratigraphy; ICS) at (a) genus-
647 level occurrences and (b) species-level occurrences.

648 Figure S3 – Sample completeness (a-c, k-l) and coverage-based rarefaction curves (d-i) for
649 Carboniferous (b, e, h, k) and Permian (c, f, i, l) intervals. Solid lines are interpolated
650 measures, points are observed data and dotted lines are extrapolated estimates.
651 Carboniferous intervals are in green and Permian intervals are in red according to the ICS
652 colours.

653 Figure S4 – Estimates of Carboniferous and Permian actinopterygian diversity using size-
654 based (classical) rarefaction of (a) occurrences of genera and (b) occurrences of species,
655 showing estimates for different sample sizes.















