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challenges and future prospects

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The early diversification of ray-finned fishes (Actinopterygii): hypotheses, challenges and future prospects

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Abstract:

Actinopterygii are the most speciose living vertebrate clade, and study of fossil members during their Palaeozoic rise to dominance has a long history of descriptive work. Although research interest into Palaeozoic actinopterygians has increased in recent years, broader patterns of diversity and diversity dynamics remain critically understudied. Past studies have investigated macroevolutionary trends in Palaeozoic actinopterygians in a piecemeal fashion, variably using existing compendia of vertebrates or literature-based searches, and there is no comprehensive occurrence-based dataset of actinopterygians spanning the whole of the Palaeozoic. Past studies typically show low levels of diversity in the Devonian with a substantial rise in the early Carboniferous in the aftermath of the end-Devonian mass extinction. However there are unresolved patterns reported for the later

42 Carboniferous and Permian. In large part, these conflicts span from a lack of publicly-

43 available occurrence data: actinopterygians are majorly underrepresented in the Paleobiology

44 Database (PBDB), for example, obscuring patterns of diversity through time. This is

45 exacerbated by major taxonomic problems pervading the Palaeozoic actinopterygian record.

46 Innumerable taxa are lumped into wide-ranging families and poorly-formulated genera, with

47 a vast number of described species concentrated in several particularly problematic 'waste-

48 basket' genera. This taxonomic confusion feeds into a limited understanding of phylogenetic

49 relationships. There is also a heavy sampling bias towards Europe and North America, with

50 other regions underrepresented despite yielding important occurrences. Scrutiny of the extent

51 to which spatial biases influence the record is lacking, as is research on other forms of bias.

52 Low richness in some time periods may be linked to geological biases, while the effect of

53 taphonomic biases on Palaeozoic actinopterygians have not yet been investigated. Efforts are

54 already underway to both redescribe poorly defined taxa and describe taxa from

55 underrepresented regions, helping address taxonomic issues and accuracy of occurrence data.

56 New methods of sampling standardisation utilising up-to-date occurrence databases will be

57 critical in teasing apart biological changes in diversity from those resulting from bias. Lastly,

58 continued phylogenetic work will enable the use of phylogenetic comparative methods to

59 elucidate the origins of actinopterygian biogeography and subsequent patterns of radiation

60 throughout their rise to dominate aquatic faunas.

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65 **CONTENTS**

99

100   **I. INTRODUCTION**

101   Reconstructions of deep time biodiversity patterns are critical to understanding the

102   evolution of life of Earth. However, deciphering whether these patterns represent true

103   changes in biodiversity is a key challenge for palaeobiologists (Raup, 1972, 1976; Sepkoski,

104   1981; Alroy *et al.*, 2008). The past 20 years have seen rapid growth in the number of

105   quantitative studies on vertebrate groups, which employ fossil occurrence data to estimate

106   patterns of diversity. The majority of work on vertebrate diversity through time focuses on

107   either individual taxonomic groups of tetrapods (e.g. Alroy, 2009; Benson *et al.*, 2010; Butler

108   *et al.*, 2011; Mannion *et al.*, 2011, 2019; Brocklehurst, Kammerer and Fröbisch, 2013; Butler,

109   Benson and Barrett, 2013; Pearson *et al.*, 2013; Cleary *et al.*, 2015, 2018, 2020; Bennett *et*

110   *al.*, 2018; Cantalapiedra, Domingo and Domingo, 2018; Brown *et al.*, 2019; Driscoll *et al.*,

111   2019; Celis *et al.*, 2020; Cantalapiedra *et al.*, 2021) and fishes (Sallan & Coates, 2010; Koot,

112   2013; Lloyd & Friedman, 2013; Sansom, Randle, & Donoghue, 2015; Romano *et al.*, 2016),

113   or more recently large scale analyses of all tetrapods (Sahney, Benton, & Ferry, 2010; Close

114   *et al.*, 2017, 2019, 2020a; Dunne *et al.*, 2018; Dunne, 2020) using large publicly available

115   databases such as the Paleobiology Database (PBDB; paleobiodb.org). Critically, these

116   studies are often able to identify biases and gaps in the fossil record, allowing insight into

117   evolutionary dynamics in deep time and the assembly of ancient and modern ecosystems.

118   Such studies can also reveal major changes in diversification, extinction, and paleoecology.

119   For example, studies of Palaeozoic vertebrates have illuminated the rise of jawed vertebrates

120   from the Silurian to the Devonian (Sansom *et al.*, 2015), a major shift from placoderm- and

121   sarcopterygian-dominated faunas to chondrichthyan- and actinopterygian-dominated faunas

122   after the end-Devonian mass extinction (Sallan & Coates, 2010), and changes in Palaeozoic

123   tetrapod diversity in relation to palaeoenvironments (Dunne *et al.*, 2018; Pardo *et al.*, 2019).

124   Despite accounting for roughly half of extant vertebrates (Nelson, Grande, & Wilson,

125   2016), research on the diversity of actinopterygians over long evolutionary timescales

126   comprises only a fraction of macroevolutionary studies. Ray-finned fishes likely evolved in

127   the Silurian (Zhu *et al.*, 2009) with the crown group originating at or about the Devonian-

128   Carboniferous boundary (Giles *et al.*, 2017), but diversity dynamics throughout the

129   Palaeozoic are poorly understood due to the limited number of studies utilising occurrence-

130   based datasets. This reflects a broader palaeontological trend of understudy into the fossil

131   record of fishes (Friedman & Sallan, 2012). Notable exceptions include Sallan and Coates'

132   (2010) diversity and faunal analyses of Middle Devonian to Mississippian gnathostomes;

133   Lloyd and Friedman's (2013) analysis of British fish richness; and Romano *et al.*'s (2016)

134   study on Permo-Triassic osteichthyans. Other studies have used compendia of first and last

135   appearances to plot counts through time (Benton, 1993; Patterson, 1994; Sepkoski, 2002;

136   Blieck, 2011; Friedman & Sallan, 2012). Additional studies examine patterns of biodiversity

137   across long periods of time using publicly available occurrence data (e.g. PBDB), though

138   they present aggregated data of numerous groups of 'fishes', or an even broader set of taxa

139 such as nektonic metazoans (e.g. Whalen and Briggs [2018]; Harper, Cascales-Miñana and

140 Servais [2020]).

141   While these studies present an important first foray into understanding Palaeozoic

142 actinopterygian evolution, there have been limited syntheses that take the accuracy of the ray-

143 fin fossil record into account, which is a major barrier to reconstructing long-term

144 evolutionary patterns. Previous attempts either focus on the UK and include non-

145 actinopterygian fishes (Lloyd & Friedman, 2013), do not cover the entire Palaeozoic (Sallan

146 & Coates, 2010; Romano *et al.*, 2016), or are broader in scope without as much focus on the

147 suitability of data and barriers to interpreting diversity patterns (Sallan, 2014). Friedman and

148 Sallan (2012) note the lack of such investigation for fishes, and, through a qualitative survey,

149 suggest that geological and taxonomic biases likely impact diversity of fishes through time.

150 Here, we summarise the current state of research on the Palaeozoic fossil record of

151 actinopterygians, and attempt to answer the following:

152 - how much is currently known about the Palaeozoic actinopterygian fossil record?

153 - what is the current state of research on actinopterygian diversity through the Palaeozoic?

154 - how do taxonomic problems and existing phylogenetic analyses hinder our interpretation of

155 the Palaeozoic actinopterygian fossil record?

156 - how do sampling and other biases affect our understanding of Palaeozoic actinopterygian

157 diversity through time?

158

159 **II. CURRENT HYPOTHESES OF PALAEOZOIC ACTINOPTERYGIAN**

160 **DIVERSITY**

161 **(1) Past studies**

162   Although our understanding of patterns of actinopterygian diversity lags behind that

163   of other groups, a number of studies over the past few decades have investigated fish

164   diversity at different taxonomic levels and geological scales (Fig. 1). Initially, these

165   approaches used published compendia to generate family- and/or genus-level diversity

166   curves. The first major attempt, by Thomson (1977), used data from Romer's (1966)

167   compendium to plot genus- and family-level diversity of Phanerozoic 'fishes' (Acanthodii,

168   Agnatha, Chondrichthyes, Chondrostei, Holostei, Placodermi, Sarcopterygii and Teleostei;

169   Fig. 1E). In subsequent years, several studies used family-level data from Benton (1993) to

170   investigate osteichthyan diversity through the Palaeozoic. Patterson (1994) plotted diversity

171   curves for osteichthyans as well as stem-actinopterygians, stem-neopterygians and stem-

172   teleosts, encompassing all Palaeozoic actinopterygians included in the parent dataset (Fig.

173   1A). Blieck (2011; Fig. 1B) and Benton (2014: fig. 2.11) also use data compiled by Benton

174   (1993) to plot family-level diversity curves of vertebrates from the Ordovician to Triassic,

175   though do not focus on actinopterygians. Additionally, Friedman and Sallan (2012) used an

176   existing marine dataset (Sepkoski, 2002) to present genus-level diversity patterns of all

177   'fishes' (vertebrates excluding Tetrapoda and including Conodonta) throughout the

178   Phanerozoic (Fig. 1C).

179   Other attempts have used literature-based datasets to interrogate patterns of diversity.

180   Sallan and Coates (2010) assembled a dataset of gnathostome occurrences from 66 localities

181   spanning the Middle Devonian (Givetian) to early Carboniferous (Serpukhovian) and

182   presented diversity curves of gnathostomes (Acanthodii, Actinopterygii, Chondrichthyes,

183   Placodermi, Sarcopterygii, Tetrapoda; Fig. 1F). Datasets assembled by Romano *et al.* (2016)

184   and Vázquez and Clapham (2017) commence in the Asselian (early Permian) and encompass

185   osteichthyans (Actinistia, Dipnoi, Holostei, 'Palaeopterygii', 'Subholostei' and

186   Teleosteomorpha: Romano *et al*. [2016]; Fig. 1F) and marine fishes (Osteichthyes [excluding

187   Dipnoi] and Chondrichthyes [excluding Acanthodii]; Vázquez and Clapham [2017]). Lloyd

188   and Friedman (2013) sourced data from a variety of sources as a means of comparing datasets

189   (Agassiz, 1833; Carroll, 1988; Benton, 1993; Sepkoski, 2002; Paleobiology Database,

190   downloaded on 31/5/12) to investigate the diversity of Phanerozoic 'fishes' (though

191   excluding Conodonta) with a particular focus on the fossil record of Great Britain (Fig. 1D).

192   These studies clearly differ greatly in their sampling and spread of taxa, but

193   collectively they provide an indication of the general patterns of changes in actinopterygian

194   diversity through time, as summarised below.

195

196   **(2) Devonian diversity patterns**

197   All studies covering the Devonian depict very low counts of actinopterygian genera or

198   families ((Thomson, 1977: fig. 7; Patterson, 1994: fig. 1; Sallan and Coates, 2010: fig. 1;

199   Blieck, 2011: fig. 2). Thomson (1977), Patterson (1994) and Sallan and Coates (2010) show a

200   gradual rise from the Middle to Late Devonian. Blieck (2011), however, figures a small peak

201   in the Frasnian, likely due to the Gogo and Gladbach faunas (Sallan & Coates, 2010). The

202   low diversity of actinopterygians also correlates with the small proportion of morphological

203   disparity that they account for among gnathostomes (Anderson *et al.*, 2011).

204   While new taxa are still being described, actinopterygians appear to be genuinely rare

205   in Devonian deposits, especially relative to other taxa (Friedman, 2015: fig. 4).

206   Reclassification of *Meemannia* Zhu *et al.* 2004 as a ray-finned fish rather than a lobe-finned

207   fish (Lu *et al.*, 2016) filled a conspicuous temporal gap in early actinopterygian evolution, but

208   this taxon remains the only actinopterygian known amongst roughly 20 species from this

209   locality. Choo *et al.* (2019) recently described a new genus from the highly diverse Frasnian

210   Gogo Formation, although ray fins account for only 5 species out of around 50 Gogo taxa

211   (Long & Trinajstic, 2010, 2017; Sallan & Coates, 2010, fig. 2). Even more recently, Newman

212   *et al.* (2021) described a new species of *Cheirolepis* Agassiz 1835 from the Givetian of

213   Svalbard, found alongside roughly 20 non-actinopterygian fishes. Similarly, a new site from

214   the Famennian of Belgium has yielded microremains of an undescribed actinopterygian,

215   amidst large numbers of other vertebrates (Olive *et al.*, 2015b, 2015a, 2016, 2020).

216   Renewed investigation into historically undersampled regions hint at previously

217   hidden actinopterygian diversity. Isolated jaw elements, body impressions and scales from

218   Famennian deposits in South Africa likely represent a single actinopterygian amid a diverse

219   array of other fishes (Gess & Whitfield, 2020), while renewed prospecting in the

220   contemporary Maïder Basin in Morocco has produced remains of a single articulated

221   actinopterygian (Frey *et al.*, 2018) amongst its well-known placoderm and chondrichthyan

222   assemblages. New South American discoveries include evidence of a stegotrachelid

223   actinopterygian from the Frasnian of Colombia (Olive *et al.*, 2019), the first actinopterygian

224   remains from the Devonian of the Parnaíba Basin of Brazil (Pais de Rezende *et al.*, 2021),

225   and a new circumpolar species from the Middle Devonian (Figueroa, Weinschütz, &

226   Friedman, 2021). As in other localities, non-actinopterygian fishes dominate these faunas

227   (Janvier, 2007; Janvier & Maisey, 2010; Figueroa & Machado, 2018). While important for

228   understanding the early evolution of the group, these scattered reports of new Devonian taxa

229   seem unlikely to change existing overarching hypotheses of actinopterygian diversity: as

230   minor faunal components represented by a small number of taxa relative to other fish groups.

231

232   **(3) Carboniferous diversity patterns**

233   Previous diversity studies consistently report a large increase in counts of

234   actinopterygians in the earliest Carboniferous, following the end-Devonian mass extinction

235   (EDME). Thomson's (1977) counts of 'chondrostean' genera (which encompasses all

236   Devonian and Carboniferous actinopterygians) rise sharply in the Mississippian, as does

237   Patterson's (1994) stem-actinopteran family-level count. Sallan and Coates (2010) show this

238   significant change in absolute and relative diversity most clearly in their presentation of

239   faunal composition from the Devonian into the Carboniferous (Sallan and Coates, 2010, fig.

240   2; see also Friedman, 2015, fig. 4). This sharp rise is especially notable because the early

241   Carboniferous (Tournaisian and early Visean) coincides with 'Romer's Gap', an apparent gap

242   in the fossil record of tetrapods (and other animals) variably explained as either a period of

243   poor sampling (Romer, 1956), low atmospheric oxygen (Ward *et al.*, 2006) or recovery

244   following the EDME (Sallan & Coates, 2010). Recent concerted efforts have begun to

245   populate Romer's Gap, indicating that poor sampling accounted for most of the apparent

246   paucity of the record (Clack *et al.*, 2019; Otoo *et al.*, 2019). The diversification of

247   actinopterygians immediately following the EDME likely represents an adaptive radiation

248   seeded by very few—or perhaps just one—actinopterygian lineages (Sallan & Friedman,

249   2012; Sallan, 2014; Giles *et al.*, 2017), although this hypothesis has not been explicitly tested.

250   The contrast between diverse (e.g. in Russia: Alekseev *et al.* [1994]) and depleted (e.g. in

251   Morocco: Frey *et al.* [2018]) early Tournaisian faunas exemplifies the uncertainty of the

252   relative contributions of extinction recovery and poor sampling to the observed Tournaisian

253   fossil record, as well as potential local variation and spatial bias.

254   Raw genus diversity increases into the Visean from the Tournaisian levels in most

255   analyses (Patterson, 1994; Sallan & Coates, 2010; Blieck, 2011). The fossil record of Great

256   Britain exhibits a particularly extreme increase in osteichthyan richness, most likely due to

257   the very richly sampled Visean deposits of Scotland (Dineley & Metcalf, 1999). This rise

258   coincides with a proliferation of new morphologies and ecologies, likely via multiple

259   independent acquisitions of key traits such as durophagy, deep-, and eel-like-bodies (Sallan &

Friedman, 2012; Sallan, 2012, 2014; Sallan & Coates, 2013; Friedman, 2015; Friedman *et al.*, 2018). This gradual rise in richness, accompanied by morphological and functional diversification, may represent a classic extinction recovery and adaptive radiation (Sallan & Friedman, 2012; Sallan, 2014).

Previous studies suggest conflicting patterns of actinopterygian raw diversity into the Serpukhovian. Patterson (1994) and Blieck (2011) report a decrease in family counts, in contrast to a slight increase in genus counts in Sallan and Coates (2010). The diversity curve of Thomson (1977) only separates data into Mississippian and Pennsylvanian bins, and therefore lacks the temporal resolution to allow comparison. Discrepancy between the trends in Sallan and Coates (2010), and Patterson (1994) and Blieck (2011) may be due to poor higher-level taxonomy in actinopterygians. For example, the highly diverse Bear Gulch fauna likely drives the rise in actinopterygian diversity in Sallan and Coates (2010), while this is not captured in higher-level family counts due to the aggregation of genera in broad, spurious families.

It is difficult to reconstruct patterns of diversity in the Late Carboniferous due to the lack of occurrence data covering the Pennsylvanian. Sallan and Coates' (2010) range ends at the Mississippian, while Romano *et al.*'s (2016) data begins in the Asselian. Thomson's (1977) genus counts decrease from the Mississippian to the Pennsylvanian, however family counts of actinopterygians increase from the Serpukhovian to the Bashkirian (Patterson, 1994; Blieck, 2011). For the Moscovian-Gzhelian the only data for actinopterygians is the family counts derived from Benton (1993); these show gradual decreases from the Bashkirian to the Moscovian, and again from the Moscovian to plateau in the Kasimovian and Gzhelian (Patterson, 1994; Blieck, 2011). Importantly, counts of families remain at roughly the same level as they were in the Tournaisian and Visean. Counts of osteichthyan genera are not

284 visible for this period in Friedman and Sallan (2012: fig. 2), and there are no Kasimovian or

285 Gzhelian occurrences in the British fossil record (Lloyd & Friedman, 2013).

286   Reported overall trends in actinopterygian diversity in the Carboniferous are unclear.

287 Genus-level counts are suggestive of a gradual rise throughout the Mississippian (Sallan &

288 Coates, 2010), with a subsequent drop in the Pennsylvanian (Thomson, 1977). This contrasts

289 with family counts, which are relatively stable except for minor deviations in the

290 Serpukhovian and Bashkirian.

291

292 **(4) Permian diversity patterns**

293   Genus- and family-level counts in previous studies agree on the general trend of

294 actinopterygian diversity in the Permian, though differ at finer timescales. The highest counts

295 are observed in the early Permian in curves derived from Benton's (1993) dataset (Patterson,

296 1994; Blieck, 2011) and Thomson's (1977) genus data. Occurrence-based datasets also show

297 a peak in the early Permian, although limited to the Asselian and Sakmarian, likely driven by

298 freshwater Lagerstätte (Romano *et al.*, 2016). Genus- and family-level trends deviate from

299 one another in the Artinskian: the family curve stays more or less stable, whereas genus

300 richness decreases substantially. Family-level counts then drop in the Kungurian and remain

301 roughly at this level, with minor fluctuations, until the end-Permian. Genus richness in

302 Thomson's (1977) curves for 'chondrostean' genus richness drop in the Middle Permian and

303 rise slightly in the Late Permian, and the Late Permian also sees the first counts of holosteans.

304 Counts in the finer-scale dataset of Romano *et al.* (2016) rises gradually from the Roadian-

305 Wuchiapingian, reaching close to Early Permian levels before dropping in the

306 Changhsingian.

307   While previous studies have established a broad understanding of general diversity

308   trends in the Palaeozoic, there has not yet been a through-Palaeozoic study focussing solely

309   on actinopterygians, and patterns differ depending on the taxonomic level and geological

310   scale investigated. At present, publicly available occurrence databases lack the level of detail

311   necessary for reconstructing long-term diversity through the Palaeozoic, and outstanding

312   issues remain concerning museum 'dark data' and taxonomic 'waste-baskets' taxa. These

313   problems need to be tackled before an accurate understanding of macroevolutionary patterns

314   can be established.

315

316   **III. MATERIALS AND METHODS**

317   **(1) Species naming and publication data**

318   To plot a collector's curve showing the number of species named over time, we

319   compiled a list of all described Palaeozoic species of actinopterygians (totalling 516 species),

320   including the authority naming the species and year the species was described.

321   To examine publication trends through time, we searched the literature for

322   publications mentioning terms typically associated with early actinopterygians –

323   "pal(a)eoniscid", "pal(a)eoniscoid", "pal(a)eonisciform" and "pal(a)eopterygian" (and their

324   equivalent formal taxonomic names, e.g. Palaeoniscidae) – using Publish or Perish 6.49

325   (Harzing, 2007) to draw literature from Google Scholar and Crossref. This comes with the

326   caveat that the resulting data does not include publications unavailable online. This may bias

327   against older literature not initially published online, however most of the key works of early

328   actinopterygian research from the 19th century are now available digitally, with text available

329   due to optical character recognition.

These terms have convoluted and interwoven histories, and the literature includes usage of these terms both informally and as formal taxonomy going back to the 19th and early 20th centuries. The family was first named by Vogt (1852), 'Die Palaeonisciden', to group six genera on the basis of their heterocercal tail and apparently unossified endoskeleton. Later works upheld this family (e.g. Owen, 1860), and the term was also subsequently used as a grouping within Chondrostei (Woodward, 1891; Hay, 1902; Watson, 1925, 1928; Stensiö, 1932). Goodrich (1909) included Palaeoniscidae in the Palaeoniscoidei, within Chondrostei, and Berg (1940) included Palaeoniscoidei within the order Palaeonisciformes, still within Chondrostei. Gardiner (1967) also considered the Palaeonisciformes to be an order in Chondrostei, and recognised Palaeoniscidae but not Palaeoniscoidei, while Lehman (1966) included Palaeoniscoidei in Palaeonisciformes, but not within Chondrostei. Gardiner (1960) referred to Palaeoniscoidea when describing Mesozoic actinopterygians, while Currey (1961) and Schultze (1968) used the same term in description of early osteichthyans whose actinopterygian affinity is not certain. Palaeoniscoidea was also described as a suborder within Palaeonisciformes (in turn within Chondrostei) by Carroll (1988). Berg, Kazantseva and Obruchev (1964) introduced Palaeonisci, including a group termed Palaeoniscida, as separate to Chondrostei, while Moy-Thomas and Miles (1971) used the term Palaeoniscida as a group including Palaeoniscoidei within Chondrostei (making it essentially equivalent to Palaeonisciformes). Kazantseva-Selezneva (1981) later included Palaeonisciformes in Palaeonisci. Lund, Poplin and McCarthy (1995) introduced a new clade, Palaeoniscimorpha, though in association with the "palaeoniscoid" term and supposedly without precise taxonomic meaning. Notably, the most recent edition of 'Fishes of the World' (Nelson *et al.*, 2016) includes only the Palaeoniscidae within the Palaeonisciformes, with the suborder Palaeoniscoidei in the previous edition having been removed by the authors.

354   Although originally used to define taxonomic ranks, these terms have gradually been

355   recognised as paraphyletic or polyphyletic groups of Palaeozoic and Mesozoic

356   actinopterygians with 'primitive' ray-fin characteristics (Patterson, 1982; Gardiner &

357   Schaeffer, 1989; Gardiner, Schaeffer, & Masserie, 2005). In recent analyses these groups are

358   paraphyletic, and most descriptions of new Palaeozoic actinopterygians do not assign taxa to

359   them (e.g. Choo *et al.*, 2019; Figueroa, Friedman and Gallo, 2019; Newman *et al.*, 2021). The

360   general trend has been towards the view that these terms are taxonomically redundant and of

361   no functional use, yet some descriptions still refer to them (Mickle, 2011) and Mickle (2012)

362   considered the Palaeonisci, Palaeoniscimorpha and Palaeonisciformes to be natural groups.

363   Some attempts have been made to introduce a term for Palaeozoic actinopterygians of

364   uncertain affinity that explicitly rejects monophyly of its constituent members. Regan (1923)

365   initially used Palaeopterygii as a taxonomic group encompassing palaeoniscoids,

366   chondrosteans and belonorhynchians. Subsequently, McCune and Schaeffer (1986) defined

367   "Paleopterygii" as a non-monophyletic group including only fossils that do not share

368   characters with modern groups. Friedman and Giles (2016) recently suggested reintroducing

369   'palaeopterygians' (*sensu* McCune and Schaeffer, 1986) as a non-taxonomic blanket term in

370   place of "palaeoniscoids".

371   This summary highlights the complexity of the taxonomic history of Palaeozoic

372   actinopterygians, particularly as they are often nested within one another (e.g.

373   Palaeoniscoidei in Palaeoniscida/Palaeonisciformes) or are essentially equivalent (e.g.

374   Palaeoniscida and Palaeonisciformes). Sallan (2014) provides a more detailed summary of

375   the usage of and interplay between these terms in the literature.

376   Our final citation dataset included 2793 publications spanning 1873–present. All data

377   transformation and plotting was conducted in R v. 4.0.3 (R Core Team, 2020).

(2) Occurrence data

We downloaded global occurrences of Actinopterygii from the Paleobiology Database (PBDB; paleobiodb.org, downloaded April 2020) to assess the coverage of actinopterygian data already entered into the PBDB and compare it with other published hypotheses of actinopterygian diversity through time. This dataset comprised 2044 accepted genera of actinopterygians from 5418 unique collections (= unique fossil localities), and 2226 species from 5629 collections. Using the PBDB download, we plotted a raw 'global' diversity curve for the Palaeozoic and Mesozoic to allow for comparison with other hypotheses of actinopterygian diversity through time. We counted the number of taxa per geological stage (as defined by the International Commission on Stratigraphy (Cohen, Harper, & Gibbard, 2021)), as well as the number of collections (= fossil localities), geological units (= formations defined in the PBDB) and occupied $50km^2$ equal-area grid cells of modern day localities to examine correlations between sampling and diversity. We also plotted local richness (the number of taxa per collection) through time (Bambach, 1977; Close *et al.*, 2019). The aim of this was not to deduce real diversity patterns, as raw counts of taxonomic occurrences generally reflect biases in the fossil record (Raup, 1972; Alroy *et al.*, 2001; Peters, 2005; Alroy, 2010; Smith & McGowan, 2011), but to assess the quality of the actinopterygian data in the PBDB and compare it with existing publications examining diversity in actinopterygians. Less than 7% of collections (= unique fossil localities) in the PBDB yielding actinopterygians were from the Palaeozoic, with 43% and 50% from the Mesozoic and Cenozoic respectively. Similarly, less than 6% of species were Palaeozoic, with 35% and ~60% from the Mesozoic and Cenozoic.

Table 1 – Percentages of collections (= unique fossil localities) and species of actinopterygians entered in the PBDB stemming from the Palaeozoic, Mesozoic and Cenozoic.

	Palaeozoic	Mesozoic	Cenozoic
Collections	7%	43%	50%
Species	6%	34%	60%

403

IV. HISTORY OF RESEARCH INTO PALAEOZOIC ACTINOPTERYGIAN DIVERSITY

(1) Collector's curves

The history of research on actinopterygian fish stretches back to the early 19th century (Blainville, 1818; Bronn, 1829; Sedgwick, 1829). Agassiz's (1833) pioneering work on palaeoichthyology kickstarted a 'golden age' for the description of new Palaeozoic taxa. Subsequent monographs throughout the 19th and early 20th centuries expanded Agassiz's initial work (e.g. Ramsay H. Traquair, 1877). This early focus is visualised by Lloyd and Friedman's (2013) asymptotic collector's curve of the British fish fossil record. This analysis compiled descriptive papers using a comprehensive taxonomic definition of fishes, comprising all non-tetrapod and non-conodont fishes, spanning every period from the Silurian to Palaeogene. Their collector's curve indicates a high degree of sampling of the fossil record in Great Britain. However, high taxonomic coverage prevents examination of the patterns in specific groups, and the limited geographic coverage prevents assessment of global-scale patterns.

We compiled collector's curves for Palaeozoic actinopterygians using both British and global data to examine whether the trend observed by Lloyd and Friedman (2013) is upheld when restricted to one taxonomic group or extended beyond Great Britain. An asymptote is observed when considering Palaeozoic actinopterygians from Great Britain

423   (black line, Fig. 2). The number of described taxa starts to plateau in the 20th century, largely

424   due to the foundational monographic descriptions of Agassiz (1833) and Traquair (1877). A

425   slight increase in recent years indicates a resurgence of interest focussed around CT-based

426   redescriptions of classic taxa (e.g. Coates and Tietjen, 2018), as well as local taxonomic

427   reviews (e.g. Elliott, 2014, 2016). While unlikely to alter large-scale diversity patterns (Lloyd

428   & Friedman, 2013) this uptick is suggestive of further hidden diversity in the fossil record of

429   Palaeozoic actinopterygians in Great Britain, particularly with regard to redescription of

430   material that has been untouched since the 19th and early 20th century.

431   Our global collector's curve, however, presents a very different trend (grey line, Fig.

432   2). During the 19th century, our global curve roughly tracks that of Great Britain, albeit with

433   slightly higher cumulative counts. This is largely due to the works of Agassiz (1833) and

434   Traquair (1877), who produced monographic descriptions of actinopterygians from Belgium,

435   France and Germany, though there were a host of other important contributions (e.g. Hancock

436   and Atthey, 1872; Frič, 1879). In the late 19th century the global curve departs from the

437   British curve, rising steadily in part due to significant contributions from Aldinger (1937) and

438   Gardiner (1969), who described new taxa from Greenland and South Africa respectively.

439   From the late 1970s the global collector's curve accelerates at a faster and steadier rate than

440   at any time previously. This corroborates statements that the fossil record of Palaeozoic

441   actinopterygians is undersampled (Sallan & Coates, 2010).

442   New Palaeozoic actinopterygian taxa continue to emerge from well-sampled regions

443   such as Europe (e.g. Elliott, 2016; Štamberg, 2016; Bakaev and Kogan, 2020; Newman *et al.*,

444   2021) and North America (e.g. Mickle, 2017, 2018; Wilson, Pardo and Anderson, 2018).

445   Importantly however, underrepresented regions such as Australia (Choo, 2012, 2015; Choo *et*

446   *al.*, 2019), and South America (Figueroa *et al.*, 2021) are also producing new taxa. In

447   addition, the widespread adoption of CT scanning allows valuable redescriptions and

448   taxonomic revisions of existing material (Giles & Friedman, 2014; Giles *et al.*, 2015, 2017;

449   Pradel *et al.*, 2016; Coates & Tietjen, 2018; Friedman *et al.*, 2018; Argyriou *et al.*, 2018;

450   Figueroa *et al.*, 2019). 'Dark data' in museums (Allmon *et al.*, 2018) will continue to play a

451   major role in unearthing new actinopterygian taxa: recent work found that museum

452   collections contained 23 times more localities than recorded in the PBDB for Cenozoic

453   marine invertebrates (Marshall *et al.*, 2018), hinting at unrecognised taxonomic diversity not

454   currently captured in publicly available occurrence databases. For example, Mickle (2017)

455   notes 'hundreds' of Tournaisian actinopterygian specimens in North American museums,

456   many referred to genera of dubious monophyly.

457

458   **(2) Publication trends**

459   Another way of assessing research interest into Palaeozoic actinopterygians is to

460   investigate the number of citations referring to them through time. We investigated use of the

461   terms "palaeoniscoid", "palaeoniscid", "palaeonisciform", and "palaeopterygian", all of

462   which are commonly associated with Palaeozoic actinopterygians (see Materials and

463   Methods).

464   There is a steady increase in the number of citations referring to Palaeozoic

465   actinopterygians over the last half century (Fig. 3), broadly coinciding with the uptick in the

466   global collector's curve. Use of the term "palaeoniscid" dominates research until the late

467   1950s, when the terms "palaeonisciforms" and "palaeoniscoids" start to become more

468   prominent. There are sporadic appearances of "palaeopterygians" in 20th century literature

469   following Regan's (1923) initial use. However, usage of the term did not increase following

470   McCune and Schaeffer's (1986) redefinition of it. A small increase in recent years may reflect

471   Friedman and Giles' (2016) renewed suggestion to use it as a term with no implications of

472   taxonomic groupings. The predominant term in 21st century literature is "palaeonisciformes",

473   though "palaeoniscoid" and "palaeoniscid" remain prevalent. From the list of terms and

474   publications above it is clear that there is a lack of convergence on a single term for

475   Palaeozoic actinopterygians and citation data reflects this.

476   The rate of description of new species of Palaeozoic actinopterygians remains high

477   (Fig. 2) and it is clear from the expanding body of literature that research interest continues to

478   grow (Fig. 3). However, the majority of studies are taxonomic or descriptive, with

479   comparatively few macroevolutionary studies (Sallan, 2014). Consequently, our

480   understanding of patterns of diversity and the impact of mass extinctions in ray-fins lags

481   behind that of other taxonomic groups.

482

483   **V. PROBLEMS IN DECIPHERING THE PALAEOZOIC ACTINOPTERYGIAN**

484   **FOSSIL RECORD**

485   **(1) Currently available occurrence data**

486   A large proportion of recent diversity studies for fossil groups rely on occurrence

487   data from the Paleobiology Database. However, most diversity studies on actinopterygians

488   rely on published compendia or datasets compiled from the literature and rarely entered into

489   the PBDB (see Vázquez and Clapham [2017] for an exception). Occurrence data from the

490   PBDB poorly represents osteichthyans (Lloyd & Friedman, 2013), and particularly ray-finned

491   fishes. We demonstrate this by generating Palaeozoic actinopterygian diversity curves for

492   genera, collections, formations and equal-area grid cells based on occurrence data currently

493   available from the PBDB (Fig. 4). The genus-level curve is almost flat, with upward trends in

494   the Tournaisian-Visean and fluctuating patterns in the Wordian–Changhsingian, and there are

495   no data for several time periods.

496   This pattern demonstrates major gaps and inaccuracies in the currently available

497   occurrence data for the bulk of the Palaeozoic. Only four genera (eight species) of

498   actinopterygians are entered for the entire Devonian; less than the number described in the

499   literature for just the Famennian (Dunkle, 1964; Dunkle & Schaeffer, 1973; Taverne, 1997;

500   Daeschler, 2000; Prokofiev, 2002; Friedman & Blom, 2006). A cursory search of the

501   literature shows ~100 published Visean localities, with many more likely represented in

502   museum 'dark data' (Sallan & Coates, 2010; Marshall *et al.*, 2018), but less than 50

503   actinopterygian taxa stemming from around 30 collections are currently recorded in the

504   PBDB for the entire Carboniferous. Inconsistencies between regional substages and ICS

505   stages mean that there are only two Serpukhovian occurrences of actinopterygians in the

506   PBDB, despite it having the highest raw count of genera in the Devonian and Mississippian

507   (Sallan & Coates, 2010). In the PBDB, no stage between the Kasimovian and Kungurian has

508   more than four genera of actinopterygians, highlighting how poor the late Carboniferous and

509   early Permian data are. This is partly due to genuinely low numbers of marine

510   actinopterygians in this period (Hurley *et al.*, 2007; Friedman, 2015; Romano *et al.*, 2016)

511   perhaps linked to a paucity of marine deposits (McGowan & Smith, 2008; Friedman &

512   Sallan, 2012). It is clear, however, that the substantial freshwater actinopterygian fossil

513   record from the late Carboniferous-early Permian is absent from the PBDB (Beltan, 1978,

514   1981; Forey & Young, 1985; Murray, 2000; Soler-Gijón & Moratalla, 2001; Evans, 2005;

515   Štamberg & Zajíc, 2008; Šimůnek & Cleal, 2020). In contrast, the late Permian

516   actinopterygian fossil record is better represented, in large part due to targeted entry of data

517   for studies relating to the End-Permian Mass Extinction (e.g. by Vázquez and Clapham

518   [2017]).

519   **(2) Taxonomic issues**

520   Deep-seated problems with Palaeozoic actinopterygian taxonomy exacerbate low

521   levels of actinopterygian genus richness, despite considerable morphological variation and

522   high numbers of species within these genera (Fig. 5). Many genera from this period have

523   apparently global distributions and stratigraphic ranges spanning nearly the entirety of the

524   Carboniferous and Permian (Gardiner, 1993; Sepkoski, 2002; Sallan, 2014). This is likely an

525   artefact of reduced researcher effort in this period in favour of earlier Devonian forms, or

526   later Mesozoic forms (Sallan, 2014). As a result, many late Palaeozoic have not been the

527   subject of detailed taxonomic work.

528   Carboniferous and Permian actinopterygians received the most attention from

529   researchers in the 19th and early 20th centuries. While much of this work was ground-breaking

530   and laid the foundations for palaeoichthyology, there are substantial problems with some

531   outcomes of the research, notably the existence of wide-ranging, poorly defined genera.

532   Often, initial descriptions of taxa were brief and erected new genera with a heavy reliance on

533   the shape of the body (e.g. deep-bodied, fusiform, slender) and scale morphology (Agassiz,

534   1833; Traquair, 1877b, 1879; Moy-Thomas & Dyne, 1938). This led to poorly defined genus

535   diagnoses, often containing large numbers of dubiously-related species – species whose

536   characteristics sometimes even contradicted generic diagnoses. Some of the most notable

537   problem genera—also termed "waste-baskets" (Evans, 2005) and "trash fish" (Coates &

538   Tietjen, 2018)—are *Palaeoniscum* Blainville 1818, *Elonichthys* Giebel 1848 and *Platysomus*

539   Agassiz 1843 (Mickle, 2017), though others exhibit similar issues (e.g. *Acrolepis* Agassiz

540   1843, *Amblypterus* Agassiz 1843 and *Rhadinichthys* Traquair 1877). Higher-level taxonomic

541   groups based on these genera, which are almost exclusively erected with generic diagnoses

542   (Sallan, 2014), suffer from the same problems. The outcome is that many Palaeozoic and

543   early Mesozoic actinopterygians jump between largely meaningless orders and families.

544   In addition to being taxonomically confusing, several early Palaeozoic

545   actinopterygian genera likely obscure a significant proportion of genus-level diversity. We

546   review three taxa below, noting problems with their initial diagnoses, valid and invalid

547   species, their temporal and geographic range, work that has been done to address these issues,

548   and what needs to be done in the future. Mickle (2017) also provides a comprehensive

549   overview of the problems associated with *Palaeoniscum*, *Elonichthys* and *Rhadinichthys* (see

550   also Appendix S1).

551   *(a)* Palaeoniscum

552   *Palaeoniscum* was erected alongside *Paleothrissum* Blainville 1818 in the early 19th

553   Century (Blainville, 1818). Not long after, Agassiz (1833), incorporated *Paleothrissum* into

554   *Palaeoniscum* and erected a new genus, *Palaeoniscus* (though the type remained that of

555   *Palaeoniscum*). Subsequent authors have used both taxon names interchangeably (Troschel,

556   1857; Traquair, 1877a, 1877b; Woodward, 1891; Jordan & Evermann, 1917), in part due to

557   its vague and unspecific diagnosis (see Supplementary Material for diagnoses and detailed

558   overview of taxonomic problems). This has led to much taxonomic confusion (Mickle, 2017),

559   and specimens ranging from the Tournasian through to the Wuchiapingian have been referred

560   to *Palaeoniscum*. This genus is almost certainly a taxonomic 'waste-basket'. Future workers

561   should refer to Aldinger's (1937) comprehensive diagnosis of the type species, *P. freieslebeni*

562   Blainville 1818, and attempt to identify shared traits to better distinguish the genus. Until that

563   point, *P. freieslebeni* could be considered the only valid species of *Palaeoniscum* (Mickle,

564   2017).

565   *(b)* Elonichthys

566   *Elonichthys* is a paraphyletic or polyphyletic waste-basket genus (Schultze &

567   Bardack, 1987; Long, 1988; Malabarba, 1988; Gardiner & Schaeffer, 1989; Schindler, 1993;

568   Mickle, 2017) reported in most Carboniferous deposits yielding actinopterygians. Poor

569   preservation of the type species (*E. germari* Giebel 1848) prevented a comprehensive

570   diagnosis, but numerous later studies referred material to the genus (Fig. 5a & b). As a result,

571   '*Elonichthys*' grew to encompass a vast number of poorly defined taxa that lack shared

572   characteristics (Long, 1988; Schindler, 1993, 2018). Though doubts about the genus were

573   noted as early as the 1890s (Woodward, 1891) it was not until recently that Schindler (2018)

574   restricted it to the type species plus *E. fritschi* Friedrich 1878 and *E. krejcii* Frič, 1895. A

575   detailed summary of the taxonomic problems associated with the genus is given in the

576   Supplementary Information.

577   '*Elonichthys*' encompasses a substantial portion actinopterygian biodiversity

578   extending from the Tournaisian through to the Anisian. The recent work of Schindler (2018)

579   is an essential first step to rectifying this. Identification of additional characters will be

580   necessary to adequately define species and determine whether they truly belong to

581   *Elonichthys*. CT scanning, particularly of cranial material, will help reveal more diagnostic

582   characters. Museum specimens collected and given labels in the 19th and 20th centuries will

583   require careful revision (e.g. '*E.*' *multistriatus* in NHM and NMS collections: S. Henderson

584   pers. obs.).

585   *(c)* Platysomus

586   The genus *Platysomus* includes 17 Palaeozoic species over a nearly 100 million time

587   period (Visean to Changhsingian) and broadly encompasses taxa with a deep-bodied

588   morphology (Fig. 5c & d). The monophyly of the genus (and higher taxonomic ranks such as

589   Platysomidae) has been questioned almost since its erection, and its relationships with other

590   deep-bodied actinopterygians such as amphicentrids and bobasatraniids is unclear. A detailed

591   overview is given in the Supplementary Information.

592   Despite poor preservation in the type species, unique characters do exist (e.g. the

593   combination of suborbitals and a dermal quadratojugal: Mickle and Bader, 2009: fig. 5b), and

594   CT-based investigations may clarify these features and identify new ones. Obvious violations

595   of the diagnoses, such as the presence of a pelvic fin in some species, should also be

596   addressed. A conservative approach may be to consider the type as the only valid species of

597   *Platysomus* and reassess all other species: Zidek (1992) suggested that all *Platysomus* species

598   should remain in the genus until revision. Poor understanding of the anatomy and taxonomy

599   of *Platysomus* species prevents their inclusion in phylogenetic analyses, with repercussions

600   for downstream analyses looking at evolutionary drivers of deep-bodied morphotypes.

601

602   *(d) Other problematic taxa*

603   While the three examples above account for a significant proportion of the taxonomic

604   uncertainty plaguing Palaeozoic actinopterygians, they are far from the only genera with

605   convoluted or questionable validity. For example, the genus *Rhadinichthys* (Fig. 5e) contains

606   24 species described from Belgium, Canada, Ireland, Poland, Russia, the UK, Uruguay and

607   the USA, and spanning the Frasnian to the early Permian, despite extremely variable

608   morphology. Similarly, 16 species belong to the genus *Amblypterus* from Czechia, France,

609   Germany, India, Russia and Spain, spanning the Kasimovian to Capitanian (Štamberg, 2013).

610   Another example that highlights the need for detailed reinvestigation is that of *Namaichthys*

611   *molyneuxi*. Woodward (1903) originally described this taxon under the genus name *Acrolepis*

612   *molyneuxi*, and Gardiner (1962) moved it to *Namaichthys*, a genus initially erected by Gürich

613   (1923). Specimens in the Natural History Museum (London) collection, however, bear the

614   label *Watsonichthys molyneuxi* (S. Henderson, personal observation).

615   In recent years, new anatomical information revealed by CT scanning has prompted

616   several reinvestigations of the validity of Palaeozoic taxa. Coates and Tietjen (2018) recently

617   redescribed a Bashkirian actinopterygian and moved it to *Trawdenia* n. gen. This specimen

618   was originally referred to *Mesopoma*, a taxon erected by Traquair (1890) in an attempt to

619   separate species belonging to *Canobius* and *Rhadinichthys*. Traquair subsequently retracted

620   the genus (Traquair, 1912), before Moy-Thomas and Dyne (1938) restored it (see Coates,

621   1993, 1998; Coates and Tietjen, 2018). *Trawdenia* exemplifies the root cause of the problem

622   with many Carboniferous and Permian actinopterygian genera: a diagnosis based on

623   characteristics prevalent in other late Palaeozoic actinopterygians and lacking unambiguous

624   synapomorphies.

625   Reinvestigation of Palaeozoic material is not simply an exercise in correcting

626   taxonomy, however. Coates (1999) and Coates and Tietjen's (2018) work revealed

627   previously-hidden features of the endocast and pectoral fin in a specimen that had been

628   known to the literature for over a century. The case of *Trawdenia*, as well as others such as

629   *Eurynotus crenatus* (Friedman *et al.*, 2018) and *Brazilichthys macrognathus* (Figueroa *et al.*,

630   2019), clearly demonstrate that reinvestigation can reveal untold anatomical, ecological, and

631   taxonomic diversity.

632   **(3) Phylogenetic issues**

633   Relationships of the four extant actinopterygian clades (Cladistia, Chondrostei,

634   Holostei, Teleostei) has reached a point of consensus through both molecular (e.g. Betancur-R

635   *et al.*, 2017; Hughes *et al.*, 2018) and morphological (e.g. Patterson, 1982; Gardiner and

636   Schaeffer, 1989; Coates, 1998; Cloutier and Arratia, 2004; Grande, 2010; Xu, Gao and

637   Finarelli, 2014; Giles *et al.*, 2017) research. Sallan (2014) provided a detailed summary of

638   previous hypotheses of living clades and the basis for this consensus. The relationships of

639   extinct forms of actinopterygians, both in relation to each other and the extant clades, however,

640   are less clear.

641   Phylogenetic hypotheses of Palaeozoic actinopterygians traditionally place the vast

642   majority of taxa within the crown, with only the Devonian taxon *Cheirolepis* consistently

643   resolved on the stem (e.g. Patterson, 1982; Gardiner, 1984; Gardiner and Schaeffer, 1989;

644   Coates, 1999). Even some of the earliest actinopterygians have been recovered as stem-

645   actinopterans (Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner *et al.*, 2005; Near *et al.*,

646   2012) or even stem-neopterygians (Hurley *et al.*, 2007), with most late Palaeozoic taxa

647   oscillating between the actinoperan and neopterygian stem. No Palaeozoic taxa are associated

648   with the polypterid or chondrostean total groups in these analyses, with the exception of the

649   late Palaeozoic-Mesozoic genus *Saurichthys* as a stem chondrostean (Gardiner *et al.*, 2005;

650   Sallan, 2014), although recent analyses refute this topology (Giles *et al.*, 2017; Latimer &

651   Giles, 2018; Argyriou *et al.*, 2018). The crown-group affinity of most Palaeozoic

652   actinopterygians was challenged by both Zhu and Schultze (2001) and Cloutier and Arratia

653   (2004), who recovered a number of taxa as branching outside of the living radiation, although

654   neither of these studies focussed on actinopterygians. Mickle, Lund and Grogan (2009) recover

655   a host of Palaeozoic taxa on the actinopterygian stem, as well as identifying stem cladistians,

656   but their analysis has a series of issues relating to taxon inclusion and character coding, as well

657   as a sub-optimal tree construction methodology (Sallan, 2014).

658   In 2017, an analysis stemming from a greatly expanded morphological character

659   matrix alongside nuclear genes posited a major upheaval of early actinopterygian

660   relationships (Giles *et al.*, 2017). Crucially, this study recognised that Triassic scanilepiforms

661   are well-supported as stem cladistians, and that the apparently primitive morphology of

662   extant cladistians is the result of several reversals and autapomorphies. A major consequence

663   of this discovery was that most Palaeozoic taxa were removed from the actinopterygian

664 crown (Fig. 6). The analysis also brought molecular estimates of clade origins more in line

665 with fossil evidence by excluding calibration points for poorly-supported nodes. Finer-scale

666 relationships amongst Palaeozoic actinopterygians remain in a state of flux, however. For

667 example, all post-Devonian taxa form a clade in (Giles *et al.*, 2017), and many Devonian

668 species form a monophyletic group. This Devonian clade is replicated by Argyriou *et al.*

669 (2018) and Figueroa, Friedman and Gallo (2019) but not by Latimer and Giles (2018) or

670 Wilson, Pardo and Anderson (2018). Wilson, Pardo and Anderson (2018) additionally

671 recover more than one radiation of post-Devonian actinopterygians. This variation is despite

672 all analyses using matrices derived from that of Giles *et al.* (2017). Relationships amongst

673 Carboniferous and Permian (and younger) stem actinopterygians are extremely volatile across

674 all analyses, with few substantiated or well-supported clades.

675   A further peculiar result is the recurrent placement of chondrosteans and cladistians as

676 sister-clades (Latimer & Giles, 2018; Argyriou *et al.*, 2018), clearly at odds with the

677 molecular and morphological consensus. These may be a result of failure to identify

678 Palaeozoic members of these radiations: huge temporal gaps exist between the fossil record

679 of definitive crown group members and the supposed origination of the clade (Sallan, 2014;

680 Friedman, 2015, fig. 3). As with the tetrapod fossil record (Pardo, Lennie, & Anderson,

681 2020), many Palaeozoic actinopterygians are morphologically distinct from even early

682 members of extant radiations, partly as a result of living groups' substantial diversification

683 (Sallan, 2014). There may be a genuine lack of early fossil members of major clades; the

684 paucity of marine late Palaeozoic deposits could be a contributing factor given the marine

685 origin of most crown groups of actinopterygians in this period (Betancur-R, Ortí, & Pyron,

686 2015). However, it is more likely that many Palaeozoic actinopterygians simply have not

687 been investigated in enough detail to determine whether they could be early members of

688 living radiations, as was the case for the early Mesozoic *Fukangichthys* (Giles *et al.*, 2017).

689   A number of factors contribute to this phylogenetic instability, not least of which is

690   choice of character matrix and taxon sampling. Absence of data in the form of missing

691   morphological codes in character-by-taxon matrices is partly responsible, as is the use of

692   composite taxa, especially for genera of dubious monophyly. However, failure to include many

693   of the Palaeozoic taxa described in the literature, as well as oversight of the many specimens

694   in museum collections, is perhaps the most significant factor. Most analyses focused on broad-

695   scale investigations of early actinopterygians contain roughly even numbers of Devonian and

696   Carboniferous taxa (Coates, 1999; Gardiner *et al.*, 2005; Giles *et al.*, 2017), despite there being

697   an order of magnitude more species described from the Carboniferous (Fig. 6). Potentially even

698   more problematic is the fact that these studies never sample more than a few Permian species,

699   despite the nearly equivalent numbers of Permian species relative to the Carboniferous (Fig.

700   6). Work remedying this is already underway using techniques such as CT-scanning (Giles *et*

701   *al.*, 2015; Pradel *et al.*, 2016; Coates & Tietjen, 2018; Friedman *et al.*, 2018; Figueroa *et al.*,

702   2019, 2021) and more traditional descriptive work (Choo, 2015; Štamberg, 2016; Mickle, 2017,

703   2018; Stack *et al.*, 2020). In particular, CT-scanning will be critical in revealing internal

704   anatomical details and increasing the number of phylogenetically informative characters

705   beyond the dermal bones, which are often very similar among Palaeozoic actinopterygians

706   (Figueroa *et al.*, 2019). Beyond this, however, numerous proposed Palaeozoic actinopterygian

707   clades are yet to be included in broader phylogenetic analyses despite either high support in

708   the literature (e.g. eurynotiforms: Sallan and Coates, 2013; Friedman *et al.*, 2018) or in-group

709   cladistic analysis (e.g. haplolepids: Elliott, 2014). In addition, important clades are often only

710   represented by a single terminal (e.g. platysomids: Giles *et al.*, 2017)). Including unrepresented

711   groups of Palaeozoic actinopterygians in phylogenetic analyses is a critical step for furthering

712   our understanding of their evolution and relies on detailed morphological descriptions.

713   At present, understanding of the relationships of early actinopterygians is extremely

714   limited. This represents a critical barrier to progressing our understanding of the evolution of

715   the Actinopterygii in their early evolutionary history, and precludes asking questions about

716   what is driving phenomena such as the emergence of novel body forms, origins of clades, and

717   responses to mass extinctions.

718

719   **(4) Fossil record biases**

720   A major obstacle to accurately interpreting the evolution of Palaeozoic actinopterygians

721   is the various forms of sampling bias that pervade their fossil record, which are related to both

722   geological, geographic and anthropogenic factors. The number of occupied grid cells has been

723   suggested as the best proxy for explaining the richness of all fishes in the fossil record of Great

724   Britain, though osteichthyan richness does not correlate with any proxy (Lloyd & Friedman,

725   2013). Investigations into the effect of geological, spatial and taphonomic biases on the

726   actinopterygian fossil record are in their infancy, and the extent to which observed patterns of

727   diversity are driven by biases is far from understood. Here we attempt a qualitative overview

728   of some of the major sampling biases affecting the Palaeozoic actinopterygian fossil record.

729   *(a) Geological biases*

730   The extent to which observed patterns of diversity are the result of rock record biases

731   and correlate with metrics such as the numbers of formations, rock volume or outcrop area is

732   the subject of much debate (Benton, 2015). There are three main hypothesised mechanisms

733   for correlation: 1) a true bias, where diversity patterns are truly dependent on the rock record

734   (Smith, 2001; Peters & Foote, 2001); 2) common cause, where another factor such as sea

735   level (and associated extent of shallow marine sea area and presence of epicontinental seas)

736   drives correlations between the rock and fossil records (Peters, 2005, 2006; Peters & Heim,

2010, 2011; Hannisdal & Peters, 2011); and 3) redundancy, where the effects of sampling on the fossil record and vice versa are redundant (Benton *et al.*, 2011, 2013). Lloyd and Friedman (2013) reject the common cause hypothesis for Great British fishes, but the mechanisms acting on the actinopterygian fossil record remain uncertain. The global actinopterygian fossil record includes both marine and freshwater components, which may be subject to different drivers, and represents an interesting test of the relative effects of these hypotheses.

Previous studies posit that changes in richness of the fossil fish record through time likely represent changes in sampling (Friedman & Sallan, 2012). A common suggestion in the literature is that the late Palaeozoic record is poorly sampled, particularly in terms of marine deposits, and that this leads to low levels of diversity (Hurley *et al.*, 2007; Near *et al.*, 2012; Broughton *et al.*, 2013). Freshwater occurrences of actinopterygians dominate much of the Permian (Romano *et al.*, 2016; Smithwick & Stubbs, 2018) and some of this skew away from marine deposits may have been linked to the formation of Pangaea and coincident reductions in coastline (Friedman & Sallan, 2012). At broad scales, the marine animal record is linked to the extent of shallow-marine sediment (Hannisdal & Peters, 2011; Smith & Benson, 2013; Close *et al.*, 2020b), although there is no significant correlation between the terrestrial tetrapod record and the non-marine rock record (Close *et al.*, 2020a). Given that actinopterygians occur across the salinity gradient in both marine and freshwater settings, it may be that different drivers are acting on different components of the actinopterygian fossil record. However, Lloyd and Friedman (2013) found no correlation between richness and geological or sampling proxies in the British fish fossil record, despite numerous palaeodiversity studies identifying strong correlations in other, though largely terrestrial, groups (e.g. Benson *et al.*, 2013, 2016; Butler, Benson and Barrett, 2013; Close *et al.*, 2017).

761   Determining the extent to which geological biases such as these drive the actinopterygian

762   record needs comprehensive occurrence-based datasets (Friedman & Sallan, 2012).

763

764   *(b) Geographic and spatial biases*

765   Europe and North America are the most intensely sampled regions in the marine

766   animal fossil record as a whole (Close *et al.*, 2020b). The vast majority of Palaeozoic

767   actinopterygian occurrences are also from Europe and North America, with important, though

768   limited, occurrences from South America, Australia and Africa: this distribution is likely due

769   to sampling intensity rather than true diversity. These biases hark back to the early

770   descriptions of actinopterygians (particularly from the UK), which are intimately linked to

771   extensive mining, extraction and industrialisation of these regions during the 19th and early

772   20th centuries (e.g. Agassiz, 1833; King, 1850; Jackson, 1851b). More broadly, recent work

773   demonstrates just how important (neo-)colonialism and European exploitation is as a

774   contributing factor to the global skew in palaeontological research outputs and therefore

775   occurrence data (Raja *et al.*, 2021).

776   For much of the Palaeozoic, what is now Europe and North America were part of the

777   same supercontinent, centred around the palaeoequator (Ziegler *et al.*, 1979; Scotese, 2001,

778   2014), which gradually drifted north and became part of Pangaea (Stampfli *et al.*, 2013). The

779   palaeolatitudinal occurrences of Palaeozoic-Mesozoic actinopterygians present in the PBDB

780   track the migration of these continents from low- to mid-palaeolatitudes (Fig. 7). Geographic

781   bias in the actinopterygian fossil record is clear from fossil occurrence data, with higher

782   sampling of low-palaeolatitudes in the Palaeozoic shifting to mid-palaeolatitudes in the

783   Mesozoic, as in the marine record (Close *et al.*, 2020b). Variation in taxonomic practice can

784   also impact richness counts depending on the number of researchers working on certain

785   groups and time periods, and whether these researchers are the same for all time periods

786   (Lloyd, Young, & Smith, 2012b, 2012c). This variation may contribute to higher diversity in

787   Europe relative to other continental regions (Close *et al.*, 2020b), though higher diversity is

788   also likely intimately linked to historical and ongoing scientific colonialism (Raja *et al.*,

789   2021).

790   Spatial biases also have a substantial impact on diversity trends at global scales due to

791   temporal variability in the fossil content, fossil quantity, and palaeogeographical coverage of

792   assemblages. The 'global' fossil record of any group in fact consists of occurrences

793   distributed heterogeneously in space and time (Benson *et al.*, 2016; Close *et al.*, 2017, 2020a,

794   2020b), and is better conceptualised as the sum of multiple regional records with different

795   attributes (Close *et al.*, 2020a). Diversity curves representing 'global' counts of taxa are

796   therefore not a true representation of the peaks and troughs in diversity of a group through

797   time, but instead a combined record of the regional diversity in sampled areas. The effect of

798   this is such that changes in diversity through time mainly mirror changes in the spatial extent

799   of the groups' fossil record between sampled intervals (Close *et al.*, 2020a, 2020b). Notably,

800   the 'common cause' (Peters, 2005, 2006; Peters & Heim, 2010, 2011; Hannisdal & Peters,

801   2011) and 'redundancy' (Benton *et al.*, 2011, 2013; Dunhill, Hannisdal, & Benton, 2014;

802   Benton, 2015) hypotheses do not explain this substantial source of sampling bias (Benson *et*

803   *al.*, 2016; Close *et al.*, 2017, 2018, 2019, 2020a). This is not to say that studies of the 'global'

804   fossil record of specific taxonomic groups are uninformative, only that patterns must be

805   carefully examined and interpreted with the knowledge that they likely exhibit significant

806   spatial structuring. Diversity at the regional scale will be informative in determining specific

807   drivers of, and biases in, the diversity signal (Crampton *et al.*, 2003; Dunhill *et al.*, 2012,

808   2013, 2014; Close *et al.*, 2020a), as will examining differences between diversity measures

809   (e.g. alpha and beta diversity), which can also be spatially dependent (Womack, Crampton, &

810   Hannah, 2021). Different spatial biases acting on the freshwater and marine records may also

811   variably impact different diversity estimates, dependent on the attributes of the sampled

812   regions (Lagomarcino & Miller, 2012). For example, the species-area effect (Hallam &

813   Wignall, 1999; Peters, 2005, 2007; Hannisdal & Peters, 2011; Close *et al.*, 2020b) may play a

814   role in levels of marine actinopterygian biodiversity, linked to changes in sea level and

815   associated features (Lagomarcino & Miller, 2012; Jones *et al.*, 2021)), whereas other factors

816   may drive freshwater actinopterygian diversity. Discrepancies in dispersal between

817   freshwater and marine actinopterygians are also likely to have an impact. These potential

818   contributing factors result in potentially complex drivers of regional heterogeneity in the

819   actinopterygian fossil record.

820

821   *(c) Taphonomic biases*

822   The impact of taphonomic processes and biases on the Palaeozoic actinopterygian fossil

823   record has not been investigated. Taphonomic biases not only obscure underlying biological

824   signals and impact perceived diversity, but likely influence understanding of other aspects of

825   actinopterygian evolution, such as the degree of functional disparity or ecospace occupation

826   (Smithwick & Stubbs, 2018). The effects of detrimental taphonomic processes varies

827   geographically, between environments and with time (Brett, 1995; Zohar *et al.*, 2008; Walker,

828   Dunhill, & Benton, 2020), though low-energy, anoxic environments in which individuals were

829   rapidly buried are usually those that best preserve vertebrates, i.e., Lagerstätten (Pardo *et al.*,

830   2020).

831   In recent years, literature has emerged on quantifying the skeletal completeness of the

832   fossil record of various vertebrate groups using both character-completeness metrics (e.g.

833   Mannion and Upchurch, 2010; Brocklehurst and Fröbisch, 2014; Cashmore *et al.*, 2020) and

834   specimen-based completeness metrics (e.g. Cleary *et al.*, 2015; Tutin and Butler, 2017; Driscoll

835   *et al.*, 2019). To date, there are no published studies investigating completeness in any groups

836   of fishes (but see Schnetz et al. [2021]), and it is likely that an anthropogenic collecting bias

837   towards more complete specimens may come into play more than in tetrapod groups. The fossil

838   record of marine tetrapod clades appear to be more complete than those of terrestrial tetrapods

839   (Cleary *et al.*, 2015; Tutin & Butler, 2017; Driscoll *et al.*, 2019), likely due to higher

840   sedimentation rates in the marine realm. Quantification of the level of skeletal completeness in

841   actinopterygians will aid interpretations of the biases acting on the fossil record, especially

842   regarding marine versus freshwater fishes.

843   An additional taphonomic factor that may detrimentally impact our understanding of

844   the actinopterygian fossil record is degree of preservation related to the size of specimens.

845   There is data to suggest that larger organisms are much more likely to preserve than smaller

846   organisms (Benson, 2018; Pardo *et al.*, 2020). The extent to which this applies to aquatic

847   vertebrates is little understood, but this is likely to be of importance to actinopterygians:

848   Sallan and Galimberti (2015) suggested that ray-finned fish were small in the aftermath of the

849   EDME. As the early Carboniferous coincides with the origin of the actinopterygian crown

850   (Giles *et al.*, 2017), and small ancestors are thought to have seeded most actinopterygian

851   clades (Romano *et al.*, 2016, Guinot and Cavin, 2018), a bias against preservation of smaller

852   organisms may contribute to the failure to identify early members of these radiations. The

853   environment of deposition is also relevant: hypothesised ancestors of most actinopterygian

854   clades existed in marine environments (Betancur-R *et al.*, 2015), which typically have higher

855   energy and disturbance levels that may bias against preservation of small actinopterygians

856   (Cooper *et al.*, 2006). Furthermore, taphonomic factors have been shown to readily destroy

857   small actinopterygian bones in particular (Smith, Stearley, & Badgley, 1988) further

858   compounding our ability to correctly interpret the early actinopterygian fossil record.

(d) Future mitigation

860   The sampling, spatial and taphonomic biases on the Palaeozoic global actinopterygian

861 record are only beginning to be explored. Future, targeted sampling in underrepresented

862 regions and environments, for example mid- to high-palaeolatitudes in the Carboniferous and

863 marine environments in the Late Carboniferous-Middle Permian, may help to redress this

864 imbalance. However, sampling biases cannot necessarily be 'fixed', and instead we should

865 attempt to mitigate these biases using analytical techniques. Understanding these biases, and

866 the interplay between them, is critical due to the potential impact that they can have on

867 taxonomy, phylogeny, and subsequent attempts to investigate the evolution of a particular

868 group such as actinopterygians.

869

870 **VI. PROSPECTS FOR PALAEOZOIC ACTINOPTERYGIAN DIVERSITY STUDIES**

871   Occurrence-based datasets are necessary for examining biases in the fossil record and

872 deducing accurate diversity trends, while phylogenetic context is generally crucial for the

873 kinds of macroevolutionary analyses that are increasingly common in the palaeontological

874 literature. Fishes are rarely the subject of such analyses, but present ample opportunities.

875 Occurrence datasets will enable sampling standardisation methods and robust phylogenetic

876 hypotheses will facilitate a broad range of techniques. In conjunction, these methods may

877 generate new hypotheses about the early evolution and diversification of actinopterygians.

878 **(1) Sampling standardisation**

879   Analytical methods of sampling standardisation (Chao, 1984, p. 198; Chao & Jost,

880 2012; Alroy, 2017, 2018, 2020), which estimate species diversity based on incomplete and

881 uneven data are invaluable when attempting to deduce real patterns of palaeodiversity from

882 the biases acting on the fossil record (Alroy, 2010; Close *et al.*, 2018). Since their

883   introduction, these methods and their application continue to be refined, moving beyond

884   temporal standardisation to spatial standardisation (Close *et al.*, 2020a; Jones *et al.*, 2021)

885   and application at different scales (Close *et al.*, 2019). Application of these methods to the

886   Palaeozoic actinopterygian fossil record could help to tease apart genuine diversity patterns

887   from the trends created by fossil record biases. However, these methods require occurrence-

888   level datasets that are not currently available for Palaeozoic actinopterygians and compiling

889   these data represents a priority for future studies.

890   **(2) Phylogenetic inference**

891   Macroevolutionary studies on early actinopterygians are in their infancy, in large part

892   due to the absence of robust phylogenetic hypotheses. Despite major reworking of

893   actinopterygian characters, stability is still low for most Palaeozoic taxa (Giles *et al.*, 2017).

894   Although the stem-group affinity of most Palaeozoic actinopterygians in recent,

895   comprehensive phylogenetic analyses (Giles *et al.*, 2017; Latimer & Giles, 2018; Argyriou *et*

896   *al.*, 2018; Figueroa *et al.*, 2019) was foreshadowed by some previous studies (Cloutier &

897   Arratia, 2004; Mickle *et al.*, 2009), these had issues with character selection, coding and

898   reversals, as well as intensely sampling the earliest actinopterygians relative to crown

899   members (Sallan, 2014). This likely exacerbates differences in character polarities and

900   precludes identification of synapomorphies (Sallan, 2014). Giles *et al.* (2017) laid the

901   foundation for an improved actinopterygian character-by-taxon matrix. Continued addition of

902   important taxa and well-formulated characters (Brazeau, 2011), as well as better methods for

903   dealing with inapplicable characters (Brazeau, Guillerme, & Smith, 2019; Goloboff *et al.*,

904   2021), will generate robust hypotheses of relationships with which to investigate key

905   evolutionary events.

906   Bayesian methods of inference, such as tip-dating, which incorporates information

907   about age into phylogenetic estimates to work out node ages and topology simultaneously,

908   have rarely been applied to actinopterygians outside of nested teleost groups (e.g. Alexandrou

909   *et al.*, 2013; Near, Dornburg and Friedman, 2014; Arcila *et al.*, 2015; Dornburg *et al.*, 2015;

910   Dornburg, Friedman and Near, 2015; Close *et al.*, 2016; Arcila and Tyler, 2017)). Tip-dating

911   methods may be able to tease apart relationships suspected to result from homoplasy (Lee &

912   Yates, 2018), for example the various deep-bodied clades of Palaeozoic actinopterygians. At

913   present, however, the temporal gaps between actinopterygian taxa in palaeontological

914   phylogenetic datasets are too great, and phylogenetic hypotheses too unstable, for tip-dating

915   to return valid hypotheses. Morphological character sets for actinopterygians also generally

916   ignore autapomorphies, which can be important for tip-dating analyses (Matzke & Irmis,

917   2018). Accuracy of tip-dating improves when more tips for calibrations are near the root

918   (Püschel *et al.*, 2020); for example, tip-dating analyses initially recovered unrealistically old

919   node ages for tetraodontiformes due to inadequate numbers of fossil taxa (Arcila *et al.*, 2015),

920   later rectified by addition of more fossil data and use of a fossilised-birth-death model (Close

921   *et al.*, 2016; Arcila & Tyler, 2017). Phylogenetic datasets therefore require inclusion of more

922   Palaeozoic actinopterygians to populate the tree and fill large temporal gaps currently only

923   inhabited by a few representative taxa before exploring inference-based and other techniques.

924   **(3) Phylogenetic comparative methods**

925   Phylogenetic comparative methods (PCMs) are a suite of methods that explicitly use

926   hypotheses of relationships when investigating macroevolutionary processes (Harmon, 2019;

927   Soul & Wright, 2021). PCMs include node-age calibrations and divergence-dating (Hedman,

928   2010; Bapst, 2014; Warnock & Wright, 2021) often as a means of calculating rates of

929   morphological evolution (Lloyd, Wang, & Brusatte, 2012a; Benson *et al.*, 2014; Wang &

930   Lloyd, 2016; Halliday, Upchurch, & Goswami, 2016; Clarke, Lloyd, & Friedman, 2016) and

931 assessing morphological disparity (Brusatte *et al.*, 2014; Lloyd, 2016; Wright, 2017; Moon &

932 Stubbs, 2020). Phylogenetic signal also plays a role in analyses of evolutionary rates

933 (Sakamoto & Venditti, 2018) and the links between morphology and ecology (Lamsdell *et*

934 *al.*, 2017).

935 PCMs offer huge potential for understanding patterns of diversity and evolution but

936 are generally yet to be applied to Palaeozoic actinopterygians. Deep-bodied actinopterygians

937 represent an obvious test case for exploring these techniques, for example by quantifying

938 convergence (Speed & Arbuckle, 2017; Arbour & Zanno, 2020), as results will be highly

939 dependent on whether they are truly independent radiations or whether there is a degree of

940 shared evolutionary history between them. Application of PCMs also has the potential to

941 identify adaptive radiations (Close *et al.*, 2015; Ezcurra & Butler, 2018; Felice & Goswami,

942 2018; Halliday *et al.*, 2019; Simões *et al.*, 2020). Previous work on neopterygians

943 investigated phenotypic evolution in holosteans and teleosts, finding that their evolutionary

944 rates and innovation were comparable through the Early Permian to Early Cretaceous (Clarke

945 *et al.*, 2016). Actinopterygians appear to diversify appreciably in the early Carboniferous.

946 However, the lack of comprehensive phylogenetic analysis prevents testing of whether this

947 pattern best fits a model of classic extinction recovery, adaptive radiation, or ecological

948 release (Schluter, 2000; Sallan & Friedman, 2012; Friedman & Sallan, 2012; Slater, 2013).

949 Other PCMs permit reconstructing ancestral states of characters (Finarelli & Flynn,

950 2006; Puttick, 2016; Sallan *et al.*, 2018; Herbst, Li, & Steel, 2019; Ponti, Arcones, & Vieites,

951 2020), correlating evolution of separate traits (Soul & Wright, 2021), identifying regime

952 shifts (Lamsdell & Selden, 2017; Soul & Wright, 2021), and assessing stratigraphic

953 congruence (Bell & Lloyd, 2015). A pertinent example is that of shifts between marine and

954 non-marine habitats (and coincident changes in morphology and disparity; Lamsdell, 2016).

955 Previous ancestral-state based hypotheses of crown group habitats have inferred both a

956   freshwater (Carrete Vega and Wiens, 2012; Betancur-R, Ortí and Pyron, 2015) and marine

957   (Guinot & Cavin, 2018) origin for actinopterygians. Given recent upheavals in established

958   schemes of phylogenetic relationships, with a particular effect on deep-branching members of

959   stem-groups (e.g. Giles *et al.*, 2017), ancestral state reconstructions should be reassessed. As

960   it may be physiologically easier to adapt from one environment to another (Betancur-R *et al.*,

961   2015), it may be prudent to explore the use of asymmetric transition models as recently used

962   to investigate the evolution of oviparity and viviparity in squamates (Blackburn, 2015).

963   More broadly, by combining palaeoecological observations with reliable phylogenetic

964   hypotheses, it will be possible to examine trends in actinopterygian ecology and

965   biogeography through time (Lamsdell *et al.*, 2017). It is unclear whether Palaeozoic

966   actinopterygians separate into biogeographical provinces and how biogeography changes

967   through time, particularly in response to mass extinctions and changing continental

968   configurations. Phylogeny is an important component in biogeographic network analyses

969   investigating these patterns (Button *et al.*, 2017; Dunne *et al.*, 2018; Kubo, 2019). Phylogeny

970   would also allow for alternative estimates of diversity such as lineage counts through time

971   (also referred to as phylogenetic diversity; Ezcurra and Butler, 2018), that would complement

972   taxic estimates of diversity patterns. Phylogenetic methods investigating survivorship and

973   selectivity through mass extinctions among and between lineages (Soul & Friedman, 2017;

974   Allen *et al.*, 2019) may reveal more detail on the effects of mass extinctions (Sallan &

975   Friedman, 2012; Sallan & Galimberti, 2015)). To understand the origins of actinopterygian

976   biodiversity and dominance, and quantify such patterns of evolution in the Palaeozoic, it is

977   necessary to improve phylogenetic hypotheses.

978

979

VII. CONCLUSIONS

(1) An understanding of both phylogenetic relationships and changes in diversity through time are critical to answering questions about the origin, rise and evolution of the Actinopterygii. However, relatively little consideration has been given to the factors that prevent an accurate picture of actinopterygian diversity through time. Existing research on actinopterygians exhibits a number of biases, paritcularly towards descriptions of European and North American taxa. Recently, however, global collector's curves show rapid increases in the rate of descriptions from other global regions, indicating unappreciated diversity in the Palaeozoic actinopterygian fossil record.

(2) The number of macroevolutionary studies on Palaeozoic fishes has not kept pace with those of other groups. Existing studies collectively point towards genuinely low diversity and disparity in the Devonian, with consistent increases in the earliest Carboniferous continuing through to the Visean. There is disagreement on Serpukhovian patterns, however, and a lack of analyses covering the Pennsylvanian render the overall Carboniferous trend unclear. Family and genus counts show consistent trends in raw counts for the Permian. To date no study has investigated the entirety of the Palaeozoic using an occurrence-based dataset, perhaps due to major gaps and inaccuracies in currently available occurrence datasets for Palaeozoic actinopterygians.

(3) Considerable, ingrained taxonomic issues plague the known Palaeozoic actinopterygian fossil record and likely obscure patterns of diversity. Efforts are already underway to address these issues, though much more work is necessary to correct the taxonomy, recognise hidden diversity and appreciate true morphological disparity in these fishes. Redescriptions will not only correct taxonomy and add to diversity counts, but also generate new morphological data for use in phylogenetic analyses.

1004 (4) There is now phylogenetic consensus about the relationships between living groups of

1005 actinopterygians, and recent upheavals have established that most Palaeozoic taxa are stem-

1006 actinopterygians. However, major temporal gaps exist between the origin age of crown

1007 groups as calculated by divergence estimates and the oldest known fossils. Inadequate

1008 representation of Carboniferous and Permian forms in phylogenies feeds into this problem.

1009 Greater sampling of Carboniferous and Permian taxa in morphological matrices is necessary

1010 to identify early crown members and accurate relationships between stem- and crown-groups.

1011 (5) Significant spatial and taphonomic biases act on the Palaeozoic actinopterygian record. It

1012 is clear that Europe and North America are the most intensely sampled regions (as in the

1013 overall vertebrate fossil record), yet the impact of all biases acting on the Palaeozoic

1014 actinopterygian record is yet to be investigated fully.

1015 (6) Future work should focus on understanding and addressing issues and biases in the

1016 actinopterygian fossil record. For example, redescription and revision of taxonomy will help

1017 address taxonomic issues, studies of skeletal completeness may help assessment of

1018 taphonomic biases, and sampling standardisation of occurrence data will be valuable in

1019 deducing genuine diversity patterns. In parallel, construction of more stable phylogenies

1020 using new morphological data from renewed descriptive work will enable investigation of

1021 more complex, specific questions on extinction recovery and adaptive radiation,

1022 morphological convergence, and biogeography and habitat transitions. Collectively, these

1023 will greatly expand our understanding of the early evolution and rise to dominance of the

1024 most speciose extant vertebrate clade, the Actinopterygii.

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1751

X. SUPPORTING INFORMATION

1753   Additional supporting information may be found online in the Supporting Information

1754 section at the end of the article. **AppendixS1**. Detailed account of the state of research on the

1755 problematic Palaeozoic actinopterygian genera *Palaeoniscus*, *Elonichthys* and *Platysomus*.

Figure 1 – Diversity of Palaeozoic fishes through time presented in previous studies. A) family-level diversity curves of actinopterygians and non-actinopterygian osteichthyans (Patterson, 1994; using data from Benson [1993]); B) family-level diversity curves of actinopterygians and non-actinopterygian fishes (Blieck, 2011; using data from Benson [1993]); C) genus-level diversity of marine osteichthyans and non-osteichthyan fishes, excluding conodonts (Friedman and Sallan, 2012; using data from Sepkoski [2002]); D) genus-level diversity of British osteichthyans and non-osteichthyan fishes (Lloyd and Friedman, 2013); E) genus-level diversity of actinopterygians and non-actinopterygian fishes (Thomson, 1977; using data from Romer [1996]); F) genus-level diversity of actinopterygians and non-actinopterygian fishes (Sallan and Coates, 2010; Romano *et al.*, 2016).

Figure 2 – Collector's curve of the global (grey) and British (black) Palaeozoic actinopterygian fossil records.

Figure 3 – Number of publications mentioning terms typically associated with Palaeozoic actinopterygians through time: 'palaeoniscid' (magenta); 'palaeonisciformes' (pink); 'palaeoniscoid' (light green); 'palaeopterygian' (dark green).
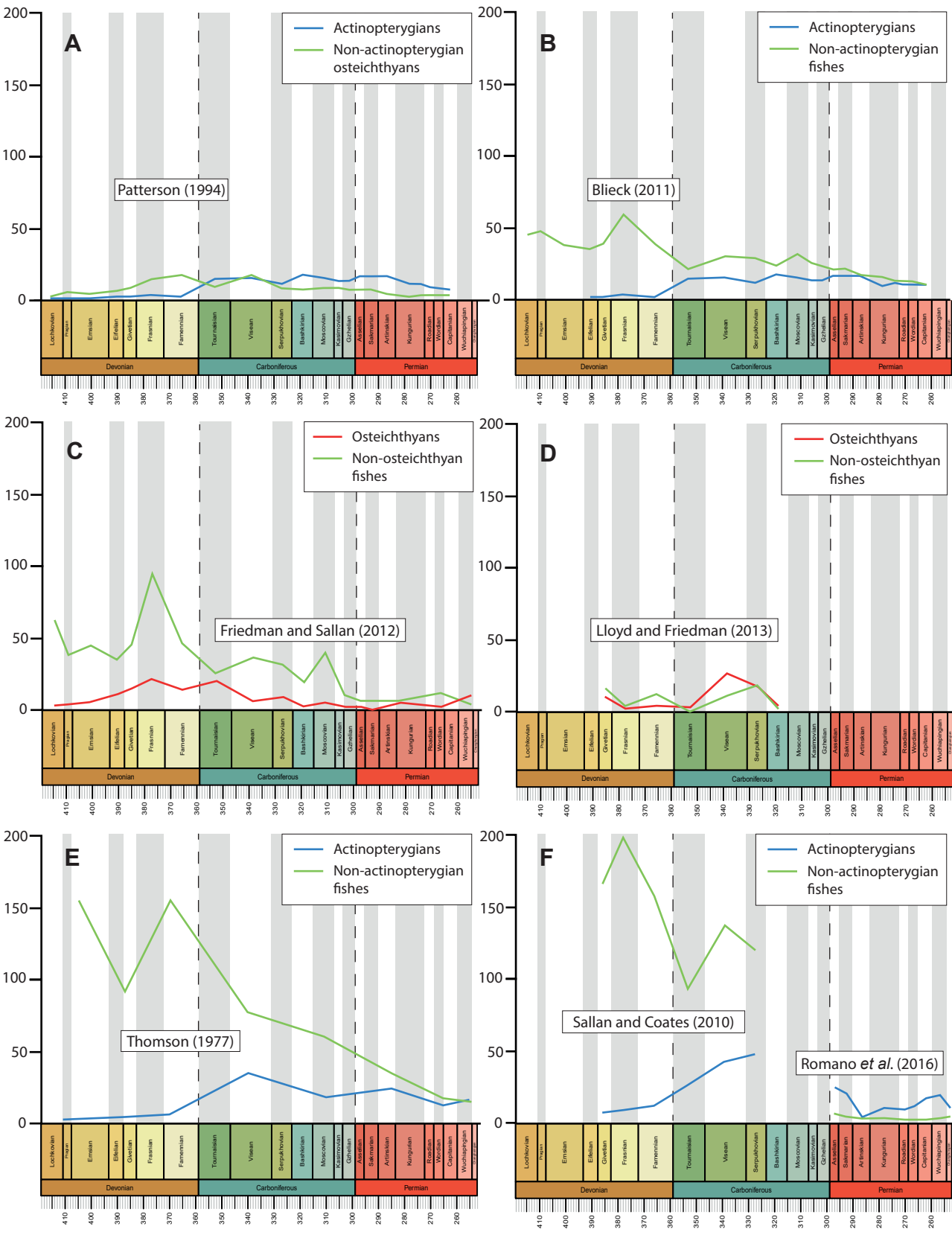
Figure 4 – Raw counts of Palaeozoic and Mesozoic actinopterygian genera (black, solid line), collections (brown, short dashed line), formations (red, dotted line) and equal-area grid cells (orange, long dashed line) entered in the PBDB.
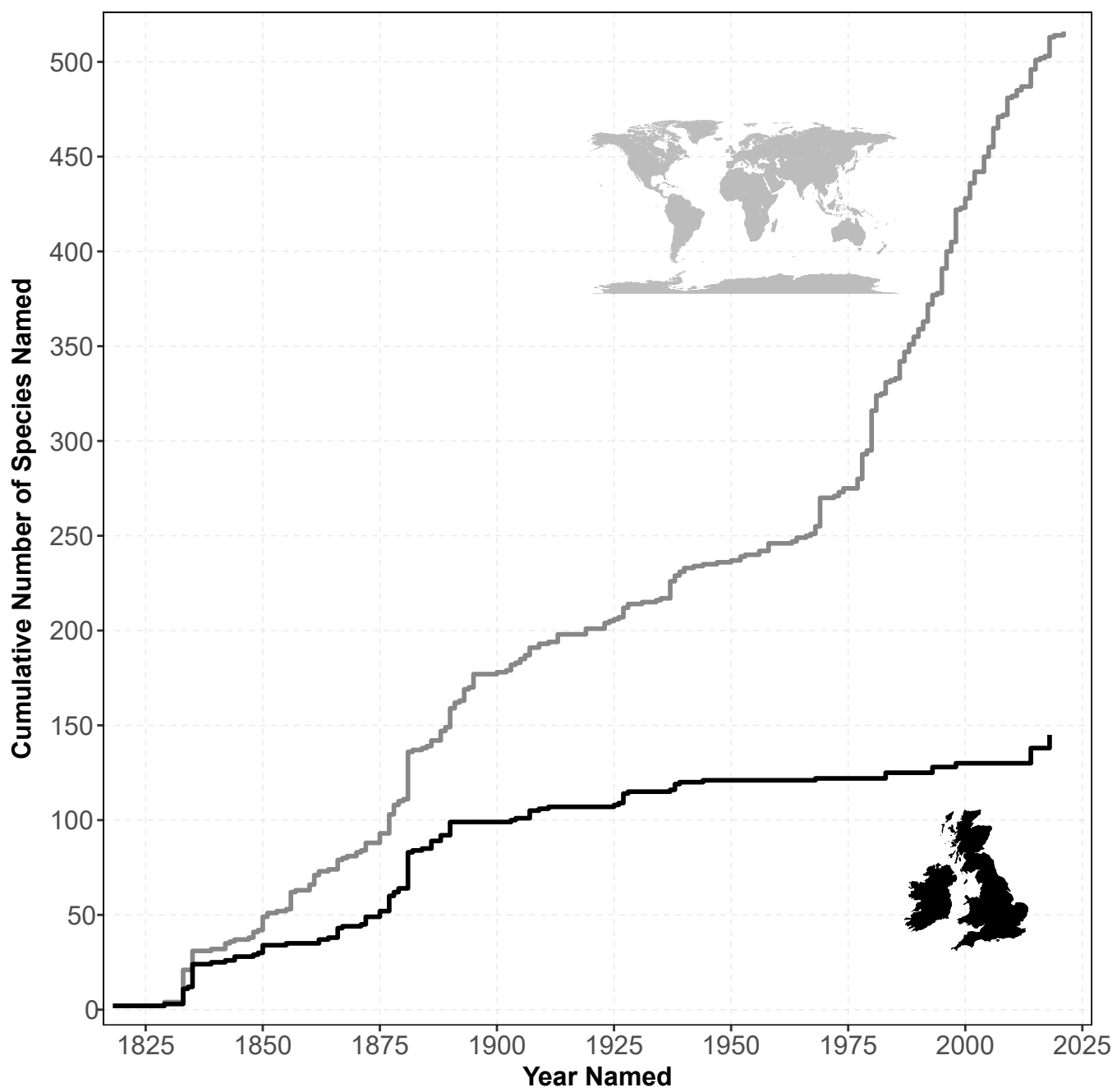
Figure 5 – Representatives of problematic Carboniferous actinopterygian taxa. Scale bars = 20 mm. A) '*Elonichthys' aitkeni* NHMUK PV P.36247; B) '*Elonichthys' egertoni* NHMUK PV P.7938; C) *Platysomus parvulus* NMS.G.1894.73.456; D) *Platysomus forsteri* NHMUK PV OR37322; E) *Rhadinichthys ornatissimus* NHM UK PV P.60940a.
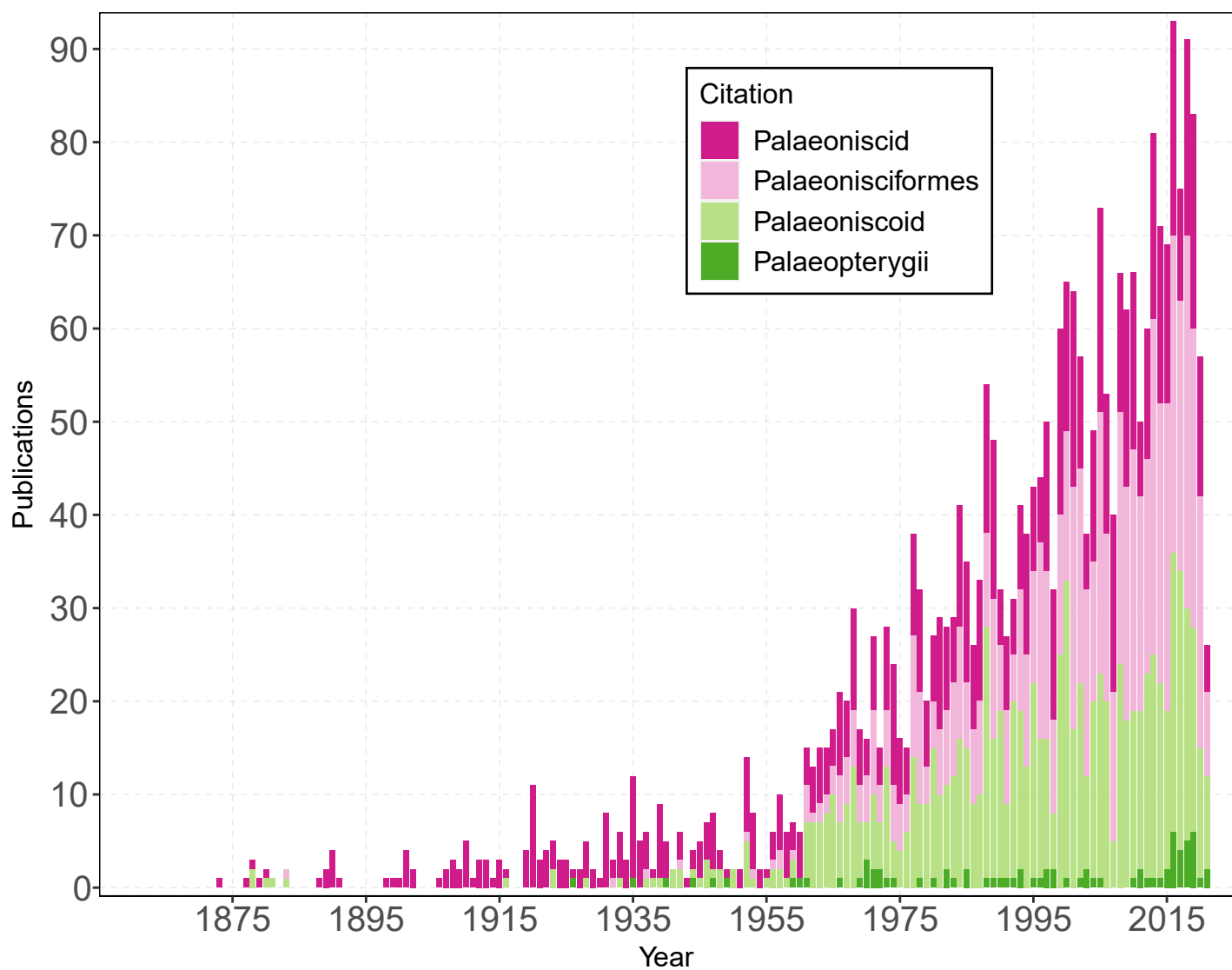
Figure 6 – A recent phylogenetic hypotheses of the interrelationships of Palaeozoic actinopterygians (redrawn from Giles *et al.* 2017) with stratigraphic ranges shown. Tips are colour coded according to geological time period. Grey lines and taxon names represent non-actinopterygian taxa. Extant clades collapsed.

Figure 7 – Alpha richness of Palaeozoic and Mesozoic actinopterygians at localities entered into the PBDB, plotted at their palaeocoordinate occurrences through geological time.
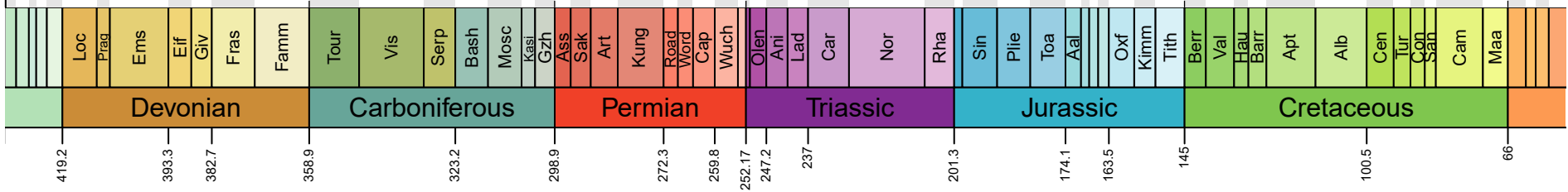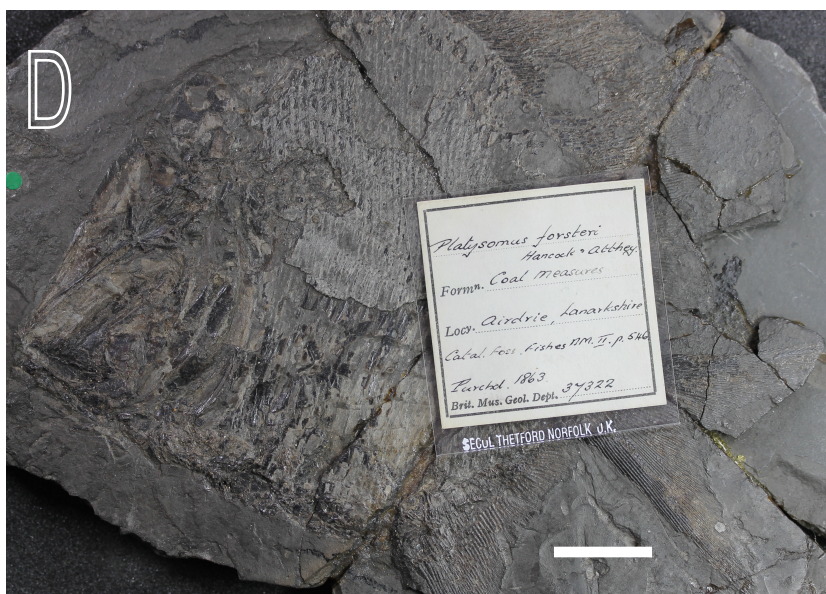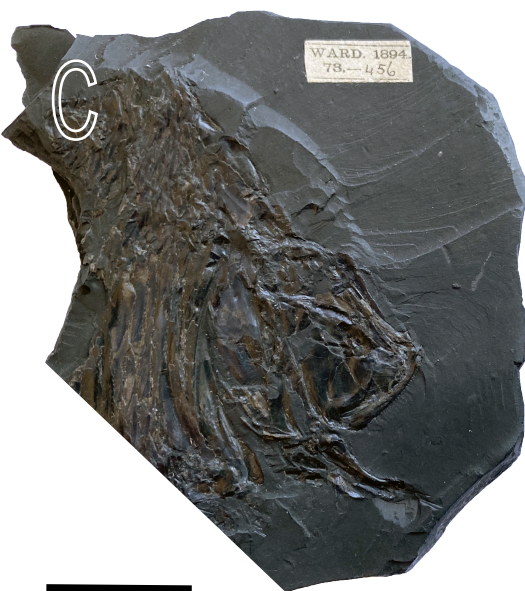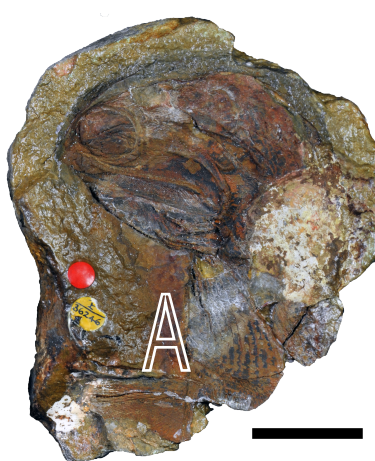
The image panels contain the following text labels:

A

B

C

WARD. 1894
78.—456

D

Platysomus forsteri
Hancock & Atthey.
Formn. Coal measures
Locy. Airdrie, Lanarkshire
Catal. Foss. Fishes B.M. II. p.546
Purchd. 1863.
Brit. Mus. Geol. Dept. 37322
SEGUL THETFORD NORFOLK U.K.

E

Dicksonosteus arcticus
Entelognathus primordialis
Cladodoides wildungensis
Ozarcus mapesae
Acanthodes bronni
Dialipina salguerioensis
Ligulalepis
Onychodus jandemarrai
Psarolepis romeri
Guiyu oneiros
Styloichthys changae
Miguashaia bureaui
Diplocercides kayseri
Porolepis sp.
Glyptolepis groenlandica
Gogonasus andrewsae
Osteolepis macrolepidotus
Eusthenopteron foordi
Meemannia eos
Cheirolepis trailli
Cheirolepis schultzei
Cheirolepis canadensis
Tegeolepis clarki
Osorioichthys marginis
Howqualepis rostridens
Donnrosenia schaefferi
Mimipiscis toombsi
Mimipiscis bartrami
Gogosardina coatesi
Raynerius splendens
Moythomasia lineata
Moythomasia durgaringa
Moythomasia nitida
Woodichthys bearsdeni
Melanecta anneae
Kentuckia deani
Trawdenia planti
Luederia kempi
Lawrenciella schaefferi
Kansasiella eatoni
Coccocephalichthys wildi
Boreosomus piveteaui
Pteronisculus stensioi
Kalops monophyrum
Cosmoptychius striatus
Beagiascus pulcherrimus
Aesopichthys erinaceus
Wendyichthys dicksoni
Cyranorhis bergeraci
Australosomus kochi
Amphicentrum granulosum
Styracopterus fulcratus
Fouldenia ischiptera
Saurichthys madagascarensis
Fukangichthys longidorsalis
Tanaocrossus kalliokoskii
S. dubia
Evenkia eunoptera
Beishanichthys brevicaudalis
POLYPTERIFORMES
Brachydegma caelatum
Birgeria groenlandica
CHONDROSTEI
Platysomus superbus
Discoserra pectinodon
Ebenaqua ritchei
Bobosatrania groenlandica
Venusichthys comptus
Dipteronotus ornatus
Peltopleurus lissocephalus
Luganoia lepidosteoides
Hulettia americana
TELEOSTEI
Macrepistius arenatus
Watsonulus eugnathoides
HOLOSTEI

CROWN ACTINOPTERYGII

Telychian | Sheinwoodian | Homerian | Gorstian | Ludfordian | Lochkovian | Pragian | Emsian | Eifelian | Givetian | Frasnian | Famennian | Tournaisian | Visean | Serpukhovian | Bashkirian | Moscovian | Kasimovian | Gzhelian | Asselian | Sakmarian | Artinskian | Kungurian | Roadian | Wordian | Capitanian | Wuchiapingian | Changhsingian | Olenekian | Anisian | Ladinian | Carnian | Norian | Rhaetian | Hettangian | Sinemurian

Silurian | Devonian | Carboniferous | Permian | Triassic | Jurassic

430 | 420 | 410 | 400 | 390 | 380 | 370 | 360 | 350 | 340 | 330 | 320 | 310 | 300 | 290 | 280 | 270 | 260 | 250 | 240 | 230 | 220 | 210 | 200
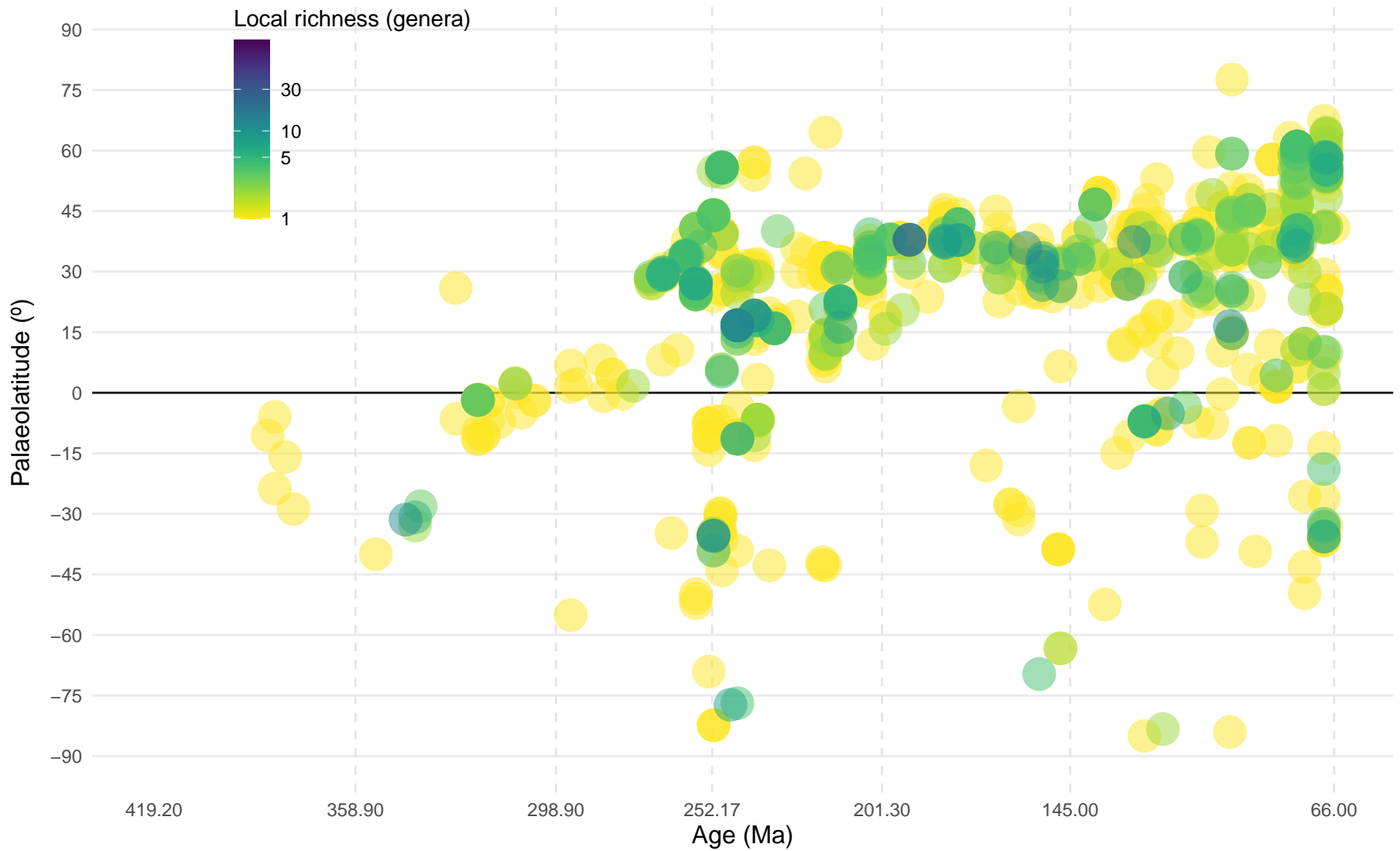
Appendix S1

Problematic Palaeozoic taxa

(a) *Palaeoniscum*

Many of the taxonomic problems associated with *Palaeoniscum* stem from its unspecific and vague diagnosis which could effectively apply to most fusiform Devonian, Carboniferous and Permian ray-fins:

"Toutes les nageoires médiocres, de petits rayons sur leurs bords; D. opposée à l'espace entre les V. et I'A. Ecailles médiocres; quelques espèces en ont d'assez grandes, et le corps plus large et plus court que les autres. Il y a toujours de grosses écailles impaires en avant de la D. et de I'A" – Agassiz (1833, p. 4). *(Translation: All small fins, with small rays on the edges; dorsal fin opposite the space between the ventral and anal fins. Small scales; some species have larger scales. There are always large, odd scales in front of the dorsal and anal fins.)*

As a consequence, fragmentary and anatomically generalised taxa have frequently been referred to the genus. Traquair (1877a) identified this problem and attempted to rectify it by limiting the number of species referred to the genus to just seven (*P. comptus, P. elegans, P. freieslebeni* (type), *P. longissimus, P. macrophthalmus, P. macropomus* and *P. magnu*s), but did not amend the diagnosis to prevent the problem from recurring. Aldinger (1937) later noted that *P. freieslebeni* is the only well-known species and revised the diagnosis to something far more comprehensive:

"Diagnose. – (Nach WESTOLL 1934, mit Ergänzungen). Mittelgrosse sehr schlanke Fische, Körper im Querschnitt rundlich oder oval, Schädel breit, nieder. Endocranium wahrscheinlich gut verknöchert. Deckknochen des Schädeldachs im ganzen wie bei den übrigen Palaeonisciformes. Parasphenoid mit Processus ascendens anterior (klein) und posterior, nach hinten bis unter die Labyrinthregion reiechend, kein Foramen hypophyseos bei erwachsenen Exemplaren. 2 Paare Extrascapularia. Parietalia klein, viereckig, Frontalia gross, hinten wesentlich breiter als vorne, etwa in der Mitte der Länge mit einem Fortsatz am lateralen Rand, die Sutur zwischen den Frontalia sehr unregelmässig. Postrostrale mässig gross, sehr stark gewölbt. Supratemporo-Intertemporale lang, mit sehr unregelmässigem Umriss, mit langem, anteromedial gerichtetem Fortsatz, der am lateralen Rand des Frontale liegt. Zwischen Dermosphenoticum und Supratemporo-Intertemporale ein kleiner schmaler Deckknochen: das Epitemporale. Zwei Reihen kleiner supraorbitaler Deckknochen zwisechen Orbita und Frontale. 4 Suborbitalia. Nasale mit Einschnitt am vorderen Rand für die vordere Nasenöffnung, caudaler Rand dieses Knochens in der Regel ohne Bucht für die hintere Nasenöffnung. Sceralring mit vier (?) Segmenten. Palatoquadratum zum Teil verknöchert. Meckelscher Knorpel im Artikularteil und vielleicht in der Nahe der Symphyse verknöchert. Hyomandibulare leicht gebogen, ohne Processus opercularis und ohne foramen fur den Truncus hhyoideomandibularis facialis. Ceratohyale lang, kraftig, etwas gebogen. Kiemenbogen verknöchert. Maxillare wie ublich. Unterkiefer lang, ohne Processus coronoideus und angularis. Praeoperculum etwa im Winkel von 110 gebogen. Operculum gross, doppelt so hoch wie breit, stark gewolbt. Suboperculum hinten wesentlich hoher als vorne, dorsaler Rand konkav. Branchiostegalstrahlen zahlreich,

ungefahr 10-11. Anordnung wie ublich. Kein Antoperculum. Die Deckknochen des Neurocraniums, der Mendibelund das Maxillare mit einem Ornament von ziemlich entfernt stehenden Ganoinrippen und Tuberkeln, Operculum und Suboperculum fast frei von Ganoin und glatt. Die Zahne auf dem Maxillare klein, spitzkonisch, auf der Mandibel zwei Reihen: sehr kleine aussere und grossere spitzknoische innere Zahnreihe auf dem Dentospleniale. Achsenskelett in den oberen und unteren Bögen verknöchert. Flossenstellung normal, die Flossen von massiger Grosse. Primarer Schultergurtel gut verknöchert, mit Processus glenoidalis (1. So benenne ich einen Fortsatz, der uber dem Margo radialis liegt und caudad gerichtet ist (siehe unten Seite 163 und 283)) und vielleicht einem Mesocoracoid. Fenestra coraco-cleithralis (2. Due Offnung zwischen dem vorderen Rand des ventralen Teils des primaren Schultergurtels und dem Cleithrum, vgl. RENDAHL, 1930, p.5) sehr klein. Vertikaler Teil des Cleithrum ziemlich schmal, schrag nach hinten oben gerichtet. Ventromediale Platte des Cleithrum lang und breit. Radialia der Pectoralflosse lange, schmale, gut verknöchert Elemente. Samtliche Lepidotrichia der Pectoralflosse mit Ausnahme des ersten gegliedert, erster Strahl etwa 1/3 bis 1/2 mal so lang wie die Flosse, mit kraftigem Trochanter (3. So benannt im Anschluss an Rendahl (1930,p.19 usw. 1933, 1934)). Beckenflosse ziemlich gross im Vergleich zur Analflosse. Dorsalflosse und Analflosse massig gross, dreieckig, Dorsalflosse mit knochernen Axonosten und Baseosten, Analflosse mit ca. 10 knochernen Axonosten, die zum Teil knovex nach vorne gebogen sind. Caudalis tief gespalten, etwas ungleichlappig. Alle Flossen mit Fuleren, die Glieder der Lepidotrichia meist hoher als breit, mit Ganoin bedeckt. Beckenflosse hinter der Mitte zwischen Pectoral- und Analflosse, Dorsalflosse gegenuber dem Raum zwischen Becken- und

Analflosse. Sinneskanalsystem des Craniums wie bei ubrigen Palaeonisciformes, mit vorderer, mittlerer und hinterer Pitlinie. Die Sinneskanale des Schadeldachs mit zahlreichen kurzen unverzweigten Tubuli. Dorsale Korpersinneslinie (4. Sie wurde an Exemplaren von Palaeoniscus freieslebeni aus dem deutschen Kupferschiefer und von Durham beobachtet) bis in die Gegend der Dorsalflosse reichend, mit spaltformigen Poren. Seitensinneslinie mit Pore in jeder zweiten bis vierten Schuppe. Foramen fur einen Zweig des Nervus lineae lateralis auf der Innenseite jeder Schuppe. Die Schuppen der Seitensinneslinie in der Mitte etwas kielartig erhoht. Schuppen rechteckig bis rhombisch, sich nicht stark uberdeckend, im grossten Teil der Abdominalregion auf den Flanken mit Dorn- und Grubenartikulation. Schuppen im ventralen Teil der Flanken nieder und lang. Oberflache der Schippen mit einer Ganoinlage bedeckt. Skulptur der Schuppen: im vorderen Teil der Oberflache kurze Rinnen oder Grubchen, die teils parallel zum ventraln Rand der Schuppe, teils schief nach unten verlaufen, in der Mitte der Schuppen einige Poren. Hinterrand der Schuppen fein gezahnt, die Rinnen zwischen den Zahnen verlaufen mehr oder weniger weit nach vorne uber die Schuppe. Vor der Dorsalflosse eine oder mehrer grosse Firstschuppen, einige massig vergrosserte Firstschuppen vor dem ventralen und dorsalen Lappen der Analflosse. Die Schuppen bestehen aus Knochen-, Kosmin- und Ganoinschicht. Die basale Knochenschicht enthalt im hinteren unteren Teil der Schuppe zahlreiche schrag nach vorne oben zur Kosminschicht aufsteigende Kanale.Die Kosmindchicht besteht aus zahlreichen im Querschnitt dreieckigen Kosminlamellen, die konzentrisch zur Peripherie der Schuppe verlaufen. Die Kosminschicht enthalt ein System von annahernd radial von assuen nach innen wellig verlaufdenden Kanalen, die ungefahr in einer Eben liegen, aber in jeder Kosminlamelle etwas nach oben ausbiegen.

Die Kanale verzweigen sich lebhaft und sind in den Kosminlamellen durch feinere Querkanale verbunden, von welchen die Kosminrohrchen nach oben und innen ausstrahlen. Die Ganoineschicht besteht aus einzelnen Lamellen die zackig zwischen die Kosminlamellen eingreigen. Zi jeder Kosminlamelle gehort eine Ganoinlamelle. Die Ganoinschicht wird im mittleren und hinteren Teil der Schuppe von einigen Kanalen durchbohrt, die korkzieherartig gewunden sind, von der Kosminschicht aufsteigen und in den Grubchen auf der Schuppenoberflache ausmunden. Die aufsteigenden Kanale sind innerhalb der Ganoinschicht von einem Mantel von Kosmin umgeben wie bei Elonichthyiden. In den First-schuppen (vor der Dorsalis usw.) ein unregelmassiger Kanalplexus in der kosminschicht und zahlreiche schrag von vorne unten nach hinten oben das Ganoin durchbohrende Kanale." – Aldinger (1937, p. 97). *(Translation: Diagnosis. – Following Westoll 1934, with additions. Medium-sized, very slender fish, round or oval body in cross-section, skull broad and low. Endocranium probably well ossified. Dermal bones of the cranial roof largely as in other Palaeonisciformes. Parasphenoid with processus ascendens anterior (small) and posterior, extending backwards to below the labyrinth region, no hypophyseal foramen in adult specimens. Two pairs of extrascapulars. Small, square parietals, large frontals broader posteriorly than anteriorly with a very irregular midline suture about halfway along the length of an extension on the lateral margin. Postrostral moderately large, very strongly arched. Long supratemporo-intertemporal with very irregular outline and a long anteromedial process lying on the lateral edge of the frontal. Between the dermosphenotic and the supratemporo-intertemporal there is a small, narrow dermal bone: the epitemporal. Two rows of small supraorbital dermal bones between the orbit and frontal. Four suborbitals.*

Nasal with notch in the anterior edge for the anterior nostril, caudal edge of this bone usually without embayment for the posterior nostril. Scleral ring with four (?) segments. Palatoquadrate partly ossified. Meckel's cartilage ossified in the articular region and possibly near the symphysis. Hyomandibular slightly curve, without the opercular process and without opercular process and without foramen for the hyomandibular nerve. Ceratohyal long, strong, slightly curved. Gill arch ossified. Maxilla as usual. Lower jaw long, without coronoid and angular processes. Preoperculum approximately bent at an angle of 110 degrees. Operculum large, twice as high as it is wide, strongly curved. Suboperculum much higher posteriorly than anteriorly, dorsal edge concave. Branchiostegal rays numerous, approximately 10-11. Arrangement as usual. No antoperculum. The dermal bones of the neurocranium, the mandible and the maxilla with an ornament of regularly separated ganoin ridges and tubercles, operculum and suboperculum almost free of ganoine and smooth. Teeth on the maxilla small, pointed conical, two rows on the mandible: very small outer and larger pointed inner row of teeth on the dentosplenial. Axial skeleton ossified in the upper and lower arches. Fin position normal and of moderate size. Primary shoulder girdle well ossified, with glenoid process [1. This is what I call an extension that lies over the radial margin and is directed caudally (see below, pp. 163 and 283)] and perhaps a mesocoracoid. Fenestra coraco-cleithralis [2. The opening between the front edge of the ventral part of the primary shoulder girdle and the cleithrum, cf. RENDAHL, 1930, p. 5] is very small. The vertical part of the cleithrum is rather narrow, sloping posterodorsally. Ventromedial plate of the cleithrum long and wide. Pectoral fin radials are long, narrow, well ossified elements. All lepidotrichia of the pectoral fin with the exception of the first articulated, first ray about

1/3 to 1/2 times as long as the fin, with a powerful trochanter [3. Named following

Rendahl (1930, p. 19 etc. 1933, 1934)]. Pelvic fin quite large compared to the anal fin.

Dorsal fin and anal fin are massive, triangular, dorsal fin with bony axonosts and

baseosts, anal fin with about 10 bony axonosts, some of which are convexly bent forward.

Caudal fin deeply split, somewhat unevenly lobed. All fins with fulcra, the limbs of the

Lepidotrichia mostly higher than wide, covered with ganoin. Pelvic fin posterior to

midpoint between the pectoral and anal fin, dorsal fin opposite the space between the

pelvic and anal fin. Sensory canal system of the cranium as in other Palaeonisciformes,

with anterior, middle, and rear pit lines. The sensory canals of the skull roof with

numerous short unbranched tubules. Dorsal lateral line [4. Observed on specimens of

Palaeoniscus freieslebeni *from German Kupferscheifer and from Durham] reaching into*

the area of the dorsal fin, with slit-shaped pores. Lateral line with pores in every second

to fourth scale. Foramen for a branch of the lateral line nerve on the inside of each scale.

The scales of the lateral line raised in the middle somewhat like a keel. Scales

rectangular to rhombic, not overlapping much, in most of the abdominal region on the

flanks with peg- and socket articulation. Scales in the ventral part of the flanks low and

long. The surface of the scales is covered with a ganoine layer. Sculpture of the scales: in

the front part of the surface short grooves or pits, some of which run parallel to the

ventral edge of the scales, some at an angle downwards, with a few pores in the middle of

the scales. The rear edge of the scales are finely toothed, the grooves between the teeth

run more or less forward over the scales. In front of the dorsal fin, one or more large

ridge scales, some massively enlarged ridge scales in front of the ventral and dorsal

lobes of the anal fin. The scales consist of bone, cosmine and ganoin layers. The basal

bone layer in the lower rear part of the scale contains numerous canals that rise obliquely upwards to the cosmine layer. The cosmine layer consists of numerous cosmine lamellae, triangular in cross section, which run concentrically to the periphery of the scale. The cosmine layer contains a system of channels, which run approximately radially from each other, undulating inwards, which lie roughly in one plane, but bend slightly upwards in each cosmine lamella. The channels branch out and are connected in the cosmine lamellae by finer transverse channels, from which the cosmine tubes radiate upwards and inwards. The ganoine layer consists of individual lamellae that jaggedly line between the cosmine lamellae. There is a ganoine lamella for every cosmine lamella. The ganoine layer is pierced in the middle and rear part of the scale by a few canals, which are twisted like a corkscrew, which rise from the cosmine layer and open into the pits on the surface of the scale. The ascending canals are surrounded by a coat of cosmine within the ganoine layer, as in elonichthyids. In the ridge scales (in front of the dorsal fin, etc.) there is an irregular canal plexus in the cosmine layer and numerous canals that pierce the ganoine at an angle from the anteroventral to posterodorsal margin.)

Despite this, many of the diagnostic characteristics are still essentially the same as for the family Palaeoniscidae (Moy-Thomas and Miles, 1971), which, aside from not being monophyletic, also includes a number of other genera including *Elonichthys* and *Rhadinichthys*. The author himself described it as "a 'hold-all' for a host of "normal forms" (Moy-Thomas and Miles, 1971, p. 102). Reliance on scale morphology is particularly problematic given that the scales of *Palaeoniscus* and *Elonichthys* are very similar (Aldinger, 1937), and in fact scale morphology is generally quite morphologically conservative among Palaeozoic actinopterygians.

Many species of *Palaeoniscum* stem from Wuchiapingian deposits of the UK and Germany (Marl Slate, Raisby, Zechstein and Kupferschiefer Formations). This includes the type species *P. freieslebeni* (sometimes erroneously spelled *P. freieslebenensis*), as well as *P. elegans* Sedgwick 1829, *P. longissimus* Agassiz 1833 (King, 1850), *P. macropthalmus* McCoy 1855, *P. glaphyrus* Agassiz 1835, *P. magnus* Agassiz 1833, *P. comtus* Agassiz 1833, and *P. macropomus* Agassiz 1833. Of these, however, the only valid species is *Palaeoniscum freieslebeni* (Aldinger, 1937; Laatsch, 1931; Westoll, 1934; Woodward, 1891). Štamberg (1997, 2007) notes three additional species (*P. katholitzkianus*, *P. moravicus* and *P. promtus* from the Asselian of Czechia) that were originally described by Rzehak (1881), though provides no further description. Other potentially valid species are *P. kasanense* Geinitz and Vetter 1880 (Aldinger, 1937), from the Roadian of Russia (Minikh and Minikh, 2009), and the Kungurian *P. daedalium* Yankevich 1998, which is based solely on scales (Minikh et al., 2016).

A number of previously described species have since been removed from the genus. Three taxa (*P. curtum* (Krotov, 1904; Nurgaliev et al., 2015), *P. netschaevi* and *P. kargalensis*) were moved to *Amblypterus* by Chabakov (1927). Aldinger (1937) determined that a further two species (*P. catopterus* (Agassiz, 1833) and *P. tscheffkini* (Eichwald, 1861; Krotov, 1904) do not belong to *Palaeoniscum* and declared *P. scutigerus* (Hay, 1902) from the Pennsylvanian of Ohio a *nomen nudum* (Aldinger, 1937). *P. bainii* (Gürich, 1923; Woodward, 1891), *P. capensis* (Evans, 2005; Gürich, 1923; Jubb and Gardiner, 1975; Murray, 2000) and *P. sculptus* (Gürich, 1923) from the Permian of South Africa are so dissimilar to *Palaeoniscum freieslebeni* that Aldinger (1937) stated uncertainty that they could even be assigned to the same family. Similarly, Anisian deposits from Australia (Hawkesbury Sandstone) yield *P. antipodeus*, *P. crassus* (Woodward, 1908) and *P. feistmantelli* (Woodward, 1891) which are actually

indeterminate beyond family level (Turner and Long, 1987). A number of other species have also been declared invalid.

Numerous fossils from throughout the Carboniferous are assigned to *Palaeoniscum* without a specific epithet, despite the type species occurring in the Wuchiapingian. Indeterminate species of *Palaeoniscum* from the Tournaisian Albert Formation of Canada highlight interwoven issues with problematic Palaeozoic genera, as previously-assigned specimens of *Palaeoniscus* sp. (Gardiner, 1966; Jackson, 1851a, 1851b) now supposedly belong to either *Rhadinichthys* or *Elonichthys* (Lambe, 1909; Mickle, 2017). Specimens with the label "*Palaeoniscum* sp." are also present in the NHM and NMS collections of fossils from Scottish deposits of Visean, Bashkirian and Moscovian age (SH, personal observation). It is likely that the disparate range of specimens referred to *Palaeoniscum* obscure a significant proportion of Carboniferous actinopterygian diversity.

(b) Elonichthys

Elonichthys is a waste-basket taxon, the early diagnoses for which (e.g. Traquair, 1877; Moy-Thomas and Dyne, 1938) suffer from being overly generalised and relying heavily on body shape, scale morphology and general cranial and fin morphology. Originally, Giebel (1848) erected the genus as an intermediate form between the deep-bodied *Amblypterus* and fusiform *Palaeoniscum* (Traquair, 1877a). The initial diagnosis:

"Fische von gestrecktem Körperbau, mit verlängertem Kopfe, schlanken, kräftigen Kiefern und sehr entwickelten Flossen. Durch die Größe dieser nähern sie sich der folgenden Gattung, stehen aber durch ihre dicken, vielfach zerschlissenen Gliederstrahlen den Paläonisten ebenso nah. Der Mangel der Schuppenbedeckung auf den Flossen

entfernt sie indes von der vorigen Gattung, indem zugleich die dick gefalteten, rhomboidalen Schmelzschuppen an gewisse Umblypteren erinnern. So zwischen Paläonisten und Umblypteren in der Mitte stehend, gewährt der Kopf- und Zahnbau die generell eigentümlichen Charaktere dieser Gattung. Die Schädelknochen haben eine runzelig gestreifte Oberfläche und zwar ist diese Streifung strahlig vom Mittelpunkt oder einer medianen Längslinie ausgehend oder sie ist überhaupt in der Längsausdehnung des Knochens angeordnet. Die Kiefer sind mit parallelen sich teilenden oder welligen Längsfalten bedeckt, welche selbst äußerst fein granuliert oder vielmehr runzelig und häufig durch eine feine Längsfurche geteilt erscheinen. Die Zwischenräume zwischen diesen Falten, bald breiter, bald schmäler als dieselben, sind ebenfalls fein gerunzelt und unregelmäßig. Nach dem Zahnrande hin verkürzen sich die Falten schnell und geben dem Kiefer hier ein höckerigrauhes Ansehen. Die Höcker ordnen sich deutlich in vertikaler Richtung an und sind von mannichfaltiger Form und Größe. Allmählig werden diese Höckerchen, je näher sie dem Zahnrande stehen, aber ohne Ordnung und Regelmäßigkeit spitzer, kegelförmig, schlanker und lassen sich den Bürstenzähnen der Umblypteren vergleichen. Zwischen denselben erheben sich jedoch größere, schlank kegelförmige Zähne in verschiedenen Abständen, wie ich dieselben weder bei den Paläonisten noch Umblypteren finde. Diese großen Zähne sind spitzig, im Durschnitt nicht immer kreisrund, sondern zuweilen leicht komprimiert, gerade, seltener sanft gekrümmt mit hackiger Spitze. Mit einer etwas verdickten Basis ruhen sie auf der Schmelzdecke des Kiefers, verdünnen sich über derselben ganz allmählig, erscheinen unter der Lupe nicht glatt und an der lebhaft glänzenden Spitze äußerst fein vertikal gestreift. Ihre Zahl ist unbestimmt, zwischen 15 und 25 schwankend. In der vorderen Kieferhälfte stehen sie

gedrängter und sind zugleich kleiner als in der hinteren, wo sie auch plumper werden. In dem Verhältnis dieser Zähne unter einander und in der Schuppenbildung erkennt man die spezifischen Differenzen. Die Arten lagern im Kohlengebirge von Wettin und ihre Überreste werden im Mineralogischen Museum in Halle aufbewahrt." Giebel (1848, p. 249). *(Translation: Fish of elongated body, with an elongated head, slender, powerful jaws and very developed fins. Due to the size of these they approximate the following genus (Amblypterus) but are just as close to* Palaeoniscus *due to their thick, often segmented fin rays. The lack of scales on the fins meanwhile removes them from the previous genus, though at the same time the thickly folded, rhomboidal enamel scales are reminiscent of certain* Amblypterus. *Intermediate between* Palaeoniscus *and* Amblypterus, *the structure of the head and teeth grants the generally peculiar characters of this genus. The cranial bones have a wrinkled, striated surface and the striae radiate from the center point or a median longitudinal line, or are generally arranged along the longitudinal extent of the bone. The jaws are covered with parallel dividing or undulating longitudinal folds, which themselves appear extremely finely granulated, or rather wrinkled and often divided by a fine longitudinal furrow. The spaces between these folds, sometimes wider, sometimes narrower than them, are also finely wrinkled and irregular. The wrinkles shorten quickly towards the edge of the teeth and give the jaw a bumpy, rough appearance. The humps are clearly arranged in a vertical direction, and are of various shapes and sizes. Gradually, the closer they are to the edge of the tooth, but without order and regularity, the little ones become more pointed, conical, slender and can be compared to the brush teeth of* Amblypterus. *Between them, however, there rise larger, slender, conical teeth in different positions, such as I do not find in either*

Palaeoniscus *or* Amblypterus. *These large teeth are pointed, on average not always circular, but at times slightly compressed, straight, more rarely gently curved with a sharp point. With a somewhat thickened base, they rest on the enamel cover of the jaw, thinning very gradually over it, appear not smooth under the magnifying glass and extremely finely vertically striped at the shiny tip. Their number is indefinite, ranging from 15 to 25. In the front half of the jaw they are more crowded and at the same time smaller than in the back, where they are also plump. The specific differences can be seen in the relationship between these teeth and in the formation of scales.)*

Subsequent diagnoses were very vague, for example:

"The body is fusiform, sometimes rather deep; the tail is large; the caudal fin deeply cleft, very inequilobate, the upper love prolonged. The dorsal fin is situated well forward, nearly opposite the interspace between the ventrals and the anal; both dorsal and anal are large, triangular, of numerous closely set and closely jointed rays. The pectorals and ventrals are acuminate, the base of the ventrals not extended; their rays are also very closely jointed, except at the commencement of the first few rays of the pectoral. The fulcra of all the fins are closely set, but very minute, usually requiring the aid of a lens to distinguish them; the V scale of the upper margin of the tail are, however, well developed. The scales are of moderate size, rhomboidal; those of the flank are slightly higher than long, with concave upper and convex lower margin; they get lower and narrower towards the belly, and diminish generally in size posteriorly, getting also more equilateral towards the tail. The anterior overlapped portion of each body-scale is very narrow, a mere margin in fact; the exposed area is brilliant, and variously ornamented with striae, or course punctures, or both; the posterior margin is often crenulated or

serrated. In many cases the scales become smooth or nearly so on the tail. There are specially large scales in front of the origin of the dorsal fin, and in front of the anal, in the region of the vent. The suspensorium is very oblique, and the gape very wide; the operculum is well developed, oblong; the interoperculum quadrate; but, as in *Palaeoniscus*, &c, there is no suboperculum. The branchiostegal plates, or rays, are numerous, sometimes numbering as many as twenty-two (*E. semistriatus*) on each side; in some other species the number is much smaller, but I feel reluctant on that account to multiply the number of genera. There is a rhomboidal median plate behind the symphysis of the jaw; and the anterior one of each lateral series is much broader than the rest. The jaws are stout, the teeth acutely conical, sharp, enamel-tipped, of two sizes, large and small, the large ones being placed in a row internal to the more closely set outer row of small ones. The ornament of the cranial bones is usually more or less tubercular; the facial bones and those of the shoulder-girdle are striated; the jaws are, however, tuberculated just at the dental margin, the tubercles appearing sometimes to pass insensibly into the outer row of minute teeth." Traquair (1877b, p. 47).

These vagaries are also seen in other diagnoses:

"Gen. Char. —Trunk more or less deeply fusiform. Mandibular suspensorium very oblique; jaws stout and dentition powerful, a close series of small conical teeth, with a spaced series of large conical teeth within. Fins large, with fulcra, the rays branching distally, covered with ganoine, and the more robust sculptured; pectoral rays all articulated; pelvic fins with short base-line; dorsal opposed to space between pelvic and anal fins; upper caudal lobe much produced, the fin deeply forked and inequilobate.

Scales very slightly overlapping, covered with ganoine, more or less sculptured; ridge-scales immediately in front of median fins much enlarged." Woodward (1908, p. 11).

These poor definitions of the genus led to many taxa being referred to *Elonichthys* from genera such as *Palaeoniscum*, *Rhadinichthys*, or *Amblypterus* (e.g. *'Elonichthys' brownii* (Mickle, 2017); *'E.' peltigerus* (Schultze and Bardack, 1987)). Taxa attributed to *Elonichthys* also show significant variation in body form and depth (cf. *'E.' serratus* and *'E.' pulcherrimus*; Moy-Thomas and Dyne, 1938). Morphological diversity is particularly noticeable in the Mazon Creek forms (Schultze and Bardack, 1987). Schindler (2018) recently redefined the genus and type species and revised the diagnoses:

> "Emended diagnosis of genus *Elonichthys* Giebel: Posterior skull roof at one species narrower, otherwise of same width as anterior part; frontal doesn't border the orbital; ratio of length of frontal to length of parietal lies between 1.77 and 2.62; ratio of length of frontal+parietal to greatest width of the median skull roof lies between 1.48 and 1.86; skull roof sculptured with tubercles and short striae, partly decorated with ganoin ridges; dermosphenotic mostly much longer than dermopterotic; dermosphenotic and dermopterotic together form a box or a more differentiated element; dermosphenotic possesses a poorly to clearly developed ventral branch; dermosphenotic contacts the nasal; position of the border dermosphenotic/dermopterotic is level or slightly anterad to the border frontal/parietal; shape of postrostral fluctuates between roundish elongated and roundish short; in one species, the nasal equals the postrostral, otherwise it is significantly shorter regarding the postrostral, the nasal occupies different positions; antorbital forms lying L to high trapezium; in older species nasal contacts the premaxilla, in contrast to most of the younger species; compared with the height of the anterior maxilla splint, the

premaxilla is equal or significantly higher; the anterior infraorbital is a single bone, its posterior end is equal or higher as its anterior end; posterior infraorbital forms a small sickle moon up to a plump half moon; the suborbitals form a high box, composed of one to three elements; anterior border of preopercular is straight to slightly concave; ratio height to length of posterior maxilla plate is 0.39 to 0.58; angle between anterodorsal border and ventral border of posterior maxilla plate is 40° to 52°; within two species the anterior border of maxilla shows an anterodorsal protrusion, otherwise it is straight; within the older species, an antopercular is present which is shorter than the opercular, within the younger species there is no such bone; ratio of height to width of the opercular ranges from 1.90 to 3.42; ventral accessory opercular is triangular; ventral extension of supracleithrum reaches from ventral border of opercular up to ventral border of subopercular; scale sculpture is type 1, at the oldest species type 4." – Schindler (2018, p. 28).

Although some specimens of the type species are missing (Schindler, 2018), this new diagnosis is a major step forward and will allow reassessment of the multitude of 'Elonichthys' species.

Following Schindler's (2018) comprehensive taxonomic revision, only three valid species of *Elonichthys* are known. The type species, *Elonichthys germari*, occurs in the Gzhelian Möhrenbach and Siebigerode Formations of Germany (Schindler, 2018; Schneider et al., 2005). The Asselian Meisenheim Formation of Germany yields the second valid species, *Elonichthys fritschi* (Friedrich, 1878; Schindler, 2017). The third species, *Elonichthys krejcii*, is from the Kasimovian (Slaný Formation) of Czechia (Štamberg, 1991; Štamberg and Zajíc, 2008).

This leaves a vast number of previously described species invalid. *Elonichthys crassidens* and *E. laevis* (Giebel, 1848) are likely synonymous with the type, *E. germari* (Schindler, 2009). Similarly, *'Elonichthys' sphaerosideritarum* is from the same deposits as and likely synonymous with *E. krejcii* (Štamberg, 2010). *Elonichthys palatinus*, originally described by Schindler (1993), has since been removed to *Meisenheimichthys* (Poschmann and Schindler, 2004). Many taxa have complicated taxonomic histories, with numerous instances of taxa being synonymised, subjected to genus and species recombinations, or referred (in part or whole) to other genera (e.g. *Amblypterus* ['*Elonichthys' punctatus*, '*E.*' *portlocki*, '*E.*' *nemopterus*]; Traquair, 1877a).

Although the type species is from the Gzhelian of Germany, taxa from five continents and spanning the Tournaisian to Wuchiapingian have previously been attributed to *Elonichthys*. The earliest of these are from the Tournaisian of Canada and Northern Ireland. There is a large concentration in the Visean of Scotland, with the West Lothian Oil Shale Formation and Gullane Formations yielding nine '*Elonichthys*', mostly described by (Traquair, 1908, 1890, 1881, 1877b). Numerous taxa are also known from the Moscovian and Bashkirian of the UK, primarily from the Pennine and Scottish Coal Measures (Egerton, 1850; Elliott, 2016; Moy-Thomas and Dyne, 1938; Traquair, 1877b; Watson, 1925), with some extending back into the Serpukhovian Millstone Grit ('*Elonichthys*' *oblongus,* Traquair, 1877b, '*E.*' *aitkeni,* Traquair, 1886; '*E.*' *caudalis*, Watson, 1928). Five '*Elonichthys*' species are named from Moscovian deposits of the USA: '*E.*' *disjunctus,* '*E.*' *hypsilepis* (='*E.*' *perpennatus*)*, '*E.*' *peltigerus,* '*E.*' *remotus* and '*E.*' *wolffi* (Bardack, 1979; Schultze and Bardack, 1987). Despite Schultze and Bardack (1987) noting major differences between these species, as well as suggesting they likely belong to different genera, these taxa have not been revised.

Occurrences of '*Elonichthys*' also extend into the Permian and Triassic. '*Elonichthys*' *gondwanus* is reported from the Permian Passa Dois Group of Brazil (Richter et al., 2000, 1985) and '*Elonichthys*' *macropercularis* from the Early Permian San Gregorio Formation of Uruguay (Beltan, 1981, 1978; Cione et al., 2010). Unfortunately, specimens of '*E.*' *macropercularis* are lost (Figueroa et al., 2019). '*Elonichthys*' sp. is present in Artinskian deposits from South Africa (Evans, 2005). Later in the Permian, scale taxa from Russia include '*Elonichthys*' *natalis* (Kungurian; Yankevich and Minikh, 1998; Minikh, Minikh and Yankevich, 2016) and '*Elonichthys*' *contortus* (Roadian; Golubev, 2001). There is only one Late Permian occurrence: '*Elonichthys*' *whaitsi* from the Wuchiapingian (Teekloof Formation) of South Africa (Bender, 2004; Jubb and Gardiner, 1975). Two taxa, '*Elonichthys*' *armatus* and '*E.*' *semilineatus*, were erected on the basis of limited, fragmentary material from the Middle Triassic (Anisian) of Australia (Woodward, 1908).

(c) Platysomus

The validity of *Platysomus* has been questioned almost since its erection. Its diagnosis is overly generic, and many species are assigned to *Platysomus* on the basis of scale or general post-cranial anatomy: genus diagnoses refer only to the general shape of the body, fins, head and scales, with little reference to individual cranial bones (e.g. Agassiz, 1833; Young, 1866; Woodward, 1891; Moy-Thomas and Dyne, 1938). The initial diagnosis was very limited:

> "Corps plat, très-élevé, court; dents en brosse; lobe supérieur de la queue allongé,
> vertébré, portant de petits rayons à son bord. D et A opposées l'une à l'autre, s'étendant
> depuis le milieu du corps jusqu'au rétrécissement de la queue; V. douteuses; P. petites. De
> Blainville range les espèces qu'il a décrites dans le genre *Stromateus*." – Agassiz (1833,

p. 6). *(Translation: Body flat, very high, short; brushed teeth; upper lobe of elongated tail, vertebrate, bearing small rays on board. Dorsal and anal fins opposed to each other, extending from the middle of the body to the narrowing of the tail; ventral fin doubtful; pelvic fin small. De Blainville ranks the species he has described in the genus Stromateus.)*

Subsequent diagnoses added some details, though were still overly generalised:

> "*Platysomus*, Agassiz, partim. Body flat, broad. Head triangular, higher than long; snout sharply angular. Premaxilla small; maxilla in a single piece; mandible slender, spatulate; all three bones armed with fine conical sharp teeth. Branchiostegal rays few, enamelled. Interopercular wanting. No ventral fins. Dorsal and anal fins opposite; their bases extended, and nearly equal in length. Tail heterocercal, equilobate. Scales oblong, vertically striated, with moderately strong lepidopleura. The marginal scales anterior to the opposite fins, more or less modified. Notochord persistent; arches ossified." Young (1866, p. 302).

> "Trunk deep, more or less rhombic, the dorsal and ventral margin being angulated or sharply rounded. Facial contour of head steep, with no marked prominence above or in advance of the orbits; margins of jaws with minute styliform teeth, tubercular within. Fin-rays closely articulated and distally bifurcating; fulcra small or absent. Pectoral fins small, inferiorly placed; pelvic fins much smaller and remote. Dorsal fin arising about the middle point of the back, much elongated, high and acuminate in front, low and fringe-like in the posterior two- thirds; anal fin similar in form, somewhat shorter, but terminating at the same point posteriorly; caudal fin deeply cleft, nearly equilobate.

Scales ornamented with more or less vertical striations, with smooth hinder border, and narrow overlapped anterior border; principal flank-scales very deep and narrow, with large anterior inner keel, and a large, broad peg- and-socket articulation often extending nearly the entire width of the scale; scales dorsally and ventrally and towards the caudal pedicle less deep in proportion to their breadth; scales of upper caudal lobe lozenge-shaped. Ridge-scales in advance of dorsal and anal fins small, those of the upper caudal lobe very large." Woodward (1891, p. 541).

Agassiz (1833), upon naming the genus, noted that while the main characteristics—i.e. the overall shape—were easy to identify, a detailed account of these characters was difficult. Young (1866) highlighted further problems with Agassiz's (1833) definition, namely that several of the original species possessed features discordant with the diagnosis, for example in possessing a pelvic fin (Mickle and Bader, 2009; Zidek, 1992). Given the absence of cranial bones in the diagnosis it is unsurprising that material has been assigned within *Platysomus* without reference to cranial data. This includes specimens that are assigned to new species despite lacking detailed cranial descriptions and being morphologically, geographically and temporally similar (e.g. *P. parvulus, P. tenuistriatus* and *P. rotundus*), as well as specimens that are designated as new species on the basis of scale material alone (e.g. *P. bashkirus*, Minikh, 1992; *P. solikamskensis*, 1998; *Platysomus forsteri*, Zidek, 1992). Other taxa, such as *Schaefferichthys leudersensis* (Dalquest, 1966), are erected on the basis of generic and specific diagnoses that are indistinguishable from *Platysomus*, as noted by Zidek (1992).

This lack of clarity surrounding *Platysomus* also precludes understanding of the diversity and drivers of deep-bodied actinopterygian radiations. A deep-bodied morphotype is a repeated motif in actinopterygian evolution, potentially evolving as many as six times (Sallan and Coates,

2013), but the relationships between deep-bodied groups is unclear. Convergence upon a deep-bodied morphology likely compounds this problem, as membership of a particular group may be determined by general body shape and proportions rather than detailed, phylogenetically informative characters. More broadly, this impacts our understanding of the sequence of morphological evolution in actinopterygians, as well as their early diversity.

The type species, *Platysomus gibbosus*, was described by Blainville (1818) from the Wuchiapingian of Germany under the genus name *Stromateus*. Agassiz (1833) later erected *Platysomus* and described four additional species (P. *rhombus, P. striatus, P. macrurus, P. parvus*). Münster (1842) added three new species, (*P. althausii*, *Platysomus intermedius* and *P. fuldai*), although the latter two were later synonymised with the type species and *P. macrurus* respectively (Geinitz, 1861). Additions and synonymisations continued over the following two decades: Williamson (1849) erected *Platysomus parvulus* on the basis of scales from the Moscovian of England, while King (1850) dissolved *P. parvus* into *P. striatus* and von Eichwald (1861) described *Platysomus biarmicus*.

Young (1866) made the first major attempt at rectifying issues with the genus, providing fuller descriptions of two taxa (*Platysomus parvulus* and *P. declivus*) mentioned but not described by Agassiz (1833), moving *Platysomus macrurus* to the genus *Eurysomus*, and limiting the species of *Platysomus* to *P. gibbosus*, *P. rhombus*, *P. striatus*, and *P. parvulus*. In subsequent years, various authors continued to add taxa from across the Carboniferous of Europe and North America to the genus, most notably *Platysomus superbus* (Traquair, 1881). A number of taxa were also revised or removed to other genera, for example *Dorypterus* (Hancock and Howse, 1870) and *Eurynotus* (Traquair, 1879). Woodward (1891) attempted another major revision, moving *Platysomus* [=*Eurysomus*] *macrurus*) to a different genus (*Globulodus*) and

regarding all of Agassiz' original erected species as synonymous with the type species, *P. gibbosus*. Three additional species were named in the early 1890s, representing the last to be erected for a century, although a number of revisions and supplemental descriptions were published in this time. Perhaps most importantly, Campbell and Phuoc (1983) redescribed the type species, *P. gibbosus*, in a broad review of the relationships of deep-bodied actinopterygians, again highlighting the pressing need for revision of *Platysomus*. Zidek (1992) carried out another review of the genus, noting the need for major revisions, naming a new species (*Platysomus schultzei*), and synonymising two taxa. In the same year Minikh (1992) described *Platysomus bashkirus* and *P. soloduchi* from the Middle Permian of Russia, with Minikh (1998) later describing *P. solikamskensis* on the basis of scales from the Kungurian of Russia. The most recently described taxa are *Platysomus swaffordae* from the Gzhelian of the USA (Mickle and Bader, 2009) and *Platysomus* sp. from the Tournaisian of Canada (Wilson et al., 2021).

On the basis of described species, *Platysomus* appears to span almost the entirety of the Carboniferous and Permian, a range of some 100 million years. The Tournaisian *Platysomus* sp. described by Wilson, Mansky and Anderson (2021) represents the oldest reliable occurrence of the genus, as well as the earliest occurrence of a deep-bodied actinopterygian; a past account of *Platysomus*? sp. from the Tournaisian of Russia is not associated with a description or illustration (Obruchev, 1977) and therefore cannot be corroborated. The earliest named species is *Platysomus superbus* from Visean marine deposits of Glencartholm in Scotland (Moy-Thomas and Dyne, 1938; Traquair, 1881). Later specimens known from the Permian appear to have conspicuous morphological distinctions from Carboniferous forms, and Campbell and Phuoc (1983) note that their validity should be reassessed. Late Permian '*Platysomus*' (especially the type species, *P. gibbosus*) have clear affinities with *Bobasatrania*, which is taxonomically

restricted to the Triassic, and it has been suggested—although not phylogenetically tested—that the taxa are related (Campbell and Phuoc, 1983).

Early phylogenetic studies included *Platysomus* as a composite group (Gardiner, 1984; Gardiner and Schaeffer, 1989), which is obviously problematic given the taxonomic issues. Only one study has included more than one species of *Platysomus*: in this, they were resolved alongside other deep-bodied actinopterygians (Mickle et al., 2009). However, this analysis has a series of issues (Sallan, 2014). The latest phylogenetic analyses (e.g. Giles *et al.*, 2017) include only *Platysomus superbus*, despite the species being temporally and morphologically remote from the type species (Moy-Thomas and Dyne, 1938). This absence of *Platysomus* in comprehensive phylogenetic studies has prevented investigation of the radiations of deep-bodied actinopterygians.

Platysomus is undoubtedly in need of urgent taxonomic revision, and calls for a major overhaul of this genus have been heard for almost the entirety of its existence (Campbell and Phuoc, 1983; Mickle and Bader, 2009; Moy-Thomas and Dyne, 1938; Weems and Windolph, 1986; Young, 1866; Zidek, 1992).

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