The early diversification of ray-finned fishes (Actinopterygii): hypotheses, 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 Carboniferous and Permian. In large part, these conflicts span from a lack of publicly-available occurrence data: actinopterygians are majorly underrepresented in the Paleobiology Database (PBDB), for example, obscuring patterns of diversity through time. This is exacerbated by major taxonomic problems pervading the Palaeozoic actinopterygian record. Innumerable taxa are lumped into wide-ranging families and poorly-formulated genera, with a vast number of described species concentrated in several particularly problematic 'waste-basket' genera. This taxonomic confusion feeds into a limited understanding of phylogenetic relationships. There is also a heavy sampling bias towards Europe and North America, with other regions underrepresented despite yielding important occurrences. Scrutiny of the extent to which spatial biases influence the record is lacking, as is research on other forms of bias. Low richness in some time periods may be linked to geological biases, while the effect of taphonomic biases on Palaeozoic actinopterygians have not yet been investigated. Efforts are already underway to both redescribe poorly defined taxa and describe taxa from underrepresented regions, helping address taxonomic issues and accuracy of occurrence data. New methods of sampling standardisation utilising up-to-date occurrence databases will be critical in teasing apart biological changes in diversity from those resulting from bias. Lastly, continued phylogenetic work will enable the use of phylogenetic comparative methods to elucidate the origins of actinopterygian biogeography and subsequent patterns of radiation throughout their rise to dominate aquatic faunas.

Keywords: fossils; ichthyology; palaeoniscids; palaeopterygians; Palaeozoic; sampling biases.

CONTENTS

I. INTRODUCTION

Reconstructions of deep time biodiversity patterns are critical to understanding the evolution of life of Earth. However, deciphering whether these patterns represent true changes in biodiversity is a key challenge for palaeobiologists (Raup, 1972, 1976; Sepkoski, 1981; Alroy *et al.*, 2008). The past 20 years have seen rapid growth in the number of quantitative studies on vertebrate groups, which employ fossil occurrence data to estimate patterns of diversity. The majority of work on vertebrate diversity through time focuses on either individual taxonomic groups of tetrapods (e.g. Alroy, 2009; Benson *et al.*, 2010; Butler *et al.*, 2011; Mannion *et al.*, 2011, 2019; Brocklehurst, Kammerer and Fröbisch, 2013; Butler, Benson and Barrett, 2013; Pearson *et al.*, 2013; Cleary *et al.*, 2015, 2018, 2020; Bennett *et al.*, 2018; Cantalapiedra, Domingo and Domingo, 2018; Brown *et al.*, 2019; Driscoll *et al.*, 2019; Celis *et al.*, 2020; Cantalapiedra *et al.*, 2021) and fishes (Sallan & Coates, 2010; Koot, 2013; Lloyd & Friedman, 2013; Sansom, Randle, & Donoghue, 2015; Romano *et al.*, 2016), or more recently large scale analyses of all tetrapods (Sahney, Benton, & Ferry, 2010; Close *et al.*, 2017, 2019, 2020a; Dunne *et al.*, 2018; Dunne, 2020) using large publicly available databases such as the Paleobiology Database (PBDB; paleobiodb.org). Critically, these studies are often able to identify biases and gaps in the fossil record, allowing insight into evolutionary dynamics in deep time and the assembly of ancient and modern ecosystems. Such studies can also reveal major changes in diversification, extinction, and paleoecology. For example, studies of Palaeozoic vertebrates have illuminated the rise of jawed vertebrates from the Silurian to the Devonian (Sansom *et al.*, 2015), a major shift from placoderm- and sarcopterygian-dominated faunas to chondrichthyan- and actinopterygian-dominated faunas after the end-Devonian mass extinction (Sallan & Coates, 2010), and changes in Palaeozoic tetrapod diversity in relation to palaeoenvironments (Dunne *et al.*, 2018; Pardo *et al.*, 2019).

Despite accounting for roughly half of extant vertebrates (Nelson, Grande, & Wilson, 2016), research on the diversity of actinopterygians over long evolutionary timescales comprises only a fraction of macroevolutionary studies. Ray-finned fishes likely evolved in the Silurian (Zhu *et al.*, 2009) with the crown group originating at or about the Devonian-Carboniferous boundary (Giles *et al.*, 2017), but diversity dynamics throughout the Palaeozoic are poorly understood due to the limited number of studies utilising occurrence-based datasets. This reflects a broader palaeontological trend of understudy into the fossil record of fishes (Friedman & Sallan, 2012). Notable exceptions include Sallan and Coates' (2010) diversity and faunal analyses of Middle Devonian to Mississippian gnathostomes; Lloyd and Friedman's (2013) analysis of British fish richness; and Romano *et al.*'s (2016) study on Permo-Triassic osteichthyans. Other studies have used compendia of first and last appearances to plot counts through time (Benton, 1993; Patterson, 1994; Sepkoski, 2002; Blieck, 2011; Friedman & Sallan, 2012). Additional studies examine patterns of biodiversity across long periods of time using publicly available occurrence data (e.g. PBDB), though they present aggregated data of numerous groups of 'fishes', or an even broader set of taxa such as nektonic metazoans (e.g. Whalen and Briggs [2018]; Harper, Cascales-Miñana and Servais [2020]).

While these studies present an important first foray into understanding Palaeozoic actinopterygian evolution, there have been limited syntheses that take the accuracy of the ray-fin fossil record into account, which is a major barrier to reconstructing long-term evolutionary patterns. Previous attempts either focus on the UK and include non-actinopterygian fishes (Lloyd & Friedman, 2013), do not cover the entire Palaeozoic (Sallan & Coates, 2010; Romano *et al.*, 2016), or are broader in scope without as much focus on the suitability of data and barriers to interpreting diversity patterns (Sallan, 2014). Friedman and Sallan (2012) note the lack of such investigation for fishes, and, through a qualitative survey, suggest that geological and taxonomic biases likely impact diversity of fishes through time. Here, we summarise the current state of research on the Palaeozoic fossil record of actinopterygians, and attempt to answer the following:

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

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

- how do taxonomic problems and existing phylogenetic analyses hinder our interpretation of the Palaeozoic actinopterygian fossil record?

- how do sampling and other biases affect our understanding of Palaeozoic actinopterygian diversity through time?

II. CURRENT HYPOTHESES OF PALAEOZOIC ACTINOPTERYGIAN DIVERSITY

(1) Past studies

Although our understanding of patterns of actinopterygian diversity lags behind that of other groups, a number of studies over the past few decades have investigated fish diversity at different taxonomic levels and geological scales (Fig. 1). Initially, these approaches used published compendia to generate family- and/or genus-level diversity curves. The first major attempt, by Thomson (1977), used data from Romer's (1966) compendium to plot genus- and family-level diversity of Phanerozoic ‘fishes’ (Acanthodii, Agnatha, Chondrichthyes, Chondrostei, Holostei, Placodermi, Sarcopterygii and Teleostei; Fig. 1E). In subsequent years, several studies used family-level data from Benton (1993) to investigate osteichthyan diversity through the Palaeozoic. Patterson (1994) plotted diversity curves for osteichthyans as well as stem-actinopterygians, stem-neopterygians and stem-teleosts, encompassing all Palaeozoic actinopterygians included in the parent dataset (Fig. 1A). Blieck (2011; Fig. 1B) and Benton (2014: fig. 2.11) also use data compiled by Benton (1993) to plot family-level diversity curves of vertebrates from the Ordovician to Triassic, though do not focus on actinopterygians. Additionally, Friedman and Sallan (2012) used an existing marine dataset (Sepkoski, 2002) to present genus-level diversity patterns of all ‘fishes’ (vertebrates excluding Tetrapoda and including Conodonta) throughout the Phanerozoic (Fig. 1C).

Other attempts have used literature-based datasets to interrogate patterns of diversity. Sallan and Coates (2010) assembled a dataset of gnathostome occurrences from 66 localities spanning the Middle Devonian (Givetian) to early Carboniferous (Serpukhovian) and presented diversity curves of gnathostomes (Acanthodii, Actinopterygii, Chondrichthyes, Placodermi, Sarcopterygii, Tetrapoda; Fig. 1F). Datasets assembled by Romano *et al.* (2016) and Vázquez and Clapham (2017) commence in the Asselian (early Permian) and encompass osteichthyans (Actinistia, Dipnoi, Holostei, ‘Palaeopterygii’, ‘Subholostei’ and Teleosteomorpha: Romano *et al*. [2016]; Fig. 1F) and marine fishes (Osteichthyes [excluding Dipnoi] and Chondrichthyes [excluding Acanthodii]; Vázquez and Clapham [2017]). Lloyd and Friedman (2013) sourced data from a variety of sources as a means of comparing datasets

(Agassiz, 1833; Carroll, 1988; Benton, 1993; Sepkoski, 2002; Paleobiology Database, downloaded on 31/5/12) to investigate the diversity of Phanerozoic 'fishes' (though excluding Conodonta) with a particular focus on the fossil record of Great Britain (Fig. 1D).

These studies clearly differ greatly in their sampling and spread of taxa, but collectively they provide an indication of the general patterns of changes in actinopterygian diversity through time, as summarised below.

(2) Devonian diversity patterns

All studies covering the Devonian depict very low counts of actinopterygian genera or families ((Thomson, 1977: fig. 7; Patterson, 1994: fig. 1; Sallan and Coates, 2010: fig. 1; Blieck, 2011: fig. 2). Thomson (1977), Patterson (1994) and Sallan and Coates (2010) show a gradual rise from the Middle to Late Devonian. Blieck (2011), however, figures a small peak in the Frasnian, likely due to the Gogo and Gladbach faunas (Sallan & Coates, 2010). The low diversity of actinopterygians also correlates with the small proportion of morphological disparity that they account for among gnathostomes (Anderson *et al.*, 2011).

While new taxa are still being described, actinopterygians appear to be genuinely rare in Devonian deposits, especially relative to other taxa (Friedman, 2015: fig. 4). Reclassification of *Meemannia* Zhu *et al.* 2004 as a ray-finned fish rather than a lobe-finned fish (Lu *et al.*, 2016) filled a conspicuous temporal gap in early actinopterygian evolution, but this taxon remains the only actinopterygian known amongst roughly 20 species from this locality. Choo *et al.* (2019) recently described a new genus from the highly diverse Frasnian Gogo Formation, although ray fins account for only 5 species out of around 50 Gogo taxa (Long & Trinajstic, 2010, 2017; Sallan & Coates, 2010, fig. 2). Even more recently, Newman *et al.* (2021) described a new species of *Cheirolepis* Agassiz 1835 from the Givetian of

Svalbard, found alongside roughly 20 non-actinopterygian fishes. Similarly, a new site from the Famennian of Belgium has yielded microremains of an undescribed actinopterygian, amidst large numbers of other vertebrates (Olive *et al.*, 2015b, 2015a, 2016, 2020).

Renewed investigation into historically undersampled regions hint at previously hidden actinopterygian diversity. Isolated jaw elements, body impressions and scales from Famennian deposits in South Africa likely represent a single actinopterygian amid a diverse array of other fishes (Gess & Whitfield, 2020), while renewed prospecting in the contemporary Maïder Basin in Morocco has produced remains of a single articulated actinopterygian (Frey *et al.*, 2018) amongst its well-known placoderm and chondrichthyan assemblages. New South American discoveries include evidence of a stegotrachelid actinopterygian from the Frasnian of Colombia (Olive *et al.*, 2019), the first actinopterygian remains from the Devonian of the Parnaíba Basin of Brazil (Pais de Rezende *et al.*, 2021), and a new circumpolar species from the Middle Devonian (Figueroa, Weinschütz, & Friedman, 2021). As in other localities, non-actinopterygian fishes dominate these faunas (Janvier, 2007; Janvier & Maisey, 2010; Figueroa & Machado, 2018). While important for understanding the early evolution of the group, these scattered reports of new Devonian taxa seem unlikely to change existing overarching hypotheses of actinopterygian diversity: as minor faunal components represented by a small number of taxa relative to other fish groups.

(3) Carboniferous diversity patterns

Previous diversity studies consistently report a large increase in counts of actinopterygians in the earliest Carboniferous, following the end-Devonian mass extinction (EDME). Thomson's (1977) counts of 'chondrostean' genera (which encompasses all Devonian and Carboniferous actinopterygians) rise sharply in the Mississippian, as does

Patterson's (1994) stem-actinopteran family-level count. Sallan and Coates (2010) show this significant change in absolute and relative diversity most clearly in their presentation of faunal composition from the Devonian into the Carboniferous (Sallan and Coates, 2010, fig. 2; see also Friedman, 2015, fig. 4). This sharp rise is especially notable because the early Carboniferous (Tournaisian and early Visean) coincides with 'Romer's Gap', an apparent gap in the fossil record of tetrapods (and other animals) variably explained as either a period of poor sampling (Romer, 1956), low atmospheric oxygen (Ward *et al.*, 2006) or recovery following the EDME (Sallan & Coates, 2010). Recent concerted efforts have begun to populate Romer's Gap, indicating that poor sampling accounted for most of the apparent paucity of the record (Clack *et al.*, 2019; Otoo *et al.*, 2019). The diversification of actinopterygians immediately following the EDME likely represents an adaptive radiation seeded by very few—or perhaps just one—actinopterygian lineages (Sallan & Friedman, 2012; Sallan, 2014; Giles *et al.*, 2017), although this hypothesis has not been explicitly tested. The contrast between diverse (e.g. in Russia: Alekseev *et al.* [1994]) and depleted (e.g. in Morocco: Frey *et al.* [2018]) early Tournaisian faunas exemplifies the uncertainty of the relative contributions of extinction recovery and poor sampling to the observed Tournaisian fossil record, as well as potential local variation and spatial bias.

Raw genus diversity increases into the Visean from the Tournaisian levels in most analyses (Patterson, 1994; Sallan & Coates, 2010; Blieck, 2011). The fossil record of Great Britain exhibits a particularly extreme increase in osteichthyan richness, most likely due to the very richly sampled Visean deposits of Scotland (Dineley & Metcalf, 1999). This rise coincides with a proliferation of new morphologies and ecologies, likely via multiple 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 visible for this period in Friedman and Sallan (2012: fig. 2), and there are no Kasimovian or Gzhelian occurrences in the British fossil record (Lloyd & Friedman, 2013).

Reported overall trends in actinopterygian diversity in the Carboniferous are unclear. Genus-level counts are suggestive of a gradual rise throughout the Mississippian (Sallan & Coates, 2010), with a subsequent drop in the Pennsylvanian (Thomson, 1977). This contrasts with family counts, which are relatively stable except for minor deviations in the Serpukhovian and Bashkirian.

(4) Permian diversity patterns

Genus- and family-level counts in previous studies agree on the general trend of actinopterygian diversity in the Permian, though differ at finer timescales. The highest counts are observed in the early Permian in curves derived from Benton's (1993) dataset (Patterson, 1994; Blieck, 2011) and Thomson's (1977) genus data. Occurrence-based datasets also show a peak in the early Permian, although limited to the Asselian and Sakmarian, likely driven by freshwater Lagerstätte (Romano *et al.*, 2016). Genus- and family-level trends deviate from one another in the Artinskian: the family curve stays more or less stable, whereas genus richness decreases substantially. Family-level counts then drop in the Kungurian and remain roughly at this level, with minor fluctuations, until the end-Permian. Genus richness in Thomson's (1977) curves for 'chondrostean' genus richness drop in the Middle Permian and rise slightly in the Late Permian, and the Late Permian also sees the first counts of holosteans. Counts in the finer-scale dataset of Romano *et al.* (2016) rises gradually from the Roadian-Wuchiapingian, reaching close to Early Permian levels before dropping in the Changhsingian.

While previous studies have established a broad understanding of general diversity trends in the Palaeozoic, there has not yet been a through-Palaeozoic study focussing solely on actinopterygians, and patterns differ depending on the taxonomic level and geological scale investigated. At present, publicly available occurrence databases lack the level of detail necessary for reconstructing long-term diversity through the Palaeozoic, and outstanding issues remain concerning museum 'dark data' and taxonomic 'waste-baskets' taxa. These problems need to be tackled before an accurate understanding of macroevolutionary patterns can be established.

III. MATERIALS AND METHODS

(1) Species naming and publication data

To plot a collector's curve showing the number of species named over time, we compiled a list of all described Palaeozoic species of actinopterygians (totalling 516 species), including the authority naming the species and year the species was described.

To examine publication trends through time, we searched the literature for publications mentioning terms typically associated with early actinopterygians – "pal(a)eoniscid", "pal(a)eoniscoid", "pal(a)eonisciform" and "pal(a)eopterygian" (and their equivalent formal taxonomic names, e.g. Palaeoniscidae) – using Publish or Perish 6.49 (Harzing, 2007) to draw literature from Google Scholar and Crossref. This comes with the caveat that the resulting data does not include publications unavailable online. This may bias against older literature not initially published online, however most of the key works of early actinopterygian research from the 19th century are now available digitally, with text available 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.

Although originally used to define taxonomic ranks, these terms have gradually been recognised as paraphyletic or polyphyletic groups of Palaeozoic and Mesozoic actinopterygians with 'primitive' ray-fin characteristics (Patterson, 1982; Gardiner & Schaeffer, 1989; Gardiner, Schaeffer, & Masserie, 2005). In recent analyses these groups are paraphyletic, and most descriptions of new Palaeozoic actinopterygians do not assign taxa to them (e.g. Choo *et al.*, 2019; Figueroa, Friedman and Gallo, 2019; Newman *et al.*, 2021). The general trend has been towards the view that these terms are taxonomically redundant and of no functional use, yet some descriptions still refer to them (Mickle, 2011) and Mickle (2012) considered the Palaeonisci, Palaeoniscimorpha and Palaeonisciformes to be natural groups.

Some attempts have been made to introduce a term for Palaeozoic actinopterygians of uncertain affinity that explicitly rejects monophyly of its constituent members. Regan (1923) initially used Palaeopterygii as a taxonomic group encompassing palaeoniscoids, chondrosteans and belonorhynchians. Subsequently, McCune and Schaeffer (1986) defined "Paleopterygii" as a non-monophyletic group including only fossils that do not share characters with modern groups. Friedman and Giles (2016) recently suggested reintroducing 'palaeopterygians' (*sensu* McCune and Schaeffer, 1986) as a non-taxonomic blanket term in place of "palaeoniscoids".

This summary highlights the complexity of the taxonomic history of Palaeozoic actinopterygians, particularly as they are often nested within one another (e.g. Palaeoniscoidei in Palaeoniscida/Palaeonisciformes) or are essentially equivalent (e.g. Palaeoniscida and Palaeonisciformes). Sallan (2014) provides a more detailed summary of the usage of and interplay between these terms in the literature.

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

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 (black line, Fig. 2). The number of described taxa starts to plateau in the 20th century, largely due to the foundational monographic descriptions of Agassiz (1833) and Traquair (1877). A slight increase in recent years indicates a resurgence of interest focussed around CT-based redescriptions of classic taxa (e.g. Coates and Tietjen, 2018), as well as local taxonomic reviews (e.g. Elliott, 2014, 2016). While unlikely to alter large-scale diversity patterns (Lloyd & Friedman, 2013) this uptick is suggestive of further hidden diversity in the fossil record of Palaeozoic actinopterygians in Great Britain, particularly with regard to redescription of material that has been untouched since the 19th and early 20th century.

Our global collector's curve, however, presents a very different trend (grey line, Fig. 2). During the 19th century, our global curve roughly tracks that of Great Britain, albeit with slightly higher cumulative counts. This is largely due to the works of Agassiz (1833) and Traquair (1877), who produced monographic descriptions of actinopterygians from Belgium, France and Germany, though there were a host of other important contributions (e.g. Hancock and Atthey, 1872; Frič, 1879). In the late 19th century the global curve departs from the British curve, rising steadily in part due to significant contributions from Aldinger (1937) and Gardiner (1969), who described new taxa from Greenland and South Africa respectively. From the late 1970s the global collector's curve accelerates at a faster and steadier rate than at any time previously. This corroborates statements that the fossil record of Palaeozoic actinopterygians is undersampled (Sallan & Coates, 2010).

New Palaeozoic actinopterygian taxa continue to emerge from well-sampled regions such as Europe (e.g. Elliott, 2016; Štamberg, 2016; Bakaev and Kogan, 2020; Newman *et al.*, 2021) and North America (e.g. Mickle, 2017, 2018; Wilson, Pardo and Anderson, 2018). Importantly however, underrepresented regions such as Australia (Choo, 2012, 2015; Choo *et al.*, 2019), and South America (Figueroa *et al.*, 2021) are also producing new taxa. In addition, the widespread adoption of CT scanning allows valuable redescriptions and taxonomic revisions of existing material (Giles & Friedman, 2014; Giles *et al.*, 2015, 2017; Pradel *et al.*, 2016; Coates & Tietjen, 2018; Friedman *et al.*, 2018; Argyriou *et al.*, 2018; Figueroa *et al.*, 2019). 'Dark data' in museums (Allmon *et al.*, 2018) will continue to play a major role in unearthing new actinopterygian taxa: recent work found that museum collections contained 23 times more localities than recorded in the PBDB for Cenozoic marine invertebrates (Marshall *et al.*, 2018), hinting at unrecognised taxonomic diversity not currently captured in publicly available occurrence databases. For example, Mickle (2017) notes 'hundreds' of Tournaisian actinopterygian specimens in North American museums, many referred to genera of dubious monophyly.

(2) Publication trends

Another way of assessing research interest into Palaeozoic actinopterygians is to investigate the number of citations referring to them through time. We investigated use of the terms "palaeoniscoid", "palaeoniscid", "palaeonisciform", and "palaeopterygian", all of which are commonly associated with Palaeozoic actinopterygians (see Materials and Methods).

There is a steady increase in the number of citations referring to Palaeozoic actinopterygians over the last half century (Fig. 3), broadly coinciding with the uptick in the global collector's curve. Use of the term "palaeoniscid" dominates research until the late 1950s, when the terms "palaeonisciforms" and "palaeoniscoids" start to become more prominent. There are sporadic appearances of "palaeopterygians" in 20th century literature following Regan's (1923) initial use. However, usage of the term did not increase following McCune and Schaeffer's (1986) redefinition of it. A small increase in recent years may reflect Friedman and Giles' (2016) renewed suggestion to use it as a term with no implications of taxonomic groupings. The predominant term in 21st century literature is "palaeonisciformes", though "palaeoniscoid" and "palaeoniscid" remain prevalent. From the list of terms and publications above it is clear that there is a lack of convergence on a single term for Palaeozoic actinopterygians and citation data reflects this.

The rate of description of new species of Palaeozoic actinopterygians remains high (Fig. 2) and it is clear from the expanding body of literature that research interest continues to grow (Fig. 3). However, the majority of studies are taxonomic or descriptive, with comparatively few macroevolutionary studies (Sallan, 2014). Consequently, our understanding of patterns of diversity and the impact of mass extinctions in ray-fins lags behind that of other taxonomic groups.

V. PROBLEMS IN DECIPHERING THE PALAEOZOIC ACTINOPTERYGIAN FOSSIL RECORD

(1) Currently available occurrence data

A large proportion of recent diversity studies for fossil groups rely on occurrence data from the Paleobiology Database. However, most diversity studies on actinopterygians rely on published compendia or datasets compiled from the literature and rarely entered into the PBDB (see Vázquez and Clapham [2017] for an exception). Occurrence data from the PBDB poorly represents osteichthyans (Lloyd & Friedman, 2013), and particularly ray-finned fishes. We demonstrate this by generating Palaeozoic actinopterygian diversity curves for genera, collections, formations and equal-area grid cells based on occurrence data currently available from the PBDB (Fig. 4). The genus-level curve is almost flat, with upward trends in the Tournaisian-Visean and fluctuating patterns in the Wordian–Changhsingian, and there are no data for several time periods.

This pattern demonstrates major gaps and inaccuracies in the currently available occurrence data for the bulk of the Palaeozoic. Only four genera (eight species) of actinopterygians are entered for the entire Devonian; less than the number described in the literature for just the Famennian (Dunkle, 1964; Dunkle & Schaeffer, 1973; Taverne, 1997;

Daeschler, 2000; Prokofiev, 2002; Friedman & Blom, 2006). A cursory search of the literature shows ~100 published Visean localities, with many more likely represented in museum 'dark data' (Sallan & Coates, 2010; Marshall *et al.*, 2018), but less than 50 actinopterygian taxa stemming from around 30 collections are currently recorded in the PBDB for the entire Carboniferous. Inconsistencies between regional substages and ICS stages mean that there are only two Serpukhovian occurrences of actinopterygians in the PBDB, despite it having the highest raw count of genera in the Devonian and Mississippian (Sallan & Coates, 2010). In the PBDB, no stage between the Kasimovian and Kungurian has more than four genera of actinopterygians, highlighting how poor the late Carboniferous and early Permian data are. This is partly due to genuinely low numbers of marine actinopterygians in this period (Hurley *et al.*, 2007; Friedman, 2015; Romano *et al.*, 2016) perhaps linked to a paucity of marine deposits (McGowan & Smith, 2008; Friedman & Sallan, 2012). It is clear, however, that the substantial freshwater actinopterygian fossil record from the late Carboniferous-early Permian is absent from the PBDB (Beltan, 1978, 1981; Forey & Young, 1985; Murray, 2000; Soler-Gijón & Moratalla, 2001; Evans, 2005; Štamberg & Zajíc, 2008; Šimůnek & Cleal, 2020). In contrast, the late Permian actinopterygian fossil record is better represented, in large part due to targeted entry of data for studies relating to the End-Permian Mass Extinction (e.g. by Vázquez and Clapham [2017]).

(2) Taxonomic issues

Deep-seated problems with Palaeozoic actinopterygian taxonomy exacerbate low levels of actinopterygian genus richness, despite considerable morphological variation and high numbers of species within these genera (Fig. 5). Many genera from this period have apparently global distributions and stratigraphic ranges spanning nearly the entirety of the Carboniferous and Permian (Gardiner, 1993; Sepkoski, 2002; Sallan, 2014). This is likely an artefact of reduced researcher effort in this period in favour of earlier Devonian forms, or later Mesozoic forms (Sallan, 2014). As a result, many late Palaeozoic have not been the subject of detailed taxonomic work.

Carboniferous and Permian actinopterygians received the most attention from researchers in the 19th and early 20th centuries. While much of this work was ground-breaking and laid the foundations for palaeoichthyology, there are substantial problems with some outcomes of the research, notably the existence of wide-ranging, poorly defined genera. Often, initial descriptions of taxa were brief and erected new genera with a heavy reliance on the shape of the body (e.g. deep-bodied, fusiform, slender) and scale morphology (Agassiz, 1833; Traquair, 1877b, 1879; Moy-Thomas & Dyne, 1938). This led to poorly defined genus diagnoses, often containing large numbers of dubiously-related species – species whose characteristics sometimes even contradicted generic diagnoses. Some of the most notable problem genera—also termed "waste-baskets" (Evans, 2005) and "trash fish" (Coates & Tietjen, 2018)—are *Palaeoniscum* Blainville 1818, *Elonichthys* Giebel 1848 and *Platysomus* Agassiz 1843 (Mickle, 2017), though others exhibit similar issues (e.g. *Acrolepis* Agassiz 1843, *Amblypterus* Agassiz 1843 and *Rhadinichthys* Traquair 1877). Higher-level taxonomic groups based on these genera, which are almost exclusively erected with generic diagnoses (Sallan, 2014), suffer from the same problems. The outcome is that many Palaeozoic and early Mesozoic actinopterygians jump between largely meaningless orders and families.

In addition to being taxonomically confusing, several early Palaeozoic actinopterygian genera likely obscure a significant proportion of genus-level diversity. We review three taxa below, noting problems with their initial diagnoses, valid and invalid species, their temporal and geographic range, work that has been done to address these issues, and what needs to be done in the future. Mickle (2017) also provides a comprehensive overview of the problems associated with *Palaeoniscum*, *Elonichthys* and *Rhadinichthys* (see also Appendix S1).

(a) Palaeoniscum

Palaeoniscum was erected alongside *Paleothrissum* Blainville 1818 in the early 19th Century (Blainville, 1818). Not long after, Agassiz (1833), incorporated *Paleothrissum* into *Palaeoniscum* and erected a new genus, *Palaeoniscus* (though the type remained that of *Palaeoniscum*). Subsequent authors have used both taxon names interchangeably (Troschel, 1857; Traquair, 1877a, 1877b; Woodward, 1891; Jordan & Evermann, 1917), in part due to its vague and unspecific diagnosis (see Supplementary Material for diagnoses and detailed overview of taxonomic problems). This has led to much taxonomic confusion (Mickle, 2017), and specimens ranging from the Tournasian through to the Wuchiapingian have been referred to *Palaeoniscum*. This genus is almost certainly a taxonomic 'waste-basket'. Future workers should refer to Aldinger's (1937) comprehensive diagnosis of the type species, *P. freieslebeni* Blainville 1818, and attempt to identify shared traits to better distinguish the genus. Until that point, *P. freieslebeni* could be considered the only valid species of *Palaeoniscum* (Mickle, 2017).

(b) Elonichthys

Elonichthys is a paraphyletic or polyphyletic waste-basket genus (Schultze & Bardack, 1987; Long, 1988; Malabarba, 1988; Gardiner & Schaeffer, 1989; Schindler, 1993; Mickle, 2017) reported in most Carboniferous deposits yielding actinopterygians. Poor preservation of the type species (*E. germari* Giebel 1848) prevented a comprehensive diagnosis, but numerous later studies referred material to the genus (Fig. 5a & b). As a result, '*Elonichthys'* grew to encompass a vast number of poorly defined taxa that lack shared characteristics (Long, 1988; Schindler, 1993, 2018). Though doubts about the genus were noted as early as the 1890s (Woodward, 1891) it was not until recently that Schindler (2018) restricted it to the type species plus *E. fritschi* Friedrich 1878 and *E. krejcii* Frič, 1895. A detailed summary of the taxonomic problems associated with the genus is given in the Supplementary Information.

'Elonichthys' encompasses a substantial portion actinopterygian biodiversity extending from the Tournaisian through to the Anisian. The recent work of Schindler (2018) is an essential first step to rectifying this. Identification of additional characters will be necessary to adequately define species and determine whether they truly belong to *Elonichthys*. CT scanning, particularly of cranial material, will help reveal more diagnostic characters. Museum specimens collected and given labels in the 19th and 20th centuries will require careful revision (e.g. '*E.*' *multistriatus* in NHM and NMS collections: S. Henderson pers. obs.).

(c) Platysomus

The genus *Platysomus* includes 17 Palaeozoic species over a nearly 100 million time period (Visean to Changhsingian) and broadly encompasses taxa with a deep-bodied morphology (Fig. 5c & d). The monophyly of the genus (and higher taxonomic ranks such as Platysomidae) has been questioned almost since its erection, and its relationships with other deep-bodied actinopterygians such as amphicentrids and bobasatraniids is unclear. A detailed overview is given in the Supplementary Information.

Despite poor preservation in the type species, unique characters do exist (e.g. the combination of suborbitals and a dermal quadratojugal: Mickle and Bader, 2009: fig. 5b), and CT-based investigations may clarify these features and identify new ones. Obvious violations of the diagnoses, such as the presence of a pelvic fin in some species, should also be addressed. A conservative approach may be to consider the type as the only valid species of

Platysomus and reassess all other species: Zidek (1992) suggested that all *Platysomus* species should remain in the genus until revision. Poor understanding of the anatomy and taxonomy of *Platysomus* species prevents their inclusion in phylogenetic analyses, with repercussions for downstream analyses looking at evolutionary drivers of deep-bodied morphotypes.

(d) Other problematic taxa

While the three examples above account for a significant proportion of the taxonomic uncertainty plaguing Palaeozoic actinopterygians, they are far from the only genera with convoluted or questionable validity. For example, the genus *Rhadinichthys* (Fig. 5e) contains 24 species described from Belgium, Canada, Ireland, Poland, Russia, the UK, Uruguay and the USA, and spanning the Frasnian to the early Permian, despite extremely variable morphology. Similarly, 16 species belong to the genus *Amblypterus* from Czechia, France, Germany, India, Russia and Spain, spanning the Kasimovian to Capitanian (Štamberg, 2013). Another example that highlights the need for detailed reinvestigation is that of *Namaichthys molyneuxi*. Woodward (1903) originally described this taxon under the genus name *Acrolepis molyneuxi*, and Gardiner (1962) moved it to *Namaichthys*, a genus initially erected by Gürich (1923). Specimens in the Natural History Museum (London) collection, however, bear the label *Watsonichthys molyneuxi* (S. Henderson, personal observation).

In recent years, new anatomical information revealed by CT scanning has prompted several reinvestigations of the validity of Palaeozoic taxa. Coates and Tietjen (2018) recently redescribed a Bashkirian actinopterygian and moved it to *Trawdenia* n. gen. This specimen was originally referred to *Mesopoma*, a taxon erected by Traquair (1890) in an attempt to separate species belonging to *Canobius* and *Rhadinichthys*. Traquair subsequently retracted the genus (Traquair, 1912), before Moy-Thomas and Dyne (1938) restored it (see Coates, 1993, 1998; Coates and Tietjen, 2018). *Trawdenia* exemplifies the root cause of the problem with many Carboniferous and Permian actinopterygian genera: a diagnosis based on characteristics prevalent in other late Palaeozoic actinopterygians and lacking unambiguous synapomorphies.

Reinvestigation of Palaeozoic material is not simply an exercise in correcting taxonomy, however. Coates (1999) and Coates and Tietjen's (2018) work revealed previously-hidden features of the endocast and pectoral fin in a specimen that had been known to the literature for over a century. The case of *Trawdenia*, as well as others such as *Eurynotus crenatus* (Friedman *et al.*, 2018) and *Brazilichthys macrognathus* (Figueroa *et al.*, 2019), clearly demonstrate that reinvestigation can reveal untold anatomical, ecological, and taxonomic diversity.

(3) Phylogenetic issues

Relationships of the four extant actinopterygian clades (Cladistia, Chondrostei, Holostei, Teleostei) has reached a point of consensus through both molecular (e.g. Betancur-R *et al.*, 2017; Hughes *et al.*, 2018) and morphological (e.g. Patterson, 1982; Gardiner and Schaeffer, 1989; Coates, 1998; Cloutier and Arratia, 2004; Grande, 2010; Xu, Gao and Finarelli, 2014; Giles *et al.*, 2017) research. Sallan (2014) provided a detailed summary of previous hypotheses of living clades and the basis for this consensus. The relationships of extinct forms of actinopterygians, both in relation to each other and the extant clades, however, are less clear.

Phylogenetic hypotheses of Palaeozoic actinopterygians traditionally place the vast majority of taxa within the crown, with only the Devonian taxon *Cheirolepis* consistently resolved on the stem (e.g. Patterson, 1982; Gardiner, 1984; Gardiner and Schaeffer, 1989; Coates, 1999). Even some of the earliest actinopterygians have been recovered as stemactinopterans (Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner *et al.*, 2005; Near *et al.*, 2012) or even stem-neopterygians (Hurley *et al.*, 2007), with most late Palaeozoic taxa oscillating between the actinoperan and neopterygian stem. No Palaeozoic taxa are associated with the polypterid or chondrostean total groups in these analyses, with the exception of the late Palaeozoic-Mesozoic genus *Saurichthys* as a stem chondrostean (Gardiner *et al.*, 2005; Sallan, 2014), although recent analyses refute this topology (Giles *et al.*, 2017; Latimer & Giles, 2018; Argyriou *et al.*, 2018). The crown-group affinity of most Palaeozoic actinopterygians was challenged by both Zhu and Schultze (2001) and Cloutier and Arratia (2004), who recovered a number of taxa as branching outside of the living radiation, although neither of these studies focussed on actinopterygians. Mickle, Lund and Grogan (2009) recover a host of Palaeozoic taxa on the actinopterygian stem, as well as identifying stem cladistians, but their analysis has a series of issues relating to taxon inclusion and character coding, as well as a sub-optimal tree construction methodology (Sallan, 2014).

In 2017, an analysis stemming from a greatly expanded morphological character matrix alongside nuclear genes posited a major upheaval of early actinopterygian relationships (Giles *et al.*, 2017). Crucially, this study recognised that Triassic scanilepiforms are well-supported as stem cladistians, and that the apparently primitive morphology of extant cladistians is the result of several reversals and autapomorphies. A major consequence of this discovery was that most Palaeozoic taxa were removed from the actinopterygian crown (Fig. 6). The analysis also brought molecular estimates of clade origins more in line with fossil evidence by excluding calibration points for poorly-supported nodes. Finer-scale relationships amongst Palaeozoic actinopterygians remain in a state of flux, however. For example, all post-Devonian taxa form a clade in (Giles *et al.*, 2017), and many Devonian species form a monophyletic group. This Devonian clade is replicated by Argyriou *et al.* (2018) and Figueroa, Friedman and Gallo (2019) but not by Latimer and Giles (2018) or

Wilson, Pardo and Anderson (2018). Wilson, Pardo and Anderson (2018) additionally recover more than one radiation of post-Devonian actinopterygians. This variation is despite all analyses using matrices derived from that of Giles *et al.* (2017). Relationships amongst Carboniferous and Permian (and younger) stem actinopterygians are extremely volatile across all analyses, with few substantiated or well-supported clades.

A further peculiar result is the recurrent placement of chondrosteans and cladistians as sister-clades (Latimer & Giles, 2018; Argyriou *et al.*, 2018), clearly at odds with the molecular and morphological consensus. These may be a result of failure to identify Palaeozoic members of these radiations: huge temporal gaps exist between the fossil record of definitive crown group members and the supposed origination of the clade (Sallan, 2014; Friedman, 2015, fig. 3). As with the tetrapod fossil record (Pardo, Lennie, & Anderson, 2020), many Palaeozoic actinopterygians are morphologically distinct from even early members of extant radiations, partly as a result of living groups' substantial diversification (Sallan, 2014). There may be a genuine lack of early fossil members of major clades; the paucity of marine late Palaeozoic deposits could be a contributing factor given the marine origin of most crown groups of actinopterygians in this period (Betancur-R, Ortí, & Pyron, 2015). However, it is more likely that many Palaeozoic actinopterygians simply have not been investigated in enough detail to determine whether they could be early members of living radiations, as was the case for the early Mesozoic *Fukangichthys* (Giles *et al.*, 2017).

A number of factors contribute to this phylogenetic instability, not least of which is choice of character matrix and taxon sampling. Absence of data in the form of missing morphological codes in character-by-taxon matrices is partly responsible, as is the use of composite taxa, especially for genera of dubious monophyly. However, failure to include many of the Palaeozoic taxa described in the literature, as well as oversight of the many specimens in museum collections, is perhaps the most significant factor. Most analyses focused on broad-scale investigations of early actinopterygians contain roughly even numbers of Devonian and Carboniferous taxa (Coates, 1999; Gardiner *et al.*, 2005; Giles *et al.*, 2017), despite there being an order of magnitude more species described from the Carboniferous (Fig. 6). Potentially even more problematic is the fact that these studies never sample more than a few Permian species, despite the nearly equivalent numbers of Permian species relative to the Carboniferous (Fig. 6). Work remedying this is already underway using techniques such as CT-scanning (Giles *et al.*, 2015; Pradel *et al.*, 2016; Coates & Tietjen, 2018; Friedman *et al.*, 2018; Figueroa *et al.*, 2019, 2021) and more traditional descriptive work (Choo, 2015; Štamberg, 2016; Mickle, 2017, 2018; Stack *et al.*, 2020). In particular, CT-scanning will be critical in revealing internal anatomical details and increasing the number of phylogenetically informative characters beyond the dermal bones, which are often very similar among Palaeozoic actinopterygians (Figueroa *et al.*, 2019). Beyond this, however, numerous proposed Palaeozoic actinopterygian clades are yet to be included in broader phylogenetic analyses despite either high support in the literature (e.g. eurynotiforms: Sallan and Coates, 2013; Friedman *et al.*, 2018) or in-group cladistic analysis (e.g. haplolepids: Elliott, 2014). In addition, important clades are often only represented by a single terminal (e.g. platysomids: Giles *et al.*, 2017)). Including unrepresented groups of Palaeozoic actinopterygians in phylogenetic analyses is a critical step for furthering our understanding of their evolution and relies on detailed morphological descriptions.

At present, understanding of the relationships of early actinopterygians is extremely limited. This represents a critical barrier to progressing our understanding of the evolution of the Actinopterygii in their early evolutionary history, and precludes asking questions about what is driving phenomena such as the emergence of novel body forms, origins of clades, and responses to mass extinctions.

(4) Fossil record biases

A major obstacle to accurately interpreting the evolution of Palaeozoic actinopterygians is the various forms of sampling bias that pervade their fossil record, which are related to both geological, geographic and anthropogenic factors. The number of occupied grid cells has been suggested as the best proxy for explaining the richness of all fishes in the fossil record of Great Britain, though osteichthyan richness does not correlate with any proxy (Lloyd & Friedman, 2013). Investigations into the effect of geological, spatial and taphonomic biases on the actinopterygian fossil record are in their infancy, and the extent to which observed patterns of diversity are driven by biases is far from understood. Here we attempt a qualitative overview of some of the major sampling biases affecting the Palaeozoic actinopterygian fossil record.

(a) Geological biases

The extent to which observed patterns of diversity are the result of rock record biases and correlate with metrics such as the numbers of formations, rock volume or outcrop area is the subject of much debate (Benton, 2015). There are three main hypothesised mechanisms for correlation: 1) a true bias, where diversity patterns are truly dependent on the rock record (Smith, 2001; Peters & Foote, 2001); 2) common cause, where another factor such as sea level (and associated extent of shallow marine sea area and presence of epicontinental seas) 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). Determining the extent to which geological biases such as these drive the actinopterygian record needs comprehensive occurrence-based datasets (Friedman & Sallan, 2012).

(b) Geographic and spatial biases

Europe and North America are the most intensely sampled regions in the marine animal fossil record as a whole (Close *et al.*, 2020b). The vast majority of Palaeozoic actinopterygian occurrences are also from Europe and North America, with important, though limited, occurrences from South America, Australia and Africa: this distribution is likely due to sampling intensity rather than true diversity. These biases hark back to the early descriptions of actinopterygians (particularly from the UK), which are intimately linked to extensive mining, extraction and industrialisation of these regions during the 19th and early 20th centuries (e.g. Agassiz, 1833; King, 1850; Jackson, 1851b). More broadly, recent work demonstrates just how important (neo-)colonialism and European exploitation is as a contributing factor to the global skew in palaeontological research outputs and therefore occurrence data (Raja *et al.*, 2021).

For much of the Palaeozoic, what is now Europe and North America were part of the same supercontinent, centred around the palaeoequator (Ziegler *et al.*, 1979; Scotese, 2001, 2014), which gradually drifted north and became part of Pangaea (Stampfli *et al.*, 2013). The palaeolatitudinal occurrences of Palaeozoic-Mesozoic actinopterygians present in the PBDB track the migration of these continents from low- to mid-palaeolatitudes (Fig. 7). Geographic bias in the actinopterygian fossil record is clear from fossil occurrence data, with higher sampling of low-palaeolatitudes in the Palaeozoic shifting to mid-palaeolatitudes in the Mesozoic, as in the marine record (Close *et al.*, 2020b). Variation in taxonomic practice can also impact richness counts depending on the number of researchers working on certain groups and time periods, and whether these researchers are the same for all time periods (Lloyd, Young, & Smith, 2012b, 2012c). This variation may contribute to higher diversity in Europe relative to other continental regions (Close *et al.*, 2020b), though higher diversity is also likely intimately linked to historical and ongoing scientific colonialism (Raja *et al.*, 2021).

Spatial biases also have a substantial impact on diversity trends at global scales due to temporal variability in the fossil content, fossil quantity, and palaeogeographical coverage of assemblages. The ‘global’ fossil record of any group in fact consists of occurrences distributed heterogeneously in space and time (Benson *et al.*, 2016; Close *et al.*, 2017, 2020a, 2020b), and is better conceptualised as the sum of multiple regional records with different attributes (Close *et al.*, 2020a). Diversity curves representing ‘global’ counts of taxa are therefore not a true representation of the peaks and troughs in diversity of a group through time, but instead a combined record of the regional diversity in sampled areas. The effect of this is such that changes in diversity through time mainly mirror changes in the spatial extent of the groups’ fossil record between sampled intervals (Close *et al.*, 2020a, 2020b). Notably, the ‘common cause’ (Peters, 2005, 2006; Peters & Heim, 2010, 2011; Hannisdal & Peters, 2011) and ‘redundancy’ (Benton *et al.*, 2011, 2013; Dunhill, Hannisdal, & Benton, 2014; Benton, 2015) hypotheses do not explain this substantial source of sampling bias (Benson *et al.*, 2016; Close *et al.*, 2017, 2018, 2019, 2020a). This is not to say that studies of the ‘global’ fossil record of specific taxonomic groups are uninformative, only that patterns must be carefully examined and interpreted with the knowledge that they likely exhibit significant spatial structuring. Diversity at the regional scale will be informative in determining specific drivers of, and biases in, the diversity signal (Crampton *et al.*, 2003; Dunhill *et al.*, 2012, 2013, 2014; Close *et al.*, 2020a), as will examining differences between diversity measures (e.g. alpha and beta diversity), which can also be spatially dependent (Womack, Crampton, & Hannah, 2021). Different spatial biases acting on the freshwater and marine records may also variably impact different diversity estimates, dependent on the attributes of the sampled regions (Lagomarcino & Miller, 2012). For example, the species-area effect (Hallam & Wignall, 1999; Peters, 2005, 2007; Hannisdal & Peters, 2011; Close *et al.*, 2020b) may play a role in levels of marine actinopterygian biodiversity, linked to changes in sea level and associated features (Lagomarcino & Miller, 2012; Jones *et al.*, 2021)), whereas other factors may drive freshwater actinopterygian diversity. Discrepancies in dispersal between freshwater and marine actinopterygians are also likely to have an impact. These potential contributing factors result in potentially complex drivers of regional heterogeneity in the actinopterygian fossil record.

(c) Taphonomic biases

The impact of taphonomic processes and biases on the Palaeozoic actinopterygian fossil record has not been investigated. Taphonomic biases not only obscure underlying biological signals and impact perceived diversity, but likely influence understanding of other aspects of actinopterygian evolution, such as the degree of functional disparity or ecospace occupation (Smithwick & Stubbs, 2018). The effects of detrimental taphonomic processes varies geographically, between environments and with time (Brett, 1995; Zohar *et al.*, 2008; Walker, Dunhill, & Benton, 2020), though low-energy, anoxic environments in which individuals were rapidly buried are usually those that best preserve vertebrates, i.e., Lagerstätten (Pardo *et al.*, 2020).

In recent years, literature has emerged on quantifying the skeletal completeness of the fossil record of various vertebrate groups using both character-completeness metrics (e.g. Mannion and Upchurch, 2010; Brocklehurst and Fröbisch, 2014; Cashmore *et al.*, 2020) and specimen-based completeness metrics (e.g. Cleary *et al.*, 2015; Tutin and Butler, 2017; Driscoll *et al.*, 2019). To date, there are no published studies investigating completeness in any groups of fishes (but see Schnetz et al. [2021]), and it is likely that an anthropogenic collecting bias towards more complete specimens may come into play more than in tetrapod groups. The fossil record of marine tetrapod clades appear to be more complete than those of terrestrial tetrapods

(Cleary *et al.*, 2015; Tutin & Butler, 2017; Driscoll *et al.*, 2019), likely due to higher sedimentation rates in the marine realm. Quantification of the level of skeletal completeness in actinopterygians will aid interpretations of the biases acting on the fossil record, especially regarding marine versus freshwater fishes.

An additional taphonomic factor that may detrimentally impact our understanding of the actinopterygian fossil record is degree of preservation related to the size of specimens. There is data to suggest that larger organisms are much more likely to preserve than smaller organisms (Benson, 2018; Pardo *et al.*, 2020). The extent to which this applies to aquatic vertebrates is little understood, but this is likely to be of importance to actinopterygians: Sallan and Galimberti (2015) suggested that ray-finned fish were small in the aftermath of the EDME. As the early Carboniferous coincides with the origin of the actinopterygian crown (Giles *et al.*, 2017), and small ancestors are thought to have seeded most actinopterygian clades (Romano *et al.*, 2016, Guinot and Cavin, 2018), a bias against preservation of smaller organisms may contribute to the failure to identify early members of these radiations. The environment of deposition is also relevant: hypothesised ancestors of most actinopterygian clades existed in marine environments (Betancur-R *et al.*, 2015), which typically have higher energy and disturbance levels that may bias against preservation of small actinopterygians (Cooper *et al.*, 2006). Furthermore, taphonomic factors have been shown to readily destroy small actinopterygian bones in particular (Smith, Stearley, & Badgley, 1988) further compounding our ability to correctly interpret the early actinopterygian fossil record.

(d) Future mitigation

The sampling, spatial and taphonomic biases on the Palaeozoic global actinopterygian record are only beginning to be explored. Future, targeted sampling in underrepresented regions and environments, for example mid- to high-palaeolatitudes in the Carboniferous and marine environments in the Late Carboniferous-Middle Permian, may help to redress this imbalance. However, sampling biases cannot necessarily be 'fixed', and instead we should attempt to mitigate these biases using analytical techniques. Understanding these biases, and the interplay between them, is critical due to the potential impact that they can have on taxonomy, phylogeny, and subsequent attempts to investigate the evolution of a particular group such as actinopterygians.

VI. PROSPECTS FOR PALAEOZOIC ACTINOPTERYGIAN DIVERSITY STUDIES

Occurrence-based datasets are necessary for examining biases in the fossil record and deducing accurate diversity trends, while phylogenetic context is generally crucial for the kinds of macroevolutionary analyses that are increasingly common in the palaeontological literature. Fishes are rarely the subject of such analyses, but present ample opportunities. Occurrence datasets will enable sampling standardisation methods and robust phylogenetic hypotheses will facilitate a broad range of techniques. In conjunction, these methods may generate new hypotheses about the early evolution and diversification of actinopterygians.

(1) Sampling standardisation

Analytical methods of sampling standardisation (Chao, 1984, p. 198; Chao & Jost, 2012; Alroy, 2017, 2018, 2020), which estimate species diversity based on incomplete and uneven data are invaluable when attempting to deduce real patterns of palaeodiversity from the biases acting on the fossil record (Alroy, 2010; Close *et al.*, 2018). Since their introduction, these methods and their application continue to be refined, moving beyond temporal standardisation to spatial standardisation (Close *et al.*, 2020a; Jones *et al.*, 2021) and application at different scales (Close *et al.*, 2019). Application of these methods to the Palaeozoic actinopterygian fossil record could help to tease apart genuine diversity patterns from the trends created by fossil record biases. However, these methods require occurrence-level datasets that are not currently available for Palaeozoic actinopterygians and compiling these data represents a priority for future studies.

(2) Phylogenetic inference

Macroevolutionary studies on early actinopterygians are in their infancy, in large part due to the absence of robust phylogenetic hypotheses. Despite major reworking of actinopterygian characters, stability is still low for most Palaeozoic taxa (Giles *et al.*, 2017). Although the stem-group affinity of most Palaeozoic actinopterygians in recent, comprehensive phylogenetic analyses (Giles *et al.*, 2017; Latimer & Giles, 2018; Argyriou *et al.*, 2018; Figueroa *et al.*, 2019) was foreshadowed by some previous studies (Cloutier & Arratia, 2004; Mickle *et al.*, 2009), these had issues with character selection, coding and reversals, as well as intensely sampling the earliest actinopterygians relative to crown members (Sallan, 2014). This likely exacerbates differences in character polarities and precludes identification of synapomorphies (Sallan, 2014). Giles *et al.* (2017) laid the foundation for an improved actinopterygian character-by-taxon matrix. Continued addition of important taxa and well-formulated characters (Brazeau, 2011), as well as better methods for dealing with inapplicable characters (Brazeau, Guillerme, & Smith, 2019; Goloboff *et al.*, 2021), will generate robust hypotheses of relationships with which to investigate key evolutionary events.

Bayesian methods of inference, such as tip-dating, which incorporates information about age into phylogenetic estimates to work out node ages and topology simultaneously, have rarely been applied to actinopterygians outside of nested teleost groups (e.g. Alexandrou *et al.*, 2013; Near, Dornburg and Friedman, 2014; Arcila *et al.*, 2015; Dornburg *et al.*, 2015; Dornburg, Friedman and Near, 2015; Close *et al.*, 2016; Arcila and Tyler, 2017)). Tip-dating methods may be able to tease apart relationships suspected to result from homoplasy (Lee & Yates, 2018), for example the various deep-bodied clades of Palaeozoic actinopterygians. At present, however, the temporal gaps between actinopterygian taxa in palaeontological phylogenetic datasets are too great, and phylogenetic hypotheses too unstable, for tip-dating to return valid hypotheses. Morphological character sets for actinopterygians also generally ignore autapomorphies, which can be important for tip-dating analyses (Matzke & Irmis, 2018). Accuracy of tip-dating improves when more tips for calibrations are near the root (Püschel *et al.*, 2020); for example, tip-dating analyses initially recovered unrealistically old node ages for tetraodontiformes due to inadequate numbers of fossil taxa (Arcila *et al.*, 2015), later rectified by addition of more fossil data and use of a fossilised-birth-death model (Close *et al.*, 2016; Arcila & Tyler, 2017). Phylogenetic datasets therefore require inclusion of more Palaeozoic actinopterygians to populate the tree and fill large temporal gaps currently only inhabited by a few representative taxa before exploring inference-based and other techniques.

(3) Phylogenetic comparative methods

Phylogenetic comparative methods (PCMs) are a suite of methods that explicitly use hypotheses of relationships when investigating macroevolutionary processes (Harmon, 2019; Soul & Wright, 2021). PCMs include node-age calibrations and divergence-dating (Hedman, 2010; Bapst, 2014; Warnock & Wright, 2021) often as a means of calculating rates of morphological evolution (Lloyd, Wang, & Brusatte, 2012a; Benson *et al.*, 2014; Wang & Lloyd, 2016; Halliday, Upchurch, & Goswami, 2016; Clarke, Lloyd, & Friedman, 2016) and assessing morphological disparity (Brusatte *et al.*, 2014; Lloyd, 2016; Wright, 2017; Moon & Stubbs, 2020). Phylogenetic signal also plays a role in analyses of evolutionary rates (Sakamoto & Venditti, 2018) and the links between morphology and ecology (Lamsdell *et al.*, 2017).

PCMs offer huge potential for understanding patterns of diversity and evolution but are generally yet to be applied to Palaeozoic actinopterygians. Deep-bodied actinopterygians represent an obvious test case for exploring these techniques, for example by quantifying convergence (Speed & Arbuckle, 2017; Arbour & Zanno, 2020), as results will be highly dependent on whether they are truly independent radiations or whether there is a degree of shared evolutionary history between them. Application of PCMs also has the potential to identify adaptive radiations (Close *et al.*, 2015; Ezcurra & Butler, 2018; Felice & Goswami, 2018; Halliday *et al.*, 2019; Simões *et al.*, 2020). Previous work on neopterygians investigated phenotypic evolution in holosteans and teleosts, finding that their evolutionary rates and innovation were comparable through the Early Permian to Early Cretaceous (Clarke *et al.*, 2016). Actinopterygians appear to diversify appreciably in the early Carboniferous. However, the lack of comprehensive phylogenetic analysis prevents testing of whether this pattern best fits a model of classic extinction recovery, adaptive radiation, or ecological release (Schluter, 2000; Sallan & Friedman, 2012; Friedman & Sallan, 2012; Slater, 2013).

Other PCMs permit reconstructing ancestral states of characters (Finarelli & Flynn, 2006; Puttick, 2016; Sallan *et al.*, 2018; Herbst, Li, & Steel, 2019; Ponti, Arcones, & Vieites, 2020), correlating evolution of separate traits (Soul & Wright, 2021), identifying regime shifts (Lamsdell & Selden, 2017; Soul & Wright, 2021), and assessing stratigraphic congruence (Bell & Lloyd, 2015). A pertinent example is that of shifts between marine and non-marine habitats (and coincident changes in morphology and disparity; Lamsdell, 2016). Previous ancestral-state based hypotheses of crown group habitats have inferred both a freshwater (Carrete Vega and Wiens, 2012; Betancur-R, Ortí and Pyron, 2015) and marine (Guinot & Cavin, 2018) origin for actinopterygians. Given recent upheavals in established schemes of phylogenetic relationships, with a particular effect on deep-branching members of stem-groups (e.g. Giles *et al.*, 2017), ancestral state reconstructions should be reassessed. As it may be physiologically easier to adapt from one environment to another (Betancur-R *et al.*, 2015), it may be prudent to explore the use of asymmetric transition models as recently used to investigate the evolution of oviparity and viviparity in squamates (Blackburn, 2015).

More broadly, by combining palaeoecological observations with reliable phylogenetic hypotheses, it will be possible to examine trends in actinopterygian ecology and biogeography through time (Lamsdell *et al.*, 2017). It is unclear whether Palaeozoic actinopterygians separate into biogeographical provinces and how biogeography changes through time, particularly in response to mass extinctions and changing continental configurations. Phylogeny is an important component in biogeographic network analyses investigating these patterns (Button *et al.*, 2017; Dunne *et al.*, 2018; Kubo, 2019). Phylogeny would also allow for alternative estimates of diversity such as lineage counts through time (also referred to as phylogenetic diversity; Ezcurra and Butler, 2018), that would complement taxic estimates of diversity patterns. Phylogenetic methods investigating survivorship and selectivity through mass extinctions among and between lineages (Soul & Friedman, 2017; Allen *et al.*, 2019) may reveal more detail on the effects of mass extinctions (Sallan & Friedman, 2012; Sallan & Galimberti, 2015)). To understand the origins of actinopterygian biodiversity and dominance, and quantify such patterns of evolution in the Palaeozoic, it is necessary to improve phylogenetic hypotheses.

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.

(4) There is now phylogenetic consensus about the relationships between living groups of actinopterygians, and recent upheavals have established that most Palaeozoic taxa are stem-actinopterygians. However, major temporal gaps exist between the origin age of crown groups as calculated by divergence estimates and the oldest known fossils. Inadequate

representation of Carboniferous and Permian forms in phylogenies feeds into this problem. Greater sampling of Carboniferous and Permian taxa in morphological matrices is necessary to identify early crown members and accurate relationships between stem- and crown-groups.

(5) Significant spatial and taphonomic biases act on the Palaeozoic actinopterygian record. It is clear that Europe and North America are the most intensely sampled regions (as in the overall vertebrate fossil record), yet the impact of all biases acting on the Palaeozoic actinopterygian record is yet to be investigated fully.

(6) Future work should focus on understanding and addressing issues and biases in the actinopterygian fossil record. For example, redescription and revision of taxonomy will help address taxonomic issues, studies of skeletal completeness may help assessment of taphonomic biases, and sampling standardisation of occurrence data will be valuable in deducing genuine diversity patterns. In parallel, construction of more stable phylogenies using new morphological data from renewed descriptive work will enable investigation of more complex, specific questions on extinction recovery and adaptive radiation, morphological convergence, and biogeography and habitat transitions. Collectively, these will greatly expand our understanding of the early evolution and rise to dominance of the most speciose extant vertebrate clade, the Actinopterygii.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article. **AppendixS1**. Detailed account of the state of research on the 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.

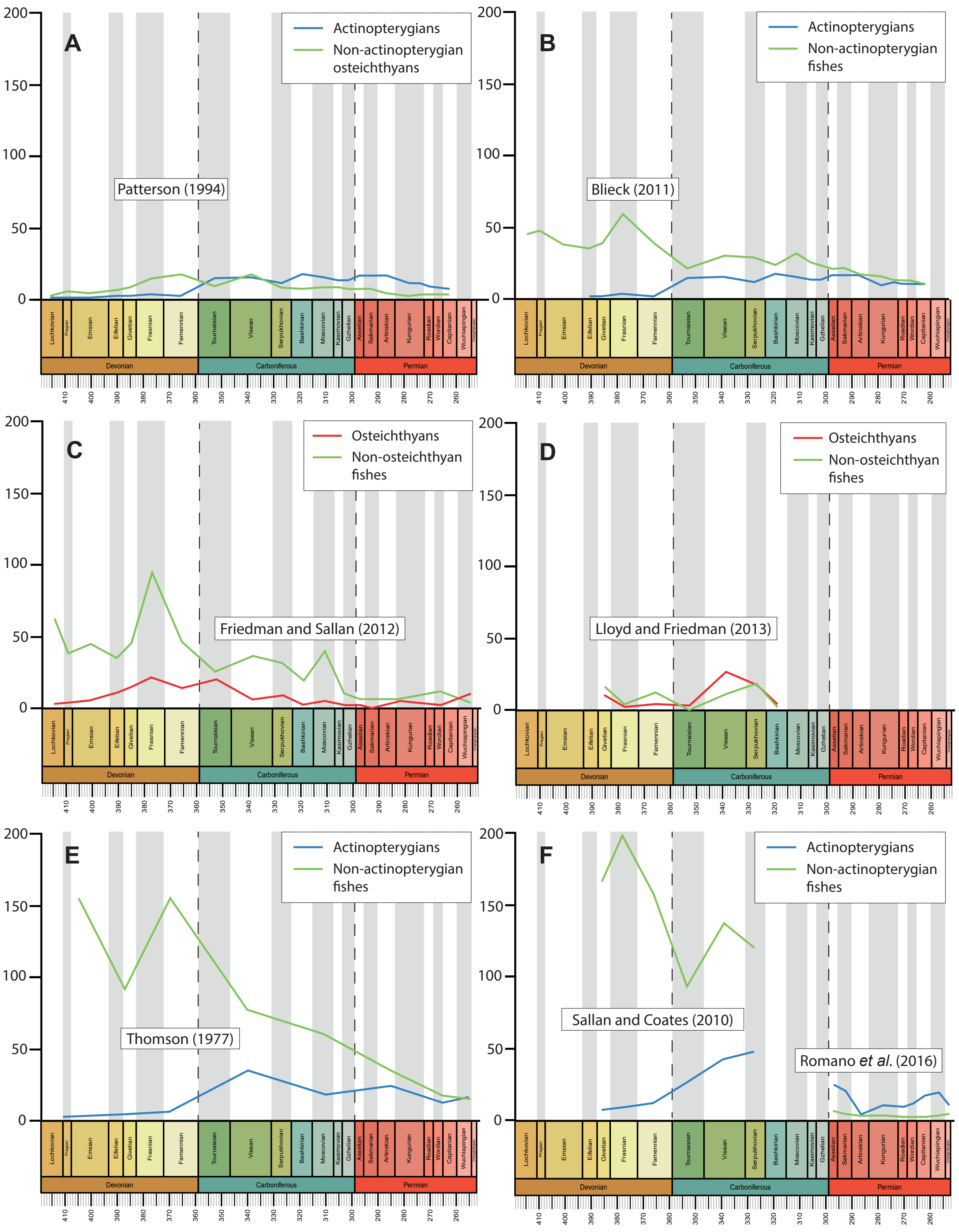
Figure 3 – Number of publications mentioning terms typically associated with Palaeozoic actinopterygians through time: 'palaeoniscid' (magenta); 'palaeonisciformes' (pink); 'palaeoniscoid' (light green); 'palaeopterygian' (dark green).

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.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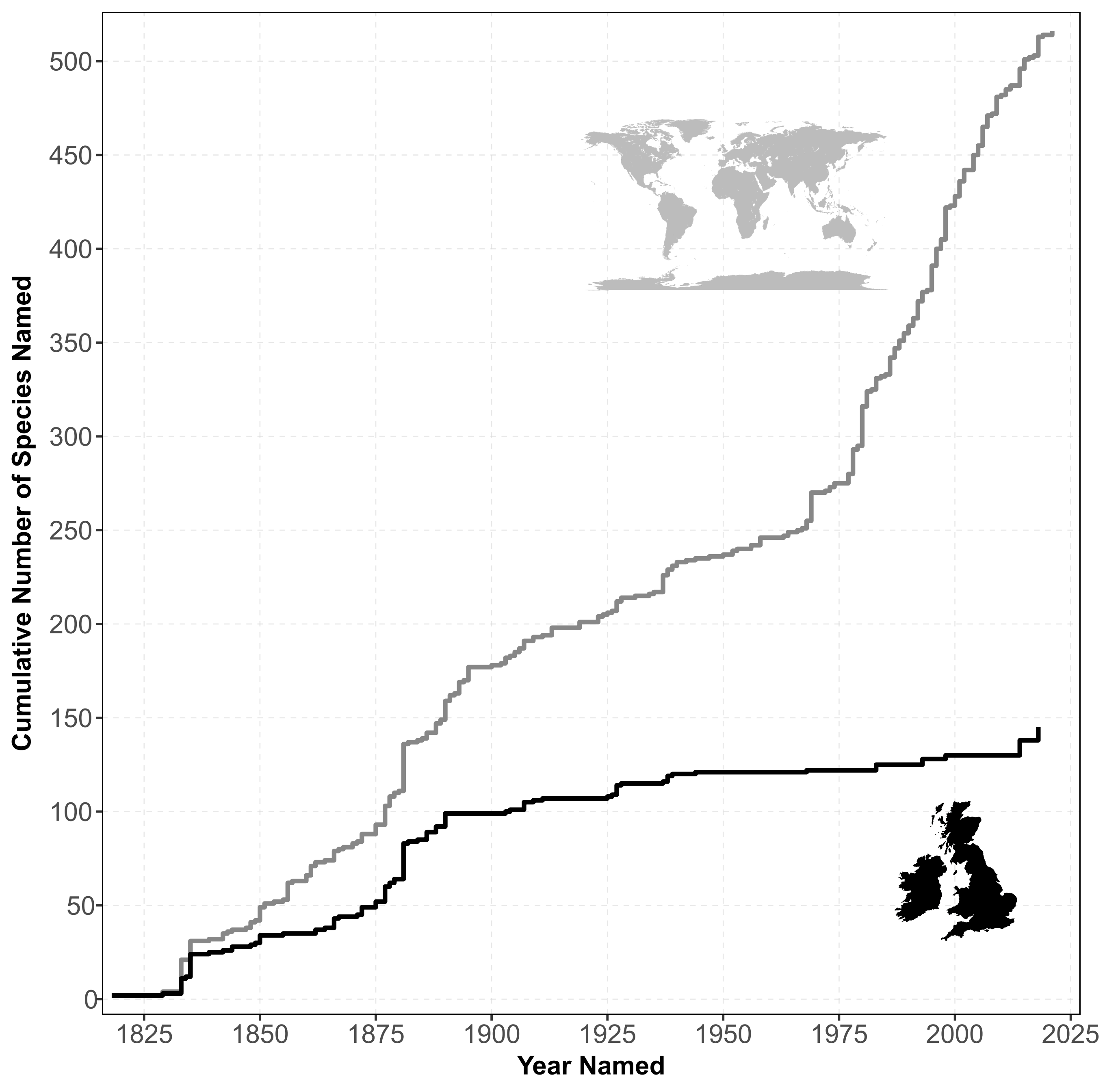
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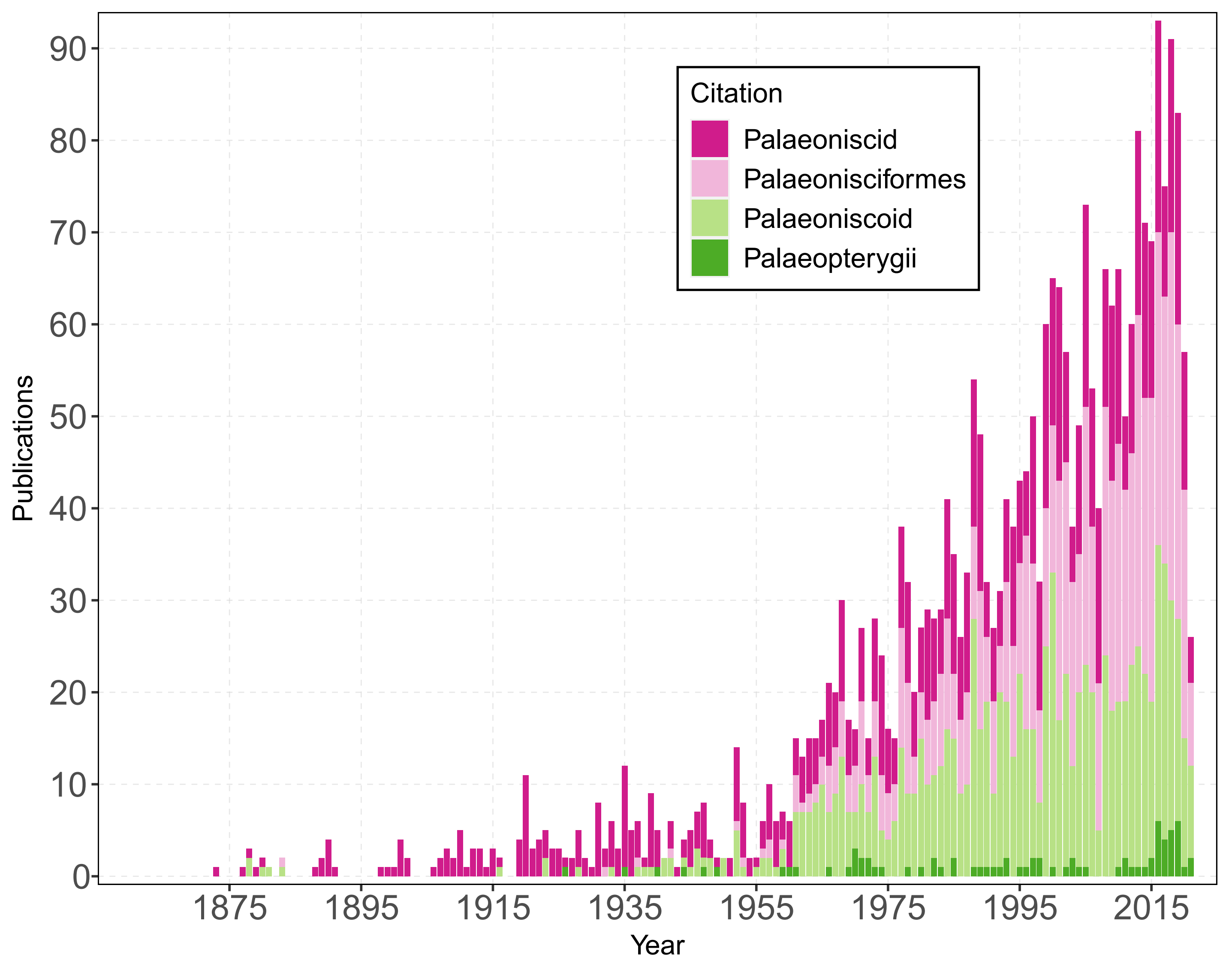
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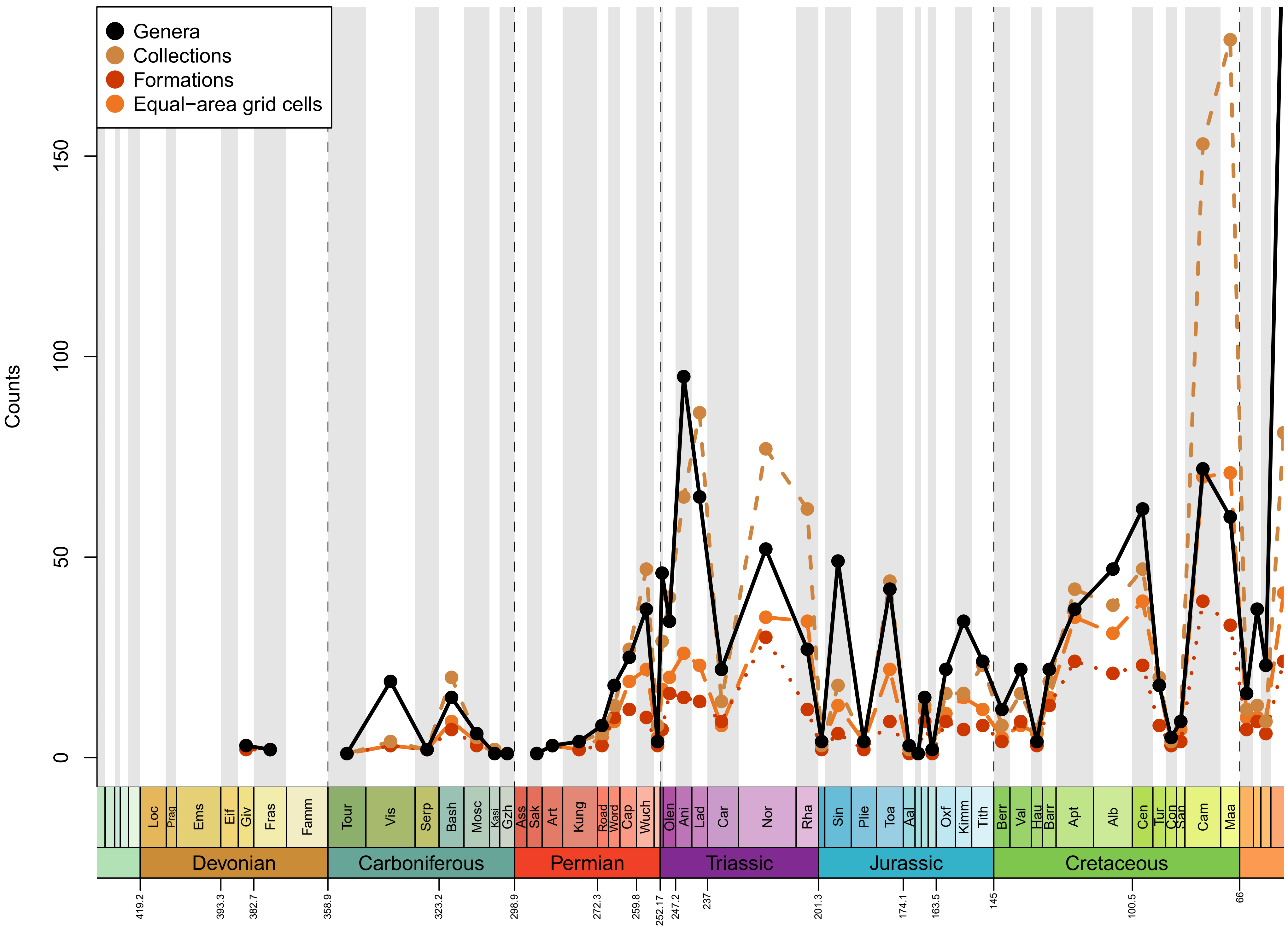

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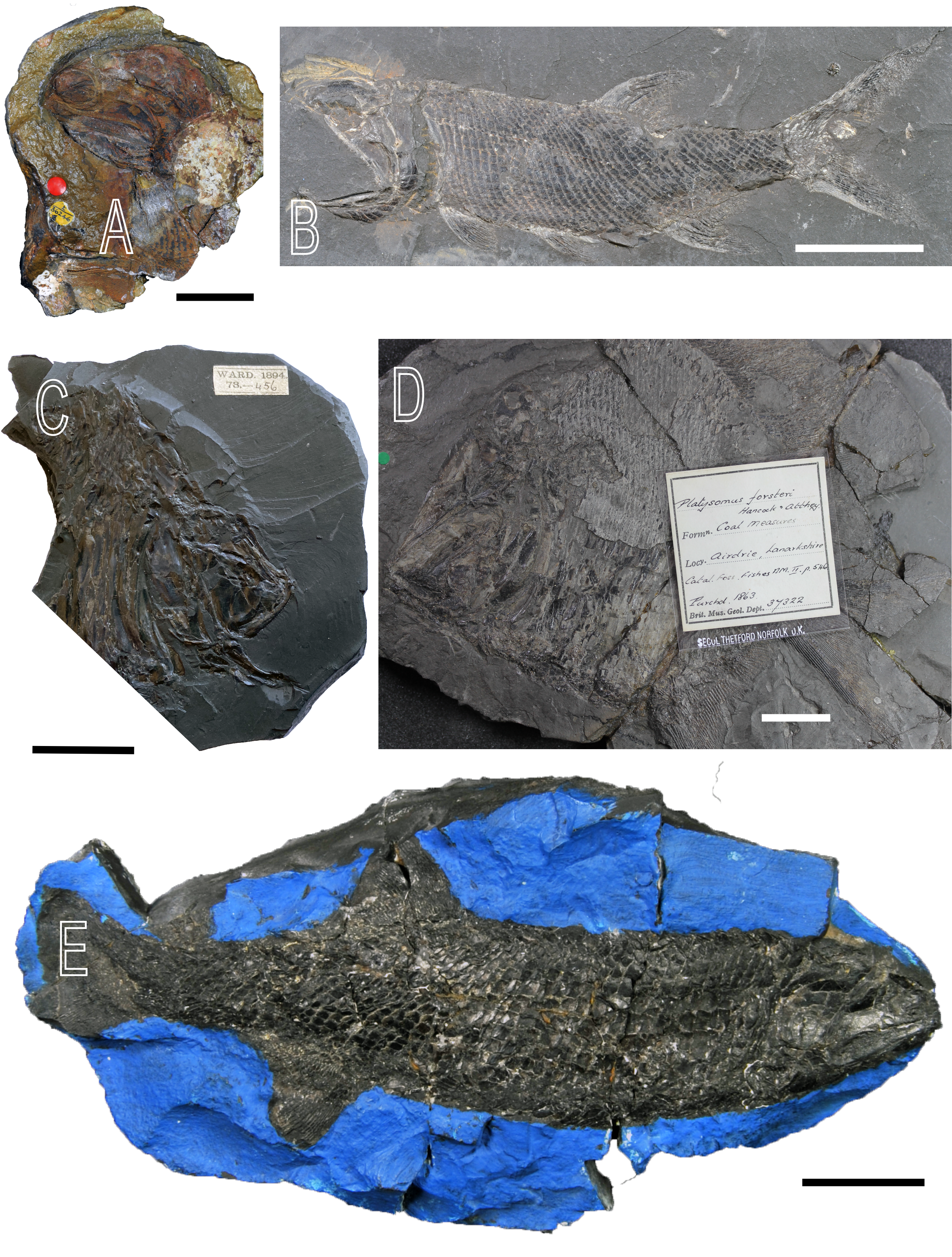
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Brit. Mus. Geol. Dept. 37322
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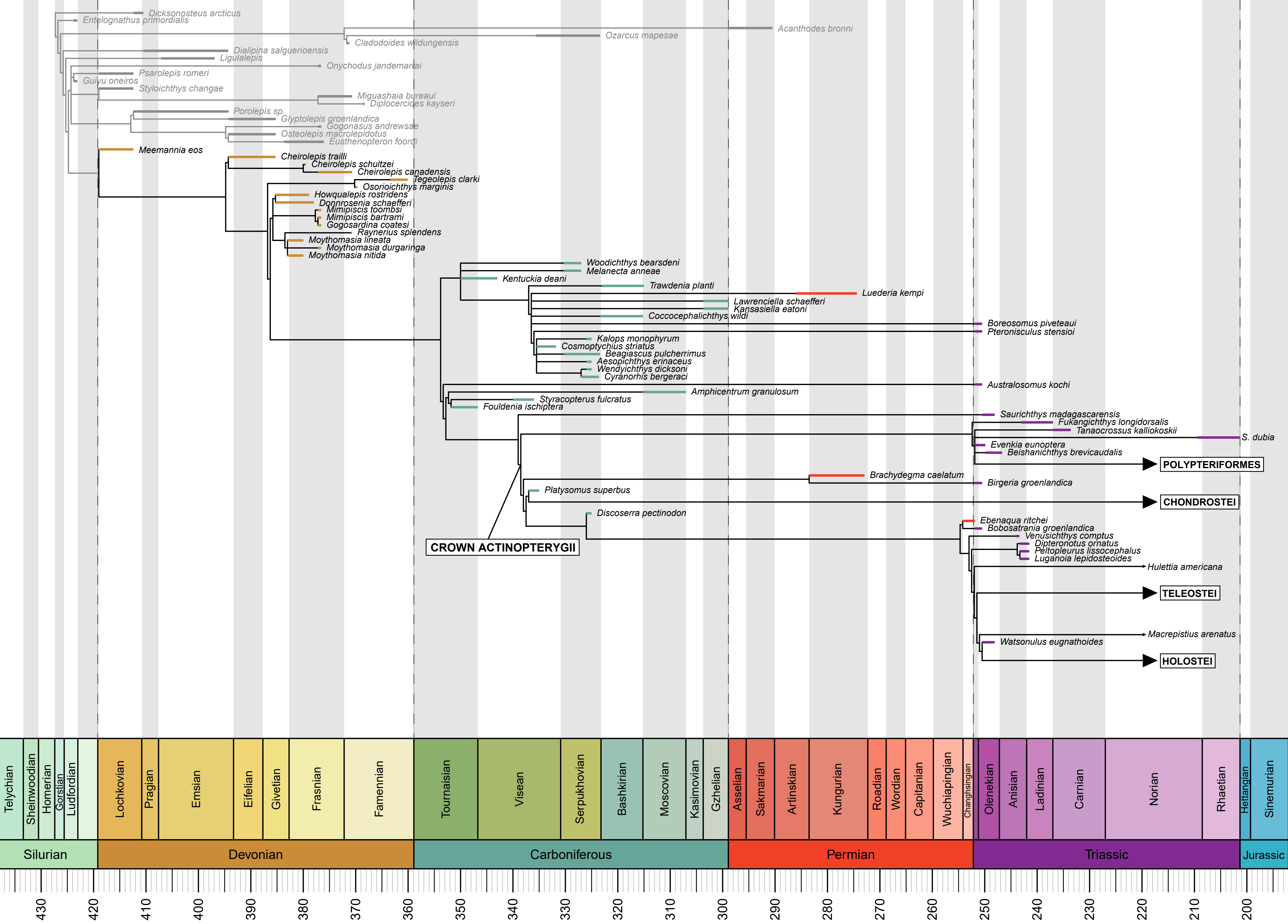

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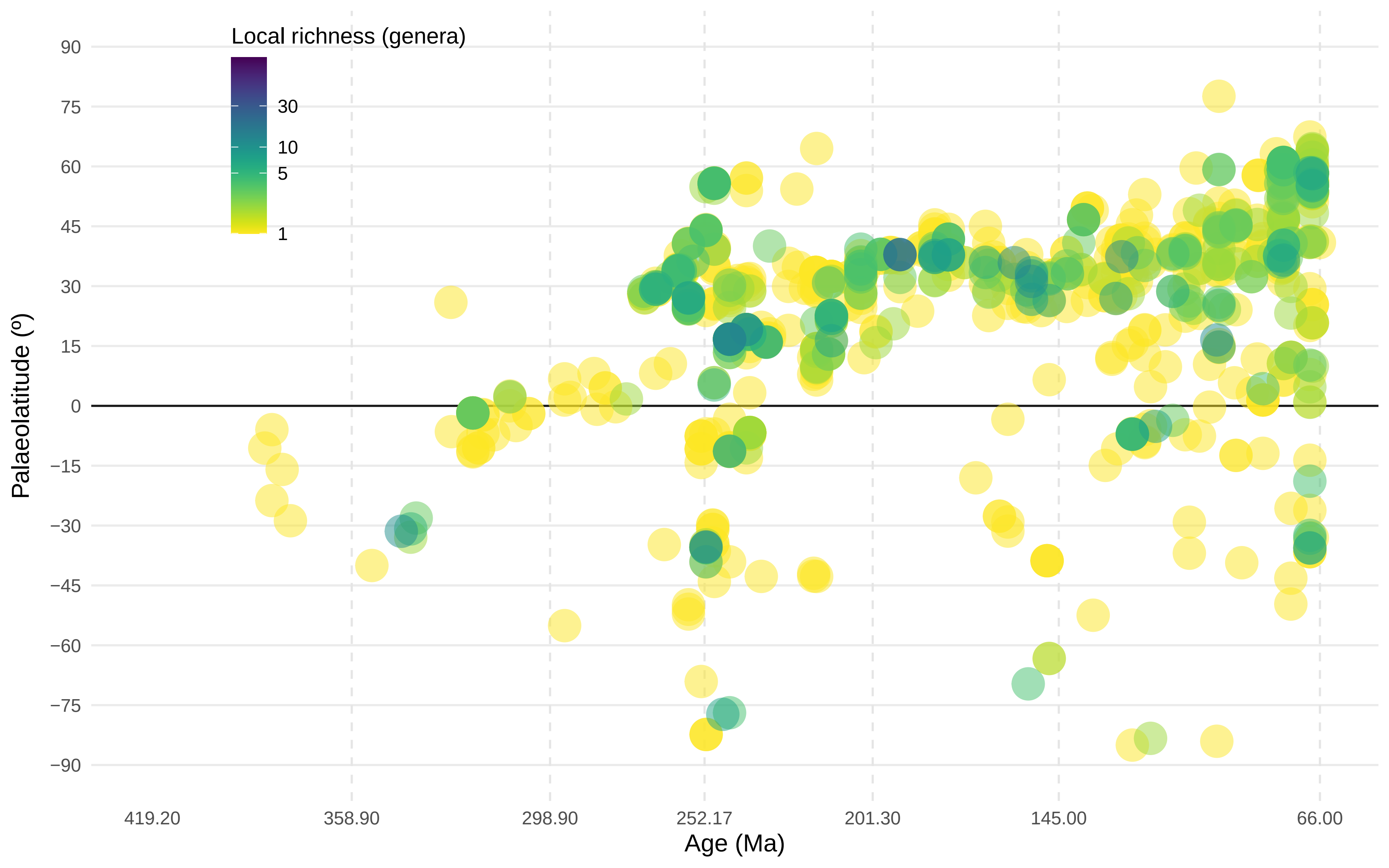
Ozarcus mapesae
Cladodoides wildungensis
Dialipina salgueriensis
Ligulalepis
Onychodus jandemarrai
Psarolepis romeri
Guiyu oneiros
Styloichthys changae
Miguashaia bureaui
Diplocercides kayseri
Porolepis sp.
Glyptolepis groenlandica
Gogonasus andrewsae
Osteolepis macrolepidotus
Eusthenopteron foordi
Meemannia 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
Platysomus superbus
CHONDROSTEI
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



Local richness (genera)
30
10
5
1
90
75
60
45
30
15
0
−15
−30
−45
−60
−75
−90
Palaeolatitude (º)
419.20
358.90
298.90
252.17
201.30
145.00
66.00
Age (Ma)

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. magnus*), 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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