

FIVE HUNDRED MILLION YEARS OF EXTINCTION AND RECOVERY: A PHANEROZOIC SURVEY OF LARGE-SCALE DIVERSITY PATTERNS IN FISHES

by MATT FRIEDMAN^{1*} and LAUREN COLE SALLAN²

¹Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, UK; e-mail: mattf@earth.ox.ac.uk

²Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA; e-mail: laurensallan@gmail.com

*Corresponding author.

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Abstract: Fishes include more than half of all living animals with backbones, but large-scale palaeobiological patterns in this assemblage have not received the same attention as those for terrestrial vertebrates. Previous surveys of the fish record have generally been anecdotal, or limited either in their stratigraphic or in their taxonomic scope. Here, we provide a broad overview of the Phanerozoic history of fish diversity, placing a special emphasis on

intervals of turnover, evolutionary radiation, and extinction. In particular, we provide in-depth reviews of changes during, and ecological and evolutionary recovery after, the end-Devonian (Hangenberg) and Cretaceous–Palaeogene (K–Pg) extinctions.

Key words: adaptive radiation, biodiversity, Chondrichthyes, durophagy, Hangenberg, K–Pg, Osteichthyes.

‘FISHES’, the paraphyletic assemblage of primitively aquatic backboned animals, comprise over half of all living vertebrate species (Nelson 2006), with a fossil record extending to the early Cambrian (Shu *et al.* 1999, 2003). Compared with marine invertebrates (Sepkoski 2002) and many other vertebrate groups (e.g. Alroy 1996; Lloyd *et al.* 2008), our understanding of large-scale diversity patterns in fossil fishes is limited. This is somewhat surprising, because fishes were the first group for which patterns of palaeobiodiversity were systematically documented, more than a century and a half ago by Louis Agassiz in his monumental *Recherches sur les Poissons fossiles* (1833–1844). Fishes should represent a obvious study system for exploring macroevolutionary contrasts between freshwater and marine environments within a single group (e.g. McKinney 1998; Vega and Wiens 2012), and the considerable body of work dissecting form–function relationships in living forms generally, and teleosts specifically (e.g. Wainwright and Bellwood 2002), make fishes a particularly attractive system for exploring questions related to ecology over geological timescales (e.g. Bellwood 2003; Friedman 2010; Anderson *et al.* 2011; Sallan *et al.* 2011; Sallan and Friedman 2012). Additionally, the impact of fishes as predators, competitors and prey on the long-term macroevolution and macroecology of other clades in the same ecosystems (e.g. invertebrates and tetrapods) has likely been substantial (Vermeij 1977; Brett and Walker 2002; Stanley 2008; Bush and Bambach

2011; Sallan *et al.* 2011). Ignorance of historical patterns of fish diversity, therefore, impedes a general understanding of aquatic biodiversity and evolutionary processes.

Several factors have prevented a synoptic picture of macroevolutionary patterns in fishes from materializing. Key among these is the sheer scope of the problem: no other vertebrate assemblage encompasses as much taxonomic richness and morphological disparity, distributed over such a long geological interval and represented by such a diverse range of preservational styles as fishes. But this extensive record remains relatively understudied, as a review of the table of contents in any issue of a palaeontological journal will illustrate. Since the time of Agassiz, the small community of fish palaeontologists has focused primarily on taxonomy, description and interrelationships. As a result, fish workers were among the early adopters and innovators of cladistic methods late in the 20th century (e.g. Nelson 1969) and among the first to apply then novel ‘tree-thinking’ approaches to the fossil record (Patterson and Rosen 1977). By contrast, the coincident ‘Palaeobiological Revolution’ (Sepkoski and Ruse 2009), with its emphasis on common macroevolutionary trends among disparate clades, was barely noted.

Macroevolutionary studies have been perceived as of secondary importance by most fish workers for many reasons: the very real need to catalogue available and newly

discovered material, assumptions of scarcity relative to the invertebrate record, and unfamiliarity with palaeobiological methods. In addition, systematic and palaeobiological analyses impose distinct demands on the worker. Cladistic analysis requires detailed investigations of a small set of exemplars, selected on the basis of group membership and phylogenetically informative characters. Macroevolutionary analysis requires large-scale surveys of diverse taxa selected on the basis of factors generally not specific to a particular group (e.g. faunal membership, ecology and age or environment).

As a result of this dichotomy, the literature concerning patterns of extinction and recovery in fishes is small and diffuse, making it difficult for workers both within and outside the field to make meaningful statements about patterns of diversity. Under the theme of extinction and recovery, our goal is to provide a broad overview of major patterns of turnover in the fossil record of fishes, so far as they can be discerned at present, and highlight areas of persistent uncertainty

that should be the target of future research. While we have attempted to present a balanced picture of Phanerozoic fish diversity patterns, this topic is vast and our review is inevitably biased towards our own areas of expertise, centred on the end-Devonian (Sallan) and end-Cretaceous (Friedman) extinctions. Our taxonomic scope encompasses the vertebrate total group exclusive of tetrapods (Fig. 1). There is mounting evidence that cyclostomes are monophyletic (Heimberg *et al.* 2010; Janvier 2011; Ota *et al.* 2011), meaning that the vertebrate crown group includes hagfishes in addition to gnathostomes and lampreys. In contrast to most previous surveys of fish diversity in the fossil record, we include conodonts in our review. There is some conflict concerning the precise systematic position of the group (e.g. Turner *et al.* 2010), but all explicit hypotheses of conodont relationships place them as members of the vertebrate total group. A summary of hypothesized relationships between major groups discussed elsewhere in this paper is given in Figure 1.

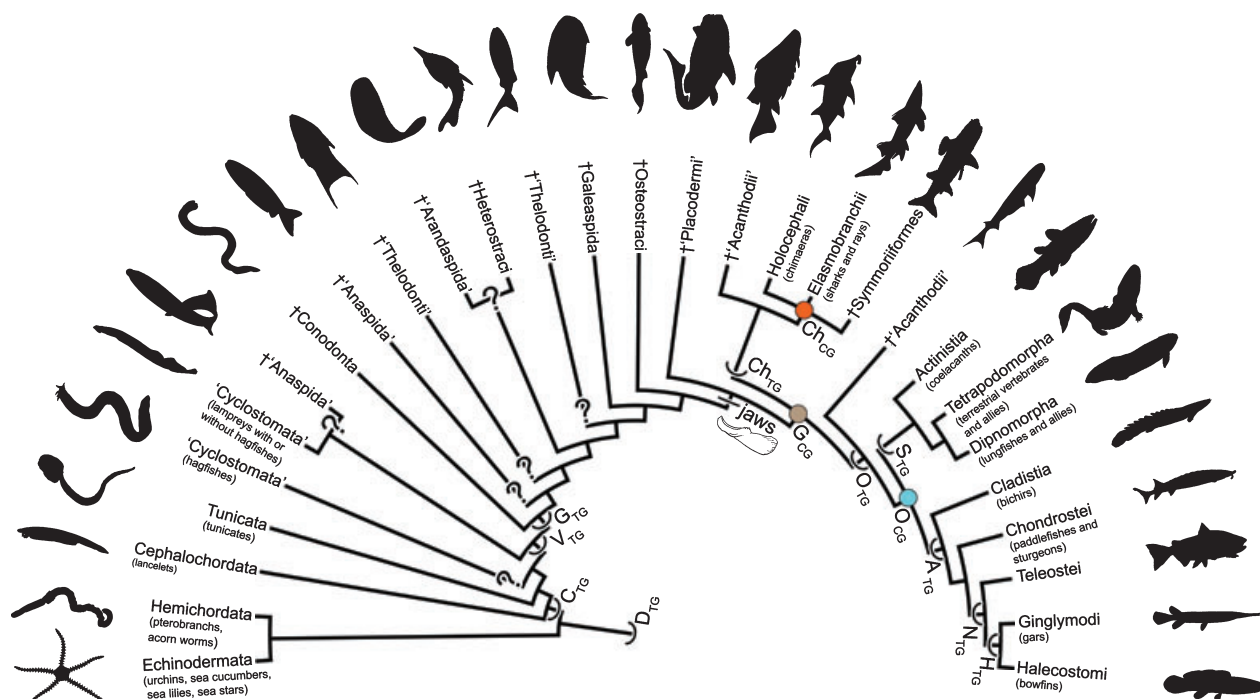


FIG. 1. A composite hypothesis of deuterostome phylogeny, with an emphasis on the interrelationships among vertebrates. Taxa preceded by the dagger symbol (+) are extinct, while those enclosed in inverted commas are possibly or likely paraphyletic. Here, 'Anaspida' includes problematic naked taxa (e.g. *Euphanerops*) typically associated with this ostracoderm assemblage. Uncertain phylogenetic placements are marked by question marks. Placoderms appear to be a grade of stem gnathostomes (Friedman 2007; Brazeau 2009), while the paraphyletic acanthodians branch from the chondrichthyan, osteichthyan and possibly gnathostome stems (the first two are shown by Brazeau's 2009 consensus topologies, while the latter is present in some source trees). Abbreviations: AT_{CG}, actinopterygian total group; Ch_{CG}, chondrichthyan crown group; Ch_{TG}, chondrichthyan total group; Co_{TG}, chordate total group; D_{TG}, deuterostome total group; G_{CG}, gnathostome crown group; G_{TG}, gnathostome total group; H_{TG}, holostean total group; N_{TG}, neopterygian total group; O_{CG}, osteichthyan crown group; O_{TG}, osteichthyan total group; S_{TG}, sarcopterygian total group; V_{TG}, vertebrate total group. Topology based on local solutions presented by: Janvier (1996), Donoghue *et al.* (2000), Coates and Sequeira (2001), Blicek and Turner (2003), Sansom *et al.* (2005), Hurley *et al.* (2007), Friedman (2007), Brazeau (2009).

AN OVERVIEW OF THE HISTORY OF FISH DIVERSITY

A detailed picture of diversity patterns in the fossil record of fishes is lacking, despite synoptic attempts dating back to the 19th century (Agassiz 1833–1844; Marsh 1877). Broad overviews are presented as range charts in relevant chapters of *The Fossil Record* (Andrews *et al.* 1967) and *The Fossil Record 2* (Aldridge and Smith 1993; Cappetta *et al.* 1993; Gardiner 1993a, b; Halstead 1993; Patterson 1993a; Schultze 1993; Zidek 1993). Richness-through-time plots have been produced for different fish groups (Fig. 1) during all (osteichthyans, or bony fishes: Patterson 1994) or part (Jurassic–Recent neoselachians (anatomically modern sharks and rays): Cappetta 1987a; Late Cretaceous–early Palaeogene neoselachians: Kriwet and Benton 2004; Late Jurassic – Late Cretaceous actinopterygians (ray-finned fishes): Cavin *et al.* 2007 Jurassic actinopterygians: Cavin 2010; Middle Triassic – Late Cretaceous neoselachians: Kriwet *et al.* 2009; Ordovician–Triassic vertebrates excluding conodonts: Blicek 2011; Devonian vertebrates excluding conodonts: Long 1993; Devonian–Carboniferous jawed vertebrates: Sallan and Coates 2010) of their evolutionary history. More synoptic spindle diagrams or ‘Romerograms’ (so-called because of their ubiquity in Romer’s classic vertebrate palaeontology text) are prolific, appearing in various formats since Agassiz (1833–1844), but these are generally schematic to the point that no precise statements might be drawn from them, and their connections to empirical counts of taxonomic diversity often seem murky at best (e.g. Carroll 1988, figs 3.1, 4.4, 5.2, 6.7). Clear diagrams of fish diversity over the Phanerozoic, where the axis representing taxonomic richness is explicitly scaled, are comparatively rare, and we are aware of only two examples. The first was constructed by Thomson (1977, fig. 1) at the genus level, based largely on taxonomic appendices to Romer’s *Vertebrate Palaeontology* (1966). The second derives from family ranges taken from *The Fossil Record 2* and appears as a small figure in an inset text box in various editions of Benton’s *Vertebrate Palaeontology* (2000, p. 34, 2005, p. 36).

Until the advent of the Paleobiology Database (PBDB), Sepkoski’s (2002) genus-level compendium represented the standard global resource for investigating extinction and recovery in the marine record, but it appears that the specific pattern of diversification for fishes recorded by this dataset has never been published. Rather, fish groups have been included as a notable but minor component of marine biodiversity curves, such as Sepkoski’s marine evolutionary faunas (1982; Bush and Bambach 2011). Here, we include a plot of Sepkoski’s data (Fig. 2), which reveals a trajectory similar to that of Thomson (1977) and Benton (2000, 2005). There are two major peaks of

richness: one in the Late Devonian and another approaching the Recent. Actinopterygians, specifically teleosts, are responsible for the latter. A shallow trough, extending from the Carboniferous to mid-Cretaceous, lies between these two intervals of apparently high richness. This long span is punctuated by a series of minor peaks and valleys that, for the most part, are not consistent between the three datasets.

Using Foote’s (2000) expressions, we made estimates of per capita rates of extinction and origination from all of Sepkoski’s (2002) fish data, as well as calculating these rates separately for the two major groups of living fishes, chondrichthyans (cartilaginous fishes, or sharks, chimaeras and their relatives) and osteichthyans (actinopterygians and lobe-finned sarcopterygians, the latter exclusive of tetrapods here) (Figs 2–4). These rates cannot be calculated for all intervals, but where they can, we have estimated 95 per cent confidence intervals about them based on binomial probability. Intervals of high extinction and origination rates are discussed in the relevant sections. These estimates appear robust to the inclusion or exclusion of conodonts. Rates of origination (raw estimates: Spearman’s $\rho = 0.77$, $p = 7.9 \cdot 10^{-7}$; first differences: Spearman’s $\rho = 0.77$, $p = 1.0 \cdot 10^{-6}$) and extinction (raw estimates: Spearman’s $\rho = 0.67$, $p = 2.9 \cdot 10^{-5}$; first differences: Spearman’s $\rho = 0.68$, $p = 3.2 \cdot 10^{-5}$) based on Sepkoski’s data including and excluding conodonts are strongly correlated over the early Ordovician to end-Jurassic interval, representing the span for which meaningful estimates can be made for both datasets and which precedes the total extinction of conodonts at the Triassic–Jurassic boundary.

Reliability of apparent diversity patterns

Historically, some of the harshest criticism levelled against taxonomic databases of fossils and the research programmes built around them have come from prominent palaeontologists (Patterson and Smith 1987, 1989; Smith and Patterson 1988), including fish workers. Such critiques of taxic palaeobiology have probably done much to discourage palaeoichthyologists from exploring large-scale diversity patterns in the fossil record of fishes, but the question remains: how unreliable are these datasets? Patterson and Smith (1989) estimated that roughly 65 per cent of the fish data used in Sepkoski’s then unpublished generic compendium represented ‘noise’: para- or polyphyletic groups, incorrectly dated monophyletic groups, and various classes of other errors. This figure agrees closely with Adrain and Westrop’s (2000) estimate of the error rate for trilobites in this same database (Sepkoski 2002). Importantly, this error appears to have been

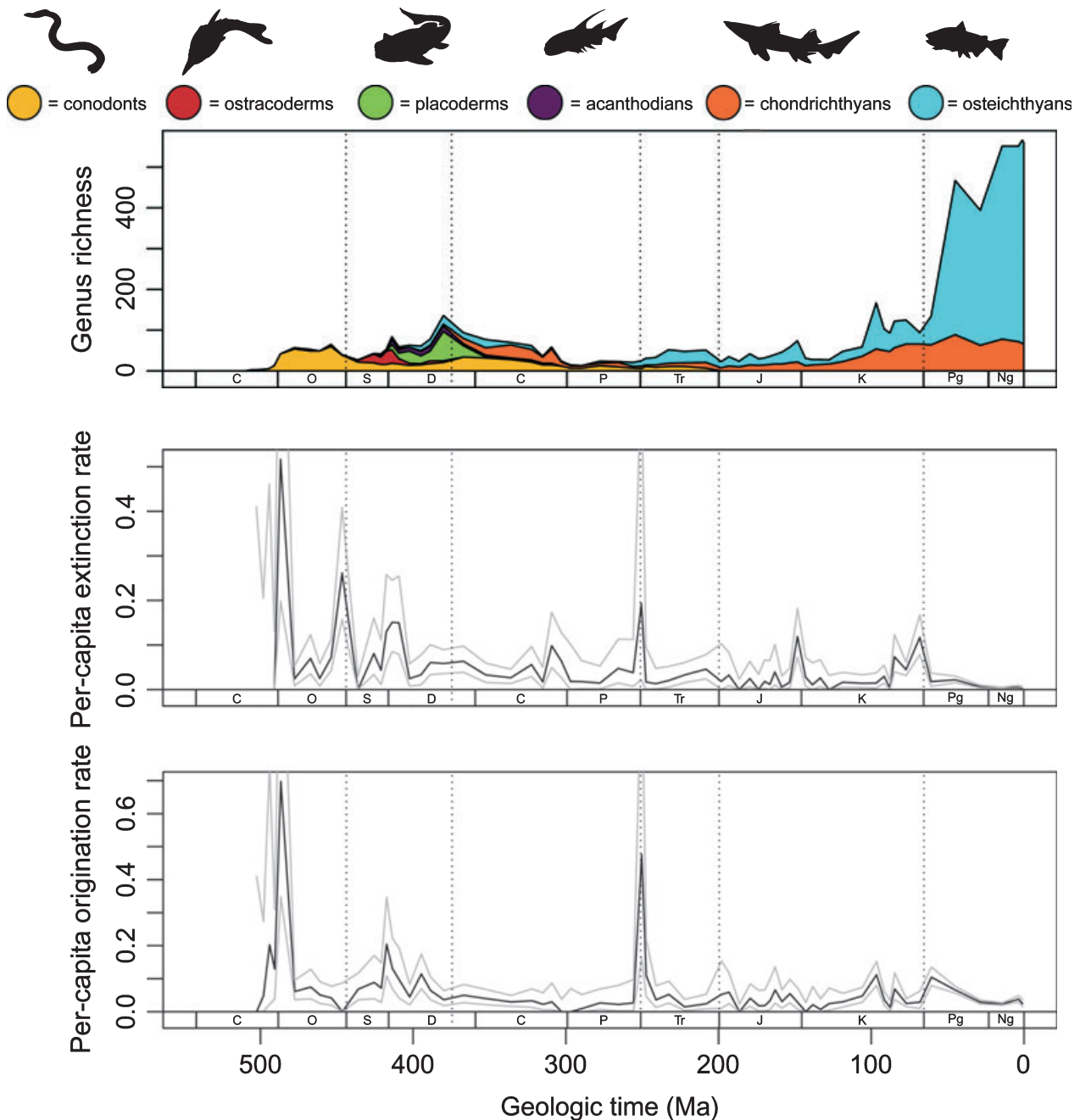


FIG. 2. Diversity patterns in marine fishes during the Phanerozoic, based on Sepkoski's (2002) compendia of marine genera. Vertical dashed lines represent the canonical 'Big Five' extinctions (Raup and Sepkoski 1982). Plots illustrate: genus richness, divided into traditional groupings (conodonts, ostracoderms, placoderms, acanthodians, and osteichthyans; second from top), per capita rates of origination for all fishes (second from bottom), and per capita rates of extinction for all fishes (bottom). Rate values were calculated using Foote's (2000) expressions. Grey lines indicate 95 per cent confidence intervals based on binomial probability. Uncertainty about some estimates is so high that it extends beyond the frame of the graph.

randomly distributed throughout the trilobite data, resulting in little net change between patterns reconstructed on the basis of Sepkoski's compendium and expert-vetted versions. This confirmed the assumptions of diversity-focused researchers that random taxonomic biases should

be cancelled out in sufficiently large datasets and that real signal should appear above a threshold level of sampling. Patterson and Smith (1987, 1989) and Smith and Patterson (1988) were largely concerned with the reliability of last appearances, and it is not clear from their analyses

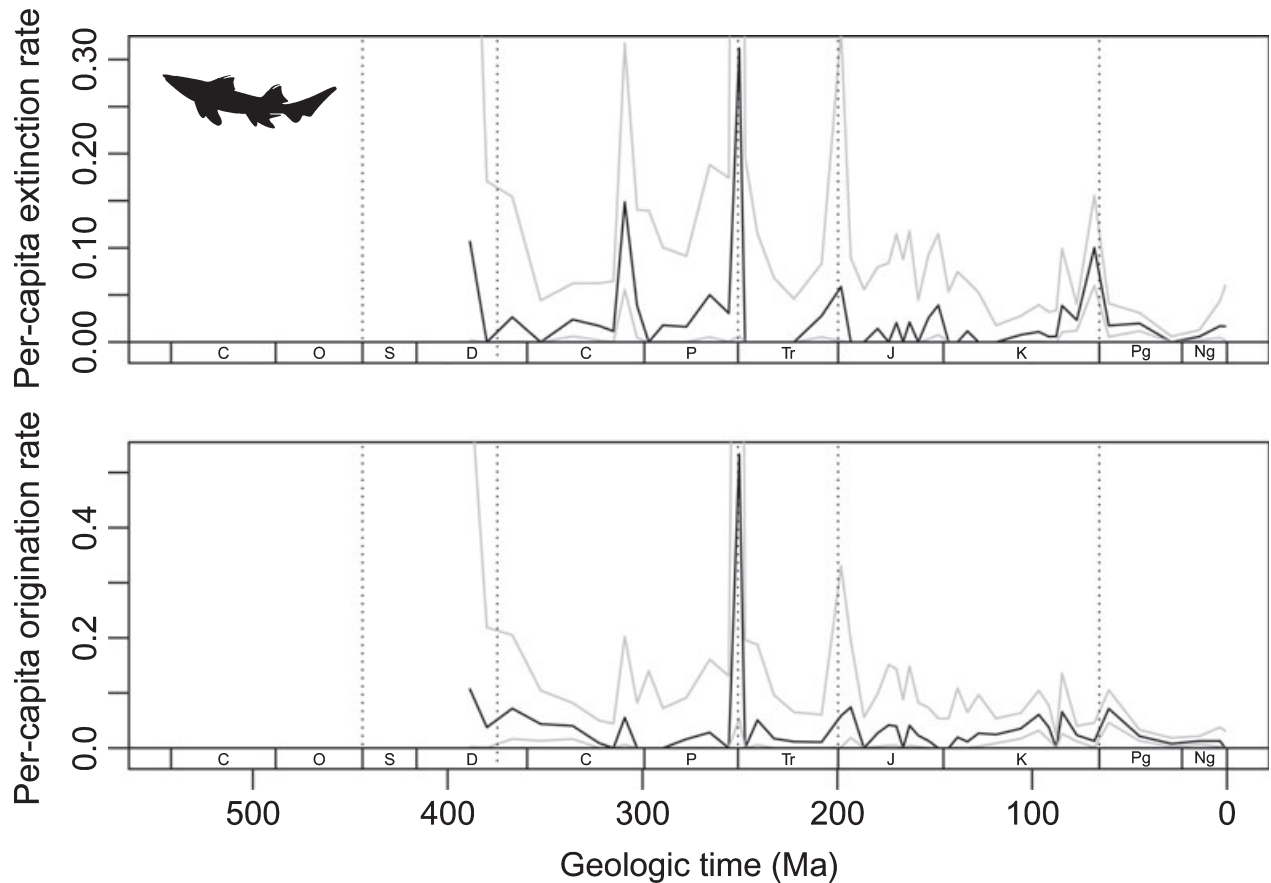


FIG. 3. Diversity patterns in marine chondrichthyans during the Phanerozoic, based on Sepkoski's (2002) compendia of marine genera. Plots illustrate: per capita rates of extinction (top), and per capita rates of origination (bottom). Rates calculated using Foote's (2000) expressions. Grey lines indicate 95 per cent confidence intervals based on binomial probability. Uncertainty about some estimates is so high that it extends beyond the frame of the graph, particularly around the first appearance of the clade in the mid-Devonian and at the P–T boundary.

the degree to which their screened fish data produce richness trajectories comparable with those reconstructed directly from Sepkoski's data.

We have not comprehensively vetted Sepkoski's genus compendium, but note the following broad issues that should be addressed in future attempts to build upon his efforts and more completely catalogue Phanerozoic fish diversity. The first is a lack of nonmarine and many euryhaline taxa. This oversight might seem obvious when discussing a marine diversity curve. However, euryhaline vertebrates are common, and many lineages have alternated between marine and freshwater habitats during their evolutionary histories, some more than once. Thus, consideration of only marine occurrences may truncate taxon ranges, creating artificial extinction and origination events. This bias is likely compounded during periods when vertebrate-bearing marine outcrop area is low, such as during the later Palaeozoic (McGowan and Smith 2008).

The second issue concerns the exclusion of major marine lineages and localities. Many taxa and faunas are

missing, such as the diverse actinopterygians found in Mississippian deposits in Glencartholm, Scotland (Dineley and Metcalf 1999; Sallan and Coates 2010). This oversight is puzzling because this same *Lagerstätte* contains a range of invertebrate taxa (Schram 1983). However, the absence of other sites might be chalked up to taphonomic bias: in many cases, shelly faunas tend to occur in layers where articulated vertebrates do not (Schram 1979; Briggs and Clarkson 1983; Baird *et al.* 1985). By contrast, Sepkoski's coverage of marine chondrichthyan ichthyoliths (isolated elements, such as scales and teeth) appears less spotty, perhaps because enamel-bearing elements are likely to co-occur with the hard parts of invertebrates (Sallan *et al.* 2011). An alternative, nontaphonomic, explanation for this pattern might be that comprehensive summaries of fossil chondrichthyan diversity have been catalogued in two volumes of the *Handbook of Palaeoichthyology* available to Sepkoski (Zangerl 1981; Cappetta 1987b), while four planned osteichthyan volumes (Dipnoi (lungfishes), Crossopterygii (nonlungfish sarcopterygian fishes),

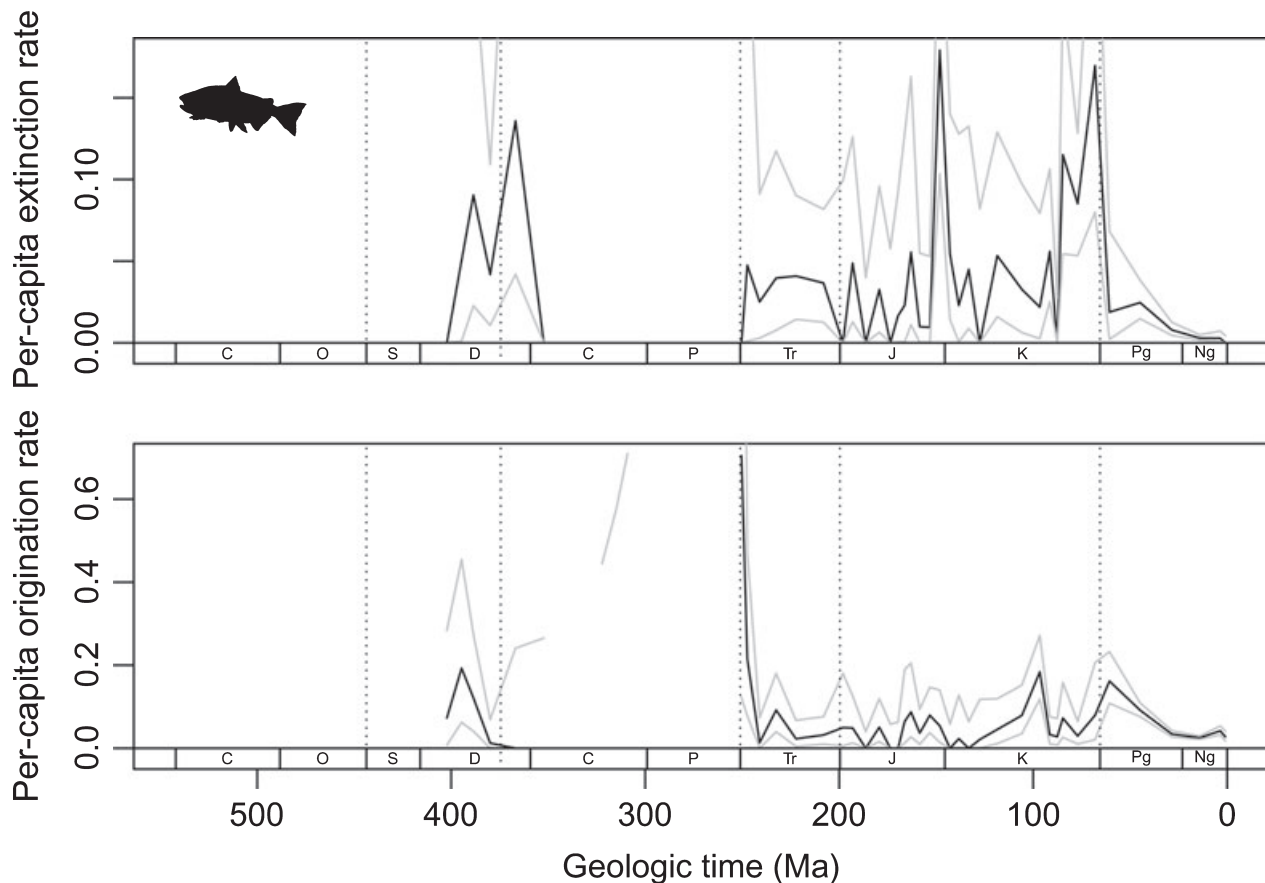


FIG. 4. Diversity patterns in marine osteichthyans during the Phanerozoic, based on Sepkoski's (2002) compendia of marine genera. Plots illustrate: per capita rates of extinction (top) and per capita rates of origination (bottom). Rates calculated using Foote's (2000) expressions. Grey lines indicate 95 per cent confidence intervals based on binomial probability. Uncertainty about some estimates is so high that it extends beyond the frame of the graph, particularly around Mesozoic boundary intervals and during the Permo-Carboniferous trough. Note the inability to calculate rates in the early Carboniferous despite the large diversity of known taxa. This illustrates the presence of significant undersampling and incorrect binning of vertebrates in Sepkoski's compendium.

Actinopterygii I, Actinopterygii II) have never been completed or published.

It should be noted that preservational issues and unfamiliarity are also likely to account for an underestimate of vertebrate occurrences in the PBDB. Vertebrates are less likely to appear in productive invertebrate collections or localities, while those that do occur may be underreported by workers unfamiliar with fish taxonomy. For example, at the time of writing the PBDB contained just three records for the Devonian antiarch placoderm (armoured fish) *Bothriolepis*, which is represented by more than seventy nominal species globally (L. C. S., pers. obs. 2011) and is often the most abundant taxon at Late Devonian vertebrate localities (E. Luksevics, pers. comm. 2009). In addition, it lacked records for any fish taxon at most of the Palaeozoic Sites of Special Scientific Interest compiled by the British Geological Survey (Dineley and Metcalf 1999).

Another issue concerns the incorrect assignment of taxon ages. As an illustration of this problem, Sepkoski

designated many long-ranging actinopterygian lineages of the later Palaeozoic as exclusively Tournaisian. Some of these genera, such as *Eurymotus*, have been known to occur in multiple stages ever since they were first described by Agassiz (1833–1844) or other 19th century palaeoichthyologists. Alternatively, other genera are given undue longevity, assigned to bins such as Carboniferous–Permian, when their more restricted ranges can be found in the literature. An additional class of error relates to outdated higher-level taxonomic assignments, which are particularly common for Palaeozoic and Mesozoic actinopterygians recorded in the PBDB. Remedying these problems will require extensive recompilation of the primary data.

Finally, there are reasons for concern about geological and taxonomic biases in all databases of raw taxonomic diversity, including Sepkoski's compendium (Raup 1979; Peters and Foote 2001; McGowan and Smith 2008). Biodiversity trends in single environments and regions can

be linked to the relative amount of outcrop area available in each bin, perhaps explaining to such phenomena as multistage troughs (e.g. the Permo-Carboniferous; Fig. 1 and below), and the 'Pull of the Recent' (Raup, 1979; Alroy *et al.* 2008). The latter is a marked, even exponential, increase in biodiversity over the Mesozoic-Cenozoic (see osteichthyans in Fig. 2). This has been linked to the appearance of diagnostic characters shared with better-sampled living taxa and an increase in pristine outcrops towards the present (Raup 1979; Alroy *et al.* 2008). However, it is possible that the correlations between deposit availability and biodiversity might reflect an interaction or a 'common cause' rather than a bias (Hannisdal and Peters 2011), and for some groups, the increase in richness towards the Recent might reflect a real pattern rather than an artefact (Jablonski *et al.* 2003; Alroy *et al.* 2008). Lastly, there is the potential that differential worker output (sampling intensity) has affected taxonomic counts in different intervals and environments (Butler *et al.* 2011; Lloyd *et al.* 2011, 2012b). However, sampling standardization, use of higher taxonomic levels (above species), total coverage of habitats and provinces can sometimes mitigate this effect (Alroy *et al.* 2008; Wall *et al.* 2009; Lloyd *et al.* 2011, 2012b). The total impact of sampling biases on our knowledge of evolutionary history continues to be an area of heavy debate in palaeobiology, and one that is yet to be explored in any meaningful way for fishes.

These problems aside, we present Sepkoski's (2002) data unaltered here as a reflection of the state of the art, and as a motivation for fish workers to combine their efforts and expertise in order to produce refined, accessible databases for investigating biodiversity patterns throughout the Phanerozoic.

EARLY TO MID-PALAEOZOIC EVENTS

The Cambrian event: the origin of vertebrates

Vertebrates, like many other metazoan groups, seem to make their first appearance in the fossil record during the Cambrian (542–488 Million years ago (Ma); throughout, interval dates based on Gradstein *et al.* 2004) explosion. Various soft-bodied taxa, largely from the lower Cambrian Chenjiang and middle Cambrian Burgess Shale *Lagerstätten* have been implicated in vertebrate origins, with *Cathaymyrus*, *Haikouichthys*, *Metaspriggina*, *Nectocaris*, *Pikaia*, mylokunmingiids, and yunnanozoons all interpreted at some point as members of either the vertebrate total or crown group (Shu *et al.* 1999, 2003; Donoghue and Purnell 2009; Sansom *et al.* 2010b). Of these, *Haikouichthys* seems to be the most likely vertebrate, with preserved features identified as definitive synapomorphies such as paired sensory capsules and vertebrae (Shu *et al.* 2003; Sansom *et al.*

2011), although the interpretation of structures preserved in these soft-bodied fossils is fraught with difficulty (Donoghue and Purnell 2009; Sansom *et al.* 2010b).

Late Cambrian to mid-Ordovician (488–444 Ma) deposits from Euramerica and Australia contain what might be the earliest armoured vertebrate: fragments of layered, dentine-bearing tissue mostly attributed to the genus *Anatolepis* (Repetski 1978; Smith *et al.* 1996; Young *et al.* 1996; Clark *et al.* 1999). This material resembles, both superficially and histologically, remains of *Porophoraspis* and *Arandaspis*, armoured agnathans (jawless fishes collectively called 'ostracoderms') known from the later Ordovician (Repetski 1978; Smith *et al.* 1996). Such fragments might mark the earliest records of the 'Arandaspida', a potentially paraphyletic assemblage branching near the base of the gnathostome stem and usually allied with Silurian and stratigraphically younger heterostracan agnathans (Janvier 1996; Sansom *et al.* 2001; Fig. 1). If the identity of *Anatolepis* and other early fossil material is correct, it would indicate that the split between cyclostomes (lamprey and hagfish) and jawed vertebrates (including all armoured agnathans along their stem) had occurred by this point (Janvier 1996; Smith *et al.* 1996), a conclusion supported by late Cambrian conodonts (Aldridge and Smith 1993; Donoghue *et al.* 2000).

The Ordovician and Silurian: the origin of gnathostomes

As in the Cambrian, Ordovician vertebrate macrofossils are rare, with the most complete available body fossils assigned to a small number of arandaspid agnathans and allied genera (*Arandaspis*, *Sacabambaspis*, *Eriptychius*, *Astrapis*, *Porophoraspis*). These earliest definitive, articulated armoured agnathans occur in second half of the Ordovician and are found at just a handful of sites in Australia (Young 2009) and the Americas (e.g. the Harding Sandstone of Colorado; Sansom *et al.* 2001; Bolivia: Gagnier *et al.* 1986). Fragments of histologically similar material have been recovered from further afield (Australia, Arabia, Siberia, South China, and possibly Mongolia and South Africa: Wang and Zhu 1997; Blicek and Turner 2003; Karatajute-Talimaa and Smith 2004; Sansom *et al.* 2009).

While the macrofossil record might indicate that fishes were neither abundant nor diverse during the Ordovician, ichthyoliths have been used to suggest otherwise (Sansom *et al.* 2001, 2009). Conodont elements, the tooth-like feeding apparati of soft-bodied agnathans, are widespread as they are throughout the Palaeozoic and are joined by a host of additional microfossils. Histological analyses have been used to identify isolated bone fragments as heterostracan- and placoderm-grade taxa, while 'odontodes' and spines have been given presumptive chondrichthyan or acanthodian ('spiny shark') status on the basis of broad

morphological similarities (Sansom *et al.* 1996, 2001, 2012; Young 1997; Smith *et al.* 2002). Such assignments have been used to argue for the origin of major gnathostome divisions (and indeed the gnathostome crown; Fig. 1) in the Ordovician or even Cambrian (Young 1997; Smith *et al.* 2002), tens of millions of years before the earliest definitive jawed body fossil (see below; Zhu *et al.* 2009). Contrary to this hypothesis, no Ordovician jaw fragments or teeth are known, and tissues (e.g. dentine) and morphological traits (e.g. pore systems) once thought to be restricted in their distribution are now known to be phylogenetically widespread (Sansom *et al.* 1992; Young *et al.* 1996). Microfossils of this age assigned to various jawed vertebrate groups lack definitive morphological characteristics and occur alongside very similar ichthyoliths belonging to thelodont and arandaspid agnathans (Sansom *et al.* 1996; Young 1997; Blicek and Turner 2003; Donoghue *et al.* 2003).

Unfortunately, the relative absence of identifiable articulated specimens, especially of putative jawed vertebrates, means little can be said about either the taxonomic or the ecological impact of the end-Ordovician Hirnantian mass extinction (444 Ma) on fishes aside from conodonts, which suffered extreme loss that is clearly expressed in our estimated rate of extinction from Sepkoski's (2002) data (Fig. 2; see also Bambach 2006). This glacial event had significant and severe impacts on marine invertebrates perhaps equivalent in scope to the end-Permian and end-Cretaceous (Raupe and Sepkoski 1982; Bambach *et al.* 2004; Bambach 2006), although ecosystem restructuring may be light relative to these other major events (Droser *et al.* 2000; McGhee *et al.* 2012). As most known Ordovician fish material derives from similar marine settings, our present inability to make more definitive statements about how this extinction affected fishes more broadly is frustrating. Some remedy might be forthcoming, as a number of new Ordovician *Lagerstätten* have recently been reported. These include Burgess Shale/Chengjiang-type preservation that could deliver the body remains of naked vertebrates such as *Haikouichthys*, stem-lampreys and hagfishes, and conodonts (Gabbott *et al.* 1995; Young *et al.* 2007; Van Roy *et al.* 2010) along with taxa bearing mineralized external skeletons.

Mass extinctions like the end-Ordovician might have long-term impacts even on clades suffering minimal direct effects, as common ecosystems are altered and new opportunities arise in the aftermath (Friedman 2010; Sallan *et al.* 2011). The Silurian (444–416 Ma) record presents a number of potential roadblocks to detecting such patterns. It is undergoing intense stratigraphic and age revision because of isotope volatility, unconformities at various boundaries, a lack of major biozonation taxa (graptolites) in those facies which preserve most other fossils, and a large number of apparent marine extinction pulses that strongly affected those same index taxa

(graptolites and conodonts; Munnecke *et al.* 2011). Despite these issues, the Silurian record does contain a greater (and better supported, in terms of precision of possible phylogenetic placement) richness of fishes than the Ordovician (Qu *et al.* 2010), allowing some diversity patterns to be parsed with appropriate caveats.

Vertebrate fossils are uncommon in the early part of the first Silurian series, the Llandovery (444–428 Ma), yet articulated material appears by the middle of the interval. These primarily consist of scaled agnathans representing the earliest articulated thelodonts (*Loganellia*; Dineley and Metcalf 1999), with scale morphologies matching Ordovician ichthyoliths (Sansom *et al.* 1996), and naked jawless forms (*Jamoytius*) attributed to lineages originating near the base of the vertebrate tree (Janvier 1996; Sansom *et al.* 2010a). The earliest armoured agnathan specimens in the Silurian appear in China (galeaspid at multiple localities: Zhao and Zhu 2007) and Canada (the possible heterostracan *Athenagis*; Janvier 1996; Soehn *et al.* 2001) in the last stage of the Llandovery. Articulated material from the subsequent Wenlock series (428–423 Ma) represents a phylogenetically broad sample of agnathan diversity, adding heterostracans and osteostracans to the body fossil record (Janvier and Blicek 1993; Wilson and Caldwell 1993; Von Bitter *et al.* 2007). This raw increase in richness, following what seems to be an earliest Silurian gap (Talimaa's Gap; Blicek 2011) in the vertebrate record lasting some 3–10 Ma, might suggest that vertebrates underwent a diversification event during or after a post-Ordovician recovery interval (Janvier 1996). However, the aforementioned uncertainties about the severity of the Hirnantian extinction, united with ambiguities surrounding the true phylogenetic affinities and abundance of some fossil material (macro and micro) from the Llandovery and Ordovician, and uncontrolled sampling, mean that the significance of this pattern remains unclear.

Osteostracans are generally considered closest jawless relatives of jawed vertebrates (Janvier 1996; Donoghue *et al.* 2000; Sansom 2009; Fig. 1) and make their debut in the Wenlock. The earliest definitive jawed fishes appear not much later; the oldest articulated placoderm, the antiarch *Silurolepis* (Zhang *et al.* 2010), occurs alongside the oldest known crown osteichthyans, the stem sarcopterygians *Guiyu* and *Psarolepis* (Zhu *et al.* 1999, 2009), in the Chinese Xiaoxing fauna of latest Ludlow age (422–418 Ma). This follows an increase in the number of solidly jawed gnathostome-like microfossils, including more plausibly chondrichthyan-like scales with crowns and necks (e.g. mongolepidids) and better characterized acanthodian-type spines (e.g. sinocanthids) in the late Llandovery (Karatajute-Talimaa, 1995; Janvier 1996; Sansom *et al.* 2005; Zhao and Zhu 2007; Žigaite *et al.* 2011), plus isolated placoderm plates and stem-osteichthyan dermal bone fragments in Wenlock-age faunas in China (Zhao and Zhu 2007; Qu

et al. 2010) and in Ludlow sites elsewhere (Janvier 1996; Friedman and Brazeau 2010).

Considering this ichthyolith evidence, it is interesting that no articulated jawed vertebrate material is known from pre-Ludlow sites with taphonomy similar to Xiaoxing or later Palaeozoic *Lagerstätten*. For example, conodonts and heterostracans are the only vertebrates known from the soft- and hard- tissue-preserving layers of the Eramosa fauna of the Canadian Wenlock (Von Bitter *et al.* 2007), while only conodont elements appear at the similarly aged hard-tissue-biased Waukesha locality in Wisconsin. Similarly, the Llandovery deposits of Lesmahagow, Scotland contain only the thelodont *Loganellia* and the naked *Jamoytius* (Dineley and Metcalf 1999). Devonian (416–359 Ma) and Carboniferous (359–299 Ma) sites with such taxa and/or preservational modes also bear articulated chondrichthyans, osteichthyans and placoderms (e.g. Hunsrückschiefer, Germany; Miguasha, Canada; Gogo, Australia; Cleveland Shale, USA; Waterloo, South Africa; Bear Gulch, USA; Mazon Creek, USA; Gess and Hiller 1995; Janvier 1996; Baird 1997; Gess *et al.* 2006). Collectively, these observations imply that if jawed vertebrates had arisen by the earliest Silurian, they existed at sufficiently low frequencies to evade preservation. An alternative explanation is that early jawed gnathostomes inhabited environments that either have been little sampled by palaeontologists or are poorly represented in the stratigraphic record. However, the abundance of gnathostome microfossils, and later macrofossils, in Silurian faunas bearing corals and other well-sampled invertebrates, and aforementioned scarcity in preservational *Lagerstätten* of similar age suggests that sampling is not the main issue (Janvier 1996; Zhao and Zhu 2007; Žigaite *et al.* 2011).

Late Silurian to mid-Devonian: the rise of ecologically modern fishes

Even though major jawed gnathostome divisions originated by the mid-Silurian, fish assemblages exclusive of conodonts were still, by and large, dominated by jawless forms into the Early Devonian. As illustrated earlier, definitive jawed vertebrate remains and associated ichthyoliths are rare in Ordovician–early Devonian deposits, with jawed fishes generally representing minor contributors to vertebrate diversity even at the best-sampled localities (Boucot and Janis 1983; Anderson *et al.* 2011). By contrast, vertebrate assemblages from the close of the Early Devonian to the Recent are composed almost exclusively of jawed gnathostomes (Anderson *et al.* 2011). This major faunal turnover is therefore not coincident with the origin of anatomically modern gnathostomes, and anecdotal scenarios linking armoured agnathan decline to jawed gnathostome competition have not been corroborated by quantitative investigation (Janvier and Blicke 1993; Anderson *et al.* 2011; Purnell 2001a).

Significantly, the earliest diverging branches of the jawed vertebrate tree represent dorsoventrally compressed forms (antiarch and petalichthyid placoderms: Friedman 2007; Brazeau 2009) that probably had benthic ecologies not dissimilar from those of the most crownward jawless members of the gnathostome stem. The origin of modern jawed vertebrates and their subsequent evolutionary success is therefore probably as much about the shift from a benthic to nektonic lifestyle in the late Silurian – Early Devonian as it is about the origin of jaws (Anderson *et al.* 2011; Klug *et al.* 2011). However, this is not the whole story, as eel-like conodonts and cyclostomes, fusiform and even deep-bodied unarmoured and scale-bearing agnathans (e.g. anaspids and thelodonts), and streamlined heterostracans were likely already nektonic in the Cambrian–Silurian (Briggs *et al.* 1983; Janvier and Blicke 1993; Wilson and Caldwell 1993; Purnell 2001a, b; Botella and Farina 2008). Many jaw-bearing fishes, both early and modern, are ram, suspension or suction feeders, acquiring mobile and planktonic prey without any major processing by the jaws or dentition (Anderson *et al.* 2011). Nektonic jawless fishes cannot be excluded *a priori* from these and other trophic strategies (Purnell 2001b), especially in the light of the functional capabilities of living agnathans (Clark and Summers 2007; Clark *et al.* 2010).

In any case, the acquisition and partitioning of novel resources among lineages with nektonic life modes does characterize an apparently slow-burning/long-fused gnathostome radiation. By the Early Devonian, jawed vertebrates had diversified to fill a wide variety of trophic roles, ranging from piscivores to durophages (Anderson *et al.* 2011). Such Siluro-Devonian diversification may be mirrored in other motile Siluro-Devonian clades, such as ammonoids and eurypterids, which likely converged on at least some vertebrate niches (Romer 1933; Packard 1972; Lamsdell and Braddy 2010; Klug *et al.* 2011). Interactions between vertebrates, ammonoids and eurypterids have been implicated in observed macroevolutionary trends among those groups (Romer, 1933; Lamsdell and Braddy 2010; Klug *et al.* 2011). Such coincident trophic diversification, coupled with indications that predatory attacks on hard-shelled invertebrates increased strikingly over the interval, and long-term elaboration of marine invertebrate armature (Signor and Brett 1984; Brett and Walker 2002; Baumiller and Gahn 2004; Klug *et al.* 2011; Kosnik *et al.* 2011; Sallan *et al.* 2011; Slotta *et al.* 2011) calls into question how revolutionary changes in Mesozoic marine ecosystems might have been (Vermeij 1977), and whether some shifts in invertebrate lifestyles and anatomy might have deeper geological roots.

A nonecological explanation has been also been offered for the abrupt diversification of jawed vertebrates

lineages long after their origin: an increase in atmospheric oxygen levels in the late Silurian and/or early Devonian that presumably allowed more energetic life modes and larger taxa (Dahl *et al.* 2010; Qu *et al.* 2010). Anderson and colleagues (2011) have noted that fish jaws reached near-peak functional diversity in the Devonian before one of the proposed causal maxima (Emsian (407–397 Ma) peak in Dahl *et al.* 2010). Regarding other peaks (e.g. Lockhovian (416–411 Ma) and Pragian (411–407 Ma): Berner *et al.* 2007; Qu *et al.* 2010) and long-term changes (e.g. Clement and Long 2010), it is not clear that there is, or should be, a general relationship between atmospheric oxygen and fish diversity. Chondrichthyans, and possibly many of the acanthodians that populate their stem (Brazeau 2009), do not possess lungs (Nelson 2006). It is not known if the most dominant and environmentally widespread group of Devonian gnathostomes, the placoderms, were capable of directly accessing atmospheric oxygen either; previous evidence of such organs in *Bothriolepis* is now regarded as ambiguous (Arsenault *et al.* 2004; Janvier *et al.* 2007). The limiting factors for oxygen uptake in living fishes seem to be physiological, morphological and behavioural (e.g. lung and gill surface area, structure and efficiency, ram speed, buccal pumping, energy spent on surfacing, trade-offs with other gill functions) rather than environmental (available oxygen) under normal conditions (Piiper 1982; Kramer 1987; McNab 2002).

If there were a relationship between oxygen levels and gnathostome success, one would expect a mass depletion of fishes coincident with a fall in oxygenation later in the Devonian (Clement and Long 2010; Qu *et al.* 2010). This is especially true because, aside from increasing energy from aerobic respiration, the link between oxygen levels and diversity is thought to run through positive correlations with plankton abundance (a key factor in most aquatic ecosystems; Berner *et al.* 2007). However, jawed vertebrate functional, faunal and size diversity remains consistent or even increase throughout multiple hypoxic events and long-term oxygen decline (Dahl *et al.* 2010; Sallan and Coates 2010; Anderson *et al.* 2011). Indeed, a previous correlation between a nadir in tetrapod abundance in the early Carboniferous ('Romer's gap': Coates and Clack 1995) and low oxygen levels (Ward *et al.* 2006) might instead be interpreted as a postextinction trough with associated environmental effects (see below; Sallan and Coates 2010).

DEVONIAN EXTINCTIONS AND CARBONIFEROUS RECOVERY

Newell (1952, 1962) was the first to identify a Late Devonian (385–359 Ma) mass extinction and associated losses

among fishes, claiming 90 per cent family-level extinction while providing few details as to specific groups. McLaren (1970) indicated the marine extinction as occurring at the Frasnian–Famennian boundary (374.5 Ma), and subsequently that horizon, or the surrounding Kellwasser deposits, was placed among the Big Five mass extinction events, albeit as the least statistically significant member (Raup and Sepkoski 1982). This uncertainty is compounded, if not caused, by the nexus of distinct bioevents in the Late Devonian that encompasses the 25-million-year 'Late Devonian Biodiversity Crisis' (Stigall 2010). The most heavily investigated of these continues to be the Kellwasser event, linked to the loss of 60 per cent of genera and up to 82 per cent of species (McGhee 1996). However, large events have also been identified at the end-Givetian (the Taghanic event; 385 Ma) and the end-Famennian (the Hangenberg event; 359 Ma) (McGhee 1996; Caplan and Bustin 1999; Racki 2005; Sallan and Coates 2010).

It has long been apparent that the vertebrate fauna changed over the later Devonian into the Carboniferous. Spurred by Agassiz (1833–1844) and confronted by a wealth of appropriately aged British and North American fossil material, 19th century fish palaeontologists noticed a number of faunal differences between the 'Age of Fishes' and the 'Age of Amphibians'. Long before the concept of a Devonian mass extinction was introduced, O. C. Marsh (1877, p. 214) remarked on the complete extinction of placoderms by the end-Devonian, followed by the rise of previously 'subordinate' chondrichthyans in 'both numbers and size'. However, this early recognition of change did not lead to further investigation of the connections with various global events, even after acceptance of vertebrate mass extinction elsewhere in the record. Nearly 120 years later, Janvier (1996) could only note that there were indeed large radiations of holocephalan chondrichthyans (chimaeras and their relatives), actinopterygians and tetrapods in the early Carboniferous. Their relationship with any extinction-associated losses of marine placoderms was merely hypothetical and the cause of such extinctions was in doubt.

In fact, many fish workers have argued for other sources of faunal change. Janvier (1985) and Ahlberg and Milner (1994) attributed the loss of Late Devonian Old Red Sandstone deposits and their associated fish fauna, and equivalent facies elsewhere, to lack of deposition, or even destruction, of appropriate sediments. Several subsequent authors proposed that a Euramerican regional biota had been swept away by invasions during a faunal interchange with Gondwana (Clement *et al.* 2004; Janvier and Clement 2005; Clack 2006). Rhizodontid and megalichthyid sarcopterygians and gyracanthid acanthodians, known from both Devonian and Carboniferous deposits, supposedly caused turnover in previously isolated ecosystems by

outcompeting or preying upon placoderms and early tetrapods (Clement *et al.* 2004; Clack 2006). Similarly, changeover from a Devonian antiarch placoderm-porolepiform sarcopterygian biota to a Carboniferous chondrichthyan-actinopterygian assemblage in Russia was dismissed as a local phenomenon (Alekseev *et al.* 1994; Clack 2006).

Even when the possibility of global turnover has been considered, change was usually assumed to be gradual and limited to the marine realm. Freshwater deposits, by contrast, were thought act as a refugium because of the absence of known extinction impacts in those environments (this is, of course, a truism, reflecting the fact that mass extinctions have been inferred on the basis of marine invertebrates). Zhao and Zhu (2007) placed this faunal turnover in the Devonian, providing no biological explanation and attributing the pattern to the inevitable replacement of stem by crown. Blicek (2011) considered marine durophagous placoderms and sarcopterygians to have been replaced by holocephalans and actinopterygians, respectively. Even Romer's gap (Coates and Clack 1995) has been linked to a lack of nonmarine or continental deposits (Clack 2007; Blicek 2011). This demonstrably false claim (Peters and Foote 2001; McGowan and Smith 2008) was made in spite of concerted exploration of such deposits (Garvey 2005), similar patterns among other terrestrial forms (e.g. arthropods: Ward *et al.* 2006), and a coincident bottleneck in tetrapod phylogeny (Ruta *et al.* 2006; Coates *et al.* 2008).

This is not to say there have not been any attempts to quantify extinction impacts on Devonian vertebrates. Stratigraphic studies provide a wealth of occurrence data, and analyses of marine impacts often include fishes present within large databases or found at invertebrate sites (McGhee 1996; Hallam and Wignall 1999; Stanley 2008). Long (1993) devoted an entire chapter of a volume on the Devonian record to the impact of mass extinctions. Using family-level and range data from published compendia, including *The Fossil Record* (Andrews *et al.* 1967) and various volumes of the *Handbook of Palaeoichthyology* (HoP), origination and extinction rates were reconstructed for all vertebrates as well as major traditional taxonomic subgroups (Long 1993). Blicek (2011) augmented this with family-level diversity curves based on *The Fossil Record 2*. Most recently, Sallan compiled genus-level occurrence and species-level faunal composition databases for the mid-Devonian through Mississippian (Sallan and Coates 2010; Sallan *et al.* 2011). These databases cover both marine and nonmarine taxa, dealing with the aforementioned issues concerning euryhaline taxa and exclusion of continental faunas from larger datasets. Here, we discuss the impacts of the Kellwasser and Hangenberg events based on these studies.

The Kellwasser event

Conodonts, armoured agnathans and all manner of marine gnathostomes have been counted among the victims of the Kellwasser extinctions, which Long (1993) estimated as the most major of all Devonian bioevents for vertebrates. Conodont faunas experience nearly complete turnover, as usual for any stage boundary (and necessary for their use in biozonation). Aldridge (1988) estimated losses of 89 per cent of conodont species, including all those bearing coniform elements, while stratigraphically important genera were reduced further. McGhee (1996), citing Sandberg and colleagues (1988), suggested that losses among conodonts took place over a time span of a few days to 20 000 years.

Armoured agnathans, including members of several divisions of jawless stem gnathostomes such as heterostracans, osteostracans, galeaspid and thelodonts (Fig. 1), are often considered victims of this same event; Long (1993) and McGhee (1996), working from different data, indicated that the youngest armoured agnathans are Frasnian (385–374 Ma) in age. However, both authors admitted that these groups had been in decline for quite some time, reduced to a handful of mostly near-shore dwellers by the Frasnian. It is now apparent that the last appearances of armoured agnathans are staggered throughout Late Devonian. Osteostracans cross the Givetian–Frasnian boundary only to make their final appearance at the Miguasha *Lagerstätte*, before or around the mid-Frasnian (Janvier 1996). Those agnathan groups which last appear closer to the end of the Frasnian–heterostracans and galeaspid – had been restricted in both diversity, abundance, habitat and range since the mid-Devonian (Halstead 1993; Janvier 1996; Jia *et al.* 2010). In addition, a thelodont ichthyolith taxon has been recovered from the early-mid Famennian (374–359 Ma) of Iran (Hairapetian and Turner 2003). It is therefore unlikely that a sudden, abiotically driven Kellwasser event was the primary cause of armoured agnathan extinction in the Devonian.

Turning to jawed vertebrates, marine placoderms were long counted among the dead. Using HoP data compiled by Denison (1978, 1979), Long (1993) and McGhee (1996) calculated losses of up to 50 per cent of species and cosmopolitan families, with another third forced into nonmarine refugia. Diversity curves published by Sallan and Coates (2010), based on an aforementioned genus-level compilation, and Blicek (2011), based on family data from the *Fossil Record 2* (Gardiner 1993a), show similar reductions in placoderm diversity. However, many of these losses are attributable to the loss of endemic species and monotypic families found only at well-sampled *Lagerstätten* situated well before the Kellwasser horizon (e.g. Gogo, Australia and Bad Wildungen, Germany: Sallan and Coates 2010) (Fig. 4), as well as a relative lack

of similarly productive marine localities within the Famennian. In fact, the proportion of placoderm species at Famennian marine faunas was unchanged relative to the Frasnian (Sallan and Coates 2010). Similarly, recorded losses among other jawed fishes were largely limited to families with low diversity, many of them in decline long before the Kellwasser event (e.g. acanthodians, diplocercid coelacanths and cheirolepidid actinopterygians: Long 1993; Sallan and Coates 2010).

In summary, there does not seem to be evidence indicating a single, sudden vertebrate extinction event at the Frasnian–Famennian boundary. Instead, differences between Frasnian and Famennian diversity were the culmination of millions of years of gradual environmental and faunal change viewed through the lens of imperfect sampling. Sallan and Coates (2010) showed that there were no significant differences in the composition of late Frasnian and early Famennian jawed vertebrate assemblages at higher taxonomic levels. The most substantial change was an increase in the number of chondrichthyans, which might be attributable to the relative abundance of ichthyolith-bearing black shales in the Famennian. Likewise, Anderson and colleagues (2011) failed to detect a statistically significant reduction in ecological diversity based on the disparity of the gnathostome jaws and dentition. The diversity of durophagous lungfishes is substantially reduced in the Famennian compared with the Frasnian (Anderson *et al.* 2011), but this might simply reflect a failure to sample suitable shallow marine environments (Sallan and Coates 2010).

Therefore, observed diversity changes in the later Devonian are probably due to greater cosmopolitanism and gradual environmental trends, as well as basic sampling issues (Long 1993). As Pangaea formed, the supercontinents of Laurussia and Gondwana were brought together around the Southern tropics, destroying the near-shore and marine habitat and facilitating migration between once isolated faunas (Copper 1986; Young 2011). Marine invertebrate losses over the later Devonian have been attributed to a long phase of low origination rather than significantly heightened extinction rates (Bambach *et al.* 2004), a phenomenon linked to invasive migrations and subsequent reduction in endemism (Stigall 2010). However, there was at least one significant bioevent around the Kellwasser that cannot be explained by these circumstances: the loss of most metazoan reef builders (e.g. corals and stromatoporoid sponges), which did not fully recover until the Carboniferous (Copper 2002; Kiessling and Simpson 2011). It is surprising that marine vertebrate lineages occupying Frasnian carbonate platform reefs were not much affected by their loss; most simply moved on to Famennian replacement habitats, such as calcified algal structures and crinoid-dominated carbonate ramps, sometimes in the same vicinity (e.g. the Canning Basin com-

plex and other Frasnian–Famennian localities around Australia; Wood 2000; Cooper 2002; Waters and Webster 2009; Young *et al.* 2010; Sallan *et al.* 2011).

The Hangenberg event

While evidence for a Kellwasser event supports the cautiousness of most Devonian fish workers towards bioevents, the Hangenberg appears to represent a real, abiotically driven mass extinction. Acknowledgement of the large magnitude of the end-Devonian event is recent and not yet universal; the extinction was long considered a second-order pulse, no larger than others throughout the Famennian (Racki 2005). The first review of the biotic impact of the event was published in 1999 (Caplan and Bustin 1999) and as recently as 2010 geologists and palaeontologists could declare the Hangenberg and associated abiotic events ‘underrated’ among Devonian extinctions (Racki 2005; Bambach 2006; Brezinski *et al.* 2010). Part of the issue was stratigraphic; Hangenberg black shales were assumed to occur within the Devonian *praesulcata* conodont zone, perhaps representing the boundary between the Famennian and the ‘Strunian’. Exact correlation was impeded by a lack of biozonation taxa, such as ammonites, conodonts and palynomorphs: all victims of the Hangenberg (Caplan and Bustin 1999; Korn 2000; Kaiser *et al.* 2008). This stratigraphic uncertainty has enabled claims that classic Devonian vertebrates (e.g. placoderms) and faunas continued above the Hangenberg horizon (Alekseev *et al.* 1994; Young 2003; Blom *et al.* 2007).

Recent work has shown that Hangenberg sediments comprise both anoxic black shales and the sandstones above them, with composition and thickness dependent on environment (Buggisch and Joachimski 2006; Brezinski *et al.* 2008, 2010; Kaiser *et al.* 2008). The Hangenberg horizon is now designated as the Devonian–Carboniferous boundary and thus the focus of concerted stratigraphic work (Kaiser *et al.* 2006; Brezinski *et al.* 2010). The unfossiliferous formations of varying height above many important end-Famennian vertebrate *Lagerstätten*, such as the Cleveland Shale in Ohio, the Chaffee Formation in Colorado, Red Hill in Pennsylvania, are Hangenberg event sediments laid down in <100 000 years (perhaps East Greenland as well: Theron 1993; Clack 2006; Brezinski *et al.* 2008, 2010; Myrow *et al.* 2011; J. E. A. Marshall, pers. comm. 2011). Many of these, particularly formations correlated with the ‘Hangenberg Sandstone’, are ice age-associated deposits. Glaciers at sea-level at both the poles and near the tropics left characteristic diamictites and mud flats, while significant sea-level fall drove the formation of deep river valleys directly atop older marine deposits (including the Cleveland Shale; Algeo *et al.* 2007;

Brezinski *et al.* 2008, 2010; Isaacson *et al.* 2008). At other vertebrate localities such as Andreyevka-2 in Russia and the Witpoort Formation in South Africa, Devonian–Carboniferous unconformities begin at the level of the Hangenberg horizon (Theron 1993; Alekseev *et al.* 1994, 1996) and it is likely that deposition was halted by marine regression (Alekseev *et al.* 1994; Hallam and Wignall 1999; Algeo *et al.* 2007). Global correlation of the Hangenberg horizon, and therefore the Devonian–Carboniferous boundary, is an ongoing project (Kaiser *et al.* 2008; Brezinski *et al.* 2009, 2010) which could reveal further examples of vertebrate faunal hiatus or sudden taxonomic turnover in even conformable deposits.

Abrupt vertebrate faunal changes were noted from around the Devonian–Carboniferous before recent stratigraphic work. Thomson (1976) pointed to a reduction from the numerous finned sarcopterygian genera at late Famennian sites to just a few megalichthyids and rhizodonts in the entire early Carboniferous (Mississippian; 359–318 Ma). Janvier (1977) remarked on the sudden end-Devonian extinction of large arthrodire placoderms, which he suggested were equivalent in scope to the loss of marine reptiles at the end-Cretaceous. This loss was linked with the Hangenberg regression (Algeo *et al.* 2007), as well as the same vague ‘internal and external’ factors used to explain the extinction of dinosaurs prior to the discovery of the Cretaceous–Palaeogene (K–Pg) iridium anomaly. In contrast, the coincident disappearance of durophagous ptyctodont placoderms was attributed to a shift of habitat into the deep sea (a habitat poorly represented in the fossil record), based on their mistaken placement as the ancestors of living bathypelagic holocephalans (and neglecting the diversity of holocephalans in shallow marine Carboniferous habitats; Janvier 1977; Sallan and Coates 2010; Sallan *et al.* 2011).

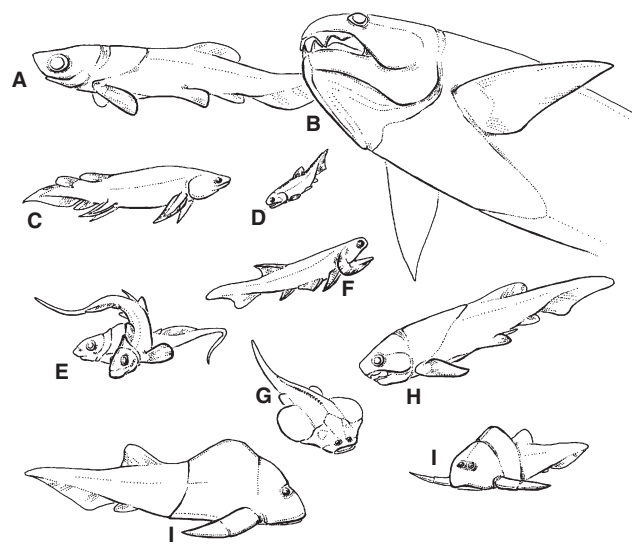
The proposed arthrodire extinction was later expanded to encompass all placoderms. Long’s (1993) family-level diversity data showed that placoderms in all habitats faced extinction over the end-Devonian or shortly thereafter. Hallam and Wignall (1999) were the first to directly attribute placoderm extinction to the Hangenberg event, even positing that the extinction enabled reported increases in actinopterygian diversity in all Carboniferous marine settings. Long (1993) also suggested an end-Devonian extinction of ischnacanthids among acanthodians, and porolepiforms, onychodonts, a few osteolepidid families, and marine lungfishes among sarcopterygians (Long 1993). The Devonian–Carboniferous extirpation of lungfishes from marine environments has been noted by a number of authors, but most discussions have failed to link it to any abiotic event (e.g. Campbell and Barwick 1986; Lloyd *et al.* 2012a). This is despite evidence for coincident and sudden changes in the habitat ranges and environmental associations of gyracanthids, rhizodonts,

elasmobranchs (Figs 5 and 6) and even eurypterids (Lamsdell and Braddy 2010). The large number of such shifts might be a mark of random refugia in different environments.

Looking to direct stratigraphic and faunal evidence, Alekseev and colleagues (1994) dated the Andreyevka-2 fauna at Tula, Russia as latest Famennian, noting the compositional similarity of the tetrapod-bearing assemblage to similarly aged sites elsewhere. This is followed by the previously mentioned, likely Hangenberg-related, hiatus in sediment deposition, which is found elsewhere in Russia (Alekseev *et al.* 1994, 1996; Algeo *et al.* 2007). In contrast to the Famennian fauna, the earliest Carboniferous assemblage in the Tula sections is similar to actinopterygian-dominated Russian and Scottish *Lagerstätten* from later in the Carboniferous. These sediments also contain chondrichthyan, megalichthyid and rhizodont sarcopterygians remains, lacking any evidence of the Porolepiform sarcopterygians antiarch placoderms and tetrapods that had previously inhabited a similar environment at the same spot (Alekseev *et al.* 1994). Alekseev suggested that the early Carboniferous actinopterygian-chondrichthyan fauna had originated at distinct Devonian localities and passed through the boundary unscathed.

There is stratigraphic evidence of extinction and turnover within chondrichthyans and actinopterygians. A vertebrate fauna in latest Famennian red sandstones at Hakkari, Turkey contains actinopterygian microfossils and ‘ctenacanth’/‘cladodont’ chondrichthyan ichthyoliths, alongside groenlandaspis placoderms, onychodontid sarcopterygians and chirodipterid lungfishes (Janvier *et al.* 1984). However, the only fossil known from the overlying Early Carboniferous formation is a cochliodont chondrichthyan tooth, appearing above an unfossiliferous shale that might be Hangenberg-related (Janvier *et al.* 1984). In Ohio, the diverse chondrichthyan fauna of the Cleveland Shale is largely absent from both the overlying Hangenberg-associated deposits and the early Tournaisian (359–345 Ma) Sunbury black shale (Hansen 1996; Brezinski *et al.* 2008, 2010). The latter has similar taphonomy to the Famennian formations, but the only chondrichthyan material is preliminarily assigned to *Stethacanthus*, belonging to a genus and clade (Symmoriiformes; figs 1, 6) common in Carboniferous Euramerica. Similarly, Randon and colleagues (2007) noted the Hangenberg-related loss of a phoeodont-jalodont chondrichthyan-dominated ichthyolith fauna in the Italian Carnic Alps, and its replacement by a taxonomically depauperate symmoriiform assemblage in conformable Tournaisian sediments. The Famennian fauna was similar to those described elsewhere and also contained actinopterygian and placoderm material. Ginter (1990) hypothesized a global Hangenberg-associated extinction of phoeodont chondrichthyans based on such samples (Ginter and Ivanov 1995). However,

Late Devonian (Frasnian), Bad Wildungen



Late Mississippian (Serpukhovian), Bear Gulch

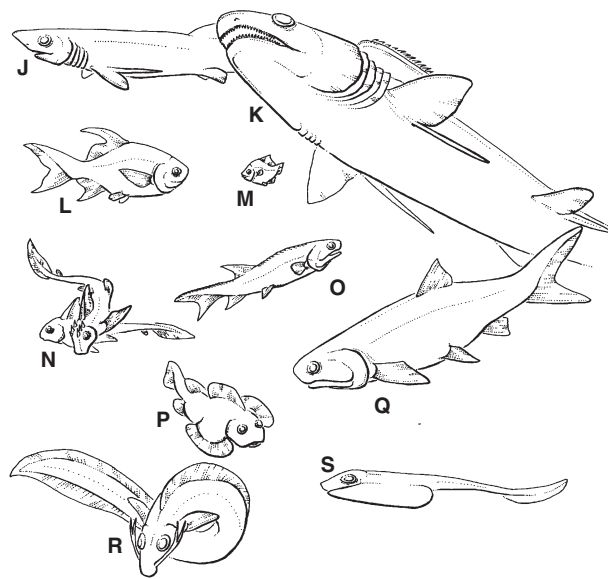


FIG. 5. Comparisons between Devonian (left) and Carboniferous (right) marine fish faunas. The Devonian assemblage derives from Frasnian age (385–374.5 Ma) deposits at Bad Wildungen, Germany. The Carboniferous assemblage derives from Serpukhovian age (328–318 Ma) deposits at Bear Gulch, Montana, USA. A, the arthrodire placoderm *Wildungenichthys*. B, the arthrodire placoderm *Erromanosteus*. C, the dipnoan sarcopterygian *Chirodipterus*. D, the actinopterygian *Moythomasia*. E, the ptactodontid placoderm *Rhynchodus*. F, the acanthodiform acanthodian *Homacanthus*. G, the rhenanid placoderm *Jagorina*. H, the arthrodire placoderm *Coccosteus*. I, the antiarch placoderm *Lepadolepis*. J, the symmoriiform chondrichthyan *Falcatus*. K, the symmoriiform chondrichthyan *Stethacanthus*. L, the actinopterygian *Aesopichthys*. M, the actinopterygian *Discoserra*. N, the holocephalan chondrichthyan *Echinochimaera*. O, the actinopterygian *Kalops*. P, the holocephalan chondrichthyan *Belantsea*. Q, the actinopterygian informally named ‘Yogoniscus.’ R, the holocephalan chondrichthyan *Harpagofututor*. S, the elasmobranch chondrichthyan *Squatinactis*.

because there is little direct association between phoeodont ichthyoliths and macrofossil material, it is not clear what these patterns might mean in an ecological sense.

Until recently, these studies represented the full extent of investigation into vertebrate faunal change over the Hangenberg event, representing a sparse and uneven sample relative to the number of vertebrate-bearing deposits from the Famennian and Tournaisian. Sallan and Coates (2010) documented the global extent and depth of faunal turnover at the Hangenberg by using both global jawed vertebrate diversity data and analyses of faunal composition at well-sampled localities from both sides of the horizon. While diversity curves indicated a 32 per cent reduction in generic diversity over the Famennian–Tournaisian, faunal analyses showed the complete loss of 44 per cent of major gnathostome clades immediately around the Hangenberg horizon (Sallan and Coates 2010) (Fig. 6). There appears to have been little selectivity and few refugia: all Devonian and Carboniferous faunas were significantly different regardless of inferred environment (continental or marine) (Figs 5 and 6). The victims included sarcopterygians, acanthodians and placoderms found in different habitats and exhibiting divergent ecomorphologies (Sallan and

Coates 2010; Anderson *et al.* 2011) (Fig. 6). Tournaisian and later Carboniferous sites were found to contain a highly homogeneous and temporally distinctive assemblages dominated by actinopterygians and chondrichthyans, with fewer lungfishes, rhizodonts, megalichthyids, coelacanth, acanthodid and gyracanthid acanthodians, and scant tetrapod material (Coates and Clack 1995; Coates *et al.* 2008; Sallan and Coates 2010) (Fig. 6).

Post-Hangenberg recovery

The Hangenberg event seems to have restructured vertebrate ecosystems worldwide and marked a bottleneck in the evolution of modern clades (Figs 5 and 6). Diversity curves show large increases in actinopterygian and chondrichthyan richness starting in the Tournaisian, followed by a postbottleneck diversification of tetrapods (Coates *et al.* 2008; Sallan and Coates 2010; Sallan *et al.* 2011). These three groups have dominated all subsequent vertebrate faunas (Nelson 2006; Sallan and Coates 2010) (Figs 5 and 6). Romer’s gap might therefore be interpreted as the post-Hangenberg recovery interval, based on the existence of a depauperate homogeneous global

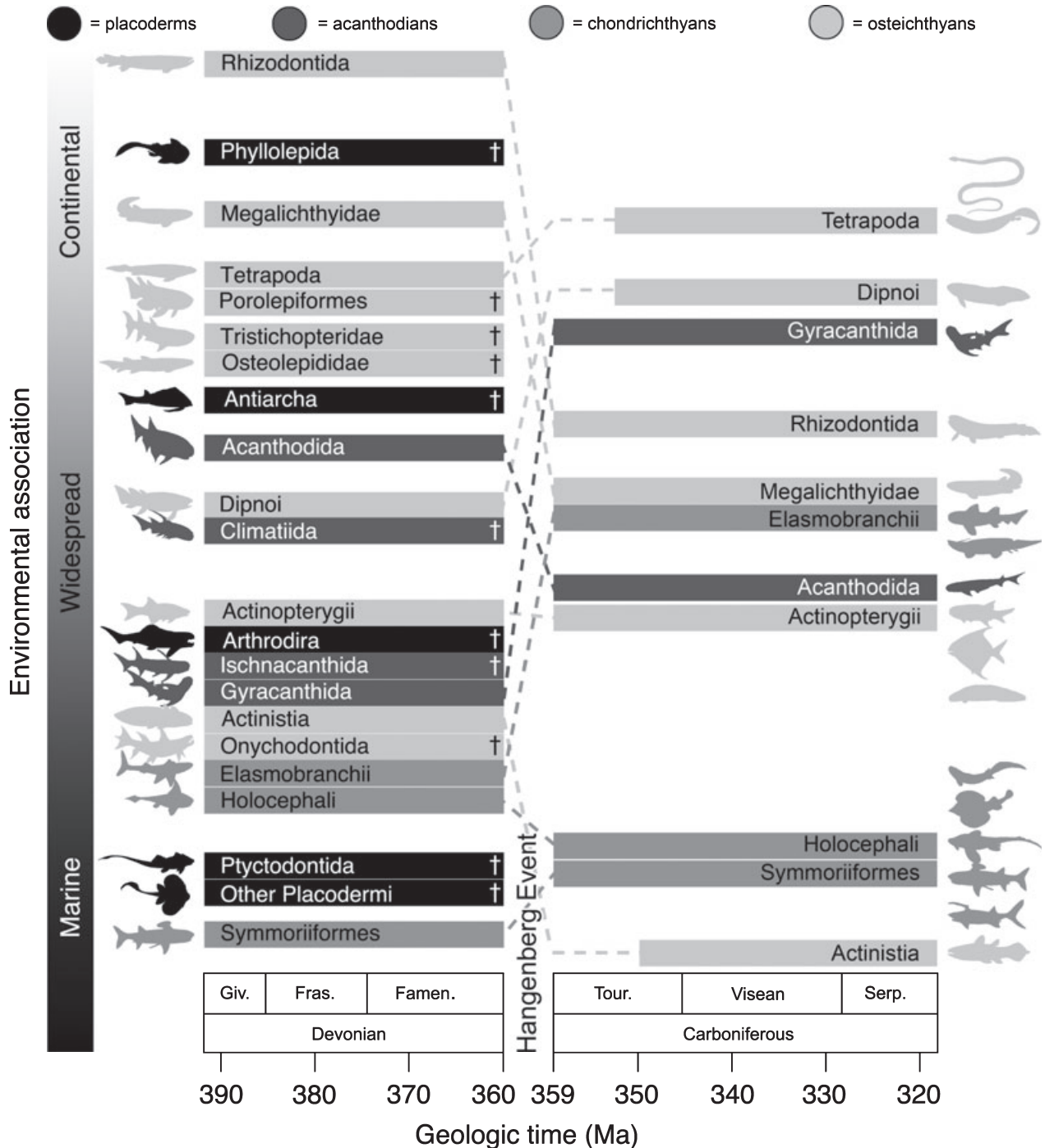


FIG. 6. Gnathostome extinction selectivity and inferred habitat changes over the Hangenberg event (360–359 Ma). Habitat preferences based on first canonical correspondence axis generated by later Devonian (391–359 Ma) or Mississippian (359–318 Ma) gnathostome faunas (data from Sallan and Coates 2010; see that analysis for justification of reconstructed habitat preference). Solid lines represent known ranges within the stages, dashed lines are ghost lineages. Dagger symbol (†) indicates the termination of lineages. 44 per cent of groups make their last appearance at or near the Hangenberg horizon, representing all vertebrate divisions and ecological categories. Three previously marine clades (Dipnoi (lungfishes), Gyracanthida (gyracanth acanthodians), Elasmobranchii (sharks)) appear to become more tightly linked to continental deposits in the Carboniferous, while two previously continental tetrapodomorph sarcopterygian fish clades (Rhizodontida and Megalichthyidae) moved into marine areas.

gnathostome fauna (Sallan and Coates 2010). This is also supported by the relative rarity of both macrofossil sites and tetrapod material, particularly during the first 10 million years post-extinction, despite concerted searches (e.g. Brazeau 2005; Garvey and Turner 2006; Smithson *et al.* 2012) and the continued availability of suitable depositional environments (Hansen 1996; McGowan and Smith 2008). At the moment, diversity patterns for all three major post-Devonian divisions, tetrapods, actinopterygians, and chondrichthyans, are suggestive of a general recovery curve (Sallan and Coates 2010; Sallan *et al.* 2011): little new diversity, significant morphological differentiation and/or abundance at both ichthyolith and macrofossil levels in the early Tournaisian, a small number of superficially similar but ecologically differentiated lineages at faunas in the late Tournaisian (e.g. the Foulden fauna of Scotland and the Horton Bluff fauna of Canada; Brazeau 2005; Sallan and Coates 2010; Smithson *et al.* 2012), and finally a peak in the appearance of novel taxa, body forms and niches by the middle to late Viséan (e.g. the various Viséan tetrapod and fish sites of the United Kingdom, such as Glencartholm and East Kirkton; Dineley and Metcalfe 1999).

The Tournaisian marks the beginning of a major round of morphological diversification in both actinopterygians and chondrichthyans, featuring the appearance of novel body shapes, jaw mechanics and dentitions (particularly durophagous and benthic types: Sallan and Coates 2010; Sallan *et al.* 2011; Finarelli and Coates 2012; Sallan and Friedman 2012) (Fig. 4). This suggests the existence of new opportunities facilitated by the loss of incumbent Devonian vertebrates at all ecological levels (Fig. 6). It is not clear why other survivors, such as acanthodians and tetrapodomorph fishes (rhizodonts and megalichthyids), did not diversify into new ecospace (Janvier 1996; Sallan and Coates 2010). Rather, a handful of genera persisted for several million years before disappearing, illustrating the postextinction phenomenon of 'Dead Clade Walking' (Jablonski 2002).

LATE PALAEOZOIC TO LATE MESOZOIC EVENTS

The late Palaeozoic to late Mesozoic interval is punctuated by two mass extinctions (the Permian–Triassic (251 Ma) and Triassic–Jurassic (200 Ma); Raup and Sepkoski 1982) and a purported reorganization of marine ecosystems (Vermeij 1977), coupled with environmental perturbations ranging from ocean anoxic events (Toarcian (183–176 Ma), early Aptian (125–112 Ma), and Cenomanian–Turonian (100–89 Ma); Schlanger and Jenkyns 1976; Jenkyns 1988) to rapid changes in global temperatures (Price 1999; Jenkyns 2003). However, the response

of fishes to these major climatic and biotic shifts is unclear. Here, we review outstanding patterns that are presently apparent in fish diversity during this lengthy interval and suggest whether these features are likely real or merely artefactual.

The late Mississippian and Permian richness trough: genuine or artefactual?

Marine invertebrate palaeontologists have proposed a bioevent equivalent to the Hangenberg and ecologically more severe than the end-Ordovician at the Viséan–Serpukhovian boundary (328 Ma), coincident with the onset of the Late Palaeozoic Ice Age (Bambach 2006; McGhee *et al.* 2012). However, Sallan and Coates (2010) found jawed fish faunal composition to be stable in the later Mississippian, perhaps in line with the onset of stasis in vertebrate morphological and taxonomic diversity (Sallan *et al.* 2011; Sallan and Friedman 2012). There is a significant reduction in marine ichthyolith sampling and the number of macrofossil localities beginning at the Serpukhovian (328–318 Ma) and persisting into the later Palaeozoic (Sepkoski 2002; Sallan *et al.* 2011). However, the Mississippian–Permian trough found in many marine generic diversity curves might be related to a general lack of appropriate marine deposits in Europe (Serpukhovian; McGowan and Smith 2008; McGhee *et al.* 2012). The absence of fossiliferous marine facies was likely driven by both the destruction of Euramerican coastlines during the formation of Pangaea and regression-driven hiatuses during long glacial cycles (which last up to 150 000 years in the Pleistocene; Falcon-Lang *et al.* 2009; McGhee *et al.* 2012). There is also a lack of nonmarine Permo-Carboniferous (c. 318–251 Ma) deposits relative to the temporal span: most productive fish localities represent coal swamps and similar nonmarine habitats which were only widespread during short interglacials (lasting at most 20 000 years as in the Pleistocene) and cyclically replaced by seasonally or perennially dry environments (Falcon-Lang and DiMichele 2010).

Therefore, the late Palaeozoic depletion apparent in Sepkoski's genus-level data might represent a sampling artefact. However, it does not occur in all data. Serpukhovian vertebrate taxon counts are boosted by the *Lagerstätten* at Bear Gulch, USA and Bearsden, Scotland, which exhibit a higher taxonomic and morphological diversity of chondrichthyans than might assumed from ichthyolith sites (Sepkoski 2002; Sallan and Coates 2010; Sallan *et al.* 2011) (Fig. 4). Blicek (2011) showed that Pennsylvanian vertebrate familial diversity rises above Mississippian levels in data from *The Fossil Record 2*, perhaps driven by the sporadic appearance of members of certain families better known from other Palaeozoic and Mesozoic intervals.

It is also possible that the Permo-Carboniferous trough is driven by the existence of stable cosmopolitan marine and freshwater faunas around Pangaea, rather than abiotic events or rock volumes. Permo-Carboniferous actinopterygian genera, such as *Elonichthys*, *Platysomus*, *Aeduella*, *Amblypterus*, *Acrolepis* and *Palaeoniscum*, seem especially widespread and long-lived, appearing at multiple disparate localities and persisting for tens of millions of years. Likewise, similar chondrichthyan teeth are known from around the Permo-Carboniferous world, with a few ranging through the entire interval (e.g. some petalodonts; Sepkoski 2002). Many of these apparently stable late Palaeozoic taxa have not undergone critical taxonomic revision in decades, with their longevity perhaps more indicative of neglect rather than true stratigraphic duration. However, their ecomorphologies do appear static (L. C. S., pers. obs.) and the same pattern occurs in marine invertebrate data, with Permo-Carboniferous benthic assemblages being particularly stable and conserved over large temporal and geographical scales (Schram 1979; Bonuso and Bottjer 2006). Bonelli and Patzkowsky (2008) noted highly homogeneous faunal composition at a single Serpukhovian site, with similar taxa appearing at all depths along a coastal gradient. In summary, reduced richness of fishes during the Permo-Carboniferous appears attributable to a lack of ecological opportunities and available habitat leading to low origination, perhaps exacerbated by poor sampling (McGowan and Smith 2008; Falcon-Lang and DiMichele 2010; McGhee *et al.* 2012).

The end-Permian event and Triassic diversification

Although classically regarded as the most catastrophic of Phanerozoic mass extinctions (Raup and Sepkoski 1982; Erwin 1990), the effects of the Permian-Triassic event on fishes remain deeply ambiguous (Janvier 1996; Blicek 2011). This reflects, we suspect, the relatively poor understanding of late Permian fishes (particularly actinopterygians; see discussion in Hurley *et al.* 2007), combined with a failure to adequately quantify patterns derived from available fossil data. Recent discussion in the literature touching on the end-Permian event as it relates to fishes is generally couched in terms of extinction recovery (Tong *et al.* 2006; Brinkmann *et al.* 2010; Hu *et al.* 2011; Wen *et al.* 2012). This is largely because Triassic (251–200 Ma) fishes are abundant and well-studied in comparison with the sparse record available for the Permian. The obvious problem is that such a research programme presupposes that patterns apparent among fishes represent recovery from extinction, without having first clearly demonstrated that fishes themselves were affected in such a way that it might be necessary to invoke recovery. We emphasize this point here because palaeontologists studying both elasmobranchs (Mutter *et al.* 2007; Mutter and Neuman 2008, Mutter 2009) and osteichthyans (Schaeffer 1973), as well as total fish diversity (Janvier 1996; Blicek 2011), have found little evidence for major taxonomic shifts associated with the end-Permian event, and no striking decline in richness is apparent in broader surveys (Fig. 1). Marine conodonts, which have best global record of any vertebrate group, were apparently little affected by the Permo-Triassic apart from a dip in abundance (Clark 1983; Clark *et al.* 1986; De Renzi *et al.* 1996). Indeed, the familial data within the *Fossil Record 2* show consistent levels of fish diversity through the Permian and into the early Triassic, leading Blicek (2011) to conclude that there was no real loss. Sepkoski's (2002) data give no indication of elevated extinction in the late Permian (Fig. 2), and his osteichthyan data are so scant that rates cannot be estimated for this major group (Fig. 3). A literal reading of Sepkoski's data would suggest that the earliest Triassic (Induan; 251–249.5 Ma) was an interval of intensive turnover among fishes (Figs 1–3), perhaps indicative of turbulent postextinction recovery. Here too, small taxonomic samples urge caution: Sepkoski (2002) records only six chondrichthyan and 13 osteichthyan genera from this interval. In the face of such evidence, we question claims that 'fishes were severely affected by the end-Permian mass extinction' (Wen *et al.* in press), at least in aggregate.

However, at least one important segment of Permo-Carboniferous fish diversity is missing from Triassic localities: nonchimaeroid holocephalans (Cappetta *et al.* 1993; Stahl 1999; Sepkoski 2002). The durophagous holocephalans became particularly diverse in the aftermath of the Hangenberg extinction (Figs 5 and 6), and many assemblages, including petalodonts, cochliodonts, deltoptychiids, pristiodonts, menaspids, and helodonts, persist through the late Palaeozoic (Stahl 1999; Sepkoski 2002; Sallan *et al.* 2011). The majority of these Palaeozoic holocephalan groups have last appearances in the late Permian. Indeed, petalodont ichthyoliths and even body fossils (e.g. *Janassa*) were widespread in end-Permian formations from Japan to Germany to Arizona (Goto 1994; Stahl 1999). Many of these holocephalan taxa are effectively repositories for morphologically similar teeth arising in different lineages (Smith and Patterson 1988; Sallan *et al.* 2011; Finarelli and Coates 2012). However, most represent clades at various levels and may serve as a proxy for ecological or functional diversity (Stahl 1999; Sallan *et al.* 2011).

In reconciling these losses with the lack of extinction signal for other fishes, it is notable that the vast majority, if not all, of Palaeozoic holocephalan material is marine (Stahl 1999) (Fig. 4). These groups co-existed with, and fed upon, known invertebrate victims of the extinction (Moy-Thomas and Miles 1971; Stahl 1999; Sallan *et al.* 2011). In contrast, the majority of unaffected elasmobranch and osteichthyan lineages were either euryhaline

(e.g. hybodonts) or completely freshwater (e.g. xenacanth) in ecology (*contra* Schultze 2009) and are well represented in the coal measures, deltas and shallow basins of Palaeozoic–Mesozoic Euramerica (Hook and Baird 1988; Dick 1998; Zajic 2000; Kriwet *et al.* 2008) (Fig. 6). As exceptions that might prove the rule, several deep-bodied, durophagous actinopterygian lineages widespread in Permo–Carboniferous sediments (e.g. *Eurynotus*, *Amphicentrum*; Moy-Thomas and Miles 1971; Dineley and Metcalfe 1999), suddenly disappear at or before the end-Permian (Gardiner 1993a). An additional datum supports marine, but not durophage, selectivity: the brush-backed symmoriiform chondrichthyans (stethacanthids) (Fig. 1), nektonic predators once widely dispersed in Palaeozoic seas (Figs 1 and 6), make their last appearance in the late Permian despite high diversity in earlier assemblages (Goto 1994; Ivanov 2005).

It is therefore possible there was a selective loss of marine and/or durophagous fishes between the Permian and Triassic. Whether these extinctions were centred on the end-Permian event or occurred more gradually is another issue. Mapes and Benstock (1988) noted a decline in holocephalan lineages over the later Permian, and Ivanov (2005) suggested that chondrichthyan tooth assemblages from that interval are less diverse than in the Carboniferous. Indeed, compendia show that the last appearances of some holocephalan lineages, such as cochliodonts, deltopychiids and chondrenchelyiforms, occurred in the early Permian or even the Late Carboniferous (Cappetta *et al.* 1993; Stahl 1999; Sepkoski 2002).

These last appearances could represent random extinctions expected over any geological interval. After all, other fishes sometimes counted among the victims of the end-Permian event – acanthodians and megaliththyid sarcopterygians – represented depauperate lineages that disappeared in geographically stepwise fashion long before the boundary (Janvier 1996; Mutter and Richter 2007; Sallan and Coates 2010). Alternatively, holocephalan losses before the end-Permian could be due to the Signor-Lipps effect: backsmearing of extinction because of incomplete sampling of the record (Signor and Lipps 1982; Foote 2007), perhaps magnified by the poor condition of the late Permian fish record. Indeed, articulated marine fishes from that interval derive almost exclusively from the Marl Slate and Kupferschiefer of the northern European Zechstein Sea (Dineley and Metcalfe 1999; Diedrich 2009) with a few scattered examples from further afield (China: Liu and Wei 1988; Greenland: Stemmerik *et al.* 2001), and these have been little studied. However, it is clear even from this scant record that many actinopterygian genera typically associated with Triassic age assemblages (*Saurichthys*: Liu and Wei 1988; *Bobasatrania*: Stemmerik *et al.* 2001) have ranges extending into the late Permian.

By contrast, the Triassic is marked by a series of well-documented and widely distributed marine *Lagerstätten* in Austria, Canada, China, Greenland, Italy, Madagascar, Spitsbergen, and Switzerland, with more minor assemblages in the United States (Tintori 1998; Brinkmann *et al.* 2010; Hu *et al.* 2011; Mutter 2011). Such Triassic deposits have been particularly important for calibrating the radiation of neopterygians, the clade that includes nearly all modern ray-finned fish diversity (Nelson 2006). In addition, the early Triassic also seems to record the onset of the neoselachian elasmobranch radiation (Underwood 2006), which includes all living chondrichthyans apart from holocephalans.

Both the neopterygian total group and crown appear to extend well into the Palaeozoic (Hurley *et al.* 2007), but crown representatives are minor components of faunas of this age, in terms of both richness and abundance (Diedrich 2009). Holosteans (bowfin, gars and their relatives) remain rare and teleosts are absent until the Late Triassic, at which point some localities record a great diversity of trophically divergent crown neopterygians. Particularly, striking is the proliferation of durophagous taxa both among total group teleosts (Pycnodontiformes) and holosteans (Macrosemiidae, Seminotidae) along with *incertae sedis* neopterygian groups (Dapediidae), occurring subsequent to the last appearances of so many Palaeozoic durophages (Tintori 1998).

In summary, although the magnitude of the end-Permian event for fishes is unclear, there is a possibility of selective extinction of marine (and particularly durophagous) fishes. In contrast, euryhaline elasmobranch and actinopterygian lineages, and marine conodonts, seem to have been largely unaffected, with multiple lineages present in devastated marine ecosystems in the Early Triassic. Just as many groups underwent habitat shifts post-Hangenberg, surviving fish clades might have moved into new marine environments, even though they would have found few resources in the immediate aftermath. Indeed, elasmobranch ichthyoliths from some Early Triassic localities are said exhibit a ‘Lilliput effect’, a reduction in size often noted after mass extinction and associated with poor productivity (Twitchett 2001; Chen *et al.* 2007; Mutter 2009). However, the significance of this reduction is unclear, because ichthyoliths from a single taxon can be variable, the size of pre-event ancestors is not always known, and oversampling of stressed environments in recovery intervals can affect recorded averages (McGowan *et al.* 2009). Holocephalans do not reappear in the record until the later Triassic, when they largely exhibit a form very similar to living chimaeroids (Stahl 1999). Mesozoic holocephalans did achieve some degree of disparity, ranging from dorsoventrally flattened skate-like forms in the Early Jurassic (Stahl 1999) and giant, but anatomically more conventional, species in the Late Cretaceous

(Cicimurri *et al.* 2008). However, they never completely refilled lost morphospace or recovered to their Palaeozoic abundance, at least outside of the deep-sea environments that Recent forms inhabit and for which Mesozoic records are poor (Stahl 1999). The apparent diversity patterns discussed previously are therefore suggestive of selective extinction and replacement of fishes at the Permo-Triassic. These are in need of detailed investigation.

Middle and late Mesozoic diversity patterns

The middle Mesozoic commenced in the aftermath of the Triassic–Jurassic extinction, but the effect of that event upon fishes seems minimal (McCune and Schaeffer 1986; Bambach *et al.* 2004). Not a single osteichthyan family listed in *The Fossil Record 2* by Gardiner (1993b) or Patterson (1993a) fails to cross the boundary (Hallam 2002). However, there is one potentially major exception: conodonts (Fig. 2). While Triassic conodont diversity paled in comparison with their Ordovician and Devonian–Mississippian peaks (Fig. 2), conodont origination preceding the Triassic–Jurassic boundary was greater than in any interval because the Mississippian and their biostratigraphic utility was undiminished until the end of the period (Clark 1983; De Renzi *et al.* 1996).

Conodonts seem to undergo a long-term decline in the second half of the Triassic (Fig. 2) (Clark 1983; De Renzi *et al.* 1996; Sepkoski 2002). During this same interval, conodont elements became more ‘generalized’ or homogeneous in form, waned in abundance, were reduced to a single family and were extirpated from faunal regions in stepwise fashion (Trammer 1974; Clark 1983; Hallam 2002; Tanner *et al.* 2004). The latter trends could be reflective of a Signor-Lipps effect driven by facies change near the extinction boundary (Signor and Lipps 1982; Clark 1983; De Renzi *et al.* 1996; Tanner *et al.* 2004). However, the selective disappearance of conodonts by the end-Triassic is not widely attributed to an abiotic marine event, but rather to long-term loss of appropriate environments and greater provincialism because of the break-up of Pangaea (De Renzi *et al.* 1996). Losses have also been credited to an unfortunate run of random extinction, after-effects of the Permo–Triassic, competition with the modern evolutionary fauna, and even anecdotal scenarios invoking predation by ichthyosaurs (Clark 1983; De Renzi *et al.* 1996).

It is difficult to favour any single or combination of options because relevant data are largely unavailable, including that for the diversity of other fishes with similar environmental preferences and ecologies. However, the Triassic–Jurassic interval is generally defined by such gradual taxonomic and ecological turnover (Hallam 2002). In

fact, the event has been termed a mass depletion without a single cause, akin to the Frasnian–Famennian (Bambach *et al.* 2004). On that note, Kriwet and colleagues (2009) have suggested that the Early Jurassic radiation of neoselachians reflects opportunistic radiation into ecological roles cleared by extinction, whether sudden or gradual, a repeated pattern by this point in the record.

The Jurassic–Cretaceous interval (200–65.5 Ma) is punctuated by several ocean anoxic events (OAEs; Schlanger and Jenkyns 1976; Jenkyns 1988), but there has been no suggestion that any of these resulted in either major extinction or faunal turnover among fishes. Indeed, some OAEs are flanked by well-studied faunas (e.g. the Hettangian–Sinemurian of Lyme Regis, England and the Toarcian of Yorkshire, England, Germany, and France in the case of the early Toarcian OAE; Wenz 1967; Hauff and Hauff 1981; Dineley and Metcalf 1999), and some even occur within continuous units that have been historically well-sampled for fishes (e.g. the English Chalk in the case of the Cenomanian–Turonian OAE; Dineley and Metcalf 1999).

There are two clear peaks in raw richness trajectories for Mesozoic fishes: one at the close of the Jurassic and another in the early Late Cretaceous (100–65.5 Ma). Both of these correspond to intervals with well-studied exceptional deposits, yielding numerous articulated actinopterygians (Late Jurassic: Cerin, France, and Solnhofen, Germany; early Late Cretaceous: Djebel Tselfat, Morocco, English Chalk, UK, Hakel, Hadjoula, and Namoura, Lebanon; Lambers 1999; Forey *et al.* 2003). Phylogeny-based techniques indicate that the Late Jurassic peak is probably a preservational artefact, at least for actinopterygians (Cavin 2010). However, the same phylogenetic test suggests that a genuine radiation among actinopterygians occurred during the Cenomanian (100–94 Ma; Cavin and Forey 2007), and Cavin *et al.* (2007) hypothesized such a pattern might have been driven by high sea surface temperatures.

THE END-CRETACEOUS EXTINCTION AND PALAEOGENE RECOVERY

The end-Cretaceous event (65.5 Ma) is perhaps the most thoroughly studied and best understood of the canonical Big Five Phanerozoic extinctions, due in large part to its relative recency combined with the charismatic nature of its most conspicuous victims. The literature concerning the mechanism of extinction is extensive, and we refer readers to the recent review of the prevailing bolide impact hypothesis presented by Schulte *et al.* (2010) and responses to it by advocates of more nuanced drivers (Archibald *et al.* 2010; Courtillot and Fluteau 2010; Keller *et al.* 2010).

In contrast to older extinction events, patterns of turnover in fishes centred on the K–Pg boundary have been the focus of numerous studies in both marine and continental environments, at scales ranging from individual sections to global surveys. Most work has focused on either marine or freshwater taxa, but the handful of analyses addressing both (e.g. Cavin and Martin 1995; Cavin 2001a) have inferred contrasting patterns in these two environmental settings. We have divided our discussion of the K–Pg extinction to reflect this dichotomy.

Patterns in continental settings

The picture of turnover in freshwater fishes is based largely on regional patterns, with a particular emphasis on sections of the Maastrichtian (71–65.5 Ma) Hell Creek Formation and overlying Danian (65.5–61 Ma) Tullock Formation in eastern Montana (Bryant 1989; Sheehan and Fastovsky 1992, 1993; Archibald 1993, 1996). Late Cretaceous to Palaeocene (84–56 Ma) continental deposits in western North America generally represent high-energy palaeoenvironments, with the consequence that most fish fossils consist of isolated, often badly abraded, bones, teeth, spines and scales recovered by screen washing (Grande and Grande 1999). This taphonomic filter generally prevents precise identification of many specimens, particularly of teleosts, although more detailed anatomical analysis has demonstrated that finer taxonomic assignment is possible (Wilson *et al.* 1992; Brinkman and Neuman 2002; Neuman and Brinkman 2005; Newbrey *et al.* 2009). Previous studies have therefore been conducted at the genus level, with probable overrepresentation by non-teleostean taxa characterized by distinctive and easily identifiable microremains (chondrichthyans, chondrosteans, holosteans). There is compelling evidence that teleosts were more significant members of Late Cretaceous freshwater communities, both in terms of numbers of individuals and taxonomic richness, than current faunal lists tend to indicate (Neuman and Brinkman 2005; Redman *et al.* 2010); consequently, patterns of fish extinction reconstructed from K–Pg sections in the Western Interior must be considered with this important caveat in mind.

Numerous studies have examined the distribution fossil fishes above and below the K–Pg boundary (Archibald and Bryant 1990; Sheehan and Fastovsky 1992, 1993; Archibald 1993, 1996), but all share a common empirical foundation: a vertebrate occurrence database initiated by Bryant (1989) that draws on more than 150 000 individual specimens. She found that 9 of the 18 genus-level fish lineages represented in the latest Maastrichtian make their last local appearance in this interval, with eight found in deposits immediately postdating the extinction event (Bryant 1989, table 1). One additional taxon, *Belonosto-*

mus, occurs in still younger deposits, but it has been argued that the single specimen upon which this range extension is based was reworked from Cretaceous sediments (Cavin 2001a). Similar patterns are reported from updated versions of this compendium (Archibald and Bryant 1990; Archibald 1996). Although limited in terms of taxonomic richness, these data have led to contrasting interpretations of extinction dynamics. Bryant (1989) parsed her fish data into divisions based on assumptions about environmental preference and salinity tolerance, noting the highest rate of extinction among the suite of putative marine-to-brackish taxa and higher survivorship in those sets of taxa inferred to have stronger ties to strictly freshwater environments. She argued that this pattern reflected the local unavailability of suitable environments for marine fishes during the Palaeocene, associated with the regression of the Western Interior Seaway, rather than any particular consequence of a global extinction, a conclusion subsequently echoed by Archibald and Bryant (1990) and Archibald (1996). Pruning these marine forms along with rare taxa, Sheehan and Fastovsky (1992, 1993) argued for higher rates of survival among freshwater taxa than terrestrial vertebrates, a pattern they attributed to the buffering of detritus-based fluvial ecosystems against collapses in primary productivity associated with post-impact reductions in insolation. Archibald (1993) questioned this analysis and its conclusions, but despite conflicting opinions, it seems clear that the best-characterized freshwater fishes from the Western Interior appear to have been little affected by global K–Pg events.

To the extent that it can be compared with microremains, the sparse articulated body fossil record of Late Cretaceous freshwater fishes in western North America provides a complementary picture of negligible turnover associated with the K–Pg extinction. With the possible exception of the *incertae sedis* rhinobatoid elasmobranch (guitarfish) *Myledaphus* (Langston 1970; Neuman and Brinkman 2005; see qualifications about possible Eocene occurrences in Cappetta 1987b) and indeterminate holosteans (Brinkman 1990), all of the fish families known from articulated remains in freshwater Campanian and Maastrichtian deposits of western North America (all are actinopterygians; Acipenseridae (sturgeons): Hilton and Grande 2006; Polyodontidae (paddlefishes): Grande and Bemis 1991; Lepisosteidae (gars): Grande 2010; Amiidae (bowfins): Grande and Bemis 1998; Osteoglossidae (gold-eyes): Li 1996; Megalopidae (tarpons): Bardack 1970; Gonorynchidae (beaked sandfishes): Grande and Grande 1999; Sorbinichthyidae (armoured herrings): Newbrey *et al.* 2010) survive the end-Cretaceous extinction (e.g. Grande 1980), with some individual genera persisting regionally to the Eocene or later (the lepisosteid *Lepisosteus*, the amiid *Cyclurus*, and the gonorynchid *Notogoneus*; Grande and Bemis 1998; Grande and Grande 1999;

Grande 2010). These rare body fossils provide a particularly important window into teleost diversity that has historically gone unrecognized in screen-washed samples and suggest that this important component of the freshwater fish fauna did not undergo radical changes associated with the K–Pg boundary in North America.

Extensive studies of fish turnover at the K–Pg in freshwater settings outside of western North America are lacking. At a local scale, suitable candidate deposits for future study include the infra- and inter-trappean sedimentary beds associated with the Deccan flood basalts of India (Woodward 1908; Hora 1937; Borkar 1973, 1975, 1984; Prasad and Sahni 1987; Rana and Sahni 1989; Rana 1990; Mohabey *et al.* 1993; Mohabey and Udhoji 2000; Arratia *et al.* 2004; Nolf *et al.* 2008) and the El Molino (Maastrichtian–Danian) and Santa Lucía (Selandian; 61–59 Ma) formations of Bolivia (Sempere *et al.* 1997; Gayet and Meunier 1998; Gayet *et al.* 2000). What can be derived from published accounts for these faunas reveals that, like contemporaneous assemblages in North America, there seem to be no major shifts in taxonomic composition across the K–Pg boundary. Although based on admittedly scant data, this coarse observation is important, because the Indian and Bolivian localities reflect lower latitude assemblages, with climatic and palaeoenvironmental profiles likely to be different from those of coeval North American sites.

The Indian sections offer considerable potential, but much of the fossil material derives from historical collections, is either poorly illustrated or unfigured and has been subjected to taxonomic and anatomical analyses of wildly varying quality. There is, however, no lack of fossils, with fishes represented by isolated bones, scales and partial to complete skeletons from both the infratrappean (Woodward 1908; Prasad and Sahni 1987; Mohabey and Udhoji 2000; Arratia *et al.* 2004) and intertrappean (Hora 1937; Borkar 1973, 1975, 1984; Prasad and Sahni 1987; Rana 1990; Mohabey and Verma 1993) beds, with collections of otoliths (actinopterygian ‘ear stones’) available for the latter (Rana and Sahni 1989; Rana 1990; Nolf *et al.* 2008).

The Bolivian faunas, although potentially less rich, offer the advantage of having been subjected to comprehensive palaeoichthyological review yielding reliable taxonomic identifications (Gayet and Meunier 1998; Gayet *et al.* 2000). Of the 23 mostly species-level lineages reported on the basis of fragmentary remains from the Maastrichtian of this sequence, 13 are also present in the overlying Palaeocene deposits (Gayet and Meunier 1998, table 1; Gayet *et al.* 2000, table 3). Taxa which fail to cross the boundary in this sequence are predominantly chondrichthyans (6 of 10), with the others belonging to actinopterygian clades typically associated with marine environments (enchodontids, pycnodonts). None of these taxa occur in the uppermost Maastrichtian section of the

El Molino Formation, suggesting that, like North American continental boundary sections, apparent patterns of turnover at this scale are likely attributable to changes in depositional environment rather than any global biodiversity crisis.

Our understanding of K–Pg extinction among freshwater fishes at a global level is limited to taxonomically coarse surveys, but reveal patterns congruent with those apparent at finer scales of taxonomic and geographic resolution. Cavin and Martin (1995) and Cavin (2001a) have argued that freshwater taxa were less affected by the K–Pg event than fishes living in other environments, based on high survivorship of families containing taxa believed to inhabit brackish or freshwater settings. Cavin (2001a, fig. 3) in particular interpreted this pattern as further support for Sheehan and Fastovsky’s (1992) hypothesis that detritus-fed continental aquatic environments were buffered to a greater extent than marine ecosystems from the drivers of the K–Pg extinction.

Patterns in marine environments

Patterns of turnover among marine fishes at the end of the Cretaceous have been addressed at scales ranging from individual sections and regions (Gallagher *et al.* 1986; Gallagher 1991, 1993, 2002, 2003; Noubhani and Cappetta 1997; Zinsmeister 1998) to global analyses (Cavin and Martin 1995; MacLeod *et al.* 1997; Cavin 2001a; Kriwet and Benton 2004; Friedman 2009, 2010). Reflecting classical divisions of research emphasis, along with profoundly different taphonomic profiles, chondrichthyans and osteichthyans have generally been treated separately outside of broad reviews that explore coarse family-level data (e.g. MacLeod *et al.* 1997). At this scale, patterns between the two major divisions of fish diversity appear similar. Estimates for extinction rates among actinopterygians at the family level vary between 10 (MacLeod *et al.* 1997) and 19 per cent (Cavin 2001a), with the larger of these two values probably representing a more accurate value. Family-level extinction rates for neoselachians are of a similar magnitude, with Kriwet and Benton (2004) reporting 17 per cent of families known from the Maastrichtian making their final appearance in that stage. For actinopterygians, raw figures for the Maastrichtian compare closely with the percentage of families making their last appearances in the preceding Campanian (12 per cent; Cavin 2001a), which has been used to argue that the K–Pg extinction was a nonevent among fishes (MacLeod *et al.* 1997). However, the K–Pg is perhaps the only clear example in Sepkoski’s fish data where a recognized mass extinction horizon is preceded by elevated rates of extinction followed by a possible recovery phase characterized by increased rates of origination (Figs 2–4).

Kriwet and Benton (2004) provided the most comprehensive overview of extinction and recovery patterns within neoselachian elasmobranchs on a global scale. A literal reading of their diversity curves (Kriwet and Benton 2004, fig. 1) suggests a Maastrichtian peak in richness, followed by a steep decline in the Danian and Selandian, with recovery to near-Maastrichtian levels by the Thanetian (59–56 Ma). Eighty-four per cent of Maastrichtian species make their last appearance in that stage, which translates losses of 56 and 17 per cent at the genus and family level, respectively. Kriwet and Benton (2004, fig. 2) presented a qualitative argument for selectivity. A curious assemblage of pelagic apex predators, shallow-water carpet sharks and durophagous rays are said to have suffered disproportionately. These putative patterns of selectivity rest on verbal arguments rather than quantitative analysis, so we have built upon Kriwet and Benton's (2004) work by testing for phylogenetic selectivity using the protocols outlined by Roy *et al.* (2009). Such a taxonomic approach, of course, does not put us in a position to comment on specific patterns of trophic selectivity; this would require quantification of ecologically relevant features that could be derived from fossil neoselachians, which, in practice, means isolated teeth. It does, however, allow us to determine whether extinctions were clustered phylogenetically. If so, this might suggest selection against common aspects of ecology that characterized closely related taxa. This procedure rejects the directional null hypothesis that victims are not clustered phylogenetically ($p = 0.032$; Fig. 7), lending some quantitative support to Kriwet and Benton's (2004) assertion of selective extinction among neoselachians.

There are also indications of selective extinction among actinopterygians at the K–Pg. From a phylogenetic perspective, comparisons drawn between actinopterygian faunas from the Late Cretaceous and early Palaeogene reveal some striking contrasts. Cretaceous assemblages, including those from the Maastrichtian (David 1946; Gallagher *et al.* 1986; Chalifa and Lewy 1992; Gallagher 1993, 2002, 2003; Khaddumi 2009; Friedman 2012), contain crown teleosts as well as an ecologically diverse array of groups that branch from the teleost stem: pycnodontiforms, pachycormiforms, aspidorhynchiforms, ichthyodectiforms and crossognathiforms (the final group has variously been assigned to the teleost stem and crown by different workers; Patterson and Rosen 1977; Cavin 2001*b*). With the exception of pycnodontiforms, which persist until the middle Eocene (56–34 Ma; Poyato-Ariza and Wenz 2002), none of these stem teleost clades are definitively known from post-Maastrichtian sediments. The pruning of radiations from teleost stem between the Cretaceous and Palaeogene is complemented by the taxonomic and morphological proliferation of some crown-group radiations in the Palaeocene and Eocene. Most prominent

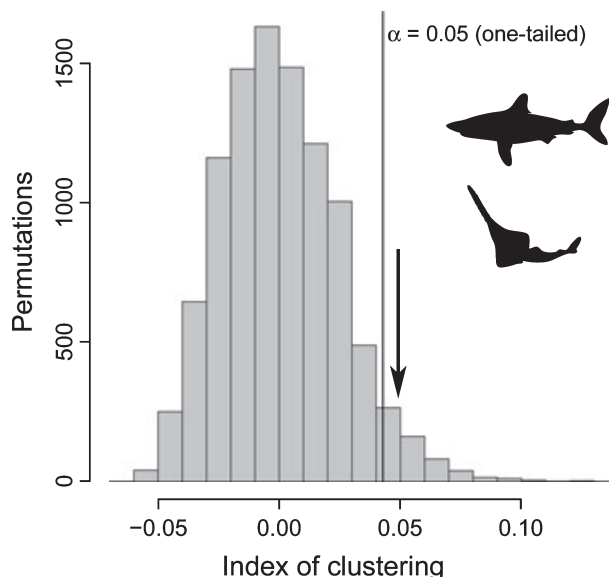


FIG. 7. Test of taxonomically structured extinction among neoselachians during the Cretaceous–Palaeogene extinction (65.5 Ma), using the taxonomic dataset assembled by Kriwet and Benton (2004). Histogram represents the null distribution of the phylogenetic clustering test statistic outlined by Roy *et al.* (2009; matrix correlation between similarity in taxonomy and response to extinction, quantified here using Spearman's rho), generated using 10 000 permutations of empirical extinction/survival data. The one-tailed hypothesis that extinctions are not phylogenetically clustered can be rejected ($p = 0.032$).

among these are the acanthomorph, or spiny-finned, teleosts, a group that today numbers nearly one of every three living vertebrate species (Stiassny *et al.* 2004; Friedman 2010; Sallan and Friedman 2012).

Many of the stem teleosts making their last appearance in the Maastrichtian represent some of the most conspicuous members of Late Cretaceous marine fish faunas (Fig. 7). These include a series of large-bodied taxa (>1 m) that appear to have had wide geographical distributions during the final stage of the Late Cretaceous: the pachycormids *Protosphyraena* and *Bonnerichthys* (Friedman *et al.* 2010; Friedman 2012), and the ichthyodectiforms *Xiphactinus* (Schwimmer *et al.* 1997), *Saurodon* (Taverne and Bronzi 1999), *Saurocephalus* (Bardack and Sprinkle 1969; Friedman 2012) and *Gillicus* (Tanimoto and Kikyo 2001). Large teleosts making their last appearance in the Maastrichtian are not limited to members of the stem, with crown representatives including the pachyrhizodontid *Pachyrhizodus* (David 1946; Friedman 2012), possibly the tselatiiform *Pentanogmus* (Chalifa and Lewy 1992; Gallagher 2003), and the aulopiforms *Apateodus*, *Cimolichthys* and *Enchodus* (David, 1946; Chalifa and Lewy 1992; Khaddumi 2009; Friedman 2012). Most of these genera have dense records leading up to the end-Cretaceous, with occurrences known from all stages

between their first and last appearances (Friedman 2009). Because of their robust bones and teeth, these large taxa are generally the easiest to recognize on the basis of isolated remains, suggesting that their complete absence from Palaeocene deposits is genuine rather than artefactual. This pattern is not simply attributable to a reduction in Chalk facies after the K–Pg. Fossils of these teleost groups are found in a range of lithologies (including shales and marls: David 1946; Russell 1988) in the Late Cretaceous and are completely unknown from early Palaeocene (Danian) chalks (Davis 1890).

The concentration of last appearances of large-bodied marine teleost groups in the Maastrichtian was first highlighted by Cavin and Martin (1995) and Cavin (2001a). Along with the decimation (dercetids) or complete extirpation (aspidorhynchids) of clades containing smaller-bodied but piscivorous taxa, these authors inferred selection against pelagic predators, which they linked to collapse of primary productivity in the open ocean. Friedman (2009) provided a quantitative test of selectivity using body size and measurements of jaw mechanics, and found that marine teleost genera making their last appearance in the Maastrichtian represented a nonrandom sample of taxa known from that stage. This result was largely driven by the extinction of all taxa occupying a region of ecomorphospace characterized by large body size and low-to-moderate jaw-closing mechanical advantage (typical of piscivorous taxa; Wainwright and Richard 1995).

The inferred extinction of many large-bodied marine teleosts during the Maastrichtian is largely built upon the recognition of disarticulated or fragmentary remains of these taxa (Friedman 2012, but see Khaddumi 2009 for articulated examples from coeval deposits), and we presently lack a clear understanding of patterns of turnover at the smaller end of the size spectrum, where articulated remains are particularly important for determining taxonomic placement. A better understanding of evolutionary patterns among small taxa forms important historical context for exploring the origins of modern reef fishes, which are increasingly used as model systems in biomechanical and evolutionary studies (e.g. Wainwright and Bellwood 2002) and appear to trace their origin to the Late Cretaceous–Palaeogene interval (Friedman 2010).

The latest well-documented Cretaceous marine site that yields complete, small fish specimens in any abundance is the latest Campanian–earliest Maastrichtian Nardò locality in southern Italy (Taverne 2010 and references therein). Younger Cretaceous assemblages yielding articulated fishes are known (e.g. Khaddumi 2009), but these specimens have not yet been formally studied. With the exception of *Chanos* and *Chanoides* (Taverne 2005, 2009), the small-bodied fish genera found at Nardò are not found in geologically younger deposits, and many of these

are assigned to monotypic families. The Nardò assemblage is particularly unusual in comparison with both pre-Maastrichtian and Cenozoic marine assemblages in its diversity of putative ostariophysian teleosts (minnows, carp, characins, catfishes, knifishes and their allies), which number nearly one quarter of the genera known from this site. Whether this represents a peculiarity of the Nardò fauna or instead reflects a more general feature of latest Cretaceous marine ichthyofaunas remains unclear.

Ecological and evolutionary recovery: building modern fish biodiversity

Some indication of the temporal scale for recovery of abundance (rather than richness) in pelagic fish communities in the aftermath of the K–Pg is provided by accumulation rates of teeth in marine cores from the South Atlantic (Shackleton *et al.* 1984; D'Hondt 2005). These show a steep drop centred about the K–Pg boundary, and only return to Maastrichtian levels some 4 million years into the Palaeocene. Such observations suggest a timescale for recovery to pre-extinction levels of productivity, but estimating the span required for evolutionary recovery is not as easily assessed and can only be discussed in qualitative terms at present.

Patterns of recovery on this scale are best illustrated by examples of putative replacement of extinct groups with new clades that appear to occupy comparable ecological roles. The loss of large-bodied, predatory taxa at or before the K–Pg represents a pattern common to both actinopterygians and chondrichthyans (Fig. 8). Similarly, both groups are marked by the Palaeocene–Eocene proliferation or appearance of large pelagic predators still found in today's oceans: carcharinids (requiem sharks; Kriwet and Benton 2004), lamnids (makos; Kriwet and Benton 2004), and scombroids (tunas and their kin; Darteville and Casier 1949) in the early Palaeocene, carangids (jacks; Bannikov and Parin 1997; Bonde 1997) and xiphioids (billfishes; Bannikov and Parin 1997; Sytchevskaya and Prokofiev 2002; Friedman and Johnson 2005) in the late Palaeocene, and sphyraenids (barracudas; Casier 1966; Blot 1980) in the early Eocene. But not all large predators in early Palaeogene oceans are familiar inhabitants of modern seas. Most striking is a short-lived invasion of marine environments by osteoglossomorph teleosts (bony tongues) in the Palaeocene and early Eocene (Bannikov and Parin 1997; Bonde 2008; Forey and Hilton 2010). These taxa were widely distributed geographically, with remains reported from North America, Asia, Europe and Africa and appear to represent multiple osteoglossomorph clades. A marine proliferation of large, predatory osteoglossomorphs is particularly striking given that modern members of this radiation are tightly linked to freshwater

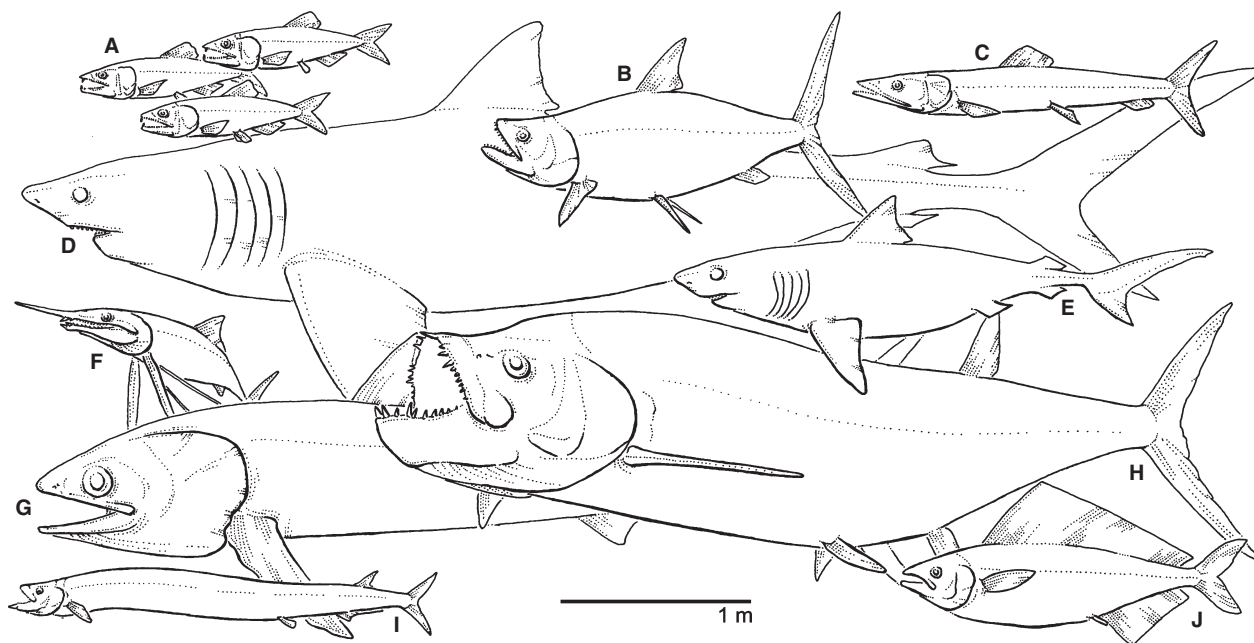


FIG. 8. Reconstructions of select large-bodied marine chondrichthyans and actinopterygian representing possible victims of the K–Pg extinction. A, the aulopiform teleost *Enchodus*. B, the pachyrhizodontid teleost *Pachyrhizodus*. C, the aulopiform teleost *Cimolichthys*. D, the cretoxyrhinid neoselachian *Cretoxyrhina* (Maastrichtian records are dubious, and this genus appears to make its last appearance in the Campanian; Kriwet and Benton 2004). E, the anacoracid neoselachian *Squalicorax*. F, the pachycormiform teleost *Protosphyraena*. G, the pachycormiform teleost *Bonnerichthys*. H, the ichthyodectiform teleost *Xiphactinus*. I, the ichthyodectiform teleost *Saurocephalus*. J, the tsselfatiiform teleost *Bananogmius*. Last appearances based on data presented by Kriwet and Benton (2004) (neoselachians), Friedman (2009, 2012) and Friedman *et al.* (2010) (teleosts).

environments (Hilton 2003). Compelling remains of osteoglossomorphs are unknown from marine deposits either before or after this Palaeocene to mid-Eocene window, and it seems likely that their brief incursion into the oceans during this time represented an opportunistic replacement of the predatory fish groups so strongly impacted at or before the K–Pg.

Other patterns of functional replacement associated with the K–Pg emphasize the need to examine extinction and subsequent recovery at a broad phylogenetic scale, extending across traditional taxonomic divisions of palaeontological research. The diversity of suspension-feeding chondrichthyans and whales in the Cenozoic (Sanderson and Wassersug 1993) has raised questions about the apparent absence of ecologically analogous vertebrates during most of the Mesozoic (Colin and Janis 1997). However, it is now clear that the role of large vertebrate suspension feeders was occupied by a subset of pachycormiform fishes until the Maastrichtian, with the familiar groups of living suspension feeders appearing in the Palaeogene (whale sharks and manta rays: Palaeocene; basking sharks: Eocene; baleen whales: Oligocene: Friedman *et al.* 2010).

Beyond these specific examples, a literal reading of any taxonomic databases documenting the Phanerozoic diver-

sity patterns in fishes suggests a striking rise in richness in the Cenozoic (Figs 2–4), with much of this attributable to a sharp increase in the number of species of acanthomorph teleost (and especially the diverse acanthomorph subgroup Percomorpha: Patterson 1993a, b, 1994; Stiassny *et al.* 2004), which show a commensurate increase in morphological disparity (Friedman 2010; Sallan and Friedman in press). Ostariophysians, like percomorph acanthomorphs, are another exceptional radiation of living teleosts (Alfaro *et al.* 2009) whose fossil record points to a Cenozoic diversification (Patterson 1994). Unlike acanthomorphs, ostariophysians are predominantly a freshwater radiation, with the consequence that their fossil record is comparatively sparse. A complete picture of the evolution of modern fish diversity demands a better understanding of the palaeontological histories of these two major clades – Acanthomorpha and Ostariophysi – which collectively make up nearly half of all living vertebrate species (Stiassny *et al.* 2004; Alfaro *et al.* 2009).

Whether the striking increase in bony fish richness in the Cenozoic reflects genuine signal, pull of the Recent, an artefact of the sedimentary record, or some combination of the three remains unclear. If this pattern survives subsequent analyses that take into account these and other biasing factors, then the true ‘Age of Fishes’ is not

the Devonian, but instead, and perhaps surprisingly, the Palaeogene and Neogene.

CONCLUSIONS AND A ROADMAP FOR FUTURE RESEARCH

1. So far as can be discerned from available data, many major marine invertebrate and terrestrial (e.g. tetrapod) extinction intervals either appear to have left much of fish diversity unscathed, or are so poorly constrained for fishes as to preclude any definitive statements. These include several of the Big Five mass extinctions, such as the Frasnian–Famennian, end-Permian and end-Triassic events. This suggests extinction patterns cannot be translated from one group to another, or different clades used as proxies for one another, even when they co-exist or interact. Morphological (and presumably ecological) diversification of fishes is common in the intervals following mass extinctions, whether or not fishes themselves appear to have been strongly impacted. These radiations usually involve movement into new environments and trophic roles, as well as ecological replacement of putative extinction victims.
2. At present, the extinctions whose impacts upon fishes are best-characterized are the end-Devonian (Hangenberg) and the end-Cretaceous (K–Pg) events. The Hangenberg extinction appears to have resulted in a phylogenetic bottleneck that radically restructured vertebrate faunas in both marine and continental environments. Selectivity appears to have been a minimal factor; taxa of every major vertebrate division, ecology and environment were lost. Chondrichthyans, actinopterygians and tetrapods radiated after this event, and these same clades continue to dominate vertebrate biodiversity today. The K–Pg extinction seems to have had strikingly different effects upon fishes inhabiting continental and marine ecosystems. Although data are scant, a series of regional studies targeting patterns of turnover among freshwater fishes across the K–Pg boundary show few, if any signs, of catastrophic extinction. By contrast, there is clear evidence for selective extinction among both marine chondrichthyans and actinopterygians. Large-bodied and predatory taxa appear to have been particularly hard hit in both clades, with new groups arising to fill vacated functional roles in the early Palaeogene.
3. The effects of geological megabiases on the fish fossil record remain unquantified, although our intuition is that many peaks and troughs in fish diversity curves are more related to sampling issues than genuine biological patterns. Assessing the strength of the relationship between the rock record and fish palaeobi-

odiversity will require new databases recording individual occurrences, rather than available compendia that archive only first and last appearances. Fish subgroups have different taphonomic profiles, preservational modes and fossilization rates (Foote and Sepkoski 1999), meaning that patterns recovered for one clade cannot be easily translated to fishes as a whole.

4. Fishes, particularly nonmarine forms, are poorly represented in current compendia of fossil diversity (Sepkoski's genus database and the PBDB being the most important and accessible) and the global diversity curves derived from them. Consequently, fishes are also neglected in large-scale studies of mass extinction and reviews of palaeobiodiversity. There are many databases that have been assembled by fish workers to address specific palaeobiological problems, but these are variable in both taxonomic and stratigraphic scope and generally include only taxon ranges (rather than occurrences). A better understanding of patterns of fish diversity will require experts on various clades and geological intervals to produce a synoptic, standardized, occurrence-based dataset for fishes that will bring the empirical dataset for this group up to modern standards. These data should be of interest to palaeobiologists more generally, because fishes are an important component of biodiversity and have played a nontrivial role in influencing evolutionary processes and ecological histories of many other clades (Stanley 2008; Sallan *et al.* 2011; Bush and Bambach 2011).

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REFERENCES

- ADRAIN, J. M. and WESTROP, S. R. 2000. An empirical assessment of taxic paleobiology. *Science*, **289**, 110–112.
- AGASSIZ, L. 1833–1844. *Recherches sur les Poissons fossiles*, V vols. Imprimerie de Petitpierre et Prince, Neuchâtel, 1420 pp.
- AHLBERG, P. E. and MILNER, A. R. 1994. The origin and early diversification of tetrapods. *Nature*, **368**, 507–514.
- ALDRIDGE, R. J. 1988. Extinction and survival in the Conodonta. In LARWOOD, G. P. (ed.). *Extinction and survival in the fossil record, Systematics Association Special Volume*, **34**, 231–256.
- and SMITH, M. P. 1993. Conodonta. 563–572. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- ALEKSEEV, A. A., LEBEDEV, O. A., BARSKOV, I. S., BARSKOVA, M. I., KONONOVA, L. I. and CHIZOVA, V. A. 1994. On the stratigraphic position of the Famennian and Tournaisian fossil vertebrate beds in Andreyevka, Tula Region, Central Russia. *Proceedings of the Geologist's Association*, **105**, 41–52.
- KONONOVA, L. I. and NIKISHIN, A. M. 1996. The Devonian and Carboniferous of the Moscow Syncline (Russian Platform): stratigraphy and sea-level changes. *Tectonophysics*, **268**, 149–168.
- ALFARO, M. E., SANTINI, F., BROCK, C., ALAMILLO, H., DORNBURG, A., RABOSKY, D. L., CARNEVALE, G. and HARMON, L. J. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of the United States of America*, **106**, 13410–13414.
- ALGEO, T. J., LYONS, T. W., BLAKEY, R. C. and OVER, D. J. 2007. Hydrographic conditions of the Devonian–Carboniferous North American Seaway inferred from sedimentary Mo–TOC relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **256**, 204–230.
- ALROY, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **127**, 285–311.
- ABERHAN, M., BOTTJER, D. J., FOOTE, M., FURSICH, F. T., HARRIES, P. J., HENDY, A. J. W., HOLLAND, S. M., IVANY, L. C., KIESSLING, W., KOSNIK, M. A., MARSHALL, C. R., MCGOWAN, A. J., MILLER, A. I., OLSZEWSKI, T. D., PATZKOWSKY, M. E., PETERS, S. E., VILLIER, L., WAGNER, P. J., BONUSO, N., BORKOW, P. S., BRENNIS, B., CLAPHAM, M. E., FALL, L. M., FERGUSON, C. A., HANSON, V. L., KRUG, A. Z., LAYOU, K. M., LECKEY, E. H., NURNBERG, S., POWERS, C. M., SESSA, J. A., SIMPSON, C., TOMASOVYCH, A. and VISAGGI, C. C. 2008. Phanerozoic trends in the global biodiversity of marine invertebrates. *Science*, **321**, 97–100.
- ANDERSON, P. S. L., FRIEDMAN, M., BRAZEAU, M. D. and RAYFIELD, E. J. 2011. Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature*, **476**, 206–209.
- ANDREWS, S. M., GARDINER, B. G., MILES, R. S. and PATTERSON, C. 1967. Pisces. 637–683. In HARLAND, W. B. (ed.). *The fossil record*. Geological Society of London, London, 826 pp.
- ARCHIBALD, J. D. 1993. Major extinctions of land-dwelling vertebrates at the Cretaceous–Tertiary boundary, eastern Montana: comment and reply. *Geology*, **21**, 90–92.
- 1996. *Dinosaur extinction and the end of an era: what the fossils say*. Columbia University Press, New York, 237 pp.
- and BRYANT, L. J. 1990. Differential Cretaceous/Tertiary extinctions of nonmarine vertebrates; evidence from northeastern Montana. *Geological Society of America Special Paper*, **247**, 549–562.
- CLEMENS, W. A., PADIAN, K., ROWE, T., MACLOED, N., BARRETT, P. M., GALE, A., HOLROYD, P., SUES, H.-D., ARENS, N. C., HORNER, J. R., WILSON, G. P., GOODWIN, M. B., BROCHU, C. A., LOFGREN, D. L., HURLBERT, S. H., HARTMAN, J. H., EBERTH, D. A., WIGNALL, P. B., CURRIE, P. J., WIEL, A., PRASAD, G. V. R., DINGUS, L., COURTILOT, V., MILNER, A., MILNER, A., BAJPAI, S., WARD, D. J. and SAHNI, A. 2010. Cretaceous extinctions: multiple causes. *Science*, **328**, 973.
- ARRATIA, G., LÓPEZ-ARBARELLO, A., PRASAD, G. V. R., PARMAR, V. and KRIWET, J. 2004. Late Cretaceous–Paleocene percomorphs (Teleostei) from India—early radiation of Perciformes. 635–663. In ARRATIA, G., WILSON, M. V. H. and CLOUTIER, R. (eds). *Recent advances in the origin and early radiation of vertebrates*. Verlag Dr. Friedrich Pfeil, Munich, 703 pp.
- ARSENAULT, M., DESBIENS, S., JANVIER, P. and KERR, J. 2004. New data on the soft tissues and external morphology of the antiarch *Bothriolepis canadensis* (Whiteaves, 1880) from the Upper Devonian of Miguasha, Quebec. 439–454. In ARRATIA, G., WILSON, M. V. H. and CLOUTIER, R. (eds). *Recent advances in the origin and early radiation of vertebrates*. Verlag Dr. Friedrich Pfeil, Munich, 703 pp.
- BAIRD, G. C. 1997. Fossil distributions and fossil associations. 21–26. In SHABICA, C. W. and HAY, A. A. (eds). *Richardson's guide to the fossil fauna of Mazon Creek*. Northeastern Illinois University, Chicago, 309 pp.
- SHABICA, C. W., ANDERSON, J. L. and RICHARDSON, E. S. Jr 1985. Biota of a Pennsylvanian muddy coast: habitats within the Mazonian Delta Complex, Northeast Illinois. *Journal of Paleontology*, **58**, 253–281.
- BAMBACH, R. K. 2006. Phanerozoic biodiversity mass extinctions. *Annual Reviews of Earth and Planetary Sciences*, **34**, 127–155.
- KNOLL, A. H. and WANG, S. C. 2004. Origination, extinction, and mass depletions of marine diversity. *Paleobiology*, **30**, 522–542.
- BANNIKOV, A. F. and PARIN, N. N. 1997. The list of marine fishes from Cenozoic (upper Paleocene–middle Miocene) localities in southern European Russia and adjacent countries. *Journal of Ichthyology*, **37**, 133–146.
- BARDACK, D. 1970. A new teleost from the Oldman Formation (Cretaceous) of Alberta. *National Museums of Canada, Publications in Paleontology*, **3**, 1–8.
- and SPRINKLE, G. 1969. Morphology and relationships of saurocephalid fishes. *Fieldiana Geology*, **16**, 297–340.

- BAUMILLER, T. K. and GAHN, F. J. 2004. Testing predator driven evolution with Paleozoic crinoid arm regeneration. *Science*, **305**, 1453–1455.
- BELLWOOD, D. R. 2003. Origins and escalation of herbivory in fishes: a functional perspective. *Paleobiology*, **29**, 71–83.
- BENTON, M. J. 2000. *Vertebrate palaeontology*, Second edition. Blackwell Science, Oxford, 452 pp.
- . 2005. *Vertebrate palaeontology*, Third edition. Blackwell Science, Oxford, 455 pp.
- BERNER, R. A., VANDENBROOKS, J. A. and WARD, P. D. 2007. Oxygen and Evolution. *Science*, **316**, 557–558.
- BLIECK, A. 2011. From adaptive radiations to biotic crises in Palaeozoic vertebrates: a geobiological approach. *Geologica Belgica*, **14**, 203–227.
- and TURNER, S. 2003. Global Ordovician vertebrate biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 37–54.
- BLOM, H., CLACK, J. A., AHLBERG, P. E. and FRIEDMAN, M. 2007. Devonian vertebrates from East Greenland: a review of faunal composition and distribution. *Geodiversitas*, **29**, 119–141.
- BLOT, J. 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). *Bulletin du Muséum National d'Histoire Naturelle, Section C, 4^e Série*, **2**, 339–396.
- BONDE, N. 1997. A distinctive fish fauna in the basal ash-series of the Fur/Ølst Formation (u. Paleocene, Denmark). *Aarhus Geoscience*, **6**, 33–48.
- . 2008. Osteoglossomorphs of the marine lower Eocene of Denmark with remarks on other Eocene taxa and their importance for palaeobiogeography. *Geological Society, London, Special Publications*, **295**, 253–310.
- BONELLI, J. R. and PATZKOWSKY, M. E. 2008. How are global patterns of faunal turnover expressed at regional scales: evidence from the Upper Mississippian (Chesterian series), Illinois Basin, USA. *PALAIOS*, **23**, 760–772.
- BONUSO, N. and BOTTJER, D. J. 2006. A quantitative study of benthic faunal patterns within the Pennsylvanian and Early Permian. *PALAIOS*, **21**, 316–324.
- BORKAR, V. D. 1973. New fossil fishes from the inter-trappean beds in Surendrangar District, Gujarat State. *Current Science*, **42**, 422–423.
- . 1975. New fossil scales from the intertrappean bed of Bamanbor, Surendrangar District, Gujarat. *Biovigyanam*, **1**, 161–166.
- . 1984. *Palaeopristolepis chipionkari*, a new fossil fish from the intertrappean bed of Bamanbor, Surendrangar District, Gujarat. *Biovigyanam*, **10**, 65–67.
- BOTELLA, H. and FARINA, R. A. 2008. Flow pattern around the rigid cephalic shield of the Devonian agnathan *Erivaspis waynensis* (Pteraspidoformes: Heterostraci). *Palaeontology*, **51**, 1141–1150.
- BOUCOT, A. J. and JANIS, C. 1983. Environment of the early Paleozoic vertebrates. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **41**, 251–287.
- BRAZEAU, M. D. 2005. A new genus of rhizodontid (Sarcopterygii, Tetrapodomorpha) from the Lower Carboniferous Horton Bluff Formation of Nova Scotia, and the evolution of lower jaws in this group. *Canadian Journal of Earth Sciences*, **42**, 1481–1499.
- . 2009. The braincase and jaws of a Devonian acanthodian and the origin of modern gnathostomes. *Nature*, **457**, 305–308.
- BRETT, C. E. and WALKER, S. E. 2002. Predators and predation in Paleozoic marine environments. *Paleontological Society Papers*, **8**, 93–118.
- BREZINSKI, D. K., CECIL, C. B., SKEMA, V. W. and STAMM, R. 2008. Late Devonian glacial deposits from the eastern United States signal an end of the mid-Paleozoic warm period. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **268**, 143–151.
- and KERTIS, C. A. 2009. Evidence for long-term climate change in the Upper Devonian strata of the central Appalachians. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 315–325.
- 2010. Late Devonian glacial and associated facies from the central Appalachian Basin, eastern United States. *The Geological Society of America Bulletin*, **122**, 265–281.
- BRIGGS, D. E. G. and CLARKSON, E. N. K. 1983. The Lower Carboniferous Granton 'shrimp-bed', Edinburgh. *Special Papers in Paleontology*, **30**, 161–177.
- and ALDRIDGE, R. J. 1983. The conodont animal. *Lethaia*, **16**, 1–14.
- BRINKMAN, D. B. 1990. Paleocology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **78**, 37–54.
- and NEUMAN, A. G. 2002. Teleost centra from the uppermost Judith River Group (Dinosaur Park Formation, Campanian) of Alberta, Canada. *Journal of Paleontology*, **76**, 138–155.
- BRINKMANN, W., ROMANO, C., BUCHER, H. and WARE, D. 2010. Palaeobiogeography and stratigraphy of advanced gnathostomian fishes (Chondrichthyes and Osteichthyes) in the Early Triassic and from selected Anisian localities (Report 1863–2009). *Zentralblatt für Geologie und Paläontologie Teil II*, **2009**, 769–812.
- BRYANT, L. J. 1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. *University of California Publications in Geological Sciences*, **134**, 1–107.
- BUGGISCH, W. and JOACHIMSKI, M. M. 2006. Carbon isotope stratigraphy of the Devonian of Central and Southern Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **240**, 68–88.
- BUSH, A. M. and BAMBACH, R. K. 2011. Paleocologic megatrends in marine Metazoa. *Annual Review of Earth and Planetary Sciences*, **39**, 241–269.
- BUTLER, R. J., BENSON, R. B. J., CARRANO, M. T., MANNION, P. D. and UPCHURCH, P. 2011. Sea level, dinosaur diversity and sampling biases: investigating the "common cause" hypothesis in the terrestrial realm. *Proceedings of the Royal Society B*, **278**, 1165–1170.
- CAPLAN, M. L. and BUSTIN, R. M. 1999. Devonian-Carboniferous Hangenberg mass extinction event, widespread organic-rich mudrock and anoxia: causes and consequences. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **148**, 187–207.

- CAPPETTA, H. 1987a. Extinctions et renouvellements fauniques chez les sélachiens postjurassiques. *Mémoires de la société géologique de France, n.s.*, **150**, 113–131.
- 1987b. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. 1–193. In SCHULTZE, H.-P. (ed.). *Handbook of paleoichthyology*, Vol. 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- DUFFIN, C. and ZIDEK, J. 1993. Chondrichthyes. 593–609. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- CARROLL, R. L. 1988. *Vertebrate paleontology and evolution*. W. H. Freeman and Company, New York, 698 pp.
- CASIER, E. 1966. *Faune ichthyologique du London Clay*. Trustees of the British Museum (Natural History), London, 496 pp.
- CAVIN, L. 2001a. Effects of the Cretaceous-Tertiary boundary event on bony fishes. 141–158. In BUFFETAUT, E. and KOEBERL, C. (eds). *Geological and biological effects of impact events*. Springer, Berlin, 310 pp.
- 2001b. Osteology and phylogenetic relationships of the teleost *Goulmimichthys arambourgi* Cavin, 1995, from the Upper Cretaceous of Goulmima, Morocco. *Eclogae geologicae Helveticae*, **94**, 509–535.
- 2010. The Late Jurassic ray-finned fish peak of diversity: biological radiation or preservational bias? 111–121. In NELSON, J. S., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Origin and phylogenetic interrelationships of teleosts*. Verlag Dr Friedrich Pfeil, Munich, 480 pp.
- and FOREY, P. L. 2007. Using ghost lineages to identify diversification events in the fossil record. *Biology Letters*, **3**, 201–204.
- and MARTIN, M. 1995. Les actinopterygiens et la limite Crétacé-Tertiaire. *Geobios, M. S.*, **19**, 183–188.
- FOREY, P. L. and LÉCUYER, C. 2007. Correlation between environment and late Mesozoic ray-finned fish evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 353–367.
- CHALIFA, Y. and LEWY, Z. 1992. Early Maastrichtian marine teleosts from the northern Negev, Israel. *Israel Journal of Earth Sciences*, **40**, 91–105.
- CHEN, L., CUNY, G. and WANG, X. 2007. The chondrichthyan fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China). *Historical Biology*, **19**, 291–300.
- CICIMURRI, D. J., PARRIS, D. C. and EVERHART, M. J. 2008. Partial dentition of a chimaeroid fish (Chondrichthyes, Holocephali) from the Upper Cretaceous Niobrara Chalk of Kansas, USA. *Journal of Vertebrate Paleontology*, **28**, 34–40.
- CLACK, J. A. 2006. The emergence of early tetrapods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 167–189.
- 2007. Devonian climate change, breathing, and the origin of the tetrapod stem group. *Integrative and Comparative Biology*, **47**, 510–523.
- CLARK, A. J. and SUMMERS, A. P. 2007. Morphology and kinematics of feeding in hagfish: possible functional advantages of jaws. *Journal of Experimental Zoology*, **210**, 3897–3909.
- MARAVILLA, E. J. and SUMMERS, A. P. 2010. A soft origin for a forceful bite: motor patterns of the feeding musculature in Atlantic hagfish, *Myxine glutinosa*. *Zoology*, **113**, 259–268.
- CLARK, D. L. 1983. Extinction of conodonts. *Journal of Paleontology*, **57**, 652–661.
- WANG, C.-Y., ORTH, C. J. and GILMORE, J. S. 1986. Conodont survival and low iridium abundances across the Permian-Triassic boundary in South China. *Science*, **233**, 984–986.
- SORENSON, J. K., LADD, A. N. and FREIHEIT, J. R. 1999. Probable microvertebrates, vertebrate-like fossils, and weird things from the Wisconsin Ordovician. *Journal of Paleontology*, **73**, 1201–1209.
- CLEMENT, A. M. and LONG, J. A. 2010. Air-breathing adaptation in a marine Devonian lungfish. *Biology Letters*, **6**, 509–512.
- CLEMENT, G., AHLBERG, P. E., BLIECK, A., BLOM, H., CLACK, J. A., POTY, E., THOREZIL, J. and JANVIER, P. 2004. Devonian tetrapod from western Europe. *Nature*, **427**, 412–413.
- COATES, M. I. and CLACK, J. A. 1995. Romer's gap: tetrapod origins and terrestriality. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **17**, 373–388.
- and SEQUEIRA, S. E. K. 2001. A new stethacanthid chondrichthyan from the lower Carboniferous of Bearsden, Scotland. *Journal of Vertebrate Paleontology*, **21**, 438–459.
- RUTA, M. and FRIEDMAN, M. 2008. Ever since Owen: changing perspectives on the early evolution of tetrapods. *Annual Review of Ecology, Evolution and Systematics*, **39**, 571–592.
- COLIN, R. and JANIS, C. M. 1997. Morphological constraints on tetrapod feeding mechanisms: why were there no suspension-feeding marine reptiles? 451–466. In CALLAWAY, J. M. and NICHOLLS, E. L. (eds). *Ancient marine reptiles*. Academic Press, San Diego, 501 pp.
- COPPER, P. 1986. Frasnian/Famennian mass extinction and cold-water oceans. *Geology*, **14**, 835–839.
- 2002. Reef development at the Frasnian/Famennian mass extinction boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **181**, 27–65.
- COURTILLOT, V. and FLUTEAU, F. 2010. Cretaceous extinctions: the volcanic hypothesis. *Science*, **328**, 973–974.
- D'HONDT, S. 2005. Consequences of the Cretaceous/Paleogene mass extinction for marine ecosystems. *Annual Review of Ecology, Evolution and Systematics*, **36**, 295–317.
- DAHL, T. W., HAMMARLUND, E. U., ANBAR, A. D., BOND, D. P. G., GILL, B. C., GORDON, G. W., KNOLL, A. W., NIELSEN, A. T., SCHOVSBO, N. H. and CANFIELD, D. E. 2010. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 17911–17915.
- DARTEVELLE, E. and CASIER, E. 1949. Les Poissons fossiles du Bas-Congo et des régions voisines. *Annales du Musée du Congo Belge, A—Minéralogie, Géologie, Paléontologie*, **2** (3), 201–256.
- DAVID, L. R. 1946. Upper Cretaceous fish remains from the western border of the San Joaquin Valley, California. Fossil Vertebrates from Western North America and Mexico. *Carnegie Institute of Washington Publication*, **551**, 83–112.
- DAVIS, J. W. 1890. On the fossil fish of the Cretaceous formations of Scandinavia. *Transactions of the Royal Dublin Society*, **4**, 363–434.

- DE RENZI, M., BUDUROV, K. and SUDAR, M. 1996. The extinction of conodonts – in terms of discrete elements – at the Triassic-Jurassic boundary. *Cuadernos de Geologica Iberica*, **20**, 247–264.
- DENISON, R. 1978. Placodermi. In SCHULTZE, H.-P. (ed.). *Handbook of paleoichthyology*, Vol. 2. Gustav Fischer Verlag, Stuttgart, 128 pp.
- 1979. Acanthodii. In SCHULTZE, H.-P. (ed.). *Handbook of paleoichthyology*, Vol. 5. Gustav Fischer Verlag, Stuttgart, 62 pp.
- DICK, J. R. F. 1998. *Sphenacanthus*, a Palaeozoic freshwater shark. *Biological Journal of the Linnean Society*, **122**, 9–25.
- DIEDRICH, C. J. 2009. A coelacanthid-rich site at Hasbergen (NW Germany): taphonomy and palaeoenvironment of a first systematic excavation in the Kupferschiefer (Upper Permian, Lopingian). *Palaeobiodiversity and Palaeoenvironments*, **89**, 67–94.
- DINELEY, D. L. and METCALF, S. J. 1999. *Fossil fishes of Great Britain*. Joint Nature Conservation Conservancy, Peterborough, 675 pp.
- DONOGHUE, P. C. J. and PURNELL, M. A. 2009. Distinguishing heat from light in debate over controversial fossils. *BioEssays*, **31**, 178–189.
- FOREY, P. L. and ALDRIDGE, R. J. 2000. Conodont affinity and chordate phylogeny. *Biological Reviews*, **75**, 191–251.
- SMITH, M. P. and SANSOM, I. J. 2003. The origin and early evolution of chordates: molecular clocks and the fossil record 190–223. In DONOGHUE, P. C. J. and SMITH, M. P. (eds). *Telling the evolutionary time: molecular clocks and the fossil record*. CRC Press, London, 288 pp.
- DROSER, M. L., BOTTJER, D. J., SHEEHAN, P. M. and MCGHEE, G. R. 2000. Decoupling of taxonomic and ecological severity of Phanerozoic mass extinctions. *Geology*, **28**, 675–678.
- ERWIN, D. H. 1990. The end-Permian mass extinction. *Annual Review of Ecology and Systematics*, **21**, 69–91.
- FALCON-LANG, H. J. and DIMICHELE, W. A. 2010. What happened to the Coal Forests during glacial phases? *Palaios*, **25**, 611–617.
- NELSON, J., ELRICK, S., LOOY, C., AMES, P. and DIMICHELE, W. A. 2009. Incised channel-fills containing conifers imply that seasonally-dry vegetation dominated Pennsylvanian tropical lowlands. *Geology*, **37**, 923–926.
- FINARELLI, J. A. and COATES, M. I. 2012. First tooth-set outside the jaws in a vertebrate. *Proceedings of the Royal Society B*, **279**, 775–779.
- FOOTE, M. 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology*, **26**, 74–102.
- 2007. Extinction and quiescence in marine animal genera. *Paleobiology*, **33**, 261–272.
- and SEPKOSKI, J. J. Jr 1999. Absolute measures of the completeness of the fossil record. *Nature*, **398**, 415–417.
- FOREY, P. L. and HILTON, E. J. 2010. Two new Tertiary osteoglossid fishes (Teleostei: Osteoglossomorpha) with notes on the history of the family. 215–246. In ELLIOT, D. K., MAISEY, J. G., YU, X. and MIAO, D. (eds). *Morphology, phylogeny, and paleobiogeography of fossil fishes*. Verlag Dr Friedrich Pfeil, Munich, 472 pp.
- LU, Y., PATTERSON, C. and DAVIES, C. E. 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. *Journal of Systematic Palaeontology*, **1**, 230–330.
- FRIEDMAN, M. 2007. *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *Journal of Systematic Palaeontology*, **5**, 289–343.
- 2009. Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 5218–5223.
- 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society B*, **277**, 1675–1683.
- 2012. Ray-finned fishes (Osteichthyes, Actinopterygii) from the type Maastrichtian, the Netherlands and Belgium. *Scripta Geologica Special Issue*, **8**, 113–142.
- and BRAZEAU, M. D. 2010. A reappraisal of the origin and basal radiation of the Osteichthyes. *Journal of Vertebrate Paleontology*, **30**, 36–56.
- and JOHNSON, G. D. 2005. A new species of *Mene* (Perciformes: Menidae) from the Paleocene of South America, with notes on the paleoenvironment and a brief review of menid fishes. *Journal of Vertebrate Paleontology*, **25**, 770–783.
- SHIMADA, K., MARTIN, L. D., EVERHART, M. J., LISTON, J., MALTESE, A. and TRIEBOLD, M. 2010. 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. *Science*, **327**, 990–993.
- GABBOTT, S. E., ALDRIDGE, R. J. and THERON, J. N. 1995. A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. *Nature*, **374**, 800–803.
- GAGNIER, P.-Y., BLIECK, A. R. M. and GABRIELA, R. S. 1986. First Ordovician vertebrate from South America. *Geobios*, **19**, 629–634.
- GALLAGHER, W. B. 1991. Selective extinction and survival across the Cretaceous/Tertiary boundary in the northern Atlantic Coastal Plain. *Geology*, **19**, 967–970.
- 1993. The Cretaceous/Tertiary mass extinction event in the northern Atlantic Coastal Plain. *The Mosasaur*, **5**, 75–154.
- 2002. Faunal changes across the Cretaceous-Tertiary (K-T) boundary in the Atlantic coastal plain of New Jersey: restructuring the marine community after the K-T mass-extinction event. *Geological Society of America, Special Paper*, **356**, 291–301.
- 2003. Oligotrophic oceans and minimalist organisms: collapse of the Maastrichtian marine ecosystem and Paleocene recovery in the Cretaceous-Tertiary sequence of New Jersey. *Netherlands Journal of Geosciences*, **82**, 225–231.
- PARRIS, D. C. and SPAMER, E. E. 1986. Paleontology, biostratigraphy, and depositional environments of the Cretaceous-Tertiary transition in the New Jersey Coastal Plain. *The Mosasaur*, **3**, 1–35.
- GARDINER, B. G. 1993a. Placodermi. 583–588. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- 1993b. Osteichthyes: basal actinopterygians. 611–619. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.

- GARVEY, J. M. 2005. An Early Carboniferous fossil assemblage from Fish Hill, Mansfield Basin, Australia. Unpublished PhD Thesis, La Trobe University, Victoria, Australia, 291 pp.
- and TURNER, S. 2006. Vertebrate microremains from the presumed earliest Carboniferous of the Mansfield Basin, Victoria. *Alcheringa*, **30**, 43–62.
- GAYET, M. and MEUNIER, F. J. 1998. Maastrichtian to early late Paleocene freshwater Osteichthyes of Bolivia: additions and comments. 85–100. In MALABARA, L. R., REIS, R. E., VARI, R. P., LUCENA, Z. M. and LUCENA, C. A. S. (eds). *Phylogeny and classification of neotropical fishes*. Edipucrs, Porto Alegre, 603 pp.
- MARSHALL, L. G., SEMPERE, T., MEUNIER, F. J., CAPPETTA, H. and RAGE, J.-C. 2000. Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **169**, 39–68.
- GESS, R. and HILLER, N. 1995. A preliminary catalogue of fossil algal, plant, arthropod, and fish remains from a Late Devonian black shale near Grahamstown, South Africa. *Annals of the Cape Provincial Museums, Natural History*, **19**, 225–304.
- COATES, M. I. and RUBRIDGE, B. S. 2006. A lamprey from the Devonian period of South Africa. *Nature*, **443**, 981–984.
- GINTER, M. 1990. Late Famennian shark teeth from the Holy Cross Mts, Central Poland. *Acta Geologica Polonica*, **40**, 69–81.
- and IVANOV, A. 1995. Middle-Late Devonian phoebeodont-based ichthyolith zone. *GEOBIOS*, **19**, 351–355.
- GOTO, M. 1994. Palaeozoic and early Mesozoic fish faunas of the Japanese islands. *The Island Arc*, **3**, 247–254.
- GRADSTEIN, F. M., OGG, J. G. and SMITH, A. G. 2004. *A geologic timescale*. Cambridge University, Cambridge, 610 pp.
- GRANDE, L. 1980. Paleontology of the Green River Formation, with a review of the fish fauna. *Geological Survey of Wyoming Bulletin*, **63**, 1–333.
- 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *American Society of Ichthyologists and Herpetologists, Special Publication*, **6**, 1–871.
- and BEMIS, W. E. 1991. Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. *Society of Vertebrate Paleontology, Memoir*, **1**, 1–121.
- 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Society of Vertebrate Paleontology, Memoir*, **4**, 1–690.
- and GRANDE, T. 1999. A new species of *Notogoneus* (Teleostei: Gonorynchidae) from the Upper Cretaceous Two Medicine Formation of Montana, and the poor Cretaceous record of freshwater fishes from North America. *Journal of Vertebrate Paleontology*, **19**, 612–622.
- HAIRAPETIAN, V. and TURNER, S. 2003. Upper Devonian fish microremains from eastern and southeastern Iran. 26–27. In SCHULTZE, H.-P., LUKSEVICS, E. and UNWIN, D. (eds). *The Gross Symposium 2: Advances In Palaeoichthyology*, Riga, Latvia, September 8–14, 2003, Abstracts. *Ichthyolith Issues, Special Publication*, **7**.
- HALLAM, A. 2002. How catastrophic was the end-Triassic mass extinction? *Lethaia*, **35**, 147–157.
- and WIGNALL, P. B. 1999. Mass extinctions and sea level changes. *Earth Science Reviews*, **48**, 217–250.
- HALSTEAD, L. B. 1993. Agnatha. 573–581. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- HANNISDAL, B. and PETERS, S. 2011. Phanerozoic earth system evolution and marine biodiversity. *Science*, **334**, 1121–1124.
- HANSEN, M. C. 1996. Phylum Chordata—vertebrate fossils. 288–369. In FELDMAN, R. M. (ed.). *Fossils of Ohio*. Bulletin 70, Division of Geological Survey, Columbus, 577 pp.
- HAUFF, B. and HAUFF, R. B. 1981. *Das Holzmadenbuch*. REPRO-DRUCK, Fellbach, 136 pp.
- HEIMBERG, A. M., COWPER-SAL-LARI, R., SÉMON, M., DONOGHUE, P. C. J. and PETERSON, K. J. 2010. microRNAs reveal the interrelationships of hagfish, lampreys, and gnathostomes and the nature of the ancestral vertebrate. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 19379–19383.
- HILTON, E. J. 2003. Comparative osteology and phylogenetic systematics of fossil and living bony-tongue fishes (Actinopterygii, Teleostei, Osteoglossomorpha). *Zoological Journal of the Linnean Society*, **137**, 1–100.
- and GRANDE, L. 2006. Review of the fossil record of sturgeons, family Acipenseridae (Actinopterygii: Acipenseriformes), from North America. *Journal of Paleontology*, **80**, 672–683.
- HOOK, R. W. and BAIRD, D. 1988. An overview of the Upper Carboniferous fossil deposit at Linton, Ohio. *Ohio Journal of Science*, **88**, 55–60.
- HORA, S. L. 1937. On some fossil fish-scales from the intertrappean beds at Deothan and Kheri, Central Provinces. *Records of the Geological Survey of India*, **73**, 267–294.
- HU, S., ZHANG, Q., CHEN, Z.-Q., ZHOU, C., TAO, L., TAP, X., WEN, W., HUANG, J. and BENTON, M. J. 2011. The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proceedings of the Royal Society B*, **278**, 2274–2282.
- HURLEY, I. A., MUELLER, R. L., DUNN, K. A., SCHMIDT, E. J., FRIEDMAN, M., HO, R. K., PRINCE, V. E., YANG, Z., THOMAS, M. G. and COATES, M. I. 2007. A new time-scale for ray-finned fish evolution. *Proceedings of the Royal Society B*, **274**, 489–498.
- ISAACSON, P. E., DIAZ-MARTINEZ, E., GRADER, G. W., KALVODA, J., BABEK, O. and DEVUYST, F. X. 2008. Late Devonian-earliest Mississippian glaciation in Gondwanaland and its biogeographic consequences. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **268**, 126–142.
- IVANOV, A. 2005. Early Permian chondrichthyans of the Middle and South Urals. *Revista Brasileira de Paleontologia*, **8**, 127–138.
- JABLONSKI, D. 2002. Survival without recovery after mass extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 8139–8144.
- ROY, K., VALENTINE, J. W., PRICE, R. M. and ANDERSON, P. S. 2003. The impact of the pull of the recent on the history of marine biodiversity. *Science*, **300**, 1133–1135.

- JANVIER, P. 1977. Les Poissons devoniens de l'Iran central et de l'Afghanistan. *Memoires de la Societe geologique de France, hors serie*, **8**, 277–289.
- 1985. Environmental framework of the diversification of the Osteostraci during the Silurian and Devonian. *Philosophical Transactions of the Royal Society, London, B*, **309**, 259–272.
- 1996. *Early vertebrates*. Clarendon Press, Oxford, 408 pp.
- 2011. Comparative anatomy: all vertebrates do have vertebrae. *Current Biology*, **21**, R661–R663.
- and BLIECK, A. 1993. The Silurian-Devonian agnathan biostratigraphy of the Old Red continent. 67–86. In LONG, J. A. (ed.). *Paleozoic vertebrate biostratigraphy and biogeography*. Johns Hopkins University Press, Baltimore, 369 pp.
- and CLEMENT, G. 2005. A new groenlandaspid arthrodire (Vertebrata: Placodermi) from the Famennian of Belgium. *Geologica Belgica*, **8**, 51–67.
- LETHIERS, F., MONOD, O. and BALKAS, O. 1984. Discovery of a vertebrate fauna at the Devonian-Carboniferous boundary in SE Turkey (Hakkari Province). *Journal of Petroleum Geology*, **7**, 147–168.
- DESBIENS, S. and WILLETT, J. A. 2007. New evidence for the controversial “lungs” of the Late Devonian antiarch *Bothriolepis canadensis* (Whiteaves, 1880) (Placodermi: Antiarcha). *Journal of Vertebrate Paleontology*, **27**, 709–710.
- JENKYN, H. C. 1988. The early Toarcian (Jurassic) anoxic event; stratigraphic, sedimentary and geochemical evidence. *American Journal of Science*, **288**, 101–151.
- 2003. Evidence for rapid climate change in the Mesozoic-Paleogene greenhouse world. *Proceedings of the Royal Society A*, **361**, 1885–1916.
- JIA, L.-T., ZHU, M. and ZHAO, W.-J. 2010. A new antiarch fish from the Upper Devonian Zhongning Formation of Ningxia, China. *Palaeworld*, **19**, 136–145.
- KAISER, S. I., STEUBER, T., BECKER, R. T. and JOACHIMSKI, M. M. 2006. Geochemical evidence for major environmental change at the Devonian-Carboniferous boundary in the Carnic Alps and the Rhenish Massif. *Palaogeography, Palaeoclimatology, Palaeoecology*, **240**, 146–160.
- — — 2008. Environmental change during the Late Famennian and Early Tournaisian (Late Devonian–Early Carboniferous): implications from stable isotopes and conodont biofacies in southern Europe. *Geological Journal*, **43**, 241–260.
- KARATAJUTE-TALIMAA, V. 1995. The Mongolepidida: scale structure and systematic position. *Geobios*, **19**, 35–37.
- and SMITH, M. M. 2004. *Tesakoviaspis concentrica*: microskeletal remains from the Ordovician and Lower Silurian of Siberia. 53–64. In ARRATIA, G., WILSON, M. V. H. and CLOUTIER, R. (eds). *Recent advances in the origin and early radiation of vertebrates*. Verlag Dr. Friedrich Pfeil, Munich, 703 pp.
- KELLER, G., ADATTE, T., PARDO, A., BAJPAI, S., KHOSLA, A. and SAMANT, B. 2010. Cretaceous extinctions: evidence overlooked. *Science*, **328**, 974–975.
- KHADDUMI, H. F. 2009. *Fossils of the Harrana fauna and the adjacent areas*. Eternal River Museum of Natural History, Amman, Jordan, 324 pp.
- KIESSLING, W. and SIMPSON, C. 2011. On the potential for ocean acidification to be a general cause of ancient reef crises. *Global Change Biology*, **17**, 56–67.
- KLUG, C., KRÖGER, B., KIESSLING, W., MULLINS, G. L., SERVAIS, T., FRÝDA, J., KORN, D. and TURNER, S. 2011. The Devonian nekton revolution. *Lethaia*, **43**, 465–477.
- KORN, D. 2000. Morphospace occupation of ammonoids over the Devonian-Carboniferous boundary. *Palaontologische Zeitschrift*, **74**, 247–257.
- KOSNIK, M. A., ALROY, J., BEHRENSMEYER, A. K., FÜRSICH, F. T., GASTALDO, R. A., KIDWELL, S. M., KOWALEWSKI, M., PLOTNICK, R. E., ROGERS, R. R. and WAGNER, P. J. 2011. Changes in shell durability of common marine taxa through the Phanerozoic: evidence for biological rather than taphonomic drivers. *Paleobiology*, **37**, 303–331.
- KRAMER, D. L. 1987. Dissolved oxygen and fish behavior. *Environmental Biology of Fishes*, **18**, 81–92.
- KRIWET, J. and BENTON, M. J. 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. *Palaogeography, Palaeoclimatology, Palaeoecology*, **214**, 181–194.
- WITZMANN, F., KLUG, S. and HEIDTKE, U. H. J. 2008. First direct evidence of a vertebrate three-level trophic chain in the fossil record. *Proceedings of the Royal Society, B*, **275**, 181–186.
- KIESSLING, W. and KLUG, S. 2009. Diversification trajectories and life-history traits in early sharks and batoids. *Proceedings of the Royal Society B*, **276**, 945–951.
- LAMBERS, P. 1999. The actinopterygian fish fauna of the late Kimmeridgian and early Tithonian ‘Plattenkalke’ near Solnhofen (Bavaria, Germany): state of the art. *Geologie en Mijnbouw*, **78**, 215–229.
- LAMSDALL, J. C. and BRADY, S. J. 2010. Cope’s rule and Romer’s theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. *Biology Letters*, **6**, 265–269.
- LANGSTON, W. Jr 1970. A fossil ray, possibly *Myledaphus* (Elasmobranchii: Batoidea) from the Late Cretaceous Oldman Formation of western Canada. *National Museums of Canada, Publications in Palaeontology*, **6**, 1–15.
- LI, G.-Q. 1996. A new species of Late Cretaceous osteoglossid (Teleostei) from the Oldman Formation of Alberta, Canada, and its phylogenetic relationships. In ARRATIA, G. and VIOHL, G. (eds). *Mesozoic fishes—systematics and paleoecology*. Verlag Dr. Friedrich Pfeil, Munich, 576 pp.
- LIU, X. and WEI, F. 1988. A new saurichthyid from the upper Permian of Zhejiang, China. *Vertebrata Palasiatica*, **26**, 77–89. [in Chinese with English summary].
- LLOYD, G. T., DAVIS, K. E., PISANI, D., TARVER, J. E., RUTA, M., SAKAMOTO, M., HONE, D. W. E., JENNINGS, R. and BENTON, M. J. 2008. Dinosaurs and the Cretaceous terrestrial revolution. *Proceedings of the Royal Society B*, **275**, 2483–2490.
- YOUNG, J. R. and SMITH, A. B. 2011. Taxonomic structure of the fossil record is shaped by sampling bias. *Systematic Biology*, **61**, 80–89.
- WANG, S. C. and BRUSATTE, S. L. 2012a. Identifying heterogeneity in rates of morphological evolution: discrete

- character change in the evolution of lungfish (Sarcopterygii; Dipnoi). *Evolution*, **66**, 340–348.
- YOUNG, J. R. and SMITH, A. B. 2012b. Comparative quality and fidelity of the deep-sea and land-based nanofossil records. *Geology*, **40**, 155–158.
- LONG, J. A. 1993. Early-middle Palaeozoic vertebrate extinction events. 54–63. In LONG, J. A. (ed.). *Paleozoic vertebrate biostratigraphy and biogeography*. Johns Hopkins University Press, Baltimore, 369 pp.
- MACLEOD, N., RAWSON, P. F., FOREY, P. L., BANNER, F. T., BOUDAGHER-FADEL, M. K., BROWN, P. R., BURNETT, J. A., CHAMBERS, P., CULVER, S., EVANS, S. E., JEFFERY, C., KAMINSKI, M. A., LORD, A. R., MILNER, A. C., MILNER, A. R., MORRIS, N., OWEN, E., ROSEN, B. R., SMITH, A. B., TAYLOR, P. D., URQUHART, E. and YOUNG, J. R. 1997. The Cretaceous-Tertiary biotic transition. *Journal of the Geological Society, London*, **154**, 265–292.
- MAPES, R. H. and BENSTOCK, E. J. 1988. Color pattern on the Carboniferous bivalve *Streblochondria*? Newell. *Journal of Paleontology*, **62**, 439–441.
- MARSH, O. C. 1877. Introduction and succession of vertebrate life in America. *American Journal of Science and Art*, **42**, 337–379.
- MCCUNE, A. R. and SCHAEFFER, B. 1986. Triassic and Jurassic fishes: patterns of diversity. 171–182. In PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic-Jurassic boundary*. Cambridge University Press, Cambridge, 381 pp.
- MCGHEE, G. R. 1996. *The Late Devonian mass extinction: the Frasnian/Famennian crisis*. Columbia University Press, New York, 303 pp.
- SHEEHAN, P. M., BOTTJET, D. J. and DROSER, M. L. 2012. Ecological ranking of Phanerozoic biodiversity crises: the Serpukhovian (early Carboniferous) crisis had a greater ecological impact than the end-Ordovician. *Geology*, **40**, 147–150.
- MCGOWAN, A. J. and SMITH, A. B. 2008. Are global Phanerozoic marine diversity curves truly global? A study of the relationship between regional rock records and global Phanerozoic marine diversity. *Paleobiology*, **34**, 80–103.
- — and TAYLOR, P. D. 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA. *Australian Journal of Earth Sciences*, **56**, 859–872.
- MCKINNEY, M. L. 1998. Is marine biodiversity at less risk? Evidence and implications. *Diversity and Distributions*, **4**, 3–8.
- MCLAREN, D. J. 1970. Time, life and boundaries. *Journal of Paleontology*, **44**, 801–815.
- MCNAB, B. K. 2002. *The physiological ecology of vertebrates: a view from energetics*. Cornell University, New York, 576 pp.
- MOHABEY, D. M. and UDHOJI, S. G. 2000. Vertebrate fauna of Late Cretaceous dinosaur-bearing Lameta Formation of Nand-Dongargaon inland basin, Maharashtra: palaeoenvironment and K-T boundary implications. *Memoir Geological Society of India*, **46**, 295–322.
- — and VERMA, K. K. 1993. Palaeontological and sedimentological observations on non-marine Lameta Formation (Upper Cretaceous) of Maharashtra, India: their palaeoecological and palaeoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **105**, 83–94.
- MOY-THOMAS, J. A. and MILES, R. S. 1971. *Palaeozoic fishes*. Chapman and Hall, London, 259 pp.
- MUNNECKE, A., CALNER, M., HARPER, D. A. T. and SERVAIS, T. 2011. Ordovician and Silurian sea-water chemistry, sea level, and climate: a synopsis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **296**, 389–413.
- MUTTER, R. J. 2009. Recovery from the end-Permian extinction event: evidence from “Lilliput *Listracanthus*”. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 22–28.
- 2011. A case study of the palaeobiogeography of Early Mesozoic Actinopterygians: the family Ptycholepididae. In UP-CHURCH, P., MCGOWAN, A. J. and SLATER, C. S. C. (eds.) *Palaeogeography and Palaeobiogeography: biodiversity in Space and Time*. CRC Press, Boca Raton. 239 pp.
- and NEUMAN, A. G. 2008. New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation of western Canada. *Geological Society of London, Special Publications*, **295**, 9–41.
- and RICHTER, M. 2007. Acanthodian remains from the Middle-Late Permian of Brazil. *Geological Journal*, **42**, 213–224.
- DE BLANGER, K. and NEUMAN, A. G. 2007. Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). *Zoological Journal of the Linnean Society*, **149**, 309–337.
- MYROW, P., STRAUSS, J. V., CREVELING, J. R., SICARD, K. R., RIPPERDAN, R., SANDBERG, C. A. and HARTENFELS, S. 2011. A carbon isotopic and sedimentological record of the latest Devonian (Famennian) from the Western U.S. and Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **306**, 147–159.
- NELSON, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History*, **141**, 475–522.
- NELSON, J. S. 2006. *Fishes of the world*. John Wiley, New York, 601 pp.
- NEUMAN, A. G. and BRINKMAN, D. B. 2005. Fishes of the fluvial beds. 167–185. In CURRIE, P. J. and KOPPELHUS, E. B. (eds.) *Dinosaur Provincial Park: a spectacular ancient ecosystem revealed*. Indiana University Press, Bloomington, 651 pp.
- NEWBREY, M. G., MURRAY, A. M., WILSON, M. V. H., BRINKMAN, D. B. and NEUMAN, A. G. 2009. Seventy-five-million-year-old tropical tetra-like fish from Canada tracks Cretaceous global warming. *Proceedings of the Royal Society B*, **276**, 3829–3833.
- — BRINKMAN, D. B., WILSON, M. V. H. and NEUMAN, A. G. 2010. A new articulated freshwater fish (Clupeomorpha, Ellimmichthyiformes) from the Horseshoe Canyon Formation, Maastrichtian, of Alberta, Canada. *Canadian Journal of Earth Sciences*, **47**, 1183–1196.
- NEWELL, N. D. 1952. Periodicity in invertebrate evolution. *Journal of Paleontology*, **26**, 371–385.
- 1962. Paleontological gaps and geochronology. *Journal of Paleontology*, **36**, 592–610.

- NOLF, D., RANA, R. S. and PRASAD, G. V. R. 2008. Late Cretaceous (Maastrichtian) fish otoliths from the Deccan Intertrappean Beds, India: a revision. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **78**, 239–259.
- NOUBHANI, A. and CAPPETTA, H. 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien–Lutétien basal)–Systématique, biostratigraphie, évolution et dynamique des faunes. *PalaeoIchthyologica*, **8**, 1–327.
- OTA, K. G., FUJIMOTO, S., OISI, Y. and KURATANI, S. 2011. Identification of vertebra-like elements and their possible differentiation from sclerotomes in the hagfish. *Nature Communications*, **2**, 373.
- PACKARD, A. 1972. Cephalopods and fish: the limits of convergence. *Biological Reviews*, **47**, 241–307.
- PATTERSON, C. 1993a. Osteichthyes: Teleostei. 621–656. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- 1993b. An overview of the early fossil record of acanthomorphs. *Bulletin of Marine Science*, **52**, 29–59.
- 1994. Bony fishes. *Short Courses in Paleontology*, **7**, 57–84.
- and ROSEN, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History*, **158**, 81–172.
- and SMITH, A. B. 1987. Is the periodicity of extinctions a taxonomic artefact? *Nature*, **330**, 248–251.
- 1989. Periodicity in extinction: the role of systematics. *Ecology*, **70**, 802–811.
- PETERS, S. E. and FOOTE, M. 2001. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology*, **27**, 583–601.
- PIIPER, J. 1982. Respiratory gas exchange at lungs, gills and tissues: mechanisms and adjustments. *Journal of Experimental Biology*, **100**, 5–22.
- POYATO-ARIZA, F. J. and WENZ, S. 2002. A new insight into the pycnodontiform fishes. *Geodiversitas*, **24**, 139–248.
- PRASAD, G. V. R. and SAHNI, A. 1987. Coastal-plain microvertebrate assemblage from the terminal Cretaceous of Asifabad, peninsular India. *Journal of the Palaeontological Society of India*, **32**, 5–19.
- PRICE, G. D. 1999. The evidence and implications of polar ice during the Mesozoic. *Earth-Science Reviews*, **48**, 183–210.
- PURNELL, M. A. 2001a. Scenarios, selection and the ecology of early vertebrates. 187–208. In AHLBERG, P. E. (ed.). *Major events in early vertebrate evolution*. Taylor & Francis, London, 418 pp.
- 2001b. Feeding in extinct jawless heterostracan fishes and testing scenarios of the early vertebrate evolution. *Proceedings of the Royal Society B*, **269**, 83–88.
- QU, Q.-M., ZHU, M. and ZHAO, W.-J. 2010. Silurian atmospheric O₂ changes and the early radiation of gnathostomes. *Palaeoworld*, **19**, 146–159.
- RACKI, G. 2005. Toward understanding Late Devonian global events: few answers, many questions. 5–36. In OVER, D. J., MORROW, J. R. and WIGNALL, P. B. (eds). *Understanding Late Devonian and Permian-Triassic biotic and climatic events. Towards an integrated approach*. Elsevier, Amsterdam, 337 pp.
- RANA, R. S. 1990. Palaeontology and palaeoecology of the intertrappean (Cretaceous-Tertiary transition) beds of the peninsular India. *Journal of the Palaeontological Society of India*, **35**, 105–120.
- and SAHNI, A. 1989. Fish otoliths from the Takli Formation (Intertrappean Beds) of Nagpur, India. *Geoscience Journal*, **40**, 145–164.
- RANDON, C., DERYCKE, C., BLIECK, A., PERRI, M. C. and SPALLETTA, C. 2007. Late Devonian-Early Carboniferous vertebrate microremains from the Carnic Alps, northern Italy. *Geobios*, **40**, 809–826.
- RAUP, D. M. 1979. Bias in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History*, **13**, 85–91.
- and SEPKOSKI, J. J. 1982. Mass extinctions in the marine fossil record. *Science*, **215**, 1501–1503.
- REDMAN, C., BRINKMAN, D. B., NEWBREY, M. G., NEUMAN, A. G. and EATON, J. G. 2010. Long-term trends in the richness of freshwater actinopterygians from the Late Cretaceous (Cenomanian-Maastrichtian) of the Western Interior of North America. *Geological Society of America Abstracts with Programs*, **42**, 257.
- REPETSKI, J. E. 1978. A fish from the Upper Cambrian of North America. *Science*, **200**, 529–531.
- ROMER, A. S. 1933. Eurypterid influence on vertebrate history. *Science*, **78**, 114–117.
- 1966. *Vertebrate paleontology*. University of Chicago Press, Chicago, 468 pp.
- ROY, K., HUNT, G. and JABLONSKI, D. 2009. Phylogenetic conservatism of extinctions in marine bivalves. *Science*, **325**, 733–737.
- RUSSELL, D. A. 1988. A check list of North American marine Cretaceous vertebrates including fresh water fishes. *Occasional Paper of the Tyrrell Museum of Palaeontology*, **4**, 1–58.
- RUTA, M., WAGNER, P. J. and COATES, M. I. 2006. Evolutionary rates in early tetrapods I. Rapid initial diversification followed by decreased character change. *Proceedings of the Royal Society of London Series B*, **273**, 2107–2111.
- SALLAN, L. C. and COATES, M. I. 2010. End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 10131–10135.
- and FRIEDMAN, M. 2012. Heads or tails: staged diversification in vertebrate evolutionary radiations. *Proceedings of the Royal Society B*, **279**, 2025–2032.
- KAMMER, T. W., AUSICH, W. I. and COOK, L. A. 2011. Persistent predator-prey dynamics revealed by mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 8335–8338.
- SANDBERG, C. A., ZIEGLER, W., DREESEN, R. and BUTLER, J. L. 1988. Part 3: late Frasnian mass extinction: conodont event stratigraphy, global changes, and possible causes. *Courier Forschungsinstitut Senckenberg*, **102**, 263–307.
- SANDERSON, S. L. and WASSERSUG, R. 1993. Convergent and alternative designs for vertebrate suspension feeding.

- 37–112. In HANKEN, J. and HALL, B. K. (eds). *The skull*, Vol. 3. University of Chicago Press, Chicago, 468 pp.
- SANSOM, I. J., DAVIES, N. S., COATES, M. I., NICHOLL, R. S. and RITCHIE, A. 2012. Chondrichthyan-like scales from the Middle Ordovician of Australia. *Palaeontology*, **55**, 243–247.
- SMITH, M. P., ARMSTRONG, H. A. and SMITH, M. M. 1992. Presence of the earliest vertebrate hard tissues in conodonts. *Science*, **256**, 1308–1311.
- and SMITH, M. M. 1996. Scales of thelodont and shark-like fishes from the Ordovician. *Nature*, **379**, 628–630.
- SMITH, M. M. and SMITH, M. P. 2001. The Ordovician radiation of vertebrates. 156–177. In AHLBERG, P. E. (ed.). *Major events in early vertebrate evolution*. Taylor & Francis, London, 418 pp.
- WANG, N.-Z. and SMITH, M. 2005. The histology and affinities of sinacanthid fishes: primitive gnathostomes from the Silurian of China. *Zoological Journal of the Linnean Society*, **144**, 379–386.
- MILLER, C. G., HEWARD, A., DAVIES, N. S., BOOTH, G. A., FORTEY, R. A. and PARIS, F. 2009. Ordovician fish from the Arabian peninsula. *Palaeontology*, **52**, 337–342.
- SANSOM, R. S. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). *Journal of Systematic Palaeontology*, **7**, 95–115.
- FREEDMAN, K., GABBOTT, S. E., ALDRIDGE, R. J. and PURNELL, M. A. 2010a. Taphonomy and affinity of an enigmatic Silurian vertebrate, *Jamoytius kerwoodi* White. *Palaeontology*, **53**, 1393–1409.
- GABBOTT, S. E. and PURNELL, M. A. 2010b. Non-random decay of chordate characters causes bias in fossil interpretation. *Nature*, **463**, 797–800.
- — 2011. Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and implications for the vertebrate fossil record. *Proceedings of the Royal Society B*, **278**, 1150–1157.
- SCHAEFFER, B. 1973. Fishes and the Permian-Triassic boundary. 493–497. In LOGAN, A. and HILLS, L. V. (eds). *The Permian and Triassic systems and their mutual boundary*. Canadian Society of Petroleum Geologists, Calgary, 766 pp.
- SCHLANGER, S. O. and JENKINS, H. C. 1976. Cretaceous oceanic anoxic events: causes and consequences. *Geologie en Mijnbouw*, **55**, 179–184.
- SCHRAM, F. R. 1979. The Mazon Creek biotas in the context of the Carboniferous faunal continuum. 159–190. In NITECKI, M. R. (ed.). *Mazon Creek fossils*. Academic, New York, 581 pp.
- 1983. Lower Carboniferous biota of Glencartholm, Eskdale, Dumfriesshire. *Scottish Journal of Geology*, **19**, 1–15.
- SCHULTE, P., ALEGRET, L., ARENILLAS, I., ARZ, J. A., BARTON, P. J., BOWN, P. R., BRALOWER, T. J., CHRISTESON, G. L., CLAEYS, P., COCKELL, C. S., COLLINS, G. S., DEUTSCH, A., GOLDIN, T. J., GOTO, K., GRAJALES-NISHIMURA, J. M., GRIEVE, R. A. F., GULICK, S. P. S., JOHNSON, K. R., KIESLING, W., KOEBERL, C., KRING, D. A., MACLEOD, K. G., MATSUI, T., MELOSH, J., MONTANARI, A., MORGAN, J. V., NEAL, C. R., NICHOLS, D. J., NORRS, R. D., PIERAZZO, E., RAVIZZA, G., REBOLLEDO-VIEYRA, M., REIMOLD, W. U., ROBIN, E., SALGE, T., SPEIJER, R. P., SWEET, A. R., URRUTIA-FUCUGAUCHI, J., VAIDA, V., WHALEN, M. T. and WILLUMSEN, P. S. 2010. The Chicxulub asteroid impact and mass-extinction at the Cretaceous-Paleogene boundary. *Science*, **327**, 1214–1218.
- SCHULTZE, H.-P. 1993. Osteichthyes: Sarcopterygii. 657–663. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- 2009. Interpretation of marine and freshwater paleoenvironments in Permo-Carboniferous deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**, 126–136.
- SCHWIMMER, D. R., STEWART, J. D. and WILLIAMS, G. D. 1997. *Xiphactinus vetus* and the distribution of *Xiphactinus* species in the eastern United States. *Journal of Vertebrate Paleontology*, **17**, 610–615.
- SEMPERE, T., BUTLER, R. F., RICHARDS, D. R., MARSHALL, L. G., SHARP, W. and SWISHER, C. C. III 1997. Stratigraphy and chronology of Upper Cretaceous-lower Paleogene strata in Bolivia and northwest Argentina. *Geological Society of America Bulletin*, **109**, 709–727.
- SEPKOSKI, J. J. Jr 2002. A compendium of fossil marine animal genera. *Bulletin of American Paleontology*, **363**, 1–560.
- SEPKOSKI, D. and RUSE, M. 2009. *The paleobiological revolution: essays on the growth of modern paleontology*. University of Chicago Press, Chicago, 568 pp.
- SHACKLETON, N. J., MOORE, T. C. JR., RABINOWITZ, P. D., BOERSMA, A., BORELLA, P. E., CHAVE, A. D., DUÉE, G., FÜTTERER, D., JIANG, M.-J., KLEINERT, K., LEVER, A., MANIVIT, H., O'CONNELL, S. and RICHARDSON, S. H. 1984. Accumulation rates in the Leg 74 sediments. *Deep Sea Drilling Project Initial Report*, **74**, 621–644.
- SHEEHAN, P. M. and FASTOVSKY, D. E. 1992. Major extinctions of land-dwelling vertebrates at the Cretaceous-Tertiary boundary, eastern Montana. *Geology*, **20**, 556–560.
- 1993. Major extinctions of land-dwelling vertebrates at the Cretaceous-Tertiary boundary, eastern Montana: comment and reply. *Geology*, **21**, 92–93.
- SHU, D.-G., LUO, H.-L., CONWAY MORRIS, S., ZHANG, X.-L., HU, S.-X., CHEN, L., HAN, J., ZHU, M., LI, Y. and CHEN, L.-Z. 1999. Lower Cambrian vertebrates from south China. *Nature*, **402**, 42–46.
- CONWAY MORRIS, S., HAN, J., ZHANG, Z.-F., YASUI, K., JANVIER, P., CHEN, L., ZHANG, X.-L., LIU, J.-N., LI, Y. and LIU, H.-Q. 2003. Head and backbone of the early Cambrian vertebrate *Haikouichthys*. *Nature*, **421**, 526–529.
- SIGNOR, P. W. III and BRETT, C. E. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology*, **10**, 229–245.
- and LIPPS, J. H. 1982. Gradual extinction patterns and catastrophes in the fossil record. *Geological Society of America Special Paper*, **190**, 291–296.
- SLOTTA, F., KORN, D., KLUG, C., KRÖGER, B. and KEUPP, H. 2011. Sublethal shell injuries in Late Devonian ammonoids (Cephalopoda) from Kattensiepen (Rhenish

- Mountains). *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, **261**, 321–336.
- SMITH, A. B. and PATTERSON, C. 1988. The influence of taxonomic method on the perception of patterns of evolution. *Evolutionary Biology*, **23**, 127–216.
- SMITH, M. P., SANSOM, I. J. and REPETSKI, J. E. 1996. Histology of the first fish. *Nature*, **380**, 702–704.
- SMITHSON, T. R., WOOD, S. P., MARSHALL, J. E. A. and CLACK, J. A. 2012. Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 4532–4537.
- SOEHN, K. L., MARSS, T., CALDWELL, M. W. and WILSON, M. V. H. 2001. New and biostratigraphically useful thelodonts from the Silurian of the Mackenzie Mountains, Northwest Territories, Canada. *Journal of Vertebrate Paleontology*, **21**, 651–659.
- STAHL, B. J. 1999. Chondrichthyes III: Holocephali. 1–164. In SCHULTZE, H.-P. (ed.). *Handbook of paleoichthyology*, Vol. 4. Verlag Dr. Friedrich Pfeil, Munich, 164 pp.
- STANLEY, S. M. 2008. Predation beats competition on the seafloor. *Paleobiology*, **34**, 1–21.
- STEMMERIK, L., BENDIX-ALMGREEN, S. E. and PIASECKI, S. 2001. The Permian-Triassic boundary in central East Greenland: past and present views. *Bulletin of the Geological Society of Denmark*, **48**, 159–167.
- STIASNY, M. L. J., WILEY, E. O., JOHNSON, G. D. and DE CARVALHO, M. R. 2004. Gnathostome fishes. 410–429. In CRACRAFT, J. and DONOGHUE, M. J. (eds). *Assembling the tree of life*. Oxford University Press, Oxford, 576 pp.
- STIGALL, A. L. 2010. Invasive species and biodiversity crises: testing the link in the Late Devonian. *PLoS One*, **5**, e15584.
- SYTCHEVSKAYA, E. K. and PROKOFIEV, A. M. 2002. First findings of Xiphioidae (Perciformes) in the late Paleocene of Turkmenistan. *Journal of Ichthyology*, **42**, 227–237.
- TANIMOTO, M. and KIKYO, T. 2001. *Gillicus* skeleton from the Upper Cretaceous Izumi Group (lower Maastrichtian) of Yura-cho, Sumoto City, Hyogo Prefecture. *Chigaku Kenkyu/Journal of the Society of Earth Scientists and Amateurs of Japan*, **50**, 41–43. [in Japanese with English summary]
- TANNER, L. H., LUCAS, S. G. and CHAPMAN, M. G. 2004. Assessing the record and causes of Late Triassic extinction. *Earth-Science Reviews*, **65**, 103–139.
- TAVERNE, L. 2005. Les poissons crétacés de Nardò. 20. *Chanoidea chardonii* sp. nov. (Teleostei, Ostariophysi, Otocephali) *Bolletino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, **29**, 39–54.
- . 2009. Les poissons crétacés de Nardò. 31. *Chanos* sp. (Teleostei, Ostariophysi, Gonorynchiformes, Chanidae). *Bolletino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, **33**, 53–58.
- . 2010. Les poissons crétacés de Nardò. 32. Trois nouveaux Perciformes: *Zorziniperca weverberghi* gen. et sp. nov., *Johnsonperca annavaccarii* gen. et sp. nov. et *Bannikovperca apula* gen. et sp. nov. (Teleostei, Percomorpha). *Bolletino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, **34**, 51–80.
- and BRONZI, P. 1999. Les poissons crétacés de Nardò. 9. Note complémentaire sur le Saurodontidae (Teleostei, Ichthyodectiformes). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, **8**, 105–116.
- THERON, J. N. 1993. The Devonian-Carboniferous boundary in South Africa. *Annales de la Société géologique de Belgique*, **116**, 291–300.
- THOMSON, K. S. 1976. Explanation of large scale extinctions of lower vertebrates. *Nature*, **261**, 578–580.
- . 1977. The pattern of diversification among fishes. 377–404. In HALLAM, A. (ed.). *Patterns of evolution as illustrated by the fossil record*. Elsevier, Amsterdam, 591 pp.
- TINTORI, A. 1998. Fish biodiversity in the marine Norian (Late Triassic) of northern Italy: the first neopterygian radiation. *Italian Journal of Zoology*, **65** (S1), 193–198.
- TONG, J., ZHOU, X., ERWIN, D. H., ZUO, J. and ZHAO, L. 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaoahu, Anhui Province, China. *Journal of Paleontology*, **80**, 146–161.
- TRAMMER, J. 1974. Evolutionary trends and pattern of extinction of Triassic conodonts. *Acta Palaeontologica Polonica*, **19**, 251–264.
- TURNER, S., BURROW, C. J., SCHULTZE, H.-P., BLIECK, A., REIF, W.-E., REXROAD, C. B., BULTYNCK, P. and NOWLAN, G. S. 2010. False teeth: conodont-vertebrate phylogenetic relationships revisited. *Geodiversitas*, **32**, 545–594.
- TWITCHETT, R. J. 2001. Incompleteness of the Permian-Triassic fossil record: a consequence of productivity decline? *Geological Journal*, **36**, 341–353.
- UNDERWOOD, C. J. 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology*, **32**, 215–235.
- VAN ROY, P., ORR, P. J., BOTTING, J. P., MUIR, L. A., VINTHER, J., LEFEBVRE, B., EL HARIRI, K. and BRIGGS, D. E. G. 2010. Ordovician faunas of the Burgess Shale type. *Nature*, **465**, 215–218.
- VEGA, C. G. and WIENS, J. J. 2012. Why are there so few fish in the sea? *Proceedings of the Royal Society B*, **279**, 2323–2329.
- VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators, and grazers. *Paleobiology*, **3**, 245–258.
- VON BITTER, P. H., PURNELL, M. A., TETREAULT, D. K. and STOTT, C. A. 2007. Eramosa Lagerstätte – exceptionally preserved soft-bodied biotas with shallow-marine shelly and bioturbating organisms (Silurian, Ontario, Canada). *Geology*, **35**, 879–882.
- WAINWRIGHT, P. C. and BELLWOOD, D. R. 2002. Eco-morphology of feeding in coral reef fishes. 33–55. In SALE, P. F. (ed.). *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, Amsterdam, 549 pp.
- and RICHARD, B. A. 1995. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*, **44**, 97–113.
- WALL, P. D., IVANY, L. D. and WILKINSON, B. H. 2009. Revisiting Raup: exploring the influence of outcrop area on diversity in light of modern sample-standardization techniques. *Paleobiology*, **35**, 146–167.

- WATERS, J. A. and WEBSTER, G. D. 2009. A re-evaluation of Famennian echinoderm diversity: implications for patterns of extinction and rebound in the Late Devonian. *Geological Society, London, Special Publications*, **34**, 149–161.
- WANG, Q.-J. and ZHU, M. 1997. Discovery of Ordovician vertebrate fossil from Inner Mongolia, China. *Chinese Science Bulletin*, **42**, 1560–1562.
- WARD, P., LABANDIERA, C., LAURIN, M. and BERNER, R. A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences United States of America*, **103**, 16818–16822.
- WEN, W., ZHANG, Q.-Y., HU, S.-X., ZHOU, C.-Y., HUANG, J.-Y., CHEN, Z. Q. and BENTON, M. J. 2012. A new genus of basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China. *Acta Palaeontologica Polonica*, **57**, 149–160.
- WENZ, S. 1967. Compléments à l'étude des poissons Actinoptérygiens du Juassique Français. *Cahiers de Paléontologie*. CNRS, Paris, 276 pp.
- WILSON, M. V. H. and CALDWELL, M. W. 1993. New Silurian and Devonian fork-tailed 'thelodonts' are jawless vertebrates with stomachs and deep bodies. *Nature*, **361**, 442–444.
- BRINKMAN, D. B. and NEUMAN, A. G. 1992. Cretaceous Esocidae (Teleostei): early radiation of pikes in North American fresh waters. *Journal of Paleontology*, **66**, 839–846.
- WOOD, R. 2000. Novel paleoecology of a postextinction reef: Famennian (Late Devonian) of the Canning basin, northwestern Australia. *Geology*, **28**, 987–990.
- WOODWARD, A. S. 1908. On some fish-remains from the Lameta Beds at Dongar-Gaon, Central Provinces. *Palaeontologia Indica, New Series*, **3**, 1–6.
- YOUNG, G. C. 1997. Ordovician microvertebrate remains from the Amadeus Basin, Central Australia. *Journal of Vertebrate Paleontology*, **17**, 1–25.
- 2003. North Gondwana mid-Paleozoic connections with Euramerica and Asia: Devonian vertebrate evidence. *Courier Forschungsinstitut Senckenberg*, **242**, 169–185.
- 2009. An Ordovician vertebrate from western New South Wales, with comments on Cambro-Ordovician vertebrate distribution patterns. *Alcheringa*, **33**, 79–89.
- 2011. Placoderms (armored fish): dominant vertebrates of the Devonian period. *Annual Review of Earth and Planetary Sciences*, **38**, 523–550.
- BURROW, C. J., LONG, J. A., TURNER, S. and CHOO, B. 2010. Devonian macrovertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld*, **19**, 55–74.
- KARATAJUTE-TALIMAA, V. N. and SMITH, M. M. 1996. A possible Late Cambrian vertebrate from Australia. *Nature*, **383**, 810–812.
- YOUNG, G. A., RUDKIN, D. M., DOBRZANSKI, E. P., ROBSON, S. P. and NOWLAN, G. S. 2007. Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. *Geology*, **35**, 883–886.
- ZAJIC, J. 2000. Vertebrate zonation of the non-marine Upper Carboniferous-Lower Permian basins of the Czech Republic. *Courier Forschungsinstitut Senckenberg*, **223**, 563–575.
- ZANGERL, R. 1981. Chondrichthyes I, Paleozoic Elasmobranchii. 1–115. In SCHULTZE, H.-P. (ed.). *Handbook of paleoichthyology*, Vol. 3A. Gustav Fischer Verlag, Stuttgart, 115 pp.
- ZHANG, G.-R., WANG, S.-T., WANG, J.-Q., WANG, N.-Z. and ZHU, M. 2010. A basal antiarch (placoderm fish) from the Silurian of Qujing, Yunnan, China. *Palaeoworld*, **19**, 129–135.
- ZHAO, W. J. and ZHU, M. 2007. Diversification and faunal shift of Siluro-Devonian vertebrates of China. *Geological Journal*, **42**, 351–369.
- ZHU, M., YU, X. and JANVIER, P. 1999. A primitive fossil fish sheds light on the origin of bony fishes. *Nature*, **397**, 607–610.
- ZHAO, W., JIA, L., LU, J., QIAO, T. and QU, Q. 2009. The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature*, **458**, 469–474.
- ZIDEK, J. 1993. Acanthodii. 589–592. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- ŽIGAITE, Z., KARATAJUTE-TALIMAA, V. and BLIECK, A. 2011. Vertebrate microremains from the Lower Silurian of Siberia and Central Asia: palaeobiodiversity and palaeobiogeography. *Journal of Micropalaeontology*, **30**, 97–106.
- ZINSMEISTER, W. J. 1998. Discovery of a fish mortality horizon at the K-T boundary on Seymour Island: re-evaluation of events at the end of the Cretaceous. *Journal of Paleontology*, **72**, 556–571.