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Nonmarine mass extinctions

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Abstract. A critical review of putative nonmarine mass extinctions associated with the so-called "Big 5 mass extinctions" of marine invertebrates (Late Ordovician, Late Devonian, end Permian, end Triassic and end Cretaceous) as well as a likely sixth mass extinction in the marine realm, the end-Guadalupian extinction, reveals little evidence of coeval marine and nonmarine mass extinctions. Little lived on land during the Ordovician other than a bryophyte-like flora that appears to have been diversifying, not going extinct, during the Late Ordovician. No case can be made for mass extinctions on land coeval with the marine extinctions of the Late Devonian-land plant diversity increased into the Carboniferous, and the tetrapod fossil record is inadequate to identify any mass extinctions. A case can be made for coeval plant/tetrapod extinctions and the end-Guadalupian marine extinctions, so this may be the first coeval marine-nonmarine mass extinction. However, problems of timing and questions about the extent of the nonmarine late/end-Guadalupian extinctions indicate that further research is needed. There were no mass extinctions of land plants, insects or tetrapods across the Permo–Triassic boundary. The Late Triassic was a time of low origination and high extinction rates on land and in the seas; there was no single end-Triassic mass extinction in either realm. The end-Cretaceous provides the strongest case for coeval land–sea mass extinctions, but there is no mass extinction of land plants, evidence of insect extinction is based on assumption-laden analyses of proxies for insect diversity and the tetrapod extinction was very selective. So, whether the nonmarine extinction at the end of the Cretaceous was a mass extinction is worth questioning. Part of the inability to identify nonmarine mass extinctions stems from taphonomic megabiases due to the relatively poor quality and uneven sampling of the nonmarine fossil record. Extinction resistance and resilience of terrestrial organisms is also a likely factor in the dearth of nonmarine mass extinctions, and this merits further investigation.

Keywords: "Big Five" mass extinctions, extinction resistance and resiliency, marine, nonmarine, taphonomic megabias

Introduction

The idea that there were five mass extinctions (substantial drops in diversity) during the Phanerozoic was originally proposed by Raup and Sepkoski (1982). These are generally considered to have been mass extinctions of marine animals, though they are not strictly comparable to each other in terms of duration, complexity and magnitude (Stanley, 2016; Racki, 2020). Here, I focus on the so-called "Big Five" mass extinctions of marine animals (Late Ordovician, Late Devonian, end Permian, end Triassic and end Cretaceous) and on a possible sixth marine mass extinction at the end of the middle Permian (end Guadalupian) (Figure 1). The question that prompted this article was, simply, are there nonmarine mass extinctions coeval with these six marine mass extinctions?

To answer that question, I review the evidence for nonmarine mass extinctions coeval with the six major marine extinctions of the Phanerozoic (Figure 1). With the exception of the end-Cretaceous extinction, this review finds little evidence of nonmarine mass extinctions correlative with the marine extinctions. I conclude by attempting to explain this result, both in terms of megabiases of the nonmarine fossil record and factors extrinsic and intrinsic to the nonmarine biota that increased its extinction resistance and resilience.

Methods

In this article, nonmarine extinctions are evaluated primarily by examining the three large groups of terrestrial taxa—land plants, insects and tetrapod vertebrates—that have a fossil record sufficient to allow identification of mass extinctions, if they took place. The analysis presented here is a review of recent conclusions regarding nonmarine mass extinctions, including my own work on these topics. The conclusions offered are not all above controversy, and some of the potential disagreements are

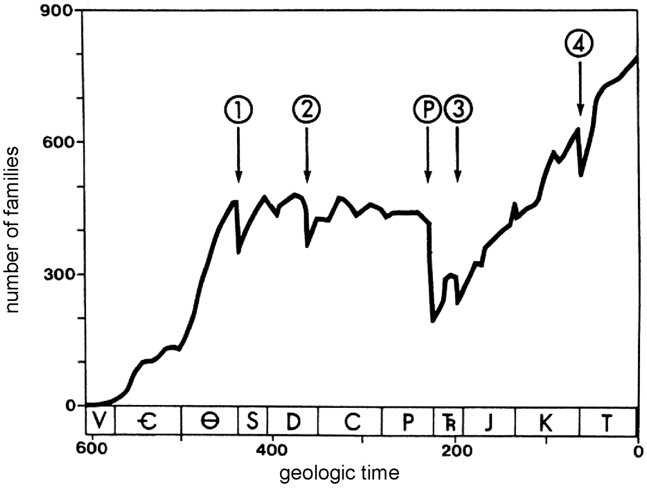

Figure 1. Marine family-level diversity curve of the last 600 million years (from Sepkoski, 1982). It shows the original five drops in diversity that have come to be known as the "Big Five" mass extinctions—Late Ordovician, Late Devonian, end Permian, end Triassic and end Cretaceous. A likely sixth marine mass extinction at the end of the middle Permian was identified later.

indicated where relevant. Although there are other putative marine and nonmarine mass extinctions that merit discussion, the focus here is on the six marine mass extinctions perceived to have been of the greatest magnitude, and possibly coeval nonmarine mass extinctions.

The literature on mass extinctions is vast. To simplify the bibliography, I primarily cite recent summaries of the six marine mass extinctions under consideration by Harper (2020), Aretz (2020), Chen and Shen (2020), Clapham (2020), Lucas (2020a) and Khosla and Lucas (2020). These articles, published in the second edition of Elsevier's *Encyclopedia of Geology*, contain many details and extensive bibliographies for readers seeking additional information.

Mass extinctions here are identified as drastic drops in diversity over relatively short intervals of geologic time (less than one million years). However, it is important to recognize that the magnitude of ecological disruption is also a measure of mass extinction (Droser *et al.*, 2000; McGhee *et al.*, 2004, 2012), so nonmarine mass extinctions are also discussed here in terms of ecological disruption.

Late Ordovician extinctions

Two substantial marine extinctions took place during the Late Ordovician, one at the beginning of the Hirnantian (last stage of the Ordovician) and the other late in the Hirnantian, at essentially the end of the Ordovician (Harper, 2020). These extinctions are correlated with an ice age in Gondwana, and are thought to have been driven largely by climate changes (Harper, 2020).

Life on land during the Late Ordovician was apparently neither extensive nor diverse. Claims of metazoans living on Ordovician landscapes based on trace fossil evidence are either questionable, or the traces are only found in marginal marine settings (Davies *et al.*, 2010; Minter *et al.*, 2016; Shillito and Davies, 2018). The spore record suggests an apparently cosmopolitan Late Ordovician bryophyte-like flora that continued into the Silurian (Cascales-Miñana, 2016; Cascales-Miñana *et al.*, 2018). Indeed, Cascales-Miñana *et al.* (2018, p. 224) concluded that during the Late Ordovician "plants were evidently undergoing a continuous and sustained diversification…."

The Late Ordovician precedes the "terrestrialization" of the global biota that took place during the Devonian–Carboniferous (Isozaki and Servais, 2017). It could thus be argued that the nonmarine fossil record of the Late Ordovician is too sparse to support definitive conclusions. Nevertheless, it does not identify a mass extinction(s) on land coeval with the Late Ordovician marine extinctions.

Late Devonian extinctions

Late Devonian marine mass extinctions are usually identified as two events, the earlier, end-Frasnian Kellwasser event (or crisis) and the later, end-Fammenian (= end Devonian) Hangenberg event/crisis (e.g., Kaiser *et al.*, 2015; Aretz, 2020). Causation of these extinctions is not agreed on.

Few have identified nonmarine mass extinctions associated with either the Kellwasser or Hangenberg crises. However, in recent reviews of the Late Devonian extinctions, Kaiser *et al.* (2015) and Aretz (2020) drew attention to the disappearance of *Archaeopteris* trees and of the miospore *Retispora lepidophyta* as evidence of a possible land-plant extinction of the Hangenberg event. They also claimed that the Hangenberg event was a bottleneck in vertebrate evolution, largely because of the extinction of the placoderm fishes, but they also suggested that there were substantial tetrapod extinctions on land at the end of the Fammenian. But, more detailed analyses (see below) do not identify mass extinctions of land plants or tetrapods during the Late Devonian.

McGhee *et al.* (2004) identified Late Devonian terrestrial extinctions as belonging to their lowest category of ecological disruption (IIb—ecosystems temporarily disrupted but recover and are not replaced post-extinction, but are re-established by new clades post-extinction). However, the lack of evidence of substantial Late Devonian terrestrial extinctions renders this categorization untenable.

Older analyses of Late Devonian land-plant diversity suggested the possibility of an end-Frasnian mass extinction (e.g., Knoll, 1986; Scheckler, 1986; Raymond and Metz, 1995). However, recent analyses do not identify any diversity crashes of land plants during the Late Devonian (Cascales-Miñana, 2016; Stephenson, 2017; Bond and Stephenson, 2019). Thus, for example, Cascales-Miñana (2016) reviewed the genus-level diversity of megafossil plants and spores to conclude that there were no Late Devonian mass extinctions of plants, but, instead, land-plant diversity increased into the Carboniferous. He concluded that "the effect of the two first 'Big Five' mass extinctions [Late Ordovician and Late Devonian] would therefore have been restricted to the marine realms" (Cascales-Miñana, 2016, p. 26).

The end Devonian thus saw increasing diversity and complexity as forests expanded to become the "Palaeophytic flora" that dominated Carboniferous landscapes (Cascales-Miñana *et al.*, 2018). However, the loss of *Archaeopteris* trees and the turnover of lycopsids across the Devonian–Carboniferous boundary may still be an ecologically important set of extinctions (DiMichele *et al.*, 2015), though not a diversity crash sufficient to qualify as a mass extinction.

No data support identification of Devonian tetrapod mass extinctions as part of the Late Devonian extinctions. McGhee (2013) argued for such tetrapod extinctions, based largely on the biostratigraphic compilation of the Devonian body-fossil record of tetrapods by Blieck *et al.* (2010). However, this compilation identified only three or four Frasnian tetrapod genera and eight or nine Fammenian genera, most of which are known from single localities based on one or a few specimens. Of course, the Devonian tetrapod body-fossil record has been augmented since the Blieck *et al.* (2010) compilation, but most of the new records continue to be of a single taxon from a single locality known from one or a few specimens (e.g. Clack and Milner, 2015; Olive *et al.*, 2016). Indeed, of the Devonian tetrapod-body-fossil taxa, only two are known from substantial numbers of specimens, *Ichthyostega* and *Acanthostega* (e.g. Marzola *et al.*, 2018).

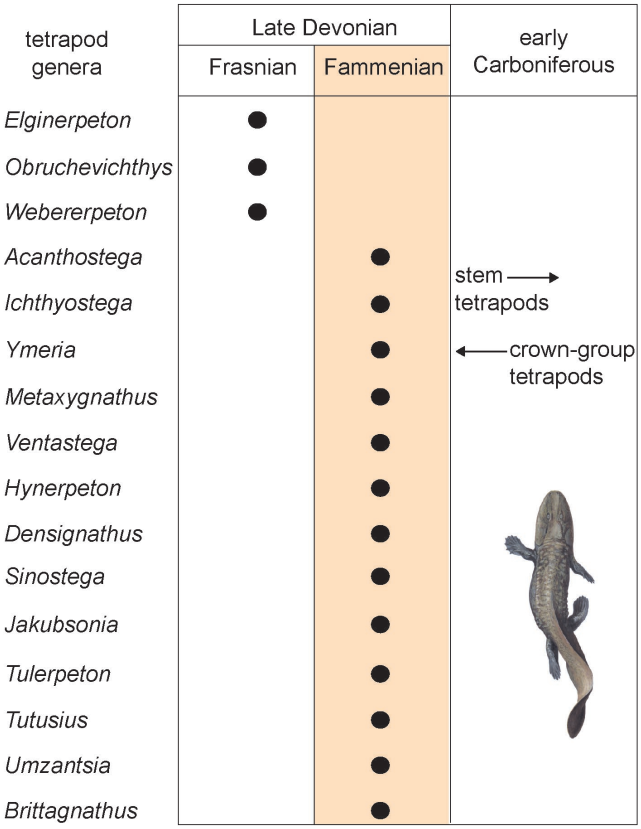

Figure 2. Geological ages of all Late Devonian tetrapod genera. Note that none of these genera have any stratigraphic range, as they are all known from one locality/area, most from a single or a few fossils. Restoration of *Acanthostega* by Frederik Spindler.

At present, there are 17 named genera of Devonian tetrapods (e.g. Clack and Milner, 2015; Olive *et al.*, 2016; Lucas, 2020b) (Figure 2). Those of Frasnian age are: (1) *Elginerpeton* from Elgin, Scotland, known primarily from its lower jaw; (2) *Obruchevichthys* from Latvia, also known from lower jaw fragments; and (3) jaw fragments named *Webererpeton* from Latvia. A greater diversity of Fammenian tetrapod genera is known: (1) *Acanthostega*, known from many specimens from Greenland; (2) *Ichthyostega*, also known from numerous specimens from Greenland; (3) *Ymeria* from Greenland, known from a skull and lower jaw; (5) *Metaxygnathus* from New South Wales, Australia, known from jaw fragments; (6) *Ventastega* from Latvia, known from an incomplete skull and lower jaw; (7) *Hynerpeton* from Clifton County, Pennsylvania, known from parts of the lower jaw and shoulder girdle; (8) *Densignathus*, known from jaw fragments, also from Clifton County, Pennsylvania; (9) *Sinostega*, based on a jaw fragment from Ningxia, China; (10) *Jakubsonia* from the Oryol region of Russia is known from a skull roof, jaw fragments and some postcrania; (11) *Tulerpeton* from Tula Province, Russia, known principally from the forelimb and hind limb bones; (12) *Tutusius*, known from a cleithrum from Waterloo Farm in South Africa; (13) also from Waterloo Farm, *Umzantsia*, known from a jaw fragment and some postcrania; and (14) *Brittagnathus* from Greenland, known from a jaw fragment. Other Devonian tetrapod records are known but are not of specimens deemed diagnostic of a genus or are awaiting full description and analysis, including fossils from the USA, Belgium, Latvia and Russia (Olive *et al.*, 2016).

The Devonian tetrapod body-fossil record is very limited in abundance and diversity (Figure 2). It lacks the stratigraphic density with which to evaluate Late Devonian diversity dynamics (Lucas, 2019, 2020b). The Devonian tetrapod footprint record is so sparse and disconnected from the body fossil record that it does not improve this situation (Lucas, 2015, 2019).

Coates *et al.* (2008) observed that any perception of an end-Devonian tetrapod extinction is largely an artifact of Romer's gap, a supposed paucity of early Carboniferous (Tournaisian) tetrapods. Sallan and Coates (2010), in their analysis of Late Devonian vertebrate extinctions, identified no dramatic Devonian tetrapod extinction events, but identified "Romer's gap" as part of a "post-extinction trough" after the Hangenberg event. However, "Romer's gap" is now known to be an artifact of sampling that is steadily being filled (e.g. Mansky and Lucas, 2013; Clack *et al.*, 2019). We now know of Tournaisian stem-tetrapod body fossils of acanthostegids, ichthyostegids and tulerpetontids (Anderson *et al.*, 2015) that indicate that stem tetrapods survived the end of the Devonian. Furthermore, recent discoveries and analyses have pushed back the radiation of typical Carboniferous tetrapods to the point where many groups must have had Devonian progenitors (e.g. Pardo *et al.*, 2017). Thus, the supposed turnover from stem tetrapods to more advanced tetrapods across the Devonian–Carboniferous boundary did not take place (Clack *et al.*, 2019). No case for Late Devonian tetrapod mass extinctions can be made based on current tetrapod body-fossil or footprint data.

Sallan and Galimberti (2015) claimed that there was a drop in tetrapod body size across the Devonian–Carboniferous boundary, a "Lilliput effect" of a Hangenberg event mass extinction. Their mean values of tetrapod body size suggest that Devonian tetrapods were about 100 cm long but only 70 cm long in the early Carboniferous. However, I see these mean values as misleading, as the largest early Carboniferous tetrapods were 250 cm long, larger than the largest Devonian tetrapods, which were 230 cm long according to their compilation (Sallan and Galimberti, 2015, table S1). The mean values simply skew the result by including some of the remarkably small and specialized early Carboniferous tetrapods, such as the aïstopods, which are not known from Devonian strata. Furthermore, tiny tetrapods (body length 25 cm) are now known from the Late Devonian (Ahlberg and Clack, 2020). There appears to have been no "Lilliput effect" on tetrapod body size across the Devonian–Carboniferous boundary.

End-Guadalupian extinction

Initial estimates of a drastic end-Permian mass extinction of marine organisms (e.g., Raup, 1979) combined the diversity drop of an earlier extinction, the end-Guadalupian (end Capitanian = end middle Permian) extinction, with the diversity drop of the end-Permian extinction, a result of the compiled correlation effect. Recognition of a separate end-Guadalupian marine extinction did not take place until the 1990s (Jin, 1991). Three different ideas about the end-Guadalupian marine extinctions are current: (1) a single mass extinction at the end of the Capitanian (e.g. Retallack *et al.*, 2006; Rampino and Shen, 2019); (2) a slightly older, within Capitanian mass extinction (e.g. Bond *et al.*, 2010); and (3) no mass extinction, but instead a steady diversity decline from the Wordian through the Changhsingian (e.g. Clapham *et al.*, 2009; Chen and Shen, 2020). There is a large igneous province (Emeishan) that erupted at the end of the Guadalupian (Huang *et al.*, 2016), and many of those who identify an end-Guadalupian marine mass extinction see it as the cause of the extinctions.

Retallack *et al.* (2006) argued for an end-Guadalupian extinction of land plants in Gondwana. And, studies in China identify a floral turnover close to the end-Guadalupian coeval with Emeishan volcanism (Bond *et al.*, 2010; Stevens *et al.*, 2011). In contrast, Cascales-Miñana and Cleal (2012, 2013) identified prolonged floral turnover beginning early in the Guadalupian (Roadian) and lasting through the end of the Permian, but no discrete land-plant extinction at the end of the Guadalupian. Thus, the case for a mass extinction of land plants at the end of the Guadalupian remains uncertain, especially because no major clades of land plants disappeared at that time.

At the end of the Guadalupian, there was an apparent, profound extinction of tetrapods, termed the dinocephalian extinction event by Lucas (2009). In the Karoo basin of South Africa, where it is best documented, the end-Guadalupian saw the total extinction of dinocephalians and substantial diversity drops in parareptiles, therocephalians and gorgonospians. The dinocephalians were the first significant evolutionary diversification of the therapsids, a group of carnivores and herbivores that included some very large and specialized forms. Younger, post-extinction tetrapod assemblages lack dinocephalians and are initially characterized in the Karoo basin by a low diversity assemblage numerically dominated (~ 85% of all specimens) by the dicynodont *Diictodon* (Smith *et al.*, 2012). Indeed, the dinocephalian extinction event set the stage for the takeover of much of the Permian tetrapod herbivore niche by dicynodonts, so it was an ecologically significant event.

Day *et al.* (2015), based on the Karoo basin record, estimated a loss of 74–80% of generic richness of tetrapods across the dinocephalian extinction event. In the Russian and Chinese sections, less extensive tetrapod records encompass assemblages with dinocephalians overlain by assemblages that lack dinocephalians, and support the idea that the dinocephalian extinction event was a global event (Lucas, 2009, 2017a). However, disagreement over the timing and magnitude of the Guadalupian marine extinctions, lack of compelling evidence of a mass extinction of land plants and a substantive tetrapod record of the dinocephalian extinction event largely confined to South Africa, render problematic the identification of coeval end-Guadalupian marine and nonmarine mass extinctions. More research is needed (and expected) here.

End-Permian extinction

The end-Permian marine extinction is seen as the most devastating marine extinction of the Phanerozoic, with estimates indicating the extinction of about 80–96% of marine species (Clapham, 2020). The consensus is that massive volcanism of the Siberian traps caused the extinctions, although the exact mechanism of this remains under discussion. On land, a mass extinction of tetrapod vertebrates has long been seen as an end-Permian event, although only a few have argued for a coeval mass extinction of land plants.

Global compilations of land plant diversity identify no substantial land plant extinction at the end of the Permian (e.g., McElwain and Punyasena, 2007; Nowak *et al.*, 2019). Analysis by Cascales-Miñana and Cleal (2012, 2013) identified two evolutionary turnovers in land plants during Permian time—through the Carboniferous-Permian boundary (Kasimovian–Asselian) and through the middle-late Permian (Roadian–Changhsingian), not a single mass extinction at any point during Permian time. These turnovers were characterized as having taken place over millions of years, and "in neither case were they discrete events" (Cascales-Miñana and Cleal, 2013, p. 196). Plant diversity dropped at the end of the Permian, but there was no mass extinction of land plants (Nowak *et al.*, 2019). Cascales-Miñana *et al.* (2015) identified a substantial extinction of land plants over several million years of Permian and Triassic time, and Cascales-Miñana *et al.* (2018) concluded that land plant evolution and extinctions across the Permo–Triassic boundary were prolonged and complex events (also see; Fielding *et al.*, 2019; Gastaldo, 2019; Nowak *et al.*, 2019).

Looy *et al.* (1999, 2001) argued that there was an end-Permian extinction of gymnosperm forests followed by an Early Triassic vegetation dominated by herbaceous lycopsids. However, Nowak *et al.* (2019) noted that Early Triassic gymnosperms are under-sampled, so this gives the appearance of a drop in gymnosperm diversity across the Permo–Triassic boundary. Furthermore, Hochuli *et al.* (2010, 2016) analyzed palynological records from Greenland and the Barents Sea to conclude that a substantial gymnosperm extinction took place during the Early Triassic, at the Induan–Olenekian boundary. They identify this extinction as an ecological crisis for land plants greater than what happened at or just before the end of the Permian (Hochuli *et al.*, 2016). This is consistent with the tetrapod fossil record, which shows a substantial extinction during the Early Triassic, at the boundary of the Lootsbergian and Nonesian land-vertebrate faunachrons, which is close to the Induan–Olenekian boundary (Lucas, 2009, 2017a, 2018a).

The fossil record of insects is heavily biased by both major gaps and Lagerstätten and is not extensive enough to speak to many possible extinctions. It identifies a Late Pennsylvanian drop in insect diversity as well as a diversity drop from the middle Permian to the Early Triassic, followed by the diversification of numerous groups of modern insects (Labandeira and Sepkoski, 1993; Labandeira, 2005; Condamine *et al.*, 2016). Thus, the Permo-Triassic boundary interval is a bottleneck in insect evolution, and it divides the archaic Paleozoic insects from the diversification of modern insects. Nevertheless, the insect fossil record lacks the stratigraphic density necessary to evaluate the precise timing of extinctions during the middle Permian–Early Triassic.

A mass extinction of tetrapods at the Permo–Triassic boundary has long been widely accepted, at least as far back as Colbert (1965). Relatively recent detailed studies in the Karoo basin of South Africa (the best tetrapod fossil record across the Permo–Triassic boundary) by MacLeod *et al.* (2000), Ward *et al.* (2000, 2005), Smith and Ward (2001) and Retallack *et al.* (2003) identified a mass extinction of tetrapods and correlated that extinction closely to the end-Permian marine mass extinction using carbon isotope stratigraphy and magnetostratigraphy. A similar scenario has been posited for the much less extensive tetrapod record in the Russian nonmarine section across the Permo–Triassic boundary (Benton *et al.*, 2004; Newell *et al.*, 2010).

Nevertheless, these conclusions have been disputed and (I conclude) refuted (Tabor *et al.*, 2007; Gastaldo *et al.*, 2009, 2015, 2019a, b, 2020; Lucas, 2009, 2017a; Neveling *et al.*, 2016a, b). What stands out are these conclusions: (1) the position of the Permo–Triassic boundary in the Karoo section is stratigraphically much higher than its long assumed position at (or near) the base of the *Lystosaurus* assemblage zone (Figure 3); (2) the actual stratigraphic ranges of Karoo tetrapods indicate a relatively prolonged and stepwise tetrapod extinction during the late Permian; (3) the amount of generic turnover of the supposed end-Permian tetrapod mass extinction is the loss of about 10 genera, which is comparable to generic turnover at land-vertebrate faunachron boundaries throughout the Permian; (4) the number of clade extinctions across the Permo–Triassic boundary is few; (5) the ecological severity of the tetrapod extinctions has been greatly over-

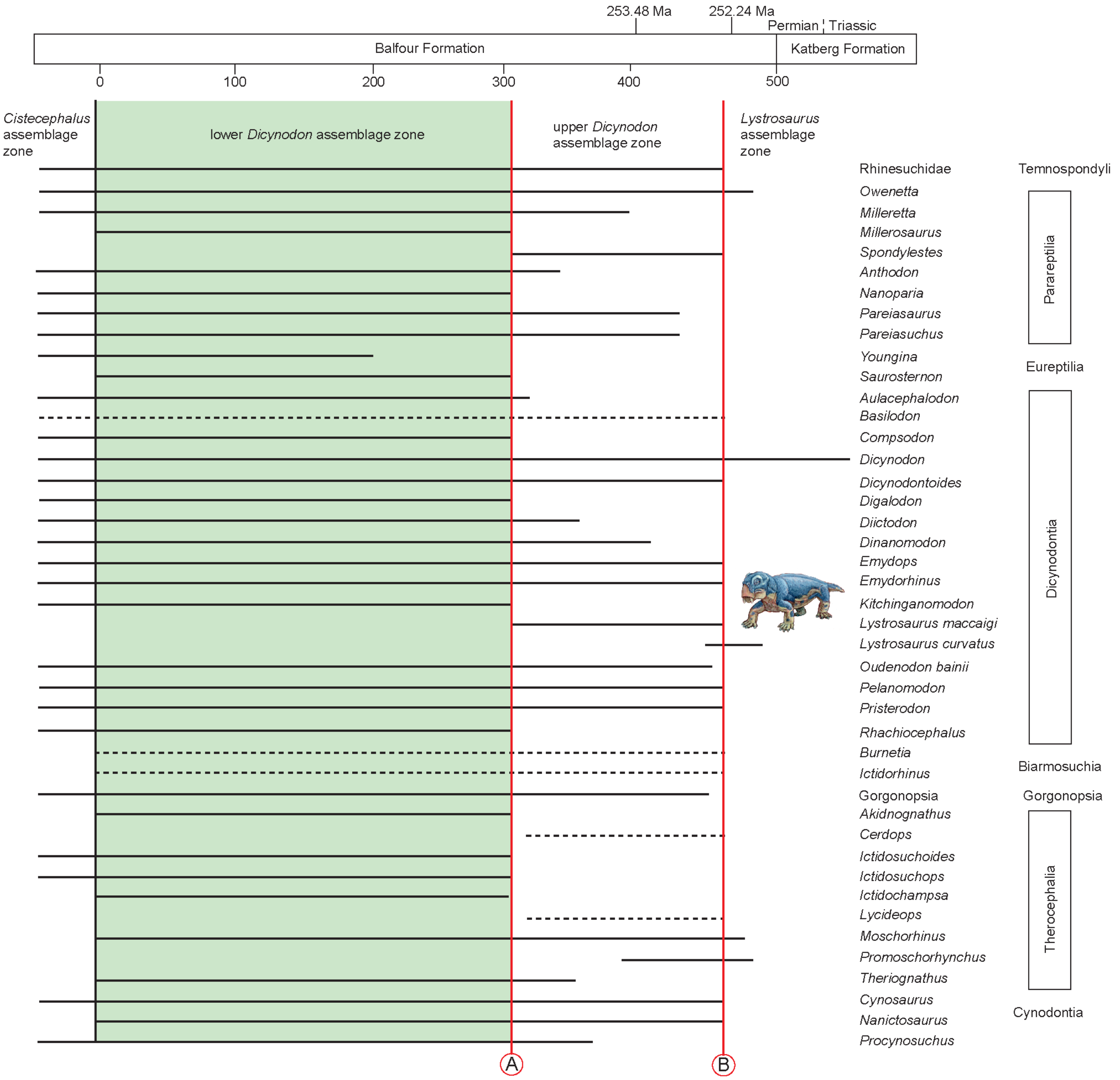

Figure 3. Stratigraphic ranges of tetrapod genera in the *Dicynodon* assemblage zone of the Karoo basin in South Africa. Note that these ranges identify two extinction events, A and B. B has generally been identified as the end-Permian mass extinction of tetrapods, even though it encompasses the extinction of very few genera and is a latest Permian datum. Modified from Viglietti *et al.* (2016) and Lucas (2017a). Restoration of *Lystrosaurus* by Matt Celeskey.

stated; and (6) the post-extinction tetrapod assemblages are not very different from the pre-extinction assemblages (Lucas, 2017a).

An important point is that different estimates indicate that there are 1131 to 4772 living reptile genera, and these numbers are minima, as there are still extant taxa that await description (Mora *et al.*, 2011; Pincheira-Donoso *et al.*, 2013; Rees *et al.*, 2020). It is impossible to say how many genera of reptiles lived during the late Permian, but the extinction of about 10 genera at that time surely is a miniscule portion of the then-extant diversity, even if late Permian reptile diversity was only half of extant reptile diversity.

McGhee *et al.* (2004) judged what they regarded as an end-Permian mass extinction on land to be a category I extinction, just like the marine extinction. Thus, they concluded that existing ecosystems collapsed and were replaced by new ecosystems post extinction, on land and in the sea. However, as Lucas (2009, 2017a) concluded, the terrestrial extinctions across the Permo–Triassic boundary are no greater than category IIb in the McGhee *et al.* scale—the pre-extinction ecosystem was disrupted temporarily but was reorganized post-extinction by the same and new clades.

Gastaldo *et al.* (2020) recently reported a high precision CA-ID-TIMS U/Pb age of 252.24 ± 0.11 Ma on an airfall ash just above the base of the *Lystrosaurus* assemblage zone in the Karoo basin (Figure 3). This predates the numerical age of the Permo–Triassic boundary of 251.9 Ma by about 300,000 years and indicates that the base of the *Lystrosaurus* assemblage zone in the Karoo basin is of late Permian age. Clearly, the lowest occurrence of *Lystrosaurus* and the highest occurrence of *Dicynodon* in the Karoo basin, biostratigraphic datums used previously to identify the Permo–Triassic boundary, are older than that boundary (Figure 3). These observations plus other age constraints place the boundary in the Katberg Formation, well above the lowest occurrence of *Lystrosaurus*, as argued by Gastaldo *et al.* (2015, 2019a, b, 2020; also see Lucas, 2020c), where there is no turnover of tetrapods. Thus, the turnover of about 10 tetrapod genera in the Karoo section, long considered the end-Permian mass extinction of tetrapods, is older than the end-Permian marine extinction. No reliable data identify a nonmarine mass extinction at the end of the Permian.

End-Triassic extinctions

An end-Triassic mass extinction continues to be cited as one of the "Big Five" mass extinctions of the Phanerozoic. However, many taxonomic groups claimed to have suffered catastrophic extinction at the end of the Triassic, such as ammonoids, marine bivalves, conodonts and tetrapod vertebrates, experienced multiple extinctions throughout the Late Triassic, not a single mass extinction at the end of the Period (e.g. Lucas and Tanner, 2018; Lucas, 2020a; Rigo *et al.*, 2020) (Figure 4). Many other groups were relatively unaffected, whereas some other groups, such as reef communities, were subject to only regional effects. Indeed, the lack of evidence of a collapse of trophic networks in the sea and on land makes the case for an end-Triassic mass extinction untenable (Lucas and Tanner, 2018). Still, marked evolutionary turnover of radiolarians and ammonoids did occur across the Triassic–Jurassic boundary. The end of the Triassic encompassed temporary disruptions of the marine and terrestrial ecosystems, driven by the environmental effects of the eruption of the flood basalts of the Circum-Atlantic Magmatic Province (CAMP), through outgassing in particular, but these disruptions did not produce a global mass extinction (Lucas and Tanner, 2018; Lucas, 2020a).

Land plants, both palynomorphs and megaflora, as well as charophytes, show no significant extinction across the Triassic-Jurassic boundary (e.g. Barbacka *et al.*, 2017; Lucas and Tanner, 2007, 2015, 2018; Lucas, 2018c, 2020a; Kustatscher *et al.*, 2018), though there are diversity crashes of local and regional extent. There is no evidence of insect extinctions across the Triassic–Jurassic boundary, but the record of nonmarine tetrapods does indicate some turnover. Thus, most of the large temnospondyl amphibians were extinct by the end of the Norian. Among reptiles, three groups of herbivores that were significant components of Middle Triassic–Carnian tetrapod communities, the rhynchosaurs, dicynodonts and traversodontid cynodonts, became extinct late in the Norian (Lucas, 2018b; Racki and Lucas, 2018; Rigo *et al.*, 2020) (Figure 4).

The classic concept of a tetrapod extinction at the Triassic-Jurassic boundary was largely predicated on the disappearance of the "thecodonts," subsequently referred to as the crurotarsans and more specifically (during the Late Triassic) encompassing the rauisuchians, aetosaurs and phytosaurs. Rauisuchians became extinct during the late Norian, aetosaurs were of low diversity after the Norian–Rhaetian boundary and became extinct during the Rhaetian or at the Triassic–Jurassic boundary, and phytosaur diversity crashed across the Norian–Rhaetian boundary, although they apparently survived at low diversity across the Triassic–Jurassic boundary (Maisch and Kapitzke, 2010; Lucas and Heckert, 2011; Lucas and Tanner, 2015; Lucas, 2018b) (Figure 4). Therefore, some turnover took place in the terrestrial tetrapods as parts of a stepwise extinction across the Triassic–Jurassic boundary that presaged the dinosaur-dominated terrestrial communities of the Jurassic–Cretaceous (Lucas, 2018b). There was no nonmarine mass extinction at the end of the Triassic.

Nevertheless, McGhee *et al.* (2004) regarded the end-Triassic "mass extinction" on land as a category I or IIa extinction. Thus, they concluded that either ecosystems on land collapsed and were replaced post extinction by new ecosystems (category I) or that there was a permanent loss of some ecosystem components, but that the disrupted ecosystems were disrupted and recovered (but were not replaced) post extinction (category IIa). However, Lucas and Tanner (2018) concluded that the disruption of terrestrial ecosystems across the Triassic–Jurassic boundary was not severe, and that at most this disruption is category IIb on the McGhee *et al.* scale.

End-Cretaceous extinction

The end-Cretaceous extinction is the most famous of the "Big Five" mass extinctions because of the extinc-

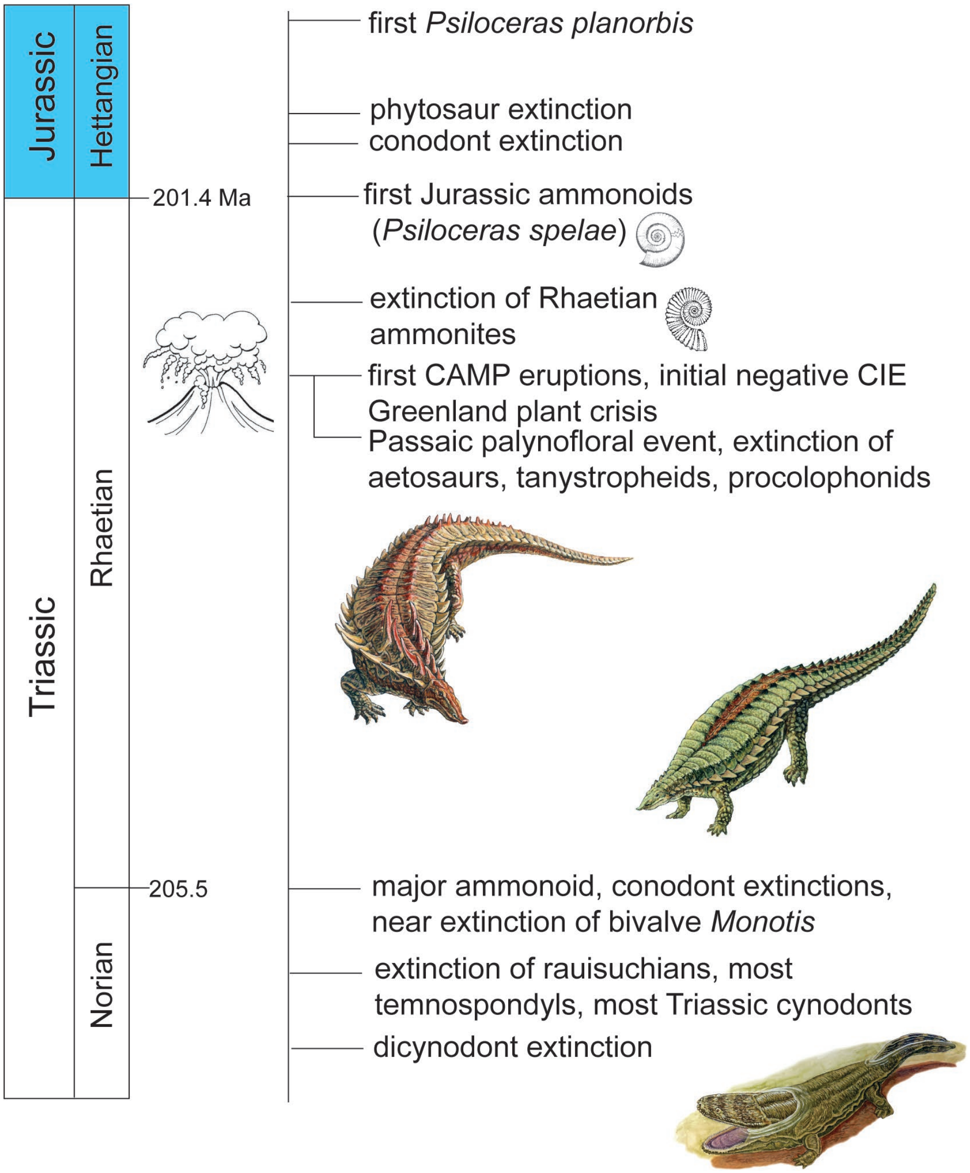

Figure 4. Some major biotic events across the Triassic–Jurassic boundary. Restorations of metoposaur and aetosaurs by Matt Celeskey.

tion of the (non-avian) dinosaurs. This extinction is correlated with the impact of an extraterrestrial body (Figure 5) and the massive eruptions of the Deccan large igneous province. Current thinking by many researchers is that extensive Deccan outgassing, atmospheric warming and oceanic acidification during the latest Maastrichtian likely provided the foundation for the mass extinction, which was culminated by the impact (Khosla and Lucas, 2020).

In the marine realm, many elements of the plankton, rudist bivalves, some sharks, marine reptiles (principally the mosasaurs) and ammonoids suffered major extinctions, notably the final disappearance of the ammonoids. On land the extinction was very selective and eliminated most of the large-bodied taxa, notably the non-avian dinosaurs and pterosaurs, as well as certain freshwater sharks, lizards and marsupial mammals (Archibald and MacLeod, 2013; but see Longrich *et al.*, 2016 for a different view of the mammal extinctions).

Most paleobotanists (exceptions include Nicholls and Johnson, 2008; Stiles *et al.*, 2020) have viewed the end-Cretaceous extinctions as an event that did not involve a mass extinction of land plants, but instead a short-lived perturbation of the terrestrial vegetation. Cascales-

Figure 5. A unique aspect of the end-Cretaceous mass extinction is that the impact of an extraterrestrial body was an evident cause. An iridium-rich clay layer documents the impact, and in the photograph is the light-colored clay layer that crosses the bottom of the rubber-covered portion of the hammer handle (hammer is 28 cm long). This outcrop is a nonmarine occurrence of the clay layer in the Raton basin of New Mexico, USA.

Miñana *et al.* (2018) thus concluded that there was an extensive die-off of land plants across the Cretaceous–Paleogene boundary, but that this was short lived, and the vegetation recovered in a matter of decades (in ecological time). In other words, there was a disruption of the flora, but no mass extinction (e.g., Tschudy and Tschudy, 1986; Traverse, 1988). No major plant clades became extinct at the end of the Cretaceous.

Global diversity data do not identify a mass extinction of insects at the end of the Cretaceous (Labandeira and Sepkoski, 1993; Labandeira, 2005; Condamine *et al.*, 2016). Nevertheless, Labandeira *et al.* (2002a, b) used the amount of insect damage of angiosperm leaves as a proxy for insect diversity across the Cretaceous–Paleogene boundary. Their studies in North America suggested a sharp drop in insect diversity across the Cretaceous–Paleogene boundary, and another study of insect damage on fossil leaves in Argentina also inferred an end-Cretaceous drop in insect diversity but one followed by a faster recovery than indicated by the North American data (Donovan *et al.*, 2016). Note, though, that this proxy only applies to herbivorous insect diversity and that ecological and taphonomic factors unrelated to diversity can impact the intensity of insect herbivory on leaves. Therefore, whether or not this proxy identifies an insect extinction is open to question.

Dinosaur extinction at the end of the Cretaceous has been viewed as either abrupt (e.g. Fastovsky and Sheehan, 2005; LeLoeuff, 2012; Brusatte *et al.*, 2015) or the final extinction of a group in which diversity was collapsing for millions of years (e.g., Archibald and MacLeod, 2013; Sakamoto *et al.*, 2016). One of the most complete known records of dinosaur extinction is in the Hell Creek Formation of southwestern North Dakota and northwestern South Dakota (Pearson *et al.*, 2002). Here, 46 genera/species of tetrapods, including 14 dinosaurs, are present in the upper part of the Hell Creek Formation and disappear in less than 10 meters of stratigraphic section. However, today the total number of tetrapod genera is on the order of 30,000 (Rees *et al.*, 2020), so is 46 a sufficient number of Late Cretaceous genera to identify a mass extinction of tetrapods?

LeLoeuff (2012) counted 104 described species of late Maastrichtian dinosaurs based on 2010 data. He then used species-area relationships to estimate an actual number of dinosaur species in the range of 628 to 1078 were alive toward the end of the Cretaceous and experienced abrupt elimination at the end-Cretaceous extinction. This analysis, however, is assumption laden, particularly regarding the degree of endemism of dinosaur species, a topic of considerable debate (e.g., Lucas *et al.*, 2016).

McGhee *et al.* (2004) identified an end-Cretaceous mass extinction on land as a category I extinction, meaning that existing ecoystems collapsed and were replaced by new ecosystems post extinction. Given that the vegetation was perturbed in ecological time, and returned quickly, a category I assignment is not merited. Nevertheless, dinosaur extinction was a significant ecological event, as it eliminated almost all of the large-bodied tetrapods on land.

The end of the Cretaceous presents the best case for coeval marine and nonmarine mass extinctions. Yet, as discussed, there are caveats to determining the magnitude and extent of the end-Cretaceous nonmarine extinctions that leave open to question whether the end Cretaceous nonmarine extinctions really amounted to a mass extinction.

Discussion

The previous analysis concludes that there is scant evidence of nonmarine mass extinctions coeval with the six perceived marine mass extinctions of the Phanerozoic. This conclusion has not been accepted or evaluated by most workers, who readily identify coeval mass extinctions in the marine and nonmarine realms at the end of the Permian, Triassic and Cretaceous, and some who advocate nonmarine mass extinctions at the end of the Devonian. The new and controversial conclusion advocated here is that there is a lack of evidence of nonmarine mass extinctions coeval with marine mass extinctions. It raises a new question, namely, why were there so few (or no) nonmarine mass extinctions? I do not know the answer to this question, but I can point to facets of possible explanations that merit further investigation.

Taphonomic megabiases

Behrensmeyer *et al.* (2000) used the term "megabias" to refer to large scale variations in the quality of the fossil record. A simple megabias relevant here is the lower quality (in terms of abundance, completeness and stratigraphic resolution) of the nonmarine fossil record when compared to the marine fossil record (e.g. Arens, 2013). Indeed, it could be argued that the apparent absence of nonmarine mass extinctions is an artifact of an incomplete fossil record (a "preservational taphonomic megabias" of Behrensmeyer *et al.*, 2000). No doubt, this is a factor in the inability to identify nonmarine mass extinctions.

Nevertheless, this conclusion, based as it is on an absence of data, is difficult to evaluate. It is important to note that increasing nonmarine fossil data have generally diminished the case for nonmarine mass extinctions and not increased it (see above). Thus, added data suggest that despite a preservational taphonomic megabias, the underlying failure to identify at least some nonmarine mass extinctions may be an accurate reading of the fossil record.

Another taphonomic bias in the fossil record, marine and nonmarine, is sampling. Clearly, the spatial and temporal aspects of sampling, as well as sampling intensity, have a direct relationship to the diversity of taxa (e.g. Longrich *et al.*, 2016; Close *et al.*, 2020). For example, the Karoo basin nonmarine section across the Permo–Triassic boundary has been intensively sampled, and it has a tetrapod record across that boundary that dwarfs other records (e.g. Lucas, 2009, 2017a). However, it is a very spatially limited record with which to judge a global extinction. And, comparable records, such as the Russian section, provide sampling at a temporal level of resolution much less than the Karoo record. Therefore, evaluation of tetrapod extinctions at the end of the Permian is very heavily influenced by both spatial and temporal limitations on the samples available.

Similar problems of spatial and temporal sampling also affect analysis of the other nonmarine extinctions, particularly the end-Cretaceous extinction. This is because for most of the putative nonmarine mass extinctions, the best sections (*sensu* Lucas, 2017b) are one or a few, and the temporal resolution of the data is very variable between different sections. Clearly, a sampling megabias is an important aspect of the nonmarine fossil record that affects the ability to identify a mass extinction.

Extinction selectivity, resistance and resilience

All mass extinctions are selective, and an extensive literature exists on extinction selectivity (e.g. Kitchell *et al.*, 1986; McKinney, 1987, 1997; Jablonski, 1989; Jablonski and Raup, 1995; Payne and Finnegan, 2007; Peters, 2008; Clapham and Payne, 2011; Harnik *et al.*, 2012; Dunhill and Wills, 2015; Payne *et al.*, 2016a, b; Donaldson *et al.*, 2019; Bush *et al.*, 2020). My reading of this literature indicates there is little agreement on what factors, extrinsic and intrinsic, create extinction resistance and/or resilience in some taxa. For example, some workers assert that rarity is associated with a high risk of extinction. But, Vermeij and Grosberg (2018) argue that rare species may have individual traits (for example, of reproductive biology and behavior) that make their populations more resistant to extinction.

The literature on extinction selectivity mostly focuses on marine organisms in terms of their extinction resistance and resilience. Few studies focus on extinction selectivity in nonmarine organisms (Robertson *et al.*, 2004 and Dunhill and Wills, 2015 are exceptions). McGowan (2013) compared nonmarine and marine mass extinctions and concluded that nonmarine organisms should be more susceptible to extinction, largely because there are more rare species on land than in the sea.

The dearth of nonmarine mass extinctions coeval with marine mass extinctions is extinction selectivity on a large scale. In other words, whatever caused the marine mass extinctions did not cause coeval nonmarine mass extinctions. This is particularly evident when examining the record of land plants.

Thus, Traverse (1988) drew attention to the fact that major changes in land plants are not coeval with the erathem boundaries of the Phanerozoic, relying on the concept of Paleophytic, Mesophytic and Cenophytic eras as marking major transitions in the global vegetation. These concepts, originally intended to be chronostratigraphic units on a par with Paleozoic, Mesozoic and Cenozoic, actually refer to biomes that tracked climate and changed in a complex, prolonged and time transgressive manner (DiMichele *et al.*, 2008; Cleal and Cascales-Miñana, 2014). At this scale, there were no abrupt changes (mass extinctions) of the global flora. As Traverse (1988, p. 277) concluded, "floral transformations have been due to gradual replacement and piecemeal, not mass extinction."

Traverse (1988) explained the disconnect between plant and animal extinctions as due to extrinsic and intrinsic factors that confer to plants more extinction resistance and resilience. These reflect basic differences between plant and animal biology. They include that land plants have minimal physicochemical requirements, and that their genetics, hybridity, polyploidy and some ontogenetic processes contribute to flexibility and survivability. Plants also have the ability to survive despite great reduc-

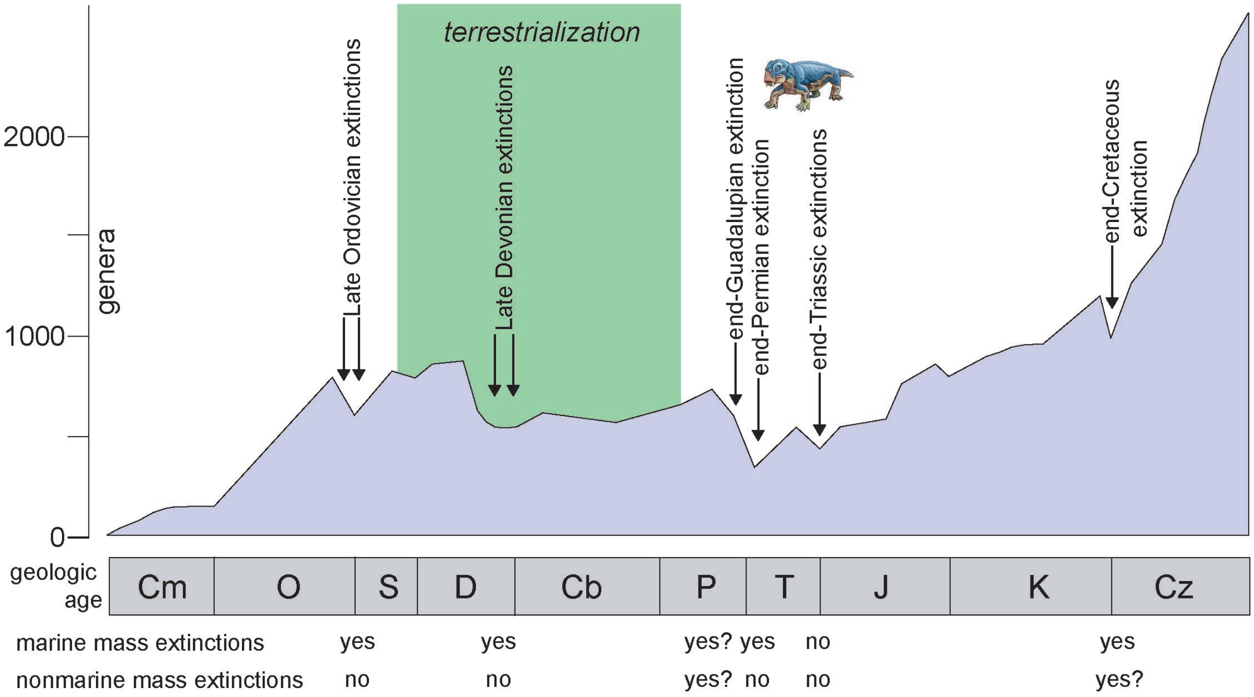

Figure 6. Phanerozoic generic diversity of marine organisms indicates important interval of middle-late Paleozoic terrestrialization and the marine and nonmarine mass extinctions and non-extinctions indicated. Based on and modified from Isozaki and Servais (2017, fig. 1). Restoration of *Lystrosaurus* by Matt Celeskey.

tions in population size, the potential dormancy and persistence of their propagules, the capacity to recover from trauma, indeterminate growth and the potential for broad deployment and migration. According to Traverse (1988), these differences from animals explain why plants do not respond to environmental crisis in the same way as do animals.

But, what about land animals? Do they respond differently to stress/crisis than do marine animals? I suspect they do, and that there are thus both extrinsic and intrinsic factors that confer greater extinction resistance and resilience to land animals than to marine animals.

Grosberg *et al.* (2012) drew attention to physical differences between marine and nonmarine settings, in part to explain the disparity in diversity in the seas and on land. These include differences between water and air in terms of density, viscosity, oxygen and CO_2 concentration, and diffusibility of gases, among others. These factors may be extrinsic factors affecting extinction resistance and resiliency.

Thus, for example, it requires much less energy for an animal to move through air than through water. This means that fleeing from an unfavorable situation (volcanism?) is much easier for animals on land than it is in the water. Furthermore, many land animals can readily burrow or otherwise take shelter to escape an environmental stressor. Note, for example that Robertson *et al.* (2004) argued that tetrapods who could shelter underground or beneath the water selectively survived the perceived effects of the end-Cretaceous impact of an extraterrestrial body. Thus, the abilities to flee more easily in the air than in the water and to shelter may explain (at least in part) why many nonmarine animals have greater extinction resistance and resilience than do many marine animals.

Different degrees of extinction resistance and resiliency of animals that live on land and in the sea may be the primary reason why there are so few nonmarine mass extinctions. This is a large subject that merits further investigation.

What could cause a nonmarine mass extinction?

Most workers have concluded that marine mass extinctions were caused by massive flood-basalt volcanism of large igneous provinces and/or the impacts of extraterrestrial bodies and associated extreme environmental conditions of climate or ocean dysoxia (e.g. Wignall, 2001; Keller, 2003; Rampino *et al.*, 2019). However, other causes, including cosmological events, are also under consideration (Isozaki, 2019).

Of course, coeval mass extinctions on land and sea may indicate a different cause than a mass extinction just in the sea or one just on land. Clearly, whatever caused the marine mass extinctions of the Late Ordovician, Late Devonian and end Permian was not sufficient to cause a coeval nonmarine extinction. The exception may be the end Cretaceous, when massive volcanism and the impact of an extraterrestrial body is what it took to force a nonmarine mass extinction. Massive eruption of a large igneous province, alone, may not be enough to cause a mass extinction on land.

It is well understood that terrestrial communities have a trophic structure based on primary consumers, the land plants. A collapse of the trophic structure on land could cause a mass extinction, but the lack of mass extinctions of land plants makes such collapse unlikely. However, in the case of the end-Cretaceous extinctions, a relatively short-lived die off of the land plants may have sufficed to cause the trophic structure to collapse, with the plants rebounding after the collapse had caused numerous animal extinctions.

Conclusions

There is no compelling evidence that identifies nonmarine mass extinctions coeval with what are generally perceived of as the six most substantial marine mass extinctions of the Phanerozoic (Late Ordovician, Late Devonian, end-Guadalupian, end-Permian, end-Triassic and end-Cretaceous extinctions) other than (perhaps) for the end-Cretaceous extinction (Figure 6). Nevertheless, there was significant though transient disruption of the terrestrial ecosystems coeval with some of these extinctions. Part of the inability to identify nonmarine mass extinctions may stem from the relatively poor quality of the nonmarine fossil record and the spatial and temporal unevenness of sampling, two taphonomic megabiases. The possibility of greater extinction resistance and resilience of nonmarine organisms may also be a factor in the dearth of nonmarine mass extinctions, and merits further investigation.

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