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Invited Review

Mapping paleocoastlines and continental flooding during the Phanerozoic

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ABSTRACT

Sea levels shape the face of the Earth, define processes of sedimentation, and influence the evolution of life via the distribution of habitats. Ancient topographies can be reconstructed using the history and understanding of tectonic processes, lithological evidence, and present-day topographies. Paleogeographic reconstructions must accommodate ever newer sources of geological data, so we can refine and improve our model of ancient topography and bathymetry. Here, we assess the accuracy of a set of Phanerozoic digital paleogeographic maps by testing the proposed distribution of flooded shallow seas and land using fossil occurrence data from the Paleobiology Database. After noting a moderate match, we modified the positions of the coastlines and continental margins of these topographic models to reflect times of maximum transgression. Using the updated paleogeographic maps, we outline the changes of land and shallow marine areas over time and suggest ways they can be used for further investigations of our planet's history.

1. Introduction

Changing sea level is one of the great themes of Earth History. The advance and retreat of the seas are the result of fundamental tectonic and paleoclimatic processes. The level of the sea at any instant in time is the result of the combined effects of plate tectonics, mantle dynamics, isostatic loading, and the slow evolution of the Earth's climate from hothouse to icehouse conditions. Local evidence of sea level change is a combination of regional (e.g. tectonic uplift) and global or "eustatic" effects (e.g., the waxing and waning of icecaps; Miller et al., 2005).

Estimating the spatial extent of continental flooding (Ronov, 1994; Sloss, 1963) over time is a key component in understanding the evolution of the biosphere. Biodiversity is expected to be directly correlated with habitat availability, both on land and in the sea. Sea level changes have been invoked as a primary control of marine biodiversity over time (Flessa and Sepkoski, 1978). As eustatic sea level increases, a larger area of the continental interior is flooded, providing additional space for marine organisms to inhabit, which in turn increases global diversity. Continental flooding was also suggested to play an important role in phytoplankton evolution (Miller et al., 2005). Observed patterns of past diversity are influenced by the distribution of fossil localities, which in turn is controlled by the degree of continental flooding (Close et al., 2020; Peters and Foote, 2001).

1.1. Previous reconstructions of shallow seas and land area

Geologists have been mapping the changing extent of land and sea for more than 200 years (Smith, 1815). One of the earliest works, Schuchert's (1910, 1955) atlas the "Paleogeography of North America", was illustrated by 50 maps describing the flooding of North America by vast epeiric seas from the Cambrian to the Pliocene. State-of-the-art paleogeographic (paleocoastline) reconstructions follow and incorporate key sources, including the work of Bozhko and Khain, 1987; Cook (1990); Cook and Bally, 1975; Cope et al. (1992); (Dercourt et al., 1985, 1993, 2000); Golonka (2000); Kazmin and Natapov (1998); Mallory (1972); McCrossan et al. (1964); (Ronov et al., 1984, 1989); Scotese (2004, 2009); Scotese, 2016); Scotese et al., (1979), Scotese and Wright (2018); Stampfli, (2000); Stampfli and Borel, (2002); Veevers, 1984, 2000; Vinogradov et al. (1967, 1968a, 1968b, 1969), Wang (1985), Ziegler et al. (1977, 1979, 1983, 1985, 1997); Ziegler (1982, 1988, 1989, 1990); Zonenshain et al. (1990). The maps produced by these paleogeographers are based on surface outcrops and sometimes extensive well data.

1.2. Digital elevation models of paleotopography and paleobathymetry

Reconstructions of deep-time topography (Scotese, 2002) are based

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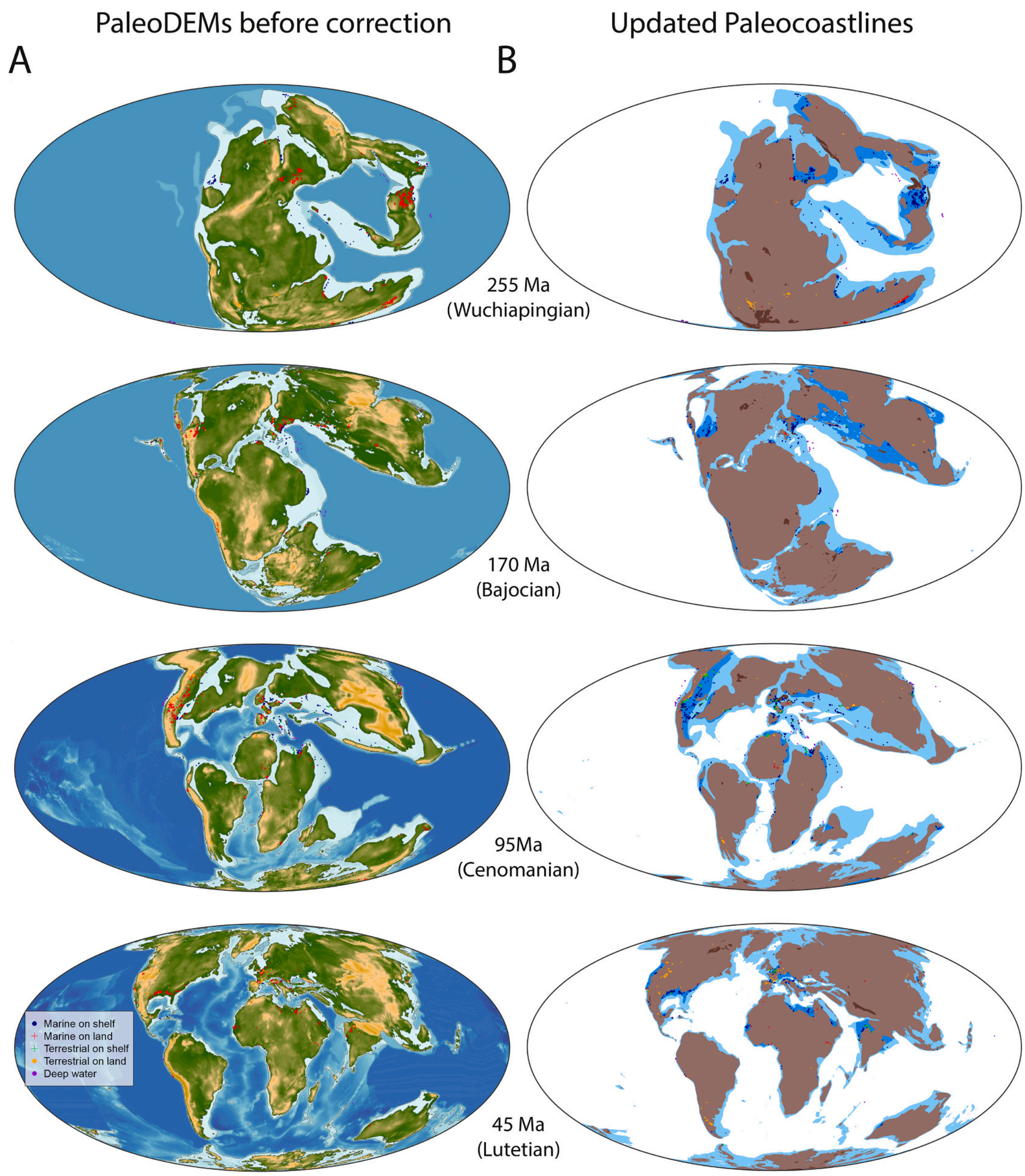

Fig. 1. Positions of fossil localities from the PBDB on selected paleogeographic reconstructions, A. The topographic models of the original PaleoDEMs, B. updated shapes to reflect maximum transgression. Marine collections that fall on flooded continental areas are marked with dark blue dots, those that incorrectly fall on land areas are marked with red plus signs. Terrestrial collections falling on flooded areas are indicated with green plus signs, those correctly falling on land are designated with orange dots. Flooded continental areas are indicated with light blue, terrestrial areas are colored brown. Dark blue and dark brown indicate areas changed to marine and terrestrial, respectively. The maps are plotted using Mollweide projection, the complete set is isavailable as Supplementary Figs. S1-5 (panel A) and S6-10 (panel B).

on digital topographic and bathymetric data sets of the modern world (Jakobsson et al., 2004; Lythe and Vaughan, 2000; Smith and Sandwell, 1997), which are rotated back to their paleopositions using the global plate tectonic model of the PALEOMAP Project (Scotese, 2016). The resulting map is a reconstruction of present-day bathymetry and topography in a paleolatitudinal and paleolongitudinal framework, which was then corrected (Scotese, 2002) based on the gradual emergence and disappearance of tectonic features, as well as using lithofacies and paleoenvironmental information. In the case of flooded shelf distribution, the broad-scale sedimentary environment indicated by lithological evidence hints at the water depth and the proximity to the coast. The result of this process is a set of digital elevation models (PaleoDEMs; Scotese and Wright, 2018) that contain topographic information characteristic of a given time interval.

1.3. Goals of the study

Reconstruction of past geography must include as much information as possible and should be validated with all available data, including the spatial stratigraphic distribution of fossils. Although the lithology-based reconstructions implicitly include information derived from the distribution of fossils, the explicit predictions made by fossil occurrences regarding paleoenvironmental settings cannot be directly evaluated using lithologic data, alone. Fossil data can be used independently to test the accuracy of the paleogeographic reconstructions in terms of predicted depositional environment for any geological interval. Earlier, Cao et al. (2017) used an older version of the Paleobiology Database (PBDB) to update a set of 24 paleogeographic maps of another reconstruction set (Golonka, 2009) that extended back to the early Devonian. In this study

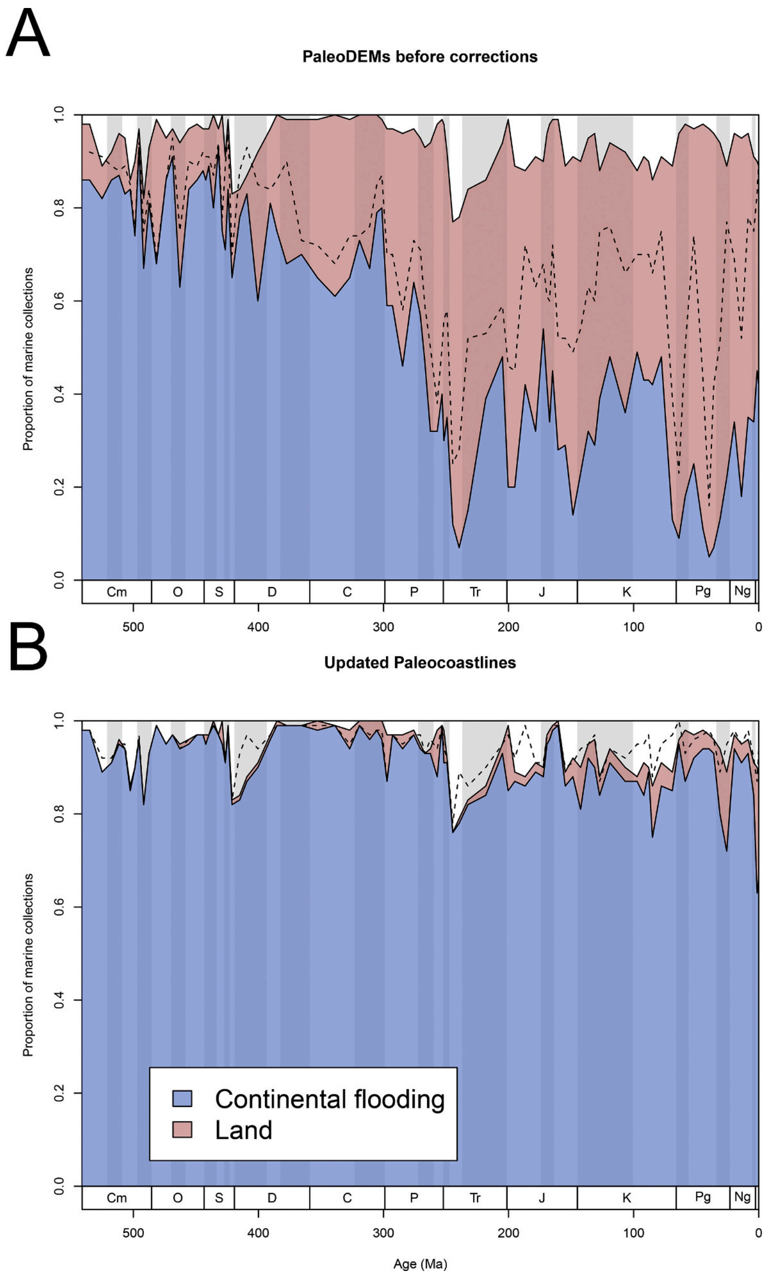

Fig. 2. The proportion of marine collections of the PBDB that fall on flooded continental areas (blue) or landmass (red) for the original coastlines of the PaleoDEMs (A) and the updated paleocoastlines (B). Note the marked increase of correctly positioned proportion of collections. Collections that fall in deep-water are reflected by the unshaded area. Dashed lines indicate the proportion of marine collections falling on the flooded continents when a 100 km buffer from the coastlines is allowed. Vertical bands indicate geologic epochs.

we 1) assess whether topographies of the PALEOMAP PaleoDEMs match the environments described by fossil occurrences from the Paleobiology Database. We 2) also use the fossil occurrence data to update the continental margins and map paleocoastlines that represent maximum transgressive surfaces for each geological stage and 3) quantify the changing distribution of shallow seas and land area during the past 540 million years.

2. Methods and data

The paleogeographic reconstructions used in this study are based on the set of digital elevation maps of paleotopography and paleobathymetry (PaleoDEMs) published by Scotese and Wright (2018). The original set of PaleoDEMs were used to produce the 109 paleogeographic maps in the PALEOMAP Paleogeographic Atlas (Scotese, 2008a–f; Scotese, 2016). The coastline (0 m contour) and continental shelf margin (−1400 m contour) were extracted from the PaleoDEMs. The 1400 m isobath was chosen to represent the continental margins (i.e., the approximate edge of continental lithosphere) because this isobath, on average, best represents the transition from the continental slope to the continental rise. While this isobath does a good job outlining the continents, it also includes some purely oceanic features such as oceanic islands and volcanic edifices.

2.1. Assessing the match of predicted marine environments and fossil occurrences

To test the accuracy of this set of paleogeographic maps, a total of 207,746 fossil collection localities were downloaded from the Paleobiology Database on August 7, 2020. The fossil dataset was then divided into marine and terrestrial collections. Only those collections that contained marine organisms were designated as “marine”. These occurrences were binned to stratigraphic stages (Ogg et al., 2016) following the Phanerozoic template of Kocsis et al. (2019). Due to a lack in stratigraphic precision, a considerable amount (~20%) of collections were omitted from the analyses. The marine fossil data from each stage

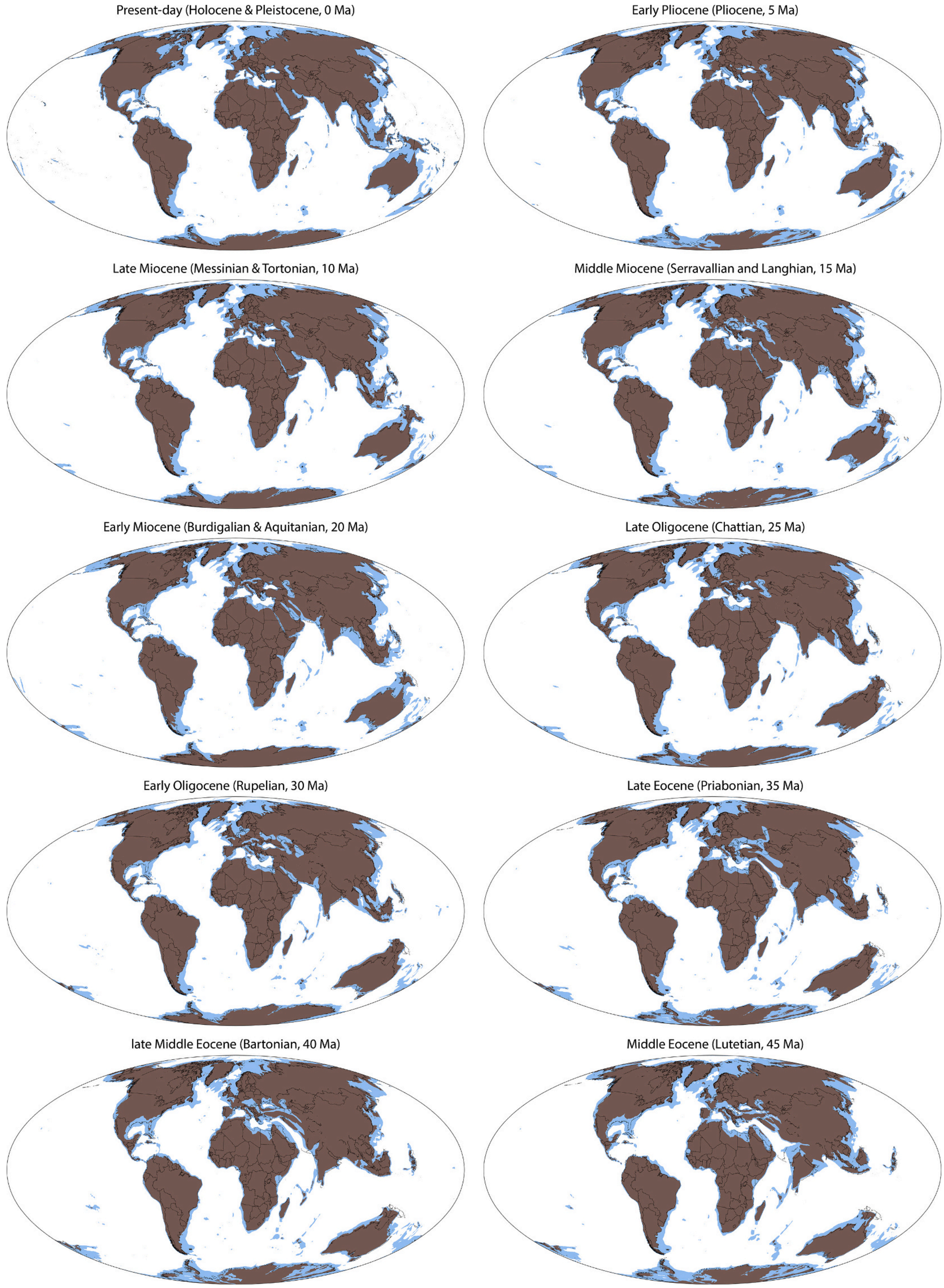

Fig. 3. Paleocoastline and continental margin reconstructions in Mollweide projection for the Present-day back to 45 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

were assigned to a PaleoDEM based on the mean age of the stage. The paleocoordinates of each sample site were reconstructed using the PALEOMAP rotation model (version 'v19o_r1c'). It is important to note that when reconstructing the fossil localities, the age of the reconstruction matched the age of the paleogeographic map, rather than the age of the fossil collections that relies on the PBDB's internal timescale. Fossil occurrence data were merged in cases when multiple stage-bins were assigned to a single paleogeographic map.

The processed terrestrial and marine fossil localities (25,766 vs 135,408 collections) were plotted on the paleogeographic reconstructions (Figs. 1A and S1). We then tabulated the proportion of collections for every stage that correctly plotted (a "hit") or incorrectly plotted (a "miss") within the appropriate environment. This "hit and miss" tabulation was repeated using a buffer of 100 km around each sample locality to take into account minor eustatic changes in sea level that may have taken place during each stage interval and also errors in the collection coordinates. In other words, if a marine fossil locality was within 100 km of the mapped paleocoastline, then the test locality was

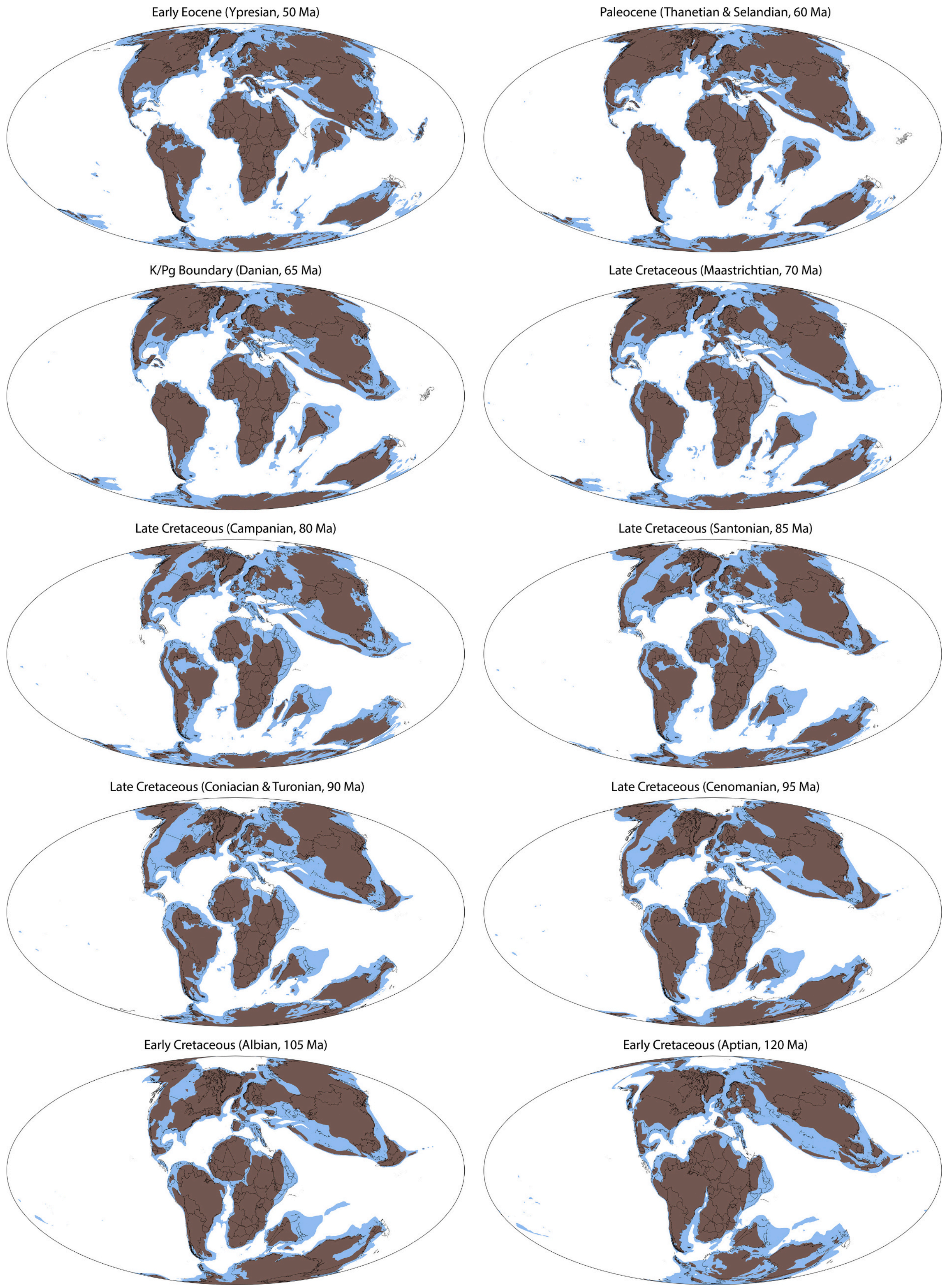

Fig. 4. Paleocoastline and continental margin reconstructions in Mollweide projection for the 50–120 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

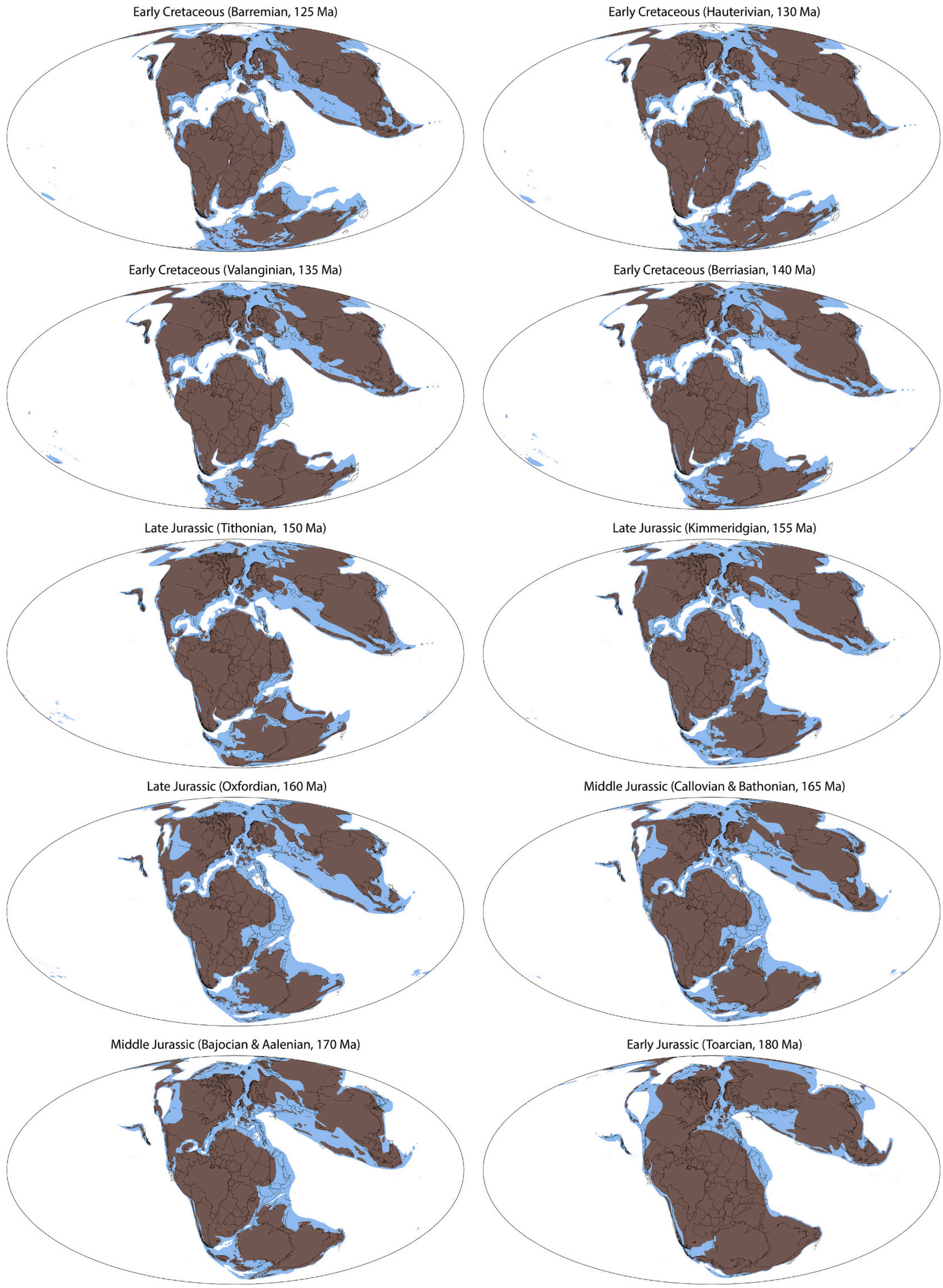

Fig. 5. Paleocoastline and continental margin reconstructions in Mollweide projection for the 125–180 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

considered to be a "hit".

2.2. Modification of paleocoastlines using fossil occurrence data from the PBDB

The location of the paleocoastlines was then adjusted and redigitized to better fit the distribution of marine and non-marine fossil localities (Fig. 1B). To improve their accuracy, the modified paleocoastlines were placed so that they were always located landward of any marine fossil localities. In some cases, when terrestrial fossil collections were available, the paleocoastline locations were further improved by mapping them between marine and the terrestrial fossil localities.

A similar methodology was used to correct the mapped edge of the continents. In some case, shallow water marine fossil localities plotted in the deep ocean. In almost every instance, this was due to the fact that these regions of continental crust were misdated and not included in the original reconstruction. These errors were rectified by changing the "appearance" age of the accreted continental crust or enlarging the area

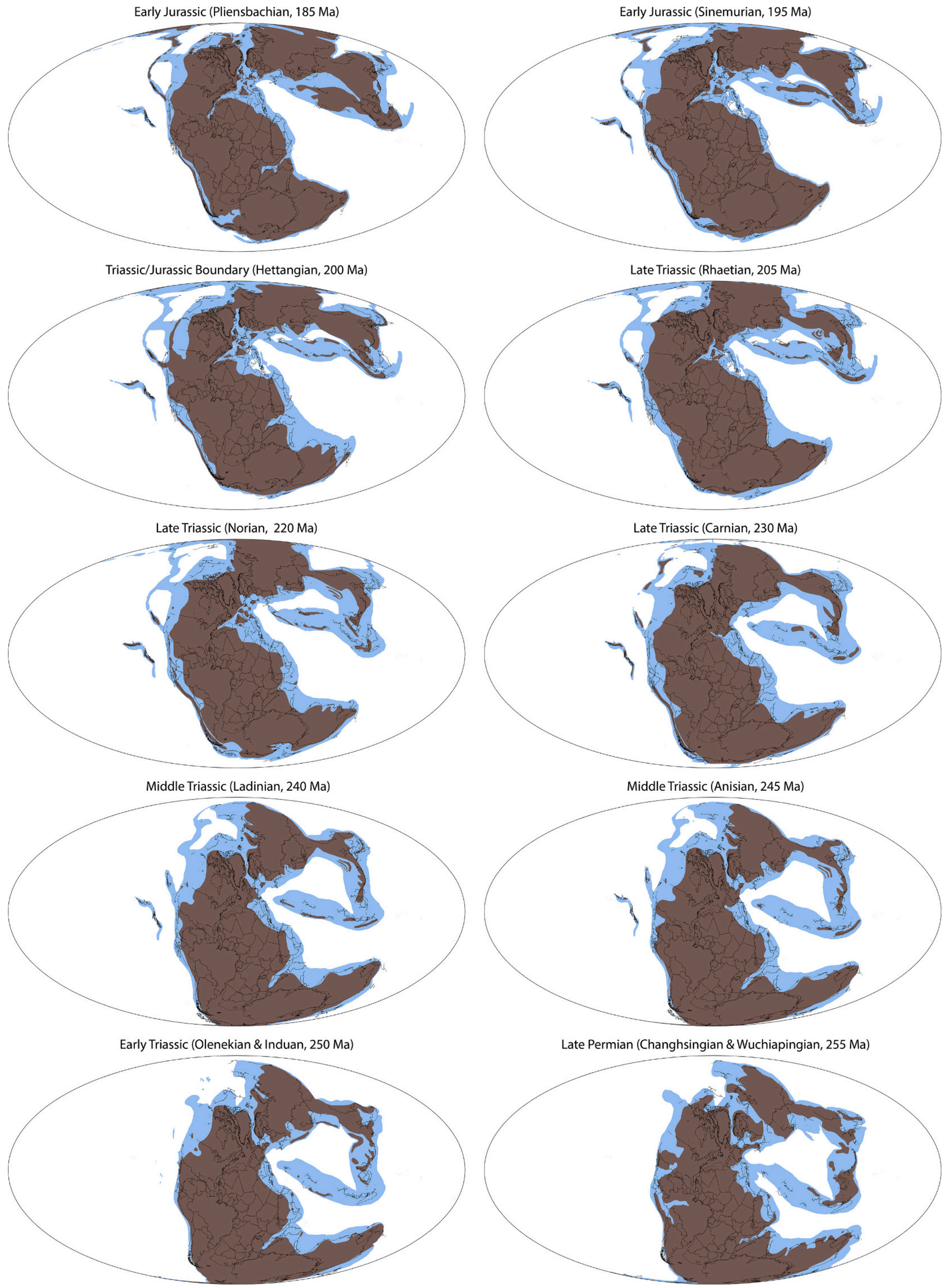

Fig. 6. Paleocoastline and continental margin reconstructions in Mollweide projection for the 185–255 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

of continental crust. In these cases, the location of the continental margin was adjusted using fossil locality information.

2.3. Measuring lengths and areas

As the length of coastlines are scale-dependent, their length was assessed using the 'yardstick' approach which resamples the coastline with equal segments (yardsticks) of different lengths (300, 500, 1000 and 1500 km; O'Sullivan and Unwin, 2010). The number of yardsticks used was tabulated for each measurement and then the yardstick length was multiplied by the number of yardsticks to get an estimate of the total length. Polygons that had a circumference smaller than the yardstick length were discarded from the calculations.

Using both the coastlines implied by the PaleoDEMs and those updated with the PBDB collections, we calculated the area of flooded continents and the area of land for every stage. The process was repeated for the polar, temperate, and tropical climate zones, which we defined using 30° latitudinal limits. The area of land and the flooded continent

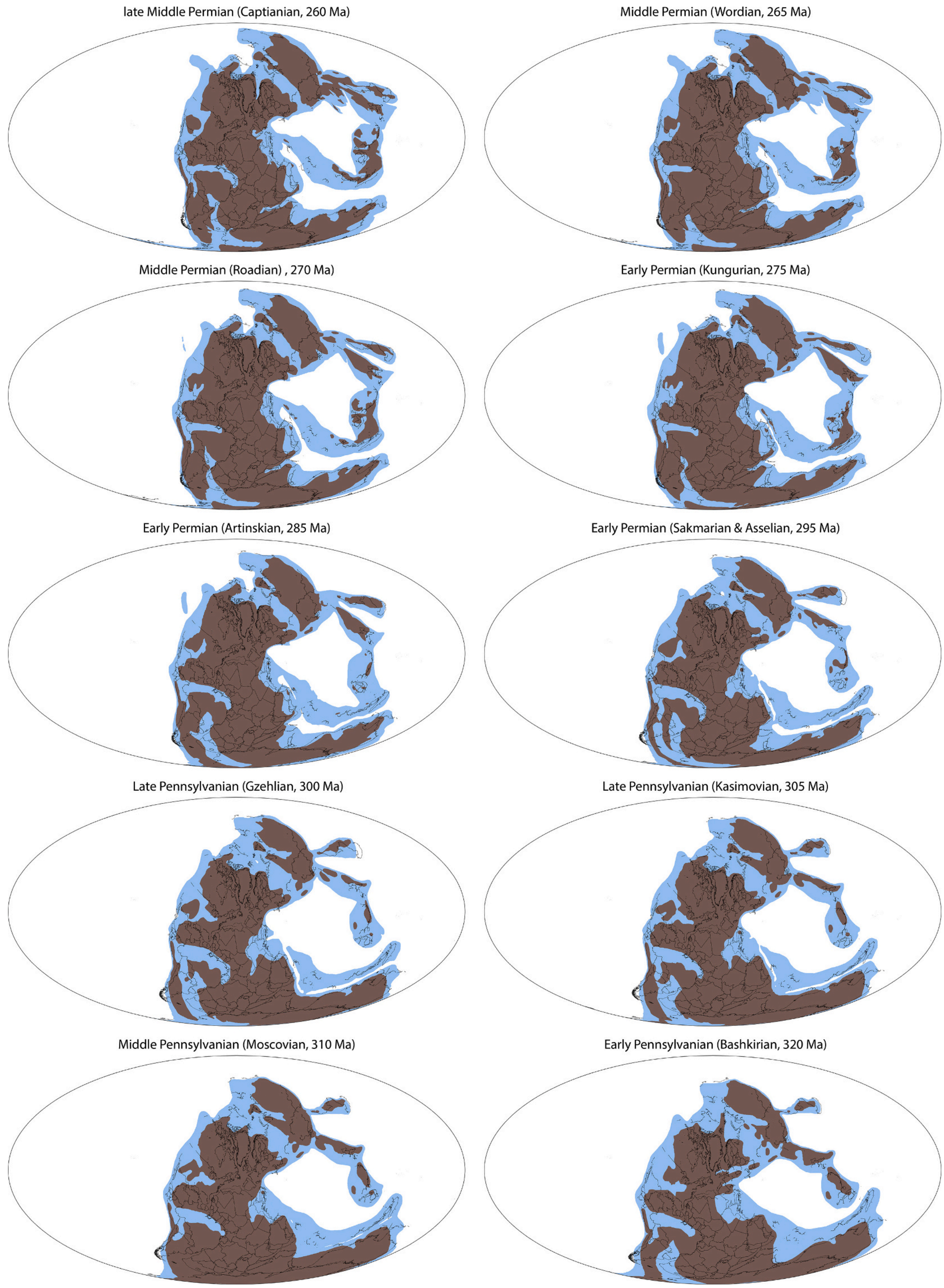

Fig. 7. Paleocoastline and continental margin reconstructions in Mollweide projection for the 260–320 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

for each stage was expressed in terms of the % of the total surface area of the Earth. Correlations were assessed with Pearson's product-moment correlation coefficient. All calculations were implemented in the R programming environment (R Development Core Team, 2020).

3. Hits, misses, and updates

3.1. *Environments implied by the original PaleoDEMs*

Before corrections to the location of the paleocoastlines were made, only about half of the marine fossil sites (47%) were "hits" (Figs. 1A and 2A). The number of "hits" improved to 67% when eustatic effects were considered and a buffer of 100 km was applied to each sample locality (Fig. 2A). Most terrestrial collections, because they are located far from

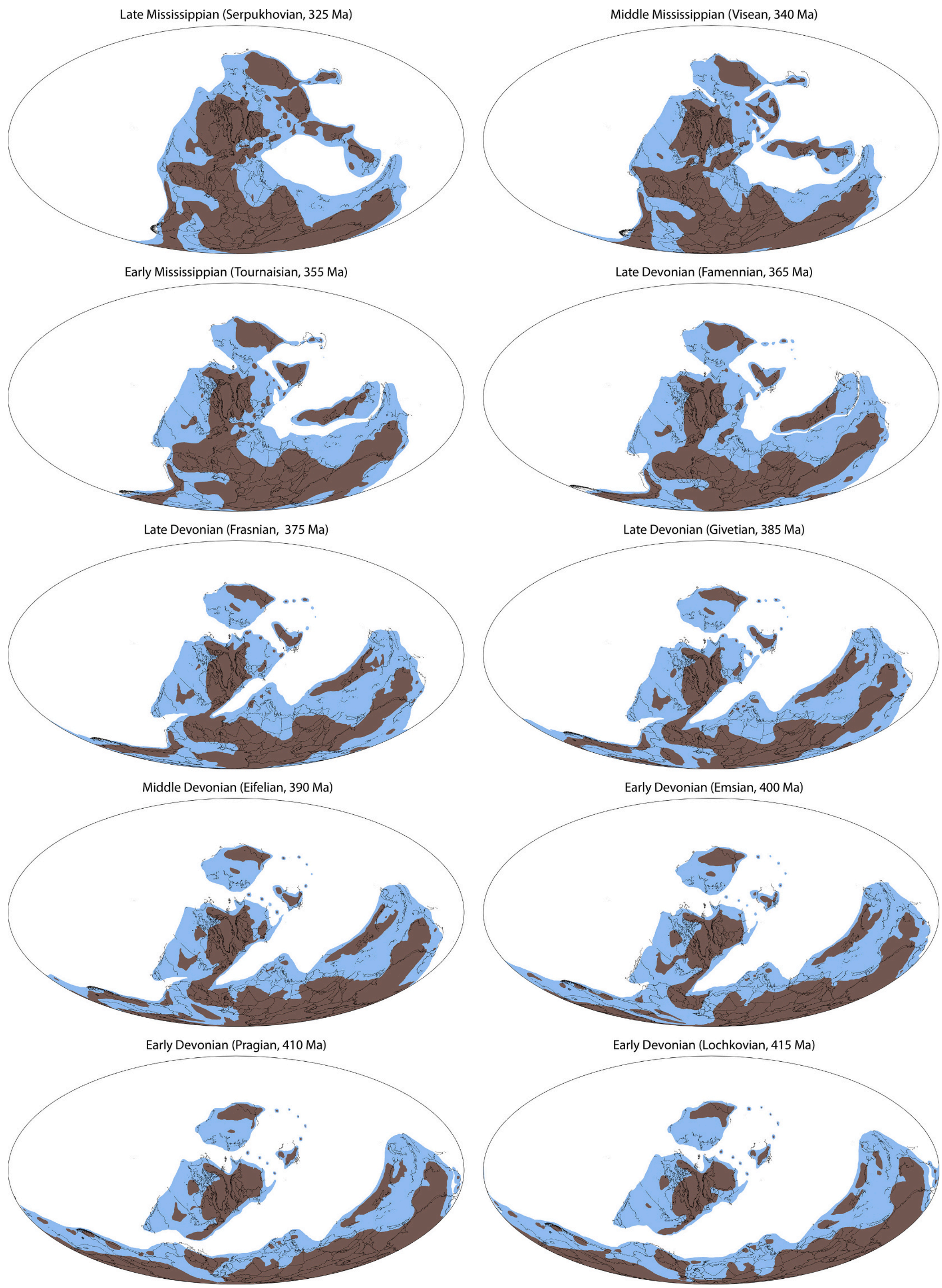

Fig. 8. Paleocoastline and continental margin reconstructions in Mollweide projection for the 325–415 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

the paleocoastline, were "hits" (90%).

It is interesting to note that the misfit of Mesozoic and Cenozoic localities was worse than the misfit of early and middle Paleozoic localities. This implies that the paleogeographic maps either: 1) underemphasized the effects of highstands of sea level, 2) overemphasized the heights of mountains and uplands during the Mesozoic and Cenozoic (especially for the Triassic and Cretaceous). 3) Another alternative explains the poor scores for Cenozoic paleogeographies. For the Cenozoic time intervals estuaries, large lakes, and landlocked inland seas (e.g. Paratethys, Lake Uinta, Chinese and Australian lakes) were often considered to be marine rather than "quasi-terrestrial" (Figs. 1A and 2A).

Mismatches could also occur for other non-systematic reasons, such as: 1) the inherent uncertainty in the location of the paleocoastline (±250 km), 2) the uncertainty in relative sea level (±100 m) and, 3) a mismatch between the stage age (Ogg et al., 2016) and the age of the plate tectonic reconstruction (Scotese and Wright, 2018). The overemphasis of land arises from the fact that areas where strata have been

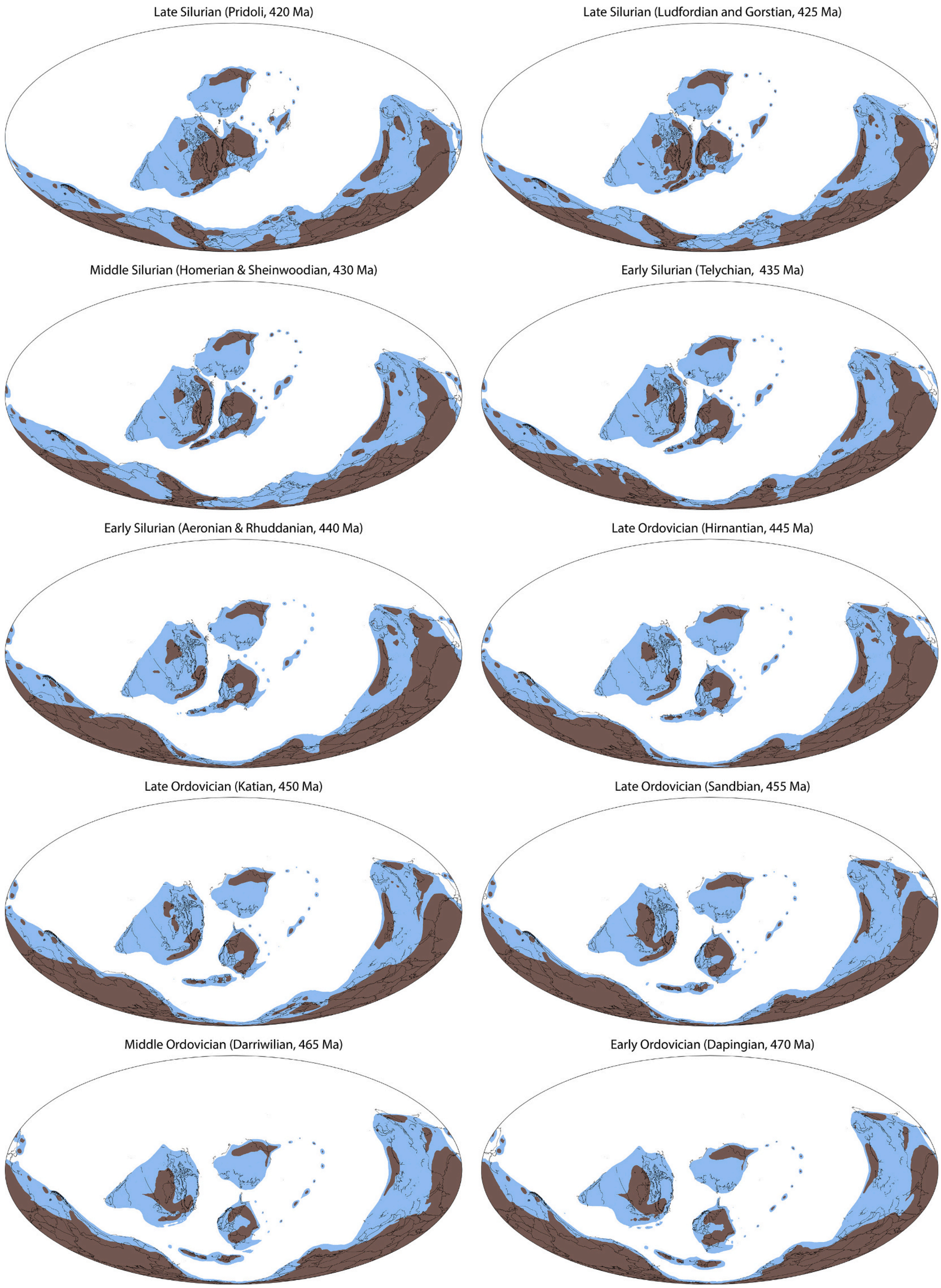

Fig. 9. Paleocoastline and continental margin reconstructions in Mollweide projection for the 420–470 Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

eroded are often classified as land. In other words, a lack of evidence of marine deposits is erroneously interpreted to be evidence of land. The solution to this bias would be to construct a set of "paleogeological" maps that describe the extent of ancient outcroppings and lithofacies belts. These maps would clearly differentiate between ancient land areas and regions where older rocks have simply been eroded. The best examples of paleogeologic maps are in the paleogeographic compilations of Ronov et al. (1989; 1984).

3.2. Updated paleocoastlines

Figs. 3–10 illustrate the updated paleocoastline maps. After the paleocoastlines were redigitized to better match the distribution of marine fossil collections, the number of "hits" dramatically increased to 90%, a significant improvement. Most of the adjustments of the paleocoastlines required lateral shifts of less than 500 km. However, in extreme cases, entire mountain ranges were removed and flattened (e.g. parts of Central Asia, Rocky Mountains and Canadian Cordillera during

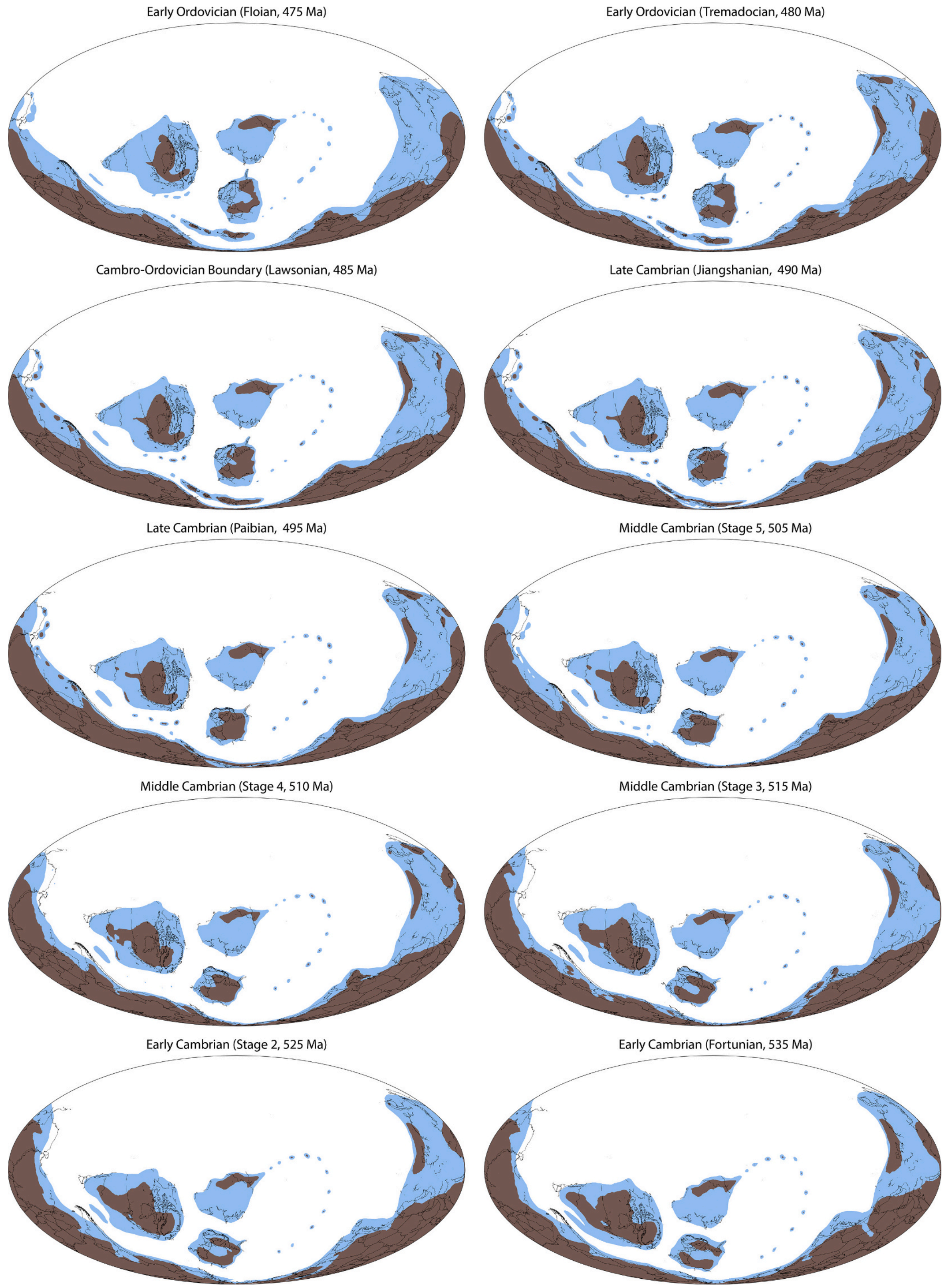

Fig. 10. Paleocoastline and continental margin reconstructions in Mollweide projection for the 475 – 535Ma after incorporating fossil occurrence data from the PBDB. The paleopositions of present-day coastlines and administrative boundaries are shown with black lines. Numeric dates indicate the ages of the paleogeographic reconstructions, geochronological names in parentheses refer to stage-level bins of the fossil occurrence data.

the mid-Cretaceous). With the addition of the 100 km highstand sea level buffer, the "hit" score improved to 95%. The poor correlation between the revised paleocoastlines and the modern fossil data is due to the different geographic resolutions of the fossil data (> 1:100,000) and the paleocoastline contours derived from the PaleoDEMs (~1:10,000,000). Though the two datasets are colinear when viewed at a global scale, when viewed at the higher geographic resolution of fossil localities, the fossil localities are likely to fall on either side of the paleocoastline.

We have made the explicit assumption that all fossil collections that are assigned to the same stratigraphic stage were truly contemporaneous. This assumption may produce a "smearing effect" that tends to overestimate sea level for any given geological stage. We argue, however, that using the resolution of geological stages represents a good compromise between the coverage of fossil collections and the accuracy of the geographic reconstructions. Although the age-model of the PBDB collections might allow a finer temporal resolution (substages, or in some cases even million years), the geographic coverage of fossils

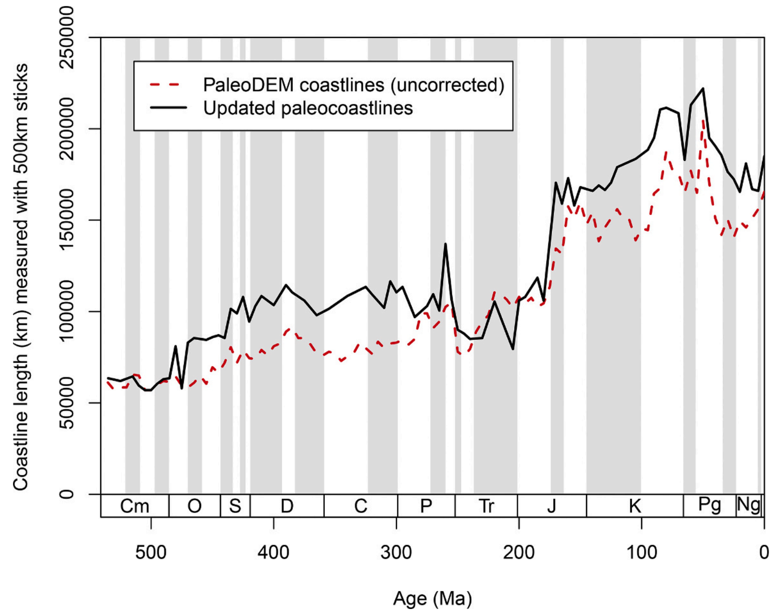

Fig. 11. Change of paleocoastline length through time before and after the updates. The length was measured with 500 km yardstick lengths. Note the abrupt increase in the Mesozoic. See Fig. S12 for trajectories of coastline lengths with 300, 1000 and 1500 km yardstick lengths. Vertical bands denote geologic epochs.

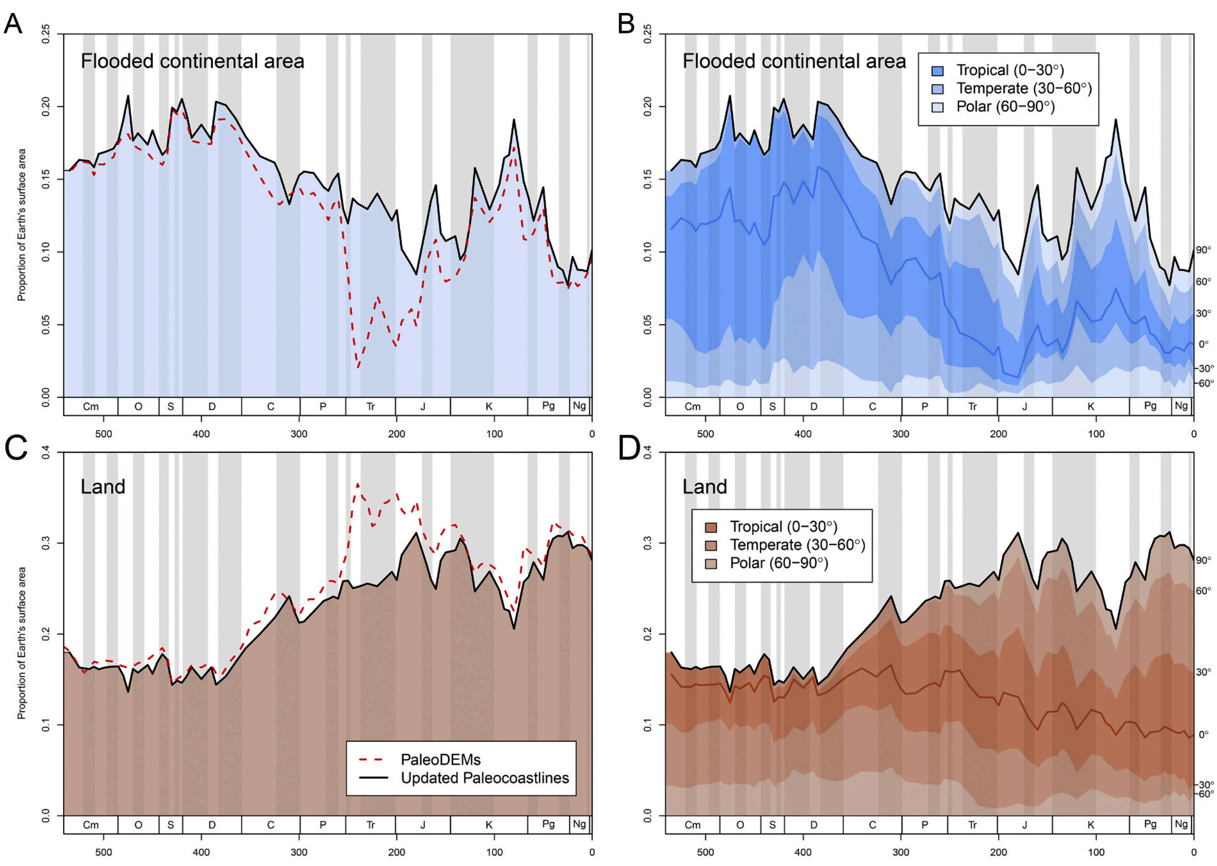

Fig. 12. Change of flooded continental plate (A, B) and land area (C, D) through time assuming maximum transgression. Left column (A, C) shows the effects of updating the paleocoastlines on the results. Dashed red lines indicate areas implied by the PaleoDEMs before, and black lines after the corrections of the paleocoastlines. The right column depicts the changes in the distribution area in tropical (0–30°), temperate (30–60°) and polar (60–90°) zones in flooded continental (B) and land (D) areas. Labels on the right-hand side of the plot indicate the boundaries between climatic zones (in degrees latitude). Vertical bands denote geologic epochs.

quickly degrades when the data are restricted to finer stratigraphic intervals. Limiting the data to such entries would exacerbate the effects of the already heterogeneous fossil sampling that suffer from spatial, preservation and taxonomic biases (Alroy et al., 2008; Close et al., 2020). Finer temporal and spatial resolution of global geographic reconstructions can be achieved by increasing the density of fossil occurrences, for instance with the integration of unpublished, "dark" data in fossil collections (Marshall et al., 2018).

4. The area of continental flooding and land over time

Updating the paleocoastlines had the overall effect of increasing their estimated length (Fig. 11). This increase is particularly apparent in the Ordovician-Carboniferous interval, where the coarse spatial resolution of the PaleoDEMs could be somewhat refined with the fossil occurrence data. The total length of paleocoastlines increases over the Phanerozoic, regardless of the yardstick length (Fig. S12) that was used to measure them. The spatial resolution of the coastlines and their information content is heterogeneous over time, and they increase abruptly after the Early Jurassic (Fig. 11) and the breakup of Pangea (Fig. 5, compare 180 Ma and 170 Ma). Extensive new coastlines were created by the rifting of northwest Africa and northern South America from eastern North America, as well as the rifting of eastern Africa from India and Antarctica. On the hand, higher spatial coverage of paleogeographic data in younger intervals also allows the systematically more detailed reconstruction of paleocoastlines.

The updated paleocoastlines markedly affect the extent of predicted flooding in the first half of the Mesozoic (Fig. 12) and suggest that sea level remained moderately high during the transition from the Paleozoic to the Mesozoic. Because continents primarily occupied the southern hemisphere, early and middle Paleozoic distribution of shallow seas was latitudinally asymmetric (Fig. 12). During the early and middle Paleozoic, there was virtually no land in the northern hemisphere (Fig. 12C). The latitudinal distribution of both land and shallow seas became more symmetric as the continents migrated northwards. The continental flooding curve shown in Fig. 12 agrees with other sea level curves that show a major sea level peaks at ~90 Ma (Haq et al., 1987; Snedden and Liu, 2010; Vérard et al., 2015) but differs from the sea level curves of Müller et al. (2018) and Wright et al. (2020), which show a major peak at 120 Ma. The reasons for these differences require further investigation.

The area of the continents (Fig. S13) gradually increases over the course of the Phanerozoic at a rate of around +1.5% of Earth's surface area per 100 million years. This trajectory matches the Phanerozoic trend of increasing land area over time. Over the course of the Phanerozoic, the percentage of land area has doubled from about 15% in the Ordovician period to the present-day value of almost 30%. A significant part of this apparent increase in continental area may be due to poor sampling of continental material far back in time.

The size of shallow seas is negatively correlated with increasing land area (Pearson's $r = -0.96$) and has declined steadily over time despite the overall growth of the continents. The greatest change in the area of both shallow seas and land environment is the interval of time from the late Devonian to the Early Jurassic, which represents the Late Paleozoic ice age, the time interval when the supercontinent of Pangea was assembled. Continental flooding has been fluctuating since the Triassic period, with a local maximum in the Late Cretaceous that also represents a minimum of land area (20%), confirming the large-scale patterns suggested by earlier works (Ronov et al., 1984, 1989).

Long-term trends in plate tectonics, and the changing area and latitude of shallow seas might have important evolutionary consequences. In coordination with biogeographic changes due to continent fragmentation (Valentine and Moores, 1970; Zaffos et al., 2017), changes in eustatic sea level has been suggested to have an effect on global diversity (Hallam and Wignall, 1999) via the control of available space that limits the number of inhabitant taxa (MacArthur and Wilson, 1963). However, the overall decline of flooded continental area since the mid-Cretaceous, suggests that sea level is an unlikely driver of the extensively-studied Cenozoic diversification in the shallow marine environment (Alroy et al., 2008; Close et al., 2020). On the other hand, the increasing area of land might be a contributing factor to terrestrial diversification (Close et al., 2019).

5. Future directions

Reconstruction of ancient geography forms the baseline of paleoenvironmental and paleontological research. The dataset of paleocoastlines presented here represents a significant advancement in the reconstruction of ancient geographies and they are the most detailed and comprehensive set of paleogeographic maps that have been produced to date. The updated dataset will be used to correct the the 3D elevation models of Scotese and Wright (2018) and produce more accurate paleotopographies. In turn, the corrected paleotopographic maps will be used to inform paleoclimate models (Haywood et al., 2019; Valdes et al., 2017), which can be used to reconstruct environmental parameters such as temperature and precipitation of fossil localities. Our study demonstrates how integrating data from the fossil record with geological and tectonic models can improve the reconstruction of ancient environments.

Author contributions

Both authors contributed equally to the study and wrote the paper. ÁTK did the calculations involving fossil occurrences, the statistical analyses, and the additional processing of GIS data. CRS provided paleogeographic reconstructions and made the corrections to the paleocoastlines and the continental margins.

Data availability

The updated continental margins and paleocoastlines are available on Zenodo (https://doi.org/10.5281/zenodo.3903163) and through the 'chronosphere' R package. The code used to conduct the analyses is also deposited on Zenodo (https://doi.org/10.5281/zenodo.4320702).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2020.103463.

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