Improving global paleogeography since the late Paleozoic using paleobiology

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Interactive comment on "Improving global paleogeography since the late Paleozoic using paleobiology" by Wenchao Cao et al.

Wenchao Cao et al.
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General Comments:

Reviewer: This is an interesting paper that does an excellent job combining two disjoint data sets (plate tectonic models & paleogeography) into a cohesive synthesis. The resulting discussion of the relationship of continental flooding to sea level and to the changing ratio of strontium isotopes in the oceans through time is clearly presented. All the figures are readable and well done. The writing is patchy, but I have made numerous suggestions for the authors. This study had four principle objectives: 1) to describe the process by which the paleogeography (Golonka) developed for one plate tectonic model (Scotese) could be reverse engineered and plotted on an alternate plate tectonic model (Matthews), 2) to improve the Golonka paleogeography by adding additional constraints from the Paleobiology Database, 3) to compare the resulting estimates of continental flooding though time with published sea level curves, and finally, 4) to explain the changing ratio of strontium isotopes in the ocean with the observed patterns of continental growth and emergence. Each of these objectives was successfully met, to varying degrees. Objective 1: The new set of paleogeographic maps produced in this paper, clear demonstrates that it is possible to transfer the paleogeographic information from one set of maps (Golonka, 2006) to another set (Matthews, 2016) – as long as plate tectonic models are available for both sets of maps. However, the methodology cannot be considered to be a universal solution. As pointed out by the authors, the paleogeography and plate models are inextricably joined, and moving the paleogeography from one plate model to a another plate model inevitably results in gaps and overlaps (see Figure 3c). Unfortunately this will always be the case. It will always be necessary to laboriously "hand edit" any attempt to transfer the paleogeography from one plate model to another.

Authors: We thank Christopher Scotese for his constructive review and detailed suggestions that have helped us to significantly improve the manuscript. We agree with the four points he raised, to be addressed in the revision. In terms of objective 1, we agree that the methodology has some limitations and we have discussed them in the revision.

Reviewer: Objective 2: There are several issues here that need to be discussed. My first major point is that I am not convinced that the "revised" coastlines are a significant improvement over the original coastlines. Though, I agree that the addition of information from the Paleobiology database can, in some areas, improve the location of the coastlines, it is not clear to me that the overall result is an improvement or merely a slight modification. There are two reasons for my skepticism. Firstly, I do not know what original data was used to draw the coastlines. Therefore I do not know how much "weight" to give the Paleobiology data with regard to the original data. For example is the original coastline is based on a dozens of coastline estimates from a variety of sources, then a few additional data points from the PBDB should not be given much weight. Conversely, if the original coastline position was an educated guess based on little or no data, then the extra information from the PBDB would be very welcomed. So, simply, we don't if the changes are an improvement or not. The second reason for doubting that any improvement has

been made is to consider what the coastline drawn on the original maps actually represents. In this case, I believe the error lies with the mapmaker, not the analysis.
Authors: The revised paleo-coastlines are significantly different, except for a few time-interval maps where there are few paleobiology data (Please see revised Figs 4, 5, 6 and a set of maps in Supplement materials). Note that in the new tests carried out on the paleogeography with paleobiology, we only use marine fossil collections to improve paleo-coastline locations and the paleogeographic geometries because the coastlines on the paleogeographic maps used in this study represent maximum transgression surfaces. The paleogeographic atlas in the study is compiled based on gathered lithologic data, which is independent with paleobiology data. Since the original data that were used to estimate the coastlines are not available for us, it is difficult to give the weight to the paleobiology data. The coastlines drawn on the original maps represent maximum transgression surfaces and we do not know much about their errors. Instead, we have systematically estimated the errors of two key steps in the workflow, including filling gaps and modifying the coastline locations and the paleogeography (see Fig. 10 in the revision) and added their discussion in the revision (lines 341-366).

Reviewer: The 24 maps in this study cover ~400 million years. That means, on average, that each map represents an interval of 17 million years. It seems very unlikely that the coastline would have remained in one place for 17 million years. A more reasonable representation of the "coastline" for this long interval would have been to show it as a "zone" that was alternately marine or terrestrial. (see my Figure 1). One way to simulate this would have been to erect a 250- 500 km buffer around the coastline, and then test only the points that lied outside of the buffer. I am not suggesting that the authors do this, but rather I am suggesting that it is likely that the "discrepancies" they point out, may in fact, be perfectly OK, given the changing location of the coastline through time. In this regard, I think the manuscript would be improved if the author's pointed out this possibility and changed their wording so that it sounds less pejorative (i.e. You made mistake and now I'm going to fix it.) In fact what would be more valuable if the authors listed all the marine data points that plotted on mountain ranges or more than 500 km from the proposed coastlines, or conversely, terrestrial deposits that plotted in the deep sea (off the edges of the continents). In these cases, changes to the paleogeographic maps should certainly be made!
Authors: In the revised version of the maps, we only use marine fossil collections to improve coastline locations and paleogeographic geometries. We have flagged all inconsistent marine fossil collections far more than 500 km inland from the nearest coastlines with red point symbology, on each time-interval map (see a set of maps in Supplement materials).

Reviewer: Objective 3: Everything here looks pretty good, however there was a little graphical confusion that needs to be fixed. It is hard to argue against a positive correlation between sea level rise and continental flooding, and I am happy to see that in Figure 9A both trends track each other well. However, it is not clear which units (y-axis) apply to which curve. This should be cleared up in the Figure caption. More problematic, however, is that the fact that the figure implies that these two very different units scale together. i.e. 40% flooding = 160m rise in sea level. This is certainly not true. The cleanest solution would be to separate these two graphs, but place them one above the other.

Authors: We have deleted the comparison between continental flooding curves and published sea level fluctuation curves as there may be some circularity in this comparison. Instead, we only compare our flooded continental area curve to previously published ones (see revised Fig. 9).

Reviewer: Objective 4. The same objection raised to Figure 9a also applies to 9b. It may be necessary to separate this figure into two diagrams.
Authors: We have deleted the comparison between emerged land area, total land area and the strontium isotope ratio curve, so this figure has been replaced.

Additional General Comments:
Reviewer: The Methods Section consistently misuses verb tense. Lines 115 – 334. You are describing actions that you did in the past. You must use the past tense, not the present tense e.g. "They are first georeferenced" should be "They were first georeferenced. " Review all verb tenses in this section and correct.
Authors: Thank you. All verb tenses throughout the manuscript in the revision have been uniform using present tense.

Reviewer: There is a confused an improper use of the terms "fossil" and "paleobiology". No fossils were used in this paper, only fossil collections that revealed paleoenvironmental conditions, i.e., marine or terrestrial.
Authors: We have corrected this throughout the manuscript in the revision.

Reviewer: When listing ranges of dates, "Ma" should appear after each date if the dates are separated by a "and" or "to", e.g. 402 Ma and 2 Ma or 402 Ma to 2 Ma. This is not necessary if the dates are separated by a dash, as in 402-2 Ma.
Authors: We have amended this in the revision.

Reviewer: Other specific comments regarding the text, figures or tables are given in the following section. Specific Comments by line: 016 Delete "time-dependent global" and "Several"
Authors: We have deleted them in the revision.

Reviewer: 018 The phrase "static maps with varying temporal resolution and fixed spatial resolution" is not clear and seems redundant and should be rewritten. Aren't all maps "static" and have a fixed "spatial resolution", i.e. "scale". So?
Authors: We have rewritten this in the revision (lines 18-19).

Reviewer: 020 Though the authors were successful in "reverse engineering" the Golonka maps, the workflow they produced is not a general or universal solution. Because of the idiosyncrasies of various plate tectonic reconstructions, each reverse engineered set of maps requires extensive hand editing to fix the resulting gaps and overlaps. This will always be true. So the claim that this new workflow fixes that problem and is a universal solution is incorrect and therefore the claim must be withdrawn or modified.
Authors: We agree and have modified the claim in the revision (lines 21-22). In addition, we have added the discussion of the limitations of the workflow developed in this study in the Discussions section (lines 341-366).

Reviewer: 022 The sentence, "Published paleogeographic . . . datasets." is not informative and should be deleted.
Authors: We have deleted this sentence in the revision.

Reviewer: 023 "fossil data" to "paleoenvironmental data".
Authors: We have amended this in the revision (line 23).

Reviewer: 023 I am not convinced that the maps were improved. See my comment above. There are some methodology problems here - both in the map making and analysis. The best I think you can say is that "the maps were modified to be more consistent with the paleoenvironmental data from the Paleobiology database." This statement does not imply that the resulting maps are "better". (I know this seems like nit-picking, but it actually is an important point!)
Authors: The paleo-maps are significantly different, except for a few time-interval maps where there have few paleobiology data (see revised Figs 4, 5, 6 and a set of maps in Supplement materials).

Reviewer: 039 A definition of what you mean by "paleogeography" might be appropriate here. I favor this definition, "paleogeographic maps describe the ancient distribution of highlands, lowlands, shallow seas, and deep ocean basins". Of the list of examples, that would disqualify Scotese (2004), but Scotese (2001 and 2004) could be substituted (see list references cited at end of review).
Authors: We have added the definition of "paleogeography" (lines 41-42) and corrected the references (lines 45, 500-502) in the revision.

Reviewer: 043 Here we go with that static .. fixed spatial resolution " business again.Why don't you just say that it is difficult to convert the maps into a digital format because of the varying map projection, different time intervals represented by the maps, and the different plate models that underlie the paleogeographic reconstructions. I agree that there is great power to having the paleogeographic data in a digital format so you can . . .. (examples). Yes, this is a worthwhile goal.
Authors: We have rewritten this part in the revision as suggested (lines 45-47). Thank you.

Reviewer: 052 use "these issues"
Authors: We have amended this in the revision (line 55).

Reviewer: 054 not "any plate model" but a "different plate model". Your workflow is not a universal solution. It is likely that any change in the plate model will create new gaps and overlap that will have to be fixed by hand.
Authors: We have changed "any plate model" to "different plate model" in the revision (lines 56-57).

Reviewer: 055 Try rewriting this sentence without the jargon. "The first step was . . . "
Authors: We have rewritten this sentence in the revision (lines 57-59).

Reviewer: 058 You didn't "reverse-engineer the global maps" (whatever that means). You "restored the ancient paleogeographic boundaries back to their modern coordinates by applying the inverse of the rotation that was used to make the ancient reconstruction." More words, but more clear.
Authors: We have amended this claim in the revision as suggested (lines 62-64).

Reviewer: 060 -062 How about saying this, "Subsequently, we used information about marine and terrestrial paleoenvironments available from the Paleobiology Database to modify the location of the paleo-coastlines."
Authors: We have rewritten this in the revision as suggested (lines 65-67).

Reviewer: 068 "modelled" should be "modeled"
Authors: Since we have deleted the comparison between emerged land area, total land area and the evolution of strontium isotopes of marine carbonates, the whole sentence here has been deleted in the revision.

Reviewer: 073 "paleoenvironmental data" not "paleontological data"
Authors: We have modified this in the revision (line 81).

Reviewer: 077 see my comments about Table 1.
Authors: We have listed three time scales of Sloss (1988), Golonka (2000) and ICS2016 in the table (see revised Table 1).

Reviewer: 084 change "a plate tectonic model" to "a mysterious plate tectonic model " - just kidding! 089 not "reverse-engineer", but " restore these paleogeographies to their present-day coordinates".
Authors: We have amended "reverse-engineer" to "restore" in the revision (line 97).

Reviewer: 091 in Figure 2 of this review I show that the plate model is identical to Scotese (1997) that was published in Scotese (2004). So the sentence should read, "are based on Scotese (1997, 2004)". My plate models have been widely available – mostly through the paleomapping programs I have written (with students) – Terra Mobilis, PaleoMap-PC, PointTracker, & PaleoGIS. Jan probably obtained a copy from me directly, or by using one of my programs. In either case, I deserve credit for the plate model (but not the paleogeography).
Authors: Sorry for the improper claim and citation. "are similar to those in Scotese (2004)" has been revised to "are based on Scotese (1997, 2004)" (line 100).

Reviewer: 106 "fossil collections" rather than "documented fossils"
Authors: We have modified this in the revision (line 116).

Reviewer: 116 This is an important sentence. It must be clear. Try, "The methodology can divided into three steps: 1) the original paleogeographic boundaries were restored to present-day coordinates by applying the inverse of the rotations used to make the reconstruction, 2) these restored boundaries were then rotated to new locations using the plate tectonic model of Matthews et al. (2016), finally, 3) the location of the paleocoastlines were adjusted using paleoenvironmental data from the Paleobiology database."

Authors: We have rewritten the sentence as suggested here (lines 126-130).

Reviewer: 117 Figure 2 illustrates the generalized workflow.
Authors: "a generalized workflow" has been revised to "the generalized workflow" (line 130).

Reviewer: 126 "to refine the rotations and ensure that the paleogeographic boundaries are restored accurately to their present-day locations."
Authors: We have modified the sentence in the revision (lines 138-140).

Reviewer: 141 Emphasize how tedious and labor intensive this procedure is. "The gaps and overlaps were fixed, feature by feature, map by map, by extending or modifying the outlines of each mismatched polygon in order to make the boundaries connect in a similar fashion to the original paleogeographies."
Authors: We have clarified this in the Discussions section in the revision (lines 346-348).

Reviewer: 151 Try "Once the gaps and overlaps were fixed, the reconstructed paleocoastlines were compared with the data from the PaleoBiology Database that described the marine and terrestrial environments of the fossil collections. These comparisons were aimed at indentifying the differences between the mapped paleocoastlines and the marine and terrestrial environments in order to modify the location of the paleocoastlines."
Authors: We have revised this part in the revision as suggested here (lines 161-164).

Reviewer: 155 change "Only the fossils" to "Only the fossil collections"
Authors: We have replaced "Only the fossils" by "Only the fossil collections" in the revision (line 166).

Reviewer: 157 change "fossils" to "collections" and "Fossils" to "Fossil collections"
Authors: We have modified this throughout the manuscript.

Reviewer: 161-165 The sentence starting with "Alternatively . . " and everything after it, should be deleted. It is unnecessary. Makes things unnecessarily complex.
Authors: We have deleted this part in the revision.

Reviewer: 169 "collections were then attached" - delete "motion"
Authors: We have deleted "motion" in the revision (line 175).

Reviewer: 170 Try, "Subsequently, a point-in-polygon test was used to determine whether the indicated terrestrial or marine fossil collection lied within the appropriate marine or terrestrial paleogeographic polygon. The results of these tests is discussed in the following section. (delete the rest of this paragraph).
Authors: We have modified this part in the revision as suggested (lines 176-178).

Reviewer: 177-178. "In the next step, we modified the location of the paleocoastlines based on the differences between the paleoenvironments indicated by the fossil collections

and the mapped paleogeography. Figures 4 & 5 illustrate how the paleocoastlines were modified. "
Authors: We have amended this part in the revision as suggested (lines 180-181).

Reviewer: 184 ". . . taken into account. (3) The boundaries . . ."
Authors: We have deleted "as valid proxies to improve marine-terrestrial boundaries" in the revision (line 185).

Reviewer: 192 "to maximize the use of the paleoenvironmental information from the fossil collection to improve . . "
Authors: We have changed "paleobiology" to "the paleoenvironmental information from the marine fossil collection" in the revision (lines 189-190).

Reviewer: 205 " when using the fossil collections. . "
Authors: We have replaced "paleobiology" by "the fossil collections" in the revision (lines 201-202).

Reviewer: 208 "deceptive fossils, however, are rare."
Authors: We have revised "deceptive fossils are rare." to "Such instances of deceptive fossil data are a potential limitation within our workflow, which we seek to minimise for example by excluding inconsistent fossils more than 500 km from previously interpreted paleoshorelines as described above." (lines 204-206)

Reviewer: 211 "4.1 Paleoevironmental Tests" - no Paleobiology used here.
Authors: We have modified "4.1 Paleobiology Tests" to "4.1 Paleo-evironmental tests" (line 209).

Reviewer: 210 -254 I still think this "consistency/inconsistency ratio " is somewhat dubious due to the changing location of the coastline (see previous discussion). Maybe if it were couched in terms of a "match ratio" , or "mixing ratio" rather than an "inconsistency ratio". A high mixing ratio (mixing of marine and terrestrial data) would indicate a widely fluctuating coastline. A low mixing ration would indicate relatively stable shorelines. Again, what should be flagged as anomalous are marine data points far removed inland from coastlines (>500 km) or terrestrial data points far removed, oceanward of coastlines. It seems nearly pointless to flag contrary indications that lie adjacent to the coastline.
Authors: Given that the coastlines on the paleo-maps used in this study represent maximum transgression surfaces, and we only use marine fossil collections to improve the paleo-coastline locations and the paleogeographic geometries in the revision, this is not the case anymore. We have used the marine fossil collections less than 500 km from the nearest coastlines in the new tests and have flagged all inconsistent marine fossil collections far removed inland from the coastlines (>500 km) with red point symbology on each time-interval map (see a set of maps in Supplement materials).

Reviewer: 254 "scarce, the fossil collections were of limited . ."
Authors: We have revised "paleobiology data is" to "the fossil collections are" (line 239).

Reviewer: 261 "Methods"

Authors: We have revised “Method” to “Methods” (line 245).

Reviewer: 264-267 Rewrite this sentence.
Authors: We have rewritten the sentence in the revision (lines 249-251).

Reviewer: 281-287 Rewrite, simplify, clarify. “380-285,81-58, and 37-2 Ma” should be “30-285 Ma, 81-58 Ma, and 37-2 Ma”
Authors: We have rewritten the sentence and modify “380-285, 81-58, and 37-2 Ma” to “30-285 Ma, 81-58 Ma, and 37-2 Ma” in the revision (lines 268-269).

Reviewer: 313 NO. The sea level curves of Haq et al. 1987 & are not inferred from the flooding ratios. They have a completely separate derivation. I would delete this sentence.
Authors: As we have deleted the comparison between continental flooding curves and published sea level fluctuations, this sentence has been deleted accordingly.

Reviewer: 310 – 323 These values are in good agreement with the flooding curve I have independently produced.
Authors: We have deleted the comparison between continental flooding curves and published sea level fluctuations. Instead, we compared the flooded continental area curve generated from our amended paleogeography to previously published ones (see revised Fig. 9).

Reviewer: 326 A similar pattern of changing areas was published by Worsley et al (1984), Fig. 7.
Authors: We have deleted the whole comparison between emerged land area, total land area and the evolution of strontium isotopes of marine carbonates in the revision.

Reviewer: 335 “402 Ma to 2 Ma”
Authors: We have deleted the paragraph in the revision.

Reviewer: 343-345 I don’t understand what you’re trying to say here. Don’t you mean “emerged”, not “submerged”?.
Authors: We have deleted the paragraph in the revision.

Reviewer: 368 “utility” rather than “flexibility”
Authors: We have deleted the paragraph in the revision.

Reviewer: 372 “variable” rather than “flexible”
Authors: We have replaced “flexible” by “variable” in the revision (line 374).

Reviewer: 375 “using paleoenvironmental data obtained from fossil collections”
Authors: We have changed “using paleobiology data” to “using paleo-environmental information indicated by the marine fossil collections from the PBDB.” in the revision (lines 377-378).

Reviewer: 397 Please include an acknowledgement to my help with the editing.

Authors: We sincerely thank the reviewer for his constructive reviews and suggestions, that we have acknowledged (lines 408-409).

Comments about Tables

Reviewer: Table 1 Nearly all of the Sloss Sequence designations are incorrect. See Table 1 Revisions. Also the timescale for the maps is not the latest ICS timescale (2012). This means the ages may be off by as much as 4-6 million years.

Authors: We have corrected the table in the revision (see revised Table 1).

Reviewer: Table 2 - OK

Authors: We have modified Table 2 in the revision (see revised Table 2).

Comments about Figures

Reviewer: Fig 1 I would arrange with oldest on bottom to match the timescale on the left.

Authors: We think the current arrangement in Fig .1 from old time to young time could better match the geological time scale.

Reviewer: Fig 2 change "Reverse Engineer" to " Restore to Present-day", change "Fix gaps" to "Fix gaps and overlaps"

Authors: We have changed "Reverse Engineer" to "Restore to Present-day" (see revised Fig. 2). We only fix the gaps.

Reviewer: Fig 3 Excellent Figure!

Fig 4 Nicely done, very clear.

Fig 5 Very clear – though I am not sue the changes are significant.

Authors: Thank you. The changes are significant and please see revised Figs 4, 5, 6 and a set of maps in Supplement materials.

Reviewer: Fig 6 I would change it to "Match Ratio". Otherwise clear.

Authors: We have amended the explanation of "Consistency ratio" in the text to be clearer.

Reviewer: Fig 7 These area nice set of maps. Well done. I think the revised coastlines are fine, however the continental margins seem cartoonish and extend far beyond the COB. The size and placement of the mountains through time are very inconsistent.

Authors: Thank you. The paleogeographic geometries in this study are all originally obtained from Golonka et al. (2006)'s paleo-maps and we use the paleo-environmental data of the marine fossil collections from the Paleobiology Database to improve the paleo-coastline locations and the paleogeographic geometries. Improving the continental margins or the size and placement of the mountains are beyond the scope of this study.

Reviewer: Fig 8 Clear.

Authors: Thank you.

Reviewer: Fig 9 Potentially misleading. Both 9a & 9b should be separate diagrams because the y-axis values are different, and not equivalent. See text comments for elaboration.

Authors: We have deleted Figure 9a and b. Instead, we have compared the flooded continental area generated from our amended paleogeography to previously published ones (see revised Fig. 9).

Comments about References Cited
In good shape, only a few things
Reviewer: 41 Blakey, 2008, is Blakey, 2003 in References
Authors: Blakey (2008) was accidentally missing and we have added it to the reference list (lines 426-427).

Reviewer: 95 Domeier and Torsvik, 2014 is missing, but there is a Domeier, 2016 that is not cited in the text.
Authors: We have added Domeier and Torsvik (2014) and have deleted Domeier (2016) in the References (lines 431).

Reviewer: 311 & 312 There is no Haq et al., 2012 in the References; Haq et al, 2008?
Authors: We have deleted the comparison between continental flooding curves and published sea level curves so they are not cited anymore.

Comments about Supplementary Materials
Reviewer: Good to have a copy of Golonka (2006) included. It would have been nice to have the rotation model used by Golonka included as well. The link to the Supplement of Golonka (2007) is no longer active.
Authors: We have attached a copy of Golonka (2006)'s digitised paleogeographic maps and the rotation model in Supplementary materials.

Reviewer: I compared some of Golonka's original maps to the updated paleogeographies. In some cases I was not able to see any of the modifications (see Figure 3). It would be good to have a complete set of maps with the red and green symbols plotted as in Figures 4 & 5. That way we could see what was changed.
Authors: The paleo-coastlines are significantly different, except for a few time-interval maps where have few fossil data. We have included a set of maps to demonstrate that (see a set of maps in Supplement materials).

Reviewer: When I loaded the Paleobiology data points in Gplates, I could not distinguish the "marine" from the "terrestrial" data points. The only attributes that I could discern were "plateid" and "end and start" times. The marine data and the terrestrial data should be in separate files.
Authors: We have provided consistent and inconsistent marine fossil collection data in separate files (see Supplement materials) as only marine fossil data are used in the revision.

Interactive comment on “Improving global paleogeography since the late Paleozoic using paleobiology” by Wenchao Cao et al.

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Reviewer: The authors attempt to produce a flexible, digital representation of Earth’s plates through most of the Phanerozoic. This representation should allow testing paleogeographic features of the original dataset against other datasets, adopting different rotation models as used in the original dataset, among other things. The authors then use a comparison of their original distributions of land and sea to that implied by the distribution of fossil organisms, to get a more accurate picture of the distributions of land and sea through Earth’s history. These ‘improved’ distributions are then used for various comparisons with eustatic sea level curves and measures for continental weathering. Although the attempt to build a flexible model of Earth’s plate movements through time is fine and useful, most of the subsequent comparisons are, in my view, redundant, insufficiently interpreted and discussed. Also the methods section needs improvements. In the present state I can only recommend to reject the manuscript, and to encourage the authors to focus on the core of their work (the model), to improve the methods section, and revamp their ‘testing’ and their discussion.
Authors: We thank the reviewer for his/her constructive review that has guided our revision of the manuscript. We have amended the paleogeographic model, given more detail in the Methods section, and changed the tests carried out on the paleogeographies using paleobiology. We have deleted the comparison between continental flooding curves and published sea level fluctuations as there may be some circularity in this comparison, and the comparison between emerged land area, total land area and the evolution of strontium isotopes of marine carbonates. Instead, we have compared our flooded continental area curve to previously published ones (see revised Fig. 9). We have estimated the terrestrial and oceanic areal change due to filling gaps and modifying the coastline locations and the paleogeographic geometries over time (see Fig. 10 in the revision), tested the marine fossil collection dataset used in this study for fossil abundances over time with two different time scales (see Fig.11 in the revision), and discussed the limitations of the workflow we develop in this study.

Reviewer: Detailed comments by line number: 106-108, there is another important bias in the PBDB: the uneven entry of fossil data.
Authors: We agree and have added this to the sentence in the revision (line 118).

Reviewer: 116-117, repetition
Authors: We have rewritten this sentence in the revision (lines 126-130).

Reviewer: 145-147, I have the feeling that the authors are trying to explain here which environmental types have gone into the gaps and overlaps, but I failed to understand it.
Authors: We have deleted this sentence to avoid any confusion.

Reviewer: 155-159, here the authors sometimes talk about ‘fossil collections’ and sometimes about ‘fossils’, though my impression is that they always mean ‘fossil collections’ – please be consistent here and throughout the ms in general.

Authors: Yes, they all mean ‘fossil collections’. This has been corrected throughout the manuscript.

Reviewer: 187-190, unclear how it was decided which ‘fossils’ (by which the authors presumably mean ‘fossil collection site’) are included in such a cluster and which aren’t. It is important to make clear how the boundaries of these clusters are drawn.
Authors: In our revised version of the maps, we only use marine fossil collections to improve paleo-coastline locations and the paleogeographic geometries (see revised Figs 4, 5, 6), because the coastlines on the paleo-maps used in this study represent maximum transgression surfaces, so this is not the case anymore.

Reviewer: 235-243, this entire test is redundant: if you’re adjusting the land-sea boundary in such a way that most inconsistencies are removed, of course does your ‘consistency index’ improve.
Authors: We have deleted the test of modified paleogeography with paleobiology, and only presented the test of unmodified paleogeography (see revised Fig. 6).

Reviewer: Paragraph 245-257, it is not clear to me what the authors are getting at with this paragraph. They discuss various biases and inhomogeneities of the fossil data, but neither do they apply a coherent test to the problem, nor do they reach any conclusion (except perhaps for “fewer fossils = fewer possibilities for adjustments”, but this again is trivial).
Authors: We have carried out a test on the marine fossil collection dataset used in this study for fossil abundances over time with two different time scales: ICS2016 and Golonka (2000) (see revised Table 1), and we have revised this paragraph (lines 231-240), deleted the trivial part, presented the result (see Fig. 11 in the revision) and discussed it in the Discussions section (lines 325-339).

Reviewer: 245-249, as for lines 106-108, uneven entry of data is another potential bias.
Authors: We have added this in the revision (lines 235).

Reviewer: 249-251, “shorter time spans contain fewer fossils” – it might be interesting to systematically test the fossil dataset for this.
Authors: We have tested the dataset used in this study for fossil abundances over time with two different time scales: ICS2016 and Golonka (2000) (see revised Table 1), presented the result (see Fig. 11 in the revision) and discussed it in the Discussions section (lines 325-339).

Reviewer: 253, “biological organisms” – organisms are biological by definition
Authors: We have removed “biological” in the revision.

Reviewer: 264-267, here I was wondering how much of the “areal change” might relate to the gap filling and overlap removal that the authors have done to fit the plate reconstructions. In their lines 144-145 they wrote that the total areal variations ranged from 5.8 to -2.7%. A comparison of these values through time to the extent of area change through time (or something along these lines) might provide valuable insights here.
Authors: We have estimated the areal change in two key steps of the methodology, including filling gaps and modifying the coastline locations and paleogeographic geometries,

presented the results (see Fig. 10 in the revision) and explained it in the Discussions section (lines 303-323).

Reviewer: 281ff, unless I've overlooked it, there is a step missing here in the explanation of the method. So far, the authors explained that in their adjustments, they exchanged 'land' for 'sea' and vice versa. But now they start discussing the quantification of different habitat types (shallow vs. deep sea, mountains vs. low lands etc.). Does this mean that when the land-sea boundary was shifted, for example, the 'new sea area' was assigned the habitat type of the fossil collection that caused the change? For example, has an area previously classified as 'mountain' sometimes been replaced by 'shallow marine' and sometimes by 'deep marine'? If so, this needs to be explained in the Methods section.
Authors: We have explained this in the Methods section (lines 188-189).

Reviewer: 310ff, this whole paragraph seems redundant. It is pretty obvious to any earth scientist that continental flooding and eustatic sea level changes are linked. Not only is it obvious that eustatic sealevel changes cause continental flooding (what else should it be?); to make matters worse, the eustatic sealevel curves are inferred from the continental flooding history as recorded in the sedimentary record so you might be looking at circularity here.
Authors: We have removed this entire paragraph as indeed there could be some degree of circularity.

Reviewer: 332, the difference between 27.7% and 27.5% isn't really great, isn't it? The authors should be a little more cautious about the errors in their own model. Could this difference of 0.2% again result from their gap filling procedure? Or could it be related to the inconsistencies in their 'improved paleogeographies'? In their lines 238-241 they write that even their 'improved paleogeographies' are still 3-5% inconsistent, which is a lot more than the 0.2% difference mentioned above. I recommend that the authors assess these inherent errors in their model (gap filling and 'consistency' index) and then discuss only variations that exceed those errors.
Authors: Since we have deleted the comparison between emerged land area, total land area and the evolution of strontium isotopes, this part has been removed accordingly. As suggested here, we have amended the paleogeographic model and updated the test carried out on the paleogeographies using paleo-environments indicated by marine fossil collections from the PBDB. We have estimated the errors of two key steps in the workflow, including filling gaps and modifying the coastline locations and the paleogeographic geometries, on the terrestrial areal change over time (see Fig. 10 in the revision) and discussed them in the Discussions section (lines 303-323).

Reviewer: 341, 3% of the world's continental area has disappeared in the Neogene? Where did it go?
Authors: The Neogene increase in mountainous areas results in a net loss of continental area.

Reviewer: 350-351, the abbreviation CGM is not explained (and perhaps not necessary?)
Authors: As we have deleted this entire paragraph, this has been deleted in the revision accordingly.

Reviewer: 363, I find it dubious to 'confirm that Sr isotope ratios have a good correlation with emerged land areas' when there is no such correlation in the Paleozoic. Doesn't this rather indicate that there may be something fundamentally wrong with this correlation? I have no solution to the problem, but it seems more scientifically to me to point out such inconsistencies rather than to uncritically reiterate some lukewarm 'conventional wisdom'.
Authors: We have deleted the comparison between emerged land area, total land area and the evolution of strontium isotopes of marine carbonates in the revision.

Reviewer: 366ff, the 'Conclusions' nicely sum up the good parts and the problems of this study. The first paragraph outlines the good part, the flexible, digital plate model that could surely be of use for a wide range of earth scientists. The second paragraph discusses the redundant correlation between emerged land and eustatic sea level changes, and the third paragraph again 'confirms' a correlation between Sr isotopes and emerged land, which apparently doesn't exist in the Paleozoic.
Authors: Our conclusions have been amended in the revision, based on the input from the reviewer.

Reviewer: Table 1. why is this awkward Sloss 1988 timetable used? As far as I can tell, it applies to the US only, and connecting it to the accepted ICS and GSA timescales and to the periods, series and stages that have been used by geologists for more than 100 years is confusing. Avoid this, it is of no use for geologists and paleontologists.
Authors: Sloss (1988) is the base of the time scale of Golonka (2000) applied to the paleogeography used in this study. We have converted the time scales of Sloss (1988) and Golonka (2000) to agree with the ICS2016 and presented them together in the table (see revised Table 1).

Reviewer: Table 2, I had difficulties relating this table to what's written in the manuscript. The table distinguishes three paleogeographies (shallow marine, landmass/mountain, ice sheet), whereas in the text and fig 8 five distinctions are made (shallow marine, deep marine, land masses, mountains, ice sheets). Please be consistent here.
Authors: We have corrected this in the revision (see revised Table 2).

Reviewer: Figure 5. colors and shapes are not explained; perhaps refer to fig. 4? And I presume you mean "fossil collection sites" rather than "fossils"? I don't see any fossils in this figure.
Authors: We have replaced Figure 5 by a new figure (see Fig. 5 in the revision) in which the colours and shapes have been explained clearly. Yes, we refer to "fossil collection sites" rather than "fossils" and we have corrected this throughout the manuscript.

Improving global paleogeography since the late Paleozoic using paleobiology

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Abstract. Paleogeographic reconstructions are important to understand Earth's tectonic evolution, past eustatic and regional sea level change, paleoclimate and ocean circulation, deep Earth resources, ~~hydrocarbon genesis,~~ and to constrain and interpret the dynamic topography predicted by ~~time-dependent global~~ mantle convection models. ~~Several~~ G~~g~~lobal paleogeographic maps have been compiled and published, but they are generally presented as static maps with varying ~~temporal resolution and fixed spatial resolution.~~ map projections, different time intervals represented by the maps, and different plate motion models that underlie the paleogeographic reconstructions. ~~Existing global paleogeographic maps are also tied to a particular plate motion model,~~This makes~~ing~~ it difficult to convert the maps into a digital form and link them to alternative digital plate tectonic reconstructions. To address this limitation, we develop~~ed~~ a workflow to ~~reverse-engineer~~restore global paleogeographic maps to their present-day coordinates and enable them to be linked to ~~any~~ a different tectonic reconstruction. ~~Published paleogeographic compilations are also tied to fixed input datasets.~~ We use~~d~~ marine fossil ~~data~~ collections from the Paleobiology Database to identify inconsistencies between ~~fossils~~their indicative paleo-environments and published paleogeographic maps, and ~~to improve~~ revise the locations of inferred ~~terrestrial-marine boundaries~~paleo-coastlines that represent the estimated maximum transgression surfaces by resolving these inconsistencies. As a result, the ~~overall~~ consistency ratio between the paleogeograph~~y~~y and the paleo-environments indicated by the marine fossil collections ~~fossil collections was~~is ~~improved~~ increased from an average 75~~6.9~~% to ~~-~~nearly full consistency (100%). The paleogeography in the main regions of North America, South America, Europe and Africa is significantly revised, especially in Late Carboniferous, Middle Permian, Triassic, Jurassic, Late Cretaceous and most of Cenozoic times. ~~96.1%. We~~ The global flooded continental areas since Early Devonian times calculated from the revised paleogeography in this study are generally consistent with results derived from other paleo-environment and paleo-lithofacies data and with the strontium isotope record in marine carbonates. We also ~~estimated~~ estimate the terrestrial areal change over time associated with transferring reconstruction, filling gaps and modifying the paleogeographic geometries based on the paleobiology test. This indicates that the variation of the underlying plate

reconstruction is the main factor that contributes to the terrestrial areal change, and the effect of revising paleogeographic geometries based on paleobiology is secondary.~~the surface areas of global paleogeographic features (shallow marine environments, landmasses, mountains and ice sheets), and reconstructed the global continental flooding history since the late Paleozoic based on the amended paleogeographies. Finally, we discuss the relationships between emerged land area and total continental crust area through time, continental growth models, and strontium isotope ($^{87}Sr/^{86}Sr$) signatures in ocean water. Our study highlights the flexibility of digital paleogeographic models linked to state-of-the-art plate tectonic reconstructions in order to better understand the interplay of continental growth and eustasy, with wider implications for understanding Earth's paleotopography, ocean circulation, and the role of mantle convection in shaping long-wavelength topography.~~

1 Introduction

Paleogeography, describing the ancient distribution of highlands, lowlands, shallow seas, and deep ocean basins, is widely used in a range of fields including paleoclimatology, plate tectonic reconstructions, paleobiogeography, resource exploration and geodynamics. ~~Several ~~G~~g~~lobal deep-time paleogeographic compilations have been published (e.g. Blakey, 2008; Golonka et al., 2006; Ronov, et al., 1984, 1989; Scotese, 2001, 2004; Smith et al., 1994). However, they are generally presented as static paleogeographic snapshots with varying map projections and different time intervals represented by the maps~~temporal resolution and fixed spatial resolution~~, and are tied to ~~a particular~~different plate motion models. ~~-~~This makes it difficult to convert the maps into a digital format, link them to alternative digital plate tectonic reconstructions, and ~~to~~ update ~~paleogeographic maps~~them when plate motion models are improved. It is therefore challenging to use paleogeographic maps to help constrain or interpret numerical models of mantle convection that predict long-wavelength topography (Gurnis et al., 1998; Spasojevic and Gurnis, 2012) based on different tectonic reconstructions, or as an input to models of past ocean and atmosphere circulation/climate (Goddéris et al., 2014; Golonka et al., 1994) and models of past erosion/sedimentation (Salles et al., 2017).

In order to address th~~is~~ese issues, we develop~~ed~~ a workflow to ~~reverse-engineer~~restore ~~published~~ the ancient paleogeographic geometries back~~es~~ to their ~~corresponding present-day~~modern coordinates so that the geometries could be attached to ~~any~~ a different plate motion model. This ~~was~~ is the first step towards the construction of paleogeographic maps with flexible spatial and temporal resolutions that are more easily testable and expandable with the incorporation of new paleo-~~-~~environmental datasets (e.g. Wright et al., 2013). In this study, we use~~d~~ a set of global paleogeographic maps (Golonka et al., 2006) covering the entire Phanerozoic time period as the base paleogeographic model. Coastlines on these paleogeographic maps represent estimated maximum marine transgression surfaces (Kiessling et al., 2003). We first ~~reverse-engineered~~restore the~~se~~ global paleogeographic ~~maps~~ geometries of Golonka et al. (2006) to their present-day coordinates by reversing the sign of the rotation angle, and then ~~then~~ reconstruct~~ed~~ them to geological times using ~~the~~ a different plate motion model ~~of~~of Matthews et al. (~~(~~2016). ~~Subsequently, w~~We then use~~d~~ paleo-environmental information from marine fossil collections~~fossil data~~ from the Paleobiology Database ~~(https://paleobiodb.org)~~ to ~~identify inconsistencies between fossils paleo-environments and the paleogeographic maps, and to improve~~modify the ~~location of~~ inferred ~~terrestrial-marine boundaries~~paleo-coastline locations and paleogeographic geometries ~~by resolving these inconsistencies~~. ~~Finally~~Next, we use~~d~~ the ~~improved~~ revised ~~reconstructed~~ paleogeography~~ies~~ to estimate the surface areas of global paleogeographic features including ~~(~~deep oceans, shallow marine environments, landmasses, mountains and ice sheets~~), to investigate the global continental flooding history since the Devonian and compare it with global sea level change over time (Haq et al., 1987; Haq et al., 2008; Müller et al., 2008)~~. In addition, we compare the global flooded continental areas since the Devonian Period calculated from the revised paleogeography with other results derived from other paleo-environment and paleo-lithofacies maps (Ronov, 1994; Smith et al., 1994; Walker et al., 2002; Blakey, 2003, 2008; Golonka, 2007b, 2009, 2012) or from the Strontium isotope record (van der Meer et al., 2017). W~~we~~e ~~discussed~~ estimate the terrestrial areal change over time associated with transferring reconstruction, filling gaps and modifying the paleogeographic geometries based on consistency test. Finally, we test the marine fossil collection dataset used in this study for fossil abundances over time using different time scales of 2016 time scale of the International Commission on Stratigraphy (ICS2016) and Golonka (2000) and discuss the limitations of the workflow we develop in this study.

~~the evolution of the modelled emerged land area and total continental area in connection with continental growth models, the strontium isotope ($^{87}Sr/^{86}Sr$) signature from the proxy records (Flament et al., 2013; van der Meer et al., 2017), and the assembly and breakup of Pangea.~~

2 Data and Paleogeographic Model

The data used in this study are global paleogeographic maps and ~~paleontological~~ paleo-environmental data for the last 402 million years (Myr), which originate from the set of paleogeographic ~~-~~maps produced by Golonka et al. (2006) and the Paleobiology Database (PBDB, paleobiodb.org)~~(https://paleobiodb.org)~~, respectively. The global paleogeographic compilation extending back to Early Devonian times of~~by~~ Golonka et al. (2006)~~, spanning the entire Phanerozoic,~~ is divided into 24~~32~~ time-interval maps using the time scale of Golonka (2000) which is based on the original time scale of Sloss (1988) (Table 1). Each map is a compilation of paleo-lithofacies and paleo-environments for each geological time interval. These paleogeographic reconstructions illustrate the changing configuration of ice sheets, mountains, landmasses, shallow marine environments (inclusive of shallow seas and continental slopes) and deep oceans ~~during~~ over the last ~ ~~544~~ 400 ~~million years~~Myr.

[Insert Table 1]

The paleogeographic maps of Golonka et al. (2006) ~~were~~ are constructed using a plate tectonic model available in the Supplement of Golonka (2007a), ~~which~~where ~~described the~~ relative plate motions are described~~between plates and terranes~~. In this rotation model, paleomagnetic data ~~were~~ are used to constrain the paleolatitudinal positions of continents and rotation of plates, and hot spots, where applicable, ~~were~~ are used as reference points to calculate paleolongtitudes (Golonka, 2007a). This rotation model is necessary to ~~accurately reverse-engineer~~restore these paleogeographic geometries~~es~~ (Golonka et al., 2006) to their present-day coordinates so that they can be attached to ~~any~~ a different ~~modern~~ plate motion model. The relative plate motions of Golonka (2006, 2007a) are ~~similar to~~based on ~~those~~ the reconstruction of~~in~~ Scotese (1997, 2004).

Here, we use a global plate kinematic model to reconstruct paleogeographies back in time from present-day locations. The global tectonic reconstruction of Matthews et al. (2016), with continuously closing plate boundaries from 410-0 Ma, is primarily constructed from a Mesozoic and Cenozoic plate model (230-0 Ma) (Müller et al., 2016) and a Paleozoic model (410-250 Ma) (Domeier and Torsvik, 2014). This model is a relative plate motion model that is ultimately tied to Earth's spin axis through a paleomagnetic reference frame for times before 70 Ma, and a moving hotspot reference frame for younger times ~~an absolute reference frame~~ (Matthews et al., 2016).

[Insert Figure 1]

The ~~Paleobiology Database~~PBDB ~~(https://paleobiodb.org)~~ is a compilation of global fossil data covering deep geological time. All fossil collections~~s~~ in the database ~~are associated with~~contain detailed metadata, including the time range (typically biostratigraphic age), present-day geographic coordinates, host lithology, and paleo-environment. Figure 1 ~~visualizes~~ represents ~~global fossil~~ distributions of the global fossil collections at present-day coordinates and shows their ~~total~~ numbers~~s~~ ~~of fossil collections on Earth~~ since the Devonian Period ~~period~~. The ~~documented~~ recorded fossil collections~~s~~ are unevenly distributed both spatially and temporally, largely due to the differences in fossil preservation, ~~and~~ the spatial sampling biases of fossil localities and the uneven entry of fossil data to the PBDB (Alroy, 2010). For this study, a total of 57,854 fossil collections with temporal and paleo-environmental assignments from 402 Ma to 2 Ma were downloaded from the database on 7 September 2016.

3 Methods

[Insert Figure 2]

The methodology can be divided into three main steps: (1) the original paleogeographic geometries are restored to present-day coordinates by applying the inverse of the rotations used to make the reconstruction, (2) these restored geometries are then rotated to new locations using the plate tectonic model of Matthews et al. (2016), (3) the paleo-coastline locations and paleogeographic geometries are adjusted using paleo-environmental data from the PBDB. ~~The methodology mainly involves the processes of paleogeographic reverse-engineering, subsequent reconstructing in another rotation model and eventually improving using paleobiology data.~~ Figure 2 illustrates the~~a~~ generalized workflow that can be applied to ~~any~~ a different paleogeography model. In order to represent the paleogeographic maps as digital geographic geometries, they are first georeferenced using the original projection and coordinate system (~~such as~~ global Mollweide in Golonka et al., 2006), and then reprojected into the WGS84 geographic coordinate system. The resulting maps are then attached to the original rotation model using the open-source and cross-platform plate reconstruction software~~,~~ *GPlates* (gplates.org). ~~(www.gplates.org).~~ Every plate is then assigned a unique plate ID that defines the rotation ~~rules~~ of the tectonic elements~~in geological times~~ so that the paleogeographic geometries~~es~~ can be rotated back to their present-day coordinates (see example in Figs~~.~~ 3a, b). We use present-day coastlines and terrane boundaries with the plate IDs of Golonka (2007a) as a reference to refine the rotations and ensure that the paleogeographic geometries are restored accurately to their present-day locations~~a high accuracy of the reverse engineering~~.

When the paleogeographic ~~maps~~ geometries in present-day coordinates are attached to a new reconstruction model, ~~e.g.~~as Matthews et al. (2016) ~~as~~ used in this study, the resulting paleogeographies ~~contain~~ result in gaps (Fig. 3c, pink) and overlaps between neighbouring polygons, when compared to the original reconstruction (Fig. 3a). These gaps and overlaps essentially arise from the differences in the reconstructions described in Matthews et al. (2016) and Golonka et al. (2006). The reconstruction of Golonka et al. (2006) ~~typically~~ has a tighter fit of the major continents within Pangea prior to the supercontinent breakup. In addition, this reconstruction contains a different plate motion history and block ~~boundaries~~ boundary definitions in regions of complex continental deformation, for example along active continental margins (e.g. Himalayas, western North America, Fig. 3c).

The gaps and overlaps cause changes~~s~~ in the total terrestrial or oceanic paleogeographic areas ~~of paleogeographies~~ at different time intervals, becoming larger or smaller, when compared with the original paleogeographic ~~-~~maps (Golonka et al., 2006). The gaps can be fixed by interactively extending the outlines of the polygons in a GIS platform to make the plates connect as in the original paleogeographic ~~-~~maps (Fig. 3a, c, ~~and~~ d). ~~The resulting paleogeographies with fixed gaps (Fig. 3d)~~ C~~c~~hanges in the~~to~~ ~~different~~ extent of ~~in~~ total terrestrial or oceanic area of the paleogeographies with filled gaps are compared with the original paleogeographies in Fig. 3d (Golonka et al., 2006). ~~The total areal variations range from the maximum 5.8% to the minimum -2.7%, with an average of -1.4%. To avoid artefacts introduced from overlapping paleogeographies, the drawing order was standardized using the following sequence: ice sheets, mountains, landmasses and finally shallow marine environments (top to bottom layering).~~

[Insert Figure 3]

Once the gaps are filled, the reconstructed paleogeographic features are compared with the paleo-environments indicated by the marine fossil collections from the PBDB. These comparisons aim to identify the differences between the mapped paleogeography and the marine fossil collection environments in order to revise the paleo-coastline locations and paleogeographic geometries.~~Once the gaps are fixed, the consistency between the reconstructed paleogeography and paleobiology data can be tested. These tests are aimed at identifying inconsistencies between fossil-derived paleo-environments and underlying paleogeographies in order to improve the accuracy of marine-terrestrial boundaries in the paleogeographic maps.~~ Fossil collections belonging to each time interval (Table 1, Golonka, 2000) a~~a~~re first ~~first~~ extracted from the dataset downloaded from the ~~Paleobiology Database~~PBDB. Only the fossil collections with temporal ranges lying entirely within the corresponding time intervals ~~were~~ are selected, as opposed to including the fossil collections that have larger temporal ranges. Fossil collections with temporal ranges crossing any time-interval boundary are not taken into consideration. As a result, a minimum number of fossil collections ~~were~~ are selected for each time interval. The selected fossil collections ~~were~~ are classified into either terrestrial or marine setting category, according to a lookup table (Table 2).~~Alternatively, the terrestrial and marine fossil data could be separately downloaded from the Paleobiology Database. In this process, each fossil with a specific environment would be automatically oriented into the corresponding terrestrial or marine groups based on the same classification scheme (Table 2). Fossil collections would then be extracted in each time interval (Table 1) from terrestrial and marine fossils subgroups, respectively.~~

[Insert Table 2]

Marine f~~F~~ossil collections are then attached to the plate motion ~~motion~~ model of Matthews et al. (2016) so they can be reconstructed at each time interval. Subsequently, a point-in-polygon test is used to determine whether the indicated marine fossil collection is within the appropriate marine paleogeographic polygon. The results of these tests is discussed in the following section.~~Subsequently, a point in polygon test is used to verify if the indicative paleo-environment (terrestrial or marine) of fossil collections is consistent with the underlying paleogeographic features. In this process, polygons are tested in the following sequence: ice sheets, mountains, landmasses and shallow marine environments. Terrestrial fossil paleo-environments correspond to landmass, mountain or ice sheet paleogeography. Fossil shallow marine environments map to marine environments in paleogeography.~~

In the next step, we modify the paleo-coastline locations and paleogeographic geometries based on the test (Fig. 4, 5 and Supplement). ~~Based on the inconsistencies between fossils paleo-environments and underlying paleogeographies, we can modify the terrestrial-marine boundaries in the paleo-maps. Figures 4 and 5 illustrate how to modify the marine-terrestrial boundaries in the paleogeographic maps based on the test results.~~ Modifications are made according to the following rules: (1) Marine f~~F~~ossil collections from the ~~Paleobiology Database~~PBDB are presumed to be well-dated, constrained geographically, not reworked and representative of their broader paleo-environments. Their indicative environments are assumed to be correct. (2) Only fossil collections~~s~~ within 5~~1~~00 km of the nearest ~~terrestrial-marine boundary~~paleo-coastline ~~(for instance, d1 ≤ 100 km in Fig. 4b)~~ are taken into account ~~as valid proxies to improve marine-terrestrial boundaries~~. (3) The paleo-coastlines and paleogeographic geometries ~~boundaries~~ are modifi~~shift~~ed until ~~the fossils~~ they ~~environments~~ are consistent with the marine fossil collection environments ~~underlying paleogeography~~ and at the same time remain ~~within~~ about 3~~2~~0 km distance from the fossil points~~s~~ used (Fig. 5~~4~~c, f, l~~e, d2 ≈ 20 km~~). (4) The adjacent ~~boundary~~ paleo-coastlines are~~is~~ accordingly adjusted and smoothed (Fig. 4, 5~~4c and Fig. 5c~~). (5) The modified area (Fig. 5b, e, k, blue) resulting from shifting the coastline is filled using the shallow marine environment. ~~(5) Occasionally, some adjacent fossils near the same boundary may indicate conflicting paleo-environments. In this case, we treat these adjacent fossils as a cluster, in which the environment represented by over 50% of fossils is considered to be indicative of the environment of the entire cluster. For example, the fossils in the black circle in Fig. 5b are regarded as a cluster, in which over 50% of fossils indicate a shallow marine environment.~~ These rules are designed to maximize the use of the paleo-environmental information obtained from the marine fossil collections ~~paleobiology~~ to improve the coastline locations and paleogeography while attempting to minimize ~~incorrect~~ spurious modifications. ~~We note that in some cases the paleogeography cannot be fully reconciled with the Paleobiology Database (for example, inconsistent terrestrial fossils in the black circle in Fig. 5b).~~

[Insert Figure 4]

[Insert Figure 5]

However, in some rare cases, outlier marine fossil data~~s~~ may be a deceptive recorder of paleogeography. For instance, Wichura et al. (2015) discussed the discovery of a ~17 Myr old beaked whale fossil 740 km inland from the present-day coastline of the Indian Ocean in the East Africa. The authors found evidence to suggest that this whale could have travelled inland from the Indian Ocean along an eastward-directed fluvial (terrestrial) drainage system and was stranded there, rather than representing a marine setting that would be implied under our assumptions. Therefore, theoretically, when using the ~~paleobiology~~ fossil collections to improve paleogeography, additional concerns about living habits of fossils and associated geological settings should be taken into account. In this study, we have removed this misleading fossil whale from the dataset. Such instances of deceptive fossil data are a potential limitation within our workflow, which we seek to minimise by excluding inconsistent fossils more than 500 km away from previously interpreted paleoshorelines described above.~~Such instances of deceptive fossils are rare.~~

4 Results

4.1 ~~Paleobiology~~ Paleo-environmental ~~Tests~~tests

Global reconstructed paleogeographic maps from 402 Ma to 2 Ma are tested against paleo-environments indicated by the marine ~~and terrestrial~~ fossil collections~~s~~ that are reconstructed in the same rotation model (Matthews et al., 2016). The ~~marine fossils~~ consistency ratio is defined by the marine fossil collections~~s~~ within shallow marine or deep ocean paleogeographic polygons as a percentage of all marine fossil collections~~s~~ at the time interval, and in contrast, the ~~marine fossils~~ inconsistency ratio, by the marine fossil collections~~s~~ not within shallow marine or deep ocean paleogeography as a percentage of all marine fossil collections~~s~~. ~~Similarly, the terrestrial fossils~~

~~consistency ratio is defined by the terrestrial fossils within landmass, mountain or ice sheet feature as a percentage of all terrestrial fossils at the time interval and the terrestrial fossils inconsistency ratio, by terrestrial fossils within shallow marine paleogeographic polygons as percentage of all terrestrial fossils at the time interval.~~ Heine et al. (2015) ~~applied~~ used a similar metric to evaluate global paleoshoreline models since the Cretaceous.

The inconsistent marine fossil collections are used to modify coastlines and paleogeographic geometries according to the rules outlined in the Methods section.~~This test shows relatively high consistency between fossil paleo-environments and the underlying paleogeographic features (Fig. 6). The results since the Cretaceous are similar to that of Heine et al. (2015). In this study,~~ T~~t~~he consistency ratios of marine ~~and terrestrial~~ fossil collections~~s~~ during 402-2 Ma ~~both~~ are all ~~generally~~ over 55~~0~~%, with an average of 75~~4.8~~% (~~marine fossils,~~ Fig. 6a, shaded area) ~~and 77.1% (terrestrial fossils, Fig. 6b, shaded area) but~~ although with large ~~both accompanying strong~~ fluctuations over time (Fig. 6). This indicates that the paleogeography of Golonka et al. (2006) has relatively high consistency with the fossil records. However, 52 fossil collections over all time intervals cannot be resolved as they are over 500 km distant from the nearest coastline (For example, red points on Fig. 5c, l). Therefore, in some cases, the paleogeography cannot be fully reconciled with the paleobiology (see Supplement). The results since the Cretaceous are similar to that of Heine et al. (2015). ~~Only at the time interval of 402-380 Ma, the terrestrial fossils consistency ratio drops to approximately 20.0%, but this result is not reliable because there are only 18 terrestrial fossil collections available for this time interval.~~

[Insert Figure 6]

~~The inconsistent marine and terrestrial fossils are used to improve marine-terrestrial boundaries in the paleogeographic maps according to the rules outlined in the Method section. Subsequently, the modified paleogeographies are tested using the same fossils. The results show the consistency ratios of marine and terrestrial fossils increased to average 97.1% (marine fossils, Fig. 6a, black line) and average 85.9% (terrestrial fossils, Fig. 6b, black line) respectively after paleogeographies are modified and the overall fossils, rising from average 76.9% before modification (Fig. 6c, shaded areas) to average 96.1% after modification (Fig. 6c, black lines). Marine fossils (Fig. 6a, black lines) show better final consistency than terrestrial fossils (Fig. 6b, black lines), mainly because marine fossils records are less sparse than terrestrial fossils through time (Fig. 6d).~~

The sums of ~~terrestrial and~~ marine fossil collections change significantly over time (Fig. 6b~~d~~), for example, more than 40~~2~~00 in total within 269-248 Ma but ~~less than~~only 2~~5~~0 during~~in~~ 37-29 Ma. These variations ~~could be~~are due to the spatiotemporal sampling bias and incompleteness of the fossil record (Benton et al., 2000; Benson and Upchurch, 2013; Smith et al., 2012; Valentine et al., 2006, Wright et al., 2013), biota extinction and recovery (Hallam and Wignall, 1997; Hart, 1996)~~, or our temporal selection criterion~~the uneven entry of fossil data to the PBDB (Alroy, 2010) and our temporal selection criterion. In addition, the differences in the duration of geological time subdivisions lead to some time-intervals having shorter time spans that contain fewer fossil records, which we discuss in a later section. ~~Specifically, marine fossils are generally more common than terrestrial fossils (Fig. 6d) as shallow marine environments can provide conditions that are more favorable to the preservation of biological organisms.~~ As for the time intervals during which fossil data are~~is~~ scarce, ~~paleobiology data~~the fossil collections are~~is~~ of limited use in improving paleogeography. ~~For instance, there are less than 300 fossil collections in total in the time interval of 380-359 Ma mainly due to the late Devonian mass extinction (McGhee, 1996).~~ However, additional records in the future will increase the usefulness of the ~~Paleobiology Database~~PBDB in such instances.

4.2 ~~Improved~~ Revised ~~Global~~ global ~~Reconstructed~~ reconstructed ~~Paleogeography~~paleogeography

Based on the PBDB test ~~testing~~ results at~~of~~ all the time intervals, we can ~~improve~~ revise the inferred ~~marine-terrestrial boundaries~~ paleo-coastlines and paleogeographic geometries ~~in the global reconstructed paleogeographic maps~~ using the approach described in the Methods section. As a result, the revised paleo-coastlines and paleogeographies are significantly improved, mainly in the regions of North America, South America, Europe and Africa during Late Carboniferous, Middle Permian, Triassic, Jurassic, Late Cretaceous and most of Cenozoic times (Figs 4, 5, 6 and Supplement). The resulting improved global paleogeographic maps since ~~the~~ Devonian times are presented in Figure 7. They ~~. Although the modifications make the areal change minimally with regards to a global context, the resulting paleogeographies can~~ provide improved ~~us more accurate marine-terrestrial boundaries~~paleo-coastlines that ~~would be~~are important to ~~generate precise paleoshorelines and therefore help~~ constrain past changes in sea level and long-wavelength dynamic topography.

[Insert Figure 7]

We subsequently calculate the area covered by each paleogeographic feature as a percentage of ~~the~~ Earth's total surface area at each time interval from 402 Ma to 2 Ma (Fig. 8~~b~~), using the HEALPix pixelization method that results in equal sampling of data on a sphere (Górski et al., 2005) and therefore equal sampling of surface areas. This method effectively excludes the effect of overlaps between paleogeographic geometries. ~~Using the resulting percentages of the paleogeographic features at each time interval, we determine their surface areas on Earth (Fig. 8a) and their percentages accounting for the Earth's total surface area (Fig. 8b) for each time interval between 402 and 2 Ma.~~

[Insert Figure 8]

As a result, the areas of landmass, mountain and ice sheet generally indicate increasing trends, while shallow marine and deep ocean areas show decreasing trends through geological time (Fig. 8). Overall, the computed areas increase ~~are sequentially becoming larger~~ in the order of ice sheet (average 1.0% of Earth surface), mountain belts (3.4%), shallow marine (14.3~~2~~%), landmass (21.3%) and deep ocean

(60.1%). Only during~~in~~ the time interval of 323-296 Ma, landmass and shallow marine areas are nearly equal at about 14.0%, and only during 359-285 Ma, ice sheet areas exceed mountain areas but ice sheets only exist during 380-285 Ma, 81-58 Ma, and 37-2 Ma. With Pangea formation during~~in~~ the latest Carboniferous or the Early Permian and breakup initiation in the Early Jurassic (Blakey, 2003; Domeier et al., 2012; Lenardic, 2016; Stampfli et al., 2013; Vai, 2003; Veevers, 2004; Yeh and Shellnutt, 2016), these paleogeographic feature~~s~~ areas significantly change ~~remarkably~~ over time (Fig. 8). During 323-296 Ma (Late Carboniferous-the earliest Permian), the landmass extent~~es~~ reach~~e~~es~~d~~ their smallest area (13.6%) and subsequently ~~underwent~~ undergoes a rapid increase until they peak~~ed~~ at 26.6~~7~~% between~~in~~ 224-203 Ma (Late Triassic). In contrast, ice sheets reach~~ed~~ their largest area (7.2%) ~~at that time~~between 323-296 Ma. In the Early Jurassic of Pangea breakup, landmass areas rapidly decrease~~d~~ from 26.6~~7~~% between~~in~~ 224-203 Ma to 234.5~~6~~% between~~in~~ 203-179 Ma but shallow marine areas ~~significantly~~ increase~~d~~ by 3.7%.

~~**4.3 Global Continental Flooding History**~~

~~[Insert Figure 9]~~

~~We calculate the global flooding ratio of continental crust from 402 to 2 Ma (Fig. 9a, blue) by dividing the shallow marine area (Fig. 8a, lightblue) by the total continental area (inclusive of shallow marine, landmass, mountain and ice sheet; Fig. 9b, blue). The continental flooding ratios rapidly decrease from about 45.2% in the Late Devonian to 27.7% in 224-203 Ma of the Late Triassic, after that it peaks, with frequent fluctuations, at 41.8% in 94-81 Ma of the Late Cretaceous. That is then followed by a quick decrease again until it reaches the lowest point at 27.6% in 11-2 Ma.~~

5 Discussions

54.1~~3~~ Global flooded ~~C~~continental ~~Flooding~~ areas~~History~~

[Insert Figure 9]

We estimate ~~calculate~~ the global flooded ~~ing ratio of~~ continental ~~crust~~areas ~~from~~since Early Devonian times ~~402 to 2 Ma (Fig. 9a, blue)~~ from the revised paleogeography in this study (Fig. 9, pink solid line) and from the original paleogeographic maps of Golonka et al. (2006) (Fig. 9, grey solid line). Both sets of results are similar, with a decrease during Pangea amalgamation from the late Devonian Period until the Late Carboniferous Period, increase from Early Jurassic times with the breakup of Pangea until Late Cretaceous times, and then decrease again until Pleistocene times. We compare the two curves (Fig. 9, pink solid line, grey solid line) to the results of other studies (Fig. 9, Ronov, 1994; Smith et al., 1994; Walker et al., 2002; Blakey, 2003, 2008; Golonka, 2007b, 2009, 2012) derived from independent paleo-environment and paleo-lithofacies data. The results are generally consistent, except for the periods 338-269 Ma and 248-203 Ma during which the flooded continental areas for this study and Golonka et al. (2006) are smaller, which reflects smaller extent of transgression in these times. van der

Meer et al. (2017, green line on Fig. 9) derived sea level and continental flooding from the strontium isotope record of marine carbonates. These results are generally consistent with the estimates from paleo-environment and paleo-lithofacies data, except during the Permian and the Late Jurassic-early Cretaceous times, during which van der Meer et al. (2017) predict larger extent of flooding than others (Fig. 9). This could indicate that the evolution of $^{87}Sr/^{86}Sr$ reflects variations in the composition of emergent continental crust (Bataille et al., 2017; Flament et al., 2013) as well as global weathering rates (e.g. Flament et al., 2013, Vérard et al., 2015, van der Meer et al., 2017).~~by dividing the shallow marine area (Fig. 8a, lightblue) by the total continental area (inclusive of shallow marine, landmass, mountain and ice sheet; Fig. 9b, blue). The continental flooding ratios rapidly decrease from about 45.2% in the Late Devonian to 27.7% in 224-203 Ma of the Late Triassic, after that it peaks, with frequent fluctuations, at 41.8% in 94-81 Ma of the Late Cretaceous. That is then followed by a quick decrease again until it reaches the lowest point at 27.6% in 11-2 Ma.~~

5.2 Terrestrial areal change associated with transferring reconstruction, filling gaps and revising paleogeography

[Insert Figure 10]

We estimate the terrestrial areas, including ice sheets, mountains and landmasses, as percentages of Earth's surface area, from the original paleogeography of Golonka et al. (2006) (Fig. 10, green), from the paleogeography reconstructed using a different plate motion model of Matthews et al. (2016) and gaps filled (Fig. 10, red), and from the paleogeography with gaps fixed and revised using the paleo-environmental information indicated by marine fossil collections from the PBDB (Fig. 10, blue). These three curves are similar and generally indicate a reverse changing trend to the flooded continental areal curves over time (Fig. 9), as expected. We also calculate the areas of the terrestrial paleogeographic geometries after transferring the reconstruction but before filling gaps and the results are nearly identical to the original terrestrial paleogeographic areas of Golonka et al. (2006). This is because the reconstruction of Golonka et al. (2006) has a tighter fit of the major continents within Pangea prior to the supercontinent breakup than the reconstruction of Matthews et al. (2016), so that transferring the paleogeographic geometries mainly produces gaps rather than overlaps. Comparing between the three curves (Fig. 10), filling gaps results in a larger terrestrial areal change than revising paleogeographic geometries based on PBDB test. Therefore, variation of the underlying plate reconstruction is the main factor that contributes to the terrestrial areal change (Fig. 10, red and green), and the effect of revising paleogeographic geometries based on paleobiology is secondary (Fig. 10, blue).

5.3 Marine fossil collection abundances in two different time scales

[Insert Figure 11]

We test the marine fossil collection dataset used in this study for fossil abundances over time with two different time scales: ICS2016 and Golonka (2000) (Table 1). The results indicate the abundances of the dataset in the two time scales are significantly different in most time intervals (Fig. 11). Generally, shorter time spans generally contain fewer data, for instance, there are about 400 marine fossil collections between 224-203 Ma using the Golonka (2000) time scale (Fig. 11, red) while there are over 1,300 collections during 232-200 Ma using the ICS2016 time scale (Fig. 11, blue). In addition, the difference of the start age and end age of the time interval could remarkably affect the fossil abundance, so that there are over 2000 marine fossil collections between 387.7-365.6 Ma in ICS2016 but less than 300 collections between 380-359 Ma using the Golonka (2000) time scale. As a result, the time scale applied to the paleobiology could significantly affect the fossil collection abundance being assigned to paleogeographic time intervals.

5.4 Limitations of the workflow

The workflow we develop in this study illustrates transferring paleogeographic geometries from one plate motion model to another and then using paleo-environmental information indicated by marine fossil collections from the PBDB to improve the paleo-coastline locations and paleogeographic geometries. However, the methodology still has some limitations. Transferring paleogeographic geometries to a different reconstruction inevitably results in gaps and/or overlaps, which can only be addressed using presently laborious methods. In addition, revising the coastlines and paleogeographic geometries based on the PBDB test is also currently achieved manually, and could be automated in the future.

Paleogeographic maps such as those considered here typically represent discrete time periods of many millions of years, whereas global plate motion models, even though also based on tectonic stages, provide a somewhat more continuous description of evolving plate configurations. A remaining question is how to provide a continuous representation of paleogeographic change that combines continuous plate motion models with paleogeographic maps that do not explicitly capture changes at the same temporal resolution. In addition, it is currently difficult to apply a time scale to the raw paleobiology data from the PBDB that is currently not tied to any time scale.

The PBDB is a widely used resource (e.g., Wright et al., 2013; Finnegan et al., 2015; Heim et al., 2015; Mannion et al., 2015; Nicolson et al., 2015; Fischer et al., 2016; Tennant et al., 2016; Close et al., 2017; Zaffos et al., 2017), yet, the spatial coverage of data is still highly heterogeneous, with relatively few data points across large areas of the globe for some time periods. Hence, it is important to combine with other geological data, such as stratigraphic data from StratDB Database (http://sil.usask.ca) and Macrostrat Database (https://macrostrat.org/) and other sources of paleo-environment and paleo-lithofacies data, to further constrain the paleogeographic reconstructions.

~~5.1 Flooding history, global sea level changes, and assembly and breakup of Pangea~~

~~The continental flooding history we calculate between 402 and 2 Ma shows trends that are generally similar to global long-term sea level change (Haq et al., 1987; Haq et al., 2002; Müller et al., 2008; Fig. 9a). The eustatic sea level of Haq et al. (1987) and Haq et al. (2002) are inferred from the flooding ratios. Continental flooding decreases during Pangea amalgamation from the late Devonian until the Late Carboniferous, which is also reflected by low eustatic sea levels. Starting from the Early Jurassic with the breakup of Pangea, continental flooding is increased rapidly until the Late Cretaceous when it peaked at about 42.0%. This rapid increase could be explained by a reduction of ocean volume basin associated with a decrease of the average age of the ocean floor and an increase in mid-ocean ridge length during Pangea breakup (Hays and Pitman, 1973; Müller et al., 2008; Müller et al., 2016; Van Avendonk et al., 2016). Since the Late Cretaceous, global continental flooding rapidly decreases again simultaneously with global sea level falling, which primarily reflects the increasing age of the ocean floor (Miller et al., 2005; Müller et al., 2008). Overall, the changes of the global continental flooding during 402-2 Ma are consistent with global long-term sea level changes.~~

~~5.2 Emerged land areas, total continental areas, continental growth models, $^{87}Sr/^{86}Sr$ of ocean water, and assembly and breakup of Pangea~~

~~We calculate the global emerged land areas since the Devonian from the improved global reconstructed paleogeographic features of landmass, mountain and ice sheet as percentages of the Earth's surface area (Fig. 9b, red). The results generally indicate ongoing increasing continental emergence varying from about 21.0% in the Devonian to nearly 30.0% in the Neogene. Emerged land areas were slightly larger between 58 and 2 Ma (up to 30%) and between 224 and 203 Ma (27.7%) than at present (27.5%). In contrast, the evolution of the emerged land areas is inverse to the global long-term sea level changes during this time (Fig. 9a), as expected.~~

~~Similarly, the total continental areas from 402 to 2 Ma are calculated from the improved global reconstructed paleogeographies including shallow marine, landmass, mountain and ice sheet. They show a sustained increase of continental areas, rising from 37.7% in 402-380 Ma to 41.1% in 11-2 Ma (Fig. 9b, green). Before the breakup of Pangea is initiated in the Late Triassic, the total continental areas generally remain constant at an average of about 38.0% of Earth's total surface area. Continental areas then increase between 203 and 179 Ma and peak at about 44.0% in the Early Neogene, followed by a sharp decrease ending up 41.1% in 11-2 Ma. The total continental areas from the latest Early Paleogene to the earliest Neogene were larger as compared to present-day continental area 42.5% of Earth's total surface area (Schubert and Reymer, 1985). Additionally, the differences between the total continental areas and emerged land areas over time indicate large submerged continental areas since the Late Paleozoic, which comprised an average of 14.0% of Earth's surface area.~~

~~A variety of continental growth models have been proposed (e.g. Armstrong, 1981; Veizer and Jansen, 1979). Flament et al. (2013) present an integrated model to investigate the emerged area of continental~~

~~crust as a function of continental growth. They predicted that the emerged land areas constantly increased from between ~21% and ~24% (CGM) at 402 Ma to 27% at 2 Ma, and the total continental area from between ~33% and ~38%(CGM) at 402 Ma to 42% at 2 Ma. Their results are generally consistent with the percentages of emerged land areas and total continental areas calculated in this study using paleogeographic features, despite some high frequency fluctuations in Early Jurassic and Late Cretaceous (Fig. 9b) indicated from our results.~~

~~The increase in the strontium isotope ratio ($^{87}Sr/^{86}Sr$) recorded in marine carbonates was previously thought to reflect continental growth (e.g. Taylor and McLennan, 1985; Veizer and Jansen, 1979). The input of high radiogenic strontium from the continents to the oceans depends on the area of emerged land and continental relief (Godderis and Veizer, 2000). Our calculated emerged land areas from Triassic to present show a similar changing trend with the evolution of $^{87}Sr/^{86}Sr$ of ocean water (McArthur et al., 2012) although not for the older times (Fig. 9b). In contrast, the continental area in the entire timeframe appears not to indicate obvious consistency with the evolution of $^{87}Sr/^{86}Sr$ of ocean water. Therefore, we confirm that $^{87}Sr/^{86}Sr$ in ocean water may have good correlation with emerged land area (Godderis et al., 2014; van der Meer et al., 2017) rather than continental crust area (Flament et al., 2013).~~

6 Conclusions

Our study highlights the flexibility of digital paleogeographic models linked to a ~~state-of-the-art~~ plate tectonic reconstructions in order to better understand the interplay of continental growth and eustasy, with wider implications for understanding Earth's paleotopography, ocean circulation, and the role of mantle convection in shaping long-wavelength topography. We present a workflow that enables the construction of paleogeographic maps with ~~flexible~~ variable spatial and temporal resolutions, while also becoming more testable and expandable with the incorporation of new paleo-environmental datasets.

We ~~also~~ develop an approach to ~~improve~~ revise the paleo-coastline locations and paleogeographic geometries~~maps~~ ~~, especially the terrestrial-marine boundaries,~~ using paleo-environmental information indicated by the marine fossil collections from the PBDB~~paleobiology data~~. Using this approach, the consistency ratio between the paleogeography and the paleobiology records since the Devonian is increased from an average 75% to nearly full consistency. The paleogeography in the main regions of North America, South America, Europe and Africa is significantly improved, especially in the Late Carboniferous, Middle Permian, Triassic, Jurassic, Late Cretaceous and most portions of the Cenozoic. The flooded continental areas since the late Devonian inferred from the revised global paleogeography in this study are generally consistent with the results derived from other paleo-environment and paleo-lithofacies data or from the strontium isotope record in marine carbonates.

Comparing the terrestrial areal change over time associated with transferring the reconstruction and filling gaps, and revising paleogeographic geometries using the paleo-environmental data from the

PBDB, indicates that reconstruction difference is a main factor to result in the paleogeographic areal change comparing with the original maps, and revising paleogeographic geometries based on PBDB test is secondary.

~~Comparing the continental flooding history since the late Devonian inferred from our improved global reconstructed paleogeographies with global long-term sea level change indicates that global continental flooding ratios are consistent with global sea level change. We calculate the global emerged land areas during 402-2 Ma from the improved global reconstructed paleogeographies. The evolution of the emerged land areas is inverse to global sea level changes during the time, as expected.~~

~~The total continental areas during 402-2 Ma, calculated from our improved reconstructed paleogeographies, shows good consistency with predictions of the long-term evolution of emerged land. The emerged land area from Triassic to present shows similar evolution with $^{87}Sr/^{86}Sr$ record of ocean water, while the total continental crust area does not. This confirms that the change of $^{87}Sr/^{86}Sr$ in ocean water through time reflects fluctuations in emerged land area rather than in continental crust area.~~

Supplementary data

We provide ~~the~~ two sets of ~~shapefiles of the~~digital global paleogeographic maps during 402-2 Ma: the paleogeography reconstructed using the plate motion model of Matthews et al., (2016) and ~~improved~~ revised using paleo-environmental information indicated by the marine fossil collections from the ~~paleobiology~~PBDB and the original paleogeography of Golonka et al. (2006), an original rotation file of Golonka et al. (2006), a set of paleogeographic maps illustrating the PBDB test and revision of paleo-coastlines and paleogeographic geometries, ~~the~~ a set of GeoTiff files of all ~~these~~ revised paleogeographic maps, ~~the~~ paleobiology data in shapefile used in this study separated into two sets of consistent marine fossil collections and inconsistent marine fossil collections, an animation for the ~~improved~~ revised global paleogeographic maps, and a README file outlined the workflow of this study. All supplementary material can be downloaded from the link (https://www.dropbox.com/s/91qhwdvm1bevmhp/bg-2017-94-supplement.zip?dl=0~~https://www.dropbox.com/sh/jzsrnnpgxrdzpaa/AAAShE5xhDxr1hmKpoBaa1G4a?dl=0~~).

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Table 1. Time scale since Early Devonian times (Golonka, 2000) used in~~of~~ Golonka et al. (2006)'s paleogeographic -maps~~ since the Early Devonian~~, the original ~~their numerical equivalents~~time scale of ~~as defined by~~ Sloss (~~(~~198~~9~~8), and 2016 time scale of the International Commission on Stratigraphy (ICS2016). Ages in italics are obtained by linear interpolation between subdivisions.~~corresponding reconstruction times.~~

Era	Sloss (1988)			Golonka (2000)					ICS2016	
	Subsequence	Start (Ma)	End (Ma)	Time Slice	Epoch/Age	Start (Ma)	End (Ma)	Reconstruction Time (Ma)	Start (Ma)	End (Ma)
Cenozoic	Tejas III	29	0	Late Tejas III	Tortonian – Gelasian	11	2	6	11.63	1.80
				Late Tejas II	Burdigigalian – Serravallian	20	11	14	20.44	11.63
				Late Tejas I	Chattian – Aquitanian	29	20	22	28.1	20.44
	Tejas II	39	29	Early Tejas III	Priabonian – Rupelian	37	29	33	37.8	28.1
	Tejas I	60	39	Early Tejas II	Lutetian – Bartonian	49	37	45	47.8	37.8
				Early Tejas I	Thanetian – Ypresian	58	49	53	59.2	47.8
Mesozoic	Zuni III	96	60	Late Zuni IV	middle Campanian – Selandian (Late Cretaceous – earliest Paleogene)	81	58	76	*79.8*	59.2
				Late Zuni III	late Cenomanian – early Campanian (Late Cretaceous)	94	81	90	*96.1*	*79.8*
	Zuni II	134	96	Late Zuni II	late Aptian – middle Cenomanian (Early Cretaceous – earliest Late Cretaceous)	117	94	105	*119.0*	*96.1*
				Late Zuni I	late Valanginian – early Aptian (Early Cretaceous)	135	117	126	*136.4*	*119.0*
	Zuni I	186	134	Early Zuni III	late Tithonian – early Valanginian (latest Late Jurassic – earliest Early Cretaceous)	146	135	140	*147.4*	*136.4*
				Early Zuni II	late Bathonian – middle Tithonian (earliest Middle Jurassic – Late Jurassic)	166	146	152	*166.8*	*147.4*
				Early Zuni I	middle Aalenian – middle Bathonian (Middle Jurassic)	179	166	169	*172.8*	*166.8*
	Absorka III	245	186	Late Absaroka III	late Hettangian – early Aalenian (Early Jurassic – earliest Middle Jurassic)	203	179	195	*200.0*	*172.8*
				Late Absaroka II	late Carnian – middle Hettangian (Late Triassic – earliest Jurassic)	224	203	218	*232*	*200.0*
				Late Absaroka I	Induan – early Carnian (Early – earliest Late Triassic)	248	224	232	252.17	*232*
Paleozoic	Absorka II	268	245	Early Absaroka IV	Roadian – Changhsingian (Late Permian)	269	248	255	272.3	252.17
				Early Absaroka III	Sakmarian – Kungurian (Early Permian)	285	269	277	295.0	272.3
	Absorka I	330	268	Early Absaroka II	Gzhelian – Asselian (latest Carboniferous – earliest Permian)	296	285	287	303.7	295.0
				Early Absaroka I	Bashkirian – Kasimovian (Late Carboniferous)	323	296	302	323.2	303.7
	Kaskaskia II	362	330	Kaskaskia IV	middle Visean – Serpukhovian (Lower Carboniferous)	338	323	328	*341.4*	323.2
				Kaskaskia III	late Fammenian – early Visean (latest Devonian – Early Carboniferous)	359	338	348	*365.6*	*341.4*
	Kaskaski I	401	362	Kaskaskia II	Givetian – early Fammenian (Middle – Late Devonian)	380	359	368	387.7	*365.6*
				Kaskaskia I	late Pragian – Eifelian (Early – Middle Devonian)	402	380	396	*408.7*	387.7

Era	Epoch	Nominal Age	Sloss (1988)		Reconstruction Time (Ma)
			Start Age (Ma)	End Age (Ma)	
Cenozoic	Tortonian-Gelasian	Late Tejas III	11	2	6
	Burdigigalian-Serravallian	Late Tejas II	20	11	14
	Chattian-Aquitanian	Late Tejas I	29	20	22
	Priabonian Rupelian	Early Tejas III	37	29	33
	Lutetian-Bartonian	Early Tejas II	49	37	45
	Thanetian-Ypresian	Early Tejas I	58	49	53
Mesozoic	Late Cretaceous-earliest Paleogene	Late Zuni IV	81	58	76
	Late Cretaceous	Late Zuni III	94	81	90
	Early Cretaceous-earliest Late Cretaceous	Late Zuni II	117	94	105
	Early Cretaceous	Late Zuni I	135	117	126
	latest Late Jurassic-earliest Early Cretaceous	Early Zuni III	146	135	140
	Middle Jurassic-Late Jurassic	Early Zuni II	166	146	152
	Middle Jurassic	Early Zuni I	179	166	169
	Early Jurassic-earliest Middle Jurassic	Late Absaroka III	203	179	195
	Late Triassic-earliest Jurassic	Late Absaroka II	224	203	218
	Early-earliest Late Triassic	Late Absaroka I	248	224	232
Paleozoic	Late Permian	Early Absaroka IV	269	248	255
	Early Permian	Early Absaroka III	285	269	277
	latest Carboniferous-earliest Permian	Early Absaroka II	296	285	287
	Late Carboniferous	Early Absaroka I	323	296	302
	Early Carboniferous	Kaskaskia IV	338	323	328
	lastest Devonian-Early Carboniferous	Kaskaskia III	359	338	348
	Middle-Late Devonian	Kaskaskia II	380	359	368
	Early-Middle Devonian	Kaskaskia I	402	380	396

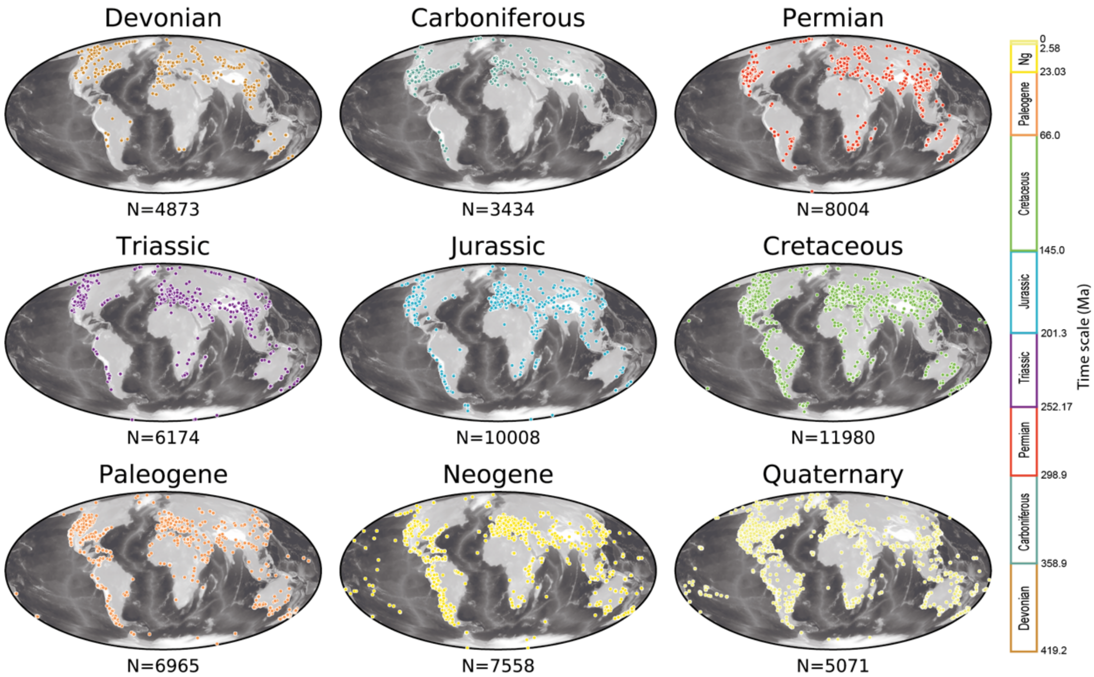
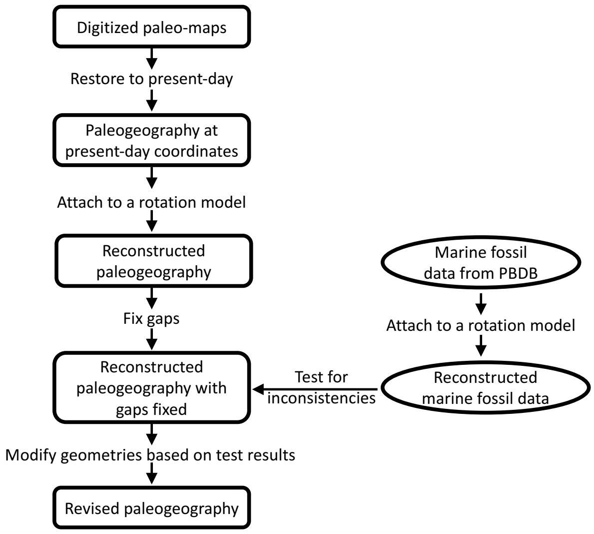


Fig. 1. Global distributions and number~~s~~ of fossil collections since the Devonian Period. The greyscale background shows global present-day topography ETOPO1 (Amante and Eakins, 2009) with lighter shades corresponding to increasing elevation. Fossil collections from the ~~Paleobiology Database~~PBDB are colored ~~according~~ following the standard used by the International Commission on Stratigraphy.



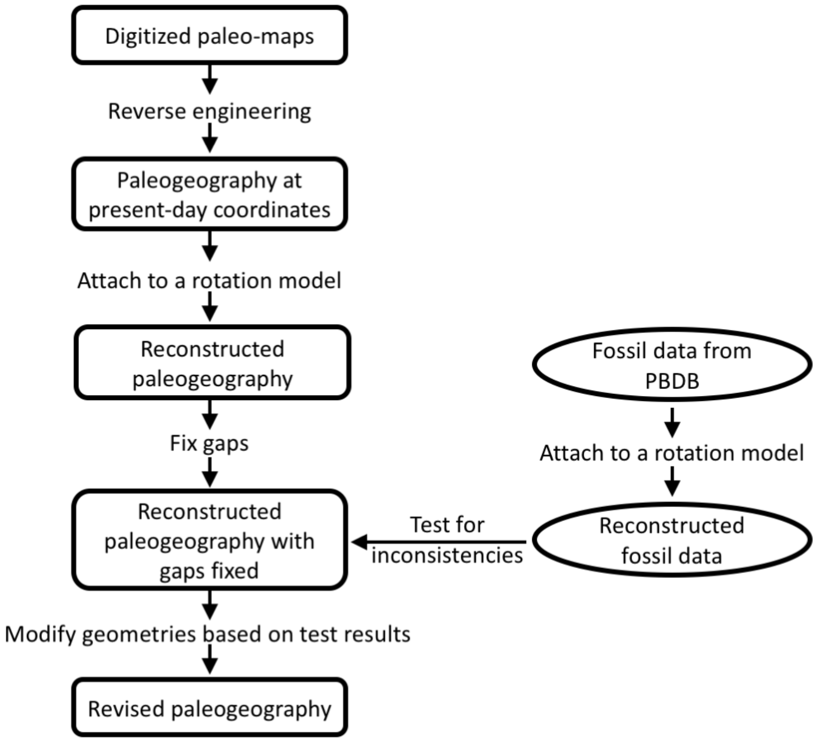
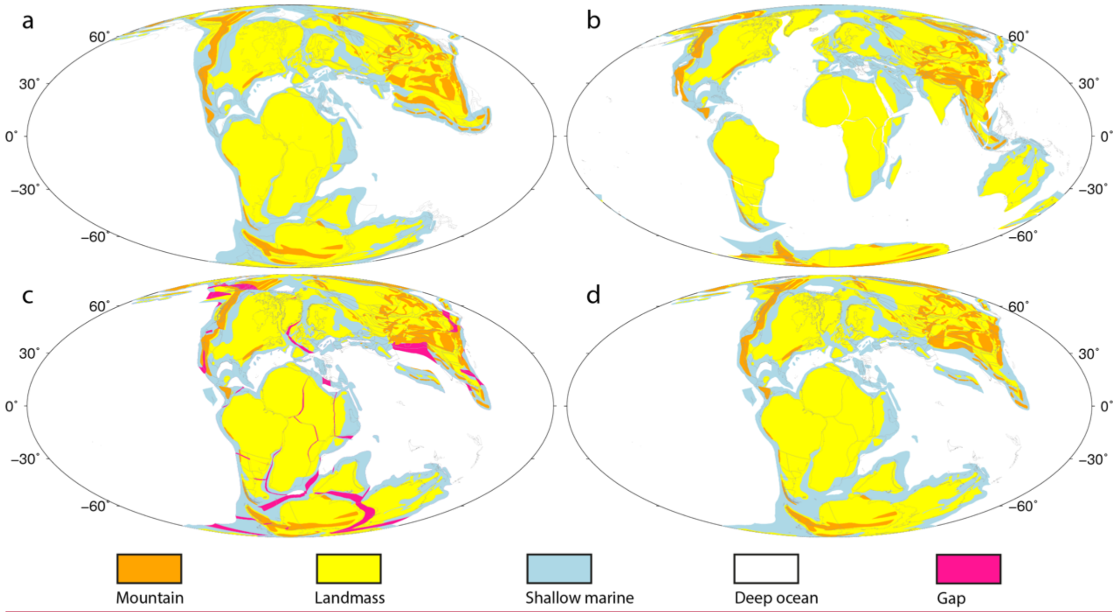


Fig. 2. Workflow used to ~~reverse-engineer~~transfer a set of paleogeographic geometries from one reconstruction ~~paleogeographic~~ to another, followed by ~~reconstructions and~~ revision~~e them~~ using paleo-environmental information indicated by marine fossil collections from the P~~p~~aleobiology D~~d~~atabase (~~,~~ PBDB)~~: Paleobiology Database~~.



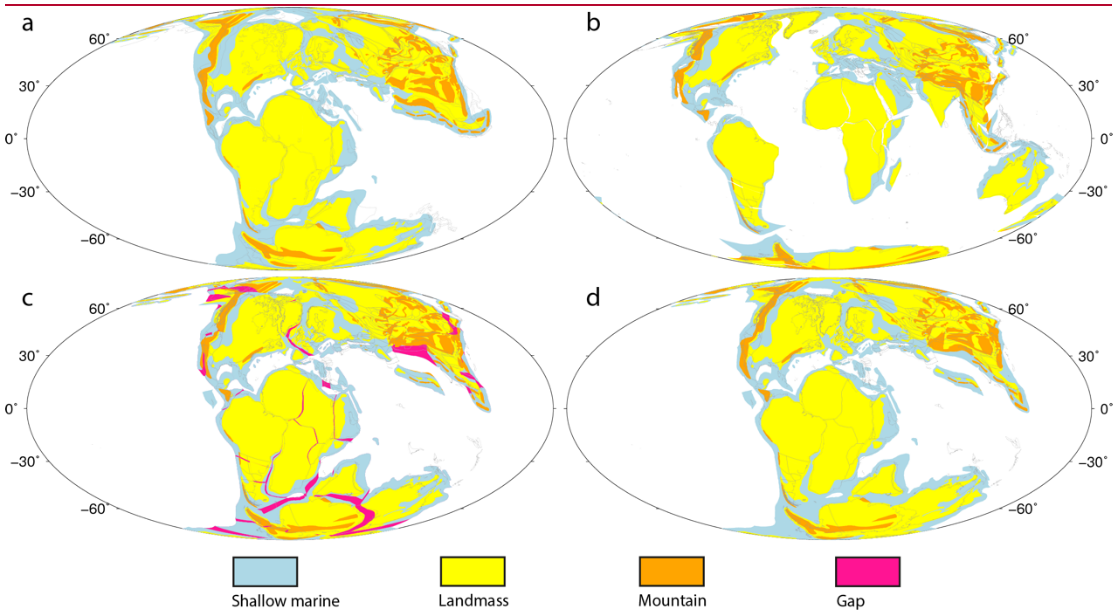
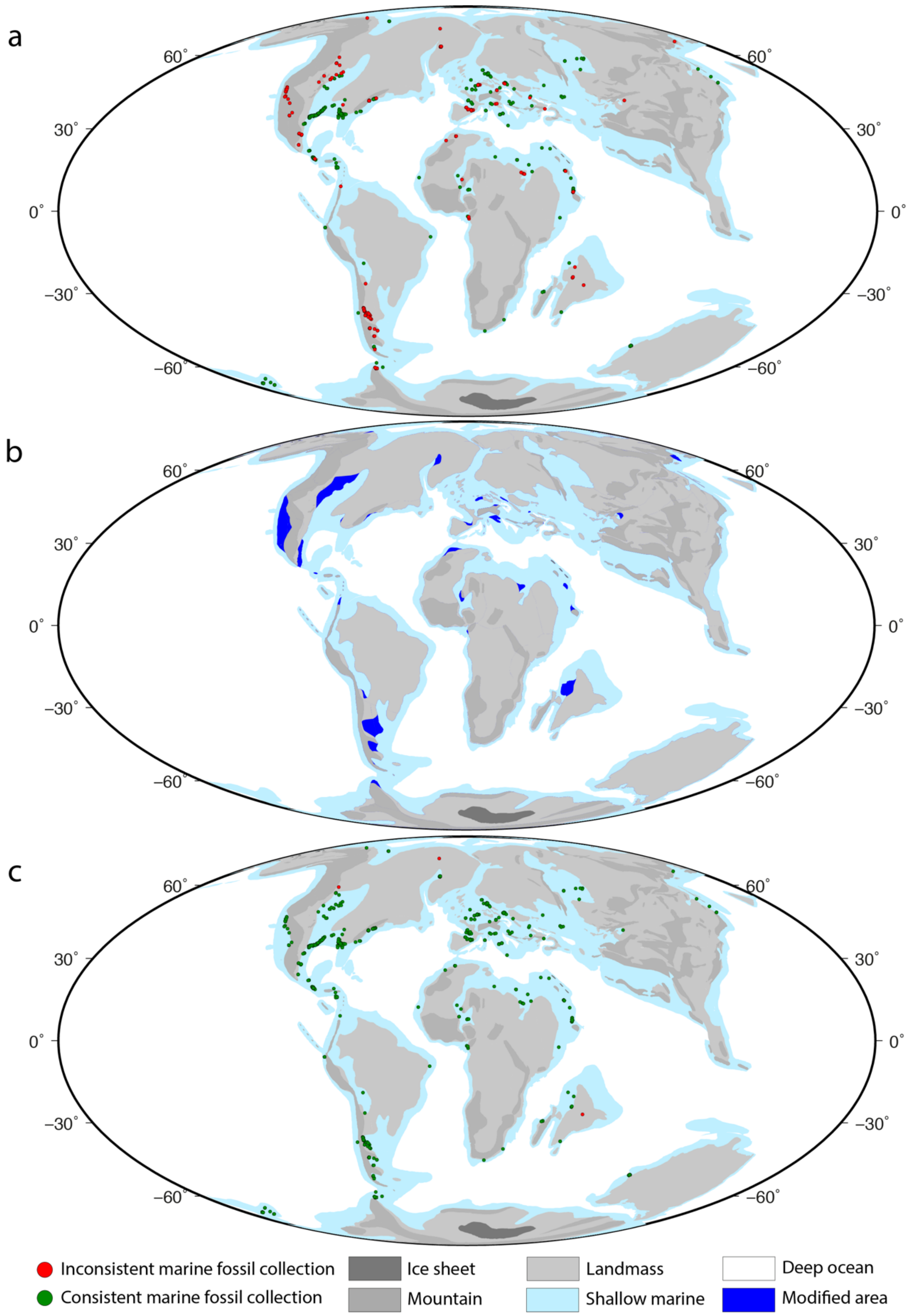


Fig. 3. (a) Original ~~Reconstructed~~ global paleogeographic map~~y~~ from Golonka et al. (2006) at 126 Ma. (b) Global paleogeographic geometries~~y~~ at 126 Ma in present-day coordinates. (c) Global paleogeography at 126 Ma reconstructed using the plate motion model of Matthews et al. (2016). Gaps are highlighted in pink. (d) Global paleogeography at 126 Ma reconstructed using the reconstruction of Matthews et al. (2016) with gaps fixed by filling with adjacent paleo-environment attributes. Gre~~a~~y lines indicate reconstructed present-day coastlines and terrane boundaries. Mollweide projection with 0°E central meridian.

Table 2. L~~A l~~ookup table to~~for~~ classify~~ing~~ fossil datas indicating different paleo-environments into marine or terrestrial settings and their corresponding paleogeographic types presented in Golonka et al. (2006). Terrestrial fossil paleo-environments correspond to paleogeographic features of landmasses, mountains or ice sheets, and marine fossil paleo-environments to shallow marine environments or deep oceans.

Marine			Terrestrial/Transitional Zone		
Paleogeography	**Fossil Paleo-environments**		**Paleogeography**	**Fossil Paleo-environments**	
Shallow marine environments/Deep oceans	marine indet.	slope	Landmasses/Mountains	terrestrial indet.	pond
	carbonate indet.	basinal (carbonate)		fluvial indet.	crater lake
	peritidal	basinal (siliceous)		alluvial fan	lacustrine delta plain
	shallow subtidal indet.	marginal marine indet.		channel lag	lacustrine interdistributary bay
	open shallow subtidal	coastal indet.		coarse channel fill	lacustrine delta front
	lagoonal/restricted shallow subtidal	estuary/bay		fine channel fill	lacustrine prodelta
	sand shoal	lagoonal		channel	lacustrine deltaic indet.
	reef, buildup or bioherm	paralic indet.		wet floodplain	lacustrine indet.
	perireef or subreef	interdistributary bay		dry floodplain	dune
	intrashelf/intraplatform reef	delta front		floodplain	interdune
	platform/shelf-margin reef	prodelta		crevasse splay	loess
	slope/ramp reef	deltaic indet.		levee	eolian indet.
	basin reef	foreshore		mire/swamp	cave
	deep subtidal ramp	shoreface		fluvial-lacustrine indet.	fissure fill
	deep subtidal shelf	transition zone/lower shoreface		delta plain	sinkhole
	deep subtidal indet.	offshore		fluvial-deltaic indet.	karst indet.
	offshore ramp	submarine fan		lacustrine - large	tar
	offshore shelf	basinal (siliciclastic)		lacustrine - small	spring
	offshore indet.	deep-water indet.	Ice sheets	glacial	

Marine			Terrestrial		
Paleogeography	**Fossil Paleoenvironments**		**Paleogeography**	**Fossil Paleoenvironments**	
Shallow marine environments	marine indet.	basinal (carbonate)	Landmasses/Mountains	terrestrial indet.	pond
	carbonate indet.	basinal (siliceous)		fluvial indet.	crater lake
	peritidal	marginal marine indet.		alluvial fan	lacustrine delta plain
	shallow subtidal indet.	coastal indet.		channel lag	lacustrine interdistributary bay
	open shallow subtidal	estuary/bay		coarse channel fill	lacustrine delta front
	lagoonal/restricted shallow subtidal	lagoonal		fine channel fill	lacustrine prodelta
	sand shoal	paralic indet.		channel	lacustrine deltaic indet.
	reef, buildup or bioherm	delta plain		wet floodplain	lacustrine indet.
	perireef or subreef	interdistributary bay		dry floodplain	dune
	intrashelf/intraplatform reef	delta front		floodplain	interdune
	platform/shelf-margin reef	prodelta		crevasse splay	loess
	slope/ramp reef	deltaic indet.		levee	eolian indet.
	basin reef	foreshore		mire/swamp	cave
	deep subtidal ramp	shoreface		fluvial-lacustrine indet.	fissure fill
	deep subtidal shelf	transition zone/lower shoreface		delta plain	sinkhole
	deep subtidal indet.	offshore		fluvial-deltaic indet.	karst indet.
	offshore ramp	submarine fan		lacustrine - large	tar
	offshore shelf	basinal (siliciclastic)		lacustrine - small	spring
	offshore indet.	deep-water indet.	Ice sheets	glacial	
	slope				


a
b
c
60°
30°
0°
−30°
−60°
Inconsistent marine fossil collection
Consistent marine fossil collection
Ice sheet
Mountain
Landmass
Shallow marine
Deep ocean
Modified area

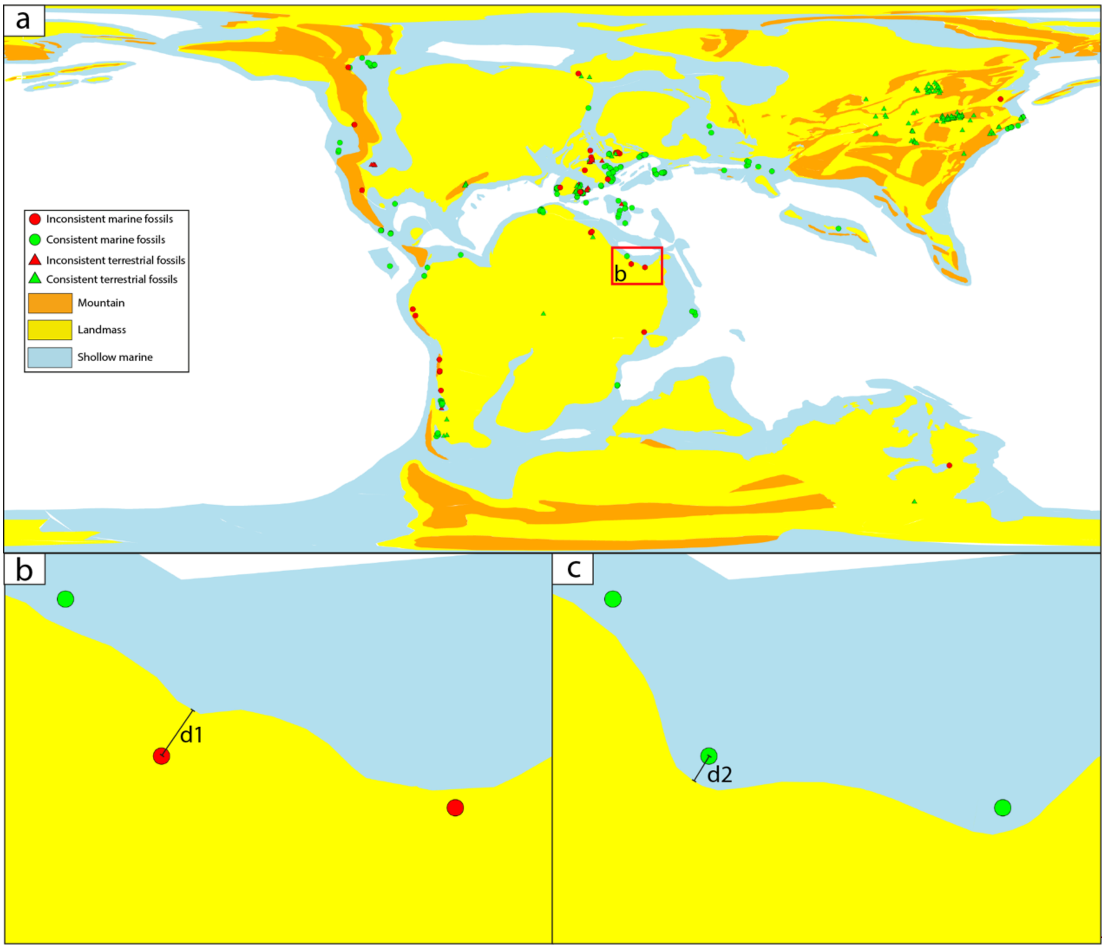
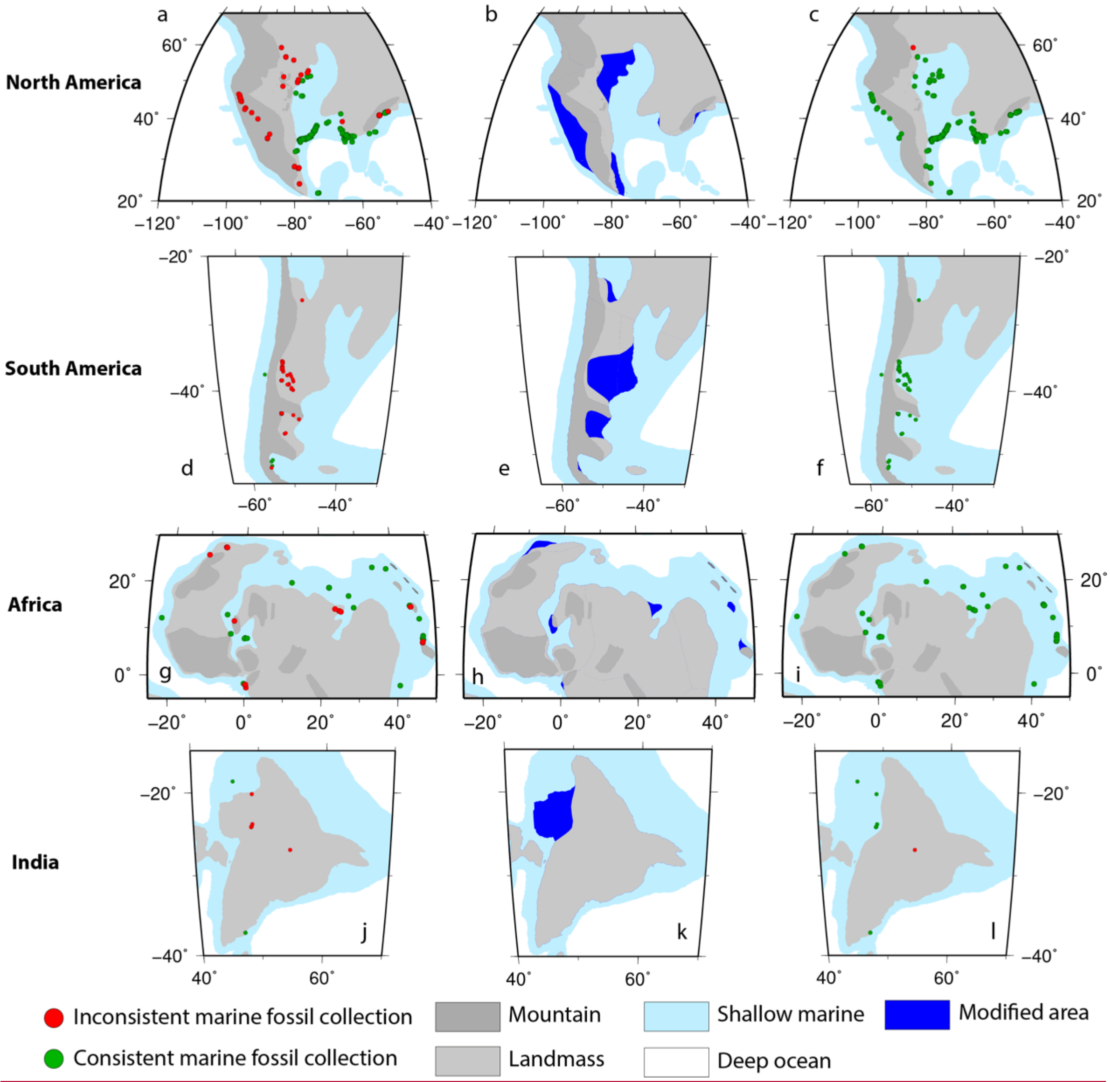


Fig. 4. (a) Test between the g~~G~~lobal paleogeography at 76~~126~~ Ma reconstructed ~~(Golonka et al., 2006) reconstructed~~ using the plate motion model of Matthews et al. (2016) with gaps fixed ~~tested against~~and the paleo-environments indicated by the ~~terrestrial and~~ marine fossil collections ~~recorded~~ from ~~in~~ the ~~Paleobiology Database~~PBDB. **(b)** Area modified (blue) to resolve the test inconsistencies~~The zoomed-in area of the small box in (a) highlights inconsistent marine fossils (red points)~~. ~~d1 ≤ 100 km is the distance between the inconsistent marine fossil and its nearest terrestrial-marine boundary.~~ **(c)** Test between the revised paleogeography at 76 Ma and the same marine fossil collections. Mollweide projection with 0°E central meridian.~~illustrates how a terrestrial-marine boundary is modified based on inconsistent fossils, the terrestrial-marine boundary is shifted until the two marine fossils are consistent with the underlying paleogeography and at the same time keep about 20 km distance from their nearest boundary, d2 ≈ 20 km is the distance between the fossil used and its nearest terrestrial-marine boundary shifted.~~



North America
South America
Africa
India
a
b
c
d
e
f
g
h
i
j
k
l
Inconsistent marine fossil collection
Consistent marine fossil collection
Mountain
Landmass
Shallow marine
Deep ocean
Modified area

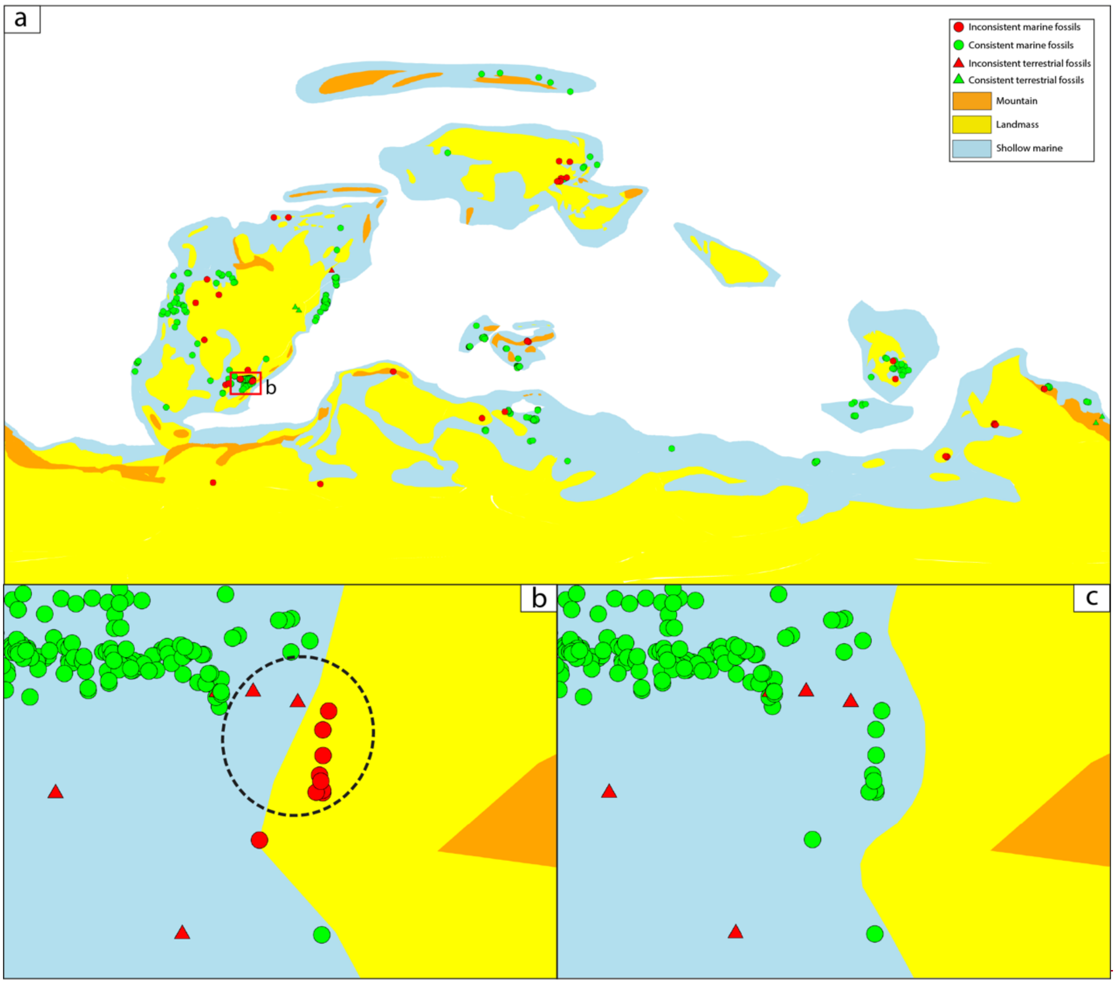
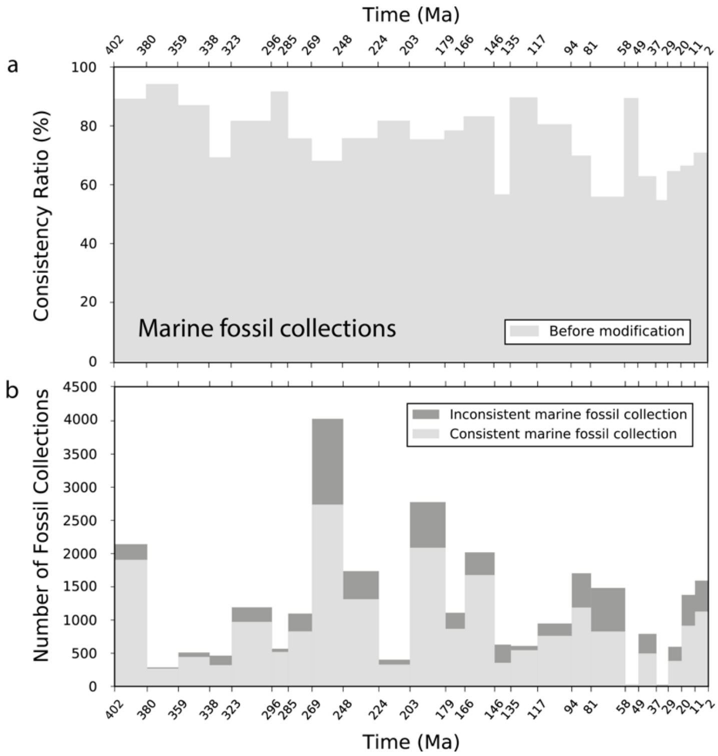


Fig. 5. ~~(a)~~ Test between unrevised and revised paleogeography at 76 Ma respectively and paleo-environments indicated by the marine fossil collections from the PBDB, and revision of the paleo-coastlines and paleogeographic geometries based on the test results, for southern North America (a, b, c), southern South America (d, e, f), northern Africa (g, h, i) and India (j, k, l). Regional Mollweide projection.~~Global paleogeography reconstructed at 396 Ma tested by terrestrial and marine fossils. (b) Zoomed-in area of the small box in (a). The fossils in the black circle are considered as a cluster, in which over 50% of fossils indicate shallow marine environment, therefore, the whole cluster is interpreted as shallow marine. (c) Illustrates how the terrestrial-marine boundary is shifted to be reconciled with fossil collections.~~


Time (Ma)
a
b
Consistency Ratio (%)
Marine fossil collections
Before modification
Number of Fossil Collections
Inconsistent marine fossil collection
Consistent marine fossil collection
402
380
359
338
323
296
285
269
248
224
203
179
166
146
135
117
94
81
58
49
37
29
20
11
2
0
20
40
60
80
100
500
1000
1500
2000
2500
3000
3500
4000
4500

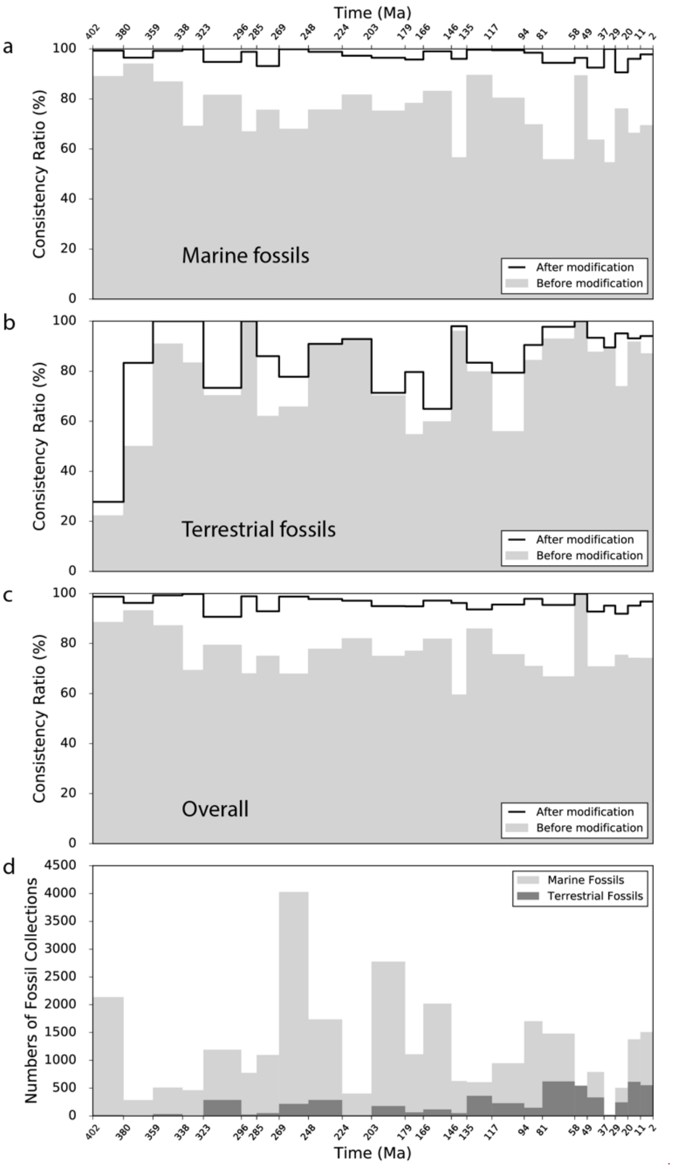
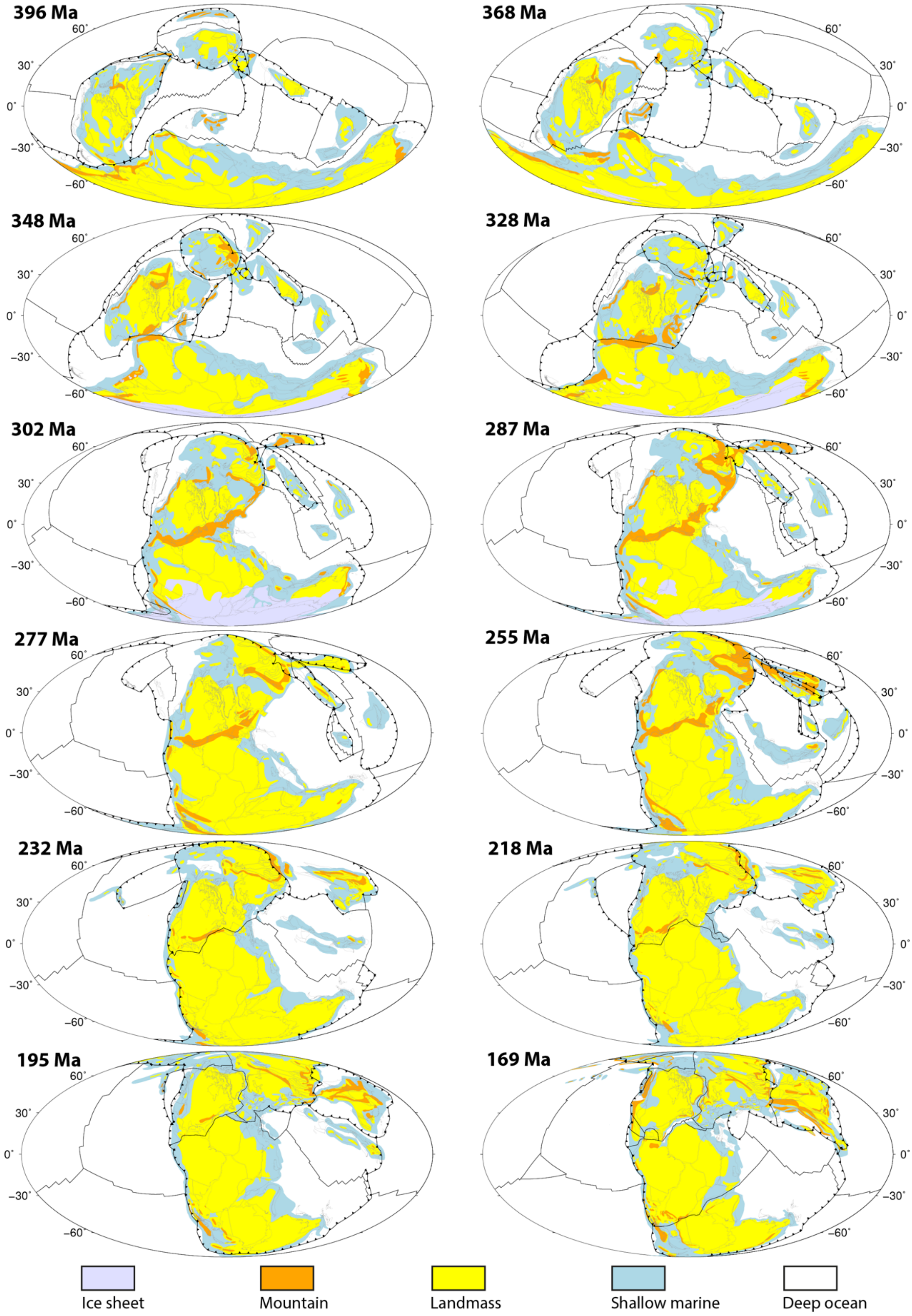
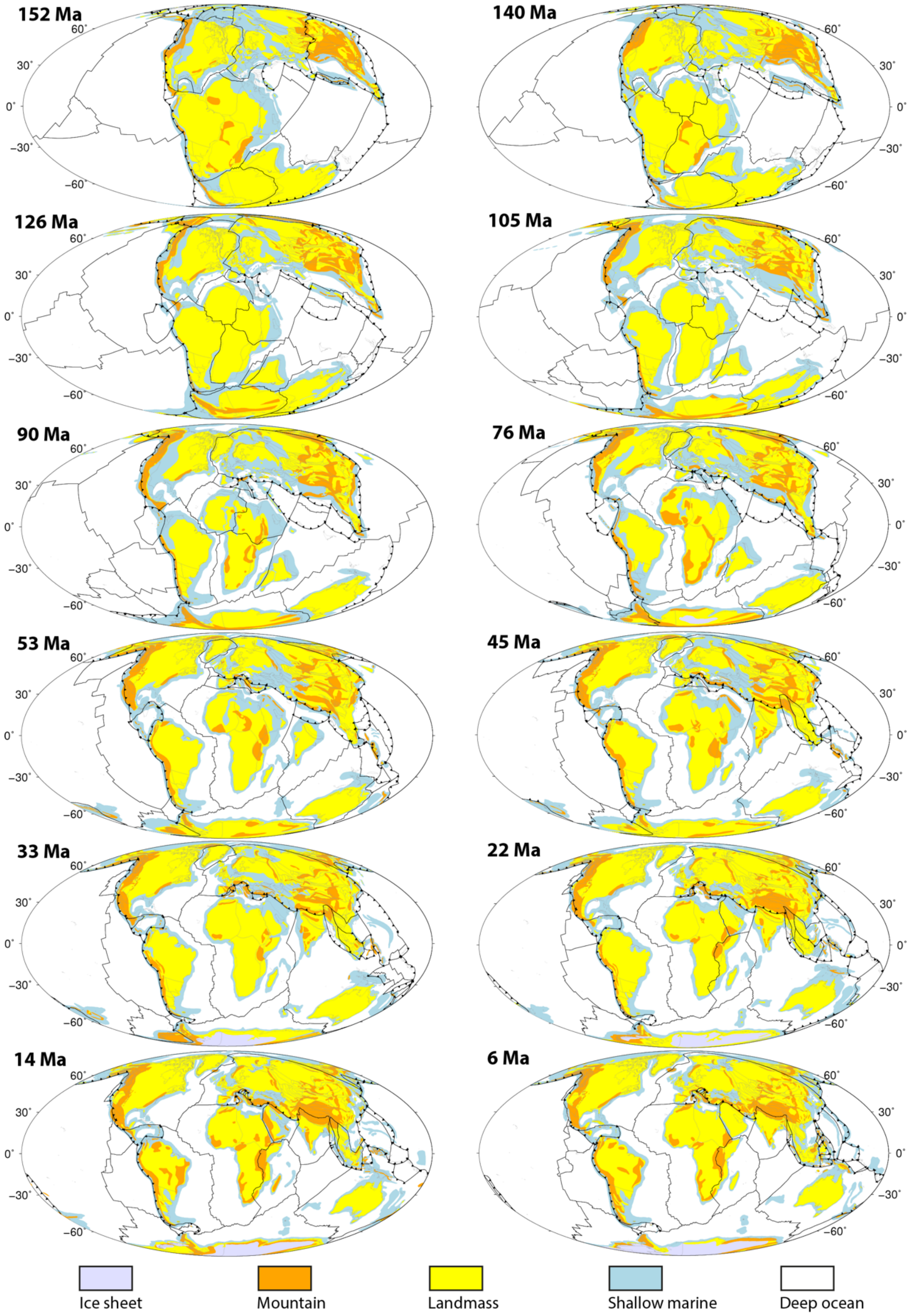


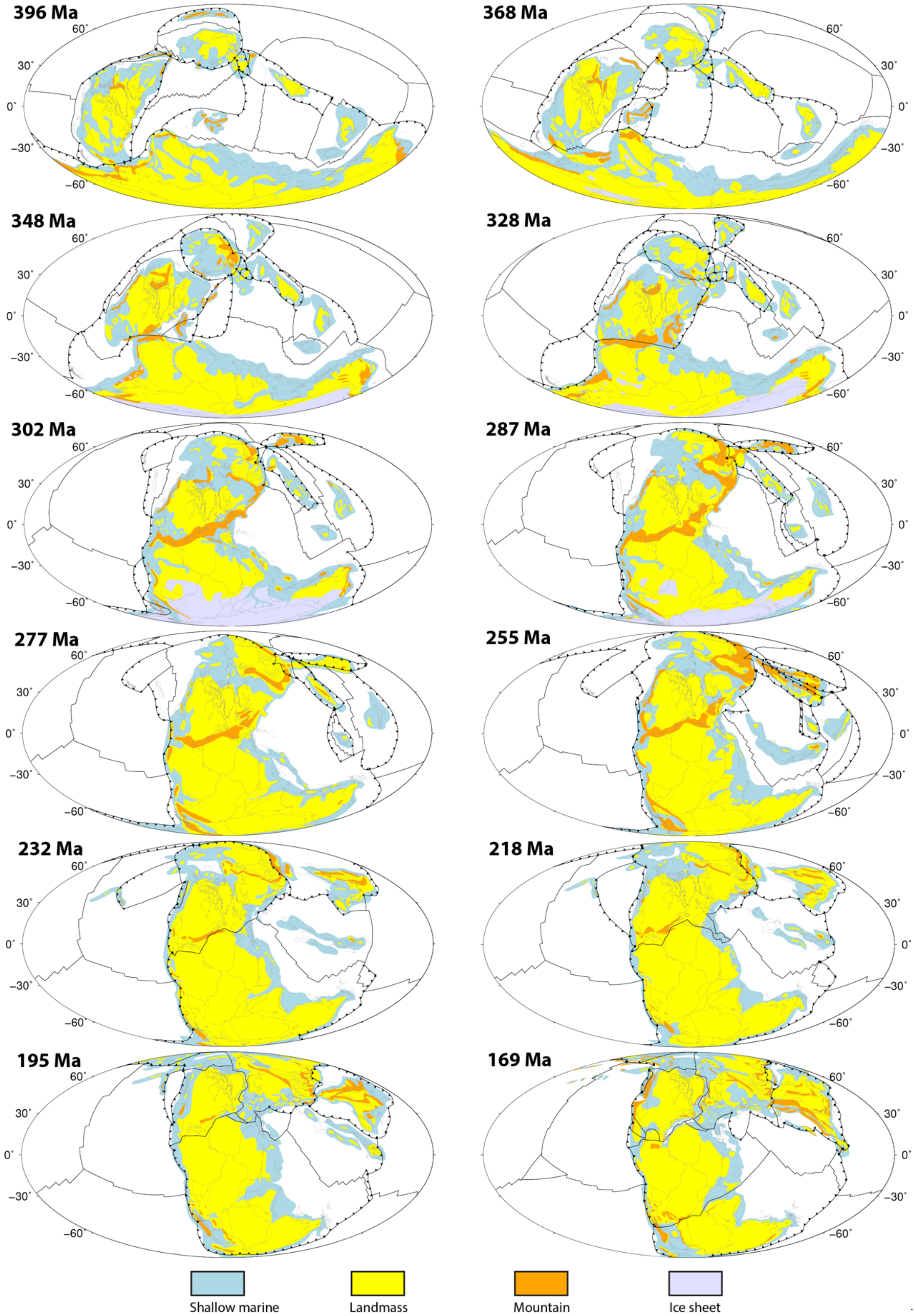
Fig. 6. (a) ~~Global~~ Consistency ratios between global paleogeography with gap filled, but before PBDB test for the period 402-2 Ma, reconstructed using the plate motion model of Matthews et al. (2016) and the paleo-environments indicated by the marine fossil collections from the PBDB~~marine fossils and underlying paleogeographies before (shaded areas) and after (black lines) modification based on fossils for each time interval between 402 and 2 Ma~~. ~~(b) Global consistency ratios between terrestrial fossils and underlying paleogeographies before (shaded areas) and after (black lines) modification for each time interval between 402 and 2 Ma. (c) Global consistency ratios between total fossils (marine and terrestrial) and underlying paleogeographies before (shaded areas) and after (black lines) modification for each time interval between 402 and 2 Ma.~~ (b~~d~~) Numbers of consistent (light grey) and inconsistent (dark grey) ~~terrestrial (shaded in dark grey) and~~ marine ~~(shaded in light grey)~~ fossil collections used in the tests for each time interval ~~between~~ from 402 Ma and 2 Ma.



396 Ma
368 Ma
348 Ma
328 Ma
302 Ma
287 Ma
277 Ma
255 Ma
232 Ma
218 Ma
195 Ma
169 Ma
Ice sheet
Mountain
Landmass
Shallow marine
Deep ocean



152 Ma
140 Ma
126 Ma
105 Ma
90 Ma
76 Ma
53 Ma
45 Ma
33 Ma
22 Ma
14 Ma
6 Ma
60°
30°
0°
−30°
−60°
Ice sheet
Mountain
Landmass
Shallow marine
Deep ocean


396 Ma
368 Ma
348 Ma
328 Ma
302 Ma
287 Ma
277 Ma
255 Ma
232 Ma
218 Ma
195 Ma
169 Ma
Shallow marine
Landmass
Mountain
Ice sheet

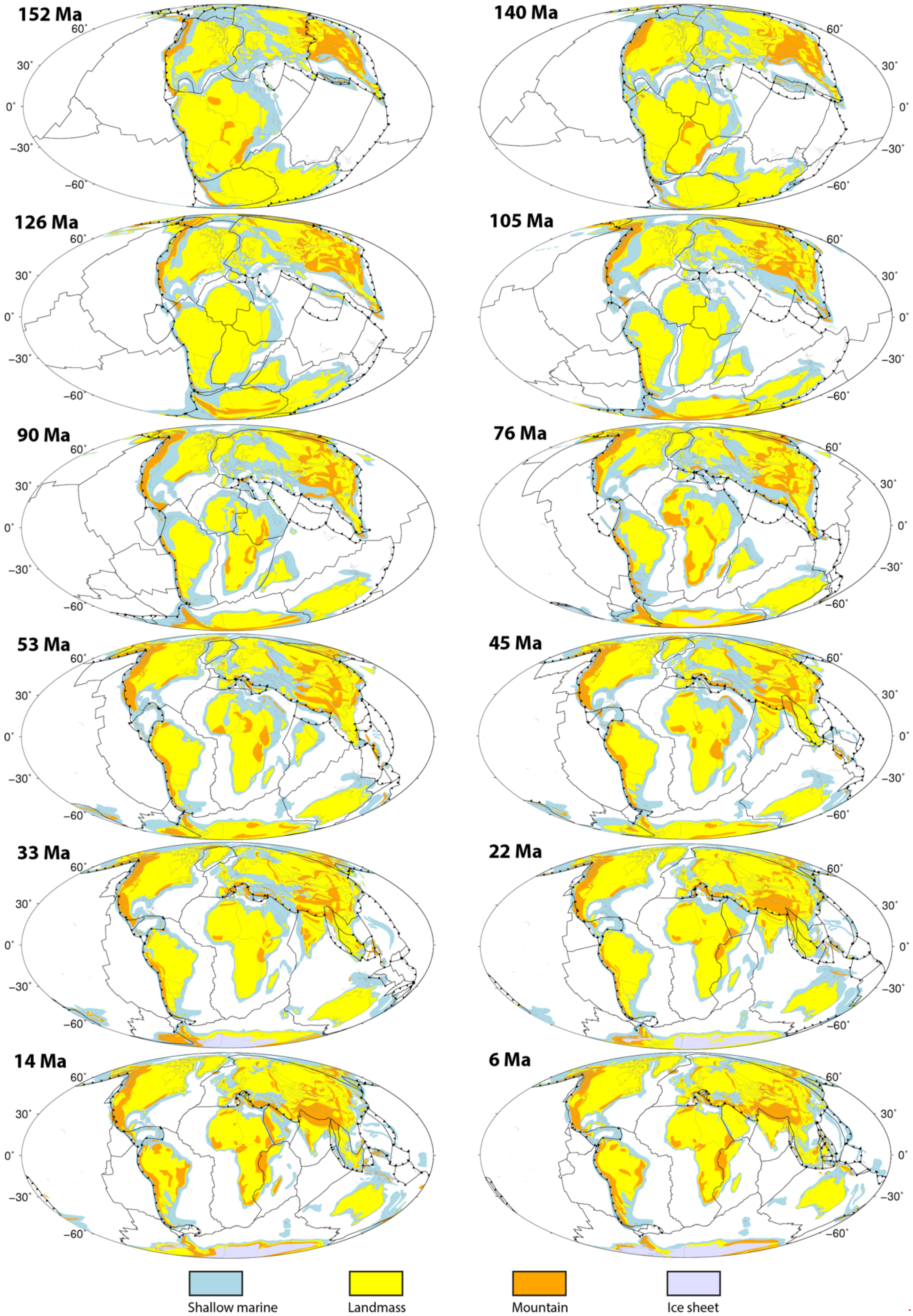
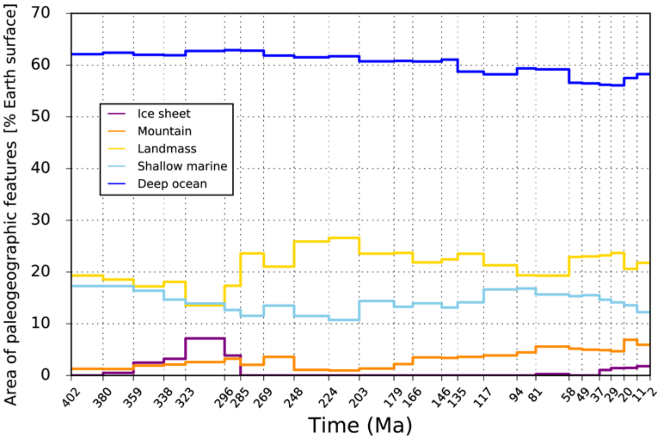


Fig. 7. Global paleogeography~~ies~~ from 402 Ma to 2 Ma reconstructed ~~with~~ using the plate motion model ~~reconstruction~~ of Matthews et al. (2016) and ~~and improved~~revised using ~~paleobiology~~ paleo-environmental data from the PBDB~~data~~. Black toothed lines indicate subduction zones, and other black lines denote mid-ocean ridges and transforms. ~~Gray~~ Grey outlines delineate reconstructed present-day coastlines and terranes. Mollweide projection with 0°E central meridian.



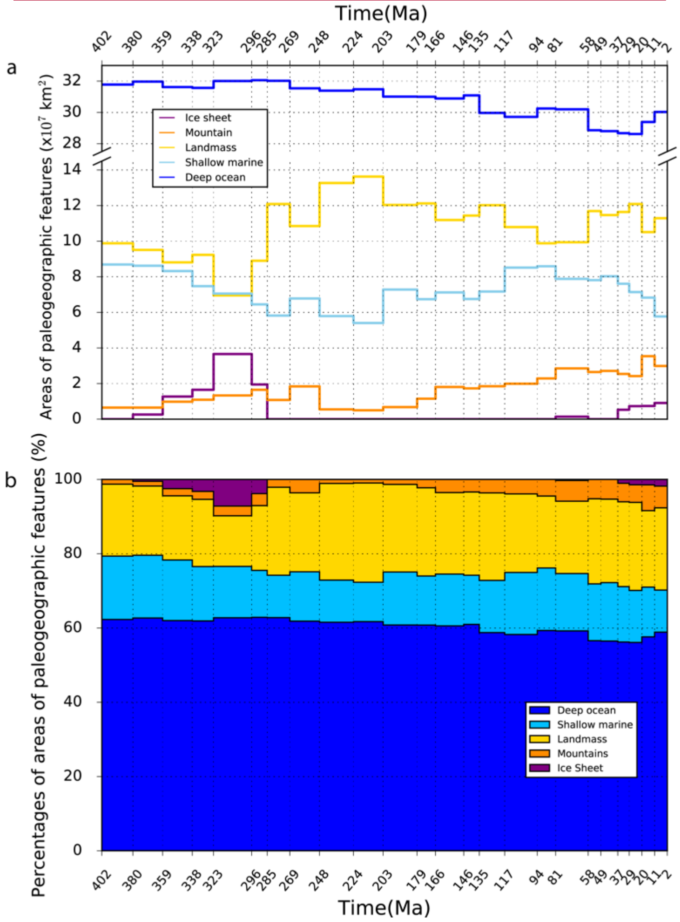
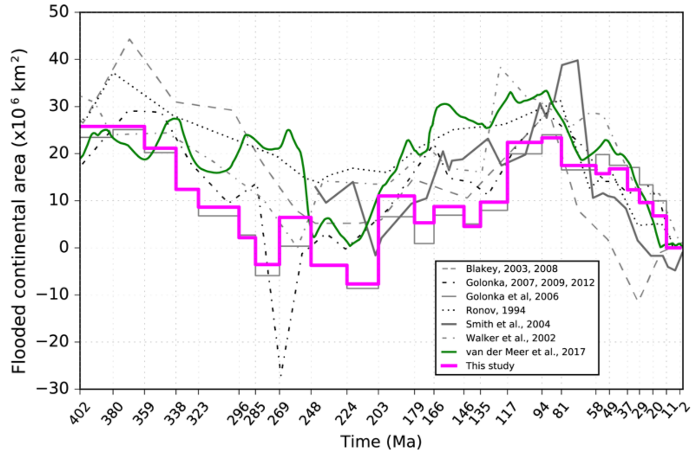


Fig. 8. ~~**(a) Global paleogeographic feature surface areas from 402 to 2 Ma. (b)**~~ **Global paleogeographic feature areas as percentages of** ~~**the**~~ **Earth's total surface area estimated from the revised paleogeographic maps** ~~**at each time interval**~~ **from 402 Ma to 2 Ma.**



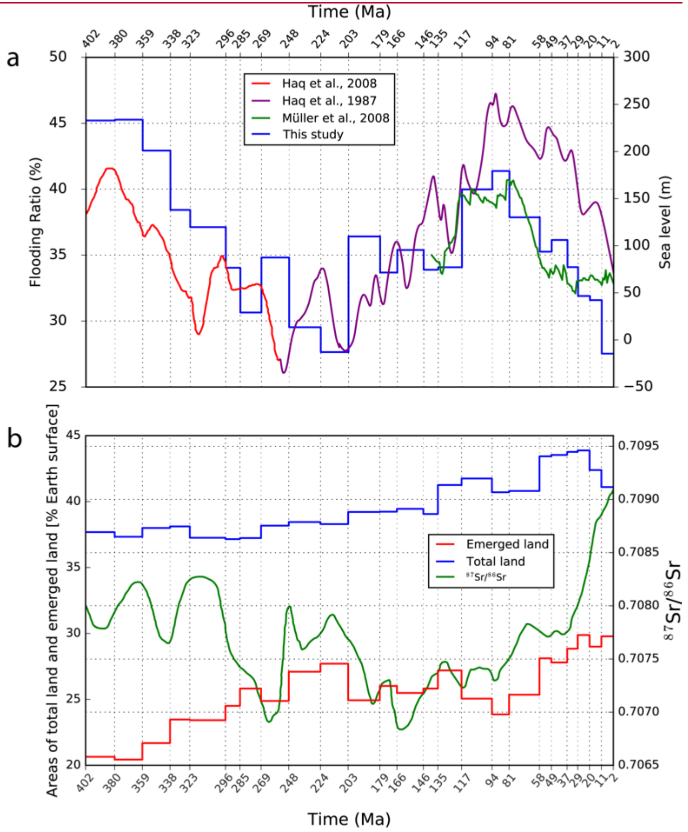


Fig. 9. ~~(a)~~ **Global flooded continental ~~flooding ratio~~area since the Early Devonian ~~(blue) and global sea level from Haq et al. (1987) (purple), Haq et al. (2008) (red) and Müller et al. (2008) (green)~~ Period from the original paleogeographic maps of Golonka et al. (2006) (grey solid line) and from the revised paleogeography in this study (pink line). Results for Blakey (2003, 2008), Golonka (2007b, 2009, 2012), Ronov (1994), Smith et al. (2004), Walker et al. (2002) are as in van der Meer et al. (2017). The van der Meer et al. (2017) curve (green line) is derived from the strontium isotope record of marine carbonates.~~. (b) Total continental areas (blue) and emerged land areas (red) as a percentage of Earth's surface area. $^{87}Sr/^{86}Sr$ record of ocean water of McArthur et al. (2012) (Green). Total continental area comprises shallow marine, landmass, mountain and ice sheet. Emerged land comprises landmass, mountain and ice sheet. Flooding ratio is defined as shallow marine area divided by the total continental area.~~**

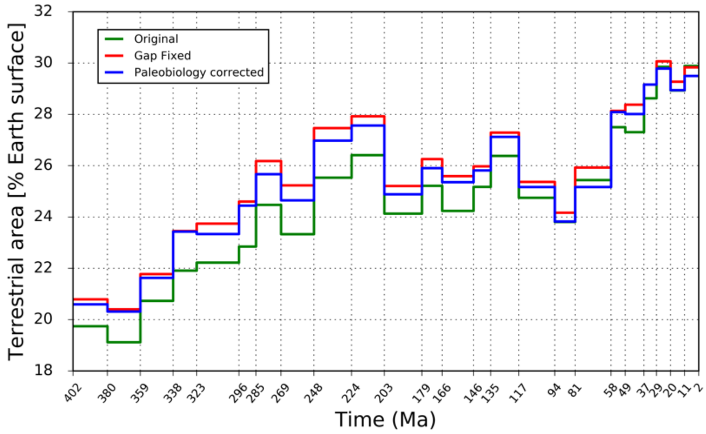


Fig. 10. Terrestrial areal change due to filling gaps and modifying the paleo-coastlines and paleogeographic geometries over time. Green: based on the original paleogeographic maps of Golonka et al. (2006); Red: based on paleogeography reconstructed using a different plate motion model of Matthews et al. (2016) and gaps filled; Blue: based on paleogeography with gaps fixed and revised using the paleo-environments indicated by marine fossil collections from the PBDB.

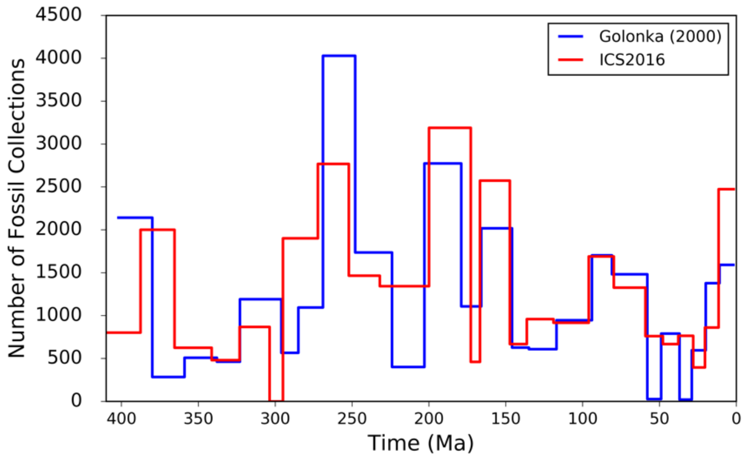


Fig. 11. Fossil abundance test on the marine fossil collection dataset used in this study with two different time scales: Golonka (2000) and ICS2016 (Table 1).