

A fully marine stem amphibian from the Late Triassic of China

Corresponding Author: Professor Ryosuke Motani

Version 0:

Decision Letter:

19th September 2025

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Professor Motani,

Your manuscript entitled "Evolutionary pathway to the first fully marine amphibian" has now been seen by 2 reviewers, whose comments are attached. The reviewers have raised a number of concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to the criticisms raised and to some editorial concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

While revising the paper, please note that substantiation of the marine lifestyle interpretation will be key for publication in NEE, so please do all you can to address reviewer comments on that aspect (as well as the other requests).

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file [OPTIONAL: in Microsoft Word format].

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

* Include a "Response to reviewers" document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

* Extended Data Figures - please ensure that any supplementary figures and tables that are crucial to the manuscript's conclusions are converted into Extended Data figures and tables to increase visibility of these data. Extended Data figures and tables are online-only (present in the online PDF and full-text HTML versions of the paper), peer-reviewed display items that provide essential background to the article but are not included in the main article due to space constraints. A maximum of ten Extended Data display items (figures and tables) is permitted.

Please use the link below to submit your revised manuscript and related files:

Link Redacted

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us

know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit <http://www.springernature.com/orcid>.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[redacted]

Reviewer expertise:

Both reviewers have expertise in early amphibian palaeontology

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

This is a fascinating manuscript describing what appears to be a solid example, the first of its kind, of a fully marine stem-amphibian. I think the data and associated interpretations are well founded. I also believe this to be of interest to Nature Ecology & Evolution's broad audience, as this contribution adds important insights into diverse aspects of vertebrate ecology and evolution.

To improve the utility of this contribution, my biggest comment for improvement is the sparse description and presentation of the actual armour itself. The main specimen figure is difficult to interpret in terms of the kind of armour that is present. Are these osteoderm-like (like in some other temnospondyls) or scale-like (like in things like embolomeres and colosteids)? What examples of armour already known does that of *G. maritimus* most closely resemble? This is particularly important as it has bearing on what the rest of the integument is doing, and thus the strength of the interpretation.

The closest text to this found on lines 168-173. Is sound from this text that the armour is most like the scale-type of structure seen in early tetrapods. If this is true, it might help to clearly state that and why. It would also help to more thoroughly explain the precise special relationship of the armour or scales to the rest of the integument. How are these "scales" thought to be organized within or upon the epidermis. I am not sure that has been explicitly stated before, and would help us understand what we think these scales are actually doing.

To achieve this, I'd request clearer description and comparisons of the armour to that of other taxa. I'd request a clear description of the interpreted resulting architecture of the integument. Do we think these scales, as seen in other fossil taxa, are embedded within the epidermis, reside atop the epidermis, etc?. Clearer images of the armour will help so that we can validate the comparisons and interpretations.

I am also not sure it's an accurate reflection of reference 23 to say that total group Amphibian had freshwater "larvae". The presence of a larva implies the presence of metamorphosis, and amphibian metamorphosis is thought to be a rather derived trait not necessarily present in stem lissamphibians (according to reference 23). Maybe just referring to them as juveniles (or early life stage) is more appropriate?

With regards to the first point, I think the reporting of these new fossils as articulated, in marine deposits, covered in body armour, and unossified carpus, are enough to make a strong case for this animal being marine.

Line 56-60 describes the limitations of modern amphibians based on their current skin. This is certainly a limiting factor among today's amphibians, but the authors rightly ask if this was the case in ancient amphibians and admit it's unclear if their skin was as permeable as it is today. I think its very possible that modern amphibians are secondarily exceptionally permeable. Taxa like *Eryops*, etc, living along side large amniotes must have had a tougher skin than a modern frog. There are also armoured terrestrial temnospondyls, e.g. *Cacops*. It has been in my head for some time that their skin must not have been modern-lissamphibian-like. Some of these questions might be enhanced by reviewing/discussing a little bit about what we know of skin evolution from a molecular perspective. There is a group led by Leopold Echart that does a lot of work on keratin protein and keratinization evolution (e.g., Carron et al. 2024; Ehrlich et al 2020).

Alternatively, if there is really no work inferring stem amphibian skin composition (I haven't kept up with the state of the field), might your fossil be a way of suggesting the presence of a somewhat amniote-like skin keratinizing program common to tetrapods? Or at least co-optable by amniotes and your new taxon? It remains hard to imagine a modern lissamphibian-like skin was present in this animal, even with dermal armour present.

But if these are indeed more scale-like structures, maybe this animal could be cast as evidence that ancient amphibians did in fact more likely have skin that was a poor barrier, since they then deployed extensive scale covering to create a better barrier. All interesting questions and problems! If any of them could be answered even a little bit more by any data presented in this paper, it would be really helpful.

Minor edits/comments/corrections:

British spelling of "armour" throughout?

Line 25: What exactly is "Such an evolutionary pathway is narrow" referring to, there is not really a pathway described in the previous sentence. Maybe you mean: "An evolutionary pathway to marine colonization is narrow, and it may have been difficult for amphibians to exploit it.", but if not please clarify.

Line 29: change "when" to "whereas"

Line 40: Not sure what "Between these two extremes" is referring to as no bounds are mentioned in the previous sentence. Presumably the authors mean "Between the extremes of Steps 1 and 5,..."

Line 52: add something like, ", and thus no fully marine representatives have been previously recorded."

Line 55: add "more"? more permeable skin? We aren't sure just how permeable it was in the fully terrestrial temnos, but it's probably reasonable to suggest it was more permeable than an amniotes?

Line 68: It is mentioned that the new specimens come from sediments where other ocean-adapted marine reptiles have been found. My question when I read this was are these also considered to be "fully" marine? I see later in the text it mentions ichthyosaurs, if these are the same specimens referred to early on, I'd put that info earlier. Have they been published on, such that there could be references added?

Line 72: remove italics for "systematic" or add them for "Palaeontology"?

Line 81: and elsewhere, "Armor" is sometime capitalized. Make lowercase.

Line 82: I think you mean "strips" instead of "stripes"?

Line 95: make "This" lowercase

Line 98: Make "Clavicle" lowercase

Line 99: make "Extra" lowercase

Line 107: perhaps change to "for sharing the diagnostic features listed in the Emended Diagnosis section above." And make "Palaeontology" capital?

Line 118: I'd add "and the presence of enhanced ossification" otherwise it sounds like it lacks it given the qualifier in the first clause.

Line 119: I'd delete the sentence about the function of the clavicular process here. It disrupts the flow and is touched upon in the discussion later.

Line 149: change to "the margin of the platform".

Line 156-8: Can references be added to this statement?

Line 162: capitalize Amphibia.

Line 182: Change to "The mode of osmoregulation"?

Reviewer #2 (Remarks to the Author):

The authors of "Evolutionary pathway to the first fully marine amphibian" present a new taxon of Gerrothorax, *G. maritimus*, represented by two extremely well preserved individuals from Falang Formation of South China. This manuscript focuses on the proposed marine adaptations of this new taxon and the uniqueness of that ecology among temnospondyl amphibians. I find these specimens intriguing and worthy of study and publication, but have some points that the authors need to address prior to a decision on publication to remove some of the speculative nature of this manuscript.

The authors describe several features of the anatomy that they say support a marine ecology, they mainly focus on the body being completely covered with armor. This is despite the close relative *G. pulcherrimus* also being covered in armor but being thought of as freshwater in its ecology. The authors use the presence of extensive armor in *G. maritimus* as indicating that the taxon most likely had a modified physiology to handle the salt issue with respect to skin permeability or lack thereof, though the evidence for this seems sparse if possible to infer at all. Rather, it seems like much of the inferred ecology instead comes from the depositional environment of the Wayao Member and the presence of other "ocean-adapted marine reptiles" in that unit. The fact that the fossils are in a marine depositional environment does not conclusively demonstrate that the taxa would have been marine-adapted. The authors should explain better why these specimens do not represent terrestrial taxa that went through a 'bloat and float' taphonomic process.

The authors' discussion of the five steps to marine adaptation also appear to focus more on diet, whereas an important aspect that did not get as much discussion is reproductive changes for a marine lifestyle. Would these amphibians be required to be viviporous? Fully marine taxa often have live birth so as to not leave the water, with the exception of sea turtles. Is there any anatomical evidence for or against this in these new specimens?

In line 184-185 the authors state "*G. maritimus* colonized the sea in the Late Triassic". This statement may be a bit misleading. Are the authors saying that the new taxon was what colonized a marine setting? Or that an ancestor was what colonized the sea and *G. maritimus* continued that lifestyle? I think the issue here is using the word "colonized", because it isn't known whether this species was the first in the lineage to become marine or if it was merely continuing an ancestral lifestyle. Furthermore, it isn't known whether the move to a marine lifestyle happened in the Late Triassic or had already

happened earlier and this is just the first known occurrence, not the true time of colonization.

*****END*****

Version 1:

Decision Letter:

15th May 2026

Dear Dr. Motani,

Thank you for submitting your revised manuscript "Evolutionary pathway to the first fully marine amphibian" (NATECOLEVOL-25082888A), and apologies for the delay in getting this next decision back to you. Your manuscript has now been seen again by the one of the original reviewers (Reviewer #1) and a new reviewer (Reviewer #3) to comment on the isotope analysis. Unfortunately Reviewer #2 was unavailable for re-review. You will find the reviewer comments pasted below. They find that the paper has improved in revision, and therefore we'll be happy in principle to publish it in Nature Ecology & Evolution, pending minor revisions to satisfy the reviewers' final requests and to comply with our editorial and formatting guidelines.

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We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in about a week. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Thank you again for your interest in Nature Ecology & Evolution. Please do not hesitate to contact me if you have any questions.

[redacted]

Reviewer #1 (Remarks to the Author):

I thank the authors for carefully considering my comments and suggestions, and for entertaining my questions. Of the questions and comments I suggested for incorporation in a revised version, I am satisfied. I appreciate the more careful description of the interpreted total integumentary arrangement in the specimen and the detailed images. It is much clearer now.

I also really appreciate the addition of the isotopic analysis. While I am not an expert, I am becoming increasingly familiar with these emerging techniques, and the analysis seems sound to me. I agree there is support for a marine existence (matching strontium ratios in the bone to sea water levels), but would defer to an expert if one were present among the reviewers.

I'd be happy to see this now published.
Thank you

Reviewer #3 (Remarks to the Author):

I am hereby just reviewing the addition of the strontium isotope analysis into the manuscript. The authors use strontium isotope analysis as a direct method to attempt to understand whether the specimens had a marine ecology or habitat or not. The testing of both the bones and the matrices provides a good study design, and the differences between the specimens and the matrices is convincing. Of course, the specimens are still very old and, as the authors note, likely to be influenced by diagenesis. Furthermore, as the authors themselves note, one component of the terrestrial landmass would also have produced values of ~0.707 which would be equifinal with a marine hypothesis. As a result I would have three main suggestions:

-The statement relating to strontium isotope analysis should make clear that the same values could also be produced by life on one component of the terrestrial landmass. However, given the difference between the matrix and the specimens the authors suggest that marine habitat is more likely. This would be reasonable and transparent.

-Perhaps the authors could spend more time discussing why the measured matrix is 0.708 given that this doesn't overlap any of the proposed terrestrial landmass components and must therefore be a mixture of them. What processes could be leading to this value? How would the mixture occur? Could there also somehow be marine influence in the matrix as part of the mixture?

-This may be beyond the scope of this study but of course more detailed taphonomic analyses through XRF or high-resolution ICP-MS would enable a more convincing discussion of diagenesis across the specimen and matrices.

In addition, the strontium Discussion paragraph could do with some grammatical editing. For example, Line 177 should be that the terrestrial landmass 'was comprised of' not 'had'.

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Reviewers' comments:

Reviewer #1 (Remarks to the Author):

“This is a fascinating manuscript describing what appears to be a solid example, the first of its kind, of a fully marine stem-amphibian. I think the data and associated interpretations are well founded. I also believe this to be of interest to Nature Ecology & Evolution’s broad audience, as this contribution adds important insights into diverse aspects of vertebrate ecology and evolution. “

Our response: Thank you.

“To improve the utility of this contribution, my biggest comment for improvement is the sparse description and presentation of the actual armour itself. The main specimen figure is difficult to interpret in terms of the kind of armour that is present. Are these osteoderm-like (like in some other temnospondyls) or scale-like (like in things like embolomeres and colosteids)? What examples of armour already known does that of *G. maritimus* most closely resemble? This is particularly important as it has bearing on what the rest of the integument is doing, and thus the strength of the interpretation.

The closest text to this found on lines 168-173. Is sound from this text that the armour is most like the scale-type of structure seen in early tetrapods. If this is true, it might help to clearly state that and why. It would also help to more thoroughly explain the precise special relationship of the armour or scales to the rest of the integument. How are these “scales” thought to be organized within or upon the epidermis. I am not sure that has been explicitly stated before, and would help us understand what we think these scales are actually doing.

To achieve this, I’d request clearer description and comparisons of the armour to that of other taxa. I’d request a clear description of the interpreted resulting architecture of the integument. Do we think these scales, as seen in other fossil taxa, are embedded within the epidermis, reside atop the epidermis, etc?. Clearer images of the armour will help so that we can validate the comparisons and interpretations. “

Our response: We have added two paragraphs describing the armour, associated by three new Extended Data Figures that provides close-up views of these structures. We also now briefly discuss the phylogenetic context of the body armour based on the literature that addressed this question.

“I am also not sure it’s an accurate reflection of reference 23 to say that total group Amphibian had freshwater “larvae”. The presence of a larva implies the presence of metamorphosis, and amphibian metamorphosis is thought to be a rather derived trait not

necessarily present in stem lissamphibians (according to reference 23). Maybe just referring to them as juveniles (or early life stage) is more appropriate? “

Our response: Thank you for pointing this out. We have changed the expression from larvae to juveniles. The changes include Fig. 4, where freshwater larvae were mentioned.

“With regards to the first point, I think the reporting of these new fossils as articulated, in marine deposits, covered in body armour, and unossified carpus, are enough to make a strong case for this animal being marine. “

Our response: Thank you. Following the lead, we have modified the text to reemphasize the preservation of unossified carpus.

“Line 56-60 describes the limitations of modern amphibians based on their current skin. This is certainly a limiting factor among today’s amphibians, but the authors rightly ask if this was the case in ancient amphibians and admit it’s unclear if their skin was as permeable as it is today. I think it’s very possible that modern amphibians are secondarily exceptionally permeable. Taxa like Eryops, etc, living along side large amniotes must have had a tougher skin than a modern frog. There are also armoured terrestrial temnospondyls, e.g. Cacops. It has been in my head for some time that their skin must not have been modern-lissamphibian-like. Some of these questions might be enhanced by reviewing/discussing a little bit about what we know of skin evolution from a molecular perspective. There is a group led by Leopold Eickholt that does a lot of work on keratin protein and keratinization evolution (e.g., Carron et al. 2024; Ehrlich et al 2020). Alternatively, if there is really no work inferring stem amphibian skin composition (I haven’t kept up with the state of the field), might your fossil be a way of suggesting the presence of a somewhat amniote-like skin keratinizing program common to tetrapods? Or at least co-optable by amniotes and your new taxon? It remains hard to imagine a modern lissamphibian-like skin was present in this animal, even with dermal armour present. But if these are indeed more scale-like structures, maybe this animal could be cast as evidence that ancient amphibians did in fact more likely have skin that was a poor barrier, since they then deployed extensive scale covering to create a better barrier. All interesting questions and problems! If any of them could be answered even a little bit more by any data presented in this paper, it would be really helpful.”

Our response: Given that the body armour was made of osteoderms and gastral plates, it is not easy to make a definitive statement about skin appendages, such as hairs, feathers, and scutes. However, by following the lead by Reviewer 1, it is possible that our animal has scutes because amphibians have at least some Epidermal Differentiation Complex (EDC) genes that are used to make scutes in reptiles. We now mention this when we describe the carapace.

Minor edits/comments/corrections:

“British spelling of “armour” throughout?”

Our response: We enforced English (UK) dictionary on the document and modified the spelling accordingly. For example, all occurrences of “armor” have been replaced by “armour”, and the same for other American spelling such as “paleontology”, “center”, etc. We also applied changes to figure captions as well as Fig. 4.

“Line 25: What exactly is “Such an evolutionary pathway is narrow” referring to, there is not really a pathway described in the previous sentence. Maybe you mean: “An evolutionary pathway to marine colonization is narrow, and it may have been difficult for amphibians to exploit it.”, but if not please clarify.”

Our response: Modified as suggested. Thank you.

“Line 29: change “when” to “whereas””

Our response: Modified as suggested. Thank you.

“Line 40: Not sure what “Between these two extremes” is referring to as no bounds are mentioned in the previous sentence. Presumably the authors mean “Between the extremes of Steps 1 and 5,...”

Our response: Modified as suggested. Thank you.

“Line 52: add something like, “, and thus no fully marine representatives have been previously recorded.””

Our response: Modified as suggested. Thank you.

“Line 55: add “more”? more permeable skin? We aren’t sure just how permeable it was in the fully terrestrial temnos, but it’s probably reasonable to suggest it was more permeable than an amniotes? “

Our response: Modified as suggested. Thank you.

“Line 68: It is mentioned that the new specimens come from sediments where other ocean-adapted marine reptiles have been found. My question when I read this was are these also considered to be “fully” marine? I see later in the text it mentions ichthyosaurs, if these are the same specimens referred to early on, I’d put that info earlier. Have they been published on, such that there could be references added? “

Our response: We added a phrase to provide the information early as suggested, with literature citation to the ichthyosaur.

“Line 72: remove italics for “systematic” or add them for “Palaeontology”?”

Our response: Modified as suggested. Thank you.

“Line 81: and elsewhere, “Armor” is sometime capitalized. Make lowercase. “

Our response: Modified as suggested. Thank you. We checked the document for all occurrences of the word Armor and Armour to make sure we did not miss any.

“Line 82: I think you mean “strips” instead of “stripes”?”

Our response: Modified as suggested. Thank you.

“Line 95: make “This” lowercase”

Our response: Modified as suggested. Thank you.

“Line 98: Make “Clavicle” lowercase”

Our response: Modified as suggested. Thank you.

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Our response: Modified as suggested. Thank you.

“Line 107: perhaps change to “for sharing the diagnostic features listed in the Emended Diagnosis section above.” And make “Palaeontology” capital?”

Our response: Modified as suggested. Thank you.

“Line 118: I’d add “and the presence of enhanced ossification” otherwise it sounds like it lacks it given the qualifier in the first clause.”

Our response: Modified as suggested. Thank you.

“Line 119: I’d delete the sentence about the function of the clavicular process here. It disrupts the flow and is touched upon in the discussion later. “

Our response: The sentence was deleted. Thank you.

“Line 149: change to “the margin of the platform”.”

Our response: The change was made. Thank you.

“Line 156-8: Can references be added to this statement? “

Our response: We have added references for the oceanic nature of these ichthyosaurs.

“Line 162: capitalize Amphibia.”

Our response: Modified as suggested. Thank you.

“Line 182: Change to “The mode of osmoregulation”?”

Our response: Modified as suggested. Thank you.

Reviewer #2 (Remarks to the Author):

“The authors of "Evolutionary pathway to the first fully marine amphibian" present a new taxon of Gerrothorax, *G. maritimus*, represented by two extremely well preserved individuals from Falang Formation of South China. This manuscript focuses on the proposed marine adaptations of this new taxon and the uniqueness of that ecology among temnospondyl amphibians. I find these specimens intriguing and worthy of study and publication, but have some points that the authors need to address prior to a decision on publication to remove some of the speculative nature of this manuscript.”

Our response: Thank you for the overall evaluation and please see below for our responses.

“The authors describe several features of the anatomy that they say support a marine ecology, they mainly focus on the body being completely covered with armor. This is despite the close relative *G. pulcherrimus* also being covered in armor but being thought of as freshwater in its ecology. The authors use the presence of extensive armor in *G. maritimus* as indicating that the taxon most likely had a modified physiology to handle the salt issue with respect to skin permeability or lack thereof, though the evidence for this seems sparse if possible to infer at all. Rather, it seems like much of the inferred ecology instead comes from the depositional environment of the Wayao Member and the presence of other "ocean-adapted marine reptiles" in that unit. The fact that the fossils are in a marine depositional environment does not conclusively demonstrate that the taxa would have been marine-adapted. The authors should explain better why these specimens do not represent terrestrial taxa that went through a 'bloat and float' taphonomic process.”

Our response: Thank you for raising the concern, which led to further improvements of our manuscript. We have three points to make regarding this question. First, we have now conducted strontium isotope analysis, which provided independent evidence suggesting

that the individuals that became the holotype and paratype grew in the sea. Second, we have strengthened our discussion of “bloat and float” by adding a new reference and emphasizing the wrist preservation, following the lead of Reviewer 1. The process of “bloat and float” has been studied for adult red-eared slider (*Pseudemys scripta elegans*) turtles, showing that the limbs and then head fell off before the body exploded and sank—none of these features is seen in our specimen. Lastly, the fact that the armour existed in the freshwater sister species does not necessarily mean that the armour could not facilitate marine adaptation. As we argue, it was an exaptation that could be used for marine adaptation

“The authors' discussion of the five steps to marine adaptation also appear to focus more on diet, whereas an important aspect that did not get as much discussion is reproductive changes for a marine lifestyle. Would these amphibians be required to be viviparous? Fully marine taxa often have live birth so as to not leave the water, with the exception of sea turtles. Is there any anatomical evidence for or against this in these new specimens?”

Our response: Possibility of viviparity and ovoviviparity was discussed in Lines 191-196 of the manuscript that was reviewed, and the section was kept in the revised manuscript that accompanies this response document. Yes, we agree that viviparity is likely based on circumstantial evidence but there is no direct fossil evidence for the reproductive style of the species or the genus as we reported. Also, we question the statement “fully marine taxa often have live birth so as to not leave the water” because there is no evidence to suggest that viviparity evolved for the purpose in those species (there is a discussion of this in ref. 3). Additionally, amniote patterns do not necessarily apply to amphibians, which do not have to leave the water for reproductive purposes because their eggs do not drown in water unlike amniote eggs. We therefore think our discussion of salt tolerance is more appropriate here.

“In line 184-185 the authors state “*G. maritimus* colonized the sea in the Late Triassic”. This statement may be a bit misleading. Are the authors saying that the new taxon was what colonized a marine setting? Or that an ancestor was what colonized the sea and *G. maritimus* continued that lifestyle? “

Our response: Thank you for pointing this out. We meant the latter and revised the text accordingly.

“I think the issue here is using the word “colonized”, because it isn't known whether this species was the first in the lineage to become marine or if it was merely continuing an ancestral lifestyle. “

Our response: It is true that whether the species colonized the sea is unknown as the reviewer pointed out—thank you. At the same time, its lineage leading to the species did. So, we prefer to keep the word “colonize” by shifting the focus from the species to the lineage. I previously had a lengthy discussion about marine invasion versus colonization with Geerat Vermeij, who convinced me that colonization was more appropriate. Going by the meaning of the words, colonization usually occurs before invasion, whereas marine adaptation takes place during the colonization stage.

“Furthermore, it isn't known whether the move to a marine lifestyle happened in the Late Triassic or had already happened earlier and this is just the first known occurrence, not the true time of colonization.”

Our response: This is a valid point—thank you for pointing it out. We now state “in the Triassic” rather than “in the Late Triassic”.

Reviewer #1 (Remarks to the Author):

Reviewer 1: I thank the authors for carefully considering my comments and suggestions, and for entertaining my questions. Of the questions and comments I suggested for incorporation in a revised version, I am satisfied. I appreciate the more careful description of the interpreted total integumentary arrangement in the specimen and the detailed images. It is much clearer now.

Response: Thank you very much again for the useful suggestions.

Reviewer 1: I also really appreciate the addition of the isotopic analysis. While I am not an expert, I am becoming increasingly familiar with these emerging techniques, and the analysis seems sound to me. I agree there is support for a marine existence (matching strontium ratios in the bone to sea water levels), but would defer to an expert if one were present among the reviewers.

Response: Thank you. We will respond to a specialist below.

Reviewer 1: I'd be happy to see this now published. Thank you

Response: Thank you again.

Reviewer #3 (Remarks to the Author):

Reviewer 3: I am hereby just reviewing the addition of the strontium isotope analysis into the manuscript. The authors use strontium isotope analysis as a direct method to attempt to understand whether the specimens had a marine ecology or habitat or not. The testing of both the bones and the matrices provides a good study design, and the differences between the specimens and the matrices is convincing. Of course, the specimens are still very old and, as the authors note, likely to be influenced by diagenesis. Furthermore, as the authors themselves note, one component of the terrestrial landmass would also have produced values of ~ 0.707 which would be equifinal with a marine hypothesis. As a result I would have three main suggestions:

-The statement relating to strontium isotope analysis should make clear that the same values could also be produced by life on one component of the terrestrial landmass.

However, given the difference between the matrix and the specimens the authors suggest that marine habitat is more likely. This would be reasonable and transparent.

Response: Thank you for the suggestion. We have incorporated the discussion of this issue in a sentence starting from line 207.

Reviewer 3: -Perhaps the authors could spend more time discussing why the measured matrix is 0.708 given that this doesn't overlap any of the proposed terrestrial landmass components and must therefore be a mixture of them. What processes could be leading to this value? How would the mixture occur? Could there also somehow be marine influence in the matrix as part of the mixture?

Response: We added a sentence starting from Line 201 to address this.

Reviewer 3: This may be beyond the scope of this study but of course more detailed taphonomic analyses through XRF or high-resolution ICP-MS would enable a more convincing discussion of diagenesis across the specimen and matrices.

Response: We appreciate the suggestion. While we agree with the value of taphonomic analysis, it is a little beyond the scope of this paper as the reviewer indicated.

Reviewer 3: In addition, the strontium Discussion paragraph could do with some grammatical editing. For example, Line 177 should be that the terrestrial landmass 'was comprised of' not 'had'.

Response: We have corrected the sentence in the original Line 177. We also read the paragraph carefully again to check for other errors.