

Evolution of terrestrial anatomy revealed by a derived stem tetrapod

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

The contribution encompasses a novel synchrotron X-ray computed-tomography of the classic early Carboniferous stem-amniote *Westlothiana lizziae* thus revealing a wealth of new anatomical data previously completely unknown, from both cranial and postcranial elements. Additionally, the paper includes a new comprehensive data matrix to explore the phylogenetic relationships of the taxon in relation to early diverging crown amniotes and their stem. The authors discuss in detail this new topology (and the calibrated one) to compare with previous alternative phylogenetic analysis on early amniotes.

I find the new topology based on the novel anatomical data important, but the paper cannot just rely on this. Most of the Introduction and Phylogenetic results and Discussion sections are paragraphs, some repetitive and convoluted, about how their new topology is more accurate/broader/larger/etc. than other contrasting phylogenies. I am happy with the new comprehensive phylogeny they obtained but I feel the contribution misses to explore the unique anatomical information they obtained from *Westlothiana*'s scans.

The paper would be much more interesting and significant for a broader audience if the authors would explore beyond the actual analysis the impact of the new data obtained in relation to the "assembly of the amniote body plan", as stated at the end of the Introduction section but not further discussed, the putative morphofunctional/paleoecological considerations based on the new anatomical data on the axial and appendicular skeleton (very briefly mentioned and figured in Extended Data Figures 5 & 6 which are in turn not cited in the text!) in the context of early tetrapod terrestrialization, a more compelling discussion about the timing of early diversification of amniotes (and stem-amniotes) beyond if its earlier or later than previously thought. Additionally, there are several statements in the text, highlighted in the attached file, that need to be discussed based on hard data and/or referenced and, in general, I think the Ms would benefit from sharpening and tightening the text.

Accordingly, I consider that in the present format the contribution is not suitable for publication in Nature after Major Revision.

Referee #3

(Remarks to the Author)

This paper uses advanced synchrotron X-ray computed tomography to reveal substantial new anatomical information of the enigmatic taxon *Westlothiana*, which has been previously identified in various phylogenetic positions and is absolutely crucial for understanding early amniote evolution. Key findings include: a detailed and revised anatomical description (of key elements in the main text, and the remainder of the holotype in the supplemental data); the new discovery of major differences between the holotype and referred specimens; fantastic 3D renderings of skeletal elements demonstrating key anatomical findings; fascinating phylogenetic results that recover an extensive amniote stem lineage, including a monophyletic Lepospondyli as stem amniotes with *Westlothiana* as the earliest diverging member of Lepospondyli; and a much earlier proposed origin for amniotes, with unappreciated early diversity. In sum, this paper makes a number of

important discoveries that will interest a wide range of workers in evolutionary biology and palaeontology.

Although *Westlothiana* has been known for three decades and described several times, details from synchrotron scans enormously increase our knowledge of the anatomy (and by extension phylogenetic placement) of this taxon, making this contribution highly original and significant.

The description (in particular that presented in the supplemental data) is very detailed and will be a tremendously valuable resource to future researchers, as will the raw CT data and 3D models made publicly available on Morphosource. I particularly commend the authors for their extensive and careful comparisons to the anatomy of other taxa in the supplementary information. The detail visible in figures, in particular the Extended Data Figure, is exquisite. The ramifications of the new phylogenetic analyses could potentially be far-reaching and will contribute to the active debate on phylogenetic relationships of early tetrapods, in particular the enigmatic lepospondyls.

The abstract and summary are clear and concise, highlighting the key findings of the study. The introduction places the work in the appropriate context and underlines the importance of understanding the anatomy of *Westlothiana*. The approach is appropriate, the quality of the anatomical data is excellent, and the presentation clear and easy to follow.

Overall - these findings represent an important advance in the field with superb new and original data, and robust interpretations.

In terms of methods, the scanning parameters are presented in great detail as are the details of the phylogenetic analyses. However, there is little detail presented on the segmentation methods (Did the authors use automated tools or was this carried out manually? Did they employ any AI technology?) or how the 3D reconstructions in Figure 2 were created - recent authors (see Rawson et al., 2021 or Porro et al., 2023) have provided transformation matrices to allow researchers to understand and replicate the movement of individual elements from their original positions to create such 3D reconstructions. The current methods lack basic information on how 3D reconstructions were generated and some elaboration is necessary.

Thus, with regards to improvements, my main suggestion is adding more detail on segmentation and 3D reconstruction. In Figure 2, the mandible reconstruction is described as a composite - presumably of the left and right mandibles? Which elements come from which side? In addition to models of the individual elements, which are very useful, can the 3D reconstructions in Figure 2 also be made available for inspection, as an STL in supplemental data or in an online repository?

Please check various issues with the figures, such as Figures 1 and 3 not being cited in the main text. There are also numerous issues with the figures and figure captions - please see annotated PDF for detailed comments.

One thing that would be useful is more references within the supplementary description to the corresponding Extended Data Figures illustrating the anatomy being discussed. On line 482 of the supplemental data you refer to an Extended Data Figure 11 - but there is no Figure 11? Please check.

It is notable that the braincase (apart from the basi- and parasphenoid) is poorly preserved in many Carboniferous tetrapods, including in this taxon. Could this be due to poor ossification of braincase elements at this stage of tetrapod evolution? Just a thought.

I cannot see a description for the surangular in the supplemental data?

Also, I agree from the figures that it is unlikely that the splenial participated in the symphysis - but is there any information preserved on symphyseal morphology? This would be very informative.

It is noted that an unusual feature of *Westlothiana* is that there is no contact between the coronoids and splenial - but it is unclear what would have filled this space on the medial aspect of the lower jaw from Figure 2 or the description. The prearticular? (From the figures the angular makes up the lateral but not the medial wall of the mandible.) How are you sure there was not a medial lamina of the splenial on the medial aspect of the mandible?

There are minor formatting errors and typos in both the main text (see annotated PDF) and in the supplementary data (for example, taxa names on lines 125, 132 286, 326, 329, etc. need to be italicised; "data" should probably be capitalised on line 392 for consistency).

Where did the anatomical data for taxa in the expanded outgroup come from? These are not in Part 3 of the supplementary data.

In general the references do appropriately credit previous work although there have been numerous anatomical studies of early tetrapods in recent years applying microCT and synchrotron data (see work by Ahlberg, Porro, Ruta, and others) that are not utilised here, which is surprising given similarity in the methodologies.

Referee #4

(Remarks to the Author)

The manuscript entitled “Synchrotron tomography of a Carboniferous tetrapod informs stem amniote diversity” provides essential new anatomical data on the Carboniferous tetrapod Westlothiana and puts it into context of its crucial role for the understanding of the evolution and early diversification of the amniote lineage.

Westlothiana has been known already since its original description in 1990, but due to its preservation many body regions that could provide important anatomical data for understanding its phylogenetic position among early tetrapods remained inaccessible and unknown. In the new study the authors are now able to provide this much needed data based on propagation phase contrast synchrotron X-ray micro computed tomography of the holotype specimen. This revealed new insights on the anatomy and configuration of the skull roof and especially on the palatal region of this taxon. This reveals a striking mixture of basal and derived characters highlighting the central role Westlothiana can play in resolving early amniote evolution more thoroughly.

The authors provide a brief, but very well-written description of those regions in the specimen that have been previously unknown and/or can be interpreted more thoroughly based on the synchrotron data. Additionally, they provide a more comprehensive description in the supplemental material, which makes a lot of sense for a study like this and will undoubtedly serve as a reference point for future studies. In the supplemental information they also provide more detailed arguments on why the second specimen, originally referred to Westlothiana, is unreferred and considered a different taxon, a point only briefly mentioned in the main manuscript.

I am pleased with the approach the authors took in this manuscript as it is well written and very clear in the way the new data is presented and reflected upon. The new insights provided by the synchrotron scans of Westlothiana are extremely important for a better understanding not only of the early evolution of amniotes, but indeed all aspects of the evolution and diversification of “lower tetrapods” and as such is well placed for a contribution to Nature. It is an important contribution to the ongoing research and progress in that field and highlights that even if and when new fossil evidence is scarce, new technologies and approaches can contribute significantly to the resolution of this important evolutionary question. In this sense, it complements and expands the data presented in recent studies on brain case morphology, allowing for an even broader perspective by integrating new and amended characters from the entire body.

Indeed, I have rarely had that little to criticize or suggest in a manuscript. There are a few minor points listed below.

- In the text figure 2 seems to come up before figure 1. I still think the current figure one makes sense to be presented first, so the authors should add a reference in the text.
- I think in figure 1 it would be beneficial if the labelled scan of the drawing would be larger. In favor of that the foot could be reduced in size as it is a less complex structure
- Something seems off in the figure caption of Extended figure 4 – there is a reference for a figure 4 somewhat in the middle of the figure caption. Please check and adjust this

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

I find the new version of the Ms suitable for publication.

I am glad that the authors have taken into consideration my previous comments and rewritten several paragraphs of the original Ms. Now the Phylogenetic Results and the Discussion of the Ms are certainly more consistent. The Discussion, in particular, is comprehensive including new data thus enriching the Ms and certainly making it more interesting for a broader audience.

My only final comment to this point is about the new article by Long et al. 2025 recently published in Nature (“Earliest amniote tracks recalibrate the timeline of tetrapod evolution”). I think the new hypothesis provided by Long et al. should be discussed in the final Discussion of the present Ms.

Sincerely,

Claudia Marsicano
Universidad de Buenos Aires
Buenos Aires, Argentina

Referee #3

(Remarks to the Author)

I am really pleased to see the changes the authors have made, in particular the greater detail in the methods used to segment the data and create the 3D reconstruction. This is a really interesting and informative paper and all of my concerns have now been addressed in this revision.

Referee #5

(Remarks to the Author)

This manuscript presents new 3D data derived from synchrotron scans of the Mississippian vertebrate *Westlothiana*, which has been suggested in the past to be a close relative of modern amniotes. In addition to this, the authors present a comprehensive reworking of the early tetrapod tree based on an amalgam of previously published characters and a few novel ones reported in this study. The former contribution is primarily relegated to the supplemental material as is traditional for short-form publication. I have some concerns about the segmented synchrotron data and description, but these could be worked out through the peer review process although this will require going back to the original data and anatomical interpretation as it is currently not in publishable form. The latter looks sleek and shiny but has critical problems. Unlike some of the previous round of referees, I do not recommend publication. I apologize in advance for the length of this review, but wanted to explain these issues.

Every phylogenetic analysis has its own problems but I think the problems in this specific analysis are worth taking into serious consideration they seem to be willful and seem to have significant impact on the major features of the phylogenetic topology as reported. Before getting into the weeds of why the phylogenetic analysis is likely problematic, I want to discuss the importance of the three major phylogenetic results the authors present here so that the impact of these specific characters and character sets can be understood. The authors here present two major innovations, which themselves are basically just returns to a previous “consensus” established in the 90s and early 2000s: (1) embolomeres/anthracosaurs as the initial grade of stem-amniote, (2) unity of disparate small-bodied early tetrapods within a monophyletic Lepospondyli clade. A third innovation, a relatively restricted amniote crown group, has been a broader theme of recent analyses arising in this working group, albeit in a range of conflicting topologies and periodically recanting of the important features of earlier high-profile analyses (e.g. a diapsid origin of varanopids, Ford & Benson 2020, quietly recanted in a series of lower-profile papers afterwards).

Placing embolomeres as stem amniotes is, *prima facie*, an appealing hypothesis because it creates a robust amniote stem group in the lower Carboniferous. However, every time it has been proposed on specific anatomical bases it has immediately been noted that the characters which unite embolomeres with amniotes are ancestral for most if not all digitated stem tetrapods (Romer 1957, Panchen 1985). The analyses here is no different: four characters unite embolomeres with amniotes: (34) absence of labyrinthine infolding, (126) lack of contact between the exoccipital and postparietal, (252) pleurocentrum-dominated vertebrae, (261) curved ribs. Of these, character 34 seemingly immediately reverts to the primitive condition because seymouriamorphs all show labyrinthine infolding (e.g. Maho & Reisz 2022). Character 126 is incorrectly scored (for instance, embolomeres do have a well-defined exoccipital-postparietal contact, see Pardo 2024 Zool J. Linn. Soc.). Character 252 is uninterpretable in embolomeres, where the pleurocentrum and intercentrum are of equal size and both articulate directly with the neural arch. Similarly, the “derived” condition of character 261 is widespread among definitive stem tetrapods, notably *Ichthyostega*, *Pederpes*, and *Whatcheeria*. The dataset here further ignores a number of recent discoveries of unambiguously primitive anatomy within embolomeres, including supraneural spines in the caudal skeleton (Clack 2011), an anocleithrum in the shoulder girdle (Adams et al. 2025), and hypophyseal and notochordal canals in the braincase (Pardo, 2024). None of these characters are incorporated into the current dataset, even though they were present in some of the datasets the authors draw upon in constructing this analysis. Their exclusion appears to be deliberate.

A monophyletic Lepospondyli is a hypothesis that posits a single adaptive radiation of small-bodied early tetrapods. Although a number of workers found a monophyletic Lepospondyli in the early 2000s (Anderson 2001, Ruta et al. 2003, Vallin & Laurin 2004), workers focused on the anatomy of these animals have consistently doubted the monophyly of the group due to the lack of a clear unifying anatomy. Most support for a monophyletic Lepospondyli comes from either the presence of spool-shaped pleurocentrum-dominated vertebrae or from small size, whereas evidence against this comes from numerous highly precise anatomical similarities across the entire body which would have had to be derived (or reversed) in parallel with the broader tetrapod tree (e.g. aistopods and neotridians must lose numerous crown tetrapod characters in parallel, recumbirostrans must gain many amniote characters in parallel). The analysis presented here falls into this same trap: the reported analysis claims this group is united by ten unambiguous characters: (1) skull < 3 cm, (7) narrow antorbital region, (29) peglike marginal teeth, (44) dorsal process of lacrimal present, (61) concave notch in posteroventral margin of postfrontal to accommodate postfrontal, (66) irregularly-shaped postorbital, (69) sigmoid-shaped anterodorsal margin of postorbital, (202) retroarticular process present, (209) dentary toothrow less than 50% of jaw length, and (311) internal trochanter not separated from surface of femur by trough. One of these (character 1) is unambiguously size-related. Several are incorrectly scored (7, 202). Others are just ancestral tetrapod conditions (29, 66). Others appear to be nonsense. An example is character 61: (large concave notch in postfrontal to accommodate postorbital): of all “lepospondyls” within and excluded by this analysis, the only one actually shows this anatomy, and that is the type specimen *Asaphestera platyrhis* (see Mann et al. 2020) which is inexplicably united here with previously attributed material that has since been reassigned to *Steenerpeton sylvae*. Interestingly this character is elsewhere seen in taxa assigned here to the amniote crown group, specifically to synapsids, which aligns with the attribution by Mann et al. (2020) of the *Asaphestera* type specimen to a probable caseasaur synapsid rather than a recumbirostran. Similarly, I have no idea where character 69 comes from: I think it is a description of the specific anatomy seen in *Westlothiana*, but I have not seen this in any other “lepospondyl.” The condition here in *Westlothiana* seems to actually be describing the presence of a syndesmosis between the skull roof and cheek, a condition actually seen in a range of stem tetrapods, including *Tiktaalik* (see Lemberg et al. 2019) and *Whatcheeria* (see Bolt & Lombard 1995 but also Rawson et al. 2021) among others. Such anatomy is also clearly apparent in embolomeres (e.g. see *Archeria*, Holmes 1989 Text-Fig 6a; *Proterogyrinus*, Holmes 1984, Figure 8; *Calligenethlon*, Adams et al. 2025, Figure 5A).

Similar problems show up in the characters associated with the definition of the clade of Lepospondyls excluding *Westlothiana*: a number of these characters are outright incorrect and reflect inaccurate coding throughout the matrix. For

instance, intercentra are widespread among recumbirostrans, a supratemporal is widespread among recumbirostrans (see Szostakiwskyj et al. 2015), the recumbirostran adductor crest (which is the only “lepospondyl” adductor crest in this dataset) preserves a prominent contribution from the posterior coronoid which is often exposed in lateral view (see Szostakiwskyj et al. 2015 as well as Pardo & Anderson 2016).

This becomes even more obvious when we look at character support for a non-microsaur clade of “lepospondyls.” This is the group which recent studies have argued are stem tetrapods unrelated to the amniote-allied recumbirostrans. This clade is mostly represented by reversions to the stem tetrapod condition: long postorbital process of the maxilla, elongate dentary with greater number of teeth, unossified carpus, single atlantal neural arch, etc. A few of the noted characters (e.g. position of the pineal) appear to be incorrectly coded as they are unambiguously positioned in the anterior third of the parietal in most groups belonging to this clade (aistopods, nectrideans). Finally, the presence of *Brachydectes* (and seemingly also *Carrolla*, although no scorings are given for this animal) in this clade should be considered highly suspect given the extensive work documenting a coherent and extensive set of recumbirostran characteristics uniting molgophids and brachystelechids within Recumbirostra (Maddin et al. 2011, Pardo et al. 2015, Pardo & Anderson 2016, MacDougall et al. 2024). There is nothing compelling here that should overturn fundamental anatomical evidence against “lepospondyl” monophyly that has been discussed by prior authors but has been mysteriously excluded in the dataset here.

So, in other words, I do not find these claims convincing because the dataset is not appropriate for addressing these questions. If the authors purported to test these two phylogenetic hypotheses, they ought to be extensively sampling known stem tetrapod groups, of which there are many well-documented forms, and of character variation important in that part of the tree, which has also been well-documented. In fact, character variation documented in previous phylogenetic analyses and which is thought to be important for defining innovation in the tetrapod stem group has actually been actively excluded here or has been folded into character statements which evade careful anatomical work. This includes character suites such as the humerus and neurocranium, as well as various others. Taxonomic sampling in the stem is poor: it is limited to five digitized tetrapod taxa: *Acanthostega*, *Whatcheeria*, *Pederpes*, *Baphetes*, and *Greererepeton*. Numerous well-represented taxa are excluded: *Ichthyostega* most notably, but also *Ossinodus*, *Crassigyrinus*, *Eoherpeton*, *Aytonerpeton*, *Eucritta*, *Ossirarus*, *Perittodus*, *Kyrinion*, and various others. Given the incomplete nature of many of the taxa included here (e.g. *Asaphestera*, *Echinerpeton*, *Eocasea*, *Erpetonyx*, *Ianthasaurus*, *Pantelosaurus*, *Vaughnictis*) it is strange that well-described animals represented by multiple complete specimens in critical parts of the tree have been excluded from the analysis. I also strongly believe that the authors must necessarily sample temnospondyls more completely: the dataset reported here only samples two dendroterpetids, one very incomplete and derived late-occurring edopoid (*Edops*) and two very advanced amphibamiform dissorophoids (*Doleserpeton* and *Gerobatrachus*). This is a massively limited sampling of a very diverse clade with real potential to bear on both the ancestral condition of the tetrapod crown as well as on specific modeling of evolutionary rates of specific characters. Finally, important “lepospondyl” taxa that need to be included (e.g. urocordylid nectrideans) are inexplicably excluded. On the other hand, a latest Permian cynodont is included for an inexplicable reason. In general, I struggle to understand the authors’ decision-making process on taxon sampling.

Some further hints as to the source of these problems comes from the table in Part 3 of the supplemental material. The authors primarily rely on relatively old references, some of which have been clearly superseded by more recent work. The most notable of these is the heavy reliance on the Carroll and Gaskill 1978 monograph on microsaur. Carroll & Gaskill is a beautifully illustrated work but unfortunately a lot of their interpretations have been overturned by direct fossil anatomy. An example here is the authors’ use of the taxon *Asaphestera intermedia*: Carroll generally regarded this animal to be the most primitive microsaur and interpreted the skull accordingly, reconstructing it as having a high narrow skull, short postorbital region, and so on. This material has been revisited by Mann et al. (2020): it is in fact a chimaera of two very different animals. The specimen bearing the name *Asaphestera platyrhis* (as referred by Steen 1934) is a skull roof and partial cheek that shows a number of characters suggestive of synapsid affinities, whereas much of the rest of the material comes from a relatively advanced recumbirostran with a relatively standard recumbirostran skull. The majority of scorings for this pivotal “basal lepospondyl” in this dataset thus appear to be entirely fictional or otherwise reflect the chimaera status of the material. Other taxa (e.g. *Micraroter*, *Tuditatus*, *Hapsidopareion*, *Cardiocephalus*) differ somewhat importantly from Carroll & Gaskill’s figures, and in some cases have been refigured more recently, or have close relatives which have been. In fact, there is an abundant recent literature carefully documenting recumbirostran anatomy and many of these taxa which have been pivotal in teasing out the amniote affinities of this group have just been outright excluded from this analysis. This applies more broadly to the literature employed in scoring decisions here, e.g. *Ianthasaurus* (note spelling) is scored solely from Reisz & Berman 1986, but at least two papers have been published on additional more complete specimens of this animal since, clarifying quite a bit of the anatomy. *Microbrachis* is scored from Carroll & Gaskill despite more recent work by Vallin & Laurin 2004 among others, and ready access to this material (both original specimens and peels).

However, part of the problem here seems to be a failure to correctly describe *Westlothiana*. Although the scans appear to be quite nice, it is actually very hard to interpret the edges of bones, and the thick black tracings imposed directly over the 3D renders is a part of that problem. In some cases, I think it is clear that the bone margins are incorrectly interpreted. There is, for instance, very clearly a sutural line between the first and second coronoid, even if the authors were unable to identify that during their segmentation. I am also unsure of their suture between the postfrontal, postorbital, and parietal; there is almost certainly a partially-displaced suture line through the element they identify as the left postfrontal (and the surface is poorly preserved on the right side) and there seems to be a slight but regular displacement through the lateral portion of the right parietal that might be a parietal-supratemporal suture, suggesting to me that they may have failed to distinguish between the parietal and temporal series on both sides of the skull. Similar problems appear in their interpretation of the postdentary bones of the lower jaw (some of the material assigned to the dentary is splenial, and there is almost certainly some postsplenial incorrectly assigned to the angular. Much of the anterior process of the prefrontal, which contacts the external naris, is assigned to the nasal, and much of the material assigned to the ectopterygoid is actually pterygoid. It appears to me

that the segmentation is primarily showing cracks rather than sutures, which makes me question a lot of the scores for *Westlothiana* in addition to the scoring for other taxa as enumerated above. There are some additional failures to interpret elements in the postcrania; the obvious one is the “axis neural arch” which is instead a pair of rounded proatlantes, as seen in some other stem tetrapods; for example, the humerus as segmented is quite strange and very distinct from how it is interpreted by Smithson et al. 1993, who reconstructed a large block-like entepicondyle and a rather standard entepicondylar foramen. Neither of these are shown here. If the authors are correctly identifying entepicondyle and ectepicondyle, this is a completely unique humerus form for a Palaeozoic tetrapod.

The authors then present a retrodeformed and reconstructed skull. I want to emphasize that this is a very flattened and deformed specimen. This is a very superficially compelling image which presents more and more problems the closer one looks at it. The most obvious biological problem I see is the positioning of the adductor fossa between the quadrate ramus of the pterygoid and the quadrate. This is incorrect: the quadrate ramus of the pterygoid forms along the surface of the palatoquadrate, which will ossify to form the quadrate posteriorly and the epipterygoid anteriorly. The palatoquadrate is always medial to the mandibular adductor musculature. Therefore, the quadrate should be broadly contiguous with the quadrate ramus here, and the adductor fossa should be located between this unit and the dermal cheek (quadratojugal, jugal, and squamosal). However, the anterior margin of the quadrate as figured in Figure 1 seems to be a zig-zagged broken edge that seems to fit into a similar broken edge on the quadrate ramus of the pterygoid (Extended Figure 3) suggesting that the pterygoid may have been massively co-ossified with the palatoquadrate rather than a distinct element as in advanced early tetrapods, and the authors are simply misidentifying a break as a suture. The quadratojugal is probably part of the slightly displaced element identified by the authors as the squamosal. I also wonder if the “adductor crest” on the mandible is an artifact of deformation; you see something similar in the definitive stem tetrapod *Sigournea*, for example. I don’t see any evidence of an obvious coronoid enlargement as seen in temnospondyls, seymouriamorphs, recumbirostrans, and uncontroversial amniotes.

These problems with the anatomical description align with additional failures to recognize clear and unambiguous stem tetrapod anatomy in *Westlothiana*. For instance, the fact the postfrontal makes up the entirety of the dorsal orbit is unlike anything seen in any “lepospondyl” but is consistent with anatomy seen in various Devonian and Mississippian stem tetrapods. The deeply-incised hooklike glenoid surface of the articular (NOT a retroarticular process) is rather typical of Mississippian stem tetrapods. The denticle field on the prearticular is a classic stem tetrapod character absent in the crown. The pterygoid denticle field that extends along the quadrate ramus of the pterygoid is a classic stem tetrapod character. The gentle convexity of the ventral margin of the lower jaw and absence of a coronoid expansion of the dentary and postdentary bones are classic stem tetrapod characteristics. Premaxillary teeth that increase in size posteriorly are a classic stem tetrapod characteristic. The absence of a well-developed bony connection between the prearticular and postdentary bones on the medial surface of the jaw would also make sense in this context if that corresponds with a broad medial exposure of the Meckel’s cartilage (typically this is ossified into Meckelian bone in better-known stem-group tetrapods but could be cartilaginous at earlier life history stages). In other words, this is an animal that is broadly consistent with a position close to the divergence between temnospondyls and amniotes, but I really do not see evidence for it being as amniote-ward as the authors claim and certainly no evidence for a close relationship between this animal and either recumbirostrans or other “lepospondyls.”

In light of these problems (critical flaws with the segmentation and associated description, critical flaws with the phylogenetic analysis) the interpretation offered in the discussion is unfortunately not of great significance. All of the anatomy here implies an animal that sits in a relatively crownward part of the tetrapod stem group, perhaps just crownward of baphetids. *Westlothiana* is probably aquatic, but that is not noteworthy in a stem tetrapod. *Westlothiana* lacks various amniote-like features, but that is expected in a stem tetrapod. Phylogeny-specific interpretations presented by the authors are effectively irrelevant. The analyses presented in Figure 9 are irrelevant because they do not sufficiently sample Mississippian stem tetrapod and temnospondyl diversity to actually estimate character evolutionary rates, whereas the authors aggressively sample even the least complete early amniotes (e.g. *Echinerpeton*). The specific character state reconstructions in Extended Figure 10 are overtly misleading even if we take the authors’ phylogeny at face value because features like a surangular crest and transverse flange of the pterygoid are widespread in temnospondyls (effectively not sampled in this analysis) which both affects the underlying topology (already suspect) as well as interpretations of character evolution i.e. these are likely ancestral characters for the tetrapod crown group that show specific reversions in various lineages due to ecomorphological factors, not parallel acquisitions among recumbirostrans and “classic” amniote taxa. Further, the authors’ claim that the absence of a transverse flange implies an undivided m. adductor mandibulae is just incorrect; the m. adductor mandibulae is divided into multiple units in all gnathostomes (see: Polypterus, Noda et al. 2017; *Neoceratodus*, Ziermann et al. 2017; *Latimeria*, Datovo & Johnson 2025; *Squalus*, Hyman 1922; *Necturus*, Hyman 1922). As stated above I do not agree with the authors’ interpretation of the subtemporal vacuity, although I do agree this animal lacked a transverse flange, but this simply implies that the m. adductor complex was comparably small. What this might indicate is that *Westlothiana* lacked an m. pterygoideus, the muscle which inserts onto the transverse flange in reptiles and caecilians (Kleinteich & Haas 2007) and which seemingly was present in the ancestral tetrapod but subsequently lost in batrachians. However, there are plenty of extant reptiles which lack a transverse flange but still retain an m. pterygoideus, so this is a more challenging argument to make on a strict comparative anatomy basis. So, the points the authors consider most discussion-worthy are either not supported by the data as presented, are not novel, or both.

This is obviously a long report (which I apologize for) so I will not add line comments, as I believe the problems with this manuscript are more fundamental than specific phrasing in the text body. I hope the authors will put in the work to ensure that the anatomy is correctly documented and that phylogenetic work engages with the extensive anatomical and phylogenetic work originating in other research groups that conflicts with this (regressive) phylogenetic hypothesis. I’m sorry I can’t be more enthusiastic at this time.

References:

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Referee #6

(Remarks to the Author)

Topics and impact: The main part of the paper addresses a classic paleontological question since the triumphant of cladistics: the exact phylogenetic position of a taxon near a key evolutionary node of poor resolution. For such taxa, three potential assignments exist: the rootward positions (often at the very base, as in this paper) within the two sister group lineages, or out of them, inclusion in the section rootward to the aforementioned sister groups. A more robust and convincing assignment normally requires newly discovered transitional taxa, or new specimens of a key taxa showing considerably greater anatomical details, or as in this paper, revisiting anatomy interpretations through technological applications, in most cases as in this paper, tomographic scanning. The rise of amniotes is certainly an important topic, and *Westlothiana* is a classic taxon in this segment of the vertebrate tree of life. Resolving it out of the conventional position within the amniote lineage is interesting, while the ecological discussion offers a refreshing update to the stereotypical portrayal of this animal. Popular literature often depicts *Westlothiana* as a terrestrial form perching on fallen trunks; this work challenges such assumptions.

Methods. this study applies standard methodologies: synchrotron scanning and reconstruction, Rendering in Blender; morphological description, phylogenetic analyses and ancestral character estimation. These are not the fanciest, but adequately used and explained and documented.

Writing. I did not participate the first round of reviewing, and I was given very limited time for a thorough review. but I found

the paper and the extensive supplementary materials are generally well-written, especially after the revision. However, structurally, I can see the two core findings, the phylogenetic position of Westlothiana and the lifestyle of early tetrapods appear disconnected, with the latter feeling tacked on. The latter topic can surely expand to another, maybe more impactful standalone paper, e.g. when and how tetrapod terrestrial adaptations evolved stepwisely, if more data and substantial update is given in that section.

The figures are functional, but unexceptional. The text figures resemble those of a descriptive paper for a professional journal, rather than a broadly accessible publication.

All in all this work is an important contribution that warrants follow-up studies and fieldwork.

Version 2:

Reviewer comments:

Referee #1

(Remarks to the Author)

The new version of this Ms is really substantially different to the previous one I read nearly a year ago. Particularly due to the radical change in the phylogenetic position of Westlothiana from crown-group Amniota to a stem-tetrapod. This change was mainly driven by a reassessment of much information in the original Ms questioned in an extended report by reviewer #5. This reviewer raised many contradictions on the 3D rendering that impacted directly on the subsequent interpretations of anatomical features in the specimen, and thus the final phylogenetic analysis and resulting position of Westlothiana.

I really appreciate that the authors took those comments into account and were able to produce a more robustly supported manuscript with a richer discussion.

Something that I really think would be interesting to expand in the Discussion is something the authors mentioned at the end of the fourth paragraph in page 6: "...then there is currently no evidence of crown amniotes before the late Carboniferous...."

Their new resulting analysis also takes away one of the last remaining crown tetrapods from the Mississippian. Essentially, all that's left is Balanerpeton (East Kirkton Fm.), after which the oldest crown tetrapods are basically from the Joggins Fm. (Pennsylvanian, Canada). That means the tetrapod calibration point for molecular clocks is likely to shift approx. 17 million years from East Kirkton Fm. to Joggins Fm. times. I think would be interesting to expand this aspect in the general final discussion of the Ms.

Referee #6

(Remarks to the Author)

The scientific question addressed by this manuscript is important. Westlothiana is a classic and historically influential taxon in discussions of early tetrapod and amniote evolution. Clarifying its anatomy and phylogenetic position therefore has significance beyond the placement of a single species. In this study, Igielman et al. provide substantially revised anatomical interpretations based on newly segmented tomographic data, offering one of the most comprehensive reassessments of this important taxon to date.

One practical suggestion concerns data accessibility. Because the anatomical interpretations presented here are central to the manuscript, I believe the tomography data should ideally be made directly available to reviewers rather than through a request-based process. Providing direct access during peer review, and depositing the data in a permanent public repository upon publication, would facilitate independent evaluation and strengthen the transparency and reproducibility of the study. I was also somewhat surprised by the absence of a quantitative morphometric assessment, given the authors' established expertise in quantitative palaeobiology. The apparent evolutionary decoupling between the cranial and appendicular skeleton in Westlothiana would seem to provide an excellent opportunity for such analyses. However, I appreciate that this may reflect the current scarcity of suitable comparative datasets among stem tetrapods.

That said, I feel that both the visual presentation and the narrative structure of the manuscript require further refinement to meet the level of accessibility and broad appeal expected of a Nature paper. The three main-text figures appear overly specialist in their current form and do not communicate the major findings as effectively as they could to a broader readership. A substantial redesign of the figure set would help highlight the principal biological messages and improve accessibility for non-specialist readers.

Similarly, portions of the detailed anatomical description could be moved to the Supplementary Information, allowing the main text to focus more clearly on the broader evolutionary implications of the study. In addition, the study by Long et al. (2025) is highly relevant to the present discussion, yet its incorporation currently feels somewhat peripheral rather than fully integrated into the central narrative. I believe its implications deserve greater emphasis and discussion.

I also noted a number of formatting and presentation issues, which are detailed below.

References

There are numerous formatting inconsistencies in the reference list. The authors should carefully check all references to ensure compliance with Nature formatting requirements. I only list a few representative examples below:

1. Long, J. A., Niedźwiedzki, G., Garvey, J., Clement, A. M., Camens, A. B., Eury, C. A., ... & Ahlberg, P. E. Earliest amniote tracks recalibrate the timeline of tetrapod evolution. *Nature* 641, 1193–1200 (2025).

-Please verify whether the author list should be abbreviated according to journal style (e.g., "Long et al.").

2. Ahlberg, P. E. *Elginerpeton pancheni* and the earliest tetrapod clade. *Nature* 373, 420–425 (1995).

-Please pay attention to page-range formatting and consistency throughout the reference list.

3. Journal titles such as *Nature Ecology & Evolution*, *Papers in Palaeontology*, *Peer Community Journal*, and *Royal Society Open Science* should follow a consistent abbreviation format where required.

-Abbreviated journal titles (e.g., *Ann. Carnegie Mus.*) should be formatted consistently, and journal names should be italicized according to journal style.

Figures

Figure 1

Panel labels appear incomplete; panel a should be clearly indicated.

Figure 2

In Fig. 2b, what is the dark opening located between the two premaxillae? Is this a genuine anatomical opening (fenestra) or a preservational artifact? Please clarify in the figure legend or main text.

The lower jaw reconstruction is reproduced at a very small size and is difficult to evaluate. Consider enlarging this panel.

Figure 3

Figure 3 currently contains relatively limited information and appears somewhat sparse for a main figure in a Nature-format paper. Since ancestral character-state estimation appears to be one of the major conclusions discussed in the manuscript, the authors may wish to incorporate some of the information currently presented in Extended Data Figure 8 into the main figure set. This would strengthen the presentation of the evolutionary implications of the study and make one of the key conclusions more accessible and visually compelling for a broader readership.

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Please find attached our manuscript entitled “**Synchrotron tomography of a Carboniferous tetrapod informs stem amniote diversity**” for consideration as an article in *Nature*. We thank all three reviewers for their positive comments and constructive feedback, and we have edited the manuscript as per their suggestions, including carefully considering the entire text of the manuscript in order to sharpen and tighten the text. We are also grateful for the suggestions to broaden the scope of the manuscript, which encouraged us to take the time to further investigate and discuss aspects that were previously insufficiently considered. In particular, we have addressed concerns about the limited scope and repetitive nature of the discussion, as well as the lack of evidence to support certain statements, by providing detailed explanations of the ecomorphological implications of traits of *Westlothiana*, fully referenced and supported by comparisons to existing literature. We have further addressed this by performing ancestral character estimation of four traits associated with terrestriality onto our tree, facilitating far more detailed exploration and robustly supported discussion of trait evolution (and the timing thereof) along the amniote stem and the assembly of the amniote body plan, for which we also provide a new figure. We have also substantially expanded the methods section to address concerns about the level of detail relating to segmentation and reconstruction.

Please find more detailed responses below.

Kind regards,

Ben Igielman.

Reviewer #1 (Remarks to the Author):

I find the new topology based on the novel anatomical data important, but the paper cannot just rely on this. Most of the Introduction and Phylogenetic results and Discussion sections are paragraphs, some repetitive and convoluted, about how their new topology is more accurate/broader/larger/etc. than other contrasting phylogenies. I am happy with the new comprehensive phylogeny they obtained but I feel the contribution misses to explore the unique anatomical information they obtained from Westlothiana's scans... and, in general, I think the Ms would benefit from sharpening and tightening the text.

Response: Thank you very much to the reviewer for these comments. They encouraged us to carefully consider the areas in which we could broaden the scope of this study and consider the implications of our new data more comprehensively. We certainly agree with the reviewer that these actions will help make the manuscript interesting to a broader audience, as the reviewer suggested. We have undergone additional work to further investigate both the ecomorphological considerations based on the anatomy of *Westlothiana*, and the evolution of the amniote body plan, in order to expand the scope of the paper, which is outlined in more detail in the subsequent paragraphs. Additionally, we have carefully revised the introduction in order to improve the writing, and we have almost entirely rewritten the phylogenetic results and discussion to remove repetitive paragraphs and sharpen the writing more generally, as well as including this new information.

The paper would be much more interesting and significant for a broader audience if the authors would explore beyond the actual analysis the impact of the new data obtained in relation to the “assembly of the amniote body plan”, as stated at the end of the Introduction section but not further discussed, the putative morphofunctional/paleoecological considerations based on the new anatomical data on the axial and appendicular skeleton (very briefly mentioned and figured in Extended Data Figures 5 & 6 which are in turn not cited in the text!) in the context of early tetrapod

terrestrialization, a more compelling discussion about the timing of early diversification of amniotes (and stem-amniotes) beyond if its earlier or later than previously thought. Additionally, there are several statements in the text, highlighted in the attached file, that need to be discussed based on hard data and/or referenced...

Response: Thank you to the reviewer for these comments that have helped make the manuscript interesting to a broader audience. This has also allowed us to address the additional comment that the reviewer noted in their supporting pdf regarding the statement **“We find that stem amniotes were highly morphologically diverse, exhibited many body plans and inhabited multiple ecological niches including large predators, burrowers, elongate, limb-reduced and snake like forms, and aquatic taxa, generally proposed to be restricted to stem tetrapods or stem reptiles during the Palaeozoic by recent studies”**, to which the reviewer noted *“This statement needs to be supported and better discussed. You do not provide any discussion based on hard data about the palaeoecology, and/or the evolution of body plans in stem amniotes in any part of your contribution”*.

We have addressed these concerns in multiple ways. We have carefully considered the ecological implications of aspects of the anatomy of *Westlothiana* by utilising referenced comparisons with both extant and extinct taxa for which the ecology has been described. This includes references to quantitative studies on modern taxa that examined, and provided hard evidence for, the correlation between the ecology and particular traits that resemble the condition in *Westlothiana*. For example, we compare the dentition of *Westlothiana* to villiform fishes (Mihalitsis & Bellwood 2019) and the proportions of the axial skeleton to sand-dwelling skinks (Camaiti et al. 2022). This has allowed us to present a far more complete picture of the possible ecology of *Westlothiana*, which we have expanded on in the discussion by the addition of two entirely novel paragraphs.

Additionally, we performed ancestral state reconstruction of four traits associated with feeding during the water-to-land transition (adductor crest on the mandible, transverse flange on the pterygoid, palatal fangs/teeth, parasphenoid plate denticles) using the Phytools package in R in order to map those traits onto our phylogeny. This allowed us to provide a more in-depth, evidenced exploration of the evolution of traits along the amniote stem, and thus how aspects of the amniote body plan were assembled. Moreover, given the ecological relevance of the traits selected, this has allowed us to investigate the evolution of the amniote body plan in the context of terrestrialisation. In particular, we have expanded the statement from the manuscript referred to above into a more detailed and thoroughly explained paragraph about how our phylogeny provides evidence for the presence of particular ecologies on the amniote stem, with reference to the specific traits that support these ecologies.

We hope that this additional work will address the issues outlined above, both considerably expanding the scope of the discussion, and providing evidence and more detailed references to support our conclusions – we are grateful to the reviewer for giving us the opportunity to do so. However, if there are any other areas that the reviewer would like us to consider, or other, more specific investigations that they had in mind, then we are happy to consider these as well.

L17: which ones?

Response: We have amended this statement to provide greater clarity by including the text “stem amniote microsaurs and other lepospondyls”

L19/20: strikethrough text “during Romer’s Gap, substantially”

Response: We have amended this by replacing the text with “occurred during the earliest Carboniferous (Tournasian)”

Line41: “These phylogenetic topologies” Which ones? All previously mentioned in the sentence?

Response: We appreciate the guidance that our continued reference to various phylogenies were somewhat ambiguous. We have substantially edited this entire paragraph of the introduction to improve the wording, including careful consideration that there is no ambiguity as to which phylogeny is being referred to, and that everything is appropriately referenced.

Line 47: "limited by the scarcity of high-resolution anatomical data" among other things

Response: Text amended to include the phrase "in part"

Line 53: "incomplete consideration of traits from other skeletal regions and of taxa with informative 53 character state combinations that may have supported older phylogenetic topologies" which is the rationale behind this comment?...that other alternative phylogenies are wrong because they do not support old topologies? This statement is really odd.

Response: Thanks for this comment. The text was supposed to communicate that the datasets of those studies had omitted character evidence that was used in older discussions. So those datasets can't be said to represent a full consideration of the evidence proposed so far. This text now reads "Some analyses have also focused on specific character sets (e.g. the braincase¹) with incomplete consideration of the traits and character states that supported older, alternative phylogenetic topologies^{16,20}, particularly from other skeletal regions. These analyses therefore have provided only an incomplete test of hypotheses about evolutionary events on the amniote stem lineage.", which we hope provides greater clarity of this point.

Line 76: Fig. 2 "cited before Fig. 1!"

Response: Thank you for pointing this out, along with multiple other notes about the inconsistent citing of figures throughout the text. We are grateful for this issue being spotted – we have taken the time to go through the text in detail and ensure that all the figures, both in the main text and extended data, are cited and in the appropriate order.

Line 134: "has four digits" preserved

Response: The text has been amended to "Four digits are preserved on the right foot"

Line 139: I recommend to separate the "Phylogenetic Results" from the general "Discussion" of all results of the paper are they are different levels of discussion.

Response: Thank you for this suggestion to improve the structure – we have taken it on board and separated the sections as suggested.

Line 186: what does this mean in this context? please elaborate

Response: Thank you for pointing out that this sentence is a little confusing. As mentioned previously, we have almost entirely rewritten the discussion section, and this particular sentence has been removed.

Line 187-194: this paragraph is rephrasing the previous two paragraphs....please avoid repeating information

Response: Thanks for pointing this out. We have rewritten the entire discussion now, to address this and other concerns. This has included combining the previous two paragraphs referred to above into a single paragraph forming the final paragraph of the phylogenetic results section, incorporating

information from this paragraph too, reducing the text and covering the information more succinctly to avoid repetition. The paragraph referred to above was also partially incorporated into the final paragraph of the discussion. After careful rewriting, we feel that the discussion section is now far less repetitive and we hope that this addresses the above concerns.

Line 206: "Romer's Gap" strikethrough, and early Carboniferous added

Response: We share the reviewer's concern about the use of the term "Romer's Gap", and we appreciate the suggestion to replace it with the less controversial reference to the early Carboniferous instead. However, this discussion of the timing of the early evolution of amniotes is in direct comparison to conclusions drawn in Pardo et al. (2017). In that manuscript, they indicate the position of Romer's Gap on their time calibrated phylogeny (Pardo et al. 2017, Fig. 3). As such, we believe that it is useful to retain some reference to Romer's Gap for a more direct point of comparison. To address this, we briefly explain what Romer's Gap is in the introduction ("an interval of the earliest Carboniferous, from approximately 359 to 340 Ma in which terrestrial tetrapod fossils are rare, sometimes referred to as 'Romer's Gap'⁸") and then have amended the text referred to in the above comment to "the early Carboniferous (Romer's Gap)"

Extended Data Fig. 5 not cited in text

Extended Data Fig. 6 not cited in text

Response: As mentioned above, we have carefully gone through the manuscript and ensured that all figures, both main text and extended data, are cited and in the correct order.

Referee #3 (Remarks to the Author)

In terms of methods, the scanning parameters are presented in great detail as are the details of the phylogenetic analyses. However, there is little detail presented on the segmentation methods (Did the authors use automated tools or was this carried out manually? Did they employ any AI technology?) or how the 3D reconstructions in Figure 2 were created - recent authors (see Rawson et al., 2021 or Porro et al., 2023) have provided transformation matrices to allow researchers to understand and replicate the movement of individual elements from their original positions to create such 3D reconstructions. The current methods lack basic information on how 3D reconstructions were generated and some elaboration is necessary.

Thus, with regards to improvements, my main suggestion is adding more detail on segmentation and 3D reconstruction. In Figure 2, the mandible reconstruction is described as a composite - presumably of the left and right mandibles? Which elements come from which side? In addition to models of the individual elements, which are very useful, can the 3D reconstructions in Figure 2 also be made available for inspection, as an STL in supplemental data or in an online repository?

Response: Thank you to the reviewer for all of their helpful comments throughout this manuscript, and in particular, for pointing out this oversight in not including this detail in the methods. We completely agree that the manuscript, as originally submitted, lacked important detail regarding the segmentation and reconstructions that have been present in other recent publications utilising similar techniques. To amend this issue, we have written two entirely novel paragraphs in the methods; one detailing the segmentation methods, and one detailing the 3D reconstruction, including the detail requested above concerning the reconstruction of the composite mandible. Additionally, though we have not been able to produce transformation matrices as in previous publications, we have made the 3D reconstructions available for inspection alongside the models of individual elements, as suggested. We hope that our level

of detail in the new methods paragraphs addresses the concerns, though if the methods are still lacking in any areas we are happy to amend them even further.

Please check various issues with the figures, such as Figures 1 and 3 not being cited in the main text. There are also numerous issues with the figures and figure captions - please see annotated PDF for detailed comments.

Response: Thank you for pointing this out – we have seen that there are several errors with the figure citations. We have been through the manuscript carefully to ensure that all of the figures, both in the main text and extended data, are cited, and in the correct order.

One thing that would be useful is more references within the supplementary description to the corresponding Extended Data Figures illustrating the anatomy being discussed. On line 482 of the supplemental data you refer to an Extended Data Figure 11 - but there is no Figure 11? Please check.

Response: We have been through the supplementary description and added many more references to the corresponding figures, as per the tracked changes. Thank you for pointing out this mistake in referencing Extended Data Fig. 11 – I'm not sure how this mistake was made, but it has been corrected to the appropriate figure citation!

It is notable that the braincase (apart from the basi- and parasphenoid) is poorly preserved in many Carboniferous tetrapods, including in this taxon. Could this be due to poor ossification of braincase elements at this stage of tetrapod evolution? Just a thought.

Response: That's a really interesting thought, and certainly possible. Unfortunately, due to the level of preservation and the necessity of retrodeformation, we are reluctant to draw conclusions that are too definitive. However, we have added text to the supplementary information to discuss this further.

I cannot see a description for the surangular in the supplemental data?

Response: An oversight on our part – thank you for pointing this out! A description has now been provided in the supplementary description.

Also, I agree from the figures that it is unlikely that the splenial participated in the symphysis - but is there any information preserved on symphyseal morphology? This would be very informative.

Response: I agree that it would be very informative to see more anatomical detail of the symphysis. Unfortunately, the anterior end of the dentary is damaged in both jaws and so nothing more can be seen! We have added a comment to the supplementary text that clarified this.

It is noted that an unusual feature of Westlothiana is that there is no contact between the coronoids and splenial - but it is unclear what would have filled this space on the medial aspect of the lower jaw from Figure 2 or the description. The prearticular? (From the figures the angular makes up the lateral but not the medial wall of the mandible.) How are you sure there was not a medial lamina of the splenial on the medial aspect of the mandible?

Response: Thank you for pointing this out – this is a really interesting point that wasn't properly considered originally. The reviewer gave us the opportunity to consider this anatomical detail further and consider in detail what may have filled this space, which has certainly helped add detail to the interpretation of the jaw. We have added comments to the supplementary information to address this point: "Nonetheless, as both the ventral margin of the coronoids, and the dorsal margin of the splenial, are well defined, with no evidence of unfinished bone or damage, this does appear to represent the genuine morphology. It is therefore unclear what would have filled the space between the coronoids and splenial; it is possible that this would have been filled by unossified cartilage."

There are minor formatting errors and typos in both the main text (see annotated PDF) and in the supplementary data (for example, taxa names on lines 125, 132 286, 326, 329, etc. need to be italicised; "data" should probably be capitalised on line 392 for consistency).

Response: Thank you for pointing out these errors – it appeared that the supplementary information needed a careful proofread. This has been done, amending non-italicised taxon names alongside the additional references to extended data figures, and we hope that all of the grammatical errors have been found and addressed! We have addressed all of those mentioned in this comment, and in the PDF, which are referred to below.

Where did the anatomical data for taxa in the expanded outgroup come from? These are not in Part 3 of the supplementary data.

Response: This was another oversight on our part, so we are grateful to the reviewer for noticing. We have added in the appropriate information to the supplementary data part 3.

In general the references do appropriately credit previous work although there have been numerous anatomical studies of early tetrapods in recent years applying microCT and synchrotron data (see work by Ahlberg, Porro, Ruta, and others) that are not utilised here, which is surprising given similarity in the methodologies.

Response: Thank you for bringing this to our attention, it is certainly a very fair point that there have been many recent studies applying microCT. Whilst we made an effort to cite as extensively as possible, we appreciate that there are also further studies that we could have cited, and we were limited to some extent by the journal restrictions. It is worth noting that, in light of the added citations for the expanded outgroup, we have added two additional references to the full reference list (Porro et al. 2015a and b) that utilise microCT, which had not been added previously by mistake. Additionally, the amended discussion has a new, additional reference to Porro et al. (2024), and the same paper has been referenced in the supplementary discussion (see below).

Line 76: Figure 1 has not been cited before Figure 2

Line 80: Extended Data Fig 1 has not been cited - either cite figures in order, or rearrange them so they are cited in order in the text.

Response: As previously noted, the figure citation issues have been addressed.

Line 76: This could only be ascertained with a 3D reconstruction of the skull, which is presented in Figure 2 - but how were these 3D reconstructions created? There is insufficient information to replicate this.

Response: As previously noted, we have substantially expanded the methods to address this.

Line 111: Unless you consider embolomeres to be anthracosaurs, in which case a pterygoid flange was reported in Eoherpeton earlier this year.

Response: Thank you for highlighting the recent publication of a pterygoid flange in *Eoherpeton*. We have amended the text accordingly by adding the word “some” to the main text, and adding a reference to the recently reported pterygoid flange in *Eoherpeton*, with the reference to Porro et al. 2024, in the supplementary information.

Line 251/252: Using automated tools, manually or both? Any AI employed in the segmentation method? In terms of the 3d reconstruction presented - how was this generated? Do you have any data (such as transformation matrices) that would allow other workers to create this from the individual elements in their original positions? If not, can the 3D models of the reconstructed cranium and mandible be made available for inspection

Response: As noted previously, this has been addressed with additional paragraphs in the methods section, and by making the reconstructed models available for inspection online alongside the individual element models.

Fig. 1: “Presumably the yellow boxes in a are the elements figured in b and c, but this should be specified.”

Response: This is correct, yes! Thank you for noting that this isn’t clear. We have added information to the figure caption to clarify this.

Please go through and cross-check all abbreviations in the figure and the figure caption please, there are already several errors a few abbreviations into the caption.” And “Please check journal rules but you may need to repeat abbreviations for this figures, especially for elements not present in Figure 1. I would also suggest using the same abbreviations in the figures (e.g., Ang vs. An for angular in Figures 1 and 2, respectively).

Response: Thank you very much for bringing up this issue – we can see that there are several issues and inconsistencies with the figure abbreviations. For clarity, we have amended the figure captions so that each figure caption contains the abbreviations from that figure, and additionally we have examined each figure carefully to ensure the captions are consistent between figures.

Whole skull - you may want to note that the dorsal aspect is labeled in Figure 1

Extended Data. Fig. 4 “Please clarify which is anterior vs. posterior views please.”

Extended Data Fig. 5 “Why does this say Figure 4? Please check.”

Response: We have been through the figures and addressed all of the above comments in the captions.

Referee #4 (Remarks to the Author):

• In the text figure 2 seems to come up before figure 1. I still think the current figure one makes sense to be presented first, so the authors should add a reference in the text.

- *I think in figure 1 it would be beneficial if the labelled scan of the drawing would be larger. In favor of that the foot could be reduced in size as it is a less complex structure*
- *Something seems off in the figure caption of Extended figure 4 – there is a reference for a figure 4 somewhat in the middle of the figure caption. Please check and adjust this*

Response: Thank you to the reviewer, firstly, for your kind comments about the manuscript. We very much appreciate your positive response, and very pleased to hear the confidence in our work. We are also very grateful to you for pointing out the issues above, which we have aimed to address.

We have been through the manuscript and ensured that all of the figures are cited, and in an appropriate order, which we hope addresses the first comment.

We have taken on board your helpful comments regarding the relative sizes of parts of figure 1. We have reduced the size of the foot and considerably increased the size of the labelled scan drawing, as suggested, though if further rescaling is required we are happy to oblige.

The figure caption for extended figure 5, referencing figure 4, was a simple mistake on our part! Thank you for pointing it out – we have corrected this accordingly.

To *Nature* editor Dr. Henry Gee,

Thank you for the opportunity to revise our manuscript on *Westlothiana*. We recognize that the time between submission and resubmission has been substantial. This delay was driven by thorough reinvestigation of the CT data following the reviewer comments. We hold ourselves to a high standard. In light of the possibility of anatomical errors, we wanted to carefully validate our observations. This process revealed numerous stem tetrapod features originally overlooked in earlier drafts of this manuscript and resulted in important conceptual changes to the manuscript. Nevertheless, it still has great importance for understanding tetrapod origins, possibly more than before even. *Westlothiana* combines highly derived limb anatomy, with striking plesiomorphies including a primitive, likely gill-bearing, branchial skeleton. It indicates a position close to the origin of the tetrapod crown-group, providing important new data at high anatomical resolution. We hope the reviewers will agree.

Reviewer #5 suggested that there were critical problems with both the anatomical segmentation and the phylogenetic analysis. Based on these comments, we conducted a detailed re-examination of *Westlothiana*. This included revising the identification of several bones (e.g., coronoids) of the palate and mandible, as well as the segmentation of additional elements in the skull, braincase, and gill arch, with cascading consequences for our character coding throughout the phylogenetic dataset. These specific anatomical observations prompted us to add an additional corresponding author (XAJ) onto the project to address reviewer comments and resegment portions of the part and counterpart of *Westlothiana*. The scope of these revisions was substantial, and required rounds of back and forth between authors.

In sum, we have:

- Resegmented the skull, correcting multiple identifications of skull roof, palate, and mandible, as well as reconstructed previously overlooked elements of the braincase and gill arch. (Note: not all of the reviewers anatomical suggestions were correct, but many of them were, and have important implications).
- Revised character scorings for *Westlothiana* and others based on recent, CT-based descriptive literature that had been overlooked in the original phylogenetic analysis
- Expanded the character matrix to incorporate characters from recent datasets (Pardo et al., Mann et al. 2026, Clack et al. 2019) that address the phylogenetic placement of lepospondyls, stem amniotes, and, now, stem tetrapods.
- Analyzed *Westlothiana* using these three independent phylogenetic datasets to test the robustness of our conclusions.

The revised manuscript now shows that *Westlothiana* is a crownward stem tetrapod rather than a stem amniote, a conclusion supported by new anatomical evidence and reinterpretation. We understand that the extended revision timeline may have created inconvenience for the editorial office and reviewers, but we are confident that the revised manuscript is greatly improved and represents an important contribution to our understanding early tetrapod evolution. Thank you for your patience.

On behalf of our coauthors,

Ben Igielman, PhD
Department of Earth Sciences
University of Oxford

Xavier A. Jenkins, PhD
Division of Paleontology
American Museum of Natural History

Response to reviewers

Referees' comments:

Referee #1 (Remarks to the Author):

I find the new version of the Ms suitable for publication.

I am glad that the authors have taken into consideration my previous comments and rewritten several paragraphs of the original Ms. Now the Phylogenetic Results and the Discussion of the Ms are certainly more consistent. The Discussion, in particular, is comprehensive including new data thus enriching the Ms and certainly making it more interesting for a broader audience.

My only final comment to this point is about the new article by Long et al. 2025 recently published in Nature (“Earliest amniote tracks recalibrate the timeline of tetrapod evolution”). I think the new hypothesis provided by Long et al. should be discussed in the final Discussion of the present Ms.

We provide a substantial review of the Long et al. results in the discussion of our revised manuscript, specifically on the presence of claw-like ungual phalanges in *Westlothiana* and numerous crownward stem tetrapods. Thank you!

Referee #3 (Remarks to the Author):

I am really pleased to see the changes the authors have made, in particular the greater detail in the methods used to segment the data and create the 3D reconstruction. This is a really interesting and informative paper and all of my concerns have now been addressed in this revision.

Thank you!

Referee #5 (Remarks to the Author):

We want to preface our point by point response to Reviewer 5 here by emphasizing our gratitude for many of this reviewer's observations, specifically on the anatomy of *Westlothiana*, below. We went through and double-checked each of the reviewer's anatomical observations here, and ended up resegmenting much of the anatomy of *Westlothiana* in response to these insights. We hope the referee will understand, based on the large efforts we undertook here, that any errors in our initial work were not deliberate. These new observations have greatly improved the paper and allowed us to reconsider the anatomy of this taxon and expand the phylogenetic dataset in light of these observations, so thank you!

This manuscript presents new 3D data derived from synchrotron scans of the Mississippian vertebrate *Westlothiana*, which has been suggested in the past to be a close relative of modern amniotes. In addition to this, the authors present a comprehensive reworking of the early tetrapod tree based on an amalgam of previously published characters and a few novel ones reported in this study. The former contribution is primarily relegated to the supplemental material as is traditional for short-form publication. I have some

concerns about the segmented synchrotron data and description, but these could be worked out through the peer review process although this will require going back to the original data and anatomical interpretation as it is currently not in publishable form. The latter looks sleek and shiny but has critical problems. Unlike some of the previous round of referees, I do not recommend publication. I apologize in advance for the length of this review, but wanted to explain these issues.

Every phylogenetic analysis has its own problems but I think the problems in this specific analysis are worth taking into serious consideration they seem to be willful and seem to have significant impact on the major features of the phylogenetic topology as reported. Before getting into the weeds of why the phylogenetic analysis is likely problematic, I want to discuss the importance of the three major phylogenetic results the authors present here so that the impact of these specific characters and character sets can be understood. The authors here present two major innovations, which themselves are basically just returns to a previous “consensus” established in the 90s and early 2000s: (1) embolomeres/antracosaurs as the initial grade of stem-amniote, (2) unity of disparate small-bodied early tetrapods within a monophyletic Lepospondyl clade. A third innovation, a relatively restricted amniote crown group, has been a broader theme of recent analyses arising in this working group, albeit in a range of conflicting topologies and periodically recanting of the important features of earlier high-profile analyses (e.g. a diapsid origin of varanopids, Ford & Benson 2020, quietly recanted in a series of lower-profile papers afterwards).

Placing embolomeres as stem amniotes is, *prima facie*, an appealing hypothesis because it creates a robust amniote stem group in the lower Carboniferous. However, every time it has been proposed on specific anatomical bases it has immediately been noted that the characters which unite embolomeres with amniotes are ancestral for most if not all digitized stem tetrapods (Romer 1957, Panchen 1985). The analyses here is no different: four characters unite embolomeres with amniotes: (34) absence of labyrinthine infolding, (126) lack of contact between the exoccipital and postparietal, (252) pleurocentrum-dominated vertebrae, (261) curved ribs. Of these, character 34 seemingly immediately reverts to the primitive condition because seymouriamorphs all show labyrinthine infolding (e.g. Maho & Reisz 2022). Character 126 is incorrectly scored (for instance, embolomeres do have a well-defined exoccipital-postparietal contact, see Pardo 2024 Zool J. Linn. Soc.). Character 252 is uninterpretable in embolomeres, where the pleurocentrum and intercentrum are of equal size and both articulate directly with the neural arch. Similarly, the “derived” condition of character 261 is widespread among definitive stem tetrapods, notably Ichthyostega, Pederpes, and Whatcheeria. The dataset here further ignores a number of recent discoveries of unambiguously primitive anatomy within embolomeres, including supraneural spines in the caudal skeleton (Clack 2011), an anocleithrum in the shoulder girdle (Adams et al. 2025), and hypophyseal and notochordal canals in the braincase (Pardo, 2024). None of these characters are incorporated into the current dataset, even though they were present in some of the datasets the authors draw upon in constructing this analysis. Their exclusion appears to be deliberate.

We have modified this phylogenetic dataset, revised numerous character scorings (e.g., exoccipital-postparietal contact), and greatly expanded our character matrix to incorporate numerous characters that test the taxonomic inclusion of the tetrapod crown group, including the addition of these three characters and numerous more derived from variations of the Pardo et al. dataset including XAJ’s work on *Hapsidoparieon*. The previous version of this phylogenetic dataset did not

consider these characters to be relevant due to the previous hypotheses of *Westlothiana* as a stem amniote, but in light of the resegmentation (see below), these characters are immediately relevant.

A monophyletic Lepospondyli is a hypothesis that posits a single adaptive radiation of small-bodied early tetrapods. Although a number of workers found a monophyletic Lepospondyli in the early 2000s (Anderson 2001, Ruta et al. 2003, Vallin & Laurin 2004), workers focused on the anatomy of these animals have consistently doubted the monophyly of the group due to the lack of a clear unifying anatomy. Most support for a monophyletic Lepospondyli comes from either the presence of spool-shaped pleurocentrum-dominated vertebrae or from small size, whereas evidence against this comes from numerous highly precise anatomical similarities across the entire body which would have had to be derived (or reversed) in parallel with the broader tetrapod tree (e.g. aistopods and nectrideans must lose numerous crown tetrapod characters in parallel, recumbirostrans must gain many amniote characters in parallel). The analysis presented here falls into this same trap: the reported analysis claims this group is united by ten unambiguous characters: (1) skull < 3 cm, (7) narrow antorbital region, (29) peglike marginal teeth, (44) dorsal process of lacrimal present, (61) concave notch in posteroventral margin of postfrontal to accommodate postorbital, (66) irregularly-shaped postorbital, (69) sigmoid-shaped anterodorsal margin of postorbital, (202) retroarticular process present, (209) dentary toothrow less than 50% of jaw length, and (311) internal trochanter not separated from surface of femur by trough. One of these (character 1) is unambiguously size-related. Several are incorrectly scored (7, 202). Others are just ancestral tetrapod conditions (29, 66). Others appear to be nonsense. An example is character 61: (large concave notch in postfrontal to accommodate postorbital): of all “lepospondyls” within and excluded by this analysis, the only one actually shows this anatomy, and that is the type specimen *Asaphostera platyrhis* (see Mann et al. 2020) which is inexplicably united here with previously attributed material that has since been reassigned to *Steenerpeton sylvae*. Interestingly this character is elsewhere seen in taxa assigned here to the amniote crown group, specifically to synapsids, which aligns with the attribution by Mann et al. (2020) of the *Asaphostera* type specimen to a probable caseosaur synapsid rather than a recumbirostran. Similarly, I have no idea where character 69 comes from: I think it is a description of the specific anatomy seen in *Westlothiana*, but I have not seen this in any other “lepospondyl.” The condition here in *Westlothiana* seems to actually be describing the presence of a syndesmosis between the skull roof and cheek, a condition actually seen in a range of stem tetrapods, including *Tiktaalik* (see Lemberg et al. 2019) and *Whatcheeria* (see Bolt & Lombard 1995 but also Rawson et al. 2021) among others. Such anatomy is also clearly apparent in embolomeres (e.g. see Archeria, Holmes 1989 Text-Fig 6a; *Proterogyrinus*, Holmes 1984, Figure 8; *Calligenethlon*, Adams et al. 2025, Figure 5A).

Similar problems show up in the characters associated with the definition of the clade of Lepospondyls excluding *Westlothiana*: a number of these characters are outright incorrect and reflect inaccurate coding throughout the matrix. For instance, intercentra are widespread among recumbirostrans, a supratemporal is widespread among recumbirostrans (see Szostakiwskyj et al. 2015), the recumbirostran adductor crest (which is the only “lepospondyl” adductor crest in this dataset) preserves a prominent contribution from the posterior coronoid which is often exposed in lateral view (see Szostakiwskyj et al. 2015 as well as Pardo & Anderson 2016).

This becomes even more obvious when we look at character support for a non-microsaur clade of “lepospondyls.” This is the group which recent studies have argued are stem tetrapods unrelated to the

amniote-allied recumbirostrans. This clade is mostly represented by reversions to the stem tetrapod condition: long postorbital process of the maxilla, elongate dentary with greater number of teeth, unossified carpus, single atlantal neural arch, etc. A few of the noted characters (e.g. position of the pineal) appear to be incorrectly coded as they are unambiguously positioned in the anterior third of the parietal in most groups belonging to this clade (aistopods, nectrideans). Finally, the presence of *Brachydectes* (and seemingly also *Carrolla*, although no scorings are given for this animal) in this clade should be considered highly suspect given the extensive work documenting a coherent and extensive set of recumbirostran characteristics uniting molgophids and brachystelechids within Recumbirostra (Maddin et al. 2011, Pardo et al. 2015, Pardo & Anderson 2016, MacDougall et al. 2024). There is nothing compelling here that should overturn fundamental anatomical evidence against “lepospondyl” monophyly that has been discussed by prior authors but has been mysteriously excluded in the dataset here.

Thank you for all this detailed attention. Our new co-author, XAJ, went through recent work on “lepospondyls” and added all characters relevant to amniote origins and the phylogenetic placement of Recumbirostra, Adelospondyli, and nectrideans on the amniote, and also tetrapod, stem. Characters 7 and 202 have been rescored, Character 61 has been reworked (this character referred to a novel anterodorsal process of the postorbital, not a vague ‘sinusoidal’ dorsal margin as originally phrased), and the scorings of all taxa in the dataset have been revised in light of new CT insights in relevant taxa.

So, in other words, I do not find these claims convincing because the dataset is not appropriate for addressing these questions. If the authors purported to test these two phylogenetic hypotheses, they ought to be extensively sampling known stem tetrapod groups, of which there are many well-documented forms, and of character variation important in that part of the tree, which has also been well-documented. In fact, character variation documented in previous phylogenetic analyses and which is thought to be important for defining innovation in the tetrapod stem group has actually been actively excluded here or has been folded into character statements which evade careful anatomical work. This includes character suites such as the humerus and neurocranium, as well as various others. Taxonomic sampling in the stem is poor: it is limited to five digitated tetrapod taxa: *Acanthostega*, *Whatcheeria*, *Pederpes*, *Baphetes*, and *Greererepeton*. Numerous well-represented taxa are excluded: *Ichthyostega* most notably, but also *Ossinodus*, *Crassigyrinus*, *Eoherpeton*, *Aytonerpeton*, *Eucritta*, *Ossirarus*, *Perittodus*, *Kyrinion*, and various others. Given the incomplete nature of many of the taxa included here (e.g. *Asaphestera*, *Echinerpeton*, *Eocasea*, *Erpetonyx*, *Ianthasaurus*, *Pantelosaurus*, *Vaughnictis*) it is strange that well-described animals represented by multiple complete specimens in critical parts of the tree have been excluded from the analysis. I also strongly believe that the authors must necessarily sample temnospondyls more completely: the dataset reported here only samples two dendrerpetids, one very incomplete and derived late-occurring edopoid (*Edops*) and two very advanced amphibamiform dissorophoids (*Doleserpeton* and *Gerobatrachus*). This is a massively limited sampling of a very diverse clade with real potential to bear on both the ancestral condition of the tetrapod crown as well as on specific modeling of evolutionary rates of specific characters. Finally, important “lepospondyl” taxa that need to be included (e.g. urocordylid nectrideans) are inexplicably excluded. On the other hand, a latest Permian cynodont is included for an inexplicable reason. In general, I struggle to understand the authors’ decision-making process on taxon sampling.

Thank you for your thoughts on taxonomic sampling. We have addressed this in two ways. Firstly, we added additional characters documenting variation among stem tetrapods as well as stem amphibians and stem amniotes. This partly resolves previous differences in phylogenetic results (resulting in a topology congruent with most recent studies on tetrapod origins). Secondly, we also incorporated *Westlothiana* into the phylogenetic datasets of Mann et al. (2026, with great temnospondyl and amniote sampling) and Clack et al. (2019, which encompasses numerous stem amniotes). In doing so, we are using the taxon samples of the previous most-up-to-date studies, which we regard as an appropriate disciplinary standard. Our new results of *Westlothiana* as a stem tetrapod are corroborated by all three phylogenetic analyses, but we note that the interrelationships (and sequence of divergence) of crownward stem tetrapods such as *Westlothiana*, aistopods, and baphetids may require revising pending future anatomical studies.

Some further hints as to the source of these problems comes from the table in Part 3 of the supplemental material. The authors primarily rely on relatively old references, some of which have been clearly superseded by more recent work. The most notable of these is the heavy reliance on the Carroll and Gaskill 1978 monograph on microsaur. Carroll & Gaskill is a beautifully illustrated work but unfortunately a lot of their interpretations have been overturned by direct fossil anatomy. An example here is the authors' use of the taxon *Asaphestera intermedia*: Carroll generally regarded this animal to be the most primitive microsauro and interpreted the skull accordingly, reconstructing it as having a high narrow skull, short postorbital region, and so on. This material has been revisited by Mann et al. (2020): it is in fact a chimaera of two very different animals. The specimen bearing the name *Asaphestera platyrhis* (as referred to by Steen 1934) is a skull roof and partial cheek that shows a number of characters suggestive of synapsid affinities, whereas much of the rest of the material comes from a relatively advanced recumbirostran with a relatively standard recumbirostran skull. The majority of scorings for this pivotal "basal lepospondyl" in this dataset thus appear to be entirely fictional or otherwise reflect the chimaera status of the material. Other taxa (e.g. *Micraroter*, *Tuditanus*, *Hapsidopareion*, *Cardiocephalus*) differ somewhat importantly from Carroll & Gaskill's figures, and in some cases have been refigured more recently, or have close relatives which have been. In fact, there is an abundant recent literature carefully documenting recumbirostran anatomy and many of these taxa which have been pivotal in teasing out the amniote affinities of this group have just been outright excluded from this analysis. This applies more broadly to the literature employed in scoring decisions here, e.g. *Ianthasaurus* (note spelling) is scored solely from Reisz & Berman 1986, but at least two papers have been published on additional more complete specimens of this animal since, clarifying quite a bit of the anatomy. *Microbrachis* is scored from Carroll & Gaskill despite more recent work by Vallin & Laurin 2004 among others, and ready access to this material (both original specimens and peels).

Our entire manuscript has been greatly revised, including the reference section, and scorings in our character matrix have been revised according to the most recent work on each taxon, rather than more historical works. Thank you for noting this, as this has resolved in numerous rescorings.

However, part of the problem here seems to be a failure to correctly describe *Westlothiana*. Although the scans appear to be quite nice, it is actually very hard to interpret the edges of bones, and the thick black tracings imposed directly over the 3D renders is a part of that problem. In some cases, I think it is clear that the bone margins are incorrectly interpreted. There is, for instance, very clearly a sutural line between

the first and second coronoid, even if the authors were unable to identify that during their segmentation. I am also unsure of their suture between the postfrontal, postorbital, and parietal; there is almost certainly a partially-displaced suture line through the element they identify as the left postfrontal (and the surface is poorly preserved on the right side) and there seems to be a slight but regular displacement through the lateral portion of the right parietal that might be a parietal-supratemporal suture, suggesting to me that they may have failed to distinguish between the parietal and temporal series on both sides of the skull. Similar problems appear in their interpretation of the postdentary bones of the lower jaw (some of the material assigned to the dentary is splenial, and there is almost certainly some postsplenial incorrectly assigned to the angular. Much of the anterior process of the prefrontal, which contacts the external naris, is assigned to the nasal, and much of the material assigned to the ectopterygoid is actually pterygoid. It appears to me that the segmentation is primarily showing cracks rather than sutures, which makes me question a lot of the scores for *Westlothiana* in addition to the scoring for other taxa as enumerated above. There are some additional failures to interpret elements in the postcrania; the obvious one is the “axis neural arch” which is instead a pair of rounded proatlantes, as seen in some other stem tetrapods; for example, the humerus as segmented is quite strange and very distinct from how it is interpreted by Smithson et al. 1993, who reconstructed a large block-like entepicondyle and a rather standard entepicondylar foramen. Neither of these are shown here. If the authors are correctly identifying entepicondyle and ectepicondyle, this is a completely unique humerus form for a Palaeozoic tetrapod.

This paragraph alone was extremely consequential for our revision, and the reason why this manuscript was so delayed in its resubmission. A new author was brought onto this manuscript to double check the tomography data and revise character scorings, and we note that the reviewer here was correct in many, though not all, of their suggestions:

- We find three coronoids and an adsymphysial (as suggested).**
- Some of the posterior portions of the parietal represented portions of the tabular and postparietal, and the prefrontal does indeed reach the external naris, which is actually visible directly on the specimen (as suggested).**
- The ‘axis neural arch’ was indeed the proatlas, and the bones as originally identified in the cervical region were labeled incorrectly (as suggested).**
- Differing from the reviewer: the parietals are wide and we basically had the sutures between the parietals and temporal series correct. This was difficult to validate and involved visiting the specimen again, making observations down the microscope, and carefully inspecting the CT data for evidence of sutures. We are very confident in our final interpretation.**
- Differing from the reviewer: the humerus is quite slender on both sides, although it is missing much of its entepicondylar region, even though an entepicondylar foramen is indeed visible; we suspect this is a result of the reduction of the entire forelimb in *Westlothiana*.**

The authors then present a retrodeformed and reconstructed skull. I want to emphasize that this is a very flattened and deformed specimen. This is a very superficially compelling image which presents more and more problems the closer one looks at it. The most obvious biological problem I see is the positioning of the adductor fossa between the quadrate ramus of the pterygoid and the quadrate. This is incorrect: the quadrate ramus of the pterygoid forms along the surface of the palatoquadrate, which will ossify to form the quadrate posteriorly and the epipterygoid anteriorly. The palatoquadrate is always medial to the mandibular adductor musculature. Therefore, the quadrate should be broadly contiguous with the quadrate

ramus here, and the adductor fossa should be located between this unit and the dermal cheek (quadratojugal, jugal, and squamosal). However, the anterior margin of the quadrate as figured in Figure 1 seems to be a zig-zagged broken edge that seems to fit into a similar broken edge on the quadrate ramus of the pterygoid (Extended Figure 3) suggesting that the pterygoid may have been massively co-ossified with the palatoquadrate rather than a distinct element as in advanced early tetrapods, and the authors are simply misidentifying a break as a suture. The quadratojugal is probably part of the slightly displaced element identified by the authors as the squamosal. I also wonder if the “adductor crest” on the mandible is an artifact of deformation; you see something similar in the definitive stem tetrapod *Sigournea*, for example. I don’t see any evidence of an obvious coronoid enlargement as seen in temnospondyls, seymouriamorphs, recumbirostrans, and uncontroversial amniotes.

We worked hard to improve this. We have segmented additional bones of the skull roof, braincase, gill arch, palate (e.g., revising the ectopterygoid-palatine-ptyerygoid relationships) and mandible and have provided a more complete reconstruction using the best preserved bone of each side and mirroring it, our originally reconstruction was flawed in using some of the more incomplete elements such as the maxilla. We fixed the adductor fossa here as well, and agree that there is no obvious ‘adductor crest’ or coronoid enlargement in *Westlothiana* as there is in definitive stem and crown amniotes.

These problems with the anatomical description align with additional failures to recognize clear and unambiguous stem tetrapod anatomy in *Westlothiana*. For instance, the fact the postfrontal makes up the entirety of the dorsal orbit is unlike anything seen in any “lepospondyl” but is consistent with anatomy seen in various Devonian and Mississippian stem tetrapods.

This is 100% correct, and we have added this as a character (Ch. 73).

The deeply-incised hooklike glenoid surface of the articular (NOT a retroarticular process) is rather typical of Mississippian stem tetrapods. The denticle field on the prearticular is a classic stem tetrapod character absent in the crown.

We’ve added this as a character (Ch. 287), and not further that our resegmentation documents that there are even denticles on the articular itself.

The pterygoid denticle field that extends along the quadrate ramus of the pterygoid is a classic stem tetrapod character.

We’ve added this as a character (Ch. 206).

The gentle convexity of the ventral margin of the lower jaw and absence of a coronoid expansion of the dentary and postdentary bones are classic stem tetrapod characteristics.

We revised these scores, as well.

Premaxillary teeth that increase in size posteriorly are a classic stem tetrapod characteristic. The absence of a well-developed bony connection between the prearticular and postdentary bones on the medial surface of the jaw would also make sense in this context if that corresponds with a broad medial exposure of the Meckel's cartilage (typically this is ossified into Meckelian bone in better-known stem-group tetrapods but could be cartilaginous at earlier life history stages).

We agree, and have added the exposure of a Meckelian canal (and number of foramina) as Characters 237 and 238.

In other words, this is an animal that is broadly consistent with a position close to the divergence between temnospondyls and amniotes, but I really do not see evidence for it being as amniote-ward as the authors claim and certainly no evidence for a close relationship between this animal and either recumbirostrans or other "lepospondyls."

In light of these problems (critical flaws with the segmentation and associated description, critical flaws with the phylogenetic analysis) the interpretation offered in the discussion is unfortunately not of great significance. All of the anatomy here implies an animal that sits in a relatively crownward part of the tetrapod stem group, perhaps just crownward of baphetids. *Westlothiana* is probably aquatic, but that is not noteworthy in a stem tetrapod. *Westlothiana* lacks various amniote-like features, but that is expected in a stem tetrapod. Phylogeny-specific interpretations presented by the authors are effectively irrelevant. The analyses presented in Figure 9 are irrelevant because they do not sufficiently sample Mississippian stem tetrapod and temnospondyl diversity to actually estimate character evolutionary rates, whereas the authors aggressively sample even the least complete early amniotes (e.g. *Echinerpeton*). The specific character state reconstructions in Extended Figure 10 are overtly misleading even if we take the authors' phylogeny at face value because features like a surangular crest and transverse flange of the pterygoid are widespread in temnospondyls (effectively not sampled in this analysis) which both affects the underlying topology (already suspect) as well as interpretations of character evolution i.e. these are likely ancestral characters for the tetrapod crown group that show specific reversions in various lineages due to ecomorphological factors, not parallel acquisitions among recumbirostrans and "classic" amniote taxa. Further, the authors' claim that the absence of a transverse flange implies an undivided m. adductor mandibulae is just incorrect; the m. adductor mandibulae is divided into multiple units in all gnathostomes (see: *Polypterus*, Noda et al. 2017; *Neoceratodus*, Ziermann et al. 2017; *Latimeria*, Datovo & Johnson 2025; *Squalus*, Hyman 1922; *Necturus*, Hyman 1922). As stated above I do not agree with the authors' interpretation of the subtemporal vacuity, although I do agree this animal lacked a transverse flange, but this simply implies that the m. adductor complex was comparably small. What this might indicate is that *Westlothiana* lacked an m. pterygoideus, the muscle which inserts onto the transverse flange in reptiles and caecilians (Kleinteich & Haas 2007) and which seemingly was present in the ancestral tetrapod but subsequently lost in batrachians. However, there are plenty of extant reptiles which lack a transverse flange but still retain an m. pterygoideus, so this is a more challenging argument to make on a strict comparative anatomy basis. So, the points the authors consider most discussion-worthy are either not supported by the data as presented, are not novel, or both.

Thank you here. Our revised phylogenetic analysis finds that *Westlothiana* is a crownward stem tetrapod, but the exact placement of derived stem tetrapods like baphetids and *Westlothiana* remain unresolved.

This is obviously a long report (which I apologize for) so I will not add line comments, as I believe the problems with this manuscript are more fundamental than specific phrasing in the text body. I hope the authors will put in the work to ensure that the anatomy is correctly documented and that phylogenetic work engages with the extensive anatomical and phylogenetic work originating in other research groups that conflicts with this (regressive) phylogenetic hypothesis. I'm sorry I can't be more enthusiastic at this time.

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Referee #6 (Remarks to the Author):

Topics and impact: The main part of the paper addresses a classic paleontological question since the triumphant of cladistics: the exact phylogenetic position of a taxon near a key evolutionary node of poor resolution. For such taxa, three potential assignments exist: the rootward positions (often at the very base, as in this paper) within the two sister group lineages, or out of them, inclusion in the section rootward to the aforementioned sister groups. A more robust and convincing assignment normally requires newly discovered transitional taxa, or new specimens of a key taxa showing considerably greater anatomical details, or as in this paper, revisiting anatomy interpretations through technological applications, in most cases as in this paper, tomographic scanning. The rise of amniotes is certainly an important topic, and *Westlothiana* is a classic taxon in this segment of the vertebrate tree of life. Resolving it out of the conventional position within the amniote lineage is interesting, while the ecological discussion offers a refreshing update to the stereotypical portrayal of this animal. Popular literature often depicts *Westlothiana* as a terrestrial form perching on fallen trunks; this work challenges such assumptions.

Methods. this study applies standard methodologies: synchrotron scanning and reconstruction, Rendering in Blender; morphological description, phylogenetic analyses and ancestral character estimation. These are not the fanciest, but adequately used and explained and documented.

Writing. I did not participate the first round of reviewing, and I was given very limited time for a thorough review. but I found the paper and the extensive supplementary materials are generally well-written, especially after the revision. However, structurally, I can see the two core findings, the phylogenetic position of *Westlothiana* and the lifestyle of early tetrapods appear disconnected , with the latter feeling tacked on. The later topic can surely expand to another, maybe more impactful standalone

paper, e.g. when and how tetrapod terrestrial adaptations evolved stepwisely, if more data and substantial update is given in that section.

The figures are functional, but unexceptional. The text figures resemble those of a descriptive paper for a professional journal, rather than a broadly accessible publication.

All in all this work is an important contribution that warrants follow-up studies and fieldwork. **Thank you for these comments, and we worked on connecting the ecological hypotheses (an important portion of the discussion) with the main text throughout, and have revised each figure following this feedback.**

To *Nature* editor Dr. Kleopatra Leontidou,

Thank you for your handling of our manuscript describing *Westlothiana* and its importance for early tetrapod evolution, we are very happy to hear that the manuscript has been provisionally accepted. We've uploaded our revised manuscript -which incorporates reviewer and editorial comments- and all associated data to the *Nature* submission site, and provide a point-by-point response to the review at the end of this letter.

Although the reviewer comments were brief this review, we modified our manuscript to address their comments and concerns wherever possible. This includes a brief expansion on the origin of crown tetrapods (e.g., *Balanerpeton*, as requested by Referee #1; and the purported Devonian tetrapod tracks, as requested by Referee #6), modifications to Figures 1-3 (such as labeling the origins of traits on our phylogenetic tree, as requested by Referee #6). Other suggestions, such as restructuring the main text (e.g., removing the description) were unclear, and we note that brief comparative descriptions is the norm in recent *Nature* papers covering paleobiology. That being said, we have therefore made modifications to the description and discussion, as well as adding informative labels to Figures 1 and 2, which hopefully make the manuscript more readily accessible to a generalist reader.

Our resubmission also includes the four requested forms (Biology editorial checklist, manuscript checklist, reporting summary, third-party rights table) uploaded as 'related manuscript files'. We've also ensured that the tomography data and code data stored on Morphosource and OSF, respectively, are now 'live' and accessible by the public.

At this stage we hope you'll agree that this manuscript, with its extensive revisions and revised figures during the course of these reviews, is ready for publication. Please let us know if we may have missed anything, and if so, we will work diligently to get the information back to you quickly.

On behalf of our coauthors,

Ben Igielman, PhD
Department of Earth Sciences
University of Oxford

Xavier A. Jenkins, PhD
Postdoctoral Fellow
Division of Paleobiology
American Museum of Natural History

Referees' comments:

Referee #1 (Remarks to the Author):

The new version of this Ms is really substantially different to the previous one I read nearly a year ago. Particularly due to the radical change in the phylogenetic position of *Westlothiana* from crown-group Amniota to a stem-tetrapod. This change was mainly driven by a reassessment of much information in the original Ms questioned in an extended report by reviewer #5. This reviewer raised many contradictions on the 3D rendering that impacted directly on the the subsequent interpretations of anatomical features in the specimen, and thus the final phylogenetic analysis and resulting position of *Westlothiana*. I really appreciate that the authors took those comments into account and were able to produce a more robustly supported manuscript with a richer discussion. **Thank you for your encouraging words!**

Something that I really think would be interesting to expand in the Discussion is something the authors mentioned at the end of the fourth paragraph in page 6: "...then there is currently no evidence of crown amniotes before the late Carboniferous...." Their new resulting analysis also takes away one of the last remaining crown tetrapods from the Mississippian. Essentially, all that's left is *Balanerpeton* (East Kirkton Fm.), after which the oldest crown tetrapods are basically from the Joggins Fm. (Pennsylvanian, Canada). That means the tetrapod calibration point for molecular clocks is likely to shift approx. 17 million years from East Kirkton Fm. to Joggins Fm. times. I think would be interesting to expand this aspect in the general final discussion of the Ms. **Yes, we agree with your comments on the origin of crown Tetrapoda. The timing of this origin hinges upon the identification of *Balanerpeton*, a taxon that has not been substantially revised in several decades, as an early temnospondyl. We added a brief line addressing this comment towards the end of our discussion.**

Referee #6 (Remarks to the Author):

The scientific question addressed by this manuscript is important. *Westlothiana* is a classic and historically influential taxon in discussions of early tetrapod and amniote evolution. Clarifying its anatomy and phylogenetic position therefore has significance beyond the placement of a single species. In this study, Igielman et al. provide substantially revised anatomical interpretations based on newly segmented tomographic data, offering one of the most comprehensive reassessments of this important taxon to date.

One practical suggestion concerns data accessibility. Because the anatomical interpretations presented here are central to the manuscript, I believe the tomography data should ideally be made directly available to reviewers rather than through a request-based process. Providing direct access during peer review, and depositing the data in a permanent public repository upon publication, would facilitate independent evaluation and strengthen the transparency and reproducibility of the study. **Thank you for this comment, we agree with the sentiment here and are huge supporters of data accessibility. However, we do not own the exclusive rights to the scan data used here, and requests for the tomography data must be reviewed by collection managers and curators at the National Museums Scotland before approval. This is currently the widely-accepted gold standard of palaeontological 3D data sharing to ensure there is no unapproved commercial usage.**

I was also somewhat surprised by the absence of a quantitative morphometric assessment, given the authors' established expertise in quantitative palaeobiology. The apparent evolutionary decoupling between the cranial and appendicular skeleton in *Westlothiana* would seem to provide an excellent opportunity for such analyses. However, I appreciate that this may reflect the current scarcity of suitable comparative datasets among stem tetrapods. **You hit the nail on the head at the end of this here. We do not have the comparative data necessary to conduct a quantitative assessment, and the crushed nature of both pectoral and pelvic girdles of *Westlothiana* means conventional methods (e.g., range of motion) are currently not available, although we are hoping to recruit students to create a synthetic, quantitative morphometric dataset in the near future.**

That said, I feel that both the visual presentation and the narrative structure of the manuscript require further refinement to meet the level of accessibility and broad appeal expected of a Nature paper. The three main-text figures appear overly specialist in their current form and do not communicate the major findings as effectively as they could to a broader readership. A substantial redesign of the figure set would help highlight the principal biological messages and improve accessibility for non-specialist readers. **We have made small changes to the text (introduction and discussion) and figures (Fig. 3, namely) to ensure that the main text is more straightforward. Furthermore, labels for important, discussed anatomy that were only labeled in the extended data figures were labeled additionally in the primary figures, which should hopefully point out some of the plesiomorphic anatomy for a generalist reader.**

Similarly, portions of the detailed anatomical description could be moved to the Supplementary Information, allowing the main text to focus more clearly on the broader evolutionary implications of the study. In addition, the study by Long et al. (2025) is highly relevant to the present discussion, yet its incorporation currently feels somewhat peripheral rather than fully integrated into the central narrative. I believe its implications deserve greater emphasis and

discussion. **Thank you for these comments, we agree here in principle, but have strove to only describe evolutionary and ecologically relevant anatomical features. In our revisions, we simplified a few of the more jargony or taxon heavy statements for a generalist reader, but have opted to include this information in the main text, as the anatomy of *Westlothiana* is what we feel is the greatest contribution of this study.**

I also noted a number of formatting and presentation issues, which are detailed below.

References

There are numerous formatting inconsistencies in the reference list. The authors should carefully check all references to ensure compliance with Nature formatting requirements. I only list a few representative examples below:

1. Long, J. A., Niedźwiedzki, G., Garvey, J., Clement, A. M., Camens, A. B., Eury, C. A., ... & Ahlberg, P. E. Earliest amniote tracks recalibrate the timeline of tetrapod evolution. *Nature* 641, 1193–1200 (2025).

-Please verify whether the author list should be abbreviated according to journal style (e.g., “Long et al.”).

2. Ahlberg, P. E. Elginerpeton pancheni and the earliest tetrapod clade. *Nature* 373, 420–425 (1995).

-Please pay attention to page-range formatting and consistency throughout the reference list.

3. Journal titles such as *Nature Ecology & Evolution*, *Papers in Palaeontology*, *Peer Community Journal*, and *Royal Society Open Science* should follow a consistent abbreviation format where required.

-Abbreviated journal titles (e.g., *Ann. Carnegie Mus.*) should be formatted consistently, and journal names should be italicized according to journal style.

Thank you, we’ve now reformatted our references following *Nature* guidelines following these comments and the provisional acceptance of this manuscript.

Figures

Figure 1

Panel labels appear incomplete; panel a should be clearly indicated. **Thank you! Yes, the left portion of the figure (with the label) was cut out in our word document.**

Figure 2

In Fig. 2b, what is the dark opening located between the two premaxillae? Is this a genuine anatomical opening (fenestra) or a preservational artifact? Please clarify in the figure legend or main text. **This is the internarial fenestra, we discuss this in the main text and label it in the supplementary data, but we’ve added a statement in the main text clarifying that this structure rests between the midline contact of the premaxillae.**

The lower jaw reconstruction is reproduced at a very small size and is difficult to evaluate. Consider enlarging this panel. **The resolution of this figure was lowered by compression in the word document during submission, all relevant anatomy should be visible in the whole version of the figure attached to the submission site.**

Figure 3

Figure 3 currently contains relatively limited information and appears somewhat sparse for a main figure in a Nature-format paper. Since ancestral character-state estimation appears to be one of the major conclusions discussed in the manuscript, the authors may wish to incorporate some of the information currently presented in Extended Data Figure 8 into the main figure set. This would strengthen the presentation of the evolutionary implications of the study and make one of the key conclusions more accessible and visually compelling for a broader readership. **Thank you, we agree that this figure was sparse. We have gone through and labeled some important origins and losses found by our ancestral state estimations here.**