

***Urokodia* illuminates the origin of chelicerae and book gills of Chelicerata**

Corresponding Author: Professor Yu Liu

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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)

This manuscript reinterprets a previously known Cambrian arthropod, *Urokodia*, as the chronologically oldest total group chelicerate (sort of, see minor comments). The stem group of chelicerates is a hotly debated topic of late, as there is a gap between the oldest fairly modern looking crown group members and stranger Cambrian relatives such as megacheirans.

Below I will compare this work to: 1) a new manuscript in press in Nature that was provided for this review (describing a new animal called *Megachelicerax* from the Wheeler Shale) and 2) published work on *Mollisonia*. The quality of material described herein with new micro-CT data is excellent, with a nice Figure 3 showing comparative morphology of two key characters, the deutocerebral appendage, and the flattened stack of trunk exites like book gills. The exites are a bit more compelling than the deutocerebral appendage (hard to say whether it should be called a chelicera here), but that is also a good complement to *Megachelicerax*, which is already in press and represents an animal that I would interpret as 1-2 nodes crownward from *Urokodia*. I could see the two papers being published successively in Nature as independent confirmation of some of the same ideas, like the two Tully monster papers in 2016.

To briefly summarize *Megachelicerax*, its most notable feature is a pair of deutocerebral appendages with an elongated proximal podomere, and terminating in a single 2 element chela. The opisthosomal region has biramous appendages with lamellate exopod surfaces, but exites are not described. So although the evidence of a chelicera is much more compelling in *Megachelicerax*, the evidence for a book gill transition is much more compelling in *Urokodia*. Herein it is also noted that *Urokodia* is the chronologically oldest – while this is true, it is not the most important emphasis, because ultimately all of these early and middle Cambrian taxa are forming various branches along the chelicerate stem lineage.

Some recent papers have suggested a similar species, *Mollisonia*, was the oldest total group chelicerate (or fanciful notions of a crown group arachnid). In my view, and that of some others, the presence of chelicerae themselves in *Mollisonia* is debatable as the figured material showed small poorly preserved humps with an “artifact” between them. There is no such concern here. The deutocerebral appendage of *Urokodia* is not a perfect example of modern-style chelicerae and also differs more from them than does *Megachelicerax*. *Urokodia* bears 4 elements (like megacheirans) which are hypothesized herein to fuse into the 2 podomeres seen in modern *Limulus*. These 4 elements of *Urokodia* are described as chelae, so I guess, though not explicitly said, their pointed morphology being borne on the deutocerebral appendage makes that appendage a “chelicera”. The prior *Mollisonia* work asserted that the chelicerate stem group was a solved problem. It was not. I do not think *Urokodia* solves the deutocerebral appendage completely either, but it is an improvement.

Overall, I do find the evidence from *Urokodia* to be complimentary to that of *Megachelicerax*, and the body parts of both animals together help to form pieces of an early chelicerate stem puzzle.

Phylogenetic comments:

It is bizarre here (and elsewhere) to privilege parsimony trees in interpretation. This has been settled in phylogenetics for over a decade. While I understand the discussion of the matrix at line 191, we also cannot cherry pick a tree because it makes writing “*Urokodia* is the oldest chelicerate” easier to word. It might be worth noting that the Bayesian posterior

probabilities at the nodes anywhere deeper than Urokodia are basically collapsible (although the same, or worse, is true of nearly every node in every parsimony tree). There are, of course, methods to visualize and/or quantify fossil phylogenetic uncertainty based on the model (such as those described by Pates et al 2022, Smith 2022, Coiro 2024) should you choose to continue emphasizing this point. That said, I agree with the main point that both positions are compatible with the Figure 3 hypothesis.

Minor:

- What exactly is a “proto-book gill” in your definition? Is it exite stack + exopod? Weirdly, I went back to the Mollisonia paper and it was never defined there.
- Figure 3: I said it was compelling above, and it is, but more labeling is required. What are the colors on the trunk appendages? Why is the Urokodia deutocerebral appendage in red and the Limulus one using colors that don't appear in the other species?
- Line 111: Kylinxia should not be described as a “transitional taxon” – transitional from what to what? It is a fossil on a branch like any other.
- Line 203: I do not think morphological phylogenetics can resolve the position of pycnogonids. They are too full of autapomorphies, as you note. Although we do not have fossil evidence of it yet (and might not even be able to identify it if we did?) there was a pycnogonid stem group sometime in the Cambrian as well. Who knows what those animals might have looked like. I would emphasize that rather than confidently stating a “continuous transformation series” – probably stem pycnogonids were similar and then evolved their current state later.
- Line 249: Thank you, this is great!
- Line 268: Interesting model.

References:

- Coiro, Mario. “Embracing Uncertainty: The Way Forward in Plant Fossil Phylogenetics.” American Journal of Botany, February 9, 2024, e16282. <https://doi.org/10.1002/ajb2.16282>.
- Pates, Stephen, Joanna M. Wolfe, Rudy Lerosey-Aubril, Allison C. Daley, and Javier Ortega-Hernández. “New Opabiniid Diversifies the Weirdest Wonders of the Euarthropod Stem Group.” Proceedings of the Royal Society B 289 (2022): 20212093. <https://doi.org/10.1098/rspb.2021.2093>.
- Smith, Martin R. “Robust Analysis of Phylogenetic Tree Space.” Systematic Biology 71, no. 5 (2022): 1255–70. <https://doi.org/10.1093/sysbio/syab100>.

Referee #2

(Remarks to the Author)

The reviewed manuscript, entitled “Urokodia – the oldest known chelicerate reveals the origin of chelicerae and book gills” describes anatomical features of the Cambrian arthropod Urokodia aequalis from the Chengjiang biota of China as revealed through X-ray microtomography of two specimens. Urokodia has previously been aligned with Mollisonia based on similarities in dorsal morphology and the reinterpretation of Mollisonia as a basal chelicerate (based on newly revealed details of the head and trunk appendages) meant the Urokodia was also considered to have chelicerate affinities. This was recently challenged based on specimens studied using micro-CT which revealed details of the appendages of Urokodia and prompted its assignment to artiopods (the group including trilobites). The present study provides a clearer view of the appendages of Urokodia and shows the assignment of the taxon to Artiopoda to be erroneous and that it instead shows affinities with megacheirans, a group considered to be the sister clade to chelicerates. The study presents a phylogenetic analysis incorporating the new data which resolves Urokodia as the basal-most chelicerate, representing the oldest currently described Chelicerata. This position makes Urokodia a potentially important taxon for understanding early chelicerate evolution, a contentious topic given the apparent conflicts between palaeontological and molecular data.

The interpretation of the morphology of Urokodia is generally compelling. The frontal appendage is shown to clearly be a great appendage similar to that found in the megacheirans Tanglangia and Haikoucaris. The suggestion that the chelicera is derived from the great appendage by the reduction of claw bearing segments from the middle of the limb is an interesting one, although I would be interested in seeing some discussion about any other cases where segments are lost from the middle of an appendage and the mechanisms for this. The main focus of the paper however is the structure of the trunk appendages which exhibit a series of stacked exites which are suggested to be precursors of the chelicerate book gill/lung. The structures seen in Urokodia do correlate well with the corresponding structures in Mollisonia – I fully agree with the inferred reinterpretation of the trunk limbs of Mollisonia based on the information from Urokodia. I am slightly concerned by the handling of overlapping exites in the phylogenetic analysis, however; the exites in Urokodia and Mollisonia appear to be arranged extremely similarly to the exites in Leanchoilia and the other megacheirans figured in the paper, however they are not coded as overlapping in the analysis. Either justification must be made as to why the megacheirans are not coded as having overlapping exites or the phylogenetic matrix should be modified; if the latter, this may have implications for the inferred position of Urokodia.

One final point is that the phylogenetic topology does not support an assignment of Urokodia to Mollisoniida; taxonomic groups should represent clades, and Mollisoniida as defined in the manuscript is rendered paraphyletic. These issues aside, it is an interesting manuscript that provides important information about basal ‘mollisoniid’ chelicerates. The reinterpretation

of Urokodia is important given its recent assignment to Artiopoda – this perhaps represents an important point regarding the potential pitfalls of interpreting CT images – and demonstrates that multiple chelicerate species were indeed present in the Cambrian.

Referee #3

(Remarks to the Author)

- Summary of the key results

This manuscript offers a novel interpretation of some Cambrian fossils from China which the authors suggest represents a basal member of the chelicerate arthropods (i.e., spiders and their relatives). These interpretations are backed up by high-quality descriptions, including the use of computed tomography to reveal anatomical details, and a phylogenetic analysis which resolves the position of these animals in the broader arthropod tree of life.

- Originality and significance: if not novel, please include reference

While various interpretations of Urokodia are known in the literature since its original description in 1989 (see also below), this appears to be the first explicit account to formally place the genus within Chelicerata – including the proposal of a new family, Urokodiidae, within the wider Mollisoniida clade. In this sense, the manuscript does represent an original contribution.

However, I would just caution that some previous authors placed Urokodia in Mollisoniidae, and when Mollisonia/Mollisoniidae was transferred to Chelicerata one could make the argument that Urokodia became, de facto, a chelicerate as well? Indeed, if you go to the 2019 Aria & Caron Nature paper and check their supplementary data they wrote under Subphylum Chelicerata and family Mollisoniidae; “Other included genera. Thelxiope Simonetta and Delle Cave, 1975; Corcorania Jell, 1980; possibly Urokodia Hou et al. 1989.” A subsequent revision of Thelxiope also more or less regarded it as a (middle) Cambrian chelicerate:

Lerosey-Aubril R, Skabelund J, Ortega-Hernández J. Revision of the mollisoniid chelicerate(?) Thelxiope, with a new species from the middle Cambrian Wheeler Formation of Utah. PeerJ. 2020 Apr 9;8:e8879. doi: 10.7717/peerj.8879. PMID: 32296605; PMCID: PMC7151752.

There is, therefore, perhaps some precedent for treating Urokodia as a chelicerate, although in fairness to the present authors they appear to be the first to resolve this result in a formal cladistic analysis.

Given that Chelicerata is one of the major divisions of the arthropods, identifying an unequivocal early Cambrian member of this lineage, which is potentially the sister-group to all other chelicerates, would be a significant advance in our understanding of arthropod evolution. It has the potential to help resolve current issues about the ground plan morphology of arachnids and their relatives, such as how their claw-like first pair of head appendages evolved, what the original division of the body was like (a prosoma and opisthosoma?), and where the lamellate gills (and later the book lungs) originated from. For these reasons publication of this data in a high-profile interdisciplinary journal would, in my opinion, be appropriate.

- Data & methodology: validity of approach, quality of data, quality of presentation

The manuscript is well written and the descriptions and figures are of high quality; but see a couple of comments on Figures 3 and 4. As noted above, the use of computed tomography is very helpful and the associated images (and videos) are extremely nice and certainly help to show the features which are important for the authors' interpretations.

- Appropriate use of statistics and treatment of uncertainties

Statistics are not really relevant here, but the phylogenetic analysis appears to have been conducted robustly using standard modern methods.

- Conclusions: robustness, validity, reliability

Over the years there have been several attempts to recognise Cambrian chelicerates (e.g. Sanctacaris, Mollisonia, etc.), which have had various levels of success based on the subsequent literature. A particular problem has been the absence of convincing evidence for a claw-like first pair of head appendages, equivalent to the chelicera which give the group its name (Chelicerata = claw bearers). For example, I personally find the putative chelicerae in Mollisonia rather unconvincing. The present authors make, I think, a better case for treating Urokodia as a putative chelicerate: both in terms of the morphology of the first head limb and the gill-like structures on the trunk appendages as possible precursors to book-gills.

- Suggested improvements: experiments, data for possible revision

However, what appears to be somewhat glossed over in the present study is the quite extensive (and superficially similar) 2024 Liu et al. study in *iScience* which analysed the same species using similar methods - microtomography - and came to rather different conclusions: namely that the first appendage is a fleshy antenna and *Urokodia* is thus a basal member of a different arthropod group: the *Artiopoda*. Implicitly the present manuscript is, in a sense, a rebuttal of the Liu et al hypothesis.

Liu et al interpreted the first appendage as a fleshy multiannulate, non-sclerotised structure, without any spine-like projections. Specifically, under Affinities they wrote: "The antermost appendages of *Urokodia* revealed in two specimens and in micro-CT data of SJZ-B16-078 are short, flesh antenniform rather than chelicerae-form as seen in *Mollisonia*. Micro-CT scanning demonstrates that the megacheiran-like artifact was derived from overlying pyritized outline of the appendage."

This is quite a fundamental difference to your interpretation, and even if you disagree with it (as per lines 133-134 where you presume they scanned a closed claw) I would have at least expected a comment on the previous suggestion that the spine like projections are simply artefacts of pyritization. The reasons why you reject this are important, because your whole manuscript relies on the interpretation of the first head appendages being hard and claw-like, not soft and annulated.

Line 60: Assuming we do have a genuine claw-like appendage, I did wonder whether you should add an emended diagnosis for *Chelicerata* as a whole? In other words, where do you draw the line (anatomically) between short great appendage arthropods and true chelicerates (see also comments below). Obviously, there would have been a continuum of characters on the stem line going up towards chelicerates, but I think for future authors trying to place other enigmatic Cambrian arthropods it would be useful to have a clear reference point where they can say, according to Yu Liu et al., if it has this character it can be treated as a chelicerate.

I believe Aria and Caron also recognised a broader *Panchelicerata* group (which you also mention in line 179) incorporating some of the stem forms, so do you regard this as useful name? Again: where would you place the cut-off point between a panchelicerate, a chelicerate and theoretically the euchelicerates (arachnids, eurypterids and horseshoe crabs)? Although you mention *Panchelicerata* I could not find a clear definition within your paper about which arthropods comprise this group (is it *Megacheira* + *Chelicerata*?) and, again, how it differs from *Chelicerata sensu stricto*?

Looking at your text (e.g. line 124), the best potential diagnostic character for *Chelicerata* in your hypothesis may be the presence of a unichelate chelicera. However, in this context, I was a little unclear about how, exactly, you define the unichelate condition? Looking at Figure 3 the morphology of the first head limb in *Haikoucaris* (which you exclude from *Chelicerata*) looks pretty similar to the morphology in *Urokodia* (which you accept as *Chelicerata*), differing only in the fact that digit II is smaller in *Haikoucaris*. So what, precisely, is the unichelate morphology: only two projections create the fixed and movable fingers of the claw? Since this is key to your interpretation of *Urokodia* as a chelicerate I think you need to be very explicit about what you mean here.

Indeed the diagnosis (line 75): says there is a peduncle with four distal podomeres, each bearing a spine. You also (line 129) refer to a chela made by element 1 and by 2 to 4 also being able to move against each other rather like the multichelate limbs of megacheirans. In essence, all these projections from the distal limb elements contribute towards a functionally raptorial appendage. So again what, exactly, in all of this is the unichelate part of this arrangement?

In general, I found your description of *Urokodia* to be quite similar to *Haikoucaris* in particular, perhaps with a difference in the number of appendage pairs in the anterior tagma. I see a slight risk that this paper is just pulling out one of the megacheiran arthropods and promoting it as the "oldest chelicerate", while excluding ostensibly similar looking forms like *Haikoucaris*. The original Chen et al. study from 2004 also made (to my mind) a fairly robust case for treating it as a chelicerate as well. In their Figure 6 chelicerates including *Haikoucaris* were defined on "compaction of the (first) antennae to four distal claw-bearing segments; peduncle unchanged (short great appendage)". This definition seems to me to be close to part of your (line 75) diagnosis of *Urokodiidae* with: "Robust chelicerae consisting of one peduncle and four distal podomeres each bearing one spine."

I think what I'm asking is whether other short great appendage arthropods could belong in *Urokodiidae*, and thus implicitly in *Chelicerata*, as well?

Figure 3: why are you using small Roman numerals (i, ii) for the branches of the chelicera in *Limulus* when supposedly homologous elements in the fossils are numbered I - IV. Surely it would be better to use the same numbering scheme throughout, to at least imply which projections from your fossils (I and IV, or I and II) were eventually adopted, in your scenario, into the fixed and free fingers of the euchelicerate chelicerate claw?

In general I have to say this *Limulus* figure looks completely wrong to me as a representation of the chelicera. In horseshoe crabs this should be a three-articled limb in which the last two articles form a small, stubby chelae claw. What you figure here has only one slender tapering claw branch, and reminds me more of the subchelate second head appendage of the living Asian horseshoe crab genus *Tachypleus* <https://link.springer.com/article/10.1007/s10661-025-14564-8>. Please check the source of your modern comparative data here.

Figure 4: Related to some of the comments the above, there is a discrepancy here in that in the cladogram you show *Urokodia* as the sister-group of *Chelicerata*, but in the text you argue that it belongs WITHIN *Chelicerata* (cf. line 60). Do you want to modify this figure to say something like "all remaining *Chelicerata*" or is there an available clade name for *Chelicerata* excluding *Urokodiidae*/ *Mollisoniida*? I guess *Euchelicerata* doesn't work so well because of the anomalous position of the

sea spiders.

Figure 4: You refer to Panchelicerata in the legend to figure 4, but (see also above) you again do not indicate on the figure which groups belong in Panchelicerata.

Line 109: I think the chelicerate prosoma is traditionally treated as six-segmented based on its limb configuration (i.e., chelicerae/pedipalps/4 pairs of walking legs). Do the seven segments you refer to here include something like the labrum or ocular segment? It would be good to clarify this, as there is embryological evidence that modern horseshoe crabs incorporate a seventh (posterior) segment into their prosoma; thus citing a seven-segmented prosoma here as a ground plan character for Chelicerata could be potentially become confusing. You interpret Urokodia as having a head with a chelate limb followed by five pairs of appendages?

- References: appropriate credit to previous work?

References are fine, but see comments above about the Liu et al. (2024) study.

- Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The manuscript is generally clearly written. However, in the summary paragraph (line 28) the phrase ‘unichelated chelicerae with multisegmented chelae’ came across as potentially confusing to me. The chelae have multiple segments, but only one claw? See also comments above. Perhaps something like “first head limb with multiple articles, two of which combine to form the opposing fingers of a chelate claw” would be better?

Also (line 34) I wasn’t quite sure what you meant by “...place megacheirans adjacent to the chelicerates...”. Do you mean in a temporal context, i.e. that both occur in the Early Cambrian? Might be worth rewording this

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

The revised manuscript has completely redone the phylogenetic analysis to use the matrix of Megachelicerax (Lerosey-Aubril and Ortega-Hernandez 2026). Given that this matrix is already published, I do not think it is appropriate to move the goalposts for Urokodia by nitpicking the previous matrix. I agree with the authors that now, all analyses place Urokodia somewhere crownward of megacheirans and stemward of Mollisonia – except equal weights parsimony, which results in a polytomy (multiple positions are equally likely for Urokodia and what seems like all megacheirans).

Given that, the authors have done a good job of responding to all reviews.

- The revision of Fig 3 is much improved.
- Table S1 is also appreciated. In its caption, it should be clarified that it follows the Bayesian and k=5 topologies.

Minor comments:

- Regarding the response to reviews, this is not a comment that needs to be re-responded to. But when your tree cannot demonstrate the character changes, that's the data! You don't prefer a worse model just because it fits your a priori view, because phylogenetics is there to test your hypothesis of homology. An ambiguous result is sometimes the result.

Referee #2

(Remarks to the Author)

This manuscript is an updated submission previously reviewed redescribing the Cambrian arthropod Urokodia as a stem chelicerate. As noted in the original submission, this is a very interesting paper that helps flesh out further our understanding of the early evolution of this important arthropod group.

The appreciate the authors engaging with my comments and suggestions of the first submission of the manuscript and think their revised manuscript adequately addresses all of the items raised in the review. I have no further comments or suggestions on the manuscript; I feel that the authors clearly illustrate and support their conclusions and that this manuscript represents a major contribution to chelicerate research.

Referee #3

(Remarks to the Author)

This is a much improved manuscript. The authors appear to have made considerable effort to address the points raised in the first round of review and have produced, in my opinion, a much neater manuscript with a clear

morphological/phylogenetic message. Taking on board the recent publication of Megachelicerax as the oldest putative member of Chelicerata sensu stricto, the present authors now offer a novel interpretation of Urokodia as a key step on the transition towards the chelicerate condition. I think the present study thus compliments the Megachelicerax paper rather nicely and merits inclusion in a similarly high-profile journal. I would now recommend acceptance and would like to add only a couple of minor comments.

line 119: "...with lower or the same number of exite flaps..."

line 200: not sure if there is still time/need to include them, but the recently published

Bolton, S. J., & Sharma, P. P. (2026). Reconciling morphology with phylogenomics in Chelicerata (Arthropoda). Zoological Journal of the Linnean Society, 206(2), zlag017.

Bolton, S. J., Friedrich, M., & Sharma, P. P. (2026). Mollisonia is probably not an arachnid. Current Biology, 36(4), R126-R127.

are somewhat more critical about the status and interpretation of some of these Cambrian fossils as chelicerates from a zoological perspective. The Bolton & Sharma study also questions the extent to which the traditional prosoma really is a key defining character for Chelicerata; although I accept that this does not affect your interpretation of the appendages. The evolutionary transition series proposed in Fig 3 remains a plausible hypothesis.

line 369: italicise "Bunaia woodwardi" in the Lustri et al reference.

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Referees' comments:

Referee #1 (Remarks to the Author):

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Below I will compare this work to: 1) a new manuscript in press in Nature that was provided for this review (describing a new animal called *Megachelicerax* from the Wheeler Shale) and 2) published work on *Mollisonia*. The quality of material described herein with new micro-CT data is excellent, with a nice Figure 3 showing comparative morphology of two key characters, the deutocerebral appendage, and the flattened stack of trunk exites like book gills. The exites are a bit more compelling than the deutocerebral appendage (hard to say whether it should be called a chelicera here), but that is also a good complement to *Megachelicerax*, which is already in press and represents an animal that I would interpret as 1-2 nodes crownward from *Urokodia*. I could see the two papers being published successively in Nature as independent confirmation of some of the same ideas, like the two Tully monster papers in 2016.

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Overall, I do find the evidence from *Urokodia* to be complimentary to that of *Megachelicerax*, and the body parts of both animals together help to form pieces of an early chelicerate stem puzzle.

- We thank the reviewer for this thoughtful and highly constructive assessment. We are especially grateful for the reviewer's positive evaluation of the new micro-CT data, the quality of the material, and the broader significance of *Urokodia* for understanding the early evolution of the chelicerate stem lineage. We also appreciate the reviewer's view that the evidence from *Urokodia* is complementary to that from other recent Cambrian taxa and that, taken together, these fossils help illuminate different aspects of the early assembly of the chelicerate body plan.

We have revised the manuscript in line with the reviewer's comments to present *Urokodia* as an important contribution to the emerging picture of early chelicerate evolution.

Phylogenetic comments:

It is bizarre here (and elsewhere) to privilege parsimony trees in interpretation. This has been settled in phylogenetics for over a decade. While I understand the discussion of the matrix at line 191, we also cannot cherry pick a tree because it makes writing "*Urokodia* is the oldest chelicerate" easier to word. It might be worth noting that the Bayesian posterior probabilities at the nodes anywhere deeper than *Urokodia* are basically collapsible (although the same, or worse, is true of nearly every node in every parsimony tree). There are, of course, methods to visualize and/or quantify fossil phylogenetic uncertainty based on the model (such as those described by Pates et al 2022, Smith 2022, Coiro 2024) should you choose to continue emphasizing this point. That said, I agree with the main point that both positions are compatible with the Figure 3 hypothesis.

- Thank you. We have taken this and other phylogeny-related comments very seriously. The point raised here is important – we were unable to demonstrate the character transitions clearly with our previous Bayesian analysis, and therefore favoured the parsimony outcome.

Fortunately, a much stronger phylogenetic framework suitable for testing our hypothesis has recently been published in the paper on *Megachelicerax*, and the authors kindly granted us access to their matrix prior to formal publication. With the new matrix, all the four new analyses (Parsimony with equal weights, $k = 5$, $k = 10$, and Bayesian inference) result in a consistent placement of *Urokodia* between the more stem-ward megacheirans and the more crown-ward chelicerate taxa such as *Mollisonia* and *Megachelicerax*, confirming our conclusion that *Urokodia* is a key bridging taxon in the early evolution of Chelicerata. Moreover, our new analyses also provide strong support for the monophyly of Cheliceromorpha.

Overall, our systematic and phylogenetic results are now in much stronger agreement. This improvement is due both to the reviewer's comments and to the newly available phylogenetic framework. Together, they enhance the position of *Urokodia* as a key transitional taxon for understanding the monophyly of Cheliceromorpha, particularly in tracing the evolutionary transition of chelicerae from the short great appendages and that of book gills from exopods and exites composed of overlapping flaps, finally solving the debate of chelicerate origins.

Minor:

- What exactly is a “proto-book gill” in your definition? Is it exite stack + exopod? Weirdly, I went back to the *Mollisonia* paper and it was never defined there.

- Thank you for raising this point. We agree that the term “proto-book gill” has been used in the literature without a sufficiently explicit anatomical definition, and that its application is complicated by the still-uncertain homology of the relevant limb structures in *Mollisonia* and related taxa. In response, we have revised the text to avoid relying on this term as a primary interpretative framework. Instead, we now focus on explicit comparison of the appendicular anatomy and limb-part homologies across megacheirans, *Urokodia*, and *Mollisonia*. In light of our new data from various megacheirans and *Urokodia* (Fig. 3a), together with our revised interpretation of the possibly inverted stacked exopodial lobes in *Mollisonia*, we have added a more detailed discussion of these structures and their homology, which also provides the basis for our updated phylogenetic coding.

- Figure 3: I said it was compelling above, and it is, but more labeling is required. What are the colors on the trunk appendages? Why is the *Urokodia* deutocerebral appendage in red and the *Limulus* one using colors that don’t appear in the other species?

- Thank you. We have improved the labeling, colouring, and explanations of this figure to increase the comparability across various taxa shown in this figure, especially with putatively homologous parts indicated by the same colours.

- Line 111: *Kylinxia* should not be described as a “transitional taxon” – transitional from what to what? It is a fossil on a branch like any other.

- That’s right. We have now replaced “transitional” with “early branching”.

- Line 203: I do not think morphological phylogenetics can resolve the position of pycnogonids. They are too full of autapomorphies, as you note. Although we do not have fossil evidence of it yet (and might not even be able to identify it if we did?) there was a pycnogonid stem group sometime in the Cambrian as well. Who knows what those animals might have looked like. I would emphasize that rather than confidently stating a “continuous transformation series” – probably stem pycnogonids were similar and then evolved their current state later.

- Yes. We agree that the pycnogonids are highly autapomorphic and that their position has long been difficult to resolve confidently using morphology alone. In response, we have removed the phrases suggesting “continuous transformation series” (see Supplementary Text).

- Line 249: Thank you, this is great!

- Thank you.

- Line 268: Interesting model.

- Thank you.

References:

- Coiro, Mario. “Embracing Uncertainty: The Way Forward in Plant Fossil Phylogenetics.” *American Journal of Botany*, February 9, 2024, e16282. <https://doi.org/10.1002/ajb2.16282>.
- Pates, Stephen, Joanna M. Wolfe, Rudy Leroosey-Aubril, Allison C. Daley, and Javier Ortega-Hernández. “New Opabiniid Diversifies the Weirdest Wonders of the Euarthropod Stem Group.” *Proceedings of the Royal Society B* 289 (2022): 20212093. <https://doi.org/10.1098/rspb.2021.2093>.
- Smith, Martin R. “Robust Analysis of Phylogenetic Tree Space.” *Systematic Biology* 71, no. 5 (2022): 1255–70. <https://doi.org/10.1093/sysbio/syab100>.

Referee #2 (Remarks to the Author):

The reviewed manuscript, entitled “*Urokodia* – the oldest known chelicerate reveals the origin of chelicerae and book gills” describes anatomical features of the Cambrian arthropod *Urokodia aequalis* from the Chengjiang biota of China as revealed through X-ray microtomography of two specimens. *Urokodia* has previously been aligned with *Mollisonia* based on similarities in dorsal morphology and the reinterpretation of *Mollisonia* as a basal chelicerate (based on newly revealed details of the head and trunk appendages) meant the *Urokodia* was also considered to have chelicerate affinities. This was recently challenged based on specimens studied using micro-CT which revealed details of the appendages of *Urokodia* and prompted its assignment to artiopods (the group including trilobites). The present study provides a clearer view of the appendages of *Urokodia* and shows the assignment of the taxon to Artiopoda to be erroneous and that it instead shows affinities with megacheirans, a group considered to be the sister clade to chelicerates. The study presents a phylogenetic analysis incorporating the new data which resolves *Urokodia* as the basal-most chelicerate, representing the oldest currently described Chelicerata. This position makes *Urokodia* a potentially important taxon for understanding early chelicerate evolution, a contentious topic given the apparent conflicts between palaeontological and molecular data.

- We thank the reviewer for this positive and accurate summary of the manuscript. We are pleased that the reviewer considers the new micro-CT data to provide a clearer view of the appendages of *Urokodia* and to support rejection of its recent assignment to Artiopoda. We also appreciate the reviewer’s recognition that *Urokodia* is potentially important for understanding early chelicerate evolution.

The interpretation of the morphology of *Urokodia* is generally compelling. The frontal appendage is shown to clearly be a great appendage similar to that found in the megacheirans *Tanglangia* and *Haikoucaris*. The suggestion that the chelicera is derived from the great appendage by the reduction of claw bearing segments from the middle of the limb is an interesting one, although I would be interested in seeing some discussion about any other cases where segments are lost from the middle of an appendage and the mechanisms for this.

- We thank the reviewer for this helpful suggestion. We agree that our proposed transformation of the short great appendage into the chelicera would benefit from broader comparative context. We have therefore added a brief discussion noting that reduction or fusion of specific podomeres, including intermediate ones, is developmentally plausible in arthropods. In extant arthropods, experimental studies have shown that perturbation of proximodistal appendage-patterning genes can reduce or fuse medial podomeres; for example, in the antenna of *Tribolium castaneum*, knockdown of *dachshund* results in reduction of medial funicle segments and fusion within that region. We also note that, in chelicerates, *evo-devo* work has suggested that the transition from a three-segmented to a two-segmented chelicera may involve loss of a *dachshund*-patterned podomere. We emphasize, however, that our fossil data do not directly demonstrate the developmental mechanism, and we therefore treat this as a hypothesis consistent with comparative arthropod developmental biology rather than as

a demonstrated pathway.

The main focus of the paper however is the structure of the trunk appendages which exhibit a series of stacked exites which are suggested to be precursors of the chelicerate book gill/lung. The structures seen in *Urokodia* do correlate well with the corresponding structures in *Mollisonia* – I fully agree with the inferred reinterpretation of the trunk limbs of *Mollisonia* based on the information from *Urokodia*.

- Thank you.

I am slightly concerned by the handling of overlapping exites in the phylogenetic analysis, however; the exites in *Urokodia* and *Mollisonia* appear to be arranged extremely similarly to the exites in *Leanchoilia* and the other megacheirans figured in the paper, however they are not coded as overlapping in the analysis. Either justification must be made as to why the megacheirans are not coded as having overlapping exites or the phylogenetic matrix should be modified; if the latter, this may have implications for the inferred position of *Urokodia*.

- Thank you for raising this point. In fact we didn't forget coding this important character in the previous version nor in the current analyses based on the new matrix from the *Megachelicerax* paper. Indeed, this comment inspired us to expand the comparison and discussion of the overlapping exite flaps across various taxa, which then leads us to give a new definition of the so-called "proto-book gill".

One final point is that the phylogenetic topology does not support an assignment of *Urokodia* to *Mollisoniida*; taxonomic groups should represent clades, and *Mollisoniida* as defined in the manuscript is rendered paraphyletic.

- As mentioned in our responses to the phylogenetic inquiries from Reviewer 1, we agree that a lower-level systematic revision of the group may be premature. We therefore decided to assign *Urokodia* to the lower taxonomic rank of Cheliceromorpha.

These issues aside, it is an interesting manuscript that provides important information about basal 'mollisoniid' chelicerates. The reinterpretation of *Urokodia* is important given its recent assignment to Artiopoda – this perhaps represents an important point regarding the potential pitfalls of interpreting CT images – and demonstrates that multiple chelicerate species were indeed present in the Cambrian.

- Thank you. This comment encouraged us to reach out to the corresponding author of that *Urokodia*–Artiopoda paper (Prof. Xingliang Zhang, Northwest University, Xi'an), who kindly provided us their original CT data and granted us the permission in written form to display the comparison between our data and our own rendering of their data (new Extended Data Fig. 3). The comparison shows close similarities between the two datasets, and most importantly, clarifies that the structures they identified as the antennae are in fact chelicerae.

Referee #3 (Remarks to the Author):

- Summary of the key results

This manuscript offers a novel interpretation of some Cambrian fossils from China which the authors suggest represents a basal member of the chelicerate arthropods (i.e., spiders and their relatives). These interpretations are backed up by high-quality descriptions, including the use of computed tomography to reveal anatomical details, and a phylogenetic analysis which resolves the position of these animals in the broader arthropod tree of life.

- Thank you for your positive evaluation. We are grateful that you find the interpretation novel and that you appreciate the scientific merits of this manuscript.

- Originality and significance: if not novel, please include references

While various interpretations of *Urokodia* are known in the literature since its original description in 1989 (see also below), this appears to be the first explicit account to formally place the genus within Chelicerata – including the proposal of a new family, Urokodiidae, within the wider Mollisoniida clade. In this sense, the manuscript does represent an original contribution.

- Thank you.

However, I would just caution that some previous authors placed *Urokodia* in Mollisonidae, and when *Mollisonia*/Mollisonidae was transferred to Chelicerata one could make the argument that *Urokodia* became, de facto, a chelicerate as well? Indeed, if you go to the 2019 Aria & Caron Nature paper and check their supplementary data they wrote under Subphylum Chelicerata and family Mollisonidae; “Other included genera. *Thelxiope* Simonetta and Delle Cave, 1975; *Corcorania* Jell, 1980; possibly *Urokodia* Hou et al. 1989.” A subsequent revision of *Thelxiope* also more or less regarded it as a (middle) Cambrian chelicerate: Lerosey-Aubril R, Skabelund J, Ortega-Hernández J. Revision of the mollisoniid chelicerate(?) *Thelxiope*, with a new species from the middle Cambrian Wheeler Formation of Utah. PeerJ. 2020 Apr 9;8:e8879. doi: 10.7717/peerj.8879. PMID: 32296605; PMCID: PMC7151752. There is, therefore, perhaps some precedent for treating *Urokodia* as a chelicerate, although in fairness to the present authors they appear to be the first to resolve this result in a formal cladistic analysis.

- Thank you for raising this. We agree that there is some prior precedent for a chelicerate affinity of *Urokodia*, particularly because Aria and Caron (2019) treated mollisoniids within Chelicerata and mentioned *Urokodia* as a possible included genus, and later work on *Thelxiope* likewise suggested a chelicerate interpretation for mollisoniid-like taxa. Our intention is therefore not to claim that a chelicerate affinity for *Urokodia* is entirely unprecedented, but rather that this study provides, to our knowledge, the first formal cladistic test and explicit anatomical documentation supporting its placement as an early branching upper stem chelicerate. On the other hand, all the four new phylogenetic analyses (parsimony with equal weights, $k = 5$ and 10, and Bayesian inference) that we undertook based on the matrix from the recent *Megachelicerax* paper consistently recovered *Urokodia* outside the mollisoniids clade, underpinning the previous assumption/inferences with solid morphological data and reliable

phylogenetic analyses for the first time.

Given that Chelicerata is one of the major divisions of the arthropods, identifying an unequivocal early Cambrian member of this lineage, which is potentially the sister-group to all other chelicerates, would be a significant advance in our understanding of arthropod evolution. It has the potential to help resolve current issues about the ground plan morphology of arachnids and their relatives, such as how their claw-like first pair of head appendages evolved, what the original division of the body was like (a prosoma and opisthosoma?), and where the lamellate gills (and later the book lungs) originated from. For these reasons publication of this data in a high-profile interdisciplinary journal would, in my opinion, be appropriate.

- Thank you for the endorsement.

- Data & methodology: validity of approach, quality of data, quality of presentation

The manuscript is well written and the descriptions and figures are of high quality; but see a couple of comments on Figures 3 and 4. As noted above, the use of computed tomography is very helpful and the associated images (and videos) are extremely nice and certainly help to show the features which are important for the authors' interpretations.

- Thank you.

- Appropriate use of statistics and treatment of uncertainties

Statistics are not really relevant here, but the phylogenetic analysis appears to have been conducted robustly using standard modern methods.

- Thank you.

- Conclusions: robustness, validity, reliability

Over the years there have been several attempts to recognise Cambrian chelicerates (e.g. *Sanctacaris*, *Mollisonia*, etc.), which have had various levels of success based on the subsequent literature. A particular problem has been the absence of convincing evidence for a claw-like first pair of head appendages, equivalent to the chelicera which give the group its name (Chelicerata = claw bearers). For example, I personally find the putative chelicerae in *Mollisonia* rather unconvincing. The present authors make, I think, a better case for treating *Urokodia* as a putative chelicerate: both in terms of the morphology of the first head limb and the gill-like structures on the trunk appendages as possible precursors to book-gills.

- Thank you.

- Suggested improvements: experiments, data for possible revision

However, what appears to be somewhat glossed over in the present study is the quite extensive (and superficially similar) 2024 Liu et al. study in *iScience* which analysed the same species using similar methods - microtomography - and came to rather different conclusions: namely that the first appendage is a fleshy antenna and *Urokodia* is thus a basal member of a different arthropod group: the Artiopoda. Implicitly the

present manuscript is, in a sense, a rebuttal of the Liu et al hypothesis. Liu et al interpreted the first appendage as a fleshy multiannulate, non-sclerotised structure, without any spine-like projections. Specifically, under Affinities they wrote: “The anteromost appendages of *Urokodia* revealed in two specimens and in micro-CT data of SJZ-B16-078 are short, flesh antenniform rather than chelicerae-form as seen in *Mollisonia*. Micro-CT scanning demonstrates that the megacheiran-like artifact was derived from overlying pyritized outline of the appendage.”

- Thank you for raising this. After comparing our rendering of the CT data of SJZ-B16-078 and the CT data from an additional specimen of ours (new Extended Data Fig. 3a, b), especially after applying the 2x digital exaggeration on both models, we found that in this case, fossil compression probably played a stronger role than pyritization in misguiding the other authors to consider the compressed short great appendages of *Urokodia* as antennae.

This is quite a fundamental difference to your interpretation, and even if you disagree with it (as per lines 133-134 where you presume they scanned a closed claw) I would have at least expected a comment on the previous suggestion that the spine like projections are simply artefacts of pyritization. The reasons why you reject this are important, because your whole manuscript relies on the interpretation of the first head appendages being hard and claw-like, not soft and annulated.

- Thank you for highlighting this crucial issue. As mentioned in the reply to reviewer 2, we solved this problem by reaching out to the corresponding author of that *Urokodia*–Artiopoda paper (Prof. Xingliang Zhang, Northwest University, Xi’an), who kindly provided us their original CT data and granted us the permission in written form to display the comparison between our data and our own rendering of their data (new Extended Data Fig. 3). The comparison shows close similarities between the two datasets, and most importantly, clarifies that the structures they identified as the antennae are in fact chelicerae. The text has been revised accordingly.

Line 60: Assuming we do have a genuine claw-like appendage, I did wonder whether you should add an emended diagnosis for Chelicerata as a whole? In other words, where do you draw the line (anatomically) between short great appendage arthropods and true chelicerates (see also comments below). Obviously, there would have been a continuum of characters on the stem line going up towards chelicerates, but I think for future authors trying to place other enigmatic Cambrian arthropods it would be useful to have a clear reference point where they can say, according to Yu Liu et al., if it has this character it can be treated as a chelicerate.

- This is an important point. In this revision, we did try to draw several lines along the stem of Chelicerata, especially a line between short great appendage arthropods and true chelicerates with *Urokodia* representing an intermediate stage. We now consider the megacheirans (i.e. short great appendage arthropods) as lower stem, *Urokodia* and mollisoniids as upper stem (grade 1), habeliidans as upper stem (grade 2), and the more crown-ward taxa as Chelicerata *sensu stricto* (Extended Data Fig. 8), each grouping supported by a set of characters (Supplementary Table 1).

I believe Aria and Caron also recognised a broader Panchelicerata group (which you also mention in line 179) incorporating some of the stem forms, so do you regard this as useful name? Again: where would you place the cut-off point between a panchelicerate, a chelicerate and theoretically the euchelicerates (arachnids, eurypetrids and horseshoe crabs)? Although you mention Panchelicerata I could not find a clear definition within your paper about which arthropods comprise this group (is it Megacheira + Chelicerata?) and, again, how it differs from Chelicerata *sensu stricto*?

- No, we don't consider Panchelicerata as a useful name. As reported by Aria and Caron themselves, Panchelicerata is a name valid under an arachnomorph scenario. In the previous phylogenetic framework, we recovered both the opposing arachnomorph and cheliceromorph scenarios in different analyses, which created some confusion. But in the new phylogenetic framework, we consistently recover the monophyly only for Cheliceromorpha. This, together with the character transitions shown by *Urokodia*, allows us to go for Cheliceromorpha, within which Chelicerata *sensu stricto* comprises the most crownward group (Extended Data Fig. 8). Please see Supplementary Table 1 for the characters.

Looking at your text (e.g. line 124), the best potential diagnostic character for Chelicerata in your hypothesis may be the presence of a unichelate chelicera. However, in this context, I was a little unclear about how, exactly, you define the unichelate condition? Looking at Figure 3 the morphology of the first head limb in *Haikoucaris* (which you exclude from Chelicerata) looks pretty similar to the morphology in *Urokodia* (which you accept as Chelicerata), differing only in the fact that digit II is smaller in *Haikoucaris*. So what, precisely, is the unichelate morphology: only two projections create the fixed and movable fingers of the claw? Since this is key to your interpretation of *Urokodia* as a chelicerate I think you need to be very explicit about what you mean here.

- Yes. Thank you. During the revision process, we realized that the term “unichelate” could be confusing and therefore replaced it with pincer-like short great appendage to describe the situation in *Urokodia* for the fact that the two smaller digits (II, III) become fused with the larger terminal digit IV to form one of the two elements of a pincer, while the most proximal digit I remains as the other element of the pincer. To our understanding, this fusion does not occur in any megacheirans including *Haikoucaris* that clearly has four separated and relatively long digits (Fig. 3a). We have improved the text to make this point clearer.

Indeed the diagnosis (line 75): says there is a peduncle with four distal podomeres, each bearing a spine. You also (line 129) refer to a chela made by element 1 and by 2 to 4 also being able to move against each other rather like the multichelate limbs of megacheirans. In essence, all these projections from the distal limb elements contribute towards a functionally raptorial appendage. So again what, exactly, in all of this is the unichelate part of this arrangement?

- See the response to the previous comment.

In general, I found your description of *Urokodia* to be quite similar to *Haikoucaris* in particular, perhaps with a difference in the number of appendage pairs in the anterior tagma. I see a slight risk that this paper is just pulling out one of the megacheiran arthropods and promoting it as the “oldest chelicerate”, while excluding ostensibly similar looking forms like *Haikoucaris*. The original Chen et al. study from 2004 also made (to my mind) a fairly robust case for treating it as a chelicerate as well. In their Figure 6 chelicerates including *Haikoucaris* were defined on “compaction of the (first) antennae to four distal claw-bearing segments; peduncle unchanged (short great appendage).”. This definition seems to me to be close to part of your (line 75) diagnosis of Urokodiidae with: “Robust chelicerae consisting of one peduncle and four distal podomeres each bearing one spine.”

I think what I’m asking is whether other short great appendage arthropods could belong in Urokodiidae, and thus implicitly in Chelicerata, as well?

- We are sorry for giving the wrong impression with the previous version of this manuscript. As shown in Extended Data Figures 5–8, none of the new phylogenetic analyses suggests the possibility of other short great appendage arthropods (i.e. megacheirans) belonging in Urokodiidae. On the other hand, despite the consistent number of digits (four) in the SGAs across various megacheirans, the morphologies of the SGAs themselves and other body parts (e.g. organization of biramous limbs, shape of exoskeleton etc.) are very different from each other – even *Haikoucaris* and *Leanchoilia illecebrosa* with the same number of trunk segments (eleven) are never grouped together (Extended Data Figures 5–8). We, therefore, consider the possibility of other short great appendage arthropods belonging in Urokodiidae is very low.

Figure 3: why are you using small Roman numerals (i, ii) for the branches of the chelicera in *Limulus* when supposedly homologous elements in the fossils are numbered I-IV. Surely it would be better to use the same numbering scheme throughout, to at least imply which projections from your fossils (I and IV, or I and II) were eventually adopted, in your scenario, into the fixed and free fingers of the euchelicerate cheliceral claw?

- Thank you. Sorry for not making our labeling system clear enough in the previous version of the manuscript. We use two different Roman numerals to indicate the corresponding elements in different taxa along the early evolution route of Chelicerata, with particular emphasis on making the fusion of digits II, III, and IV in *Urokodia* easier to follow.

In general I have to say this *Limulus* figure looks completely wrong to me as a representation of the chelicera. In horseshoe crabs this should be a three-articled limb in which the last two articles form a small, stubby chelae claw. What you figure here has only one slender tapering claw branch, and reminds me more of the subchelate second head appendage of the living Asian horseshoe crab genus *Tachypleus* <https://link.springer.com/article/10.1007/s10661-025-14564-8>. Please check the source of your modern comparative data here.

- Thank you, we received this image courtesy of Dr. Russel Bicknell who published this in a paper entitled “A 3D anatomical atlas of appendage musculature in the chelicerate arthropod *Limulus polyphemus*”. In order to remove any possible confusion, the green segment/peduncle in the original image has been removed from the new Fig. 3a.

Figure 4: Related to some of the comments the above, there is a discrepancy here in that in the cladogram you show *Urokodia* as the sister-group of Chelicerata, but in the text you argue that it belongs WITHIN Chelicerata (cf. line 60). Do you want to modify this figure to say something like “all remaining Chelicerata” or is there an available clade name for Chelicerata excluding Urokodiidae/Mollisoniida? I guess Euchelicerata doesn’t work so well because of the anomalous position of the sea spiders.

- Thank you. We have improved this by running new phylogenetic analyses that resulted in a much better topology. We now consider *Urokodia* as an upper stem chelicerate with a unique combination of characters (Supplementary Table 1). The text has also been modified accordingly.

Figure 4: You refer to Panchelicerata in the legend to figure 4, but (see also above) you again do not indicate on the figure which groups belong in Panchelicerata.

- See the response to the previous comment.

Line 109: I think the chelicerate prosoma is traditionally treated as six-segmented based on its limb configuration (i.e., chelicerae/pedipalps/4 pairs of walking legs). Do the seven segments you refer to here include something like the labrum or ocular segment? It would be good to clarify this, as there is embryological evidence that modern horseshoe crabs incorporate a seventh (posterior) segment into their prosoma; thus citing a seven-segmented prosoma here as a ground plan character for Chelicerata could be potentially become confusing. You interpret *Urokodia* as having a head with a chelate limb followed by five pairs of appendages?

- Yes. In saying *Urokodia* bears a seven-segmented head, we mean the ocular segment, the SGA segment, and the subsequent five segments each bearing a pair of biramous appendages. The labrum is considered non-appendicular and hence a non-segmental structure. We have improved the text to make this point clearer.

- References: appropriate credit to previous work?

References are fine, but see comments above about the Liu et al. (2024) study.

- Thank you. We have now addressed all the points raised around Liu et al. (2024).

- Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The manuscript is generally clearly written. However, in the summary paragraph (line 28) the phrase ‘unichelated chelicerae with multisegmented chelae’ came across as potentially confusing to me. The chelae have multiple segments, but only one claw? See also comments above. Perhaps something like “first head limb with multiple articles, two of which combine to form the opposing fingers of a chelate claw” would

be better?

- Thank you. We have re-written the summary paragraph and made this point clearer there and elsewhere in the main text.

Also (line 34) I wasn't quite sure what you meant by "...place megacheirans adjacent to the chelicerates...". Do you mean in a temporal context, i.e. that both occur in the Early Cambrian? Might be worth rewording this.

- Thank you. With the new results from our phylogenetic analyses we have reworded the context about the phylogenetic placement of megacheirans and other taxa thoroughly.

Referee #1 (Remarks to the Author):

The revised manuscript has completely redone the phylogenetic analysis to use the matrix of *Megachelicerax* (Lerosey-Aubril and Ortega-Hernandez 2026). Given that this matrix is already published, I do not think it is appropriate to move the goalposts for *Urokodia* by nitpicking the previous matrix. I agree with the authors that now, all analyses place *Urokodia* somewhere crownward of megacheirans and stemward of *Mollisonia* – except equal weights parsimony, which results in a polytomy (multiple positions are equally likely for *Urokodia* and what seems like all megacheirans).

- Thank you.

Given that, the authors have done a good job of responding to all reviews.

- The revision of Fig 3 is much improved.

- Table S1 is also appreciated. In its caption, it should be clarified that it follows the Bayesian and k=5 topologies.

- Done.

Minor comments:

- Regarding the response to reviews, this is not a comment that needs to be re-responded to. But when your tree cannot demonstrate the character changes, that's the data! You don't prefer a worse model just because it fits your a priori view, because phylogenetics is there to test your hypothesis of homology. An ambiguous result is sometimes the result.

- Totally agree. Thank you.

Referee #2 (Remarks to the Author):

This manuscript is an updated submission previously reviewed redescribing the Cambrian arthropod *Urokodia* as a stem chelicerate. As noted in the original submission, this is a very interesting paper that helps flesh out further our understanding of the early evolution of this important arthropod group.

- Thank you.

The appreciate the authors engaging with my comments and suggestions of the first submission of the manuscript and think their revised manuscript adequately addresses all of the items raised in the review. I have no further comments or suggestions on the manuscript; I feel that the authors clearly illustrate and support their conclusions and that this manuscript represents a major contribution to chelicerate research.

- Thank you.

Referee #3 (Remarks to the Author):

This is a much improved manuscript. The authors appear to have made considerable effort to address the points raised in the first round of review and have produced, in my opinion, a much neater manuscript with a clear morphological/phylogenetic message. Taking on board the recent publication of *Megachelicerax* as the oldest putative member of Chelicerata *sensu stricto*, the present authors now offer a novel

interpretation of *Urokodia* as a key step on the transition towards the chelicerate condition. I think the present study thus compliments the *Megachelicerax* paper rather nicely and merits inclusion in a similarly high-profile journal. I would now recommend acceptance and would like to add only a couple of minor comments.

- Thank you.

line 119: "...with lower or the same number of exite flaps..."

- Corrected.

line 200: not sure if there is still time/need to include them, but the recently published

Bolton, S. J., & Sharma, P. P. (2026). Reconciling morphology with phylogenomics in Chelicerata (Arthropoda). *Zoological Journal of the Linnean Society*, 206(2), zlag017.

Bolton, S. J., Friedrich, M., & Sharma, P. P. (2026). *Mollisonia* is probably not an arachnid. *Current Biology*, 36(4), R126-R127.

are somewhat more critical about the status and interpretation of some of these Cambrian fossils as chelicerates from a zoological perspective. The Bolton & Sharma study also questions the extent to which the traditional prosoma really is a key defining character for Chelicerata; although I accept that this does not affect your interpretation of the appendages. The evolutionary transition series proposed in Fig 3 remains a plausible hypothesis.

- Citations of both recently published papers added at the end of the Discussion (lines 288-290).

line 369: italicise "*Bunaia woodwardi*" in the Lustri et al reference.

- Done.