

Jurassic flightless bird reveals early ecological diversity of avialans

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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)

Dear authors,

I have read with attention the manuscript about the newly discovered Yuezhurnis, and I must say that the anatomical evidence afforded for the specimen is not convincing enough for its location as a basal avialan more derived than Archaeopteryx. As you correctly expose in the manuscript, the new taxon exhibits troodontid features in the skull and dentition, in joint with plesiomorphic proportions in the forelimb bones, plesiomorphic shape of coracoid, and several pelvic and hindlimb features that are widely present in several paravian taxa close to the Avialae node. Of course, you also introduce the existence of a new, yet-unpublished avialan taxon, which seems closely related to Yuezhurnis, and this fact may lend support to the avialan affiliation you advocate for Yuezhurnis.

In the attached pdf of your manuscript I made some comments and suggestions that, hopefully, become useful for your work.

Sincerely yours,

Fernando Novas

Referee #2

(Remarks to the Author)

Overall, I have sufficient doubts about the most important inferences in the paper, that I do not recommend publication of this fossil in Nature.

The paper reports a Late Jurassic theropod, which the authors suggest belongs within Avialae as a secondarily flightless member of the group. That would be a very interesting discovery - a secondarily flightless bird living at the same time as Archaeopteryx. However, I have numerous reservations about this, which include: (1) I'm not confident that this is a member of Avialae, rather than a non-avian paravian (e.g. similar to Anchiornis), and (2) I'm not totally sure it gives strong evidence of flightlessness, the forelimb:hindlimb length ratio is similar to that of Anchiornis, so it potentially consistent with some form of volant behaviour, similar to either Anchiornis or Microraptor.

Indeed, the ulna:humerus length ratio is higher in this new specimen than in e.g. Anchiornis and Microraptor. Normally, flightless birds have reduced the relative length of the ulna segment (see Gatesy & Middleton 2000 "Theropod forelimb design and evolution", e.g. Fig. 4), but that has not happened here. See Fig. 3b: the forelimb proportions are similar to terrestrial flying birds, but not to strictly flightless birds. The text states, rather selectively, that the forelimb proportions of the new taxon are similar to 'flightless' pheasants. However, these pheasants aren't strictly flightless and, more importantly, the forelimb proportions are almost equally similar in some birds that are capable of sustained flight, including Podilymbus (grebe), Branta (goose) and Anser (duck). Although those birds aren't agile flyers, they certainly can fly.

The fossil is quite poorly-preserved. So currently, not as much anatomy is visible as we ideally would be able to see to support this, but various features are highlighted as being shared with Anchiornis. These make me suspicious of the support for the hypothesis that the new taxon it belongs to Avialae, rather than an outgroup of Avialae.

- The proportion of forelimb length (humerus+radius+metacarpal1) to hindlimb length (femur+tibia+metatarsus) is 0.67 here, and 0.69 in Anchiornis, very similar.
- Both have small, closely-packed premaxillary and anterior maxillary teeth (which are absent in other avialans).
- Teeth and ziphodont, serrated, and the maxillary tooth row extends further than in avialans (see ms).
- The jugal morphology is similar to Anchiornis and different to avialans (see ms).
- Anterior surface of the coracoid with numerous pits (see ms).
- Low angle of circular rami, differing from Avialae.
- Pubic apron morphology shared with troodontids.
- ...etc (see text)

The authors do not present statistical tests of alternative phylogenetic hypotheses. So it is not clear that the anatomy statistically rejects a placement outside Avialae, for the new taxon. That is important because, if it is outside Avialae, then it isn't a secondarily flightless avialan.

Anchiornis is much better known, and older (Middle Jurassic). So the new fossil may be confirmation that Anchiornis-like taxa continued to be present into the Late Jurassic (which has already been suggested at Solnhofen).

DETAILED COMMENTS

Abstract

"The origin and early diversification of birds remain one of the most debated transitions in vertebrate evolution"

>>This seems incorrect. The origins of turtle, snakes, placental mammals, vertebrates themselves, and even squamates (for which there is no consensus on which Triassic fossils might be stem squamates) seem more 'debated'. The origin and early diversification of birds of course is very interesting, with various unanswered questions, but specifically the statement that it is 'one of the most debated' seems incorrect.

"Our study challenges the prevailing notion that aerodynamic selection was the determinant force of early avialan evolution. Instead, it demonstrates that birds underwent rapid ecological diversification and specialized niche colonization—including the loss of flight—shortly after their emergence."

>>I can't swallow this text. The paper documents an early transition to flightlessness in one lineage of Avialae. Sure, that's very interesting. But it doesn't actually contradict the idea that aerodynamic selection (i.e. flight) explains the main anatomical transitions involved in bird origins or the early evolution of Avialae. Consider alternative ways of explaining the significance of the observation of an early flightless taxon. (But note: I don't think the authors have provided sufficiently strong evidence of that).

Results

>>References to 'stem avialans' are confusing. Crown birds have a stem group that includes all (non crown bird) dinosaurs, pterosaurs etc etc. Avialae does not have a stem. But if it did, then it should also include other dinosaurs, pterosaurs etc. Maybe just say 'early avialans' or 'early-diverging avialans'.

>>Anterior caudal transverse processes are described as facing posterolaterally. But they appear to face anterolaterally in the images - or all these vertebrae have been reversed during disarticulation?

"As in stemward avialans and non-avialan theropods^{12,52}, the ulna is shorter than the humerus"

>>Very slightly shorter only (add 'slightly' to text).

"The ulna is bowed, rather than being straight"

>>The ulna is close to being straight. It is only weakly bowed. Consider adding the word 'weakly'

"The robust radius measure around 90% of the width of the ulna, comparable to that of basal theropods; whereas the bone is relatively slender in other paravians^{5,15,54,55}."

>>The radius diameter seems similar in Anchiornis (Rui et al 2017)

"We tentatively interpret the ungual that articulates with the shortest phalanx as III-4 (Fig. 1b)".

>>Please explain the evidence for this. It is an isolated phalanx + ungual phalanx, not connected to other elements.

"The ventral margin of the preacetabular process is deeply concave, as in Cratonavis and some enantiornithines⁴³, contrasting with the straight form seen in Archaeopteryx and Jeholornis²²"

>>But also similar to Anchiornis (Hu et al 2009; Rui et al 2017)

"The postacetabular process narrows posteriorly, lacking the ventral deflection that is present in Anchiornis and some dromaeosaurids⁴⁸"

>>These seem similar to me. Rui et al (2017, fig. 18) show the ilium of Anchiornis, with the dorsal margin sloping down the page. But if you rotate it so the dorsal margin is horizontal, then the outline of the posterior margin is fairly similar to that shown here in the new specimen.

"The pubic peduncle is anteroposteriorly wider than the ischiatic peduncle"

>>I agree that this differs from e.g. Anchiornis.

"The calcaneus and astragalus are unfused with one another or the tibia. In contrast to what is observed in most other Jurassic avialans and non-avian paravians¹⁸"

>>Could be more specific about which taxa. They are unfused in Anchiornis and Archaeopteryx.

"The metatarsus measures approximately 63% of the length of the femur, much shorter than in other stem avialans in which the length ratio is greater than 0.8"

>>I measured images from four individuals referred to Anchiornis, from Hu et al (2009) and Rui et al (2017). The ratio was 0.81 in BMNHC PH822, 0.78 in BMNHC PH804, 0.69 in PKUP V1068, and 0.675 in LPM-B00169. The last two aren't very different to the ratio in the new specimen (0.631). I don't know what explains the variation among measurements of individuals referred to Anchiornis. But the similarity of some of them to the specimen here seems important and is consistent with the hypothesis that this is related to Anchiornis or otherwise belongs outside of Avialae.

>>Note that when I confirmed the measurements of the current ms, but measuring Fig. 1, I found that the scale bar was incorrect. Maybe it is a 20 mm scale bar and not a 10 mm scale bar.

>>In the statement "much shorter than stem avialans", I don't know which taxa are considered to be stem avialans, either (1) non-avian stem birds (i.e. excluding e.g. Archaeopteryx) or just early members of Avialae (i.e. including Archaeopteryx).

"The metatarsals are not ginglymoid"

>>I'm looking at ED Fig. 6. I agree that it doesn't look ginglymoid. But how sure can you be, given the style of preservation? Please indicate in the text.

"Presence of deinonychosaurs-like digit II phalanges in Archaeopteryx, Xiaotingia, and Anchiornis was acknowledged in earlier studies^{42,50,53} but called into question by recent work²²"

>>As-phrased, it isn't clear whether the authors are saying that a large pedal claw was present in these taxa, or not. They show a large pedal claw in their skeletal reconstruction of the new taxon (ED Fig. 1). But no such claw is actually preserved. The presence of a large claw, and the hyper extensible nature of the claw, seem to be independent of each other. For example, it is possible that a hyper extensible digit is present but has a regular-sized claw, as in Xiaotingia (see below).

>>In Xiaotingia, Xu et al (2011). The claw is not enlarged, but is proposed as being hyper extensible based on the following anatomy: "The second pedal digit is similar to those of Archaeopteryx¹⁶ (Fig. 3h), Anchiornis⁵ and other deinonychosaurs in having a prominent dorsal expansion and a dorsally located lateral collateral ligament fossa at the distal ends of both phalanx II-1 and phalanx II-2 (Fig. 2e), indicating that the second digit was highly extensible."

Morphometric analyses

"Yuezhornis exhibits features relating to terrestrial adaptation (e.g., short forelimb, and extensible pedal digits)..."

>>The forelimb:hindlimb length ratio, based on the dataset provided here, is 0.67 in the new taxon, and 0.69 in Anchiornis, and 0.73 in Microraptor. This is clear in Fig. 4 here. Those are very similar numbers. So I'm not convinced that this is a secondarily flightless animals instead of representing the general condition for some early paravians with some kinds of volant behaviours. That depends partly on its phylogenetic position.

>>The analyses presented seem to examine only the proportions -within- the forelimb.

"Yuezhornis compares favorably with some flightless pheasants (Francolinus afer and Crossoptilon crossoptilon) in limb proportions..."

>>It isn't really correct to call these pheasants 'flightless'. They are burst flyers, that lack the ability for sustained flight. Nevertheless, they can fly. Their form of flight is very derived and is unlikely to be present in the earliest paravians. I don't think they are appropriate comparisons.

"Forelimb elongation has been viewed as the major skeletal modification across the dinosaur-bird transition^{3,8,72}, with the fundamental flight-adapted limb proportions (forelimb longer than hindlimb) acquired before the origin of avialans^{9,52,73}.

However, contrasting with all the other early avialans (Supplementary Table 2), in *Yuezhornis* the forelimb is shorter than the hindlimb, and the humerus is shorter than the femur"

>>If we accept that *Yuezhornis* is secondarily flightless, for the moment, that does not contradict the idea that forelimb elongation was invalid in bird origins. So the statement here, as written, seems misleading.

"...The results reveal that *Yuezhornis* has prominently short forelimb and humerus (only longer than the flightless ornithomorph *Patagopteryx* among Mesozoic paravians), even shorter than some fast-running dromaeosaurids such as *Bambiraptor* and *Buitreraptor*"

>>We don't actually know that those animals (e.g. *Bambiraptor*) were flightless, strictly speaking. We guess this, but don't observe it directly. Comparisons with *Anchiornis* and *Microraptor* seem more relevant (see above).

"Both morphometric analyses and focal features (e.g., wide interclavicular angle, reduced deltopectoral crest, and short forelimb) strongly indicate that *Yuezhornis* was flightless and adapted to terrestrial environments"

>>These are potential indicators of flightlessness, but these aspects are also consistent with the anatomy of some volant non-avian paravians. Note that the authors say, later in their discussion: "Recent studies suggested powered flight capability for anchiornithines and other early avialans". If *Anchiornis* is considered to have powered flight then the anatomy of *Yuezhornis* does not rule it out either.

Referee #3

(Remarks to the Author)

This intriguing paper describes what is purported to be a Jurassic-aged flightless bird, and thus the oldest flightless bird in the fossil record. It is a big and exciting claim. Unfortunately, I think the authors have not demonstrated a strong case.

The fossil itself is important and well worthy of publication. It is a new derived theropod (paravian) from the Zhenghe Fauna of China, one of the most exciting new fossil sites. For the first time, this site is preserving a range of Jurassic small theropods, including early birds like *Bambiraptor*. It is our best window into the diversity of the first birds and their close theropod relatives, from around the time that these dinosaurs were first flying. Undoubtedly this new fossil is an important new record, and its diagnosis as a new species is strong. And I completely agree with the authors that this was not a flying animal. The arms are simply too short to have supported a wing big enough to fly, plus features of the shoulder girdle and furcula also seem too 'primitive' for a flying animal.

What I am not convinced of is that it is a flightless bird. Let me unpack what that means. If it were a flightless bird, that means that: 1) it is a member of the clade Avialae (the 'bird' clade capable of powered flapping flight: *Archaeopteryx* + modern birds) and more derived than *Archaeopteryx*; 2) it evolved from flying ancestors. I think neither of these things is clear.

First, I will note that the authors have not attempted to make a case based on the anatomy that this specimen has characteristic features of the arms, chest, and other body regions seen in modern birds (or fossil birds) that have lost flight. There is an enormous literature on flightlessness in birds, and how the skeleton has been modified as birds give up the flight of their volant ancestors. Flight has been lost repeatedly in birds, and there are commonalities to how this happens. At a minimum, this literature must be engaged with. The authors need to show that this new fossil has hallmarks of the ways in which birds are known to lose flight. As it stands, to me, this skeleton looks remarkably similar to many dromaeosaurids and troodontids—it looks like what I would expect for a small Jurassic theropod close to the origin of Avialae, but not yet past that threshold of powered flapping flight. I don't see anything obvious that indicates that it had ancestors that once flew. More than anything, the arm looks like a normal dromaeosaurid or troodontid arm to me, and nothing like the highly modified arms of 'ratites' or various extinct birds that evolved from flying ancestors.

What the authors have done is shown that the limb proportions, especially of the forelimb, fall within the range of terrestrial birds. But this is to be expected of any non-flying close relative of avialans, and indeed is the case for dromaeosaurids and troodontids in their dataset. Also, there is something of a linguistic sleight of hand in the manuscript: the authors regularly talk about how the skeleton has features of 'terrestrial birds' and use this somewhat synonymously with 'flightless bird.' These are different things. There are plenty of birds today that spend much time on the ground and have limbs (particularly the hindlimbs) suited for this lifestyle. In their plots, especially in figure 3, the authors need to make clear which modern birds are totally flightless and which simply spend much time in a terrestrial setting

Because the authors have not based their interpretations on flightless anatomy in the specimen, their story hinges entirely on the phylogenetic placement of this new species, which they find within Avialae, slightly more derived than *Archaeopteryx*: one node up, 'in between' *Archaeopteryx* and all more derived birds. They find this result with both parsimony and Bayesian analysis of a suitable dataset. However, it is not clear how strongly supported this result is. The relationships of the earliest avialans and their closest paravian relatives (dromaeosaurids, troodontids, anchiornithids) are notoriously labile, and in alternative analyses these branches regularly move around—sometimes even when adding a single new specimen to an often-used dataset, such as the TWiG dataset the authors are using. Let's play devil's advocate, and say that the new species moved one node basally. Then it would be out of the *Archaeopteryx* + modern bird clade. Out of the clade of unequivocal volant flapping birds. And just another small bird-like paravian in the troodontid and dromaeosaurid zone.

Thus, everything hinges on those features that place the new species as more derived than *Archaeopteryx*. And I'm not clear

what those features are. They need to be front and center in this manuscript. In the discussion, the authors note two features that place the new species in the Archaeopteryx + modern bird clade—which seems like very weak support when we know the positions of taxa in this part of the tree are so labile. But, even if this is strongly supported, those features might just tell us that the new species groups with Archaeopteryx and modern birds in a more inclusive clade. What we need to know is those features that place the new species more derived than Archaeopteryx—in a unique relationship with the lineage that led to modern birds.

And, here I will raise another troubling point: even if the phylogenetic analysis in the paper is correct, and the new species is more derived than Archaeopteryx, and positioned between Archaeopteryx and the clade of more derived avialans, that might mean that it lost flight from an Archaeopteryx-like ancestor. But: there would be an equally parsimonious scenario: the ancestor of all of these animals was not a flier, and Archaeopteryx developed flight independently than all other avialans, and then the clade of birds more derived than the new species evolved flight on its own. In this scenario, the new species would not have evolved from a flying ancestor and would not have lost flight. This is why it is critical to not simply rely on the results of a phylogenetic analysis to make a big claim about flightlessness, but to document features of the anatomy that independently support evolution from a flying ancestor.

When it comes down to it, this new species is incredibly similar in anatomy to dromaeosaurids, troodontids, and anchiornithids. The authors themselves acknowledge this repeatedly throughout the manuscript. If all you had of this animal was the skull, then you would surely think it was a deinonychosaur (troodontid/dromaeosaurid), and probably a troodontid. I'm pretty confident that a phylogenetic analysis would position it there too—if all we had was the skull. Also, the ratios of the humerus-femur and forelimb-hindlimb are very similar to deinonychosaurs, and the metatarsus is as well—and it would be very short for an early avialan. Remarkably, the new species has a hyperextensible second pedal digit! That is amazing! Or it would be amazing if it truly was an avialan, more derived than Archaeopteryx. Because this is a classic deinonychosaur feature. And I think, ultimately, a giant red flag: if this species has a classic deinonychosaur feature, then it most likely is a deinonychosaur. I will admit that the pelvis looks quite bird-like, especially the ilium. But: could this just be convergence? As the most detailed similarities are shared with enantiornithines, which are a more derived subgroup of birds—and clearly this new species is not an enantiornithine.

Three other things to note:

- Much of the discussion, and the phylogenetic analysis, relies on another paper not yet published, under review in Science Advances. Really this other paper should be published first, as it is describing another new species that is highly relevant to the arguments in this paper.

- Figure 3—There are so many points and so many colors that it is hard to tell where the other Jurassic paravians (Archaeopteryx, Anchiornis, etc.) fall out in the plots. Please label them with their name and arrow as well, as you've done with Yuezuornis.

- The skeletal reconstruction should be shown in the main paper, not just as a supplementary figure. It's important that readers can immediately see the body proportions, especially the size of the arms versus the legs, without having to wade into the supplement.

In conclusion, I think this is a very interesting new fossil. It is a new species. It is worthy of publication. But I don't think the authors have demonstrated that it is a flightless bird. To do so, they need to make a very robust case that it is more derived phylogenetically than Archaeopteryx, and need to identify features of the skeleton that are hallmarks of flightlessness in birds. And they really need to convince us that it is not a deinonychosaur.

Referee #4

(Remarks to the Author)

A. Summary of Key Results: Liming Xu et al (Nature 2026-02-03370-Jurassic flightless bird reveals early ecological diversity of avialans) provide descriptive/comparative and functional analyses on a new Late Jurassic stem bird, Yuezuornis yangyuanensis, representing another new taxon of early branching avialan from the Zhenghe Fauna (China). The fossil discovery and highlighted anatomical interpretations provide the basis for inferring the occurrence of the first stem bird lineage to realize a flightless ecomorphotype, underscoring rapid ecological diversification among avialans very early in their evolutionary history.

In addition to characterizing those traits shared among early avialans and closely related paravians (allowing an explicit phylogenetic consideration of the new form), the team provides an estimation of body size (@ 821 g), and forelimb/hind limb proportions to establish a general functional/ecological signal related to flightlessness (a key point of the paper).

The occurrence of "deinonychosaurian" characteristics (e.g., dental count, tooth size, tooth shape [blade-like], jugal with reduced QJ process, etc.) combined with mixed avialan/troodontid (e.g., L-shaped quadratojugal lacking a posterior process) OR avialan/dromaeosaurid characteristics (e.g., lacrimal with straight dorsal margin, etc.) continues the trend of anatomical mosaicism that we see among stem birds/paravians (as recently noted in several papers by this research team and others; e.g., Xu et al., A new avialan theropod from an emerging Jurassic terrestrial fauna; Nature 621: doi.org/10.1038/s41586-023-06513-7) and shouldn't be surprising. It is messy (anatomically and phylogenetically) in this part of the paravian tree.

The coauthors provide additional background and context for the new specimen as part of the Zhenghe Fauna, emphasizing both the importance of its temporal occurrence and the broader phylogenetic context of its biota. In sum, this paper presents important new data on early branching avialans from the Late Jurassic, this time emphasizing the possibility of an early avialan exploiting/succeeding in an ecological role related to flightlessness.

Finally, the team closes with a discussion on the significance of the mosaic nature of *Yuezhornis* (e.g., deinonychosaurs-like hyperextensible pedal phalanges, short forelimb, etc.) in the context unique niche utilization by stem (very early stem) avialans. I am not sure that I agree that this challenges the 'traditional notion' that selection for powered flight was the primary force structuring the early avialan Bauplan—more importantly, I think it emphasizes that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of a clade in this one region. In either case, this important datapoint allows us to further consider the morphological range (disparity) of avialans/near-avialans in the Zhenghe Fauna—which is proving to be very interesting.

B. Originality and Significance: This is a very significant new specimen from the Late Jurassic...a time period in avialan history for which there are very few fossils from outside of a handful of locations. The significance of the specimen is apparent, as highlighted by the exhaustive treatment (phylogenetic and functional) given the new fossil.

Again, of note re: mosaicism in another early diverging avialan continues the trend based on discoveries from this region/basin/strata and is not surprising as new fossils are recovered. This does not take away from the impact of this new fossil...and the research diligence and originality provided by the research team is exemplary. Of particular mention here is that the team employs a broad range of phylogenetic, and importantly, functional and comparative analyses (e.g., morphometric, geometric morphometric, phylogenetic comparative) to emphasize the ecological/functional relevance of the new specimen. This is far more interesting than just another new early bird/feathered dinosaur, as has become common place in recent years. Nice work on this front.

The work is original and significant, both for its description and comparative quantitative framework in which the new specimen is presented.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The data (i.e., a new fossil, its descriptive anatomy, and phylogenetic characters associated with it) are clear and represent standard approaches in how the authors have presented them. The phylogenetic approaches (MP for the topologies and Bayesian for the tip dating) employed by the group are now standard, as we have seen in many recent papers.

The anatomical description is appropriately detailed, emphasizing those portions of the skeleton/dentition essential for considering the phylogenetic context of the specimen (and by extension, the ambiguity of traits distributed among paravians).

Finally, the authors have provided repository information and note that access to phylogenetic/morphometric matrices/data/code, etc. are available via FigShare—these are not currently accessible during review.

D. Appropriate use of statistics and treatment of uncertainties: The approaches used by the authors include the typical complement of phylogenetic and morphometric analyses used for fossil data such as those at the focus of the paper. The dual use of both MP and tip-date informed Bayesian Inference analyses are appropriately applied for the morphology-based phylogenetics work, as are the morphometric and geometric morphometric approaches in the context of both ecological/functional characterization. Uncertainty measures for all phylogenetic, morphometric, geometric morphometric, and ecological/functional are appropriately considered.

E. Conclusions: robustness, validity, reliability

The conclusions of this paper are very interesting, and should be easily reproducible for all phylogenetic, geometric morphometric, and phylo comparative purposes. The new fossil is certainly exciting, with a team who has provided the requisite comparative work to highlight its significance.

Two specific things for the team to address:

Lines 302 – 304: This is a fine statement. But is the notably short forelimb a retention of the 'ancestral theropod' condition (as stated here)? Or does this perhaps reflect ecological specialization (i.e., does it reflect homoplasy/reversal) in the context of flightlessness in a form derived from an otherwise flight capable group of early branching avialans? I appreciate early ecological specialization (implying flightlessness, and presumably morphologies indicative of such) could be either derived or potentially retentions). How do we differentiate between the possibilities? Can we?

Lines 730 -732: The result shows the phalanx of IVPP 730 V34427 can be referred into deinonychosaurs-1 morphotype with a probability of 95%, 731 whereas its assignment to other morphotypes is highly unlikely ($p < 2\%$). So, does this represent additional evidence for retention of a deinonychosaurian feature? Homoplasy? Or does it represent homology (and group belonging for IVPP V34427 as a deinonychosaurian, rather than an avialan)? To which characters do you give the most weight? This is something for the team to further consider and discuss in the revision.

F. Suggested Improvements/Line Edits:

In addition to the points raised above concerning the amount of detailed anatomy in the main text, I have noted several line-specific edits below.

General Comments:

Anatomical nomenclature: The anatomical description is well written throughout most of the manuscript (see a few minor suggestions/edits below). However, the use of single (vs. plural) for anatomical structures could be used throughout (e.g., prezygapophysis vs. prezygapophyses; Lines 137 – 141), but I'll leave that decision to the editorial team. Also, hindlimb could be changed to hind limb throughout.

Bold Paragraph

Lines 36-38 (Bold Paragraph): I don't so much think this discovery challenges a prevailing notion that aerodynamic selection was the determinant force of early avialan evolution—just that this discovery underscores the rapid ecological (and morphological) specialization that early avialans underwent (which is what your next line indicates)...I would delete this sentence.

Main Text

Line 43: Delete the word 'the' before terrestrial

Lines 44-46: alter text as follows: encompassing extensive changes in musculoskeletal and neural systems, epidermal structures, and hypothesized behavioral and physiological adaptations. (This distinguishes morphological systems in which you can observe/derive direct data [e.g., musculoskeletal, neural, and integumentary systems] from inferred behavioral/physiological 'adaptations.'). Also, neurological is derived from neurology—which specifically related to the medical study of the nervous system—just use 'neural' to capture the point you are trying to make.

Line 46: Delete the word 'The' at the beginning of the sentence.

Line 47: Suggested change: Change 'event' to 'transformation' (or series of changes).

Line 48: insert the word 'the' between 'Yet' and 'fossil'

Line 49: Suggested change: "...critical gap in early avialan diversification^{5,6}."

Lines 50-52: Delete the words 'which' (in both cases)...and add '.' after gen.

Line 50: delete "which we named" and just leave *Yuezhurnis yangyuanensis*, gen. et sp. nov.—

Line 50: Add full stop (period) after gen (i.e., gen.)

Line 51: delete the word 'which' after the word 'China' (suggest that you change this to something like...a unit that has yielded some of the oldest avialans....).

Systematic Palaeontology

Line 66: Delete the '.' after et

Line 65: I would delete the fam. nov. designation (as it has no/little biological meaning). It is fine to formalize the *Zhengeornithidae* (but leave it without the Linnean rank designation).

Description

Line 136: change to 'twice as long as high' (re: caudal vertebral

Line 136: Delete 'Their', replace with 'The'

Line 137: Delete 'the' after 'whereas'

Line 139: Length/depth OR length/height? I think the latter is more appropriate.

Line 140: Change 'posteriorly' to 'posterior'

Line 143 - 145:

1st: "ancestral condition" for 'theropod'? Theropoda? Or Neotheropoda? Paravians? Etc. Please be more precise.

2nd: whereas this bone is strut-like in *Baminornis* and more crownward taxa.

Line 145 – 146: Add "a feature that is otherwise only known in *Anchiornis* among theropods⁴⁸.

Lines 143 – 148: Suggest to reorganize to highlight anatomy in the following sequence: Sternum, Furcula, then coracoid.

Line 198: add 's' to 'extend' = 'extends'

Line 225: Add 'A' to beginning of the sentence.

Line 227 – 228: ...it is interspersed within morphospace occupied by extant terrestrial birds.

Lines 233 – 234: Alternative wording suggestion: ...all the other early avialans (Supplementary Table 2), the forelimb in *Yuezhurnis* is shorter than the hind limb, with the humerus also being shorter than the femur.

Line 235: Replace 'applied' with 'conducted'

Line 257: Delete the 's' on deinonychosaurs. (the same suggested edit for Line 263, Line 817 & Line 294 and likely elsewhere throughout MS and SI).

Lines 276 – 277:

1st: Alter the sentence as follows: *Zhengeornithids* further differ from other...

2nd: ...in having a short, robust second metatarsal (or just MT II)

Lines 279 – 280: Despite a closer relationship between *Zhengeornis* and *Yuezhurnis*, the two forms are readily distinguishable from one another, including the presence in *Yuezhurnis* of penultimate manual phalanges with a well-developed hallux, deinonychosaurs-like pedal phalanges, and an elongate tail.

Lines 281 – 282: please clarify the size comparison with specific names.

Lines 288 – 289: change wording to: straight, posterior process of lacrimal (posterodorsally curved in early avialans).

Methods

Line 574: Change 'detail' to 'detailed'

Lines 578 – 579: Suggested change: ...we sampled the right tibial ~mid-shaft for histological analysis.

Lines 590 - 593: Three lines of arrested growth can be recognized in some regions but cannot be traced around the full cross section due to fragmentation of the cortex. Taken together, these features indicate that growth had slowed or ceased entirely at the time of death⁸¹; thus, IVPP V34427 is here interpreted as a subadult or adult.

Line 614: Delete the words 'the' and 'software'.

Line 817: Delete the 's' on deinonychosaurs.

Line 884: PC 3? Or PC 2? Figure indicates PCs 1 and 2.

Figures: The figures in the MS (both main figures and extended data figures) are generally good and convey the main points of the paper. Please double check abbreviations used throughout.

Extended Data Fig 2: More detail on where (anatomically speaking) in the tibia, how the section was developed (see comments on the methods section).

G. References: appropriate credit to previous work
Appropriate references for the paper.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions.
The new specimen is well contextualized through both the opening of the paper (i.e., the bold paragraph), the description (although some of this might be a bit too long for Nature), the discussion, and via the figures. The main theme of the paper is tracked throughout.
The final paragraph of the main text attempts to summarize the importance of this new fossil, emphasizing the ecological significance to the broader audience—this is a very nice change of pace from many standard 'new species' descriptions of Mesozoic birds/avialans.

Supplementary Information Comments:

The SI developed for this paper is adequate for the additional figures, tables, character definitions, and matrix used for the analyses. A more comprehensive differentiation for all Zhenghe fauna paravians would be very useful in the beginning of the SI. I realize that an abbreviation version of this is developed in the methods section...but it is fairly telegraphic and only focused on Yuezhornis and Zhengheornis.

Very nice work. Quite worth of publication in Nature. I look forward to seeing a revised version of this paper.

Patrick O'Connor
Denver Museum of Nature & Science/Ohio University

Version 2:

Reviewer comments:

Referee #1

(Remarks to the Author)

Dear Dr Liming Xu and co-authors,

I feel honored to review your ms about the Yuezhornis, which demonstrates a complex history for the base of avialan diversification. Your second version of the manuscript accepted most of my original concerns, and you kindly responded each one in your kind rebuttal letter.

I am now attaching my second review, which has some new questions and suggestions, but that I trust you will be able to solve easily. My observations are marked in the main text of the manuscript, but are also listed below in this box.

I hope see it finally published in Nature.

Sincerely,

Fernando Novas

- LINES 38-39: "Our study demonstrates that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of birds".

COMMENT: I agree with authors, but I ask whether such pattern also applies to other parts of the phylogenetic tree of Avialae (in other words, it is not unique of the "basal diversification" stage).

- LINES 53-56: Our comparative analyses show that Yuezhornis compares favorably with living terrestrial birds in limb proportions, indicative of terrestrial, flightless lifestyle, shedding new light on ecological diversification of early-diverging avialans.

- COMMENT: I agree with this, but it is reasonable to expect that Yuezhornis ALSO shared similar proportions with the terrestrial non-avian paravians. In fact, all these theropods (INCLUDING early birds) were "terrestrial": they walked on land using similarly constructed hindlimbs. The differences are between volant vs non-volant theropods. By sure Yuezhornis was terrestrial (like other dinosauriforms), but a non-volant bird (an evolutionary reversal).

- LINES 132-133: "The four caudals preserved near the mid-length of the right tibia are twice as long as high."

- COMMENT: This information fits well as part of a text-figure, but here I believe that authors may offer morphological / proportional reasons to indicate the approximate position in the caudal series. After all, saying "caudals preserved close to

the tibia" circumstantially occur only in the holotype specimen, and is not anatomically informative.

- LINES 242-245: "Both morphometric analyses and focal features (e.g., wide interclavicular angle, short coracoid, reduced deltopectoral crest, LONG BONY TAIL, and shortened forelimb) STRONGLY indicate that Yuezhuornis was non-volant, but adapted to terrestrial ENVIRONMENTS."

- COMMENT ON "LONG BONY TAILS": Why? Is it as long/longer than in Archaeopteryx, Microraptor and other early volant paravians? Probably the kind of plumage coat is more important than how long was the bony tail. Please, justify.

- COMMENT ON "STRONGLY": Probably better is to say "congruently indicate", instead of "strongly"

- COMMENT ON "ENVIRONMENTS": Apparently all these paravians lived in a "terrestrial environment" (vs shoreline environment). Let me suggest to say "terrestrial mode of life".

- LINES 246-265: "Phalanx X"

- COMMENTS: If "phalanx X" was preserved as forming part of a complete foot, then no doubts will exist that it is the phalanx II-2. The same identification is obtained by conducting comparisons with available three-dimensionally preserved digits of other paravians, the identity of such isolated pedal bone will be easily solved. Then, first, I still believe that the statistical analysis conducted by the authors is not required (think about applying a statistical method to support the identity that an "isolated femur" is a femur). Second, the positive aspect is that authors demonstrate (through their statistical analysis) the absence of deinonychosaurian features in Archaeopteryx and Anchiornis, modifying previous interpretations. Third, and most important, is the fact that the foot of Yuezhuornis retained the condition of deinonychosaurian digit II. In sum, the statistical analysis allows recognize different shapes of digit II among early avians (a welcome result of the present manuscript), but it is not required to demonstrate that "phalanx X" is a ph. II-2.

- LINES 268-270: "Our phylogenetic analyses consistently recovered Yuezhuornis as the sister taxon to Zhengheornis, and the new clade emerged just crownward of Archaeopteryx as one of the earliest diverging avialans"

- COMMENTS: This is an original and highly interesting result!

- LINES 274-277: "(character state 82.0 in Supplementary information); extensive pubic apron without a slit (character state 179.0); interclavicular angle greater than or equal to 90° (character state 330.0); and distal end of tibia approximately equal to its midshaft in width (character state 421:1)."

- COMMENTS: I understand that authors recovered this list of synapomorphies after their phylogenetic analysis. However, it calls my attention that most of these features are widely present among outgroups of Avialae. For example, "extensive pubic apron" represents an Archosauriformes condition, while a reduction of the pubic apron occurred in the course of pygostilian / ornithothoracine evolution. Regarding ch. 330.0, the condition represents the plesiomorphic one, and it was listed above (line 243) as evidence of the non-volant capabilities of Yuezhuornis, and also on lines 321-322 where it is said that Yuezhuornis exhibits the "ancestral theropod condition" (i.e., interclavicle angle obtuse).

-

- LINE 337: "flight"

- COMMENTS: As it is, the phrase taxatively supports a dual origin of flight, once in Archaeopterygids, and (separately) in Jeholornis+Pygostilia. Probably more appropriate is inserting (also) the alternative hypothesis, the one supporting the loss of flying capabilities in Zhengheornithidae.

Referee #2

(Remarks to the Author)

Ok. Thanks to the authors for cleaning up the manuscript nicely. I'm a lot more convinced now than I was first time around. The study is clearly very interesting. The fossil seems important, and it's nice to know more about the Jurassic radiation of Avialae. For more than a century we relied entirely on Archaeopteryx. This now fossil seems to illuminate an early radiation that we previously knew basically nothing about.

So I recommend acceptance after a few revisions:

Abstract

"The origin and early diversification of birds remain one of the most debated transitions in vertebrate evolution"

>>This is not correct (see my previous review). In your response you said. That you wanted to communicate that there were various things that still remain unknown. That's true and I agree with it. But is not the same as saying "is one of the most debated transitions in vertebrate evolution". I agree that it is important that you emphasise the importance of the work, but also that the words remain scientifically correct. So please rephrase this.

"While macroevolutionary models suggest a Jurassic radiation"

>>"macroevolutionary models" is a little vague. Could you instead say "timescaled phylogenies" or "estimates of the evolutionary timescale".

"Our study demonstrates that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of birds"

>>"Evolution works fast" seems a little informal.

Figures

In the PCA plot (Fig. 3), it would be great to show the morphological changes corresponding to each axis more clearly. Currently they are very tiny and not visible.

Extended Data Fig.1: Please check the measurements on this image compared to the real specimen (Fig. 1). The humerus seems much smaller and more slender in EDF 1 than in Fig. 1. I want to confirm that the true scale is used rigorously.

Referee #3

(Remarks to the Author)

I thank the authors for their revision, and their careful responses to my comments. The paper is now much improved. There is no doubt this is an important new taxon. I agree that this is a flightless paravian close to the origin of Avialae, and although character support for major nodes around Avialae is labile and relationships often change depending on analysis and method, I find that the authors have presented a compelling case that this new taxon is an avialan more crownward than Archaeopteryx. And the authors have certainly presented a compelling case that this animal could not fly. I have no doubt about that. What this comes down to is the importance of the discovery. Initially, I had thought the authors were arguing that this new taxon was the oldest instance of a secondarily flightless bird in the fossil record—a big claim, but if true, a major discovery. Now they have been quite clear in their responses and in the revised manuscript that they did not mean to imply that it was secondarily flightless, only that it didn't fly. In fact, they argue that it never had flying ancestors. And therefore, flight must have evolved multiple times in avialans. But the multiple-origin scenario for flight is well established. It was the subject of a major paper by Pei et al. in 2020 (Current Biology), and over the last decade or so, several Mesozoic paravians have been found to be non-flying species within Avialae or very close to it. It is great that this new fossil supports the multiple-origin scenario. It is probably one of the strongest pieces of new support for the hypothesis. But is that enough for a Nature paper in 2026? I think the paper as written is sound. I don't have any suggestions for further improvement in terms of the writing or framing or anatomical details. If the other referees are strongly supportive of publication in Nature, I would not object. So I leave this in the hands of the editors: the science in this paper is good, the fossil is interesting and important, but it mostly confirms a hypothesis that has been around for quite some time, and is supported by many other lines of evidence.

Referee #4

(Remarks to the Author)

A. Summary of Key Results: Liming Xu et al (Nature 2026-02-03370B-Jurassic flightless bird reveals early ecological diversity of avialans) provide descriptive/comparative and functional analyses on a new Late Jurassic stem bird, *Yuezuornis yangyuanensis*, representing another new taxon of early branching avialan from the Zhenghe Fauna (China).

The team has now completed a revision of the manuscript, addressing the distribution of characters supporting the assignment to Avialae (rather than the substantially longer tree length necessary to assign to Deinonychosauria), along with an extensive 'response to reviewers' following the first round of reviews. To my reading, the authors are supporting assignment to Avialae, fully acknowledging the admixture of character states present in any form from this part of the tree (i.e., they are explicit and acknowledge that rampant mosaicism of traits makes this assignment a challenge for researchers).

As I stated previously, the occurrence of "deinonychosaurian" characteristics (e.g., dental count, tooth size, tooth shape [blade-like], jugal with reduced QJ process, etc.) combined with mixed avialan/troodontid (e.g., L-shaped quadratojugal lacking a posterior process) OR avialan/dromaeosaurid characteristics (e.g., lacrimal with straight dorsal margin, etc.) continues the trend of anatomical mosaicism that we see among stem birds/paravians (as recently noted in several papers by this research team and others; e.g., Xu et al., A new avialan theropod from an emerging Jurassic terrestrial fauna; Nature 621: doi.org/10.1038/s41586-023-06513-7) and shouldn't be surprising. This will continue to be an interestingly challenging part of the paravian/avialan distribution to sort out, even with contemporary approaches in comparative biology/paleontology.

The team retains necessary background and context for *Yuezuornis* (and Zhengheornithidae more generally) as part of the Zhenghe Fauna, emphasizing the significance of the temporal occurrence as critical for de-tangling/elucidating inter-relationships among Jurassic paravians. Again, this paper presents important new data on early branching avialans from the Late Jurassic, this time emphasizing the possibility of an early avialan (or interesting non-avialan paravian?) exploiting/succeeding in an ecological role that differs from other closely related taxa.

B. Originality and Significance: This is a very significant new specimen from the Late Jurassic...a time period in avialan history for which there are very few fossils from outside of a handful of locations. The significance of the specimen is apparent, as highlighted by the exhaustive treatment (phylogenetic and functional) given the new fossil.

The revised manuscript is original and significant, both for its description and comparative quantitative framework in which the new specimen is presented. The revision continues to emphasize the significance of the new specimen...and provides a clearer emphasis on those traits essential for interpreting the specimen. The revision also provides needed clarity on the interpretation of a specimen like this for assignment to Avialae vs. non-avialan paravians.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The data (i.e., a new fossil, its descriptive anatomy, and phylogenetic characters associated with it) are clear and represent standard approaches in how the authors have presented them.

The anatomical description is appropriately detailed, emphasizing those portions of the skeleton/dentition essential for considering the phylogenetic context of the specimen (and by extension, the ambiguity of traits distributed among paravians)

The revision provides a cleaned-up version, continuing to emphasize those parts of the skeleton most relevant for assessing the phylogenetic affinities of the new specimen.

D. From my original review: Appropriate use of statistics and treatment of uncertainties: The approaches used by the authors include the typical complement of phylogenetic and morphometric analyses used for fossil data such as those at the focus of the paper. The dual use of both MP and tip-date informed Bayesian Inference analyses are appropriately applied for the morphology-based phylogenetics work, as are the morphometric and geometric morphometric approaches in the context of both ecological/functional characterization. Uncertainty measures for all phylogenetic, morphometric, geometric morphometric, and ecological/functional are appropriately considered. The revision maintains these analytical approaches.

E. Conclusions: robustness, validity, reliability

The conclusions of this revised paper are very interesting, and should be easily reproducible for all phylogenetic, geometric morphometric, and phylo comparative purposes. The new fossil is certainly exciting, with a team who has provided the requisite comparative work to highlight its significance.

F. Suggested Improvements/Line Edits:

G. References: appropriate credit to previous work

Appropriate references for the paper.

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

The new specimen is well contextualized through both the opening of the revised paper (i.e., the bold paragraph), the description, the discussion, and via the figures. The main theme of the paper is consistent throughout, albeit with more clarity on interpretation in the revised manuscript.

The final paragraph of the main text attempts to summarize the importance of this new fossil, emphasizing the ecological significance to the broader audience—this is a very nice change of pace from many standard 'new species' descriptions of Mesozoic birds/avialans.

Patrick O'Connor

Ohio University/Denver Museum of Nature & Science

Version 3:

Reviewer comments:

Referee #1

(Remarks to the Author)

Dear Editor and Authors,

I have enjoyed by reading and learning the manuscript by Xu et al. describing *Yuezhurnis* and its evolutionary implications. I have pointed out some minor interpretive aspects of the current manuscript (enumerated below) which I trust the authors will be solve or explain easily.

1. Comments on MAIN TEXT

Page 7 – line 131 – Replace “displaced” for “preserved”

Page 7 – line 135 – Modify “indicating that they are located posterior to the transition point” for “indicating that they may correspond to the transition point”

Page 7 – line 142 – Authors say: “The coracoid is trapezoidal (Fig. 2d), an ancestral condition for Theropoda”. Let me suggest apply the term “trapezoidal” (i.e., dorsoventrally deep coracoid, with angled anteroventral margin) for PARAVIAN theropods, in contrast to an elliptical-shaped and dorsoventrally shallower one of non-paravian theropods. In sum, let me suggest replace “an ancestral condition for Theropoda” for “an ancestral condition for Paraves”.

Page 10 – line 206 - Replace “has” for “had”, because the capability to hyperextend the digit was a function / behaviour, which took place when the animal was alive.

Page 11 – line 213. Authors say: “*Yuezhurnis* exhibits features relating to non-volant adaptation (e.g., short forelimb, trapezoidal coracoid...”. Regarding the shape of coracoid as mirroring flying capabilities, I agree that a trapezoidal coracoid is widely present among non-volant paravians (e.g., *Deinonychus*, *Unenlagiids*). However, it is also present in *Microraptor* and *Archaeopteryx*, for which (and due to wing-feather development) most authors agree were volant. Thus, there is no univocal relation between this shape of the coracoid with the flying capabilities.

Page 11 – line 213. Authors say: “*Yuezhurnis* exhibits features relating to non-volant adaptation (e.g ...extensible pedal

digits)". I am unable to tie flying capabilities with "extensible pedal digits". Please, explain.

Page 16 – lines 317-318. Authors say: "The pectoral girdle and forelimb of Yuezhuornis exhibit the ancestral theropod condition". Let me suggest replacing "theropod condition" for "paravian condition".

Page 16 – line 333. Let me suggest replacing "... slightly younger than..." for "... slightly geologically younger than..."

2. Comments on SUPPLEMENTARY INFORMATION

Page 1. Author say: "The coracoid is trapezoidal, a feature widely distributed among non-avian theropods". In my view, the trapezoidal condition applies for Paraves, but not for non-paravian theropods. Besides, a trapezoid-shaped coracoid is present in the early avian Archaeopteryx. Thus, let me recommend saying that the feature is "widely distributed among early paravian theropods".

Page 1. Authors say: "A trapezoidal-shaped coracoid independently evolved in anchiornithines and the Cretaceous avian Sapeornis". I am surprised for this statement, because a trapezoid-shaped coracoid is present in dromaeosaurids, unenlagiids, troodontids, Archaeopteryx, Anchiornis, Yuezhuornis, Confuciusornis and Sapeornis, and the only exception (among basal Avialae) is currently Jeholornis. Then, alternative hypothesis that "a strut-like coracoid evolved once in Jeholornis and once in Ornithothoraces" probably results more appropriate.

3. Comments on FIGURE 1 (EXTENDED DATA):

Please, review drawing because the knee seems dislocated (femoral distal condyles are anteriorly displaced respect to proximal end of tibia).

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In cases where reviewers are anonymous, credit should be given to 'Anonymous Referee' and the source.

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Dear Dr. Henry Gee,

We thank you, Drs. Fernando Novas, Patrick O'Connor, and two anonymous reviewers for their detailed and constructive comments, which have significantly improved the manuscript. More importantly, the questions raised by the reviewers are truly inspiring, which enable us to further dig into this bizarre specimen. We have submitted a revised version of our manuscript, figures, and Supplementary information, in which we have addressed your comments and those of the reviewers. Please find below our detailed response on the remarks of each reviewer. In order to be specific, all comments of each reviewer are listed and explained one by one.

Response to Dr. Fernando Novas:

First, we are truly grateful to Dr. Novas for constructive comments and particularly providing an annotated PDF.

1. I have read with attention the manuscript about the newly discovered *Yuezhurnis*, and I must say that the anatomical evidence afforded for the specimen is not convincing enough for its location as a basal avialan more derived than *Archaeopteryx*. As you correctly expose in the manuscript, the new taxon exhibits troodontid features in the skull and dentition, in joint with plesiomorphic proportions in the forelimb bones, plesiomorphic shape of coracoid, and several pelvic and hindlimb features that are widely present in several paravian taxa close to the Avialae node. Of course, you also introduce the existence of a new, yet-unpublished avialan taxon, which seems closely related to *Yuezhurnis*, and this fact may lend support to the avialan affiliation you advocate for *Yuezhurnis*.

Response: We thank Dr. Novas for these comments. Frankly speaking, we thought this specimen was a troodontid at the very beginning. While, after detailed observation, comparison, and phylogenetic analyses, especially taking your and other reviewers' comments into consideration, we re-conducted morphological and phylogenetic analyses. The results still support that *Yuezhurnis* is an avialan and it is derived than

Archaeopteryx. Meanwhile, the manuscript that describes the other new species *Zhengheornis* (sister taxon to *Yuezhurnis*) has been accepted and in press status now.

For morphological comparison: *Yuzhuornis* exhibits several derived cranial features that speak clearly to its avialan affinity, such as slender cranial elements (e.g., jugal, postorbital, and dentary), whereas these elements are much robust in troodontids and dromaeosaurids. The T-shaped lacrimal has a short anterior process, as in some Cretaceous avialans such as *Jeholornis* and enantiornithines (O'Connor and Chiappe, 2011; Hu et al., 2022). By contrast, in most troodontids and dromaeosaurids, the anterior process is much longer than the posterior process (Xu and Wu, 2001; Turner et al., 2012; Yin et al., 2018). Like early avialans, the T-shaped postorbital has three rod-like slender processes, contrasting to the strap-like form that is seen in non-avialan paravians. As in *Archaeopteryx* and other early avialans, the middle and posterior maxillary teeth are sparsely spaced, contrasting to the closely packed condition in troodontids. The slender dentary has parallel dorsal and ventral margins, as in *Archaeopteryx* and more crownward avialans. By contrast, the bone is stout and triangular in lateral view in most non-avialan paravians such as *Xiaotingia*, *Caihong*, and *Linheraptor* (Currie, 1995; Xu et al., 2011, 2015). Anchiornithines, troodontids, and dromaeosaurids typically have a deep lateral dentary groove that widens posteriorly (Agnolin et al., 2019; Xu et al., 2011), but this groove is absent in *Yuezhurnis* and other avialans.

Yuezhurnis also exhibits features in postcranial elements that support its avialan affinity. Specifically, the prezygapophyses and postzygapophyses of posterior caudal vertebrae are short, rather than being markedly elongate as in troodontids and dromaeosaurids. The ilium is readily distinguishable from that of troodontids and dromaeosaurids in having a preacetabular process that is convex cranially and markedly longer than the postacetabular process; whereas the pre- and postacetabular processes are subequal in length in *Anchiornis* and most deinonychosaurs (Extended Data Fig. 5; Rhodes et al., 2021; Turner et al., 2012). As in avialans such as *Xiaotingia* and *Fujianvenator*, and some unenlagiids (Agnolin et al., 2019), the preacetabular process is anteriorly convex, rather than being straight as in some troodontids or concave as in

Anchiornis and some dromaeosaurids (Xu et al., 2009; Hwang et al., 2002). Overall, the ilium is dorsoventrally narrow and anteroposteriorly long, contrasting with the short and deep form seen in non-avian paravians, including *Unenlagia* (Agnolin et al., 2019). The right and left fibulae are preserved in *Yuezhornis*. The left fibula was cut by a crack along its mid-length. However, the combined length of the proximal and distal parts of the left fibula is equal to the right fibula (the latter is completely preserved here). The distal end of the left fibula is complete and fully exposed (see Extended Data Fig. 6c), showing that preserved morphology of its distal extremity is genuine. All these observations show that the length of the fibula is not biased by preservation, and the fibula is much shorter than the tibia. The fibula rapidly tapers distally to a splint-like end, which terminates far proximal to the distal end of the tibia. This is a derived condition of avialans that is widely distributed among Cretaceous avialans (O'Connor, 2009; Botelho et al., 2016). By contrast, the fibula reaches the proximal tarsals in deinonychosaurs (Botelho et al., 2016), anchiornithines (Pei et al., 2017), and *Archaeopteryx* (Rauhut et al., 2018; O'Connor et al., 2025). Lastly, unlike troodontids and dromaeosaurids (Makovicky and Norell, 2004; Norell and Makovicky, 2004; Turner, 2012; Novas et al., 2018), the foot is non-archimetatarsal, a typical condition of avialans.

To explore the phylogenetic position of *Yuezhornis*, we performed both maximum parsimony and Bayesian tip-dating analyses. The maximum parsimony analysis was performed using TNT package implementing both equal weights (EW) and implied weighting methods (IW). Both EW and IW analyses recovered *Yuezhornis* as sister taxon to *Zhengheornis*, and the new clade constitutes the outgroup of other avialans except *Archaeopteryx* (Extended Data Figs. 8-10, Supplementary Fig. 1)

Given the presence of deinonychosaur-like traits, we further evaluated alternative phylogenetic position of *Yuezhornis*. A constrain was applied, which forced *Yuezhornis*, troodontids, and dromaeosaurids as a monophyly, and *Yuezhornis* to be an outgroup of avialans. The constrain-induced topology is far less parsimonious (**14 steps longer** than the most parsimonious trees obtained without the constrain); and a **negative Bremer support value (-13)** was recovered to support the clade uniting

Yuezhurnis and Deinonychosauria (Supplementary Fig. 2).

Our Bayesian tip-dating analysis also recovered *Yuezhurnis* as an avialan, a result consistent with the topology obtained using parsimony analysis. Given the comprehensive morphological comparison (lacking key diagnostic features of troodontids and dromaeosaurids) and phylogenetic analyses that incorporates different analytical methods (equal weights, implied weighting, constrain search, and Bayesian tip-dating), we suggest that the avialan affinity of *Yuezhurnis* is much better supported by all the evidence available, and a deinonychosaurian affinity of *Yuezhurnis* is highly unlikely. We have revised the Discussion section and added additional morphological comparison (“*Yuezhurnis* compared with other paravian theropods”) in the supplementary information.

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- Rauhut, O. W., C. Foth, and H. Tischlinger. 2018. The oldest *Archaeopteryx* (Theropoda: Avialae): a new specimen from the Kimmeridgian/Tithonian boundary of Schamhaupten, Bavaria. PeerJ 6:e4191.
- Rhodes, M. M., D. M. Henderson, and P. J. Currie. 2021. Maniraptoran pelvic musculature highlights evolutionary patterns in theropod locomotion on the line to birds. PeerJ 9:e10855.
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- Yin, Y., R. Pei, and C. Zhou. 2018. Cranial morphology of *Sinovenator changii* (Theropoda: Troodontidae) on the new material from the Yixian Formation of western Liaoning, China. PeerJ 6:e4977.

2. This is right, but it is more appropriate for the present discussion citing that such condition is widespread among non-avian theropods. Afterall, authors must demonstrate that *Yuezhornis* is a "flightless bird" rather than a "flightless basal paravian with avian like features".

Response: Yes, we revised this paragraph accordingly.

3. Since the beginning of the manuscript, authors advocate (before exposing reasons for that) that *Yuezhornis* is a bird. However, the short forelimbs immediately open doubts if the new taxon is not a bird, but a basal paravian with avialan characteristics (currently plenty of examples like this).

Response: Please find our response above. Based on morphological comparison and phylogenetic analyses, we suggest that *Yuezhornis* belong to the Avialae.

4. But this does not warrant that it is a bird (a member of Avialae)

Response: Yes, we agree. Similar limb proportion does not suggest close affinity on its

own. Here, we just pointed it out that *Yuezhornis* has comparable limb proportions to terrestrial living birds.

5. I don't understand why the humerus is listed here, separately from "forelimb one-third shorter than hindlimb", when both form part of a same feature (i.e., limb proportions).

Response: The humerus is shorter than the femur, a typical condition in non-avian theropods, but the opposite is true in avialans. The condition that forelimb is shorter than the hindlimb does not equal to the condition that humerus is shorter than the femur. For example, in *Fujianvenator*, the humerus is much longer than the femur, but the hindlimb is longer than the forelimb.

6. Line 143: theropods (plural).

Response: Yes, we corrected.

7. The coracoid of the Patagonian alvarezsaurid *Bonapartenykus ultimus* exhibits a pattern of well-marked grooves on its outer surface (see Agnolín et al., 2012. New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs. *Cretaceous Research* 35: 33-56).

Response: We thank the Reviewer for this comment. Yes, we have revised this paragraph.

8. Aside for the possible separation between both pubes in *Unenlagia*, and the very narrow, slit like perforation present in *Buitreraptor*, these unenlagiids shows a similar condition of pubic apron to *Yuezhornis*.

Response: Yes, we agree and have revised this. This comment adds to the list of

evidence that convergence is not that rare among paravians, as we argued in the manuscript.

9. The same applies to *Unenlagia*.

Response: Yes, we have revised this accordingly.

10. The ilium of *Yuezhornis* fits well among paravians close to Avialae as well as early avialans. However, I don't see why it is especially comparable with Enantiornithes.

Response: In *Yuezhornis*, the ilium is dorsoventrally narrow and anteroposteriorly long, contrasting with many non-avian paravians, and some early avialans such as *Sapeornis*. Meanwhile, the preacetabular process is much longer than the postacetabular process, which is subequal in many non-avian paravians. As in avialans, the anterior margin of the ilium is convex, but it is concave in *Anchiornis* and some dromaeosaurids such as *Microraptor*, and in troodontids it is nearly straight. We have removed the sentence that highlights its resemblance with enantiornithines.

11. I highly recommend improving the definition of the available images with the aim to understand better the morphology of the distal end of fibula and (if possible) proximal surface of calcaneum. In other words, authors must demonstrate that the fibula is anatomically shorter, and not broken due postmortem distortion.

Response: Yes, we thank the reviewer for this comment, and have revised the corresponding figures. We added a detail figure that show the distal extremity of the left fibula in Extended Data Fig. 6c. The right and left fibulae are preserved in *Yuezhornis*. The left fibula was cut by a crack along its mid-length. However, the combined length of the proximal and distal parts of the left fibula is equal to the right fibula (the latter is completely preserved here). The distal end of the left fibula is complete and fully exposed (see Extended Data Fig. 6c), showing that preserved

morphology of its distal extremity is genuine. All these observations show that the measurement of the fibula is not biased by preservation, and the fibula is much shorter than the tibia. The fibula rapidly tapers distally to a splint-like end, which terminates far proximal to the distal end of the tibia.

12. Line: Replace "expect" for "except"

Response: Yes, corrected.

13. I recommend quantifying the degree of "pinching", because it varies among paravians.

Response: We thank the reviewer for this comment. Following previous studies, it is generally classified into three types: arctometatarsal, sub- arctometatarsal, and non-arctometatarsal. It is clearly that metatarsal III is fully exposed anteriorly along its full length, showing that the foot is non-arctometatarsal.

14. Illustrated pedal phalanx matches well with pedal ph.2.II of paravians (e.g., *Deinonychus*, *Neuquenraptor*) in bearing a prominent posteroventral heel, proximally exceeding the level of the posterodorsal lip. Phalanx 1.II does not exhibit such features, and proximal end depicts a uniform circled outline with both proximodorsal and proximoventral lips equally extended proximally. In sum, pedal "phalanx X" is, not doubt, a ph.2.II. That implies that discussions and analyses about this pedal element have to be considerably shortened.

Response: We agree with the reviewer that the disarticulated phalanx (here referred to 'phalanx X') matches well with pedal phalanx II-2 of deinonychosaurs. While, for colleagues that are not specialized in or familiarly with pedal morphology of theropods, it could be challenging to argue its affinity just based on morphological comparison. For instance, previous studies (e.g., Xu et al., 2011) suggest deinonychosaur-like II-2

in *Archaeopteryx* and *Anchiornis* based on morphological observation. To substantiate this conclusion, we utilized geometric morphometrical analyses to explore the affinity of 'phalanx X' across broad sample of paravian phalanges sample. Our result not only supports the presence of deinonychosaur-like II-2 in *Yuezhornis*, but also points out that II-2 of *Archaeopteryx* and *Anchiornis* is more comparable to that of avialans rather than deinonychosaurs.

Reference:

Xu, X., H. You, K. Du, and F. Han. 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475:465-470.

15. Without dismissing this conclusion, comparisons have to be made with closely related, flightless basal paravians. Authors have to take into account that they didn't demonstrate (up to this part of their manuscript) that *Yuezhornis* is a bird and not a non-avian paravian.

Response: We agree with the reviewer that comparison should be made with other basal paravians. Therefore, we included the Jurassic basal paravians *Caihong*, *Anchiornis*, *Fujianvenator*, and *Archaeopteryx* in the forelimb and hind limb comparison. We have denoted these taxa in the revised Figure 3a.

16. Again, and typical of many non-avian theropods.

Response: Yes, we have added this content.

17. in my view, this long paragraph can be considerably shortened or removed, because "phalanx X" can be easily identified as pedal digit 2.II. Notably, authors arrive to this conclusion, and --most important-- the identification of such phalanx doesn't modify neither the phylogenetic allocation (either *Yuezhornis* being an avialan or a non-avian paravian), nor the ecological interpretation (it was a flightless paravian, of

terrestrial habits).

Response: We are delighted that review agreed with our identification of this disarticulated phalanx. While, as we explained above, we want to substantiate this conclusion based on both morphological comparison and statistical analyses. Also, our finding that a deinonychosaur-like pedal II-2 is absent in *Archaeopteryx* and *Anchiornis* is also meaningful, showing that a statistical analyses should also be considered in future studies.

18. Line 267: "consistently" instead of "uniformly"?

Response: Yes, corrected.

19. Authors present the discovery of a paravian theropod which they recover as a bird more derived than *Archaeopteryx*. However, I am worried that just two features were identified in support of this assertion, and that such features consist in subtle distinctions among paravians. At least pubes that meet extensively medially is present in the unenlagiid *Buitreraptor* and the troodontid *Jianianhualong*, and tibiae slightly expanded distally is a condition documented in many gracile paravians. It seems contradictory that *Yuezhornis*, which depicts several troodontid-like characters in the skull, and that are in tandem with proportionally short forelimbs (constituting the plesiomorphic condition for paravians), result as a bird more derived than *Archaeopteryx*. Let me encourage the authors to expose their reasons for interpreting *Yuezhornis* as not a troodontid nor a dromaeosaur.

Response: Yes, we agree with the reviewer that the new specimen indeed exhibits some features shared with troodontids and dromaeosaurids. However, many diagnostic features of troodontids and dromaeosaurids are absent in *Yuezhornis*, such as the elongate anterior process of the lacrimal, strap-like processes of the lacrimal, well-developed quadratojugal process of the jugal, a robust dentary with a lateral groove that

widens posteriorly, closely packed middle and posterior maxillary teeth, elongate prezygapophyses and postzygapophyses of posterior caudals, and the sub- or arctometatarsal foot. Meanwhile, *Yuezhaoornis* exhibits several derived cranial features that speak clearly to its avialan affinity such as slender cranial elements (e.g., jugal, postorbital, and dentary), short anterior process of lacrimal sparsely spaced middle and posterior maxillary teeth, fewer dentary teeth, reduced zygopophyses of posterior caudals, elongate preacetabular ilium, short fibula, reduced fifth metatarsal, and non-arctometatarsal foot. Our phylogenetic analyses using different methods (maximum parsimony using equal weight and implied weighting, Bayesian tip-dating), and a constrain search (forcing *Yuezhaoornis* as a deinonychosaurs), consistently supports its referral to the Avialae. We have extensively revised the manuscript to strengthen our conclusion and added additional content in the supplementary information (see “*Yuezhaoornis* compared with other paravian theropods” section).

20. Could you quantify the development of this crest? Regarding the humerus of *Yuezhaoornis* (and the remaining forelimb bones), no good images are provided, neither comparative drawings with other paravians.

Response: We mean the deltopectoral crest is poorly developed, much narrower than the humeral shaft. A line drawing of the humerus can be found in Fig. 1a.

21. Line 294: Remove "s"

295: Let me suggest "recognized / identified" rather than "captured"

303: Before in the present manuscript, the coracoid is described as "trapezoidal". Please, choose the best option

305: Sincerely, I cannot identify features uniting the ilium of *Yuezhaoornis* preferently with enantiornithines

309: Remove "s"

310: Remove "s"

317: "extraordinary"?

Response: We thank the Reviewer for this detail comments, and all these mistakes have been corrected.

22. Motta and co-authors (Motta et al. 2025. Phylogenetic relationships of Unenlagiidae among Paraves) criticized results of the TWG matrix, and investigated different alternatives for phylogenetic relationships among paravian theropods. Although I am not indicating that current authors must employ Motta et al. 's views, it could be convenient express (somewhere in the text) that other options about troodontid relationships are possible.

Response: Yes, we agree with Dr. Novas that the phylogenetic relationships among early-diverging paravians is debated. Recent studies (e.g., Agnolín and Motta et al., 2019; Gianechini et al., 2018) suggest different hypotheses. We have specified these alternative phylogenetic relationships and cited relevant references in the manuscript (see Discussion section).

References:

- Agnolín, F. L., M. J. Motta, F. Brissón Egli, G. Lo Coco, and F. E. Novas. 2019. Paravian phylogeny and the dinosaur-bird transition: an overview. *Frontiers in Earth Science* 6.
- Gianechini, F. A., P. J. Makovicky, S. Apesteguía, and I. Cerda. 2018. Postcranial skeletal anatomy of the holotype and referred specimens of *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín 2005 (Theropoda, Dromaeosauridae), from the Late Cretaceous of Patagonia. *PeerJ* 6:e4558.

23. These extinct taxa are members of Avialae (except for *Caihong*, depending on authors). Did you include taxa of non-avialan paravians? I will say, a prior, that *Yuezuornis* will fall close to many of the latter taxa

Response: In the phylogenetic comparative analyses of forelimb evolution, we included a broad sample of non-avian and Mesozoic avian theropods.

24. I believe this analysis is unnecessary.

Response: As we explained in previous comments, a statistical analyses could help explore the affinity of this phalanx.

25. If it is a left tibia (which I agree), then the bone is exposed in posterior view. That means that we are unable to observe the anterolateral facet for reception of the fibular shaft. I am not telling that the fibula is as long as the tibia, but that evidence is not clear enough to support that the fibula was distally reduced. Also, the shape of proximal end of the calcaneum may offer some evidence about if was in articulation or not with the fibula.

Response: We think this fibula is the left one, and it is exposed anteriorly. We added a detail figure that show the distal extremity of the left fibula in Extended Data Fig. 6c. The right and left fibulae are preserved in *Yuezhornis*. The left fibula was cut by a crack along its mid-length. However, the combined length of the proximal and distal parts of the left fibula is equal to the right fibula (the latter is completely preserved here). The distal end of the left fibula is complete and fully exposed (see Extended Data Fig. 6c), showing that preserved morphology of its distal extremity is genuine. All these observations show that the measurement of the fibula is not biased by preservation, and the fibula is much shorter than the tibia. The fibula rapidly tapers distally to a splint-like end, which terminates far proximal to the distal end of the tibia.

26. About Figure 2. I ask the authors to insert a better image of the coracoid, as well as a line drawing clarifying the outline of the bone. This bone also deserves better comparative figures with selected coracoids of other basal paravians, with the aim to visualize if it fits within the derived kind of basal birds (*Archaeopteryx*) or within the

less derived, more rounded one of other non-avian theropods.

Why this figure of an isolated pedal phalanx is so large?

Response: Yes, we have added a line drawing of the coracoid in the revised figure. The isolated pedal phalanx is a diagnostic feature of this new fossil, and we intended to show its deinonychosaur-like morphology here.

27. About Extended Data Fig. 1. I have counted 29 presacral vertebrae, which contrast with most early paravians in which the count does not surpass 23 presacral elements.

Ungual of digit II seems large. Is that big?

Response: We thank the Reviewer for these comments. Yes, we have revised this reconstruction accordingly. The ungual of digit II was incorrectly reconstructed, and this has been fixed now.

28. Let me say that *Buitreraptor* exhibits a block-like, proximoventral process ("flexor tubercle") on manual phalanx 3.III (see Novas et al., 2017. Postcranial osteology of *Buitreraptor*). Please, check three-dimensionally preserved paravians such as *Deinonychus* and *Velociraptor*.

Response: We thank the Reviewer for bringing out this information. Yes, we have added this content in the revised manuscript, showing that similar feature is observed in some non-avian paravians such as *Buitreraptor*.

29. About Extended Data Fig. 6. In the image, at least, it is very difficult to discern whether the fibula extends (or not) up to the level of distal tibia.

Response: We added an enlarged view of the distal end of the left fibula, which shows that the distal end of the fibula is far proximal to the distal tibia.

Response to Reviewer 2:

1. I'm not confident that this is a member Avialae, rather than a non-avian paravian (e.g. similar to *Anchiornis*)

Response: Yes, we agree with the Reviewer that phylogenetic position of this new fossil is a hard question, and we thought this specimen could be a *Anchiornis*-like taxon, or could a troodontids given its shared cranial and tooth morphologies. While, after detailed observation, comparison, and phylogenetic analyses, we re-examined all the morphological features and performed comprehensive phylogenetic analyses. The results collectively support our original conclusion that *Yuezhornis* is an avialan that is derived than *Archaeopteryx*.

Yuezhornis exhibits several derived cranial features that suggest its avialan affinity: as in other long-tailed avialans such as *Archaeopteryx* and *Jeholornis*, the prezygapophyses and postzygapophyses of posterior caudal vertebrae are short, whereas these structures are significantly elongate in troodontids and dromaeosaurids (Makovicky and Norell, 2004; Norell and Makovicky, 2004). The main cranial elements such as jugal, postorbital, and dentary are slender, in stark contrasting to the robust condition in troodontids and dromaeosaurids (Xu et al., 2011, 2015). The T-shaped lacrimal has a short anterior process, as in some Cretaceous avialans such as *Jeholornis* (Hu et al., 2022) and enantiornithines (O'Connor and Chiappe, 2011). By contrast, the anterior process is much longer than the posterior process in *Anchiornis* and most troodontids and dromaeosaurids (Xu and Wu, 2001; Turner et al., 2012; Yin et al., 2018; Wang et al., 2025). Like early avialans, the T-shaped postorbital has three rod-like slender processes, contrasting to the strap-like, triangular form that is seen in *Anchiornis* (Wang et al., 2025) and non-avian paravians (Xu et al., 2015). As in *Archaeopteryx* and other early avialans, the middle and posterior maxillary teeth sparsely are spaced, contrasting to the closely packed condition in troodontids. The slender dentary has parallel dorsal and ventral margins, as in *Archaeopteryx* and more crownward avialans. By contrast, the bone is stout and triangular in lateral view in most non-avian paravians such as *Xiaotingia*, *Caihong*, and *Linheraptor* (Currie, 1995; Xu

at al., 2011, 2015). In Anchiornithines, troodontids, and dromaeosaurids, the dentary characteristically bears a lateral groove that widens posteriorly (Agnolin et al., 2019; Xu et al., 2011), but this groove is absent in *Yuezhornis* and other avialans.

Yuezhornis also exhibits traits in postcranial elements that support its avialan affinity. Specifically, the ilium is readily distinguishable from that of troodontids and dromaeosaurids in having a preacetabular process that is convex cranially and markedly longer than the postacetabular process; whereas the pre- and postacetabular processes are subequal in length in *Anchiornis* and most deinonychosaurs (Extended Data Fig. 5; Rhodes et al., 2021; Turner et al., 2012). As in avialans such as *Xiaotingia* and *Fujianvenator*, and some unenlagiids (Agnolin et al., 2019), the preacetabular process is anteriorly convex, rather than being straight as in some troodontids or concave as in *Anchiornis* and some dromaeosaurids (Xu et al., 2009; Hwang et al., 2002). Overall, the ilium is dorsoventrally shallow and anteroposteriorly long, contrasting with the short and deep form seen in non-avialan paravians, including *Unenlagia* (Agnolin et al., 2019). The right and left fibulae are preserved in *Yuezhornis*. The fibula is much shorter than the tibia, a derived condition of avialan that is otherwise unknown in *Anchiornis* and non-avialan paravians (O'Connor, 2009; Botelho et al., 2016). By contrast, the fibula reaches the proximal tarsals in deinonychosaurs (Botelho et al., 2016), anchiornithines (Pei et al., 2017), and *Archaeopteryx* (Rauhut et al., 2018; O'Connor et al., 2025). Lastly, unlike troodontids and dromaeosaurids (Makovicky and Norell, 2004; Norell and Makovicky, 2004; Turner, 2012; Novas et al., 2018), the foot is non-arctometatarsal, a typical condition of avialans.

To explore the phylogenetic position of *Yuezhornis*, we performed both maximum parsimony and Bayesian tip-dating analyses. The maximum parsimony analysis was performed using TNT package implementing both equal weights (EW) and implied weighting methods (IW). Both EW and IW analyses recovered *Yuezhornis* as sister taxon to *Zhengheornis*, and the new clade constitutes the outgroup of other avialans except *Archaeopteryx* (Extended Data Figs. 8-10, Supplementary Fig. 1)

Given the presence of deinonychosaur-like traits, we further evaluated alternative phylogenetic position of *Yuezhornis*. A constrain search was applied, which forced

Yuezhurnis, troodontids, and dromaeosaurids as a monophyly, and *Yuezhurnis* to be an outgroup of avialans. The constrain-induced topology is **far less parsimonious (14 steps longer than the most parsimonious trees obtained without the constrain)**; and **a negative Bremer support value (-13)** was recovered to support the clade uniting *Yuezhurnis* and Deinonychosauria (Supplementary Fig. 2).

Our Bayesian tip-dating analysis also recovered *Yuezhurnis* as an avialan, a result consistent with the topology obtained using parsimony analysis.

Given the comprehensive morphological comparison (lacking key diagnostic features of troodontids and dromaeosaurids) and phylogenetic analyses that incorporates different analytical methods (equal weights, implied weighting, constrain search, and Bayesian tip-dating), we suggest that the avialan affinity of *Yuezhurnis* is much better supported by all the evidence available, and a deinonychosaurian affinity of *Yuezhurnis* is highly unlikely. We have revised the Discussion section and also added additional morphological comparison (“*Yuezhurnis* compared with other paravian theropods”) in the supplementary information.

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- Novas, F. E., F. Brissón Egli, F. L. Agnolin, F. A. Gianechini, and I. Cerda. 2018. Postcranial osteology of a new specimen of *Buitreraptor gonzalezorum* (Theropoda, Unenlagiidae). Cretaceous Research 83:127-167.
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- O'Connor, J., A. Clark, P.-C. Kuo, Y. Kiat, M. Fabbri, A. Shinya, C. Van Beek, J. Lu, M. Wang, and H. Hu. 2025. Chicago *Archaeopteryx* informs on the early evolution of the avian bauplan. Nature 641:1201–1207.
- Pei, R., Q. Li, Q. Meng, M. A. Norell, and K.-Q. Gao. 2017. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of northeastern China. Bulletin of the American Museum of Natural History:1-67.
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2. I'm not totally sure it gives strong evidence of flightlessness, the forelimb: hindlimb length ratio is similar to that of *Anchiornis*, so it potentially consistent with some form of volant behaviour, similar to either *Anchiornis* or *Microraptor*

Response: We agree that *Yuezhornis* is comparable with *Anchiornis* in limb proportion. However, as the reviewer mentioned, there clearly exist variations among the reported specimens of *Anchiornis*: in specimen LPM-B00169 (Hu et al., 2009), the humerus is longer than the femur (ratio: 1.04), and the forelimb is shorter than the hindlimb (0.69); whereas in the specimens reported in Pei et al. (2017), the humerus is shorter than femur (ratio varies from 0.81 to 0.95), and forelimb/hindlimb ratio is 0.63 (the other three specimens lack metatarsal II). Also, as in Pei et al. (2017), the reported specimens of

Anchiornis exhibit many different morphologies, which indicate that the known specimens of *Anchiornis* could be different species. However, taxonomical revision of *Anchiornis* is beyond the scope of this study (personally, I do believe these reported specimens are not the same species). Whereas, *Microraptor* has proportionately longer forelimb (length ratio 0.73), and forelimb proportion is quite different from that of *Yuezhornis* (specifically, the metacarpal is much shorter in *Yuezhornis*). The most notable difference is that the metacarpal in *Yuezhornis* is much shorter than in *Anchiornis* and *Microraptor* (0.15 compared with 0.21 in *Anchiornis*, and 0.24 in *Microraptor*). We performed morphological analyses that include *Anchiornis* and *Microraptor*, which shows that *Yuezhornis* is widely spaced from these two taxa in morphospace (Fig. 3 and Extended Data Fig. 7). In all our morphometric analyses, *Yuezhornis* never falls into the morphospace of arboreal birds, and *Yuezhornis* exhibits the typical forelimb proportion of flightless birds characterized by the combination of short metacarpals and long humerus (Middleton and Gatesy, 2000). The deinonychosaur-like hyperextensible pedal digits, shortened forelimb with reduced deltopectoral crest, short coracoid, a primitive furcula with large angle, long bony-tail, combined with the troodontid-like dental morphologies, suggest that *Yuezhornis* is highly unlikely to be volant.

References:

- Hu, D., L. Hou, L. Zhang, and X. Xu. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461:640-643.
- Middleton, K. M., and S. M. Gatesy. 2000. Theropod forelimb design and evolution. *Zoological Journal of the Linnean Society* 128:149-187.
- Pei, R., Q. Li, Q. Meng, M. A. Norell, and K.-Q. Gao. 2017. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of northeastern China. *Bulletin of the American Museum of Natural History*:1-67.

3. Indeed, the ulna:humerus length ratio is higher in this new specimens than in e.g. *Anchiornis* and *Microraptor*. Normally, flightless birds have reduced the relative length

of the ulna segment (see Gatesy & Middleton 2000 "Theropod forelimb design and evolution", e.g. Fig. 4), but that has not happened here. See Fig. 3b: the forelimb proportions are similar to terrestrial flying birds, but not to strictly flightless birds. The text states, rather selectively, that the forelimb proportions of the new taxon are similar to 'flightless' pheasants. However, these pheasants aren't strictly flightless and, more importantly, the forelimb proportions are almost equally similar in some birds that are capable of sustained flight, including *Podilymbus* (grebe), *Branta* (goose) and *Anser* (duck). Although those birds aren't agile flyers, they certainly can fly.

Response: Yes, we agree with the Reviewer that the ulna/humerus length ratio is useful to distinguish flightless from flight taxa. In our morphometric analyses, *Yuezhornis* is more comparable with some pheasants (*Francolinus afer* and *Crossoptilon crossoptilon*) in forelimb and hind limb proportions, and it is widely spaced from *Anchiornis* (Fig. 3). When we only focused on forelimb proportion, *Yuezhornis* differs greatly from other Jurassic paravians, instead having the typical forelimb proportion of flightless birds characterized by the combination of short metacarpals and long humerus, and it is interspersed within morphospace occupied by extant terrestrial birds (Fig. 3c). Again, *Yuezhornis* is widely spaced from other Jurassic paravians such as *Anchiornis*. Yes, we agree that these pheasants could perform burst fly to escape predator, but these modern birds have a skeleton that could support such specialized flight behavior, such as keeled sternum, robust humerus with well-developed deltopectoral crest, and a pygostyle. However, all these flight-related morphological features are absent in *Yuezhornis*, and it is really challenging to argue that *Yuezhornis* could perform similar burst flight as these modern pheasants. We have removed the word "flightless pheasants" to avoid ambiguity.

4. The fossil is quite poorly-preserved. So currently, not as much anatomy is visible as we ideally would be able to see to support this, but various features are highlighted as being shared with *Anchiornis*. These make me suspicious of the support for the hypothesis that the new taxon belongs to Avialae, rather than an outgroup of Avialae.

Response: Please see our response above. Our revised morphological comparison and phylogenetic analyses show that *Yuezhornis* is not anchiornithine, but emerged slightly derived than *Archaeopteryx*. We have revised the text to highlight the morphological differences between *Yuezhornis* and anchiornithine. Admittedly, the preservation is not that good, but it does provide some new information that are of importance to piece together the early evolution of avialans during the Jurassic. Currently, the known Jurassic paravians are exceedingly rare and spatiotemporally restricted, with only two localities known before—Solnhofen Limestones in Germany and the Yanliao Biota in China. Our recent fieldwork has been able to find the third Jurassic avialan-bearing locality in southeast China, which we named Zhenghe Fauna. Unlike previously known avialans from Zhenghe Fauna, this study reports the first avialan that preserve a skull from this locality. And Jurassic avialan skull is quite rare. Our morphological and phylogenetic analyses show that the new specimen represents one of the earliest-branching avialan. As such, *Yuezhornis* fills a critically undersampled phylogenetic and temporal interval of early avialan diversification in Late Jurassic, and further provides previously unrecorded and unrecognized cranial features that have been hindered by rarely preserved Jurassic skulls.

4. -The proportion of forelimb length (humerus+radius+metacarpal1) to hindlimb length (femur+tibia+metatarsus) is 0.67 here, and 0.69 in *Anchiornis*, very similar.
5. -Both have small, closely-packed premaxillary and anterior maxillary teeth (which are absent in other avialans).
6. -Teeth and ziphodont, serrated, and the maxillary tooth row extend further than in avialans (see ms).
7. -The jugal morphology is similar to *Anchiornis* and different to avialans (see ms).
8. -Anterior surface of the coracoid with numerous pits (see ms).
9. -Low angle of circular rami, differing from Avialae.
10. -Pubic apron morphology shared with troodontids.
11. The authors do not present statistical tests of alternative phylogenetic hypotheses.

So it is not clear that the anatomy statistically rejects a placement outside Avialae, for the new taxon. That is important because, if it is outside Avialae, then it isn't a secondarily flightless avialan.

12. *Anchiornis* is much better known, and older (Middle Jurassic). So the new fossil may be confirmation that Anchiornis-like taxa continued to be present into the Late Jurassic (which has already been suggested at Solnhofen).

Response: We thank the Reviewer for these instructive comments, which lead us to re-examine the morphologies of this fossil. For morphological comparison: the new specimen indeed exhibits some features shared with troodontids and dromaeosaurids. However, many diagnostic features of troodontids and dromaeosaurids are absent in *Yuezhornis*, such as the elongate anterior process of the lacrimal, strap-like processes of the lacrimal, well-developed quadratojugal process of the jugal, a robust dentary with a lateral groove that widens posteriorly, closely packed middle and posterior maxillary teeth, elongate prezygapophyses and postzygapophyses of posterior caudals, and the sub- or arctometatarsal foot. Meanwhile, *Yuezhornis* exhibits several derived cranial features that speak clearly to its avialan affinity such as slender cranial elements (e.g., jugal, postorbital, and dentary), short anterior process of lacrimal sparsely spaced middle and posterior maxillary teeth, fewer dentary teeth, reduced zygopophyses of posterior caudals, elongate preacetabular ilium, short fibula, reduced fifth metatarsal, and non-arctometatarsal foot.

For statistical tests of alternative phylogenetic hypotheses: we performed both maximum parsimony and Bayesian tip-dating analyses. The maximum parsimony analysis was performed using TNT package implementing both equal weights (EW) and implied weighting methods (IW). Both EW and IW analyses recovered *Yuezhornis* as sister taxon to *Zhengheornis*, and the new clade constitutes the outgroup of other avialans except *Archaeopteryx* (Extended Data Figs. 8-10, Supplementary Fig. 1)

Given the presence of deinonychosaur-like traits, **we further evaluated alternative phylogenetic position of *Yuezhornis*. A constrain search was applied, which forced *Yuezhornis*, troodontids, and dromaeosaurids as a monophyly, and *Yuezhornis***

to be an outgroup of avialans. The constrain-induced topology is far less parsimonious **(14 steps longer than the most parsimonious trees obtained without the constrain);** and a **negative Bremer support value (-13) was recovered to support the clade uniting *Yuezhurnis* and Deinonychosauria** (Supplementary Fig. 2).

Our Bayesian tip-dating analysis also recovered *Yuezhurnis* as an avialan, a result consistent with the topology obtained using parsimony analysis.

Given the comprehensive morphological comparison (lacking key diagnostic features of troodontids and dromaeosaurids) and phylogenetic analyses that incorporates different analytical methods (equal weights, implied weighting, constrain search, and Bayesian tip-dating), we suggest that the avialan affinity of *Yuezhurnis* is much better supported by all the evidence available, and a deinonychosaurian affinity of *Yuezhurnis* is highly unlikely. We have revised the Discussion section and also added additional morphological comparison (see section titled “*Yuezhurnis* compared with other paravian theropods”) in the supplementary information.

Yes, we agree with the Reviewer that the anchiornithine lineage likely persistent into Late Jurassic. However, this conclusion is not supported by the new specimen reported here, but instead by *Fujianvenator* which is also discovered from the Zhenghe Fauna, because our previous study has recovered *Fujianvenator* as a member of the Anchiornithine (Xu et al., 2023).

Reference:

Xu, L., M. Wang, R. Chen, L. Dong, M. Lin, X. Xu, J. Tang, H. You, G. Zhou, L. Wang, W. He, Y. Li, C. Zhang, and Z. Zhou. 2023. A new avialan theropod from an emerging Jurassic terrestrial fauna. *Nature* 621:336–343

13. The origin and early diversification of birds remain one of the most debated transitions in vertebrate evolution"

>>This seems incorrect. The origins of turtle, snakes, placental mammals, vertebrates themselves, and even squamates (for which there is no consensus on which Triassic fossils might be stem squamates) seem more 'debated'. The origin and early

diversification of birds of course is very interesting, with various unanswered questions, but specifically the statement that it is 'one of the most debated' seems incorrect.

Response: Yes, we agree with the Reviewer that the origins of turtle, snakes, placental mammals, vertebrates themselves, and even squamates are of importance and debated. Although our understanding about the origin of birds has been advanced by recent discoveries, many questions are still needed to be addressed; for instance, the phylogenetic relationship among the earliest-branching paravians, the poor Jurassic records of troodontids and dromaeosaurids. Here, we just simply want to address this issue.

14. "Our study challenges the prevailing notion that aerodynamic selection was the determinant force of early avialan evolution. Instead, it demonstrates that birds underwent rapid ecological diversification and specialized niche colonization—including the loss of flight—shortly after their emergence." >>I can't swallow this text. The paper documents an early transition to flightlessness in one lineage of Avialae. Sure, that's very interesting. But it doesn't actually contradict the idea that aerodynamic selection (i.e. flight) explains the main anatomical transitions involved in bird origins or the early evolution of Avialae. Consider alternative ways of explaining the significance of the observation of an early flightless taxon. (But note I don't think the authors have provided sufficiently strong evidence of that).

Response: We thank the Reviewer for this comment, and help us clarify the main finding here. We have deleted the paragraphs relating to flight loss. *Yuezhornis* exhibits few morphological modifications that relates to powered flight, which is corroborated by morphometric analyses. Although recent studies suggest flight capability of anchiornithines, this clade lack flight-related features (e.g., elongate forelimb, keeled ossified sternum, and asymmetrical remiges). In addition to *Yuezhornis*, the long-legged avialan *Fujianvenator* is also unlikely to be volant. These early-branching avialans show that flight evolved more than once in bird evolution. We

have removed the sentence “Our study challenges the prevailing notion that aerodynamic selection was the determinant...”, and revised the manuscript to say that “these new fossils exemplify an early departure from that adaptive mainstream in this localized area, highlighting the extraordinary breadth of ecological and morphological diversification that took place close to the origins of avialans”.

15. References to 'stem avialans' are confusing. Crown birds have a stem group that includes all (non crown bird) dinosaurs, pterosaurs etc. Avial does not have a stem. But if it did, then it should also include other dinosaurs, pterosaurs etc. Maybe just say 'early avialans' or 'early-diverging avialans'.

Response: Yes, we have revised all these words accordingly.

16. Anterior caudal transverse processes are described as facing posterolaterally. But they appear to face anterolaterally in the images - or all these vertebrae have been reversed during disarticulation?

Response: We think the anterior caudal vertebrae are disarticulated, and they are not reversed. The transverse processes are directed posterolaterally, as in other paravians.

17. "As in stemward avialans and non-avian theropods, the ulna is shorter than the humerus" >>Very slightly shorter only (add 'slightly' to text).

18. "The ulna is bowed, rather than being straight" >>The ulna is close to being straight. It is only weakly bowed. Consider adding the word 'weakly'

19. "The robust radius measure around 90% of the width of the ulna, comparable to that of basal theropods; whereas the bone is relatively slender in other paravians⁵" >>The radius diameter seems similar in *Anchiornis* (Rui et al 2017)

Response: We are grateful to the Reviewer for these detailed comments and have corrected all these mistakes.

20. Please explain the evidence for this. It is an isolated phalanx + ungual phalanx, not connected to other elements.

Response: There are three manual unguals preserved, and they are different in size, showing that they belong to different digits. In most known paravians with three clawed digits, the shortest penultimate phalanx is III-3. Therefore, we tentatively referred the ungual that is associated with the shortest penultimate phalanx as the ungual of digit III.

21. "The ventral margin of the preacetabular process is deeply concave, as in *Cratonaia* and some enantiornithines, contrasting with the straight form seen in *Archaeopteryx* and *Jeholornis*"

>>But also similar to *Anchiornis* (Hu et al 2009; Rui et al 2017)

Response: Yes, we have revised this paragraph.

22. "The postacetabular process narrows posteriorly, lacking the ventral deflection that is present in *Anchiornis* and some dromaeosaurids⁴⁸"

>>These seem similar to me. Rui et al (2017, fig. 18) show the ilium of *Anchiornis*, with the dorsal margin sloping down the page. But if you rotate it so the dorsal margin is horizontal, then the outline of the posterior margin is fairly similar to that shown here in the new specimen.

Response: All the specimens described in Pei et al. (2017) are poorly preserved regarding the ilium (either broken or overlain by other elements). Instead, this bone is nicely preserved in the holotype of *Anchiornis* (Xu et al. 2009), and a reconstruction is provided therein. Based on Xu et al. (2009), the postacetabular process of *Anchiornis* is ventrally deflected.

Reference:

Pei, R., Q. Li, Q. Meng, M. A. Norell, and K.-Q. Gao. 2017. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of northeastern China. *Bulletin of the American Museum of Natural History*:1-67.

Xu, X., Q. Zhao, M. Norell, C. Sullivan, D. Hone, G. Erickson, X. Wang, F. Han, and Y. Guo. 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chinese Science Bulletin* 54:430-435.

23. "The calcaneus and astragalus are unfused with one another or the tibia. In contrast to what is observed in most other Jurassic avialans and non-avian paravians18" >>Could be more specific about which taxa. They are unfused in *Anchiornis* and *Archaeopteryx*.

Response: No, we intended to mean that the fibula reaches the proximal tarsals in *Anchiornis* and *Archaeopteryx* here, not about the fusion degree of calcaneus and astragalus.

24. "The metatarsus measures approximately 63% of the length of the femur, much shorter than in other stem avialans in which the length ratio is greater than 0.8" >>I measured images from four individuals referred to *Anchiornis*, from Hu et al (2009) and Rui et al (2017). The ratio was 0.81 in BMNHC PH822, 0.78 in BMNHC PH804, 0.69 in PKUP V1068, and 0.675 in LPM-B00169. The last two aren't very different to the ratio in the new specimen (0.631). I don't know what explains the variation among measurements of individuals referred to *Anchiornis*. But the similarity of some of them to the specimen here seems important and is consistent with the hypothesis that this is related to *Anchiornis* or otherwise belongs outside of Avialae.

Response: Yes, we thank the Reviewer for pointing out this issue. Actually, not only these measurements, the reported specimens of *Anchiornis* show different morphological features (as said in Pei et al., 2017), and they are also different from the holotype specimen of *Anchiornis huxleyi*. It is unclear whether these differences are

intraspecific or interspecific, or ontogenetic variations. Honestly, I really do not think all these specimens can be confidently referral to the taxon *Anchiornis huxleyi*. Taxonomical revision of all the known *Anchiornis* specimens is much needed.

Reference:

Pei, R., Q. Li, Q. Meng, M. A. Norell, and K.-Q. Gao. 2017. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of northeastern China. *Bulletin of the American Museum of Natural History*:1-67.

25. Note that when I confirmed the measurements of the current ms, but measuring Fig. 1, I found that the scale bar was incorrect. Maybe it is a 20 mm scale bar and not a 10 mm scale bar.

Response: Yes, we have corrected this mistake.

26. In the statement "much shorter than stem avialans", I don't know which taxa are considered to be stem avialans, either (1) non-avialan stem birds (i.e. excluding e.g. *Archaeopteryx*) or just early members of Avialae (i.e. including *Archaeopteryx*).

Response: We have removed the word “stem”. Here, we mean early-diverging avialans such as *Anchiornis* and *Archeopteryx*. We have removed this paragraph, because this comparison is not that informative.

27. "The metatarsals are not ginglymoid"

I'm looking at ED Fig. 6. I agree that it doesn't look ginglymoid. But how sure can you be, given the style of preservation? Please indicate in the text.

Response: Yes, in the revised manuscript we indicated that the distal ends of the metatarsals showed no sign of intertrochlear incisures.

28. "Presence of deinonychosaurs-like digit II phalanges in *Archaeopteryx*, *Xiaotingia*, and *Anchiornis* was acknowledged in earlier studies, but called into question by recent work" >>As-phrased, it isn't clear whether the authors are saying that a large pedal claw was present in these taxa, or not. They show a large pedal claw in their skeletal reconstruction of the new taxon (ED Fig. 1). But no such claw is preserved. The presence of a large claw, and the hyper extensible nature of the claw, seem to be independent of each other. For example, it is possible that a hyper extensible digit is present but has a regular-sized claw, as in *Xiaotingia* (see below). >>In *Xiaotingia*, Xu et al (2011). The claw is not enlarged, but is proposed as being hyper extensible based on the following anatomy: "The second pedal digit is similar to those of *Archaeopteryx* (Fig. 3h), *Anchiornis* and other deinonychosaurs in having a prominent dorsal expansion and a dorsally located lateral collateral ligament fossa at the distal ends of both phalanx II-1 and phalanx II-2 (Fig. 2e), indicating that the second digit was highly extensible."

Response: We are sorry for this ambiguity. Here we intended to say that a hyperextensible digit II, represented by the specialized morphology of phalanges II-1 and II-2, is present in *Yuezhornis*, which is comparable to that of deinonychosaurs. Previous studies suggest similar pedal phalanges (II-1 and II-2) is present in *Anchiornis*, *Xiaotingia*, and *Archaeopteryx*, and that conclusion has been challenged by recent study. Here, we did not compare the claw. We have revised the reconstruction in Extended Data Fig. 1, and the claw has been resized.

29. "*Yuezhornis* exhibits features relating to terrestrial adaptation (e.g., short forelimb, and extensible pedal digits)..."

>>The forelimb: hindlimb length ratio, based on the dataset provided here, is 0.67 in the new taxon, and 0.69 in *Anchiornis*, and 0.73 in *Microraptor*. This is clear in Fig. 4 here. Those are very similar numbers. So I'm not convinced that this is a secondarily flightless animals instead of representing the general condition for some early paravians with some kinds of volant behaviour. That depends partly on its phylogenetic position.

Response: We did not suggest *Yuezhornis* is secondarily flightless, and instead we posit that *Yuezhornis* is highly unlikely to be volant. Yes, the limb proportions between *Yuezhornis* and *Anchiornis* is comparable, but their forelimb is proportionately shorter than *Microraptor*. The asymmetric remiges on both forelimb and hindlimb of *Microraptor* suggest flight capability in this animal. However, *Microraptor* is deeply nested within the Dromaeosauridae, and it is phylogenetically distant from and geologically younger than *Yuezhornis* and *Anchiornis*. Therefore, direct comparison with *Microraptor* is not appropriate. As for *Anchiornis*, despite recent studies suggest flight potential of *Anchiornis* based on morphometric analyses (Pei et al., 2020), the flight capability of this taxon should be treated with caution as mentioned in that study. Also, *Anchiornis* lacks key flight-related morphological modifications, including elongate forelimb, keeled ossified sternum, and asymmetric remiges. *Yuezhornis* exhibit few morphologies that relate to volant behavior, given its large interclavicular angle, short forelimb, and elongate bony tail. The presence of deinonychosaur-like hyperextensible pedal digits also suggest that *Yuezhornis* is well adapted to terrestrial locomotion. Our phylogenetic analyses recovered *Yuezhornis* as an early-branching avialan that is slightly derived than *Archaeopteryx*. These observations suggest that flight evolved more than once since the origin of avialans.

30. >>The analyses presented seem to examine only the proportions -within- the forelimb.

"*Yuezhornis* compares favorably with some flightless pheasants (*Francolinus afer* and *Crossoptilon crossoptilon*) in limb proportions... "

>>It isn't really correct to call these pheasants 'flightless'. They are burst flyers, that lack the ability for sustained flight. Nevertheless, they can fly. Their form of flight is very derived and is unlikely to be present in the earliest paravians. I don't think they are appropriate comparisons.

Response: In this study, we first analysed both the forelimb and hind limb, and then

focused on the forelimb and hindlimb, respectively. When both the forelimb and hind limb analyzed together, *Yuezhornis* falls close to *Francolinus afer* and *Crossoptilon crossoptilon* in the morphospace (Fig. 3A). Yes, we removed the word “flightless” now. As the Reviewer said, these pheasants could only perform short burst but not sustained flight. Such specialized volant behavior is unlikely present in early avialans such as *Yuezhornis*, given its primitive skeleton.

31. Forelimb elongation has been viewed as the major skeletal modification across the dinosaur-bird transition, with the fundamental flight-adapted limb proportions (forelimb longer than hindlimb) acquired before the origin of avialans. However, contrasting with all the other early avialans (Supplementary Table 2), in *Yuezhornis* the forelimb is shorter than the hindlimb, and the humerus is shorter than the femur"

>>If we accept that *Yuezhornis* is secondarily flightless, for the moment, that does not contradict the idea forelimb elongation was invalid in bird origins. So the statement here, as written, seems misleading.

Response: We thank the Reviewer for this comment and have revised the corresponding paragraph. Here, we did not argue that *Yuezhornis* is secondarily flightless, and just suggest that *Yuezhornis* is unlikely to be volant given its overall skeletal features and the results of morphometric analyses. So, we suggest that some of the earliest avialans are poor fliers or non-volant, such as *Yuezhornis* and *Fujianvenator*.

32. "...The results reveal that *Yuezhornis* has prominently short forelimb and humerus (only longer than the flightless ornithuromorph *Patagopteryx* among Mesozoic paravians), even shorter than some fast-running dromaeosaurids such as *Bambiraptor* and *Buitreraptor*"

>>We don't actually know that those animals (e.g. *Bambiraptor*) were flightless, strictly speaking. We guess this, but don't observe it directly. Comparisons with *Anchiornis* and *Microraptor* seem more relevant (see above).

Response: Yes, we agree with the Reviewer that reconstruction of ecology of distinct vertebrates is notoriously difficult. The two dromaeosaurids cited are generally interpreted as adapted to terrestrial locomotion, and as far as we are aware, few studies suggest these animals could be volant. Yes, we have added comparison with *Anchiornis* and *Microraptor* in the revised manuscript.

33. "Both morphometric analyses and focal features (e.g., wide interclavicular angle, reduced deltopectoral crest, and short forelimb) strongly indicate that *Yuezhornis* was flightless and adapted to terrestrial environments"

>>These are potential indicators of flightlessness, but these aspects are also consistent with the anatomy of some volant non-avian paravians. Note that the authors say, later in their discussion: "Recent studies suggested powered flight capability for anchiornithines and other early avialans". If *Anchiornis* is considered to have powered flight, then the anatomy of *Yuezhornis* does not rule it out either.

Response: Some recent studies (e.g., Pei et al., 2020) suggested potential powered flight potential for *Anchiornis* based on morphometric analyses. But they clearly said "The potential for powered flight in anchiornithines should be treated cautiously though. This is because aspects of their anatomy might have affected their flight-relevant forelimb capabilities negatively, e.g., lack of functionally asymmetrical feathers....." (Pei et al., 2020). Therefore, whether *Anchiornis* and its kins are volant or not is not conclusively resolved. Relating to this matter, we reported an anchiornithine *Fujianvenator* from the Zhenghe Fauna that also yielded *Yuezhornis* (Xu et al., 2023). *Fujianvenator* is certainly non-volant, given its surprisingly elongated distal hindlimb element, reduced deltopectoral crest, and long bony tail (Xu et al., 2023). All these fossils show that powered flight evolved more than once since the origin of the Avialae, at least some anchiornithines and *Yuezhornis* is non-volant. We have revised the corresponding sentences to clarify this issue.

Reference:

- Pei, R., M. Pittman, P. A. Goloboff, T. A. Dececchi, M. B. Habib, T. G. Kaye, H. C. E. Larsson, M. A. Norell, S. L. Brusatte, and X. Xu. 2020. Potential for powered flight neared by most close avialan relatives, but few crossed its thresholds. *Current Biology* 30:4033-4046.e8.
- Xu, L., M. Wang, R. Chen, L. Dong, M. Lin, X. Xu, J. Tang, H. You, G. Zhou, L. Wang, W. He, Y. Li, C. Zhang, and Z. Zhou. 2023. A new avialan theropod from an emerging Jurassic terrestrial fauna. *Nature* 621:336–343

Response to Reviewer 3:

1. The fossil itself is important and well worthy of publication. It is a new derived theropod (paravian) from the Zhenghe Fauna of China, one of the most exciting new fossil sites. For the first time, this site is preserving a range of Jurassic small theropods, including early birds like *Baminornis*. It is our best window into the diversity of the first birds and their close theropod relatives, from around the time that these dinosaurs were first flying. Undoubtedly this new fossil is an important new record, and its diagnosis as a new species is strong. And I completely agree with the authors that this was not a flying animal. The arms are simply too short to have supported a wing big enough to fly, plus features of the shoulder girdle and furcula also seem too ‘primitive’ for a flying animal.

Response: We thank the Reviewer for this positive comment, and more importantly sharing the feeling with us about this exciting new fossil locality.

2. What I am not convinced of is that it is a flightless bird. Let me unpack what that means. If it were a flightless bird, that means that: 1) it is a member of the clade Avialae (the ‘bird’ clade capable of powered flapping flight: *Archaeopteryx* + modern birds) and more derived than *Archaeopteryx*; 2) it evolved from flying ancestors. I think neither of these things is clear.

Response: We appreciated the Reviewer for unpacking these two scenarios. We have carefully re-examined the morphologies, checked all the character coding, and re-ran the phylogenetic analyses using different approaches, such as maximum parsimony (using both equal weights and implied weighting) and Bayesian tip-dating methods. Also, to explore the possibility that this new fossil may be a non-avialan paravian, we conducted constraint search, which forced the new specimen as a member of deinonychosaurs but not a member of avialan. Both the maximum parsimony and Bayesian tip-dating analyses recovered *Yuezhornis* as an avialan that is more derived than *Archaeopteryx* (Fig. 4A, Extended Data Figs. 9 and 10, Supplementary Fig. 1). The constrain search shows that 14 additional steps would be needed to recover *Yuezhornis* as deinonychosaurs rather than avialan, and a negative Bremer support value of -13 was obtained (Supplementary Fig. 2). As such, we suggest that *Yuezhornis* is an avialan. Given that the earliest diverging avialans such as *Fujianvenator* and now *Yuezhornis* are unlikely to be volant, we think powered flight evolved more than once within the Avialae. Previous studies suggest that flight evolved independently among pennaraptora, at least in scansoriopterygids and *Microraptor*-like taxa (Sullivan et al., 2017; Pei et al., 2020; Xu, 2024; but see Kiat and O'Connor, 2024). This does not mean that *Yuezhornis* is a secondary flightless, and we did not bring out this conclusion.

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- Kiat, Y., and J. K. O'Connor. 2024. Functional constraints on the number and shape of flight feathers. PNAS 121:e2306639121.
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- Sullivan, C., X. Xu, and J. K. O'Connor. 2017. Complexities and novelties in the early evolution of avian flight, as seen in the Mesozoic Yanliao and Jehol Biotas of Northeast China. Palaeoworld 26:212-229.

Xu, X. 2024. Inferring aerial behavior in Mesozoic dinosaurs: Implications and uncertainties. PNAS 121: e2401482121.

3. First, I will note that the authors have not attempted to make a case based on the anatomy that this specimen has characteristic features of the arms, chest, and other body regions seen in modern birds (or fossil birds) that have lost flight. There is an enormous literature on flightlessness in birds, and how the skeleton has been modified as birds give up the flight of their volant ancestors. Flight has been lost repeatedly in birds, and there are commonalities to how this happens. At a minimum, this literature must be engaged with. The authors need to show that this new fossil has hallmarks of the ways in which birds are known to lose flight. As it stands, to me, this skeleton looks remarkably similar to many dromaeosaurids and troodontids—it looks like what I would expect for a small Jurassic theropod close to the origin of Avialae, but not yet past that threshold of powered flapping flight. I don't see anything obvious that indicates that it had ancestors that once flew. More than anything, the arm looks like a normal dromaeosaurid or troodontid arm to me, and nothing like the highly modified arms of 'ratites' or various extinct birds that evolved from flying ancestors.

Response: We thank the Reviewer for clarifying this matter to us. Actually, what the Reviewer suggested is our main conclusion, that is, *Yuezhornis* is not volant. We did not intend to argue that *Yuezhornis* is a secondarily flightless, and we have revised the manuscript to clarify this ambiguity. As the Reviewer mentioned, taxa close to the origin of avialans most likely have not yet pass the threshold of powered flight (Sullivan et al., 2017). For instance, morphometric analysis suggested that the closest common ancestor of avialans fails the lift threshold of powered flight (Pei et al., 2020); and that flight potential of anchiornithines should be treated with caution, given the lack of flight-related features such as ossified and keeled sternum, elongate forelimb, asymmetrical remiges (Zheng et al., 2014). *Yuezhornis* exhibit few or no flight-related morphological transformations, instead preserving features indicative terrestrial locomotion such as elongate hindlimb and extensible pedal phalanges. Yes, the forelimb

exhibits similar features with that of dromaeosaurids and/or troodontids, and this reflect evolutionary mosaicism. We have added this content in the revised manuscript.

Responses:

- Pei, R., M. Pittman, P. A. Goloboff, T. A. Dececchi, M. B. Habib, T. G. Kaye, H. C. E. Larsson, M. A. Norell, S. L. Brusatte, and X. Xu. 2020. Potential for powered flight neared by most close avialan relatives, but few crossed its thresholds. *Current Biology* 30:4033-4046.e8.
- Sullivan, C., X. Xu, and J. K. O'Connor. 2017. Complexities and novelties in the early evolution of avian flight, as seen in the Mesozoic Yanliao and Jehol Biotas of Northeast China. *Palaeoworld* 26:212-229.
- Zheng, X., J. O'Connor, X. Wang, M. Wang, X. Zhang, and Z. Zhou. 2014. On the absence of sternal elements in *Anchiornis* (Paraves) and *Sapeornis* (Aves) and the complex early evolution of the avian sternum. *PNAS* 111:13900-13905.

4. What the authors have done is shown that the limb proportions, especially of the forelimb, fall within the range of terrestrial birds. But this is to be expected of any non-flying close relative of avialans, and indeed is the case for dromaeosaurids and troodontids in their dataset. Also, there is something of a linguistic sleight of hand in the manuscript: the authors regularly talk about how the skeleton has features of 'terrestrial birds' and use this somewhat synonymously with 'flightless bird.' These are different things. There are plenty of birds today that spend much time on the ground and have limbs (particularly the hindlimbs) suited for this lifestyle. In their plots, especially in figure 3, the authors need to make clear which modern birds are totally flightless and which simply spend much time in a terrestrial setting.

Thus, everything hinges on those features that place the new species as more derived than *Archaeopteryx*. And I'm not clear what those features are. They need to be front and center in this manuscript. In the discussion, the authors note two features that place the new species in the *Archaeopteryx* + modern bird clade—which seems like very weak support when we know the positions of taxa in this part of the tree are so labile.

But, even if this is strongly supported, those features might just tell us that the new species groups with *Archaeopteryx* and modern birds in a more inclusive clade. What we need to know is those features that place the new species more derived than *Archaeopteryx*—in a unique relationship with the lineage that led to modern birds.

Response: Yes, we agree with the Reviewer that ‘flightless birds’ and ‘terrestrial birds’ should not be treated synonymously. We have revised the corresponding paragraphs and specified that “*Yuezhornis* compares favorably with some terrestrial birds (pheasants *Francolinus afer* and *Crossoptilon crossoptilon*) in limb proportions”. These pheasants, despite spending much of their time on ground, can perform burst flight to escape predator. However, such specialized flight capability is unlikely the case for this Jurassic avialan, given its morphologies (long bony tail, short arm, large interclavicular angle, short coracoid, etc.). So, we posit that the similar limb proportions between *Yuezhornis* and pheasants indicates that *Yuezhornis* is adapted to terrestrial locomotion.

5. Because the authors have not based their interpretations on flightless anatomy in the specimen, their story hinges entirely on the phylogenetic placement of this new species, which they find within Avialae, slightly more derived than *Archaeopteryx*: one node up, ‘in between’ *Archaeopteryx* and all more derived birds. They find this result with both parsimony and Bayesian analysis of a suitable dataset. However, it is not clear how strongly supported this result is. The relationships of the earliest avialans and their closest paravian relatives (dromaeosaurids, troodontids, anchiornithids) are notoriously labile, and in alternative analyses these branches regularly move around—sometimes even when adding a single new specimen to an often-used dataset, such as the TWiG dataset the authors are using. Let’s play devil’s advocate, and say that the new species moved one node basally. Then it would be out of the *Archaeopteryx* + modern bird clade. Out of the clade of unequivocal volant flapping birds. And just another small bird-like paravian in the troodontid and dromaeosaurid zone.

Response: Yes, we agree with the Reviewer that much of the discussion hinges on the phylogenetic position of the new specimen. Honestly speaking, this question also hovered over our mind for a long time. While, after detailed observation, comparison, and phylogenetic analyses, we re-conducted morphological and phylogenetic analyses, and the result still support the conclusion that *Yuezhurnis* is an avialan that is derived than *Archaeopteryx*. Please find our detail explanation:

Yuezhurnis exhibits several derived cranial features that indicates its avialan placement. These feature include slender cranial bones, such as jugal, postorbital, and dentary, whereas these elements are much robust in troodontids and dromaeosaurids. As in some Cretaceous avialans such as *Jeholornis* (Hu et al., 2022) and enantiornithines (O'Connor and Chiappe, 2011), the T-shaped lacrimal has an anterior process that is shorter than the posterior process. By contrast, in *Anchiornis*, most troodontids, and dromaeosaurids, the anterior process is much longer than the posterior process (Xu and Wu, 2001; Turner et al., 2012; Yin et al., 2018; Wang et al., 2025). As in early avialans such as enantiornithines (Wang et al., 2021; Hu et al., 2020), the T-shaped postorbital has three rod-like slender processes, contrasting to the strap-like form that is seen in non-avialan paravians such as *Linheraptor*. As in *Archaeopteryx* and other early avialans (O'Connor et al., 2025; Wang et al., 2021), the middle and posterior maxillary teeth sparsely are spaced, contrasting to the closely packed condition in troodontids (Makovicky and Norell, 2004). The slender dentary has parallel dorsal and ventral margins, as in *Archaeopteryx* and more crownward avialans. By contrast, the bone is stout and triangular in lateral view in most non-avialan paravians such as *Xiaotingia*, *Caihong*, and *Linheraptor* (Currie, 1995; Xu et al., 2011, 2015). A deep lateral dentary groove that widens posteriorly is exclusively present in anchiornithines, troodontids, and dromaeosaurids (Agnolin et al., 2019; Xu et al., 2011), but this groove is absent in *Yuezhurnis* and other avialans.

Yuezhurnis also exhibit features in postcranial elements that support its avialan affinity. Specifically, the ilium is readily distinguishable from that of troodontids and dromaeosaurids in having a preacetabular process that is convex cranially and markedly longer than the postacetabular process; whereas the pre- and postacetabular processes

are subequal in length in *Anchiornis* and most deinonychosaurs (Extended Data Fig. 5; Rhodes et al., 2021; Turner et al., 2012). As in avialans such as *Xiaotingia* and *Fujianvenator*, and some unenlagiids (Agnolin et al., 2019), the preacetabular process is anteriorly convex, rather than being straight as in some troodontids or concave as in *Anchiornis* and some dromaeosaurids (Xu et al., 2009; Hwang et al., 2002). Overall, the ilium is dorsoventrally shallow and anteroposteriorly long, contrasting with the short and deep form seen in non-avian paravians, including *Unenlagia* (Agnolin et al., 2019). The right and left fibulae are preserved in *Yuezhornis*. The left fibula was cut by a crack along its mid-length. However, the combined length of the proximal and distal parts of the left fibula is equal to the right fibula (the latter is completely preserved here). The distal end of the left fibula is complete and fully exposed (see Extended Data Fig. 6C), showing that preserved morphology of its distal extremity is genuine. All these observations show that the measurement of the fibula is not biased by preservation, and the fibula is much shorter than the tibia. The fibula rapidly tapers distally to a splint-like end, which terminates far proximal to the distal end of the tibia. This is a derived condition of avialan that is widely distributed among Cretaceous avialans (O'Connor, 2009; Botelho et al., 2016). By contrast, the fibula reaches the proximal tarsals in deinonychosaurs (Botelho et al., 2016), anchiornithines (Pei et al., 2017), and *Archaeopteryx* (Rauhut et al., 2018; O'Connor et al., 2025). Lastly, unlike troodontids and dromaeosaurids (Makovicky and Norell, 2004; Norell and Makovicky, 2004; Turner, 2012; Novas et al., 2018), the foot is non-archimetatarsal, a typical condition of avialans.

To explore the phylogenetic position of *Yuezhornis*, we performed both maximum parsimony and Bayesian tip-dating analyses. The maximum parsimony analysis was performed using TNT package implementing both equal weights (EW) and implied weighting methods (IW). Both EW and IW analyses recovered *Yuezhornis* as sister taxon to *Zhengheornis*, and the new clade constitutes the outgroup of other avialans except *Archaeopteryx* (Extended Data Figs. 8-10, Supplementary Fig. 1)

Given the presence of deinonychosaur-like traits, we further evaluated alternative phylogenetic position of *Yuezhornis*. A constrain was applied, which forced

Yuezhurnis, troodontids, and dromaeosaurids as a monophyly, and *Yuezhurnis* to be an outgroup of avialans. The constrain-induced topology is far less parsimonious (**14 steps longer** than the most parsimonious trees obtained without the constrain); and a **negative Bremer support value (-13)** was recovered to support the clade uniting *Yuezhurnis* and Deinonychosauria (Supplementary Fig. 2).

Our Bayesian tip-dating analysis also recovered *Yuezhurnis* as an avialan, a result consistent with the topology obtained using parsimony analysis.

Given the comprehensive morphological comparison (lacking key diagnostic features of troodontids and dromaeosaurids) and phylogenetic analyses that incorporates different analytical methods (equal weights, implied weighting, constrain search, and Bayesian tip-dating), we suggest that the avialan affinity of *Yuezhurnis* is much better supported by all the evidence available, and a deinonychosaurian affinity of *Yuezhurnis* is highly unlikely. We have revised the Discussion section and also added additional morphological comparison (“*Yuezhurnis* compared with other paravian theropods”) in the supplementary information.

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- O'Connor, J., A. Clark, P.-C. Kuo, Y. Kiat, M. Fabbri, A. Shinya, C. Van Beek, J. Lu, M. Wang, and H. Hu. 2025. Chicago *Archaeopteryx* informs on the early evolution of the avian bauplan. *Nature* 641:1201–1207.
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6. And, here I will raise another troubling point: even if the phylogenetic analysis in the paper is correct, and the new species is more derived than *Archaeopteryx*, and positioned between *Archaeopteryx* and the clade of more derived avialans, that might mean that it lost flight from an *Archaeopteryx*-like ancestor. But: there would be an equally parsimonious scenario: the ancestor of all of these animals was not a flier, and *Archaeopteryx* developed flight independently than all other avialans, and then the clade of birds more derived than the new species evolved flight on its own. In this

scenario, the new species would not have evolved from a flying ancestor and would not have lost flight. This is why it is critical to not simply rely on the results of a phylogenetic analysis to make a big claim about flightlessness, but to document features of the anatomy that independently support evolution from a flying ancestor.

Response: Yes, we agree, and based on our phylogenetic analyses and recent studies, we suggest that powered flight evolved more than once within avialans. Although recent studies suggest flight capability of anchiornithines (Pei et al., 2020), this clade lack flight-related features in this clade (e.g., elongate forelimb and keeled ossified sternum). It has been argued that the most recent common ancestor of avialans were flightless (Xu, 2024). The discovery of *Yuezhuornis*, together with the co-occurring long-legged anchiornithine *Fujianvenator* lend further support to the multiple-origin scenario for powered flight in paravians (Pei et al., 2020; Xu, 2024).

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7. When it comes down to it, this new species is incredibly similar in anatomy to dromaeosaurids, troodontids, and anchiornithids. The authors themselves acknowledge this repeatedly throughout the manuscript. If all you had of this animal was the skull, then you would surely think it was a deinonychosaur (troodontid/dromaeosaurid), and probably a troodontid. I'm pretty confident that a phylogenetic analysis would position it there too—if all we had was the skull. Also, the ratios of the humerus-femur and forelimb-hindlimb are very similar to deinonychosaurs, and the metatarsus is as well—and it would be very short for an early avialan. Remarkably, the new species has a

hyperextensible second pedal digit! That is amazing! Or it would be amazing if it truly was an avialan, more derived than *Archaeopteryx*. Because this is a classic deinonychosaur feature. And I think, ultimately, a giant red flag: if this species has a classic deinonychosaur feature, then it most likely is a deinonychosaur. I will admit that the pelvis looks quite bird-like, especially the ilium. But: could this just be convergence? As the most detailed similarities are shared with enantiornithines, which are a more derived subgroup of birds—and clearly this new species is not an enantiornithine.

Response: We could not agree more with the Reviewer. Yes, when we first looked at the skull and the teeth, we were more than sure thought it was a deinonychosaur. However, when we took a deeper look, and compared every morphological characters with other paravians, we hesitated. The cross reexamination and phylogenetic analyses (taking different hypotheses into consideration) led us to suggest that this new specimen is an avialan rather than a non-avialan paravian. Previous studies show that the cranium is evolutionary conservative in theropod, attesting to many ancestral dinosaurian features that are still present in Cretaceous birds such as enantiornithines (Hu et al., 2019; Felice et al., 2020; Wang et al., 2021, 2022). Specifically, the plesiomorphic diapsid temporal configuration and dinosaurian palate were present in enantiornithines (Wang et al., 2021), and some primitive features even retained by *Ichthyornis* (Field et al., 2018). Meanwhile, the highly modified feeding apparatus in *Archaeopteryx*, the ancestrally clawed manual digits in Cretaceous avialans, and the sudden appearance of the pygostyle in the Jurassic avialan *Baminornis*, all demonstrate that the early avialan evolution has been deeply shaped by mosaicism.

References:

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Wang, M., T. A. Stidham, J. K. O'Connor, and Z. Zhou. 2022. Insight into the evolutionary assemblage of cranial kinesis from a Cretaceous bird. *eLife* 11: e81337.

8. Much of the discussion, and the phylogenetic analysis, relies on another paper not yet published, under review in *Science Advances*. Really this other paper should be published first, as it is describing another new species that is highly relevant to the arguments in this paper.

Response: Yes, this manuscript has been accepted by *Science Advances* and now in press status.

9. Figure 3—There are so many points and so many colors that it is hard to tell where the other Jurassic paravians (*Archaeopteryx*, *Anchiornis*, etc.) fall out in the plots. Please label them with their name and arrow as well, as you've done with *Yuezhornis*.

Response: Yes, we have labeled *Archaeopteryx*, *Anchiornis*, and other Jurassic avialans in this figure.

10. The skeletal reconstruction should be shown in the main paper, not just as a supplementary figure. It's important that readers can immediately see the body proportions, especially the size of the arms versus the legs, without having to wade into the supplement.

Response: Yes, we have put this reconstruction into Fig. 4. However, due to the limited figure number allowed by the journal, we have to leave it to the Extended Data Figure. I think this figure should be visible along with the main text.

11. In conclusion, I think this is a very interesting new fossil. It is a new species. It is worthy of publication. But I don't think the authors have demonstrated that it is a flightless bird. To do so, they need to make a very robust case that it is more derived phylogenetically than *Archaeopteryx*, and need to identify features of the skeleton that are hallmarks of flightlessness in birds. And they really need to convince us that it is not a deinonychosaur.

Response: We thank the Reviewer for pointing out the weakness of the original draft. Based on these comments, we have revised the manuscript and particularly strengthened the phylogenetic analysis of this specimen. We are looking forward to further suggestion to improve our understanding

Response to Dr. Patrick O'Connor:

1. Finally, the team closes with a discussion on the significance of the mosaic nature of *Yuezhornis* (e.g., deinonychosaurs-like hyperextensible pedal phalanges, short forelimb, etc.) in the context unique niche utilization by stem (very early stem) avialans. I am not sure that I agree that this challenges the 'traditional notion' that selection for powered flight was the primary force structuring the early avialan Bauplan—more importantly, I think it emphasizes that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of a clade in this one region. In either case, this important datapoint allows us to further consider the morphological range (disparity) of avialans/near-avialans in the Zhenghe Fauna—which is proving to be very interesting.

Response: We thank Dr. O'Connor for these positive comments. Yes, we agree that this

single fossil has not challenged the traditional notion that selection for powered flight was the primary force structuring the early avialan bauplan. We have revised the corresponding paragraph into “Our study demonstrates that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of birds”.

2. Lines 302 – 304: This is a fine statement. But is the notably short forelimb a retention of the ‘ancestral theropod’ condition (as stated here)? Or does this perhaps reflect ecological specialization (i.e., does it reflect homoplasy/reversal) in the context of flightlessness in a form derived from an otherwise flight capable group of early branching avialans? I appreciate early ecological specialization (implying flightlessness, and presumably morphologies indicative of such) could be either derived or potentially retentions). How do we differentiate between the possibilities? Can we?

Response: We thank the Reviewer for this comment. *Yuezhornis* has a short humerus and forelimb, and it is slightly shorter than in *Anchiornis*, but certainly shorter than *Archaeopteryx*. As such, it appears that the short forelimb was inherited from their common ancestor, and elongation of the forelimb took place latter during avialan evolution.

3. Lines 730 -732: The result shows the phalanx of IVPP 730 V34427 can be referred into deinonychosaurs-1 morphotype with a probability of 95%, 731 whereas its assignment to other morphotypes is highly unlikely ($p < 2\%$). So, does this represent additional evidence for retention of a deinonychosaurian feature? Homoplasy? Or does it represent homology (and group belonging for IVPP V34427 as a deinonychosaurian, rather than an avialan)? To which characters do you give the most weight? This is something for the team to further consider and discuss in the revision.

Response: This is an interesting question. *Yuezhornis* lacks many diagnostic features of troodontids and dromaeosaurids, such as the elongate anterior process of the lacrimal,

strap-like processes of the lacrimal, well-developed quadratojugal process of the jugal, a robust dentary with a lateral groove that widens posteriorly, closely packed middle and posterior maxillary teeth, elongate prezygapophyses and postzygapophyses of posterior caudals, and the sub- or arctometatarsal foot. Meanwhile, *Yuzhuoornis* exhibits several derived cranial features that speak clearly to its avialan affinity such as slender cranial elements (e.g., jugal, postorbital, and dentary), short anterior process of lacrimal sparsely spaced middle and posterior maxillary teeth, fewer dentary teeth, reduced zygapophyses of posterior caudals, elongate preacetabular ilium, short fibula, reduced fifth metatarsal, and non-arctometatarsal foot. Our phylogenetic analyses using different methods (maximum parsimony using equal weight and implied weighting, Bayesian tip-dating), and a constrain search (forcing *Yuezhurnis* as a deinonychosaurs), consistently supports its referral to the Avialae. We have extensively revised the manuscript to strengthen our conclusion and added additional content in the supplementary information (see “*Yuezhurnis* compared with other paravian theropods” section). Given its avialan affinity, and the absence of deinonychosaur-like pedal features in *Archaeopteryx* and *Anchiornis*, we suggest this pedal feature represents homoplasy between *Yuezhurnis* and deinonychosaurs.

4. Anatomical nomenclature: The anatomical description is well written throughout most of the manuscript (see a few minor suggestions/edits below). However, the use of single (vs. plural) for anatomical structures could be used throughout (e.g., prezygapophysis vs. prezygapophyses; Lines 137 – 141), but I’ll leave that decision to the editorial team. Also, hindlimb could be changed to hind limb throughout.

Response: Yes, we have revised these according to the suggestion.

5. Lines 36-38 (Bold Paragraph): I don’t so much think this discovery challenges a prevailing notion that aerodynamic selection was the determinant force of early avialan evolution—just that this discovery underscores the rapid ecological (and morphological) specialization that early avialans underwent (which is what your next line indicates) ...I

would delete this sentence.

Response: Yes, we have removed this sentence.

6. Line 43: Delete the word ‘the’ before terrestrial

Lines 44-46: alter text as follows: encompassing extensive changes in musculoskeletal and neural systems, epidermal structures, and hypothesized behavioral and physiological adaptations. (This distinguishes morphological systems in which you can observe/derive direct data [e.g., musculoskeletal, neural, and integumentary systems] from inferred behavioral/physiological ‘adaptations.’). Also, neurological is derived from neurology—which specifically related to the medical study of the nervous system—just use ‘neural’ to capture the point you are trying to make.

Line 46: Delete the word ‘The’ at the beginning of the sentence.

Line 47: Suggested change: Change ‘event’ to ‘transformation’ (or series of changes).

Line 48: insert the word ‘the’ between ‘Yet’ and ‘fossil’

Line 49: Suggested change: “...critical gap in early avialan diversification^{5,6}.”

Lines 50-52: Delete the words ‘which’ (in both cases)...and add ‘.’ after gen.

Line 50: delete “which we named” and just leave *Yuezhornis yangyuanensis*, gen. et sp. nov.—

Line 50: Add full stop (period) after gen (i.e., gen.)

Line 51: delete the word ‘which’ after the word ‘China’ (suggest that you change this to something like...a unit that has yielded some of the oldest avialans...).

Line 66: Delete the ‘.’ after et

Line 65: I would delete the fam. nov. designation (as it has no/little biological meaning). It is fine to formalize the Zhengheornithidae (but leave it without the Linnean rank designation).

Line 136: change to ‘twice as long as high’ (re: caudal vertebral

Line 136: Delete ‘Their’, replace with ‘The’

Line 137: Delete ‘the’ after ‘whereas’

Line 139: Length/depth OR length/height? I think the latter is more appropriate.

Line 140: Change ‘posteriorly’ to ‘posterior’

Line 143 - 145:

1st: “ancestral condition” for ‘theropod’? Theropoda? Or Neotheropoda? Paravians? Etc. Please be more precise.

2nd: whereas this bone is strut-like in Baminornis and more crownward taxa.

Line 145 – 146: Add “a feature that is otherwise only known in Anchiornis among theropods”⁴⁸.

Lines 143 – 148: Suggest to reorganize to highlight anatomy in the following sequence: Sternum, Furcula, then coracoid.

Line 198: add ‘s’ to ‘extend’ = ‘extends’

Line 225: Add ‘A’ to beginning of the sentence.

Line 227 – 228: ...it is interspersed within morphospace occupied by extant terrestrial birds.

Lines 233 – 234: Alternative wording suggestion: ...all the other early avialans (Supplementary Table 2), the forelimb in Yuezhuornis is shorter than the hind limb, with the humerus also being shorter than the femur.

Line 235: Replace ‘applied’ with ‘conducted’

Line 257: Delete the ‘s’ on deinonychosaurs. (the same suggested edit for Line 263, Line 817 & Line 294 and likely elsewhere throughout MS and SI).

Lines 276 – 277:

1st: Alter the sentence as follows: Zhengheornithids further differ from other...

2nd: ...in having a short, robust second metatarsal (or just MT II)

Lines 279 – 280: Despite a closer relationship between Zhengheornis and Yuezhuornis, the two forms are readily distinguishable from one another, including the presence in Yuezhuornis of penultimate manual phalanges with a well-developed hallux, deinonychosaurs-like pedal phalanges, and an elongate tail.

Lines 281 – 282: please clarify the size comparison with specific names.

Lines 288 – 289: change wording to: straight, posterior process of lacrimal (posterodorsally curved in early avialans).

Line 574: Change ‘detail’ to ‘detailed’

Lines 578 – 579: Suggested change: we sampled the right tibial ~mid-shaft for histological analysis.

Lines 590 - 593: Three lines of arrested growth can be recognized in some regions but cannot be traced around the full cross section due to fragmentation of the cortex. Taken together, these features indicate that growth had slowed or ceased entirely at the time of death⁸¹; thus, IVPP V34427 is here interpreted as a subadult or adult.

Line 614: Delete the words ‘the’ and ‘software’/

Line 817: Delete the ‘s’ on deinonychosaurs.

Line 884: PC 3? Or PC 2? Figure indicates PCs 1 and 2.

Response: We thank Dr. O’Connor for these detailed comments, and we have corrected all these mistakes accordingly.

7. Extended Data Fig 2: More detail on where (anatomically speaking) in the tibia, how the section was developed (see comments on the methods section).

Response: Yes, we added an outlined box in Figure 1 to denote the position of the histological sample.

8. The SI developed for this paper is adequate for the additional figures, tables, character definitions, and matrix used for the analyses. A more comprehensive differentia for all Zhenghe fauna paravians would be very useful in the beginning of the SI. I realize that an abbreviation version of this is developed in the methods section...but it is fairly telegraphic and only focused on *Yuezhurnis* and *Zhengheornis*.

Response: Yes, we have added additional comparison in the Supplementary information (titled “*Yuezhurnis* compared with other paravian theropods”).

We hope that the revised version of the manuscript can be accepted for publication and look forward to your decision.

Sincerely,

Min Wang

wangmin@ivpp.ac.cn

Dear Dr. Henry Gee,

We thank you, Drs. Fernando Novas, Patrick O'Connor, and two anonymous reviewers for their detailed and constructive comments in the second round of review, which have significantly improved the manuscript. We have submitted a revised version of our manuscript, figures, and Supplementary information, in which we have addressed your comments and those of the reviewers. Please find below our detailed response on the remarks of each reviewer. In order to be specific, all comments of each reviewer are listed and explained one by one.

Response to Editorial comments:

1. The number of references should generally not exceed 60. Currently you have 82 references

Response: We have shortened the reference list to 64 references, which will not affect the content of the manuscript.

2. Please remove the main figures from the article file and re-supply them individually in an acceptable format such as EPS, AI, PS, PDF, PPT, PSD or XLS (for graphs) with editable vector files.

Response: Yes, we did.

3. You have more than one account on EJP. Please contact Nature Manuscripts (naturemanuscripts@nature.com) to confirm all accounts which belong to you, and your primary email address.

Response: I have checked the system and make sure that I only have one account on EJP, the login name is: wangmin21, and the email address is wangmin@ivpp.ac.cn. I'm not sure how this matter occurred.

4. There are potential third party rights issues in the figures. Please check the sources of all illustrations and clarify whether permissions are needed to adapt or reproduce them. Please make sure to include the relevant details in third party rights table when you resubmit (more information below). If Biorender or a similar software has been used, please also ensure to provide relevant licenses. In particular please check figure/s: main figures 1,2, 3, 4, and figure 1-6,

Response: All the figures, including the drawings in Figures 1, 2, 3, 4, and Extended Data Figures 1-10, and the supplementary figures 1-4, were originally created by the corresponding author (Min Wang).

5. Please make sure to provide a third party rights table (more information below) when you resubmit. If Biorender or similar software has been used, please also ensure to provide relevant licenses.

Response: Because all the figures have been created originally by the authors in this study, this is no need for a third-party rights table.

6. Please ensure that the text size in all figures is at least 5 pt Arial.

Response: Yes, we confirm.

7. Please remove the Extended data figures from the article file and re-supply them individually in EPS, JPEG or TIF format.

Response: Yes, we did.

8. Please provide a funding section as a separate section.

Response: Yes, we did.

9. The web-link provided in the code availability statement

(<https://doi.org/10.6084/m9.figshare.31228414>) is not valid/ currently not accessible.

Please provide a valid and accessible web-link.

Response: The figshare link (<https://doi.org/10.6084/m9.figshare.31228414>) was generated when I submitted the manuscript by the Nature online manuscript submission and tracking system. I think this link should be activated automatically by the system when this manuscript is published.

Response to Dr. Fernando Novas:

1. LINES 38-39: "Our study demonstrates that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of birds".

COMMENT: I agree with authors, but I ask whether such pattern also applies to other parts of the phylogenetic tree of Avialae (in other words, it is not unique of the "basal diversification" stage).

Response: I think this pattern could work in other parts of the avialan phylogeny. For instance, the rapid occurrences of the crown groups following the K/P event, and the independent losses of flight within the paleognaths. Unfortunately, this is beyond the scope of this study, and in this study, we highlight this pattern took place in the early evolution of avialans.

2. LINES 53-56: Our comparative analyses show that *Yuezhornis* compares favorably with living terrestrial birds in limb proportions, indicative of terrestrial, flightless lifestyle, shedding new light on ecological diversification of early-diverging avialans.

- COMMENT: I agree with this, but it is reasonable to expect that *Yuezhornis* ALSO

shared similar proportions with the terrestrial non-avian paravians. In fact, all these theropods (INCLUDING early birds) were "terrestrial": they walked on land using similarly constructed hindlimbs. The differences are between volant vs non-volant theropods. By sure *Yuezhornis* was terrestrial (like other dinosauriforms), but a non-volant bird (an evolutionary reversal).

Response: Yes, we agree and have revised this paragraph to say that *Yuezhornis* share similar limb proportions with some non-avian paravians.

3. LINES 132-133: "The four caudals preserved near the mid-length of the right tibia are twice as long as high. "

- COMMENT: This information fits well as part of a text-figure, but here I believe that authors may offer morphological / proportional reasons to indicate the approximate position in the caudal series. Afterall, saying "caudals preserved close to the tibia" circumstantially occur only in the holotype specimen, and is not anatomically informative.

Response: Yes, we intent to refer the four caudals that were located near the mid-length of the right tibia. The free caudals are disarticulated and incomplete, making it challenge to identify the real anatomical position of these caudals. We have revised the sentence as "the four caudals displaced near the mid-length of the right tibia" to clarify this issue.

4. - LINES 242-245: "Both morphometric analyses and focal features (e.g., wide interclavicular angle, short coracoid, reduced deltopectoral crest, LONG BONY TAIL, and shortened forelimb) STRONGLY indicate that *Yuezhornis* was non-volant, but adapted to terrestrial ENVIRONMENTS."

- COMMENT ON "LONG BONY TAILS": Why? Is it as long/longer than in *Archaeopteryx*, *Microraptor* and other early volant paravians? Probably the kind of plumage coat is more important than how long was the bony tail. Please, justify.

- COMMENT ON “STRONGLY”: Probably better is to say "congruently indicate", instead of "strongly"
- COMMENT ON “ENVIRONMENTS”: Apparently all these paravians lived in a "terrestrial environment" (vs shoreline environment). Let me suggest to say "terrestrial mode of life".

Response: We thank Dr. Novas for these comments. We have revised these accordingly. Here the bony tail refers to that the tail is not shortened to the degree seen in the pygostylians. An elongate tail increases drags and impacts flight performance. We did not intent to say that *Yuezhornis* has a longer bony tail than in *Archaeopteryx* or other paravians, because the caudal series is incomplete and disarticulate, preventing estimation of its real length.

5. - LINES 246-265: “Phalanx X”

- COMMENTS: If "phalanx X" was preserved as forming part of a complete foot, then no doubts will exists that it is the phalanx II-2. The same identification is obtained by conducting comparisons with available three-dimensionally preserved digits of other paravians, the identity of such isolated pedal bone will be easily solved. Then, first, I still believe that the statistical analysis conducted by the authors is not required (think about applying a statistical method to support the identity that an "isolated femur" is a femur). Second, the positive aspect is that authors demonstrate (through their statistical analysis) the absence of deinonychosaurian features in *Archaeopteryx* and *Anchiornis*, modifying previous interpretations. Third, and most important, is the fact that the foot of *Yuezhornis* retained the condition of deinonychosaurian digit II. In sum, the statistical analysis allows recognize different shapes of digit II among early avians (a welcome result of the present manuscript), but it is not required to demonstrate that "phalanx X" is a ph. II-2.

Response: We thank the Reviewer for the comments. Yes, the preserved morphology of this phalanx exhibits shared features with phalanx II-1 or II-2 of

deinonychosaurians, which is supported by the geometric morphometric analysis. And as the reviewer said, it is importantly to find out that phalanx II-1 and II-2 of *Archaeopteryx* and *Anchiornis* differ from that of deinonychosaurians.

6. - LINES 268-270: “Our phylogenetic analyses consistently recovered *Yuezhornis* as the sister taxon to *Zhengheornis*, and the new clade emerged just crownward of *Archaeopteryx* as one of the earliest diverging avialans”

- COMMENTS: This is an original and highly interesting result!

Response: Thanks.

7. - LINES 274-277: “(character state 82.0 in Supplementary information); extensive pubic apron without a slit (character state 179.0); interclavicular angle greater than or equal to 90° (character state 330.0); and distal end of tibia approximately equal to its midshaft in width (character state 421:1).”

- COMMENTS: I understand that authors recovered this list of synapomorphies after their phylogenetic analysis. However, it calls my attention that most of these features are widely present among outgroups of Avialae. For example, "extensive pubic apron" represents an Archosauriform condition, while a reduction of the pubic apron occurred in the course of pygostylian / ornithothoracine evolution. Regarding ch. 330.0, the condition represents the plesiomorphic one, and it was listed above (line 243) as evidence of the non-volant capabilities of *Yuezhornis*, and also on lines 321-322 where it is said that *Yuezhornis* exhibits the "ancestral theropod condition" (i.e., interclavicle angle obtuse).

Response: We thank the Reviewer for these comments. We share the same feelings now. With the continuing discoveries of paravians, it shows that convergent evolution or mosaicism has systematically shaped the diversification of stem avialans, and some characters that are used to diagnose the Avialae are phylogenetically widely distributed. Therefore, the combination of character states, rather than single

character, is more phylogenetically informative. The characters listed here are the results obtained from our phylogenetic analysis.

8. - LINE 337: “flight”

- COMMENTS: As it is, the phrase taxatively supports a dual origin of flight, once in Archaeopterygids, and (separately) in *Jeholornis*+Pygostilia. Probably more appropriate is inserting (also) the alternative hypothesis, the one supporting the loss of flying capabilities in Zhengheornithidae.

Response: Yes, we thank the Dr. Novas for pointing out the alternative hypothesis, and we have added this content in the revised manuscript.

Response to Reviewer 2:

1. Ok. Thanks to the authors for cleaning up the manuscript nicely. I'm a lot more convinced now than I was first time around. The study is clearly very interesting. The fossil seems important, and it's nice to know more about the Jurassic radiation of Avialae. For more than a century we relied entirely on Archaeopteryx. This now fossil seems to illuminate an early radiation that we previously knew basically nothing about.

Response: we thank the Reviewer for the positive comment.

2. Abstract: "The origin and early diversification of birds remain one of the most debated transitions in vertebrate evolution"

>>This is not correct (see my previous review). In your response you said. That you wanted to communicate that there were various things that still remain unknown. That's true and I agree with it. But is not the same as saying "is one of the most debated transitions in vertebrate evolution". I agree that it is important that you emphasize the importance of the work, but also that the words remain scientifically correct. So please rephrase this.

Response: Yes, we have revised this sentence into “The origin and early diversification of birds remain highly debated in vertebrate evolution”.

3. "While macroevolutionary models suggest a Jurassic radiation"

>>"macroevolutionary models" is a little vague. Could you instead say "time-scaled phylogenies" or "estimates of the evolutionary timescale".

Response: Yes, we revised accordingly.

4. "Our study demonstrates that evolution works fast as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of birds"

>>"Evolution works fast" seems a little informal.

Response: We have revised this sentence into “Our study demonstrates that evolution works extensively as exemplified by the occurrence of multiple, divergent ecological pathways being exploited in the initial diversification of birds”

5. Figures: In the PCA plot (Fig. 3), it would be great to show the morphological changes corresponding to each axis more clearly. Currently they are very tiny and not visible.

Response: Yes, we have resized the corresponding skeletal elements to show the changes along the PC axes.

Extended Data Fig.1: Please check the measurements on this image compared to the real specimen (Fig. 1). The humerus seems much smaller and slenderer in EDF 1 than in Fig. 1. I want to confirm that the true scale is used rigorously.

Response: Yes, we have revised Extended Data Fig. 1. The humerus, as well as other elements (e.g., femur), in Extended Data Fig. 1 appears relative slender, because they exposed in different view compared with Figure 1 (laterodorsal view compared with dorsal view).

Response to Reviewer 3:

I thank the authors for their revision, and their careful responses to my comments. The paper is now much improved. There is no doubt this is an important new taxon. I agree that this is a flightless paravian close to the origin of Avialae, and although character support for major nodes around Avialae is labile and relationships often change depending on analysis and method, I find that the authors have presented a compelling case that this new taxon is an avialan more crownward than *Archaeopteryx*. And the authors have certainly presented a compelling case that this animal could not fly. I have no doubt about that. What this comes down to is the importance of the discovery. Initially, I had thought the authors were arguing that this new taxon was the oldest instance of a secondarily flightless bird in the fossil record—a big claim, but if true, a major discovery. Now they have been quite clear in their responses and in the revised manuscript that they did not mean to imply that it was secondarily flightless, only that it didn't fly. In fact, they argue that it never had flying ancestors. And therefore, flight must have evolved multiple times in avialans. But the multiple-origin scenario for flight is well established. It was the subject of a major paper by Pei et al. in 2020 (*Current Biology*), and over the last decade or so, several Mesozoic paravians have been found to be non-flying species within Avialae or very close to it. It is great that this new fossil supports the multiple-origin scenario. It is probably one of the strongest pieces of new support for the hypothesis. But is that enough for a Nature paper in 2026? I think the paper as written is sound. I don't have any suggestions for further improvement in terms of the writing or framing or anatomical details. If the other referees are strongly supportive of publication in Nature, I would not object. So I leave this in the hands of the editors: the science in this paper is good, the fossil is interesting and important, but it mostly confirms a

hypothesis that has been around for quite some time, and is supported by many other lines of evidence.

Response: We thank the Reviewer for these positive comments, and the previous comments indeed help us strengthen the manuscript.

Response to Reviewer 4:

1. A. Summary of Key Results: Liming Xu et al (Nature 2026-02-03370B-Jurassic flightless bird reveals early ecological diversity of avialans) provide descriptive/comparative and functional analyses on a new Late Jurassic stem bird, *Yuezhornis yangyuanensis*, representing another new taxon of early branching avialan from the Zhenghe Fauna (China).

The team has now completed a revision of the manuscript, addressing the distribution of characters supporting the assignment to Avialae (rather than the substantially longer tree length necessary to assign to Deinonychosauria), along with an extensive ‘response to reviewers’ following the first round of reviews. To my reading, the authors are supporting assignment to Avialae, fully acknowledging the admixture of character states present in any form from this part of the tree (i.e., they are explicit and acknowledge that rampant mosaicism of traits makes this assignment a challenge for researchers).

As I stated previously, the occurrence of “deinonychosaurian” characteristics (e.g., dental count, tooth size, tooth shape [blade-like], jugal with reduced QJ process, etc.) combined with mixed avialan/troodontid (e.g., L-shaped quadratojugal lacking a posterior process) OR avialan/dromaeosaurid characteristics (e.g., lacrimal with straight dorsal margin, etc.) continues the trend of anatomical mosaicism that we see among stem birds/paravians (as recently noted in several papers by this research team and others; e.g., Xu et al., A new avialan theropod from an emerging Jurassic terrestrial fauna; Nature 621: doi.org/10.1038/s41586-023-06513-7) and shouldn’t be surprising. This will continue to be an interestingly challenging part of the paravian/avialan distribution to sort out, even with contemporary approaches in

comparative biology/paleontology.

The team retains necessary background and context for Yuezhuornis (and Zhengheornithidae more generally) as part of the Zhenghe Fauna, emphasizing the significance of the temporal occurrence as critical for de-tangling/elucidating inter-relationships among Jurassic paravians. Again, this paper presents important new data on early branching avialans from the Late Jurassic, this time emphasizing the possibility of an early avialan (or interesting non-avialan paravian?) exploiting/succeeding in an ecological role that differs from other closely related taxa. Originality and Significance: This is a very significant new specimen from the Late Jurassic...a time period in avialan history for which there are very few fossils from outside of a handful of locations. The significance of the specimen is apparent, as highlighted by the exhaustive treatment (phylogenetic and functional) given the new fossil.

The revised manuscript is original and significant, both for its description and comparative quantitative framework in which the new specimen is presented. The revision continues to emphasize the significance of the new specimen...and provides a clearer emphasize on those traits essential for interpreting the specimen. The revision also provides needed clarity on the interpretation of a specimen like this for assignment to Avialae vs. non-avialan paravians.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The data (i.e., a new fossil, its descriptive anatomy, and phylogenetic characters associated with it) are clear and represent standard approaches in how the authors have presented them.

The anatomical description is appropriately detailed, emphasizing those portions of the skeleton/dentition essential for considering the phylogenetic context of the specimen (and by extension, the ambiguity of traits distributed among paravians) The revision provides a cleaned-up version, continuing to emphasize those parts of the skeleton most relevant for assessing the phylogenetic affinities of the new specimen.

D. From my original review: Appropriate use of statistics and treatment of

uncertainties: The approaches used by the authors include the typical complement of phylogenetic and morphometric analyses used for fossil data such as those at the focus of the paper. The dual use of both MP and tip-date informed Bayesian Inference analyses are appropriately applied for the morphology-based phylogenetics work, as are the morphometric and geometric morphometric approaches in the context of both ecological/functional characterization. Uncertainty measures for all phylogenetic, morphometric, geometric morphometric, and ecological/functional are appropriately considered. The revision maintains these analytical approaches.

E. Conclusions: robustness, validity, reliability

The conclusions of this revised paper are very interesting, and should be easily reproducible for all phylogenetic, geometric morphometric, and phylo comparative purposes. The new fossil is certainly exciting, with a team who has provided the requisite comparative work to highlight its significance.

F. Suggested Improvements/Line Edits:

G. References: appropriate credit to previous work

Appropriate references for the paper.

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

The new specimen is well contextualized through both the opening of the revised paper (i.e., the bold paragraph), the description, the discussion, and via the figures. The main theme of the paper is consistent throughout, albeit with more clarity on interpretation in the revised manuscript.

The final paragraph of the main text attempts to summarize the importance of this new fossil, emphasizing the ecological significance to the broader audience—this is a very nice change of pace from many standard ‘new species’ descriptions of Mesozoic birds/avialans.

Response: We thank Dr. O'Connor for these positive comments. And yes, it is much exciting to find this fossil that provides important information regarding the origin of birds.

We hope that the revised version of the manuscript can be accepted for publication and look forward to your decision.

Sincerely,

Min Wang

wangmin@ivpp.ac.cn

Dear Dr. Henry Gee,

We thank you, and the Reviewer 1 for the detailed and constructive comments in the third round of review, which have significantly improved the manuscript. We have submitted a revised version of our manuscript, figures, and Supplementary information, in which we have addressed your comments and those of the reviewers. Please find below our detailed response on the remarks of each reviewer. In order to be specific, all comments of each reviewer are listed and explained one by one.

Response to Reviewer 1:

1. Comments on MAIN TEXT

Page 7 – line 131 – Replace “displaced” for “preserved”

Page 7 – line 135 – Modify “indicating that they are located posterior to the transition point” for “indicating that they may correspond to the transition point”

Page 7 – line 142 – Authors say: “The coracoid is trapezoidal (Fig. 2d), an ancestral condition for Theropoda”. Let me suggest applying the term "trapezoidal" (i.e., dorsoventrally deep coracoid, with angled anteroventral margin) for PARAVIAN theropods, in contrast to an elliptical-shaped and dorsoventrally shallower one of non-paravian theropods. In sum, let me suggest replacing "an ancestral condition for Theropoda" for "an ancestral condition for Paraves".

Page 10 – line 206 - Replace "has" for "had", because the capability to hyperextend the digit was a function / behaviour, which took place when the animal was alive.

Response: Yes, all these revision have been done.

Page 11 – line 213. Authors say: “Yuezhornis exhibits features relating to non-volant adaptation (e.g., short forelimb, trapezoidal coracoid...”. Regarding the shape of coracoid as mirroring flying capabilities, I agree that a trapezoidal coracoid is widely present among non-volant paravians (e.g., Deinonychus, unenlagiids). However, it is also present in Microraptor and Archaeopteryx, for which (and due to wing-feather development) most authors agree were volant. Thus, there is not a univocal relation

between this shape of the coracoid with the flying capabilities.

Page 11 – line 213. Authors say: “Yuezhurnis exhibits features relating to non-volant adaptation (e.g ...extensible pedal digits)”. I am unable to tie flying capabilities with "extensible pedal digits". Please, explain.

Response: Yes, we agree with the Reviewer that the direct causal relationship between the trapezoidal coracoid, extensible pedal digits and flight capability is not clearly established, and we have removed these words.

Page 16 – lines 317-318. Authors say: “The pectoral girdle and forelimb of Yuezhurnis exhibit the ancestral theropod condition”. Let me suggest replacing “theropod condition” for “paravian condition”.

Page 16 – line 333. Let me suggest replacing “... slightly younger than...” for “... slightly geologically younger than...”

Response: Yes, we have revised all these paragraphs.

2. Comments on SUPPLEMENTARY INFORMATION

Page 1. Authors say: “The coracoid is trapezoidal, a feature widely distributed among non-avian theropods”. In my view, the trapezoidal condition applies for Paraves, but not for non-paravian theropods. Besides, a trapezoid-shaped coracoid is present in the early avian Archaeopteryx. Thus, let me recommend saying that the feature is "widely distributed among early paravian theropods".

Response: Yes, we revised this sentence accordingly.

Page 1. Authors say: “A trapezoidal-shaped coracoid independently evolved in anchiornithines and the Cretaceous avian Sapeornis”. I am surprised for this statement, because a trapezoid-shaped coracoid is present in dromaeosaurids, unenlagiids, troodontids, Archaeopteryx, Anchiornis, Yuezhurnis, Confuciusornis

and Sapeornis, and the only exception (among basal Avialae) is currently Jeholornis. Then, alternative hypothesis that "a strut-like coracoid evolved once in Jeholornis and once in Ornithothoraces" probably results more appropriate.

Response: Yes, we changed the sentence accordingly.

3. Comments on FIGURE 1 (EXTENDED DATA):

Please, review drawing because the knee seems dislocated (femoral distal condyles are anteriorly displaced respect to proximal end of tibia).

Response: Yes, we have revised this figure and replaced the tibia.

We hope that the revised version of the manuscript can be accepted for publication and look forward to your decision.

Sincerely,

Min Wang

wangmin@ivpp.ac.cn