

Independent assembly of the flight apparatus in a non-avian dinosaur clade

Corresponding Author: Dr Andrea Cau

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

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors describe a new very well-preserved skeleton of microraptorine dromaeosaurid from the Jiufotang Formation of Liaoning, China. The describers give sufficient detail in the text and in the illustrations to characterize this fossil and to justify the assessment of it as a new taxon.

One item that should be included is a statement about the circumstances of the discovery of this fossil: the year of discovery; the discoverer's name (if known); the situation of its acquisition by MHGU (Did their team collect it? Was it discovered by some other person or group and the museum purchased it or it was donated to them? Etc.)

Beyond the description of the new fossil, the primary contribution of this study is the detailing of the acquisition of flight-associated derived states in the anatomy of microraptorines and in avialians. The authors show how basally-diverging dromaeosaurids (and even early branches of Microraptorinae) lack the aerial traits shared between derived microraptorines and derived avialians: this is strong evidence for the convergence (or parallelism) of these attributes and against an aerial mode of locomotion for basal Paraves. This helps resolve one of the main matters of debate currently ongoing in paravian studies (that is, how many times did powered flight evolve in maniraptorans on the way to Neornithes).

The data are sufficiently provided for replication of phylogenetic analyses.

One thing that seems to be lacking from the manuscript is a simplified version of one of the phylogenetic analyses (retaining the expanded details of Microraptorinae but reducing other clades to single branches) as part of the illustrations in the body of the paper. As one of the primary aspects of this paper is increased resolution of microraptorine relationships, this information should be up front rather than tucked away in the Supplementary Data.

Reviewer #2

(Remarks to the Author)

Dear Authors,

Thank you for the opportunity to read your new research "Independent assembly of the flight apparatus in a non-avian dinosaur clade". This is a topic I follow with great interest and was excited to read your work. The description of a new small bodied theropod is of obvious importance and should certainly be published. This paper is well-organized and reads very clearly, I noted very few places where any small changes needed to be made (I note only three below). I commend the authors for their consideration of homology and ontogeny. The differences in the maxillary fossa are particularly distinct, though I am happy to see that other features of the skeleton distinguish it from other microraptorines. I have two concerns which I recommend addressing before publication: a correction and a suggestion for elaboration.

1. In the abstract and histology sections the claim is made that the paper will "describe for the first time forelimb osteohistological features for that clade [Microraptorinae]" (lines 11-12). This is incorrect. Poust et al. 2020, which you cite described the osteohistology of the mid-diaphysis of the humerus of Wulong and the radius of Sinornithosaurus. The authors even cite this study in the context of radial histology (e.g. line 236). The claims that this is the first study need to be removed. However, as I will stress to the editors, I do not believe that this reduces impact or importance of this paper. The forelimb

histology descriptions of Poust et al. are short and written in support of the hindlimb data. The current study includes fuller descriptions, which is very worthwhile. It also extends the forelimb histology record to a new taxon and gives the opportunity to compare the patterns seen with the previous records. The fact that the radius sample is directly comparable to that of *Sinornithosaurus* is of particular importance. I would recommend adding additional comparisons in this section. Then, if the authors wanted to, they could rightfully claim that the paper included the first comparison of histology from similar forelimb elements, which would allow at least an initial assessment of whether these patterns applied generally in the group.

2. The concept of “deep homology” is complex, as discussed in the paper by Scotland that you cite as well as in Shubin’s initial formulation. Because we do not yet know with any precision the context in which any instance of flight has evolved, it is difficult to know whether the pressures that led to the selection for the component parts of the flight apparatus happened in the same way or even in the same order. To make a hypothetical comparison using an example brought up in the paper, postcranial pneumatization in two distinct branches would traditionally be judged to be independently evolved if it was discovered to have proceeded cranio-caudally in one branch and back to front in another. But that difference would not necessarily rule out genetic/developmental features present in the common ancestor that allow the pneumatization to occur at all. Similarly, a shared developmental pattern might be expressed in a different order under related but not identical selective regimes, or a set of deeply homologous features might add together to form a functional unit (such as the flight apparatus), which would itself be convergent or analogous even though made of homologous parts.

As Scotland states, “...the phrase deep homology is no substitute for a specified phylogenetic level and precise conditional phrase”.

One relatively easy change that could help with this would be to add the words “a single” to the final statement (as in “acted as a single “deep homology” igniting...”). That helps to define for the reader the phylogenetic level at which your data is beginning to rule out deep homology, that is to say: the order of acquisition of features is different, which suggests that the flight apparatus as a whole unit cannot be deeply homologous. Further explanation would help, but this could be an efficient part of a way to address this complexity.

Small suggestions:

Line 23: should be plural “gut contents”

Line 215: word “however” is unnecessary

Line 484: in main text the zone3 osteocyte organization is mentioned, but that doesn’t seem to be described here. I would suggest adding a description of that to this section.

Good luck, I look forward to seeing this work published.

Sincerely,

Ashley Poust

Reviewer #3

(Remarks to the Author)

Dear authors and editors,

I congratulate for the discovery of the new microraptorine *Norellraptor*, illustrating about the anatomy of this remarkable clade of paravians. However, I don’t feel that it impulse a novel view about the aquisition of flight related characteristics.

My main concerns about the submitted ms are ennumerated as follows:

1. Several papers by Argentine paleontologist (e.g., Agnolín and Novas, 2013; Agnolín et al 2019; Novas et al., 2020, 2021; Motta et al., 2025) offered valuable information about the anatomy of unenlagiid paravians and --most important-- how they modify previous conceptions about paravian phylogeny and acquisition of flight. Notably, none of these papers and interpretations are cited in the present manuscript. I recommend to read the above cited contributions.

2. The text lacks references to unenlagiids, albeit one of the phylogenetic trees provided by the authors indicates Unenlagiidae as sister group of Avialae. Also important is to say that the tree topology matches well with that recently published by Matías Motta and colleagues (Matías J. Motta, Federico L. Agnolín, Federico Brissón Egli, Sebastián Rozadilla & Fernando E. Novas (2025) Phylogenetic relationships of Unenlagiidae among Paraves (Dinosauria), *Journal of Systematic Palaeontology*, 23:1, 2529608, DOI: 10.1080/14772019.2025.2529608).

3. Considering that authors opted to submit their ms to Nature, I believe the following description is redundant with already published descriptions of other members of Microraptorina. I believe that a description of a new taxon for a paper in Nature must contain outstanding novelties, which I am unable to see in the present version.

The alternative to submit the ms to a "classic" journal devoted to paleontology seems more appropriate, and authors may use present, well done description to increase in anatomical details and, particularly, in detailed comparisons with other paravian taxa.

Comparative figures of *Norellraptor* with other currently known microraptorans (which do not form part of the current ms) will benefit the presentation of the new discovery.

In the context of a more "classic" description, even the osteohistological features of *Norellraptor* will be quite adequate (as they are here exposed, are unrelated with the main topic considered in the ms: the independent origin of flight features in different paravian clades).

Regarding the independent aquisition of flight capabilities in different paravian groups, the topic has been already

considered in different publications of previous authors, thus it is not novel by itself.

Finally, although the hypothesis that different characteristics evolved separately (and in different order) among Microraptoria and Avialae seems probable, it must be said that a similar process of "mosaicism" occurred among different clades of early avialans (confuciusornithids, junguoforthids, sapeornithiforms, Jeholornis, etc. etc): these early avians DIFFERENTIALLY share derived characteristics related with improved flying abilities. I guess such an evolutionary process widely applies to all clades of the Tree of Life.

4. Osteohistological information is welcome, of course. However, it constitutes a detailed description of the osteohistological features of the specimen, lacking considerations about physiological aspects of these theropods. It could be great that authors expand their ideas on this particular topic. However, these descriptions and considerations can not be easily integrated with the main purpose of the present ms: independent avian acquisition in Microraptoria.

5. No explanations are provided for the figures forming part of the main text.

A corrected version of the ms is attached. I hope my comments become useful for the authors.

Sincerely yours,
Fernando Novas

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors have sufficiently addressed the issues raised by myself and the other reviewers. I do not see the need of further revisions.

Reviewer #2

(Remarks to the Author)

Thank you for your work in responding to reviewer comments. My substantive concerns have been addressed and I believe the paper is ready for submission.

Reviewer #3

(Remarks to the Author)

Dear authors,

I like very much the corrected version of your manuscript. Thanks for explaining point by point each of the issues I raised in the previous version. I am attaching the pdf of your contribution with some minor observations. I hope to see it published in Nature Communications.

Sincerely,
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Please, see below a point-to-point reply to the reviewers (our reply marked in **bold**).

REVIEWER COMMENTS

Reviewer #1:

The authors describe a new very well-preserved skeleton of microraptorine dromaeosaurid from the Jiufotang Formation of Liaoning, China. The describers give sufficient detail in the text and in the illustrations to characterize this fossil and to justify the assessment of it as a new taxon.

One item that should be included is a statement about the circumstances of the discovery of this fossil: the year of discovery; the discoverer's name (if known); the situation of its acquisition by MHGU (Did their team collect it? Was it discovered by some other person or group and the museum purchased it or it was donated to them? Etc.)

The specimen was discovered by a local farmer near Lamadong Town (Jianchang County, western Liaoning, China), and donated to the museum of Hebei GEO University in 2023. Our team checked the integrity of the specimen and ascertained the fossil locality. We have added this information in the manuscript.

Beyond the description of the new fossil, the primary contribution of this study is the detailing of the acquisition of flight-associated derived states in the anatomy of microraptorines and in avialians. The authors show how basally-diverging dromaeosaurids (and even early branches of Microraptorinae) lack the aerial traits shared between derived microraptorines and derived avialians: this is strong evidence for the convergence (or parallelism) of these attributes and against an aerial mode of locomotion for basal Paraves. This helps resolve one of the main matters of debate currently ongoing in paravian studies (that is, how many times did powered flight evolve in maniraptorans on the way to Neornithes).

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We agree with the reviewer with this suggestion, and thank them: a simplified version of the strict consensus topology has been included as new Figure in the main manuscript.

Reviewer #2:

Dear Authors,

Thank you for the opportunity to read your new research "Independent assembly of the flight apparatus in a non-avian dinosaur clade". This is a topic I follow with great interest and was excited to read your work. The description of a new small bodied theropod is of obvious importance and should certainly be published. This paper is well-organized and reads very cleanly, I noted very few places where any small changes needed to be made (I note only three below). I commend the authors for their consideration of homology and ontogeny. The differences in the maxillary fossa are particularly distinct, though I am happy to see that other features of the skeleton distinguish it from other microraptorines. I have two concerns which I recommend addressing before publication: a correction and a suggestion for elaboration.

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We thank the reviewer for the comments and the suggestion: we have edited the sentences and expanded the comparative section mentioned.

2. The concept of “deep homology” is complex, as discussed in the paper by Scotland that you cite as well as in Shubin’s initial formulation. Because we do not yet know with any precision the context in which any instance of flight has evolved, it is difficult to know whether the pressures that led to the selection for the component parts of the flight apparatus happened in the same way or even in the same order. To make a hypothetical comparison using an example brought up in the paper, postcranial pneumatization in two distinct branches would traditionally be judged to be independently evolved if it was discovered to have proceeded cranio-caudally in one branch and back to front in another. But that difference would not necessarily rule out genetic/developmental features present in the common ancestor that allow the pneumatization to occur at all. Similarly, a shared developmental pattern might be expressed in a different order under related but not identical selective regimes, or a set of deeply homologous features might add together to form a functional unit (such as the flight apparatus), which would itself be convergent or analogous even though made of homologous parts.

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We thank much the reviewer for the comments and suggestions, which we have followed in the edited manuscript.

Small suggestions:

Line 23: should be plural “gut contents”

Line 215: word “however” in unnecessary

Line 484: in main text the zone3 osteocyte organization is mentioned, but that doesn’t seem to be described here. I would suggest adding a description of that to this section.

We have added a description of the section.

Good luck, I look forward to seeing this work published.

Sincerely,

Ashley Poust

Reviewer #3 (Remarks to the Author):

Dear authors and editors,

I congratulate for the discovery of the new microraptorine Norellraptor, illustrating about the anatomy of this remarkable clade of paravians. However, I don't feel that it impulse a novel view about the aquisition of flight related characteristics.

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1. Several papers by Argentine paleontologist (e.g., Agnolín and Novas, 2013; Agnolín et al 2019; Novas et al., 2020, 2021; Motta et al., 2025) offered valuable information about the anatomy of unenlagiid paravians and --most important-- how they modify previous conceptions about paravian phylogeny and acquisition of flight. Notably, none of these papers and interpretations are cited in the present manuscript. I recommend to read the above cited contributions.

We thank the reviewer for the suggestions. In the last 25 years, the microraptorines have been considered key taxa in both phylogenetic and functional discussions of avian flight origins. As discussed in our manuscript, the significance of the microraptorines in bird evolution needs to be re-evaluated. In fact, we agree with the reviewer that the unenlagiids have redefined both topology of the paravian relationships and the earliest phases of the avialan evolution, and that both further corroborate our main argument about the status of the microraptorines in this topic. Accordingly, in the edited manuscript we have included an explicit mention to the above-listed studies on the unenlagiids.

2. The text lacks references to unenlagiids, albeit one of the phylogenetic trees provided by the authors indicates Unenlagiidae as sister group of Avialae. Also important is to say that the tree topology matches well with that recently published by Matías Motta and colleagues (Matías J. Motta, Federico L. Agnolín, Federico Brissón Egli, Sebastián Rozadilla & Fernando E. Novas (2025) Phylogenetic relationships of Unenlagiidae among Paraves (Dinosauria), Journal of Systematic Palaeontology, 23:1, 2529608, DOI: 10.1080/14772019.2025.2529608).

We agree with the reviewer that the similar placement of the unenlagiines (among Paraves) obtained by our phylogenetic analysis and by the above-mentioned study is a significant result: in fact, our phylogenetic analysis represents the first independent replication of the scenario discussed by Motta and colleagues. Accordingly, we have added a new paragraph discussing the implications of this result and mentioned the relevant literature.

Yet, we remark that the phylogenetic placement of Unenlagiidae relative to Dromaeosauridae and Avialae does not represent the main topic of our analysis, which instead focuses on the assembly of the flight-related features along Microraptorinae and its significance in interpreting the evolution of flight among the taxa traditionally included in Avialae. As explicitly stated by the reviewer himself, unenlagiids are not members of Avialae (*sensu stricto*: the least inclusive clade containing *Archaeopteryx* and extant birds), but a sister taxon of the avialans. Although we concur with the reviewer that Unenlagiidae is significant in revealing key information about the *ancestral* avialan body plan, the clade that has been usually compared to the microraptorines in term of flight adaptations is Avialae *sensu stricto*. The latter was thus the target of our analysis. Nevertheless, it should be remarked that the main

conclusion of our study (focusing on the microraptorines) is an independent support to the arguments by Motta et colleagues (focusing on the unenlagiines), because both studies - even if from different perspectives - concur in considering the wing apparatus of the microraptorines less relevant than usually assumed for understanding the origin of the wing apparatus in Avialae.

3. Considering that authors opted to submit their ms to Nature, I believe the following description is redundant with already published descriptions of other members of Microraptoria. I believe that a description of a new taxon for a paper in Nature must contain outstanding novelties, which I am unable to see in the present version.

The alternative to submit the ms to a "classic" journal devoted to paleontology seems more appropriate, and authors may use present, well done description to increase in anatomical details and, particularly, in detailed comparisons with other paravian taxa.

We disagree with the reviewer. As demonstrated by this list of papers focusing on non-avian dinosaurs and Mesozoic birds, published in Nature Communications (linked below), our manuscript broadly fits the scopes of this journal in both content and structure.

Kurri Rogers et al.: <https://www.nature.com/articles/ncomms1578>

Carney et al.: <https://www.nature.com/articles/ncomms1642>

Goswami et al.: <https://www.nature.com/articles/ncomms2716>

Evans et al.: <https://www.nature.com/articles/ncomms2749>

Fanti et al.: <https://www.nature.com/articles/ncomms3080>

Godefrot et al.: <https://www.nature.com/articles/ncomms2389>

Zanno et al.: <https://www.nature.com/articles/ncomms3827>

Han et al.: <https://www.nature.com/articles/ncomms5382>

Lü et al.: <https://www.nature.com/articles/ncomms4788>

Xing et al.: <https://www.nature.com/articles/ncomms12089>

Pu et al.: <https://www.nature.com/articles/ncomms14952>

Xu et al.: <https://www.nature.com/articles/ncomms14972>

Hu et al.: <https://www.nature.com/articles/s41467-017-02515-y>

Knoll et al.: <https://www.nature.com/articles/s41467-018-03295-9>

Xu et al.: <https://www.nature.com/articles/s41467-018-05128-1>

Bailleul et al.: <https://www.nature.com/articles/s41467-019-09259-x>

Reisz et al.: <https://www.nature.com/articles/s41467-020-16045-7>

Wang et al.: <https://www.nature.com/articles/s41467-021-24147-z>

Ibiricu et al.: <https://www.nature.com/articles/s41467-025-63793-5>

Comparative figures of Norellraptor with other currently known microraptorans (which do not form part of the current ms) will benefit the presentation of the new discovery.

We have added a new figure focusing on the diagnostic features differentiating *Norellraptor* from other microraptorines.

In the context of a more "classic" description, even the osteohistological features of Norellraptor will be quite adequate (as they are here exposed, are unrelated with the main topic considered in the ms: the independent origin of flight features in different paravian clades).

Regarding the independent acquisition of flight capabilities in different paravian groups, the topic has been already considered in different publications of previous authors, thus it is not novel by itself.

We believe that the reviewer here somewhat misrepresented our study. The mere recognition of flight convergences among different paravian lineages (the topic mentioned by the reviewer) does not necessarily equate to determining if the assembly patterns among each paravian group expressed a shared developmental model inherited by all paravians (the aim of our investigation). Our manuscript focused on the assembly of the flight apparatus in Microraptorinae, a clade which has been mentioned in several studies as expressing a potential ancestral stage in the evolution of the flight apparatus of birds. Our investigation is novel in explicitly showing for the first time that the evolutionary sequences in these two lineages cannot be considered the expression of a shared developmental pattern.

Finally, although the hypothesis that different characteristics evolved separately (and in different order) among Microraptoria and Avialae seems probable, it must be said that a similar process of "mosaicism" occurred among different clades of early avialans (confuciusornithids, junguoforthids, sapeornithiforms, Jeholornis, etc. etc): these early avians DIFFERENTIALLY share derived characteristics related with improved flying abilities. I guess such an evolutionary process widely applies to all clades of the Tree of Life.

It is important to distinguish between 1) mosaicism in the expression of homoplastic features widespread among closely-related clades (the phenomenon mentioned by the reviewer), 2) the step-wise acquisition of hierarchically-nested synapomorphies (which is the basis for inferring a cladistic pattern), and 3) the parallelism in the assembly of a novel adaptation due to a "deep homology" in the development shared by related groups (which is the main topic of our manuscript).

As correctly stated by the reviewer, each lineage among Avialae expresses a differential level of similarity with the living birds. In fact, it is the differential degree of similarity which supports the topological relationships among the various Mesozoic bird groups and the living avians (and, in general, every phylogenetic structure in the whole Tree of Life).

Yet, this is not necessarily pertinent to the main topic discussed in our manuscript, which is whether the patterns driving the independent acquisition of the flight-related features between Avialae (as a whole) and Microraptorinae are the expression of a shared developmental regime or not.

4. Osteohistological information is welcome, of course. However, it constitutes a detailed description of the osteohistological features of the specimen, lacking considerations about physiological aspects of these theropods. It could be great that authors expand their ideas on this particular topic. However, these descriptions and considerations can not be easily integrated with the main purpose of the present ms: independent avian acquisition in Microraptoria.

We thank the reviewer for the suggestion: the relative paragraphs have been implemented and integrated with the rest of the manuscript. In particular, we suggest that the analysis of the growth patterns in the microraptorine appendicular skeleton, inferred from the osteohistological information, could represent an independent test for our evolutionary scenario.

5. No explanations are provided for the figures forming part of the main text.

Inadvertently, the captions of the figures were excluded from the first version of the submission. The captions were included during the online submission process but did not appear in the document sent to the reviewers. This issue has been resolved in the resubmission.

A corrected version of the ms is attached. I hope my comments become useful for the authors.

Sincerely yours,
Fernando Novas

Our point-by-point reply to the reviewers' comments is marked in bold:

Reviewer #1 (Remarks to the Author):

The authors have sufficiently addressed the issues raised by myself and the other reviewers. I do not see the need of further revisions.

We thank the reviewer for their constructive remarks.

Reviewer #2 (Remarks to the Author):

Thank you for your work in responding to reviewer comments. My substantive concerns have been addressed and I believe the paper is ready for submission.

We thank the reviewer for their constructive remarks.

Reviewer #3 (Remarks to the Author):

Dear authors,

I like very much the corrected version of your manuscript. Thanks for explaining point by point each of the issues I raised in the previous version. I am attaching the pdf of your contribution with some minor observations. I hope to see it published in Nature Communications.

Sincerely,

Fernando Novas

Reviewer #3: Lines 299-304: This is a very interesting and novel point of the present ms. However, please review the grammar of the paragraph, because it involves different concepts and it is somewhat confusing in its structure.

We have re-written the paragraph breaking the long sentences and arranging them more linearly.

Reviewer #3: Line 322-323: Apologies if I misunderstood the issue, but such a pattern of growth, does equally apply to altricial birds and precocial ones? This is because you mention below (lines 333-336) that Microraptorines had precocially-developing forelimb, different from living FLYING avians. Then, I ask if by saying "flying birds" you are excluding poor fliers and precocial birds such as Gallus.

I sum, let me recommend clarify this highly interesting paragraph (lines 319-336).

We have added details about the living birds mentioned in the paragraph and have made clearer the different growth patterns which are compared to the microraptorines.