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Discussion

Reply to comments on "A well-preserved pelvis from the Maastrichtian of Romania suggests that the enigmatic *Gargantuavis* is neither an ornithurine bird nor an insular endemic"

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ABSTRACT

We appreciate the comments of Buffetaut and Angst on our recent study of a *Gargantuavis*-like pelvis from the Late Cretaceous of Romania. We consider some of their points to be valid, but maintain our conclusion on the likely absence of a glycogen body in *Gargantuavis* and the lack of fusion of the pelvic elements in the acetabular region. Both characters conflict with a classification of the taxon into Ornithurae. We also uphold our hypothesis that *Gargantuavis* is possibly related to the enigmatic theropod *Balaur bondoc*.

1. Association of other bones with the *Gargantuavis* pelves

Buffetaut and Angst (2020) may be correct that the femora from sites in France and Spain belong to *Gargantuavis*. In this case, our tentative proposal that the Romanian *Gargantuavis*-like pelvis may be associated with the Romanian *Elopteryx* femora would be wrong. However, even though we raised this hypothesis, we were well aware of its speculative nature and did not make any definitive assignment. The femora from France and Spain, which were found a short distance away from *Gargantuavis* pelves, show remarkably different morphologies and sizes, and Buffetaut and Angst themselves now consider one of the originally referred femora to have been erroneously assigned to *Gargantuavis philoinos*. We therefore conclude that an unambiguous association of other postcranial remains with *Gargantuavis* pelves is not possible and has to await future fossils of partial skeletons.

Buffetaut and Angst also mention a referred cervical vertebra of *Gargantuavis*, which was described by Buffetaut and Angst (2016) and exhibits heterocoelous articulation facets. However, even if correctly assigned to *Gargantuavis*, this vertebra does not provide unambiguous evidence for ornithurine affinities of the taxon, because heterocoelous cervical vertebrae have also been reported for the enantiornithine taxa *Pengornis* (Zhou et al., 2008), *Piscivorenantiornis* (Wang and Zhou, 2017), and *Shanyang* (Wang and Zhou, 2019). Heterocoelous vertebrae were also reported for some non-avian theropods (e.g., Novas et al., 2018).

2. Lines of arrested growth

Buffetaut and Angst are correct in noting that lines of arrested growth are not restricted to the two palaeognathous taxa listed by Mayr et al. (2020). Their occurrence in extant birds is, however, uncommon, and the presence of lines of arrested growth in

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Gargantuavis was not our main argument against ornithurine affinities of the taxon.

3. Pelvis proportions

We concur with Buffetaut and Angst that the pelvis of moas is wider than the pelves of most other palaeognathous birds. Still, however, the proportions of the *Gargantuavis* pelvis are utterly different from those of any terrestrial ornithurine birds including moas and the dodo (Fig. 1B–D). Although a wide pelvis occur in some extant birds (Mayr et al., 2020), most of these are highly aerial species and there is no terrestrial ornithurine bird in which the pelvis is almost as wide as it is long and in which the preacetabular portion is as short as in *Gargantuavis*.

4. Systematic affinities

We tried to be cautious in our discussion of the systematic affinities of *Gargantuavis*, and in light of the conflicting character evidence, we did not present a definitive phylogenetic placement. Buffetaut and Angst are more determined in their classification and maintain a position of *Gargantuavis* within Ornithurae. At present, however, only a single character supports this hypothesis, that is, the comparatively high number of fused synsacral vertebrae.

4.1. Lack of fusion of ilium, ischium, and pubis

Buffetaut and Angst note that the pubic and ischiadic peduncles are broken in all *Gargantuavis* pelves from France and Spain. We concur that the ventral surfaces of these structures are damaged in the fossils, but we note that the specimens from France and Spain show a fair degree of breakage and abrasion, so that damage of the peduncles is not unexpected. Buffetaut and Angst consider this damage to be evidence for a fusion of the pelvic bones in the acetabular region, but we think that the opposite is more likely. Actually, the region around the acetabulum is one of the most robust portions of the pelvis, and given the comparatively high number of *Gargantuavis* pelves known so far, one would expect this region to be present in its entity in one of the fossils, if ilium, pubis, and ischium were fused in *Gargantuavis*. We admit, however, that our sentence that unfused ilium, ischium, and pubis of *Gargantuavis* are “also indicated by the morphology of the tips of the pubic and ischiadic preduncles, which do not show signs of breakage” may have been misleading, and this sentence only refers to the Romanian pelvis.

In the Romanian *Gargantuavis*-like fossil, the surface of the peduncles is well preserved and Buffetaut and Angst raise the possibility that the apparent lack of a fusion of ilium, ischium, and pubis may be due to a juvenile condition of the specimen. However, we are confident that the Romanian pelvis is not from a juvenile, in which case one would not expect a complete fusion of the synsacral

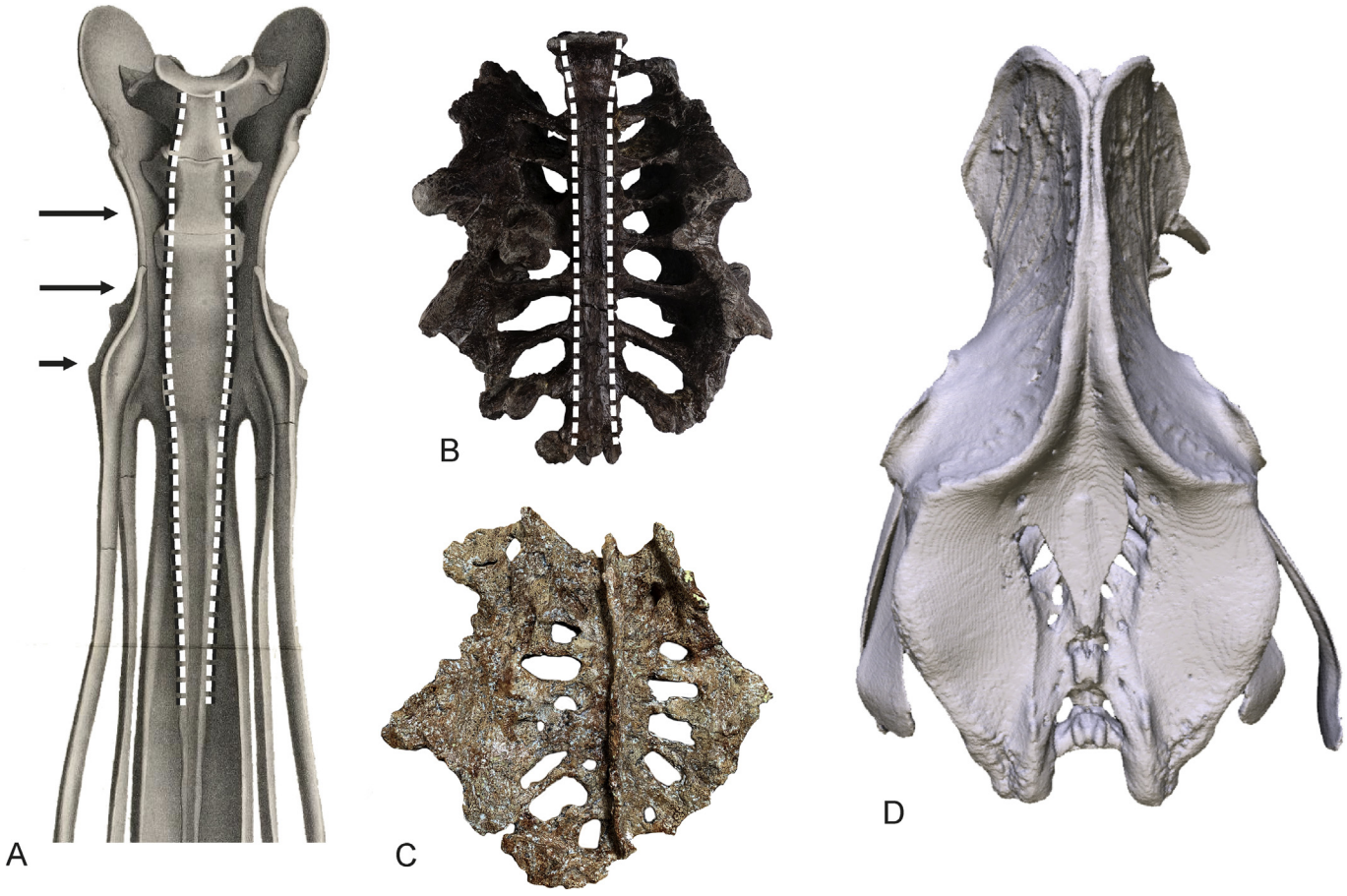

Fig. 1. **A**, pelvis of *Hesperornis regalis* in ventral view (from Marsh, 1880). **B**, *Gargantuavis*-like pelvis from Romania in ventral view. **C**, pelvis of *Gargantuavis philoinos* in dorsal view. **D**, 3D model of the pelvis of the Heavy-footed Moa *Pachyornis elephantopus* (Dinornithidae) in dorsal view; image from sketchfab (https://sketchfab.com/3d-models/heavy-footed-moa-p-elephantopus-pelvis-196f1d5629a840c39e08287b9b531131), used with permission and slightly modified. The dashed lines in **A** and **B** indicate the outline of the synsacrum; the arrows in **A** denote its widening. The figures are not to scale.

vertebrae, which do not show any visible sutures in the fossil. In juvenile birds the bone surfaces furthermore have an "unfinished", textured or porous structure, which is not present in the *Gargantuavis*-like fossil from Romania. Therefore, we maintain our observation that the absence of fusion of ilium, ischium, and pubis in at least the Romanian fossil is a true feature and represents the adult condition.

4.2. Synsacrum widening and glycogen body

Mayr et al. (2020) discussed the putative absence of a glycogen body in *Gargantuavis*, with this pelvic feature not having been considered by most previous authors describing Mesozoic birds. Occurrence of a glycogen body is accompanied by a widening of the midsection of the synsacrum, and Buffetaut and Angst note that the Hesperornithiformes, which are uncontroversial early representatives of the Ornithurae, do not show such a widening of the synsacrum. In our opinion, however, their figure (Buffetaut and Angst, 2020: fig. 1) actually documents the opposite. It is true that in hesperornithiforms the cranialmost synsacral vertebra is wider than all caudally following ones owing to its wide articulation facet. However, it is not the width of the vertebra as such, which is of interest here, but the width of the portion around the neural canal. We did not directly examine hesperornithiform pelves ourselves, but the reconstruction of the *Hesperornis regalis* pelvis in Marsh (1880) clearly shows a widening of the bodies of the second to fifth synsacral vertebrae (Fig. 1A). The weak development of this widening may be due to the fact that the pelvis of hesperornithiforms is extremely elongated. In the well-preserved new Romanian *Gargantuavis*–like fossil, by contrast, the synsacral vertebrae are of subequal width (Fig. 1B), and this condition is clearly different from all ornithurine birds including hesperornithiforms.

5. Palaebiogeography

We did not aim to propose that *Gargantuavis* lineages evolved independently in the Ibero-Armorican and Haţeg islands, which is indeed an unlikely assumption. Instead, we hypothesized that the stem species of *Gargantuavis* lived at a time when land connections still existed between the two islands. Buffetaut and Angst are right in noting that *Gargantuavis* may have dispersed from one island to the other by swimming. This is a valid hypothesis we did not consider and cannot refuse. However, if *Gargantuavis* was able to cross considerable distances (Csiki-Sava et al., 2015) by swimming, it is difficult to maintain the assumption that the taxon was restricted to the Ibero-Armorican and Haţeg islands, which would in turn challenge an evolution of flightlessness under insular conditions.

Gargantuavis coexisted with various potential predators in the European archipelago, and it remains difficult to understand how flightlessness could have evolved under such circumstances and which selective advantages favored the loss of flight capabilities in such a palaeoenvironment. Buffetaut and Angst note that flightless birds today also occur in areas with potential predators. We concur, but emphasize that these birds, such as the palaeognathous ostriches and nandus, usually are highly self-defensive, cursorial species, which have a very long evolutionary history (Mayr, 2017). Currently, there exists no unambiguous evidence that the stem species of any of the extant flightless palaeognathous birds lost its flight capabilities in a palaeoenvironment with a high predation pressure (all flightless neognathous birds are confined to oceanic islands with no or only a few mammalian predators). Clearly, some of these birds today occur in areas with large carnivores, but the initial stages in the evolution of flightlessness, where birds are particularly prone to predation, is unlikely to have occurred under such conditions. Rheidae, for example, lost their flight capabilities in the early Paleogene of South America, at a time where there were no large carnivorous mammals (Mayr, 2017). Where exactly the stem species of ostriches lived is uncertain and the group may have evolved in Eurasia (Mayr, 2017). The earliest, early Miocene, fossil ostriches from Africa were already large-sized, cursorial birds and their flightless ancestor must have lived in the Paleogene. Even if ostriches originated in Africa, they would therefore have lost their flight capabilities well before carnivorans dispersed on the continent (although hyaenodont carnivores were diversified in the Paleogene of Africa, most were probably less agile predators than true carnivorans; Van Valkenburgh, 1985).

6. Conclusions

We concur with Buffetaut and Angst that alternatives exist for the phylogenetic and biogeographic hypotheses we presented in our study, but we also think that we were cautious in our conclusions. Clearly, the evidence for a systematic placement of *Gargantuavis* is controversial, and in our study we raised the possibility that the taxon may be closely related to the enigmatic theropod *Balaur bondoc* (Brusatte et al., 2013), with which it has not been compared before. Buffetaut and Angst did not comment on this hypothesis, even though we listed some striking similarities of both taxa, most notably the presence of well-developed supratrochanteric processes. Like *Gargantuavis*, *Balaur* has a well-developed antitrochanter and the midsection of the synsacral vertebrae does not show a widening. Certainly, possible affinities between *Gargantuavis* and *Balaur* will have to be considered in more detail in future studies. In any case, however, the discovery of the latter taxon has shown that the Late Cretaceous European archipelago was inhabited by very unusual theropods, which were unknown at the time *Gargantuavis* was first reported and considered to be an ornithurine bird.

Pelvis remains of *Gargantuavis* are surprisingly common in fossil sites of the Late Cretaceous European archipelago, which sharply contrasts with the fact that – with the exception of the above-mentioned femora – no unambiguously ornithurine limb elements, such as tibiotarsi or tarsometatarsi, have yet been discovered at these sites. We would not be surprised if such bones already exist in current collections but defy an identification, because their morphologies conflict with the presumed ornithurine affinities of *Gargantuavis*.

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References

Brusatte, S.L., Vremir, M., Csiki-Sava, Z., Turner, A.H., Watanabe, A., Erickson, G.M., Norell, M.A., 2013. The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. Bulletin of the American Museum of Natural History 374, 1–100.

Buffetaut, E., Angst, D., 2016. The giant flightless bird *Gargantuavis philoinos* from the Late Cretaceous of southwestern Europe: a review. In: Khosla, A., Lucas, S.G. (Eds.), Cretaceous Period: Biotic Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin, vol. 71, pp. 45–50.

Buffetaut, E., Angst, D., 2020. *Gargantuavis* is an insular basal ornithurine: a comment on Mayr et al., 2020, 'A well-preserved pelvis from the Maastrichtian of Romania suggests that the enigmatic *Gargantuavis* is neither an ornithurine bird nor an insular endemic'. Cretaceous Research in press.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and

extinction of land-living vertebrates on the Late Cretaceous European archipelago. ZooKeys 469, 1–161.
Marsh, O.C., 1880. Odontornithes: A monograph on the extinct toothed birds of North America. U.S. Government Printing Office, Washington.
Mayr, G., 2017. Avian evolution: The fossil record of birds and its paleobiological significance. Wiley-Blackwell, Chichester.
Mayr, G., Codrea, V., Solomon, A., Bordeianu, M., Smith, T., 2020. A well-preserved pelvis from the Maastrichtian of Romania suggests that the enigmatic *Gargantuavis* is neither an ornithurine bird nor an insular endemic. Cretaceous Research 106, 104271.
Novas, F.E., Egli, F.B., Agnolin, F.L., Gianechini, F.A., Cerda, I., 2018. Postcranial osteology of a new specimen of *Buitreraptor gonzalezorum* (Theropoda, Unenlagiidae). Cretaceous Research 83, 127–167.
Van Valkenburgh, B., 1985. Locomotor diversity within past and present guilds of large predatory mammals. Paleobiology 11, 406–428.
Wang, M., Zhou, Z., 2017. A morphological study of the first known piscivorous enantiornithine bird from the Early Cretaceous of China. Journal of Vertebrate Paleontology 37, e1278702.
Wang, M., Zhou, Z., 2019. A new enantiornithine (Aves: Ornithothoraces) with completely fused premaxillae from the Early Cretaceous of China. Journal of Systematic Palaeontology 17, 1299–1312.
Zhou, Z., Clarke, J., Zhang, F., 2008. Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. Journal of Anatomy 212, 565–577.