PALÆO VERTEBRATA

ARTICLE

A femur of the Late Cretaceous giant bird *Gargantuavis* from Cruzy (southern France) and its systematic implications

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Abstract: A large avian femur recently discovered at the Late Cretaceous Montplo-Nord locality at Cruzy (Hérault, southern France) is referred to the giant bird *Gargantuavis philoinos*. The estimated mass of the bird is 57 kg, within the range of living cassowaries. The specimen provides new evidence about the anatomy of *G. philoinos*, notably showing that the distal end of the femur was similar to that of modern birds in having a condylus lateralis subdivided into two semicondyles. A new diagnosis of *Gargantuavis philoinos* is provided and the taxon is placed in a new family of basal ornithurines.

Keywords: Aves, Late Cretaceous, France, *Gargantuavis*, femur, systematic position

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INTRODUCTION

The giant bird *Gargantuavis philoinos* Buffetaut & Le Loeuff, 1998, is known from relatively scanty remains from a few Late Cretaceous localities in southern France and northern Spain (Buffetaut & Angst, 2016a,b; Angst & Buffetaut, 2017; Angst *et al*., 2017). Many aspects of its osteology remain unknown, so that its systematic position within Aves is still uncertain. A recently discovered well preserved femur from Cruzy (southern France), described below, complements the information available from an incomplete and poorly preserved specimen from Villespassans (southern France) described by Buffetaut & Le Loeuff (1998) and provides important additional anatomical evidence about *Gargantuavis* that sheds new light on its systematic affinities.

Institutional abbreviations: MACN – Museo Argentino de Ciencias Naturales, Buenos Aires (Argentina); MC – Musée de l'Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois, Cruzy (Hérault, France); MDE – Musée des Dinosaures, Espéraza (Aude, France).

GEOGRAPHICAL AND GEOLOGICAL SETTING

The specimen described in the present paper was found in April 2016 in the course of excavations conducted by the Centre National de la Recherche Scientifique and the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois at the Montplo-Nord locality, near the village of Cruzy. The sedimentary environment (red clays with sandy to conglomeratic lenses) suggests deposition in a floodplain setting. The locality has yielded an abundant vertebrate assemblage including fishes, turtles, squamates, crocodiles, pterosaurs and dinosaurs (titanosaurian sauropods, abelisaurid and dromaeosaurid theropods, rhabdodontid ornithopods and nodosaurid ankylosaurs).

The predominance of titanosaurians and rhabdodontids, and the absence of hadrosaurs, indicates a late Campanian to early Maastrichtian age, as for other *Gargantuavis* localities in France and Spain (Buffetaut & Angst, 2016a,b).

The Montplo-Nord locality has already yielded a cervical vertebra (Buffetaut & Angst, 2013) and pelvic elements (Buffetaut & Angst, 2016b) of *Gargantuavis philoinos*. Although the specimens were not found in direct association, they come from the same sedimentary layer and were found a short distance from each other and may belong to a single individual.

DESCRIPTION

The anatomical description generally follows Baumel & Witmer (1993) and Zinoviev (2010), except for the distal end of the bone, for which Elzanowski's terminology is used (Elzanowski, 2008).

The specimen (Fig. 1) is a well preserved right femur (MC-MN 1335, already illustrated in Angst & Buffetaut, 2017, fig. 8.4), that has only undergone moderate crushing of parts of the shaft, notably in the proximal region of its cranial face and the distal region of its caudal face. The crista supracondylaris medialis is incompletely preserved.

The proximal part of the bone shows a well defined semi-spherical caput femoris, separated from the rest of the bone by a fairly well defined neck (collum femoris). The caput femoris bears a shallow oval fovea ligamenti capitis which faces craniocaudally. The facies articularis antitrochanterica forms a craniocaudally narrow, rather flat surface that slopes down mediocaudally from the trochanter femoris and merges with the proximal surface of the caput femoris. It strongly overhangs the caudal face of the bone. The trochanter femoris is well defined but does not protrude much proximally. In proximal view, it is concave cranially and convex caudally. There is a thick, rounded crista trochanteris. The space between the crista trochanteris and the caput femoris on the cranial face of the bone is deeply concave (this may be somewhat exaggerated by crushing). On the caudal face of the bone, there is a deep teardrop-shaped scar between the trochanter femoris and the proximal inception of the linea intermuscularis caudalis. This must correspond to the insertion of a powerful muscle, possibly the musculus iliofemoralis (Zinoviev, 2010). Another well-marked depression in a more dorsolateral position may correspond to the insertion of the musculus obturatorius medialis (Zinoviev, 2010).

The rather robust shaft has a straight lateral margin and a concave medial margin. In lateral or medial view, it shows a distinct sigmoid curvature. Originally it probably had an oval, slightly craniocaudally flattened cross-section, now distorted by crushing. On the cranial face, the linea intermuscularis cranialis, which runs obliquely from the crista trochanteris towards the condylus medialis, forms a sharp ridge in its middle part but becomes fainter distally. On the caudal surface, the linea intermuscularis caudalis, which runs from the above-mentioned deep muscle scar towards the condylus lateralis, is also well marked, especially in its proximal portion. As revealed when it was accidentally broken during preparation, the shaft is hollow, with 3 to 4 mm thick bony walls.

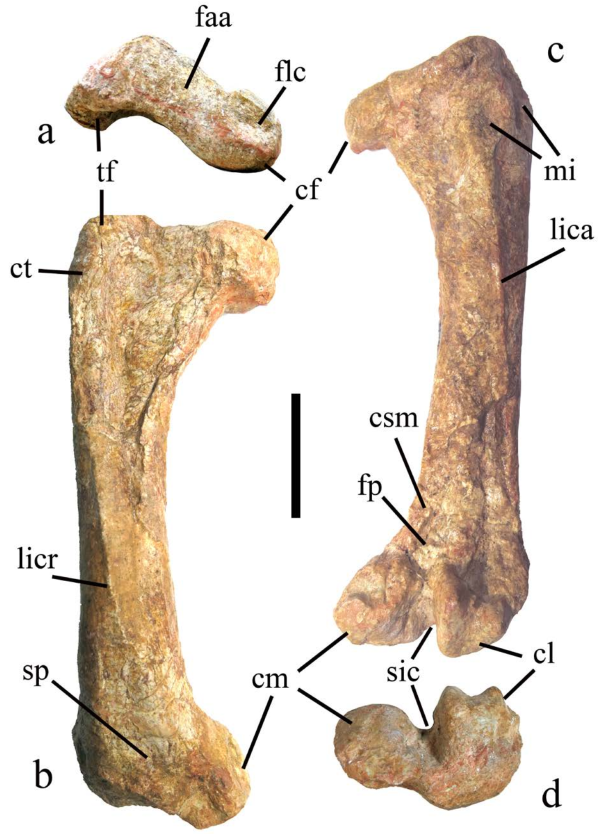

Figure 1. Right femur of *Gargantuavis philoinos* from Montplo-Nord (Cruzy), MC-MN 1335, in proximal (a), cranial (b), caudal (c) and distal (d) views. Abbreviations: cf: caput femoris; cl: condylus lateralis; cm: condylus medialis; csm: crista supracondylaris medialis; ct: crista trochanteris; faa: facies articularis antitrochanterica; flc: fovea ligamenti capitis; fp: fossa poplitea; lica: linea intermuscularis caudalis; licr: linea intermuscularis cranialis; mi: muscle insertions; sic: sulcus intercondylaris; sp: sulcus patellaris; tf: trochanter femoris. Scale bar: 50 mm.

The distal end of the bone is generally well preserved, although the caudal face of the distal end of the shaft has undergone severe crushing. A point worth mentioning is that the condylus medialis extends significantly farther distally than the condylus lateralis, whereas the opposite condition is observed in many modern birds (including ratites). The sulcus patellaris is shallow and separated from the very deep sulcus intercondylaris by a strong oblique bony ridge. There is a long straight ridge along the lateral margin on the cranial face merging into that oblique ridge. On the caudal face, the fossa poplitea is long and narrow and occupies only the medial half of the bone. It is limited laterally by a well-marked longitudinal ridge issuing from the semicondylus tibiofibularis (see below), which separates it from a similarly shaped fossa in the lateral half of the caudal face of the bone.

The distal condyles are well-preserved and separated by a sulcus intercondylaris that is very deep distally and caudally. The condylus medialis slants mediodistally; it is narrow and parallel-sided. Its medial surface bears a deep depression (impressio ligamenti collateralis medialis femori). Its caudal surface bears a deep transverse groove which may be accidental. The condylus lateralis is divided into two semicondyles (*sensu* Elzanowski, 2008). Medially, there is a large, caudally prominent semicondylus tibiofibularis forming a sharp longitudinal ridge (the crista tibiofibularis). Separated from it by a V-shaped groove (the sulcus fibularis), the semicondylus fibularis forms a relatively small knob followed proximolaterally by a well-marked epicondylus lateralis. This is completely similar to the condition in modern birds, but different from that in non-avian theropods, in which there are a cranial and a caudal semicondyles separated by a distal groove (Elzanowski, 2008). The lateral surface of the semicondylus lateralis bears a deep impressio ligamenti collateralis lateralis femori.

There is no evidence of pneumatic foramina anywhere on the bone.

COMPARISON WITH THE PURPORTED *GARGANTUAVIS* FEMUR FROM COMBEBELLE

Buffetaut & Le Loeuff (1998) referred to *Gargantuavis philoinos* a large avian femur (MDE A-08) from the Combebelle locality at Villespassans (Hérault). That bone was used for a histological study by Chinsamy *et al*. (2014) that confirmed its avian nature. At first sight, that specimen looks rather different from the newly discovered femur from Montplo-Nord (Fig. 2). However, the differences are more apparent than real. The femur from Combebelle, which lacks the distal end, is badly crushed and distorted, and has been pieced together from many fragments, so that its original shape has been altered. Similarities between MDE A-08 and MC MN 1335 include the proximal outline of the caput femoris and the narrow facies articularis antitrochanterica which merges with the dorsal surface of the caput femoris and strongly overhangs the caudal face of the bone. A further resemblance is the very similarly located and developed linea intermuscularis cranialis.

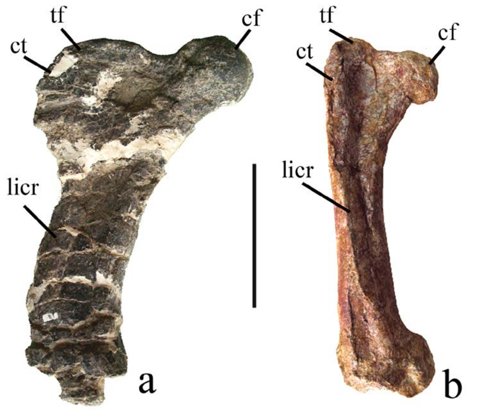

Figure 2. *Gargantuavis* femora from Combebelle (Villespassans), MDE A08 (a), and Montplo-Nord (Cruzy), MC-MN 1335 (b) in cranial view. The apparent morphological differences are very probably due to heavy crushing and distortion of MDE A08. Abbreviations: see Fig. 1. Scale bar: 100 mm.

In MDE A-08, however, the region of the trochanter femoris and crista trochanteris has undergone very severe compression and deformation, and a large amount of bony matter is missing on the caudal surface, so that this area now appears as a proximolaterally rounded thin bony flange, a shape that is not the original one and can easily be derived from the condition seen in MC MN 1335. Moreover, the whole proximal part of the bone is no longer in real contact with the shaft, the intermediate region being reconstructed with plaster, so that its orientation relative to the shaft is hypothetical. To judge from the much better preserved MC MN 1335, the caput femoris was probably directed less proximally and more medially than in its present position. Although badly crushed craniocaudally, the shaft of MDE shows a concave medial margin, as in MC MN 1335 and a straighter lateral margin.

In view of the severe deformation undergone by MDE A-08, that can explain the observed differences, it may be assumed that the femora from Combebelle and Montplo-Nord belong to the same taxon. However, MDE A-08 is significantly larger than MC-MN 1335, and that cannot be explained by post-mortem deformation. The minimum circumference of the femur of MC MN 1335 is 100 mm, whereas it is 148 mm in MDE A-08 (this measurement may be somewhat overestimated because of crushing and displacement of bone fragments). Similarly, the diameter of the caput femoris is 88 mm in MC-MN 1335 versus 125 mm in MDE A-08. The femur from Combebelle is thus about 40% larger than that from Montplo-Nord. As there are no signs of juvenility on MC-MN 1335, it seems unlikely that this size difference reflects a difference in individual age. This may suggest sexual dimorphism, as observed in many extant and extinct large ground birds, but more material will be needed to check that hypothesis.

However, it may be argued that MDE A-08 and MC-MN 1335 are in fact too different to be placed in the same taxon. If that turned out to be the case, it should be remembered that the femur from Combebelle was simply referred to *Gargantuavis philoinos* by Buffetaut & Le Loeuff (1998) – the holotype being the synsacrum from a different locality (Bellevue at Campagne-sur-Aude). At Combebelle, femur MDE A-08 was not associated with any other avian material. The situation is different at Montplo-Nord, where, as mentioned above, femur MC-MN 1335 was in the same layer as and at a short distance from pelvic elements which closely agree morphologically with the holotype of *Gargantuavis philoinos* (Buffetaut & Angst, 2016b) and with pelves from Fox-Amphoux referred to that taxon by Buffetaut *et al*. (2015). As noted above, all the large avian elements from Montplo-Nord may belong to a single individual. There is therefore every reason to accept that femur MC-MN 1335 does belong to *Gargantuavis philoinos*. If the femora from Montplo-Nord and Combebelle belong to different taxa, then femur MDE A-08 should no longer be referred to *Gargantuavis philoinos* and might be referred to as cf. *Gargantuavis*.

SIZE AND MASS ESTIMATES

The overall length of the bone is 235 mm (from the proximal tip of the trochanter femoris to the distal extremity of the condylus medialis). By comparison with present-day ratites (mean femoral lengths from Dickison, unpublished Ph.D. Thesis, Duke University, 2007), it is longer than the femora of the emu (*Dromaius novaehollandiae*: 219 mm) and slightly shorter than that of the one-wattled cassowary (*Casuarius unappendiculatus*: 245 mm). Even though the ostrich (*Struthio camelus*) has a significantly longer femur (mean length: 300 mm), as far as the femur is concerned, this suggests that *Gargantuavis philoinos* was in the size range of the large living ratites. The femur from Montplo-Nord is also in the length range of those of some of the smaller New Zealand moas, such as *Megalapteryx* and *Euryapteryx* (see length ranges in Worthy, 1988). However, since only a few elements of the skeleton of *Gargantuavis philoinos* are currently known, its body proportions cannot be reliably reconstructed. Therefore, although the length of the femur from Montplo-Nord certainly suggests a very large bird, it is not possible to provide an estimate of its size, especially in terms of height since the length of its neck is unknown.

Nevertheless, its body mass can be estimated, using Campbell & Marcus's equation that links body mass to least circumference of the femur (Campbell & Marcus, 1992). The least circumference of MC-MN 1335 is 100 mm, corresponding to a mass of about 57 kg. By comparison, Dunning (2008) gives the following masses for some of the living ratites (in kg):

		Mean	**Minimum**	**Maximum**
Struthio camelus		110	86	145
Casuarius casuarius		44	29.2	58.5
Dromaius novaehollandiae	**(male)**	31.5	17.7	46.5
	(female)	36.9	25.9	48
Rhea americana		23	10.5	40
Pterocnemia pennata		23.9	19.1	28.6

With a body mass of 57 kg, *Gargantuavis philoinos* is thus within the range of present-day cassowaries and there is little doubt that it was flightless. Buffetaut & Le Loeuff (1998) estimated the mass of *Gargantuavis philoinos* at 141 kg (the weight of a large male ostrich) by applying the method of Anderson *et al*. (1985), which uses the midshaft circumference of the femur, to the specimen from Combebelle. The method of Campbell & Marcus (1992) provides an estimated mass of 147 kg for that individual. However, mass estimates based on the Combebelle femur should be taken with some caution because the crushing and deformation of the specimen make it difficult to measure the least circumference of the shaft with complete accuracy.

COMPARISON WITH OTHER CRETACEOUS BIRDS AND SYSTEMATIC POSITION OF *GARGANTUAVIS PHILOINOS*

Because of the scarcity of the available material, the systematic position of *Gargantuavis philoinos* has long remained uncertain. Mainly on the basis of pelvic and femoral characters, Buffetaut & Le Loeuff (1998) suggested that it was more advanced than enantiornithines but less derived than ornithurines and noted possible similarities with *Patagopteryx deferrarisii*, from the Late Cretaceous of Argentina. Because of the highly heterocoelous condition of the cervical vertebra from Montplo-Nord, Buffetaut & Angst (2013, 2016a,b) considered that *Gargantuavis* could be placed within Ornithuromorpha (the group that includes all birds more advanced than Enantiornithes), was not very closely related to *Patagopteryx*, and was close to or within Ornithurae (the group that includes Neornithes (modern birds) and some more basal Cretaceous groups such as Hesperornithiformes and Ichthyornithiformes). Beyond confirming some previous observations (e.g. the absence of a posterior trochanter, which separates it from other Cretaceous birds such as enantiornithines), the well-preserved femur from Montplo-Nord provide important new evidence about the systematic position of *Gargantuavis*. In particular, the morphology of the distal end, the evolutionary significance of which was highlighted by Elzanowski (2008), shows that this bird was more advanced than many other Mesozoic avians. The subdivision of the condylus lateralis into two well-defined semicondyles is a derived character, not found in archaic birds such as Enantiornithes, in which the lateral condyle is undivided and ball-shaped (Chiappe & Walker, 2002; O'Connor & Forster, 2010; Walker & Dyke, 2010). The condition in *Patagopteryx*, which may be a basal ornithuromorph (see Mayr, 2017, for a discussion), is unclear. Chiappe (1996, p. 218) noted that "the condylar area is damaged in all the available specimens" and that the condition of the tibiofibular crest was unknown in that taxon. Later, Chiappe (2002, p. 303) described "a well-developed tibiofibular crest that delimits a large, lateral area for the articulation for the fibula". Among *Patagopteryx* femora in the Museo Argentino de Ciencias Naturales, only specimen MACN N11 shows a reasonably well preserved distal end. The general appearance of that region is very different from what it is in MC MN 1335; notably, the condylus medialis is smaller and does not project much distally in the specimen from Argentina (Fig. 3). Unlike the condition in the French specimen, the condylus lateralis is very large and bulbous. Its distal end is damaged, but it seems to be divided into two parts by a longitudinal groove. Whether this groove is an original feature of the bone or an artefact is unclear. However that may be, direct comparison between MC MN1335 and *Patagopteryx* femora confirms what was already suggested by the cervical vertebra from Montplo-Nord (Buffetaut & Angst, 2013), viz. that *Gargantuavis* is not especially closely related to *Patagopteryx.* Its condylus lateralis, which is very similar to that of modern birds, suggests that *Gargantuavis* is more advanced than *Patagopteryx*. Late Cretaceous birds showing a condylus lateralis divided into two semicondyles include ornithurines such as *Ichthyornis* and related forms from North America (Marsh, 1880; Clarke, 2004) and the hesperornithiforms from Laurasia (Marsh, 1880; Bell & Chiappe, 2016). When exactly the peculiar morphology of the condylus lateralis was acquired in the course of avian evolution is uncertain, partly because the morphology of that condyle is unobservable or has not been described in detail in many Early Cretaceous ornithuromorphs, notably those from the Jehol Biota of north-eastern China. As noted above, it is not present in enantiornithines, and its presence in *Patagopteryx* is uncertain. *Hollanda luceria*, from the Late Cretaceous of Mongolia, considered as a basal ornithuromorph by Bell *et al*. (2010), shows a divided condylus lateralis, but the morphology of the distal end of the femur is very different from that of the Montplo-Nord femur, which more closely approximates the condition seen in modern birds.

Taken together with the advanced heterocoelous condition of its cervical vertebrae (Buffetaut & Angst, 2013) and the number of synsacral vertebrae (at least ten: Buffetaut & Le Loeuff, 1998; Buffetaut *et al*., 2015), the "modern" morphology of the distal end of its femur suggests that *Gargantuavis philoinos* is certainly an ornithuromorph, and in all likelihood a basal ornithurine. A more precise placement will have to wait until more elements of the skeleton are discovered.

A feature of *Gargantuavis philoinos* worth mentioning in this respect is its peculiar type of skeletal pneumatisation. As shown by pneumatic foramina and passages within the bones, it shows a pronounced pneumatisation of the cervical vertebrae, the synsacrum and the ilia (Angst *et al*., 2017; Buffetaut & Angst, 2013, 2016b; Buffetaut *et al*., 2015). However, as noted above, its femur shows no evidence of pneumatic foramina (unlike that of, for instance, modern ratites). O'Connor (2009) distinguished several pneumaticity levels among extant birds, ranging from a 'reduced pattern', in

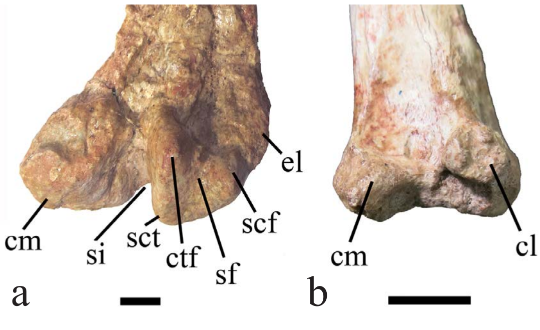

Figure 3. Close ups of the distal ends of the femora of *Gargantuavis philoinos* (MC-MN 1335) and *Patagopteryx deferrarisii* (MACN N11, mirror image for easier comparison) in caudal view. Abbreviations: cl: condylus lateralis; cm: condylus medialis; ctf: crista tibiofibularis; el: epicondylus lateralis; scf: semicondylus fibularis; sct: semicondylus tibiofibularis; sf: sulcus fibularis; si: sulcus intercondylaris. Nomenclature after Elzanowski (2008). Scale bars: 10 mm.

which there is no postcranial pneumatisation (e.g. penguins), to a hyperpneumaticity pattern, in which pneumatisation encompasses the whole postcranial skeleton, including the distal elements of the limbs (e.g. pelicans, vultures). Intermediate levels include the 'common' pattern, in which pneumaticity is restricted to portions of the cervicothoracic vertebral column (e.g. shorebirds) and the 'expanded' pattern, in which pneumatisation extends to the whole axial skeleton, the pelvis and the proximal limb elements (e.g. geese). *Gargantuavis philoinos* exhibits a type of pneumatisation that does not fit any of the patterns described by O'Connor, since the vertebral column and the pelvis are pneumatised, but not the femur. The exact pneumatisation pattern of many Mesozoic birds is unknown, but the peculiar pattern seen in *Gargantuavis* is noteworthy, as it does not seem to have an equivalent among extant birds (including ratites, in which the femur is pneumatised).

TAXONOMY

On the basis of the new information provided by the femur from Montplo-Nord, it is possible to provide a new diagnosis of *Gargantuavis philoinos* that supersedes those provided by Buffetaut & Le Loeuff (1998) and Buffetaut & Angst (2016a). In view of the fact that no close similarities with other Cretaceous ornithurines are apparent, it seems justified to place it in a family of its own.

Class Aves Linnaeus, 1758
Subclass Ornithurae Haeckel, 1866
Gargantuaviidae fam. nov.

Diagnosis: as for the single genus and species in the family.

Type genus: ***Gargantuavis*** Buffetaut & Le Loeuff, 1998

Gargantuavis philoinos Buffetaut & Le Loeuff, 1998

Revised diagnosis: A very large bird with a broad pelvis, on which the acetabulum is placed in a very anterior position relative to the synsacrum, at the level of the third and fourth synsacral transverse processes. The robust and relatively short synsacrum, which is markedly arched ventrally, consists of at least ten completely fused vertebrae. The ilia do not meet each other dorsally. A well developed antitrochanter is present posterodorsally to the relatively large acetabulum. Synsacrum and ilium extensively pneumatized. Pneumatized, strongly heterocoelous cervical vertebra with a remarkably narrow caudal articular surface. Non-pneumatized femur with a trochanteric crest but no posterior trochanter. On the distal end of the femur, the condylus lateralis is divided into two semicondyles and the condylus medialis extends farther distally than the condylus lateralis. Differs from non-ornithurine avians by the advanced heterocely of the cervical vertebrae, the relatively large number of synsacral vertebrae and the condylus lateralis divided into two semicondyles. Differs from modern birds (Neornithes) in the very anterior position of the acetabulum relative to the synsacrum and in the complete lack of dorsal contact between the ilia.

CONCLUSION

The new femur from Montplo-Nord provides much new evidence about the morphology of that bone in *Gargantuavis philoinos*, which leads to reconsider the information provided by the poorly preserved and incomplete specimen from Villespassans. The condition of the distal end of the bone confirms that *Gargantuavis* was more advanced than enantiornithines and should be placed among ornithurines, in a family of its own. The previously suggested similarities with *Patagopteryx* are apparently not supported by this new specimen. Despite these advances in our knowledge of *Gargantuavis philoinos*, many parts of its osteology remain unknown, so that a reconstruction of the skeleton remains impossible. Although the mass estimated from the Montplo specimen is lower than that derived from the Villespassans femur, it still shows that *Gargantuavis philoinos* was in the mass range of some of the larger present-day ratites, such as cassowaries, and remains the largest known Cretaceous bird. The size difference between the femora from Villespassans and Montplo-Nord suggests the possibility of sexual dimorphism.

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