

New remains of the giant bird *Gargantuavis philoinos* from the Late Cretaceous of Provence (south-eastern France)

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Abstract: Two incomplete pelves of the giant bird *Gargantuavis philoinos* are described from Late Cretaceous deposits at Fox-Amphoux (Var, south-eastern France). They consist of synsacra with attached parts of the ilia. One of them has undergone considerable dorsoventral compression, which makes it very similar in appearance to the holotype pelvis of *Gargantuavis philoinos* from Campagne-sur-Aude (Aude, southern France). The second specimen has suffered some lateral distortion but is uncrushed dorsoventrally. Because of this, its avian characters (including an arched synsacrum and widespread pneumatisation) are especially clear. These new specimens confirm the avian nature of *Gargantuavis* and reveal new details about its pelvic anatomy, but provide little new evidence about its systematic position within Aves. The geographical distribution and general rarity of *Gargantuavis* are discussed.

Keywords: Gargantuavis, Aves, Pelvis, Late Cretaceous, South-eastern France

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INTRODUCTION

The first indication of the presence of a giant bird (roughly the size of an ostrich: Buffetaut & Le Loeuff, 1998) in the Late Cretaceous of southern France was an incomplete synsacrum (Buffetaut et al., 1995) found at the Bastide-Neuve locality at Fox-Amphoux (Var, south-eastern France). On the basis of more complete material, including a partial pelvis and a femur, found at other localities farther west (Bellevue, Aude and Combebelle, Hérault), the taxon Gargantuavis philoinos was erected by Buffetaut & Le Loeuff (1998). More recently, a large cervical vertebra from the Montplo-Nord locality at Cruzy (Hérault) was referred to Gargantuavis philoinos (Buffetaut & Angst, 2013). Despite claims to the contrary (Mayr, 2009), the avian nature of Gargantuavis is clearly supported by osteological (Buffetaut & Le Loeuff, 2010) and histological (Chinsamy et al., 2014) evidence. Among other characters, Gargantuavis philoinos is remarkable for its broad pelvis, with the acetabulum placed in an anterior position, and its synsacrum consisting of relatively few vertebrae. Although systematic excavations are currently carried out at several Late Cretaceous localities in southern France, finds of Gargantuavis remains are uncommon (see Fig. 1 for a location map). The discovery by two of us (P. M. and A. M.S.) of two Gargantuavis pelves, consisting of synsacra with remains of the ilia, at the Bastide-Neuve locality is therefore worth reporting, all the more so that these finds provide valuable new information about the anatomy of that giant bird.

Figure 1. Map of southern France showing the location of *Gargantuavis* localities. 1: Fox-Amphoux (Var); 2: Campagne-sur-Aude (Aude); 3: Villespassans (Hérault); 4: Cruzy (Hérault). Map background: Google Earth.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Bastide-Neuve locality is near the village of Fox-Amphoux, in the northern part of department Var, in Provence. Fox-Amphoux is located in a small syncline, filled with Late Cretaceous to Early Tertiary continental deposits consisting of conglomerates, sandstones and marls (Lapparent, 1947). Late Cretaceous vertebrate remains have been known from that area since the first half of the 19th century (Buffetaut et al., 1993) and are known to occur at various sites in the basin. The Bastide-Neuve locality has yielded an abundant and diverse assemblage including fishes, turtles (Tong et al., 1998), crocodilians (Martin, 2007), pterosaurs (Buffetaut et al., 2006), various kinds of non-avian dinosaurs, including theropods (Le Loeuff & Buffetaut, 1998; Chanthasit & Buffetaut, 2009), sauropods (Le Loeuff et al., 1989), ornithopods and ankylosaurs, and birds. The bird remains hitherto reported from Bastide-Neuve were the above-mentioned Gargantuavis synsacrum fragment (Buffetaut et al., 1995) and an enantiornithine tibiotarsus (Buffetaut et al., 2000).



Although it is difficult to provide a very precise age for the non-marine Late Cretaceous deposits of the Fox-Amphoux syncline, the composition of the vertebrate fauna from Bastide-Neuve, where the ornithopod *Rhabdodon* is abundant but no remains of hadrosaurs have been found, suggests a Late Campanian to early Maastrichtian age (Buffetaut et al., 2006).

MATERIAL AND METHODS

The specimens described in the present paper (BN 758 and BN 763) belong to the Mechin collection, registered with the Esperaza Dinosaur Museum. A cast of BN 763 is in the collections of the museum of the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois at Cruzy (Hérault).

The osteological terminology used in the present paper generally follows Baumel & Witmer (1993).

DESCRIPTION

The new material from Bastide-Neuve consists of two large incomplete pelves that differ notably in their preservation and appearance. The differences are clearly linked to different types of fossilisation in two different types of sediment. One of the specimens (BN 758) was discovered in soft siltstone and shows considerable dorsoventral crushing. The other one (BN 763) comes from a much harder sandstone bed and is much less crushed, although it exhibits some lateral distortion.

Specimen BN 758 (Fig. 2) is dorsoventrally flattened and not very well preserved. It consists of part of the synsacrum and of the ilia. The anterior part of the synsacrum is destroyed, so that the cranial articular surface is missing. The neural canal (canalis synsacri) is small and oval in outline. Longitudinally, the synsacrum has a concave ventral margin. In its cranial part, it is convex transversally; more caudally a longitudinal depression or furrow (the sulcus ventralis synsacri), becomes visible, as on the type specimen of *Gargantuavis philoinos*. The

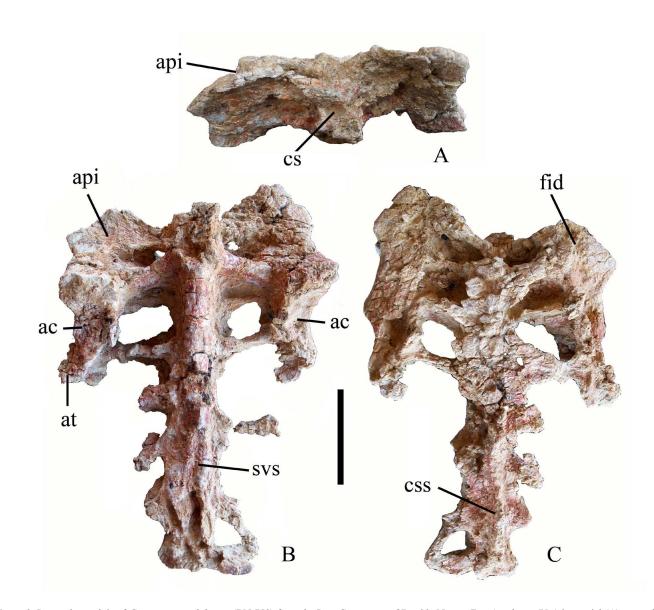


Figure 2. Incomplete pelvis of *Gargantuavis philoinos* (BN 758) from the Late Cretaceous of Bastide-Neuve, Fox-Amphoux (Var) in cranial (A), ventral (B) and dorsal (C) views. Scale bar: 50 mm. Abbreviations: ac: acetabulum; api: ala preacetabularis ilii; at: antitrochanter; cs: canalis synsacri; css: crista spinosa synsacri; fid: fossa iliaca dorsalis; svs: sulcus ventralis synsacri.

fusion of the synsacral vertebrae is complete, without any trace of sutures between the vertebrae. The transverse processes are moderately well preserved. Eight of them are visible on both sides, but several more are broken at their base, and it can be estimated that there were 10, as on the holotype specimen. The processes are more robust cranially, at the level of the cranial part of the acetabulum. More caudally, they become thinner and are directed more caudally. The processes are tall and two-pronged where they meet the fused centra. The cup-shaped acetabulum is preserved on both sides. It opens ventrally. The antitrochanter is visible on the right side, in a posterodorsal position relative to the acetabulum (this is an avian character, also observable on the holotype, MDE C3-525). Anterior to the acetabulum, the ala preacetabularis ilii forms a vault-like ventrally concave surface. The dorsal part of the specimen is poorly preserved. The fused neural spines of the synsacral vertebrae form a continuous crista spinosa synsacri. The crista iliaca dorsalis is preserved only on the right side and it can be observed that the ilia did not meet dorsally above the synsacrum, as in the holotype.

On the whole, this specimen is very similar to the holotype

of *Gargantuavis philoinos*, in its preservation, its morphology and its size.

Measurements:

Length of synsacrum as preserved:	180 mm
Length of acetabulum:	40 mm
Greatest width as preserved:	140 mm

The second specimen (BN 763, Fig. 3), which comes from a layer of hard sandstone, shows no dorsoventral flattening, but a certain amount of lateral compression, the left ilium having been pushed forward and towards the midline. This lateral compression is clearly evidenced by the visible distortion, accompanied by some splitting, of the transverse processes on the left side. Similarly, the fused centra show some lateral crushing. The right ilium is not preserved. The synsacrum is markedly arched, with a strongly concave ventral margin. Fusion of the individual vertebrae is as advanced as in BN 758,

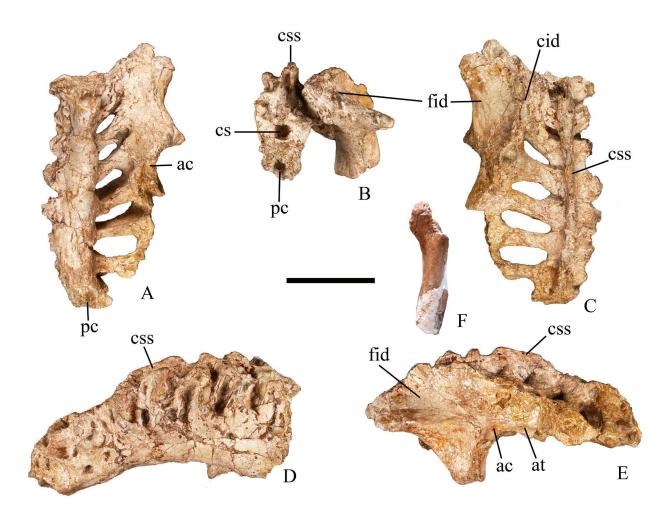


Figure 3. Incomplete pelvis of *Gargantuavis philoinos* (BN 763) from the Late Cretaceous of Bastide-Neuve, Fox-Amphoux (Var) in ventral (A), cranial (B), dorsal (C), right lateral (D) and left lateral (E) views. Abbreviations: ac: acetabulum; at: antitrochanter; cid: crista iliaca dorsalis; cs: canalis synsacri; css: crista spinosa synsacri; fid: fossa iliaca dorsalis; pc: pneumatic canal. F: bone fragment (rib?) associated with BN 763. Scale bar: 50 mm.

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so that their number cannot be directly determined, since no clear limits can be seen between them, but only estimated on the basis of the number of transverse processes. It is taller cranially than caudally. The cranial end being destroyed, the cranial articular face is not preserved, but the left prezygapophysis is partly preserved, showing that not much is missing. The anterior end of the synsacrum shows that the neural canal (canalis synsacri) has a more or less circular outline. More ventrally, the centrum is taller than wide. It is markedly pneumatised, with a broad more or less circular canal in its ventral part. This canal is also visible at the caudal end of the synsacrum, where the bone is also broken. It therefore appears that the canal extended along the whole length of the synsacrum. A canal in a similar position occurs in some modern birds (Boas, 1933), but pneumatic spaces also seem to occur dorsal to the neural canal, unlike the condition in BN 763. Eight more or less complete transverse processes are visible. They are tall but relatively thin craniocaudally, especially at mid-height, where fairly deep recesses are visible close to the contact with the fused centra. On the right side, where the processes are incompletely preserved, it can be seen that they are thicker ventrally than dorsally and concave cranially and convex caudally. Various openings can be seen between them. Comparison with modern birds (Boas, 1933) suggests that some of them are openings for nerves of the plexus lumbosacralis, while others are pneumatic openings. The neural spines of the synsacral vertebrae are fused to form a continuous crista spinosa synsacri. Cranially, this bony ridge is partly broken, exposing pneumatic cavities. The left ilium is partly preserved. Cranially, it shows a slightly concave roof-like dorsal surface (fossa iliaca dorsalis). The crista iliaca dorsalis is poorly preserved, but it can be seen that the ilia did not meet dorsally. The rim of the acetabulum is not well preserved, but the anterior part of the antitrochanter can be distinguished in a posterodorsal position. The position of the acetabulum relative to the transverse processes can be established with some precision: its cranial rim appears to be at the level of the 4th process, and its caudal rim at that of 5th process.

Measurements:

Length of synsacrum as preserved: 120 mm Maximum width as preserved: 60 mm

Two bone fragments are associated with that pelvis. One is a small piece of a long, hollow bone, with part of an articular region (Fig. 3F). However, it seems too small to be a fragment of the femur and is more likely the incomplete proximal end of a rib, with its pneumatic cavity. The other element may be a part of the right ilium, but is so fragmentary that it cannot really be identified.

DISCUSSION

At first sight, the two partial pelves from Bastide-Neuve seem to differ in various respects. In particular, BN 758 appears to be wider and flatter than BN 763. However, a closer examination shows that the observed differences can certainly be explained by different types of preservation. BN 763 has obviously suffered much less dorsoventral compression than BN 758, but it has undergone some lateral compression, as a result of which some of the transverse processes have been bent and partly broken. BN 763 therefore seems proportionally higher and narrower than BN 758. However, when the observed deformations are corrected, the bones become very similar. Even though BN 763 at first sight appears significantly smaller than BN 758, once deformation has been corrected, the size difference becomes less apparent, although BN 763 may have belonged to a somewhat smaller individual than BN 758. An apparent difference is that in BN 758 (as well as in the holotype), the spaces between the transverse processes appear to be significantly larger than in BN 763 (Fig. 4). However, it appears that dorsoventral compression has splayed apart the processes in BN 758. When this flattening is corrected, they become taller and less divergent and the spaces between them become

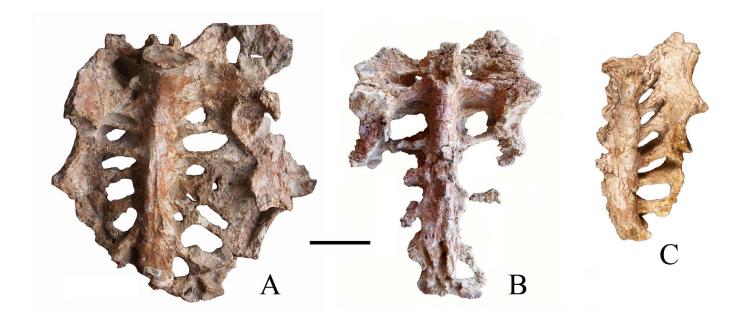


Figure 4. Comparison between three *Gargantuavis philoinos* incomplete pelves, in ventral view: A, holotype MDE C3-525, from Campagne-sur-Aude; B: BN 758, from Fox-Amphoux; C: BN 763, from Fox-Amphoux. Scale bar: 50 mm.

narrower. Conversely, when the lateral distortion of BN 763 is corrected (Fig. 5), the spaces become somewhat wider. The observed differences can therefore be interpreted as resulting from differential compression of bones that were heavily pneumatised, which certainly facilitated deformation. Interestingly, the holotype of Gargantuavis philoinos, a partial pelvis (Espéraza Dinosaur Museum, n° MDE C3-525) from Bellevue (Campagne-sur-Aude, Aude), is dorsoventrally compressed in much the same way as BN 758 from Bastide-Neuve. The new specimens share many significant characters with the holotype, including an anteriorly positioned acetabulum, ilia that do not meet dorsally and a synsacrum comprising a relatively low number of fused vertebrae (at least ten, possibly more, but no specimen is complete enough to provide a fully reliable count). However, despite this remarkable anatomical similarity with the type specimen, the new fossils from Bastide-Neuve lead to a reconsideration of some of the skeletal characters of Gargantuavis philoinos. The pelvis was apparently narrower and relatively taller than what appeared on the basis of the holotype. The synsacrum was markedly arched, and the tall transverse processes were separated by spaces which were narrower than previously accepted. This on the whole makes the pelvis more bird-like. Mayr (2009, p 21) noted that "the wide pelvis of Gargantuavis is very unlike the narrow one typically found in large groundbirds". As remarked by Buffetaut & Le Loeuff (2010), some large terrestrial birds, such as the moas, had wide pelves, but, be that as it may, to judge from the new material from Bastide-Neuve, the pelvis of Gargantuavis was not as wide as originally appeared from the dorsoventrally flattened holotype. On the other hand, a notable feature initially observed on the holotype, viz the fact that the ilia did not meet dorsally, is confirmed by the new specimens.

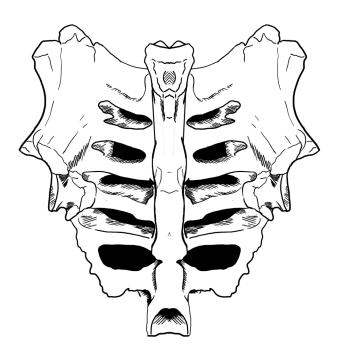


Figure 5. Schematic reconstruction of synsacrum BN 763 after correction of mediolateral crushing and restoration of missing parts on the right side. Ventral view. No attempt has been made to reconstruct the missing parts of the poorly preserved ilia or the posterior part of the synsacrum.

CONCLUSIONS

The specimens from Bastide-Neuve provide various kinds of new information about Gargantuavis. This giant bird is clearly an uncommon element in the Late Cretaceous vertebrate assemblages of southern France. Despite active field work at a number of localities during the last twenty years, only six specimens of Gargantuavis are currently known from France. A synsacrum from the Laño locality in north-western Spain, currently under study (Pereda-Suberbiola et al., 2015), is in all likelihood referrable to Gargantuavis. At most localities where it occurs (Bellevue, Combebelle, Montplo-Nord), only a single specimen has been found so far. From this point of view, Bastide-Haute appears as something of an exception, as three specimens have already been found there. It is difficult to find a clear explanation for this relative abundance, since the sedimentary environment, taphonomic conditions and faunal assemblage at Bastide-Neuve at first sight do not seem to differ very much from those at other Gargantuavis localities.

Another point worth noting is that currently *Gastornis philoinos* is mainly represented by synsacra, often with parts of the ilia attached (three at Bastide-Neuve, one at Bellevue). This probably reflects the fact that the synsacrum of birds is a rather resistant part of their skeleton, with a good potential for fossilisation (isolated synsacra are relatively abundant at some fossil bird localities, for instance in the Aquitanian of the Saint-Gérand-le-Puy area in central France). Nevertheless, the scarcity of other skeletal elements remains puzzling, unless it indicates that *Gargantuavis philoinos* usually inhabited areas that were not conducive to fossilisation.

From an anatomical point of view, the new specimens both confirm previous observations, correct some interpretations, and shed light on previously unknown features. The synsacrum of Gargantuavis philoinos was relatively short, consisting of about ten completely fused vertebrae. This figure must however be considered as a minimum, since no specimen is really complete caudally and it cannot be excluded that a few additional vertebrae were included in the synsacrum. Nevertheless, the synsacrum of Gargantuavis clearly included a relatively small number of vertebrae, and this should probably be regarded as a plesiomorphic feature. Another presumably archaic feature confirmed by the new finds is that the ilia did not meet dorsally above the synsacrum. As mentioned above, the unusually great width of the pelvis that was suggested by the holotype specimen is largely a result of dorsoventral compression, as shown by the relatively uncrushed specimen BN 763. Once deformation has been taken into account, however, it still remains that Gargantuavis had a relatively broad pelvis, suggesting graviportal rather than cursorial adaptations (Buffetaut & Le Loeuff, 2010). Generally speaking, specimen BN 763, being uncrushed dorsoventrally, shows that the pelvis of *Gargantuavis* was more bird-like than appears from the crushed holotype and from BN 758. In particular, the synsacrum is markedly arched, and the transverse processes of the synsacral vertebrae are tall, narrow and generally bird-like. The widespread development of pneumatic spaces, especially in the synsacrum, is also worth noting. Although the avian nature of Gargantuavis philoinos has been questioned (Mayr, 2009), histological evidence shows that it was indeed a bird (Chinsamy et al., 2014). The new material from Bastide-Neuve, especially the well preserved synsacrum BN 763, fully supports this interpretation.

Beyond confirming its avian nature, the new specimens from

Bastide-Neuve do not provide much new evidence about the uncertain systematic position of Gargantuavis within Aves. The presence of at least 10 synsacral vertebrae suggests that it is more advanced than Enantiornithes (O'Connor et al., 2011). The well developed antitrochanter in a caudodorsal position also is an advanced character (O'Connor et al., 2011), but it occurs in at least some enantiornithines (Walker & Dyke, 2010). The acetabulum appears to be rather large, which is a basal character in birds (O'Connor et al., 2011), but it is difficult to really estimate its size relative to that of the ilium, since no complete ilia have yet been found. The advanced heterocoelous cervical vertebra from Cruzy suggests a position within Ornithuromorpha and close to Ornithurines (Buffetaut & Angst, 2013), but the pelvis, as mentioned above, shows various basal features. It should be admitted that much remains obscure about Late Cretaceous basal ornithuromorphs, and it may be difficult to get a better idea of the systematic position of the probably endemic (Buffetaut & Angst, 2013) Gargantuavis until more complete material is found.

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