Early Eocene birds from La Borie, southern France

ESTELLE BOURDON, CECILE MOURER-CHAUVIRÉ, and YVES LAURENT

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The early Eocene locality of La Borie is located in the village of Saint-Papoul, in southern France. These Eocene fluvio-lacustrine clay deposits have yielded numerous vertebrate remains. Mammalian taxa found in the fossiliferous levels indicate an age near the reference level MP 8–9, which corresponds to the middle Ypresian, early Eocene. Here we provide a detailed description of the avian remains that were preliminarily reported in a recent study of the vertebrate fauna from La Borie. A maxilla, a quadrate, cervical vertebrae, a femur and two tibiotarsi are assigned to the giant ground bird *Gastornis parisiensis* (Gastornithidae). These new avian remains add to the fossil record of *Gastornis*, which is known from the late Paleocene to middle Eocene of Europe, early Eocene of Asia and early Eocene of North America. *Gastornis parisiensis* differs from the North American *Gastornis giganteus* in several features, including the more ventral position of the narial openings and the slender orbital process of quadrate. Two tibiotarsi and one tarsometatarsus are assigned to a new genus and species of Geranoididae, *Galligeranoides boriensis* gen. et sp. nov. So far, this family was known only from the early and middle Eocene of North America. The fossils from La Borie constitute the first record of the Geranoididae in Europe. We show that *Gastornis* coexisted with the Geranoididae in the early Eocene of both Europe (La Borie) and North America (Willwood Formation). The presence of Geranoididae and the large flightless bird *Gastornis* on either side of the present-day North Atlantic provides further evidence that a high-latitude land connection existed between Europe and North America in the early Eocene.

Key words: Aves, Geranoididae, *Gastornis*, *Galligeranoides*, palaeobiogeography, Ypresian, Eocene, France.

Estelle Bourdon [EBourdon@snm.ku.dk], The Natural History Museum of Denmark, Section of Biosystematics, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark.
Cécile Mourer-Chauviré [cecile.mourer@univ-lyon1.fr], Université Claude Bernard Lyon 1, Laboratoire de Géologie de Lyon, Terre, Planètes et Environnement, UMR 5276, 2 rue Dubois, F-69622 Villeurbanne Cedex, France.
Yves Laurent [Yves.LAURENT@mairie-toulouse.fr], Association Paléontologique du Sud-Ouest, 13 chemin des Telles, F-31360 Roquefort-sur-Garonne, France, and Muséum d'Histoire Naturelle de Toulouse, 35 allées Jules Guesde, F-31000 Toulouse, France.

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Introduction

The early Eocene locality of La Borie is located in the village of Saint-Papoul, around 20 km north-west of Carcassonne, in southwestern France (Laurent et al. 2010: fig. 1). This locality belongs to the formation of the "Argiles rutilantes d'Issel et de Saint-Papoul", which corresponds to fluvio-lacustrine deposits composed of thick ochre clay layers and thinner grey clay layers (Laurent et al. 2010). These clay deposits are interpreted as standing water bodies, suddenly invaded by sand and gravel during successive waterways floods (Laurent et al. 2010). La Borie has yielded a very rich vertebrate fauna, including turtles, crocodiles, mammals and birds (Laurent et al. 2010 and references therein). The mammalian taxa found in the fossiliferous levels indicate an age near the reference level MP8–9, which corresponds to the middle Ypresian, early Eocene (Laurent et al. 2010; Danilo et al. 2013).

The first avian fossil reported from La Borie is an isolated tibiotarsus that was assigned to the giant ground bird *Gastornis parisiensis* Hébert, 1855 (Buffetaut 2008). The preliminary study by Laurent et al. (2010) reported new avian remains that were assigned to *Gastornis* (Gastornithidae) and *Eogrus* sp. (Eogruidae). Here we provide a detailed description of these avian remains. The new gastornithid material is referred to *Gastornis parisiensis* Hébert, 1855. To date, *Gastornis* is known to occur in the Paleocene to middle Eocene of Europe (Martin 1992; Buffetaut 1997, 2008; Angst and Buffetaut 2013; Hellmund 2013), early Eocene of China (Hou 1980; Buffetaut 2013) and early Eocene of North America (Andors 1988, 1992; Eberle and Greenwood 2012). In the first publication on La Borie locality (Laurent et al. 2010), some avian fossils were assigned to the extinct genus

Eogrus (Eogruidae). This attribution was based on the very elongate shape of the tarsometatarsus and on the presence of a strongly projecting crista lateralis hypotarsi. Actually, the appearance of this crest is due to a taphonomic process which has produced a strong compression of the shaft in mediolateral direction. The morphological characteristics of the tibiotarsi are different from those of the Eogruidae and agree better with those of the Geranoididae. So far, the latter taxon was known only from the early and middle Eocene of North America (Cracraft 1969; Mayr 2009). Hence, the fossils from La Borie constitute the first record of the Geranoididae in Europe. Fossils of *Gastornis* come from three fossiliferous sites within the locality of La Borie, including SP1, SP2, and SP5 (see Laurent et al. 2010: fig. 2). Geranoididae remains come from the sites SP2 and SP5. SP2 is found in grey clays containing strongly pyritised organic matter, and SP1 and SP5 are located in sandstone banks (Laurent et al. 2010: fig. 2).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; APSO, Association Paléontologique du Sud-Ouest, Toulouse, France; BR, Muséum National d'Histoire Naturelle, Mont-de-Berru collections, Paris, France; MHNL St.G., Muséum d'Histoire Naturelle de Lyon, Saint-Gérand-le-Puy collections, Lyon, France; MHNT, Muséum d'Histoire Naturelle, Toulouse, France; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMNH, National Museum of Natural History, Washington, USA; NHM, Natural History Museum, London, UK; R, Muséum National d'Histoire Naturelle, Cernay-lès-Reims collections, Paris, France.

Other abbreviations.—SP, fossiliferous sites in the locality of La Borie.

Material and methods

The fossil material described here is deposited in the collections of the MHNT and APSO. Anatomical terminology follows Baumel et al. (1993) and Livezey and Zusi (2006).

Systematic palaeontology

Class Aves Linnaeus, 1758

Order Gastornithiformes Stejneger, 1885

Family Gastornithidae Fürbringer, 1888

Genus *Gastornis* Hébert, 1855

Type species: *Gastornis parisiensis* Hébert, 1855; the "Conglomérat de Meudon", Ypresian, early Eocene, Meudon, France.

Gastornis parisiensis Hébert, 1855

Figs. 1–4.

Referred material.—MHNT.PAL.2013.15.1, maxilla; MHNT.PAL.2013.15.2, right os quadratum; MHNT.PAL.2013.15.3–8, six vertebrae cervicales; MHNT.PAL.2013.15.9, shaft of left femur; MHNT.PAL.2013.15.10, left tibiotarsus; APSO.2006.SP1-62, right tibiotarsus; from La Borie, Saint-Papoul, department of Aude, southern France; middle Ypresian, early Eocene, age close to reference level MP8–9.

Measurements (in mm).—Maxilla MHNT.PAL.2013.15.1: height, 166.0; length as preserved, 178.0; distance between rostral margin of right apertura nasi ossea and apex of rostrum maxillare, 100.0; distance between dorsal margin of right apertura nasi ossea and culmen, 93.2; distance between ventral margin of right apertura nasi ossea and crista tomialis, 54.0; length of right apertura nasi ossea, 34.0; height of right apertura nasi ossea, 17.0. Quadratum MHNT.PAL.2013.15.2: height, 77.0; width of processus oticus, 35.1; length of processus mandibularis (from caudal margin of condylus lateralis and cotyla quadratojugalis to rostral margin of condylus medialis), 62.6. Vertebra MHNT.PAL.2013.15.3: estimated length of arcus transversus at midline, 29.3; estimated length of dorsal part of corpus vertebrae at midline, 50.0. Vertebra MHNT.PAL.2013.15.5: width at processus transversi, 153.0; length of dorsal part of corpus vertebrae at midline, 59.2; width of facies articularis caudalis, 39.3; length from tip of zygapophysis caudalis to tip of zygapophysis cranialis, 91.5. Vertebra MHNT.PAL.2013.15.6: estimated height of facies articularis caudalis, 32.0; length from tip of zygapophysis caudalis to tip of zygapophysis cranialis, 83.0. Vertebra MHNT.PAL.2013.15.7: width at zygapophyses caudales, 85.4; length of arcus transversus at midline, 34.0; length of dorsal part of corpus vertebrae at midline, 47.1; width of facies articularis caudalis, 42.1; length from tip of zygapophysis caudalis to tip of zygapophysis cranialis, 63.0. Vertebra MHNT.PAL.2013.15.8: width at zygapophyses caudales, 74.8; length of arcus transversus at midline, 24.0; length of dorsal part of corpus vertebrae at midline, 39.1; width of facies articularis caudalis, 35.8. Femur MHNT.PAL.2013.15.9: length as preserved, 262.0; width of corpus femoris at mid-shaft, 49.6; depth of corpus femoris at mid-shaft, 38.4. Tibiotarsus MHNT.PAL.2013.15.10: length as preserved, 415.0; width of corpus tibiotarsi at mid-shaft, 38.3; depth of corpus tibiotarsi at mid-shaft, 25.1; length of crista fibularis, 107.0; depth of condylus lateralis, 55.2. Tibiotarsus APSO.2006.SP1-62: length as preserved, 430.0; width of corpus tibiotarsi at mid-shaft, 46.9; depth of corpus tibiotarsi at mid-shaft, 32.5; length of crista fibularis, 110.0; width of extremitas distalis, 93.0; depth of condylus lateralis, 60.1; depth of condylus medialis (estimated, due to imperfect preservation), 78.0. NB: measurements were not provided for vertebra MHNT.PAL.2013.15.4 because it is very badly preserved.

Description.—Maxilla: The maxilla (MHNT.PAL.2013.15.1) comes from site SP5 (Laurent et al. 2010: fig. 2), along with a quadratum, vertebra cervicalis and tibiotarsus (see below). The maxilla is massive, tall and laterally compressed (Fig. 1A). It has a convex culmen about 2 cm thick, and lacks a hooked tip (hamulus rostri). MHNT.PAL.2013.15.1 is partly damaged at the tip and in the caudal part that lies

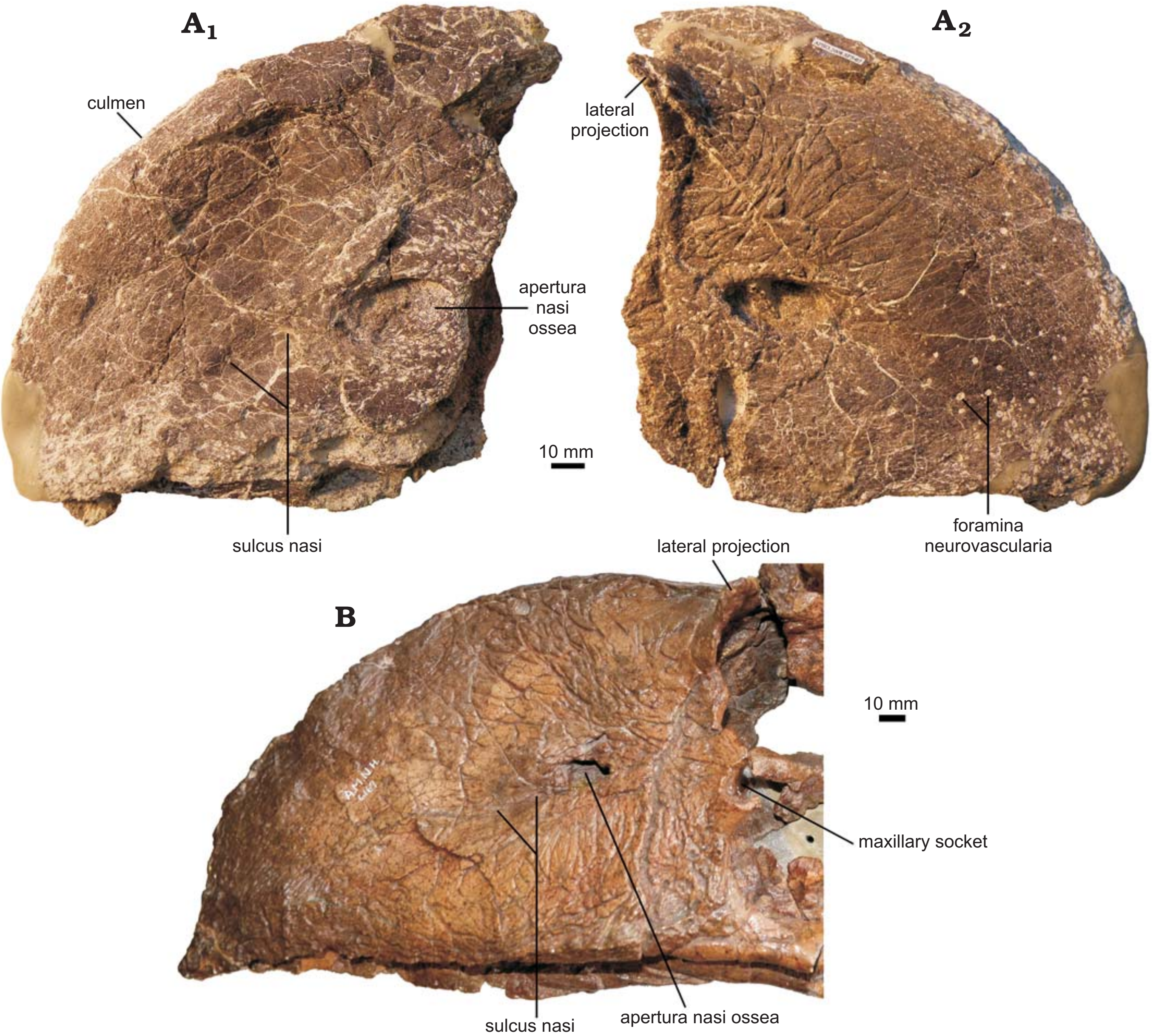

Fig. 1. Maxilla of early Eocene gastornithid birds. **A**. *Gastornis parisiensis* Hébert, 1855 MHNT.PAL.2013.15.1, La Borie, France, in left (A_1) and right (A_2) lateral views. **B**. *Gastornis giganteus* (Cope, 1876) AMNH6169, Willwood Formation, Wyoming, USA, in left lateral view.

in front of the orbita. The "maxillary socket" for the arcus jugalis found in *Gastornis giganteus* (Cope, 1876) (Fig. 1B; Andors 1988) is not preserved. The lateral projection which contacts the os lacrimale is partially preserved on the right side (Fig. 1A_2). The distance between the caudal rim of the apertura nasi ossea and the orbita was at least 2 cm. The apertura nasi ossea is in ventral position and its dorsal rim is located one-third the height from the lower border of the maxilla up to the culmen. A short furrow (sulcus nasi) extends in front of apertura nasi ossea on the lateral surface of the bill. Numerous grooves are found dorsal to the apertura nasi ossea. Some foramina neurovascularia are present on the distal part of the rostrum maxillae.

The maxilla from La Borie is similar to that of *G. giganteus* (AMNH6169) (Fig. 1B; Matthew and Granger 1917: pl. 20A, B), albeit slightly smaller. MHNT.PAL.2013.15.1 differs from *G. giganteus* in several features. The apertura nasi ossea is in more ventral position in *Gastornis parisiensis* Hébert, 1855 than in *G. giganteus* (Fig. 1). In the latter species, the dorsal rim of the apertura nasi ossea is located at mid-height of the maxilla (Fig. 1B; Matthew and Granger 1917: pl. 20A, B). The portion located rostral to the apertura nasi ossea is proportionally shorter in the maxilla from la Borie than in *G. giganteus*. In MHNT.PAL.2013.15.1, the apertura nasi ossea is slightly larger and faces more laterally than in *G. giganteus*, and the sulcus nasi is shallower (Fig. 1).

The maxilla R2583 from Cernay-lès-Reims (Martin 1992: fig. 1) is too large to fit with the tarsometatarsus described as the type specimen of *Gastornis russelli* Martin, 1992 (Martin 1992: fig. 6), but its size is much smaller than those of MHNT.PAL.2013.15.1 and AMNH6169. Some anatomical details suggest that this maxilla might belong to a juvenile individual of *G. parisiensis*: the contact between processus frontalis of os premaxillare and processus premaxillaris of os nasale is not fully ossified (open sutura) and is visible on the dorsal edge of the maxilla and on the ventral border of the pila supranasalis, which is not the case in adult individuals of *Gastornis*. The apertura nasi ossea is also very large with a relatively slender pila supranasalis, which is probably due to an incomplete ossification of the bones in this region.

Quadratum: The right os quadratum (MHNT.PAL.2013. 15.2) probably belongs to the same individual as the maxilla described above, because both fossils were found close to each other within the same layer, in site SP5. The os quadratum of *Gastornis parisiensis* is well preserved except the tip of the processus orbitalis and medial margin of the processus oticus (Fig. 2A). The quadratum is large and stout, with a well-developed processus orbitalis that is depressed on the medial side. The processus oticus has a single head with two distinct facets (condyli), and its curved rostral border is continuous with a large tuberculum musculi adductor mandibulae ossis quadrati (eminentia articularis) (Fig. $2A_1$, A_2). The elongate processus mandibularis bears only two condyli (Fig. $2A_4$), and the cotyla quadratojugalis is shallow (Fig. $2A_5$).

Comparisons were made with: (i) a quadratum from the late Paleocene of Cernay-lès-Reims (R3561; Fig. 2C) and two quadrata from the late Paleocene of Mont-de-Berru (BR617, which is represented in Fig. 2B, and BR12461) which also belong to *G. parisiensis* (Martin 1992); (ii) the quadrata of *Gastornis giganteus* (AMNH6169). MHNT.PAL.2013.15.2 is comparable in size to R3561 and AMNH6169 and slightly larger than the two specimens from Berru.

G. parisiensis (MHNT.PAL.2013.15.2) differs from *G. giganteus* in the relatively more slender and pointed processus orbitalis (Fig. $2A_1$). In *G. giganteus*, this structure is extremely stout and truncated at the extremity (Matthew and Granger 1917: pl. 22: 2a). The processus orbitalis is not preserved in the quadrata from Cernay and Berru assigned to *G. parisiensis* (Fig. 2C). In *G. parisiensis*, the condyli are aligned with each other, and the lateral edge of the processus mandibularis is convex (Fig. $2A_4$). In *G. giganteus*, the condylus medialis is more deflected medially with respect to the condylus lateralis and a distinct depression separates the two condyli (Matthew and Granger 1917: pl. 22: 2c). The medial edge of the condylus medialis exhibits a process in MHNT.PAL.2013.15.2 (Fig. $2A_3$). This convexity is also present in the quadrata from Cernay and Berru, albeit less prominent, and absent in *G. giganteus*. In *G. parisiensis*, a sharp ridge delimits the condylus medialis rostrolaterally and extends medial to the condylus pterygoideus (Fig. $2A_2$, A_3). This "rostral ridge" occurs in the quadrata from La Borie and Cernay/Berru. In *G. giganteus*, this ridge is absent.

MHNT.PAL.2013.15.2 exhibits features which are absent in the quadrata from the eastern Paris Basin (Cernay and Berru) and in the quadrata of *G. giganteus*: in MHNT.PAL.2013.15.2, the tuberculum musculi adductor mandibulae is oval in shape and continuous with a sharp curved ridge that constitutes the rostral border of the processus oticus (Fig. $2A_1$, A_2). In the quadrata from Cernay and Berru, the tuberculum is very prominent and pointed, somewhat "hooked" ventrally (Fig. 2B, C). In *G. giganteus*, the tuberculum musculi adductor mandibulae is large and rounded (Matthew and Granger 1917: pl. 22: 2a, b), and there is no ridge at the rostral edge of the processus oticus. Among the *G. parisiensis* specimens, differences occur between the quadratum from the early Eocene of La Borie and the quadrata from the late Paleocene of the eastern Paris Basin. In the quadratum from La Borie, the processus mandibularis is slender, lateromedially narrow, and the concavity that separates the two condyli is shallow (Fig. $2A_4$). In the quadrata from Cernay and Berru, the processus mandibularis is markedly wider and shorter, and the condyli are more convex and separated by a deeper depression (Fig. 2B, C). The cotyla quadratojugalis of MHNT.PAL.2013.15.2 is shallow (Fig. $2A_1$, A_5), as in *G. giganteus*. In contrast, the cotyla quadratojugalis of the quadrata from Cernay and Berru is deep, circular, surrounded by a thick edge (Fig. 2B, C). Part of these differences might be due to preservation, since the specimen from La Borie appears lateromedially compressed compared to other examined *Gastornis* quadrata. Some of these differences probably reflect intraspecific variation within *G. parisiensis*, in addition to the fact that the specimens from the eastern Paris Basin and the specimen from La Borie are Thanetian and Ypresian in age, respectively.

Vertebrae cervicales: Vertebral remains include six vertebrae cervicales that are broken and/or crushed to various degrees. Four of them (MHNT.PAL.2013.15.3–6) were found in close proximity to one another and in the same layer, along with a left tibiotarsus (see below), in locus SP1. These vertebrae most probably come from the same individual. MHNT. PAL.2013.15.6 belongs to the cranial series (sectio I, facies articularis cranialis facing ventrally) (Fig. 3A), and the three other vertebrae (MHNT.PAL.2013.15.5 represented in Fig. 3D) belong to the beginning of the intermediate series (sectio II, facies articularis cranialis facing dorsally). A vertebra cervicalis (MHNT.PAL.2013.15.8) of the intermediate series was found in site SP5, in close association with cranial remains (see above) and right tibiotarsus (see below). It is well preserved, undistorted, and lacks the left ansa costotransversaria (Fig. 3C). An isolated vertebra cervicalis (MHNT. PAL.2013.15.7) of the intermediate series was found in site SP2, at the bottom of the fossiliferous layer, along with turtle remains. It is well preserved, undistorted, and lacks part of the left ansa costotransversaria (Fig. 3B). This vertebra is slightly larger in size than other vertebral remains.

The vertebrae cervicales are heterocoelous, extremely massive and greatly shortened craniocaudally. The corpus vertebrae is short and wide. The zygapophyses are stout and their facies articulares are large, round and flat. The processus costales are short and blunt at the tip (Fig. $3D_1$). The cranial vertebra cervicalis exhibits a small foramen arcocostalis cranialis and its arcus vertebrae is longer than in

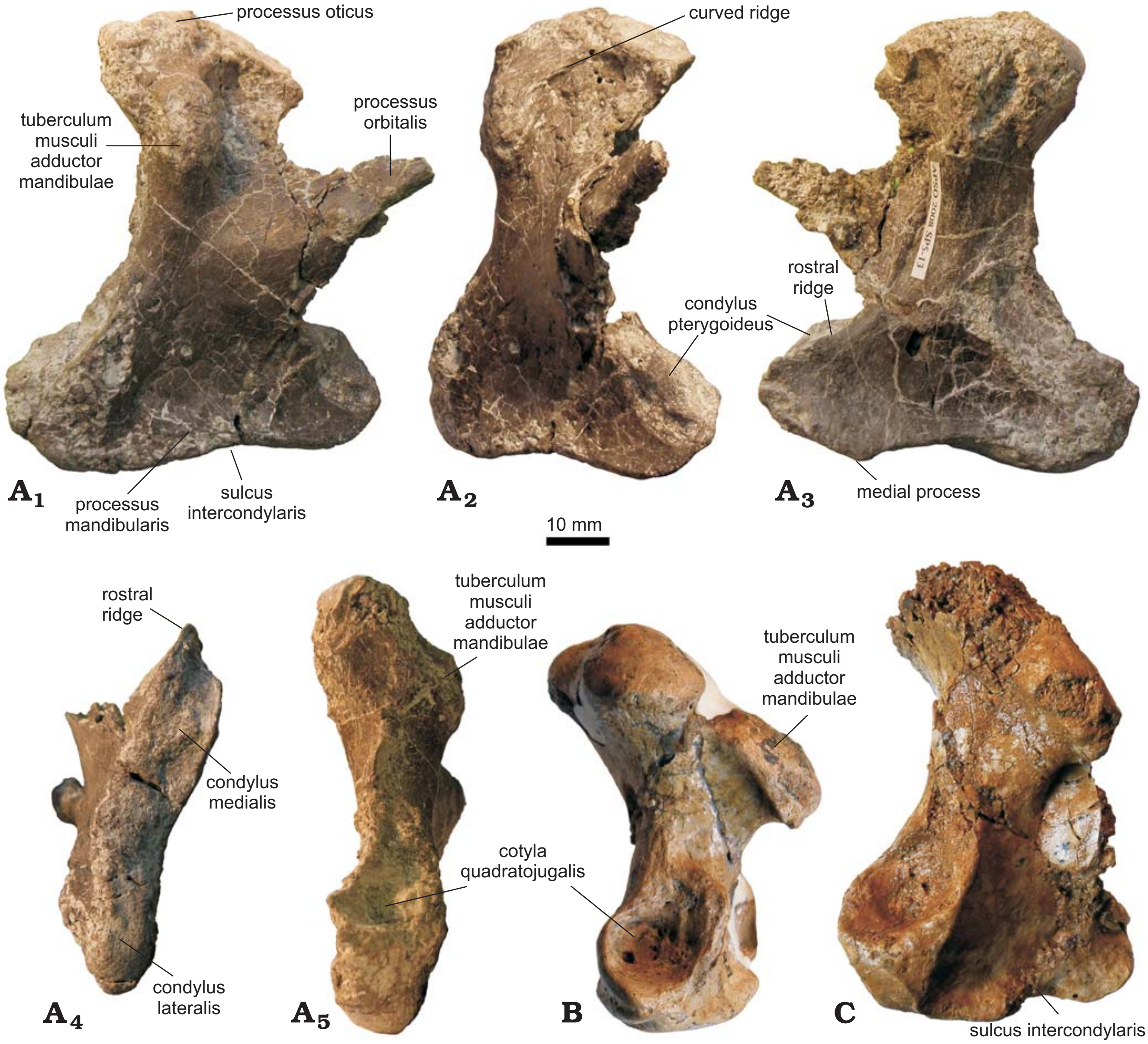

Fig. 2. Quadrata of gastornithid bird *Gastornis parisiensis* Hébert, 1855. **A**. MHNT.PAL.2013.15.2 (right), early Eocene, La Borie, France, in lateral (A_1), craniolateral (A_2), medial (A_3), distal (A_4), and caudal (A_5) views. **B**. BR617 (reversed left), late Palaeocene, Berru, France, in laterocaudal view. **C**. R3561 (right), late Palaeocene, Cernay, France, in lateral view.

intermediate vertebrae cervicales (Fig. 3A). The vertebrae cervicales of the intermediate series have stout processus transversi (Fig. 3D_1) and very large foramina transversaria (Fig. 3B_3, C_2). The arcus vertebrae is very short craniocaudally and has marked area ligamenti elastici on either side (Fig. 3B_3). The facies articularis cranialis is separated from the bottom of the corpus vertebrae by a deep ventral furrow (Fig. 3D_1). Caudalmost vertebrae of the intermediate series (MHNT.PAL.2013.15.7 and MHNT.PAL.2013.15.8) exhibit well developed processus carotici and a deep sulcus caroticus (Fig. 3B_3, C_2). The facies articulares of the zygapophyses craniales and caudales are separated from each other by a very short distance (Fig. 3B_2). The vertebrae cervicales from La Borie are exceedingly similar to the two vertebrae cervicales from Cernay-lès-Reims (listed in Martin 1992) and one vertebra cervicalis from Mont-de-Berru also deposited in the collections of the MNHN (BR 14568, not listed in Martin 1992). The vertebrae cervicales of *Gastornis parisiensis* closely resemble those preserved in *Gastornis giganteus* (Matthew and Granger 1917: pls. 23–25).

Femur: The left femur (MHNT.PAL.2013.15.9) was found in site SP2, at the top of the fossiliferous layer, in contact with a gravel bar. This specimen does not preserve many diagnostic features. MHNT.PAL.2013.15.9 consists of the shaft, and the proximal and distal extremities are broken. On the facies cranialis, the distal end of the crista trochanteris is visible and continuous with an oblique linea intermuscularis cranialis. The facies caudalis (Fig. 4A) preserves an impressio musculi iliotrochantericus, most of the fossa poplitea, and a large, ovoid tuberculum musculi gastrocnemius pars

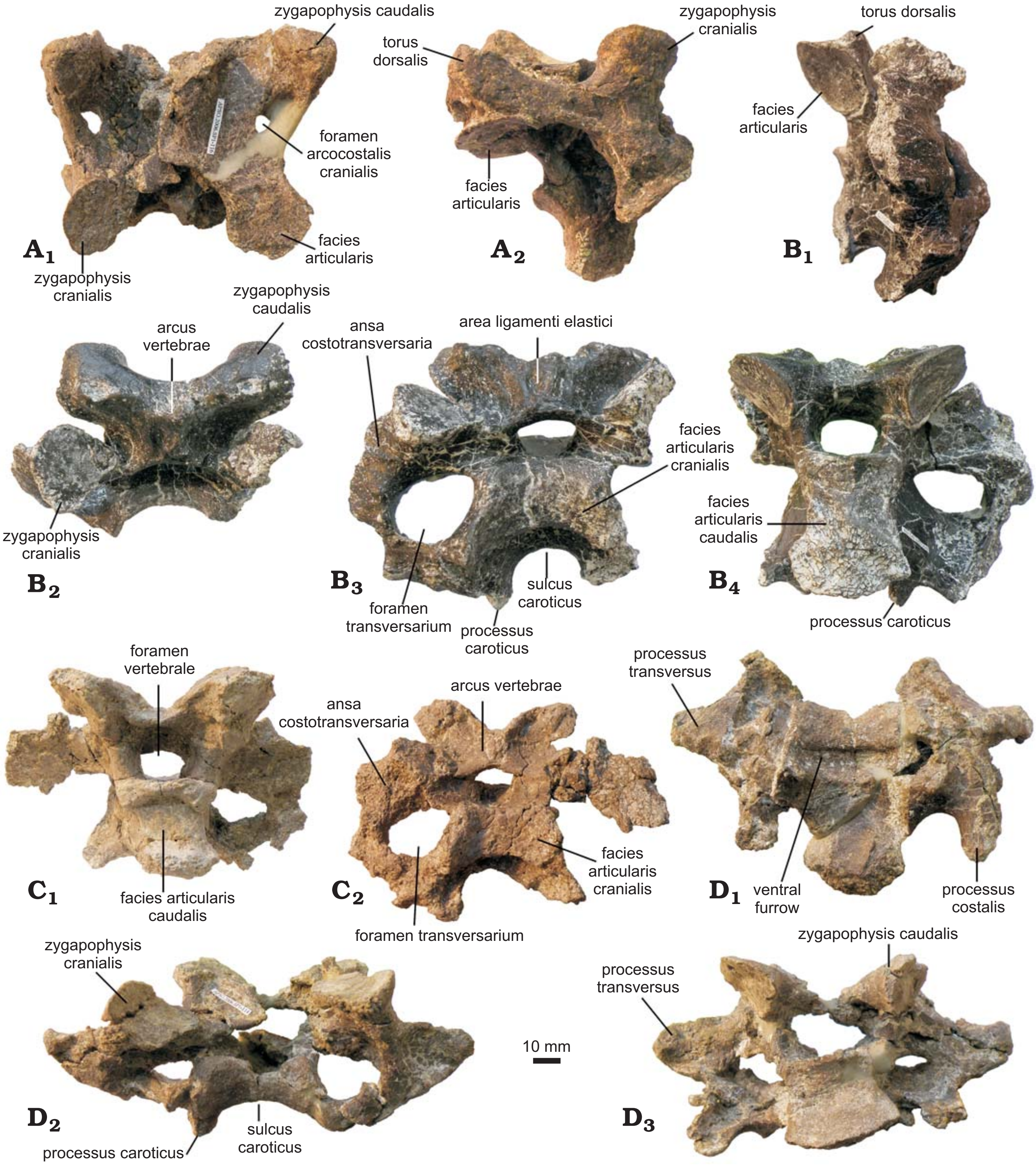

Fig. 3. Vertebrae cervicales of gastornithid bird *Gastornis parisiensis* Hébert, 1855, early Eocene, La Borie, France. **A**. MHNT.PAL.2013.15.6, in dorsal (A_1) and right lateral (A_2) views. **B**. MHNT.PAL.2013.15.7, in right lateral (B_1), dorsal (B_2), cranial (B_3), and caudal (B_4) views. **C**. MHNT.PAL.2013.15.8, in caudal (C_1) and cranial (C_2) views. **D**. MHNT.PAL.2013.15.5, in ventral (D_1), cranial (D_2), and caudal (D_3) views.

lateralis, which is located at the base of the condylus lateralis. The crista trochanteris extends far distally on the shaft. The latter is craniocaudally compressed and distinctly deflected medially towards the base of the condylus medialis. The fossa poplitea is deep and the tuberculum musculi gastrocnemius pars lateralis is an oval concavity. The femur MHNT. PAL.2013.15.9 possibly belongs to a juvenile individual, because it is smaller than the tibiotarsi described below. This

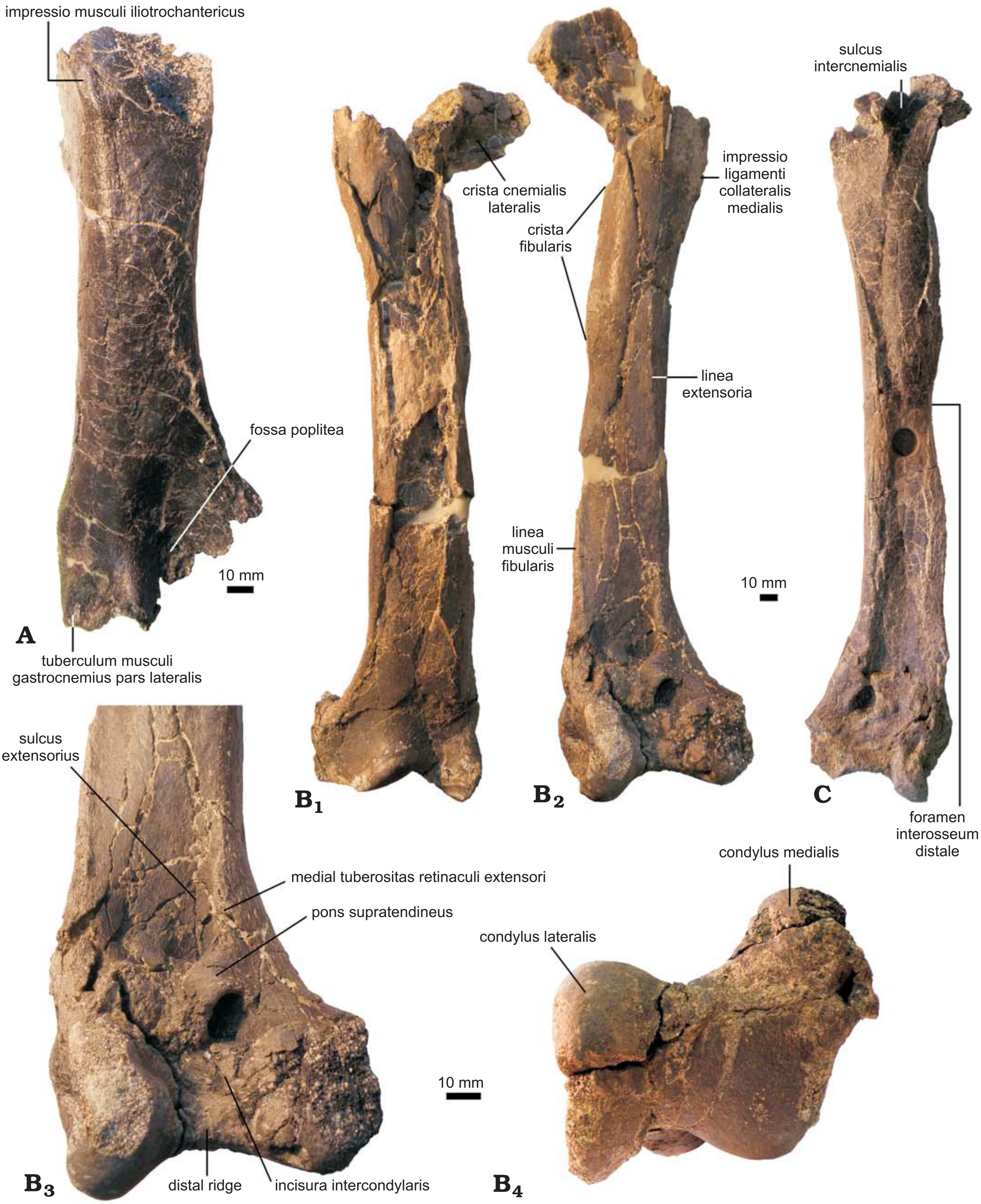

Fig. 4. Hindlimb of gastornithid bird *Gastornis parisiensis* Hébert, 1855, early Eocene, La Borie, France. **A**. Left femur MHNT.PAL.2013.15.9, in caudal view. **B**. Right tibiotarsus APSO.2006.SP1-62, in caudal (B_1) and cranial (B_2) views, distal part in cranial (B_3) and distal (B_4) views. **C**. Left tibiotarsus MHNT.PAL.2013.15.10, in cranial view.

is also supported by the fact that this specimen was found isolated from other *Gastornis* remains.

Tibiotarsi: The left tibiotarsus (MHNT.PAL.2013.15.10) was found associated with cranial remains and a vertebra, in site SP5. MHNT.PAL.2013.15.10 includes the base of the cristae cnemiales, the shaft, and a badly preserved extremitas distalis (Fig. 4C). The right tibiotarsus (APSO.2006.SP1-62) was found next to a series of vertebrae cervicales in site SP1. APSO.2006.SP1-62 includes an incomplete extremitas proximalis that only preserves the crista cnemialis lateralis, the slightly crushed shaft, and a well-preserved extremitas distalis (Fig. 4B). These specimens are from two different individuals because the left tibiotarsus is slightly smaller than the right one, and because they come from two different sites.

The cristae cnemiales are strongly deflected laterally, as in the *Gastornis parisiensis* tibiotarsus previously described from the same locality (Buffetaut 2008: fig. 2). The crista cnemialis lateralis is proximally prominent and its thick lateral margin is slightly twisted caudally (Fig. 4B_1, B_2). The crista fibularis is thick and elongate (Fig. 4B_1, B_2, C). The shaft is straight and craniocaudally compressed. Its lateral margin shows a slight concavity that corresponds to the foramen interosseum distale, just distal to the crista fibularis (Fig. 4C). The linea musculi fibularis is well marked and extends to the condylus lateralis. A drop-shaped impressio ligamenti collateralis medialis is located on the facies medialis of the shaft, level with the proximal end of the crista fibularis (Fig. 4B_2). The linea extensoria extends from the distal end of the crista cnemialis cranialis down to the tuberositas retinaculi extensori located medial to the sulcus extensorius (Fig. 4B_2). The extremitas distalis is curved medially (Fig. 4B_3). The pons supratendineus is about 4 mm thick and 15 mm wide. It is oblique and located in the medial part of the tibiotarsus, its lateral margin being at the level of the midpoint of the shaft, as in the specimen previously described from La Borie (Buffetaut 2008). The incisura intercondylaris is wide and bounded distally by a prominent ridge that joins the distal edges of the condyli. A similar ridge is clearly visible in the tibiotarsus of *G. parisiensis* (Martin 1992: fig. 2), *Gastornis giganteus* (Matthew and Granger 1917: pl. 32) and *Gastornis xichuanensis* (Hou, 1980) (Buffetaut 2013: fig. 2a). The condylus medialis protrudes further cranially than the condylus lateralis (Fig. 4B_4). The size and shape of the new tibiotarsi from La Borie match well with those of other specimens of *G. parisiensis* (Martin 1992; Buffetaut 1997, 2008; and references therein).

Stratigraphic and geographic range.—Thanetian (Late Paleocene) to Ypresian (early Eocene); France (Meudon, Passy, Berru, Cernay, Saint-Papoul), England (Croydon), and Belgium (Mesvin).

Order Gruiformes (Bonaparte, 1854)

Suborder Grues Bonaparte, 1854

Family Geranoididae Wetmore, 1933

Genus *Galligeranoides* nov.

Type species: *Galligeranoides boriensis* sp. nov.; monotypic, see below.

Etymology: Combination of the ancient name of France, *Galli*, and the type genus of the extinct family Geranoididae.

Diagnosis.—As for the type species.

Stratigraphic and geographic range.—Ypresian (Early Eocene), southern France.

Galligeranoides boriensis sp. nov.

Figs. 5A, 6, 7.

Etymology: From La Borie, the name of the quarry; in langue d'Oc language *borie*, large farm.

Type material: Holotype: MHNT.PAL.2013.16.3, distal part of left tibiotarsus (Fig. 5A). Paratypes: MHNT.PAL.2013.16.1, right tibiotarsus (Fig. 6A); MHNT.PAL.2013.16.2, subcomplete right tarsometatarsus (Fig. 6B).

Type locality: La Borie, Saint-Papoul, Department of Aude, Southern France.

Type horizon: Middle Ypresian, early Eocene, close to reference level MP8–9.

Diagnosis.—Tibiotarsus with condylus medialis projecting cranially and slightly deeper than condylus lateralis; cranial surface of distal end flat with a well-developed ridge along the medial side of this flat area; canalis extensorius located on the medial side and with two tiny openings; muscular tubercle located in the median axis of the bone and extended proximally by tuberositas retinaculi extensori; distinct groove between muscular tubercle and condylus lateralis; flattened surface on the lateral side of the tuberositas retinaculi extensori and proximal to condylus lateralis; trochlea cartilaginis tibialis bordered by bladelike projecting cristae trochleares.

Measurements (in mm).—MHNT.PAL.2013.16.3, distal part of left tibiotarsus (holotype): width of shaft on the cranial side, just proximal to the condyli, 16.9; depth of condylus medialis, 21.8; depth of condylus lateralis, 20.0; estimated distal width on the cranial side, 16.5; estimated width of trochlea cartilaginis tibialis, 13.7; width of condylus medialis on the cranial side, 6.5; width of condylus lateralis on the cranial side, 7.0. MHNT.PAL.2013.16.1, right tibiotarsus: total length (as preserved), 252.0; width at mid-shaft (as preserved), 12.3; depth at mid-shaft (as preserved), 9.8; width of shaft on the cranial side, just proximal to the condyli, 14.7; distal width (as preserved; condylus lateralis is incomplete), 16.0; depth of condylus medialis (as preserved; trochlea cartilaginis tibialis is incomplete), 17.0; width of condylus medialis on the cranial side, 6.5. MHNT.PAL.2013.16.2, right tarsometatarsus: total length (as preserved), 232.0; proximal depth from eminentia intercotylaris to cristae hypotarsi (as preserved), 21.5; depth of cotyla medialis, 12.0; depth at mid-shaft (as preserved), 11.4; width of sulcus flexorius at mid-shaft, 8.1; distal width, 24.7; distal depth, 16.1; width of trochlea metatarsi (TM) II, 6.0; depth of TM II (as preserved), 10.6; width of TM III, 11.0; depth of TM III, 11.2; width of TM IV, 7.1; depth of TM IV (as preserved), 11.0.

Description.—*Tibiotarsi*: The distal part of tibiotarsus MHNT.PAL.2013.16.3 (holotype) was found in site SP5. This left tibiotarsus is crushed and distorted. The cranial surface of the shaft is flat and shows a longitudinal ridge on its medial border. The openings of the canalis extensorius are very small and hardly visible. The pons supratendineus is very elongate in proximodistal direction. The muscular tubercle that is located at the distal part of the pons supratendineus is strongly projecting. It is situated in the median axis of the bone and is continuous with a strong crest which corresponds to the tuberositas retinaculi extensori. The tubercle is separated from the condylus lateralis by a deep groove. The condylus medialis is almost as wide as the condylus lateralis and the incisura intercondylaris is very narrow. The condylus medialis is strongly projecting cranially, partly because of distortion. It is, however, longer in craniocaudal direction than the condylus lateralis. The slight distal protrusion of the condylus medialis relative to the latter is due to crushing. The epicondylus medialis is well developed; the distal outline of the condylus is incompletely preserved but there is an indication of the presence of a notch. The trochlea cartilaginis tibialis is bounded on either side by strongly projecting, bladelike cristae trochleares. It is possible, however, that these cristae have been sharpened by crushing. The trochlea itself is narrow and deep. The distal outline of the condylus lateralis is flattened and shows no indentation. The epicondylus lateralis is weakly projecting. A flattened ligamentary insertion for the retinaculum musculi fibularis is located proximal to the condylus lateralis (Fig. 7A).

The tibiotarsus MHNT.PAL.2013.16.1 (also from site SP5) is broken and crushed. The proximal part is missing. The shaft is preserved up to the base of the crista cnemialis lateralis, but it is not possible to see the crista fibularis. The distal part lacks the trochlea cartilaginis cranialis and the cristae trochleares. The condylus lateralis and part of the shaft proximal to it are incompletely preserved. The preserved part of the distal end is similar to that of the holotype: the openings of the canalis extensorius are tiny; the pons supratendineus is proximodistally wide; the muscular tubercle is prolonged proximally by a crest located in the medial axis of the bone, and is separated from the condylus lateralis by a deep groove. The condylus medialis is relatively wide and strongly projected cranially, and the incisura intercondylaris is narrow.

Tarsometatarsus: The tarsometatarsus MHNT.PAL.2013.16.2 (found in site SP2) is almost complete. The lateral part of the extremitas proximalis and part of TM IV are broken. The lateral rim of TM III is slightly eroded on the lateral and plantar sides. The wings of TM II and IV are also eroded. The proximal part and about 2/3 of the shaft are crushed in mediolateral direction. The eminentia intercotylaris is rounded and cranially projected, but rather flattened on the proximal articular surface. The cotyla medialis has a quadrangular outline. The fossa infracotylaris dorsalis is very deep and shows two foramina vascularia proximalia located almost at the same level. The preserved crista hypotarsi is plantarly prominent and rather medially directed. The rest of the hypotarsus is

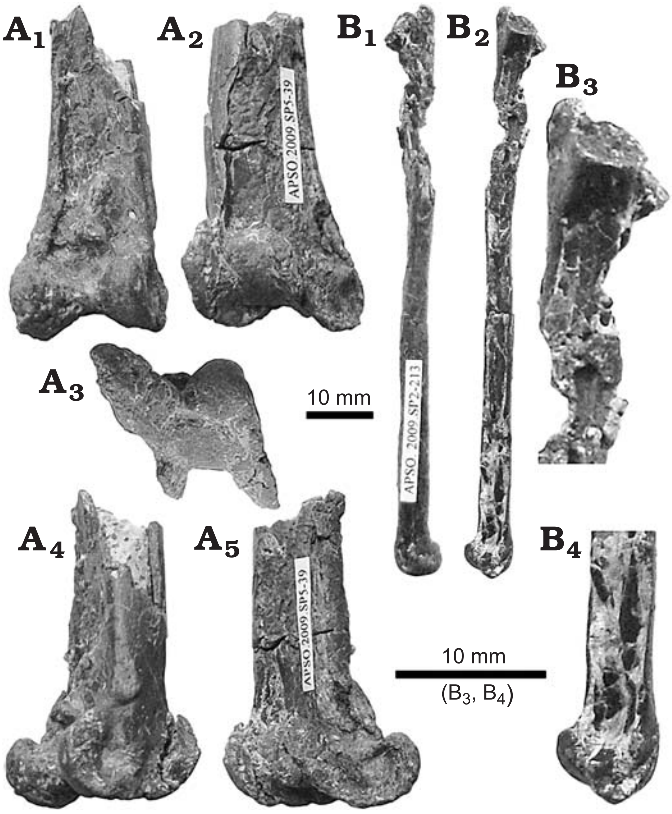

Fig. 5. Limb bones of early Eocene birds, La Borie, France. **A**. Geranoidid *Galligeranoides boriensis* gen. et sp. nov., left tibiotarsus, MHNT.PAL.2013.16.3 (holotype), in cranial (A_1), caudal (A_2), distal (A_3), lateral (A_4), and medial (A_5) views. **B**. Undetermined bird, left ulna, MHNT.PAL.2013.16.4, in dorsal (B_1), ventral (B_2), proximal part in ventral (B_3) and distal part in ventral (B_4) views.

crushed but it is possible to see the trace of a canalis hypotarsi, which opened on the proximal articular surface, and extended distally over 3 cm (Fig. 7B). The sulcus extensorius is deep, but this character is strongly exaggerated by the crushing of the shaft. The sulcus extensorius extends over 4/5 of the shaft. The crista hypotarsi extends over a length of about 4 cm; the well developed cristae plantares extend over 4/5 of the shaft and border a wide, shallow sulcus flexorius. The distal part of TM III is wide, with two symmetrical rims. The distal part of TM IV reaches the mid-length of TM III, and TM II is slightly shorter than TM IV. In distal view the TM are disposed along a weakly curved line. TM II is slightly more plantarly displaced than TM IV. On the cranial face TM III is continued proximally as a wide, flattened, weakly projecting ridge. The foramen vasculare distale is very wide and opens at the distal end of a short groove. The incisurae intertrochleares are very wide, especially the lateral one. There is no indication of a fossa metatarsi I. The fossa supratrochlearis plantaris is wide and shallow. The opening of the canalis interosseus distalis is proximal to the incisura intertrochlearis lateralis and just distal to the opening of the foramen vasculare distale. TM III is not raised above the surface of the fossa supratrochlearis plantaris and ends proximally into a small circular depression.

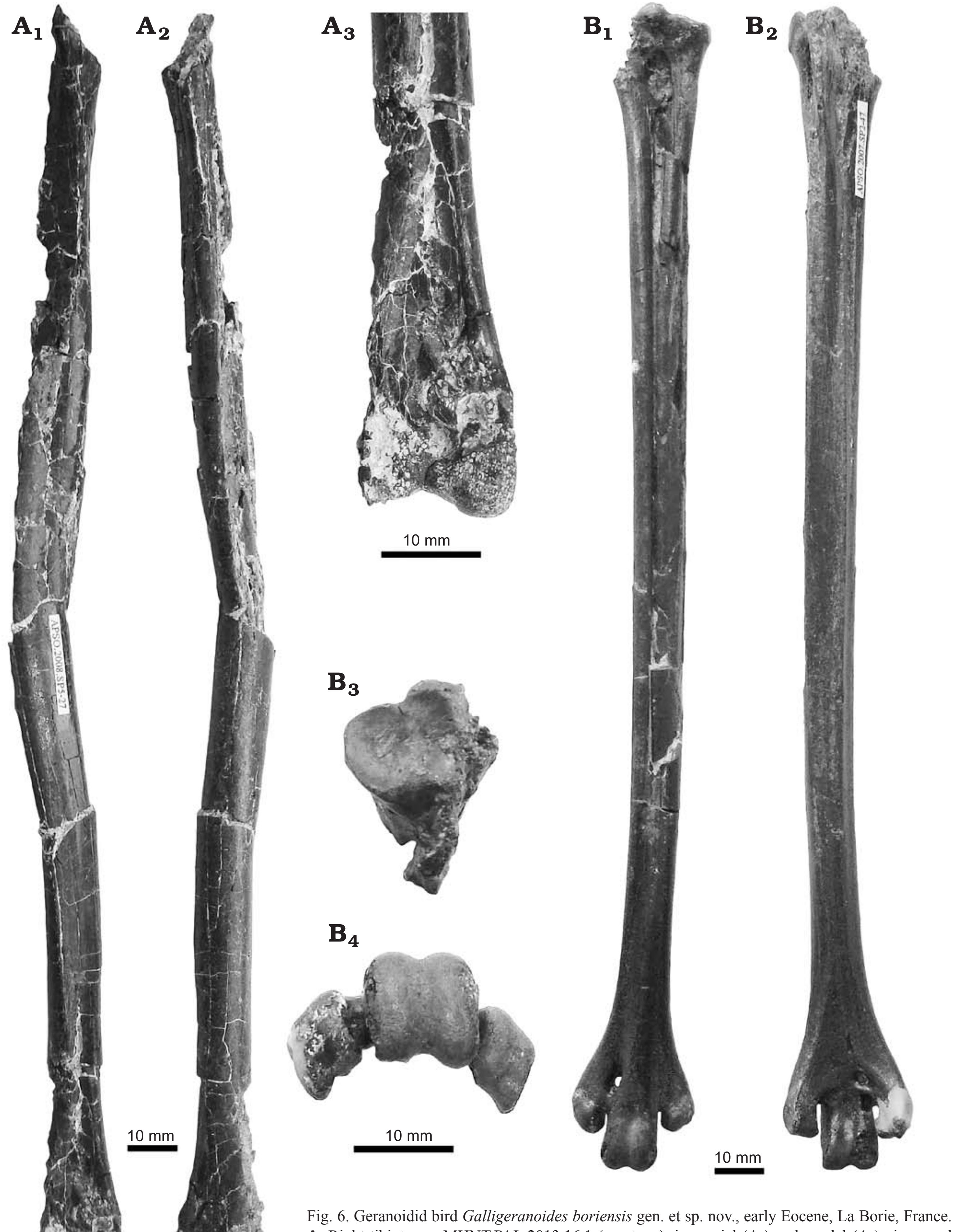

Fig. 6. Geranoidid bird *Galligeranoides boriensis* gen. et sp. nov., early Eocene, La Borie, France. **A**. Right tibiotarsus MHNT.PAL.2013.16.1 (paratype), in cranial (A_1) and caudal (A_2) views and distal part in cranial view (A_3). **B**. Right tarsometatarsus MHNT.PAL.2013.16.2 (paratype), in cranial (B_1), plantar (B_2), proximal (B_3), and distal (B_4) views.

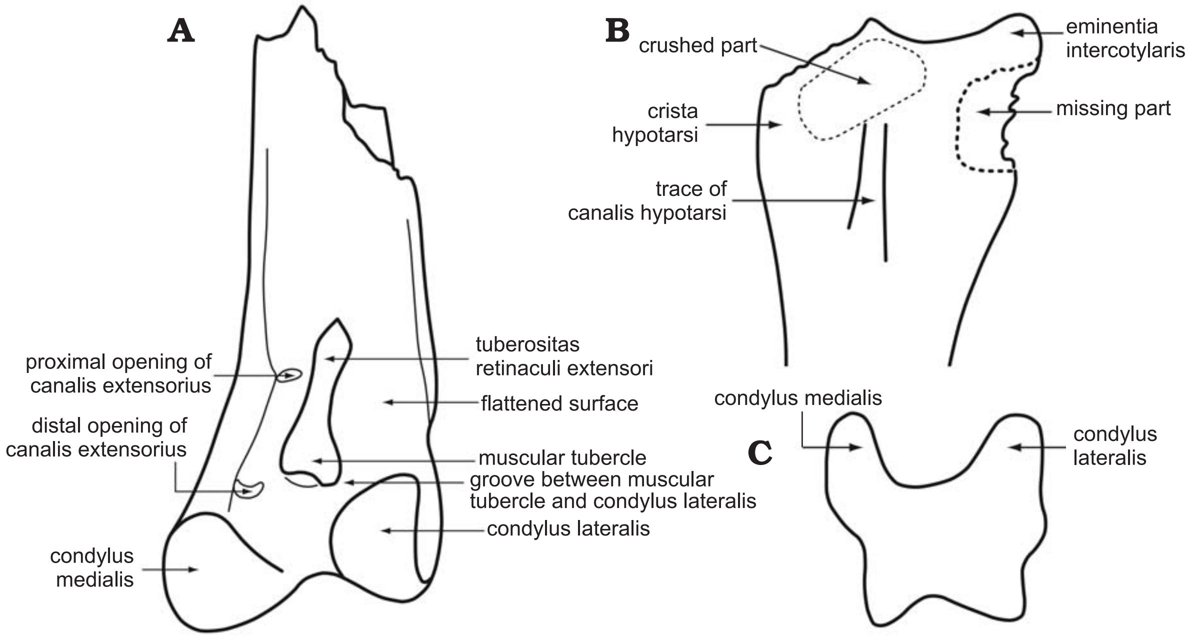

Fig. 7. Diagrams of limb bones of geranoidid bird *Galligeranoides boriensis* gen. et sp. nov., early Eocene, La Borie, France (**A**, **B**) and *Grus grus* (Linnaeus, 1758), extant, Eurasia and Africa (**C**). **A**. Distal part, cranial view of left tibiotarsus MHNT.PAL.2013.16.3. **B**. Proximal part, medial view of right tarsometatarsus MHNT.PAL.2013.16.2. **C**. Distal end of left tibiotarsus, showing the discontinuity in alignment of the condylus medialis.

Comparison with the Geranoididae.—The family Geranoididae includes five genera and seven species, mainly from the early Eocene of the Willwood Formation, and also from the middle Eocene of the Bridger Formation (Cracraft 1969; Mayr 2009). So far it was known only from the West of the United States. These taxa are almost uniquely known by distal parts of tibiotarsi and by proximal and distal parts of tarsometatarsi. Their morphological characteristics were given by Cracraft (1969). The characteristics of the distal part of tibiotarsus are as follows: distal part not strongly elongated medially; distal outline of the condylus lateralis flattened (rounded in the genus *Geranodornis*); distal outline of the condylus medialis showing a notch; condyli almost parallel to each other and incisura intercondylaris narrow; tubercle on the pons supratendineus moderately developed; condylus medialis not very cranially elongate and almost the same size as the condylus lateralis. On some of the tibiotarsi illustrated by Cracraft (1969), it is possible to see that the tubercle on pons supratendineus is extended proximally by a longitudinal ridge, and that this tubercle is separated from the condylus lateralis by a wide groove (e.g., in *Geranoides jepseni*, *Eogeranoides campivagus*, and *Geranodornis aenigma*; Cracraft 1969: figs. 1, 6, and 10). Concerning *Paragrus shufeldti*, Cracraft (1969: 11) writes: "The tubercle is situated nearly in the middle of the bone, being offset slightly to the external side, and separated from the external condyle by a rather broad groove". Also in *Palaeophasianus meleagroides* "there is a well-pronounced tubercle separated from the external condyle by a moderately broad groove" (Cracraft 1969: 20).

The *Galligeranoides* tibiotarsi show the morphological characteristics of the Geranoididae, with some small differences. These differences are as follows: condylus medialis more craniocaudally elongate than condylus lateralis (almost equal in other Geranoididae); openings of the canalis extensorius very narrow whereas they are generally wider in other Geranoididae (though they are very narrow in *Geranodornis*); flattened surface between the tubercle and its extending crest and the lateral side of the shaft (in Geranoididae the tubercle and crest are generally closer to the lateral side); wide, deep groove between the tubercle and the condylus lateralis (shallower in other Geranoididae); two projecting bladelike crests on the facies caudalis (less projecting in other Geranoididae).

For the tarsometatarsus, the main characteristics indicated by Cracraft (1969) for the Geranoididae, which occur on La Borie tarsometatarsus, are as follows: eminentia intercotylaris relatively pointed and not broad; TM II and TM IV slightly plantarly displaced relative to TM III (TM II more than TM IV); incisurae intertrochleares relatively broad (lateral more so than medial). These features are present in *Galligeranoides*. The proximal part of the tarsometatarsus is known in *Eogeranoides* and *Palaeophasianus*, and the distal part in *Paragrus* and *Palaeophasianus*. In the two latter genera, TM IV reaches 2/3 of TM III whereas it is shorter in *Galligeranoides* and reaches only the mid-length of TM III. There is still, in these two genera, a larger difference in the relative lengths of TM II and IV. TM II is clearly shorter than TM IV whereas in *Galligeranoides* TM II is only slightly shorter than TM IV. Lastly, in the description of *Geranoides jepseni* Wetmore (1933: 115) writes: "facet for articulation of first toe small but evident". In *Galligeranoides* this facet is not visible.

Comparison with the Eogruidae.—The Eogruidae are a family of large, long-legged birds which spanned from the middle Eocene to the early Pliocene of Eurasia (Clarke et al.

2005; Mayr 2009). They are mainly known by distal parts of tibiotarsi and by tarsometatarsi. These tarsometatarsi are very elongate and show a projecting crest along the lateral border of their plantar surface. They are also characterized by the progressive reduction, then disappearance, of TM II over time (Kurochkin 1976, 1981; Mayr 2009).

The distal part of tibiotarsus MHNT.PAL.2013.16.3 is very different from the tibiotarsi of the genus *Eogrus* (see Wetmore 1934: fig. 4; Cracraft 1973b: fig. 47; Clarke et al. 2005: fig. 8). On the paratype tibiotarsus of *Eogrus aeola* (Wetmore 1934: fig. 4), the canalis extensorius has two wide openings and is situated close to the middle of the facies cranialis. The pons supratendineus is proximodistally short. The muscular tubercle is weakly developed. Both condyli are almost the same depth in craniocaudal direction and almost the same width on the facies cranialis. The tibiotarsus of *Eogrus wetmorei* Brodkorb, 1967, from the Miocene of China, figured in Clarke et al. (2005: fig. 8A) shows the same characteristics.

On the tarsometatarsus of *Eogrus aeola*, the three trochleae are arranged on a weakly curved line, but TM II is much narrower than TM IV, whereas in *Galligeranoides* they have nearly the same width. In addition, TM II is much shorter than TM IV and hardly reaches 1/3 of TM III length. TM II is still shorter on the tarsometatarsus AMNH 2937. These characteristics are conspicuous on the tarsometatarsi figured in Clarke et al. (2005: figs. 2, 3, 5, 6). The tarsometatarsi of Eogruidae are also characterized by the presence of a plantarly projecting crest, on the facies plantaris of the shaft, on the lateral side (Kurochkin 1981: fig. 10; Mayr 2009). In *Galligeranoides*, the crista plantaris lateralis is not more projected than the crista plantaris medialis, but the shaft has been mediolaterally compressed.

Comparison with the Parvigruidae.—This family is based on the taxon *Parvigrus pohli* Mayr, 2005, from the Early Oligocene of Luberon, France. In *Parvigrus*, the distal part of the tarsometatarsus looks similar to those of Aramidae and *Balearica*. Its TM II is plantarly displaced and is shorter than TM III, but it is not as short as in the Gruidae. *Rupelrallus saxoniensis* Fischer, 1997, from the Early Oligocene of Weißelsterbeckens near Leipzig, Germany, was described as a Rallidae but, according to Mayr (2006, 2009, 2013) it can be attributed to the family Parvigruidae. The tibiotarsi and tarsometatarsus of *Galligeranoides* differ from this taxon because in *Rupelrallus* the tibiotarsus lacks a tubercle at the pons supratendineus, the condylus lateralis is very elongate in proximal direction along the craniolateral angle, and the trochlea cartilaginis tibialis is narrow. In *Rupelrallus*, the tarsometatarsus has a very short and strongly plantarly displaced TM II (see Fischer 1997: figs. 13a, b, 15a, b).

Comparison with the Gruidae.—The extant family Gruidae appeared in the middle Eocene with the genus *Palaeogrus*. In the Gruidae, on the distal part of the tibiotarsus, in distal view, the condylus medialis is parallel to the condylus lateralis, and then shows a discontinuity in alignment (Fig. 7C). This morphological characteristic is very slightly visible also in *Psophia*, but not in *Aramus*.

Palaeogrus princeps Portis, 1884 is known by a distal part of left tibiotarsus from the Lutetian of Italy (Portis 1884: pl. 1: 1–4). On the facies cranialis, it is only possible to see the wide proximal opening of the canalis extensorius, located almost in the middle of the cranial surface, but other morphological details are not visible “because the rest is masked by the still adherent sediments” (Portis 1884: 363, our translation from Italian). The lateral, caudal, and distal views of this tibiotarsus show the characteristic shape of the Gruidae, with the medial shift of the condylus medialis.

Palaeogrus hordwelliensis (Lydekker, 1891), from the late Eocene of England, is also known by a distal part of right tibiotarsus. *Palaeogrus excelsa* (Milne-Edwards, 1871) from the early and middle Miocene of France (Cheneval 2000; Mlíkovský 2002) is known by a large number of elements of the postcranial skeleton. *Palaeogrus mainburgensis* Göhlich, 2003, from the middle Miocene of Germany is also known by several elements including a distal part of tibiotarsus (Göhlich 2003). In these three species, the distal tibiotarsus shows the characteristics of the Gruidae: wide openings of the canalis extensorius; presence of a tubercle on the laterodistal border of the pons supratendineus; cranial end of condylus medialis thin; condylus medialis craniocaudally longer than condylus lateralis and showing a medial shift in distal view. In *Palaeogrus excelsa*, the distal part of the tarsometatarsus (visible on the specimen MHNL St.G. 64) shows that TM II is very short and strongly plantarly displaced. In this respect, *P. excelsa* is more similar to the Recent genus *Grus* than to the Recent genus *Balearica*. The species *Palaeogrus geiseltalensis* Lambrecht, 1935, from the middle Eocene of Geiseltal, has been placed in synonymy with *Palaeotis weigelti* Lambrecht, 1928 by Houde and Haubold (1987). These authors assign the genus *Palaeotis* to the Struthionidae.

The extinct genus *Geranopsis* was described from the late Eocene of England. It included two species, *Geranopsis hastingsiae* Lydekker, 1891, and *Geranopsis elatus* Milne-Edwards, 1892, from the Eocene or Oligocene of the Phosphorites du Quercy, in France. *Geranopsis elatus* has been transferred to the genus *Occitaniavis* and to the family Idiornithidae, suborder Cariamae (Mourer-Chauviré 1983). The holotype of *G. hastingsiae* is a left coracoideum which has been placed in the Gruidae probably because of the presence of a large pneumatic fossa on the dorsal surface, just proximal to the facies articularis sternalis (Cracraft 1973b; Harrison and Walker 1976). Later, Harrison and Walker tentatively referred to this species an omal part of coracoideum, three distal ends of tibiotarsi, and a proximal part of tarsometatarsus from the early Oligocene of England (Harrison and Walker 1979). Mayr (2005: 523 and 2009: 51, 103) remarked that the coracoideum of *G. hastingsiae* is morphologically very similar to the coracoideum of *Anserpica kiliani* Mourer-Chauviré, Berthet, and Hugueney, 2004, from the late Oligocene of France, which has been attributed to the Anseranatidae (Mourer-Chauviré et al. 2004). The coracoideum of *Geranopsis* differs from the Gruidae because its omal part is much shorter, compared to its total length, than in the latter taxon. In Gruidae the length of the omal part (from the top of processus acrocoracoideus to the sternal border of the cotyla scapularis) corresponds to about half of the internal length (from the top of processus acrocoracoideus to the angulus medialis of the facies articularis sternalis), while in *Geranopsis* the omal part is less developed and corresponds to about 30% of the internal length. In our opinion, the holotype coracoideum of *G. hastingsiae* probably does not belong to the Gruidae, and other elements referred to this species should be revised. The distal parts of tibiotarsi differ from *Galligeranoides* because they are wider than deep in distal view, and because both condyli are weakly projecting cranially. In addition, they are much smaller in size.

Stratigraphic and geographic range.—Ypresian (early Eocene), southern France.

Neornithes incertae sedis

Fig. 5B.

Material.—Left ulna, MHNT.PAL.2013.16.4 from La Borie, Saint-Papoul, department of Aude, Southern France; middle Ypresian, early Eocene, age close to reference level MP8–9.

Measurements (mm).—Total length, 84.0; proximal depth from the cranial border of cotyla ventralis to the top of olecranon, 7.5; width of cotyla ventralis, 4.9; depth of condylus ventralis, 7.0.

Description and comparison.—The ulna is crushed and dorsoventrally flattened. The shaft is very rectilinear. The olecranon is narrow at its base and strongly projecting proximally. The cotyla ventralis is deep and has a regular circular shape. The condylus dorsalis is proximodistally short and strongly projecting caudally. This ulna shows some similarities with the genus *Limnofregata*, from the early Eocene of the Green River Formation (Olson 1977). These similarities are as follows: a very rectilinear shape; a circular cotyla ventralis; a narrow and proximally projecting olecranon, which is sharply set off from the cotyla ventralis; a proximodistally short condylus dorsalis. In *Limnofregata* there is a "very large, roughly triangular prominence for the anterior articular ligament, which has a tapering extension along the lower margin of the impression of M. brachialis anticus" (Olson 1977: 22). In the La Borie specimen, this part shows a flat triangular surface. In addition, this ulna corresponds to a bird much smaller than the two known species of *Limnofregata*, *L. azygosternon*, and *L. hasegawai* (Olson 1977; Olson and Matsuoka 2005).

Discussion

The avifauna from La Borie is composed of three distinct taxa, including the gruiform bird *Galligeranoides boriensis* gen. et sp. nov. (Geranoididae), the giant flightless bird *Gastornis parisiensis* (Gastornithidae), and an undetermined bird. *Galligeranoides boriensis* gen. et sp. nov. is represented by three different individuals in the La Borie deposits. The two tibiotarsi clearly belong to different individuals, since MHNT.PAL.2013.16.3 is more robust than MHNT.PAL.2013.16.1. The right tarsometatarsus MHNT.PAL.2013.16.2 does not belong to the same individual as the right tibiotarsus MHNT.PAL.2013.16.1 because the cotyla medialis of the tarsometatarsus is too large compared to the condylus medialis of this tibiotarsus. In addition, these two elements were found in different sites, SP5 for the tibiotarsus and SP2 for the tarsometatarsus. The size difference could be related to sexual dimorphism, the left tibiotarsus MHNT.PAL.2013.16.3 and the right tarsometatarsus MHNT.PAL.2013.16.2 belonging to males, and the right tibiotarsus MHNT.PAL.2013.16.1 belonging to a female.

The *Gastornis* material is the most abundant and likely belongs to four different individuals: the maxilla, quadratum, a vertebra cervicalis and a tibiotarsus were found in close proximity to one another and in the same layer, in site SP5 (Laurent et al. 2010: fig. 2). All these specimens are almost certainly from the same adult individual. *Gastornis* remains from SP1 include a tibiotarsus and a series of vertebrae cervicales. They most probably belong to the same individual, which is comparable in size to the individual from SP5. However, stratigraphical evidence suggests that SP1 is older than SP5 (Laurent et al. 2010: fig. 2). The vertebra cervicalis from SP2 pertains to an adult individual which was slightly larger than the individuals from SP1and SP5. The femur from SP2 belongs to a subadult individual that was smaller than all other *Gastornis* specimens.

Aside from the gigantic size, the 11 elements described above can be assigned to *Gastornis*, based on the following features: the maxilla is massive, tall, laterally compressed and devoid of hooked tip. The apertura nasi ossea is small and in ventral position. The quadratum exhibits a single-headed processus oticus bearing two condyli, a well-developed processus orbitalis, and a huge tuberculum musculi adductor mandibulae ossis quadrati. The elongate processus mandibularis has only two condyli. The vertebrae cervicales are heterocoelous, extremely massive and greatly abbreviated craniocaudally. The zygapophyses are stout and their facies articulares are large, round and flat. The femur has an elongate crista trochanteris, a craniocaudally compressed shaft that is distinctly deflected medially towards the base of the condylus medialis, and a deep fossa poplitea. The tibiotarsus has laterally deflected cristae cnemiales and a craniocaudally compressed shaft. The extremitas distalis is curved medially and bears an oblique pons supratendineus. The incisura intercondylaris is bounded distally by a prominent ridge that joins the distal edges of the condyli. The condylus medialis protrudes further cranially than the condylus lateralis.

Remains of the giant flightless bird *Gastornis* were first described from the early Eocene "Conglomérat de Meudon" near Paris (Hébert 1855). Since then, a large number of specimens have been reported as either *Gastornis* or *Diatryma* (for a detailed account of subsequent discoveries and interpretations see Buffetaut 1997; Buffetaut and Angst 2013). Andors (1992) and Martin (1992) considered that *Gastornis* is similar to, but not congeneric with, *Diatryma*. Buffetaut (1997, 2000) emphasized the similarities between the two taxa and suggested that *Diatryma* is a junior synonym of *Gastornis*. This treatment has been followed by subsequent authors (Mlíkovský 2002; Mayr 2009). To date, *Gastornis* is known from the middle Paleocene (Selandian) of Germany (Weigelt 1939; Mayr 2007); the late Paleocene (Thanetian) of France (Lemoine 1878, 1881; Martin 1992; Buffetaut 1997; Angst and Buffetaut 2013) and Belgium (Dollo 1883); the early Eocene (Ypresian) of France (Hébert 1855; Milne-Edwards 1867–1868; Schaub 1929; Buffetaut 2008), England (Newton 1885, 1886), North America (Cope 1876; Matthew and Granger 1917; Andors 1988, 1992; Eberle and Greenwood 2012) and China (Hou 1980; Buffetaut 2013); and the middle Eocene (Lutetian) of Germany (Fischer 1962; Berg 1965; Fischer 1978; Hellmund 2013).

Hellmund (2013) listed five species of *Gastornis*, including *G. parisiensis*, *G. russelli*, *G. sarasini*, *G. giganteus*, and *G. geiselensis*. An additional species, *G. xichuanensis*, is known from the early Eocene of China (Buffetaut 2013). However, the number of species of *Gastornis* is still uncertain, because a thorough revision of all the available material has not been undertaken yet. In particular, whether the poorly known *G. sarasini* (early Eocene of France; Schaub 1929) is conspecific with either *G. parisiensis* (late Paleocene of France and Belgium; early Eocene of France and England; Martin 1992; Buffetaut 1997, 2008; Angst and Buffetaut 2013) or *G. geiselensis* (middle Eocene of Germany; Hellmund 2013) remains unclear (Mlíkovský 2002; Mayr 2009; Hellmund 2013).

The avian remains from La Borie (Buffetaut 2008; this study) constitute the southernmost occurrence of *G. parisiensis* in France and in Europe. The morphology of the quadratum from the Ypresian of La Borie is slightly different from those of the quadrata from the Thanetian of Mont-de-Berru and Cernay-lès-Reims. Aside from preservation, the wide geographical and temporal distribution of *G. parisiensis* implies an important intraspecific variation both in size and shape, including possible sexual dimorphism. A marked size variation has already been noted in *G. parisiensis* (Martin 1992) and *G. geiselensis* (Hellmund 2013), and shape variation also occurs in the tibiotarsus of *G. parisiensis* (Buffetaut 2008, 2013).

Although *Gastornis* has been widely regarded as a predator showing similarities with Phorusrhacidae (see Buffetaut and Angst 2013 for review), there is growing evidence that *Gastornis* had an herbivorous diet (Andors 1988, 1992; Buffetaut and Angst 2013; Angst et al. 2014). No well preserved maxilla had hitherto been described for *G. parisiensis*. We confirm that the tip of the beak is not hook-shaped in *G. parisiensis*, a condition which also occurs in the North American species *G. giganteus* (Andors 1988, 1992). Hence, the new specimen from La Borie gives additional support to the hypothesis that *Gastornis* was herbivorous.

We show that *G. parisiensis* can be differentiated from the North American *G. giganteus* (formerly *Diatryma gigantea* or *D. steini*) by several new features, including the shorter maxilla, the more ventral position of the apertura nasi ossea and the shallower sulcus nasi. Compared with *G. giganteus*, the quadratum of *G. parisiensis* has a more slender processus orbitalis and the condylus medialis is less deflected medially with respect to the condylus lateralis. Consistent with the shorter maxilla, the mandibula is shorter in *G. parisiensis* (Angst and Buffetaut 2013: figs. 2, 3) than in *G. giganteus* (Matthew and Granger 1917: pl. 21). Martin (1992) noted salient differences between the two species: the extremitas sternalis of the scapulocoracoideum is wider in *G. giganteus* than in *G. parisiensis*; concerning the tarsometatarsus, the TM III is larger and the TM IV is more divergent in the North American species than in the European one. Some additional differences (EB, personal observation) are as follows: in *G. giganteus*, the humerus exhibits a tuberculum ventrale that is projected proximally and an epicondylus ventralis that is strongly deflected ventrally and distally (Matthew and Granger 1917: pl. 31), and these features are not found in *G. parisiensis* (Martin 1992: fig. 3A, B). There is a pronounced widening of the shaft of the tarsometatarsus towards the extremities in *G. giganteus* (Martin 1992: fig. 5I, J), whereas the shaft is of even width in *G. parisiensis* (Martin 1992: fig. 5A, B; Buffetaut and Angst 2013: fig. 2). A tarsometatarsal shaft of event width also occurs in the small species *G. russelli* from the Paleocene of France (Martin 1992: fig. 6), but not in *G. geiselensis* from the middle Eocene of Germany (Hellmund 2013: fig. 7a, c).

The extinct family Geranoididae is reported here for the first time in Europe. Among the seven previously described geranoidid species, six species come from the lower Eocene deposits of the Willwood Formation, Wyoming (Cracraft 1969). *Palaeophasianus meleagroides* is also possibly present in the middle Eocene of the Bridger Formation, Wyoming (Cracraft 1969). The seventh species, *Geranodornis aenigma*, is known only from the middle Eocene of the Bridger Formation (Cracraft 1969). The lower Eocene deposits of the Willwood Formation have also yielded the most abundant material of *G. giganteus* (Andors 1988, 1992). Our study has shown that *Gastornis* coexisted with the Geranoididae in the lower Eocene deposits of La Borie. Previous authors noticed that the early Eocene vertebrate faunas of Europe and North America were very similar (e.g., McKenna 1975; West and Dawson 1978; Estes and Hutchison 1980), including bird faunas (see Mayr 2009). Sedimentological, floral and faunal data indicate that the early Eocene *Gastornis* localities in both Europe and North America benefited from a warm temperate to tropical climate with a humid, well-vegetated environment (Andors 1988; Russell et al. 1990; Andors 1992; Hooker et al. 2009; Laurent et al. 2010). It is well known that there was a great interchange of mammalian faunas between Europe and North America in the early Eocene (Rose 2006). The presence of both *Gastornis* and Geranoididae on either side of the present-day North Atlantic provides further evidence that a high-latitude land connection existed between Europe and North America at that time (Cracraft 1973a; McKenna 1983; Andors 1992). The occurrence of *Gastornis* in the early Eocene of Ellesmere Island, Canada (Eberle and Greenwood 2012) suggests that dispersal of this giant flightless bird was via an Arctic route (Buffetaut 2013). The mild climate that prevailed in the ice-free Arctic at that time (Eberle and Greenwood 2012) facilitated dispersal of terrestrial organisms between North America and Europe. *Gastornis* shows its longest stratigraphic range in Europe, where it is known from the late Paleocene to the middle Eocene (Buffetaut 2013). In North America and Asia, *Gastornis* is restricted to the early Eocene. At face value, stratigraphic evidence seems to support the hypothesis that gastornithids originated in Europe and reached North America via a North Atlantic land corridor which connected these continents at the onset of the Eocene (Buffetaut 1997, 2013). Future discoveries may change this scenario, but Buffetaut (2013) mentioned that the Paleocene fossil record of terrestrial vertebrates in North America and Asia is good and does not include *Gastornis*, which suggests that this bird was not present in these continents in the Paleocene.

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