

Giant Birds from the Uppermost Paleocene of Rivecourt (Oise, Northern France)

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Resumo

Dois fragmentos de restos de aves gigantes provenientes de depósitos do Paleocénico Superior da localidade de Petit-Pâtis em Rivecourt (Oise, norte da França) são descritos. Um deles é uma zygapofisis isolada de uma ave muito grande, identificada como pertencente à ave Neognata *Gastornis* sp. A outra é uma vértebra cervical posterior incompleta referida à ave Paleognata *Remiornis*. Ambos os táxones também ocorrem em localidades clássicas do Thanetiano na área de Reims, mais a leste. Os espécimes de Rivecourt mostram que, mesmo no final do Paleocénico, os maiores tetrápodes terrestres da Europa eram aves gigantes herbívoras. Enquanto o *Gastornis* sobreviveu ao Eocénico e se dispersou pela Europa e daí para a América do Norte e para a Ásia. O género *Remiornis* parece ter-se extinguido no final do Paleocénico.

Palavras-chave: Aves, Paleocénico, França, *Gastornis*, *Remiornis*.

Résumé

Deux restes fragmentaires d'oiseaux géants du Paléocène terminal du site du Petit-Pâtis à Rivecourt (Oise, Nord de la France) sont décrits. L'un est une zygapophyse isolée identifiée comme appartenant au néognathe *Gastornis* sp. L'autre est une vertèbre cervicale postérieure rapportée au paléognathe *Remiornis* sp. Ces deux taxons sont aussi associés dans les gisements thanétiens classiques de la région de Reims plus à l'est. Les spécimens de Rivecourt montrent qu'à la fin du Paléocène en Europe les plus grands tétrapodes terrestres étaient des oiseaux géants herbivores. Alors que *Gastornis* a survécu jusque dans l'Eocène et s'est répandu d'Europe jusqu'en Amérique du Nord et en Asie, *Remiornis* semble s'être éteint à la fin du Paléocène.

Mots-clés: Aves, Paléocène, France, *Gastornis*, *Remiornis*.

Abstract

Two fragmentary remains of giant birds from uppermost Paleocene deposits at the Petit-Pâtis locality at Rivecourt (Oise, northern France) are described. One is an isolated zygapophysis of a very large bird, identified as belonging to the neognath *Gastornis* sp. The other one is an incomplete posterior cervical vertebra referred to the palaeognath *Remiornis*. Both taxa also occur together at classical Thanetian localities in the Reims area farther east. The specimens from Rivecourt show that right at the end of the Paleocene the largest terrestrial tetrapods in Europe were herbivorous giant birds. While *Gastornis* survived into the Eocene and dispersed from Europe to North America and Asia, *Remiornis* appears to have become extinct at the end of the Paleocene.

Key words: Aves, Paleocene, France, *Gastornis*, *Remiornis*.

1. INTRODUCTION

The uppermost Paleocene beds of the Petit Pâtis locality at Rivecourt (Oise, northern France) have yielded a diverse assemblage of fossil vertebrates, including a few avian remains

(Smith *et al.*, 2014). In this paper, we describe two specimens which, although fragmentary, clearly belong to distinct taxa of very large birds. They can be identified to the genus level and allow comparisons with avian assemblages from other Early Tertiary localities in Europe.

2. GEOGRAPHICAL AND GEOLOGICAL SETTING

The Petit-Pâtis locality at Rivecourt (Oise) is located about 60 km NE of Paris, in the valley of the river Oise, about 10 km SW of the city of Compiègne (Fig. 1). There, a vast pit opened for the extraction of Pleistocene sands and gravels exposed underlying fossil-bearing Paleocene beds. A detailed description of the geology and palaeontology of the locality was given by Smith *et al.* (2014). The fossiliferous Paleocene beds consist of lignite-bearing sands (Sparnacian facies) in the upper part of the Sables de Bracheux Formation. They were deposited in a fluvial to fluvio-estuarine environment and contain abundant remains of plants, fishes, amphibians, squamates, choristoderans, turtles, crocodylians and mammals. Only a few bird remains have been discovered, including a vertebra, a tibiotarsus and the distal part of a tarsometatarsus belonging to small birds which remain unidentified. Very large birds are represented by the fragmentary specimens described below, which were initially identified as avian by one of us (G. de P.).

Stratigraphical and palaeontological evidence indicates that the fossil-bearing beds at Petit-Pâtis are latest Paleocene (MP6b level) in age, coeval with the Clarkforkian Land Mammal Age in North America (Smith *et al.*, 2014). This suggests an age of about 56-57 My (Vandenberghe *et al.* 2012).

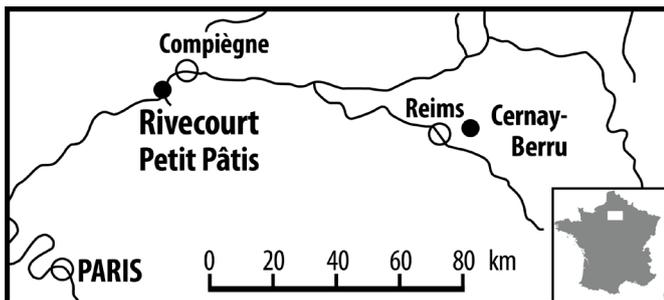


Fig. 1. Map of part of northern France showing the location of fossil localities mentioned in text.

Institutional abbreviations:

MNHN: Muséum national d'Histoire naturelle, Paris;

MV: Musée Vivanel, Compiègne.

3. SYSTEMATIC DESCRIPTION

Systematic Description

Gastornis: *isolated zygapophysis*

CLASS Aves Linnaeus, 1753

NEOGNATHAE Pycraft, 1900

FAMILY Gastornithidae Fürbringer, 1888

GENUS *Gastornis* Hébert, 1855

Gastornis sp.

Gastornis is represented at Rivecourt by a single isolated zygapophysis, MV riv. PP 0828 (Fig. 2). The specimen essentially shows a flat articular surface, more or less oval

in outline (its dimensions being 28 x 24 mm). The highly cancellous condition of the interior of the bone indicates that it belongs to a bird. In shape and size, this zygapophysis is very similar to those of *Gastornis* vertebrae from the Thanetian of Cernay and Berru (Marne, eastern France) in the collections of the MNHN. Comparisons suggest that it is probably a postzygapophysis.

The specimen is therefore referred to *Gastornis*, the largest bird to have been reported from the Paleocene of France. Several *Gastornis* species have been described from the Thanetian of France (Buffetaut & Angst, 2014; Angst & Buffetaut, 2017) and are in need of revision. In terms of size, the zygapophysis from Rivecourt is similar to the corresponding skeletal element in the largest of them, *Gastornis parisiensis*. However, because of the incompleteness of the specimen it seems more advisable to refer to it as *Gastornis* sp.



Fig. 2. *Gastornis* sp. Isolated zygapophysis, MV riv. PP 0828, in external (A) and internal (B) views. The internal view shows a typically avian highly cancellous structure.

Systematic Description

Remiornis: *cervical vertebra*

PALAEOGNATHAE Pycraft, 1900

FAMILY Remiornithidae Martin, 1992

GENUS *Remiornis* Lemoine, 1881

Remiornis sp.

The palaeognath *Remiornis* is represented by an incomplete posterior cervical vertebra (MV riv. PP 0718) (Fig. 3), which was much damaged by quarrying equipment before it was found by one of us (G. de P.); some of the fragments could not be pieced together. While the facies articularis caudalis is well preserved, the facies articularis cranialis is very incomplete, the processus spinosus is incomplete, too, the zygapophyses are missing and the cranial part of the ventral surface is destroyed. The centrum was clearly heterocoelous, with a wide cranial articular area, the central part of which is missing; its lateral surfaces form flat facets. The facies articularis caudalis is markedly saddle-shaped and broader ventrally than dorsally. Its ventral part extends much farther caudally than its dorsal part. Its ventral and caudal margins are markedly concave. In ventral view the elongate centrum shows a deep longitudinal groove, the sulcus caroticus; its lateral edges form well-marked ridges. Although the cranial part of the ventral surface is missing, it seems that there was no hypapophysis. Caudally,

the ventral face broadens and forms two lobes corresponding to the ventral part of the facies articularis caudalis. The right side of the centrum is better preserved than the left side, it shows a large pneumatic foramen just posterior to the processus transversus, its opening being subdivided by a thin oblique bony lamina. The neural canal was more or less circular in outline, becoming wider cranially with a funnel-shaped cranial opening. Little is left of the processus spinosus. Its broad cranial face shows an oval depression subdivided by a vertical bony ridge, which indicates a ligamentous insertion, the anterior area ligamenti elastici. The caudal face of the processus spinosus is poorly preserved but shows a rugose concave area, the posterior area ligamenti elastici. Its caudal extent cannot be estimated. The processus transversus is better preserved on the right side than on the left one, although it is broken cranially, exposing highly cancellous bone. Caudally, the processus transversus overhangs a strong horizontal bony buttress. It is perforated caudodorsally by a slit-like canal. At the junction between the processus transversus and the processus spinosus there is a pneumatic foramen. Laterally the processus transversus is directed ventrolaterally but its tip is broken. It is therefore difficult to determine whether it completely encircled a foramen transversarium. No evidence of ribs is preserved.

Measurements

Ventral length of centrum: 70 mm.

Posterior width (ventral): 23 mm.

Diameter of neural canal: 8 mm.

Dorsal width of facies articularis caudalis: 20 mm.

The great elongation of the centrum and the absence of a hypophysis suggest that it is a posterior cervical vertebra (rather than an anterior dorsal as mentioned in Smith *et al.*, 2014), possibly the 16th vertebra by comparison with the vertebrae of living ‘‘ratites’’ (Mivart, 1874, 1877). This vertebra is definitely smaller and less robust than those of *Gastornis* and it is generally ratite-like in morphology. A palaeognathous bird, *Remiornis*, has been known for a long time (Lemoine, 1881 ; Martin, 1992) from Paleocene (Thanetian) localities (Cernay, Berru) of the north-eastern Paris basin. However, its skeleton is incompletely known and no cervical vertebrae have so far been reported so that comparisons are not easy. It is nevertheless likely that the vertebra from Rivecourt belongs to *Remiornis*. Its dimensions are compatible with those of an anterior dorsal vertebra from Berru (MNHN R 3572) described by Martin (1992). Morphological similarities include a very deep sulcus caroticus and possibly a pneumatic foramen dorsal to the processus transversus.

The specimen from Rivecourt is nearly the size of the corresponding vertebra in the living ostrich, *Struthio camelus*. The latest Paleocene *Remiornis* could therefore reach quite a large size. For the slightly older *Remiornis* from Cernay, Lambrecht (1933) suggested a size similar to that of the emu.

4. DISCUSSION

Although giant birds are represented at the Petit-Pâtis locality only by scanty remains, identifications are possible at

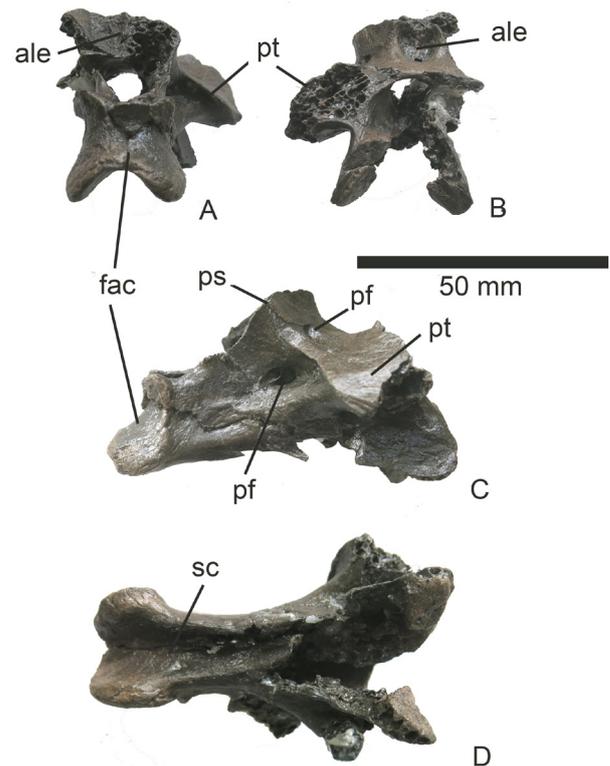


Fig. 3. *Remiornis* sp. Posterior cervical vertebra, MV riv. PP 0718, in caudal (A), cranial (B), right lateral (C) and ventral (D) views. Abbreviations: **ale**: area ligamenti elastici; **fac**: facies articularis caudalis; **pf**: pneumatic foramen; **ps**: processus spinosus; **pt**: processus transversus; **sc**: sulcus caroticus.

the genus level, showing that both *Gastornis* and *Remiornis* are present. This association is completely similar to that found in the Thanetian localities of the Reims area (Cernay, Berru), where both these genera are present. Both *Gastornis* and *Remiornis* were therefore present in the latest Paleocene of Europe, the Petit-Pâtis locality being considered as equivalent in age to the Clarkforkian North American Land Mammal Age. The stratigraphic range of gastornithids in Europe extends from the Selandian to the Lutetian (Buffetaut & Angst, 2014a, b), the oldest record so far being possibly a fragmentary femur of a putative small gastornithid from the Selandian of Maret, in Belgium (Mayr & Smith, 2019). *Remiornis* is currently known only from the Thanetian of France (Buffetaut & Angst, 2014a, b), the specimen from Rivecourt being its latest known occurrence. There is no evidence so far that *Remiornis* persisted into the Eocene. The somewhat enigmatic Eocene palaeognath *Palaeotis weigelti* Lambrecht, 1928, from Messel and the Geiseltal (Houde & Haubold, 1987; Peters, 1988; Mayr, 2015), is a significantly smaller bird and the presence of a pons supratendineus on the tibiotarsus shows that it is not very closely related to *Remiornis*, which lacks such an ossified bridge. The same applies to the Early Eocene *Gallogeranoides boriensis* Bourdon, Mourer-Chauviré & Laurent, 2016, from the Lower Eocene of France, considered by Mayr (2019) as the earliest known palaeotidid.

A point worth noting is that the giant birds *Gastornis* and *Remiornis* are the largest terrestrial tetrapods in the faunal assemblage from Rivecourt. The largest mammal in the Rivecourt fauna is the laurasiatherian *Arctocyon*, the size of a large dog. *Gastornis* was up to 2 m tall (Angst & Buffetaut,

2017), with an estimated mass of about 135-156 kg (Angst *et al.*, 2014a). No accurate mass estimate has been published for *Remiornis*, but if it was the size of an emu, it may have weighed up to 55 kg (Elphick, 2019), or more if it reached nearly the size of an ostrich. As shown by isotopic and anatomical evidence (Angst *et al.*, 2014b), *Gastornis* was herbivorous. No isotopic evidence is available for *Remiornis*, but all known “ratites” are principally herbivorous, and there is little doubt that *Remiornis* was a plant-eater, too. The largest herbivores in the Rivecourt fauna thus were giant birds, which was the general situation in Europe during the Paleocene (Buffetaut & Angst, 2014b), but very different from that in later, Early Eocene, faunas in which that ecological role was at least partly taken up by large mammals (e.g. *Coryphodon*, *Lophiodon*). *Gastornis* and *Remiornis* probably had different diets and occupied distinct niches. *Gastornis* has been shown to be herbivorous on the basis of isotopic evidence and its powerful adductor musculature suggests that its massive jaws could be used to crush hard plant food (Angst *et al.*, 2014b). The skull of *Remiornis* is not known, but its palaeognathous affinities suggest that, like other “ratites”, it had a small head and jaws and fed on various kinds of plants and occasionally small animals. In Europe, the Paleocene/Eocene boundary thus seems to correspond to a notable change in the trophic structure of terrestrial tetrapod communities, when giant birds ceased to be the only large herbivores, with the appearance of large herbivorous mammals through dispersal from other land masses. It is worth noting that although *Gastornis* dispersed from Europe to North America and Asia in the Early Eocene (Buffetaut, 2013; Buffetaut & Angst, 2014b), *Remiornis* did not, probably for the simple reason that it became extinct at the end of the Paleocene.

5. CONCLUSION

Although fragmentary, the remains of giant birds from the latest Paleocene Petit Pâtis site at Rivecourt (northern France) indicate the presence of two taxa, *Gastornis* and *Remiornis*. This assemblage of very large birds is similar to the somewhat earlier one from the Reims area and confirms that up until the end of the Paleocene the largest terrestrial tetrapods in Europe were giant herbivorous birds. While *Gastornis* survived well into the Eocene in Europe, and dispersed to Asia and North America, *Remiornis* is unknown in Eocene localities and seems to have become extinct at the Paleocene/Eocene boundary.

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