First evidence of the giant bird *Gastornis* from southern Europe: a tibiotarsus from the Lower Eocene of Saint-Papoul (Aude, southern France).

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ABSTRACT - A well preserved tibiotarsus from the Early Eocene locality of Saint-Papoul (Aude, southwestern France) is described as belonging to the giant ground bird *Gastornis parisiensis* Hébert, 1855, on the basis of close resemblances with the lectotype of that species. Small and variable differences in the tibiotarsi of European and North American gastornithids are considered as insufficient to justify a separation between *Gastornis* and *Diatryma*, the latter being considered as a junior synonym of the former. The discovery of *Gastornis* in southern France lends weight to the hypothesis according to which the large bird eggs found in the continental Lower Eocene of southern France may have been laid by gastornithids.

Key words: *Aves, Gastornis, Tibiotarsus, Eocene, France, Eggs.*

Première découverte de l'oiseau géant *Gastornis* dans le Sud de l'Europe : un tibiotarse de l'Eocène inférieur de Saint-Papoul (Aude, Sud de la France) - Un tibiotarse bien conservé provenant du gisement Eocène inférieur de Saint-Papoul (Aude, Sud-Ouest de la France) est décrit comme appartenant à l'oiseau géant terrestre *Gastornis parisiensis* Hébert, 1855, sur la base de ses ressemblances étroites avec le lectotype de cette espèce. Les petites différences variables observées sur les tibiotarses de gastornithidés européens et nord-américains sont considérées comme insuffisantes pour justifier une séparation entre *Gastornis* et *Diatryma*, ce dernier étant considéré comme synonyme du premier. La découverte de *Gastornis* vient à l'appui de l'hypothèse selon laquelle les gros œufs d'oiseaux trouvés dans l'Eocène inférieur continental du Sud de la France auraient été pondus par des gastornithidés.

Mots clés: *Aves, Gastornis, Tibiotarse, Eocène, France, Oeufs.*

INTRODUCTION

The giant bird *Gastornis* was first described by Hébert (1855) from the basal Eocene "Conglomérat de Meudon" in the suburbs of Paris (see Buffetaut, 1997a, for a detailed account of the discovery and subsequent interpretations). Since then, a number of additional specimens have been reported, either as *Gastornis* or as *Diatryma* (here considered as a junior synonym of *Gastornis*, see Buffetaut, 1997b, 2000, and discussion below), from various localities (Fig.1) in northwestern and central Europe (see Mlikovský, 2002, for a detailed list), including eastern France (Lemoine, 1879, 1881a, 1881b), England (Newton, 1885, 1886), Belgium (Dollo, 1883) and Germany (Weigelt, 1939; Fischer, 1962, 1978; Berg, 1965; Mayr, 2007). *Gastornis* remains are also widely distributed in North America, with finds from both the western and eastern United States and from Arctic Canada (see Andors, 1988, 1992, for reviews). An apparently very closely related form, *Zhongyanus*, is known from the Eocene of China (Hou, 1980). So far, no *Gastornis* remains had been reported from southern Europe. The southernmost European specimen hitherto referred to "*Diatryma*" was *Diatryma (?) cotei*, described by Gaillard (1936, 1937) from the Eocene of the Mont d'Or, near Lyon, on the basis of a fragmentary tarsometatarsus. Andors (1992, p.112) considered it as "utterly different from any diatrymid" and referred it to "Aves incertae sedis", a conclusion fully shared by the author of the present paper after examination of the specimen.

The present paper describes a *Gastornis* tibiotarsus from the Lower Eocene of southwestern France which extends the geographical distribution of the genus to southern Europe, confirms the generic identity of *Gastornis* and *Diatryma*, and has a bearing on the question of large bird eggs found in the Early Tertiary non-marine deposits of southern France.

Figure 1 - Map of western and central Europe showing main *Gastornis* localities (circles - see text for details). The Saint-Papoul locality in southern France is shown by a star.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The specimen described in the present paper was discovered by Mr Henri-Pierre Labarrère, who kindly presented it to the Esperaza Dinosaur Museum, in a large clay pit near the village of Saint-Papoul, about 20 km north-west of the city of Carcassonne, in the *département* of Aude, in southwestern France (Fig.1; see also location maps in Richard, 1946). The Early Tertiary non-marine sediments exposed in the quarry have yielded a fairly large amount of vertebrate material, which has been only partly studied. In addition to *Gastornis*, the Saint-Papoul vertebrate fauna includes fishes, turtles (see Julien & Tong, 2004, for a recent review), crocodilians (Vasse, 1992) and mammals. On the basis of the mammals, it is referred to the Early Eocene (Ypresian). According to Sudre *et al.* (1992), some unpublished data lead to refer it to reference level MP10 ("Grauves"). However, according to H.P. Labarrère (pers.com.), on the basis of undescribed mammal remains, an age close to the MP8-9 ("Avenay") reference level may be more likely. According to recent correlation schemes (BiochroM'97, 1997), the Saint-Papoul locality would therefore be coeval with the Meudon Conglomerate (reference level MP8-9), which yielded the type material of *Gastornis parisiensis*, or slightly more recent than it.

The *Gastornis* tibiotarsus was found at the base of a sandy channel containing lignite lenses. The sedimentological environment suggests a wooded marshy plain crisscrossed by deep channels (H.P. Labarrère, pers.com.).

DESCRIPTION

Class Aves Linnaeus, 1758
Order Gastornithiformes Stejneger, 1885

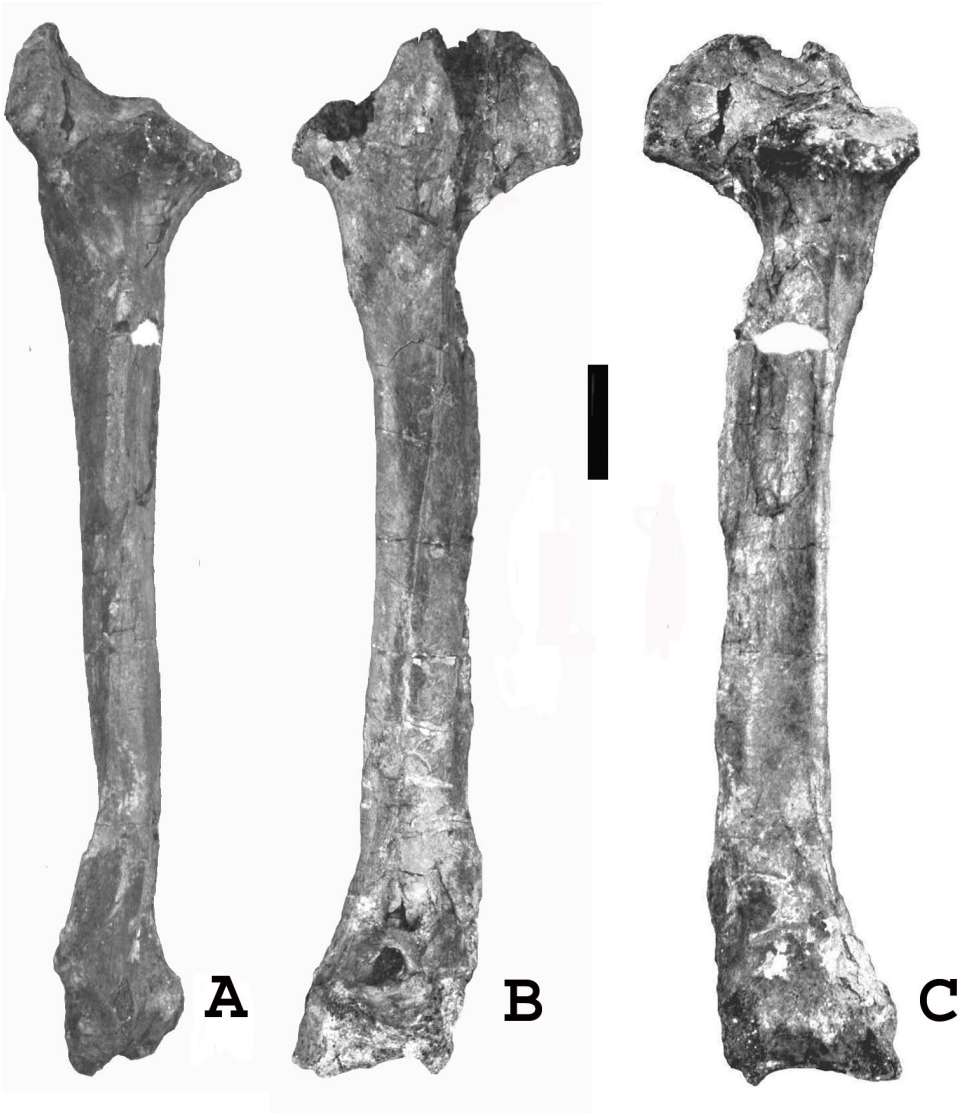

Figure 2 - Left tibiotarsus of *Gastornis parisiensis*, Early Eocene of Saint-Papoul (Aude, France), Musée des Dinosaures d'Espéraza, MDE-A18. A: lateral view. B: anterior view. C: posterior view. Scale bar: 50 mm.

Family Gastornithidae Fürbringer, 1888
Genus *Gastornis* Hébert, 1855
Gastornis parisiensis Hébert, 1855

The *Gastornis* bone from Saint-Papoul (Musée des Dinosaures, Espéraza, MDE-A18) is a fairly complete and well preserved left tibiotarsus, which has suffered very little crushing or distortion (Fig.2). Some abrasion has occurred in the proximal part, damaging some of the crests and processes, and the cranial parts of the distal condyles are missing.

The proximal part of the bone (Fig.3) shows a strong hook-like Crista cnemialis lateralis, with a thickened, well-rounded proximocranial edge. The lateral surface of the Crista is markedly concave. The Crista cnemialis cranialis is incompletely preserved proximally. It forms a sharp ridge extending much farther down the shaft than the Crista cnemialis lateralis, and becoming thicker proximally. It is separated from the Crista cnemialis lateralis by a well-marked Sulcus intercristalis. On the proximal articular surface of the bone (Fig.3), the articular facet for the medial condyle of the femur (Facies articularis medialis) is well-preserved and kidney-shaped; it strongly overhangs the shaft posteromedially. The smaller Facies articularis lateralis (for the lateral condyle of the femur) is poorly preserved but seems to have been oval in shape. At the anterior junction between the facets, there is a well-marked rounded tubercle, which probably served as attachment for ligaments (Andors, 1988). Anteriorly to the Facies articularis lateralis, there is a pair of depressions, the Fossae retrocristales, separated from each other by an S-shaped ridge which issues from the tubercle and extends towards the Crista cnemialis lateralis.

Although it is much less crushed, the proximal part of the tibiotarsus from Saint-Papoul closely resembles the proximal end of a tibiotarsus (LR BR A4) from the Thane-

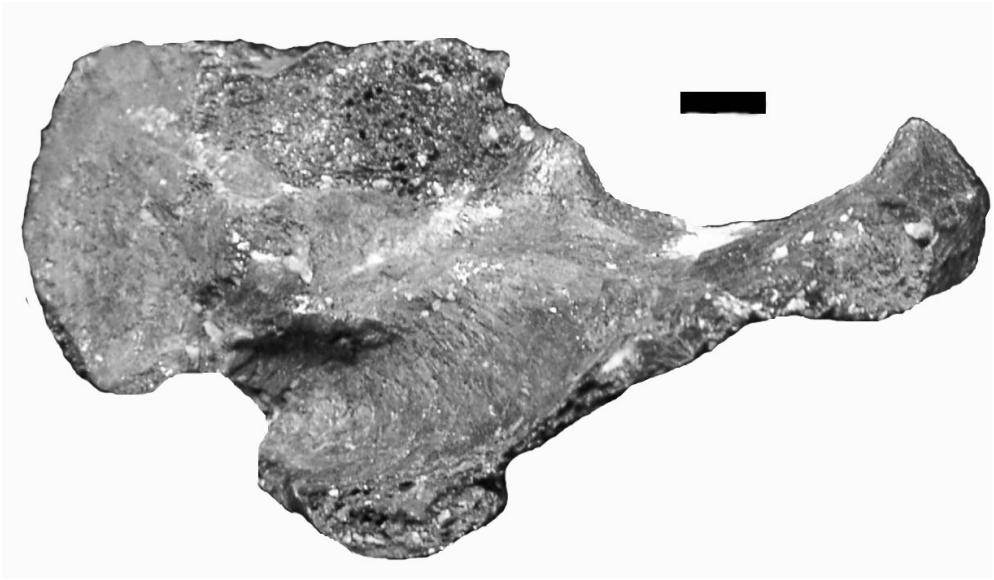

Figure 3 - Left tibiotarsus of *Gastornis parisiensis*, Early Eocene of Saint-Papoul (Aude, France), Musée des Dinosaures d'Espéraza, MDE-A18. Proximal view. Scale bar: 10 mm.

tian of Berru identified as *Gastornis parisiensis* by Buffetaut (1997b), as well as that of *Gastornis giganteus* (= "*Diatryma" gigantea*) from North America as described by Andors (1988). Direct comparison with a cast of the tibiotarsus of the skeleton kept at the American Museum of Natural History (AMNH 6169) confirms this very close resemblance.

The shaft is well-preserved in the Saint-Papoul specimen, with very little crushing. It is mostly straight, except distally, where it curves medially, as in the lectotype of *Gastornis parisiensis* (Milne-Edwards, 1867-1868) and North American forms (Sinclair, 1928). The Crista fibularis, separating the caudal from the cranial surface in the proximal half of the shaft, is very strong and thick. The Linea extensoria continues the Crista cnemialis cranialis down the shaft, dividing the cranial from the medial side; although it becomes fainter distally, it can be traced all the way to the medial margin of the Sulcus extensorius. The Margo caudalis, at the junction of the medial and caudal surfaces, is rounded. As a result of the development of these ridges, at mid-shaft, the section of the bone is roughly triangular.

On the medial surface of the shaft, close to the distal end, two well-marked insertion areas for muscles or tendons are visible, one of them sub-circular in outline, and the other teardrop-shaped. Fischer (1978) described two muscular scars in the same position on the tibiotarsus of *"Diatryma geiselensis"*, from the Middle Eocene of the Geiseltal. In the distal half of the shaft, the Crista fibularis is replaced at the junction of the cranial and caudal surfaces by a strong peroneal ridge which extends distally to the lateral condyle.

In the distal part of the bone (Fig.4), the Sulcus extensorius is deep and forms a canal (Canalis extensorius) when it passes beneath the bridge, or Pons supratendineus. The latter is well-preserved and about 2 mm thick. It is broad at its medial and lateral ends, narrower in the middle, and its lateral end is broader than the medial one. Lateral to the lateral end of the bridge, there is a short but sharp oblique ridge, at the bottom of a well-defined depression limited laterally by the peroneal ridge. In his revised diagnosis of *Gastornis*, Martin (1992) considered that in *Gastornis* the supratendinal bridge is more proximal and central than in *Diatryma*. In the specimen from Saint-Papoul, the bridge is located mostly in the medial part of the bone, its lateral edge being more or less at the level of the mid-point of the shaft. Comparisons with casts of various specimens of *Gastornis* (from Meudon and Croydon) and "*Diatryma*" (from various North American localities), and with tibiotarsi from the Geiseltal referred by Fischer (1962) to *Diatryma*, did not reveal significant differences in this respect: in all specimens, the bridge is displaced medially rather than being in a central position. The same applies to the Chinese form *Zhongyanus* (Hou, 1980). Similarly, it does not appear to be placed more proximally in *Gastornis* than in "*Diatryma"* on specimens in which the distal end of the tibiotarsus is relatively well preserved. In the specimen from Saint-Papoul, in which the cranial parts of the condyles are missing, the position of the bridge relative to the Incisura intercondylaris is not different from what is seen in North American specimens. The supratendinal bridge on the Saint-Papoul specimen is oblique rather than transverse, its lateral end being somewhat more distal than its medial end. Fischer (1978) considered that an oblique rather than transverse bridge distinguished *"Diatryma geiselensis"* from the North American representatives of the genus. In this regard, the bone from Saint-Papoul would seem to be more similar to the German form than to the North American one. However, there seems to be some individual variation in this character (see the figures in Martin, 1992), and its significance should not be overestimated.

As mentioned above, the condyles are poorly preserved: their cranial parts are missing, and the caudal parts are damaged, so that few osteological details can be seen. In distal view, a rather deep depression (Impressio lig. intercondylaris) can be seen in the Incisura intercondylaris.

Measurements (those of the proximally incomplete

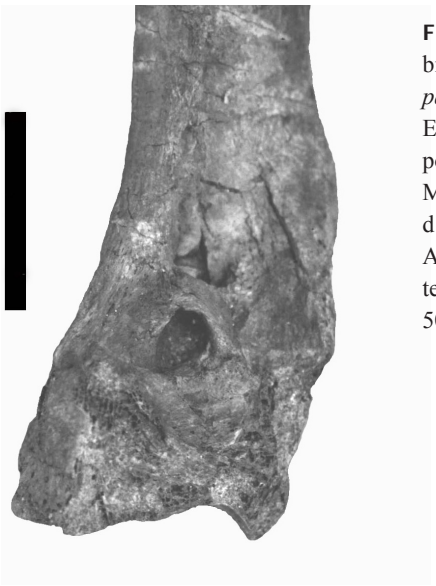

Figure 4 - Left tibiotarsus of *Gastornis parisiensis*, Early Eocene of Saint-Papoul (Aude, France), Musée des Dinosaures d'Espéraza, MDE-A18. Distal end in anterior view. Scale bar: 50 mm.

lectotype of *Gastornis parisiensis*, from Meudon, taken from Milne-Edwards (1867-1868), are given for comparison):

Specimen:	Saint-Papoul	Meudon
Total length (preserved):	436 mm	430 mm
Width at mid-shaft:	41 mm	46 mm
Width of proximal end:	121 mm	95 mm

The main conclusion to be drawn from this description of the rather well-preserved tibiotarsus from Saint-Papoul is that it very closely resembles the lectotype of *Gastornis parisiensis* from Meudon (see figures in Owen, 1856 and Milne-Edwards, 1867-1868), as confirmed by direct comparisons with a cast of the latter in the collection of the Natural History Museum, London (the original specimen, which was at the Ecole Normale Supérieure in Paris and should now be at the Paris Natural History Museum, is lost). This close resemblance justifies its inclusion in the same species, *Gastornis parisiensis* Hébert, 1855. Moreover, it also closely resembles other gastornithid tibiotarsi from Europe and North America that have been referred either to *Gastornis* (the specimens from Cernay and Berru in eastern France, and those from Croydon in England) or to *Diatryma* (the North American specimens and those from the Geiseltal in Germany). Variations do occur from one specimen to another, but they are small and do not appear to clearly separate the European specimens from the North American ones. The generic identity of *Gastornis* and *Diatryma*, advocated by Buffetaut (1997b, 2000) and formally accepted by Mlikovský (2002), is therefore supported by the characters of the fairly well preserved tibiotarsus from Saint-Papoul. The question of how many species of *Gastornis* should be distinguished is beyond the scope of this paper, as it can be answered only by a detailed revision of all the available European material and comparison with the North American specimens.

GASTORNIS AND THE LARGE EARLY TERTIARY BIRD EGGS FROM SOUTHERN FRANCE

The Late Cretaceous continental deposits of Provence and Languedoc, in southern France, are well known for their abundant dinosaur eggs (see Cousin, 2002, and references therein). It is less well known that fossil eggshell fragments, indicative of large eggs, also occur in some abundance in the continental Early Tertiary sediments of the same region. They were first reported from Provence in the late 1950s and early 1960s (Dughi & Sirugue, 1959; Fabre-Taxy & Touraine, 1960; Touraine, 1960), and slightly later from Languedoc (Villatte, 1966). Dughi and Sirugue (1962) erected a new oogenus, *Ornitholithus*, for this eggshell material, with several oospecies, the identification of which is questionable (Mikhailov, 1997). They also attempted to use them for biostratigraphic purposes (Dughi & Sirugue, 1968), despite an initial controversy about their exact stratigraphic position, precise correlations of the continental eggshell-bearing formations of Provence with the standard stratigraphic scale being fraught with difficulties (see Touraine, 1961). According to Dughi and Sirugue (1968), in Provence the *Ornitholithus* type of fossil eggshell occurs in both the Thanetian and the Sparnacian, although Kerourio and Aujard (1987) consider that they are all "Sparnacian". In Languedoc, the eggshell fragments from the Aude localities (which are geographically closest to Saint-Papoul) have been referred to the Sparnacian (Early Eocene) on the basis of correlations with marine ingressions (Dughi *et al.*, 1969). They are therefore roughly coeval with the tibiotarsus described in the present paper.

The Early Tertiary bird eggs from southern France are usually far from complete, consisting of scattered fragments, which are sometimes found in great abundance. Although differences in thickness, ornamentation and microstructure may suggest that they were laid by more than one species of bird, the available evidence does indicate eggs of considerable size. Touraine (1960) mentions eggshell thicknesses varying from 13 to 31 mm. Egg dimensions have been estimated on the basis of a few relatively complete eggs seen in cross-section *in situ*. According to Touraine (1960), the eggs with a thicker eggshell had a greater diameter of about 24 cm and a smaller diameter of about 15 cm, which makes them larger than ostrich eggs, but smaller than *Aepyornis* eggs. According to Dughi and Sirugue (1962), the dimensions of *"Ornitholithus biroi"* eggs were about 15x12 cm, whereas *"Ornitholithus arcuatus"* eggs could reach dimensions of 20x40 cm (which is the size of an *Aepyornis* egg). However, in view of the extreme scarcity of well-preserved eggs, these size estimates should be treated with caution.

The problem of the identity of the egg-layer(s) was posed as soon as the first specimens were reported. In 1959, Dughi and Sirugue noted that it was tempting to refer them to the gastornithids of the European Eocene, although it was difficult to reach a conclusion in the absence of skeletal remains. In 1960, Touraine remarked that an attribution to ra-

tites was difficult, because no ratite remains were known in the Early Tertiary; however, the occurrence at that time of very large carinates such as *Gastornis* and *Diatryma* suggested the possibility that the large eggs from Provence had been laid by such giant birds. Touraine wisely concluded that only an association between eggs and skeletal remains could verify this hypothesis. In 1962, Dughi and Sirugue found that the *Ornitholithus* eggshell type showed a mixture of characters, some reminiscent of the ratites, some of the carinates, and concluded that this was in agreement with an attribution to the "Diatrymiformes". This suggestion was considered likely by Cailleux (1969) in his study of gastroliths associated with eggshells from Provence. Mikhailov (1997) considered that shell structure and thickness were generally in accordance with an assignment to gastornithid or diatrymid birds. Bousquet and Vianey-Liaud (2001) went even farther, considering that the *Ornitholithus* eggshells had been laid by *Diatryma*.

A dissenting opinion was voiced by Kerourio and Aujard (1987), who considered that the microstructure and the morphology of the pore system of *Ornitholithus* eggs led to refer them to ratites, and, more precisely, to Aepyornithiformes. This conclusion does not seem to have been accepted by any other researcher, and there is currently no skeletal evidence of Aepyornithiformes in the Palaeocene and Eocene of Europe, although ratites such as *Remiornis*, *Eleutherornis* and *Paleotis* are known (Martin, 1992; Schaub, 1940; Houde & Haubold, 1987) .

Despite rather widespread agreement in favour of a gastornithid origin for the large eggs from the Early Eocene of southern France, this hypothesis was based only on the fact that gastornithids occur in formations of that age in other parts of Europe, such as the Paris Basin. Considering the palaeogeography of Europe at that time, it was not unlikely that that type of ground bird also occurred in southern Europe. However, no skeletal evidence of gastornithids had so far been recorded from the Lower Eocene of southern France (or, more generally, southern Europe). The *Gastornis* tibiotarsus from Saint-Papoul demonstrates that this group of giant birds was indeed present in that part of the world in the Early Eocene. The *Ornitholithus* localities of Aude are only a few tens of kilometres distant from Saint-Papoul.

The discovery of *Gastornis* at Saint-Papoul thus lends weight to the hypothesis according to which *Ornitholithus* eggs were laid by gastornithids. However, one should keep in mind that loose associations between fossil eggs and potential egg-layers are hazardous. The only way to uncontrovertibly demonstrate that *Ornitholithus* eggs are indeed *Gastornis* eggs would be to find a *Gastornis* embryo inside such an egg, or at least a clear association between an adult *Gastornis* skeleton and such eggs. It should also be kept in mind that, in addition to gastornithids, there were also other types of fairly large ground birds in Early Tertiary Europe, such as the ratites *Remiornis*, from the Thanetian of eastern France (see Martin, 1992, for a review), *Palaeotis*, from the Middle Eocene of the Geiseltal (Houde & Haubold, 1987), and *Eleutherornis*, from the Middle Eocene of Switzerland (Schaub, 1940). Although these birds were not as large as gastornithids, they may have laid fairly large eggs, and in view of the supposed occurrence of several eggshell types in the Lower Eocene of southern France, the possibility that more than one kind of large bird was involved cannot be dismissed.

ACKNOWLEDGMENTS

I am very grateful to Mr Henri-Pierre Labarrère, who kindly donated the *Gastornis* bone described in the present paper to the Musée des Dinosaures (Espéraza), and provided very useful information about the Saint-Papoul locality. I also thank Angela Milner and Sandra Chapman for access to the excellent collection of *Gastornis* casts in the Natural History Museum (London).

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