ORYCTOS, Vol. 1 : 131 - 136, Octobre 1998

FIRST EVIDENCE OF ENANTIORNITHINE BIRDS FROM THE UPPER CRETACEOUS OF EUROPE : POSTCRANIAL BONES FROM CRUZY (HÉRAULT, SOUTHERN FRANCE)

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Abstract : A coracoid and an incomplete femur from a newly discovered Late Campanian to Early Maastrichtian locality at Cruzy (Hérault, France) are described and identified as the first remains of enantiornithine birds to be reported from the Upper Cretaceous of Europe. This find extends to Europe the already wide known geographical distribution of Late Cretaceous Enantiornithes, and confirms the important part played by this peculiar group of birds in avifaunas in many parts of the world until late in the Cretaceous.

Key words : Aves, Enantiornithes, Late Cretaceous, France.

Premiers restes d'Enantiornithes (Aves) du Crétacé supérieur d'Europe : ossements post-crâniens trouvés à Cruzy (Hérault, Sud de la France)

Résumé : Un coracoïde et un fémur incomplet provenant d'un nouveau gisement d'âge Campanien supérieur à Maastrichtien inférieur à Cruzy (Hérault, France) sont décrits et identifiés comme les premiers restes d'oiseaux du groupe des Enantiornithes à être signalés dans le Crétacé supérieur d'Europe. Cette découverte étend à l'Europe la distribution géographique connue déjà vaste des Enantiornithes au Crétacé supérieur, et confirme que ce groupe particulier d'oiseaux jouait un rôle important dans les avifaunes de nombreuses parties du monde jusque tard dans le Crétacé.

Mots clés : Aves, Enantiornithes, Crétacé supérieur, France.

Résumé français étendu : Les avifaunes du Crétacé supérieur européen demeurent mal connues. Un oiseau de grande taille, incapable de voler, a été décrit sous le nom de *Gargantuavis philoinos* dans quelques gisements d'âge Campanien supérieur à Maastrichtien inférieur du Sud de la France, mais les formes volantes de petite taille étaient jusqu'ici inconnues. Le gisement de Massecaps, récemment découvert près de Cruzy (Hérault), a livré quelques ossements d'oiseaux, parmi une riche faune de vertébrés comprenant des poissons, des amphibiens, des chéloniens, des squamates, des crocodiliens et des dinosaures. Ces derniers sont représentés notamment par l'ornithopode *Rhabdodon* et le sauropode *Ampelosaurus*, assemblage qui indique un âge Campanien supérieur à Maastrichtien inférieur. Les oiseaux sont représentés par un coracoïde et un fragment proximal de fémur, qui montrent tous deux des traits caractéristiques du groupe éteint des Enantiornithes. Le coracoïde présente une grande expansion postérieure, et les processus procoracoïde et latéraux des oiseaux modernes sont absents à son extrémité antérieure, ce qui est caractéristique des Enantiornithes. Il suggère un animal de la taille d'un goéland actuel. Le fragment de fémur se caractérise par une dépression caudolatérale marquée, limitée latéralement par ce qui est probablement l'homologue du trochanter postérieur des Dromaeosauridae et d'*Archaeopteryx* ; il s'agit là encore d'un caractère présent chez les Enantiornithes. A partir du matériel actuellement disponible, on peut dire que l'oiseau de Cruzy appartient très clairement aux Enantiornithes, mais il n'est guère possible de l'identifier plus précisément. En Europe, les Enantiornithes n'étaient jusqu'ici connus que dans le Crétacé inférieur d'Espagne ; les spécimens de Cruzy constituent la première preuve de leur existence au Crétacé supérieur dans cette partie du monde. Cette découverte étend à l'Europe l'aire de répartition connue déjà vaste des Enantiornithes au Crétacé supérieur (Amérique du Sud, Amérique du Nord, Asie), et confirme que ces oiseaux jouaient un rôle important dans les avifaunes de nombreuses parties du monde jusque tard dans le Crétacé. Il n'est donc pas impossible qu'ils aient été victimes de l'extinction en masse de la limite Crétacé-Tertiaire.

INTRODUCTION

The Late Cretaceous avifauna of Europe is still largely unknown. Purported bird bones from the Maastrichtian of Transylvania (Harrison & Walker, 1975) are now usually regarded as belonging to troodontid dinosaurs (Osmolska & Barsbold, 1990) , although they are in need of a revision in the light of recent discoveries of Cretaceous birds. As far as southwestern Europe is concerned, Sauvage (1897-1898) reported remains of a bird from the Late Cretaceous Vizo (also spelled Viso) locality in Portugal, but he neither described nor illustrated them. Whether this purported bird material consisted of the specimens from Viso later briefly mentioned (but not figured) as caudal vertebrae of a pterosaur by Lapparent and Zbyszewski (1957) is uncertain. Pending a revision of the specimens from Viso, nothing definite can be said about them. So far, the only undisputed record of Late Cretaceous birds from Europe was that of a very large bird known from several specimens from the Upper Cretaceous of Provence and Languedoc, which has been described as *Gargantuavis philoinos* (Buffetaut *et al,* 1995 ; Buffetaut & Le Loeuff, 1998); smaller flying birds had not yet been reported. The discovery of a very distinctive coracoid and a fragmentary femur at a Late Cretaceous vertebrate locality at Cruzy near Béziers in southern France now reveals that representatives of the peculiar group of Cretaceous birds known as Enantiornithes were present in Europe during the Late Cretaceous.

GEOLOGICAL AND PALAEONTOLOGICAL SETTING

The fossils described here were found in the course of systematic excavations at the Massecaps locality near the village of Cruzy (Hérault, southern France), conducted by the Association Culturelle et Archéologique Cruziate, the Musée des Dinosaures d'Espéraza, and the Centre National de la Recherche Scientifique. This newly discovered locality has yielded an abundant and diverse vertebrate fauna, which includes lepisosteid fish, amphibians, turtles, large varanid lizards, ornithopod, sauropod and theropod

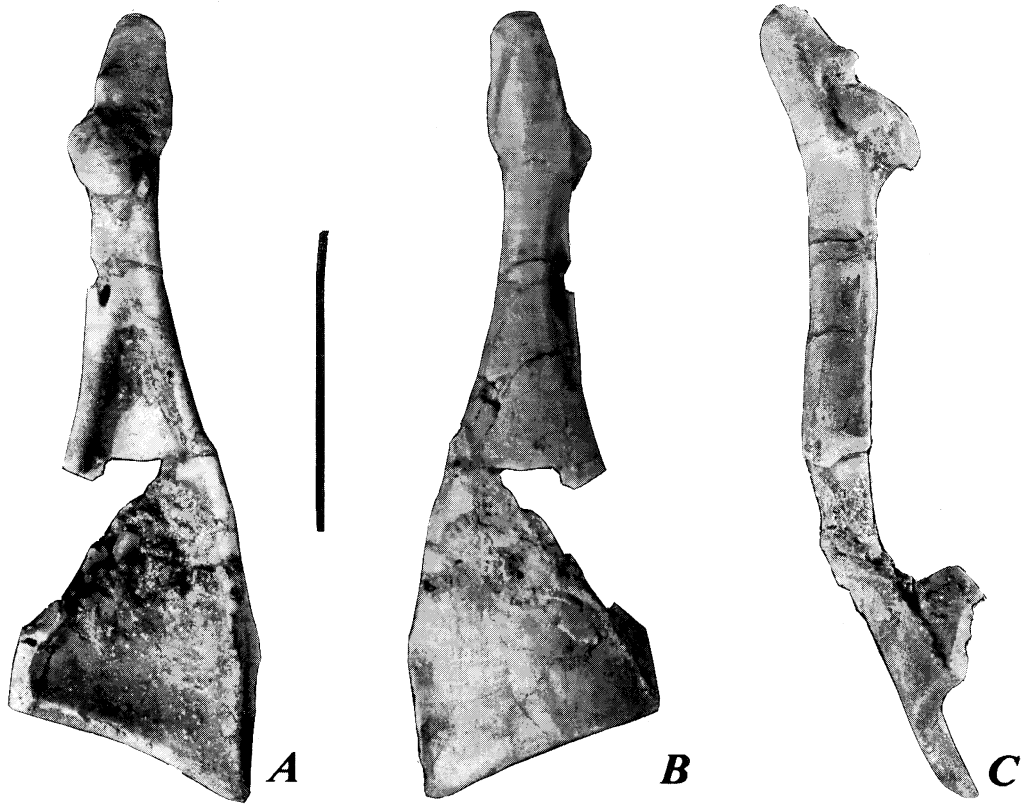

Figure 1. Right coracoid of enantiornithine bird from the Upper Cretaceous (Late Campanian/Early Maastrichtian) of Cruzy (Hérault, France) , Musée de Cruzy, M192.
A : dorsal view ;
B : ventral view ;
C : medial view.
Scale bar : 20 mm.
Photographs by Claude Abrial.
Coracoïde droit d'enantiornithe du Crétacé supérieur (Campanien supérieur / Maastrichtien inférieur) de Cruzy (Hérault, France), Musée de Cruzy, M192.
A : vue dorsale ;
B : vue ventrale ;
C : vue médiale.
Echelle : 20 mm.
Photos : Claude Abrial.

dinosaurs, and birds. The bones occur as disarticulated elements in variegated clays apparently indicative of a fluvial deposit. The dinosaur assemblage, dominated by the ornithopod *Rhabdodon* and the titanosaurid sauropod *Ampelosaurus*, is that usually found in Late Campanian to Early Maastrichtian vertebrate sites in southern France (Le Lœuff *et al.* 1994 ; Buffetaut & Le Lœuff, 1997 ; Buffetaut *et al.*, 1997). The available bird material, kept at the Cruzy Museum, consists of a nearly complete coracoid and the proximal end of a femur.

CORACOID

The first bird bone found at Cruzy by Didier Clavel, in 1996, is a fairly well preserved right coracoid (Cruzy Museum, M192) which exhibits the very peculiar features characteristic of the Enantiornithes (the recognition of the peculiar character of the Enantiornithes, or « opposite birds », was originally largely based on the unusual structure of the pectoral girdle : Walker, 1981). The coracoid from Cruzy (Fig. 1) is nearly complete, although part of the posterior expansion is destroyed. It is triangular in shape, with an anterior elongated apex. The posterior part of the bone forms a triangular plate of bone which is deeply excavated dorsally. Its lateral margin is markedly convex, whereas its posterior (sternal) and medial margins are concave. Just anteromedial to the anterior tip of the dorsal fossa, the supracoracoidal nerve foramen perforates a medial bony ridge and opens into a groove on the medial surface. This foramen opens inside the fossa in some enantiornithes, but in the Cruzy specimen it opens outside it, as in *Enantiornis leali* (Chiappe, 1996 a). The anterior part of the bone lacks the procoracoid and lateral processes of modern birds ; obviously, the triosseal canal, at the junction between the coracoid, the scapula and the furcula, was surrounded more by the scapula than by the coracoid, which is a characteristic feature of the Enantiornithes (Walker, 1981 ; Martin, 1995 ; Chiappe, 1996b). The contribution of the coracoid to the triosseal canal in the Cruzy bird is in the form of a notch for the supracoracoideus tendon, just anterior to the convex articular facet for the scapula, and separated from the acrocoracoid process by a well-marked tubercle (as in *Enantiornis leali* : Chiappe, 1996a). The anteriormost tip of the bone (the acrocoracoid process) is blunt, with a well-marked groove on its ventrolateral surface.

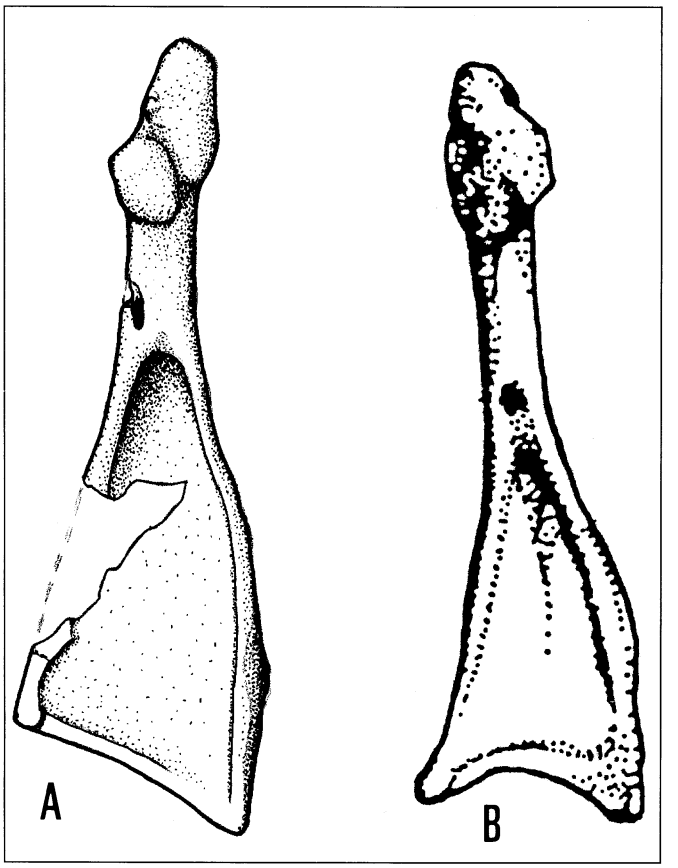

Fig.2. A comparison between the enantiornithine coracoid from Cruzy (A ; drawing by H. Tong) and the coracoid of *Enantiornis leali* (B), from the Maastrichtian of Argentina (mirror image after Walker, 1981). Both specimens in dorsal view, brought to the same size (the coracoid of *Enantiornis* is in fact about twice the length of the one found at Cruzy).
Comparaison entre le coracoïde d'enantiornithe de Cruzy (A ; dessin de H. Tong) et le coracoïde d'*Enantiornis leali* (B), du Maastrichtien d'Argentine (image inversée d'après Walker, 1981). Les deux spécimens sont en vue dorsale, et ramenés à la même taille (le coracoïde d'*Enantiornis* est en fait à peu près deux fois plus long que celui trouvé à Cruzy).

The bird coracoid from Cruzy is in all respects very similar to previously described enantiornithine coracoids (Walker, 1981 ; Martin, 1995 ; Chiappe, 1996a,b), such as those of *Enantiornis leali* (see Fig.2), from the Maastrichtian of Argentina (Walker, 1981), *Neuquenornis volans*, from the Coniacian-Santonian of Argentina (Chiappe & Calvo, 1994), and *Concornis lacustris*, from the Barremian of Spain (Sanz *et al.*, 1995). Its posterior triangular

expansion seems to be somewhat broader than in *Neuquenornis volans* and in *Nanantius valifanovi*, from the Upper Cretaceous (probably Late Campanian) of Mongolia (Kurochkin, 1996), but figured specimens of the latter seem to be incompletely preserved in that area. Although the general shape is the same, the anterior part of the coracoid from Cruzy seems to exhibit stronger reliefs than in the enantiornithine *Gobipteryx minuta*, from the Upper Cretaceous of Mongolia (Elzanowski, 1995), but the differences may be due to the embryonic condition of the latter. The coracoids of the Enantiornithes are very different from those of other birds, but within the group, there seems to be relatively little variation. The coracoid from Cruzy is 53 mm long, which suggests a bird about the size of a herring gull *(Larus argenteus)*.

FEMUR

A second bird bone was discovered at Massecaps at the end of the summer excavations of 1997. It is the proximal head of a femur (M193), with only a small portion of the hollow shaft preserved (Fig.3).

This specimen shows a well-defined, rounded articular head , which is medially and slightly dorsally oriented, and separated from the shaft by a a very distinct « neck ». There may be a small fossa on the articular head for insertion of the ligamentum capitis femoris, but this region has undergone some abrasion and details are not easily discernible. Lateral to the «neck », there is a trochanteric crest, as in other enantiornithines (Chiappe, 1996b). The most striking enantiornithine character of this fragment is a rather deep excavation on the caudolateral face of the bone, close to its proximal end. This excavation opens caudally and is limited ventrolaterally by a sharp border. This is very similar (Fig.4) to the condition described and illustrated by Chiappe and Calvo (1994) in enantiornithine femora from the Maastrichtian of El Brete (Argentina).

In *Neuquenornis volans*, the lateral border extends farther proximally (Chiappe & Calvo, 1994). According to Chiappe (1991, 1996b) and Chiappe and Calvo (1994), this structure is homologous to the posterior trochanter of dromaeosaurids and *Archaeopteryx*, and very well developed in enantiornithines.

CONCLUSIONS

Although both the coracoid and the femoral fragment from Cruzy exhibit characteristic features of the Enantiornithes, it is difficult to be more specific in

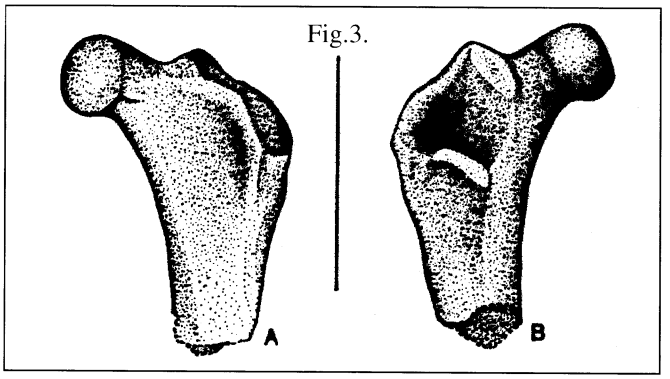

Fig.3. Proximal end of enantiornithine left femur from Cruzy, in cranial (A) and caudal (B) views. Scale bar : 20 mm. Drawing by H. Tong.
Extrémité proximale de fémur gauche d'enantiornithe de Cruzy, en vues craniale (A) et caudale (B). Barre d'échelle : 20 mm. Dessin de H. Tong

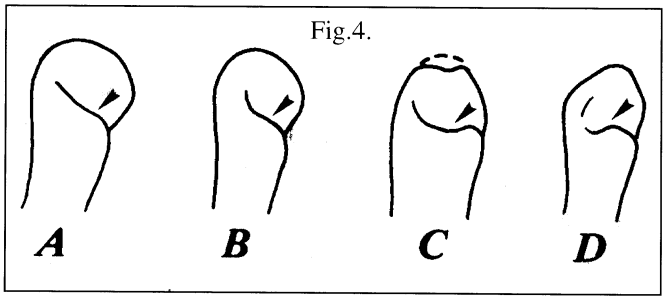

Fig.4. Proximal ends of enantiornithine left femora, in lateral view, showing the posterior trochanter (arrows). A, B : two enantiornithines from the Maastrichtian Lecho Formation of El Breta, Argentina. C : *Neuquenornis volans,* from the Coniacian - Santonian of Neuquen, Argentina. D : enantiornithine femur from Cruzy (M193). Not to scale. A,B,C after Chiappe and Calvo (1994).
Extrémités proximales de fémurs gauches d'enantiornithes, en vue latérale, montrant le trochanter postérieur (flèches). A,B : deux enantiornithes de la Formation Lecho (Maastrichtien) d'El Brete, Argentine. C : *Neuquenornis volans*, du Coniacien-Santonien de Neuquen, Argentine. D : fémur d'enantiornithe de Cruzy (M193). Echelles différentes. A,B,C d'après Chiappe et Calvo (1994).

their identification. As far as the coracoid is concerned, the closest resemblances seem to be with that of *Enantiornis leali* Walker, 1981, a member of the family Enantiornithidae, of the order Enantiornithiformes (following Martin's classification, 1995), or Alexornithiformes (following Kurochkin's classification, 1996), although they are clearly not identical (Fig.2), but it may be safer at the moment to simply refer the bird material from Cruzy to the subclass Enantiornithes, pending the discovery of additional material

Previously known European enantiornithine birds were *Concornis*, and possibly *Iberomesornis* and *Noguerornis* from the Lower Cretaceous of Spain (see Chiappe, 1996b ; Kurochkin, 1996), but the group was so far unknown in the Upper Cretaceous of Europe. The discovery of an enantiornithine bird in the late Campanian or early Maastrichtian of France shows that the group was still present in that part of the world late in the Cretaceous. It extends to Europe the known Late Cretaceous distribution of the Enantiornithes, which were already known from the Upper Cretaceous of Argentina, Mexico, the United States, and Central Asia (see reviews in Martin, 1995 ; Kurochkin, 1996), and confirms the very vast distribution of this group of birds until late in the Mesozoic. In Europe as in many other parts of the world (Martin, 1983, 1995 ; Chiappe, 1995 ; Feduccia, 1996 ; Kurochkin, 1996), enantiornithine birds seem to have been a significant component of the Late Cretaceous avifauna. Although their fossil record for the last million years of the Cretaceous is still too scanty to provide a detailed picture of the last stages of their evolutionary history, the idea that the enantiornithine radiation came to an end during the mass extinction of the Cretaceous-Tertiary boundary (Feduccia, 1995, 1996) finds some support in their continued presence in many parts of the world until late in the Cretaceous and their complete absence in the Tertiary. As already suggested elsewhere (Buffetaut, 1996), the fact that the Enantiornithes, to judge from their bone histology, had a less advanced, more reptile-like, physiology than modern birds (Chinsamy *et al* 1995) may help to explain why they did not survive into the Tertiary while other birds did.

ACKNOWLEDGMENTS

Field work at Cruzy was supported by the Institut National des Sciences de l'Univers (CNRS), the Association Culturelle et Archéologique Cruziate, and the Musée des Dinosaures (Espéraza). I thank all the volunteers who took part in the excavations. Special thanks to all members of the Association Culturelle et Archéologique Cruziate , and their president Francis Fages for their invaluable help. I am grateful to Angela Milner (The Natural History Museum, London), for access to casts in her care, and to Lionel Cavin, Joëlle Salomon and Haiyan Tong for their help in the first stages of the identification of the enantiornithine coracoid from Cruzy.

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Note reçue le 01-10-1997
acceptée le 31-10-1997