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DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of
Peter Wellnhofer**

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B28

DAVID W. E. HONE & ERIC BUFFETAUT (Eds)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;
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Late Cretaceous pterosaurs from France: a review

By
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Abstract

The scanty Late Cretaceous pterosaur record from France is reviewed. Cenomanian pterosaurs are represented by isolated teeth and fragmentary bones, referred to ornithocheirids, from the Charentes region of SW France. A putative pterosaur bone from the Coniacian Chalk of northern France is in fact a phalanx of a marine turtle. Bones from the Campanian Chalk of Oise, in the northern Paris Basin, originally described as belonging to birds, may have belonged to pterosaurs but the whereabouts of the specimens are unknown. The best record is from the Campanian and Maastrichtian non-marine deposits of southern France, which have yielded pterosaur remains at several localities since the 1990s. A newly discovered distal carpal from Cruzy (Hérault) is described as probably belonging to an azhdarchid. All identifiable pterosaur specimens from these formations are referable to azhdarchids. The details of the transition from a pterosaur assemblage dominated by toothed forms to a later one consisting of azhdarchids cannot be documented because of a gap in the record covering the Turonian-Santonian time interval.

Key words: Mesozoic, stratigraphy, pterosaurs

Zusammenfassung

Die dürftige Pterosaurierfunde aus der Oberkreide Frankreichs werden kurz beschrieben. Von Flugsauriern aus dem Cenomanium sind nur isolierte Zähne und fragmentäre Knochen erhalten. Sie gehören der Familie Ornithocheiridae an und stammen aus der Region Charentes im SW Frankreichs. Ein vermeintlicher Knochen eines Flugsauriers aus dem Coniacium von Nordfrankreich wurde tatsächlich als Phalange einer marinen Schildkröte identifiziert. Knochen aus dem Campanium von Oise, nördlich des Pariser Beckens, wurden ursprünglich als Vogelknochen identifiziert. Diese könnten möglicherweise von Flugsauriern stammen, leider ist der Verbleib dieser Individuen unbekannt. Der beste Fossilienbericht besteht aus den nicht marinen Schichten des Campanium und Maastricht von Südfrankreich, aus diesen gehen die Überreste

von Flugsauriern an mehreren Lokalitäten seit 1990 hervor. Ein kürzlich entdeckter distaler Carpalia von Cruzy (Hérault) stammt laut Beschreibung von einem Individuum der Familie der Azhdarchidae. Alle Flugsaurier dieser Formationen die als solche identifiziert werden konnten können den Azhdarchidae zugeordnet werden. Wann ein Übergang von den meist bezahnten früheren Formen der Flugsaurier zu den späteren Azhdarchidae stattgefunden hat ist auf Grund einer Lücke im Fossilienbericht zwischen Turonium und Santonium nicht dokumentiert.

Schlüsselwörter: Stratigraphie, Mesozoikum, Flugsaurier

1. Introduction

The French pterosaur record is relatively scanty, although it extends from the Late Triassic to the Late Cretaceous (MAZIN et al. 2001). One of the reasons for this situation is that few *Lagerstätten* allowing exceptional preservation of pterosaur specimens (BUFFETAUT 1995) are known in France (the Late Jurassic lithographic limestones of Cerin and Canjuers are exceptions, but they have yielded few pterosaur specimens). For a long time, very few pterosaur remains were known from the extensive Late Cretaceous deposits of France. The situation has changed in recent years, largely because of systematic excavations at various localities in southern France. The purpose of the present paper is to briefly review the French Late Cretaceous pterosaur record, including some hitherto unpublished finds – and also to show that some purported pterosaur specimens are dubious or were erroneously assigned to that group of vertebrates.

Late Cretaceous pterosaur remains have been reported from three main regions of France (Fig. 1), in rocks formed in different depositional environments. The oldest group of remains is from Cenomanian paralic deposits which crop out near the Atlantic coast of western France, in the Charentes region. A few specimens have been reported from the Coniacian and Senonian Chalk of northern France, but, as shown below, one of them is clearly not pterosaurian, while the others must be considered as dubious. Finally, the non-marine, mostly fluvial

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Figure 1: Map of France showing localities mentioned in text. 1: Charentes, Cenomanian: Ornithocheiridae indet. (see VULLO 2007 for details). 2: Lezennes-les-Lille (Nord), Coniacian: bone erroneously identified as pterosaurian, in fact from a turtle. 3: Notre-Dame-du-Thil (Oise), Campanian: possibly pterosaurian bones. 4: Fox-Amphoux (Var), late Campanian-early Maastrichtian: Azhdarchidae indet. 5: Pourrières (Var), late Campanian-early Maastrichtian: Pterosauria indet. 6: Cruzy (Hérault), early Maastrichtian: Azhdarchidae indet. 7: Campagne-sur-Aude (Aude), late Campanian-early Maastrichtian: Pterosauria indet. 8: Fontjoncouse (Aude), late Maastrichtian: Pterosauria indet. 9: Mérignon (Ariège), late Maastrichtian: Azhdarchidae indet.

deposits of Campanian and Maastrichtian age in southern France, from Provence to the foothills of the Pyrenees, have yielded pterosaur bones at several localities. All these finds are listed below in ascending stratigraphic order.

2. Cenomanian of western France: Ornithocheiridae indet.

Several localities in the paralic Cenomanian deposits of the Charentes area of western France have recently yielded

relatively abundant vertebrate remains, including fish, amphibians, squamates, dinosaurs and mammals (VULLO et al. 2005; VULLO 2007). Pterosaurs are represented by four isolated teeth and two hollow bone fragments (one of which identified as an incomplete femur) from several sites in department Charente-Maritime (Fig. 1.1), some of which are early Cenomanian, and others late Cenomanian in age. Two tooth morphotypes, differing in the curvature of the crown, can be distinguished; according to VULLO (2007), they probably correspond to two distinct taxa referred to as indeterminate Ornithocheiridae.



Figure 2: Bone from the Coniacian Chalk at Lezennes-lez-Lille (Nord), erroneously identified by Barrois (1875) as a pterosaur tibia, in fact in all likelihood a phalanx of a marine turtle. Muséum d'Histoire Naturelle de Lille, n° MGL 4158. Scale bar: 10 mm.

3. Coniacian of northern France: not a pterosaur

In 1875, BARROIS reported a pterodactyl tibia found by a M. DÉCOQ in the White Chalk (“Craie blanche”) which was then exploited in underground quarries at Lezennes (department Nord – now in the suburbs of the city of Lille; Fig. 1.2). The Lezennes Chalk is referred to the Coniacian stage. BARROIS referred the specimen to *Pterodactylus giganteus*, a species from the English Chalk. Although no detailed description or illustration was provided, the occurrence of a pterosaur in the Lezennes Chalk was later mentioned in works on local geology (GOSSELET 1881) and in lists of French pterosaurs (KNOLL 2001; MAZIN et al. 2001). The specimen, kept at the Lille Natural History Museum (MGL 4158), is an elongate, more or less cylindrical bone (Fig. 2), with poorly differentiated and only slightly expanded articular ends, which is not hollow but shows a spongy bone texture. It does not resemble a pterosaur tibia (or any other pterosaur bone) in any way. Comparisons reveal that the so-called pterosaur tibia from Lezennes is in all likelihood a phalanx of a marine reptile. Among Late Cretaceous marine reptiles, plesiosaurs have proportionally much shorter phalanges. In mosasaurs, the phalanges are elongate but more hourglass-shaped than the specimen from Lezennes. The greatest similarities seem to be with phalanges of marine turtles, which show a comparable degree of elongation and proximal and distal expansion (BUFFETAUT 2004). Incidentally, a turtle shell is known from the Lezennes Chalk (CHELLONEIX & ORTLIEB 1869).

4. Campanian of Oise (northern France): bird or pterosaur?

GRAVES (1847) reported “*Ornitholithes*” from the White Chalk (Campanian) of Notre-Dame-du-Thil (now part of the city of Beauvais, in department Oise, northwest of Paris; Fig. 1.3). He only briefly mentioned these supposed bird fossils as “indeterminable” long bone fragments, probably a radius and ribs. GERVAIS (1848–1852) suggested that these specimens in fact probably belonged to pterosaurs. He based his opinion on BOWERBANK’s demonstration that fossils from the Chalk of England previously referred to birds were in fact pterosaur bones (BOWERBANK 1846). GERVAIS’s suggestion was

tentatively accepted by KNOLL (2001) and MAZIN et al. (2001), who referred to GRAVES’s specimens as *Pterosauria* indet. (?). However, when GERVAIS discussed that material, no birds were known from the Late Cretaceous, whereas pterosaurs were. Since we now know that birds were abundant in the Cretaceous, the possibility that the bones from Notre-Dame-du-Thil actually belonged to birds cannot be completely excluded, and GRAVES may have been correct in his initial interpretation. Re-examination of the specimens to confirm their identity is not possible, however, because their present whereabouts is unknown. Like a large part of GRAVES’s collection, they were probably kept at the Musée départemental de l’Oise in Beauvais, where the geology collections were largely destroyed by Luftwaffe bombings in 1940. It therefore seems unlikely that the exact zoological affinities of GRAVES’s *Ornitholithes* will ever be ascertained.

5. Late Cretaceous of southern France: azhdarchid-dominated assemblages

Vertebrate remains have been known in the continental Late Cretaceous deposits of southern France since the early 19th century, when CUVIER (1824) described crocodylian remains from lignite beds near Marseilles. Subsequently, fairly abundant remains of dinosaurs, turtles and crocodylians were described from various localities in these formations, which extend in a discontinuous belt from the hills of Provence in the East to the valley of the Garonne and the foothills of the Pyrenees in the West (see BUFFETAUT et al. [1997] for a review). However, it is only recently that pterosaur remains were first reported, from a late Maastrichtian locality in the Corbières area (BUFFETAUT et al. 1996). Since then, more specimens have been collected in the course of systematic excavations at several sites.

Dating the vertebrate-bearing non-marine sediments of southern France has proved problematic, because of the scarcity of stratigraphically useful fossils, the lack of volcanic intercalations and the difficulty of correlation with the marine domain (except in the westernmost area; see LAURENT et al. [2001] for a review). However, contrary to older assumptions, the vertebrate remains show changes over time which reveal at least two successive faunal assemblages (LE LOEUFF et al. 1994; BUFFETAUT et al. 1997; LAURENT et al. 2001):

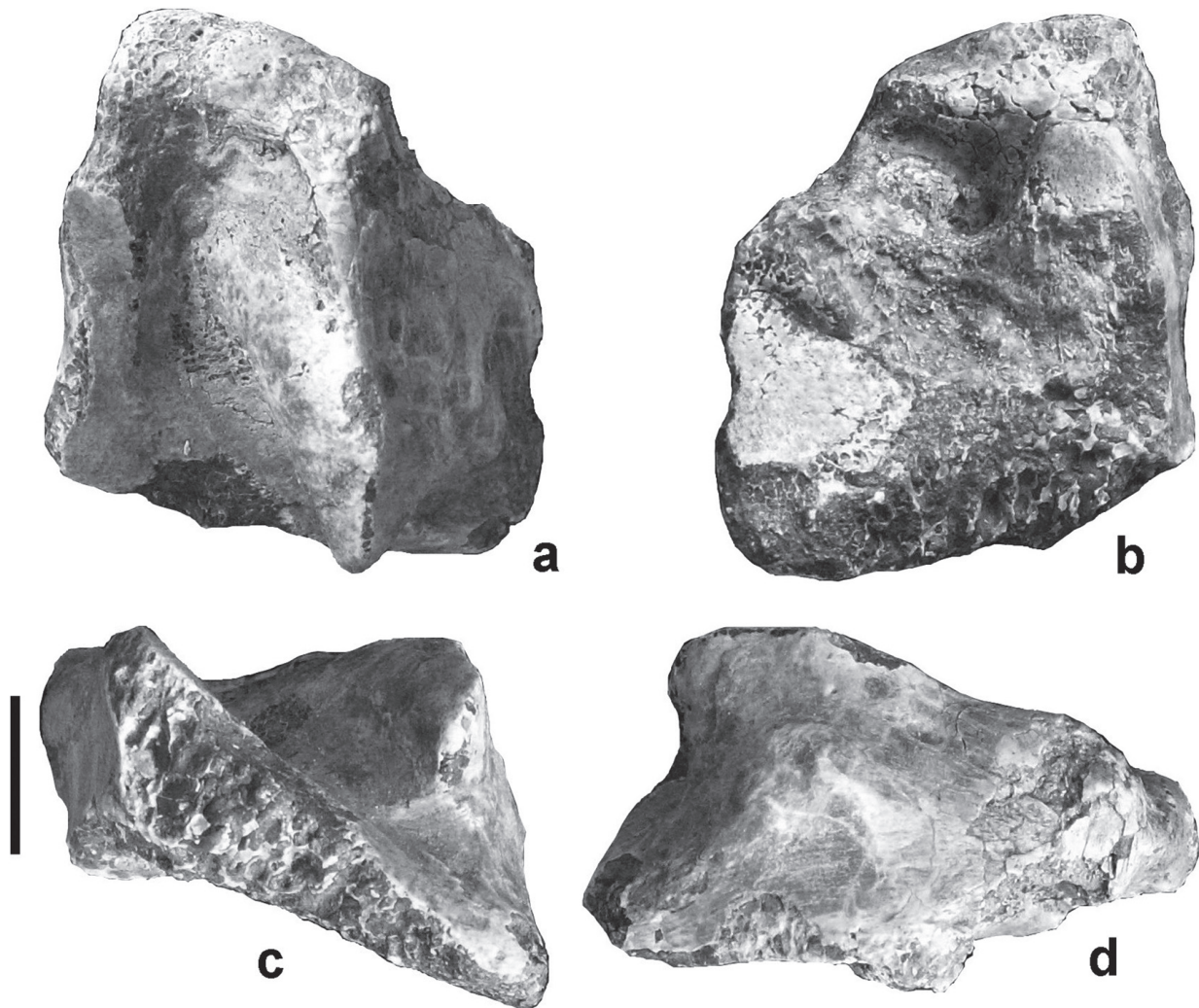


Figure 3: Right distal syncarpal of an azhdarchid from the early Maastrichtian of Masecaps, Cruzy, Hérault (Musée de l'Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois, Cruzy, n° M3929); a: proximal view; b: distal view; c: posterior view; d: dorsal view. Scale bar: 10 mm.

-an earlier assemblage, apparently of Campanian to early Maastrichtian age, which is characterised by the occurrence of the ornithopod dinosaur *Rhabdodon* and the abundance of titanosaurid sauropods;

-a later assemblage in which *Rhabdodon* no longer occurs, sauropods may be less abundant, and hadrosaurid ornithopods become abundant; this assemblage is late Maastrichtian in age.

Pterosaur remains have been found in both types of faunal assemblages. The localities and the pterosaur material they have yielded are listed below, roughly in ascending stratigraphical order. All the material comes from fluvial deposits, generally consisting of variegated marls with sandstone intercalations.

5.1 Late Campanian-Early Maastrichtian localities

Fox-Amphoux (Var)

The area around the village of Fox-Amphoux, in the hills of the Upper Var area of Provence (Fig. 1.4), has been known for its Late Cretaceous fossil vertebrates since the 1840s

(see review in BUFFETAUT et al. 2006), but the first pterosaur specimen was described in 2006. It is a right humerus from the Bastide-Neuve locality, at which sandy marls have yielded a varied assemblage comprising turtles, crocodylians, dinosaurs and birds (BUFFETAUT et al. 2006). The specimen was referred to the family Azhdarchidae on the basis of the shape and position of the proximal articular head and deltopectoral crest. On the basis of the length of that humerus, wing span was estimated at about 3 metres.

Pourrières (Var)

In course of emergency excavations along the A8 motorway in the eastern part of the Aix-en-Provence basin, conducted by the Aix-en-Provence Natural History Museum in 2006, pterosaur remains have been found in sandstone layers at two distinct localities near the village of Pourrières (Var; Fig. 1.5). They include the distal end of a middle-sized humerus, and a fairly robust quadrate showing the typical helical articulation for the lower jaw. Both specimens, kept in the collections of the Aix-en-Provence Natural History Museum, are currently under study by the author of the present paper.

Cruzy (Hérault)

Pterosaur remains have been found at two localities near the village of Cruzy (Fig. 1.6). A broken cervical vertebra was surface-collected at the Sainte-Foy locality and described by BUFFETAUT (2001) as belonging to a small azhdarchid (estimated wing span about 3 metres), notably because the neural chord is enclosed in a very thin-walled bony tube “hanging” inside the elongate hollow centrum, as described by FREY & MARTILL (1996), and MARTILL et al. (1998) in *Arambourgiania*.

Other pterosaur remains have been found in the course of systematic excavations at the Masecaps locality, which has yielded an abundant and diverse vertebrate assemblage (review in BUFFETAUT 2005), preserved in variegated clays with intercalated sandy layers. They include a poorly preserved, considerably crushed wing metacarpal, and a relatively well preserved right distal syncarpal (Musée de Cruzy, n° M3929, Fig. 3), which is described below. The bone shows all the characteristics of a pterosaur distal carpal (as described by, e.g., WELLNHOFER [1985] and KELLNER & TOMIDA [2000]), with two large steeply sloping articular surfaces, separated by a deep longitudinal, slightly curved groove. The ventral articular surface is significantly narrower than the dorsal one. The anterior face of the bone forms a convex, oval articular surface for the preaxial carpal. The dorsal and ventral faces of the bone show no evidence of pneumatic foramina, contrary to the condition in several of the pterosaurs from the Santana Formation described by WELLNHOFER (1985), and in *Pteranodon* (BENNETT 2001). The distal face has suffered some abrasion, exposing the spongy bony tissue covered by only a very thin layer of outer compact bone; morphological details are therefore partly obliterated, and the large facet for the articulation of metacarpal IV is largely destroyed. The deep pit or fovea for the articulation of a process of metacarpal IV is in an anterior rather than central position. This bone differs from the general morphology described by UNWIN (2003) for the “ornithocheiroid carpus” in the squarish rather than rounded outline of the distal face and in the shape and orientation of the facet for the preaxial carpal. There are closer resemblances with the distal carpals referred by WELLNHOFER (1985) to *Santanadactylus spixi*, which are considered by UNWIN (2003) as probably belonging to *Tupuxuara*. This would suggest azhdarchoid affinities for the distal carpal from Cruzy. Unfortunately, no detailed description of the azhdarchid carpus is available. However, comparison with a cast of a distal carpal of *Quetzalcoatlus* in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG, Munich) reveals notable similarities, particularly in the shape and arrangement of the sloping articular facets on the proximal face. The specimen from Cruzy is therefore tentatively referred to the family Azhdarchidae.

Campagne-sur-Aude (Aude)

The Bellevue vertebrate locality in the valley of the Aude river, above the village of Campagne-sur-Aude (Fig. 1.7), has yielded a rich vertebrate assemblage, including turtles, crocodylians, various types of dinosaurs (notably *Rhabdodon* and the sauropod *Ampelosaurus*) and birds, preserved in variegated marls with some sandstone intercalations. Pterosaurs are represented only by a few poorly preserved hollow bones (BUFFETAUT 1998). One of them, showing a marked curvature and a triangular cross-section, was tentatively identified as a

terminal phalanx of the wing finger. Because in cross-section it differs from the T-shaped wing phalanges of azhdarchids, it was speculated that it probably did not belong to the family Azhdarchidae (BUFFETAUT 1998). However, identification as a wing phalanx should be considered as dubious – a pterosaur rib may show a similarly triangular cross-section (BENNETT 2001). It thus seems premature to conclude that a non-azhdarchid pterosaur is present at Bellevue on the basis of this single specimen.

5.2 Late Maastrichtian localities

Fontjoncoue (Aude)

The first pterosaur specimen to be described from the Late Cretaceous of southern France was found at the Bexen locality near the village of Fontjoncoue (Fig. 1.8), in the Corbières hills. Besides pterosaurs, the vertebrate fauna from the Bexen locality contains crocodylians, dromaeosaurid theropods and hadrosaurs (LE LOEUFF et al. 1993), preserved in red clays. The presence of hadrosaurs indicates a late Maastrichtian age, which is confirmed by local stratigraphy. The pterosaur specimen is a 95 mm long fragment of the shaft of a hollow, very thin-walled bone, possibly a first wing phalanx (BUFFETAUT et al. 1996). Its pterosaurian nature was confirmed by a histological study. Because of its fragmentary condition, this specimen could not be identified beyond Pterosauria.

Méridon (Ariège)

The Méridon locality, in the foothills of the Pyrenees (Fig. 1.9), has yielded a large cervical vertebra which clearly belongs to a giant pterosaur (BUFFETAUT et al. 1997). The locality, consisting of alternating sandstones and marls, has also yielded hadrosaur remains; it belongs to the Marnes d’Auzas Formation, a freshwater to brackish formation with some marine intercalations which is well dated as late Maastrichtian. The elongate and dorsoventrally flattened centrum resembles those of *Quetzalcoatlus* and other azhdarchids (although it differs from that of *Arambourgiania*) and the Méridon specimen was therefore referred to the Azhdarchidae. A wing span estimate of about 9 metres was obtained, placing the Méridon pterosaur among the largest known flying reptiles.

The azhdarchid material from southern France exhibits considerable size differences. Whether this reflects differences in individual age or indicates the occurrence of several taxa cannot be decided on the basis of the morphology of the available material, although histological studies could possibly prove useful in this regard.

6. Conclusions

The French Late Cretaceous record of pterosaurs is still scanty, although it has been growing noticeably during the last decade, largely thanks to systematic excavations at various localities in southern France. With the exception of the recently discovered specimens from the Cenomanian of Charente-Maritime, very little is known about pterosaurs from the lower part of the Late Cretaceous. The extensive Late Cretaceous marine deposits (Chalk) of northern France have so far yielded no remains that can safely be attributed to pterosaurs, although the

bones from the Campanian of Notre-Dame-du-Thil may have belonged to that group. Most of the Late Cretaceous pterosaur material from France comes from the non-marine Campanian and Maastrichtian deposits of southern France. Although fossil vertebrates began to be collected from these formations during the first half of the 19th century, these pterosaur specimens have all been found since the mid-1990s. This is largely a result of the development of systematic excavations using modern collecting techniques in recent years – most of the earlier discoveries of fossil vertebrates resulted from surface collecting, during which the delicate bones of pterosaurs had relatively little chance of being found. The new finds from southern France illustrate the fact that even in relatively coarse, high-energy sediments pterosaur remains can be found – although they tend to be rather fragmentary.

The Late Cretaceous pterosaur record from France is too patchy to reveal details of faunal evolution. The small Cenomanian assemblage seems to be dominated by ornithocheirids, but this may reflect the fact that it consists mostly of teeth. Toothless pterosaurs may have been present, too, but cannot be identified on the basis of the available material. The Campanian-Maastrichtian record from southern France includes no teeth, despite the fact that large-scale screen-washing, which should have revealed them if they were present, has been conducted at several localities. It thus seems reasonable to assume that only toothless pterosaurs were present at that time. All the identifiable remains from southern France described so far show azhdarchid characters (as mentioned above, the purported non-azhdarchid specimen from Campagne-sur-Aude is in fact of highly uncertain affinities), and it is highly likely that azhdarchids were the dominant, if not the only, group of pterosaurs in that part of Europe during the last stages of the Cretaceous. This is in agreement with the known record of pterosaurs from other parts of Europe, such as Romania (BUFFETAUT et al. 2003), Spain (BUFFETAUT 1999; COMPANY et al. 1999) and Hungary (ÖSI et al. 2005), for that time interval. The only exception may be the material from the Campanian Gosau beds of Muthmannsdorf, Austria, which was referred to *Ornithocheirus* by SEELEY (1881). However, as noted by WELLNHOFER (1980, 1991), the pterosaur material from Muthmannsdorf, which consists of fragmentary phalanges, an incomplete humerus and the articular region of a mandible, cannot be referred to *Ornithocheirus* (or even Ornithocheiridae) with any certainty. The shape of the proximal articular area and deltopectoral crest of the humerus from Muthmannsdorf would certainly not preclude an attribution to the Azhdarchidae.

The French record indicates that in that part of the world sometime during the Late Cretaceous, pterosaur assemblages containing toothed forms (“ornithocheirids”) were succeeded by others in which azhdarchids were dominant. It seems likely that the Azhdarchidae were the only pterosaur family to be present in Campanian and Maastrichtian times in France. How and when this replacement took place remains very poorly understood, for lack of reasonably good pterosaur remains for the long time span from the Cenomanian to the Campanian – a time interval for which the French fossil record is poor for all groups of non-marine vertebrates.

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