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A terminal Cretaceous giant pterosaur from the French Pyrenees

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Abstract

A very large pterosaur cervical vertebra is described from the Upper Maastrichtian deposits of Mérigon, in the foothills of the French Pyrenees. It resembles the vertebrae of *Quetzalcoatlus*, from the Maastrichtian of Texas, more than those of *Arambourgiania*, from the Maastrichtian of Jordan. The estimated wing span of the Mérigon pterosaur is close to 9 m, which makes it one of the largest known flying creatures. Giant pterosaurs still had a wide geographical distribution at the end of Maastrichtian time, which is not suggestive of a declining group, although it is difficult to obtain an accurate estimate of taxonomic diversity of terminal Cretaceous pterosaurs on the basis of available data.

1. Introduction

We report the discovery of a cervical vertebra of a huge pterosaur of the family Azhdarchidae in the Upper Maastrichtian sediments of the foothills of the French Pyrenees. The specimen is identified as a pterosaur because of its hollow centrum and the shape of its posterior articular region, with well-marked exapophyses. It is referred to the Azhdarchidae because of its great elongation and close resemblances with the giant azhdarchid *Quetzalcoatlus*. The Azhdarchidae, a group of very large pterosaurs with greatly elongated neck vertebrae, were among the last of the pterosaurs (Wellnhofer, 1991). Azhdarchids have been reported from a small number of Maastrichtian localities. The most abundant and complete material hitherto reported is that of *Quetzalcoatlus* (Lawson, 1975; Langston, 1981), with probably two species, the very large *Q. northropi* and a smaller, still unnamed one (Kellner & Langston, 1996), from localities close to the Cretaceous–Tertiary boundary in the late Maastrichtian Javelina Formation of the Tornillo Group of Texas. Another late Maastrichtian azhdarchid is known from the Lance Formation of Wyoming (Estes, 1964). *Arambourgiania philadelphiae* (Arambourg, 1954, 1959 ; Frey & Martill, 1996), from the phosphates of Jordan, is Maastrichtian, but probably older than the North American forms (see stratigraphic section in Frey & Martill, 1996) ; its referral to the Azhdarchidae is debatable (Frey & Martill, 1996). Azhdarchid specimens from Senegal (Monteillet, Lappartient & Taquet, 1982) and Spain (Astibia *et al.* 1990) may be late Campanian or early Maastrichtian in age.

Previously described pterosaur remains from the Upper Maastrichtian deposits of southern France (Buffetaut, Clarke & Le Loeuff, 1996) consist of wing bone fragments from the Corbières (Department Aude) which, although undoubtedly pterosaurian, could not be definitely identified at the family level, and indicate a large (possible wing span about 5 m) but not gigantic pterosaur.

2. Geological setting

The French specimen was found at the base of a thick bed of coarse sandstone overlying a bed of sandy clay, exposed on a hillside near the village of Mérigon (Department Ariège), in the part of the foothills of the French Pyrenees known as the Plantaurel. Fossil bones were first reported from Mérigon in 1863, by a local priest, Abbé Cabibel, the vicar of the nearby village of Montardit. In a letter to Abbé Jean-Jacques Pouech, a famous local geologist and palaeontologist who was the first to report remains of Mesozoic vertebrates from that part of France (Le Loeuff, 1992, Buffetaut, 1992), Cabibel explained that he had collected reptile bone fragments of a blackish to rusty brown colour above the village of Mérigon (incidentally, his description of the colour of the fossils perfectly fits the pterosaur bone described below). The fossil vertebrates from Mérigon then seem to have been forgotten until 1979, when Ségura (F. Ségura, unpub. thèse de doctorat de 3e cycle, Université Paul Sabatier, Toulouse) reported the presence of fossil bones in his description of the late Cretaceous section at Mérigon.

The fossil locality is in the uppermost sequence of the Marnes d'Auzas Formation (Bilotte & Ségura, 1991), a freshwater to brackish deposit with some marine intercalations (Bilotte, 1985; Lepicard, 1985) which is late Maastrichtian in age and underlies Danian beds. It has also yielded remains of turtles, crocodilians and hadrosaurid dinosaurs (Le Loeuff *et al.* 1994). In southern France, hadrosaurids are currently unknown prior to late Maastrichtian time (Le Loeuff, Buffetaut & Martin, 1994).

Stratigraphical and palaeontological evidence thus indicates that the Mérigon azhdarchid is one of the latest known pterosaurs, approximately coeval with the Texan *Quetzalcoatlus*.

3. Description

The specimen (Musée des Dinosaures, Espéraza, n° ME1 04) is the ventral part of a very large and elongated cervical vertebra. As preserved, it is 460 mm long, but it is incomplete both anteriorly and posteriorly, and its actual length probably reached 550 mm, which would make it longer than the longest known cervical vertebra of the 'small' species of *Quetzalcoatlus*, usually referred to as *Quetzalcoatlus* sp. (length of complete vertebra 480 mm; no cervical vertebrae referrable to the larger *Q.*

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Figure 1. Location map showing the position of the late Maastrichtian vertebrate locality at Mérigon (star), in the foothills of the Pyrenees.

northropi are currently known, W. Langston, pers. comm.), but shorter than the type of *Arambourgiania* (preserved length 620 mm, estimated total length 770 mm ; Frey & Martill, 1996). The centrum is hollow and partly matrix-filled, with lateral walls which are fairly thick by pterosaur standards, varying from 2 to 6 mm. This, however, is relatively little by comparison with the width of the bone, which reaches 80 mm at mid-length. The anterior and posterior ends of the centrum consist of highly cancellous bone. Anteriorly, the ventral face bears a blunt ridge corresponding to the hypapophysis. The anterior articular region is missing. The posterior part broadens ventrally to form a Y-shaped pair of exapophyses, separated by a broad groove. Laterally, the bases of the postzygapophyses can be seen. They are separated from each other medially by the incompletely preserved posterior articular condyle, which is dorsoventrally flattened. Anterior to the condyle, a smooth surface corresponding to the floor of the medullary canal is clearly visible; more anteriorly, the canal apparently became confluent with the hollow space inside the centrum, but this may in fact be due to destruction of the thin bony tube which may have enclosed the medulla inside the centrum (if the condition was similar to that described by Nessov (1984) in *Azhdarcho* and also observed in *Arambourgiania:* E. Frey, pers. comm.).

In the dorsoventral compression of the condyle, the breadth of the exapophyses and the bluntness of the hypapophysis, the Mérigon vertebra is much more reminiscent of *Quetzalcoatlus* than of *Arambourgiania,* which has a deeper centrum, a higher than wide condyle, less divergent exapophyses and a sharper hypapophysis (Frey & Martill, 1996). The French specimen may therefore provisionally be referred to as cf. *Quetzalcoatlus*. On the basis of Langston's reconstruction of *Quetzalcoatlus* (Langston, 1981), assuming that the Mérigon vertebra was the longest cervical, the estimated wing span of the French pterosaur was about 8.5 m, which places it between the 'small' species of *Quetzalcoatlus* (wing span about 5.5 m) and *Q. northropi* (wing span about 11 m) and *Arambourgiania philadelphiae* (wing span possibly reaching 12 m according to Frey & Martill, 1996; however, this estimate is based on the hypothetical maximum length of a vertebral centrum; if one uses the actual length of the specimen instead, the estimated wing span is a little less than 9 m: Frey & Martill, 1996). To estimate the wing span of *Arambourgiania* on the basis of the type cervical vertebra, Frey & Martill (1996) have used scaling indices derived from several specimens of *Quetzalcoatlus*. When the same method is used for the Mérigon vertebra, on the basis of the same measurements of *Quetzalcoatlus* specimens, the resulting estimated wing span is close to 9 m. There is no doubt that the Mérigon pterosaur was among the largest known flying creatures.



Figure 2 . The azhdarchid pterosaur vertebra from the Upper Maastrichtian of Mérigon (French Pyrenees) in ventral view (anterior end up). Musée des Dinosaures, Espéraza, n° ME1 04. Missing parts are reconstructed in outline. Scale bar: 10 cm. e: exapophysis; h: hypapophysis; p: base of postzygapophysis. Photo by Claude Abrial.

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4. Conclusions

The discovery of a *Quetzalcoatlus*-like form in the Upper Maastrichtian of France extends the distribution of terminal Cretaceous giant azhdarchids to Europe (the previously reported azhdarchid remains from Laño are smaller and significantly older than the Mérigon specimen), and shows that these huge pterosaurs had a wide geographical distribution until the very end of the Cretaceous Period. Although their mode of life probably was favourable to dispersal over wide areas, this is not especially suggestive of a declining group on its way to extinction, and should be taken into consideration when discussing the final stages of pterosaur history prior to the Cretaceous–Tertiary boundary. The supposed rarity of pterosaurs at the end of the Cretaceous Period may well be more apparent than real, and linked to a taphonomic bias against the preservation of recognizable pterosaur bones in non-marine and non-lacustrine environments. The fossil record of pterosaurs is strongly affected by a Lagerstätten effect (Buffetaut, 1995): a few localities with exceptional preservation of pterosaur remains have yielded abundant and diverse specimens which contrast with the more 'normal', far scantier record of pterosaurs from 'usual' localities. Campanian and Maastrichtian pterosaurs are still relatively poorly known, being represented mostly by isolated finds from continental, often fluviatile deposits which do not provide the best opportunities for pterosaur preservation, as contrasted with some marine, lagoonal or lacustrine environments (see Buffetaut, Clarke & Le Loeuff, 1996, for a more detailed review). The best late Cretaceous pterosaur record is from the Santonian Niobrara Chalk of North America, which has yielded a very large number of specimens belonging to the families Pteranodontidae (with several species of *Pteranodon*) and Nyctosauridae (see review and literature in Wellnhofer, 1991). The Campanian and Maastrichtian records are much scantier, consisting of mostly isolated finds (the Texas *Quetzalcoatlus* localities being an exception), and a simple comparison may suggest a decline of pterosaurs during the last stages of the Cretaceous Period, prior to their final extinction. Nevertheless, the available data indicate that two distinct families (Azhdarchidae and Nyctosauridae) were clearly present during Maastrichtian time, and a third one may be represented by material from New Zealand (for a recent review, see Buffetaut, Clarke & Le Loeuff, 1996). It is difficult, however, to assess the true diversity of those terminal Cretaceous pterosaurs at lower taxonomic levels, because few really productive pterosaur localities are known for that time interval, and none that can compare with the remarkable sites in the Niobrara Chalk. Although we suspect that the purported decline of pterosaurs during the last stages of the Cretaceous Period is largely due to a taphonomic bias and therefore more apparent than real (Buffetaut, 1996 ; Buffetaut., Clarke & Le Loeuff, 1996), it should be admitted that is still difficult to produce an accurate estimate of taxonomic diversity on the basis of the currently available Campanian and Maastrichtian pterosaur record.

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References

ARAMBOURG, C. 1954. Sur la présence d'un Ptérosaurien gigantesque dans les phosphates de Jordanie. *Comptes Rendus de l'Académie des Sciences de Paris* **238**, 133–4.

ARAMBOURG, C. 1959. *Titanopteryx philadelphiae* nov.gen., nov.sp., Ptérosaurien géant. *Notes et Mémoires sur le Moyen-Orient* **7**, 229–34.

ASTIBIA, H., BUFFETAUT, E., BUSCALIONI, A. D., CAPPETTA, H., CORRAL, C., ESTES, R., GARCIA-GARMILLA, F., JAEGER, J. J., JIMENEZ-FUENTES, E., LE LOEUFF, J., MAZIN, J. M., ORUE-ETXEBARRIA, X., PEREDA-SUBERBIOLA, J., POWELL, J. E., RAGE, J. C., RODRIGUEZ-LAZARO, J., SANZ, J. L. & TONG, H. 1990. The fossil vertebrates from Laño (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. *Terra nova* **2**, 460–6 .

BILOTTE, M. 1985. Le Crétacé supérieur des plates-formes est-pyrénéennes. *Strata* **5,** 1–438.

BILOTTE, M. & SÉGURA, F. 1991. Stratigraphie séquentielle des séries du Sénonien supérieur dans la zone sous-pyrénéenne (Petites Pyrénées, Dômes annexes, SW France). *Comptes Rendus de l'Académie des Sciences de Paris II* **312**, 393–8.

BUFFETAUT, E. 1992. La place de l'Abbé Pouech dans la paléoherpétologie du XIXe siècle. In *Actes du Colloque Jean-Jacques Pouech*, pp. 37–43. Pamiers: Société Historique et Archéologique de Pamiers et de la Basse-Ariège.

BUFFETAUT, E. 1995. The importance of "Lagerstätten" for our understanding of the evolutionary history of certain groups of organisms : the case of pterosaurs. In *II International Symposium on Lithographic Limestones, Extended Abstracts*, pp.49–52. Madrid: Ediciones de la Universidad Autonoma de Madrid.

BUFFETAUT, E. 1996. Pterosaur extinction : decline and fall or just fall? *Journal of Vertebrate Paleontology* **16** (supplement to 3), 24A–25A.

BUFFETAUT, E., CLARKE, J. B. & LE LOEUFF, J. 1996. A terminal Cretaceous pterosaur from the Corbières (southern France) and the problem of pterosaur extinction. *Bulletin de la Société géologique de France* **167**, 753–9.

ESTES, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. *University of California Publications in the Earth Sciences* **49**, 1–180.

FREY, E. & MARTILL, D. M. 1996. A reappraisal of *Arambourgiania* (Pterosauria, Pterodactyloidea): one of the world's largest flying animals. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **199**, 221–47.

KELLNER, A. W. A. & LANGSTON, W. 1996. Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology* **16**, 222–31.

LANGSTON, W. 1981. Pterosaurs. *Scientific American* **244**, 122–36.

LAWSON, D. A. 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. *Science* **187**, 947–8.

LE LOEUFF, J. 1992. L'Abbé Pouech et les dinosaures du Plantaurel. In *Actes du Colloque Jean-Jacques Pouech*, pp.23–30. Pamiers: Société Historique de Pamiers et de la Basse-Ariège.

LE LOEUFF, J., BUFFETAUT, E., CAVIN, L., LAURENT, Y., MARTIN, M., MARTIN, V. & TONG, H. 1994. Les hadrosaures des Corbières et des Petites Pyrénées. *Bulletin de la Société d'Etudes Scientifiques de l'Aude* **94**, 19–21.

LE LOEUFF, J., BUFFETAUT, E. & MARTIN, M. 1994. The last stages of dinosaur faunal history in Europe: a succession of Maastrichtian dinosaur assemblages from the Corbières (southern France). *Geological Magazine* **131**, 625–30.

LEPICARD, B. 1985. Le Crétacé terminal et le Paléocène basal

https://doi.org/10.1017/S0016756897007449 Published online by Cambridge University Press

dans les Petites Pyrénées et les Dômes Annexes. Biostratigraphie – Sédimentologie. *Strata* **2**, 1–276.

MONTEILLET, J., LAPPARTIENT, J. R. & TAQUET, P. 1982. Un Ptérosaurien géant dans le Crétacé supérieur de Paki (Sénégal). *Comptes Rendus de l'Académie des Sciences de Paris II* **295**, 409–14.

NESSOV, L.A. 1984. Upper Cretaceous pterosaurs and birds from Central Asia. *Paleontologicheskii Zhurnal* **1**, 47–57 [in Russian].

WELLNHOFER, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. London: Salamander Books, 192 pp.

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