

Pterosaurs from the Lower Cretaceous (?Berriasian) of Anoual, Morocco

Fabien KNOLL*

*Laboratoire de paléontologie, UMR 8569 CNRS,
Muséum national d'histoire naturelle, 8, rue Buffon, 75005 Paris, France*

(Received 14th January 2000; accepted after revision 7th August 2000)

Abstract — A report on the pterosaurian remains from the Lower Cretaceous of Anoual, Morocco, is presented. The material consists of teeth possibly documenting two groups. One of them cannot be clearly established but might be ornithocheirid, while the most numerous teeth are reminiscent of those of gnathosaurine. This possible attribution might be consistent with a Berriasian age for the calcareous lens containing the microvertebrate assemblages of Anoual. © 2000 Éditions scientifiques et médicales Elsevier SAS

Pterosauria / Gnathosaurinae / Lower Cretaceous / Morocco

Résumé — Les ptérosaures du Crétacé inférieur (Berriasien ?) d'Anoual (Maroc). L'étude des restes de ptérosaures du Crétacé inférieur d'Anoual est présentée. Le matériel consiste en un ensemble de dents pouvant témoigner de la présence de deux groupes distincts. Un de ceux-ci ne peut être déterminé avec précision mais pourrait s'intégrer aux Ornithocheiridae, alors que les dents les plus fréquentes rappellent celles des Gnathosaurinae. Cette identification serait en accord avec l'attribution d'un âge Berriasien à la lentille calcaire de laquelle proviennent les microvertébrés d'Anoual. © 2000 Éditions scientifiques et médicales Elsevier SAS

Pterosauria / Gnathosaurinae / Crétacé inférieur / Maroc

* Correspondence and reprints. knoll@mnhn.fr

INTRODUCTION

Despite recent discoveries the pterosaur fossil record remains very patchy and the evolutionary history of the group is still only poorly known. This is especially true of Africa where pterosaurs have only been reported from a handful of localities of Late Jurassic [11, 14, 27, 28, 38], Early Cretaceous [3, 19, 30, 32, 33] and Late Cretaceous [17, 18, 21, 22, 25, 34, 46] ages. Thus, due to the rarity (and rather fragmentary condition) of African pterosaurs, the representatives of this group from Anoual [32, 33] deserve attention despite being represented so far merely by isolated teeth.

The Moroccan microvertebrate locality of Anoual is situated in the Eastern High Atlas Mountains, 100 km east of the city of Talsint, close to a fort called Ksar Met Lili. The site was sampled, along with some 20 others, during a 1983 field expedition from the Muséum national d'histoire naturelle (Paris) and the ministère marocain de l'Énergie et des Mines (Rabat), led by M. Monbaron (Institut de géographie, Fribourg). In view of the promising results from the Anoual locality, field crews returned there to make further collections in 1986 and 1988. The site is highly important in having produced a diversity of microvertebrates: mammals, saurischians, ornithischians, pterosaurs, crocodylians, squamates, sphenodontians, turtles, amphibians and fishes [4, 7, 10, 29, 31–33], but most of them have yet to be described in detail. The aim of this paper is to give an account of the pterosaurian remains from Anoual.

GEOLOGICAL SETTING

The calcareous lens containing the microvertebrate assemblage can be described as a microbreccia of bones and fish scales about 20 cm thick and covering an area of about 200 square meters. The lens is sandwiched between marine beds, suggesting that it formed part of a deltaic sedimentary environment close to the sea. Studies of the calcareous nannofossils (holococcoliths) present at the same level suggest a basal Cretaceous (Berriasian) age for the lens [33].

Altogether, some 700 kg of calcareous sediment were treated with acid, and about two-thirds of the resulting residues have been sorted for microvertebrate and plants remain. The sediment is very rich in microvertebrates, especially ganoid scales like those of *Lepidotes*. Most of the remains are small, the larger elements (bones) usually being broken, but they show little sign of polishing or abrasion. This would suggest some transportation, but with deposition in relatively quiet conditions. This could also indicate short transportation in a high-energy flow of mud mixed with debris (Frey, pers. comm., 2000).

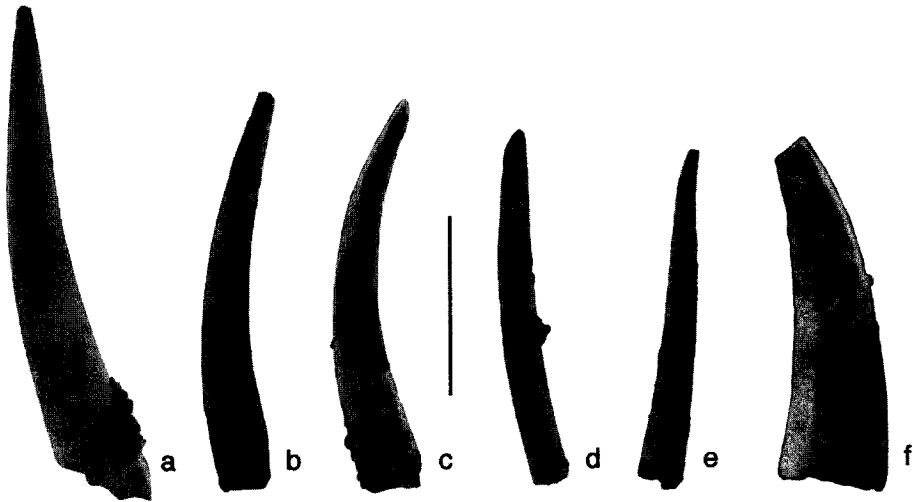


Figure 1a–f. Isolated pterosaurian teeth from the Lower Cretaceous (?Berriasian) of Anoual (Morocco). Scale bar: 3 mm (photos 1a–e: provisional specimen numbers SA 100–104) and 5.5 mm (photo 1f: provisional specimen number SA 105).

Figure 1a–f. Dents isolées de ptérosaures du Crétacé inférieur (Berriasien ?) d'Anoual (Maroc). Barre d'échelle : 3 mm (photos 1a–e : numérotation provisoire des spécimens SA 100–104) et 5.5 mm (photo 1f : numérotation provisoire du spécimen SA 105).

DESCRIPTION

Pterosaurs from Anoual are represented by nearly 300 complete or fragmentary teeth housed in the collections of the Laboratoire de paléontologie, Muséum national d'histoire naturelle (Paris). They are generally relatively well preserved despite their fragility. According to their morphology, they can be assigned to two categories.

Most of the pterosaurian teeth from this site (*figures 1a–e*) are very slender and elongated with a marked curvature. Two 'changes of curvature' are even visible along the most tapered teeth, giving a subtle sigmoid shape to them (*figure 1e*). Distal to the smooth base of the teeth, the enamel in most specimens is finely longitudinally grooved toward the apex.

The second category is represented by rare, generally somewhat stronger and smoother teeth (*figure 1f*). They are more or less oval in cross-section at the base, with one (or two) carina(e).

COMPARISONS

The teeth of the most common type are quite close to those of some non-pterosaurian taxa such as, for instance, teleosaurid crocodiles (see e.g. [9], pl. 11). But this is only a morphological resemblance: pterosaur teeth are characterised by a peculiar enamel pattern [44, 45] (Frey, pers. comm., 1999); they only have an enamel cap and lack enamel at the basal part of the crown, while in crocodiles the whole crown is coated with enamel.

These teeth have been suggested by K. Padian [32, 33] to be reminiscent of those of ‘rhamphorynchoid’ pterosaurs. This would be an interesting discovery as the long-tailed ‘rhamphorynchoid’ pterosaurs are known otherwise only from strata of Triassic and Jurassic ages [43]. The ‘Rhamphorhynchoidea’ have been considered as the group from which the Pterodactyloidea derived and are supposed to represent a paraphyletic group [12, 16, 26, 36, 37]. The type genus of the family Rhamphorhynchidae, *Rhamphorhynchus*, has teeth that look like those from Anoual, although they are smooth and oval in section. Moreover, in *Rhamphorhynchus*, there is a coating of enamel, along both carinae, toward the base of the teeth [41]. Therefore the small Anoual teeth do not appear to be referable to ‘rhamphorynchoid’ pterosaurs.

They are most reminiscent of those of the pterodactyloid pterosaurs *Ctenochasma* and *Gnathosaurus* (‘Ctenochasmatidae’) [40, 43]. According to the results of the phylogenetic analysis of Jouve [15], *Ctenochasma* and *Gnathosaurus* can now be ranked among the Pterodactylidae, the definition of which would be: *Pterodactylus antiquus*, *Ctenochasma elegans*, their most recent common ancestor and all descendants (node-based taxon). They have indeed a long and thin shape and show a circular or sub-circular cross-section. This holds especially true for the teeth in figures 1d and 1e. This is not so obvious for the teeth in figures 1b and 1c but still they can be referred to the same tooth type. The tooth in figure 1a, which tapers relatively strongly, may look more like an ornithocheirid tooth (Unwin, pers. comm., 2000) but it has not such a compressed shape with distinct labial and lingual surfaces: it is rather nearly circular in cross-section. The teeth of the *Ctenochasma* specimen studied by Taquet [35] and Jouve [15] are smooth (pers. obs.). Moreover, the teeth of this genus only taper at or near the tip. The Anoual specimens may be morphologically closer to the teeth of *Gnathosaurus*. These are indeed somewhat larger, more robust (i.e. not so ‘needle-like’), than those of *Ctenochasma*; likewise, the teeth of Gnathosaurinae tend to taper from base to tip. Thus, the teeth of the first type from Anoual are tentatively assigned here to the Gnathosaurinae (*sensu* Unwin, pers. comm., 2000, see below), though it seems unlikely that they can be assigned to a particular genus. It has to be noticed that slender, recurved pterosaur teeth from the Purbeck Limestone Formation (Tithonian-Berriasian) at first identified as those of small ‘rhamphorynchoid’ pterosaurs [8] were subsequently interpreted as teeth possi-

bly referable to 'ctenochasmatid' pterodactyloids such as *Gnathosaurus* and *Plataleorhynchus* [13].

The most robust pterosaurian teeth from Anoual (*figure 1f*) seem to be relatively too robust to be gnathosaurine, and may well be ornithocheirid even if a determination to genus level cannot be achieved for the available material. The principal genera of the Ornithocheiridae are *Ornithocheirus*, *Coloborhynchus* and *Anhanguera* [1]. They show some variations in the dentition type but all of them possessed relatively powerful teeth (cf. e. g. [24], pl. 57: figure 6). Teeth of this kind have been previously described from Morocco (Early Cenomanian; e. g. [46]). Compared with the latter, the tooth of *figure 1f* is more particularly reminiscent of the morphotype I of Wellnhofer and Buffetaut ([46], figure 6), namely by its degree of curvature and the carina developed at the caudal edge only. The teeth of *Anhanguera* [42, 44] have caudal and rostral carinae. Likewise, strong ridges mark their labial surface. This latter character is lacking in *Ornithocheirus* and *Coloborhynchus*; the tooth of *figure 1f* thus refers possibly to a taxon closer to these genera than to *Anhanguera*.

DISCUSSION

According to Unwin (pers. comm., 2000), the subfamily Gnathosaurinae is composed of *Gnathosaurus* [23], *Plataleorhynchus* [13], *Huanhepterus* [5] and *Cearadactylus* [20]. The age of the formations of the Zhidan group of China, from where *Huanhepterus* comes, are not precisely known but are now assigned to the Early Cretaceous [6]. *Gnathosaurus* is known from the Tithonian-?Berriasian of Europe [13, 40] whereas *Plataleorhynchus* is restricted so far to the Late Tithonian or Early Berriasian of the British Isles [13]. *Cearadactylus* is known from the Brazilian Aptian [39] but its phylogenetic position is at present controversial [2]. Thus, the attribution of a Berriasian age to the Lower Cretaceous Moroccan microvertebrate locality of Anoual is consistent with the presence of Gnathosaurinae possibly close to *Gnathosaurus*. On the other hand, confirmation of this age would emphasise the extension of the Gnathosaurinae biochron into the Lower Cretaceous.

CONCLUSION

The pterosaurs from the Lower Cretaceous microvertebrate assemblages of Anoual are represented by isolated teeth. On a morphological basis, they can be distributed into two major groups.

The rarer and more robust teeth are reminiscent of the Ornithocheiridae but an accurate identification cannot be made on such a poor material. The most numerous teeth are elongate and quite similar to those of some Gnathosaurinae such as *Gnathosaurus*. If this attribution is confirmed, the Anoual fauna will have to be considered as containing some of the rare (maybe unique) Cretaceous Gnathosaurinae, which could then well be the latest known representatives of the subfamily while being the first discovery of African Gnathosaurinae. The nature of the pterosaurian material from Anoual might be consistent with a Berriasian age while not constituting a supporting element or confirmation for it.

Acknowledgements — D. Sigogneau-Russell (Muséum national d'histoire naturelle, Paris) entrusted the Anoual pterosaurian material to the author and kindly improved the manuscript as did E. Frey (Staatliches Museum für Naturkunde, Karlsruhe). The comments of the referee, D.M. Unwin (Museum für Naturkunde, Berlin), were of considerable help; he kindly sent me a copy of part of one of his papers, then in press [39]. C. Weber-Chancogne, D. Serrette, and H. Lavina (Muséum national d'histoire naturelle, Paris) produced the excellent SEM photographs (*figures 1a–e*), the other picture (*figure 1f*), and arranged the illustrations in *figure 1* respectively. The work of the author is supported by a grant from the Chancellerie des universités de Paris.

REFERENCES

- [1] Bakhurina N.N., Unwin D.M., A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia, *Hist. Biol.* 10 (1995) 197–245.
- [2] Benton M.J., Reptilia, in: Benton M.J. (Ed.), *The Fossil Record 2*, Chapman & Hall, London, 1993, pp. 681–715.
- [3] Benton M.J., Bouaziz S., Buffetaut E., Martill D., Ouaja M., Soussi M., Trueman C., Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 157 (2000) 227–246.
- [4] Broschinski A., Sigogneau-Russell D., Remarkable lizard remains from the Lower Cretaceous of Anoual (Morocco), *Ann. Paléontol.* 82 (1996) 147–175.
- [5] Dong Z., [On a new Pterosauria (*Huanhepterus quingyangensis* gen. and sp. nov.) from Ordos, China], *Vert. Pal. Asiat.* 20 (1982) 115–121.
- [6] Dong Z., *Dinosaurian faunas of China*, China Ocean Press, Beijing, 1992.
- [7] Duffin C.J., Sigogneau-Russell D., Fossil shark teeth from the early Cretaceous of Anoual, Morocco, *Belgian Geol. Surv. Prof. Pap.* 264 (1993) 175–190.
- [8] Ensom P.C., Evans S.E., Milner A.R., Amphibians and reptiles from the Purbeck Limestone Formation (Upper Jurassic) of Dorset, in: *5th Symposium on Mesozoic Terrestrial Ecosystems and Biota, Extended Abstracts*, 1991, pp. 19–20.
- [9] Eudes-Deslongchamps J.-A., Note sur trois espèces de Téléosauriens du Calcaire de Caen, se rapprochant du premier type créé par Geoffroy-Saint-Hilaire, sous le nom de *Teleosaurus cadomensis*, *Bull. Soc. Linn. Normandie 2^e sér.* 1 (1866) 326–353.

- [10] Evans S.E., Sigogneau-Russell D., New sphenodontians (Diapsida: Lepidosauromorpha: Rhynchocephalia) from the Early Cretaceous of North Africa, *J. Vert. Paleontol.* 17 (1997) 45–51.
- [11] Galton P.M., Avian-like tibiotarsi of the pterodactyloids (Reptilia: Pterosauria) from the Upper Jurassic of East Africa, *Paläontol. Zeit.* 54 (1980) 331–342.
- [12] Howse S.C.B., On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria), *Zool. J. Linn. Soc.* 88 (1986) 307–328.
- [13] Howse S.C.B., Milner A.R., The pterodactyloids from the Purbeck Limestone Formation of Dorset, *Bull. Nat. Hist. Mus. (Geol. Ser.)* 51 (1995) 73–88.
- [14] Janensch W., Die Gliederung der Tendaguru-Schichten im Tendaguru-Gebiet und die Entstehung der Saurier-Lagerstätten, *Arch. Biontol.* 3 (1914) 227–261.
- [15] Jouve S., Un crâne de *Ctenochasma* (Archosauria, Pterosauria) de l'Est de la France, suivi de commentaires sur l'ontogénie des Ctenochasmatoidea et d'une analyse phylogénétique des Pterodactyloidea, DEA, Muséum national d'histoire naturelle, 2000 (unpublished).
- [16] Kellner A.W.A., The relationships of the Tapejaridae (Pterodactyloidea) with comments on pterosaur phylogeny, in: 6th Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short papers, 1995, pp. 73–77.
- [17] Kellner A.W.A., Mader B.J., First report of Pterosauria (Pterodactyloidea, Azhdarchidae) from Cretaceous rocks of Morocco, *J. Vert. Paleontol.* 16 (1996) 45A.
- [18] Kellner A.W.A., Mader B.J., Archosaur teeth from the Cretaceous of Morocco, *J. Paleontol.* 71 (1997) 525–527.
- [19] Le Loeuff J., Buffetaut E., Cuny G., Laurent Y., Ouaja M., Souillat C., Srarfi D., Tong H., Mesozoic continental vertebrates of Tunisia, in: 5th European Workshop on Vertebrate Palaeontology, Abstracts, 2000, p. 45.
- [20] Leonardi G., Borgomanero G., *Cearadactylus atrox* nov. gen., nov. sp.: novo Pterosauria (Pterodactyloidea) da Chapada do Araripe, Ceará, Brasil, *Col. trab. Paleontol. Sér. Geol.* 27 (1985) 75–80.
- [21] Mader B.J., Kellner A.W.A., First occurrence of Anhangueridae (Pterosauria, Pterodactyloidea) in Africa, *J. Vert. Paleontol.* 17 (1997) 62A.
- [22] Mader B.J., Kellner A.W.A., A new Anhanguerid pterosaur from the Cretaceous of Morocco, *Bol. Mus. Nac. Geol.* 45 (1999) 1–11.
- [23] Meyer H. von, *Gnathosaurus subulatus*, ein Saurus aus dem lithographischen Schiefer von Solnhofen, *Mus. Senckenb.* 1 (1834) 3.
- [24] Milner A.C., Reptiles, in: Smith A.B. (Ed.), *Fossils of the chalk*, The palaeontological Association, London, 1987, pp. 266–280.
- [25] Montillet J., Lappartient J.R., Taquet P., Un Ptérosaurien géant dans le Crétacé supérieur de Paki (Sénégal), *C. R. Acad. Sci. Paris sér. II* 295 (1982) 409–414.
- [26] Padian K., Rayner J.M.V., The wings of pterosaurs, *Am. J. Sci.* 293-A (1993) 91–166.
- [27] Parkinson J., *The dinosaur in East Africa*, H.F. & G. Witherby, London, 1930.
- [28] Reck H., Die deutschostafrikanischen Flugsaurier, *Centralbl. Mineral. Geol. Paläontol.* (1931) 321–336.

- [29] Richter A., Lacertilia aus der Unteren Kreide von Üna und Galve (Spanien) und Anoual (Marokko), Berliner geowiss. Abh. 14 (1994) 1-147.
- [30] Sereno P.C., Beck A.L., Dutheil D.B., Gado B., Larsson H.C.E., Lyon G.H., Marcot J.D., Rauhut O.W.M., Sadleir R.W., Sidor C.A., Varricchio D.D., Wilson G.P., Wilson J.A., A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids, *Science* 282 (1998) 1217–1372.
- [31] Sigogneau-Russell D., Découverte de mammifères dans le Mésozoïque moyen d’Afrique, *C.R. Acad. Sci. sér. II* 307 (1988) 1045–1050.
- [32] Sigogneau-Russell D., Evans S.E., Levine J.F., Russell D.A., The Early Cretaceous microvertebrate locality of Anoual, Morocco: a glimpse at the small vertebrate assemblages of Africa, *New Mexico Mus. Nat. Hist. Sci. Bull.* 14 (1998) 177–181.
- [33] Sigogneau-Russell D., Monbaron M., De Kacnel E., Nouvelles données sur le gisement à mammifères mésozoïques du Haut-Atlas marocain, *Geobios* 23 (1990) 461–483.
- [34] Swinton W.E., A Cretaceous pterosaur from the Belgian Congo, *Bull. Soc. Belge Géol. Paléontol. Hydrol.* 77 (1948) 234–238.
- [35] Taquet P., Un crâne de *Ctenochasma* (Pterodactyloidea) du Portlandien inférieur de la Haute-Marne, dans les collections du Musée de Saint-Dizier, *C.R. Acad. Sci. Paris sér. D* 274 (1972) 362–364.
- [36] Unwin D.M., The phylogeny of the Pterosauria, *J. Vert. Paleontol.* 12 (1992) 57A.
- [37] Unwin D.M., Preliminary results of a phylogenetic analysis of the Pterosauria (Diapsida: Archosauria), in: 6th Symposium on Mesozoic Terrestrial Ecosystems and Biota. Short papers, 1995, pp. 69–72.
- [38] Unwin D.M., Heinrich W.D., On a pterosaur jaw from the Upper Jurassic of Tendaguru (Tanzania), *Mitt. Mus. Nat.kd. Berl., Geowiss. Reihe* 2 (1999) 121–134.
- [39] Unwin D.M., Lü J., Bakhurina N.N., On the systematic and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China, *Mitt. Mus. Nat.kd. Berl., Geowiss. Reihe* 3 (2000) in press.
- [40] Wellnhofer P., Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands, *Abh. Bayer. Akad. Wiss. Math.-naturwiss. Kl. N.F.* 141 (1970) 1–133.
- [41] Wellnhofer P., Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands, I: Allgemeine Skelettmorphologie, *Palaeontographica A* 149 (1975) 1–33.
- [42] Wellnhofer P., Neue Pterosaurier aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien, *Palaeontographica A* 187 (1985) 105–182.
- [43] Wellnhofer P., *The illustrated Encyclopedia of Pterosaurs*, Salamander Books, London, 1991.
- [44] Wellnhofer P., Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien, *Palaeontographica A* 215 (1991) 43–101.
- [45] Wellnhofer P., *The illustrated Encyclopedia of Prehistoric Flying Reptiles*, Barnes & Noble, New York, 1996.
- [46] Wellnhofer P., Buffetaut E., Pterosaur remains from the Cretaceous of Morocco, *Paläontol. Zeit.* 73 (1999) 133–142.