

RAPID COMMUNICATION

The pterosaurian remains from the Grünbach Formation
(Campanian, Gosau Group) of Austria: a reappraisal
of ‘*Ornithocheirus buenzeli*’

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Abstract

The fragmentary pterosaur material from the Campanian Grünbach Formation (Gosau Group) of Muthmannsdorf (Austria), previously identified as *Ornithocheirus buenzeli* Bunzel, 1871, is revised. A lower jaw fragment shows a helical type of articulation, which is known in several families of pterosaurs, and cannot be identified with great accuracy. The proximal part of a humerus shows distinctive features that allow it to be referred to as a member of the family Azhdarchidae, which is widespread in the Late Cretaceous Period of Europe. *Ornithocheirus buenzeli* is considered a *nomen dubium*. The pterosaur material from the Grünbach Formation cannot be used as evidence for the presence of ornithocheirids in the Late Cretaceous of Europe.

Keywords: Cretaceous, Austria, Pterosauria, Azhdarchidae.

1. Introduction

A diverse vertebrate assemblage has been known from the Upper Cretaceous Gosau beds of Muthmannsdorf (Lower Austria) since the 19th century. A first description of this assemblage was provided by Bunzel (1871), followed by a thorough revision by Seeley (1881) and a short discussion by Nopcsa (1926). Since then, reappraisals of various elements of this fauna have been published by several authors (choristoderes: Buffetaut, 1989; crocodylians: Buffetaut, 1979; ankylosaurs: Pereda-Suberbiola & Galton, 2001; ornithopods: Sachs & Hornung, 2006). The occurrence of pterosaur remains in the Muthmannsdorf assemblage was first noted by Seeley (1881), who mentioned crushed phalangeal fragments, the proximal portion of a humerus and the articular region of a lower jaw. The latter specimen had been figured and described by Bunzel (1871) as *Lacerta* sp. Seeley (1881) erected the species *Ornithocheirus Bünzeli* for this material. Since then, the pterosaur material from Muthmannsdorf has been mentioned in various papers dealing with the whole assemblage (Nopcsa, 1926), or with pterosaurs in general (Wellnhofer, 1978, 1980a, 1991), and redescribed in detail by Wellnhofer (1980b). Following

Seeley's original suggestion, *Ornithocheirus buenzeli* has usually been placed in the family Ornithocheiridae. In the light of present knowledge of Cretaceous pterosaurs, however, this attribution is questionable, as shown in the present paper, which is based on a re-examination of the original material kept at the Palaeontological Institute of the University of Vienna.

Institutional abbreviations: UWPI – Paläontologisches Institut der Universität Wien; SMNK – Staatliches Museum für Naturkunde Karlsruhe.

2. Geographical and geological setting

As noted by Bunzel (1871), the first vertebrate element discovered in the coal-bearing beds at Muthmannsdorf, west of Wiener Neustadt (Lower Austria), was a dinosaur tooth found by Ferdinand Stoliczka in 1859, during an excursion led by Eduard Suess. Subsequently, 'Prof. Suess was so fortunate as to obtain the assistance of Bergverwalter Pawlowitsch in conducting excavations' in the coal seam, which resulted in the discovery of 'a perfect cemetery of the remains of Cretaceous reptiles' (Seeley, 1881, p. 621).

The vertebrate-bearing beds at Muthmannsdorf, in the eastern part of the Calcareous Alps, belong to the Gosau Group, a succession of Upper Cretaceous to Palaeocene mainly marine sediments (see Summesberger, Machalski & Wagneich, 2007 for a recent synthetic section of the Gosau Group). Although Suess (1881) initially thought they were older than Turonian, it is now clear that the vertebrate-bearing beds are in fact Campanian (Plöschinger, 1961; Thenius, 1974; Summesberger, Machalski & Wagneich, 2007). In current stratigraphic nomenclature (Summesberger *et al.* 2000), they are placed in the Grünbach Formation of the Lower Gosau Subgroup. The Grünbach Formation is referred to the early Campanian on the basis of microfossils (foraminifera, spores and pollen) and of marine fossils in the underlying and overlying formations (see Kvaček & Herman, 2004 for a recent review). The vertebrate fauna from the Grünbach Formation includes chelonians, squamates, choristoderes, crocodylians, dinosaurs (ornithopods, ankylosaurs and theropods) and pterosaurs (Sachs & Hornung, 2006).

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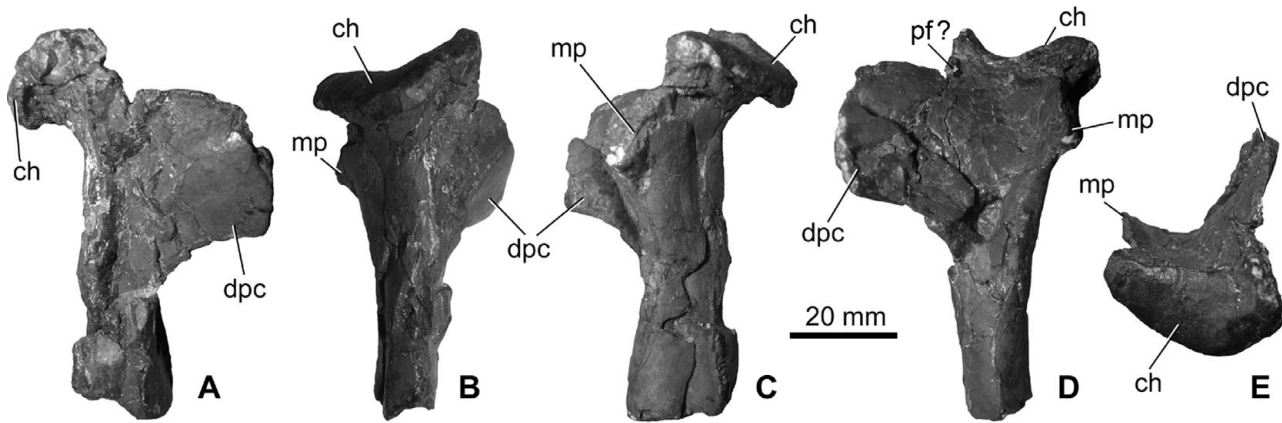


Figure 1. Proximal part of a right azhdarchid humerus (UWPI 2349/102) from the Lower Campanian Grünbach Formation of Muthmannsdorf (eastern Austria). (a) anterior; (b) dorsal; (c) posterior; (d) posteroventral; (e) proximal views. Abbreviations: ch – caput humeri; dpc – deltopectoral crest; mp – medial process; pf? – pneumatic foramen (?).

3. Previous interpretations of the pterosaurian material from Muthmannsdorf

As noted by Seeley (1881) and Wellnhofer (1980*b*), the pterosaur material from Muthmannsdorf consists of fragmentary phalanges (which are too incomplete to be of any systematic use), the proximal part of a humerus and the left articular region of a lower jaw.

Seeley, who consistently misspelled Bunzel's name as 'Bünzel', used the name *Ornithocheirus Bünzeli* for this material (and was followed in this by Sauvage, 1882 and Newton, 1888); according to the current rules of zoological nomenclature, the specific name should therefore be *buenzeli*. Wellnhofer (1978, 1980*b*) suggested that it should be emended to *Ornithocheirus bunzeli*, but, as remarked by Sachs and Hornung (2006), this emendation is not acceptable under the ICZN. Wellnhofer (1980*b*) also indicated that the name proposed by Seeley (1881, p. 701) only applies to the lower jaw fragment, presumably because Seeley considered it as 'the only specimen of importance' and specifically referred to the illustration provided by Bunzel (Bunzel, 1871, pl. VI, figs 6, 7).

Seeley did not clearly explain why the pterosaur material from Muthmannsdorf was referred to the genus *Ornithocheirus*, and only mentioned that 'this jaw seems to be well distinguished from the species already described' (Seeley, 1881, p. 701). Nopcsa (1926) merely confirmed the identification of the specimen as pterosaurian. Wellnhofer referred to the jaw fragment as '*Ornithocheirus bunzeli* and placed it in the *Ornithocheiridae incertae sedis* (Wellnhofer, 1978) or '*Ornithocheiridae von unsicherer systematischer Stellung*' (Wellnhofer, 1980*a*). In his detailed revision of the material from Muthmannsdorf, Wellnhofer (1980*b*, p. 102) referred to the jaw fragment as *Ornithocheirus bunzeli* and to the humerus as *Ornithocheirus* sp., but remarked that the genus *Ornithocheirus* is poorly characterized and concluded that 'aufgrund der oben gegebenen Charakterisierung ist eine eindeutige Zuordnung der vorliegenden Pterosaurierreste aus der Gosau zur Gattung *Ornithocheirus* nicht möglich' ('on the basis of the characters given above, an unequivocal attribution of these pterosaur remains from the Gosau to the genus *Ornithocheirus* is not possible'). Nevertheless, Wellnhofer (1991, p. 116) referred to the jaw fragment from Muthmannsdorf as *Ornithocheirus bunzeli* and to the humerus as *Ornithocheirus*. Jianu, Weishampel & Şticuă (1997) noted that the humerus did not appear to belong to a pteranodontid, because it lacks a warped deltopectoral crest and a caudally directed ulnar crest, and considered that it

may be a member of the Nyctosauridae on the basis of a supposedly hatchet-shaped deltopectoral crest.

Buffetaut (2008, p. 254) briefly mentioned the pterosaur material from Muthmannsdorf and noted that 'the shape of the proximal articular area and deltopectoral crest of the humerus from Muthmannsdorf would certainly not preclude an attribution to the Azhdarchidae'.

In our revision of the pterosaur material from Muthmannsdorf, we have considered the humerus and the jaw fragment separately. They are unlikely to be from the same individual, as the jaw fragment seems to be from a larger animal than the humerus. As noted by Seeley (1881) and Wellnhofer (1980*b*), the phalanx fragments are too incomplete to be identified beyond Pterosauria and are not discussed here. Photographs of the humerus and jaw fragment are published here for the first time (Figs 1, 2); for excellent drawings of this material, see Wellnhofer (1980*b*).

4. The humerus

Contrary to Seeley's opinion, who thought that the humerus (UWPI 2349/102) was 'of no importance' to the anatomist (Seeley, 1881, p. 701), this specimen (Fig. 1), although it has undergone crushing and lacks the distal part, shows a number of characters that allow a relatively precise systematic assignment to the family level. Despite some deformation, the spatial arrangement of the caput humeri and deltopectoral crest is well preserved, as already noted by Wellnhofer (1980*b*). In proximal view the caput humeri is regularly rounded, with a roughly oval outline. Ventrally, the articular surface is clearly separated from the more distal part of the bone by a well-marked step-like sulcus. Dorsally, the edge of the articular surface strongly overhangs the shaft; although this has probably been exaggerated by compression, it is a characteristic feature of the proximal articular region. The deltopectoral crest lacks its tip, but its insertion on the shaft is well preserved and shows that it is broad and unwarped. More distally, it is gently curved, with more or less parallel sides, and there is no indication that it was 'hatchet-shaped' as in nyctosaurids, contrary to the claim of Jianu, Weishampel & Şticuă (1997), which may have been based on Wellnhofer's (1980*b*) reconstruction that showed a hypothetical slightly expanded tip of the deltopectoral crest. The specimen actually does not support this interpretation and rather suggests that the tip of the crest had a rounded outline. The medial process is incomplete, but it can be seen that it was at right angles to the deltopectoral crest in proximal view. Although this

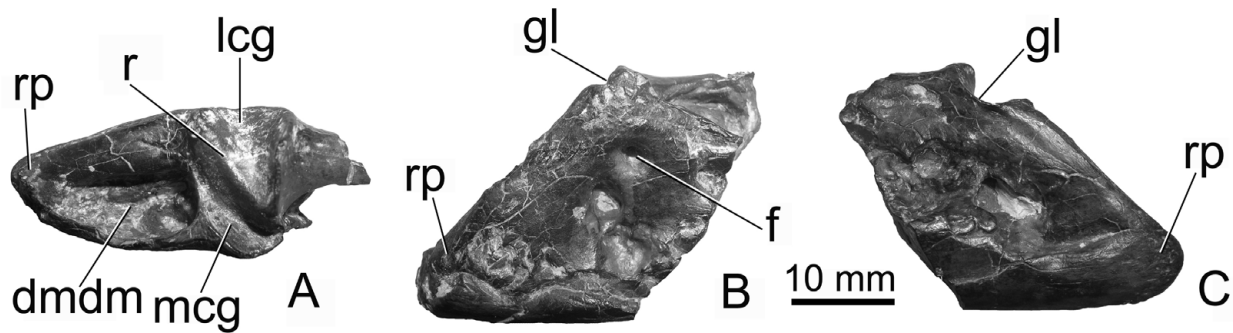


Figure 2. Pterodactyloidea indet. distal lower jaw fragment (UWPI 2349/101) from the Lower Campanian Grünbach Formation of Muthmannsdorf (eastern Austria). (a) dorsal; (b) medial; (c) lateral views. Abbreviations: dmdm – depression for musculus depressor mandibulae; f – foramen; gl – glenoid; lcg – lateral cotyle of the glenoid; mcg – medial cotyle of the glenoid; r – ridge; rp – retroarticular process.

whole area is poorly preserved, what is possibly a pneumatic foramen can be seen on the ventral surface of the bone, between the caput humeri and the proximal inception of the deltopectoral crest. Although a pneumatic foramen in such a position is frequently considered an azhdarchoid feature (Unwin, 2003; Witton, Martill & Green, 2009), inter- as well as intraspecific variability in pneumatic features is a well-known phenomenon among birds (O'Connor, 2004) and has also been reported in *Rhamphorhynchus* (Ösi & Prondvai, 2009), so the significance of this character should perhaps not be overestimated.

As already noted by Wellnhofer (1980b), the humerus from Muthmannsdorf is clearly different from those of *Pteranodon* and *Nyctosaurus*. The deltopectoral crest of *Nyctosaurus* (and other nyctosaurids, Frey *et al.* 2006) shows a characteristic hatchet-like shape, viz. it has concave proximal and distal margins (Williston, 1903; Price, 1953), of which there is no indication in the Austrian specimen. In *Pteranodon*, the deltopectoral crest is notably warped (Bennett, 2001), unlike that of the Muthmannsdorf humerus. A warped deltopectoral crest is an ornithocheiroid character (Unwin, 2003). The unwarped crest of the Muthmannsdorf specimen thus shows that it cannot be placed among the ornithocheiroids. Wellnhofer (1980b) noted similarities between the specimen from Muthmannsdorf and a humerus from the Cambridge Greensand described and illustrated by Owen (1859, pl. 3, figs 14, 15). Contrary to Wellnhofer's (1980b) statement, Owen did not refer to this bone as *Ornithocheirus* sp. (in 1859, the name *Ornithocheirus* had not yet been erected by Seeley, 1869). Although Seeley later referred much (Seeley, 1869) and then practically all (Seeley, 1870) of the pterosaur material from the Cambridge Greensand to *Ornithocheirus*, a recent revision (Unwin, 2001) has shown that the pterosaur assemblage from the Cambridge Greensand is in fact much more diverse than previously recognized, and that taxa other than ornithocheirids (such as lonchodectids and pteranodontids) also occur. Although not mentioned by Unwin (2001), azhdarchids may be present in the Cambridge Greensand (E. Buffetaut, unpub. data). To judge from the unwarped deltopectoral crest shown on Owen's figure, the humerus from the Cambridge Greensand mentioned by Wellnhofer, which does resemble the specimen from Austria, certainly does not belong to an ornithocheirid.

The characters visible on the humerus from Muthmannsdorf are strongly reminiscent of those of azhdarchid humeri. Features in common include the unwarped deltopectoral crest and the thick, oval caput humeri, which overhangs the dorsal side of the shaft and is separated from its ventral side by a well-marked step-like sulcus. Although the

unwarped crest appears to be the plesiomorphic condition in pterosaurs, the general morphology of the proximal part of the humerus in azhdarchids, including the caput humeri, the deltopectoral crest and the medial process, seems to be characteristic of that group of pterosaurs. It has been described or illustrated in *Quetzalcoatlus* from the Maastrichtian of Texas (Lawson, 1975), *Hatzegopteryx thambema* from the Maastrichtian of Romania (Buffetaut, Grigorescu & Csiki, 2003), two azhdarchids from the Late Cretaceous of Montana (an unnamed large form, Padian & Smith, 1992; and *Montanazhdarcho minor*, McGowen *et al.* 2002), an azhdarchid from the Campanian of Alberta (Godfrey & Currie, 2005) and an azhdarchid from the Late Cretaceous of Provence (Buffetaut, Mechin & Mechin-Salessy, 2006). On the basis of these similarities, it seems reasonable to refer the humerus from Muthmannsdorf to the Azhdarchidae. An attribution to the Tapejaridae, which are often considered as the sister-group of Azhdarchoidea, although different interpretations have also been put forward (e.g. Witton, Martill & Green, 2009), could also be envisioned. Few details have been published about the morphology of the humerus in tapejarids, although Kellner (2004) noted that the medial process is massive. According to Lü & Yuan (2005), in *Huaxiapterus jii*, the deltopectoral crest is elongate with a long axis roughly perpendicular to the long axis of the shaft, a rounded extremity and more or less parallel margins; in these respects, the humerus is similar to that of azhdarchids. Our observations on tapejarid humeri, including a specimen identified as *Tapejara wellnhoferi* (SMNK – PAL 1137) and one belonging to an indeterminate tapejarid (SMNK – PAL 3856 (2./4)), show that the proximal part is indeed very similar to that of azhdarchids, notably in the shape and orientation of the deltopectoral crest. However, some differences can be seen in the morphology of the caput humeri, which in tapejarids is less expanded dorsoventrally, less prominent dorsally and not separated by a distinct step-like sulcus from the ventral surface of the bone. In these respects, the specimen from Muthmannsdorf is more reminiscent of azhdarchids than of tapejarids.

Comparison with the humeri of thalassodromids and chaoyangopterids, which have also been considered as closely related to azhdarchids (Witton, Martill & Green, 2009), is difficult because the humeri of these pterosaurs have not been described in great detail: most known chaoyangopterid specimens, from the Early Cretaceous of China, are crushed (Witton, Martill & Green, 2009). In the chaoyangopterid *Shenzhoupterus chaoyangensis*, the deltopectoral crest is described as markedly elongate, with a rounded distal termination (Lü *et al.* 2008), which suggests some similarity with azhdarchids and tapejarids.

The humerus of the thalassodromid *Tupuxuara*, as figured by Unwin (2003) and Witton, Martill & Green (2009), bears a deltopectoral crest that is less displaced distally, and a caput humeri that seems to be less ventrodorsally expanded, than in the Muthmannsdorf specimen, and in azhdarchids generally. Similarly, the 'Wessex humerus' from the Early Cretaceous of England, considered as belonging to a thalassodromid or a chaoyangopterid (Witton, Martill & Green, 2009), shows a less distally displaced deltopectoral crest and a less expanded caput humeri than azhdarchids and the Muthmannsdorf humerus. In these respects, the Austrian specimen appears to be closer to azhdarchids than to thalassodromids and chaoyangopterids.

It should also be mentioned that tapejarids, thalassodromids and chaoyangopterids have so far not been reported from the Late Cretaceous of Europe, whereas azhdarchids are known from many European localities of that age (in France, Spain, Hungary, Romania and Russia; see Barrett *et al.* 2008).

5. The jaw fragment

The left articular region of a pterosaur jaw (UWPI 2349/101) from Muthmannsdorf, originally described as *Lacerta* by Bunzel (1871), and then as *Ornithocheirus Bünzeli* by Seeley (1881), was redescribed in great detail by Wellnhofer (1980b), who interpreted it in functional terms. There is no need to provide here one more detailed description of this well preserved, although incomplete, specimen (Fig. 2). Instead, we shall focus on its distinctive characters, which may provide evidence concerning its systematic position. As noted by Wellnhofer (1980b), one of the important features of the specimen is the shape of the fossa articularis mandibulae, which is divided into two cotyles by an oblique ridge extending in a posterolateral to anteromedial direction. This peculiar structure has implications for the opening of the jaws and has been interpreted as resulting in a wide gape (Wellnhofer, 1980b, but see Bennett, 2001 for a different interpretation). Its systematic significance is even more uncertain, because this oblique ridge is found in various, not closely related groups of pterosaurs. Wellnhofer (1980b) noted that it is present in *Pteranodon* (see also Bennett, 2001) and reported it in a jaw fragment referred to *Ornithocheirus* from the Cambridge Greensand (see also Wellnhofer, 1985 for a description of a helical jaw joint in an ornithocheirid from Brazil). However, this type of 'helical' jaw joint is also known in *Quetzalcoatlus* (Kellner & Langston, 1996). In *Hatzegopteryx thambema*, from the Maastrichtian of Transylvania, the articular is not known, but the quadrate articulation shows two condyles separated by an oblique groove (Buffetaut, Grigorescu & Csiki, 2003), which indicates that the fossa articularis mandibulae must have been similar in structure to that of *Quetzalcoatlus*. Williston (1902) described a similar condition in *Nyctosaurus*. Since the helical jaw joint occurs in pteranodontids, ornithocheirids, nyctosaurids and azhdarchids, and in fact appears to be rather common in pterosaurs (Wellnhofer, 1985), its systematic significance is limited. Moreover, not all azhdarchids show this type of articulation. In *Bakonydraco galaczi*, from the Santonian of Hungary, the morphology of the fossa articularis mandibulae is different from that of the Muthmannsdorf specimen. In the Hungarian form, the glenoid fossa is mediolaterally enlarged and S-shaped but is not separated into lateral and medial cotyles (Ösi, Weishampel & Jianu, 2005), so the helical type of jaw articulation is not as developed as in *Quetzalcoatlus* and the Austrian specimen. An additional difference is that in *Bakonydraco galaczi*, the fossa depressoria, on the dorsal side of the retroarticular process, is not as elongate and deep as that of the fragment

from Muthmannsdorf (as described by Wellnhofer, 1980b). It thus appears that the jaw mechanics of the Hungarian and Austrian forms were different.

In conclusion, the morphology of the jaw articulation in the Muthmannsdorf specimen does not preclude its inclusion in the Azhdarchidae, nor does it demonstrate it. Other groups of pterosaurs, such as pteranodontids and nyctosaurids, show a similar kind of jaw articulation, and some azhdarchids, such as *Bakonydraco*, do not exhibit it.

6. Conclusions

Contrary to what other authors may have thought, among the pterosaur remains from Muthmannsdorf, the jaw fragment turns out to be less significant from a systematic point of view than the humerus. The helical type of jaw joint is known in various, not closely related groups of pterosaurs, notably pteranodontids, nyctosaurids and azhdarchids, so that no precise systematic assignment is possible on the basis of this character alone. Conversely, the morphology of the proximal part of the humerus can be used to distinguish various groups of pterosaurs (Bennett, 1989). The unwarped deltopectoral crest of the humerus from Muthmannsdorf shows that it cannot belong to an ornithocheirid, and the general morphology of the proximal region of the bone supports an attribution to the Azhdarchidae.

The validity of the taxon *Ornithocheirus buenzeli* is worth a brief discussion. Although Wellnhofer (1980b) claimed that this name should be used only for the jaw fragment, Seeley (1881) did not designate a holotype. As shown above, the humerus cannot be referred to the genus *Ornithocheirus*. As to the jaw fragment, its systematic position is uncertain and its fragmentary nature makes it insufficient for the erection of a distinct taxon. We therefore consider *Ornithocheirus buenzeli* as a *nomen dubium*.

This reappraisal of the pterosaur material from Muthmannsdorf raises the question of the persistence of ornithocheirids until the later stages of the Late Cretaceous in Europe. Buffetaut (2008) noted that the French pterosaur record suggests a replacement of ornithocheirid-dominated assemblages by azhdarchid-dominated assemblages during Late Cretaceous time. This probably applies to Europe as a whole, but the timing and mode of this replacement remain largely obscure because of insufficient fossil evidence for a large part of the Late Cretaceous Period. Whether ornithocheirids were still present in the Campanian–Maastrichtian of Europe is highly uncertain, and the pterosaur material from the Grünbach Formation cannot be used as evidence for their occurrence during this time interval.

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