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On two pterosaur humeri from the Tendaguru beds (Upper Jurassic, Tanzania)

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ABSTRACT

Jurassic African pterosaur remains are exceptionally rare and only known from the Tendaguru deposits, Upper Jurassic Tanzania. Here we describe two right humeri of Tendaguru pterosaurs from the Humboldt University of Berlin specimens MB.R. 2828 (cast MN 6661-V) and MB.R. 2833 (cast MN 6666-V). MB.R. 2828 consists of a three dimensionally preserved proximal portion. The combination of the morphological features of the deltopectoral crest not observed in other pterosaurs suggests that this specimen belongs to a new dsungaripteroid taxon. MB.R. 2833 is nearly complete, and because of a long and round proximally placed deltopectoral crest it could be referred to the Archaeopterodactyloidea. It is the smallest pterosaur from Africa and one of the smallest flying reptiles ever recorded. These specimens confirm the importance of the Tendaguru deposits for the Jurassic pterosaur record. This potential, however, has to be fully explored with more field work.

Key words: Tendaguru, Tanzania, Africa, Upper Jurassic, Pterosauria.

INTRODUCTION

Africa shows a great potential for pterosaur material due to the extensive outcrops in several areas. However, pterosaur remains have been found only in nine African countries (Kellner et al. 2007) and, prior to 1997, just postcranial material had been reported (Reck 1931, Galton 1980, Mader and Kellner 1999, Wellnhofer and Buffetaut 1999). Recently new deposits were found with associated bones, including a partial wing from Lebanon (Dalla Vecchia et al. 2001) and a sequence of five cervical vertebrae from Morocco (Pereda-Suberbiola et al. 2003). The red beds of Albian Cenomanian age from Morocco and Late Jurassic Tendaguru beds, located approximately 75 km northwest of Lindi, Tanzania (Maier 1997), are the most potential deposits

in providing isolated remains up to now (Kellner 1996, Mader 1997, Wellnhofer and Buffetaut 1999, and Kellner 1999).

Regarding Tendaguru beds, four species were established by the pioneer studies of Reck (1931): “*Rhamphorhynchus*” *tendagurensis* (based on radius and ulna), “*Pterodactylus*” *maximus* (based on a comparatively large ulna), “*Pterodactylus*” *brancai* (based on a tibiotarsus, fibula and the first phalanx of the wing finger), and “*Pterodactylus*” *arningi* (based on the first phalanx of the wing finger). Later, Galton (1993) reviewed the tibiotarsus from “*Pterodactylus*” *brancai* and reclassified it as “*Dsungaripterus brancai*” (Dsungaripteridae). However, all those specimens are fragmentary or incomplete for any determination.



a short section of a mandibular symphysis. Afterward Sayão and Kellner (2001) briefly discussed part of Tendaguru pterosaur collection and mentioned the existence of the two humeri, which are here described in detail. We follow Kellner and Tomida (2000) regarding the orientation of the bones.

GEOLOGICAL SETTING

The deposits of the Tendaguru beds are divided into Lower, Middle and Upper Saurian beds (Janensch 1914). Transitional deposits between the Saurian beds and the marine units were formally recognized as Transitional Sands (*Übergangsschichten*) (Heinrich 1999). Most of pterosaur remains were possibly recovered from the Upper Saurian bed and the Transitional Sand at the base of the Upper Saurian bed (Reck 1931). According to Unwin and Heinrich (1999), pterosaurs are rare in the Middle Saurian bed and absent in the Lower Saurian bed and marine units, but this can be due to collecting bias (Fig. 1).

Although isolated, all known pterosaur elements from those deposits are preserved in three dimensions, albeit some crushing is perceptible.

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Dsungaripteroidea Young, 1964

Dsungaripteroidea indet.

Material: Proximal portion of a right humerus housed at the Naturkundemuseum of the Humboldt University (MB.R. 2828), Berlin; cast at the Museu Nacional/UFRJ (MN 6661-V), Rio de Janeiro.

Description: The specimen MB.R. 2828 (Fig. 2; Table I) has a slightly dorso-ventral compression, showing several fractures. It possesses the characteristic saddle-shaped proximal articular head, common to the pterosaur humeri. The deltopectoral crest is well developed and inclined proximoventrally. It is tongue-shaped with a rounded distal end. In lateral view the proximal mar-

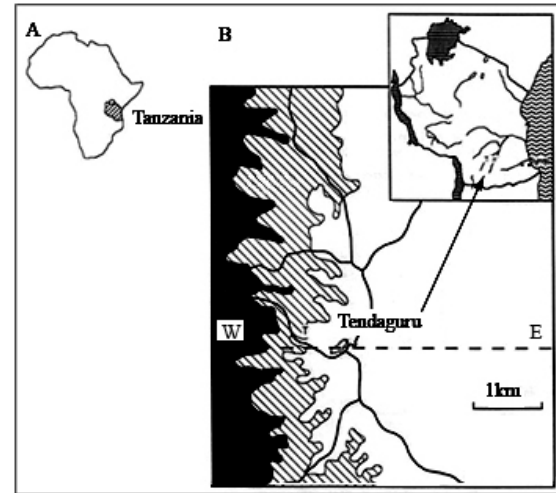


Fig. 1 – Locality map. A. Africa, showing the location of Tanzania. B. Tendaguru site (adapted from Unwin and Heinrich 1999).

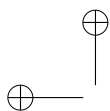
to the proximal edge, and is likely an attachment of a flight muscle (*m. pectoralis*, see Bennett 2003). There is an elongated concavity on the medial side, close to the distal margin, whose function is unknown. The ulnar crest is blunt and slightly crushed laterally. The dorsal margin shows a well developed pneumatic foramen, located close to the lateral side.

Archaeoptero-dactyloidea Kellner, 2001

Archaeoptero-dactyloidea indet.

Material: Complete right humerus housed at the Naturkundemuseum of the Humboldt University (MB.R. 2833), Berlin; cast at the Museu Nacional/UFRJ (MN 6666-V), Rio de Janeiro.

Description: The specimen MB.R. 2833 (Fig. 3; Table II) is nearly complete, lacking only the lateral portion of the ulnar crest. It is quite small (total length of 25.5 mm) but, based on the bone texture and the articulation surface, appears not to represent a very ontogenetically immature animal (Bennett 1993, Kellner and Tomida 2000). It lacks pneumatic foramina both at ventral and dorsal surfaces. The deltopectoral crest is proximally placed with the main axis directed almost perpen-



TWO PTEROSAUR HUMERI FROM TENDAGURU

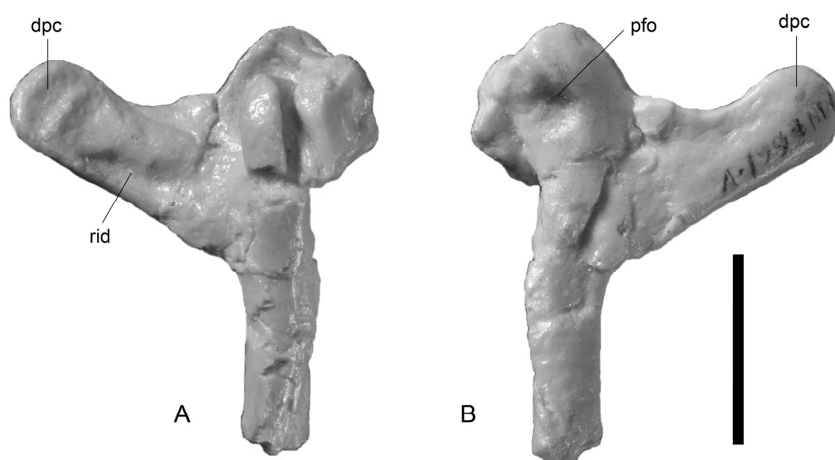


Fig. 2 – Specimen MB.R. 2828 in: A. medial view, B. lateral view; dpc – deltopectoral crest; pfo – pneumatic foramen; rid – ridge (scale 2 cm).

TABLE I
Measurements (in mm) of MB.R. 2828.

Measurement	Value
Deltopectoral crest length	22.20
Length of attachment of deltopectoral crest	17.90
Proximal width	38.65

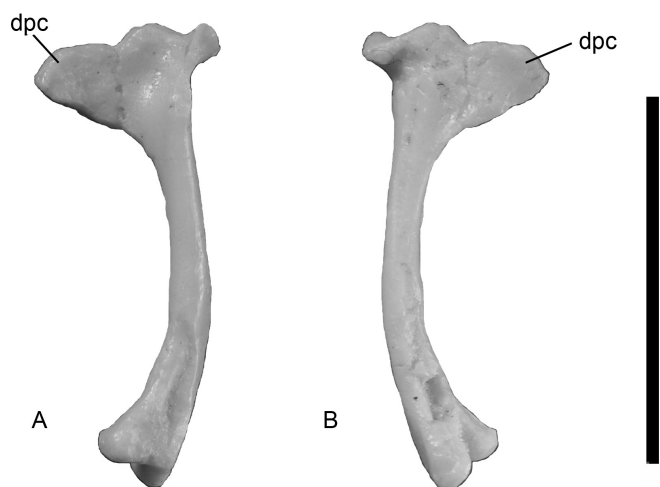


Fig. 3 – MB.R. 2833 in: A. medial view, B. lateral view; dpc – deltopectoral crest (scale 2 cm).

The humerus shaft is bowed, with its diameter remaining constant for most of its length. At the distal

lateral condyle being more prominent and pr when compared to the roller shaped medial cond



TABLE II
Measurements (in mm) and proportions of MB.R. 2833.

Measurements	Values
Humeral length	25.50
Deltopectoral crest length	5.95
Length of attachment of deltopectoral crest	4.80
Deltopectoral crest/humeral length	0.23
Proximal width	10.44
Proximal width/humeral length	0.41
Distal width/humeral length	0.22
Minimum shaft diameter	2.04
Minimum shaft diameter/humeral length	0.08

COMPARISON AND DISCUSSION

Both humeri from the Tendaguru deposits described here show a developed deltopectoral crest, which allows their allocation within Pterosauria. The deltopectoral crest of MB.R. 2828 differs from the most basal non-pterodactyloid pterosaurs by being longer and having the proximal margin curved and not straight such as reported in *Sordes* and *Jeholopterus* (Sharov 1971, Wang et al. 2002, Kellner 2003, Wang et al. 2009). It further lacks the hatched-shaped condition reported in the Rhamphorhynchidae and the sub-rectangular condition of the Campylognathoididae (Wellnhofer 1975, Wild 1978, Kellner 2003, Padian 2008). The most similar humerus of a non-pterodactyloid pterosaur is the one of *Dorygnathus* (Padian 2008). However, since MB.R. 2828 shows a well developed pneumatic foramen on the dorsal surface absent in all basal taxa, this specimen is referred to the Pterodactyloidea.

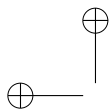
Pterodactyloid pterosaurs are divided into the Archaeopterodactyloidea and the Dsungaripteroidea. Up to date, no archaeopterodactyloid shows a pneumatic foramen on the humerus (Kellner 2004), leading us to classify MB.R. 2828 in the Dsungaripteroidea. Within that derived clade of pterosaurs, MB.R. 2828 does not show any particular affinity. This humerus lacks the warped and the hatched-shaped deltopectoral crest of the Pteranodontoidea and Nyctosauridae, respectively (Bennett 2001, Wang et al. 2005). It further differs from

phological features suggests that this specimen belongs to a new dsungaripteroid taxon, whose close affinities cannot be determined at this point.

The classification of the second specimen (MB.R. 2833) is less complicated. It differs from primitive pterosaurs by the shape of the deltopectoral crest and also differs from the Dsungaripteroidea by the lack of pneumatic foramen. MB.R. 2833 is similar to the humerus of several archaeopterodactyloids (e.g., *Pterodactylus*) and therefore is referred to this clade. Within the Archaeopterodactyloidea, all taxa show similar humeri with a long, proximally placed and curving ventrally deltopectoral crest, and the absence of pneumatic foramina. A sub-triangular distal end of the humerus is also observed in the Pteranodontoidea (Kellner 2003, Wang et al. 2009). However, no pteranodontoid pterosaur shows a well developed intertrochlear sulcus that is present in this Tendaguru specimen. Therefore, MB.R. 2833 is regarded as representing an undetermined species of Archaeopterodactyloidea. Based on the size and comparisons with other archaeopterodactyloid pterosaurs, this specimen represents a small individual, with an estimated wing-span around 35 cm, making it the smallest pterosaur recorded from Africa so far.

CONCLUSION

As has been pointed out several times in the literature, the record of pterosaurs in terrestrial deposits is gener-



TWO PTEROSAUR HUMERI FROM TENDAGURU

As we have already discussed, there is no possibility to compare the humeri studied here (MB.R. 2828 and MB.R. 2833) with previously described pterosaur material from Tendaguru. *Tendaguripterus recki* was regarded as a Germanodactylidae (Unwin and Heinrich 1999) but is now considered as belonging to a distinct group of pterosaurs (Tendaguripteridae) whose relationships cannot be established at present (Kellner et al. 2007). Nonetheless, the presence of a *Pterodactylus*-like flying reptile as suggested by Reck (1931) or a similar archaeopterodactyloid species is corroborated by MB.R. 2833. The second specimen (MB.R. 2828), albeit representing a dsungaripteroid taxon, is sufficiently different from *Dsungaripterus* and other similar taxa.

Humerus has been used to diagnose new taxa (Price 1953, Buissonjé 1980, Wang et al. 2008) particularly concerning distinct shapes of the deltopectoral crest. In this respect, MB.R. 2828 indicates the presence of a new dsungaripteroid species in Africa whose close affinities cannot be established at this point. This new taxon lacks the diagnostic features of the Tapejariidae, Azhdarchidae, Pteranodontoidea and Nyctosauridae, suggesting that it might represent a new group of pterosaurs in the Jurassic of Africa. However, since the material is incomplete, we refrain from naming a new taxon, hoping that more complete material comes to light and allows a better characterization. Nonetheless, the fact that the humeri described here differ from each other indicates the presence of a diversified pterosaur fauna in Tendaguru during the Late Jurassic.

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RESUMO

Fragmentos de pterossauros africanos do Jurássico são tipicamente raros e conhecidos apenas dos depósitos de Tendaguru, Jurássico Superior, Tanzânia. Este estudo descreve dois úmeros direitos de pterossauros de Tendaguru depositados na Universidade Humboldt de Berlim: espécimes MB.R. 2828 (réplica MN 6661-V) e MB.R. 2833 (réplica MN 6661-V). MB.R. 2828 consiste em uma porção proximal completa de um úmero tridimensional. Características morfológicas como a crista deltopeitoral não observadas em outros pterossauros sugerem que este espécime pertença a um novo dsungaripteróide. MB.R. 2833 é quase completo e, apesar de sua crista deltopeitoral extensa e arredondada, proximamente, pode ser associado a Archaeopterodactylus. De qualquer forma, este é o menor pterossauro da África e um dos menores já registrados. Estes espécimes corroboram a importância dos depósitos de Tendaguru para registro de pterossauros jurássicos. Este potencial, no entanto, precisa ser mais amplamente explorado com um maior número de espécimes de campo.

Palavras-chave: Tendaguru, Tanzânia, África, Jurássico Superior, Pterosauria.

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