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Humeral torsion in multituberculate mammals

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The humeri of small mammals are rarely preserved unbroken in fossil state. Only four complete humeri of multituberculate mammals have been described so far. These belong to the Eocene ?*Lambdopsalis bulla* Chow & Qi, 1978 (two specimens), from the Bayn Ulan Beds, Eocene, Bayn Ulan, China (Kielan-Jaworowska & Qi 1990; Kielan-Jaworowska & Gambaryan 1994; Gambaryan & Kielan-Jaworowska 1997), and to *Bulganbaatar nemegtbaataroides* Kielan-Jaworowska, 1974 (left and right humerus of the same individual), from the Djadokhta Formation, ?early Campanian, Bayn Dzak, Gobi Desert, Mongolia (Sereno & McKenna 1995; Gambaryan & Kielan-Jaworowska 1997; see also Kielan-Jaworowska & Hurum 1997 for age estimates).

Kielan-Jaworowska & Gambaryan (1994) and Gambaryan & Kielan-Jaworowska (1997) argued that multituberculates had a sprawling stance and that the degree of torsion in ?*Lambdopsalis* varies between 24 and 38°. Sereno & McKenna (1995), on the other hand, argued that multituberculates had a parasagittal posture, similar to that in *Didelphis*, and that the degree of torsion in *Bulganbaatar* is approximately 15°. These authors also concluded that the parasagittal posture in mammalian evolution evolved only once, in the common ancestors of multituberculates and therians, some time before the Late Jurassic. This opinion has been questioned by Rougier *et al.* (1996), and recently by Hu *et al.* (1997) who found the sprawling stance in a symmetrodont mammal from the Late Jurassic or Early Cretaceous of China. It should be also mentioned that the humeri of other Mesozoic therians *sensu lato*, such as the 'eupantothere' *Henkelotherium* (Krebs 1991: fig. 8 and 'Tafel' 1) and in the prototribosphenid *Vincelestes* (Rougier 1993: figs 84 and 85) show a considerable humeral torsion, apparently related to a sprawling or half-sprawling stance.

A Polish-Mongolian team visited the Gobi Desert in 1995 and collected fossils at various localities. Among others they collected ten mammal skulls, one of a eutherian and nine of multituberculates, at Ukhaa Tolgod on the Gobi Desert (Dashzeveg *et al.* 1995). The specimens were found in sandstone nodules, at the northern part of Ukhaa Tolgod. The Ukhaa Tolgod Beds may be an equivalent of the Djadokhta Formation (Novacek *et al.* 1997). This small collection is housed at the Institute of Geology, Mongolian Academy of Sciences in Ulan Bator (abbreviated GI).

In a specimen of *Kryptobaatar* sp. from Ukhaa Tolgod (GI 5/302, Fig. 1), in addition to a skull which is 22.7 mm long, there are fragments of the postcranial skeleton. The complete right humerus (Figs 1, 2), exposed in ventral view, has been preserved together with the skull. The length of the humerus is about 15.3 mm. Although the humerus is complete, I did not remove all the matrix which supports the humeral head and the dorsal side of the bone, because of the fragility of the specimen.

The fossils collected by the Polish-Mongolian team at Ukhaa Tolgod are commonly preserved without the compact layer of the bone, which has a tendency to fall away during weathering, leaving – in the case of long bones – a cast of the medullary cavity. Such

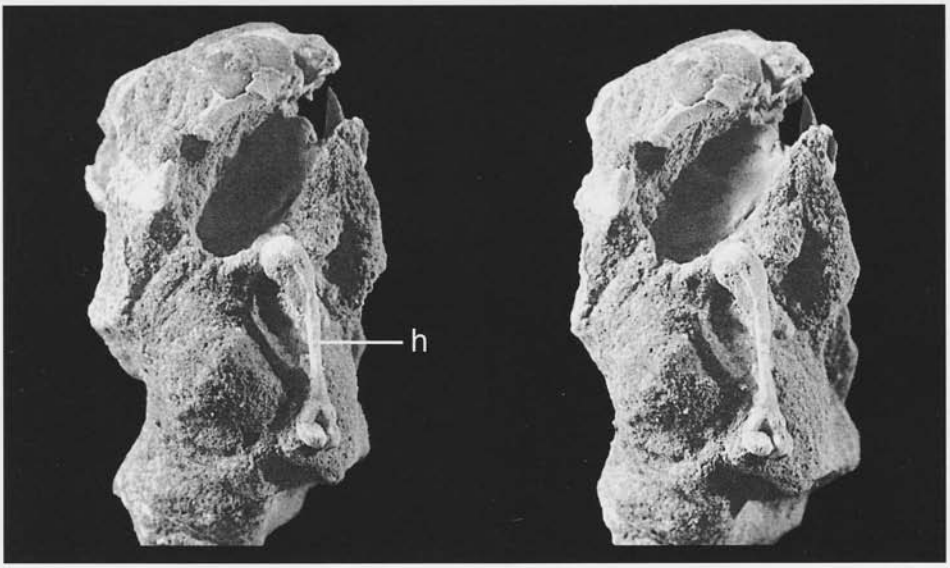

Fig. 1. *Kryptobaatar* sp., GI 5/302, Late Cretaceous, ?Djadokhta Formation, Northern Ukhaa Tolgod, Nemegt Basin, Gobi Desert, Mongolia. Skull associated with both dentaries (right lateral view) and complete right humerus (h). Stereo-photograph × 2.

preservation is characteristic for the humerus GI 5/302 (Fig. 2), in which the medullary cavity has been apparently replaced by calcite. The shaft of the humerus on its ventral side is devoid of the compact layer, which has been preserved only on the medial side (right side of the photographs in Fig. 2), and on the unexposed dorsal side. The compact bone is completely preserved on the distal epiphysis and the margin along which it has been broken off is well seen. On the proximal epiphysis the compact layer has been partly preserved, being seen as white, irregularly distributed patches. Because of this state of preservation the shaft of the humerus appears unusually thin, especially in relation to the distal epiphysis, on which the compact bone has been completely preserved. In spite of the lack of the compact bone on the shaft, details of its structure (such as a wide intertubercular groove) are preserved, but this groove is less deep than in bones with the compact layer preserved.

The humerus GI 5/302 displays typical multituberculate features (Figs 1, 2): the head overhangs the shaft dorsally, the lesser tubercle is wider than the greater, and the intertubercular groove is wide. The shaft looks relatively very slender because of the lack of the compact layer and because the crest of the greater tubercle has been broken off. The distal epiphysis is very extensive, with large entepicondyle and narrow ectepicondyle, oval ulnar condyle and spherical radial condyle, both very prominent and large. There is an obliquely arranged entepicondylar foramen (barely visible in Fig. 2B) and an extensive fossa coronoidea.

The torsion of the humerus is well seen at first sight. I measured the degree of torsion using method of Simpson (1928: fig. 52) and obtained 31°. I could not use the method of Kielan-Jaworowska & Gambaryan (1994: fig. 46), because the head remained partly obscured by the matrix. The humeral torsion is also evident when examining the two stereo-photos of the humerus in ventral view. The first photo (Fig. 2A), taken at the horizontal position of the ventral surface of the greater and lesser tubercles, shows the distal epiphysis obliquely arranged; the ectepicondyle is not exposed. The second one (Fig. 2B), taken at the horizontal position of the distal epiphysis,

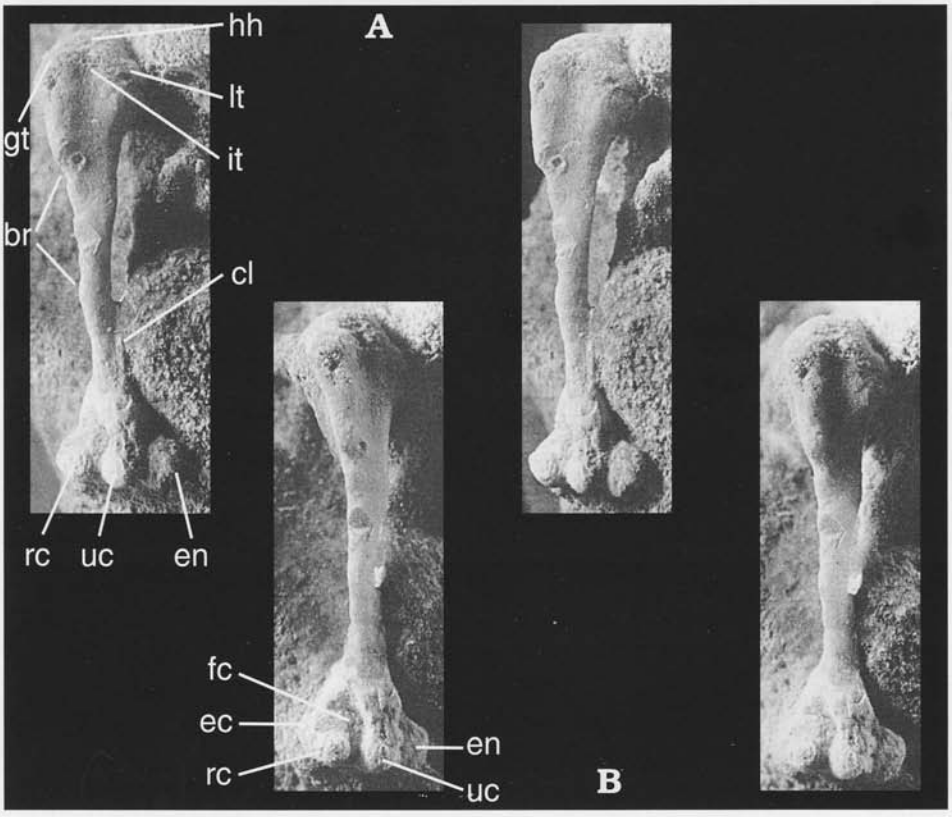

Fig. 2. ·*Kryptobaatar* sp., GI 5/302, Late Cretaceous, ?Djadokhta Formation, Northern Ukhaa Tolgod, Nemegt Basin, Gobi Desert, Mongolia. **A**. Right humerus in ventral view. Photo taken at the horizontal position of the proximal part. **B**. The same, photo taken at the horizontal position of the distal part. Stereo-photographs, × 4, coated with ammonium chloride. Abbreviations: br – broken area of the crest of greater tubercle, cl – compact layer, ec – ectepicondyle, en – entepicondyle, fc – fossa coronoidea, gt – greater tubercle, hh – humeral head, it – intertubercular groove, lt – lesser tubercle, rc – radial condyle, uc – ulnar condyle.

shows all its structures, including ectepicondyle, and the oblique position of the surface passing through both tubercles.

The discovery of a slender, twisted humerus in the small multituberculate *Kryptobaatar* demonstrates that the humeral torsion previously found in ?*Lambdopsalis* is not related to its fossorial habits or to a relatively large size (the two humeri of ?*Lambdopsalis*, described by Kielan-Jaworowska & Qi 1990, are 36.5 mm and 38.6 mm long).

With the new find, complete humeri are now known in three multituberculate taxa: ?*Lambdopsalis bulla*, *Kryptobaatar* sp., and *Bulganbaatar nemegtbaataroides*, the two first of which show a considerable degree of torsion (varying around 30°), the last one only a small torsion (15°). Numerous incomplete humeri described, among others, by Gidley (1909), Simpson (1928), Deischl (1964), Kielan-Jaworowska & Dashzeveg (1978), Krause & Jenkins (1983), Kielan-Jaworowska & Gambaryan (1994 and references therein) apparently show also a considerable torsion.

This find rises further skepticism (see also Gambaryan & Kielan-Jaworowska 1995; Rougier *et al.* 1996, and Hu *et al.* 1997) against the idea of Sereno & McKenna (1995, 1996) that parasagittal stance made its appearance in mammalian history only once, in the common ancestors of multituberculates and therians.

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