

Limb posture in early mammals: Sprawling or parasagittal

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The limb posture in early mammals is a matter of controversy. Kielan-Jaworowska and Gambaryan presented arguments for a sprawling posture in multituberculates, based mainly on three characters of the hind limbs (deep pelvis, mediolateral diameter of the tibia larger than the craniocaudal, and position of MtV, which fits the peroneal groove on the calcaneus and is not aligned with the axis of tuber calcanei). Here we present two more arguments for sprawling hind limbs in early mammals. One is the presence of an os calcaris, supporting the probably venomous spur in hind legs of docodontans, multituberculates, eutriconodontans, and “symmetrodontans”, similar to those of extant monotremes. We argue that early mammals (except for boreosphenidans) had sprawling limb posture and venomous spur; acquisition of the parasagittal stance was apparently characteristic only of boreosphenidans, in which the spur has not been found. The second argument is based on taphonomic evidence from lacustrine conditions (e.g., Early Cretaceous Jehol Biota), in which the mammalian skeletons, except for boreosphenidans (*Sinodelphys* and *Eomaia*), have been preserved compressed dorso-ventrally, suggesting sprawling stance. In similar conditions of the Eocene Messel Biota the skeletons of boreosphenidan mammals (except for bats and pangolins) are preserved lying on flanks, suggesting parasagittal stance. Sereno argued that forelimbs in multituberculates were parasagittal, based on the stated presence of a ventrally facing glenoid, a mobile shoulder joint, and an elbow joint with enhanced flexion-extension capability. However, these characters are not unequivocally indicative of parasagittalism. We demonstrate that the structure of the distal end of the multituberculate humerus is condylar, with no tendency for developing a trochlea. We reconstruct multituberculates and other early mammals with sprawling stance in resting position as plantigrade.

Key words: Mammalia, Multituberculata, Monotremata, os calcaris, spur, venomous mammals, sprawling posture, parasagittalism, Mesozoic.

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Introduction

Reconstruction of the posture of fossil mammals is possible when the entire or almost entire postcranial skeleton is known and especially if it shows similarities to those of any modern mammals.

The best known postcranial skeletons of early mammals belong to multituberculates, which do not have living relatives. For many years mostly isolated bones of the multituberculate skeleton have been known (Cope 1882a, b; Marsh 1889; Gidley 1909, Simpson and Elftman 1928; Granger and Simpson 1929; McKenna 1961; Deischi 1964, Sahni 1972; Kielan-Jaworowska and Dashzeveg 1978; Kielan-Jaworowska 1989; Kielan-Jaworowska and Qi 1990; Szalay 1994). Simpson (1928a) described several isolated postcranial elements, but none of them could be assigned to multituberculates with any certainty. From the famous fauna of the Guimarota coal mine in Portugal (see Martin and Krebs 2000 for review), which yields the oldest (Kimmeridgian) uncontested multituberculates, no single multituberculate postcranial fragment has so far been described (e.g., Hahn 1969, 1993, and other papers by this author).

The first articulated multituberculate skeleton was described by Krause and Jenkins (1983), who studied a nearly complete skeleton of Paleocene *Ptilodus kummae* Krause and Jenkins, 1983, in comparison with isolated postcranial elements of other North American multituberculates. Better preserved materials of multituberculate postcranial skeletons are from the Mongolian part of the Gobi Desert (Kielan-Jaworowska 1969, 1979, 1998; Kielan-Jaworowska and Gambaryan 1994; Sereno and McKenna 1995; Gambaryan and Kielan-Jaworowska 1997; Minjin 2001, 2003; Sereno 2006). Another source of Mesozoic mammalian skeletons preserved in articulation is from the famous Early Cretaceous Yixian Formation (Jehol Biota) of China, which, however, has so far yielded a single skeleton of a multituberculate (*Sinobaatar lingyuanensis* Hu and Wang Y.-Q., 2002a), described only preliminarily (Hu and Wang Y.-Q. 2002a, b).

Simpson and Elftman (1928) reconstructed the hind limb musculature of a Paleocene multituberculate referred to *Eucosmodon* sp. on the basis of a fairly complete hind limb skeleton, consisting of isolated bones. They stated (p. 3): “The foot, as clearly shown in its almost completely known osteology, is unusually primitive. It is pentadactyl and plantigrade, of gras-

ping type with partially opposable hallux." The presence of an opposable hallux has not been confirmed in multituberculate feet from Mongolia (see e.g., Kielan-Jaworowska and Gambaryan 1994). With respect to the stance Simpson and Elftman (1928: 7) concluded: "The disadvantages of retaining a somewhat more reptilian posture were compensated in *Eucosmodon* to a considerable degree by the freedom of rotation." However, one year later Granger and Simpson (1929: 672) stated: "The posture of the monotremes would also seem to be inherited in large part from the reptilian ancestry, and here again the multituberculates are more highly evolved."

Simpson (1928b) commented on the multituberculate shoulder girdle and forelimb on the basis of fragments of the scapulocoracoid and humerus in *Ptilodus* and *Djadochtherium*, and regarded them as of the same general pattern as in primitive marsupials and placentals. He stated that the glenoid (1928b: 11) was "exactly that of higher mammals and fundamentally unlike that in monotremes".

Sloan and Van Valen (1965: 3) on the basis of isolated elements of the postcranial skeleton of *Mesodma* from the Hell Creek Formation concluded that "movement of the humerus is apparently in the same plane as the blade of the scapula", thus accepting the premise that movements were as in therian mammals. Krause and Jenkins (1983) concluded (p. 200) that: "[...] at least some multituberculates were arboreal"; and further (p. 235) that "multituberculate shoulder girdle posture and mobility were comparable to those of modern therians."

The first reconstruction of multituberculate posture was provided by Krause and Jenkins (1983: fig. 31), and Jenkins and Krause (1983: fig. 2, see also the reconstruction on the cover of *Science* vol. 220, no. 4598, 1983), for Paleocene *Ptilodus*, who reconstructed it as an arboreal mammal. Alexander N. Kuznetsov, who does not believe that *Ptilodus* was arboreal (personal communication June, 2006), suggested to us that if one turns any of these figures clockwise by 90 degrees and removes the tree trunk, it will look rather like a tachyglossid with sprawling stance and reversed hind limbs. Kielan-Jaworowska and Gambaryan (1994: fig. 61; see also Gambaryan and Kielan-Jaworowska 1997, and Kielan-Jaworowska 1998), provided the second reconstruction of multituberculate posture, this time for the Late Cretaceous *Nemegtbaatar*, showing sprawling stance. This was challenged by Sereno and McKenna (1995) and Sereno (2006), who advocated a parasagittal posture for multituberculate mammals. The latter authors also suggested that parasagittalism evolved only once among mammals; that is, in the common ancestor of multituberculates and therians (boreosphenidans¹ in our terminology).

Conclusions concerning limb posture in fossil mammals should be based on analysis of the structure of both the forelimbs and hind limbs, and of their movements. Sereno

and McKenna (1995) and Sereno (2006) limited their conclusions to the forelimbs only, neglecting the evidence from the hind limbs.

In this paper we evaluate the evidence provided by Kielan-Jaworowska and Gambaryan (1994), Gambaryan and Kielan-Jaworowska (1997), Sereno and McKenna (1995), and Sereno (2006), and discuss two more arguments for the sprawling stance of multituberculates, and as far as available material permits, of other early mammals. The first of the new arguments is the presence of a spur in the tarsus (Hurum et al. 2006; see also our Figs. 1 and 2). The second argument derives from taphonomic evidence (Figs. 3–5); the way in which, depending on their limb posture, early mammals are preserved in lacustrine sediments of the Jurassic, Cretaceous, and Eocene ages in China, Portugal, and Germany (Schaal and Ziegler 1992; Koenigswald and Storch 1998; Martin and Krebs 2000; Habersetzer and Schaal 2004; Chang et al. 2005).

We reconstruct multituberculate feet in resting position as plantigrade (as suggested also by Simpson and Elftman 1928 and *contra* Kielan-Jaworowska and Gambaryan 1994), accepting the results of Bolortsetseg Minjin and Xingyou Zang (personal communication April, 2006), who, adopting the method of Carrano (1997), demonstrated that two multituberculate genera were plantigrade. We also speculate, but less conclusively, that mammals with a venomous spur probably were plantigrade, as the spur would act more effectively when situated at the very end of the moment arm of a force (in this case the length of the standing hind limb), than when placed higher on the leg. The feet of multituberculates were probably plantigrade in resting position, but apparently digitigrade when running fast and jumping (as in most plantigrade mammals).

The postcranial skeletons of other early mammals, except for those of the Late Cretaceous boreosphenidans that are preserved mostly in the Late Cretaceous sandstones of the Gobi Desert (Kielan-Jaworowska 1977, 1978; Szalay and Trofimov 1996), are rare and generally poorly known. An articulated skeleton has been preserved in the "eupantotherian" *Henkelotherium guimarotae* Krebs, 1991 from the Kimmeridgian Guimarota beds of Portugal, described by Krebs (1991). Another but more fragmentary skeleton from the same beds belongs to the docodontan *Haldanodon* (Henkel and Krusat 1980; Krusat 1991). Martin (2005) described in detail the skeleton of *Haldanodon exspectatus* Kühne and Krusat, 1972, and several well preserved isolated bones, among which, however, the bones of the foot have not been found. He reconstructed the posture of *Haldanodon* as sprawling and its life style as fossorial.

In the last decade a number of complete skeletons belonging to different groups of early mammals have been found in China, the best known of which come from the famous Jehol

¹ We follow Luo et al. (2001) in referring to mammals with tribosphenic molars that originated on the northern hemisphere as Boreosphenida, rather than Theria, because the term Theria has been used in various meanings; for example, including only extant Marsupialia and Placentalia; including these groups and their fossil ancestors with tribosphenic molars; and including also "symmetrodontans" and "eupantotherians" = Holotheria of Hopson (1994) and Wible et al. (1995).

Biota, collected from sediments of the Early Cretaceous Yixian Formation (see Chang et al. 2003 and Zhou et al. 2003 for reviews). The other Chinese formation yielding so far one articulated mammalian skeleton is the Middle Jurassic Jiulongshan Formation of northwestern China (Ji Q. et al. 2006). Both formations represent lacustrine sediments in which the skeletons are somewhat flattened, not as well preserved as in terrestrial (aeolian) sediments of the Gobi Desert. Most of the taxa from the two Chinese formations are represented by single specimens, so far only preliminarily described. In this situation the detailed functional analyses of the postcranial skeletons have not been made and that is why our paper is confined mostly to the discussion and posture reconstruction of multituberculates, other groups being treated mostly in comparison with them.

Institutional abbreviations.— CAGS, Chinese Academy of Geological Sciences, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts, USA; PM, Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PMO, Paleontological Museum, Oslo, Norway; PSS-MAE, Mongolian-American Museum Expeditions (the collections are for the time being housed at the American Museum of Natural History in New York); ZIN, Zoological Institute Russian Academy of Sciences, St. Petersburg, Russia; ZMO, Zoological Museum, University of Oslo, Norway; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Evaluation of available material

Evidence from the forelimbs.—The most complete multituberculate shoulder girdle and forelimbs belong to *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1969, PSS-MAE 103, from the Late Cretaceous Djadokhta Formation of Bayan Zag in the Gobi Desert, Mongolia. This unique specimen was originally tentatively referred by Sereno and McKenna (1995) to *Bulganbaatar* Kielan-Jaworowska, 1974.

Sereno and McKenna (1995) reconstructed the posture of the forelimbs in “*Bulganbaatar*” as parasagittal, based on the glenoid fossa facing ventrally, alleged presence of a trochlea at the distal end of the humerus, and lack of humeral torsion. After the criticism of Gambaryan and Kielan-Jaworowska (1997), who demonstrated that in all known multituberculate humeri, the distal extremity shows a condylar, rather than trochlear structure, Sereno (2006) did not argue anymore for the trochlear structure of the multituberculate humerus, but replaced “the trochlear structure” by the “cam-shaped ulnar condyle”, which we discuss below.

With respect to the third of the mentioned characters, Sereno (2006: 351) stated that Gambaryan and Kielan-Jaworowska (1997) postulated a sprawling stance for the multi-

tuberculate forelimb on four attributes of the humerus, one of which is the “[...] high degree of humeral torsion”. This is a misquotation, as Gambaryan and Kielan-Jaworowska (1997) argued that there seems to be a considerable degree of variability of humeral torsion among multituberculate mammals, and demonstrated on numerous examples, *contra* their earlier opinion (Kielan-Jaworowska and Gambaryan 1994), that lack of torsion is not indicative of parasagittalism.

Of the three characters of Sereno and McKenna (1995) only one—the ventrally facing glenoid—has been retained by Sereno (2006). In the latter paper the author provided detailed discussion on posture in *Kryptobaatar*, summarized as follows (p. 360): “Evidence in favor of a more parasagittal forelimb posture in multituberculates includes the small ventrally facing glenoid, mobile shoulder girdle, cam-shaped ulnar condyle of the humerus, and elbow joint with enhanced flexion-extension capability.” We discuss these four characters below.

(1) *Ventrally facing glenoid.*—The state of preservation of PSS-MAE 103, studied by Sereno (2006) leaves no doubt that the glenoid fossa in this specimen faces ventrally. However, the question arises as to whether the ventrally facing glenoid unambiguously indicates a parasagittal stance?

In Recent monotremes the major part of the glenoid fossa, formed by the scapula, faces ventrally; only a small coracoid portion faces laterally. A ventrally facing glenoid occurs also in the Early Cretaceous eutriconodontan *Jeholodens jenkinsi* Ji Q., Luo, and Ji S.-A., 1999, from the Yixian Formation of China. *Jeholodens* has an advanced boreosphenidan-like structure of the scapula, not only with an infraspinous fossa present, but also with fully developed supraspinous fossa, a prominent scapular spine, and a small coracoid process. This type of scapula occurs also in the Early Cretaceous eutriconodontan *Gobiconodon ostromi* Jenkins and Schaff, 1988, from the Cloverly Formation, and is regarded as characteristic of Eutriconodonta as a whole (Ji Q. et al. 1999; Kielan-Jaworowska et al. 2004). The eutriconodontans have always been reconstructed as having sprawling posture (see Kielan-Jaworowska et al. 2004 for review).

Another early mammal with a ventrally facing glenoid fossa and abducted forelimbs is the “symmetrodon” *Zhangheotherium quinquecuspidens* Hu, Wang Y.-Q., Luo, and Li Ch.-K., 1997, also from the Yixian Formation of China (Hu et al. 1997, 1998; Luo and Ji Q. 2005). Hu et al. (1997: 141) characterized its posture as follows: “A mobile clavicle-interclavicle joint that allows a wide range of movement of the forelimb has an ancient origin in the mammalian phylogeny. The abducted forelimb inferred for *Zhangheotherium* and other archaic therians suggests that early therian mammals lacked the more parasagittal limb posture of most living therians.”

The other well preserved “symmetrodon” skeleton from the Yixian Formation is *Akidolestes cifellii* Li G. and Luo, 2006, in which the authors characterized the shoulder girdle and forelimbs as (p. 196) “[...] similar to those of zhangheotheriids”.

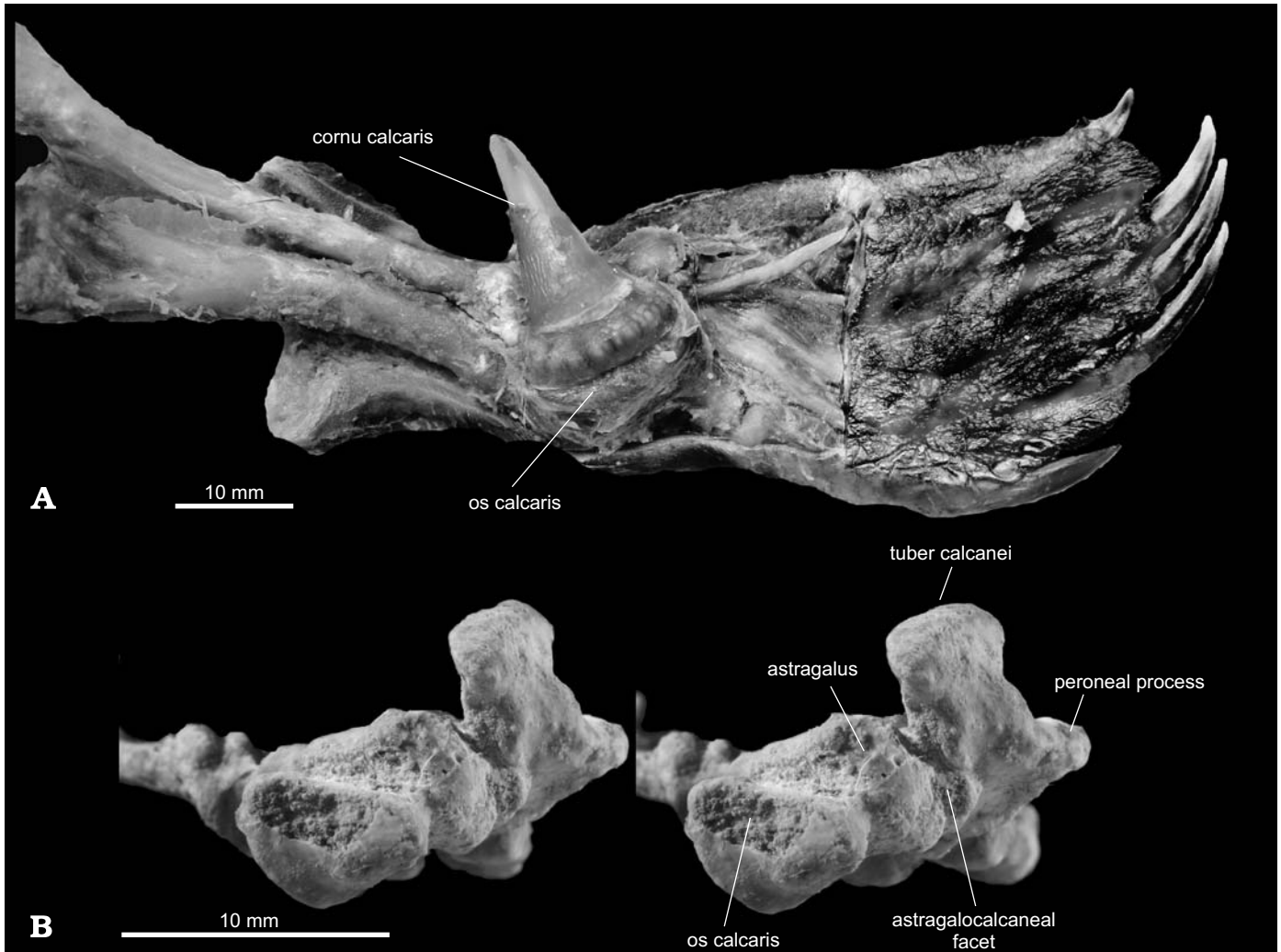


Fig. 1. Comparison of os calcaris in a Recent monotreme and a Cretaceous multituberculata. **A.** The left tarsus of monotreme *Ornithorhynchus anatinus* (Shaw, 1799), ZMO 11793, an adult male, showing the well-preserved venomous cornu calcaris facing medially. **B.** Proximal part of the left tarsus of *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), showing os calcaris in proximal view. PM 120/107, Late Cretaceous red beds of Hermin Tsav, (?late Campanian), Hermin Tsav I, Gobi Desert, Mongolia. Note the roughly triangular shape of os calcaris in *C. catopsaloides* and its undulating surface, indicating the presence of cornu calcaris upon it.

Sereno (2006) challenged the ideas of Hu et al. (1997), and Ji Q. et al. (1999), concluding that in *Zhangheotherium* (p. 333): “The forelimb may well have had a more parasagittal, than sprawling, posture that emphasized the hinge-like flexion-extension at the elbow, as in *Jeholodens*.” It is beyond the scope of the present paper to discuss the controversy between Sereno (2006) and Hu et al. (1997), and between Sereno (2006) and Ji Q. et al. (1999), concerning the forelimb posture in *Zhangheotherium* and *Jeholodens*, especially in view of the fact that we have not had an opportunity to examine the relevant specimens. However, for discussion of the forelimb structure in multituberculata, which continues below, it is important to cite the conclusion of Ji Q. et al. (1999: 329), who stated: “*Jeholodens jenkinsi* shows a mosaic of derived, therian-like characters for many parts of the pectoral girdle [...] and the humerus, but very primitive characters for the vertebral column, pelvic girdle, hindlimb and pes [...]”.

(2) *Mobile clavicle-interclavicle articulation*.—In extant mammals the mobile shoulder girdle never occurs in forms having an abducted humerus. The mobile clavicle-interclavicle articulation is characteristic not only of the multituberculata *Kryptobaatar*, but also of a eutriconodontan *Jeholodens* (Ji Q. et al. 1999).

(3) *Cam-shaped ulnar condyle of the humerus*.—All tetrapods with a primary sprawling stance have a condylar structure of the elbow joint, as is characteristic of multituberculata (see, e.g., Gambaryan and Kielan-Jaworowska 1997: fig. 3). We agree with Sereno (2006) that in multituberculata humeri the ulnar condyle is cam-shaped and smaller than the ball-shaped radial condyle. The ulnar condyle may be provided with a distinct ridge, best seen in *Catopsalis* from the Hell Creek Formation, MCZ 19529, figured by Jenkins (1973: pl. 1: 19). Sereno (2006: 342) regarded the cam-shaped structure of the ulnar condyle as a transitional stage to the development of the

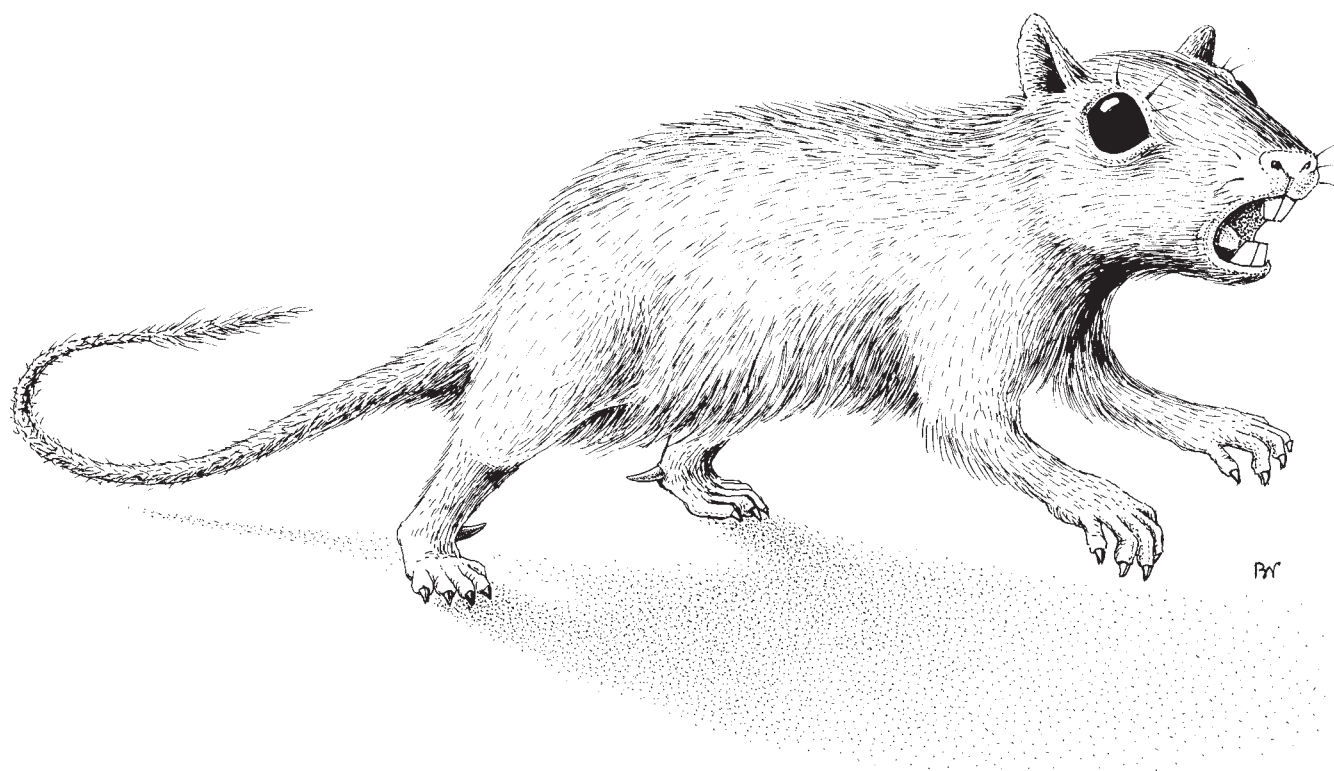


Fig. 2. Reconstruction of the posture of the Late Cretaceous multituberculate *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974) from the Gobi Desert, Mongolia, as a plantigrade mammal with sprawling limbs. Skull length is about 60 mm. The size of the spur has been reconstructed based on the length of the male spur in *Ornithorhynchus* in comparison to the length of the foot. The animal is reconstructed in aggressive position, ready for attack, with mobile spurs projecting medially. (Artwork by Bogusław Waksmundzki.)

trochlea, stating: “In multituberculates the cam is developed only on the anterior half of the ulnar condyle adjacent to the bulbous, hemispherical portion of the radial condyle (Fig. 10.11B). In therians, the ulnar condyle is cam-shaped posteriorly as well, which, together with the broadened intercondylar groove, forms the trochlea (Fig. 10.11C). An ulnar condyle that is, at least in part, cam-shaped is transitional to a fully developed therian trochlea”. We agree that the cam-shaped ulnar condyle in boreosphenidans indicates an incipient origin of the trochlear structure, but as the trochlea never developed in multituberculates, the structure of the multituberculate ulnar condyle cannot be regarded as “transitional”. All multituberculates, including the Paleocene forms, show the condylar structure of the humerus (see, e.g., Krause and Jenkins 1983: figs. 11 and 12). The third point of Sereno’s list—“cam-shaped ulnar condyle of the humerus” has been, in our opinion, wrongly interpreted. As pointed out by Jenkins (1973: 281): “The primitive therian trochlea evolved by enlargement of the intercondylar groove separating the ulnar and radial condyles [...]” In spite of the cam-shaped ulnar condyle in multituberculates, the intercondylar groove is not enlarged in any known humerus.

The distal part of the humerus in *Jeholodens* (not figured in detail) has a condylar structure on its anterior (dorsal) aspect, but Ji Q. et al. (1999) recognized the presence of an in-

ipient ulnar trochlea on its posteroventral aspect. They reconstructed the hind limbs of *Jeholodens* as sprawling, but the forelimbs as having a “more derived” position, which means more close to the parasagittal position, or in other words only partly abducted.

(4) *Elbow joint with enhanced flexion-extension mobility.*—Sereno (2006) argued that structure of the elbow joint which enabled a wide flexion-extension capability might suggest a more parasagittal posture of the forelimbs. It should be remembered, however, that such a structure of the elbow joint has been interpreted by Hu et al. (1997) and Ji Q. et al. (1999) as occurring in forms recognized by these authors as having sprawling or half-sprawling forelimbs. There is no evidence that parasagittalism increases the flexion-extension mobility, as e.g., in lizards and urodelans (personal communication from Alexander N. Kuznetsov, June, 2006) the flexion-extension amplitude in the elbow joint is approximately equal to that in mammals.

Evidence from the hind limbs.—Kielan-Jaworowska and Gambaryan (1994) discussed three important characters in the structure of the pelvic girdle and hind limbs that indicate a sprawling posture of multituberculates. Here we provide a fourth anatomical character, based on the study of Hurum et al. (2006), which is the presence of a supporting bone (os

calcaris) for a spur in the multituberculate tarsus, not known at the time of Kielan-Jaworowska and Gambaryan's writing.

(1) The first line of evidence is based on the structure of the pelvis. In boreosphenidan mammals with a parasagittal stance, the pelvis is much shallower than in therapsid reptiles with a sprawling posture. Although the multituberculate pelvis has a typical mammalian pattern with a strongly elongated ilium, it is relatively deeper in its ischio-pubic part than in boreosphenidan mammals. Kielan-Jaworowska and Gambaryan (1994) demonstrated that in multituberculates the femoral adductors originated ventral to the acetabulum, rather than posterior to the vertical line extending ventrally from the acetabulum, as in placental mammals of similar size with parasagittal limbs (e.g., *Rattus*). This resulted in an oblique position of the femur during the propulsive phase in multituberculates (as illustrated for *Nemegtbaatar gobiensis* Kielan-Jaworowska, 1974), rather than a vertical position as in *Rattus* (Kielan-Jaworowska and Gambaryan 1994: figs. 48, 49), indicating a sprawling stance of the multituberculate hind limb.

(2) The second line of evidence derives from measuring the diameters of the tibia. In mammals with parasagittal limbs, the craniocaudal (anteroposterior) diameter of the tibia is larger than the mediolateral diameter (Kummer 1959a, b). In multituberculates, in contrast, the mediolateral diameter of tibia is relatively larger than in modern boreosphenidan mammals with parasagittal limbs. Kielan-Jaworowska and Gambaryan (1994) assigned the increase of the mediolateral diameter of tibia in multituberculates to the abducted position of limbs, as during the propulsive phase the stress on the tibia was directed medially. They stated (1994: 63): "In *Kryptobaatar* (ZPAL MgM-I/41) the craniocaudal diameter of the tibia is 54% of the mediolateral diameter, in *Nemegtbaatar* (ZPAL MgM-I/110) 60% and in *Eucoelodon* 63% in the proximal part and 65% in the distal part. In modern boreosphenidan mammals these values are 81% in *Marmosa* sp. (ZIN 1110), 107% in *Elephantulus roseti* (ZIN 1380) and 105–150% in different species of rodents cited in Table 2." In *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974) studied by us (PM 120/103) the mediolateral diameter of tibia is distinctly larger than the craniocaudal one, but as both tibiae have been slightly compressed, we refrain from providing the measurements.

(3) The third line of evidence is based on the structure of the multituberculate tarsus and the position of the foot related to it. Kielan-Jaworowska and Gambaryan (1994: 74) stated: "In cursorial therian mammals the pes as a rule is situated parallel to both the sagittal plane and to the direction of movement. In animals with abducted limbs the pes may be placed in various positions." These authors argued that in multituberculates metatarsal III is abducted 30–40 degrees from the longitudinal axis of the tuber calcanei; in other words, it was not parallel to the sagittal plane and direction of movement. Such a position of multituberculate pedes suggests also the sprawling position of their hind limbs.

(4) The new anatomical evidence derives from the presence of a supporting bone (os calcaris) for a spur in the tarsus

of multituberculates. Hurum et al. (2006) reviewed the occurrence of the os calcaris in Mesozoic mammals. The extratarsal spur is well known to occur in the tarsus of extant monotremes, being venomous in the platypus (*Ornithorhynchus*, Fig. 1A) and possibly secondarily non-venomous in the echidnas (*Tachyglossus* and *Zaglossus*). In adult *Ornithorhynchus* the spur occurs only in males. It consists of an os calcaris and a hollow, keratinous cornu calcaris inwardly directed (Nowak and Paradiso 1983). The dangerous cornu calcaris is mobile, and when the animal is ready for attack, it is directed medially from the tarsus (as reconstructed by us for a multituberculate *Catopsbaatar* in Fig. 2). Only juvenile male platypuses have spurs when they leave the nesting burrows. The spur is housed in a chalky sheath, which eventually breaks away to expose the spur itself. The spur would normally be completely exposed by October in a male which had left the nesting burrow in February. In the juvenile female, no spur develops within the small remnant sheath (<0.5 cm long) which persists for about eight to ten months after emergence (Griffiths 1978; Grant 1995).

With respect to echidnas, Griffiths (1968: 3) stated: "On the inside of the ankle in all males and in some females is a hollow perforated spur 0.5–1.0 cm long from the base of which a duct leads up the leg to a gland buried among the muscles just below the knee. [...] The spur and the glandular apparatus is not poisonous [...]."

The most primitive known mammals with an os calcaris and fused to it an ossified cornu calcaris to support the venomous extratarsal spur are the docodontans. Ji Q. et al. (2006: fig. 1) figured this structure in a relatively large Middle Jurassic Chinese docodontan *Castorocauda lutrasimilis* Ji Q., Luo, Yuan, and Tabrum, 2006, from northeastern China, which shows adaptations for burrowing and swimming (see also our Fig. 5A).

The os calcaris with fused ossified cornu calcaris in eutriconodontan mammals was described by Jenkins and Schaff (1988) from the North American Early Cretaceous Cloverly Formation *Gobiconodon* and re-described and re-figured by Hurum et al. (2006). It has not been preserved in the only specimen of the eutriconodontan *Jeholodens* from the Yixian Formation (Ji Q. et al. 1999) discussed above, nor in an older (from the basal member of the Yixian Formation) Chinese genus *Repenomamus*, closely related to *Gobiconodon* (Wang Y.-Q. et al. 2001). Two species of *Repenomamus* are known: *Repenomamus robustus* Li J.-L., Wang Y., Wang Y.-Q., and Li Ch.-K., 2001 and *Repenomamus giganticus* Hu, Meng, Wang Y.-Q., and Li Ch.-K., 2005. During the Early Cretaceous, *Repenomamus* and *Gobiconodon* had a wide geographical distribution, and are known (in particular *Repenomamus*) from several specimens, only parts of which have been so far described (Wang Y.-Q. et al. 2001; Li J.-L. et al. 2001; Li Ch.-K. et al. 2003); we presume that the finding of an os calcaris and probably an ossified cornu calcaris in this taxon is a matter of time. It remains an open question whether the lack of an os calcaris and ossified cornu calcaris in the specimen of *Jeholodens* could be evidence for sexual

dimorphism as seen in *Ornithorhynchus*, where only the males have spurs.

Among “symmetrodontans”, an os calcaris fused with the ossified cornu calcaris is known in the first specimen of *Zhangheotherium* (described by Hu et al. 1997, and originally assigned to the Spalacotheriidae). In the second specimen of *Zhangheotherium*, described by Luo and Ji Q. (2005), os calcaris has not been preserved. These elements have been also found in another “symmetrodontan” from the Yixian Formation, *Maotherium sinensis* Rougier, Ji Q., and Novacek, 2003. The authors did not mention the os calcaris or ossified cornu calcaris in the text, but it is seen in their plate 1 (see also Hurum et al. 2006, and our Fig. 4G). Rougier et al. (2003) erected for *Zhangheotherium* and *Maotherium* the new family Zhangheotheriidae. The third “symmetrodontan” found in Yixian Formation is *Akidolestes* described by Li G. and Luo (2006), who assigned it to the Spalacotheriidae. As with the two other “symmetrodontans” from the Yixian Formation, the os calcaris fused with the ossified cornu calcaris has been preserved on both hind legs of the *Akidolestes* specimen (Li G. and Luo 2006: fig. 1) and even imprints of the keratinous spur are seen (our Fig. 4H). The structure of *Akidolestes* is unusual. As stated by Li G. and Luo (2006: 195): “[...] this new mammal revealed some surprisingly convergent features to monotremes in the lumbar vertebrae, pelvis and hindlimb.” And further (p. 196): “The shoulder girdle and forelimb are similar to those of zhangheotheriids [...]. However, *Akidolestes* differs from zhangheotheriids but is similar to monotremes in many features of the posterior part of the skeleton [...]. Of the six lumbar vertebrae, five have unfused ribs [...], similar to the condition in monotremes, *Repenomamus* [...] and many premammalian cynodonts [...].”

Hurum et al. (2006) described for the first time the structure of the os calcaris in multituberculates, best preserved in *Catopsbaatar* PM 120/107 (Fig. 1B), from the Campanian of Mongolia (see also Kielan-Jaworowska et al. 2002; and Kielan-Jaworowska et al. 2005). In the Jehol Biota so far only a single specimen of a multituberculate has been found, dubbed by Hu and Wang Y.-Q. (2002a, b) *Sinobaatar lingyuaenensis*, and figured also by Chang et al. (2003). In the beautiful book edited by Chang et al. (2003) a counterpart of the specimen illustrated by Hu and Wang Y.-Q. (2002a, b) as the holotype of *Sinobaatar lingyuaenensis* has been illustrated. The specimen is distorted and only preliminarily described. The study of its pictures published by Hu and Wang Y.-Q. (2002a: pl. 1a) and by Chang et al. (2003: fig. 200) lead us to the conclusion that os calcaris might be preserved in it (see our Fig. 4A).

The affinities of the Late Jurassic mammal from the Morrison Formation of Colorado—*Fruitafossor windscheffeli* Luo and Wible, 2005, showing digging adaptations, are uncertain. It has (Luo and Wible 2005: 103): “[...] highly specialized teeth similar to those of xenarthrans and tubulidentate placental mammals and different from the generalized insectivorous or omnivorous dentitions of other Jurassic mammals. [...] Par-

simony analysis suggests that this fossil represents a separate basal mammalian lineage with some dental and vertebral convergences to those of modern xenarthran placentals [...]”. Judging by the reconstruction of *Fruitafossor* (Luo and Wible 2005: fig. 2A), a large part of the postcranial skeleton has been preserved, but the specimen as found has not been illustrated. It has been reconstructed as having a sprawling posture, but the os calcaris or ossified cornu calcaris (and the entire tarsus) have not been preserved.

Hurum et al. (2006) also demonstrated that in several well preserved Cretaceous boreosphenidan tarsi (e.g., Kielan-Jaworowska 1977, 1978; Szalay 1994; Szalay and Trofimov 1996) no trace of an os calcaris has been found. Also in two boreosphenidan mammals described from the Jehol Biota, the eutherian *Eomaia scansoria* Ji Q., Luo, Yuan, Wible, Hang, and Georgi, 2002 and metatherian *Sinodelphys szalayi* Luo, Ji Q., Wible, and Yuan, 2003, no trace of os calcaris or ossified cornu calcaris has been found. Finally, in australosphenidan mammals the cornu calcaris and os calcaris is known only in recent monotremes, as in the fossil australosphenidans the postcranial skeleton has not been preserved. It is not known whether the loss of the spur in boreosphenidans was related to the acquisition of the parasagittal posture, or was rather related to other unknown factors.

Of the early mammals, the os calcaris or ossified cornu calcaris has not been found as yet in morganucodontans, the postcranial skeleton of which is incompletely known (Jenkins and Parrington 1976); in “eupantotherians”, the only incomplete skeleton of which has been preserved in *Henkelotherium* from the Kimmeridgian of Portugal (Krebs 1991; Henkel and Krebs 1977; see also our Fig. 5B); and in “tribotherians” and gondwanatherians, the postcranial skeletons of which are not known (Kielan-Jaworowska et al. 2004). We believe that the spur might have been present in all early mammals, except for the boreosphenidans.

Taphonomic evidence

We observed that the skeletons of mammals preserved in lacustrine sediments may have different positions, depending on their limb posture (Figs. 3–5). This is well documented in the classic study of Weigelt (1927, English translation of 1989). Weigelt introduced the term “passive position”, for a position in which the animal dies. He stated in a discussion of an opossum carcass (1989: 86): “[...] we often find slightly damaged water carcasses in a completely passive position similar to the natural structure of the body” and he continues: “We find this strictly lateral, passive position of the opossum carcass extraordinarily often in fossils”. Weigelt described the passive position in reptiles (1989: 87) as dorsal or ventral: “Fossil reptiles furnish us with many, many examples of the typical passive position of water carcasses. The first that come to mind are the Solnhofen saurians. The dorsal and ventral position is the norm; lateral position seldom occur.”

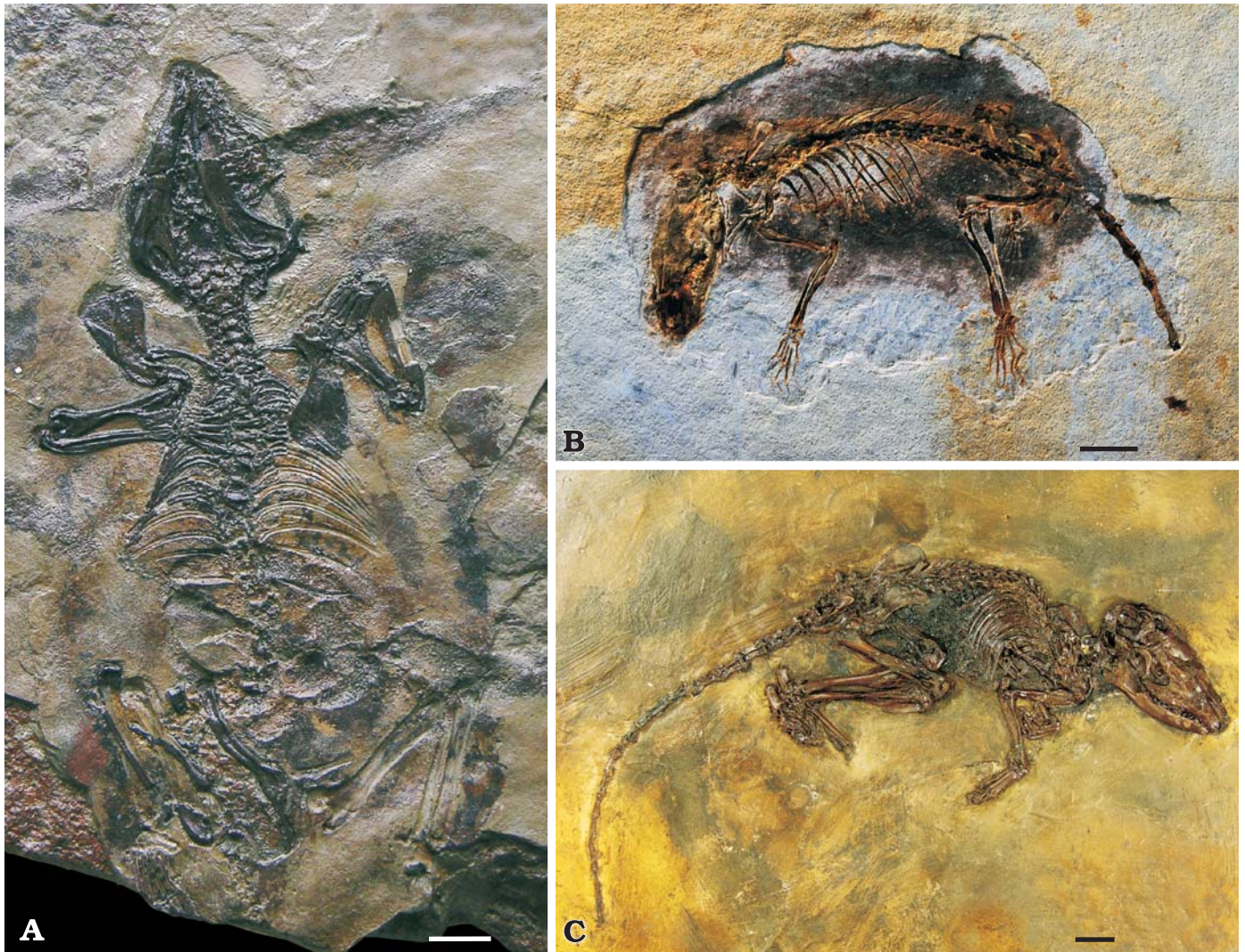
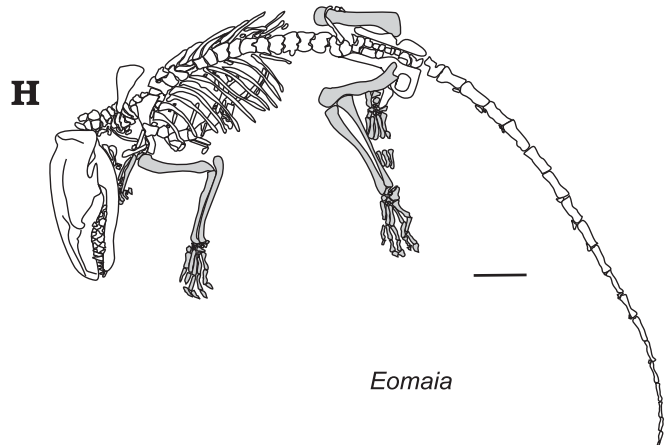
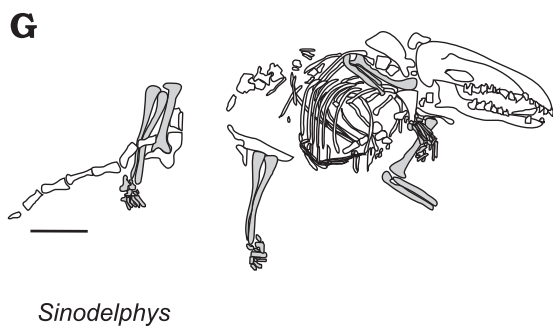
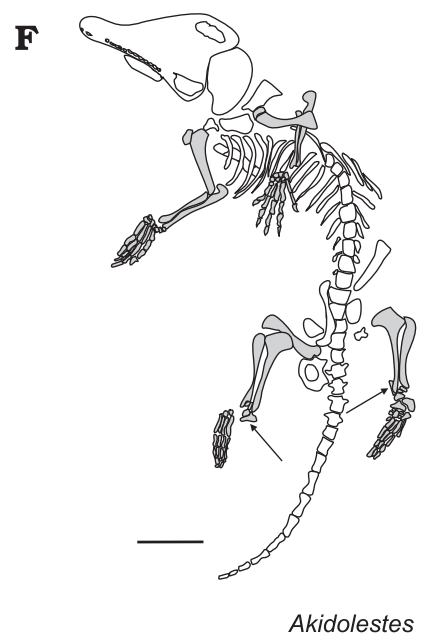
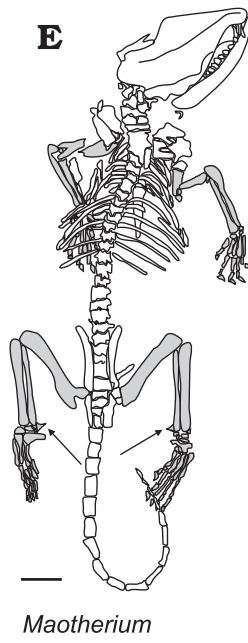
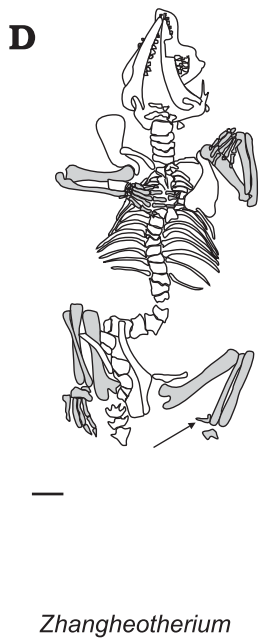
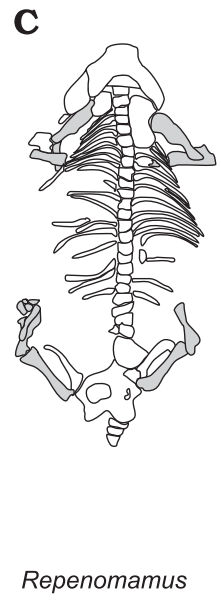
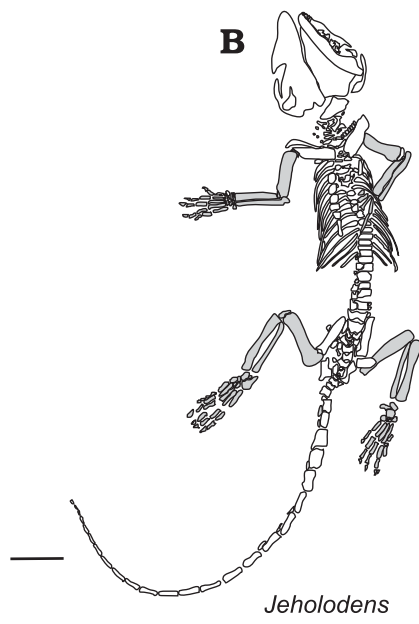
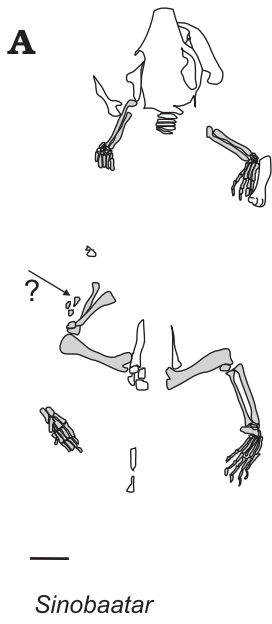


Fig. 3. A comparison of the state of preservation of the skeletons of two Early Cretaceous mammals from the Yixian Formation of Jehol Biota in China (A, B), and an Eocene eutherian mammal from Messel in Germany (C), all preserved in lacustrine sediments. A. “Symmetrodontan” *Zhangheotherium quinquecuspidens* Hu, Wang Y.-Q., Luo, and Li Ch.-K., 1997 (cast of IVPP V7466). B. Early eutherian *Eomaia scansoria* Ji Q., Luo, Yuan, Wible, Hang, and Georgi, 2002. (CAGS 01-IG-1). C. Amphilemurine insectivore *Macrocranium tupaodon* Weitzel, 1949 (PMO 207.791). *Eomaia* and *Macrocranium* are eutherians with parasagittal limbs and are preserved lying on their sides, *Zhangheotherium* belongs to “symmetrodontans” with sprawling limbs and has been preserved in a position characteristic of animals with sprawling posture, lying on its back. Scale bars 10 mm.

Fig. 4. Diagrammatical drawings of the skeletons of Mesozoic mammals from the Jehol Biota (Early Cretaceous Yixian Formation) preserved in lacustrine sediments, re-drawn and simplified from the original photographs or published drawings, showing different states of preservation depending of the position of the limb posture. All are rendered to approximately the same length. Limb bones are shaded in grey. The arrows point to the os calcaris. A–F. Skeletons of early mammals with a sprawling posture, preserved dorso-ventrally compressed and exposed in dorsal or ventral views, showing abducted limbs. G, H. Skeletons of boreosphenidan mammals with parasagittal posture, preserved lying on their flanks, as the presence of parasagittal limbs did not allow preservation in another position. A. *Sinobaatar lingyuanensis* Hu and Wang Y.-Q., 2002a, a multituberculata in dorsal view, drawn from Hu and Wang Y.-Q. (2002a: pl. 1a). B. *Jeholodens jenkinsi* Ji Q., Luo, and Ji S.-A., 1999, a eutriconodontan in dorsal view, based on Ji Q. et al. (1999: fig. 1a). C. *Repenomamus robustus* Li J.-L., Wang Y., Wang Y.-Q., and Li Ch.-K., 2001, a eutriconodontan in dorsal view, based on Hu et al. (2005: fig. A in supplementary online data). D. *Zhangheotherium quinquecuspidens* Hu, Wang Y.-Q., Luo, and Li Ch.-K., 1997, a “symmetrodontan” in ventral view, based on Hu et al. (1997: fig. 1b). E. *Maothierium sinensis* Rougier, Ji Q., and Novacek, 2003, a “symmetrodontan” in dorsal view, based on Rougier et al. (2003: pl. 1). F. *Akidolestes cifellii* Li G. and Luo, 2006, a “symmetrodontan” in ventral view, based on Li G. and Luo (2006: fig. 1b). G. *Sinodelphys szalayi* Luo, Ji Q., Wible, and Yuan, 2003, a metatherian in side view, based on Luo et al. (2003: SOM-fig. 1 in supplementary online data). H. *Eomaia scansoria* Ji Q., Luo, Yuan, Wible, Hang, and Georgi, 2002, a eutherian in side view, based on Ji Q. et al. (2002: fig. 1b). Scale bars 10 mm. →



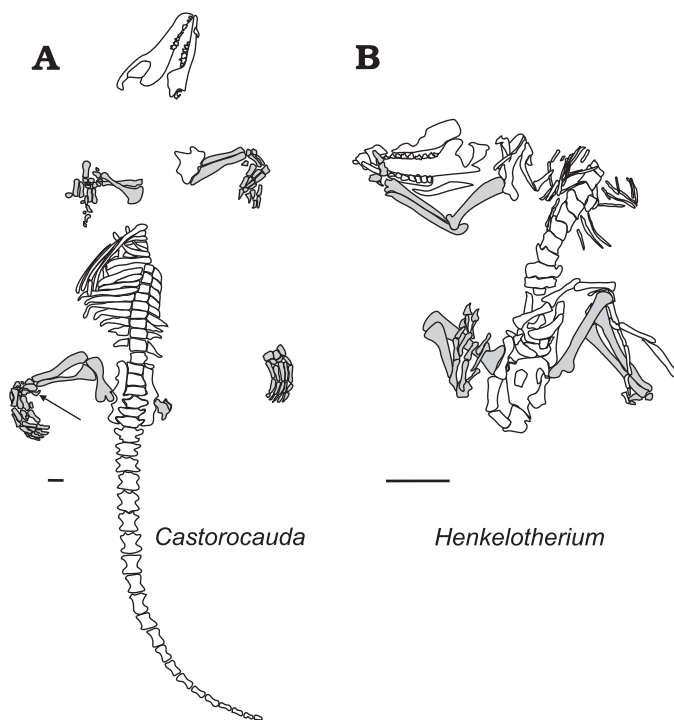


Fig. 5. Diagrammatic drawings of two skeletons of Mesozoic mammals from lacustrine sediments, re-drawn and simplified from the published drawings. Limb bones are shaded in grey. The arrow points to os calcaris. Both skeletons show sprawling posture. They are preserved dorso-ventrally compressed and exposed in ventral views, showing abducted limbs (as those in Jehol Biota, illustrated in Fig. 4A–F). **A.** *Castorocauda lutrasimilis* Ji Q., Luo, Yuan, and Tabrum, 2006, a Middle Jurassic docodontan from north-west China, in ventral view, based on Ji Q. et al. (2006: fig. 1b). **B.** *Henkelotherium guimarotae* Krebs, 1991, a “eupantotherian” from the Kimmeridgian of Portugal, in ventral view, based on Henkel and Krebs (1977). Scale bars 10 mm.

In the well known Eocene locality of Messel in Germany, in which the bulk of mammalian taxa belongs to placental mammals, and two to marsupials, all the skeletons (except for bats, e.g., representatives of *Archaeonycteris* and *Palaeochiropteryx*, and pangolins, including several skeletons of *Eomanis waldi* Storch, 1978 and one skeleton of *Eomanis krebsi* Storch and Martin, 1994) have been preserved lying on their flanks in the typical mammalian passive position (Schaal and Ziegler 1992; Koenigswald and Storch 1998; Habersetzer and Schaal 2004; see also our Fig. 3C). The reason for this passive positioning is obvious, as boreosphenidan mammals (both marsupials and placentals) presumably acquired parasagittal posture sometime during the Early Cretaceous, or even earlier, and their common resting (and dying) position, as nowadays, is on the side. The different position of the skeletons of bats is also obvious, due to the transformation of their forelimbs into wings, and in pangolins due to the scaly integument. The reptiles and amphibians from the same locality are mostly preserved in the typical reptilian/amphibian passive position, dorso-ventrally compressed.

In a similar taphonomic setting of the Early Cretaceous Jehol Biota from China, the majority of the mammal skeletons have been differently preserved (Fig. 4A–F). Out of eight mammal genera: *Sinobaatar*, *Jeholodens*, *Repenomamus* (represented by two species), *Zhangheotherium*, *Maothierium*, *Akidolestes*, *Sinodelphys*, and *Eomaia*, so far described from the Jehol Biota, only the two boreosphenidan mammals *Sinodelphys* (Fig. 4G) and *Eomaia* (Figs. 3B, 4H) have been preserved lying on their flanks. The passive position of these two boreosphenidan genera is the same as those of Eocene mammals from Messel (Fig. 3C), indicating a parasagittal posture for *Sinodelphys* and *Eomaia*. The passive positions of lizards and amphibians from the Jehol Biota are mostly dorsoventrally compressed, as in the Messel locality. This rule is less rigorous for preservation of dinosaur skeletons. For example Ji Q. et al. (2001: fig. 1) published the dorso-ventrally compressed skeleton of a small dromaeosaurid dinosaur from the same Biota, characteristic for taxa with sprawling posture, rather than parasagittal as characteristic for dinosaurs. Dromaeosaurids, however, are bipedal, and hence very different from early mammals discussed herein. The specimen is a juvenile with possibly more movement in the joints than more mature individuals. To our knowledge, most other non-avian theropods from the locality are preserved lying in a lateral passive position (e.g., *Caudipteryx*, *Sinosauropteryx*, *Protarchaeopteryx*; see pictures in Chang et al. 2003). This issue would require a special study, which is beyond the scope of our paper.

We speculate that the six skeletons of early mammals from the Jehol Biota, belonging to multituberculates, eutriconodontans, and “symmetrodontans” (Fig. 4A–F), are preserved in their passive position, i.e., dorso-ventrally compressed due to their sprawling stance. This means that the resting and dying position lying on their bellies or backs, rather than on the side, is indicative of the posture of their legs. Two other early mammal taxa, illustrated in Fig. 5, the docodontan *Castorocauda* (Fig. 5A), from the Middle Jurassic of north-west China, and the “eupantotherian” *Henkelotherium* (Fig. 5B) from the Kimmeridgian Guimarota coal mine of Portugal, have also been preserved lying on their backs, as characteristic of animals with sprawling legs. They are both preserved in lacustrine sediments and compressed similarly to Jehol Biota specimens. Uncompressed specimens from the Late Cretaceous of the Gobi Desert, preserved in sand dunes or other terrestrial environments, display different taphonomic conditions and are not comparable to those preserved in lacustrine sediments.

The two species of *Repenomamus* were found in the lowermost Yixian Formation (Lujiatun bed) and are preserved in tuffs. These tuffs show less compacting than the younger, more silty sediments of the Jianshangou and Dawangzhangzi beds, which contain the other mammals from the Jehol Biota discussed in this paper. The specimens figured by Hu et al. (2005: fig. 2) of *Repenomamus giganticus*, and *Repenomamus robustus* (Hu et al. 2005: fig. 3, and Fig. 4C herein)

still show the sprawling hind limbs in both species, and sprawling forelimbs in *Repenomamus robustus*.

Maothierium sinensis, a “symmetrodon” from the Yixian Formation (Fig. 4E), shows another interesting taphonomic feature. It is the only mammal from the Jehol Biota in which the humeri are broken into several pieces. We presume that this resulted from post mortem damage, caused perhaps by a more parasagittal posture of the forelimbs than the hind limbs. As the skeleton has been preserved lying on its belly, as characteristic for the preservation of individuals with sprawling hind limbs, the humeri arranged more parasagittally have been broken, when forced to acquire a sprawling position.

Out of eight taxa showing a sprawling stance, illustrated in Figs. 4A–F and 5A, B, the uncontested evidence of a spur, the os calcaris with co-ossified cornu calcaris (marked by an arrow), has been preserved in four of them, but we also mark a possible os calcaris present in *Sinobaatar* (Fig. 4A). In our opinion it is possible that the spur might have been present in all the taxa of early mammals showing sprawling posture.

Discussion and conclusions

When boreosphenidan mammals acquired a parasagittal posture, sometime during the Early Cretaceous or even latest Jurassic, the evolution from the sprawling to the fully parasagittal posture was gradual and certainly involved several intermediate stages. It is also possible that in some instances (see, e.g., Ji Q. et al. 1999) forelimbs and hind limbs changed at a different rate, as a rule the forelimbs acquired a more parasagittal posture earlier than the hind limbs. Using cineradiography, Jenkins (1971) demonstrated that in non-cursorial small Recent mammals (echidna, opossum, tree shrew, hamster, rat, and ferret), the humerus is abducted 90 degrees from the parasagittal plane in echidna (which has a fully sprawling posture), and varies between 10 to 30 degrees of abduction from the parasagittal plane in studied boreosphenidan mammals, the posture of which has generally been previously referred to as parasagittal. Another interesting result of Jenkins’ study is that the degree of femoral abduction in studied non-cursorial mammals is higher than for the humerus, and varies between 20 to 50 degrees from the parasagittal plane. By the current scheme of phylogeny of Mesozoic mammals (Luo et al. 2002; Kielan-Jaworowska et al. 2004; Luo and Wible 2005), the mammalian forelimbs might have acquired a more parasagittal posture earlier than the hind limbs. This is also evident from studies of the mammalian gait. The main propulsive force comes from the hind limbs. When extended forward they pass lateral to the forelimbs, and are therefore less parasagittal. On the other hand, the hind limbs are more parasagittal than the forelimbs in monotremes and also in crocodiles (personal communication from Alexander N. Kuznetsov, June, 2006).

As the cineradiographic method cannot be adopted in studies of fossil mammals, reconstruction of posture is fairly

arbitrary and results in usage of poorly defined terms such as “somewhat more reptilian posture”, “more highly evolved [posture]”, “more parasagittal forelimb posture”, etc. The different interpretations of the forelimb posture in a “symmetrodon” *Zhangheotherium* by Hu et al. (1997, 1998) and Sereno (2006), and similarly in the eutriconodontan *Jeholodens* by Ji Q. et al. (1999) and Sereno (2006), who in both cases studied the same single specimens, show how different conclusions may be, based on studies of the same fossil material.

The controversy in interpretation of multituberculate posture between Kielan-Jaworowska and Gambaryan (1994) and Gambaryan and Kielan-Jaworowska (1997) on one hand, and Sereno and McKenna (1995) and Sereno (2006) on the other, appears to be related to the fact that these two groups of authors studied different girdles and limbs. Kielan-Jaworowska and Gambaryan (1994) concentrated mostly on analysis of the pelvic girdle and the hind limbs. In their subsequent paper (Gambaryan and Kielan-Jaworowska 1997) they discussed the evidence from the structure of the humerus (the shoulder girdle was at that time incompletely known). On the other hand Sereno and McKenna (1995) and Sereno (2006) studied only the shoulder girdle and forelimbs.

As discussed under “Evidence from the forelimbs”, only one of the four points listed by Sereno (2006: 360)—the mobile clavicle-interclavicle articulation, might possibly indicate parasagittalism; the three remaining are equivocal.

In particular the third point of Sereno’s list “cam-shaped ulnar condyle of the humerus” has been, in our opinion, wrongly interpreted. Jenkins (1973: 281) argued that the therian trochlea evolved by enlargement of the intercondylar groove. In spite of the cam-shaped ulnar condyle in multituberculates, the intercondylar groove is not enlarged in any known humerus.

If parasagittalism would indeed have originated in a common ancestor of multituberculates and boreosphenidan mammals, as advocated by Sereno and McKenna (1995) and Sereno (2006), one should expect the development of structures indicating parasagittalism in boreosphenidans and multituberculates of the same age. While the Campanian eutherian *Barunlestes* (see Gambaryan and Kielan-Jaworowska 1997: fig. 4C), and the oldest known Campanian metatherian *Asiatherium* (Szalay and Trofimov 1996: figs. 14–16) show an incipient trochlea, indicating beginning of parasagittalism, no Cretaceous multituberculate humerus shows such a structure (Deischl 1964; Kielan-Jaworowska and Dashzeveg 1978; Kielan-Jaworowska and Gambaryan 1994). The difference is even more striking among the Paleocene forms. Early Paleocene marsupials, e.g., *Pucadelphys* and *Mayulestes* from Bolivia (Marshall and Sigogneau-Russell 1995; Muizon 1998), show a fully developed humeral trochlea. The same concerns all Paleocene eutherians in which the postcranial skeleton is known, see e.g., numerous papers reviewed in *The Rise of Placental Mammals*, edited by Rose and Archibald (2005). In contrast, the Paleocene multituberculates of North America: *Stygimys*, *Ptilodus*, and *Mesodma* (Gidley 1909; Jenkins 1973;

Krause and Jenkins 1983), as well as the Chinese Eocene multituberculate *Lambdopsalis* (Kielan-Jaworowska and Qi 1990; Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1997), show a fully developed condylar structure of the humerus, with a narrow intercondylar groove. This demonstrates that multituberculates retained the structure characteristic of tetrapods with primitively sprawling posture till the end of their existence.

The difference between multituberculate and boreosphenidan humeri may be also observed on an example of fossorial boreosphenidans, which secondarily acquired a sprawling or half-sprawling stance. The humerus in the fossorial boreosphenidans differs from that of the tetrapods with a primarily sprawling stance in having a trochlea and radial condyle (see Gambaryan and Kielan-Jaworowska 1997: figs. 4, 5), but no ulnar condyle, which is preserved in all the multituberculates.

With respect to the pelvic girdle and hind limbs, the data discussed by Hurum et al. (2006) provide additional evidence in favor of the sprawling posture hypothesis forwarded by Kielan-Jaworowska and Gambaryan (1994) with respect to multituberculates. We speculate that all mammals that possessed an extratarsal spur (docodontans, multituberculates, eutriconodontans, "symmetrodontans"), and possibly also other non-boreosphenidan Mesozoic mammals, in which the os calcaris and a fused ossified cornu calcaris are still to be found, had (like monotremes) a sprawling posture of the hind limbs.

There are, however, several unresolved problems related to the presence of a spur in Recent and fossil mammals. Calaby (1968) described how the venomous spur of platypuses was used for defense, and can inflict serious injuries on much larger mammals, such as humans. If it is used for defense, the question arises as to why it has disappeared in females of platypus? On the other hand it is present in some females of echidna, albeit not poisonous (Griffiths 1968). In his second book, Griffiths (1978) demonstrated that there is clear evidence that the spur in platypus is used for territorial defense (competition between males). He also cited the Ph.D. thesis of Temple-Smith (1973, not available to us), who demonstrated that the venomous secretions in platypus vary with the reproductive cycle. The available material of fossil spurs is too limited to venture an opinion whether in fossil mammals the spur has disappeared in females or not. To our knowledge, nothing is known either on the origin of the os calcaris and cornu calcaris.

As discussed under "Introduction", we reconstruct the multituberculate foot as plantigrade in resting position, but as digitigrade (as in most plantigrade mammals), when running fast and jumping (see Fig. 2).

In summary, we accept the hypothesis that multituberculate hind limbs had a sprawling posture (Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1997). As discussed above, it cannot be demonstrated with any certainty whether the forelimbs in multituberculate and in some other early mammals might have had a more parasagittal posture than the hind limbs. The idea of Sereno and

McKenna (1995) and Sereno (2006), that parasagittalism developed in mammalian evolution in a common ancestor of multituberculates and boreosphenidan (therian) mammals, does not hold in the light of available facts and oversimplifies a wide range of variation of forelimb structures that are best considered to have a varying degree of parasagittal posture (Rougier et al. 1996; Hu et al. 1997, 1998).

Evidence from taphonomy of early mammals preserved in lacustrine environments is also considered to indicate the abducted limbs in non-boreosphenidan mammals.

We believe that parasagittalism developed in the evolution of mammals only once, however, not in the common ancestors of multituberculates and boreosphenidans, but rather in early boreosphenidans.

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