CRURO-PEDAL STRUCTURE OF THE PAULCHOFFATIID RUGOSODON EURASIATICUS AND EVOLUTION OF THE MULTITUBERCULATE ANKLE

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Here we describe the osteological structures of the lower hind limb and foot of the Late Jurassic Rugosodon eurasiaticus, the earliest-known postcranial fossil of a multituberculate mammal. This fossil extends the key cruro-tarsal apomorphies, previously known from multituberculates of the Cretaceous and Paleogene, to the paulchoffatiid multituberculates of the Jurassic. Multituberculates as a group can now be diagnosed by derived features of the astragalus, the navicular, and the entocuneiform. These features are correlated with the mobility of the upper ankle joint and pedal digit I, indicating that early multituberculates acquired new locomotor functions of the limb and foot. However, the standing pedal posture of the basal multituberculates is plantigrade, typical of primitive mammaliaforms. The digitigrade posture appeared later in derived multituberculates of the Late Cretaceous and Paleogene, and was accompanied by several derived features of the calcaneus: elongation of the calcaneal tuber, development of the peroneal process and groove, and medio-lateral compression of the proximal part of calcaneus. These derived features enhanced locomotor function by increasing the in-lever of the Achilles muscles to lift the calcaneal heel off the substrate. The derived calcaneo-cuboidal features also facilitated a wider range of movement (including abduction) of the distal pedal elements. We concur that derived multituberculates may have had digitigrade pedal posture, although only facultatively. New fossils of the Jurassic Rugosodon and Early Cretaceous Sinobaatar have revealed fresh evidence that the astragalar features of the earliest paulchoffatiids are correlated with sophisticated cruro-tarsal rotation as in other multituberculates. Rugosodon provides the ancestral condition from which more diverse calcaneal features for more versatile functions evolved in geologically vounger and more derived multituberculates.

Key words: Hind limb, tarsals, multituberculates, mammal evolution, Jurassic.

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INTRODUCTION

Multituberculates are the most diverse mammals of the Mesozoic. They are not only speciose (Kielan-Jaworowska *et al.* 2004; Rose 2006; Luo 2007), but also show significant morphological disparity and variation in body size during the Late Cretaceous (Wilson *et al.* 2012). Multituberculates have a range of dental morphological features that indicate versatile feeding adaptation from animal-dominated omnivory to herbivory (Wilson *et al.* 2012). They also have very distinctive tarsal characteristics related to their locomotor functions (Simpson 1926; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994; Yuan *et al.* 2013).

The paulchoffatiids represent the basal-most clade of multituberculates (Hahn 1969, 1993; Hahn and Hahn 1998, 2000; Kielan-Jaworowska *et al.* 2004). They are almost entirely Late Jurassic (Hahn and Hahn 1998; Kielan-Jaworowska *et al.* 2004), with one possible exception in the Early Cretaceous of North America (Cifelli *et al.* 2013). The morphological features of paulchoffatiids are informative about the ancestral condition of multituberculates, and are also useful for distinguishing multituberculates from other mammaliaforms. The type specimen of *Rugosodon* is the only skeletal fossil known, so far, from the family Paulchoffatiidae. It is also the earliest-known skeletal fossil of any multituberculate. Previously, the hind limb and tarsal features of *Rugosodon eurasiaticus* only received a brief description in a preliminary study (Yuan *et al.* 2013). Here we offer a detailed description of these features and explore their ramifications for the skeletal evolution of multituberculates as a whole.

Multituberculates of the Late Cretaceous and Paleogene have been long known for their derived hind limb and pedal features (Simpson and Elftman 1928; Kielan-Jaworowska 1979, 1989; Jenkins and Krause 1983). Some of the better-preserved postcranial skeletal fossils have been documented by detailed studies (Krause and Jenkins 1983; Kielan-Jaworowska and Qi 1990; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008). Our present study of *Rugosodon* reveals that many derived hind limb and pedal features, hitherto known in the Cretaceous and Paleogene multituberculates, can now be traced to the basal-most paulchoffatiids of the Jurassic, and are therefore diagnostic of all multituberculates (inclusive of paulchoffatiids; Yuan *et al.* 2013).

Our comparative study can now also demonstrate that multituberculates show a range of disparity of their hind limb and pedal structures. These morphological differences can be attributable to diverse locomotor functions among different multituberculates, and suggest that different Mesozoic multituberculates may have developed preferences for different substrates. Their limbs and pedes show a significant ecomorphological diversity, as was already known from the functional morphology of their teeth.

Institutional abbreviations. — BMNH, Beijing Museum of Natural History, Beijing, China; CAGS, Chinese Academy of Geological Sciences, Institute of Geology, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NGMC (GMV), National Geological Museum of China, Beijing, China; PM, Paleontological Center of Mongolian Academy of Sciences; ZPALMgM, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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FOSSIL MATERIAL

Holotype specimen. — The holotype of *Rugosodon eurasiaticus* (BMNH 1142) consists of the main slab (1142A) and the counter-slab (1142B) (Figs 1–5). The fossil was originally found at the Daxishan fossil site of the Jurassic Tiaojishan Formation, and was later acquired by Beijing Museum of Natural History. The site has been dated to between 158.5 ± 1.6 ma and 161.0 ± 1.44 ma (Liu *et al.* 2012). These dates for the site have been corroborated by an independent study (Wang *et al.* 2013).

The holotype slabs were preserved with two specimens of the small estheriid conchostracan *Qaidames-theria* (*sensu* Liao and Huang 2014). This is an index invertebrate fossil from the main fossiliferous layers of the Tiaojishan Formation. Shale and mudstone slabs of vertebrate fossils from the several quarries of the Daxishan site are typically preserved with a moderate abundance of *Qaidamestheria* specimens (Liao and Huang 2014; Huang 2015; Huang *et al.* 2015). The presence of the small conchostracan *Qaidamestheria* on the slabs of this mammal fossil helped to authenticate that the specimen is from the Daxishan site.

Taxonomy. — *Rugosodon eurasiaticus* (BMNH 1142) is assigned to the paulchoffatiid clade by its dental features. The lower molars of *R. eurasiaticus* are nearly identical to those of *Plesiochoffatia*, a paulchoffatiid multituberculate from the Late Jurassic Guimarota Mines of Portugal (Hahn and Hahn 1998, 1999, 2000). *Rugosodon* and *Plesiochoffatia* show strong similarities in the occlusal surfaces of both upper and lower molars: dense pits, ridges, grooves, and a highly corrugated middle valley, rimmed by crenulated tooth margins with coalesced cusps. The lower molars are also similar in having a tall and trenchant anterolingual cusp, and in overall oblong shape of the occlusal basin (Yuan *et al.* 2013, figs S3, S4). The M2 is similar to M2s assigned to *Plesiochoffatia* and the upper molars of other paulchoffatiids in having a crenulated antero-buccal ridge or shelf (Hahn 1969, 1993; Hahn and Hahn 2000). M2 of *Rugosodon* and paulchoffatiids from the Late Jurassic of Portugal are also similar in that the middle valley is posteriorly closed by a cusp or ridge (Hahn and Hahn 1998; see also Yuan *et al.* 2013, figs S3, S4). *Rugosodon* can be distinguished from most non-paulchoffatiid multituberculates in having these derived features (Yuan *et al.* 2013).

Of all paulchoffatiid multituberculates, *Rugosodon* is most similar to *Plesiochoffatia* but it is 150% to 200% larger than *Plesiochoffatia* by the size of lower m1. Also its occlusal surfaces are more densely ornamented than those of *Plesiochoffatia* (Yuan *et al.* 2013).

Orientation of fossil structure on slabs. — Because the same bones and their impressions and mold outlines are preserved on both the main slab (1142A) and the counter-slab (1142B), it is necessary to establish the right versus the left sides of the skeleton, for descriptive purposes. We designate, *a priori*, the right side versus the left side of the skeleton, as seen on the main slab (BMNH 1142A) (Figs 1, 2, 4). The right vs. left sides of the skeletal structures (or the impressions thereof) on the counter-slab (BMNH1142B; Figs 3, 5) are determined according to the left-right orientation on BMNH1142A.

CRURAL MORPHOLOGY

The proximal part of the tibia possesses an anterior tibial tuberosity, a medial tuberosity, and a large, hook-like lateral process (Figs 5, 6). The latter process is also known as proximolateral process (Kielan-Jaworowska and Gambaryan 1994). This is homologous to the "lateral condyle" of extant therian mammals (*sensu* Evans 1995). The proximal end of the tibia is asymmetrical because the lateral process is much larger and longer than the medial tuberosity (Fig. 6). A low anterior tibial crest extends from a prominent anterior tibial crest is interpreted to be the area of origination for M. tibialis anterior (*sensu* Kielan-Jaworowska and Gambaryan 1994). This is similar to the tibialis anterior fossa of extant small placentals (Neveu and Gasc 2002). The shaft of the tibia is relatively straight (Figs 5, 6), and is not bowed medially as seen in the Late Cretaceous *Chulsanbaatar*, *Nemegtbaatar*, and *Catopsbaatar* (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008).

The distal extremity of the tibia is distinctly longer than the distal extremity of the fibula (Figs 5, 6). It shows a distinctive suture between the epiphysis and the diaphysis (shaft). The distal end of the tibial epiphysis has a medial malleolus, called the medial tibial condyle (*sensu* Krause and Jenkins 1983). Although the



Fig. 1. The paulchoffatiid Rugosodon eurasiaticus Yuan et al., 2013 (BMNH1142A), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China. Pedal structure preserved on the main slab of the type specimen. A. Skeleton and the location of the right and left pedes, photo (A₁) and explanatory drawing (A₂). B. Right pes in dorsal view. C. Left pes on main slab in dorsal view.

distal part of the tibia is not fully exposed in distal view due to its intact association with the astragalus, the medial tibial condyle can be seen in the anterior view of the tibia (Figs 4, 6). In anterior view, the profile of the distal tibia is similar to those of *Ptilodus* and *Eucosmodon* (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994); thus we interpret *Rugosodon* as having the medial and lateral articulating condyles on the tibia, for the corresponding structures on the astragalus (Figs 6, 7), as in the Paleocene multituberculates *Ptilodus* and *Eucosmodon*.

A large and plate-like parafibula is present, and abuts the proximal end of the fibula (Figs 5, 6), but it is not fused with the fibula, thus differing from those of monotremes (Lessertisseur and Saban 1967; Gambaryan *et al.* 2002), or as seen in the spalacotherioid *Akidolestes* (Li and Luo 2006; Chen and Luo 2013). The overall features of the parafibula and the proximal fibula are similar in *Sinobaatar* (NGMC3000).

The unfused parafibula of *Rugosodon* (Figs 5, 6) is shared by all other multituberculates in which the relevant anatomy is preserved (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Hu and Wang 2002; Bolortsetseg 2008). The condition in *Rugosodon* suggests that a separate parafibula is a plesiomorphy of all multituberculates including paulchoffatiids. The bone, however, is much larger in *Rugosodon* than in *Kryptobaatar* and *Chulsanbaatar* (Kielan-Jaworowska and Gambaryan 1994) and *Sinobaatar* (Wang *et al.* 2003; personal observation).

Implications of the parafibula for functional comparison with other mammals will be discussed below in the "Functional Morphology" section of this paper.

The fibula has a straight shaft (diaphysis; Figs 5, 6), not bowed as those of several Cretaceous multituberculates (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008). The fibular head is bilaterally compressed and fan-shaped. It is significantly wider than the shaft. *Rugosodon* lacks the hook-like posterior projection from the proximal end of the fibula, as seen in several Cretaceous multituberculates.

The distal fibula has a clear suture between the diaphysis and the epiphysis (Fig. 4). The articulating surface is relatively flat to slightly convex (Figs 4, 6). By our assessment, it does not show a distinctive, pointed lateral malleolus, as in *Kryptobaatar* (Kielan-Jaworowska and Gambaryan 1994, fig. 2), *Ptilodus* (Krause and Jenkins 1983), and *Eucosmodon* (Szalay 1993). As preserved, the distal end of the fibula clearly contacted the calcaneus (Fig. 6), in addition to the astragalo-fibular contact. However, the fibula of *Rugosodon* does not show a dividing crest that separates the astragalo-fibular facet from the calcaneo-fibular facets (Figs 4, 6). Together, the distal end of the fibula and the distal extremity of the tibia form a curved contact with the astragalus and the calcaneus (Fig. 6D), as characterized for *Nemegtbaatar*, *Chulsanbaatar* and *Catopsbaatar* (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008), *Ptilodus* (Krause and Jenkins 1983), and other multituberculates (Szalay 1993). In all essential respects, *Sinobaatar* is similar to *Rugosodon* in these features.



Fig. 2. Foot and tarsal elements of *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (A, B; BMNH1142A, Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China) and *Eucosmodon* sp. (C, D; AMNH 16325, locality near Kimbetoh, Nacimiento Formation, early Paleocene, New Mexico, USA). A. Left pes in dorsal view, stereo photographs (A₁) and explanatory drawing (A₂); proximal and intermediate phalanges of digit V are missing. Details of tarsals and metatarsals in dorsal view (A₃); the navicular is ajar from the astragalus; the astragalus is slightly displaced relative to the calcaneus (in Yuan *et al.* 2013: fig. 2, this illustration was incorrectly identified as "ventral view"). B. Articulated entocuneiform and MT I in oblique dorsal view. C. Entocuneiform in medial view and metatarsal in dorsal view, showing the reciprocal saddle-shaped joint on the distal end of entocuneiform and the proximal end of MT I. D. Astragalus in dorsal view (or tilted dorsal view). Abbreviations: Ip, intermediate phalanx; MT, metatarsal; Pp, proximal phalanx; Tp, terminal phalanx.

TARSAL MORPHOLOGY

The calcaneus is the largest of all tarsal bones of *Rugosodon* (Figs 1–6). The peroneal shelf has a rectangular outline and is mediolaterally broad (Fig. 8). It lacks the distinctive peroneal process (or peroneal tuber of some authors) separated by a peroneal groove (*sensu* Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). The calcaneal body is dorsoventrally compressed and wide mediolaterally between the sustentacular area on the medial side and the lateral (peroneal) border (Fig. 8E). The calcaneal tuber is short, being less



Fig. 3. *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142B), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China; left pes preserved in outlines and impressions in dorsal view on the counter slab. Stereo photographs (A), explanatory drawing (B). Proximal and intermediate phalanges of digit V are missing. Abbreviations: Ip, intermediate phalanx; MT, metatarsal; Pp, proximal phalanx.

than 20% of the total length of the calcaneus, and it is pointed (Figs 4–6). The cuboid facet is on the mediodistal corner of the calcaneus. Although its surface is not fully exposed, we infer from its exposed dorsal margin that, overall, the cuboidal facet is concave. The astragalar facet on the calcaneus is convex (Figs 4, 6), as seen in other multituberculates (Krause and Jenkins 1983; Szalay 1994). However, the sustentacular area of the calcaneus is not exposed. As preserved in the intact ankle (Figs 4, 6), the calcaneo-fibular contact appears to be extensive but the tibia has no possibility to contact the calcaneus (Figs 4, 6, 9), as interpreted for several Paleogene multituberculates (Krause and Jenkins 1983; Szalay 1993).

The astragalus is exposed in dorsal view on the left pes (Fig. 2) and in dorso-medial view on the right (Fig. 4). The bone is ajar from the calcaneus in the right pes in such a way that the flexed surface (under side) of the right astragalus is partially visible (Figs 4, 6B). This reveals the calcaneo-astragalar contact to some extent. The curvature and the shape of the calcaneo-astragalar contact (Fig. 6B) are similar to those of the isolated calcaneus and astragalus of other multituberculates (Jenkins and Krause 1983; Krause and Jenkins, 1983; Szalay 1993, 1994; Kielan-Jaworowska and Gambaryan 1994; Hurum *et al.* 2008). The calcaneo-astragalar facet appears to be separate from the sustentacular facet in the right astragalus, as in other mammals. However, the dividing sulcus is not well preserved; the part of the sulcus where the astragalar foramen would be located in an intact astragalus (Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008) is not exposed, so our interpretation of these two facets is tentative.

The proximal (posterior) part is narrower than the distal (anterior) end. The dorsal aspect of the astragalus has extensive contact with the fibula. On the medial (proximal) surface the astragalus has two shallow depressions, which we interpret to be the medial astragalo-tibial facet and the lateral astragalo-tibial facet (*sensu* Jenkins and Krause 1983), respectively for articulation with the medial tibial condyle and the lateral tibial condyle (Figs 2B, C, 6C). These shallow facets are not distinctively demarcated from each other, similar to the condition of several Late Cretaceous multituberculates as noted in some previous studies (Szalay 1993, p. 121; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008) but different from the distinctive crest of the two facets as seen in *Eucosmodon* (Krause and Jenkins 1983; Szalay 1994).

The navicular facet on the distal aspect of the astragalus is a curved groove. It is concave in dorso-ventral plane and also slightly curved from the medial side to the lateral side. Overall, the astragalo-navicular contact is somewhat like a saddle (Figs 2, 7). This morphology is similar to the astragalo-navicular joint well described for other multituberculates (Krause and Jenkins 1983; Szalay 1994; Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008).

We identify the os calcaris bone for supporting the extratarsal spur in the left foot of the main slab (BMNH1142A; Fig. 2). The bone has a crescent shape. As preserved, it is attached to the posterior aspect of the astragalus. A similar association of the os calcaris and the astragalus has been documented for several



Fig. 4. *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142A; Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China); right lower leg and pes preserved on the main slab in dorsal view. **A**. Stereo photographs. **B**. Explanatory drawing. The right pes is mostly preserved in bones on BMNH1142A, and its corresponding impression and mold outlines are on BMNH1142B. MT, metatarsal.

Late Cretaceous multituberculates, including *Kryptobaatar dashzevegi* (ZPALMgM-I/41) and *Catopsbaatar catopsaloides* (PM120/107) (Hurum *et al.* 2006, p. 5, fig. 5; Hurum and Kielan-Jaworowska 2008). A less likely possibility is that this bony piece would belong to a disarticulated tibial epiphysis of the left hind limb of the specimen. This can be ruled out because the preserved left tibia has at least a part of its epiphysis in situ and still attached to the diaphysis of the tibia. The identification of the os calcaris in multituberculates and other extinct mammaliaforms is ultimately based on a similar association of the os calcaris and the astragalus in extant monotremes (Hurum *et al.* 2006; Ji *et al.* 2006; Kielan-Jaworowska and Hurum 2006; Zhou *et al.* 2013; Luo *et al.* 2015). Because the os calcaris is embedded in the soft-tissues of the ankle region but not directly articulated with the astragalus in extant monotremes, its close proximity to the astragalus is the only way to identify this structure (Hurum *et al.* 2006).

The cuboid has a square-like outline in dorsal view and is antero-medial (disto-medial) to the calcaneus in *Rugosodon* (Fig. 2). The bone fits, obliquely, into the concave proximo-medial margin of the calcaneus. It is medial to the imaginary proximo-distal (long) axis of the calcaneus. In the proximo-distal orientation of the calcaneus and the cuboid, this facet faces antero-medially (Fig. 6C). The facet appears to be oriented vertically for the dorso-ventral orientation. This orientation of the cuboid-calcaneus and the dorsal extent of the cuboidal facet on the calcaneus, as documented here for *Rugosodon*, is plesiomorphic for multituberculates (Fig. 9).

The navicular has a triangular outline in dorsal view (Figs 2, 4). The navicular is slightly ajar from the astragalus on the left pes (Fig. 2) but appears to be intact and articulated with the astragalus on the right pes (Fig. 4). We interpret that the proximal part of the navicular contacts the saddle-shaped navicular facet of the astragalus (Fig. 2: an-groove), as shown by previous studies for other multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008) (Fig. 7). The ectocuneiform and the mesocuneiform show oblong outlines in dorsal view (Figs 4, 6). They are small and only half the size of the cuboid and the entocuneiform. The entocuneiform is twice as long proximo-distally as the ectocuneiform and the mesocuneiform in *Rugosodon* (Figs 2–4), and it is a bilaterally compressed bone, as well illustrated for other multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994). The entocuneiform of the left pes on the main slab (BMNH1142A) clearly shows the saddle-shaped joint to the metatarsal I. Its distal end is concave dorsoventrally and slightly convex mediolaterally. This articulating surface fits the saddle-shaped proximal end of metatarsal I.



Fig. 5. *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142B), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China; right crus and pes preserved on the counter slab, mostly in impression and mold outlines (mostly in dorsal view). **S**tereo photographs (**A**), explanatory drawing (**B**).

METATARSALS AND PHALANGES

Metatarsal (MT) I is wider in the proximal end than the distal, and its proximal end has a saddle joint that is mediolaterally concave and dorso-ventral convex (Figs 2, 7). The shape of this contact surface reciprocates the saddle shaped joint of the entocuneiform, and is thus called here "reciprocal saddle joint." This is a unique and diagnostic feature of all multituberculates (Krause and Jenkins 1983; Szalay 1993, 1994; Kielan-Jaworowska and Gambaryan 1994; Yuan *et al.* 2013).

MT II–IV are bilaterally compressed in the proximal ends, which are slightly narrower than the distal ends. MT II–IV are also tightly packed together near their proximal ends. MT V is about 80% of the length of MT II–IV. It is the shortest of all metatarsals, but is also the widest in its proximal end among all metatarsals. A peroneal process (*sensu* Bolortsetseg 2008) or the proximolateral tubercle of MT V is present in both pedes (Figs 2, 3, 6). All metatarsals show distinctive distal epiphyseal sutures between the epiphyses and the diaphyses, but there are no epiphyseal sutures in the proximal ends of any metatarsals. The articulating surface of the distal epiphysis is uniformly convex and almost dome-shaped for digits I–IV. Although the epiphysis of MT V is slightly obscured by a fracture, we interpret that it, too, is dome-shaped, as in the other metatarsals.

Absence of the proximal epiphyseal growth plate of MT II–IV is a uniform feature of extant therian mammals (Reno *et al.* 2006, 2007). We add that this is also the case for MT II–IV of multituberculates. However, in MT I of extant therians, it is the proximal end of the bone that has an epiphyseal suture and a growth plate in the sub-adult stages. By contrast, in *Rugosodon*, an epiphysis and a distinctive epiphyseal suture are preserved on its distal end on the intact MT I on the left pes (Figs 2, 3). In this regard, *Rugosodon* is distinctive from extant therians, in that the single epiphysis is on the opposite end of MT I. According to our observation, MT I of *Sinobaatar* also has a distal epiphyseal suture. A distal epiphyseal suture is also visible in the published photo of MT I belonging to *Kryptobaatar* and *Catopsbaatar* (Hurum and Kielan-Jaworowska 2008). Thus multituberculates, as a group, are different from extant therians in the distal location of the epiphysis on MT I.

Proximal phalanges of pedal digit rays I–IV are generalized; the proximal phalanx for digit V is missing on both feet. Their proximal ends are preserved well enough to show a slight lip along the dorsal rim of the concave proximal end. The proximal ends are slightly wider and thicker than the distal ends. The distal end of this phalangeal segment shows an epiphyseal suture on at least proximal phalanges of digits II–IV. The distal articulating surface of the epiphysis is transversely cylindrical.



Fig. 6. Rugosodon eurasiaticus (A–D), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China; composite reconstruction of cruro-pedal structure and Eucosmodon sp. (E), distal tibia (AMNH 16325), locality near Kimbetoh, Nacimiento Formation, early Paleocene, New Mexico, USA. A. Reconstruction of the right cruro-pedal features from camera lucida drawings, tibia in anterior view, proximal part of fibula rendered in lateral view. B. Details of preserved tarsals and meta-tarsals (based on right side of BMNH1142A), most bones seen in dorsal view. C. Reconstruction of the right pes in dorsal view.
D. Reconstruction of distal tibia and fibula, right side in anterior view. E. Tibia in distal view (redrawn from photos of Krause and Jenkins 1983 and Kielan-Jaworowska and Gambaryan 1994). MT, metatarsal.

The intermediate phalanges are preserved on digital rays II–IV. Each of these is slightly wider (thicker) on the proximal end than the distal end. The proximal end is flat to slightly concave without epiphyseal suture on digits II–IV. But the distal epiphyseal suture is visible in at least two proximal phalanges. On the intermediate phalanx of digit IV, the distal surface of the epiphysis has a grooved contact surface for the terminal phalanx.

The terminal phalanx is only preserved on digit I. It is transversely wide and has a dorsal lip over its proximal articular surface. It clearly lacks a high and arch-like dorsal profile and is not bilaterally compressed. Functional inference on the proportions of the metatarsals and phalanges will be discussed below.

FUNCTIONAL MORPHOLOGY OF JOINTS

Hip and knee joints. — The socket of the acetabulum lacks a continuous dorsal margin in that the articular facets of the ilium and ischium in the acetabulum are not dorsally continuous in *Rugosodon*. The same is true of well-preserved pelves belonging to several other multituberculates. This would have permitted the femur to rotate dorsally, such that the femur could be held in a strongly abducted orientation (Simpson and Elftman 1928; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994).

Based on osteological characteristics of the femur, tibia, and parafibula, we interpret the knee of *Rugosodon* as asymmetrical. Although the femur is flattened in slab preservation, the size and shape differences of its two distal condyles are still distinctive. The lateral condyle of the femur is much wider and slightly lower than the medial condyle. The condyle and its ectepicondylar prominence are markedly more pointed than the medial condyle and the entepicondyle (not illustrated). The extensor aspect of the distal



Fig. 7. Rugosodon eurasiaticus (A), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China, cruro-tarsal joint functions (modified from Yuan et al. 2013), compared to the cimolodontan Eucosmodon sp. (B–D), site near Kimbetoh, Nacimiento Formation, early Paleocene, New Mexico, USA. A. Pes in dorsal view, showing abduction-adduction of digit I (arrow) on the reciprocal saddle joint of the entocuneiform and MT I. B. Astragalus in dorsal view, showing pivotal rotation (gray dot) of the astragalus relative to the tibia, which represents the contact of the medial condyle of distal tibia to the medial astragalo-tibial facet of the astragalus. The arrow shows the lateral condyle of the distal tibia, which glides along the lateral astragalo-tibial facet.
C. Astragalus in ventral view showing the grooved and saddle-shaped astragalo-navicular joint; the arrow indicates movement of the navicular relative to the astragalus. D. Dorsiflexion and plantarflexion of MT I at the reciprocal saddle joint. Phylogenetic topology is based on the Adam's consensus tree in Yuan et al. (2013). MT, metatarsal.

femur of *Rugosodon*, as exposed in the right femur on the main slab of the fossil (BMNH1142A), is similar to that illustrated for other multituberculates. Krause and Jenkins (1983) noted that, in *Ptilodus*, both condyles are largely confined to the flexor side of the femur and do not extend around to be continuous with the patellar groove on the extensor side of the distal femur. They suggest that this is consistent with a crouched stationary posture of the knee. Kielan-Jaworowska and Gambaryan (1994, figs 51–53) postulated, similarly, a flexed knee posture for Late Cretaceous multituberculates.

The tibia of *Rugosodon* is noticeably asymmetrical mediolaterally, on its proximal end. This is similar to extant *Ornithorhynchus*, in which the proximal tibia is asymmetrical. With this pattern of tibial distal condyles, the knee joint is obligately flexed, related to the sprawling posture of the hind limb (Gambaryan *et al.* 2002; Li and Luo 2006, fig. 4).

The presence of a large parafibula is also consistent with a crouched posture of the knee. In monotremes (Gambaryan *et al.* 2002; Li and Luo 2006), the knee can only flex in sprawling posture because the parafibula projects dorsally behind the lateral femoral condyle. This would exclude the possibility for the knee to bend if the femur and the crus had been aligned parasagittally. In other words, the femur and the crus had been aligned parasagittally. In other words, the femur and the crus had to be sprawling in a crouched posture, given the large size and the location of the parafibula. Similar to *Rugosodon*, another Mesozoic mammal, the spalacotheriid *Akidolestes*, has also been interpreted as having a habitually flexed knee, as constrained by the hypertrophied parafibular process of the fibula (Li and Luo 2006, fig. 4; 2013, fig. 20).

For *Rugosodon* and *Sinobaatar*, the sprawling hind limb is consistent with evidence of taphonomic preservation. As noted by Kielan-Jaworowska and Hurum (2006), the Mesozoic mammals interpreted to have sprawling hind limb by osteological characters also tend to show a sprawling posture in typically passive preservation in lacustrine rock slabs. Mammaliaform skeletons that were determined to have crouched posture by osteological characters (Gambaryan and Kielan Jaworowska 1997) are also predominantly preserved in dorso-ventral compression of the skeleton, with sprawling fore and hind limbs. This differs from the limbs of crown therian mammals, which, if passively preserved in rock slabs, tend to be preserved on their lateral flanks (Kielan-Jaworowska and Hurum 2006). The lateral flank preservation is more consistent with their presumptive parasagittal limb postures. So far, the skeleton of *Rugosodon* and several skeletal specimens of *Sinobaatar (e.g.*, the holotype of *S. lingyuanensis*, IVPP V12517; see Hu and Wang 2002) found in lacustrine shales are preserved also in dorso-ventral compression with sprawling posture. In sum, the osteological interpretation of an abducted femur and a flexed knee of *Rugosodon* here is consistent with ancillary, but supportive evidence of its taphonomic preservation on shale slabs.



Fig. 8. Morphological disparity and evolutionary pattern of calcanei among multituberculates and their outgroups. A. Basal mammaliaform *Morganucodon* in ventral view. B. Eutriconodont *Jeholodens* in ventral view. C. Spalacotherioid *Zhangheotherium* in ventral view. D. Spalacotheriid *Akidolestes* in ventral view. E. Eaulchoffatiid multituberculate *Rugosodon* in dorsal view. F. "Plagiaulacidan" multituberculate *Sinobaatar* in dorsal view. G. Djadochtatherian multituberculate *Kryptobaatar* in dorsal view. H. Eucosmodontid multituberculate *Stygimys* in ventral view. I. Ptilodontid multituberculate *Ptilodus* in ventral view. Proportional changes in evolution of the calcaneus (upper panel): the distal part of the calcaneus becomes narrower, and the proximal part (the calcaneal tuber) is elongate in the more derived taxa. Drawings are either original to this study or adapted with modification from Luo and Wible (2005), Chen and Luo (2013), Zhou *et al.* (2013), and Yuan *et al.* (2013). Several are composite drawing from photos published by Szalay (1994), Kielan-Jaworowska and Gambaryan (1994), Hurum and Kielan-Jaworowska (2008), and Bolortsetseg (2008). Cladogram based on the Adam's consensus tree of Yuan *et al.* (2013). Nodes (1) Mammaliaformes; (2) Theriimorpha; (3) Theriiformes (in part); (4) Multituberculata; (5) clade ("plagiaulacidans" + Cimolodonta); (6) Cimolodonta; (7) unnamed clade.

Functional developmental interpretation of parafibula. — In the development of extant monotremes, the parafibula is a separate embryonic element and then in the later growth stages becomes fused completely to the proximal end of the fibula, to become the enlarged parafibular process (Pearson and Davin 1921; Barnett and Lewis 1958; Vickeryous and Olsen 2007). In marsupials, the parafibula is a separate ossification associated with the proximal end of the fibula in development, and it remains as a separate, small bone in adults (Pearson and Davin 1921; Barnett and Lewis 1958; Lessertisseur and Saban 1967; Argot 2002; Kielan-Jaworowska and Gambaryan 1994). A hypertrophied parafibula, either fused or a separate bone as in *Rugosodon* (Fig. 5), is similar in shape to the fully fused to the fibula in monotremes. Thus *Rugosodon* and

monotremes only differ in whether the parafibulo-fibular suture is fused, or not. The large parafibula, with or without the adult suture to fibula, can provide more area for origination of the peroneal muscles, the M. gastrocnemius lateralis, the M. tibialis posterior, and the M. extensor digitorum hallucis (Lessertisseur and Saban 1967; Kielan-Jaworowska and Gambaryan 1994; Argot 2002; Gambaryan *et al.* 2002). The gastrocnemius and the tibialis posterior join the Achilles tendon on the calcaneal tubercle for plantar-flexion of the peroneus longus) have the function of rotating and everting the foot via the peroneal shelf or the peroneal groove of the calcaneus (Szalay 1994; Kielan-Jaworowska and Gambaryan 1994; Argot 2002; Szalay and Sargis 2005).

Most placental mammals lack a separate parafibula (Pearson and Lewis 1921; Lessertisseur and Saban 1967). Accordingly, they have smaller bone surface area for muscles attached to the proximal end of the fibula (Evans 1995; Neveu and Gasc 2002). By contrast, in marsupials, the presence of a parafibula can augment the attachment area for origination of several muscles to dorsiflex (or extend) the metatarsals (*e.g.*, M. extensor hallucis longus) and to plantarflex pedal digits (*e.g.*, M. peroneus longus) (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). In monotremes, the fused parafibula process of the fibula (Vickeryous and Olsen 2007) adds a significantly expanded surface of origination for these muscles (Gambaryan *et al.* 2002).

In this light, we interpret that, with a larger parafibula, the proximal region of fibula including the parafibula would have had a broader attachment of the muscles in *Rugosodon* than in mammals with a smaller parafibula or without a parafibular process of the fibula. We further speculate that, with this extra bony element of the parafibula, there would be a greater volume of muscles for plantarflexion, eversion and dorsiflexion of the ankle, in locomotion.

The parafibula shows systematic variation among multituberculates. It is larger in *Rugosodon* and *Sinobaatar* than in the cimolodontan multituberculates (including *Ptilodus*; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008). Currently, it is not yet feasible to assess the further differences of muscles resulting from the large (and un-fused) parafibulae of *Rugosodon* and *Sinobaatar* versus the smaller parafibula of other, derived multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994, fig. 44). The functional differences of disparate sizes of the parafibula among multituberculates can only be understood after the skeletomuscular differences of the parafibula of disparate sizes among marsupials are more fully explored (Argot 2002).

Upper ankle joint. — The upper ankle joint (UAJ, *sensu* Szalay 1994) of *Rugosodon* is highly mobile (Fig. 7), as in other multituberculates (Jenkins and Krause 1983; Szalay 1993; Kielan-Jaworowska and Gambaryan 1994). The medial distal condyle and the lateral distal condyle of the tibia (*sensu* Jenkins and Krause 1983) are, respectively, in contact with the medial astragalo-tibial facet and the lateral astragalo-tibial facet of the astragalus (Fig. 7). The main movement of the upper ankle joint involves pivoting of the peg-like medial condyle on the medial astragalar facet and gliding between a spiral lateral condyle in the distal end of the tibia with the curved lateral astragalar facet. With this pivotal rotation the pes as a whole can increase its range of abduction and adduction relative to the crus (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994).

This rotation of the distal end of the crus relative to the astragalus was originally proposed for the Paleogene *Eucosmodon* and *Ptilodus* by Jenkins and Krause (1983; also Krause and Jenkins 1983) and for Late Cretaceous multituberculates (Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). Because the observable features of the tibio-astragalar articulation in *Rugosodon* are identical to those of *Eucosmodon* and *Ptilodus*, we can now interpret the function of the upper ankle joint in *Rugosodon* accordingly (Fig. 7). The wide range of possible movement of the lateral tibial condyle relative to the medial tibial condyle, and the lack of constraint by the fibula on the upper ankle joint facilitate rotation (both abduction and eversion) of the hind foot at this joint (Jenkins and Krause 1983, fig. 1). For *Ptilodus*, Jenkins and Krause (1983; see also Krause and Jenkins 1983) suggested that the foot, in normal stance, would be capable of abduction of 30 to 40 degrees (longitudinal axis of the foot passing through MT III deviated from a sagittal plane). We interpret that *Rugosodon* was capable of a similar range of eversion, although we are unable to quantify the scope of this eversion, due to the fact that the medial and lateral distal condyles of tibia are partially obscured by their association with the astragalus.

Movement at the UAJ depends on the absence or presence of the fibular malleolus. An absence of this structure would be permissive for the movement, while the presence (or the size variation of this structure if present) would tend to limit this movement. Historically, there was uncertainty as to how the distal end of

the fibula would be involved in crural rotation at the UAJ, as pointed out by Szalay (1993). This previously unclear issue can now be clarified by the *in situ* preservation of the fibula with the tarsals in *Rugosodon* (Fig. 4) and in *Sinobaatar* (Z-X L, personal observation). The distal fibula has a contact with the calcaneus, in addition to its contact with the astragalus. However, it lacks a distinctive lateral malleolus, thus this contact does not constrain the range of the upper ankle joint movement. The wide cruro-tarsal rotation is, at least, a functional adaptation of paulchoffatiids (Yuan *et al.* 2013) through the Paleogene multituberculates (Krause and Jenkins 1983). A fibular malleolus was identified in one specimen of *Kryptobaatar* by Kielan-Jaworowska and Gambaryan (1994, fig. 8), and a similar structure is also described in another specimen of *Kryptobaatar* (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008). It is possible that the range of cruro-tarsal rotation at the upper ankle joint is more limited in *Kryptobaatar*, but less constrained in other contemporary multituberculates. For multituberculates as a whole, we suggest that the degree of possible rotation at the upper ankle joint may be variable in different taxa.

Lower ankle joint. — The lower ankle joint (LAJ, sensu Szalay 1993) is between the astragalus and the calcaneus. The astragalus and the calcaneus are in juxtaposition horizontally and side-by-side in *Rugosodon*: the astragalus is not superposed on top of the calcaneus (Figs 2, 4, 6, 9, 10). This is also the case in the eobaatarid Sinobaatar (Hu and Wang 2002, fig. 1). Similarly, the Late Cretaceous Kryptobaatar, Chulsanbaatar, and Catopsbaatar lack a direct superposition of the astragalus on top of the calcaneus, although this absence of superposition was somewhat obscured by the fact that the metapodials and phalanges are strongly abducted toward the calcaneal tuber, preserved in situ in these fossils (Kielan-Jaworowska and Gambaryan 1994, figs 6, 25; Hurum and Kielan-Jaworowska 2008, figs 11, 13). For *Ptilodus*, in which the tarsals preserved in three dimensions are more reliable for this assessment, the astragalus was reconstructed as obliquely overlapping on the calcaneus (Krause and Jenkins 1983), although the exact extent of this overlap may be quite limited, as compared to therians. The calcaneo-astragalar facet of the astragalus overlaps the calcaneus, but the sustentacular facet of the astragalus is juxtaposed side-by-side with the calcaneus (Jenkins and Krause 1983, fig. 1). The superposition of the astragalus on top of the calcaneus, by both the calcaneo-astragalar facet and the sustentacular facet, as seen in extant therians (sensu Jenkins 1970; Szalay 1993), is not developed in Ptilodus or Eucosmodon. Fossils of Rugosodon and Sinobaatar can now extend this plesiomorphic condition (juxtaposition of the astragalus and calcaneus) to the basalmost taxa of the multituberculate clade (Figs 9, 10).

Jenkins and Krause (1983) interpreted that, in *Ptilodus* and *Eucosmodon*, the LAJ was capable of pivoting at the sustentacular facets of the astragalus and calcaneus. The calcaneus has translational movement relative to the astragalus, at the calcaneo-astragalar facets. Taken together, this movement can facilitate the plantarflexion and inversion of distal pedal elements (Krause and Jenkins 1983). Although the sustentacular and calcaneo-astragalar facets of the calcaneus and the astragalus are only partially exposed in the *Rugosodon* type specimen, the exposed aspects of the astragalus and the calcaneus appear to be similar to those of *Ptilodus* and *Eucosmodon*. By extension, we speculate that *Rugosodon* may be similar in mechanical function of the joint between the astragalus and the calcaneus, as proposed previously for other multituberculates (Jenkins and Krause 1983; Kielan-Jaworowska and Gambaryan 1994).

Astragalo-navicular joint. — The grooved or saddle-shaped anterior surface of the astragalar head would permit hinge-like rotation of the navicular relative to the astragalus in dorso-ventral direction, permitting significant dorso- and plantarflexion of the navicular to the astragalus, and also side-to-side movement, especially abduction (Fig. 7). This enhances the mobility of the hind foot in general.

We interpret the navicular to have been aligned distal to the astragalus in *Rugosodon* (Fig. 9A). By contrast, the navicular is more ventro-distal to the astragalus in some Late Cretaceous and Paleogene multituberculates (Fig. 9B). In three-dimensional preservation of the astragalus in some multituberculates (*Eucosmodon*, Szalay 1994, figs 5.8, 5.9; *Catopsbaatar*, Hurum and Kielan-Jaworowska 2008, fig. 12; *Kryptobaatar*, Bolortsetseg 2008, figs 36, 37), the navicular facet is more ventrally inclined, facing ventro-distally in plantar view. The navicular is also positioned ventro-distal to the astragalus in several intact pedes (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008).

Calcaneo-cuboid joint. — In a majority of multituberculates, the calcaneo-cuboid joint faces medio-distally ("antero-medially") in the dorsal view of the pes (Figs 7, 8). But the dorso-ventral orientation of the calcaneus-cuboid joint can show systematic variation among multituberculates (Fig. $9A_1$ versus Fig. $9B_1$). The plesiomorphic pattern of the calcaneo-cuboid joint is a vertical orientation of its surface in the dorsal-ventral



Fig. 9. Schematic patterns of the astragalo-navicular articulation among multituberculates. A. Plesiomorphic pattern: the astragalus and the calcaneus in juxtaposition. The groove-like astragalo-navicular contact is oriented more vertically and less inclined on the distal end of the astragalus. The calcaneo-cuboid contact is also more vertically oriented and less inclined on the distal end of the calcaneus. The peroneal shelf is not differentiated into the peroneal process separated by a groove. A₁, distal ("anterior") view of the astragalus with a more dorsally placed navicular contact, and the calcaneus with a more dorsally placed cuboid contact (stylistic drawing after Szalay 1993, fig. 9.11); A₂, schematic alignment of the navicular and the astragalus; A₃, the plesiomorphic astragalo-navicular alignment tends to be correlated with the plantigrade pedal posture. B. Apomorphic pattern of some derived multituberculates. B₁, distal ("anterior") view of the astragalus with a more ventrally inclined cuboid contact as well (stylistic drawing after Szalay 1993, fig. 9.11); B₂, schematic alignment of the more ventrally placed and inclined navicular contact, and the calcaneus with a more ventrally inclined cuboid contact as well (stylistic drawing after Szalay 1993, fig. 9.11); B₂, schematic alignment of the more ventrally positioned and inclined navicular to the astragalus; B₃, the derived condition of the astragalo-navicular alignment tends to be correlated with the facultative digitigrade pedal posture, as reconstructed for derived multituberculates of the Late Cretaceous (*e.g.*, Kielan-Jaworowska and Gambaryan 1994, fig. 54). MT, metatarsal.

direction. The cuboid facet of calcaneus of *Rugosodon* appears to be this type: the calcaneo-cuboid facet is vertically oriented on the calcaneus (Fig. $9A_1$). But in dorsal view, the calcaneo-cuboid contact is oriented medio-distally from the long axis of the calcaneus (Fig. 7). This interpretation needs to be confirmed when additional specimens with separated calcaneus and cuboid become available for *Rugosodon*.

An apomorphic pattern involves positioning of the calcaneo-cuboid joint surface on the antero-medio-ventral side of the calcaneus (Fig. 9B₁). In this pattern of orientation, the cuboidal contact surface is more ventrally inclined, and is extensively visible on the ventral aspect of the calcaneus, as shown in the Cretaceous ptilodontoid calcanei (Szalay 1994, fig. 5.8) and the eucosmodontid *Stygimys* (Krause and Jenkins 1983, fig. 26; also Kielan-Jaworowska and Gambaryan 1994, fig. 55; Kielan-Jaworowska *et al.* 2004). We interpret this type of calcaneo-cuboid articulation to have been more conducive for the distal tarsal bones to plantarflex and to invert, relative to the calcaneus.

The ventrally tilted calcaneo-cuboid joint, combined with the above-mentioned flexion at the astragalo-navicular joint, augments the scope of flexion of the metatarsal and phalanges of digit I. Increased plantarflexion would be compatible with a digitigrade stance, at least facultatively, for the standing pedal posture.



Fig. 10. Evolutionary pattern of the astragalus, the calcaneus, and pedal posture among multituberculates and their outgroups. A. Manda cynodont. B. Basal mammaliaform morganucodontan, *Morganucodon*. C. Basal mammaliaform haramiyidan, *Megaconus*. D. Basal mammalian triconodontan, *Jeholodens*. E. Basal multituberculate paulchoffatiid, *Rugosodon*.
F. Multituberculate *Sinobaatar*. G. *Kryptobaatar*, a djadochtatherian multituberculate. H. *Eucosmodon*, a ptilodontoid multituberculate. We hypothesize that multituberculates (node 4) ancestrally have a wide distal region of calcaneus and relatively short calcaneal tuber that are plesiomorphies. These are related to a plantigrade pedal posture, a functionally generalized feature. In the derived clade (node 6) including Cretaceous djadochtatherians of Cretaceous through ptilodontoids and taeniolabidids of the Paleogene, the distal calcaneus becomes narrower and the calcaneal tuber becomes more elongate. The narrower calcaneus and elongate calcaneal tuber, among other features, have a longer in-lever for plantarflexion at the ankle, and help achieve a facultatively digitigrade stance. A–C from Zhou *et al.* (2013); D, H from Ji *et al.* (1999); E–G are original to this study. Cladogram nodes (1) Mammaliaformes; (2) Theriimorpha; (4) Multituberculata; (5) unnamed clade ("Plagiaulacidans"+Cimolodonta); (6) Cimolodontans. Cladogram node designation is the same as in Fig. 8.

Entocuneiform-MT I joint. — *Rugosodon* is identical to Late Cretaceous and Paleogene multituberculates in the saddle-shaped distal surface of the entocuneiform, reciprocated by a curved groove of the proximal end of MT I (Fig. 6C; see also Krause and Jenkins 1983; Szalay 1994; Kielan-Jaworowska and Gambaryan 1994). This joint is permissive of a vertical rotation of MT I to the entocuneiform, which could further amplify the dorso- and plantar-flexion of the phalanges of pedal digit I (Fig. 7D). In extant *Didelphis* (Szalay 1994), the long tendon of M. peroneus longus inserts on the plantar base of MT I, and pulls to flex pedal digit I at the saddle shaped entocuneiform-metatarsal joint. In the multituberculate reconstruction by Kielan-Jaworowska and Gambaryan (1994, fig. 57), the tendon of M. peroneus longus passes in the peroneal groove onto the plantar side of the pes and inserts on the plantar base of MT I. The M. extensor digitorum hallucis inserts on the dorso-distal part of MT I, for the extension of pedal digit I (Fig. 7). M. peroneus longus and the M. extensor digitorum hallucis are antagonistic muscles for plantarflexion and dorso-extension of digit I, but both muscles originated from near the enlarged parafibula at the knee joint in *Rugosodon* (Fig. 6).

We note that, in *Rugosodon*, MT I was not habitually abducted at the entocuneiform joint. Pedal digit I is not divergent from other pedal digits. In the articulated foot bones of *Sinobaatar*, pedal digit I is not divergent either (personal observation; see also Hu and Wang 2002). In *Kryptobaatar*, *Chulsanbaatar*, and *Catopsbaatar*, for which most pedal bones are intact, MT I is not divergent (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008). Therefore we suggest that multituberculates did not have divergent digit I or an opposable hallux (Fig. 6), as previously speculated by Simpson and Elftman (1928). Rather, pedal digit I was facultatively capable of a wider range of abduction, thanks to the development of the reciprocal saddle joint of the entocuneiform permissive of such abduction of MT I (Jenkins and Krause 1983, fig. 1). The enhanced mobility and wide range of abduction, plantar- and dorsoflexion of MT I is a derived condition in multituberculates as a whole, unique among Mesozoic mammal clades (Jenkins and Krause 1983).

PEDAL POSTURE

Pedal abduction and eversion. — In both feet of *Rugosodon, in situ* metatarsals are not strongly abducted laterally from the tarsals; neither is MT V strongly abducted from the more central digit rays. This appears to be a habitual and resting posture of the metatarsals with respect to the tarsals for paulchoffatiids, a basal clade of multituberculates. Because the Paleogene multituberculates show no eversion of the pes either (Krause and Jenkins 1983; Szalay 1993), we interpret the ancestral multituberculate condition to have not involved either habitual eversion or abduction in a resting posture.

We interpret that metatarsals were capable of a range of eversion and abduction relative to the calcaneus, at lease in some multituberculate taxa. In the holotype of *Sinobaatar lingyuanensis* (IVPP V12517), the metatarsals are preserved in a strongly everted position (Hu and Wang 2002, fig. 1; Wang *et al.* 2003, fig. 200). However, in another specimen of *Sinobaatar* (NGMC3100), the foot is preserved with distal pedal bones along the axis of the crus and the calcaneus, and there is no eversion of metatarsals from the tarsals, thus different from the type specimen of *Sinobaatar lingyuanensis*. Different degrees of abduction of the metatarsals preserved in different specimens of *Sinobaatar* are not conflicting with each other. This suggests that metatarsals of this taxon were capable of a range of everting positions relative to tarsals.

Kielan-Jaworowska and Gambaryan (1994) interpreted that, in some Late Cretaceous multituberculates, metatarsals were habitually abducted and everted, such that the proximal end of MT V would have contacted the peroneal process of the calcaneus, in a standing and resting posture. This was based on *Kryptobaatar* and *Chulsanbaatar* whose *in situ* metatarsals are strongly flexed. MT I–V are also strongly adducted toward the plantar midline of the pes. Kielan-Jaworowska and Gambaryan (1994, fig. 54) argued that this was the habitual posture in standing pose, an opinion that was further expanded by Hurum and Kielan-Jaworowska (2008, p. 563).

As shown by the *Sinobaatar* fossil materials, the metatarsals can be abducted and everted relative to the calcaneus in one specimen (Wang *et al.* 2003) but show little or no abduction in others (*e.g.*, NGMC3100). Such a strong eversion/abduction as seen in some multituberculates may not be the habitual standing posture (Hu and Wang 2002). Instead, it may represent the outer limit of the permissible abduction and eversion, for a range of facultative eversion. The degree of facultative eversion in multituberculates is also partly dependent on cruro-tarsal rotation at the UAJ, as the latter joint movement can augment overall pedal abduction and eversion.

Pedal posture. — We propose a plantigrade standing pedal posture for *Rugosodon*, based on several cruro-pedal features. The plantigrade pedal posture is defined by the cruro-tarsal joint as the primary joint of flexion of the foot. But for a digitigrade pedal posture, the primary joint of flexion is the metatarso-phalangeal joint, and the inter-phalangeal joints, in standing position (Carrano 1997). Plantigrade, digitigrade, and unguligrade stances are represented by a continuum of postural grades among placental mammals. Nonetheless, there are some qualitative differences that can help to distinguish these grades of posture (Carrano 1997).

Plantigrade therian mammals are characterized by several osteological characters. Commonly they have less restrictive structure of the cruro-tarsal joint, which is capable of a wider range of lateral rotation (abduction and adduction), and less parasagittal (fore-aft) rotation arc at the tibio-tarsal joint than digitigrade mammals (Wang 1993; Carrano 1997). Within the placental carnivoran clade, the arboreal plantigrade forms have a lesser trochlear arc than the cursorial digitigrade forms (Wang 1993). Plantigrade mammals tend to have a shorter calcaneal tuber and a longer proximal part of the calcaneus relative to the overall calcaneal length, than digitigrade mammals (Carrano 1997). Plantigrade mammals tend to have a relatively wider sustentacular region than digitigrade mammals of the same clade (Polly 2008; Polly and MacLeod 2008). Also, plantigrade mammals tend to have a wider spread of metapodials, with MT I and MT V more abducted from the longitudinal axis of the foot, in contrast to the more convergent metapodials with side digits (MT I and MT V) adducted toward the pedal axis in digitigrade mammals (Carrano 1997).

We offer another observation: that plantigrade mammals tend to have a greater combined breadth of the calcaneus and the astragalus, as evidenced by the transversely wide astragalus and calcaneus in extant monotremes, which are plantigrade. By contrast, extant mammals with a digitigrade stance are characterized by a narrower combined width of the calcaneus and the astragalus, thanks to a more complete superposition of the astragalus over the calcaneus (Jenkins 1970; Szalay 1993), in addition to the narrower width of

each bone. We note that extant therian mammals with plantigrade stance lack the inclined orientation of the astragalo-navicular and the calcaneo-cuboid joints that can lift the calcaneus and the astragalus up from the substrates, in habitual standing posture.

Rugosodon has a combination of the characteristics for plantigrade posture: the calcaneal body is mediolaterally wide and dorso-ventrally compressed, and the peroneal shelf is also wide. The calcaneal tuber is short relative to the calcaneal length. The calcaneo-cuboid joint is vertical (not so much inclined). Finally, the metatarsals are divergent (with medial and lateral metatarsals abducted from the midline of the foot), as preserved in both pedes. These plantigrade features are also present in *Sinobaatar lingyuanensis* (Hu and Wang 2002; Wang *et al.* 2003) and in other *Sinobaatar* specimens (Z.-X. Luo, personal observation).

PHALANGEAL PROPORTIONS

It is now feasible to use the segment proportions of the pedal digits to estimate the substrate preference of an extinct mammal, by morphometric comparison with extant mammals having known substrate preferences and locomotor adaptations (Zheng *et al.* 2013; Bi *et al.* 2014). As initially proposed for the manus (*e.g.*, Lemelin 1999), the phalangeal index is the sum of lengths of the proximal and intermediate phalanges divided by the length of metacarpal of the same digit (commonly digit III) (Kirk *et al.* 2008). Zheng *et al.* (2013) extended this metric to the pedal bones, and estimated the likely substrate preferences of extinct mammals by comparing their phalangeal indices to those of extant mammals with known habits and substrate preference. In general, the higher the phalangeal index, the more likely the pes would have a capacity for gripping or branch-walking, related to climbing function and arboreal adaptation (Kirk *et al.* 2008; Zheng *et al.* 2013; Bi *et al.* 2014). The pedal phalangeal index of *Rugosodon* is 114%. This is higher than *Sinobaatar* at 97%, which was likely a terrestrial mammal (Zheng *et al.* 2013). The phalangeal index value of *Rugosodon* and *Sinobaatar* are close to those Mesozoic mammals considered to be terrestrial, such as *Jeholodens* (Table 1).

EVOLUTIONARY PATTERNS

In the first study to address limb functional anatomy of multituberculates, Simpson and Elftman (1928, p. 4) interpreted that the pes of *Eucosmodon* "is pentadactyl and plantigrade, of grasping type with partially opposable hallux." Although it is now clear that multituberculates did not have an opposable hallux, Simpson and Elftman (1928) were correct in proposing that *Eucosmodon* was plantigrade, as an exemplar of multituberculate pedal posture. The question of plantigrade vs. digitigrade pedal postures was not explicitly discussed by Krause and Jenkins (1983). However, it is implicit in their discussion on the grasping capability of the pes, the tibio-astragalar rotation, and their graphic reconstruction of divergent and spread digit rays that *Ptilodus* and *Eucosmodon* had a plantigrade posture (see also Granger and Simpson 1929, fig. 23).

The plantigrade pedal posture is also phylogenetically plesiomorphic for multituberculates as a whole, by comparison to outgroups that are independently inferred to have been plantigrade by osteological characters. In current phylogenies, multituberculates are the sister group to the trechnotherian clade. The basal-most taxa of trechnotherians, *Zhangheotherium* and *Akidolestes*, have a dorso-ventrally flattened and mediolaterally wide calcaneal body (Luo and Ji 2005; Hurum *et al.* 2006). *Akidolestes* has a short calcaneal tuber (Li and Luo 2006; Chen and Luo 2013). Outside the multituberculate-trechnotherian clade (Figs 8, 10: node 2), eutricono-donts (Ji *et al.* 1999; Hu 2006) also have a wide calcaneus (Fig. 8). Outside crown Mammalia (Fig. 8: node 1), *Morganucodon, Agilodocodon* and the haramiyid *Megaconus* have similarly plesiomorphic calcaneal structures (Jenkins and Parrington 1976; Szalay 1994; Zhou *et al.* 2013; Meng *et al.* 2015; Luo *et al.* 2015). Recent discoveries of tarsals in these stem mammaliaform have augmented the earlier evidence from *Megazostrodon* (Jenkins and Parrington 1976, fig. 18) that mammaliaforms as a whole are plantigrade (Zhou *et al.* 2013).

While the basal taxa of Multituberculata, such as *Rugosodon* and *Sinobaatar*, had the plesiomorphic plantigrade posture, not all multituberculates were plantigrade. Pedal posture of more derived multituberculates was more varied, and may have been digitigrade, if only facultatively. Kielan-Jaworowska

Comparative Mesozoic	Hypothesized sub-	Metatarsal	Proximal pha-	Intermediate	Pedal phalan-	Specimens/
mammaliaforms	strate preference	length	lanx length	phalanx ength	geal index	references
Agilodocodon scansorius	arboreal?	3.91	2.89	2.33	134%	BMNH1138
Eomaia scansoria	arboreal?	4.35	3.15	2.4	128%	CAGS01-IG1A
Jeholodens jenkinsi	terrestrial?	3.92	2.48	1.88	111%	GMV 2139A
Maotherium sinensis	terrestrial?	7.3	4.1	3.15	99%	Rougier et al. 2003
Rugosodon eurasiaticus	terrestrial?	9.59	6.48	4.47	114%	BMNH1143
Sinobaatar lingyuanensis	terrestrial?	6.3	3.2	2.8	95%	Zheng et al. 2013
Sinodelphys szalayi	arboreal?	2.9*	2.5*	2.3*	165%	CAGS00-IG03

Table 1. Pedal phalangeal measurements (mm) and indices for digit III of *Rugosodon eurasiaticus* and comparison with other Mesozoic mammals.

* In the type specimen of *Sinodelphys szalayi*, the pedal bones are associated but partially displaced relative to each other; thus the length measurements of metatarsal, proximal phalanx and intermediate phalanx are provisional.

and Gambaryan (1994, fig. 54) reconstructed a digitigrade pedal posture for several Late Cretaceous multituberculates: *Kryptobaatar*, *Chulsanbaatar*, and *Nemegtbaatar*. The plantar flexure of the calcaneus-cuboid and the astragalus-navicular is preserved intact (or nearly so) in *Kryptobaatar*, *Chulsanbaatar*, and *Catopsbaatar* (Hurum and Kielan-Jaworowska 2008, p. 563), as well as in a new and un-named multituberculate (Bolortsetseg 2008). Given a strong pedal plantarflexion, the calcaneus, when held horizontal, is lifted from the substrate (Fig. 9B, Fig. 10: node 6). The primary contact to the substrate would be by metatarsals, or metatarsal-phalanges in a digitigrade posture (Kielan-Jaworowska and Gambaryan 1994, fig. 54).

The digitigrade hypothesis for Cretaceous multituberculates is supported by the tightly adducted metatarsals in intact feet (Kielan-Jaworowska and Gambaryan 1994; Bolortsetseg 2008; Hurum and Kielan-Jaworowska 2008). These are different from the more divergent digit rays of *Rugosodon* (Yuan *et al.* 2013) and of extant therians having plantigrade posture (Szalay 1994; Carrano 1997). Furthermore, these Late Cretaceous multituberculates show a more elongate calcaneal tuber and a more bilaterally compressed calcaneal body than in *Rugosodon* and *Sinobaatar* (Figs 8–10).

Based on the flexed foot in Late Cretaceous multituberculates, Kielan-Jaworowska and Gambaryan (1994, fig. 55) also re-interpreted *Eucosmodon* to have had a strongly flexed tarsus and a digitigrade pedal posture. By our re-evaluation, however, the case for digitigrady in *Eucosmodon* is not strong, although we would agree that *Eucosmodon* could have been facultatively digitigrade during at least some phases of active locomotion.

In terms of evolution of pedal structure and function (Figs 7–10), the basal-most known *Rugosodon* has many diagnostic features of multituberculates as a whole. These are correlated with enhanced mobility in the cruro-tarsal rotation at the UAJ, and high mobility in the astragalo-navicular joint, and in plantarflexion and dorsiflexion of MT I at its joint to the entocuneiform. Thus, the earliest evolution of multituberculates was accompanied by new cruro-pedal locomotor functions (Fig. 7, Fig 10: node 4).

However, a majority of the calcaneal characters of the Jurassic *Rugosodon* and Early Cretaceous *Sinobaatar* are plesiomorphic compared to other multituberculates. These calcaneal features happen to be related to inferred plantigrade pedal posture. Further evolution of the calcaneal structures for versatile functions occurred in a more derived subclade of multituberculates (Fig. 10: node 6). The most prominent apomorphic feature is the elongation of a more bilaterally compressed calcaneal tuber, relative to the calcaneus length in derived multituberculates (Fig. 8). A longer calcaneal tuber increases the in-lever for the gastrocnemius and other muscles to pull the Achilles tendon on the calcaneal tuber. The narrower proximal part of the calcaneus in such derived multituberculates as *Kryptobaatar* and *Eucosmodon* (Krause and Jenkins 1983) has been hypothesized to correlate with a more digitigrade pedal posture (Kielan-Jaworowska and Gambaryan 1994), or to a facultatively digitigrade posture (Fig. 9, Fig. 10: node 6). This interpretation can be supported by comparative evidence from placental mammals that digitigrade taxa tend to have a narrower proximal part of the calcaneus than do plantigrade taxa of the same group (Wang 1993; Carrano 1997; Polly 2008; Polly and MacLeod 2008).

In the derived multituberculates, the peroneal process and groove are separate structures. The tendon of M. peroneal longus has been reconstructed as passing through the peroneal groove (Kielan-Jaworowska and Gambaryan 1994). These bony characters and their soft-tissue correlates are clearly apomorphic, by comparison to the undifferentiated peroneal shelf of *Rugosodon* and *Sinobaatar*, and most of the outgroups to multituberculates (Fig. 8). In the latter taxa, the tendon of M. peroneus longus passed through the gap between the peroneal shelf, the cuboid, and the proximal end of MT V, but without a distinctive peroneal groove.

In both configurations of the course for the tendon of M. peroneal longus, it inserts on the plantar base of MT I and the M. peroneal brevis tendon inserts on the plantar base of MT V, as exemplified by extant didelphid marsupials (Szalay 1994). These structures are correlated with the functions in the eversion of the metatarsals, plus some plantarflexion in didelphids. However, the functional difference of the tendon passage in a distinct groove, or without a groove, is still unclear.

The more disparate morphologies of the tarsals of the derived multituberculates (Fig. 10: node 6) with potentially more diverse locomotor functions are also consistent with the independent observations on dentition that the Late Cretaceous multituberculates evolved a great disparity of dental patterns and more diverse feeding functions before the radiation of ptilodontoids and taeniolabidoids in the Paleocene (Wilson *et al.* 2012).

SUMMARY

- The new fossil of *Rugosodon* provides diagnostic cruro-tarsal characters for multituberculates as a whole, and shows that multituberculates developed novel structures of the astragalus, the navicular and the entocuneiform that increased the mobility of the all joints of these bones, very early in their phylogenetic history.
- *Rugosodon* shows plesiomorphic features of the calcaneus and the cuboid. This helps to establish the ancestral condition from which the more derived djadochtatherian multituberculates of the Late Cretaceous and taeniolabidoids and ptilodontoids of the Paleogene evolved more apomorphic calcaneal features that can be correlated with more versatile functions of the ankle.
- Multituberculates have a relatively wide range of morphologies of the tarsals and presumed pedal postures. We propose that the ancestral pedal posture of multituberculates was plantigrade without a strong abduction of metatarsals, whereas some of the derived multituberculates of the Late Cretaceous and Paleogene evolved facultative digitigrady and a wider range of pedal abduction and eversion.
- *Rugosodon* had a sprawling (crouched) hind limb posture and habitually flexed knee. It was more likely a terrestrial than an arboreal mammal, based on its pedal phalanges.

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