MAMMALS OF THE EOCENE LOCALITY TORU AJGYR (KYRGYZSTAN)

by

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This paper is dedicated to the memory of Dr. Valerij JUREVICH RESHETOV (1946-1993), who participated in excavations at the Toru-Ajgyr locality and provided detailed descriptions of *Lophialetes expeditus* from Mongolia.

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RESUME

Les restes de mammifères collectés à Toru Ajgyr (NE-Kyrgyzstan) en 1997 et 1998 dans le cadre d'une coopération entre l'Université Martin-Luther de Halle (Allemagne), l'Institut Zoologique de St. Pétersbourg (Russie) et l'Institut Sismologique de Bishkek (Kirghizstan) sont ici décris. Les taxons identifiés appartiennent aux perissodactyles *Lophialetes* sp., *Teleolophus* sp. et brontothères. Les Olseniidae, un groupe d'ongulés primitifs, sont représentés par un pied complet attribué a *Olsenia* sp. En outre, nous décrivons du materiel post-cranien appartenant à *Gobiatherium mirificum* (Dinocerata) et à différents artiodactyles. L'assemblage de mammifères trouvés à Toru Ajgyr indique un âge Eocene moyen inférieur, équivalent à l'age mammalien asiatique Arshantan (ALMA), qui est corrélable au Bridgerien nord americain (NALMA) et à la partie inférieure et moyenne du Geiseltalien en Europe.

ABSTRACT

Morphological descriptions are given of Eocene mammals from the locality Toru Ajgyr (NE-Kyrgyzstan) that were excavated in 1997 and 1998 in a cooperation between the Martin-Luther-University Halle (Germany), the Zoological Institute in St. Petersburg (Russia) and the Seismological Institute in Bishkek (Kyrgyzstan). The species found belong mostly to perissodactyls, as *Lophialetes* sp., *Teleolophus* sp. and brontotheres. The primitive ungulate family Olseniidae is represented by a complete foot skeleton of cf. *Olsenia* sp. In addition, postcranial materials of *Gobiatherium mirificum* (Dinocerata) and of artiodactyls have been collected and are described herein. Based on mammals, the locality is part of the Asian Land Mammal Age Arshantan and is stratigraphically equivalent with the Bridgerian Land Mammal Age in North America and with the lower and middle Geiseltalian of the European Middle Eocene.

KURZFASSUNG

Es werden die in den Jahren 1997 und 1998 durch die Martin-Luther-Universität Halle (Deutschland) in Zusammenarbeit mit dem Zoologischen Institut St. Petersburg (Russland) und dem Seismologischen Institut in Bishkek (Kirgisistan) geborgenen eozänen Säugetierfunde von Toru Ajgyr morphologisch beschrieben. Zu den nachgewiesenen Taxa gehören hauptsächlich die Perissodactyla *Lophialetes* sp., *Teleolophus* sp. und Brontotherien. Neu ist die ungulate Familie Olseniidae, die durch ein vollständiges Fußskelett belegt ist. Weiterhin konnten Dinocerata mit *Gobiatherium mirificum* und nicht näher bestimmbares postcraniales Material von Artiodactylen nachgewiesen werden. Nach dem Auftreten der o.g. Taxa und deren phylogenetischen Entwicklung ist das Vorkommen stratigraphisch präziser einzustufen und wird mit dem Arshantan Asiens korreliert. Damit ist Toru Ajgyr stratigraphisch äquivalent mit dem Bridgerian Nordamerikas und den unteren und mittleren Geiseltalium des europäischen terrestrischen Mitteleozäns.

INTRODUCTION

The Russian geologist Vokhmintsev discovered the Eocene locality Toru-Ajgyr during geological mapping of the Kungei-Alatau Mountain Range north to Lake Issyk-Kul in Northern Kyrgyzstan (Plate 1a, b). The first note about this discovery was made by Zhukov (1970). Tarasov (1968b) described two new species of perissodactyls from Toru-Ajgyr in the abstract (non public "avtoreferat") of his dissertation: "*Deperetella kungeica*" and "*Prothyracodon zhukovi*". Although Tarasov provided diagnoses for these taxa, they are not available according to article 8.2 of the ICZN (Kraus, 2000), but they are not *nomina nuda*, as was thought by Russell & Zhai (1987: 189, 191). In 1968, 1971 and 1975 the Palaeontological Institute of Moscow (PIN) organised further excavations, of which the last two were particularly large. In 1973 a team from the Zoological Institute of Alma-Ata also collected fossils. Original materials, sampled by Tarasov and described in his dissertation, were deposited in the latter Institute (Tarasov, pers. com. 2000). None of the Moscow and Alma-Ata collections were fully studied and published. In their papers concerning Central Asian perissodactyls, Reshetov (1975, 1979), Nesmeyanov *et al.* (1977), Reshetov *et al.* (1978), Dmitrieva & Nesmeyanov (1982) and Badamgarav *et al.* (1985) mentioned briefly preliminary determined mammals from Toru Ajgyr. The first overview of this fauna was given by Russell & Zhai (1987: 190-191). In 1999, Agadjanian & Kondrashov described skulls of *Gobiatherium* from the PIN collection, which were formerly found in this locality and Lucas (2001) revised this genus. Erfurt & Averianov (2005) described the Olseniidae as a new ungulate family.

The geological setting of Toru Ajgyr is described by Dmitrieva & Nesmeyanov (1982), Russell & Zhai (1987), and Erfurt *et al.* (1999). The fossils were deposited in a clay bed of the Chonkurchak Svita over a basalt layer (Figure 1), for which absolute dates of 55-56 MYR were determined (Krylov 1960; Zhukov 1970; Nesmeyanov *et al.* 1977); roughly equal to the Paleocene-Eocene boundary (Berggren & Aubry 1998: 2.2). The calculations using decay constants accepted in western countries give a somewhat older age of 57.35 MYR (Lucas 2001). However, the mammal assemblage from Toru-Ajgyr has a typical Middle Eocene aspect, implying a considerable gap in deposition between basalts and the mammal bed or that the radioisotop age is unreliable. Therefore, two expeditions to Toru-Ajgyr were organised by the Geological Institute (Halle) in co-operation with the Zoological Institute (Saint Petersburg) and the Seismological Institute (Bishkek) in 1997 and 1998. The best preserved fossil materials are presented here. For a complete description of the fauna see Erfurt & Averianov (2006).

MATERIALS AND METHODS

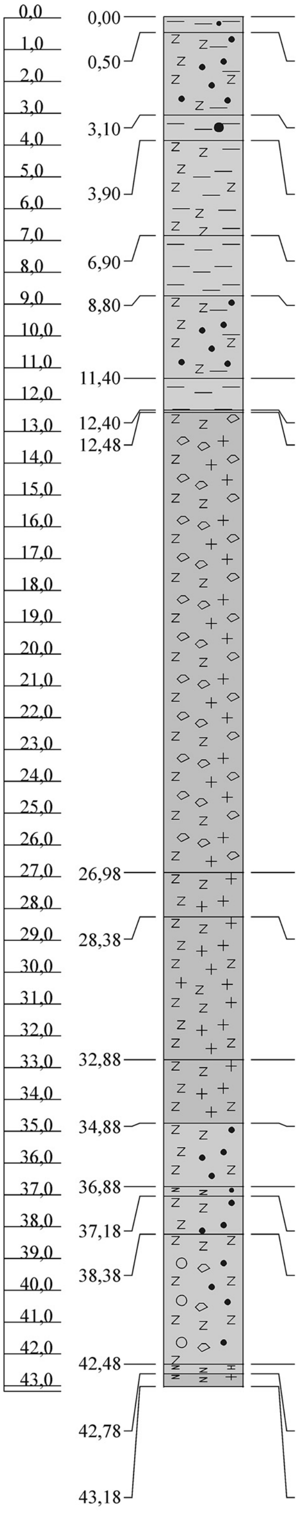
All materials were found near the village Toru Ajgyr on the northwest border of Lake Issyk-Kul in Kyrgyzstan (Russell & Zhai 1987; Erfurt *et al.* 1999). The materials are housed in the Institute of Geological Sciences of the Martin-Luther-University Halle (GIH). 1441 teeth and bones were catalogued; the number of bone splinters is much higher (Table 7). Only 55% of the excavated bone fragments and bones were anatomically or taxonomically determinable. The fossils were embedded in different layers of sands and clays from the lower part of the Chonkurchak Svita. They are up to 3m thick and partly cemented. The upper part of this svita is eroded and the fossils are only superimposed by relatively thin layers of marl, sands, chalk or clay (Figure 1). The lacustrine character of the sediments is demonstrated by the mineralogical content, such as montmorillonite and bentonites (Dmitrieva & Nesmeyanov 1982: 57). The preservation is good within the uncemented clays and bones are mostly articulated. Bones, around which the matrix is already eroded, are very fragile (site VII), as are those in cemented matrix (site IV). Fragile bones were hardened with a special lack ("Archäocoll") in the field and plaster jackets were used for larger specimens. If the concentration of bone splinters was high on the surface, a systematic excavation was undertaken.

The material around the unearthed bones was sieved and additional material was taken for screen-washing in order to detect microfossils. However, during screen-washing only splinters of larger bones were found and microvertebrate remains were lacking. The labels of the Toru Ajgyr material (TA) contain three parts: First, a Roman number corresponding to the local excavation site within the Toru-Ajgyr complex. Second, an Arabic number was given to assign closely attached bones, which could represent one individual. Third, if such specimens consist of several bones, each bone got an additional Arabic number after a hyphen (for example GIH TA I/57-1). The taxonomical classification generally follows McKenna & Bell (1997). The anatomical terminology is according to Dobberstein & Hoffmann (1961) and Starck (1979); the dental terminology is taken from Dashzeveg & Hooker (1997: fig. 24). For the use of Latin terms see also Osborn (1929a).

All measurements are in millimetres with an accuracy of 0.5 mm. For postcranial bones "length" is used as extension in the dorsoventral direction. "Width" refers to mediolateral measurements and "height" to an anteroposterior direction (Figure 3). Other orientations are diameters according to Duerst (1926). Data in round brackets are taken from incomplete specimens and represent minimal values. Rectangular brackets indicate measurements from drawings. Both types of data should be used as orientation only. In the drawings, broken areas are hatched, smaller fractures are not indicated.

Acronyms for institutions: AMNH: American Museum of Natural History, New York; CM: Carnegie Museum of Natural History, Pittsburgh; GIH: Institute of Geological Science and Geiseltalmuseum, Halle; PIN: Paleontological Institute, Russian Academy of Sciences, Moscow; ZMB: Museum für Naturkunde, Berlin.

Anatomical abbreviations: art.: articulation; D: diameter; dext.: dexter; dist.: distal; frag.: fragmentary; H: height; L: length; MC: metacarpus; MT: metatarsus; proc.: processus; prox.: proximal; sin.: sinister; W: width.



17. Marl: slightly sandy, brown; 0,5m

16. Pattum (local name): Mixture of sand, chalk and clay with slightly rounded argillite up to 1.5 cm; spottet coloured: grey-blue, brown, pale-brown; contains fossil canals filled with reddish brown clay and **bone fragments**; 2,6m

15. Mergel: sandy, reddish-brown, lumpy with fine fragments of quartz and argillite; contains fossil root tubes; 0,8m

14. Clay: colour changes from dirty green, red to reddish brown; slightly lithified, gypsum bearing and contains **fragments of fossil roots and bones**; 3,0m

13. Marl: reddish-brown; with fine fragments of quartz and argillite; 1,9m

12. Mixture of sand, chalk and clay: with slighlty rounded fragments of quartz and argillite; pale gray - blueish; 2,6m

11. Marl: pale brown, with fragments of limestone and argillite up to 0,5 cm in diameter; 1,0m

10. Basalts: kaolinised, pale grey; 0, 08m

9. Basalts: grey - dark grey; fine crystalline and solid; mosaic like pattern of parts with tonsils and without; seldom with reddish scree; 14,5m

8. Basalts: grey - pale grey; with tonsils, up to 50% content in the upper layer; about 1,4m

7. Basalts: dark grey; solid and fine crystalline, with isolated fragments of argillite; rarely with tonsils; 4,5m

6. Basalts: heavily eroded or decomposed; dark grey; contain many tonsils, which are filled with pale secondary minerals; 2m

5. Sandstone: intensely red to raspberry - red; weakly sorted; 2m

4. Sandstone: reddish; with weakly rounded fragments of chalk, which are greenish up to cream-coloured; 0,3m

3. Sandstone: reddish; with greenish intermediate layers of clay; 1,2m

2. Rough sandstone or fine conglomerate: weakly sorted; grey with translocated bone splinters; slightly rounded and up to 3 cm in diameter; 4,1m

1. Basal layer:

b) carbonaceous stones with some grains of quartz and sand; lumpy with a coal-like substance in thin veins and crusts; 0,3m

a) heavily eroded granits; kaolinised spotted colour: pale grey, blueish, reddish; 0,3 - 0,4m

Figure 1.— Profile of the lower part of the Chonkurchak Svita in Toru-Ajgyr site I. Profile taken by J. BUCHANTSCHENKO (GIH) in 1998. Top of the profile: 2138m above sea level.

SYSTEMATIC PALAEONTOLOGY

Class Mammalia LINNAEUS, 1758
Order Dinocerata MARSH, 1873a
Family Uintatheriidae FLOWER, 1876

Genus ***GOBIATHERIUM*** OSBORN & GRANGER, 1932
Gobiatherium mirificum OSBORN & GRANGER, 1932
(Figure 2 a,b)

Synonymy

This list is focussed on Toru Ajgyr material; for more details see Lucas (2001: 592).

= *Gobiatherium mirificum*: Dmitrieva & Nesmeyanov 1982: 57.
= *Gobiatherium mirificum*: Agadjanian & Kondrashov 1999:102.
= *Gobiatherium* cf. *mirificum*: Erfurt *et al.* 1999: 115.
not *Gobiatherium* cf. *mirificum*: Erfurt *et al.* 1999: plate 1/b.
= *Gobiatherium mirificum*: Lucas 2001: 592.

Material

- GIH TA I/19: navicular sin.; GIH TA II/28: frag. MC IV prox. dext.

Discussion

In our field campaign, *Gobiatherium* is less frequent than other mammals, although the large bones are very conspicuous. Probably, this species was selectively collected by former expeditions. The new material supports the identification of *Gobiatherium* from Toru Ajgyr by Beljaeva (1974), Agadjanian & Kondrashov (1999) and Lucas (2001). The osteological determination is based on the size of the bones and the shape of their facets (fig. 2 a, b). GIH TA II/28 is regarded as MC IV due to a small lateral facet for an adjacent metacarpal (MC V). In contrast to a MC II of *G. mirificum* (Osborn & Granger 1932: fig. 18B), the proximal facet is not flat but convex similar to a MC III. In contrast to brontotheriids, our metapodial is anteroposteriorly elongated, tall and the proximal articulation facet comes down to the anterior side. There, the facet ends in a straight line.

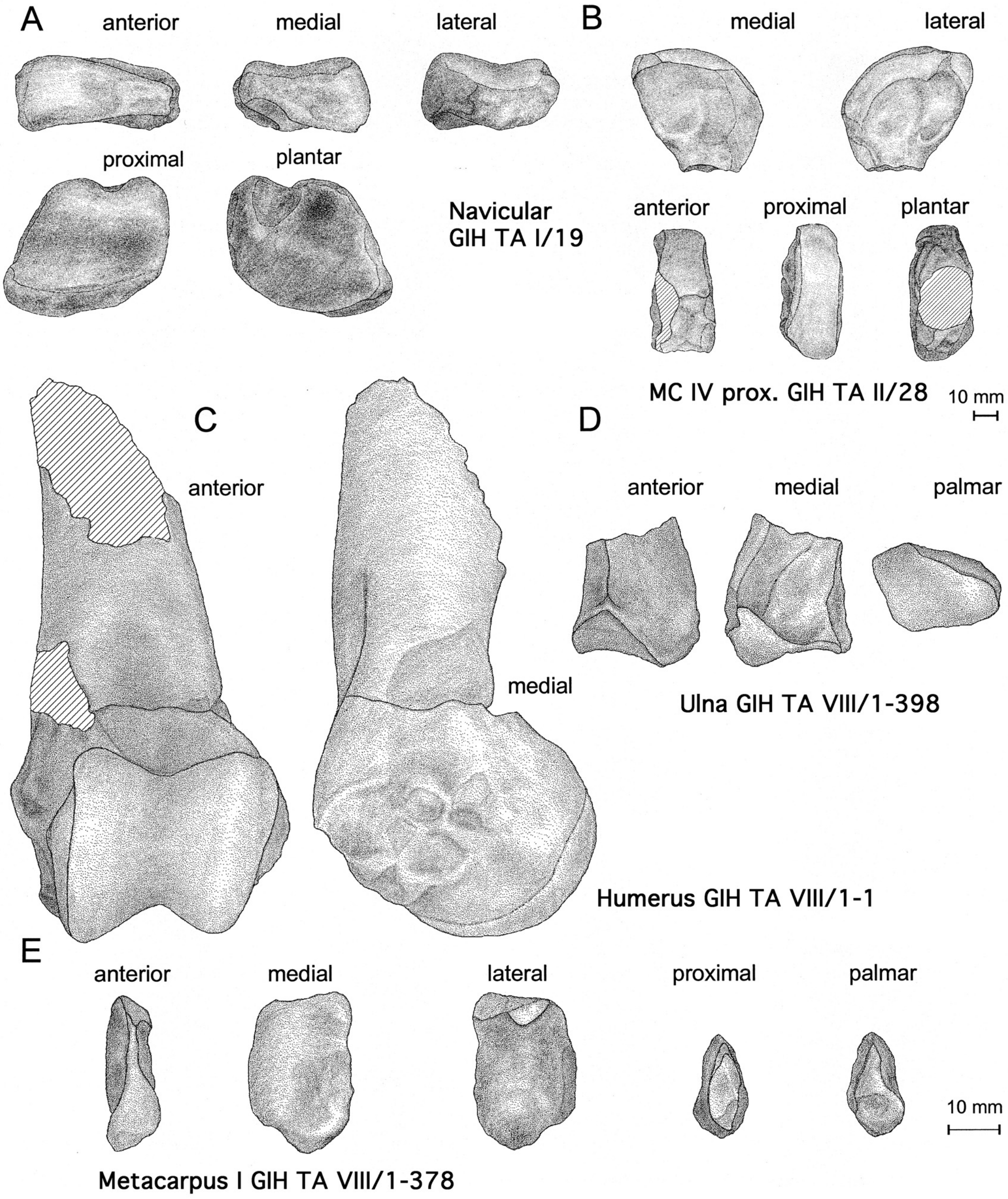


Figure 2.— *Gobiatherium mirificum* and Brontotheriidae from Toru Ajgyr.

A - B: *Gobiatherium mirificum,* same scale; C - E Brontotheriidae indet., same scale.

Order Perissodactyla OWEN, 1848
Suborder Ceratomorpha WOOD, 1937
Superfamily Brontotherioidea MARSH, 1873b

***Brontotheriidae** indet.*
(Figure 2 c-e, figure 3 - figure 6, plate 1 c , plate 2 c)

Synonymy

= "*Triplopus*?"sp.: Erfurt *et al.* 1999: 116.

Material

- GIH TA I/75: skeleton with 69 fragmental postcranials including vertebras, patella, tibia, tarsals, phalanges and sesamoids;
- GIH TA VIII/1: skeleton with 401 fragmental bones including vertebras, humerus, radius, ulna, carpals, metacarpals, phalanges, sesamoids, femur, patella, tibia, tarsals;
- isolated bones: GIH TA I/31: frag radius dist.; GIH TA VII/2: frag. ulna dist.; GIH TA VII/102: frag. trapezoideum sin. juv.

Further material is available at sites I and II, which likely is referable to brontotheriids. All bones are multiply broken and only epiphyses are preserved.

Discussion

These materials indicate medium sized, relatively heavy, mesaxonic animals with ungual phalanges and morphologically pentadactyl but functionally tetradactyl manus. Remarkable are the articulated first (GIH TA VIII/1-220) and second (GIH TA VIII/1-221) phalanx, which proof a residual first finger (Figure 4, Plate 2c).

Forelimb

The scaphoid (GIH TA VIII/1-379) is more compact than in *Teleolophus* sp. and is much larger than *Lophialetes* sp. (Figure 3). A shared character with brontotheres is the serial, but not taxeopode (Rasmussen *et al.*, 1990) construction of the basipodium. The carpals are aligned proximodistally with minimal interlocking between the proximal and distal row. In contrast to hyraxes and proboscideans, the magnum articulates only with the scaphopid, not with the lunate. Our material displays two main power transmission units (Granger & Gregory 1943). The first unit comprises the lunate and triquetrum, which articulate via a large unciform with MC V, MC IV and the lateral MC III. The second unit is represented by the scaphoid, which is in contact via magnum and trapezoideum with MC II and the medial MC III. In American Eocene brontotheres, the proximal carpal row is relatively high compared with the magnum and trapezoideum (Osborn 1929b: fig. 512). The lunate is especially large and overlays mainly the unciform (*Eotitanops*, *Mesatirhinus* and *Paleosysops*). In anterior view, the lunate has an oblique and short contact to the magnum and scaphoid and lunate are of about the same height. So, the lunate does not reach the magnum and has no additional laterodistal facet for the unciform. Therefore, the load of MC III is sustained primarily by the magnum.

The metapodium is unspecialised: there is neither an elongation nor a special thickening of bones. This condition is more similar to that in Eocene brontotheres and tapiromorphes than in hippomorphs, which display cursorial adaptations and are smaller. The medial side of the proximal MC III does not display any articulation areas; supporting the idea that MC II stands higher than MC III and articulates with trapezoideum and magnum only. This condition is regarded as typical for brontotheres.

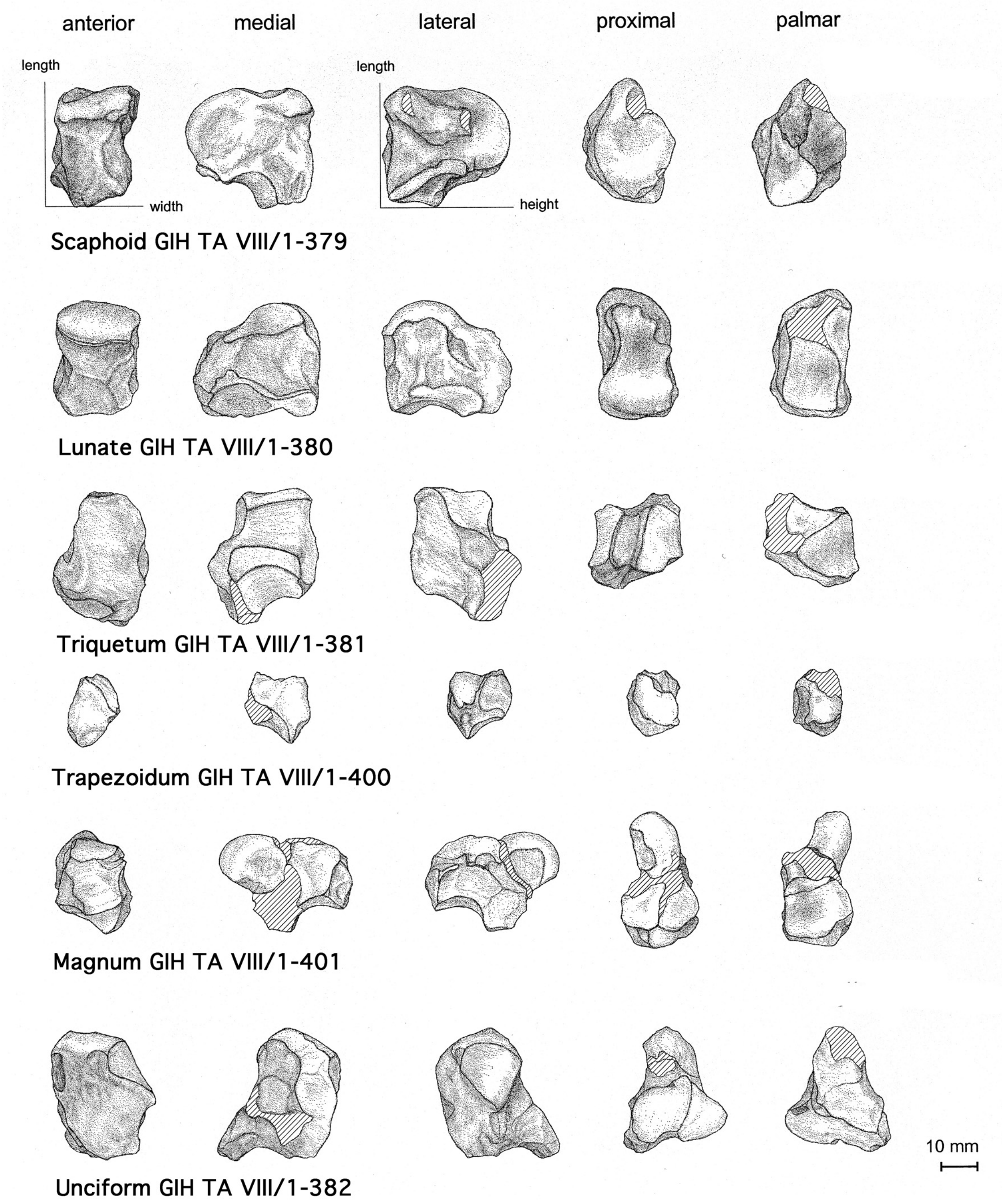


Figure 3.— Carpals of Brontotheriidae indet. from Toru Ajgyr. Except or the magnum, all bones belong to th left side

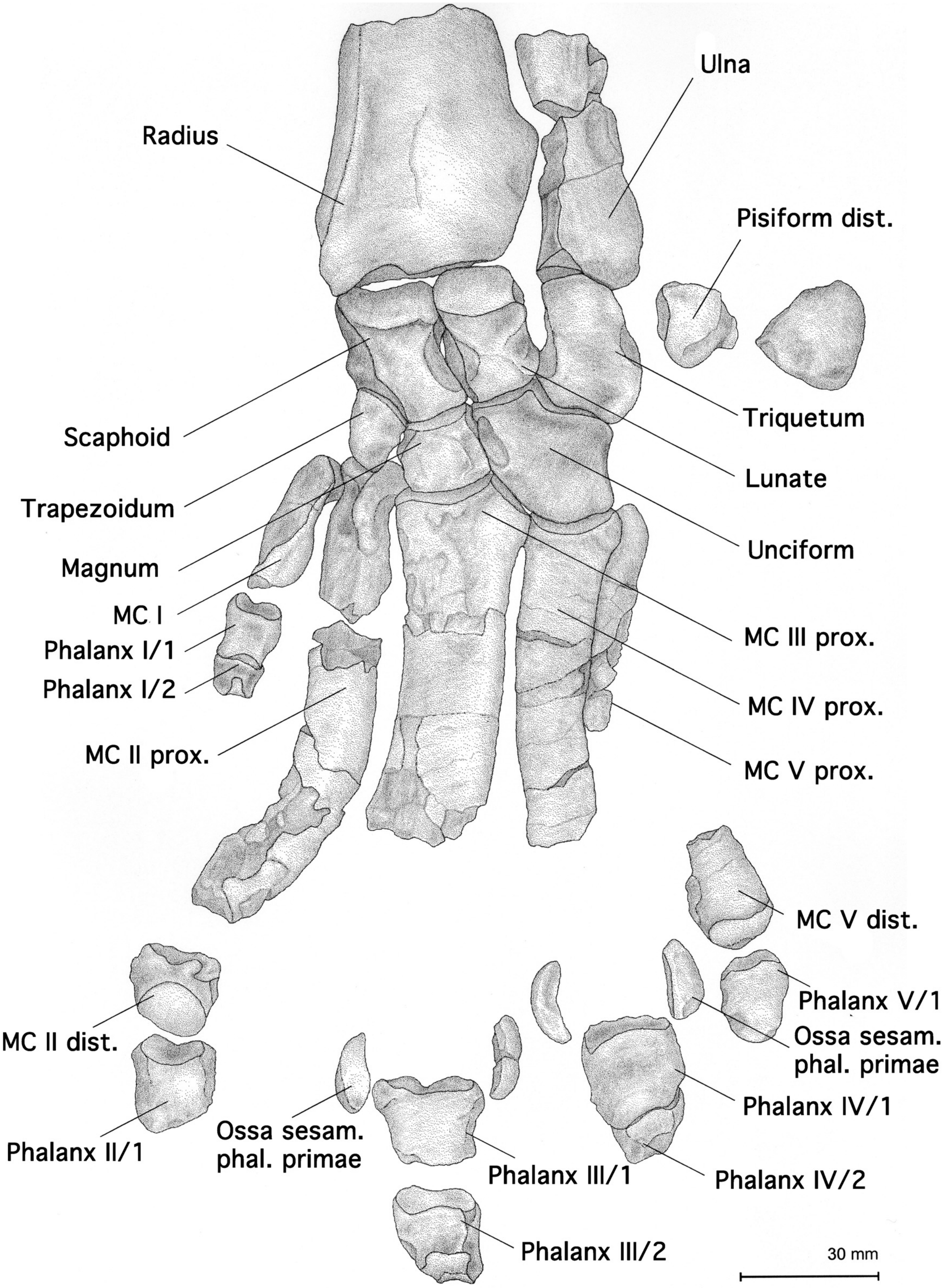


Figure 4.— Reconstructed left manus of Brontotheriidae indet. from Toru Ajgyr, dorsal view. Metapodials fragmentary, distal joints are in estimated position.

For example, in *Metatitan* (Yanovskaya, 1980: fig. 37), the proximal MC II and MV C are relatively broad. The body mass is more or less equally shared among four metacarpals with the result that the diaphyses of MC II through MC V are more or less equally thick, and trapezoideum and unciform display large distal facets. This principle is suggested in GIH TA VIII/1, where the latter carpals are large and the magnum is small compared with tapiroids. In tapiroids, the magnum represents larger distal carpals and transmits mesaxonically the body weight to MC III. In the Toru Ajgyr material, the lunate is not tapering in the palmar (distal) direction and the width on the proximal side is nearly equal to the palmar width. In contrast, the lunate of upper Eocene brontotheres is wedge-like in correlation to their higher mass.

Hindlimb

Combined fragments of the hindlimb (GIH TA I/75) suggest a total tibia length of

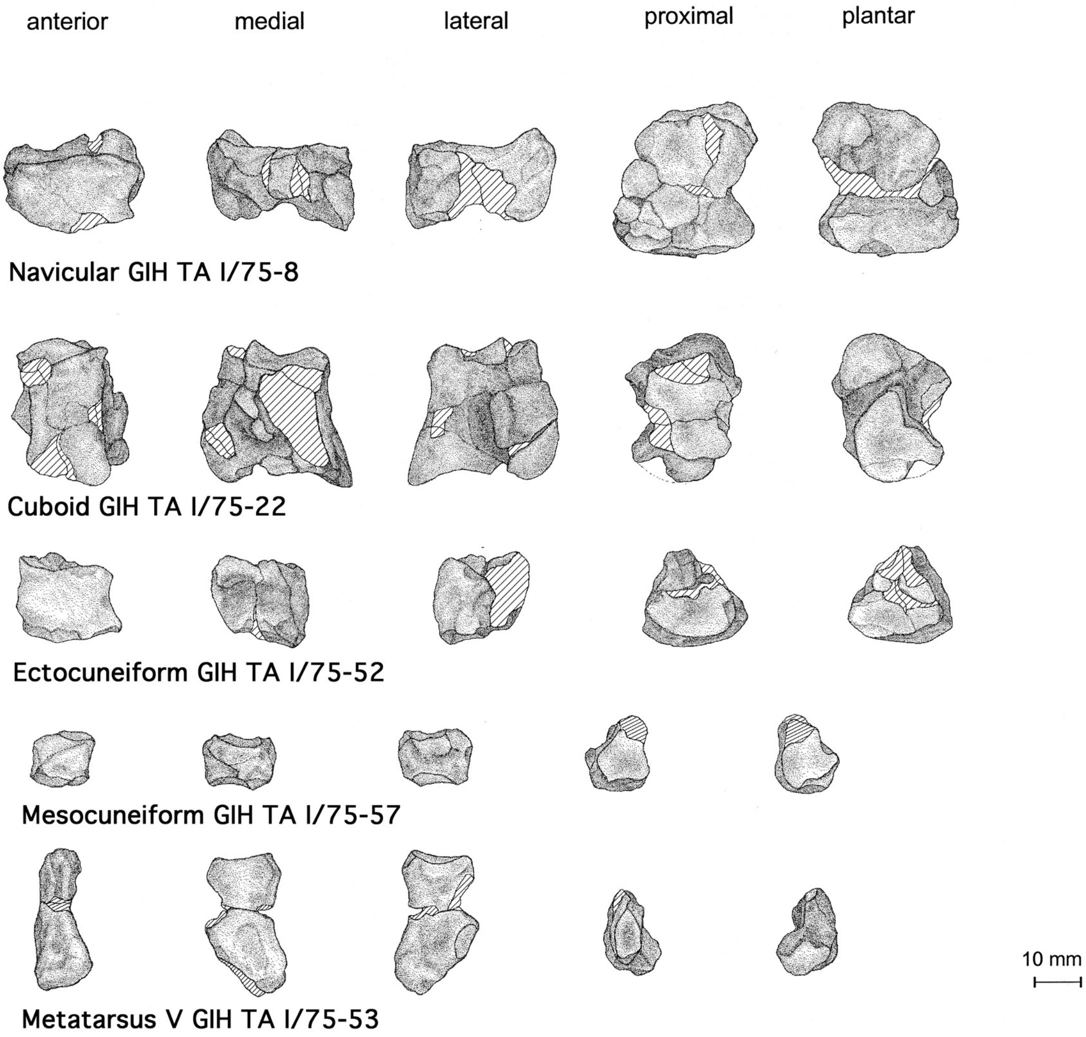


Figure 5.— Left tarsals and right MT V of Brontotheriidae indet. from Toru Ajgyr.

at least 310 mm. Based on this size, we exclude all hippomorphs as well as gracile and/or tridactyl ceratomorphs. In contrast to other perissodactyls from Toru Ajgyr, GIH TA I/75 is larger than expected for *Teleolophus* and similar to *Deperetella cristata* AMNH 81844 from Ula Usu (Radinsky 1965b: 257, fig. 38c, 39b).

In contrast to *D. cristata*, there is medially no hump for ligaments on the distal tibia, the malleolus tibiae is shorter and the anterior border is marked by a styloid process that is standing medially, not centrally. In addition, the facet for MT IV is not laterally open in the cuboid. The terminal phalanx of the third toe (GIH TA I/75-69) displays a fissure, but not as large as in *D. cristata*. Furthermore, this phalanx is shorter. The only similar specimen with *Deperetella* is GIH TA I/75-53, which resembles an entocuneiforme (Radinsky, 1965b: fig. 38-40).

In contrast to his determination, we regard this bone as MT V owing to the articulation facet with the cuboid. Unfortunately, deperellids cannot be definitely excluded because postcranials are not known for all taxa. Within the Rhinocerotoidea (Heissig 1989), most amynodontids (Colbert 1938 and Xu 1966) are larger. Only *Lushiamynodon* is similar-sized, of which the foot bears thickened metatarsals. Among similar sized hyracodontoids, only *Forstercooperia* and *Juxia* are valid according to Lucas & Sobus (1989: 358). *Forstercooperia (F. sharamurense*) can be excluded due to the tetradactyl manus and because of the phalanges in the hind limb, which are longer in the second toe than those of the fourth (Radinsky 1967a: fig. 10). *Uintaceras radinskyi* (formerly associated with *Forstercooperia*, Holbrook & Lucas, 1997) is different due to larger size, relatively compact metapodials and MC II stands at the same level as MC III. *Juxia* is only known by skull remains. Based on the similarities to *Forstercooperia* (Dashzeveg, 1991) this genus is probably not referable to our material. The most appropriate determination of GIH TA I/75 would be that of an unspecialised brontotheriid.

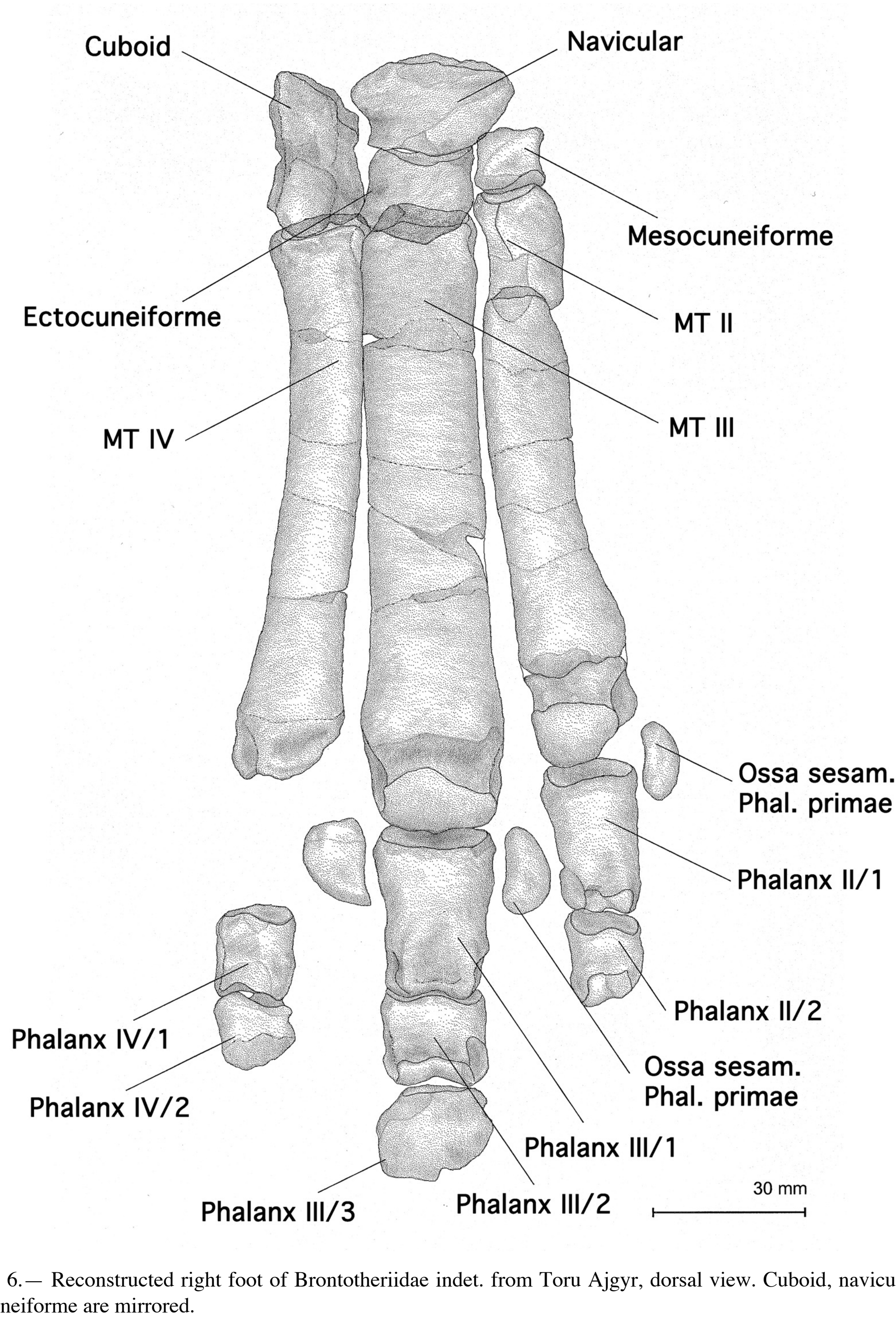


Figure 6.— Reconstructed right foot of Brontotheriidae indet. from Toru Ajgyr, dorsal view. Cuboid, navicular and ectocuneiforme are mirrored.

Infraorder Tapiromorpha HAECKEL, 1866
Superfamily Tapiroidea GRAY, 1825
Family Deperetellidae RADINSKY, 1965b

Genus ***TELEOLOPHUS*** MATTHEW & GRANGER, 1925a

Teleolophus sp.

(Figure 7 - Figure 8, Plate 2b)

Synonymy

= *Teleolophus beljaevi*: Biryukov 1974:78; Russell & Zhai 1987: 191.

= *Teleolophus* sp.: Nesmeyanov *et al.* 1977: 84; Dmitrieva & Nesmeyanov 1982: 57.

= *Deperetella kungeica*: Nesmeyanov *et al.* 1977: 84; Dmitrieva & Nesmeyanov 1982: 57.

= *Teleolophus beliajevi*: Reshetov 1979: 37.

= *Teleolophus* cf. *beliajevi*: Erfurt *et al.* 1999: 115.

Deperetella kungeica mentioned by Nesmeyanov *et al.* (1977) and Dmitrieva & Nesmeyanov (1982) refer to the unpublished dissertation of Tarasov, which is only partly available as "avtoreferat" (Tarasov, 1968b). This avtoreferat contains the statement that this work should not be considered as a publication. According to Lucas *et al.* (1997: 243) *T. beljaevi* is a junior subjective synonym of *T. medius* Matthew & Granger, 1925a.

Material

- GIH TA IV/1-48: limb bones of partly articulated individuals in superposition;

- isolated bones: GIH TA II/24 to 25: corpus vert. thor.; GIH TA II/38: frag. phalanx I prox.

At site IV, manganese crystals in the form of little black dots and stripes covered those parts of the skeleton lying deeper in the sediment. The density of these spots gives hints concerning the anatomical positions of the bones.

Discussion

The tridactyl and mesaxonic manus (Figure 8) supports the classification as perissodactyl. Within this group, many ancylopods are to be excluded because they are larger. Smaller ancylopods display specialized phalanges and stronger developed MC V. Most hippomorpha are different due to the lack of MC V. The only exceptions are hyracotherines, which are of smaller size such as *Hyracotherium* (Kitts 1956). In addition, the trapezoideum and magnum are relatively large. Anteriorly viewed, the magnum is only half the size of the unciform (Figure 7) in the Toru Ajgyr material. Finally, our classification as ceratomorph perissodactyl is established on the slender, medium-sized limbs with primitive carpal skeleton and the reduced MC V.

Within ceratomorphs, most of the rhinocerotoid forms can be excluded due to their short and stout legs and larger size. Only hyracodontids - mostly known from North America - contain smaller representatives. Estimated by dentitions, *Forstercooperia* and *Paraceratherium* are larger (Radinsky, 1967a; Chow & Xu, 1961). *Triplopus* bears a tridactyl manus and is smaller. *Prothyracodon* (possibly a synonym of *Triplopus*, see Radinsky 1967a: 7) displays a relatively high proximal carpal row, stouter metacarpals (Peterson 1919: pl. 46/2) and it is smaller. The limbs of other hyracodontids are not known and, therefore, this group cannot be definitely excluded.

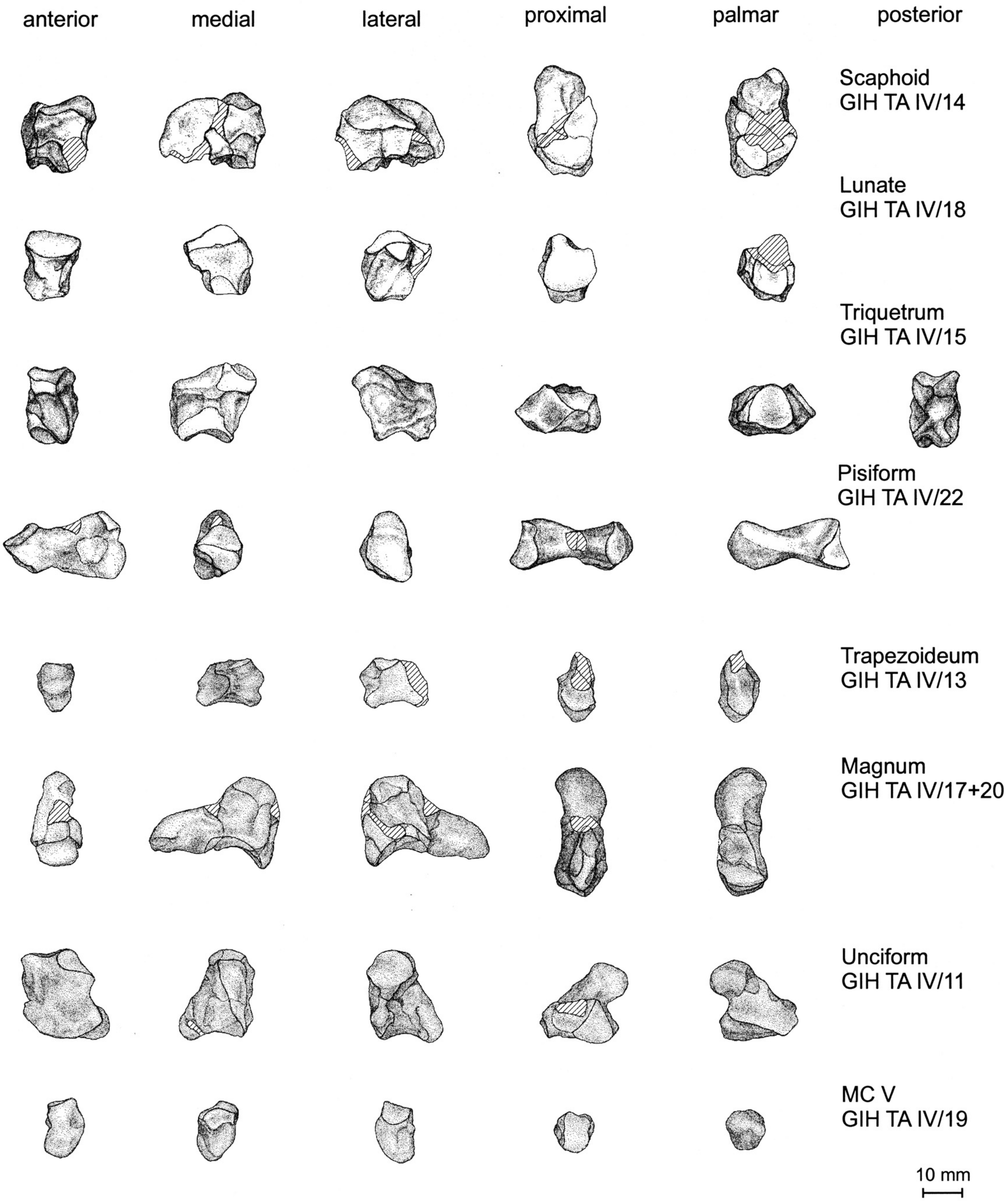


Figure 7.— Left carpals of *Teleolophus* sp. from Toru Ajgyr.

Nearly all of the families mentioned above are known only by their dentitions. This is the reason for phylogenetic and systematic uncertainties (Dashzeveg & Hooker, 1997; Lucas *et al.*, 1997). Asian Helaletidae, like *Helaletes* and *Colodon* (Borissiak 1918:27), are characterised by a strong bilophodont molar structure. They are excluded based on the relation between teeth and limb dimensions. *Cymbalophus* and *Heptodon* are also excluded owing to their dimensions (Radinsky, 1965a).

bone	measurement	Toru Ajgyr	[mm]	Ula Usu	[mm]
Humerus	largest width of distal epiphysis	TA IV/35,30	41.5	AMNH 81827[1]	69
Radius	total length	TA IV/45, 44	(220)	AMNH 81828[1]	315 - 335
Ulna	largest height of the distal epiphysis	TA IV/47+26	14.5	AMNH 81829[1]	[19]
Scaphoid	largest length (dorsoventrally)	TA IV/14	(20)	AMNH 81808[1]	[30]

Table 1.— Limb measurements of *Teleolophus* sp. from Toru Ajgyr compared with *Deperetella cristata* from Ula Usu.

[1] measured after Radinsky (1965b: 252, 259, fig.35, 40).

Isectolophidae are primitive in having a bunoselenodont dentition and a short or lacking postcanine diastema (Holbrook *et al.* 2004). Thus, the morphology of hand and foot is expected to be more primitive than in the specimens described here. In addition, these forms are of smaller size (Radinsky 1967b; Lucas *et al.* 2003). Lophialetidae are also small and have no MC V.

In the Deperetellidae, the forelimbs of *Deperetella cristata* are larger (Table 1). The distal ulna is thicker and the ratio of the largest width to the largest height of the distal epiphysis is about 1:1 (Radinsky 1965b: fig. 35/d, e), whereas in our material this ratio is about 1:1.5. In addition, metatarsus and phalanges are more elongated. On the pisiform, there is no facet for the radius as indicated for *D. cristata*. In this species from Ula Usu, there is a round and flat scaphoid facet on the palmar side of the lunate. In our materials (Figure 7), this facet lies below the distal margin of the scaphoid and obviously articulates with the magnum. The scaphoid of *Teleolophus* sp. is shorter than that of *D. cristata* (Table 1). Furthermore, there is no second, palmar facet for the lunate. The trapezoideum GIH TA IV/13 is neither as stout as AMNH 81813 nor AMNH 81812 from Ula Usu. In the unciform, the proximal facets joining together at an angle of about 45°, which is steeper than figured for *D. cristata* (Radinsky, 1965b: fig. 36). A further difference is given in MC V, which tapers distally in *D. cristata*. In our material, this bone is stout is rounded at its end. In combination, these characters would most likely determine the described manus as *Teleolophus*, which fits in size.

The presence of *Teleolophus* in Toru Ajgyr is also confirmed by dental remains described by Tarasov (1968b) see Table 2. This concerns specimen N 119, a left p3 that is referred to *Teleolophus* sp. and N 120, a left maxillary fragment with M2-3 (the holotype of the unavailable taxon "*Deperetella kungeica*"). The p3 bears a sharp lingual accessory crest on the paraconid, which is a diagnostic character for *Teleolophus* (Dashzeveg & Hooker 1997). The morphology and measurements of the molars (Table 2) fit into the range of *Teleolophus medius* from northern China and southern Kazakhstan (Radinsky 1965b; Lucas *et al.* 1997).

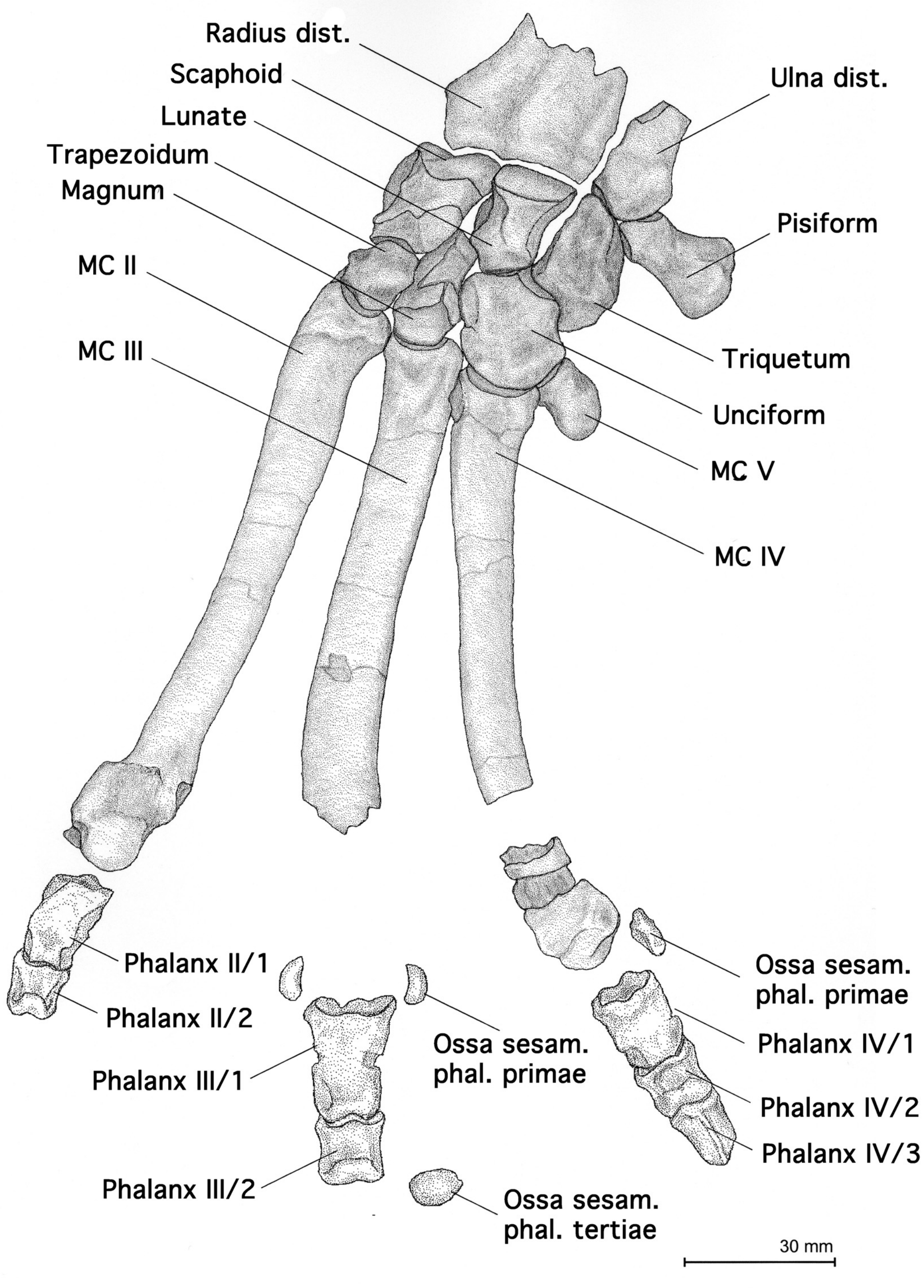


Figure 8.— Reconstructed left manus of *Teleolophus* sp. from Toru Ajgyr, dorsal view. All bones were found articulated, distal phalanges eroded.

Measurement	Toru Ajgyr[1]	Irdin Manha[2]	Ulan Shireh[2]	Shinzhaly[3]
L M2	20.0	19.0, 21.9	19.6-20.0, M=19.8, n=3	21.0
W M2	20.0	18.1, 22.2	18.9-20.0, M=19.3, n=3	21.7
L M3	21.0	21.1	19.0-21.0, M=20.1, n=4	21.8
W M3	21.0	22.6, 25.8	19.5-21.2, M=20.3, n=4	23.0
L p3	12.3	12.3	-	-
W p3	7.5	7.6	-	-

Table 2.— Teeth measurements of *Teleolophus* sp. from Toru Ajgyr compared with *Teleolophus medius* from China and Kazakhstan.

If available, the statistical range is indicated. M = mean, n = number of specimens. [1] Tarasov (1968b: tabs. 11, 12), [2] Radinsky (1965b: tabs. 11, 12), [3] Lucas *et al.* (1997: 242).

Family Lophialetidae MATTHEW & GRANGER, 1925a
Genus ***LOPHIALETES*** MATTHEW & GRANGER, 1925a

Lophialetes sp.

(Figure 9 - Figure 12, Plate 2a)

Synonymy

= *Lophialetes expeditus*: Reshetov 1979: 124; Russell & Zhai 1987: 191.

= *Lophialetes* cf. *expeditus*: Erfurt *et al.* 1999: 115, pl.2.

Material

- GIH TA I/7: skeleton with 23 frag. bones including scapula, ribs, metatarsals, phalanges, sesamoids;
- GIH TA I/11: skeleton with 71 frag. bones including radius, carpals, tibia, tarsals, metapodials;
- GIH TA I/76: skeleton with 77 frag. bones including skull with P3-4, M1-3 dext., P2-4 sin., mandibular symphysis with (i1-3), c1, p1 dext., (i1-3), c1, p1 sin., frag. mandible with p2, (p3), p4, m1-2 dext.; (p3-4), m1-2 sin., radius, carpals, metacarpals, phalanges;
- isolated bones: GIH TA I/2: frag. femur dist. sin.; I/3: frag. femur dist. dext.; I/5: frag. tibia dist. sin.; I/9: frag. tuber calcanei; I/12: frag. humerus prox. dext.; I/17: frag. tibia dist. sin.; I/26: frag. tuber calcanei; I/27: frag. vert. thor.; I/28: frag. humerus prox. sin.; I/33: ecto- and mesocuneiforme dext.; I/35: frag. scapula prox. dext.; I/42: frag. femur dist. dext.; I/43: frag. femur dist. sin.; I/46: frag. tibia prox. sin.; I/65: frag. calcaneus dist. sin.; I/66: frag. calcaneus dist. dext.; I/69: frag. metapodium dist.; I/70: lower jaw with 3 frag.; I/73: frag. calcaneus dist. dext.; I/74: frag. vert. thor.; I/77: frag. tibia prox.; I/78: frag. tibia dist. sin.; I/79: frag. vert. thor.; I/88 to 91: frag. vert. cerv.; I/92 to 93: frag. vert. cocc.; I/118: frag. humerus prox. dext.; I/123: frag. mandibula with m2; IV/84: frag. calcaneus; IV/142: phalanx (III?)/1; IV/143 to 144: frag. corpus vert. cocc.; IV/145: phalanx (III?)/2; IV/146: frag. corpus vert. cocc.; IV/209: frag. femur dist. dext.; VIII/1: frag. femur dist. dext.

Discussion

Although the dentition is worn and fragmentary, GIH TA I/76 could be confidently attributed to Lophialetidae by a unique combination of the following primitive (-) and derived (+) characters: postcanine diastema (+), non-molariform premolars (-), P2-4 with protoloph-metaloph loop (+), p1 one-rooted (+) and "rhinocerotoid-like" molar pattern, particularly with prominent paralophids and metalophids (-).

Among lophialetids, the Toru-Ajgyr material is close to *Schlosseria* MATTHEW & GRANGER, 1926, *Lophialetes* MATTHEW & GRANGER, 1925a and *Eoletes* BIRYUKOV, 1974 in having a complete postcanine formula P 1-4/1-4 M 1-3/1-3. In contrast, the number of premolars is reduced in *Breviodon* RADINSKY, 1965b. Our taxon differs from *S. magister* by at least two derived characters: 30% larger size (counted by upper molar length) and a series of upper premolar shorter than molars. Both series would be about the same length in *Schlosseria*. In the molar structure, the Toru-Ajgyr specimens are indistinguishable from *Lophialetes expeditus*. Radinsky (1965b: 192) noted that the variation in tooth measurements in *L. expeditus* is higher than expected for a single species. He suggested that the sample he studied "includes more than one population, or encompasses a long enough time span to reflect evolutionary size variation". The latter was confirmed by Dashzeveg & Hooker (1997: 107) who described *Lophialetes* sp. with smaller and lower crowned molars from the stratigraphically older locality Mergen in Mongolia. In these parameters and morphology, the Mergen sample is intermediate between *Schlosseria* and the typical *L. expeditus* from Irdin Manha. By molar sizes and other characters (see below), the material from Toru-Ajgyr is intermediate between Arshanto and the topotypical sample of *Lophialetes* (Table 3).

Locality	L	W	Reference	Remark
Shara Murun	11.2	11.97	RADINSKY 1965b: tab.3	mean value
Mergen	11.2	12.6	DASHZEVEG & HOOKER 1997: tab.1	M1 or M2
Arshanto	12.4	13.0	QI 1987: tab.11	
Khaychin Ula III	[12.6]	[13.7]	RESHETOV (1979: fig. 10)	adult specimen
Toru-Ajgyr	12.0	13.0	ERFURT et al. 1999: tab.4	
Irdin Manha	12.45	13.08	RADINSKY 1965b: tab.1	mean value

Table 3.— M1 - measurements of *Lophialetes* from different localities.

On the other hand, our material differs from Inner Mongolian samples by primitive dental characters: by relatively larger premolars, by longer premolar series and by less reduced p1. The length of p1 makes 17% of the lower premolar series length in GIH TA I-76/2. In contrast, there are 14% in a specimen tentatively assigned to *L. expeditus* (AMNH 26109) from Shara Murun. Unfortunately, no p1 was found in association with other lower premolars in *Schlosseria* and *Eoletes* (Radinsky 1965b; Qi 1987; Lucas *et al.* 1997). However, the tooth measured in AMNH 26109 could be, in fact, a dp1. According to Radinsky (1965b: 191) p1 is "normally crowded by p2, since in most examined specimens it was lost during life". About 5% of specimens lack the p1 alveolus. All this may refer actually to dp1, which become "crowded" by later erupting permanent p2, normally shed out and not replaced by permanent p1. So, its alveolus becomes closed in more aged specimens. If true, this would be a significant difference between *L. expeditus* and *Lophialetes* sp. from Toru Ajgyr, which apparently had a replacement of dp1 by p1, judging from the difference in wear between p1 and p3-4 (see Figure 9). In this character, the form from Toru Ajgyr would be more primitive than *L. expeditus,* in which the p1 is reduced. Although known lophialetids have a very similar premolar and molar pattern, they can be distinguished by skull structure. The most important modifications include an increasing of the postcanine diastema (accompanied by shortening of the premolar series and reduction of anterior premolars in most derived taxa), increasing of the mandibular symphysis length, and development of a deeply retracted nasal incision, terminating posteriorly at M1 level in the most derived *Lophialetes*. The latter character and the short nasal bones (Reshetov 1979: fig. 9) reflect the development of a mobile proboscis in this lineage. This character and the elongation of the cervical vertebra suggest that *Lophialetes* was a specialized top browser, and probably all lophialetids were evolving these adaptations (Radinsky 1965b; Reshetov 1979). Unfortunately, the nasal region is not known for *Lophialetes* sp. from Toru Ajgyr. In *Eoletes* (Lucas *et al.* 1997: fig. 5A, B) and *Schlosseria* (Radinsky 1965b: fig. 2), the lower postcanine diastema and mandibular symphysis are shorter.

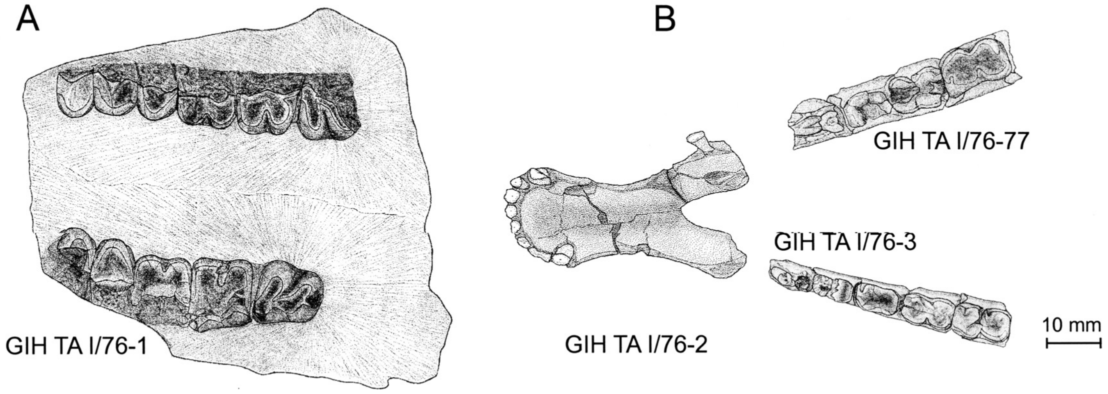


Figure 9.— Cranial fragments of *Lophialetes* sp. from Toru Ajgyr.

Radinsky noted a relatively short mandibular symphysis for *L. expeditus*, "terminating midway between the canine and first premolar", but this may refer to less adult individuals. In some older specimens from Khaychin Ula III, the mandibular symphysis is extending to beneath p2 (Reshetov 1979: fig. 13b). The specimen GIH TA I/76-2, with a mandibular symphysis of about 70% from the diastema length, belongs to quite an old individual judging from the teeth abrasion, and should be compared with aged specimens of the Mongolian *L. expeditus*. Thus, in the relative length of the mandibular symphysis it would be more primitive than in the Mongolian material. The relatively small foramina mentalia in GIH TA I/76-2 also could be a primitive character compared with *L. expeditus*. GIH TA I/76-1 is similar with *L. expeditus* in that the anterior root of the maxillary zygomatic process starts at the level of the middle of M2 or between M2-3. In *Eoletes* and *Schlosseria* this process begins more anteriorly, between M1 and M2. Therefore, our material is referred to *Lophialetes* sp. without a specific determination. Compared within the genus, there are smaller differences to *L. expeditus* from Irdin Manha (AMNH collection) as well as *L. expeditus* from Khaychin Ula III (PIN collection). In GIH TA I/76, the anterior root of the proc. zygomaticus begins at the level of the middle of M2. Thus, the anterior border of the orbita should be above M2 in contrast to *L. expeditus* (Radinsky 1965b: 237; Reshetov 1979: fig. 8), in which the orbita begins above the anterior edge of M3.

The associated postcranial bones of *Lophialetes* sp. indicate further differences to *L. expeditus*. In the scaphoid GIH TA I/76-66, the trapezoideum facet (6 mm x 5.3 mm) is relatively smaller than that in *L. expeditus* from Irdin Manha, and closer to the condition shown by specimen PIN 3403-28. Reshetov (1979: 74) noted a high variability of the scaphoid in size and shape of the articulation facets, and our observation can also be a matter of variation.

The lunate GIH TA I/76-67 is distinctly more convex than in specimens from China and Mongolia. Compared to AMNH 81705, the facet for the hump of the magnum is posteriorly displaced, with little overlap to the distal scaphoid facet. A more similar condition is seen in PIN 3403-32 (Reshetov 1979: fig. 24-3v). In accordance to the articulation with the unciform, a mediodistal prolongation is expected in the triquetrum (GIH TA I/76-71). This suggestion does not accord with the figures of Reshetov (1979: fig. 24-4v) and Radinsky (1965b: fig. 27), where no medial prolongation is visible. In contrast to the drawings of each isolated bone, the triquetrum looks very broad as incorporated in the reconstruction of the basipodium by Reshetov (1979: fig. 24, 1) compared with Figure 11. On the posterior edge of the lateral trapezoideum, there is a small triangular and convex facet, which is interpreted as a hint of the trapezium. This facet is about 3.5 mm long and at least 4 mm high. The Chinese *L. expeditus* (Radinsky 1965b: fig. 28) shows a similar facet, but the position is posterior there, not posteromedial. The scaphoid facets on the hump of the magnum provide a further similarity to the Mongolian material. Despite the fact that Reshetov (1979: 77, fig. 25-3v) did not mention a second facet on the magnum PIN 3403-107, the corresponding facet on the scaphoid (Reshetov 1979: fig. 24-2g) suggests its presence.

In GIH TA I/76-65, this facet is preserved in a similar form but is shorter than in AMNH 81707. In addition, the facet for the unciform is broadly contacting the lunate facet proximally in our material. In contrast, both facets are well separated in *L. expeditus* from Irdin Manha. Similar to PIN 3403-107, the distal facet for the trapezoideum is quite small, crescent-shaped and attached to the proximal edge of the more pronounced facet for MC II.

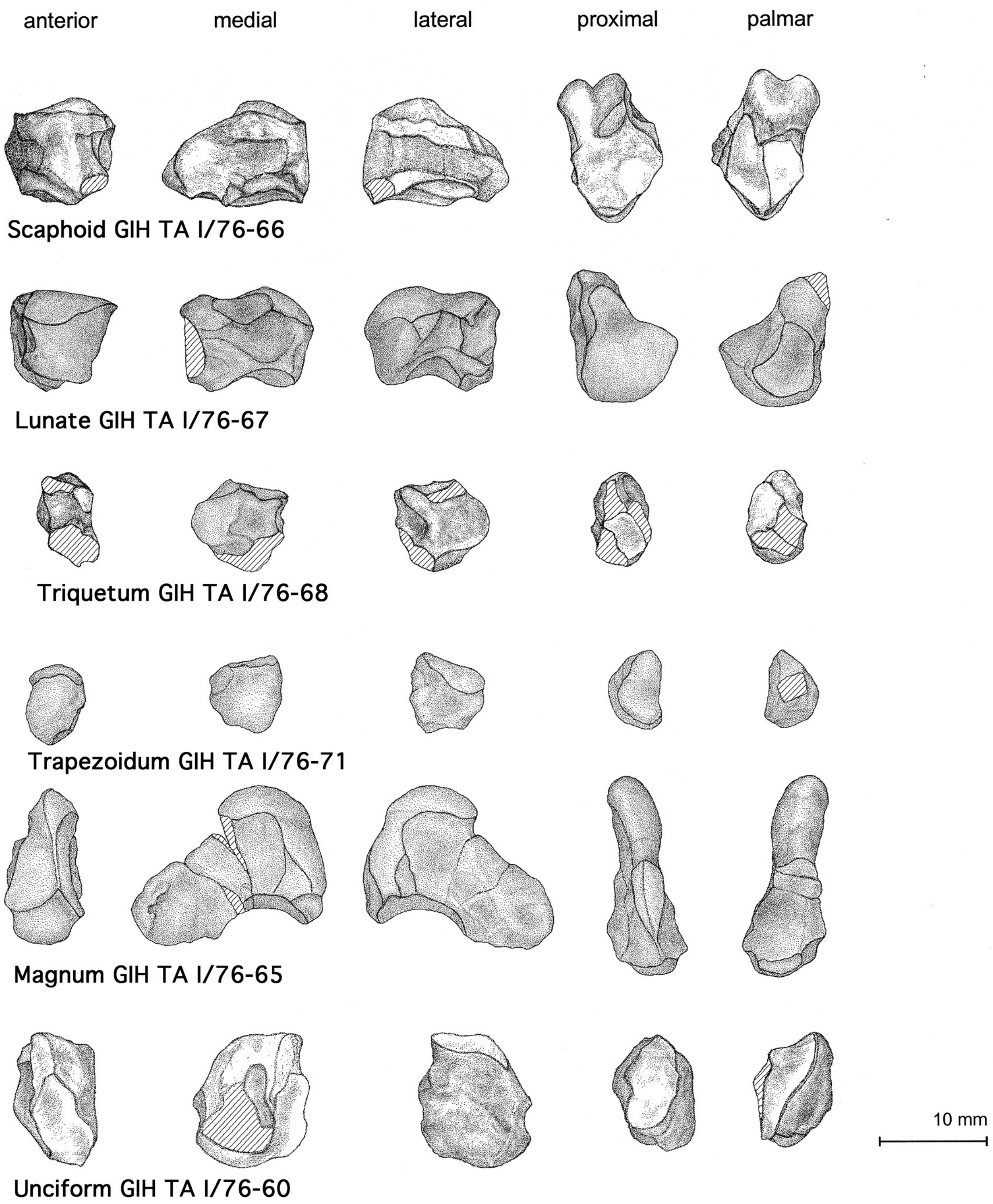


Figure 10.— Left carpals of *Lophialetes* sp. from Toru Ajgyr

Furthermore, the distal trapezoideum facet is larger than those for MC II in AMNH 81707. As with Mongolian material, our unciform is longer than wide and shorter than the specimens from Irdin Manha.Regarding bone measurements, *Lophialetes* sp. from Toru-Ajgyr is smaller than the Mongolian and the Chinese form (Table 4).

The separation from *L. expeditus* is strengthened by qualitative differences in isolated postcranial materials. The humerus bears a weaker tuberositas deltoidea and a smaller tuberculum majus (GIH TA I/12, GIH TA I/28) compared with *L. expeditus* from Khaychin Ula III. In the femur, the direction of the trochanter major is more medially deflected in contrast to our material in which the trochanter is a more vertically

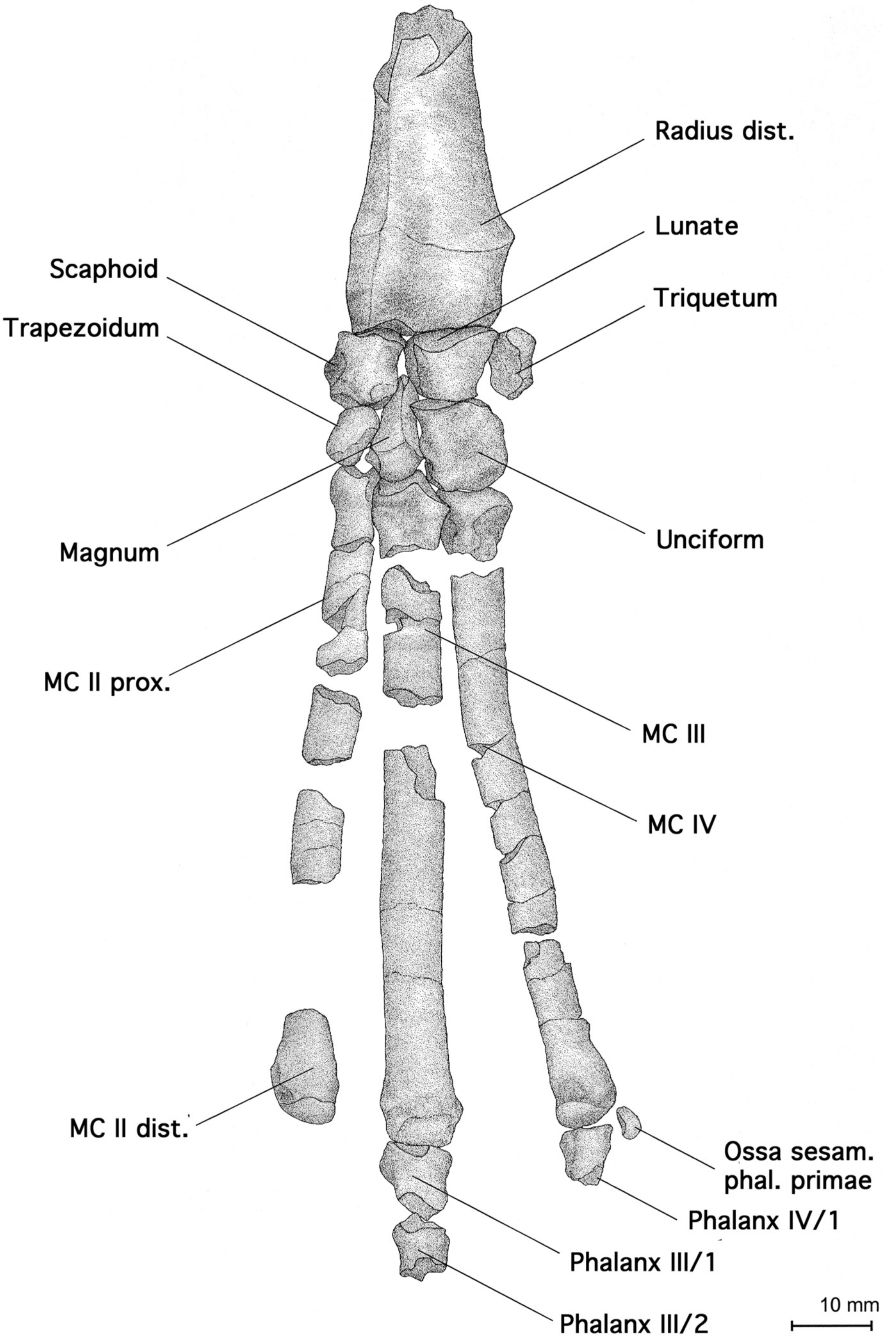


Figure 11.— Reconstructed left forelimb of *Lophialetes* sp. from Toru Ajgyr, dorsal view. The unciform is drawn slightly rotated in order to show the articulation surfaces.

orientated. In the Mongolian tibia, both tuberculi intercondylare are of the same height. In our material and the Chinese material, the lateral tuberculum is about twice as long and high as the medial one.

bone	measurement	Toru Ajgyr	[mm]	Khaychin Ula III[1]	[mm]	Irdin Manha[2]	[mm]
Humerus	largest width of the prox. epiphysis via trochanter minor	TA I/28	25.5	PIN 3403-17	26.0	AMNH 81702	[28]
MC II	largest width of dist. epiphysis	TA I/76-47	6.7	PIN 3403-39	7.8	composite	[7]
MC III	largest width of dist. epiphysis	TA I/76-44	9.8	PIN 3403-42	16.7	composite	[18]
MC IV	largest width of dist. epiphysis	TA I/76-48	6.2	PIN 3403-47	8.7	composite	[8]
Astragalus	total length	TA I/11-39	20.8	PIN 3403-59	23.2	AMNH 81715	[23]
Calcaneus	total length	TA IV/84	44.5	PIN 3403-66	46.0	AMNH 81714	[44]
MT II	total length	TA I/7-3	88.9	PIN 3403-89	99.0	AMNH 81702[3]	[92]

Table 4.— Limb measurements of *Lophialetes* sp. from Toru Ajgyr compared with *Lophialetes expeditus* from Khaychin Ula III and Irdin Manha.

[1] Reshetov (1979), [2] Radinsky (1965b), [3] specimen from Ulan Shireh.

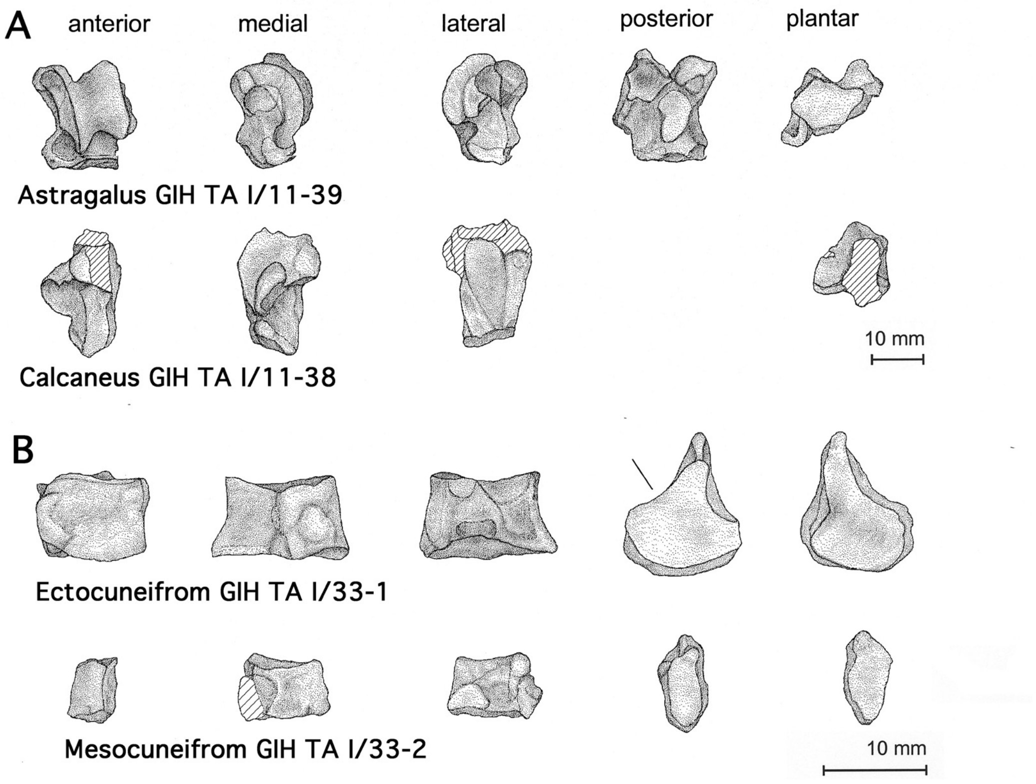


Figure 12.— Tarsals of *Lophialetes* sp. from Toru Ajgyr.

A: left side; B: right side. The arrow indicates the position of the mesocuneiforme.

In contrast to the Irdin Manha material, the astragalus (GIH TA/I/11-39) is more primitive due to a small, convex navicular facet. This facet figured by Radinsky (1965b: fig. 30) is larger and more concave, indicating a higher cursorial adaptation. The ectocuneiforme (os cuneiforme III), which was articulated found with the mesocuneiforme (os cuneiforme II) in site I, displays laterally a longish groove parallel to the plantar border (Figure 12). This facet is not mentioned in Radinsky (1965b) or Reshetov (1979). All metatarsals are relatively slender, as in the reconstruction of Radinsky (1965b: fig. 32). It is more likely that MT III was longer than MT II and MT IV. In contrast, the hind foot shown by Reshetov (1979: fig. 32) is shorter and the metatarsals are of about the same size.

Despite the possibility of age dimorphism, most of the differences mentioned above can be referred to a somewhat older geological age compared with the Mongolian form. Taking into account a high degree of infraspecific variation within the genus, *Lophialetes* sp. from Toru-Ajgyr could be formally referred to *L.* cf. *expeditus*. Considering it's more primitive nature compared with the latter, our form also may belong to a distinct species.

Order Artiodactyla OWEN, 1848
Artiodactyla indet.

Synonymy

not Artiodactyla indet. Russell & Zhai, 1987: 191

Material

- GIH TA I/1: frag. ilium and ischium.

Discussion

At site I, a fragmentary pelvis was found, which fits in size to the well preserved pelvis of *Lophialetes expeditus* described by Reshetov (1979: 82, fig. 26). In contrast to his description, the ala ilii is less bent and the spina iliaca dorsalis cranialis is not elongated. On the lateral side, the linea glutea is not pronounced as in *L. expeditus*. In the latter taxon, the fossa muscularis in front of the acetabulum is deep. In our material, there is only a shallow groove, which is about 8 mm long and 3 mm high. The described morphology of a cranially rounded ilium is more typical for artiodactyls, like in *Amphirhagatherium weigelti* from the Eocene Geiseltal in Germany (Erfurt 2000). Unfortunately, no other bones were found that would support the existence of artiodactyls in Toru Ajgyr.

Order Cete LINNAEUS, 1758
Family Olseniidae ERFURT & AVERIANOV (2005)
cf. ***Olsenia*** sp.

(Figure 13 - Figure 16, Plate 3)

Synonymy

= Mesonychidae *inc. sed.*: Erfurt *et al.* 1999: 116.

Material

- GIH TA II/75: left foot skeleton with 22 partly fragmental bones including tibia, tarsals, metatarsals, phalanges and sesamoids.

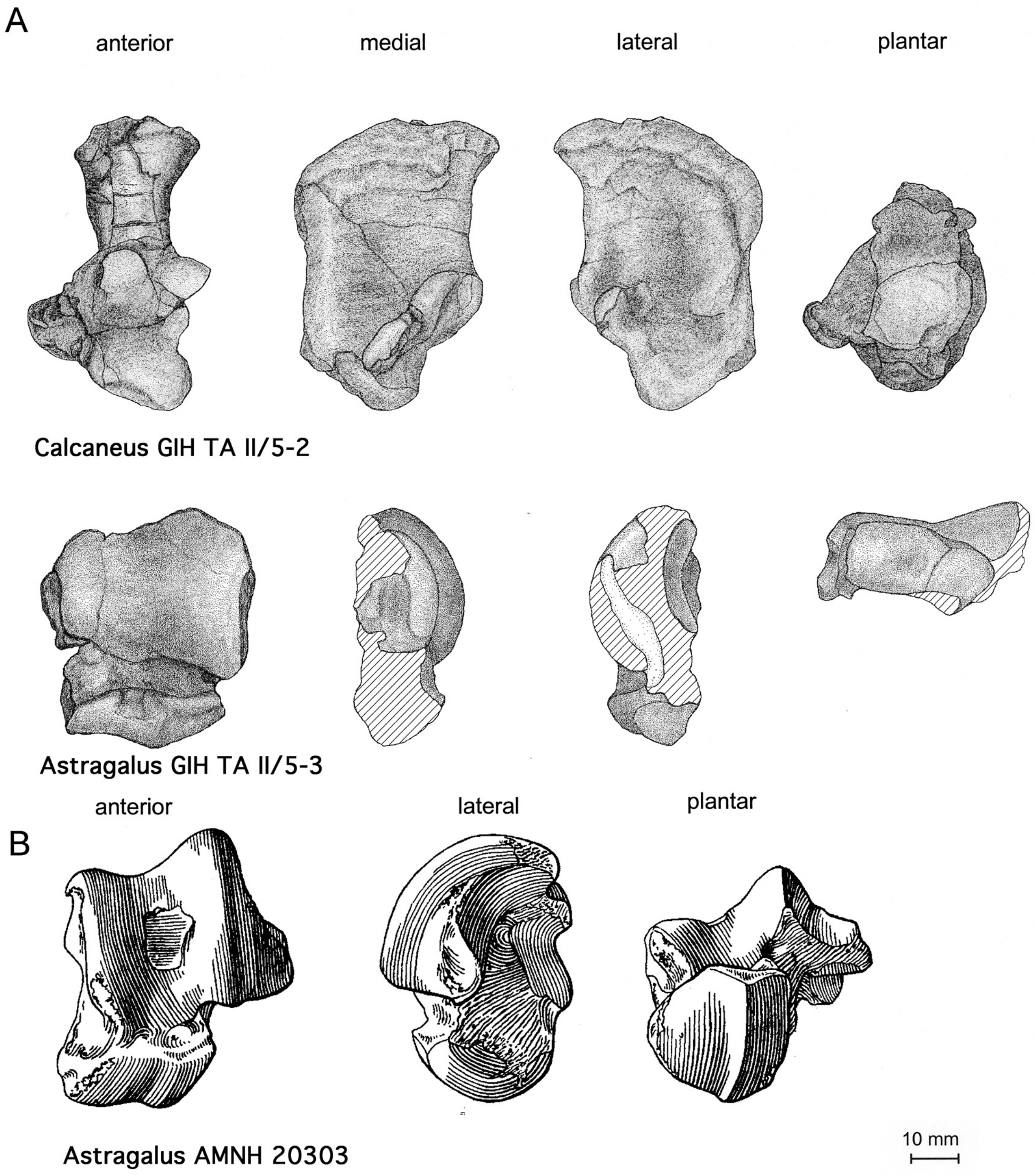


Figure 13.— Comparison of Tarsals in Olseniidae.

A: cf. *Olsenia* sp. GIH TA II/5-2,3 from Kyrgyzstan; B: *Olsenia mira* AMNH 20303 from China (Szalay & Gould, 1966: fig. 9).

Navicular, cuboid and ectocuneiforme are still connected with the metatarsals. All phalanges and the sesamoids were articulated. The mesocuneiforme and the residual MT I were displaced from the tarsus prior to the fossilisation. Due to the embedding near the surface, the distal tibia and the proximal tarsals are fragmentary.

Discussion

The determination as Olseniidae (Erfurt & Averianov 2005) is based on a unique combination of mesonychid, perissodactyl and artiodactyl foot characters. The metapodium is paraxonic and artiodactyl-like but the astragalus does not have a double trochlea. This bone is similar to *Olsenia mira* AMNH 20303 from the Shara Murun Formation near Baron Sog Lamasery (Inner Mongolia, China; Matthew & Granger 1925b: fig. 3).

Matthew & Granger provisionally attributed *O. mira* to mesonychids due to the upper premolar AMNH 20319 that was found nearby. Later, Matthew (1929: 519) saw similarities with chalicotheres and referred *O. mira* to that group. In his revision of Asian chalicotheres, Colbert (1934:385) had doubts about Matthew 's conclusion but he did not offer an alternative determination. Owing to the lack of correlated dental and postcranial characters, Szalay & Gould (1966:152) regarded *O. mira* as a nomen dubium. McKenna & Bell (1997) referred *Olsenia* to Acreodi incertae sedis with a note that they are possibly mesonychids. Based on the mosaic pattern of the character set, *Olsenia* is now regarded as stem taxon within a "Paraxonia" clade (Geisler 2001: 3). Olseniidae are probably nested with Artiodactyla, Cetacea, Mesonychidae, Hapalodectidae and *Andrewsarchus*. The systematic rank as family is given in the complexity of the character set, which describes in detail the foot as the most characteristic skeletal part of an ungulate taxon.

	Measurement	cf. *Olsenia* sp.	*Olsenia mira*[1]	*Pachyaena ossifraga*[2]	*Pachyaena gigantea*[2]
		GIH TA II/5-3	AMNH 20303	AMNH 15730	AMNH 2959 / AMNH 15228[2]
A	height from trochlea to navicular facet	(48)	[58]	38.8	56.4 / 61.6[2]
B	largest width via the epicondyles	(47)	[48]	32.3	57.0 / 60.0[2]
C	largest width via the trochlea	(42)	[36]	19.3	32.8, 32.9[2]
D	width of caput tali	(33)	[32]	[23]	[40], [16[2]]
E	length of caput tali (anterior-posterior)	-	[30]	[17]	[26], [13[2]]

Table 5.— Astragalus measurements of cf. *Olsenia* sp. from Toru Ajgyr compared with mesonychids.

[1] Szalay & Gould (1966: pl. 20), [2] Matthew (1915: 99, fig. 83).

All known ungulate groups are somehow different from cf. *Olsenia* sp. Mesonychids display the similar basic foot pattern but they possess an astragalar canal and there are differences in shape and arrangement of the astragalar facets. Based on the correlation of teeth measurements to postcranial dimensions in *Pachyaena* (Table 5), *Andrewsarchus* is much larger and *Dissacus, Ankalagon* and *Synoplotherium* are too small (Scott 1886: 166; Matthew & Granger 1915; Dehm & Öttingen-Spielberg 1958: 12ff; Chow 1965:291; Osborn 1924; Szalay & Gould 1966: tab. 2-5; Gingerich 1989: tab. 18*;* Zhou *et al.* 1995: tab. 1; Archibald 1998: 318ff). The North American *Mesonyx* (Scott 1886: 168) is also much smaller and the calcaneus is slender and bears a wide, distal part. In our material, the calcaneus tapers on the plantar side, giving space for the astragalus - cuboid articulation. In *Pachyaena* (Szalay & Gould 1966: pl. 20) as well as in many "condylarths" and perissodactyls, the trochlea is rotated against the caput tali and the navicular facet is not squarely separated from the cuboid facet.

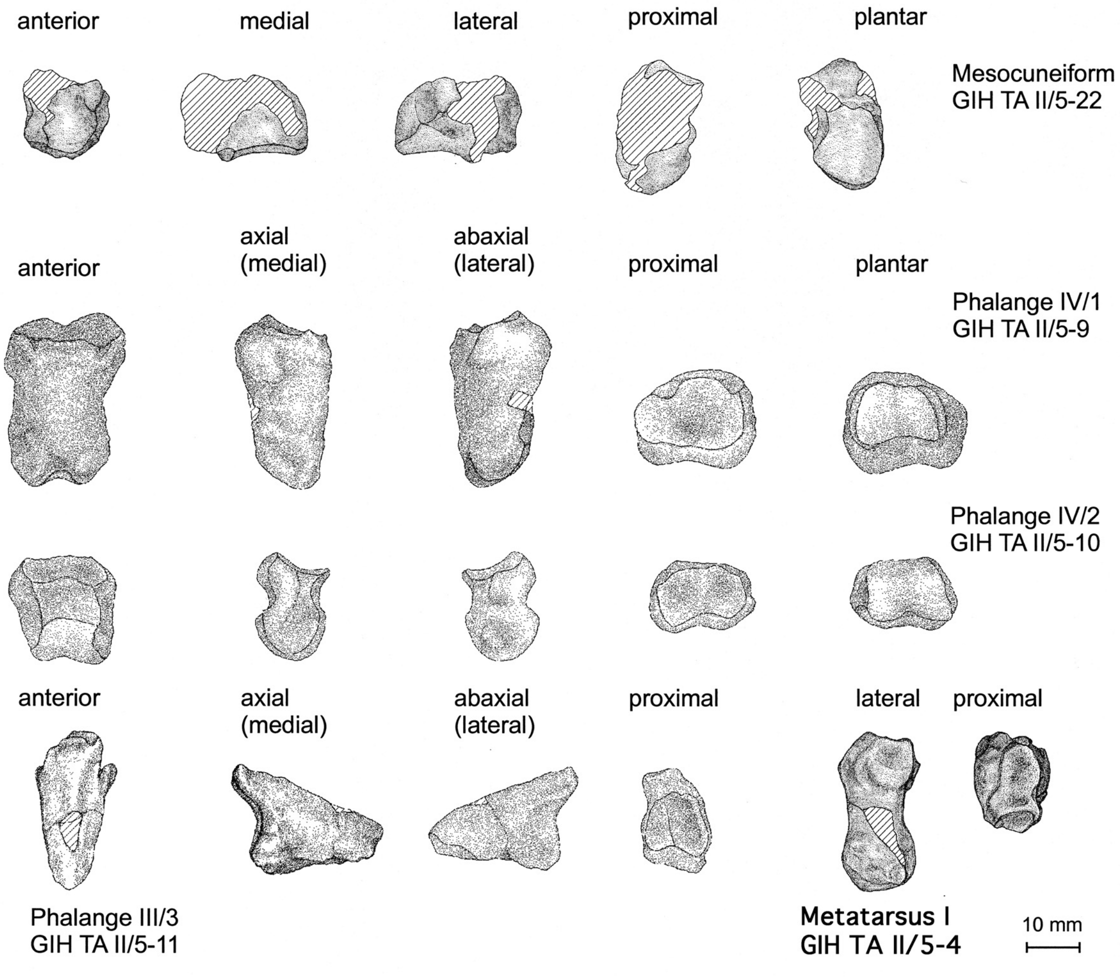


Figure 14.— Left foot - skeleton of cf. *Olsenia* sp. from Toru Ajgyr.

In cf. *Olsenia* sp. the cuboid facet is relatively wide, about one third of the navicular facet. In contrast, the cuboid facet is much narrower in mesonychids (O'Leary & Rose 1995, fig. 14). The latter difference is one of the arguments for the family rank of the Olseniidae (Erfurt & Averianov 2005) as stem group of cetiartiodactyla, see comparison with hippos below. In all mesonychids, of which the foot skeleton is known, there are the terminal phalanges fissured and claw-like. The phalanges of cf. *Olsenia* sp. are not fissured (Figure 14) and intermediate between claws and hoofs owing to their lateral compression.

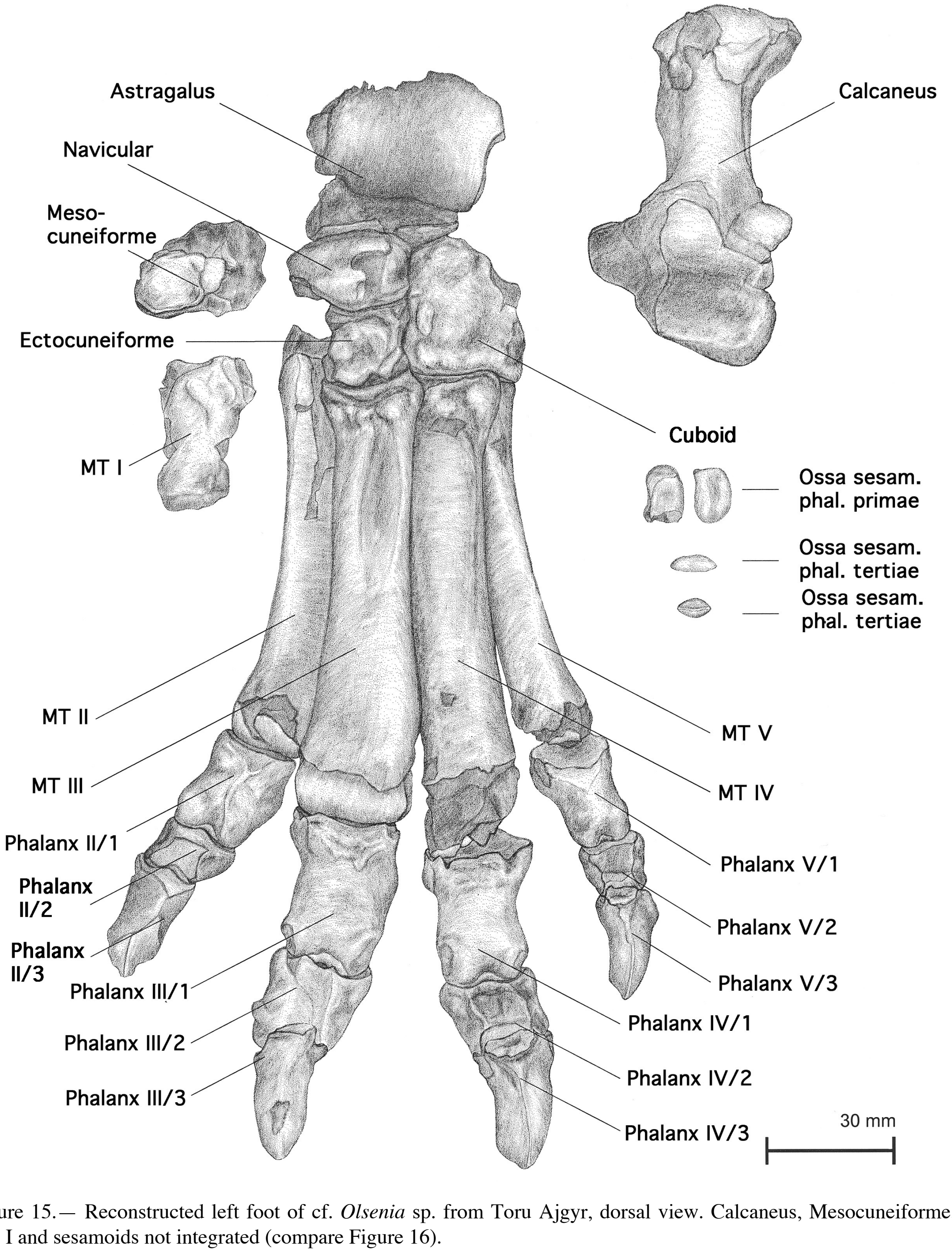


Figure 15.— Reconstructed left foot of cf. *Olsenia* sp. from Toru Ajgyr, dorsal view. Calcaneus, Mesocuneiforme, MT I and sesamoids not integrated (compare Figure 16).

Perissodactyls are characterised by mesaxonic limbs, but the postcranial morphology of older taxa (Chalicotheres) is not known. GIH TA II/5 represents a functionally paraxonic and tetradactyl metapodium with residual first metatarsal. The second and fifth metatarsals are only a few millimetres shorter than the main metatarsals (Figure 15). Significant are also the terminal phalanges, which are usually broader and more hoof-like in perissodactyls. Smaller differences are to be seen in the pentagonal shape of the cuboid (anteriorly viewed), which reaches its maximum length in the medial part directly above MT IV. As mentioned already by Colbert (1934), there are similarities to older chalicotheres such as the similar sized *Grangeria gobiensis*. There, the hind foot is tridactyl, the astragalus articulates only with the navicular and the phalanges are significantly shorter (Table 6) and different in their shape (Coombs *et al.*, 2001; Geraads *et al.,* 2001). Unfortunately, postcranial materials of other primitive chalicotheres are not known and phylogenetic relationships between these groups and cf. *Olsenia* sp. can also not be excluded.

bone	measurement	cf. *Olsenia* sp.	[mm]	*Grangeria gobiensis* [1]	[mm]	*Choeropsis liberiensis*	[mm]
Astragalus	largest width trochlea	TA II/5-21	(42)	AMNH 26655-6	24	ZMB 5237	31.5
Calcaneus	largest length	TA II/5-2	82.8	AMNH 26655-6	67	ZMB 5237	83.7
MT III	largest length	TA II/5-1	(109)	AMNH 26655-6	103	ZMB 5237	70.3
Phalanx III-1	largest length	TA II/5-12	41.5	AMNH 26655-6	[15]	ZMB 5237	40.8

Table 6.— Limb measurements of cf. *Olsenia* sp. from Toru Ajgyr compared with *Grangeria gobiensis* and *Choeropsis liberiensis*.

[1] Colbert (1934: 371, fig. 6).

Worth mentioning are the principle similarities with recent hippos in the arrangement of the tarsals as well as the relation of length within the metatarsals (Figure 16).

Except for the reduction of the MT I and the form of the terminal phalanges, astragalus and calcaneus display the main differences between both families. The proximal trochlea of the astragalus is laterally rotated, not medially as in hippos. The calcaneus is stout in cf. *Olsenia* sp. whereas this bone is more elongated in *Hippopotamus*. In contrast, the tarsals and metatarsals are stouter in hippos and longer in cf. *Olsenia* sp. Both animals display graviportal adaptations in different skeletal elements. Therefore, the similarities mentioned above are regarded as convergent development in phylogenetically separate lineages with similar habit and locomotion. A closer relation between Olseniidae and hippos is less likely. New findings of Eocene whales from Pakistan (Gingerich 1997, 1998, Gingerich *et al.* 1993; Thewissen *et al.* 1996, 1998; Gingerich *et al.* 2001) reinforced the discussion about the cetiartiodactyl clade (Archibald 1998; Gatesy 1997; Gatesy *et al.* 1999; Geisler 2001; Geisler & Luo 1998; Luckett & Hong 1998; Madar *et al.* 2002; Madsen *et al.* 2001; O'Leary 1999; O'Leary & Geisler 1999; Shimamura *et al.* 1999; Thewissen *et al.* 2001). Regarding the morphology of astragalus and calcaneus, Rose (2001) proposed the transformation of a mesonychid-like form via a cetacean stage to the double trochleated artiodactyl form. As primitive and typical for mesonychids he mentioned the form of the astragalus with taller caput tali (distal trochlea) than the proximal trochlea. In this stage, the proximal trochlea is shallow, the caput tali displays a broad facet for navicular and a small one for the cuboid. There also exists a foramen for blood vessels and nerves on the proximal side of the astragalus. Early cetaceans are intermediate to artiodactyls in possessing this foramen, as well as an already more superposed position of both trochlear facets. In artiodactyls, this foramen is lost and the distal trochlea broadens. In addition, there is a step between the articulation of the cuboid with the calcaneus and its articulation with the astragalus. The calcaneus reaches farther down in plantar direction (Geisler 2001: fig. 7). In our material, the astragalus (Figure 13) displays another combination for these characters: lack of the above mentioned foramen, large size and relatively straight superposition of both trochleas, shallow proximal trochlea, tall distal joint, large cuboid facet and an intermediate position concerning the plantar extension of the articulation between calcaneus and cuboid. In combination with the paraxonic

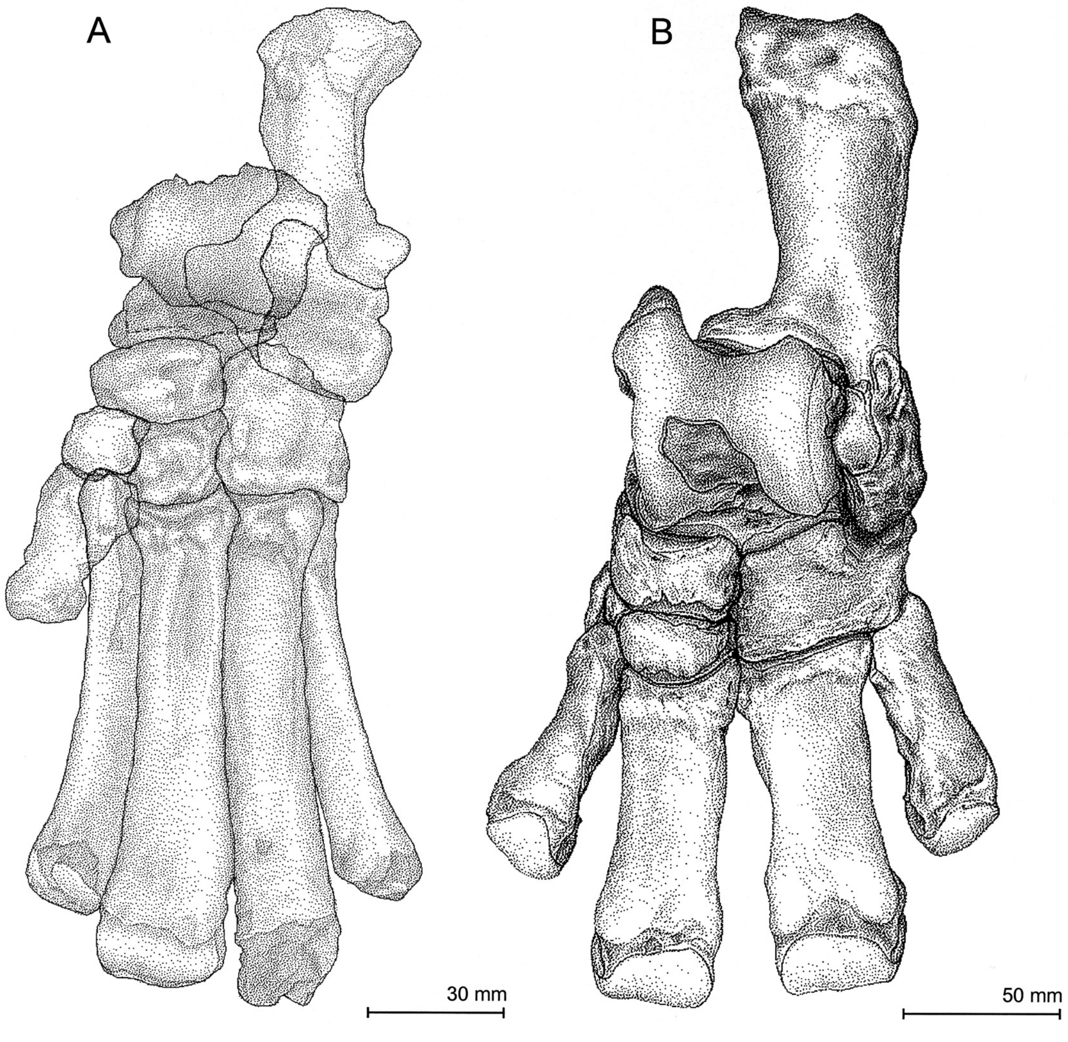


Figure 16.— Comparison of the foot skeletons in Olseniidae and Hippopotamidae

pattern of the metapodium (Figure 15), this represents a further intermediate stage to mesonychians, perissodactyls, cetaceans and artiodactyls. *Olsenia* could be regarded as a taxon near the common ancestry of whales and artiodactyls. We hope in the near future that *Olsenia* will be included in an actual phylogenetic analysis.

A parallel evolution of paraxonic limbs would be also possible starting from perissodactyls. Consequently, even-numbered manual and pedal fingers are not an autapomorphy of artiodactyls. Similarities to lower Eocene brontotheres like *Lambdotherium* or *Palaesyops* give hints to a common origin from which graviportal lines and more cursorial lines developed. In size the Toru Ajgyr material corresponds to Bridgerian brontotheres such as *Mesatirhinus* and *Limnohyops* (Osborn 1929a: figs. 526, 527). A definitive interpretation of the Olseniidae and their phylogenetic significance is not possible at the moment. More material is needed, especially dental remains.

General discussion

Taphonomical aspects

Except for site VII, the Toru Ajgyr fossil complex includes sites that cover an area of 100000 m^2 (Erfurt *et al.*, 1999: tab.1). The distance from site I to VII is about 1.5 km in a south-east direction and indicates a larger extension of the fossil complex (Plate 1a). Taking only the excavated areas of each site into account, the spatial density is estimated at 5 bones/m^2 including splinters. Bones and teeth were found isolated on the surface as well as in articulated skeletal parts in the finding layer. Unfortunately, complete skeletons with limbs and skulls were not preserved. The main orientation of partial skeletons is NNW to SSE and most of the specimens are in lateral position.

site	total of specimens	articulated bones	isolated bones or splinters	taxa
I	592	456	136	Lophialetes sp., Gobiatherium mirificum, Brontotheriidae indet., Artiodactyla indet., Teleolophus sp.
II	80	23	57	Teleolophus sp., Gobiatherium mirificum, cf. Olsenia sp.
III	1	0	1	Mammalia indet.
IV	229	0	229	Lophialetes sp., Teleolophus sp.
V	1	0	1	Mammalia indet.
VI	1	0	1	Mammalia indet.
VII	127	0	127	Brontotheriidae indet.
VIII	411	401	10	Lophialetes sp., Brontotheriidae indet.
sum	1442	880	562	

Table 7.— Distribution and preservation of Eocene fossils in Toru Ajgyr.

The fossils are embedded in fine laminated, weakly lithified, lacustrine clays from the lower part of the Chonkurchak Svita (Figure 1). In addition, some bones were found in grey coloured sandstones, which are intercalated with the clays. The clay in the embedding matrix indicates low transport energy. In the founding layer, stones and gravel are rare and are less than 3cm in diameter. Owing to the low transport energy, there results an allochthonous situation with short transport paths that is also indicated in the following taphonomical aspects. Table 7 displays the number and preservation of specimens in the different sites. Sites III, V and VI are not intensively investigated. In partial skeletons, each bone was counted separately. Therefore, the percentage of articulated bones is high relative to bone splinters.

site	articulated skeletal parts	Voorhies Group 1 [%]	Voorhies Group 2 [%]	Voorhies Group 3 [%]	adult [%]	articulated [%]	corroded [%]	broken [%]
I	6	65,7	31,8	4,4	91,2	42,0	12,9	61,0
II	2	82,9	9,7	7,3	75,6	75,6	26,8	92,7
IV	3	81,5	18,5	0	100	99,2	0	60
VII	1	62	38	0	46	16	62	38
VIII	2	50,3	48,6	0	87,0	64,9	1,1	70,3
all	**14**	**65,2**	**32,9**	**2,4**	**87,6**	**58,8**	**11,8**	**63,5**

Table 8.— Assemblage data from the Eocene Toru Ajgyr fauna.

Voorhies groups according to Voorhies (1969). Sites III, V and VI not included due to poor material.

All sites of the fossil complex contain smaller and larger species, and adult individuals dominate (Table 8). Based on counting of bones from one side of the body, the minimal number of individuals was calculated. Accordingly, *Lophialetes* sp. is the most common mammal in Toru Ajgyr: five fragments of the right and two fragments of the left distal femur are preserved, which were found at three different sites. Other bones, such as the left calcaneus or the left distal tibia, allow a similar estimation of at least 5 individuals. Furthermore, three brontotheriids are indicated and two *Teleolophus* sp. The latter taxon occurs at site II with isolated phalanges, which are not surely indicating a third individual. In spite of their larger and better preserved bones, mammals such as uintatheres and brontotheres are under-represented. The latter fact is regarded as the result of selective sampling of bigger or more significant bones in former times. For example, the astragalus, a frequently preserved bone in other mammal assemblages, is under-represented (only 3 specimens). In total, there are at least 15 individuals of 6 mammal taxa that can be distinguished in Toru Ajgyr.

The small amount of separable individuals in comparison to the high number of bones (Table 8) stresses the high degree of undetermined materials but also the high percentage of articulated bones. Especially frequent are distal limb remains, which partly belong to the same individual. Correspondingly, the most frequent bones are those of Voorhies Group 1 (least dense elements, such as vertebrae and ribs) and Voorhies Group 2 (limb elements). In contrast, skull fragments (Voorhies Group 3), as well as pelvis fragments, are rare. The short scratches in GIH I/76 and IV/47 are artificial. There is no evidence for in situ scavenging. In site VII, the bones were found near the surface and were corroded by weathering.

The distribution of bones, which belong to different skeletal parts (for example eroded teeth TA I/76-1 and not ossified femur TA I/76-5 of *Lophialetes* sp.), verify a mixture and transport before the embedding. On the other hand, the completeness of the limb parts indicates that there was not enough time for a complete dismemberment of the carcass and that the transport was relatively short. Remains of the forelimb are more frequent than hindlimbs because they are the most easily detached part of the carcass. This observation supports the idea of short distance transport and an accumulation of the disintegrated but still complete body parts as in the Eocene Geiseltal (Germany).

Some modifications in the anatomical arrangement of the skeletal parts are artificial. For example, the angle between the distal metatarsals and the first phalanges was about 80 in the foot skeleton of cf. *Olsenia* sp. (GIH TA II/5). The acropodium was bent beyond the normal position and pressed against the metapodium. More than 60% of the bones are broken and display fractures with clay intruded into the spongiosa and into the medullar cavity (Erfurt & Averianov in press). These fillings resemble vascular canals (see astragalus in cf. *Olsenia* sp.) and indicate the anatomical order within the phalanges in GIH TA II/5. In other specimens, found near the surface, the clay fillings are responsible for a size increase owing to clay swelling (Bones with indications of swelling were not included in the measurements).

According to Weigelt (1930, 1989) preservation without adjustment would be typical for animals that died and that were embedded on land. Regarding the orientation in our materials, a drifting of the carcasses is supposed rather than a sticking in the mud of a former lake. The drifting could be initiated by a sudden inundation. The carcasses were then accumulated and floated into a lateral position. A quick embedding would avoid the access of land scavengers to the carcasses. The dissection should have taken only a little time because of the high decomposition speed under warm conditions, as indicated by the pollen analysis (Fortuna & Erfurt 2006). Finally, parautochthonous conditions resulted, which allowed - with reservations - paleoecological interpretations of the mammal fauna.

Biostratigraphical aspects

Despite the fact that small mammals have recently played an important role in the biostratigraphy of Central Asia (Averianov 1994, 1996a, b; Averianov *et al.* 1996), Toru Ajgyr was formerly dated by perissodactyls only. Tarasov (1968a) correlated the fauna of Toru Ajgyr with Shinzhaly (Kazakhstan), Khaychin Ula III (Mongolia) and Irdin Manha (China). The validity of the taxa he mentioned (for example *Triplopus zhukovi*) is problematic due to the loss of the original material and incompleteness of former descriptions. On the basis of the taxa mentioned in this paper, there are new relationships to Chinese and Mongolian faunas as shown in Table 9.

Russell & Zhai (1987) referred this fauna to the Irdinmanhan Asian Land Mammal Age (ALMA) *sensu lato*, but Erfurt *et al.* (1999: 121), as well as Lucas (2001), to the Arshantan ALMA. The latter attribution is supported by the occurrence of *Gobiatherium*, which is known only from the Arshanto and Yuhuangding fauna (Ma & Cheng, 1991). *G. mirificum* is regarded as the index fossil for the Arshantan (Lucas 2001). This ALMA is correlated with the North American Land Mammal Age (NALMA) Bridgerian (Lucas *et al.* 2003). The revised list of mammals from Toru Ajgyr now includes, except for *G. mirificum* and an unidentified brontothere, the lophialetid *Lophialetes* sp., the deperetellid *Teleolophus* sp. (="*Deperetella kungeica*") and the ungulate cf. *Olsenia* sp. Reshetov (1979: 123) indicated also the presence of *Schlosseria* in Toru Ajgyr, but such is obviously a mistake: he did not mention this taxon again in his faunal lists (Reshetov 1979: 124, tab. 30). *Lophialetes* and brontotheres are present in both, the Arshantan and the Irdinmanhan sensu stricto, but *Teleolophus* was thought to be restricted to the latter biostratigraphic unit (Tong *et al.* 1995; Lucas 2001). It should be noted that *Teleolophus* is present also in the Andarak fauna in southern Kyrgyzstan (Averianov & Godinot, 2005), distinctly older than the Toru Ajgyr fauna. As *Teleolophus* has a wider stratigraphic range, it cannot be used for defining the Irdinmanhan *sensu stricto* LMA.

Locality Author / Taxon	*Gobiatherium*	*Lophialetes*	*Teleolophus / Irdinolophus*	*Deperetella*	*Ardynia / Forstercooperia*
Toru Ajgyr; Kyrgyzstan, this paper	*G. mirificum*	*L.* sp.	*T.* sp.	*D.* sp. (*D. kungeica*)	-
Arshanto; China[1]	*G. mirificum*	*L. expeditus*	*T.* sp. (*T. primarius*)	-	*F. grandis*?
Khaychin-Ula II, III, V; Mongolia[1]	-	*L. expeditus*	*T. magnus*[4]	*D. khaitchinulensis*	*F. totadentata*
Zaysan, Obayla Subsvita; Kazakhstan[1]	-	*L.* cf. *expeditus*	*T.* cf. *medius*	-	*F.* cf. *grandis*
Irdin Manha, Irdin Manha Fm.; China[1]	-	*L. expeditus*	*T. medius*	-	*F. totadentata*
Ulan Shireh, Ulan Shireh Fm.; China[1]	-	*L. expeditus*?	*T. medius*?	-	*F.* cf. *grandis*
Lushi Basin, Lushi Fm.; China[2]	-	*L. minutus*	-	*D.* sp.	*F.* sp.
Mergen; Mongolia[4]	-	*L. expeditus*?	*I. mongoliensis*	-	*Ardynia* sp.
Guanzhuang, Guanzhuang Fm.; China[1]	-	*L.* sp.	*T. shandongensis* *T.* sp.	-	-
Hetaoyuan, Hetaoyan Fm.; China[3]	-	(*Schlosseria*) *hetaoyuanensis*	*T. danjiangensis*	*D. sichuanensis*	-
Bose Basin, Dongjun Fm.; China[1]	-	-	*T.* sp.	-	*F.* sp.
Khoer Dzan, Sevkhul member; Mongolia[4]	-	-	*T. magnus*	*D.* cf. *birmanica*	-

Table 9.— Fauna of Toru Ajgyr compared with other Asian Eocene faunas.

[1] Russell & Zhai (1987); [2] Chow *et al.* (1973); [3] Tong & Lei (1984); [4] Dashzeveg & Hooker (1997); not stratigraphically ordered.

Despite the fact that there are still considerable gaps in the fossil record, Toru Ajgyr and other localities, which were of uncertain biostratigraphical age, are now better correlated to Central Asian reference localities. Including perissodactyl determinations on the family level, the faunas are characterized by the following taxa and may overlap (beginning with the oldest):

1) Wutu Fauna (Isectolophidae [*Homogalax*], ?Lophialetidae [*Ampholophus*], Eomoropidae, "Phenacodonta" *Olbitherium*) see Tong & Wang (1995), Tong et al (2004);

2) Chakpaktas Fauna (Isectolophidae [*Homogalax*], Helaletidae [*Helaletes*], Lophialetidae [*Rhodopagus*], Hyracodontidae [*Triplopus*]);

3) Lower Obayla Fauna (Brontotheriidae [*Palaeosyops*], Isectolophidae, Helaletidae, Lophialetidae [*Rhodopagus*; *Breviodon* by Russell & Zhai (1987: 167) known only by one tooth, see Reshetov (1975: Fig. 10)], Hyracodontidae, Rhinocerotoidea indet. [?Amynodontidae]);

4) Andarak Fauna (Lophialetidae [*Eoletes*], Deperetellidae [*Teleolophus*], Hyracodontidae [*Pataecops*], Amynodontidae [*Sharamynodon*]);

5) Shinzhaly Fauna (Brontotheriidae, Lophialetidae [*Eoletes, Breviodon, Rhodopagus*], Deperetellidae [*Teleolophus*], Hyracodontidae [*Prohyracodon*]);

6) Arshanto Fauna (Brontotheriidae [*Microtitan, Desmotitan*], Lophialetidae [*Lophialetes, Schlosseria, Breviodon*], Deperetellidae [*Teleolophus*], Helaletidae [*Colodon, Hyrachyus*], Hyracodontidae [*Urtinotherium*]);

7) Toru Ajgyr Fauna (Brontotheriidae, Lophialetidae [*Lophialetes*], Deperetellidae [*Teleolophus*], Olseniidae [cf. *Olsenia*]);

8) Mergen Fauna (Lophialetidae [*Breviodon, Lophialetes*], Deperetellidae [*Irdinolophus*], Hyracodontidae [*Ardynia*]);

9) Khaychin Fauna (Brontotheriidae [*Protitan, Microtitan*], Lophialetidae [*Lophialetes, Breviodon*], Deperetellidae [*Teleolophus, Deperetella*], Hyracodontidae, Amynodontidae, Mesonychidae);

10) Kholboldzhi Fauna (Brontotheriidae, Isectolophidae, Lophialetidae [*Lophialetes, Breviodon, Rhodopagus, Schlosseria*], Hyracodontidae [*Pataecops*], Amynodontidae);

11) Khoer Dzan Fauna (Brontotheriidae, Helaletidae [*Colodon*], Deperetellidae [*Irdinolophus, Teleolophus, Deperetella*], Hyracodontidae [*Ardynia*]);

12) Irdin Manha Fauna (Brontotheriidae [*Protitan, Metatalmatherium, Microtitan, Epimanteoceras, Gnathotitan*], Lophialetidae [*Lophialetes, Breviodon, Rhodopagus, Eoletes*], Deperetellidae [*Teleolophus*], Helaletidae [*Helaletes*], Hyracodontidae).

So defined, the Arshantan is also seen as partly equivalent to the European Land Mammal Ages (ELMA) upper Grauvian and lower Geiseltalian (early Lutetian) and the Irdinmanhan s. str. to the upper Geiseltalian and lower Robiacian (late Lutetian). The Sharamurunian would be considered as the equivalent to the upper Robiacian (Bartonian) and lower Headonian (Priabonian) in Europe.

Ecological aspects

The species diversity is probably not fully represented by the Toru Ajgyr assemblage due to lack of small mammals and other vertebrates. Likewise, the total amount of perissodactyls and artiodactyls (5 taxa) is also too small. In the middle Eocene Geiseltal fauna (Germany) there are at least 37 taxa (Haubold & Krumbiegel 1984; Erfurt 1995). In order to discuss comprehensively the ecosystem, further collections and sedimentological studies are necessary. At the moment there are only autecological hints given from larger mammals.

Lophialetes and *Teleolophus* are cursorially adapted by the functionally tridactyl limbs with long metapodials and hooflike terminal phalanges. Reshetov (1979) pointed out that *L. expeditus* displays a higher cursorial adaptation than other middle Eocene perissodactyls. Our limb material supports this statement also for *Lophialetes* sp. from Toru Ajgyr. In *Teleolophus* and Brontotheriidae indet., the limbs are less cursorial. In *Lophialetes* sp., all distal parts of the limbs are elongated. Hence, MC III is the longest metacarpal, MC II and MC IV are reduced to a thinner diameter but they still reached the ground. MC V is not preserved in Tory Ajgyr. In the Chinese specimen AMNH 22091, it is reduced to a short triangular nodule (Radinsky 1965b: 244). The carpals are elongated antero-posteriorly and display, like the proximal metacarpals, relatively large insertion areas for muscles. This result concerns especially the musculus extensor carpi radialis and musculus extensor carpi ulnaris, which are larger than in non-cursorial mammals. In addition, there was a large musculus extensor carpi ulnaris, which is functionally a flexor in recent equids, suoids and bovids, supporting the dorsal flexion of the hand (Dobberstein & Hoffmann 1961). In cursorially more primitive perissodactyls (brontotheres) or mesonychids (*Pachyaena*), this function was only realised by flexors in the strict sense such as the musculus flexor carpi ulnaris, which inserts at the pisiform. There, the other carpals are not anteroposteriorly elongated (Figure 3). In the hind limb of *Lophialetes* sp., the caput femoris is round and the tibia is elongated. A less advanced cursorial character is the short shallow groove at the end of the tuber calcanei, which indicates a weaker insertation of muscles compared to recent cursorial mammals. The cervical vertebras of *Lophialetes* sp. indicate an elongated neck as reconstructed for the Mongolian *L. expeditus* (Reshetov 1979). Based on the slim limbs, Reshetov proposed a similar morphology as in the recent gerenuk (*Litocranius*) and classified *L. expeditus* as a top browser. Our material underlines that this genus was highly specialized for top browsing. In contrast to the Mongolian *L. expeditus*, the Toru Ajgyr form is slightly smaller (Table 4) and the body mass is less (Table 10).

measurement	Function W in [kg];	Brontotheriidae indet. [kg]	*Teleolophus* sp. [kg]	*Lophialetes* sp. [kg]	cf. *Olsenia* sp. [kg]
width caput humeri	$\log W=2.7311*(\log H_{Dcaput})+0.27311$	180	107	36	-
width humerus distal	$\log W=2.6246*(\log H_{Wdist.})+0.2756$	184	79	-	-
width radius distal	$\log W=2.4824*(\log R_{Wdist.})+0.4635$	134	60	15	-
largest femur length	$\log W=3,5526*(\log F_{L})-2.9997$	-	-	27,7	-
width tibia proximal	$\log W=2,8850*(\log T_{Wprox.})-0.2758$	213	-	11	-
width tibia distal	$\log W=2,8409*(\log T_{Wdist.})+0.3222$	191	-	13	428

Table 10.— Body mass estimations for Eocene mammals from Toru Ajgyr.
Calculations after Scott (1983); abbreviations: H = humerus, R = radius, F = femur, T = tibia (see chapter methods).

Regarding the relatively high abundance in Toru Ajgyr and in other localities, *Lophialetes* sp. appears as an ecological equivalent for smaller recent artiodactyls such as gazelles. The largest and heaviest mammal in Toru Ajgyr was *Gobiatherium* *mirificum*, for which 600 kg is roughly estimated. With a weight of about 400 kg, cf. *Olsenia* sp. also counts in the group of large mammals. In contrast to other middle Eocene localities, the brontotheres are relatively small in Toru Ajgyr. A body mass of about 180 kg is comparable to recent tapirs.

Teleolophus sp. takes an intermediate position. In this form there results an average of 80 kg from the estimation in Table 10. This mass is less than in recent perissodactyls and only comparable with artiodactyls. *Teleolophus* would be an ecological equivalent to larger cervids and antelopes. According to the dentition, there are similarities to tapirs. In all Eocene Asian forms, the molars are high-crowned and lophodont. The lower jaw displays a relatively long symphysis and is elongated. Unfortunately, all skull materials are poorly preserved. It is unclear whether or not there was a trunk as reconstructed for *Lophialetes* by Reshetov (1979: fig. 15). The latter would support the characterisation as a browser, which is indicated by the dentition.

In cf. *Olsenia* sp., the intermediate claw/hooflike form of the terminal phalanges could be interpreted differently as an adaptation for digging or for scavenging. The orientation of the facets between metatarsals and first phalanges, as well as the orientation of the facets between the phalanges, determines a divergence of the toes, see Figure 15. This spreading of the metapodium enlarges the foot surface and is known for heavy animals or species living on soft grounds. This foot structure marks an ecological differentiation to similar sized but slender mesonychids. Further ecological interpretations are not possible due to the lack of preserved dentitions, skulls or gut contents.

The occurrence of higher cursorially adapted perissodactyls in Toru Ajgyr (and in other Eocene Asian localities) was very probably contemporaneous with significant changes in the environment, in particular with the expansion of open semi-arid to arid savannah-like thorny woodlands. The number of hypsodont species increased, which were able to use the harder food in the dryer landscapes at the boundary between the lower and middle Eocene in Central Asia. Unfortunately, the Asian fossil record is still poorly described in detail. Even if not exactly determinable, associated postcranial materials play an important role in order to complete our morphological and taxonomical knowledge and to give a basis for palaeoecological interpretations.

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PLATE CAPTIONS

PLATE 1

A) View of the fossil complex, Toru Ajgyr locality in Kyrgyzstan from the south.

(The arrow indicates fossil site I.)

B) View of site I, Toru Ajgyr from the north.

(Arrows indicate several levels with bones in the finding layer.)

C) Combined left foot-bones of Brontotheriidae indet. from Toru Ajgyr site I. Dorsal view.

PLATE 1

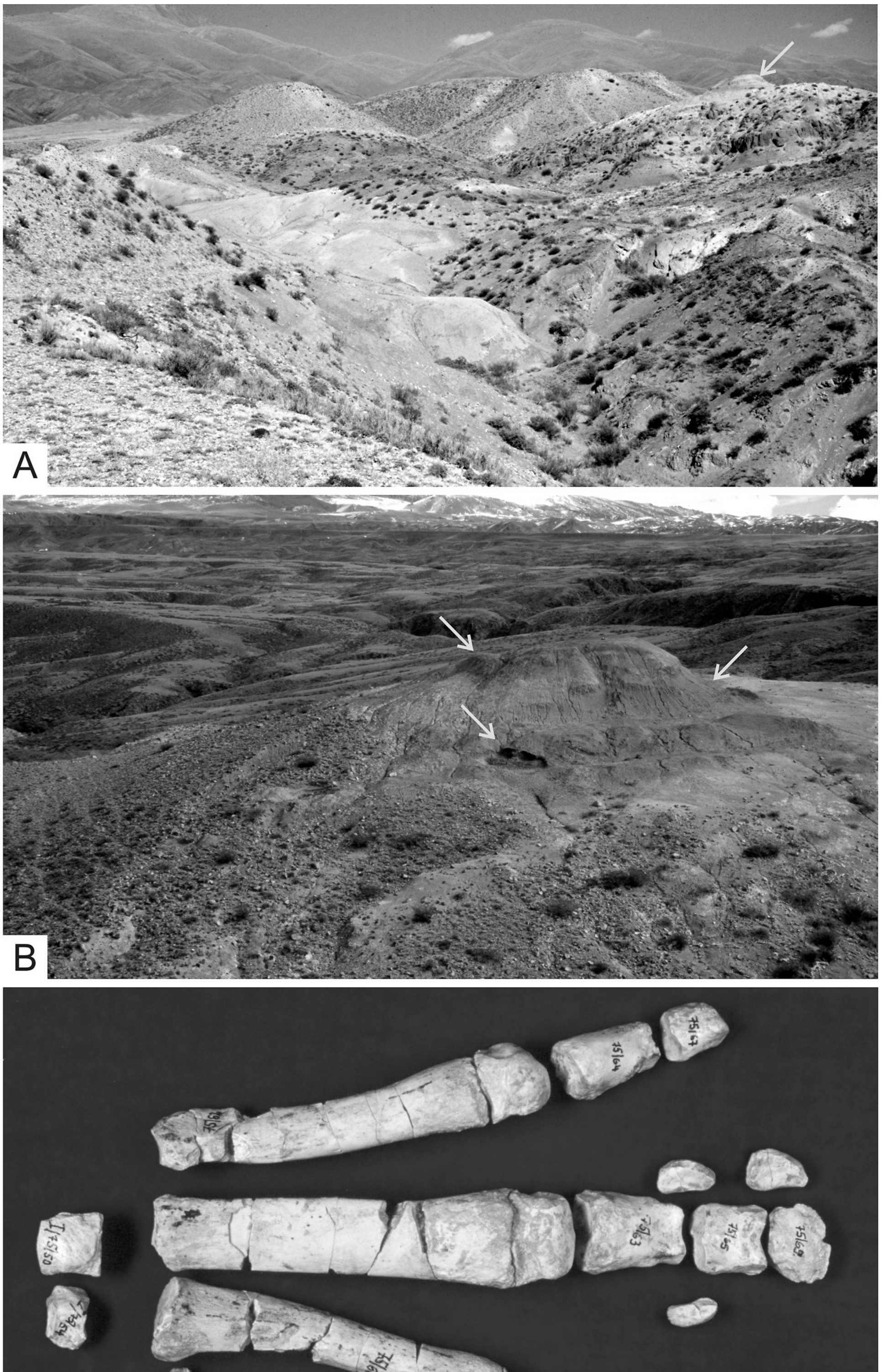

PLATE 2

A) Combined left hand-bones of *Lophialetes* sp. from Toru Ajgyr site I. Dorsal view.

B) Combined left hand-bones of *Teleolophus* sp. from Toru Ajgyr site IV. Dorsal view.

C) Combined left hand-bones of Brontotheriidae indet. from Toru Ajgyr site VIII. Dorsal view.

PLATE 2

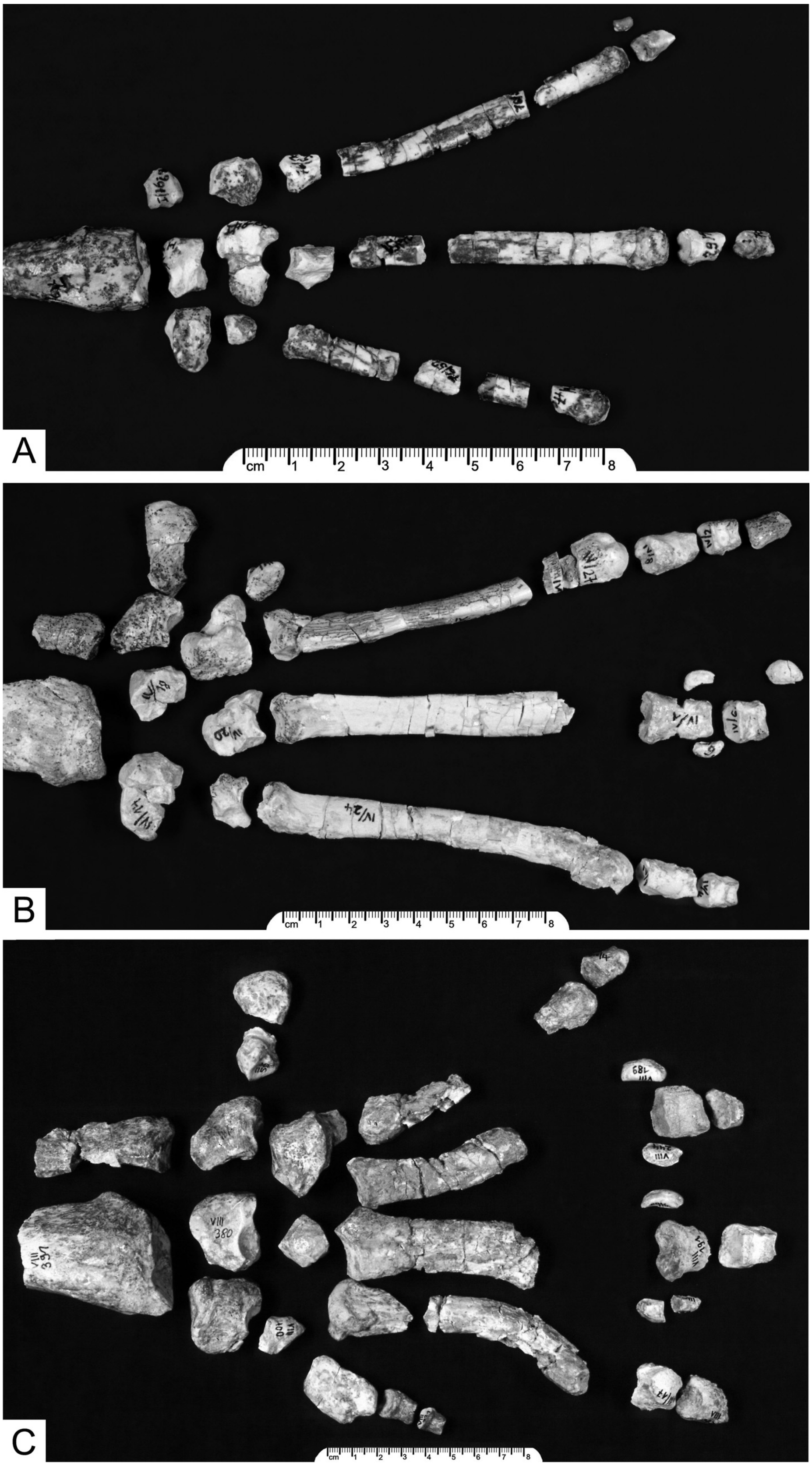
A
cm 1 2 3 4 5 6 7 8
B
cm 1 2 3 4 5 6 7 8
IV/24
C
cm 1 2 3 4 5 6 7 8
VIII 337
VIII 380

PLATE 3

A) Combined left foot skeleton of cf. *Olsenia* sp. from Toru Ajgyr site II in dorsal view.

B) Detail of Plate 3/A: Calcaneus in dorsal view.

C) Detail of Plate 3/A: Calcaneus in lateral view.

D) Detail of Plate 3/A: Calcaneus in medial view.

E) Detail of Plate 3/A: Astragalus in dorsal view.

F) Detail of Plate 3/A: Astragalus in medial view.

G) Detail of Plate 3/A: Astragalus in lateral view.

PLATE 3