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Gomphos elkema (Glires, Mammalia) from the Erlian Basin: Evidence for the Early Tertiary Bumbanian Land Mammal Age in Nei-Mongol, China

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ABSTRACT

Dental and postcranial specimens of *Gomphos elkema*, including lower and upper dentition and pedal elements, from the Huheboerhe locality, Erlian Basin, Nei-Mongol (Inner Mongolia), are described. Postcranial elements of *Gomphos* are similar to those of *Mimolagus*, suggesting affinity with lagomorphs. *Gomphos elkema* is a typical Bumbanian taxon, previously known only from Mongolia. *Gomphos elkema* specimens at Huheboerhe indicate occurrence of Bumbanian-equivalent beds and fauna in the region and suggest potential presence of the Paleocene–Eocene boundary in the Huheboerhe section.

INTRODUCTION

The Mongolian Plateau has been a major source of data for studies of Asian Tertiary vertebrate paleontology and stratigraphy

since the Central Asiatic Expeditions (CAE) of the American Museum of Natural History in the 1920s. This region is important in its abundance of fossil mammals from many localities where strata ranging from the late Pa-

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leocene to Miocene are exposed. Most type localities for biostratigraphic and chronostratigraphic units of the terrestrial Tertiary of Asia are in this region. These units form the framework for much of the Asian Paleogene. Initially much of this framework rested on research by the CAE, but numerous studies conducted over the last few decades have now expanded our knowledge of this critical region (e.g., Radinsky, 1964; Mellett, 1968; Szalay and McKenna, 1971; Rose, 1981; Jiang, 1983; Li and Ting, 1983; Qi, 1987; Russell and Zhai, 1987; Dashzeveg, 1982; 1988; Meng, 1990; Meng et al., 1998). One key result of the more recent studies was the discovery of a new fauna, the type assemblage for the Bumbanian Asian Land Mammal Age (ALMA), and the suggestion that the Paleocene–Eocene boundary lies below that new faunal level, at the transition between the Naran Member and Bumban Member of the Naran-Bulak Formation in the Nemegt region, Mongolia (Dashzeveg, 1988). The fauna from the Bumban Member remains the richest early Eocene vertebrate assemblage in central Asia.

Here we report a new occurrence of fossil mammals that we argue is correlative to the Bumban fauna. The new fauna was discovered during the field season of 2002 in a stratigraphic section along Huheboerhe cliff, an area near the Camp Margetts area of the CAE (Radinsky, 1964; Meng, 1990). Although a section in the vicinity was previously reported by the local geological mapping team (Jiang, 1983; Qi, 1987), only the probable late Paleocene Nomogen Formation and probable middle Eocene Arshanto and Irдин Manha beds were recognized in that section; a disconformity was described between the Nomogen and Arshanto Formations. Our new section shows no significant sedimentological hiatus within the interval encompassed by the Nomogen and Arshanto Formations. In addition, fossils, dominated by the gliroid *Gomphos elkema*, were found within this sequence. *Gomphos* is a common element in Bumbanian faunas of Mongolia, and recent work has shown that some (if not all) of the Bumbanian ALMA is earliest Eocene in age (Bowen et al., 2002). Below this level in the section, *Prodinoceras*, a fossil typical of the Late Paleocene Gashatan

ALMA, was found. Above this level, typical Arshanto and Irдин Manha fossils, predominantly perissodactyls, are abundant. These biostratigraphic observations indicate the potential presence of earliest Eocene strata and the Paleocene–Eocene (P-E) boundary in this sequence, the first evidence of this boundary in Nei-Mongol (Inner Mongolia). The discovery of the new faunal level in the Huheboerhe section could lead to enhanced correlation of faunas across the P-E boundary in central Asia.

The P-E boundary is marked by a dramatic, short-term global warming event and by carbon cycle perturbations that produced a distinctive carbon isotope excursion recorded in both marine and terrestrial sediments (Burchardt, 1978; Hubbard and Boulter, 1983; Rea et al., 1990; Koch et al., 1992; Bown and Kraus, 1993; Gunnell et al., 1993; Wing and Greenwood, 1993; Zachos et al., 1993; Meng and McKenna, 1998; Bowen et al., 2002). These events are roughly coincident with the first appearances of several modern orders of placental mammals in North America and Europe (Koch et al., 1992; Hooker 1998; Cojan et al., 2000; Bowen et al., 2001), and several of these same taxa have been associated with the P-E boundary carbon isotope excursion in southern China (Bowen et al., 2002). Therefore, the discovery of the new fossil level and recognition of the P-E boundary in Nei-Mongol (Inner Mongolia) should shed new light on faunal evolution coincident with environmental change during this critical interval in central Asia.

Thus far there is only one named species of *Gomphos*, *G. elkema* Shevyreva, 1975, from the Lower Eocene of Mongolia. This species is based on a fragmentary lower jaw, which was first named by Shevyreva (1975, in Shevyreva et al., 1975) and redescribed by Zhegallo and Shevyreva (1976) and by Dashzeveg and Russell (1988). *Gomphos* specimens, consisting of teeth and jaws, have previously been reported from the Bumban Member of the Naran-Bulak Formation in Tsagan-Khushu, Nemegt Basin, and from Bumban equivalent beds in the Gashato Formation, Ulan-Nur Basin of Mongolia (Dashzeveg and Russell, 1988; Dashzeveg, 1988). The specimens described here are the first

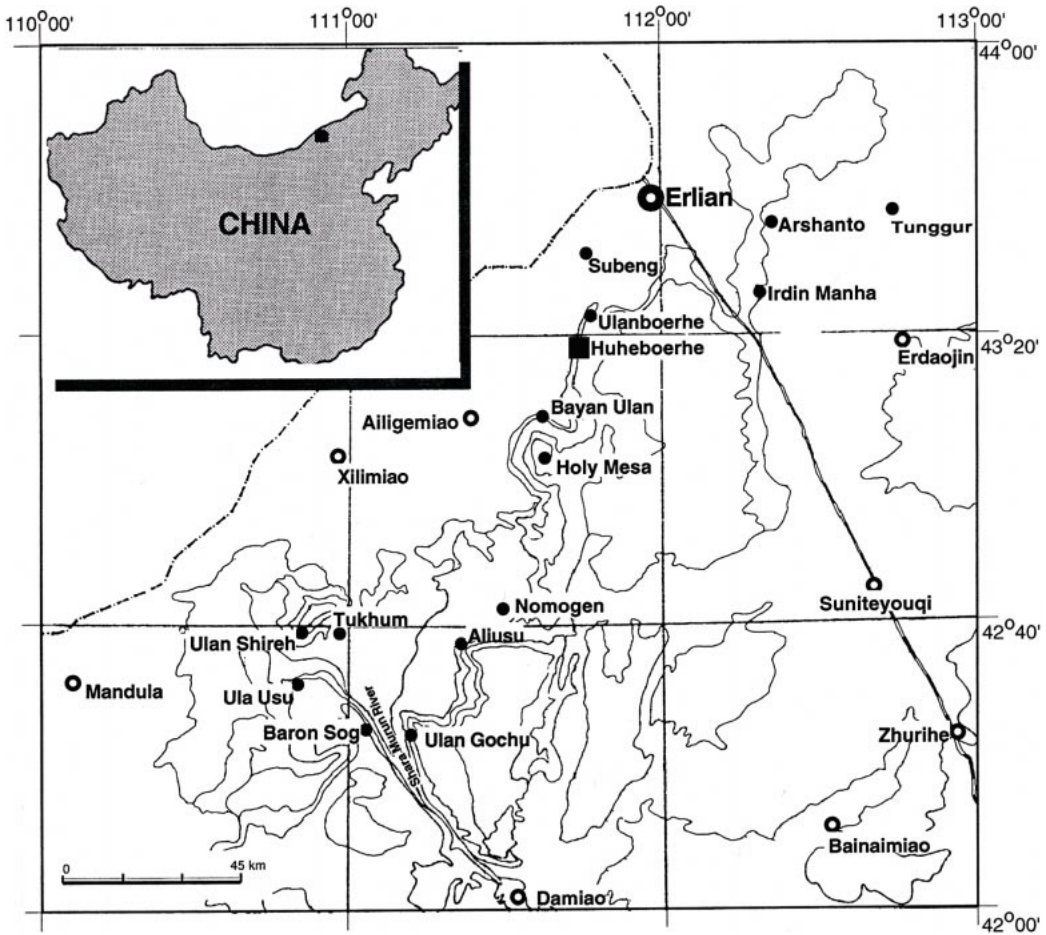


Fig. 1. Locality map of the Erlian Basin (after Meng et al., 1998).

record of this taxon from Nei-Mongol in China. Several postcranial elements are assigned to this taxon, and additional dental morphology of the species is described. With the identification of this typical Bumbanian fossil, we present a preliminary discussion on the correlation and probable location of the P-E boundary in the Huheboerhe section.

MATERIALS AND METHODS

All material reported here was collected at the Huheboerhe section except for two astragali that came from Bayan Ulan, approximately 25 km to the southwest. The fauna is dominated by specimens of *Gomphos*, a stem taxon of lagomorphs. The specimens are fragmentary jaws and isolated postcranial elements. By the frequency of occurrence,

size, and morphology we are able to associate the upper and lower dentition as well as postcranial elements of *Gomphos*. Similarities to the foot bones of *Mimolagus* (Bohlin, 1951) and to those of articulated mimotonid specimens from the Bumban member of Mongolia (unpublished material) also help to associate the teeth and postcranial elements.

INSTITUTIONAL ABBREVIATIONS: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; AMNH, American Museum of Natural History.

STRATIGRAPHY

The locality is indicated in figure 1. Fossil-bearing strata in this area were first discovered by the CAE (Radinsky, 1964), and were

further investigated by workers from the local geological mapping team (Jiang, 1983) and the IVPP (Qi, 1987; Meng, 1990). The locality is in an area that is now an active oil field. A section with a total thickness of 57.8 meters is described below.

Huheboerhe section (starting point coordinate: 43°21.895'N, 110°44.186'E):

1. Fine-grained sandstone with light gray-green bands; some microbands cross-bedded; locally containing light brown muddy siltstone. 4.2 m thick.
2. Grayish white calcareous fine-grained sandstone; fresh rock hard and darkly banded, but friable after weathering. 0.6 m thick.
3. Fine-grained sandstone with grayish green banding, locally containing light brown siltstone. 13.5 m thick.
4. Interbedded light green-brown sandstone and medium-coarse grained sandstone containing pebble conglomerates; pebbles are primarily hollow, columnar, calcareous nodules. 10.5 m thick.
5. Light brown, thinly layered fine grained sandstone. 3 m thick.
6. Grayish green mudstone and claystone. 2.5 m thick.
7. Light brown mudstone and claystone, fresh surface showing black manganese nodules, weathered surface light red. 5.5 m thick.
8. Light brownish yellow fine-grained sandstone, weathered surface pale white. 1 m thick.
9. Brown claystone. 1.5 m thick.
10. Gray mudstone and claystone, fresh surface with black manganese nodules, upper beds richly fossiliferous and dominated by *Gomphos*. 10 m thick.
11. Reddish brown sandy claystone. The base of the unit is at 48.3 m (43°21.720'N; 111°45.063'E) and contains white calcareous nodules. (A small perissodactyl and a possible palaeoryctoid were found in this bed.). 7.5 m thick.
12. Grayish white, medium-coarse grained sandstone with pebble conglomerates and crossbedding. Bottom layers characterized by fine pebble conglomerates comprised predominantly of quartz grains, which is typical of basal Irдин Manha Formation. Rich in fossil fragments of perissodactyls, including tapiroids. 2 m thick.

SYSTEMATIC PALEONTOLOGY

MAMMALIA LINNAEUS, 1758

GLIRES LINNAEUS, 1758

MIMOTONIDAE LI, 1977

Gomphos elkema Shevryeva, 1975

REVISED DIAGNOSIS: Similar to other mimotonids but differing from other Glires in having two pairs of lower incisors. Differing from *Mimotona* in having less transverse upper teeth, separated paracone and metacone, a longer trigonid, and presence of a mesostyle on upper molars and a mesoconid on lower molars. Differing from *Anatolmys* in having a shallow horizontal ramus (see also Averianov, 1994). Differing from *Mimolagus* in being smaller and having higher crowns of cheekteeth with distinctive cusps and ridges.

REFERRED SPECIMENS: IVPP V13509.1, a right mandible with m1–m3; V13509.2, a left mandible with m2–m3; V13509.3, a right mandible with m2–m3; V13509.4, a right maxilla with P4–M2; V13509.5, a left maxilla with P3–M1; V13509.6, right P4–M1; V13509.7, a right mandible with partial incisor; V13509.8, anterior portion of a right mandible with the major incisor and the alveolus of the minor incisor; V13510.1, a right calcaneus; V13510.2, a left astragalus; V13510.3, a right cuboid; and V13510.4, a right navicular. In addition to the numbered specimens, many unnumbered fragmentary jaws without teeth, isolated incisors, four additional naviculars, seven cuboids, 23 complete and partial astragali, 140 complete and partial calcanea from Huheboerhe, and two calcanea from Bayan Ulan were referred to the species.

LOCALITIES AND AGE: Upper beds of the “Nomogen Formation” in the Huheboerhe section, Erlian Basin of Nei-Mongol (Inner Mongolia), China; the Bumban Member of the Naran-Bulak Formation in Tsagan-Khushu, Nemegt Basin; Members II and III in the Gashato Formation, Ulan-Nur Basin of Mongolia (Dashzeveg and Russell, 1988; Dashzeveg, 1988); and probably the upper part of the Nomogen Formation at Bayan Ulan. The fauna contained in the Bumban Member has been conventionally considered as early Eocene (Dashzeveg, 1988; Ting,

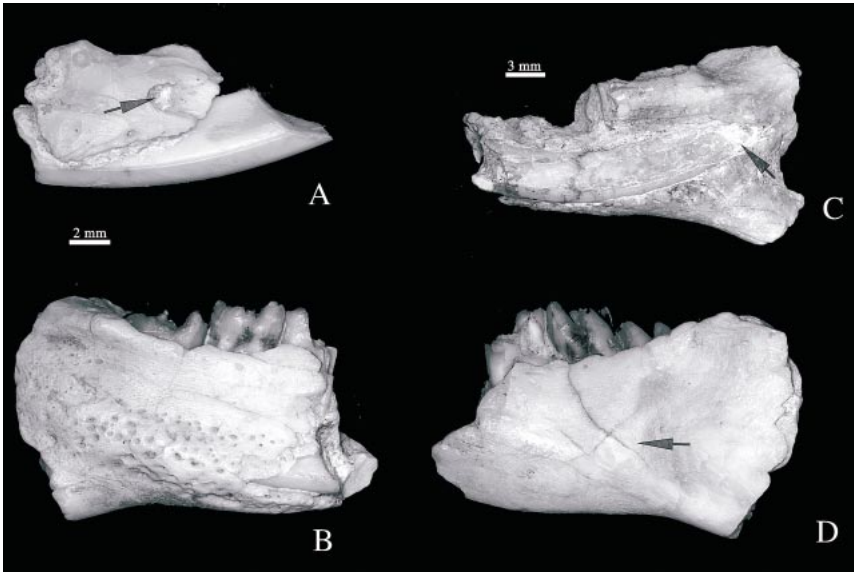


Fig. 2. Lower jaw fragments of *Gomphos elkema*. **A.** lateral view of the anterior portion of right mandible (IVPP V13509.8); arrow indicates alveolus of the second lower incisor. **B.** Medial view of left partial mandible, showing the fenestrae on the ventral portion of the bone (V13509.2). **C.** Medial view of partial right mandible, with arrow pointing to the posterior end of the lower incisor (V13509.7). **D.** Lateral view of partial left mandible, with arrow pointing to the anterior edge of the masseteric fossa (V13509.2). Panels A, B, and D, are at the same scale.

1998), although an alternative hypothesis that the Bumbanian fauna is of Late Paleocene age exists (Beard, 1998). *Gomphos* is known only from Bumbanian faunas, by which the beds containing the taxon in Huheboerhe are biostratigraphically correlative to rocks bearing Bumbanian fossils elsewhere on the Mongolian Plateau (see below).

DESCRIPTION

MANDIBLE AND MAXILLA: No cranial elements have been discovered except partial maxillae. The roots of the cheekteeth are exposed on the maxillary floor of the orbit, and the bony floor bears numerous tiny fenestrae. The posterior edge of the anterior root of the zygomatic arch aligns with the anterior half of M2. The infraorbital foramen is probably above the anterior edge of P3. Fragmentary mandibles are preserved (fig. 2). The body of the mandible is thick. The angular process aligns in roughly the same plane as the incisor. The ventral margin of the horizontal ramus is gently curved in lateral view; the deepest portion of the ramus occurs below

the m1. There are probably two mental foramina: one lateral to p3 and the other lateral to the posterior half of the p4. Along the ventral part of the medial surface of the dentary there are numerous tiny fenestrae (fig. 2B). The masseteric fossa extends anteriorly to a point even with the anterior edge of m3, ending at a blunt, rounded knot (fig. 2D). The fossa is shallow and broad, lacking a distinct upper crest. The symphyseal area is narrow, roughly surfaced, and unfused. The position of the mandibular foramen cannot be determined.

TEETH: The dental specimens are fragmentary. Still, we recognize the dental formula of *Gomphos* as $2?-0-3-3/2-0-2-3$ based on jaw specimens that preserve teeth, alveoli, and contact facets on teeth.

Numerous isolated upper and lower incisors are available. The enlarged upper incisors are typical of gliroid mammals in being transversely compressed with enamel covering their anterior (labial) surfaces, wrapping slightly onto the lateral and medial sides, and extending longitudinally the entire length of

the tooth. The labial surface is gently rounded and the enamel band forms the widest part of the tooth in cross-section. The incisor tip is chisel-shaped, with the lingual surface bearing a curved wear facet. The incisor pulp cavity is narrow in cross-section. No upper incisors were found in situ. The major lower incisor is presumably the di2 (Lockett, 1985; Meng and Wyss, 2001; Meng et al., 2003), which lies in the same plane as the cheek-teeth and is ventral to the roots of the cheek-teeth; its posterior end extends posterior to the m3 (fig. 2C). The exposed section of the lower incisor above the alveolus is short, and in life the tip of the lower incisor was lower than the occlusal surface of the cheekteeth. A minor lower incisor (presumably i2) is present. Although the tooth crown was broken, the alveolus of this tooth in V13509.8 indicates that it is small, procumbent, and posterolateral to the enlarged major incisor (fig. 2A).

P2 is not preserved, but a partial alveolus in IVPP V13509.5 suggests its presence. P3 is oval in occlusal view (fig. 3A). The lingual side of the tooth is significantly higher than the labial side. A single centrolabial cusp is conical, strong, and lateral to the protocone; it is the highest cusp of the tooth. Its lingual base has a weak ridge connecting to the protocone. The protocone is crestlike, sending two strong lophs labially. The anterior loph forms the anterior edge of the tooth and extends to the anterolabial corner of the center cusp. The posterior loph is longer than the anterior one and extends to the posterolabial corner of the tooth. Between the posterior loph and the center cusp, a broad, concave shelf basin is formed. No hypocone is present. A cuspule is present posterolabial to the center cusp. No cingulum is present on lingual and labial sides of the tooth.

P4 is similar to P3 but is more unilaterally hypsodont and more transversely elongate (figs. 3, 4; table 1). The unilateral hypsodonty decreases from P4 posteriorly. As in P3, a low ridge connects the single, transversely extended centrolabial cusp to the protocone. The anterior and posterior lophs extend farther labially and surround the centrolabial cusp more completely than in P3.

M1 differs from the premolars in being more angular and in having a hypocone on

the lingual side and the paracone and metacone on the labial side (figs. 3, 4). The hypocone is strong and is lower than the protocone. It extends labially as a strong posterior loph (or postcingulum). After wear, a large facet is formed on the protocone and hypocone. The enamel is thick around the protocone and paracone, both along the edge and on the occlusal surface of the tooth, and gradually becomes thinner labially. The anterior edge of the tooth is only slightly higher than the posterior edge of the preceding tooth. These structures suggest that grinding is the main function of the cheekteeth in *Gomphos*. The lingual surface of the tooth is rounded, with a flat area between the protocone and hypocone; a groove is not present between the two cusps. The paracone and metacone are labially positioned. The paracone is teardrop shaped and at the anterolabial corner of the tooth; its tip connects to the broad loph that comes from the protocone. The metacone is slightly more lingual than the paracone. The metaconule is not distinct and is confluent with the metacone after wear, such that a broad ridge is formed and directed toward the protocone. The ridge connecting the metaconule and protocone is narrow. The three main cusps and crests between them form a V shape. A triangular trigon basin is present. A distinct mesostyle is present on the labial margin and between the paracone and metacone. The tip of the wedge-shaped mesostyle extends lingually to the trigon basin between the bases of the paracone and metacone. There is no lingual or labial cingulum. M2 is nearly identical to M1 except being slightly narrower (fig. 4). M3 is not preserved, but its presence is indicated by a contact facet on the posterior surface of M2 in V13509.4.

Lower premolars are not preserved. Fragmentary mandibles bearing roots and alveoli of cheekteeth (not illustrated) show that there are two premolars. The p3 is a single-rooted, small, tooth. The p4 is double-rooted and is as long as, but narrower than, the m1. The m1 and m2 are similar, with the former being slightly larger; both are somewhat square shaped (figs. 5, 6). The paraconid is absent. The metaconid aligns with the protoconid at the same level. The metaconid is as thick as, and is higher than, the protoconid. The tri-

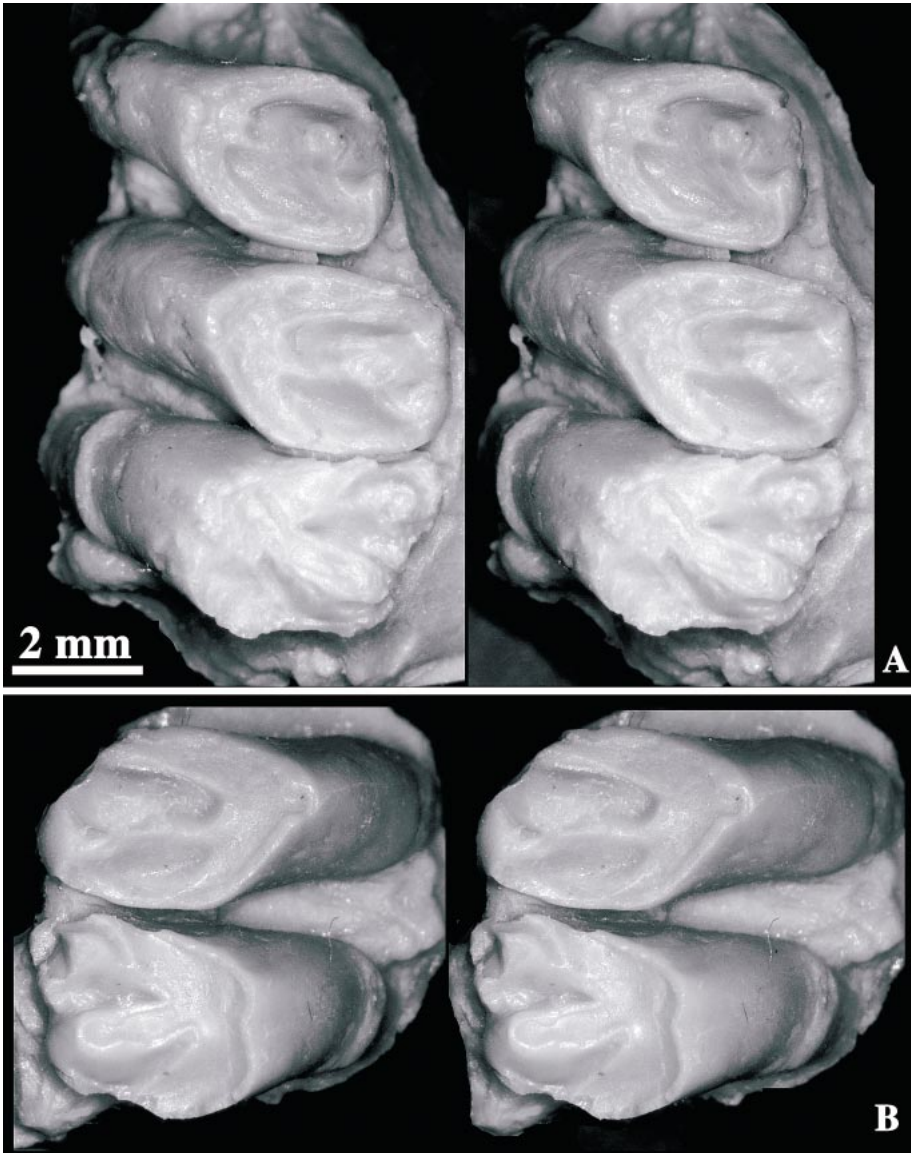


Fig. 3. Upper teeth of *Gomphos elkema*. **A.** Occlusal view of left P3–M1 (IVPP V13509.5). **B.** Occlusal view of right P4–M1 (V13509.6).

gonid is anteroposteriorly short. Anterior (paralophid) and posterior (protolophid) ridges extend from the protoconid to join the anterior and posterior side of the metaconid, respectively. A small trigonid basin is present between the two ridges. The talonid is lower than the trigonid and about twice as long. Immediately posterior to the trigonid, at the longitudinal axis of the tooth, is an inflated mesoconid, which occupies much the

position of the cristid obliqua. The hypoconid is large and is separated from the protoconid by a deep, narrow hypoflexid. Similar to the protoconid, the hypoconid is somewhat laterally extended. On the lingual side of the talonid, the mesostylid and entoconid are close to each other, with their bases being confluent. The mesostylid is slightly smaller than the entoconid. The hypoconulid is at the longitudinal axis of the tooth and protrudes

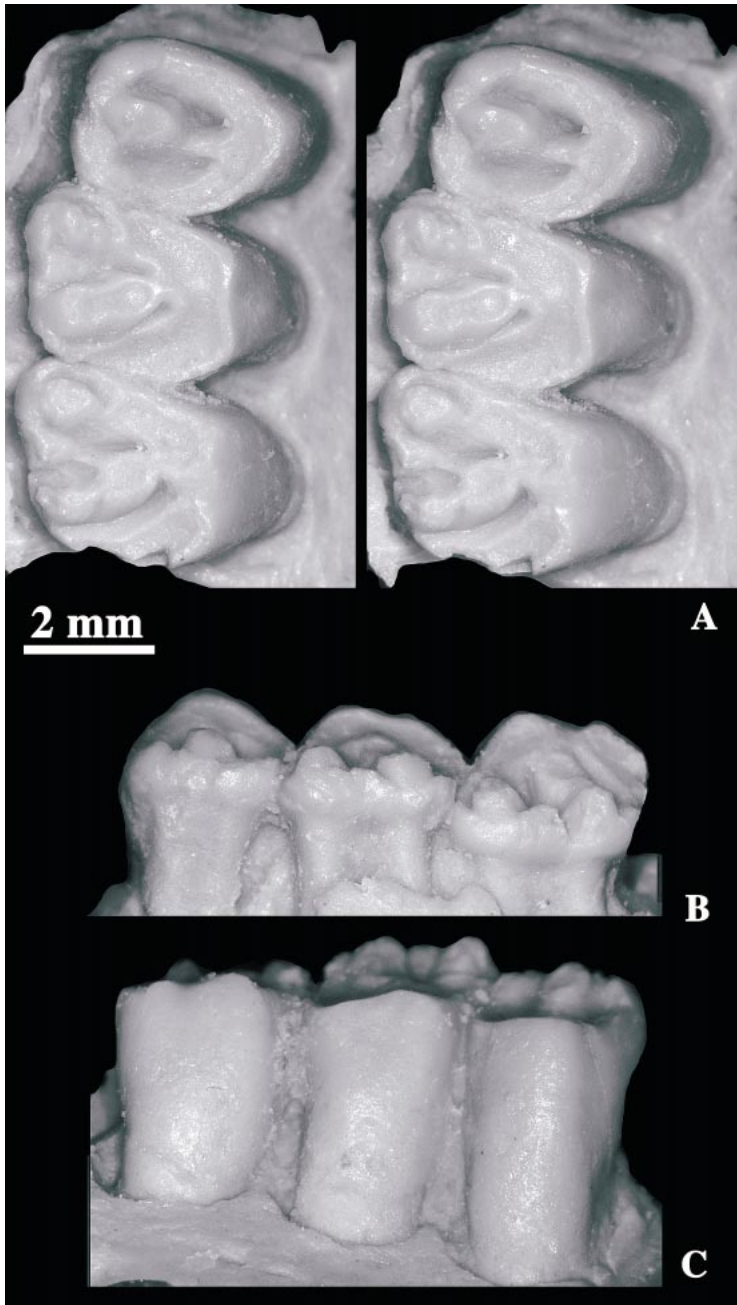


Fig. 4. Upper teeth of *Gomphos elkema* (IVPP V). A–C. Occlusal, labial, and lingual views of right P4–M2 (IVPP V13509.4).

backward as the most posterior point of the tooth. Wear facets are present on the occlusal surfaces of all teeth, particularly on the protoconid and hypoconid. There is no shear

facet along the posterior surface of the trigonid, which again suggests that grinding is the main chewing function of *Gomphos*.

The m3 differs from m1 and m2 in having

TABLE 1
Measurements (in mm) of Teeth of
Gomphos elkema

Specimen	Tooth	Width	Length
V13509.1	m1	3.12	3.32
	m2	3.28	3.30
	m3	3.42	4.56
V13509.2	m2	3.12	3.50
	m3	3.35	4.55
V13509.3	m2	3.15	3.30
	m3	3.10	4.22
V13509.4	P4	5.30	2.93
	M1	5.18	3.13
	M2	5.07	2.86
V13509.5	P3	5.23	2.85
	P4	5.55	2.98
	M1	5.52	3.32

a more inflated entoconid and hypoconulid such that a posterior lobe is formed (figs. 5, 6).

POSTCRANIAL ELEMENTS: The astragalus is ventrodorsally (or anteroposteriorly) flat (fig. 7). The astragalus head is transversely extended. In distal view, the long axis of the convex astragalonavicular facet has a 30–40° angle to the axis of rotation of the bone (fig. 7F). The same facet extends posteriorly on the medial surface to the midpoint of the bone. Breakage is present on the facet in the illustrated specimen, but other specimens show a continuous, elongated articular surface, which is broader laterally than medially. There is no distinct boundary indicating the facet for articulation with the cuboid, but a narrow area at the ventrolateral side of the head may contact the cuboid. This area and the astragalonavicular facet make a blunt angle. In dorsal and ventral views, the head is large compared to the rest of the bone. The astragalonavicular facet does not extend to the ventral side of the bone to contact the sustentacular facet, but extends somewhat to the dorsal side of the bone. The neck of the astragalus is short and broad. The trochlea is transversely broad and shallow; it is extensive on the dorsal side but weak on the ventral side. Therefore, the distal astragalotibial facet is almost absent on the ventral side. The lateral rim of the trochlea is sharper and

much longer than the medial one, and it is more posteriorly extended. Anterior to the medial rim of the trochlea, the bone has a large concave area, so that the bone is thin in this region.

On the ventral astragalar surface, the sustentacular facet is large, convex, and roughly oval in outline. This facet is separated from the astragalonavicular facet by a broad, shallow valley that forms the neck of the bone. The sulcus astragali is well defined as a narrow, deep trough between the sustentacular facet and the calcaneoastragalar facet. The sustentacular hinge is short and shallow. There is no astragalar foramen. The calcaneoastragalar facet is extensive and concave and is oriented diagonal to the long axis of the astragalus.

In lateral view, the astragalar head appears thicker than the rest of the bone. The astragalofibular facet is a narrow, semilunar shaped area, and is nearly perpendicular to the calcaneoastragalar facet.

The calcaneus is dominated by a long tuber, which is about half of the total length of the bone (measured from the posterior edge of the calcaneoastragalar facet) (fig. 8). In dorsal (cranial) view, it gradually thickens distally. The distal end of the tuber is rough-surfaced, suggesting attachment of tendons in life. In dorsal view, the calcaneoastragalar facet and the sustentacular facet are aligned at the same level. The calcaneoastragalar facet is a narrow convex band in a proximodistal orientation, nearly parallel to the long axis of the bone. The sustentacular facet is rounded and concave. A narrow sulcus calcanei separates the two facets.

In plantar view, the anterior plantar tubercle is low and blunt. The peroneal process is strong. Between the process and the anterior plantar tubercle is a broad, concave area. A distinct pit is present on the plantar side of the peroneal process. On the dorsal side of the peroneal process is the calcaneoastragalar facet. In distal view, the calcaneocuboid facet is large, concave, and oblique, with the lateral edge extending more distally than the medial one. Therefore, the calcaneocuboid facet faces anteromedially. The medial edge of the facet is notched. Between the notch and the broad groove for the tendon of the flexor fibularis, which is on the plantar side

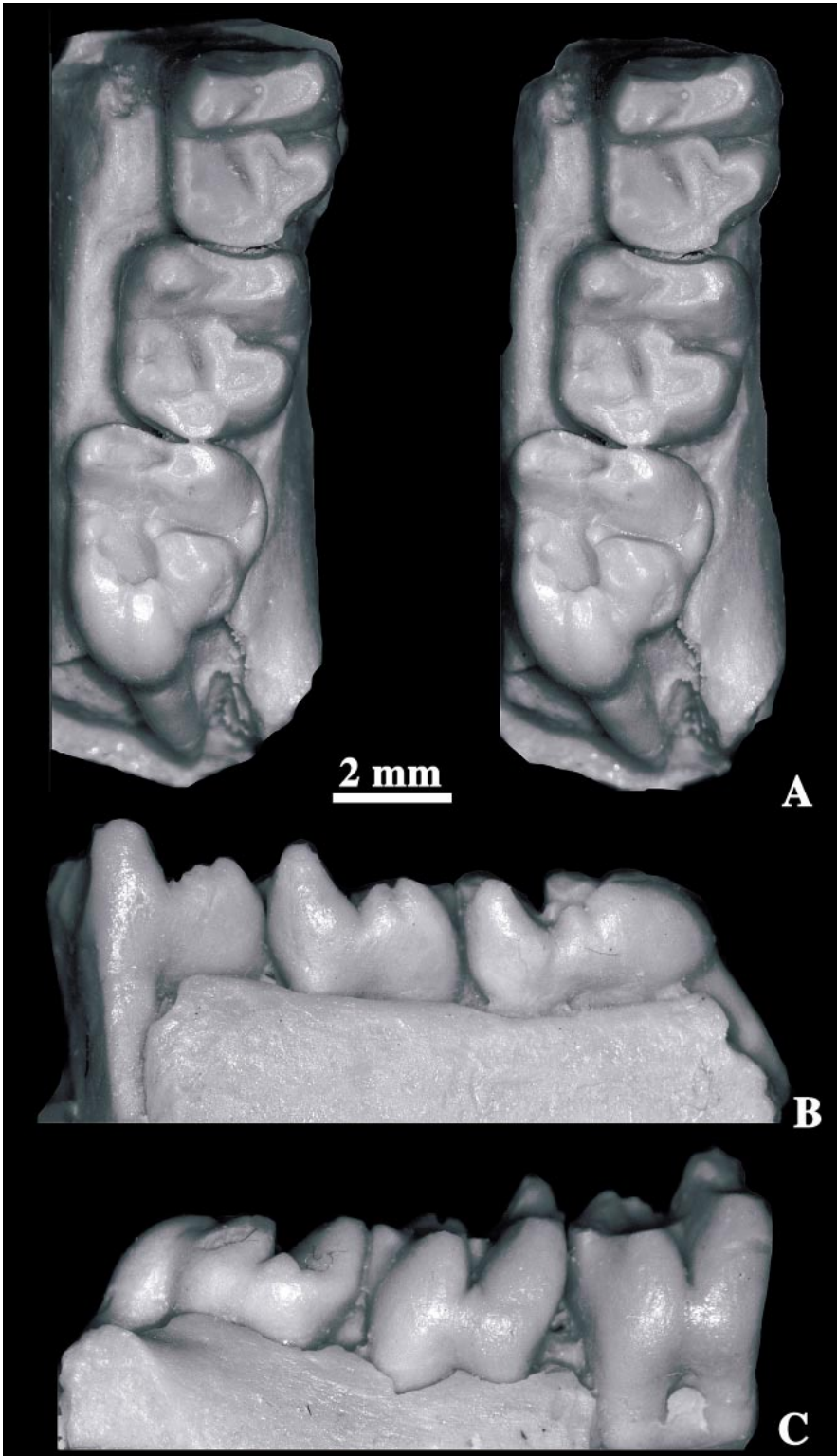


Fig. 5. Lower teeth of *Gomphos elkema*. A–C. Occlusal, lingual, and labial views of right m1–m3 (IVPP V13509.1).

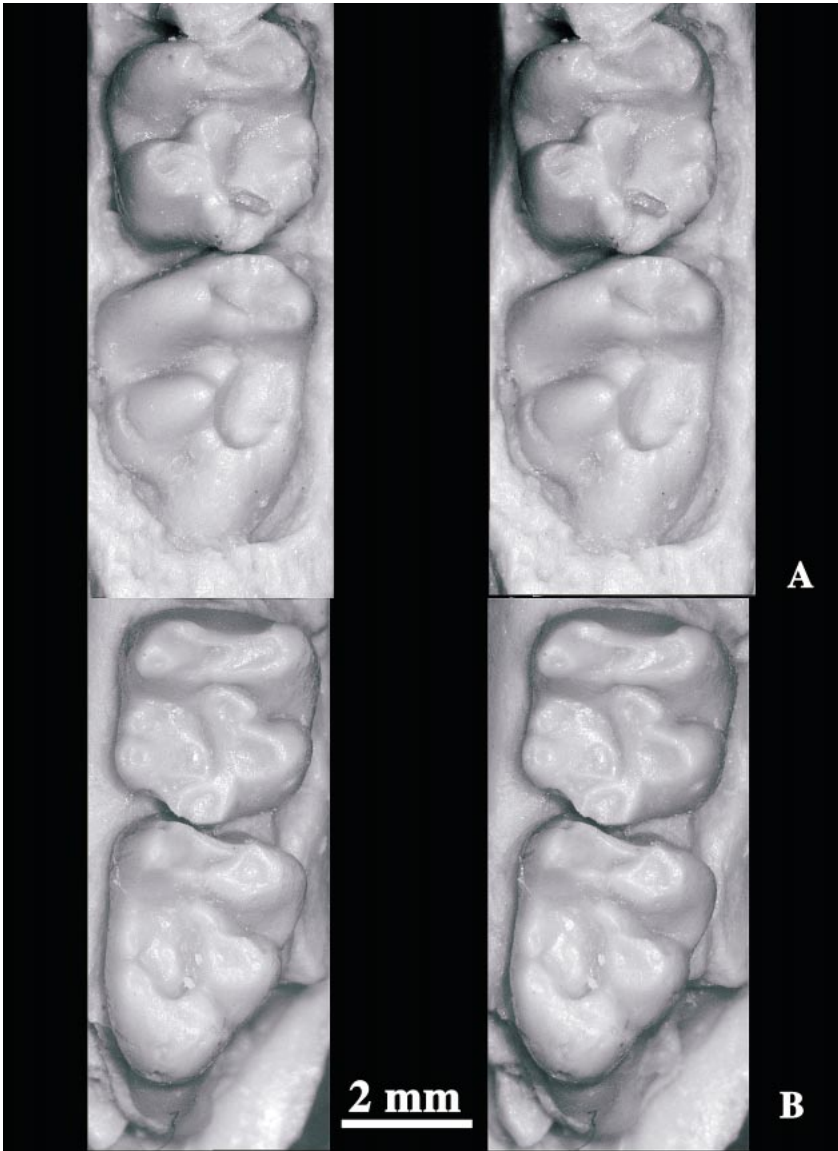


Fig. 6. Lower teeth of *Gomphos elkema*. A–B. Occlusal views of left and right m1–m3, respectively (IVPP V13509.2, V13509.3).

of the process bearing the sustentacular facet, is a concave area with a rough surface, in which there is a small foramen of unknown function. There is no calcaneal canal.

The cuboid is shorter than it is wide (fig. 9). The proximal articular surface (or calcaneal facet) is flat and rounded except that the medial side is irregular. This surface is inclined, with the dorsal edge being more distally located than the ventral edge. The distal

articular surface (facet for metatarsals IV and V) is roughly triangular and concave; its ventrolateral edge is ridge-shaped. In ventral view, the plantar tubercle is prominent, projecting ventrally from the midportion of the cuboid body. This process is better illustrated in medial and lateral views. Ventral (or distal) to the tubercle is a broad peroneal groove. On the medial side, a central process bears two articular facets, the proximal one

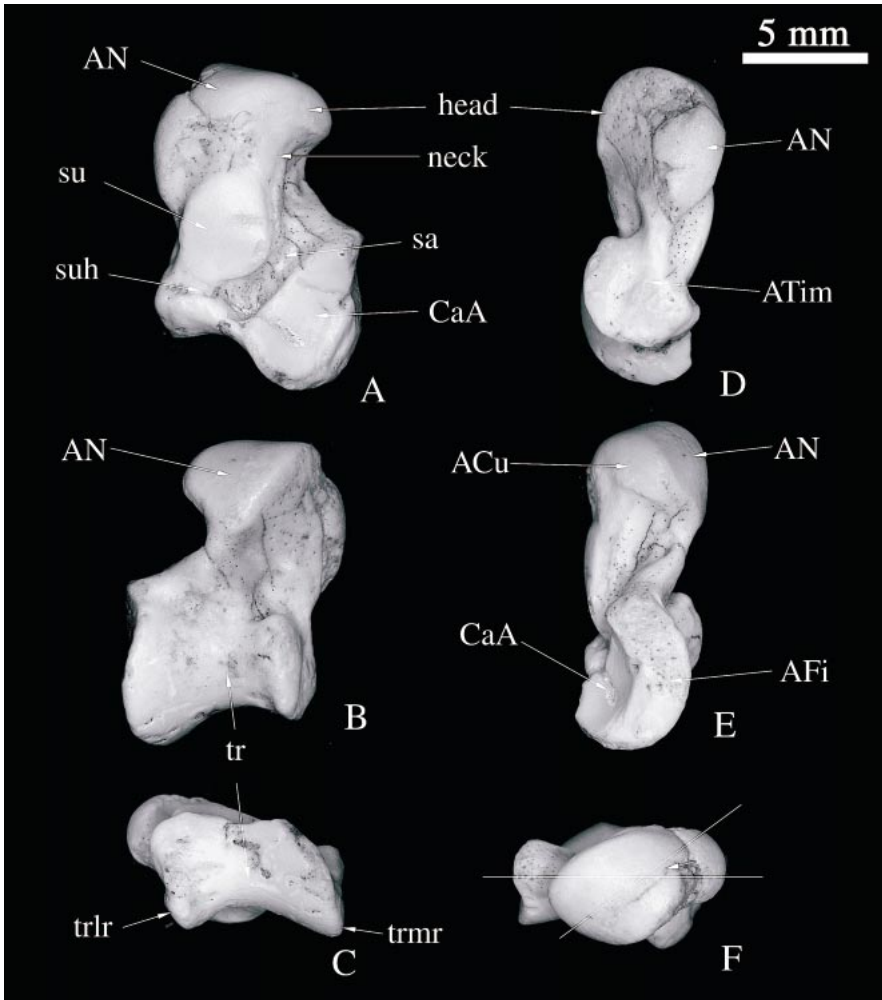


Fig. 7. A–F. Ventral, dorsal, posterior, medial, lateral, and distal views of left astragalus of *Gomphos elkema* (IVPP V13510.2). Abbreviations: ACu, astagalocuboid facet; AFi, astragalofibular facet; AN, astragalonavicular facet; ATim, medial astragalotibial facet; CaA, calcaneoastragal facet; sa, sulcus astragali; su, sustentacular facet; suh, sustentacular hinge; trlr, lateral rim of astragal trochlea; trmr, medial rim of astragal trochlea.

for the navicular and the distal one for the ectocuneiform; both facets are small. There is no indication of a contact between the cuboid and the astragalus. The dorsal side of the cuboid is smooth and featureless.

The body of the navicular is proximodistally short (fig. 10). Its proximal surface, which receives the astragal head, is a semi-lunar, smoothly concave fossa that is dorsoventrally elongated. The lateral edge of this fossa is notched. The distal surface is flat and presumably contacts the ectocuneiform and

the mesocuneiform, but there is no boundary to show the two facets. On the lateral side of the body, the facet for the cuboid is small and concave. The dorsal and the lateral surfaces of the body are confluent and convex. The plantar process of the navicular is robust and short.

Fragmentary distal ends of tibiae are preserved (not illustrated). The tibia bears a moderate medial malleolus and a weak posterior process; the fibula would not be fused to the tibia.

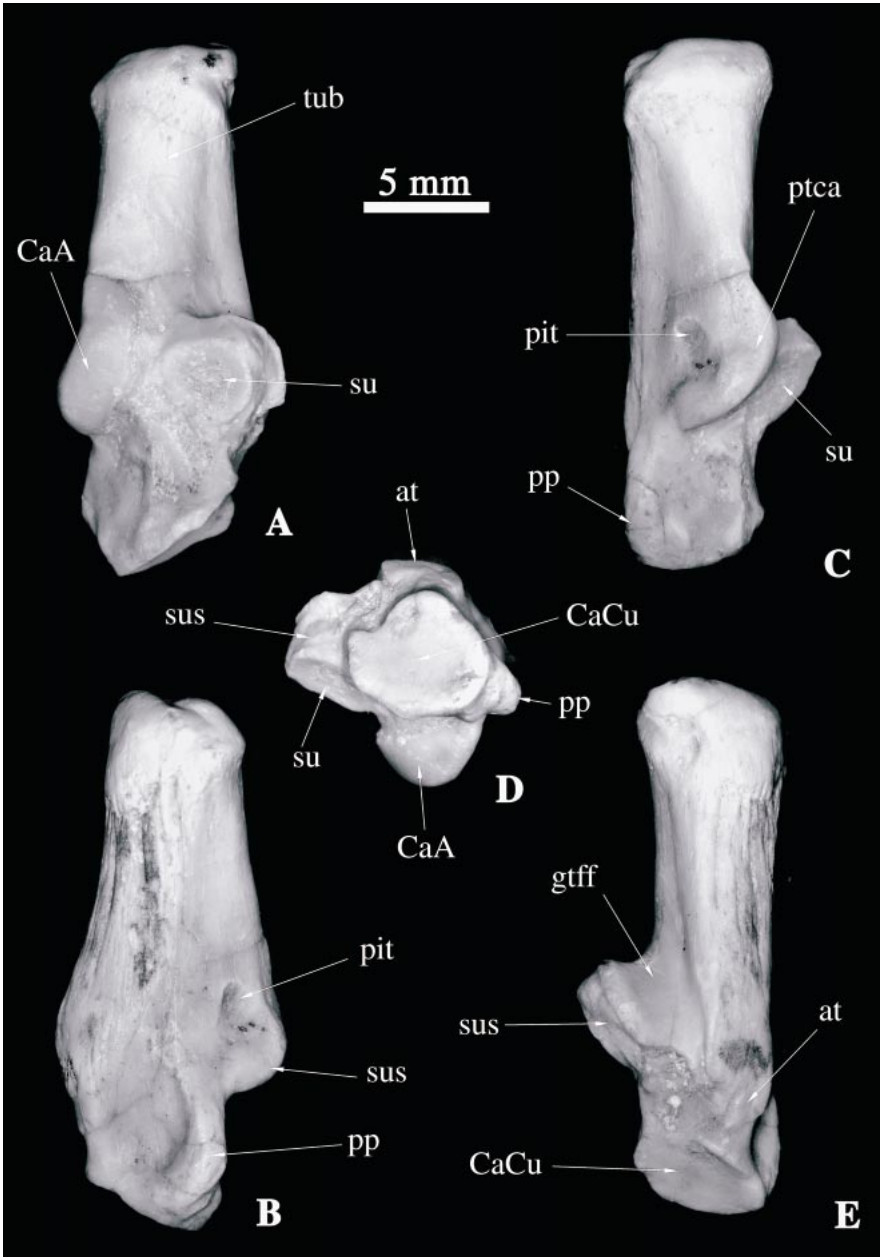


Fig. 8. A-E, Dorsal, ventral, lateral, distal, and medial views of the right calcaneus of *Gomphos elkema* (IVPP V13510.1). Abbreviations: at, anterior plantar tubercle; CaA, calcaneoastagalar facet; CaCu, calcaneocuboid facet; gtff, groove for the tendon of *M. flexor fibularis*; pp, peroneal process; ptca, calcaneal protuberance; su, sustentacular facet; sus, sustentaculum talus; and tub, tuber of the calcaneus.

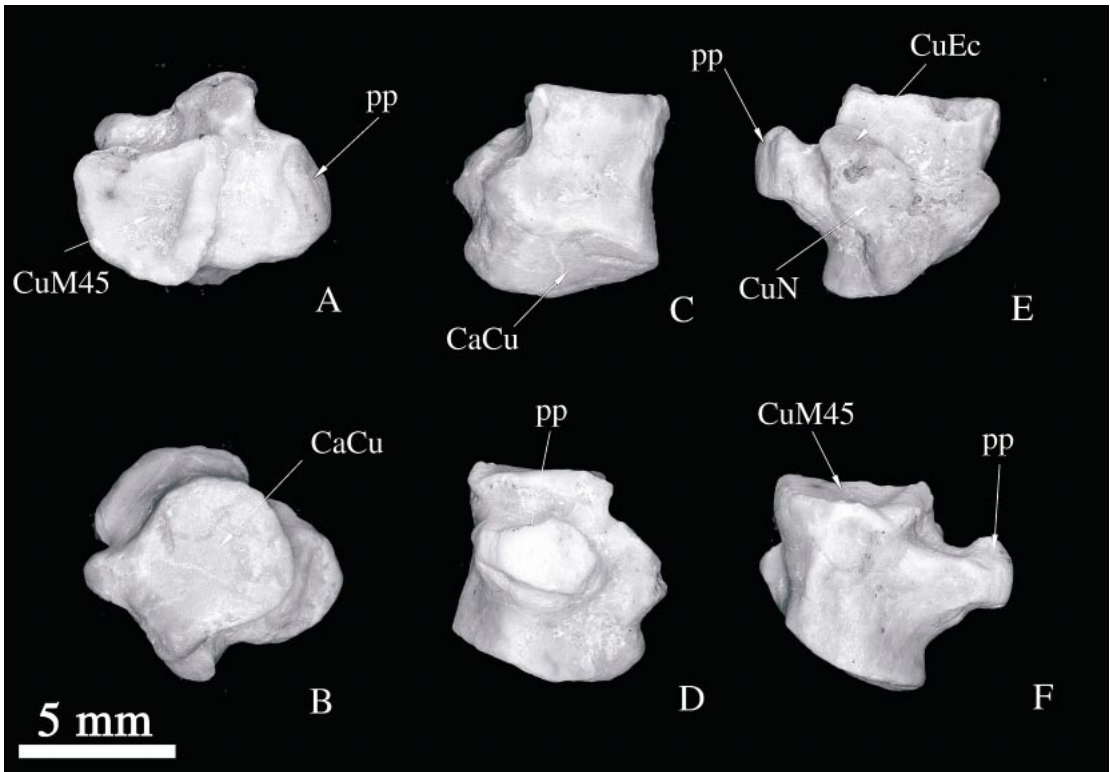


Fig. 9. A–F, Distal, proximal, dorsal, ventral, medial, and lateral views of the right cuboid of *Gomphos elkema* (IVPP V13510.3). Abbreviations: CaCu, calcaneocuboid facet; CuEc, facet for ecto-cuneiform; CuM45, facet for metatarsals IV and V; CuN, cuboidonavicular facet; and pp, plantar process.

COMPARISON

Zhegallo and Shevyreva (1976) compared *Gomphos* primarily with Tertiary rodents such as *Paramys*, *Reithroparamys*, and *Lepotomus*. However, because the type and only specimen known to these authors was a fragmentary lower jaw with m1–m2, distinctive features, such as the second pair of lower incisors and upper dentition, were not available. A more complete comparison was made between *Gomphos* and *Rhombomylus* by Dashzeveg and Russell (1988) in order to facilitate identification of specimens collected from Tsagan-Khushu. They recognized that *G. elkema* differs from *R. turpanensis* by the presence of two lower incisors; by an elongate p3; by a molariform p4 with a much wider talonid; by the lower cheekteeth tending to be subquadrate and the m3 being shorter with no enlarged third lobe formed by the hypoconulid; by the columns formed

by the protoconid and hypoconid being very close together; and by a greater degree of unilateral hypsodonty. According to Dashzeveg and Russell (1988: 151), the upper teeth of *Gomphos* differ from those of *Rhombomylus* by the subcircular contour of P4 in occlusal view; by the presence on P4 of a single centrolabial cusp (four cusps in *Rhombomylus*); by P4–M2 being greatly inflated lingually and more sloping with considerable unilateral hypsodonty; by the absence of a vertical groove between the protocone and hypocone; by the paracone being circular and cusped, becoming lophlike only with advanced wear, and being well separated from the anterior and labial cingula; by the stronger metaconule; and by the presence in the molars of a possible mesostyle. These differences appear constant except that the four-cusped P4 in *Rhombomylus* is not confirmed by a study involving many more complete

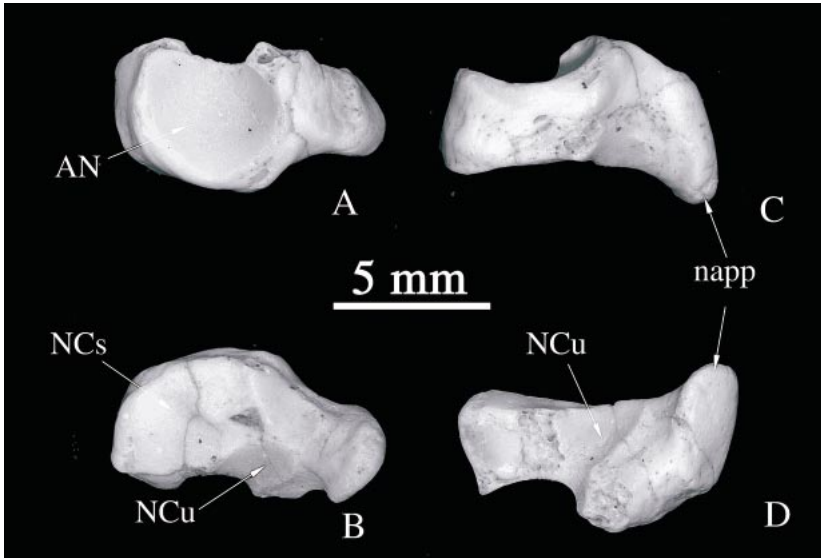


Fig. 10. A–D, Proximal, distal, medial, and lateral views of the right navicular of *Gomphos elkema* (IVPP V13510.4). Abbreviations: AN, astragalonavicular facet on navicular; napp, plantar process of navicular; NCs, articular facet for cuneiforms on the distal surface of navicular; and NCu, naviculocuboid facet on the lateral surface of navicular body.

specimens of *Rhombomylus* (Meng et al., 2003). *Rhombomylus* also differs from *Gomphos* in having a broader hypocone shelf on upper cheek teeth and in lacking a mesoconid on the lower molars. In addition, the molars of *Rhombomylus* have a pair of strong shearing facets between the anterior edge of an upper molar and the posterior surface of the corresponding lower molar. The enamel distribution is thicker along the cutting edges of *Rhombomylus* teeth (Meng et al., 2003). The cheekteeth of *Gomphos* are more suitable for grinding than for shearing, in which a pair of shear facets is not present. The enamel on the occlusal surface of the cheek teeth is also thick in *Gomphos*.

In Dashzeveg and Russell (1988), *Matutinia* was considered to be a junior synonym of *Rhombomylus*. Following recent studies (Ting et al., 2002; Meng et al., 2003) *Matutinia* is regarded as a valid taxon, which differs from *Rhombomylus* in several aspects, such as cheekteeth crowns relatively lower, p3 single-rooted, a partial vertical groove on lingual side of upper cheekteeth, the paracone and metacone more conical and more distantly separated, and the hypocone shelf relatively less well developed. The differenc-

es between *Gomphos* and *Rhombomylus* are applicable to *Matutinia*.

The presence of two pairs of lower incisors readily distinguishes *Gomphos elkema* from species frequently referred to as eurymylids, rodents, *Mimolagus*, and lagomorphs. Double lower incisors of *Gomphos* are shared with *Mimotona* and *Anatolmylus*. *Mimotona* (Li, 1977; Li and Ting, 1985, 1993) differs from *Gomphos* in having smaller body size, less developed mesoconid on the lower molars, shorter trigonid, a more elongated talonid on m3, a less molariform p4, absence of the mesostyle on upper molars, upper cheekteeth anteroposteriorly shorter, and lower degree of hypsodonty.

Averianov (1994: 401) recognized that *Anatolmylus* “Differs from *Mimotona* and *Gomphos* by extremely deep and relatively short horizontal ramus of mandible with distinctly more curved tooth row and incisor (i2). Diastema is short, shorter than in *Mimotona*. The lower and upper cheek teeth with unilateral hypsodonty; p4 molariform. Paraconid on the lower molars virtually absent. On the upper molars paraconule and metaconule absent, the mesostyl[e] small.” Except for depth of the mandible, these differ-

ences between *Gomphos* and *Anatolmylus* are not fully demonstrated because of the fragmentary specimens (Zhegallo and Shevryeva, 1976; Dashzeveg and Russell, 1988; Averianov, 1994).

The astragalus and calcaneus of *Gomphos* are very similar to those of *Mimolagus* (Bohlin, 1951; Bleefeld and McKenna, 1985; Szalay, 1985) in several aspects: the tuber of the calcaneus gradually expanding distally; the calcaneoastragalar and the sustentacular facets being aligned at the same level; the calcaneoastragalar facet being a narrow convex band in a distoproximal orientation, nearly parallel to the long axis of the bone; a distinctive pit being present on the plantar side of the process bearing the calcaneoastragalar facet; astragalonavicular facet on the head of the calcaneus with similar orientation; and the astragalus being ventrodorsally (or anteroposteriorly) narrow. They differ in that in *Mimolagus* a longitudinal ridge is present on the plantar surface of the calcaneus, the head of the astragalus is transversely narrower, the astragalonavicular facet is less medially extended, and the trochlear rims are more sharply delineated. This combination of features makes the ankle bones distinctive from other gliroids, such as *Rhombomylus* (Li and Ting, 1993; Meng et al., 2003), *Tribosphenomys* (Meng and Wyss, 2001), and early rodents (Wood, 1962). The astragalus and calcaneus of *Gomphos* are also different from those that were referred to "Mixodontia sp." from the early Eocene of Kirgizia (Averianov, 1991). The astragalus and calcaneus of "Mixodontia sp." described by Averianov (1991) are more elongate. The general shape and the condition of calcaneoastragalar facet and sustentacular facet aligned at the same level, with the calcaneoastragalar facet being a narrow convex band in a distoproximal orientation, are similar to those of lagomorphs. However, in both *Gomphos* and *Mimolagus* a calcaneofibular facet is absent on the calcaneus and the distal portion of the calcaneus is not elongated. In addition, the astragalus is transversely broader than that of lagomorphs (Dawson, 1958; Szalay, 1985). Nonetheless, the foot bones of *Gomphos* are similar to *Mimolagus* in being more lagomorphlike, not rodentlike.

The head of the astragalus articulates ex-

clusively with the navicular in most eutherians, but in anagalids (Simpson, 1931; Bohlin, 1951) and macroscelideans (Szalay, 1985) it also has a small contact with the cuboid. As in *Gomphos*, the contact is absent in lagomorphs (Szalay, 1985) but is present in *Mimolagus* (Bleefeld and McKenna, 1985; Szalay, 1985).

In most eutherians, the calcaneoastragalar facet is either somewhat rounded or is elongate but oriented diagonal to the long axis of the calcaneus body. In mimotonids (Averianov, 1991), *Mimolagus* (Bohlin, 1951; Szalay, 1985), and lagomorphs the calcaneoastragalar facet is oriented such that the major axis is nearly parallel to the long axis of the calcaneus body. A similar condition is present in *Gomphos*.

The sustentaculum on the calcaneus is anteromedial to the calcaneoastragalar facet and in most eutherian taxa the two facets are separated by a distinctive sulcus calcanei. In contrast, the sustentaculum in lagomorphs is immediately medial to the calcaneoastragalar facet. *Mimolagus* and *Gomphos* are similar to each other and comparable to lagomorphs in this condition.

Primitively, the calcaneus does not extend farther distally than does the astragalus; therefore, the astragalar-navicular articulation and the calcaneus-cuboid articulation are roughly at the same level and the ankle is more flexible in rotation. In some lagomorphs, the calcaneus is distally extended to contact the navicular. The foot bones are more firmly interlocked such that sideward movement of the foot is limited but fore-and-aft movement of the foot is emphasized (Dawson, 1958). In some early lagomorphs, such as *Palaeolagus haydeni* and *Megalagus turgidus*, the astragalus reaches approximately the same distance distally as does the calcaneus; in others, such as *Hypolagus* and the recent leporids, the calcaneus extends farther distally than does the astragalus, making possible a calcaneonavicular contact (Dawson, 1958). The calcaneonavicular contact is not present in ochotonids (McKenna, 1982). The calcaneonavicular facet also occurs on the calcaneus of *Mimolagus* (Bohlin, 1951; Szalay, 1985), suggesting that the calcaneus extended farther distally than did the astragalus.

The calcaneal canal is a perforation present in the mammalian calcaneus to provide channels for small blood vessels. In lagomorphs, the canal starts from the lateral side of the calcaneal tuber as a circular foramen, traverses the calcaneal body diagonally, and exits the calcaneus via an aperture situated between the sustentaculum and the cuboid facet (Bleefeld and Bock, 2002). According to Bleefeld and Bock (2002), the calcaneal canal is a feature that appeared early in the history of this order, and it occurs in all recognized Recent and fossil lagomorph calcanea. The ancientness of the calcaneal canal and its ubiquity among lagomorphs emphasize the monophyly of the order. The canal is greatly reduced, or lost, in extant leporids, which is regarded as a derived lagomorph feature (Bleefeld and Bock, 2002). Because the calcaneal canal is unknown in the calcaneus of any rodent, or other suggested Recent or fossil lagomorph relatives (e.g., macroscelidids, anagalids), Bleefeld and Bock (2002) concluded that the morphological distinctiveness of the earliest recognized pedes of lagomorphs from those of macroscelidids and anagalids may indicate a long evolutionary separation of those mammalian orders.

Mimolagus and *Gomphos* are stem taxa to Lagomorpha and share many derived similarities with lagomorphs (Meng and Wyss, 2001; Meng et al., 2003). The calcaneus does not have the calcaneal canal in either taxa. This indicates that the calcaneal canal characterizes only Lagomorpha, but not Duplicitata that includes Lagomorpha and its stem taxa (Meng and Wyss, 2001). The oldest lagomorph calcanei observed by Bleefeld and Bock (2002) are from the early Oligocene Hsanda Gol Formation of Mongolia. It is probable that in earlier lagomorphs the calcaneus may have had the calcaneal canal. Nonetheless, because the age of *Mimolagus* is roughly early Oligocene (Bohlin, 1951), it seems that the morphological distinctiveness in the calcaneal structure may not adequately indicate the relative timing of the evolutionary separation between Lagomorpha and its stem taxa.

Because several recent phylogenetic studies of Glires have shown that *Gomphos* is a stem taxon to Lagomorpha (Meng and Wyss, 2001; Meng et al., 2003; Meng, in press), we

will not provide additional phylogenetic analyses concerning this taxon in the present study. However, we note that the foot bones of *Gomphos* are apparently similar to those of lagomorphs in several aspects, which undoubtedly strengthens the position of *Gomphos* as a stem taxon to lagomorphs. Our discussion will focus on the implications for faunal correlation of the presence of *Gomphos* in Nei Mongol.

STRATIGRAPHY

LITHOSTRATIGRAPHY: Rock units relevant to the discussion include the Nomogen, Arshanto, and Irдин Manha Formations. The Nomogen Formation was first described by Zhou et al. (1976), who noted the earlier, informal use of the name by the Geological Survey of Inner Mongolia mapping team. At the type locality, Haliut, the formation consists of three levels of approximately 16 m aggregate thickness (reported as 14 m in Russell and Zhai, 1987; see also Meng et al., 1998) and produced a mammalian fauna traditionally considered to be late Paleocene (Zhou et al., 1976; Zhou and Qi, 1978). The formation is mainly composed of red sandy claystone of lacustrine origin (Russell and Zhai, 1987). The bottom of the formation is not exposed.

The second locality where the Nomogen Formation is known is Bayan Ulan, at the northern foot of the Holy Mesa (Meng, 1990; Meng et al., 1998). Qi (1979) formally recognized the Bayan Ulan Fauna for a fossil assemblage derived from this area and assigned these fossiliferous deposits to the "Bayan Ulan Formation", a name first used by the geological mapping team (see also Jiang, 1983; fig. 2). Qi's listing of mammalian taxa from Bayan Ulan did not include detailed stratigraphic information or descriptions of the fossils. In addressing the general stratigraphic context, however, Qi suggested that at Bayan Ulan the "Bayan Ulan Formation" is continuous with the underlying Nomogen Formation. Further, Qi observed that most species from the Bayan Ulan and Nomogen formations are the same, excepting the occurrence of *?Lambdotherium* sp. and *?Heptodon* sp. at Bayan Ulan. The first description of the "Bayan Ulan Formation" at

the Bayan Ulan locality occurs in the summary of the 1:200,000 mapping study on the early Tertiary in the Erlian Basin (Jiang, 1983). Because the "Bayan Ulan Formation" was based primarily on its fossil content, instead of its lithology, the designation of "Bayan Ulan Formation" has been abandoned (Qi, 1987; BGMRNMAR, 1991; Meng et al., 1998). Meng et al. (1998) suggested that the basal beds at Bayan Ulan are the lateral extension of the Nomogen Formation.

The type section of the Arshanto Formation is about 30 km southeast of the Erlian Basin and was first studied in the 1920s (Berkey and Morris, 1924; Mathew and Granger, 1925). At the type locality the Arshanto Formation is a sequence of dark reddish sandy claystone and siltstone beds (Zhou et al., 1976; Russell and Zhai, 1987) and is overlain by the coarser rocks of the Irdin Manha Formation. The base of the Arshanto Formation is not visible. The exposed portion is less than 10 m thick (Zhou et al., 1976). Red beds of similar lithology assignable to the Arshanto Formation are present throughout the basin, but the thickness of the formation varies significantly from one place to another.

In a later study Qi (1987) considered instead that the CAE's "Arshanto Formation" can be divided into three units, the late Paleocene Nomogen beds, the early Eocene Bayan Ulan beds, and the middle Eocene Arshanto beds. Qi grouped the Nomogen and Bayan Ulan beds into the Nomogen Formation, whereas the Arshanto beds and overlying Irdin Manha beds were associated in the Irdin Manha Formation. Although Qi (1987) suggested that the Nomogen Formation (his definition) could be distinguished from the Arshanto beds by the presence of celestite nodules therein, the features of these two units are not otherwise distinctive (Meng, 1990). Also, because the Arshanto and Irdin Manha rocks are lithologically distinctive, Meng (1990) disagreed with Qi's placement of the two sets of deposits into the Irdin Manha Formation. The complexities and uncertainties associated with the definition and division of these units hamper efforts to correlate the early Tertiary red beds in Nei Mongol in general and at Huheboerhe in particular.

At Huheboerhe, the rock sequence potentially contains the conventionally defined Nomogen, Arshanto, and Irdin Manha Formations. A stratigraphic section from the Huheboerhe region was previously published (Jiang, 1983; Qi, 1980), although the section was subdivided differently in the two studies (Meng, 1990; Meng et al., 1998). For the present study, we choose not to assign the lower beds (beds 1 to 11) to any named rock unit, but recognize that the top of these beds is truncated by an erosional surface marking the base of the Irdin Manha Formation (bed 12). In our opinion, this erosional surface and grain-size change represents the most distinctive and regionally traceable stratigraphic datum for this part of the early Paleogene sedimentary package of the Erlian Basin. Contrary to previous studies in this region (Jiang, 1983; Qi, 1987), we do not note evidence for significant sedimentological hiatuses in the Huheboerhe section, with the exception of that marking the base of the Irdin Manha Formation. We do, however, note distinctive stratigraphic changes in the lithologic characteristics of the rocks underlying the Irdin Manha Formation at Huheboerhe. There is a significant color transition between beds 10 and 11 in the above section, and a large number of white calcareous nodules in the bottom of bed 11 are indicative of paleosol formation under conditions different from those during the deposition of the underlying beds. The presumably Bumbanian fauna, dominated by *Gomphos*, occurs in the upper part of bed 10.

BIOSTRATIGRAPHY: The faunas relevant to our discussion include those of the Gashatan and Bumbanian Asian Land Mammal Ages (ALMA). The Gashato fauna of Mongolia comes from Member I of the Gashato (Khashat) Formation at the Ulan-Nur Basin, which is overlain by Members II and III that produced only one mammal taxon, *Gomphos elkema* (Dashzeveg, 1988). These beds were first studied by Morris in 1923 (Mathew and Granger, 1925; Russell and Zhai, 1987). The name Gashato was first published in Mathew and Granger (1925) in describing the Gashato fauna, but without a description or definition for the rock unit. The Gashato Formation was formally proposed in 1927 by Berkey and Morris. The only datable bed at

the type locality, a basalt, was found above the Member II, but dates for the basalt are too contradictory to be of use: one is 51 ± 2 Ma (Dashzeveg, 1988) and the other is 37 ± 1 Ma (Devyatkin 1981, 1994).

The Gashatan ALMA was based on the Gashato and its equivalent faunas, and it was defined by Ting (1998) on the basis of the first appearance of Rodentia as represented by *Tribosphenomys* (but see Meng and Wyss, 1994, 2001; Wyss and Meng, 1996). This definition was considered to be less than felicitous (Beard, 1998) because *Tribosphenomys* is known only from the Bayan Ulan locality (Meng et al., 1994, 1998), although there are specimens collected from Subeng, a locality about 50 km northeast of Bayan Ulan (unpubl. data). Defining the Gashatan on the basis of the first appearance of the more commonly encountered *Prodinoceras* was considered to be more stable and easily recognized. Indeed, among many typical Gashatan species (Dashzeveg, 1988; Meng and McKenna, 1998), *Prodinoceras martyr* is one of the most common taxa. It was found in the Zhigden and Naran members of the Naran Bulak Formation, Mongolia, as well as in the Nomogen Formation at Nomogen (Chow and Qi, 1978), Bayan Ulan (Meng et al., 1998), and Subeng (unpubl. data), Nei-Mongol of China.

Prodinoceras was one of the taxa commonly used to establish the correlation between the Gashatan ALMA and the Clarkforkian North American Land Mammal Age (Szalay and McKenna, 1971; Dashzeveg, 1988; Krause and Maas, 1990), although this correlation may be problematic. *Prodinoceras* was proposed by Matthew et al. (1929) and was thought to be a senior subjective synonym of nine other junior names (Schoch and Lucas, 1985), including *Bathyopsoides* from North America. Although Lucas (1989) considered *Prodinoceras* an indicator of late Paleocene, lumping all these names into a single genus decreases the precision of *Prodinoceras* as an age indicator because it increases the geological age distribution of the taxon. *Prodinoceras*, as defined by Schoch and Lucas (1985), has a distribution from the late Paleocene to early Eocene in North America; consequently, faunal correlations using the genus *Prodinoceras* are less precise

than previously thought. Nonetheless, the faunas that contain the species *Prodinoceras martyr* in central Asia are all considered to be Gashatan equivalent, and the species has not been reported from the younger faunas of the Bumbanian ALMA (Meng et al., 1998; Ting, 1998). Isotopic and paleomagnetic correlation suggests that Gashatan ALMA is entirely restricted to the late Paleocene (Bowen et al., 2002).

The Bumbanian ALMA is based on the Bumban fauna from the Bumban Member of the Naran Bulak Formation, Nemegt Basin (Dashzeveg, 1988). *Gomphos elkema* is one of the typical Bumbanian species and is also known from Members II and III of the Gashato Formation (Dashzeveg, 1988). This species was only known from Mongolia until this study and is not found in any of the Gashatan faunas.

At Huheboerhe, we have found *Prodinoceras martyr* in the lower part of the section and numerous specimens of *Gomphos elkema* in bed 10. Along with *Gomphos elkema*, fragmentary fossils possibly representing *Homogalax* and a creodont are also found in bed 10. Fossils representing later ALMAs (probably Arshantan and Irдинmanhan) are found on the upper part of the section. Based on the presence of fossils with Gashatan and Bumbanian affinities and the traditional views regarding the ages of these faunas, it is possible that the stratigraphic section at Huheboerhe spans the Paleocene–Eocene boundary.

THE PALEOCENE–EOCENE BOUNDARY: The position of the Paleocene–Eocene boundary in Asia has usually been determined by biostratigraphic correlation to North America. In recent years the position of the boundary in North America has shifted relative to the boundary defined in the marine stratotype (Gunnell et al., 1993; Wing, 1984; Archibald et al., 1987; Woodburne and Swisher, 1995), largely due to changes in the operational definition of the boundary. It seems likely that the marine boundary will be formally placed at the position equivalent to the short term warming and carbon-cycle perturbations discussed in the introduction, at about 55 Ma. This position is precisely coincident with the boundary between the Clarkforkian and Wasatchian North American Land Mammal

Ages, when Artiodactyla, Perrisodactyla, and the family Hyaenodontidae all make their first appearance (Bowen et al., 2001). Thus, accepting this definition, the correlation of the Paleocene-Eocene boundary from North America to Asia essentially involves the correlation of this major event in mammalian history between the two continents.

Based on mammalian faunal composition, the Paleocene–Eocene boundary of Mongolia has been suggested to be at the bottom of the Bumban Member within the Naran-Buluk Formation (Dashzeveg, 1988; Ting, 1998). While acceptance of this boundary is perhaps the most obvious choice, existing problems merit discussion. Correlations based on faunal composition implicitly assume the synchronicity of episodes of evolution, extinction, and dispersal at regional to global scales. For basin-scale correlations the uncertainty imparted by this assumption is perhaps small (see, however, Gunnell and Bartels, 2001), but at the continental to global scale geographic and climatic barriers to dispersal and the potential for diachronous extinction of isolated populations represent significant sources of uncertainty. Even though faunal changes occur across the Naran–Bumban boundary (Dashzeveg, 1988), these changes are not in themselves sufficient to indicate the Paleocene–Eocene boundary. Without a temporal framework developed independently of faunal composition, the Naran–Bumban boundary can only be regarded as a boundary between lithological units and between biozones. The recognition of the P–E boundary is a different, unsettled issue.

Independent of the potential problems associated with assuming the equivalence of biostratigraphic and chronostratigraphic boundaries, differences of opinion exist among workers as to the proper correlation of Asian and North American land mammal ages. Although the Clarkforkian–Gashatan intercontinental correlation is commonly cited (Szalay and McKenna, 1971; Dashzeveg, 1988; Krause and Maas, 1990; Meng et al., 1998; Ting, 1998), other opinions exist. Wang et al. (1998) suggested that the Tiffanian–Clarkforkian boundary lies within the Gashatan, so that the Gashatan is correlative in part with the latter part of the Tiffanian, a view supported by Beard (1998). Beard ar-

gued that *Tribosphenomys*, known only from the Gashatan of Asia, is more primitive than its close relative, *Alagomys*, a genus found in the Bumbanian of Asia (Dashzeveg, 1990) and in the Clarkforkian of North America (Dawson and Beard, 1996). He further suggested that this relationship indicates that *Alagomys* likely originated on the Asian continent and dispersed to North America prior to early Clarkforkian time, giving reason to think that the Gashatan record of *Tribosphenomys* in the Bayan Ulan fauna antedates the Clarkforkian record of *Alagomys* at Big Multi Quarry, Wyoming (Dawson and Beard, 1996; Beard, 1998). In contrast, Lucas (1999) has proposed, based on the distribution of coryphodontid pantodonts, that faunas considered here to be Gashatan correlate with the latter part of the Clarkforkian and the early Wasatchian.

Most workers have considered the Bumbanian to be correlative with the North American Wasatchian and the European Sparnacian (McKenna, 1975; Savage and Russell, 1983; Russell and Zhai, 1987; Dashzeveg, 1982, 1988; Krause and Maas, 1990; Stucky, 1992; Meng and McKenna, 1998; Ting, 1998). However, Beard (1998) argued that this correlation likely underestimates the antiquity of at least some Bumbanian mammal faunas, which more likely correlate with the North American Clarkforkian. The traditional correlation of Bumbanian with Wasatchian is based primarily on the appearance of Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae in the Bumban fauna (Dashzeveg, 1988). The inverse relationship of multituberculate and rodent diversity (i.e., extinction of multituberculates and radiation of rodents) across the Naran–Bumban boundary is also comparable to that at the Paleocene–Eocene boundary in North America and Europe (Krause, 1986; Stucky, 1992; Legendre and Hartenberger, 1992). Beard (1998) pointed out that phylogenetic and biostratigraphic data support an Asian origin for Perissodactyla, Artiodactyla, euprimates, and Hyaenodontidae (the East of Eden model), all of which share North American first appearance datum (FADs) at the beginning of the Wasatchian and European FADs at the beginning of the Sparnacian. Among these taxa, hyaenodontids and questionable peris-

sodactyls are known from the Gashatan Bayan Ulan fauna (Meng et al., 1998). Beard (1998) argued that if these taxa did indeed originate in Asia, there is no reason to assume that their earliest records on that continent are synchronous with their North American and/or European FADs. Therefore, the Bumbanian may correlate, at least in part, with the North American Clarkforkian, and the P-E boundary may well be within the Bumbanian. A recent chronostratigraphic study shows that the Bumbanian ALMA cannot confidently be assigned a later Paleocene age, but neither can it be confidently assigned in its entirety to the early Eocene (Bowen et al., 2002).

Thus, the presence of Gashatan and Bumbanian taxa suggests that the Huheboerhe section may contain the Paleocene–Eocene boundary and that it is also possible that the epoch boundary may lie above the *Gomphos* level. Assuming that the climatic changes that affected the marine realm at the end of the Paleocene were manifested in the Asian interior, these may have forced sedimentological changes in the Erlian Basin. We therefore suggest that likely locations for the placement of the Paleocene–Eocene boundary in our section include the contact between beds 10 and 11, which is above the *Gomphos* assemblage, or at the unconformity at the base of the Irdin Manha Formation (also above the *Gomphos* level). Alternatively, the Paleocene–Eocene transition may not be expressed as a significant lithological boundary at Huheboerhe, and it may occur within bed 10 or in the underlying strata, predating the deposition of the *Gomphos*-bearing sediments. Our ongoing isotope and paleomagnetic studies may help to pinpoint the Paleocene–Eocene boundary in the Huheboerhe section, clarifying the relationship between the Bumbanian Land mammal age and the Paleocene–Eocene boundary.

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