

**THE CTENODACTYLIDAE (RODENTIA) FROM THE OLIGOCENE
OF ULANTATAL
(INNER MONGOLIA, CHINA)**

by

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Key-words: Ctenodactylidae, Rodents, Oligocene, Mongolia, Adaptative radiation.

ABSTRACT

This paper proposes a systematic revision of the Oligocene Mongolian Ctenodactylidae, on the basis of abundant material obtained by screen/washing operations in stratified localities of the Ulantatal area (Inner Mongolia) (UTL1, 2, 3, 4, 5, 7, 6 & 8). A Chinese-German team has collected several thousands of isolated rodent teeth, and a number of fragmentary jaws. A new genus is identified (*Alashania* nov. gen. *tengkoliensis* nov. sp.), and eight former species are reevaluated, *Karakoromys decessus*, *Tataromys sigmodon*, *T. minor*, *T. plicidens*, *Yindirtemys ulantatalensis*, *Y. bohlini*, *Y. deflexus*, with several synonymies. A new *Yindirtemys* species is described: *Y. shevyrevaevae* nov. sp. and another one close to that: *Y. aff. shevyrevaevae* nov. sp. Four new species, which are rare in the localities, remain in open nomenclature because they are not well-represented. *Yindirtemys* differs from the other genera by the permanence of crescentic structures, while the other genera show a general reduction of the trigonoid area (= anterior valley). We define a range of size variation for each well documented population. Although the dental morphology shows a wide range of variation, given that transitional morphologies occur in a single locality, it is possible to provide a clear definition for most species. We show that dental patterns of the different genera can be derived from the pattern of *Karakoromys*. As a number of Tataromyinae have been determined in several localities from China, Kazakhstan and Mongolia, usually on the basis of scarce material, or surface collections, the present study would be used to re-evaluate their attribution inasmuch as the taxa are now placed in the Oligocene stratigraphy. The diversity of sizes and forms reflects the adaptive radiation of the family during the Oligocene, within a forested environment where the vegetation was probably abundant.

RESUME

Cet article propose une révision des Ctenodactylidae de la région de Ulantatal (Mongolie chinoise). Une expédition Sino-Allemande a échantillonné 7 localités en superposition stratigraphique (UTL1, 3, 4, 5, 7, 6 & 8). Plusieurs milliers de dents isolées et quelques mâchoires de Ctenodactylidae ont été ensuite obtenus par lavage-tamassage des sédiments. Au moins une nouvelle espèce représentant un nouveau genre a été identifiée (*Alashania tengkoliensis*), et 8 espèces précédemment décrites ont été redéfinies (*Karakoromys decessus*, *Tataromys sigmodon*, *T. minor*, *T. plicidens*, *Yindirtemys ulantatalensis*, *Y. bohlini*, *Y. shevyrevaevae* nov. sp., *Y. deflexus*), tandis que des synonymies sont proposées. Quatre nouvelles espèces, rares dans les localités, sont laissées en nomenclature ouverte. Le genre *Yindirtemys* diffère des autres genres par la permanence des structures sélénodontes, tandis que les autres genres montrent une plus ou moins forte réduction de la région du trigonoïde. L'étendue de la variation de taille est définie pour chaque population suffisamment abondante. La variation des caractères morphologiques peut aussi être importante, mais elle peut être appréhendée grâce aux formes de transition existant au sein des populations. Les schémas dentaires des différents genres peuvent dériver du plan dentaire de *Karakoromys*. Comme de nombreux Tataromyinae ont été signalés dans diverses localités de Chine, du Kazakhstan et de Mongolie, souvent sur la base de matériel isolé, ou de récoltes de surface, la présente étude pourra être utilisée pour ré-évaluer leur attribution taxonomique, d'autant plus que les taxons définis sont replacés dans la stratigraphie de l'Oligocène. La diversité, tant des formes que des tailles, permet de décrire la radiation adaptative de la famille à l'Oligocène, dans un environnement où les ressources végétales, et les insectes, devaient être abondants.

INTRODUCTION

The paleontological potential of the Ulanatal area was discovered in the late 70s of the last century by teams of Chinese paleontologists. This is situated about 60 km north of the small town Bayanhaote in the county Alxa Zuoqi, Nei Mongol (Inner Mongolia). Initial geological description of the area was provided by Huang (1982) and extensive surface collection followed. The larger part of the fossil micromammals found during this period has been studied and published by Huang in several articles (insectivores 1982, ctenodactylid rodents 1985, and lagomorphs 1986). Later, Wang (1994, 1997) revised several taxa erected by Huang. In 1987, a Chinese/German expedition supported by the Academia Sinica, China, and the Max Planck Gesellschaft, Germany, returned to the area. During this time geological study and extensive screen/washing operations of fossiliferous sediments were undertaken. Considering the material obtained, only a small part has been published thus far (zapodids rodents: Huang, 1992). In this paper, we describe the main part of the ctenodactylid rodents, which appears to be the more diverse rodent family. The ctenodactylid material from Ulanatal comprises species nearly entirely belonging to the subfamily Tataromyinae. Only few medium hypsodont specimens, which show a combination of characters unknown from that taxonomic unit, are not included in the Tataromyinae. Their dental characters are much more consistent with the *Sayimys*-group, belonging to the subfamily Ctenodactylinae.

Geological Setting

During the Chinese/German expedition to the Ulanatal area in 1987 fossiliferous horizons suitable for washing and screening were found, and geological observations have produced a lithostratigraphy and a geological map of the most interesting part of the Ulanatal area (fig. 1 and 2). Due to the very slight dipping of the beds and the gentle topography with small hills and gullies, the thickness of the exposed sediments could not easily be measured. Nevertheless, it seems that the thickness of 20 meters given by Huang (1982), and reported in Russell & Ren-Jie (1987), is underestimated. As can be seen from the location of the section in his topographical sketch (fig. 1), Huang did not get the complete sequence of the sediments. In a later paper (1992) the same author mentions a total thickness of the series of more than 100 meters. The field data taken during the work of the Chinese/German expedition of 1987 indicate a thickness probably about 60 meters.

The Paleogene sediments in the Ulanatal area represent a coarsening upward sequence. Following the vertical facies development and the change of color of the beds, three lithostratigraphical units could be distinguished. This made it possible to delimit the stratigraphic position of the fossil horizons exploited. A closer study of well-exposed parts revealed that relevant concentrations of microvertebrates could be found in small shallow channels of about five to eight meters transversal extension. Their fill mainly consisted of reworked clay pebbles with intraclast diameters of about one to two centimeters diameter and admixed white bone fragments of about the same size. The channels with their intraformational fillings are indicative of a low energy regime of

transportation so that it can be supposed that the fossil accumulations are not derived from very far sources.

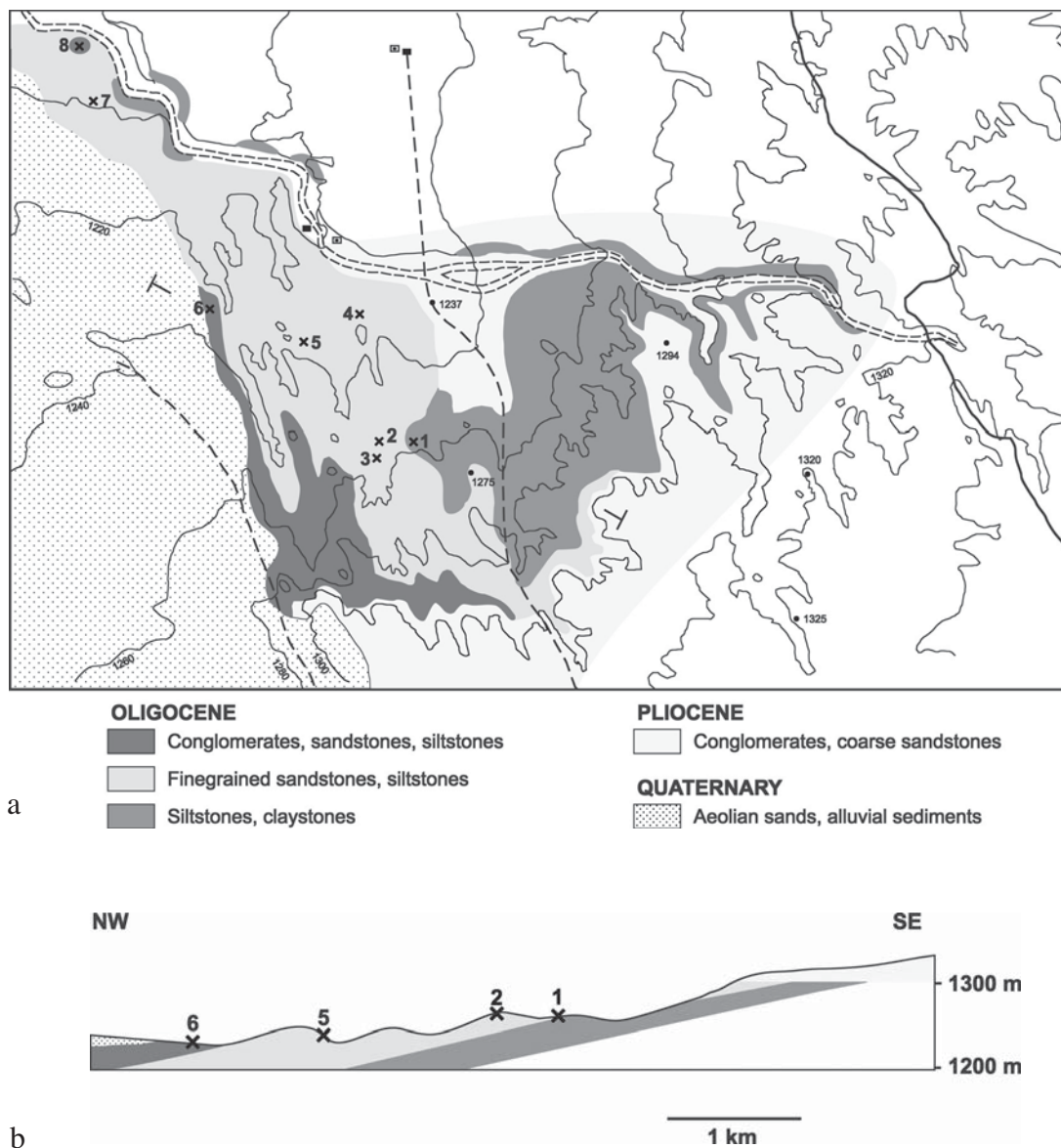


Figure 1.— Geographical and lithostratigraphical localization of the fossiliferous localities in the Ulantatal area (Inner Mongolia, China); 1a: map; 1b: schematic section.

It seems that the sedimentary conditions did not change significantly during the deposition of the larger part of the series. Only at locality UTL8 can a marked facies change be observed. There, conglomeratic coarse quartz sand with an erosive base is exposed. It occupies the top of a small hill that forms the northwestern extreme of the exposed area. The bed is most probably part of a larger channel that unconformably overlies the rest of the deposited sequence. From the abrupt facies change it can be

inferred that a relevant period of non-deposition preceded the formation of the channel. The gap seems to correspond to a shift of the sedimentary parameters leading to modified drainage conditions in the area. The channel is considered to belong to the uppermost sedimentary unit. Possibly it even corresponds to a younger event. Its fossil content also supports this conclusion (Fig. 2).

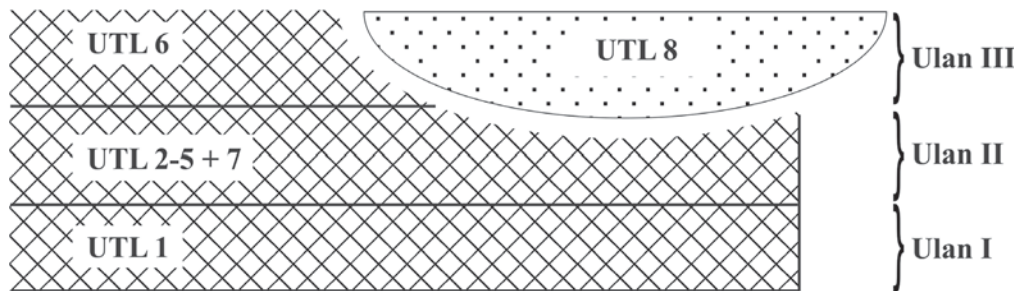


Figure 2.— Biostratigraphy of the Ulan area Oligocene localities. Three biozones are defined, Ulan I (UTL1) = partly lower Oligocene; Ulan II (UTL2, 3, 4, 5, 7) = early Upper Oligocene; Ulan III (UTL6,8) = late Upper Oligocene.

The study of the ctenodactylids from these fossiliferous localities leads to suggest that the Ulanatal sequence (notwithstanding its modest thickness) covers a large part of the Oligocene. More reliable indications will be possible through correlation with the Oligocene micromammal bearing series in Central Mongolia, which has radiometric dates (Höck *et al.* 1999). The study of the ctenodactylid rodents found in these beds will be published soon (Schmidt-Kittler *et al.* in prep).

	UTL1	UTL3	UTL4	UTL5	UTL7	UTL6	UTL8
<i>Karakaromys decessus</i> Matthew & Granger 1923	+						
<i>Tataromys sigmodon</i> Matthew & Granger 1923	+		+		+		+
<i>Tataromys minor</i> (Huang 1985)	+	+	+	+	+	+	
<i>Tataromys plicidens</i> Matthew & Granger 1923	+		+	+	+		
<i>Alashania tengkoliensis</i> nov. gen., nov. sp.	+		+				+?
<i>Yindirtemys ulantatalensis</i> (Huang 1985)	+		+		+	+	+
<i>Yindirtemys bohlini</i> (Huang 1985)			+			+	+
<i>Yindirtemys shevyrevae</i> nov. sp.	+		+		+	+	+
<i>Yindirtemys</i> aff. <i>shevyrevae</i> nov. sp.						+	
<i>Yindirtemys deflexus</i> (Teilhard de Chardin 1926)						+	+
Tataromyinae nov. gen.1, nov. sp.1	+	+	+	+			+
Tataromyinae nov. gen. 1 or 2, nov. sp.2						+	
Tataromyinae nov. gen.1 or 2, nov.sp.3							+
Tataromyinae nov. gen.1 or 2, nov.sp.4							+
Semi - hypsodont ctenodactylid	+		+				
Minimum Ctenodactylid specific diversity	9	2	9	3	5	7	9

Table 1.— Localities and tataromyine ctenodactylid occurrences in Ulanatal area.

MATERIAL AND METHODS

Before screen/washing operations at the different localities, surface collections were undertaken. The dental material gathered by this approach was systematically separated from the remains obtained by washing, and were identified "a" and "b", respectively. The description in the present article is exclusively limited to the screen-washed material. As such, the index specification "b" is not given in the text. It can appear, however, in the figures. As it is common for material obtained by screen-washing, fossils predominantly consist of isolated teeth. Jaw fragments are relatively rare.

The teeth were drawn using a camera lucida on a Leica binocular microscope and photographs were taken using a stereoscan Jeol 6300F.

Terminology and definition of morphotypes

The terminology used is basically that proposed by Wang (1997), but modified with regard to several elements. In lower teeth the central cuspid sometimes developed at the junction of the ectolophid with the posterior arm of the protoconid (e. g. in *Yindirtemys*) is called a mesoconid. The labial (= buccal) and lingual valleys on upper molars are named "synclines" and "sinuses", respectively, and in lower molars they are called "sinusids" and "synclinids" (fig. 3). The small anterior valley is named "trigonoid", as we demonstrate that it is not homologous to the primitive trigonoid. Teeth have been measured (maximum width and length: see marks on figure 3) with a Nikon measuroscope 10.

We have observed variations in the junctions and in the orientation of the posterior lophes of the upper molars: for comparisons, we have defined five morphotypes (A, B, C, D, E: fig. 4)



Figure 3

3a.— Terminology for occlusal dental morphology of the upper and lower cheek teeth of primitive ctenodactyl rodents (modified after Wood and Wilson [1936] and Wang [1997]); a) upper left premolar, b) upper left molar, c) lower left premolar, d) lower left molar.

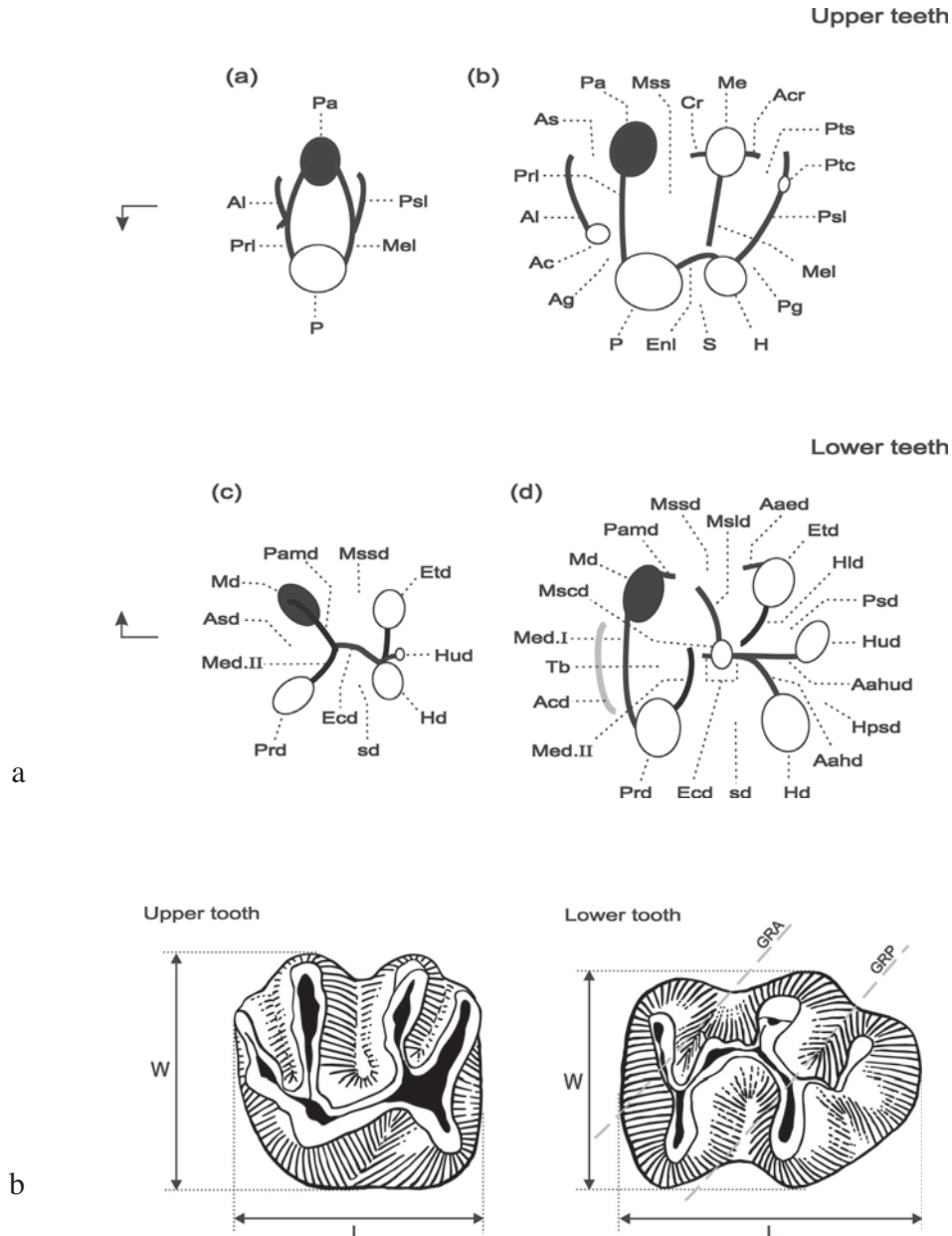
Upper teeth: **Ac:** anterocone, **Acr:** anticrochet, **Ag:** anterior groove, **Al:** anteroloph (=anterior cingulum), **As:** anterior syncline, **Cr:** crochet, **Enl:** endoloph, **H:** hypcone, **Me:** metacone, **Mel:** metaloph, **Mss:** meosyncline, **P:** protocone, **Pa:** paracone, **Pg:** posterior groove, **Prl:** protoloph, **Psl:** posteroloph, **Ptc:** postrerocone, **Pts:** posterior syncline, **S:** sinus.

Lower teeth: **Aaed:** anterior arm of entoconid, **Aahd:** anterior arm of hypoconid, **Aahud:** anterior arm of hypoconulid, **Acd:** anterior cingulid, **Asd:** anterior sinusid, **Ecd:** ectolophid, **Etd:** entoconid, **Hd:** hypoconid, **Hld:** hypolophid (= anterior arm of entoconid), **Hpsd:** hyposinusid, **Hud:** hypoconulid, **Md:** metaconid, **Med I:** metalophid I, **Med II:** metalophid II (= posterior arm of protoconid), **Mscd:** mesoconid, **Mslid:** mesolophid, **Mssd:** mesosynclinid, **Pamd:** posterior arm of metaconid, **Prd:** protoconid, **Psd:** posterior synclinid, **Sd:** sinusid, **Tb:** trigonoid basin.

3b.— References for measurement and position of occlusal wear grooves on lower molars. GRA: anterior groove; GRP: posterior groove.

Collections

The material belongs to the collection of the Institute of Vertebrate Paleontology, Beijing (IVPP, China), and it is presently housed in München (Germany). For this paper, the specimens are numbered after the abbreviation of their locality in Ulanatal (UTL1, UTL3, UTL4, UTL5, UTL6 and UTL8). They will be later integrated in the catalogous of the IVPP collections.



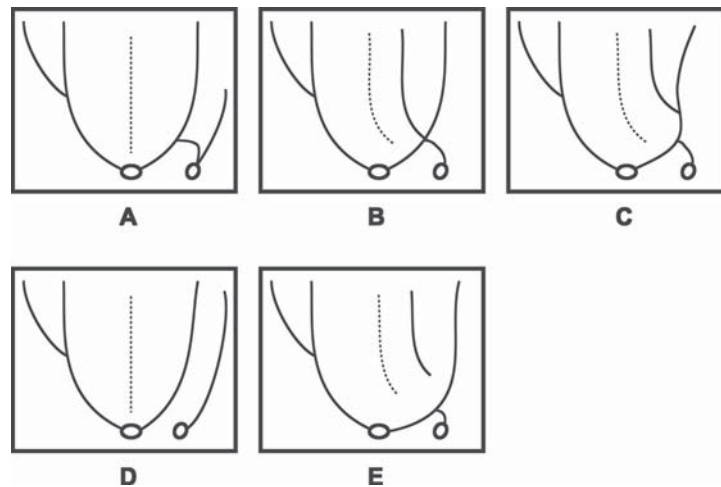


Figure 4.— Morphological variations of the posterior part of molars of Tataromyinae. Morphotype A: metaloph curved forward and directly connected to the protocone; hypocone linked to the metaloph by its anterior arm; short posteroloph connected to the posterior arm of the hypocone. Morphotype B: metaloph curved backward and connected to the posteroloph-anterior arm of the hypocone junction. Morphotype C: the same, but the junction between the metaloph and the posteroloph is moved labially. Morphotype D: like morphotype A, but hypocone separated from the metaloph. Morphotype E: orientations like morphotype C, but the metaloph do not reach the posteroloph.

Taxonomy

Thanks to the diversity and abundance of some populations, the morphological parallelisms and the variation of tooth sizes along the dental rows can be well assessed. We have followed several steps in our analyses. First, within two rich localities (e.g. UTL4 and UTL7), using the preserved lower and upper jaws as morphological standards, the populations of isolated teeth of different sizes were separated. Then the distinct samples were measured and the clusters tested, taking into account the size, the characters of cusps and lophs and the wear facets.

A common difficulty in tataromyine taxonomic descriptions is that the genera or species have been erected on upper jaws, isolated upper teeth, lower jaws or isolated lower teeth. So, the morphological variability within one population is often ignored. Sometimes in the diagnoses of species (e. g. in Wang 1997), the characters and sizes of specimens of different localities, for which contemporaneity is not well established, are mixed together.

Table 2 displays the dental characters found in the various species and genera arranged corresponding to their primitive or derived state. Table 3 groups features as they characterize key genera.

<i>Primitive dental characters</i>	<i>Derived dental characters</i>
<i>General:</i>	<i>General:</i>
1-Swollen cusps	1-Cusps compressed into lophs or crescentic cusps and lophs
2-Incomplete lophs and lophids	2-Continuous lophs and lophids
3-P3	3-P3 lost
4-Occurrence of p4-P4 and dp4-DP4	4-Permanent deciduous dp4 - DP4
5-Small talonid on P4-p4	5-Reduced P4 - p4 (reduced talonid)
6-non-molarized dp4-DP4	6-molarized dp4 - DP4
7-M3-m3 shorter than M2-m2	7-M3-m3 longer than M2-m2
<i>Lower teeth:</i>	<i>Lower teeth:</i>
8-Ectolophid low, connected only at the bottom of the posterior arm of the protoconid and at the anterior arm of the hypoconid	8-Ectolophid reduced at a junction between the posterior arm of the protoconid with the anterior arm of the hypoconid or Ectolophid high,
9-Ectolophid intermediate between lingual position and medial position	9-Ectolophid central or lingual
10-Mesoconid low, localized at the middle of the ectolophid	10-Mesoconid high, closer to the posterior arm of the protoconid or absent
11-Hypoconulid more or less medial and prominent	11-Hypoconulid linked with entoconid or anterolingual arm of hypoconid
12-Trigonoid well developed in comparison to talonid	12-Trigonoid reduced
13-Trigonoid higher than talonid	13-Talonid as high as Trigonoid
<i>Upper teeth:</i>	<i>Upper teeth:</i>
14- Metaconule present	14-Metaconule absent
15-Protocone close to hypocone, sometimes connected by an endoloph	15-Protocone distant to hypocone, both connected by the posterior arm of the protocone more (long sinus) or less oblique (short sinus)
16-Incomplete metaloph	16-Complete metaloph
17-Lophs transverse, with metaloph connected with the posterior arm of the protocone (morphotypes A, D)	17-Metaloph curved posteriorly (morphotypes B, C, E)

Table 2.— Primitive and derived states of dental characters of the studied species.

SYSTEMATICS

<i>Tataromys</i>	<i>Alashania</i> nov. gen.	<i>Yindirtemys</i>	nov. gen. indet 1
1-Cusps and cuspids compressed; 2- Thin lops and lophids; 3-No crescentic structures	1-Cusps and cuspids less compressed; 2-Lops and lophids less thin; 3-No crescentic structures	1-Cusps and cuspids swollen, prominent 2-Lops and lophids generally low and short 3-A part of cusps (cuspids) and lops (lophids) crescentic	1-Cusps and cuspids compressed; 2- Thin lops and lophids; 3-No crescentic structures
4-Wear nearly horizontal; one main groove on the lower molars; 5-DP3 absent 6-Upper P4 of the same width of M1 7-Anterocone weak, or not prominent within the anteroloph; 8-Anteroloph short, connected with the protocone, with anterosinusid generally absent or weak; 9- Protocone arms generally strongly asymmetrical 10- Short sinus 11-Morphotypes B and C (metaloph posteriorly curved linked to the posteroloph);	4-Cusp profiles worn in open angle (close to 90°); wear pattern on lower molars with two grooves; 5-DP3 6-Upper P4 of the same width of M1 7-Anterocone weak a few prominent in the anteroloph; 8-Anteroloph short, connected with the protocone, with anterosinusid generally absent or weak; 9- Protocone arms generally a few asymmetrical 10- Short sinus 11-Morphotypes A and D (metaloph and protoloph parallel, generally connected with the protocone); morphotypes B rares (only on some M3) 12- Posteroloph prominent 13-Lingual part of the posteroloph sometimes inflated in a posterocone on M3 14-Mesoconid reduced or absent 15-p4 with labial entoconid	4-cusp profiles worn in more acute angle (less than 90°); wear pattern on lower molars with two grooves 5-DP3 6-Upper P4 of the same width of M1 7-Anterocone strong, prominent in the anteroloph; 8-Anteroloph often short and low; with anterosinusid well individualized; 9- Protocone arms generally a few asymmetrical 10-Sinus relatively long 11-Morphotypes A (generally on M1-2) and B (on main M3) 12- Posteroloph prominent 13-Lingual part of the posteroloph sometimes inflated in a posterocone on M3 14-Mesoconid generally well developed 15-p4 with labial entoconid	4-Cusp profiles worn in more acute angle (less than 90°); wear pattern on lower molars with two grooves 5-DP3 absent ? 6-Upper P4 wider than M1 7-Anterocone strong, prominent in the anteroloph; 8-Anteroloph often short and low; with anterosinusid well individualized; 9- Protocone arms generally symmetrical (V shaped) 10-Sinus relatively long 11-Mainly morphotypes D, (sometimes F in M1), B and C in M3 12- Posteroloph prominent 13-Lingual part of the posteroloph sometimes inflated in a posterocone on M3 14-Mesoconid absent 15-p4 with median entoconid due to lack of hypoconid 16-Ectolophid short and lingual 17-Trigonoid basin absent
16-Ectolophid of molars straight and more or less lingually situated; 17-Trigonoid basin present, more or less reduced within one population, and along the dental row; 18-Hypoconulid always connected at the posterior arm of the hypoconid.	16-Ectolophid of molars straight and lingually situated; 17-Trigonoid basin absent 18-Hypoconulid connected with the entoconid, by a loph parallel to the hypolophid, making a long and narrow hyposinusid at least on dp4 and m1	16-Ectolophid in the mid part of the lower molars to the lingual 1/3 of the tooth 17-Wide Trigonoid basin, closed or labially open 18-Hypoconulid always connected at the posterior arm of the hypoconid	16-Ectolophid short and lingual 17-Trigonoid basin absent 18-Hypoconulid connected with the entoconid, by a loph parallel to the hypolophid, making a long and narrow hyposinusid on all dp4 and molars, except a few m3

Table 3. — Key dental characters of the genera described from the Ulanatal area.

Subfamily TATAROMYINAE LAVOCAT, 1961

Included genera: *Karakoromys* MATTHEW & GRANGER, 1923; *Tataromys* MATTHEW & GRANGER, 1923; *Yindirtemys* BOHLIN, 1946; *Alashania* nov. gen.; ? *Euryodontomys* WANG, 1997.

Karakoromys represents a primitive evolutionary stage of the Tataromyinae. Wang (1994) places the genus in a new subfamily, the Karakoromyinae, considering that it is also a primitive grade for Ctenodactylinae, with which it shares supposed derived characters. The so-called derived characters are "wide cheek teeth, large hypocone, well developed entoloph and relatively extended posteriorly posterior arm of the protoconid". These features are not distinctive at the subfamily level. The wide cheek teeth and the large hypocone are also seen in the Tataromyinae. The "entoloph" is not in a lingual position; it corresponds to the posterior arm of the protocone, more or less oblique and backwards displaced in *Karakoromys* as in the Tataromyinae. It is lower in *Karakoromys* than in the other Tataromyinae. The posterior arm of the protoconid is extended posteriorly when the trigonoid is wide: that can be the case in *Karakoromys*, as it does in some Tataromyinae. Wang (1997) describes another genus from Ulanatal area, *Euryodontomys*, with a wide trigonoid, and the figure of the holotype shows a triangular unit at the place of the mesoconid. She underlines similarities with *Karakoromys* that she considers as derived. Among them: the posterior extension of the posterior arm of the protoconid, the "cone" shaped entoconid, and the sinus "less" oblique. None of these characters are derived characters. The first is related with the central position of the ectolophid and the wide trigonoid, and the second and the last are linked to the bunodonty and brachyodonty. All of them appear primitive for Tataromyinae. The characters and the figures given by Wang are insufficient to decide of the validity of the genus and of the assemblage between upper and lower teeth. They do not allow a reliable comparison with the material described here.

Genus *KARAKOROMYS* MATTHEW & GRANGER, 1923

Type species: *Karakoromys decessus* MATTHEW & GRANGER, 1923

Karakoromys decessus MATTHEW & GRANGER, 1923

Holotype and type locality: AMNH19070, "lower jaw, both rami with cheek teeth and left incisor complete", from Hsanda Gol Formation, red beds, Loh (Central Mongolia)

Stratigraphical and geographical range: Early Oligocene, Ulan Tatal formation: level Ulan I, in the Ulan Tatal area (Western Inner Mongolia, China); Wulanbulage Formation and Buran formation, Level A & B in the Valley of lakes, Hsanda Gol Formation (Central Mongolia), Kazakhstan.

Original diagnosis: "p4 present, much smaller and simpler than molars. Molars increasing slightly in size from first to third, moderately brachyodont, longer than wide,

the crown with high transverse crests, a principal anterior (trigonid) and posterior (talonid) crest connected by a commissure, and a hypoconulid crest extending posterointernally from a point on the outer half of the talonid crest. P4 with a single transverse crest and a wide but short posterior heel"

Emended diagnosis (Wang, 1997): Sphenopalatine foramen situated above junction of P4 and M1; wide metaloph with or without distinct metaconule on upper molars; metaconid usually isolated and hypoconulid usually distinct on p4.

New emended diagnosis: Cheek teeth brachyodont; low endoloph on upper molars; metacone only weakly connected to the posteroloph; lower premolars with well-developed hypoconid; lower molars and fourth deciduous premolar with ectolophid forming a protruding angle; no connection between ectolophid and metaconid.

Material and measurements:

1 m2 from UTL1 (1.97 mm x 1.55 mm) and 1 m3 (1.96 mm x 1.53 mm)

Description (Fig. 5)

Only two lower molars are preserved, from locality UTL1. Because they are still unworn and perfectly preserved, the characters can be assessed in details. The cusps are slightly bunodont and sharpened at their tip. The ectolophid is low and descends rather steeply from the protoconid and hypoconid to the center of the tooth. Its lingualmost extension does not pass beyond the sagittal middle axis of the crown. There is no trace

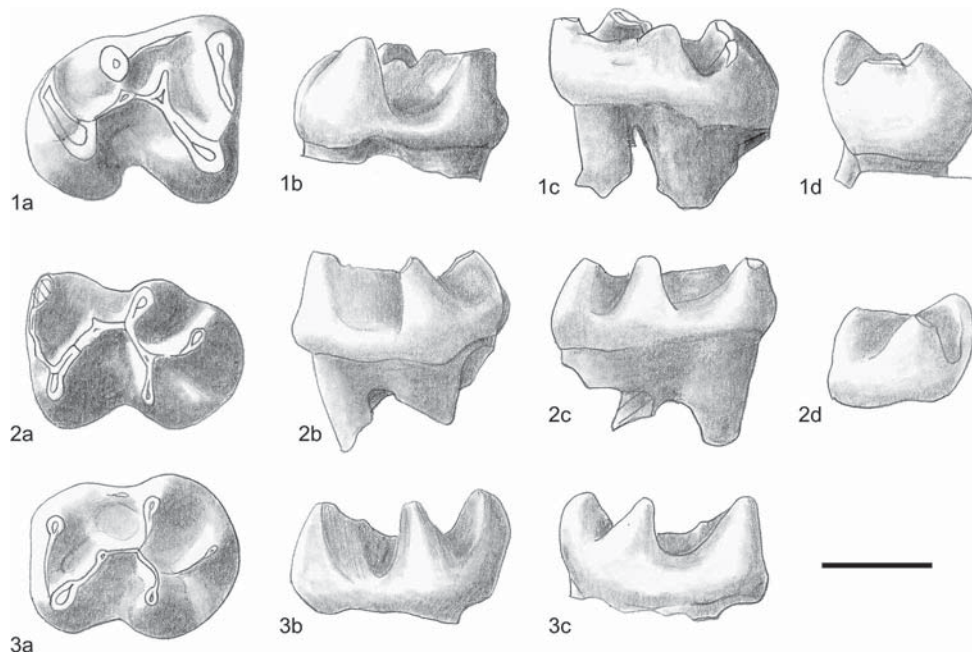


Figure 5.— *Karakoromys decessus* from UTL1, m1-2 and m3, compared to m3 of *K. decessus* from locality TGR-A/13, n°110/0001 (Valley of Lakes, Central Mongolia): 1: UTL1-1, right m3, 1a: occlusal view, 1b: labial view, 1c: lingual view, 1d: front view; 2: TGR-A/13, n°110/0001, left m3, 2a: occlusal view, 2b: labial view, 2c: lingual view, 2d: front view; 3: UTL1-2, left m2, 3a: occlusal view, 3b: labial view, 3c: lingual view.

of a connection between the ectolophid and the metaconid. The connective crests attaching the entoconid (hypolophid) and the hypoconulid to the ectolophid (anterior arm of the hypoconulid) are only weakly developed. The metalophid-I is weak and rather low. On the m3, the hypoconulid is connected closely to the hypoconid: there is no clear hyposinusid.

Discussion

The characters of the described isolated teeth clearly correspond to the typical features found in the lower molars of *Karakoromys decessus*. With this, there is no doubt about the identification of this species. No further dental material of *Karakoromys decessus* is documented from UTL1 or any other of the exploited Ulantatal localities. Huang (1985) described a mandible fragment found in the area during surface collection as belonging to the same species. In studying the original specimen, it could be ascertained that the determination is right. Given that the very rich localities UTL4 and UTL7 overlying UTL1 did not yield any trace of that taxon, it can be concluded that the *Karakoromys* lineage became extinct in the lower part of the Ulantatal section. This means that Huang's specimen comes probably from a rather low sedimentary level of the Ulantatal area.

Genus *TATAROMYS* MATTHEW & GRANGER, 1923

Type species: *Tataromys plicidens* MATTHEW & GRANGER, 1923

Included species: *T. sigmodon* MATTHEW & GRANGER, 1923; *T. minor* HUANG, 1985

Diagnosis (Wang, 1997, p. 8): "Dorsal part of the frontal shorter than nasal, interparietal large and triangular in form, temporal fossae large, temporal crest distinct but lacking temporal foramen, orbit large and situated completely lateral to frontal, masticatory and buccinator foramina separated, palate comparatively wide, maxilla long and palatine shift posteriorly, posterior palatine foramen located at maxillary-palatine suture opposite to M2, choana wide; cheek teeth brachydont to moderately high-crowned, with compressed cusps and thin lophs; P4 protoloph straight or slightly curved, anterior cingulum weakly developed: on upper molars protoloph transverse and slender; p4 with long and lingually situated ectolophid and wide, U-shaped mesosinusid and sinusoid; on lower molars trigonid short, posterior arm of protoconid narrow, with no swollen middle and short lingual joining with metaconid, trigonid basin small, closed or absent, ectolophid straight and lingually situated, mesosinusid wide and shallow, sinusoid deep, hypoconid, entoconid, hypoconulid flat and anterior cingulum absent."

Emended diagnosis : "*Dorsal part of the frontal shorter than nasal, interparietal large and triangular in form, temporal fossae large, temporal crest distinct but lacking temporal foramen, orbit large and situated completely lateral to frontal, masticatory and buccinator foramina separated, palate comparatively wide, maxilla long and palatine shift posteriorly, posterior palatine foramen located at maxillary-palatine*

suture opposite to M2, choana wide"; incisive foramen ending opposite of P4; palate wider than the molars; cusps and cuspids compressed; loph and lophids thin; wear nearly horizontal; only one main groove on the lower molars; anterocone weak, or not prominent within the anteroloph; anteroloph short, connected with the protocone, with an antesisinus generally absent or weak; short sinus; morphotypes of molars B and C (metaloph posteriorly curved and linked to the posteroloph); ectolophid of molars straight and more or less lingually situated; trigonoid basin more or less reduced within one population, and along the dental row; hypoconulid always connected at the posterior arm of the hypoconid.

***Tataromys sigmodon* MATTHEW & GRANGER, 1923**

Synonymy: *Leptotataromys gracilidens* BOHLIN, 1946; *Leptotataromys gracilidens* BOHLIN, in HUANG, 1985; *Tataromys sigmodon* MATTHEW & GRANGER, in WANG, 1997.

Matthew & Granger (1923) defined the species, on the basis of a palate showing the two tooth rows, from the Hsanda Gol Formation (Loh), as being smaller than *T. plicidens* from the same formation. Later, Bohlin (1946) erected the genus *Leptotataromys* and the species *gracilidens* for a mandible with two teeth from Shargaltein (Sh 35) of the same size as *T. sigmodon*. Huang (1985) described as *Leptotataromys gracilidens* some lower and upper jaws, and isolated teeth from the Ulantatal Formation.

On the bases of two skulls and their associated lower jaws, Wang (1997) put in synonymy both genera *Tataromys* and *Leptotataromys*. She considered that the Ulantatal population described by Huang as *L. gracilidens* includes the morphotype and size of *T. sigmodon*. She named this population *T. sigmodon*. We agree on the basis of the characters of the holotypes, considering the variation of two populations stratigraphically controled, UTL7 and UTL4. The following description of the upper tooth variations includes indeed the characters of the teeth of the holotype palate of *T. sigmodon*, as well as the variations of the lower m2 thought to typify *L. gracilidens*.

	n	Length			width		
		minimum	maximum	average	minimum	maximum	average
p4	29	1,14	2,27	1,87	1,28	1,92	1,57
m1	48	2,40	3,04	2,65	1,60	2,13	1,87
m2	73	2,56	3,36	3,05	1,92	2,56	2,32
m3	62	2,56	3,68	3,16	1,76	2,62	2,27
DP4	1			2,13			2,24
P4	28	1,44	2,08	1,72	1,84	2,56	2,24
M1	38	1,84	2,72	2,34	1,93	2,72	2,29
M2	49	2,27	3,04	2,78	2,13	3,04	2,68
M3	47	2,32	3,20	2,87	2,24	2,96	2,65

Table 4. — Size of *T. sigmodon*, after Wang, 1997.

In contrast, the size variations of some species given by Wang (1997; this paper: Table 4), including *T. sigmodon*, seem misleading. She gathers material from different

Oligocene localities, probably heterochronous, and gives the size variability as if it is one unique population.

Our observations and measurements of chronologically homogeneous populations, coming from a single locality, provide a more reliable estimation for the variability of the species (Fig. 6 to 8, & Table 5 to 10). Elsewhere, the two lower jaws figured by Wang (1997, fig. 13 & 14) clearly belong to two different species, even if their size is close. That casts doubt on the reliability of the assemblage considered by Wang as being one species, *T. sigmodon*. The specimen AMNH 85750 (Wang, o.c., Fig. 14) shows both size and characters of *T. sigmodon*, especially a small trigonoid basin and a short hyposinusid. The horizontal ramus of the mandible is relatively narrow, with a foramen mentale low in position, close to the lower margin of the dentary, and under the anterior root of m1. IVPP V 10541 shows the characters of the species described here as *A. tengkoliensis* nov. sp., which displays a long hyposinusid and no trigonoid basin. The horizontal ramus of the dentary is higher than in the former one, with a foramen mentale at mid-height, that runs from the posterior root of p4 to the anterior part of m1 crown.

Holotype & Type-Locality: AMNH 19079, palate with two tooth rows P4-M3, Loh: Hsanda Gol Formation

Localities in Ulanatal area, Inner Mongolia (China): UTL4, UTL7, UTL1, UTL8 (Lower to Upper Oligocene, from base to top: ULAN I, II, III Units)

Diagnosis (in Wang 1977, p. 18-19): "smaller than *Tataromys plicidens* in size ; sphenopalatine foramen located above M1; P4 metaloph extending more posteriorly, complete or incomplete, anterior cingulum usually joining protoloph, lingual part of posterior cingulum weak or lacking; on upper molar, mesosinus L-shaped and posterosinus short, metaloph strongly curved, meeting posteroloph on M1 and M2, posteriorly oblique and joining posteroloph on M3; on lower molars trigonid relatively longer, usually with slightly larger closed basin, hypoconulid usually joining arm of hypoconid".

Emended diagnosis:

Id. above for cranial characters; smaller than *T. plicidens* and greater than *T. minor*;

dp4/DP4 more bunodont than molars and slightly wider than P4/p4; asymmetrical P4, flattened anteriorly and rounded posteriorly; anteroloph reduced or absent, variable connections between metacone and posteroloph; general increase of length from lower p4/dp4 to m3, and from P4/DP4 to M2; great size variation of M3;

On upper molars, mesosyncline L-shaped and posterosyncline short, metaloph strongly curved, reaching posteroloph on M1 and M2, posteriorly oblique and joining posteroloph on M3: morphotypes B, C, E;

On lower molars, trigonoid relatively long, usually with a relatively wide and closed basin, generally closed lingually, but sometimes superficially open on moderately worn teeth; hypoconulid usually joining arm of hypoconid;

Size close to that of *Alashania tengkoliensis* nov. gen. nov. sp.; differs from

Alashania by the shape of the dentary and the location of the foramen mentale; the development of a trigonoid basin, a short hyposinusid due to the direct junction between hypoconulid and hypoconid; metaloph joining the posteroloph (generally morphotypes B and C).

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	7	2,1	2,33	2,21	0,07303	1,30	1,40	1,36	0,03055
p4	12	1,67	2,42	1,98	0,17857	1,33	1,71	1,53	0,12513
m1	11	2,54	2,82	2,63	0,09209	1,57	1,93	1,73	0,105495
m2	13	2,96	3,63	3,19	0,20402	1,88	2,77	2,21	0,22336
m3	5	3,02	3,55	3,28	0,20555	2,21	2,44	2,28	0,09149
DP4	1			1,84				1,65	
P4	5	1,62	1,90	1,77	0,10296	2,00	2,29	2,20	0,11640
M1	9	2,14	2,60	2,32	0,13911	1,76	2,24	2,05	0,15411
M2	10	2,73	3,12	2,93	0,12184	2,40	2,77	2,66	0,10796
M3	11	2,50	3,28	2,85	0,26212	2,12	2,86	2,44	0,21729

Table 5.— Measurements of *Tataromys sigmodon* from UTL7.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	19	1,98	2,48	2,18	0,14596	1,16	1,85	1,41	0,14955
p4	41	1,55	2,15	1,94	0,14205	1,16	1,91	1,48	0,15840
m1	53	2,52	3,23	2,82	0,13958	1,58	2,42	1,98	0,16153
m2	39	2,66	3,85	3,17	0,18742	1,96	2,56	2,35	0,13336
m3	24	2,79	3,53	3,29	0,20599	2,03	2,61	2,37	0,15203
DP4	28	1,81	2,16	1,97	0,09314	1,70	2,15	1,89	0,11519
P4	34	1,51	1,94	1,74	0,10806	1,88	2,37	2,11	0,12934
M1	33	2,28	2,61	2,45	0,08731	2,13	2,46	2,31	0,07115
M2	29	2,71	3,32	2,95	0,15754	2,53	3,02	2,75	0,14636
M3	30	2,73	3,53	2,94	0,18485	2,37	3,06	2,66	0,14796

Table 6.— Measurements of *Tataromys sigmodon* from UTL4.

	n	length			width		
		Min.	Max.	Average	Min.	Max.	Average
p4	2	1,73	2,11		1,33	1,36	
m1	1			2,24			1,61
m2	1			2,55			1,93
m3	1			2,87			1,86
DP4	1			2,18			1,92
M2	2	2,58	2,95		2,32	2,57	

Table 7.— Measurements of *Tataromys sigmodon* from UTL1.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
p4	2	1,73	1,94			1,24	1,30		
m1	2	2,49	2,54			1,47	1,55		
m2	1			2,70				1,94	
m3	2	2,79	2,93			1,77	1,82		
DP4	1			1,99				1,95	
P4	5	1,46	1,77	1,64	0,11371	1,65	1,97	1,80	0,12775
M1	4	2,00	2,33	2,19	0,14387	1,95	2,13	2,03	0,08016
M2	7	2,57	3,09	2,90	0,20295	2,18	2,86	2,50	0,22811
M3	3	2,45	2,79	2,63	0,17039	1,98	2,43	2,21	0,22517

Table 8.— Measurements of *Tataromys sigmodon* from UTL5.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
p4	2	1,73	1,84			1,28	1,36		
m2	1			3,20				2,59	
m3	1			2,54				1,81	
P4	2	1,57	1,66			1,83	1,90		
M1	2	2,19	2,39			1,80	1,95		
M2	3	2,53	2,73	2,64	0,10263	2,27	2,39	2,35	0,06658
M3	1			2,76				2,25	

Table 9.— Measurements of *Tataromys sigmodon* from UTL8.

In UTL4, a few teeth are intermediate in size between the majority of specimens referred to *T. sigmodon* and those identified as *T. minor* (see p.) (Table 10, Fig. 7, Plate 3, fig. 1-9, 11-12). The same is true for the few specimens from UTL1 (Plate 3, fig. 10).

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	3	1,28	1,45	1,37	0,08622	0,79	0,94	0,84	0,08386
p4	6	1,37	1,49	1,43	0,05076	1,00	1,19	1,10	0,07167
m1	5	1,96	2,38	2,14	0,18133	1,32	1,62	1,45	0,12696
m2	7	1,86	2,25	2,11	0,13844	1,43	1,67	1,52	0,08343
m3	4	1,98	2,18	2,11	0,10132	1,32	1,66	1,48	0,13961
DP4	1			1,54				1,45	
P4	11	1,19	1,39	1,30	0,06262	1,23	1,75	1,55	0,16613
M1	4	1,73	1,83	1,79	0,04435	1,56	1,70	1,62	0,06455
M2	6	1,83	2,05	1,92	0,08430	1,63	1,98	1,83	0,11215
M3	12	1,51	1,89	1,75	0,12944	1,44	1,78	1,60	0,10384

Table 10.— Measurements of *Tataromys* cf. *sigmodon* or *minor*? (Only complete teeth) from UTL4.

Description

Lower teeth (Plate 1)

p4: The higher cuspids are the metaconid and protoconid. From both cuspids, two lophids dive into the talonid basin and generally converge to build an ectolophid connected to the entolophid. These characters are close to those of *Yindirtemys ulantatalensis*, but the hypoconid and the hypoconulid are not well individualized as in that species. Only one tooth shows an anterior metalophid, which marks the boundary of

a closed trigonoid basin.

dp4 and molars : We note a slight increase of tooth size from dp4 to m3 (fig. 6). The dp4 and the molars show similar dental patterns.

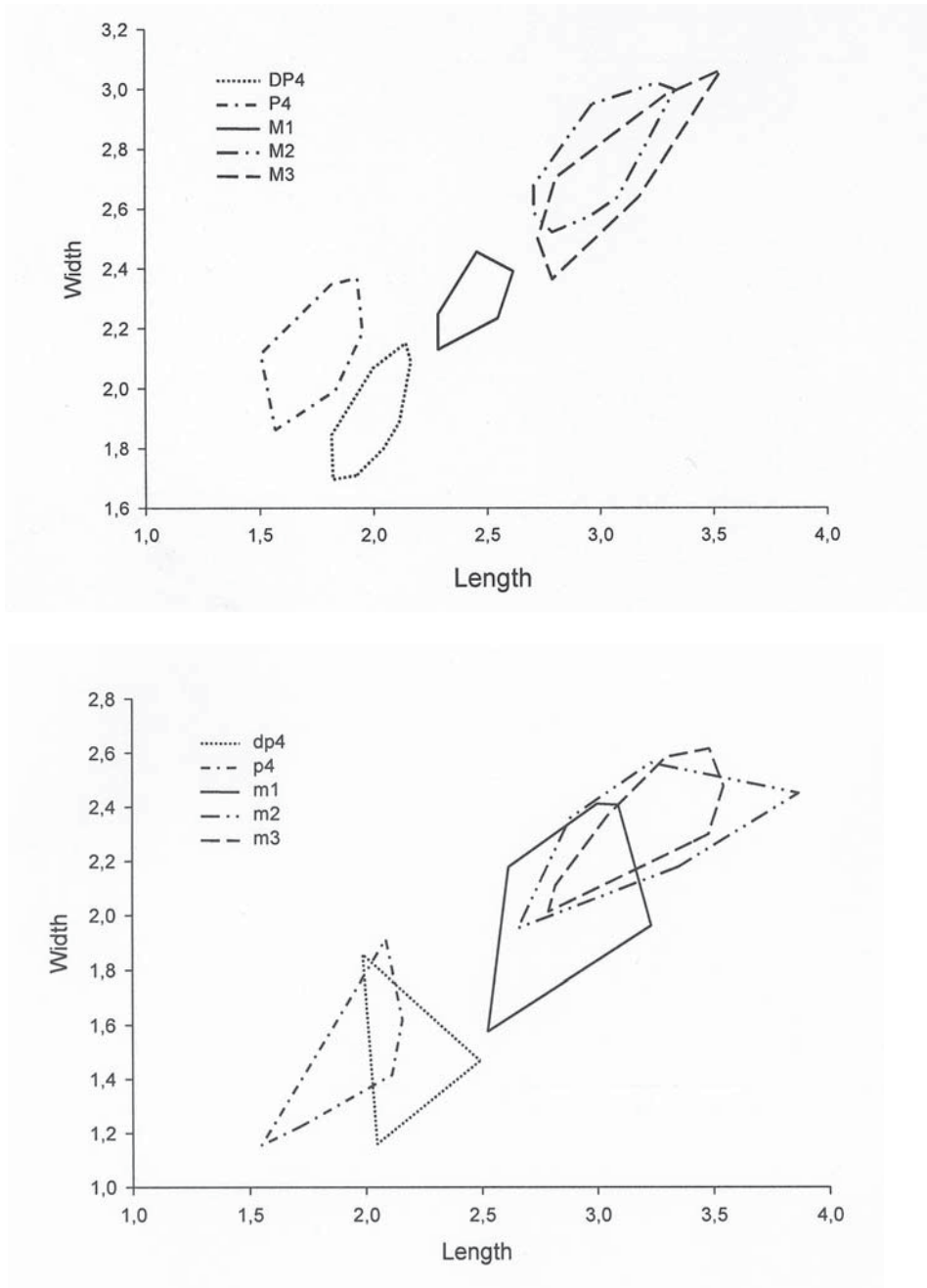


Figure 6. — Bivariate graph (width/length) of the upper and lower teeth of *Tataromys sigmodon* from UTL7.

- the trigonoid bears a closed basin;
- the ectolophid occurs in the middle to the lingual border of the tooth;
- the hypoconulid is connected to the hypolophid, parallel to the entolophid.

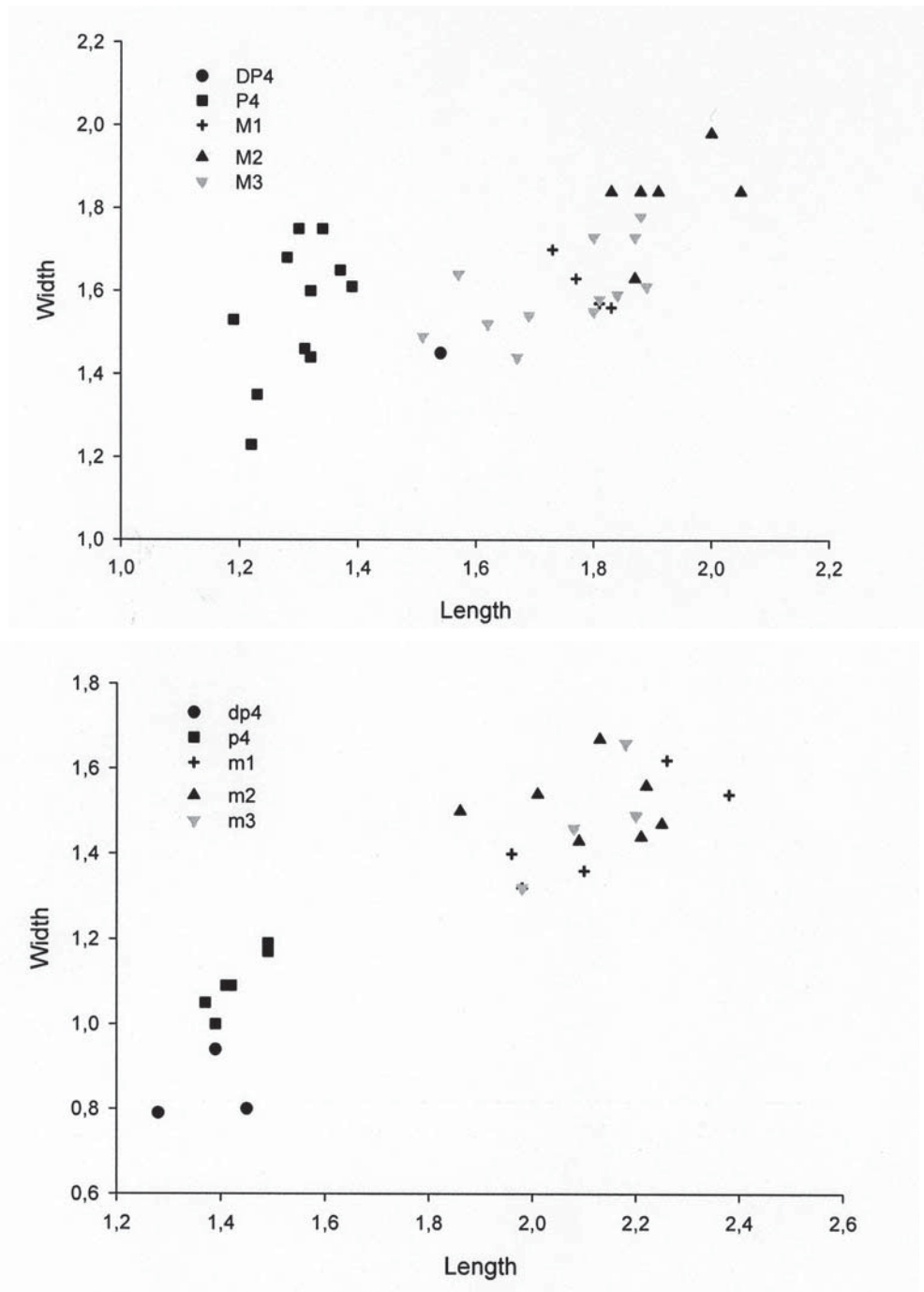


Figure 7.— Bivariate graph (width/length) of the upper and lower teeth of *Tataromys* cf. *minor* or *sigmodon* from UTL4.

However, we note a morphological gradient from dp4 or m1 to m3. If the trigonoid basin is always broad on dp4, m1 and m2, it can be significantly reduced on m3. This reduction is linked to lingual displacement of the ectolophid, which reaches the lingual quarter on m3 (fig. 15 to 19, plate 1).

A few variations of the closing of the trigonoid basin are observed on superficially worn teeth. On a few m2 (UTL4: 5/58; UTL7: 2/18) and m3 (UTL4: 2/15; UTL7: 4/13), there is no crest closing the basin, or it is incomplete or broken by a short gap (fig. 7 & 14, plate 1). On worn teeth, the trigonoid basin, which is shallow, can disappear. As seen on tooth rows, wear begins from the front part of the row, on m1, to the end, on m3. Two specimens display, within the trigonoid basin, a short longitudinal crest stemming from the anterolophid.

Molar wear is oblique. We notice only one well-marked groove, crossing from the junction hypolophid/arm of the hypoconulid to the junction entolophid/ectolophid (GRP = posterior groove). Functionally, the hypoconulid leans against the anterior part of the following tooth, and a clear wear surface continues from the surface of the protoconid and its two arms, to the postero-lingual ends of the hypoconulid and entoconid of the precedent tooth (fig. 8b, Plate 1).

Upper teeth (Plate 2)

P4: Smaller than those of *T. plicidens*, they have about the same size as those of *Alashania tengkoliensis* nov. gen. nov. sp. and slightly smaller than those of *Yindirtemys ulantatalensis*. They are more asymmetrical than *A. tengkoliensis* and *Y. ulantatalensis*, and more lengthened labio-lingually. Their anterior slope is flattened, while the posterior slope is asymmetrically rounded. From the metacone, an oblique posterior arm is connected with the posterior arm of the protocone, at the middle, or slightly labially. Sometimes this loph is interrupted at this level, and prolonged by a fairly low posterior cingulum. The posterior cingulum can also be situated more labially. The junction of the anterior arm of the protocone and that of the metacone is frequent, enclosing a central small valley as a result. Frequently, on slightly worn teeth, the anterior arm of the protocone is absent, and the central valley is anteriorly open. A short and very low anteroloph (cingulum) can be present, linked or not to the protocone.

DP4 and molars: Morphologies and tooth proportions are close to the teeth of *Tataromys minor*, but with a greater size. Both show an increase of length from DP4 to M2. The size variation of M3 is larger than that of M2 in UTL7 (Fig. 6, Fig. 8), and encompass that of M2 + M3 in UTL 4. On unworn or slightly worn teeth, the lingual cusps are not prominent over the loph. The anterior cingulum, without a prominent anterocone, is linked to the protoloph. The anterosinus is present, even if it is short. In occlusal view, the protoloph is transverse and regularly thin. The orientation of the metaloph is more variable, and it is slightly widened at its middle part. The metaloph is not connected directly to the protocone. It can be transverse, and its relationship with the posteroloph is very scarcely realized by a short longitudinal loph (morphotype A, table 9). The most frequent connections are oblique backwards: the metaloph is directly attached to the hypocone (morphotype B) or more lingually on the posteroloph, behind the hypocone (morphotype C). Such connections (morphotypes B et C) are observed on

the teeth of the holotype of *T. sigmodon*. The loph and cusp patterns are very stable. Only one M3 from UTL7 has two small « crochets » on the protoloph and the metaloph, directed towards the mesosinus.

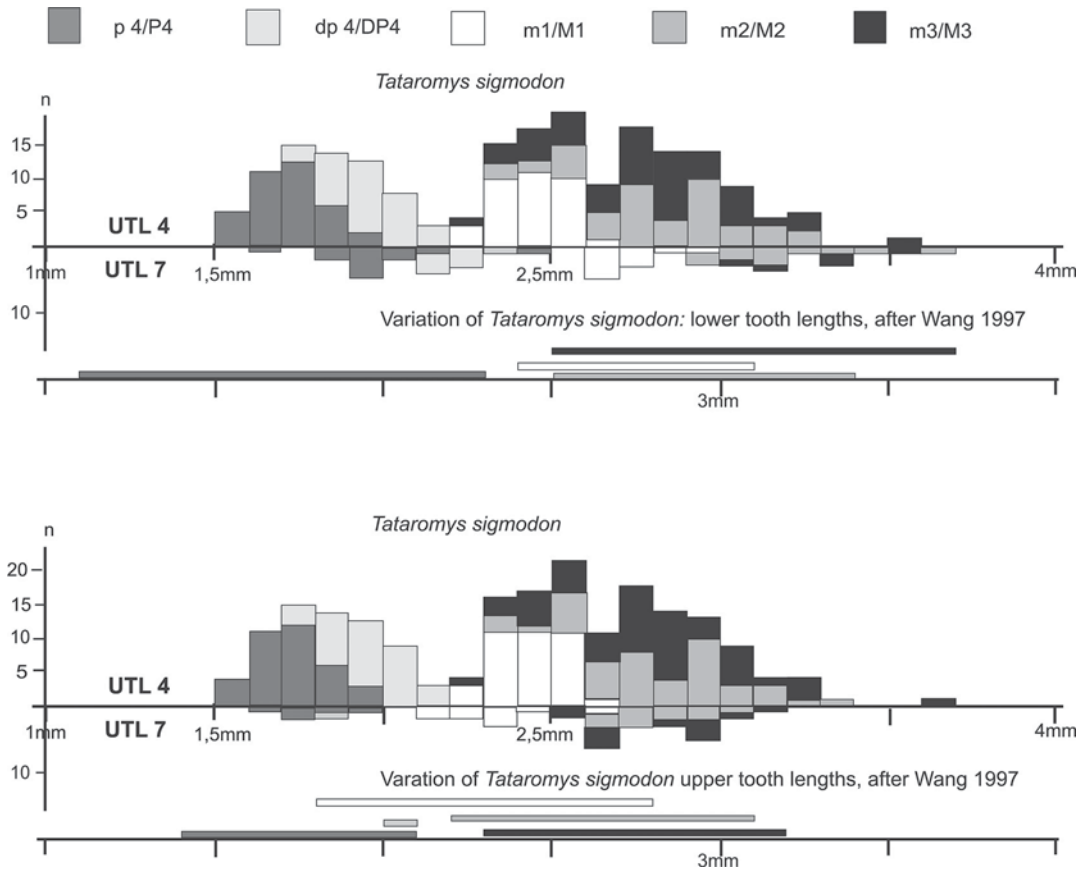


Figure 8.— Histograms of lengths of the lower and upper teeth of *Tataromys sigmodon* from UTL4 and UTL7; variation of the length of *T. sigmodon*, after Wang, 1997.

localité	DP4				M1				M2				M3				
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	
UTL1		2															
UTL7		3		2		6				12						13	
UTL4	2	28			1	38			6	28			1		34		
	1	4		1	2	3			3	14			2		25		
UTL8						2				3					1		

Table 11.— Morphotype occurrences on upper teeth of *Tataromys sigmodon*.

From UTL4, some (complete or fragmentary) teeth are intermediate in size between *T. sigmodon* and *T. minor* (Table 10). Among them, some show thicker lophs, with more prominent cusps: a few display morphotypes A, and one morphotype D is

observed (metaloph directed to the protocone, not linked with the hypocone). These teeth are indicated in italics on Table 11. The other small specimens display the same morphology as typical *T. sigmodon*.

Discussion

The localities where *T. sigmodon* is the most abundant are those from level Ulan II (UTL4 and UTL7). In UTL1, there are only a few teeth, smaller than those of these localities.

We have identified only a few teeth from UTL8, of the youngest stratigraphical level (Ulan III). For the lower teeth, two p4, and one m2, with a wide trigonoid, are present. The morphotypes of the six upper molars (Table 11) are common for *T. sigmodon* (3B, and one C).

Tataromys minor (HUANG, 1985)

Synonymy: *Leptotataromys minor* HUANG, 1985; *T. parvus* WANG, 1997.

The species has been erected by Huang (1985) from a mandibular fragment with a worn m1, from the Ulantatal area. Huang underlined the morphological similarities between this tooth and those of *L. gracilidens* (= *T. sigmodon*). Wang (1997) provided a new diagnosis, including the upper teeth. But, she described as *T. minor*, material that does not belong to the species named by Huang. Moreover, this material includes teeth from various localities and areas (Ulantatal, but also Saint Jacques Quianlishan district, Wulanbulage and Shargaltein).

In the material from Ulantatal, mainly in UTL7 and UTL4, but also in the other localities, except UTL8, we have found a great number of teeth and jaws, for which morphological variations include the morphotype of the Huang's holotype. We will see that their characters (for the smaller teeth) are reminiscent of those of *T. sigmodon*.

The two lower jaws figured by Wang (fig. 17, B, AMNH 19075; CD: AMNH 84208) from Wulanbulage or Hsanda Gol (?) certainly do not belong to *T. minor*, but to another species, belonging to the new genus *Alashania* described here from UTL4, UTL1, and UTL8.

Upper jaws and upper teeth that we associate to *T. minor* in Ulantatal material also show a great morphological similarity with the upper teeth of *T. sigmodon*.

In all cases, they differ from the two specimens bearing upper teeth named *T. minor* by Wang (o.c., fig 15). The maxillary from Saint Jacques (V 10545), and the other from an unspecified locality (AMNH 22077) (o.c. fig. 15A, B, p. 23) belong to a new species, which is described below. The maxillary selected by Wang as the type of *T. parvus* (o.c. fig. 15C) cannot be distinguished from *T. minor*. The specimens that we name *minor* in Ulantatal are similar to those named *T. parvus* by Wang (o.c. fig. 15C, p. 23, upper jaw with P4-M2) from Shargaltein. We propose to consider *T. parvus* as a junior synonym of *T. minor*.

Holotype and Type Locality: V7347, Huang, 1985: fragment of right lower jaw with worn m1 and root of P4, Ulanatal area (surface collection: imprecise locality)

Other localities and stratigraphical range: Ulanatal area, Inner Mongolia (Ulan I to III, Lower to Upper Oligocene: UTL1, UTL3, UTL4, UTL5, UTL6)

Original diagnosis: "Lower molars identical to those of *L. gracilidens* morphologically, but much smaller, m1 being 1.7 mm in length and 1.1 mm in width "

Emended diagnosis: Small *Tataromys* (Holotype: m1 = 1.7 mm x 1.1 mm; measurements of one population: see Table 12 or Table 13); incisive foramen ending at the level of front part of P4; dental morphology similar to that of *T. sigmodon*, for a much smaller size. M3/m3 smaller than M2/m2; lower molars (dp4 to m3) with a trigonoid basin less and less frequent from m1 to m3; ectolophid localized in the lingual quarter of the teeth; upper molars (from DP4 to M3) with metaloph generally oriented backward, with its disto-lingual end connection varying from the level of the hypocone to the middle of the anteroloph; anteroloph linked with the protoloph, without anterocone; anterior groove not or weakly marked.

Material and measurements (Fig. 9 & Fig. 10)

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	33	1,10	1,37	1,23	0,06147	0,71	0,90	0,82	0,04917
p4	140	0,91	1,33	1,07	0,06567	0,65	1,21	0,81	0,08498
m1	202	1,27	1,81	1,52	0,08245	0,96	1,27	1,10	0,06906
m2	305	1,48	1,99	1,70	0,09005	1,03	1,50	1,26	0,08121
m3	164	1,36	1,95	1,64	0,09973	1,01	1,48	1,19	0,07894
DP4	35	0,97	1,30	1,09	0,07306	0,96	1,22	1,07	0,05281
P4	125	0,81	1,15	0,95	0,07080	1,00	1,45	1,18	0,09216
M1	152	1,10	1,47	1,30	0,066021	0,99	1,34	1,21	0,06526
M2	172	1,37	1,66	1,51	0,05858	1,11	1,54	1,35	0,06941
M3	217	1,25	1,64	1,44	0,07314	0,90	1,40	1,13	0,09858

Table 12.— Measurements of *Tataromys minor* from UTL4.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	6	1,06	1,24	1,15	0,07118	0,62	0,81	0,75	0,06834
p4	25	0,94	1,17	1,05	0,05664	0,67	0,72	0,75	0,06423
m1	37	1,33	1,65	1,48	0,07464	0,99	1,10	0,99	0,07016
m2	32	1,52	1,8	1,64	0,06648	1,09	1,31	1,20	0,13346
m3	23	1,53	1,90	1,66	0,09383	1,03	1,31	1,13	0,14898
DP4	8	1,06	1,14	1,11	0,03457	0,97	1,09	1,01	0,04348
P4	21	0,82	0,98	0,90	0,04383	0,98	1,11	1,10	0,08255
M1	24	1,17	1,41	1,28	0,06633	1,12	1,24	1,09	0,07946
M2	31	1,35	1,7	1,51	0,07860	1,2	1,5	1,28	0,09327
M3	42	1,27	1,56	1,43	0,05914	1,09	1,22	1,19	0,07289

Table 13.— Measurements of *Tataromys minor* from UTL7.

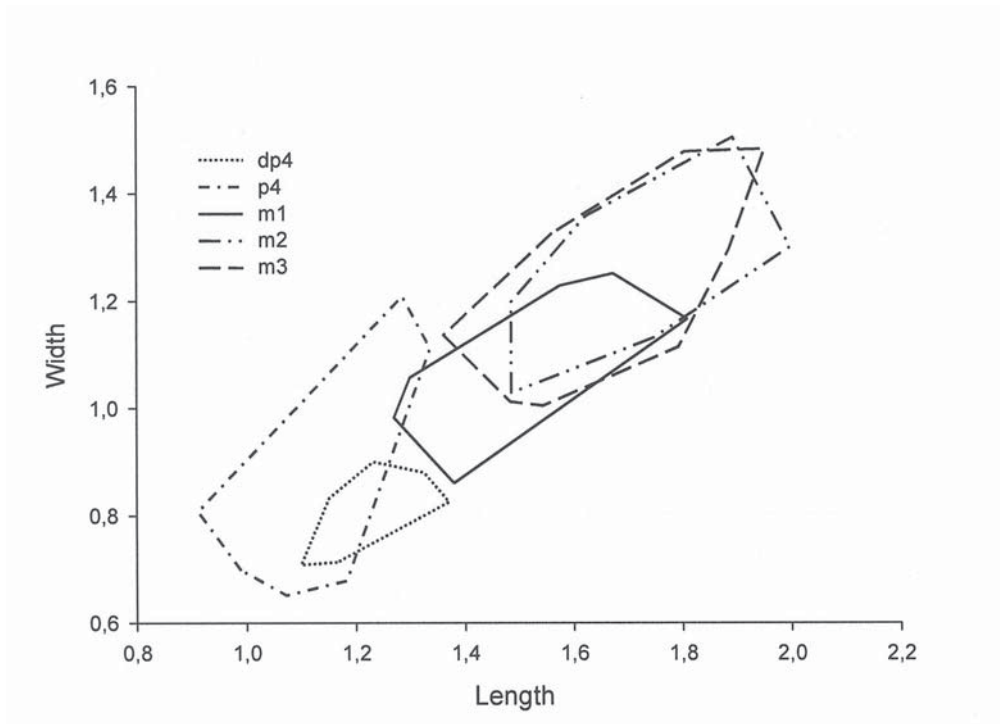
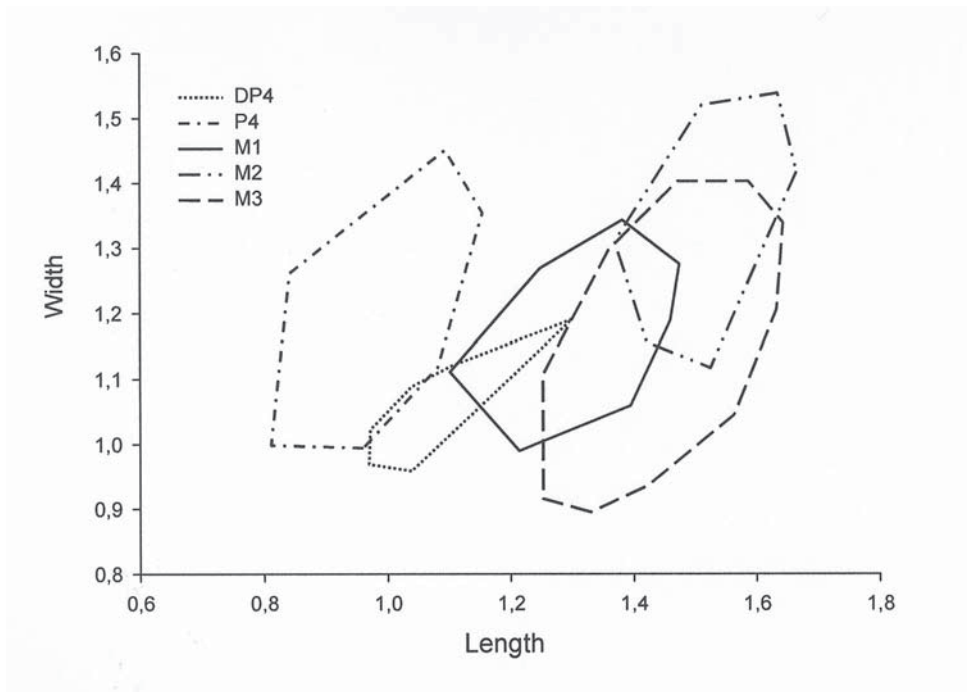


Figure 9. — Bivariate graph (width/length) of the upper and lower teeth of *Tataromys minor* from UTL4.

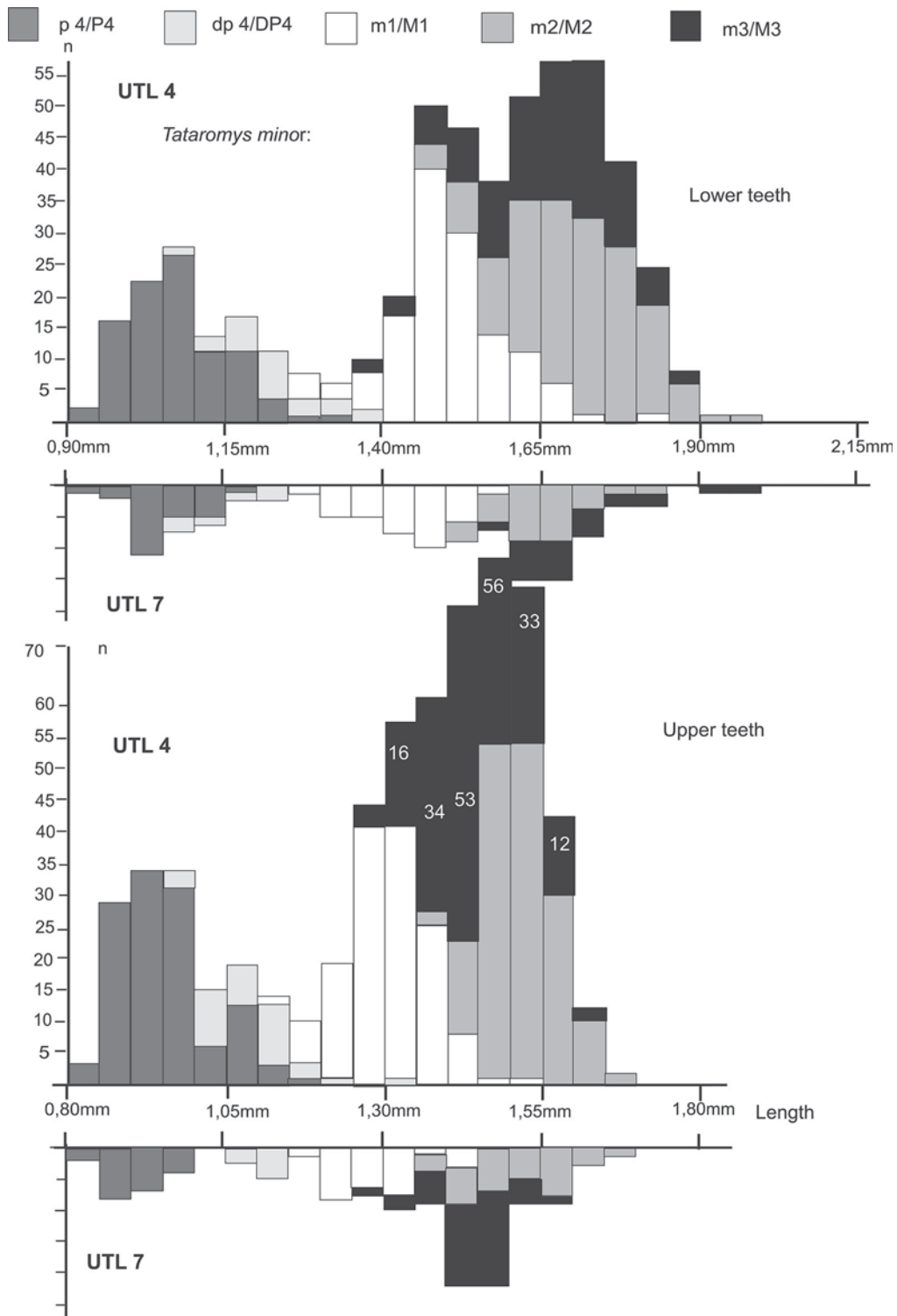


Figure 10. — Histograms of lengths of the lower and upper teeth of *Tataromys minor* from UTL4 and UTL7.

Description

Lower teeth (Plate 4, fig. 1-23)

p4: Several small ctenodactylid species occur in the Ulanatal localities. Among them, *T. minor* and a small *Yindirtemys*, referred to a new species *Y. shevyrevae*, are of the same size. Some p4, associated with m1 or other molars on mandible fragments, show that the morphology is hardly distinguishable between the two species. In *T. minor*, the entoconid is generally not followed by an entolophid, while it is sometimes present in *Y. shevyrevae* nov. sp. The p4 of *T. minor* is very simple, with three sharp cuspids. A wide-open V-shaped crest frequently connects the metaconid and protoconid. The tooth is generally triangular, much thinner posteriorly.

dp4: Their morphology resemble that of the dp4 of *T. sigmodon*. Narrow anteriorly, the protoconid and metaconid are generally separated (30/36 in UTL4, 5/6 in UTL7). They are rarely connected by a metalophulid I, closing the trigonoid basin (6/36 et 1/6).

Lower molars: m1 is smaller than m2. m2 and m3 are of similar size. The trigonoid basin is relatively more reduced than in *T. sigmodon*, and as a consequence, the ectolophid is generally more lingual. The frequency of the trigonoid basin decreases from m1 to m3 (UTL4: 143/230 m1, 101/222 m2, 38/185 m3; UTL7: 23/38 m1, 22/34 m2, 8/36 m3). The dental pattern does not vary significantly on m1-2-3, except for more or less strong reduction of the trigonoid basin. It can be completely closed or open mesially or distally. Exceptional accessory crests have been detected on 3 of the m3.

As in *T. sigmodon*, there is only one posterior groove (GRP) for the cusp movements during occlusion and chewing.

Upper teeth (Plate 3, fig. 24-30)

P4: They are oval, with an anterior slope flattened, while the posterior slope is asymmetrically rounded. The anteroloph joins the paracone and the protocone. It is generally underlined by a short and low antero-labial cingulum. The central valley is either open posteriorly or completely closed.

DP4: Most show an oblique metaloph directed backward (morphotypes B/C or only C in UTL4). Only three teeth (among 40) display the morphotype D, with the metaloph attached to the protocone. They show, for this character, a similarity with *Yindirtemys shevyrevae* nov. sp. It seems to be a primitive character.

Upper molars: M1 is smaller than M2 and M3, and M3 smaller than M2. The lophes are thin and the lingual cusps only slightly prominent from the ectoloph. The anteroloph, lacking a prominent anterocone, is connected to the protoloph. The metaloph orientation is more constant than in *T. sigmodon*. It is more generally curved backward making morphotypes B and C (B: connection metaloph-hypocone; C: connection metaloph to the middle of the posteroloph). For exemple, in UTL4, M1: 190B/6C, M2: 178C/30B, M3: 240B, C rare, with connection close to the hypocone. We have not observed other variations.

Discussion: If the populations of that species are abundant in the localities of Ulan II, it is not the case for Ulan I and Ulan III. For that reason, it is not possible to discriminate

any evolutionary trend.

Tataromys plicidens MATTHEW & GRANGER, 1923

Holotype: palate with right P4-M3 (AMNH 19082); Hsanda Gol formation of Loh (Central Mongolia).

Original diagnosis (Matthew & Granger, 1923, p. 5-6): "Premolar smaller than the molars, trigon with three submarginal crests, not at all molariform in pattern, but of fair size. Molars with two principal transverse crests connected by an external commissure; on M2 and M3 supplementary anterior and posterior crests obliquely inward from the main crests commissure. The lower molars reverse this pattern in the usual manner, but the arrangement is less regular"

Emended diagnosis (Wang, 1997, p. 11, and modified in this paper): The largest form known for *Tataromys*; sphenopalatine foramen above the junction of M1-M2; cheek teeth with compressed cusps and lophs; P4 anterior cingulum low; upper molars with slightly curved metaloph, weak anterocone, mesosyncline wide U-shape; anterosyncline and posterosyncline transverse; molars of morphotype A (metaloph connected to the hypocone by a short crest; variability of lower molars not well known: sometimes having very short trigonoid with or without small closed basin, or no trigonoid; hypoconulid usually joining entoconid or both entoconid and hypoconid or hypoconid on m1 and meeting hypoconid on m2 and m3.

Other localities and stratigraphical range: Ulantatal area, Inner Mongolia (ULAN I to II , Lower to early Upper Oligocene: UTL1, UTL4, UTL5, UTL7)

Discussion

The holotype is a palate, and the paratypes, including upper and lower jaws are not figured nor described precisely. Material referred by Wang (1997) to this species comes from different basins and localities. Wang emended the diagnosis of the species on the basis of heterogeneous material, from late early Oligocene to late (?) Oligocene. Thus, we cannot know if the variability given for the size, or for some characters, like the connections of the hypoconulid on the different lower molars, is fairly the variability of one chronospecies, or if it is artificial. The only indication for the type is about 14 mm length for the P4-M3 row. If we consider the average given by Wang, the addition of P4 + M1 + M2 + M3 is about 14 mm.

The material found in the different localities of Ulantatal is not so abundant for providing a complete range of the *T. plicidens* variability.

Measurements:

<i>L-W mm</i>	<i>DP4</i>	<i>P4</i>	<i>P4</i>	<i>P4</i>	<i>M1</i>	<i>M2</i>	<i>M3</i>	<i>M3</i>	<i>M3</i>	<i>M3</i>
UTL1	2.41-2.22	-	-	-	3.12+-2.45	3.48-3.24	-	3.37-2.72	-	-
UTL4	2.82-2.42	2.60-3.02	2.39-2.75	2.51-2.86	3.47-2.69	-	4.07-3.63	4.36-3.52	3.74-3.17	3.41-3.16
UTL5	-	-	-	-	-	4.12-3.44	-	4.01-3.32	-	-
<i>L-W mm</i>	<i>dp4</i>	<i>p4</i>	<i>p4</i>	<i>p4</i>	<i>m1</i>	<i>m2</i>	-	<i>m3</i>	<i>m3</i>	<i>m3</i>
UTL1	-	2.60-1.97	-	-	3.49-2.30	-	-	4.66-3.04	4.03-2.62	4.06-2.46
		2.72-2.32								
UTL4	-	2.81-2.33	2.77-2.01	-	-	-	-	4.38-2.87	-	-
UTL5	-	-	-	-	3.56-2.16	-	-	-	-	-
UTL7	-	-	-	-	-	-	-	3.74-2.63	-	-

Table 14. — Size of *Tataromys plicidens* from several localities of Ulanatal.

Description (Plate 5, fig. 1-9)

Lower teeth

The lower p4 are close to those of *T. sigmodon*, but they are bigger, and the ectolophid is clearly lower. Wang notes, as it can be seen on figure 9 for IVPP V 10534.1 or figure 10 c & d (Wang 1997), that the hypoconulid is connected with the entoconid on m1. The only two m1 from Ulanatal (UTL1 and UTL5) show that the connection is made from the hypoconulid to the protolophid. On the two available m1, the trigonoid is absent, and the ectolophid is lingual. The variation in size of the m3 is important and the smallest reach the upper limit of the *T. sigmodon* m3. The biggest m3 (UTL1) has a clear trigonoid basin. Another, also from UTL1, has a reduced trigonoid, and one from UTL1 has no trigonoid and a lingual ectolophid. It is the same for the m3 from UTL7.

Upper teeth

Only one DP4 (UTL4) can be referred to *T. plicidens*. Without knowing the variability of this character due to the scarcity of the sample, the anteroloph is low, longer than in *Alashania* nov. gen. or in *T. sigmodon*. It reaches the level of the top of the protocone, whereas it reaches only the anterior arm of the protocone in *Alashania*. The hypocone is either separated from the trigon (morphotype D) or connected by a low crest (morphotype A).

Three P4, from UTL4, seem less asymmetrical than in *T. sigmodon*, with an anteroloph not connected with the protoloph, low, and occupying the middle of the teeth. The posteroloph is connected at the junction of the posterior arms of the protocone and paracone. The size fits with that of the holotype. The few M1 and M2, in UTL4, UTL1 and UTL5, are morphotypes A or B. The antesisinus is weak, and the sinus short, but well defined.

Six M3 occur in three localities (UTL4, UTL5 and UTL1). They are also of morphotype A, with the mesosyncline U-shaped and nearly symmetrical. The antesisinus and the sinus are weaker than in M1. One M3 from UTL1 shows an extra-cusp, low, at the bottom of the sinus. Kowalski (1974, p.164) observed this cusp on the two M3 of the palate MgM-III 44 described as *T. plicidens*. A labial longitudinal crest connects the protoloph and metaloph of the UTL1 M3 (Plate 5, fig. 8).

Genus *ALASHANIA* nov. gen.

Type species: *Alashania tengkoliensis* nov. sp.

Diagnosis: Palate "rectangular" (tooth rows parallel); on the dentary, foramen mentale under the posterior root of p4.

On lower molars: wear pattern with two grooves (GRA & GRP, fig. 3); ectolophid of molars straight and lingually situated; trigonoid basin absent; hypoconulid connected to entoconid, by way of a loph, which is parallel to the hypolophid, making a long and narrow hyposinusid at least on dp4 and m1.

On upper molars: anterocone evident or prominent, within the anteroloph; anteroloph short, separated from the protocone, with an antesisinus generally absent or weak; sinus long; morphotypes A and D frequent; protoloph and metaloph parallel, generally connected with the protocone (morphotypes A and D): posteroloph joining hypocone by a short and low entoloph; morphotype B rare (in which posteroloph is connected directly to hypocone).

Differs from *Yindirtemys* by the characters of ectolophid and of hyposinusid, the absence of trigonoid and strong reduction or absence of mesoconid, and the non-crescentic structures;

Differs from *Tataromys* by the characters of ectolophid and of hyposinusid, the absence of trigonoid; its cusps and cuspids less compressed, and loph and lophids less thin.

Differs from *Karakaromys* mainly by the development of loph, the absence of trigonoid, the long hyposinusid and the lingual ectolophid.

Alashania tengkoliensis nov. sp.

Synonymy: *Tataromys sigmodon*, Wang, 1997, p. 20, fig. 13.

Derivatio nominis: After the names of the small hills (Alashan) and of the Chinese desert : Ting-Ko li (Sha-mo) (see The Times Atlas of China, p. 114, for the transcription from Chinese to English)

Holotype & Type Locality: UTL1-24, incomplete left dentary, with p4-m3. From UTL1, Lower Oligocene, Ulantatal area (Inner Mongolia):

Other localities: Ulantatal area: UTL4 (ULAN II, early Upper Oligocene); Saint Jacques (Wang, 1997, p.20)

Diagnosis: *Alashania* with long and narrow hyposinusid generally on dp4 (8/10 at UTL4; 3/3 at UTL1; 2/2 at UTL1), on some of the molars but more often on m1 than on m2 than on m3; Slightly smaller than *Y. ulantatalensis* and *T. sigmodon*. (Holotype: p4: 1.66 mm x 1.28 mm, m1: 2,26 mm x 1.58 mm, m2: 2,50 mm x 1,97 mm, m3: 2,79 mm x 1,93 mm; syntypes: see Table 15)

Measurements:

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	3	2.07	2.18	2.13	0.05508	1.11	1.26	1.17	0.07767
p4	37	1.35	2.45	1.66	0.27297	0.89	1.76	1.23	0.24246
m1	38	1.91	3.14	2.27	0.32274	1.13	1.94	1.47	0.24007
m2	47	2.02	3.44	2.47	0.38087	1.27	2.27	1.70	0.28005
m3	26	2.22	3.37	2.63	0.35333	1.24	2.46	1.71	0.30384
DP3	2	0.59	0.70	0.65	-	0.58	0.68	0.63	-
DP4	11	1.40	2.19	1.73	0.22593	1.21	1.91	1.47	0.22686
P4	30	1.23	2.05	1.48	0.21337	1.36	2.42	1.68	0.22585
M1	35	1.73	2.68	1.99	0.24708	1.39	2.39	1.74	0.23813
M2	40	1.92	3.17	2.34	0.37626	1.58	2.82	2.03	0.33696
M3	44	1.76	2.87	2.23	0.31885	1.53	2.60	1.90	0.25458

Table 15.— Measurements of *A. tengkoliensis* nov. sp. from UTL1.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	9	1.52	2.35	1.78	0.27286	0.79	1.20	0.98	0.14379
p4	19	1.30	1.70	1.49	0.10936	0.99	1.40	1.13	0.10650
m1	34	1.79	3.01	2.19	0.30856	1.14	1.79	1.38	0.18861
m2	26	1.97	3.15	2.46	0.34730	1.24	2.06	1.71	0.21266
m3	20	1.84	3.10	2.34	0.30614	1.36	1.80	1.53	0.14128
DP4	5	1.36	1.54	1.44	0.06504	1.17	1.38	1.30	0.08426
P4	12	1.40	2.06	1.67	0.20362	1.71	2.74	1.98	0.32449
M1	22	1.73	2.38	1.98	0.20931	1.55	2.16	1.76	0.18020
M2	21	1.85	2.93	2.21	0.33731	1.55	2.68	1.96	0.33040
M3	14	1.86	3.02	2.27	0.33898	1.59	2.55	1.92	0.26442

Table 16.— Measurements of *A. tengkoliensis* nov. sp. from UTL4.

	n	Length			width		
		Min.	Max.		Min.	Max.	
m1	1			1.98			1.12
m3	2	2.23	2.43		1.52	1.55	
P4	1			1.27			1.29
M1	1			1.76			1.57
M2	1			1.90			1.97
M3	1			1.91			1.59

Table 17.— Measurements of *A. tengkoliensis* nov. sp. from UTL5.

Size variations (fig. 11, 12, 13)

From the material of five localities (UTL4, UTL7, UTL1, UTL3, UTL5, UTL8), we have found teeth displaying the characteristics of *Alashania*, but the size variation seems strong. In poorly fossiliferous localities, we have either small teeth or larger ones. At UTL1, where the material is the most abundant, the sizes distribution is not normal, as shown in figures 11 and 13. Does it mean that there are two species, or a dimorphism within one species? At first, we thought that two species of *Alashania* were documented, as well in poor localities as in richer ones. On the basis of the comparison with the variation of an abundant population, like *Tataromys minor* of UTL4, we have

noticed that it is hardly greater than that observed within one species. Nevertheless, the statistical distribution of the size is not as normal as in *T. minor* or in *T. sigmodon*, which suggests the occurrence of more than one species.

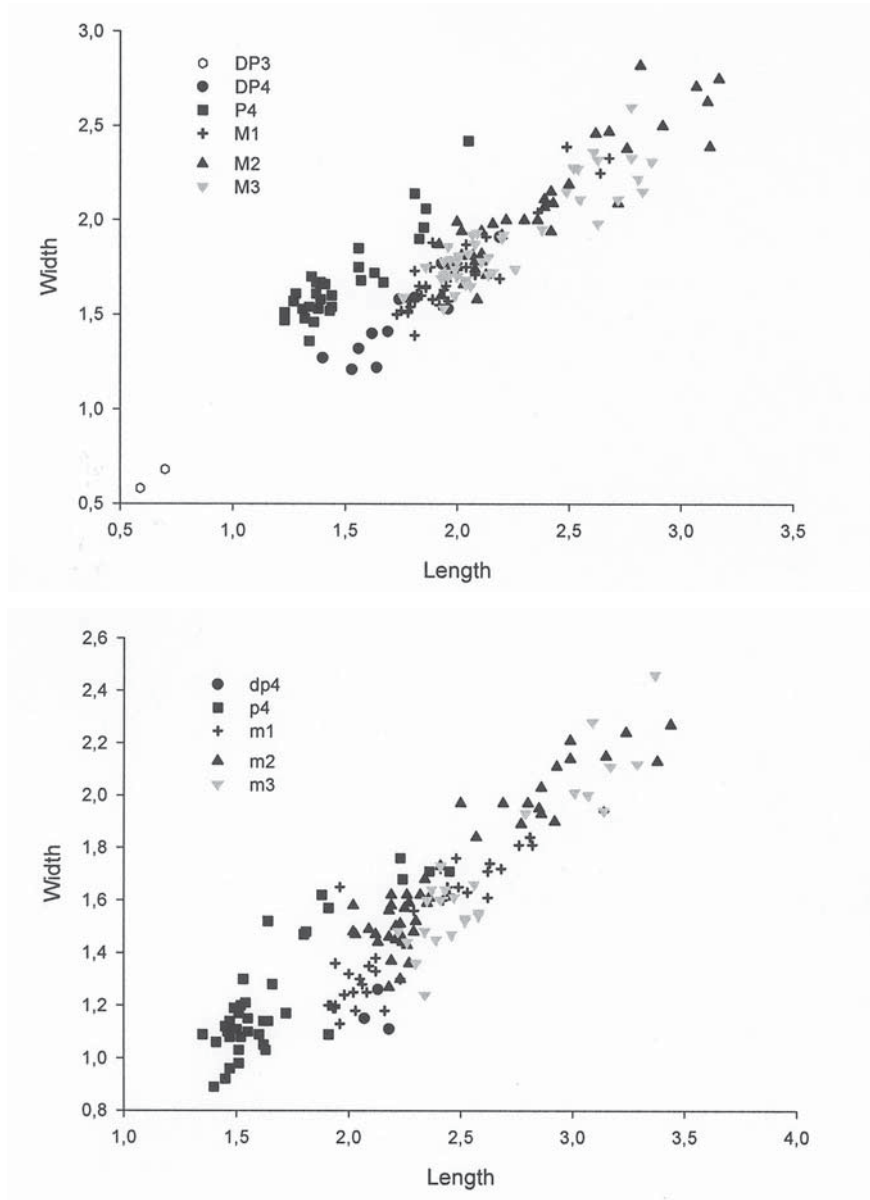


Figure 11.— Bivariate graph (width/length) of the upper and lower teeth of *Alashania tengkoliensis* from UTL1.

Even if there are important differences of size for the maximum to the minimum, and that a bi-modal distribution is suspected for premolars or second and third molars, the material is not abundant enough in the different localities for differentiating two species at present time, either on the basis of the morphology or on the size distribution. The holotype, from UTL1, is a medium size individual. In UTL4, the size distribution seems more normal than in UTL1. Three upper P4 are bigger than the others (fig. 12),

and could be P4 of another species.

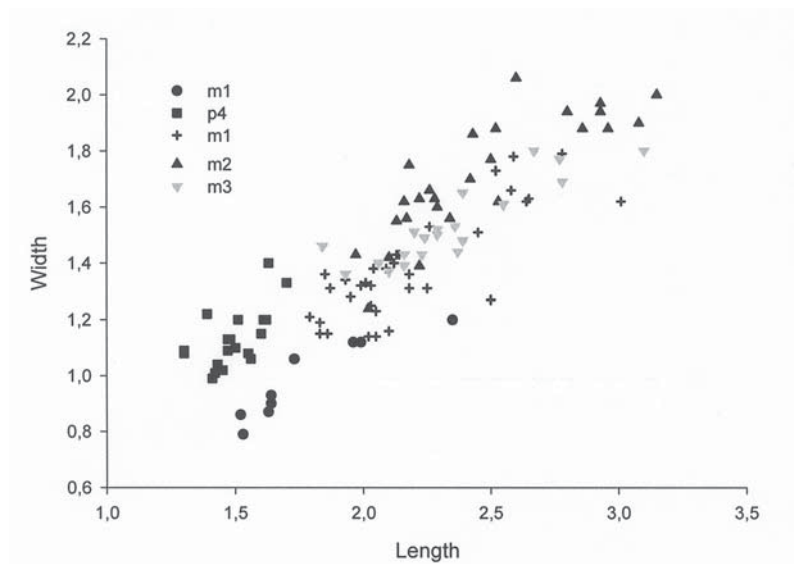
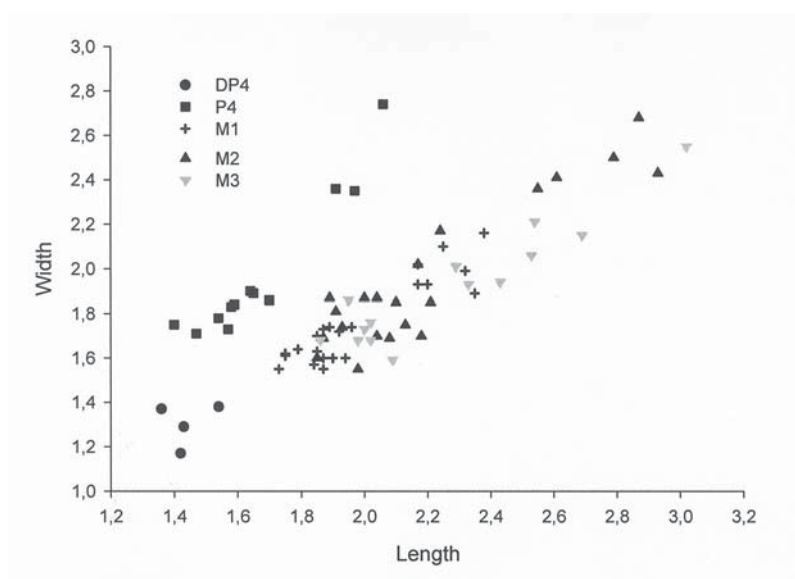


Figure 12.— Bivariate graph (width/length) of the upper and lower teeth of *Alashania tengkoliensis* from UTL4.

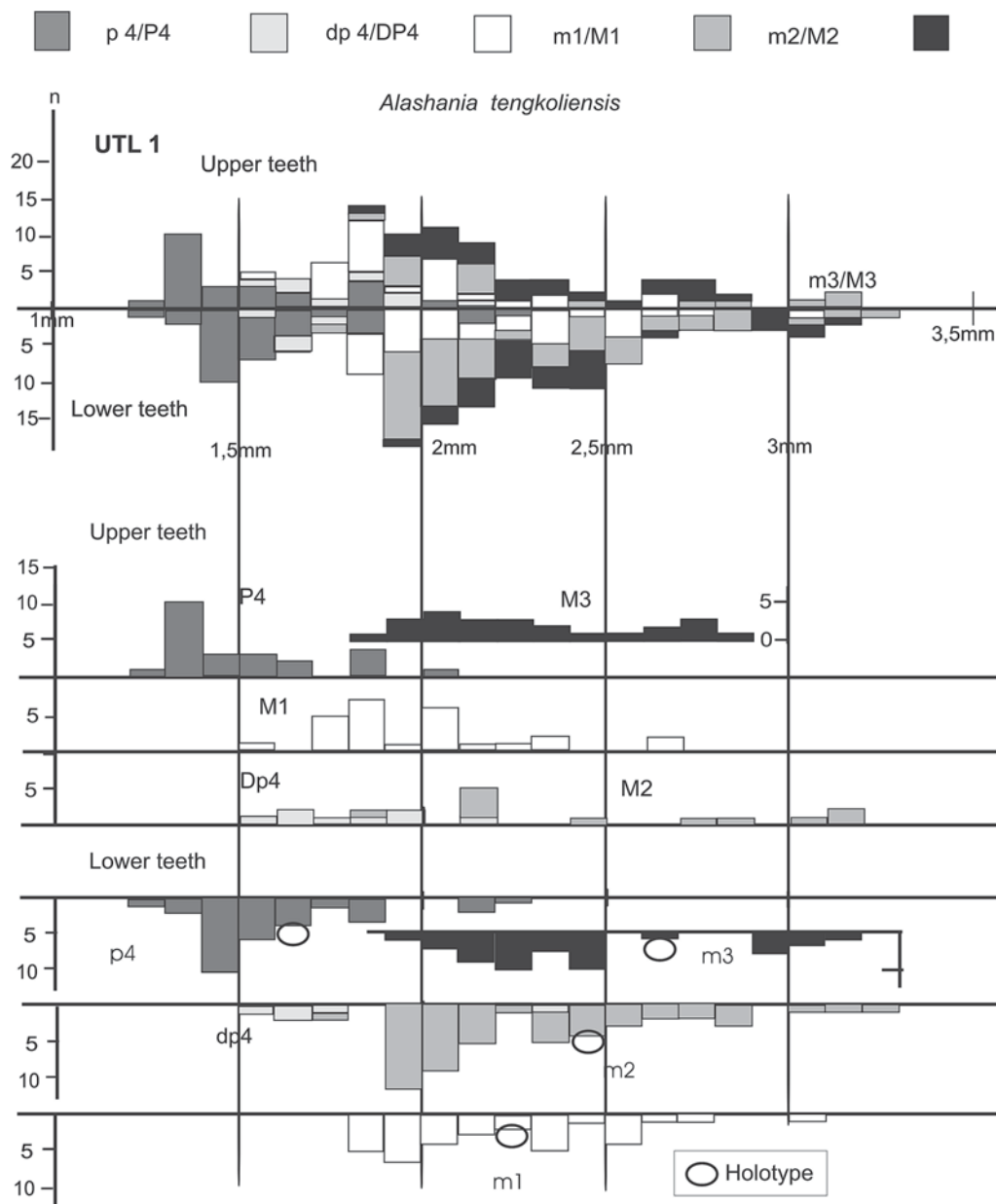


Figure 13.— Histograms of lengths of the lower and upper teeth of *Alashania tengkoliensis* from UTL1.

Description (Plate 5, fig. 21-22, Plate 6, Plate 7)

Dentary: Foramen mentale under the posterior root of p4

Palate: The palate is nearly rectangular, with the two tooth rows slightly convergent anteriorly. The incisive foramen ends at the mid of P4, and the posterior palatine foramen occurs at the level of the posterior half of M2.

Dentition: The wear pattern of upper and lower molars shows two grooves (GRA & GRP) less deep than in *Yindirtemys ulantatalensis*, between two oblique ridges. Cusps

profiles are worn in rectangular angle (close to 90°)

Lower teeth

dp4: The protoconid and metaconid are close and connected by a low protolophid. The ectolophid is low mainly at its junction with the entoconid. The hyposinusid is deep.

p4: The premolar is nearly as wide posteriorly as anteriorly, and clearly lophodont. The junctions of the posterior arms of both protoconid and metaconid draw a widely open V-shape. The ectolophid is medial. The entoconid and entolophid are well-developed, the latter bearing a long labial appendix.

m2 and m3 are of same size, and clearly greater than m1, which is more elongated than m2/m3. The molar ectolophid is quite lingual. On m1, the entoconid is generally connected to the hypoconulid, whereas on m2/m3 the hypoconulid is more frequently linked to the hypoconid. Rarely, a short labial spur can be more or less developed, arising from the angle of the lingual arm of the hypoconulid, and highlighting the hyposinusid. It is the case for a few specimens from UTL1 (the holotype, Plate 6, fig 14; and fig. 13) and for about 10% of the lower molars from UTL4. Lower molars are generally without trigonoid. Rarely, a tiny mesoconid is visible on the ectolophid, close to the metaconid (see table 18), mainly on small specimens of m3.

Localities	UTL4			UTL1		
	m1	m2	m3	m1	m2	m3
Long hyposinusid (hypoconulid connected with the entoconid)	14	11	6	34	3	0
Short hyposinusid (hypoconulid connected with the hypoconid)	6	14	18	1	32	32
Tiny mesoconid on the ectolophid (number of unworn teeth)	2(4)	2(2)	5(7)	1(3)	1(5)	3(12)

Table 18.— Lower molar morphotypes of *Alashania tengkoliensis* nov. gen. nov. sp. within two localities: UTL4 and UTL1 .

Upper teeth

DP3: Two maxillary fragments bear a unicuspid DP3 in front of the anterior root of the DP4.

DP4 bears a small anterocone. The metaloph-posteroloph relation is of type A or intermediate A/B on the few observed specimens, but the short ridge linking the trigon to the posteroloph is very low.

P4: They are larger than those in *T. sigmodon*. The anterior wall is straight and oblate whereas the posterior one is convex. On the three specimens, the central valley is closed. Two cingulae (antero-labial and postero -labial) border the crown.

M1 and M2 are quadrangular. Protoloph and metaloph are not swollen. A little morphological variation is observed in the relationships between the trigon and the posteroloph. The morphotype A is the most frequent, with a transverse metaloph linked to the posteroloph by a short longitudinal crest (cf. table 19). The morphotypes B and C or intermediates (metaloph directly attached to the hypocone or more lingually to the posteroloph, behind the hypocone) are rare on M1/M2. Morphotype B seems to be more frequent on the M3.

Locality	M1/M2					M3			
	▼ morphotype →	A	A/B	B	B/C	D	A	B	B/C
UTL1		29	1	2	1		8	15	0
UTL4		29		8		5M1	2	3	3

Table 19.— Upper molar morphotypes within two localities : UTL1 and UTL4.

The anterosinus is short, due to the relatively weak anterocone. It is yet more marked on M1 than on M2.

Genus *YINDIRTEMYS* BOHLIN, 1946

Synonymy: *Bounomys* WANG, 1997.

Type species: *Tataromys grangeri* BOHLIN, 1946, *non Yindirtemys woodi* BOHLIN, 1946 (Wang, 1997).

Included species

Yindirtemys grangeri (BOHLIN, 1946); *Yindirtemys deflexus* (TEILHARD de CHARDIN, 1926); *Yindirtemys gobiensis* (KOWALSKI, 1974) ; *Yindirtemys suni* (LI and QIU, 1980) ; *Yindirtemys bohlini* (HUANG, 1985); *Yindirtemys ulantatalensis* (HUANG, 1985); *Yindirtemys birgeri* BENDUKIDZE, 1993; *Yindirtemys xiningensis* WANG, 1997; *Yindirtemys ambiguus* WANG, 1997; *Yindirtemys shevyrevae* nov. sp.

Original diagnosis (Bohlin, 1946): "Small tataromyoid rodents with isolated anteroloph, shallow lingual re-entrant and the two posterior buccal re-entrants divided into an outer portion, open buccally, and an inner portion forming a lake. Roots as in *Tataromys*."

Emended diagnosis (Wang, 1997): "Small to large sized ctenodactylid, palate very narrow; cheek-teeth brachydont, uppers having crowns higher lingually than buccally, lowers moderately high; on cheek teeth main cusps swollen and bulbous, loph swollen; P4 protoloph and metaloph complete, equally developed; upper molar anterocone large, sometimes metacone with antecrochet; p4 ectolophid short; lower molars having anterior cingulum, posterior arm of protoconid swollen and crescentic, trigonid basin relatively large, ectolophid situated at the middle, entoconid, hypoconid and hypoconulid crescentic in shape".

Emended diagnosis (this paper): Tataromyinae of small to large size; palate broad to narrow; cheek teeth brachydont and bunio-selenodont: cusps swollen at their base and acute at their top, at least some of them being crescentic (protocone, mesoconid, hypoconulid), generalization of the selenodonty in the most derived species; characteristic wear pattern, producing two main sliding grooves, anterior and posterior (GRA and GRP); mesoconid always present on lower molars; low anterior cingulid

always present, but more or less long; ectolophid varying from occupying the half to the lingual one-third of the teeth.

On upper molars, anterocone always well developed; variable junction of the distal end of the metaloph, from the anterior arm of the hypocone to the beginning of its posterior arm; occurrence of transverse accessory crests (crochet and anti-crochet of the metaloph) variable.

Differs from *Tataromys* in its wear pattern, the selenodonty and the generally strong development of the mesoconid.

Discussion

The characters used by Wang (1997, p.42) to define her genus *Bounomys* are primitive characters found in the species *T. bohlini* Huang, 1985 and *T. ulantatalensis* Huang 1985, such as the swollen cusps, the weak loph, the brachyodonty, and the wide palate. As these two species share derived characters, like an enlarged crescentic mesoconid and other crescentic cusps, we include them in the genus *Yindirtemys*.

***Yindirtemys ulantatalensis* (HUANG, 1985)**

Synonymy: *Tataromys ulantatalensis* HUANG, 1985; *Bounomys ulantatalensis* (HUANG), in WANG 1997.

The species was defined by Huang (1985, p. 28 & 38, fig. 1, pl. I) on lower jaws and isolated cheek teeth only. In the original diagnosis neither the bunodonty nor the occurrence of a mesoconid were indicated. But these characters are significant for distinguishing *Tataromys* from *Yindirtemys*. On the contrary, Wang (1997) underlined the bunodonty of this species in order to include it in her new genus *Bounomys*. Moreover, she described the characters of the upper molars, based on material from two different areas, Ulantatal and Saint Jacques. She mentioned nothing about bunodonty or a mesoconid.

Holotype and type locality: incomplete lower jaw bearing p4-m3, V7341, (p4 = 1,5 mm x 1,5 mm, m1 = 2,7 mm x 2 mm, m2 = 2,8 mm x 2,3 mm, m3 = 3,0 mm x 2,3 mm); from Ulantatal (precise locality unknown).

Paratype and other material: fragmentary lower jaw with dp4-m3; 17 dentary fragments with teeth.

Other localities and stratigraphical range: Ulantatal area (Inner Mongolia): UTL1, UTL4, UTL7, UTL6, UTL8; ULAN I to III (Lower and Upper Oligocene).

Original diagnosis: "Size about *T. sigmodon*; lower molars with accessory longitudinal lingual crests and ectolophids relatively situated in the middle."

Emended diagnosis (Wang 1997): "About 1.5 times the size of *Bounomys bohlini*. On

upper molars, paracone and metacone swollen, metacone larger than paracone, protoloph and metaloph short, anterior cingulum joining protoloph, sinus separated from posterosinus; lower molars usually having a large central basin closed by longitudinal anterior arm and transverse posterior arm of entoconid."

Emended diagnosis (this paper): Medium sized *Yindirtemys* (smaller than *Y. deflexus* and larger than *Y. bohlini*); palate nearly as wide as the molars; bucco-selenodont molars, with high cusps, swollen at their bottom and acute at their top; weakly expressed and low loph and lophids;

On lower molars, high and crescentic mesoconid, at midline of the teeth; mesoconid limited by two vertical grooves, the anterior drawing a clear sinus between metaconid and mesoconid; wide trigonoid basin; additional crests present;

On upper molars, anterocone high, short antesinus; clear posterosinus; morphotypes A and B most frequently observed (A: metaloph curved forward and directly connected to the protocone; hypocone linked to the metaloph by its anterior arm; short posteroloph connected to the posterior arm of the hypocone; morphotype B: metaloph curved backward and connected to the posteroloph-anterior arm of the hypocone junction); additional crests mainly on M3 (crochet, anti-crochet, double junction anterocone-protocone-protoloph)

Measurements:

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	7	2.00	2.16	2.08	0.06075	1.36	1.56	1.46	0.07047
p4	20	1.74	2.04	1.89	0.08379	1.41	1.67	1.54	0.07281
m1	29	2.29	2.91	2.65	0.16128	1.83	2.25	2.00	0.11328
m2	20	2.67	3.45	3.07	0.22100	2.13	2.71	2.40	0.13347
m3	32	2.64	3.74	3.33	0.26268	1.94	2.57	2.35	0.14540
DP4	19	1.72	2.14	1.94	0.11015	1.60	2.00	1.79	0.11754
P4	29	1.58	2.00	1.81	0.09218	1.99	2.43	2.19	0.09603
M1	26	2.10	2.61	2.43	0.15106	1.92	2.48	2.27	0.11886
M2	30	2.56	3.24	2.89	0.17995	2.32	2.96	2.69	0.14650
M3	23	2.45	3.22	2.86	0.20006	2.25	2.88	2.65	0.15798

Table 20.— Measurements of teeth of *Yindirtemys ulantatalensis* (Huang) from UTL7.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	27	1.78	2.36	2.08	0.13873	1.26	1.56	1.43	0.08331
p4	36	1.54	1.97	1.81	0.10424	1.19	1.60	1.40	0.09432
m1	54	2.33	2.97	2.66	0.14045	1.77	2.28	2.02	0.10128
m2	30	2.62	3.47	3.05	0.20425	2.09	2.60	2.36	0.12798
m3	19	2.89	3.66	3.36	0.21513	2.09	2.59	2.41	0.14380
DP4	25	1.76	2.25	2.01	0.12600	1.63	2.08	1.89	0.11337
P4	16	1.79	2.09	1.96	0.08547	1.98	2.37	2.16	0.11396
M1	62	2.01	2.77	2.36	0.21600	1.84	2.61	2.22	0.19406
M2	53	2.07	3.12	2.66	0.27626	2.03	2.93	2.45	0.23646
M3	33	2.41	3.46	2.87	0.49707	2.23	3.09	2.62	0.44477

Table 21.— Measurements of teeth of *Yindirtemys ulantatalensis* (Huang) from UTL4.

L-W m2	L-W m3	L-W M2	L-W M3
2,98-2,11	3,06-2,03	2,43-2,21	2,14-2,27
	3,31-2,18	2,45-2,17	2,17-1,88
	3,34-1,98	2,56-2,33	2,37-2,29
		2,67-2,21	
		2,84-2,26	

Table 22.— Measurements of teeth of *Yindirtemys ulantatalensis* (Huang) from UTL8.

Size analysis (Table 20-22, Fig. 14-16)

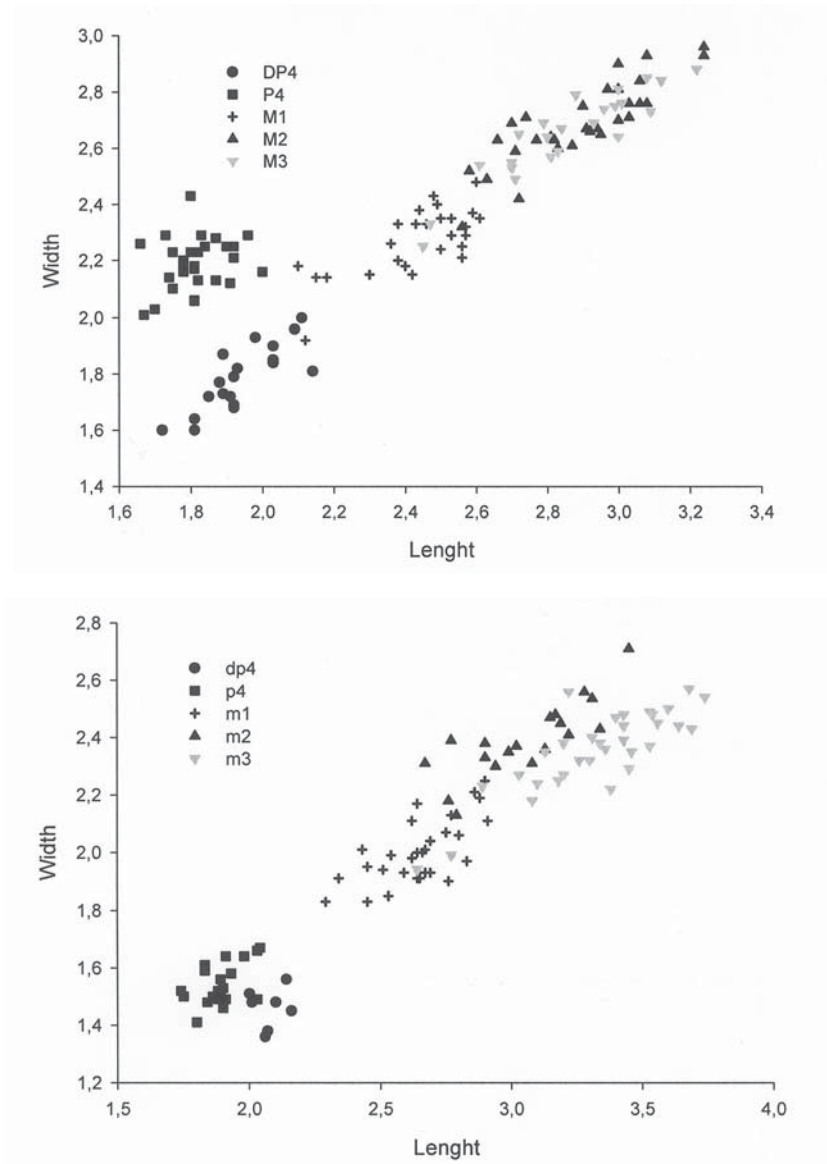


Figure 14.— Bivariate graph (width/length) of the upper and lower teeth of *Yindirtemys ulantatalensis* from UTL7.

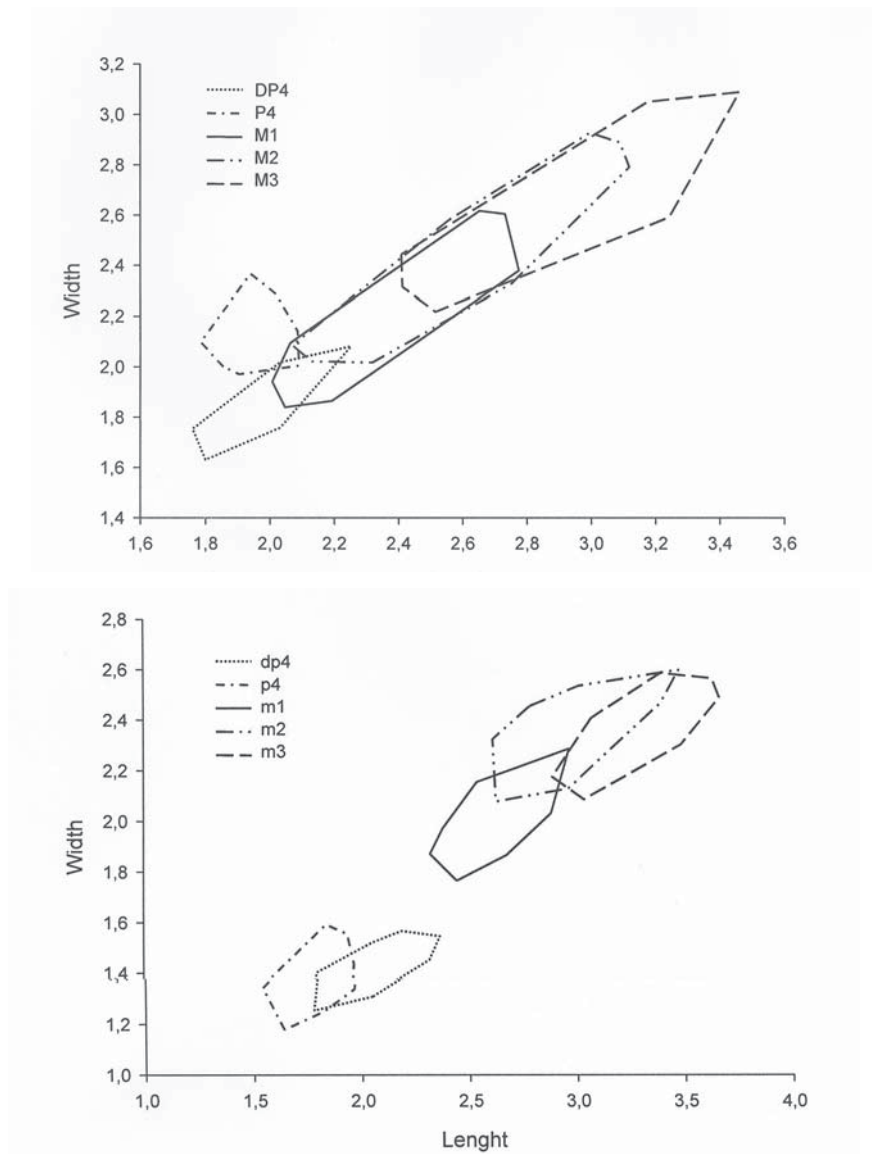


Figure 15.— Bivariate graph (width/length) of the upper and lower teeth of *Yindirtemys ulantatalensis* from UTL4.

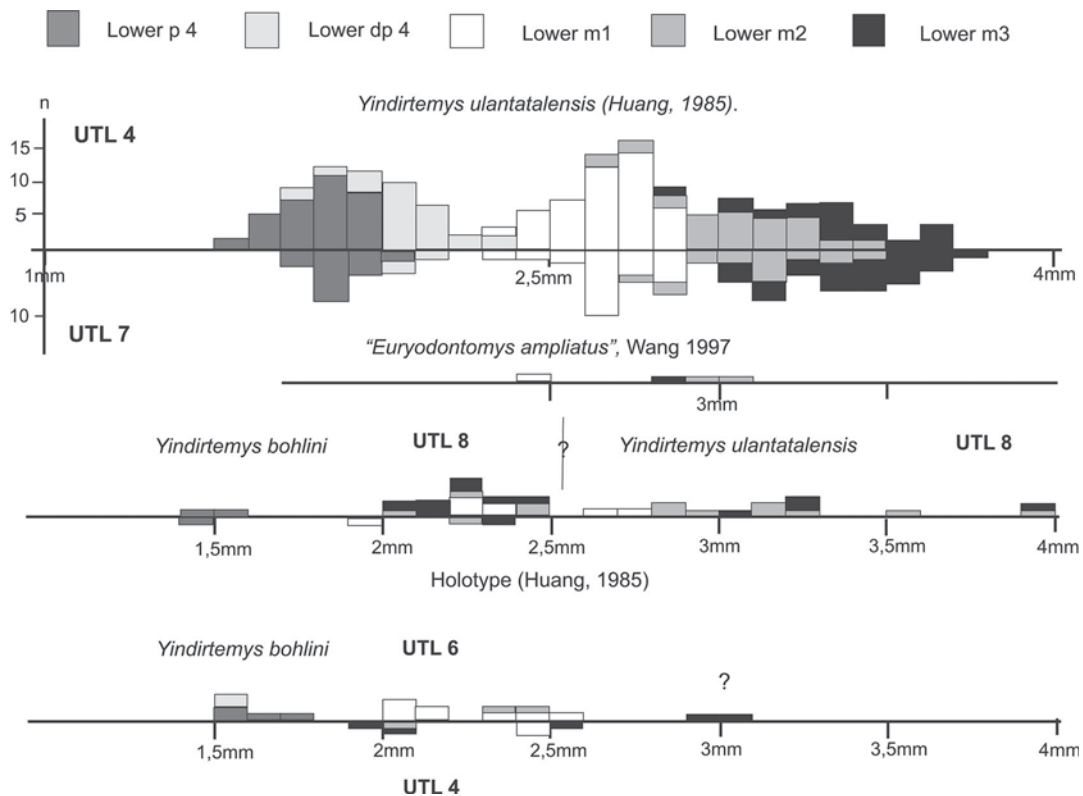


Figure 16. — From top to bottom: Histograms of lengths of lower teeth of *Yindirtemys ulantatalensis* from UTL7 and UTL4; below: Holotype of *Euryodontomys ampliatus* (Wang, 1997); below: *Yindirtemys bohlini* from UTL8, and Holotype after Wang 1997, *Yindirtemys ulantatalensis* from UTL8; below: *Yindirtemys bohlini* from UTL6 and UTL4. ?: limit between *bohlini* and *ulantatalensis*?

The richest locality is UTL4, with a total of 355 teeth. The size distribution (length) on each tooth category, lower and upper, seems normal. A few upper Oligocene teeth (UTL6 and UTL8) fall within this variation (Fig. 16).

p4 and dp4 have the same width, what is logical, in terms of functional adaptation, whereas the dp4 are generally longer than the p4. P4 have the same length as DP4, but the range of variation is less. Despite an overlap of their dimensions, m1/M1 are smaller than m2/M2, m2/M2 shorter than m3/M3. But the overlap of their sizes is greater for upper molars than lower molars. It is the same in UTL7 and UTL8. The holotype of *Y. ulantatalensis* fits the observed variation. Due to the overlap of successive molar dimensions, it is probable that a few teeth were misassigned (m2 versus m3 for example).

Description (Plates 8-10)

Material from UTL7

Dentary: Only one fragmentary dentary shows the beginning of the masseteric crest, at the level of m1. The horizontal ramus seems deeper than that of *A. tengkoliensis* from UTL1. The longitudinal incisor axis draws an angle with the axis of

the tooth row greater than in *A. tengkoliensis* from UTL1. This is probably related to a different movement of mastication, more oblique in *ulantatalensis*.

Lower teeth

p4: It is difficult to separate the p4 of *ulantatalensis* from those of *T. sigmodon*, because of their close size and above all when they are unworn. On the slightly worn specimens, the plunging wear facets, like in the other teeth, could be a means of distinction, as well as the crescentic entoconid + entolophid. A V-shaped crest joins the metaconid and the protoconid, and is open anteriorly. A short ectolophid connects it to the entolophid. Neither hypoconid nor hypoconulid is present. Sometimes a short crest linked at the middle of the entolophid is the only remnant of its arm.

dp4: These teeth, generally weakly worn, have acute cusps, swollen at their bottom. The lophids are narrow and low. The mesoconid is close to the metaconid and protoconid, both the latter close together. Lower crests can connect these cusps. The mesoconid-hypoconid junction is crescentic, and forms a mure, more or less high, oblique, limiting the main oblique valley of the tooth. The main wear plan is located there. It is indicated, on worn teeth, by plunging facets posteriorly on this mure, and on the metaconid, mesoconid and hypoconid, as on the anterior slope of the hypoconid and entoconid. These two cusps can be, or not, connected by a crescentic loph, from the anterior arm of the hypoconulid and the posterior arm of the entoconid. A low small cuspid can develop on the labial shelf of the sinusid, and on the lingual end of the mesosynclinid.

m1-2-3: Their striking characters are the prominent metaconid, and the crescentic lophids connecting the cusps, oblique to the longitudinal axis of the teeth. These cusps are swollen at their bottom, and acute at their top. Another one is the orientation of the wear plans. On dp4, we have noted the oblique groove (GRP) defined by the posterior slopes of the metaconid/mesoconid/hypoconid, opposite to the anterior slopes of the hypoconulid/entoconid. An anterior groove is added on the molars, shorter than the first, limited by the posterior slopes of the protoconid/metalophid on one hand, and, on the other hand, by the anterior slopes of the metaconid/mesoconid (GRA). This last groove starts on the precedent tooth, where it is marked on the posterolingual arm of the hypoconulid. Wear facets of these two grooves give a peaked roof shape to the mesoconid.

m1 is the smallest molar, with its anterior width shorter than the posterior. m2 is slightly larger, and rectangular, with a posterior cingulum lingually curved from the hypoconulid. m3, larger than m2, shows a more prominent hypoconulid.

The morphological variability is the same for the three molars. They do not show a true anterior cingulum, but a weak shelf at 1/3 height of the crown. It is well marked on a single m3. Metaconid and protoconid are connected by the metalophid I. The mesoconid can be longitudinally connected directly to the metalophid I. It is more often connected both to the posterior arm of the metaconid by the way of the mesolophid, and to the posterior arm of the protoconid. A short lingual longitudinal crest joins the end of the mesolophid to the entoconid. Sometimes, it is interrupted and the entolophid is related with the ectolophid. In most cases, the mesolophid is connected to the hypolophid by the intermediate ectolophid. A weak crest prolongates posteriorly

this connection, on the hypoconulid arm.

Upper molars

The shape of the cusps and the peculiar disposition of the wear facets, complementary to the lower ones, are very helpful to distinguish *Y. ulantatalensis* upper molars. The loph including the protocone is crescentic, and sculptured by two opposite wear facets making a peaked roof. The cusps are thus sharpened by the sliding movements. We find also oblique wear striations on the enamel surfaces, as observed in lower molars. The first groove is delimited on the anterior slope of the protocone, and the posterior slopes of the anterocone and paracone. The second one, parallel to the first, acts on the posterior slope and arm of the protocone, on that of the metacone/metaloph, as well as on the anterior slopes of the hypocone/posteroloph, in continuity with the anterior slope of the anteroloph of the following tooth. The wear and cusp patterns are similar from the DP4 to the M3.

P4: Most of them are oval and symmetrical, wider and shorter than the DP4. They generally show two cusps (paracone and protocone) connected anteriorly by a high protoloph, and posteriorly by the two posterior arms of these cusps. This « metaloph » is related with a short postero-labial cingulum, sometimes prolonged by a short lingual crest. The anterior cingulum can be absent, or reduced to a small central or lingual anterocone, sometimes lingually elongated. The central basin is exceptionally open distally (2/31).

DP4: The anteroloph is much shorter, more often limited to an anterocone, or extended to half the width of the tooth. The trigon basin occurs as (14/22) a slightly asymmetrical triangle, posteriorly bordered by the metaloph, and anteriorly by the protoloph (Plate 9, fig. 21-22). On eight specimens, a very low longitudinal metaloph-posteroloph connection exists, and only on three DP4, does this connection distort the mesosyncline backwards.

Molars: M1 and M2 are quadrangular, M2 being quite larger than M1. M3 are as long as M2, sometimes slightly shorter, with a hypocone and posterior cingulum reduced. The base of cusps are swollen, and their apex acute. They are linked by narrow lophs, very low in the central part of the teeth. The anterocone, frequently prominent, is situated at the midline of the tooth and it is prolonged by a narrow antero-labial cingulum. A low crest to the posterior base of the anterocone connects the protoloph. The metaloph is sometimes preceded by a short anterior crochet (M1: 1/25; M2: 7/28), or it is only swollen at this level. On the M1 and M2, the posterior arm of protocone and the metaloph converge towards a short endoloph, connecting them to the hypocone. The junction of protocone and metacone on the hypocone can be, rarely, separated on M2. This separated junction is more frequent on M3.

The mesosyncline is slightly asymmetrical, slightly oblique backwards, drawing a 100° angle at the level of the junction of the two posterior arms. A prolongation of this mesosyncline is deeper backwards on M3, or on the other molars displaying a separated junction of the two arms on the hypocone. In all cases, molars show a clear posterolingual sinus and a short anterosinus. The latter is never observed on *T. sigmodon*.

Material from UTL4

The size variation is somewhat stronger, but this fact can be the result of better fossil representation: the teeth are more numerous in UTL4. For example we can observe variations of the height of the metaloph. On M3, the sinus is more or less deep. The effects of wear accentuate this: at the top of the crown, the sinus is short, but is lengthened downward. On these M3, the frequent occurrence of a "crochet" on the anterior wall of the metacone can be noted (Plate 10, fig. 11a, 21a) (21 / 38). In one specimen (Plate 10, fig. 12a), it even exhibits a weak basal connection to the posterior wall of the paracone as a first indication of the "deflexus" structure found in more modern populations of the species *Y. bohlini* of UTL6 and *Y. ulantatalensis* of UTL8 (see below) and in *Yindirtemys deflexus* (p. 164-165). On M1-M2, the "crochet" is only exceptionally present (2 / 80). It has not been observed on DP4 (0 / 27). For the rest, the morphological characters and the size are similar.

Material from UTL6

It is difficult to identify this species in the scarce material from UTL6. About thirty upper and lower teeth share characters of the species *Y. ulantatalensis*, but also of *Y. bohlini*. The main difference with *Y. ulantatalensis* is that the M3 exhibit a well developed crest between metacone and paracone described later as "deflexus" structure (Plate 10, Fig. 23a & 24). This crest connecting the metacone with the paracone is typically described for the species *Yindirtemys deflexus* (see below). As for size the material from UTL6 is smaller than that of UTL4, and better corresponds to *Y. bohlini*, so those teeth are referred to the species *bohlini* (see below).

Material from UTL8

Few teeth from UTL8 can be referred to *Y. ulantatalensis*. Their general characters are not different from the characters of the UTL4 and UTL7 populations. However, the cusps and crests, especially the ectolophid, are somewhat higher and the relief produced by wear is flatter, which is more easily visible on the anterior profile of lower molars. Some of the upper third molars possess the "deflexus" structure. Two teeth (1m3 and 1m1-2) are larger but do not display distinctive features. The size range of the molars (m1-m3) in the lower tooth range is moved toward larger dimensions for m1 to m3. It can be stated that there is a slight increase of size (see Fig. 16) and of "hypsodonty" in the *Y. ulantatalensis* of UTL8 compared to UTL4 and UTL7. The stronger ectolophid in the lower molars, and connected to this, the more flattened relief of wear, and further the "deflexus" structure in the M3, indicate a more advanced evolutionary stage for this *Y. ulantatalensis* population.

Yindirtemys bohlini (HUANG, 1985)

Synonymy: *Tataromys bohlini* HUANG, 1985; *Boumymys bohlini* (HUANG), in WANG 1997; *Euryodontomys exiguus* new species, Wang 1997.

Among the jaws originally assigned to the species *bohlini* (Huang 1985), Wang

(1997) separated a mandible (IVPP V 7350.4) as holotype of a species newly described by her as *Euryodontomys exiguus*. Since the dentition of the specimen is strongly worn and because no other material was included in the taxon, its tooth pattern partly remains unknown. Nevertheless, contrary to Wang (1997: 56), closer relationships to *Karakoromys decessus* can be excluded, since in the latter no connection between the ectolophid and the metaconid exists. The occlusal picture produced in progressive wear stages is completely different: in *Karakoromys* the enamel crest delimiting the dentine area posterior to the metaconid is not straight but instead shows a marked sinus, and no enamel pit occurs within the dentinal area. As to the proportion of the cusps of the lower molars in Wang's specimen, the hypoconulid-complex is relatively short. This is a common feature of the species *bohlini*. There are actually no characters, in the specimen considered by Wang that would suggest its separation from Huang's species.

Holotype: V7348, (IVPP) fragmentary skull, with complete tooth rows, and mandibles.

Type locality: Ulantatal area, Central Mongolia (surface collection: imprecise locality)

Localities in Ulantatal area and stratigraphical range: UTL4, UTL6, UTL8 (ULAN II-III, Late Oligocene).

Original diagnosis (Huang, 1985, p.29-31, 38): "A small *Tataromys*, size about those of *T. grangeri* or *Karakoromys decessus*; anteroloph not connected with protocone; external valley straight and not bent backwards interiorly on the upper molars. Lower molars similar to those of *T. ulantatalensis* morphologically, but without accessory longitudinal crests on the lingual side; hypolophid II poorly developed and entoconid rather isolated."

Emended diagnosis: Size about that of *Tataromys grangeri* or *Karakoromys decessus*; anteroloph may be not connected with protocone on unworn teeth, but always connected after moderate wear. Lower molars similar to those of *Yindirtemys ulantatalensis* morphologically, with well developed mesoconid separated from the posterior wall of the protoconid by a vertical groove, but cuspids less crescentic, and accessory crests less numerous.

Measurements (Figure 16 and Tables 23-25)

	Length	Width
m1	2,43	1,83
	2,47	1,91
m2	2,04	1,67
m3	1,98	1,56
	2,04	1,67
	2,08	1,71
	2,56	1,99

Table 23.— Measurements of lower teeth of *Yindirtemys bohlini* (Huang) from UTL4.

L-W dp4	L-W p4	L-W m1	L-W m2	L-W m3	L-W DP4	L-W P4	L-W M1	L-W M2	L-W M3
1,71-1,13	1,66-1,46 1,66-1,54 1,86-1,73	1,96-1,47 2,05-1,57 2,08-1,48 2,12-1,63 2,20-1,70 2,36-1,86 2,48-1,74 2,59-1,93	2,40-1,92 2,49-2,07 2,69-2,03	3,00-2,06 3,05-2,20	1,96-1,80 2,08-2,04	1,32-1,77 1,46-1,88 1,49-2,08 1,54-1,74 1,64-1,86	2,16-2,13 2,19-2,06 2,21-2,14	2,36-2,15 2,47-2,46	2,03-1,99 2,08-2,05 2,18-2,21

Table 24.— Measurements of (complete) teeth of *Yindirtemys bohlini* (Huang) from UTL6.

L-W p4	L-W m1	L-W m2	L-W m3	L-W DP4	L-W P4	L-W M1	L-W M2	L-W M3
1,41-1,05	2,10-1,50	2,03-1,48	2,11-1,64	1,51-1,46	1,27-1,41	1,75-1,45	1,96-1,76	1,72-1,76
1,44-0,94	2,26-1,59	2,24-1,63	2,14-1,63		1,34-1,47	1,91-1,54	2,07-1,95	1,78-1,62
1,54-1,26	2,29-1,53	2,45-1,76	2,26-1,71				2,11-1,82	1,91-1,66
1,56-1,12	2,29-1,72		2,37-1,68				2,15-2,12	1,95-1,66
	2,32-1,62		2,37-1,74				2,21-1,88	1,99-1,68

Table 25.— Measurements of (complete) teeth of *Yindirtemys bohlini* (Huang) from UTL8.

<i>Y. grangeri</i>	Lxw p4 mm	Lxw m1 mm	Lxw m2 mm	Lxw m3 mm
Tb 586 TYPE	1.2x1.1	1.5x1.3	1.5x1.4	1.9x1.5
Tb 588	1.1x1.1	1.4x1.3	1.4x1.5	1.6x1.5
<i>Y. woodi</i>	L x w M3 mm			
TYPE	1.7x1.6			
<i>Y. bohlini</i>	Lxw P4 mm	Lxw M1 mm	Lxw M2 mm	Lxw M3 mm
TYPE	1.4x2.0	1.8x1.9	2.1x2.3	2.1x2.0
	Lxw p4 mm	Lxw m1 mm	Lxw m2 mm	Lxw m3 mm
	1.4x1.3	2.0x1.6	2.2x2.05	2.3x2.0

Table 26.— Measurements of the holotype and syntypes of *Yindirtemys grangeri*, *Y. woodi* and *Y. bohlini*.

Description (Plate 10, fig. 23-25, Plate 11)

Material from UTL4

A few lower teeth (1 m2, 2 m1, 4 m3), smaller than those of *Y. ulantatalensis* of the same locality, are referred to *Y. bohlini*. The cusps are slightly less crescentic, and the accessory crests not frequent. Peculiarly, the lingual wall connecting the entoconid and metaconid is not developed as in *Y. ulantatalensis*. However, a short and low crest, less lingual, can join partly or completely the entoconid with the mesoconid, and another incomplete one with the hypolophid. The mesoconid is limited anterolabially by a vertical groove. Respectively on their labial and lingual border, the sinusid and the mesosynclinid are limited by a low cingulum.

It is difficult, even impossible, to identify the upper teeth of *Y. bohlini*. With their size, their swollen cusps, their modes of wear and their pattern (morphotypes A and D), they resemble those of the smallest teeth of *Y. ulantatalensis* or of *Alashania tengkoliensis* nov. gen. nov. sp., or with the largest teeth of *Y. shevyrevae* nov. sp. The great difference in size between the successive molars along the tooth row adds to these difficulties. It would be necessary to get complete tooth rows, and much more material, for distinguishing various sources of variability, and thereby, for establishing the tiny

diagnostic characters for the upper molars.

Material from UTL6 (Plate 11, fig. 1-6)

Teeth smaller than those of typical *Y. ulantatalensis* can also be distinguished in UTL6 material, and determined as *Y. bohlini*. (5 p4, 8 m1, 10 m3; 5 P4, 2 M1, 6 M2?, 1 M3). The lower p4, not recognized in UTL4, is a "miniature" of the *Y. ulantatalensis* corresponding tooth. Features of lower molars are the same as in UTL4. We have been able to identify upper molars of *Y. bohlini* in this locality, because their size is clearly out of the *Y. ulantateleensis* range, even if, once more, their morphology appears to be a miniature of that of *Y. ulantatalensis*.

Material from UTL8 (Plate 10, fig. 15-20 and 22-25)

A few teeth, also smaller than those of typical *Y. ulantatalensis*, (4 p4, 8 m1-2, 6 m3; 2 P4, 3 M1?, 5 M2, 5 M3) diverge clearly from the evolutionary trends towards elevation of lophs, increasing selenodonty and flattening of the occlusal surface of *Y. ulantatalensis* from this locality. They seem more conservative, with the general pattern quite similar to that of *Y. bohlini* from UTL4 and UTL6: no accessory crests, a medial ectolophid, a little crescentic mesoconid and hypoconulid, a mesolophid short and connected with the posterior arm of the metaconid. On only one m3, two crests connect the mesoconid to both the entoconid and the ectolophid. The P4 is rounded, with an anteroloph and a posteroloph. On the DP4, the hypocone + the posteroloph are separated from the protocone (morphotype D). M1 and M2 show a connection between the posterior arm of the protocone and the hypocone (morphotype A). The anterocone is isolated or connected with the protoloph. Twice, a medial connection between the anteroloph and the protocone separate a lingual pit from the labial part of the anterosyncline. The antesisinus is short, whereas the sinus is deep. The main difference with the small population of *Y. bohlini* from UTL6 is the "generalization" of the "deflexus" structure: with a central pit in the mesosyncline. But it is necessary to keep in mind that only a few teeth of this hypothetical *Y. bohlini* lineage are known.

Discussion

In the light of the Ulantatal material, some taxonomic ambiguities can be underlined. It is the case for the species *Y. grangeri*, *Y. woodi* and *Y. bohlini*. Bohlin (1946) described the species *Y. grangeri* on the basis of lower teeth from Taben Buluk (holotype Tb 586). Wang (1997) clearly shown that the isolated M3, holotype of *Y. woodi*, can be synonymized with *Y. grangeri*. The diagnosis of Wang for the two remaining species was not really discriminant, because she listed primitive characters (transverse lophs, transverse mesosinus) and common derived features ("lunar-shaped", i.e. crescentic, cusps). The main difference is the complex connexion of the M3 metacone, with the protocone, the posteroloph, and the anterior arm of the hypocone, but we have seen that this character is variable in different *Yindirtemys* populations. *Y. grangeri* is described from the Upper Oligocene Hsanda Gol formation, and *Y. bohlini* from an undetermined locality in the Ulantatal formation. Our studies show that the species also occurred during the Upper Oligocene. If the type

of *Y. grangeri* seems to be smaller than *Y. bohlini*, the differences of size observed between them are not quite important compared to the variation observed in well-documented tataromyine populations in Ulanatal area. However, due to the small sample sizes, we cannot definitely synonymize the two species.

Yindirtemys shevyreva nov. sp.

The taxon newly described here exhibits a small mesoconid on its lower molars and, hence, possesses a feature exclusively found only in species of the genus *Yindirtemys* and not present in any other ctenodactylid species. This is why it is as well included in *Yindirtemys*. Within this genus it is, however, somewhat apart because this feature, i.e., the mesoconid, is less strong and there is no vertical groove separating its posterobuccal wall from the posterior wall of the protoconid. Also no indication of selonodonty is visible. Additional material will probably allow separation from *Yindirtemys* as an independent genus.

Derivatio nominis: in memory of the Russian vertebrate paleontologist Nina Shevyreva.

Holotype: fragmentary left dentary with p4 to m3, UTL7-86 (length x width in mm: p4: 1,10 x 0,88; m1: 1,57 x 1,21; m2: 1,76 x 1,47; m3: 1,79 x 1,41)

Type Locality and stratigraphical range: UTL7, from Ulanatal area, Inner Mongolia (China), Upper Oligocene, Unit ULAN II

Localities and stratigraphical range: UTL1, UTL4, UTL6, UTL8, from Ulanatal area, western part of Inner Mongolia (China), Upper Oligocene, Unit Ulanatal I to Ulanatal III; Unit B in the sections of the Tsagan Noor basin, Valley of the Lakes (Central Mongolia).

Diagnosis: Comparable to *Tataromys minor* and *Yindirtemys grangeri* in its size; mesoconid of lower molars present but smaller and less prominent than in the species *Y. grangeri*; no vertical groove on the posterior wall of the protoconid separating mesoconid and protoconid developed; cones more rounded than in *Tataromys minor* and less selonodont than in *Yindirtemys grangeri*; in the upper molars connection between metaloph and hypocone or posteroloph variable with most frequent morphotypes B, B/C and C.

Measurements (Table 27-31, fig. 17)

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	5	1.24	1.30	1.26	0.02608	0.78	0.90	0.85	0.04868
p4	8	0.98	1.20	1.07	0.07386	0.82	0.92	0.87	0.03583
m1	12	1.36	1.73	1.55	0.10475	0.95	1.31	1.21	0.09764
m2	9	1.58	1.92	1.78	0.11681	1.27	1.52	1.43	0.09460
m3	11	1.44	1.89	1.73	0.14812	1.01	1.46	1.28	0.13710
DP4	1			1.40				1.23	
P4	4	0.98	1.02	1.00	0.01708	1.22	1.26	1.24	0.01826
M1	5	1.35	1.60	1.51	0.09680	1.31	1.47	1.36	0.06348
M2	9	1.53	1.71	1.62	0.06652	1.41	1.64	1.55	0.07794
M3	10	1.33	1.62	1.52	0.09134	1.29	1.55	1.46	0.09546

Table 27.— Measurements of teeth of *Yindirtemys shevyreva* nov.sp. from UTL7.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	9	1.10	1.39	1.23	0.11489	0.67	0.91	0.82	0.07280
p4	22	0.90	1.16	1.00	0.06192	0.69	0.95	0.81	0.05720
m1	42	1.30	1.78	1.50	0.08944	0.96	1.26	1.13	0.07041
m2	71	1.40	1.95	1.67	0.12039	1.11	1.62	1.32	0.09633
m3	63	1.23	1.94	1.68	0.17685	0.92	1.60	1.25	0.14350
DP4	12	1.07	1.25	1.16	0.06281	1.04	1.25	1.12	0.06708
P4	18	0.97	1.19	1.09	0.05345	1.21	1.49	1.34	0.08795
M1	76	1.25	1.61	1.45	0.08021	1.17	1.55	1.35	0.08921
M2	50	1.26	1.76	1.57	0.11343	1.24	1.74	1.48	0.10753
M3	65	1.29	1.80	1.52	0.11820	1.16	1.69	1.42	0.12126

Table 28.— Measurements of teeth of *Yindirtemys shevyreva* nov.sp. from UTL4.

	n	Length				width			
		Min.	Max.	Average	sd	Min.	Max.	Average	sd
dp4	8	1,07	1,36	1,22	0,10063	0,73	0,79	0,75	0,02507
p4	7	1,01	1,13	1,07	0,04776	0,74	0,86	0,80	0,04670
m1	16	1,25	1,65	1,47	0,11337	0,80	1,16	1,01	0,11094
m2	25	1,46	1,86	1,66	0,09566	1,11	1,38	1,23	0,06718
m3	11	1,42	1,98	1,69	0,19173	1,04	1,43	1,23	
DP4	7	1,07	1,35	1,18	0,08923	0,88	1,25	1,01	0,15395
P4	3	1,04	1,14	1,10	0,05508	1,25	1,45	1,36	0,10263
M1	27	1,23	1,57	1,38	0,08400	1,06	1,41	1,22	0,10606
M2	25	1,37	1,70	1,54	0,08863	1,16	1,51	1,37	0,08335
M3	31	1,22	1,67	1,45	0,10704	1,11	1,53	1,28	0,10331

Table 29.— Measurements of teeth of *Yindirtemys shevyreva* nov.sp. from UTL1.

L-W dp4	L-W p4	L-W m1	L-W m2	L-W m3	L-W P4	L-W M1	L-W M2	L-W M3
1,31-0,91	1,41-1,20	1,41-1,13	1,79-1,39	1,63-1,24	1,19-1,43	1,57-1,33	1,63-1,57	1,41-1,35
	1,41-1,30	1,42-1,11	1,83-1,40	1,72-1,36	1,21-1,46	1,59-1,44	1,72-1,70	1,47-1,38
	1,42-1,27	1,49-1,23	1,84-1,50	1,99-1,33	1,28-1,50		1,87-1,79	1,53-1,48
	1,46-1,34	1,56-1,29	1,85-1,56	2,07-1,77	1,37-1,62		1,88-1,82	1,86-1,68
	1,47-1,26	1,60-1,23	1,87-1,48				1,94-1,83	
		1,62-1,33	1,89-1,42				1,99-1,91	
		1,68-1,38					2,00-1,74	

Table 30. — Measurements of teeth of *Yindirtemys shevyreva* nov.sp. from UTL6.

L-W m1	L-W m2	L-W m3	L-W M1	L-W M2	L-W M3
1,37-1,07	1,67-1,30	1,92-1,47	1,41-1,43	1,57-1,53	1,48-1,46
1,44-1,22	1,67-1,44	1,93-1,47	1,45-1,45	1,73-1,65	1,51-1,40
1,49-1,13	1,68-1,38	2,00-1,53	1,51-1,51	1,74-1,61	
1,55-1,22	1,76-1,41	2,04-1,58			
1,56-1,15	1,76-1,47				
1,58-1,24	1,79-1,41				
1,64-1,23	1,83-1,48				
1,68-1,24	1,88-1,47				
	1,88-1,50				

Table 31. — Measurements of teeth of *Yindirtemys shevyreva* nov.sp. from UTL8.

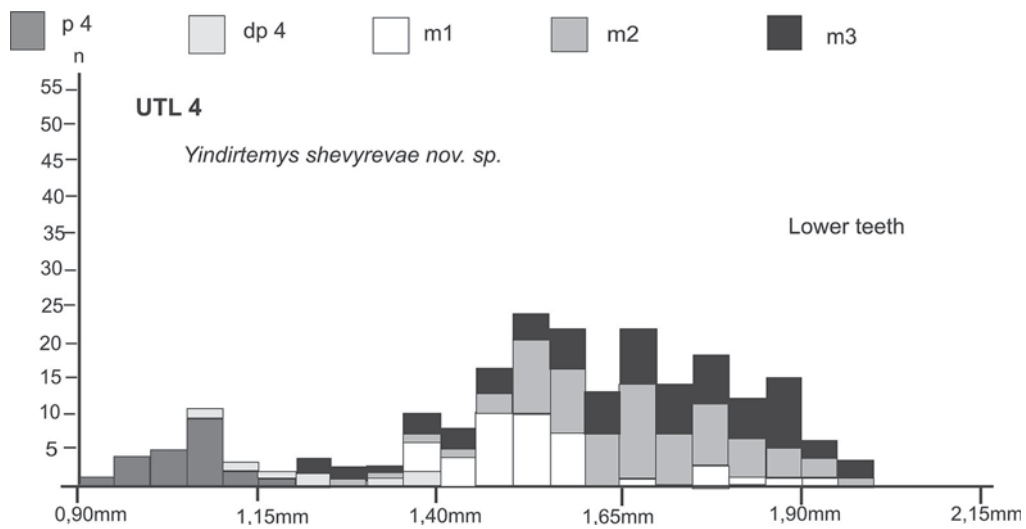


Figure 17. — Histograms of lengths of lower teeth of *Yindirtemys shevyreva* nov. sp., from UTL4.

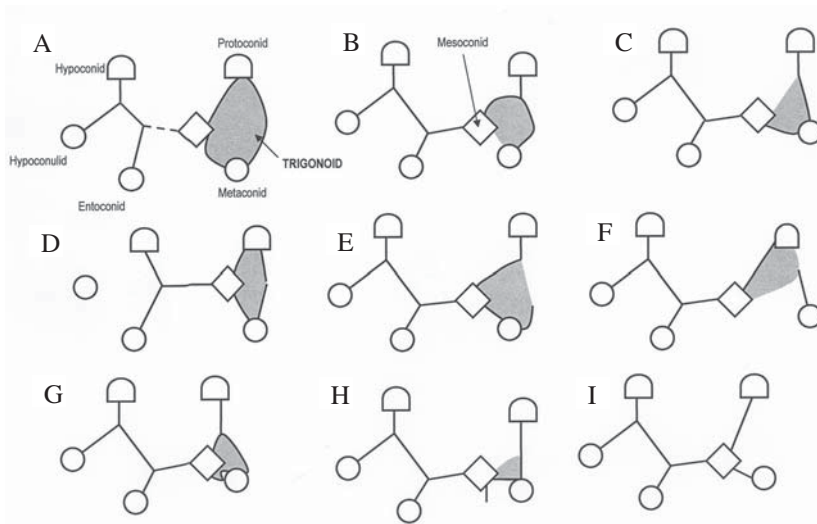


Figure 18.— Variation of the trigonoid area and of the ectolophid position in *Yindirtemys shevyreva* nov. sp. m3 from UTL4 (Ulanatal area, Inner Mongolia, China). A: large trigonoid; H-I: trigonoid incipient or absent; B to G: transitional variations.

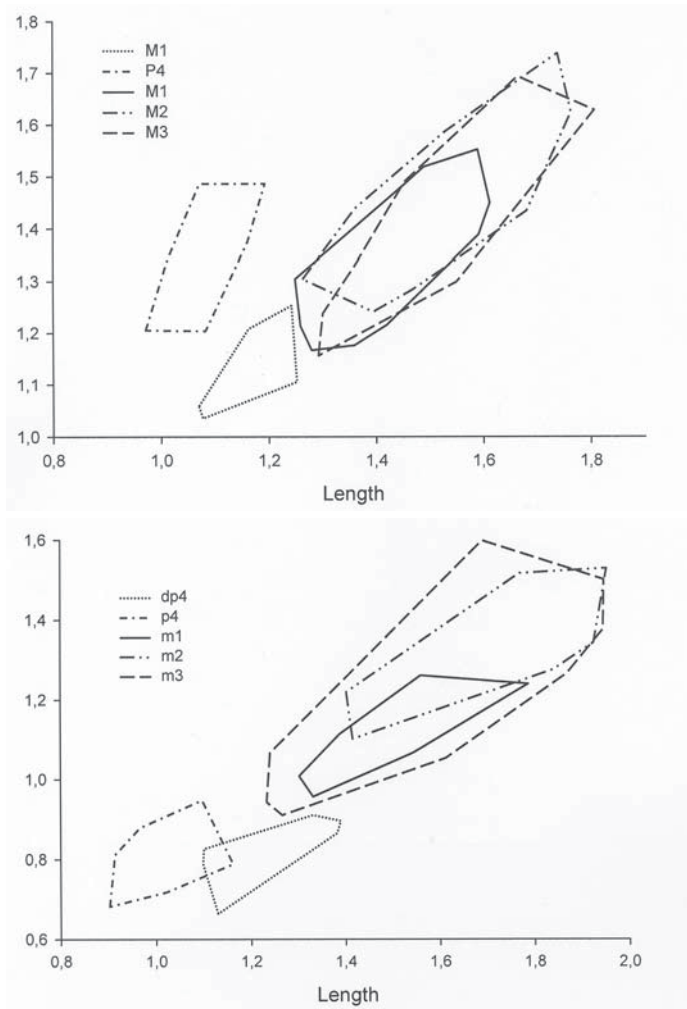


Figure 19.— Bivariate graph (width/length) of the upper and lower teeth of *Yindirtemys shevyreva* from UTL4.

The size variation of the molars is the same as that observed in *Tataromys minor*. Within the upper and lower tooth ranges, the second molar is the largest. The last molar is only slightly smaller while the first molar is clearly smaller than the second one. The size of the teeth from the two youngest Ulanatal localities, UTL6 and UTL8, are situated in the upper variation of the UTL1, 7 and 4, and m3 appears to be relatively larger. The population is not abundant enough to characterize another evolutionary grade.

Description (Plates 12-14)

Lower teeth

The size of p4 is close to that of *T. minor*. Considering the holotype (Plate 12, fig. 1; mandible UTL7-86) as jaw of reference, about twenty specimens could be separated from the respective size class of the sample of UTL4. The posterior part of the tooth crown is broader and the cones are less sharpened than in *T. minor*. The angle of the V shaped crest between the protoconid and metaconid is more acute than that in *T. minor*. The entoconid sometimes continues as an entolophid.

In dp4 the metaconid and protoconid are close. Their ectolophid is continuous. The triple point of the trigonoid formed by the connection of the posterior arms of the protoconid and metaconid with the ectolophid is usually strengthened to form a weak mesoconid. (UTL4: 7/9, UTL7: 3/6). The trigonoid is sometimes closed anteriorly by the formation of an anterolophid between protoconid and metaconid (closed: UTL4: 3/9, UTL7: 3/6; open: UTL4: 4/9, UTL7: 1/6). In some cases the ectolophid continues only to the metaconid. The hypolophid has sometimes a free end or reaches the entoconid or the hypoconid or is connected to both at the same time.

The lower molars show the same type of variation (fig. 18). The mesoconid may be strong and occupy the center of the crown. In this case the trigonoid pit is generally well-developed and the ectolophid is placed near the sagittal middle axis of the tooth. In the locality UTL4 most m1 (42/48) and m2 (44/52) and about the half of the m3 (27/54) exhibit a trigonoid pit of this type (Fig. 18 A). Sometimes, the ectolophid and mesoconid are removed more lingually together with a reduction and even disappearance of the trigonoid pit (Fig. 18 H-I) (UTL4: 7/54 m3, 5/52 m2, 5/48 m1; UTL1: 4/8m3, 1/33m2). In these cases, interruptions of connections between the three anterior conids also can be observed. And there are, of course, transitional morphotypes (UTL4: 3/52 m2, 10/54 m3) (Fig. 18 B, C, D, E, F, G). It can be noted that the ectolophid normally occupies a more central position than in *T. minor* and only in some cases has a more lingual position. Beyond the more irregular lophids and the more swollen cusps, the presence of the mesoconid is the more significant character to distinguish the two species.

In molars of older individuals the wear of the mesoconid produces a peaked roof shape with two divergent slopes, like in *Y. ulantatalensis*. In even more advanced stages the surface of wear becomes flattened very quickly. As found in *Y. ulantatalensis*, two grooves guide the movement of the teeth during occlusion, while in *T. minor* only one wear facet is formed. The posterior one runs obliquely with the same direction as the ectolophid, and affects the junction of the anterior arms of the

hypoconulid and entolophid with the ectolophid. The anterior one crosses obliquely the basin of the trigonoid.

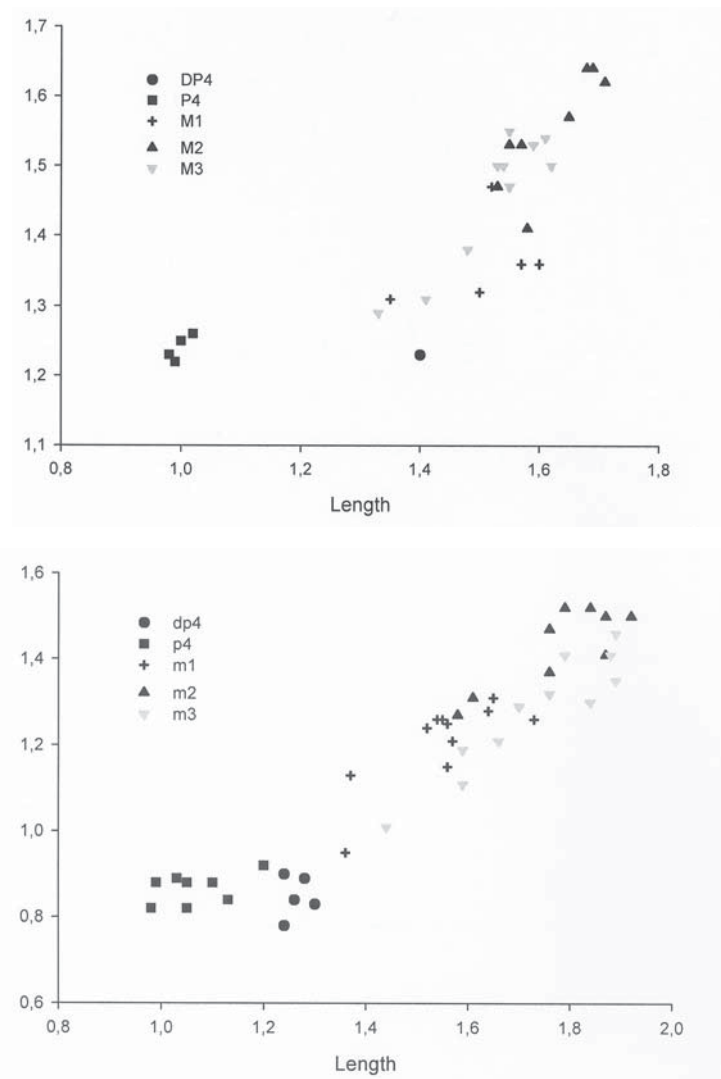


Figure 20. — Bivariate graph (width/length) of the upper and lower teeth of *Yindirtemys shevyrevae* from UTL7.

Some rare supplementary structures can also be found in the m2 and m3. In one single UTL4 m2 a proper mesolophid is present. Predominantly the anterior arm of the hypoconulid is connected to the posterobuccal arm of the hypocone (UTL4: 47/48 m1, 57/58 m2, 49/49 m3). Only in two specimens the connection is interrupted and a tendency of the hypoconulid to join the entoconid can be observed. In one m2 an accessory lingual crest is developed, which has the same orientation as the ectolophid and runs from the entoconid to the mesoconid. Finally various small accessory crests can be found within the trigonoid structure (UTL4: 5/58 m2; UTL7: 1 m2, 1 m3).

The main striking difference with *Y. bohlini* is the absence of a vertical groove along the mesoconid, and the lesser development of that cusp.

A few lower teeth seem to be smaller than the others (UTL4: 13 m1, 9m2, 5m3), but their morphology is quite similar, and can be integrated in the variation of the population.

Upper teeth

P4: Some teeth can be referred to *Yindirtemys shevyreva* nov. sp., despite the lack of a maxillary with complete tooth row. Among small isolated P4 from UTL4 and UTL7, some differ from *Tataromys minor* in their more rounded outline. The anterior slope is less flattened. A low and short anterolabial cingulum can occur, and be reduced to a small cusp. There is rarely an anteroloph: paracone and protocone are separated, and the central valley is open anteriorly. Frequently, the paracone has only an oblique posterior arm, joining the posterior arm of the protocone to the posterior cingulum.

DP4: Most DP4 display a primitive connection between the trigon and the posteroloph: the metaloph runs towards the protocone, with which it is fused (UTL4: 6/17 morphotypes A) or separated (UTL4: 4/17 morphotypes D). Two specimens show a metaloph directly attached at the hypocone (morphotype B).

Three DP4 are wider than the others, although as long. The metaloph, oblique backwards, is either connected at the hypocone (1 morphotype B), or, posteriorly, at the posteroloph (2 morphotypes C). They may represent this species, or not.

Upper Molars:

UTL4 molars	Morphotypes						
	A	A/B	B	B/C	C	D	E
M1	7	3	7	13	7	4	10
M2	6	4	10	10	14	1	5
M3	4	-	12	5	23	-	3

Table 32.— Molar morphotypes of *Yindirtemys shevyreva* nov. sp. from UTL4.

The cusps of the molars are more prominent than the lophs. The anterocone, developed on the anteroloph, is well marked and mostly connected with the anterior arm of the protocone. It is unusually separated from it by a shallow notch. A "posterocone", resulting of the inflation of the posteroloph, is visible on about the half of the M3, and occasionally on the M2. The orientation of the metaloph is variable. Only rarely, it is directly connected with the protocone (morphotype D). More frequently, it is connected to the beginning of the endoloph. It is mostly directly connected with the hypocone (morphotype B) or more obliquely directed backward to meet the posteroloph posterobuccally of the hypocone (morphotype C). The latter pattern is most frequent on the M3.

The movements of the worn teeth in occlusion are canalized by two grooves. The anterior one crosses obliquely the anteroloph-posteroloph junction. The posterior one follows the valley that separates the metaloph from the posteroloph and cuts into the posterior arm of the protocone. The molar movements have sculptured three edges. The first one, in the continuity of the posterior edge of the preceding tooth, concerns the metacone and protocone. In the first steps of wear, the latter has the shape of a peaked

roof, as observed in *Y. ulantatalensis*. This shape dims on older individuals. On all the M1-M2, the sinus is well-marked. On the M3, it can be weakly marked, and thus, the endoloph is lingual. On one M3, there is neither hypocone nor sinus: it is the very end of the variation, or another species. A few M3 seem to be less bunodont, and their protoloph and metaloph are slender, parallel and oriented backwards. On these teeth, the endoloph is lingual. Once more, it is not possible to decide if it represents extreme variation, or another species.

Yindirtemys aff. *shevyrevae* nov. sp.

A few teeth (Plate 15, fig. 2-4, 8) from late Oligocene locality UTL6 (one m2, three M1-2) can be distinguished from the typical *Y. shevyrevae* of the same locality. The lower molar shows a well-developed trigonoid, with a visible metaconid. On the upper teeth, the main cusps, as well as the anterocone, are prominent. The anteroloph is not linked to the protoloph, and the metaloph is connected to the endoloph.

The main differences with the typical *Y. shevyrevae* are the acute shape of the cusps, the isolation of the anterocone, and a higher crown.

Yindirtemys deflexus (TEILHARD de CHARDIN, 1926)

Synonymy: *Tataromys deflexus* n. sp., Teilhard de Chardin 1926 : 28 ; *Tataromys* Material of larger species (pars), Bohlin 1946: 95; *Tataromys sp.*, Stehlin and Schaub 1951: 125, fig. 181; *Yindirtemys deflexus* (TEILHARD de CHARDIN, 1926), Wang 1997: 30.

Holotype and type locality: Fragment of maxilla with right M2 and M3, from Saint Jacques (Inner Mongolia, China), Teilhard de Chardin (1926: fig. 15B).

Stratigraphical range: late Oligocene. Units UlanII & UlanIII, Ulantatal area (Western Inner Mongolia, China); Level C1, Valley of the Lakes (Central Mongolia).

Geographical distribution: Western part of Inner Mongolia, Gansu province China, Tsagan Noor basin (Valley of the Lakes, Central Mongolia).

Original diagnosis: Teilhard de Chardin (1926, p. 28): "les dents sont notablement plus grandes que celles de *T. plicidens* (longueur M3-M2 = 10,5 au lieu de 6); mais surtout leur dessin est sensiblement différent. Le paralophe et le métalophe, au lieu d'être transverses, sont fortement infléchis en avant ; et le métacône émet un crochet qui, rejoignant un anté-crochet issu du paracône, détermine un puits d'émail sur les dents moyennement usées. Le bourrelet cingulaire antérieur est assez fortement développé pour esquisser un troisième lobe sur la muraille interne de la dent ».

Emended diagnosis: Large *Yindirtemys* species with tendency of developing additional crests on upper molars; M3 sometimes with longitudinal crest connecting metaloph and paraloph; M3 and M2 frequently with longitudinal crest connecting the metacone with the posteroloph; lower molars exhibiting the *Yindirtemys* pattern as found in *Yindirtemys grangeri* and the more recent *Yindirtemys ulantatalensis*.

Material and measurements:

Eleven specimens from UTL8 (Table 33) and three from UTL6: L-W p4: 2,27-2,06; L-W m1: 4,06-2,57; L-P4: 2,43-broken.

L-W p4	L-W m1-2	L-W m3	L-W P4	L-W M1-2	L-W M3
3,13-2,25	4,63-3,41	5,27-3,51	2,75-2,97	4,06-3,67	4,14-3,65
2,75-1,98				4,48-3,55	
2,72-2,12				4,95-3,92	
2,73-2,12					

Table 33.— Measurements of teeth of *Yindirtemys deflexus* from UTL8.

Description (Plate 5, fig. 10-19; Plate 8, fig. 10)

An upper third molar (UTL8, Plate 8, fig. 10) exhibits a well developed crest connecting the metaloph and paraloph. This structure is found in the holotype described by Teilhard de Chardin (1926) and was considered a diagnostic feature of that species by Kowalski (1974) and Wang (1997). New material of large *Yindirtemys* from Central Mongolia currently under study reveals that the crest is present only on a minor fraction of M3 (Schmidt-Kittler *et al.* in prep.). The two second molars documented from the same locality are provided with a small anti-crochet crest. Together with the metaloph and the posteroloph it delimits a small enamel pit. But since the fusion of the metaloph and the posteroloph extends far buccally in these teeth, the pit is extremely small. The m3 and m2 of a mandible fragment with the same provenance show the typical slightly selenodont occlusal pattern found in advanced *Yindirtemys* (e.g. also *Y. grangeri*). The trigonoid structure is lingually closed. The lower premolar preserved lacks the hypoconid. As to the size of the teeth they are somewhat inferior to that of the type specimen (Holotype: M3+M2 = 10,5 mm, Teilhard de Chardin, 1926,28) the material can represent an earlier evolutionary stage of the *Yindirtemys deflexus* lineage. A lower molar and some lower tooth fragments from UTL6 can be identified as belonging to the same species, with respect to their morphology and size.

In addition to *Yindirtemys deflexus*, other large species were described from the Upper Oligocene (*Y. gobiensis*, *Y. suni*). However, it could not be demonstrated up to now that they really represent separate taxa. This problem is more intensively discussed on the basis of more material in Schmidt-Kittler *et al.* (in prep.).

Tataromyinae nov. gen. 1 nov. sp. 1

Synonymy: *Tataromys minor* HÖCK *et al.* 1999, fig. 20/7.

Measurements:

L-W dp4	L-W m1	L-W m2	L-W m3	L-W M1	L-W M2	L-W M3
1,36-0,87	1,67-1,14	1,71-1,04	1,83-1,13	1,40-1,08	1,59-1,16	1,79-1,15
1,45-0,92		1,62-1,01	1,93-1,07	1,45-1,17	1,61-1,10	1,73-1,15
1,38-0,94		1,69-1,04		1,42-1,09	1,61-1,14	1,67-1,26
1,50-0,89				1,32-1,15	1,64-1,11	1,65-1,15
						1,70-1,27
						1,67-1,31
						1,77-1,28

Table 34.— Measurements of *Tataromyinae* nov. gen. nov. sp. 1 from UTL1.

L-W m2	L-W m3	L-W P4	L-W M1	L-W M2	L-W M3
UTL3					
1,80-0,98	2,05-1,04	1,28-1,41	1,51-1,13	1,66-1,22	
	1,99-1,04			1,62-1,21	
	1,87-1,14				
UTL5					
1,74-1,05				1,55-1,12	1,71-1,09

Table 35.— Measurements of *Tataromyinae* nov. gen. nov. sp. 1 from UTL3 and UTL5.

L-W dp4	L-W p4	L-W m1	L-W m2	L-W m3	L-W DP4	L-W M1	L-W M2	L-W M3
1,30-0,89	1,26-0,83	1,68-0,87	1,84-1,12	1,93-1,18	1,20-0,90	1,48-1,07	1,65-1,06	1,76-1,24
1,30-0,75	1,20-0,83	1,75-1,10	1,84-0,92	1,89-1,07	1,06-0,78	1,53-1,13	1,66-1,20	1,70-1,14
	1,30-0,99	1,77-0,97	1,83-1,09	1,92-1,29		1,38-0,98	1,65-1,06	1,75-1,19
	1,34-1,14	1,84-1,09	1,85-1,10	1,88-1,01		1,50-0,96	1,66-1,22	1,71-1,12
	1,28-1,09	1,67-1,03	1,82-0,97	1,84-0,90				1,88-1,28
	1,31-1,12	1,68-0,88	1,79-1,08	1,74-1,06				
	1,31-1,12	1,81-1,00	1,82-1,21					
	1,30-1,15	1,76-1,15	1,90-1,11					
		1,71-0,99	1,79-0,97					
		1,81-1,11						

Table 36.— Measurements of *Tataromyinae* nov. gen. nov. sp. 1 from UTL4.

Description

In all localities of the Ulantatal area a small ctenodactylid of the size of *Tataromys minor* and *Yindirtemys shevyreva* is present. This taxon clearly differs from these species in several features. Its molars are elongated, which is particularly clear in the upper molars. The upper premolar is broader than the M1. The upper molars possess a cusp-like anterocone and a very prominent posteroloph provided with a posterocone removed far buccally. Another significant feature of all lower molars and dp4 is the crest connecting directly the entoconid with the hypoconulid. Hence, there is a complete separation of the hypoconulid from the anterolingual arm of the hypoconid. As a consequence there is a deep and far lingually reaching hyposinusid. There is no

trace of a trigonoid structure.

The combination of these morphological characters is clearly different from the known brachyodont ctenodactylids and justifies the definition of a new genus. However, since the new form is also present in the material gathered from the Valley of Lakes in Central Mongolia (Höck *et al.* 1999) and even with more complete specimens (comprising also jaws) it was decided to erect the new taxon on the basis of the latter (Schmidt-Kittler *et al.*, in prep.).

The morphotype exhibited by all lower molars of the new form appears as well in *Alashania tengkoliensis* newly described above, the difference being that the connection of the hypoconulid with the anterobuccal arm of the entoconid only occurs in the m1 and occasionally in the m2 but never in m3. Another clear difference is the elongation of the molars of the new form.

Tataromyinae nov. gen. 1 or 2 nov. sp. 2, nov. sp. 3, nov. sp. 4

Three new and scarcely represented forms of Tataromyinae occur in UTL6 and UTL8. They are until now recognized by upper teeth. They could belong to one or more new genera, but the elongated anterior molar recalls what is observed in the Tataromyinae nov. gen. 1, even if the posterior molar is not elongated. Due to the scarcity of the material, we do not create now a new genus.

Stratigraphical range: late Oligocene, UTL6 and UTL8, Units Ulan II and III (Ulanatal area, Inner Mongolia, China).

UTL6: nov. sp. 2: 2 M1-2 (Plate 15, fig. 1, 5-6).

These teeth are slightly elongated anteroposteriorly. The anterocone is closer to the median axis of the tooth than in *Yindirtemys*. The anteroloph is reduced on one molar, and the second exhibits a short anteroloph and low anti-crochet posterior to the metacone. They have a reduced hypocone and posteroloph, but basically they exhibit the same dental pattern. The mesosyncline is widely open labially on the two molars. The metaloph is connected to the protocone (morphotype D). The hypocone is as high as the protocone. The posteroloph, long and sinuous, is higher than the endoloph, when the endoloph is developed, and occasionally bears a posterocone. The sinus is wide and shallow. The crown is clearly higher than in the other observed genera.

UTL8: nov. sp. 3: 4M1-2, ? 2M3 (Plate 15, fig. 7, 9-11, 13, 14).

The M1-2 of nov. sp. 3 are bigger than nov. sp. 2 from UTL6. The anteroloph is longer and extended to the middle of the anterior flank of the paracone. There is a short anti-crochet starting posteriorly from the metacone. It begins at the tip of the metacone and joins the sinuous posteroloph. The protoloph ends slightly more labially than on the two molars of nov. sp. 2 from UTL6. The lophs are transverse. One M1 shows a vertical edge on the hypocone, limiting the lingual posterior border of the sinus. The cusps do not seem as acute as in nov. sp. 2 of UTL6. The molars are less elongated anteroposteriorly than nov. sp. 4, but basically exhibit the same pattern. The position of the anterocone is closer to the sagittal middle axis of the tooth. Only a short anti-crochet

starting from the metacone posteriorly is developed, instead of a connection between the posteroloph and the metacone.

The two M3 are not elongated, but shortened. It may be expected that both teeth do not belong to the same species. However, their features are reminiscent of the M1: pattern of anterocone, cusps, loph, and anti-crochet on one.

UTL8: nov. sp. 4: 2 damaged upper molars (Plate 15, fig. 12, 15).

Possibly another new form of Tataromyinae is documented by two somewhat fragmentary upper molars. These molars exhibit a dental pattern that is largely similar to that of the nov. sp. 3 discussed above and is comparable to this also by the marked elongation of the tooth crown. But the metaloph and paraloph are more obliquely oriented, running posterolingually to anterobuccally. The anti-crochet originates at mid-length of the metaloph, more lingually than in the species described above.

The protocone is very large and occupies the middle of the lingual wall of the tooth. In one of the specimens, a part of the anterocone is preserved. It is placed on the lingual wall in front of the protocone and is separated from the latter only by a very shallow vertical depression. The sinus is removed far caudally and very narrow. The hypocone is connected to the trigon by a very prominent but very short crest. The hypocone occupies the lingualmost extremity of the posteroloph. This latter is very prominent and runs to the buccal wall of the tooth where it bends in anterobuccal direction to form the smoothly curved posterobuccal margin of the tooth. No posterocone is developed. However, there is a strong longitudinal crest that connects the posteroloph with the metacone.

Subfamily CTENODACTYLINAE HINTON, 1933

Type genus: *Ctenodactylus* GRAY, 1828.

Ctenodactylinae nov. gen. nov. sp.

This sub-family includes the Miocene to recent genera of the Ctenodactylidae (see Wang, 1997, p.59-60).

A few hypsodont teeth (1 m2, 1 M1, 1 M2, 1 M3) from Oligocene localities of Ulantatal area (UTL1 and UTL4) can be referred to a new genus and new species of Ctenodactylinae (Schmidt-Kittler & Vianey-liaud, in prep. 2).

These teeth are more hypsodont than any tataromyine species of the Ulantatal localities, and the upper molars are semi-hypsodont (lingual wall higher than labial one). Their occlusal pattern is close to that of *Prosayimys* (Baskin, 1996), even if they are less hypsodont.

This Oligocene new species can represent the ancestral group of the modern Ctenodactylinae.

DISCUSSION AND CONCLUSION

The systematic analysis of the ctenodactylid rodents collected by a Chinese-German team in the Ulanatal area (Inner Mongolia) was the main aim of our study. Their abundance allowed us to analyse these rodents at the population level in the richest localities, UTL4, UTL7 and UTL1. On the one hand we had a rich and varied material, and on the other hand, we had at our disposal a revised Ctenodactylidae systematic frame (Wang, 1994, 1997). It appeared soon that our observations did not fit that framework. Some striking features, like the crescentic mesoconid or the long and narrow hyposinusid (in *Alashania*, or Tataromyinae nov. sp. 1), had not been identified by Wang. Some other characters previously considered as derived appear clearly to be primitive, like the bunodonty or the wide trigonoid. Above all, our material allowed us to understand the morphological and size variation among several ctenodactylid species. The morphological variation can be large, but as transitional morphologies occur in a single locality, it is possible to define the range of the variation clearly for most of the species. On that basis, several previously named genera and species are placed in synonymy, as is the case for the genus *Bounomys*. At least one new genus and new species has been identified (*Alashania tengkoliensis*), seven previous species are re-evaluated, and a new species (*Y. shevyrevae*) is described. Four new other species, rare in the localities, are left in open nomenclature.

Systematics and relationships

Considering the studied genera *Karakoromys*, *Yindirtemys*, *Tataromys*, *Alashania*, and Ctenodactylinae nov., it clearly appears that the five represented patterns are related. Comparing the lower tooth pattern, the basic one is *Karakoromys*, with a central mesoconid, a short mesolophid and a wide anterior synclinid. We have named it a trigonoid, because it is not homologous of the trigonid (no paraconid, no basin anterior to the metalophid-I). The other genera can derive from this initial condition. *Yindirtemys* differs from the other genera in the permanence of crescentic structures, whereas the other genera show a more or less strong reduction of the trigonoid area. The oldest known Ctenodactylinae is identified in the early Oligocene localities (UTL1 and UTL4).

In some species of *Yindirtemys*, like *Y. shevyrevae*, we follow the reduction of this trigonoid with the antero-lingual shifting of the ectolophid and mesoconid. In *Y. ulantatalensis* or *Y. bohlini*, or *Y. deflexus*, the trigonoid remains wide and the crescentic mesoconid, central.

In *Tataromys sigmodon*, *T. plicidens* or *T. minor*, the mesoconid disappears, and the trigonoid varies with the strong lingual shifting of the ectolophid. In Tataromyinae nov. sp. 1, there is no trigonoid, no mesoconid, whereas in *Alashania*, a very faint anterior mesoconid can remain or disappear, but there is also no trigonoid.

The lineages documented by these genera diverge whether they have crescentic structures, and additional crests, or not, whether they develop transverse or oblique posterior crests on upper molars.

Hypsodonty is not properly developed on the Ulantatal species before UTL8, except on a few teeth of the lower part of the sequence (UTL1 and UTL4), which clearly announce the *Sayimys*-like morphology.

Diversity, ecological niches and diets

Among Ulantatal rodents, only Zapodidae have been exhaustively published (Huang, 1992), with six species described (Table 37).

	UTL3	UTL4	UTL7	UTL6	UTL8
<i>Parasminthus asiae-centralis</i> Bohlin, 1946	+	+		+	+
<i>Parasminthus tangingoli</i> Bohlin, 1946	+	+		+	+
<i>Parasminthus parvulus</i> Bohlin, 1946	+	+	+		+
<i>Gobiosminthus qiui</i> Huang, 1992		+	+		
? <i>Gobiosminthus</i> sp., Huang, 1992		+		+	
<i>Shamosminthus tongi</i> Huang, 1992	+	+			+
Minimum Zapodid species diversity	4	6	2	3	4

Table 37.— Localities and Zapodid (Dipodidae) occurrences in Ulantatal area (Huang, 1992).

The Cricetidae are now under a PhD study, and there are at least four species in one locality. The present paper shows that there are up to nine species of ctenodactylids in the localities where the fossils are abundant (Table 1). On the basis of previous works (Huang 1982, 1985, 1992; Russell & Ren-Jie 1987; Wang 1994, 1997) and on that present study, it appears that the Ulantatal rodent fauna is much diversified. Taking into account that there are also relatively large fossorial rodents such as Tsaganomyidae and Cylindrodontidae, and a few Aplodontidae, the rodent diversity could be more than 25 species.

Within the Ctenodactylidae, the size extends from tiny rodents which have tooth row lengths less than 5 mm (*Tataromys minor* or *Yindirtemys shevyreva*), to medium sized rodents, bigger than rats, with tooth row lengths more than 18 mm (*Tataromys plicidens* or *Yindirtemys deflexus*). Such diversity corresponds to a wide range of ecological niches within this single family, which could have been concentrated in the fluvial deposits, or could represent nearby environments.

The following discussion on jaw movements and diets is based on qualitative characters established in our systematic study of the ctenodactylid teeth from Ulantatal area. The quantification of the various parameters (wear facets and microwear striations) is the subject of another study, now in progress.

Most of the Ulantatal ctenodactylids show brachyodont teeth and a tendency toward selenodonty. There are several species displaying the same range of size, but not the same morphology. For example, *Alashania tengkoliensis*, *Tataromys sigmodon* and *Yindirtemys ulantalensis* display virtually the same size range and variation. But the shape of the cusps, crescentic or not, the modes of wear, horizontal on *T. sigmodon* with compressed thin loph and lophids, oblique sharpening of the cusps in a more (*Yindirtemys*) or less (*Alashania*) acute angle between the opposite facets, indicate different shearing modes, related to different kinds of food intake. As a consequence,

they indicate various vegetarian diets, and different modes of exploitation of the environments, suggesting separate ecological niches.

In most tataromyine genera from Ulanatal, wear affects molars obliquely, as proved by the orientation of edges and grooves, but also by the wear striations visible on the wear facets and occlusal surface. The opposite wear facets of the cusps and cuspids line up the edges, and are drawn on the profiles for the various species, or sometimes on the occlusal surfaces (see the different Plates).

Alashania and Yindirtemys

The grinding movements have a predominant transverse component in *Alashania* and *Yindirtemys*, and high cusps relief is maintained during life. The movements of the teeth during occlusion and grinding are canalized by two grooves, between three oblique edges.

In the lower teeth, the posterior groove runs obliquely with the same direction as the ectolophid, and affects the junction of the anterior arms of the hypoconulid and entolophid with the ectolophid. The anterior one crosses obliquely the basin of the trigonoid.

In the upper teeth, the anterior groove crosses obliquely the anteroloph-posteroloph junction. The posterior one follows the valley that separates the metaloph from the posteroloph and cuts into the posterior arm of the protocone. Consequently, the molar movements have sculptured three edges. The first one, in the continuity of the posterior edge of the preceding tooth, concerns the metacone and protocone. In the first steps of wear, the latter has the shape of a peaked roof, as observed for example in *Y. ulantatalensis*. The relief fades on older individuals.

The crescentic or bunodont shape of cusps and cuspids is the more significant difference between *Alashania* and *Yindirtemys*. It has been noticed that selenodonty allied to brachyodonty is a feature of arboreal rodents, correlated with a vegetarian and frugivorous diet (Wood, 1976), fully available in forested environments. *Yindirtemys shevyrevae* and *Y. bohlini* have crescentic cusps and may have a soft vegetarian diet. In such an environment, insects and other terrestrial arthropods are also abundant.

In a small species like *Yindirtemys shevyrevae*, the acute and hooked cusps, especially of the lower p4, could indicate an insectivorous diet for young individuals, and perhaps for adults, because of the acute sharpening of the main molar cusps. In UTL8, at least two taxa, *Yindirtemys* aff. *shevyrevae* and one unnamed new species (nov. sp. 2), show higher crowns and more acute cusps and we can suppose a case of insectivorous diet.

In the small population of *Y. ulantatalensis* from the younger localities UTL6 and UTL8, the lophids seem less swollen at their bottom, while the occlusal surface becomes flattened very quickly. The crescentic cuspids, the hypoconid, mesoconid and metaconid, are much more oriented mesio-distally. The orientation of the movements turns from clearly oblique to nearly mesio-distal. The tendency to a propalinal movement of the jaws during the power stroke, has to be confirmed by the study of the rare wear facets and microwear striations preserved on the scarce material. The wear

surface displays indeed more antero-posterior (faint) grooves and microwear striations. If this propalinal movement is proved, it will indicate a change of diet in the *Yindirtemys ulantatalensis* lineage by the end of the Oligocene, probably towards more abrasive food. It could be the same for the largest *Yindirtemys*, *Y. deflexus*. This species is not frequent in Ulantatal unit II and III. Its best record is in the later locality UTL8, even if the teeth are not numerous. The occlusal surface flattens rapidly, because of the loph and lophids nearly as high as the apex of the cusps. The upper molars show a tendency towards a weak semi-hypsodonty (increasing lingual wall). The enamel of the crown often shows small blisters.

In *Alashania*, where the cusps are not crescentic, wear produces lower reliefs and the lophs are transverse. Wear tends to flatten the occlusal surface of the molars, while the cusps of deciduous molars and premolars are less elevated.

Tataromys

The plane of wear is horizontal in *Tataromys*. The top of the cusps and cuspids is compressed within thin loph and lophids, even if they are swollen at the very bottom of the crown. The direction of edges, groove and wear striations are slightly less oblique than in *Yindirtemys*. In *Tataromys*, only one well-marked groove guides jaw movements. It crosses the tooth from the junction hypolophid/arm of the hypoconulid to the junction entolophid/ectolophid (GRP = posterior groove). Functionally, the hypoconulid leans against the anterior part of the following tooth, and a clear wear surface is continued from the protoconid and its two arms, to the postero-lingual ends of the hypoconulid and entoconid of the precedent tooth. After moderate wear, the occlusal surface is flattened.

Tataromyinae nov. gen. 1 or 2 nov. sp. 2, nov. sp. 3, nov. sp. 4

These four taxa of small to medium size, are poorly recorded but document other evolutionary tendencies and diets. Some characters of nov. sp. 1 suggest insectivorous diet during its life. They are: the elongated teeth, the slimming of loph and lophids since mid-height and, on p4, the sharp metaconid and protoconid and hooked hypoconid. The upper teeth of nov. sp. 2 show a clear increase of semi-hypsodonty, while the cusps are included in thin lophs which are not deeply separated, especially on their lingual wall. Also striking is the reduction of the anteroloph to a tiny acute anterocone. The larger species nov. sp. 3 shows a parallel increase of semi-hypsodonty, but it does not involve the individualisation of the cusps, which remain swollen and a bit more deeply separated on the lingual side. However, there is a development of the lophs, mainly in the posterior part of the molars, with a long posteroloph and anti-crochet. The very fragmentary molars of nov. sp. 4 represent a close pattern with nov. sp. 3, but the surface appears flat and basined, with thin lophs. The last two taxa can represent the same kind of abrasive food as is indicated by the largest species of *Yindirtemys* in UTL8, and thus may be linked to a change in vegetation, and climatic condition, during the late Oligocene. The data are presently too tenuous to be sure. The current study of cricetids, as well as the detailed and quantitative occlusal wear analysis of these two rodent families in Ulantatal should provide new data on that issue.

However, the adaptive diversity, size and diets, seem to demonstrate during ULAN I, II and III units, a mosaic of landscapes with rich vegetation: forest gallery, close to the river, for some ctenodactylids, thick soils for fossorial rodents like tsaganomyids, savanna and bushes elsewhere for other ctenodactylids, maybe some cricetids or zapodids. Höck *et al.* (1999) described such varied environments in Central Mongolia, with contrasted climate (episodic droughts and heavy rainfall, "which occasionally follow long dry periods").

Biostratigraphy

Based on field data and paleontological information a biostratigraphic subdivision of the Ulanatal sequence into three units is proposed (fig. 2). According to the correlation with Central Mongolia (Höck *et al.* 1999), it seems to encompass a large part of the Oligocene period, about 8 millions years. Independently from the lithostratigraphical indications (fig. 1 & 2) the micromammal bearing localities of the Ulanatal area can be ranged in a succession because of their fossil content. As usual for biochronological zonations, the last occurrence or first appearance of species can be used and, as an independent argument, also the evolutionary degree of lineages.

Even if rare, in locality UTL1 *Karakoromys decessus* could be determined with high reliability. *Karakoromys decessus* occurs in association with other Tataromyinae (*T. sigmodon*, Biozone B, Höck *et al.* 1999) in localities of Central Mongolia between the two basalts dated as 30.4-32.1 millions years (basalt I) and 27-29 millions years (basalt II), respectively. However, it is lacking in UTL4, which occupies a higher stratigraphic position (fig. 2). Because of the very rich documentation of micromammals from UTL4 the non-occurrence of this species is indicative (with high probability) of its extinction in this area prior to the deposit of that fossil level.

Following the same line of argumentation, the documentation of the *Yindirtemys deflexus* lineage in UTL6 and UTL8 (not known from UTL4) can be interpreted as new appearance of this taxon. Besides this, the first occurrence of *Tachyoryctoides obrutschewi* in UTL6 can be stated. This last species occurs only in the late Oligocene in Central Mongolia, above basalt II (Level C, Daxner-Höck *et al.* 1997, Höck *et al.* 1999)

The less rich localities UTL3 to 5 and UTL7 can be ranged in the same biostratigraphic position as UTL4 because of their lithostratigraphic correspondence to the latter. UTL6 and UTL8 are not only located in a higher position within the section but are also distinguished by the first occurrence of the *Yindirtemys deflexus* lineage. At the same time the small populations of *Yindirtemys bohlini* (UTL6) and *Y. ulantatalensis* (UTL8) exhibit more advanced morphological features. In the M3 of that species from UTL6, the "deflexus" structure is developed for the first time. The same is true for *Y. ulantatalensis* from UTL8. However, this population exhibits an even more advanced evolutionary stage (see above).

It has not been possible yet to discriminate morphological or size evolutionary grades for *Tataromys sigmodon*, *T. minor* or *Yindirtemys shevyrevae* among the Ulanatal levels, due probably to the quite uneven richness of the successive populations and, seemingly, to morphological stability. A more detailed and quantitative study is in

progress, in order to better discriminate the different populations, and possible grades, on the basis of quantitative data, wear facets and microwear striations.

Tataromyinae have been reported from the Zaisan Depression (Kazakhstan) to Mongolia and several provinces in China (Russell & Ren-Jie, 1987; Qiu & Gu, 1988; Shevyreva 1994a, 1994b; Wang, 1991, 1997; Emry *et al.* 1998). On the basis of our systematic study of the Tataromyinae, and of the established stratigraphic succession, it will be possible to re-evaluate their taxonomic attributions, and to make the correlations between these Asian localities more precise.

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PLATE CAPTIONS

PLATE 1

Tataromys sigmodon MATTHEW & GRANGER, 1923, from Oligocene localities UTL4 and UTL7 (Ulanatal area, Inner Mongolia): Lower teeth

- Fig. 1a: right dp4, UTL7-1; occlusal view
- Fig. 1b: right dp4, UTL7-1; lingual profile
- Fig. 2: left dp4, UTL7-2; occlusal view
- Fig. 3a: left p4, UTL7-3; occlusal view
- Fig. 3b: left p4, UTL7-3; lingual profile
- Fig. 4a: left p4, UTL7-4; occlusal view
- Fig. 4b: left p4, UTL7-4; lingual profile
- Fig. 5a: left p4, UTL7-5; occlusal view
- Fig. 5b: left p4, UTL7-5; lingual profile
- Fig. 6a: right m1, UTL7-6; occlusal view
- Fig. 6b: right m1, UTL7-6; lingual profile
- Fig. 6c: right m1, UTL7-6; labial profile
- Fig. 7: left m2, UTL7-7; occlusal view
- Fig. 8a: left m1-m2, UTL7-8; occlusal view
- Fig. 8b: left m1-m2, UTL7-8; labial profile
- Fig. 9a: right m2, UTL7-9; occlusal view
- Fig. 9b: right m2, UTL7-9; lingual view
- Fig. 10a: left m2, UTL7-10; occlusal view
- Fig. 10b: left m2, UTL7-10; lingual view
- Fig. 10c: left m2, UTL7-10; labial view
- Fig. 11: left m3, UTL7-11; occlusal view
- Fig. 12a: right m3, UTL7-12; occlusal view
- Fig. 12b: right m3, UTL7-12; lingual view
- Fig. 13: right m2, UTL7-13; occlusal view
- Fig. 14: left m2, UTL7-14; occlusal view
- Fig. 15: right m3, UTL7-15; occlusal view
- Fig. 16: left m3, UTL7-16; occlusal view
- Fig. 17: left m3, UTL4-1; occlusal view
- Fig. 18: left m3, UTL4-2; occlusal view
- Fig. 19: right m3, UTL4-3; occlusal view

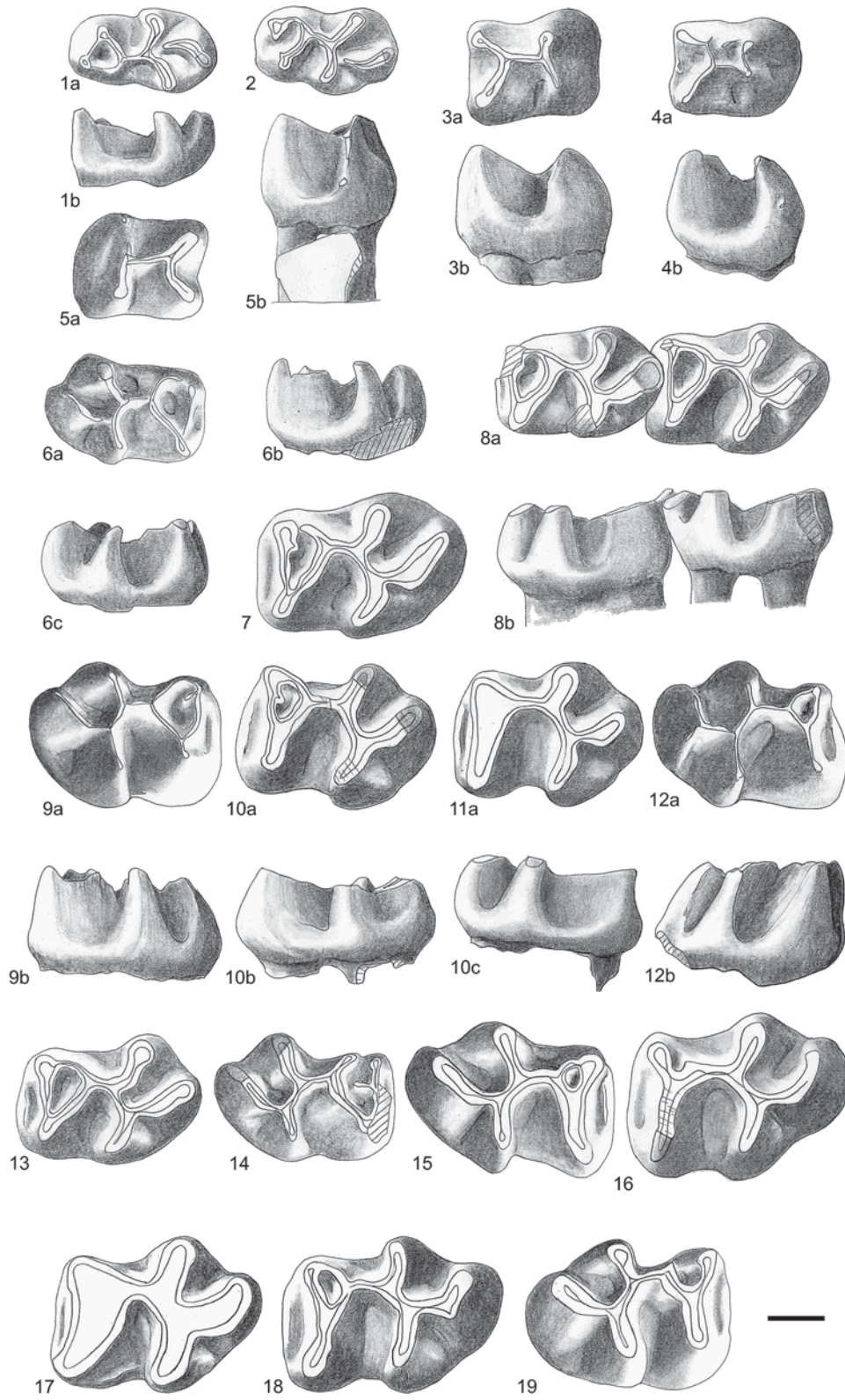


PLATE 2

Tataromys sigmodon MATTHEW & GRANGER, 1923, from Oligocene localities UTL4 and UTL7 (Ulanatal area, Inner Mongolia): Upper teeth.

- Fig. 1: left P4, UTL4-4; occlusal view
- Fig. 2: right P4, UTL4-5; occlusal view
- Fig. 3: left P4, UTL4-6; occlusal view
- Fig. 4: left P4, UTL4-7; occlusal view
- Fig. 5: right M1-DP4, UTL4-8; occlusal view
- Fig. 6a: left P4, UTL7-17; occlusal view
- Fig. 6b: left P4, UTL7-17; front view
- Fig. 7a: right P4, UTL7-18; occlusal view
- Fig. 7b: right P4, UTL7-18; lingual profile
- Fig. 8a: right P4, UTL4-9; occlusal view
- Fig. 8b: right P4, UTL4-9; front view
- Fig. 9a: left M1, UTL7-19; occlusal view
- Fig. 9b: left M1, UTL7-19; lingual profile
- Fig. 10a: left DP4-M1, UTL7-20; occlusal view
- Fig. 10b: left M1, UTL7-20; lingual profile of M1
- Fig. 11a: right M2, UTL7-21; occlusal view
- Fig. 11b: right M2, UTL7-21; lingual profile
- Fig. 12a: right M2, UTL7-22; occlusal view
- Fig. 12b: right M2, UTL7-22; lingual profile
- Fig. 13a: left M2, UTL7-23; occlusal view
- Fig. 13b: left M2, UTL7-23; lingual profile
- Fig. 14: left M3, UTL7-24; occlusal view
- Fig. 15: left M3, UTL7-25; occlusal view
- Fig. 16: left M3, UTL7-26; occlusal view
- Fig. 17: right M2, UTL7-27; occlusal view
- Fig. 18: left M2, UTL7-28; occlusal view
- Fig. 19: right M3, UTL7-29; occlusal view

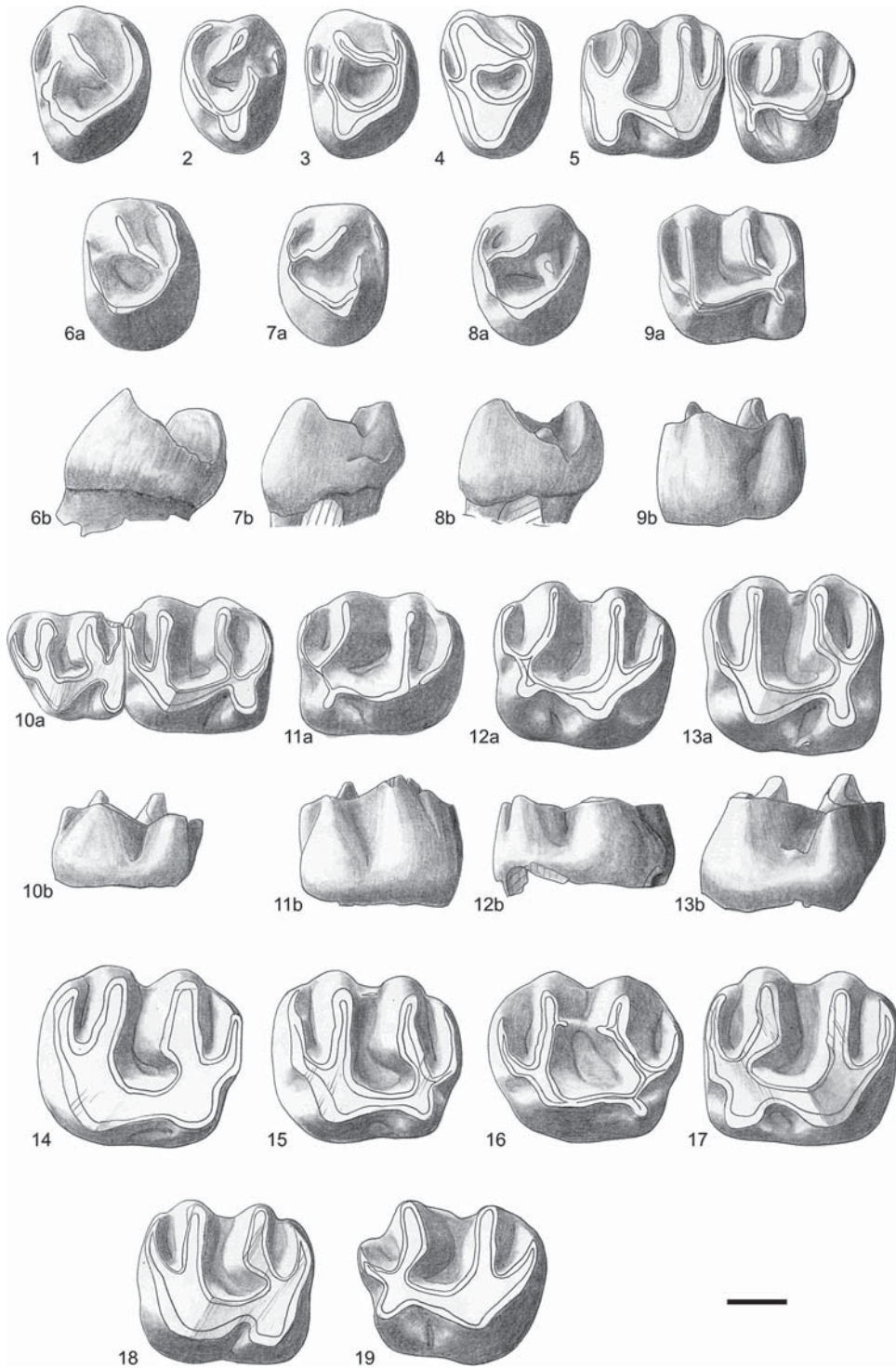


PLATE 3

Tataromys cf sigmodon Matthew & Granger, 1923, from Oligocene localities UTL4 and UTL1 (Ulanatal area, Inner Mongolia):

Fig.1: right dp4, UTL4-10; occlusal view
Fig.2a: right m1, UTL4-11; occlusal view
Fig.2b: right m1, UTL4-; labial profile
Fig.3: right m2, UTL4-12; occlusal view
Fig.4a: right m2, UTL4-13; occlusal view
Fig.4b: right m2, UTL4-13; labial profile
Fig.5a: left m3, UTL4-14; occlusal view
Fig.5b: left m3, UTL4-14; labial profile
Fig.6a: left m3, UTL4-15; occlusal view
Fig.6b: left m3, UTL4-15; labial profile
Fig.7a: left m3, UTL4-16; occlusal view
Fig.7b: left m3, UTL4-16; labial profile
Fig.8a: left m3, UTL4-17; occlusal view
Fig.8b: left m3, UTL4-17; labial profile
Fig.9a: right DP4, UTL4-18; occlusal view
Fig.9b: right DP4, UTL4-18; lingual profile
Fig.10a: left M1-M3, UTL1-30; occlusal view
Fig.10b: left M1-M3, UTL1-30; lingual profile
Fig.11a: left M2, UTL4-20; occlusal view
Fig.11b: left M2, UTL4-20; lingual profile
Fig.12a: right M2, UTL4-21; occlusal view
Fig.12b: right M2, UTL4-21; lingual profile

Tataromyinae nov. gen. nov. sp. 1:

Fig.13a: left p4, UTL4-22; occlusal view
Fig.13b: left p4, UTL4-22; labial profile
Fig.13c: left p4, UTL4-22; lingual profile
Fig.14a: right dp4, UTL4-23; occlusal view
Fig.14b: right dp4, UTL4-23; lingual profile
Fig.15a: right m1, UTL4-24; occlusal view
Fig.15b: right m1, UTL4-24; lingual profile
Fig.15c: right m1, UTL4-24; lingual profile
Fig.16a: left m2, UTL4-25; occlusal view
Fig.16b: left m2, UTL4-25; lingual profile
Fig.17a: left m3, UTL4-26; occlusal view
Fig.17b: left m3, UTL4-26; lingual profile
Fig.18: left DP4, UTL4-27; occlusal view
Fig.19: right M1, UTL4-28; occlusal view
Fig.20: right M2, UTL4-29; occlusal view
Fig.21: right M3, UTL4-30; occlusal view

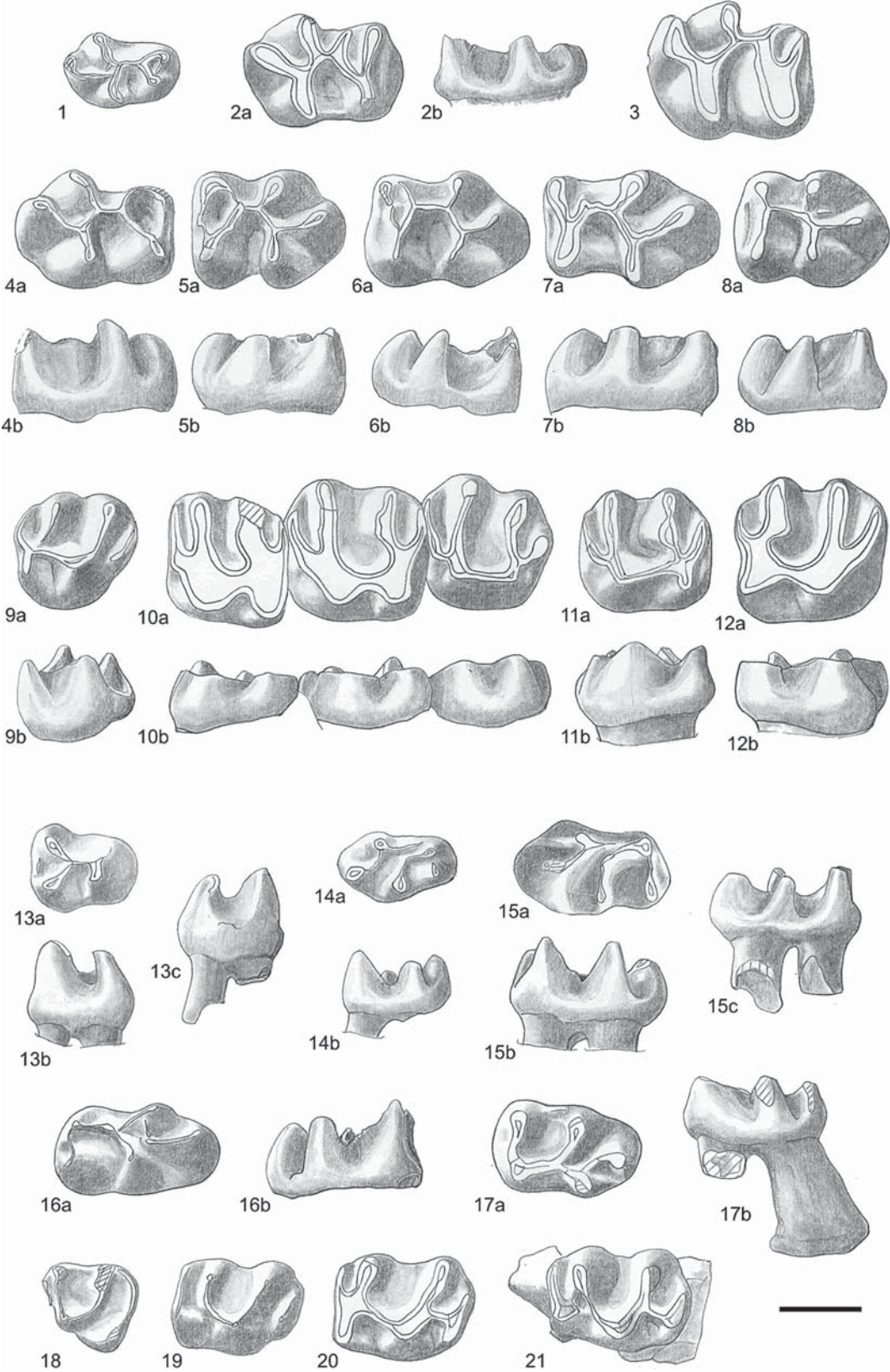


PLATE 4

Tataromys minor (Huang, 1985), from Oligocene localities UTL4 and UTL7 (Ulanatal area, Inner Mongolia):

- Fig.1a: left dp4, UTL7-30; occlusal view
Fig.1b: left dp4, UTL7-30; labial profile
Fig.1c: left dp4, UTL7-30; lingual profile
Fig.2a: left dp4, UTL7-31; occlusal view
Fig.2b: left dp4, UTL7-31; labial profile
Fig.2c: left dp4, UTL7-31; lingual profile
Fig.3a: left p4, UTL7-32; occlusal view
Fig.3b: left p4, UTL7-32; lingual profile
Fig.4a: right p4, UTL7-33; occlusal view
Fig.4b: right p4, UTL7-33; lingual profile
Fig.5a: right p4, UTL7-34; occlusal view
Fig.5b: right p4, UTL7-34; lingual profile
Fig.6a: right m1-m3, UTL7-35; occlusal view
Fig.6b: right m1-m3, UTL7-35; lingual profile
Fig.7a: right p4-m1, UTL7-36; occlusal view
Fig.7b: right p4-m1, UTL7-36; lingual profile
Fig.8a: right dp4, UTL4-31; occlusal view
Fig.8b: right dp4, UTL4-31; labial profile
Fig.9a: right dp4, UTL4-32; occlusal view
Fig.9b: right dp4, UTL4-32; labial profile
Fig.10a: right m1, UTL7-37; occlusal view
Fig.10b: right m1, UTL7-37; lingual profile
Fig.11: left m1-m3, UTL4-33; occlusal view
Fig.12: right m3, UTL4-34; occlusal view
Fig.13: right m3, UTL4-35; occlusal view
Fig.14: right m3, UTL7-38; occlusal view
Fig.15: left m3, UTL7-53; occlusal view
Fig.16: right m3, UTL7-53; labial profile
Fig.17: left m1, UTL7-39; occlusal view
Fig.18: left m1, UTL7-40; occlusal view
Fig.19: left m3, UTL7-41; occlusal view
Fig.20: right m2, UTL7-42; occlusal view
Fig.21: right m2 or 3, UTL7-43; occlusal view
Fig.22: right m2, UTL7-120; occlusal view
Fig.23: left m2, UTL7-44; occlusal view
Fig.24a: fragment of left maxillary, with DP4, UTL7-45; occlusal view
Fig.24b: fragment of left maxillary, with DP4, UTL7-45; occlusal view
Fig.25a: fragment of right maxillary, with P4-M1, UTL7-46; occlusal view
Fig.25b: right P4-M1, UTL7-46; occlusal view
Fig.26a: fragment of right maxillary, with M2-M3, UTL7-47; occlusal view
Fig.26b: right M2-M3, UTL7-47; occlusal view
Fig.27: left M1-M3, UTL7-48; occlusal view
Fig.28a: left M2, UTL7-49; occlusal view
Fig.28b: left M2, UTL7-49; lingual profile
Fig.29a: left M2, UTL7-50; occlusal view
Fig.29b: left M2, UTL7-50; lingual profile
Fig.30a: left M2, UTL7-51; occlusal view
Fig.30b: left M2, UTL7-51; lingual profile
Fig.30c: left M2, UTL7-51; labial profile
Fig.31a: right P4-M2, UTL7-52; occlusal view
Fig.31b: right P4-M2, UTL7-52; lingual profile
Fig.32: left M3, UTL7-54; occlusal view
Fig.33: left M3, UTL4-37; occlusal view

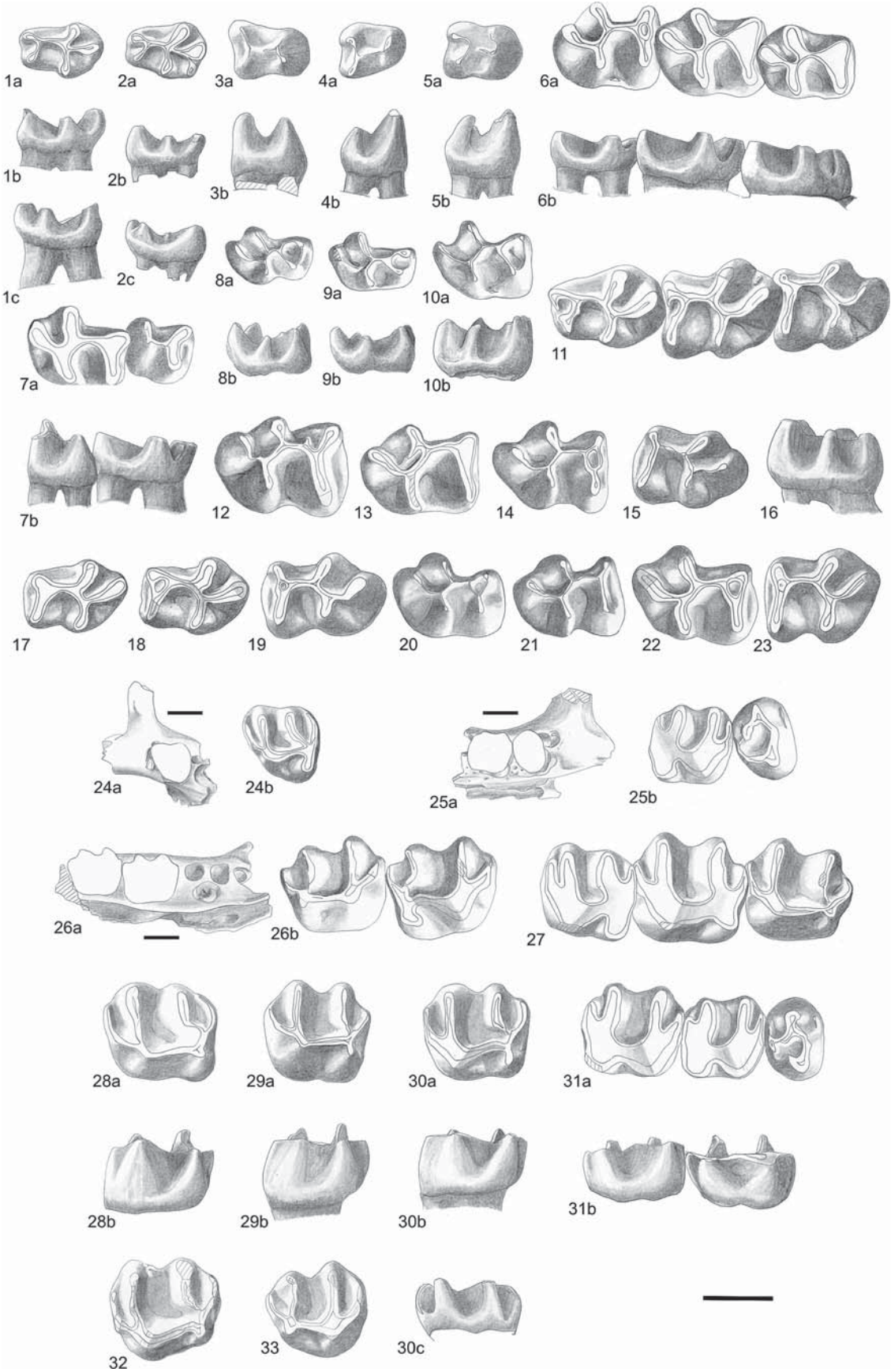


PLATE 5

Tataromys plicidens Matthew & Granger, 1923, from Oligocene locality UTL1,5,7 (Ulanatal area, Inner Mongolia):

- Fig.1a: left p4, UTL1-1; occlusal view
- Fig.1b: left p4, UTL1-1; labial profile
- Fig.1c: left p4, UTL1-1; front view
- Fig.2: right m2-3, UTL1-2; occlusal view
- Fig.3: left m3, UTL1-3; occlusal view
- Fig.4: right m3, UTL1-4; occlusal view
- Fig.5: left M2, UTL1-5; occlusal view
- Fig.6a: right m3, UTL1-6; occlusal view
- Fig.6b: right m3, UTL1-6; labial profile
- Fig.7a: left m1, UTL5-1; occlusal view
- Fig.7b: left m1, UTL5-1; labial profile
- Fig.7c: left m1, UTL5-1; lingual profile
- Fig.7d: left m1, UTL5-1; front view
- Fig.8a: left M3, UTL1-7; occlusal view
- Fig.8b: left M3, UTL1-7; lingual profile
- Fig.9a: left M2-M3, UTL1-8; occlusal view
- Fig.9b: left M3, UTL1-8; lingual profile

Yindirtemys deflexus (Teilhard de Chardin, 1926):

- Fig.10a: left m2-m3, UTL8-1; occlusal view
- Fig.10b: UTL8-1; lingual profile of m3
- Fig.11a: fragmentary right m2, UTL8-2; occlusal view
- Fig.11b: fragmentary right m2, UTL8-2; lingual profile
- Fig.12: right P4, UTL8-3; occlusal view
- Fig.13: right p4, UTL8-4; occlusal view
- Fig.14: left p4, UTL8-5; occlusal view
- Fig.15: right p4, UTL8-6; occlusal view
- Fig.16: left M1, UTL8-7; occlusal view
- Fig.17a: right M3, UTL8-8; occlusal view
- Fig.17b: right M3, UTL8-8; lingual profile
- Fig.18a: left M2, UTL8-9; occlusal view
- Fig.18b: left M2, UTL8-9; lingual profile
- Fig.19a: left M2, UTL8-10; occlusal view
- Fig.19b: left M2, UTL8-10; lingual profile

Yindirtemys ulantatalensis (Huang, 1985):

- Fig.20a: right m3, UTL8-11; occlusal view
- Fig.20b: right m3, UTL8-11; labial profile
- Fig.20c: right m3, UTL8-11; lingual profile
- Fig.23: left m2, UTL8-12; occlusal view
- Fig.24a: right m1-2, UTL6-1; occlusal view
- Fig.24b: right m1-2, UTL6-1; lingual profile

Alashania tengkoliensis nov.gen. nov.sp.:

- Fig.21: right M2, UTL8-13; occlusal view
- Fig.22: right m2, UTL8-14; occlusal view

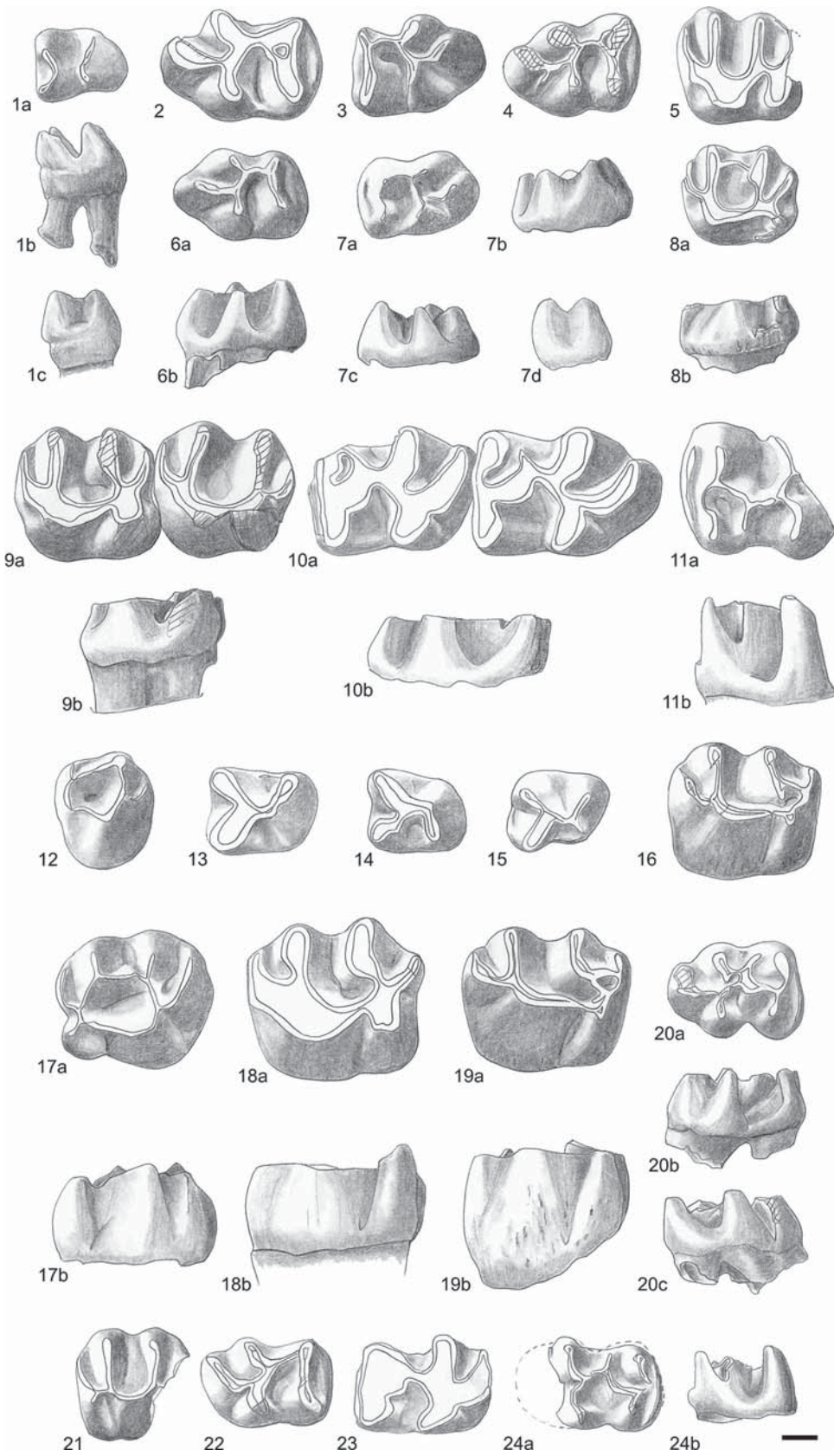


PLATE 6

Alashania tengkoliensis nov.gen. nov.sp., from Oligocene locality UTL1 & UTL4
(Ulanatal area, Inner Mongolia):

- Fig.1a: left P4, UTL1-9; occlusal view
- Fig.1b: left P4, UTL1-9; front view
- Fig.2a: left P4, UTL1-10; occlusal view
- Fig.2b: left P4, UTL1-10; front view
- Fig.2c: left P4, UTL1-10; labial profile
- Fig.3a: left P4, UTL1-11; occlusal view
- Fig.3b: left P4, UTL1-11; posterior profile
- Fig.3c: left P4, UTL1-11; front view
- Fig.4a: left DP4, UTL1-14; occlusal view
- Fig.4b: left DP4, UTL1-14; lingual profile
- Fig.5a: left M3, UTL1-15; occlusal view
- Fig.5b: left M3, UTL1-15; lingual profile
- Fig.6a: right M1, UTL1-16; occlusal view
- Fig.6b: right M1, UTL1-16; lingual profile
- Fig.7a: right M1, UTL1-17; occlusal view
- Fig.7b: right M1, UTL1-17; lingual profile
- Fig.8a: right M2, UTL1-18; occlusal view
- Fig.8b: right M2, UTL1-18; lingual profile
- Fig.8c: right M2, UTL1-18; labial profile
- Fig.8d: right M2, UTL1-18; front view
- Fig.9a: right M2, UTL1-19; occlusal view
- Fig.9b: right M2, UTL1-19; lingual profile
- Fig.9c: right M2, UTL1-19; labial profile
- Fig.9d: right M2, UTL1-19; front view
- Fig.10a: left M3, UTL1-15; occlusal view
- Fig.10b: left M3, UTL1-15; lingual profile
- Fig.10c: left M3, UTL1-15; labial profile
- Fig.10d: left M3, UTL1-15; front view
- Fig.11a: right M3, UTL1-17; occlusal view
- Fig.11b: right M3, UTL1-17; lingual profile
- Fig.11c: right M3, UTL1-17; labial profile
- Fig.11d: right M3, UTL1-17; front view
- Fig.12a: right M2, UTL1-22; occlusal view
- Fig.12b: right M2, UTL1-22; lingual profile
- Fig.13: right m1-m3, UTL1-23; occlusal view
- Fig.14: right p4-m3, UTL1-24; occlusal view, HOLOTYPE
- Fig.15: right dp4, UTL4-38; occlusal view
- Fig.16: right dp4, UTL4-39; occlusal view
- Fig.17a: right m1, UTL4-40; occlusal view
- Fig.17b: right m1, UTL4-40; labial profile
- Fig.18: right m2-m3, UTL1-25; occlusal view
- Fig.19: left m1, UTL4-41; occlusal view
- Fig.20: left m2, UTL4-42; occlusal view
- Fig.21a: right m3, UTL4-43; occlusal view
- Fig.21b: right m3, UTL4-43; labial view

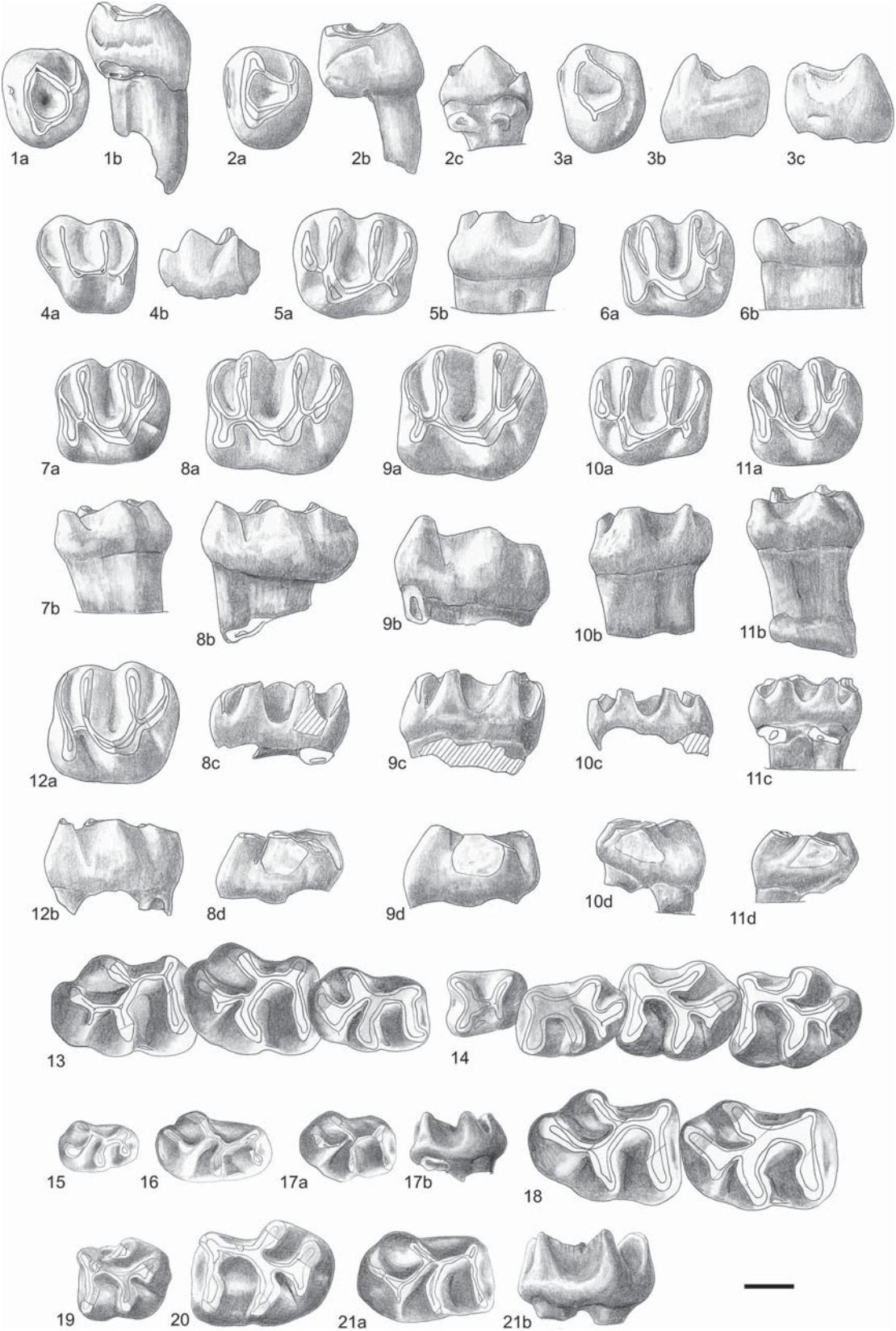


PLATE 7

Alashania tengkoliensis nov.gen. nov.sp., from Oligocene locality UTL1 (Ulanatal area, Inner Mongolia):

Fig. 1a: left P4-M3, UTL1-26; occlusal view

Fig. 1b: fragmentary palate bearing left P4-M3 and right P4-M1, UTL1-26; palatine view

Fig. 1c: fragmentary palate bearing left P4-M3 and right P4-M1, UTL1-26; front view

Fig. 2a: left fragmentary maxillary with P4-M2, UTL1-27; occlusal view

Fig. 2b: left fragmentary maxillary with P4-M2, UTL1-27; labial view

Fig. 2c: left fragmentary maxillary with P4-M2, UTL1-27; lingual view

P.P.F.: posterior palatine foramen.

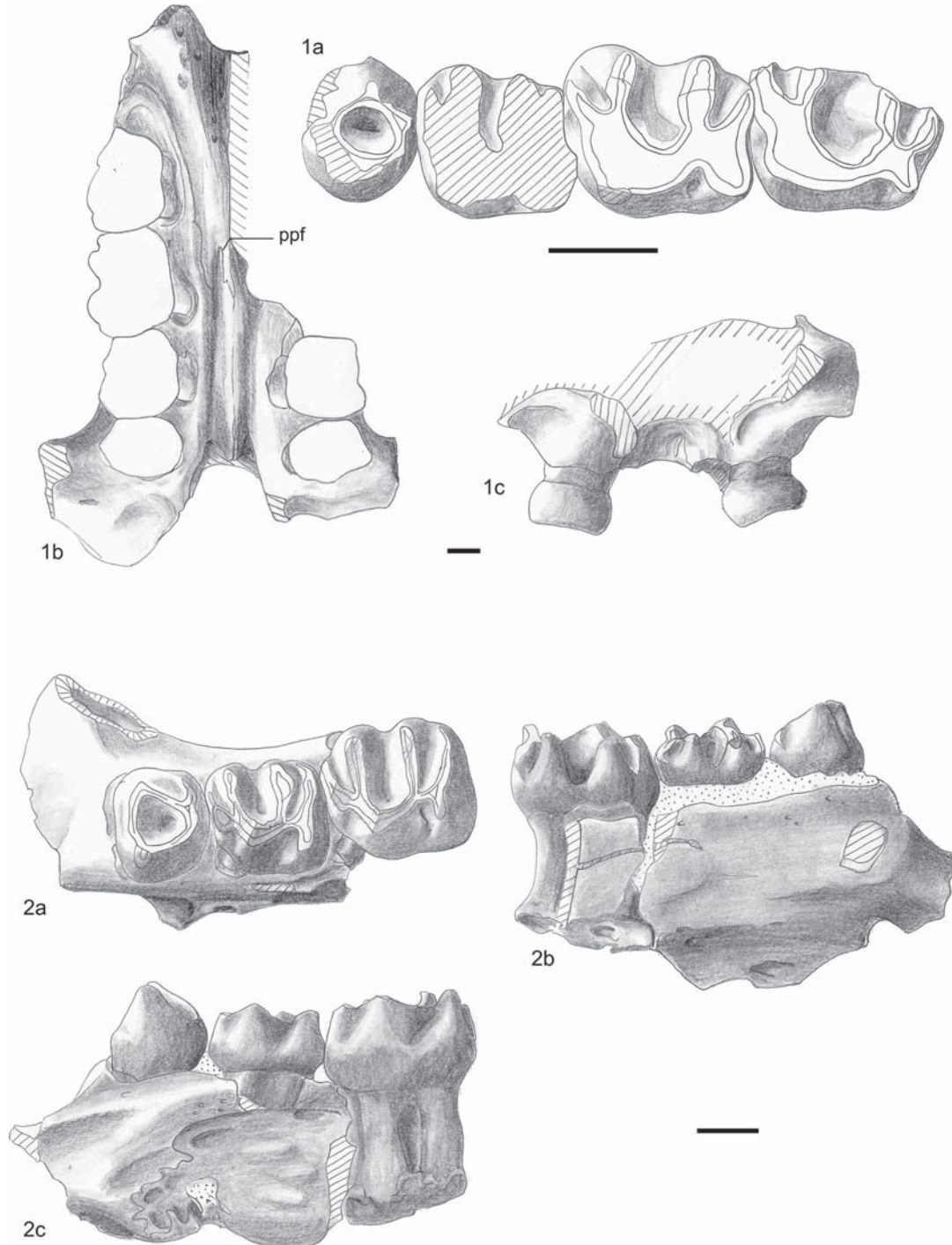


PLATE 8

Yidirtemys ulantatalensis (Huang, 1985), from Oligocene locality UTL4 (Fig. 1-9,11) and *Yindirtemys deflexus* (Teilhard de Chardin, 1926) from locality UTL8 (Fig. 10) (Ulantatal area, Inner Mongolia):

- Fig.1: left dp4, UTL4-44; occlusal view
- Fig.2: right p4, UTL4-45; occlusal view
- Fig.3: left m1, UTL4-46; occlusal view
- Fig.4: left m2, UTL4-47; occlusal view
- Fig.5: right m3, UTL4-48; occlusal view
- Fig.6: right DP4, UTL4-49; occlusal view
- Fig.7: right M1, UTL4-50; occlusal view
- Fig.8: left M2, UTL4-51; occlusal view
- Fig.9: left M3, UTL4-52; occlusal view
- Fig.10: right M3, UTL8-15; occlusal view
- Fig.11: left fragment of maxillary, with M2-M3, UTL4-53; occlusal view

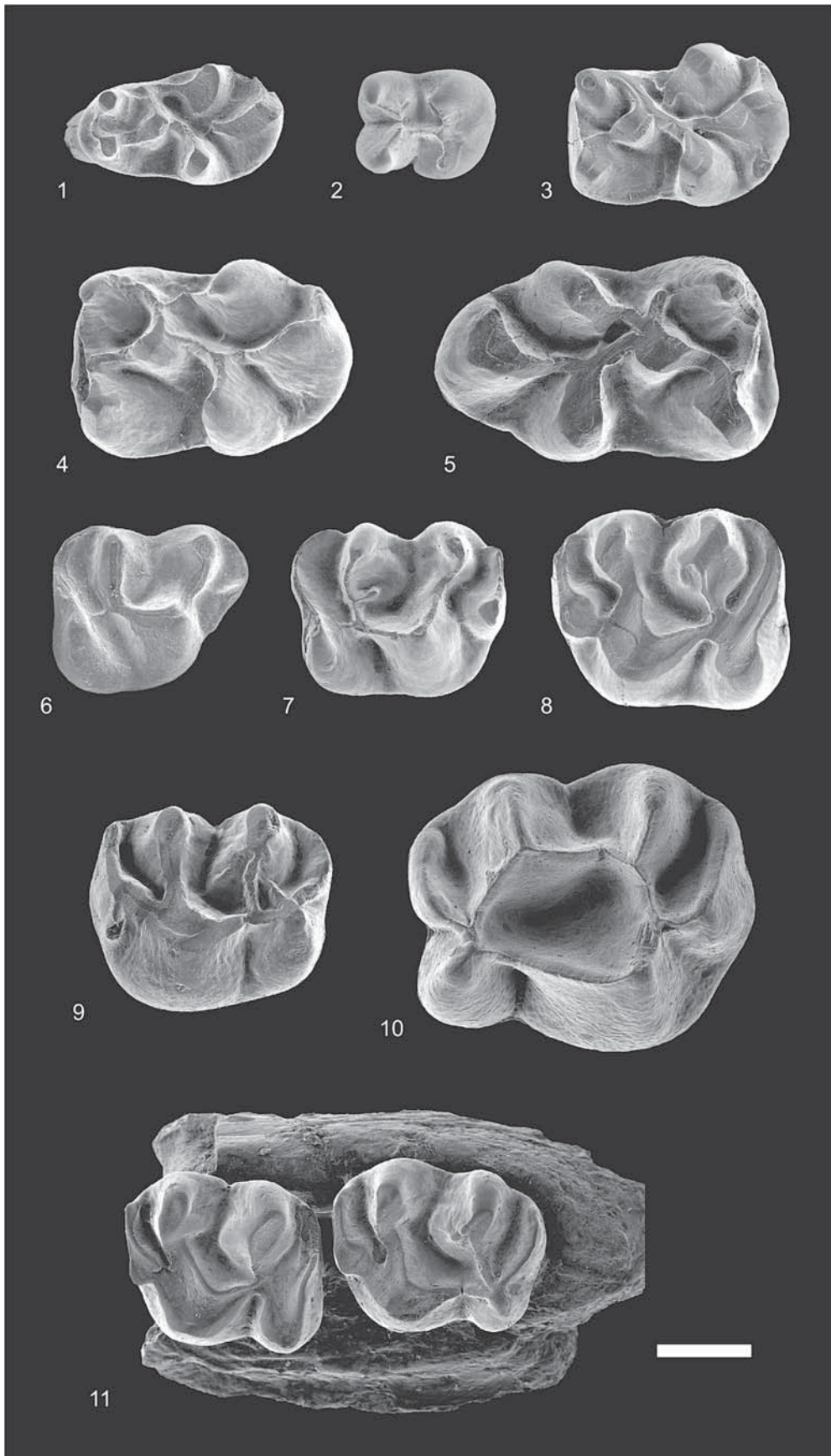


PLATE 9

Yidirtemys ulantatalensis (Huang, 1985), from Oligocene locality UTL7 (Ulantatal area, Inner Mongolia):

Fig.1a: right teeth row with p4-M3, UTL7-56; occlusal view

Fig.1b: right teeth row with p4-M3, UTL7-56; labial profile

Fig.2a: right p4, UTL7-57; occlusal view

Fig.2b: right p4, UTL7-57; labial profile

Fig.3a: left p4, UTL7-58; occlusal view

Fig.3b: left p4, UTL7-58; lingual profile

Fig.4a: left p4, UTL7-59; occlusal view

Fig.4b: left p4, UTL7-59; lingual profile

Fig.5a: left dp4, UTL7-60; occlusal view

Fig.5b: left dp4, UTL7-60; lingual profile

Fig.6a: left dp4, UTL7-61; occlusal view

Fig.6b: left dp4, UTL7-61; labial profile

Fig.6c: left dp4, UTL7-61; lingual profile

Fig.7a: left dp4, UTL7-62; occlusal view

Fig.7b: left dp4, UTL7-62; lingual profile

Fig.8a: left m1, UTL7-63; occlusal view

Fig.8b: left m1, UTL7-63; antero - lingual view

Fig.9: right m1, UTL7-64; occlusal view

Fig.10: left m1, UTL7-65; occlusal view

Fig.11: left m2, UTL7-66; occlusal view

Fig.12: left m3, UTL7-67; occlusal view

Fig.13: left m3, UTL7-68; occlusal view

Fig.14a: right m2, UTL7-69; occlusal view

Fig.14b: right m2, UTL7-69; antero - lingual view

Fig.15a: left m2, UTL7-70; occlusal view

Fig.15b: left m2, UTL7-70; labial profile

Fig.15c: left m2, UTL7-70; lingual profile

Fig.15d: left m2, UTL7-70; antero - lingual view

Fig.16a: left m3, UTL7-71; occlusal view

Fig.16b: left m3, UTL7-71; lingual profile

Fig.16c: left m3, UTL7-71; antero - lingual view

Fig.16d: left m3, UTL7-71; anterior profile

Fig.17a: left m3, UTL7-74; occlusal view

Fig.17b: left m3, UTL7-74; labial profile

Fig.17c: left m3, UTL7-74; lingual profile

Fig.18a: right m3, UTL7-75; occlusal view

Fig.18b: right m3, UTL7-75; posterior profile

Fig.18c: right m3, UTL7-75; anterior profile

Fig.19a: left m3, UTL7-76; occlusal view

Fig.19b: left m3, UTL7-76; postero - lingual view

Fig.20a: right P4, UTL7-77; occlusal view

Fig.20b: right P4, UTL7-77; anterior profile

Fig.20c: right P4, UTL7-77; posterior profile

Fig.21a: right DP4, UTL7-78; occlusal view

Fig.21b: right DP4, UTL7-78; lingual profile

Fig.22a: right DP4, UTL7-79; occlusal view

Fig.22b: right DP4, UTL7-79; lingual profile

Fig.23a: right M1, UTL7-80; occlusal view

Fig.23b: right M1, UTL7-80; lingual profile

Fig.24a: left M1, UTL7-81; occlusal view

Fig.24b: left M1, UTL7-81; lingual profile

Fig.25a: left P4, UTL7-82; occlusal view

Fig.25b: left P4, UTL7-82; anterior profile

Fig.25c: left P4, UTL7-82; posterior profile

Fig.26a: right M3-M2, UTL7-83; occlusal view

Fig.26b: right M3-M2, UTL7-83; labial profile

Fig.27: right M1, UTL7-84; occlusal view

Fig.28: right M1-DP4, UTL7-85; occlusal view

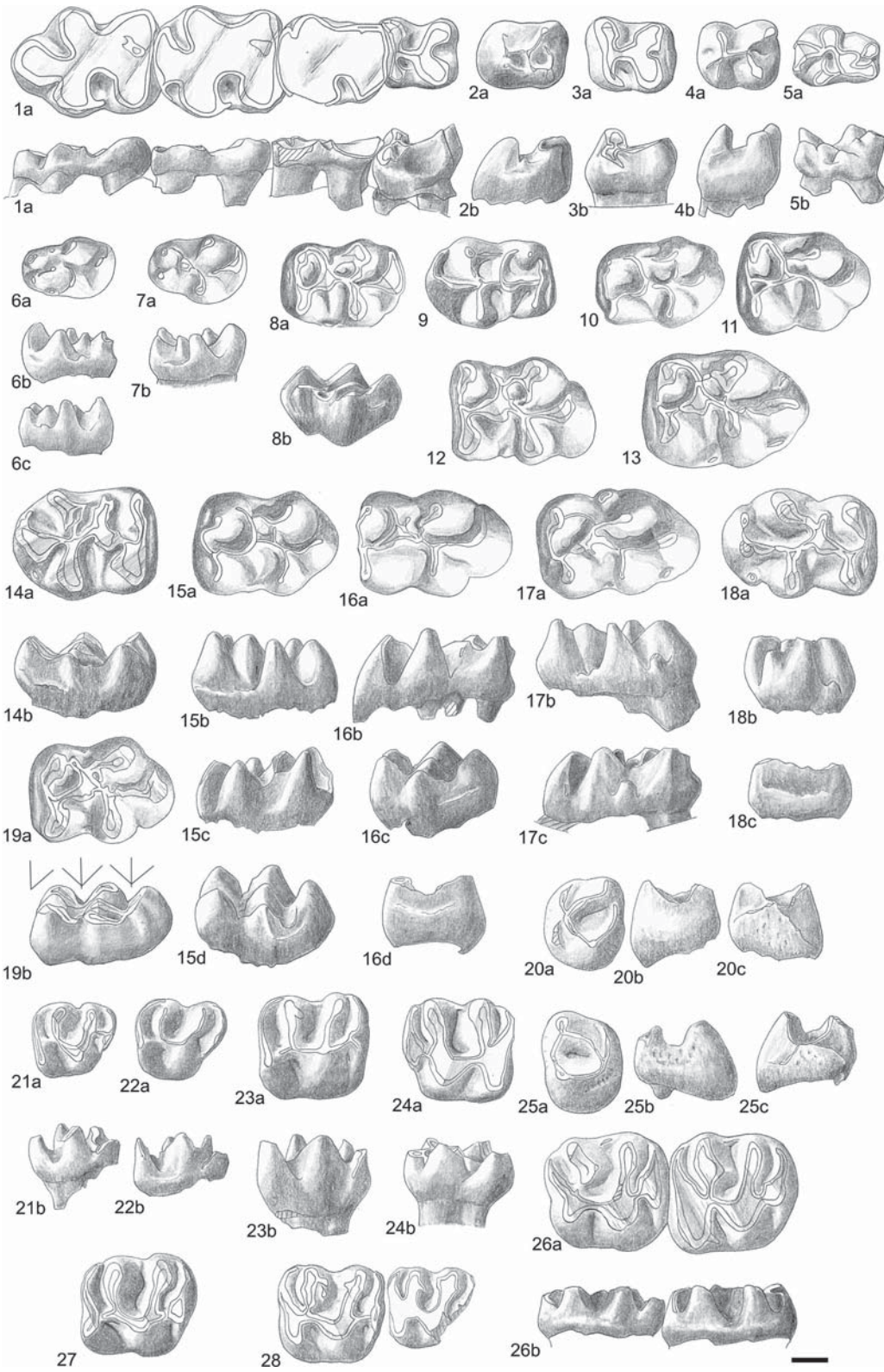


PLATE 10

Yidirtemys ulantatalensis (Huang, 1985), from Oligocene locality UTL4 & UTL8 (Ulantatal area, Inner Mongolia), and *Yidirtemys bohlini* (Huang, 1985) from UTL6 (Fig. 23-24) and UTL8 –Fig.22, 25):

- Fig.1a: right M2, UTL4-54; occlusal view
- Fig.1b: right M2, UTL4-54; lingual profile
- Fig.2a: left M2, UTL4-55; occlusal view
- Fig.2b: left M2, UTL4-55; lingual profile
- Fig.3a: right M2, UTL4-56; occlusal view
- Fig.3b: right M2, UTL4-56; lingual profile
- Fig.4a: right M2or3, UTL4-57; occlusal view
- Fig.4b: right M2or3, UTL4-57; lingual profile
- Fig.5a: right M1, UTL4-58; occlusal view
- Fig.5b: right M1, UTL4-58; lingual profile
- Fig.6a: left M1, UTL4-59; occlusal view
- Fig.6b: left M1, UTL4-59; lingual profile
- Fig.7a: right P4, UTL4-60; occlusal view
- Fig.7b: right P4, UTL4-60; anterior profile
- Fig.8a: right DP4, UTL4-61; occlusal view
- Fig.8b: right DP4, UTL4-61; anterior profile
- Fig.9a: right DP4, UTL4-62; occlusal view
- Fig.9b: right DP4, UTL4-62; anterior profile
- Fig.10a: right M2-M1, UTL4-63; occlusal view
- Fig.10b: right M2-M1, UTL4-63; lingual profile
- Fig.11a: left M3, UTL4-64; occlusal view
- Fig.11b: left M3, UTL4-64; lingual profile
- Fig.12a: right M3, UTL4-65; occlusal view
- Fig.12b: right M3, UTL4-65; lingual profile
- Fig.13a: *Y. ulantatalensis* or *Y. bohlini*: left M3, UTL4-66; occlusal view
- Fig.13b: *Y. ulantatalensis* or *Y. bohlini*: left M3, UTL4-66; lingual profile
- Fig. 14: right M2-M1-P4, UTL4-68; occlusal view
- Fig. 15: left m3, UTL8-16; occlusal view
- Fig. 16: *Y. ulantatalensis* or *Y. bohlini*: left M3, UTL8-17; occlusal view
- Fig.17a: right m1, UTL8-18; occlusal view
- Fig.17b: right m1, UTL8-18; labial profile
- Fig.17c: right m1, UTL8-18; lingual profile
- Fig.17d: right m1, UTL8-18; anterior profile
- Fig.18a: right m2, UTL8-19; occlusal view
- Fig.18b: right m2, UTL8-19; lingual profile
- Fig.19a: right m3, UTL8-20; occlusal view
- Fig.19b: right m3, UTL8-20; lingual profile
- Fig.20a: right M2, UTL8-21; occlusal view
- Fig.20b: right M2, UTL8-21; lingual profile
- Fig.21a: left M3, UTL4-69; occlusal view
- Fig.21b: left M3, UTL4-69; lingual profile
- Fig.22a: right M3, UTL8-22; occlusal view
- Fig.22b: right M3, UTL8-22; lingual profile
- Fig.23a: left M3, UTL6-20; occlusal view
- Fig.23b: left M3, UTL6-20; lingual profile
- Fig.24: right M3, UTL6-21; occlusal view
- Fig.25: right M3, UTL8-32; occlusal view

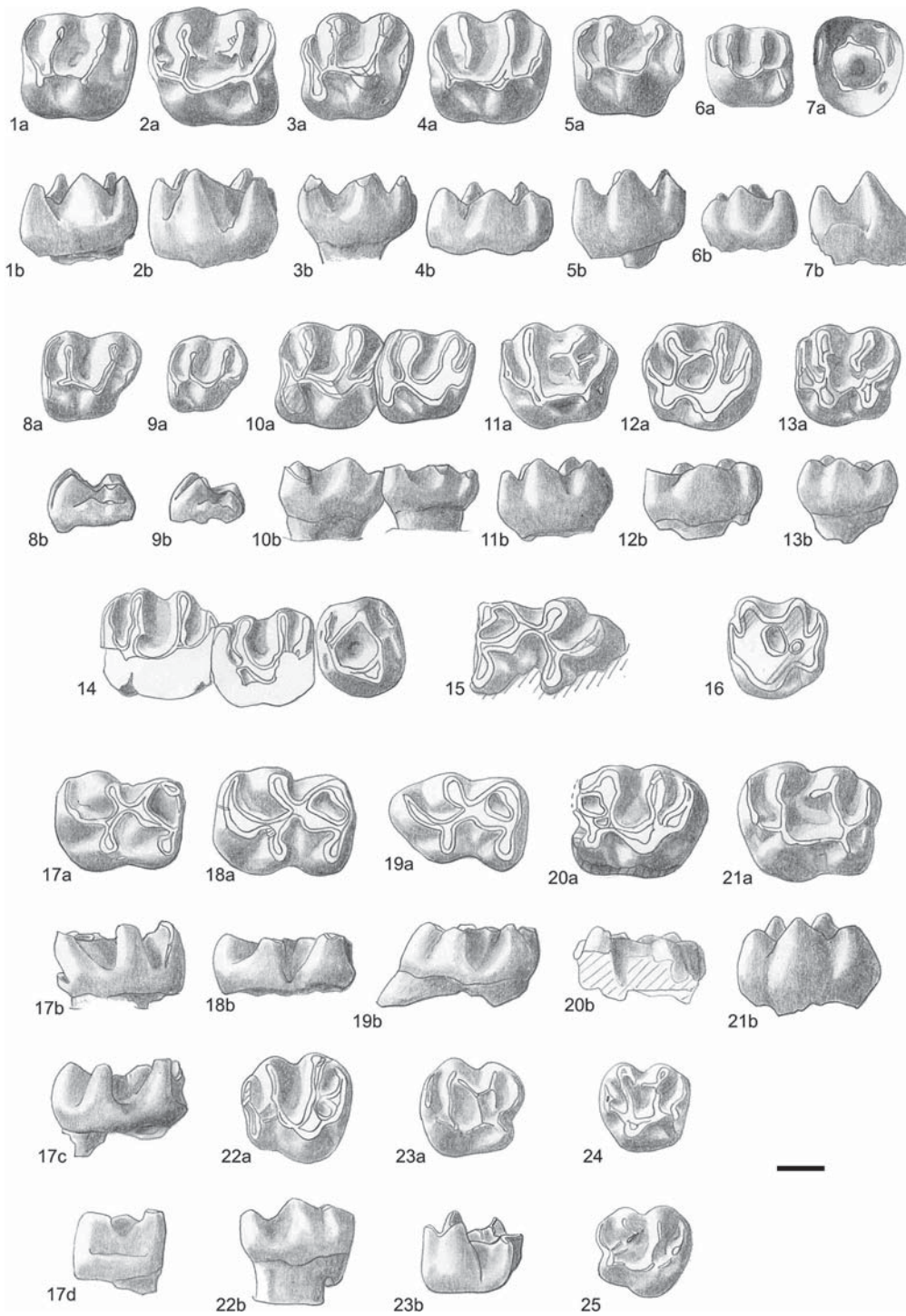


PLATE 11

Yidirtemys bohlini (HUANG, 1985), from Oligocene localities UTL4 & UTL6 (Ulanatal area, Inner Mongolia).

- Fig. 1: right p4, UTL6-5; occlusal view
- Fig. 2: left m1, UTL6-6; occlusal view
- Fig. 3: right m2, UTL6-7; occlusal view
- Fig. 4: right P4, UTL6-8; occlusal view
- Fig. 5: right M1, UTL6-9; occlusal view
- Fig. 6: left M1, UTL6-10; occlusal view
- Fig. 7: right m2, UTL4-71; occlusal view
- Fig. 8: left m2, UTL4-72; occlusal view (*Y. bohlini* or *Y. ulantatalensis*?)
- Fig. 9: right m3, UTL4-73; occlusal view
- Fig. 10: left m3, UTL4-74; occlusal view
- Fig. 11: left m3, UTL4-75; occlusal view
- Fig. 12: right m3, UTL4-76; occlusal view

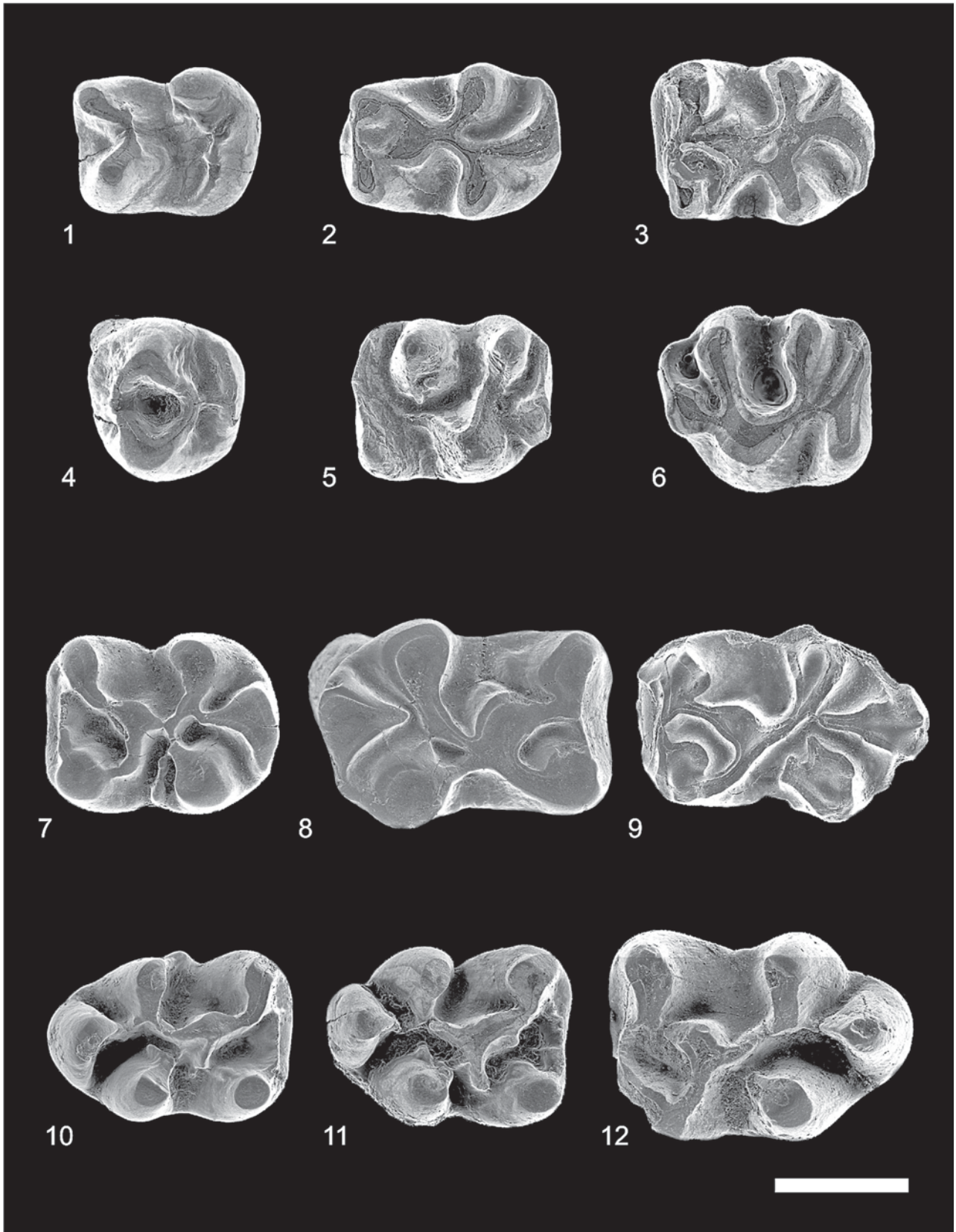


PLATE 12

Yindirtemys shevyrevae nov. sp., from Oligocene locality UTL7 (Ulantatal area, Inner Mongolia); lower teeth:

Fig.1: left lower row p4 to m3, UTL7-86; occlusal view HOLOTYPE

Fig.2a: right p4, UTL7-87; occlusal view

Fig.2b: right p4, UTL7-87; lingual profile

Fig.3a: left dp4, UTL7-88; occlusal view

Fig.3b: left dp4, UTL7-88; lingual profile

Fig.4a: left dp4, UTL7-89; occlusal view

Fig.4b: left dp4, UTL7-89; lingual profile

Fig.5a: right dp4, UTL7-90; occlusal view

Fig.5b: right dp4, UTL7-90; lingual profile

Fig.6a: left m1, UTL7-91; occlusal view

Fig.6b: left m1, UTL7-91; lingual profile

Fig.6c: left m1, UTL7-91; postero - lingual view

Fig.7a: right m1, UTL7-92; occlusal view

Fig.7b: right m1, UTL7-92; lingual profile

Fig.8a: left m1, UTL7-93; occlusal view

Fig.8b: left m1, UTL7-93; lingual profile

Fig.9a: right m1, UTL7-94; occlusal view

Fig.9b: right m1, UTL7-94; lingual profile

Fig.10: left m1, UTL7-95; occlusal view

Fig.11a: left m1, UTL7-91; occlusal view (same as fig. 6)

Fig.11b: left m1, UTL7-91; lingual profile (same as fig. 6)

Fig.12a: right m2, UTL7-97; occlusal view

Fig.12b: right m2, UTL7-97; lingual view

Fig.13a: left m2, UTL7-98; occlusal view

Fig.13b: left m2, UTL7-98; lingual view

Fig.14a: left m3, UTL7-99; occlusal view

Fig.14b: left m3, UTL7-99; lingual view

Fig.15a: left m3, UTL7-99; occlusal view (same as fig. 14)

Fig.15b: left m3, UTL7-99; lingual view (same as fig. 14)

Fig.16a: left m3, UTL7-101; occlusal view

Fig.16b: left m3, UTL7-101; lingual view

Fig.17a: left m3, UTL7-102; occlusal view

Fig.17b: left m3, UTL7-102; lingual view

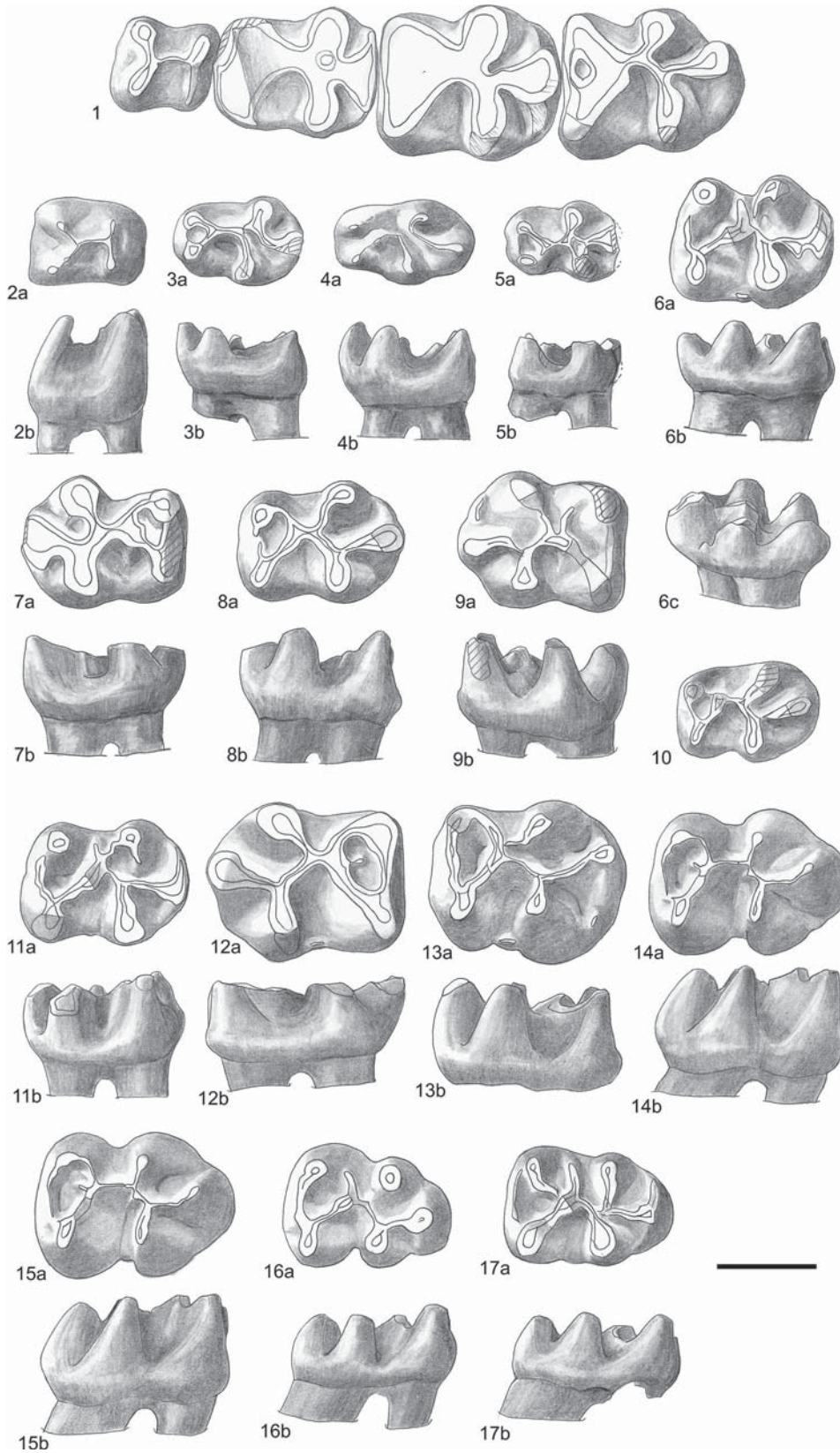


PLATE 13

Yindirtemys shevyrevaе nov. sp., from Oligocene locality UTL7 (Ulantatal area, Inner Mongolia); upper teeth:

- Fig.1a: right DP4, UTL7-103; occlusal view
- Fig.1b: right DP4, UTL7-103; lingual profile
- Fig.2a: left M1, UTL7-104; occlusal view
- Fig.2b: left M1, UTL7-104; lingual profile
- Fig.3a: left M1, UTL7-105; occlusal view
- Fig.3b: left M1, UTL7-105; lingual profile
- Fig.4a: right M1, UTL7-106; occlusal view
- Fig.4b: right M1, UTL7-106; lingual profile
- Fig.5a: right M2, UTL7-108; occlusal view
- Fig.5b: right M2, UTL7-108; lingual profile
- Fig.6a: right M2, UTL7-109; occlusal view
- Fig.6b: right M2, UTL7-109; lingual profile
- Fig.7a: left M2, UTL7-110; occlusal view
- Fig.7b: left M2, UTL7-110; lingual profile
- Fig.8a: left M2, UTL7-111; occlusal view
- Fig.8b: left M2, UTL7-111; lingual profile
- Fig.9a: left M3, UTL7-112; occlusal view
- Fig.9b: left M3, UTL7-112; lingual profile
- Fig.10a: right M3, UTL7-113; occlusal view
- Fig.10b: right M3, UTL7-113; lingual profile
- Fig.11a: right M3, UTL7-114; occlusal view
- Fig.11b: right M3, UTL7-114; lingual profile

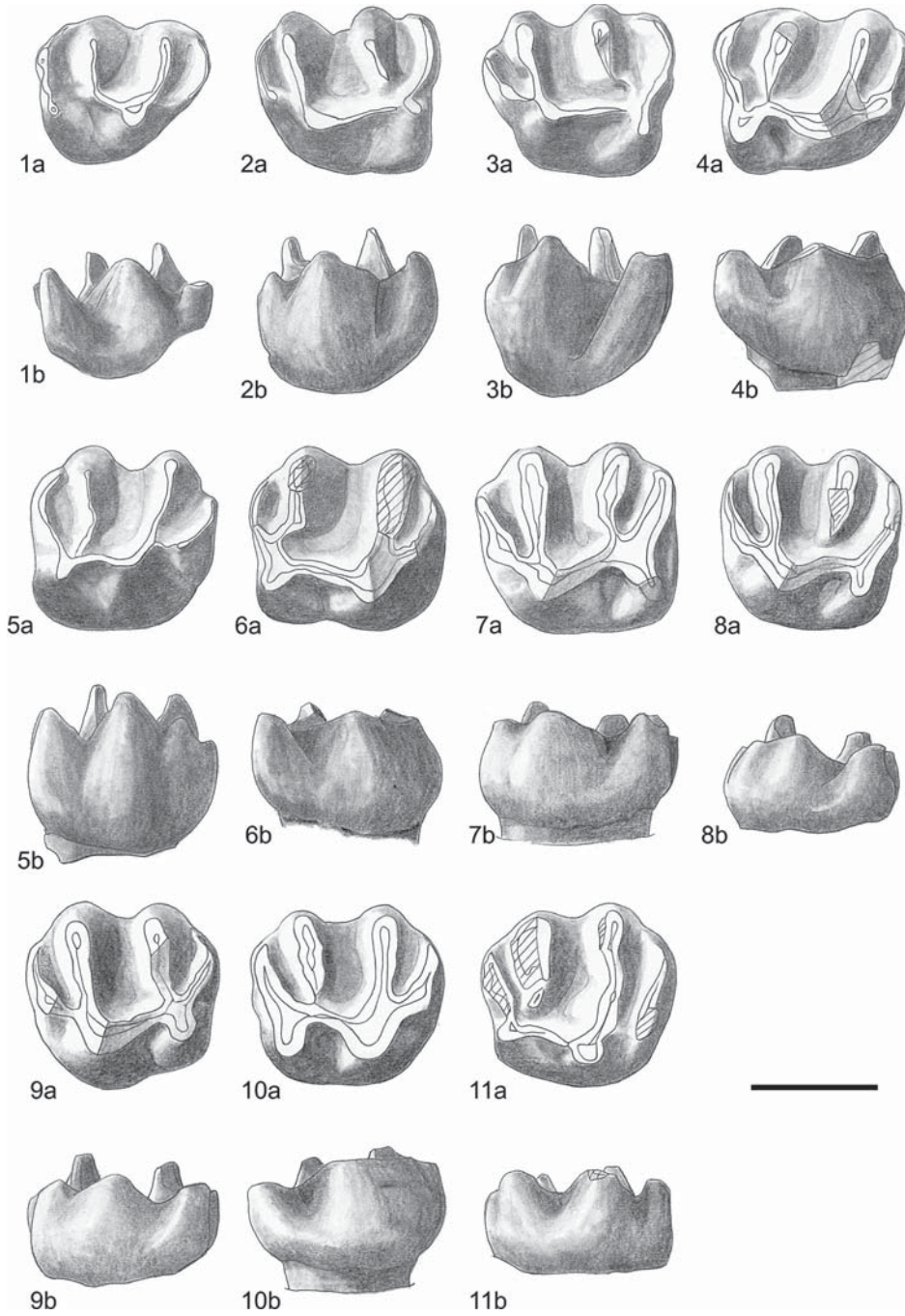


PLATE 14

Yindirtemys shevyrevae nov. sp., from Oligocene locality UTL1 (Ulantatal area, Inner Mongolia); upper and lower teeth:

- Fig.1a: right upper teeth row, with M3 – P4, UTL1-40; occlusal view
- Fig.1b: right upper teeth row, with M3 – P4, UTL1-40; lingual profile
- Fig.1c: right upper M3, the same, UTL1-40; more lingual profile
- Fig.2a: left M3, UTL1-41; occlusal view
- Fig.2b: left M3, UTL1-41; lingual profile
- Fig.3a: left m1-m3, UTL1-42; occlusal view
- Fig.3b left m1-m3, UTL1-42; lingual profile
- Fig.4a: left m2-m3, UTL1-43; occlusal view
- Fig.4b: left m2-m3, UTL1-43; lingual profile

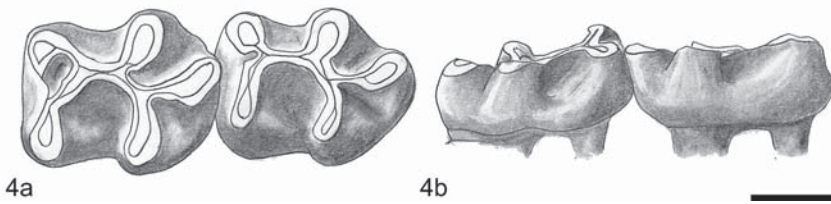
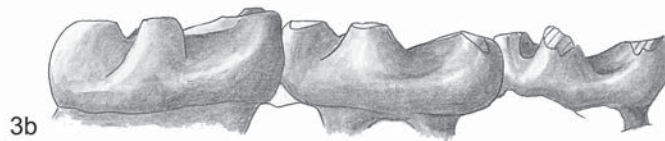
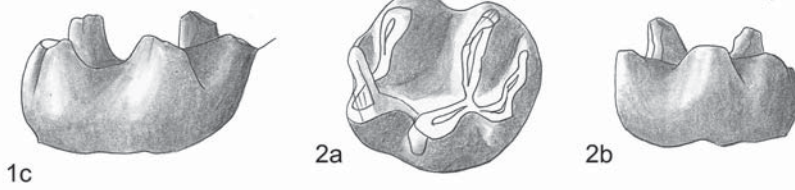
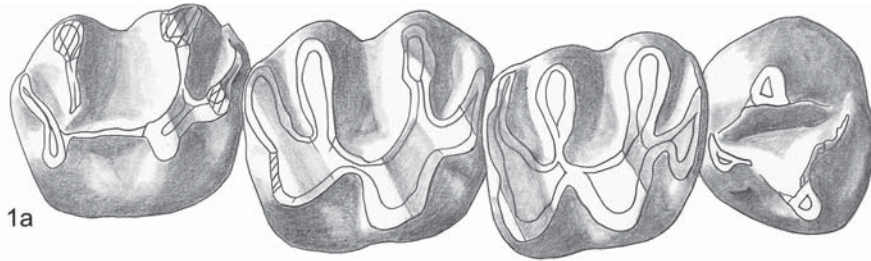


PLATE 15

Yindirtemys aff. *shevyrevae* nov. sp., From UTL6 (Ulanatal area, Inner Mongolia):

Fig.2a: left M1, UTL6-11; occlusal view
Fig.2b: left M1, UTL6-11; lingual profile
Fig.2c: left M1, UTL6-11; labial profile
Fig.2d: left M1, UTL6-11; anterior profile
Fig.3a: right M2, UTL6-12; occlusal view
Fig.3b: right M2, UTL6-12; lingual profile
Fig.3c: right M2, UTL6-12; labial profile
Fig.3d: right M2, UTL6-12; anterior profile

Fig.4a: right M2, UTL6-13; occlusal view
Fig.4b: right M2, UTL6-13; lingual profile
Fig.4c: right M2, UTL6-13; labial profile
Fig.4d: right M2, UTL6-13; anterior profile
Fig.8a: left m2, UTL6-17; occlusal view
Fig.8b: left m2, UTL6-17; lingual profile

Tataromyinae nov.gen.1 or 2, nov. sp.2, from Late Oligocene locality UTL6 (Ulanatal area, Inner Mongolia):

Fig.1a: left DP4, UTL6-14; occlusal view
Fig.1b: left DP4, UTL6-14; lingual profile
Fig.5a: left M1-2, UTL6-15; occlusal view
Fig.5b: left M1-2, UTL6-15; lingual profile
Fig.5c: left M1-2, UTL6-15; labial profile
Fig.5d: left M1-2, UTL6-15; anterior profile

Fig.6a: left M1-2, UTL6-16; occlusal view
Fig.6b: left M1-2, UTL6-16; lingual profile
Fig.6c: left M1-2, UTL6-16; labial profile
Fig.6d: left M1-2, UTL6-16; anterior profile

Tataromyinae nov.gen.1 or 2, nov. sp.3, from Late Oligocene locality UTL8 (Ulanatal area, Inner Mongolia):

Fig.7a: left M3, UTL8-23; occlusal view
Fig.7b: left M3, UTL8-23; lingual profile
Fig.7c: left M3, UTL8-23; labial profile
Fig.7d: left M3, UTL8-23; anterior profile
Fig.9a: right M1-2, UTL8-24; occlusal view
Fig.9b: right M1-2, UTL8-24; lingual profile
Fig.9c: right M1-2, UTL8-24; labial profile
Fig.9d: right M1-2, UTL8-24; anterior profile
Fig.10a: left M2, UTL8-25; occlusal view
Fig.10b: left M2, UTL8-25; lingual profile
Fig.10c: left M2, UTL8-25; labial profile

Fig.10d: left M2, UTL8-25; anterior profile
Fig.11a: right M2, UTL8-26; occlusal view
Fig.11b: right M2, UTL8-26; lingual profile
Fig.11c: right M2, UTL8-26; labial profile
Fig.11d: right M2, UTL8-26; anterior profile
Fig.13a: right M2, UTL8-27; occlusal view
Fig.13b: right M2, UTL8-27; lingual profile
Fig.13c: right M2, UTL8-27; labial profile
Fig.13d: right M2, UTL8-27; anterior profile
Fig.14a: right M3, UTL8-28; occlusal view
Fig.14b: right M3, UTL8-28; lingual profile

Tataromyinae nov.gen.1 or 2, nov. sp.4, from Late Oligocene locality UTL8 (Ulanatal area, Inner Mongolia):

Fig.12a: left M2, UTL8-29; occlusal view
Fig.12b: left M2, UTL8-29; lingual profile
Fig.12c: left M2, UTL8-29; labial profile

Fig.12d: left M2, UTL8-29; anterior profile
Fig.15a: left M2, UTL8-30; occlusal view
Fig.15b: left M2, UTL8-30; lingual profile

