Multituberculate mammals from the Cretaceous of Uzbekistan

ZOFIA KIELAN-JAWOROWSKA and LEV A. NESSOV



Kielan-Jaworowska, Z. & Nessov, L. A. 1992. Multituberculate mammals from the Cretaceous of Uzbekistan. Acta Palaeontologica Polonica **37**, 1, 1-17.

The first western Asian multituberculates found in the Bissekty Formation (Coniacian) of Uzbekistan are described on the basis of a lower premolar (p4), a fragment of a lower incisor, an edentulous dentary, a proximal part of the humerus and a proximal part of the femur. Uzbekbaatar kizylkumensis gen. et sp. n. is defined as having a low and arcuate p4, possibly without a posterobuccal cusp; it presumably had two lower premolars, as inferred from the presence of a triangular concavity at the upper part of the anterior wall of p4, and p3 less reduced in relation to p4 than in non-specialized Taeniolabidoidea and Ptilodontoidea. Uzbekbaatar is placed in the Cimolodonta without indicating family and infraorder. It might have originated from the Plagiaulacinae or Eobaatarinae.

Key words: Multituberculata, Mammalia, Cretaceous, Coniacian, Uzbekistan.

Zofia Kielan-Jaworowska, Paleontologisk Museum, Universitetet i Oslo, Sars Gate 1, N-0562 Oslo, Norway.

Лев А. Несов, Институт Земной Коры, Санкт-Петербургский Университет, 199034 Санкт-Петербург, Россия (Lev A. Nessov, Institute of the Earth Crust, Sankt-Petersburg University. 199034 St. Petersburg, Russia).

Introduction

The Multituberculata is the first mammalian order to have adapted to herbivorous niches, although many may have been omnivorous (Krause 1982). Known from the Late Triassic to the Early Oligocene (Hahn & Hahn 1983), this order of mammals was dominant throughout the Mesozoic in most of the local faunas studied. In spite of this there are still numerous gaps in the multituberculate geographic and stratigraphic record. Until the work of Bonaparte (1986; see also Krause *et al.*, 1992) on the Late Cretaceous multituberculates from Argentina, and of Sigogneau-Russell (1991) who described a multicuberculate tooth from the Early Cretaceous of Morocco, the multituberculates were not known from Gondwanaland. Although Clemens & Kielan Jaworowska (1979: p. 100) stated: 'From the Late Jurassic onward through the Cretaceous every well sampled Holarctic local fauna contains one or more species of multitubeculates...', until now no single multituberculate specimen was known from the vast territory that was previously the Soviet Union.

The stratigraphic record of the Multituberculata is punctuated. Kielan-Jaworowska (1974a) summarized the multituberculates known at that time and stated that the gaps in their fossil record covered at least 73 million years. One of these gaps embraced the first part of the Late Cretaceous (Cenomanian-Early Santonian), referred to by Kielan-Jaworowska (1974a) as Cenomanian-Coniacian or Santonian (because of the ambiguity concerning the age of the Gobi Desert Djadokhta Formation, which yielded numerous multituberculates). In this paper we accept that the Djadokhta Formation is of ?Late Santonian and/or ?Early Campanian age (Gradziński *et al.* 1977).

After 1974 some of the gaps in the multituberculate fossil record were filled. As far as the early part of the Late Cretaceous is concerned Krause & Baird (1979) described a multituberculate lower incisor from the Cenomanian east of the North American Western Interior Seaway. Eaton (1987, 1988) and Eaton & Cifelli (1988) recorded the presence of multituberculates in the Late Turonian Smoky Hollow member of the Straight Cliffs Formation (Kaiparowits Plateau, Utah) and in the Coniacian/Santonian John Henry Member of the same formation. These findings, important as they are, are rare and confined only to the North American continent. Multituberculates have not been reported as yet from the early part of the Late Cretaceous of other parts of the world.

Multituberculates were apparently very rare on southwestern coastal plains of Cretaceous Asia. The latest Albian, Early Cenomanian and Early Santonian-Middle Campanian mammals of these regions are represented only by eutherians while multituberculates are not known (Nessov & Kielan-Jaworowska 1991). Only the Coniacian of Uzbekistan has yielded uncontested multituberculates, which represent not more than one percent of the known mammalian specimens. This contrasts with the Late Cretaceous assemblages from Mongolia and North America (Lillegraven *et al.* 1979 and references therein) where multituberculate specimens represent 50% to 70% of the mammalian fauna, but in the Hell Creek (Sloan & Van Valen 1965) and Lance (Krause 1986) formations they are even more numerous.

Since 1978 one of us (LAN) has been collecting Early and Late Cretaceous mammals in Uzbekistan (Nessov 1987, 1988 and references therein; Kielan-Jaworowska & Nessov 1990). Nessov & Kielan-Jaworowska (1991) reported that four multituberculate specimens had been found in the Late Turonian and Coniacian strata. A closer examination of these specimens shows that the single specimen from the Early Turonian, a fragment of an edentulous dentary, cannot be assigned with certainty to the Multituber-



Fig. 1. Uzbekbaatar kizylkumensis gen. et sp. n. Holotype CCMGE 100/12455, right **p4**, outcrop CBI-14, Bissekty Formation, Coniacian, Dzhyrakuduk, Kizylkum Desert, Uzbekistan. □A. SEM stereo-micrograph, occlusal view. □B. Stereo-photograph, buccal view. □C. Stereo-photograph, lingual view. □D. SEM micrograph, buccal view. C and D coated with ammonium chloride. All × 13.

culata. During the field work in 1991 two more multituberculate specimens were found by LAN in the Coniacian beds.

We describe here these five multituberculate specimens from the Coniacian Bissekty Formation at the locality CBI-14, Dzhyrakuduk, Kizylkum Desert, Uzbekistan, which are the first multituberculates found in western Asia. They belong to few multituberculates known from the time interval Turonian-Early Santonian of the world (see Eaton 1987, 1988; Eaton & Cifelli 1988, for data on North American findings).

Institutional abbreviations: CCMGE, Czernyshev's Central Museum of Geological Exploration, St. Petersburg; DORCM, Dorset County Museum, Dorchester, Dorset; FMNH, Field Museum of Natural History, Chicago; MNA, Museum of Northern Arizona, Flagstaff; PIN, Paleontological Institute, Academy of Sciences, Moscow; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Descriptions

Premolar (the holotype of Uzbekbaatar kizylkumensis gen. et sp. n. - see p. 14; Figs 1, 3C).- In buccal view p4 is moderately arcuate, slightly overhanging the posterior and anterior roots. The crown (with missing anterior margin) is 3.1 mm long, 2.4 mm high along the middle of the exodaenodont lobe, 1.6 mm high above the interradicular crest, and 1.2 mm wide across the middle of the exodaenodont lobe. There are nine serrations, first eight of which bear ridges on both buccal and lingual sides. The distances between the first four ridges are smaller than between the successive ones. The ridges become more prominent posteriorly, the 6th and 7th are the widest, the 8th less prominent again. The 5th and 6th ridges are the longest and extend onto the exodaenodont lobe; their lower parts are, however, very faint. The anterior serrations are less prominent than the posterior ones. The distance between the 8th and 9th serrations is about 1.5 times as long as between the 7th and 8th. As the ridges are directed obliquely anteroventrally, there is a relatively large smooth surface without ridges on the posterior one third of the crown. We presume that the posterobuccal cusp was absent in U. kizylkumensis; as, however, the enamel is partly missing on the posterior part of the buccal side (Fig. 1B, D), the absence of this cusp cannot be unequivocally demonstrated. On the posterior margin there is a deep incurvature near the lower margin of the crown (Fig. 1B, C).

In lingual aspect the crown is lower than in the buccal, 1.4 mm deep above the interradicular crest. The ridges are more prominent than on the buccal side.

In occlusal view the crown widens anteriorly and is asymmetrical, as the buccal side in the area of the exodaenodont lobe protrudes more strongly buccally than the lingual side (Fig. 1A).

In anterior view (Fig. 3C) the broken part of the crown is exposed as an irregular, small surface. As this part (and the missing part) overhangs the root, we presume that the triangular area with crenulated margins, which in the Plagiaulacidae contacts the $\mathbf{p3}$ (see below), was not developed. The root extends upwards until this broken surface and in its upper parts is surrounded by the flaring margins of the crown, the buccal distinctly longer than the lingual, forming an unequilateral triangle. There are two longitudinal ridges on the root, with a furrow between them, presumably for reception of $\mathbf{p3}$. In posterior view on the surface of the crown there is a deep, short, roughly triangular (pointed upwards) concavity, wider than long.

The anterior root is 1.0 mm long anteroposteriorly (measured at the base, in buccal view), the posterior is 0.8 mm long. The internadicular crest

Fig. 2. Changes in number and structure of premolars in the evolution of multituberculates. Reconstruction of the skull, upper teeth and lower molars of *Plagiaulax* is hypothetical, based on *Bolodon* and *Ctenacodon*. Not to scale. (Modified from Simpson 1928, 1937; Krause 1982; Hahn 1985, and Kielan-Jaworowska 1991).





is broken off, but its basal part is preserved, better seen in lingual than in buccal view.

Comparisons.– The discussed tooth is similar to the undescribed **p4**'s (e.g., FMNH PM 1751, PM 662 and PM 1008) from the Albian Antlers Formation, Trinity group, of Texas (see Krause *et al.* 1990) in having a relatively low crown. It differs from the Texas specimens in the apparent absence of a posterobuccal cusp (large in Texas specimens), in having 9 serrations (7 in Texas specimens) and in its smaller size. Eaton (1988) described forty multituberculate taxa from Utah (Albian through Campanian), mostly upper teeth. Of the two **p4**'s figured by him, only the Campanian *Cimexomys* sp. cf. *C. judithae*, MNA V5312 (Eaton 1988: Fig. 66A, B) from the Kaiparowits Formation invites a comparison with the new Asian species. The Utah **p4** is 3.05 mm long, has a relatively low crown with 9 serrations, which are more prominent and differently distributed than in our species, and which extend to the posterior end of the crown. The posterobuccal cusp, not recognizable in our species, is present in the Utah specimen.

Number of lower premolars.– Although only **p4** of *Uzbekbaatar* is known, we assume there might have been two lower premolars for the following reasons.

(1) The primitive multituberculates, Paulchoffatoidea and Plagiaulacoidea (Simpson 1928; Hahn 1969, 1978; Hahn & Hahn 1983; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska & Ensom 1992) have three or more lower premolars which are parallel-sided (Fig. 2).

We did not study the contact between **p3** and **p4** in the Paulchoffatoidea or the structure of the anterior wall of **p4**. In Plagiaulacoidea the contact between **p3** and **p4** is only in the upper parts of the teeth (see Kielan-Jaworowska & Ensom 1992: Pl. 2: 1). Among the plagiaulacine p4's available to us, the anterior wall of **p4** is exposed only in Bolodon osborni, DORCM GS 201 (Fig. 3A). The preserved anterior wall consists of two parts. The upper part forms a narrow triangle with crenulated margins and a deep longitudinal middle furrow. The lower part, which corresponds to the upper part of the anterior root (which is partly broken), is wider and relatively flat, with a very weak medial furrow. Only the upper triangular part was in contact with **p3**. In a plagiaulacid eobatarine, Eobaatar magnus (Fig. 3B), an upper triangular part with crenulated margins is similar in anterior aspect of **p4**, to that in Bolodon, but smaller; also, a longitudinal furrow on the anterior root extends to this small triangular part. If **p3** in *Eobaatar* was in contact only with the small triangular surface with crenulated margins on **p4** (as in Bolodon), then it was smaller than in Bolodon.

(2) Arginbaatar (from the ?Aptian or Albian of the Gobi Desert; the only member of the Arginbaataridae suborder *incertae sedis* - see Kielan-Jawo-rowska & Ensom 1991, 1992) is possibly the only multituberculate with three premolars, of which **p4** is strongly arcuate, rather than parallel-sided. In Arginbaatar, as shown by Kielan-Jaworowska *et al.* (1987: e.g., Pls 13; 14: 1a, b, 2a, b; 16: 2b, c; 17: 2a, b), only a small, upper part of **p3**



Fig. 3. $\Box A.$ Bolodon osborni Simpson 1928, DORCM GS 201, left **p4**, anterior view, Purbeck Limestone Formation, Cherty Freshwater Member, Sunnydown Farm Quarry near Langton Matravers, Southern England. $\Box B.$ Eobaatar magnus Kielan-Jaworowska, Dashzeveg, & Trofimov 1987, PIN 3101/60, epoxy resin cast of right **p4**, anterior view, Khovboor Beds (?Aptian or Albian), Khovboor, Guchin Us, Gobi Desert, Mongolia. $\Box C.$ Uzbekbaatar kizyl-kumensis gen. et sp. n. Holotype CCMGE 100/12455, right **p4**, anterior view, outcrop CBI-14, Bissekty Formation, Coniacian, Dzhyrakuduk, Kizylkum Desert, Uzbekistan. $\Box D.$ Kryptobaatar dashzevegi Kielan-Jaworowska 1970, ZPAL MgM-I/37, right dentary, anterobuccal view, Djadokhta Formation (?Middle Campanian), Bayn Dzak, Gobi Desert, Mongolia. All stereo-photographs, coated with ammonium chloride. A-C × 13, D × 6.

is in contact with the upper portion on the anterior wall of **p4**, which is oblique, rather than vertical, as in the Plagiaulacidae. In the top part of the anterior wall of **p4** a small triangular concavity, embraced on both sides by the margins of the buccal and lingual blades of the crown (Kielan-Jaworowska *et al.*, 1987: Pl. 19: 2), contacts **p3**. Below this triangle the anterior root of **p4** is convex in anterior view (rather than concave as in *Eobaatar*).

(3) The advanced multituberculates, Cimolodonta (Taeniolabidoidea and Ptilodontoidea), are characterized by an arcuate **p4**, and only two (or one in the derived forms) lower premolars (Clemens & Kielan-Jaworowska 1979). Usually **p3** is very small, peg-like and fits tightly the anterior wall

of the anterior root of **p4**, below the overhanging crown (e.g., *Kryptobaatar*, Fig. 3D).

Our small sample of isolated **p4**'s shows that in Plagiaulacoidea, there is a triangular area with crenulated margins on the upper part of the anterior wall of **p4**, for the reception of **p3**. In Cimolodonta, in contrast, the peg-like **p3** contacts only the anterior root of **p4**, on which, as a rule, is a longitudinal furrow. However, in *Eobaatar*, an advanced plagiaulacoid (Plagiaulacidae, Eobaatarinae), there is a small triangular area at the top part of the crown, below which there extends the anterior root with a longitudinal furrow (Fig. 3B).

In the discussed specimen (Fig. 3C), the anterior part of the crown that overhangs the anterior root is broken. The root extends high onto the crown, and has a longitudinal furrow. The anterior wall is somewhat intermediate between that of **p4** of *Eobaatar* and *Kryptobaatar*. The crown overhangs the root as in *Kryptobaatar*, but less strongly, and the furrow on the root extends higher upwards. The size and shape of this furrow is similar to that of *Eobaatar*, but possibly without the triangular surface with crenulated margins as in *Eobaatar*, although the relevant part of the *Uzbekbaatar* **p4** is partly broken. The shape of **p4** and the structure of its anterior wall allow speculation on the shape and size of **p3** and possibly on the number of lower premolars. The morphology of **p4** of *Uzbekbaatar* suggests that its jaw possibly had only two lower premolars, **p3** being peg-like, but larger than in eucosmodontid Taeniolabidoidea and Ptilodontoidea.

An edentulous dentary, described below, shows in front of the alveoli for $\mathbf{p4}$ an alveolus for a single-rooted $\mathbf{p3}$ (Fig. 4E). This alveolus is relatively larger than in the Late Cretaceous members of Taeniolabidoidea from Mongolia, which indicates that the $\mathbf{p3}$ was not very strongly reduced. This dentary does not seem conspecific with the premolar of *U. kizylkumensis*, but shows that the Coniacian multituberculates of Uzbekistan attained the two-premolar level.

Dentary (Multituberculata indet. sp. A; Fig. 4D-F).– Only the anterior part of the right dentary, with alveoli for the incisor and p3-m2, has been preserved. The coronoid process is broken off; its base starts opposite the **m1-m2** embrasure. In the anteroventral prolongation of the coronoid process there is a swelling on the buccal wall, below and somewhat to the rear of the anterior root of **p4**. The masseteric crest starts opposite the **p4-m1** embrasure. It is relatively weak anteriorly and more prominent to the rear, but its posterior part is broken off. The anterior part of the anterior prolongation of the coronoid process and the base of this process from above, is roughly triangular and well defined. It is not divided into two fossae, as is characteristic of most taeniolabidoid and ptilodontoid multituberculates (see e.g. Clemens & Kielan-Jaworowska 1979: Figs 6, 7A and Kielan-Jaworowska 1974b: Fig. 5c). The pterygoid fossa is large and deep; its anterior margin lies opposite the middle of **m2**. There is a



Fig. 4. \Box A-C. ?Multituberculata indet. - ?right lower incisor CCMGE 102/12455. A. Buccal view. B. Dorsal view. C. Lingual view. \Box D-F. Multituberculata indet. sp. A. CCMGE 101/12455, right dentary. D. Buccal view. E. Stereo-photograph, occlusal view. F. Lingual view. Locality CBI-14, Bissekty Formation, Coniacian, Dzhyrakuduk, Kizylkum Desert, Uzbekistan. All coated with ammonium chloride, × 6.

single, large opening (the entrance to the mandibular canal) in the upper part of the anterior wall of the fossa. The ramus separating the pterygoid and the masseteric fossae projects lingually to form the wide, horizontal floor to the pterygoid fossa. The dentary is roughly parallel-sided at the level of **p3-p4**; below the middle of **m1** it starts to increase in depth posteriorly, the lower margin being incurved at this point. When examined in ventral view the dentary is relatively narrow anteriorly and increases in width posteriorly.

The mental foramen is situated relatively high, about 1.6 mm in front of the alveolus for **p3**. There are several nutrient foramina, slightly smaller than the mental foramen, distributed at random on the buccal and lingual sides and one between the alveoli for **p3** and **p4**. The positions of the alveoli show that the premolars and molars were situated obliquely in respect to the longitudinal axis of the dentary, but somewhat less obliquely than in advanced Taeniolabidoidea (see e.g. Kielan-Jaworowska *et al.* 1987: Fig. 6B) and Ptilodontoidea (e.g. Clemens & Kielan-Jaworowska 1979: Figs 6, 7B). The alveolus for **p3** is 0.44 mm in diameter. The buccal and posterior margins of the anterior alveolus for **p4** are partly broken off, the estimated diameter of the alveolus is 1.1 mm. The posterior alveolus for **p4** is 0.65 mm long. Between these two alveoli there is a third minute alveolus, 0.28 mm in diameter for an interradicular crest. The tentative estimations of the lengths of the teeth from the alveoli are: $\mathbf{p4}$ - 2.7 mm, $\mathbf{m1}$ - 1.4 mm, $\mathbf{m2}$ - 1.2 mm.

Humerus (Multituberculata indet. sp. B; Fig. 5A-D).– Only the proximal part of the right humerus has been found. The greatest width of the humerus across the tuberosities is 4.3 mm, the width of the head - 2.9 mm. The head is somewhat more flat proximally than in other multituberculates, e.g. in *Ptilodus montanus* (Krause & Jenkins 1983), in an unidentified taeniolabidoid from Bayn Dzak (Kielan-Jaworowska 1989) and in ?Lambdopsalis bulla (Kielan-Jaworowska & Qi 1990). The head overhangs the shaft in a similar way as in the unidentified taeniolabidoid from Bayn Dzak (Kielan-Jaworowska 1989: Pl. 18: 2b, d). The greater tuberosity is situated only slightly more proximally than the lesser. The sulcus for the musculus brachialis is very wide, relatively wider and shallower than in the taeniolabidoid from Bayn Dzak. The deltopectoral crest is moderately prominent. The lesser tuberosity is proximally confluent with the head, it bears a small prominent medial tubercle. In ventral view the lesser tuberosity is prominent only in the very proximal part, and more distally it gently merges with the wide bicipital groove. The greater tuberosity is more prominent than the lesser and more sharply separated from the bicipital groove. Only a tiny part of the entepicondylar flange has been preserved, and although its surface is partly damaged, one can see that it was developed as a wide, rounded ridge.

Femur (Multituberculata indet. sp. C; Fig. 5E-G).– The incomplete, proximal part of a left femur has been found. The head and lesser trochanter are broken off. The greater trochanter is robust, about 2.7 mm long. The expanded apex bears a rugose area for insertion of gluteal musculature. Proximally the area is divided by a shallow furrow into two inflated parts. Distally the insertion area is prolonged along the lateral aspect of the shaft as a triangular area that passes into a sharp gluteal crest (Fig. 5E). Medial to this area (in dorsal aspect), at mid length on the trochanter there is a small longitudinal pit. Another, somewhat longer pit is seen in the dorsal aspect distomedially to the first one, along the distal prolongation of the medial margin of the greater trochanter. The digital fossa is very narrow and deep. There is also a second larger, very deep fissure-like fossa between the lesser trochanter medially and gluteal crest laterally, regarded by Granger & Simpson (1929), and Simpson & Elftman (1928) as part of a divided digital fossa, referred to below as the distal digital fossa. The shaft is oval in cross section, slightly compressed laterally, its maximal diameter at the distal margin of the distal digital fossa described above is 2.3 mm. In the structure of the greater trochanter, the proximal part of which is divided into two inflated parts, and in the presence of a very deep fissurelike distal digital fossa, the described femur is more similar to that of the ptilodontoid *Ptilodus*, which is about twice as large (Krause & Baird 1979; Krause & Jenkins 1983), than to that of the Asian taeniolabidoid Kryptobaatar (Kielan-Jaworowska 1969, 1979b). The described femur belonged



Fig. 5. \square A-D. Proximal part of the right multituberculate humerus CCMGE 103/12455. A. Stereo-photograph, ventral view. B. Dorsal view. C. Medial view. D. Lateral view. \square E-G. Proximal part of the left multituberculate femur CCMGE 104/12455. E. Stereo-photograph, dorsal view. F. Stereo-photograph, ventral view. G. Stereo-photograph, ventromedial view. Locality CBI-14, Bissekty Formation, Dzhyrakuduk, Kizylkum Desert, Uzbekistan. All coated with ammonium chloride, × 6.

to a species slightly smaller than *Kryptobaatar dashzevegi* and larger than *Chulsanbaatar vulgaris* (Kielan-Jaworowska 1974b).

Incisor (?Multituberculata indet.; Fig. 4A-C).- Fragment of a ?right lower incisor is gently bent, narrows posteriorly and, less strongly anteriorly. Its maximum depth is 1.7 mm in buccal view. The tooth is broken at both ends. At the anterior end of the preserved fragment the enamel is partly damaged on the ventral and buccal sides. Otherwise the tooth appears to be completely covered by enamel; at the anterodorsal corner of the preserved part, there is a minute plate with an additional layer of enamel. There is a weak, longitudinal furrow on the buccal side, the anterior end of which is not preserved due to damage of the enamel. On the lingual side there is also a longitudinal furrow, somewhat deeper than the buccal one, which disappears before reaching the anterior end of the preserved part. The lingual side is somewhat flattened at the area of the furrow. Longitudinal, but deeper furrows on both buccal and lingual sides of the lower incisor occur in Eobaatar sp. a of Kielan-Jaworowska et al. (1987: Pl. 8: 5). The discussed specimen differs from the lower incisor of *Eobaatar* sp. a in being possibly completely covered with enamel, which, however, because of the incompleteness of the tooth cannot be demonstrated with any certainty. It cannot be also excluded that the incisor from Uzbekistan did not belong to a multituberculate.

Discussion

Sloan & Van Valen (1965) regarded a limited enamel band on the lower incisor as an apomorphy of the Taeniolabidoidea (see also Krause & Carlson 1987). Recently, limited enamel on the lower incisor was found in a 'plagiaulacoid' from the Morrison Formation (latest Jurassic) of North America (Engelmann *et al.* 1990). Among the isolated ?Aptian or Albian teeth from Guchin Us in the Gobi Desert two lower incisors of different shape, both with limited enamel, were assigned to *Eobaatar* sp. a, and *Eobaatar* sp. b (Kielan-Jaworowska *et al.* 1987). An occurrence of incisors with limited enamel in plagiaulacoids from the Late Jurassic of North America and Early Cretaceous of Mongolia indicates that this character cannot be regarded as an apomorphy of the Taeniolabidoidea.

As demonstrated by Krause & Jenkins (1983) the postcranial skeleton of ptilodontoid and taeniolabidoid multituberculates cannot help in subordinal assignment. Fossorial adaptations of a multituberculate skeleton were described by Kielan-Jaworowska & Qi (1989), but our postcranial fragments do not show such adaptations.

The femur described above is possibly more similar to that of the ptilodontoid *Ptilodus* than to the femur of the Asian taeniolabidoid *Kryptobaatar*, but small differences in femoral structure, related to different musculature and habits, are not infraordinally diagnostic.

Uzbekbaatar gen. n., based on a single premolar tooth, has characters that do not allow assignment to any known family. It cannot belong to a member of the Paulchoffatoidea, as it is long and arcuate, possibly without a posterobuccal cusp, rather than being quadrangular or oval and short, with many posterobuccal cusps (Hahn 1969, 1978). Neither can it be assigned to the Plagiaulacoidea because of its arcuate shape and presumed presence of two lower premolars in the jaw, whereas there are three or four lower premolars in Plagiaulacoidea and the **p4** is parallel-sided. Two lower premolars, arcuate **p4** (with a posterobuccal cusp) and peg-like p3 occur in non-specialized members of the Taeniolabidoidea and Ptilodontoidea. The Kizylkum species may belong in either of these infraorders. If its lower incisor was completely covered with enamel, an assignment to the Ptilodontoidea would be more justified; however, this group has not yet been recorded from Asia (Kielan-Jaworowska 1979a). We assign Uzbekbaatar to the Cimolodonta, infraorder and family incertae sedis, because we cannot demonstrate whether it is a taeniolabidoid or a ptilodontoid.

It seems possible that *Uzbekbaatar* arose from the Plagiaulacinae or Eobaatarinae by loss of one lower premolar, and by the acquisition of a more arcuate **p4**. If *Uzbekbaatar* lost indeed the posterobuccal cusp on **p4**, it does not lie in the evolutionary line leading to known Taeniolabidoidea or Ptilodontoidea, because this cusp is retained in non-specialized members of these infraorders.

It is not possible to demonstrate whether the five multituberculate specimens from the Bissekty Formation are conspecific or even congeneric. Although they roughly fit each other in size, there are differences. The length of the isolated **p4** is 3.1 mm, while the estimated length of **p4** in the edentulous dentary is 2.8 mm. Also the posterior root of the isolated premolar is more robust than the posterior alveolus for **p4** in this dentary. This suggests that it possibly belonged to a different, smaller species. The fragmentary lower incisor is larger than the missing incisor in the dentary.

The fragment of humerus is 3.3 mm in diameter below the head, while the femur is 2.3 mm in diameter below the distal digital fossa. The humerus/femur width ratio is 1.49. In the Late Cretaceous multituberculates from the Gobi Desert, humeri and femora are preserved together only in a few specimens, but only in *Nemegtbaatar gobiensis* ZPAL MgM-I/81 were we able to measure this ratio, which is 1.12. This suggests that the humerus from Kizylkum belongs either to a different (larger) species than the femur, or to a much older individual.

It follows that at least two multituberculate species are represented in the Bissekty Formation.

Taxonomy

Suborder Cimolodonta McKenna 1975

Remarks.– We described above five multituberculate specimens from the Coniacian of Uzbekistan, which we assign to the Cimolodonta McKenna 1975. McKenna (1975), in his classification of multituberculates, recognized only two suborders: the Haramiyoidea and Plagiaulacoidea, the latter including the Plagiaulacida and the new infraorder Cimolodonta. The Cimolodonta was erected to include the 'parvorders' Ptilodontoidea and Taeniolabidoidea, but was not defined. As McKenna did not discuss his classification, it was ignored by subsequent authors. The cladistic analysis of multituberculate taxa by Archibald (1982) and by Krause & Carlson (1987) confirmed the monophyly of the Ptilodontoidea and Taeniolabidoidea, and thus the retention of Cimolodonta appears justified. We will not discuss the higher rank systematics of the Multituberculata; we tentatively regard the Cimolodonta as a suborder, with two infraorders the Ptilodontoidea.

Infraorder incertae sedis

Family incertae sedis

Uzbekbaatar gen. n.

Type species: Uzbekbaatar kizylkumensis sp. n.

Etymology: Uzbek - from Uzbekistan. baatar - Mong. a hero. a suffix often used for multituberculate genera.

Diagnosis.– As for the type species.

Comparison.– The new genus differs from Plagiaulacoidea (*sensu* Kielan-Jaworowska & Ensom, 1991, 1992) in having **p4** arcuate (rather than parallel-sided), without a row of posterobuccal cusps. Differs from most Plagiaulacinae and Eobaatarinae in presumable presence of two lower premolars, and possibly in lack of triangular plate at upper part of anterior wall of **p4** for reception of **p3**. Shares with non-specialized Cimolodonta two lower premolars and structure of the anterior wall of **p4**, but differs from them in presumable lack of a posterobuccal cusp on **p4** and in having **p3** possibly less reduced in relation to size of **p4**. Shares with Arginbaataridae presumable lack of posterobuccal cusp, but differs from it in having **p4** that does not rotate during ontogeny, smaller number of serrations, and less arcuate crown, completely covered with enamel.

Uzbekbaatar kizylkumensis sp. n.

Figs 1, 3C.

Holotype: CCMGE 100/12455, right p4, the only specimen known.

Type horizon and locality: Locality CBI-14 (Nessov 1987) of the Bissekty Formation (Coniacian) of Dzhyrakuduk, Kizylkum Desert, Uzbekistan.

Etymology: kizylkumensis - found in Kizylkum Desert.

Diagnosis.– Lower premolar p4 relatively low, with nine serrations and eight ridges. Distance between 8th and 9th serrations distinctly longer than between preceding ones. First ridges weak, the 6th and 7th most prominent. Posterior one third of buccal side smooth. Deep, short incurvature on the posterior surface of p4.

Acknowledgements

We thank Prof. David W. Krause (State University of New York at Stony Brook) and Mr Paul C. Ensom (Yorkshire Museum, York) who reviewed the first draft of this paper and provided useful comments. We are grateful to Dr. Jerzy Dzik for making Fig. 2. The work of ZKJ has been supported by Norges Allmenvitenskapelige Forskningsråd, grant no. ABC/LR 441. 92/003. The photographs were taken by ZKJ and Per Aas, the SEM micrographs by LAN, with a help of Hans-Arne Nakrem, all at the Paleontological Museum, University of Oslo. LAN wishes to express his gratitude to A. O. Averianov (Zoological Institute, St. Petersburg) for field assistance.

References

- Archibald, J.D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. University of California Publications, Geological Sciences 122, I-XVI + 1-286.
- Bonaparte. J.F. 1986. Sobre Mesungulatum houssayi y nuevos mamíferos Cretácicos de Patagonia, Argentina. Actas IV Congreso Argentino de Paleontologia **2**, 48-61.
- Clemens, W.A. & Kielan-Jaworowska, Z. 1979. Multituberculata, In: J. A. Lillegraven, Z. Kielan-Jaworowska, & W.A. Clemens (eds) Mesozoic Mammals: The First Two-Thirds of Mammalian History, 99-149. University of California Press. Berkeley.

- Eaton, J.G. 1987. Stratigraphy, depositional environments, and age of Cretaceous mammalbearing rocks in Utah, and systematics of the Multituberculata (Mammalia). Ph. D. dissertation, XV + 308 pp. University of Colorado, Boulder.
- Eaton, J.G. 1988. Cretaceous multituberculate (Mammalia) from Utah. Journal of Vertebrate Paleontology 8. Abstracts, 13A-14A.
- Eaton, J.G. & Cifelli, R.L. 1988. Preliminary report on Late Cretaceous mammals of the Kaiparowits Plateau, southern Utah. University of Wyoming Contributions to Geology 26, 45-55.
- Engelmann, G.F., Greenwald, N.S., Callison, G., & Chure, D.J. 1990. Cranial and dental morphology of a Late Jurassic multituberculate mammal from the Morrison Formation. *Journal of Vertebrate Paleontology* 10, Abstracts, 22A.
- Gradziński, R., Kielan-Jaworowska, Z., & Maryańska, T. 1977. Upper Cretaceous Djadokhta, Barun Goyot and Nemegt formations of Mongolia including remarks on previous subdivisions. Acta Geologica Polonica 27, 281-318.
- Granger, W. & Simpson, G.G. 1929. A revision of the Tertiary Multituberculata. Bulletin of the American Museum of Natural History 56, 601-676.
- Hahn, G., 1969. Beiträge zur Fauna der Grube Guimarota Nr. 3. Die Multituberculata. *Palaeontographica A* **133**, 1-100.
- Hahn, G. 1978. Neue Unterkiefer von Multituberculaten aus dem Malm Portugals. *Geologica et Palaeontologica* **12**, 177-212.
- Hahn, G. 1985. Zum Bau des Infraorbital-Foramens bei den Paulchoffatiidae (Multituberculata, Ober-Jura). Berliner geowissenschaftliche Abhandlungen A **60**, 5-27.
- Hahn, G. & Hahn, R. 1983. Multituberculata. In: F. Westphal (ed.) Fossilium Catalogus. I: Animalia, Pars 127, 409 pp. Kugler Publications, Amsterdam.
- Kielan-Jaworowska, Z. 1969. Discovery of a multituberculate marsupial bone. Nature 222, 1091-1092.
- Kielan-Jaworowska, Z. 1974a. Migrations of the Multicuberculata and the Late Cretaceous connections between Asia and North America. Annals of the South African Museum 64, 231-243.
- Kielan-Jaworowska, Z. 1974b. Multituberculate succession in the Late Cretaceous of the Gobi Desert (Mongolia). In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, pt. V. Palaeontologia Polonica 30, 23-44.
- Kielan-Jaworowska, Z. 1979a. Absence of ptilodontoidean multituberculates from Asia and its palaeogeographic implications. *Lethaia* 13, 169-173.
- Kielan-Jaworowska, Z. 1979b. Pelvic structure and nature of reproduction in Multituberculata. Nature 277, 402-403.
- Kielan-Jaworowska, Z. 1989. Postcranial skeleton of a Cretaceous multituberculate mammal. Acta Palaeontologica Polonica 34, 75-85.
- Kielan-Jaworowska, Z. 1991. Ewolucja na Lądach. 66 pp. Wydawnictwa Geologiczne, Warszawa.
- Kielan-Jaworowska, Z. & Ensom, P.C. 1991. Suprageneric taxa of Late Jurassic and Early Cretaceous multituberculate mammals. In: Z. Kielan-Jaworowska, N. Heintz, & H.-A. Nakrem (eds) Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota: Extended Abstracts. Contributions from the Paleontological Museum, University of Oslo 364, 35-36.
- Kielan-Jaworowska, Z. & Ensom, P.C. 1992. Multituberculate mammals from the Upper Jurassic Purbeck Limestone Formation of Southern England. *Palaeontology* 35, 95-126.
- Kielan-Jaworowska, Z. & Nessov, L.A. 1990. On the metatherian nature of the Deltatheroida, a sister group of the Marsupialia. *Lethala* 23, 1-10.
- Kielan-Jaworowska, Z. & Qi, T. 1990. Fossorial adaptations of a taeniolabidoid multituberculate mammal from the Eocene of China. *Vertebrata PalAsiatica* **28**, 83-94.
- Kielan-Jaworowska, Z., Dashzeveg, D., & Trofimov, B.A. 1987. Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms. Acta Palaeontologica Polonica 32, 3-47.
- Krause, W.D. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate Ptilodus. Paleobiology 8, 265-281.

- Krause, W.D. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. *Contributions to Geology*, *University of Wyoming Special Paper* **3**, 95-117.
- Krause, W.D. & Baird, D. 1979. Late Cretaceous mammals east of the North American Western Interior Seaway. *Journal of Paleontology* 53, 562-565.
- Krause, W.D. & Carlson, S.J. 1987. Prismatic enamel in multituberculate mammals: tests of homology and polarity. *Journal of Mammalogy* 68, 755-765.
- Krause, W.D. & Jenkins, F.A. 1983. The postcranial skeleton of North American multituberculates. Bulletin of the Museum of Comparative Zoology 150, 199-246.
- Krause, W.D., Kielan-Jaworowska. Z., & Bonaparte, J.F. 1992. Ferugliotherium Bonaparte, the first known multituberculate from South America. Journal of Vertebrate Paleontology 12, 351-376.
- Krause, W.D., Kielan-Jaworowska, Z., & Turnbull, W.D. 1990. Early Cretaceous Multituberculata (Mammalia) from the Antlers Formation, Trinity Group, in North-Central Texas. *Journal of Vertebrate Paleontology* 9, Abstracts, 31A.
- Lillegraven, J.A., Kielan-Jaworowska, Z., & Clemens, W.A. (eds) 1979. Mesozoic Mammalis: The First Two-Thirds of Mammalian History. 311pp. University of California Press, Berkeley.
- McKenna, M.C. 1975. Toward a phylogenetic classification of the Mammalia. In: W.P. Luckett & F.S. Szalay (eds) *Phylogeny of the Primates*, 21-46. Plenum Press, New York.
- Nessov, L.A. (Несов, Л.А.). 1987. Результаты поисков и исследования меловых и раннепалеогенновых млекопитающих на територии СССР. *Ежегодник Всесоюзного Палеонтологического Общества* **30**, 199-219.
- Nessov, L.A. (Несов, Л.А.) 1988. Комплексы позвоночных позднего мезозоя и палеоцена Средней Азии. В: Т.Н. Богданова и М.В. Ошуркова (ред.) Становление и Еволюция Континентальных Биот, 93-101. Труды XXXI Сесии Всесоюзного Палеонтологического Общества. Издательство "Наука". Ленинград.
- Nessov, L.A. & Kielan-Jaworowska, Z. 1991. Evolution of Cretaceous Asian therian mammals. In: Z. Kielan-Jaworowska. N. Heintz, & H.A. Nakrem (eds) Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Extended Abstracts. Contributions from the Paleontological Museum, University of Oslo 364, 51-52.
- Sigogneau-Russell, D. 1991. First evidence of Multituberculata (Mammalia) in the Mesozoic of Africa. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte B **2**, 120-126.
- Simpson, G.G. 1928. A catalogue of Mesozoic Mammalia in the Geological Department of the British Museum. X + 215 pp. British Museum (Natural History), London.
- Simpson, G.G. 1937. Skull structure of the Multituberculata. *Bulletin of the American Museum of Natural History* **73**, 727-763.
- Simpson, G.G. & Elftman, H.O. 1928. Hind limb musculature and habits of a Paleocene multituberculate. *American Museum Novitates* **333**, 1-19.
- Sloan, R.E. & Van Valen. L. 1965. Cretaceous mammals from Montana. Science 148, 220-227.

Streszczenie

Praca zawiera opis pięciu okazów multituberkulatów z późnej kredy (z formacji Bissekty, należącej do koniaku) z pustyni Kizylkum w Uzbekistanie. Są to pierwsze multituberkulaty z terytorium byłego Związku Radzieckiego i jedne z nielicznych na świecie z pierwszej połowy późnej kredy. Ssaki kredowe zostały ostatnio odkryte na terenie Uzbekistanu i Kazakstanu, reprezentowane prawie wyłącznie przez ssaki łożyskowe i deltateroidy; multituberkulaty, znalezione tylko w formacji Bissekty, obejmują 1% okazów ssaków. Ta proporcja różni się bardzo od stosunków w większości odsłonięć górnej kredy Azji i Ameryki północnej, gdzie multituberkulaty z reguły stanowią 50 - 70% znajdowanych okazów ssaków, a w formacjach Lance i Bug Creek w Ameryce północnej nawet więcej.

Uzbekbaatar kizylkumensis gen. et sp. n., został opisany na podstawie czwartego dolnego zeba przedtrzonowego (p4). Zab ten ma stosunkowo niską, łukowato wygiętą koronę, z dziewięcioma grzebieniami i przypuszczalnie bez tylnego guzka policzkowego. Uzbekbaatar został zaliczony do podrzędu Cimolodonta, szczepu i rodziny incertae sedis. Cimolodonta charakteryzują się obecnością dwóch dolnych przedtrzonowych: p3 i p4, przy czym **p4** jest duży i łukowato wygięty; przewiesza się on nad silnie zredukowanym p3, który jest jednokorzeniowy i ma kształt patyczka przylegającego do przedniego korzenia **p4**. Dwa szczepy zaliczone do Cimolodonta: Ptilodontoidea i Taeniolabidoidea różnia się budowa dolnego siekacza. Ponieważ siekacz ten u Uzbekbaatar nie jest znany, przynależność nowego rodzaju do szczepu nie mogła zostać ustalona. Uzbekbaatar nie może być zaliczony do podrzędów Paulchoffatoidea lub Plagiaulacoidea ze względu na łukowaty kształt p4 i przypuszczalną obecność tylko dwóch dolnych zębów przedtrzonowych, gdy w obu tych podrzędach p4 ma kształt prostokatny i występują trzy lub cztery dolne zeby przedtrzonowe.

Ponadto w pracy opisano okazy oznaczone jako Multituberculata indet. sp. A, B, C, reprezentujące bezzębną żuchwę, proksymalną część kości ramiennej i proksymalną część kości udowej. W żuchwie zachowały się zębodoły zębów przedtrzonowych i trzonowych, wskazujące że multituberkulat ten miał dwa przedtrzonowe. Porównania rozmiarów tych okazów, oraz przedtrzonowego opisanego jako *Uzbekbaatar kizylkumensis* wykazują, że opisane multituberkulaty należą przynajmniej do dwóch taksonów. Ponadto w pracy opisano fragment dolnego siekacza z tych samych warstw, zaliczonego z zastrzeżeniem do multituberkulatów.

Zilustrowane zostały również czwarte zęby przedtrzonowe przedstawicieli Plagiaulacoidea i Taeniolabidoidea, oraz przeprowadzono powrównania między nimi, z których wynika, że budowa czwartego dolnego przedtrzonowego (który często zachowuje się sam) pozwala wnioskować o budowie i rozmiarach trzeciego przedtrzonowego, a także o liczbie dolnych przedtrzonowych.