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POSTCRANIAL SKELETON OF A CRETACEOUS MULTITUBERCULATE MAMMAL

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The fragmentary postcranial skeleton of an unidentified taeniolabidoid multituberculate from the Upper Cretaceous Djadokhta Formation at Bayn Dzak, Gobi Desert, Mongolia, is described. It consists of cervical vertebrae 2-7, manubrium of the sternum, sternebra, incomplete scapula and proximal part of the humerus. Cervical vertebrae and the manubrium of the sternum are described for the first time in the Multituberculata. The individual to which the skeleton belonged was intermediate in size between Kryptobaatar dashzevegi and Catopsalis matthewi. The fusion of the axis with the third vertebra, the relatively large manubrium with a strong ventral ridge and the relatively stout humerus indicate that the species to which the skeleton belonged may have been specialized for digging.

Key words: Multituberculata, Mammalia, fossorial adaptations, Cretaceous, Mongolia.

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INTRODUCTION

Although multituberculates had the longest span of any order of mammals, their postcranial skeleton and habits are still incompletely known. Partial limbs and girdles, or vertebrae have been described or discussed in XIX century by Cope (various papers) and Marsh (see Krause and Jenkins 1983 for review), and later by Gidley (1909), Broom (1914), Simpson (1926, 1928, 1937), Simpson and Elftman (1928), Granger and Simpson (1929), McKenna (1961), Clemens (1963), Sloan and Van Valen (1965), Kielan-Jaworowska (1969, 1979a), Sahni (1972), Jenkins (1973), Kielan-Jaworowska and Dashzeveg (1978), Jenkins and Weijs (1979) and Krause and Baird (1979). Krause and Jenkins (1983, see also Jenkins and Krause 1983) described an almost complete skeleton of the Paleocene *Ptilodus kummae* and discussed all known postcranial skeletons of North American multituberculates. In spite of all these papers, some parts of the multituberculate skeleton such as the cervical vertebrae, except one cervical — 6th or 7th, described but not figured by Gidley (1909), the sternum and part of the manus have not been described as yet.

In the collection of Late Cretaceous mammals from Mongolia housed in the Zakład Paleobiologii PAN in Warsaw (abbreviated ZPAL), there are several multituberculate skeletal parts. Most complete are the skeletons of Kryptobaatar dashzevegi (ZPAL MgM-I/41) from the Djadokhta Formation, and of Nemegtbaatar gobiensis (ZPAL MgM-I/81) and Chulsanbaatar vulgaris (ZPAL MgM-I/83), from the Red Beds of Khermeen Tsav. The latter beds are a stratigraphic equivalent of the Barun Goyot Formation (see Gradziński et al. 1977 for the discussion of the age of these beds and formations). The detailed description of these specimens will take some time due to their small size and the long process of preparation. In the same collection there is a partial multituberculate postcranial skeleton from the Djadokhta Formation (ZPAL MgM-I/165). As some structures in this specimen may be interpreted as adaptations to semi-fossorial habits, unknown previously in multituberculates, I have thought it desirable to describe this specimen separately, before the description of all the remaining multituberculate postcranial material is completed.

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SYSTEMATIC PALEONTOLOGY

Multituberculata Suborder Taeniolabidoidea Taeniolabidoid, fam., gen. et sp. indet.

(pls. 15-18; figs. 1-3)

Material. — ZPAL MgM-I/165 — fragmentary postcranial skeleton from the ?Late Santonian and/or ?Early Campanian Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia, consisting of cervicals 2-d to 7th with missing arches, manubrium of the sternum, one sternebra, incomplete left scapula, proximal part of the right humerus and fragments of ribs.

Remarks on systematic assignment. — The structure of the scapula and humerus

indicates that the specimen is a multituberculate. Its familial, generic and specific assignments pose difficulties. All known Djadokhta Formation multituberculates belong to the Taeniolabidoidea (Kielan-Jaworowska 1980). Of the six described Djadokhta Formation multituberculate genera (Simpson 1925, 1928, Kielan-Jaworowska 1970, 1974, Kielan-Jaworowska and Dashzeveg 1978, Kielan-Jaworowska and Sloan 1979), the incomplete postcranial skeleton has been described in Catopsalis matthewi, referred to earlier as Djadochtatherium (Simpson 1925, 1928, McKenna 1961), but see also Simmons and Miao (1986), and the pelvis in Kryptobaatar dashzevegi (Kielan-Jaworowska 1969, 1979). Additional postcranial skeletal material, as yet undescribed, is housed in the Zakład Paleobiologii PAN in Warsaw. Associated with the above mentioned pelvis of Kryptobaatar are the hind limbs, an incomplete scapula and fragments of neck vertebrae. From the Djadokhta Formation are also postcranial elements of Sloanbaatar, Kamptobaatar and of an undetermined genus, all consisting of incomplete pelvic girdles and hind limbs.

A comparison of the cervical vertebrae of ZPAL MgM-I/165 with the poorly preserved cervicals of Kryptobaatar dashzevegi (ZPAL MgM-I/41) shows that the two specimens are very different from one another. ZPAL MgM-I/165 is larger than K. dashzevegi and has a differently shaped axis which is fused with the third vertebra (they are not fused in Kryptobaatar). The humerus of ZPAL MgM-I/165 is larger than that of Tugrigbaatar saichanensis (Kielan-Jaworowska and Dashzeveg 1978) which is of approximately the same size as that of K. dashzevegi.

A comparison with the described fragments of the postcranial skeleton of Catopsalis matthewi (which may belong to Djadochtatherium), shows that ZPAL MgM-I/165 is approximately intermediate in size between K. dashzevegi and C. matthewi. Of such a size is a poorly known Djadokhta Formation species, Bulganbaatar nemegtbaataroides. However, the identification of ZPAL MgM-I/165 as B. nemegtbaataroides cannot be demonstrated and therefore the described specimen is identified as a taeniolabidoid fam., gen. et sp. indet.

Description.— The axis and the third vertebra (pl. 15, 16; fig. 1) are fused and will be referred to here as the fused vertebrae. On the ventral surface is a suture between the two component bodies. On the dorsal surface the suture is not discernible and the place of fusion is indicated only by the large intervertebral foramen at the base of the arch. On the axis itself there is no suture corresponding to the line of fusion between the atlantal and the axial parts of the body, such as seen in e.g. Eozostrodon (Jenkins and Parrington 1976) and in Zalambdalestes (Kielan-Jaworowska 1978).

The length of the fused vertebrae (without the dens) is 5 mm; the length of the dens is 1.2 mm and its width 1.4 mm. The dens is roughly rectangular and directed horizontally. The body is strongly compressed dorsoventrally. The anterior articular processes are large and form in ventral view a crescent-like convex area, which protrudes ventrally. There is a prominent ventral crest. The lateral depressions are very deep, especially immediately behind the anterior articular processes. In the axial part, on each side of the depressions, are two oblique furrows directed posterolaterally. In the third vertebra, a roughly longitudinal furrow lies on either side of the ventral crest. Lateral to this furrow is a deep oblique furrow lying parallel to the second transverse process. The fused vertebrae are provided with two processes, which are long and evidently correspond to the cervical ribs, although the suture is not discernible. It is not discernible either on the remaining cervical vertebrae. Unlike in Ornithorhynchus the transverse processes appear to be pointed rather than rounded at the ends, although the tips are broken off. Each of the transverse processes arises by two roots: a ventral one from the body, visible in the ventral view as an oblique crest directed in lateral aspect nearly horizontally, and

a dorsal one from the arch, directed more obliquely downwards. The transverse foramina are present. Extending anterodorsally from the transverse foramen is a short furrow on the transverse process. The posterior articular processes are large and nearly horizontal, as they are on the 4th vertebra (not preserved on the other vertebrae). The fused vertebrae are provided with a single arch, only the base of which has been preserved. The dorsal side of the body is flat and smooth, perforated by 4 pairs of small nutrient foramina.

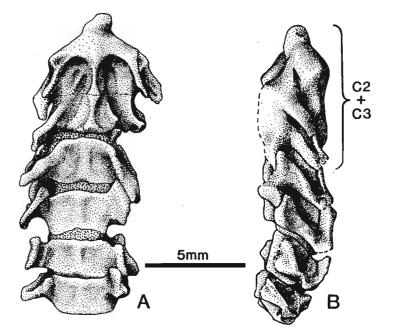


Fig. 1. Taeniolabidoid, fam., gen. et sp. indet., ZPAL MgM-I/165, Cervical vertebrae 2-7. A, ventral view; B, right lateral view

Cervical vertebrae four to seven (pl. 15, 16: 1; fig. 1). In all the vertebrae the arches are missing. The bodies of all the vertebrae are compressed dorsoventrally, and their lengths decrease in size posteriorly: C4 is 2.2 mm long, C5-2 mm, C6 1.8 mm, and C7-1.8 mm. The body of C4 is narrower anteriorly than posteriorly. The ventral crest is much less prominent than on the fused vertebrae. On C5 and C6 the ventral crest is absent, but it is present on C7. The lateral depressions on C4 are concave, with a deep, lateral furrow, arranged obliquely posterolaterally, parallel to the transverse process. The bodies of C5 to C7 are in ventral view more rectangular than that of C4.

On the fourth vertebra the ventral branch of the transverse process joins in the posterior part of the body and is directed more transversely than on the fifth and sixth vertebrae. On all of the vertebrae the dorsal branch of the transverse process arises directly below the anterior articular process. The fifth and sixth vertebrae differ from the fourth in having the ventral branches of the transverse processes more prominent and joining the body more anteriorly; they project ventrally as distinct vertical plates with anteroventral projections; however, the inferior lamella (Howell 1926) characteristic of the sixth vertebra of therian mammals is not developed. The seventh vertebra has a short transverse process, joining the anterior part of the body. Its base is perforated by a transverse foramen. The dorsal surfaces of the bodies are flat. There is one pair of large nutrient foramina in the middle of each vertebra.

Sternum (pl. 17: 1; fig. 2). The manubrium is about 7.5 mm wide and 9.7 mm long. It consists of a wide, fan-shaped anterior part and a long narrow posterior stem which widens at the end. The jugular notch is gently concave. The obliquely arranged clavicular notches are seen on its sides. A depression for the reception of the first costal cartilage is preserved only on the left lateral border, immediately behind the clavicular notch.

In dorsal view, in the anterior part, there are triangular lateral parts, which embrace the middle, bowl-shaped part from both sides. In the posterior part of the bowl, along its mid-line, starts a longitudinal ridge, which continues along the stem and merges into the expanded foot. The stem is about 3 mm wide anteriorly, narrows posteriorly to 1.2 mm width a short distance in front of the posterior margin and widens to 2.1 mm at the foot. In posterior view, the foot is quadrangular with rounded corners, and has a dorsoventral diameter of 2.5 mm. Its expanded posterior surface is slightly convex.

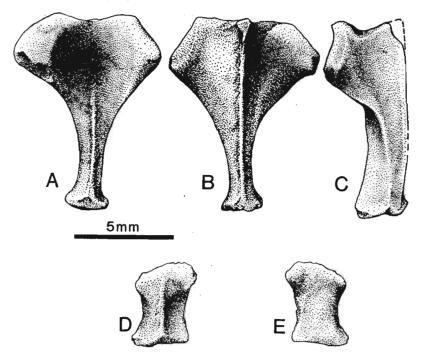


Fig. 2. Taeniolabidoid, fam. gen., et sp. indet., ZPAL MgM-I/165. A—C, manubrium sterni, dorsal, ventral and right lateral views; D—E, sternebra, ventral and dorsal views

In ventral view the manubrium is strongly convex transversely. The longitudinal ridge (keel) is prominent. It is deeper and somewhat narrower anteriorly; on the stem it is lower and wider and merges posteriorly into the expanded foot.

A single preserved sternebra is 3.5 mm long and has incurved lateral margins. The anterior margin is damaged, but the posterior margin is 2.5 mm wide. The dorsal surface is flat and the ventral surface has a longitudinal median ridge. The sternebra is wider than the foot of the manubrium, indicating that the preserved sternebra is not the first and that the sternum widened posteriorly.

Scapula (pl. 16: 2, pl. 3: 3). The preserved part of the left scapula is 13 mm long. There is a large spine and, as the posterior border of the scapula is strongly everted (partly due to the deformation), there is a very deep trough-like infraspinous fossa. The glenoid fossa is only partly preserved, the coracoid process is missing and the tip of the acromion process is broken off.

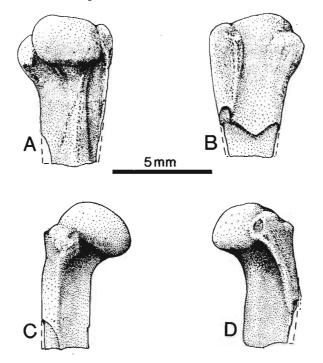


Fig. 3. Taeniolabidoid, fam., gen. et sp. indet., ZPAL MgM-I/165. Proximal part of the right humerus. A, posterior, B, anterior, C, left lateral, D, right lateral views

Humerus (pl. 18: 2; fig. 3). Only the proximal part of the right humerus has been preserved. The preserved part is stout. The head is 3.3 mm wide. With the shaft oriented vertically, the head strongly overhangs the shaft posteriorly. It is flanked anterolaterally by the greater tuberosity and anteromedially by the lesser tuberosity. The greater tuberosity is higher and lies closer to the head than the lesser. The bicipital groove is wide, especially well-defined on the side of the greater tuberosity. The posterior crest is rounded and sulcus m. brachialis is very deep, especially so proximally. The crescent-shaped prominence on the ridge below the lesser tuberosity is present, as in all multituberculate humeri, but as it is partly broken off, one cannot state whether it was very prominent. The preserved part of the shaft is roughly triangular in cross-section (the characteristic shape of multituberculate humeri), one wall of the triangle being concave, because of the depth of the sulcus m, brachialis. The deltopectoral crest is broken off.

DISCUSSION

Digging is a common habit in various orders of mammals. Fossorial forms occur in Monotremata, Marsupialia, Insectivora, Rodentia, Edentata,

Pholidota, Tubulidentata, Carnivora and Palaeanodonta. Some of the burrowing mammals, such as most of the Talpidae, Chrysochloridae, Spalacidae and Notoryctidae burrow extensively and spend most of their lives underground. The others are more or less semifossorial, spending more time on the surface and digging only occasionally.

The literature on fossorial mammals is very large (see Gambaryan 1960, Dubost 1968, Hildebrand 1974, Nevo 1979, and Rose and Emry 1983 for reviews).

It follows from these studies that, as there are several different ways in which mammals may be adopted to a fossorial mode of life, there are no skeletal adaptations which are common to all fossorial mammals. However, in spite of this, one can recognise skeletal structures, which, when occurring together, indicate underground life. To such adaptation, among others, belong: the tendency towards fusion of the cervical vertebrae; the shortening and increase in robustness of the fore-limbs; and changes in the structure of the manubrium of the sternum and of the pelvis.

Scientists have speculated on the locomotor habits of multituberculates since Gidley (1909) concluded that the North American Paleocene *Ptilodus* was saltatorial. Simpson (1926: 247) regarded *Ptilodus* as "probably swiftly moving and agile quadruped" and (p. 249) stated: "... it would be remarkable if many [multituberculates] were not at least semi-arboreal".

Krause and Jenkins studied the known postcranial skeletons of North American multituberculates and found (1983: 242): "... substantial homogenity in postcranial structure among North American multituberculates of the suborders Ptilodontoidea and Taeniolabidoidea". On the basis of a nearly complete postcranial skeleton of *Ptilodus*, with special attention being paid to its hind foot and the tail, and the hind limb skeleton of *Eucosmodon*, they concluded that these two multituberculates were arboreal. They stated (cit. op.: 143): "We conclude that some multituberculates, at least, were arboreal in habit".

My preliminary studies of the multituberculate postcranial skeletons from the Late Cretaceous of the Gobi Desert, housed in ZPAL in Warsaw, as well as of the partial postcranial skeleton of the Paleocene Lambdopsalis bulla in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing (Kielan-Jaworowska and Qi, in preparation) show that there was a diversity of skeletal adaptations among Asian taeniolabidoid multituberculates. The structure of the robust humerus of Lambdopsalis bulla indicates an undoubted fossorial mode of life, a conclusion supported by the fused second and the third cervicals.

The postcranial skeleton of Cretaceous Kryptobaatar dashzevegi (Kielan-Jaworowska and Gambaryan, in preparation) shows that this animal was possibly a fast runner living in a semidesert environment, similar in its habits to modern Gerbilus.

The fragmentary skeleton described in this paper does not show adap-

tations that unequivocally indicate mode of life. Fused second and third cervical vertebrae, similar to those present in Lambdopsalis, might indicate similar digging habits. However, the humerus of Lambdopsalis shows obvious fossorial adaptations, while the fragmentary humerus described here does not show them, although it is relatively more stout than e.g. the humerus of Cretaceous Tugrigbaatar (Kielan-Jaworowska and Dashzeveg 1978). The prominent ventral ridge and relatively large manubrium indicate the development of large pectoral muscles. Although inconclusive, I suggest that the described skeleton belongs to an animal species which was semi-fossorial in its habits.

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ZOFIA KIELAN-JAWOROWSKA

SZKIELET POZACZASZKOWY KREDOWEGO MULTITUBERKULATA (SSAKI)

Streszczenie

W pracy opisano niekompletny szkielet pozaczaszkowy multituberkulata (wymarła grupa ssaków mezozoicznych i paleogeńskich) z późnokredowej formacji Dżadochta, z miejscowości Bajn Dzak na pustyni Gobi w Mongolii. W skład szkieletu wchodzą kręgi szyjne (2—7), rękojeść mostka, jeden odcinek trzonu mostka (sternebra), niekompletna łopatka oraz proksymalna część kości ramiennej.

Kręgi szyjne i mostek multituberkulatów nie były dotychczas znane i są opisane w tej pracy po raz pierwszy.

Osobnik, do którego należał opisany szkielet, miał wymiary pośrednie między Kryptobaatar dashzevegi i Catopsalis matthewi. Takie wymiary miał Bulganbaatar nemegtbaataroides z formacji Dżadochta (znany tylko z niekompletnej czaszki), jednakże nie ma podstaw aby zaliczyć opisywany szkielet do Bulganbaatar. Ponieważ wszystkie multituberkulaty znane dotychczas z późnej kredy Mongolii należą do podrzędu Taeniolabidoidea (Kielan-Jaworowska 1980), szkielet ten został zaliczony do Taeniolabidoidea, fam., gen. et sp. indet.

Zrośnięcie drugiego i trzeciego kręgu szyjnego, szeroka rękojeść mostka z wydatnym grzebieniem, oraz stosunkowo mocno zbudowana kość ramienna wskazują że osobnik, do którego należał opisany szkielet, mógł prowadzić częściowo ryjący tryb życia.

Przystosowania do ryjącego trybu życia nie były dotychczas u multituberkulatów znane.

EXPLANATIONS OF PLATES 15-18

Taeniolabidoid, fam., gen. et sp. indet

All the specimens figured in plates 1—4 belong to ZPAL MgM-1/165, and are from the Late Cretaceous Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia.

Plate 15

1a. Cervical vertebrae 2-7, ventral view.
1b. The same, left lateral view.
1c. The same, right lateral view.
All stereo-photographs ×6

Plate 16

1. Cervical vertebrae 2-7, dorsal view.

2a. Partial left scapula, outer view.

2b. The same, inner view.

All stereo-photographs $\times 6$

Plate 17

1a. Manubrium of the sternum, ventral view.

1b. The same, right lateral view.

1c. The same, dorsal view.

- 2. Left scapula, distal view.
 - All stereo-photographs $\times 6$

Plate 18

- 1a. The specimen, as it has been found, showing the manubrium of the sternum in the upper left of the photograph, the sternebra to the right of it and a broken rib below, $\times 3$.
- 1b. The same from the other side, showing the cervical vertebrae in dorsal view, the left scapula in the upper left and the right humerus in the upper right part of the photograph, $\times 3$.
- 2a. Proximal part of the right humerus, proximal view.
- 2b. The same, left lateral view.
- 2c. The same, posterior view.
- 2d. The same, right lateral view.
- 2e. The same, anterior view.

Figs. 2a-2e are $\times 6$, all excepted 2c are stereo-photographs

