

中国始新世纹齿兽科多瘤齿兽对 掘土的适应

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关键词 内蒙古 始新世 哺乳纲 多瘤齿兽目 斜剪齿兽 掘土适应

本文记述了内蒙古沙拉木伦地区下始新统巴彦乌兰层(脑木根组)内采集到的多瘤齿兽类(鼓泡斜剪齿兽)部分颅后骨骼。这些材料包括:愈合的第2-3颈椎(C2-C3),第4颈椎(C4)的部分神经弧,完整的第5-7颈椎(C5-C7),第1-3胸椎(T1-T3),以及两块首次报道的肱骨。

第2和第3颈椎的愈合,具十分粗大三角肌脊的肱骨的强壮结构及其具有突出的桡骨踝和尺骨踝的宽大的远端都显示出鼓泡斜剪齿兽掘土的生活方式。

周明镇和齐陶(1978)记述过一种来自内蒙古晚古新世地层的多瘤齿兽类——鼓泡斜剪齿兽。其后, Kielan-Jaworowska 和 Sloan (1979)对它的结构进一步加以评论。苗德岁(1988)又对它的头骨详加研究,认为斜剪齿兽可能是掘土类型的动物。Kielan-Jaworowska 对蒙古晚白垩纪 Djadohta 组中未确定分类位置的多瘤齿兽类的颅后骨骼的研究也得到相近的结论。她的结论也来自对古脊椎所采到的斜剪齿兽肱骨和颈椎的初步观察。内蒙古的化石是齐陶(1981)在巴彦乌兰采到的。与这些暂时归入斜剪齿兽颅后骨骼一起发现的还有带着牙齿的下颌骨和头骨碎片。除此之外,该层还发现了其它两种多瘤齿兽 *Sphenopsalis* 和 *Prionessus*。

生活习性的重建:对鼓泡斜剪齿兽部分颅后骨骼的研究表明这种多瘤齿兽可能是适应于掘土(苗德岁, 1988; Kielan-Jaworowska, 1989)。目前有不少文章记述了现生哺乳动物对掘土的生活方式的适应(见 Gambarjan, 1960; Dubost, 1968; Nevo, 1979, 以及 Hildebrand, 1985)。Gambarjan (1960) 认出现生于欧亚大陆上的哺乳动物有7类是适应掘土的。他将其中的三类动物归于单一型的挖掘方式而将另四类动物归于双重型的挖掘方式。Dubost (1968) 则指出了适应掘土的三个主要类型:第一类是利用短而粗、肌肉强壮而有大的爪子的前肢来掘土;第二类是用大的而且不断快速生长的门齿掘土;而第三类则是两者的结合。Hildebrand (1985) 不仅研究了哺乳动物,而且也研究了其它掘土的四足动物。他认为有6类掘土动物。他指出(1985: p. 94),“...在这些动物内,某些动物不能和其它动物截然分开,而且它们在掘土时采用的不只是一种方式”。

鼓泡斜剪齿兽(?) 颅后材料还不足以对其生活模式做出明确的结论。更困难的是, 我们不能十分肯定本文记述的颅后骨骼是属于鼓泡斜剪齿兽的。如果进一步的发现表明这些肱骨和颈椎是属于 *Sphenopsalis* 或 *Prionessus*, 而不是斜剪齿兽的话, 我们的结论将为这两个属所取代。应当强调的是, 以上三属动物关系密切, 被归入同一科中(苗德岁, 1988) 因而不能排除它们都适应于掘土的生活方式(程度有所不同)。

鼓泡斜剪齿兽(?) 的肱骨结构粗壮, 但与 *Talpidae* 科 (Slonaker, 1920; Dubost, 1968) 的成员的肱骨有很大不同, 该科成员主要靠十分粗壮而具大爪的前肢掘土。另一方面, 如苗德岁(1988)复原的那样, 鼓泡斜剪齿兽的头部并没有显示出成为那些专门用门齿掘土、用头推土的那些种动物特点的适应性。那些动物, 例如大多数 *Spalacidae* 科的成员 (Gambarjan, 1953, 1960; Krapp, 1965; Nevo, 1961; Dubost, 1968) 都具有长长的门齿, 大的枕骨板(由枕髁向前上方倾斜)以及突出的人字嵴。

鼓泡斜剪齿兽(?) 的肱骨粗壮并具一突出的三角肌嵴。它的宽大的远端和巨大的尺骨髁表明一块大的尺骨的存在。这似乎是说多瘤齿兽能用爪掘土。人们可能推测: 鼓泡斜剪齿兽(?) 是否既用爪也用门齿掘土。这种掘土方式发现在新大陆现生的 *Geomyidae* 科 (Holliger, 1916; Hill, 1937; Orcutt, 1940; Lehman, 1963) 和渐新世的 *Tsaganomyidae* 科 (Vinogradov 和 Gambarjan, 1952; Gambarjan 引用, 1960) 的一些动物之中。然而, 相对短的门齿(苗德岁, 1988) 和头部结构并不表示此种适应。

鼓泡斜剪齿兽(?) 的头骨很宽、很扁; 头骨的枕骨板是垂直的; 而脖颈短, 颈骨中有两个或三个是愈合在一起的。所有这些特征都表明鼓泡斜剪齿兽可能是用头排土的。如果真是这样, 那么, 我们暂做结论: 鼓泡斜剪齿兽(?) 属于 Gambarjan (1960) 所指出的第 6 种类型动物, 即: 掘土时既用爪又用头。这种掘土方式可见于现代的金鼯鼠——*Eremitalpa* (具相对大而从枕髁向前上方倾斜的枕骨板, 见 Hildebrand, 1985), 以及 *Myospalax* 这类仓鼠之中 (Gambarjan, 1960; Dubost, 1968)。不能排除的情况是: 今后当斜剪齿兽有更多的颅后骨骼被发现时, 关于其习性的结论可能有相当大的变化。

中生代哺乳动物的颅后骨骼很少发现, 只是最近才对它们掘土的生活方式有所报道。Henkel 和 Ktrusat (1980) 提到了晚侏罗纪的 docodonts, Bleefeld (1987) 举出了晚白垩纪的真兽类, 而 Kielan-Jaworowska (1989) 则报道了晚白垩纪多瘤齿兽对掘土的种种适应。对掘土的各种适应在渐新世的 palaeonodonts (Rose and Emry, 1983), 一类位置不明的始新世哺乳动物 (Robinson, 1963), 以及中新世的鼯鼠 (Baronsky, 1981, 1982) 中均已有所记述。早期哺乳动物(特别是多瘤齿兽类)对掘土的种种适应可能比过去想象的更为普遍。

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FOSSORIAL ADAPTATIONS OF A TAENIOLABIDOID MULTITUBERCULATE MAMMAL FROM THE EOCENE OF CHINA

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Abstract

Fragments of the postcranial skeleton of a taeniolabidoid multituberculate, *?Lambdopsalis bulla*, from the Eocene of China are described. These consist of cervical vertebrae C2-C3 (fused), a fragment of the neural arch of C4, and complete C5-C7, thoracic vertebrae T1-T3, and two humeri, which are the first complete multituberculate humeri ever described. The fusion of C2 and C3, and the stout structure of the humerus with a very large deltopectoral crest, a wide distal end, and prominent radial and ulnar condyles, indicate a fossorial mode of life for *?L. bulla*. These postcranial elements and a wide flattened, skull with a vertical occipital plate, suggest adaptations seen in some modern golden moles and cricetid rodents such as *Myospalax* that dig with claws and displace the soil with the head.

Introduction

Chow and Qi (1978) described the skull of an unusual multituberculate, *Lambdopsalis bulla*, from the Nomogen Formation (Late Paleocene) of Inner Mongolia; Kielan-Jaworowska and Sloan (1979) commented further on its structure. Subsequently the skull of *Lambdopsalis* was described in detail by Miao (1988), who suggested that *Lambdopsalis* may have been fossorial. A similar conclusion was reached independently by Kielan-Jaworowska (1989), who described a partial postcranial skeleton of an unidentified taeniolabidoid multituberculate from the Djadokhta Formation (Late Cretaceous) of Mongolia. Her conclusion was based on a preliminary examination of *Lambdopsalis* humeri and cervical vertebrae in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing. These latter specimens were collected by Qi Tao in 1981, at the Bayan Ulan locality in the Bayan Ulan beds (Early Eocene) in the Shara Murum Region, Inner Mongolia. The remnants of *Lambdopsalis bulla* were found (lower jaws with teeth and skull fragments, associated with fragments of postcranial skeletons tentatively assigned also to *L. bulla*).

In addition these beds yielded also remnants of multituberculates *Sphenopsalis* and *Prionessus*.

The description of the postcranial fragments from this collection, consisting of the cervical vertebrae C2-C3 (fused), a fragment of the neural arch of C4, complete but separate C5-C7, thoracic vertebrae T1-T3, and two humeri is the objective of the present paper.

An assignment of the specimens described in this paper to *Lambdopsalis bulla* cannot be demonstrated with certainty. The cervical and thoracic vertebrae that we describe were found in a block of celestite that also yielded cranial fragments, lower jaws, and teeth of *L. bulla*. Although the vertebrae were not found in anatomical arrangement with the skull, they correspond in size to the skull of *L. bulla*, and it is probable that they belong to this species. Among the cervical vertebrae found in this block, C2 and C3 are fused, while the remaining cervicals are not. Miao (1988, p.82) when describing the skull of *L. bulla*, mentioned "the complete fusion of the cervical vertebrae". However, both Dr. Desui Miao and Prof. James A. Hopson now believe (pers. comm., 1989 to ZKJ) that, in the postcranial material found by Miao, C2-C4 are fused, while C5-C7 are separate. This postcranial material was not found in anatomical arrangement with the skull either. In addition, part of the collection of *L. bulla* described by Miao is from the Late Paleocene Nomogen Formation, while the collection that we describe here is from the Early Eocene Bayan Ulan Formation. Nevertheless, there are no doubts that the cranial and dental fragments of *Lambdopsalis* yielded by the rocks of both formations are conspecific.

If the species described by Miao (1988) has C2-C4 fused, while in the species which we describe only C2 and C3 are fused, then either we and Miao are dealing with postcranial fragments belonging to two different species (and possibly to different genera), or we are dealing with the same species which shows a considerable variability in the degree of fusion of the cervical vertebrae. The latter possibility appears more probable, as in the described specimen the suture between C2 and C3 is still preserved, which shows that the fusion of these vertebrae was not complete as yet.

The two humeri that we describe were found in the same area that yielded numerous fragments of *L. bulla*, but again not in anatomical arrangement with the skull. They differ slightly in size and proportions (see Table 1) and may belong to different species or genera. As this cannot be demonstrated with any certainty, and as they roughly correspond in size to the skull of *L. bulla*, we assign both humeri to ?*L. bulla* and regard the observed differences as owing to the individual variation.

Two (or three) other multituberculate species that occur in the Bayan Ulan

beds are known from teeth and incomplete skull fragments (Matthew and Granger, 1925; Matthew, Granger and Simpson, 1928; Granger and Simpson, 1929; Miao, 1986, 1988). They are either too large with respect to the postcranial elements described herein (*Sphenopsalis nobilis*, *Sphenopsalis* sp.), or too small (*Prionessus lucifer*). In addition, specimens of *Lambdopsalis* are much more common than are those of *Sphenopsalis* and *Prionessus*. However, because of the ambiguity we assign all the described postcranial remnants to *Lambdopsalis bulla* tentatively.

Although numerous partial postcranial skeletons of multituberculates have been described (see Krause and Jenkins, 1983, and Kielan-Jaworowska, 1989 for reviews) some parts are still poorly known or unknown. Kielan-Jaworowska (1989) described the first multituberculate cervical vertebrae (C2-C7) but the atlas has not been found as yet. Many fragmentary multituberculate humeri have been described and reconstructed (Gidley, 1909; Simpson, 1928, Kielan-Jaworowska and Dashzeveg, 1978; Krause and Jenkins 1983; Jenkins and Krause, 1983), none of them being complete. In this paper we describe the first complete multituberculate humeri known.

Abbreviations

IVPP-Institute of Vertebrate Paleontology and Paleoanthropology, Beijing

ZPAL-Institute of Paleobiology (Zaklad Paleobiologii) of the Polish Academy of Sciences, Warsaw.

Systematic Paleontology

Order Taeniolabidoidea Sloan and Van Valen, 1965

Family Taeniolabididae Granger and Simpson, 1929

?*Lambdopsalis* Chow and Qi, 1978

?*Lambdopsalis bulla* Chow and Qi, 1978

(Plates 1-4, Text figs. 1-2)

Material Cervical vertebrae C2-C3 (fused), fragment of the left side of the neural arch of C4, and cervical vertebrae C5-C7, thoracic vertebrae T1-T3-IVPP V9052; two left humeri-IVPP V8408 and IVPP V9051. All of the above are from the Bayan Ulan beds, Bayan Ulan, Shara Murum Region, Inner Mongolia, People's Republic of China.

Description

Axis and cervical vertebra three C2 and C3 are fused and will be referred to here as the fused vertebrae. Their length, without the dens, which is damaged, is about 10mm. The width across the anterior articular processes is 10mm. On the

ventral surface a suture between the two component bodies is preserved but, on the

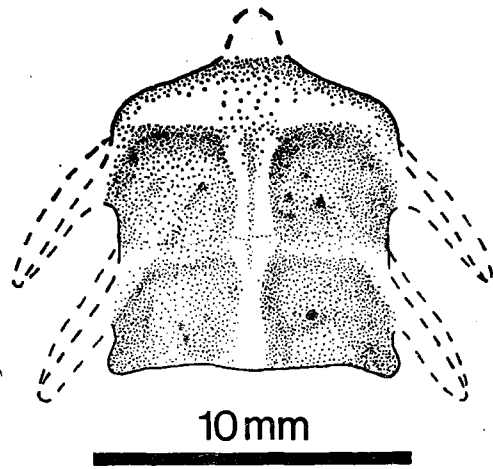


Fig. 1 ?*Lambdopsalis bulla* Chow and Qi, 1978
Reconstruction of the fused vertebrae C2-C3,
ventral view

dorsal surface the suture is less obvious. The body is strongly compressed dorso-ventrally; its caudal extremity is flat. On the basis of the preserved part it is impossible to state with any certainty whether the arches of the fused vertebrae were or were not completely fused. The damaged arch, which was preserved on the left side (Pl. I, fig. 1) but was partly broken during preparation, was directed slightly posteriorly. It shows a possible suture between the two component parts. On the basis of a comparison with a taeniolabidoid from Bayn Dzak (Kielan-Jaworowska, 1989) it is concluded

that there were two transverse processes on each side of the fused vertebrae

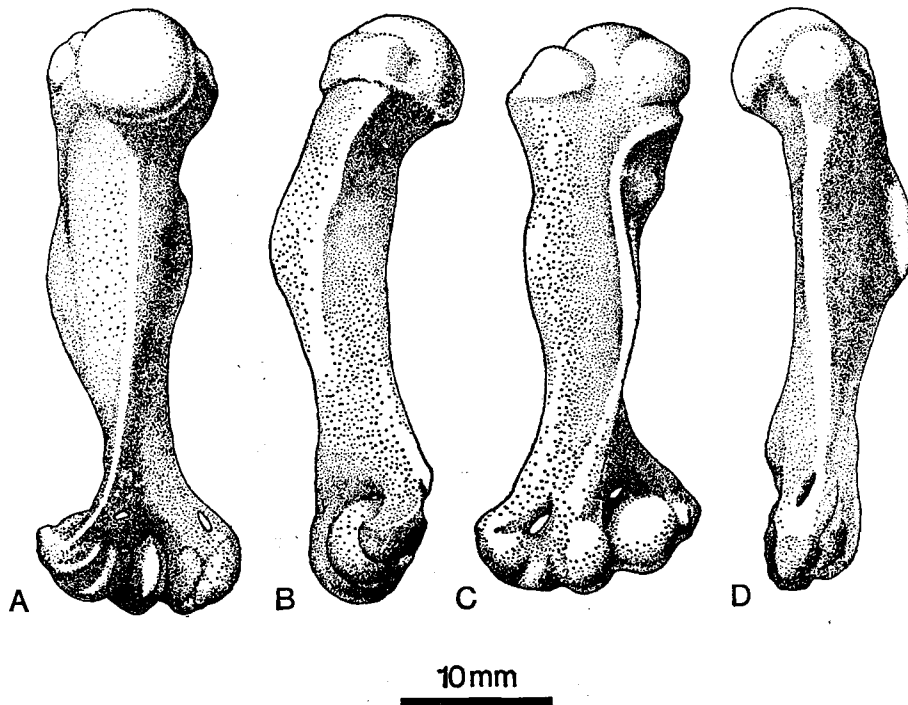


Fig. 2 ?*Lambdopsalis bulla* Chow and Qi, 1978
Reconstruction of the left humerus, based mostly on IVPP V9051, A. posterior; B.
lateral; C. anterior; and D. medial views

(broken off on both sides). Each of the transverse processes arises by two roots: a ventral one from the body, visible in the ventral view as an oblique crest and directed in lateral aspect nearly horizontally, and a dorsal one from the arch, directed in lateral aspect more obliquely downward.

Table 1
?Lambdopsalis bulla Measurements of the humeri (in mm)

	IVPP V8408	IVPP V9051
Length	36.5	38.6
Width of the head	8.0	9.0
Proximal width	11.2	13.0
Distal width	16.1	15.8

Right and left anterior articular processes are confluent with each other and form in ventral view a convex area that protrudes ventrally. Extending posterolaterally from the lateral corner of the anterior articular process is the ventral root of the first transverse process. The middle part of the anterior articular processes extends posteriorly as the ventral crest. The crest is prominent anteriorly and constricted along the midlength of the axial part. It is less prominent on C3 and is also constricted at its midlength. A medial furrow extends along the axial part of the ventral crest and disappears on C3. The lateral depressions are deep immediately behind the anterior articular processes and shallow posteriorly. On each side of the depressions there are three shallow, irregular furrows, separated by faint ridges. The medial of these ridges, which is hardly discernible, widens posteriorly and reaches the lateral corner of the posterior margin of the fused vertebrae. The lateral ridge is more prominent. It reaches the posterior part of the lateral margin of the body and continues posterolaterally as the ventral root of the second transverse process. The ventral side of the body is perforated by numerous nutrient foramina, four of which are larger than the others. The caudal articular process, preserved on the left side is flat and directed anteroventrally, more vertical than horizontal.

In the middle of the dorsal side of the body there is a low, flat prominence surrounded by two pairs of depressions on both sides. The whole area is perforated by nutrient foramina. Extending laterally between the two depressions is a transverse groove leading to the intervertebral foramen, which originally separated the axis and C3.

Cervical vertebrae four to seven Only a fragment of the right side of the arch has been preserved (Pl. I, Fig. 1). The bodies of C5-C7 are less compressed dorsoventrally than in the fused vertebrae. All are slightly damaged and therefore the measurements given below are somewhat tentative. C5 (along the ventral crest) is 3,6 mm long and 7mm wide, C6 is 3,5 mm long and about 6.6 mm wide, C7

is 3,2 mm long and slightly narrower than C6. The ventral crest in C5 is less prominent than in the fused vertebrae; in C6 and C7 it is hardly discernible. The bodies; when seen in ventral view, are perforated by nutrient foramina. In all three vertebrae the transverse processes are broken off. Along the lateral sides of the bodies in ventral view there are distinct traces of broken off ventral branches of the transverse processes, directed longitudinally. Both cranial and caudal articular processes are well preserved on both sides of all three cervicals. They form oval, flat surfaces, directed obliquely anteroventrally. The basal parts of the arches are preserved in all three cervicals. They arise upwards above the posterior articular processes and are slightly inclined anteriorly. A distinct caudal costal fovea is preserved on the left lateral part of the body of C7, in the posterodorsal corner.

Thoracic vertebrae one to three The length of the thoracic vertebrae increases in size posteriorly. T1 (along the midlength) is 3,4 mm long, T2 4,6 mm, and T3 4,8 mm. The bodies are in ventral view trapezoidal rather than rectangular, the anterior margins being longer than the posterior ones. Because of *post mortem* damage, the width of the vertebrae cannot be given. The ventral crests are hardly developed. The cranial and caudal costal foveae are seen in both ventral and lateral aspects. The caudal fovea is larger than the cranial one, which causes the above mentioned trapezoidal shape of the bodies. The transverse processes are broken off. The middle part of the dorsal side of the body (seen only in T3) is elevated. As on the cervical vertebrae, there are numerous nutrient foramina. The caudal and cranial extremities of the bodies are flat. The basal part of the arch is preserved on T1. This appears to be directed somewhat anteriorly, as are the arches of the cervical vertebrae. The fragments of the damaged arches of T2 and T3 allow one to judge that these were possibly directed vertically and were longer than the arches of the cervical vertebrae.

Humerus (Measurements—see Table 1). For descriptive purposes the humerus is oriented vertically. The surface referred to as the posterior one was in life posterodorsal, while the anterior one was anteroventral. The two humeri differ slightly in size and proportions, but we assign them tentatively to the same species. The proximal and distal parts of the humerus are twisted relative to one another, a plane through the tubercles and deltopectoral crests lies approximately 35° to the plane through the epicondyles. The humerus is stout. The head strongly overhangs the shaft posteriorly. The surface of the prominent head incorporates more than one half of a sphere. The greater tuberosity is higher and lies closer to the head than does the lesser tuberosity. In proximal view the lesser tuberosity stands apart from the head as a major prominence; the greater tuberosity is almost confluent with the head.

The shaft, as characteristic of multituberculate humeri, is more or less triangular in cross section, which is disturbed in the proximal part by the presence of a very large deltopectoral crest. The latter is broken off in the proximal part in IVPP V8408 but is more completely preserved in V9051, allowing its reconstruction. It has a thickened margin. It stands apart from the shaft as a crescent-shaped prominence, well seen in both lateral and anterior views. Distally the prolongation of the deltopectoral crest is divided into two weak branches. The medial one of them reaches the ulnar condyle, whereas the lateral one merges into the entepicondyle. The oval, obliquely arranged entepicondylar foramen lies between these two branches. It is about 2 mm long in both humeri. The ridge of the lesser tuberosity has a thickened margin and bears in its proximal part a small crescent-shaped prominence, as is usual in multituberculates. The ectepicondylar flange (posterior crest of Kielan-Jaworowska and Dashzeveg, 1978) starts as a rounded ridge below the humeral head. On both sides the ectepicondylar flange the surface of the shaft is slightly concave. Distally it continues as a sharp ridge that merges into the ectepicondyle. The bicipital groove is wide and relatively shallow, deeper on the side of the greater tuberosity.

The distal end of the humerus is very wide and robust. The entepicondyle is very prominent, much larger than the ectepicondyle. Both radial and ulnar condyles are large and are well separated by a deep intercondylar groove. In anterior view the radial condyle appears enormous and completely spherical. It is separated by a deep furrow from the ectepicondyle. In posterior view the radial condyle appears small and has a medial longitudinal ridge, while it is the ulnar condyle that dominates. The latter, however, is more elongated longitudinally and not so completely spherical as the radial condyle. There is a small prominence (longitudinal ridge) separating the ulnar condyle from the entepicondyle, seen both in posterior and distal views. In distal view the radial condyle is spherical, more rounded than the ulnar condyle, which is slightly compressed laterally and arranged obliquely. There is a deep olecranon fossa perforated by a foramen. The presence of an ectepicondylar foramen cannot be determined with any certainty.

Comparisons

The only multituberculate cervical vertebrae hitherto described belong to an unidentified taeniolabidoid (ZPAL MgM-I/165) from the Late Cretaceous of Bayn Dzak in Mongolia (Kielan-Jaworowska, 1989). ?*L. bulla* (IVPP V9052) is more than twice as large as the taeniolabidoid from Bayn Dzak, but is reminiscent of it in having the axis fused with C3. The fused vertebrae in IVPP V9052 differ from those in ZPAL MgM-I/165 in having less prominent ventral crest. The broken ma-

rgins of the fused vertebrae in IVPP V9052 show that there were two transverse processes, similarly arranged as in ZPAL MgM-I/165. In other respects the fused and the remaining cervical vertebrae are in both forms similar, although the lack of transverse processes in IVPP V9052 and of neural arches in ZPAL MgM-I/168 makes further comparisons impossible.

The two humeri described above are possibly the most stout multituberculate humeri so far described. They are more stout than the gracile one reconstructed for *Tugrigbaatar* (Kielan-Jaworowska and Dashzeveg, 1978) and possibly also more stout than that of *Ptilodus*, ?*Mesodma* sp., ?*Stygimys kuszmauli* (all figured by Krause and Jenkins, 1983; see also Gidley, 1909), and of *Catopsalis mathewi* (referred to also as *Djadochtatherium*-see Simpson, 1928; Kielan-Jaworowska and Sloan, 1979; Simmons and Miao, 1986). In all these multituberculate humeri the distal end is very wide and stout, relatively wider than in other Mesozoic mammals. In the unidentified taeniolabidoid from Bayn Dzak (Kielan-Jaworowska, 1989) only the proximal part of the humerus has been preserved and the deltopectoral crest was broken off. It seems that the humeral head in ?*L. bulla* encompasses a somewhat greater portion of a sphere than in previously known multituberculate humeri. A well developed deltopectoral crest was figured by Krause and Jenkins (1983) for *Ptilodus montanus*, it was, however, possibly less prominent than in ?*L. bulla*.

The distal part of the Upper Jurassic mammalian humerus of Colorado, described by Prothero and Jensen (1983) may belong to a multituberculate (suggested as one of the possibilities by the authors). It resembles the humerus of ?*L. bulla* possibly more closely than it does other multituberculate humeri, having, however, a more slender shaft.

The humerus of ?*L. bulla* resembles also in some features that of *Eozostrodon* (Jenkins and Parrington, 1976), differing in having a lesser twisting of the anterior and posterior parts in relation to each other, more prominent head, much larger deltopectoral crest and larger ulnar and radial condyles. The humerus of the Early Cretaceous triconodont *Gobiconodon* (Jenkins and Schaff, 1988) resembles that of ?*L. bulla* in having a robust deltopectoral crest, but differs in having a differently shaped distal end, with grooved trochleae as in advanced mammals.

Reconstruction of life habits

Preliminary investigations of the postcranial fragments of ?*L. bulla* (Miao, 1988; Kielan-Jaworowska, 1989) indicate that this multituberculate was possibly adapted for digging. There are numerous papers on adaptations of modern mammals to a fossorial mode of life (see Gambarjan, 1960; Dubost, 1968; Nevo, 1979; and Hildebrand, 1985 for summaries). Gambarjan (1960) recognized seven different types in

which Recent Eurasian mammals may be adapted for digging, three of which he classified within a single-phase mode of digging, the remaining four within a double-phase mode. Dubost (1968) recognized three main types of fossorial adaptations: in the first type the digging is done primarily by robust and short, heavily-muscled and large-clawed forelimbs; in the second type by large, rapidly evergrowing incisors and in the third type by a combination of both. Finally Hildebrand (1985) dealing not only with mammals, but also with other groups of fossorial quadrupeds, recognized six categories of digging. He pointed out (1985: 94) that: "... some of these [categories] are not sharply set off from others, and many burrowers dig in more than one way".

The postcranial material of ?*L. bulla* that we describe here is insufficient for drawing unequivocal conclusions on the mode of life. The difficulty is increased by the fact that we cannot demonstrate with any great degree of certainty that the described postcranial elements belong to *L. bulla*. In the discussion that follows, however, we tentatively accept that they belong to *L. bulla*. If it would be demonstrated by future investigations that the humeri or the cervical vertebrae which we describe belong to *Sphenopsalis*, or to *Prionessus*, rather than to *Lambdopsalis*, our conclusions may hold for those genera instead. It should be also stressed that the three above-mentioned genera are closely related, assigned to the same family (Miao, 1988), and it cannot be excluded that all of them may have been adapted (possibly at various degrees) to a fossorial mode of life.

The humerus of ?*L. bulla* has a stout structure, but is very different from those in the Talpidae (Slonaker, 1920; Dubost 1968) in which the digging is done primarily by very strong, short, large-clawed forelimbs. On the other hand the head in *L. bulla*, as reconstructed by Miao (1988), does not show the adaptations characteristic of forms that dig exclusively with the incisors and that bulldoze with the head. In such forms, e. g. in most Spalacidae (Gambarjan, 1953, 1960; Krapp, 1965; Nevo, 1961; Dubost, 1968), the incisors are long, the occipital plate is large, sloping forwards and upwards from the condyles, and the lambdoidal crests are prominent.

The humerus in ?*L. bulla* is stout and has a prominent deltopectoral crest. The wide distal end of the humerus and the enormous ulnar condyle indicate the presence of a large ulna. It seems possible that this multituberculate may have used claws for digging. One may speculate whether ?*L. bulla* used both the claws and incisors for digging. This type of digging is found among others in modern rodent New World family the Geomyidae (Holliger, 1916; Hill, 1937; Orcutt, 1940; Lehman, 1963), and in some Oligocene Tsaganomyidae (Vinogradov and Gambarjan, 1952, cited in Gambarjan, 1960). However, relatively short incisors (Miao, 1986) and

the structure of the head do not indicate such adaptations.

The head of ?*L. bulla* is very wide and flattened, the occipital plate vertical and the neck is short, with two or three fused vertebrae. All these characters indicate that ?*L. bulla* might have used the head for displacing the soil. If so, it may be tentatively concluded that ?*L. bulla* would belong to the sixth category recognized by Gambarjan (1960), in which the digging is done using both claws and head. This type of digging occurs in the modern golden mole *Eremitalpa* (which, however, has a relatively larger occipital plate sloping forward and upward from the condyles, Hildebrand, 1985), and in the cricetid rodents such as *Myospalax* (Gambarjan, 1960; Dubost, 1968). It cannot, however, be excluded that when more complete postcranial skeleton of *Lambdopsalis* is known, the conclusions concerning its habits may be considerably changed.

Postcranial skeletons of Mesozoic mammals are rarely found and it is only recently that the adaptations to the fossorial mode of life have been reported among them. Henkel and krusat (1980) mentioned fossorial adaptations in Late Jurassic docodonts, Bleefer (1987) cited them in Late Cretaceous eutherians, while Kielan-Jaworowska (1989) reported them in Late Cretaceous multituberculates. Fossorial adaptations have been described in the Oligocene palaeodonts (Rose and Emry, 1983), in an unidentified Eocene mammal (Robinson, 1963), and in Miocene moles (Barnosky, 1981, 1982). It seems possible that the adaptations for digging were more common among early mammals, and in particular among the multituberculates, than previously thought.

Acknowledgments

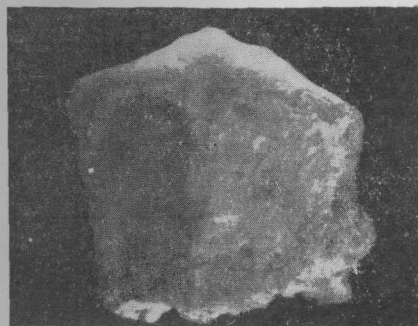
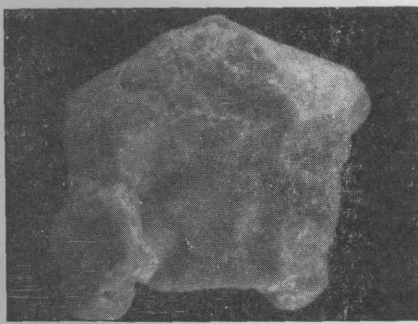
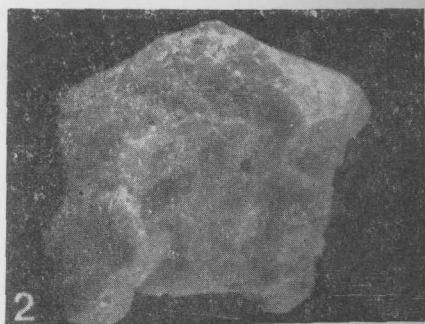
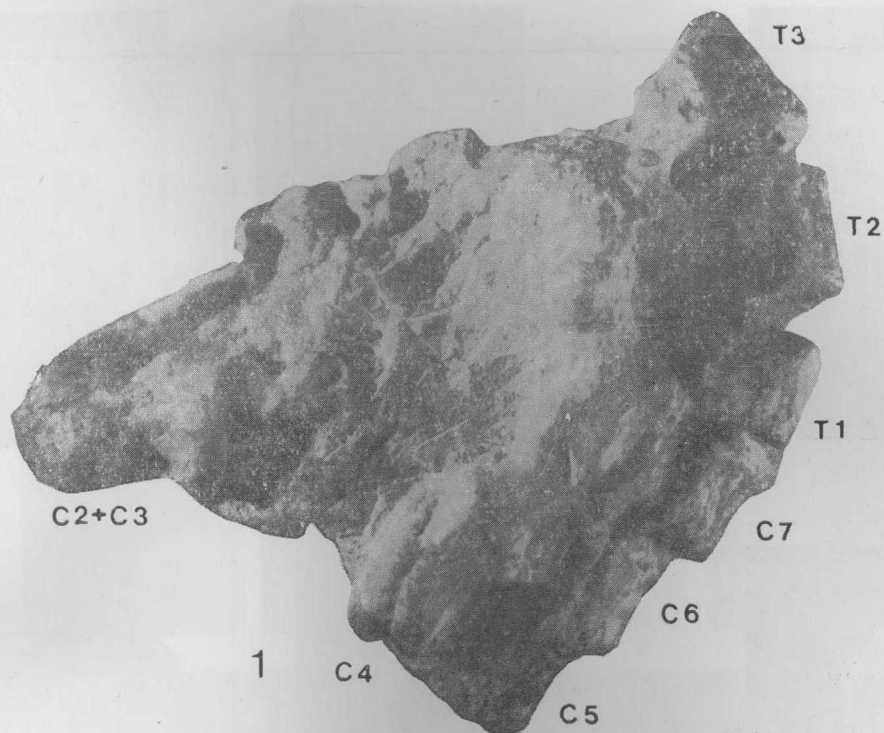
Prof. P. P. Gambarjan's (Zoological Institute, USSR Academy of Sciences, Leningrad) knowledge of postcranial anatomy and habits of fossorial modern mammals has been an invaluable resource in this study. Prof. David W. Krause (Department of Anatomical Sciences, State University of New York, Stony Brook) kindly read the manuscript and provided useful comments. The photographs were taken by Mr Per Aas (Paleontological Museum, the University of Oslo) and the drawings were made (after ZKJ pencil sketches) by Mr Bogdan Bocianowski. The research of ZKJ was funded by Norges Allmennvitenskapelige Forskningsrad Grant No. ABC/SDU 441.89/004. To all these persons and institutions we would like to express our sincere thanks and gratitude. This paper is the Contribution from the Paleontological Museum, the University of Oslo No. 355.

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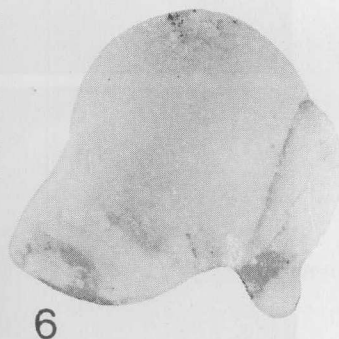
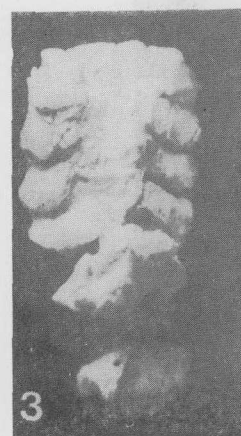
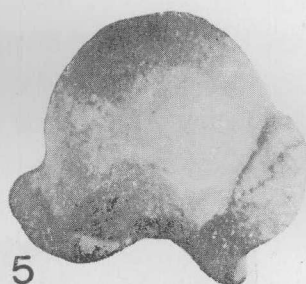
?Lambdopsalis bulla Chow and Qi, 1978

All the specimens are from the Bayan Ulan beds (Early Eocene), Bayan Ulan, Inner Mongolia

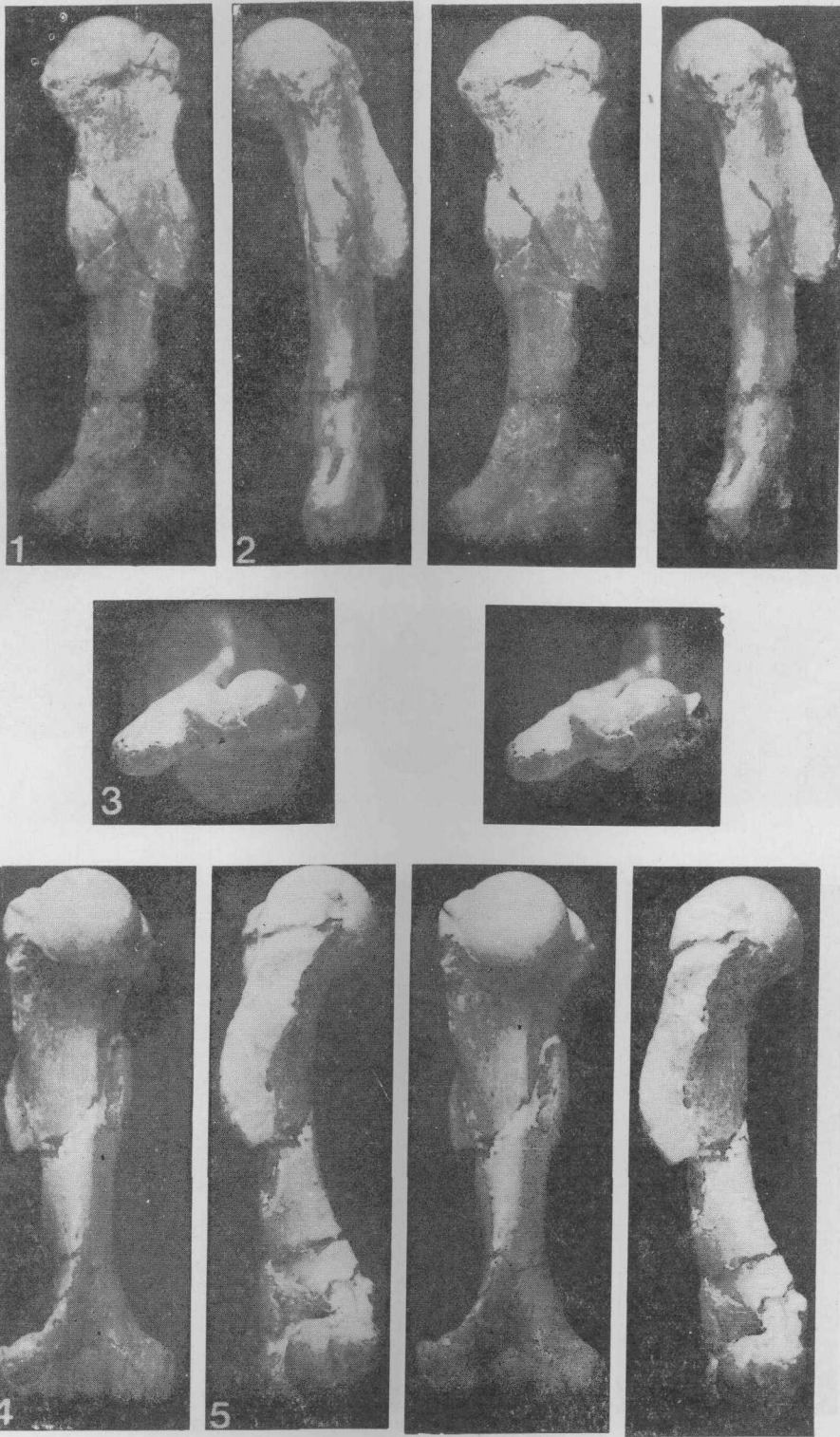
1. Cervical vertebrae C2—C3 (fused), neural arch fragment of C4, C5—C7 and thoracic vertebrae T1—T3, as found, lateral view, IVPP V9052, $\times 4$ (see also Plate II);

2. Stereophotograph of the fused cervical vertebrae C2—C3 of the same specimen, dorsal view, $\times 4$;

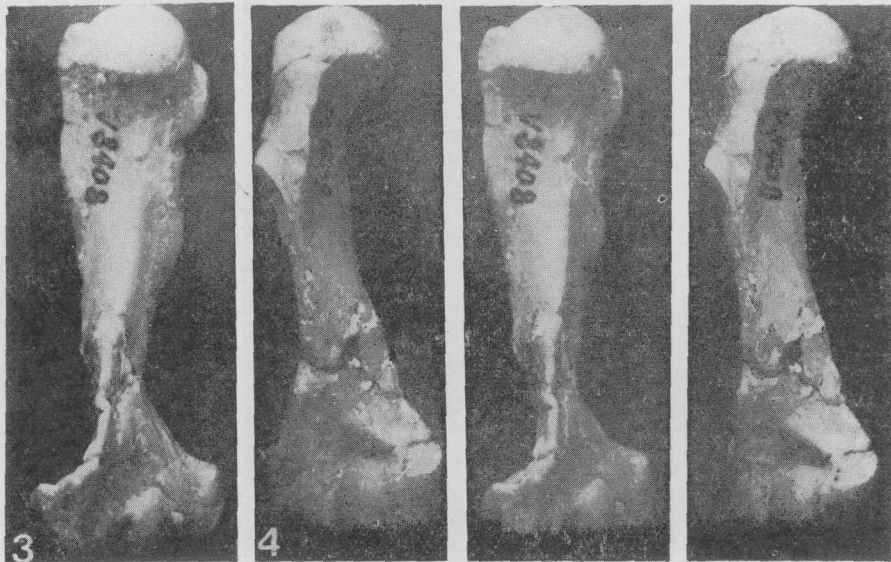
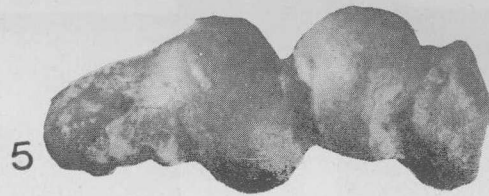
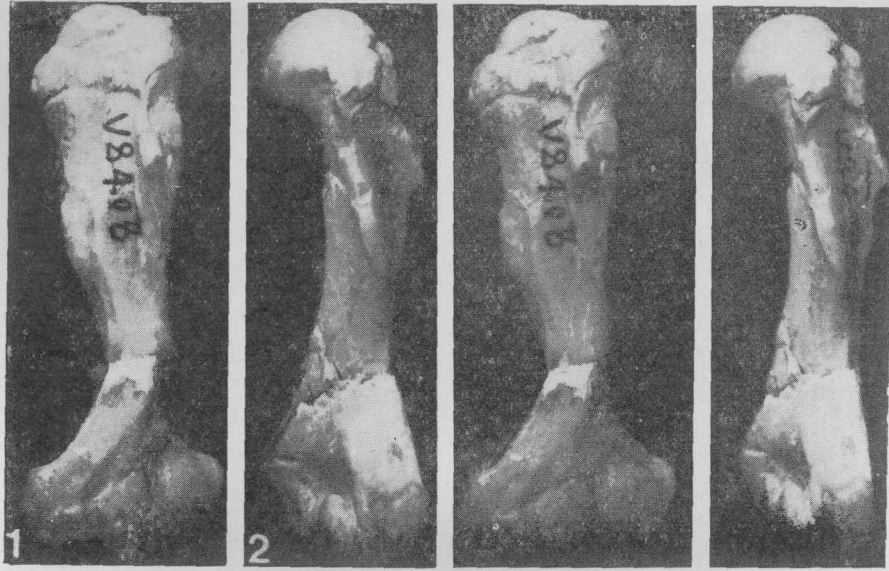
3. Stereophotograph of the same, ventral view, $\times 4$



1. Cervical vertebrae C5—C7 and thoracic vertebrae T1—T3, ventral view (thoracic vertebrae in plane of focus), stereophotograph, IVPP V9052, $\times 2$, (see also Plate I);
2. Stereophotograph of the same, lateral view, $\times 2$;
3. Stereophotograph of the same, dorsal view, $\times 2$;
4. The same, ventral view (cervical vertebrae in plane of focus), $\times 2$;
5. Left humerus, proximal view, IVPP V8408, $\times 4$ (see also Plate IV);
6. Left humerus, proximal view, IVPP V9051, $\times 4$ (see also Plate III)



1. Left humerus, anterior view, IVPP V9051 (see also Plate II);
2. The same, medial view;
3. The same, distal view;
4. The same, posterior view;
5. The same, lateral view;
All stereophotographs, $\times 2$



1. Left humerus, anterior view, IVPP V8408 (see also Plate 1);
2. The same, medial view;
3. The same, posterior view;
4. The same, lateral view;
- All stereophotographs, $\times 2$;
5. Distal view of the same. $\times 4$