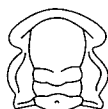


Characters of multituberculates neglected in phylogenetic analyses of early mammals

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Multituberculate anatomy is compared with that of other mammals, with an emphasis on the characters that have either been neglected or misinterpreted in previous analyses of early mammal relationships. These are: brain structure, backward masticatory power stroke (along with aspects of cranial design), and foot structure. New data on ear ossicles and a controversy concerning multituberculate posture are also discussed. The following characters of multituberculate skull and lower jaw are interpreted to be related to the backward masticatory power stroke: anterior orbital area roofed dorsally and without a floor (characteristic of advanced multituberculates), parietal postorbital process, lack of the angular process and a more anterior position of the coronoid process and masseteric fossa than in all other mammals. It is argued that the parallel development in the cranial structure of multituberculates and other mammals was limited by the backward masticatory power stroke of multituberculates that resulted in different configuration of the masticatory musculature and related osteology. In the postcranial skeleton the parallelism was limited by the structure of the multituberculate foot, in which the calcaneum contacts the fifth metatarsal (MtV) and the middle metatarsal (MtIII) is abducted 30° from the longitudinal axis of the tuber calcanei. Backward masticatory power stroke and related skull design do not show unequivocally whether multituberculates originated from some 'triconodonts' (a polyphyletic group), or independently from all other mammals from cynodonts. The foot structure refutes the origin of multituberculates from the Morganucodontidae. The brain structure allies the multituberculates with the Triconodontidae, the postcranial skeleton of which remains unknown. New data on ear ossicles suggest close relationships of multituberculates to all modern mammals. Lack of uncontested pre-Kimmeridgian multituberculates disproves the separate origin of multituberculates from cynodonts. □ *Mammalia, Multituberculata, evolution, parallelism, Mesozoic.*

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The uniqueness of multituberculates among mammals was recognized in the previous century by Marsh (1880), who placed them in a subclass of their own, the Allotheria. When Simpson (1945) wrote his classic monograph *The Principles of Classification and a Classification of Mammals*, multituberculates were relatively poorly known. He followed Marsh in placing Multituberculata in a separate subclass and stated (Simpson 1945, p. 168): 'The multituberculate structure was so radically distinctive throughout their history that it seems hardly possible that they are related to other mammals except by a common origin at, or even before, the appearance of the class as such, a conclusion that necessitates placing them in a separate subclass as well as order.'

This attitude has been followed until now by most professional text-books and reviews. In recently published papers dealing directly or indirectly with the origin of mammals, early mammals are synonymized with the Morganucodontidae (often assigned to 'Triconodonta' – see 'Terminology'), while the multituberculates, as a rule, are not discussed, or mentioned only peripherally (Jenkins 1984; Crompton & Sun 1985; Gow 1985; Crompton & Hylander 1986; Hopson & Barghusen 1986; Hopson 1987, 1991; Graybeal *et al.* 1989; Crompton & Luo 1993; Bonaparte & Crompton 1994; Luo & Crompton, 1994; Luo 1994; and others). The papers by Miao (1991, 1993) and Hopson (1994) are exceptions in this respect. Neither did Kemp (1982, 1983) include multitu-

berculates in discussing the relationships of cynodonts and early mammals.

The approach of Lillegraven & Krusat (1991) to multituberculates was ambiguous. In an attempt to find the systematic position of the docodont *Haldanodon*, they produced a cladogram including Cynodontia, *Haldanodon*, *Sinoconodon*, Morganucodontidae and 'Other mammals'. It appears from the description of the node 'Other mammals' that multituberculates are included in this group, as on p. 126 we read: 'Premaxillary dorsal median process absent (except in certain multituberculates)'. Some characters, however, scored in their Appendix 2 under 'Other mammals', do not, in fact, occur in multituberculates. In addition, in the discussion on the polyphyletic origin of mammals, the authors did not discount the possibility that multituberculates were derived from a different cynodont stock than other mammals.

Novacek (1993), in a comprehensive review of mammalian skull anatomy, did not treat multituberculates. Gauthier *et al.* (1988) and Rowe (1988) had defined Mammalia as containing only extant and fossil taxa that stem from the last common ancestor of all living groups: monotremes, marsupials, and eutherians. Rowe (1988) included the Multituberculata in this newly defined Mammalia (see Lucas & Luo 1993 for criticism of Rowe's definition). Novacek (1993) accepted this definition and was aware of the inclusion of the Multituberculata, but nevertheless omitted them (as all other groups of fossil mammals) from his considerations. Weijs (1994), in a review of mammalian masticatory motor pattern, although dealing primarily with extant Theria, discussed the evolutionary development of the mammalian jaw apparatus on the basis of well-studied data from the cynodont–morganucodontid transition, but did not mention the multituberculates.

The reason for the frequent omission of Multituberculata from the discussion of mammal origins is probably that, in contrast to the early (Early Jurassic) 'triconodonts', known from skulls and postcranial skeletons (K.A. Kermack *et al.* 1973, 1981; Crompton 1974; Jenkins & Parrington 1976; Gow 1986), the record of multituberculates of the same age is scanty and uncertain. The Late Triassic – Early Jurassic Haramiyidae, known only from isolated teeth, were regarded by Hahn (1973) and tentatively by Sigogneau-Russell (1989) as the earliest multituberculates. Butler & MacIntyre (1994) regarded the haramiyids as a sister-group of the multituberculates (see also Sigogneau-Russell & Hahn 1994). Jenkins *et al.* (1996) reported the discovery of haramiyid mandibles, a maxilla and other skeletal remains in the Late Triassic Fleming Fjord Formation of East Greenland. Occlusal pattern evidences predominantly orthal jaw movement, which casts doubts on the relationship of the haramiyids and multituberculates.

The earliest purported multituberculate is *Mojo* from the Lower Rhaetian (Late Triassic) of Belgium, known only from an incomplete upper(?) premolar (Hahn *et al.* 1987; Hahn 1993). The oldest multituberculate lower jaws and skulls are from the Kimmeridgian or Oxfordian (Late Jurassic) of Guimarota in Portugal, referred to further as Kimmeridgian (Hahn 1969; Hahn & Hahn 1994 and references therein; see also Lillegraven & Krusat 1991, for discussion of the age of the Guimarota beds). The pre-Kimmeridgian 'multituberculates', in addition to *Mojo*, are represented by isolated teeth (Freeman 1979; K.A. Kermack 1988 and references therein). There is a collection of Bathonian (Middle Jurassic) isolated teeth, possibly related to multituberculates being studied by Dr. K.A. Kermack, but these specimens have not been described as yet (personal communication, February 1995).

The multituberculate skull was described *inter alia* by Gidley (1909), Granger & Simpson (1929), Broom (1914), Simpson (1937), Hahn (1969, 1977, 1987, 1988; Hahn & Hahn 1994), Kielan-Jaworowska (1970, 1971, 1974), Kielan-Jaworowska & Dashzeveg (1978), Kielan-Jaworowska & Sloan (1979), Clemens & Kielan-Jaworowska (1979, and references therein), Kielan-Jaworowska *et al.* (1986), Miao (1988, 1993), Hurum (1994) and Gambaryan & Kielan-Jaworowska (1995), Rougier, Novacek & Dashzeveg (in press) and Kielan-Jaworowska & Hurum (in press). The Guimarota lower jaws are well preserved, but the skulls are not complete and some details of their structure are unknown. If *Mojo* is a multituberculate, then the time span between the oldest multituberculates and the skulls from Guimarota is in the order of 70 million years, which is more than the duration of the Tertiary, during which enormous changes in therian mammal lineages took place. The oldest completely preserved multituberculate skulls are from the Late Cretaceous of Asia (Kielan-Jaworowska 1970, 1971, 1974; Kielan-Jaworowska *et al.* 1986; Hurum 1994; Gambaryan & Kielan-Jaworowska 1995). The time span between these Late Cretaceous fossils and *Mojo* embraces about 90 million years.

The situation is still more frustrating in the case of the postcranial skeletons, which are known practically only from the Late Cretaceous and Paleocene of Asia (Kielan-Jaworowska 1979; Kielan-Jaworowska & Gambaryan 1994 and references therein; Sereno & McKenna 1995) and from the Paleocene of North America (Granger & Simpson 1929; Krause & Jenkins 1983; Szalay 1993).

Although the multituberculate cranial and postcranial material from the Cretaceous and Paleocene is abundant and well preserved, some important characteristics of their structure have been neglected or misinterpreted in current analyses of the relationships of early mammals. In this account I discuss a suite of such characters and some new, recently published data on multituberculate structure.

Terminology

It appears from cladograms in papers by Crompton & Sun (1985), Rowe (1988, 1993), Wible & Hopson (1993), and Wible *et al.* (1995), and from data discussed in this paper, that the 'Triconodonta' is a polyphyletic group, and therefore it is cited here in quotation marks.

I use the term Theria in a traditional sense, i.e. embracing Metatheria and Eutheria and their extinct ancestors 'eupantotheres' (which is a paraphyletic group, see, e.g., McKenna 1975 and Prothero 1981) and symmetrodonts. In this old concept the therians do not include the Monotremata, which might in fact be therians (Kielan-Jaworowska *et al.* 1987). Rowe (1993) reserved the term therians for the Marsupialia and Placentalia, and Hopson (1994) introduced an informal term 'holotheres' (p. 201): "to refer to the entire group of mammals characterized by a 'reversed triangles' molar pattern".

I use the term Mammalia for a group characterized by the possession of the dentary condyle in contact with the glenoid on the squamosal (K.A. Kermack & Mussett 1958; Hopson 1991, 1994; Rougier *et al.* 1992, and many others). Such a group corresponds to *Sinoconodon* plus Rowe's (1988) Mammaliaformes, which includes *Haldanodon*, Morganucodontidae, Megazostrodonidae, later 'Triconodonta', Multituberculata, Monotremata and all the Theria.

Current views on multituberculate position

Recent studies of braincase structure of early and extant mammals (Presley & Steel 1976, 1978; Presley 1980, 1981; Kielan-Jaworowska *et al.* 1986; Miao 1988; Wible 1991; Rougier *et al.* 1992; Wible & Hopson 1993; Hopson & Rougier 1993; Hurum 1994) demonstrated the general homogeneity of the internal structure of the skull and vascular system of all mammals including the multituberculates. Zeller (1989a, b, 1993) expressed, however, a different opinion, summarized as follows (1993, p. 98): "The morphogenesis of the head does not provide evidence for close phylogenetic relationships among the Monotremata, Triconodonta, Multituberculata, or Pantotheria."

In order to find out what differences there are between multituberculates and other mammals, it would be desirable to establish the plesiomorphies, synapomorphies and autapomorphies of multituberculates. However, this is difficult because of the lack of adequate materials of the oldest (Late Triassic) purported multituberculate cited in the previous section.

In recent phylogenetic analyses of early mammals, the Multituberculata are regarded as:

- 1 The sister taxon of the Theria, i.e. placed in cladograms, phylogenetic trees or discussions between the Monotremata and Theria, for example, by Kemp (1983, tentatively), Rowe & Greenwald (1987), Rowe (1988, 1993), Lucas & Luo (1993), Luo (1994, implicitly) and Sereno & McKenna (1995). The conclusions of Rowe & Greenwald and Rowe are largely, but not entirely, based on similarities between the multituberculate and therian postcranial skeleton, although cranial characters were also used, while those of Sereno & McKenna (1995) are based on the analysis of forelimb structure in one multituberculate taxon. The conclusions of Lucas & Luo (1993) are based on an analysis of some cranial characters, preserved in an incomplete basicranium of the oldest known mammal, *Adelobasileus*. Luo (1994) treated the multituberculates only peripherally.
- 2 The sister taxon of Monotremata plus Theria, i.e. placed between the 'Triconodonta' (including Morganucodontidae) and Monotremata, or between 'Triconodonta' and early Symmetrodonta, for example, by Crompton & Sun (1985), Miao & Lillegraven (1986), Miao (1991), Wible (1991), Meng (1992), Rougier *et al.* (1992), Lillegraven & Hahn (1993) and Szalay (1993, implicitly). A somewhat different concept is that of Wible & Hopson (1993) and Meng & Wyss (1995), who regarded the Multituberculata as a sister taxon of the Monotremata, both groups together being a sister taxon of the Theria. In this concept Multituberculata plus Monotremata form a monophyletic group. The conclusions of Wible (1991), Rougier *et al.* (1992) and Wible & Hopson (1993) were based on an analysis of the details of braincase structure and reconstruction of the cranial vasculature of early mammals, while those of Meng & Wyss (1995) were based on multituberculate ear ossicles.
- 3 The sister taxon of all other mammals, i.e. placed between advanced Cynodontia and 'Triconodonta', for example, by McKenna (1987), Hahn *et al.* (1989) and Miao (1993). The conclusions of McKenna (1987) are based on an analysis of both cranial and postcranial characters of non-mammalian and mammalian synapsids, those of Hahn *et al.* (1989) on an analysis of the dentition of the early multituberculates and related groups known only from isolated teeth, and those of Miao (1993) mostly on an analysis of multituberculate cranial anatomy and a comparison with other mammals.

The selected characters employed by Rowe (1988) in the first of these options have been analyzed and refuted by Wible (1991), Meng (1992), Miao (1993), Lillegraven & Hahn (1993) and Kielan-Jaworowska & Gambaryan (1994), and others. In order to choose between the three

options, it would be desirable to discuss all the known multituberculate and other early mammal characters, which is beyond the scope of this paper. The internal structure of the skull and cranial vasculature has been discussed in detail by Kielan-Jaworowska *et al.* (1986), Wible (1991), Rougier *et al.* (1992), Wible & Hopson (1993) and Hurum (1994), the postcranial skeleton by Krause & Jenkins (1983), Kielan-Jaworowska & Gambaryan (1994), Sereno & McKenna (1995) and Gambaryan & Kielan-Jaworowska (in press), the external structure of the skull by Gambaryan & Kielan-Jaworowska (1995), Kielan-Jaworowska & Hurum (in press) and Rougier, Novacek & Dashzeveg (in press). Here I discuss only those multituberculate characters that were either omitted or misinterpreted in previous phylogenetic analyses, or are controversial. These are: brain structure, ear region (including ear ossicles), the backward masticatory power stroke (and the associated configuration of the masticatory musculature and skull design), the mandibular condyle, the pterygoideus shelf and lack of the angular process, the foot and pelvis structure, and the multituberculate posture.

I compare the multituberculates mainly with the Morganucodontidae, Triconodontidae, Theria and Monotremata. With respect to the postcranial skeleton, I chose Theria, rather than Monotremata, as a model for comparisons, because of the greater similarity of the multituberculate skeleton to that of therians (especially rodents).

The three living monotreme genera are powerful diggers, and in addition *Ornithorhynchus* is adapted for swimming. If of all the Theria only the moles had survived until today, the comparison of multituberculate and therian structure would probably be as fruitless as the comparison of the monotremes and multituberculates is now. (This does not detract from the fact that some multituberculates may have been fossorial; Kielan-Jaworowska & Qi 1990.) Although monotremes retain many primitive characters in their postcranial skeleton, some of which are shared with multituberculates, e.g., large iliosacral angle, interclavicle, abducted limbs (Kielan-Jaworowska & Gambaryan 1994; Gambaryan & Kielan-Jaworowska, in press; but see Sereno & McKenna 1995), etc., the overall arrangement of the skeleton is too different in the two groups to invite a close comparison.

Evaluation of neglected or controversial multituberculate characters

Brain structure

Jerison (1973, p. 1) in his classic book *Evolution of the Brain and Intelligence* wrote: 'Among the facts of brain evolution none are more certain than those obtained from endocasts (casts of the endocranial cavities) of fossil ani-

mals, although like all the facts these must be interpreted with care.' It is therefore astonishing that, in studies on mammalian origins and the relationships of early mammals published in the last decade, brain structure inferred from investigation of endocranial casts has been almost completely neglected. In two impressive volumes from the *Mammal Phylogeny* symposium in New York, edited by Szalay *et al.* (1993), brain structure was not discussed at all, and only twice was there mention (Crompton & Luo 1993; Rowe 1993) of the shape of the skull related to the expansion of the brain.

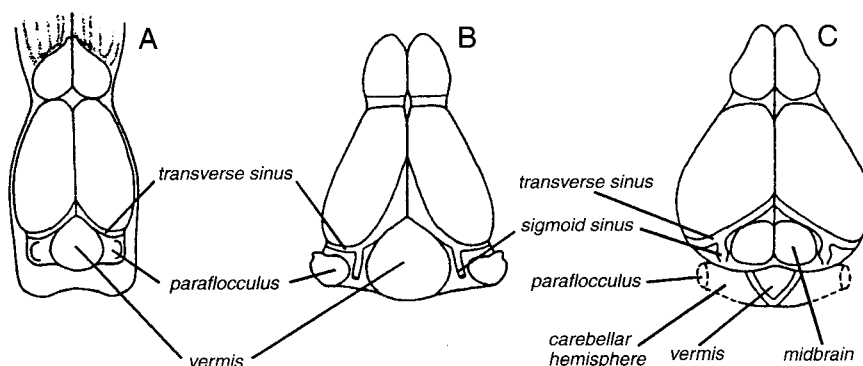
Gauthier *et al.* (1988) gave mostly a soft-tissue diagnosis of the Mammalia, including their brains, which is hardly applicable to the study of endocranial casts. Rowe (1988), when regarding Multituberculata as a sister taxon of the Theria, did not mention that these groups differ fundamentally in their brain structure. Ariëns Kappers *et al.* (1960) stated that the mammalian cerebellum differs from those of all other vertebrates by the greater development of its transverse diameter (presence of cerebellar hemispheres and paraflocculi) and regarded monotremes as an exception in this respect. Studies of Holst (1986), however, demonstrated that the monotreme (especially tachyglossid) brain is generally therian-like; she identified the lateral parts of the cerebellum as the cerebellar hemispheres, in addition to large paraflocculi and very small flocculi.

I showed (Kielan-Jaworowska 1986) that there are two types of brain in Mesozoic mammals (Fig. 1 herein), designated the cryptomesencephalic type (characterized by a very large vermis, no cerebellar hemispheres and no dorsal midbrain exposure) and the eumesencephalic type (characterized by a wide cerebellum, presence of cerebellar hemispheres and a large dorsal midbrain exposure). The midbrain is exposed dorsally in cynodonts (Hopson 1979) and its exposure is a plesiomorphic feature for mammals. The cryptomesencephalic brain occurs in Multituberculata and in *Triconodon*; the eumesencephalic brain is characteristic of Cretaceous Theria, some primitive extant therians and possibly of *Morganucodon* (see below).

Quiroga (1979, 1980, 1984) studied the development of the neocortex at the reptilian-mammalian transition and claimed that the neocortex was present at least in the cynodonts *Probainognathus* and *Therioherpeton*. I reviewed his data and generally agreed with his conclusion, stating: '... on the basis of expansion of cerebral hemispheres, one may tentatively conclude that the neocortex possibly was well developed in all Mesozoic mammals, and in some (e.g., *Probainognathus* and *Therioherpeton*), but not all, cynodonts (Kielan-Jaworowska 1986, p. 30).

In order to establish the relationship of multituberculates with other mammals, it is crucial to know at which stage of evolution these two types of brain made their appearance. The oldest adequately preserved multituber-

Fig. 1. Brain reconstructions in some primitive mammals, based on endocranial casts. □A. 'Triconodont' *Triconodon*. □B. Multituberculate *Chulsanbaatar*. □C. Eutherian *Barunlestes*. A, B, cryptomesencephalic type; C, eumesencephalic type. In the endocranial cast of *Barunlestes* the division of the exposed part of the midbrain into anterior and posterior colliculi is not visible, which may be due to the state of preservation. Modified from Kielan-Jaworowska (1986). Not to scale.



culate and therian braincasts are from the Late Cretaceous of Mongolia (Kielan-Jaworowska 1986 and references therein). Hahn (1969) reconstructed the dorsal aspect of the brain of the Kimmeridgian *Paulchoffatia*, on the basis of skull structure and a comparison with Simpson's (1937) reconstruction of the brain of the Paleocene *Ptilodus*. Krause & Kielan-Jaworowska (1993) demonstrated that the widening of the olfactory bulbs in Simpson's reconstruction is an artefact. Hahn's (1969) reconstruction of the *Paulchoffatia* endocast generally resembles that of Cretaceous and Tertiary multituberculates, indicating that the cryptomesencephalic type of brain was possibly present in Late Jurassic forms.

The only 'triconodont' endocast of which the dorsal aspect has been reconstructed belongs to the Purbeckian (latest Jurassic) *Triconodon mordax*, based on several, poorly preserved specimens (Simpson 1927, 1928; Kielan-Jaworowska 1986). This brain is cryptomesencephalic, but has a relatively smaller vermis than in multituberculates (Fig. 1). Another partially reconstructed endocast (based on the ventral aspect of the cranial roof) is that of *Sinoconodon* (Patterson & Olson 1961) from the Liassic (Early Jurassic) of China, regarded as a sister group of other mammals (Crompton & Sun 1985; Crompton & Luo 1993). The preserved endocast was interpreted by Patterson & Olson as representing the caudal end of the hemispheres and the anterior part of the cerebellum. Quiroga (1984) commented on it and argued that in this specimen the dorsal surface of the midbrain is exposed, rather than the cerebellum. As I have not seen the specimen I cannot venture an opinion as to which of these views is more probable.

K.A. Kermack *et al.* (1981, Fig. 76) reconstructed the brain of *Morganucodon* in lateral view; it is not possible from this reconstruction to say whether the brain was eumesencephalic or cryptomesencephalic. In the same paper (Fig. 99B) they reconstructed the tentorium in the *Morganucodon* skull in medial view. The tentorium separates the cerebral and cerebellar cavities. It appears from that reconstruction that the cerebellum in *Morganucodon*

was very short longitudinally, and, if so, the brain was eumesencephalic rather than cryptomesencephalic. This means that *Morganucodon* and *Triconodon* differed dramatically in their brain structure.

If the eumesencephalic brain with a large dorsal midbrain exposure were to have originated from the cryptomesencephalic brain, this would have involved reversal of the primitive cynodont condition in which the midbrain was exposed dorsally (Hopson 1979). Nor, apparently, could the cryptomesencephalic brain have originated from the eumesencephalic brain, as this would involve a reduction of the newly developed character, the cerebellar hemispheres, which seems unlikely.

If the cryptomesencephalic condition were characteristic only for the Multituberculata, then one could imagine a relatively simple scenario: the cryptomesencephalic brain of multituberculates developed directly from that of cynodonts and apparently eumesencephalic brain of *Morganucodon* type (leading to the brains of the Theria) developed in parallel from cynodonts. However, the presence of cryptomesencephalic brain in *Triconodon* obscures this scenario. The differences in the brain structure of *Morganucodon* and *Triconodon* support the idea that the 'Triconodonta' is a polyphyletic group (see above). The dramatic differences in tooth replacement between the 'triconodont' families (Jenkins & Schaff 1988) point also to the polyphyly of the 'Triconodonta'. If one were to construct a phylogeny based on the brain structure, Multituberculata could have originated from the *Triconodon*-like forms (family Triconodontidae), but not from the Morganucodontidae.

Obviously the brain structure of early mammals should be more extensively studied and employed in the phylogenetic analyses. Skulls of Mesozoic mammals, except for materials from the Late Cretaceous of the Gobi Desert, are very rare. It should be possible, however, to obtain some endocranial casts from the collections in various museums, by a careful removal of the cranial roof and exposure of endocranial casts in some skulls, or to reconstruct the endocranial cavities using computer tomography.

Ear region

K.A. Kermack (1963) described isolated petrosals of the two triconodontid taxa *Trioracodon ferox* and *Triconodon mordax* from the English Upper Jurassic (Purbeck). I compared (Kielan-Jaworowska 1971, Fig. 12) the ventral view of the *Trioracodon* petrosal with those of the Cretaceous multituberculates *Kamptobaatar* and *Sloanbaatar* and pointed out some similarities between the three taxa. The epitympanic recess is shallower in *Trioracodon* than in multituberculates, but otherwise the ventral side of the *Trioracodon* petrosal is similar to that of multituberculates (K.A. Kermack 1963; Kielan-Jaworowska 1971). The petrosal of *Morganucodon* differs considerably from that of *Trioracodon* (K.A. Kermack *et al.* 1981), as well as from those of the multituberculates. The so-called Khoboor (referred to also as Khovboor and Khoobur) petrosal, from the Early Cretaceous of Mongolia, placed by Wible *et al.* (1995) in a trichotomy with Triconodontidae and Prototribosphenida (*Vincelestes* + Theria) differs from those of multituberculates in many characters (see Appendix 2 in Wible *et al.* 1995) and does not invite a comparison.

The evidence from the similarities between the choanal region of *Kamptobaatar* and *Triconodon*, showing that in the Triconodontidae the pterygoid bones were apparently situated medial to the lateral walls of the choanal channels, as in multituberculates (Kermack 1963, Fig. 11; Kielan-Jaworowska 1971, Fig. 13), should also be taken into account in establishing relationships between the multituberculates and the triconodontids.

Luo & Ketten (1991), using computer tomography, reconstructed the vestibule in two multituberculate petrosals (Late Cretaceous *Meniscoessus* and Paleocene *Catopsalis*) as unusually large and concluded that the enlarged vestibule is probably a synapomorphy of Multituberculata. Hurum *et al.* (1996) argued that the sections of the skull of *Nemegtbaatar* published by Kielan-Jaworowska *et al.* (1986) and of *Chulsanbaatar* (J.H. Hurum, unpublished) show that in these taxa the cross-sectional diameter of the vestibule is about twice that of the cochlea, and in most extreme cases about three times. This corresponds approximately to the ratio of vestibular to proximal cochlear diameter in neonatal therians and is not five or seven times that of the cochlea, as illustrated by Luo & Ketten (1991) for *Meniscoessus* and *Catopsalis*, respectively.

Multituberculate ear ossicles were described by Miao & Lillegraven (1986) for the Paleocene *Lambdopsalis*. Subsequently, Miao (1988) reconstructed the ear ossicles and ectotympanic in the ventral aspect of the *Lambdopsalis* skull. In these papers the malleus has been reconstructed with the manubrium pointing roughly posteriorly, rather than anteriorly or anteromedially as in other mammals

(e.g., Fleischer 1973, 1978; Maier 1989, 1990, and many others). Allin & Hopson (1992, p. 604, on the basis of the work of Miao 1988) stated: '... the entire middle ear [in *Lambdopsalis*] is reoriented so that its morphologic lateral aspect is anterior, as a result of great expansion of the vestibule of the inner ear in this peculiar multituberculate'.

Meng (1992) described a columelliform stapes with a slit-like stapedia foramen in *Lambdopsalis*, in contrast to the stout stapes reconstructed by Miao & Lillegraven (1986). Meng argued that in *Lambdopsalis* the stapes is directed anteriorly, rather than laterally as in other mammals, and regarded the anterior contact of the stapes with the incus as a possible multituberculate autapomorphy.

Hurum *et al.* (1995) reported the finding of the stapes, several specimens of the incus, and a fragment of an apparent malleus in the Late Cretaceous taeniolabidoid multituberculate from Mongolia *Chulsanbaatar*. They believed that the orientation of the malleus in Miao & Lillegraven (1986) and Miao (1988) papers was correct, and accordingly reconstructed the malleus with its anterior process lying in line with the crus breve of the incus and the manubrium mallei pointing posteromedially.

New discoveries demonstrated that the reconstructions of Miao & Lillegraven (1986), Miao (1988), and, consequently, of Hurum *et al.* (1995) require revision. Meng & Wyss (1995) found a partial tympanic and partial malleus of *Lambdopsalis*. They reconstructed the ear ossicles in *Lambdopsalis* arranged as in modern mammals. Rougier, Wible & Novacek (in press) described partial malleus, ectotympanic, stylohyal, and a fragment of a possible stapes of the Late Cretaceous *Kryptobaatar* from Mongolia, arranged as in modern mammals. They also argued that a part of the ossicle of *Lambdopsalis*, identified by Miao & Lillegraven as a manubrium, represents a fragment of an ectotympanic. Hurum *et al.* (1996) described several incudes and two fragments of an anterior process of the malleus in *Chulsanbaatar*. The incus in all the preserved specimens is roughly A-shaped, with a crus longum (medial leg of the A-shaped structure) contacting the head of the stapes, and the crus breve (lateral leg) lying parallel to the outer margin of the deep epitympanic recess. These fragments, although poorly preserved, indicate the presence of a malleus with a long anterior process, similarly arranged to those in *Lambdopsalis* (Meng & Wyss 1995), *Kryptobaatar* (Rougier, Wible & Novacek, in press), monotremes, and in embryos of extant therian mammals (Fleischer 1973; Maier 1989, 1990).

The presence of three ear ossicles in multituberculates arranged as in modern mammals suggests that the mammalian triossicular system evolved only once, as proposed earlier by, e.g., Kemp (1983), Novacek (1993) and recently by Meng & Wyss (1995). This suggests the monophyletic origin of mammals including multituberculates.

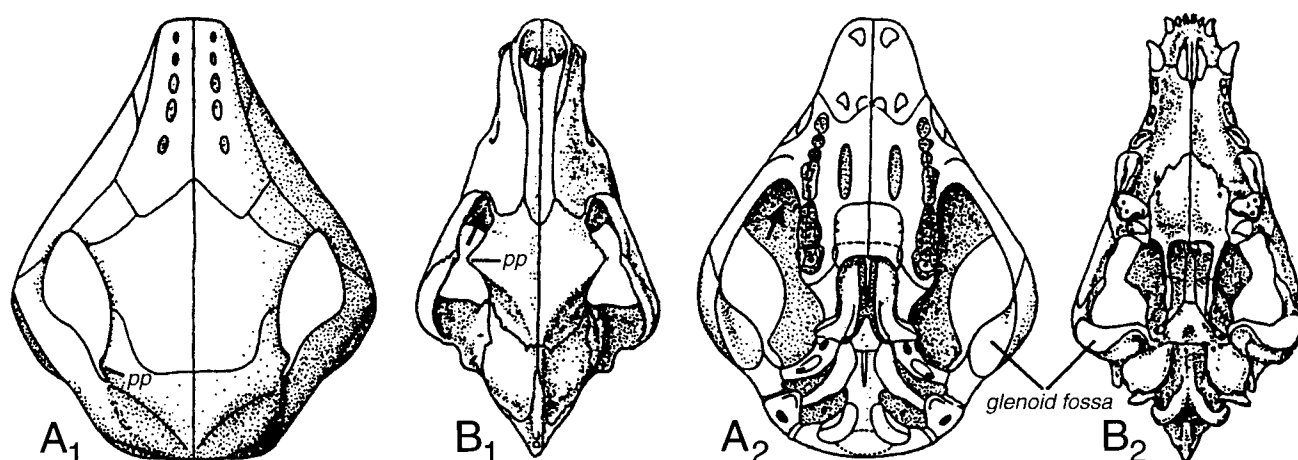


Fig. 2. Diagrammatical comparison of advanced multituberculate and therian skulls. □A. Multituberculate *Nemegtbaatar*. □B. Therian *Canis*. A₁, B₁, dorsal views; A₂, B₂, ventral views. Note differences in the structure of the orbit, glenoid fossa and position of the postorbital process (pp), on the frontal in therians and on the parietal in multituberculates. The arrow in B₁ points to the floor of the orbit, in A₂ to the orbital pocket. The orbital pocket has not been found in the Paulchoffatiidae. Not to scale.

Backward masticatory power stroke and associated cranial characters

Multituberculates are unique among mammals in having a backward (palinal) masticatory power stroke (Gingerich 1977; Krause 1982). A backward power stroke occurred also in gomphodont and tritylodontid cynodonts (Crompton 1972; Sues 1986) and has been proposed for the Haramiyidae (Butler & MacIntyre 1994), but the discovery of haramiyid mandibles with teeth and a maxilla (Jenkins *et al.* 1996) suggests predominantly orthal movement. Crompton & Luo (1993, p. 42) stated: 'We suggest that the gomphodonts and tritylodontids evolved a postcanine dentition in conjunction with a posteriorly directed occlusal stroke, whereas the transversely directed occlusal stroke of tritheledontids and mammals arose later from forms with a simple orthal jaw movement during occlusion.' Crompton & Luo (1993) did not venture an opinion on the origin of the power stroke in multituberculates.

Gambaryan & Kielan-Jaworowska (1995) demonstrated that the backward chewing stroke in multituberculates had a great impact on the configuration of their masticatory muscles and in relation to this on the external structure of the skull.

In therians primitively (e.g., Kielan-Jaworowska 1981), but also in *Sinoconodon* (Crompton & Luo 1993), in docodonts (Lillegraven & Krusat 1991) and in morganucodontids (K.A. Kermack *et al.* 1981) the orbit has no roof but has a floor and the eye is situated in its anterior part (in some advanced eutherians, for example in primates, the orbit has both floor and roof). In the Late Cretaceous Asian multituberculates the orbital space is prolonged anteriorly into an orbital pocket which is roofed dorsally

and laterally but lacks a floor (Fig. 2). Hahn (1987, Pl. 1: 2) demonstrated the presence of an orbital floor in the specimen designated Paulchoffatiinae, gen. et sp. indet. Professor Gerhard Hahn also informed me (personal communication, March, 1996) that he has not found an orbital pocket in the Paulchoffatiidae, which, however, may be due to the poor state of preservation of Guimarota material. The roofed orbital pocket of advanced multituberculates is not unique among mammals, as it occurs also rarely in specialized Theria, e.g., in extinct South American marsupials, the Argyrolagidae (Simpson 1970), and among hystricomorph rodents in the Bathyergidae (Boller 1970).

In therians the postorbital process as a rule is situated on the frontal, with a few, apparently secondary exceptions, e.g., *Procavia* and *Castor*, where it is situated on the fronto-parietal boundary or on the parietal. In multituberculates the postorbital process is not known in the Plagiaulacoidea, but in all well-preserved Late Cretaceous Asian djadochtatherian skulls it is situated on the parietal (the Late Cretaceous Mongolian multituberculates, traditionally referred to the Eucosmodontidae and Taeniolabididae, have been assigned by Kielan-Jaworowska & Hurum, in press, to a separate suborder Djadochtatheria. See also Rougier, Novacek & Dashzeveg, in press, who independently reached the conclusion that most of the Mongolian Late Cretaceous multituberculates form an endemic clade). Miao (1988) described the postorbital process in *Lambdopsalis* on the frontal, covered dorsally by the parietal, but Jin Meng informed me (personal communication, February 1995) that in *Lambdopsalis* specimens studied by him it is situated on the parietal.

Gambaryan & Kielan-Jaworowska (1995) reconstructed the masticatory musculature of Asian Late Creta-

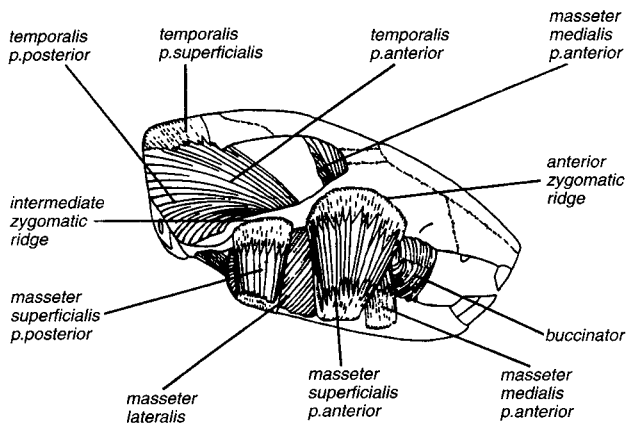


Fig. 3. Reconstruction of the superficial layer of the masticatory musculature in multituberculate *Nemegtbaatar*. Masseter lateralis profundus is referred to as masseter lateralis. Skull length is about 4 cm. p. = pars. Modified from Gambaryan & Kielan-Jaworowska (1995).

ceous dajdochtatherian (referred to as taeniolabidoid) multituberculates (Fig. 3) and compared it with that of rodents. Rodents were chosen for comparison because of the superficial similarity of the skull and lower jaw structure and arrangement of the dentition between the two groups and because in both the rodents and multituberculates the lower jaw moves anteroposteriorly (propalially) during the chewing stroke (see, e.g., Weijs 1975; Butler 1986). As in rodents, the masseter complex in multituberculates consisted of three layers. The difference is that the masseter superficialis, which in rodents and all therian mammals is not divisible, in multituberculates probably consisted of two bellies; these originated below two prominent ridges on the zygomatic arch, designated anterior and intermediate zygomatic ridges (Fig. 3).

In front of the masseteric fossa of Asian Late Cretaceous dajdochtatherians is another small fossa, designated by Gambaryan & Kielan-Jaworowska (1995) the masseteric fovea. The masseter medialis pars anterior was reconstructed as originating from the large orbital pocket in front of the orbitonasal ridge and inserting in the masseteric fovea (Fig. 3). In relation to the presence of the orbital pocket and the posterior position of the postorbital process, Gambaryan & Kielan-Jaworowska (1995, Fig. 19) reconstructed the eye in Asian dajdochtatherian multituberculates as very large and situated far posteriorly (see also Fig. 6 in this paper).

In multituberculates the masseteric fossa is situated more anteriorly than in all other mammals (Gambaryan & Kielan-Jaworowska 1995). The masseteric fovea (not present in therian mammals) is placed in multituberculates more anteriorly than the most anterior insertion of masseter muscles in any other mammal. This more anterior insertion of all the masticatory muscles is related to the backward masticatory power stroke. Another effect of

the backward chewing is that the resultant force of all the masticatory muscles had, in multituberculates, a retractory horizontal component; this is protractory in Theria. I compared the lower jaw of multituberculates with those of the monotremes and with the published drawings or photographs of the lower jaws of *Sinoconodon*, *Haldanodon*, *Morganucodon* (see references above) and later 'triconodonts' (e.g., *Gobiconodon*, Jenkins & Schaff 1988). These comparisons show that the masticatory muscles in multituberculates inserted not only more anteriorly than those of therians (Gambaryan & Kielan-Jaworowska 1995, Fig. 12), but also more anteriorly than in all other mammals.

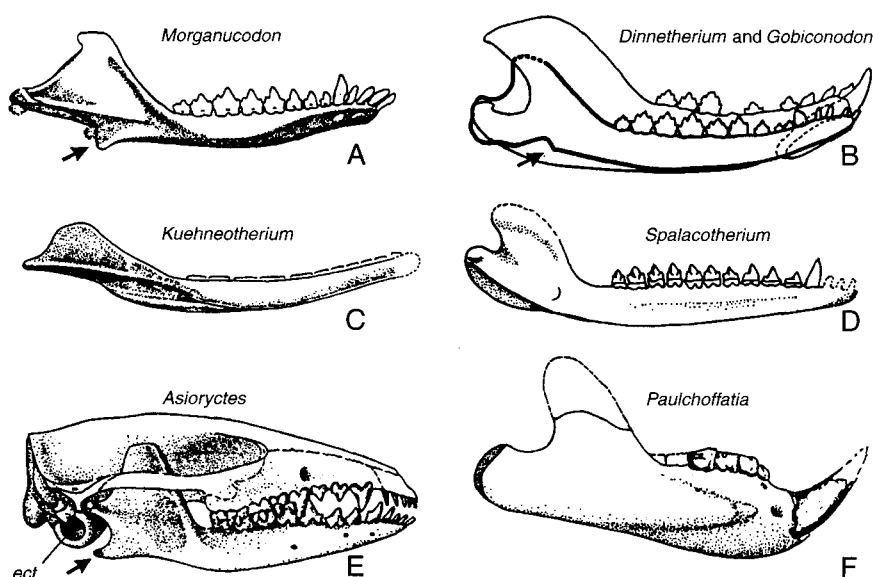
It should be mentioned that Ride (1959) related the forward insertion of the masseter muscles in the Macropodinae, where they enter the masseteric canal, to the presence of the so-called plagiaulacoid premolars in this group of kangaroos. He stated (p. 49): '... there is the direct mechanical advantage that is to be gained by inserting the deep masseter as close as possible to the position at which the shearing surface of the premolar is to be applied'. The question whether and to what extent the anterior insertion of masseter muscles in multituberculates is related also to the control of their plagiaulacoid premolars requires a special study and is beyond the scope of this paper.

Gambaryan & Kielan-Jaworowska (1995) demonstrated that the coronoid process in multituberculates (on which the temporal muscles insert) is situated more anteriorly than in therian mammals. It is also placed more anteriorly than in all other mammals listed above. Mammalian temporal muscles originate to the rear of the postorbital process. As the postorbital process in multituberculates is situated more posteriorly than in therian mammals, the multituberculate temporal muscles (both temporalis pars anterior and temporalis pars posterior) were arranged less vertically than in generalized therians.

Summing up, the reconstruction of the position of the main masticatory muscles allowed Gambaryan & Kielan-Jaworowska (1995) to interpret the following characters of the multituberculate skull as related to the backward masticatory power stroke: the roofed orbit, the backward displacement of the postorbital process onto the parietal, the anterior position of the coronoid process and of the masseteric fossa, as well as the lack of an angular process (discussed in the next section).

The question arises whether the other peculiarities of multituberculate skull structure discussed by Gambaryan & Kielan-Jaworowska (1995) are all related to the backward masticatory power stroke? These are: the medial position of the jugal (Hopson *et al.* 1989), presence of the zygomatic ridges and the structure of the glenoid fossa, which is large, flat, slopes backwards and stands out from the braincase, rather than being concave and transversely elongated as in most therians – see Fig. 2 (but not in

Fig. 4. Diagrammatical lateral views of dentaries (skull in *Asioryctes*) in some primitive mammals, rendered to the same length. Arrows point to the angular process; ect – ectotympanic bone. □A, B. 'Triconodonts'. Heavy line in B denotes *Dinnetherium*, light line *Gobiconodon*. □C, D. Symmetrodonts (but see text for doubts concerning the symmetrodont nature of *Kuehneotherium* lower jaw). □E. Therian (eutherian). □F. Multituberculate. Modified from: A – K.A. Kermack *et al.* (1973); B – Jenkins & Schaff (1988); C – D.M. Kermack *et al.* (1968); D – Simpson (1928); E – Kielan-Jaworowska (1975); F – reconstructed after the photographs of Hahn (1969).



rodents). These characters may be caused by the configuration of the muscles, but their relation to the backward power stroke cannot be so unequivocally demonstrated as in the case of the first group of characters discussed above.

Another question is whether all these characters, best observed on multituberculate skulls from the Late Cretaceous of Mongolia, were characteristic of all multituberculates. As mentioned earlier, the first multituberculate skulls and lower jaws are known from the Kimmeridgian of Portugal. These mandibles (Hahn 1969, 1978) show the typical multituberculate condylar process (Fig. 4F), lack of the angular process, anterior position of the coronoid process and the masseteric fossa, and the presence of the masseteric fovea and pterygoideus shelf. The skulls are not so well preserved as the lower jaws, but on the preserved part of the zygomatic arches the anterior zygomatic ridge is present. The anterior part of the orbital area and the postorbital process have not been preserved in these Kimmeridgian skulls. It may be inferred, however, from the arrangement of the masticatory muscles, apparently similar to that in the Cimolodonta and Djadochtatheria, that the orbital pocket was present and the eye was situated fairly posteriorly. It cannot be excluded that the postorbital process in the paulchoffatiids was developed on the parietal as in Late Cretaceous Asian multituberculates.

The above discussed main characters of the multituberculate mandible occur also in Paleocene forms, although the size of the coronoid process and the position of the condylar process may vary (see Wall & Krause 1992 and Gambaryan & Kielan-Jaworowska 1995). The anterior margin of the orbital area is rarely preserved, but the orbital pocket is found in the Paleocene *Ectypodus* (Sloan 1979) and in the highly specialized Paleocene tae-

niolabidid *Taeniolabis* (Sloan 1981). The orbital pocket is small in another highly specialized Paleocene taeniolabidid *Lambdopsalis* (Desui Miao, personal communication, December, 1994). The Taeniolabidae differ from most multituberculates and share this character with some Djadochtatheria, in having strong, gnawing incisors. In relation to this the temporalis muscles increased in size, the postorbital process migrated anteriorly and the orbit and consequently the eye were relatively small (see reconstruction of *Taeniolabis* skull in Hahn & Hahn 1983, upper figure before p. 1) and situated more anteriorly than in, e.g., *Nemegtbaatar* (Gambaryan & Kielan-Jaworowska 1995, Fig. 19; see also Fig. 6 herein) and in other Asian Late Cretaceous multituberculates.

This summary shows that multituberculates are a very homogeneous group as far as skull structure and cranial musculature is concerned. We do not know when the suite of characters related to the backward power stroke developed, but it seems probable that it made its appearance at the beginning of multituberculate evolution. Gambaryan & Kielan-Jaworowska (1995, p. 101) argued: 'Given that in rodents the forward power stroke (with only a limited transverse component) developed from forms with a transversely directed power stroke (Weijjs 1994), the origin in multituberculates of the backward power stroke may have been from triconodonts with a transversely directed power stroke.'

It follows that the external structure of the multituberculate skull cannot demonstrate unequivocally whether multituberculates originated from a subgroup of 'triconodonts' (apparently from the common ancestors with the Triconodontidae) or developed in parallel to them from an insectivorous cynodont stock.

Mandibular condyle, pterygoideus shelf and angular process

In many cynodonts, for example, *Trirachodon*, *Exaeretodon*, *Probainognathus*, *Pachygenelus*, *Kayentatherium*, and others (see for example Allin & Hopson 1992, Fig. 28.9), there is an angular process and a concavity on the posteroventral margin of the dentary above it. This concavity houses some of the post-dentary bones.

Early mammals, namely *Sinoconodon* (Crompton & Sun 1993), *Morganucodon*, *Dinnetherium*, *Megazostrodon* and possibly all other Late Triassic – Early Jurassic ‘triconodonts’ (K.A. Kermack *et al.* 1973, 1981; Jenkins *et al.* 1983; Gow 1986), docodonts (Kron 1979; Lillegraven & Krusat 1991 and references therein) have a double jaw joint. The double jaw joint was also present in an edentulous lower jaw described by D. M. Kermack *et al.* (1968) as a symmetrodont *Kuehneotherium*. However, the conspecificity of this lower jaw with teeth assigned to *Kuehneotherium* has not been demonstrated and one cannot be sure if it belongs in fact to Symmetrodonta. Allin & Hopson (1992) reconstructed postdentary bones in the ‘eupantothere’ *Amphitherium*. In all these forms the post-dentary bones are housed in a trough at the posteroventral end of the inner side of the dentary and extend posteriorly behind it. In *Morganucodon* (Fig. 4A), *Sinoconodon*, and docodonts there is a concavity at the posteroventral margin of the dentary, similar to that in the above-mentioned cynodonts, housing a part of post-dentary bones (the angular and articular). The angular process surrounds anteroventrally the reflected lamina of the angular. In the early ‘triconodont’ *Dinnetherium* (Fig. 4B) the concavity is reduced to a small subtriangular depression on the ventral margin of the dentary. In later ‘triconodonts’ (see below) the concavity disappears and there is no trace of the angular process. In *Kuehneotherium* (Fig. 4C), in which the post-dentary bones have not been preserved and their presence is inferred only from the presence of a trough, the angular process is lacking, but a shallow concavity at the posteroventral margin of the dentary is present. In all later symmetrodonts, e.g., *Spalacotherium* (Fig. 4D), there is no trace of the angular process.

In embryos of extant mammals (e.g., Allin 1975; Maier 1990 and many others) there is a concavity between the articular and angular processes similar to that in cynodonts, early ‘triconodonts’ and docodonts. This concavity houses some of the post-dentary bones. In non-specialized fossil and extant therians the remnant of this housing is retained as a concavity on the posterior margin of the dentary, e.g., in the Late Cretaceous *Asioryctes* in which the ectotympanic bone (homologue of angular) fits into this concavity (Fig. 4E). The concavity and the angular process related to it are secondarily absent in, e.g., large herbivores, primates and many other therian mammals. The angular process is vestigial in *Tachyglos-*

sus and absent in *Ornithorhynchus* (Griffiths 1968), but present in *Obdurodon* (J.A. Hopson, personal communication, May, 1995).

The homology of the angular process of non-therian mammals (and non-mammalian synapsids) with that of therians is debated. Simpson (1928) regarded these processes as homologous and was supported by Parrington (1959) and K.A. Kermack *et al.* (1973). The homology was questioned by Patterson (1956), Patterson & Olson (1961) and more recently by Jenkins *et al.* (1983). The last-mentioned authors argued that in an early ‘triconodont’ *Dinnetherium* (Fig. 4B in this paper), posterior to the angular process (which they called the pseudoangular process) there is a bony flange continuous with the masseteric fossa which they interpret as a neomorphic angular region that is characteristic of therian mammals. They pointed out that in cynodonts, ‘triconodonts’ and other early mammals the angular process is situated more anteriorly than in therians and claimed that the angular process of later mammals did not originate through the posterior growth of the process present in cynodonts and ‘triconodonts’, but as a separately evolved structure. The idea of Jenkins *et al.* (1983) was challenged by Sues (1986) and not accepted by Allin (1986), Allin & Hopson (1992) and Gambaryan & Kielan-Jaworowska (1995). Sues (1986) argued that the angular processes in cynodonts, non-therian mammals and therians are homologous. He stated (p. 254): “‘Fusion’ of this process [angular process of Jenkins *et al.*] with the ‘pseudoangular process’ could have produced the condition in the Multituberculata, Symmetrodonta, and Triconodonta (Simpson 1928, Figs. 9, 19) where the ventral margin of the dentary is continuous from symphysis to condyle.”

The angular process is prominent in *Morganucodon* and docodonts, where the concavity is conspicuous; it is much less significant in the Megazostrodonidae (*Megazostrodon* and *Dinnetherium*). In later ‘triconodont’ families Triconodontidae, Amphilestidae and Gobiconodontidae (e.g., *Gobiconodon*), the angular process is absent. The condition in Megazostrodonidae is morphologically intermediate between that of *Morganucodon* and the more advanced ‘triconodonts’, such as *Gobiconodon* (Fig. 4A, B).

The angular processes of cynodonts, non-therian mammals and therians are homologous not only in the masticatory musculature that inserts upon them, but also with respect to the bones that are in contact with them (in embryos of therians). In all cases the angular process surrounds anteroventrally the reflected lamina of the angular (ectotympanic). In adult non-advanced therians (e.g., Fig. 4E) the process similarly surrounds the relevant part of the ectotympanic. With the reduction in the size of the post-dentary bones in the lineage leading from cynodonts to mammals (Allin 1975), the angular process moved posteriorly. Accepting the scenario of Jenkins *et al.* (1983), it

would be difficult to visualize what happened to the angular bone and the tympanic membrane when the original 'pseudoangular' process disappeared and the new process developed.

If the angular processes of non-therians and therians are homologous, the question arises: when did the angular process make its appearance in the therian line? It is absent in the dentary of the apparent earliest known therian *Kuehneotherium* (Fig. 4C), generally regarded on dental evidence as ancestral to the therian line. If this dentary belongs indeed to *Kuehneotherium*, and *Kuehneotherium* originated from forms with the angular process, then one should assume that this process disappeared in symmetrodonts and then appeared again in 'eupantotheres'. If so, the angular process is a synapomorphy for 'eupantotheres' and tribosphenic mammals, as generally accepted (e.g., Prothero 1981 and references therein). Another possibility is that *Kuehneotherium* dentary does not belong to the symmetrodonts, or that *Kuehneotherium* and other symmetrodonts are a side-branch of mammals and 'eupantotheres' originated from an unknown ancestor with *Kuehneotherium*-like teeth and an angular process. As long as *Kuehneotherium* and other early therians are poorly known it is difficult to speculate on which of these scenarios is more probable.

The oldest known multituberculate lower jaws from the Kimmeridgian of Portugal (Fig. 4F) have a fully developed dentary-squamosal joint (Hahn 1978 and references therein). The only 'reptilian' bone found in the multituberculate lower jaw is the coronoid of *Kuehneodon* (Hahn 1977). The structure of Kimmeridgian multituberculate lower jaws shows that the transformation of the bones forming the reptilian jaw joint into ear ossicles took place very early in multituberculate evolution or, in case they originated from a subgroup of 'triconodonts', in their ancestors. As noted by Granger & Simpson (1929, p. 612): '... in *Taeniolabis*, and in multituberculates generally, there is no angular process, strictly speaking, and this region is fundamentally distinct from either marsupials or placentals.'

The semicircular posterior margin of the dentary, with the condylar process forming at least a part of it, is characteristic of the Kimmeridgian Paulchoffatiidae and has been retained in most multituberculates. Gambaryan & Kielan-Jaworowska (1995) regarded it as a multituberculate autapomorphy and demonstrated that only in advanced families such as the Taeniolabidae (part of which is now assigned to the Djadochtatheria) and Sloanbaataridae did the condylar process migrate upwards. The high position of the condylar process in these multituberculate groups was possibly an adaptation for cutting hard seeds. It was also argued that the so-called pterygoideus shelf or floor of the pterygoid fossa in multituberculates incorporates not only the angular process (as suggested earlier by Cope 1881 and Miao 1988) but also the entire

ventral margin of the dentary below the mandibular canal. It is, however, unknown whether the angular process was present in multituberculate ancestors. Both the extensive pterygoideus shelf in multituberculates and the angular process in therians are sites for insertion of the m. pterygoideus and thus are homologous in the musculature that inserts upon them. The different portions of the dentaries that are inflected in multituberculates and in therians suggest that the inflection occurred separately. In marsupials the remnant of the housing of the postdentary bones is well seen above the posterior end of the inflected angular process, while in multituberculates this remnant cannot be discerned even in the most completely preserved dentaries.

Gambaryan & Kielan-Jaworowska (1995) speculated on why the angular process is absent in multituberculates. In Theria the presence of the angular process causes an increase of the protractor horizontal component of the vector of masseter superficialis that inserts upon it. Because of the backward chewing stroke in multituberculates the masseter superficialis inserted more anteriorly than in Theria. Had there been a large protractor component associated with an angular process in multituberculates, the muscles inserting upon the angular process would pull the lower jaw forwards, preventing a backward power stroke. It follows that the absence of an angular process in multituberculates is related to the backward masticatory power stroke.

As the characters of the lower jaw discussed in this section are related to the backward masticatory power stroke, the conclusion is similar to that of the previous section dealing with the cranial characters. The multituberculate condyle, the pterygoideus shelf and lack of the angular process possibly originated at the very beginning of multituberculate lineage and may have developed irrespective of whether multituberculates originated from cynodonts or from a subgroup of 'triconodonts'.

Foot, pelvis and posture

Kielan-Jaworowska & Gambaryan (1994) argued that multituberculates differ considerably from extant therians in having abducted limbs and a different structure of the foot. The multituberculate foot was reconstructed for the first time by Granger & Simpson (1929) for the Paleocene *Eucosmodon* on the basis of almost all foot elements, preserved in isolation. They found that in the multituberculate calcaneum the facet for articulation with the cuboid (which in therians is placed distally) is placed obliquely mediodistally. In relation to this they reconstructed (Granger & Simpson 1929, Fig. 23) the multituberculate foot with the calcaneum not supported distally by any bone. In Granger & Simpson's reconstruction the tuber calcanei was arranged subparallel to the main axis (third ray) of the foot. This reconstruction was accepted until recently (see e.g., Krause & Jenkins 1983 and Szalay 1993).

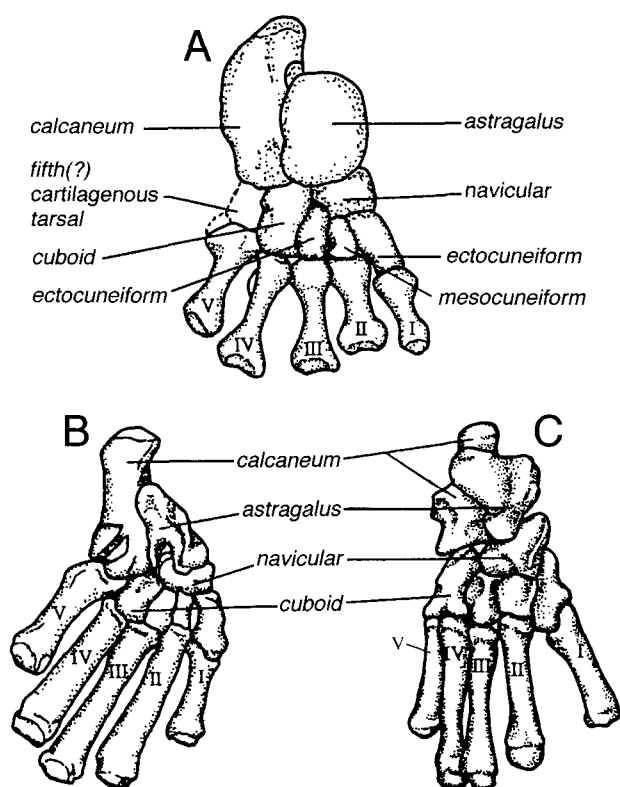


Fig. 5. Diagrammatical comparison of ankle joints. □A. *Manda cynodont*. □B. Multituberculate *Eucosmodon*. □C. Recent therian *Didelphis*. I – V metatarsals. Modified from: A – Szalay (1993); B – Kielan-Jaworowska & Gambaryan (1994). Not to scale.

In material from the Gobi Desert studied by Kielan-Jaworowska & Gambaryan (1994) there are three feet preserved in articulation. On the basis of these specimens and on a comparison with the original material of *Eucosmodon*, a new reconstruction of the multituberculate foot was offered, in which the middle metatarsal (MtIII) is abducted by 30° from the longitudinal axis of the tuber calcanei and the calcaneum distally contacts the fifth metatarsal (MtV) (Fig. 5B).

One of the multituberculate postcranial skeleton autapomorphies, namely the pelvis with a ventral keel (Kielan-Jaworowska 1979), hindered prolongation of the gestation period and therefore might have been responsible for the competitive inferiority of multituberculates to placentals. Kielan-Jaworowska & Gambaryan (1994, p. 87) argued: '... the keel in the multituberculate pelvis might have been developed as a response to the origin of femoral adductors ventral to the acetabulum; this in turn was related to the abducted position of their hind limbs. If this is true, one may speculate that the abducted position of multituberculate limbs would restrict their evolutionary possibilities also by limiting their reproductive strategy.'

The multituberculate foot as reconstructed by Kielan-Jaworowska & Gambaryan (1994) is unique for mammals (Fig. 5B). In morganucodontids and therians (Szalay 1993 and references therein) the calcaneum articulates distally with the cuboid (Fig. 5C). The complete foot of morganucodontids has not been reconstructed, although partial foot has been preserved in *Megazostrodon* (Jenkins & Partridge 1976). The distinct distal cuboid facet on the calcaneum in *Morganucodon* (*Eozostrodon*) (Jenkins & Partridge 1976; Szalay 1993), however, demonstrates that the calcaneocuboid contact in morganucodontids was generally of the same type as in therians. In monotremes the calcaneum is modified and there is a large peroneal tubercle directed laterodistally and a calcaneal–MtV ligament; still the calcaneal cuboid facet is distal and it articulates with the lateral side of the cuboid (Szalay 1993, Fig. 9.2). Monotreme feet represent a modification of the foot characteristic for a morganucodontid–therian line and are very different from those of multituberculates.

How might these two different types of foot structure (multituberculate type and morganucodontid–therian type) have originated? In cynodonts and in most therapsids (Schaeffer 1941a, b; Jenkins 1971; Szalay 1993) the fifth distal tarsal bone, characteristic of early reptiles (Romer & Parsons 1986), is not preserved. Schaeffer (1941b) maintained that it was still present, but cartilaginous in *Bauria*. It is not known whether it was also present in the so-called *Manda cynodont* (Jenkins 1971; Szalay 1993), but such a possibility cannot be excluded (Fig. 5A).

Kielan-Jaworowska & Gambaryan (1994) speculated that when the fifth tarsal disappeared in the lineage leading to mammals, two different types of mammalian foot developed. In the 'triconodont' (morganucodontid) – therian line the cuboid extended laterally, supporting the distal end of the calcaneum and the cuboid facet on the calcaneum acquired a distal position. In the multituberculate line, in contrast, the calcaneum came into contact with the fifth metatarsal; at the same time the cuboid facet on the calcaneum shifted from nearly distal to a medio-distal position, which is unique for mammals. The origin of multituberculate foot from that of morganucodontid–therian line is improbable, as first the cuboid would have to extend laterally to acquire the morganucodontid–therian position and then migrate medially again to leave the place for calcaneo–MtV contact. Therefore these authors concluded that the multituberculate foot apparently developed directly from that of cynodonts. It should, however, be remembered that the foot structure in the Triconodontidae is not known. As I assume that the Triconodontidae are more closely related to multituberculate ancestors than are any other 'triconodonts', discovery of their postcranial skeleton may be crucial for finding an answer to the problem of multituberculate origin.

Kielan-Jaworowska & Gambaryan (1994) argued that a deep multituberculate pelvis, with femoral adductors originating ventral to the acetabulum (rather than posteroventral as in Theria) and large mediolateral diameter of the tibia, indicate abduction of the femora by 30–60°. The first complete multituberculate humeri ever described are those of ?*Lambdopsalis* from the Eocene of China (Kielan-Jaworowska & Qi 1990). They are twisted up to 38°, have a very wide intertubercular groove and strongly expanded distal end with prominent radial and ulnar condyles. Sereno & McKenna (1995) suggested that multituberculate posture was parasagittal, similar to that of *Didelphis*. They based their hypothesis on the structure of the shoulder girdle and forelimbs in a Late Cretaceous multituberculate, *Bulganbaatar*, from Mongolia, the humerus of which shows a small degree of torsion (15°), on the structure of the distal end of the humerus and structure of the glenoid fossa. Sereno & McKenna (1995, p. 147) concluded: '... a forelimb posture with the elbow near the body arose only once, some time before the Late Jurassic, in a common ancestor of multituberculates, therians and their extinct allies'.

In reply to critique by Presley (1995) and Rougier *et al.* (1996), Sereno & McKenna (1996, p. 379) argued that both Presley and Rougier *et al.* '[a]s evidence against the therian-like structure and function of the multituberculate pectoral girdle and hind limb [...] cite the greater degree of torsion in the shaft of another multituberculate (*Lambdopsalis*). Marked humeral torsion and fossorial habits, however, are clearly correlated among mammals (for example, moles [sic] among living therians). Increased humeral torsion in this avowed fossorial multituberculate from the Paleogene can thus not be interpreted with confidence as a "residuum of the primitive torsion between the humeral head and elbow condyle."'.

Gambaryan & Kielan-Jaworowska (in press) argued that in terrestrial tetrapods with primary sprawling posture, which use symmetrical diagonal gaits (Lacertilia, Crocodylia and Monotremata), the humerus shows a relatively high torsion (up to 60°), wide intertubercular groove, lesser trochanter wider than the greater, and the condylar type of the elbow joint, with spherical radial condyle and oval, convex ulnar condyle. Abducted forelimbs occur also in Anura, which use asymmetrical jumps and have a straight humerus (without torsion). Therian mammals acquired a trochlea probably during the Late Jurassic, retained vestigial radial condyle in Late Cretaceous forms, but lost this condyle in the Paleocene. Fossorial mammals that secondarily acquired half-sprawling or sprawling stance, differ from tetrapods with primary sprawling stance in having a trochlea and radial condyle, but no ulnar condyle, and in having a narrow intertubercular groove. Among fossorial therians humeral torsion occurs only in Chrysochloridae. The Spalacidae, which are fossorial, have no radial condyle, only a trochlea, as their forelimbs work in a parasagittal plane.

Small degree of humeral torsion (15°) found in one multituberculate taxon (*Bulganbaatar*) does not imply a parasagittal posture (as proposed by Sereno & McKenna 1995), as lack of torsion occurs also in forms with sprawling posture, such as the Anura, and in several digging therians, with secondarily abducted forelimb trajectories. *Bulganbaatar* has no trochlea, but has prominent radial and ulnar condyles, characteristic of forms with primary abducted forelimbs. Multituberculate humeri vary in the degree of torsion. It cannot be excluded that relatively notable torsion of *Lambdopsalis* is, at least in part, related to its semi-fossorial mode of life. However, the structure of the multituberculate humerus, with spherical humeral head, wide intertubercular groove, lesser trochanter wider than the greater, spherical radial condyle and prominent ulnar condyle, indicates the primary sprawling stance of the forelimbs.

Gambaryan & Kielan-Jaworowska (in press) also demonstrated that the structure of multituberculate scapula, which is narrow and has convex medial side (subscapular fossa), indicates that the scapula was more movable than in any therian mammal. The rotation at the shoulder joint was ensured by both the rotation of the scapula and the rotation of the humerus. The structure of the multituberculate elbow joint, with spherical radial condyle and very extensive articular circumference on the proximal end of the radius, suggests extensive rotation of the antebrachium and independent rotation of the radius about its longitudinal axis, as characteristic of abducted limbs.

Kielan-Jaworowska & Gambaryan (1994) concluded on the basis of analysis of multituberculate hind limbs and structure of lumbar vertebrae with long transverse and high spinous processes, that multituberculates had sprawling limb posture and were adapted for asymmetrical gait with steep jumps. Gambaryan & Kielan-Jaworowska (in press) demonstrated that the range of humeral excursion at flexion-extension in the shoulder joint in multituberculates was much smaller than in *Didelphis* and the joint was more extended, as characteristic for mammals during jumps. This questions the hypothesis of Sereno & McKenna (1995) on *Didelphis*-like locomotion of multituberculates, and gives support to Kielan-Jaworowska & Gambaryan (1994) supposition that multituberculates were adapted for asymmetrical jumps with abducted limbs.

The fact that multituberculates never developed a trochlea and retained condylar structure of the elbow joint throughout their history, while the ancestors of therians acquired the trochlea possibly during the Late Jurassic and very early lost the ulnar condyle, gives evidence that the parasagittal posture arose in mammalian evolution only once in therians, and not in common ancestors of therians and multituberculates. Reconstruction of multituberculate stance and movements thus does not support a multituberculate–therian sister-group relationship.

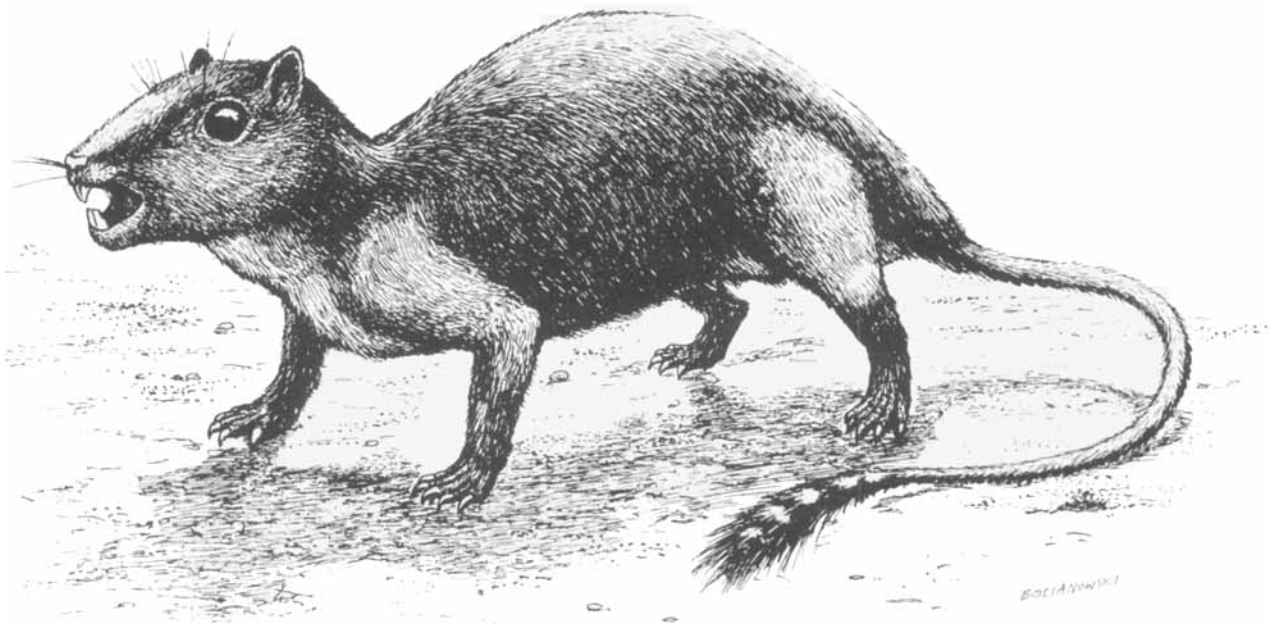


Fig. 6. Reconstruction of the posture of multituberculata *Nemegtbaatar*. Modified from Kielan-Jaworowska & Gambaryan (1994).

Conclusions

The present account shows that although Multituberculata and Theria developed several characters in parallel, there are limits to this parallelism. In the skull structure the differences are caused primarily by the backward masticatory power stroke in multituberculata, which resulted in a different configuration of the masticatory musculature than in Theria and in all other mammals and, in consequence, a different osteological design. In the postcranial skeleton the differences concern in the first place the foot and pelvis structure, different from those of Theria (and all other mammals). As may be seen from the foregoing discussion, the multituberculata limb posture (Fig. 6) does not demonstrate close multituberculata–therian relationship.

The multituberculata brain was very different from those of the Theria and possibly also from the Morganucodontidae (*Morganucodon*), but was of the same type as in the Triconodontidae (*Triconodon*). As argued under 'Brain structure' the possible differences between the *Morganucodon* and *Triconodon* brains indicate the polyphyly of the 'Triconodonta', as assumed earlier by many authors. Similar conclusions may be drawn from the differences in tooth replacement between the 'triconodont' families. Jenkins & Schaff (1988) demonstrated that in *Gobiconodon* (Gobiconodontidae) the molari-form teeth are replaced, which is unique not only for the 'triconodonts' but also for mammals. In *Morganucodon* and *Triconodon* the last premolar is replaced and there is no evidence for replacement of any other premolar (Mills 1970).

The brain and foot structure of the Morganucodontidae refute the morganucodontid origin of the Multituberculata. The brain structure of *Triconodon* allies the Triconodontidae with the Multituberculata. The relationships of Multituberculata and the Triconodontidae may possibly, but less convincingly, be inferred from the structure of the petrosal and the choanal region. Other details of triconodontid skull anatomy are poorly known, and their postcranial skeleton is virtually unknown, which makes conclusions on this relationship uncertain.

New data on the ear ossicles of Paleocene *Lambdopsalis* (Meng & Wyss 1995) and of the Late Cretaceous *Kryptobaatar* (Rougier, Wible & Novacek, in press) and *Chulsanbaatar* (Hurum *et al.* 1996) may refute the diphyletic origin of multituberculata and living mammals.

The remaining characters discussed in this paper, such as the backward masticatory power stroke and associated skull and lower jaw design, could possibly have developed either if multituberculata had a common ancestry with a subgroup of 'triconodonts' or if they developed from the cynodonts separately from the 'triconodonts'.

I discuss in this paper a suite of characters that (except for the structure of the ear region) have been almost completely neglected in previous analyses of early mammal relationships. These characters do not decisively indicate the phylogenetic position of multituberculata. However, they may prove critical to the balance of evidence necessary for resolving the basal relationships of mammals.

The difficulty in establishing the phylogenetic position of multituberculata resides in the lack of adequate materials of their earliest representatives, as well as in limited knowledge of 'triconodont' structure and their interrela-

tionships. The Haramiyidae apparently are not related to the multituberculates (Jenkins *et al.* 1996) and the material of the pre-Kimmeridgian purported multituberculates consists of a few broken teeth known only from Europe (Hahn *et al.* 1987; Freeman 1979; K.A. Kermack 1988 and references therein). The multituberculate affinity of these teeth is possible, but it cannot be unequivocally demonstrated. The lack of uncontested pre-Kimmeridgian multituberculates disproves the separate origin of multituberculates from cynodonts, and may be taken as an argument for their origin from a common ancestor with the Triconodontidae.

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