PHYLOGENY AND SYSTEMATICS OF MULTITUBERCULATE MAMMALS

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ABSTRACT. We present a synopsis of high-rank multituberculate systematics and a manually generated cladogram illustrating multituberculate interrelationships. We divide the Multituberculata into the paraphyletic suborder 'Plagiaulacida', an apparently monophyletic suborder Cimolodonta, and one family *incertae sedis*. Within 'Plagiaulacida' we recognise three informal lines: paulchoffatiid (three families), plagiaulacid (three families) and allodontid (two families and the genus *Glirodon*). The Cimolodonta are divided into an informal *Paracimexomys* group; three superfamilies: Ptilodontoidea, Djadochtatherioidea (new), and Taeniolabidoidea (restricted to Taeniolabididae); and five families (superfamily *incertae sedis*): Eucosmodontidae, Microcosmodontidae, Cimolodontidae, Boffiidae, and Kogaionidae; and some genera *incertae sedis*. New characters used in our analysis are (1) a tendency of molar cusps to coalesce; and (2) ornamentation of grooves, pits, and ridges on the molars. We argue that the Ptilodontoidea, and less certainly also the Cimolodontidae and Boffiidae, might have originated from among the plagiaulacid line, a possible intermediate link being the *Paracimexomys* group. The remaining Cimolodonta might have originated from unknown members of the *Paracimexomys* group with separated molar cusps and smooth enamel. The origin of two types of prismatic enamel and a relationship between them are stumbling blocks in understanding the origin of the Cimolodonta; we conclude that microprismatic enamel made its appearance only once. Revised diagnoses of high-rank multituberculate taxa, including lists of all known genera, are given.

KEY WORDS: Multituberculata, Allotheria, Mammalia, systematics, phylogenetic reconstructions, Mesozoic.

MULTITUBERCULATE mammals were conspicuous, biotically significant elements of Mesozoic and early Tertiary terrestrial communities. They are also the most completely known of all Mesozoic mammals but, paradoxically, their systematics and phylogeny are poorly understood. In this paper we present an attempt at resolving interrelationships of high-rank multituberculate subgroups.

The use of algorithm-based cladistic analyses for resolving high rank relationships of vertebrate groups is now widely accepted. However, previous studies of multituberculate systematics that employed algorithm-based cladistic analyses have resulted in very poor resolution. Simmons (1993), using 49 genera and a hypothetical ancestor, and 67 cranial and dental characters, obtained from the PAUP program of Swofford (1989) 10,000 equally parsimonious trees and a strict consensus tree with a resolution of 66 per cent. Rougier *et al.* (1997), using a modified version of Simmons' matrix of 67 characters, 50 genera, and a hypothetical ancestor, obtained in a slightly different version of the same program (Swofford 1993) 20,000 equally parsimonious trees, before exhausting the available computer memory.

Small scale cladistic analyses (limited to members of selected genera or families) which used PAUP programs (e.g. Simmons and Miao 1986; Weil 1998; and the PhD thesis of Weil 1999, unpublished and not available to us, but reported in Montellano *et al.* 2000) did not provide more reliable results. The most striking example is in Weil's thesis. She examined 48 multituberculate species scored for 36 dental characters. These were summarised by Montellano *et al.* (2000, p. 338) as follows: 'Multiple heuristic analyses using PAUP* 4.0.d64 for DOS, written by D. L. Swofford, yielded 395,743 shortest trees in seven islands, summarized as seven consensus hypotheses of relationships ...'.

Previously we (Kielan-Jaworowska and Hurum 1997) also offered a computer-generated cladistic analysis of 11 Mongolian Late Cretaceous multituberculate genera, five of the best known genera from other territories, a hypothetical ancestor, and 43 characters, using the Pee-Wee and NONA programs (Goloboff 1996 and 1993 respectively). With Pee-Wee we obtained only two trees and have chosen one of

them. The results based on an analysis using NONA were less reliable. However, our method has been criticised by an anonymous reviewer and colleagues, who suggested that Pee-Wee is less objective because it involves weighting of characters. In addition, as PAUP is now most widely used for this type of analysis, we were advised to use PAUP in future studies, because otherwise our results would not be compatible with those of other researchers.

In view of this criticism we originally made an attempt at using PAUP in an algorithm-based cladistic analysis for the present paper (see Appendix for character list). With a taxon-character matrix (Appendix) of 62 characters, 32 taxa and a hypothetical ancestor, we obtained 17,783 equally parsimonious trees with PAUP version 4.0b4a (Swofford 1998). Again, the strict consensus tree produced by the program did not provide meaningful results and we do not publish it.

Rougier et al. (1997) suggested that a large amount of missing data probably accounts for the high number of trees and poor resolution of the strict consensus tree in their paper. We agree that incompleteness is of great importance. For example, since members of the plesiomorphic family Paulchoffatiidae have never been found with upper and lower dentitions in occlusion, Hahn (1993) divided them (with exception of Kuehneodon) into upper dentition and lower dentition genera. As a result, in strict consensus trees obtained from different PAUP analyses (e.g. Simmons 1993; Rougier et al. 1997; and our unpublished results), the paulchoffatiid genera usually appear in a polytomy, mixed with members of the Plagiaulacidae, Allodontidae, and even sometimes the Arginbaataridae.

We are of the opinion that the reason for the lack of detailed, robust results in resolving multituberculate interrelationships by cladistic computer-supported methods is, in addition to the incompleteness of data, a high level of parallelism, especially in development of the dentition. For example, the Djadochtatherioidea are defined by skull characters, which differentiate them from other Cimolodonta (Kielan-Jaworowska and Hurum 1997). Within the Djadochtatherioidea one observes evolution of the dentition in different directions. One, exemplified by the Bulganbaatar/Nemegtbaatar line, involves elongation of the last upper premolar and molars, and an increase in their cusp numbers. A similar tendency exists in the Ptilodontoidea. For example, the shape and proportions of upper cheek teeth in the ptilodontoidean Ectypodus approach those of the djadochtatherioid Nemegtbaatar (Text-fig. 1). This similarity is so striking that if only upper teeth were known, these genera might have been assigned to the same family. In the course of this study we also found a high level of parallelism in development of the lower dentition among high rank multituberculate subgroups.

In view of the difficulties and doubts concerning the utility of computer analysis, we present instead a systematic division of the Multituberculata, based on synapomorphies that we consider to be of greatest importance and utility, associated with selected plesiomorphies. We offer also a manual cladogram illustrating what we believe to be the most parsimonious hypothesis of multituberculate phylogeny, based on available evidence. Because of the incompleteness of data other interpretations are also possible, and we discuss some of them.

Below we discuss multituberculate interrelationships, as far as the available data permit us, pointing out unresolved problems in understanding multituberculate phylogeny, such as interrelationships between 'plagiaulacidan' lines, origins of Cimolodonta, origins of gigantoprismatic enamel, and relationships between gigantoprismatic and microprismatic enamels (Carlson and Krause 1985; Fosse et al. 1985; Krause and Carlson 1987). We base our systematics on data from previous work on multituberculate morphology and systematics, including papers and references cited by Matthew and Granger (1921, 1925), Matthew et al. (1928), Simpson (1928, 1929, 1937), Granger and Simpson (1929), Jepsen (1930, 1940), Clemens (1963, 1973), Kielan-Jaworowska and Sochava (1969), Lillegraven (1969), Kielan-Jaworowska (1970, 1971, 1974, 1997), Fox (1971, 1976, 1980, 1989, 1999), Holtzman and Wolberg (1977), Krause (1977, 1982a, b, 1992), Clemens and Kielan-Jaworowska (1979), Sloan (1979, 1981), Vianey-Liaud (1979, 1986), Archibald (1982), Hahn and Hahn (1983, 1999a), Krause and Jenkins (1983), Fosse et al. (1985), McKenna (1975), Kielan-Jaworowska et al. (1986), Krause and Carlson (1986, 1987), Eaton and Cifelli (1988), Miao (1988), Eaton and Nelson (1991), Kielan-Jaworowska and Ensom (1992, 1994), Hahn (1993), Simmons (1993), Kielan-Jaworowska and Gambaryan (1994), Eaton (1995), Gambaryan and Kielan-Jaworowska (1995), Râdulescu and Samson (1996), Kielan-Jaworowska and Hurum (1997), Rougier et al.(1997), Weil (1998), Engelmann and Callison (1999), Montellano et al. (2000), and many others.
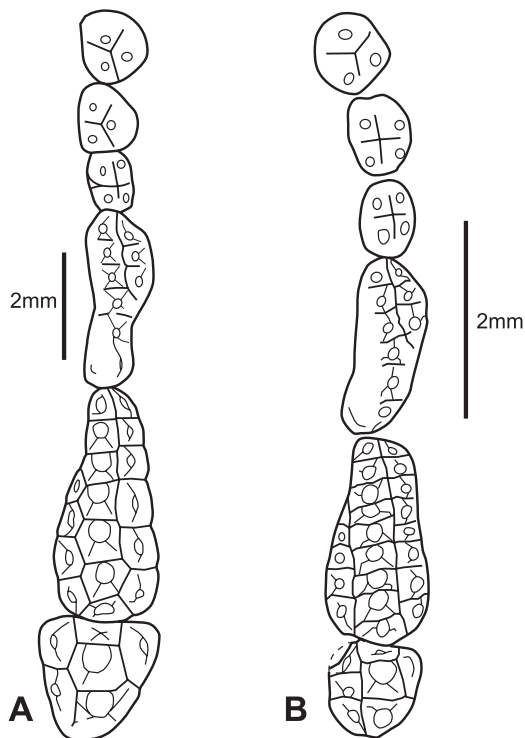
TEXT-FIG. 1. Slightly diagrammatic *camera lucida* drawings of left upper premolars and molars. A, djadochtatherioid *Nemegtbaatar gobiensis* (ZPAL MgM-I/81). B, ptilodontoidean *Ectypodus tardus* (PU 17674; drawing based on a cast). This comparison shows a high level of parallelism in the development of the upper dentition in groups that differ dramatically in skull and dentary structure, lower dentition and enamel microstructure.

Abbreviations. We use upper case characters I, C, P, M, for upper incisors, canine, premolars, and molars respectively; and lower case characters i, c, p, m, for corresponding lower teeth. AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London [previously British Museum (Natural History)]; DINO, Dinosaur National Monument, Jensen; DORCM, Dorset County Museum, Dorchester, Dorset; MNA, Museum of Northern Arizona, Flagstaff; OMNH, Oklahoma Museum of Natural History, Norman; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PU, Princeton University, Princeton (collection now housed at the Yale Peabody Museum); UA, The University of Alberta, Edmonton; YPM, Yale Peabody Museum, New Haven; and ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

HISTORICAL REVIEW OF HIGH RANK MULTITUBERCULATE SYSTEMATICS

Simpson (1945) divided the order Multituberculata Cope, 1884 into three families: Plagiaulacidae Gill, 1872, Ptilodontidae Gregory and Simpson, 1926 (= Chirogidae Cope, 1887), and Taeniolabididae Granger and Simpson, 1929. Simpson did not recognise any multituberculate suborders at that time, although earlier he mentioned (Simpson 1925) the suborder Plagiaulacoidea and formally diagnosed it three years later (Simpson 1928). Simpson (1945), however, treated the Plagiaulacoidea as a synonym of Multituberculata as opposed to Tritylodontoidea, which he also regarded as allied to multituberculates. Sloan and Van Valen (1965) raised the family Ptilodontidae to subordinal rank (Ptilodontoidea) and erected a new suborder, Taeniolabidoidea.

Hahn (1969) revised, re-diagnosed and enlarged the scope of the Plagiaulacoidea. McKenna (1971) proposed the suborder Plagiaulacida, but subsequently (1975) he used the suborder Plagiaulacoidea; he also proposed within Plagiaulacoidea a new infraorder Cimolodonta but did not diagnose it. Hahn and Hahn (1983) recognised within the Multituberculata (in addition to Haramiyoidea), three multituberculate suborders: Plagiaulacoidea, Ptilodontoidea, and Taeniolabidoidea. Archibald (1982) presented the first cladistic analysis of Multituberculata, based on the distribution of 16 dental characters. On that basis he removed the Cimolomyidae from the Taeniolabidoidea; he also regarded the Ptilodontoidea and Taeniolabidoidea as separate clades.

Fosse et al. (1978) hypothesised that the two advanced multituberculate suborders Taeniolabidoidea and Ptilodontoidea differ in enamel microstructure. Very large prisms (gigantoprismatic enamel, referred to also as large arcade-shaped prisms by Carlson and Krause 1985) characterise the Taeniolabidoidea, while in the Ptilodontoidea the prisms are smaller, comparable to those of eutherian mammals. The latter type of enamel has been referred to subsequently by various authors as small circular prisms, small prismatic enamel, or microprismatic enamel. Carlson and Krause (1985) and Fosse et al. (1985) studied the distribution of prismatic enamel in numerous multituberculate taxa and confirmed the conclusion of Fosse et al. (1978). In addition Fosse et al. (1985) found that two plagiaulacoid genera have non-prismatic enamel ('prismless' in the terminology of Koenigswald and Sander 1997). Subsequently Krause and Carlson (1986) studied the distribution of enamel microstructure in 30 out of 41 Late Cretaceous and Tertiary multituberculate genera recognised at that time, as well as 22 characters of gross dental morphology. Krause and Carlson (1986) concluded that small circular prisms are homologous in all multituberculates in which they occur; the same concerns large, arc-shaped prisms, which are homologous in all the genera, with exception of *Neoliotomus*. This genus has microprismatic enamel as is characteristic of the Ptilodontoidea, but has been traditionally assigned to the Taeniolabidoidea. Krause and Carlson (1986) concluded that microprismatic enamel is derived with respect to gigantoprismatic and apparently made its appearance twice.

Kielan-Jaworowska and Ensom (1992) proposed a new suborder, Paulchoffatoidea (assigning a new rank to the family Paulchoffatiidae). Hahn (1993) rejected it and restored the family status of the Paulchoffatiidae, a course followed by Gambaryan and Kielan-Jaworowska (1995).

Simmons (1993) provided a large-scale cladistic analysis of the Multituberculata, using the PAUP program (see Introduction for details). She recognised the paraphyly of the Plagiaulacoidea ('Plagiaulacida' in the terminology used herein) and monophyly of the Cimolodonta. She further claimed that the Ptilodontoidea are monophyletic if the genera *Boffius* and *Liotomus* are removed to the Taeniolabidoidea, while monophyly of the Taeniolabidoidea is possible but not certain. Rougier et al. (1997), using a modified version of Simmons' matrix, came to the conclusion that Asian Late Cretaceous genera (excluding *Buginbaatar*), together with North American Palaeocene *Pentacosmodon*, form a monophyletic group. Kielan-Jaworowska and Hurum (1997) reached a similar conclusion on the monophyly of Late Cretaceous Mongolian taxa and erected the suborder Djadochtatheria (= superfamily Djadochtatherioidea herein) for this group (*Buginbaatar* excluded) and tentatively assigned to Djadochtatheria the North American *Pentacosmodon* and *Paracimexomys*.

McKenna (*in* Stucky and McKenna 1993) considered the Cimolodonta and Plagiaulacida as orders within the infraclass Multituberculata. McKenna and Bell (1997), however, eliminated the order Plagiaulacida, regarding it as a paraphyletic unit. These authors assigned various paulchoffatiid, plagiaulacid, and allodontid genera (belonging to different well-defined families) to the Plagiaulacidae, while one plagiaulacid genus, *Bolodon,* was placed by them in the Bolodontidae (which we regard as a synonym of Plagiaulacidae), together with members of the Eobaataridae. This procedure, neglecting the meticulous and very competent work of Prof. Gerard Hahn, completely obscured the relationships between early multituberculate subgroups. McKenna and Bell also assigned superfamily rank to the suborders Taeniolabidoidea and Ptilodontoidea, which we follow.

Hahn and Hahn (1999a) provided a systematic division of the Plagiaulacoidea, within which they recognised eight families. They suggested that the Ptilodontoidea might have originated from the Allodontidae and Taeniolabidoidea from the Plagiaulacidae, and argued that if this is true, the suborder Cimolodonta should be abandoned.

After our paper was originally submitted for publication, we read an abstract by Fox (1999), who had independently come to some conclusions that are similar to those expressed in this paper. Fox (1999) challenged the monophyly of Taeniolabidoidea (*sensu* Sloan and Van Valen 1965) and classified Microcosmodontidae (new rank assigned by Fox to the subfamily Microcosmodontinae), Eucosmodontidae, Cimolomyidae, and Taeniolabididae as families *incertae sedis* within the Cimolodonta. Thus his conclusions have priority in this systematic arrangement.

Another paper published after submission of our paper, which is worth mentioning, is that by Montellano *et al*. (2000). These authors described the fairly complete and well-preserved dentition, dentary and skull fragments of *Cimexomys judithae* from the Campanian of Montana and argued that *Cimexomys* is too primitive to be included among either the Taeniolabidoidea or Ptilodontoidea. This agrees with our conclusion as we tentatively place *Cimexomys* in the informal '*Paracimexomys* group', which we erect for plesiomorphic, poorly known members of the Cimolodonta.

In the present paper we use the suborder 'Plagiaulacida' in inverted commas because of its paraphyly. This suborder includes the Plagiaulacoidea (Simpson, 1925; G. Hahn, 1969). The subordinal name Plagiaulacoidea would be in line with traditional use. However, according to the International Commission on Zoological Nomenclature (1999, Article 29.1): 'The suffix – OIDEA is used for a superfamily name . . .'. As superfamilies are now used in multituberculate systematics (e.g. McKenna and Bell 1997 and this paper), we choose the existing name 'Plagiaulacida' (as corrected by McKenna 1971) for the suborder, to avoid confusion with superfamily names. As McKenna changed only the ending of Simpson's suborder, Simpson (1925) remains the author.

PHYLOGENETIC ANALYSIS

Outgroup

Hennig (1966) argued that if one can find the closest relative or relatives of the group one is working on, then one has basic tools for deciding which characters are plesiomorphic and which are apomorphic. According to Hennig, search for outgroups is the essence of phylogenetic analysis. Finding an outgroup for the Multituberculata, however, is the first difficulty which one encounters in an attempt at phylogenetic analysis of this order. The problem is that the origins of the Multituberculata are obscure and in recent phylogenetic analyses of early mammals, multituberculate relationships have been a subject of vigorous controversy.

Traditionally palaeontologists believed that multituberculates might have originated from cynodonts independently from all other mammals, or diverged from other mammals at a very early stage of mammalian evolution. Simpson (1945, p. 168) stated: '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 class as such . . .'. More recently the idea that multituberculates might be a sister taxon of all other mammals has been supported by, among others Hahn *et al*. (1989) and Miao (1993). On the other hand, studies of the last two decades on the skull structure of multituberculates and other early mammals (e.g. Kielan-Jaworowska *et al*. 1986; Miao 1988; Wible 1991; Rougier *et al*. 1992; Wible and Hopson 1993, 1995; Hurum 1994, 1998*a*, *b*) demonstrated the homogeneity of the internal structure of the skull and vascular system of all mammals, including multituberculates. The same concerns the discovery of multituberculate ear ossicles, which display the same pattern as those of all other mammals (Hurum *et al*. 1996; Rougier *et al*. 1996*a*).

The notion that multituberculates might form a sister taxon of all other mammals is related to the idea that they are close relatives to the Haramiyidae, a family represented until recently only by isolated teeth, with numerous cusps arranged in longitudinal rows, known from the Late Triassic and Early Jurassic mostly in Europe. Hahn (1973) proposed for the Haramiyidae the suborder Haramiyoidea within the Multituberculata and later (Hahn *et al*. 1989) raised it to an ordinal rank as Haramiyida. Butler and McIntyre (1994) regarded the Haramiyida as a sister group of the Multituberculata and assigned them to ?Mammalia, Allotheria (see also Sigogneau-Russell 1989). The year 1997 brought a long awaited discovery. Jenkins *et al*. (1997) described from the Upper Triassic of Greenland *Haramiyavia clemmenseni*, assigned to the Haramiyidae, represented by dentaries and partial maxillae with teeth and

fragments of the postcranial skeleton. *Haramiyavia* has been interpreted as having orthal jaw movement. On this basis Jenkins *et al.* excluded the Haramiyida from the Allotheria, which have propalinal (fore-and-aft) movement of the dentary and backward (palinal) power stroke. In turn Butler (2000) revised all known allotherians and argued that dental resemblance supports the hypothesis that the Multituberculata originated from the Haramiyida.

It should be stressed that in rigorous cladistic analyses of early mammals the Haramiyidae (and Theroteinidae, another early allotherian family known from isolated teeth: e.g. see Sigogneau-Russell *et al.* 1986) have been omitted, because of the incompleteness of the available material. For example, Simmons (1993, p. 148) stated: 'Haramiyidae and Theroteinidae, taxa that are known only from isolated teeth, do not represent useful outgroups to Multituberculata because they cannot be yet demonstrated to share any unequivocally derived character states with multituberculates . . .'.

Rowe and Greenwald (1987), Rowe (1988, 1993), Lucas and Luo (1993), and Sereno and McKenna (1995), among others, regarded the Multituberculata as a sister taxon of Theria (Marsupialia + Placentalia). Similarly Simmons (1993), in the first computer-generated analysis of all multituberculate taxa, used Theria *sensu stricto* as an outgroup. This has been followed by Rougier *et al.* (1997), who used a modified version of Simmons' matrix. Sister group relationships of Theria and Multituberculata, based mostly on superficial similarity of the postcranial skeleton, have been criticised by, among others, Kielan-Jaworowska and Gambaryan (1994), Presley (1995), Rougier *et al.* (1996*b*), and Gambaryan and Kielan-Jaworowska (1997). The selected characters employed by Rowe (1988) have been analysed and refuted by, among others, Wible (1991), Meng (1992), Miao (1993), and Lillegraven and Hahn (1993). Finally, the most recent analyses of mammalian relationships, including analysis of the skeleton of a symmetrodont *Zhangheotherium* (Hu *et al.* 1997), and the skeleton of the eutriconodont *Jeholodens* (Ji *et al.* 1999), did not support multituberculate-therian sister-group relationship. In both of these papers the Multituberculata are placed between Monotremata (*Ornithorhynchus*) and Symmetrodonta (*Zhangheotherium*), being a sister taxon of all the Holotheria.

A somewhat different concept was expressed earlier by Crompton and Sun (1985), Miao and Lillegraven (1986), Miao (1991), Meng (1992), Rougier *et al.* (1992), and Lillegraven and Hahn (1993), who regarded the Multituberculata as a sister taxon of Monotremata + Theria *sensu lato* (Holotheria); i.e., placed between the Triconodonta (including Morganucodontidae) and Monotremata, or between the Triconodonta and early Symmetrodonta. On the other hand, Wible and Hopson (1993) and Meng and Wyss (1995) regarded the Multituberculata as a sister taxon of the Monotremata, both groups together being the sister taxon of the Theria.

It should be pointed out that none of these analyses took into account the structure of the brain, which, as argued by Kielan-Jaworowska (1997), is one of several characters neglected in phylogenetic analyses of early mammals. The multituberculate brain, designated cryptomesencephalic (characterised by an expanded vermis, no cerebellar hemispheres, and lack of the dorsal midbrain exposure) is very different from that in Theria, which originally had eumesencephalic brains (characterised by a wide cerebellum with extensive cerebellar hemispheres and large dorsal midbrain exposure). The cryptomesencephalic brain characteristic of multituberculates otherwise occurs only in eutriconodonts. Another character neglected until recently in phylogenetic analyses of early mammals involves the foot structure. In the multituberculate foot the middle metatarsal (MIII) is abducted from the longitudinal axis of the tuber calcanei, while the calcaneus contacts distally the fifth metatarsal (Kielan-Jaworowska and Gambaryan 1994). This type of foot appeared at that time to be unique among mammals, but Ji *et al.* (1999) described a similar type of foot in the eutriconodont *Jeholodens*. It follows that there are two groups of characters related to brain and foot structure, which ally multituberculates with eutriconodonts.

Out of an array of various hypotheses of sister group relationships of the Multituberculata, discussed above, the two that appear most probable to us are with the Haramiyida or the Eutriconodonta; the latter has not, however, been supported as yet by dental evidence. That is why we follow the opinion of haramiyid students (in particular G. Hahn, D. Sigogneau-Russell, P. M. Butler and others, expressed in various papers cited above), and we choose the Haramiyida as an outgroup of the Multituberculata. We base characters of a hypothetical ancestor in the taxon-character matrix on Haramiyida-Multituberculata sister-group relationships.

Characters used

In our phylogenetic analysis we use numerous dental and cranial characters employed in previous analyses of multituberculate interrelationships (Archibald 1982; Krause and Carlson 1987; Simmons 1993; Kielan-Jaworowska and Hurum 1997; Rougier *et al*. 1997), with the exclusion of the metric characters adopted by Simmons, and Rougier *et al*. We do not use postcranial characters because the postcranial skeleton is known only in a few multituberculate taxa (see Krause and Jenkins 1983, and Kielan-Jaworowska and Gambaryan 1994 for reviews) and appears to be unified in all multituberculates.

We do not use the size of the coronoid process of the dentary, which primitively is large, but its size varies within particular groups in relation to dietary preferences (Gambaryan and Kielan-Jaworowska 1995).

We observed that there are two characters of dental morphology, often associated: cusp fusion and ornamentation, and separated cusps with smooth enamel. These features have seldom been used in previous phylogenetic analyses or mentioned in descriptions. Kielan-Jaworowska *et al*. (1987) recognised the presence of cusp coalescence and grooves in m2 of *Eobaatar*. Subsequently, Kielan-Jaworowska and Ensom (1992) used both characters in their diagnosis of the Plagiaulacidae (including Eobaatarinae), pointing out that members of the Plagiaulacidae differ in this respect from members of the Allodontidae. Krause *et al*. (1992) used both characters in their analysis of the relationships of the gondwanatherian *Ferugliotherium* within the Multituberculata (assigned now to Mammalia *incertae sedis*: see Pascual *et al*. 1999; not discussed herein). Krause *et al*. (1992) also commented on the presence of grooves in the Ptilodontoidea and their absence from the Taeniolabidoidea.

We introduced these characters in our character list as follows: molar enamel smooth, not ornamented, or enamel covered with grooves and pits (character 39). The other character is molar cusps well separated or tending to coalesce. As a rule, this character is more obvious on lower than upper molars and is sometimes difficult to define. Because of ambiguity we use this character in the character list only with respect to lower molars (characters 32 and 33).

As coalescence of cusps does not occur in the Haramiyidae (but it occurs in the Theroteinidae) (e.g. see figures in Hahn 1973; Sigogneau-Russell 1989; and Butler and MacIntyre 1994), we regard well-separated cusps as plesiomorphic, while coalescence is considered to be derived. Similarly the ornamentation of grooves and pits does not occur in the Haramiyida, and we regard smooth enamel as plesiomorphic, while ornamented enamel is interpreted to be derived.

Defining both characters may be dubious in some instances, as, for example in the Paulchoffatiidae m2 is basin-like, with a single cusp showing a very strong degree of cusp coalescence, but m1 and the upper molars may have well-separated cusps (the same concerns the poorly known Pinheirodontidae, based on isolated teeth). If only one of the teeth in a given taxon shows coalescence or ornamentation, we score it as having coalesced cusps or ornamented enamel. In other families, such as the Plagiaulacidae and Eobaataridae, all known genera show a tendency toward cusp fusion (at least in peripheral aspect), associated with ornamentation of grooves and pits. On the other hand in the Allodontidae, *Glirodon* and all Djadochtatherioidea the molar cusps are well separated and molar enamel is smooth.

We figure examples of forms with well-separated cusps and smooth enamel in Plate 1, figures 3–5; Plate 2, figures 7–8; and Plate 3, figures 7 and 9. In Plate 2, figures 1–6 and 9–10, and Plate 3, figures 1–4, 6, 8 and 10, there are examples of coalesced or partly coalesced cusps and ornamented enamel. In the specimen in Plate 3, figure 5, the cusps are not obviously coalesced, but enamel is ornamented.

For character list and taxon-character matrix, see Appendix.

Computer-generated analysis

We obtained 17,783 equally parsimonious trees using PAUP version 4.0b4a (Swofford 1998) with a length of 210 steps. In the strict consensus tree generated by this analysis, two main groups were produced: one containing all 'Plagiaulacida' and Arginbaataridae, the other containing all of the Cimolodonta. In the first group, all the branches collapsed forming a polytomy; in the second group we received a polytomy, except

for two cases: *Lambdopsalis–Taeniolabis*, and *Eucosmodon–Stygimys*. Because of the poor resolution obtained we refrain from publishing the cladogram and present only the taxon-character matrix, which was used by the program. Instead we have produced the manual cladogram (Text-fig. 2) described below.

Description of the cladogram

On the basis of analysis of the 'character list' (Appendix) and 'taxon-character matrix' (Appendix), we propose a hypothesis of multituberculate interrelationships, shown in Text-figure 2 (in which the numbers show distribution of selected characters). We have constructed this cladogram using the apomorphic characters for groups of genera (used in the taxon-character matrix; Appendix) and the genera that share the same characters, but have not been included in the matrix. As may be seen from the cladogram, several characters appear independently in various lines because of homoplasy. We regard unique associations of characters (apomorphies, occurring together with some plesiomorphies) as diagnostic for the families. Not all the characters have been shown in the cladogram; for complete lists of characters used in our analysis, see sections on phylogeny and systematic palaeontology below.

0. Hypothetical ancestor at allotherian non-multituberculate grade of evolution. Three upper incisors; lower molars with two parallel rows of cusps of different height; lower canine present, four lower premolars not modified as 'blades', molar cusps separate; enamel surface smooth, more than one lower incisor. Propalinal jaw movement not developed or incipient.
1. Containing all except ancestor; see diagnosis of Multituberculata in systematic palaeontology section below.
2. 2^1, 2^2. I3 small and single-cusped, or with main cusp and basal cuspule (allodontid line and some Cimolodonta, homoplasy or common ancestry?).
3. 3^1, 3^2. Loss of buccal cusps on p3 (plagiaulacid and allodontid lines, ?homoplasy).
4. 4^1, 4^2. The p4 increased in size with respect to p3 (plagiaulacid and allodontid lines, ?homoplasy, more strongly expressed in plagiaulacid than in allodontid line).
5. 5^1, 5^2. Incipient lingual ridge on M1 (plagiaulacid and allodontid lines, ?homoplasy).
6. I3 enlarged, with 3–4 cusps (paulchoffatiid and plagiaulacid lines).
7. m2 with coalesced buccal cusps (paulchoffatiid and plagiaulacid lines).
8. Incipient ornamentation of molar enamel (paulchoffatiid and plagiaulacid lines).
9. I3 roughly quadrangular or trapezoid in occlusal view, 3–4 cusped, with main cusps arranged obliquely forming a ridge (paulchoffatiid line).
10. m2 basin-like (paulchoffatiid line) differing in details in three families (see diagnoses of Paulchoffatiidae, Hahnodontidae and Pinheirodontidae in systematic section below).
11. 11^1, 11^2. Anterior lower premolars roughly triangular in buccal view (plagiaulacid line and Arginbaataridae, homoplasy).
12. Enlarged I3 (smaller than in Paulchoffatiidae), roughly triangular in occlusal view, with three cusps (plagiaulacid line).
13. Tendency of molar cusps to coalesce (retaining two-row structure of m2), more strongly expressed in the lowers than in the uppers (Plagiaulacidae, Eobaataridae, *Paracimexomys* group, and are less strongly expressed in the Ptilodontoidea).
14. Ornamentation of grooves and pits on the molars (Plagiaulacidae, Eobaataridae, *Paracimexomys* group, and are less strongly expressed in the Ptilodontoidea, Cimolomyidae and Boffiidae).
15. Unusually large p4, with limited enamel, rotating during ontogeny over p2 and p3, which gradually disappear (arginbaatarid autapomorphy).
16. 16^1, 16^2, 16^3. Gigantoprismatic enamel (appearing ?independently in *Glirodon, Arginbaatar, Eobaatar* and characteristic also of the Cimolodonta, except for the Ptilodontoidea).
17. 17^1, 17^2, 17^3 17^4. Limited enamel band on lower incisor (appearing independently at least four times in *Glirodon, Eobaatar, Neoliotomus*, and five groups of non-ptilodontoidean Cimolodonta, possibly separately in each of them).
18. 18^1 and 18^2. Arcuate p4 (appearing independently at least twice, homoplasy, in the Cimolodonta and Arginbaataridae).
19. Loss of I1 (apomorphy of Cimolodonta).
20. Loss of P4 (apomorphy of Cimolodonta).
21. 21^1, 21^2. Loss of p1 (Arginbaataridae, Eobaataridae and a few other plagiaulacid genera, the latter not shown in the
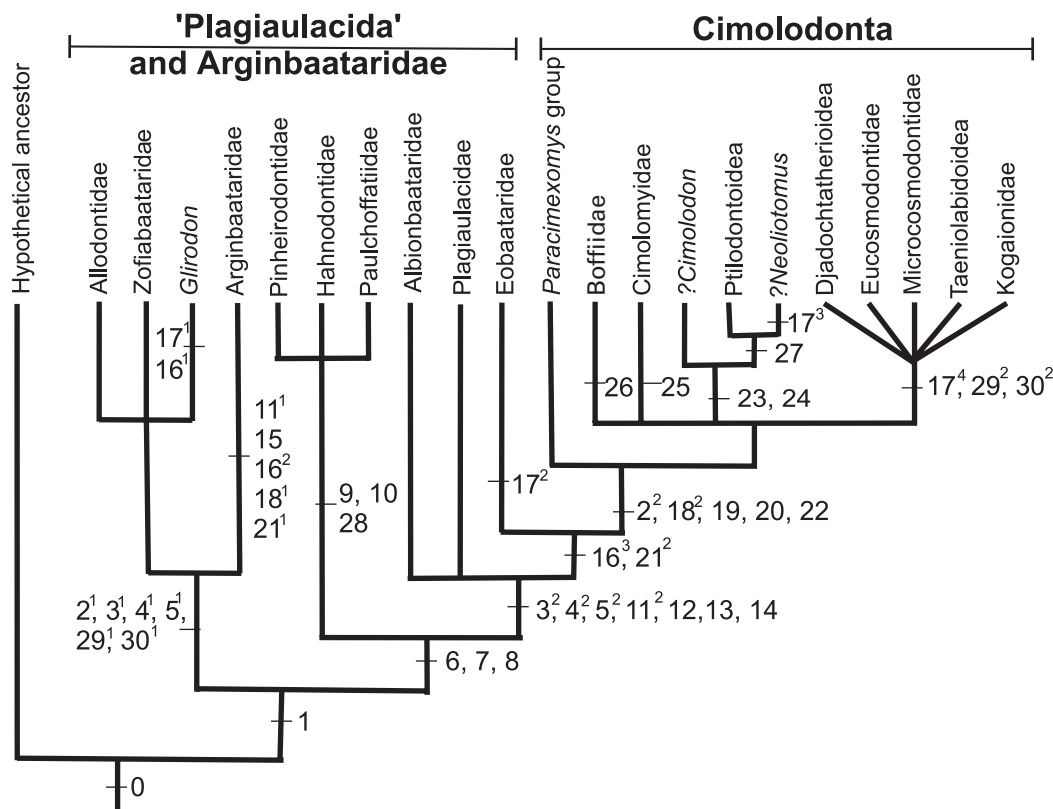
TEXT-FIG. 2. Cladogram showing hypothetical interrelationships of the Multituberculata. The numbers show distribution of selected characters. If a character appears twice or several times, the same number is repeated, marked by different indices, e.g. 3^1, 3^2. The Arginbaataridae, which are a very specialised side-branch of the Multituberculata, have been placed together with 'Plagiaulacida' for technical reasons. See text for explanation of the numbers; for characters defining all of the groups, see systematic section.

cladogram, and Cimolodonta, homoplasy; between Eobaataridae and Cimolodonta possibly because of the common ancestry).

22. Change of p3 into a peg-like non-functional tooth (apomorphy of Cimolodonta).

23. Increase of size of p4, which becomes strongly arcuate with numerous ridges and protrudes dorsally over the level of the molars (apomorphy of Ptilodontoidea).

24. Lower incisor very gracile (apomorphy of Ptilodontoidea, except *Neoliotomus*, tentatively assigned).

25. Molar cusp pyramidal to crescentic, correlated with reduction of upper premolars and enlargement of the molars, enamel grooves only on m1 (apomorphies of Cimolomyidae).

26. Upper molars strongly enlarged with three rows of cusps; strong ribbing of upper premolars and molars, weak on m1, grooves absent (apomorphies of Boffiidae).

27. Acquisition of microprismatic enamel (apomorphy of Ptilodontoidea, which appears once after the separation of *Cimolodon*, tentatively assigned, from the main ptilodontoidean line).

We also use three plesiomorphic characters:

28. Plesiomorphic structure of p3, with buccal cusps present (paulchoffatiid line).

29^1, 29^2, 29^3. Lower molar cusps separated (not coalesced) (allodontid line, Arginbaataridae and five cimolodontan groups in polytomy).

30^1, 30^2, 30^3. Molar enamel smooth (allodontid line, Arginbaataridae and five cimolodontan families in polytomy).

PHYLOGENY

We present below a phylogeny of Multituberculata, which should be read in conjunction with the cladogram in Text-figure 2 (throughout the discussion we refer to the numbers in that figure).

'Plagiaulacida'

As apparent from the cladogram in Text-figure 2, the 'Plagiaulacida' are a grade characterised by three upper incisors, lower incisor completely covered with enamel (except *Glirodon* and *Eobaatar*), five upper premolars (with the exception of two paulchoffatiid genera), and four (three in advanced forms) blade-like lower premolars, rectangular or triangular in lateral view (Text-fig. 3). Blade-like lower premolars are an apomorphy of the Multituberculata and differentiate them from other mammals (except for a few marsupials, homoplasy), including the Haramiyidae, which we regarded as the sister-group of the Multituberculata (see also Hahn 1973; Sigogneau-Russell 1989; Butler and MacIntyre 1994; Butler 2000).

The 'Plagiaulacida' include eight families and *Glirodon*, placed by Engelmann and Callison (1999) in 'Plagiaulacida' *incertae sedis*. The families assigned to the 'Plagiaulacida' may be divided into three informal, apparently monophyletic lines: (1) *Allodontid line*: Allodontidae, Zofiabaataridae, and *Glirodon*; (2) *Paulchoffatiid line*: Paulchoffatiidae, Hahnodontidae, and Pinheirodontidae; (3) *Plagiaulacid line*: Plagiaulacidae, Albionbaataridae, and Eobaataridae.

Allodontid line (numbers 2^1, 3^1, 4^1, 5^1, 29^1, 30^1). It is difficult to decide whether the allodontid or paulchoffatiid line is more plesiomorphic; both lines are characterised by different mixtures of plesiomorphic and derived characters. We tentatively accept that members of the allodontid line might be the most plesiomorphic multituberculates, as they retain the plesiomorphic structure of the lower molars with two rows of well-separated cusps, smooth enamel (lack of grooves and ribbing on the upper and lower molars) and a small I3 (Simpson 1929; Bakker and Carpenter 1990; Carpenter 1998; Engelmann and Callison 1999; and Pl. 1). They all retain five upper and four lower premolars. They are, however, more advanced than members of the paulchoffatiid line in the structure of the lower premolars and in possessing a larger angle between the tooth row and the longitudinal axis of the dentary, which is very low in at least one paulchoffatiid genus, *Paulchoffatia*. The Allodontidae also have a slightly younger geological occurrence than the Paulchoffatiidae (Simpson 1928, 1929; Hahn 1969, 1993; Kielan-Jaworowska and Ensom 1992; Carpenter *et al.* 1998; Engelmann and Callison 1998).

Upper premolars are smooth in *Ctenacodon* and *Glirodon*, but ornamented in *Psalodon* (Simpson 1929, pl. 5, fig. 2). The buccal cusps on m2 in *Ctenacodon scindens* (Pl. 1, fig. 5) are strongly worn and it cannot be demonstrated whether they were coalesced or not. However, in *Ctenacodon* sp., figured by Simpson (1929, pl. 1, fig. 3), both buccal and lingual cusps are well preserved and separated.

EXPLANATION OF PLATE 1

Comparison of dentition in members of the allodontid line. All except 5 are SEM micrographs; 1–2 and part of 3 are stereo-pairs; all are epoxy resin casts. All specimens are from the Upper Jurassic Morrison Formation; note the lack of grooves and ridges and lack of cusp coalescence.

Fig. 1. *Psalodon fortis* (Marsh), YPM 11760; I2 and I3, lateral view; Quarry 9 of Simpson (1929), Como Bluff, Wyoming; ×5.

Figs 2–3. *Glirodon grandis* Engelmann and Callison, DINO 10822; holotype, occlusal view; Dinosaur National Monument, Utah. 2, fragment of the right side of the snout with broken I2, I3 and C. 3, left side of the palate with I2, alveolus for I3, C, P1–P5, M1 and M2; only the teeth P4-M2 are stereo-photographs. Both ×10.

Fig. 4. *Ctenacodon laticeps* (Marsh), YPM 11761; Como Bluff, Wyoming; left side of the maxilla with P1–P5, M1, M2, occlusal view; ×10.

Fig. 5. *Ctenacodon scidens* Simpson, YPM 10366; Como Bluff, Wyoming; right m1 and m2 (anterior is to the right) in buccal view; ×15.

PLATE 1
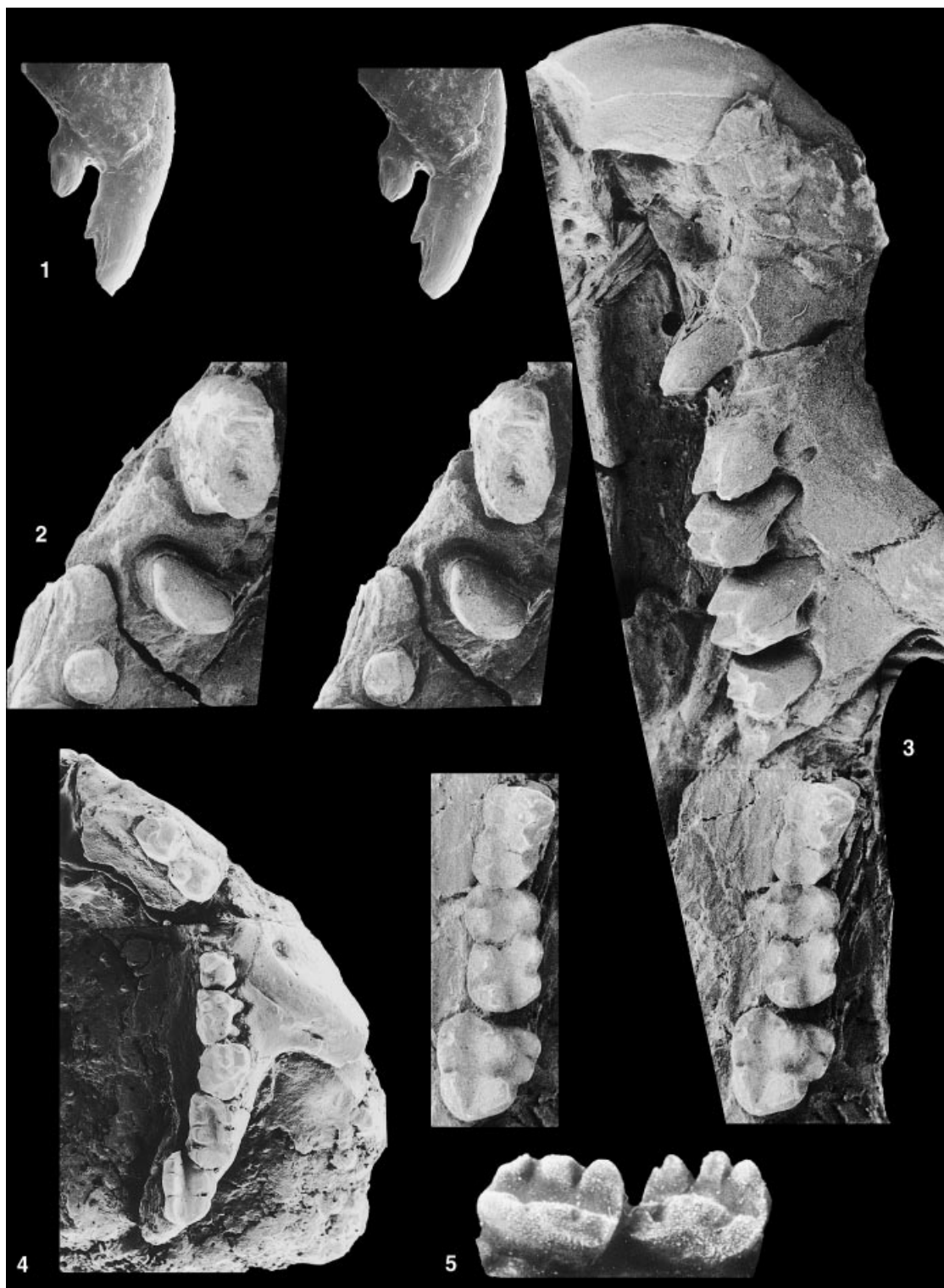
KIELAN-JAWOROWSKA and HURUM, multituberculates
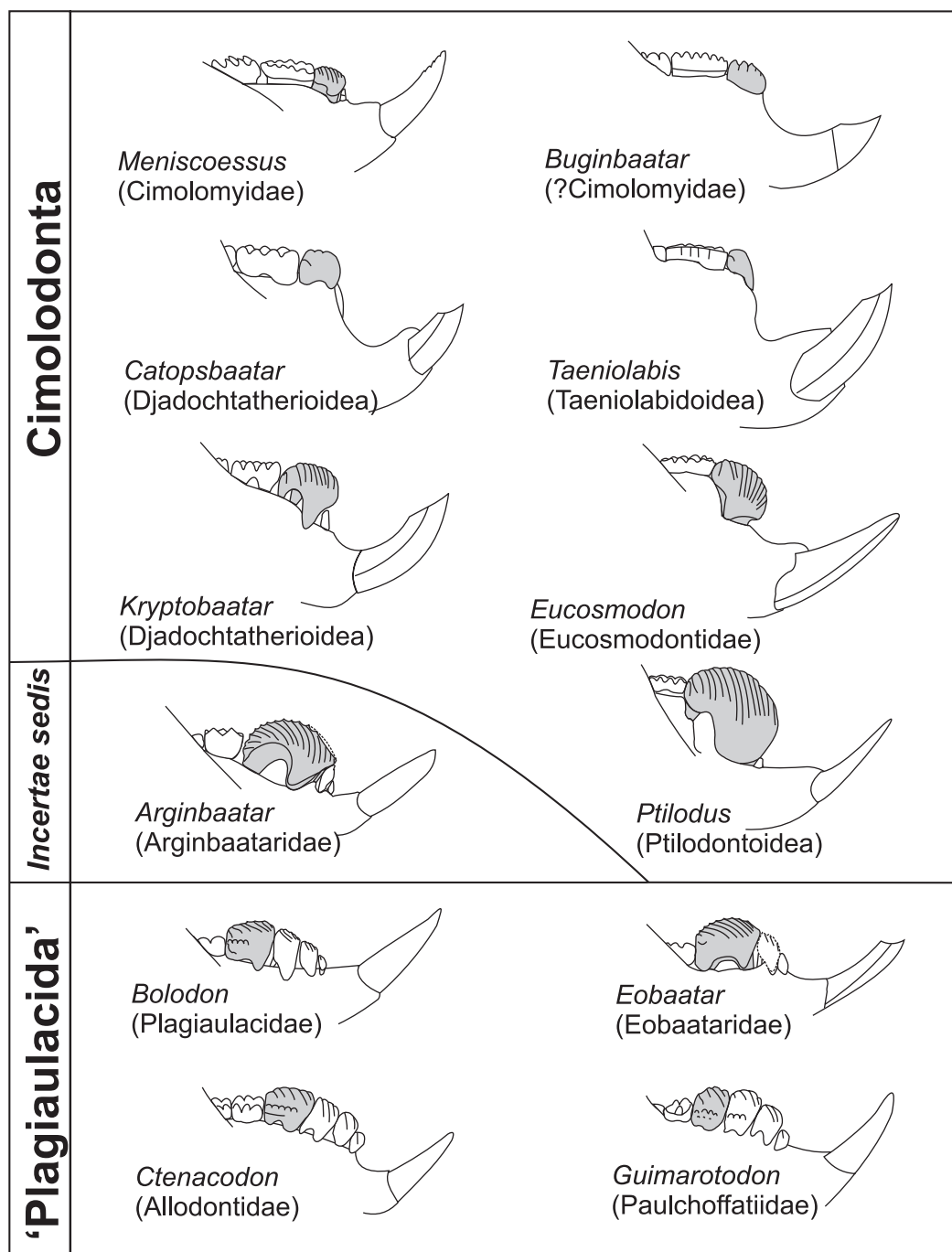
TEXT-FIG. 3. Diagrammatic comparison of lower dentitions exposed in buccal view of selected multituberculates. All jaws rendered to approximately the same length, p4 hatched. Reconstructions based on original material and casts, or modified from various sources.
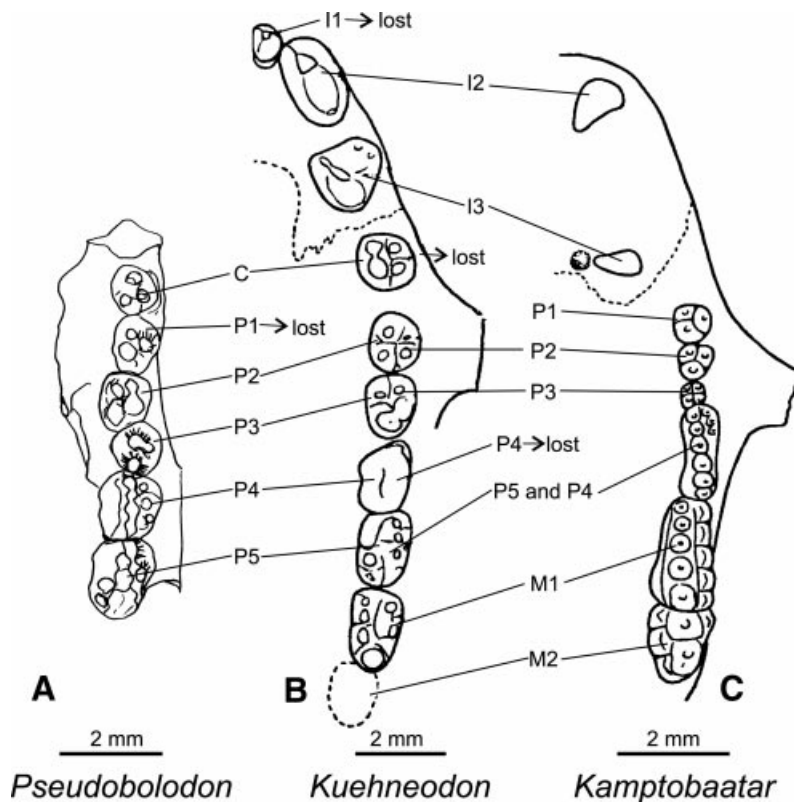
TEXT-FIG. 4. Comparison of the left upper dentition in palatal view, in Late Jurassic 'plagiaulacidans' (A–B) and a Late Cretaceous cimolodontan (C), showing tooth homology. We accept (following Hahn 1978) that in paulchoffatiid *Kuehneodon* P1 disappeared, but we follow Clemens (1963) in accepting that in Cimolodonta P1 is retained and 'plagiaulacidan' P4 has been lost. Dentition in A–C is based respectively on Hahn (1977), Hahn (1969), and Kielan-Jaworowska (1971).

Upper incisors are unknown in *Ctenacodon*. In *Psalodon,* I1 (not preserved) is small, I2 is enlarged and two-cusped, and I3 is small, with a strong main cusp and a minute basal cuspule (Pl. 1, fig. 1). In *Glirodon* I3 is single-cusped (Pl. 1, fig. 2). Simmons (1993) and Rougier *et al.* (1997) scored I3 of *Psalodon* together with *Paulchoffatia* and *Bolodon* as multicusped. This is misleading because the small I3 in *Psalodon* is very different from the enlarged, 3–4-cusped I3 in the Paulchoffatiidae and Plagiaulacidae. In addition Simmons (1993) and Rougier *et al.* (1997) mistakenly scored I3 in *Kuehneodon* (see Text-fig. 4), *Henkelodon*, and *Bolodon* as single-cusped.

The Allodontidae share with the Plagiaulacidae (homoplasy, number 4) the loss of the buccal cusps on p3, an increase in the length of p4 (Text-fig. 3), and an incipient posterolingual ridge on M1 (Pl. 1, fig. 4).

Zofiabaatar Bakker and Carpenter, 1990, assigned by Bakker (1992) to a monotypic family, Zofiabaataridae (see also Bakker 1998), is a specialised genus from the Morrison Formation, known only from the dentary with p1–p4 and m1. Carpenter (1998) assigned *Zofiabaatar* to the Plagiaulacidae. However, the Plagiaulacidae are characterised by lower molars with coalescing cusps, while in *Zofiabaatar* cusps are well-separated, as in the Allodontidae. We regard the Zofiabaataridae as belonging to the allodontid line.

Engelmann and Callison (1999) assigned *Glirodon* (numbers 16[1], 17[1]) from the Morrison Formation, to the Plagiaulacoidea *incertae sedis*. *Glirodon* retains the plesiomorphic 'plagiaulacidan' dental formula and

shares with the Allodontidae the structure of the upper premolars and molars (Pl. 1, figs 2–4). It differs from the Paulchoffatiidae and Plagiaulacidae in having a single-cusped I3. It is more advanced than *Ctenacodon* in the structure of M2 (with three rows of cusps), but less advanced in lacking incipient posterolingual ridges on M1. The gigantoprismatic enamel (unique for multituberculates among mammals: see Fosse *et al.* 1985; Carlson and Krause 1985), and lower and upper incisors with a limited enamel band, appear in *Glirodon* for the first time in multituberculate evolution. *Glirodon* shares these characters with the Early Cretaceous Mongolian *Eobaatar*, which belongs to the plagiaulacid line, and with numerous Cimolodonta (see below).

Paulchoffatiid line. The paulchoffatiid and plagiaulacid lines are more closely related to one another (numbers 6–8) than either of them is to the allodontid line. The shared derived characters of the two lines are enlarged I3 with 3–4 cusps, the structure of m2 with no buccal cusps, and ornamentation of at least the lower molars, however less constant and only incipient in the paulchoffatiid line. These three character states differentiate both lines from the allodontid line. However, in spite of the general similarity, the details of I3, p3, and m2 structure, as well as ornamentation, are different in the paulchoffatiid and plagiaulacid lines (numbers 9–10, 28).

Members of the paulchoffatiid line (as exemplified by Paulchoffatiidae) are more plesiomorphic in the structure of the dentary and lower premolars than members of the allodontid line. They retain plesiomorphic molar cusps of different height, but at the same time show features of specialisation in the structure of the upper incisors and lower molars. The autapomorphies of this line are an almost complete coalescence of cusps in m2, producing a basin-like tooth with only a single cusp in the Paulchoffatiidae, and enlarged 3–4-cusped I3, roughly quadrangular or trapezoid in occlusal view. Both m2 and I3 differ in details from other families of this line and from the Plagiaulacidae (see systematic palaeontology). Hahn (1971) accepted that a small I3 is plesiomorphic for multituberculates, while an enlarged I3 is apomorphic for the plagiaulacid and paulchoffatiid lines; we agree. This view, however, has been challenged by Van Valen (1976) who argued on the basis of isolated, presumably haramiyid incisors (possible plesiomorphic sister taxon of the Multituberculata) described by Parrington (1947) and Peyer (1956) that a multicusped I3 may be plesiomorphic for the Multituberculata. Among isolated incisors attributed to the Haramiyidae, Sigogneau-Russell (1989) described two types considered to be possible uppers, one of which was two-cusped, the other three-cusped, but of simpler structure than in the Paulchoffatiidae. On the other hand, the upper incisors in *Haramiyavia* (assigned by Jenkins *et al.* 1997 to the Haramiyidae; see also Butler 2000) are all single-cusped. Therefore it seems to us more probable that a single-cusped I3 or with a basal cuspule is plesiomorphic for the Multituberculata.

The Paulchoffatiidae are plesiomorphic in having a row of buccal cusps on p3 (absent in other families) and in being almost as long as p4 (Text-fig. 3). *Paulchoffatia* is unique among multituberculates in retaining a very low angle (7 degrees) between the tooth row and the longitudinal axis of the dentary (examined in dorsal view), and in this respect it is the most plesiomorphic of all known multituberculates. Molars and premolars may show complicated ornamentation. Hahn (1969, 1971) argued that the basin-like structure of m2 is apomorphic for the Paulchoffatiidae (the whole paulchoffatiid line in our division), and excludes the Paulchoffatiidae from the ancestry of the Cimolodonta. We follow this opinion (see also Hahn 1993) and regard the Paulchoffatiidae as a monophyletic dead-end of the 'Plagiaulacida'.

For descriptions of the two other families of the paulchoffatiid line, see the systematic section below.

Plagiaulacid line (numbers 3[2], 4[2], 5[2], 11[2], 12–14). Members of the plagiaulacid line, Plagiaulacidae, Eobaataridae (Text-fig. 3) and the tentatively assigned Albionbaataridae, are more advanced than those of the paulchoffatiid line. The Plagiaulacidae share with the Paulchoffatiidae the basic similarities in structure of I3 and m2, ornamentation of the enamel, incipiently developed in some representatives of the Paulchoffatiidae (Simpson 1928, 1929; Hahn 1969, 1993; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska and Ensom 1992), but differ in having several apomorphies (see systematic section). The plagiaulacid I3 is roughly triangular in occlusal view, with three cusps and the absence of the oblique ridge that is characteristic of the Paulchoffatiidae. They share with the paulchoffatiid line the coalescence of buccal cusps on m2, but differ in having separated lingual cusps and a longitudinal valley along the tooth

(Pl. 2, fig. 2), rather than having a basin-like m2. A tendency of molar cusps to coalesce, and distinct ornamentation of molar enamel with grooves, pits and ridges, incipient in the Paulchoffatiidae, is well expressed in the Plagiaulacidae and we regard it as characteristic of the plagiaulacid line (Pl. 2, figs 1–3; Pl. 3, figs 1–2). Another characteristic feature is the strong ribbing of the upper premolar cusps and cuspules (e.g. see Kielan-Jaworowska and Ensom 1992, pl. 4, figs 8–9), which is shared with some of the Paulchoffatiidae (e.g. *Kielanodon*; see Hahn 1987). The Plagiaulacidae also share with the Paulchoffatiidae a robust lower incisor and low position of the dentary condyle.

The Eobaataridae (numbers 16^3 17^2, and Text-fig. 3) are closely allied with the Plagiaulacidae as indicated by the structure of molars with coalescing cusps, grooves and ribbing on the molars (Pl. 2, figs 1–3; Pl. 3, figs 1–2) and strong ribbing and similar shape of the upper premolars (Kielan-Jaworowska *et al*. 1987, pls 4–5). They differ from the Plagiaulacidae by several apomorphies (see systematic section for description of the Eobaataridae and Albionbaataridae).

Arginbaataridae. We leave this specialised family (numbers 11^1, 15, 16^2, 18^1, 21^1, and Text-fig. 3), endemic to the Early Cretaceous of Mongolia, in the suborder *incertae sedis*, because it shows a mixture of characters of the 'Plagiaulacida' and the Cimolodonta (Trofimov 1980; Kielan-Jaworowska *et al.* 1987; see also systematic section). *Arginbaatar*, as seen in Text-figure 2, shares several characters with members of the allodontid line, and apparently has its origin within this group.

Cimolodonta

The Cimolodonta (numbers 2^2, 18^2, 19–20, 22), which embrace some Early Cretaceous (Aptian–Albian) and all the Late Cretaceous and Tertiary multituberculates, have prismatic enamel. They might be monophyletic, as argued by Simmons (1993), but see Archibald (1982) and Hahn and Hahn (1999*a*) for alternative opinions. They are well defined by at least five apomorphies (see systematic section and Text-figs 2–3). Their origin remains a mystery. It has not been demonstrated with any certainty which of the five upper premolars characteristic of the 'Plagiaulacida' disappeared in the line leading to the Cimolodonta. Clemens (1963) speculated that it was P4, while Hahn (1978, fig. 10) suggested that it was rather P1. In favour of G. Hahn's hypothesis, one may argue that the shortening of the cheek tooth row in mammals usually begins either from the anterior or from the posterior end. Hahn (1977) demonstrated that in *Kuehneodon*, a member of the Paulchoffatiidae, P1 has been lost, as there is a diastema between C and P2 (Text-fig. 4). However, the Paulchoffatiidae, as argued by Hahn (1993) and accepted herein, is not in the evolutionary line leading to the Cimolodonta. On the other hand there are examples in various mammal groups of loss of a tooth in the middle of the premolar series. Cifelli (2000) argued that in early eutherian mammals, which had five premolars, it was the middle one, referred to by him as px (fig. 1 in his paper), which was lost. Similarly in some Djadochtatherioidea (e.g. *Catopsbaatar* and *Tombaatar*) with three upper premolars, it was P2 and not P1 that disappeared, leaving a short diastema between P1 and P3. This loss of a tooth in the middle of the tooth row in these taxa gives additional support to Clemens' (1963) hypothesis, which is accepted here (Text-fig. 4).

Paracimexomys group. The most plesiomorphic of the Cimolodonta (and apparently paraphyletic) is a group of poorly known Aptian–Albian–Maastrichtian, mostly North American genera, referred to previously (e.g. Archibald 1982; Eaton and Cifelli 1988) as the *Paracimexomys* grade. Members of this group, *Paracimexomys* Archibald, 1982 and related forms, are known almost exclusively from isolated teeth (Lillegraven 1969; Sahni 1972; Archibald 1982; Eaton and Cifelli 1988; Eaton and Nelson 1991; Eaton 1995; Cifelli 1997). However, *Cimexomys*, which we only tentatively assign to this group, is known from almost complete upper and lower dentitions, and fragments of skull and dentary (Montellano *et al*. 2000). It has four upper premolars of cimolodontan pattern, a slender lower incisor, completely covered with enamel, p4 not protruding dorsally over the level of the molars, and molar cusps (especially in m2) showing a tendency to coalesce, with cusps covered with grooves. *Paracimexomys* and *Dakotamys*, assigned here, resemble the Eobaataridae in the structure of the upper and lower molars, with cusps showing a tendency to coalesce, and with ornamentation of grooves and ribs on the molars (compare Pl. 2,

figs 3–4, 6, 8 with Pl. 3, figs 2, 4, 6). Another genus, *Bryceomys* (Pl. 2, fig. 5; Pl. 3, figs 3, 5) shares with the two former genera the characteristic ornamentation of the molars and coalescence of cusps of m2, but differs in having the cusps of M2 separated.

Members of this group apparently differ from the Eobaataridae in having a slender lower incisor uniformly covered with enamel, or with enamel thinner on the dorsal side, but not sharply limited (Eaton 1995), and share with the Eobaataridae gigantoprismatic enamel. The similarities of isolated molars (especially M2) of *Paracimexomys*, *Bryceomys* and *Dakotamys* to *Eobaatar* are striking (see Plate 3). However, the genera of the *Paracimexomys* group differ from *Eobaatar* and other members of the plagiaulacid line, in having an arcuate, rather than a rectangular p4 and a cimolodontan dental formula. Ornamentation of molars and molar cusp arrangement (especially on M2) of the members of *Paracimexomys* group, are also similar to those of the Ptilodontoidea, discussed in the next section.

On the other hand, the genera of the *Paracimexomys* group share a small number and similar arrangement of cusps on M1 with some Djadochtatherioidea, for example with *Kryptobaatar*, *Sloanbaatar* and *Chulsanbaatar* (e.g. see Pl. 3, figs 3, 7, 9). Also P4s of the members of this group, figured by Eaton (1995), are strikingly similar to P4s in the Djadochtatherioidea (e.g. Kielan-Jaworowska 1970, 1974; Kielan-Jaworowska and Hurum 1997). It follows that the *Paracimexomys* group embraces forms intermediate in some respects between the plagiaulacid line and at least some Cimolodonta.

Origin of the Ptilodontoidea, Cimolomyidae and Boffiidae. In all of the 'Plagiaulacida' the cutting edge of p4 is above the level of the molars (Text-fig. 3). Among the Cimolodonta, only in the Ptilodontoidea does the p4 protrude dorsally over the level of the molars; however, it differs considerably from that in the 'Plagiaulacida', where it is rectangular. The arcuate, strongly enlarged p4, with numerous ridges and serrations, is an apomorphy of the Ptilodontoidea (number 23). The presence of uniform enamel on the lower incisor is a plesiomorphic character, albeit the gracile incisor is an apomorphy of the Ptilodontoidea (number 24).

The Ptilodontoidea are the only Cimolodonta that share with the *Paracimexomys* group the coalescence of molar cusps associated with grooves, which is also characteristic of the plagiaulacid line (see figures in Fox 1971; Krause 1977; Vianey-Liaud 1986, and many others; discussion in Krause *et al.* 1992; Pl. 2, figs 9–10; Pl. 3, figs 8, 10). *Cimolodon* seems to be more closely related to the *Paracimexomys* group than are other ptilodontoideans (e.g. compare M1 of *Cimolodon electus* in Fox 1971, fig. 5, with our

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EXPLANATION OF PLATE 2

Comparison of lower molars of selected multituberculates, oriented with anterior margin up except for 3–4, in which anterior margin is to the right. SEM micrographs; all except 3–4 are stereo-pairs. All are in occlusal view except 4, which is in lingual view; all except 2–3 and 6 are epoxy resin casts. Note grooves and ribbing and/or cusp coalescence at least in peripheral aspect, in all except the specimen in 7.

Figs 1–2. *Bolodon osborni* Simpson. 1, DORCM GS4; left m1. 2, DORCM GS 206; left m2. Purbeck Limestone Group (Berriasian), Sunnydown Farm Quarry, Langton Matravers, southern England. Both ×20.

Figs 3–4. *Eobaatar magnus* Kielan-Jaworowska *et al.*, PIN 3101/53; left m1 and m2 in fragment of a dentary in two views; Khoboor beds (Aptian or Albian), Khoboor, Guchin Us county, Gobi Desert, Mongolia. Both ×15.

Fig. 5. *Bryceomys fumosus* Eaton, OMNH 25448; left m2; Straight Cliffs Formation, Smoky Hollow locality, south-western Utah; ×20.

Figs 6, 8. *Paracimexomys* sp. cf. *P. robinsoni* Eaton and Nelson. 6, MNA V 6365; right m2. Dakota Formation (Cenomanian), locality 1067 of Eaton (1995), south-western Utah; ×20. 8, MNA V 7473, left m1; Straight Cliffs Formation (Turonian), Smoky Hollow, locality 995 of Eaton (1995), south-western Utah; ×10.

Fig. 7. *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/8; right m1 and m2; Djadokhta Formation (?lower Campanian), Bayn Dzak, Gobi Desert, Mongolia; ×10.

Fig. 9. *Ptilodus montanus* Douglass, AMNH 35271; left m1 and m2; Fort Union Formation (lower Tiffanian), Gidley Quarry, Crazy Mountains Field, Montana; ×10.

Fig. 10. *Parectypodus laytoni* (Jepsen), PU 14162; left m1 and m2; Fort Union Formation (lower Tiffanian), Princeton Quarry, Clark Fork Basin, Wyoming; ×24.

PLATE 2
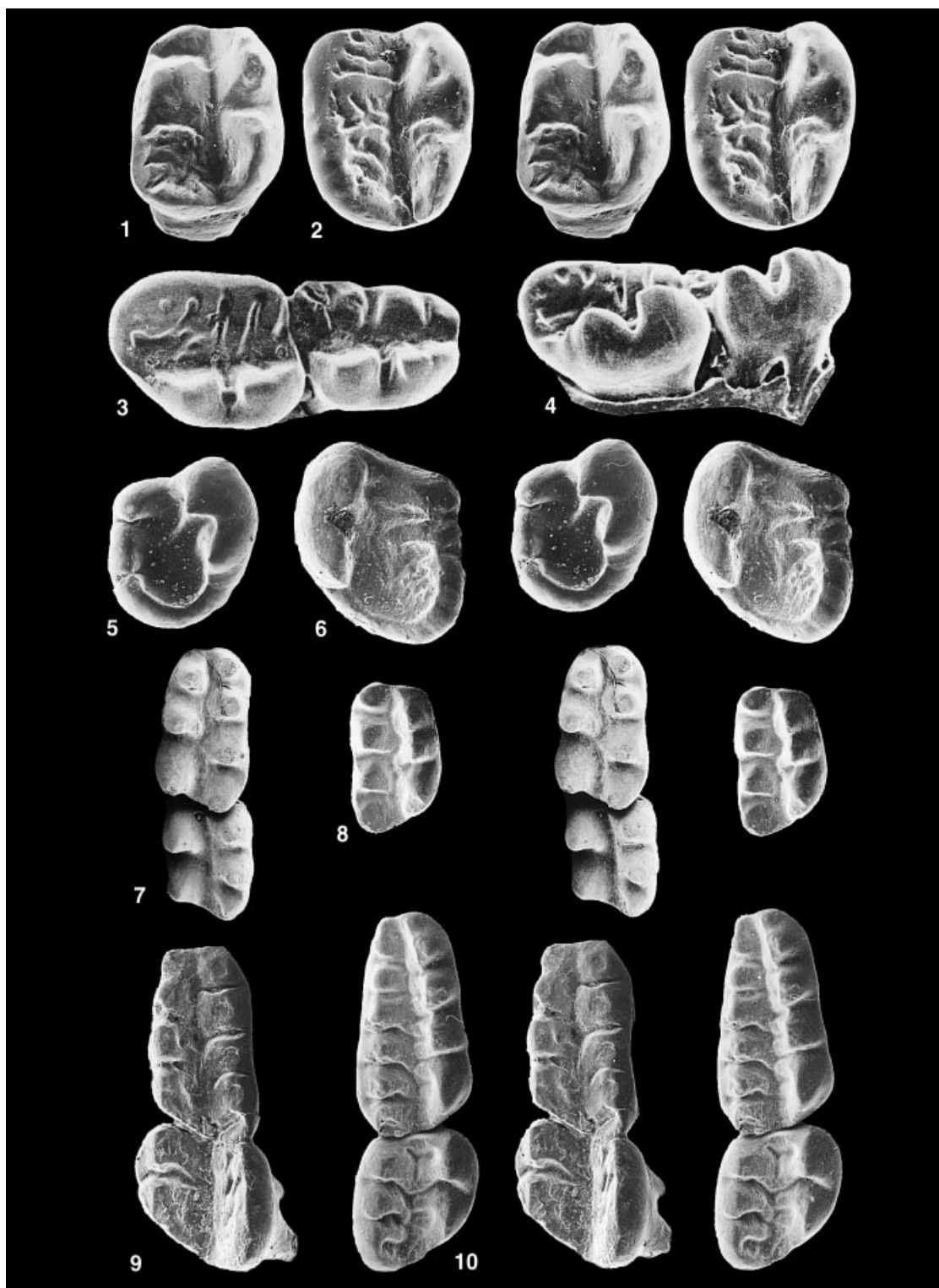
KIELAN-JAWOROWSKA and HURUM, multituberculates

Pl. 3, figs 5–6). The Cimolodontidae, to which Hahn and Hahn (1983) referred *Cimolodon*, *Anconodon*, and *Liotomus*, are assigned to the Ptilodontoidea, with which they share a very high p4, protruding dorsally over the level of the molars and slender lower incisor, completely covered with enamel (Clemens 1963; Lillegraven 1969). *Cimolodon* differs from other cimolodontid genera in retaining gigantoprismatic enamel, which is a more plesiomorphic character than the microprismatic (Carlson and Krause 1985). We suggest that the Ptilodontoidea acquired microprismatic enamel (number 27) after separation of *Cimolodon* (which we tentatively assign to the Ptilodontoidea) from the main ptilodontoidean line.

On the basis of the foregoing comparisons we suggest that the Ptilodontoidea originated from among the plagiaulacid line, the intermediate links being forms close to the Eobaataridae and *Paracimexomys* group. *Eobaatar* apparently had a limited enamel band on the lower incisor, and therefore cannot be related to the Ptilodontoidea. However, as a limited enamel band made its appearance several times in multituberculate evolution, one can imagine the existence of forms close to eobaatarids with their incisors completely covered with enamel, especially in so far as such incisors are characteristic of the *Paracimexomys* group (Eaton 1995; Montellano *et al.* 2000).

The similarities of the *Paracimexomys* group to *Eobaatar* on the one hand and the Ptilodontoidea (*Cimolodon*) on the other, have also been recognised by Eaton (1995), who noted that members of this group share with *Eobaatar* an alternating arrangement of cusps on M1. With respect to the similarity to the Ptilodontoidea he stated (p. 782): '*Dakotamys* could be considered morphologically transitional between *Paracimexomys* and *Cimolodon*. Both *Dakotamys* and *Cimolodon* have a pocket labial to the anteriormost cusps of the external row of M1, *Dakotamys* shows some tendency toward the ribbed pyramidal cusps and pitted valleys found in some species of *Cimolodon*, and both taxa have straight central valleys on M1s'.

Neoliotomus Jepsen, 1930, previously assigned to the Eucosmodontidae (see Krause 1982*b*), shares with the Ptilodontoidea microprismatic enamel and p4 protruding dorsally over the level of the molars. It differs from other Ptilodontoidea in having a very robust lower incisor with a limited enamel band (number 17^3). But as a limited enamel band made its appearance several times in multituberculate evolution (Text-fig. 2), it is possible that it appeared also in a ptilodontoid. On this basis we assign *Neoliotomus* tentatively to the Ptilodontoidea.

Another genus with microprismatic enamel, which was originally assigned to Eucosmodontidae, is *Xyronomys* Rigby, 1980. It is incompletely known, represented only by p4 and P4. Its eucosmodontid attribution was based on the presence of a low, roughly triangular p4. Because of its possession of microprismatic enamel we assign it to the Neoplagiaulacidae within the Ptilodontoidea.

EXPLANATION OF PLATE 3

Comparison of upper molars of selected multituberculates, oriented with anterior margin up and in occlusal view. SEM micrographs except for 2; all except 7 are stereo-pairs; all are epoxy resin casts except for 2, 7, and 9. Note grooves and ribbing and/or cusp coalescence at least in peripheral aspect, in all except the specimens in 7 and 9.

Fig. 1. *Bolodon osborni* Simpson, BMNH 47735A; right M1 and M2; Purbeck Limestone Group (Berriasian), Marly Freshwater Member, Durlston Bay, near Purbeck, Swanage, southern England; ×20.

Fig. 2. *Eobaatar magnus* Kielan-Jaworowska *et al.*; PIN 3101/62; right M2; Khoboor beds (Aptian or Albian), Khoboor, Guchin Us county, Gobi Desert, Mongolia; ×15.

Figs 3, 5. *Bryceomys fumosus* Eaton. 3, MNA V7427; right M1; Straight Cliffs Formation (Turonian), Smoky Hollow Member, locality 795 of Eaton (1995), south-western Utah. 5, MNA V 7404; left M2; same horizon and locality. Both ×20.

Figs 4, 6. *Dakotamys malcolmi* Eaton. 4, MNA V6232; right M1; Dakota Formation (Cenomanian), locality 1067 of Eaton (1995), south-western Utah. 6, MNA V 5392; right M2; same horizon, locality 1064 of Eaton (1995). Both ×20.

Figs 7, 9. *Kryptobaatar dashzevegi* Kielan-Jaworowska. Djadokhta Formation (?lower Campanian), Bayn Dzak, Gobi Desert, Mongolia. 7, ZPAL MgM-I/ 52; left M1. 9, ZPAL MgM-I/8; left M1 and M2. Both ×10.

Fig. 8. *Ptilodus kummae* Krause, UA 10330 (right M1) and UA 9837 (right M2), composite; Ravenscrag Formation (Tiffanian), Roche Percée, Saskatchewan, Canada; ×10.

Fig. 10. *Neoplagiaulax hazeni* (Jepsen), PU 14432; right M1 and M2; Fort Union Formation (lower Tiffanian) Princeton Quarry, Clark's Fork Basin, Wyoming; ×10.

PLATE 3
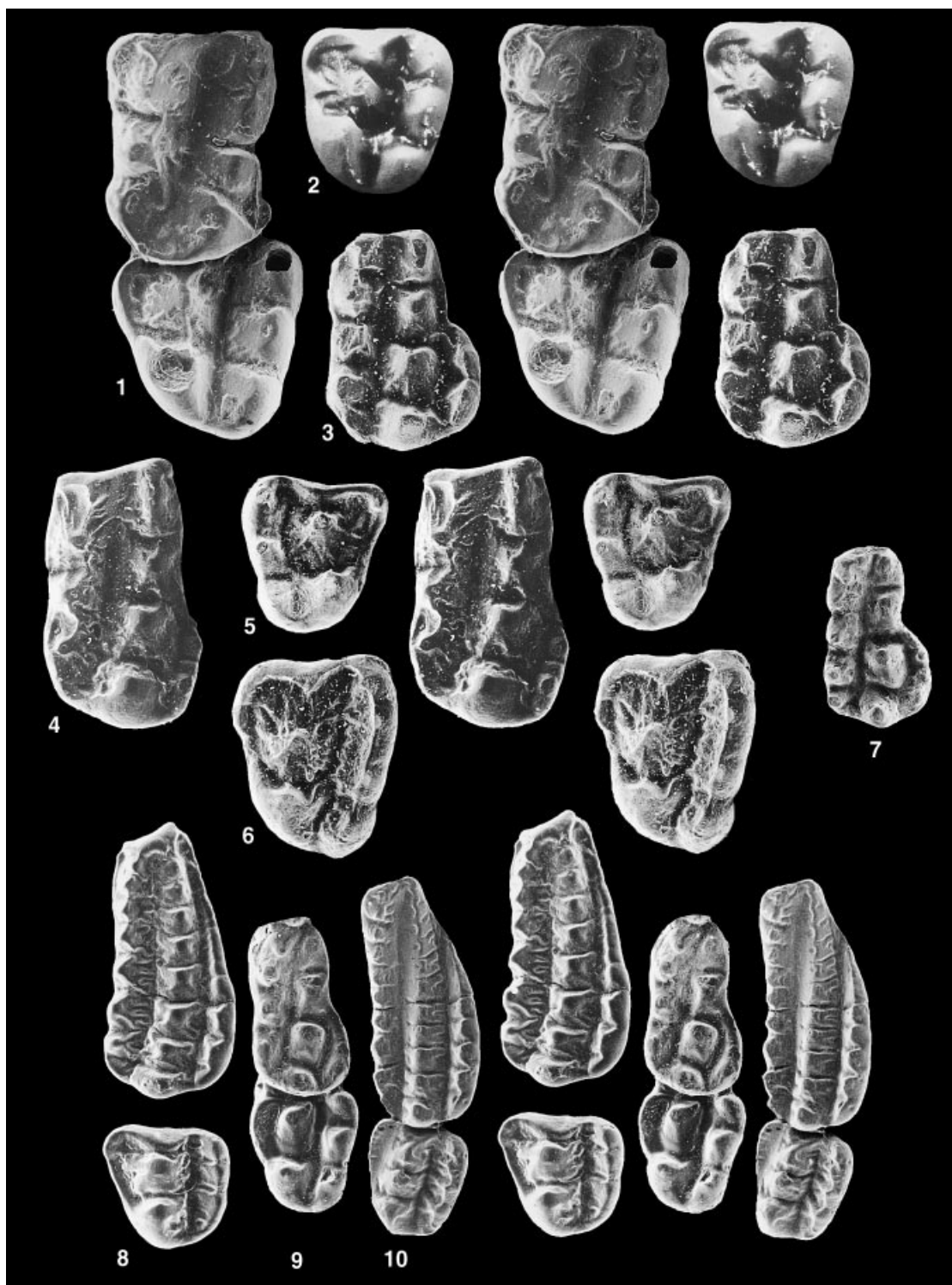
KIELAN-JAWOROWSKA and HURUM, multituberculates

The Cimolomyidae (number 25), of which the best known is *Meniscoessus*, approach the Ptilodontoidea in having the lower incisor completely covered with enamel, albeit in the Cimolomyidae it is robust (which is a plesiomorphic character), rather than slender as in the Ptilodontoidea. Another similarity is ornamentation; e.g. see the photographs of upper and lower molars of *Meniscoessus* in Sahni (1972) and Fox (1976, 1980), which show heavily ribbed cusps with groove-like valleys between the ribs. The same applies to *Cimolomys* (Archibald 1982). The tentatively assigned *Essonodon* differs from other multituberculates in having transverse ridges between the molar cusps and shares this character only with a gondwanatherian *Ferugliotherium* (Krause *et al*. 1992). The Cimolomyidae differ from the Ptilodontoidea in having differently built upper dentition with a strongly reduced upper premolar row and crescentic molar cusps. The p4 is small and low, very different from the enlarged p4 in the Ptilodontoidea, and resembles rather that in the Djadochtatherioidea (Text-fig. 3). We tentatively assign to the Cimolomyidae the incompletely known Asian *Buginbaatar* (Kielan-Jaworowska and Sochava 1969; Trofimov 1975; see also Text-fig. 3). As the Cimolomyidae are generally poorly known, their origin from members of the *Paracimexomys* group (with which they share ornamentation) remains uncertain.

Boffius (number 26), a relatively large taxon with upper molars bearing three rows of cusps, was originally assigned to the Ptilodontoidea. Hahn and Hahn (1983) erected the family Boffiidae within the Ptilodontoidea. Carlson and Krause (1985) demonstrated that *Boffius* has gigantoprismatic enamel. McKenna and Bell (1997) assigned to the Boffiidae the rank of a tribe Boffiini; they attributed to the Boffiini four genera, *Boffius, Essonodon, Liotomus* and *Neoliotomus*. We regard the Boffiidae as a monotypic family, assigned to superfamily *incertae sedis*. The Boffiidae resemble the Cimolomyidae in an increase in number of molar cusps and grooves and ridges on P4 and M1. Vianey-Liaud (1986, fig. 56) derived *Boffius* from the Cimolomyidae. As in the case of the Cimolomyidae the origin of the Boffiidae from the *Paracimexomys* group (with which they share ornamentation) is uncertain.

Origin of the Djadochtatherioidea, Eucosmodontidae, Microcosmodontidae, Taeniolabidoidea, and Kogaionidae (numbers 17^4, 29^2, 30^2). The origin of these five groups appears to be more enigmatic than those previously discussed. We did not find apomorphies that would allow uniting the five groups in question into a higher rank taxon. They share with one another a limited enamel band on the lower incisor (except some Djadochtatherioidea), a character which also occurs in some 'Plagiaulacida' and the ptilodontoidean *Neoliotomus*. Other characters uniting them are shared with all other cimolodontans. Members of these subgroups differ from the *Paracimexomys* group, the Ptilodontoidea, Cimolomyidae, and Boffiidae in lacking enamel ornamentation (except for upper incisors in some cases and anterior upper premolars, which might be ribbed) and in having well-separated molar cusps. The most plesiomorphic of these five groups are perhaps the Djadochtatherioidea, some members of which (e.g. *Kryptobaatar*), share with members of the *Paracimexomys* group a small number of cusps and general shape of m1, and of upper premolars and molars (compare Pl. 2, figs 7–8; Pl. 3, figs 3, 7, 9). They differ, as mentioned above, in lacking ornamentation and in having well-separated molar cusps.

The Djadochtatherioidea and Eucosmodontidae approach one another in some characters of the dentary and skull, which in the Eucosmodontidae is known only from a single, incomplete rostrum of *Stygimys* (Sloan and Van Valen 1965). Resolving the problem of Djadochtatherioidea-Eucosmodontidae relations is not possible as long as the details of the upper dentition and skull structure of eucosmodontids remain largely unknown.

Sloan and Van Valen (1965) assigned the Eucosmodontidae, Taeniolabididae, and Cimolomyidae to their suborder Taeniolabidoidea (now a superfamily). We agree with Fox (1999) that there are no apomorphies uniting the Taeniolabidoidea *sensu* Sloan and Van Valen (1965), and we restrict it to the Taeniolabididae.

The superfamily assignment of the aberrant Late Cretaceous–Palaeocene European family Kogaionidae Râdulescu and Samson, 1996, of which the dentary and lower dentition remain unknown, cannot be resolved. The skull shape is similar to that of the Taeniolabidoidea in being roughly rectangular (Costin Râdulescu, pers. comm. 1999), but the upper dentition differentiates them from all other multituberculates. The Palaeocene-Cretaceous genus *Hainina*, known from Belgium (Vianey-Liaud 1979), France (Vianey-Liaud 1986), and Romania (Csiki and Grigorescu 2000), shows in the general morphology of the molars

some resemblance to those of *Kogaionon*, as suggested by the latter authors. *Hainina* was originally assigned by Vianey-Liaud (1979) to the ?Cimolomyidae and Carlson and Krause (1985) demonstrated that it has gigantoprismatic enamel, which has also recently been found in *Kogaionon* (G. Fosse and C. Râdulescu, pers. comm. 2000). We assign *Hainina* to the Kogaionidae (superfamily *incertae sedis*); it differs from *Kogaionon* in having ornamented enamel, while the enamel is smooth in *Kogaionon*.

If the Cimolodonta are monophyletic (Text-fig. 2), one should search for the closest relatives of these five subgroups within the plagiaulacid line, perhaps via the *Paracimexomys* group. It would be difficult to visualise the origin of forms with well-separated molar cusps and smooth enamel from such forms as *Paracimexomys* and *Dakotamys,* in which discrete buccal cusps, e.g. in m2, disappeared. However, one observes in some teeth of members of the *Paracimexomys* group (e.g. M2, but not m2 of *Bryceomys*; see Pl. 2, fig. 5) the separation of cusps. Another possible candidate close to ancestral forms of the discussed cimolodontans might be the poorly known Mongolian Early Cretaceous *Monobaatar*, which has well-separated molar cusps (Kielan-Jaworowska *et al*. 1987), and which has been only tentatively assigned to the Eobaataridae.

SYNOPSIS

The cladogram presented in Text-figure 2 shows a very high level of homoplasy in multituberculate evolution. Several characters appear two, three or four times (or perhaps even more; e.g. acquisition of a limited enamel band on the lower incisor).

The Cimolodonta as defined herein are characterised by at least five apomorphies (numbers 2^2, 18^2, 19–20, 22 in Text-fig. 2). Algorithm-based analyses (Simmons 1993; Rougier *et al.* 1997) have supported the monophyly of the Cimolodonta, although these authors did not suggest which 'plagiaulacidan' subgroup may be ancestral to them. In Text-figure 2 we offer a hypothesis accepting that the Cimolodonta are monophyletic, and originated from among the plagiaulacid line, the *Paracimexomys* group being in some respects intermediate between 'plagiaulacidans' and the remaining cimolodontans. According to this hypothesis, the origin of two superfamilies (Djadochtatherioidea and monotypic Taeniolabidoidea) and three families (Eucosmodontidae, Microcosmodontidae and Kogaionidae) from among known members of the *Paracimexomys* group would require the disappearance of a tendency for coalescence of molar cusps (acquisition of separate cusps) and the disappearance of the ornamentation of grooves and ridges on the molars (acquisition of smooth enamel)**.** However, it cannot be excluded that they originated from unknown members of this group, characterised by molars with well-separated cusps and smooth enamel. As we accept that the Haramiyida are a sister-group of the Multituberculata, and as a tendency to coalescence and incipient ornamentation does not occur in the Haramiyidae (although it is characteristic of the Theroteinidae), the separated cusps and smooth enamel are regarded as plesiomorphic.

One can also visualise another hypothesis, less probable in our opinion, that five cimolodontan units, in polytomy, united in our cladogram by numbers 17^4, 29^2, 30, originated separately from all other Cimolodonta from among the allodontid line (Pl. 1), with which they share smooth enamel, lack of coalescence of molar cusps and single-cusped I3. This would require acceptance that five or more synapomorphies of the Cimolodonta made their appearance in parallel twice, which seems highly improbable.

The origin of two types of prismatic enamel is one of the stumbling blocks in understanding the roots and interrelationships of the Cimolodonta. Wood *et al.* (1999, p. 203) stated: '... no extant animals are known to have gigantoprisms. No living ameloblasts large enough to secrete enamel into a single gigantoprism have been observed. The ontogeny of gigantoprisms therefore remains a mystery, as does any possible mechanism for the conversion of one to a small prism, or vice versa'. Carlson and Krause (1985) demonstrated that some species of *Microcosmodon* (family Microcosmodontidae) have both micro- and gigantoprisms in their enamels, which, however, does not elucidate the problem of the origin of enamel.

Hahn and Hahn (1999*a*) argued that an independent double origin of gigantoprismatic enamel appears improbable. We agree, but for the time being we cannot otherwise explain the presence of giganto-prismatic enamel in *Eobaatar*, a member of the plagiaulacid line, and in *Glirodon*, which is a member of the allodontid line, in view of the fact that the primitive members of these two lines have prismless enamel.

It is possible that future discoveries will reveal forms with gigantoprismatic enamel ancestral to both *Eobaatar* and *Glirodon.* So far, however, such forms remain unknown.

According to our hypothesis microprismatic enamel made its appearance only once in multituberculate evolution, *contra* Krause and Carlson (1986, 1987) and Clemens (1997). The latter author suggested that microprismatic enamel evolved from the gigantoprismatic type as many as three and possibly four times.

We are aware that the cladogram presented by us is inconclusive, because many taxa are known only from fragments. The origin of the Cimolodonta must remain unresolved until more missing links between the 'Plagiaulacida' and the Cimolodonta are found. The missing links needed should be searched for in the Upper Jurassic, Lower Cretaceous and lower Upper Cretaceous deposits. In view of this, it is astonishing that the collection of Trinity (Albian) multituberculates from Texas, assembled almost half a century ago, remains undescribed.

Hahn and Hahn (1999*a*) proposed a different scenario of cimolodontan origins. They argued (p. 136) that: 'The Ptilodontoidea can be derived structurally without difficulties from the Allodontidae, the Taeniolabidoidea from forms close to the Eobaataridae (but with the buccal cusps on m$_2$ preserved)'. There are, however, no characters known that would ally the Allodontidae more closely with the Ptilodontoidea than with other Cimolodonta. On the contrary, as discussed above, we believe that if the Cimolodonta were diphyletic, the Ptilodontoidea would have their roots among the plagiaulacid line, while five cimolodontan groups placed in our cladogram in polytomy (which with the exclusion of the Kogaionidae belong to the former suborder Taeniolabidoidea) would be allied to the allodontid line.

On the basis of the foregoing discussion we offer a classification of the Multituberculata presented in the next section. This classification is asymmetrical as the 'Plagiaulacida' are divided into families, while the Cimolodonta are divided into superfamilies. It would be possible to assign, for example, a superfamily rank to the three informal lines within the 'Plagiaulacida' recognised by us. We regard, however, assigning superfamily rank to 'plagiaulacidan' lines premature, pending further discoveries, which might cast new light on the problem of multituberculate interrelationships.

SYSTEMATIC PALAEONTOLOGY

Order MULTITUBERCULATA Cope, 1884

Diagnosis. Monophyletic order of the subclass Allotheria Marsh, 1880 characterised by multicusped premolars and molars, covered with longitudinal rows of low cusps of subequal height (except Paulchoffatiidae and Pinheirodontidae where molar cusps may differ in height). Three or two upper incisors, upper canine present only in a few early taxa, five upper premolars in most 'Plagiaulacida' (two 'plagiaulacidan' genera have four upper molars), 4–1 in Cimolodonta; two upper molars; single lower incisor, no lower canine, 4–1 lower premolars and two lower molars. M2 shifted lingually with respect to M1, lower premolars blade-like, with serrated upper margin and oblique ridges that extend along the buccal and lingual surfaces. The skull differs from those of most therian mammals in being wide and dorsoventrally rather than laterally compressed. Jugal placed on the medial side of the zygomatic arch, cochlea bent but not coiled; three ear ossicles as in other mammals. Multituberculates had a backward power stroke of the mandible, which resulted in a more anterior insertion of the masticatory muscles than in any other mammal group. Epipubic bones present, pelvis very narrow, with pubes and ischia fused ventrally to form a keel, calcaneo-Mt V contact in ankle joint; they had a sprawling posture. Multituberculate brain, referred to as cryptomesencephalic, is characterised by lack of midbrain exposure on the roof, deep vermis deeply inserted between the cerebral hemispheres, and very large parafloculi. This type of brain occurs also in eutriconodonts, and is different from that of therian mammals. Most multituberculates were small, of shrew or rat size, an exception being the Palaeocene *Taeniolabis* of beaver size.

Suborders. 'Plagiaulacida' Simpson, 1925 [*nomen correctum* McKenna, 1971 *ex* Plagiaulacoidea]; Cimolodonta McKenna, 1975; suborder *incertae sedis*: family Arginbaataridae G. Hahn and R. Hahn, 1983.

Distribution. ?Middle Jurassic (Bathonian) to lower Tertiary (Eocene) of the Northern Hemisphere and Gondwana, except the Australian region and Antarctica. Until recently the oldest uncontested multituberculates were from the Kimmeridgian of Portugal. Freeman (1976) described from the Middle Jurassic Forest Marble of Dorset, England, a strongly worn, three-rooted tooth, and from the Middle Jurassic of Oxfordshire (1979) an incisor, which might be records of multituberculates. P. M. Butler (pers. comm. 1999) informed us that in the collection from the Bathonian Forest Marble at Kirtlington, Oxfordshire, housed in The Natural History Museum, London, there are isolated multituberculate upper and lower premolars (see also Kermack *et al.* 1998 for description of multituberculate-like teeth from Kirtlington). The only named pre-Bathonian multituberculate is *Mojo*, represented by an incomplete ?upper premolar (Hahn *et al.* 1987); its attribution to the Multituberculata remains uncertain. Given the scant record and the great hiatus between *Mojo* and the first uncontested multituberculates, we restrict the distribution of the Multituberculata to a Middle Jurassic origin. Argentinean Late Cretaceous Ferugliotheriidae, assigned previously to the Multituberculata (e.g. Krause *et al.* 1992) are now regarded as Mammalia *incertae sedis* (Pascual *et al.* 1999). We accept this attribution with the exclusion of a few specimens described as ?*Ferugliotherium*. These are: a dentary with blade-like premolar (Kielan-Jaworowska and Bonaparte 1996) and upper premolars (Krause *et al.* 1992), which show multituberculate affinities. These poorly known specimens (not discussed herein) demonstrate that a branch of multituberculates apparently lived during the Late Cretaceous in South America.

Suborder 'PLAGIAULACIDA' Simpson, 1925
[*nomen correctum* McKenna, 1971 *ex* PLAGIAULACOIDEA]

Diagnosis. Plesiomorphic, paraphyletic suborder of Multituberculata with dental formula: 3.1-0.5-4.2 / 1.0.4-3.2. The p4 is blade-like, rectangular in lateral view, with a row of buccal cusps (single cusp in Eobaataridae, cusps missing or replaced by pits in some Pinheirodontidae). I2 enlarged and 2-cusped, I3 either enlarged 3–4-cusped, or small single-cusped or with a main cusp and basal cuspule; canine, if present, premolariform; 5–4 upper premolars, 4–3 lower premolars, p3 in buccal view primitively rectangular, triangular in later forms; third lingual row of cusps in M1 absent or developed as incipient, smooth posterolingual ridge. Lower incisor completely covered with enamel (except *Glirodon* and *Eobaatar*), enamel prismless (except *Glirodon* and *Eobaatar*, which have gigantoprismatic enamel). Dentary condyle placed on the level of the molars and facing posteriorly in all of the groups in which it is known, except for Zofiabaataridae.

Families. Allodontidae Marsh, 1889; Zofiabaataridae Bakker, 1992; Paulchoffatiidae G. Hahn, 1969; Hahnodontidae Sigogneau-Russell, 1991; Pinheirodontidae G. Hahn and R. Hahn, 1999*a*; Plagiaulacidae Gill, 1872; Albionbaataridae Kielan-Jaworowska and Ensom, 1994; Eobaataridae Kielan-Jaworowska *et al.*, 1987; and *Glirodon* Engelmann and Callison, 1999, assigned to 'Plagiaulacida' *incertae sedis*.

Distribution. ?Middle Jurassic (Bathonian)–Lower Cretaceous (Barremian) of Europe; Upper Jurassic of North America; Lower Cretaceous (Aptian or Albian) of Asia; Lower Cretaceous (?Berriasian) of Morocco.

Allodontid line

Comment. Informal group erected to include the families Allodontidae Marsh, 1889; Zofiabaataridae Bakker, 1992; and *Glirodon* Engelmann and Callison, 1999, assigned to 'Plagiaulacida' *incertae sedis*.

Family ALLODONTIDAE Marsh, 1889

Diagnosis. Dental formula 3.0.5.2/1.0.4.2. I1 small, I2 large two-cusped, I3 small, spatulate, or with main cusp and a small cuspule. Differ from Plagiaulacidae in having P4 and P5 with no or a single buccal cuspule and shorter in relation to M1. Share with the Plagiaulacidae (homoplasy) incipient posterolingual ridge on M1. The p3 lacks buccal cusps (characteristic of the Paulchoffatiidae) rectangular in buccal view; p4 about 1·5 times longer in buccal aspect than p3. Differ from the Plagiaulacidae and share with the

Paulchoffatiidae anterior lower premolars quadrangular rather than triangular in buccal view. Differ from the Paulchoffatiidae, Plagiaulacidae, and Eobaataridae in having lower molars with two rows of subequal, well-separated cusps, without traces of coalescence (plesiomorphy), and lack of ornamentation of grooves and ridges on the posterior upper premolars and molars (except *Psalodon*, which has distinctly ornamented upper premolars).

Genera. Ctenacodon Marsh, 1879; *Psalodon* Simpson, 1926; not *Ctenacodon brentbaatar* Bakker, 1998.

Distribution. Upper Jurassic (Morrison Formation) of North America.

Family ZOFIABAATARIDAE Bakker, 1992

Diagnosis. Monotypic family (*Zofiabaatar* Bakker and Carpenter, 1990, type genus). Only the dentary is known, dental formula 1.0.4.2. Differ from Allodontidae in having p4 distinctly longer than p3, and share this character and structure of the premolars with Plagiaulacidae. Differ from Allodontidae and Plagiaulacidae in having very short m1 with two cusps in two rows, and from Plagiaulacidae in having lower molar cusps separated. *Zofiabaatar* differs from all 'plagiaulacidans' in having the condyle facing upwards, rather than posteriorly, and shares this character with some advanced Djadochtatherioidea and Taeniolabidoidea. It differs also from other 'plagiaulacidan' genera in having strongly enlarged pterygoid fossa.

Distribution. Upper Jurassic Morrison Formation of North America.

Family *incertae sedis*
Genus GLIRODON Engelmann and Callison, 1999

Diagnosis (emended after Engelmann and Callison 1999). Monotypic genus (*G. grandis* Engelmann and Callison, 1999, type species). Differs from other 'plagiaulacidans' (except *Eobaatar*) in having restricted enamel on lower incisor and I2; differs from the Paulchoffatiidae and Plagiaulacidae in having single-cusped I3; shares with the Allodontidae structure of the lower molars with two rows of separate cusps (not coalesced), but differs from them in having M1 without incipient posterolingual ridge and in having an advanced structure of M2 with a third row of cusps. Differs from the Cimolodonta in having a complete plesiomorphic dental formula 3.1.5.2/1.0.4.2. Differs from 'plagiaulacidans' (except *Eobaatar*) and shares with the Arginbaataridae, and all of the Cimolodonta except the Ptilodontoidea, gigantoprismatic enamel.

Distribution. Upper Jurassic Morrison Formation of North America.

Paulchoffatiid line

Comment. Informal group, erected to include the families Paulchoffatiidae G. Hahn, 1969; Hahnodontidae Sigogneau-Russell, 1991; and Pinheirodontidae G. Hahn and R. Hahn, 1999*a*.

Family PAULCHOFFATIIDAE G. Hahn, 1969

Diagnosis (based on Hahn 1969, 1993, emended). Side branch of 'Plagiaulacida', retaining many plesiomorphic characters. Dental formula: 3.1-0.5-4.2 / 1.0.4-3.2. Apomorphies: m1 with anterior cuspidate cingulum and enlarged anterobuccal cusp, m2 basin-shaped, with cuspules and only one anterolingual cusp, P4–P5 not shearing, molariform with two rows of cusps, sometimes with additional

external row of cuspules, in some genera (e.g. *Kielanodon*) strongly ribbed; large M2 with 2–3:3–6 cusps. In some genera a third row of cusps may be developed on upper and lower premolars (Hahn 1993). Share with the Plagiaulacidae incipient ornamentation of the molar enamel (less strongly pronounced than in the Plagiaulacidae), enlarged I3 and coalesced buccal cusps on m2. Differ from the Plagiaulacidae in having I3 roughly quadrangular or trapezoid in occlusal view, with 3–4 cusps (triangular with three cusps in the Plagiaulacidae), and with main cusp arranged as an oblique ridge, directed antero-lingually to postero-buccally. Another difference is presence of only one lingual cusp in m2 in the Paulchoffatiidae. Plesiomorphies: molar cusps of different height, rudimentary coronoid sometimes present, M1 without posterolingual ridge; p1–p3 oval or rectangular rather than triangular in buccal view; p3 with a row of buccal cusps, almost as long as p4; p4 short with no more than four serrations with ridges. Angle between tooth row and the longitudinal axis of the dentary 7–20 degrees. Angle between the lower margin of the dentary and a horizontal level of the molars is low.

Subfamilies and genera. Paulchoffatiinae G. Hahn, 1971 [*Paulchoffatia* Kühne, 1961, type genus; *Bathmochoffatia* G. Hahn and R. Hahn, 1998*a*; *Guimarotodon* G. Hahn, 1969; *Henkelodon* G. Hahn, 1987; *Kielanodon* G. Hahn, 1987; *Meketibolodon* G. Hahn, 1993; *Meketichoffatia* G. Hahn, 1993; *Plesiochoffatia* G. Hahn and R. Hahn, 1999*b* (replacing *Parachoffatia*, preoccupied); *Pseudobolodon* G. Hahn, 1977; *Xenachoffatia* G. Hahn and R. Hahn, 1998*a*]. Kuehneodontinae G. Hahn, 1971 (*Kuehneodon* G. Hahn, 1969, type genus). Subfamily *incertae sedis* (*Galveodon* G. Hahn and R. Hahn, 1992; *Sunnyodon* Kielan-Jaworowska and Ensom, 1992).

Distribution. ?Middle Jurassic (Bathonian) or Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Barremian) of Europe.

Family HAHNODONTIDAE Sigogneau-Russell, 1991

Diagnosis. Poorly known, monotypic family, including only the type genus *Hahnodon* Sigogneau-Russell, 1991, with a single species, *H. taqueti* Sigogneau-Russell, 1991, known from a single m2. Shares with the Paulchoffatiidae basin-like structure of m2, but differs from them in having m2 with two high cusps and one cuspule (rather than a single lower cusp as in Paulchoffatiidae), deeper basin of m2 and smooth enamel.

Distribution. ?Berriasian of Morocco.

Family PINHEIRODONTIDAE G. Hahn and R. Hahn, 1999*a*

Diagnosis (based on Hahn and Hahn 1999*a*, emended). Family established on about 250 isolated teeth. Dental formula unknown; cusps on lower molars of different height. I2 with several small posterior cuspules arranged in a semicircle. Share with the Paulchoffatiidae enlarged I3, but differ in details of its structure. Upper canine present, single-rooted. Share with other 'plagiaulacidans' 3–5-cusped P1–P3; P4 with two rows of cusps, the buccal shorter than the lingual. Share with the Paulchoffatiinae and Albionbaataridae P5 with three rows of cusps. M1 with two rows of cusps. M2 with two rows of cusps and a small pit that separates the first from the second buccal cusps. Lower incisor completely covered with enamel. Basal cusps on p4 either present (*Bernardodon*), or absent (*Pinheirodon*), or replaced by a row of pits (*Iberodon*), a character unique among multituberculates. Share with the Paulchoffatiidae and Plagiaulacidae a tendency to enlarge the second buccal cusp in m1 and diminish the first and the third. Share with Paulchoffatiidae m2 with central basin and reduced buccal cusps.

Genera. *Pinheirodon* G. Hahn and R. Hahn, 1999*a*, type genus; *Bernardodon* G. Hahn and R. Hahn, 1999*a*; *Ecprepaulax* G. Hahn and R. Hahn, 1999*a*; *Gerhardodon* Kielan-Jaworowska and Ensom, 1992; *Iberodon* G. Hahn and R. Hahn, 1999*a*; *Lavocatia* Canudo and Cuenca-Bescós, 1996.

Distribution. Lower Cretaceous (Purbeck Limestone Group; Berriasian) of England; Barremian of Spain; Berriasian of central Portugal.

Plagiaulacid line

Comment. Informal group erected to include the families Plagiaulacidae Gill, 1872; Albionbaataridae Kielan-Jaworowska and Ensom, 1994; and Eobaataridae Kielan-Jaworowska *et al.*, 1987**.**

Family PLAGIAULACIDAE Gill, 1872

Synonym. Bolodontidae Osborn, 1887.

Diagnosis. Dental formula 3.0.5.2/1.0.4-3.2. Differ from the Allodontidae and Paulchoffatiidae in the following apomorphies: elongated p4 1·5−2 times longer than p3, with 5−7 serrations with ridges; p2 and p3 triangular rather than rectangular in buccal view. Differ from Allodontidae and Paulchoffatiidae in having m1 and m2 with two rows of coalescing cusps. Differ from the Allodontidae in having ornamentation of irregular grooves, pits and ribs on the molars, and share these characters with the Eobaataridae, members of the *Paracimexomys* group, and with some Ptilodontoidea. Share with the Paulchoffatiidae enlarged I3 with more than one cusp (2−3), but differ in having roughly triangular shape of the tooth in occlusal view and in lack of oblique arrangement of the main cusp. Share with Paulchoffatiidae m2 with obliterated buccal cusps, but differ in lack of a basin on that molar, and in presence of lingual cusps. Share elongation of p4 with respect to p3 with the Zofiabaataridae and Eobaataridae. Differ from the Paulchoffatiidae in having incipient posterolingual ridge in M1, shearing P4−P5, and smaller number of cusps on M2 (2−3:3). Differ from the Allodontidae in having P4 and P5 with numerous ribbed cuspules and share this character with some Paulchoffatiidae, e.g. *Kielanodon*. Differ from the Eobaataridae in having p4 with a row of buccal cusps (mistakenly quoted by Kielan-Jaworowska and Ensom 1992 as having single cusp in *Bolodon osborni* Simpson, 1928).

Genera. Plagiaulax Falconer, 1857; *Bolodon* Owen, 1871, ?new genus to be erected for '*Bolodon' elongatus*; and undescribed plagiaulacid mandible from north-east China (Wang *et al*. 1995). '*Ctenacodon*' *brentbaatar* Bakker, 1998 (upper P5) from the Morrison Formation may also belong here.

Distribution. Lower Cretaceous (Berriasian) of Europe; Upper Jurassic Morrison Formation of North America; ?Valanginian or ?Hauterivian of north-east China (Wang *et al*. 1995).

Family ALBIONBAATARIDAE Kielan-Jaworowska and Ensom, 1994

Diagnosis. Shrew-sized taxa that differ from all other multituberculates in having relatively flat, multi-cusped anterior upper premolars, with 10−14 cusps arranged in three rows, rather than 3−4, rarely up to nine high cusps in two rows, and in having lingual slope of all premolars covered by prominent, subparallel ridges. Differ from most multituberculates, except for specialised Ptilodontoidea (homoplasy) in having P5 with three rows of numerous small cusps. Differ from the Paulchoffatiidae in having P5 distinctly longer relative to the width. Differ from the Plagiaulacidae in lack of dramatic difference in size of cusps on the same upper premolar, but share with them a generally similar morphology of P5 with a roughly horizontal ventral surface with rows of cusps and an extensive oblique lingual slope. Hahn and Hahn (1999*a*) argued that three rows of cusps on anterior premolars, characteristic of the Albionbaataridae, are unknown in other multituberculates, but occur on P4 and P5 in some Paulchoffatiidae. On this basis they presumed that the Albionbaataridae might be descendants of the Paulchoffatiidae. We describe them provisionally within the plagiaulacid line, pending further discoveries, which may demonstrate their relationships to the Paulchoffatiidae.

Genera. *Albionbaatar* Kielan-Jaworowska and Ensom, 1994; *Proalbionbaatar* G. Hahn and R. Hahn, 1998*b*; and undescribed upper premolars similar to *Albionbaatar* (Wang *et al*. 1995).

Distribution. Upper Jurassic (Kimmeridgian) and Lower Cretaceous (Berriasian) of Europe; ?Valanginian or ?Hauterivian of north-east China (Wang *et al*. 1995).

Family EOBAATARIDAE Kielan-Jaworowska, Dashzeveg and Trofimov, 1987

Diagnosis. Estimated dental formula ?.?.5.2/1.0.3.2. Differ from most 'plagiaulacidans' (except *Glirodon*) in having lower incisor with limited enamel band and gigantoprismatic enamel. Differ from other 'plagiaulacidans' in having single buccal cusp on p4 rather than a row of cusps. Share with the Plagiaulacidae and with some members of the *Paracimexomys* group the structure of m1 and m2 with coalescing cusps (buccal cusps in m2 obliterated). Share with members of the *Paracimexomys* group the structure of M2 with straight anterior margin (sigmoid in the Plagiaulacidae), anterior rim confluent with the first cusp of the medial row, and enlarged second cusp of the medial row. Share with the Plagiaulacidae and some members of the *Paracimexomys* group and some of the Ptilodontoidea ornamentation of grooves, pits and ridges on the molars. Share with the Plagiaulacidae generally similar structure of the upper premolars (five in number) and differ in having a more prominent incipient lingual ridge on M1. Share with *Bolodon, Plagiaulax*, and *Zofiabaatar* similar p3/p4 length ratio and with *Plagiaulax* the presence of only three lower premolars.

Genera. *Eobaatar* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987, type genus; *Loxaulax* Simpson, 1928; *Parendotherium* Crusafont-Pairó and Adrover, 1966. ?*Monobaatar* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987, which has isolated cusps on M2, probably does not belong to the Eobaataridae, but because it is very incompletely known we place it tentatively herein.

Distribution. Lower Cretaceous: Aptian or Albian of Asia (Mongolia); Berriasian of Great Britain; Barremian of Spain.

Suborder *incertae sedis*
Family ARGINBAATARIDAE G. Hahn and R. Hahn, 1983

Diagnosis. Monotypic family (*Arginbaatar* Trofimov, 1980, type genus). Estimated dental formula ?.1.5.2./1.0.3.2. This family shows a mixture of 'plagiaulacidan' and cimolodontan characters. Shares with some 'Plagiaulacida' three lower premolars and apparently five upper premolars, and presence of an upper canine, but differs from them and from all other multituberculates in structure of p4. The arginbaatarid p4 is arcuate as in the Cimolodonta, but is unique in having the enamel limited to a part of the crown, and during ontogeny rotating anteroventrally over the worn p2 and p3, which gradually disappear. Share with *Glirodon*, *Eobaatar,* and most Cimolodonta (except the Ptilodontoidea) giganto-prismatic enamel, and with most 'Plagiaulacida' lower incisor completely covered with enamel.

Distribution. Lower Cretaceous (Aptian or Albian) of Asia (Mongolia).

Suborder CIMOLODONTA McKenna, 1975

Diagnosis. Multituberculates with prismatic enamel; dental formula: 2.0.1-4.2/1.0.1-2.2. Differ from the 'Plagiaulacida' in the following apomorphies: two upper incisors (I1 lost); I2 single- or two-cusped, I3 small, single-cusped; no more than four upper premolars (apparently 'plagiaulacidan' P4 lost); no more than two lower premolars (p1 and p2 lost); p3, if present, peg-like, non-functional. The p4 is primitively arcuate with oblique ridges (shared with Arginbaataridae, homoplasy), rather than rectangular as in 'Plagiaulacida'. Single posterobuccal cusp on p4, which may disappear, rather than

a row of cusps as in 'Plagiaulacida' except *Eobaatar*. Two main evolutionary tendencies occur in parallel: (1) increase in number of ridges of p4 and its size; (2) reduction in size of p4 and reduction of premolar number.

Superfamilies. Djadochtatherioidea nov.; Taeniolabidoidea (Sloan and Van Valen, 1965) McKenna and Bell, 1997; Ptilodontoidea (Sloan and Van Valen, 1965) McKenna and Bell, 1997; and superfamily *incertae sedis*: *Paracimexomys* group.

Families. Cimolomyidae Marsh, 1889; Boffiidae G. Hahn and R. Hahn, 1983; Eucosmodontidae Jepsen, 1940; Kogaionidae Rădulescu and Samson, 1996; and Microcosmodontidae Fox 1999.

Genera. *Uzbekbaatar* Kielan-Jaworowska and Nessov, 1992 and *Viridomys* Fox, 1971 left in superfamily and family *incertae sedis* and not discussed herein.

Distribution. Lower Cretaceous (Aptian–Albian) to Lower Tertiary (Eocene) of Northern Hemisphere.

PARACIMEXOMYS group

Diagnosis. Most plesiomorphic, apparently paraphyletic informal group of Cimolodonta, members of which are known mostly from isolated teeth. Differ from most 'Plagiaulacida' (but not from *Eobaatar* and *Glirodon*) in having gigantoprismatic enamel. Differ from the 'Plagiaulacida' in having arcuate p4 (cimolodontan apomorphy), and cimolodontan dental formula. Share with the Plagiaulacidae and Eobaataridae structure of the molars (especially m2) with coalescing cusps, ornamentation of grooves and ribs on lower and upper molars, and often very similar cusp arrangement (especially in M2). Share with some Djadochtatherioidea P4 with a row of main cusps and short anterobuccal row of 3–4 cusps, and M1 with small number of cusps and a short posterobuccal ridge with a few cusps.

Genera. *Paracimexomys* Archibald, 1982; *Bryceomys* Eaton, 1995; *Dakotamys* Eaton, 1995; and tentatively assigned *Cimexomys* Sloan and Van Valen, 1965, and ?*Barbatodon* Rădulescu and Samson, 1986.

Distribution. Lower Cretaceous (Aptian–Albian) through Maastrichtian of North America; ?Maastrichtian of Europe. The oldest described record of *Paracimexomys* is that of Cifelli (1997), based on ?*P. crossi* from the Aptian–Albian of Oklahoma, but the record does not improve until the Albian–Cenomanian, from which Eaton and Nelson (1991) published several species. As *Barbatodon* is only tentatively assigned, the occurrence of this group in Europe is not certain.

Superfamily DJADOCHTATHERIOIDEA nov.

Diagnosis. A clade of Cimolodonta with skull length varying between 20 and 70 mm, dental formula 2.0.3-4.2/1.0.2.2. Synapomorphies: large frontals pointed anteriorly in the middle, inserted between the nasals; U-shaped fronto-parietal suture; a sharp edge between the lateral and palatal walls of premaxilla (rounded in other multituberculates), parietal postorbital process. A large, roughly rectangular facial surface of lacrimal exposed on the cranial roof may be a plesiomorphy. Lower incisor with limited enamel band or thicker on ventrolateral surface. Share with *Meniscoessus* and *Stygimys* I3 placed on the palatal part of premaxilla; share with most Cimolodonta (except most Ptilodontoidea), and with *Glirodon* and *Eobaatar* gigantoprismatic enamel.

Comment. This superfamily replaces the suborder Djadochtatheria Kielan-Jaworowska and Hurum, 1997.

Families and genera. Sloanbaataridae Kielan-Jaworowska, 1974 (*Sloanbaatar* Kielan-Jaworowska, 1970, type genus; *Nessovbaatar* Kielan-Jaworowska and Hurum, 1997; ?*Kamptobaatar* Kielan-Jaworowska, 1970); Djadochtatheriidae

Kielan-Jaworowska and Hurum, 1997 (*Djadochtatherium* Simpson, 1925, type genus; *Catopsbaatar* Kielan-Jaworowska, 1994; *Kryptobaatar* Kielan-Jaworowska, 1970; *Tombaatar* Rougier, Novacek and Dashzeveg, 1997); and family *incertae sedis* (*Bulganbaatar* Kielan-Jaworowska, 1974; *Chulsanbaatar* Kielan-Jaworowska, 1974; *Nemegtbaatar* Kielan-Jaworowska, 1974). *Pentacosmodon* Jepsen, 1940, tentatively assigned to the Djadochtatheria by Kielan-Jaworowska and Hurum (1997, see also Rougier *et al.* 1997) is attributed to the Microcosmodontidae (see Weil 1998).

Distribution. Upper Cretaceous of Asia. Occurrence of this superfamily in the Palaeocene of North America is doubtful.

Family EUCOSMODONTIDAE (Jepsen, 1940) Sloan and Van Valen, 1965

Diagnosis. Snout (known only in *Stygimys*) incurved in front of zygomatic arches; palatal vacuities present. Dental formula 2.0.4.2/1.0.1-2.2, gigantoprismatic enamel, lower incisor with limited enamel band. Differ from other Cimolodonta except the Cimolomyidae and *Catopsalis* in having two-cusped I2. Differ from the Djadochtatherioidea in lack of p3, and greater number of cusps (ridges on p4) on the premolars and molars, but share with them (and *Meniscoessus*) I3 placed on the palatal part of premaxilla. Share with the Djadochtatherioidea and Cimolomyidae arcuate p4, not protruding over the dorsal level of the molars, and with the Djadochtatherioidea P4 with lower margin almost straight in lateral view (triangular in the Cimolomyidae and Ptilodontoidea). Differ from the Taeniolabidoidea in having four upper premolars and larger arcuate p4 (rather than triangular).

Genera. *Eucosmodon* Matthew and Granger, 1921, type genus; *Stygimys* Sloan and Van Valen, 1965; and tentatively assigned *Clemensodon* Krause, 1992.

Distribution. Upper Cretaceous–Lower Eocene of North America; Lower Palaeocene–Lower Eocene of Europe.

Family MICROCOSMODONTIDAE (Holtzman and Wolberg, 1977) Fox, 1999

Diagnosis (based on Weil 1998 and Fox 1999). Small multituberculates with enlarged lower incisor with restricted enamel band; p4 small, shorter than m1, with 5–6 serrations; p4 crown height subequal or greater than crown length. Differ from the Eucosmodontidae and Djadochtatherioidea in having I3 located at the palatal margin of premaxilla, rather than medially. Enamel microstructure, at least in some species of *Microcosmodon*, with both microprisms and gigantoprisms (Carlson and Krause 1985).

Genera. *Microcosmodon* Jepsen, 1930, type genus; *Pentacosmodon* Jepsen, 1940; and *Acheronodon* Archibald, 1982.

Distribution. Upper Cretaceous (see Fox 1989)–Palaeocene of North America.

Superfamily TAENIOLABIDOIDEA (Sloan and Van Valen, 1965), McKenna and Bell, 1997, Fox, 1999

Diagnosis. Monotypic superfamily (see Fox 1999 who limited the Taeniolabidoidea to a single family), including the largest known multituberculates (skull length in Palaeocene *Taeniolabis* reaching 16 cm), with gigantoprismatic enamel. Dental formula 2.0.1-2.2/1.0.1.2. Apomorphies: snout short and wide with anterior part of zygomatic arches directed transversely, resulting in a square-like shape of the skull (shared with Kogaionidae); frontals small, pointed posteriorly, almost or completely excluded from the orbital rim. Differ from all multituberculates in having only one upper premolar (two in one taxon), long diastema between I3 and premolars, P4 and p4 triangular in lateral view, strongly reduced in proportion to enlarged multicusped molars. Share strong, self-sharpening incisors, with limited enamel band with most Djadochtatherioidea and Eucosmodontidae. Differ from the Djadochtatherioidea, Cimolomyidae, and Eucosmodontidae in position of I3 on the margin of the premaxilla, close to I2. Upper and lower molars

strongly enlarged, wide, M1 with three rows of cusps in most advanced forms with inner ridge extending for the entire length of the tooth (the latter character shared with the Boffiidae).

Family and genera. Taeniolabididae Granger and Simpson, 1929 (*Taeniolabis* Cope, 1882, type genus; *Catopsalis* Cope, 1882; *Lambdopsalis* Chow and Qi, 1978; *Prionessus* Matthew and Granger, 1925; *Sphenopsalis* Matthew, Granger and Simpson, 1928); see also Simmons and Miao (1986).

Distribution. Upper Cretaceous–Palaeocene of North America and Asia. *Catopsalis joyneri*, traditionally considered of Late Cretaceous age (e.g. Sloan and Van Valen 1965), is now believed to be restricted to the Palaeocene, at least in Montana (Lofgren 1995), but the Cretaceous record is based on an occurrence in Canada (Fox 1997).

<div style="text-align:center">

Superfamily *incertae sedis*
Family KOGAIONIDAE Râdulescu and Samson, 1996

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Diagnosis. Dental formula, known only for upper dentition 2.0.4.2. Apomorphies: differ from other Cimolodonta in having all upper premolars strongly elongated, of which P3 is the longest, premolar row twice as long as molar row, short and wide M1 with cusp formula in *Kogaionon* 3:4:3. The p4, known only in *Hainina* Vianey-Liaud, 1979, if correctly attributed (Vianey-Liaud 1986), is arcuate and protrudes dorsally over the level of the molars as in Ptilodontoidea, from which they differ in having gigantoprismatic enamel. I2 with limited enamel band, which suggests limited enamel also on the lower incisor (dentary unknown). Molar enamel smooth in *Kogaionon*, but ornamented with grooves in *Hainina*. Share with Taeniolabidoidea the general shape of the skull, with anterior part of zygomatic arches directed roughly transversely and very short basicranial region, which gives the skull a square-like appearance, but differ from them in having a strongly elongated snout and different dentition.

Genera. *Kogaionon* Râdulescu and Samson, 1996, and *Hainina* Vianey-Liaud, 1979.

Distribution. Upper Cretaceous and Palaeocene of Europe.

<div style="text-align:center">

Superfamily PTILODONTOIDEA Sloan and Van Valen, 1965 (McKenna and Bell, 1997)

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Diagnosis. Dental formula 2.0.4.2 /1.0.2.2. Apomorphies: microprismatic enamel (except for tentatively assigned *Cimolodon*, which has gigantoprismatic enamel); gracile lower incisor completely covered with enamel (robust lower incisor covered with enamel occurs in most 'Plagiaulacida' and Cimolomyidae, but slenderness is an apomorphy of the Ptilodontoidea). In tentatively assigned *Neoliotomus* the lower incisor is robust, with limited enamel band. The p4 is very large, arcuate, strongly protruding dorsally over the level of the molars (apomorphy). Snout is wide, gently incurved in front of zygomatic arches. Share with the Taeniolabididae small frontals pointed posteriorly (convergence) and differ in this respect from the Djadochtatherioidea. I2 probably single-cusped, I3 placed on the margin of premaxilla. P4 elongated, in lateral view shaped as isosceles triangle, protruding ventrally over the level of the anterior premolars and molars. Share with the Plagiaulacidae, Eobaataridae and *Paracimexomys* group ornamentation of grooves and ridges on the molars and tendency of molar cusps to coalesce.

Families and genera. Neoplagiaulacidae, Ameghino, 1890 (*Neoplagiaulax* Lemoine, 1882, type genus; *Cernaysia* Vianey-Liaud, 1986; *Ectypodus* Matthew and Granger, 1921; *Krauseia* Vianey-Liaud, 1986; *Mesodma* Jepsen, 1940; *Mimetodon* Jepsen, 1940; *Mesodmops* Tong and Wang, 1994; *Parectypodus* Jepsen, 1930; *Xanclomys* Rigby, 1980; *Xyronomys* Rigby, 1980). Ptilodontidae Cope, 1887 (*Ptilodus* Cope, 1881, type genus; *Baiotomeus* Krause, 1987; *Kimbetohia* Simpson, 1936; *Prochetodon* Jepsen, 1940). Cimolodontidae Marsh, 1889 (?*Cimolodon* Marsh, 1889, type genus; *Anconodon* Jepsen, 1940; *Liotomus* Cope, 1884, and ?*Essonodon* Simpson, 1927); and tentatively assigned, family *incertae sedis,* ?*Neoliotomus* Jepsen, 1930.

Distribution. Upper Cretaceous of North America and Europe; Palaeocene–Eocene of North America, Europe and Asia.

Superfamily *incertae sedis*
Family CIMOLOMYIDAE Marsh, 1889

Diagnosis. Dental formula: 2.0.4.2/1.0.2.2. Apomorphies: differ from other Cimolodonta in having stout lower incisor completely covered with enamel and four upper premolars strongly reduced in width and length in proportion to enlarged molars, P4 triangular in buccal view strongly protruding ventrally over the level of the premolars and molars, molar cusps crescentic. Share with Eucosmodontidae two-cusped I2 (known only in *Meniscoessus)* and with the Djadochtatherioidea and Eucosmodontidae I3 placed on the palatal part of premaxilla and arcuate p4 at the level of the molars. Share with the Taeniolabidoidea M1 with three rows of cusps, the inner row as long or almost as long as the other rows. Share with the Plagiaulacidae, Eobaataridae and *Paracimexomys* group ornamentation of grooves and ridges on m1, and weak ribbing on M1, but differ in lack of obvious coalescence of cusps characteristic of these groups. Share with all Cimolodonta except the Ptilodontoidea, and with *Eobaatar* and *Glirodon*, gigantoprismatic enamel. Molar cusps pyramidal to crescentic; upper and lower first molars in *Meniscoessus* and *Cimolomys* develop multiple accessory roots.

Genera. Cimolomys Marsh, 1889; *Meniscoessus* Cope, 1882; and tentatively assigned *Essonodon* Simpson, 1927, and *Buginbaatar* Kielan-Jaworowska and Sochava, 1969.

Distribution. Upper Cretaceous of North America and ?Asia.

Family BOFFIIDAE G. Hahn and R. Hahn, 1983

Diagnosis. Monotypic family including type genus *Boffius* Vianey-Liaud, 1979, relatively large multituberculate, known from isolated teeth. Lower incisor is completely covered with enamel. Share with Cimolomyidae certain reduction in the size of upper premolars, but differ in having relatively larger P4 with three rows of cusps, and enlarged M1 with three full rows of cusps. Enlarged M1 with three complete rows of cusps is shared with some Taeniolabidoidea (homoplasy). Share with plagiaulacid line and *Paracimexomys* group strong ribbing of upper premolars and molars (weaker on m1), but differ in lack of grooves and lack of a tendency of molar cusps to coalesce.

Distribution. Palaeocene (Montian) of Belgium.

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ADDENDUM

After our paper was accepted for publication, a paper by Peláez-Campomanes *et al.* (2000) was published. These authors argue that the Kogaionidae, to which they assign *Kogaionon* and *Hainina*, had five upper premolars, and identified the four premolars in *Kogaionon* as P2–P5. This conclusion has been based on an assumption that all the isolated teeth of multituberculates found in the Paleocene locality Fontllonga 3, in the Southern Pyrenees, are conspecific. They did not take into account the possibility that either one of the P4s found there may be deciduous, or that the two P4s may belong to different taxa. In our opinion the upper premolars of *Kogaionon* represent P1–P4, as only one of these teeth, P4, shows shearing structure, whereas P3, although elongate, has a structure that is typical for multituberculate anterior upper premolars, with large piercing cusps, and is not similar to P4s in 'Plagiaulacida'.

PALÁEZ-CAMPOMANES, P., LÓPEZ-MARTÍNEZ, N., ÁLVAREZ-SIERRA, M. A. and DAAMS, R. 2000. The earliest mammal of the European Paleocene: the multituberculate *Hainina*. *Journal of Paleontology* **74**, 701–711.

APPENDIX

Character list

Plesiomorphic characters are scored as (0), unknown as (?), not applicable as (-).

1. Enamel microstructure: prismless (= preprismatic of Simmons 1993) (0), gigantoprismatic (1), small prismatic (2).
2. Number of upper incisors: 3 (0) or 2 (1).
3. I2 two-cusped (0), single cusped (1).
4. I3: single or 2-cusped (0), 3–4-cusped (1).
5. Canine present (0), absent (1).
6. Number of upper premolars: 5 (0), 4 (1), 3 (2), 2 or 1 (3).
7. Cuspules on posterior upper premolars absent (0) or present (1).
8. Upper premolars / upper molars length ratio 1·5 or more (0), 1·5–0·5 (1), 0·5 or less (2).
9. Last upper premolar with two rows of cusps (0), two rows of cusps and additional buccal cuspules (1), one main row and a shorter buccal one (anterior or posterior) (2), one row only (3).
10. M1 cusp formula 2-3:2-4 (0), 3-5:4-5:smooth ridge-5 (1), 5-7:5-8:2-5 (2), 5-11:7-10:6-11 (3).
11. M1 posterolingual wing to M1 length, wing absent (0), below 0·2 (1), between 0·2 and 0·5 (2), more than 0·5 (3).
12. M1 posterolingual wing smooth (0), with cusps (1).
13. I3 situated on the margin of premaxilla (0), on the palatal part (1).
14. Anterior upper premolars double-rooted (0) or single-rooted (1).
15. Diastema between transverse levels of I3 and first maxillary teeth : length of upper premolars and molars ratio, below 0·09 (0), between 0·1–0·19 (1), between 0·2–0·3 (2), above 0·3 (3).
16. Infraorbital foramen double (0), single (1).
17. Palatal vacuities absent (0), single (1), double (2).
18. P4 cusp formula 0-5:1-4:0-5 (0), 0-5:5-10:0-5 (1), 5-7:5-8:2-5 (2).
19. Width of P4:M1 more than 0·9 (0), 0·9–0·6 (1), 0·6–0·45 (2), 0·44–0·2 (3).
20. Enamel covering of lower incisor of uniform thickness (0), thicker on ventro-labial surface (1), completely restricted to ventro-labial surface of tooth (2).
21. Lower incisor robust (0), gracile (1).
22. p1 present (0), absent (1).

23. p2 present (0), absent (1).
24. p3 cusp count 3–5 (0), 1–2 (1), p3 absent (2).
25. Shape of p3: two rows of cusps (0), blade-like rectangular (1), blade-like triangular (2), peg-like (3).
26. Basal cusps on p3 present (0), absent (1).
27. p4 in lateral view rectangular (0), arcuate (1), triangular (2).
28. p4 serration count 5 or less (0), 6–10 (1), more than 10 (2).
29. p3/p4 maximum length 1·0–0·55 (0), 0·54–0·11 (1), 0·10 or less (2).
30. Basal cuspules on p4: several (0), single (1), lacking (2).
31. Ratio of p4:m1 length: less than 0·6 (0), 0·6–1·7 (1), above 1·7 (2).
32. m1 with two rows of subequal, well-separated cusps (0), with anterior cuspidate cingulum and a large buccal cusp (1), with two rows of cusps, both tending to coalesce (2).
33. m2 with two rows of well-separated cusps (0), basin-shaped (1), with buccal cusps coalesced (2).
34. Dorsal margin of p4 on the level of molars (0), protruding dorsally over molars (1).
35. Angle between the lower margin of the dentary and a horizontal level of the molars 11–17 degrees (0), 18 or above (1).
36. m1 cusp count 4:4 or lower (0), 5:4 (1), 6:4 or higher (2).
37. m2 cusp count 2-3:2-3 (0), 1 (1), 4-5:2-6 (2).
38. Cusp shape on molars conical (0), cresentic (1).
39. Molar enamel smooth, not ornamented (0), covered with grooves, pits and ridges (1).
40. Ridge between the palate and lateral walls of premaxilla absent (0), present (1).
41. Shape of the snout in dorsal view: incurved in front of the zygomatic arches with anterior part directed posterolaterally (0), incurved with anterior part of zygomatic arches directed transversely (1), trapezoid, not incurved in front of the zygomatic arches (2).
42. Number of pairs of vascular foramina on nasal 1 (0), 2 (1), more (2).
43. Infraorbital foramen positioned dorsal to P1 (0), dorsal to P2 (1), dorsal to P3 or P4 (2).
44. Base of zygomatic arch as marked by posterior edge dorsal to P4 or more anterior (0), dorsal or posterior to P5/M1 or P4/M1 embrasure (1).
45. Postorbital process short (0), long (1).
46. Snout length <49 per cent of total skull length (0), >50 per cent of skull length (1).
47. Frontals deeply inserted between the nasals (0), pointed anteriorly and not deeply inserted between the nasals (1), with subtransverse anterior margins (2).
48. Frontal-parietal suture roughly V-shaped (0), U-shaped (1).
49. Contacts between nasals and parietals absent (0), present (1).
50. Facial surface of lacrimal very small and arcuate (0), large, roughly rectangular (1).
51. Thickening in palatal process of premaxilla absent (0), present (1).
52. Incisive foramen situated within premaxilla (0), limited posteriorly by maxilla (1).
53. Foramen ovale inferium placed medial to foramen masticatorium (0), posterior to foramen masticatorium (1).
54. Jugular fossa small and shallow (0), large and deep (1).
55. Anterior part of promontorium (*sensu* Hurum *et al.* 1996) oval (0), irregular with incurvatures on both sides (1).
56. Glenoid fossa length (anterolateral to posteromedial):width ratio more than 1·7 (0), below 1·69 (1).
57. Angle of coronoid process relative to tooth row steep >45 degrees (0), low <45 degrees (1).
58. Coronoid process parallel to the rest of the outer wall of the dentary (0), flared laterally (1).
59. Posttemporal fossa large (0), reduced to a small foramen (1).
60. Mandibular condyle opposite or below the level of the molars (0), above the level of the molars (1).
61. Width of the snout:skull length ratio below 0·3 (0), 0·3–0·39 (1), above 0·4 (2).
62. Skull width:skull length ratio 0·79 and below (0), above 0·8 (1).

Taxon-character matrix

In this we use only a selected number of the genera of each family, choosing the most completely known ones and representative in our opinion for higher rank groups. We do not use poorly known monotypic families, based on single specimens such as, for example, the Hahnodontidae. We do not use either member of the Pinheirodontidae, which are based on several, but isolated teeth. Plesiomorphic characters are scored as (0), unknown as (?), not applicable as (−).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	39	30	31
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	−	0	−	?
Ctenacodon	?	0	0	0	?	0	0	0	0	0	1	0	0	0	?	0	?	0	1	0	0	0	0	0	1	1	1	1	0	0	0
Zofiabaatar	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	0	1	1	0	1
Glirodon	1	0	?	0	0	0	0	0	1	0	0	−	0	0	0	0	0	0	1	2	0	0	0	0	1	1	0	0	0	0	1
Meketichoffatia	0	0	?	0	0	0	1	0	0	0	0	−	0	0	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Paulchoffatia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0	0	0	0	0	0
Henkelodon	?	0	0	1	1	0	1	0	1	0	0	−	0	0	1	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?
Kuehneodon	0	0	0	1	0	1	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Bolodon	0	?	?	1	?	0	1	0	1	0	1	0	?	0	?	0	?	0	0	0	0	0	0	0	2	1	0	1	1	0	0
Plagiaulax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	0	2	1	0	1	1	0	0
Eobaatar	1	?	?	?	?	0	0	0	?	0	2	0	?	0	?	?	?	?	?	2	0	1	0	0	2	1	0	1	?	1	?
Arginbaatar	1	?	?	?	0	0	0	?	?	0	1	0	?	0	?	0	?	?	?	0	0	1	0	1	2	1	1	2	1	2	2
Cimexomys	1	?	?	?	?	1	0	1	2	2	3	1	?	0	?	1	?	1	0	0	0	0	0	1	3	1	1	1	2	1	1
Boffius	1	?	?	?	?	?	?	?	1	3	3	1	?	?	?	?	?	1	1	1	0	?	?	?	?	?	?	?	?	?	?
Meniscoessus	1	1	0	0	1	1	0	1	2	2	3	1	1	0	2	0	2	0	2	0	0	1	1	1	3	1	1	1	2	1	0
Buginbaatar	?	?	?	?	?	?	0	?	2	3	3	1	?	?	?	?	?	1	3	0	0	1	1	2	−	−	1	0	−	2	0
Cimolodon	1	?	?	?	?	1	0	1	2	2	3	1	?	0	?	?	?	1	0	0	?	1	1	1	3	1	1	2	1	1	1
Ectypodus	2	1	?	0	1	1	0	1	2	2	2	1	?	0	1	1	1	1	0	1	1	1	1	1	3	1	1	2	2	1	0
Mesodma	2	1	0	1	1	1	0	1	2	2	2	1	0	0	?	1	?	1	0	0	1	1	1	1	3	1	1	2	2	1	1
Ptilodus	2	1	1	0	1	1	0	0	2	2	2	1	0	0	0	1	1	1	0	0	1	1	1	1	3	1	1	2	2	1	1
Neoliotomus	2	?	1	?	?	1	0	1	2	3	3	1	?	0	?	?	?	1	1	2	0	1	1	1	3	1	1	2	2	1	1
Pentacosmodon	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2	−	−	1	0	−	1	0
Catopsbaatar	1	1	1	0	1	2	0	1	0	2	3	1	1	0	0	1	0	1	2	2	0	1	1	1	3	1	0	0	2	1	1
Kamptobaatar	1	1	1	0	1	1	0	1	2	1	1	0	1	0	0	1	0	1	2	1	0	1	1	1	3	1	1	1	2	1	1
Chulsanbaatar	1	1	1	0	1	1	0	1	2	1	1	0	1	0	0	1	0	1	2	2	0	1	1	1	3	1	1	1	2	1	1
Kryptobaatar	1	1	1	0	1	1	0	1	2	1	1	1	1	0	0	1	0	1	2	2	0	1	1	1	3	1	1	1	2	1	1
Nemegtbaatar	1	1	1	0	1	1	0	1	2	1	2	1	1	0	1	1	1	1	1	2	0	1	1	1	3	1	1	1	2	1	1
Eucosmodon	1	1	0	0	1	2	0	?	2	?	?	?	?	1	?	1	?	?	?	2	0	1	1	2	−	−	1	2	−	1	1
Stygimys	1	1	0	0	1	1	0	1	2	2	2	1	1	1	1	1	1	1	2	2	0	1	1	2	−	−	1	2	−	1	1
Microcosmodon	?	?	0	?	?	?	?	?	?	2	2	1	?	?	?	?	?	?	?	2	0	1	1	1	−	−	1	0	−	1	0
Lambdopsalis	1	1	1	0	1	3	0	2	3	2	3	1	0	1	3	1	0	0	3	2	0	1	1	2	−	−	2	0	−	2	2
Taeniolabis	1	1	1	0	1	3	0	2	3	2	3	1	0	1	3	1	0	0	3	2	0	1	1	2	−	−	2	0	−	1	2
Kogaionon	?	1	1	0	1	1	0	0	3	1	3	1	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?

	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Ancestor	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenacodon	0	0	1	1	0	0	0	0	?	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Zofiabaatar	0	?	1	1	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	?	?
Glirodon	0	0	1	1	0	0	0	0	0	0	1	1	0	?	?	2	?	0	?	?	1	?	?	?	?	0	0	?	1	?	?
Meketichoffatia	?	?	?	?	?	?	?	?	0	0	?	2	0	?	0	0	?	?	?	?	1	1	0	0	0	?	?	?	?	1	0
Paulchoffatia	1	1	1	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Henkelodon	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kuehneodon	1	1	1	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bolodon	2	2	1	0	0	?	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plagiaulax	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	?	?
Eobaatar	2	2	?	?	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Arginbaatar	0	?	1	1	0	?	0	0	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cimexomys	0	0	0	?	2	0	0	1	?	?	2	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boffius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Meniscoessus	0	0	0	0	1	2	1	1	0	0	?	2	1	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?
Buginbaatar	0	0	0	0	2	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?
Cimolodon	0	0	1	0	2	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?
Ectypodus	0	0	1	1	2	2	0	1	?	2	?	2	1	0	?	0	?	0	?	?	1	1	0	0	0	0	?	?	1	1	0
Mesodma	0	0	1	0	2	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?
Ptilodus	0	0	1	0	1	2	0	1	0	0	1	2	0	?	0	2	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Neoliotomus	0	0	1	0	2	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pentacosmodon	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	1	?	?
Catopsbaatar	0	0	0	1	0	0	0	0	1	2	1	2	1	1	1	1	1	0	1	1	0	?	1	1	1	0	0	0	1	2	1
Kamptobaatar	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	1	0	1	1	1	0	1	0	0	1	1	0	1	1	0
Chulsanbaatar	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	0	0	0	0	0
Kryptobaatar	0	0	0	0	0	0	0	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	2	1
Nemegtbaatar	0	0	0	0	1	0	0	0	1	0	2	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0	0	0	1	0
Eucosmodon	0	0	0	1	1	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?	?
Stygimys	0	0	0	0	2	0	0	0	?	0	?	0	0	?	?	?	?	?	1	1	?	?	?	?	1	0	?	?	?	?	?
Microcosmodon	0	0	0	0	2	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Lambdopsalis	0	0	0	1	1	2	1	0	0	1	2	2	1	0	0	0	1	0	0	1	?	1	1	?	0	1	1	1	1	1	1
Taeniolabis	0	0	0	0	2	2	0	0	0	1	?	2	?	0	0	0	1	0	0	?	?	?	?	?	0	0	1	1	1	1	1
Kogaionon	?	?	?	?	?	?	?	0	0	1	2	2	0	0	0	2	0	0	?	?	1	?	1	?	1	?	?	?	?	1	0