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Mesozoic mammals of China: implications for phylogeny and early evolution of mammals

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Abstract

All Mesozoic mammaliaforms reported from China are briefly documented herein. These forms can be divided into at least five major assemblages: Lufeng, Yanliao (Daohugou), Jehol, Fuxin and Bayan Mandahu, ranging from the Early Jurassic to the Late Cretaceous periods. Although the temporal and geographic distributions of these mammaliaforms are not dense, the records do reveal a pattern that is generally consistent with patterns that have been recognized globally. The initial stage of mammalian evolution was represented by stem mammaliaforms or primitive ‘triconodonts’ from the Lufeng. This was followed by the Middle-Late Jurassic Yanliao episode that showed a high diversity and disparity of mammaliaforms in which terrestrial, swimming, arboreal and gliding species were present. The disparity, at least in molar morphology and types of locomotion, decreased but the diversity persisted into the Cretaceous, a period that was dominated by eutriconodontans, multituberculates and trechnotherians. The superb specimens from nearly all major groups of Mesozoic mammals in China provided a great amount of information that

contributed to our understanding on some major issues in phylogeny and the early evolution of mammals, such as divergences of mammals and the evolution of the mammalian middle ear. A hypothesis on the transformation of the allotherian tooth pattern is proposed as an example to illustrate the potential for future studies of mammalian evolution.

Key words: Mammals, Mesozoic, phylogeny, evolution, China

Introduction

Mammals are a monophyletic vertebrate group to which we human beings belong. The early mammals that were coeval with dinosaurs in the Mesozoic are of particular importance in understanding the origin, evolution, phylogeny and early life of the group. They have therefore been the focus of numerous studies during the last two centuries. The first scientifically documented Mesozoic mammal was discovered in 1812 from England, which was formally reported by Broderip [1]. Owen made a more definitive and systematic treatment of Mesozoic mammals in his iconic monograph published in 1871, which recorded all British Mesozoic mammals known at that time. Owen's [2] work, along with those of Marsh's [3-5], on the Jurassic and Cretaceous mammals from North America provided the basis for the more detailed documentation and interpretation of all Mesozoic mammal fossils then known from Europe and North America. Furthermore, studies by Simpson [6, 7] described several new genera. Substantial progress has been made in the study of Mesozoic mammals since Simpson's treatments, synthesized in two works: Lillegraven et al. [8] and Kielan-Jarowowska et al. [9]. Due to their small size and fragile skeletons, most of the Mesozoic mammals were known only from fragmented material, typically teeth and jaws; a fact reflected from Owen's [2] monograph to the more recent work [9]. As noted by Lillegraven and Clemens ([10]: vii): "The study of Mesozoic mammals continues to be dominated by examination of dentitions... Despite our best efforts, however, discoveries of high-quality articulated skeletal remains of Mesozoic mammals continue to be extraordinarily rare." In part due to the limited information available from fragmentary material of Mesozoic mammals, many problems remain regarding the early evolution of mammals, including timing and places of origin of almost all major groups of mammals, the affinities of multituberculates, higher-level

phylogenies of mammals and the discrepancy on the divergence time between the fossil record and the molecular clock, as noted by Lillegraven and Clemens [10].

During the last two decades, a great amount of data on Mesozoic mammals has become available, owing to discoveries made from both southern and northern continents, part of which have been incorporated in Kielan-Jaworowska et al. [9]. Of particular importance are some findings from the southern continents, or the landmasses of the ancient Gondwana, that include fossils from various groups of mammals previously known only in the northern continents [11-20], as summarized in some recent studies [21,22]. Although these materials are mostly fragmentary, they provided accumulating evidence - although in some cases ambiguous (e.g., presence of multituberculates in Gondwana landmasses [22]) - that major groups of mammals most likely had a cosmopolitan distribution during their evolution in the Jurassic and Cretaceous [23].

However it is reasonable to assume that the most exciting and informative findings of Mesozoic mammals during the last two decades came from the Jurassic and Cretaceous periods of China. These discoveries have increased the diversity of nearly all major groups of Mesozoic mammals and provided a great amount of information about their morphology and biology, thanks to the superb preservation of those fossils. In the context of the studies on Mesozoic mammals at the time, Lillegraven and Clemens ([10], viii) wrote: "These studies have tended to conclude that we already know about most of the taxonomic diversity that existed among Mesozoic mammals. We predict that another quarter-century of fieldwork will show that conclusion is far from the truth." These authors are absolutely correct, however we do not have to wait for another 25 years to witness the impressive increase in taxonomic diversity of Mesozoic mammals and other vertebrates, as exemplified by the Chinese record during the last decade. The new data on the Mesozoic mammals have inevitably stimulated rigorous discussions on the morphology, diversity, disparity, phylogeny, biogeography, evolution, divergence time and biology of early mammals, some of which are summarized and briefly discussed below.

In this study I briefly review what is known about the fossil record of Mesozoic mammals in China, which provides a current data source for those who are interested in the subject. Among many important studies that were based on the Chinese fossils, I try to highlight, as examples, contributions to some important scientific problems that

were related to mammalian evolution and phylogeny. Furthermore, To show the the potential to address many interesting topics with the data amassed during the last two decades, I present a hypothesis, based on recent research, on the evolution of the allotherian tooth pattern, which has remained as a long-lasting obstacle in understanding the higher-level phylogeny of mammals and their evolution. Thus, the work presented here is more than just a review or summary on what is known. Rather, I hope it will trigger future research efforts in the study on mammalian evolution.

In this study, mammals are defined as the clade consisting of the most recent common ancestor of living monotremes and therians and all descendants of that ancestor [24]. Mammals so defined are also referred to as crown Mammalia or crown mammals, but for simplicity in this report, the terms mammals or Mammalia will be used where the descriptor “crown” is considered unnecessary. An alternative and more traditional definition of Mammalia is the clade that shares a common ancestor of *Sinoconodon*, morganucodontans, docodontans, Monotremata, Marsupialia, and Placentalia, plus any extinct taxa that are shown to be nested with this clade by parsimony analyses [9]. “Mammals” so defined are equivalent to Mammaliaformes of Rowe [24]. Mammaliaforms will be used in the text to refer to animals in the Mammaliaformes.

Diversity and distributions

The first Mesozoic mammal reported from China was *Manchurodon simplicidens* [25], whose age was arguably mid-Jurassic [26,27]. About 46 years later, Zhang [26] reviewed the Mesozoic mammaliaforms in China and compiled a list of seven species, excluding several synonymous taxa (see [28-31]), and three unnamed mammals known at the time. The discoveries of Mesozoic mammals over the next decade were sparse since that review [26]. The report of the first Jehol mammal, *Zhangheotherium quinquecuspidens* [32] from the Lower Cretaceous Yixian Formation triggered the explosive discoveries of Mesozoic mammals in China over the last 20 years, some of which have been reviewed in several studies [9,33,34,35]. Since then, the number of Mesozoic mammaliaforms from China has grown dramatically, as shown in Fig. 1.

Most of the Mesozoic mammaliaforms discovered over the last 20 years were from Northeast China in three time intervals, represented by three assemblages that belong to the Middle-Late Jurassic Yanliao (Daohugou), Early Cretaceous Jehol and late Early

Cretaceous Fuxin biotas The distributions of the three assemblages largely overlap geographically, as shown in the locality map (Fig. 2). Another two regions that generated a considerable number of Mesozoic mammals in China are the Late Cretaceous Bayan Mandahu locality of Inner Mongolia [36-38] and the Jurassic sites in the Junggar basin of northern Xinjiang (mainly from the Qigu and Shishugou formations) [39-43]. For the Middle-Late Jurassic biota from the Northeast China, two names have been used: Yanliao and Daohugou [44,45]; their potential as interchangeable equivalent terms has been noted [45]. As the contents (at least the species of mammaliaforms) referred to in the Yanliao or Daohugou Biota overlap, I prefer to use Yanliao for the biota because it implies an area consisting of the Liaoning Province and the northern part of Hebei Province, whereas Daohugou is a village (locality) name only.

In counting the species diversity, I generally adopt the original taxonomic assignments of each species, but understand that taxonomic positions of some taxa at generic and higher levels remain uncertain. For instance, *Acuodulodon* [42] was considered to be a junior synonymy of *Dsungarodon* [43], but because of the fragmentary nature of the specimens that both taxa were based on, more evidence is needed to confirm the synonymy [46]. In either case, however, the species remains valid so that the diversity count at the species level is not affected. I also compiled taxa that are identifiable at the generic level, including *Tegotherium* sp. [43] and *Kennalestes* sp. [36]. Taxa that are identifiable only at a higher taxonomic level, for example Eutriconodonta indet. [43], were not included. The known species belong to nearly all major clades of Mesozoic mammaliaforms from the northern continents and are listed below and in Fig. 3. In addition to the species list, Fig. 3 also illustrates the localities, temporal distributions, higher-level taxonomy and phylogeny in a simplified frame. Main evolutionary stages are represented as assemblages from several geological intervals.

Sinoconodon (Although several species names had been proposed in early studies, *Sinoconodon rigneyi* [47] is the only species that is generally recognized today from Lufeng, Yunan [26,28-31].

Morganucodonta (*Morganucodon oehleri* [48]; *M. heikoupengensis* [30,49]; *Hadrocodium wui* [50]). Given that *Hadrocodium* was reinterpreted as having

postdentary bones (see references 23 and 51 for discussion), I consider it highly possible that *Hadrocodium* will be placed in Morganucodonta in future studies; therefore I tentatively list it here.

Megaconus mammaliaformis [52]. *Megaconus* was considered to be a “haramiyidan” [52], but its morphology displays some uncertainties as discussed elsewhere [23]. Here I list it separately.

Docodonta (*Castorocauda lustrasilis* [53]; *Dsungarodon zuoi* [41]; *Acuodulodon sunae* [42]; *Tegotherium sp.* [43]).

Volaticotherium antiquum [54]. This species was originally recognized as belonging to an order of its own, Volaticotheria, but others considered it a specialized eutriconodontan [55]. It is a highly specialized species and probably has close relatives from the southern continents [55]. For the purpose of this study, I list it separately here and in Fig. 3, and keep its phylogeny open for future study.

Shuotheridia (*Shuotherium dongi* [56]; *S. shilongi* [57]; *Pseudotribos robustus* [58]). *Pseudotribos robustus* was originally placed in Yinotheria [58], a higher taxon also proposed by Chow and Rich [56]. Given that the content and definition of Shuotheridia are identical to those of Yinotheria, I follow others and place *P. robustus* in the Shuotheridia [46].

Eutriconodonta (*Meiconodon lii* [59]; *M. setoguchii* [59]; *Jeholodens jenkinsi* [60]; *Yanoconodon allini* [61]; *Liaconodon hui* [62]; *Gobiconodon zofiae* [63]; *Gobiconodon luodianus* [64]; *Hangjinia chowi* [65]; *Meemannodon lujiatunensis* [66]; *Repenomamus robustus* [63,67]; *Repenomamus giganticus* [68]; *Chaoyangodens lii* [69]; *Juchilestes liaoningensis* [70]; *Klamelia zhaopengi* [39]; *Liaotherium gracile* [27]). Eutriconodontans are the most diverse group in the Jehol Biota. The taxa reported thus far are well established, but species identification on a large number of specimens with differing sizes may prove challenging in the future [35].

Euharamiyida (*Sineleutherus uyguricus* [43]; *Shenshou lui* [23]; *Xianshou linglong* [23]; *X. songae* [23]; *Arboroharamiya jenkinsi* [71]). Euharamiyida, as a newly recognized clade, forms the sister taxon of Multituberculata in a recent study [23]. These species are possibly among the most important discoveries in Mesozoic mammals from China. They provided a suite of new morphological features that supports the mammalian affinity of the group that has been known since at least the 1840s. *Shenshou lui* was based on four well-preserved specimens, providing the only

example of a new mammal species being named on the basis of more than one specimen from the Jehol and Yanliao biotas. Because the conventional “haramiyidans” were considered as a paraphyletic group [72-74], a view supported by phylogenetic analysis [23], I will use “haramiyidans”, with the name placed between quotation marks, in my discussion.

Multituberculata (*Rugosodon eurasiaticus* [75]; *Sinobaatar lingyuanensis* [76]; *Sinobaatar xiei* [77]; *S. fuxinensis* [77]; *Kryptobaatar mandahuensis* [37]; cf. *Tombaatar* sp. [38]; *Liaobaatar changi* [77]; *Heishanobaatar triangulus* [78]; *Kielanobaatar badaohaoensis* [78]; Multituberculata gen. et sp. nov. [personal observation]). Most multituberculate species in the list came from the coal mine of Fuxin. The Late Cretaceous Bayan Mandahu locality in the Inner Mongolia also produced a considerable number of multituberculate and other mammal specimens, but most of them are yet to be described. In addition to *Kryptobaatar mandahuensis*, a potential new genus and species, currently treated as cf. *Tombaatar* n. sp., was mentioned from Bayan Mandahu [38] and is included in the study. Moreover, there are specimens representing at least two new mammals from the Upper Cretaceous Qiupa Formation of Luanchuan County, Tantou Basin, Henan Province [79]. One mammal is a new genus and species of multituberculates and is currently being investigated by my colleagues and myself. As the study is completed (although yet to be published) I will include it here as Multituberculata gen. et sp. nov. The other mammal is probably a metatherian, represented by multiple skulls and skeletons, but is not included in the diversity count because its status of study is unclear.

“Symmetrodontans” (*Zhangheotherium quinquecuspidens* [32]; *Maotherium sinensis* [80]; *Maotherium asiaticus* [81]; *Akidolestes cifellii* [82]; *Heishanlestes changi* [83]; *Manchurodon simplicidens* [25]). Taxonomy and phylogeny of “symmetrodotans” are poorly known and probably paraphyletic. I follow Kielan-Jaworowska et al. [9] and use “symmetrodontans” in a descriptive, not taxonomic, sense.

“Eupantotherians” (*Nanolestes mckennnai* [43]; *Mozomus shikamai* [84]). I follow Kielan-Jaworowska et al. [9] in treating “eupantotherians” as stem cladotherians.

Metatheria (*Sinodelphys szalayi* [85]). *Sinodelphys szalayi* is by far the only known species assigned to Metatheria from the Jehol Biota. As in the case of *Eomaia*

and *Acristatherium*, the holotype specimens of these species are either crushed or the upper and lower dentitions are in locking occlusion. Therefore, some of the dental features on the tooth crown that are most diagnostic for eutherians and metatherians are not known.

Eutheria (*Juramaia sinensis* [86]; *Acristatherium yanensis* [87]; *Eomaia scansoria* [86]; *Kennalestes sp.* [36]; *Endotherium niinomii* [88]; *Zhangolestes Jilinensis* [89]). As discussed below, *Juramaia* was considered a eutherian from the Middle-Late Jurassic (*ca.* 160 Ma) and is 35 million years older than *Eomaia*. Although there is no reason to doubt the presence of eutherians in the Jurassic or earlier, it is preferable not to consider the age of *Juramaia* as being assured, because the age determination of these floating specimens requires more convincing evidence and should be cautiously used.

Age determinations for the biotas remain open to debate. The most complex ones concern the Jehol and Yanliao biotas because the fossils grouped into the two biotas originate from multiple localities that are tens or hundreds of kilometers apart. In my own field observations, rock sequences in most localities have a restricted exposure and their accurate stratigraphic division and correlation is challenging. Numerous studies on radiometric dating and biostratigraphic correlations of the strata generating the biotas have been conducted, as reviewed recently for the Jehol Biota [90] and for the Yanliao Biota [45], respectively. The authors concluded that the Jehol Biota comprises organisms from a series of localities (Fig. 2) that span a time interval of approximately 10 million years from 130 to 120 Ma [90]. The views regarding the temporal range of the Yanliao Biota are more diverse, partly because of the uncertainty on stratigraphic correlations between the Daohugou beds and the Tiaojishan and Jiulongshan formations [91-94]. The Yanliao Biota was tentatively considered to be close to the Middle-Upper Jurassic boundary [45]. Given that the ages of the strata producing the Yanliao mammal fossils were usually referred to the Callovian or Oxfordian (see Sullivan et al. [45] for detailed discussion), it seems that these sites may be regarded as spanning a time interval of roughly nine million years from the base of the Callovian (166.1 Ma) to the end of the Oxfordian (157.3 Ma) [95]. Thus, there is a 30 Ma temporal gap between the youngest component of the Yanliao Biota and the oldest component of the Jehol Biota [45].

Relevant to the Yanliao Biota are the mammaliaforms from the Junggar Basin of northern Xinjiang. Fossils of mammaliaforms were reported from two strata: the Qigu Formation [43] and the Shishugou Formation [39,42]. The Qigu Formation was considered to be Late Jurassic (Oxfordian) based on palynomorph data [43]. The isotopic age of the tuff from the lower part of the Qigu Formation gave the age of 164.6 ± 1.4 Ma [96,97]. Based on the Geological Time Scale 2004 [98], in which the base age of the Calovian was 164.7 ± 4.0 Ma and that of the Oxfordian was 161.2 ± 4.0 Ma, it was concluded that the bulk of the Qigu Formation was formed during the Callovian, that is, the latest Middle Jurassic [97]. However, in the Geological Time Scale 2012 [95] (also in the International Chronostratigraphic Chart issued by the International Commission of Stratigraphy 2014), the base ages for the Calovian and Oxfordian were adjusted to 166.1 Ma and 163.5 Ma, respectively. Therefore, the Qigu Formation most likely traverses the boundary of the Middle-Late Jurassic. Similarly, the age of the Shishugou Formation probably spans the latest Middle Jurassic and the earliest Late Jurassic [99]. The $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the intercalated tuff at the Wucaiwan section yielded dates between 158.7 ± 0.3 Ma and 161.2 ± 0.2 Ma [100], which fall in the middle of the Oxfordian [95]. If these dates are correct, it is likely that the Shishugou mammal assemblage is slightly younger than that of the Qigu. Mammals known from the Jurassic of the Junggar Basin are dominantly euharamiyidans and docodontans [42,43]. Based on the dating data and mammaliaforms, I consider the Shishugou/Qigu assemblage to be roughly correlative to the Yanliao Biota, and despite differences at the generic level, these mammaliaforms as a whole represent an evolutionary stage similar to that of the Yanliao Biota.

Disparity and evolutionary patterns of mammals

Many specimens of the Chinese Mesozoic mammals discovered during the last two decades are well-preserved skeletons, although in most cases crushed. A few examples of the specimens are illustrated in Fig. 4 to show the quality of the preservation. The superb preservation of the specimens, particularly those from the Yanliao and Jehol biotas, may be attributed to various mass mortality events and taphonomic processes related to volcanism [57,101,102], but the mechanisms that resulted in various qualities of preservation may be complicated. These iconic fossils present a great amount of morphological data previously unknown in Mesozoic mammals and thus shed light on

biology and life styles of previously poorly known Mesozoic mammals, for example the “haramiyidans” [23,52,71]. This has significantly contributed to the understanding of evolutionary patterns of mammaliaforms during the Jurassic and Cretaceous periods.

From their temporal distributions, the known Chinese Mesozoic mammaliaforms may be divided into at least five or six evolutionary stages, represented by the Early Jurassic Lufeng, Middle-Late Yanliao, Early Cretaceous Jehol, late Early Cretaceous Fuxin, Late Cretaceous Bayan Mandahu and perhaps latest Cretaceous Luanchuan assemblages (Fig. 3). These assemblages show an interesting evolutionary pattern in which the Early Jurassic species of mammaliaforms, typically represented by *Sinoconodon* and *Morganucodon*, represent the initial diversification of basal mammaliaforms in the fossil record of China. These forms were generally primitive, have small body sizes and possess the postdentary bones (including *Hadrocodium*; see comments in reference 23). They are characterized by having the typical “triconodont” teeth in which three main cusps are aligned mesiodistally. During the Middle to Late Jurassic, mammaliaforms experimented with major adaptive radiation for various life styles [103]. In addition to the general terrestrial life style, represented by *Pseudotribos*, *Megaconus* and *Rogosodon* [52,58,75], there were morphologically specialized forms adapted for swimming (*Castorocauda* [53]) and gliding (*Volanticotherium* [54]). Most recent findings of the euharamiyidans [23,71] show that this early group of mammals was exclusively tree dwellers. Compared to the early therians that were interpreted to be scansorial/arboreal [85, 86], the gracile body and limbs of euharamiyidans provide the most convincing evidence for scansorial/arboreal life among major groups of Mesozoic mammals. The forestry life style of “haramiyidans” may explain their poor fossil record despite being known since the Late Triassic [72-74].

The Early Cretaceous Jehol was dominated with eutriconodontans and trechnotherians (“symmetrodontans and therians). The late Early Cretaceous Fuxin Biota has more multituberculates, although eutriconodontans and trechnotherians are also common. In the Cretaceous biotas, docodontans and euharamiyidans appeared to be absent (Fig. 3). It is interesting that the taxonomic diversity and the functional morphologies represented by Chinese Mesozoic mammals are generally consistent with the conclusion that there was a decline in diversity of molar types of mammals during the mid-Cretaceous angiosperm radiation [104]. Moreover, at least in the known

Chinese records, it appears that types of locomotion, such as swimming, climbing (arboreal) and gliding, also decreased along with the molar types during the same period of time. Conversely, the body size of eutriconodonts reached an extreme among Mesozoic mammals in the Jehol Biota, as represented by *Repenomamus giganticus* [68] (Fig. 4d). The body size and complexity of the tooth pattern in multituberculates also increased, demonstrating an adaptive shift towards increased herbivory. This trend continued into the Cenozoic, as recognized by Wilson et al. [105]. In the Late Cretaceous eutriconodontans faded away and multituberculates and therians continued to diversify. This pattern is clearer when the fossil records from other parts of Asia, such as those from the Djadokhta Formation of South-central Mongolia [36], are also considered.

The morphological disparity shown in the Chinese Mesozoic mammals not only showed us the adaptive experiments in early mammals, but also provided evidence to test some hypotheses for mammalian evolution. For instance, one hypothesis attributed the success of therians to their scansorial or arboreal locomotion as many early therians were considered to be scansorial or arboreal [85,86,106-109]. It was argued that arboreality increases longevity in mammals [106] and that the grasping ability and flexion in arboreal mammals could have played a key role in the radiation of therians [107]. However, in all known Mesozoic mammals, euharamiyidans as a group are the ones that possess perhaps the most convincing morphological evidence for arboreal or tree dwelling life. Of the euharamiyidans whose skeletal materials were known [23,71], all have a gracile skeleton; this is also true for *Haramiyavia* [110]. In particular, the manus and pes of euharamiyidans are characterized by having relatively short metapodials and long phalanges, an adaptation for grasping as in many extant arboreal mammals [23,71]. Thus, this arboreal group may function as an “experimental control” that contrasts the arboreality-advantage hypothesis for therian radiations. They show that arboreality alone did not give euharamiyidans any advantage over other contemporary mammals. This is particularly interesting when euharamiyidans are compared with multituberculates as both groups have a similar tooth pattern and palinal chewing motion in mastication. Multituberculates survived into the Cenozoic and their diversity and disparity increased significantly around the K-Pg boundary [105], whereas euharamiyidans probably survived into the Early Cretaceous, if the Hahnodontidae were interpreted as “haramiyidans” [74,111]. It would be an interesting

research topic to explore whether the declination, or perhaps extinction, of this arboreal mammal group resulted from changing floras owing to the angiosperm radiation [112-114] and the accompanied radiation of insect pollinators in the Early Cretaceous [115-117].

Divergence of placentals and therians

The higher-level phylogeny of mammals, especially when Mesozoic mammals are considered, remains unresolved. Fig. 5 presents four hypotheses that were simplified from some recent phylogenetic studies [23,52,118-120]. The phylogenetic relationships are directly related to understanding the divergence time and evolutionary pattern of mammals during geological history. Among many existing issues, I focus my discussion in this section on phylogenetic relationships and divergence times of placentals and therians, to which the Mesozoic mammals from China have contributed considerable data. However, this additional data may complicate the issues even further

During the last two decades, numerous studies investigated the relationships and divergence time of placental mammals based on molecular data and on morphological or combined data. A considerable discrepancy between research results from the two schools is that the divergence time of placental mammals extended into the Cretaceous by estimation of molecular clocks in many studies [121-127], much older than the earliest known fossil records. For instances, the divergence time of the placental mammals was estimated as 98.5 Ma [124], 101.3 [125], 88–90Ma [127], or 72–108 Ma [126]. In contrast, phylogenetic analyses based primarily on morphological data have not demonstrated the presence of unambiguous placental mammals that predated the Cretaceous-Paleogene (K-Pg) boundary at about 66 Ma [85,86,109,128,129], although there is an indication of potential placental mammals in the Latest Cretaceous [130]. The uncertainty derived from the discrepancy was illustrated by a question mark associated with a dashed line in Fig. 5. The divergence time of therians seems less controversial, but differences are also present between the fossil record and molecular dates. The molecular clock estimated the divergence time of therians (the split of lineages containing marsupials and placentals, respectively) as 147.7 Ma [124], 190 Ma [125], 168–178 Ma [127] or 168.5–191.5 Ma [126]. By far, the earliest known eutherian mammal is *Juramaia* from the Middle-Late Jurassic Tiaojishan Formation (~160 Ma) [108]. *Eomaia*, another eutherian species, from the Yixian Formation was

considered to be 125 Ma [86], coeval with the oldest known metatherian *Sinodelphys* [85]. The age determination of *Eomaia* was regarded as less reliable than that of *Acristatherium*, however the two eutherians were deemed to be equivalent in age within a range from 123 to 125 Ma and *Acristatherium* was phylogenetically more basal than *Eomaia* [87]. Recent phylogenetic analyses based on morphological data [23,52,71,75,85,108] show that *Juramaia* and *Eomaia* were stem eutherians, whereas *Sinodelphys* was a stem metatherian. If the age of *Juramaia* is correct, then the crown therians have a divergence age at least as old as 160 Ma. However, excepting the estimate of 147.7 Ma [124], which is younger than the age of the oldest known eutherian *Juramaia*, most of molecular dates are older than the age of known fossils. *Juramaia* and *Eomaia* as basal eutherians do not provide much insight on the resolution of placental divergence, but their placement within the crown Theria was thought to reduce and resolve the discrepancy between the previous fossil record and the molecular estimate for the placental–marsupial divergence [108].

In an effort to resolve the discrepancy between the fossil record and the molecular estimate, new methods have been employed in some molecular analyses, which have generated relatively young divergence ages for placental mammals [131,132]. However, the discrepancy will probably persist not only because the molecular dates remain controversial [126] but also because challenges in the fossil record. For instance, the earliest eutherians were mainly from the Early Cretaceous during a time interval from 112 to 125 Ma [9], leaving a 35-million-year gap in the fossil record between *Juramaia* and the next oldest eutherian. In addition, the morphology of *Juramaia* does not seem to be significantly more primitive than those of early Cretaceous eutherians, such as *Eomaia*, *Acristatherium*, *Prokennalestes* [133,134] and *Montanalestes* [135], which would suggest an unusually low rate of morphological change in the eutherian evolution during the 35 million years. Nevertheless, any eutherian fossils unearthed in future fieldwork from strata dated between 160 and 125 Ma would be highly significant in understanding the evolution of eutherians. It is also helpful if another specimen of *Juramaia* is recovered from strata with a similar age of the holotype; it will greatly increase the confidence level on the age of the earliest eutherian.

Furthermore, if the placental mammals diversified immediately after the K-Pg boundary [109], there is a considerable time lag of *ca* 95 million years between

Juramaia, or 60 million years between *Eomaia* or *Acristatherium*, and the origin of placental mammals. Even compared with the maximum date (108 Ma) of placental divergence estimated by the molecular clock [126], the time lag is still significant. If considering only the molecular dates in the studies cited above, the time lag between the metatherian/eutherian split and the origin of placental mammals could range from about 40 million years to 120 million years. These age differences from both fossil records and molecular dates imply that the origin of placental mammals took place following a long “fuse” [136] after eutherians split from metatherians.

Divergence of mammals

Similar to therians, the divergence of mammals is not so rigorously debated as in the case of placental mammals. The molecular clock either fixed the divergence time of mammals at 166.2 Ma [124] or estimated it as 217.8 Ma [125], 174-192 Ma [127] or 162-193 [126]. The divergence time of mammals estimated from fossils depends on both the age of the fossils and the higher-level phylogeny that involves major groups of Mesozoic mammals, particularly the phylogenetic placement of Allotheria [3], an extinct group that include “Haramiyida” and Multituberculata. Multituberculates are the most diverse and best-known group of Mesozoic mammals [9, 137]. The oldest known multituberculate (*Kermackodon*) is from the Middle Jurassic [111] and the youngest species persisted into the Eocene [138,139]. Fossils of “haramiyidans” were known at least as early as in 1847 [140], but this archaic group has been known primarily from isolated teeth [43,72,111,141-150]. The oldest “haramiyidans”, such as *Theroteinus* [145] and *Haramiyavia* [110] came from the Late Triassic, coeval with morganucodonts [74,111,143]. *Haramiyavia*, represented by dentition and some postcranial materials, has remained the best-known taxon of the group until recent reports of several euharamiyidans from the Yanliao Biota [23,71]. *Megaconus* was also from the Yanliao Biota and placed in “Haramiyida” [52], but as mentioned above, its morphology is uncertain; it could be a stem mammal or a multituberculate [23]. If the former, then the allotherian-type tooth pattern would have to evolve independently at least twice.

As members of “haramiyidans” were among the oldest mammaliaforms, the phylogenetic position of “haramiyidans” significantly affects the divergence of mammals [151]. If “haramiyidans” were separated from multituberculates and placed

outside the mammals, and multituberculates fell within the mammals (Fig. 5b, d), then mammals would take their origin in the Middle Jurassic. This indicates that numerous similar craniodental and postcranial features must have evolved independently in “haramiyidans” and multituberculates during different periods of time [23,151]. If Allotheria (multituberculates + “haramiyidans”) as a clade was placed outside the mammals (Fig. 5c), then numerous similar cranial and postcranial features in allotherians and other mammals must still have evolved independently. In contrast, if multituberculates and “haramiyidans” form the clade Allotheria that are placed within mammals [23,71] (Fig. 5a), the similar craniodental and postcranial features in euharamiyidans and multituberculates, as well as those between allotherians and other mammals, can be interpreted as homologous acquisitions instead of parallelisms. This phylogeny suggests an explosive model [136] for the origin of mammals in the Late Triassic [23,151] (Fig. 5a), which is older than estimates of mammalian divergence by some molecular studies (e.g., Bininda-Emonds et al. [124]; dos Reis et al. [126,127]). A Late Triassic origin of mammals actually gains support from the fact that some Late Triassic “symmetrodontans”, such as *Kuehneotherium* and *Woutersia*, co-existed with the Late Triassic “haramiyidan” *Theroteinus* [152-154]. As “symmetrodontans” were universally considered as mammals [9], their oldest fossil records would suggest a Late Triassic origin of mammals even if allotherians were placed outside of the crown.

The phylogeny proposed by Bi et al. [23] has some novel relationships of mammals. Within mammals a new clade Euharamiyida was recognized that forms the sister group of Multituberculata. In addition, primitive “haramiyidans”, such as *Haramiyavia* and *Thomasia*, are positioned as stem allotherians. This relationship suggests that euharamiyidans and multituberculates probably evolved from a *Haramiyavia*-like common ancestor, supporting the view that multituberculates evolved from the “haramiyidan” stock [74]. If the teeth with an allotherian-like crown from the Lower Triassic of South Africa were not from mammals, but rather belong to a nonmammalian cynodont [155], then the diversity and geological and geographic occurrences of the earliest known mammals in Eurasia, along with accumulating evidence of related taxa from the Mesozoic of Gondwana landmasses [22], suggest that mammals originated in landmasses belonging to Laurasia at a minimum oldest age of the Late Triassic and had a cosmopolitan distribution into the Jurassic and Cretaceous. I consider this phylogeny [23] to be the most parsimonious hypothesis that best

incorporates available data of morphology, phylogeny and fossil records of earliest mammals and is consistent with results of many other recent phylogenetic analyses [71,75,119,156]. It refocuses our research efforts on a basic issue: how the allotherian tooth pattern evolved during the early evolution of mammals (see below).

Evolution of mammalian middle ear

The Mesozoic mammals discovered during the last two decades in China have provided a suite of new data for us to understand the character evolution of early mammals. Notably, these include researches on evolution of obtuse-angled molars [70], tribosphenic molars [58], limb and foot structures [58,60,76,82,85,86] and vertebral column [23,61]. The most important contribution, however, came from studies related to the evolution of the mammalian middle ear complex on which I will focus my discussion. The incorporation of the lower jaw elements and the quadrate of reptilian precursors into the middle ear in the cranium is an innovative character complex of mammals and the transformation has been considered as a classic example of gradual evolution in vertebrates, a subject that has attracted extensive studies (see references 62 and 157). Characters from this complex apparatus are also influential in higher-level phylogenetic analyses of mammals [23, 71,75,119,156,157].

Developmental studies [158,159] have long revealed the homologies of the mammalian ear ossicles. These studies recognized that the malleus is a composite element consisting of the articular and prearticular, that the incus is derived from the quadrate, and that the ectotympanic is from the angular (Fig. 6). It is also known from fossil records that during the synapsid evolution toward mammals, the postdentary bones in the lower jaw of non-mammalian cynodonts were gradually reduced in size and eventually migrated to the middle ear [160-162] (Fig. 6a). In stem mammaliaforms, such as *Morganucodon*, the postdentary bones were greatly reduced in size but still attached to the dentary, serving a dual function for hearing and feeding [161,163,164]. Such a mandibular middle ear in *Morganucodon* [9] has been generally accepted as the prototype that gave rise to the definitive mammalian middle ear (DMME) [161,162]. A key issue during the transformation from the mandibular ear to the DMME concerns the detachment of the postdentary bones from the dentary [61,157,162,165-167], which involves two main events: separation of the ossicles from the dentary and degeneration

of the Meckel's cartilage in adult individuals. The transformation from the mandibular middle ear to the DMME has remained unclear for many decades.

A critical feature that casts light on the transformation came from *Repenomamus*. In the original study of *Repenomamus*, a bony element attached to the distomedial side of the lower jaw was identified as the "postdentary bar" [168], which would be a primitive feature for mammals. Based on the identification, *Repenomamus* was considered as a relic member of a primitive reptile-like mammal, as the name implies. The "postdentary bar" was later reinterpreted as the ossified Meckel's cartilage (OMC) [67,166] because its morphology and relationship with the dentary are closely comparable to the Meckel's cartilage of prenatal and some postnatal extant mammals [167,169-171] (Fig. 6b-c). The OMC was later reported from other eutriconodontans, including *Gobiconodon zofiae* [63], *Yanoconodon allini* [61]; *Liaoconodon hui* [62] and *Chaoyangodens lii* [69]. It was also present in the "symmetrodontan" *Zhangheotherium* [166] and *Maothierium asiaticus* [81]. The presence of the OMC and/or a persistent Meckel's cartilage may be inferred in other mammals that have the Meckelian groove on the medial side of the dentary [166].

The relationship of the OMC with the middle ear was further explored and interpreted as a paedomorphic resemblance to the embryonic Meckel's cartilage of modern mammals [61, 81]. In this scenario, for an adult individual of eutriconodontans and "symmetrodontans" to retain a permanent connection of the ear ossicles to the mandible, it required relatively premature ossification of Meckel's cartilage and its fusion with the ectotympanic [61,81]. The most convincing evidence on the role of the OMC, however, came from *Liaoconodon* [62] (Figs. 4a, 6), which preserved the unambiguous morphology of middle ear ossicles intermediate between the mandibular middle ear of *Morganucodon* and the DMME (Fig. 6); it also retained a clear relationship between the ossicles, OMC and the dentary. The middle ear of *Liaoconodon* shows that the postdentary bones have been detached from the dentary and became the ear ossicles, but they were still associated with the dentary via the OMC and thus affected by mastication. This intermediate condition was defined as the transitional mammalian middle ear (TMME) [62]. The OMC in the TMME was interpreted as a stabilizing mechanism for the detached ossicles that were yet to be supported by any cranial structures. Instead of being a paedomorphic resemblance to the embryologic condition of extant mammals, the TMME was considered as a

phylogenetic stage in mammalian middle ear evolution; the embryonic pattern of the Meckel's cartilage in modern mammals [167,169-175] was regarded as a recapitulation of the phylogenetic stage [62]. Moreover, it was also recognized that the transformation from the mandibular middle ear to the TMME and then to the DMME was a complex process that involved not only the detachment of the postdentary bones from the dentary but also numerous structural changes that were associated with the functions of mastication and hearing [62].

Another issue surrounding the evolution of the mammalian middle ear is whether this complex evolved once or multiple times [162]. Hahn and Hahn ([74]: 190) pointed out: "Thus, the formation of three ear ossicles must have evolved for three times independently among mammals, in the Pantotheria, Australosphenida and Allotheria." If "haramiyidans" were separated from multituberculates and placed outside the mammals, while multituberculates fall within the mammals [52] (Fig. 5b, d), then detachment of the postdentary bones from the dentary could have evolved at least four times independently in "haramiyidans", multituberculates, monotremes and therians. New evidence, however, showed that euharamiyidans are similar to multituberculates in that they lack the postdentary trough and Meckelian groove, suggesting the presence of the DMME [23]. If the reinterpretation that *Haramiyavia* has only the Meckelian groove, not the postdentary trough [23,150], and *Hadrocodium* was reinterpreted as having the postdentary bones (see discussions in references 23 and 175), then detachment of the postdentary bones may have evolved twice independently: in the clade leading to the monotremes and the clade containing Eutricondonta, Allotheria and Trechnotheria; thus the latter groups probably have evolved from a common ancestor that had the TMME.

Evolution of allotherian tooth

If the morphology revealed by the new euharamiyidans helped to resolve the mammalian affinity of this archaic group [23], a fundamental obstacle in our understanding of mammalian character evolution is the question of how the allotherian tooth pattern evolved. This involves both the tooth morphology and masticatory function [72,73,147]. With this problem in mind, I choose to write an unconventional review in which I provide not only a brief summary of what is known, but also cultivate the potential for future research on mammalian evolution. For that purpose I propose a

hypothesis, along with review of related research, on the evolution of the allotherian tooth pattern in the remainder of this text.

The basic allotherian tooth pattern consists of two rows of multiple cusps in the upper and lower molars and is capable of a palinal (posterior), not transverse, chewing motion (Fig. 7c-i). This tooth pattern differs from those of other mammals that evolved from a “triconodont”-like tooth pattern (Fig. 7a, b) to a tribosphenic tooth pattern, in which the lateral side of the lower molar is in contact with the lingual side of the upper molar to form the unilateral occlusion and a chewing motion with a transverse component [72,73,176]. Although morphologies of jaws and teeth have differentiated to reflect trophic specializations in the earliest mammaliaforms, such as the Late Triassic-Early Jurassic *Morganucodon* and *Kuehneotherium* [177], the tooth morphology and chewing motion in contemporary allotherians (“haramiyidans”) are more complex and different from those of *Morganucodon* and *Kuehneotherium*. The allotherian tooth pattern apparently represents a distinctive type of trophic specialization, but phylogenetically it is unclear how this tooth pattern evolved.

Kielan-Jaworowska et al. ([9]: 524) wrote: “One of the most prominent cases of character conflicts resulting in uncertainty in phylogenetic placement concerns multituberculates. Molars of multituberculates resemble those of haramiyidans and nonmammalian tritylodontids. Based on molar characteristics alone, multituberculates are certainly more comparable to haramiyidans. However, multituberculates are far more derived than haramiyidans and tritylodontids in mandibular characters, and in these characters they are more closely comparable to the more derived mammalian clades in the mammalian crown group.” This statement was made at the time when the mandible of “haramiyidans” was known only from *Haramiyavia*, a taxon from the Late Triassic of Greenland in which the presence of the postdentary trough was inferred [110]. However, this feature has now been disputed [23,175] and the discoveries of euharamiyidans from the Jurassic of China have considerably changed the view on the character conflicts in multituberculates and “haramiyidans” by showing the mammalian features of the latter.

Wherever allotherians are placed in the phylogeny of mammaliaforms, it is equally difficult to derive the allotherian tooth pattern from any known mammaliaforms or their close kin, including tritylodontids. The phylogeny [23] (Fig. 5a) indicates that the allotherian tooth pattern must have derived from a “triconodont”-like or even a

reversed triangular (an obtuse-triangle) tooth pattern by adding an additional cusp row on the tooth. With the preferred phylogeny [23], the complex problems surrounding allotherians, in both tooth evolution (and many other cranial and postcranial structures) and their relationships, can be reduced to one basic issue: whether the tooth pattern of primitive allotherians, represented by *Haramiyavia*, can be derived by developing extra cusp row, or rows, from a “triconodont”-like tooth. Whether the *Haramiyavia*-like tooth can give rise to those of the euharamiyidans and multituberculates is also an important issue but is probably less complex. The hypothesis I propose on the evolution of the allotherian tooth pattern is illustrated in Fig. 7, based on new data available recently [23, 71].

In interpreting the tooth evolution of allotherians from a “triconodont” tooth, two assumptions need to be made. The first assumption is that the continuity of the tooth contact and function must be maintained in the upper and lower dentitions during the evolution of these tooth patterns. If we call the wear facets on the buccal sides of the lower cusps and lingual sides of the upper molar in the “triconodont” tooth as the primary wear facets, then wear facets homologous to these primary wear facets should be traceable in allotherians even if additional cusp rows were added (Fig. 7). In addition, the primary wear facets on successive teeth, such as M1 and M2 in the same dentition, must align mesiodistally with each other to keep the chewing function working properly.

The second assumption is that the occlusal relationship of *Haramiyavia* should be consistent with what we observed in the euharamiyidans. Contrasting to the conventional view that the labial cusp row of the lower molar occludes with the lingual row of the upper molar in “haramiyidans” [72,73,110,147], a critical feature revealed by the euharamiyidans from the Jurassic of China is that in “haramiyidans” the lingual cusps of the lower molar occlude in the valley of the upper molar, similar to the occlusal relationship of M2/m2 in multituberculates [178,179]. This occlusal relationship was reinterpreted to be in *Haramiyavia* [23,71] (Fig. 7d), which differs from the original interpretation [110]. Butler [73] noted that the single specimen of *Haramiyavia* is little worn and no wear scratches have been reported. In addition, the lingual portions of m1-2 of *Haramiyavia* were broken, so that wear facets on those teeth are unknown. Therefore, new evidence is needed to clarify the occlusal relationship of *Haramiyavia*. It is clear, however, that row A cusps of *Haramiyavia* are

the largest cusps of the upper molar and a1 is the largest cusp of the lower molar, consistent with those of euharamiyidans from the Jurassic of China and with M2/m2 of multituberculates ([9,137]; personal observations). Moreover, the reinterpreted occlusal relationship of *Haramiyavia* (Fig. 7d) better explains the development of C cusps on the buccal side of the upper molars because the buccal cusps of the lower molar may have occluded between A and C cusps of the upper molar.

Under these two assumptions, if the allotherian tooth pattern, as represented by *Haramiyavia*, was derived from a “triconodont” tooth by adding secondary cusp rows, the primary wear facets can only be on the buccal surfaces of the lingual cusp row of the lower molars (Fig. 7). The lingual cusps of the lower molar should therefore be the primary cusps, presumably homologous with the main cusps of “triconodont” tooth. The buccal cusp row has to be secondary. With the occlusal constraint from the lower molars, the primary wear facets should be on the lingual sides of row A cusps of *Haramiyavia* (Fig. 7). In other words, A cusps should be homologous with the main cusps of the upper “triconodonts” tooth. Row B (lingual) and C cusps (not a cusp row yet) on the buccal side of row A in upper molars of *Haramiyavia* must be secondary.

It was considered that development of extra cusps on the lingual cingula is common, but buccal cingula are rare on lower molars [72] except for *Hallautherium* [144]. However, orientation of isolated teeth in early mammals is not always certain, as has been demonstrated in the case of eleutherodontids, in which a left tooth was probably identified as the right one [23, 71]. It was noted that the teeth of *Haramiyavia* are more similar to those of *Sinoconodon* and *Morganucodon* than to those of multituberculates in the lateral view [180], but the tooth pattern of *Haramiyavia* is more comparable to those of *Woutersia*, a taxon that co-existed with *Theroteinus*, another Late Triassic “haramiyidan” [153,154]. There is no convincing evidence to rule out the possibility that the additional (minor) tooth cusps were buccal in *Woutersia* (assuming they are lower teeth). Parrington ([141]: 269) already noted that “Finally the discovery of lower molars of *Eozostrodon*, which have developed a series of small cusps on their outer [buccal] faces, lends some support to the view that the Triconodonta might also be ancestral to the Multituberculata, a view already made possible by the teeth known as haramiyids.” The p4 morphology in some early multituberculates may also lend support for development of cusps on the buccal side. When commenting on Hahn’s work [181,182], Van Valen ([178]: 198) pointed out: “Further, Hahn has shown that the

last premolar of *Paulchoffatia* had a row of cingulum cusps like the second row of m1, and that the premolars primitively functioned more or less like the molars.” The “cingulum cusps” referred to by Van Valen were on the buccal side of the ultimate premolars of paulchoffatiids, such as those *Kuehneodon* and *Guimarotodon* [181-183]. Butler and MacIntyre ([72]: 452) further commented that “In both cases the buccal row of cusps is confined to the posterior part of the tooth, and the cutting blade of multituberculates seems to be an exaggeration of the A row.” These studies show that cusps and cuspules could be added on the buccal side of the main cusp row of lower cheek teeth in allotherians. The fact that the buccal cusps of lower molars in *Haramiyavia*, *Thomasia* and all euharamiyidans are always smaller than the lingual molars suggest the former to be more likely secondary. Based on these data, I illustrated a hypothetical stage (Fig. 7j2) that represents the initial development of the secondary cusp row.

Related to the tooth morphology is the transformation of the chewing motion from the “triconodont” tooth to the allotherian tooth pattern. In allotherians the chewing motion is palinal, that is, the lower jaw (teeth) could only move distally, which differs from the unilateral occlusion with transverse jaw movement in “triconodonts” and its derivatives in which a triangular arrangement of main tooth cusps are gradually developed [72,73,176,184]. An intermediate condition for the transformation could be the orthal occlusion in *Haramiyavia* [110]. However, it was considered that a palinal component, probably less than in *Thomasia*, may exist in the chewing motion of *Haramiyavia*, but the little worn specimen can not confirm this [73]. Nevertheless, Hahn and Hahn [74] thought that the main evolutionary step from *Thomasia* to the oldest multituberculates is the change from orthal to palinal mastication and correlated that the mandible adapted to the new mode of chewing. Modification of the chewing function requires changes of the masticatory apparatus, such as reshaping the mandibular condyle and glenoid fossa, as in euharamiyidans [23] and multituberculates [9] in which the mandibular condyle is more vertically orientated and the glenoid fossa is mesiodistal without the postglenoid process. In short, although evidence is far from robust, there seems to be enough evidence to support the possibility that the primitive allotherian tooth pattern was derivable from a “triconodont”-like tooth in the Late Triassic or earlier.

From the *Haramiyavia*-like dentition to those of euharamiyidans and multituberculates, the common and most significant difference is that *Haramiyavia* has three upper and lower molars, but all known euharamiyidans and multituberculates have only two upper and lower molars. In a recent communication my colleague (Anne Weil, May 13, 2014) raised the possibility that P4/p4 of multituberculates may actually be homologous with M1/m1 of other mammals. Although this is a novel and interesting topic for allotherian tooth evolution, I will not discuss it in this work, but focus my discussion on tooth pattern evolution within allotherians.

For euharamiyidans, M1 and M2 are aligned mesiodistally as in *Haramiyavia*. Thus, euharamiyidans could simply retain the occlusal pattern and wear facets of *Haramiyavia* with the exception of the loss of C cusps in the upper molar. For multituberculates, the occlusal relationship is more complicated because M2 is one cusp row lingual to M1. In commenting on the work on paulchoffatiids by [181,182], Van Valen ([178]: 198) already noted that “The structure of m2, however, is largely duplicated in the enigmatic Rhaetic family Haramiyidae, for which only isolated teeth are known (e.g. [141,142]). A haramiyid ancestry of multituberculates was suggested long before the recognition of paulchoffatiid m2's and, as Hahn notes, the latter teeth support this view.” The problem, however, remains on how we interpret the development of a different cusp row arrangement between M1 and M2 in multituberculates.

In questioning Hahn's early view that M2 is directly distal to M1 in Paulchoffatiidae, Van Valen ([178]: 198) noted “This would (in the most nearly normal occlusion) require that the labial side of both m1 and m2 occlude into the central basin of the respective upper molar. In other multituberculates this is true for M1, but with the more lingual position of M2 it is the lingual side of m2 that occludes there.” Clemens and Kielan-Jaworowska [185] raised similar doubt. Krause and Hahn [179] finally settled the issue in demonstrating that M2 of paulchoffatiids was also one cusp row lingual to M1, as in other multituberculates, and that the lingual cusps of m2 occlude in the valley of M2, as in euharamiyidans (Fig. 7). Thus, the M2/m2 occlusion pattern is present in both “haramiyidans” and multituberculates and is unique among mammals; it is perhaps a synapomorphy of allotherians.

It remains uncertain, however, how the multituberculate M1 condition evolved in relation to M2. Given the first assumption (made above), the only possible primary

wear facet on M1 in multituberculates (the primitive condition in which there are only two cusp rows) must be on the lingual side of the lingual cusp row, which is mesiodistally aligned with the facet on the lingual wear of the buccal cusp row of M2. Considering the tooth of *Haramiyavia* as the prototype, the different cusp row arrangements and occlusal relationships of M1 and M2 in multituberculates may result from the following modifications: C cusps of *Haramiyavia* were developed into a full buccal cusp row but B cusps were suppressed in M1 of multituberculates. In contrast, as in euharamiyidans, C cusps were lost to give rise to the cusp pattern of M2 in multituberculates (Fig. 7g). The resultant pattern is that M2 is one cusp row lingual to M1 in multituberculates.

Finally, in some advanced multituberculates, such as cimolodonts, an additional ridge or cusp row has developed on the lingual side of M1 and the buccal side of M2 [9, 137]. Therefore, the lingual wear facet on the lingual cusp row of m1 is caused by contact with the additional lingual cusps of M1 and is therefore not homologous with that of m2. Similarly, the buccal wear facet on the buccal cusp row of m2, if any, is not homologous with that of m1 in these advanced multituberculates.

Future work

Numerous important specimens were discovered from the Jurassic and Cretaceous periods of China during the last two decades. Many of the specimens were preserved in superb conditions, based on which a considerable number of species belonging to major Mesozoic groups of mammals were recognized. These discoveries provided a great deal of new information on the diversity and disparity of Mesozoic mammals that are largely consistent with the global pattern of evolution in Mesozoic mammals. They allow us to address several problems related to dental, cranial and postcranial structures in early mammals and to reassess higher-level phylogenies of mammals. In particular, the divergences of placentals, therians and mammals as well as evolution of the mammalian middle ear and allotherian tooth pattern are elaborated. However, it is appropriate to mention that a great amount of work is still required. For instance, many of the named species were briefly described, sufficient only for taxonomic purposes and for addressing some outstanding problems in mammalian evolution, but as a useful source of data to be shared by those who are interested in the subjects, those specimens need thorough and systematic descriptions and sufficient illustrations; it is pivotal to

provide robust and convincing morphological data to support current phylogenetic hypotheses and conclusions. In addition to the studies on traditional taxonomy, higher-level phylogenies and evolution of critical characters still need to be explored in depth. Multidisciplinary analyses on biology, taphonomy, ecology, sedimentology, biogeography and geology of these Mesozoic mammals need more attention and probably require a broader collaborative research effort.

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Figure captions

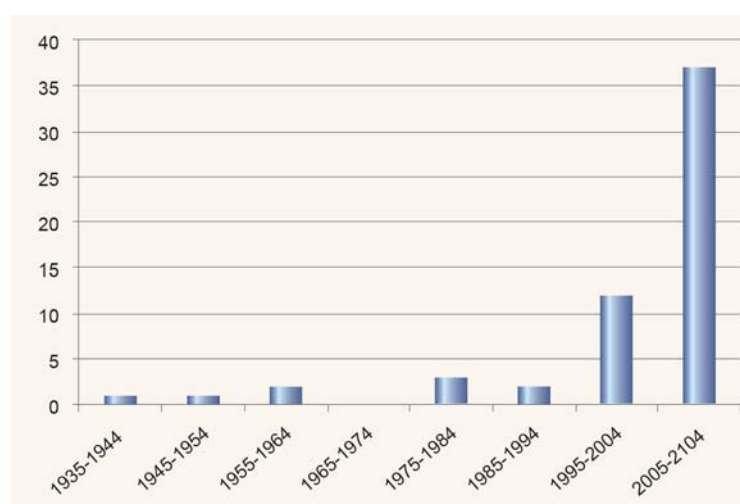


Fig. 1. Number of Mesozoic mammal species of China reported in the last 80 years. See Fig. 3 and Diversity and Distributions for more details.

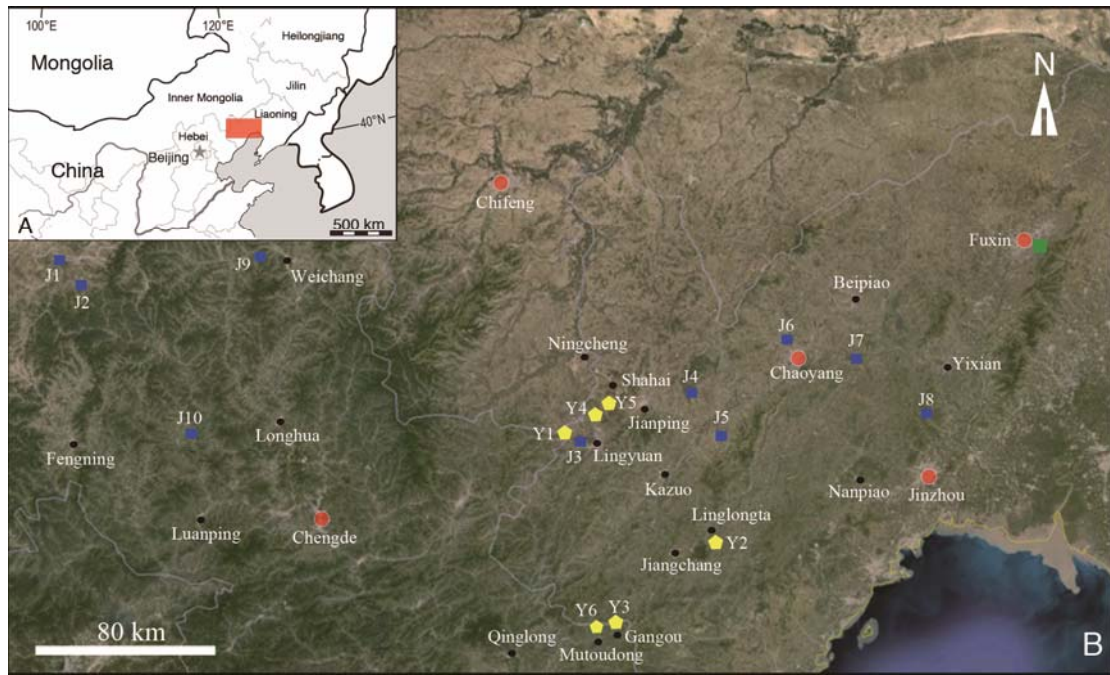


Fig. 2. Geographic map of main fossil localities that yield the Yanliao (Daohugou), Jehol and Fuxin biotas in Northeast China. The red-ish rectangular area in A is shown in detail in B. Red dots represent main cities and black dots are small towns. Yellow pentagons represent localities of the Yanliao (Daohugou) Biota (Y1, Daohugou; Y2, Daxishan [Daxigou]; Y3, Zhuanshanzi; Y4, Wubaiding; Y5, Guancailiang; Y6, Bawanggou [Mutoudeng]). Blue squares indicate localities of the Jehol Biota (J1, Sichakou; J2, Senjitu; J3, Dawangzhangzi [=Fanzhangzi, Y-H Pan personal communication]; J4, Boluochi; J5, Meileyingzi; J6, Shangheshou; J7, Sihetun; J8, Jingangshan; J9, Weichang; J10, Fengshan). The green square represents sites in vicinity of Fuxin and Badaohao, Liaoning. The site map is based primarily on several studies [45,78, 90].

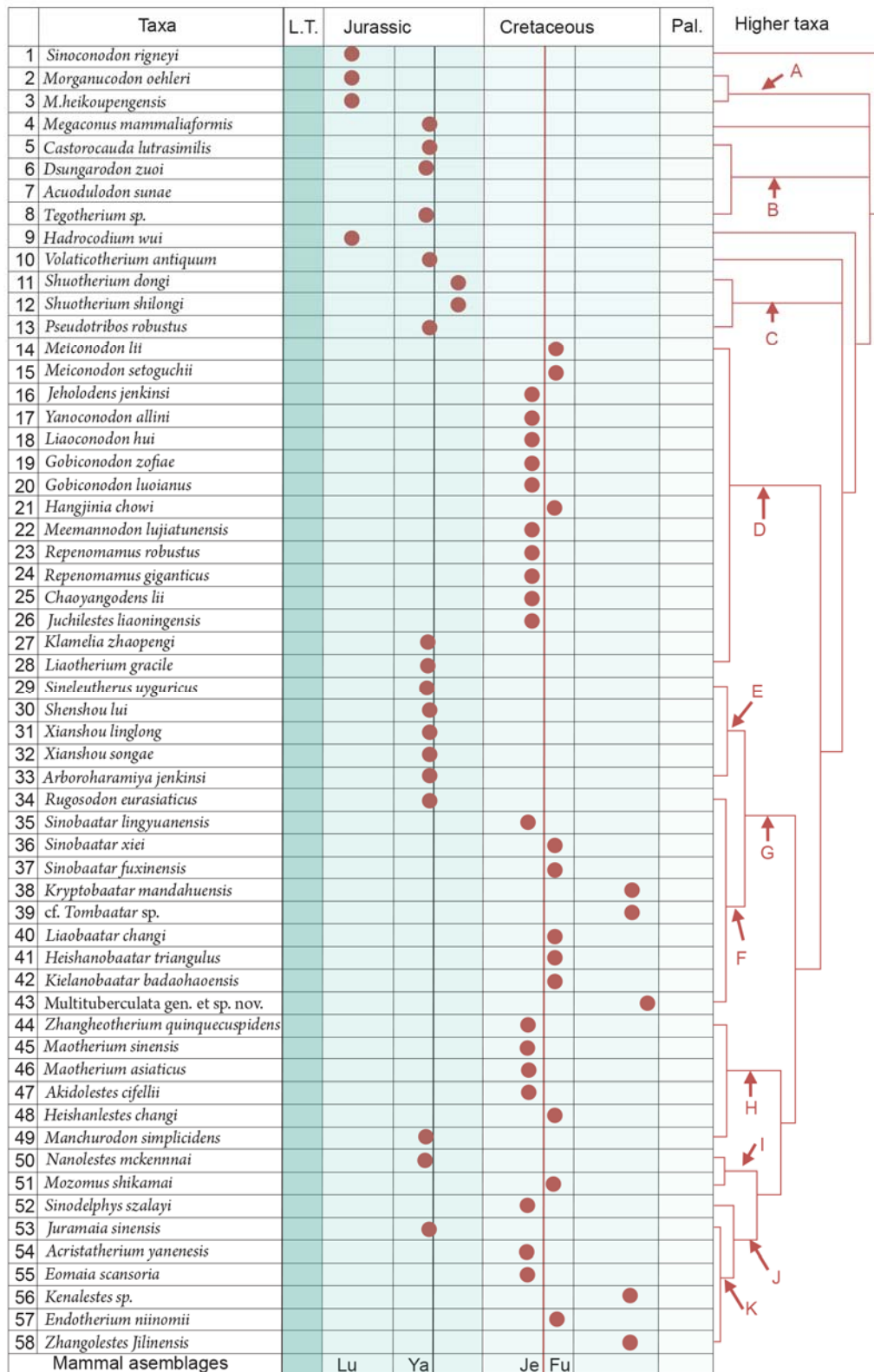


Fig. 3. Temporal distributions of Mesozoic mammals in China. 1-58, Species of Mesozoic mammals in China. **A**, Morganucodontidae; **B**, Docodonts; **C**, Shuotheriids; **D**, Eutriconodonts; **E**, Euharamiyids; **F**, Multituberculata; **G**, Allotheria; **H**, “Symmetrodontans”; **I**, “Eupantotherians”; **J**, Theria; **K**, Eutheria. The simplified

phylogenetic relationship is based on several studies [23,52,71]. The red line separates the Jehol mammals (left) from the Fuxin mammals (right; except for *Hanjinia*) in the Early Cretaceous. The mammal assemblage abbreviations are Lufeng (**Lu**), Yanliao (**Ya**, =Daohugou), Jehol (**Je**), Fuxin (**Fu**) and Bayan Mandahu (**Ba**). Please refer to the original references for detailed information of the biotas and localities for each species in Diversity and Distribution. The mammal assemblage abbreviations at the bottom of the figure are Lufeng (**Lu**), Yanliao (**Ya**, =Daohugou), Jehol (**Je**), Fuxin (**Fu**) and Bayan Mandahu (**Ba**). The chronological frame is based on Gradstein et al. [186].

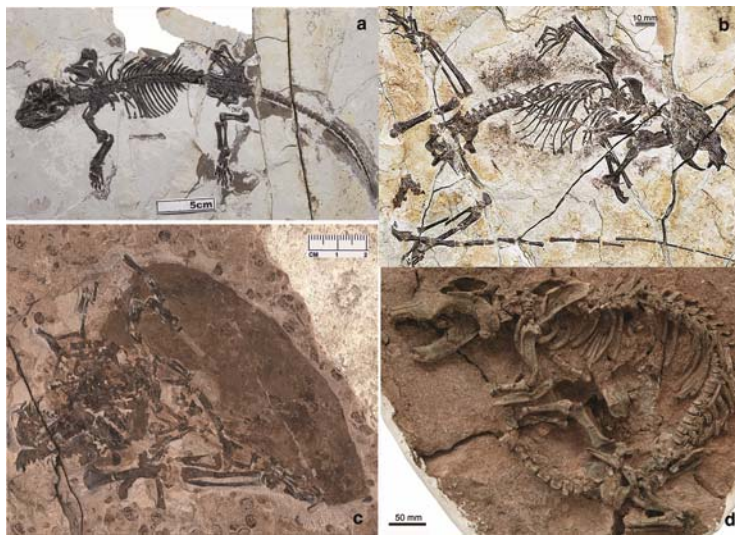


Fig. 4. Mammal fossils from the Yanliao (Daohugou) and Jehol biotas. **a**, *Lioconodon hui* [62]; **b**, *Shenshou lui* [23]; **c**, *Volanticotherium antiquum* [54]; **d**, *Reptomamus giganticus* [68].

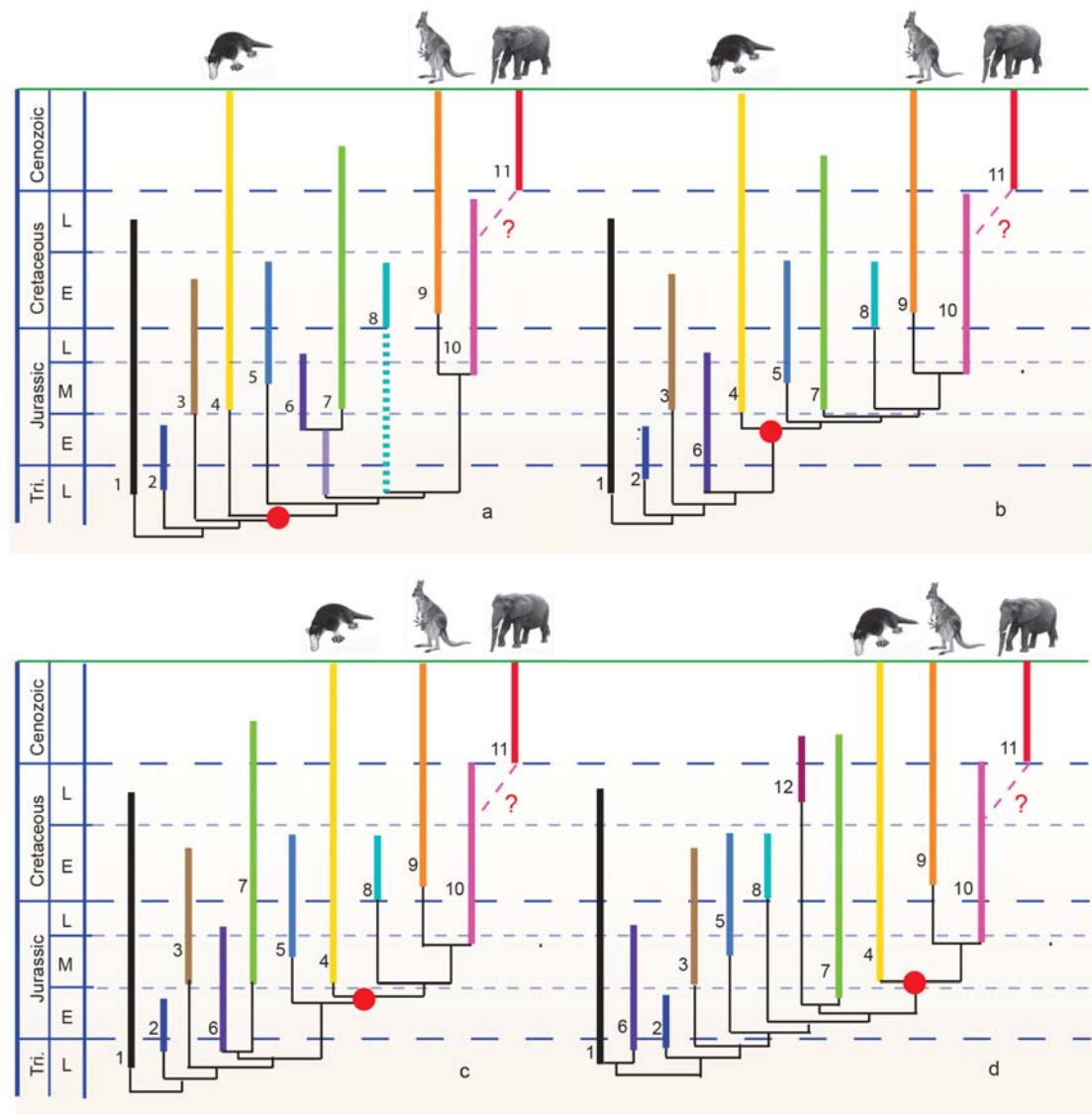


Fig. 5. Four phylogenetic hypotheses of mammals. The red dot indicates the node of Mammalia in each hypothesis. In a-d, the dashed line and question mark between stem eutherians (pink) and placentals (red) indicate the uncertainty about the divergence time of placental mammals. **a**, Hypothesis in which allotherians (multituberculates and haramiyidans) are nested within mammals, modified from several studies [23,71,119]. The light colored stem for groups 6 and 7 represents stem allotherians, such as *Haramiyavia* and *Thomasia*. The dashed part of line 8 indicates older members of “symmetrodontans” (usually not included in phylogenetic analyses, such as *Kuehneotherium* and *Woutersia*) that co-existed with primitive “haramiyidans” in Late Triassic. **b**, Hypothesis in which “haramiyidans” are separated from multituberculates and placed out side of mammals, modified from reference 52. **c**, Hypothesis in which “haramiyidans” and multituberculates form a clade that inserts between *Sinoconodon*

and/or *Morganucodon* and the clade containing eutriconodontids and mammals, modified from Luo et al. [118]. **d**, Hypothesis in which multituberculates are grouped with Gondwanatheria, but the clade is placed outside mammals, whereas “haramiyidans” are clustered with tritylodonts, modified from Gurovich and Beck [120]. **1**, Non-mammaliaform cynodonts (here primarily referred to tritylodonts based on Gurovich and Beck [120] and Liu and Olsen [187]). A similar tree topology, without Gondwanatheria, was presented in Rougier et al. [188] in which multituberculates are the immediate outgroup of the mammals. **2**, *Sinodonodon* and/or morganucodontids (these two taxa are not a natural group; for simplicity of the figure they are merged). **3**, Docodonta; **4**, Australosphenidans (distribution of the clade is based on Rougier et al., [189]). **5**, Eutriconodontans. Eutriconodontans are considered as a natural group that does not include taxa such as *Sinodonodon* and *Morganucodon* [9] but they were also recognized to be paraphyletic in some recent studies [13,23,119,188,189]. **6**, “Haramiyidans” (In hypothesis a, “haramiyidans” are divided into euharamiyidans represented by the dark purple bar and stem “haramiyidans” are represented by the light purple bar.). **7**, Multituberculates. **8**, “Symmetrodontans”. **9**, Metatherians (Marsupials). **10**, Stem eutherians. **11**, Placentals. **12**, Gondwanatheria. In a-d, the dashed line and question mark between stem eutherians and placentals indicate the uncertainty about the divergence time of placental mammals.

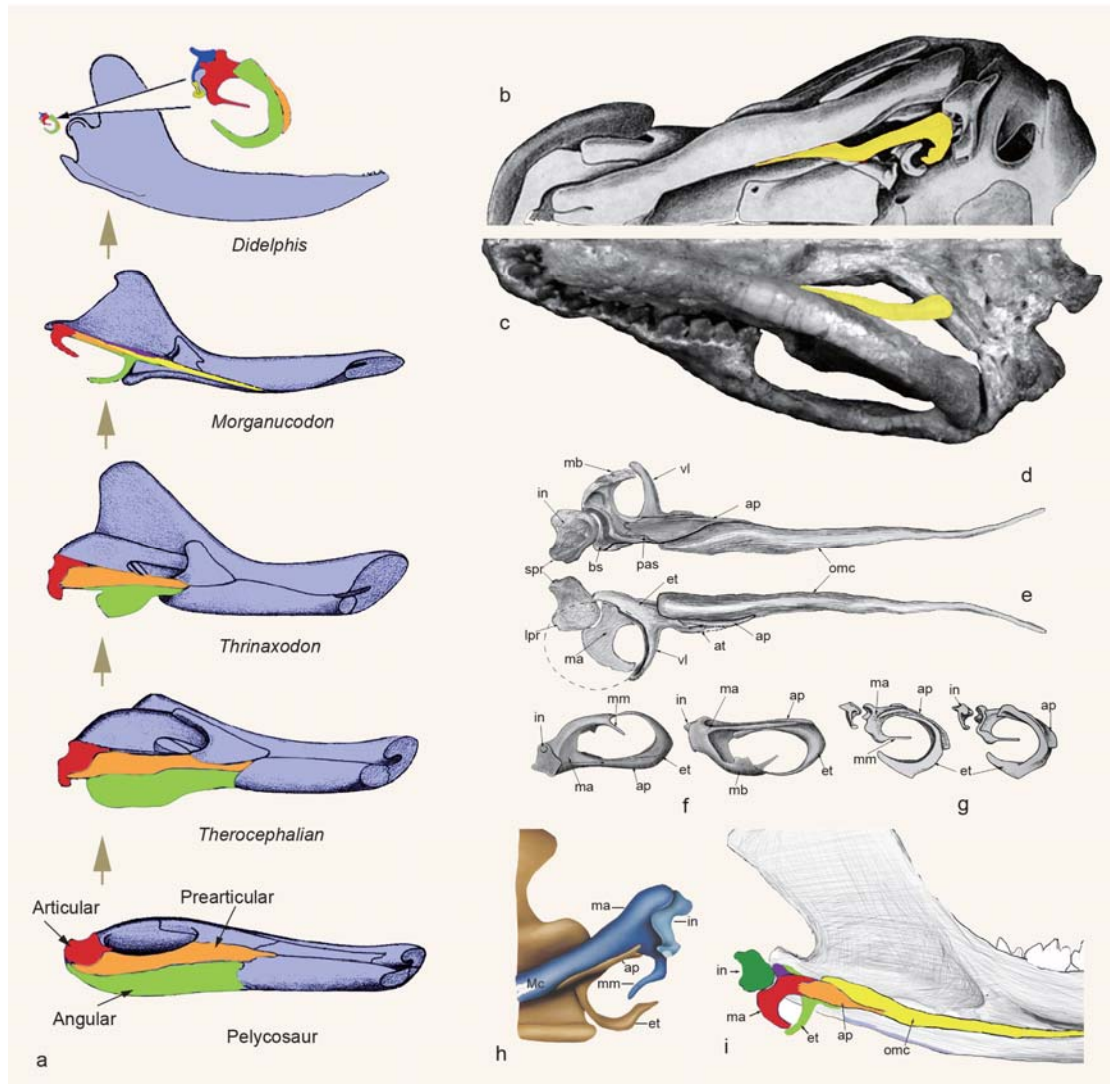


Fig. 6. Homology and transformation of the mammalian middle ear ossicles. **a**, Transformation (reduction) of the postdentary bones from a primitive condition in pelycosaur to the mammalian middle ear as shown in fossils. **b**, Ventral view of the embryological cranium of *Ornithorhynchus* with the Meckel's cartilage marked in yellow. **c**, Ventral view of the skull of *Repenomamus* with the ossified Meckel's cartilage marked in yellow. **d-e**, Medial (dorsal) and lateral (ventral) views of the middle ear ossicles and OMC of *Liaococonodon*. **f**, Dorsal and ventral views of the ossicles of *Ornithorhynchus anatinus*. **g**, Medial and lateral views of the ossicles of *Didelphis*. Ossicles are not on the same scale. **h**, Medial view of the right ear ossicles, ectotympanic and Meckel's cartilage of a pouch young *Macropus rufogriseus*. **i**, Medial view of the transitional mammalian middle ear (TMME) with the ear ossicles detached from the dentary but still associated with the latter via the OMC in *Liaococonodon*. Abbreviations: ap, anterior process of malleus (prearticular); at, anterior

process of the tympanic; bs, boss of surangular; et, ectotympanic (angular); in, incus (quadrate); lpr, long process of the incus; ma, body of malleus (articular); mb, manubrial base of malleus (retroarticular process); Mc, Meckel's cartilage; mm, manubrium of malleus; omc, ossified Meckel's cartilage; pas, prearticular-articular suture; spr, short process of the incus; vl, ventral limb of ectotympanic (reflected lamina of angular). Images are modified from the following works: A [125,162,166,190]; B ([170], with permission from the author); C [67], D-G and I [62]; F [62,171], G [62,161]; H ([173], with permission from the author).

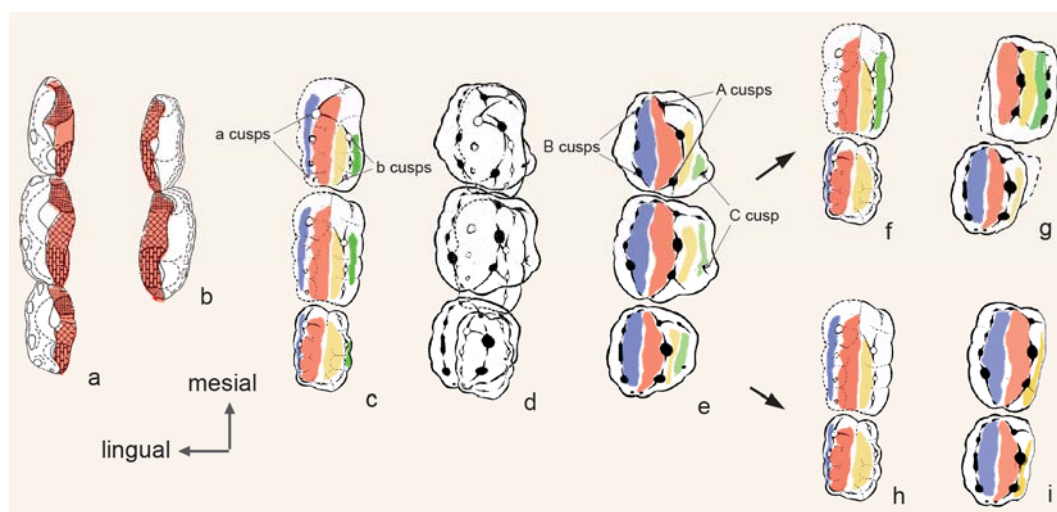


Fig. 7. A hypothesis for transformation of the allotherian tooth pattern from a “triconodont” tooth pattern. **a-b**, Crown views of three lower and two upper molars of *Eozostrodon*, in which the primary wear facets are marked in red on the buccal (lateral) sides of the primary cusps of lower teeth and lingual side of primary cusps of upper teeth. **c-e**, Crown views of lower molars (cusp with empty circle), occlusal relationship of the upper and lower molars and crown views of upper molars (cusp with solid circle) in *Haramiyavia*. Given the reinterpreted occlusal relationship in d, the primary wear facets homologous with those of “triconodont” tooth must be on the buccal side of lingual cusps of the lower molars and lingual side of buccal cusps of the upper molars, indicated in red. **f-g**, Crown views showing the lower and upper molars of primitive multituberculate; they were presumably derived from the *Haramiyavia*-tooth pattern. During the evolution, M2/m2 retained the occlusal relationship of *Haramiyavia* except for loss of C cusps and related wear facets. The primary wear facet (in red) of m1 must be aligned mesiodistally with that of m2 to keep a continuous chewing function; the primary wear facet of M1 must be on the lingual side of the lingual teeth. This is

presumably derived by suppression of B cusps but development of C cusps of *Haramiyavia*. The resultant upper molar relationship in multituberculates is that M2 is one cusp row lingual than M1. (For convenience of comparison, I slightly modified the tooth drawings of *Haramiyavia* to represent those of multituberculates). The dashed line indicates additional ridge or cusp row developed on M1 and M2 in some advanced multituberculates. **h-i**, Crown views showing the tooth pattern of euharamiyidans that are comparable to those of *Haramiyavia*, except for reduction of C cusps in the upper teeth and related wear facets. **j**, Diagram showing the occlusal relationship of the upper and lower molars in cross-sectional view (1, “triconodont”; 2, a hypothetical stage in which secondary cusps were developed on the lingual side of upper molars and buccal side of lower molars (see discussion in the text). 3, *Haramiyavia*, as I interpret; 4, euharamiyidan; 5, M1/m1 of multituberculates; 6, M2/m2 of multituberculates). In box J, A-C and a-b represent cusps of the upper molar and lower molar, respectively. Wear facets presumably homologous are represented by the same color in occlusal views (a-i) and in cross sections (1-6 in j). Sources of figures: a-b modified from Crompton and Jenkins [176]; c-i modified from Jenkins et al. [176].