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The mammal fauna in the Early Cretaceous Jehol Biota: implications for diversity and biology of Mesozoic mammals

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Eleven species belonging to five major groups of mammals (multituberculates, eutriconodontans, 'symmetrodontans', metatherians and eutherians) have been described from the Jehol Biota, Liaoning, China. These fossils came from three horizons of the Yixian Formation: Lujiatun (lowest), Jianshangou and Dawahgzhangzi (highest) beds. Ages and correlations of these beds are still in debate, but are generally accepted as Early Cretaceous. Biostratigraphic distributions of some Jehol mammals corroborate the Early Cretaceous age of the biota. Many species are represented by skulls and articulated skeletons, although in most cases a species is known only from a single holotype that is squashed. These fossils furnish a wealth of morphological data for Mesozoic mammals, from which large character data sets have been amassed to generate competing higher-level phylogenetic hypotheses of mammals. The Early Cretaceous divergence of eutherians is first documented as skull and skeletal fossils. The Jehol mammals indicate a diverse mammal fauna in which species range from 25 g to 14 000 g in body masses, have insectivorous, omnivorous and carnivorous diets (as reflected by their dentitions and by stomach content), and acquire scansorial, possibly arboreal and terrestrial habits (as inferred from articulated skeletons). The well-preserved material helps to clarify some anatomical uncertainties in the study of early mammals, such as an ossified Meckel's cartilage as the occupant for the internal groove on the lower jaw of some Mesozoic species and a dental formula I3-C1-P3-M4/i2-c1-p2-3-m5 for gobiconodontids as suggested by dentitions of several Jehol eutriconodontans. Evidence from cranial specimens of Jehol eutriconodontans also disfavours the brain-expansion model for the detachment of middle ear ossicles from the dentary during evolution of mammals. Copyright © 2006 John Wiley & Sons, Ltd.

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1. INTRODUCTION

The Early Cretaceous is an important period of time in mammalian evolution, during which diverse groups are found in Asia, Europe, North America, South America, Africa and Australia (Lillegraven *et al.* 1979; Kielan-Jaworowska *et al.* 2004). Some of these groups include eutriconodontans, 'symmetrodontans', multituberculates and basal tribosphenic mammals, that were related to metatherians and eutherians. In the last decade numerous excellent specimens of mammals have been discovered from the Early Cretaceous Yixian Formation, Liaoning, northeast China. These specimens encompass about a dozen species representing the major clades of Mesozoic mammals known to date, and provide a considerable amount of morphological data that are critical for understanding the biology, phylogeny and evolution of early mammals.

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The first mammal, a 'symmetrodontan', reported from the Yixian Formation was *Zhangheotherium quinquecuspidens* (Hu *et al.,* 1997). Other species known thereafter include a multituberculate (*Sinobaatar lingyuanensis* Hu and Wang, 2002), five eutriconodontans (*Jeholodens jenkinsi* Ji Q *et al.*, 1999b; *Gobiconodon zofiae* Li *et al.*, 2003; *Meemannodon lujiatunensis* Meng *et al.*, 2005; *Repenomamus robustus* Li *et al.*, 2000; *R. giganticus* Hu *et al.*, 2005), two 'symmetrodontans' (*Maotheirum sinensis* Rougier *et al.*, 2003; *Akidolestes cifellii*, Li and Luo, 2005), a stem metatherian (*Sinodelphys szalayi* Luo *et al.*, 2003) and a stem eutherian (*Eomaia scansoria* Ji *et al.*, 2002).

As Lillegraven and Clemens (in Kielan-Jaworowska *et al.* 2004) pointed out, the study of Mesozoic mammals continues to be dominated by examination of dentition and despite our best efforts, discoveries of high-quality articulated skeletal remains of Mesozoic mammals continue to be extraordinarily rare. The Early Cretaceous Jehol mammal fossils prove to be exceptional in their preservation, most of the described species are preserved as skulls and skeletons and provide a spectrum of morphologies in their dentition, cranium and postcranium. They vary greatly in body sizes, ranging from a mouse-sized creature typical of Mesozoic mammals to dog-sized creatures that are uncommon in early mammals. These species also show diverse life styles from scansorial to terrestrial walker. Tooth morphologies and stomach contents indicate that these species have adapted to various diets, such as omnivorous in multituberculates, insectivorous in 'symmetrodontans' and tribosphenic mammals, and carnivorous in large eutriconodontans. This diversity in species composition, morphologies, body sizes, diets and behaviours, bears importantly on the understanding of the biology of Mesozoic mammals and the relationships of mammals with other vertebrates of the fauna and the environments.

Although the study of Jehol mammals is still at an early stage, in which many reported specimens are still under detailed description and new taxa are to be named, it is a good opportunity to briefly review the published data concerning Jehol mammals. We will first summarize the preservation and occurrences of the Jehol mammals in the Yixian Formation and the diversity of known species, and discuss the age and taxonomic issues. Then we will explore the implications of the Jehol mammals to mammalian phylogeny and divergences, the biology of early mammals, including body mass, diet and locomotion, and finally, the anatomical significance in two selected areas, the ossified Meckel's cartilage and the tooth formula.

For taxonomic terminology used in the review, we follow Rowe (1988) for the crown-group concept of Mammalia. The crown clade of Placentalia includes all living placental mammals and their immediate common ancestor, plus all its descendants, and that of Eutheria consists of Placentalia and its stem taxa. The crown clade of Marsupialia includes all living marsupials and their immediate common ancestor, plus all its descendants, whereas Metatheria include Marsupialia and the stem taxa to it (Rougier *et al.* 1998). Triconodonts, which are taxa traditionally included in the Triconodonta (Jenkins and Crompton 1979), are used informally, because this group of mammals has been shown to be polyphyletic (Rougier *et al.* 1996a, 1999; Kielan-Jaworowska and Dashzeveg 1998; Ji Q *et al.* 1999b; Kielan-Jaworowska *et al.* 2004). Eutriconodonta (Kermack *et al.* 1973) was recently resurrected by Kielan-Jaworowska *et al.* (2004). Whether it is monophyletic is yet to be tested. Among eutriconodontans, Triconodontidae have been considered a monophyletic group (Crompton and Jenkins 1968; Hopson and Crompton 1969; Jenkins and Crompton 1979; Rougier *et al.* 1996a, 1996b; Cifelli *et al.* 1998, Ji Q *et al.* 1999b). Gobiconodontidae are probably also a monophyletic group, but its content is subject to discussion (see below). The nature of other eutriconodontan groups, such as amphilestids, remains uncertain. 'Symmetrodonta' is probably a paraphyletic group (Kielan-Jaworowska *et al.* 2004), but for convenience in this review we still follow McKenna and Bell (1997) in using the name.

2. PRESERVATION AND OCCURRENCES

2.1. Preservation

The Jehol Biota comes from the rock sequence of the Jehol Group, which consists of two formations: the Yixian Formation and the overlying Jiufotang Formation. A composite sequence is presented in Figure 1. Jehol mammals

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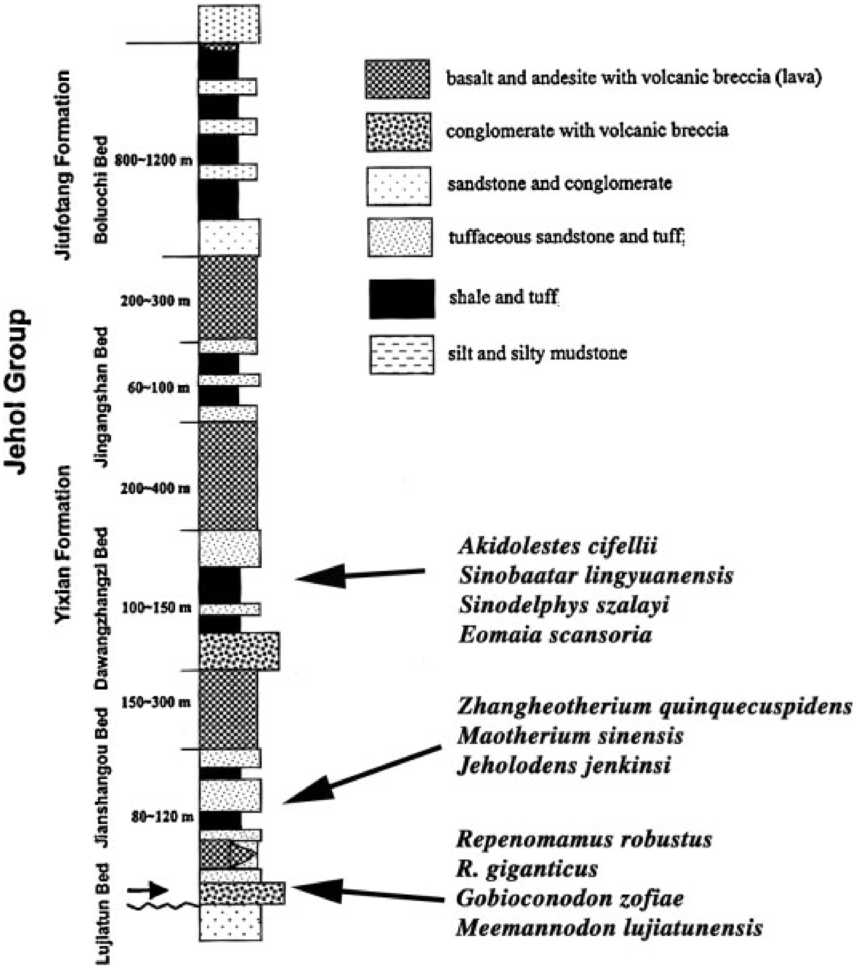

Figure 1. Composite stratigraphic column of the Jehol Group showing the horizons of occurrences of mammals. Modified from Wang and Zhou (in Chang *et al.* 2003). See text for alternative views on age determinations of the beds.

have been reported only from the Yixian Formation that contains four subunits ranging from bottom up: Lujiatun, Jianshangou, Dawangzhangzi and Jingangshan beds (Zhou *et al.* 2003; Wang and Zhou 2003). Superpositional relationships of the beds are not fully observable in the field, which has resulted in rigorous debates on the relationships of these rock units as well as their relative ages that have been postulated as being either Late Jurassic, transitional Jurassic-Cretaceous, or Early Cretaceous (see Wang *et al.* 1999, Zhou *et al.* 2003, Chang *et al.* 2003 for reviews). More recent biostratigraphic correlations and radiometric dating (Barrett 2000; Smith *et al.* 2001; Swisher *et al.* 1999, 2002; Wang *et al.* 2001; Chen *et al.* 2004) have converged on the conclusion that the Yixian Formation is of Early Cretaceous age. The time interval represented by the Jehol Group is still an on-going subject of research. It could have spanned over 18 million years, from 128 to 110 million year (Zhou *et al.* 2003; Wang and Zhou 2003), or a much shorter period, given the new dating of the Jiufotang Formation as 120 million year old (He *et al.* 2004) and the possible equivalence of the Lujiatun beds with the Jianshangou beds (Chen *et al.* 2004), which have been dated about 125 million year (Swisher *et al.* 1999, 2002; Chen *et al.* 2004) or 123.2 million year old (He *et al.* 2006).

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The sedimentary rocks of the Yixian Formation are intercalated with thick basalt and andesite volcanic rocks and vary in their thicknesses from locality to locality. Most of the sedimentary rocks are sandstones and shales that are of freshwater lacustrine origin and are characterized by laminated to finely bedded siliciclastic sediments from a low-energy setting. The Lujiatun Bed represents a different type of sedimentation, of which the nature of origin has not been fully explored. This bed is primarily light-coloured tuffaceous conglomerates, sandstones and silty mudstones of alluvial deposits that have little bedding structures and are considered to be from a nearly simultaneous mass mortality event (Zhou *et al.* 2003; Wang and Zhou 2003). Fossils from a named bed, such as the Jianshangou Bed, actually came from various pits and localities. Their recognition as from the same bed or horizon is based on bio- and lithological correlations. It is better to regard these fossils as coming from an interval of beds, rather than from a clearly defined horizon.

Articulated skeletons of mammals have been found in both the Lujiatun deposits and the above lacustrine shale. Fossil preservations of the two depositional environments are drastically different. Specimens from the shale are squashed into nearly two-dimensions, whereas those from the Lujiatun beds are three-dimensional (Figure 2). Mammal specimens preserved in the shale are relatively rare and are all from small species. These animals died and

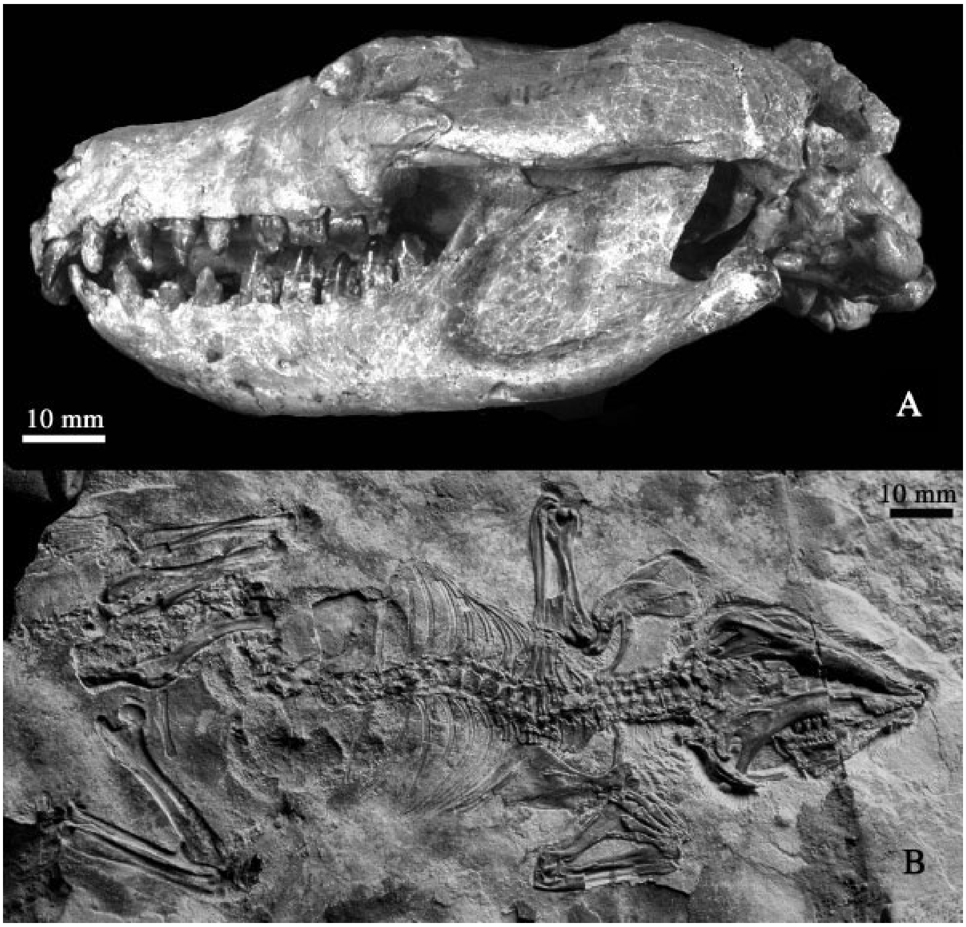

Figure 2. Contrast of preservation conditions of Jehol mammals. A, a three-dimensional skull of *Repenomamus robustus* from the Lujiatun beds; B, the squashed specimen of *Zhangheotherium quinquecuspidens* (Hu *et al.*1997; holotype, IVPP V 7466; Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science) from the shale of Jianshangou beds (10 mm scale bar).

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were buried with little disturbance in a low-energy condition at the lake bottom, covered with tuffs that sealed the fossil-bearing sediments and helped to preserve the organisms in exceptional delicacy and details (Zhou *et al.* 2003; Chang *et al.* 2003; Ji *et al.* 2004). Relatively greater numbers of mammal specimens from the geographically more restricted Lujiatun beds indicate that mammal specimens in these beds are more concentrated both in taxa and number of individuals. This is probably partly owing to the preservational condition and large body sizes of the species contained. Invertebrates are unknown from these beds and large mammal species, such as *Repenomamus robustus* and *R. giganticus*, are only known from these beds.

Not only preserved as articulated specimens, the Lujiatun fossils often display the postures as if the animals were in sleeping or resting position at the time they died. This is supported by the sleeping dinosaur *Mei long* (Xu and Norell 2004), a resting herd of juvenile *Psittacosaurus* dinosaurs crowded together with an adult (Meng *et al.* 2004), and probably the holotype of *Repenomamus giganticus* (Hu *et al.* 2005), which is a curled skeleton displaying a posture similar to a sleeping fox. Based on the articulated specimens and cluster of individuals, it has been postulated that the death of the grouped juvenile psittacosaurids might be caused by burial by volcanic debris, entrapment in a collapsed underground burrow, or flooding of a nest or other surface excavation (Meng *et al.* 2004). However, because animals from three different groups, which may well have different resting sites and behaviours, appear to have died peacefully and probably simultaneously, another scenario is that they were killed while sleeping by poisonous volcanic gas, and were soon buried by ‘a single, catastrophic mass mortality event’ (Zhou *et al.* 2003, p. 808). If, as the taphonomic data indicate, these animals died simultaneously, the composition of the fossil assemblage from the Lujiatun beds reflects, at least partly, the true composition of a coeval fauna.

2.2. *Occurrences*

The occurrences of known fossil mammals in the Yixian sequence are illustrated in Figure 1. Current records show that mammals came from at least three horizons, Lujiatun, Jianshangou, and Dawangzhangzi beds. The compositions of the three assemblages are different. The Lujiatun beds preserved primarily eutriconodontans, including *Repenomamus robustus* (Li *et al.* 2000), *R. giganticus* (Hu *et al.* 2005), *Gobiconodon zofiae* (Li *et al.* 2003), and *Meemannodon lujiatunensis* (Meng *et al.* 2005). Immediately above the Lujiatun assemblage are the ‘symmetrodontan’ *Zhangheotherium quinquecuspidens* (Hu *et al.* 1997; Luo and Ji 2005) and *Maotherium sinensis* (Rougier *et al.* 2003) and the eutriconodontan *Jeholodens jenkinsi* in the Jianshangou beds. The multituberculate *Sinobaatar lingyuanensis* (Hu and Wang 2002), ‘symmetrodontan’ *Akidolestes cifellii* (Li and Luo 2006), metatherian *Sinodelphys szalayi* (Luo *et al.* 2003) and eutherian *Eomaia scansoria* (Ji *et al.* 2002) are from the still younger Dawangzhangzi beds. No mammal has been reported from the top Jingangshan beds of the formation. Large eutriconodontans have not been found in Jianhshangou or younger beds, whereas metatherian and eutherian species are unknown from the beds lower than the Dawangzhangzi beds.

Although metatherian and eutherian mammals are phylogenetically more derived than other mammals, it is unclear whether the occurrences of the Yixian mammals in the sequence simply result from chance preservation or actually reflect some kind of evolutionary stages in mammal evolution. There is evidence to consider fossils from the same beds as from a coeval fauna, but those from different beds remain to be a challenging case. For instance, it is not certain whether the Lujiatun and Jianshangou assemblages come from two distinct faunas of different ages and, if so, how much time difference lags between them, or whether they are actually coeval faunas but have been preserved in different taphonomic conditions. Chen *et al.* (2004), in contrast to others (Zhou *et al.* 2003; Wang and Zhou 2003), considered the Lujiatun beds to represent a different facies, and thus a lateral extension of the Jianshangou beds.

For convenience in this review, we treat the Jehol mammals as from one biota, but note that they come from three beds of the Yixian Formation, of which the relationships are not universally agreed upon. This should be borne in mind when we discuss composition and diversity of the Jehol mammal fauna.

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3. DIVERSITY

3.1. Taxa

A total of 11 species have been described from the Yixian Formation, as listed below. A docodontan mammalia form has been recently reported from Daohugou locality, Inner Mongolia (Ji *et al.* 2006), which we consider as from a pre-Jehol assemblage and is not counted in the 11 Jehol mammals (see below). This list is not a systematic treatment of these mammals; it only presents the diversity of the Jehol mammals. These species are represented only by holotypes in the published record, except for a few specified below. The type specimens are housed in the following institutions: Chinese Academy of Geological Sciences, Institute of Geology (CAGS-IG), Beijing; Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing; Jinzhou Museum of Paleontology (JZMP), Jinzhou City, Liaoning Province; Nanjing Institute of Geology and Paleontology (NIGPS), Nanjing; National Geological Museum of China (NGMC; also abbreviated as GMV in Ji Q *et al*. 1999b), Beijing.

Multituberculata Cope, 1884
Eobaataridae Kielan-Jaworowska, Dashzeveg and Trofimov, 1987
Sinobaatar lingyuanensis Hu and Wang, 2002

The holotype (IVPP V12517) is a skeleton of a subadult individual, preserved mainly in impressions of both dorsal and ventral sides on the slate and its counterpart. The specimen came from the Dawangzhangzi Bed of the Yixian Formation at Dawangzhangzi locality, Lingyuan City. A lower jaw of *Sinobaatar* has been identified as part of the stomach content of a small carnivorous dinosaur, *Sinosauropteryx prima*, from the Yixian Formation, with the beds unidentified (Hurum *et al.* 2006).

Eutriconodonta Kermack Mussett and Rigney, 1973
Jeholodens jenkinsi Ji, Luo and Ji, 1999b

The holotype (GMV2139) is a skeleton consisting of a partial skull and the postcranial skeleton preserved as part and counterpart that are from the Jianshangou Bed of the Yixian Formation at Sihetun site, about 32 km east of Chaoyang City.

Gobiconodontidae Chow and Rich, 1984
Gobiconodon zofiae Li, Wang, Hu and Meng, 2003

The holotype (IVPP V12585) is a partial skull with partial associated lower jaws from the Lujiatun Bed of the Yixian Formation at Lujiatun locality, Shangyuan, Beipiao City.

Meemannodon lujiatunensis Meng, Hu, Wang and Li, 2005

The holotype (IVPP V13102) is a left lower mandible with complete dentition from the Lujiatun Bed of the Yixian Formation at Lujiatun locality.

Repenomamidae Li, Wang, Wang and Li, 2000
Repenomamus robustus Li, Wang, Wang and Li, 2000

The holotype (IVPP V 12549) is a skull and articulated mandibles with partial skeleton from the basal beds of the Yixian Formation at Lujiatun locality. Additional specimens known include a skull (Wang *et al.* 2001; Meng *et al.* 2003a) and a skeleton associated with fragmentary bones of a juvenile *Psittacosaurus* (Hu *et al.* 2005); both from the same locality of the holotype.

Repenomamus giganticus Hu, Meng, Wang and Li, 2005

The holotype (IVPP V14155) is a partial skull with associated right mandible and articulated partial postcranium from the Lujiatun Bed of the Yixian Formation at Lujiatun locality.

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‘Symmetrodonta’
Zhangheotheridae Rougier, Ji and Novacek, 2003
Zhangheotherium quinquecuspidens Hu, Wang, Luo and Li, 1997

The holotype (IVPP V7466) is a partial skull with most of the postcranial skeleton from the Jianshangou Bed of the Yixian Formation at the Jianshangou locality about 32 km east of Chaoyang City. Another specimen of a skeleton from a juvenile individual from the Yixian Formation of Sihetun site was referred to the species (Luo and Ji 2005). The specific beds for the specimen was not mentioned, but it most likely comes from the Jianshangou Bed, the main outcrops distributed at Sihetun (Chang *et al.* 2003). In addition, two lower jaws referred to *Zhangheotherium* were identified as part of the stomach content of the same specimen of *Sinosauropteryx prima*, associated with the lower jaw of *Sinobaatar* (Hurum *et al.* 2006). *Zhangheotherium* was originally placed in the family Spalacotheriidae under ‘Symmetrodonta’ (Li *et al.* 1995; Hu *et al.* 1997). A new family, Zhangheotheridae, based on *Zhangheotherium* was proposed and placed in Trechnotheria by Rougier *et al.* (2003).

Maotheirum sinensis Rougier, Ji and Novacek, 2003

The holotype (NGMC-97-4-15) is a skeleton with hair and body contour impressions from ‘Lower part of the Lower Jurassic Yixian Formation, also referred to as the Chaomidianzi member of the Yixian Formation approximately 30 km east of Chaoyang, Lioming Province, NE China’ (Rougier *et al.* 2003, p. 8). As mentioned above, it has become a common view that the Yixian Formation is Early Cretaceous; the ‘Lower Jurassic’ referred to the Yixian Formation by Rougier *et al.* (2003) is unquestionably an error. The ‘Chaomidianzi member’ was originally proposed as a formation (Ji SA *et al.*, 1999) for a set of sediments at Sihetun locality, which is roughly equivalent to the Jianshangou Bed adopted in this review. The ‘Chaomidianzi Formation’ was also cited in other studies (Ji Q *et al.* 1998, 1999a). Sun *et al.* (2001) argued that the same sequence should be better named as the ‘Jianshangou Formation’. In a more recent synthetic study Ji *et al.* (2004) apparently abandoned ‘Chaomidianzi Formation’ or ‘Chaomidianzi member’ and adopted instead the Jianshangou Bed as the term for the sequence in question.

Family Spalacotheriidae
Akidolestes cifellii Li and Luo, 2005

The holotype (NIGPAS139381), a skeleton with partial skull preserved in part and counterpart, is from the ‘Yixian lacustrine beds at the Dawangzhangzi locality, Lingyuan, Liaoning, China. The locality is correlated with other localities in Liaoning dated to be 124.6 Million year, of the Barremian stage of the Lower Cretaceous.’ (Li and Luo 2005, p. 196). We regard the beds generating the specimen as equivalent to the Dawangzhangzi Bed.

Metatheria
Sinodelphys szalayi Luo, Ji Wible and Yuan, 2003

The holotype (CAGS00-IG-03) is an incomplete, flattened skeleton with some preserved soft tissues from the Dawangzhangzi Bed of the Yixian Formation at the Dawanzhangzi locality, Lingyuan, Liaoning.

Eutheria
Eomaia scansoria Ji, Luo, Yuan, Wible, Zhang and Georgi, 2002

The holotype (CAGS01-IG-1) is a skeleton with an incomplete, flattened skull partially represented by impressions with some preserved soft tissues, such as costal cartilages and fur from the Dawangzhangzi Bed of the Yixian Formation at the Dawanzhangzi locality, Lingyuan, Liaoning.

Docodonta
Family incertae sedis
Castorocauda lutrasimilis Ji, Luo, Yuan and Tabrum, 2006

The holotype (JZMP-04-117) consists of an incomplete, flattened skeleton with partial skull and impressions of fur and scales from the Jiulongshan Formation at Daohugou locality, Ningcheng County, Inner Mongolia. Other

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vertebrates from the same locality include three genera and species of salamanders, two genera and species of pterosaurs and two genera and species of feathered maniraptoran dinosaurs (Wang *et al.* 2005). No fish and birds have been reported from this locality. By citing other works (Chen *et al.* 2004; Liu and Liu 2005), Ji *et al.* (2006) adopted the age of Daohugou beds as Middle Jurassic, about 164 million years old. In contrast, Wang *et al.* (2005, p. 2369) considered that the Daohugou 'assemblage is closer to that of the Early Cretaceous Jehol Biota than to any other biota' and that 'it was incorrect to correlate the Daohugou Bed with the Middle Jurassic Jiulongshan Formation'. Because of these controversial opinions on the age of Dauhegou beds, we tentatively regard *Castorocauda* as from an assemblage predating the conventional Jehol mammal fauna that comes from the Yixian Formation and will not include this interesting semiaquatic mammal in the following discussion.

3.2. Species identifications

The true diversity of Jehol mammals, as well as other organisms, may not be known because some species may not be preserved as fossils, or preserved but never found. Nonetheless, the fossil assemblages collected give us a good sense of the diversity of Jehol biota. However, at least three issues need to be dealt with in recognizing the diversity of the biota: (1) coexistence of species (discussed above); (2) identification of species; and (3) classification of higher-level taxa.

Fossil species are morphological species, and most of the Mesozoic species are based only on dentitions. Although such species are diagnostic, at least for specialists, features used to diagnose them are often limited and biased. It is not uncommon that when a limited number of specimens is available, species recognition appears simple, whereas a large number of specimens often presents problems on species identification because of potential intraspecific and interspecific variations. Many mammal taxa from the Jehol Biota are represented by a limited number of specimens, often known only from the holotype. Eutriconodontans from the Lujiatun Bed present a challenging case for species identification because numerous specimens of various sizes from the same group have been recovered. Eutriconodontans from other areas are represented primarily by dental and fragmentary jaw material; relatively complete non-Jehol specimens were known only from the North American *Gobiconodon ostromi* (Jenkins and Schaff 1988), in which, however, little of the skull is preserved. In contrast, four species belonging to three genera and two families have been reported from the Lujiatun beds: *Gobiconodon zofiae, Meemannodon lujiatunensis, Repenomamus robustus*, and *R. giganticus.* All, except for *Meemannodon*, are represented by well-preserved skull material. It can be expected that new species will be discovered in the future. When numerous specimens with various sizes and morphological variations are obtained, one may ask whether the differences are due to intraspecific age differences and/or sexual dimorphisms.

Age difference is related not only to the size and morphological differences between a young individual and an adult of a species, but also to a more fundamental issue: whether the growth of early mammals is determinate, as in extant mammals, or continuous, as in some 'reptiles', during the life history of an individual. It is relatively easy to tell a young individual from an old one by a combination of size difference, tooth eruption, degree of tooth wear, fusion of skull elements, and fusion of the epiphyses and shafts of long bones. For instance, in the holotype of *Repenomamus giganticus* (IVPP V14155) the last lower molariform (m5) is just erupted, bears no wear, and is located at the anterior base of the coronoid process in a position higher than other cheek teeth (Hu *et al.* 2005). Therefore, compared to adult specimens of *R. robustus* in which all cheek teeth were erupted and deeply worn, IVPP V14155 represents a relatively younger individual. This shows that the much larger body size of *R. giganticus*, in relation to *R. robustus*, is not related to individual age.

Two lines of evidence can be used to interpret the growth pattern of fossil mammals: whether its ontogenetic growth is determinate or continuous. First, during the ontogenetic growth of mammals, a long bone increases in length only at the cartilaginous plates that separates it from its epiphyses. If these plates are obliterated at maturity, the long bone stops increasing in length. Because the epiphysis and the shaft of the long bone are already fused in the skeletons of *R. giganticus* and *R. robustus* (Hu *et al.* 2005), the long bones have stopped growth in these species, which have considerably different body sizes. Second, if a mammal grew continuously, their skull and lower jaws

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would become larger with ageing. To match the larger skull and lower jaws, their teeth would increase accordingly. The specimens of *Repenomamus* show that molariform teeth from different generations of the same individual are similar in size (Hu *et al.* 2005). In addition, teeth from an adult individual are no bigger than those of a young individual. Commonly, adult teeth may turn out to be smaller because of wear. Therefore, we can exclude age difference and growth pattern as the causes for body size and morphological differences that have been used as features to differentiate species, such as *Repenomamus robustus* from *R. giganticus*.

It is not so easy, however, to tell sexual size dimorphism within fossil species. Sexual size dimorphism is the difference in size between males and females of the same species (Lammers *et al.* 2001). Sexual selection is the most popular hypothesis for the origin and maintenance of sexual size dimorphism (Trivers 1972), but other factors, such as latitude, population density, and physiological mechanisms that affect growth patterns, are also attributable to the formation of sexual size dimorphism, which in turn can have important consequences for animal ecology, behaviour, population dynamics and the evolution of life-history traits (Isaac 2005). Sexual size dimorphism is most common in relatively large and derived groups of mammals, such as primates, ungulates, whales and proboscideans. It may be speculated that in Mesozoic mammal sexual size dimorphisms would not be distinct. For the two described species of *Repenomamus*, they differ in several dental and cranial features and in body size (Hu *et al.* 2005). The significant differences in body size and estimated body mass between adults of *R. giganticus* and *R. robustus* exceed those between dimorphic sexes of a species in most extant terrestrial mammals (Nowak 1999; Silva and Downing 1995).

Thus, it is convincing that eutriconodontans from the Lujiatun Bed represent several genera and species, indicating that the Jehol mammal fauna is quite diverse. In commenting on recent statistical analyses of mammal diversity based upon available samples in museum collections, Lillegraven and Clemens (2004, p. 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’. We may not wait for another quarter-century to witness the prediction.

3.3. Gobiconodontidae and Repenomamidae

Species referred to gobiconodontids have been reported from the Jurassic and Lower Cretaceous of Mongolia (Trofimov 1978; Kielan-Jaworowska and Dashzeveg 1998; Rougier *et al.* 2001), China (Chow and Rich 1984; Godefroit and Guo 1999; Li *et al.* 2003; Meng *et al.* 2005), North America (Jenkins and Schaff 1988), and Russia (Maschenko and Lopatin 1998). The only Jurassic species referred to Gobiconodontidae is *Klamelia zhaopengi* (Chow and Rich, 1984). However, with more knowledge of gobiconodontid morphology in recent years, Rougier *et al.* (2001) considered that this species is not closely related to *Gobiconodon* and has uncertain affinities with other groups of mammaliaforms; these authors treated *Klamelia* as Mammaliaformes *incertae sedis*. Therefore, gobiconodontids are now known only from the Early Cretaceous.

Gobiconodontids were ranked as a subfamily by Kielan-Jaworowska and Dashzeveg (1998) within the family Amphilestidae (Simpson 1928; Mills 1971; Jenkins and Crompton 1979), while Rougier *et al.* (2001) considered Amphilestidae to be paraphyletic. Gobiconodontidae is recognized in recent works (Rougier *et al.* 2001; Li *et al.* 2003; Kielan-Jaworowska *et al.* 2004; Meng *et al.* 2005) to include at least three genera: *Gobiconodon, Hangjinia* (Godefroit and Guo 1999) and *Meemannodon* (Meng *et al.* 2005).

A controversial issue concerns the taxonomic position of *Repenomamus*. When first described, the genus was placed in a new family of its own, Repenomamidae. Luo *et al.* (2003) regarded *Repenomamus* a gobiconodontid and Kielan-Jaworowska *et al.* (2004) treated Repenomamidae as a junior synonym of Gobiconodontidae. When originally described, little cranial material was known in related taxa, such as *Gobiconodon*. Some of the anatomical identifications of *Repenomamus* were erroneous. For instance, the zygomatic process of the squamosal was identified as the jugal and the ossified Meckel’s cartilage, an unusual element preserved in Mesozoic mammals, was identified as the postdentary bar. Because of some primitive features in teeth and skull structures, Li *et al.* (2000) thought *Repenomamus* represented a primitive branch of Mesozoic mammals, a relic group. With further study on the numerous well-preserved specimens, more is known about the genus (Wang *et al.* 2001; Meng *et al.* 2003a; Hu *et al.* 2005).

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Kielan-Jaworowska *et al.* (2004, p. 241) provided the diagnosis for Gobiconodontidae that includes *Repenomamus.* Some of the diagnostic features for the family include 'i1, the only lower incisor, is procumbent and enlarged', 'anterior molariform teeth replaced ontogenerically in a sequential fashion', and 'upper molariforms wide transversely, with well-developed labial and lingual cingula and characterized by increasing triangulation of principal cusps from M1 to M5'. All these features are not present or unclear in *Repenomamus.*

The number of incisor of *Repenomamus* is I3/i2 (Li *et al.* 2000; Wang *et al.* 2001; Li *et al.* 2003; Meng *et al.* 2003a, 2005; Hu *et al.* 2005), which is based primarily on the well-preserved skull specimens of the genus in which the premaxilla-maxillary suture is clear so that the position of the upper canine can be defined. Anterior to the canine, three upper incisors occur in the premaxilla. The unequivocal occlusal relationships of the lower and upper teeth reveal two lower incisors in *Repenomamus*, not one. Moverover, the medial incisor, identified as i1, is not enlarged, nor is it procumbent in *Repenomamus*. As our collection shows, all molariforms of *Repenomamus*, including the last upper and lower ones, replace during ontogeny. For instance, in IVPP V14240, a relatively young individual of *R. robustus*, the locus for the last molariform (M4 in our identification) contains the teeth of two generations. In CT-scan data of several skulls of *R. robustus*, replacement of molariforms in both upper and lower jaws is observed. Both CT-data and direct observation of the dentitions of *Repenomamus* do not display a clear sequential pattern of replacement. The upper molariforms of *Repenomamus* are transversely expanded, but cingula are generally weak and usually absent on the labial side of a molariform tooth. Moreover, although cusp A is inflated, the principal cusps do not show a triangular arrangement. Thus, until a thorough phylogenetic analysis is conducted, the taxonomic position of *Repenomamus* remains open; for that reason, we prefer to maintain the family Repenomamidae.

4. PHYLOGENY AND DIVERGENCE

4.1. Phylogeny

The Jehol mammals belong to five major clades of mammals: multituberculates, 'symmetrodontans', eutriconodontans, metatherians and eutherians; the first three are extinct. Well-preserved dentocranial and postcranial specimens from the Jehol Biota represent a true burst of morphological data for these Mesozoic mammals. Although the study of Jehol mammals is still at an early stage, several phylogenetic analyses based on sizable data sets have been generated (Hu *et al.* 1997; Ji Q *et al.* 1999b, 2002; Wang *et al.* 2001; Luo *et al.* 2003). The results of these phylogenetic analyses are not always consistent because the selected taxa and characters differ among the analyses. In all analyses, metatherians and eutherians always form a clade, to which 'symmetrodontans' are more closely related than are either eutriconodontans or multituberculates. The phylogenetic positions of eutriconodontans and multituberculates, particularly in relation to monotremes, appear to be unstable. In Hu *et al.* (1997) and Ji *et al.* (1999), multituberculates form the sister-group of the clade containing *Zhangheotherium* and crown-group mammals (also called Trechnotheria), with monotremes and eutriconodontans being successive outgroups. In Wang *et al.* (2001), multituberculates and monotremes cluster as a sister-group; this clade, Trechnotheria and Triconodontidae form an unresolved clade. In Ji *et al.* (2002) and Luo *et al.* (2003), eutriconodontans are within the crown-group mammals, but placed outside the clade of multituberculates and Trechnotheria. Monotremes are grouped with some fossil taxa as Australosphenida.

Because of the fast pace of discoveries of Jehol mammals, there is no current phylogenetic analysis that encompasses all known Jehol mammal species. Figure 3 is a composed cladogram that is primarily based on Wang *et al.* (2001), which illustrates one possible relationship of the Jehol mammals and their relationships with other mammals.

4.2. Divergence

One of the major issues in the recent discussions on evolution of mammals is the divergence time of the various groups of mammals, in particular, the placental mammals to which humans belong. Palaeontological records show

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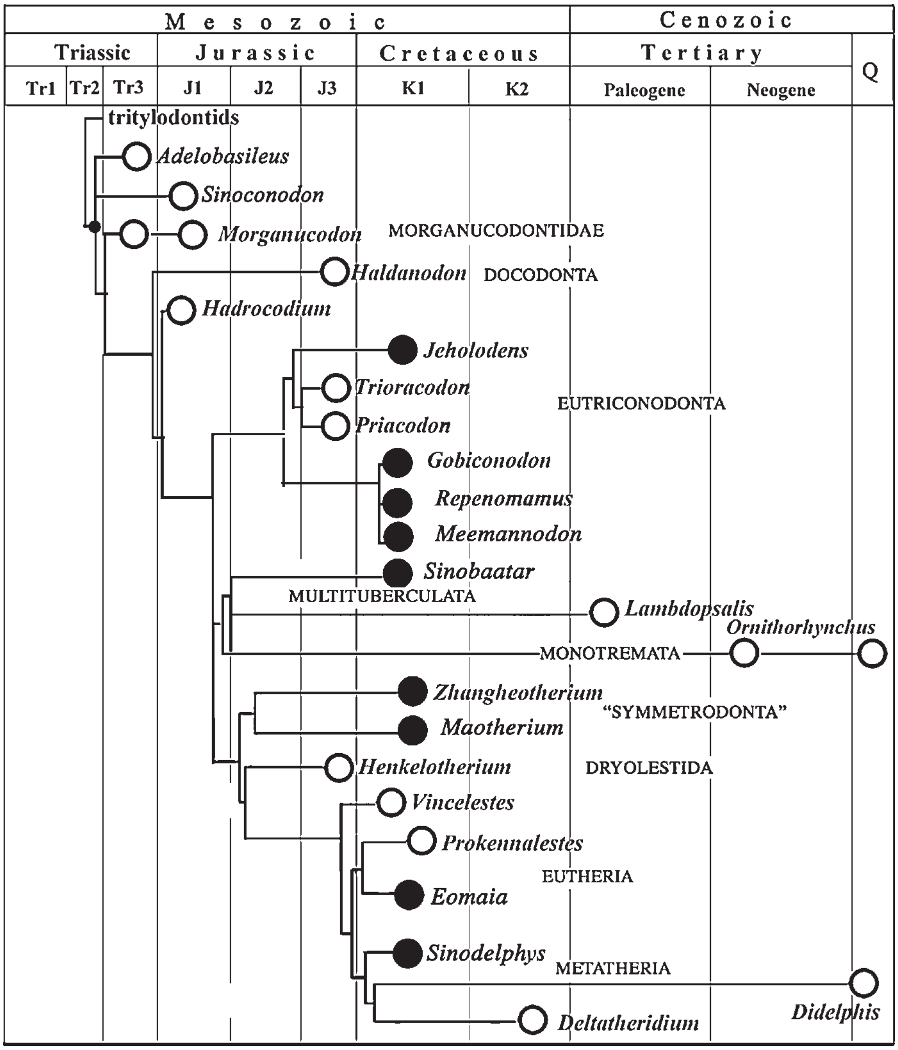

Figure 3. A possible relationship for the Jehol (K_1) mammals (represented by black dots) and other mammals (represented by white dots). The cladogram is modified from Wang *et al.* (2001); additions of *Eomaia* and *Sinodelphys* to the cladogram are based on Luo *et al.* (2003).

that the earliest members of placental orders postdate the Cretaceous-Tertiary boundary about 65 million years ago, although some analyses imply a few possible exceptions (Archibald *et al.* 2001; Meng *et al.* 2003b; O'Leary *et al.* 2004). In contrast, molecular studies, based on the molecular-clock method, predict much older divergence dates for various cladogenetic events within mammals (Janke *et al.* 1994; Hedges *et al.* 1996; Kumar and Hedges 1998; Springer *et al.* 2003; Springer *et al.* 2005). The Jehol mammals are basal members of Mammalia and bear little on the relationships and divergences within the placental mammals, but they are relevant to the issues on the divergences of metatherians and eutherians. Recent molecular estimates for the Eutheria-Metatheria dichotomy range between extremes of 190 (Woodburne *et al.* 2003) and 130 (Janke *et al.* 2002) million years, which is again generally earlier than palaeontological records. The earliest known eutherian, *Eomaia*, and the earliest metatherian, *Sinodelphys* both come from of the Early Cretaceous Jehol Biota, roughly about 125 million years ago. Other Early Cretaceous eutherians have been reported from the lower Cretaceous, such as *Murtoilestes* from the upper Barremian–middle Albian of eastern Russia (Averianov and Skutschas 2001), and *Prokennalestes* (Kielan-Jaworowska and Dashzeveg 1989) and *Montanalestes* (Cifelli 1999) from the Albian-Aptian of Mongolia and

North America. Thus, palaeontological data indicate a split of Eutheria and Metatheria at least in the Early Cretaceous. Discoveries of *Sinodelphys* and *Eomaia* and phylogenetic analyses including them suggest that divergence of metatherians and eutherians had taken place in Asia no later than 125 million years ago, followed by the evolution of deltatheroidan-like taxa in both Asia and North America during the late Early Cretaceous (120 to 100 Ma); then there was a major metatherian diversification in North America in the Late Cretaceous (100 to 65 Ma) and finally, the diversification of proximal relatives to crown marsupials occurred in South America during the Paleocene (Luo *et al.* 2003).

It should be noted, however, that the Early Cretaceous records of therians, such as *Eomaia* and *Sinodelphys*, provide little evidence on the divergence time for placental mammals, which is still an issue in debate (see Rose and Archibald 2005). Given the phylogenetic position of *Eomaia* to Placentalia (Ji *et al.* 2002), one could predict that the divergences of the lineage ultimately giving rise to Placentalia and the one containing *Eomaia* are equally ancient, but that does not show *a priori* how old the crown Placentalia might be. Given that relationship, the divergence of placental mammals may still postdate the K-T boundary, as we currently have palaeontological evidence for (Rose and Archibald 2005; Asher *et al.* 2005), even though the stem of Placentalia may extend to the Early Cretaceous.

The palaeogeographic distributions of gobiconodontids indicate that there were dispersal events between Asian and North American mammals during the Early Cretaceous. This seems not surprising because Laurasia still remained essentially a supercontinent (Smith *et al.* 1994; Zharkov *et al.* 1998). The Jehol mammals are also informative for biostratigraphic correlations (Li *et al.* 2003). Among known vertebrates of the Jehol Biota, *Gobiconodon* is the only genus present in Asia, Europe and North America. This genus has been found in Mongolia (Trofimov 1978; Kielan-Jaworowska and Dashzeveg 1998; Rougier *et al.* 2001), Siberia (Maschenko and Lopatin 1998), North America (Jenkins and Schaff 1988; Cifelli *et al.* 1998), other regions of China (Tang *et al.* 2001), and Spain (Cuenca-Bescós and Canudo 2003). The fossil record indicates that the stratigraphic distribution of *Gobiconodon* is limited to the Early Cretaceous. Similarly, eobaatarid multituberculates, to which *Sinobaatar* belongs, are also known only from the Early Cretaceous (Hu and Wang 2002). Thus, the findings of *Sinobaatar* and *Gobiconodon* support an Early Cretaceous age for the Jehol Biota.

5. BIOLOGY

Lillegraven and Clemens (2004, p. vii) wrote: 'When most of us think about mammals from the Mesozoic Era we use our imaginary time-viewing machines to see furry little creatures with relatively large beady eyes and wiggly noses. We see them scampering through moonlit forests capturing insects, tearing apart fruits from early flowering plants, sometimes lapping nectar, and universally marking their territories with diverse body exudates . . . The food chain of their generally warmer ecosystems are seen to be capped by dinosaurs, crocodiles, and birds. . .' This description vividly portray Mesozoic mammals as small, nocturnal, insectivorous or omnivorous, and overwhelmed by dinosaurs. The Jehol mammals furnish a unique source of data on the biology of early mammals. Based on the diverse and well-preserved Jehol mammals, we will consider three aspects of their biology: body mass, dentition and diet, and locomotion.

5.1. Body mass

Most Mesozoic mammals and their close relatives, such as kuehneotheriids and morganucodontids in the Late Triassic-Early Jurassic, were small and considered to be nocturnal insectivores (Hopson 1973; Jerison 1973); the same is true of most later Mesozoic mammals (Lillegraven *et al.* 1979; Kielan-Jaworowska *et al.* 2004). The reason for the miniscule nature of Mesozoic mammals is uncertain (Lillegraven 1979), but it has often been hypothesized that diurnal reptilian carnivores and herbivores of various sizes, particularly dinosaurs, dominated the Mesozoic land and prevented mammals from invading those niches, so that mammals did not have the chance to 'experiment' with large body size (Lillegraven *et al.* 1979). Exploitation of niches may be related to many factors other than body

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size, such as key innovations that enable organisms to involve adoption of new foraging modes (Mitter *et al.* 1988; Hunter and Jernvall 1995) or new modes of reproduction (Slowinski and Guyer 1993) or to promote reproductive divergence (Vrba 1987). However, the number of niches is potentially greatest for small-sized mammals, as known from living mammals (Gardezi and Silva 1999), so that mammals may have a chance to survive as being small.

For fossil mammals, body size is one of the most important factors influencing life strategy (Carbone *et al.* 1999). A larger animal can live longer and move faster; they also need more food supply and larger home range (Van Valkenburgh and Jenkins 2002). Home range size varies with body size and is influenced by energetic requirements (McNab 1963; Harestad and Bunnell 1979; Lindstedt *et al.* 1986; Swihart *et al.* 1988), and integrates behaviour, physiology and population density and strongly depends on organism size (Damuth 1981; Holling 1992; Reiss 1988; Haskell *et al.* 2002). Many characteristics of animals, including basal metabolic rate, brain size, heart size and rate of blood circulation, litter size and size of offspring at birth, maximum life-span, median, dispersal distances, and the frequency distribution of body sizes, are body-size related (Peters 1983; Brown *et al.* 1993; Van Vuren 1998; Kelt and Van Vuren 1999; Damuth and MacFadden 1990).

Body size and masses of Jehol mammals vary considerably. Figure 4 contrasts the body sizes of two species, *Repenomamus giganticus* and *Eomaia scansoria*, that are known from the biota. Luo *et al.* (2003) estimated the body masses of *Eomaia* and *Sinodelphys* ranging from 25 to 40 g, although Ji *et al.* (2004) presented slightly different figures on body lengths and masses of these species. Luo *et al.* (2003) also estimated the body masses as 45–79 g for *Zhangheotherium* and *Maotherium*, 20–25 g for *Jeholodens* and *Sinobaatar*, and 200–3000 g for gobiconodontids, which in their usage include *Gobiconodon zofiae* and *Repenomamus robustus*. The methods used by these authors to estimate the body mass for these species are unknown to us. To our knowledge, body mass estimate has not been conducted in any other original descriptions of the Jehol mammals, except for Hu *et al.* (2005). Nonetheless, it is obvious that most of the known Jehol mammals are small, as is usually the case for Mesozoic mammals.

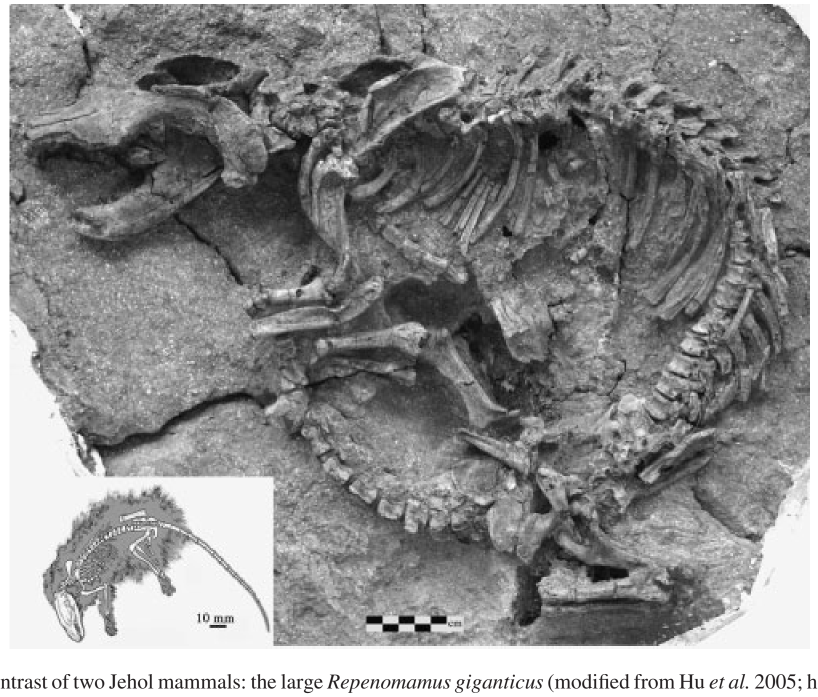

Figure 4. Body size contrast of two Jehol mammals: the large *Repenomamus giganticus* (modified from Hu *et al.* 2005; holotype, IVPP V14155) and the small *Eomaia scansoria* (modified from Ji *et al.* 2002; holotype, CAGS01-IG1; Chinese Academy of Geological Sciences, Institute of Geology). The two photos are roughly to the same scale (10 mm scale bar).

Discovery of *Repenomamus giganticus* (Hu *et al.* 2005) greatly expanded the body size range for the Jehol mammals. This species may actually be the largest known Mesozoic mammal. It is unquestionably the largest Mesozoic mammal represented by substantial material. Based on data from various groups of living mammals (Alexander *et al.* 1979; Damuth and MacFadden 1990; Silva and Downing 1995), several empirical regression equations expressing exponential relationships between body mass and dimensions of skeletal elements have been generated. Some of the equations have been used to estimate body masses of extinct mammals (Gingerich 1990; Damuth and MacFadden 1990). Two equations, one from Alexander *et al.* (1979) and the other from Van Valkenburgh (1990), have been employed to estimate the body mass of *Repenomamus*. The averaged estimates are 12–14 kg for *R. giganticus* and 4–6 kg for *R. robustus* (Hu *et al.* 2005). Thus, the body masses of the Jehol mammals range from 25 g to 14 000 g, much broader than what we knew before (Lillegraven *et al.* 1979; Kielan-Jaworowska *et al.* 2004). *R. giganticus* significantly expands the upper limit of body size of Mesozoic mammals. The size of *Repenomamus* actually exceeds those of several small dinosaurs, particularly dromaeosaurid dinosaurs, from the same fauna (Xu and Norell 2004; Chang *et al.* 2003; Ji *et al.* 2004). This body mass spectrum reflects to some degree diverse adaptations of life styles of these early Cretaceous mammals.

5.2. Dentition and diet

Because most Mesozoic mammals are preserved as and identified by teeth, their teeth remain central in interpreting the early history, diversity and biology of early mammals. Diet of a mammal may be inferred from its dentition and the way it uses its teeth. It has been known that most Mesozoic mammals are insectivorous and some may be omnivorous based on their tooth structures (Lillegraven *et al*. 1979; Kielan-Jaworowska *et al*. 2004). For Jehol mammals, the lower jaw structures and tooth morphologies may be classified into four types: therian, 'symmetrodontan', multituberculate and eutriconodontan (Figures 5 and 6).

Eomaia and *Sinodelphys* are the two currently known therians and are similar in their jaw and tooth morphologies. The therian lower jaw is slender, long and shallow. The dentition occupies a large proportion of the length of the dentary bone. One of the therian lower jaw features that does not exist in other Jehol mammals is the

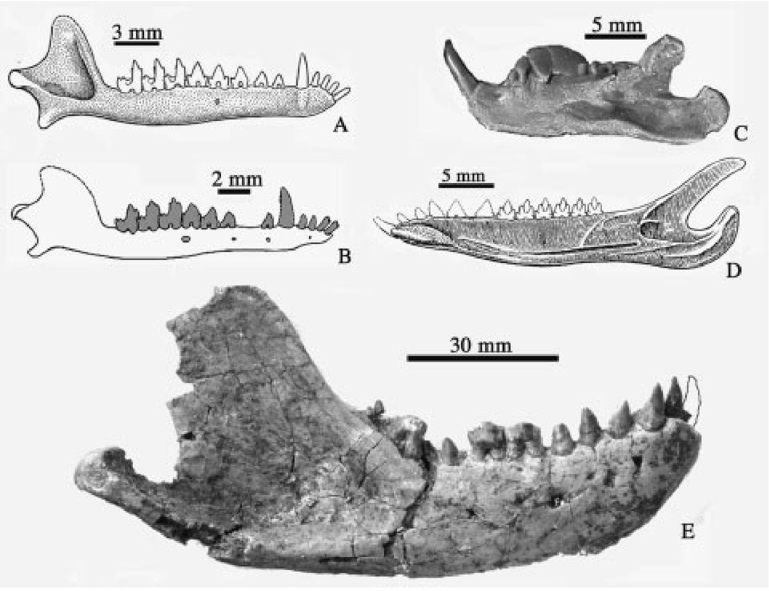

Figure 5. Lower jaw morphologies of Jehol mammals. A, *Eomaia scansoria* (from Ji *et al.* 2002); B, *Sinodelphys szalayi* (from Luo *et al.* 2003); C, *Sinobaatar lingyuanensis* (from Hu and Wang 2002); D, *Zhangheotherium quinquecuspidens* (from Hu *et al.* 1997); E, *Repenomamus giganticus* (from Hu *et al.* 2005). See text for discussion.

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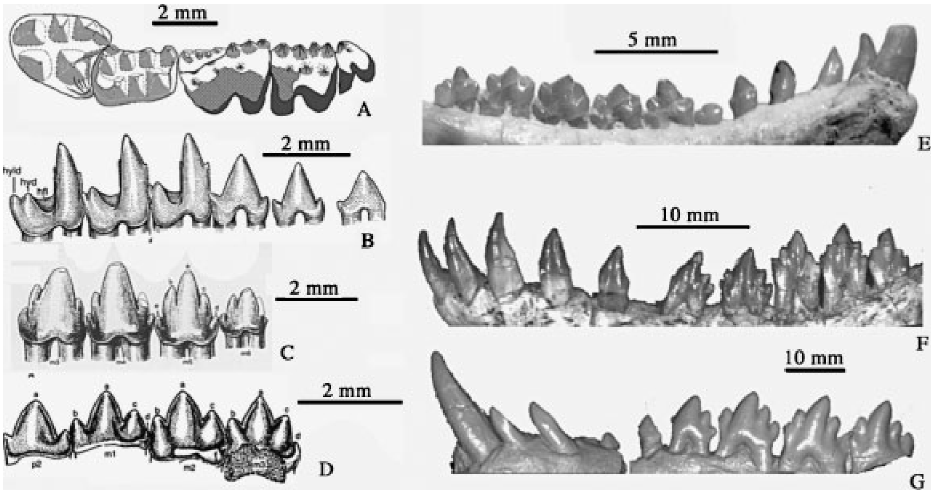

Figure 6. Tooth morphologies of Jehol mammals. A, *Sinobaatar lingyuanensis* (from Hu and Wang 2002); B, *Eomaia scansoria* (from Ji *et al.* 2002); C, *Zhangheotherium quinquecuspidens* (from Hu *et al.* 1997); D, *Jeholodens jenkinsi* (from Ji Q *et al.* 1999); E., *Gobiconodon zofiae* (from Li *et al.* 2003); F, *Repenomamus robustus* (an undescribed specimen of IVPP); G, *Meemannodon lujiatunensis* (from Meng *et al.* 2005).

angular process, which in living mammals is the site for attachment of the lateral masseteric muscle. Although different in dental formula, *Eomaia* and *Sinodelphys* are similar in many aspects of their teeth (Ji *et al.* 2002; Luo *et al.* 2003; Figures 5, 6). The fundamental feature shared by them is the fully developed tribosphenic pattern of the molars. Tribosphenic molars have embrasure shearing between vertical shearing surfaces, such as between the anterior edge of an upper molar trigon and the posterior edge of a corresponding lower molar trigonid. In addition, a crushing or grinding function is provided between the protocone of an upper molar and the talonid of the lower molar, when the former bites into the latter (Crompton 1971). During occlusion, each lower jaw moves in a triangular trajectory that contains a transverse component; the trigonid of a lower molar shears past the labial portion of the upper one, and then the talonid crushes against the protocone in the more lingual part of the upper molar (Crompton and Hiiemae 1969). The piercing cusps of the teeth, the function of these teeth and the small body size suggest that these animals are insectivorous.

Zhangheotherium and *Maotherium* are the two ‘symmetrodontans’ from the Jehol Biota. The symmetrodont lower jaw is also long, slender and shallow (Figures 5D and 6C). It differs from that of therians in having a narrower and more posteriorly inclined coronoid process, a relatively long and posterodorsally extended condyle and a more anteriorly extended masseteric fossa (at least in *Maotherium* [Rougier *et al.* 2003]), and in lacking the angular process. The cheek teeth of ‘symmetrodontans’, as represented by the three Jehol species, are more primitive than the tribosphenic ones seen in *Eomaia* and *Sinodelphys* (Figures 5, 6). The main cusps of the molars are arranged in a triangular pattern and shearing is the primary function of the cheek teeth. The leading edges of the shearing surfaces are maintained by differential wear, in which the apical wear takes place more rapidly than does the occlusal wear (Crompton *et al.* 1994). The masticatory cycle of these ‘symmetrodontans’ consisted of considerable lateral translation and rotation of the mandible (Crompton 1971; Fox 1976; Cifelli and Madsen 1999). Given their small body sizes and the molar structures that are good at embrasure shearing and puncturing, these ‘symmetrodontans’ are probably insectivorous.

Sinobaartar is the only multituberculate known from the Jehol Biota, although the group represents the most common Mesozoic mammals. The multituberculate lower jaw resembles that of a rodent, in having a single, enlarged incisor, a distinct diastema between the incisor and cheek teeth, and an anteriorly extended masseteric fossa (Figure 5C). However, the lower jaw in multituberculates has a low-positioned condyle relative to the tooth row; its masseteric fossa is situated more anteriorly than in all other mammals (Gambaryan and Kielan-Jaworowska

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1995). More importantly, multituberculates developed a mastication pattern characterized by backward movement of the lower jaw during the power stroke of mastication (Gingerich 1977; Krause 1982; Fox 2005), which differs from the forward movement of the power stroke in rodents. The cheek teeth of multituberculates were multicuspate, and the numerous cusps are subequal in height in most species of the group (Figure 6A). Multituberculates from the Late Jurassic to Paleogene show evolutionary trends in several dental features, including reduction of premolars, increasing the number of ridges on the last lower premolar, and increasing of the molar cusps (Clemens and Kielan-Jaworowska 1979). These changes may indicate the evolution of multituberculates, as omnivorous animals, in a tendency to process food items more effectively (Hu and Wang 2002). Conventionally, multituberculates were considered to be herbivorous based on their jaw structure and tooth morphology (Simpson 1926), but recent works show that they are omnivorous and were able to eat, for instance, hard seeds (Krause 1982; Wall and Krause 1992).

The most novel knowledge on dentition and diet of Mesozoic mammals gained from the Jehol mammals is from the eutriconodontans, particularly *Repenomamus*. Similar to those of multituberculates and 'symmetrodontans', the lower jaw of *Repenomamus* lacks the angular process. However, the coronoid process and the masseteric fossa are large, indicating attachment of large jaw muscles (Figure 5E). The molar pattern of eutriconodontans is the most primitive of the molars seen in Jehol mammals, characterized by three main cusps that align in a row anteroposteriorly on a transversely compressed crown (Figure 6D–G). Early studies documented transverse wear facets on upper molars of fragmentary specimens of *Gobiconodon* (Kielan-Jaworowska and Dashzeveg 1998), but these transverse facets do not indicate transverse movement of the lower jaw during occlusion. Specimens of *Repenomamus* show that the lower jaw moves vertically, with the labial surface of the lower cheek teeth shearing with the lingual side of the uppers. However, a peculiar feature is that the upper molariforms curl inward, which may be a way to extend the usage of the teeth. When the lower tooth occludes past the upper one, wear facets or grooves are created across the upper tooth crown. If an isolated upper molariform of *Repenomamus* is placed in a normal tooth position as in other mammals, the wear facets would appear transversely oriented.

Although it has been suggested that some 'triconodonts' are probably carnivorous, based on the large body size and tooth morphology (Jenkins and Crompton 1979; Jenkins and Schaff 1988), direct evidence is not available until recently (Hu *et al.* 2005). The fossilized stomach content associated with a skeleton of an adult individual of *R. robustus* shows remains of a juvenile *Psittacosaurus*, an herbivorous dinosaur that is very common in the Jehol Biota (Meng *et al.* 2004). Among the disarticulated and displaced skeletal elements of the juvenile *Psittacosaurus* are a few long bones in their original articulations. This indicates that the baby *Psittacosaurus* was dismembered and swallowed in as large pieces in the last meal of the *R. robustus*. The large and pointed incisors and similarly shaped canines and premolariforms of *Repenomamus* form an apparatus for catching, holding and ripping prey. This apparatus is powered by strong jaw musculature, as indicated by the robust dentary and zygoma, large temporal fossa, and deep masseteric fossa. Large pointed anterior teeth followed by small posterior teeth characterize many carnivorous non-mammalian synapsids (Van Valkenburgh and Jenkins 2002). The molariform teeth in the back of the dentition can assist processing food, but their small size, blunt crowns, and side-to-side occlusal contacts suggest a minor role in food processing.

Kielan-Jaworowska *et al.* (2004) have speculated that *Gobiconodon* and *Repenomamus* relied partly on scavenging. As Hu *et al.* (2005) noted, it is not easy to assess whether *Repenomamus* is a predator or scavenger. Scavengers are relatively rare among mammals. Among extant carnivorous mammals, only two hyenas are habitual scavengers (Nowak 1999; Van Valkenburgh *et al.* 2004). Compared to their hunting cousins, these hyenas have smaller second upper incisors and decreased jaw muscle leverage, which probably reflect their inability to capture and handle live prey. In contrast, the enlarged incisors and strong jaw muscles of *Repenomamus* are well shaped to catch small animals; on the other hand, the cheek teeth of *Repenomamus* are not strong enough for bone crushing. In fact, the skeletal elements preserved in the stomach of *R. robustus* do not show any sign of bone crushing. These seem to favour *Repenomamus* as a predator over a scavenger. Kielan-Jaworowska *et al.* (2004) also suggested that some of the large eutriconodontans may have fed on prey that tended to be larger than the predator. *R. giganticus* is much larger than *R. robustus* and they probably could take down larger prey than a 160 mm long juvenile *Psittacosaurus*. However, whether these large eutriconodontans could hunt down prey larger than their body size, such as an adult *Psittacosaurus*, remains unknown. If they did, they may have done that in pack hunting,

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so that many individuals could share the prey; this in turn implies some social behaviours in the population of *Repenomamus*, for which we do not have any evidence. In any case, the fact that *Repenomamus* fed on juvenile dinosaurs indicates that the large mammals must have been one of the carnivores occuping the top trophic level in the ecosystem of the Jehol Biota.

Interestingly, there are no exclusively herbivorous mammals in the Jehol Biota even though various plants flourished there, and this is probably also true for other Mesozoic faunas. It may be because the niches for herbivores were occupied by other vertebrates, particularly dinosaurs. If the number of niches is potentially greatest for small-bodied taxa (Gardezi and Silva 1999), then mammals may have a better chance of survival being small. Insectivorous and omnivorous diets are probably better ways for small and endothermic mammals to obtain sufficient nutrition.

5.3. Locomotion

Although there is no definitive indicator of the habits for early mammals, skeletal features can be suggestive of patterns of locomotion. In this regard, the specimens of Jehol mammals illustrate several types of habits that also add to the diverse life styles of the early mammals.

The metatherian *Sinodelphys* and eutherian *Eomaia* are similar in their skeletal structures. Their forefeet and hindfeet show similar phalangeal proportions and curvature to the grasping feet of extant arboreal mammals. In phalangeal features, *Eomaia* and *Sinodelphys* are more similar to arboreal mammals than to some scansorial species such as the tree shrew and opossum in several aspects. The proximal manual phalanx is arched dorsally; some phalanges have two protuberances for the fibrous tendon sheaths of the flexor digitorum; the proportions of the intermediate phalanx to the proximal phalanx is intermediate between the fully arboreal and scansorial species and the claws lack the broad and thickened dorsal margin found in *Jeholodens*, *Zhangheotherium* and multituberculates and are laterally compressed as in extant mammals capable of climbing. These features in combination suggest that *Sinodelphys* and *Eomaia* are agile, scansorial mammals capable of grasping and branchwalking, and active both on the ground and in trees or shrubs and that scansorial and arboreal adaptations in therian mammals have a very ancient evolutionary origin and can be dated at least to about 125 million years ago (Ji *et al.* 2002; Luo *et al.* 2003).

In contrast to their diverse dental morphologies, the postcranial elements of multituberculates are more conservative. This may suggest that patterns of locomotions in various multituberculates were similar (Hu and Wang 2002). With relatively generalized skeletons, multituberculates can live on a variety of substrates. Some groups show a tendency to be limitedly arboreal, such as *Ptilodus*, an arboreal taxon with a long and prehensile tail from the North American Paleogene (Krause and Jenkins 1983; Jenkins and Krause 1983); others are terrestrial, such as the Late Cretaceous Asian multituberculates (Kielan-Jaworowska and Gambaryan 1994). The tibial condyle and astragalotibial joint of *Sinobaatar* resemble those of *Ptilodus*; therefore, *Sinobaatar* is probably capable of arboreal locomotion. The wrists of *Sinobaatar* are not significantly specialized and may represent the prototype mammalian wrist, suitable for locomotion on uneven substrates (Hu and Wang 2002).

The forelimb and manus of *Zhangheotherium* are well preserved (Hu *et al.* 1997; Hu *et al.* 1998). The smooth articulation between the ulna and radius permits pronation-supination of its forearm to a degree similar to that of North American multituberculates. The manus of *Zhangheotherium* can flex and extend considerably, but may not have grasping ability. Its claws are similar to those of terrestrial mammals. Skeletal structures suggest that *Zhangheotherium* is capable of both climbing and walking, but would spend more time on the ground than in trees, as do most extant insectivores and rodents (Hu *et al.* 1998).

The skeleton of the smallest triconodont, *Jeholodens jenkinsi*, is characterized by a mosaic combination of derived, therian-like pectoral girdle and humerus, and primitive characters of the vertebral column, pelvic girdle, hindlimb and pes. Derived features such as a fully developed supraspinous fossa of the scapula, acromion and metacromion on the scapular spine, incipient ulnar trochlea and reduced epicondyles of the humerus are considered to be convergences with those of therians (Ji Q *et al.* 1999b). Its claviculointerclavicle articulation had some degree of mobility, similar to those of multituberculates and therians, although this ability is also independently acquired,

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given the phylogeny presented by Ji Q *et al.* (1999b). *Jeholodens jenkinsi* was interpreted as a ground-dweller that had a plantigrade gait and some capability for climbing on uneven substrates, but not an arboreal mammal.

As the largest mammals from the Jehol Biota, *Repenomamus* has a relatively long trunk but short, robust limbs. Its well differentiated vertebral column, scapula-humerus joint, offset femoral head in relation to the shaft, and short and broad plantigrade pes and manus suggest that the limb excursion of *Repenomamus* is more similar to those of non-cursorial therian mammals than to those of monotremes (Hu *et al.* 2005). The large ulnar olecranon and posteroventrally directed femoral condyles allow a semi-erect posture, as in the majority of small- to medium-sized extant therian mammals. The postcranial skeleton of *Repenomamus* is most similar to that of *Gobiconodon ostromi* (Jenkins and Schaff 1988). Jenkins and Schaff realized that *G. ostromi* does not have vertebral features developed in mammals that are capable of rapid locomotion and that the phalanges and other postcranial structures are indicative of ambulatory rather than scansorial or cursorial habits. Therefore, *G. ostromi* was probably more methodical than agile in habits, and as a predator had a greater advantage in its size than in its speed. This conclusion is readily applicable to the unquestionably terrestrial *Repenomamus.*

6. ANATOMICAL SIGNIFICANCE

The well-preserved specimens of the Jehol mammals furnished a wealth of morphological data for early mammals, such as presence of fur in an early eutherian (Ji *et al.* 2002) and 'symmetrodontan' (Rougier *et al.* 2003) and presence of the epipubic bones in eutriconodontans (Ji Q *et al.* 1999b; Hu *et al.* 2005) and in the eutherian *Eomaia* (Ji *et al.* 2002). Some of the specimens help to clarify several uncertainties in the anatomy of early mammals that have been puzzling palaeontologists for decades, such as the occupant of the internal groove on the medial surface of the dentary bone of early mammals, and the tooth count and eruption of molariform teeth.

6.1. Ossified Meckelian cartilage

A groove that extends longitudinally along the medial surface of the dentary is a common but puzzling feature present in many Mesozoic mammals and their relatives known since the 19th century (see Meng *et al.* 2003a for a review). For most Mesozoic mammals, such as eutriconodontans and 'symmetrodontans', there is no direct evidence of what the groove actually holds. Interpretation of the function of the internal groove bears importantly on the origin of the definitive mammalian middle ear. For instance, because *Peramus* and *Amphitherium* are within Trechnotheria of Mammalia (McKenna and Bell 1997), interpretation of the presence of the postdentary unit in these taxa argues for multiple origins of the definitive mammalian middle ear (Allin and Hopson 1992).

Evidence from *Repenomamus* and *Gobiconodon* (Wang *et al.* 2001; Li *et al.* 2003; Meng *et al.* 2003a) demonstrates that an ossified Meckel's cartilage occupies their internal groove. Because the internal groove in eutriconodontans is similar to that of *Repenomamus*, it is probably true that it also lodges a persistent Meckel's cartilage in other eutriconodontans. The finding indicates that in early mammals, including *Peramus* and *Amphitherium*, an ossified Meckel's cartilage should be considered as a potential occupant for the groove in question. This weakens the hypothesis that postdentary elements are still attached to the dentary of some early mammals, such as *Peramus* and *Amphitherium*; rather, these mammals may have developed the definitive mammalian middle ear.

The position of the ossified Meckel's cartilage in *Repenomamus* and *Gobiconodon* also provides evidence for the relationship of Meckel's cartilage with the definitive mammalian middle ear in early mammals, which is otherwise inferred only from embryological evidence of living mammals. The specimens show that, while the anlage of the malleus is reduced, or posteriorly shifted, to form a small malleus, a significant middle portion of Meckel's cartilage persisted and even ossified in adults of some early mammals and close relatives. This supports the assumption that a persisting and possibly ossified Meckel's cartilage that connects the malleus to the lower jaw was present in the common ancestor of mammals (Zeller 1993).

One of the important issues in the evolution of the definitive mammalian middle ear is how the postdentary unit became detached from the dentary, and translocated to the basicranium as ear ossicles (Hopson 1966; Allin 1975, 1986; Maier 1990; Allin and Hopson 1992; Zeller 1993; Rowe 1996a, 1996b). Rowe (1996a, 1996b) suggested that there is a negative allometry of growth of the auditory chain in relation to that of the brain, that is, the ear ossicles approach their mature size during early stage of development while still attached to the lower jaws, while the brain continues to grow for a much longer time during postnatal development. As the brain expands, the distance between the secondary craniomandibular joint and the ear region is widened and the ear ossicles are torn away from the mandible and carried backwards to their adult position behind the jaw. This mechanism was considered to account for detachment of the ear ossicles in both mammalian ontogeny and phylogeny (Rowe 1996a, 1996b).

Specimens of Jehol eutriconodontans provide evidence against the brain-expansion model for ear ossicle detachment during mammalian evolution. For instance, the ear ossicles of *Repenomamus* are considered to be detached from the dentary, but the maximum ratio of the estimated brain vault to the skull width (Meng *et al.* 2003a) is smaller than those of *Sinoconodon* and *Morganucodon* in which the postdentary unit is still attached to the dentary (Kermack *et al.* 1981; Crompton and Sun 1985; Luo *et al.* 2001). This and other evidence indicate that detachment of the ear ossicles is not necessarily associated with expansion of the brain during mammalian evolution and that separation of the postdentary bones from the dentary does not require increase of distance between the ear and the mandible (Wang *et al.* 2001; Meng *et al.* 2003a). Meng *et al.* (2003a) proposed an alternative hypothesis for ear ossicle detachment. The position of the ossified Meckel's cartilage in *Repenomamus* suggests that the embryonic dentary is probably in an inclined or horizontal orientation and reorients to a vertical position in later stage, as in early development of marsupials (Maier 1987, 1990). Reduction of the postdentary bones increasingly weakened their tie to the dentary until a critical point was reached that the dentary, while erecting to a more vertical position during ontogeny, no longer seized the postdentary bones. The postdentary bones were moored at the basicranium by connective tissue as exclusively auditory ossicles.

6.2. Tooth formula

In addition to tooth morphology, as introduced above, identification of the incisors, canines, premolars and molar is also crucial in establishing tooth homology of mammals, which in turn forms one of the major data sources for phylogenetic analysis. In extant mammals, designations of teeth are based on morphology, ontogeny, and position of an individual tooth (Clemens and Lillegraven 1986; Butler and Clemens 2001). 'The benchmark for positional characters is the upper canine, which is defined as the tooth whose alveolus is at or immediately behind the premaxillary-maxillary suture' (Butler and Clemens 2001, p. 2). The corresponding lower tooth is usually a half tooth anterior to its upper counterpart. Because of incomplete preservation of specimens, such a relationship is not always easy to establish in early mammals.

In known species of gobiconotontids, the designations of these teeth are not conclusive (Trofimov 1978; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Rougier *et al.* 2001; Li *et al.* 2003). The dental formula is ? · ? · ? · 5/1 · 1 · 4 · ? for *G. borissiaki*, ? · ? · 4 · 5/1 · 1 · 4 · 5 for *G. hoburensi* (Kielan-Jaworowska and Dashzeveg 1998) and 2 · 1 · ? · ?/1 · 1 · 3-4 · 5 for *G. ostromi* (Jenkins and Schaff 1988). None of the tooth designations was referred to un unequivocal position of the upper canine because either the canine is not preserved or skull material is not available to show the premaxillary-maxillary suture.

Although complete dentitions and skull material are preserved in *G. zofiae* from the Lujiatun beds (Li *et al.* 2003), the premaxillary-maxillary suture is unclear in the holotype. Therefore, the designations of the non-molariform teeth in *G. zofiae* were tentative and the tooth formula was considered I2-C1-P4-M4/i1-c1-p4-m5. It clarifies, however, that there are 4, instead of 5, upper molariforms in *Gobiconodon.* The tooth identified as the lower canine appears too anterior in the tooth row of *G. zofiae;* it does also in *G. ostromi.*

Repenomamus from the Jehol Biota preserves complete skulls and associated lower jaws, as well as associated upper and lower dentitions (Li *et al.* 2000; Wang *et al.* 2001; Hu *et al.* 2005). Several skulls of *Repenomamus* show clearly the premaxillary-maxillary suture that helps to determine the upper canine and thus other non-molariform teeth. The tooth formula of *Repenomamus* is I3-C1-P2-3-M4/i2-c1-p2-3-m5. The i2 of *Repenomamus* is similar to the tooth designated as the lower canine in *G. ostromi* and *G. zofiae*, although in the former the i1 is not enlarged. A recently described taxon from the Lujiatun beds, *Meemannodon*, has an enlarged i1 but a proportionally reduced i2. In light of the dental formula of *Repenomamus*, it is probable that the tooth formula for gobiconodontids may well be I3-C1-P3-M4/i2-c1-p2-3-m5, similar to that of *Repenomamus*.

Sinodelphys and *Eomaia* present intriguing issues for the dental formulae of metatherians and eutherians. The dental formula is I5-C1-P5-M3/i4-c1-p5-m3 for *Eomaia* (Ji *et al.* 2002) and I4-C1-P4-M4/i4-c1-p4-m3 for *Sinodelphys* (Luo *et al*. 2003). Although the premaxilla-maxillary suture is not always clear, such as in the case of *Sinodelphys*, the morphology of the landmark upper canine is usually characteristic in eutherians and metatherians. This is true in *Asioryctes* and *Kennalestes*, in which the last upper incisor is located either at the premaxilla-maxillary suture or in the maxilla posterior to the suture and is recognized by its shape (Kielan-Jaworowska 1975). The incisor count of *Eomaia* is similar to those of other early eutherians, such as *Asioryctes* and *Ukhaatherium* (Kielan-Jaworowska 1975; Kielan-Jaworowska *et al.* 2004) and to the primitive marsupials in having five upper and four lower teeth (Clemens and Lillegraven 1986). The I5/i4 condition is probably shared by the common ancestor of metatherians and eutherians. However, given that the earliest and most basal metatherian *Sinodelphys* has only four upper incisors (Luo *et al.* 2003), it may be interpreted that reduction of upper incisors is either an apomorphic feature for *Sinodelphys* or that marsupials postdating *Sinodelphys* regain the last upper incisor.

The premolars and molars of *Sinodelphys* also display a unique formula. The primitive metatherian tooth formula for postcanine teeth is P3/p3-M4/m4 (Clemens and Lillegraven 1986; Kielan-Jaworowska *et al.* 2004). *Sinodelphys* appears to be primitive in having four upper and lower premolars but derived in having three lower molars compared to other metatherians. Given the phylogenetic position of *Sinodelphys*, absence of the m4 is probably an automorphic feature for the taxon, or presence of m4 in later metatherians is a secondary acquisition. Because the last upper molar of *Sinodelphys* does not occlude to a lower tooth, as inferred from Luo *et al.* (2003: Figure 1), the functional significance of that tooth remains to be explained.

7. CONCLUSIONS

Since the first report of mammals in 1997 (Hu *et al.* 1997), a total of 11 species belonging to five major groups of mammals have been described from the Jehol Biota, Liaoning, China. These include the ‘symmetrodontan’ *Zhangheotherium quinquecuspidens* (Hu *et al.*, 1997), *Maotheirum sinensis* (Rougier *et al.*, 2003) and *Akidolestes cifellii* (Li and Luo, 2006), multituberculate *Sinobaatar lingyuanensis* (Hu and Wang, 2002), eutriconodontan *Jeholodens jenkinsi* (Ji Q *et al.*, 1999b), *Gobiconodon zofiae* (Li *et al.*, 2003; *Meemannodon lujiatunensis* (Meng *et al.*, 2005), *Repenomamus robustus* (Li *et al.*, 2000) and *R. giganticus* (Hu *et al.*, 2005), stem metatherian *Sinodelphys szalayi* (Luo *et al.*, 2003) and stem eutherian *Eomaia scansoria* (Ji *et al.*, 2002). These mammals are known from the Lujiatun, Jianshangou and Dawangzhangzi beds of the Yixian Formation. Ages and correlations of these beds from various localities are still controversial, although a converged view of Early Cretaceous emerges recently. The time range of the Jehol Group could be as long as 18 million years, from 128 to 110 million year, or as short as about 3 million years, from 123.2 to 120 million year. Because mammals are unknown from the Jiufotang Formation, the time span for the mammal fauna known to date could be much shorter than 3 million years. A more accurate chronology of the Yixian Formation is apparently critical for understanding evolution of Mesozoic mammals in general and faunal composition of the Jehol mammals in particular.

Specimens of Jehol mammals are preserved in two types of condition: some three-dimensional from the sandstones of Lujiatun Bed and others nearly two-dimensionsal from shales of Jianshangou and Dawangzhangzi beds. Based on these specimens, large character data matrixes have been generated, although these data sets have generated competing phylogenetic hypotheses. While future refinement of these data sets based on detailed detailed description of specimens is anticipated, our knowledge of phylogeny and divergence of early mammals and their relatives has been significantly advanced because of the Jehol mammals. The coeval existence of *Sinodelphys* and *Eomaia* documents at least an Early Cretaceous divergence of mammal lineages that lead to their extant relatives. The well-preserved material provide convincing morphological evidence pertinent to several previously uncertain

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features, such as the dental formula of some eutriconodontans and detachment of the middle ear ossicles from the lower jaw in some Mesozoic mammals. The Jehol mammals possess a variety of life styles, as reflected by their body masses, diets and locomotions, and display some evidence of faunal dynamics. We have, for the first time, direct evidence that not only small mammals are food of carnivorous dinosaurs, but also large carnivorous mammals could have lived on eating young dinosaurs.

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REFERENCES

Alexander RMcN, Jayes AS, Maloiy GMO, Wathuta EM. 1979. Allometry of limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *Journal of Zoology, London* **189**: 305–314.

Allin EF. 1975. Evolution of the mammalian middle ear. *Journal of Morphology* **147**: 403–438.

Allin EF. 1986. Auditory apparatus of advanced mammal-like reptiles and early mammals. In *The ecology and biology of mammal-like reptiles*, Hotton N, MacLean PD, Roth JJ, Roth EC (eds). Smithsonian Institution Press: Washington; 283–294.

Allin EF, Hopson JA. 1992. Evolution of the auditory system in Synapsida ('mammal-like reptiles' and primitive mammals) as seen in the fossil record. In *The evolutionary biology of hearing*, Webster DB, Fay RR, Popper AN (eds). Springer-Verlag: New York; 587–614.

Archibald JD, Averianov AO, Ekdale EG. 2001. Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals. *Nature* **414**: 62–65.

Asher RJ, Meng J, Wible JR, McKenna MC, Rougier GW, Dashzeveg D, Novacek MJ. 2005. Stem Lagomorpha and the antiquity of Glires. *Science* **307**: 1091–1094.

Averianov AO, Skutschas PP. 2001. A new genus of eutherian mammal from the Early Cretaceous of Transbaikalia, Russia. *Acta Palaeontologica Polonica* **46**: 431–436.

Barrett PM. 2000. Evolutionary consequences of dating the Yixian Formation. *Trends in Ecology and Evolution* **15**: 99–103.

Brown JH, Marquet PA, Taper ML. 1993. The evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* **142**: 573–584.

Butler PM, Clemens WA. 2001. Dental morphology of the Jurassic holotherian mammal *Amphitherium*, with a discussion of the evolution of mammalian postcanine dental formulae. *Palaeontology* **44**: 1–20.

Carbone C, Mac GM, Roberts SC, Macdonald DW. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**: 286–288.

Chang MM, Chen PJ, Wang YQ, Wang Y (eds). 2003. *The Jehol Biota: the emergence of feathered dinosaurs, beak birds and flowering plants*. Shanghai Scientific and Technical Publishers: Shanghai.

Chen W, Ji Q, Liu DY, Zhang Y, Song B, Liu XY. 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* **23**: 1165–1169. (in Chinese)

Chen PJ, Wang QF, Zhang HC, Cao MZ, Li WB, Wu SQ, Shen YS. 2004. Comments on Jianshangou beds. *Science in China D* **34**: 883–895 (in Chinese).

Chow MZ, Rich THV. 1984. A new triconodontan (Mammalia) from the Jurassic of China. *Journal of Vertebrate Paleontology* **3**: 226–231.

Cifelli RL. 1999. Tribosphenic mammal from the North American Early Cretaceous. *Nature* **401**: 363–366.

Cifelli RL, Madsen SK. 1999. Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA. *Geodiversitas* **21**: 167–214.

Cifelli RL, Wible JR, Jenkins FA. 1998. Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. *Journal of Vertebrate Paleontology* **18**: 237–241.

Clemens WA, Kielan-Jaworowska Z. 1979. Multituberculata. In *Mesozoic mammals: The first two-thirds of mammalian history*, Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds). University of California Press: Berkeley; 99–149.

Clemens WA, Lillegraven JA. 1986. New Late Cretaceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. *Contributions to Geology, University of Wyoming, Special Paper* **3**: 55–85.

Crompton AW. 1971. The origin of the tribosphenic molar. In *Early Mammals*, Kermack DM, Kermack KA (eds). *Zoological Journal of the Linnean Society* **50** (Suppl. 1):65–87.

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Crompton AW, Hiiemae KM. 1969. Functional occlusion in tribosphenic molars. *Nature* **222**: 678–679.

Crompton AW, Jenkins FA. 1968. Molar occlusion of Late Triassic Mammals. *Biological Review* **43**: 427–458.

Crompton AW, Sun AL. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. *Zoological Journal of the Linnean Society* **85**: 99–119.

Crompton AW, Wood CB, Stern DN. 1994. Differential wear of enamel: a mechanism for maintaining sharp cutting edges. *Advances in Comparative and Environmental Physiology* **18**: 321–346.

Cuenca-Bescós G, Canudo JI. 2003. A new gobiconodontid mammal from the Early Cretaceous of Spain and its palaeogeographic implications. *Acta Palaeontologica Polonica* **48**: 575–582.

Damuth J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. *Biological Journal of the Linnean Society* **15**: 185–193.

Damuth J, MacFadden BJ (eds). 1990. *Body size in mammalian paleobiology: Estimation and biological implication*. Cambridge University Press: Cambridge.

Fox RC. 1976. Additions to the mammalian local fauna from the upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian Journal of Earth Sciences* **13**: 1105–1118.

Fox RC. 2005. Microcosmodontid multituberculates (Allotheria, Mammalia) from the Paleocene and Late Cretaceous of western Canada. *Palaeontographica Canadiana* **23**: 1–109.

Gambaryan PP, Kielan-Jaworowska Z. 1995. Masticatory musculature of Asian taeniolabidoid multituberculate mammals. *Acta Palaeontologica Polonica* **40**: 45–108.

Gardezi T, Silva J. 1999. Diversity in relation to body size in mammals: A comparative study. *American Naturalist* **153**: 110–123.

Gingerich PD. 1977. Patterns of evolution in mammalian fossil records. In *Patterns of evolution*, Hallam A (ed.). Elsevier Science Publishers: Amsterdam; 469–500.

Gingerich PD. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. *Contributions from the Museum of Paleontology, University of Michigan* **28**: 79–92.

Godefroit P, Guo DY. 1999. A new amphilestid mammal from the Early Cretaceous of Inner Mongolia (P.R. China). *Bulletin de l'Institut royal des Sciences naturelles de Belgique* **69** (Suppl B):7–16.

Harestad AS, Bunnell FL. 1979. Home range and body weight-A reevaluation. *Ecology* **60**: 389–402.

Haskell JP, Ritchie ME, Olff H. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* **418**: 527–530.

He HY, Wang XL, Zhou ZH, Wang F, Boven A, Shi GH, Zhu RX. 2004. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China, and its implications. *Geophysical Research Letters* **31**: L12605.

He HY, Wang XL, Zhou ZH, Jin F, Wang F, Yang LK, Ding X, Boven A, Zhu RX. 2006. ^{40}Ar/^{39}Ar dating of Lujiatun Bed (Jehol Group) in Liaoning, northeastern China. *Geophysical Research Letters* **33**: L04303.

Hedges SB, Parker P, Sibley G, Kumar S. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**: 226–229.

Holling CS. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* **62**: 447–502.

Hopson JA. 1966. The origin of the mammalian middle ear. *American Zoologist* **6**: 437–450.

Hopson JA. 1973. Endothermy, small size and the origin of mammalian reproduction. *American Naturalist* **107**: 446–452.

Hopson JA, Crompton AW. 1969. Origin of mammals. *Evolutionary Biology* **3**: 16–72.

Hu YM, Wang YQ. 2002. *Sinobaatar*gen. nov.: First multituberculate from the Jehol Biota of Liaoning, Northeast China. *Chinese Science Bulletin* **47**: 933–938.

Hu YM, Wang YQ, Luo ZX, Li CK. 1997. A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature* **390**: 137–142.

Hu YM, Wang YQ, Li CK, Luo ZX. 1998. Morphology of dentition and forelimb of *Zhangheotherium*. *Vertebrata PalAsiatica* **38**: 102–125.

Hu YM, Meng J, Wang YQ, Li CK. 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature* **433**: 149–152.

Hunter JP, Jernvall J. 1995. The hypocone as a key innovation in mammalian evolution. *Proceedings of the National Academy of Sciences USA* **92**: 10718–10722.

Hurum JH, Luo ZX, Kielaa-Jaworowska Z. 2006. Were mammals originally venomous? *Acta Palaeontologica Polonica* **51**: 1–11.

Isaac JL, 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review* **35**(1): 101–115.

Janke A, Feldmaier-Fuchs G, Thomas WK, von Haeseler A, Pääbo S. 1994. The marsupial mitochondrial genome and the evolution of placental mammals. *Genetics* **137**: 243–256.

Janke A, Magnell O, Wieczorek G, Westerman M, Arnason U. 2002. Phylogenetic analysis of 18S rRNA and the mitochondrial genomes of the wombat, *Vombatus ursinus*, and the spiny anteater, *Tachyglossus aculeatus*: increased support for the Marsupionta hypothesis. *Journal of Molecular Evolution* **54**: 71–80.

Jenkins FA, Krause DW. 1983. Adaptation for climbing in North American multituberculates (Mammalia). *Science* **220**: 712–715.

Jenkins FA, Schaff CR. 1988. The Early Cretaceous mammal *Gobiconodon*from the Cloverly Formation in Montana. *Journal of Vertebrate Paleontology* **8**: 1–24.

Jenkins FA, Crompton AW. 1979. Triconodonta. In *Mesozoic Mammals: the first two-thirds of mammalian history*, Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds) .University of California Press: Berkeley; 74–90.

Jerison HJ. 1973. *Evolution of the brain and intelligence*. Academic Press: New York.

Ji Q, Currie PJ, Norell MA, Ji SA. 1998. Two feathered dinosaurs from northeastern China. *Nature* **393**: 753–761.

Ji Q, Ji SA, Ren D, Lu LW, Fang XS, Guo ZG. 1999a. On the sequence and age of the Protobird-bearing deposits in Sihetun-Jianshangou area, Beipiao, western Liaoning Province. *Professional Papers of Stratigraphy and Palaeontology* **27**: 74–80.

Ji Q, Luo ZX, Ji SA. 1999b. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* **398**: 326–330.

Ji SA, Ji Q, Padian K. 1999. Biostratigraphy of new pterosaurs from China. *Nature* **398**: 573–574.

Ji Q, Luo ZX, Yuan CX, Wible JR, Zhang JP, Georgi JA. 2002. The earliest known eutherian mammals. *Nature* **416**: 816–822.

Ji Q, Chen W, Wang WL, Jin XC, Zhang JP, Liou YQ, Zhang H, Yao PY, Ji SA, Yuan CX, Zhang Y, You HL. 2004. *The Mesozoic Jehol Biota of western Liaoning and a synthetic study of related stratigraphic sequences* (in Chinese). The Geological Press: Beijing.

Ji Q, Luo ZX, Yuan CX, Tabrum AR. 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science* **311**: 1123–1127.

Kelt DA, Van Vuren D. 1999. Energetic constraints and the relationship between body size and home range area in mammals. *Ecology* **80**: 337–340.

Kermack KA, Mussett F, Rigney HW. 1973. The lower jaw of *Morganucodon*. *Zoological Journal of the Linnean Society* **53**: 87–175.

Kermack KA, Mussett F, Rigney HW. 1981. The skull of *Morganucodon*. *Zoological Journal of Linnean Society* **71**: 1–158.

Kielan-Jaworowska Z. 1975. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. *Palaeontologia Polonica* **33**: 5–16.

Kielan-Jaworowska Z, Dashzeveg D. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. *Zoologica Scripta* **18**: 347–355.

Kielan-Jaworowska Z, Dashzeveg D. 1998. Early Cretaceous amphilestid ('triconodont') mammals from Mongolia. *Acta Palaeontologica Polonica* **43**: 413–438.

Kielan-Jaworowska Z, Gambaryan PP. 1994. Postcranial anatomy and habits of Asian multituberculate mammals. *Fossils and Strata* **36**: 1–92.

Kielan-Jaworowska Z, Cifelli RL, Luo ZX. 2004. *Mammals from the age of dinosaurs: origins, evolution, and structure*. Columbia University Press: New York.

Krause DW. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. *Paleobiology* **8**: 265–281.

Krause DW, Jenkins FA. 1983. The postcranial skeleton of North American multituberculates. *Bulletin of the Museum of Comparative Zoology* **150**: 199–246.

Kumar S, Hedges SB. 1998. A molecular timescale for vertebrate evolution. *Nature* **392**: 917–920.

Lammers AR, Dziech HA, German RZ. 2001. Ontogeny of sexual dimorphism in *Chinchilla lanigera*(Rodentia: Chinchillidae). *Journal of Mammalogy* **82**: 179–189.

Li G, Luo ZX. 2006. A Cretaceous symmetrodont therian with some monotreme-like postcranial features. *Nature* **439**: 195–200.

Li CK, Wang YQ, Hu YM, Zhou MZ. 1995. A symmetrodont skeleton from the Late Jurassic of western Liaoning, China. In *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Sun AL, Wang YQ (eds). China Ocean Press: Beijing; 233.

Li JL, Wang Y, Wang YQ, Li CK. 2000. A new family of primitive mammal from the Mesozoic of western Liaoning, China. *Chinese Science Bulletin* **45**: 2545–2549 (in Chinese)

Li CK, Wang YQ, Hu YM, Meng J. 2003. A new species of *Gobiconodon*(Triconodonta, Mammalia) and its implication for the age of Jehol Biota. *Chinese Science Bulletin* **48**: 1129–1134.

Lillegraven JA. 1979. Introduction. In *Mesozoic mammals: The first two-thirds of mammalian history*, Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds). University of California Press: Berkeley; 1–6.

Lillegraven JA, Clemens WA. 2004. Foreword. In *Mammals from the age of dinosaurs: origins, evolution, and structure,*Kielan-Jaworowska Z, Cifelli RL, Luo ZX. Columbia University Press: New York; vii–ix.

Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds.) 1979. *Mesozoic mammals: The first two-thirds of mammalian history*. University of California Press: Berkeley.

Lindstedt SL, Miller BJ, Buskirk SW. 1986. Home range, time, and body size in mammals. *Ecology* **67**: 413–418.

Liu Y, Liu Y. 2005. Comment on '^{40}Ar/^{39}Ar dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic age for the overlying Daohugou Bed' by H. Y. He *et al.*, *Geophysical Research Letters* **32**: L12314.

Luo ZX, Crompton AW, Sun AL. 2001. A new mammaliaform from Early Jurassic and evolution of mammalian characteristics. *Science* **292**: 1535–1540.

Luo ZX, Ji Q. 2005. New study on dental and skeletal features of the Cretaceous 'symmetrodontan' mammal *Zhangheotherium*. *Journal of Mammalian Evolution* **12**: 337–357.

Luo ZX, Ji Q, Wible JW, Yuan CX. 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. *Science* **302**: 1934–1940.

Maier W. 1987. Der Processus angularis bei *Monodelphis domestica*(Didelphidae; Marsupialia) und seine Beziehungenzum Mittelohr: Eine ontogenetische und evolutionsmorphologischeUntersuchung. *Gegenbaurs Morphologisches Jahrbuch* **133**: 123–161.

Maier W. 1990. Phylogeny and ontogeny of mammalian middle ear structures. *Netherlands Journal of Zoology* **40**: 55–74.

Maschenko EN, Lopatin AV. 1998. First record of an Early Cretaceous triconodont mammal in Siberia. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **68**: 233–236.

McKenna MC, Bell SK. 1997. *Classification of mammals above the species level*. Columbia University Press: New York.

McNab BK. 1963. Bioenergetics and the determination of home-range size. *American Naturalist* **97**: 133–140.

Meng J, Hu YM, Wang YQ, Li CK. 2003a. The ossified Meckel's cartilage and internal groove in Mesozoic mammaliaformes: implications to origin of the definitive mammalian middle ear. *Zoological Journal of Linnean Society* **138**: 431–448.

Meng J, Hu YM, Li CK. 2003b. The osteology of *Rhombomylus* (Mammalia, Glires): implications for phylogeny and evolution of Glires. *Bulletin of the American Museum of Natural History* **275**: 1–247.

Meng QJ, Liu JY, Varricchi DJ, Huang T, Gao CL. 2004. Palaeontology: Parental care in an ornithischian dinosaur. *Nature* **431**: 145–146.

Meng J, Hu YM, Wang YQ, Li CK. 2005. A new triconodont (Mammalia) from the Early Cretaceous Yixian Formation of Liaoning, China. *Vertebrata PalAsiatica* **43**: 1–10.

Mills JRE. 1971. The dentition of *Morganucodon*. In *Early mammals*, Kermack DM, Kermack KA (eds). *Zoological Journal of Linnean Society* **50** (Suppl. 1):29–63.

Mitter C, Farrell B, Wiegmann B. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *American Naturalist* **132**: 107–128.

Nowak RM. 1999. *Walker's mammals of the world* (6th edn). The Johns Hopkins University Press: Baltimore.

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DOI: 10.1002/gj

O'Leary MA, Allard M, Novacek MJ, Meng J, Gatesy J. 2004. Building the mammalian sector of the tree of life: combining different data and a discussion of divergence time for placental mammals. In *Assembling the tree of life*, Cracraft J, Donoghue MJ (eds). Oxford University Press: New York; 490–516.

Peters RH. 1983. *The ecological implications of body size*. Cambridge University Press: Cambridge.

Reiss M. 1988. Scaling of home range size: body size, metabolic needs and ecology. *Trends in Ecology and Evolution* **3**: 85–88.

Rose KD, Archibald JD (eds). 2005. *The rise of placental mammals: origins and relationships of the major extant clades*. The Johns Hopkins University Press: Baltimore.

Rougier GW, Wible JR, Hopson JA. 1996a. Basicranial anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the Late Jurassic of Colorado, and a reappraisal of mammaliaform interrelationships. *American Museum Novitates* **3183**: 1–38.

Rougier GW, Wible JR, Novacek MJ. 1996b. Middle-ear ossicles of the multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: implications for mammaliamorph relationships and the evolution of the auditory apparatus. *American Museum Novitates* **3187**: 1–43.

Rougier GW, Wible JR, Novacek MJ. 1998. Implications of *Deltatheridium* specimens for early marsupial history. *Nature* **396**: 459–463.

Rougier GW, Isaji S, Manabe M. 1999. An Early Cretaceous Japanese triconodont and a revision of triconodont phylogeny. *Journal of Vertebrate Paleontology* **19** (Suppl. 3):72A.

Rougier GW, Novacek MJ, McKenna MC, Wible JR. 2001. Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. *American Museum Novitates* **3348**: 1–30.

Rougier GW, Ji Q, Novacek MJ. 2003. A new symmetrodont mammal with fur impressions from the Mesozoic of China. *Acta Geologica Sinica* **77**(1): 7–14.

Rowe T, 1988. Definition, diagnosis and origin of Mammalia. *Journal of Vertebrate Paleontology* **8**: 241–264.

Rowe T. 1996a. Coevolution of the mammalian middle ear and neocortex. *Science* **273**: 651–654.

Rowe T. 1996b. Brain heterochrony and origin of the mammalian middle ear. *Memoirs of the California Academy of Sciences* **20**: 71–95.

Silva M, Downing JA. 1995. *CRC handbook of mammalian body mass.* CRC Press: Boca Raton.

Simpson GG. 1926. Mesozoic Mammalia. IV. The multituberculates as living animals. *American Journal of Science* **11**: 228–250.

Simpson GG. 1928. *A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. Trustees of the British Museum: London.

Slowinski JB, Guyer C. 1993. Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist* **142**: 1019–1024.

Smith AG, Smith DG, Funnell BM. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press: Cambridge.

Smith JB, Harris JD, Omar GI, Dodson P, You HL. 2001. Biostratigraphy and avian origins in northeastern China. In *New perspectives on the origin and early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom*, Gauthier J, Gall LF (eds). Peabody Museum of Natural History: New Haven; 549–589.

Springer MS, Murphy WJ, Eizirik E, O'Brien SJ. 2003. Placental mammal diversification and Cretaceous-Tertiary boundary. *Proceedings of the National Academy of Sciences USA* **100**: 1056–1061.

Springer MS, Murphy WJ, Eizirik E, O'Brien SJ. 2005. Molecular evidence for major placental clades. In *The rise of placental mammals: origins and relationships of the major extant clades*, Rose KD, Archibald JD (eds). The Johns Hopkins University Press: Baltimore; 37–49.

Sun G, Zheng SL, Dilcher DL, Wang YD, Mei SW. 2001. *Early angiosperms and their associated plants from western Liaoning, China.* Scientific and Techonological Education Publishing House: Shanghai.

Swihart RK, Slade NA, Bergstrom BJ. 1988. Relating body size to the rate of home-range use in mammals. *Ecology* **69**: 393–399.

Swisher CC, Wang YQ, Wang XL, Xu X, Wang Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* **398**: 58–61.

Swisher CCIII, Wang XL, Zhou ZH, Wang YQ, Jin F, Zhang JY, Xu X, Zhang FC, Wang Y. 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new ^{40}Ar/^{39}Ar dating of the Yixian and Tuchengzi formations. *Chinese Science Bulletin* **47**: 135–138.

Tang F, Luo ZX, Zhou ZH, You HL, Georgi JA, Tang ZL, Wang XZ. 2001. Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. *Cretaceous Research* **22**: 115–129.

Trivers RL. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*, Campbell B (ed.). Aldine Publishing: Chicago; 136–179.

Trofimov BA. 1978. The first triconodonts (Mammalia, Triconodonta) from Mongolia. *Doklady Akademii Nauk SSSR* **243**: 213–216 (in Russian).

Van Valkenburgh B. 1990. Skeleton and dental predictors of body mass in carnivores. In *Body size in mammalian paleobiology: Estimation and biological implication*, Damuth J, MacFadden BJ (eds). Cambridge University Press: Cambridge; 181–205.

Van Valkenburgh B, Jenkins I. 2002. Evolutionary patterns in the history of Permo-Triassic and Cenozoic synapsid predators. *Paleontological Society Papers* **8**: 267–288.

Van Valkenburgh B, Sacco T, Wang XM. 2004. Pack hunting in Miocene Borophagine dogs: Evidence from craniodental morphology and body size. *Bulletin of the American Museum of Natural History* **279**: 147–162.

Van Vuren D. 1998. Mammalian dispersal and reserve design. In *Behavioral ecology and conservation biology*, Caro TM (ed.). Oxford University Press: New York; 369–393.

Vrba ES. 1987. Ecology in relation to speciation rates: some case histories of Miocene-Recent mammal clades. *Evolutionary Ecology* **1**: 283–300.

Wall CE, Krause DW. 1992. A biomechanical analysis of the mascatory apparatus of *Ptilodus*(Multituberculata). *Journal of Vertebrate Paleontology* **12**: 172–182.

Wang XL, Zhou ZH. 2003. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. *Chinese Science Bulletin* **48**: 16–23.

Wang XL, Wang YQ, Jin F, Xu X, Wang Y, Zhang JY, Zhang FC, Tang ZL, Li C, Gu Z. 1999. The Sihetun fossil vertebrate assemblage and its geological setting in western Liaoning, China. *Palaeoworld* **11**: 310–327 (in Chinese with English abstract).

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DOI: 10.1002/gj

Wang YQ, Hu YM, Meng J, Li CK. 2001. An ossified Meckel's cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science* **294**: 357–361.

Wang XL, Zhou ZH, He HY, Jin F, Wand YQ, Zhang JY, Wang Y, Xu X, Zhang FC. 2005. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chinese Science Bulletin* **50**: 2369–2376.

Woodburne MO, Rich TH, Springer MS. 2003. The evolution of tribospheny and the antiquity of mammalian clades. *Molecular Phylogenetics and Evolution* **28**: 360–385.

Xu X, Norell M. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* **431**: 838–841.

Zeller U. 1993. Ontogenetic evidence for cranial homologies in monotremes and therians, with special reference to Ornithorhynchus. In *Mammal phylogeny, Vol. 1: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*, Szalay FS, Novacek MJ, McKenna MC (eds). Springer-Verlag: New York; 95–107.

Zharkov MA, Murdmaa IO, Filatova NI. 1998. Paleogeography of the Berriasian–Barremian Ages of the Early Cretaceous. *Stratigraphy and Geological Correlation* **6**(1): 49–72.

Zhou ZH, Barrett PM, Hilton J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**: 807–814.

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