

中国中生代哺乳动物研究进展¹⁾

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摘要:迄今为止,中国已知的中生代哺乳动物共有 26 属 29 种(包括 3 个未定种),时代分布从早侏罗世至晚白垩世。在中国新近发现的中生代哺乳动物中,除少数几种材料比较零星之外,大多数都有保存很好的头骨和骨架为代表。它们提供了认识哺乳动物高阶元之间的系统发育关系以及早期演化过程中特征转变的重要信息。过去几年中发现的中生代哺乳动物多数产于热河生物群中。这些化石代表了不同的哺乳动物大类,同时显示了在个体大小、运动姿态以及食性方面的较高的分异。多方面的分异确保了它们在同一个生态系统中能够占据不同的生态位。频繁的火山活动被认为是辽宁西部地区动物大量死亡的主要原因。像巨爬兽(*Repenomamus giganticus*)一样以睡眠姿势保存的标本,很可能意味着随火山喷发释放出的有毒气体参与造成了这样的灾难。

关键词:中国,中生代,哺乳动物,研究进展

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REVIEW OF RECENT ADVANCES ON STUDY OF MESOZOIC MAMMALS IN CHINA

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Abstract Twenty-six named species of 23 genera have been known in China from the deposits ranging from the Early Jurassic to Late Cretaceous. Except a few taxa, most of recently discovered Mesozoic mammals in China are represented by well-preserved skulls and skeletons. They have greatly improved our knowledge of the relationships of the major mammalian lineages and the character transition during the evolution of early mammals. Some localities of the Jehol Biota produced most Mesozoic mammal fossils in the past several years. These fossils represent different major groups and show high diversity in body size, locomotory adaptation, and dietary. Such diversification ensures them to occupy different niches in the common ecosystem. Frequent volcanic eruptions in western Liaoning were primarily responsible for the massive death of animals. Specimens preserved in sleeping posture, like the type specimen of *Repenomamus giganticus*, may indicate that the emission of poisonous gas with the volcanic eruption was probably involved in causing the disaster.

Key words China, Mesozoic, mammals, recent advances

1 Introduction

Mammals have dominated the continental environments for about 65 myr in Cenozoic after

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the great extinction of dinosaurs and other large reptiles at the end of Mesozoic, but more than two-thirds of mammalian evolution occurred in the Mesozoic Era (Lillegraven et al., 1979; Kielan-Jaworowska et al., 2004). Compared to the Cenozoic records, Mesozoic mammals are quite rare. It is also the case in China. The first Chinese Mesozoic mammal, *Manchurodon simplicidens*, was described in 1938 (Yabe and Shikama, 1938), but only 13 named species had been reported before 2000 (Wang YQ et al., 2001a). In recent years, discoveries of Mesozoic mammals in China, especially those from the Jehol Biota, have greatly increased the information for understanding the early radiation and phylogeny of mammals. Since 2000, 14 species of Mesozoic mammals, including 13 new species (as many as the named species in the previous 60 years), have been described from 6 localities. These localities are: Lufeng in Yunnan Province (Early Jurassic), Liuhuanggou of Urumqi in Xinjiang Uigur Autonomous Region (Late Jurassic), Sihetun and Lujiatun of Beipiao, Dawangzhangzi of Lingyuan, and Badaohao of Heishan in Liaoning Province (Early Cretaceous) (Fig. 1). In addition, some undescribed gobiconodontid specimens were collected from the Early Cretaceous Xinminbao Formation in Mazongshan area of Gansu Province (Tang et al., 2001).



Fig. 1 A sketch map showing the Chinese localities where yielded Mesozoic mammals in recent years 1. Lufeng, Yunnan; 2. Badaohao, Heishan, Liaoning; 3. Sihetun-Lujiatun area, Beipiao, Liaoning; 4. Dawangzhangzi, Lingyuan, Liaoning; 5. Mazongshan, Gansu; 6. Liuhuanggou, Urumqi, Xinjiang

2 New findings

Since 2000, 14 species of Mesozoic mammals have been described in China. Most of them were represented by well-preserved specimens including skulls and skeletons, and only a few were named on the basis of fragmentary materials. They were classified into 13 genera and fall into seven major groups: triconodonts, docodonts, multituberculates, symmetrodonts, “eupantotherian”, metatherians, and eutherians.

2.1 Triconodonts

In the past several years, triconodonts were the most commonly reported mammaliaforms in

China, and recently described only from two sites: Lufeng, Yunnan Province, southwestern China, and Lujiatun, Beipiao, Liaoning Province, northeastern China (Li et al., 2000; Luo et al., 2001; Li et al., 2003; Hu et al., 2005b; Meng et al., 2005). The triconodont from Lufeng was named *Hadrocodium wui* (Luo et al., 2001). It was collected from the Upper Red Beds of the Lower Lufeng Formation, which is considered to be the Early Jurassic Sinemurian in age (Luo and Wu, 1994, 1995). Its dental formula is $5 \cdot 1 \cdot 2 \cdot 2 / 4 \cdot 1 \cdot 2 \cdot 2$. Each molar has three main cusps and two accessory cuspules in alignment on the laterally compressed crown. Primary lower cusp occludes in the embrasure between the opposite upper molars. It has relatively large brain capacity, from which derived its genus name. According to the original description, the type specimen has no postdentary trough on the mandible, indicating the separation of the middle ear bones from the mandible (Luo et al., 2001). Further examination shows that the trough exists on the internal surface of the mandible. Wang YQ et al. (2001b) considered that the type specimen is a postsuckling juvenile, based on a number of features (see Wang YQ et al., 2001b, p. 360), and further doubted whether *Hadrocodium* has evolved the definitive mammalian middle ear. No further information supports the juvenile condition of its type specimen, but the presence of the internal trough weakens the evidence for separation of middle ear bones from the lower jaw.

Other named triconodonts were all collected from the First Member of the Yixian Formation at Lujiatun site (Wang XL et al., 1998). The site has yielded a number of triconodont specimens, some of which have been referred to four species of three genera: *Repenomamus robustus*, *R. giganticus*, *Gobiconodon zofiae*, and *Meemannodon lujiatunensis* (Li et al., 2000; Li et al., 2003; Hu et al., 2005b; Meng et al., 2005). *Repenomamus* was allocated into its own family Repenomamidae (Li et al., 2000; Hu et al., 2005b). *Gobiconodon* and *Meemannodon* were the representatives of the family Gobiconodontidae (Li et al., 2003; Meng et al., 2005). Both families are closely related to each other (Wang YQ et al., 2001b; Li et al., 2003; Hu et al., 2005b; Meng et al., 2005). Repenomamids differ from gobiconodontids in having three upper incisors, i1 not enlarged, higher and more piecing molariform teeth, and more inflated cusp a on lower molariforms. Based on the examination of a number of specimens, the dental formula for *Repenomamus* has been designated as $3 \cdot 1 \cdot 2 \sim 3 \cdot 4/2 \cdot 1 \cdot 2 \sim 3 \cdot 5$ (Li et al., 2000; Wang YQ et al., 2001b; Hu et al., 2005b), whereas $2 \cdot 1 \cdot 3 \sim 4 \cdot 4/2 \cdot 1 \cdot 2 \sim 3 \cdot 5$ for the gobiconodontids (Meng et al., 2005), which is in contrast to the previous opinion that *Gobiconodon* has one lower incisor (Jenkins and Schaff, 1988; Li et al., 2003). On the type specimen of *G. zofiae* and *R. robustus*, and some additional *Repenomamus* specimens, a rod-like bone attached to the internal groove of the lower jaw was recognized as the ossified Meckel's cartilage (Wang YQ et al., 2001b; Meng et al., 2003; Li et al., 2003). Such ossified Meckel's cartilage was also recognized on the type specimen of *Zhangheotherium quinquecuspidens* (Meng et al., 2003), which indicates a wide distribution of such structure in Mesozoic mammals.

Identification of the ossified Meckel's cartilage leads to the conclusion that *Repenomamus* and *Gobiconodon* have three ear ossicles, detached from the lower jaw and forming the definitive mammalian middle ear (Wang YQ et al., 2001b; Meng et al., 2003). It provides the direct fossil evidence indicating the relationships of Meckel's cartilage to the middle ear in early mammals. This discovery shows that the internal groove on the mandible of many early mammals is probably functioned as holding the Meckel's cartilage, instead of holding dental nerves and arteries (Simpson, 1928; Jenkins and Schaff, 1988) or as attachment of the postdentary bones in *Peramus* and *Amphitherium* (Allin and Hopson, 1992). On the basis of the widely adopted mammalian phylogeny, the interpretation weakens the hypothesis of multiple origins of the definitive mammalian middle ear, proposed by Allin and Hopson (1992).

The most uncertain issue in the evolution of the definitive mammalian middle ear is how the postdentary bones became detached from the dentary, and translocated to the basicranium as ear

ossicles. Two models have been previously proposed for interpreting the origin of the definitive mammalian middle ear (Maier, 1987, 1990; Rowe, 1996a, b; Sánchez-Villagra et al., 1997, 2002). Both models require brain expansion as the initial factor for the detachment of ear ossicles during mammalian evolution. Compared to the most primitive mammaliaform *Morganucodon* and *Sinoconodon*, however, the braincase of *Repenomamus* is proportionally narrow or small. Since the postdentary bones are still attached to the dentary in *Morganucodon* and *Sinoconodon* (Kermack et al., 1981; Crompton and Sun, 1985; Luo et al., 2001), both models are not supported by the new findings. Instead, an alternative hypothesis was proposed that modifications in both feeding and hearing apparatuses toward efficient functions have led to the development of the definitive mammalian middle ear (Wang YQ et al., 2001b; Meng et al., 2003).

Repenomamus is among the largest Mesozoic mammals. The larger species, *R. giganticus*, was estimated 14 ~ 16 kg in weight, and the smaller one, *R. robustus*, 4 ~ 6 kg (Hu et al., 2005b). Some features of *Repenomamus*, such as large and pointed incisors and similarly shaped canines and premolariform teeth, strong jaw musculature as suggested by the robust dentary and zygoma, indicate that it was a carnivore. The stomach contents of a *R. robustus* individual provide direct evidence to support this opinion. Some fragmentary postcranial bones and jaws with teeth of a juvenile *Psittacosaurus* were recognized in the stomach contents. This confirms that this animal was a meat-eater and could feed on small dinosaurs. Since some limb bones were still articulated, *Repenomamus* must have eaten its prey by swallowing in large pieces without chewing, which means that chewing as a derived feature in mammals was probably not present in *Repenomamus* (Hu et al., 2005b).

The gobiconodontid specimens from the Mazongshan area have not been described yet, and may represent a new taxon (Tang et al., 2001). They were collected in two stratigraphic levels. Based on the correlation of associated fauna, its geologic age was considered to be Barremian to Aptian (Tang et al., 2001), contemporaneous with the gobiconodontids in the Jehol Biota.

2.2 Docodonts

This small group of extinct mammals had not been discovered in China until a few years ago. In 2005, Pfretzschner et al. (2005) described, for the first time, some dental materials of a docodont from the upper part of the Qigu Formation (Oxfordian) of the Junggar Basin, Xinjiang Uigur Autonomous Region, northwestern China, which was previously reported as from the Middle Jurassic (Callovian) Toutunhe Formation by Martin and Pfretzschner (2003). It was named a new taxon, *Dsungarodon zuoi* (Pfretzschner et al., 2005).

Based on the lower molar characters, Pfretzschner et al. (2005) performed a phylogenetic analysis. According to their result, *Dsungarodon* and *Simpsonodon* are closely related, while *Borealestes*, *Haldanodon*, and *Docodon* form a monophyletic group which is different from the result of Sigogneau-Russell (2003). All the docodont taxa except *Haldanodon* were only represented by fragmentary materials. Phylogenetic analysis to resolve the relationship of genera within docodonts is thus on the basis of very few dental characters, e. g., Pfretzschner et al. (2005). Different interpretation for even one character may lead to a completely different result. Establishment of more convincing relationship within the order requires the discovery of better preserved specimens of different forms.

Pfretzschner et al. (2005) also concluded that *Dsungarodon* and *Simpsonodon* had developed extensive grinding functions in their molars. Their chewing model for *Dsungarodon* shows that the cusp b on lower molar occludes within the trigon basin of corresponding upper molar during the occlusion, while the main lingual cusp of upper molar, Cusp X, occludes neither within "pseudotalonid" nor with the talonid part of corresponding lower molar (Pfretzschner et al., 2005). Such kind of occlusal pattern might mainly perform crushing and/or puncturing function rather than grinding function.

2.3 Multituberculates

Skulls of Late Cretaceous multituberculate, *Kryptobaatar*, were collected from the equivalent of the Mongolian Djadohta Formation in China's Nei Mongol (Inner Mongolia) (Dong, 1993), but the only described Mesozoic specimen came from the Early Cretaceous Yixian Formation at Dawangzhangzi of Lingyuan, western Liaoning. It was named *Sinobaatar lingyuanensis* (Hu and Wang, 2002). Its dental formula is $3 \cdot ? \cdot 5 \cdot 2 / 1 \cdot 0 \cdot 3 \cdot 2$. Unlike later multituberculates, the first lower incisor of *Sinobaatar* is conical and completely covered by enamel. The blade-like middle portion of the lower dentition involves three premolars. *Sinobaatar* has similar dental morphology-especially of the cheek teeth, and same dental formula as some Early Cretaceous multituberculates from Mongolia (Kielan-Jaworowska et al., 1987; Kielan-Jaworowska and Hurum, 2001). They are all referred to the family Eobaataridae.

The holotype of *Sinobaatar lingyuanensis* is the most complete pre-Late Cretaceous multituberculate specimen. It provides some morphological information of postcranial skeleton for early multituberculates. In contrast to the significant changes of their dental features, the available information shows little change in the postcranial morphology of multituberculates during their history. This may suggest that the locomotory patterns in different multituberculates did not change much during evolution (Hu and Wang, 2002).

2.4 Symmetrodonts

The type specimen of the Cretaceous symmetrodont mammal, *Zhangheotherium quinquecupedens*, is a nearly complete skeleton and was published in 1997 (Hu et al., 1997). It provides much morphological information for symmetrodont cranium, ear region, and postcranial skeleton (Hu et al., 1997, 1998). A partial skeleton of *Z. quinquecupedens* was recently reported from the same stratigraphic unit, the Yixian Formation, as the type specimen at Dawangzhangzi of Lingyuan, western Liaoning (Luo and Ji, 2005). Its dentaries were macerated, and all dental alveoli, roots of functional teeth, partially formed tooth crown and the crypt for developing permanent teeth are exposed. Based on this material, the lower dental formula of *Zhangheotherium* has been revised as $3 \cdot 1 \cdot 3 \cdot 5$ (Luo and Ji, 2005). However, the tooth assigned as p3 is morphologically like a molariform. In contrast to extant mammals, some primitive mammals replaced their molariform teeth as well as premolariform ones (Jenkins and Schaff, 1988; Zhang et al., 1998). The assignment of the third postcanine tooth to p3 thus needs reconsideration. Consequently, whether it has the diphyodont replacement of premolars depends on the assignment of that tooth. This fossil also provides new information on the vertebral column, the pelvis, the hindlimb and pes. Its calcaneus and astragalus in the ankle joint lack superposition, which shows that the symmetrodont has retained the primitive condition of mammaliaforms (Luo and Ji, 2005).

After the report of *Zhangheotherium quinquecupedens*, three additional symmetrodont taxa, *Maotherium sinensis*, *Heishanlestes changi*, and *Akidolestes cifellii*, were described on the basis of Chinese Mesozoic materials (Rougier et al., 2003; Hu et al., 2005a; Li and Luo, 2006). *Maotherium* is represented by a complete skeleton. It shares, with *Zhangheotherium*, many morphological features of cranium, dentition, and postcranial skeleton, and differs from the latter in some details. *Maotherium* has one more lower molar than *Zhangheotherium*. The postcranial skeleton of *Maotherium* differs from that of *Zhangheotherium* in the limb proportions, the number of vertebrae, and having unfused sternum, etc. (Rougier et al., 2003).

Akidolestes cifellii is another spalacotheriid symmetrodont, recently reported from the Yixian Formation at Dawangzhangzi, Lingyuan in western Liaoning (Li and Luo, 2006). The dental formula of *Akidolestes* is $4 \cdot 1 \cdot 5? \cdot 5? / 4 \cdot 1 \cdot 5 \cdot 6$. *Akidolestes* differs from *Zhangheotherium* and *Maotherium* in having higher protocristid on molars, longer (larger) posterior premolars than anterior molars, and more premolars (Li and Luo, 2006).

The shoulder girdle and forelimb of *Akidolestes* are similar to those of *Zhangheotherium* (Hu et al., 1997, 1998; Luo and Ji, 2005) and *Maotherium* (Rougier et al., 2003). In many features in the posterior part of the skeleton, however, *Akidolestes* differs from *Zhangheotherium* and *Maotherium* but is similar to monotremes. These features include unfused lumbar ribs, a prominent tubercle on pubis for the psoas minor muscle, a hypertrophied parafibular process of the fibula, a short femoral neck, and a curved tibia with a distal malleolus, etc. Based on the similarities, a sprawling hindlimb posture was postulated for *Akidolestes* (Li and Luo, 2006).

Another symmetrodont, *Heishanlestes changi*, was collected from the Early Cretaceous Shaha Formation at Badaohao, Heishan County, Liaoning Province (Hu et al., 2005a). It is the first described mammal from the area after collecting specimens for 10 years. The Shaha Formation is considered to be late Aptian to early Albian in age (Wang YQ et al., 2001a; Li et al., 2005). *Heishanlestes* was represented by three pieces of lower jaws and has a lower dental formula of $? \cdot 1 \cdot 4 \cdot 6$. Its four premolars are tightly positioned and procumbent. The lower molars form three discontinuous morphological sets. The first one has a low, broadly obtuse trigonid angle. The $m2 \sim 4$ have the trigonids constructed of tall crests and the trigonid angle is acute, as in the lower molars of typical spalacotheriid symmetrodonts. The last two molars have a large neomorphic cusp in the center of the trigonid, a feature not seen in other mammals. The dental morphology and the wear facets show that the animal probably uses the premolars to crush its prey before shearing it with the molars. Because of the small sample size, it is arguable whether the neomorphic cusp of $m5 \sim 6$ in *Heishanlestes* is a diagnostic character or just represents an individual variation. Nevertheless, the presence of the cusp on two teeth indicates a developmental phenomenon. Alteration in the ontogenetic pattern may affect its crown morphology, and further result in the formation of a new, large cusp in the middle of the trigonid (Hu et al., 2005a, c).

2.5 “Eupantotherians”

From the same locality and stratigraphic horizon as those of *Heishanlestes changi*, a lower jaw with the last two premolars and four molars was collected. Similar to *Kielantherium* (Dashzeveg, 1975; Dashzeveg and Kielan-Jaworowska, 1984), it has four molars with paraconid higher than metaconid. It was thus previously mentioned as an aegialodontid mammal (Wang et al., 1995). Further examination of the specimen shows that it has a submolarized last premolar, relatively large unbasined talonids on molars without wear facet 5. These characters indicate that the animal does not have a tribosphenic molar pattern, and is not a representative of tribosphenic mammals. It was therefore referred to “Eupantotheria” and named *Mozomus shikamai*. Due to its differences from the known “eupantotherians”, the family Mozomuridae was proposed for it (Li et al., 2005).

2.6 Eutherians and metatherians

Primitive eutherian and metatherian were also reported recently from the Mesozoic in China. They were both from the Early Cretaceous Yixian Formation at Dawangzhangzi, Lingyuan, Liaoning Province (Ji et al., 2002; Luo et al., 2003), where yielded the type specimen of *Sinobaatar lingyuanensis* (Hu and Wang, 2002). They were dated about 125 Ma ago (Swisher et al., 1999, 2002; Wang SS et al., 2001b) and are the earliest representative of their own group, respectively. The metatherian specimen is a complete skeleton, preserved on a slab of lacustrine deposit. It was named *Sinodelphys szalayi*. It has many metatherian apomorphies in the skeleton and anterior dentition. The dental formula is $4 \cdot 1 \cdot 4 \cdot 4 / 4 \cdot 1 \cdot 4 \cdot 3$. $I3 \sim 4$ are compressed mediolaterally and lanceolate in lateral view. $P1$ is procumbent and close to the upper canine, followed by a large diastema behind. Its lower molars have developed an approximation of the entoconid to the hypoconulid. However, it lacks the twined entoconid and hypoconid, and the inflected mandibular angular process of the more derived metatherians. It has proportionally hypertrophied hamate, enlarged triquetrum

and scaphoid. Its trapezium is small and bean-shaped. The astragalar head of *Sinodelphys* is asymmetrical with regard to the main axis of the astragalar neck, which is typical in Cretaceous metatherians. Its supraspinous fossa is much wider than infraspinous fossa at midlength of the scapula. All these features show that *Sinodelphys* has metatherian affinity (Luo et al., 2003).

The eutherian mammal is also represented by a complete skeleton, preserved on the slab and counterpart slab of lacustrine deposit (Ji et al., 2002). It has a typical primitive eutherian dental formula, $5 \cdot 1 \cdot 5 \cdot 3/4 \cdot 1 \cdot 5 \cdot 3$. The animal has specialized limb and foot features that are only known from scansorial (climbing) and arboreal (tree-dwelling) extant mammals, quite different from the terrestrial or cursorial (running) features of other Cretaceous eutherians. Because of its early age and scansorial adaptation, it was named *Eomaia scansoria* (Ji et al., 2002).

The fore- and hindfeet of both *Eomaia* and *Sinodelphys* show similar phalangeal proportions and curvature to the grasping feet of extant arboreal mammals. In *Eomaia* and *Sinodelphys*, the proximal manual phalanx is arched dorsally. Some phalanges have two protuberances for the fibrous tendon sheaths of the flexor digitorum. Sesamoid bones are present at interphalangeal joints. The ratio of the intermediate phalanx to the proximal phalanx in both *Eomaia* and *Sinodelphys* is intermediate between those of fully arboreal and scansorial mammals, and is far greater than that of the fully terrestrial ones. These features suggest that *Eomaia* and *Sinodelphys* were agile animals with climbing skeletal adaptations, capable of grasping and branch walking, and active both on the ground and in trees or shrubs (Ji et al., 2002; Luo et al., 2003). The diversification of the earliest metatherians and eutherians appears to be associated with evolution of scansorial adaptations that may have facilitated the spread of these derived clades into more niches than were accessible to the terrestrial stem lineages of Mesozoic mammals (Luo et al., 2003).

3 Discussion and concluding remarks

1) Recent discoveries of Mesozoic mammals in China have provided much information about the evolution of early mammals. They extend the geological and geographical distribution of Mesozoic mammals in China. Except for a few taxa based on fragmentary specimens, most of them are represented by the well-preserved skulls and skeletons. They greatly increased our knowledge about the transition of characters during the evolution of early mammals. For example, the ossified Meckel's cartilage found in mammals of the Gobiconodontidae + Repenomamidae clade is indicative of relationship between Meckel's cartilage and the middle ear of mammals. The recently discovered Chinese Mesozo-

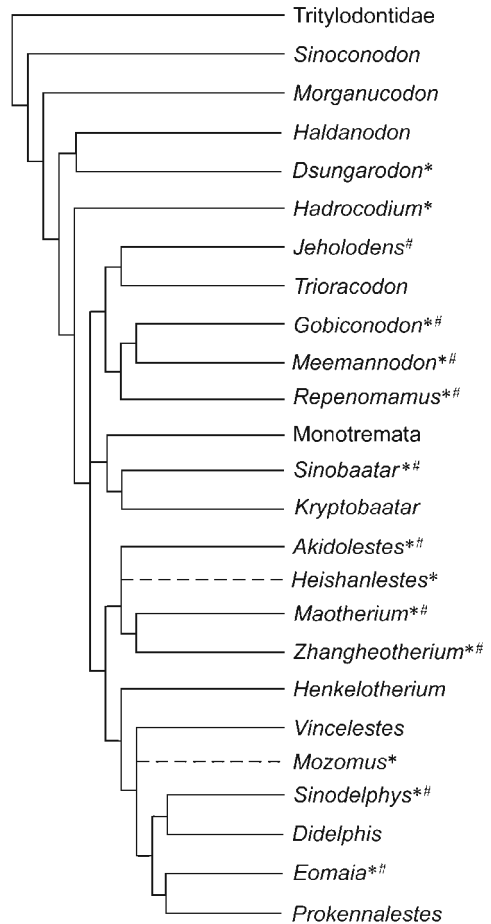


Fig. 2 Cladogram of mammalian phylogeny, combining results of different analyses, showing the phylogenetic position of the recently described Chinese Mesozoic mammals * denotes the taxa discussed in the text; # indicates the taxa from the Jehol Biota; dashed line refers to the taxon that is plotted in the cladogram based on the comparison of morphological features

ic mammals have also provided new insights into the relationships of the major lineages of mammals. They represent different major groups, occupying different phylogenetic position in the mammalian history (Fig. 2). In particular, specimens from the Jehol Biota are among the most informative representatives of several major groups. The symmetrodont skeletons, discovered only in China's western Liaoning, indicate a high diversification of this group during the Early Cretaceous, and are the unique resource for the information about cranial and postcranial morphology of symmetrodonts. Both *Eomaia* and *Sinodelphys* in the Jehol Biota are the earliest and most primitive member of eutherian and metatherian, respectively. They exhibit the morphological features for the early evolutionary stage of both groups. Some extraordinarily well-preserved specimens reveal the ecological adaptation of those mammals.

2) Ten genera and 11 species of mammals have been reported from the Yixian Formation in western Liaoning, northeastern China (Fig. 2). These fossils have shown high diversity in both biological and ecological respects. They represent five major groups of the Mesozoic mammals: triconodonts, multituberculates, symmetrodonts, metatherians, and eutherians. The body size of these animals varies from 15 cm long, such as *Jeholodens* and *Eomaia*, to over 1 meter in length, e. g. *Repenomamus*. The larger species of *Repenomamus* are estimated to be 14 ~ 16 kg. These animals also have a broad range of locomotory adaptations. All the symmetrodonts, including *Zhangheotherium*, *Maotherium*, and *Akidolestes*, and triconodonts, such as *Repenomamus*, are terrestrial mammals, whereas *Eomaia* and *Sinodelphys* have evolved scansorial adaptations. They also have different adaptation to the food resource. The dental morphology indicates that most Jehol mammals mainly feed on insects. These include symmetrodonts, *Jeholodens*, *Sinodelphys*, and *Eomaia*. The only multituberculate *Sinobaatar* is a vegetarian and eats plants. The stomach content of *Repenomamus robustus* and the dental and jaw features of the genus provide strong evidence for meat-eating behavior. Different adaptation in wide respects clearly suggests that the Mesozoic mammals have greater diversification than previously thought. These mammals have evolved to occupy different niches and share the common ecosystem.

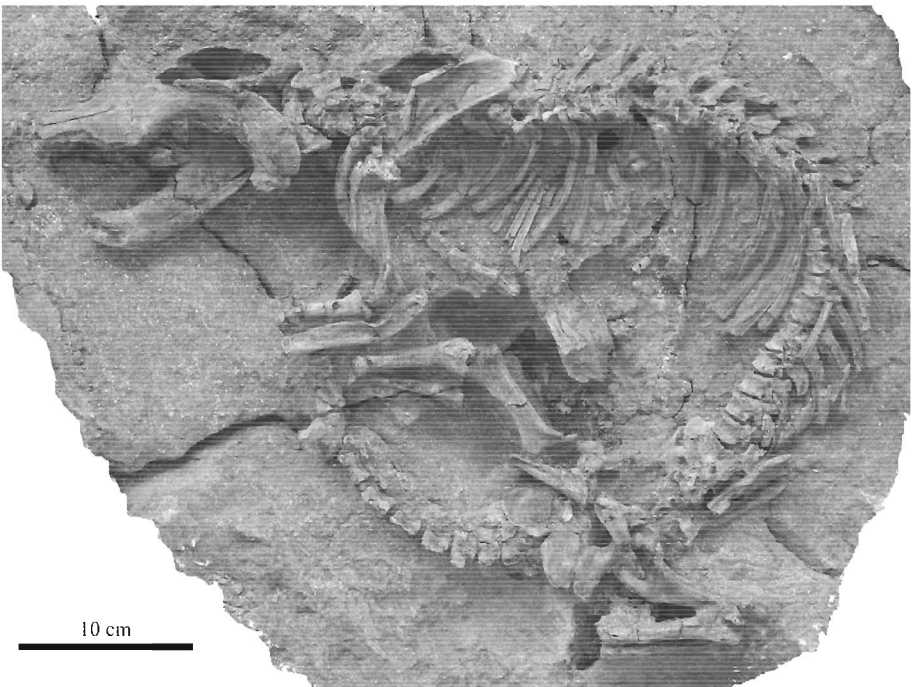


Fig. 3 The type specimen of *Repenomamus giganticus* (IVPP V 14155), preserved in sleeping posture

3) Unlike the two dimensional preservation of fossil vertebrates in other localities of the Jehol Biota, the triconodonts and other fossils, from the First Member of the Yixian Formation at the Lujiatun site, were preserved in three dimensions in the thick tuffaceous deposits. The radiometric dating for the tuff has not been finished, but the measurement of the overlying basaltic andesite from the Second Member of the formation gave an average $^{40}\text{Ar}/^{39}\text{Ar}$ age of 128.2 ± 0.8 Ma, which suggests that the age of the First Member is possibly around 130 Ma (Wang SS et al., 2001a). The type specimen of *R. giganticus* is preserved in a sleeping or resting posture like some extant carnivores (Fig. 3), which indicates that this animal died peacefully. A troodontid dinosaur, *Mei long*, and other undescribed vertebrate specimens were also preserved in similar posture (Xu and Norell, 2004). Frequent volcanic eruptions in western Liaoning were primarily responsible for the massive death of the animals (Wang et al., 1999; Zhou et al., 2003). Specimens preserved in sleeping posture imply that the emission of poisonous gas with the volcanic eruption probably involved in causing the disaster.

4) To date, 17 localities have been reported to produce Mesozoic mammals in China. Twenty-six named species of 23 genera were collected from the deposits ranging from the Early Jurassic to Late Cretaceous. The following table summarizes the basic information of Chinese Mesozoic mammals (Table 1).

Table 1 Summary of Mesozoic mammals known from China

| Locality | Formation | Age | Fossil Mammals | References |
|-----------------------------------|---------------------|------------------------|---|--|
| Lufeng, Yunnan | Lower Lufeng Fm. | Sinemurian | <i>Sinoconodon rigneyi</i> <i>Morganucodon oehleri</i> <i>M. heikuopengensis</i> <i>Hadrodiodium wui</i> Tooth fragment | Patterson & Olson, 1961 Rigney, 1963 Young, 1978; Luo & Wu, 1994 Luo et al., 2001 |
| Luchang, Huili, Sichuan | Lower Yimen Fm. | Early Jurassic | | Chow & Rich, 1984b |
| Wafangdian, Liaoning | Wafangdian Fm. | Middle Jurassic | <i>Manchurodon simplicidens</i> | Yabe & Shikama, 1938 |
| Fangshen, Lingyuan, Liaoning | Jiulongshan Fm. | ? Bathonian | <i>Liaotherium gracile</i> | Zhou et al., 1991 |
| Shilongzhai, Nanjiang, Sichuan | Upper Shaximiao Fm. | Oxfordian-Kimmeridgian | <i>Shuotherium dongi</i> | Chow & Rich, 1982 |
| Laoshangou, Klameli, Xinjiang | Shishugou Fm. | Late Jurassic | <i>S. shilongi</i> | Wang YQ et al., 1998 |
| Liuhuanggou, Urumqi, Xinjiang | Qigu Fm. | Late Jurassic | <i>Klamelia zhaopengi</i> <i>Dsungarodon zuoi</i> | Chow & Rich, 1984a Pfretzschner et al., 2005 |
| Huanggutai, Klameli, Xinjiang | Shengjinkou Fm. | Early Cretaceous | Jaw fragment | Chow & Rich, 1984b |
| Lujiatun, Beipiao, Liaoning | Yixian Fm. | Barremian | <i>Repenomamus robustus</i> <i>R. giganticus</i> <i>Gobiconodon zofae</i> <i>Meemannodon lujiatunensis</i> <i>Zhangheotherium quinquecupidens</i> | Li et al., 2000 Hu et al., 2005b Li et al., 2003 Meng et al., 2005 Hu et al., 1997 |
| Jianshangou, Beipiao, Liaoning | | | <i>Z. quinquecupidens</i> | Luo & Ji, 2005 |
| Sihetun, Beipiao, Liaoning | | | <i>Jeholodens jenkinsi</i> <i>Maotherium sinensis</i> | Ji et al., 1999 Rougier et al., 2003 |
| Dawangzhangzi, Lingyuan, Liaoning | | | <i>Sinobaatar lingyuanensis</i> <i>Eomaia scansoria</i> | Hu & Wang, 2002 Ji et al., 2002 |
| Mazongshan, Gansu | Xinminbao Fm. | Barremian - Aptian | <i>Sinodelphys szalayi</i> <i>Akidolestes cifellii</i> | Luo et al., 2003 Li & Luo, 2006 |
| Hangjin Qi, Nei Mongol | Ejinhoro Fm. | Early Cretaceous | gobiconodontid | Tang et al., 2001 |
| Badaohao, Heishan, Liaoning | Shahai Fm. | ? Aptian or Albion | <i>Hangjina chowi</i> <i>Heishanlestes changi</i> <i>Mozomus shikamai</i> | Godefroit & Guo, 1999 Hu et al., 2005a Li et al., 2005 |
| Xinqiu, Fuxin, Liaoning | Fuxin Fm. | Aptian | <i>Endotherium ninomii</i> | Shikama, 1947 |
| Tsondolein-Khuduk, Nei Mongol | Ulan Hoshao Fm. | Cenomanian | <i>Khuduklestes bohlini</i> | Bohlin, 1953; Nessov et al., 1994 |
| Bayan Mandahu, Nei Mongol | "Djadohta" Fm. | Campanian | <i>Kennalestes</i> sp. <i>Zalambdalestes</i> sp. <i>Kryptobaatar</i> sp. | Dong, 1993 |

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References

- Allin E F, Hopson J A, 1992. Evolution of the auditory system in Synapsida (‘mammal-like reptiles’ and primitive mammals) as seen in the fossil record. In: Webster D B, Fay R R, Popper A N eds. The evolutionary biology of hearing. New York: Springer-Verlag. 587 ~ 614
- Bohlin B, 1953. Fossil reptiles from Mongolia and Kansu. Sino-Swedish Expedition Publication, 37, VI. Vertebrate Palaeontology, **6**: 1 ~ 113
- Chow M C, Rich T H V, 1982. *Shuotherium dongi* n. gen. et sp., a therian with pseudo-tribosphenic molars from the Jurassic of Sichuan, China. Aust Mammal, **5**: 127 ~ 142
- Chow M C, Rich T H V, 1984a. A new triconodontan (Mammalia) from the Jurassic of China. J Vert Paleont, **3**(4): 226 ~ 231
- Chow M C, Rich T H V, 1984b. New Mesozoic mammal sites from China. Alcheringa, **8**: 304
- Crompton A W, Sun A L, 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. Zool J Linn Soc, **85**: 99 ~ 119
- Dashzeveg D, 1975. New primitive Therian from the Early Cretaceous of Mongolia. Nature, **256**: 402 ~ 403
- Dashzeveg D, Kielan-Jaworowska Z, 1984. The lower jaw of an aegialodontid mammal from the Early Cretaceous of Mongolia. Zool J Linn Soc, **82**: 217 ~ 227
- Dong Z M, 1993. The field activities of the Sino-Canadian Dinosaur Project in China, 1987 – 1990. Can J Earth Sci, **30**(10 ~ 11): 1997 ~ 2001
- Godefroit P, Guo D Y, 1999. A new amphilestid from the Early Cretaceous of Inner Mongolia (P. R. China). Bull Inst R Sci Nat Belg, Sci Terre, **69**(suppl B): 7 ~ 16
- Hu Y M, Fox R C, Wang Y Q et al., 2005a. A new spalacotheriid symmetrodont from the Early Cretaceous of northeastern China. Am Mus Novit, (3475): 1 ~ 20
- Hu Y M, Meng J, Wang Y Q et al., 2005b. Large Mesozoic mammals fed on young dinosaurs. Nature, **433**: 149 ~ 152
- Hu Y M, Wang Y Q, 2002. *Sinobaatar* gen. nov.: first multituberculate from the Jehol Biota of Liaoning, Northeast China. Chinese Sci Bull, **47**(11): 933 ~ 938
- Hu Y M, Wang Y Q, Fox R C et al., 2005c. Novel dental pattern in Mesozoic mammal. Chinese Sci Bull, **50**(7): 713 ~ 715
- Hu Y M (胡耀明), Wang Y Q (王元青), Li C K (李传夔) et al., 1998. Morphology of dentition and forelimb of *Zhangtherium*. Vert Palasiat (古脊椎动物学报), **36**(2): 102 ~ 125 (in Chinese with English summary)
- Hu Y M, Wang Y Q, Luo Z X et al., 1997. A new symmetrodont mammal from China and its implications for mammalian evolution. Nature, **390**: 137 ~ 142
- Jenkins F A Jr, Schaff C R, 1988. The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. J Vert Paleont, **8**(1): 1 ~ 24
- Ji Q, Luo Z X, Ji S A, 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. Nature, **398**: 326 ~ 330
- Ji Q, Luo Z X, Yuan C X et al., 2002. The earliest known eutherian mammal. Nature, **416**: 816 ~ 821
- Kernack K A, Mussett F, Rigney W H, 1981. The skull of *Morganucodon*. Zool J Linn Soc, **71**: 1 ~ 158
- Kielan-Jaworowska Z, Cifelli R L, Luo Z X, 2004. Mammals from the age of dinosaurs: origin, evolution and structure. New York: Columbia Univ Press. 1 ~ 630
- Kielan-Jaworowska Z, Dashzeveg D, Trofimov B A, 1987. Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms. Acta Palaeont Pol, **32**(1 ~ 2): 3 ~ 47
- Kielan-Jaworowska Z, Hurum J H, 2001. Phylogeny and systematics of multituberculate mammals. Palaeontology, **44**(3): 389 ~ 429
- Li C K (李传夔), Setoguchi T, Wang Y Q (王元青) et al., 2005. The first record of “eupantotherian” (Theria, Mammalia) from the late Early Cretaceous of western Liaoning, China. Vert Palasiat (古脊椎动物学报), **43**(4): 245 ~ 255

- Li C K, Wang Y Q, Hu Y M et al. , 2003. A new species of *Gobiconodon* (Triconodonta, Mammalia) and its implication for the age of Jehol Biota. *Chinese Sci Bull*, **48**(11): 1129 ~ 1134
- Li G, Luo Z X, 2006. A Cretaceous symmetrodont therian with some monotreme-like postcranial features. *Nature*, **439**: 195 ~ 200
- Li J L (李锦玲), Wang Y (王原), Wang Y Q (王元青) et al. , 2000. A new family of primitive mammal from the Mesozoic of western Liaoning, China. *Chinese Sci Bull (科学通报)*, **45**(23): 2545 ~ 2549 (in Chinese)
- Lillegraven J A, Kielan-Jaworowska Z, Clemens W A, 1979. *Mesozoic Mammals: the First Two-thirds of Mammalian History*. Berkeley: Univ Calif Press. 1 ~ 311
- Luo Z X, Crompton A W, Sun A L, 2001. A new mammaliaform from the Early Jurassic and evolution of mammalian characteristics. *Science*, **292**: 1535 ~ 1540
- Luo Z X, Ji Q, 2005. New study on dental and skeletal features of the Cretaceous mammal *Zhangheotherium*. *J Mammal Evol*, **12**(3/4): 337 ~ 357
- Luo Z X, Ji Q, Wible J R et al. , 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. *Science*, **302**: 1934 ~ 1940
- Luo Z X, Wu X C, 1994. The small tetrapods of the Lower Lufeng Formation, Yunnan, China. In: Fraser N C, Sues H-D eds. *In the shadow of the dinosaurs — early Mesozoic tetrapods*. New York: Cambridge Univ Press. 251 ~ 270
- Luo Z X, Wu X C, 1995. Correlation of Vertebrate Assemblage of the Lower Lufeng Formation, Yunnan, China. In: Sun A L, Wang Y Q eds. *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. Beijing: China Ocean Press. 83 ~ 88
- Maier W, 1987. Der Processus angularis bei *Monodelphis domestica* (Didelphidae, Marsupialia) und seine Beziehungen zum Mittelohr: Eine ontogenetische und evolutionsmorphologische Untersuchung. *Gegenbaurs Morph Jahrb*, **133**: 123 ~ 161
- Maier W, 1990. Phylogeny and ontogeny of mammalian middle ear structures. *Netherlands J Zool*, **40**: 55 ~ 74
- Martin T, Pfretzschner H-U, 2003. Functional morphology and evolution of docodont molars (Mammalia) from the middle Jurassic of Junggar Basin (NW China). *J Vert Paleont*, **23**(suppl 3): 76A
- Meng J, Hu Y M, Wang Y Q et al. , 2003. The ossified Meckel's cartilage and internal groove in Mesozoic Mammaliaforms: Implications to origin of the definitive mammalian middle ear. *Zool J Linn Soc*, **138**: 431 ~ 448
- Meng J (孟津), Hu Y M (胡耀明), Wang Y Q (王元青) et al. , 2005. A new triconodont (Mammalia) from the Early Cretaceous Yixian Formation of Liaoning, China. *Vert PalAsiat (古脊椎动物学报)*, **43**(1): 1 ~ 10
- Nessov L A, Sigogneau-Russell D, Russell D E, 1994. A survey of Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. *Palaeovertebrata*, **23**(1 ~ 4): 51 ~ 92
- Patterson B, Olson E C, 1961. A triconodontid mammal from the Triassic of Yunnan. Brussels: International colloquium in the evolution of lower and non-specialized mammals. 129 ~ 191
- Pfretzschner H-U, Martin T, Maisch M W et al. , 2005. A new docodont mammal from the Late Jurassic of the Junggar Basin in Northwest China. *Acta Palaeont Pol*, **50**(4): 799 ~ 808
- Rigney H W, 1963. A specimen of *Morganucodon* from Yunnan. *Nature*, **197**: 1122 ~ 1123
- Rougier G W, Ji Q, Novacek M J, 2003. A new symmetrodont mammal with fur impressions from the Mesozoic of China. *Acta Geol Sin*, **77**(1): 7 ~ 14
- 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. *Mem Calif Acad Sci*, **20**: 71 ~ 95
- Sánchez-Villagra M R, Gemballa S, Nummela S et al. , 2002. Ontogenetic and phylogenetic transformations of the ear ossicles in marsupial mammals. *J Morph*, **251**: 219 ~ 238
- Sánchez-Villagra M R, Smith K K, 1997. Diversity and evolution of the marsupial mandibular angular process. *J Mammal Evol*, **4**: 119 ~ 144
- Shikama T, 1947. *Teilhardosaurus* and *Endotherium*, new Jurassic Reptilia and Mammalia from the Husin Coal-Field, South

- Manchuria. Proc Japanese Acad, **23**(7): 76 ~ 84
- Sigogneau-Russell D, 2003. Docodonts from the British Mesozoic. Acta Palaeont Pol, **48**(3): 357 ~ 374
- Simpson G G, 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London: William Clowes and Sons, Ltd. 1 ~ 215
- Swisher C C, Wang X L, Zhou Z H et al., 2002. Further support for a Cretaceous age for the feathered dinosaur beds of Liaoning, China; new $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Yixian and Tuchengzi formations. Chinese Sci Bull, **47**(2): 136 ~ 138
- Swisher C C, Wang Y Q, Wang X L et al., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature, **400**: 58 ~ 61
- Tang F, Luo Z X, Zhou Z H et al., 2001. Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. Cret Res, **22**: 115 ~ 129
- Wang S S (王松山), Hu H G (胡华光), Li P X (李佩贤) et al., 2001a. Further discussion on the geologic age of Sihetun vertebrate assemblage in western Liaoning, China — evidence from Ar-Ar dating. Acta Petrol Sin (岩石学报), **17**(4): 663 ~ 668 (in Chinese with English summary)
- Wang S S, Wang Y Q, Hu H G et al., 2001b. The existing time of Sihetun vertebrate in western Liaoning, China. Chinese Sci Bull, **46**(9): 779 ~ 782
- Wang X L (汪筱林), Wang Y Q (王元青), Wang Y (王原) et al., 1998. Stratigraphic sequence and vertebrate-bearing beds of the lower part of the Yixian Formation in Sihetun and neighboring area, western Liaoning, China. Vert Palasiat (古脊椎动物学报), **36**(2): 85 ~ 101 (in Chinese with English summary)
- Wang X L (汪筱林), Wang Y Q (王元青), Xu X (徐星) et al., 1999. Record of the Sihetun vertebrate mass mortality events, western Liaoning, China; caused by volcanic eruptions. Geol Rev (地质论评), **45**(suppl): 458 ~ 467 (in Chinese with English abstract)
- Wang Y Q, Clemens W A, Hu Y M et al., 1998. A probable pseudo-tribosphenic upper molar from the Late Jurassic of China and the early radiation of the Holotheria. J Vert Paleont, **18**(4): 777 ~ 787
- Wang Y Q, Hu Y M, Li C K et al., 2001a. Recent advances on the study of Mesozoic mammals in China. Asoc Paleont Argent, Publ Espec, (7): 179 ~ 184
- Wang Y Q, Hu Y M, Meng J et al., 2001b. An ossified Meckel's Cartilage in two Cretaceous mammals and origin of the mammalian middle ear. Science, **294**: 357 ~ 361
- Wang Y Q, Hu Y M, Zhou M Z et al., 1995. Mesozoic mammal localities in western Liaoning, Northeast China. In: Sun A L, Wang Y Q eds. Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. Beijing: China Ocean Press. 221 ~ 227
- Xu X, Norell M A, 2004. A new troodontid dinosaur from China with avian-like sleeping posture. Nature, **431**: 838 ~ 841
- Yabe H, Shikama T, 1938. A new Jurassic Mammalia from South Manchuria. Proc Imp Acad, **14**(9): 353 ~ 357
- Young C C (杨钟健), 1978. New materials of *Eozostrodon*. Vert Palasiat (古脊椎动物学报), **16**(4): 222 ~ 224 (in Chinese with English summary)
- Zhang F K (张法奎), Crompton A W, Luo Z X (罗哲西) et al., 1998. Pattern of dental replacement of *Sinoconodon* and its implication for evolution of mammals. Vert Palasiat (古脊椎动物学报), **36**(3): 197 ~ 217 (in Chinese with English summary)
- Zhou M Z (周明镇), Cheng Z W (程政武), Wang Y Q (王元青), 1991. A mammalian lower jaw from the Jurassic of Lingyuan, Liaoning. Vert Palasiat (古脊椎动物学报), **29**(3): 165 ~ 175 (in Chinese with English summary)
- Zhou Z H, Barrett P M, Hilton J, 2003. An exceptionally preserved Lower Cretaceous ecosystem. Nature, **421**: 807 ~ 814