

Recent advances on the study of Mesozoic mammals from China

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Abstract. History of the study of Chinese Mesozoic mammals can be traced back to over 60 years ago when Yabe and Shikama described *Manchurodon simplicidens* Yabe and Shikama, an amphidontid "symmetrodont" from northeastern China in 1938. So far, a dozen of localities yielding Mesozoic mammals have been reported from China, representing a wide range of Mesozoic mammal groups, including sinoconodontids, morganucodontids, triconodonts, multituberculates, symmetrodonts, shuotheriids, and eutherians, etc. Complete skeletons of *Zhangheotherium quinquecuspidens* Hu *et al.*, a symmetrodont, and *Jeholodens jenkinsi* Ji *et al.*, an eutriconodont, from the same early Cretaceous lacustrine deposits as those bearing the feathered dinosaurs and the primitive birds, offer new insight into the relationships of the major lineages of mammals and the evolution of the mammalian skeleton. Discovery of an upper molar of *Shuotherium shilongi* Wang *et al.* from the same locality as *S. dongi* Chow and Rich, the type species of the genus, confirms the existence of the pseudo-tribosphenic molar pattern, in contrast to tribosphenic one, and indicates that Yinotheria represents a separate lineage in early therian diversity.

Keywords. China. Mesozoic mammals. History. New information.

Introduction

Mammals have dominated the continental environments for about 65 Ma in Cenozoic after the great extinction of dinosaurs and other large reptiles at the end of Mesozoic. The early evolution of mammals in Mesozoic era played an important role in their history. Since the Mesozoic mammals are comparatively rare, any new findings can update our knowledge on mammal evolution. Like in all other countries, the Mesozoic mammals found in China also provide important information in understanding the early evolution of mammals.

History of discovery

The first Chinese Mesozoic mammal was found at a small coal mine in northeastern China. It is only represented by the type specimen, a right lower jaw with 7 cheek teeth, from Zhaziyao (Sakusyo), Wafangdian (Gaboten), Liaoning Province (figure 1.1). Yabe and Shikama (1938) named it *Manchurodon simplicidens* under the family Amphidontidae of the Symmetrodonta. It was originally considered to be of Middle Jurassic age (Yabe and Shikama, 1938), but the Late Jurassic and Early Cretaceous were also pro-

posed later (Teilhard de Chardin and Leroy, 1942; Chow, 1953; Patterson, 1956; Zhang, 1984). Further work suggested a Middle Jurassic age for the mammal-bearing beds (Zhou *et al.*, 1991). Also from a coal mine at Xinqiu (Hsinchiu), Fuxin (Husin), western Liaoning (figure 1.2), an eutherian mammal, *Endotherium niinomii*, was reported by Shikama in 1947. This taxon is represented by a lower jaw with 3 molars. The original author proposed a new family Endotheriidae for this new fossil mammal (Shikama, 1947), but it was considered to be similar to *Zalambdalestes* (Shikama, 1947; Chow, 1953), which was further questioned by Wang *et al.* (1995). *Endotherium niinomii* has been usually accepted as an eutherian mammal (Kielan-Jaworowska *et al.*, 1979), but its taxonomic position remains uncertain. Its geologic age was first thought to be Late Jurassic (Shikama, 1947) and then Early Cretaceous (Chow, 1953; Patterson, 1956; Zhou *et al.*, 1991). More recent work provides evidence for an Early Cretaceous age, probably Aptian (Wang *et al.*, 1995).

An axis of a Mesozoic mammal was collected by the Sino-Sweden Expeditions during 1930-31 in Tsondolein-Khuduk, Inner Mongolia (figure 1.7). It was not reported until twenty years later by Bohlin (1953) who identified it as *Mammalia indet.* Nessov *et al.* (1994) named it *Khuduklestes bohlini* under Eutheria incert. sed., but it was referred to Deltatheroidea by McKenna and Bell (1997). Its age is considered to be the Cenomanian (Nessov *et al.*, 1994).

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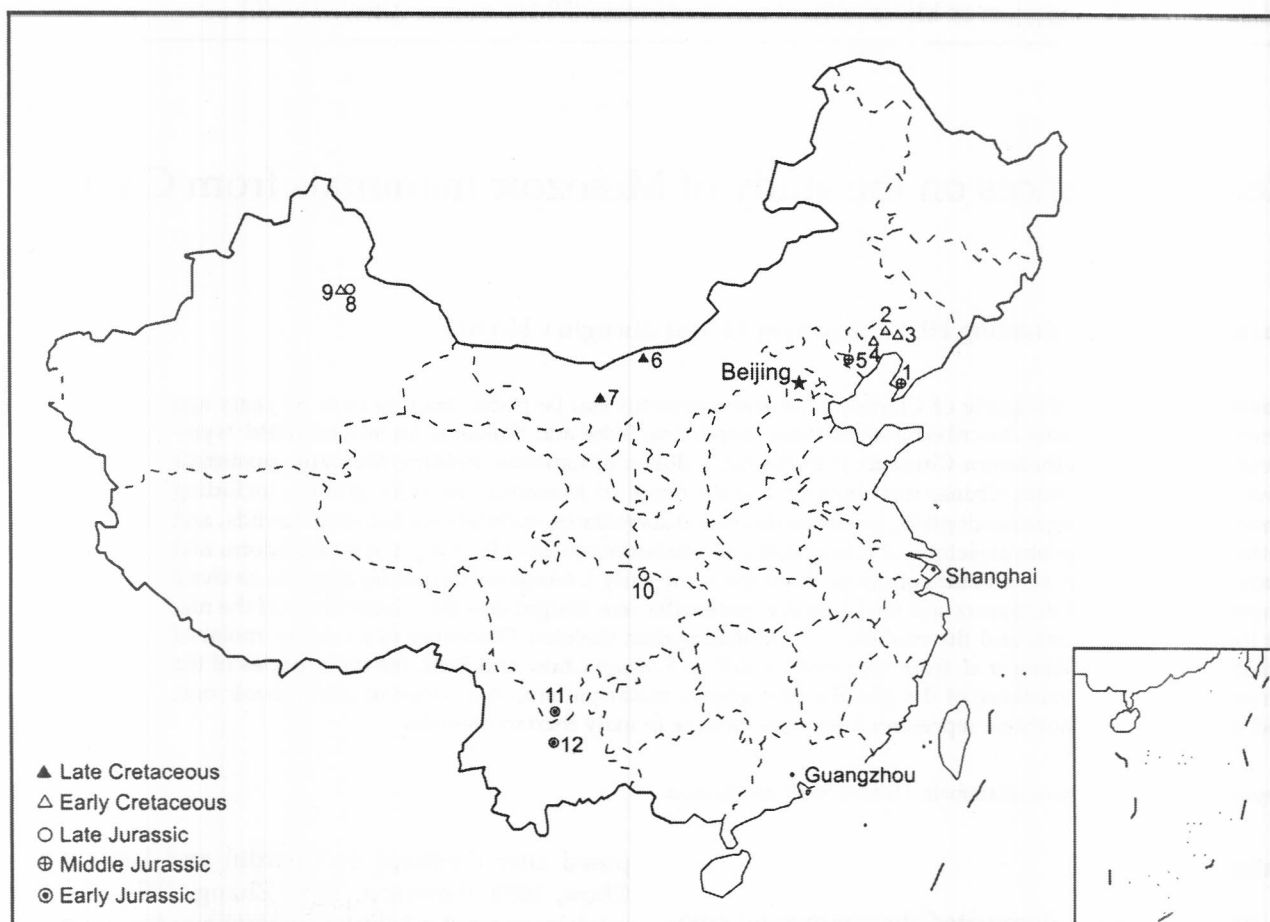


Figure 1. A sketch map showing the distribution of Mesozoic mammal localities in China. 1, Wafangdian, Liaoning; 2, Fuxin, Liaoning; 3, Badaohao, Heishan, Liaoning; 4, Sihetun area, Beipiao, Liaoning; 5, Fangshen, Lingyuan, Liaoning; 6, Bayan Madahu, Inner Mongolia; 7, Tsondolein-Khuduk, Inner Mongolia; 8, Laoshangou, Klameli, Xinjiang; 9, Huangnitan, Klameli, Xinjiang; 10, Shilongzhai, Nanjiang, Sichuan; 11, Luchang, Huili, Sichuan; 12, Lufeng, Yunnan.

From southwestern China, some specimens of the Mesozoic mammals were collected from Lufeng, Yunnan (figure 1.12). Patterson and Olson (1961) first reported *Sinoconodon rigneyi*. After that, two new species of *Sinoconodon*, *S. parringtoni* Young (1982) and *S. yangi* Zhang and Cui (1983), and a new genus and species, *Lufengoconodon changchiawaensis* Young (1982), were described from the same sites. However, the latter three species were thought to represent different ontogenetic stages of *Sinoconodon* and should be regarded as junior synonyms of *S. rigneyi* (Crompton and Luo, 1993; Luo and Wu, 1994; Zhang *et al.*, 1998). Two species of *Morganucodon*, *M. ohleri* Rigney (1963) and *M. heikuopengensis* (Young, 1978), were also recovered from these sites. Both *Sinoconodon* and *Morganucodon* are representatives of the earliest Chinese Mesozoic mammals. The geologic age of the fossil-bearing Lower Lufeng Formation was in dispute for a long time. Now, it is considered to be Early Jurassic (Luo and Wu, 1994; Dong, 1995), probably Hettangian-Pliensbachian (Luo and Wu, 1995).

After the above mentioned fossil localities discov-

ered before 1940s, no more sites of Mesozoic mammals were reported until 1980s. Chow and Rich (1982) reported a mammal jaw from the Late Jurassic of Nanjiang, Sichuan (figure 1.10) and named it *Shuotherium dongi*. This species has a peculiar dentition with a talonid-like structure, pseudo-talonid, in front of the trigonid rather than behind it. Chow and Rich (1982) proposed the term pseudo-tribosphenic for its obviously different occlusal relationship between the upper and lower molars, in contrast to the tribosphenic pattern. The age of the fossil-bearing beds has been considered to be Oxfordian-Kimmeridgian (Dong, 1995). Recently, Wang Y.q. *et al.* (1998) described an upper molar from the same quarry and named it a new species of the genus, *S. shilongi*. It provides new information about the occlusal relationship between upper and lower molars of the pseudo-tribosphenic pattern.

Chow and Rich (1984a) described a triconodont mammal from the Early Cretaceous of Laoshangou, Klameli, Xinjiang, northwestern China (figure 1.8). The fossil was referred to the Amphilestidae and named *Klamelia zhaopengi* (Chow and Rich, 1984a).

Chow and Rich (1984a) also considered that it is close to *Gobiconodon*. However, later studies diminished such possibility (Jenkins and Schaff, 1988; Zhou *et al.*, 1991).

Besides these fossils, some fragmentary mammal specimens are also reported from China in 1980s and early 1990s. They include a tooth fragment from the Early Jurassic Lower Yimen Formation (probably equivalent of the Lower Lufeng Formation) of Huili, Sichuan (figure 1.11) and a lower jaw fragment from the Early Cretaceous Shenjinkou Formation of Klameli, Xinjiang (figure 1.9) (Chow and Rich, 1984b). Another fragmentary lower jaw with the broken last molar was reported from the Middle Jurassic Jiulongshan Formation (= Haifanggou Formation) of Lingyuan, Liaoning (figure 1.5) (Zhou *et al.*, 1991). It was named *Liaotherium gracile* and tentatively referred to the Amphilestidae.

In late 1980s and 1990s, some new discoveries were made in China. During the Sino-Canadian Dinosaur Project, a new locality of Mesozoic mammals was found at Bayan Mandahu, Inner Mongolia (figure 1.6). Some skulls of multituberculates, such as *Kryptobataar*, and eutherians, such as *Kennalestes* and *Zalambdalestes*, were uncovered from the equivalent of the Djadohta Formation (Dong, 1993). The age of this locality is considered to be Campanian (Jerzykiewicz *et al.*, 1993).

Recently, discovery of primitive birds (Hou, 1996; Hou *et al.*, 1995, 1996, 1999; Ji *et al.*, 1999a) and feathered dinosaurs (Chen *et al.*, 1998; Ji *et al.*, 1998; Xu *et al.*, 1999a, 1999b) from the Sihetun area of Beipiao, western Liaoning (figure 1.4) attracted worldwide attention of scientists and the public. From the same locality and horizon, two complete skeletons of Mesozoic mammals were described (Hu *et al.*, 1997; Ji *et al.*, 1999b). Both are from the lower part of the Yixian Formation. *Zhangheotherium quinquecuspidens* Hu *et al.* (1997) is a representative of the Spalacotheriidae of the Symmetrodonta. Phylogenetic analyses based on the dental, cranial and postcranial characters support that multituberculates are a sister-group of therian mammals including symmetrodonts (Hu *et al.*, 1997). It represents an intermediate stage of the evolution of mammalian pectoral girdle morphology and forelimb posture between primitive and advanced therian mammals (Hu *et al.*, 1998).

Jeholodens jenkinsi Ji *et al.* (1999b) is a representative of an eutriconodont mammal. Its pectoral girdle and forelimbs are highly derived, but it has primitive pelvic girdle and hindlimbs, which shows a mosaic of characters of postcranial skeleton (Ji *et al.*, 1999b).

In the past few years, some new mammal specimens were collected from two different levels in western Liaoning, northeastern China. One is the

Early Cretaceous Fuxin Formation in Fuxin area (figure 1.2), same as that of the famous *Endotherium niinomii*, and the other is the underlying Shapai Formation at Badaohao (figure 1.3) (Wang *et al.*, 1995). The mammal fossils from this area include triconodonts, multituberculates, symmetrodont, aegialodontid, and eutherians. All the specimens are under description. Both levels are stratigraphically higher than the *Zhangheotherium*-bearing bed and possibly of Aptian age.

Up to this date, twelve localities yielding Mesozoic mammals have been reported. They range from the Early Jurassic to the Late Cretaceous. The specimens collected from these localities represent 8 mammalian groups including sinoconodontids, Morganucodontids, triconodonts, multituberculates, symmetrodonts, shuotheriids, aegialodontid, and eutherians. The Mesozoic mammals found in China are summarized in table 1.

Recent advances

Mammals are considered to have their special tooth replacement pattern. All deciduous premolars are replaced once in eutherians, whereas only the last premolar is replaced in marsupials (Luckett, 1993; Cifelli *et al.*, 1996). Examination of new materials of *Sinoconodon* from the Early Jurassic Lower Lufeng Formation shows that there are "more than three alternate replacements of the incisors, at least five replacements of the canines, and one replacement of the premolars and the posterior molars" in *Sinoconodon* (Zhang *et al.*, 1998). *Sinoconodon* has a wide range of ontogenetic variation (Crompton and Luo, 1993). Its skull length ranges from about 30 mm to over 60 mm (Luo, 1994).

Zhangheotherium quinquecuspidens, represented by a nearly complete skeleton, has the dental formula 3.1.2.5/3.1.2.6. There is a hypertrophied cusp B' on its upper molars. The lower molars lack lingual and labial cingulids that are common on the lower molars of other spalacotheriids. The reduced postaxial cervical ribs are unfused in adult, as in Morganucodontids and multituberculates. This animal has separate interclavicle (Hu *et al.*, 1997). Phylogenetic analysis, based on the overall characters, supports a sister-group relationship between multituberculates and therian mammals including the spalacotheriid symmetrodonts and more derived mammalian forms (Hu *et al.*, 1997, 1998). Its mobile clavicle-interclavicle joint allows a wide range of movement of the forelimb (Hu *et al.*, 1997). *Zhangheotherium* possesses several forelimb features characteristic of therians, such as the trochlear articulation at the humero-ulnar joint, narrow intertubercular groove of the humerus, the greater tubercles wider than lesser one, and so on.

Table 1. Summary of Mesozoic mammals known from China.

Locality	Formation	Age	Fossil mammals	References
Lufeng, Yunnan	Lower Lufeng Fm.	Hettangian-Pliensbachian	<i>Sinocondon rigneyi</i>	Patterson and Olson, 1961
			<i>Morganucodong oehleri</i>	Rigney, 1963
			<i>M. heikuopengensis</i>	Young, 1978; Luo and Wu, 1994
Luchang, Huili, Sichuan	Lower Yimen Fm.	Early Jurassic	Tooth fragment	Chow and Rich, 1984b
Wafangdian, Liaoning	Wafangdian Fm.	Middle Jurassic	<i>Manchurodon simplicidens</i>	Yabe and Shikama, 1938
Fangshen, Lingyuan, Liaoning	Jiulongshan Fm.	?Bathonian	<i>Liaotherium gracile</i>	Zhou <i>et al.</i> , 1991
Shilongzhai, Nanjiang, Sichuan	Upper Shaximiao Fm.	Oxfordian-Kimmeridgian	<i>Shuotherium dongi</i>	Chow and Rich, 1982
			<i>S. shilongi</i>	Wang Y.q. <i>et al.</i> , 1998
Laoshangou, Klameli, Xinjiang	Shishugou Fm.	Late Jurassic	<i>Klamelia zhaopengi</i>	Chow and Rich, 1984a
Huangnitan, Klameli, Xinjiang	Shengjinkou Fm.	Early Cretaceous	Jaw fragment	Chow and Rich, 1984b
Jianshangou, Beipiao, Liaoning	Yixian Fm.	Barremian	<i>Zhangheotherium quinquecuspidens</i>	Hu <i>et al.</i> , 1997
Sihetun, Beipiao, Liaoning			<i>Jeholoden jenkinsi</i>	Ji <i>et al.</i> , 1999b
Badaohao, Heishan, Liaoning	Shahai Fm.	?Aptian	Under description	Wang <i>et al.</i> , 1995
Xinqiu, Fuxin, Liaoning	Fuxin Fm.	Aptian	<i>Endotherium niinomii</i>	Shikama, 1947
Tsondolein-Khuduk, Inner Mongolia	Ulan Hoshao Fm.	Cenomanian	<i>Khuduklestes bohlini</i>	Bohlin, 1953; Nessov <i>et al.</i> , 1994
Bayan Mandahu, Inner Mongolia	"Djadohta" Fm.	Campanian	<i>Kennalestes</i> sp. <i>Zalambdalestes</i> sp. <i>Kryptobataar</i> sp.	Dong, 1993

However, it still retains some primitive characters, such as twisted humerus and condylar articulation between humerus and ulna, common feature in nontherian mammals having sprawling posture (Hu *et al.*, 1998). Morphological features of its forelimb and pectoral girdle suggest that it lacks parasagittal forelimb posture of most living mammals (Hu *et al.*, 1997). The forelimb posture in *Zhangheotherium* represents a transitional stage between the more primitive sprawling and more derived parasagittal postures (Hu *et al.*, 1998).

Recently reported *Jeholodens jenkinsi*, a triconodont mammal, is also represented by a complete skeleton (Ji *et al.*, 1999b). Its dentition is typical of triconodonts. Evidence from the type specimen shows that *Jeholodens* is more closely related to the triconodontids than the amphilestids and gobiconodontids (Ji *et al.*, 1999b). Based on a mosaic of derived, therian-like characters of the pectoral girdle and the humerus, but very primitive characters for the vertebral column, pelvic girdle, hindlimb and pes, the authors concluded that "the pectoral girdles and forelimbs for early mammals underwent extensive convergent evolution" (Ji *et al.*, 1999b).

The geological age of the Yixian Formation that

has yielded the primitive birds, feathered dinosaurs and mammals, has been considered to be Late Jurassic, Late Jurassic to Early Cretaceous or Early Cretaceous. Recently, $^{40}\text{Ar}/^{39}\text{Ar}$ dating gave an age of 124.61 ± 0.20 Ma for the tuff sample 50 cm above *Zhangheotherium*-bearing bed. Thus, the fossil-bearing beds is of Early Cretaceous age (Swisher *et al.*, 1999).

After Chow and Rich (1982) reported *Shuotherium*, a few researchers disputed its phylogenetic position (e.g. Kermack *et al.*, 1987; Tatarinov, 1994). The hypothesized reconstruction of upper molar of *Shuotherium* by Chow and Rich (1982) was questioned by Butler (1988) and Hopson (1995). An upper molar from the same quarry as the type specimen of *Shuotherium* was referred to the genus and named *S. shilongi*, based on analysis of occlusal relationship, coincidence of apparently derived morphological characters, particularly the high, flat, nearly vertically oriented faces of the occluding buccal side of the pseudo-protocone and lingual side of the pseudo-hypoconid (Wang Y.q. *et al.*, 1998). This is corroborated by an independent study of the *Shuotherium*-like fossils from England (Sigogneau-Russell, 1998). Reconstruction of occlusal relationship between the

lower dentition of *S. dongi* and the upper molar of *S. shilongi* indicates that the occlusal pattern of *Shuotherium* appears to be analogous to that hypothesized for an early stage in evolution of the tribosphenic dentition (Wang Y.q. *et al.*, 1998). The Yinotheria, represented by mammals with the pseudo-tribosphenic molar pattern, comprise a separate lineage in early therian diversity. Discovery of *Shuotherium*-like mammal from the upper Bathonian in England (Sigogneau-Russell, 1998) suggests a wider distribution of this group and indicates that this lineage separated from the other mammal groups at least no later than Middle Jurassic.

In the past few years, field work of an IVPP group resulted in the discovery of some new materials of Mesozoic mammals from two stratigraphic levels in Fuxin area, where *Endotherium* was collected (Wang *et al.*, 1995). All the specimens are under description. Some eutherian specimens may help in determining the systematic position of *Endotherium*, which has been considered as Eutherian indet. for many years due to the loss of the type and only specimen during World War II. Of two mammal-bearing levels, the lower one, the Shahai Formation at Badaohao, was considered to be Valanginian or Hauterivian (Wang *et al.*, 1995). Recent stratigraphic work and radiometric dating of the Yixian Formation bearing feathered dinosaurs and *Zhangheotherium* and *Jeholodens* (Wang X.I. *et al.*, 1998; Swisher *et al.*, 1999) indicates the Shahai Formation is possibly Aptian in age.

Concluding remarks

Twelve localities in China have yielded a wide range of Mesozoic mammals, including sinoconodonts, morganucodonts, triconodonts, multituberculates, symmetrodonts, shuotheriids, and eutherians, etc. Recent work on the Chinese Mesozoic mammals provides new knowledge in understanding the origin and early evolution of mammals.

1) *Sinoconodon*, the representative of the most primitive mammal group Sinoconodontidae, has a tooth replacement pattern more primitive than that of all the other mammals and represents an intermediate stage of character transformation from advanced cynodonts to mammals (Zhang *et al.*, 1998).

2) Complete skeleton of a symmetrodont mammal, *Zhangheotherium quinquecuspidens* from the early Cretaceous lacustrine deposits, provides new evidence for the sister-group relationship between multituberculates and therian mammals including spalacotheriid symmetrodonts and more derived mammals. The morphological features of its pectoral girdle and forelimbs indicate that the parasagittal posture developed in therian mammals more derived than spalacotheriid symmetrodonts (Hu *et al.*, 1997, 1998).

3) The mosaic of both derived and primitive characters of *Jeholodens jenkinsi*, an eutriconodont from the same site as that of *Zhangheotherium*, suggests the existence of extensive convergent evolution of the pectoral girdles and forelimbs for early mammals (Ji *et al.*, 1999b).

4) An upper molar of *Shuotherium shilongi* from the same locality as *S. dongi*, the type species of the genus, shows some derived and possibly autapomorphic features related to occlusion that match those of the lower dentition. It confirms the existence of a lingual cusp on *Shuotherium* upper molars and that the Yinotheria represents a separate lineage in early therian diversity. The upper and lower dentition of pseudo-tribosphenic molar pattern mainly has shearing and puncture function and demonstrates the trend to grinding (Wang Y.q. *et al.*, 1998).

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