

Middle-Eocene artiodactyls from Shanghuang (Jiangsu Province, Coastal China) and the diversity of basal dichobunoids in Asia

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Abstract A new assemblage of basal dichobunoid artiodactyls from the middle-Eocene Shanghuang fissure fillings includes the diacodexeid *Jiangsudon shanghuangensis* gen. and sp. nov., a new species of the lantianine dichobunoid *Elaschitherium*, *Elaschitherium crepaturus* sp. nov., and an indeterminate suoid which is presently the earliest record of this clade. Diacodexeids are also represented by two forms provisionally referred to cf. *Diacodexis* sp. and to an indeterminate Diacodexidae, respectively. The occurrence of diacodexeids in Shanghuang contrasts with the early and earliest middle-Eocene chronological range of the family in Europe and North America and suggests that the stratigraphic range of the family in Asia extends up to the middle Eocene. This may reflect particular habitats in coastal China that may have been relatively stable during the early and middle Eocene, thus preserving forest-dwelling artiodactyls that became extinct in the other Holarctic regions. Compared to other supposedly coeval North American, European, and

Asian faunas, the Shanghuang mammalian assemblage is most similar to early Uintan faunas of North America but is also remarkable in recording forms close to taxa that are characteristic of the Wasatchian and Bridgerian North American Land Mammal Ages. The Irindmanhan age of the Shanghuang fauna is supported by the mammalian assemblage recovered from the fissure D, but an Arshantan age cannot be completely ruled out at this point. Although the Shanghuang assemblage is biased towards preservation of small components of the mammalian fauna, the Shanghuang fauna provide an important and unique window into the Eocene diversity and early evolution of cetartiodactyls in eastern Asia.

Keywords Cetartiodactyla · Middle Eocene · Shanghuang · China

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Introduction

The karstic infillings into the Triassic Shangqinglong limestone near the Shanghuang village, Liyang County, southern Jiangsu Province, coastal China (Fig. 1) have yielded diversified assemblages of middle-Eocene mammals (Qi et al. 1991, 1996; Beard et al. 1994; Wang and Dawson 1994; Qi and Beard 1996; Dawson and Wang 2001; Dawson et al. 2003). Five distinct fissures (Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) localities 93006A-E) have been sampled, and artiodactyl remains have been retrieved after screen washing from all the fissures. However, fossil mammals are of unequal abundance in these fissures since approximately 70% of the total fossil material comes from the fissure D. This fissure has produced abundant dental and postcranial material of the tiny lantianine dichobunoid *Elaschitherium qii*

Fig. 1 Map of the Shanghuang fissure fillings in Jiangsu Province (Eastern China)



(Métais et al. 2004) and much rarer elements of the homacodontid *Limeryx chimaera* (Métais et al. 2005). Age of fissures is based on biostratigraphic correlations established with mammals, and the fissures D and E have been correlated with the Irđinmanhan Asian land mammal ages (ALMA) and the fissures A, B, and C with the early Sharamuronian ALMA. Each fissure is believed to represent a relatively short interval of middle-Eocene times, which is supported by the relative homogeneity of the faunas extracted from each fissures (Beard et al. 1994; Wang and Dawson 1994; Qi and Beard 1996; Qi et al. 1996).

Artiodactyls are relatively common small and medium-sized mammals in the early and middle Eocene of Europe and North America. However, their fossil record in Asia for the same time interval remains extremely limited. It is generally admitted that dichobunoids represent a heterogeneous and paraphyletic assemblage of generalized bunodont to bunoselenodont artiodactyls that inhabited the three Holarctic continents from the basal Eocene to the Oligocene. Dichobunoids were morphologically close to modern tragulids, and they are likely involved in the origin of all the modern groups of cetartiodactyls including ruminants, camels, pigs, and probably whales and hippos (e.g., Geisler and Uhen 2005).

These early Selenodontia (in the sense of Gentry and Hooker 1988; i.e., extinct forms that are more closely related to extant ruminants and camels than to pigs and hippos-Cetacea) are designated as “homacodonts” in North America where they are documented by at least eight

genera recorded from the Wasatchian North American Land Mammal Age (NALMA) to the Duchesnean NALMA (Stucky 1998). The peak of their generic diversity is registered in the late Uintan NALMA with five distinct forms. In Europe, middle-Eocene dichobunoids are represented by the Dichobunidae, which are subdivided into Eurodexeinae and Dichobuninae (Erfurt and Sudre 1996). Métais et al. (2004) tentatively reattached the Lantianinae to the Dichobunidae on the basis of dental resemblance, but Lantianinae may belong to an independent group of Asian hypoconiferous dichobunoid (Theodor et al. 2007).

Among the dichobunoids, the Diacodexidae are the most primitive, and their first appearance in the fossil record marks the base of the Wasatchian Land Mammal Age (LMA) in North America. This family of small-stem cetartiodactyls is moderately common in the early Eocene of Europe and North America, but their record in Asia is restricted to the early Eocene of Pakistan (Thewissen et al. 1983). Diacodexids are characterized by their basic tribosphenic upper molars retaining smaller and equally developed paraconule and metaconule. The main cusps are generally bulbous and conules are moderately crested. The hypocone is usually absent, but an accessory cuspule or spur, sometimes interpreted as an incipient hypocone, is present on the distolingual cingulum.

Here, we report new diacodexeid and lantianine cetartiodactyls from different fissures of the karstic system of Shanghuang. The fissures B and C have only yielded sparse artiodactyl assemblages, and the fissure E has not yielded dental remains referable with certainty to artiodactyls.

Although still poorly documented, this new assemblage of early artiodactyls provides critical new evidence on the morphology, diversity, and biogeography of early artiodactyls in Asia. This report is the first part of the study of the artiodactyl fauna from Shanghuang. The selenodont forms which are moderately diversified in Shanghuang will be described in a second and separate report.

Systematic paleontology

Superorder Cetartiodactyla, Montgelard et al. 1997

Family Diacodexidae (Gazin 1955)

Jiangsudon shanghuangensis, gen. et sp. nov. (Fig. 2a)

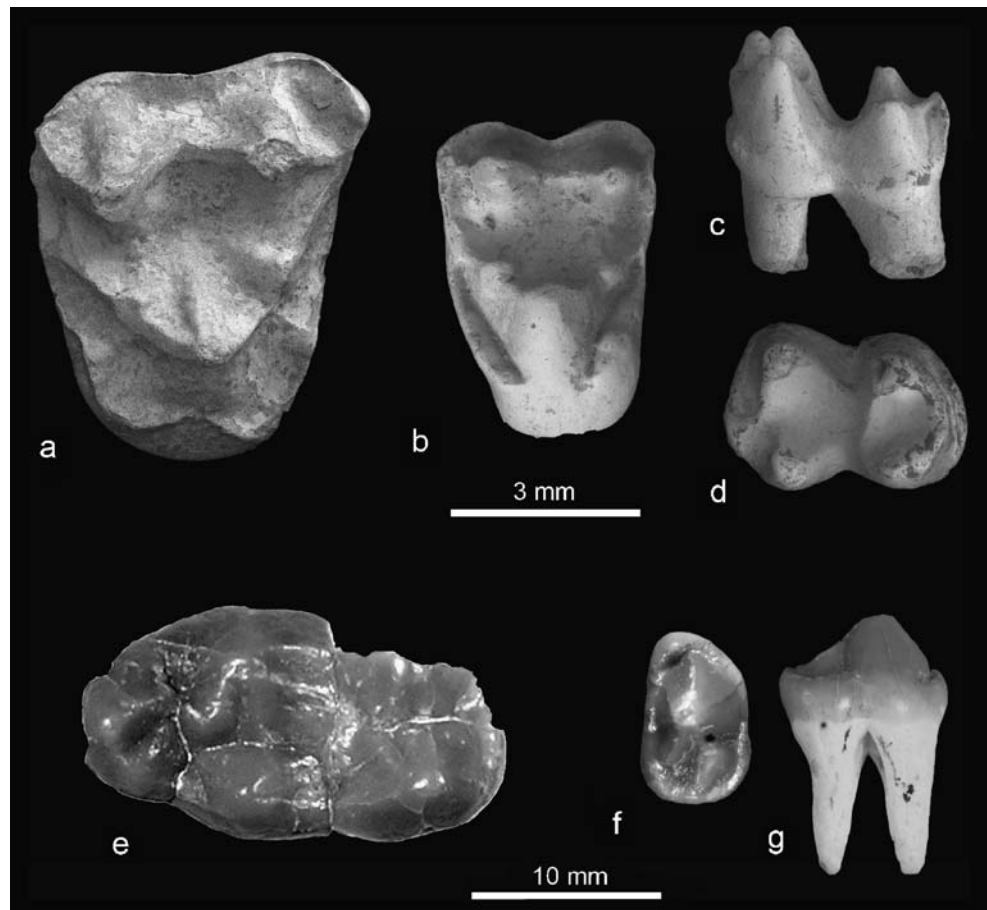
Diagnosis Upper molars shows a basic tribosphenic pattern and subtriangular outline with central protocone, lacking distinct hypocone and mesostyle; paracone is higher on the tooth crown and more expanded than the metacone; protocone is prominent with a narrow labial rib; paracone and metacone are acute and show a distinct rib (more accentuated on the paracone) on their labial face; metacone is more lingual than the paracone; labial cingular shelf is particularly well developed in the parastylar area; there are

incipient accessory cusps and spurs on the cingular shelves that are well developed mesiolingually and distolingually; the lingual cingulum is thinner. It differs from other diacodexids in its large size and in a distinct parastyle on upper molars. It differs from North American antiacodontines in the lesser development of conules and the transverse elongation of upper molars. It further differs from Wasatchian *Hexacodus*, Bridgerian *Homacodon* and *Microsus*, and Uinta “homacodonts” in the lack of hypocone and the equal development of conules on upper molars. *J. shanghuangensis* differs from European eurodexeine dichobunoids in lacking true hypocone, the lesser development of conules, and the presence of a strong parastylar shelf labially.

Holotype Its holotype is IVPP V12761.1, an isolated right upper molar (probably M2; Fig. 2a), from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural history, Pittsburgh.

Etymology The generic name refers to the Jiangsu Province, and the specific name alludes to the village of Shanghuang, near the provenance of the holotype and so far unique specimen.

Fig. 2 *J. shanghuangensis* gen. et sp. nov., **a** IVPP V12761.1 (holotype), an isolated upper molar (probably M2). *Diacodexis* sp., **b** cf. IVPP V12762.1, left upper molar (probably M2). Diacodexidae indet., **c** IVPP V12763.1, left lower molar (probably m2) in labial and occlusal views. Suoidea indet. 1, **d** IVPP V12763.1, an isolated left lower molar (m3). Suoidea indet. 2, **e** IVPP V12763.1, an isolated right p4 in occlusal and labial views. All specimens are in occlusal view, and only the specimens e, f, and g go with the bar scale 10 mm



Type locality The type of locality is IVPP locality 93006A (Fissure A) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Distribution Distribution is Middle Eocene, fissure A, which is probably late Irudinmanhan–early Sharamurunian in age (Wang and Dawson 1994) and geographically restricted to the type locality so far, central coastal China (see “Discussion”).

Description The holotype is a right upper molar of subtriangular occlusal outline and is transversely elongated (length, 5.1 mm; width, 6.3 mm). The protocone is central and thick cingula lines its basal mesial and distal sides; mesial and distal cingula exhibit distinct spurs that can be interpreted as incipient pericone and hypocone, respectively; there is a distinct labial rib on the protocone; paracone and metacone are equal in size, relatively acute, but the metacone is more lingual, and its labial rib is not as convex as that of the paracone. Conules are moderately developed and weakly winged, and the paraconule is larger and forms a triangular platform lingual to the base of the paracone. The central basin is wide, suggesting the presence of a widely expanded hypoconid on the lower molars. There is a surface showing evidence of abrasion at the base of the distal side of the metacone, but this is certainly a postmortem artifact. The parastyle is part of the thick labial cingular shelf and forms a spur rather than a real cusp. There is no trace of metastyle or mesostyle and the labial cingular shelf is straight longitudinally.

Discussion Although naming a new taxon based on fragmentary material can be problematic, IVPP V12761.1 displays a combination of primitive (central protocone, weak development of conules, thick buccal cingulum and protocone relatively central in position on upper molars) and derived (well-developed parastylar area) dental features that are unique among Eocene artiodactyls. This distinctive combination of characters clearly distinguishes *J. shanghuangensis* from the few Eocene basal artiodactyls that are known from Asia. Reference of *J. shanghuangensis* to the Diacodexidae is based on the central position of the protocone, lack of hypocone and mesostyle, presence of crested conules, and bulbous paracone and metacone (Stucky 1998). This family is particularly poorly documented in Asia, and affinities of most early–middle-Eocene artiodactyls remains poorly understood, and their familial assignment is mostly on a tentative basis. The Asian landmass is vast, and our knowledge about early artiodactyls is based on few spots, mostly in the Indo-Pakistani region, Central Asia, and South East Asia.

Artiodactyl faunas from the Indian Subcontinent range in age around the early–middle-Eocene boundary (Thewissen

et al. 2001; Gingerich 2003), and their affinities with cotemporaneous faunas from Europe and North America are poorly understood. *Gujaratia pakistanensis* was first recognized as belonging to the genus *Diacodexis* (Thewissen et al. 1983), and it is generally thought to be the stem and most primitive taxon of this local radiation of artiodactyls. The upper molars of *G. pakistanensis* are more bunodont, triangular in occlusal outline, and less transversely elongated than that of *J. shanghuangensis*; the Pakistani form lacks parastylar extension and labial cingular shelf. Among the nonraoellids dichobunoids from Indo-Pakistan, *Dulcidon gandaensis* shares with IVPP V12761.1 the labial extension of upper molar through a thick labial cingular shelf and a parastyle connected to the straight and sharp preparaconule crista, but the unique upper molar known for *D. gandaensis* is smaller and of triangular outline and retains strongly winged conules. The upper dentition of *Pakibune* is not known and, although comparable in size, *Chorlakkia* and *Haqueina* from the Kuldana Formation show more bulbous cusps on upper molars and lack the labial cingular shelf and parastyle, as well as mesiolingual and distolingual cingula with accessory cuspule as in *J. shanghuangensis*. Raoellids all exhibit marked bunodont dentition which set them apart from all the dichobunoids (sensu lato) reported in the three Holarctic landmasses.

Jiangsudon can be easily distinguished from *Aksyiria oligostus* from the early–middle-Eocene Obayla Formation in the Zaysan Basin, Kazakhstan (Gabunia 1973, Gabounia 1977). The unique upper molar which *A. oligostus* is based on is square in occlusal outline and does not show expanded parastyle or labial cingular shelf as in *Jiangsudon*. Our knowledge of *A. oligostus* is still very limited since no additional material was reported since the original description by Gabunia (1973), and the affinities of the genus are consequently unclear. It is worth noting that the upper molar NMMP-KU 1556 from the late middle-Eocene Pondaung Formation, Central Myanmar, figured in Tsubamoto et al. (2005) and referred by these authors to “Artiodactyla indeterminate 1” is actually very similar to the holotype of *A. oligostus*. If correct, this identification would extend the geographical distribution and the chronological range of the genus *Aksyiria*, previously restricted to its type locality.

Comparisons with early bunoselenodont artiodactyls from Europe are particularly instructive because Europe apparently experienced sporadic faunal interchange with Asia during the middle Eocene (Qi et al. 1996). In that respect, the ongoing study of ungulates from Shanghuang may well provide additional biogeographic information. Diacodexids in Europe are more taxonomically diverse than those from North America (Sudre et al. 1983), even though both areas were geographically connected until the

European Mammal Zone MP 8/9, which roughly corresponds to the middle Wasatchian. *Bunophorus* is clearly distinctive from *Jiangsudon*, and European *Diacodexis*, although morphologically closer, also shows very few of the dental characters seen in *Jiangsudon*: their upper molars are smaller (with the exception of *Diacodexis varleti*), cusps are more bulbous, and molars lack the labial cingular shelf and parastylar area, which characterize IVPP V12761.1. Closer resemblance can be seen in the early eudexine dichobunoid *Eurodexis* from the Prémontré (MP10; Sudre and Erfurt 1996) and Geiseltal (MP11–13; Erfurt and Sudre 1996). However, upper molars of *Eurodexis* can be clearly differentiated in having less transversely isolated upper molars, less salient parastyle, and generally smaller size. It is worth noting that the limited material currently available for *Jiangsudon* prevents any extensive comparisons, but it appears that the form from Shanghuang shows a similar evolutionary stage to that of the European Eurodexeinae.

Extensive comparisons with North American diacodexids, antiacodontines, leptocherids, and “homacodonts” show that *Jiangsudon* possesses a mosaic of dental characters that set it apart from the Bridgerian and Uintan representatives of early Selenodontia (in the sense of Gentry and Hooker 1988). The relative small size of conules and the lack of true hypocone in *Jiangsudon* prevent its reattachment to antiacodonts and the position and size of the metaconule does not indicate close affinities with homacodonts. Likewise, the lack of the characteristic “cusp inflation” of leptocherids suggests no special affinities with this North American family. In fact, it is the early-Eocene diacodexids that appear to be the most closely related to *Jiangsudon*, although the morphology of IVPP V12761.1 is atypical within the Diacodexidae, and this allocation is tentative pending additional material.

cf. *Diacodexis* sp. (Fig. 2b)

Referred material The referred material is IVPP V12762.1, an isolated left upper molar (probably M2; Fig. 2b) from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural history, Pittsburgh.

Locality The locality is IVPP locality 93006D (Fissure D) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Description This taxon is represented by a single upper molar (length, 3.1 mm; width, 4.6 mm) provisionally assigned to *Diacodexis*, pending additional material that will allow definitive taxonomic assignment. This molar (probably a M2) is much smaller than the holotype of *J. shanghuangensis* and displays a quite distinct morphology.

IVPP V12762.1 is subtriangular in occlusal outline; conules are reduced in size, poorly crested, and located near the protocone; the preprotocrista and postprotocrista are poorly expressed and reach down the lingual margin of the tooth; cingula are particularly well developed along the mesial and distal sides of the protocone; the distal cingular shelf is particularly sharp, forming lingually a distinct bulb that can be interpreted as an incipient hypocone; the labial cingulum is present; styles are absent; paracone and metacone are equal in size and connected through a straight mesocrista.

Discussion This upper molar is referred to *Diacodexis* because of the central position of the protocone, bulbous paracone and metacone, the lack of a true hypocone and mesostyle, and the presence of conules. However, the specimen from Shanghuang is distinguished in having poorly expressed conular wings, thick cingular shelves on the mesial and distal side of the protocone, and higher transverse length. All the species referred to the genus *Diacodexis* show upper molars with a larger protocone, larger and winged conules, and thinner mesial and distal cingula. IVPP V12762.1 is close in size to *Diacodexis antunesi* (Estravis and Russell 1989) and *Diacodexis gazini* (Godinot 1978), both from the earliest Eocene (MP 7) of Europe. IVPP V12762.1 is also comparable in size to *Diacodexis illicis* from the basal Wasatchian (Wa0) of the Bighorn Basin, Wyoming (Gingerich 1989), but comparisons are limited since the upper dentition of the latter species is unknown. The specimen from Shanghuang is also comparable in size to *Diacodexis* sp. and *Eolantianius russelli* reported from the early Eocene of Andarak 2, Kyrgyzstan (Averianov 1996). The partly damaged upper molar from Andarak 2 referred to *Diacodexis* sp. (Averianov 1996: plate 1B) is transversely shorter than IVPP V12762.1, and it lacks the precingulum. The upper molars of *Eolantianius* are clearly distinctive because of the continuous lingual cingulum and strong hypocone on upper molars. Comparison with *D. gandaensis* (Dehm and Oettingen-Spielberg 1958) which is based on a single upper molar from the early-Eocene Kuldana Formation (Pakistan) shows a similar molar structure, but the molar from Pakistan is more triangular in occlusal outline, less extended transversely, and displays a well-developed cingular shelf labially. At this point, it appears difficult to go farther in the determination due to the scarcity of available material.

The occurrence in Shanghuang of a diacodexid close to *Diacodexis* suggests that the chronological range of the family in Asia extends up to the middle part of the middle Eocene. The specimen is from the fissure D which is believed to correlate with the Irindmanhan ALMA (Dawson and Wang 2001) but evidence remains weak partly because of the apparent provincialism that obviously affected

eastern Asia during the middle Eocene (Dawson et al. 2003). Diacodexids, the most basal cetartiodactyls known so far, appear from the base of the Eocene in Europe (Smith et al. 1996) and North America (Gingerich 1989) where their first appearance datum marks the onset of Eocene. However, the stratigraphic range of the family in these two continents does not extend beyond the early middle Eocene (Theodor et al. 2007). The earliest occurrence of the Diacodexidae in Asia is represented by the genus *G. pakistanensis* from the late early Eocene of Pakistan (Thewissen et al. 2001) and possibly by *Tsaganohyus pecus* from the base of the Bumban Member of the Naran Bulak Formation in Mongolia (Kondrashov et al. 2004). The upper dentition of *T. pecus* is unknown and its inclusion within diacodexids remains tentative. The upper molars of *Gujaratia* are less extended transversely, and labial cusps are more bulbous than in the specimen from Shanghuang. In regard to its general structure and pending additional fossil evidence, this upper molar from Shanghuang is best left as *Diacodexis* sp.

Diacodexidae indet. (Fig. 2c–d)

Referred material The referred materials are IVPP V12763.1, an isolated left lower molar (probably m2; Fig. 2c) and IVPP V12763.2, an isolated left lower molar (probably m2), from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural History, Pittsburgh.

Locality The locality is IVPP locality 93006D (fissure D) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Description These two isolated lower molars (IVPP V12763.1: length, 3.3 mm; width, 2.1 mm. IVPP V12763.2: length, 3.5; width, 2.1 mm) are within the size range of *E. qii*'s m1, but they differ morphologically by several characters including their higher trigonid and the position of the paraconid which is closely appressed to and twinned with the metaconid. In *Elaschitherium*, the paraconid of molar is lower and more labially situated, and the lingual cuspids are generally more bulbous. IVPP V12763.1 is slightly smaller than the Wasatchian *Diacodexis minutus* (Krishtalka and Stucky 1985) and *D. illicis* (Gingerich 1989), which is the smallest North American representative of the genus. The specimens from Shanghuang also differ from these species by the higher position of the paraconid and the narrowness of their talonid. In *Diacodexis*, the basin of the talonid is wider due to the more distolingual position of the entoconid which is usually very close to the hypoconulid; this character is related to

the relative large protocone on the *Diacodexis*' upper molars that occlude in a relatively large basined talonid. IVPP V12763.1 and V12763.2 show a different pattern with a voluminous and acute entoconid situated on the same transverse line as the crescent-shaped hypoconid. Therefore, the talonid basin is much narrower, and the corresponding upper molar is expected to show a less voluminous protocone than that of *Diacodexis*' upper molars.

Discussion The general morphology of these lower molars and height of the trigonid with respect to the talonid are reminiscent of arctocyonid condylarths such as *Chriacus*. However, the lower molars of *Chriacus* are more expanded transversely, the paraconid is both weaker and lower than the metaconid, and the entoconid is more distolingually situated making the talonid wider. Comparisons with lower molars of early-Eocene artiodactyls *T. pecus* (Kondrashov et al. 2004) and *Wutuhyus primiveris* (Tong and Wang 1998, 2006) reveals a clearly distinct dental pattern that suggests no special relation with the Shanghuang specimens. Among North American artiodactyls, two forms show some resemblances with these two lower molars from Shanghuang: *Antiacodon* and *Hexacodus*. The lower molars of *Antiacodon* display twinned paraconid and metaconid (with the paraconid generally larger than the metaconid), but the oblique orientation of the strong cristid obliqua which connects to the metaconid is characteristic of the North American Antiacodontinae and absent in IVPP V12763.1 and IVPP V12763.2. The lower molars of *Hexacodus* are transversely wider, the trigonid is more expanded mesiodistally, and the paraconid is generally smaller and lower than the metaconid. Moreover, the cuspids of *Hexacodus* tend to be more inflated, a character also present in the late Wasatchian species of *Diacodexis* (Krishtalka and Stucky 1985, 1986). The morphological differences noted above with *Elaschitherium* suggest that these two molars may represent a new genus, but the morphological evidence is still too weak and the material is too fragmentary for a formal description. In the course of this study, we came upon the question of whether or not these lower molars should be associated to the unique upper molar tentatively referred to *Diacodexis* sp. (IVPP V12762.1). As mentioned above, the relatively narrow talonid of "Diacodexidae indet" implies that the protocone of the occluding upper molar was smaller than that seen in *Diacodexis*' upper molars (IVPP V12762.1). The specimen referred to cf. *Diacodexis* sp. above displays a smaller protocone, but the proportion of this tooth, especially the transverse length, suggests rather that this upper molar may belong to another taxon. These two lower molars are provisionally referred to diacodexids, pending additional material that will allow definitive taxonomic assignment.

Suborder Suiformes, Jaeckel 1911

Several isolated specimens are tentatively referred to the “suiforms” (in the sense of McKenna and Bell 1997). These specimens are generally larger than the average size of the artiodactyl material of the Shanghuang fissures. We suspect that several new taxa are represented, but these are not formally named here because of the paucity of material currently available.

Indeterminate (1) Suoidea, Gray 1821 (Fig. 2e)

Referred material The referred material is IVPP V12764.1, an isolated left lower molar (m3) from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural history, Pittsburgh.

Locality The locality is IVPP locality 93006B (Fissure B) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Description The tooth is moderately worn, and the labial side of the protoconid is lacking, but the trigonid was certainly slightly wider transversely than the talonid. The molar (length, 22.3 mm; width, 12.1 mm) is brachyodont and bunodont, with five main cuspids and additional cuspules on the lingual margin of the third lobe bearing the hypoconulid. There is no paraconid; the weak and low postprotocristid and postmetacristid connect medially at the rear of the trigonid. The entoconid is the most bulbous cuspid although it is less transversely expanded than the hypoconid; a low V-shaped transverse crest connects the entoconid and hypoconid. Although this structure is not obvious due to the wear, the mesial side of the hypoconid shows a distinct longitudinal groove; the posthypocristid forms a swollen bulge and ends medially. The second and third lobes are separated by a distinct transverse groove which is connected to the longitudinal valley separating the entoconid and hypoconid. The hypoconulid lobe consists of two bulbous cusps separated by an oblique and narrow groove. The tooth is damaged labially, and it is not possible to state whether a cingulid occurred between the protoconid and the hypoconid. The tooth enamel is finely wrinkled in the valleys and at the base of the crown.

Discussion This specimen is assigned to the Suoidea on the basis of its overall bunodony, the cusped hypoconulid, and the system of grooves and bulbous crests that we interpret as an incipient furchenplan (von Hünemann 1968). IVPP V12763.1 differs from the early entelodontid *Eoentelodon* from middle Eocene of China (Chow 1958) in having attenuated transverse crests and longitudinal or oblique grooves and the absence of paraconid. Although much

larger, the Shanghuang specimen resembles bunodont raoellids such as *Khirtharia* from the middle Eocene of India and Pakistan (Thewissen et al. 1987). But beyond the size, *Khirtharia* further differs from the Shanghuang specimen in having a trigonid longitudinally narrower, a more reduced hypoconulid lobe on m3, more developed transverse crests, and absence of accessory grooves on lower molars. Moreover, the Shanghuang specimen clearly differs from the more bunoselenodont Asian helohyids like *Gobiohyus* and *Pakkokuhys* which are known from the late middle Eocene of Mongolia (Coombs and Coombs 1977) and Myanmar (Holroyd and Ciochon 1995), respectively.

IVPP V12763.1 compares most closely with earliest suoids known from the late Eocene of Asia. Although, the system of swollen crests and grooves (furchenplan) remains poorly developed on the Shanghuang specimen, it shares morphologic affinities with the early suoid *Siamochoerus* including the general arrangement of cuspids and crests, the trigonid transversely wider than the talonid, and the duplicated hypoconulid on the m3. Moreover, the hypoconid and entoconid are linked by a swelling of the enamel that originates from the lingual face of the hypoconid and from the buccal face of the entoconid, and which might be interpreted as incipient massive crests. IVPP V12763.1 is close in size and proportion to *Siamochoerus banmarkensis* from Krabi (Ducrocq et al. 1998) and about 20% smaller than *Siamochoerus viriosus* from the Nadu Formation, Guangxi, southern China (Liu 2001).

The early history of suoids (suoids and tayasuids) has remained obscure. Until the recent discoveries of Eocene suoid fossils from south Asia, the geological range of suoids was considered to be early Oligocene to Recent. The oldest suoid fossils now known are from the late Eocene of China (Tong and Zhao 1986; Liu 2001) and Thailand (Ducrocq 1994; Ducrocq et al. 1998). Although the evidence is still sparse and incomplete, it would appear that suoids originated in eastern Asia during the Eocene, subsequently dispersing into the New World (Tayassuidae) and elsewhere in the Old World (Suidae) during the Oligocene (Ducrocq 1994; Ducrocq et al. 1998; Liu 2001).

In Asia, the “palaeochoerids” is a paraphyletic assemblage of basal suoids that appeared as early as the late Eocene (Liu 2003). If our identification is correct, the Shanghuang specimen increases the number of suoid remains in the Paleogene of Southeast Asia and further confirms that this group underwent an important and early differentiation during the middle Eocene. More specimens are required to document this taxon which represents the earliest record of suoids known so far.

Indeterminate (2) Suoidea, Gray 1821 (Fig. 2f–g)

Referred material The referred material is IVPP V12764.2, an isolated right premolar (p4) from the collection of the

IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural History, Pittsburgh.

Locality The locality is IVPP locality 93006D (fissure D) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Description The premolar (length, 8.7 mm; width, 5.4 mm) is robust, with a strong and continuous cingulid surrounding the base of the crown; the paraconid is small and barely emerges from the cingulid; the protoconid is inflated; there are two crests running from the top of the protoconid down to the small posterolingual talonid which is bordered lingually by the strong cingulid; the labial postprotocristid is connected to a small posterolabial cuspid which is heavily worn on IVPP V12764.2.

Discussion This specimen is assigned to the *Suoidea* on the basis of its overall bunodonty but could equally be referred to the early-Eocene genus *Bunophorus* in regard to its size and morphology. However, the p4 of *Bunophorus* is generally more mesiodistally elongated and lacks the continuous cingulid. Additional material is necessary to illuminate the familial identity of this enigmatic p4 from Shanghuang.

Family? Dichobunidae, Turner 1849

Subfamily Lantianinae, Métais et al. 2004

Genus *Elaschitherium*, Métais et al. 2004

Elaschitherium crepaturus sp. nov.

(Fig. 3a–g,p)

Diagnosis Differs from the upper molars of the type species *E. qii* in being significantly larger, in having more salient conule cristae, small accessory cusps emerging from the lingual cingulum, slightly larger styles on upper molars; stronger metaconid on p4, and absence of paraconid on p3.

Holotype The holotype is IVPP V12765.1, an isolated right upper molar (probably M2; Fig. 3c), from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural History, Pittsburgh.

Referred material The referred materials are 6M1 (IVPP V12765.2-7); 6M2 (IVPP V12765.8-13); 12M3 (IVPP V12765.14-25); 9 P4 (IVPP V12765.26-34); 5 P3 (IVPP V12765.35-39); 6m1 (IVPP V12765.40-55); 7m2 (IVPP V12765.56-62); 4m3 (IVPP V12765.63-66); 3 p4 (IVPP V12765.67-69); 5 p3 (IVPP V12765.70-74); 2

DP4 (IVPP V12765.74-75); 2 dp4 (IVPP V12765.76-77); and 2 astragali (IVPP V12765.78-79).

Etymology The species name derives from *crepatura*, fissure in Latin.

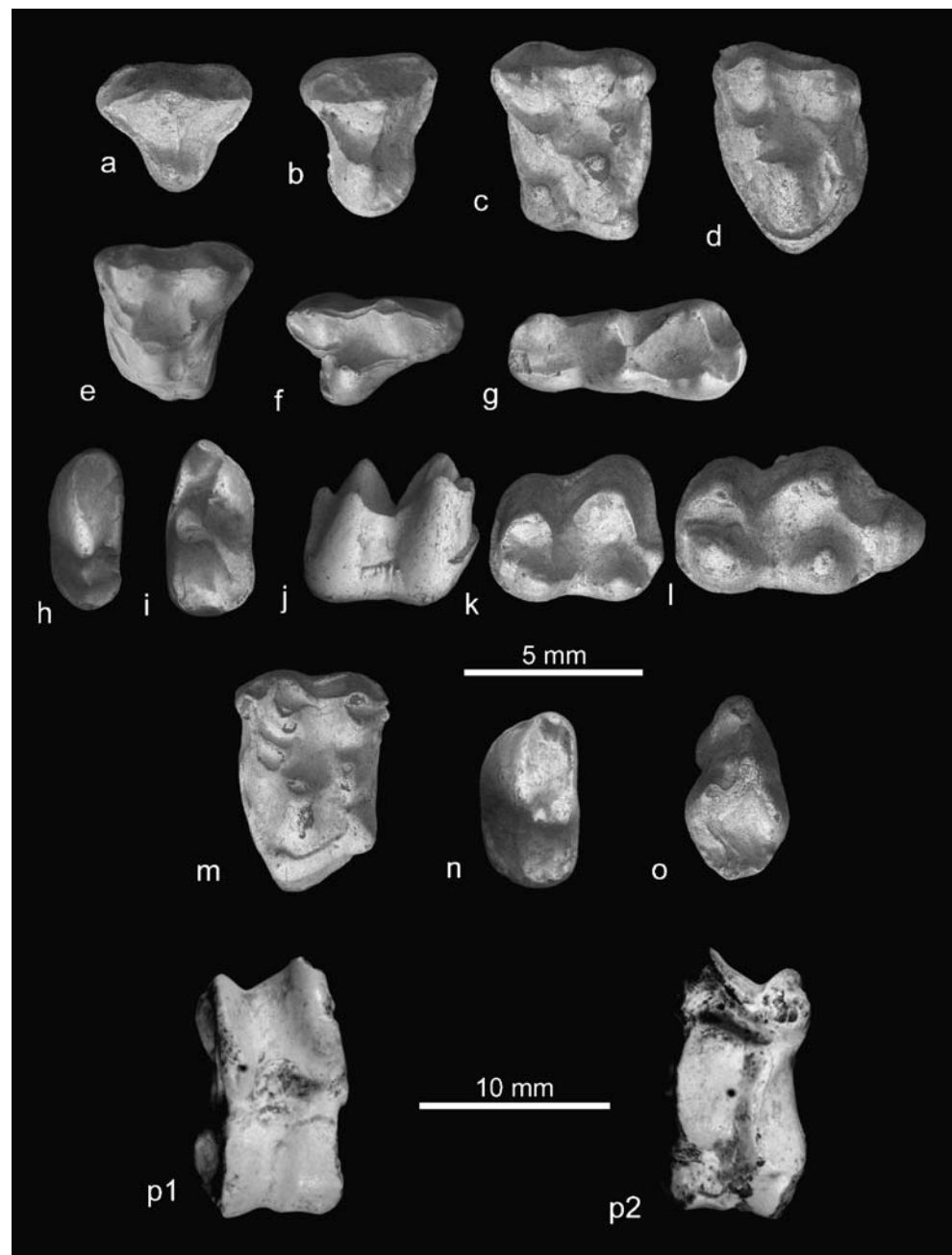
Type locality The type locality is IVPP locality 93006D (fissure D) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Distribution The distribution is Middle Eocene, reported from fissures A, B, D, and E which are probably middle Irdirmanhan (D, E) to early Sharamurunionian (A, B) in age (Dawson and Wang 2001) and geographically restricted to the type locality so far, central coastal China (see “Discussion”).

Description The dental morphology of the type species *E. qii* has been described in detail in Métais et al. (2004), and *E. crepaturus* shows roughly the same morphological traits.

Upper dentition P3 is longer than it is wide; the small conical lingual protocone is linked to the base of the labial paracone by a very weak transverse crest. Cingula are well developed except lingually and near the midline of the labial border of the premolar. The P4 is much broader transversely than long; the conical protocone is connected to a tiny parastyle by a sharp preprotocrista; a weaker oblique crest runs labially from the protocone to the base of the paracone; cingula are well developed except on the mesial margin of the tooth. Like P3, P4 is supported by three roots. The upper molars are rectangular in occlusal outline and wider transversely than long; conules are well developed and subequal in size; the hypocone emerges from the lingual cingulum and is well developed on M1-2, reduced to a spur on M3; unlike *Diacodexis* and as a consequence of the well-developed and cusped hypocone, the protocone is more mesially situated (especially in M1-2); cusps bear weak crests, and the labial cingulum is moderately developed; M1 is smaller than M2-3, and M3 is slightly smaller than M2 (Table 1). The conical paracone and metacone are equal in size on M1-2, but the latter cusp is reduced and more lingually situated on M3; the labial flank of the paracone is more ribbed than that of the metacone; the centrocrista is straight, and the parastyle is barely visible; the preprotocrista extends labially and fuses with the preparaconule crista to form a straight transverse crest which joins the preparaocrista; the postprotocrista joins the metaconule; the postmetaconule crista extends toward the distolabial corner of the molar; the postparaconule crista and the premetaconule crista are better developed than in *E. qii* and extend toward the base of paracone and metacone, respectively; there is no metastyle nor mesostyle; a small

Fig. 3 *E. crepaturus* sp. nov., **a** IVPP V12764.33, left P3, **b** IVPP V12764.43, left P4, **c** IVPP V12764.1 (holotype), an isolated right M2, **d** IVPP V12764.13, left M3, **e** IVPP V12764.33, right DP4, **f** IVPP V12764.41, right DP3, **g** IVPP V12764.60, right dp4, **h** IVPP V12764.37, left p3, **i** IVPP V12764.37, right p4, **j** IVPP V12764.37, right m1 in labial view, **k** IVPP V12764.38, right m2, **l** IVPP V12764.39, right m3. cf. *Elaschitotherium* sp., **m** IVPP V12765.1, left upper molar (M1?). cf. *Elaschitotherium* sp., **n** IVPP V12765.1, left p4. *Dichobunoidea* indet., **o** IVPP V12766.1, right p4. *E. crepaturus* sp. nov., IVPP V12789.1, left astragalus in ventral (**p1**) and dorsal (**p2**) views. All the specimens are in occlusal view (unless otherwise specified above)



and cusate pericone is present on M1-2 farther mesially on the lingual cingulum, at the lingual base of the protocone. The DP4 is built with the same overall morphology as the M1-2, but it is more triangular in occlusal outline; it is shorter transversely and, as a consequence of the reduction of the lingual margin, the paraconal lobe appears more salient. The DP3 consists of two labial cusps located on a strong mesiodistal crest; the lingual lobe bears an acute cusp; the lingual cingulum is well developed on the posterior half of the tooth.

Lower dentition The p3 is triangular in lateral view and displays a very simple structure, consisting of a prominent

protoconid and a distinct small and sharp tubercle that emerges from the longitudinal postprotocristid which connects distally to a tiny talonid heel at the base of the crown; an incipient slightly inflected lingually positioned paraconid occurs at the base of the preprotocristid. The lower p4 is much more robust than p3 (Table 1), and its crests and cusps are better expressed; the protoconid is slightly compressed transversely, and the postprotocristid connects to the posterior spur of the tooth (hypoconid); a conical metaconid occurs on the posterolingual side of the protoconid, but it is lower than the latter cusp; the paraconid is conical and clearly displaced lingually with respect to the preprotocristid; no cingulids occur on p4. The

Table 1 Measurements of *E. crepaturus* sp. nov. from the Shang-huang fissures

Tooth position	Number	Mean	Range
Upper dentition			
P3 L	5	4.8	4.2–5.8
P3 W	5	3.6	3.4–4.0
P4 L	9	4.1	3.7–4.9
P4 W	9	5.1	4.6–6.0
DP4 L	2	4.2	4.1–4.3
DP4 W	2	4.1	4.0–4.3
M1 L	6	4.5	4.2–5.0
M1 W	6	5.7	5.4–6.1
M2 L	6	4.7	4.5–4.8
M2 W	6	6.4	6.2–7.0
M3 L	12	4.1	4.0–4.5
M3 W	12	5.8	5.3–6.1
Lower dentition			
p3 L	5	5.1	4.9–5.5
p3 W	5	2.2	2.0–2.4
p4 L	3	5	4.9–5.1
p4 W	3	2.7	2.6–2.9
dp4 L	2	5.8	5.7–5.9
dp4 W	2	2.7	2.6–2.8
m1 L	6	4.5	4.2–4.8
m1 W	6	3.4	3.0–3.8
m2 L	7	4.9	4.5–5.2
m2 W	7	3.7	3.4–4.1
m3 L	4	5.3	5.1–5.5
m3 W	4	3.1	3.0–3.2

Values are in millimeters

dp4 is trilobed and shows a hexacuspoid pattern as in all terrestrial cetartiodactyls; the mesial lobe is narrower, and it consists of two transversely compressed cuspids bordering a subcircular depression; the distal lobe is the wider transversely of the two and built on the same model as the talonid of permanent molars; the distal cuspid is equivalent to the hypoconulid and is well developed and connected to the crescent-shaped hypoconid through a bent postprotocristid. The m2 is the shortest and transversely widest lower molar (Table 1); the talonid is wider than the trigonid on m1-2, and the latter cusp is slightly higher than the talonid; the trigonid is anteroposteriorly compressed; on m1-2, the paraconid is smaller and lower than the metaconid and closely appressed to the mesiolabial flank of the latter cusp; the paraconid is barely visible on m3; the metaconid is slightly compressed transversely and lies lingual and slightly distally displaced with respect to the crescentic protoconid; the hypoconid is crescent-shaped and labially inflated (especially on m2); the cristid obliqua extends mesiolingually and terminates near the center of the posterior trigonid wall; the posthypoconid is transversely oriented, but it bends posteriorly at its lingual extremity to

join a well-developed hypoconulid which lies on a strong distal cingulid; the entoconid is conical and situated directly lingual to the hypoconid; there is an incipient preentocristid extending mesially on m1-2; there is no labial cingulid, but a distinct cingulid extends along the mesial border of the molars; the m3 hypoconulid is centrally situated and directly connected to the posthypoconid.

Postcranial elements Astragali here referred to *E. crepaturus* are larger (length, 11.7 mm; transverse diameter, 5.3; anteroposterior diameter, 5.9) but show similar proportion and are nearly identical in morphology to those referred to *E. qii*; the tibial trochlea is not moderately deep, and its lateral flank is clearly higher but less sharp-edged than the medial one; the distal trochlea is slightly rotated medially and relatively shallow, and it displays a weak ridge separating the articular surfaces for the cuboid and navicular; the sustentacular facet is flat to slightly convex mediolaterally and is limited medially by a strong oblique ridge; the distal part of the cuboid facet is less extended than that of the navicular facet; the calcaneal facet is small and oval in outline. Métais et al. (2004) found some resemblance between the astragalus of *Elaschitherium* and that of *Messelobunodon* from the early middle Eocene of Germany (MP 11, Franzen 1983). This is mostly based on the shape of the sustentacular facet although this articular facet is less extended laterally in *Elaschitherium*, and the ridge separating the articular surfaces for the cuboid and navicular is less attenuated than in *Messelobunodon*. Franzen (1981, 1983) proposed a running–jumping mode of locomotion for *Messelobunodon*, roughly similar to the extant water chevrotain *Hyemoschus*.

Discussion The proportion of dental and skeletal elements described above clearly indicates the presence of an *Elaschitherium* species distinct from the type species *E. qii*. At present, size distinguishes the new species best from *E. qii*. *E. crepaturus* is approximately 40% larger than the type species, and the few morphological differences include the presence of a cuspidate pericone on m1-2, more marked conular wings, and the slightly larger metaconid in the fourth premolar. Estimation of the body mass from the area of m1 (Legendre 1989) and the size of astragali (Martinez and Sudre 1995) provides values ranging between 1.3 and 1.5 kg for *E. crepaturus*.

cf. *Elaschitherium* sp. (Fig. 3j)

Referred material The referred material is IVPP V12765.1, an isolated left upper molar (probably M1; Fig. 3), from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural History, Pittsburgh.

Locality The locality is IVPP locality 93006A (fissure A) in the Shanghuang limestone Quarry, near Shanghuang Village, in southern Jiangsu Province, Eastern China.

Description The only specimen is an upper molar (length, 3.9 mm; width, 5.1 mm) of uncertain affinities. The specimen is partially abraded and its enamel has been partially dissolved. It differs from the upper molars referred to *E. crepaturus* by its strong cingula and larger parastyle. The labial cingulum is well developed; the conules are weathered and lacks much of their enamel.

Discussion This specimen is possibly referable to *E. crepaturus* in regard to its size and global arrangement of cusps. However, the development of cingula may indicate the presence of an additional species of *Elaschitherium* in the Shanghuang fissures. The specimen is too badly preserved to make a taxonomic decision; only more material can bring a solution.

Dichobunoidea indet. (Fig. 3k)

Referred material The referred material is IVPP V12766.1, an isolated right lower premolar (p4), from the collection of the IVPP, Chinese Academy of Sciences, Beijing. Cast of the specimen is housed at the Carnegie Museum of Natural History, Pittsburgh.

Locality The locality is IVPP locality 93006D (fissure D) in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Description This p4 (length, 5.0 mm; width, 3.1 mm) is moderately worn and shows a pattern very distinct that of the p4 referred to *E. crepaturus*. The talonid is particularly wide transversely and lacks the characteristic postprotocristid that connects the posterior spur of the tooth (hypoconid) in *E. crepaturus*. The conical metaconid occurs on the posterolingual side of the protoconid, but it is smaller than in *E. crepaturus*; the paraconid is larger and not clearly displaced lingually; no cingulids occur on this premolar.

Discussion This specimen falls into the size range of *E. crepaturus* but is slightly wider than the observed range of this species. The shape and greater size of the talonid contrast with the lantianine morphology of the p4 known from Shanghuang. Unfortunately, no other specimen with such morphology has been noticed in the studied material, and we provisionally assign this premolar to an indeterminate dichobunoid, pending additional fossil evidence.

General discussion

Significance of the dichobunoid assemblage from Shanghuang

The three forms here referred to Diacodexidae are very rare in the mammal assemblages recovered in the Shanghuang fissures. *J. shanghuangensis* is based on a single specimen from the fissure A and is unexpectedly not represented among the abundant fossil material of fissure D; the two other forms are restricted to fissure D. Isolated postcranial material could possibly be referred to *J. shanghuangensis*, but specimens are generally fragmentary and our knowledge on this form is presently too incomplete to refer these isolated postcranial remains with certainty. More than 70% of the artiodactyl material identified at Shanghuang belongs to the tiny lantianine dichobunoid *E. qii*, which is based on abundant dental and postcranial material mostly from the fissure D (Métais et al. 2004). Fossil material referable to *E. crepaturus* is less abundant, but the species is represented in all the fissures, including fissures B and C which are otherwise poorly sampled. Other poorly defined bunodont forms represent less than 3% of the isolated skeletal and dental specimens from the Shanghuang fissures. The rest of the artiodactyls material consists of early selenodonts (including protoruminants and related forms) that will be described elsewhere.

The artiodactyl fauna of Shanghuang reveals an unexpected diversity of basal forms with at least three forms showing a molar pattern characteristic of diacodexids. These taxa are still poorly defined, and they are geographically restricted to the Shanghuang fissure deposits. In contrast with the fossil record known in Europe and North America, these typical early-Eocene artiodactyls are associated in Shanghuang with bunoselenodont forms (including early ruminants) that first appeared during the middle Eocene in Europe and North America. Our knowledge of the diversity and stratigraphic range of early–middle-Eocene artiodactyls in Asia is still very primitive, and comparisons are therefore limited. Several basal artiodactyls have been reported from early and middle Eocene of Asia (Kondrashov et al. 2004; Tong and Wang 2006), but their affinities with European and North American forms remain obscure. Diacodexids are represented in the late early Eocene of Pakistan and India by the genus *Gujaratia* (Bajpai et al. 2005) which was long considered as an Asian species of *Diacodexis* (Thewissen et al. 1983). Averianov (1996) reported *Diacodexis* sp. from the ?early-Eocene locality Andarak 2, southwestern Kyrgyzstan. However, the diacodexids from Shanghuang appear morphologically closer to Asian lantianines than to any other group of basal Asian artiodactyls, with the exception of *Jiangsudon* which is larger and certainly more derived with respect to the

development of the parastyle and crests on upper molars. The Shanghuang diacodexoids exhibit a fairly unique dental structure that is reminiscent of the North American representatives of this family although the combination of characters such as the narrowness of lower molars, the height of the trigonid, and the position and size of the entoconid are unique among the Diacodexidae. Moreover, diacodexoids and the early homacodontid *Hexacodus* are distinctive by their characteristic transversely expanded lower molar and more robust upper molars. These characters have also been used to differentiate the North American diacodexoids from the European material (Sudre and Erfurt 1996).

Métais et al. (2004) noted the dental resemblances between primitive European hyperdichobunines and Asian lantianines, although this does not necessarily imply close phylogenetic relationships between the two groups. However, this similar dental morphology certainly influenced the provisional familial assignment of *Elaschitherium* to the Dichobunidae, a family ranging chronologically from the middle Eocene to the early Oligocene in Europe. In regard to the dental differences between European dichobunoids and Asian lantianines, the latter group is likely to acquire familial status when postcranial characters of lantianines become better documented. *Elaschitherium* probably documents in Asia the preselenodont grade of dichobunoids. The high degree of similarity among North American homacodonts and European dichobunoids has been noted by several authors (e.g., Stucky 1998) suggesting remarkable degrees of convergent evolution and homoplasy or several episodes of immigration between Europe and North America. As initially suggested by Gazin (1955) and subsequently developed by Sudre (1978), the acquisition of selenodont molars may have evolved several times independently in different geographic regions during the middle Eocene. The present fossil record of Asia is still insufficient to document the transition from the basal bunodont tribosphenic molar pattern to the bunoselenodont grade represented at Shanghuang by *Limeryx* (Métais et al. 2005).

The age of Shanghuang artiodactyls fauna and the reliability of intercontinental biochronologic correlations

The stratigraphic range of diacodexoids in Europe is from MP7 to MP11 (Sudre and Erfurt 1996), and their last occurrence in North America does not exceed the base of the Bridgerian NALMA (Stucky 1998; Robinson et al. 2004). The occurrence of diacodexoids in Shanghuang indicates that the range of the family extends up to the late middle Eocene in eastern Asia. The age of Shanghuang fissure fillings is based on several mammal taxa that are either reported from the Irдин Manha Formation of

Mongolia or congeneric with typical Uintan taxa known in North America. The cricetid rodents from Shanghuang (Wang and Dawson 1994) are close to but more primitive than those reported from the lower Heti Formation, dated to late middle Eocene on the basis of mammal assemblage. Beard et al. (1994) identified the omomyid primate *Macrotarsius macrorhysis* at Shanghuang, which is known from the early Uintan in North America. Further evidence were provided by the occurrence at Shanghuang of the brontothere *Microtitan* sp., cf. *Microtitan mongoliensis*, which is based on material from the Irдин Manha Formation, Inner Mongolia, China (Qi and Beard 1996). Because most of the artiodactyls from Shanghuang represent new taxa, they bring very little information for further constraining the age of the Shanghuang fissures. In North America, early Uintan faunas lack diacodexoids and are dominated by homacodontids which are also represented in Shanghuang (Métais et al. 2005). It is worth noting that none of the artiodactyl taxa reported from Shanghuang have been reported so far from the relatively well-known stratified deposits of Mongolia and Inner Mongolia (China) on which the Asian Eocene land mammal ages have been based (Romer 1966; Li and Ting 1983; Russell and Zhai 1987; Meng and McKenna 1998). However, correlation between Eocene mammal faunas from Inner Mongolia and the Shanghuang assemblages are hampered by several problems. First, the lack of geochronological control for the Irдин Manha Formation and the directly underlying Arshanto Formation, which has produced the mammal assemblage that defines the Arshantan Asian Land Mammal Age, makes the age of these formations uncertain. Moreover, artiodactyls are virtually unknown in the Arshanto Formation (Qi 1987), and the stratigraphic range of most mammal taxa characterizing the Irдинmanhan ALMA remains uncertain in Asia (Russell and Zhai 1987). As a result of the absence of a geochronological framework, the Arshantan and Irдинmanhan ALMAs are calibrated to the well-defined North American LMAs, with the assumption that the occurrence of a taxon in North America and Asia (at the specific or generic level) necessarily implies similar age. Asia has long been thought as an important center of evolution for placental mammals (e.g., Beard 1998), with several subsequent episodes of immigration to Europe and North America. Therefore, the occurrence of stem taxa in Asia makes intercontinental correlations at best tenuous in regard to the absence of reliable isotopic calibration for the Eocene terrestrial deposits of Inner Mongolia that have produced abundant fossil mammals.

While there is certainly a bias towards the preservation of large mammals in the Shanghuang fissures, the absence of small- and medium-sized artiodactyls in the Irдин Manha Formation (with the exception of *Archaeomeryx*) may also reflect taphonomic and/or collecting biases. However, the

absence of record of small dichobunoids in the well-sampled Irdin Manha deposits may be related to distinct environment as well. In fact, the combined effect of differences in taphonomy, sampling, and geography make it very difficult to attempt proper biochronologic correlation between coastal China and Inner Mongolia. It is frequently argued that a fauna collected in a karst infill generally gives a faunal spectrum different from that obtained in a basin locality. This is certainly true for the Shanghuang mammal assemblages since nocturnal birds of prey are generally the source of bone and tooth accumulations, thus introducing a bias towards the abundance of small mammals. This bias at Shanghuang also contributes to distort the precision and accuracy of correlations with stratified sequences of Inner Mongolia. Additional sampling of fossil mammals associated with a rigorous stratigraphic framework in the region is needed to substantiate preliminary age assessment for most Chinese mammal localities, including that of Shanghuang fissure fillings.

The “provincialism effect” in China during the early–middle Eocene

The problem in the reliability of biochronologic correlations in China during the Eocene is accentuated by a significant provincialism reflected by the various mammal assemblages along a north–south transect (Tong et al. 1996; Tsubamoto et al. 2004). This latitudinal zonation is also exhibited by independent sources of data such as paleobotanical and pollen evidences. Leopold et al. (1992) identified an extensive semiarid belt across China extending from the southeast (present) coast northwestward to the Xinjiang region during the Paleocene through mid-Eocene, and Sun and Wang (2005) identified three latitudinal vegetation zones during the Eocene. These data indicate that mixed evergreen and deciduous forests associated with warm and humid climates occurred in northern China during the middle Eocene. In contrast, the Shanghuang region was part of the middle zone extending from the Xinjiang Province to coastal China which was warm and dry with the occurrence of arid to semiarid vegetation. However, Sun and Wang (2005) suggested that a clear longitudinal climatic differentiation also indicates that coastal China was probably more humid and tropical than the eastern part of this middle vegetational zone.

Dawson et al. (2003) used rodent assemblages to suggest the existence of a biogeographic province including coastal China and the Yuanqu and Lushi Basin of inland China during the late Paleogene. This coastal province may have consisted of forested tropical habitats that may have contrasted with habitat of Inner Mongolia during the middle–late Eocene. Although faunal data supporting this provincialism are still thin, the persistence of small tragulid-

like forms such as diacodexoids in the middle Eocene of Shanghuang is congruent with very stable ecological conditions in coastal China throughout the early and middle Eocene. The late middle Eocene (Uintan NALMA in North America) records the climatic deterioration in the higher and middle latitudes that led to the loss of tropical habitats that characterized the Wasatchian and Bridgerian times (Zachos et al. 2003) and the subsequent radiation of selenodont artiodactyls. This important climatic event seems to have been global (Prothero 1994) and may have accentuated the climatic zonation in China.

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