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A NEW BUNOSELENODONT ARTIODACTYL FROM THE MIDDLE EOCENE OF CHINA AND THE EARLY RECORD OF SELENODONT ARTIODACTYLS IN ASIA

GRÉGOIRE MÉTAIS¹, TAO QI², JIANWEI GUO², and K. CHRISTOPHER BEARD¹, ¹Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh PA 15213, U.S.A., metaisg@carnegiemnh.org; ²Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P. O. Box 643, Beijing 100044, China

The vast continent of Asia is thought to have played a major role in the origin and early differentiation of several extant groups of ungulate mammals, including artiodactyls (e.g. Beard, 1998). According to Gentry and Hooker (1988), Selenodontia are a major division within Artiodactyla encompassing many extinct forms that are more closely related to extant ruminants and camels than to pigs and hippos (Bunodontia). Living ruminants are characterized by their highly derived digestive system, which is not preserved in fossils. Bony features that are closely correlated with this critical physiological innovation have yet to be identified. The incisiform lower canine and the loss of upper incisors are dental features that help to define extant ruminants, but these characters are rarely preserved in the fossil record. Moreover, *Archaeomeryx* from the middle Eocene of Mongolia, which is classically regarded as the earliest known ruminant, still retains its upper incisors (Matthew and Granger, 1925). In terms of osteology, the main apomorphic feature uniting all Ruminantia is the fusion of two tarsal bones (cuboid and navicular), although this feature may have evolved at least twice during in the evolutionary history of selenodont artiodactyls (Sudre and Blondel, 1995). Accordingly, it can be problematic to distinguish a “true ruminant” from the multitude of extinct proto-selenodont forms that radiated during the middle Eocene in the Northern Hemisphere. Moreover, the poor record of early Selenodontia in Asia greatly hampers our understanding of their origin and early evolution. Except for *Archaeomeryx*, which is known from several fairly complete skeletons from Mongolia (Matthew and Granger, 1925; Colbert, 1941; Webb and Taylor, 1980; Vislobokova, 1998, 2001), the early selenodonts of Asia are limited to fragmentary jaws and isolated teeth from the middle and late Eocene (Guo et al., 2000; Métais et al., 2001; Tsubamoto et al., 2003).

Here, we describe a new genus and species that is characterized by a combination of primitive ‘dichobunoid’ dental features together with derived dental characters that are reminiscent of early ruminants. The fossils were collected by screen-washing the fossiliferous clays from the middle Eocene fissure-filling complex near the village of Shanghuang in southern Jiangsu Province, People’s Republic of China (Fig. 1). Five distinct fissure fillings (designated A through E) have been sampled from the Triassic Shangqinglong limestone at Shanghuang. Artiodactyl remains have been retrieved from all the fissures, but the taxon described here is known so far only from fissure-filling D, which has also yielded a lantianine dichobunid (Métais et al., 2004), brontotheriid perissodactyls (Qi and Beard, 1996, 1998), primates (Beard et al., 1994; MacPhee et al., 1995), rodents (Wang and Dawson, 1994; Dawson and Wang, 2001), and other mammals that are currently under study. According to Dawson & Wang (2001), fissure D is middle Eocene in age and probably correlates with the Irudinmanhan Asian Land Mammal Age (see Russell and Zhai, 1987).

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Suborder SELENODONTIA Scopoli, 1777
Family HOMACODONTIDAE Marsh, 1849
LIMERYX CHIMAERA, gen. et sp. nov.
(Fig. 2)

Diagnosis—Medium-sized bunoselenodont artiodactyl slightly smaller than extant African tragulid *Hyemoschus*. Upper and lower molars with

weakly crescentic cusps and cuspids. Upper molars with buccal cingulum thick, parastyle and mesostyle well developed, buccally deflected centrocrista, paraconule and metaconule distinct, metaconule subcrescentic and not fully lingual in position, and protocone relatively central in position. Lower molars retaining straight hypolophid and minute paraconid. Differing from *Asiohomacodon* in having less crescentic and more inflated cusps (especially on lower molars), less developed cingula and lack of wrinkled enamel on upper molars, shorter posthypocristid and presence of both distinct hypolophid and *Zhailimeryx* fold on lower molars (Fig. 2). Differing from all North American ‘homacodonts’ in having *Zhailimeryx* fold and short posthypocristid (Fig. 2) not connected to postcingulid on lower molars, and in labially deflected centrocrista, distinct mesostyle, and stronger metaconule and parastyle on upper molars. Further differing from *Homacodon* and *Microsus* in more nearly selenodont structure of upper molars, extreme reduction of lower molar paraconids, and greater mesiodistal length of lower molar trigonids. Further differing from *Mesomeryx*, *Pentacemylus* and *Bunomeryx* in lacking lingual cingulum, showing stronger development of parastyle and mesostyle on upper molars, and weaker ribbing on buccal side of both paracone and metacone. Differing from European *Hyperdichobune* and *Mouillacitherium* in lacking hypocone, showing less development of styles and cingula on upper molars, and in having relatively longer lower molars with *Zhailimeryx* fold and straight transverse hypolophid joining entoconid to hypoconid.

Holotype—IVPP V12760.1, an isolated upper molar (probably M2; Fig. 2A-B). Collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

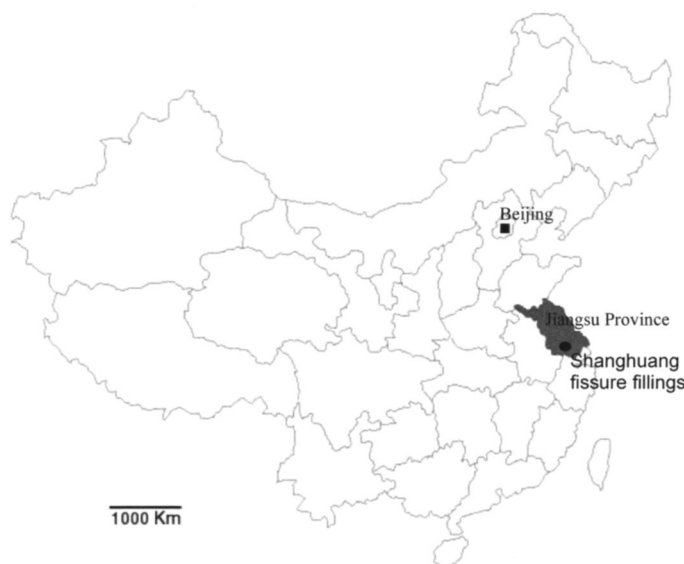


FIGURE 1. Location map of the Shanghuang fissure-fillings in Jiangsu Province (Eastern China).

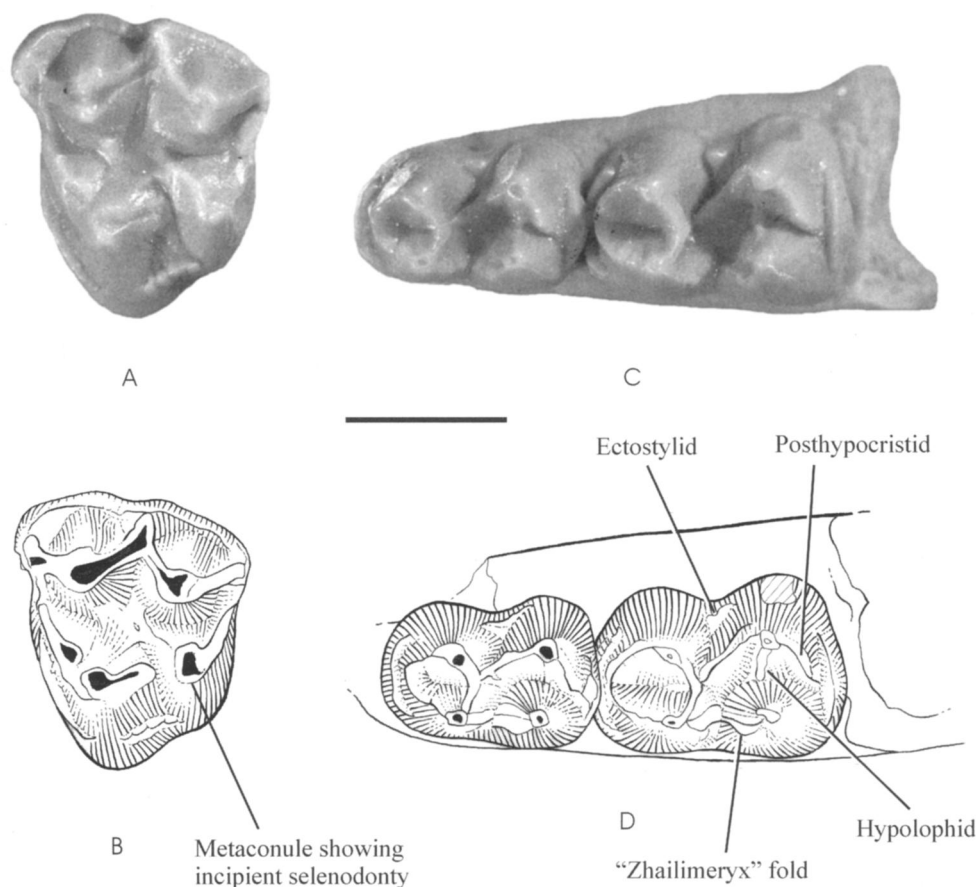


FIGURE 2. *Limeryx chimaera* gen. and sp. nov. **A**, IVPP 34567.1 (holotype), left M2 in occlusal view. **B**, interpretative drawing of **A**. **C**, IVPP 34567.2 (paratype), fragmentary right lower jaw preserving m1-2 in occlusal view. **D**, interpretative drawing of **C**. Scale bars equals 5 mm.

Hypodigm—The holotype and a fragmentary dentary preserving right m1-2 (IVPP V12760.2, Fig. 2C, D).

Etymology—The generic name is for our friend and mentor, Professor Li Chuankuei, who facilitated fieldwork at the Shanghuang fissure-fillings. The specific name alludes to the distinctive combination of primitive and derived features in the dentition of this animal.

Type locality—Fissure D in Shanghuang Quarry (within the Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, China (Fig. 1).

Distribution—Middle Eocene, Irudinmanhan Land Mammal Age (Wang and Dawson, 1994), southern Jiangsu Province, China, and possibly extending to the Sharamuronian of Shanxi Province, central China (see discussion).

Description—The holotype upper molar (length = 7.5 mm; width = 8.3 mm) is trapezoidal in occlusal outline (Fig. 2A, B). The contact facets that occur along the base of both the mesial and distal sides of the crown suggest it is either M1 or M2. Because its size corresponds well with the referred m2, we tentatively regard the holotype as a M2. The crown supports four main cusps and a tiny paraconule. The latter cuspule is situated close to the protocone, being partly incorporated within the preprotocrista, which connects the protocone with the rounded parastyle. There is no trace of a hypocone. The centrocrista is weak and oriented mesiodistally. The metaconule is incipiently crescentic, and the trigon basin is expansive. The buccal side of the paracone supports a distinctly convex rib. A similar, but less convex rib occurs on the buccal side of the metacone. The centrocrista is strongly deflected buccally, where it joins a distinct mesostyle that emerges from the thick and continuous buccal cingulum. A weak cingulum lines the mesial side of the protocone, and a weak cingular shelf occupies space that separates the protocone and metaconule lingually.

The lower molars are bunoselenodont and low-crowned, and m2 (length = 7.5 mm; width = 5.4 mm) is larger than m1 (length = 6.3 mm; width = 4.3 mm). On each lower molar, the trigonid is closed lingually

by a sharp premetacristid that is mesially continuous with the curved paracristid (Fig. 2C, D). No distinct paraconid can be observed on the present material, but a small bulge at the junction of the paracristid and premetacristid on m1 can be interpreted as the remnant of a paraconid. The entoconid is conical, and its mesial side displays a distinct longitudinal groove (or *Zhailimeryx* fold). The hypoconid is crescentic, and the posthypoconistid is abbreviated, thereby failing to reach the postcingulid. A weak transverse hypolophid extends from the hypoconid toward the entoconid. Mesial and distal cingulids are present, but there is no distinct buccal cingulid. Rather, a weak ectostylid (Fig. 2D) emerges from the cingular shelf between the protoconid and hypoconid.

DISCUSSION

Limeryx chimaera displays a combination of primitive (weakly crescentic cusps and cuspid, thick buccal cingulum, protocone relatively central in position on upper molars, retention of a minute paraconid on lower molars) and derived (well-developed parastyle and mesostyle, buccally deflected centrocrista on upper molars, and presence of both a hypolophid and a *Zhailimeryx* fold on lower molars) dental features that are unique within Selenodontia. This distinctive combination of characters clearly distinguishes *Limeryx chimaera* from the Eocene bunoselenodont artiodactyls that are known from North America and Europe. 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.

The earliest representative of the hyperdichobunine dichobunids in Europe, *Hyperdichobune* cf. *H. hammeli* from La Defense (MP 13; Sudre and Ginsburg, 1993) and Saint-Maximin (MP 13; Sudre, 1997), represents the earliest proto-selenodont form from which the endemic European selenodonts (amphimerycids and xiphodontids) of the late Eocene may

have evolved (Sudre, 1978). *Hyperdichobune* and *Mouillacitherium* are much smaller than *Limeryx*, and their upper molar cusps are more bunodont, while their lower molars are mesiodistally narrower. These comparisons suggest that the evolution of a selenodont dental pattern occurred in a different way in Europe, where the first amphimericyid (*Pseudamphimericyx*) displays upper molars with a centrally located protocone and strongly crescentic conules. Similarly, xiphodontids differ from North American and Asian selenodonts in dentition, suggesting an endemic origin for this European clade as well (Sudre, 1978). It is worth noting that these proto-selenodont forms first appeared slightly later in Europe than in North America, where the first evidence of a trend towards selenodonty occurred as early as the early Uintan, which correlates with the famous Geiseltal localities in Europe. The Geiseltal artiodactyls include choeropotamids and eurodixine dichobunids, each showing a fully bunodont dentition (Erfurt, 1993; Erfurt and Sudre, 1995, 1996).

Extensive comparisons with North American “homacodonts” show that *Limeryx* possesses a mosaic of dental characters that set it apart from the Bridgerian and Uintan representatives of early Selenodontia. Intriguingly, the upper molar morphology of *Limeryx* is derived with respect to that of its known lower dentition. The lower molars of *Limeryx* are strikingly similar to those of *Homacodon*, while upper molars of the latter are much closer to those of *Diacodexis* in having a more primitive, tribosphenic, bunodont pattern and in the retention of a well developed hypocone. In contrast, the upper molars of *Limeryx* display a W-shaped ectoloph, cingula, and a reduced paraconule, all of which are reminiscent of upper molars of *Mesomeryx* or those of a new primitive ruminant from the Pondaung Formation of Myanmar (Métais, in press). Although *Limeryx* is still too poorly documented to allow for any detailed discussion of its phylogenetic relationships with other early Selenodontia, it appears to share many dental features with the putative Asian homacodont *Asiohomacodon* from the late middle Eocene Pondaung Formation (Tsubamoto et al., 2003). However, the latter genus is definitely more advanced toward the selenodont dental pattern. This is especially true with respect to the lower molar characters of *Asiohomacodon*, which show fully crescentic labial cuspids and less bulky but more transversely compressed lingual cuspids. Moreover, the posthypocristid is invariably linked to the lingual part of the postcingulid, and the hypolophid is lacking. Interestingly, the M1–2 of *Asiohomacodon* are more square in occlusal outline due to the more prominent development of the metaconule, which is otherwise more crescentic in shape.

The most remarkable dental feature exhibited by *Limeryx* is the presence of the *Zhailimeryx* fold, which is otherwise found in the earliest known lophimericyid *Zhailimeryx* (Guo et al., 2000). This groove on the mesial side of the entoconid is an important character suggesting that *Limeryx* may be closely related to traguloid ruminants. This possibility is corroborated by some upper molar features in *Limeryx*, including: the strongly developed preprotocrista and premetacrista, giving these molars an incipient lopho-selenodont appearance; the prominent and rounded parastyle and the weakly ribbed buccal side of the metacone, which are clearly reminiscent of *Zhailimeryx* upper molars. Although the possibility of a close relationship between *Limeryx* and *Zhailimeryx* must be tested with additional morphological data, it would be consistent with an Asian origin of traguloids as suggested by Métais et al. (2001). This, in turn, would conflict with any derivation of ruminants from North American homacodonts, as has been suggested by some authors (e.g., Stucky, 1998).

Finally, a unique specimen from Locality 7 in the Rencun Member of the Heti Formation in the Yuanqu Basin (Henan Province, China), formerly referred to *?Dichobune* sp. by Zdansky (1930), can be assigned to *Limeryx* by the similarities in lower molars. The Yuanqu Basin specimen, a dentary bearing the crowns of p4 and m2, differs from that of *Limeryx* in that m2 of the former has a shelf-like distal cingulid bearing a distinct hypoconulid and in lacking a definitive *Zhailimeryx* fold. However, in light of their shared dental features, we suspect that this specimen may document a second species of *Limeryx*. The Yuanqu Basin specimen clearly differs from that of the European genus *Dichobune* in that p4 in the Yuanqu Basin specimen exhibits a strong and pinched paraconid and a well-developed metaconid that is linked to the protoconid by a strong transverse crest. The metacristid extends posteriorly before turning lingually to form a subrectangular talonid basin. This unique p4 morphology clearly distinguishes the Yuanqu Basin form from all North American homacodonts and pencontemporaneous European bunoselenodont artiodactyls. If our tentative generic allocation for this specimen proves

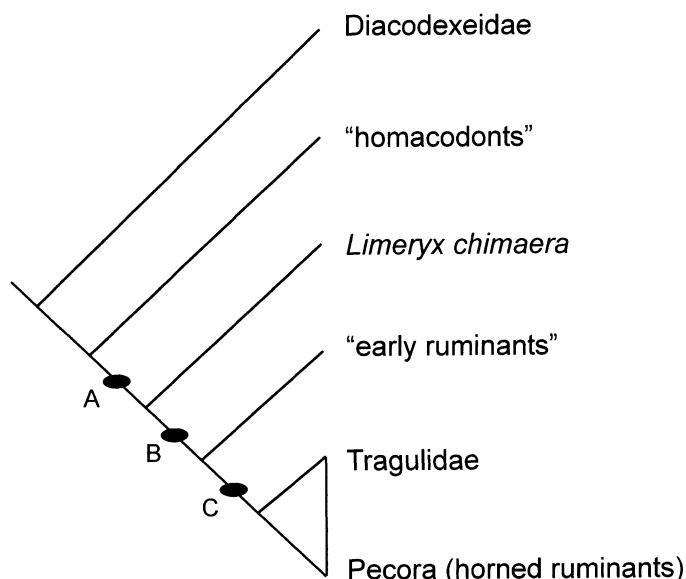


FIGURE 3. Simplified cladogram illustrating the putative phylogenetic position of *Limeryx chimaera* within Selenodontia (as defined by Gentry and Hooker, 1988). The term “early ruminants” designates a heterogeneous assemblage of extinct hornless traguline and pre-pecoran ruminants known in the Eocene and Oligocene of the northern hemisphere landmasses. “Homacodonts” include small bunoselenodont artiodactyls from the Eocene of Asia and North America as defined by Stucky (1998). Some important autapomorphic features for each clade are indicated. **Abbreviations:** **A**, selenodonty; **B**, loss of paraconule on upper molars; **C**, incisiform lower canine, loss of upper incisors, fused cuboid and navicular.

to be correct, it would extend the stratigraphic range of *Limeryx* to the Sharamuruni (Tong et al., 1995; Huang et al., 2001).

Although its affinities are to be tested by additional data, *Limeryx* improves the known record of early Selenodontia. Additional material of this animal—especially postcranial elements that would establish whether or not the cuboid and navicular were fused—will be needed to provide a more definitive assessment of its phylogenetic position (Fig. 3). The mosaic of “dichobunoid” and ruminant features found in *Limeryx* may ultimately prove to be of considerable phylogenetic interest, because it could well approximate the ancestral dental morphotype for all Ruminantia.

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