New records of archaic ungulates from the Lower Eocene of Sanshui Basin, Guangdong, China

4 AUTHORS, INCLUDING:

Fangyuan Mao
Chinese Academy of Sciences

8 PUBLICATIONS   6 CITATIONS

SEE PROFILE

Qian Li
Chinese Academy of Sciences

12 PUBLICATIONS   82 CITATIONS

SEE PROFILE

Xun Jin
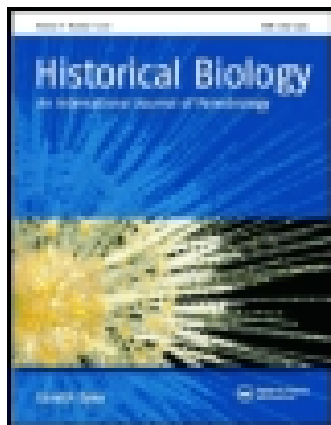Chinese Academy of Sciences

10 PUBLICATIONS   69 CITATIONS

SEE PROFILE

New records of archaic ungulates from the Lower Eocene of Sanshui Basin, Guangdong, China

Fang-Yuan Mao[a], Yuan-Qing Wang[a], Qian Li[a] & Xun Jin[a]

[a] Key Laboratory of Vertebrate Evolution and Human Origin, Institute of Vertebrate
Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
Published online: 24 Apr 2015.

Click for updates

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis
Taylor & Francis Group

New records of archaic ungulates from the Lower Eocene of Sanshui Basin, Guangdong, China

Fang-Yuan Mao*, Yuan-Qing Wang, Qian Li and Xun Jin

Key Laboratory of Vertebrate Evolution and Human Origin, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

Phenacolophidae is a group of little known archaic ungulates from the Late Paleocene to Middle Eocene of Asia. Its phylogenetic relationships with other altungulates have remained uncertain, partly because most phenacolophids are represented by poorly preserved material. Here we report a new phenacolophid, *Sanshuilophus zhaoi* gen. et sp. nov., from the Lower Eocene Huayong Formation of the Sanshui Basin, Guangdong, China. Although still fragmentary, the new specimens show that the new taxon is characterised by relatively large body size (except for *Zaisanolophus*), sub-molariform premolars, relatively higher bilophodont molars that lack the mesostyle, and tooth enamel microstructure with true prisms and typical Hunter-Schreger bands (HSB). With the new specimens and a review of the published phenacolophid material, we are able to provide an alternative identification for the tooth loci for the type specimen of *Phenacolophus* and further present an emended diagnosis for Phenacolophidae. The tooth morphology and enamel microstructure provide new evidence to support the notion that phenacolophids differ from species of Embrithopoda in having low-crown teeth, considerably slanting lophids, distinct paralophids and lacking the arsinoitheriid radial enamel. Phenacolophidae should not be included in Tethytheria but probably represent a stem group for altungulates, if not for all archaic ungulates.

Keywords: Mammalia; Altungulata; Phenacolophidae; *Sanshuilophus*; Guangdong; Sanshui Basin

Introduction

Phenacolophids were a group of archaic ungulates with bilophodont molars and were known from the Late Paleocene to Middle Eocene of Asia. It is an important group of archaic ungulates because its members were interpreted as primitive embrithopods, and for the reason that phenacolophids were included in Embrithopoda under Tethytheria and Paenungulata in some early studies (McKenna and Manning 1977; Wells and Gingerich 1983; Ray et al. 1994). More recent studies considered phenacolophids to be the stem taxa of altungulates or tethytheres, which contain fossil and extant species of African clades of mammals and have close affinity with Perissodactyla (Gheerbrant, Domning, et al. 2005; Rose 2006; Gheerbrant 2009; Sanders et al. 2010, 2014; Sen 2013; Holbrook 2014; Rose et al. 2014). Although this relationship has not been convincingly demonstrated, it suggests the possibility of an Asiatic origin of Altungulata. During the last two decades phenacolophids have played a critical role in various phylogenetic analyses that involved Afrotheria and Perissodactyla using both morphological and molecular data as well as fossil and extant taxa (Fischer and Tassy 1993; Gheerbrant, Domning, et al. 2005; Tabuce, Marivaux, et al. 2007; Gheerbrant 2009; Holbrook 2014; Rose et al. 2014). The phylogenetic placement of phenacolophids bears importantly on interpretation of the early evolution and biogeography of

altungulates, particularly tethytheres (Sanders et al. 2010; Sen 2013).

The conventional Phenacolophidae was most likely paraphyletic (Gheerbrant, Domning, et al. 2005), but all taxa previously referred to phenacolophids are so poorly known that their precise taxonomic and phylogenetic positions remain open. The type genus *Phenacolophus*, for instance, was assigned either to Condylarthra (Matthew and Granger 1925), the family Arsinoitheriidae in the order Embrithopoda (McKenna and Manning 1977), or even Pantodonta (Flerow 1957; Chow and Wang 1979; Zhang 1979; Gabunia 1998). Other genera referred to this group included *Yuelophus* Zhang 1978, *Minchenella* (= *Conolophus* Zhang 1978) Zhang 1980, *Ganolophus* Zhang 1979, *Tienshanilophus* Tong 1979, *Radinskya* McKenna et al. 1989 and *Zaisanolophus* Gabunia 1998. *Minchenella* was originally referred to the family Phenacolophidae (Zhang 1978) but was later treated as a possible ancestor of Anthracobunidae, Desmostylia and Proboscidea (Wells and Gingerich 1983; Domning et al. 1986; Gheerbrant, Domning, et al. 2005; Gheerbrant, Sudre, et al. 2005) that may occupy a position as a basal tethythere close to the origin of Proboscidea (Ray et al. 1994; Gheerbrant, Domning, et al. 2005). Gheerbrant, Domning, et al. (2005, 94) concluded that: '*Minchenella* would be indeed better placed closer to anthracobunids than to "Phenacolophidae"' and assigned

it as a family with a question mark under Altungulata (=Pantomesaxonia).

Radinskya was originally assigned to 'Family Phenacolophidae, incertae sedis' (McKenna et al. 1989). This genus was later identified as the most primitive member of Altungulata (McKenna and Bell 1997; Gheerbrant, Domning, et al. 2005; Gheerbrant, Sudre, et al. 2005) and more closely related to perissodactyls (McKenna et al. 1989; Fischer and Tassy 1993; Holbrook 2005, 2014). Gheerbrant, Domning, et al. (2005, Table 7.1) considered it as the most basal member of Altungulata and assigned it to an unnamed family of its own. Furthermore, a more recent phylogenetic analysis including *Radinskya* did not support its inclusion in Phenacolophidae (Holbrook 2014). Based on various studies on *Radinskya* (Wells and Gingerich 1983; Domning et al. 1986; Gheerbrant 2009; Holbrook 2014) and *Minchenella* (Wells and Gingerich 1983; Domning et al. 1986; Gheerbrant, Domning, et al. 2005; Gheerbrant, Sudre, et al. 2005), with which we agree based on our own observations and comparisons of the type specimens of the two taxon, we exclude them from Phenacolophidae and will not consider them further in the study.

The new phenacolophid, *Sanshuilophus zhaoi* gen. and sp. nov., is based on material collected from the Early Eocene Huayong Formation in the Sanshui Basin near the industrial estate of the Shishan Town, Nanhai District, Foshan City, Guangdong Province, China (Zhang et al. 2008). Vertebrate fossils from other localities of the basin include Paleocene Bemalambdidae (*Hypsilolambda*) from the Buxin Group exposed at the northeastern margin of the basin (Zhang 1981; Wang and Zhang 1997) and the Early Eocene tapiromorph, *Meridiolophus expansus* (Bai et al. 2014) that was discovered about 3 km north of the new locality. Other vertebrate fossils, including fish (Wang et al. 1981) and a ciconiiform bird (Wang et al. 2012), were reported from localities of the Eocene Huayong Formation.

The new species reported here fills a temporal gap between the Late Paleocene forms and the Middle Eocene *Zaisanolophus* and demonstrates again that phenacolophids were widely distributed in central and southeastern Asia during the Paleogene. Although still fragmentary, the new specimens provide some dental morphologies, particularly the unambiguous morphology of the upper premolars, molars, incisors and enamel microstructures, which were previously poorly known for the group. In reporting the new species of phenacolophids in the study, our discussion will focus on the description of the new specimens and comparisons with other species that are bracketed in Phenacolophidae, including *Phenacolophus*, *Yuelophus*, *Ganolophus*, *Tienshanilophus* and *Zaisanolophus*. Given the limited information known from all these species and some unconfirmed characteristics of *Phenacolophus*, as we will discuss below, we find it premature to conduct a meaningful phylogenetic analysis of phenacolophids.

Nonetheless, we provided a tentative emended diagnosis for Phenacolophidae based purely on morphological comparison rather than a phylogenetic relationship. We hope that the addition of the new species and the new information of dental morphology will help to deepen our understanding of this archaic group of ungulates.

Institutional abbreviations

AMNH, American Museum of Natural History, Division of Paleontology, New York; AN PIN, Academy of Sciences of the USSR, Paleontological Institute, Moscow; IPB, Institute of Paleobiology, Academy of Sciences of Georgia, Georgia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

Systematic Paleontology

Altungulata Prothero and Schoch 1989

Family Phenacolophidae Zhang 1978

Type genus: *Phenacolophus* Matthew and Granger 1925 (= *Procoryphodon* Flerow 1957), Gashato Formation, Omono Gobi, south-central Mongolian People's Republic (Matthew and Granger 1925; Flerow 1957; McKenna and Manning 1977).

Included genera: *Tienshanilophus* Tong 1979, Taizicun Formation, Subashi locality, Lianmuqin locality and Shengjinkou locality, Turpan Basin, Xinjiang Province (Tong 1979); *Ganolophus* Zhang 1979, Datangyu Member, Nongshan Formation, Luofozhai Group, Nanxiong Basin, Guangdong Province (Zhang 1979); *Yuelophus* Zhang 1978, Lannikeng Member, Chijiang Formation, Lannikeng locality, Dayu, Jiangxi Province (Zhang 1978); *Zaisanolophus* Gabunia 1998, Obaila Formation, Zaisan Depression, Kazakhstan (Gabunia 1998); *Sanshuilophus* gen. nov (This paper).

Distributions: Late Paleocene to Middle Eocene of Asia.

Emended diagnosis: Differs from embrithopods (Gabunia 1998) in that lower molars possess a less reduced paralophid, considerably slanting lophids and low crowns. Differs from tethytheres (Gheerbrant, Domning, et al. 2005; Gheerbrant 2009) in lacking the postentoconulid and metacristid in lower molars, lacking the postentoconule in the upper molars, and possessing the postprotocrista in P3-4. Differs from Hyracoidea (Gheerbrant, Domning, et al. 2005) in lacking tusklike incisor and having low crowned cheek teeth that are bilophodont but not lopho-selenodont. Differs from *Radinskya* (McKenna et al. 1989; Hooker and Dashzeveg 2004) in that the metaloph does not connect the hypocone and the metaconule; instead, the metaloph reaches the ectoloph on upper molars. Differs from phenacodontids (McKenna et al. 1989; Gheerbrant 2009) in having lower degree of (more primitive) bilophodonty and less reduced M3. Differs from Perissodactyla in

having a small hypoconulid that merges lingually with a steeply ascending and wide posterior cingulid on lower molars (McKenna and Manning 1977), and p2 premolariform and p3-4 sub-molariform (Zhang 1978, 1979).

The known species of phenacolophids are characterised by a combination of the following features: Dental formula 3.1.4.3/3.1.4.3. Incisors stout; lower incisors subvertical. Canine small and having no diastema mesial or distal to the canine. Cheek teeth low-crowned and bilophodont. p1 small, simple and single-rooted. p2 small, premolariform and double-rooted. p3-4 well developed and sub-molariform; lower molars with low and weak paraconid but prominent metaconid that is separated from the protoconid by a groove; the talonid pronounced with a distinct talonid basin and cusps; the metaconulid small and weak, lacking entoconulid; lophids oblique; the protolophid and hypolophid deeply notched in the middle, distinctively; the cristid obliqua not strong; the hypoconulid cone-shaped on m3, completely separated from the entoconid and hypoconid and forms a third lobe; the trigonid and talonid V-shaped and the tooth height gradually decreasing distally. Upper premolar with prominent protocone and the protocrista connecting paraconule and metaconule; the preprotocrista longer than postprotocrista; all lophs separated by a groove in the middle. Upper molars bilophodont with six main cusps still discernible on occlusal surface; the paracone arc-shaped; the hypocone isolated and distinct; the paraloph connecting the metaloph through the ectoloph, which is notched by a groove in the middle; the paracingulum, postcingulum and metacingulum continuous; the parastyle weak and located on the paracingulum.

Comment: We place Phenacolophidae within Altungulata (Paeungulata + Perissodactyla) (Prothero and Schoch 1989; McKenna and Bell 1997), following Gheerbrant, Domning, et al. (2005) and Rose (2006). Phenacolophids as a group of archaic ungulates were considered to be the stem taxa of altungulates or tethytheres and have played a critical role in various phylogenetic analyses that involved Afrotheria and Perissodactyla using both morphological and molecular data as well as extinct and extant taxa (Fischer and Tassy 1993; Gheerbrant, Domning, et al. 2005; Rose 2006; Tabuce, Marivaux, et al. 2007; Gheerbrant 2009; Sanders et al. 2010, 2014; Sen 2013; Holbrook 2014; Rose et al. 2014). Altungulata as a higher-level taxon contains mammals that belong to Afrotheria and Laurasiatheria, respectively (Gheerbrant, Domning, et al. 2005; Rose 2006). Phenacolophidae was placed under Tethytheria (Gheerbrant, Domning, et al. 2005; Rose 2006), which implies that they were more closely related to Afrotheria, or even nested in Afrotheria (Tabuce, Marivaux, et al. 2007). Recent morphological studies continue to support the concept of Altungulata (Kondrashov and Lucas 2012; Rose et al. 2014). However, the concept of Altungulata is generally incompatible with molecular data that recognised a distant relationship between perissodactyls and afrotherians (Madsen et al. 2001; Bininda-Emonds et al. 2007; Springer et al. 2007; Meredith et al. 2011; dos Reis et al. 2012). Thus, we follow the paleontological convention in placing Phenacolophidae in Altungulata but note the discrepancy between the schools of morphologic and molecular researches.

Genus *Sanshuilophus* gen. nov

Type species: *Sanshuilophus zhaoi* sp. nov.
Diagnosis: Differs from other phenacolophids in having the following characters: Large body size (except for *Zaisanolophus*). m1-2 with weak paracone and paralophid; the metaconulid small and distinct, but the metaconid and entoconid strong; the grooves on the protolophid and the hypolophid deep; cristid obliqua weak and orientated strongly transversal, connecting the protolophid at its lingual end; postcingulid fan-shaped, without any coniformed prominence but with a ridge-like edge. The third lobe of m3 possessing one semi-conical and prominent hypoconulid and lacking other cusps. The cusps on P3? and P4 blunt and isolated; the lingual cingulum well developed and consistent. The upper molars lacking of mesostyle and possessing a isolated hypocone; the parastyle small, connecting paracone through a weak crista; metacone coniform with weak V-shaped ridge, cingulum well developed and surrounding the whole tooth as a circle.
Etymology: '*Sanshui*' is after Sanshui Basin where the holotype specimen was collected; the Greek '*lophus*' means crest, a commonly used surfix in naming early altungulates.

Sanshuilophus zhaoi gen. et sp. nov

Holotype: IVPP V 20147 (Figure 1), a left lower mandible fragment with m1-2.
Etymology: The species' name is dedicated to Mr. Canhui Zhao, who discovered the type locality of the new species.
Paratypes: IVPP V 20148.1, an isolated right I1?; V 20148.2, an isolated right I3?; V 20148.3, an isolated left i3?; V 20148.4, an isolated right P3?; V 20148.5, an isolated right P4; V 20148.6, an isolated right M2; V 20148.7, an isolated left M3; V 20148.8, an isolated left m2; V 20148.9, an isolated left m3; V 20148.10, an isolated left m3.
Diagnosis: Same as for the genus.
Locality and horizon: Lower Eocene Huayong Formation, Sanshui Basin, Guangdong Province, China.

Description
Upper teeth
The upper incisors are stout in labial or lingual view (Figure 2(a),(b)). The mesial and distal edges of both upper
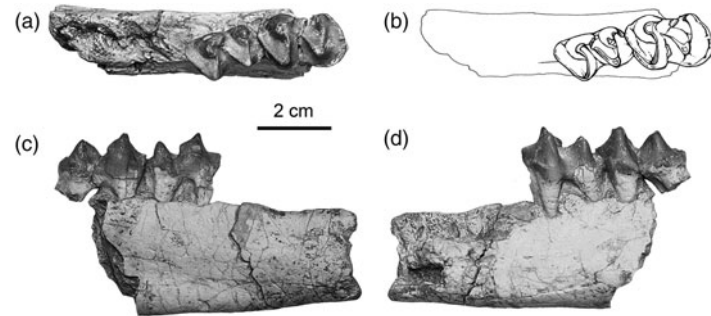
Figure 1.   Fragmentary left mandible of *Sanshuilophus zhaoi* with m1-2 (IVPP V 20147, holotype). (a) Occlusal view; (b) line drawing of the occlusal view; (c) lingual view; (d) labial view.

incisors are sharp, with the distal one longer than the mesial one, which usually is more distinct on the mesial incisor (Figure 2(a),(b)). For the significant different between the two crowns of the incisors, they are tentatively identified as I1? (V 20148.1, Figure 2(a)) and I3? (V 20148.2, Figure 2(b)). I1? and I3? both have a discontinuous cingulum near the crown base either on the lingual or the labial surface. The cingulum on the I3? is more prominent and located closer to the base of the tooth than that on the I1?. The labial surface and the basal portion of the lingual surface are convex and smooth on both incisors (Figure 2(a),(b)), but the upper portion of the lingual surface of I1? is concave (Figure 2(a2)). The apical portion of the lingual surface on I3? is also concave but has a ridge in the middle that bifurcates into two branches that merge with the cingulum on the labial and lingual sides, respectively (Figure 2(b2)). The enamel surface below the ridge of I3? is flat, whereas the tooth surfaces on both sides of the ridge are concave so that the lingual surface of I3? is trisected (Figure 2(b2)).

The two premolars are similar in morphology but differ in size with the small one being a quarter smaller than the large one. Both teeth are roughly triangular with an obtuse outline and differ from P2 of *Phenacolophus fallax* (DP4 of AN PIN 476-6 in the identification of McKenna and Manning (1977), which is reinterpreted as a P2 in this study as detailed below) that has a sharp outline. We tentatively treat the small premolar as possibly the P3 and the large one as P4, for the reason that the latter possesses a comparable size with the upper molar, but we cannot exclude the possibility that the small premolar is a P2. The width of P3? (IVPP V 20148.4, Figure 3(a)) and P4 (V 20148.5, Figure 3(b)) is longer than the length. The paracones, metacones and protocones are all blunt and round (Figure 3(a1-2),(b1-2)), with the protocone being the lowest of the three main cusps (Figure 3(a3),(b3)); the main cusps are higher than the conules on the P3? (Figure 3(a4)), but subequal in height with the conules on P4 (Figure 3(b4)). The paracone on each premolar was broken but the preserved portion indicates that it is slightly larger and higher than the metacones and is more centrally positioned. The labial two

cusps are only partly separated and each is slightly transversely compression (Figure 3(a1-2),(b1-2)). The preprotocrista is usually longer than the postprotocrista. The notchs on the ectoloph between the paracone and metacone, between the ectoloph and paraconule, and between the ectoloph and metaconules are all conspicuous. However, these notches are deeper on P3? than on P4 (Figure 3(a1-2),(b1-2)). The precingulum and postcingulum are moderate and equal to each other in size. The lingual cingulum is continuous on the P4 (Figure 3(b3)) but is interrupted in the middle of P3? (Figure 3(a3)). There is a weak ectocingulum on P4 (Figure 3(b1-2)) but no ectocingulum is discernable on P3? (Figure 3(a1-2)).

M2 (V 20148.6, Figure 3(c)) was slightly compressed transversely in preservation so that a crack was created in the trigon and the tooth is slightly distorted in that the mesial portion became slightly narrower than it should be. The tooth is roughly quadrate in outline with the anterior part being longer than the posterior. The tooth crown is brachyodont and also displays lophodonty in occlusal view
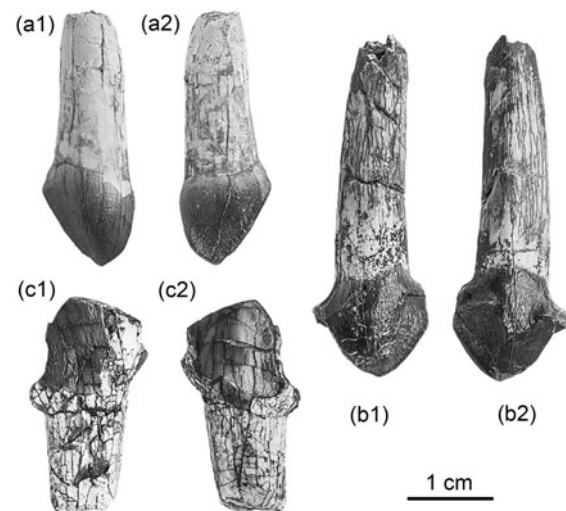

Figure 2.   Isolated incisors of *Sanshuilophus zhaoi*. (a) Right I1? (IVPP V 20148.1); (b) right I3? (V 20148.2); (c) left i3? (V 20148.3). 1. Labial side; 2. lingual side.
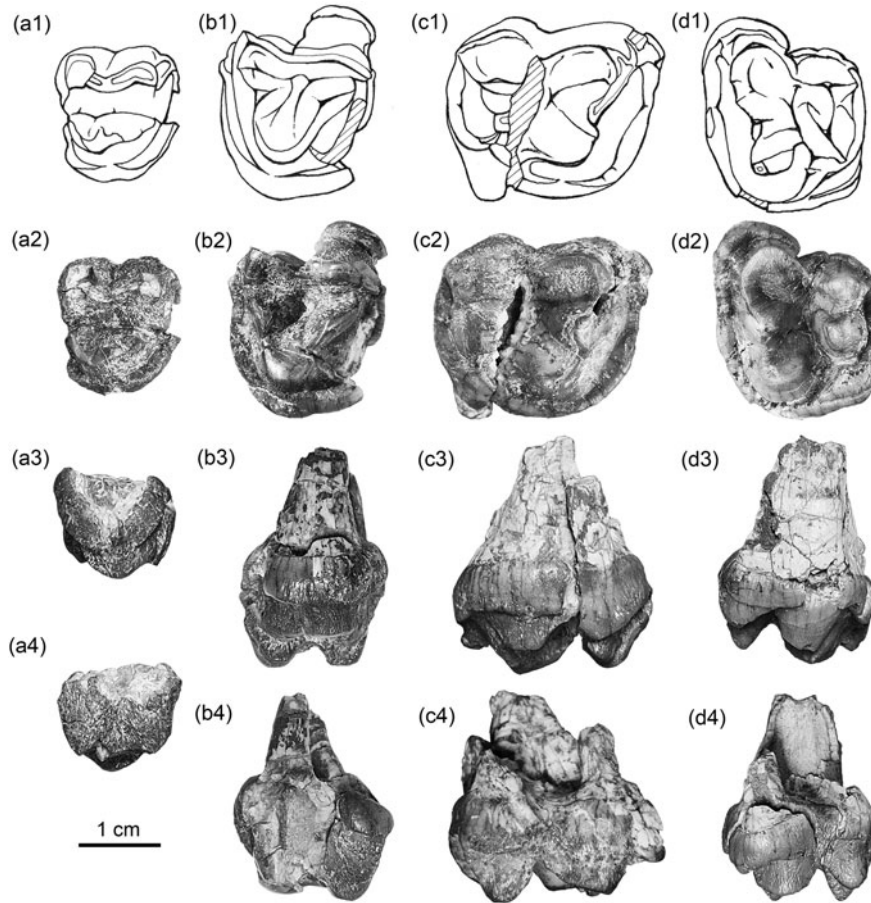
Figure 3. Upper cheek teeth of *Sanshuilophus zhaoi*. (a) Right P3? (IVPP V 20148.4); (b) right P4 (V 20148.5); (c) right M2 (V 20148.6); (d) left M3 (V 20148.7). 1. Line drawings of the occlusal view; 2. occlusal view; 3. lingual view; 4. labial view.

(Figure 3(c1-2)). There is a contact facet on the mesial and distal surface of the tooth, respectively, for M1 and M3. The conical paracone, paraconule and protocone of M2 are somewhat inflated and have similar height, with the protocone being slightly lower (Figure 3(c3-4)). Because of the inflation of the cusps, the protoloph connecting the cusps is short Figure 3(c1-2)). The protocone is blunt and cone-shaped. The preprotocrista connects the paraconule and forms the lingual part of the paraloph. There is no postprotocrista. The paraconule is sharp and conical, and is delimited by a groove from the protocone lingually and the parastyle labially. The paracone is well developed and crescent shaped. From the paracone, an arc-shaped ridge descends to the valley between the paracone and the metacone on the ecoloph. Lingually, the ridge connects the paraconule and merges to the paraloph. A weak ridge also anterolaterally connects the apex of the paracone with the small parastyle that is projected from the precingulum. There is no mesostyle. The metacone and metaconule are connected by the metaloph, and the hypocone is nearly isolated. The three cusps are located more nearly the lingual portion than the three cusps on the anterior portion

of the tooth, partially for the reason that the tooth is compressed transversely. The height of the three cusps is gradually reduced from the labial side to the lingual. The metacone has a weak V-shaped ridge, it is lower than the paracone but slightly higher than the metaconule. The metaconule is conical and with its posterior wing of the weak V-shaped ridge being one section of the metaloph and connecting the metacone. The anterior wing is broken and extends in the valley of two transverse lophs. A small and flat sheet-like hypocone is just located on the lingual side of the metaconule; the two limbs of the hypocone are jointed into the complete cingulum like what the parastyle does. The cingulum is continuous. The ectocingulum and lingual cingulum are weak relative to the well-developed precingulum, and postcingulum.

M3 (V 20148.7, Figure 3(d)) is so identified because its shape is more likely a M3 and because there is no contact facet on the distal surface of the tooth whereas the contact facet on its mesial surface for M2 is clear. It differs from M2 in being smaller and slightly wider than long in its crown outline. The anterior half of the tooth is wider than the posterior (Figure 3(d1-2)). The cusps on the lingual

side of M3 are more distinctive, but the cusps on the labial side are opposite, except the parastyle (Figure 3(d3-4)). The V-shaped ridge of the metacone is less developed than that of the M2. The hypocone is more prominent, and the precingulum and postcingulum are less conspicuous than those of M2.

Lower teeth

The lower incisor (V 20148.3, Figure 2(c)) is nearly square in labial view and the crown is mesiodistally flat, with a smooth lingual surface and a gently convex labial surface. The mesial and distal sides of the tooth are ridge-like and define an angle about 70°. The length of the distal edge is twice that of the mesial one, thus it may be a distal incisor and we identified it as i3?. There is a wear facet on the lower part of the distal edge. A weak cingulid is located at the base of the labial surface and bears a conulid in the middle.

IVPP V 20147 is a lower left mandible that has m1-2. The teeth have light colored enamel, compared to other teeth in the collection and are only slightly worn (Figure 1). The two teeth are smaller than other lower molars (Figure 4, see Table 1), we consider them to be m1-2 instead of deciduous teeth, because their positions on the dentary and the X-ray image reveals no dental germ in the dentary bone (Figure 8(b)). In addition, the morphologies of the two teeth of V 20147 are comparable to the m2

(V 20148.8, Figure 4(a)) that is from an older individual. We think that V 20147 represents a sub-adult. There is insufficient evidence to consider or rule out the possibility that the size difference reflects sexual dimorphism, even though sexual dimorphism usually does not express itself in molar size differences.

In occlusal view, the crowns of m1-2 are double V-shaped (Figures 1 and 4). The trigonid of m1 is similar to the talonid in morphology except that the trigonid is higher and slightly wider than the talonid. The angles of the V-shaped lophids on the trigonid and talonid are both near 35°. The protoconid and hypoconid on the labial side of the lower molar are sharp and mesiodistally compessed. The metaconid and entoconid are blunt and conical. There is no sign of the hypoconulid. The height of the protoconid is equal to that of the metaconid, and the height of the hypoconid is equal to that of the entoconid. There is a small but distinct metaconulid presented posterior and lingual to the metaconid. The metaconulid has a ridge extending to the metaconid. The paraconid is low and incorporated into the slender and nearly straight paralophid. The length of the paralophid is shorter than that of the protolophid. The protolophid and the hypolophid are high and strong, and both are not straight but have a notch separating the hypoconid and hypoconulid in the middle. The precingulid is weak and the ectocingulid is absent, but the postcingulid is
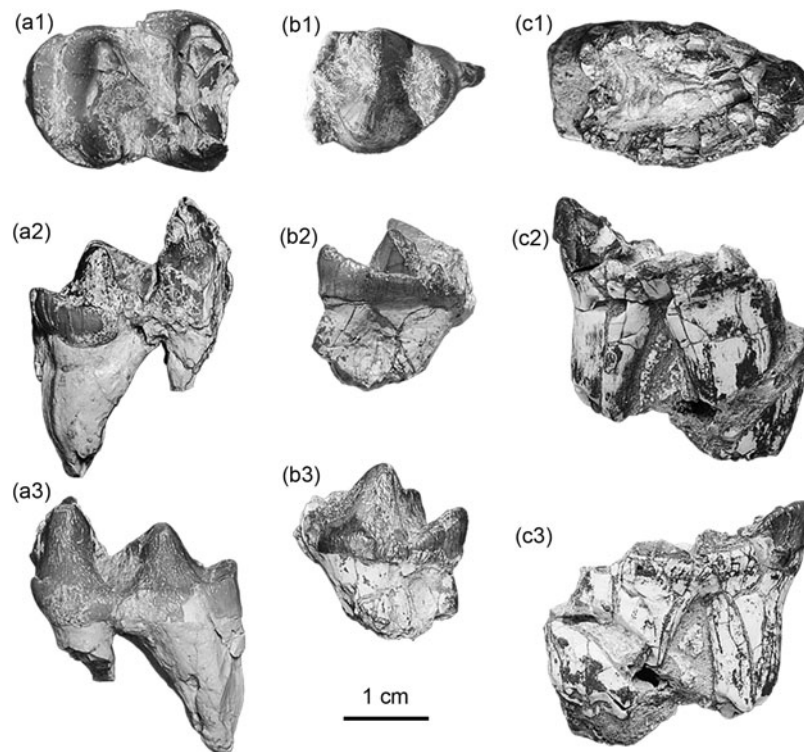

Figure 4.   Lower molars of *Sanshuilophus zhaoi*. (a) Left m2 (IVPP V 20148.8); (b) posterior portion of a left m3 (V 20148.9); (c) a broken left m3 (V 20148.10). 1. Occlusal view; 2. lingual view; 3. labial view.

Table 1. Measurements of the teeth of phenacolophids (in mm).

	Sanshuilophus	*Zaisanolophus*	*Phenacolophus*	*Tienshanilophus*	*Yuelophus*	*Ganolophus*
Lower	V 20148	V 20147				
i1			5.8/4.6			
i2			4.6/4.7			
i3			4.8/7.0			
c			4.5/5.0			
p1			7.2/4.9			
p2			9.7/5.9		5.9/5.3	
p3			12.2/6.4		9.0/7.2	8.5/5
p4			12.2^a/7.4	12.5/7.9	10.3/8.3	9.1/6.1
m1		21.0/13.6	14.9/9.5		11.0/8.1^a	11.0/7.1
m2	25.0^a/19.8	24.2/15.5	16.0/10.3	15.2/10.8	13.7/9.0	12.9/8.0
m3	27.9^a/17.9^a	41/21.5				15.7/9.5
Upper	V 20148					
I1	8.2/11.9					
I3	8.7/14.8		6.0^a/3.7^a			
C						
P1			5.7^a/4.6^a			
P2			10.9/9.4			
P3	16.0/18.2					
P4	19.8/25.8		12.0^a/13.2^a			
M1			13.5/^{a}/14.9^a			
M2	26.5/23.7		14.7/16.2	14.3/18.1		
M3	22.8/25.3			14.4/17.0		

Note: Some data of *Phenacolophus* are from McKenna and Manning (1977) and Zhang (1978); data of *Tienshanilophus*, *Yuelophus* and *Ganolophus* are from Zhang (1978, 1979), data of *Zaisanolophus* are from Gabunia (1998). ^{a}Based on estimated length.

well-developed to form a fan-shaped projection with a ridge-like distal edge, which does not project dorsally to form a cusp. The postcingulid surrounds the distal end of the tooth from the lingual side to the labial. The cristid obliqua is moderately developed and connects the protolophids at the lingual base near the metastylid.

The m2 of V 20147 (Figure 1) and V 20148.8 (Figure 4(a)) are similar to but slightly larger than the m1 of V 20147 (Figure 1). The protoconid and hypoconid angles are also slightly greater than that of m1. The paralophid is shorter than that of m1. The postcingulid is broader and its ridge-like end is more raised than that of m1. The m2 of V 20148 bears some wear, so that the metaconulid appears small.

The m3 of IVPP V 20148.9 only has the posterior part preserved, which contains the talonid and the third lobe that is formed by the postcingulid and hypoconulid (Figure 4(b)). The hypoconid angle of m3 is about 45° and greater than those in other lower molars. The small and isolated metaconulid is at the lingual edge of the tooth. The groove between the hypoconid and the entoconid is not as clear as in other lower molars. Unlike m1-2, the postcingulid of m3 is considerably narrower than the rest of the tooth and projects dorsally to form the third lobe distal to the talonid. It is completely separated from the entoconid and the hypoconid and bears a hypoconulid in the centre of the lobe. The root of the talonid expands distally and a small root supporting the third lobe is fused with it as indicated by a line of fusion.

IVPP V 20148.10 (Figure 4(c)) is a badly damaged m3 except that the third lobe is preserved. This tooth resembles V 20148.10 in the length/width ratio of the remaining parts and the morphology of the third lobe. However, the root under the talonid does not seem to expand distally to form a fused root that supports the third lobe.

Tooth enamel microstructure

Fortelius (1984) first illustrated 'pronounced grooves and valleys' in the occlusal surface of the enamel ridge of *Arsinoitherium*, which was further defined by von Koenigswald et al. (2011) as cross-ridges and was believed to have a close connection with the development of HSB. von Koenigswald (1997b, 2013) confirmed the presence of true HSB in the middle layer between the inner and outer zones of radial enamel in the tooth of *Phenacolophus*. The HSB is distinctly different from the enamel microstructure of true embrithopodids represented by the 'arsinoitheriid radial enamel (ARE, von Koenigswald 2013)' or the 'modified radial enamel (MRE, Pfretzschner 1994)' in the inner layer in which all the prisms are parallel to one another and there is no prism decussation (von Koenigswald 2013). The enamel of *Sanshuilophus* also has the intensive bifurcation of strips on the surface (Figure 5(h)), and we took a small fragment of the lower molar (m1 or m2) bearing a metaconid of *Sanshuilophus* to
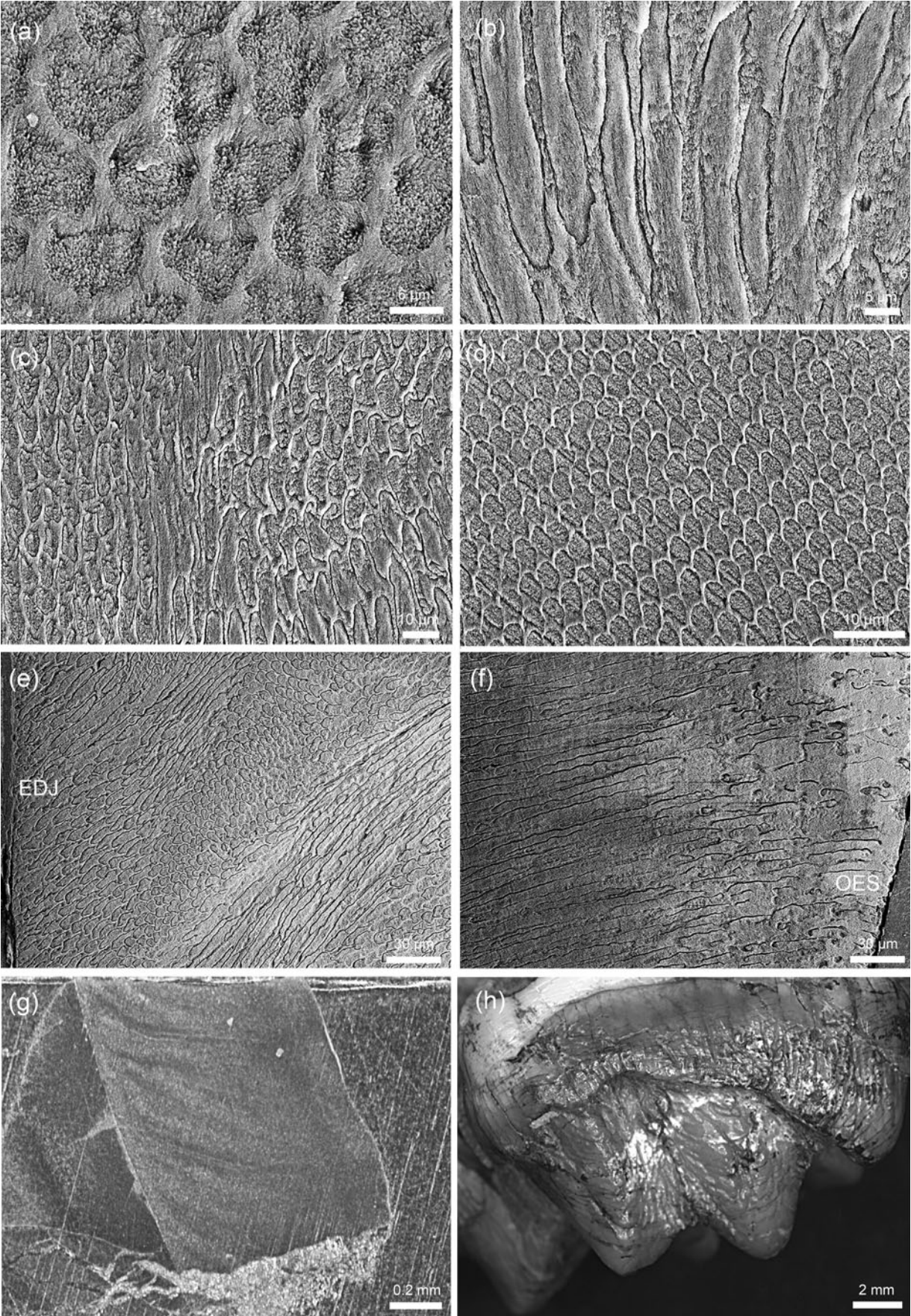
examine its enamel microstructure and enhance comparison with *Phenacolophus*.

In the cross section of prisms, the prism shape of *Sanshuilophus* is round and the prism sheaths are generally open to one side (Figure 5(a)). The prisms are closely lined up in parallel and the head of the prism combined with the dimidiate tail that showed as a keyhole pattern, which together may be classified as prism type 3B in the widely used prism type system (Boyde 1964). The diameter of the prism head is about 5 μm and is relatively consistent in the inner zone. The interprismatic matrix (IPM) always surrounds the prism and the crystallites of it are oriented vertically to the crystallites of prism head. The angle of the crystallites between the prism head and the IPM in the longitudinal section of prisms show the same oriented sets comparing to the cross section (Figure 5(b)).

The Schmelzmuster of *Sanshuilophus* is composed of two blurry differentiated zones either in the longitudinal section (Figure 5(c),(d)) or in the cross-section (Figure 5(e)–(g)). The prisms are bounded into HSBs in the inner layer (Figure 5(c),(e)), whereas the prisms in the outer zone are all oriented in parallel and perpendicular to the enamel–dentine junction (EDJ) (Figure 5(d),(f)). The enamel in the outer zone consists of parallel prisms that are characteristic of radial enamel (RE). The HSBs are roughly perpendicular to the EDJ and radial in their orientation (Figure 5(e)), forming nearly the inner half of the enamel (Figure 5(g)). There are about eight prisms in each band with some variations (Figure 5(c),(e)). The prism near the outer enamel surface (OES) seems larger in diameter than the prism in the inner layer.

Unlike in the *Arsinoitherium* in which the strips only occur on the occlusal surface of the enamel ridge (Fortelius 1984), the enamel surface of *Sanshuilophus* is fully covered with dense bifurcated strips, which are present even on the cingulum and cingulid (Figures 1–4 and 5(h)). A similar condition is also present on the enamel surface of the incisors (Figure 2). The strips are stubby and roughly vertical to the occlusal surface and have some waveform in addition to dense bifurcations. In general, the strips are thicker and more irregular than those of *Arsinoitherium* (von Koenigswald 2013).

Comparisons

Sanshuilophus shares with other phenacolophids the features that are listed in the emended diagnosis of the family, and differs from other genera as diagnosed for the genus. It also differs from other genera in many details, and we will further compare them below. To assist with the comparison, we provide some photographs of the teeth from several species that we have the access to (mostly type specimens) (Figures 6–8). Most of the images were presented in the original works but were usually illustrated in poor quality except for those of *Phenacolophus fallax,* which was well figured by McKenna and Manning (1977). In Figure 6, we also illustrated three fragmentary mandible specimens of *Phenacolophus* (AMNH 20430) that were not shown in previous studies (McKenna and Manning 1977). These edentulous mandibles display the root condition, which help us to show the single-rooted condition of p1 and double-rooted condition of following teeth.

Phenacolophus

The teeth of *Sanshuilophus* differ with those of *Phenacolophus* in being larger (Table 1, Figures 6(a)–(c), 7) and having a higher degree of biolophodonty. The upper premolars of *Sanshuilophus* are more molariform in that they are proportionally longer and with a more developed lingual portion where the protocone, conules, and lingual cingulum are more distinctive and the preprotocrista is longer than the postprotocrista. On the upper molars of *Sanshuilophus*, the mesostyle is missing, but the paracone and parastyle are more prominent, whereas the metacone, metaconule and hypocone are less so; the hypocone is flat sheet-like with two cristae anteroposteriorly joining into the postcingulum and lingual cingulum, in contrasting to the hypocone of *Phenacolophus* that is cone-shaped and lacks connection to the cingulum; no postprotocrista; no crista from the apex of paraconule stretching into the valley of two lophs; the postparacrista is longer; the V-shaped crista of metacone is weaker than that of *Phenacolophus*. The lower molar of *Sanshuilophus* has a stronger and distinctive metaconid and hypoconulid; the small but distinctive metaconulid is distal to the metaconid; the cristid oblique is low and extends more lingually to join the protolophid near the metastylid. The cristid obliqua of *Phenacolophus* is more labially extended and connects the protolophid in the mid-point. The postcingulid is distinct in the m1-2 of *Sanshuilophus*, and surrounds the talonid to give the talonid a fan-shape in occlusal view. The postcingulid in m1-2 of *Phenacolophus* is less developed. The third lobe of m3 of *Sanshuilophus* is linguiform and prominent.

Figure 5.   Tooth enamel microstructure in *Sanshuilophus zhaoi.* (a) Prism shape on the cross-section of prisms; (b) longitudinal section of prisms; (c) HSB in the inner layer of the enamel; (d) primitive radial enamel in the outer layer; (e) enamel type of the inner layer with HSBs; (f) enamel type of the outer layer with radial enamel; (g) Schmelzmuster on the cross section of the tooth enamel; (h) cross-ridges on the enamel surface of M3. (a)–(d) Longitudinal sections of the tooth enamel; (e)–(g) cross sections of the tooth enamel. (a)–(g) All sections are from the same lower molar (m1 or m2) fragment bearing a metaconid.
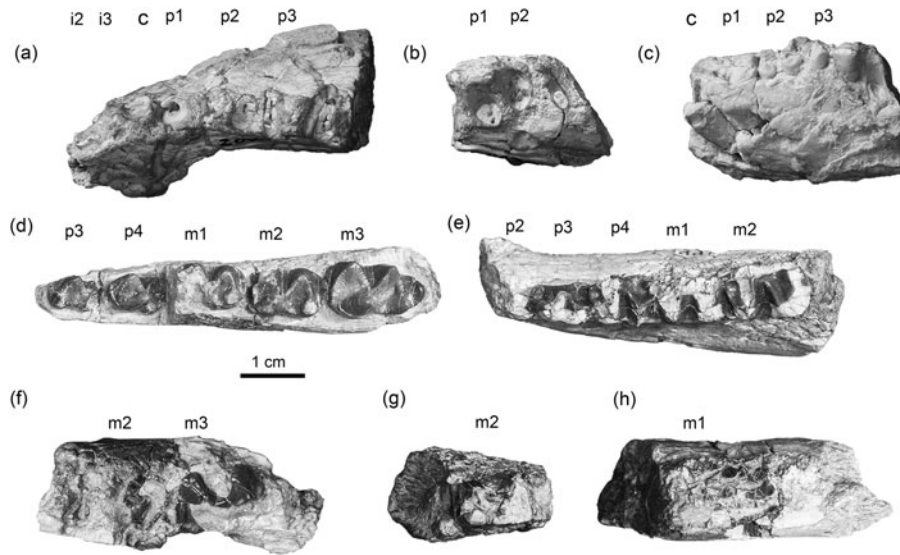
Figure 6.   Some specimens of other phenacolophid species. (a)–(c) Three mandible fragments of *Phenacolophus*, (a) the right mandible fragment with alveoli for i2-3, lower canine and p1-3 (AMNH 20430); (b) the left mandible fragment with alveoli for p1-2? (AMNH 20430); (c) symphysial part of a mandible fragment with left alveoli for the canine and p1-3 (AMNH 20430); (d) the right mandible fragment with p3-m3 of *Ganolophus lanikenensis* (V 5041, holotype, Zhang 1979, Figure 1; plate I, Figure 1); (e) left mandible fragment with partial p2, p3-m2 of *Yuelophus validus* (V 5601, holotype, Zhang 1978, plate I, Figures 1, 2(a),(b)); (f)–(h) left mandible fragment with a broken m3 (V4058, Tong 1979, Figure 6), right mandible fragment with a broken m2 (V4058, Tong 1979, Figure 8) and right mandible with a broken m1 (V4058.1) of *Tienshanilophus subashiensis*.

Ganolophus

The holotype of *Ganolophus lanikensis* is a sub-adult right mandible with erupting p3-4 and barely worn m1-3 (V 5041, Figure 6(d); Zhang 1979). *G. lanikensis* is the smallest known phenacolophid and shows some primitive characters compared to other phenacolophids. Its teeth are the least lophodont and the V-shaped lophids on the trigonid and talonid are more open, with angles of about 55°. The lower premolar has a coniform paraconid, a basined talonid, and a high hypoconid. The lower molars have high protoconids and hypoconids. The metaconids and entoconids are high and inflated. The ectopostcingulid is broad and ridge-like. The entoconulid is small but distinct. The cristid obliqua and paralophid are relatively weak and short, with the former connecting the mid-point of the protolophid. The metaconulid is very small but bears a weak cristid that joins the metaconid. The postcingulid is conspicuously upraised and crested. The ectocingulid is small but almost continuous. The third lobe of m3 is small with a central conulid. The m3 talonid is notably smaller and lower than trigonid.

Yuelophus

The holotype of *Yuelophus validus* is a left mandible fragment with p2-m2 with damaged crowns (Zhang 1978; Figure 6(e)). *Y. validus* is most similar to *G. lanikensis* in size and in having a low degree of lophodonty, the paraconid isolated and coniform, a basined talonid and a

hypoconid on the lower premolar. However, *Y. validus* differs from *G. lanikensis* in that the lower premolar has a larger talonid, the cristid obliqua of the lower molar is closer to the metaconid, and the postcingulid is absent. The lower molar of *Yuelophus* differs from that of *Sanshuilophus* in having less developed postcingulid and ectocingulid but more open angles of the V-shaped lophids on the trigonid and talonid.

Tienshanilophus

Three species of *Tienshanilophus* were based on specimens from the Late Paleocene Taizicun Formation from three localities, respectively, in the Turpan Basin, northwestern China (Tong 1979; Figure 6(f)–(h)). Tong considered *Tienshanilophus* as belonging to an unnamed new family under Condylarthra, but Zhang (1978) placed it in Phenacolophidae, which was followed by others (Gabunia 1998). In addition to the difference in body size (see Table 1), Tong (1979) considered that *Tienshanilophus* differs from *Phenacolophus* in having a weaker paraconid on lower molar and no cristid that extends distally from the apex of the paraconid. In addition, the m3 talonid is longer, and there is no lingual cingulum on the upper molars in *Tienshanilophus*. According to Tong (1979), *T. lianmuqinensis* differs from *T. subashiensis* in that the hypocone on M2 of the former is more developed, and the height of hypocone equals with that of metaconule; the hypocone and the metaconule are connected tightly
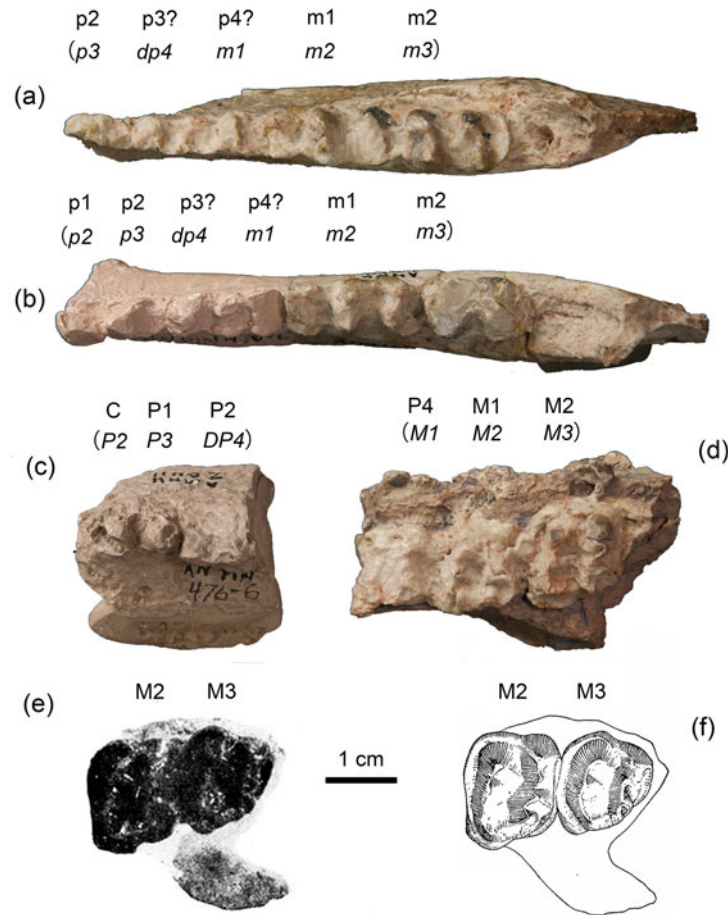
Figure 7. (Colour online) Comparison for cheek teeth of *Phenacolophus* and *Tienshanilophus* and another possible tooth loci for the type specimen of *Phenacolophus*. (a) Right lower mandible fragment with p2, p3?, p4? and m1-2 (AMNH 20411); (b) left lower mandible fragment with patial p4?, m1, m2 (AMNH 20411) with attached mandible fragment cast of AN PIN 476-6 showing p1, p2, p3?, patial p4?; (c) cast of CP1P2 in right maxillary fragment included in AN PIN 476-6; (d) fragmentary right maxilla with battered remains of P4M1M2 (AMNH 20411); (e) occlusal view of fragmentary right maxilla with M2 and M3 (IVPP V4084, holotype of *Tienshanilophus lianmuqinensis*, according to Tong, 1979, plate I, Figure 10A); (f) drawing of IVPP V4084 (according to Tong 1979, Figure 1). Tooth identification indicated in normal font on the left is from this paper. Tooth identification in italic on the right is from McKenna and Manning (1977).

thus the groove between them is less prominent. *T. shenjinkouensis* differs from *T. lianmuqinensis* in having a lower and flatter heel on m3. In *T. shenjinkouensis*, the hypoconulid and its cristid on lower molars are weaker, the distance between the postcristid and the hypolophid is longer, and the postcingulid is thicker.

Compared to *T. subashensis*, the lingual cingulum of the upper molar in *Sanshuilophus* is more prominent and
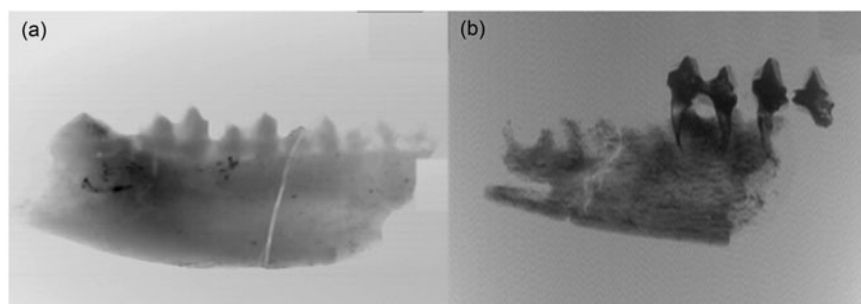

Figure 8. X-ray images of lower jaws. (a) *Phenacolophus* (AMNH 20411, right lower mandible fragment with cheek teeth); (b) *Sanshuilophus* (V 20147, left lower mandible fragment with m1-2).

continuous. The precingulum and postcingulum are better developed. The hypocone is small but distinct with its cristae merging into the cingulum. The postcingulid of the lower molar is more developed and fan-shaped. Although the lower molars of *T. subashensis* were broken, it is still discernible that the cristid oblique of the lower molar is well developed and connects the protolophid at the mid-point (Figure 6(f)–(h)). In contrast, the cristid obliqua in *Sanshuilophus* joins the protolophid more lingually.

T. lianmuqinensis is based on a partial right maxilla with M2-3 (Tong 1979). It differs from *Sanshuilophus* in that the hypocone of *T. lianmuqinensis* is relatively larger, with equal height with the metaconule; the two cusps are closely packed. In *T. lianmuqinensis* there is a weak postprotocrista that connects the apex of the protocone and the metaconule and that the precingulum and lingual cingulum are stronger and surround the protocone. In *T. lianmuqinensis*, the grooves on the protoloph and the metaloph are more conspicuous. *Sanshuilophus* further differs from *T. lianmuqinensis* in having proportionally longer upper molars, a better-developed paraconule, and lacking the ridge connecting the hypocone and metaconule. The cingulum is less developed but surrounds the entire molars without interruption.

T. shengjinkouensis was based exclusively on lower teeth (Tong 1979). According to Tong, *T. shengjinkouensis* differs from the other two species of the genus in that the talonid of m3 is lower and flat; the hypoconulid and the hypoconulid crest are weaker; the distance between the protolophid and hypolophid on m1-2 are bigger; the postcingulid is stronger and lies more distantly from the hypolophid; the entoconid of p4 is weaker. *Sanshuilophus* differs from *T. shengjinkouensis* in that the protoconid and the hypoconid of the lower molars are sharper, the metaconid and the hypoconulid expand more, the cristid obliqua joins the protolophid more lingually and the third lobe of m3 is higher but proportionally smaller.

Zaisanolophus

Zaisanolophus was based on one tooth: a right m3 (IPB. Z-413), from the Middle Eocene Obaila Formation of the Zaisan Depression of Kazakstan (Gabunia 1998). It is the latest and largest representative of the family, with the m3 length being about 2.5 times of that of *Phenacolophus* (Table 1). In addition, the m3 of *Zaisanolophus* differs from that of *Phenacolophus* in having a prominent and bicuspid third lobe and a stronger cristid obliqua (Gabunia 1998). These features are also distinctive from *Sanshuilophus*. From the sketch of Gabunia (1998), we can also see that the cingulid of *Zaisanolophus* is well developed and without interruption, especially the entocingulid is small but distinct; the protolophid and hypolophid are more transverse.

Discussion

Dentition of phenacolophids

The dentition of phenacolophids is best known from *Phenacolophus,* although it is still subject to interpretation, which in turn affects interpretation of the relationship of phenacolophids with other ungulates. Two collections of *Phenacolophus* were made separately from the same locality of the Upper Paleocene Gashato Formation in Mongolia. One was collected by the Central Asiatic Expedition (CAE) in 1924 and housed in the American Museum of Nature History. These specimens were designated as the type specimens of *Phenacolophus* (Matthew and Granger 1925). The second collection was made by the Soviet-Mongolian Expedition in 1948, housed in the Paleontological Institute of the Soviet Academy of Sciences and initially studied by Flerow (I957). McKenna and Manning (1977) made a systematic study of the specimens from both collections. In describing those materials, McKenna and Manning (1977) recognised that dp4, instead of p4, was present in the type specimen of *P. fallax*. The tooth was identified as dp4 because it is long, highly molariform, worn deeper than molars (although this is obscured by the weathered condition). In addition, the trigonid of the tooth is almost as low as the talonid and is more open, occupying a relatively greater part of the tooth on the left mandible. The right mandible of the type specimen (AMNH 20411) was believed to bear p3, dp4, and m1-3 (Figure 7(a)) and the left mandible bear p2, p3, dp4 and m1-3 (Figure 7(b)). Moreover, p2-p3 were considered as being not molariform, p2 single rooted with the crown possessing a high protoconid and a flattened lingual side but lacking the talonid, p2 rotated in the jaw, and p4 is molariform (McKenna and Manning 1977).

McKenna and Manning (1977) considered the ultimate three teeth in the type specimen are m1-3 (Figure 7(a),(b)) and that the type specimen for '*Procoryphodon primaevus*' Flerow 1957 (Figure 1; AN PIN 476-1) was a left mandible fragment with damaged m2-3, although they noted that Flerow may have meant the two teeth to be m1-2 (McKenna and Manning 1977, 64). This is because Flerow (1957, 74) also reported 'a piece of right lower jaw with a broken m2 and anterior part of m3' and considered it probably 'belongs to the same specimen as type'. McKenna and Manning (1977, 64) described the same specimen as 'a right jaw fragment with an erupting ?m3, labeled AN PIN 476.2'.

In light of the new material of *Sanshuilophus* and our reexamination of the specimens of *Ganolophus* and *Yuelophus* (Zhang 1978, 1979; Figure 6(d),(e)) that were not available to McKenna and Manning (1977) when they re-described the material of *Phenacolophus*, we found that the dentition of *Phenacolophus* displays some interesting differences from other phenacolophids. The other phenacolophids show that p3 are both sub-molarizform

and double rooted (Figure 6(d),(e)), while the p3 of *Phenacolophus* is single rooted with one main cusp (Figure 7(b)); the postcingulid of m1-2 are well developed and fan-shaped but do not project dorsally to form a cusp (hypoconulid) (Figures 1, 4(a), 6(d),(e)); the distal lobe of m3 is narrower than the rest part of the tooth but unlike the flat postcingulid of m1-2, it bears a hypoconulid that projects dorsally (Figures 4(b),(c), 6(d),(e)). It seems that the m2-3 as designated in the type of *Phenacolophus* (Figure 7(a),(b)) and the specimen originally described by Flerow (1957) are more similar to m1-2 rather than to m2-3 of other phenacolophids (Figures 1, 4, 6). In the type of *Phenacolophus*, the p2 is single rooted and rotated relative to the dentition (Figure 7(b)). We have observed that the rotation is present in the single-rooted tooth, which is usually the mesial cheek tooth in the dentition of archaic ungulates and ungulate-like mammals, such as most perissodactyls, paenungulates, pantodonts and dinoceratans that we examined.

Moreover, if the first two teeth on the maxillary fragment (AN PIN 476-6, Figure 7(c)) were identified as P2 and P3 (McKenna and Manning 1977), then the P2-3 in the type of *Phenacolophus* are unusually small and single rooted and have one single main cusp (Figure 7(c)), which cannot match with its p2-3 (Figure 7(a),(b)) in size and shape. The P3? of *Sanshuilophus* is three-rooted and molariform (Figure 3) and has the suitable size compared with the lower molars (Figure 1, Table 1). The ultimate tooth on the maxillary fragment (AN PIN 476-6, Figure 7(c)) was identified as DP4 by McKenna and Manning (1977), which is premolarised but not sub-molarised. It is considerably smaller than M1 in an unusual diminution and has a relatively shaper outlines than the two premolar of *Sanshuilophus* (Figure 7(d)), while the P4 of *Sanshuilophus* is only slightly smaller than the molars and possesses a broader lingual portion (Figure 3, Table 1). In our view, the three teeth on the maxillary fragment (AN PIN 476-6) are better interpreted as the upper canine and P1-2, which is also fit to the location of the sutural fusion.

In accordance with the reidentification of the lower teeth in the mandibles of type specimen of *Phenacolophus*, the upper teeth on the type maxilla fragment, presumably from the same individual of AMNH 20411, need to be reinterpreted. These teeth were originally designated as M1-3 by Matthew and Granger (1925), but we think they should be reinterpreted as P4, M1 and M2. The P4 differs from the other two upper molars and M1-2 of other phenacolophids in that its outline is more or less subtriangular to sub-square and its two lophs are not parallel with each other but seems like cross on the lingual size. The identification of the ultimate tooth as M2 is reasonable because the posterior half of M3 is usually reduced and the M3 is usually the smallest molar in other ungulates (this is also true in the dentitions of *Sanshuilophus* and *Tienshanilophus*, Figures 3(c),(d), 7(e),(f)).

There were also some conflicts in the documentation of the specimens assigned to *Phenacolophus*. The two edentulous mandibles of AMNH 20430, for instance, show that p1 is single rooted and the other premolars are double rooted (Figure 6(a),(c)) which is different from the condition of the type (Figure 7(a),(b)). The left p2 of AMNH 20411 appears identical to the p1 of AN PIN 476-5.

To clarify the problem, we further took the X-ray image of the holotype (the right lower mandible fragment; AMNH 20411, Figure 8(a)) of *Phenacolophus* and the holotype left lower mandible fragment (V 20147, Figure 8(b)) of *Sanshuilophus*. The images are not very clear due to preservation of the specimens, but it is clear that there is no trace of dental germ under the purported dp4 in AMNH 20411, whereas there seems to be a fuzzy germ-like shape ventrodisal to the ultimate erupted tooth in the jawbone. Such a condition appears to be uncommon, although in some large bodied ungulates m3 erupts after eruption of other cheek teeth (Smith 2000). If this is correct, then an alternative interpretation of the tooth loci for AMNH 20411 is that the left mandible bears p1-4 and m1-2, the right mandible has p2-4 and m1-2, and the right maxilla bears P4-M2 (Figure 7). However, the second and the third teeth in the right lower mandible fragment of AMNH 20411 are long and molariform and worn deeper than molars as noted by McKenna and Manning (1977). Thus, we cannot rule out the possibility that they are deciduous teeth based on available evidence. Nonetheless, we tentatively identify the second and the third teeth in the right lower mandible fragment and the third and fourth teeth in the left lower mandible fragment of AMNH 20411 as possible p3 and p4 because there is no trace of tooth germ under these teeth in the mandible. The deeply worn appearance of these teeth may also be attributable to might weathering of the specimen, because the deeply worn condition is not that obvious in the left lower mandible fragment of the same individual. A conclusive identification of the dentition of *Phenacolophus* has to wait for better-preserved material.

Enamel microstructures

Tooth enamel yields information for taxonomic and phylogenetic research in mammals (von Koenigswald and Clemens 1992; von Koenigswald 1997a), which also facilitates resolution of existing difficulty in the determination of phylogenetic relationships among Paenungulata and especially Tethytheria (Fortelius 1985; Pfretzschner 1994; Maas et al. 1998; Tabuce, Delmer, et al. 2007; Tabuce, Marivaux, et al. 2007; von Koenigswald 2013).

In Embrithopoda, the conspicuous light and dark stripes on the occlusal surface of *Arsinoitherium* were first regarded as vertical HSB (Fortelius 1984), which were treated as a resemblance with those frequently observed in large body-sized mammals (Rensberger and von Koenigs-

wald 1980; von Koenigswald et al. 2011). However, Pfretzschner (1994) could not find any decussation of prisms in the enamel of *Arsinoitherium*. He diagnosed the Schmelzmuster as having an inner layer of modified radial enamel (MRE), which is a subtype of radial enamel (RE) with prisms aligned in radial rows and trapped in thick intercalated sheets of IPM (inter-row sheets), and an outer layer of primitive RE. von Koenigswald (2013) reinvestigated the enamel microstructure of *Arsinoitherium* and reported that the Schmelzmuster of *Arsinoitherium* showed a unique differentiation of radial pattern: the Schmelzmuster is composed of two zones, of which the outer zone of the enamel is more homogenous with straight prisms surrounded by IPM, consisting of RE. The inner zone, in contrast, shows a distinctive pattern of light and dark stripes, oriented perpendicular to the EDJ. In one set of the stripes in inner zone, narrow prisms occur in stripes with IPM sheets, whereas in the other, rounded prisms in those with surrounding IPM (von Koenigswald 2013). In contrast with the true MRE, both sets of stripes in the inner zone do not have inter-row sheets. Thus, according to the two sets of radial prism stripes surrounding by or trapped in different IPMs, von Koenigswald (2013) defined another subtype of radial enamel, *Arsinoitherium* radial enamel (ARE). In the enamel microstructure of two other embrithopods, *Crivadiatherium* and *Palaeoamasia*, the prism type showed a layer with the inter-row sheets, or at least with a tendency to form with inter-row sheets (von Koenigswald 2013).

von Koenigswald (2013) also reported that true HSB present in the middle of two RE layers and that the crystallites of the IPM and the prism head are oriented at an angle in the tooth enamel of *Phenacolophus*. He concluded that the different enamel microstructure provides another argument for the exclusion of *Phenacolophus* from the Embrithopoda. The Schmelzmuster of *Phenacolophus* is similar to that of *Sanshuilophus* in having true HSB in both the inner layer of the enamel and the outer zone that consists of typical primitive RE. This type of Schmelzmuster is common in tooth enamel of large body-sized mammals, such as perissodactyls, archaic ungulates and ungulate-like mammals (von Koenigswald 2013). The Schmelzmuster shows that the tooth enamel of *Phenacolophus* and *Sanshuilophus* is different from those of embrithopods and thus do not support the placement of phenacolophids in embrithopods.

Conclusion

With the alternative interpretation of the tooth loci for the type specimen of *Phenacolophus* (AMNH 20411) in this paper, all phenacolophids appear consistent in their molar and premolar morphologies in that they differ embrithopods in having low crowned and bilophodont cheek teeth

and true HSB in the inner layer of the enamel. They differ Pantodonta in having sub-molariform premolars, different shape of the third lobe of m3 and considerably different morphology in upper molars. Based on the comparison we made in this study, we concur that Phenacolophidae may not be considered as members of Pantodonta (Flerow 1957; Xu 1976; Zhang 1978, 1979; Chow and Wang 1979; Tong 1979) or embrithopods (Simons 1960; Szalay and McKenna 1971; McKenna and Manning 1977; Gingerich and Russell 1981). However, the tooth loci for *Phenacolophus* and related dental features for Phenacolophidae still need to be clarified with more complete and well-preserved specimens. Although still not conclusive, the current placement of Phenacolophidae as a primitive altungulate or Altungulata *incertae sedis* (Sen and Heintz 1979; Radulesco and Sudre 1985; Prothero et al. 1988; Court 1992; Gheerbrant, Domning, et al. 2005; Gheerbrant, Sudre, et al. 2005; Gheerbrant 2009; Sen 2013) is favored by this study. The conventional Phenacolophidae was most likely paraphyletic (Gheerbrant, Domning, et al. 2005), but after we exclude *Radinskya* and *Minchenella* from the family and reinterpret the tooth loci of *Phenacolophus*, the remaining genera become more coherent in morphology than those included in the conventional Phenacolophidae. Nonetheless, whether or not Phenacolophidae forms a monophyletic group needs to be tested with future phylogenetic analyses that are based on better material.

References

Bai B, Wang Y, Meng J, Li Q, Jin X, Beatty BL. 2014. New early Eocene basal tapiromorph from Southern China and its phylogenetic implications. PloS One. 9(10):e110806. doi:10.1371/journal.pone. 0110806.

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A. 2007. The delayed rise of present-day mammals. Nature. 446(7135): 507–512. doi:10.1038/nature05634.

Boyde A. 1964. The structure and development of mammalian enamel [Ph.D. thesis]. London: The London Hospital Medical College. 193 pp.

Chow MC, Wang BY. 1979. Relationship between the Pantodonts and Tillodonts and classification of the order Pantodonta. Vertebrat Palasiatic. 17(1):37–48 [In Chinese with English summary].

Court N. 1992. A unique form of dental bilophodonty and a functional interpretation of peculiarities in the masticatory system of *Arsinoitherium* (Mammalia, Embrithopoda). Hist Biol. 6(2):91–111. doi:10.1080/10292389209380421.

Domning DP, Ray CE, McKenna MC. 1986. Two new Oligocene desmostylians and a discussion of tethytherian systematics. Smithson Contrib Paleobiol. 59:1–56. doi:10.5479/si.00810266.59.1.

dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang Z. 2012. Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. Proc R Soc B Biol Sci. 279(1742):3491–3500. doi:10.1098/rspb.2012.0683.

Fischer MS, Tassy P. 1993. The interrelation between Proboscidea, Sirenia, Hyracoidea, and Mesaxonia: the morphological evidence. In: Szalay FS, Novacek MJ, editors. Mammal phylogeny: placentals. New York (NY): Springer-Verlag; p. 217–243.

Flerow CC. 1957. A new Coryphodont from mongolia and on evolution and distribution of Pantodonta. Vertebrat Palasiatic. 1(2):73–81.

Fortelius M. 1984. Vertical decussation of enamel prisms in lophodont ungulates. In: Fearnhead R, Suga S, editors. Tooth enamel IV. Amsterdam: Elsevier; p. 427–431.

Fortelius M. 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. Acta Zool Fenn. 180:1–76.

Gabunia LK. 1998. The Phenacolophidae (Mammalia, Pantodonta) from the Eocene of the Zaisan Depression (Eastern Kazakhstan). Paleontol J, translated from Paleontologicheskii Zhurnal. 32(1):78–81.

Gheerbrant E. 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. Proc Natl Acad Sci. 106(26):10717–10721. doi:10.1073/pnas.0900251106.

Gheerbrant E, Domning DP, Tassy P. 2005. Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives). In: Rose KD, Archibald David J, editors. The rise of placental mammals: origins and relationships of the major extant clades. Baltimore (MD): Johns Hopkins University Press; p. 84–105.

Gheerbrant E, Sudre J, Tassy P, Amaghzaz M, Bouya B, Iarochene M. 2005. New data on *Phosphatherium escuilliei* (Mammalia, Proboscidea) from the early Eocene of Morocco, and its impact on the phylogeny of Proboscidea and lophodont ungulates. Geodiversitas. 27(2):239–333 [In French with English summary].

Gingerich PD, Russell DE. 1981. *Pakicetus inachus*, a new archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contrib Mus Paleontol Univ Mich. 25(22):235–246.

Holbrook LT. 2005. On the skull of *Radinskya* (Mammalia, ?Phenacolophidae) and its affinities. J Vert Paleontol. 25(Suppl 3):70A–71A.

Holbrook LT. 2014. On the skull of *Radinskya* (Mammalia) and its phylogenetic position. J Vert Paleontol. 34(5):1203–1215. doi:10.1080/02724634.2014.854249.

Hooker JJ, Dashzeveg D. 2004. The origin of chalicotheres (Perissodactyla, Mammalia). Palaeontology. 47(6):1363–1386. doi:10.1111/j.0031-0239.2004.00421.x.

Kondrashov PE, Lucas SG. 2012. Nearly complete skeleton of *Tetraclaenodon* (Mammalia, Phenacodontidae) from the early Paleocene of New Mexico: morpho-functional analysis. J Paleontol. 86(1):25–43. doi:10.1666/11-009.1.

Maas MC, Thewissen JGM, Kappelman J. 1998. *Hypsamasia seni* (Mammalia: Embrithopoda) and other mammals from the Eocene Kartal Formation of Turkey. Bull Carnegie Mus Nat Hist. 34:286–297.

Madsen O, Scally M, Douady CJ, Kao DJ, DeBry RW, Adkins R, Amrine HM, Stanhope MJ, de Jong WW, Springer MS. 2001. Parallel adaptive radiations in two major clades of placental mammals. Nature. 409(6820):610–614. doi:10.1038/35054544.

Matthew WD, Granger W. 1925. Fauna and correlation of the Gashato Formation of Mongolia. Am Mus Nat Hist. 189:1–12.

McKenna MC, Bell SK. 1997. Classification of mammals above the species level. New York (NY): Columbia University Press. 631 p.

McKenna MC, Chow MC, Ting SY, Luo ZX. 1989. *Radinskya yupingae*, a perissodactyl-like mammal from the late Paleocene of China. In: Prothero DR, Schoch RM, editors. The evolution of perissodactyls. New York (NY); Oxford: Clarendon Press; Oxford University Press; p. 24–36.

McKenna MC, Manning E. 1977. Affinities and palaeobiogeographic significance of the Mongolian Paleogene genus *Phenacolophus*. Geobios. 10(Special 1):61–85. doi:10.1016/S0016-6995(77)80008-9.

Meredith RW, Janecka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC, Goodbla A, Eizirik E, Simao TLL, Stadler T, et al. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science. 334(6055):521–524. doi:10.1126/science.1211028.

Pfretzschner HU. 1994. Biomechanics of the enamel microstructure of large mammals. Palaeontographica Abteilung A. Band A. 234-(Leiferung 1–3):1–88. [In German with English summary].

Prothero DR, Manning EM, Fischer M. 1988. The phylogeny of the ungulates. In: Benton MJ, editor. The phylogeny and classification of the tetrapods. Oxford: Clarendon Press; p. 201–234.

Prothero DR, Schoch RM. 1989. Origin and evolution of the Perissodactyla: summary and synthesis. In: Prothero DR, Schoch RM, editors. The evolution of perissodactyls. New York (NY); Oxford: Clarendon Press; Oxford University Press; p. 504–529.

Radulesco C, Sudre J. 1985. *Crivadiatherium iliescui* n. sp., nouvel embrithopode (Mammalia) dans le Paléogène ancien de la Dépression de Hateg (Roumanie). Palaeovertebrata. 15:139–157 [In French with English summary].

Ray CE, Domning DP, McKenna MC, Berta A, Deméré TA. 1994. A new specimen of *Behemotops proteus* (Order Desmostylia) from the marine Oligocene of Washington. Proc San Diego Soc Nat Hist. 29:205–222.

Rensberger JM, von Koenigswald W. 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology. 6(4):477–495.

Rose KD. 2006. The beginning of the age of mammals. Baltimore (MD): The Johns Hopkins University Press.

Rose KD, Holbrook LT, Rana RS, Kumar K, Jones KE, Ahrens HE, Missiaen P, Sahni A, Smith T. 2014. Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. Nat Commun. 5(5570):1–9.

Sanders WJ, Nemec W, Aldinucci M, Janbu NE, Ghinassi M. 2014. Latest evidence of *Palaeoamasia* (Mammalia, Embrithopoda) in Turkish Anatolia. J Vert Paleontol. 34(5):1155–1164. doi:10.1080/02724634.2014.850430.

Sanders WJ, Rasmussen DT, Kappelman J. 2010. Embrithopoda. In: Werdelin L, Sanders WJ, editors. Cenozoic mammals of Africa. Berkeley (CA): University of California Press; p. 115–122.

Sen S. 2013. Dispersal of African mammals in Eurasia during the Cenozoic: ways and whys. Geobios. 46(1–2):159–172. doi:10.1016/j.geobios.2012.10.012.

Sen S, Heintz E. 1979. *Palaeoamasia kansui* Ozansoy 1966, embrithopode (Mammalia) de l'Eocène d'Anatolie. Annales de Paléontologie (Vértébres). 65:73–91.

Simons EL. 1960. The Paleocene Pantodonta. Trans Am Phil Soc. 50(6):3–99. doi:10.2307/1005810.

Smith BH. 2000. 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. In: Teaford MF, Smith MM, Ferguson MWJ, editors. Development, function and evolution of teeth. New York (NY): Cambridge University Press; p. 212–227.

Springer MS, Burk-Herrick A, Meredith R, Eizirik E, Teeling E, O'Brien SJ, Murphy WJ. 2007. The adequacy of morphology for reconstructing the early history of placental mammals. Syst Biol. 56(4):673–684. doi:10.1080/10635150701491149.

Szalay FS, McKenna MC. 1971. Beginning of the age of mammals in Asia: the late Paleocene Gashato fauna, Mongolia. Bull Am Mus Nat Hist. 144:271–317.

Tabuce R, Delmer C, Gheerbrant E. 2007. Evolution of the tooth enamel microstructure in the earliest proboscideans (Mammalia). Zool J Linnean Soc. 149(4):611–628. doi:10.1111/j.1096-3642.2007.00272.x.

Tabuce R, Marivaux L, Adaci M, Bensalah M, Hartenberger JL, Mahboubi M, Mebrouk F, Tafforeau P, Jaeger JJ. 2007. Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. Proc R Soc B Biol Sci. 274(1614):1159–1166. doi: 10.1098/rspb.2006.0229.

Tong YS. 1979. Late Paleogene mammalian fauna from Taizicun, Xinjiang. In: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, editor. Paleontological investigation report (3). Beijing: Science Press; p. 82–101 [In Chinese].

von Koenigswald W. 1997a. Evolutionary trends in the differentiation of mammalian enamel ultrastructure. In: von Koenigswald W, Sander PM, editors. Tooth enamel microstructure. Rotterdam: Balkema; p. 203–235.

von Koenigswald W. 1997b. The variability of the enamel structure at the dentition level. In: von Koenigswald W, Sander PM, editors. Tooth enamel microstructure. Rotterdam: Balkema; p. 193–201.

von Koenigswald W. 2013. Unique differentiation of radial enamel in *Arsinoitherium* (Embrithopoda, Tethytheria). Hist Biol. 25(2): 183–192. doi:10.1080/08912963.2012.714658.

von Koenigswald W, Clemens WA. 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. Scanning Microsc. 6(1):195–218.

von Koenigswald W, Holbrook LT, Rose KD. 2011. Diversity and evolution of Hunter-Schreger band configuration in tooth enamel of perissodactyl mammals. Acta Palaeontol Pol. 56(1):11–32. doi:10.4202/app.2010.0021.

Wang BY, Zhang W. 1997. Mammalian fossils from Sanshui Basin, Guangdong, China. Vertebrat Palasiatic. 35(1):44–48 [In Chinese with English summary].

Wang JK, Li GF, Wang JS. 1981. The early Tertiary fossil fishes from Sanshui and its adjacent basin. Guangdong Palaeontol Sin. New Series C. (22):1–89 [In Chinese].

Wang M, Mayr G, Zhang JY, Zhou ZH. 2012. New bird remains from the Middle Eocene of Guangdong, China. Acta Palaeontol Pol. 57(3): 519–526. doi:10.4202/app.2011.0061.

Wells NA, Gingerich PD. 1983. Review of Eocene Anthracobunidae (Mammalia: Proboscidea) with a new genus and species, Jozaria palustris, from the Kuldana Formation of Kohat (Pakistan). Contrib Mus Paleontol Univ Mich. 26:117–139.

Xu YX. 1976. Some new forms of the Coryphodontidae from the Eocene of Xichuan, Henan. Vertebrat Palasiatic. 14(3):185–193 [In Chinese with English summary].

Zhang W. 1981. Mammalian fossils from the Paleocene of Sanshui Basin, Guangdong. Vertebrat Palasiatic. 19(3):293–294 [In Chinese].

Zhang XQ, Li G, Yang RL, Li HM. 2008. Palaeogene Ostracods from the Sanshui Basin of Guangdong. Acta Micropalaeontol Sin. 25(3): 235–265 [In Chinese with English summary].

Zhang YP. 1978. Two new genera of Condylarthan Phenacolophids from the Paleocene of Nanxiong Basin, Guangdong. Vertebrat Palasiatic. 16(4):267–274 [In Chinese with English summary].

Zhang YP. 1979. A new genera of Phenacolophids from the Paleocene of Chijiang Basin, Jiangxi. In: Institute of Vertebrate Paleontology and Paleoanthropology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, editor. The Mesozoic and Cenozoic red strata of the South China. Beijing: Schience Press; p. 416–432 [In Chinese].

Zhang YP. 1980. *Minchenella*, new name for *Conolophus* Zhang, 1978. Vertebrat Palasiatic. 18(3):257 [In Chinese with English summary]