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Systematic Palaeontology (Vertebrate Palaeontology)

Systematics and functional morphology of *Molarochoerus yuanmouensis* (Suidae, Mammalia) from the Late Miocene of Yunnan, China

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Abstract

The discovery of a propotamochoerine suid with unique features of the dentition and skull led to the naming of *Molarochoerus yuanmouensis* Liu & Pan [6]. Further study of the material reveals that this species was better adapted than *Sus scrofa* for the 'rooting' behaviour and that its dentition has morphological features indicating that it was eating hard food items. The posterior premolars are completely molarised, hence the generic name, the first time that any suid has been shown to possess almost perfectly molariform P4/s and p/4s. In lateral view the curvature of the occlusal surface of the upper cheek teeth is convex ventrally, the opposite of the usual situation in suids. The origins of the rostral musculature are exceptionally well developed, and the nasal bones are much more robust than is usually the case in Suinae, indicating powerful musculature and fortified osseous structures presumably for 'rooting' in hard ground or for extended periods of time. The masseteric musculature appears to have been more massive than it is in *Sus, Microstonyx* and *Propotamochoerus*. ***To cite this article: M. Pickford et al., C. R. Palevol 3 (2004)***.

Résumé

Systématique et morphologie fonctionnelle de *Molarochoerus yuanmouensis* (Suidae, Mammalia) du Miocène supérieur de Yunnan, Chine. La découverte d''un Suidae Propotamochoerini présentant des caractères dentaires et crâniens uniques a conduit à la création de *Molarochoerus yuanmouensis* Liu & Pan [6]. Une étude du matériel montre que cette espèce

Abbreviations: PD, refers to the "Pan Den Program"; YV, is the serial number of vertebrate specimens housed in the Institute of Culture Relics and Archaeology, Yunnan Province.

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était bien mieux adaptée au fouissage que *Sus scrofa*. Par ailleurs, les caractères morphologiques de sa dentition indiquent qu'il se nourrissait d'aliments coriaces. Les prémolaires postérieures sont complètement molarisées, d'où le nom générique, et c'est la première fois qu'un Suidae présente des P4 supérieures et inférieures presque parfaitement molariformes. En vue latérale, la courbure de la surface occlusale des dents jugales supérieures est convexe ventralement, différant ainsi de la morphologie classique des Suidae. La musculature rostrale est exceptionnellement bien développée et les os nasaux sont beaucoup plus robustes que chez les autres Suinae, suggérant des structures musculaires et osseuses puissantes, probablement liées au fouissage, soit dans des sols, soit sur une longue durée. Les muscles massétériens sont plus puissants que dans les genres *Sus, Microstonyx* et *Propotamochoerus*. ***Pour citer cet article : M. Pickford et al., C. R. Palevol 3 (2004)***.

Keywords: Yuanmou; Yunnan; China; Late Miocene; Suidae; Propotamochoerini

Mots clés : Yuanmou ; Yunnan ; Chine ; Miocène supérieur ; Suidés ; Propotamochoerini

1. Introduction

Excavations were made at Yuanmou, Yunnan, China (Fig. 1), from 1987 to 1998, during which a large quantity of mammalian fossils was collected, including abundant suids. According to their dimensions, the suid fossils from the site comprise three taxa of which the medium sized species was thought by Pan [11] to belong to Suinae, but to an unknown genus. As the specimens accumulated, and especially when a skull and mandibles were recovered, a better idea of the affinities of this species emerged and it was named *Molarochoerus yuanmouensis* by Liu and Pan [6]. The unique cranial and dental morphology of this suid prompt us to examine its systematic position and functional morphology in greater detail.

2. Geochronology of Yuanmou

The age distribution of *Propotamochoerus* is similar in Europe and the Indian Subcontinent. In Europe it ranges from MN 10–MN 13, and in the Indian Subcontinent it spans the Nagri, Dhok Pathan and lower Soan units [13]. All known Chinese Propotamochoerini suids are Late Miocene in age [7,15]. Because *Molarochoerus yuanmouensis* possesses some progressive characters, it is probably a late member of the Propotamochoerini lineage. It suggests an age for Yuanmou younger than Kaiyuan, (Xiaolongtan) China [2,15,21] Chiang Muan, Thailand [16] and the Dhok Pathan succession in Pakistan [9,13,17] but is closer in age to Lufeng, China [10] and Lantian, China [8,22].

This conclusion is supported by the other suoids from the site, the suids *Chleuastochoerus stehlini* and *Hippopotamodon hyotherioides* and the palaeochoerid *Yunnanochoerus lufengensis*. For example, the range of variation in length of M3/ and m/3 of *Hippopotamodon hyotherioides* is almost the same for Lufeng (32–36.5 mm for M3/, 34–36 mm for m/3) and Yuanmou (31–36 mm for M3/, 34–36.5 mm for m/3), and shorter than the propotamochoerine material from northern China (37–44 mm for M3/, 37–46 mm for m/3) [15] (Fig. 2). The rodents [19] and palaeomagnetism [20] provide supportive evidence that the age of Yuanmou is ca 8–7 Ma.

3. Systematic description

Artiodactyla Owen, 1848
Suidae Gray, 1821
Suinae Gray, 1821
Propotamochoerini Pickford, 1988
***Molarochoerus* Liu & Pan, 2003**

Type species: *Molarochoerus yuanmouensis* Liu & Pan, 2003

Species *Molarochoerus yuanmouensis* Liu & Pan, 2003

Holotype: skull (PDYV 2000) lacking much of the neurocranium (Figs. 3 and 4).

Paratypes: left and right maxillae with P1/–M1/ (PDYV 0070 + 0071), right mandible with p/3–m/3 (PDYV 1666), left mandible with m/2–m/3 (PDYV 0766).

Referred material: right maxilla with P2/–P4/ (PDYV 1750), right maxilla with P3/–P4/ (PDYV 0844), right P2/–P4/ (PDYV 0428), left mandible with m/1–m/3 (PDYV 0878), left mandible with dm/4–m/1

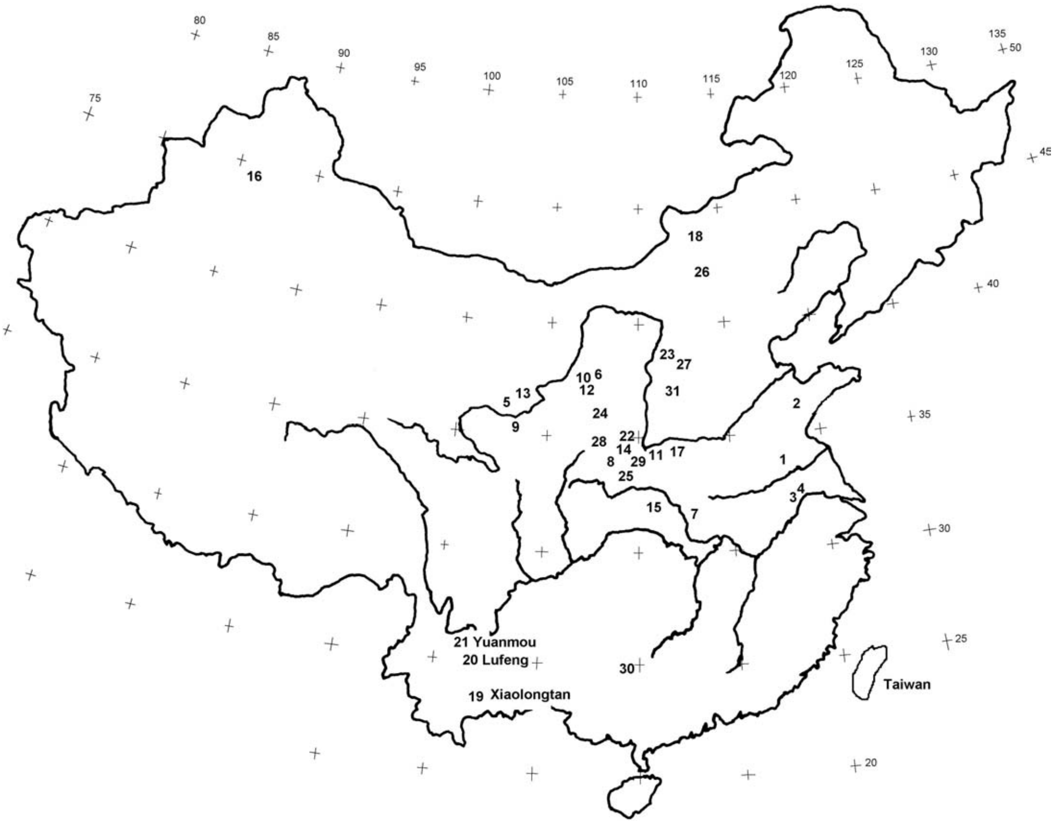

Fig. 1. Location of Neogene suid localities in China. **1**. Sihong (Xiacaowan); **2**. Shanwang, **3**. Puzhen, **4**. Lingyanshan, **5**. Lierbao (Nanhawangou), **6**. Yehuli Jianzhi, **7**. Zhongxiang, **8**. Koujiacun, **9**. Guanghe, **10**. Maerzuizhigou, **11**. Xin'an (Jianshan), **12**. Jingzuizhigou, **13**. Xianshuihe, **14**. Lengshuigou, **15**. Erlanggang, **16**. Halamagai, **17**. Tungshapo, **18**. Tung Gur, **19**. Xiaolongtan (Kaiyuan), **20**. Lufeng, **21**. Yuanmou, **22**. Binxian, **23**. Baode, **24**. Qingyang, **25**. Liu Lao Po (Lantian), **26**. Ertemte, **27**. Jingle, **28**. Leijiahe, **29**. Youhe, **30**. Liucheng, **31**. Qinxian (Chinhsien).

Fig. 1. Localisation des gisements néogènes à suidés de Chine.

(YV 18), left mandible with m/1–m/2 (YV 10) and about 99 isolated teeth.

Etymology: 'molar' (English) refers to the molarised condition of the P4/ and p/4, 'choer' (Greek) for 'pig'; '*yuanmouensis*' signifies the discovery locus of the species.

Type locality and horizon: Xiaohe, Luilao, Yuanmou, Yunnan Province, China; late Late Miocene (ca 8–7 Ma).

Diagnosis (modified from Liu & Pan [6]): medium sized Suidae, Suinae, Propotamochoerini with orbits far back in relation to the face and palate; zygomatic arches depart from maxilla at right angles opposite M1/ and are expanded and thickened anteriorly; parietal crests converge sharply towards each other from immediately behind the post-orbital processes running obliquely disto-sagittally; no diastema between P1/ and P2/, but a short diastema exists between p/1 and p/2; P4/ and p/4 are fully molarised; anterior lophid of p/4 is wider than the posterior lophid; p/4 has two main anterior cusps which widen the anterior part. Talonid of p/4 large and high, with three cusps (hypoconid, entoconid and hypoconulid). The p/4 hypoconid and entoconid wide apart, and hypoconulid close to the postero-lingual corner of the hypoconid. No posterior cingulum; P4/ consists of two buccal cusps and two lingual cusps (behind the protocone there is a distinct hypocone), and its mesio-distal length is slightly greater than the bucco-lingual breadth. P4/ with small cusplets in sagittal valley; P3/ with large and inflated lingual cusp, main cusp of P3/ oriented diagonally, forming an angle of about 30° with the sagittal plane of the skull; molar enamel

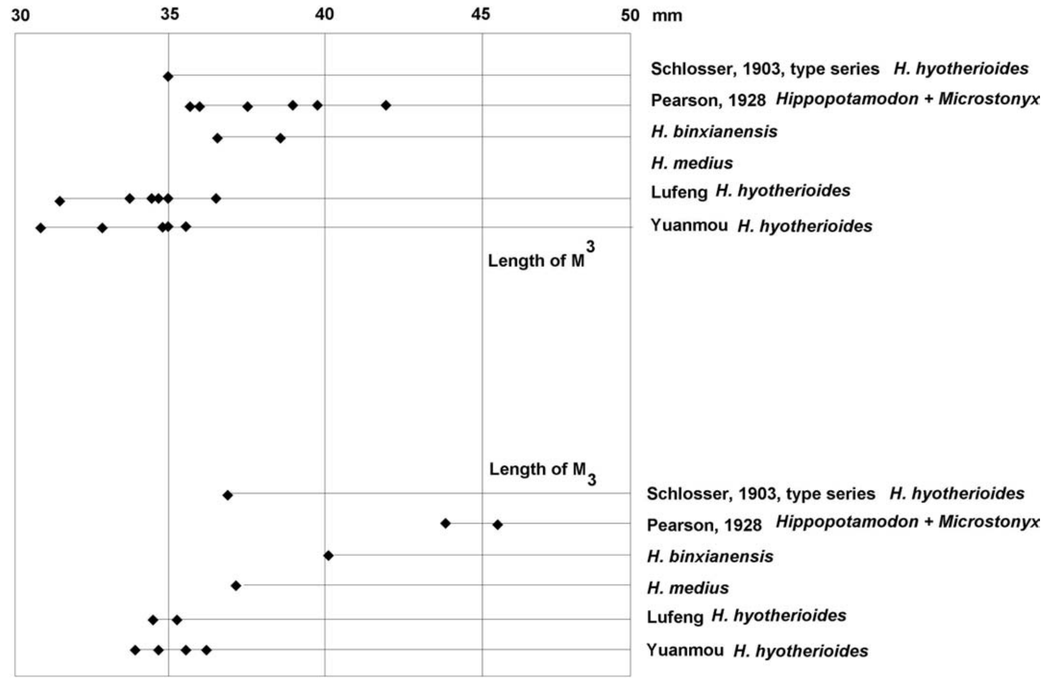

Fig. 2. Variability in length of third molars in large Late Miocene Chinese suines. Note the close similarity in the ranges of variation of lengths of M3/ and m/3 at Lufeng and Yuanmou.

Fig. 2. Variabilité des longueurs des dernières molaires chez les grands suidés du Miocène supérieur de Chine. Noter la similitude dans les variations de longueur des M3/ et m/3 de Lufeng et de Yuanmou.

thickness moderate to thick, enamel surface complexly wrinkled, furchen shallow, the male mandible is robust and that of the female is slender. In lateral view upper tooth row is convex occlusally (lower tooth row concave occlusally). Origin of *m. levator rostri* greatly enlarged. Nasals robust.

4. Differential diagnosis

Molarochoerus differs from all other genera of Propotamochoerini (*Miochoerus, Chleuastochoerus, Microstonyx, Hippopotamodon, Eumaiochoerus* and *Propotamochoerus*) by its possession of almost completely molarised P4/ and p/4, and partly molarised P3/ and p/3, the exaggerated development of the origins of the facial musculature, and the robustness of the nasal bones.

5. Description

5.1. Skull

PDYV 2000 is a complete but bilaterally compressed snout and dentition that has also suffered some plastic deformation (Figs. 3 and 4). It lacks most of the neurocranium. The right anterior part of the zygomatic arch is preserved.

Lateral view: the snout is long, the anterior tip of the nasal bone is broken, but it terminates slightly behind the anterior extremity of the premaxilla (Fig. 4-1). The flange above the canine is not very developed, nor is it elongated antero-posteriorly. The anterior root of the zygomatic arch extends laterally, and it departs from the maxilla at a right angle opposite M1/, while the rear part of the zygomatic root is below the anterior of the orbit. The anterior edge of the arch is relatively slender, but the lateral and posterior parts are robust with extensive fossae for the origin of the levator rostri musculature (Fig. 4-1). The anterior edge of the orbit lies above the pterygoid process of the palatine, the orbit is rounded and of medium size. The supraorbital process is distinct, the supraorbital crest is well developed, and the infraorbital foramen is above P3/ and P4/. The distance from the anterior edge of the orbit to the front of the premaxilla is 260 mm.

Ventral view: the palatine (Fig. 3-2) is long and on the left side it is possible to see that palatine foramen is opposite to the postero-lingual side of M2/. The incisive foramen is opposite to the postero-lingual end of I1/ and the antero-lingual part of I2/, and is elliptical in outline. All three incisor alveoli are preserved, those for I1/ and I2/ are large and deep, but the alveolus of I3/ is small and located on the lateral surface of the snout immediately above a low occlusal ridge on the premaxilla, and behind the alveolus of I2/. According to the preserved section of the canine in the alveolus, it was not very large. The P1/ is preserved on the right side, the P2/–M1/ are heavily worn, but the M2/ and M3/ are lightly worn, suggesting that the individual was fully adult when it died but was not senile. There is no diastema between P1/ and P2/, but between P1/ and the upper canine there is a gap of 10 mm, and between the canine and I3/ the diastema is 22 mm long. P1/–M3/ is 132 mm, the premolar row (P1/–P4/) is 62 mm, M1/–M3/ is 70 mm, and the distance from the pterygoid process of the palatine to the anterior tip of the premaxilla is 266 mm. The pterygoid process of the palatine and sphenoid is situated 25 mm behind the M3/.

Occipital view: the neurocranium is missing and only the left frontal sinus can be observed.

Dorsal view: the facial part is much narrower than it would have been in life due to the compression and distortion that the specimen has undergone (Fig. 3-1). The nasals and anterior part of the frontals are compressed and have been deformed into a wide crest. The frontals and anterior part of the parietals have been crushed, the posterior portion of the parietals is missing. The supraorbital foramen is located above the orbit, and is oval in outline. Behind the postorbital process the two parietal crests run posteriorly and quite sharply sagittally and approach each other closely, but because the neurocranium is broken at this point it is not possible to determine whether they joined to form a sagittal crest.

5.2. Maxilla

PDYV 0070 and PDYV 0071 are two maxillae with P1/–M1/, belonging to the same individual. Although they are separated at the midline of the palate, palatal width at P2/ can be estimated to be ≥ 44 mm. In the left maxilla (PDYV 0070), the diastema between P1/ and C1/ is 12 mm, whereas on the right one (PDYV 0071) it is 10 mm. The length of the left premolar row (P1/–P4/) is 59.5 mm, while on the right side it is 55.5 mm. The left maxilla is slightly distorted.

5.3. Upper dentition (Table 1)

The central upper incisor (Fig. 5-1a and b) is typical of the Propotamochoerini, with several ridges and grooves on the occlusal and distal aspects, and a smoother labial surface.

The first upper premolar (Fig. 5-2) consists of a central main cusp with rounded anterior and posterior margins, and there are lingually curved anterior and posterior crests ending in accessory cusplets, and there is a disto-lingual cingulum. It has two roots.

The second upper premolar (Fig. 5-3) is a larger and wider version of P1/, and there is a bigger disto-lingual cusplet, the base of the cusp is inflated on its lingual side, from which a beaded lingual cingulum runs anteriorly and posteriorly. It has two roots.

The P3/ (Figs. 5-4 and 5-6) is approximately triangular in occlusal outline, the lingual cusp is located forwards of its usual position in suids, being almost at the same level as the main cusp, and for this reason the widest part of the tooth is in the middle. The lingual cusp is almost as high as the main cusp. The main cusp of P3/ is oriented diagonally, forming an angle of about 30° to the sagittal plane of the skull. Behind the main cusp there is a closely applied secondary cusp, which blends into the main cusp after slight wear. The lingual cingulum is developed forwards to connect with the anterior cusplet and backwards to connect with the posterior cusplet. In the sagittal valley there is small beaded cusplet. The tooth has three roots, one anterior and two posterior.

The P4/ (Figs. 5-5 and 5-6) is trapezoidal in occlusal outline, and is almost completely molarised, being comprised of four main cusps arranged in two transverse pairs. Most specimens are slightly longer mesiodistally than bucco-lingually. The two buccal cusps are wide apart, and lingually there is a distinct cusp (hypocone) behind the protocone. The protocone is displaced forwards in line with the paracone, and the hypocone is the smallest cusp. There is a small cusplet in the sagittal valley. The anterior accessory cusp is distinct, but there is no distal one. The lingual cingulum is well developed and the lingual flare is marked. There are three roots, two buccal ones and one lingual.

The M1/ (Fig. 5-7) is approximately rectangular in occlusal outline, and it has four similar sized main cusps, with anterior, median and posterior accessory cusplets, and anterior and posterior cingula. The main

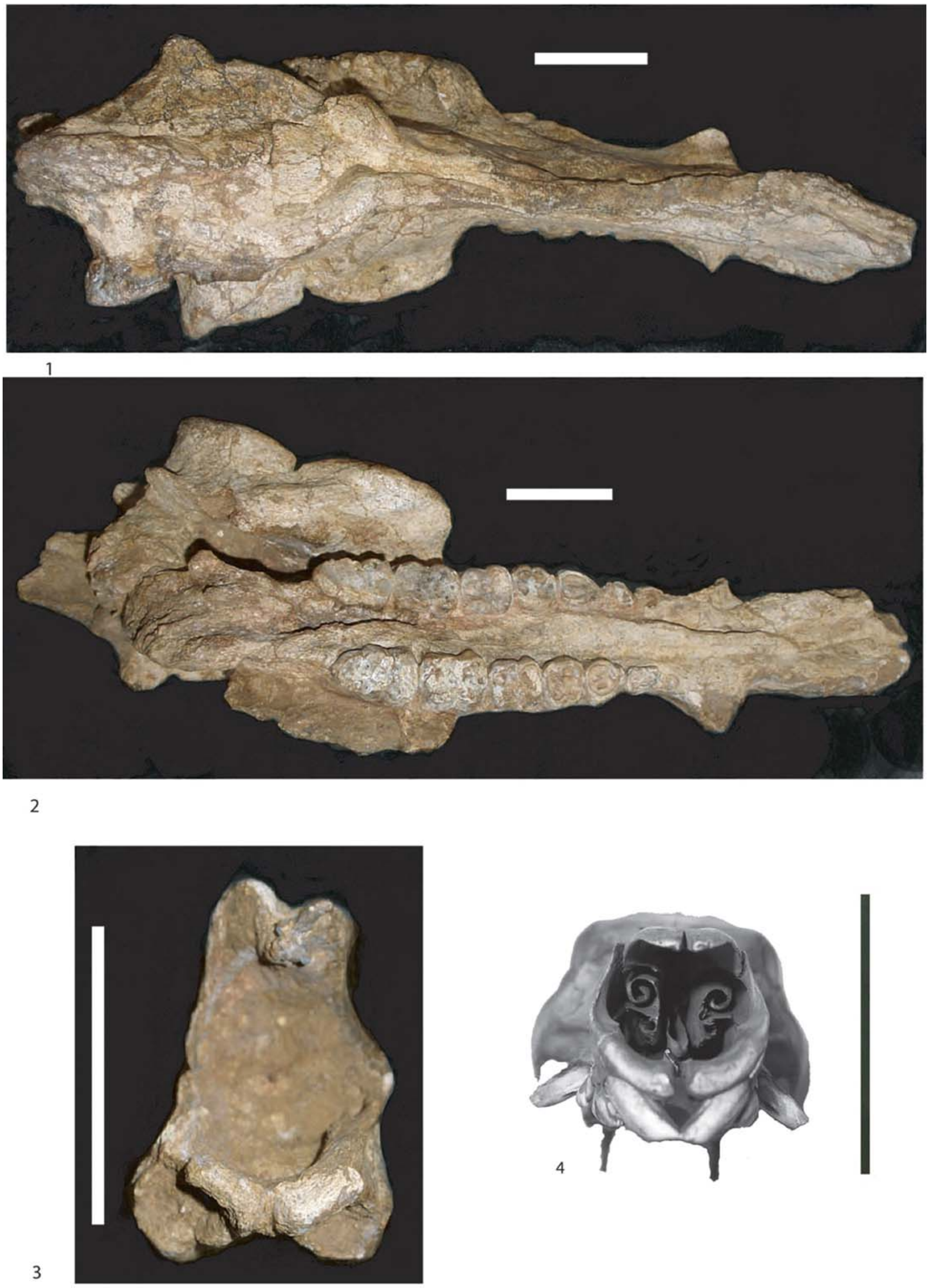
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Fig. 4. Comparison of snout musculature in *Molarochoerus yuanmouensis* and *Sus scrofa*. (lr = origin of *m. levator rostri*; dr = origin of *m. depressor rostri*; dnl = origin of *m. dilatator naris lateralis*) (scale: 10 cm). **1**. *Molarochoerus yuanmouensis* PDYV 2000. **2**. *Sus scrofa*.
Fig. 4. Comparaison des muscles faciaux de *Molarochoerus yuanmouensis* et *Sus scrofa*. (lr = origine du *m. levator rostri*; dr = origine du *m. depressor rostri*; dnl = origine du *m. dilatator naris lateralis*) (échelle : 10 cm). **1**. *Molarochoerus yuanmouensis* PDYV 2000. **2**. *Sus scrofa*.

Fig. 3. *Molarochoerus yuanmouensis* and *Sus scrofa* (scale: 10 cm). **1**. Dorsal view of holotype snout of *Molarochoerus yuanmouensis* PDYV 2000. Note the bilateral compression. **2**. Palatal view of holotype of *Molarochoerus yuanmouensis* PDYV 2000. **3**. Anterior view of holotype snout of *Molarochoerus yuanmouensis* PDYV 2000. Bilateral compression has occurred. Note the robustness of the nasal bones. **4**. Anterior view of snout of *Sus scrofa*. Note the slender nasal bones.
Fig. 3. *Molarochoerus yuanmouensis* et *Sus scrofa*. (échelle : 10 cm). **1**. Vue dorsale du museau de l'holotype de *Molarochoerus yuanmouensis* PDYV 2000. Noter la compression bilatérale. **2**. Vue palatine de l'holotype de *Molarochoerus yuanmouensis* PDYV 2000. **3**. Vue antérieure de l'holotype de *Molarochoerus yuanmouensis* PDYV 2000. Noter la présence d'une compression bilatérale et la robustesse des nasaux. **4**. Vue antérieure du museau de *Sus scrofa*. Noter la gracilité des nasaux.

cusps are not high, the enamel is moderately thick and is wrinkled, the *furchen* are shallow, and the median transverse valley is not wide.

The M2/ (Fig. 5–8, Fig. 5–10) is a larger version of M1/, but is proportionally longer.

The M3/ (Fig. 5-11) is approximately trapezoidal in occlusal outline, and is composed of four main cusps and a talon, The anterior two lophs are morphologically similar to M2/, the talon is about 1/4 of the total length of the tooth, and consists of three flat cusps, the lingual one being the largest, the buccal cusp being small. The rear half of the tooth narrows perceptibly distally.

The dM4/ (Fig. 5-9) is similar to M1/ save for its more trapezoidal outline, and the less well pronounced main cusps.

5.4. Mandible

PDYV 1666 is part of a horizontal ramus of a mandible carrying p/3–m/3, but the ascending ramus is missing. The mandibular body is slender, and the cheek teeth are in medium wear.

PDYV 0878 is a slender horizontal ramus preserving its ventral margin, containing m/1–m/3.

PDYV 0766 is a well-preserved left horizontal ramus where m/2–m/3, c/1 to m/1 have been lost, but the roots are preserved, part of m/2 is damaged, but the m/3 is intact (Fig. 5-17). The body is robust, and the base of the mandible broadens anteriorly. The root of the canine preserved in the alveolus is large, from which we infer that the jaw probably represents a male individual. There is a pair of mental foramina below the p/1, which are close together, and there is a field of small pits above them, presumably for firm attachment of the skin or other superficial tissue. There is also a foramen below p/2–p/3.

5.5. Measurements of the mandibles

In PDYV 0766 the basal mandibular width at p/2 is 38 mm, the diastema between p/1 and p/2 is 9 mm, the length of the premolar row (p/1–p/4) is 131 mm, and p/2–m/3 is 114 mm. Other measurements of the mandible are provided in Table 2.

5.6. Lower dentition

Canines are of the 'verrucose' type, some specimens are larger than the others, perhaps reflecting sex differences.

The p/3 (Fig. 5-12) has an elongate crown, and there is a shallow groove behind the main cusp, which would

Table 1
Molarochoerus yuanmouensis measurements (in mm) of the upper teeth (L = length; B = breadth, ? = no measurement possible).
Mensurations (en mm) des dents supérieures de *Molarochoerus yuanmouensis* (*L* = longueur; *B* = largeur, ? = mesure impossible)

P1/		P2/		P3/		P4/		M1/		M2/		M3/	
L	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*
10.6	6.0	14.0	10.0	15.3	16.3	16.3	15.6	18.1	15.7	21.2	18.0	27.4	17.8
10.3	5.6	13.0	9.4	16.6	15.0	16.1	16.3	18.1	16.1	21.4	18.3	27.0	16.0
10.8	5.6	13.0	9.1	16.6	16.4	15.9	15.3	17.1	16.4	20.4	18.8	27.1	17.1
10.1	5.7	14.9	10.5	15.0	14.6	16.2	16.3	17.5	16.4	21.1	17.0	27.9	17.8
?	5.7	13.9	9.6	15.3	14.3	16.1	15.8	17.4	16.0	21.7	19.1	27.0	17.2
11.0	?	14.2	10.0	15.5	?	17.0	15.6	18.0	16.2	21.3	18.6	25.3	17.0
		15.0	10.4	15.7	14.8	?	16.1	17.7	16.2	23.4	20.1	28.6	17.4
		12.8	9.9	14.1	14.5	14.7	15.9	19.6	16.6	23.1	19.1	28.0	?
		13.3	?	16.5	16.2	16.1	16.5	19.6	18.9	22.3	17.6	28.4	18.5
		13.4	10.0	16.4	16.1	16.4	16.1	19.2	15.5	22.1	18.1	28.0	17.8
		15.0	10.3	17.2	16.0	18.0	17.9					28.2	16.1
		14.1	?	18.0	16.1	17.6	17.0					?	19.5
		13.8	10.5	14.2	14.2	14.1	15.0					22.5	17.9
		13.2	9.4	15.4	14.2	15.6	14.9					28.4	18.8
				15.9	14.3							27.2	18.7
												25.0	16.7
												27.0	18.0
												27.8	18.0
												27.5	18.5

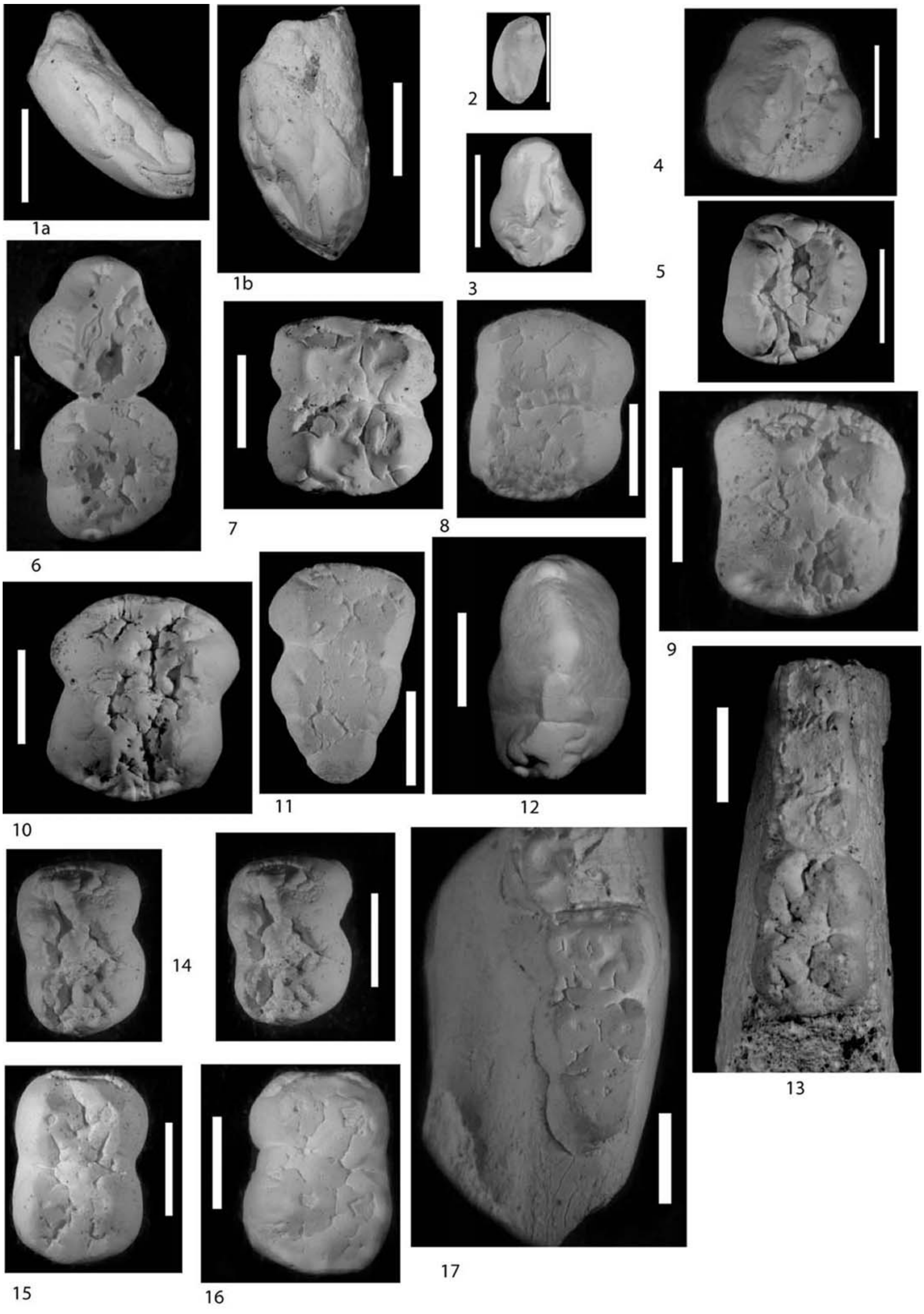
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Table 2
Measurements (in mm) of the mandibles of *Molarochoerus yuanmouensis*.
Mensurations (en mm) des mandibules de *Molarochoerus yuanmouensis*

Specimen	Length p/3–m/3	Length p/3-p/4	Length m/1–m/3	Width of mandible at m/1	Depth of mandible at m/1	Width of mandible at m/3	Depth of mandible beneath m/3	Depth of mandible beneath p/2
PDYV 1666	100	33	67	—	—	—	—	—
PDYV 0878	—	—	68	18 (lower edge)	45	11 (lower edge)	28	—
PDYV 0766	—	—	70	30	50	19	55	52

disappear with light wear. The anterior accessory cusp is half the height of the crown, the talonid is high, and there is a groove separating it from the main cusp. The talonid is somewhat inflated on its lingual side. In fact, this tooth looks like a p/4 of *Propotamochoerus*.

The p/4 (Fig. 5-14) of *Molarochoerus* is approximately rectangular in occlusal outline, the anterior part being slightly wider than the posterior half. This tooth is completely molarised, possessing four main cusps arranged in two transverse pairs. The two main anterior cusps (protoconid and metaconid) are separated by a deep and wide groove, the lingual cusp is almost the same height as the buccal one, and is slightly posterior to it. The antero-buccal cusp is obliquely oriented and its anterior crest runs obliquely anteriorly towards the lingual side, terminating at the base of the anterior part of the lingual cusp where it forms a small, low anterior accessory cusp. The posterior crest of the antero-buccal cusp runs slightly obliquely towards the buccal end of the floor of the median transverse valley. In some specimens this posterior crest is not well developed, and in these few teeth the antero-buccal cusp is lower. There is a well-developed median accessory cusp behind the two main cusps, which is lower than the main cusp and has a crest linking it to the buccal main cusp, which itself is slightly obliquely oriented. The talonid is nearly the same height as the main cups, and its morphology recalls the posterior part of m/1, the entoconid and hypoconid being located at the same level opposite one another but separated from each other by a deep groove. The hypoconulid is situated to the postero-lingual side of the hypoconid. There is an anterior cingulum, but none posteriorly. The tooth has three roots, one anteriorly (incipiently bifid) and two posteriorly.

The m/1 (Figs. 5-13 and 5-15) is rectangular in occlusal outline with four main cusps. The crown is low, the lingual cusps being slightly higher than the buccal ones. The median accessory cusp and groove system are well developed. There are one or two basal pillars in the buccal end of the median transverse valley, the lingual side not having any. The anterior and posterior cingula are well developed. The hypoconulid is strong but the anterior accessory cusp is indistinct.

The second lower molar (Figs. 5-16 and 5-17) is an enlarged version of m/1.

The m/3 (Fig. 5-17) consists of four main cusps and a talonid. The two anterior lophs are similar to the m/2, behind which there are three small cusps forming the talonid. Of these the buccal one is the largest. The talonid is narrower than the two anterior lophs and is

Fig. 5. Casts of upper and lower teeth of *Molarochoerus yuanmouensis*. (scale: 10 mm). 1. Left I1/, YVY 87-003, **(1a)** occlusal and **(1b)** distal views. **2**. Right P1/, YVY 87-032, occlusal view. **3**. Right P2/, PDYV 1845, occlusal view. **4**. Right P3/, YV 04, occlusal view. **5**. Right P4/, PDYV 0143, occlusal view. **6**. Right P3/–P4/ in maxilla fragment, PDYV 0844, occlusal view. **7**. Left M1/, YV 05, occlusal view. **8**. Left M2/, PDYV 0293, occlusal view. **9**. Left dM4/, PDYV 1793, occlusal view. **10**. Left M2/, YV 06, occlusal view. **11**. Right M3/, PDYV 0102, occlusal view. **12**. Left p/3, YVY 87-015, occlusal view. **13**. Left dm/4–m/1 in mandible, YV 18, occlusal view. **14**. Right p/4, YV 14, stereo occlusal view. **15**. Right m/1, PDYV 1841, occlusal view. **16**. Left m/2, PDYV 0347, occlusal view. **17**. Left m/2–m/3 in mandible, PDYV 0766, occlusal view.
Fig. 5. Moulages des dents supérieures et inférieures de *Molarochoerus yuanmouensis* (échelle : 10 mm). **1**. I1/ gauche, YVY 87-003, vues **(1a)** occlusale et **(1b)** distale. **2**. P1/ droite, YVY 87-032, vue occlusale. **3**. P2/ droite, PDYV 1845, vue occlusale. **4**. P3/ droite, YV 04, vue occlusale. **5**. P4/ droite, PDYV 0143, vue occlusale. **6**. P3/–P4/ droites dans maxillaire, PDYV 0844, vue occlusale. **7**. M1/ gauche, YV 05, vue occlusale. **8**. M2/ gauche, PDYV 0293, vue occlusale. **9**. dM4/ gauche, PDYV 1793, vue occlusale. **10**. M2/ gauche, YV 06, vue occlusale. **11**. M3/ droite, PDYV 0102, vue occlusale. **12**. p/3 gauche, YVY 87-015, vue occlusale. **13**. dm/4–m/1 gauches dans fragment de mandibule, YV 18, vue occlusale. **14**. p/4 droite, YV 14, vue occlusale stéréoscopique. **15**. m/1 droite, PDYV 1841, vue occlusale. **16**. m/2 gauche, PDYV 0347, vue occlusale. **17**. m/2–m/3 gauche dans mandibule, PDYV 0766, vue occlusale.

positioned towards the buccal side of the crown, and it comprises 1/4 of the length of the tooth.

The dm/4 (Fig. 5-13) is composed of three lophs, the anterior part is narrower than the posterior part, and there is a distinct accessory cusplet in the centreline of the tooth behind each loph.

6. Taxonomic discussion

There are four recognised tribes within the subfamily Suinae: Propotamochoerini, Hippohyini, Suini and Phacochoerini [14]. Phacochoerini occur only in Africa, and they have peculiar cranial and dental characters related to their herbivorous diet and savannah environment [3]. Hippohyini is a highly specialised tribe of pigs, with short faces, anteriorly positioned orbits, hypsodont cheek teeth, thin molar enamel, vertically implanted incisors and lower cheek teeth with no buccal pillars [13]. These two groups clearly differ from the Yuanmou specimen.

The Yuanmou species has some similarities to the tribe Suini, including p/4 with a high talonid and a distinct cusplet behind the protocone in P4/. These similarities are probably plesiomorphic at the tribal level, as they are shared between Propotamochoerini and Suini in general. Out of all the tribes of the subfamily Suinae, we consider that the Yuanmou species belongs to Propotamochoerini for the following reasons. **(1)** All the Propotamochoerini possess a 'Dicoryphochoerine' p/4, and although the Yuanmou p/4 is molarized its underlying morphology accords with this configuration, and it is likely derived from this type. **(2)** The Yuanmou zygomatic arch departs from the face of the maxilla laterally at M1/ forming a right angle with the surface of the snout, whereas in Suini the zygomatic arch departs at a gentle angle from the maxilla. **(3)** The zygomatic arches are inflated and occupied by sinuses in Propotamochoerini and are slender without sinuses in Suini. **(4)** The orbit in the Yuanmou fossil is more posteriorly positioned compared with Suini. **(5)** The Yuanmou specimen has well-developed lingual cingula and talons in P2/ and P3/. 5. M3/ and m/3 of Suini have better developed talon/ids.

Six genera have been attributed to Propotamochoerini by Pickford [14], while Chen [1] added a seventh named *Miochoerus*. *Molarochoerus* is the eighth genus to be attributed to the tribe. The others are *Chleuastochoerus* Pearson, 1928, *Microstonyx* Pilgrim, 1926, *Hippopotamodon* Lydekker, 1877, *Eumaiochoerus* Hurzeler, 1982, and *Propotamochoerus* Pilgrim, 1926.

The measurements of the teeth of *Molarochoerus youanmouensis* are provided in Tables 1 and 3. The

Table 3
Molarochoerus yuanmouensis measurements (in mm) of the lower teeth (L = length; B = breadth, ? = no measurement possible).
Mensurations (en mm) des dents inférieures de *Molarochoerus yuanmouensis* (*L* = longueur; *B* = largeur, ? = mesure impossible)

p/3		p/4		m/1		m/2		m/3		dm/4	
L	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*
15.8	10.4	17.0	13.0	18.2	12.8	19.2	14.4	30.6	16.3	21.6	9.5
14.9	9.8	17.5	12.1	20.4	13.0	21.2	14.7	30.7	16.9	21.1	9.5
16.3	10.2	18.6	13.5	18.7	12.8	20.4	13.1	29.4	15.2		
		17.8	13.0	19.2	13.1	22.0	16.2	32.8	17.0		
		17.4	12.8	18.6	12.7	22.2	15.0	30.4	16.6		
		18.2	12.0	18.7	12.6	20.5	14.6	29.6	15.2		
		17.5	13.1	18.2	12.9	21.3	15.5	28.5	16.5		
		18.0	13.0	17.9	12.8	21.4	14.8	29.4	15.5		
		18.2	12.0	17.5	12.3	22.0	15.6	28.5	15.5		
		17.0	12.0	17.5	?	20.1	15.3				
		17.6	12.1	18.2	13.0	20.2	15.0				
		16.9	11.0	18.7	13.0	20.5	15.4				
		16.5	11.9			22.8	15.0				
		18.0	13.0			22.5	15.4				
		18.6	13.0								
		18.0	12.0								
		16.4	13.4								

Yuanmou species is much smaller than species of *Microstonyx* and *Hippopotamodon*, and is much bigger than *Chleuastochoerus* and *Miochoerus. Microstonyx* is typically found in Europe and northern China [7] whereas *Hippopotamodon* occurs in southeastern Europe, the Indian subcontinent [13], Thailand [16] and southern China respectively [13]. Both these genera are both large, and possess a number of similarities in skull and dental morphology, but *Microstonyx* differs from *Hippopotamodon* by its elongated snout, more parallel parietal ridges, smaller canine and absent p/1 [7,13]. *Eumaiochoerus* is an endemic island form from the Upper Miocene of Tuscany, Italy [5]. It differs from the Yuanmou suid by: **(1)** p/1 often absent, **(2)** the talonid of m/3, consisting of two large cusps, **(3)** its larger size.

Chleuastochoerus is a small endemic Late Miocene suid of China [12]. Its zygomatic arch extends abruptly laterally, its anterior root departing from the maxilla at right angles opposite M1/, the orbit is located posteriorly, and the P4/ has a cusplet behind the protocone. These characters are similar to the Yuanmou species, but *Chleuastochoerus* is a diminutive suid, the teeth are more primitive and shorter, the P4/ does not have a sagittal cusplet, the M3/ has a small talonid, the facial part is relatively short, the tip of the nasal is more distally located compared to the tip of premaxilla, and it has a well-developed highly recurved canine flange [12].

7. Functional morphology of the face and dentition

7.1. Facial musculature

In lateral view the origin of the *levator rostri* musculature in *Molarochoerus* occupies a vast area extending from behind the infraorbital foramen anteriorly to the orbital margin posteriorly and from the naso-maxillary suture dorsally to the ventral edge of the zygomatic arch ventrally (Fig. 4(1)). This area is huge when compared with the conformation in *Sus scrofa* (Fig. 4(2)). It is much larger than in *Propotamochoerus hysudricus* [13] and *Microstonyx major* [7], but its position and the lateral flare of the zygomatic arches of these genera are comparable, suggesting that *Molarochoerus* is closely related to them, and was probably derived from one or other of them, most probably the former. In *Molarochoerus*, the origins of the *depressor rostri* and *dilatator naris lateralis* muscles are located beneath the zygomatic arch in an area where the arch thickens medio-laterally, as in *Propotamochoerus* and *Microstonyx*. The homologous muscle origins in *Sus scrofa* occur on the lateral surface of the maxilla, separated from that of the *levator rostri* by a prominent but low crest. In addition, in *Sus* the ventral margin of the zygomatic arch is slim, and not at all medio-laterally expanded (Fig. 4–2), [18] unlike *Microstonyx* in which it is inflated and occupied by extensive sinuses [7]. The impression obtained from the vastness of the origin of the *levator rostri* muscle in *Molarochoerus*, allied to the depth of the fossa and the robustness of the surrounding bone margin is one of immense muscular power. The same impression is obtained when examining the ventral margin of the zygomatic arch, indicating powerful *depressor rostri* and *dilatator naris lateralis* muscles.

The function of all these muscles relates to the rostral disc, which in pigs occurs at the anterior extremity of the snout [3,4]. The disc is rotated dorsally, ventrally and laterally depending on which muscle is acting. When more than one muscle is functioning, complex movements of the disc are possible, including during the well-known ‘rooting’ behaviour of pigs, when the snout is used as a ‘plough’ to uproot bulbs, tubers, corms, roots, truffles and other underground food resources from soft soil. Bushpigs (*Potamochoerus larvatus* and *Potamochoerus porcus*) can produce 5–10–m-long, 10-cm-wide and 15–20-cm-deep ‘trenches’ in humid to wet soil during extensive rostral ploughing bouts.

The vastness of the facial musculature in *Molarochoerus* suggests that the rooting behaviour in this genus was extremely well developed, and it may indicate that the genus could plough in relatively hard substrates, or for extended periods of time. In support of the former suggestion, it is noted that the nasal bones in *Molarochoerus* appear to be dorso-ventrally thickened in comparison with those of *Sus scrofa* (Fig. 3-3), making them much more robust and thus stronger, presumably for resisting damage or bending forces while rooting.

7.2. Dentition

The cheek tooth rows of *Molarochoerus* are unique within a suine framework, on account of the ventrally convex curvature of the occlusal surface of the upper cheek teeth in lateral view. In other suines, the upper cheek tooth row, in lateral view, is concave and the lower one is convex. This convex upper tooth row (and concave lower tooth row) curvature occurs in all adequately preserved material from Yuanmou, and is not due to post–mortem distortion.

Other unique features of the dentition of *Molarochoerus* concern the molarization of the posterior premolars, and the anterior shift of the area of maximal chewing forces from the molars towards the premolars. In the snout, PDYV 2000, wear of the cheek tooth row is greatest at P3/, P4/ and M1/, and the same applies to the mandible PDYV 1666. These teeth are at the centre of the curved cheek tooth row, and evidently absorb the greatest masticatory forces during chewing. Enlarged buccal roots of the upper teeth are clearly evident on the lateral surface of the maxilla, much more so than in *Sus scrofa*, for example, also indicating the concentration of masticatory forces in this region of the snout. In *Sus scrofa* and most other suines the chewing forces are concentrated further back along the tooth row, between M1/ and M3/, the latter tooth being the largest in the molar row. In *Molarochoerus* in contrast, the M3/ and m/3 are relatively small, the front two lophs of M3/ and m/3 being smaller than the M2/ and m/2, respectively.

The power of the masticatory forces appears to have been greater in *Molarochoerus* than it was in either *Propotamochoerus* or *Microstonyx*. The disto-sagittally directed parietal crests in the former genus differ from the more distally directed crests that occur in *Microstonyx* [7], which are almost parallel to each other, those of *Propotamochoerus*, which converge distally at a more gentle angle [13], indicating that there is more room for expanded masseter muscles in the anterior part of the post-orbital vacuity in *Molarochoerus* than in either of the other two genera. This morphology accords with the dental evidence. The anterior expansion of the space for the masseter muscles in the post-orbital region also accords with the suggestion that greater masticatory loads occurred anteriorly in the tooth row in comparison with the posterior tooth loading that typifies most suines.

The male mandible PDYV 0766 has an exceptionally robust anterior body, but the female specimens have more slender lower jaws.

All in all, it would appear that, not only was *Molarochoerus* endowed with massive snout musculature, but it was also provided with powerful chewing musculature. From this we infer that its masticatory behaviour was divergent from that of *Sus scrofa*, and species of *Microstonyx* and *Potamochoerus*. The observed splanchnocranial and dental differences suggest that the Yuanmou suid was 'rooting' in relatively hard substrates, perhaps for extended periods, and that the food that it ingested required tremendous masticatory forces.

8. Conclusions

In general, the dental and osteological characters of *Molarochoerus* are closest to those of Propotamochoerini among the Suinae.

Propotamochoerus is similar to the Yuanmou suid in the following features: **(1)** its comparable size, **(2)** the facial part of the skull is longer than the neurocranial part, **(3)** the zygomatic arches depart from the maxilla at right angles opposite M1/ and are inflated and filled with sinuses, **(4)** its molar enamel thickness is moderate, and molar furchen are shallow, **(5)** it possesses sagittal cusplets in the sagittal valley of P4/, **(6)** the p/4 has two anterior main cusps, and the rostral musculature originates on the superior and inferior surfaces of the anterior zygomatic root. *Molarochoerus* differs from *Propotamochoerus* in the following ways: **(1)** the P4/ and p/4 are completely molarised, **(2)** the P3/ has a large and inflated lingual cusp, and the main cusp is oriented diagonally, **(3)**) the orbits are more posteriorly located, **(4)** there is diastema between p/1 and p/2, **(5)** the anterior part of the zygomatic arches and the maxillary surface above them has a unique shape (representing an enlarged insertion area for the *levator rostri* musculature), **(6)** the parietal crests converge more sharply towards each other, **(7)** the curvature of the occlusal surface of the upper cheek teeth is convex downwards in lateral view.

On the basis of the unique features of the snout, mandible and dentition, Liu & Pan [6] considered that the Yuanmou specimens represented a new genus and species of Propotamochoerini, which they named *Molarochoerus yuanmouensis*. *Molarochoerus* is a highly derived Propotamochoerini in many features of its snout, mandible and dentition. It is likely that *Molarochoerus* descended from *Propotamochoerus* during the Late Miocene.

The enlarged areas for the origins of the rostral musculature indicate that *Molarochoerus yuanmouen-*

sis was well adapted for the 'rooting' behaviour, an inference supported by the observation that the nasal bones are considerably more robust than they are in *Sus scrofa*, itself a well-adapted 'rooter'. Particularities of the dentition of *Molarochoerus* (curvature of the occlusal surface of the cheek teeth, anterior displacement of the principal masticatory forces, molarisation of the posterior premolars, reduction of the third molars) suggests that its diet consisted predominantly of hard foods and that the chewing action was different from that in *Sus*, the main masticatory forces being concentrated at the P3/–M1/ sector of the dentition. The orientation of the parietal crests which results in the enlargement of the post-orbital space for the anterior part of the masseter musculature also suggests increased chewing forces and an anterior position of maximum tooth loading, in accordance with the molarisation of the posterior premolars, slight reduction of the third molars, and the wear gradient of the cheek teeth.

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