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Suoidea from the Upper Miocene hominoid locality of Lufeng, Yunnan province, China

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ABSTRACT

The Suoidea from Lufeng (Yunnan, China) belong to the following taxa: *Yunnanochoerus* nov. gen. *lufengensis* (Han, 1983), a peccary and the suids *Propotamochoerus wui* nov. sp., *Propotamochoerus hyotherioides* (Schlosser, 1903) and *Chleuastochoerus* sp.

Taxonomy and phylogeny of the genera *Yunnanochoerus, Taucanamo, Schizochoerus, Propotamochoerus* and *Chleuastochoerus* are reviewed.

Y. lufengensis is the probable ancestor of *Yunnanochoerus gandakasensis* (Pickford, 1977) from the Dhok Pathan Formation (Pakistan). For this reason the Lufeng locality is placed in the lower part of the Upper Miocene and correlates with the Nagri Formation in Pakistan. This stratigraphic position is slightly lower than the correlation based on rodents.

The high number of suoid species in Lufeng indicates a warm and humid climate, which confirms earlier interpretations of the environment.

INTRODUCTION

The locality of Lufeng is located near the village of Shihuiba in the Lufeng Basin (fig. 1). A description of the geology and a faunal list are given by Qi (1985a), Wu and Xu (1985) and Badgley et al. (1988). The fossils come from six layers, having a total thickness of approximately 6 meters (layers 1–6 in fig. 1). The locality was excavated by the IVPP and the Yunnan Provincial Museum from 1975 to 1983.

The following articles have been published on Lufeng material, most of them in Chinese with English abstracts.

Table 1. Measurements of the cheek teeth of *Yunnanochoerus lufengensis* n. gen. from Lufeng in mm.

	P_1 DAP	DTa	DTp	P_2 DAP	DTa	DTp	P_3 DAP	DTa	DTp	P_4 DAP	DTa	DTp	M_1 DAP	DTa	DTp	M_2 DAP	DTa	DTp	M_3 DAP	DTa	DTp	DTpp
holotype	+8.3	—	+4.0	10.8	4.6	5.0	11.8	4.9	5.6	11.7	5.1	6.9	—	—	—	12.7	—	+8.8	16.5	9.4	7.3	4.5
isolated teeth	>6.5	..	4.1				11.8	5.3	5.6							14.3	8.1	8.0	—	—	8.0	4.8
							>11.1	5.5	6.0							13.7	8.4	9.0	17.1	9.6	7.5	5.0
																—	—	8.6				
	M^3 DAP	DTa	DTp																			
isolated teeth	13.3	10.0	6.8																			

The first hominoid fossils and the first faunal lists were published by Xu and Lu (1979), Qi (1979) and Zhang et al. (1981).

The fishes were studied by Liu (1985), emydidid turtles by Yeh (1981, 1985), birds by Hou (1985), carnivores by Qi (1983, 1985a) and Qiu and Qi (1989, 1990), elephants by Zhang (1982), artiodactyls by Han (1983, 1985, 1986), insectivores by Storch and Qiu (1991), the tupaiid by Qiu (1986), lagomorphs by Qiu and Han (1986), rodents in general by Qiu, Han, Qi and Lin (1985), platacanthomyids by Qiu (1989) and the remains of a plant by Tao and Han (1990).

The hominoids were studied by Kelley and Xu (1991), Lu, Xu and Zheng

Table 2. Measurements of the lower cheek teeth of *Propotamochoerus wui* n. sp. from Lufeng in mm.

	P_1 DAP	DTa	DTp	P_2 DAP	DTa	DTp	P_3 DAP	DTa	DTp	P_4 DAP	DTa	DTp	M_1 DAP	DTa	DTp	M_2 DAP	DTa	DTp	M_3 DAP	DTa	DTp	DTpp
mandibles																						
holotype, l	9.8	3.5	3.6	12.3	4.6	5.6	12.9	5.9	7.0	12.4	8.0	9.3	11.7	9.6	10.1	16.6	13.0	14.0				
holotype, r	9.9	3.7	3.8	—	—	—	12.9	5.9	6.9	12.6	8.0	9.3	11.8	9.8	10.1	16.7	13.0	14.0	26.1	14.0	13.5	10.6
							13.2	5.6	6.2	12.4	7.5	8.3	12.3	9.3	9.8	16.8	12.2	12.9	24.0	13.5	12.3	9.0
							13.4	5.9	6.1	13.0	7.7	8.9	12.9	9.7	9.9	16.7	12.7	13.3	25.4	14.0	12.6	8.9
							12.4	+6.5	+6.4	12.5	8.0	9.2	—	—	--	16.3	14.2	13.4	25.2	14.1	13.4	9.6
							11.3	5.4	5.9	12.4	7.4	7.9	—	—	—	<18.9	+12.8	12.6	23.1	13.7	12.2	9.0
							--	—	7.2	12.3	7.6	9.0	12.6	>8.9	≥11.4	+15.9	—	—	—	—	12.9	8.4
																—	--	12.7	--	13.7	12.0	9.0
							13.6	6.8	6.7	12.8	9.0	9.3										
													13.8	9.6	10.2	17.8	13.1	14.3	24.5	13.9	12.7	9.0
													—	9.9	--	16.2	12.6	13.4				
										12.0	7.5	8.3	13.5	9.4	9.6							
													13.5	8.9	9.1	17.5	12.3	12.6				
										11.7	8.6	9.0	14.3	9.9	10.7	16.8	—	—				
													13.5	9.7	9.8	17.3	12.8	13.2				
							..	..	..	12.9	..	..										
mandibles mean	9.9	3.6	3.7	12.3	4.6	5.6	12.8	5.9	6.6	12.5	7.9	8.9	13.0	9.6	9.9	16.9	12.9	13.3	24.7	13.8	12.7	9.2
isolated teeth	10.3	3.7	3.8	12.4	4.8	5.4	13.3	6.1	6.8	12.6	8.0	8.8	14.5	9.4	10.0	16.7	12.3	13.0	26.6	14.0	12.8	9.1
	8.5	—	—				12.7	5.0	6.0	12.1	7.3	8.1	13.4	9.3	9.3	16.7	12.6	13.7	24.1	12.9	12.4	8.3
	>8.6	4.1	+3.3				13.4	5.9	—	13.3	7.8	8.9	--	--	10.0	17.2	12.0	12.5	24.1	12.8	11.8	10.3
	8.7	3.2	3.4				13.2	5.6	6.3	12.3	7.5	8.4	—	—	10.2	17.4	11.8	12.5	24.4	12.5	11.6	8.5
	10.2	3.8	4.0				>12.7	+6.3	6.0	12.3	7.1	7.9	12.6	8.8	8.9	16.7	12.5	13.4	25.0	>13.2	>12.6	9.6
							14.0	6.2	6.2	13.0	--	--	14.1	9.1	9.7	17.6	12.6	13.5	26.1	13.4	13.6	7.1
							--	--	6.0	13.2	9.1	9.4	13.8	9.3	10.0	18.7	12.2	13.0	29.0	16.0	14.2	11.2
							>12.5	6.5	7.2	13.1	8.2	9.6	13.3	>8.3	>8.5	+17	12.1	12.7	27.4	14.8	13.6	11.2
							13.2	5.8	6.4	13.6	—	9.4	--	--	10.7	17.2	13.0	13.7	26.8	14.7	13.9	9.9
							—	—	6.3	12.6	7.2	8.0	13.3	>8.2	9.3	17.8	12.5	13.3	28.3	15.0	14.1	10.4
							13.4	≥6.4	7.4	12.4	7.5	8.7	13.9	9.0	9.5	17.9	13.0	13.4	26.9	—	—	10.1
										12.3	7.8	8.6	—	9.0	--	—	12.4	—	27.6	14.5	13.5	11.0
										11.9	7.8	9.0				--	—	13.6	27.6	14.3	13.3	10.7
										12.5	8.0	8.8				≥17.7	12.5	12.6	--	--	--	11.0
										12.9	8.0	8.8				—	--	12.4	26.4	13.7	12.4	9.1
																—	—	13.9	—	—	--	9.4
																—	--	13.3	--	14.7	--	--
																—	—	12.7	--	--	12.4	9.3
																			--	--	12.8	10.8
																			—	--	≥13.4	10.5
mean all teeth	9.6	3.7	3.7	12.4	4.7	5.5	13.1	5.9	6.5	12.6	7.9	8.7	13.3	9.3	9.8	17.1	12.6	13.2	25.9	14.0	12.9	9.7
n	6	6	5	2	2	2	14	13	17	26	23	24	18	17	19	20	22	28	20	20	22	27
SD	0.8	0.3	0.2	0.7	0.1	0.1	0.6	0.5	0.5	0.5	0.5	0.5	0.8	0.4	0.5	0.6	0.5	0.5	1.6	0.8	0.7	1.0
V	8.1	8.2	6.1	5.7	3.0	2.5	4.9	7.8	7.6	3.6	6.5	5.7	6.1	3.7	4.9	3.6	4.0	4.0	6.2	5.8	5.8	10.7
V'	19	25	16	1	4	4	21	31	23	15	23	20	21	12	18	14	18	13	23	25	20	45

(1981), Martin (1991), Schwarz (1990), Wu, Han, Xu, Lu, Pan, Zhang, Zheng and Xiao (1981), Wu, Han, Xu, Qi, Lu, Pan, Chen, Zhang and Xiao (1982), Wu (1987), Wu and Oxnard (1983 a and b), Wu and Xu (1985), Wu, Xu and Lu (1983, 1986), Xu and Lu (1979, 1980) and Xu, Lu, Pan, Qi, Zhang and Zheng (1978). A gibbon was published by Wu and Pan (1984, 1985b), Pan (1988), Meldrum and Pan (1988) and Pan, Waddle and Fleagle (1989) discussed sexual dimorphism of the species and gave a catalog of the material. Wu and Pan (1985a), Pan and Wu (1986) and Wu and Wang (1988) described an adapid.

Qi (1985b) summarized the stratigraphy of Lufeng. Rhizomyid rodents were compared to those of Pakistan (Flynn and Qi, 1982 and Qi, 1986) and indicated an age of 8 Ma, but the murids suggested a somewhat younger age, equivalent to the Middle Turolian (MN 12; Neogene Mammal Units, Mein, 1990) of Europe (Qiu and Storch, 1990).

Chen (1986) made a sedimentologic description of the site and the paleoenvironment was reconstructed by Sun and Wu (1980). Badgley et al. (1988) and Qi (1993), using all available evidence, including pollen, concluded that the fossiliferous deposits were formed in a fresh water swamp surrounded by hills covered with humid tropical forest with open glades.

This paper describes the four species of Suoidea in Lufeng, compares them to other Suoidea, studies the phylogeny of these species and interpretes their presence in Lufeng in terms of stratigraphy and paleoecology.

Table 3. Measurements of the upper cheek teeth of *Propotamochoerus wui* n. sp. from Lufeng in mm.

	p1			p2			p3			p4		M1			M2			M3			
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
maxillas										9.6	11.3	>13.4	--	--	+18.0	--	15.1	20.8	16.5	13.5	+6.6
										9.6	11.3	13.4	11.7	11.6	16.5	15.5	15.1				
							11.0	8.3	9.7	10.1	11.9	13.1	12.2	--	17.4	15.4	15.4	25.2	16.3	14.4	9.6
				>11.2	5.6	7.0	11.2	8.0	10.3	9.8	12.6	--	--	--	>17.3	16.6	16.2				
							10.4	7.2	9.8	9.3	11.7	13.3	11.8	11.9	16.5	<15.1	<14.9				
							10.8	7.8	10.3	9.6	12.9	14.9	<12.8	12.7	17.6	16.4	16.1	25.9	18.5	15.8	7.2
							10.8	8.0	10.2	9.9	12.0	14.0	12.3	12.4	17.2	15.0	14.8				
															18.2	16.5	16.6	24.3	18.3	15.8	7.3
	+11.2	3.8	--	11.3	5.9	9.0	10.3	8.2	10.4	9.6	12.7	13.0	12.7	13.0	17.2	15.6	15.4				
	10.5	4.3	4.6	--	5.6	--	10.9	8.1	--												
mean maxillas	10.5	4.1	4.6	11.3	5.7	8.0	10.8	7.9	10.1	9.7	12.1	13.6	12.1	12.3	17.2	15.9	15.6	24.1	17.4	14.9	8.0
isolated teeth	9.5	..	4.6	12.3	5.4	--	12.2	8.4	10.1	10.2	12.3	13.3	12.2	12.3	16.5	15.1	15.9	25.6	18.4	15.5	7.2
							--	--	--	9.9	>11.2	14.0	12.2	11.8	18.1	15.4	15.9	23.1	16.4	12.9	6.4
										10.9	11.0	13.3	12.4	11.8	17.0	16.0	15.3	21.1	16.7	14.0	7.3
										9.6	11.3	13.2	12.1	12.3	16.8	15.8	15.5	23.9	17.3	15.7	11.7
										10.5	12.1	13.5	12.2	12.1	17.2	15.7	14.8	24.5	18.5	15.4	9.1
												13.6	11.9	12.3	17.0	15.7	14.8	--	--	15.3	12.0
															17.5	15.8	16.2	20.9	15.0	13.7	6.4
															18.1	16.0	15.3	23.3	17.0	14.1	8.9
															16.6	15.0	15.8	21.5	16.2	13.9	6.7
															16.7	15.9	14.1	--	--	14.7	9.2
															17.8	17.0	16.4	22.0	15.3	13.5	7.7
															17.6	17.7	16.7	22.6	18.5	14.9	9.0
															17.8	17.7	15.2	22.8	16.6	14.3	--
															18.6	15.5	15.4	--	--	15.3	11.2
															17.9	16.6	16.2	--	--	15.7	--
															>17.7	>16.6	17.5	--	16.8	--	--
															>17.4	16.6	17.2				
															18.1	--	16.7				
															18.4	15.9	16.4				
															19.0	15.6	16.7				
															19.1	16.3	--				
															--	16.8	--				
mean all teeth	10.5	4.1	4.6	11.3	5.7	8.0	10.8	7.9	10.1	9.7	12.1	13.6	12.1	12.3	17.2	15.9	15.6	24.1	17.4	14.9	8.0
n	2	2	2	1	3	2	8	8	7	13	12	12	11	11	26	27	28	15	16	19	16
S	0.7	0.4	0	0	0.2	1.4	0.6	0.4	0.3	0.4	0.6	0.5	0.3	0.4	0.7	0.7	0.8	1.7	1.1	0.9	1.8
V	7.1	8.6	0	0	3.0	17.6	5.3	4.7	2.6	4.4	5.2	3.9	2.3	3.4	4.3	4.5	5.1	7.4	6.9	6.2	22.5
V'	10	26	o	0	5	25	17	15	7	16	16	13	8	11	15	17	22	22	21	20	61

MATERIAL AND METHODS

Of the 369 teeth examined, we attribute 14 to *Yunnanochoerus lufengensis*, 300 to *Propotamochoerus wui*, 63 to *Propotamochoerus hysudricus* (Stehlin, 1899) and 19 to *Chleuastochoerus* sp. *Chleuastochoerus* (Pearson, 1928) is found only in layer 3, *Yunnanochoerus* in layers 3 and 6 and both species of *Propotamochoerus* (Pilgrim, 1925) are found in beds 1 to 6.

In our analysis we used the common biometrical and morphological methods, including DAP–DT and DTa–DTp scatter diagrams (see next section on abbreviations). In addition we expressed the length and width of cheek teeth as a percentage of the length and width of the first molar (Van der Made, 1989): the DAP′ and DT′ values. In some cases it was more practical to relate the size of a tooth to the size of the M2 (DAP″ and DT″ or DAP* and DT*). Variability of these values for the canines are illustrated using a population of recent pigs (see section on canine size).

We emphasize characters that are of value for taxonomy (or recognition of the species) and phylogeny, as well as in the determination of the type of tooth (premolar versus deciduous molar etc.). Where necessary the importance of the character is indicated in the description. Bearing in mind that the material is

Table 4. Measurements of the incisors and canines of *Propotamochoerus wui* n. sp., *Propotamochoerus hyotherioides* and *Chleuastochoerus* sp. from Lufeng in mm.

	I_1 DLL	DMD	I_2 DLL	DMD	I_3 DLL	DMD	C_m Li	La	Po	C_f DAP	DT
Chleuastochoerus isolated teeth	6.8	4.6	7.2	5.3			9.3	6.4	7.2		
Propotamochouerus wui mandibles											
holotype left	--	4.5	8.8	+4.1			>10.4	9.3	10.1		
right	+9.2	4.3	9.0	+4.8			11.7	8.0	10.6		
symphysis left	--	+8.5	9.0	5.3						8.7	6.4
right	>8.5	5.3	9.4	5.2						8.7	6.7
isolated teeth	>7.4	>4.7	8.4	4.9	5.0	8.5	--	--	--	--	--
	7.5	4.7	8.2	5.0	4.4	9.2	12.8	8.8	9.6	9.4	5.7
	7.3	4.7	9.2	5.2	6.0	--	9.6	8.6	7.5		
	8.8	5.2	--	4.5			11.5	9.2	9.0		
	9.0	5.7	>8.2	5.0			9.8	8.1	7.3		
	--	5.0	8.4	5.2							
	>7.4	5.5	--	5.3							
	6.8	4.6									
	8.3	4.5									
	--	6.6									
DI_2			4.8	3.1							
Propotamochoerus hyotherioides isolated teeth	>12.5	6.2	>12	7.5	9.5	5.4	18.0	15.7	13.3		
	13.0	7.7	12.3	6.8	9.0	8.4	17.4	14.9	12.2		
	>12.4	>7.1	>11.0	7.6			21.5	19.3	17.2		
	12.1	>6.8	14.6	8.5			21.6	18.0	14.9		

	I^1 DMD	DMDo	DLL	I^2 DMD	DLL	I^3 DMD	DLL	C^m DAP	DT
Propotamochoerus wui isolated teeth	>11.3	>13.7	5.3	16.0	6.1	12.2	4.2	12.6	11.1
	--	--	--	15.6	5.6			13.1	11.7
	12.8	--	--	15.2	5.2				
	--	--	6.3	16.4	5.3				
	--	19.1/16.1	6.0						
	10.2	16.7/12.3	5.5						
DI^1	6.5	11.0/8.7	3.6						
Propotamochoerus hyotherioides isolated teeth	15.0	29.0/20.4	9.2	19.4	8.1			25.0	26.1
	17.6	--/--	10.8	18.6	7.5			--	--
				--	7.4				

suoid we did not think it necessary to indicate that, for example, the first molar has four main cusps.

Abbreviations and definitions

Measurements are given in mm and they are taken as indicated in fig. 2. Measurements and indices of teeth are indicated with the following abbreviations:*

DAP Length (fig. 2 a, f and g; see also Van der Made, 1991a).

DAPd Distal antero-posterior diameter in a bone.

DAPp Proximal antero-posterior diameter in a bone.

DAP′ Length of a tooth expressed as a percentage of the length of the first molar DAP′ = (DAP / DAP M1) × 100% (for upper teeth the length of the M^1 is used as a standard, for lower teeth the M_1).

DAP″ Length of a Cm expressed as a percentage of the width of the second molar DAP″ = (DAP Cm / DT M2) × 100%.

DAP* Length of a Cm expressed as a percentage of the length of the second molar DAP* = (DAP Cm / DAP M2) × 100%.

DLL Linguo-labial diameter (fig. 2 a, b and c).

DLL″ Linguo-labial diameter expressed as a percentage of the width of the second molar DMD″ = (DAP Ix / DT M2) × 100 %.

DMD Meso-distal diameter (fig. 2 a, b and c).

DMD″ Meso-distal diameter expressed as a percentage of the width of the second molar DMD″ = (DAP Ix / DT M2) × 100 %.

DMDo Meso-distal diameter of I^1, measured along the occlusal surface either as a total length of the crown or of the occlusal surface (fig. 2 b).

DT Maximum width (fig. 2 f; see also Van der Made, 1991a).

DT′ Width of a tooth expressed as a percentage of the width of the first molar DT′ = (DT / DT M1) × 100%.

DT″ Width of a Cm expressed as a percentage of the width of the second molar DT″ = (DT Cm / DT M2) × 100%.

DT* Width of a Cm expressed as a percentage of the length of the second molar DT* = (DT Cm / DAP M2) × 100%.

DTa Width of first lobe of a cheek tooth (fig. 2 e, f, g).

DTd Distal width in a bone.

Table 5. Measurements of the deciduous molars of *Propotamochoerus wui* n. sp. and *Propotamochoerus hyotherioides* from Lufeng in mm.

	D_4				D^2			D^3			D^4		
	DAP	DTa	DTm	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DTp
Propotamochoerus wui	--	--	6.7	8.0	--	3.7	4.3	13.2	6.3	9.2	11.7	9.5	9.6
	16.6	5.9	6.4	7.7	--	4.5	--	13.1	6.3	9.3	12.1	8.8	9.7
	--	--	7.0	7.5				14.5	6.6	9.8	11.4	9.9	10.4
	--	5.3	6.0	--							--	--	9.4
	20.4	8.3	8.9	10.5									
Propotamochoerus hyotherioides	20.4	8.3	8.9	10.5							16.0	13.1	12.8
	--	--	--	9.0							±15.6	13.1	12.7
	16.6	5.6	6.7	7.4									

DTm Width of the middle lobe of a cheek tooth in D_4.

DTp Width of second lobe of a cheek tooth (fig. 2 e, f and g), or in a bone, the proximal width.

DTpp Width of third lobe of a cheek tooth (in M3; fig. 2 e and g).

I Index (DAP / DT) × 100% or (DMD / DLL) × 100%.

L Length of a bone.

La Width of the labial side of the C_m (fig. 2 d).

La″ Width of the labial side of the C_m as a percentage of the width of the M_2.

Li Width of the lingual side of the C_m (fig. 2 d).

Li″ Width of the lingual side of the C_m as a percentage of the width of the M_2.

Po Width of the posterior side of the C_m (fig. 2 d).

Po″ Width of the posterior side of the C_m as a percentage of the width of the M_2.

V′ Measure of variability (Freudenthal and Cuenca, 1984):

$$V' = \frac{200 \times (\text{maximum-minimum})}{(\text{maximum} + \text{minimum})}.$$

The suoids from Lufeng were compared with material from the following institutions:

AFS Accademia dei Fisiocritici, Siena.

GSP Geological Survey of Pakistan, Islamabad.

HLD Hessisches Landesmuseum, Darmstadt.

IGF Istituto di Geologia, Firenze.

IM Indian Museum, Calcutta.

IPS Instituto de Paleontología, Sabadell.

IVAU Instituut Voor Aardwetenschappen, Utrecht.

IVPP Institute for Vertebrate Paleontology and Paleoanthopology, Academia Sinica, Beijing.

SLJ Steiermärkisches Landesmuseum Joanneum, Graz.

MHMN Museu Històric Municipal de Novelda.

Table 6. Measurements of the cheek teeth of *Propotamochoerus hyotherioides* from Lufeng in mm.

	P_3 DAP	DTa	DTp	P_4 DAP	DTa	DTp	M_1 DAP	DTa	DTp	M_2 DAP	DTa	DTp	M_3 DAP	DTa	DTp	DTpp
isolated teeth	17.4	8.3	8.9	16.2	9.5	10.7	19.3	12.8	14.2	23.7	17.9	17.6	35.2	21.1	18.1	16.0
	16.7	8.5	9.0	17.6	10.2	11.8				23.8	17.1	17.6	34.5	19.0	17.2	12.5
				17.0	10.5	11.1				--	--	17.8	--	--	--	11.1
				16.9	12.0	13.2				--	--	16.1				
										23.0	16.6	16.7				
										22.6	15.7	16.5				
										21.8	14.3	14.9				
										--	15.4	15.3				

	p2 DAP	DTa	DTp	p3 DAP	DTa	DTp	p4 DAP	DT	M^2 DAP	DTa	DTp	M^3 DAP	DTa	DTp	DTpp
isolated teeth	15.4	7.8	9.5	17.5	11.2	--	15.7	17.2	24.0	22.3	23.1	34.8	23.3	21.4	12.1
	16.7	7.2	9.4	--	11.1	--	14.8	16.4	23.3	--	--	34.3	24.7	21.7	9.0
	16.1	7.2	8.7				15.4	16.8	--	--	--	31.3	20.3	17.5	10.8
									22.2	19.5	19.8	33.5	22.5	19.0	9.7
												36.3	26.9	22.5	10.1
												34.5	23.5	21.1	11.4
												33.6	24.7	22.0	11.6

MNCN	Museo Nacional de Ciencias Naturales, Madrid.
MNHN	Muséum National d'Histoire Naturelle, Paris.
MPV	Museo Paleontológico de Valencia.
MTA	Maden Tetkik ve Arama, Ankara.
NMB	Naturhistorisches Museum, Basel.
RMNHL	Rijksmuseum voor Natuurlijke Historie, now called, Nationaal Natuurhistorisch Museum, Leiden.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.
UCBL	Université Clade Bernard, Lyon.
ZMA	Zoölogisch Museum, Amsterdam.

DESCRIPTION AND COMPARISON

Separation into different species

In the Lufeng suoid fossils, lophodont molars can easily be separated from the bunodonts. Associated with the lophodont molars, premolars were found. These teeth were described as *Lophochoerus lufengensis* by Han (1983). *Lophochoerus* Pilgrim, 1926 is a suid, while the teeth from Lufeng are tayassuid and require a new taxon.

Some of the bunodont molars represent a larger species, without overlap with the smaller suids (figs. 3 and 4), which we identified as *Propotamochoerus hyotherioides* (Schlosser, 1903).

The small bunodont *Propotamochoerus wui* n. sp. and *Chleuastochoerus* sp. can be recognised by morphology and small size differences (figs. 3 and 4).

Incisors, canines and deciduous dentition were assigned to one of the species on the basis of morphology, size and association.

SUOIDEA Cope, 1887

TAYASSUIDAE Palmer, 1897

Palaeochoerinae Matthew, 1924

Yunnanochoerus new genus

Table 7. Measurements of the cheek teeth of *Chleuastochoerus* sp. from Lufeng in mm.

	P_4 DAP	DTa	DTp	M_1 DAP	DTa	DTp	M_2 DAP	DTa	DTp	
mandibles	12.0	6.7	7.0	12.4	8.0	8.9	15.6	10.2	11.1	
	12.0	6.6	6.7	13.0	7.8	8.6	16.3	10.7	11.1	
isolated teeth				12.9	8.1	9.5	16.8	11.1	10.7	
							14.0	10.7	10.4	
							15.9	11.1	11.6	
							15.5	11.0	11.6	
							--	--	11.7	
	p^2 DAP	DTa	DTp	p^3 DAP	DTa	DTp	M^3 DAP	DTa	DTp	DTpp
isolated teeth	11.7	4.9	5.9	10.9	7.3	8.2	17.9	17.8	13.8	7.9
				12.9	8.3	8.7	21.6	18.4	14.6	10.2

Table 8. The size of the male lower canine as related to the length (*) or to the width ('') of the M_2. Dimensions in mm. In is indicated whether means of a population is used or the mandible of one individual (right or left): m, r, l.

		C_m Li	La	Po	M_2 DAP	DT	Li*	La*	Po*	Li''	La''	Po''
Taucanamo sansaniense												
Sansan, Sa 4663, MNHN	r	6.9	5.1	5.3	11.4	7.5	61	44	46	92	68	71
Schizochoerus vallesiensis												
Yassiören, Yas 27, MNHN	r	9.5	9.3	7.5	--	≥11.6	--	--	--	≤81	≤80	≤65
Doliochoerus quercyi												
Quercy, cast MNCN	l	9.6	8.3	8.4	13.5	11.4	71	61	62	84	73	74
Barberahyus castellensis												
holotype, IPS	l	8.5	5.1	5.9	9.3	7.4	91	55	63	114	69	80
Hyotherium meissneri												
Cetina de Aragon, CT 468, MNCN		7.6	5.2	5.1	13.7	10.7	55	38	37	71	49	48
Kubanochoerus gigas												
Tongxin, IVPP	l	35.0	27.1	18.0	39.0	28.5	90	69	46	122	95	63
	r	34.8	28.2	19.7	37.8	28.8	92	75	52	121	98	68
Bunolistriodon latidens												
Veltheim, holotype, Winterthur	l	11.2	12.2	9.0	20.1	15.9	56	61	45	70	77	56
Sivachoerus												
Indian subcontinent, B 1, IM		31.6	±20	±23	27.4	23.3	115	±73	±84	136	±86	±99
Sahabi, Roma		27.1	22.0	20.8	27.0	--	100	81	77	--	--	--
Potamochoerus porcus, recent												
Equatorial Guinea, MNCN	r	14.6	11.7	10.2	21.8	16.9	67	54	47	86	69	60
South Africa, RMNHL	l	17.3	14.2	12.0	22.9	17.2	76	62	52	101	83	70
Liberia, RMNHL	l	19.0	12.7	15.2	24.2	16.9	79	52	63	112	75	90
Propotamochoerus wui												
holotype, Lufeng, IVPP	l	>10.4	9.3	10.1	16.6	14.0	>63	56	61	>74	66	72
	r	11.7	8.0	10.6	16.7	14.0	70	48	63	83	57	76
Lufeng, IVPP	m	11.1	8.7	9.0	16.9	13.3	66	51	53	83	65	68
Propotamochoerus hyotherioides												
Lufeng, IVPP	m	19.6	17.0	14.4	23.0	16.5	85	74	63	119	103	87
Propotamochoerus palaeochoerus												
Ballestar, IPS	l	16.6	--	--	21.4	16.8	78	--	--	99	--	--
	r	16.9	--	--	20.5	--	82	--	--	--	--	--
Hippopotamodon												
Eppelsheim, Din 2, HLD		17.1	16.5	13.7	30.4	>22.0	56	54	45	--	--	--
Indian subcontinent, B 740, IM		≤24.5	22.3	18.1	32.1	21.9	≤76	69	56	≤112	102	83
Microstonyx major												
Terrassa	m	±12.4	13.9	12.2	27.7	19.7	±44	50	44	±63	71	62
Sus strozzii												
Valdarno, IGF 424, IGF	l	32.4	30.7	22.0	27.5	18.7	118	112	80	173	164	118
Valdarno, IGF 417, IGF		28.5	25.4	19.4	25.6	18.8	111	99	76	152	135	103
Valdarno, IGF 429, IGF		28.6	+27.4	20.4	25.1	18.5	114	+110	81	155	+148	110
Valdarno, IGF 433, IGF		26.9	25.9	18.0	25.4	18.7	106	102	71	144	139	96
Valdarno, IGF 439, IGF	l	28.1	26.8	21.3	26.0	19.3	108	103	82	146	139	110
Olivola, IGF 4006, IGF	l	27.5	26.7	19.1	>28	19.4	--	--	--	142	138	98
Olivola, IGF 4007, IGF	r	26.1	25.0	17.3	28.2	19.1	93	89	61	137	131	91
Sus peii												
Liucheng, V 5825.16, IVPP	l+r	18.0	16.8	15.3	24.0	17.1	75	70	64	105	98	89
Sus scrofa, recent												
Lerida, spain, MNCN	l	16.7	10.3	13.9	20.4	13.0	82	50	68	128	79	107
Burgos, Spain, MNCN	l	18.1	12.0	14.0	20.8	13.4	87	58	68	135	90	104
Doñana, Huelva, Spain, MNCN		19.3	11.2	15.9	19.7	13.6	98	57	81	142	82	117
Guadalajara, Spain, MNCN, subadult		13.4	8.6	8.7	25.4	15.3	52	34	34	88	56	57

Diagnosis: tayassuid with lophodont molars, enlarged elongated premolars and a P_4 with one main cusp.
Remarks: Currently the Tayassuidae are divided into two subfamilies Tayassuinae (new world peccaries) and Palaeochoerinae Matthew, 1924 (= Doliochoerinae Simpson, 1945 = old world peccaries). At present, the phylogeny of the old world peccaries is not well understood. Our diagnosis separates the new genus from all other peccaries on tooth characteristics and contains characters that are of taxonomical importance at the subfamily or tribal level.
Derivatio nominis: pig (choerus) from the province of Yunnan.
Genotype: *Yunnanochoerus lufengensis* (Han, 1983).
Other species: *Yunnanochoerus gandakasensis* (Pickford, 1977).

Yunnanochoerus lufengensis (Han, 1983)
Plate 1; Plate 2; Plate 4, figs. 1 and 2.

Synonymy

1983 *Lophochoerus lufengensis* Han, p. 22–26, figs. 1 and 2, not fig. 3.

Diagnosis: a small *Yunnanochoerus* species with a relatively small M_3.
Remarks: This is opposed to *Yunnanochoerus gandakasensis* which is larger (estimated body weight 45 versus 70 kg) and which has a relatively larger M_3 (DAP′ M_3 of approximately 150 or 160 versus 183).
Holotype: remains of a left mandible with P_2, P_3, P_4, M_2 and M_3 and a broken P_1, filed under the number V 6891 in the IVPP. Pl. 1, fig. 4; Plate 2, fig. 3. Figs. 1 and 2 of Han (1983).
Type locality: Lufeng, Yunnan, China.
Age of type locality: Late Miocene.

Material

Besides the holotype there is an isolated right M_3, a fragmentary left M_3, a left M^3, two left M_2, the posterior part of a right M_2, a right P_1, a right and a left P_3. All these teeth are filed under number V 6891. This material was found in layers 3 and 6 (fig. 1).

Description and comparison

The $\mathbf{P_1}$ (pl. 1, fig. 4; table 1 for the size) of the holotype has two divergent roots, but in an isolated P_1 (pl. 1, fig. 3) the roots are fused. Both specimens lack the tip of the crown, but the crown must have been high, with steep anterior and posterior edges, as is common in tayassuids.

The $\mathbf{P_2}$ (pl. 1, fig. 4) has a similar morphology, but it is larger. The posterior ridge is not bifurcated or ornamented with cusplets. It has two roots.

The $\mathbf{P_3}$ (pl. 1, figs. 1, 2 and 4) is still larger and it resembles the P_2, save for the posterior ridge, of which the lower half is bifurcated. The tooth has a symmetrical outline and no posterior flare like a suid P_3.

The $\mathbf{P_4}$ (pl. 1, fig. 4) resembles the P_3, but has two posterior ridges; a long labial one and a short lingual one. Both edges depart from the tip of the tooth. *Lophochoerus* (pl. 3, fig. 7) does not have two posterior ridges and is much wider. *Schizochoerus vallesiensis* (Crusafont and Lavocat, 1954) has two main cusps (pl. 3, figs. 6A and 6C). The *Taucanamo* (Simpson, 1945) P_4 has an individualized talonid cusp and does not have two posterior ridges (pl. 3, fig. 5A). The talonid is very low in *Schizochoerus*, intermediate in *Yunnanochoerus* and high in *Taucanamo* (pl. 3, figs. 5A and 5C; pl. 1, figs. 4A and 4C; pl. 3, figs. 6A and 6C). The two roots are fused and convergent.

Unlike in suids, none of the *Yunnanochoerus* premolars has well developed anterior or posterior additional cusplets.

The $\mathbf{M_2}$ (pl. 2, figs. 1 and 3; pl. 4, fig. 1) is (imperfectly) lophodont. The protoconid and metaconid have transverse ridges that meet near the axis of the tooth, a little behind both cusps and at a lower level. The same structure is found be-

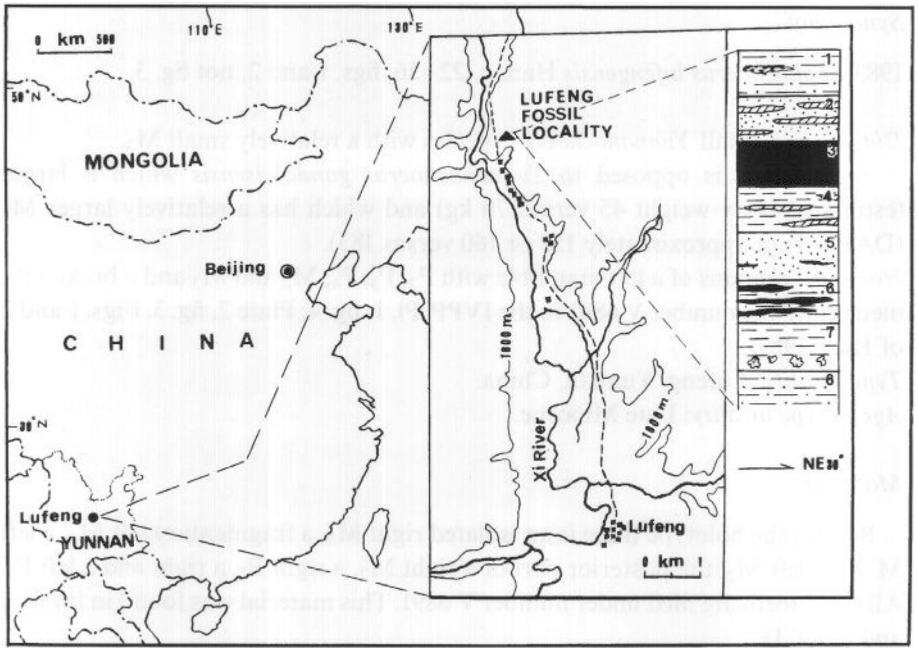

Fig. 1. The geographic position of the fossil locality of Lufeng and its stratigraphic column (from Badgley et al. 1988). The fossils were found in layers 1 to 6. Legend: 1. Yellow sandy clay with sand and gravel lenses. Thickness 0.5–2 m. 2. Interbedding of blackish brown carbonaceous clay and sand and fine grayish white sand. Thickness 0.7–3 m. 3. Blackish brown massive lignite. Thickness 0.3–1.4 m. 4. Interbedding of black carbonaceous clay and fine grey sand. Thickness about 0.2–1.8 m. 5. Grey uniform and pure fine sand with intercalations or lenses of black carbonaceous clay and lignite. Thickness 1.5–2.5 m. 6. Lignite consisting of two or three laminated layers. Thickness 0.5 m. 7. Grayish white and blackish grey clay with small pebbles of quartz and nodules of pyrite. Thickness about 1.6 m (in the test pit of 1981). 8. Purplish red, orange red, yellowish brown sandy clay. Thickness about 0.8 m (in the test pit of 1981).

tween the entoconid and hypoconid (see in particular pl. 2, fig. 1B and pl. 4, figs. 1A and 1C). A ridge departs from the protoconid, is directed antero-lingually and ends near the axis of the tooth. A similar ridge departs from the hypoconid, it lowers rapidly towards the transverse valley, but runs up at the middle of the back of the anterior lophe. In a similar fashion a small ridge departing rom the hypoconulid runs up the back of the second lophe. The hypoconulid is a single cusp, undivided sitting on the posterior cingulum. The molars of *Y. lufengensis* have higher cusps than those of *Schizochoerus* (compare pl. 2, fig. 1A and pl. 3, fig. 1B), but after wear low lophes are formed which are similar in both species (compare M_3 pl. 2, fig. 2C and M_1 pl. 3, fig. 2). The lower molars of *Taucanamo sansaniense* (Lartet, 1851) differ in having an individualized central cusp instead of the low ridge crossing the median valley (pl. 3, fig. 4). *Schizochoerus* does not have a central cusp (pl. 3, figs. 1A and 1C) and is like *Yunnanochoerus*.

The $\mathbf{M_3}$ (pl. 2, figs. 2 and 3) has a large hypoconulid, which forms a small third lobe.

The M^3 (pl. 4, fig. 2) is truly lophodont, although the anterior lophe is somewhat lower in the middle (pl. 4, fig. 2E). The paraconule forms part of the anterior lophe and is not fused to the cingulum. There is an anterior cingulum, which is elevated in the middle, but does not have a large cusp there. From the protocone a narrow and low ridge runs in the direction of the middle of the posterior

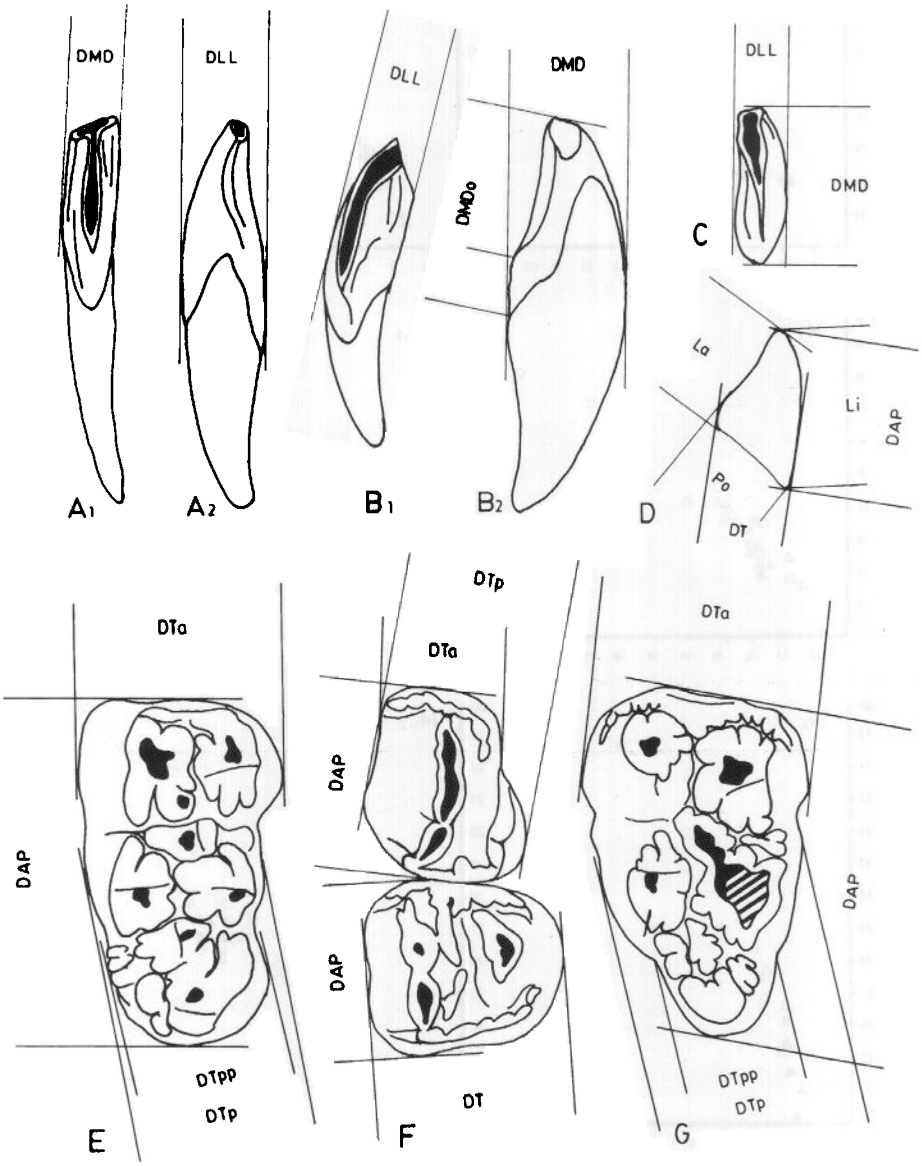

Fig. 2. The way of measuring. For abbreviations, see section on abbreviations and definitions. (a) lower incisors (I_1 figured); (b) first upper incisor; (c) second and third upper incisors (I^2); (d) male lower canines (section); (e) lower molars (M_3); (f) premolars (P^3, P^4); g) upper molars (M^3). C^f and C_f are measured like premolars. C^m are measured in an essentially similar way as the C^f, although the tooth has rotated. See also Van der Made, 1991a, fig. 1.

lophe. In the same way a ridge runs down from the hypocone to the talon. The lophes of this upper tooth are much better formed than those in the lower teeth and resemble those of *Schizochoerus* (pl. 3, fig. 3).

All molars differ from most suid molars, but resemble primitive tayassuid

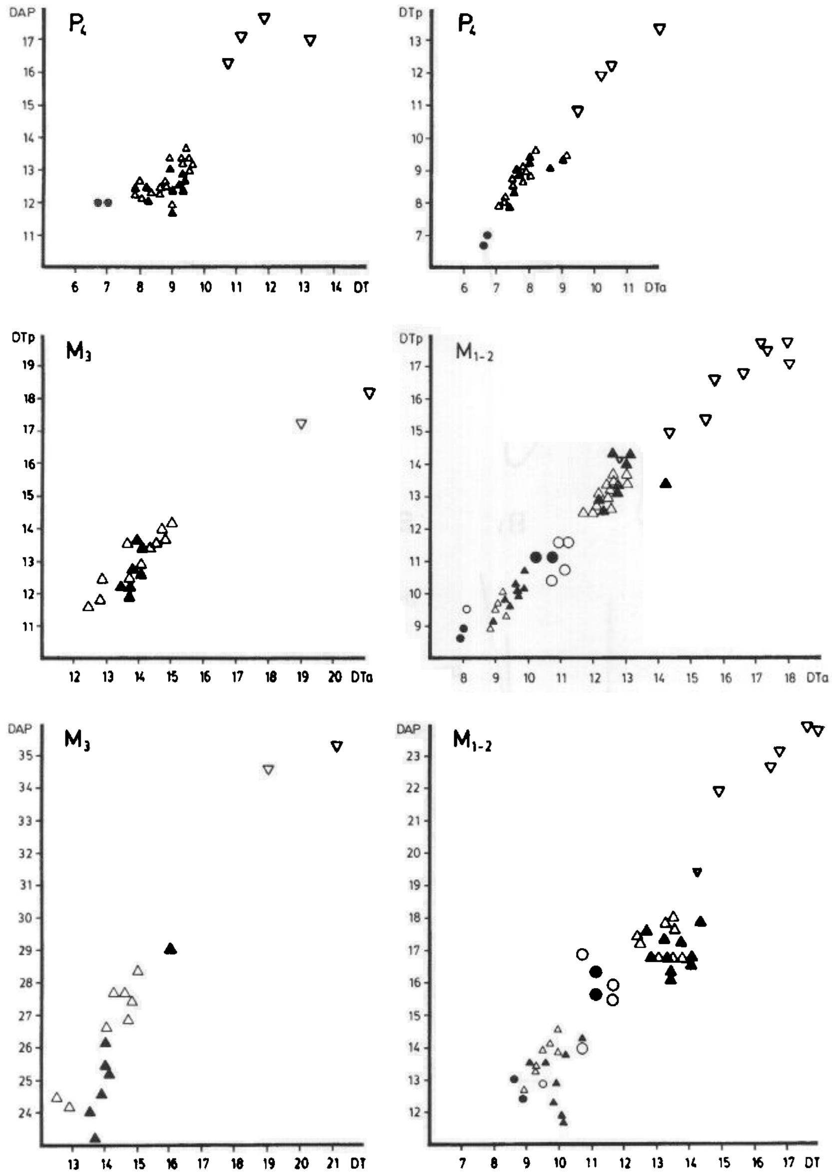

Fig. 3. DAP-DT and DTa-DTp diagrams of the P_4 and lower molars of the Suidae from Lufeng. Dots = *Chleuastochoerus*, triangles with the point downwards = *Propotamochoerus hyotherioides* and the triangles with the point upwards = *Propotamochoerus wui* n. sp.. Black symbols indicate teeth of a tooth row and white symbols are isolated teeth. The small symbols indicate the smaller tooth of a couple that resembles each other (M1 and M2, P2 and P3).

molars in having smooth enamel, without the formation of additional cusps. The crests in these teeth are smooth and thin, the valleys are wide with concave walls. All structures have their homologues in suids, but in suids the ridges are swollen. These ridges are folds in the enamel and give a complicated pattern with wear, as is seen in *Lophochoerus* (compare the M_2 in pl. 3, fig. 7A with the M_3 in pl. 2, fig. 2A). As a result of the swollen cusps in suids the valleys are narrower and have

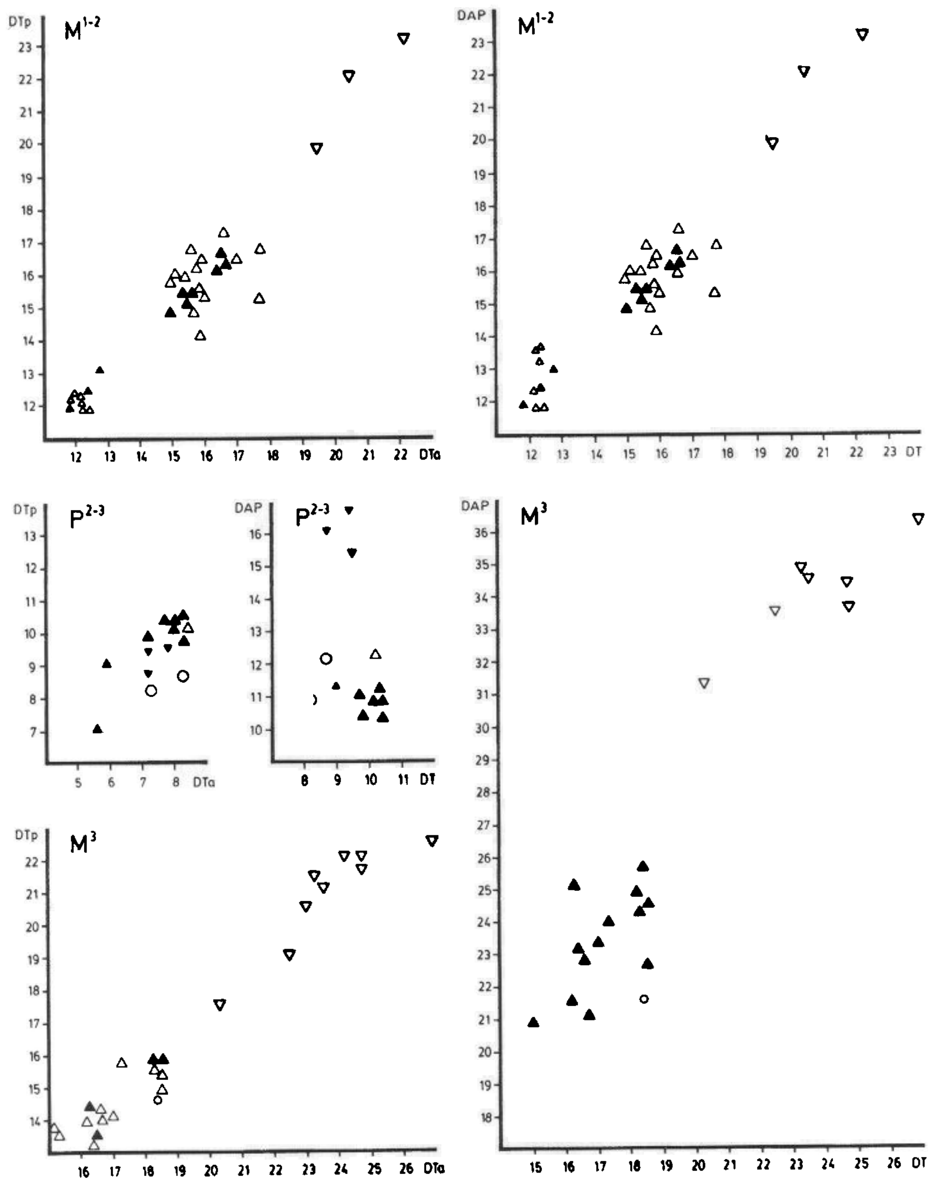

Fig. 4. DAP-DT and DTa-DTp diagrams of the P^2, P^3 and upper molars of the Suidae from Lufeng. Symbols as in fig. 3

convex walls. The morphology of the molars of *Y. lufengensis* is intermediate between *Taucanamo* and *Schizochoerus* in the degree of development towards lophodonty.

The ascending ramus of the **mandible** (pl. 2, fig. 1) starts to rise far behind the M_3. The massetric fossa is deep and has a sharp outline.

Discussion

Han (1983) described most of this material as a new species of the genus *Lophochoerus*. Pilgrim (1926) gave the name *Lophochoerus* to a small suid because of the supposed lophodont molars. When worn, the dentine of metaconid and protoconid of *Lophochoerus* molars makes contact and the same occurs in the second lobe of the tooth, giving it a lophodont appearance (pl. 3, fig. 7A), which is common in worn suoid molars. Other resemblances between *Lophochoerus* and *Yunnanochoerus* are enlarged premolars and a P_4 with only one main cusp.

The P_4 of *Lophochoerus* has a typical tetraconodontine morphology (Pickford, 1988a); it has one main cusp, from this cusp one ridge descends to a cusp on the talonid, it is inflated, it has a marked postero-labial swelling and it is wide relative to its length. The P_4 of *Y. lufengensis* differs in having two posterior ridges and no cusp on the talonid and in being more elongate and less inflated.

The simple structure of the premolars (no small cusps on the talonids, high crowns with steep slopes) and molars (smooth enamel, structures in the form of slim and sharp instead of swollen ridges, paraconule not fused to the cingulum) indicate that *Y. lufengensis* is not a tetraconodontine, nor another suid, but a tayassuid.

The known old world Tayassuidae are *Odoichoerus* Tong and Zhao, 1986 (Eocene, China), *Propalaeochoerus* Stehlin, 1899, *Palaeochoerus* Pomel, 1847 and *Doliochoerus* Filhol, 1882 (Oligocene and lowermost Miocene, Europe), *Taucanamo* (lower Miocene to upper Miocene, Europe and Turkey) and *Schizochoerus* (upper Miocene, Europe and Turkey). The Miocene genera *Sanitherium* Von Meyer, 1866 (SE Europe, Africa, Indo-Pakistan-Subcontinent), *Pecarichoerus* Colbert, 1933 (Indo-Pakistan-Subcontinent), *Albanohyus* Ginsburg, 1974 (= *Barberahyus* Golpe, 1977; Europe) and *Cainochoerus* Pickford, 1988b (Africa) are either no tayassuids or not well known and in any case they are clearly different from the Lufeng tayassuid. (Fortelius et al. in press, Hendey, 1976; Van der Made, 1990c and in press; Van der Made and Hussain 1992; Pickford, 1977, 1978, 1984 and 1988b; Pickford and Ertürk, 1979; Tong and Zhao, 1986.)

We will compare *Y. lufengensis* which is lophodont and has elongate premolars to lophodont *Schizochoerus* and *Taucanamo* which has elongate premolars and discuss the biometry of these genera. Other genera are not considered since they are not lophodont nor have elongate premolars.

In figs. 5 and 6 the lengths and widths of the cheek teeth are represented as a percentage of *Taucanamo sansaniense* and also the index I is indicated. *T. grandaevum* (Fraas, 1870) (the tayassuid from Steinheim; see Fortelius et al. in

press) resembles *T. sansaniense* in its proportions, but is on average 10% smal.
(figs. 5 and 6). *T. inonuensis* Pickford and Ertürk, 1979 measures on average 107%
of *T. sansaniense*, but has relatively small P^1 and P^2 (fig. 6). It has diastemas between the upper canine and the P^1 and between the P^1 and the P^2. This points to

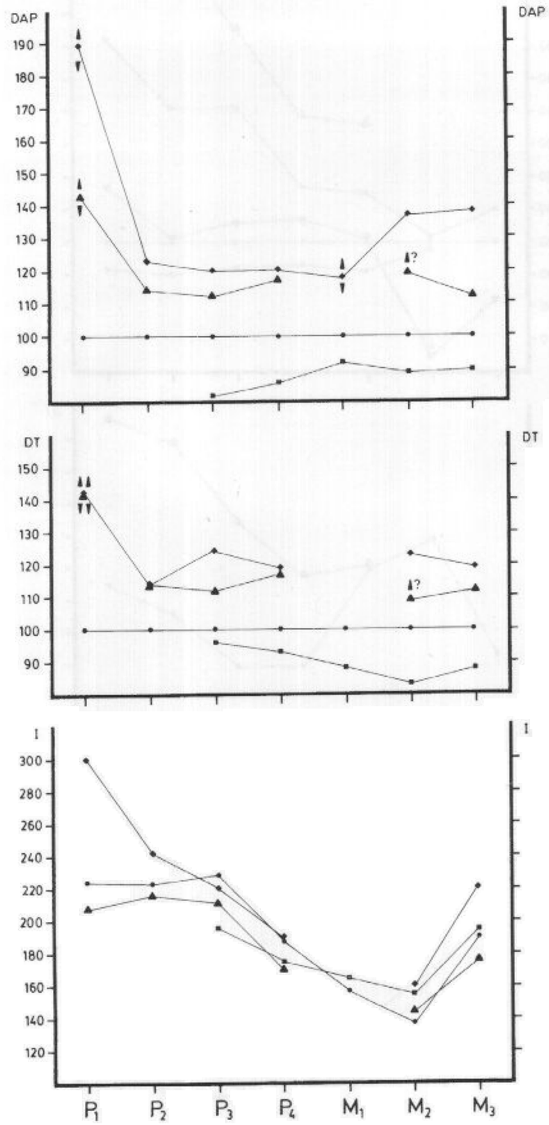

Fig. 5. Lower cheek teeth of *Taucanamo* and *Yunnanochoerus*. The upper part of the figure (DAP) shows the length and the next part (DT) the greatest width as a percentage of *Taucanamo sansaniense*. The lower part of the figure shows the index I. Dots = *Taucanamo sansaniense*, mean of population from Sansan (MNHN); squares = *Taucanamo grandaevum*, mean of population from Steinheim (SMNS); diamonds = *Yunnanochoerus gandakasensis*, holotype (data from Pickford, 1977); triangles = *Yunnanochoerus lufengensis*, holotype (IVPP). Arrows and questions marks indicate ≤, ≥, >, < and ± for the DAP and DT diagrams. In the DT diagram, P_1 of two species have the same approximate value.

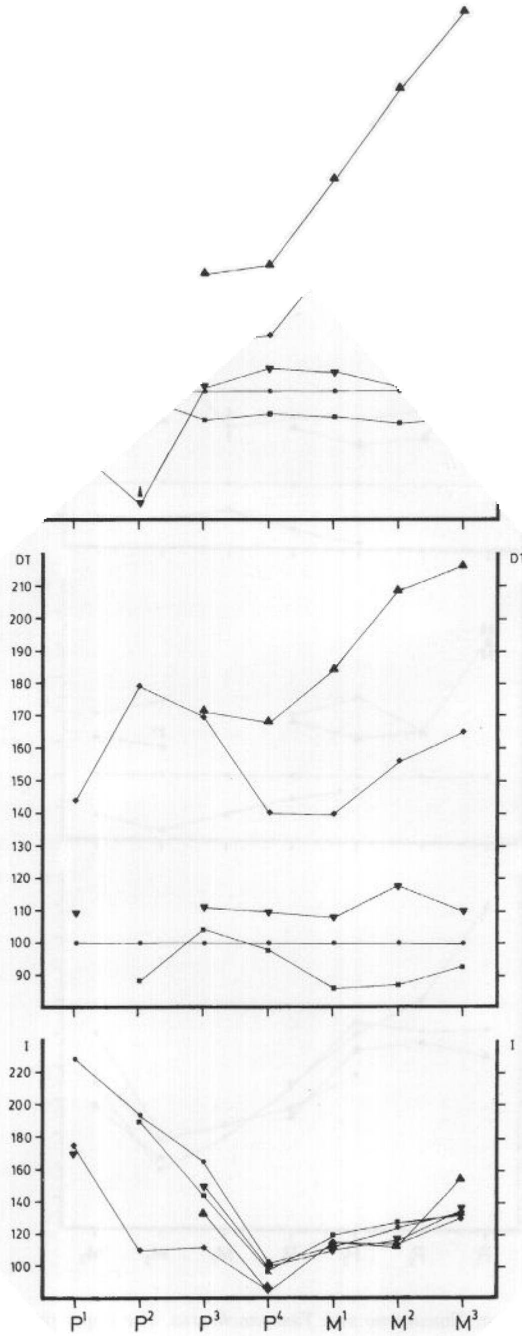

Fig. 6. Upper cheek teeth of *Taucanamo* and *Schizochoerus*, length, width and index I are indicated as in fig. 5. Dots = *Taucanamo sansaniense*, mean of population from Sansan (MNHN); squares = *Taucanamo grandaevum*, mean of population from Steinheim (SMNS); diamonds = *Schizochoerus* 'cf. *gandakasensis*' as described by Pickford and Ertürk (1979); triangles with the point downwards *Taucanamo inonuensis*, holotype from Inönü, data from Pickford and Ertürk (1979); triangles with the point upwards = *Schizochoerus vallesiensis* from Sinap (MNHN).

size reduction of the anterior premolars. Size increase of premolars in a first stage and size reduction of the anterior premolars and formation of diastemas in a next stage seems to be a common pattern in suoid evolution (Van der Made, 1989).

In *Schizochoerus*, the premolars are relatively short and wide and have a low index I (fig. 6) and the P_4 has two main cusps (pl. 3, fig. 6). A further difference with *T. sansaniense* is the large size of the M^2 and M^3. There are two sizes of *Schizochoerus*, *S. vallesiensis*, which measures on average 180% of *T. sansaniense* and '*Schizochoerus gandakasensis*' as described by Pickford and Ertürk (1979), which measures on average 142% of *T. sansaniense*.

Y. lufengensis (holotype) measures on average 106% of *T. sansaniense*. It has elongated premolars like *T. sansaniense* and it has a relatively large P_1, like *Y. gandakasensis*.

Yunnanochoerus gandakasensis (Pickford, 1977) has an average size of 120% of *T. sansaniense* and had long and narrow premolars (fig. 5).

It is evident that among the premolars there are two types, short and wide premolars (*Schizochoerus vallesiensis* and '*Schizochoerus* cf. *gandakasensis*') and long elongate premolars (*Taucanamo* spp., *Y. lufengensis* and *Y. gandakasensis*) (figs. 5 and 6, note especially fig. 6 DT diagram). Both types are a deviation from the most common type, which is intermediate in its index value I. Hence, it is obvious that *Y. gandakasensis* cannot be related to '*Schizochoerus* cf. *gandakasensis*' from Sinap. The small *Schizochoerus* from Sinap represents an unnamed species.

Y. gandakasensis was originally described as a *Taucanamo* species (Pickford, 1977), but was later placed in *Schizochoerus* because it is lophodont (Pickford, 1979).

In *Schizochoerus* lophodonty is best developed in the first lobe of the upper molars and least in the lower molars.

Y. lufengensis is lophodont, although the lophes are not perfectly formed in the lower molars. The degree of lophodonty in *Y. gandakasensis* is comparable to that of *Y. lufengensis*. Both species have elongate premolars and a P_4 with one main cusp. They differ from *Taucanamo* in the development of lophodonty. This is why we place the two species in the new genus *Yunnanochoerus*.

Y. gandakasensis is approximately 15% larger than *Y. lufengensis* and its M_3 is approximately 30% larger. Most tayassuids are small animals with small M3. So it is likely that *Y. gandakasensis* is a descendant from *Y. lufengensis*, although it is also possible that there are two lineages.

Y. gandakasensis is from the lower part of the Dhok Pathan Formation (Pickford, 1977). This suggests that Lufeng might be correlated with the upper part of the Nagri Formation (not with a much older horizon because of the presence of *Hipparion* in Lufeng; see also discussion on *Chleuastochoerus*) or the very lowest part of the Dhok Pathan Formation. This is close to the age of 8 Ma found by Flynn and Qi (1982) and Qi (1986) and slightly older than the age given by Qiu and Storch (1990), who correlated with MN 12, which is approximately 7 Ma (Opdyke et al., 1990). Flynn Qiu found the same species of rhizomyids in

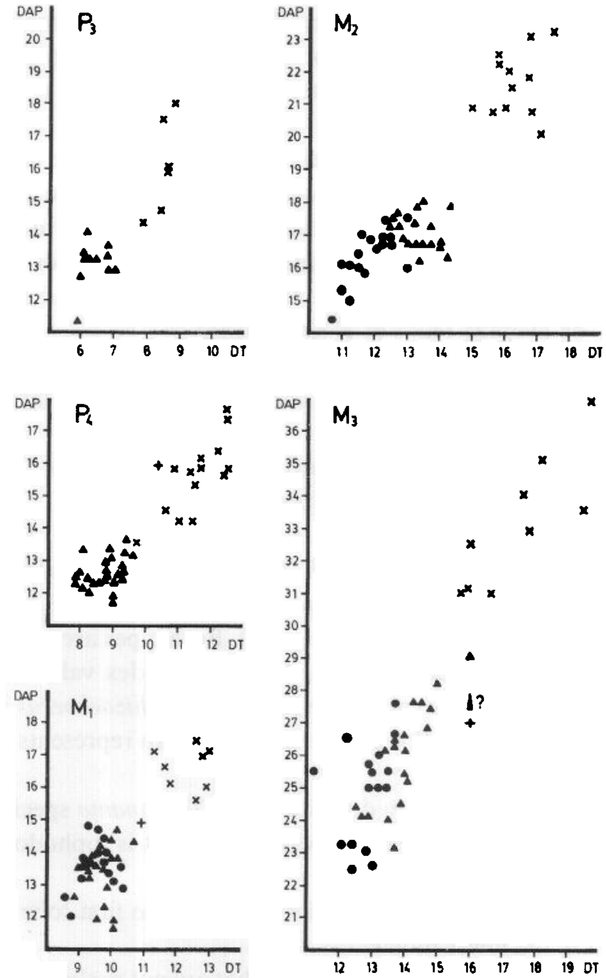

Fig. 7. Scatter diagrams of the lower cheek teeth. Triangles = *Propotamochoerus wui* n. sp. from Lufeng; oblique crosses = *Propotamochoerus hysudricus* from Pakistan and India (GSP and IM); crosses = *Propotamochoerus* sp. from Padri 40, Dhok Pathan Formation (IVAU); dots = *Chleuastochoerus* from Lagrelius locality 49 (data from Pearson, 1928).

Pakistan and Lufeng, and considered both areas to belong to one general biogeographical province. The presence of *Propotamochoerus* and *Yunnanochoerus* in Pakistan and in southern China (although with different species) is in accordance with their findings. The fact that rodents and suids indicate that both areas are not separated might be used as an argument in favor of the single lineage model in *Yunnanochoerus*.

SUIDAE Gray, 1821

Suinae Zittel, 1893

Dicoryphochoerini Schmidt-Kittler, 1971

Revised diagnosis: Suidae with a Dicoryphochoerine-type P_4 (P_4 with two main cusps, a large labial one and a somewhat smaller lingual or postero-lingual one) and with elongated I^2.
Remarks: A more detailed description and discussion of the characters mentioned in this diagnosis and the diagnoses of *Propotamochoerus* and *P. hyotherioides* is given by Van der Made and Moyà-Solà (1989).
Type genus: *Hippopotamodon* (Lydekker, 1877) (=*Dicoryphochoerus*, Pilgrim, 1926).

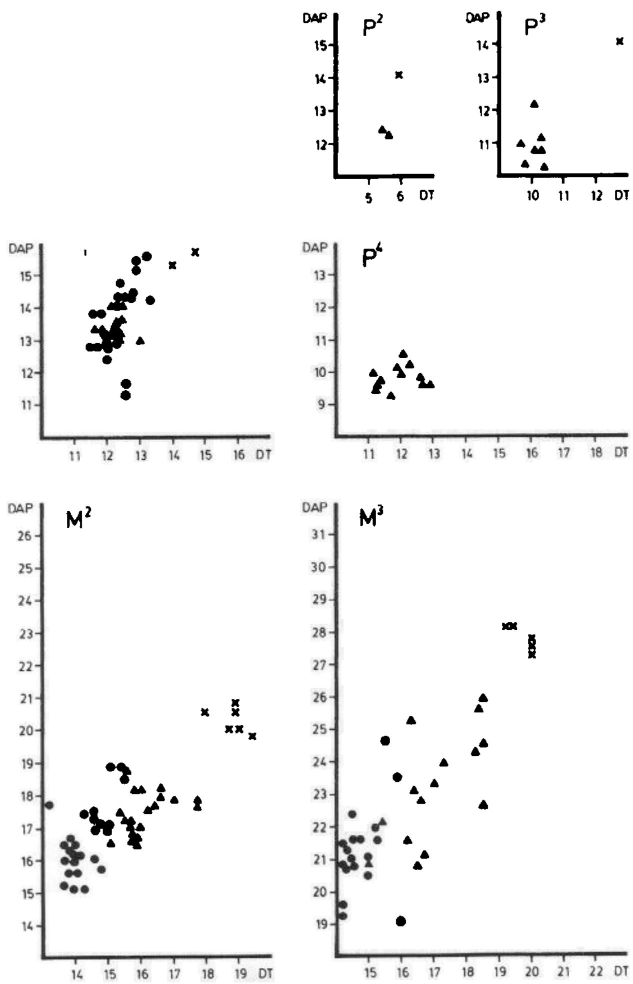

Fig. 8. Scatter diagrams of the length (DAP) and width (DT) of the upper cheek teeth in mm. Triangles = *Propotamochoerus wui* n. sp. from Lufeng; oblique crosses = *Propotamochoerus hysudricus* from Pakistan and India (GSP and IM); dots = *Chleuastochoerus* from Lagrelius locality 49 (data from Pearson, 1928).

Propotamochoerus Pilgrim, 1925

Revised diagnosis: Small Dicoryphochoerini, with canines that are not much reduced.
Type species: *Propotamochoerus hysudricus* (Stehlin, 1899).
Other species: *P. palaeochoerus* (Kaup, 1833), *P. hyotherioides* (Schlosser, 1903), *P. provincialis* (Gervais, 1859) and *P. wui* n. sp. Several species belonging to this genus were described by Pilgrim (1926) from the Indian subcontinent, but Pickford (1988) did not recognize any species other than *P. hysudricus*. No other species belonging to this genus are known to us, except for the small fossils from the Dhok Pathan Formation mentioned in the description and some material from the Chinji Formation that is close to *P. hysudricus*, but differs in having a small M3.

Propotamochoerus wui nov. sp.

Plate 4, figs. 3, 4 and 6; Plates 5–12.

Diagnosis: Very small *Propotamochoerus* (linear measurements 78% of *P. hysudricus*).
Derivatio nominis: named in honor of Wu Rukang because of his important contribution to the palaeontology of China.
Holotype: Mandible with left I_1-I_2, C_m-M_2 and right I_1-I_2, C_m-P_1, P_3-M_3. The piece was broken transversely in the area of the P_2 and is restored with plaster. It is figured in pl. 5, figs. A to E and it is filed in the IVPP under number V 9942.1.
Type locality: Lufeng, Yunnan, China.
Age of the type locality: Late Miocene.

Material

Lower teeth: 18 Mandibles or tooth rows (including holotype) with 2 I_1, 2 I_2, 2 C_m, 2 P_1, 1 P_2, 9 P_3, 11 P_4, 13 M_1, 13 M_2 and 8 M_3; one symphysis with 2 I_1, 2 I_2 and 2 C_f; isolated lower teeth: 10 I_1, 7 I_2, 3 I_3, 2 C_f, 5 C_m, 5 P_1, 1 P_2, 11 P_3, 15 P_4, 12 M_1, 18 M_2, 20 M_3, 1 DI_2, 5 D_4; 10 maxillas or tooth rows with, 2 P^1, 3 P^2, 7 P^3, 8 P^4, 8 M^1, 9 M^2 and 4 M^3; isolated upper teeth: 6 I^1, 4 I^2, 1 I^3, 2 C^m, 1 P^1, 1 P^2, 2 P^3, 5 P^4, 6 M^1, 22 M^2, 16 M^3, 2 D^2, 3 D^3, 4 D^4; a first falange. This material was recovered from layers 1 to 6 (Fig. 1) and is filed in the IVPP under number V 9942.

The measurements are given in tables 2–5.

Description and comparison

Comparisons with other species of *Propotamochoerus* will be made, as well as with *Chleuastochoerus*, a sympatric contemporaneous species of similar size. The teeth are very similar to those of *P. hysudricus* and an imperfectly known small *P.* aff. *hysudricus* from the Dhok Pathan Formation. However, these species, which are the next smallest *Propotamochoerus*, are clearly larger (figs. 7 and 8). Pearson (1928) gave only measurements of the molars of *Chleuastochoerus*.

The *Chleuastochoerus* from locality 49 is the largest and the molars are slightly smaller than those of *P. wui*, although there is overlap (figs. 7 and 8). If the figs. given by Pearson (1928; text-figs. 19–22) are reliable to size, the premolars are clearly smaller and no overlap occurs.

The $\mathbf{P_1}$ (pl. 5, figs. A and B; pl. 11, fig. 3) has a low and elongate crown, the tip is placed much forward and it has two separate roots.

The $\mathbf{P_2}$ (pl. 11, fig. 2) and $\mathbf{P_3}$ (pl. 4, fig. 4; pl. 7, figs. 1 and 5; pl. 8, fig. 1; see also pl. 6, figs. 1 and 3) have a posterior flare and are less symmetrical than those of *Chleuastochoerus*. The premolars of *P. wui* have a posterior profile with several small cusps, which however disappear with wear (pl. 7, fig. 5, no wear versus pl. 7, fig. 1, worn), in *Chleuastochoerus* the profile is straighter.

The $\mathbf{P_4}$ is of the Dicoryphochoerini type (Schmidt-Kittler, 1971; Van der Made and Moyà-Solà, 1989), there are two main cusps on the trigonid and there is a

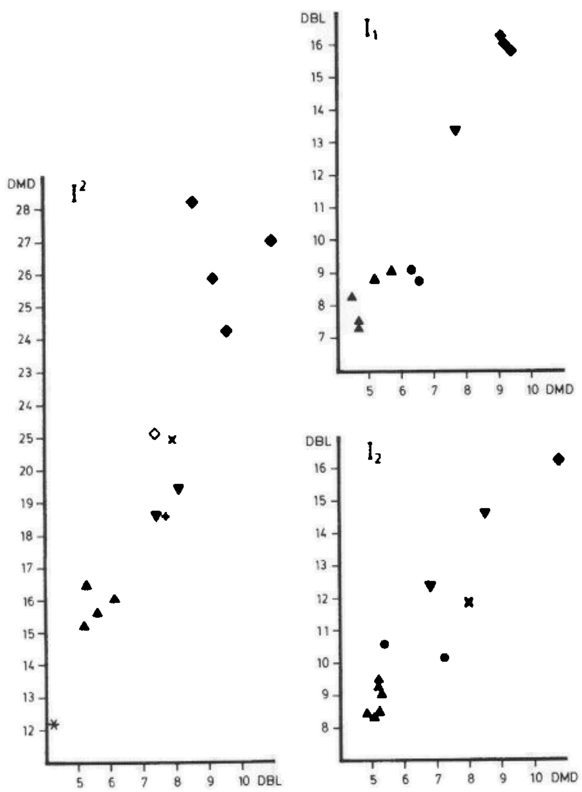

Fig. 9 Scatter diagram for the I^2, I_1 and I_2 of the Dicoryphochoerini; in two cases the I^3 is plotted in the diagram for the I^2: triangles with the point upwards = *Propotamochoerus wui* from Lufeng (IVPP); triangles with the point downwards = *P. hyotherioides* from Lufeng (IVPP); dots = *P. hysudricus* from Pakistan and India (GSP, IM, IVAU); crosses = *P. palaeochoerus* from Hostalets (IPS); oblique crosses = *P. provincialis* from Venta del Moro (MNCN); asterisk = I^3 of *P. provincialis* from Venta del Moro (MNCN) in the diagram for the I^2; diamonds = *Microstonyx* from Crevillente 2, Terrassa, Cerro de la Garita and Samos (MHMN, IPS, IPS, NMB); open diamond = I^3 of *Microstonyx* from Samos (NMB) in the diagram for the I^2.

lower cusp on the talonid, the anterior cingulum is elevated. Several authors gave great importance to this tooth and Pilgrim (1926) created a number of new taxa for different types of P_4 and believed them to belong to very different branches of the Suidae. Pickford (1984) lumped most of those taxa. The Lufeng sample is

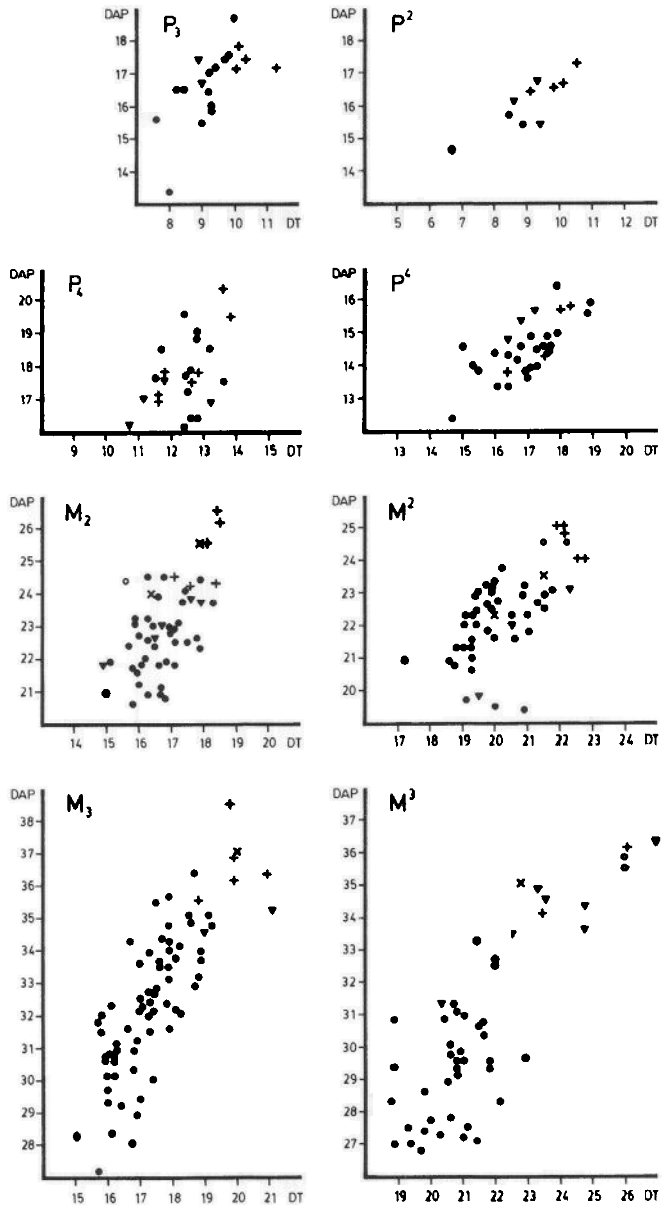

Fig. 10. Scatter diagrams for the cheek teeth of the larger species of *Propotamochoerus*. Dots = *P. palaeochoerus* from the Deinotheriensande, Germany (data from Hünermann, 1968); crosses = *P. provincialis* from the European localities Arenas del Rey (IPS), Casino (AFS), Montpellier (UCBL), Ptolemais Kardia (IVAU), Venta del Moro (MNCN); oblique crosses = *P. hyotherioides* from China (data from Schlosser, 1903); circles = *P. hyotherioides* from locality 49 (data from Pearson, 1928); triangles = *P. hyotherioides* from Lufeng (IVPP).

large and shows great variability in the position and degree of separation of the main cusps but cannot be split into two well defined groups, coroborating Pickford's idea that variability in these characters may be great in a monospecific sample. Relative to the labial cusp, the lingual cusp may be placed nearly exactly posteriorly, being displaced only slightly lingually (pl. 7, fig. 7; worn state pl. 7, fig. 3) or it may be placed much more forward (pl. 7, fig. 6; pl. 8, fig. 1, worn state pl. 7, fig. 2). The distance between the cusps is variable and the outline of the trigonid, if seen from the side may be sharp (pl. 7, fig. 7) or blunt (pl. 7, fig. 8). The anterior cingulum is elevated and tends to become a stylid; there is variation as to the degree of elevation (pl. 7, fig. 7 versus figs. 4, 6 and 8). This character has its importance as it is one of the differences with the P_4 of *Sus* Linnaeus, 1758. Some P_4 seem to be more hypsodont (pl. 11, fig. 1, worn) than others (pl. 7, fig. 8, unworn but less hypsodont). In some P_4 the talonid seems to be relatively wide (pl. 7, figs. 2, 4 and 6), but in the DTa-DTp scatter diagram this is not apparent. The tooth is smaller than that of *P. hysudricus* and no overlap occurs. The P_4 of *P. wui* has the same length as the one of *Chleuastochoerus*, but is wider. The *Chleuastochoerus* P_4 has the main cusps wider apart and its lingual cusp is placed more forward.

The **M_1** (pl. 6, figs. 1 and 3) have nearly the same size as in *Chleuastochoerus*, but the **M_2** (pl. 11, fig. 5; also pl. 6, figs. 1 and 3) are slightly larger, however, overlap is great (fig. 7).

The **M_3** (pl. 9, figs. 1–4) has a simple third lobe, consisting of one large cusp which is placed on, or very slightly labially of the axis of the tooth. There is not so much variability in third lobe morphology as in dicoryphochoerines like *Microstonyx* Pilgrim, 1926 (Van der Made et al. 1992) and *P. provincialis* (one or two cusps). The last cusp of the lingual cingulum is in some cases slightly enlarged (pl. 9, fig. 3), which is the very beginning of the formation of a second cusp in the third lobe. None of the M_3 of *Chleuastochoerus* figured by Pearson has a large posterior cusp, although the M_3 in this species may be more elongated (fig. 7).

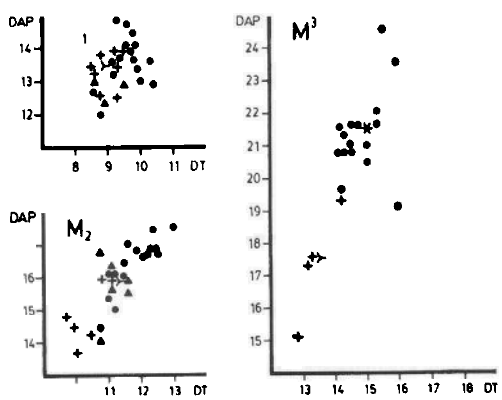

Fig. 11. Scatter diagram of the M_1, M_2 and M^3 of *Chleuastochoerus*: crosses = *Chleuastochoerus* from locality 73 (data from Pearson, 1928); dots = *Chleuastochoerus* from locality 49 (data from Pearson, 1928); triangles = *Chleuastochoerus* from Lufeng (IVPP); three pointed starr = *Chleuastochoerus stehlini*, cotypes (data from Schlosser, 1903).

The M_3 of *P.* aff. *hysudricus* from the Dhok Pathan Formation (IVAU) differs in having two equally large cusps in the third lobe.

The $\mathbf{P^1}$ is a low and elongate tooth (pl. 4, fig. 6; pl. 11, figs. 4 and 6), with two roots that are not always very well separated.

The $\mathbf{P^2}$ (pl. 11, figs. 4 and 6) has a high crown and a wide postero-lingual cingulum. The P^2 in *Chleuastochoerus* is narrower because it does not have a well developed postero-lingual cingulum.

The $\mathbf{P^3}$ (pl. 8, fig. 2) has a large conical main cusp, which, as is common in Dicoryphochoerini, is only slightly laterally compressed; however, the P^3 of *Chleuastochoerus* is much more compressed.

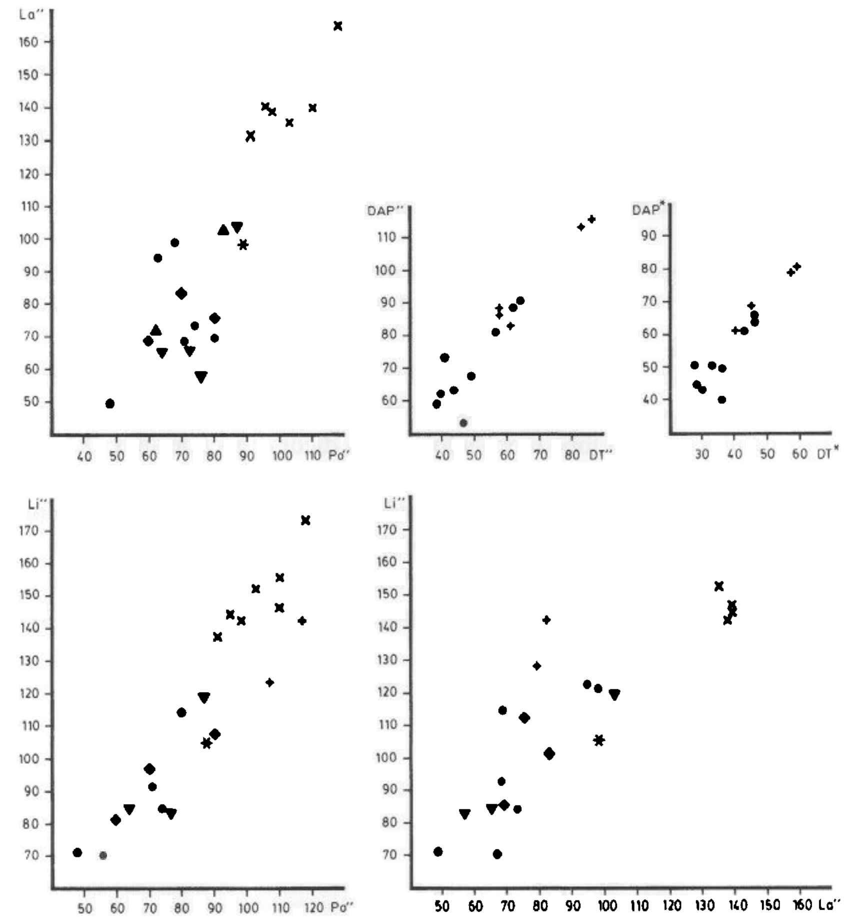

Fig. 12. Scatter diagrams of C_m. DAP'' DT'' and DAP* DT* diagrams of *Sus scrofa*, Deli: dots = subadults, crosses = adults. Other diagrams: dots = Tayassuidae, Hyotheriinae and Listriodontinae; crosses = recent *Sus scrofa* from Guadalajara, Huelva, Lerida and Burgos, Spain (MNCN); triangles with the point downwards = *Propotamochoerus* from Ballestar (IPS) and Lufeng (IVPP); triangles with the point upwards = *Hippopotamodon/Microstonyx* from Eppelsheim (HLD), the Indian subcontinent (IM) and Terrassa (IPS); diamonds = recent *Potamochoerus porcus* (Linnaeus, 1758) from Africa (RMNHL, MNCN); oblique crosses = *Sus strozzii* from Valdarno (IGF); asterisks = *Sus peii* Han, 1987 from Liucheng (IVPP).

The $\mathbf{P^4}$ has two well separated labial cusps. There is a sagittal cusp (sensu Pickford, 1988a) (pl. 8, figs. 2–4), which is not the case in *Chleuastochoerus* (Pearson, 1928). The base of the crown at the labial side is slightly lower (pl. 8, fig. 3C) or much lower (pl. 8, fig. 4C) than at the other sides.

The $\mathbf{M^1}$ (pl. 8, fig. 5) and $\mathbf{M^2}$ (pl. 10, fig. 5) have the paraconule fused to the cingulum. This is also the case in *Chleuastochoerus*. The M^1 has the same size as in *Cleuastochoerus* from locality 49, but on average the M^2 is slightly larger (fig. 8).

The $\mathbf{M^3}$ has a talon which may consist of a posterior cingulum that is enlarged lingually of the median plane of the tooth (pl. 10, fig. 7) or which may have a well developed cusp at that place (pl. 10, figs. 2 and 3), there may be a constriction separating this cusp from the second lobe of the tooth (pl. 10, fig. 4) and there may even be an additional cusp buccally of the talon, but this seems to be an abnormality (pl. 10, fig. 1). The second morphology is the most common. *Chleuastochoerus* has a simple morphology like the first one described, but is slightly smaller (fig. 8).

The $\mathbf{I^1}$ is compressed in linguo-labial direction and elongated in meso-distal direction (pl. 11, fig. 7; pl. 12, fig. 1). With wear a large undulating linguo-apical wear facet develops. This type, its crown height and its wear is intermediate between the primitive suoid incisor and the incisor of *Sus* (Van der Made, 1990b). All *Propotamochoerus* I^1 are elongated to some degree in meso-distal direction compared to the I^1 of primitive suoids. In being compressed in linguo-labial direction it is like the I^1 of *P. hysudricus* and *P. provincialis* and differs from the one of *P. palaeochoerus* which has meso-lingually a wide cingulum, making it less compressed. The I^1 of *P. palaeochoerus* has also a small distal cusplet, which seems to be typical of the species. The I^1 is much like the one of *Sus scrofa* Linnaeus, 1758, but is much less hypsodont. The I^1 of *Chleuastochoerus* is not clearly figured by Pearson, but if it is like in other Hyotheriinae than it is less hypsodont and less compressed than in *P. wui*.

The $\mathbf{I^2}$ (pl. 12, figs. 3 and 4) have low and elongated crowns (I = 262, 279, 292, 309 and 311). The Suinae *Sus*, *Propotamochoerus Hippopotamodon* and *Micro-*

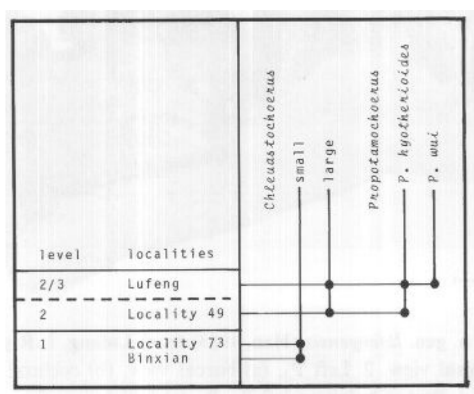

Fig. 13. Synthetic stratigraphy of Chinese localities with *Chleuastochoerus* and *Propotamochoerus*. Level numbers indicate levels recognizable with suoids, above the entry of *Hipparion*.

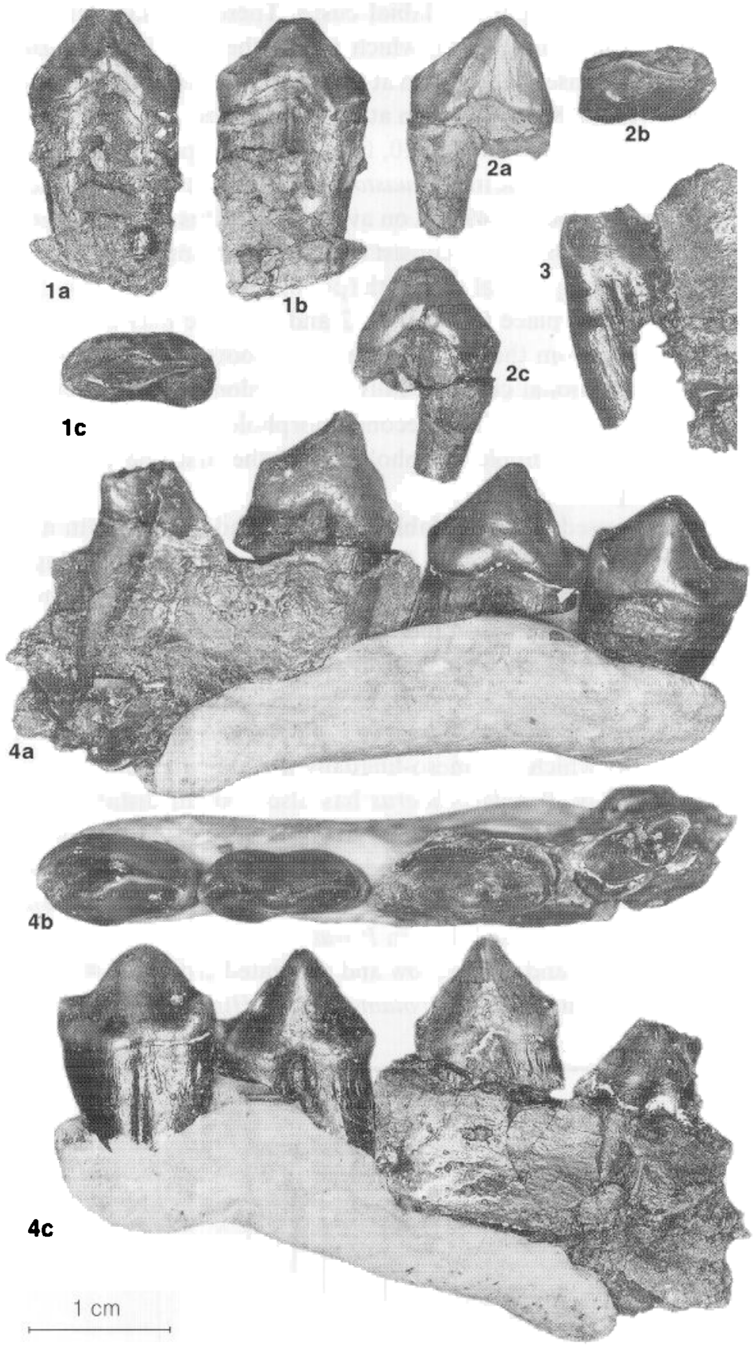

Plate 1. *Yunnanochoerus* n. gen. *lufengensis* (Han, 1983) from Lufeng. 1. Right P_3, (a) lingual view, (b) buccal view, (c) occlusal view. 2. Left P_3, (a) buccal view, (b) occlusal view, (c) lingual view. 3. Right P_1, lingual view. 4. Part of holotype, left P_1 P_4, (a) labial view, (b) occlusal view, (c) lingual view. The scale in the plates is approximate; individual figures may show minor deviations.

stonyx have such I^2 and it may be a common derived character of these Suinae, but also *Sivachoerus* Pilgrim, 1926 / *Nyanzachoerus* Leakey, 1958 have such I^2, which is a parallelism. In *P. palaeochoerus* from Hostalets (IPS) I = 245, in *P. provincialis* from Venta del Moro (MNCN) I = 264 and 281, in *Microstonyx major* (Gervais, 1848–1852) from Crevillente II, Cerro de la Garita and Terrassa (respectively MHMN, IPS, IPS) I = 245, 312, 248 and *Microstonyx erymanthius* (Roth and Wagner, 1854) from Samos (NMB) I = 280, 328 and in *Eumaiochoerus* Hürzeler, 1982 from Baccinello (NMB) I = 290 and 305. There is a postero-lingual cingulum, which is not commonly found in *Sus*. The I^2 is the smallest assigned to Dicoryphochoerini (fig. 9) and its size is relatively the same as in other species of the genus. Average DMD″ and DLL″ are respectively 98 and 34 for *P. wui*. For *P. hyotherioides* these values are 88 and 36 and for *P. provincialis* from Venta del Moro 99 and 36. For the following species the same method is used on material from different localities, and the values should be seen as very superficial indications: *P. palaeochoerus* 95 and 34, *M. major* 96 and 39 and for *M. erymanthius* 111 and 34. The I^2 of *Chleuastochoerus* does not seem to be elongated (Pearson, 1928), in *Hyotherium meisneri* (Von Meyer, 1829), which is also a hyotheriine, DMD″ and DT″ are 65 and 36 (data from Van der Made, in press).

The $\mathbf{I^3}$ has a low and elongated crown (I = 290), like the I^2, but the postero-lingual cingulum is absent (pl. 12, fig. 6). In most suids other than Suinae the I^3 does not have an elongated and low crown. With use a large posterior wear facet may develop, which is caused by the lower canine (compare *P. provincialis*, Morales, 1984, plate 4, fig. 6 and *Microstonyx major*, Van der Made et al. 1992, plate 3, fig. 11). The index I of the I^3 in *P. provincialis* from Venta del Moro (MNCN) is 219, 226 and 244, in *P. palaeochoerus* from Castell de Barberà (IPS) this is 224, 227, 233 and 242 and in *Microstonyx erymanthius* from Samos (NMB) this is 285, a worn I^3 of *M. major* from Crevillente II (MHMN) has an I of 199, it probably had a value between the *Propotamochoerus* and *M. erymanthius* values. Although only few specimen are known, the degree of elongation of the I^3 seems to be of interest for Dicoryphochoerini-phylogeny. In *Chleuastochoerus* the I^3 is not elongated (Pearson, 1928, text-fig. 14b).

The $\mathbf{C^m}$ (pl. 11, fig. 8) is a hypsodont outward curved tooth with anterior and posterior crests which are covered by narrow enamel bands. In addition, there is a wide lingual or ventral band of enamel with longitudinal ribs. The section is nearly circular. In *Sus*, the section may have a kidney shape. In *Chleuastochoerus* the canines are placed within a bony structure and cannot be as large as in *P. wui*, certainly not the part below the wear facet.

The $\mathbf{I_1}$ and $\mathbf{I_2}$ are teeth with roughly the same morphology, but the former is nearly symmetrical and the latter is clearly asymmetrical and has a distal wear facet with the I^2 (pl. 12, figs. 2 and 5; pl. 6, fig. 2). The degree of hypsodonty is intermediate between Hyotheriinae, such as *Chleuastochoerus* (Pearson, 1928, text-figs. 19–22) and advanced Suinae, such as *Sus* and *Microstonyx* (Van der Made et al. 1992, plate 2, fig. 10). The incisors are the smallest attributed to Dicoryphochoerini (fig. 9).

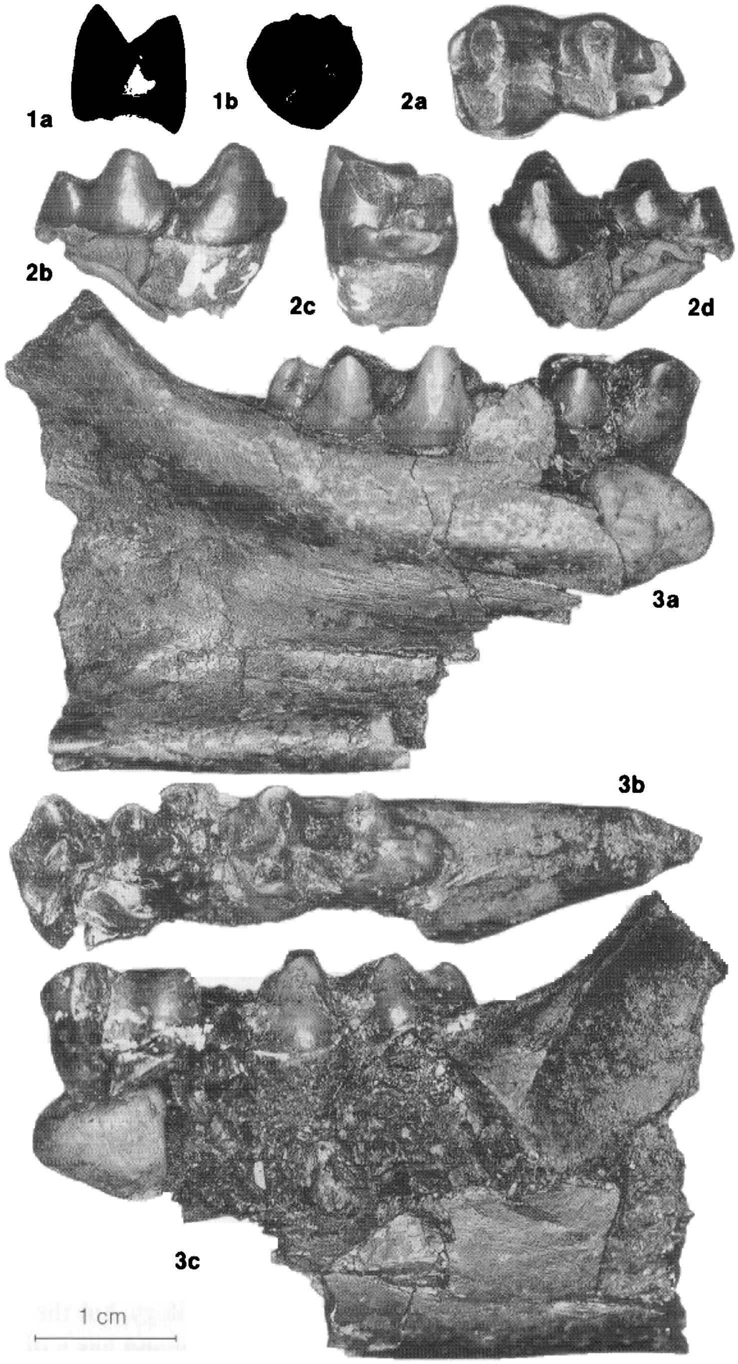

Plate 2. *Yunnanochoerus* n. gen. *lufengensis* (Han, 1983) from Lufeng. 1. Left M_2, (a) posterior view, (b) occlusal view. 2. Left M_3, (a) occlusal view, (b) lingual view, (c) anterior view, (d) labial view. 3. Part of holotype, left M_2–M_3, (a) lingual view, (b) occlusal view, (c) buccal view.

The I_3 (pl. 12, fig. 7) has the same structural elements as in *P. hyotherioides*, but it is less symmetrical, much more flattened in labio-lingual direction, has a higher crown and the median crista is not so well developed.

The C_f (pl. 4, fig. 3), is relatively large (it is not reduced as in some Dicoryphochoerini) and, like in *S. scrofa*, the middle of the posterior side is not covered with enamel. Many suids, including *Microstonyx major* (which evolved from *Propotamochoerus*) have the posterior side of the female canine completely covered with enamel, so this character may be of special interest for the study of the Suinae.

The C_m (pl. 5, figs. A and B) has a verrucosic section.

The D_3 is smaller and lower compared to its length and width than the P_2 and P_3 and it has a triangular outline if seen from the side. The posterior edge of the triangle tends to be straight.

The D_4 is easily recognizable because of its three lobes (pl. 10, fig. 6).

The D^3 has three cusps, one large anterior cusp and two posterior cusps. The posterior part of the tooth resembles a molar.

The D^4 has an antero-buccally protruding corner unlike the molars (pl. 8, fig. 6).

The DI^1 (pl. 12, fig. 8) has roughly the same morphology as the I^1, but is smaller. It is not the incisor of *Chleuastochoerus* as it differs from that tooth in the same way as the I^1 of *P. wui*, it is linguo-labially compressed.

The DI_2 is a much smaller tooth than the I_2 and has thin enamel. The section of the tooth approaches more a cylinder, whereas the permanent tooth is generally more compressed. The I_2 of *Chleuastochoerus* is larger, has thicker enamel and probably has a relatively lower crown.

The **diastema** between C_m and P_1 is small (pl. 5, figs. A and B). The only mandible which might have shown the diastema between the P_1 and P_2 is damaged in this area. There is no evidence for a diastema between P_2 and P_3. In some of the mandibles of *Chleuastochoerus* figured by Pearson (1928) such a diastema exists. In two tooth rows (probably belonging to the same individual) the P^1 is in contact with the P^2 (pl. 11, figs. 4 and 6). In all nine *Chleuastochoerus* skulls figured by Pearson (1928), including males and females, the P^1 was separated from the P^2 by a diastema, although the length of the diastema varied from very small to more than the length of the P^1.

The **mandible** (pl. 6, figs. 1 and 3; pl. 5, figs. A and B) is deep and wide, as is normal in suids. If seen from buccally the ascending ramus does not hide the posterior part of the M_3 (this character may be age dependent). The symphysis starts at the back of P_2 (this character is age and sex dependent and is higly variable as indicated by the same samples of *Sus* that were studied for sexual bimodality by Van der Made, 1991).

Only one foot bone was found, a **first falange** of a central toe, right of the axis. The proximal facet shows a vertical grove, which is still deep at the dorsal side, as is common in Suidae, but in Tayassuidae, this grove may be shallow or absent dorsally. DAPp = 11.9; DTp = 10.9; L = 24.6; DAPd = 8.3; DTd = 8.8. It is referred to *P. wui* because it is small and this is the most abundant small suoid.

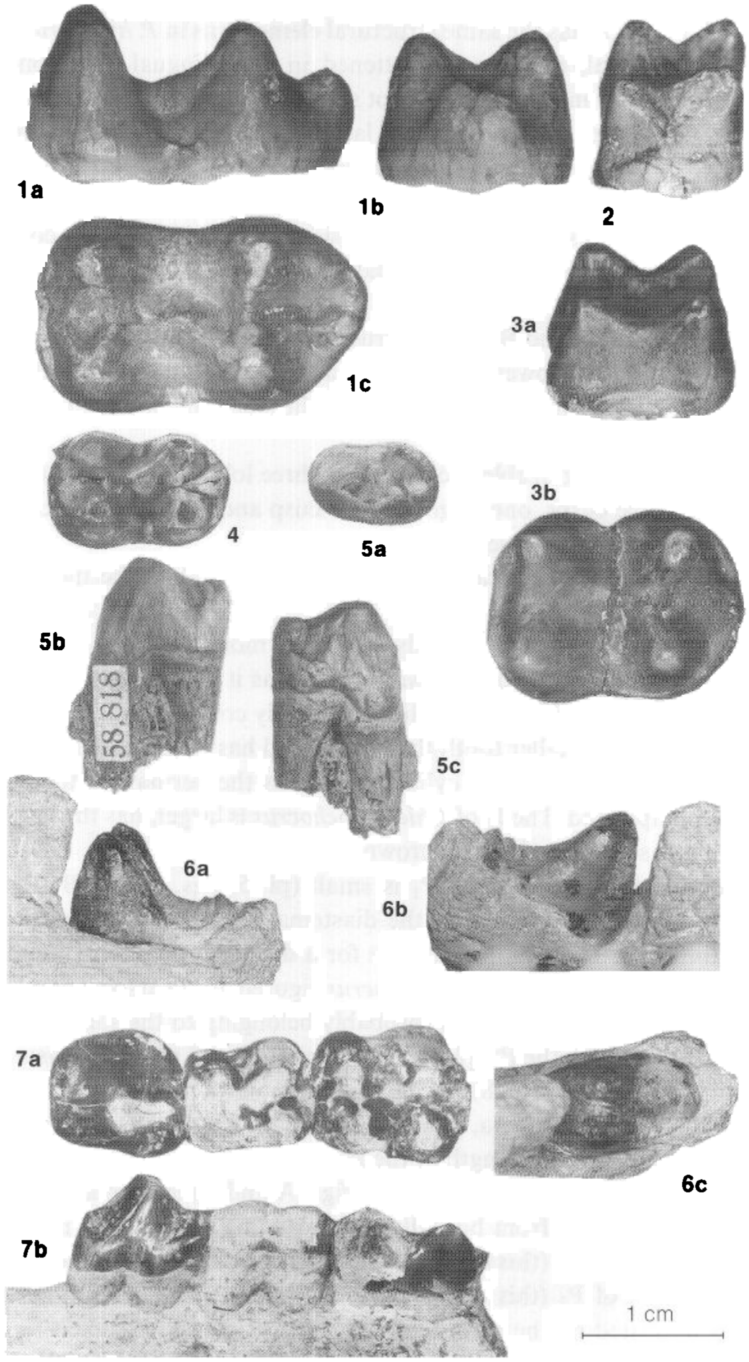

Plate 3. *Schizochoerus vallesiensis* Crusafont and Lavocat, 1954, *Taucanamo sansaniense* Lartet, 1851 and *Lophochoerus nagrii* Pilgrim, 1926. Figures 1–3 syntypes of *S. vallesiensis* from Villadecavalls (IPS). 1. IPS 1928, left M_2, (a) buccal view, (b) posterior view, (c) occlusal view. 2. IPS 1926, right M_1, anterior view. 3. IPS 1927, (a) anterior view, (b) occlusal view. Figures 4–5 *T. sansaniense* from Göriach (SLJG). 4. 58.817, right M_2, occlusal view. 5. 58.818, right P_4, (a) occlusal view, (b) lingual view, (c) buccal view. Figure 6 *S. vallesiensis* from Sinap (MNHN), Yas 27, left P_4, (a) buccal view, (b) lingual view, (c) occlusal view. Figure 7 *L. nagrii* from Haritalyangar (IM), B 693, right P_4–M_2, (a) occlusal view, (b) lingual view.

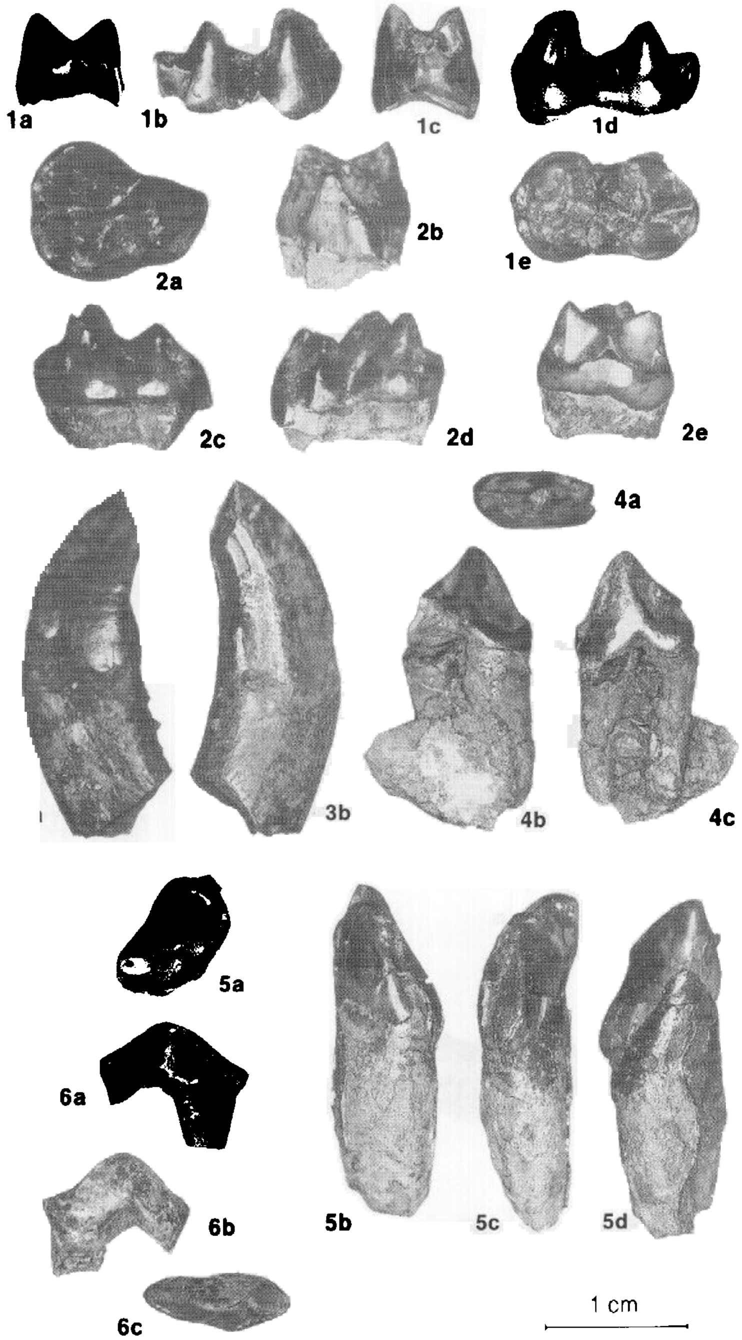

Plate 4. *Yunnanochoerus* n. gen. *lufengensis* (Han, 1983), *Propotamochoerus wui* n. sp. and *Propotamochoerus hyotherioides* Schlosser, 1903 from Lufeng. Figures 1–2 *Y. lufengensis*. 1. Left M_2, (a) posterior view, (b) lingual view, (c) posterior view, (d) buccal view, (e) occlusal view. 2. Left M^3, (a) occlusal view, (b) posterior view, (c) lingual view, (d) labial view, (e) anterior view. Figures 3, 4 and 6 *P. wui*. 3. Right C_f, (a) lingual view, (b) buccal view. 4. Left P_3, (a) occlusal view, (b) lingual view, (c) buccal view. 6. Right P^1, (a) buccal view, (b) lingual view, (c) occlusal view. Figure 5. Left I_3, (a) apical view, (b) distal view, (c) lingual view, (d) mesial view.

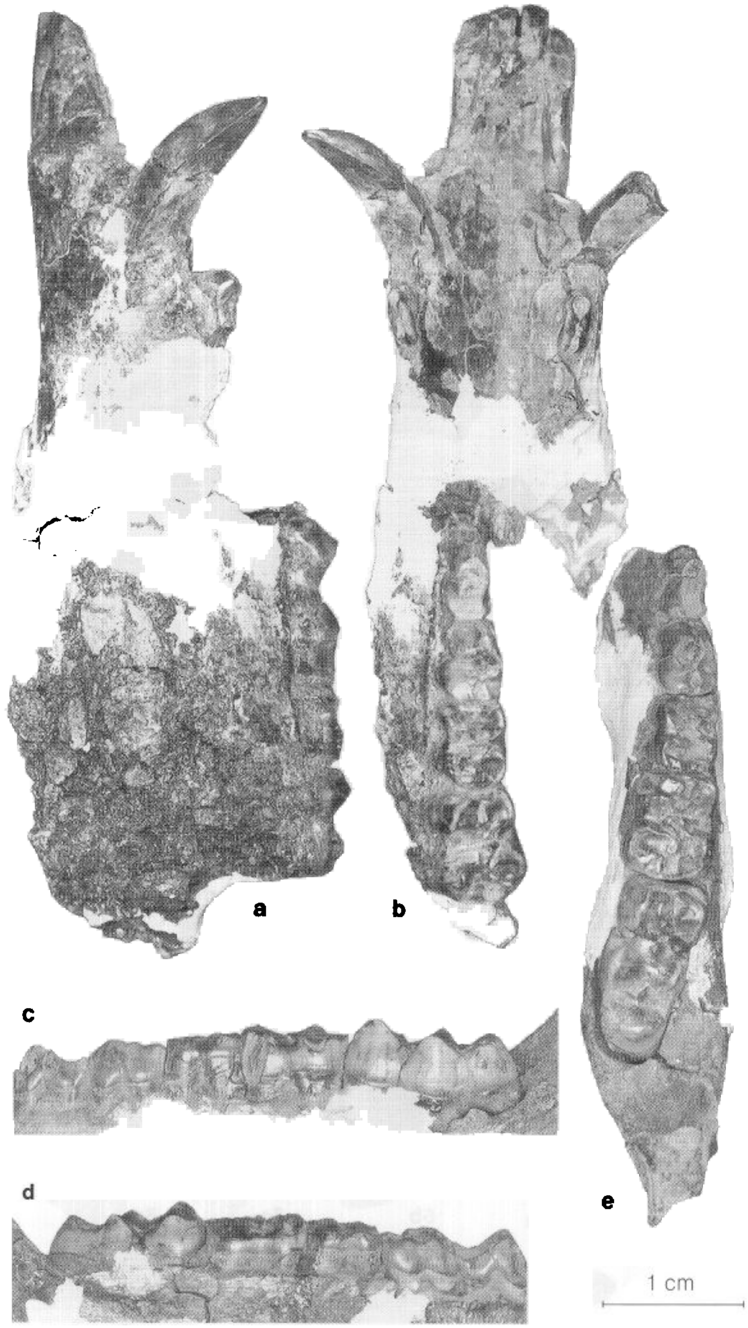

Plate 5. *Propotamochoerus wui* n. sp. from Lufeng. Holotype, (a) left mandible P_3–M_2 and symphysis with P_1, C_m and I_{1-2}, buccal view (b) left mandible P_3–M_2 and symphysis with left and right P_1, C_m, I_1 and I_2, occlusal view, (c) right P_3–M_3 lingual view, (d) right P_3–M_3, buccal view, (e) right mandible P_3–M_3, occlusal view. The white spots are restauration plaster.

Discussion

The morphologies of the P_4, I^2 and also I^1 indicate that this suid must belong to the Dicoryphochoerini. This tribe contains the large *Hippopotamodon* and *Microstonyx* and the small *Propotamochoerus*.

We used a sample of 11 *P. hysudricus* mandibles, that preserve both P_4 and M_3, in the IM and GSP as a standard for the size. Similarly, a reference sample of maxillaries was selected. The means of the measurements of *P. hysudricus* were taken as 100% and means of measurements on the teeth of the other species were expressed as a percentage. *P. wui* measured 78% of *P. hysudricus*, *P. palaeochoerus* 104% (measurements from Hünermann, 1968), *P. hyotherioides* 107% (Lufeng fossils) and *P. provincialis* 110% (various European localities).

There are no important morphological differences between the dentitions of *P. hysudricus* and *P. hyotherioides*. *P. provincialis* may have an M_3 with a third lobe with one or two cusps. *P. palaeochoerus* has a simple M_3, but differs in some characters from all others, including *P. wui*: 1) the I^1 is not linguo-labially compressed and has a distal cusplet, 2) the M3 is shorter, 3) the anterior premolars are reduced in size. The differences are small, but constant.

P. wui differs from *Chleuastochoerus* in: 1) having larger anterior premolars (relative to the other cheek teeth) without indication of diastemas other than between P_1 and P_2, 2) a wide P^2, 3) P^4 with a sagittal cusp, 3) having the two main cusps of the P_4 closer together with the lingual cusp less forward, 4) a relatively large M2, 5) a larger talon of the M^3, 6) morphology of the third lobe of the M_3, 7) more hypsodont I_1 and I_2 and a distal side of the base of the crown of the I_2 inwardly curved (which is distally lower) and 8) elongate I^2 and I^3.

Propotamochoerus hyotherioides (Schlosser, 1903)

Synonymy

1903 *Sus hyotherioides* n. sp. – Schlosser, p. 92–93, pl. 8, figs. 6, 9–14.

1928 *Propotamochoerus hyotherioides* Schlosser–Pearson, p. 58–62, text-fig. 32 (?), plate 5, partially (material from localities 44, 49 and probably 44, the remaining material possibly belonging to *Sus*).

1949 *Sus hyotheroides* – Kuhn, p. 303, fig. 235a.

non 1950 *Potamochoerus (Postpotamochoerus)* nov. subgen. *hyotherioides* Thenius, p. 25–36.

Emended diagnosis: Large *Propotamochoerus* (linear measurements 107 % of *P. hysudricus*), intermediate in size between *P. palaeochoerus* and *P. provincialis*, with large lower canines in the males.
Cotypes: 2 M_1, 2 M_2, 1 M_3, 1 D_4, 1 P^3, 2 M^1, 2 M^2 and 1 M^3, figured by Schlosser, 1903, pl. VIII, figs. 7 and 9–14.
Type locality: the pieces are from somewhere in China, probably from different localities.
Age of the type locality (or type localities): unknown.

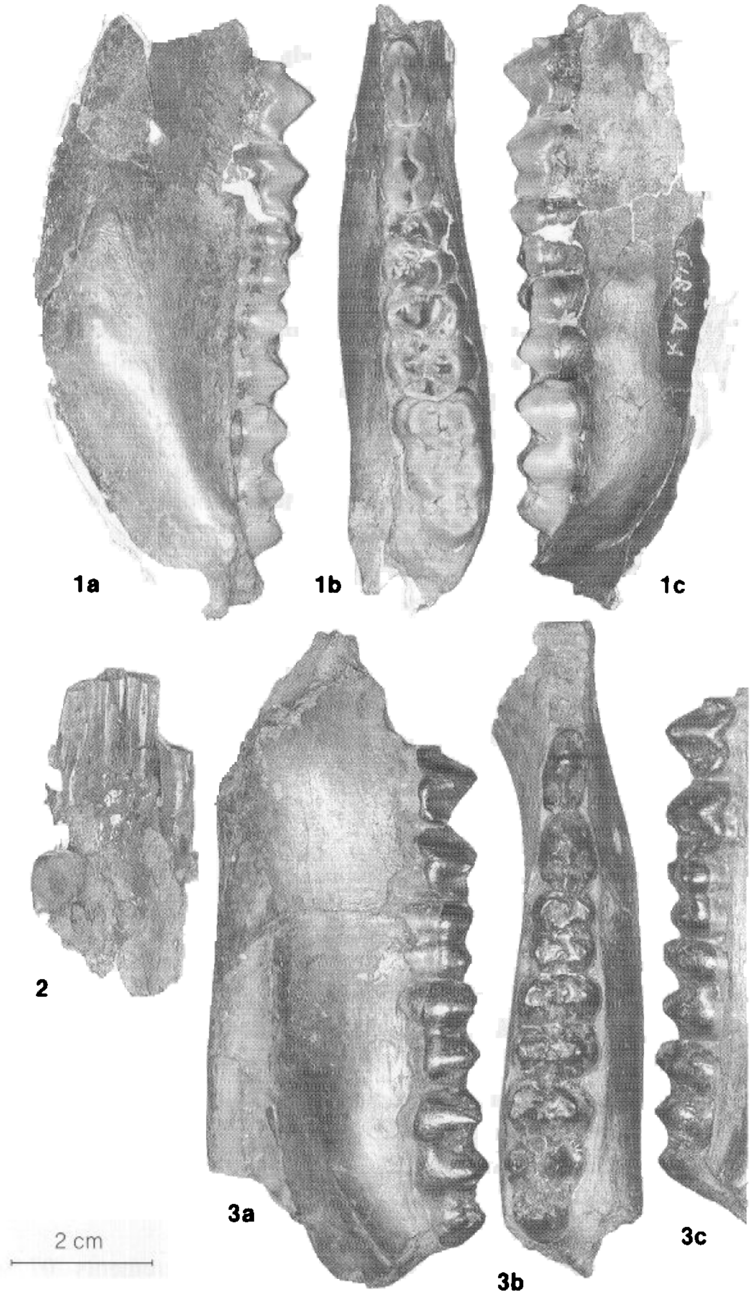

Plate 6. *Propotamochoerus wui* n. sp. from Lufeng. 1. Left mandible with P_3–M_3, (a) buccal view, (b) occlusal view, (c) lingual view. 2. Right mandible with P_3–M_3 and roots of P_2, (a) lingual view, (b) occlusal view, (c) buccal view. 3. Symphysis with left and right I_1 and I_2, lingual view.

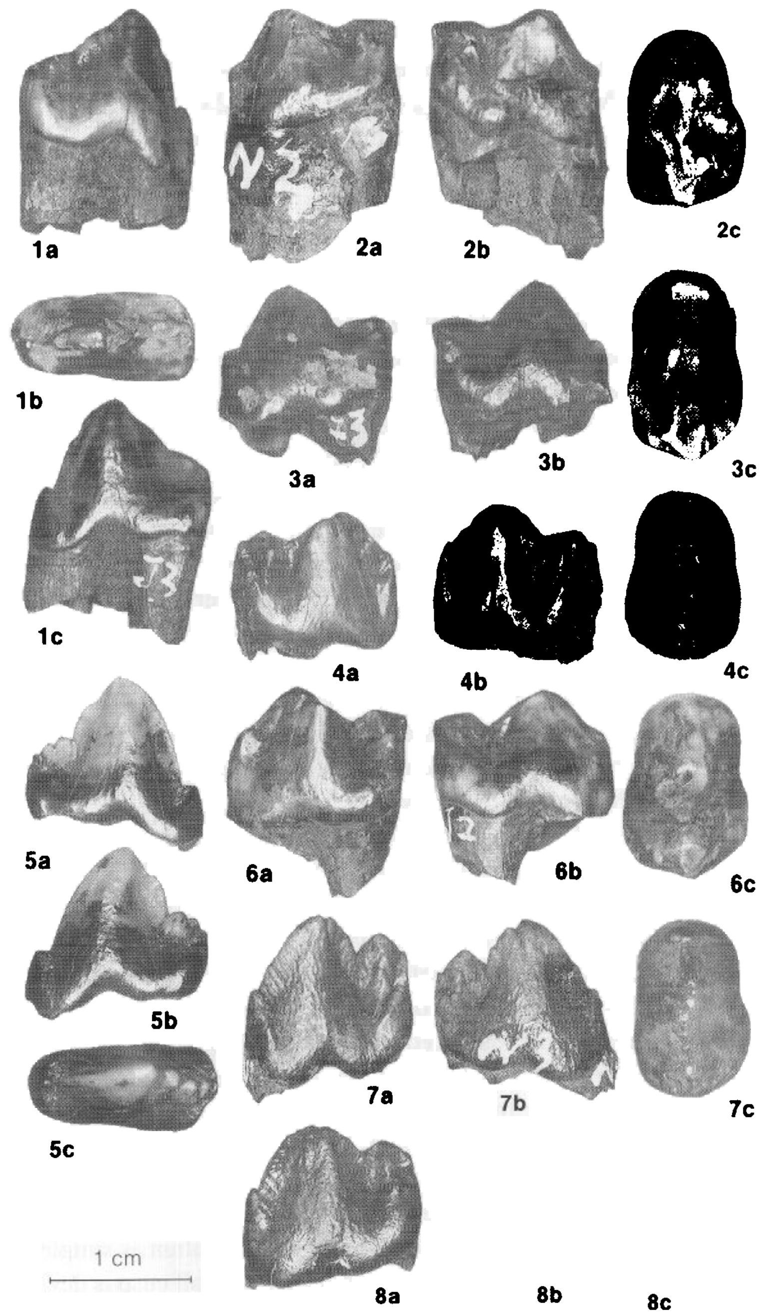

Plate 7. *Propotamochoerus wui* n. sp. from Lufeng. 1. Left P_3, (a) lingual view, (b) occlusal view, (c) buccal view. 2. Right P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 3. Right P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 4. Left P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 5. Left P_3, (a) lingual view, (b) buccal view, (c) occlusal view. 6. Right P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 7. Right P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 8. Right P_4, (a) lingual view, (b) labial view, (c) occlusal view.

Material

All teeth assigned to this species are isolated: 2 P_3, 4 P_4, 1 M_1, 8 M_2, 3 M_3, 3 P^2, 2 P^3, 3 P^4, 4 M^2, 7 M^3, 4 I_1, 4 I_2, 2 I_3, 4 C_m, 2 I^1, 3 I^2, 2 C^m, 3 D_4 and 2 D^4. These fossils were found in beds 1–6 (Fig. 1) and are filed in the IVPP under number V 4493. Measurments are given in Tables 4–6.

Description and comparison

P. hyotherioides, as represented by the teeth described by Schlosser (1903), a mandible and palate described by Pearson (1928), and the teeth from Lufeng are intermediate in size between the smaller *Propotamochoerus palaeochoerus* and the larger *P. provincialis*. However, overlap with both species occurs (Fig. 10). The teeth of *P. hyotherioides* from Lufeng resemble those of *P. wui* in morphology, but differ by their larger size (figs. 3 and 4).

The $\mathbf{P_3}$ (pl. 16, figs. 1 and 2) have one main cusp and a small cusp on the talonid.

The $\mathbf{P_4}$ have two main cusps that are placed close together, the lingual cusp postero-lingually of the labial cusp. There is some variability in the degree of separation of the cusps (pl. 14, fig. 1 – close together versus figs. 2 and 3 – wider apart). Also the height of the crown is variable (pl. 14, fig. 3 – low versus fig. 2 – high; both teeth have the same degree of wear). The anterior cingulum is much elevated forming low lingual and labial styles in a similar way as is in *Sus* the high styles are formed. Also the posterior cusp and cingulum are elevated (in pl. 13, fig. 1 nearly as high as the main cusp). The morphology coincides with that of the P_4 figured by Pearson (1928, pl. IV, figs. 1 and 2).

The $\mathbf{M_1}$ and $\mathbf{M_2}$ (pl. 16, fig. 8) can be separated on size only. In Dicoryphochoerini the M_2 has DAP′ and DT′ values of about 130%. This means that the ranges for the M_1 of the large and the M_2 of the small species overlap and determination of isolated molars is subjective.

The $\mathbf{M_3}$ have simple third lobes with only one main cusp, which may be placed on the axis (pl. 15, fig. 4) or labially of the axis of the tooth in which case a small cusp is formed between the displaced cusp and the lingual cingulum (pl. 16, fig. 6). The M_3 figured by Schlosser (pl. VIII, fig. 14) is intermediate in this character and for the rest very similar to the Lufeng M_3. The M_3 of *P. provincialis* may have either one cusp in the third lobe (Morales, 1984, pl. 4, fig. 10) or two equally large ones.

The $\mathbf{P^2}$ have the same width as the P^3 of *P. wui*, but are much longer (fig. 4), the main cusps are lower, narrower and the posterior cingulum is simple and does not protrude much lingually. Behind the main cusp a small cusp is developed (pl. 13, fig. 3; pl. 14, fig. 5). The talon is much smaller than in the P^2 of *P. wui*. The teeth resemble the P^2 figured by Pearson (pl. IV, fig. 3).

The $\mathbf{P^3}$ has one massive slightly compressed cone-like main cusp (pl. 13, fig. 2). The P^3 figured by Pearson (1928) has a larger cingulum and the main cusp seems to be less inflated than in the P^3 figured by Schlosser (1903). The cingulum is not preserved in our specimen.

The $\mathbf{P^4}$ have two well separated labial cusps. The sagittal cusps (sensu Pick-

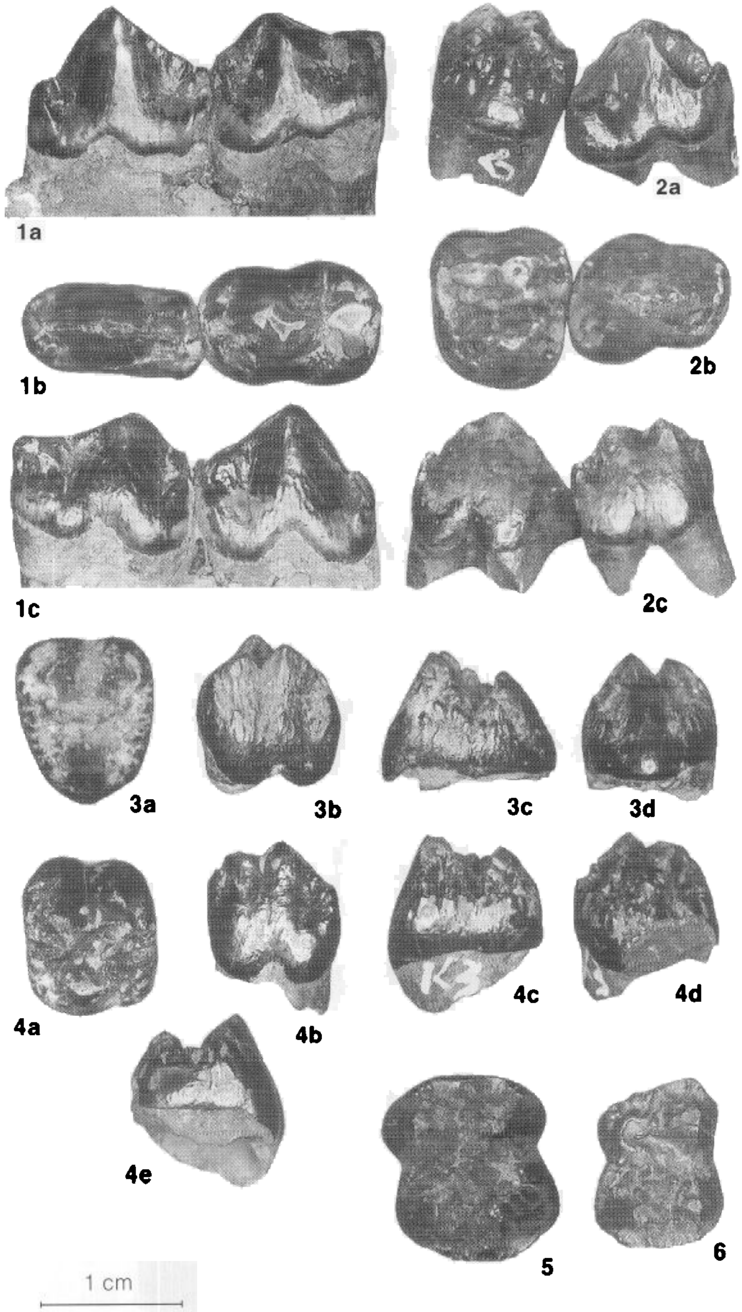

Plate 8. *Propotamochoerus wui* n. sp. from Lufeng. 1. Right P_3–P_4, (a) lingual view, (b) occlusal view, (c) buccal view. 2. Right P^3–P^4, (a) lingual view, (b) occlusal view, (c) buccal view. 3. Left P^4, (a) occlusal view, (b) buccal view, (c) anterior view, (d) lingual view. 4. Left P^4, (a) occlusal view, (b) buccal view, (c) anterior view, (d) lingual view, (e) posterior view. 5. Right M^1, occlusal view. 6. Left D^4, occlusal view.

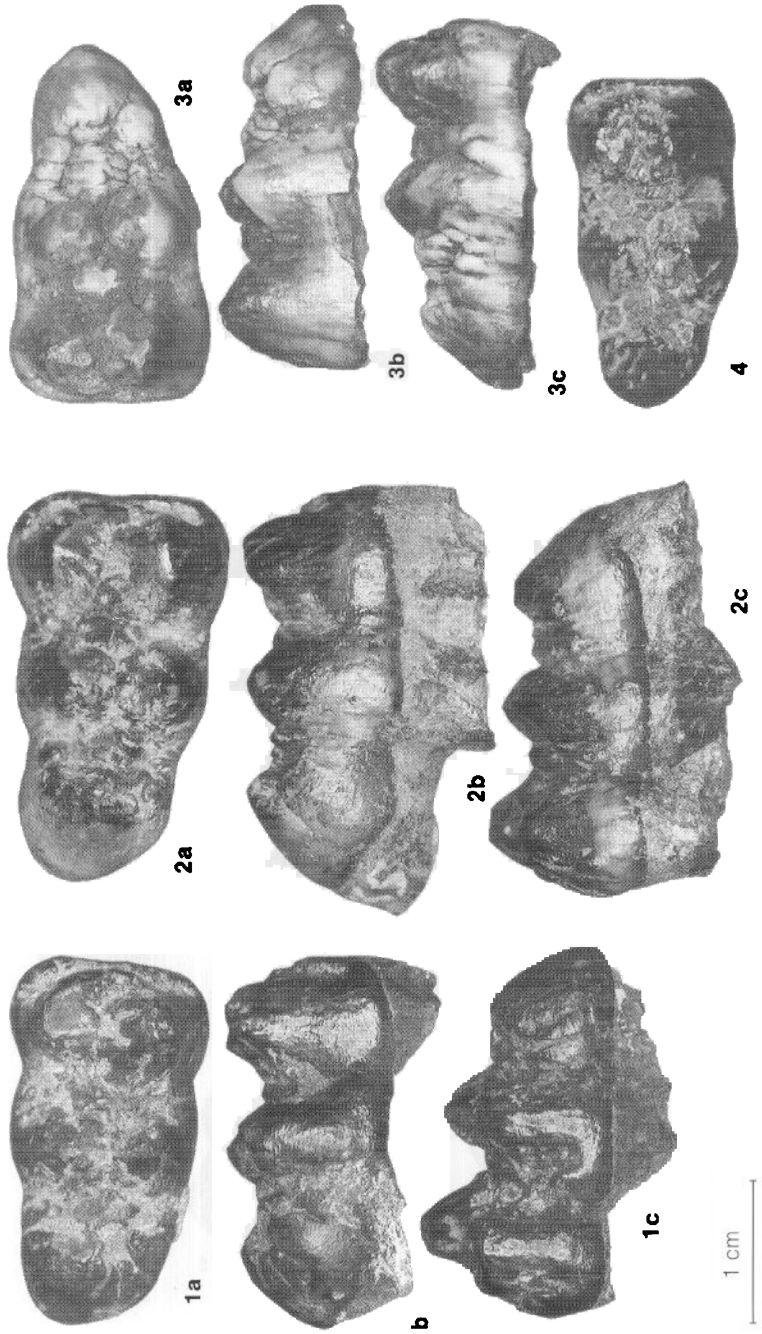

Plate 9. *Propotamochoerus wui* n. sp. from Lufeng. 1. Left M_3, (a) occlusal view, (b) lingual view, (c) buccal view. 2. Left M_3, (a) occlusal view, (b) lingual view, (c) buccal view. 3. Right M_3, (a) occlusal view, (b) lingual view, (c) buccal view. 4. Left M_3, occlusal view.

ford, 1988) do not seem to be well individualized in any of the P^4 (pl. 13, fig. 4) and unite with the labial cusps with little wear (pl. 16, fig. 3). The presence of sagittal cusps was chosen by Pickford (1988) to define the Suinae.

The largest molars are $\mathbf{M^2}$ of the large species, no M^1 have been assigned to this species.

The $\mathbf{M^3}$ have simple talons made up of a small lingual cusp (pl. 15, fig. 5; pl. 16, fig. 7) or a larger cusp that extends more labially (pl. 15, fig. 6). The M^3 illustrated by Schlosser has the same morphology as the Lufeng M^3 of pl. 15, fig. 5. The right M^3 figured by Pearson (1928) has an aberrant labial cusp, like one of the M^3 of *P. wui* (pl. 10, fig. 1).

The $\mathbf{I^1}$ (pl. 16, fig. 5) is like other *Propotamochoerus* incisors, save those of *P. palaeochoerus*, which are less compressed and have a lower crown.

The $\mathbf{I^2}$ has a postero-lingual cingulum which consists of some irregular cusps as in *P. provincialis* and not of a smooth and continuous ridge as in *P. palaeochoerus* (pl. 16, fig. 4; Morales, 1984; Van der Made and Moyà-Solà, 1989).

The $\mathbf{I_1}$ and $\mathbf{I_2}$ have crowns with a well defined lower rim and are intermediate in height between the primitive suids and advanced forms like *Sus* (pl. 13, fig. 6; pl. 14, fig. 4). The I_1 and I_2 are large compared to the incisors of *P. provincialis*, but the I^2 are smaller (fig. 9).

The $\mathbf{I_3}$ (pl. 13, fig. 5; pl. 4, fig. 5) is, like the I_1 and I_2, intermediate in crown height between primitive and more advanced suids, such as *Microstonyx major* (Van der Made, et al., 1992). However, in advanced species of *Sus* the I_3 does not occlude anymore and became irregular in morphology.

The $\mathbf{C_m}$ (pl. 15, figs. 2 and 3) have a verrucosic section (table 4), and are large for Dicoryphochoerini (table 8).

The $\mathbf{C^m}$ also are large and have a great radius of curvature (pl. 15, fig. 1).

$\mathbf{D^4}$ has an oblique anterior border, which serves to separate it from the permanent molars of *P. wui*.

The $\mathbf{D_4}$ has three lobes and is slightly smaller than the *P. provincialis* D_4.

Discussion

'*Sus*' *hyotherioides* Schlosser, 1903 was based on isolated molars, a D_4 and a P^3. On the basis of color Schlosser assumed that at least part of the fossils came from eastern China. No holotype was indicated. Thus, it is not known where and from how many localities the fossils originate and whether the teeth represent one species. The cotypes do not include teeth of importance in taxonomy and cannot be assigned to a genus and not even to a subfamily.

Pearson (1928) described some fossils as *Propotamochoerus hyotherioides* Schlosser, including a mandible and palate with teeth that resemble the teeth described by Schlosser, but also containing teeth that are of importance in taxonomy and show proportions of the teeth relative to each other.

In the discussion on *Propotamochoerus wui* we have seen that *P. hysudricus* (100%), *P. palaeochoerus* (104%), *P. provincialis* (110%) and the larger Lufeng material (107%) differ very little in size. '*Dicoryphochoerus*' *medius* Liu, Li and

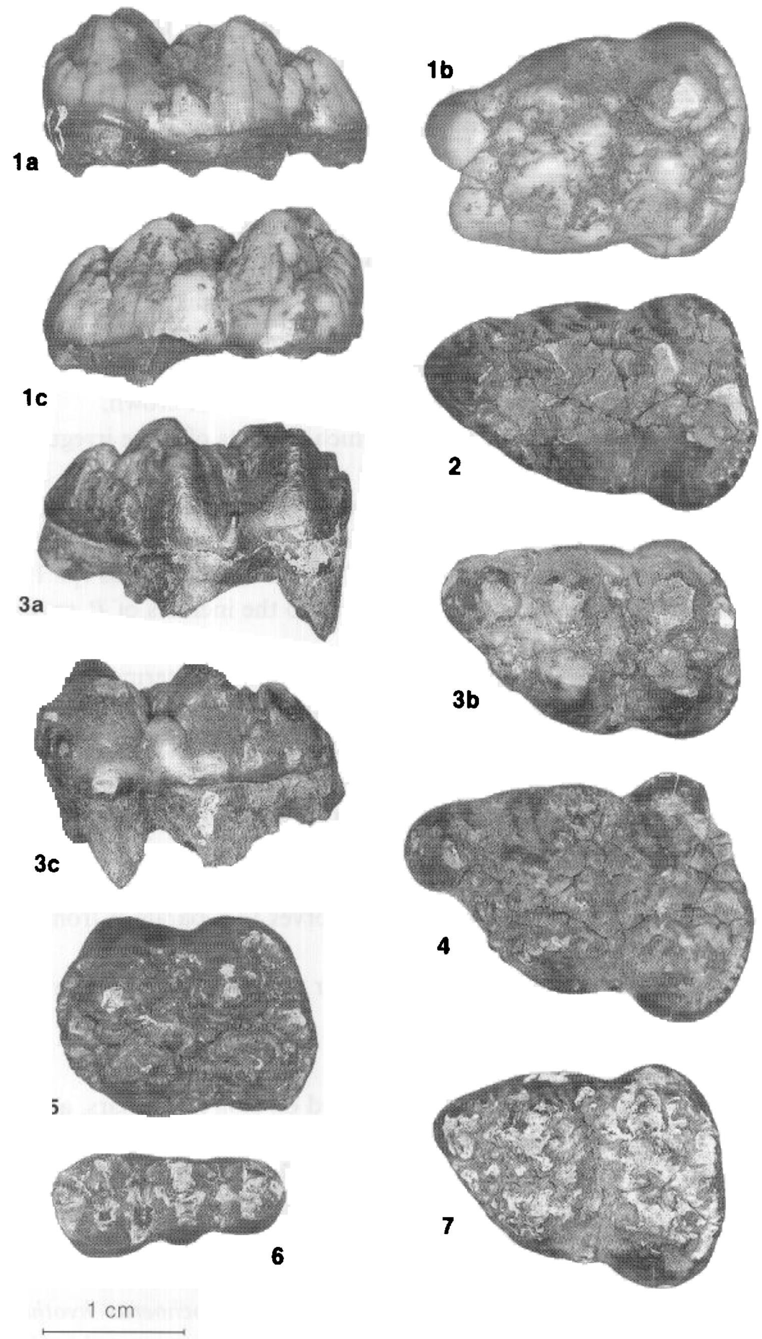

Plate 10. *Propotamochoerus wui* n. sp. from Lufeng. 1. Left M^3, (a) lingual view, (b) occlusal view, (c) buccal view. 2. Left M^3, occlusal view. 3. Left M^3, (a) buccal view, (b) occlusal view, (c) lingual view. 4. Left M^3, occlusal view. 5. Left M^2, occlusal view. 6. Right D_4, occlusal view. 7. Left M^3, occlusal view.

Zhai, 1978 and '*D.*' *bingxianensis* (Tang, Liu, Chen and Chen, 1985) are larger than *P. provincialis*, but smaller than the smallest species of *Microstonyx*. The reduction of the P2 indicates that these species might be more related to *Microstonyx* and *Hippopotamodon*.

The larger Lufeng cheek teeth coincide in size with *P. hyotherioides* as described by Schlosser (1903) and Pearson (1928), but there is overlap with both *P. palaeochoerus* and *P. provincialis* (fig. 10). In morphology there are no important differences with *P. provincialis* and the smaller *P. hysudricus*. The third lobe in the M_3 in the former species may have two cusps (a progressive character); in the latter species only M_3 with one cusp in the third lobe are known. The importance of this character is not known until more M_3 are found. Differences between the large suid from Lufeng and *P. palaeochoerus* are that the I^1 is compressed and the M3 and anterior premolars are larger (note the P2).

P. hyotherioides (both Lufeng fossils and the teeth described by Schlosser and Pearson) is close to *P. provincialis*. There are no important morphological differences, nor in size (one measures 107% and the other 110% of *P. hysudricus*). We do not know the skull structure of *P. hyotherioides* and we did not study large samples of the dentitions of the two other species. When more material becomes available, *P. hyotherioides* may prove to be synonymous with *P. provincialis* or be lowered to subspecific rank. In any case, we assume a close relationship and we think *P. hyotherioides* to be ancestral to *P. provincialis*.

Hyotheriinae Cope, 1888

Chleuastochoerus Pearson, 1928

Diagnosis: 'Its skull, otherwise simple and primitive in structure, is at once marked off from that of any other known type of pig by the great bony arch over the canine teeth of the male and by the curious shelf-like expansion of the anterior end of the zygomatic arch' (Pearson, 1928).
Type species: *Chleuastochoerus stehlini* (Schlosser, 1903).

Chleuastochoerus sp.
Plate 17, figs. 1–5.

Material

A right and a left series both with P_4 to M_2 and isolated teeth: 1 M_1, 5 M_2, 1 P^2, 2 P^3, 2 M^3, 1 I_1, 1 I_2 and a right lower canine of a male. This material is filed in the IVPP under number V 9944 and was found in layer 3 (fig. 1).

The measurements are given in Table 7.

Description and comparison

The $\mathbf{P_4}$ have two well separated main cusps, the lingual one is placed nearly as much forward as the labial one, differing in both characters from *P. wui* (pl. 17,

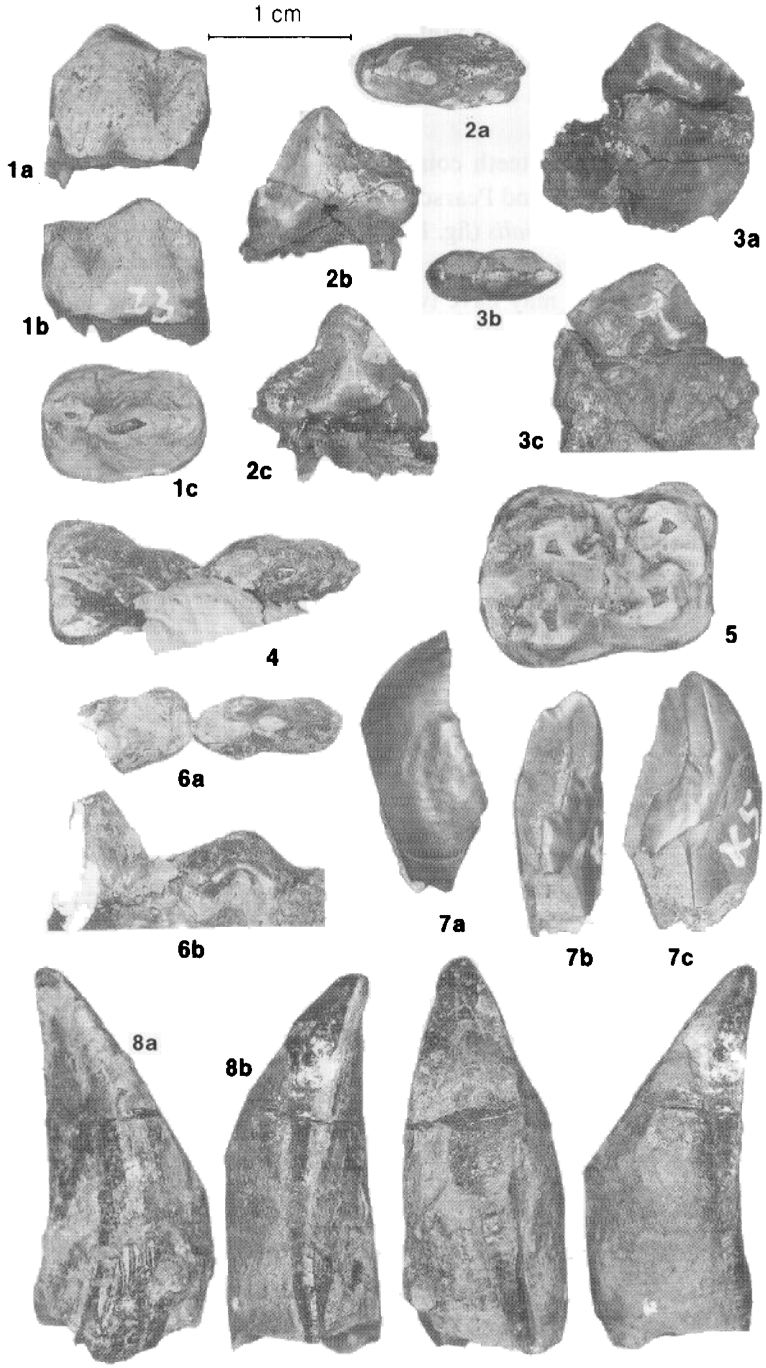

Plate 11. *Propotamochoerus wui* n. sp. from Lufeng. 1. Left P_4, (a) buccal view, (b) lingual view, (c) occlusal view. 2. Right P_2, (a) occlusal view, (b) lingual view, (c) labial view. 3. Left P_1, (a) buccal view, (b) occlusal view, (c) lingual view. 4. Right P^1 and P^2, occlusal view. 5. Left M_2, occlusal view. 6. Left P^1, and P^2, (a) occlusal view, (b) buccal view. 7. Right I^1, (a) labial view, (b) linguo-distal view, (c) linguo-mesial view. 8. Left C^m, (a) inferior ('lingual') view, (b) posterior view, (c) anterior view, (d) superior ('labial') view.

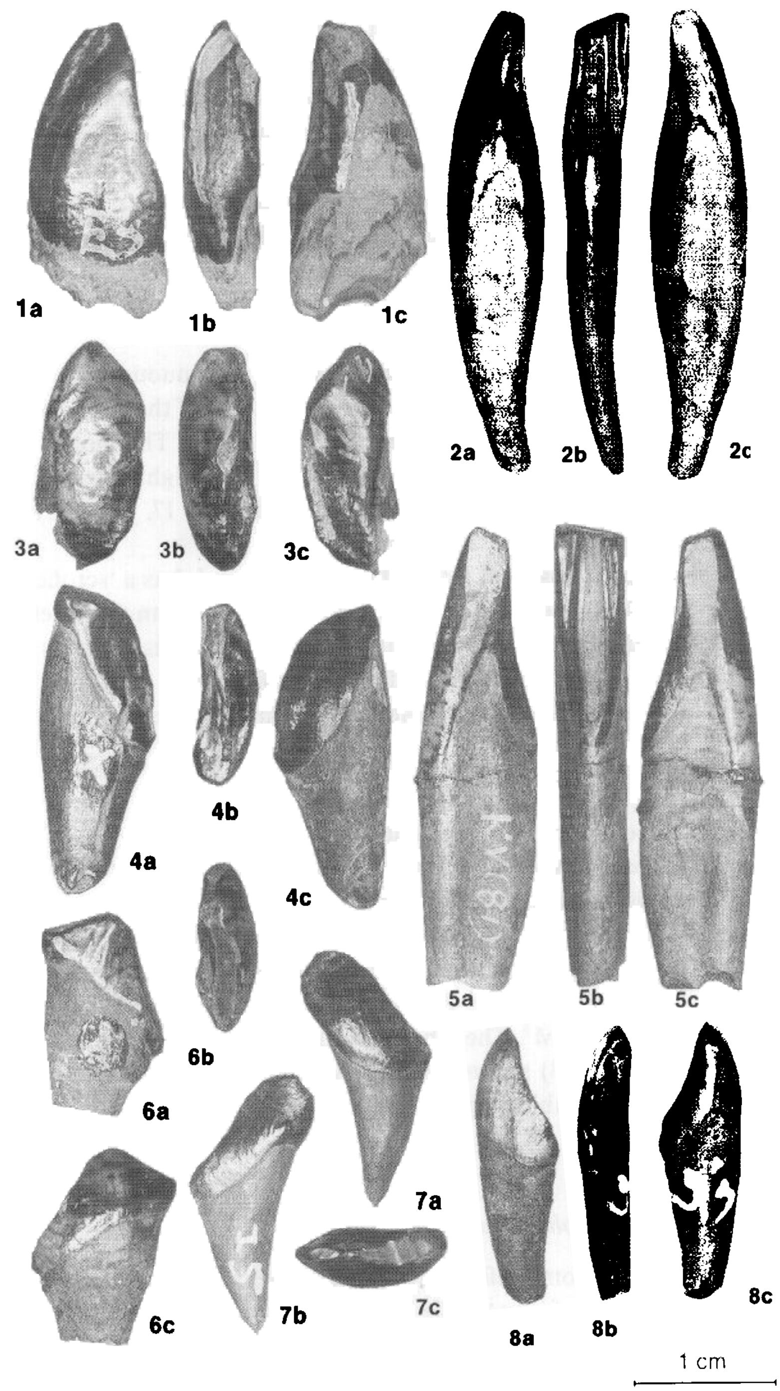

Plate 12. *Propotamochoerus wui* n. sp. from Lufeng. 1. Right I^1, (a) labial view, (b) linguo-distal view, (c) linguo-mesial view. 2. Left I_2, (a) distal view, (b) lingual view, (c) mesial view. 3. Right I^2 (a) labial view, (b) occlusal view, (c) lingual view. 4. Left I^2, (a) lingual view, (b) occlusal view, (c) labial view. 5. Right I_1, (a) mesial view, (b) lingual view, (c) distal view. 6. Left I^3, (a) lingual view, (b) occlusal view, (c) labial view. 7. Right I_3, (a) labial view, (b) linguo-mesial view, (c) apical view. 8. Right DI^1, (a) labial view, (b) linguo-distal view, (c) linguo-mesial view.

figs. 4B and 5A versus pl. 7). The posterior cusp (on the talonid) and the anterior cingulum tend to be less elevated than in *P. wui* (pl. 17, figs. 4A, 4C, 5B and 5C versus pl. 7). The tooth is narrower than in *P. wui*, but has the same length (fig. 3). In morphology of the main cusps, the anterior cingulum and the talonid cusp the premolars from Lufeng closely resemble *Chleuastochoerus* (Pearson, 1928).

The $\mathbf{M_1}$ and $\mathbf{M_2}$ (pl. 17, figs. 4 and 5) are small in comparison to those of *P. wui*, especially the M_2 and the M_1 in the DTa (fig. 3), but have the same size as in *Chleuastochoerus* from Pearson's (1928) locality 49 (fig. 11).

The $\mathbf{P^3}$ is longer and narrower than the P^3 in *P. wui*, but is too small to be a P^2 of *P. hyotherioides* (fig. 4).

The two $\mathbf{M^3}$ differ from those of *P. wui* in having a continuous labial cingulum and in being short, both absolutely and relatively because of the talon (pl. 17, figs. 1 and 2), which tends to be smaller than in *P. wui* (pl. 10). The molars are also wider than the M^3 of *Chleuastochoerus* (fig. 11), but this might be caused by the extension of the crown over a part of the lingual root (pl. 17, figs. 1A and 2A). The protoconule is fused to the cingulum.

A small **canine** (pl. 17, fig. 3) is referred to this species. It has a 'scrofic section' and no enamel at the posterior side. The canine is smaller than those referred to *P. wui* (Table 4) and the labial side is relatively narrower and its crown is lower. It has exactly the size of canines in a mandible in the BNHM.

An $\mathbf{I_1}$ and an $\mathbf{I_2}$ are smaller than those of *P. wui* and are less hypsodont.

Discussion

This suid is close in size to *P. wui*, but can be separated from *P. wui* by morphology, relative size of M_2, M^3, P_4 and P^2, absolute size of the M_2, lesser hypsodonty of the incisors and a different canine.

The morphology of the P_4 suggests affinities with the 'waste basket taxon' for primitive suids: the Hyotheriinae, size and morphology placing it close to *Chleuastochoerus* (as described by Pearson, 1928 from her locality 49), but there is a difference in its wide M^3. The labial cingulum on the M^3 is typical. The M^3 figured by Schlosser (1903) shows a clear cingulum and the maxilla figured by Pearson (1928) show variable cingula.

DISCUSSION

Canine size in the Dicoryphochoerini

Most of the suoids from Lufeng are Dicoryphochoerini and the size of the canines in this tribe is of systematic interest. Ideally, the size of the canines should be related to M1 size, as is done with the other teeth. However, the M_2 is used as a standard for the practical reason that in this particular case the M_1 is damaged or under-represented in the pieces or populations we want to compare. The widths of the lingual, labial and posterior sides of the lower male canines may increase from the top of the tooth downward at different rates. At some distance of the tip changes in width of the sides become less. The measurements

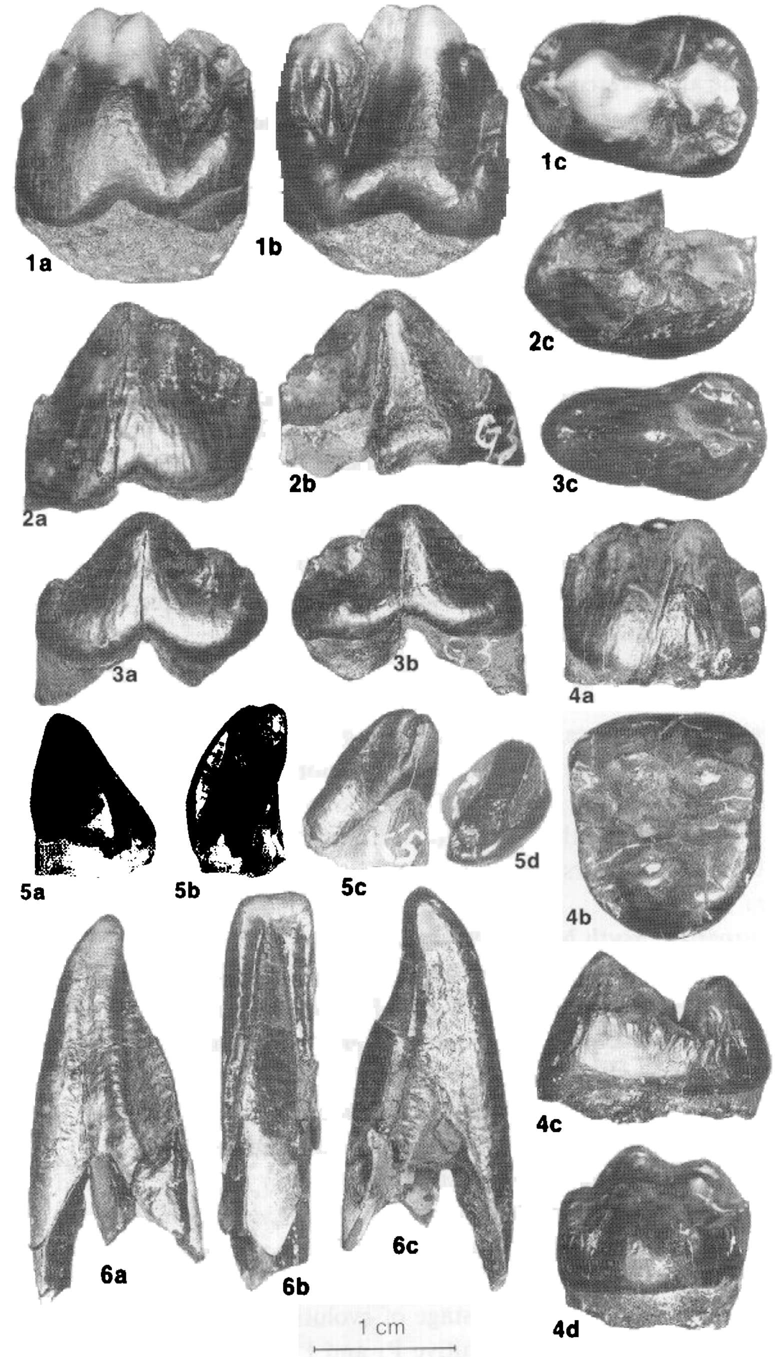

Plate 13. *Propotamochoerus hyotherioides* (Schlosser, 1903) from Lufeng. 1. Right P_4, (a) lingual view, (b) labial view, (c) occlusal view. 2. Left P^3, (a) labial view, (b) lingual view, (c) occlusal view. 3. Right P^2, (a) buccal view, (b) lingual view, (c) occlusal view. 4. Left P^4, (a) buccal view, (b) occlusal view, (c) anterior view, (d) lingual view. 5. Right I_3, (a) distal view, (b) lingual view, (c) mesial view, (d) apical view. 6. Left I_1, (a) distal view, (b) lingual view, (c) mesial view.

(table 8) are taken as far as possible from the tip and close to basis of the crown which usually is hidden in the mandible. The lingual and antero-labial sides of the canine are covered with enamel and the posterior facet is devoid of enamel. In some cases the enamel of the lingual or labial sides ends anteriorly of the edge of the side, which often is rounded. The widths of the sides are not measured at the limit of the enamel, but at the maximum posterior extension of the side (see fig. 2).

In a sample of *Sus scrofa* from Deli, Sumatra, Indonesia (ZMA), the length and width of the canines were measured. These measurements illustrate the variability of the size of the C_m. Figure 12 gives the measurements of adult males (with M3 completely erupted) and subadult males (with M2 erupted, but M3 not yet completely erupted). The size of the canines increases in the subadults, but there is no evidence of continued size increase in the adults. It was expected that DAP″ and DT″ values might have a lesser variability than DAP* and DT* values, because of growth of the canine and decrease of DAP of the molar by wear. However, V′ values (Freudenthal and Cuenca, 1984) are approximately the same, DAP″ and DT″ have V′ of 74 and 75, DAP* and DT* have V′ of 67 and 77. V′ values for the DAP′ M_3 of adults of the same sample are slightly larger than V′ values for the DAP of the C_m.

Size of the canines varies independently of body size (fig. 12 and table 8). Primitive suoids like old world Tayassuidae, Hyotheriinae and Listriodontinae have relatively small canines, which may be slightly 'scrofic' or slightly 'verrucosic': having the labial side smaller than the posterior side as in *Sus scrofa*, or wider as in *S. verrucosus* Müller, 1840. The Tetraconodontinae may develop large canines (table 8). This means that size and shape of the canines changed too often to predict these characters for the first Suinae on the basis of the evolution of the Suoidea.

Sus strozzii Forsyth Major, 1881 has very large verrucosic canines. *Sus scrofa* has large scrofic canines. Both morphologies probably depart from an intermediate type as in *Potamochoerus* Gray, 1854 where the labial and posterior sides have about the same width. *Propotamochoerus* either has intermediate or slightly scrofic canines.

The Dicoryphochoerini *Hippopotamodon* and *Microstonyx* have either large or small canines; *Microstonyx* is known to have reduced the size of its canines. *Propotamochoerus palaeochoerus* still has relatively large canines and is thought to be close to the origin of *Microstonyx* and *Hippopotamodon* (Van der Made and Moyà-Solà, 1989). The size of the canine of *Potamochoerus* is slightly larger than the reduced canines.

Potamochoerus is probably a stage of evolution anterior to *Sus* and Dicoryphochoerini (because of its primitive P_4 and I^2 morphologies). The shape and relative size of the *Potamochoerus* canine may be primitive for Suinae, it is also like in most of the primitive suoids.

P. hyotherioides has relatively large canines and *P. wui* has very small canines and the differences are probably real, considering the variability in *Sus scrofa* (fig. 12). Canines can have increased or decreased in size in the different *Propo-*

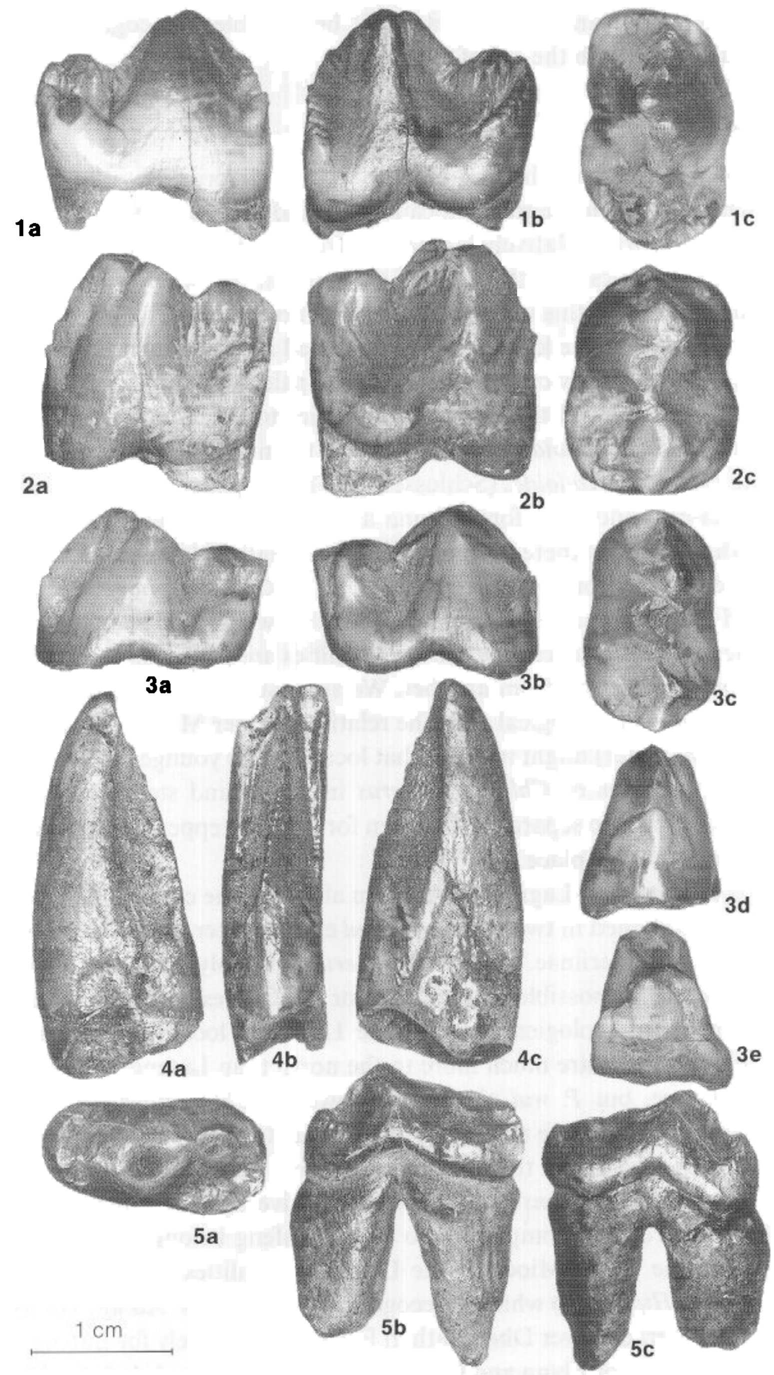

Plate 14. *Propotamochoerus hyotherioides* (Schlosser, 1903) from Lufeng. 1. Left P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 2. Right P_4, (a) lingual view, (b) buccal view, (c) occlusal view. 3. Right P_4, (a) lingual view, (b) labial view, (c) occlusal view. 4. Left I_2, (a) distal view, (b) lingual view, (c) mesial view. 5. Left P^2, (a) occlusal view, (b) lingual view, (c) buccal view.

tamochoerus species and in future it might be possible to recognise lineages in this difficult group with the aid of canines.

Age of Lufeng

Chleuastochoerus from the Lagrelius collection, described by Pearson (1928), has a small form (from Lagrelius localities 73 and 43 and some other localities) and a large form with relatively larger M3 (from Lagrelius locality 49). Pearson showed with statistics that the sizes of the populations where significantly different. She considered this to be local size variation (localities 43 and 49 are at a distance of at most some kilometers) and warned against the 'crude methods of species-making generally current in systematic paleontology'.

Kurtén (1952) showed the Lagrelius localities to represent two different environments. The '*dorcadoides* localities' are in the north-west and have a steppe fauna and *Gazella dorcadoides* (Schlosser, 1903). The '*gaudryi* localities' are more to the south-east and have forest fauna and *Gazella gaudryi* (Schlosser, 1903). Between the two areas there are mixed faunas. Small *Chleuastochoerus* is found in both steppe and forest faunas and the large *Chleuastochoerus* is found in mixed and steppe faunas. This indicates that the two sizes are not separated by environment. The distances between the localities are too small to allow for isolation of one population from another. We suggest that the size differences indicate differences in geological age. The relatively larger M3 (in many lineages a progressive character) might indicate that locality 49 is younger. The presence of both evolutive stages of *Chleuastochoerus* in mixed and steppe environments might indicate that the separation between forest and steppe faunas persisted for some time at the same place.

P. wui is absent in the Lagrelius collection although the collection is abundant. This may be explained in two ways: 1) *P. wui* entered later. In a general way Suinae replaced Hyotheriinae. *Propotamochoerus* probably lived on longer than *Chleuastochoerus*. A possible stratigraphy for the Chinese faunas is given in fig. 13. 2) There is an ecological reason. The Lagrelius localities have abundant *Chleuastochoerus* and are much more to the north than Lufeng, where *Chleuastochoerus* is rare, but *P. wui* abundant. However, *Chleuastochoerus* has been found in supposedly steppe and forest environment, which makes the ecological explanation less likely than the stratigraphical one.

Yunnanochoerus lufengensis indicated a tentative age for Lufeng older than Dhok Pathan, probably comparable to Nagri. Lufeng belongs to the second or third level in the upper Miocene (the Lagrelius localities with small *Chleuastochoerus* have *Hipparion*) which is recognizable with suids. An age comparable to the upper Nagri or lower Dhok Pathan Formations is likely for Lufeng. This is close to the findings of Flynn and Qi (1982) and Qi (1986) and slightly older than the age given by Qiu and Storch (1990), all based on rodents.

Palaeoecology

Excluding detailed analyses on the suoids (such as, on dental wear), two types

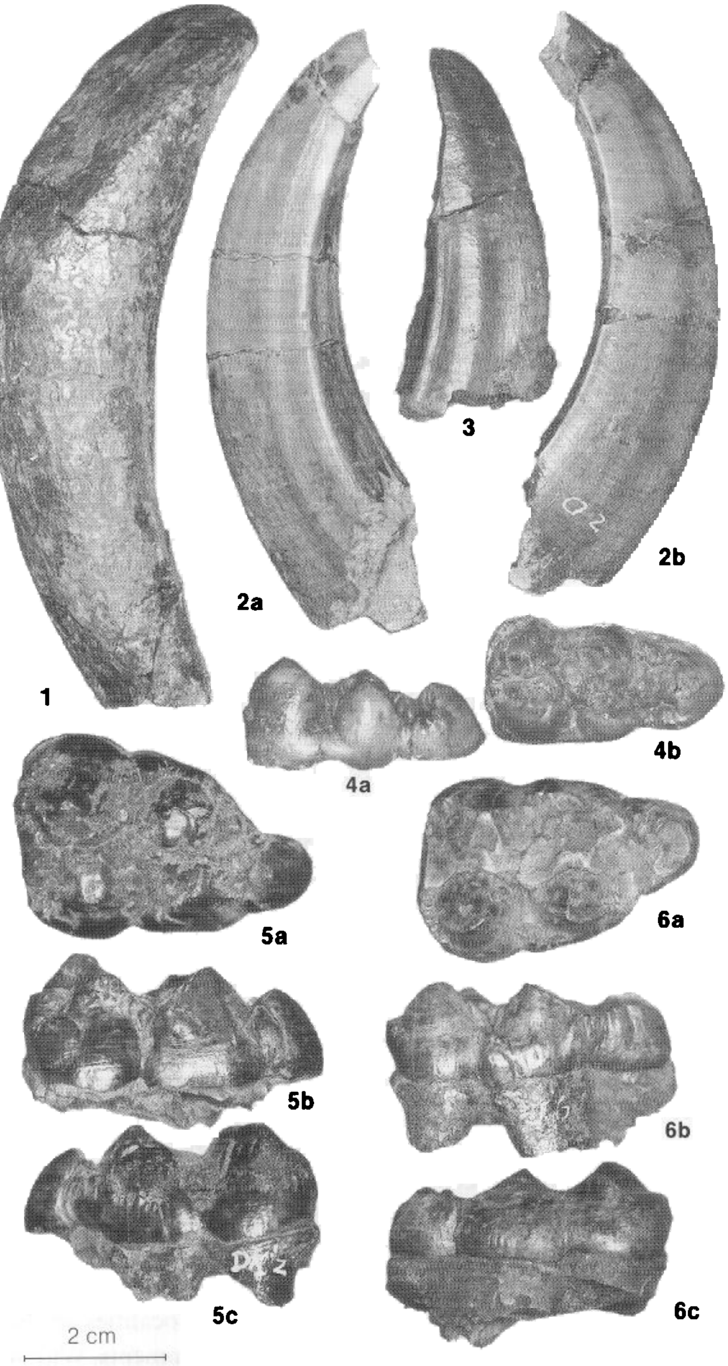

Plate 15. *Propotamochoerus hyotherioides* (Schlosser, 1903) from Lufeng. 1. Right C^m, anterior view. 2. Left C_m, (a) labial view, (b) lingual view. 3. Right C_m, labial view. 4. Right M_3, (a) lingual view, (b) occlusal view. 5. Left M^3, (a) occlusal view, (b) lingual view, (c) buccal view. 6. Right M^3, (a) occlusal view, (b) buccal view, (c) lingual view.

of data may help to interpret the palaeoenvironment of Lufeng: the number of suoid species and their body weight.

In the European Miocene, the number of contemporaneous suoid species ranged from 4 to 9 till the middle of the Vallesian, when it dropped from 8 to 2. In Pakistan, south China and in Africa species number remained high till long after the Vallesian. The strong decrease in species number in Europe was thought to be related to changes in temperature (Van der Made, 1991b). Although the influence of temperature changes on distribution of taxa is not straightforward (Van der Made, 1992), the high number of suoid species in Lufeng (4) might indicate a high temperature.

A regular pattern of size differences was found in sympatric congeneric artiodactyls; they tend to differ 15% in linear size of the cheek teeth (Van der Made, 1990a, in press). Several species of such a series may occur together, which may be a way of using the habitat in an optimal way, and conversely the coocurrence of several such species may indicate optimal conditions (Van der Made, 1992). *P. wui* is 73% of *P. hyotherioides*. 85% of 85% is 72%; these species seem to fit the pattern of regular size differences and indicate optimal conditions for the genus. Biogeography of the genus might suggest that aridity might be a limiting factor. However, further research is necessary to substantiate this.

Analysis of cenograms (Legendre, 1986) showed that in an environment the (logarithm of the) body weights of the different mammal species differ from each other in a regular manner and that the differences in body weight (the slope of the cenogram) decrease with humidity. Besides, it seems that the total number of large species (over 8 kg) also increases with humidity (Legendre, 1986).

The body weight of mammals can be estimated from the size of the M_1 (Legendre, 1986). The M_1 of *Y. lufengensis* is not preserved, but the genus *Taucanamo* has M_2 and M_3 in similar proportions, with the M_2 approximately 115% of the M_1; a common value in primitive tayassuids. The estimated M_1 size indicates a body weight of approximately 45 kg for *Y. lufengensis* (and *Y. gandakasensis* would have weighed some 70 kg). The estimated weight of *P. wui* is 53 kg. Comparing *P. hyotherioides* with *P. wui*, the estimated body weight is 143 kg. *Chleuastochoerus* sp. may have weighed 44 kg. The three smaller species are close to each other in body weight, this might indicate a relatively humid environment.

In the Indo-Pakistan subcontinent up to 8 species are found in Nagri equivalent strata (although some species are very rare, and their true provenance is disputed in some cases). Their estimated body weights are: 19, 19, 70, 92, 92, 215, 298, 468 and 1177 kg. For the Dhok Pathan equivalent strata this is: 70, 92, 298 and 468 kg. A direct comparison with Lufeng cannot be made, because diversity tends to be lower in a single locality than in a group of localities of similar age, which have the potential of representing different environments. With 44, 45, 53 and 143 kg Lufeng has predominantly small species and is not comparable to the Nagri and Dhok Pathan equivalent strata from the Indo-Pakistan Subcontinent. European early Vallesian localities may have up to 5 species of 59, 142, 162, 171, 396 kg (the extremes are the least common species). Large suoids might defend themselves against predators, rather than flee and hide and are thus not re-

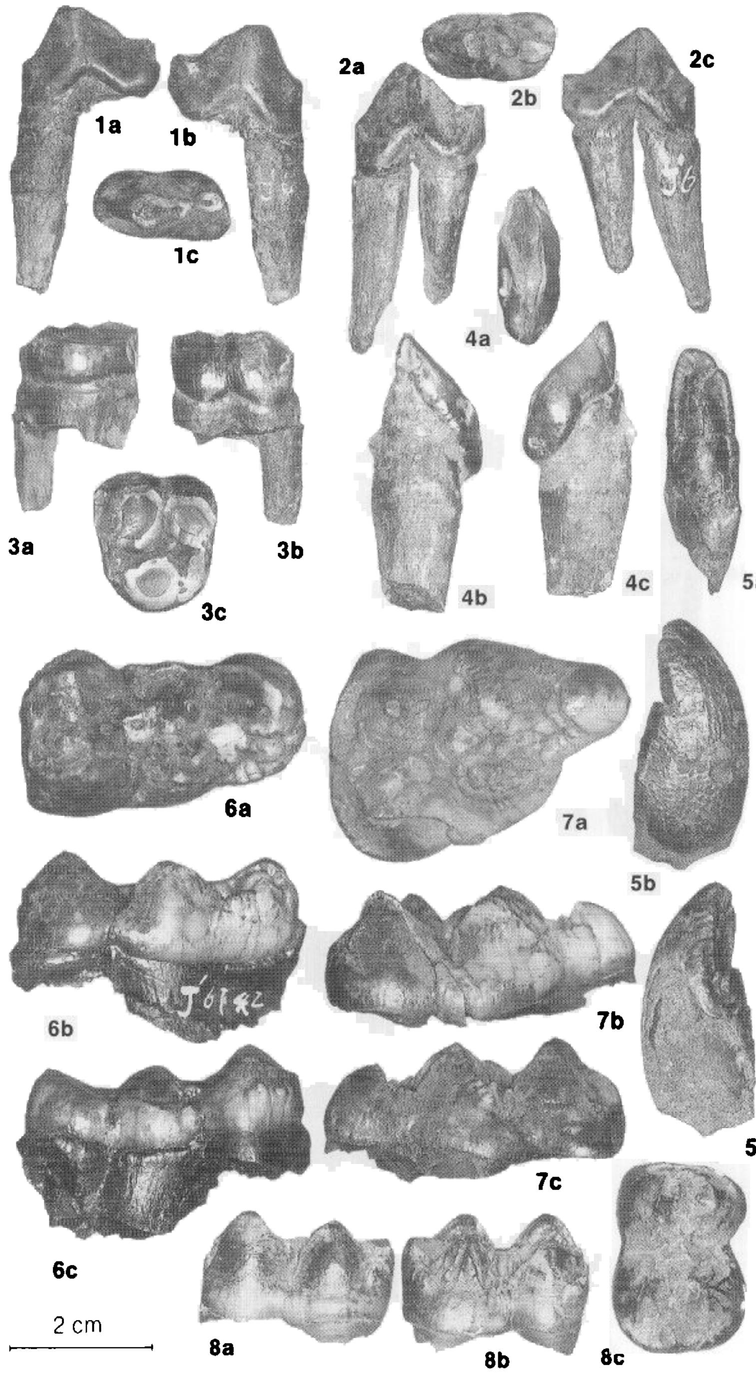

Plate 16. *Propotamochoerus hyotherioides* (Schlosser, 1903) from Lufeng. 1. Right P_3, (a) lingual view, (b) buccal view, (c) occlusal view. 2. Left P_3, (a) buccal view, (b) occlusal view, (c) lingual view. 3. Left P^4, (a) lingual view, (b) buccal view, (c) occlusal view. 4. Left I^2, (a) occlusal view, (b) lingual view, (c) labial view. 5. Left I^1, (a) linguo-distal view, (b) labial view, (c) linguo-mesial view. 6. Right M_3, (a) occlusal view, (b) lingual view, (c) buccal view. 7. Right M^3, (a) occlusal view, (b) buccal view, (c) lingual view. 8. Right M_2, (a) lingual view, (b) buccal view, (c) occlusal view.

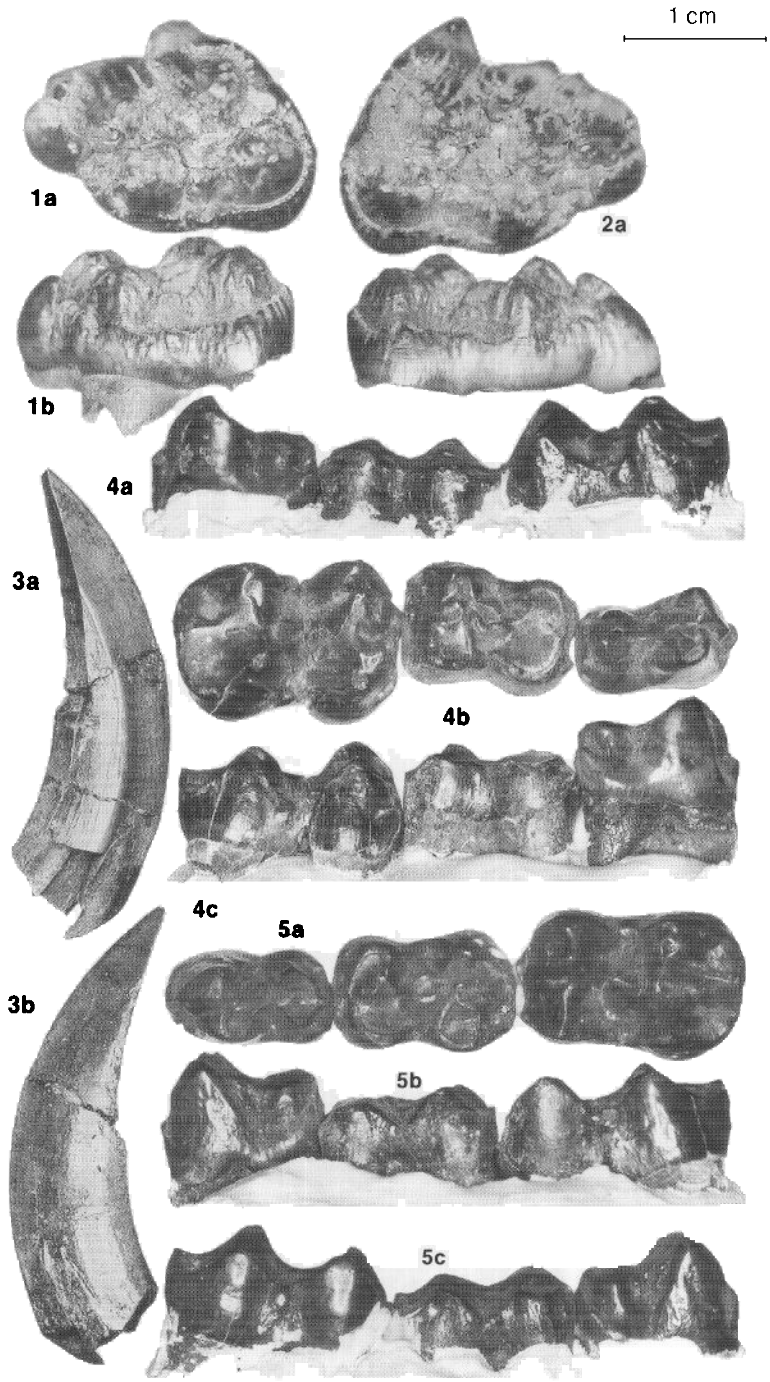

Plate 17. *Chleuastochoerus* sp. from Lufeng. 1. Left M^3, (a) occlusal view, (b) buccal view. 2. Right M^3, (a) occlusal view, (b) buccal view. 3. Right canine of a male, (a) labial view, (b) lingual view. 4. Left P_4–M_2, (a) buccal view, (b) occlusal view, (c) lingual view. 5. Right P_4–M_2, (a) occlusal view, (b) lingual view, (c) buccal view.

stricted to closed habitats. The Nagri equivalent strata might represent several habitats and Lufeng, European localities and Dhok Pathan might represent a sequence from closed to more open landscapes.

Our assumptions, suggesting that the suoid species in Lufeng indicate a warm and probably moist closed environment, are confirmed by Badgley et al. (1988), who based their interpretation on the total fauna and flora.

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