

New materials of *Hippopotamodon* (Artiodactyla, Mammalia) from southern China

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Abstract New materials of *Hippopotamodon ultimus* associated with *Gigantopithecus* have been collected in the systematic excavations carried out at Chongzuo since 2004. The taxonomic position of the former “*Dicoryphochoerus*” *ultimus* from Guangxi, Guizhou and Chongqing has been revised from *Dicoryphochoerus* to *Hippopotamodon* based on the study on both new and old materials, and *H. ultimus* is a valid species of *Hippopotamodon*. It is a suid larger than all known *Sus* with elongated snout, developed diastema between the P1 and the P2, short and narrow third lobe of the M3, *verrucosus* type lower canine, the main cusp of the p4 cleft at the tip into twin summits, double cusped third lobe of the m3. *H. ultimus* ranges only in South China. Its chronological distribution is limited from the early to the middle stages of the Early Pleistocene. It is an ultimate representative of *Hippopotamodon*.

Key words Guangxi, Early Pleistocene, Artiodactyla, *Hippopotamodon*, “*Dicoryphochoerus*”

1 Introduction

The excavations carried out from 1956 to 1963 at *Gigantopithecus* Cave in Liucheng, Guangxi Autonomous Region, resulted the rich collection of mammalian fossils associated with *Gigantopithecus*. Many suid taxa were identified from these fossils, including a new species “*Dicoryphochoerus ultimus*” (Han, 1987). *Dicoryphochoerus* was supposed to range from the Middle Miocene to the Pliocene, and the new species from the Early Pleistocene deposits was considered as the ultimate relict of the Neogene relatives as indicated by the specific name (Han, 1987). Besides “*D. ultimus*”, “*D. medius*” and “*D. binxianensis*” were reported from North China (Liu et al., 1978; Tang et al., 1985), and *Dicoryphochoerus* sp. was reported from Yunnan (Dong, 1987). *Dicoryphochoerus* was a genus established in 1926 by Pilgrim for some Siwaliks suids characterized by “the main central cusp of the last lower premolar, instead of being single as in the *Conohyus* and *Potamochoerus* lines, is divided into two of approximately equal value” (Pilgrim, 1926) and the genus was considered as an Asian form (Viret, 1961). During his revision of the Miocene Siwaliks suids, Pickford (1988)

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indicated that *Dicoryphochoerus* was a junior synonymy of *Hippopotamodon* Lydekker, 1877. The Siwaliks species previously referred to *Dicoryphochoerus* were consequently either revised as *Hippopotamodon*, or regrouped into *Propotamochoerus* and *Conohyus* (Pickford, 1988). The *Dicoryphochoerus* sp. from Kaiyuan was revised to *Hippopotamodon hyotherioides* (Pickford and Liu, 2001). *D. medius* and *D. binxianensis* from the Late Miocene of North China were reassigned to *Microstonyx major* based on the new complete materials from Hezheng (Liu et al., 2004). But “*D. ultimus*” from South China remained unresolved (Liu, 2003).

A series of karstic caves bearing *Gigantopithecus* and associated mammalian faunas have been excavated since 2004 in Chongzuo, Guangxi (Jin et al., 2009). Some new suid materials from Chongzuo were identified similar to those of Han’s “*D. ultimus*” from Liucheng and Daxin. These new materials are described in the present paper with taxonomic revision of the “*D. ultimus*”.

The suid dental terminology proposed by Pickford (1988) is mostly followed in the present paper. The institutional abbreviations are as follow: GBB, Baeryan Locality at Bijie Municipality in Guizhou Province; H MV, vertebrate specimens of Hezheng Paleontological Museum; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; PDYV, vertebrate specimens collected by the “State Key Project of the 9th Five-Year Plan—Origin of Early Human and Environmental Background” and housed at Yunnan Institute of Cultural Relics and Archaeology.

2 Systematic description

Mammalia Linnaeus, 1758

Artiodactyla Owen, 1848

Suoidae Cope, 1887

Suidae Gray, 1821

Suinae Gray, 1821

Propotamochoerini Pickford, 1993

***Hippopotamodon* Lydekker, 1877**

***Hippopotamodon ultimus* (Han, 1987)**

1982 *Dicoryphochoerus ultimus*, Han, p.59

1987 *Dicoryphochoerus ultimus*, Han, p.137

1991 *Dicoryphochoerus ultimus*, Huang et al., p.127

2009 *Dicoryphochoerus ultimus*, Jin et al., p.793

2010a “*Dicoryphochoerus*” *ultimus*, Dong et al., p.61

2010b “*Dicoryphochoerus*” *ultimus*, Dong et al., p.215

Revised diagnosis A suid larger than the other known *Sus*. The snout is long, canine

flanges in the female are small. The diastema between P1 and P2 is developed. Entocingulum is often present in P2 and P3 but with varied development. P4 is nearly rectangular in occlusal view with beaded anterior and posterior cingula. The third lobe of M3 is short and narrow, the lower canine is *verrucosus* type, the main cusp of the p4 is cleft at the tip into twin summits, the third lobe of m3 is double cusped, all molars brachyodont, the enamel folds on cusps are not developed, the main cusps of molars are separate well from each other.

New materials A partial broken skull (IVPP V 18400.1), 3 isolated M1 (V 18400.2-4), 3 isolated M2 (V 18400.5-7), 3 isolated M3 (V 18400.8-10), 5 isolated m1 (V 18400.11-15), 3 isolated m2 (V 18400.16-18) and 4 isolated m3 (V 18400.19-22) from Sanhe Cave of Chongzuo in Guangxi.

Referred materials Partial maxillae with palates and both left and right P4-M3 (GBB14-1), 2 right M3 (GBB14-2-3), a right p3 (GBB14-5), a left p4 (GBB14-6), a right m1 (GBB14-4) from Baeryan, Bijie, Guizhou Province (Dong et al., 2010b). Five isolated teeth (IVPP V 17751.1-5) from Boyueshan, Chongzuo, Guangxi (Dong et al., 2010a).

Description The specimens from Chongzuo include some published isolated teeth from Boyueshan Locality (Dong et al., 2010a) and the new findings from Sanhe Cave. They are morphologically the same as those from Bijie (Dong et al., 2010b), and they are thus described together in order to give the specific information as comprehensive as possible. The broken skull (IVPP V 18400.1) includes partial nasals, nearly complete premaxillae, partial maxillae and partial palates (Fig. 1C). The preserved part of nasals indicates that the nasals are narrow and long in dorsal view and thin in lateral view; and the lateral sides of nasals are parallel to each other in dorsal view. Right premaxilla is better preserved. The incisor row forms a sharp angle with median sagittal plan. The I2 contacts with I1, but there is a diastema of about 9.2 mm between I2 and I3. The diastema between I3 and C is 13.9 mm. The palatine fissures (incisive foramina) are oval and elongated with an average longitudinal diameter of about 13 mm. The dorsal parts of maxillae are broken, but the ventral parts are well preserved. In lateral view, the canine flange is evident but not strong. The weakly developed canine and canine flange indicates that the specimen is a female. The left infraorbital foramen is located about 27 mm above the P4, its diameter measures about 10 mm; the right one is located about 24 mm above the contact between P3 and P4, and its diameter is 9.5 mm. An infraorbital fovea with a diameter of about 6.5 mm is situated about 6 mm below the posterior side of the infraorbital foramen. In ventral view, the left and right cheek teeth rows are parallel to each other. The diastema between C and P1 measures 17 mm, and that between P1 and P2 measures 5.3 mm. No diastema between the rest cheek teeth. The palatine sulcus beside the cheek teeth row is shallow and it deepens on the palatine near the major palatine foramen.

The upper dentition is better preserved on the right side of the broken skull V 18400.1.

The I1 is not available in the materials studied, but the right I1 alveolus is preserved in V 18400.1. Its buccolingual diameter measures 17.5 mm and its mesiodistal one 17.6 mm.

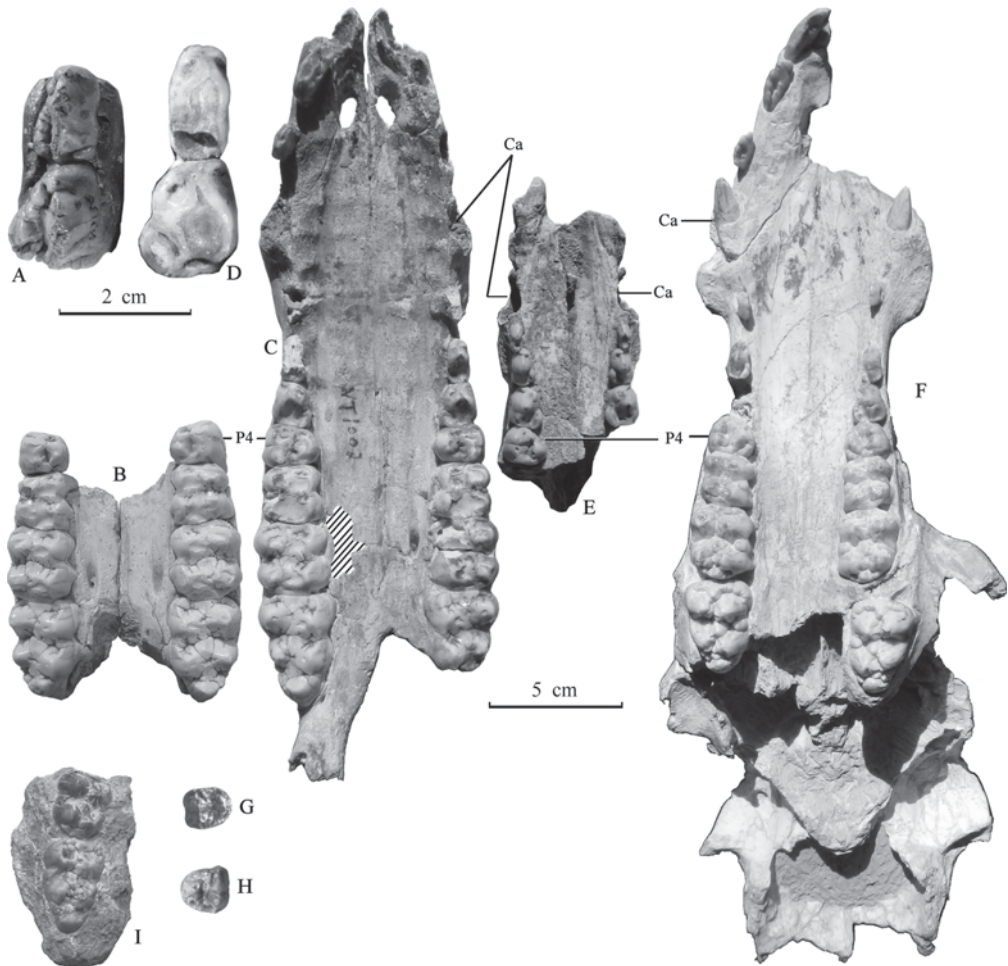


Fig. 1 Occlusal view of some Propotamochoerini and *Sus peii*

A. left maxillary fragment with P2-3 (IVPP V 03136) of *Microstonyx major* from Lantian; B. maxillary fragment with right and left P4-M3 (GBB14-1) of *Hippopotamodon ultimus* from Bijie; C. broken female skull with premaxilla and maxilla (V 18400.1) of *H. ultimus* from Chongzuo; D. left P2-3 from the broken skull (V 18400.1); E. skull fragment of *S. peii* from Liucheng (V 5825.14); F. female skull of *M. major* from Hezheng, Linxia (HMY 0977); G-I. *H. hyotherioides* from Yuanmou, G. right P4 (PDYV1587); H. left P4 (PDYV1224); I. right M2-3 (PDYV25)

Abbreviation: Ca. canine alveolus. The dentitions are aligned with P4 for comparison

The I2 is represented only by a tooth in the broken skull V 18400.1. The tooth crown is elongated along the alveolus in occlusal view with a mesiodistal diameter of 19.1 mm, a buccolingual one of 8.2 mm, much narrower than that of I1, and a crown height of 7.1 mm. It is worn and not evident to judge the number of the main cusps. But it is clear that its lingual base is protruding as a cingulum.

The I3 is also represented only by one tooth. It is much smaller than I2 and composed of one main cusp only. The tooth crown is also elongated along the alveolus in occlusal view with

a mesiodistal diameter of 13.3 mm, a buccolingual one of 6.5 mm and a crown height of 6.1 mm. No cingulum is visible.

The C is not available in the materials concerned, but both alveoli are preserved in V 18400.1. The mesiodistal diameter of the alveolus measures 18.7 mm for the right one and 17.1 mm for the left one, and its buccolingual one 12.9 mm for the right one and 11.7 mm for the left one. The occlusal view of the alveolus is oval.

The P1 is present only in the partial skull V 18400.1. The preserved part of the right P1 is only a posterior root, the tooth crown and the anterior root are all lost; and that of the left P1 is the base of the tooth crown and its two roots. The occlusal view of the crown is elongated oval with one main cusp.

The P2 is represented by a pair of teeth in the partial skull V 18400.1. The left one is median worn but well preserved and the right one is broken. It is elongated oval in occlusal view and triangular in lateral view. The tooth is composed of one main cusp and a precingulum at the anterior base of the main cusp, as well as a talon at the posterior base of the main cusp. The lingual cusplet and cingulum are absent.

The P3 is represented by a pair of well preserved teeth in the partial skull V 18400.1. The tooth crown is triangular both in occlusal and lateral views. The crown is also composed of a main cusp and a precingulum at the anterior base of the main cusp, as well as a cusplet or “talon” at the posterior base of the main cusp, but the cusplet is much wider and better developed than that in P2. The entocingulum is developed in the anterior and fused with the precingulum, but it is weak in the posterior. A lingual cusplet is present at the posterior base of the crown.

The P4 is represented by a pair of well preserved teeth in the partial skull V 18400.1 and another well preserved pair in the maxillae GBB14-1. Its outline in occlusal view is roughly square. The lingual side of the tooth crown is a little shorter than the buccal one. The crown is composed of three main cusps, a strong lingual bunodont one (protocone) and two buccal less bunodont ones (paracone and metacone), and some irregular accessory cusplets. The buccal main cusps have a tendency to fuse with each other. Precingulum is developed, and sagittal valley, too.

The M1 is represented by seven teeth, a pair in V 18400.1, a pair in GBB14-1, and three isolate teeth. Its outline in occlusal view is trapezoid. The tooth crown is composed of four main bunodont cusps, protocone and hypocone on the lingual side, paracone and metacone on the buccal side. The lingual cusps are evidently larger than the buccal ones. The basal pillar is moderately present on the buccal side but absent on the lingual side. The precingulum is evident on the anterior base of paracone. Postcingulum is not evident.

The M2 is also represented by a pair in V 18400.1 and another in GBB14-1, and three isolated teeth. It is evidently bigger than M1. Besides four main bunodont cusps as in the M1, median accessory cusplet and hypoconule are well present, precingulum and postcingulum are well developed. Basal pillar is weak on the buccal side and absent on the lingual side.

The M3 is represented by a pair in V 18400.1, another in GBB14-1, and five isolated

teeth. Its outline in occlusal view is nearly triangular (Fig. 1B). The tooth crown is composed of five main bunodont cusps, i.e. protocone and hypocone on the lingual side, paracone and metacone on the buccal side, and talon on the distal side. Median accessory cusplet and hypoconule are well present. Precingulum is well developed on the anterior base of paracone. Postcingulum is absent.

Tables 1-2 lists the measurements of cheek teeth of *H. ultimus* from Sanhe of Chongzuo.

The lower dentition is represented by some isolated teeth only; p1 and p2 are not available.

The p3 is represented only by a right p3 (GBB14-5). The tooth crown is composed of a main cusp, i.e. a protoconid, a moderate precingulum and a developed talonid. The crown is trapezoid in occlusal view and triangular in lateral view.

The p4 is represented only by a left p4 (GBB14-6). It is composed of anterior and posterior two main cusps (equivalent to protoconid and metaconid respectively), and the anterior one is evidently larger than the posterior one. The main cusp of the p4 is cleft at the tip into twin summits. An anterior honing facet and a posterior one are present on the anterior main cusp. The anterior facet inclines forward and downward, and the posterior facet appears undulated. Another anterior honing facet is present on the posterior main cusp, but no posterior facet is present on the cusp. A weak precingulum is present on the anterior base of the crown.

Table 1 Measurements of teeth of *Hippopotamodon ultimus* (IVPP V 18400.1) from Sanhe (mm)

	Length (left)	Width (left)	Height (left)	Length (right)	Width (right)	Height (right)
P1	13.8	6.5		13.6	6.6	
P2	16.8	9.3	8.2	18.3	9.2	
P3	18.3	15.1	9.8	18.0	15.2	14.7
P4	16.3	19.3	10.5	17.0	21.2	11.7
M1	23.1	23.5	7.8	23.2	23.7	8.3
M2	27.0	26.3	11.2	27.1	27.0	11.0
M3		27.5	13.6	39.3	27.7	14.5
P1-M3				155.0		
P1-P4	67.7			65.2		
M1-3				67.0		

The m1 is represented by six isolated teeth (IVPP V 18400.11-15 and GBB14-4). It is trapezoid in occlusal view and composed of four bunodont main cusps. The protoconid and metaconid are close to each other to form the anterior lobe; hypoconid and endoconid are also close to each other to form the posterior lobe. The median accessory cusplet and hypoconulid are all well developed. Both precingulum and sagittal valley are developed on all specimens.

The m2 is represented by three isolated teeth (V 18400.16-18). The morphology of the tooth is very similar to that of the m1 but its size is evidently larger, and its buccal basal pillar more developed.

Table 2 Measurements of isolated cheek teeth of *Hippopotamodon ultimus* from Sanhe (mm)

	Length	Width	Height	IVPP number	Field number
M1 left	22.3	20.88	10.88	V 18400.2	DXO:32
M1 right	22.46	21.9	8.64	V 18400.3	D1001
M1 right	23.2	23.7	9.77	V 18400.4	—
M2 left	27.82	22.78	12.16	V 18400.5	T0237
M2 left	26.76	23.22	12.76	V 18400.6	T0037
M2 right	26.22	20.3	10.88	V 18400.7	T0214
M3 left	38.2	24.02	12.86	V 18400.8	DXO:11
M3 right	37.62	24.22	8.7	V 18400.9	T0032
M3 right	41.58	24.72	15.0	V 18400.10	DXO:14
m1 right	23.86	18.4	11.44	V 18400.11	DXO:43
m1 left	22.44	16.5	8.84	V 18400.12	CSD0030
m1 left	23.02	16.9	8.62	V 18400.13	06GCHDXO:4
m1 right	22.9	16.84	11.18	V 18400.14	DXO:21
m1 right	24.52	16.2	10.62	V 18400.15	D2020
m2 right	25.92	17.56	11.58	V 18400.16	DXO:2
m2 left	26.4	17.14	11.1	V 18400.17	D2017
m2 left	24.4	18.78	8.4	V 18400.18	DXO:19
m3 right	39.54	19.32	10.82	V 18400.19	T0091
m3 right	39.38	20.4	13.78	V 18400.20	05F(2)0:37
m3 right	41.22	19.96	12.5	V 18400.21	05F(2)0:47
m3 right	38.96	19.12	11.48	V 18400.22	T0036

The m3 is represented by four isolated teeth (V 18400.19-22). The anterior two thirds of the tooth crown is morphologically the same as the m2, i.e. the four bunodont main cusps form two lobes, the precingulid developed in the anterior base of the anterior lobe, the median accessory cusplet between the two lobes and the hypoconulid behind the second lobe. But the posterior third lobe of the tooth, or talonid, is morphologically varied. It is generally composed of three main cusps, two anterior ones and a posterior one. If analogous to the second lobe, the anterior two are similar to the endoconid and hypoconid, and the posterior one to the hypoconulid. The posterior cusp is the most varied component. When it is moderately developed, it looks like a cusplet as a hypoconulid (Fig. 2I, K); but when it is over developed, it looks like a talonid and makes the anterior two cusps look like the third lobe of the m3 (Fig. 2J).

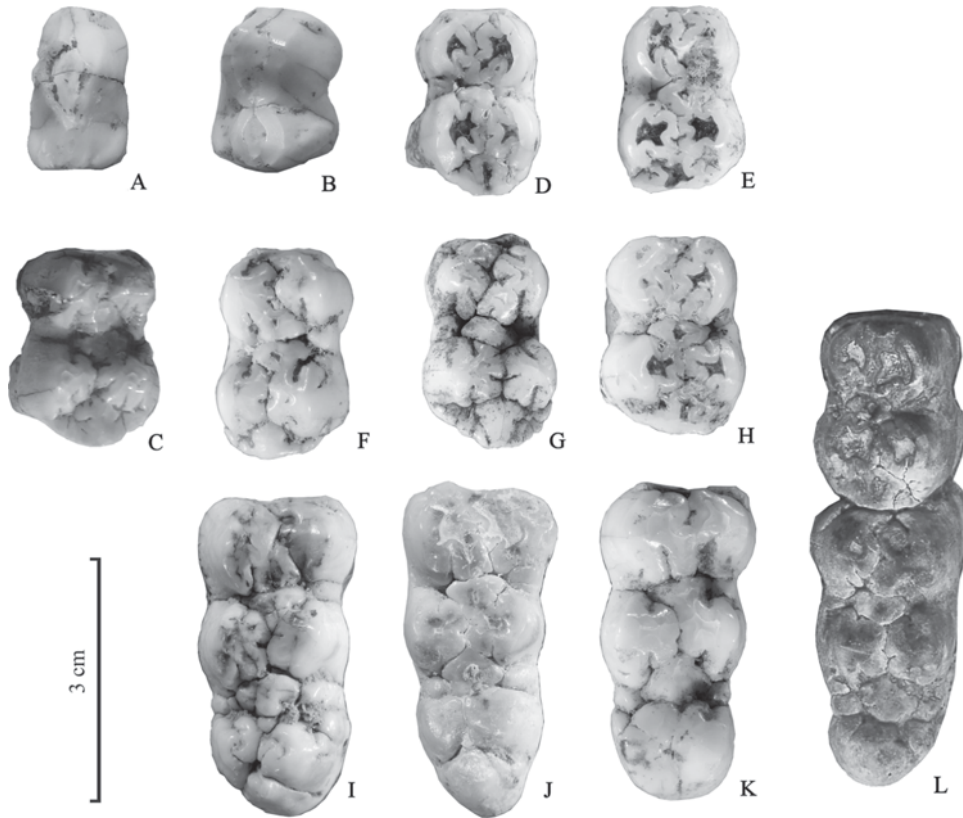


Fig. 2 Occlusal view of some lower cheek teeth of *Hippopotamodon ultimus* and *H. hyotherioides*. A. right p3 (GBB14-5) from Bijie; B. left p4 (GBB14-6) from Bijie; C. right m1 (GBB14-4) from Bijie; D. left m1 (V 18400.13); E. right m1 (V 18400.14); F. right m2 (V 18400.16); G. left m2 (V 18400.17); H. left m2 (V 18400.18); I. right m3 (V 18400.20); J. right m3 (V 18400.21); K. right m3 (V 18400.22); L. *H. hyotherioides* from Yuanmou, left m2-m3(PDYV322)

3 Comparison

As mentioned in the introduction, “*Dicoryphochoerus*” was a genus formally named by Pilgrim (1926) but considered as invalid by Pickford (1988). The *Dicoryphochoerus* from the Late Miocene of North China were reassigned to *Microstonyx major* (Liu et al., 2004), the *Dicoryphochoerus* sp. from Kaiyuan was revised to *Hippopotamodon hyotherioides* (Pickford and Liu, 2001), but “*D. ultimus*” from South China remained unresolved (Liu, 2003). The generic attribution of the new materials is either one of the closely related *Hippopotamodon*, *Propotamochoerus* and *Microstonyx*, or *Sus*.

3.1 Comparison with *Hippopotamodon* from southern China

The first reported *Hippopotamodon* in China was *H. hyotherioides*. The *Dicoryphochoerus* sp. (Dong, 1987) from Xiaolongtan, *Propotamochoerus hyotherioides* from

Lufeng (Made and Han, 1994) were all considered to be *H. hyotherioides* (Pickford and Liu, 2001). Some Yuanmou materials (Fig. 1G-I, 2L) were also included into *H. hyotherioides* (Pan et al., 2006). The similarities between the new materials and *H. hyotherioides* are that the main cusp of the p4 is cleft at the tip into twin summits; P4 is nearly rectangular in occlusal view, its precingulum and postcingulum are developed and beaded, its lingual cusp is nearly as long as its two buccal cusps altogether; molars relatively simple with developed precingulum and furchenplan, the median accessory cusplets in molars are well present but not developed; the enamel folds on cheek teeth is not well developed. The differences are that dimensions of *H. ultimus* are slightly larger than those of *H. hyotherioides*, the third lobe of m3 is better developed in *H. ultimus* than in *H. hyotherioides*.

3.2 Comparison with *Propotamochoerus* from southern China

Propotamochoerus is a genus closely related to *Hippopotamodon* that their generic statuses are sometimes controversial (Pickford, 1993; Made and Han, 1994; Chen, 1997; Pickford and Liu, 2001; Pan et al., 2006). For example, the *H. hyotherioides* from Lufeng for Made and Han (1994) is *Propotamochoerus* but for Pickford and Liu (2001) and Pan et al. (2006) is *Hippopotamodon*. The *Propotamochoerus* with no controversy in China is found only in Yunnan Province, e.g. *P. parvulus* from Xiaolongtan (Chang, 1974; Dong, 1987; Pickford and Liu, 2001) and *P. hysudricus* from Yongren (Liu and Ji, 2004). Although the *P. wui* from Lufeng nominated by Made and Han (1994) was considered as a synonym of *P. parvulus* (Pickford and Liu, 2001), its generic status is undoubted. Compared with these *Propotamochoerus* from Yunnan, the *H. ultimus* is evidently larger sized, the snout is evidently longer, the main cusp of the p4 is cleft at the tip into twin summits, the differences from *Propotamochoerus* are obvious.

3.3 Comparison with *Microstonyx* from northern China

In fact, the first reported “*Dicoryphochoerus*” in China is “*D. medius*” from Lantian (Liu et al., 1978), and Liucheng materials were assigned into “*Dicoryphochoerus*” by following the same methods for classifying the Lantian materials (Han, 1987). The Lantian materials were reassigned into *Microstonyx major* by Liu et al. (2004), together with Binxian materials described by Tang et al. (1985) and “*Sus (Microstonyx) erymanthius*” described by Pearson (1928). The difference of the p4 between Lantian and Liucheng materials is that, as indicated by Han (1987), the dimidiating of the protoconid is not equal, the lingual part looks as an accessory cusplet pasted on the distolingual side of the main cusp, the anterior slope of the main cusp is small, the talonid is lower than the main cusp in Lantian materials; but it is on the contrary in Liucheng materials. In addition, the fold in molar enamel is complicated in Lantian materials but simple in Liucheng ones; the talonid of the m3 is contracted in Lantian materials but double cusped in Liucheng ones. The Lantian materials are unfortunately lost during several moves of the IVPP collections except a maxillary fragment with P2-3 (IVPP V 03136,

Fig. 1A) which is still available. As can be seen in Fig. 1A, D, the occlusal view of the P2 is oval in *H. ultimus* from Chongzuo but triangular in *M. major* from Lantian, the entocingulum is beaded on the P2 in *M. major* from Lantian but absent in *H. ultimus* from Chongzuo; the main cusp of P3 is better developed in *H. ultimus* from Chongzuo and that the entocingulum of P3 is better developed in *M. major* from Lantian.

The best preserved materials of *M. major* found in China are the skulls and mandibles from Hezheng, Linxia Basin (Liu et al., 2004). Compared with the Linxia materials, the general morphology is similar, e.g. long snout, large size, presence of diastema between P1 and P2, presence of precingulum on the molars, etc. The differences are that the female skull V 18400.1 from Chongzuo (Fig. 1C), although a partial one, has much smaller canine flanges than those in Linxia female skull HMV 0977 (Fig. 1F). In addition, the diastema between the C and the P1, that between the P1 and the P2 in the Chongzuo skull, are much shorter than those in the Linxia skull; the distance between the C and the P2 in V 18400.1 is 32 mm, and that in HMV 0977 is 44 mm; the entocingulum on P3 is developed in Linxia skull but weak in Chongzuo one; the precingulum of the P3 is better developed in Chongzuo materials; the width index of P4 is greater in Chongzuo skull (121.55) than in Linxia skull (116.8); the buccal main cusps of P4 are better developed in Chongzuo skull than in Linxia one.

3.4 Comparison with *Sus* from southern China

Five species of *Sus* were identified from southern China, *S. bijiashanensis* from Liujing (Han et al., 1975), *S. xiaozhu*, *S. liuchengensis*, *S. australis* and *S. peii* from Liucheng (Han, 1987). *S. bijiashanensis* is characterized by shortened upper last molars, whose third lobe is a very contracted talon, and the species is evidently different from *H. ultimus*. *S. xiaozhu* is characterized by its small size, also evidently different from *H. ultimus*. *S. liuchengensis* is a median sized *Sus* between *S. xiaozhu* and *S. peii*. Although it is morphologically similar to *S. peii*, it can still be distinguished from *S. peii* and *H. ultimus* by dimensions, particularly when complete dentitions are available (Han, 1987). *S. australis* is morphologically and metrically similar to *S. peii*. The only differences between them are that the mandibular symphysis and the lower last molars in *S. australis* are longer, the m3 has an extra fourth lobe. Nevertheless, such differences were regarded as intraspecific variation and *S. australis* was considered as a synonym of *S. peii* (Chen, 2004). Among the available species of *Sus* from southern China, *S. peii* is therefore the only one the closest to *H. ultimus*.

S. peii was nominated in the same paper as *H. ultimus* for the materials from Liucheng (Han, 1987). It has been found in many localities south of Yangtze River, e.g. Longgudong at Jianshi (Xu et al., 1974; Chen, 2004), Bijiashan at Liuzhou (Han et al., 1975; Chen, 2004), Longgupo in Chongqing (Huang et al., 1991), Mohui at Tiandong (Wang et al., 2007), Renzidong at Fanchang (Dong et al., 2009), as well as Sanhe at Chongzuo (Jin et al., 2009). It was sometimes uncovered with *H. ultimus* in the same localities, e.g. *Gigantopithecus* Cave (Han, 1987), Longgupo (Huang et al., 1991) and Sanhe (Jin et al., 2009).

The partial broken skull of *H. ultimus* (Fig. 1C) and that of *S. peii* (Fig. 1E) are both female adults judging by the canine sizes and permanent dentitions. Compared with *S. peii*, the snout of *H. ultimus* is much longer, the palates evidently wider, the diastema between the upper canine and the upper first premolar clearly longer, a remarkable diastema between the P1 and P2 present in *H. ultimus* but absent in *S. peii*.

Besides the dimidiate protoconid of p4 in *H. ultimus*, Han (1987) pointed out that the P2 and P3 of *H. ultimus* have developed entocingulum, the molars are brachyodont, the small folds on the main cusps are few, the main cusps of molars are more away from each other, enamel is thick. A few of these characters are sometimes also found in *S. peii*, e.g. the skull fragment from Liucheng (V 5825.14) also has the left P3 with evident entocingulum (Fig. 1E). In addition, the occlusal view of the P2 shows that its outline is olivary in *H. ultimus* but triangular in *Sus peii*; a posterior lingual accessory cusplet is present in *S. peii* but absent in *H. ultimus* (Fig. 1C, E). The outline of P4 is nearly rectangular in *H. ultimus* but triangular in *S. peii*, the protocone is better developed and longer in *H. ultimus* than in *S. peii* (Fig. 1C, E). The dimensions of cheek teeth, the lengths of premolar and molar rows in *H. ultimus* are evidently greater than those in *S. peii*, especially the length of premolar rows (Table 3). The median accessory cusplets and enamel folds in *H. ultimus* are less developed than in *S. peii*.

Table 3 Comparison between *Hippopotamodon ultimus* and *Sus peii* on the dimensions of isolated cheek teeth (mm)

	<i>H. ultimus</i>			<i>S. peii</i>		
	Sanhe	Liucheng ¹⁾	Bijie ²⁾	Sanhe	Liucheng ¹⁾	Jianshi ³⁾
P1 L	13.6–13.8				10.0–10.42	
P1 W	6.5–6.6				4.8	
P2 L	18.3–16.8	15.5–19.6			13.14–14.98	10.4–14.4
P2 W	9.2–9.3	9.7–12.2			8.36–9.1	7.7–9.5
P3 L	18.0–18.3	16.3–18.6		13.00–14.28	15.4–15.46	12.9–14.8
P3 W	15.1–15.2	14.8–18.5		10.86–12.10	12.36–13.2	10.2–15.0
P4 L	16.3–17.0	15–17.6	14.9–15.2	12.96–15.36	14.16	12.3–14.8
P4 W	19.3–21.2	18–22.6	19.3	15.06–18.32	16.7	14.2–16.8
P1-4 L	66.6–69.5				53.1	
M1 L	22.3–23.2	20–22.5	21.3–21.7	18.10–21.80	16.8–16.3	16.0–19.2
M1 W	20.88–23.7	17.6–21.0	20.2–20.6	16.10–19.36	16.5	14.8–17.3
M2 L	26.22–27.82	25.4–29.6	27.6–27.7	22.66–25.78	23.1–23.5	19.7–25.7
M2 W	20.3–27.0	22–26.4	23.2–23.9	20.00–23.22	21.8–22.2	18.2–22.4
M3 L	38.2–41.58	33.6–41.5	35.3–42.0	33.66–39.18	34.6–41.7	30.1–38.7
M3 W	24.02–27.7	23.2–29.6	25.2–27.0	19.08–24.02	21.3–25.2	19.0–24.4
M1-3 L	87.0		85.2–85.7		78.2	

Continued						
	<i>H. ultimus</i>			<i>S. peii</i>		
	Sanhe	Liucheng ¹⁾	Bijie ²⁾	Sanhe	Liucheng ¹⁾	Jianshi ³⁾
p1 L					11.2	8.5–11.3
p1 W					5.0	4.2–6.1
p2 L		14.7–17.2			12.0–13.2	10.7–14.1
p2 W		7.2–9.3			6.0–7.5	4.9–8.2
p3 L		17.0–19.5	19.4		14.3–15.3	12.3–14.9
p3 W		9.2–12.6	11.5		8.2–10.0	7.0–9.4
p4 L		17.3–21.5	19.4		15.2–16.6	13.6–16.8
p4 W		13.2–16.2	14.2		11.4–12.8	9.2–13.0
m1 L	22.44–24.52	20.5–24.7	21.9	18.00–20.86	15.5–19.0	15.8–20.5
m1 W	16.2–18.4	13.3–18.5	16.6	13.70–17.80	14.0–15.0	12.0–13.4
m2 L	24.4–25.92	24.0–29.0		21.98–25.60	22.0–26.5	20.9–25.3
m2 W	17.14–18.78	19.0–22.5		15.50–18.06	17.3–19.5	14.8–17.3
m3 L	38.96–39.54	34.5–45.0		34.14–41.20	35.2–40.9	33.7–41.2
m3 W	19.12–20.4	20.0–26.5		16.16–19.88	16.2–22.9	15.8–20.3

1) Han, 1987; 2) Dong et al., 2010b; 3) Chen, 2004; L. length; W. width.

4 Discussion

The discovery of the “*Dicoryphochoerus*” *ultimus* enriched the fauna data of the region as well as the information for suid phylogeny, but also started its taxonomically intricate story. Although the formal nomination of this species was officially published in 1987, the species name appeared already in a research paper on the mammalian fauna associated with *Gigantopithecus* from Heidong (Dark Cave) at Daxin (previously spelled as Tahsin) County in Guangxi (Han, 1982). The Daxin materials were collected in 1955 and not numerous: only an isolated left P3 and an isolated left M3; but those from Liucheng were collected from 1956 to 1963 with impressive quantity: more than 400 isolated teeth and some jaw fragments. Especially, the taxonomically important p4 is absent from Daxin but more than 50 from Liucheng. This is why the nomination of the species was based on the materials from Liucheng. The paper on the Daxin fauna is not very long and was submitted to a journal, and those on the Liucheng fauna are very long and were submitted to a memoir. The publication of the memoir was probably delayed due to various reasons and the formal nomination of the species was published in 1987, five years later than the journal.

During the study on Liucheng suids, Han (1987) followed Pilgrim’s methods for the taxonomic classification on suids, i.e. based mainly on the morphology of the p4 to divide the

suids into four groups: protoconid splitting into two at its summit, such as “*Dicoryphochoerus*”; protoconid remaining as an integrative cusp, such as *Potamochoerus*; the anterior and posterior of tooth crown being elevated nearly at the same height of protoconid, such as *Sus*; the tooth being bulky but still composed of a sole cusp of protoconid, such as *Conohyus*, *Sivachoerus*, *Tetracondon*. The materials from Liucheng with the p4 having dimidiate protoconid were assigned to “*Dicoryphochoerus*”.

Even though the first materials of “*Dicoryphochoerus*” in China were found in 1955 at Daxin, the first published materials of “*Dicoryphochoerus*” in China were collected nine years later by Han at Jiulaopo, Lantian County, Shaanxi Province (Liu et al., 1978; Han, 1987). Their morphology is between that of “*Dicoryphochoerus*” from the Siwaliks nominated and described by Pilgrim (1926) and that of *Sus*. A new species “*D. medius*” was erected by Liu et al. (1978) for Lantian materials.

The second formally reported materials of “*Dicoryphochoerus*” in China were discovered by Coal Geology Prospecting Team No.186 of Shaanxi in 1982 at Potoucun, Binxian County, Shaanxi Province (Tang et al., 1985). The materials were morphologically similar to “*D. chisholmi*” from the Siwaliks and “*D. medius*” from Lantian, but the talonid of the p4 is larger and simpler, the enamel layer is smooth with little folding. A new species, “*D. binxianensis*”, was established for the Binxian materials (Tang et al., 1985).

Dong (1987) reported the presence of “*Dicoryphochoerus*” sp. in the Late Miocene mammalian fauna of Xiaolongtan, Kaiyuan County, Yunnan Province. The specimens are morphologically similar to those of “*D. cf. vagus*” and “*Sus advena*” from the Siwaliks and comparable to those of “*D. medius*” from Lantian. The Xiaolongtan form was considered as a transitional form from “*Dicoryphochoerus*” to *Sus* (Dong, 1987; Dong, 2001).

“*Dicoryphochoerus*” was a genus formally named by Pilgrim in 1926 when he described the suids from the Siwaliks. But Pickford (1988) pointed out that Pilgrim was “incorrect in his erection of the new genus *Dicoryphochoerus*, as *Hippopotamodon* Lydekker, 1877 was already available and valid” and *Dicoryphochoerus* is therefore invalid as it is a junior synonym of *Hippopotamodon*. The latter is a common genus of Neogene hominoid fauna of the Siwaliks. The “*Dicoryphochoerus* sp.” from Xiaolongtan was consequently reassigned to *Hippopotamodon hyotherioides* (Pickford and Liu, 2001). In addition, the *Propotamochoerus hyotherioides* from Lufeng hominoid site (Made and Han, 1994) was also moved to *H. hyotherioides* (Pickford and Liu, 2001). The materials from Yuanmou hominoid site were included into *H. hyotherioides* as well (Pan et al., 2006).

Pilgrim (1926) formally nominated *Dicoryphochoerus* and other six new genera with type species and generic description. He also proposed, in his introduction, the generic name *Microstonyx* for some European suids “belonging to the *Sus major-erymanthus* group, on account of their small verrucose male lower canines and the exceptional elongation of their snout” (Pilgrim, 1926). This nomination is so informal that neither type species nor generic diagnosis were defined. *Microstonyx* has nevertheless been accepted as valid for large-sized

Late Miocene (Pontien) “*Sus*” with small canines and long snout, especially for European forms (Viret, 1961; Made and Hussain, 1989; Made and Moya Sola, 1989; Made et al., 1992; Kostopoulos et al., 2001; Liu et al., 2005). Liu et al. (2004) reattributed “*D. medius*” and “*D. binxianensis*” from North China into *Microstonyx major* during their study on the suid materials from Hezheng. But the “*Dicoryphochoerus*” *ultimus* from South China was left unresolved (Liu, 2003).

“*D.*” *ultimus*, including the new materials, from South China has generic similarities with *H. hyotherioides* such as molar relatively simple with well developed furchenplan, labial cusps in lower molar lower crowned than lingual ones, etc., based on the comparison mentioned above. In addition, it is a member of *Gigantopithecus* fauna, and the latter is more related to *Lufengpithecus* fauna of South China than to the *Hipparion* fauna of North China. It is therefore more reasonable to reassign “*D.*” *ultimus* from South China to *Hippopotamodon* than to *Microstonyx* of North China. Furthermore, *Gigantopithecus* fauna of the Early Pleistocene might evolve from the *Lufengpithecus* fauna of the Neogene for their characteristic of hominoid components, *H. ultimus* is likely evolved from *H. hyotherioides* as the last Pleistocene relic of *Hippopotamodon* from the Neogene. The differences between *H. ultimus* and *H. hyotherioides* showed in the comparison mentioned above indicate that *H. ultimus* is a valid species of *Hippopotamodon*.

5 Conclusion

The former “*Dicoryphochoerus*” *ultimus* is reassigned into the genus *Hippopotamodon* based on the available materials and up-to-date knowledge on suids. *H. ultimus* is a valid species of *Hippopotamodon*. It is one of the Neogene relics in the *Gigantopithecus* fauna. The localities yielding *H. ultimus* so far include the type locality *Gigantopithecus* Cave of Liucheng, and other localities such as Heidong at Daxin (Tahsin), Boyueshan and Sanhe at Chongzuo, Baeryan at Bijie and Longgupo at Wushan. That is to say, its geographic ranges limit only in the southern China south of the Yangtze River. According to the specimen numbers, Liucheng population is the largest, followed by Sanhe, and then Bijie, with Heidong the smallest. Correlated to the biochronological sequence of *Gigantopithecus* faunas of East Asia proposed by Jin et al. (2009), the chronological sequence of *H. ultimus* populations from the oldest to the youngest is Wushan (1.9 Ma, Huang et al., 1995), Bijie, Liucheng, Sanhe (1.2 Ma, Jin et al., 2009), Boyueshan, and Daxin.

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华南河马齿河猪(偶蹄目, 哺乳纲)的新材料

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摘要: 2004年以来, 广西崇左系统发掘出土了一些与巨猿共生的早更新世最后河马齿河猪(*Hippopotamodon ultimus*)的新材料。根据新材料及以前积累的各地点材料, 产于广西、贵州和重庆的原“最后双齿尖河猪(*Dicoryphochoerus ultimus*)”的系统分类位置由“双齿尖河猪”属修订到河马齿河猪属(*Hippopotamodon*), 而最后河马齿河猪(*H. ultimus*)是河马齿河猪属中的有效种。这种猪的个体较大, 大于猪属(*Sus*)的成员。其鼻吻部很长, P1和P2间的齿隙发育, M3第三叶相对窄小, 下犬齿*verrucosus*型, p4主尖在顶部分裂成双尖, m3的第三叶由两个主尖组成。最后河马齿河猪仅分布于华南地区, 其时代分布局限于早更新世早期和中期, 是河马齿河猪的最晚代表。

关键词: 广西, 早更新世, 偶蹄目, 河马齿河猪, “双齿尖河猪”

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