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A new species of *Kubanochoerus* (Suidae, Artiodactyla) from the Linxia Basin, Gansu Province, China

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Abstract A new specimen of *kubanochoeres* has been discovered from the Maida locality, Linxia Basin, Gansu Province, China, and a new species, *Kubanochoerus parvus* sp. nov., has been created based on the unique partially broken cranium. The new species has a relatively small body size similar to *K. massai* and *K. minheensis*. The new species, which possesses relatively wide cheek teeth that resemble those of *K. massai* and many derived characters that are similar to *K. gigas*, may represent a separate lineage of the Eurasian *kubanochoeres*. The horizon of the Maida locality is speculated to be the upper Hujialiang Formation or lower Liushu Formation, and the new species is possibly the youngest known *kubanochoere*. Based on the comparison of the known *kubanochoere*, *Libycochoerus* is suggested to be a synonym of *Kubanochoerus*, while *K. robustus* and *K. lantienensis* are synonyms of *K. gigas*. There is not sufficient evidence to support the subdivision of *K. gigas* at the subspecies level. *Kubanochoerus gigas* is speculated to have derived from more primitive forms that existed earlier than *K. massai*, and the new species may be derived from *K. massai* or other earlier forms. *Kubanochoerus minheensis*, which bears a relatively small body size and rudimentary sub-lophodont dentition, is suggested to be another separate lineage of the Eurasian *kubanochoeres*.

Key words Linxia Basin, Neogene, Suidae, Listriodontinae, *Kubanochoerus*

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1 Introduction

Kubanochoeres belong to a group of giant bunodont suids that are found from the Early to Middle Miocene deposits of the Old World. *Kubanochoere* fossils were first discovered in China and later in other Eurasian countries and Africa, which have been reported as *Listriodon* (Pearson, 1928; Liu and Lee, 1963), *Kubanochoerus* (Gabunia, 1955, 1958, 1960; Qiu et al., 1988; Ye, 1989; Guan and van der Made, 1993), *Bunolistriodon* (Wilkinson, 1976; Qiu et al., 1981), *Libycochoerus* (Arambourg, 1961, 1963; Pickford and Ertürk, 1979; Pickford, 1986),

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Hemimastodon (Pickford, 1987), and *Megalachoerus* (Pickford, 1993).

The classification of kubanochoeres has been a highly controversial topic. The first described kubanochoere fossils were found in China and classified as *Listriodon gigas* (Pearson, 1928). Gabunia (1955) erected *Kubanochoerus robustus* for a giant mandible found in Belometchetskia, part of the Caucasus region, and later erected a separate subfamily, Kubanochoerinae, for these giant suids, after a “horned” cranium was discovered from the same locality (Gabunia, 1958). Arambourg (1961) described a large mandible from Gebel Zelten, Libya, named *Libycochoerus massai*. After the discovery of a “hornless” cranium found from the same locality, Arambourg (1963) validated the genus name *Bunolistriodon* instead of *Kubanochoerus* and *Libycochoerus* based on the similar cranial morphology of *Lib. massai* and *Lis. jeanneli*. Gabunia (1973), however, listed differences between *K. robustus* and *Lis. lockharti*, confined *Bunolistriodon* to *B. lockharti*, and maybe also to *B. jeanneli* as well, and claimed *Libycochoerus* to be a synonym of *Kubanochoerus*. Leinders (1975) questioned the generic difference between *B. lockharti* and *Lis. splendens*, and considered *Bunolistriodon* to be a nomen nudum and suggested the reuse of *Libycochoerus*. Wilkinson (1976) again followed the classification of Arambourg (1963) and placed all kubanochoere fossils in *Bunolistriodon*; he also named a new species, *B. khinzikebirus*, which has larger body size than *B. gigas*. However, Cooke and Wilkinson (1978) later transferred these large forms and *B. jeanneli* to *Kubanochoerus* within the subfamily Listriodontinae. Contemporaneously, the Chinese kubanochoeres were attributed to *Listriodon* (Liu and Lee, 1963) or *Bunolistriodon* (Qiu et al., 1981), and the genus name *Kubanochoerus* has not been mentioned. Pickford (1986) accepted the viewpoint of Gabunia (1973) and Leinders (1975) when reviewing the African Suidae; he confined the genus *Libycochoerus* to the giant suid from Africa, and *Kubanochoerus* to the giant Eurasian forms; and enlarged the subfamily Kubanochoerinae to contain both the large-sized *Libycochoerus* and *Kubanochoerus*, and the small-sized *Nguruwe* and *Kenyasus*. Qiu et al. (1988) suggested that *Kubanochoerus*, *Libycochoerus*, and *Bunolistriodon* are all valid genus of Listriodontinae; they placed the large-sized Eurasian kubanochoere materials to *Kubanochoerus*, and moved materials of *B. jeanneli* to *Libycochoerus*. Guan and van der Made (1993) again denied the validity of *Libycochoerus*; they put all the giant forms to one single genus, *Kubanochoerus*, and merged all the “horned” fossils to one species, *K. gigas*. Van der Made (1996) nomen transferred Kubanochoerinae Gabunia, 1958, to Kubanochoerini Gabunia, 1958, moved *Nguruwe* to Lopholistriodontini, and excluded *Kenyasus* from Listriodontinae. However, McKenna and Bell (1997), Liu (2003), and Harris and Liu (2007) still followed the classification of Pickford (1986) and admitted to the validity of the Kubanochoerinae, *Libycochoerus* and *Kubanochoerus*. The recent cladistic analyses mostly followed the classification of van der Made (1996), taking *Kubanochoerus* as the only genus of the large forms, and the results suggest that *Kubanochoerus* is a sister group of the small to medium sized listriodonts within the subfamily Listriodontinae, and *Nguruwe* and *Kenyasus* are excluded from the Listriodontinae (Orliac, 2009, 2013; Orliac et al., 2010; Hou and Deng, 2014).

In this paper, a partially broken cranium found from the Linxia Basin, China, is described and compared with the known *kubanochoeres*. The new specimen was purchased by a local farmer named Zhao Rong from Dalang Town, Hezheng County. Now it is housed at the Hezheng Paleozoological Museum. The specimen was allegedly dug out from a hillside tunnel west to the Maida village, Maijiayi Town, Hezheng County, Gansu Province, China (Fig. 1). In order to verify Zhao's statement about the provenance of the fossil we examined the locality twice. Based on a close comparison of the cranium part with other fossils unearthed from the tunnel and the lithology exposed nearby, it is safe to assume that the cranium under study came from this tunnel. The fossiliferous layer is composed mainly of brownish red silty mudstone or muddy siltstone with thin intercalated layers of small calcareous concretions. There are at least seven conglomerate layers or lenses above the fossil cave as well as one conglomerate layer two meters below the tunnel. Based on comparison with a relatively continuous section west of the Maida Locality (Chawanling Section), the horizon of the fossiliferous layer is speculated to be top of the Hujialiang Formation or bottom of the Liushu Formation, correlating to the latest Middle Miocene or earliest Late Miocene. Judging by the accompanying fossils of *Gobicyon*, the age of the fossiliferous layer is a little younger than the Tongxin fauna.

The cranium is relatively small compared with those of other *kubanochoeres*, and differs from the other *kubanochoeres* in both the cranial and dental morphologies. Therefore, a new species, *Kubanochoerus parvus* sp. nov., is erected. The new species sheds new light on the

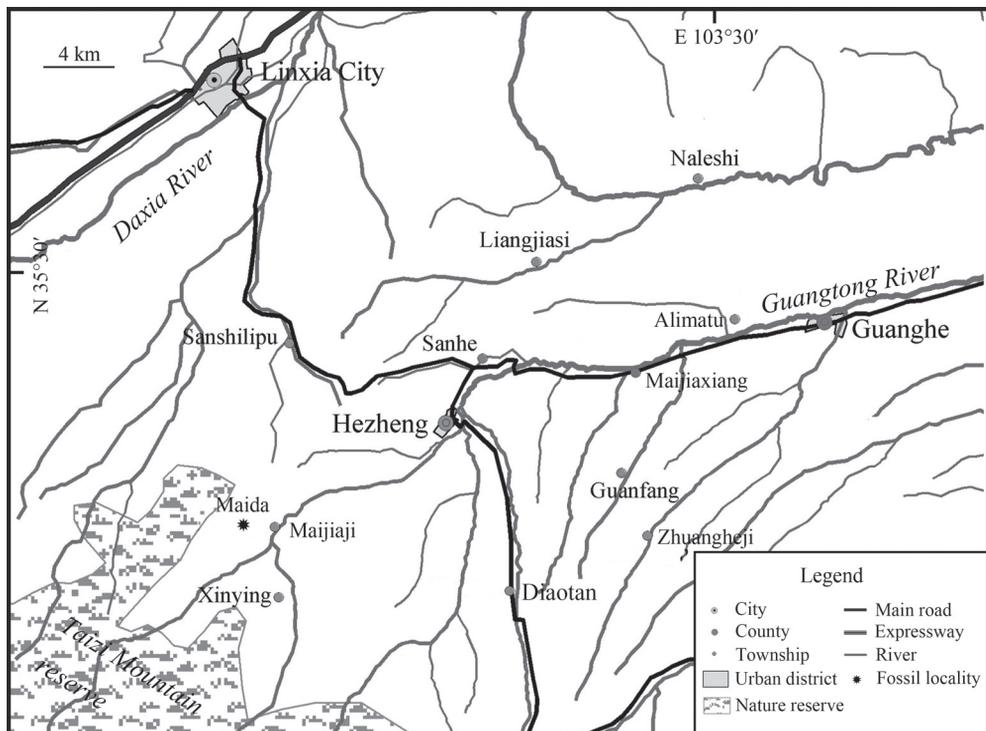


Fig. 1 Location map of the area studied in the Linxia Basin

classification and evolution of kubanochoeres.

The tooth orientation and the dental nomenclature of the common features on all tooth crowns (main cusps and accessory cusps) used here mostly follow Pickford (1986, 1988), and the work of Boisserie et al. (2010) is also considered for the nomenclature of the crest on the premolars. Tooth measurement follows van der Made (1996). Tooth width was measured at the widest part of the base of the crown.

Abbreviations DLL, labio-lingual diameter of incisor; DMD, mesio-distal diameter of incisor; L, length of premolar and molar; W, maximum width of premolar and molar; I, index, $(L/W) \times 100$ or $(DLL/DMD) \times 100$. BMNH, Beijing Natural History Museum; H MV, prefix of the catalogue number at the Hezheng Paleozoological Museum.

2 Systematic paleontology

Artiodactyla Owen, 1848

Suidae Gray, 1821

Listriodontinae Simpson, 1945

Kubanochoerini Gabunia, 1958

***Kubanochoerus* Gabunia, 1955**

***Kubanochoerus parvus* sp. nov.**

(Figs. 2–4; Tables 1–3)

Holotype H MV 1985, anterior half of an adult cranium, which is slightly laterally compressed. The posterior part the cranium is broken off from the post-median part of the orbit on the right side, and from anterior of the orbit on the left side. The posterior part behind the palate is missing. The crowns of the left I1–I2 and the left P1 are broken off; the right canine is broken at the tip; the right P1 retains only its root; the right M3 crown is largely shattered, and the left I3 and the right P1 are not preserved.

Locality and horizon Maida Locality (LX 200601, N35°21'19.7", E103°11'58.0"), latest Middle Miocene or earliest Late Miocene.

Etymology *Parvus*, Latin, small.

Diagnosis Small *Kubanochoerus* (cheek teeth is similar to *K. massai*, about 90% of *K. minheensis*, and 75%–80% of *K. gigas*) with complex features of *K. massai* (wide cheek teeth) and *K. gigas* (derived characters like fused premaxillae, more mesio-distally enlarged I1, tightly arranged I1–I3, large I3–C diastema, more posteriorly extended palate, relatively small P1, large P1–P2 diastema), and unique upper canine (relatively long and straight, projecting antero-laterally, and only slightly inferior).

3 Description

Cranium lateral view The dorsal border of the nasal bone is straight and slowly rises posteriorly (Fig. 2). The facial part seems unnaturally high, which is likely the result of the

lateral depression (Table 1). The premaxillae are stout, and their nasal processes steeply rise posteriorly. The premaxillo-maxillary suture forms an angle of about 60° with the horizontal plane, and its rear-end meets the naso-maxillary suture before the level of P2. The facial surface of the maxillary is broad and weakly concave. The preorbital fossa is very shallow, lacking a clear margin. On the right side of the skull, two round infraorbital foramina appear in a common fossa separated by a thin lamella above P3/P4 (Fig. 2B). The lacrimal bone is small and triangular with an acute angle pointing anteriorly (length: 48 mm, maximum width: 34 mm). The orbit is highly situated, and its anterior rim is slightly posterior to the M3. The zygomatic arch originates above the anterior border of the M3. The facial crest is faintly shown.

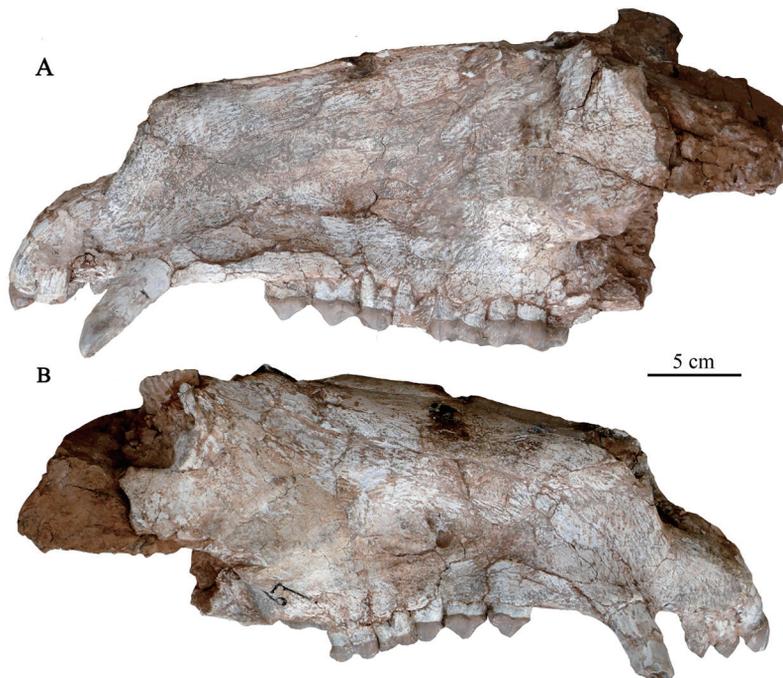


Fig. 2 Cranium of *Kubanochoerus parvus* sp. nov. (HMV 1985) from the Linxia Basin
A. left view; B. right view

Ventral view The incisors are arranged in a wide and gentle arc (Fig. 3A). The I1s are implanted nearly transversely, and the I2–I3 form an angle of about 45° with the I1s. There is no niche in front of the upper canine. The palate is slightly broadened at the level of the upper canine alveoli. The palatine fissures are comparably long, extending from the level of the anterior of the I3s to the anterior of the upper canines, and slightly converge anteriorly. The median palatine suture forms a weak crest. The posterior part of the palate is broken off, but what remains still extends the M3 length far behind the tooth rows. The anterior part of the zygomatic arch does not markedly expand laterally, which forms an angle of about 30° with the axis of the skull.

Dorsal view The nasal bones are long and narrow, and their dorsal surfaces are convex in transversal direction (Fig. 3B). There is a sagittal groove along the nasal suture, which is

Table 1 Measurements and comparison of cranium of *Kubanochoerus parvus* sp. nov. (HMV 1985) from the Linxia Basin, and some other kubanochoere species (mm)

	<i>K. parvus</i> sp. nov. HMV 1985	<i>K. gigas</i>		<i>K. massai</i> Gebel Zelten (Arambourg, 1963)
		IVPP V 8501 Koujiacun (Qiu et al., 1988)	N 33 Belometchetskia (Gabunia, 1960)	
Premaxillae–M3	287.9	402	385	300
Premaxillae–posterior border of palate	>330	490	451	312
Width of palate at C	~80			
Width of palate at P1	53	69	69.6	42
Width of palate at M3	43	59.5	73.9	42
Width of cranium at P2	73	90	92	60
Width of cranium at M3	~166	215	~292	174
Height of cranium at P2	103	96.7		81
Height of cranium at M1	122.1	~120		117
Height of cranium at M3	139			
P1–M3		237	235	205
P1–P4		121	120.5	102
P2–P4	67.9	85.3	90	70.5
M1–M3	91.2	119	112	102
I3–C diastema	21.5	30	30	~12
P1–P2 diastema	21	15.5	21.5	~9

slender and weakens posteriorly. The tips of the nasal bones are slightly broken, reaching beyond the upper canines. The posterior part of the nasal bones is broken off, so the naso-frontal suture cannot be observed. The premaxillae are fused at the anterior part, with a sagittal-groove on the dorsal surface, which widens and deepens posteriorly. The upper canine alveoli are large and bulging labially. The dorsal surface of the canine alveoli, triangular in shape, is smooth and slopes down slightly.

Dentition The I1 crown is mesio-distally enlarged; though heavily worn, it is still notably longer than the crowns of the I2 and I3 (Fig. 3A; Table 2). A longitudinal groove is developed at the mesial 2/5 part on the labial side, which separates the crown into two parts. The distal portion of the labial surface is broken, so whether or not there is another groove present is unknown. A small facet is present on the mesial side of the crown, indicating a contact point with its counterpart. The labial surface is smooth and strongly convex, and there is no labial cingulum. The lingual surface is flat, and the lingual cingulum forms a narrow platform. The crown is worn essentially apical, and the wear facet narrows at the distal part. The root, cross section of which conforms to that of the crown, is strong, but smaller and more rounded. The I2 is about 1/3 the size of the I1. It leans posteriorly against the linguo-distal part of the I1, and forms an angle of about 45° with the I1. The transverse section of the I2 crown is a narrow diamond. The labial surface of the I2 is only slightly convex, with a shallow depression at the mesial part. The labial cingulum is thin and only developed at the mesial end. The root is strong and rounded in transverse section. There is a small diastema between the roots of the I1 and I2. The I3 is similar to the I2, but smaller. The lingual cingulum is strong. There is a short I2–I3 diastema (ca. 4–5 mm), and a long I3–C diastema (Table 1).

Table 2 Measurements of the upper incisors and canine of *Kubanochoerus parvus* sp. nov. (HMV 1985) from the Linxia Basin (mm)

	I1 (DMD×DLL)	I2 (DMD×DLL)	I3 (DMD×DLL)	C (L×W)
Right	33.8×19.1	20.1×12.2	16×8.8	23.8×22.2

Abbreviations: DLL. labial-linguo diameter in incisors; DMD. meso-distal diameter in incisors; L. length; W. width.

The upper canine (Figs. 2–3; Table 2) is moderately robust. Its crown is nearly straight, projecting mainly antero-laterally, and only slightly inferior, which forms an angle of about 45° with the palate. It is compressed dorsoventrally, so the cross section is oval in shape. There is a longitudinal groove developing on the dorsal side of the canine, which extends to the middle-upper part of the canine. The enamel layer cannot be observed. There are two worn facets on the canine, the larger one at the middle-to-upper part of the ventral surface, and the smaller one at the tip of the posterior surface. There is a long C–P1 diastema (14.6 mm).

The upper cheek teeth (Fig. 4; Table 3) are arranged in a straight line. The P1–P2 diastema is long, making the premolar row relatively longer than the molar row. The molars are simple, brachyodont and bunodont. The enamel of the molar is thick.

The P1 only preserved the alveolus, which is situated slightly labially to the P2–M3 row and forms an angle of about 15° with the P2–M3. Judged from the alveolus, the P1 should be notably smaller than the P2. The root of the P1 is bifid and inclines posteriorly. There is a long P1–P2 diastema. The P2 is triangular from the occlusal view. The preparacrista and postparacrista are both well developed, forming an angle of about 30° with the tooth row; and the postparacrista is longer than the preparacrista. There is a weak crest at the antero-labial corner of the paracone. The talon of the P2 expands lingually, so the posterior width of the P2 is larger than the anterior width. The main cusplet of the talon is large, connected with the postparacrista by two small protuberances of irregular form. The lingual cingulum is high and thick, and the posterior cingulum is relatively low. The labial cingulum is only developed anteriorly and posteriorly, connecting with the anterior and posterior cingula. The P3 is similar to the P2 but larger. The P3 talon has a large main cusplet fused with the lingual and the posterior cingula. The lingual cingulum is as strong as in the P2, and the labial cingulum is uncontinuous. There is a worn facet at the anterior part of the paracone, so the preparacrista lies on the same plane with the antero-labial crest. The P4s seems *in situ* but is rotated 180°, which may represent a case of maleruption. The crown of the P4 is round in occlusal view. The paracone and the metacone are well separated. The protocone forms a wide crest due to wear, and there is no groove on either the labial or the lingual surface of the labial crest, so the presence of a hypocone is unknown. There is one small accessory cusplet present in the sagittal valley, which is fused with the main cusps and the anterior cingulum at the base. The anterior and the posterior cingula are thick and continuous, the lingual cingulum is thick but discontinuous in the middle, and there is no labial cingulum.

The first lobe of the M1 is narrower than the second lobe. The four main cusps are completely worn; therefore, no detailed morphology can be observed. There is a large protostyle. The M2 crown is rectangular in occlusal view, with its being width slightly greater

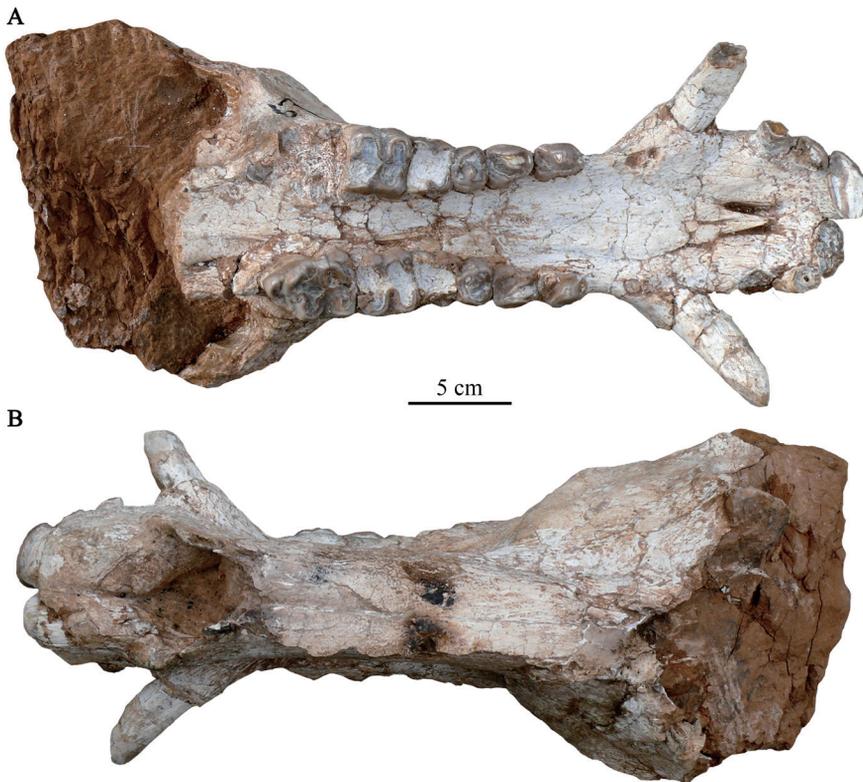


Fig. 3 Cranium of *Kubanochoerus parvus* sp. nov. (HVM 1985) from the Linxia Basin
A. ventral view; B. dorsal view

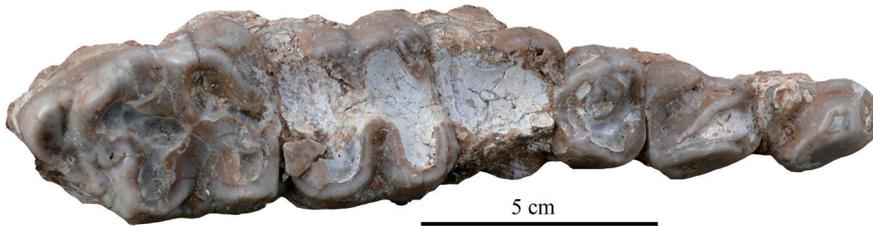


Fig. 4 Left upper tooth row with the P2–M3 of *Kubanochoerus parvus* sp. nov. (HVM 1985)
from the Linxia Basin, occlusal view

Table 3 Measurements of the upper cheek teeth of *Kubanochoerus parvus* sp. nov. (HVM 1985)
from the Linxia Basin (mm)

	P2 (L×W)	P3 (L×W)	P4 (L×W)	M1 (L×W)	M2 (L×W)	M3 (L×W)
Left	24.6×17.3	24.7×21.4	19.7×21.6	20.6×–	29×31.8	42.9×33
Right	25×18.2	25×21.7	20.3×21.8	21.5×26.4	28.5×31.5	

Abbreviations: L. length; W. width.

than the length. The main cusps are simple, inflated, and slightly elongated labiolingually on the worn surface. The protostyle is notable. The labial valley is deeply U-shaped. The anterior and median accessory cusps cannot be observed on the worn surface. The anterior cingulum is weak and continuous, the posterior cingulum is moderately developed, the labial cingulum

only exists at the labial valley, and the lingual cingulum is absent. The main cusps of the M3 are similar as in the M2. The anterior accessory cusp is small and round, connected with the protocone when worn. The median accessory cusp is large and inflated, connected with the hypocone and the metacone when worn. The M3 talon is small, mainly formed by a round hypoconule that connects with the hypocone, and a small and simple cusplet that originates from the posterior cingulum and connects with the hypocone by one small cusplet and with the metacone by the serrated postero-labial cingula. There is also a serrated cingulum-like ridge connecting the hypocone and the metacone at the base. The anterior cingulum is moderately developed and continuous, with a strong protostyle. The labial cingulum is only serrated at the labial valley, and the lingual cingulum is absent.

4 Comparative discussion

The new specimen from the Maida locality in the Linxia Basin was previously recognized as *Listriodon mongoliensis* according to its relatively small size (Deng, 2009). The new specimen is approximately the same size as *Kubanochoerus massai* (Fig. 5), and is larger than any known *Listriodon* and *Bunolistriodon*. The I1 of the new specimen is bilobate, differing from the usually multilobate I1 of *Listriodon* and *Bunolistriodon*. The I index of I1 is 177 in the new specimen, which is within the range of *K. massai*, and smaller than many Early to early Middle Miocene forms of *Bunolistriodon* and *Listriodon*. The M3 of the new specimen is relatively simple and bunodont, differing from the fully lophodont teeth of *Listriodon* and the sub-bunodont to lophodont teeth of progressive *Bunolistriodon*. All these differences suggest a closer relationship to the large bunodont kubanochoere than to *Listriodon* or *Bunolistriodon*. Therefore, the new specimen undoubtedly belongs to the kubanochoere group.

In the known species of kubanochoeres, *K. khinzikebirus*, *K. mancharensis* and *Megalochoerus* are giant forms. *Kubanochoerus khinzikebirus* is about 150% the size of the new specimen, *K. mancharensis* is even larger, and *Megalochoerus* is the largest, thus, the new specimen cannot be attributed to either of them. *Kubanochoerus marymunnguae* only preserved the P2 and M3 of the upper dentition; its P2 is larger than the P2 of the new specimen and proportionally longer, and its M3 is notably wider than the M3 of the new specimen; so, the new specimen cannot be *K. marymunnguae* either.

The new specimen resembles *Kubanochoerus massai* in the relatively small body size and wide cheek teeth (Fig. 5), but differs in the following characters, *K. massai* in bracket: 1) premaxillae meet anteriorly in the mesial plane, with a sagittal-groove moderately developed on the dorsal surface (a notable V-shaped gap presents anteriorly between premaxillae); 2) the I1s more mesio-distally enlarged (Fig. 6), and meets the counterpart at both the crown and the root (less mesio-distally enlarged, and neither the crown nor the root of the I1s meet each other); 3) the I1–I3 are arranged tightly, and the I1 is notably larger than the I2 (large I1–I2 diastema, and the I2 only moderately decreased); 4) labial longitudinal groove of the I1

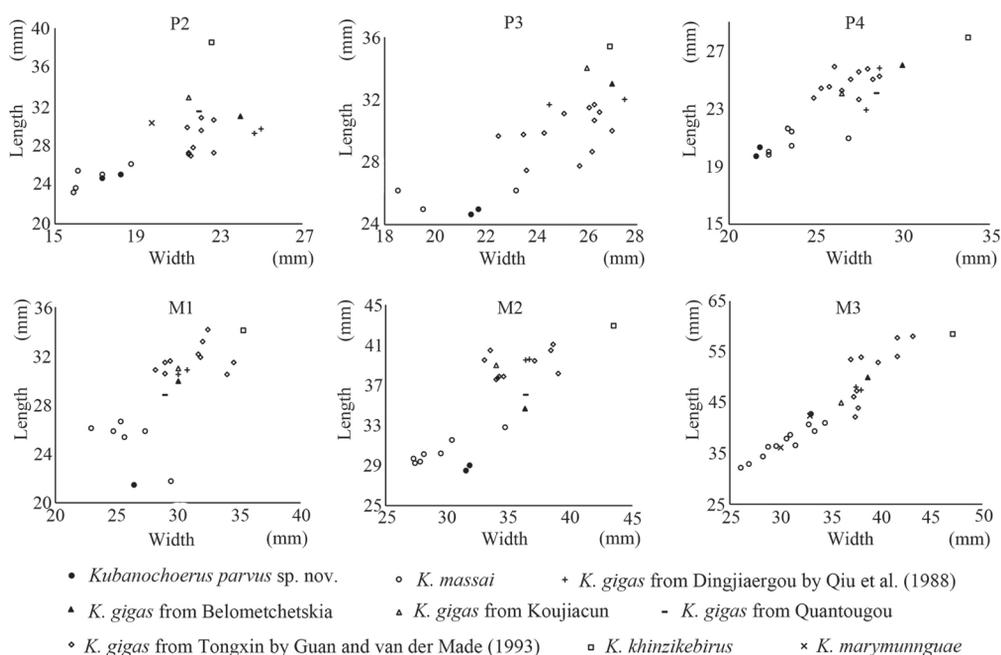


Fig. 5 Bivariate plot of the upper cheek teeth of *Kubanochoerus parvus* sp. nov. (HMV 1985) from the Linxia Basin, and other kubanochoeres

is shallow and at the mesial 2/5 part of the crown (relatively deep and closely situated in the middle); 5) upper canine relatively strong, alveolus expand evidently, worn facet developed at the base of the ventral surface and the tip of the posterior surface, no niche developed anterior to the upper canine (upper canine and its alveolus weak, worn facet only developed on the anterior surface, small niche exists anterior to the upper canine); 6) palate relatively wide, exceeding far behind the M3 (narrow, near the M3); 7) palatine fissures slender, located posteriorly (short, located anteriorly); 8) P1 small (relatively large); 9) the I3–C, C–P1 and P1–P2 diastemas have similar length, which are relatively large (the C–P1 diastema much longer than the I3–C and P1–P2 diastemas). Therefore, the new specimen cannot be attributed to *K. massai*.

On the other hand, the new specimen resembles the Eurasian *Kubanochoerus* in most of the characters above that differentiate it from *K. massai*, for instance: the fused premaxillae, the relatively large and wide I1, the tightly arranged I1–I3, the stronger upper canine, the large I3–C diastema, the slender palatine fissure, the more posteriorly extended palate, the relatively small P1, the large P1–P2 diastema, etc. The new specimen is smaller than all known Eurasian *Kubanochoerus* (Fig. 5). It is about 75%–80% of *K. gigas* (includes *K. lantienensis* and *K. robustus*). The facial region of the new specimen is relatively broad and the dorsal profile of its skull rises posteriorly, while in *K. gigas* the facial region is narrower and the dorsal profile of skull is nearly horizontal from the tip of the nasal bone to the base of the frontal appendix. The new specimen also differs from *K. gigas* in the following characters (the characters of the latter are in bracket): 1) weaker sagittal-groove on the dorsal surface of the premaxillae

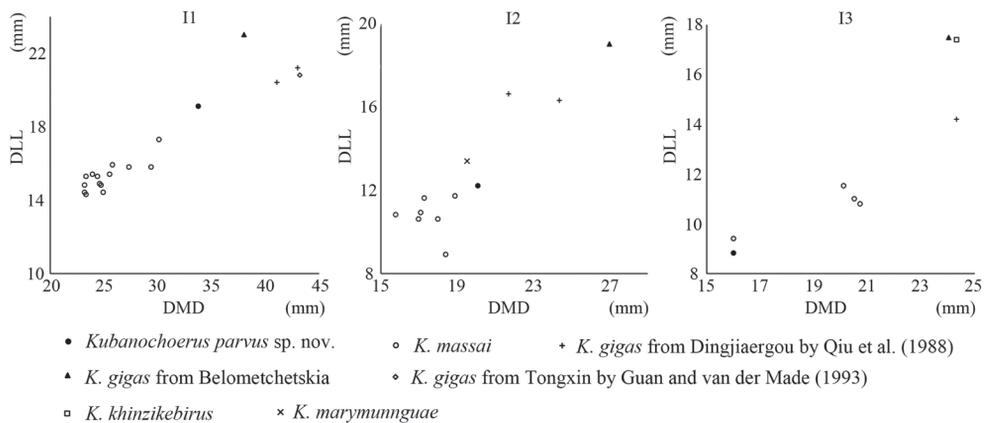


Fig. 6 Bivariate plot of the upper incisors of *Kubanochoerus parvus* sp. nov. (HMV 1985) from the Linxia Basin, and other kubanochoeres

(notable); 2) posterior ends of the palate fissures reach almost the anterior ends of the upper canine alveoli (only slightly posterior to the rear end of the I3); 3) upper canine and the canine alveolus are relatively small, upper canine relatively straight, projecting antero-laterally and only slightly inferior (relatively large, upper canine projects postero-laterally); 4) the paracone and metacone of the P4 are well-separated (partly separated). Therefore, the new specimen cannot be assigned to *K. gigas*.

Kubanochoerus minheensis from Liebao, Minhe County, Qinghai Province (Qiu et al., 1981), represents another relatively small kubanochoere form. Both the new specimen and *K. minheensis* have relatively small distal incisors ($I3[DMD]/I1[DMD] = 0.47, 0.58-0.63$, and $I3[DLL]/I1[DLL] = 0.46, 0.71-0.76$, respectively in the new specimen and *K. gigas*; $i3[DMD]/i2[DMD] = 0.85$ in *K. minheensis*, and $0.83-1.03$ in *K. gigas*) and long P1–P2/p1–p2 diastemas. *Kubanochoerus minheensis* bears a more reduced p1, larger hypoconid of the lower premolars, weakly separated metaconid and protoconid of the p4, strong preprotocristid of the p4, a blunt ridge emerging lingually from the hypoconid of the p4, and strong furrows of the lower molar; which indicates a tendency to form a sub-lophodont pattern dentition. All these characters suggest a possible relatively more progressive status for *K. minheensis* than for the other *Kubanochoerus* forms. The new specimen also has some derived characters, like more mesio-distally enlarged central incisors, the P4 has well-separated paracone and metacone, and a relatively large M3 hypoconule. On the other hand, the new specimen is smaller than *K. minheensis*, about 90% the tooth dimension of the latter (the p1–m3 length, m1–m3 length, and m2 length of *K. minheensis* is about 89.9%, 88.7%, and 81.9% of *K. gigas*, and the P2–P4 length, M1–M3 length, and M2 length of the new specimen is about 79.6%, 76.6%, and 74.4% of *K. gigas*). The main cusps of the molars in the new specimen appear relatively rounded compared with those of *K. minheensis*. The new specimen has relatively wide molars, which have a similar proportion to those of *K. massai*, while *K. minheensis* has relatively narrow molars that more resemble those of *K. gigas*. Therefore, though both are relatively small in size

and bear some derived characters, the new specimen and *K. minheensis* may represent separate lineages of kubanochoeres.

Based on all the comparisons mentioned above, a new species, *Kubanochoerus parvus* sp. nov., is erected for the new specimen from the Maida Locality, Linxia Basin, which represents a relatively small but progressive kubanochoere, and the name “*parvus*” is selected for its relatively small size.

The classification of kubanochoeres, as we mentioned in the introduction, has been disputed ever since their discovery, and the main controversy revolves around whether or not they deserve a separate subfamily rank, and the validity of the reported taxa. As van der Made (1996) claimed, the Listriodontinae share unique central canine morphology, where the I1/i1 and i2 have wide and low crowns and the right and left I1s form a transverse ridge. Gabunia (1958) erected Kubanochoerinae for giant “horned” kubanochoeres, however, the similarity of kubanochoeres to bunodont listriodonts was noted by many researchers (Arambourg, 1963; Wilkinson, 1976; Cooke and Wilkinson, 1978; Qiu et al., 1988). Pickford (1986, 1988, 1993) also separated the Kubanochoerinae from Listriodontinae, but has not given diagnoses. Pickford (1988) has summarized the characters of both Listriodontinae and Kubanochoerinae, however, it seems that most of the characters were based on the observation of the African kubanochoeres. Pickford (1988) mentioned that the Listriodontinae have U-shaped posterior choanae which open up a long distance behind the M3, long canine-premolars diastema, reduced or lost p1; while the Kubanochoerinae were suggested to have V-shaped posterior choanae that open immediately behind the M3, premaxillae which do not meet anteriorly, short canine-premolars diastema, robust p1, and the I3 larger than I2. However, the U-shaped posterior choanae that open up a long distance behind the M3 is indeed a common character shared by the Eurasian kubanochoeres, the premaxillae have already fused in many Eurasian kubanochoeres, there are also long diastema in Eurasian kubanochoeres, the P1/p1 have been reduced or lost in many Eurasian kubanochoeres, and the I3 is smaller than the I2 in most specimens of Eurasian kubanochoeres. Moreover, there are also many other shared morphologies between the Listriodontinae and Kubanochoerinae mentioned in his summary, such as the enlarged snout, long diastema, absence of canine flanges, and outwards projected upper canines, etc. All these above-mentioned commonalities suggested a closer relationship of kubanochoeres to listriodonts than to other suids. The recent cladistic analyses also supported classifying kubanochoeres as a sister group of listriodonts within the subfamily Listriodontinae (Orliac, 2009, 2013; Orliac et al., 2010; Hou and Deng, 2014). Therefore, in this paper we also agree that kubanochoeres be viewed as a separate tribe within the Listriodontinae. The cladistic analyses were performed based on a revised systematic of the Listriodontinae that was partly consistent with the one proposed by van der Made (1996) where *Libycochoerus* was suggested to be a junior synonym of *Kubanochoerus*, and *K. robustus* and *K. lantienensis* be synonyms of *K. gigas*. Considering there are different opinions on the general and species level classifications of van der Made (1996) (Pickford and Morales, 2003; Harris and Liu, 2007), a

brief comparison and discussion on the classification and evolution of the known *kubanochoere* taxa follows.

Qiu et al. (1988) have listed several differences between *Kubanochoerus* and *Libycochoerus* when studying *K. lantienensis* from China, most of which were argued by Guan and van der Made (1993) to be either sexual or individual, or only differing at the species level. The most unique character raised by Qiu et al. (1988) was a frontal bony “horn” in the Eurasian *Kubanochoerus*. The holotype of *Lib. massai* is a female skull; Guan and van der Made (1993) have also mentioned a female individual from Dingjiaergou that lacks a frontal “horn”; all these factors make it difficult to determine whether the frontal “horn” is a diagnostic or dimorphism. The cranium of the new species was broken off posteriorly, so whether it bears a frontal “horn” or not is unknown; but a “hornless” individual, perhaps male judged from the relatively strong canine, was found from the Qinghai Province recently (in preparation), which proves that the frontal “horn” may not simply be a sexual dimorphism but a diagnostic in certain species like *K. gigas*, *K. lantienensis*, and *K. robustus*. The shape and position of the palate were other important pieces of evidence raised by Qiu et al. (1988) to separate the Eurasian and African *kubanochoeres*. The posterior border of the palate is U-shaped and extends far behind the M3 in the Eurasian *Kubanochoerus*, and V-shaped and near to the M3 in the African *Libycochoerus*. Guan and van der Made (1993) and van der Made (1996) claimed that the palatine shape was variable in age and sex based on their statistical analysis within the large sample of *Sus scrofa vittatus*. Though the palatine position difference between *Kubanochoerus* and *Libycochoerus* was greater than those within the *S. s. vittatus* group, van der Made (1996) believed it was not beyond the interspecies variation between *S. s. vittatus* and *S. barbatus*. Based on our observation, the palatine extension possibly developed parallelly in different branches of the Listriodontinae, as the posteriorly expanded palate can also be found in *Lopholistriodon kidogosana* and *Listriodon*. The known Eurasian *Kubanochoerus* all have a more posteriorly extended palate than observed in *Lib. massai*, which may suggest a relatively more progressive status of the former compared to the latter. Similar to the palate, the premaxillae of *Lib. massai* and the Eurasian *Kubanochoerus* also indicate an evolutionary sequence: the premaxillae of *Lib. massai* are separated by a V-shaped gap at the anterior end, and the I1s do not meet; while in *K. gigas*, the premaxillae are fused, only a conspicuous sagittal-groove is developed on the dorsal side of the premaxillae, and the I1s meet at the crown; and in the new species, the premaxillae are fused, the sagittal-groove on the dorsal side is weaker than in *K. gigas*, and the I1s meet at both the crown and the root. Moreover, the more mesio-distally enlarged central incisors, the more reduced or lost first premolars, the elongated P1–P2/p1–p2 diastema, and the relatively short premolar row also suggest a more derived status for the Eurasian *Kubanochoerus* than *Lib. massai*. The materials of *Libycochoerus* were suggested to have relatively wide cheek teeth compared to those of the Eurasian *Kubanochoerus* (Qiu et al., 1988; van der Made, 1996). The new species, however, has similar dental proportions to those of *Lib. massai*, which are wider than in other

Eurasian *Kubanochoerus*. On the other hand, the cranial morphology of the new species more closely resembles that of the Eurasian *Kubanochoerus* than that of *Libycochoerus* in its more posteriorly exceeding palate, fused premaxillary, enlarged central incisors, and elongated P1-P2 diastema, etc. Considering all the characters above, we agree with Guan and van der Made (1993) that there are no generic differences between the Eurasian and African kubanochoeres, and *Libycochoerus* is a junior synonym of *Kubanochoerus*. The Eurasian *Kubanochoerus* are suggested to represent more derived kubanochoere forms than *K. massai* from Africa.

The Eurasian *Kubanochoerus* fossils that bear a frontal appendix (frontal “horn”) have been attributed to two subspecies of *K. gigas* by Guan and van der Made (1993): *Kubanochoerus gigas gigas* consisting of the holotypes of *K. gigas*, *K. robustus*, and *K. lantienensis*, and *K. g. lii* consisting of fossils found from Dingjiaergou, Tongxin, by BMNH. The *K. lantienensis* skull from Dingjiaergou, described by Qiu et al. (1988), was placed to *K. g. gigas* with the need for further inquiry (Guan and van der Made, 1993). According to Guan and van der Made (1993), *K. g. lii* was progressive due to its more meso-distally enlarged central incisors, smaller premolars and larger last molars. Based on our comparison, the lower central incisors of *K. g. lii* do have larger absolute and relative length ($i3[DMD]/i1 [DMD] = 0.66-0.73$ of *K. g. lii*, and 1.20 of *K. lantienensis* from Dingjiaergou; I index of $i1 = 103-108$ in *K. g. lii*, and 74 in *K. lantienensis* from Dingjiaergou); however, the upper central incisors of *K. g. lii* have similar size and proportions to *K. lantienensis* from Dingjiaergou, and are more labiolingually compressed than the I1 of *K. robustus* (Fig. 6; $I3[DMD]/I1[DMD] = 0.62$ of *K. g. lii*, 0.58 of *K. lantienensis* from Dingjiaergou, 0.63 of *K. robustus*; I index of I1 = 208 in *K. g. lii*, 201–203 in *K. lantienensis* from Dingjiaergou, and 165 in *K. robustus*). The first premolars of both *K. g. lii* and *K. lantienensis* from Dingjiaergou, though relatively small, are still present; while *K. robustus* has a strong P1 but lost its p1; and *K. gigas* lost its P1. The M3/m3 of *K. lantienensis* from Dingjiaergou and *K. robustus* are similar to the mean value of the M3 of *K. g. lii*; the holotype of *K. gigas* and *K. lantienensis* has smaller last molars, but are still within the variation of *K. g. lii*. Given these results, we concur with Guan and van der Made (1993) that *K. robustus* and *K. lantienensis* are synonyms of *K. gigas*, but we do not believe there is sufficient evidence to separate *K. g. lii* from *K. g. gigas*.

The age of the type locality of *K. massai* is approximately equivalent to MN4 (van der Made, 1992; van der Made and Hussain, 1992). *Kubanochoerus khinzikebirus*, which is contemporary to *K. massai* (MN 4, van der Made, 1992), was suggested to represent a separated lineage due to its significantly larger size and wider cheek teeth (Guan and van der Made, 1993). Later, van der Made (1996) erected *K. marymunnguae* and *K. mancharensis*, and suggested a size increase, *K. marymunnguae* (MN 4e) - *K. khinzikebirus* (MN 4) - *K. mancharensis* (MN 4–6). *K. gigas* is known from Belometchetskia (15Ma by Steininger, 1999; late MN5 by Qiu et al., 2013), Dingjiaergou (late MN5 by Qiu et al., 2013), Halamagai (late MN 5 by Qiu et al., 2013), Quantougou (early MN 6 by Qiu et al., 2013), Koujiacun (late MN7/8 by Qiu et al., 2013), and the Hujialiang Formation of the Linxia Basin (7/8

by Qiu et al., 2013; Deng et al., 2013). The morphology of *K. gigas*, as we have discussed above, is notably different from *K. massai*, suggesting this species represents a separate lineage. The skull and dental morphology of *K. gigas* indicate a more progressive status than *K. massai*. Guan and van der Made suggested a lineage *K. g. gigas* - *K. g. lii* based on their study. Our study, however, suggests that specimens of *K. g. lii* and *K. g. gigas* share complex morphologies and cannot be separated at the subspecies level. Moreover, *K. gigas* from Belometchetskia and Quantougou, which were attributed to *K. g. gigas* and suggested to be relatively primitive by Guan and van der Made (1993), appear to be more derived than those from Dingjiaergou or Koujiacun in the absence of the P1/p1 and the larger talon/talonid of the third molars. *Kubanochoerus minheensis* from Lierbao resembles *K. massai* in its relatively small body size, but differs from the latter by displaying narrower cheek teeth and the sub-lophodont tendency of the cheek teeth. There is no paleomagnetic data of the locality that yielded *K. minheensis*, so the age of *K. minheensis* is unknown. Qiu et al. (2013) speculated the fossils from Lierbao to be a mixed fauna and suggested *K. minheensis* was more primitive than those found in the Dingjiaergou fauna. However, the current study indicates that *K. minheensis* might be a relatively derived form based on its more reduced third incisors and first premolars, long p1-p2 diastema, and tendency to form a sub-lophodont tooth pattern. The new species from Maida also preserves a relatively small body size and wide cheek teeth that resemble those of *K. massai*; its cranium and dentition show some more progressive morphology than both *K. massai* and *K. gigas*; the age of the Maida locality is also relatively young, approximately around the boundary of MN 7/8 and MN 9; therefore, the new species may represent the known youngest kubanochoere. The relatively wide cheek teeth of the new species resemble those from Africa. The P4 of *K. massai* usually has separated metacone and protocone, the metacone of the P4 in *K. gigas* is usually weakly or partially separated from the paracone, and the paracone and metacone of the P4 are well separated in the new species. Therefore, *K. gigas* may have derived from some early species before *K. massai*, and the new species may be derived from *K. massai* or earlier forms.

5 Conclusions

A new species, *Kubanochoerus parvus* sp. nov., is erected for the new specimen from the Linxia Basin, based on cranial and dental dimensions and morphology. Bearing many derived characters, the new species is suggested to perhaps represent the youngest known kubanochoeres. The genus *Libycochoerus* is proved to be junior synonym of *Kubanochoerus*, and the species *K. robustus* and *K. lantienensis* are proved to be junior synonyms of *K. gigas*. The validity of *K. g. gigas* and *K. g. lii* is denied, and *K. gigas* from Belometchetskia and Quantougou are suggested to be relatively more derived forms than those from Dingjiaergou and Koujiacun. The new species and *K. gigas* are suggested to represent separated lineages of the Eurasian kubanochoeres, *K. gigas* may have derived from more primitive forms that evolved earlier than *K. massai*, and the new species may be derived from *K. massai* or earlier

forms. *Kubanochoerus minheensis* is suggested to represent another separate lineage of kubanochoeres, which retains a relatively small body size, but has the tendency to develop a sub-lophodont dentition.

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甘肃临夏盆地库班猪属(猪科, 偶蹄目)一新种

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摘要: 描述了甘肃省临夏盆地麦大地点库班猪类化石的一件部分破损的头骨标本, 建立了库班猪属的一个新种——小库班猪(*Kubanochoerus parvus* sp. nov.)。新种个体较小, 与 *K. massai* 和 *K. minheensis* 类似; 颊齿较宽, 与 *K. massai* 类似; 其他进步的特征如增大的中央门齿、愈合的前颌骨、显著向后延伸的腭骨、长的 P1-P2/p1-p2 齿隙等则与 *K. gigas* 类似; 它代表了欧亚大陆库班猪的一个单独的支系。麦大地点的层位大致相当于虎家梁组的顶部或者柳树组的底部, 因此新种可能是目前已知时代最晚的库班猪化石。根据对已知库班猪类化石的对比, *Libycochoerus* 被认为是 *Kubanochoerus* 的同物异名, *K. robustus* 和 *K. lantienensis* 被认为是 *K. gigas* 的同物异名, 且没有足够的证据支持将 *K. gigas* 划分为两个亚种。*Kubanochoerus gigas* 可能演化自较 *K. massai* 更早的原始类型, 而新种可能演化自 *K. massai* 或者更原始的类型。*Kubanochoerus minheensis* 则代表了欧亚大陆库班猪的另外一个独立的支系, 该种保持了较小的体型, 但牙齿有亚脊型化的趋势。

关键词: 临夏盆地, 新近纪, 猪科, 利齿猪亚科, 库班猪属

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