

Fossil Suidae from Dingjiaergou Near Tongxin, China

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Abstract

The upper Lower Miocene locality of Dingjiaergou (Tongxin, Ningxia, China) has yielded two species of suids, *Bunolistriodon intermedius* and *Kubanochoerus gigas*, both belong to the Listriodontinae. *B. intermedius* helps us to date the locality. *K. gigas* is represented by a unique collection of 6 skulls and 5 mandibles or parts of mandibles. This material improves our understanding of the taxonomy and phylogeny of the genus.

Several species of *Bunolistriodon* lived during the early Miocene (up to MN 5), but only the *B. latidens* lineage is known to have lived on during the middle Miocene (MN 6) in Turkey and southeast Europe. The material from Dingjiaergou is referred to the Chinese species *B. intermedius*, which might be identical with later *B. lockharti* or might be a true intermediate between *Bunolistriodon* and *Listriodon*. Dingjiaergou probably belongs to the Lower Miocene (MN 5) and Inönü I, with *B. latidens*, to the Middle Miocene (lower part of MN 6).

The only skull of *Libycochoerus* known belonged to a female (which is indicated by the canines) and has two small protuberances above the orbits. All skulls of *Kubanochoerus* that are known, belonged to males and have the same small protuberances and in addition a large median ossicone on the frontals. The ossicone more likely is an example of sexual dimorphism than a character to separate two genera and *Libycochoerus* is a junior synonym of *Kubanochoerus*.

The holotypes of *K. gigas*, *K. robustus* and *K. lantienensis* resemble each other very much in morphology and the variation in size is less than in the sample from Dingjiaergou. Only the name *Kubanochoerus gigas* is retained. The population of Dingjiaergou is progressive in reducing the size of the premolars and increasing the size of the last molars, for this reason a new subspecies name is given, *K. gigas lüi* n. subsp.

Three lineages in *Kubanochoerus* are proposed: *Kubanochoerus* sp. — *K. massai* — *K. minheensis* (approximately MN 3/4 to MN 6, or even later), *K. khazikebirus* (approximately MN 3/4 — 6) and *K. gigas gigas* — *K. gigas lüi* (approximately MN 5 to MN 7/8).

Introduction

The first scientific recognition of fossils in Tongxin area was by the Sino—Soviet Paleontological Expedition in 1960 (some *Gomphotherium* sp. fossils were recorded). In 1979, the expedition team of the Beijing Natural History Museum (BNHM) did a large scale survey in northwestern China. From a drugstore they obtained some very well preserved molars and shovel-like incisors, which came from Tongxin. The team visited Tongxin and since then, collected over 15 times in Tongxin. The collection consists of many well preserved fossils, including complete skulls and skeletons and is stored in the BNHM.

Since the 1910's the farmers living near Tongxin supplement their income by excavating deep tunnels into the Miocene sediments in order to obtain fossils, which they then sell as medicinal "dragon bones". The specimens described in this paper, have been collected from one of these artificial "dragon bone" tunnels (Guan & Rice, 1990). In the tunnel, the Miocene sequence and the fossiliferous layer can easily be recognized so that we know the exact stratigraphic position of the fossils.

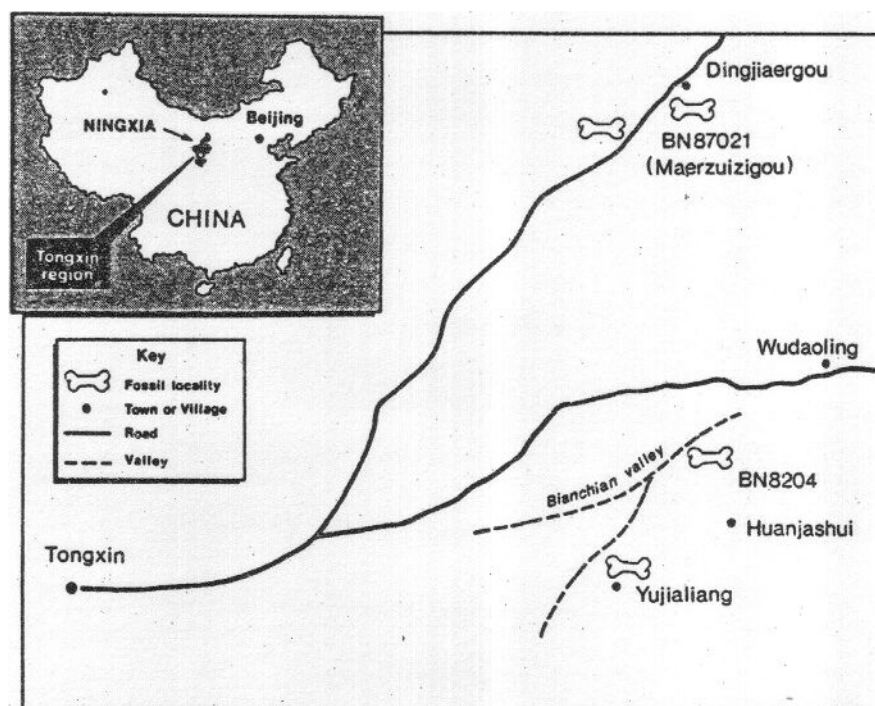


Figure 1 The location of Dingjiaergou and other localities in the Tongxin area and stratigraphical section of the locality. BN87021 is the Maerzuizigou where most Miocene Suids came from Farther south in Bianchian Valley is located BN8204 yielding some suid too (Following Harrison *et al* 1991)

The fossil locality (37°N, 104°E) is situated in the Ningxia geological basin (Guan, 1988), which geographically belongs to the eastern part of the northwestern Plateau of the P. R. China. The Miocene deposits are exposed in an area of about 350km².

In the north of the basin, the fossils are found in fluvio-lacustrine sediments consisting of medium to fine grained yellowish-grey sandstone, interbedded with gypsum sandstones and brownish clays and gravels. The texture of the sediments (accumulative curve of the grain size of the sand) indicate a fluvial facies. An analysis of the sediments of the locality which yielded the *Kubanochoerus* material, shows that there is abundant evidence that the remains of this suid were deposited in a delta facies (Guan 1988). There is evidence for flood events, in particular in the fossiliferous layers.

Near Dingjiaergou and Gujiazhuang, in the northern part of the basin, about 15km to the northeast of the county capital Tongxin town, more than ten fossiliferous sites (see Figure 1) have been reported. Most of these localities are distributed in two major fossiliferous horizons (levels two and three in table 1). In the south of the basin, near Bianchiagou and Wudaoling there are four fossiliferous horizons (levels one to four).

The fauna from level three in Tongxin is somewhat older than the rich fauna from Tung Gu-er (Nei Mong-gol) and correlates well with other faunas of the northwestern Chinese bioprovince, such as Lengshuigo in Shaanxi and Chetuoguo in Qinghai (Li et al. 1984; Guan 1988; Qiu 1990). The fauna is very similar to the fauna of one of the levels of Guanghe (nearby in Gansu Province) and sedimentation in both areas was apparently simultaneous (Table 1).

Several papers on the fauna and stratigraphy of the Tongxin area were published by a number of authors. An introduction to the Tongxin and the history of the collection of fossils is given by Guan & Rich (1990). Guan, Zhang & Ma (1981) gave an overview of localities in the area, their positions, lithologies and faunal lists. Guan (1988) gave a geological map, stratigraphical sections, sedimentology, faunal lists, biostratigraphy and a description of some new elephant and rhino species (*Amebelodon tobieni*, *Serbelodon zhongningensis* and *Caementodon tongxinensis*). Based on large mammals, Guan (1988) recognised three biostratigraphic levels prior to the entry of *Hipparion*.

The first paper was by Chen (1978), who reported the new elephant *Gomphotherium tongxinensis* from Gujiazhuang near Tongxin. Proboscidea remain the most frequently studied animals from the Tongxin area; Ye (1986, 1990), Guan (1988, in press) and Tobien, Chen & Li (1986).

Wu, Ye & Zhu (1991) described the lagomorph *Alloptox* from many different localities in the area and they recognised many different lithostratigraphical levels, also above the fauna with *Kubanochoerus*.

Qiu, Ye & Cao (1988) described a new species of hyena, *Percrocuta primordialis* from a level just below Maerzuizigou.

Remains of the gibbon-like ape *Pliopithecus* were described by Qiu & Guan (1986) and Delson, Guan & Harrison (1990), Harrison, Delson & Guan (1991) named the new species, *P. zhanxiangi*. Some of the specimens of this ape come from the same locality as the suids described here.

		P ₁		P ₂		P ₃		P ₄		M ₁		M ₂		M ₃										
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp							
—	l								18.7	—	±13.5	17.6	—	≤14.3	21.4	17.4	16.4	34.8	20.9	17.6	15.0			
—	r													32.7	20.7	21.9	39.4	27.2	27.6	99.5	31.3	28.6	23.3	
BPV-900	l	≥17.0	..	..	29.5	..	13.6	32.6	..	..	32.2	..	..	31.4	..	..	39.3	..	..	..	..	..	..	
	r	±15.6	..	..	—	—	—	32.6	..	..	32.1	..	..	—	..	..	40.0	..	..	55.6	..	..	..	
BPV-903	l	17.9	≥8.7	9.2	≥26.2	12.7	14.0	33.2	15.5	17.6	32.2	19.1	22.0	—	—	—	42.5	30.7	≥29.6	61.4	32.9	29.4	24.8	
	r	16.7	9.2	≥8.5	≥27.5	12.6	14.0	30.0	14.4	16.8	32.8	18.8	21.4	31.3	≥21.8	23.8	41.2	29.7	29.3	63.7	33.2	29.2	24.9	
BPV-905	l	18.9	9.6	7.4				30.9	15.6	17.8	32.0	19.3	21.2	29.9	22.1	23.7	37.8	27.9	28.9					
	r				27.5	13.0	14.1	31.8	15.3	18.1	32.4	19.4	20.5	—	—	—	41.0	28.6	29.0	64.1	32.2	29.7	24.3	
BPV-906	l													—	—	—	25.2	38.0	30.6	30.8	38.8	33.3	30.3	25.2
BPV-908	r													—	—	—	25.2	38.2	>29.7	31.0	58.5	33.5	29.9	24.1

		p ₁			p ₂			p ₃			p ₄			M ¹			M ²			M ³			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
—	l	21.0	10.1	12.4	27.2	15.8	>22.7	31.7	19.2	26.3	25.7	28.0	±34.2	29.5	≤32.4	38.2	39.0	37.5	57.8	41.6	37.6	22.7	
	r	>20.3	10.4	14.6	≥29.8	15.9	21.4	31.5	19.0	26.1	25.5	27.5	33.2	±30.7	32.0	41.1	38.6	38.1	58.2	43.1	38.2	25.4	
BPV-900	l	≥18.0	..	..	29.5	16.3	22.1	28.7	±19.5	26.2	25.2	28.7	28.1	..	..	40.1	..	..	..	..	..	..	
	r	—	—	—	..	..	..	29.7	16.5	22.5	25.3	..	±29.2	..	..	40.5	..	..	..	..	..	..	
BPV-901	l	18.9	9.1	11.0	—	—	—	29.9	19.0	24.3	24.4	25.3	31.5	28.0	28.9	37.9	34.6	34.3	47.4	37.6	36.9	24.8	
	r	19.4	10.6	9.2	—	—	—	29.8	19.2	23.5	23.7	24.9	31.6	27.0	29.3	37.9	34.2	33.5	46.2	37.1	37.5	20.6	
BPV-902	l				26.9	16.1	21.6	27.8	19.0	25.7	24.5	25.8	30.6	27.5	28.9	37.7	34.1	34.3	42.2	37.4	33.1	??	
	r	18.9	<10.3	10.7	27.2	16.9	21.5	27.5	20.7	23.6	24.2	26.5	30.9	26.9	28.1	37.6	34.0	33.9	44.0	37.7	33.9	??	
BPV-909	l	20.4	10.9	12.9	30.6	17.0	22.7	32.1	20.3	25.1	25.9	26.1	32.2	—	31.6	40.5	38.4	37.2	54.1	41.6	39.3	18.7	
	r	20.2	10.1	12.8	30.8	17.1	22.1	30.7	20.0	26.3	25.0	28.3	31.9	30.4	31.8	39.4	37.0	37.1	53.0	39.7	35.0	21.0	

Table 1 The species of Guanghe and Tonsxin (adapted from Guan, 1988). The numbers refer to different fossiliferous levels in the areas.

Table 2 Measurements of the cheek teeth of *Bunolistriodon intermedius* (the smaller specimens) and *Kubanochoerus gigas* (all other specimens) from Dingjiaergou. (Measurements in mm).

Qiu, Ye & Huo (1988) described a suid skull and referred it to *Kubanochoerus lantienensis*. This skull is stored in the IVPP and is not included in our sample. It was collected in Maerzuizigou, but not from the tunnel, where the BNHM collection comes from. Ye, Qiu & Zhang (1992) studied *Bunolistriodon* from various localities in the area.

The unique BNHM-collection of *Kubanochoerus* skulls and mandibles allows us to study variability in size and morphology and a revision of the genus is one of the objectives of this study. In the section on systematics a new subspecies of *Kubanochoerus gigas* will be defined. A mandible of *Bunolistriodon* helps us to date Dingjiaergou. However, in order to do that, some aspects of the evolution of *Bunolistriodon* have to be discussed. The stratigraphic distribution of the species of *Kubanochoerus* will be discussed.

Measurements and abbreviations

All measurements in this paper are in mm. The way of measuring is indicated in Figure 2.

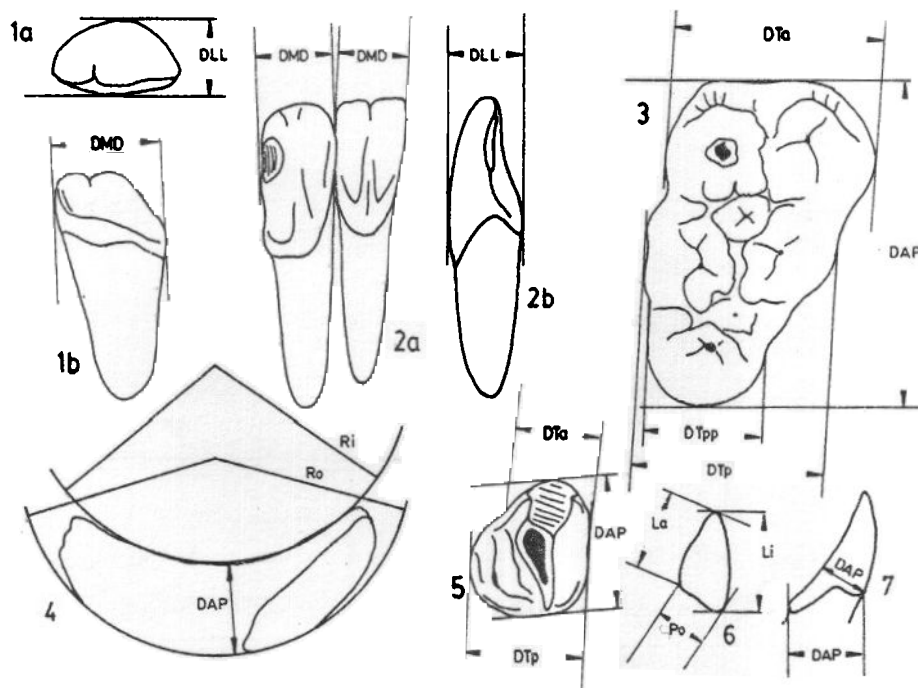


Figure 2 The way of measuring. Symbols are explained in the section on symbols measurements.

DAP Antero-posterior diameter in molars (3), premolars (5), upper canines (4) and lower female canines (7). In molars, DAP is measured perpendicular to the anterior edge. In the female canines DAP might be measured in two ways, giving different results.

DAP' The DAP of a tooth expressed as a percentage of the DAP' of the M₁. $DAP's Mx = (DAP Mx / DAP M1) \times 100\%$. For upper teeth, the M¹ is taken as a standard, for lower the M₁.

DLL Labio-lingual diameter in upper (1b) and lower incisors (2a).

DMD Meso-distal diameter in upper (1a) and lower incisors (2b).

DT Maximum transverse diameter (either DTa or DTp).

DT The DT of a tooth expressed as percentage of the DT of the M₁.

DTa Transverse diameter of the first lobe in molars (3) and premolars (5).

DTp Transverse diameter of the second lobe in molars (3) and premolars (5).

- DTpp Transverse diameter in the third lobe in M3 (3).
 Li Width of the lingual side of the male lower canine (6).
 La Width of the labial side in male lower canines (6).
 Po Width of the posterior side in male lower canines (6).
 R Radius of curvature in male canines (4); Ri inner radius, Ro outer radius.
 V' A measure of variability (Freudenthal & Cuenca, 1984).

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

The material described in this paper is stored in the Beijing Natural History Museum. In addition we studied material from many collections for comparison. These collections are listed here, as well as the abbreviation of their names, as used in this paper.

- BNHM Beijing Natural History Museum
 BSOHGM Bayerische Staatssammlung für Paläontologie und historische Geologie, München
 IM Indian Museum, Calcutta
 IPS Instituto de paleontologia de Sabadell
 IVAU Instituut voor Aardwetenschappen Utrecht, Faculteit Geologie en Geofysica, Rijksuniversiteit te Utrecht
 IVPP Institute for Vertebrate Paleontology and Paleoanthropology, Beijing
 KNM Kenya National Museums, Nairobi
 MNHN Museum national d'Histoire naturelle, Paris
 MTA Maden Tetkik ve Arama, Genel Müdürlüğü, Jeoloji Etüdleri, Ankara
 NSSW Naturwissenschaftliche Sammlungen der Stadt Winterthur
 PIMUZ Paläontologisches Institut und Museum der Universität, Zürich
 PDTFAU Paleontoloji, Dil ve Tarih Coğrafya Fakültesi, Ankara Üniversitesi
 PMNH Pakistan Natural History Museum, Islamabad
 RGM National Museum of Natural History, Leyden
 UCBL Université Claude Bernard, Lyon.
 ZMA Zoological Museum of Amsterdam

DESCRIPTION AND COMPARISON OF THE MATERIAL FROM DINGJIAERGOU

Bunolistriodon intermedius?

Material:

BPV—1670 A left mandible of a female with P₁—M₁ and the roots of P3 and a small canine; P₁ and M₁ are damaged. Plate 1, figure 1.

BPV—928a Left mandible with M₁ and M₂.

BPV—928b Right mandible with M₁ and M₂. identical in morphology and wear to BPV—928a and very likely of the same individual.

BPV—929 Right mandible with P₁—M₁.

BPV—930 Skull. Dorso-ventrally compressed. The snout anterior of P^3 is lacking, otherwise complete. Left P^3 , M^2 and M^3 , right P^4 — M^3 .

BPV—952 Posterior half of left M^3 .

Description and comparison

The molars are still bunodont, but the two cusps in each lobe seem to be on their way to form a lophe as in *Listriodon* (Plate I, figure 1). Such molars are called sublophodont (Fortelius & Bernor, 1990). The "degree of lophodonty" is intermediate between European *Bunolistriodon* and *Listriodon*. However most of the European *Bunolistriodon* is from MN 4 and presumably older (MN, Neogene Mammal Units, Mein, 1990). The size of the talon of the M^3 is variable, it is long in BPV—930 and short in BPV—952. Such a variability in the size of the talon is common in Listriodontinae.

The P_4 has two main cusps, which are equally large and which are placed in such a way that they also resemble a lophe. One of the specimens (BPV—929) has a large cusp on the anterior cingulum (paraconid?); this is not the case in the other specimen. The P_3 is a simple tooth with one main cusp from which a single ridge descends to the talonid.

Below the P_3 of BPV—929 the root of a canine can be seen. It is a small root with an oval or "8-shaped" section. As males have large root—less canines and a triangular section at the base, this individual must have been a female.

The cheek teeth from Dingjiaergou are not as elongate as those from Pasalar, they are larger than those of *Bunolistriodon latidens* from Veltheim and Inöndü I, and they are close in size to those of *B. lockharti* and *Bunolistriodon* sp. from the Calatayud area (Figure 1).

The Skull has a narrow brain case and a parietal crest. The frontals are wide and flat and there is no indication of thickening of the bone or any kind of ornamentation. The distance between the postorbital processes of the frontal is 127 mm. The zygomatic arc is a thin structure, although it may have stood out wide before the bone that is preserved in this area is smooth without any relieve. Although the posterior part of the palate is not well preserved, it seems likely, that the palate extended some distance behind the M^3 . The approximate width of the palate between P^4 and M^3 is 50 and 52 mm respectively.

Discussion

The only suid of this size with sublophodont molars is *Bunolistriodon*. Moreover the locality of Dingjiaergou is approximately of the age that this animal was very abundant. Species described that (probably) belong to *Bunolistriodon* are:

B. lockharti (Pomel, 1848) from the Sables de l'Orleanais, France;

B. latidens (Biedermann, 1873) from Veltheim, Switzerland;

B. affinis (Pilgrim, 1908) from Khumbi, Bugti Hills, Pakistan;

B. guptai (Pilgrim, 1926) from Bhagothoro, Sind, Pakistan;

B. jeanelli (Arambourg, 1933) from Moruorot, Kenya;
B. intermedius (Liu & Lee, 1963) from Koujiacun (= Kou Chia Tsun), Lantien Hsien, Shaanxi, China;
B. fategadensis (Prasad, 1967) from Fategad, Kutch, India;
B. robustus (Yan, 1979) from Erlanggang, Fangxian, Hubei, China and besides;
B. aff. latidens from Pasalar, Turkey ("Listriodon sp. nov." of Fortelius & Bernor, 1990);
Bunolistriodon sp., some European localities have a *Bunolistriodon* of a size that seems consistently intermediate between *B. lockharti* and *B. latidens*, for instance in the Calatayud area (Armantes I, Munébrega I, Munébrega II, Munébrega AB and Torralba I, Spain).

B. affinis and *B. guptai* are known from poor material and are of a size comparable to *B. latidens* and *B. jeanelli*. *B. jeanelli* has P4 without a well separated second main cusp and *B. fategadensis* has a very large m1, indicating a much greater body size than the other species. None of these species will be considered.

B. latidens is smaller than the fossil from Dingjiaergou and *B. lockharti* is of about the same size; *B. aff. latidens* has cheek teeth that are more elongate (Figure 3). The Calatayud material is slightly smaller and might represent a different species or belong to *B. lockharti* or *B. latidens*. This material (or at least most of it) differs in its lesser development of lophodonty.

B. intermedius is known only from the posterior lobe of an M₁ or M₂; the width is 16 mm. Ye Qiu & Zhang (1992) assigned material from various localities in Tongxin to *B. intermedius*. *B. robustus* was initially placed in *Listriodon*, but is not fully lophodont. All this material is similar to the material from Maerzuizigou in size and in degree of lophodonty, assuming that the holotype of *B. intermedius* is an M₁. *B. intermedius* has priority over *B. robustus*, but it seems preferable to use the species name that is attached to good type material, after all it is not known which tooth the holotype of *B. intermedius* represents.

The fact that the *Bunolistriodon* from Maerzuizigou is intermediate in its degree of development of the lophes between *Listriodon* and most other *Bunolistriodon* is interesting. European *Bunolistriodon* from MN 5 is rare and "intermediate" forms similar to the Chinese ones might turn up in Europe and indeed some of the European specimens do seem to be more advanced. At present it is not yet clear what is due to individual variability and what to evolution. It is possible that the Tongxin and Erlanggang material represents a later stage of evolution, that also is found in Europe. On the basis of the present data, it seems justified to maintain *B. intermedius* (or *B. robustus*) as a separate species.

The skull from Tongxin resembles the skull of *L. splendens* from Simorre (in the MNHN), but skulls of *Bunolistriodon* are rare and the value of the resemblance cannot yet be assessed. More material, such as the I1 which has three lobes in *B. lockharti* and two lobes in *Listriodon*, is needed to determine the place of the *Bunolistriodon* from Tongxin in the evolution of the Listriodontinae. However, the material from Maerzuizigou is certainly different from the *B. aff. latidens* which is found in Pasalar. This last observation is of importance for the interpretation of the age of Maerzuizigou.

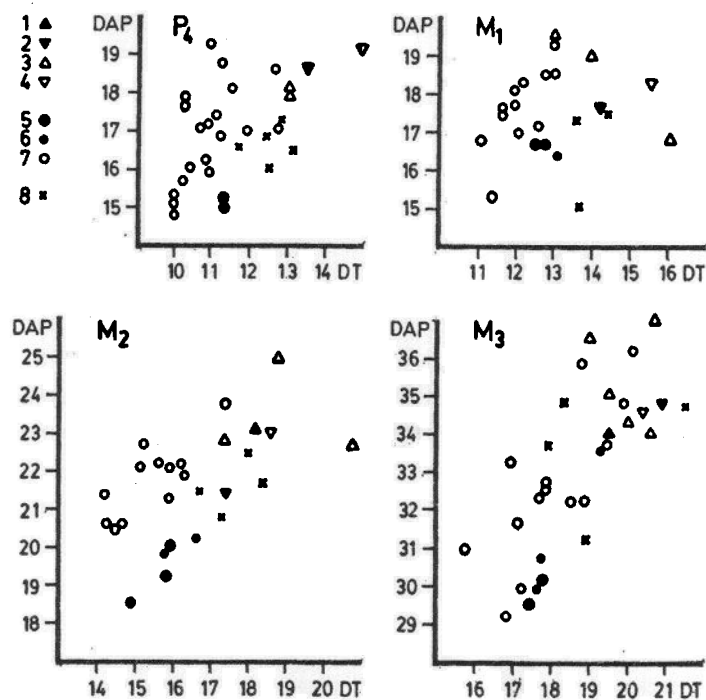


Figure 3 Scatter diagrams of the lower cheek teeth of *Bunolistriodon*. Legend, 1) the holotype of *Bunolistriodon lockharti* from the Sables de l'Orleanais (MNHN); 2) *Bunolistriodon intermedius* from Dingjiaergou (BNHM); 3) *Bunolistriodon lockharti* from Monteagudo (measurements from Astibia et al. , 1987); 4) *Bunolistriodon intermedius* from Erlanggang (data from Yan, 1979); 5) the holotype of *Bunolistriodon latidens* from Veltheim (NSSW); 6) *Bunolistriodon latidens* from Inönd I (MTA); 7) *Bunolistriodon* aff. *latidens* from Pasalar (PDTFAU & PIMUZ); 8) *Bunolistriodon* sp. from the Calatayud area (Armantes I, Munébrega I, Munébrega I , Munébrega II , Munébrega AB and Torralba I ; IVAU).

Kubanochoerus gigas lii n. subsp.

Material

- BPV Skull and mandibles of a male. All cheek teeth, upper incisors, upper canines and the left lower canine are preserved. The anterior part of the symphysis is lacking and the posterior part of the skull is deformed and broken off behind the orbits. Most of the teeth cannot be measured because of the sediment that holds together the skull and mandibles.
- BPV-901 Skull of a male with left C^m , P^1 and P^3-M^3 and right I^1 , C^m , P^1 and P^3-M^3 . The posterior part of the skull is broken off some 6 cm behind the M^3 . Because the area of the frontals is damaged, no trace of a frontal ossicone can be seen.
- BPV-902 Skull of a male with left P^3-M^3 and right C^m-M^3 . The frontals have still the basis of an ossicone. The anterior part of the premaxillaries is broken off.
- BPV-903 the alveoles of both C^m . The frontal ossicone is preserved.
- BPV-904 Left C^m .
- BPV-905 Mandible of a male (?) with left P_1, P_2-M_2 and the root of C_x and right C_x, P_2-M_2 and the alveoles of the P_1 . The right M_1 is not well formed, it was never used and it is below the occlusal plane of the other teeth, apparently a pathology.
- BPV-906 Right mandible with M_{1-3} and roots of the P_4 . The teeth are well worn.
- BPV-907 Right and left mandibles of a male with right and left I_1 and I_2-M_2 . The left M_1 is in a very bad state.
- BPV-908 Left mandible with M_{1-3} and posterior root of P_4 . The piece is identical to BPV-906 and may have belonged to the same individual.
- BPV-909 Skull of a male, with all left and right cheek teeth and alveoles of the incisors and canines. Part of the premaxillaries is broken off. A frontal ossicone is entirely preserved.
- BPV-910 Nearly complete skull of a young male. Frontals preserved; there is a beginning of a frontal ossicone. Only part of the occipital lacking. All teeth present, save for right and left I^2 .
- BPV-911 Left and right mandible with all teeth save for the left I_1 .
- BPV-921 Right C^m .
- BPV-922 Left MT II.
- BPV-923 Left calcaneus.
- BPV-924 Left astragalus.
- BPV-1671 Right mandible with M_{1-3} .

Description and comparison

The morphology of the molars and premolars is similar in the different species of *Kubanochoerus* and is described in several papers (Arambourg, 1961 & 1963; Gabunia, 1960; Liu & Lee, 1963; Pickford, 1986; Pearson, 1928; Pickford & Ertürk, 1979; Qiu, Li & Wang, 1981; Qiu, Ye & Huo, 1988; Wilkinson, 1976 & 1978). Here, only some elements will be highlighted.

The P_4 has one main cusp, but its shape is like that, that one might also say that there are three

cusps very close to each other. But then these cusps are placed behind each other, in most species of *Bunolistriodon* there are two cusps next to each other. The P_1 does not have two well separated roots, like the P^1 . Both P^1 have a low crown, indicating reduction. Measurements of the molars and premolars are given in Table 2.

The canines are large (Table 3). The male upper canines (C^m) have a curvature with a great radius, BPV-921 has $R_i=11$ cm and $R_o=15$ cm and BPV-904 has $R_i=10$ cm and $R_o=14$ cm. BPV-921 does not show an enamel band, but the tip is worn away completely. BPV-900, BPV-901, BPV-902 and BPV-904 have enamel bands at the ventral side, which may have a width of 30 mm. A canine from Gebel Zelten has enamel bands only in the upper 6 cm of the tooth. The lower canines are slightly scrofic in section, which means that the width of the labial side is less than the width of the posterior side (Table 3).

		I_1 DMD	DBL	I_2 DMD	DBL	I_3 DMD	DBL
BPV-907	l	20.8	19.3			+13.7	22.5
	r	19.8	19.3			14.6	+21.0
		I_1 DMD	DBL	I_2 DMD	DBL	I_3 DMD	DBL
BPV-900	l	39.9	..	..	..	24.8	..
	r	+39.0	..				
BPV-901	r	43.2	20.8				
		DAP		DT		Width of facet	
						ling	lab post
C_f or C_m BPV-905	r	19.3/25.3		14.2		19.4	18.1 12.7
C^m BPV-900	l	31.0		31.0			
	r	..		..			
BPV-901	l	29.3		31.6			
	r	30.5		31.2			
BPV-902	r	33.3		35.0			
BPV-904	l	35.6		37.2			
BPV-921	r	38.6		39.5			
C_m BPV-900	l					..	≥ 20.9 ≥ 17.4
BPV-907	l					30.6	22.7 28.1
	r					33.5	22.6 28.3

Table 3 Measurements of the incisors and canines of *Kubanochoerus gigas* from Dingjaergou. (Measurements in mm.)

One mandible (BPV-905) shows the tip of a robust canine. The section is verrucose (posterior

side narrower than labial side) and there is no enamel at the posterior side. It is not clear whether this is the canine of a male or of a female. Canines of females of *Listriodon* (unlike in most other suids) also lack enamel at the posterior side. The tooth does not project much from the jaw, indicating that the individual might be a female. But the enamel is very thick (unlike in female *Listriodon*) and disappears into the alveolus (whereas in females usually, the lower limit of the crown can be seen). This suggests that they are male canines, that did not fully erupt. Usually the canine is one of the first permanent teeth to erupt. The same mandible has also a pathologic right M_1 that did not erupt, the M_2 is still fresh, but the P_4 are worn. In the upper end of a canine, the width of the posterior side may decrease more (a "scrofic" canine may be "verrucose" near the tip). It is not clear whether this individual was a female or a male, but we are inclined to think it was a male.

Skull BPV—910 has canines that are just erupting. The canines must be male, because of the wide very rugose lingual bands of enamel, which is very unlike in female listriodontine canines. In this skull the M^3 just erupted and is not yet worn. Usually suid canines erupt at an early stage. The skull is in a slightly earlier stage of dental development than mandible BPV—905, since its P^4 have not yet fully erupted. Either skull and mandible belonged to two individuals with an abnormal tooth eruption patterns, or the canines erupt late in *Kubanochocerus*.

The incisors have the typical morphology of the Listriodontinae. The I_1 is wide, but within this subfamily it is among the narrowest (Figure 4 shows an increase in DMD/DLL ratio, *Listriodon* is not plotted, but it has wider incisors than *Bunolistriodon*, save for the MN 6 form). The I_1 has a very low crown and appears even narrower (less listriodontine like) than the first two incisors. The measurements are given in Table 3. The I^1 is as wide (DMD/DLL ratio) as those of the earlier *Bunolistriodon*. There are two well separated lobes. There are many I^1 from Gebel Zelten and they show that there is a great variability, both in size and in the degree of separation of the two lobes. The I^1 from Dingjiaergou are close in size to the I^1 from Belometchetskaya (holotype of *K. robustus*), Quantougou (= Chuan Tou Kou, paratype of *K. gigas*, width approximately 40 mm, taken from figure 2, Pearson 1928) and Koujiacun (holotype of *K. lantienensis*, width 39.5 mm, Liu & Lee, 1963). These teeth are much larger than those from Gebel Zelten (Figure 4). Compared to *K. massai* the incisors of these species are some 150 % as large, but those of Maerzuizigou even up to 170%.

The mandibles are deep. In BPV—905 the lower edge of the mandible is 77 mm below P_3 , 72 mm below P_4 and M_1 and 73 mm below M_2 . In the same specimen, the length of the symphysis is 145.5 mm, measured from the lingual edge of the alveolus of I_1 to the posterior side of the symphysis. The thickness, measured perpendicular is approximately 30.4 mm. In BPV—907 the length of the section of the symphysis is approximately 18 cm. The posterior end of the symphysis is below the P_3 . The area with the symphysis and incisors is wide in comparison with non-listriodontine suids. Lengths of diastemas and distances between teeth in the canine region are given in Table 4.

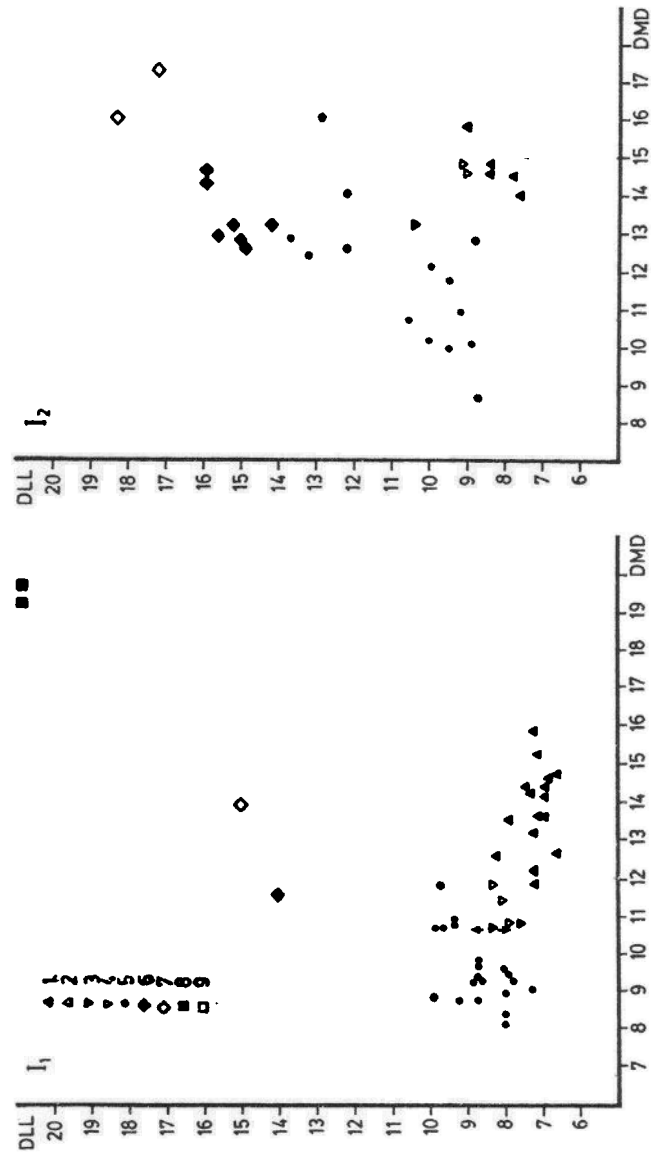


Figure 4 Scatter diagrams of the incisors of *Bunolistriodon* and *Kubanochoerus*. Legend: 1) *Bunolistriodon* aff. *latidens* from Pasalar (PDTF AU & PIMUZ); 2) *B. aff. latidens* from Candir (PIMUZ), I^1 only; 3) the holotype of *B. latidens* from Veltheim (NSSW), lower incisors only; 4) *B. latidens* from Inönü I (MTA); 5) West European *Bunolistriodon*; 6) *Kubanochoerus massaj* from Gebel Zelten (MNHNP); 7) the holotype of *K. minheensis* from Nanhawangou (IVPP), lower incisors only; 8) *K. gigas* from Dingjiaergou, I_1 and I^1 ; 9) the holotype of *K. robustus* (measurements from Gabunia, 1960), I^1 only.

All skulls belonged to males, as can be derived from the canines or alveoles for the canines. There is no cresta alveolaris above the canines. The most striking character are the frontal ossicones in the middle of the frontals. The ossicone is directed forward and slightly upward. In side view it is curved slightly so that it is more inclined at the basis and more horizontal at the tip. The ossicone of BPV—909 is 18 cm long and it has a width of 6 cm in the middle and 7.3 cm at the base. It has a transverse section that is oval, but in BPV—903 the ossicone is narrow, with a round section and the basis of the ossicone which is preserved in BPV—902 indicates also a narrow ossicone, as in the specimen from Maerzuizigou, Tongxin described by Qiu, Ye & Huo (1988). Qiu et al. described a "horn" that sits on top of a separate pedicle. The pedicle was supposed to be an outgrowth of the frontals and that the "horn" a separate bone that later in ontogeny would fuse to the frontals. In our specimens no suture separating a horn and a pedicle can be seen. Someone found the "horn" on the ground, whereas the skull was still in the rock. It is possible that the "horn" was sticking out of the rock and broke off, later on erosion obliterated the plane of the fracture. Above the orbits there are low conical protuberances as in the skull of a female of *K. massai* from Gebel Zelten, but they project more laterally. Skull BPV—910 has only the base of a pedicle. At the level of the orbits, there is a transverse elevation with a protuberance in the middle, the anterior surface is vertical and overturning and the posterior surface is gently inclined. The structure looks like a breaking wave. It is still a young individual, as appears from the M^3 and canines which have just erupted, and it is likely that the pedicle too was being formed at the time of the death of the animal. We assume, that the pedicle grew out of the frontals.

No lacrymal foramina were found at the place where they are present in modern suids. There is no deep preorbital fossa and the anterior part of the zygomatic arc forms a wide flat surface below the relatively small orbits. In our specimens, the lower border of the upper molars, but Qiu et al. (1988) state that is lower in their specimen. The parietal and occipital area slopes down backwards and the occipital crest (as inferred, since it is not preserved in any of our specimens) is in a low position. In other suids the occipital region tends to be the highest part of the skull. There is a sagittal crest, as in other Listriodontinae, but it is very pronounced. The occipital condyles and foramen magnum are large in comparison to the other elements at the back of the skull. In BPV—909 occipital surface is well preserved and the nuchal crest is seen to be narrow compared to the condyles (DAP 73 mm) and foramen magnum (DT 23 mm). In most specimens the posterior part of the palate is broken off, but the remains extend over 105 mm behind the last molars. The length of the skulls is about equal, some 70 cm. The lengths of the diastemas are indicated in Table 4.

The premaxillaries extend to above the P^3 . In the specimens that are not compressed, the premaxillaries at the level of the incisors are twice as wide as the palate between the cheek teeth. In BPV—910 the diastema between I^3 and I^2 is 20 mm. The distance of the I^3 to the posterior margin of the C^4 is 46 mm.

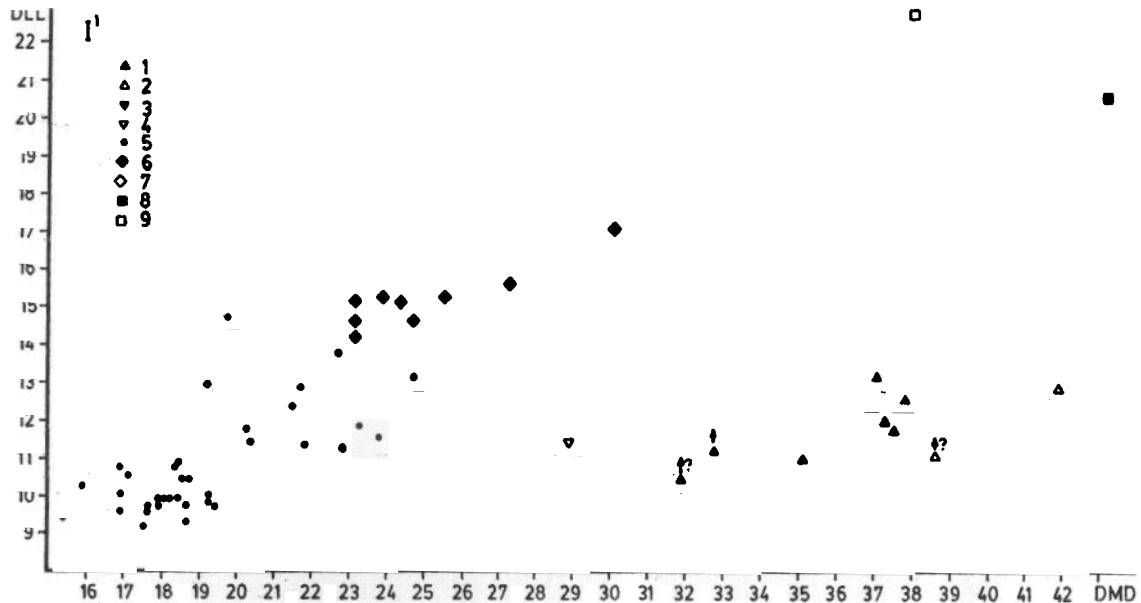
	r/l	P ₁ -P ₂	P ₁ -C _f	P ₂ -C _f	P ₃ -C _f	P ₃ -I ₃	P ₃ -I ₂
BPV-905	l	26.7	--	--	--	--	--
	r	33.5	5.8	57.4	85.8	796.2	7104.4
	r/l	p ¹ -p ²	p ¹ -c ^m	p ² -c ^m	p ³ -c ^x		
BPV-902	l	27.1/22.8	7.4	53.8	85.0		
	r	29.3/22.2	7.5	56.3	89.3		
BPV-909	l	18.6/21.0	--	44.6	79.7		
	r	21.0/24.7	+12.7	+51.2	+86.1		

Table 4 Distances between premolars and canines in *Kubanochoerus gigas* from Dingjiaergou. Measurements in mm, taken as indicated by Van der Made (1991).

	p ¹		p ²		p ³		p ⁴		M ¹		M ²		M ³		mean
	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	all
Gebel Zelten, mean	108	90	87	72	86	86	83	88	92	88	78	81	79	82	
Quantougou, holotype			109	--	99	--	96	106	92	99	92	100	--	93	98
Belometchetskaja, holotype	114	137	108	112	110	108	104	112	98	100	89	100	99	98	
Koujiacun, holotype	86	90	117	97	115	101	96	100	99	98	95	95	91	93	
Gebel Zelten, holotype	141	139	132	102	117	115	111	132	123	126	108	121	117	123	
Tingjiaergou small material as % of large	108	128	106	102	109	107	104	105	106	110	103	112	124	111	110
	P ₁		P ₂		P ₃		P ₄		M ₁		M ₂		M ₃		mean
	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	DAP	DT	all
Gebel Zelten, mean	94	86	89	88	85	78	80	80	87	86	77	81	76	78	85
Nanhawangou, holotype	74	88	92	102	86	88	101	88	88	87	81	87	82	88	82
Belometchetskaja, holotype			120	119	109	114	107	103	110	103	99	99	96	100	106
Koujiacun, holotype	94	104	125	115	107	108	97	99	106	98	95	98	81	89	100
Gebel Zelten, holotype			111	117	112	117	102	117					105	108	118

Table 5 Sizes of *Kubanochoerus* compared; mean of *K. massai* from Gebel Zelten, holotype of *K. minheensis* from Nanhawangou, holotype of *K. gigas* from Quantougou, holotype of *K. robustus* from Belometchetskaja, holotype of *K. lantienensis* from Koujiacun, holotype and paratypes of *K. khazikebirus* from Gebel Zelten. The mean of the sample from Dingjiaergou is taken as 100%. In the same way the large and the small teeth from Dingjiaergou are compared.

The astragalus differs from the *Listriodon* and *Bunolistriodon* astragalus in having a ridge bordering the sustentacular facet, substantiating the idea of Leinders (1976) that the flat sustentacular facet in *Listriodon* is a derived character (but see remarks Van der Made, in Gebel Zelten the character is variable. The Gebel Zelten astragali measure 62% of the Tongxin specimen, but are not so wide (length measurements 68%, width measurements 55% n = 2 or 3). Measurements for Tongxin, external length 82.2, internal length 71.5 and length in the middle 62.6 mm; proximal width 46.0, distal width 52.0 mm, width of the facet for the cuboid 19.9 mm and radius of the proximal roller 44.7 mm.



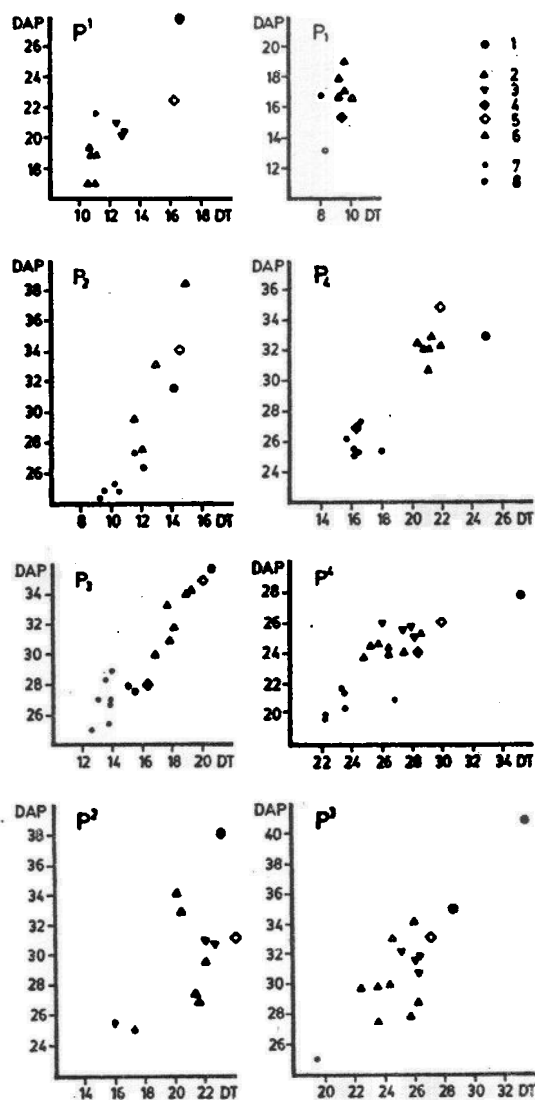


Figure 6 Scatter diagrams of the premolars of *Kubanochoerus*. Legend for figures 5 and 6, 1) *K. khinzikebirus* from Gebel Zelten (measurements from Wilkinson, 1976); 2) *K. gigas* from Dingjiaergou (BNHM); 3) upper cheek teeth of the three larger skulls from Dingjiaergou (BNHN); 4) *Kubanochoerus* from Quantougou, the holotype of *K. gigas* (upper cheek teeth) and *K. minheensis* (P_3 and P_4) (cast of holotype in the IVPP and measurements from figures, Pearson, 1928); 5) the holotype of *K. robustus*, Belometchetskaya (Measurements from Gabunia, 1960); 6) the holotype of *K. lantienensis* from Koujiacun (Liu & Lee, 1963); 7) *K. massai* from Gebel Zelten (MNHNP); 8) *K. minheensis* from Nanhawangou (only lower cheek teeth; IVPP).

The lower dentition is homogenous in size. In the upper dentition the teeth of three skulls are larger (Figures 5 & 6). Only the Length of the M^3 is much greater (Table 5). These teeth have the greatest coefficients of variation and V^3 . The M^3 in the larger specimens are also more elongate. Presumably the large specimens are just extremes and do not represent another taxon.

In Figures 5 and 6 there are three main clusters; the small species *K. massai* and *K. minheensis*, the large *K. khinzikebirus* and the intermediate *K. gigas*, *K. robustus*, *K. lantienensis* and the material from Dingjiaergou. A P_3 and P_4 of "*K. gigas*" from Quantougou have the size of *K. minheensis*, it is more likely that they belong to *K. minheensis*. This is not strange as two species of one genus may have been sympatric. If the averages of the sizes of the cheek teeth are compared and if the Tongxin sample is taken as 100% then *K. massai* is 85%, *K. minheensis* 82%, *K. khinzikebirus* 118% and the other species are about the same size (98, 100, 106%). Note that 85% of 117 is 100 and that the smaller species are about 15% smaller and *K. khinzikebirus* as much larger. Size differences in related sympatric species tend to be 15% (Vander Made, 1990 b).

Discussion

The species described that in our opinion have to be placed in *Kubanochoerus* are;

K. gigas (Pearson, 1928) from Quantougou (= Chuan Tou Kou), Ping Fan Hsien, Gansu, China;

K. robustus Gabunia, 1955 from Belometchetskaia, Stavropol region, Russia.

K. massai (Arambourg, 1961) from Gebel Zelten, Libya;

K. lantienensis (Liu & Lee, 1963) from Koujiacun (= Kou Chia Tsun), Lantien Hsien, Shaanxi, China;

K. khinzikebirus (Wilkinson, 1976) from Gebel Zelten, Libya;

K. minheensis (Qiu, Li & Wang, 1981) from Nanhawangou, Lierbao, Minhe county, China.

As we have seen, in the cheek teeth there are three sizes of *Kubanochoerus* and it is obvious that the animal from Dingjiaergou might be identical only with the intermediate species, *Kubanochoerus gigas*, *K. robustus* and *K. lantienensis*. If these species are compared to each other no important morphological differences can be found and the sizes are very similar to each other. The cheek teeth of the three holotypes usually show less variation in size than the populations from Dingjiaergou and Gebel Zelten. We consider them as synonyms, the valid name is *Kubanochoerus gigas*.

There are some differences however, between the fossils from Dingjiaergou and the three holotypes. The typical *K. gigas* tends to have longer premolar rows, specially the P_2 is longer and the M_3 tend to be relatively small (Figures 5 & 6). Later, this will be discussed in more detail. The differences are small and part of the Dingjiaergou population is still at the level of evolution of the three holotypes. As the Dingjiaergou population indicates a new trend in the evolution of the species it is useful to reflect this in taxonomy at the subspecies level (see section on systematics).

The skull from Tongxin, described by Qiu, Ye & Huo (1988) tends to have large premolars (P^3 ,

P₂, P³) and small M³. We do not know whether this skull is a "conservative member" of a population with the same stage of development as our sample or whether it is an average representative of an older population that was less advanced in reduction of premolars and enlargements of M³. Also its I¹ are on the small side.

EVOLUTION AND SYSTEMATICS OF *Kubanochoerus*

The most intriguing feature of *Kubanochoerus* is the ossicone on the frontals and it is used to define the genus. Several authors recognize another genus of gigantic suid, *Libycochoerus* Arambourg, 1961, with type species "*Libycochoerus*" *massai* and place the two genera in a separate subfamily Kubanochoerinae Gabunia, 1958 (for instance, Pickford, 1986). The only skull assigned to *Libycochoerus*, is the skull of a female of *Kubanochoerus massai* from Gebel Zelten (as inferred from the canines, which are different in females). This skull has two small protuberances, one above each orbit, but no ossicone in the middle of the head (Arambourg, 1963). The ossicone is used to separate the two genera, along with some characters of lesser importance like, size and implantation of the upper incisors, the shape of the posterior part of the palate, the state of reduction of the premolars, the shape of the nasals and the degree of elongation of cheek teeth. The size of the first premolar is used to place *Bunolistriodon jeanelli* in *Libycochoerus* (Pickford, 1986, 1988; Qiu et al. 1988).

The sample from Tongxin includes a female without ossicone and several males with ossicone. It is clear that the character is subject to sexual dimorphism and cannot be used to separate *Kubanochoerus* and *Libycochoerus*. The ossicone is a striking difference between the two types of skulls and draws the attention away from a peculiar common derived character, the protuberances above the orbits. There are no other suids that have such structures. In addition to having the same general skull shape, the same kind of dentition and a gigantic size the skulls share this unique character; these two "genera" cannot be related to another species than to each other.

The shape of the posterior part of the palate was used to separate *Kubanochoerus* and *Libycochoerus*. *Sus barbatus* has a palate that extends very much behind the last molars and *S. scrofa* has a palate that extends only very little posteriorly and there is a whole range of morphologies of the posterior border of the palate in the genus *Sus*. We agree that the character may be a useful one, however, for separating the species of *Kubanochoerus*, not for separating genera. In *K. massai* the palate extends approximately 1 cm behind the last molars, in *K. gigas* over 10 cm. A fragmentary skull of *K. minkeensis* in the BNHM also has the palate extending much behind the last molars.

The elongation of cheek teeth (increase of length compared to width) is a common trend in many different lines of Suoidea. *K. massai* has cheek teeth with a similar degree of elongation as *K. gigas* and *K. minkeensis*, but the cheek teeth of *K. khazikebirus* and *Kubanochoerus* sp. (Van der Made, 1992 b) from Baragol and West Stephanie are wider. The type species of *Libycochoerus* is *K. massai*, the elongation of cheek teeth cannot be used to separate *Kubanochoerus* and *Libycochoerus*.

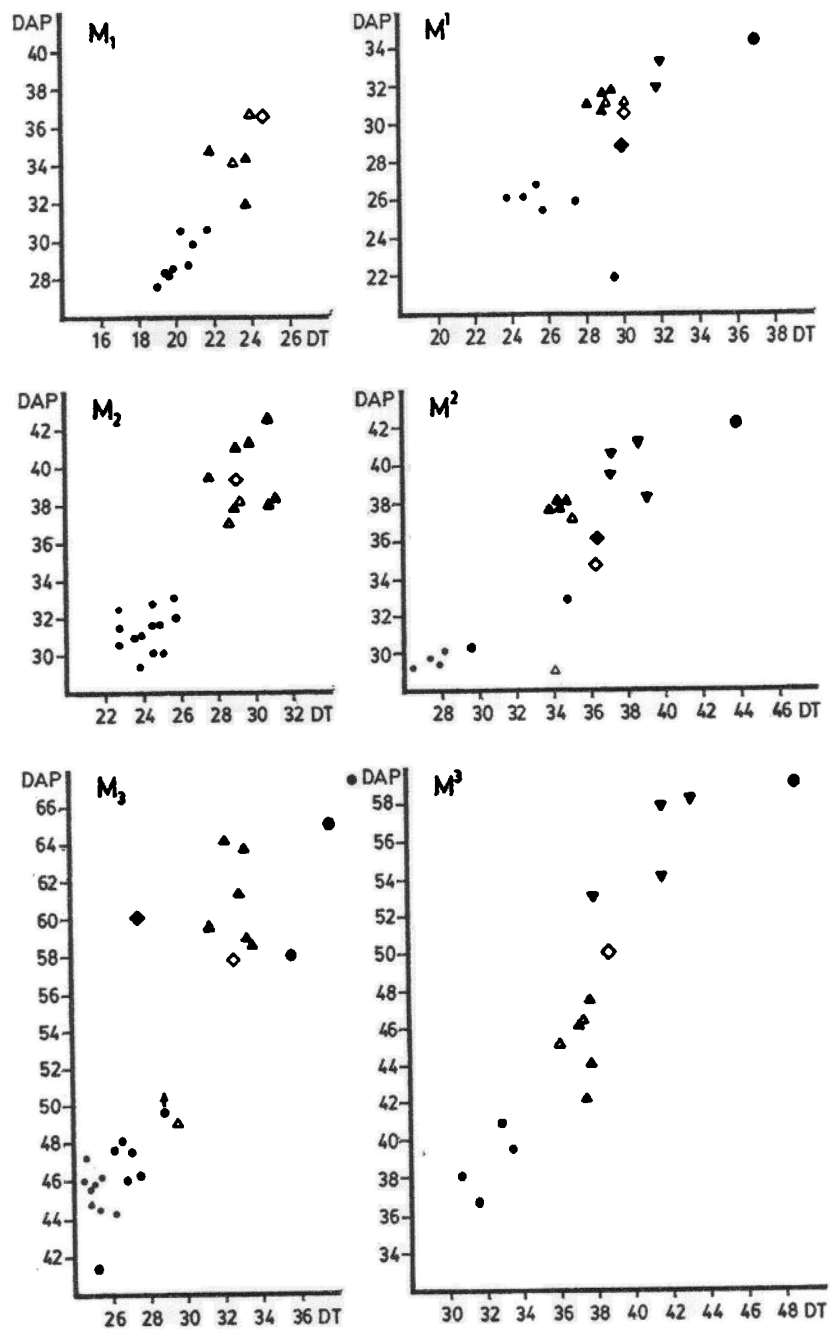


Figure 7 Scatter diagrams of the molars of *Kubanochoerus*. Legend as in figure 5.

The other characters used to separate the "genera", like size increase or reduction of cheek teeth, such as the P1, and the size of diastema, should be studied with care, preferentially larger amount of material should be compared and variability in a population should taken into account. The length of diastema is highly sexually bimodal (Van der Made, 1991).

In Suidae, most of the teeth are subject to size increase or reduction in one or another lineage, like reduction of the premolars and increase in relative size of the M3 in species with herbivorous specializations. This is another thing as that the entire animals changes in size. The size changes are relative size changes. Body weight of mammals is related to the size of the first molar (Legendre, 1986). To study the relative sizes of cheek teeth, the sizes of these teeth are expressed as percentages of the size of the first molar; DAP' and DT' (see section on abbreviations). Changes in the relative sizes of the premolars follow a certain pattern (Van der Made, 1989); first the premolars become longer, later they may be reduced and diastemas start to grow. Ideally such a sequence may be like this; first there are no diastemas and there is a size increase from P1 to P4, then premolar size start to increase, the size increases more in P3 than in P4 and even more in the P2, the longest premolar becomes the P3, in a later stage the P2. During this process the premolars become also more elongate, P2 becomes more elongate than P3 etc. and diastemas are formed. Reduction starts in the P1, later when the P1 is very small it starts to affect the second premolar, but the P3 and P4 are not affected at all at this stage, only if the P2 becomes very small the p3 will be affected etc. In a similar way the last molars change their sizes; the M3 becomes much larger and elongated, the M2 is less affected.

In Figure 7, DAP' — DT' scatter diagrams are given for the Listriodontinae. For comparison similar diagrams are given for a population of *Sus scrofa villatus* (the same sample was studied for sexual bimodality, Van der made, 1991). One thing should be borne in mind, the variability cannot be compared directly. The DAP' of the M3 of *S. scrofa* has values from 201 to 241%, a range of 40% and the DAP' of the listriodontinae varies between 142 and 213%, a range of 61%. Since in the first case all values are much higher, the range is relatively smaller, expressed in V'; 18 for the first case, 35 in the second case. From Figure 7, it is apparent that *B. jeanelli* had significantly larger P1 and P3 and that *Listriodon* reduced the size of its premolars up to the P3 and P2, but it is not apparent that all species that were placed in *Libycochoerus* have longer premolars than those that were placed in *Kubanochoerus* or other species of *Bunolistriodon*. From this point of view all *Kubanochoerus* and *Bunolistriodon* are intermediate between *B. jeanelli* and *Listriodon*. On the basis of these data, nothing more can be said than that *B. jeanelli* might be the ancestor of all other *Bunolistriodon*, *Kubanochoerus* and *Listriodon*. As long as there is no evidence of a real ossicone, or protuberances above the orbits in *B. jeanelli* we prefer to retain the genus in *Bunolistriodon*.

Comparing the variability in *Sus* and *Kubanochoerus* in Figure 8, it appears that size differences in P2 and P3 between the Dingjiaergou and other localities are very likely significant. It is also apparent that the variability in DAP' of the M3 is great ($V' = 24$) and there seem to be two clusters; in this population the last molar may have been in the act of evolving larger and longer. This is a common trend.

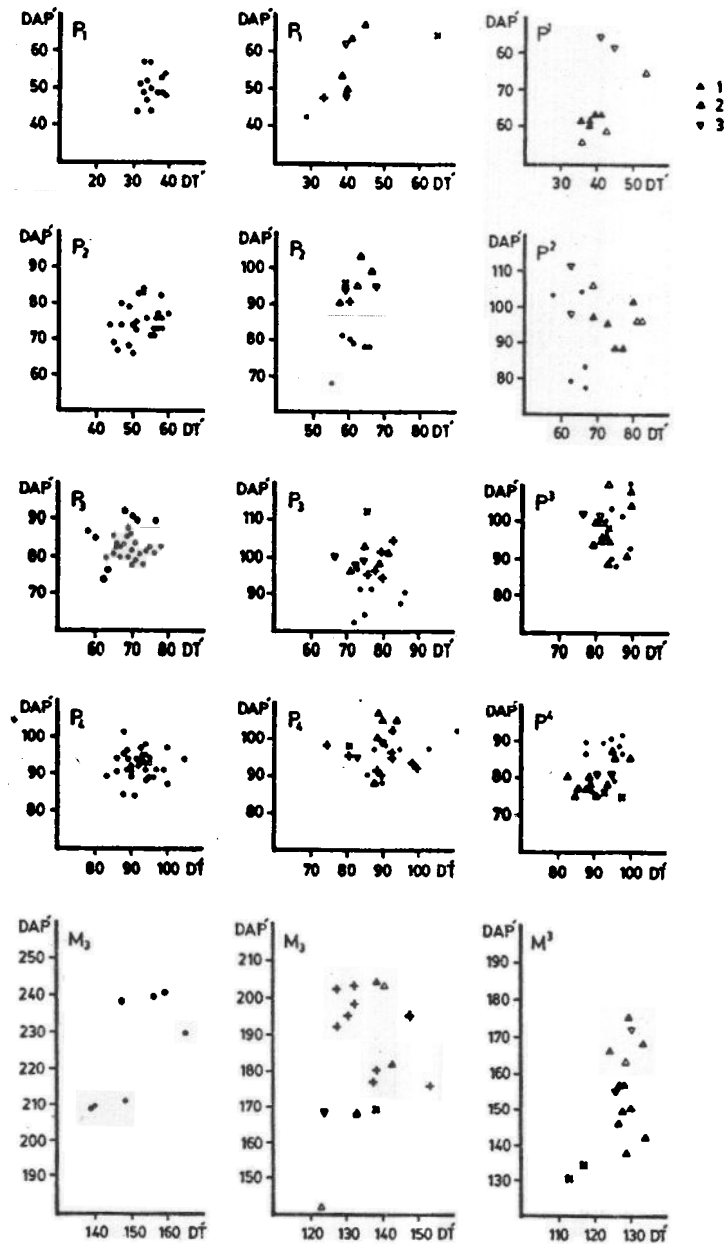


Figure 8 Scatter diagrams of DAP' and DT'. Left column, *Sus scrofa*; middle and right columns Listrionodontinae. Legend, 1) *Kubanochoerus gigas* from Dingjiaergou (BNHN); 2) *K. gigas* from other localities; 3) other species of *Kubanochoerus*; 4) *Bunolistriodon jeanelli*; 5) other species of *Bunolistriodon*; 6) *Listriodon* (not for M3); 7) male *Sus scrofa villatus* from Deli, Sumatra, Indonesia (ZMA); 8) female *Sus scrofa villatus* from Deli, Sumatra Indonesia (ZMA);

Increasing size and meso-distal diameter of "width" of the incisors. and in particular the I1, is a common tendency in Listriodontinae, see the section on stratigraphy of *Kubanochoerus*. It is possible to treat the subject in the same way as for the premolars, but we will not do that here and just note that incisors of *K. gigas* and *K. minkeensis* are relatively larger than those of *K. massai*. The incisors from Dingjiaergou are large, but not always larger than those of *K. gigas* from other localities. There still might be a trend in size increase within the species, although the individuals from Dingjiaergou might just be larger.

We lack important data on *K. khazikebirus*, and *Kubanochoerus* sp. from Kenya, which is characterized by wide cheek teeth. Nevertheless we try to give a tentative model of evolution of *kubanochoerus*. Initial *Kubanochoerus* had wide cheek teeth, and gave rise to the large *K. khazikebirus* and the smaller *Kubanochoerus* sp. from West Stephanie and Baragol. *K. khazikebirus* may have become even larger, as specimens from Maboko, Nyakach and Inōnd I are large in comparison to those from Gebel Zelten. *Kubanochoerus* sp. may have decreased the width of its cheek teeth and became *K. massai*. *K. massai* might have evolved into the equally large *K. minkeensis* by elongating the palate and increasing the size of the incisors. *K. gigas* might be an offshoot of that lineage, it shares the two characters with *K. minkeensis*, but is larger.

One observation may be of interest for finding the origins of the Listriodontinae. Recent Tayassuidae do not have foramina lacrymalia, the same seems to be the case in *Kubanochoerus*, *Listriodon* and *Lopholistriodon* (Van der Made, 1992 b). Recent Suidae have foramina lacrymalia. The same is the case with *Hyotherium*. In *Chleuastochoerus* (also placed in the hyotheriinae), foramina lacrymalia may lack, but usually are present (Stuenkel, personal communication). Listriodontinae are commonly derived from Hyotheriinae (For instance, Wilkinson, 1976 and Thenius, 1979). Also the genus *Kenyasus* is thought to be a primitive member of (what we call) the Listriodontinae (Pickford, 1986). *Kenyasus* seems to have foramina lacrymalia (Van der Made, 1992 a) and unless foramina lacrymalia disappeared in different lineages neither *Kenyasus* belongs to the Listriodontinae, nor did the Hyotheriinae evolve into the Listriodontinae.

Below, we give our view of the systematics of *Kubanochoerus*, including the new subspecies from Dingjiaergou.

Listriodontinae Lydekker, 1884

Emended diagnosis, Suidae with I1, I1 and I2 with wide and low crowns.

Type genus, *Listriodon* Von Meyer, 1846

Listriodon Von Meyer, 1846

Emended diagnosis, lophodont listriodontinae with high crowned C^m that curve outward and upward.

Type species, *Listriodon splendens* Von Meyer, 1846.

Bunolistriodon Arambourg, 1963

Emended diagnosis; Listriodontinae that are not (fully) lophodont and in which the males do not have an ossicone ("horn") in the middle of the frontal; the incisors tend to be moderately to very wide for Listriodontinae.

Type species; *Bunolistriodon lockharti* (Pomel, 1848).

Kubanochoerus Gabunia, 1955

Synonymy; *Kubanochoerinae* Gabunia, 1958

Libycochoerus Arambourg, 1961

Emended diagnosis; Large Listriodontinae in which the males have an ossicone ("horn") on the frontals.

Type species; *K. gigas* (Pearson, 1928) (originally *Kubanochoerus robustus* Gabunia, 1955, but this is a synonym of *K. gigas*).

Kubanochoerus gigas (Pearson, 1928)

Kubanochoerus gigas gigas (Pearson, 1928)

Synonymy;

1928 *Listriodon gigas* sp. nov. ; Pearson, pages 8—12 partially, Text-figures. 1, 2, 3, 4e, 5.

1960 *Kubanochoerus robustus* Gabunia, 1955; Gabunia, 87—97, plates I — V.

1963 *Listriodon lantienensis* sp. nov. ; Liu & Lee, pages 293—296 and 301—302, text-figures 2 & 3, plates I, II and N.

1963 *Listriodon gigas* Pearson; Liu & Lee, pages 292—293 and 300—301, plate I.

? 1963 ? *Listriodon* sp. ; Liu & Lee, 297—299 and 303; plate V, figures 2—8.

1973 *Kubanochoerus robustus* Gabunia; Gabunia, pages 76—94, figures 18, 19, 20, 22b; plate VI, figures 3—6; plate VI, figures 1—4.

? 1988 *Kubanochoerus lantienensis* (Liu et Lee, 1963); Qiu, Ye & Huo, pages 1—19, text-figures 1—5, plates I — III.

1989 *Kubanochoerus* sp. ; Ye, pages 37—38 and 50.

Emended diagnosis of *K. gigas*; *Kubanochoerus* of intermediate size (surface M_1 approximately 751 mm²), with relatively large incisors and the palate extending far behind the M^3 .

Lectotype; a left maxilla with P^3 — M^3 , figured by Pearson, 1928, text-figure 1; stored in Upsala.

Type locality and horizon; Quantougou (=Chuan Tou Kou), Ping Fan Hsien, Gansu, China, horizon unknown, probably lower Miocene, equivalent to MN 5.

Other localities; Belometchetskaia and Koujiacun. Ye (1989) cited *Kubanochoerus* sp. from Halamagai. It has the size of *K. gigas*. On the basis of the probable age of the locality (see section on stratigraphy) the piece is tentatively assigned to *K. gigas gigas*.

Kubanochoerus gigas lii subsp. nov.

Synonymy,

1988 *Kubanochoerus lantianensis*; Guan, pages 3, 15 and 20.

Diagnosis of *K. gigas lii* subsp. nov.: *Kubanochoerus gigas* with premolars that are reduced in size, M3 that are longer and I¹ that have a greater meso-distal diameter.

Derivation nominis; the subspecies is named in honor of Prof. Li Chuankui.

Holotype, BPV-909 the skull of a male, stored in the Beijing Natural History Museum.

Type locality and horizon; maerzuizigou near Dingjiaergou village, Tongxin county, Ningxia, China; Tongxin level 2, Lower Miocene, approximately MN 5.

Other localities; Qiu (1990) assigned an incisor from Tung-Gur to a large species of *Kubanochoerus* on the basis of size. We have observed that there seems to be an increase in the size of the incisors of *Kubanochoerus gigas*, it seems more likely that the incisor belongs to *K. gigas lii* than to *K. khazikebirus*, the only other large species, which however never was cited from China.

Kubanochoerus massai (Arambourg, 1961)

Synonymy,

1961 *Libycochoerus massai* nov. gen. nov. sp.; Arambourg, page 108, figure b.

1963 *Bunolistriodon massai* (Arambourg); Arambourg, pages 903 — 911, figures 1 — 3; text-text-plates 1 — II; plate X X IV.

1975 *Bunolistriodon massai* (Arambourg); Pickford & Wilkinson, pages 133-134.

1975 *Libycochoerus massai* Arambourg; Leinders, pages 199 — 203, figure 1 (no. 7).

1976 *Bunolistriodon massai* (Arambourg); Wilkinson, page 226 229, plate V, figures d-g.

1978 *Kubanochoerus massai* (Arambourg 1961); wilkinson, 446.

1986 *Libycochoerus massai* Arambourg; 1961; Pickford, pages 40 and 45 — 46, figures 47 — 49.

Emended diagnosis; small *Kubanochoerus* (cheek teeth approximately 85% linear size of *K. gigas*) with relatively small M3 and the palate not extending much behind the M³.

Holotype; 1961 — 5 — 8, a left mandible with P₂ — M₃, stored in the MNHN, figured by Arambourg (1961; figure b).

Type locality and horizon; Gebel Zelten, Libya, lower Miocene, approximately equivalent to MN 4.

Kubanochoerus minheensis (Qiu, Li & Wang, 1981)

Synonymy,

1928 *Listriodon gigas* sp. nov.; Pearson, page 11 partially, text—figures 4 a—d.

1981 *Bunolistriodon minheensis* sp. nov.; Qiu, Li & Wang, pages 164 — 166 and 172, plate I, 3—4.

Emended diagnosis; small *Kubanochoerus*, cheek teeth approximately 85% of those of *K. gigas*,

with elongated M3, enlarged incisors and with a palate that extends far behind the M¹.

Holotype, V6021, a mandible with all teeth except for the right I₂ and canine the left P₁, stored in the IVPP, figured by Qiu, Li & Wang (1981, plate I, 3).

Type locality and horizon, Nanhawangou, Lierbao, Minhe county, China, middle Miocene.

Other localities, Guanghe level 2 and Quantougou.

Material from Guanghe is assigned to the species mainly because of its size. The P₂ and P₄ from Quantougou (the paratypes of *K. gigas*) are close in size to *K. massai* and *K. minheensis*, the upper premolars however are larger than those from Dingjiaergou and we assume that the lower premolars belong to *K. minheensis* (or *K. massai*). The material from the latter localities might also represent *K. massai*, but the association with more advanced Listriodontinae, indicate that they are younger than Gebel Zelten and probably contemporaneous with *K. minheensis*. Pearson implicitly indicated a large maxilla as a holotype for *K. gigas*, so this observation does not bring about any taxonomical complications.

Kubanochoerus khazikebirus (Wilkinson, 1976)

Synonymy,

1975 *Bunolistriodon* sp. nov. A; Pickford & Wilkinson, pages 133 — 134.

1976 *Bunolistriodon khazikebirus* sp. nov.; Wilkinson, pages 230 — 236, plate VI, figures a—d.

1979 *Libychoerus khazikebirus* (Wilkinson, 1976); Pickford & Ertürk, page 145, figure 4.

1978 *Kubanochoerus khazikebirus* (Wilkinson 1976); Wilkinson, page 446.

1984 *Libychoerus khazikebirus* (Wilkinson) 1976; Pickford, pages 45 and 48, figures 49a, 49b, 50a, 50b?.

Emended diagnosis, large *Kubanochoerus*, cheek teeth approximately 117% the size of those of *K. gigas* and comparatively wide.

Holotype, Bu 6416 — 82 a — e, right P₂₋₄ and M₂₋₃; stored in the Bristol University Geology Department; figured by Wilkinson, plate 6, a.

Type locality and horizon, Gebel Zelten, Libya, lower Miocene, probably equivalent to MN 4.

Other localities, Material from Karungu, Nyakach, Maboko and probably Mfwangano was assigned to this species (Van der Made, 1992 b) as well as from Inöndü I (Pickford & Ertürk, 1979).

Kubanochoerus sp.

Synonymy,

1992 *Kubanochoerus* sp.; Van der Made, 1992 b & c, pages 91 and 97.

Characters, length of cheek teeth as in *K. massai*; cheek teeth comparatively wide; width of the cheek teeth is superior to cheek teeth of *K. massai*.

Localities, West Stephanie-Buluk and Baragol.

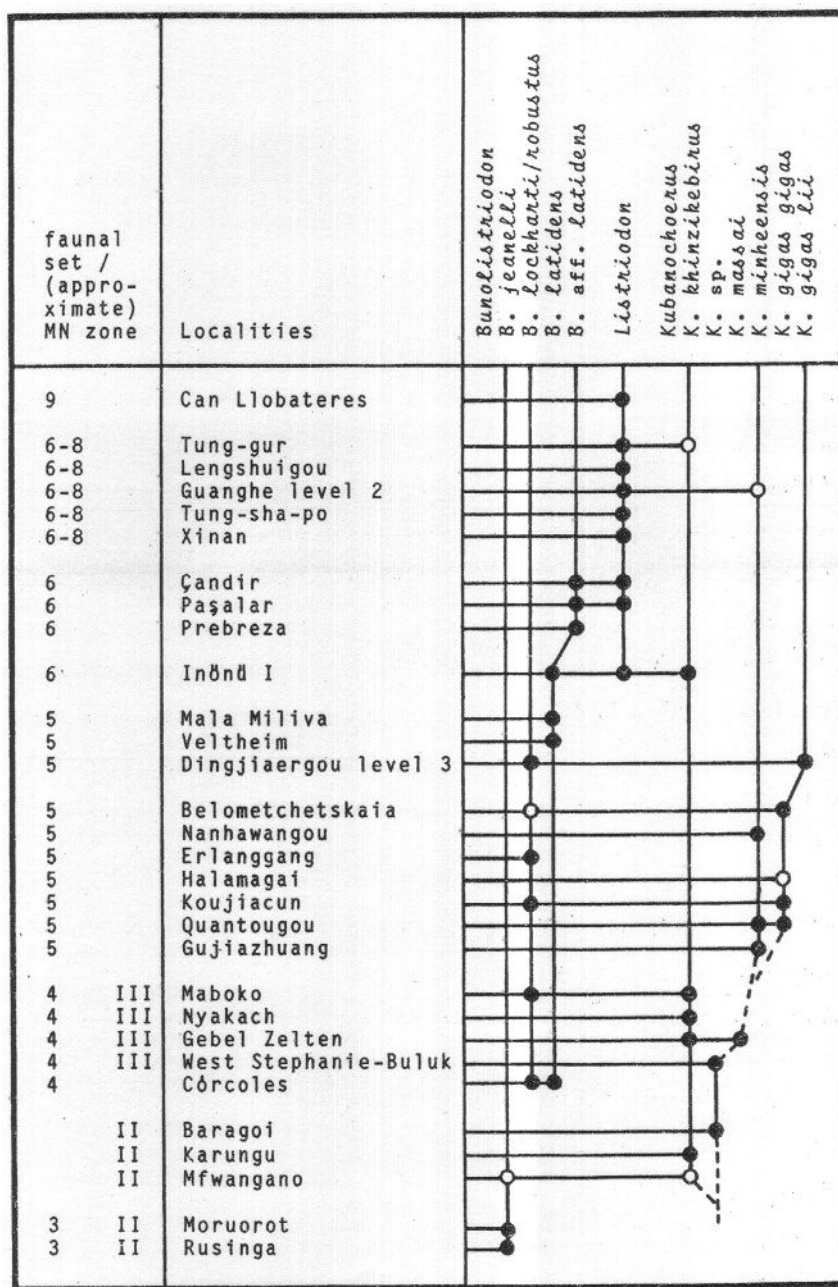


Figure 9 The stratigraphic ranges of *Kubanochoerus*, *Bunolistriodon* and *Listriodon* and stratigraphic position of the localities mentioned in the text. Stratigraphic position of localities according to Pickford (1981) for the Faunal Sets and Mein (1989) for the MN zones (Mein, 1989), Van der Made & Hussain (1992), Van der Made (1992 c) and this paper (see section on stratigraphy).

THE AGE OF MAERZUIZIGOU AND STRATIGRAPHY OF THE GENUS *Kubanochoerus*

Bunolistriodon is found in several localities with *Kubanochoerus* and gives information on the age of these localities. These localities are, apart from Maerzuizigou, also Koujiacun, Inöndü I and probably Belometchetskaya. Figure 8 will help the reader to keep track of the localities and their inferred stratigraphic positions.

In Europe and presumably in India *Bunolistriodon* was replaced abruptly by *Listriodon* (Van der Made, 1990 a). Since the genera were found together nowhere, it was widely assumed that one genus evolved into the other and many paleontologists have described what they thought were intermediate species or transitions in many different places, including Africa (Leinders, 1976 & 1977; Liu & Lee, 1963; Paraskevaidis, 1940; Wilkinson, 1976). Possibly none of these "transitions" are the real transition and for Africa it is not even certain that *Listriodon* ever occurred there (Van der Made, 1992 b). The last *Bunolistriodon* from Western Europe is from MN 5, in the Indian subcontinent from Kamlial equivalent beds and in Africa from Set III and might even be anterior to MN 5 (Van der Made, 1992 c). Figure 9 shows the age of the faunas with *Bunolistriodon* and *Kubanochoerus* in Euroasia

Pickford & Ertürk (1979) and Fortelius & Bernor (1990) described sympatric *Bunolistriodon* and *Listriodon* from Turkey (F. & B.'s *Listriodon* cf. *splendens* and *Listriodon* sp. nov.). Fortelius et al. (in press) assigned this *Bunolistriodon* and that of Mala Miliva and Prebreza to the lineage *Bunolistriodon latidens*-*Bunolistriodon* sp. nov., which is characterized by increasing incisor size. *B. latidens* has small cheek teeth (Figure 3), but wide incisors (I_1 and I_2 , Figure 4). In west and central Europe, earlier *Bunolistriodon* may be small, like *B. latidens* (Van der Made & Alférez, 1988), however, large incisors have not been found, in other localities than Veltheim. This suggests that the Turkish and southeast European *Bunolistriodon* is later (late MN 5 or MN 6). The trend of increase in hypsodonty in *Caprotragoides* (material in the IVAU and the material described by Köhler, 1987, which was stored in the IPS) indicates that Pasalar and Candir are probably older than Arroyo del Val. This implies that the survival of the *B. latidens* lineage in MN 6 was only during the earlier part of this unit.

The localities with *Bunolistriodon*, claimed to be MN 6 or younger either have a later stage of development of the *B. latidens* lineage, Inöndü I, Prebreza, Pasalar, Candir and possibly Chios or they have another species not belonging to this lineage, Belometchetskaya, Dingjiaergou, Erlanggang and Maboko. The sole piece described from Belometchetskaya (Gabunia, 1973) is an I^2 or I^3 . It is small, which makes it more likely to be *B. lockharti* or a similar form, than either *Listriodon* or *B. latidens*. Belometchetskaya has archaic elements such as a large anthracothere of the size that occurs in the lower Manchar Formation below the entry of *Listriodon*. More and more early bovids are found, so that the bovids need not be an argument for placing Belometchetskaya in a younger biozone. "*Oioceros*", *Anchitherium* and "*Listriodon*" were used to correlate Erlanggang with the Tung Gur Formation (Yan, 1979), but the suid is *Bunolistriodon* and seems to be similar but possibly slightly more lophodont than *B. lockharti*, *Anchitherium* entered much earlier (MN 3) and an "*Oioceros*" (*Hypsodontus*) is also

present in Belometchetskaya. Chen (1988) indicated that the "*Oioceros*" has still a temporal ridge, which is a primitive character, not known from any other bovid. The presence of *Hypsodontus* like bovids cannot be an indication for a late age. Maboko was placed in the Middle Miocene (Pickford, 1986), but the "*Listriodon*" from that locality belongs to *Bunolistriodon* close to *B. intermedius* in molar morphology and to *B. lockharti* in incisor proportions and the locality is likely to be older than the Middle Miocene (Van der Made, 1992 b, c). If these *Bunolistriodon* (or one of them) really are an intermediate from which *Listriodon* evolved, this certainly is an indication that these localities are earlier than MN 6, since *Listriodon* enters very early in that unit.

Unless there is strong evidence for the contrary, these localities, including Maerzuizigou, as well as the last occurrence of *Bunolistriodon* other than the *B. latidens* lineage may be placed in MN 5 or the lower Miocene.

K. massai is known from Gebel Zelten only. This locality is placed in Set III (Pickford, 1986) and may be as old as MN 4 (Van der Made & Hussain, 1992; Van der Made, 1992 c).

K. minkeensis is known from Nanhawangou, Quantougou and Guanghe level 2. Qiu (1990) believed Nanhawangou to be older than the Tongxin (that is Tongxin, level 3) fauna. Considering the evolutionary level of the species MN 5 or even late MN 4 might be good approximations. From Quantougou no other fauna is known than *Kubanochoerus* (Qiu, 1990), but considering that *K. gigas* from that locality is more primitive than from Tongxin level 3, and age of MN 5 or maybe late MN 4 is possible. In Guanghe level 2, *Listriodon* is found (Guan, 1988, in prep.).

Localities with *K. khazikebirus* include, Gebel Zelten, Karungu, Nyakach, Maboko, Inōnd I and probably Mfwangano and Tung-Gur. Karungu and Mfwangano are Set I and Nyakach, Maboko and Gebel Zelten Set III (Pickford, 1986) and most of these localities are believed to be MN 4 or older (Van der Made, 1992 c). Inōnd I is believed to belong to MN 6 (see discussion above) and Tung-Gur MN 7/8 (Qiu, 1990).

K. gigas is known from Maerzuizigou (Tongxin level 2), Belometchetskaya, Koujiacun, Quantougou and Halamagai. Tongxin level 2 seems best be correlated with late MN 5. On the level of evolution of *K. gigas* Belometchetskaya, Koujiacun and Quantougou are thought to be slightly older. Halamagai was assigned to MN 7/8 by Qiu (1990), or to MN 6—7 by Ye (1989). "*Eotragus*" *halamagaiensis* does not seem to be *Eotragus*, but a primitive member of the *Hypsodontus/Taurocerus* group. Because of its primitive horn cores it resembles *Eotragus*, which is also a primitive form. Its state of evolution suggests an earlier age than Oandir, Belometchetskaya and Mala Milliva, that is no say MN 5 or earlier (Van der Made, in preparation). *K. gigas gigas* may have occurred in the earlier part of MN 5 and maybe MN 4, *K. gigas* *lii* n. subsp. may have occurred in the upper part of MN 5, data on later occurrences are lacking.

ECOLOGY OF *Kubanochoerus*

The different species of *Kubanochoerus* have regular size differences of 15% (linear measurements

of the dentition). *K. gigas* is taken as 100%, *K. massai* is 85%, *K. minhoensis*, based on a single mandible has nearly the same value as *K. massai*, and *K. khinzikobirus* is 118% (Table 6). This is a common pattern in Suidea (Van der Made, 1990 b). A favorable habitat may support more than one species of a genus, but it seems that size differences are necessary to avoid competition. The estimated size differences for the species are (using the method of Legendre, 1986): *K. massai* and *K. minhoensis* 518 kg, *K. gigas* 823 kg and *K. khinzikobirus* 1345 kg.

	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
Tongxin mean	19.80	10.20	11.94	28.70	16.44	21.50	29.94	19.21	24.96	24.94	26.79	31.25	28.22	30.08	39.09	36.23	35.74	50.36	39.48	35.91	22.20
n	6	6	7	6	7	6	10	9	10	10	9	8	6	7	10	8	8	8	8	8	6
Gebel Zeiten mean	21.4	10.75	9.55	25.02	13.78	16.35	25.80	16.53	21.35	20.68	23.68	25.57	24.27	25.92	30.41	29.48	28.27	39.60	32.54	27.27	14.20
n	2	2	2	5	6	6	3	3	2	6	6	7	6	6	7	5	6	6	5	9	10

	P1			P2			P3			P4		M1			M2			M3				
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Tongxin mean	17.8	9.4	8.3	28.5	12.8	13.9	31.9	15.2	17.6	32.3	19.2	21.3	31.3	21.4	23.96	39.96	39.71	29.43	60.23	32.73	29.52	24.43
n	3	2	2	2	3	4	6	4	4	6	4	4	4	2	5	9	6	6	7	6	6	6
Gebel Zeiten mean	16.8	8.1	7.4	25.50	11.32	12.20	27.16	13.35	13.77	25.90	15.59	17.03	27.21	19.61	20.50	30.72	23.72	23.85	45.79	25.43	22.72	17.74
n	1	1	1	6	10	6	9	14	9	13	10	9	9	8	9	13	10	11	18	16	29	31

Table 6 Means and numbers of measurements (n) of the cheek teeth of *Kubanochoerus gigas* from Tongxin and *Kubanochoerus massai* from Gebel Zeiten.

Kubanochoerus as well as other Listriodontinae, do not have a deep fossa infraorbitalis. This indicates that the muscles for the rhinarium were not well developed. Rooting was probably not very important for these suids. This is in line with Leinders' interpretation (1977) of the incisor morphology. Listriodontinae probably browsed in a tapir-like way.

Figure 10 shows the geographic distribution of the localities with *Kubanochoerus*. It should be noted that the northernmost localities both in China, Turkey and southern Russia are just over 40° latitude. This may be the reason why the genus never entered western Europe; passing north of the Alps into western Europe may have been impossible, because it would have to go north nearly as far as 50° and enter a different climatical zone. The sediments in which the fossils have been found, contain large amounts of gypsum (Guan, 1988). Gypsum precipitation in the soil in significant quantities, nowadays occurs in arid regions, where the mean monthly potential evaporation exceeds the mean monthly precipitation (Watson, 1985). In MN 5 and 6 extensive peats were formed in Austria (the

localities of Münzenberg-Leoben, Seegraben-Leoben, Göriach etc. are in peats). It might be possible that *Kubanochoerus* preferred a somewhat dryer or hotter climate (which does not automatically mean that it ate abrasive food) and for that reason did not pass into Europe.

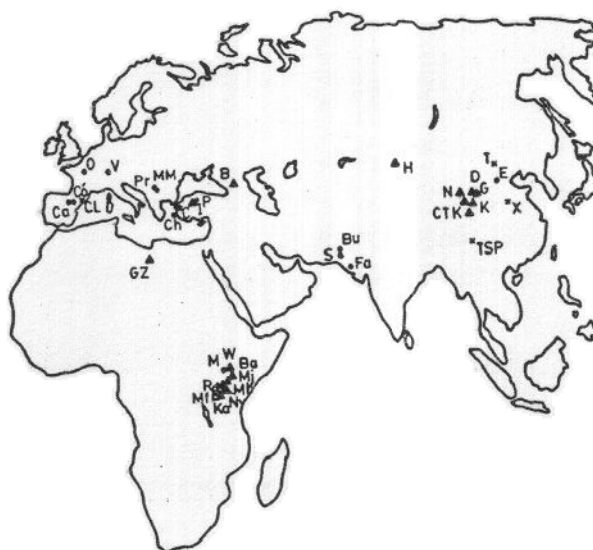


Figure 10 The geographic position of the localities with *Kubanochoerus* (indicated by triangles), the localities with *Bunolistriodon*, mentioned in the text (indicated by dots) and the localities with *Listriodon* (crosses). Legend; B) Belometchetskaya; Ba) Baragoi; Bu) Khumbi in the Bugti Hills; C) Candir; Ca) Calatayud; Ch) Chios; CL) Can Llobateres; Co) Córcoles; CTK) Quantougou; D) Dingjiaergou; E) Erlanggang; Fa) Fategad in Kutch; G) Guanghe; GZ) Gebel Zelten; H) Halamagai; I) Inönü I; K) Koujiacun; Ka) Karungu; M) Moruorot; Mb) Maboko; Mf) Mfwangano; MM) Mala Milliva; N) Nanhawangu; Ny) Nyakach; O) Sables d'Orleanais; P) Pasalar; Pr) Prebreza; R) Rusinga; S) Bhagothoro in Sind; T) Tunggur; TSP) Tung Sha Po, V) Veltheim, X) Xining.

The geographical distribution of bovids of the *Hypsodontus*/—*Turcoceros* type coincides with that of *Kubanochoerus* (China, south USSR, Turkey, Kenya and probably Libya, often the same localities). Köhler (1987) interpreted these bovids as specialised for open landscapes. The geographical distribution also coincides with *Platybelodon grangeri* like proboscideans (Tobien, Chen & Li, 1986). These animals not only lived in the same area, but also in the same period and may have been specialised to the same type of habitat.

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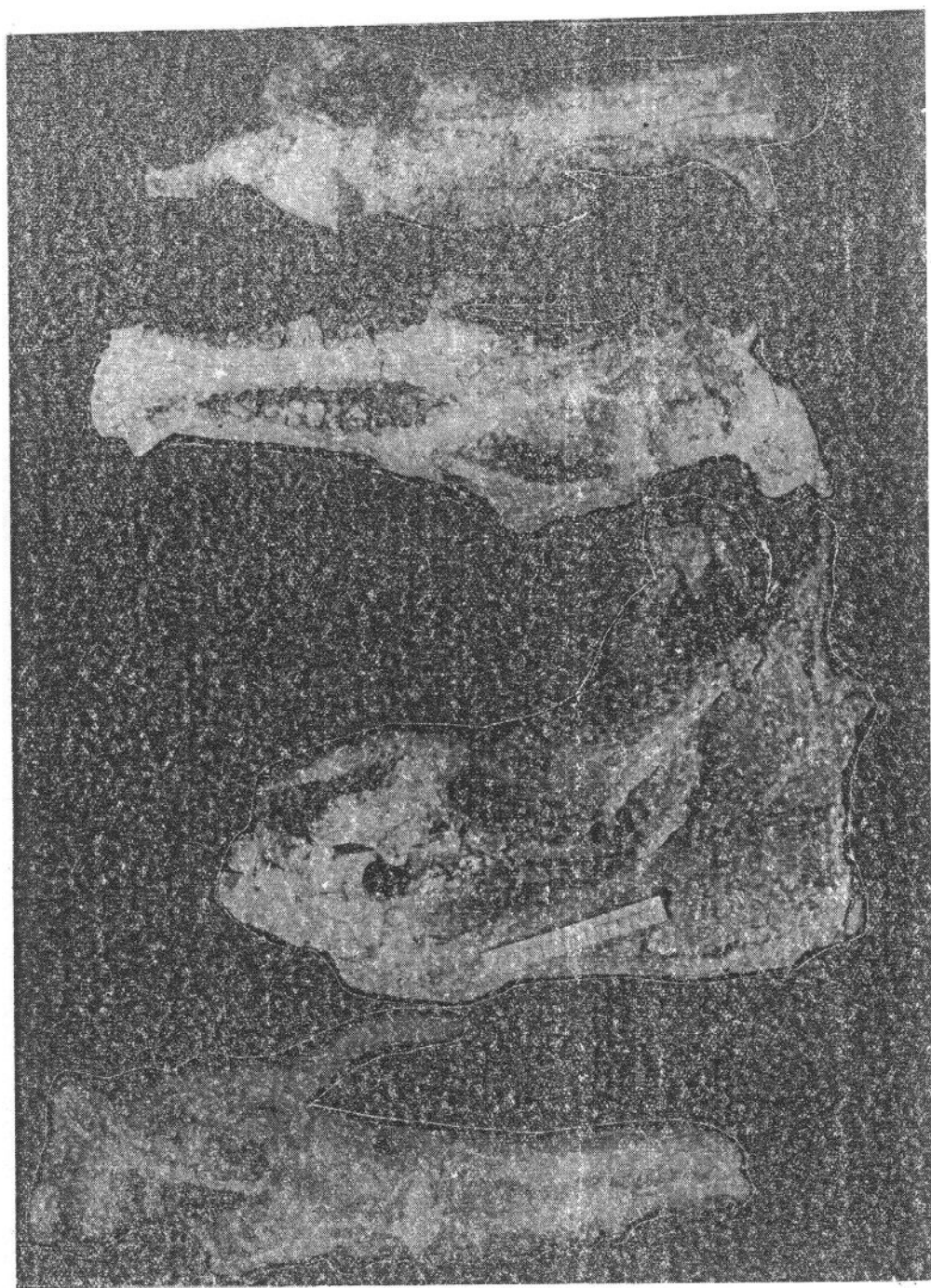
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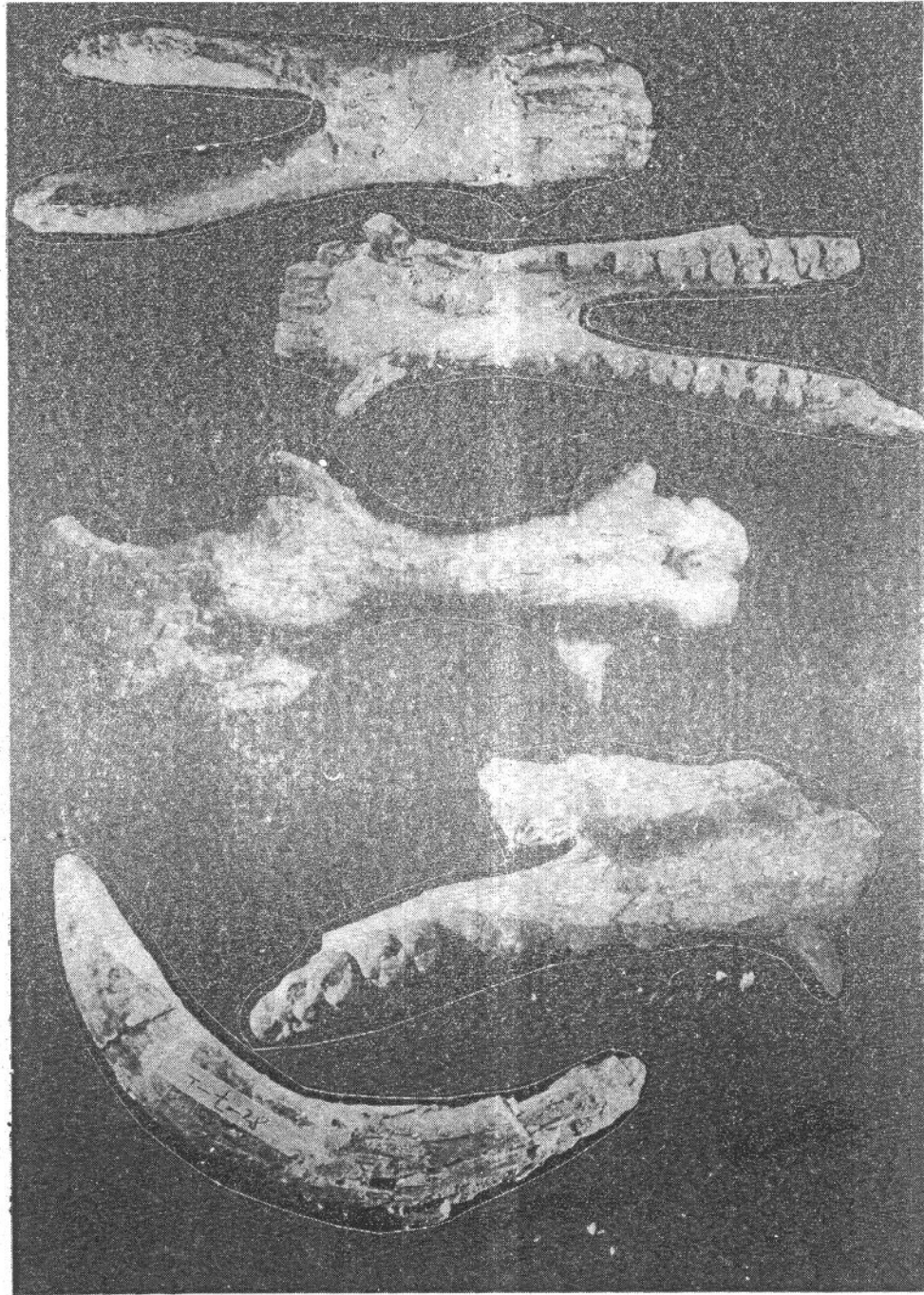
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BPV-903, dorsal view of upper jaw x 6
BPV-903, ventral view of upper jaw x 5.2
BPV-1066, lateral view of skull x 8
BPV-xxx (T-S-72) lateral view of upper jaw x 6



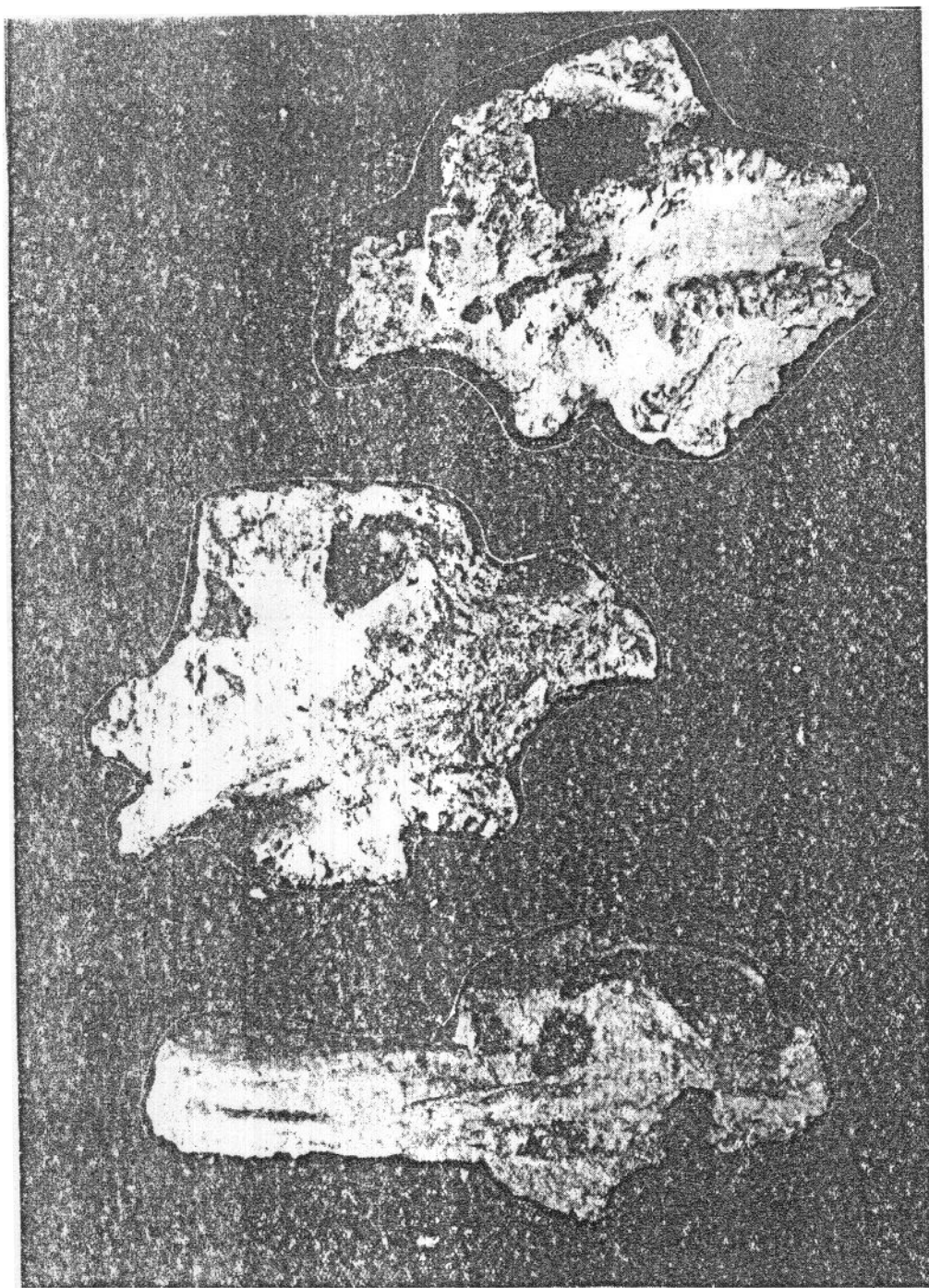
BPV-930, ventral view of mandible x 4.5

BPV-930, dorsal view of mandible x 4.5

BPV-1620, dorsal view of upper jaw x 6

BPV-1623, dorsal view of mandible x 4.8

BPV-1621, lateral view of upper canini x 2.6



BPV-908, ventral view of mandible x 5.2

BPV-908, dorsal view of mandible x 5.2

BPV-1620, dorsal view of upper jaw x 6

宁夏同心的中新世猪类化石

关 健

(北京自然博物馆)

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关键词: 宁夏同心丁家二沟·猪科·利齿猪亚科·丘齿型利齿猪·库班猪·利比考猪·性别二向性

摘 要

宁夏同心中新世地层中的猪类化石包括两种: 丘齿型利齿猪 (*Bunolistriodon* sp.) 和巨库班猪 (*Kubanochoerus gigas*), 均属于利齿猪亚科 (Listriodontine)。同心的库班猪材料包括六具较完整的头骨和五具不同程度完整的下颌骨。本文对这些材料进行了系统描述和讨论, 从而进一步了解了此类的特征、分布及这一属的系统发育和分类位置。

丘齿型利齿猪的几个种的时代分布为早中新世 (到 MN5), 仅有 *B. aff. latidens* 发现于中中新世早期 (MN6)。丘齿型利齿猪可帮助确定含库班猪的地层的时代, 它在同心丁家二沟的出现说明了同心含此类化石的地层的时代与吉尔吉斯库班地区的 Stanitza 产库班猪化石的地层的时代均为下中新世 (MN5), 而艾努努 (Inōnōu) 的时代应为中中新世 (MN6 下部)。

已知的利比考猪 (*Libyoochoerus*) 的唯一一具头骨属雌性。在其眼眶上方两侧各有一“角”状突起 (protuberances)。所有的已知属于雄性个体的库班猪 (从犬齿可分辨出) 的头骨上也具此两侧的“角状突”。同心的标本还具大的前颧突 (“角”, ossicone)。这个巨大的前颧突 (“角”) 明显地应被视为这一属动物的性别二向性 (性别区别) 特征, 而不是种一级的鉴别特征。本文认为利比考猪 (*Libyoochoerus*) 应归属于库班猪属。

K. gigas, *K. robustus* 和 *K. lantienensis* 在形态特征上极为相似, 个体大小变化未超出同心库班猪材料的变异范围。本文仅保留巨型库班猪 (*Kubanochoerus gigas*)。同心库班猪在前臼齿退化、最后臼齿增大等特征上表现为更进步一些的特征, 因此本文确立一巨型库班猪新亚种, 李氏巨库班猪 (*Kubanochoerus gigas lii* nov. subsp.)。

从目前材料判断, 库班猪沿着三个方向发展, 即 *K. massai*—*K. minkeensis* (大约在 MN4—MN6 或稍晚); *K. kingitebirus* (大约在 MN4—MN6) 和 *K. gigas* (包括 *K. gigas lii*, 大约在 MN5—MN8)。