

The differentiation of bunodont Listriodontinae (Mammalia, Suidae) of Africa: new data from Kalodirr and Moruorot, Kenya

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Received 12 June 2008; accepted for publication 9 September 2008

The early Miocene sites of Moruorot and Kalodirr (Kenya, 17.5 Myr) have yielded a rich collection of mammals. New listriodont material from these localities, including a complete skull and a partial mandible, provide long awaited information on cranial features of early bunodont Listriodontinae. The evolution and systematics of the group are highly debated, especially regarding its first representatives. The new material described here sheds light on the differentiation of bunodont Listriodontinae in Africa and clarifies the systematics of the group. The first phylogenetic analysis of the Listriodontinae is here performed and supports close relationships between *Kubanochoerus* and a clade (*Eurolistriodon*, *Listriodon*). *Lopholistriodon* is the most basal representative of the listriodontine clade. These first results stress the role of the African continent in the biogeographical history of the Listriodontinae.

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doi: 10.1111/j.1096-3642.2008.00525.x

ADDITIONAL KEYWORDS: auditory region – early Miocene – phylogeny – suid – systematics.

INTRODUCTION

The Miocene localities of the Lothidok Formation in Kenya have yielded an abundant collection of land mammals (Arambourg, 1933, 1943; Madden, 1972; Leakey, Leakey & Walker, 1988a, b). The sites of Kalodirr and Moruorot are located near the western shore of Lake Turkana and are about 10 km distant from each other. The locality of Moruorot is part of the lower section of the Kalodirr series in the Lothidok formation, and its age is estimated at 17.5 Myr (Boschetto, Brown & McDougall, 1992) which corresponds to the upper part of the lower Miocene. The site of Moruorot is the type locality of two species of Listriodontinae: *Listriodon jeanneli* Arambourg (1933) and *Lopholistriodon moruoroti* Wilkinson (1976).

Listriodontinae constitutes a peculiar subfamily of suids that developed sublophodont to lophodont cheek teeth during the early Miocene and middle Miocene,

probably as an adaptation to folivory (Hunter & Fortelius, 1994). They are characterized by a specialization of the incisor area: the anterior part of the snout is enlarged with a concurrent widening of the incisors, especially the central ones, the crowns of which form a transverse ridge used as a cropping device. Representatives of the subfamily are known from the upper part of the lower Miocene of Africa and India until the basal late Miocene of Europe. The listriodonts from Moruorot and Kalodirr are therefore among the first African members of the group.

The systematics and phylogeny of the Listriodontinae are highly debated topics and successive revisions of the group (Pickford, 1993, 2007b; Van der Made, 1996, 1997; Pickford & Morales, 2003) have failed to reach a consensus about the entities composing the subfamily and the relationships amongst them. From an historical point of view, the partial cranium from Moruorot, holotype of the species *Lis. jeanneli* and the only listriodont known from the locality, is the starting point of major nomenclatural and systematic debates. When Arambourg

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(1933) erected the species *Lis. jeanneli* it was the first record of bunodont Listriodontinae in Africa. On the basis of major cranial differences from the European lophodont forms and of dental similarities with European bunodont species [*Listriodon lockharti* (Pomel, 1848) and *Listriodon latidens* (Biedermann, 1873)], Arambourg (1933) informally proposed the gathering of the bunodont listriodonts of Europe and Africa at the generic level into the genus *Bunolistriodon*. The genus *Bunolistriodon* is nowadays one of the problematic points of listriodont systematics. Its nomenclatural validity has been rejected (Pickford & Moyá Solá, 1995) because the mention of the name *Bunolistriodon* by Arambourg (1933) did not constitute a valid nomenclatural act. However, in the description of '*Bunolistriodon*' *massai* Arambourg (1963) makes the name valid from a nomenclatural point of view by providing a type species to the genus (Van der Made, 1997). Besides nomenclatural concerns, some authors have considered that *Bunolistriodon* Arambourg, 1963 is a junior synonym of *Listriodon* Von Meyer, 1846 (Leinders, 1975; Pickford, 1986, 1993, 2007b; Pickford & Morales, 2003). It is noteworthy that the skull from Gebel Zelten upon which Arambourg (1963) built the diagnosis of the genus *Bunolistriodon*, belongs in fact to the kubanochoeres (Leinders, 1975; Pickford, 1986; Van der Made, 1996). This group, which exhibits frontal appendages, is regarded as a tribe of the Listriodontinae (Van der Made, 1996, 1997) or as a separate subfamily (Pickford, 1986, 1993, 2007a, b; Liu, 2003; Harris & Liu, 2007). Given the various classifications of listriodonts used in parallel by different authors, the species are referred to in the descriptive part of this paper by the original binomial name accompanying their first assignation to Listriodontinae.

Reflecting the instability of listriodont systematics and the lack of clear synapomorphies defining the different taxa, the holotype of *Lis. jeanneli* has had various subsequent generic assignations, and has been referred either to the Listriodontinae ('*Bunolistriodon*' *jeanneli*, Wilkinson, 1976; Van der Made, 1996) or to the Kubanochoerinae ('*Libycochoerus*' *jeanneli*, Pickford, 1986, 1993, 2001, 2007a, b; Qiu, Ye & Huo, 1988). The material referred to the species *Lis. jeanneli* comes from the localities of Moruorot (Kenya) and Fategad (Cutch, Gujrat, India). In Moruorot, the species is exclusively represented by its upper dentition, with the partial holotype cranium (MNHN 1933 9) and a DI1 (KNM MO10; Van der Made, 1996: pl. 13 fig. 8). The lower dentition of *Dicoryphochoerus fadegadensis* Prasad, 1967 from Fategad (IM GSI 18098, Cutch, Gujarat, India, Lower Miocene) was attributed to the species '*B. jeanneli*' by Van der Made (1996) the same material being attributed to *Libycochoerus fadegadensis* by Pickford (1988). Some listriodont remains from

Rusinga (Kenya), comprising the lower dentition, have also been attributed to the species by Pickford (1986, 2001) and Pickford & Morales (2003) but placed in the genus *Libycochoerus*. Van der Made (1996) created the species *Bunolistriodon anchidens* for the same material and, finally, Pickford (2007a, b) recognized this new species but assigned it to the genus *Libycochoerus*.

New material from Moruorot described in this paper, a mandible and a few upper teeth assigned to the same male individual, allows the first non-ambiguous association of upper and lower teeth. A new complete female cranium from the locality of Kalodirr is also assigned here to the species *Lis. jeanneli*. This specimen, slightly more recent than the material from Moruorot (Boschetto *et al.*, 1992), exhibits the same feature as the fragmentary cranium from the type locality and complements our knowledge of the cranial morphology of the species.

Cranial remains of listriodonts are very scarce and, furthermore, the listriodont specimens from Kalodirr and Moruorot represent the most ancient cranial remains of African bunodont Listriodontini. Thus, they provide data of crucial importance for the systematics and phylogeny of Listriodontinae. To clarify the systematics of the Listriodontinae and the phylogenetic relationships of the species *Lis. jeanneli*, a phylogenetic analysis based on 22 taxa and 76 craniodental characters is performed.

MATERIAL AND METHODS

COMPARATIVE MATERIAL

The new material described in this paper is curated at the Kenyan National Museum (KNM) in Nairobi, Kenya and was collected by M. G. Leakey, R. E. Leakey, and A. Walker between 1983–1987/1990 in the localities of Moruorot and Kalodirr. Comparative material comes from the Muséum National d'Histoire Naturelle, Paris, France (MNHN); the Muséum d'Histoire Naturelle, Toulouse, France (MHNT); the Université Claude Bernard, Lyon, France (UCBL); the Universidad Complutense, Madrid, Spain (UCM); the Museo Nacional de Ciencias Naturales, Madrid, Spain, (MNCN); the Museo Paleontológico de la Universidad de Zaragoza, Spain (MPZ); the Institut Paleontologic Dr. Miguel Crusafont, Sabadell, Spain (IPS); the Naturwissenschaftliche Sammlungen der Stadt Winterthur, Switzerland (NSSW); the Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany (BSPHGM); the Indian Museum, Calcutta, India (IM) and the Institut for vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China (IVPP). A time scale with the regional distribution of the different listriodont species mentioned is given in Figure 1.

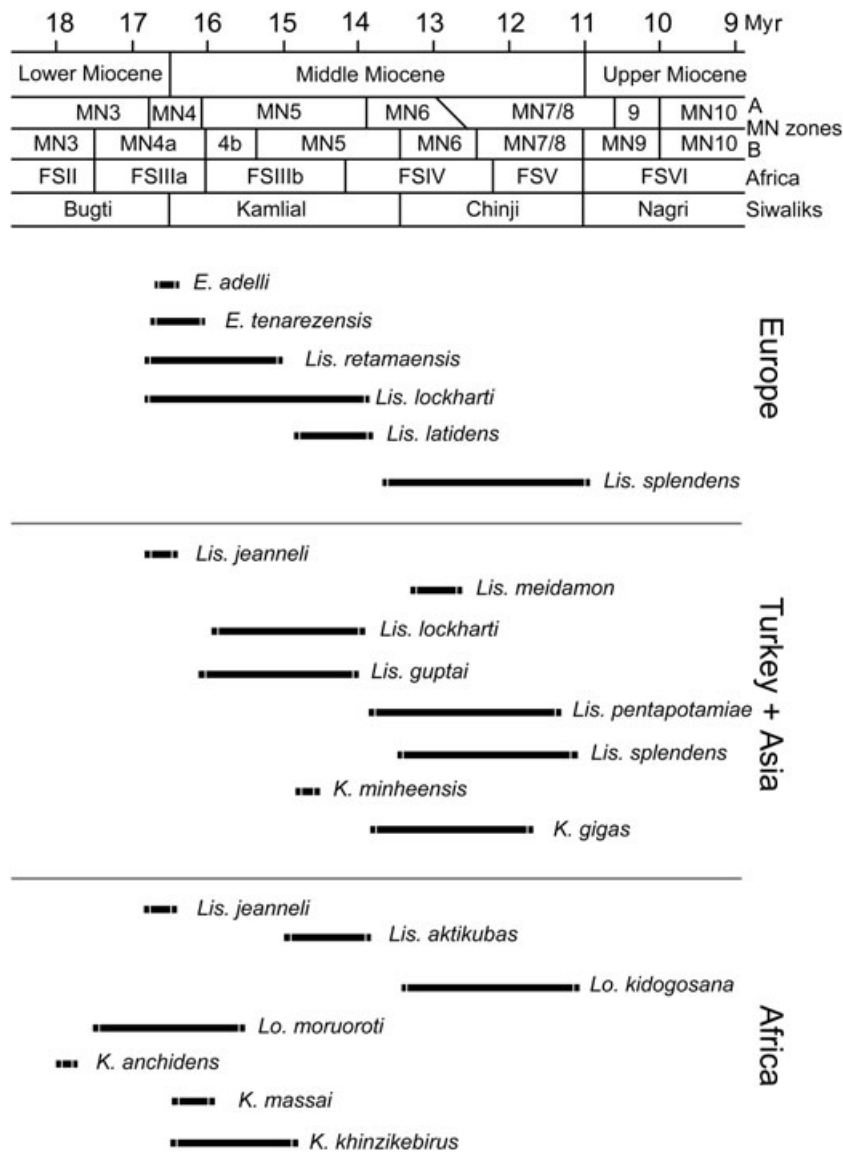


Figure 1. Stratigraphical and regional distribution of the listriodont taxa mentioned in the present article. Miocene subdivisions are from Berggren *et al.* (1995); European mammalian Neogene zones (MN zones) given are from (A) Van der Made (1996) and (B) Pickford & Morales (2003). Correlations between European mammalian zones and African and Siwaliks faunal zones are respectively from Pickford & Senut (1997) and Welcomme *et al.* (2001); correlations between mammalian Neogene zones and time scale are given by Van der Made (1997) and Pickford & Morales (2003). Most common synonymies are: Turkey + Asia, *Listriodon jeanneli* = *Libycochoerus fategadensis* (Prasad, 1967); *Listriodon splendens* = *Listriodon xinanensis* Chen, 1986; *Listriodon lockharti* = *Listriodon intermedius* Liu & Lee, 1963; *Kubanochoerus gigas* = *Kubanochoerus robustus* Gabunia, 1960 = *Listriodon lantiensis* Liu & Lee, 1963; Africa, *Lopholistriodon moruoroti* = *Namachoerus moruoroti*.

MEASUREMENTS

Tooth measurements were taken with a precision of 0.1 mm. The mesiodistal length corresponds to the maximal length of the teeth, parallel to the sagittal plan, and the buccolingual width is measured perpendicular to the mesiodistal length and corresponds to the maximal width of the tooth.

MORPHOLOGY

The dental nomenclature follows that of Orliac (2006) derived from Van der Made (1996). The names of secondary structures, such as crests, are constructed as follows: the name of the structure (crisid/crista, fossid/fossa) is combined with the name of the cusp that bears it, and a prefix indicates the position of the

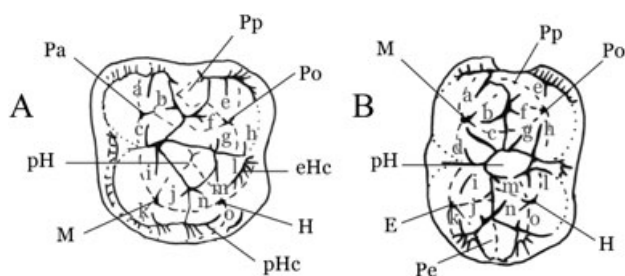


Figure 2. Nomenclature of: A, upper molar and B, lower molar of bunolophodont listriodonts. Grooves are figured in full lines, crests in dotted lines. Abbreviations: Equivalent for Hünemann's (1986) coordinates corresponding to the lower molars are given in parentheses; a, ectometafossa/id (1); b, premetafossa/id (2); c, endometafossa/id (3); d, postmetafossa/id (3i); E, entoconid; e, ectoprotoconid (4); eHc, ectohypocrista; f, preprotofossa/id (5); g, endoprotofossa/id (6); H, hypocone/id; Hpe, prehypoconule/id; h, postprotofossa/id (6a); i, pre-entofossa/id (7); j, endoentofossa/id (8); k, postentofossa/id (9); l, ectohypofossa/id (10); M, metacone/id; m, prehypofossa/id (10v); n, entohypofossa/id (11); o, posthypofossa/id (12); Pa, paracone; Pe, pentaconid; pHe, posthypocrista; Po, protocone/id; Pp, preprotoconule/id.

secondary structure. The groove between two cristids is named after the crest in front of it. For instance, a crest on the metaconid located in an anterobuccal position is called a 'premetacristid'. Pickford (1986) stressed the importance of the 'groove pattern' already emphasized and described by Hünemann (1968). Here, the groove pattern has been carefully studied because it is linked to the degree of tooth lophodonty, the former being reduced when the latter is developed. The nomenclature of the groove pattern of bunolophodont listriodonts is given in Figure 2 for the second upper and lower molar. Capital letters are used for upper teeth (I, C, P, M), and lower-case for lower teeth (i, c, p, m).

SYSTEMATICS

FAMILY SUIDAE GRAY, 1821

SUBFAMILY LISTRIODONTINAE GERVAIS, 1859

TRIBE LISTRIODONTINI

GENUS *LISTRIODON* VON MEYER, 1846

LISTRIODON JEANNELI ARAMBOURG, 1933

Bunolistriodon jeanneli – Arambourg, 1963: 910

Dicoryphochoerus fategadensis – Prasad, 1967: 11, fig. 2

Bunolistriodon jeanneli – Madden, 1972: 2, 6

Bunolistriodon jeanneli – Van Couvering & Van Couvering, 1976: 203 (only the specimen from Moruorot)

Bunolistriodon jeanneli – Wilkinson, 1976: 217–225 (only the specimen from Moruorot)

Libycochoerus jeanneli – Pickford, 1986: 36–37 (only the specimen from Moruorot)

Libycochoerus affinis – Pickford, 1987: 305 (only the specimen from Fategad)

Libycochoerus fategadensis – Pickford, 1988: 35, fig. 64

Libycochoerus affinis – Pickford, 1988: 947–948 (only the specimen from Cutch)

Libycochoerus jeanneli – Qiu *et al.*, 1988: 16–18 (only the specimen from Moruorot)

Bunolistriodon jeanneli – Fortelius, Van der Made & Bernor, 1996: 160

Bunolistriodon fategadensis – Fortelius *et al.*, 1996: 160

Bunolistriodon jeanneli – Van der Made, 1996: 70–71, pl. 13, figs 3, 8, 9; pl. 14, figs 5, 6, 10, 12

Bunolistriodon jeanneli – Van der Made, 1997: 156

Libycochoerus jeanneli – Pickford, 2001: 194–198

Libycochoerus jeanneli – Pickford, 2007a: tab. 2

Libycochoerus jeanneli – Pickford, 2007b: fig. 4

Differential diagnosis: Dental characters – upper male canine smaller than that of European Listriodontinae, backwardly orientated as in *Eurolistriodon* but in contrast to other European listriodonts which exhibit upwardly directed canines in males, sharp postanticipline as in *Lis. lockharti* and *Listriodon splendens* but contrasting with *Eurolistriodon* in which the postanticipline is rounded; **Cranio-mandibular characters** – general aspect of the cranium shallow in comparison to lophodont listriodonts; orbit located in an anterior position: anterior border located at the level of M2–M3, whereas it is located at the level of the rear of the M3 in other known representatives of the Listriodontini (*Eurolistriodon*, *Lis. splendens*, *Listriodon pentapotamiae*); zygomatic arch particularly robust in its anterior portion, being wider and lower than that of *Lis. splendens*; presence of a lateral protuberance as in *kubanochoeres*; glenoid surface lying in a low position compared to *Eurolistriodon* and other European listriodonts, close to the occlusal plane; post-tympanic process well developed as in *Lis. splendens*, absence of postglenoid process contrasting with *Eurolistriodon*.

Holotype: MNHN 1933-9, a portion of cranium comprising the palate from P4 to M3 and anterior portion of zygomatic arches.

Type locality: Moruorot, Losodok Formation (Kenya) = Muruorot (Madden, 1972).

Other localities: Kalodirr (Kenya), Fategad (Cutch, India).

DESCRIPTION AND COMPARISONS

NEW MATERIAL FROM KALODIRR

Comparisons were made with the type specimen of *Lis. jeanneli* and with listriodont remains from Rusinga primarily attributed to *Libycochoerus jeanneli* by Pickford (1986) and Pickford & Morales (2003), transferred to the species *B. anchidens* by Van der Made (1996), and finally recognized as *Libycochoerus anchidens* by Pickford (2007b). The new material from Kalodirr, belonging to a female individual, is also compared to other known female crania of the subfamily Listriodontinae: the cranium of *Libycochoerus massai* Arambourg (1961) from Gebel Zelten (Libya, c. 17 Myr, MNHN LBE 563), the snout of *Listriodon retamaensis* Pickford & Morales, 2003 from Retama (Huete, Spain, MN4a, MNCN RET 740), and the crania of *Lis. splendens* Von Meyer, 1846 from Toril (Spain, MPZ MN7, TO3B 129) and from Xinan (Henan, China, middle Miocene, IVPP V 8285 figured by Chen, 1986: pl. III, 1–2).

Cranium

The female cranium (Fig. 3) is one of the most complete specimens of Listriodontinae known and the best preserved cranium of a bunodont Listriodontini. Its three-dimensional shape has only been slightly altered by a slight dorsoventral compression affecting the right side of the frontal bone; and by a slight lateral toppling of the anterior part of the snout. The proportions of the left side are preserved and this side gives access to: the height of the cranium, the position of the zygomatic arch and of the orbit relative to the tooth row, and the height of the glenoid surface; the suprameatic process is intact. Cranial sutures are obliterated in this fully adult specimen. The cranium is missing: a portion of the right zygomatic arch, the right zygomatic process of the frontal bone, and the posterior part of the palate, broken at the level of the M1. The guttural area, highly damaged, is broken with no distortion. The left auditory bulla lies in its original position, whereas the right one is detached from the cranium but perfectly preserved.

The dental formula is complete. The anterior dentition and the P1 are represented by their alveoli. The left side of the cranium preserves the canine and the P2–M3, the right side only bears a fragment of canine and M2–M3, the M2 being reduced to its distal lobe. The morphology of the upper canine clearly indicates that this specimen is a female (Fig. 3). The maximum anteroposterior length of the cranium is 372 mm.

Dorsal view (Fig. 3A): the snout is short. The nasal cavity is wide and rounded. The height of the narial opening is 38 mm and its maximal width is 46 mm. The shape of the anterior border of the nasals is rounded and their anterior extension is not as anterior as the anterior margin of the premaxilla. This peculiar morphology of the anterior part of the snout is also seen in other Listriodontinae and suggests a more flexible ability of the rostral organ (Orliac, 2007b). The infraorbital foramen lies at the level of the middle of the P3.

Laterally, the origin of the levator rostri muscle forms a shallow depression just in front of the orbit. It is overhung by a thickening of the frontal located above and anterior to the orbit. This structure lies laterally to the sulci joining the supraorbital foramina. The position of the latter cannot be determined. The lacrymal bears a clear foramen lacrimale, located in the internal aspect of the orbit, as it is the case in *Eurolistriodon adelli* Pickford & Moyá Solá, 1995 from Els Casots (Spain, IPS 9096) and *Lis. retamaensis* from Bezian (France, MNHN Be A-69-22), but contrary to *Lis. splendens* from Toril and Xinan, which are devoid of lacrymal foramina (Pickford & Morales, 2003). The orbit lies above the first lobe of the M3. This position is more anterior than in *Lib. massai*, where it lies above the rear of the M3. The position of the orbit is also high, almost reaching the level of the cranial roof. The orbit exhibits the typical listriodontine shape with the indentation anterior to the orbital process of the jugal. The postorbital constriction is marked compared to that of female specimens of *Lis. splendens* known from Spain and China. The sagittal crest is sharp and high. Its anteroposterior extension is estimated at 60 mm and its posterior outline is concave. There is no trace of parietal foramina. The external volume of the neurocranium is lower than that of European Listriodontini and of the female specimen of *Lis. splendens* known from China, but similar to that of *kubanochoeres* [*Lib. massai*, MNHN LBE 563; *K. gigas* (Pearson, 1928); Gabunia, 1960]. The external occipital protuberance (Protuberantia occipitalis externa) is thin and its posterior profile is incurved. In dorsal view, the occiput is narrow in comparison to that of *E. adelli* (IPS 9096) and *Lis. splendens* (MNHN Sa 10141), which present a wider occipital protuberance, without sagittal inflexion.

Ventral view (Fig. 3B): the incisive part of the premaxilla is short and widened. The incisor alveoli form an arch, separated from the canine alveolus by a short depressed diastema. The extension of the snout anterior to the canine is similar to that of the type specimen of *Lis. retamaensis* (MNCN RET 574). The alveoli are rounded and opened ventrally, indicating that the incisors were implanted much more verti-

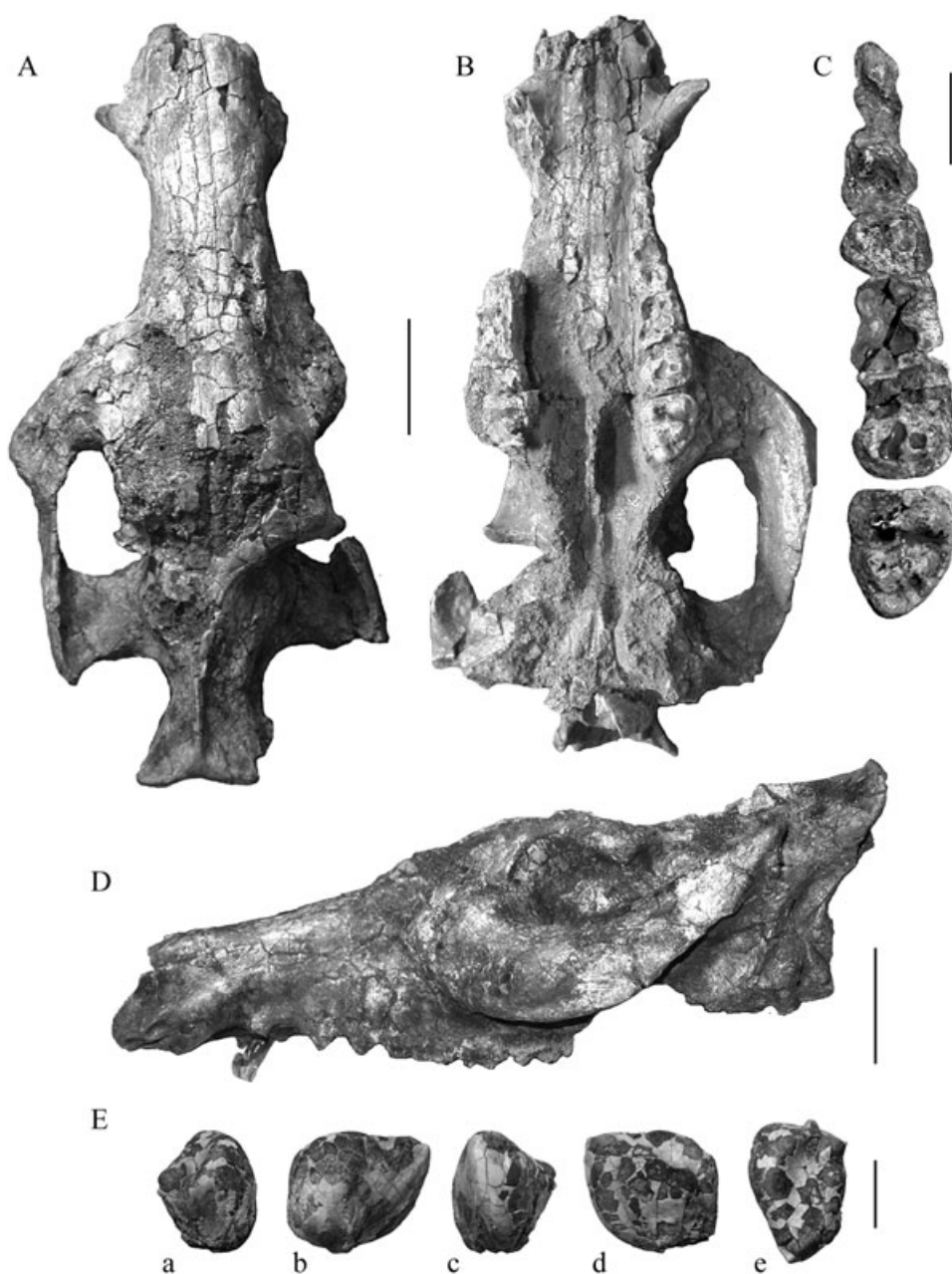


Figure 3. Cranium of *Listriodon jeanneli* KNM WK-17127 in A, dorsal view; B, ventral view; C, detail of the left cheek teeth row in occlusal view; D, lateral view; E, right auditory bulla associated to the cranium in a, posterior; b, medial; c, anterior; d, lateral; e, anterior view. Scale bars: A, B, D = 50 mm; C, E = 20 mm.

cally than in European bunodont Listriodontinae. An even more pronounced vertical implantation, is also found in *Lib. massai*. The I1 alveolus is rounded and of reduced mesiodistal extension, suggesting that the I1 has a reduced mesiodistal diameter. Its medial margin is quite far from the sagittal plan in comparison to other Listriodontinae, also recalling kubanochoerine morphology. The palatine fissure is reduced and hardly extends posteriorly to the rear of the I3

alveolus as in *Lib. massai* and *Lis. retamaensis*. The precanine diastema is estimated to be about 15 mm. The breadth of the snout anterior to the canine is 76 mm, which is slightly larger than in *Lis. retamaensis* (breadth = 59 mm). The development of the incisive part of the snout is more important in the females of *Lis. splendens* from Spain and China, a species with more pronounced sexual dimorphism. The P1 lies just behind the canine alveolus and is

separated from the P2 by a short diastema of 15 mm. The palate is wide (38 mm between the P3) and flat.

The zygomatic arches rise with a shallow angle at the level of the P4–M1. The anterior part of the arch is wide and thick, and is preceded by a domed expansion supporting the origin of the depressor rostri muscle. This extension of the zygomatic arch emphasizes the brevity of the snout. The ventral profile of the zygomatic arch forms a wide continuous edge reaching a prominent lateral protuberance supported by the jugal. Posterior to the lateral protuberance, the arch becomes slender and straight. Other Eurasiatic Listriodontini are devoid of a protuberance on the jugal. However, a lateral protuberance is also found on the jugal of *Lib. massai*, but the zygomatic arch of the latter is much more slender. The medial aspect of the arch, at the protuberance level, is concave in *Lib. massai*, which is not the case in *Lis. jeanneli*. Unlike in extant suids, there is no facial crest.

The posterior extension of the palatines is unknown, the palate being broken at the level of the M1. The pterygoid processes of the palatine are also broken off and the shape of the posterior margin of the palate is unknown. The glenoid process is flat and consists of a very thin strip of bone. The level of the glenoid surface is located 45 mm above the tooth row, this position being low compared to that of bunodont Listriodontinae, as indicated by the comparison of the ratio of the height of the glenoid surface to the length of the snout given in Table 1.

There is no delineation between the articular surface and the mandibular fossa. The rear of the fossa is fused to the post-tympanic process (ptp) and no groove remains between the two structures. The ptp is well developed ventrolaterally in a sharp bony crest and is prolonged ventromedially by a strong tympanic neck (a structure described in Suiformes by Pearson, 1928). There is no postglenoid process (pgp). This configuration of the external auditory duct is similar to that of *Lis. splendens* from Sansan (France, MNHN Sa 10141, male specimen) and Toril (Spain, MPZ TO 3B 129, female specimen) and to that of *Lis. pentapotamiae* (Kundal Nala2, Chinji formation, BSPHGM 1956II37, figured by Van der Made, 1996: pl. 14, fig. 1). Unfortunately

the morphology of the female skull of *Lis. splendens* from Xinan has not been directly controlled on the original material but from the literature only and cannot be clearly observed on the figures provided by Chen (1986) and Van der Made (1996). The morphology of the external auditory duct of *Lis. jeanneli* differs markedly from *Lib. massai* and *Eurolistriodon tenarezensis* which exhibit a clear pgp (Orliac, 2006; Orliac & Ladevèze, 2007). Differences amongst the taxa are illustrated in Figure 4.

The preservation of the right auditory bulla is exceptional (Fig. 3E). The size of the bulla is impressive compared to the overall size of the cranium (Fig. 3B, length is 42 mm and breadth is 28.5 mm). The bulla is heart-shaped and dorsoventrally elevated (height is 39.5 mm). The anterior part of the bulla tightly contacts the pterygoid process. The left occipital condyle is intact. It is narrow and does not have the globular shape found in *Lib. massai* or *Lis. splendens*. Its shape is similar to that of *Eurolistriodon* (Pickford & Moyá Solá, 1995; Orliac, 2006).

Posterior view (Fig. 4E): the occipital face is narrow and low, with a maximal height of 66.7 mm. The suprameatic process is salient and overhangs the opening of the acoustic meatus. The ventral extension of the ptp is important and hides the posterior margin of the glenoid surface. The overall morphology of the auditory region is very close to that of *Lis. splendens* and differs greatly from that of *Lib. massai*. The difference in the structure of the false auditory meatus clearly appears in posterior view: the occipital part of the squamosal of *Lib. massai* is very reduced and the pgp is clearly visible (Fig. 4D). There is a wide gap between the ptp and the distal border of the rear of the articular zone, whereas in the cranium from Kalodirr there is no gap and the ptp is the only visible structure and forms a sharp ridge lining the false external meatus (Fig. 4E, F). If the ventral extension of the pgp of the cranium from Kalodirr is important, the dorsal development of the occipital portion of the squamosal is reduced and hardly reaches the level of the nuchal crest. The left occipital condyle is preserved. It is narrow in comparison to the more globulous condyle of *Kubanochoerus* (Qiu

Table 1. Height of the glenoid surface relative to the occlusal plan (H) and length of the snout expressed by the mesiodistal distance I1–M3 (L) of representatives of the Listriodontinae

	<i>Listriodon splendens</i>	<i>Eurolistriodon tenarezensis</i>	<i>Listriodon jeanneli</i>	<i>Lopholistriodon kigodosana</i>	<i>Libychoerus massai</i>
H	100	60	45	37	80
L	266	230	240	145	310
(H/L) × 100	37,6	26	18,6	25	25

Measurements are expressed in mm.

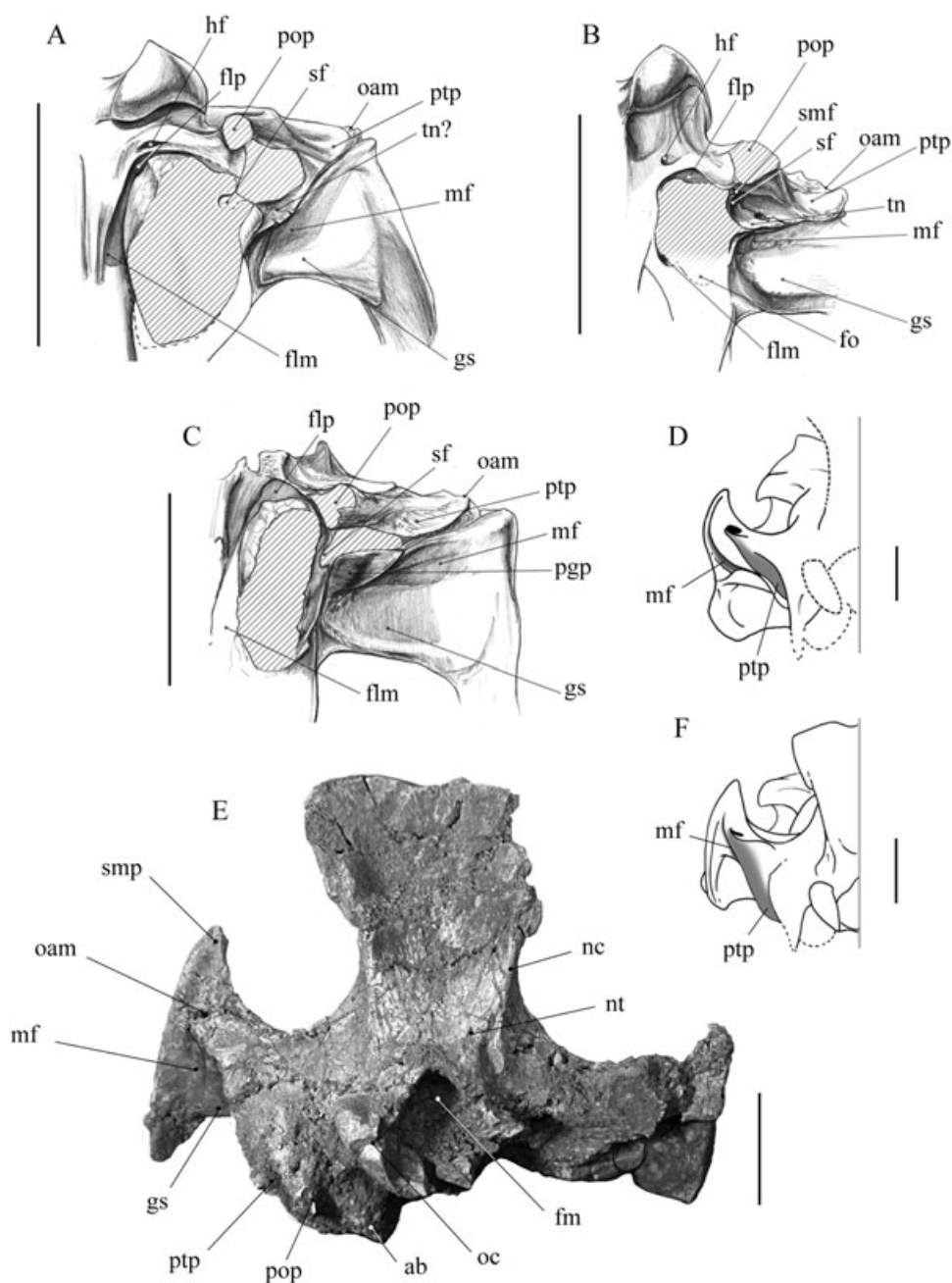


Figure 4. Basicranium and nuchal face of *Listriodon jeanneli* and comparisons with other listriodonts. A–C, drawings of the ventral view of the auditory region, of A, *Lis. jeanneli* (KNM WK-17127); B, *Listriodon splendens* (MNHN Sa 10141); C, *Libycochoerus massai* (MNHN LBE 563). E–F, dorsal view of the skull KNM WK-17127 of *Lis. jeanneli*; comparison with D, dorsal view of the skull MNHN LBE 563 of *Lib. massai*. Abbreviations: ab, auditory bulla; flm, foramen lacerum medium (median lacerate foramen); flp, foramen lacerum posterior (posterior lacerate foramen = foramen jugulare); fm, foramen magnum; fo, foramen ovale; hf, hypoglossal foramen; gs, glenoid surface; mf, mandibular fossa; nc, nuchal crest; nt, nuchal tubercle; oam, opening of the auditory meatus (opening of the external acoustic meatus); oc, occipital condyle; ppg, postglenoid process; pop, paroccipital process; ptp, post-tympanic process; sf, styloid foramen; smf, stylomastoid foramen; smp, suprameatic process; tn, tympanic neck. Scale bars: A–C = 50 mm; D–F = 50 mm.

et al., 1988). Its shape is similar to that of *Eurolistriodon* (Pickford & Moyá Solá, 1995; Orliac, 2006). The nuchal tubercles are reduced in comparison to those of extant suids; in the Kalodirr cranium, they are laterally doubled by a small tuberosity that is found neither in *E. adelli* nor in *Lis. splendens* (MNHN Sa 10141). This structure may correspond to the rugosity that replaces the mastoid process in suids. The latter is present in similar proportions in *Hyotherium major* (Pomel, 1847) from Saint-Gérard-le-Puy (female cranium, MNHN SG 3554). The overall morphology of the nuchal face of the Kalodirr cranium is close to that of *H. major*. The paroccipital processes are broken but the shape of the base of the left one indicates that it was rather conical. The orientation of the paroccipital processes has a strong vertical component as in *Lib. massai*. However, the global morphology of the occipital part of the cranium of *Lib. massai* is very different.

Dental remains (Fig. 3C)

Teeth are heavily worn and the cranial dentition does not provide much information. The upper canine is a typical female canine: its size, enamel band pattern, and implantation are similar to those of known European bunodont listriodontine females. This tooth is more slender than that of *Lib. massai*. The crowns of P1 are broken but the roots are still in the maxilla. It is possible to say that this tooth was well developed with a crown length of about 10 mm. P2–3 are elongated teeth with a clear lingual basin bearing inter-

nal enamel knobs lining the lingual cingulum. The P4 bears two buccal cusps tightly close to each other. The protocone lies in a mesial position.

The two first molars are greatly eroded. However, the presence of a postprotocrista in the M2 is highly probable judging from the shape of the dentine surface visible at the level of the hypocone. M2–3 bear a clear lingual cingulum interrupted at the paracone level on the M2 and fully developed on the buccal side of the M3. The latter presents large and rounded cusps, with small endocristae. The preprotoconule inserts between the two mesial cusps and contacts the endoprotocrista. The sublophodont character of the teeth is increased by the distal position of the median accessory cusp, stuck between the two distal cusps, strongly connected to the hypocone. The talon of the M3 bears a well-developed pentacone cusp. Tooth measurements are given in Table 2.

Comparison with the type of *Lis. jeanneli*

Although it has been restricted in the literature to a fragmentary palate, providing information on the dental characters of the species (Pickford, 1986: 37; Van der Made, 1996: 70), the holotype of *Lis. jeanneli* is a cranium that provides enough data to infer general morphological features such as its height, the position of the orbit, and the morphology of the zygomatic arches.

As the temporal part of the parietal bone is preserved on the right face of the cranium, it is possible to determine the position of the anterior origin of the

Table 2. Measurements of the dental remains attributed to *Listriodon jeanneli* and *Bunolistriodon anchidens*

<i>Lis. jeanneli</i>			<i>Lis. jeanneli</i>			<i>Lis. jeanneli</i>			<i>Lis. jeanneli</i>			<i>B. anchidens</i>		
Kalodirr			Kalodirr			Moruorot			Fategad			Rusinga		
MNHN 1933 9			KNM WK 17127			KNM MO 18127			GSI 18098			Ru 2785-2780A		
MDD	BLD		MDD	BLD		MDD	BLD		MDD	BLD		MDD	BLD	
P3	21.3	18.0	P3	> 17.5	17.5							P3	19.7	11.5
P4	16.0	20.1	P4	15.3	19.5	P4	14.5	17.0				P4	13.5	17.7
M1	21.4	20.8	M1	22.0	–	M1	20.0	18.3				M1	18.1	19.5
M2	24.4	24.8	M2	23.4	–	M2	22.7	22.5				M2	21.5	22.2
M3	28.0	24.4	M3	28.3	25.3	M3	30.0	–				M3	27.8	25.4
			M3	28.4	24.3									
						p3	20.0	12.0				p3	19.0	10.8
						p4	18.8	13.8	p4	18.8	14.2	p4	17.9	11.4
						m1	20.4	14.2	m1	22.3	16.7	m1	18.7	14.3
						m2	23.0	17.5	m2	24.0	19.0	m2	21.4	15.6
						m3	> 24.7	20.0	m3	33.6	20.0	m3	31.8	19.2

Measurements of *Lis. jeanneli* from Fategad are those taken by Pickford (1988: 35). Measurements are expressed in mm. BLD, buccolingual diameter; MDD, mesiodistal diameter.

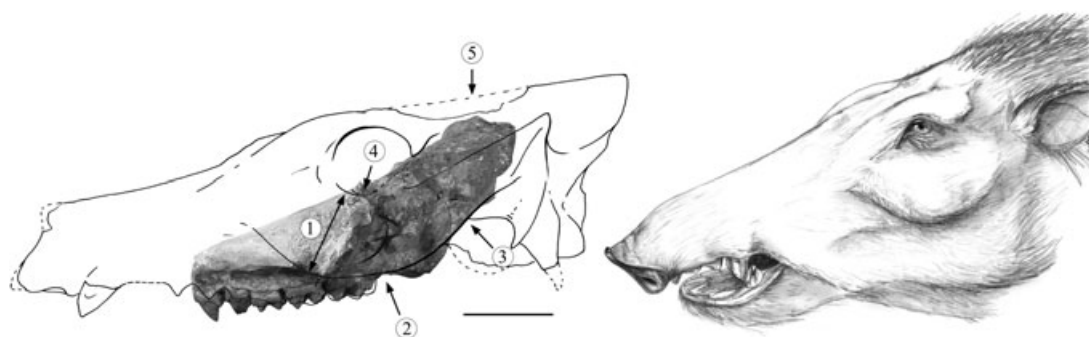


Figure 5. Comparison of the lateral profile of the skull KNM WK-17127 from Kalodirr and the left profile of the holotype of *Listriodon jeanneli* from Moruorot (MNHN 1933-9) with a reconstruction of the living appearance of *Lis. jeanneli*. The corresponding features and placemarks are the following: 1, thickness of the zygomatic arch; 2, distal edge of the palatal part of the maxilla; 3, basis of the pterygoids; 4, position of the fossa for the oblique ventral muscle (fossa musculus obliquus ventralis); 5, level of the anterior origin of the sagittal crest. Scale bar = 50 mm.

sagittal crest on the holotype (Fig. 5, placemark 5). The volume of the braincase is small. The pterygopalatine fossa opens 14 mm above the basis of the crown of the M3. This position is very low in comparison to that of *Lis. splendens* from Sansan in which the pterygopalatine fossa opens 31 mm above the base of the crown of the M3, which is considerable given that the two crania have approximately the same length. This character is congruent with the very shallow aspect of the cranium described by Arambourg (1933). The root of the zygomatic arch lies in a very low position in the holotype of *Lis. jeanneli*: the ventral face rises just above the level of the alveolar margin of the M3. This character, present in the Kalodirr cranium, also suggests a shallow aspect of the cranium. The thickness of the anterior part of the zygomatic arch is important in the holotype and also in the case of the specimen from Kalodirr (Fig. 5, feature 1).

Despite the lack of the major part of the lacrymal bone, the frontal, and the jugal, the position and height of the orbit on the holotype can be determined and is congruent with what is observed on the Kalodirr cranium. The ventral part of the anterior margin of the orbit is preserved and bears the imprint of a large sulcus corresponding to the lacrymal duct. The internal anterior part of the orbit bears a wide fossa for the oblique ventral muscle (fossa musculus obliquus ventralis) just above the pterygopalatine fossa; this feature is also observable in the Kalodirr cranium (Fig. 5, placemark 4). In suids, the base of the pterygoid process corresponds to the level of the glenoid; the level of the glenoid on the holotype is estimated at about 40 mm above the palatal plan, a value congruent with that of the specimen from Kalodirr (height = 45 mm, Fig. 5, placemark 3). The base of the anterior part of the sagittal crest is preserved on the holotype, giving an idea of the

height of the cranium. The base of the sagittal crest lies 98 mm above the palatal plan, which is congruent with the measurements of the Kalodirr cranium (height = 109 mm). The typical cranial characters of the species, described by Arambourg (1933) but since neglected despite their interest, are found in the Kalodirr cranium.

Comparison of the dental characters of the kalodirr cranium and the holotype is more difficult because of the advanced state of wear of the Kalodirr specimen. The dental measurements of the latter are slightly larger than those of the holotype (see Table 2). The structure of the molars is best observed on the M3. Both specimens present a clear buccal cingulum; however, the distal part of the Kalodirr specimen bears a well-developed pentacone contrary to the holotype, which only presents a bulge of the cingulum. In both specimens the distal part of the M3 consists of a distinct lobe and the development of the pentacone is considered here as individual variation.

The female cranium from Kalodirr KNM WK 17127 exhibits the typical characters of *Lis. jeanneli* described by Arambourg (1933) and is thus attributed to the same species.

NEW CRANIODENTAL AND POSTCRANIAL REMAINS FROM THE LOCALITY OF MORUOROT, KENYA

The listriodont dental remains from Moruorot (KNM MO 18127, Figs 6, 7) are all referred to the same male individual. They consist of a right portion of mandible preserving p3–m3, a right portion of maxilla with P4–M2, two isolated M3, and two isolated upper male canines. A few postcranial remains (Fig. 8) were also collected from the same area: an atlas, a fragment of vertebra and a proximal end of an ulna.

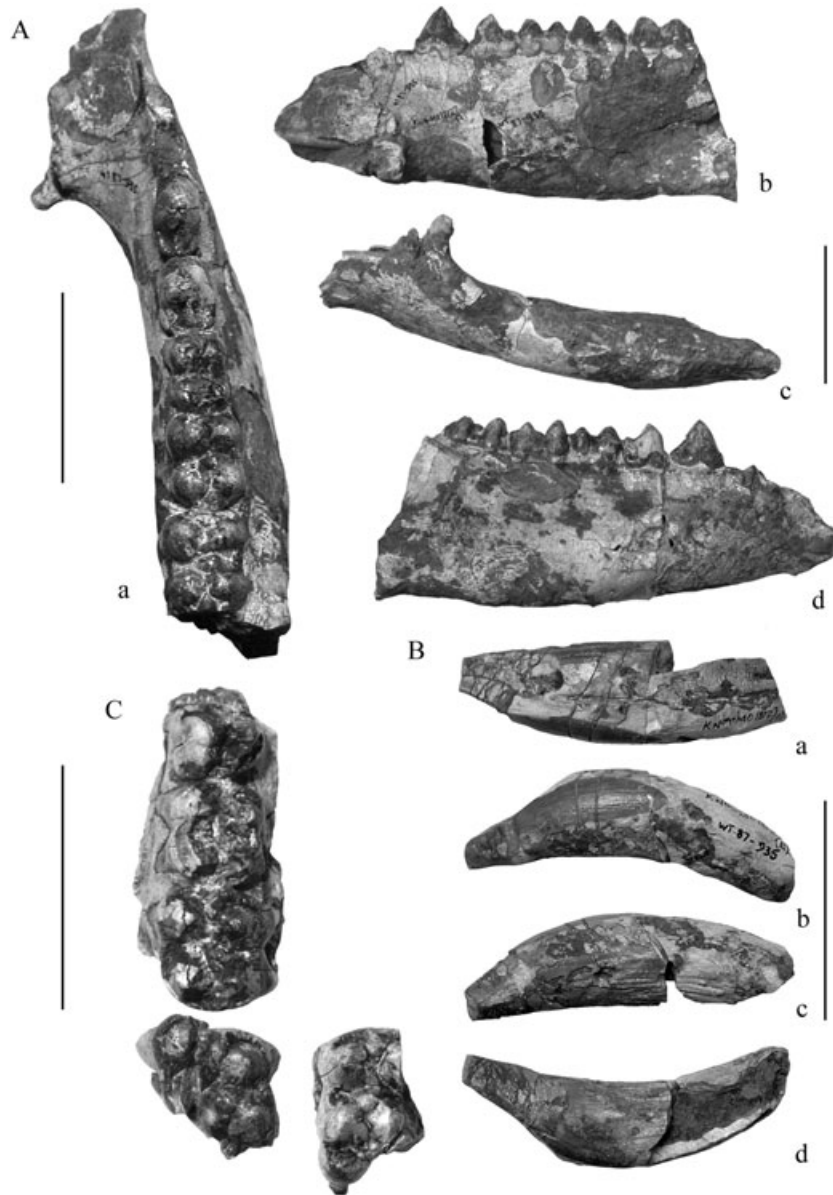


Figure 6. Craniodental remains of *Listriodon jeanneli* from Moruorot (KNM MO 18127): A, fragment of mandible with right p3–m3 in view a, occlusal; b, lingual; c, ventral; d, buccal; B, left upper male canine in view a, anterior; b, ventral; c, posterior; d, dorsal; C fragment of maxilla with right P4–M2 with associated right and left M3. Scale bar = 50 mm.

This new material from the type locality of *Lis. jeanneli* allows the first non-ambiguous association of upper and lower dentition of the species, the lower dentition being so far unknown from the type locality. The dental remains from Moruorot are here primarily compared to the listriodont remains from Fategad and Rusinga.

Mandible and lower dentition (Fig. 6)

The hemimandible KNM MO 18127 (Fig. 6A) is broken just anteriorly to the p1–2 diastema and pos-

teriorly to the vascular incisura. The body of the mandible is wide and massive, and bears two foramina located at the level of the p3 and p4. The vascular incisura is present but shallow; the lingual face is covered by a mineral deposit of calcite hiding the spina lingualis and thus hiding whether the structure is absent or broken. The posterior margin of the symphysis forms a wide arch and is thicker than that of the specimen from Rusinga (Fig. 7A vs. B).

The mandible from Fategad is more gracile than the specimen from Moruorot. This difference could be

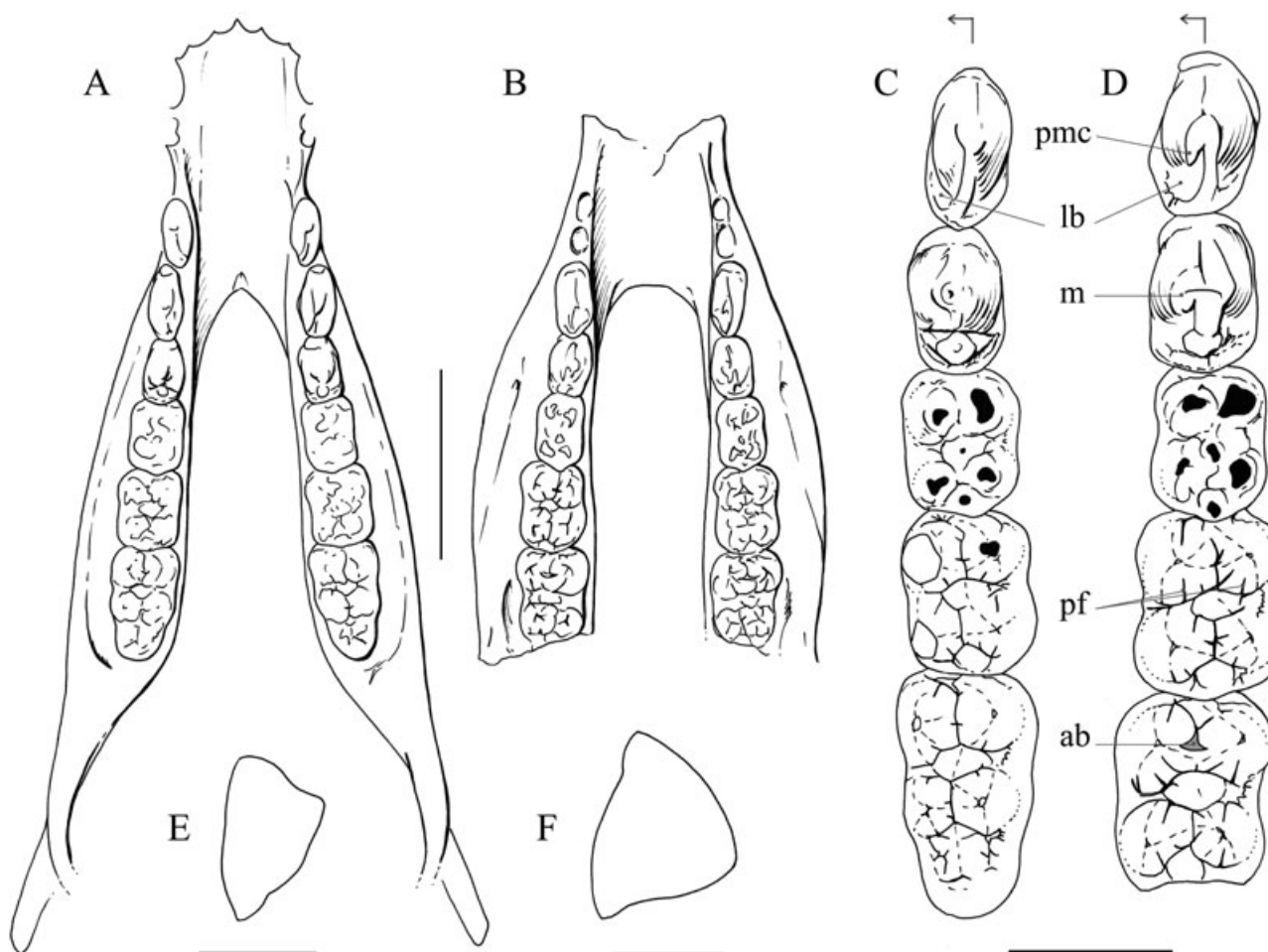


Figure 7. Comparison of mandibles and lower cheek teeth of *Listriodon jeanneli* from Moruorot (KNM MO 18127, B, D, F) and *Kubanochoerus anchidens* Rusinga (KNM RU 2785, A, C, E). A–B, occlusal views; C–D, detail of the jugal teeth; E–F, right male lower canine section, postfacet orientated downwards. A and B are reconstructions of the original specimens. Abbreviations: ab, anterior basin; lb, lingual basin; m, metaconid; pf, postfossid; pmc, postmetacristid; Scale bars: A–B = 50 mm, C–F = 20 mm.

a result of sexual dimorphism, but unfortunately, it is impossible to determine the sex of the Fategad individual, the specimen being broken in front of the p2. The specimen from Fategad also presents a very shallow vascular incisura.

Lower male canine: the section of the right lower male canine is visible on the mandible. The size of the tooth is superior to that of Rusinga and its section is clearly different. The ectofacet of the specimen from Moruorot is wide, conferring a verrucosic shape to the section of the tooth (Fig. 7F), whereas the canine from Rusinga presents a very short ectofacet compared to the postfacet (Fig. 7E), making the section of the tooth more scrofic in shape.

Premolars: the p3 bears strong mesial and distal cingulids, the main cuspid is high, more than that of p4. Two cristids run from the apex of the main cuspid:

the postprotocristid and a short one that could be assimilated to an incipient metaconid or to the postmetacristid (Figs 6A, 7D). This structure is not found in the p3 from Rusinga (Fig. 6C), which presents only a postprotocristid with accessory conules. The p3 of the specimen from Rusinga is more slender and more elongated than that of the specimen from Moruorot, its size being even larger than that of the p4. The lingual basin of the posterior part of the p3 from Rusinga is more reduced than that of the specimen from Moruorot.

The p4 bears a reduced metaconid located at the protoconid level (Fig. 6A). The preprotocristid is well developed, in contrast to the specimen from Rusinga in which this structure is absent (Fig. 7C). The distal part of the tooth is not wide and the hypoconid consists of a simple rounded cuspid lying in a

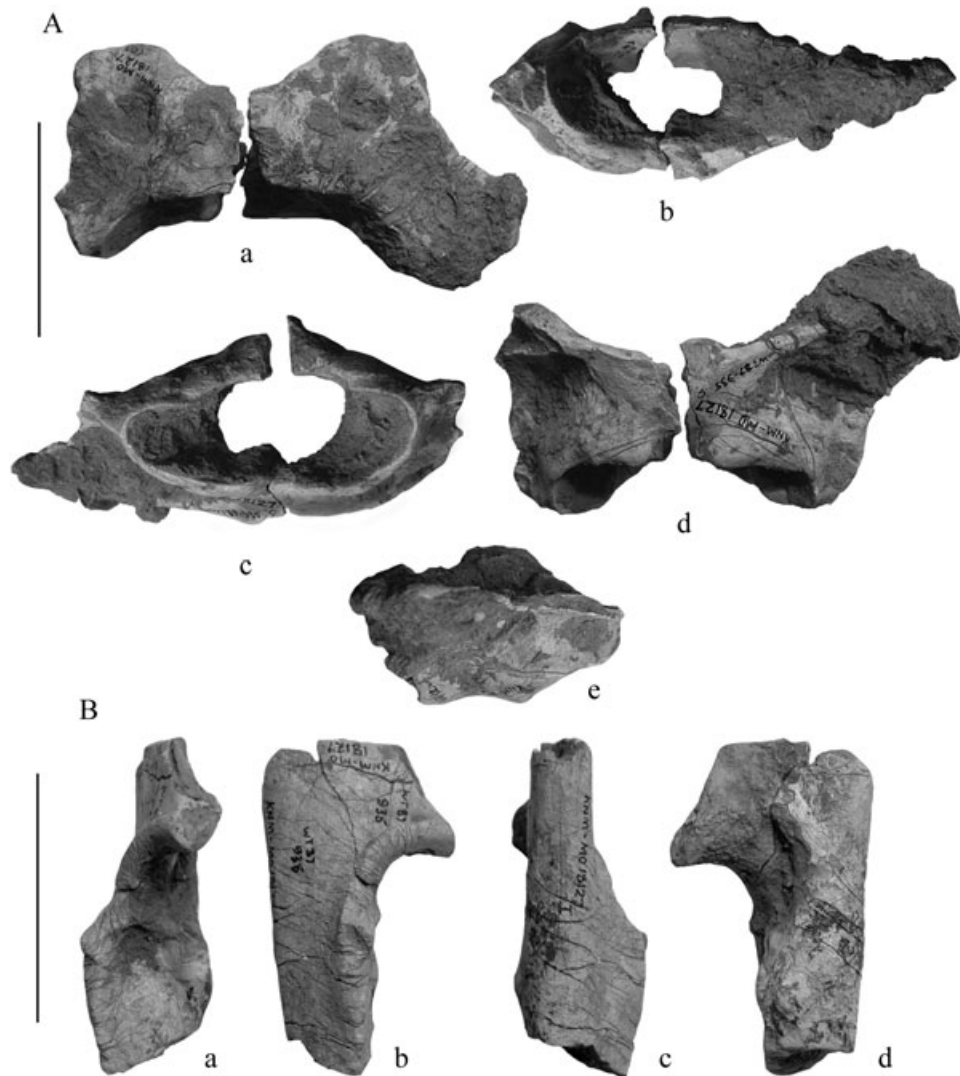


Figure 8. Postcranial remains of *Listriodon jeanneli* (KNM MO 18127). A, atlas in view: a, dorsal; b, posterior; c, anterior; d, ventral; e, lateral; B, proximal right ulna in view: a, anterior; b, lateral; c, posterior; d, medial. Scale bars = 50 mm.

subcentral position. The p4 from Fategad (IM GSI 18098; figured by Van der Made, 1996: pl. 13, 3) exhibits the same structure. However, the morphology of the p4 from Rusinga is close to that of *Lib. massai*: the tooth has no differentiated metaconid and the preprotocristid is reduced or lacking, the distolingual part of the tooth has no basin and no bulge, and the buccolingual diameter of the tooth is thus smaller than that of the p4 of Moruorot and Fategad (Fig. 7C).

Lower molars: the specimen from Moruorot presents a clear reduction of the width of the m1 compared to the m2 (Figs 6A, 7D). The cuspids are high and narrow, with angular crests. The groove pattern is of the listriodontine type, with an anterior basin

resulting from the confluence of the prefossids and the groove separating the protoconid from the preprotoconulid (Orliac, 2006).

The reduction of the m1 compared to the m2 is also found in the specimen from Fategad. The groove pattern of the type specimen of *D. fategadensis* figured by Van der Made (1996: pl. 13, 3, 9, 11) is similar to that of the specimen from Moruorot. The morphology of the lower molars of the bunodont listriodont from Rusinga differs greatly from that of the specimens from Moruorot and Fategad: there is no reduction of the width of the m1; the cuspids are lower and larger; the groove pattern is similar to that of kubanochoeres with a wide endometacristid; no

anterior basin or postfossids on the mesial lobe of the molars; and the enamel is thicker and more rugose (Fig. 7C).

Upper dentition

Male upper canine (Fig. 6B): the tooth is small compared to that of European Listriodontini. The curvature is very slight and the positions of the ventral enamel band, the major wear facet, and the cervix indicate that the tooth was orientated backward, with the apex slightly turned upward. The male canine bears three enamel bands: anterior, dorsal, and ventral, the latter being the largest. The shape of the postanticleine is difficult to determine, but the dorsal enamel band is slightly displaced on the posterior face, which is congruent with the slight upward orientation of the apex. This morphology is close to that of the specimen (KNM RU 952) from Rusinga; however, the Moruorot specimen is larger, the size difference being more important for the canine than for the cheek teeth. Only the part covered by enamel is preserved on the specimen from Rusinga. The dorsal enamel band is not shifted on the posterior face, and the apex is not turned upward as in the specimen from Moruorot.

P4: the P4 bears two buccal cusps. The metacone is slightly smaller than the paracone and clearly separated from it by a groove (Fig. 6C). The protocone lies in an anterior position. The postprotocrista is low and narrow, constituted of many enamel knobs. It joins the cingulum distally and the endometacrista buccally. The lingual cingulum is interrupted at the protocone level. The P4 from Rusinga also bears a clear metacone, but it is smaller than the paracone. The holotype of *Lis. jeanneli* also presents a P4 with a reduced metacone; however, the protocone and the postprotocrista of Rusinga are more massive. This structure joins the distal cingulum, but does not contact the metacone, which is devoid of endocrista. The distal part of the P4 from Rusinga is simpler than that from Moruorot, and the structures of the protocone are clearly separated from those originating from the metacone.

Upper molars: the upper molars from Moruorot bear high and angular cusps. Crests are well differentiated and separated by clear grooves. The preprotoconule intercalates between the two anterior cusps and contacts the endoprotocrista, which is elongated and inserts between the paracone and the pretetraconule. The two first molars bear a sharp ectohypocrista. On the M2 the two distal prefossa form a small basin, this structure, also found in the holotype of *Lis. jeanneli*, is lacking in the specimen from Rusinga. The M2 also bears a complete posthypocrista; this structure is also found in the holotype of *Lis. jeanneli* and in European listriodonts, but is incomplete in the specimen from Rusinga. The lingual cingulum is

interrupted at the paracone level in the specimen from Moruorot whereas the specimens from Rusinga exhibit a strong and unbroken buccal cingulum.

Postcranial remains

Atlas (Fig. 8A): the specimen is slightly dorsoventrally compressed and the transversal processes (wings) of the bone are damaged. However, the straight posterior margin of the dorsal face undoubtedly indicates that it can be referred to Suidae (ruminants present a deep inflexion of this margin). The general morphology of the bone is very close to that of extant suids. However, the atloideous fossa (Fossa atlantis) is shallower and the dorsal and ventral tubercles are clearly reduced. The dorsal tubercle has a weak posterior extension. The ventral tubercle is weakly salient ventrally. Compared to *Sus scrofa*, the lateral extension of the transversal process is more prominent and similar to that of *Phacochoerus aethiopicus*.

This observed morphology is congruent with that of the few known specimens of European bunodont listriodonts. One atlas of *E. adelli* is known from Els Casots (Spain, IPS 9096-20) and two specimens of *Lis. retamaensis*, one complete and perfectly preserved (MNHN BE 8412), are known from Beziau (France), both exhibiting the same morphology. The specimen of *Lib. massai* from Gebel Zelten stored at the MNHN (MNHN LBE 693) is too fragmentary to give an idea of the bone shape. However, the preserved part presents the same characteristics as other listriodont atlases. The atlas of *B. anchidens* is unfortunately unknown.

Ulna (Fig. 8B): only the proximal articular surface of the ulna is preserved. In the listriodonts, the proximal ulna differs markedly from that of extant suines. The radio-ulnar contact is much wider and flatter in Listriodontini and the facet corresponding to the capitulum of the humerus is lacking (Orliac, 2006).

The proximal part of the bone, at the level of the contact with the radius is medially shifted, the medial face of the bone being more developed than in extant taxa.

The ulnar proximal extremity of *Lis. jeanneli* is very close to that of *Eurolistriodon* from Els Casots (Spain) and Béon1 (Orliac, 2006), and of *Lis. lockharti* from Córcoles (M. J. Orliac & F. Alférez, unpubl. data), the only difference being a slightly more lateral orientation of the olecranon that may be a result of deformations.

DISCUSSION

SPECIFIC ASSIGNATION OF THE LISTRIODONT REMAINS FROM MORUOROT AND KALODIRR

The morphological similarity between the holotype of *Lis. jeanneli* and the listriodont remains from

Moruorot and Kalodirr justifies assignation of this latter material to the same species. The morphological correspondence of the mandible from Moruorot and the holotype of *Dicoryphochoerus fategadensis* Prasad, 1967 validates the synonymy between the African and Indian taxa proposed by Van der Made (1996), *Lis. jeanneli* Arambourg, 1933 having priority.

There has been a long-running debate about the generic assignation of the species described by Arambourg (1933) as *Lis. jeanneli*. Arambourg (1963) transferred the species to *Bunolistriodon* when he erected this genus to gather together European and African bunodont and bunolophodont listriodonts. This attribution was followed by Wilkinson (1976) when he added the material from Rusinga to the hypodigm of the species. Then Pickford (1986), on the basis of the characters of type material and of the material from Rusinga, placed the species in the genus *Libychoerus* (a kubanochoere) especially on: posterior margin of the palate located immediately behind M3 and V shaped; canine small pointed laterally; p4 with incipient innerhugel (metaconid); lower molars strictly bunodont. In his revision of the subfamily, Van der Made (1996) placed the species in the genus *Bunolistriodon* but without making any comments about the generic assignations of the material.

The new cranial material from Kalodirr reveals that the basicranial morphology of *Lis. jeanneli*, with a derived auditory region, is similar to that of most advanced Eurasian lophodont forms of *Listriodon* and suggests the attribution of the species to this genus. As this species is bunolophodont, it also puts forward the synonymy of *Bunolistriodon* with *Listriodon* already proposed by several authors (Leinders, 1975; Pickford & Morales, 2003; Orliac, 2006). Meanwhile, there are also some clear differences between the cranial architecture of *Lis. jeanneli* and the lophodont species such as *Lis. splendens*; notably: (1) the position of the orbit; (2) the level of the glenoid surface; (3) the general height of the cranium; and (4) the morphology of the zygomatic arches. This is not surprising as the listriodont cranium from Kalodirr and *Lis. splendens* represent two clearly different species, separated in time by at least 3 Myr. *Listriodon splendens* represents the most derived listriodont species and exhibits an elongated snout (correlated to the posterior position of the orbit) and an elevated braincase (correlated to the high glenoid fossa). The four cranial features mentioned above may probably appear in their primitive state in *Lis. jeanneli* and thus could not be put forward for a generic separation. Unfortunately, the scarcity of cranial remains of European bunolophodont *Listriodon* makes it impossible for now to determine if the cranial features seen in *Lis. jeanneli*, such as the particularly shallow

aspect of the cranium, are typical of bunodont *Listriodon* and could help to define the genus *Bunolistriodon*. When Arambourg (1963) proposed the grouping of the European and African bunodont listriodonts in the genus *Bunolistriodon*, he mentioned several cranial characters based on a listriodont cranium from Gebel Zelten (Libya). However, this cranium was revealed to be a kubanochoere (Leinders, 1975; Pickford, 1986; Van der Made, 1996) and the cranial characteristics of Eurasiatic bunolophodont listriodonts remain unknown.

The association in *Lis. jeanneli* of a bunolophodont dentition and a derived auditory region similar to that of most advanced lophodont Listriodontini (such as *Lis. splendens*) indicates that the acquisition of a derived auditory region precedes the acquisition of advanced lophodonty. The morphological divergence between the auditory region of *Lis. jeanneli* and *Kubanochoerus* is similar to that observed between *Eurolistriodon* and *Listriodon* described by Orliac (2006). Nevertheless, the cranium of *Lis. jeanneli* presents some similarities with the kubanochoerine cranium, such as: (1) the shape of the palate posterior margin; (2) the presence of cranial protuberances (here only jugal); (3) the shape of the premaxilla anterior margin; and (4) the shallow aspect of the cranium. These characters were proposed by Gabunia (1960), Pickford (1986, 1993), and Pickford & Moyá Solá (1995) for distinguishing listriodonts and kubanochoeres at a familial level. Some of them have already been examined by Van der Made (1997). I can add that the shape of the posterior border of the palate is unfortunately unknown for European bunodont Listriodontini, the guttural area of the two craniums of *Eurolistriodon* (IPS 9096, Pickford & Moyá Solá, 1995; MHNT G2 587, Orliac, 2006) being deeply deformed. It is thus impossible to comment on this character distribution for now. Concerning the maxillary protuberance, the morphology of this structure is quite different in *Lis. jeanneli* and in *Kubanochoerus*: the internal surface of the zygomatic arch is slightly domed in *Lis. jeanneli* and concave in *Kubanochoerus* (MNHN LBE 563, *Lib. massai*). Concerning the shallow aspect of the cranium, the comparison of the ratio of the height of the glenoid surface to the length of the snout (Table 1) indicates that *Lis. jeanneli* presents the lowest glenoid surface relative to the occlusal plane. Furthermore, a low glenoid surface is also observed in *Eurolistriodon* and *Lopholistriodon* and is most likely primitive among Listriodontinae. The shape of the premaxilla anterior margin is correlated to the presence of a mesial contact between the upper incisors; noncontacting premaxillae are also observed in *Eurolistriodon* (Orliac, 2006) and this character, observed in Namachoerini (*Lopholistriodon moruoroti*, PQ ad 138) and

in Kubanochoerini (*Kubanochoerus massai* MNHN LBE 243) is primitive among Listriodontinae *sensu* Van der Made (1996).

COMMENTS ON THE MATERIAL FROM RUSINGA

Van der Made (1996) erected the species *B. anchidens* for the small listriodont of Rusinga, referred to *B. jeanneli* by Wilkinson (1976) and *Lib. jeanneli* by Pickford (1986). Van der Made (1996, 2003a, b) proposed a lineage comprising *Bunolistriodon affinis*, *B. anchidens*, and *B. jeanneli* based on increase in size, whereas Pickford (1986), on the basis of morphological differences between the mandible of Rusinga and those of European listriodonts, attributed the material from Moruorot and Rusinga to the genus *Libycochoerus*.

Several mandibular and dental characters differentiate the Moruorot material, here attributed to *Lis. jeanneli*, from that of Rusinga, beyond the simple size difference advocated by Van der Made (1996): (1) p3 from Rusinga simple, without double postcristid and lingual basin; (2) mesiodistal diameter of the p3 is superior to that of the m1 from Rusinga; (3) the p4 from Rusinga is more simple and narrow, with reduced precristid; (4) the morphology of the lower molar mesial lobe of the specimens from Rusinga is similar to that of Kubanochoeres; (5) in Rusinga specimens, the wear of the lower cheek teeth is more apical, whereas in Moruorot specimens the wear is more distal and vertical; (6) the Rusinga molar cusps are wide, mesial and distal cusps contacting each other at their bases, whereas Moruorot cusps are narrower and separated by a short plateau; (7) the posthypocrista is not fully developed in Rusinga specimens; and (8) the horizontal ramus of the mandible is narrower in Rusinga specimens.

All these characters indicate different lineages and justify a systematic separation, not only at the specific level as suggested by Van der Made (1996), but also as a generic level as supported by Pickford (1986, 2001) and Pickford & Morales (2003). Pickford (1986, 1988, 1993, 2001) recognized five genera among the kubanochoeres: *Kenyasus*, *Nguruwe*, *Libycochoerus*, *Kubanochoerus*, and *Megalochoerus*. *Kubanochoerus* differs from *Libycochoerus* by the presence of a frontal 'horn', and *Megalochoerus* differs from the two other genera by a buccal enlargement of the upper molars. However, it is not possible to verify the presence of cranial appendages in *Libycochoerus* as no male cranium is known so far for this genus. Therefore, this character cannot be advocated as a discriminant character. The genus *Libycochoerus* Arambourg, 1961 is here considered as a junior synonym of *Kubanochoerus* Gabunia, 1960. The material from Rusinga is here referred to the species *Kubanochoerus anchidens*.

Beyond taxonomic distinction, the differences observed between the specimens from Rusinga on the one hand, and Moruorot, Kalodirr, and Fategad on the other, indicate different masticatory movements and feeding habits. The premolars are higher and sharper and the molarization of the p4 and the development of internal crests of the molars are more advanced in Moruorot specimens. The wear facets are more distal and more vertical in Moruorot, which indicates a more reduced range of masticatory movements involving sharper cutting edges. In *K. anchidens*, wear facets are much more extended and cusps are more rounded with thick enamel suggesting a diet based on quite hard elements.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis based on 76 dental and cranial characters controlled for 22 taxa was performed in order to define how *Lis. jeanneli* and *B. anchidens* relate to each other and to other bunodont Listriodontinae *s.l.* (listriodonts + kubanochoeres). The present analysis was not intended to provide a complete picture of the phylogenetic relationships within Listriodontinae, it rather consisted of a test of the systematic conclusions resulting from the morphological observations. The ingroup included African and Eurasian bunodont to sublophodont Listriodontinae. Poorly known species represented only by scarce dental remains were not included in the analysis. The palaeochoere *Palaeochoerus* and the suids *Hyotherium* and *Sus* were chosen as outgroups. The taxa and character lists are given in Supporting Information Appendix S1 and in Appendix 1; the dental characters are illustrated in Appendix 2. The data matrix is provided in Appendix 3. The data were treated under the assumptions of unweighted parsimony, using PAUP 3.1 (Swofford, 1993), with the exact 'Branch & Bound' algorithm.

RESULTS

The strict consensus of the 27 shortest trees [length (L) = 153; consistency index (CI) = 0.55; retention index (RI) = 0.77] is presented in Figure 9. Only the unambiguous synapomorphies are discussed hereafter. The distribution of character states at each node is given in Supporting Information Appendix S2. The resolution is satisfactory and only a few polytomies are observed, at the nodes D, I, and L. However, several nodes are weakly supported (Bremer support of 1).

Monophyly of Listriodontinae

The cladistic analysis shows one main clade, recognized here as the Listriodontinae. This clade is

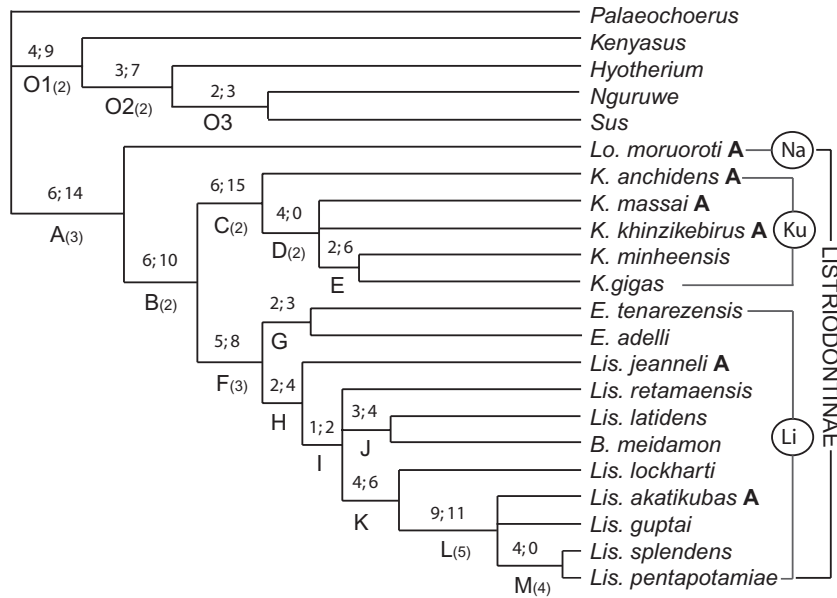


Figure 9. Phylogenetic relationships of the Listriodontinae: strict consensus of the 27 parsimonious trees (length = 153; consistency index = 0.55; retention index = 0.77). Above the nodes are the number of unambiguous synapomorphies followed by the total number of synapomorphies (ACCTRAN optimization). Bremer support (Bremer, 1994) superior to 1 is in parentheses after the letter corresponding to the node. A indicates the African taxa. Abbreviations: Na, Namachoerini; Ku, Kubanochoerini; Li, Listriodontini.

supported by six non-ambiguous synapomorphies, of which four are nonhomoplastic: upper central incisor with paraconal and metaconal part in the same plan (1^1 ; RI = 0.67); lower incisors with three apical lobes (10^2 ; RI = 0.85); upper male canine with a circular section (20^1 ; RI = 0.66); upper male canine pointed backwards (22^1 ; RI = 0.75); P3 with accessory cusps in the lingual basin (26^1 ; RI = 1.00); buccal cingulum of the lower premolar developed mesially and distally (39^1 ; RI = 1.00).

The monophyly of the Listriodontinae *sensu* Van der Made (1996) is not supported because *Nguruwe kijivium* is excluded from the clade corresponding to the subfamily and gathers with *Hyotherium* and *Sus scrofa* in clade O2 (Fig. 9). The latter is defined by four non-ambiguous synapomorphies: the presence of a dorsal groove on the upper male canine (17^1 ; RI = 1.00); a lack of groove on the endofacet of the lower male canine (25^0 ; RI = 0.66); the presence of an hypoconule on the upper molars (35^1 ; RI = 0.83); endocristids of the first lobe posterior and low (53^1 ; RI = 0.87).

Structure of the Listriodontinae

Amongst Listriodontinae, the three tribes proposed by Van der Made (1996) can be recognized: the Namachoerini represented by *Lo. moruoroti*, the Kubanochoerini, and the Listriodontini. Kubanochoerini and

Listriodontini form a monophyletic group and share six non-ambiguous synapomorphies: a lack of posterior carena in the upper canine (18^0 ; RI = 0.75); M2 bearing a sharp ectohypocrista (33^1 ; RI = 0.75); p2–4 not clearly increasing in size from mesial to distal (40^1 ; RI = 0.80); an infraorbital fossa on the jugal (63^1 ; RI = 1.00); the anterior border of the orbit located at the level of the M3 (65^1 ; RI = 0.50); a lack of precanine constriction (68^1 ; RI = 0.66).

The tribe Listriodontini, gathering together European, Asiatic, and African species, is unambiguously defined by five synapomorphies: an asymmetrical crown of the I2 (9^1 ; RI = 0.75); i2 with a wide base of the distal fossa (13^1 ; RI = 1.00); a wide open space between the endocristids of the mesial lobe of the lower molars (47^1 ; RI = 1.00); postfossids on the mesial lobe of the lower molars (51^1 ; RI = 1.00); and a lingual spine on the mandible (76^1 ; RI = 1.00).

Listriodon jeanneli belongs to clade H (Fig. 9) that gathers the members of the genus *Listriodon* and members of the genus *Bunolistriodon* and appears to be paraphyletic. Clade H is defined by two non-ambiguous synapomorphies of the auditory region: a reduction of the postglenoid process (71^1 ; RI = 0.75) and a well-developed post-tympanic process (72^1 ; RI = 0.66). *Listriodon jeanneli* appears to be the most basal member of clade H. Indeed, this species does not exhibit the upwardly directed male canine (22^2 ;

RI = 0.75) observed in more derived species of the clade. *Listriodon latidens* and *Listriodon meidamon* form the small clade J defined by three non-ambiguous synapomorphies: a wide I1 (8²; RI = 0.66); a complete anterior lophid of the lower molars (48¹; RI = 0.66); and an opening of the anterior basin of the m2–3 (50¹; RI = 0.66). These characters, traducing some degrees of lophodonty, are respectively convergently present in clades M and L. *Listriodon lockharti* gathers with *Listriodon akatikubas*, *Listriodon guptai*, *Lis. splendens*, and *Lis. pentapotamiae* in clade K. Clade K is defined by: a bulge of the endosynclinid of the i2 (14¹; RI = 1.00); an upper male canine with a small ray of curvature (20¹; RI = 0.50); and the mesiodistal length of the lower premolars increasing from p2 to p4 (40¹; RI = 0.80). *Listriodon akatikubas* and *Lis. guptai* gather with *Lis. splendens* and *Lis. pentapotamiae* in clade L on the basis of seven non-ambiguous synapomorphies: I1 with several apical grooves divided into two principal lobes by a deep median groove (6¹; RI = 1.00); full anterior lophe on upper molars (30¹; RI = 0.75); posthypocrista of the M3 merged to the distal cingulum (37¹; RI = 1.00); linguobuccal diameter of the distal part of the p4 wider than the protoconid (43¹; RI = 0.75); hypoconid of the p4 developed lingually (44¹; RI = 1.00); anterior lophid complete (48¹; RI = 0.66); distance between the metaconid and entoconid wide in lingual view (49¹; RI = 1.00); opening of the anterior basin of the m2–m3 (50¹; RI = 0.66). Taxa of this clade are listriodonts with advanced or full lophodonty.

Kubanochoerus anchidens and the tribe Kubanochoerini

These results indicate that *Lis. jeanneli* undoubtedly differs from the listriodont from Rusinga (Kenya, c. 18 Myr) previously attributed to this species by Wilkinson (1976) and Pickford (1986) and referred to '*B. anchidens*' by Van der Made (1996). *Kubanochoerus anchidens* belongs to the Kubanochoerini clade. This tribe is here non-ambiguously defined by: lower incisors divided in two apical lobes (10¹; RI = 0.85); i2 with a thick distal edge (15¹; RI = 1.00); lower male canine devoid of groove on the entofacet (25⁰; RI = 0.66); a premolar row of the lower cheek teeth longer than the molar row (38¹; RI = 1.00); linguobuccal length of m1 not clearly inferior to that of the m2 (45⁰; RI = 0.60); and the size of the endometacristid of the m3 larger than the endoprotocristid (55¹; RI = 0.80).

The kubanochoere from Rusinga appears to be the most basal member of the Kubanochoerini. More derived members of the tribe gather in clade D supported by four non-ambiguous synapomorphies: a wide postprotocrista on the P4 (27¹; RI = 1.00); hypo-

conule on the M3 (35¹; RI = 0.83); the presence of an endometacristid more developed than the endoprotocristid (55¹; RI = 0.80); and a lack of vascular incisura (75¹; RI = 0.66).

SYSTEMATIC IMPLICATIONS

These results support a close relationship between kubanochoeres and listriodonts, both groups being sister taxa of *Lo. moruoroti*. Given the morphological divergence existing between other suid subfamilies, and given the numerous morphological characters uniting *Lo. moruoroti* (Namachoere), kubanochoeres, and listriodonts in the same clade, I recognize these taxa as three tribes within an enlarged concept of the subfamily Listriodontinae as suggested by Van der Made (1996). This result will have to be tested by the inclusion of additional species of the genus *Lopholistriodon*. Besides, the name *Listriodon* comes from the Latin *listrion* which means 'small spade' and particularly fits the spatulated upper central incisors of the members of the group. The three tribes considered here all present spatulated upper incisors (1¹) and I propose that the name Listriodontinae should apply to the clade defined, at least, by this character traditionally mentioned in the literature (Stehlin 1899/1900; Pearson, 1928; Leinders, 1975; Pickford, 1986; Van der Made, 1996). Furthermore, this clade is one of the major clade of the Suidae (Orliac, 2007a; M. J. Orliac, unpubl. data) and, as the other major clades of the family are recognized as subfamilies, it seems more appropriate to recognize one subfamily: the Listriodontinae, which gathers three tribes: Namachoerini, Kubanochoerini, and Listriodontini.

The results of the present cladistic analysis provide a clear definition for the two tribes discussed in this paper, Listriodontini and Kubanochoerini. The kubanochoeres are not regarded here as a subfamily but as part of the Listriodontinae clade for the reasons given above (*contra* Pickford, 1986, 1993, 2001, 2007a, b; Pickford & Moyá Solá, 1995; Liu, 2003; Harris & Liu, 2007).

The medium size bunodont listriodont from Rusinga referred to *Bunolistriodon anchidens* by Van der Made (1996) unambiguously belongs to the Kubanochoerini tribe as previously proposed by Pickford (2007a, b). Pickford (1993, 2007a, b) recognized five genera of kubanochoeres: *Nguruwe*, *Kenyasus*, *Libycochoerus*, *Kubanochoerus*, and *Megalchoerus*. *Kenyasus* and *Nguruwe* are here excluded from Listriodontinae and additionally from the tribe Kubanochoerini.

Two genera can be recognized amongst the tribe Listriodontini: *Eurolistriodon* and *Listriodon*. The species *K. anchidens* apart, the genus *Bunolistriodon* appears to be paraphyletic and represents a grade of nonlophodont listriodonts. The taxa of clade H are

here all recognized as members of the genus *Listriodon*. Therefore, the name *Bunolistriodon* Arambourg, 1963 is considered as a junior synonym of *Listriodon* Von Meyer, 1946. The results of the present analysis indicate that the bunodont listriodont from Moruorot and Kalodirr belongs to the genus *Listriodon* and should be named *Listriodon jeanneli*.

REMARKS ON THE ORIGIN AND EVOLUTION OF LISTRIODONTINAE

Pickford (1993, 2001, 2007b) considered *Kenyasus* to be a basal representative of the kubanochoeres. However, the results of the present analysis indicate that *Kenyasus* is not closely related to this group and cannot be regarded as a plausible ancestor of the kubanochoeres. Van der Made (1996) attributed the genus *Nguruwe* to the tribe Namachoerini and proposed this taxon as the most basal member of the group. However, he also mentioned that, in Namachoerini, 'the fossil shows no unique common derived character uniting all species' (Van der Made, 1996: 125) and the species are arranged according to their size and stratigraphical position. The present analysis indicates that *Nguruwe* exhibits derived characters of clade O1 that gathers *Sus* and *Hyotherium*, such as the presence of a dorsal groove on the upper male canine (17¹) or the presence of an hypoconule on the M3 (35¹), and is not part of the Namachoerini. The taxonomic sampling of the present analysis is not accurate enough to understand the position of Listriodontinae within Suidae. However, the subfamily does not appear as a sister taxon of *Hyotherium* and is clearly separated from this genus that is proposed as the 'ancestral stock' from which the Listriodontinae originated (Wilkinson, 1976; Pickford, 1993; Pickford & Moyá Solá, 1995; Pickford & Morales, 2003). It is also worth noting that the most basal member of the Listriodontinae is a member of the Namachoerini, *Lo. moruoroti*. The representatives of the tribe Namachoerini are all exclusively known from Africa. Furthermore, the first members of the Kubanochoerini are also African taxa as it is the case for the first representative of the genus *Listriodon*. Thus, the question of an African origin of the subfamily Listriodontinae should be considered, as the group might probably have undergone its first radiation on the African continent.

Amongst Listriodontinae, the first representatives of Kubanochoerini and of the genus *Listriodon* are present in Kenya, in Rusinga (*K. anchidens*) and Moruorot (*Lis. jeanneli*). The material from these two localities has in the past been referred to the same species (Wilkinson, 1976; Pickford, 1986). In fact,

being the least differentiated kubanochoere, *K. anchidens* is morphologically close to Listriodontini. However, *K. anchidens* and *Lis. jeanneli* exhibit clear morphological differences and belong to different clades. Wilkinson (1976) indicated that the material from Rusinga exhibits some plesiomorphic characters also observed in hyotheres and kubanochoeres. The present analysis indicates that some characters traditionally considered as primitive in kubanochoeres, such as the strict bunodonty, are in fact derived amongst Listriodontinae and are present convergently in *Hyotherium*.

During the lower and middle Miocene, the upper and lower cheek teeth of Kubanochoerini became increasingly robust. The Kubanochoerini developed bilobate upper central incisors and lower incisors, the latter being more massive and more vertically implanted than those of Namachoerini and Listriodontini. The premolars are particularly robust and the premolar row is longer than the molar row (38¹). Their crown is high and the mesiodistal length of the p3 is greater than that of the m1. The m1 breadth is not reduced compared to that of m2–3 (45⁰). The lower molars also present a robust structure with low and backward orientated endocristids (53¹). The robustness of the teeth, the vertical implantation of the upper incisors, and the lack of developed transverse structure suggest that kubanochoeres withdrew from the lophodont way and from the folivorous diet for a more diverse diet including tougher food. A tougher food supply might be correlated to the more arid periods suggested by palaeoenvironmental data of the Hiwegi formation of the site of Rusinga (Andrews, 1992; Bestland & Krull, 1999). The structure of the kubanochoerine teeth gets even more robust with, at clade D, the acquisition of a massive postcrista on the P4, molarizing the tooth and playing the role of a second lingual cusp. The important development of the endometacristid also reinforces the crushing surface of the lower molars. Listriodontini and Kubanochoerini acquire convergently upwardly directed upper canines in males (22²).

Listriodon jeanneli is the first African representative of the tribe Listriodontini, at 17.5 Mya. This species, the most basal member of the genus *Listriodon*, is also known from the Indian locality of Fategad. *Listriodon affinis* (Pilgrim, 1908) from the Bugti Beds (Kumbhi, Pakistan) is traditionally regarded as the most ancient and most primitive member of the Listriodontini (Fortelius, Van der Made & Bernor, 1996; Van der Made, 1996). However, the scarcity of these remains (a maxilla fragment with P4–M1) prevents me from attributing with certainty *Lis. affinis* to the Listriodontini or Kubanochoerini.

CONCLUSIONS

The new listriodont remains from the late early Miocene localities of Moruorot and Kalodirr considerably improve our knowledge of the species *Lis. jeanneli*. This species exhibits a characteristic cranial architecture with a general shallow aspect of the cranium expressed by a very low glenoid surface, and a derived auditory region that regroups this species with the European lophodont species *Lis. splendens* in the same clade. The results of the cladistic analysis led to two major conclusions concerning the systematics of the Listriodontinae: (1) the subfamily Listriodontinae is monophyletic and includes the three tribes recognized by Van der Made (1996, 1997): Namachoerini, Kubanochoerini, and Listriodontini, the monophyly of the latter two also being confirmed; and (2) the genus *Bunolistriodon*, being paraphyletic, should be abandoned and *Listriodon* should be used to name bunodont as well as lophodont species.

Even if the presence of cranial appendages in kubanochoeres is a clear distinctive trait of the group, the assignation to kubanochoeres or to listriodonts of material when this feature was not observable has often been problematic in the literature. However, a list of key synapomorphies of the two listriodontine tribes has been established on the basis of the cladistic results and the observations made in this paper. The tribe Kubanochoerini presents a clearly more robust dentition and can be defined by characters other than cranial appendages, such as a lower pre-molar row longer than the molar row. The Listriodontini tribe can be defined by several dental characters, such as an asymmetrical crown of the I2; i2 with a wide basis of the distal fossa; and a wide open space between the endocristids of the mesial lobe of the lower molars.

Furthermore, this first general overview of the phylogeny of Listriodontinae through a cladistic analysis stresses the role of Africa in the biogeographical history of listriodonts. This role needs to be carefully investigated.

ACKNOWLEDGEMENTS

I am grateful to M. G. Leakey for having granted access to the new material from Kalodirr and Moruorot. I am also indebted to the following institutions and individuals for access to the specimens that form part of this study: E. Mbua and M. Muungu, National Museums of Kenya; J. Morales and B. Sánchez Chillón, Museo Nacional de Ciencias Naturales, Madrid; B. Azanza, Universidad de Zaragoza; A. Galobar Lorrente, Institut Paleontològic Dr Miguel Crusafont, Sabadell. Many thanks to J.-R. Boissérie, J. M. Harris, P. Tassy, and D. Germain for critical

comments on early versions of the manuscript and to A. Grossman for providing additional information about the Kenyan sites. I thank J. Van der Made for fruitful discussions on Listriodontinae. Many thanks to M. Pickford for discussions on suids and for kindly providing good photos of the specimen from Fategad. This work was supported by a MRT grant (ED 227) of the French Ministry of Research and University Education, by the Muséum National d'Histoire Naturelle UMR 5143, and the département Histoire de la Terre.

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APPENDIX 1

List of the characters used in the data matrix.

INCISORS

1. I1, shape of the crown: paraconal part of the teeth forming an angle with the metaconal part (0); paraconal part in the same plan with the metaconal part (1)
2. upper incisors, wear: essentially apical (0); essentially lingual (1)
3. I1, cingular fossa: narrow (0); wide (1)
4. I1, slide of the metaconal part of the crown: absent (0); present (1)
5. I1, number of lobes of the crown: one (0); two (1); several (2)
6. I1, crown with several lobes, depth of the apical grooves: similar (0); medial groove deeper dividing the crown into two lobes
7. I1, mesial contact: absent (0); present (1)
8. I1, average of the index I [defined by Van der Made, 1996, $I = (\text{mesiodistal diameter} / \text{labiolingual diameter}) \times 100$]: inferior to 150 (0); between 150 and 200; over 200
9. I2, shape of the crown: symmetric (0); asymmetric (1).
10. i1–2, number of apical lobes: one (0); two (1); three (2)
11. i2, inflexion of the distal edge: absent (0); present (1)
12. i2, lingual view, endosynclinal: absent (0); present (1)
13. i2, basis of the distal fossa: narrow (0); wide (1)
14. i2, bulge of the endosynclinal: absent (0); present (1)
15. i2, proximal part of the distal edge of the tooth: slender (0); thick (1)
16. i3, lingual view, bulge of the distal part of tooth: absent (0); present (1)

CANINE

17. upper male canine, dorsal groove: absent (0); present (1)
18. upper male canine, posterior carina: absent (0); present (1)
19. upper male canine, third enamel band: absent (0); incipient (1); complete (2)
20. upper male canine, section: mediolaterally compressed (0); circular (1)
21. upper male canine, ray of curvature: wide (0); small (1)
22. upper male canine, orientation of the tooth: downward (0); backward (1); upward (2)

23. lower male canine, section: postfacet similar to ectofacet (0); postfacet wider than ectofacet (1); postfacet inferior to ectofacet (2)
24. lower male canine, angle formed by ectofacet and postfacet: inferior to 90° (0); superior to 90° (1)
25. lower male canine, groove on the endofacet: absent (0); present (1)

UPPER CHEEK TEETH

26. P3, accessory cusps in the lingual basin: absent (0); present (1)
27. P4, postprotocrista: narrow (0); wide (1)
28. fusion of the lingual roots of the upper molars and of the anterior lophid of the lower molar: absence (0); presence (1)
29. upper molars, anterior accessory cusp: posterior, not included in the anterior cingulum (0); anterior, included in the anterior cingulum (1)
30. upper molars, anterior loph: not complete (0); complete (1)
31. upper molars, contact between the metacone and median accessory cusp: present (0); absent endoprotocrista intercalates between the two structures (1)
32. upper molars, median accessory cusp: present as an individualized structure (0); impossible to differentiate from the prehypocrista (1)
33. M2, sharp ectohypocrista: absent (0); present (1)
34. M2, posthypocrista: interrupted (0); continuous (1)
35. M3, hypoconule: absent (0); present (1)
36. M3, third lobe: absent (0); present (1)
37. M3, posthypocrista: independent from the posterior cingulum (0); merged to the posterior cingulum (1)
44. p4, shape of the hypoconid: circular (0); lingually elongated (1)
45. lower molars, reduction of the width of the m1: absent (0); present (1)
46. lower molars, anterior basin: formed by the prefossids (0); formed by the prefossids and the groove separating the preprotoconid from the protoconid (1)
47. lower molars, groove between the prefossids: narrow (0); wide (1)
48. lower molars, anterior lophid: not complete (0); complete (1)
49. lower molars, lingual view, distance between the metaconid and the entoconid: V shape (0); U shape (1); very wide (2)
50. m2–m3, opening of the anterior basin: absent (0); present (1)
51. m2, ectocristids delimited by ectofossids on the anterior lobe: absent (0); present (1)
52. m2–m3, groove isolating the prehypoconulid: absent (0); present (0)
53. m2–m3, endocristids of the first lobe: transversal and high (0); posterior and low (1)
54. m3, posterior lophid: absent or incomplete (0), complete (1)
55. m3, size of the endometacristid: similar to the endoprotocristid (0); larger than the endoprotocristid
56. m3, metaendoconulid: absent (0); present (1)

SKULL

LOWER CHEEK TEETH

38. cheek teeth, relative importance of the premolar and molar row: molar row longer than the premolar row (0); premolar row longer than the molar row (1)
39. lower premolar, buccal cingulum: reduced (0); developed anteriorly and posteriorly (1)
40. mesiodistal length of the lower premolars: increasing clearly from p2 to p4 (0); of similar size (1)
41. p4, metaconid: as a well-developed cusp (0); reduced (1)
42. p4, width of the anterior part of the teeth: slenderer or equal to the central cusp (0); wider than the central cusp (1)
43. p4, width of the distal part of the teeth: slenderer than the central cusp (0); wider than the central cusps (1)
57. zygomatic arches, orientation: ventral (0); subhorizontal (2)
58. supraorbital sulcus: parallel (0); convergent (1)
59. implantation of the upper incisors: vertical (0); subhorizontal (1)
60. canine niche in males: absent (0); present (1)
61. location of the infraorbital foramina: p3–4 level or anteriorly (0); above p4 or beyond (1)
62. preorbital fossa: absent (0); present (1)
63. infraorbital fossa: absent (0); present (1)
64. bone protuberance on the maxillary: absence (0); presence (1)
65. level of the anterior margin of the orbit: anterior to the M3 (0); at the level of the M3 (1); posterior to the M3 (2)
66. supraorbital cranial appendix(s): absent (0); present (1)
67. parietal foramina: present (0); absent (1)
68. constriction precanine: absent (0); present (1)
69. P1–P2 diastema: short (0); long (1)
70. posterior extension of the palate: anterior to the M3 (0); posterior to the M3 (1); far posterior to the M3 (2)

71. postglenoid process: more developed than the post-tympanic process (0); reduced in comparison to the post-tympanic process (1)
 72. post-tympanic process: reduced (0); forming a ventral flange (1)
 73. shape of the tympanic bulla: heart-shaped (0); elongated (1)
 74. post-tympanic part of the squamosal: not developed above the level of the opening of the auditory meatus (0); developed above the level of the opening of the auditory meatus (1)
 75. mandible, vascular incisura: present (0); absent (1)
 76. mandible, spina lingualis: absent (0); present (1)

APPENDIX 2

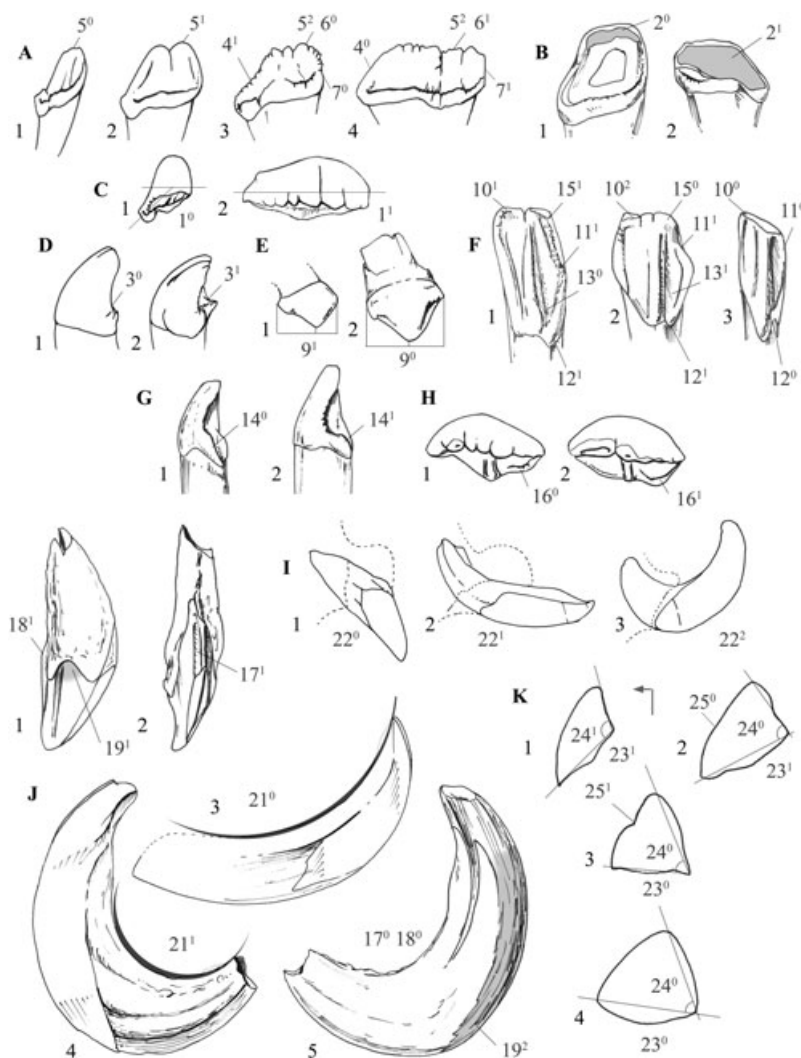
Illustration of dental characters

Plate 1: A–D, I1 of: A1, *Hyotherium lacaillei* (MHNT Béon 92 G3 111); A2, *K. massai* (MNHN LBE 368); A3, *E. tenarezensis* (MHNT Béon 2003 SN 25); A4, *Lis. splendens* (MNHN Si 270); B1, *K. anchidens* (KNM Ru 8322,); B2, *E. tenarezensis* (MHNT Béon 2003 SN 3,); C1, *H. lacaillei* (MHNT Béon 92 G3 111); C2, *Lis. splendens* (MNHN Si 270); D1, *K. massai* (MNHN LBE 368); D2 *Lis. splendens* (MNHN Si 270); E, I2 of: E1, *H. major* (MNHN SG 3554); E2, *K. massai* (MNHN LBE 561); F–G, i2 of: F1 (MNHN LBE 400); F2 *E. tenarezensis* (MNHN PEL 162); F3, *H. lacaillei*; G1, *E. tenarezensis* (MNHN PEL 483); G2 *Listriodon lockharti* (MNHN FP 1029); H, i3 of: H1, *Lis. lockharti* (MNHN Ba 449); H2 *Lis. splendens* (MNHN Si 274); I–J, upper male canine of: I1, *Hyotherium major* (MNHN SG 3618); I2 *E. tenarezensis* (MHNT Béon G2 588); I3, *Lis. splendens* (MNHN Si 429); J1–2 *H. major* (MNHN SG 3618); J3, *Lis. latidens* (NSSW 14612); J4–5 *Lis. Lockharti* (MNHN CHE 32); K, lower male canine of: K1, *Sus scrofa*; K2, *Lis. splendens* (MNHN Si 431); K3, *Lis. lockharti* (MNHN CHE 135); K4, *K. massai* (MNHN LBE 423).

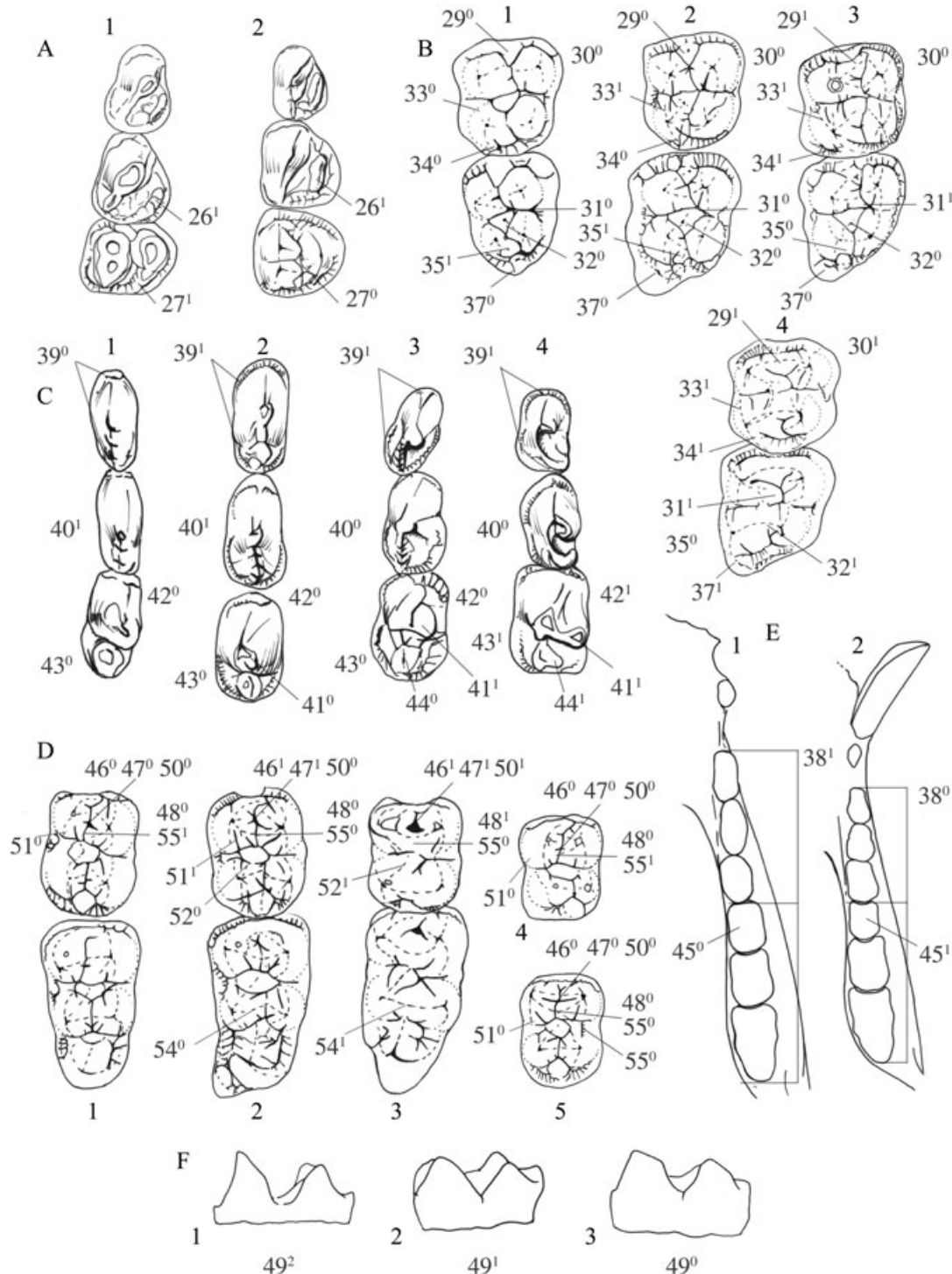


Plate 2: A, P2–4 of: A1, *K. massai* (MNHN LBE 563); A2, *Lis. retamaensis* (UCN Co 4400); B, M2–3 of B1, *H. major* (MNHN SG 3554); B2, *K. massai* (MNHN LBE 479); B3, *Lis. lockharti* (MNHN Ba 430–438); B4, *Lis. splendens* (MNHN Si 428); C, p2–4 of: C1, *H. soemmeringi* (MNHN 1959 II 313); C2, *K. massai* (MNHN 449); C3, *Lis. lockharti* (MNHN FSL 320 095); C4, *Lis. splendens* (MNHN Si 155); D, m2–3 of: D1, *K. massai* (MNHN LBE 354); D2, *Lis. lockharti* (MNHN Ba 459); D3, *Lis. splendens* (MNHN Si 307); D4, m2 of *H. soemmeringi* (MNHN SG 3554); D5 m2 of *Kenyasus rusingensis* (KNM Ru 2701); E, left lower cheek teeth of: E1, *K. anchidens* (KNM Ru 2785); E2, *Lis. lockharti* (UCBL FS 320095); F, lingual view of the m2 of: F1, *Lo. moruoroti* (KNM MB 10318); F2, *Lis. splendens* (MNHN Si 307); F3 *Lis. latidens* (NSSW 99) .

APPENDIX 3

Data matrix showing the distribution of 76 dental and cranial characters amongst 22 taxa. '?' denotes unknown data and '-' refers to non-applicable characters.

<i>Palaeochoerus</i>	00--0-0000	00??000100	?02010-100	-00000-00?	0000001000	0000000??0	????0??001	00??00
<i>Hyoherium</i>	00000-1010	000-001110	-011000010	0000110000	0000001000	0110110001	1100000000	100010
<i>Sus</i>	00--0-1-10	000-000021	1211000010	0010110000	0010101000	0110110000	1100101111	11-110
<i>Kenyasus</i>	00--0-0001	100-0011?0	-000000?10	0000110000	000?101000	0110000?00	00???0000?	00?1??
<i>Nguruwe</i>	10010-00?0	000-?01110	-001?00010	0000110?0?	-000?0100-	011011????	??????????	??????
<i>E. tenarezensis</i>	1100200112	1110000021	0100110000	1011010011	0000110000	1100001111	??1010?1?1	00?101
<i>E. adelli</i>	11002001?2	1110??0021	0100110000	10100100??	0000110000	1100001111	??1010?111	000101
<i>Lis. lockharti</i>	1111201112	1111000021	1200110000	1011010010	0100110000	110000????	??????????	????01
<i>Lis. retamaensis</i>	1111201112	1110000021	02?0110000	101101001?	0?00110000	110000?111	00??10?101	????01
<i>Lis. latidens</i>	111120?2?2	1110000021	02???100??	???????011	0000110101	110000????	???????10?	????0?
<i>B. meidamon</i>	1111201212	1110000021	0220110000	1011010?1?	0000110101	110000????	??????????	??????
<i>Lis. jeanneli</i>	??????????	??????0021	-100110000	101101001?	0000110000	110000010?	001110110?	11010?
<i>Lis. splendens</i>	1111211212	1111010021	1200010001	1111011010	0111110111	-001000110	0010101112	111101
<i>Lis. pentapotamiae</i>	1111211212	1111010021	1200?10001	1111011010	0111110111	-001000?1?	?0??10??1?	11?101
<i>Lis. akatikubas</i>	1111211112	111101????	??????0001	1011011?10	0111110111	-10000????	??????????	??????
<i>Lis. guptai</i>	11102101??	??????????	??????10001	1011011?1?	0011110111	110000????	??????????	??????
<i>K. anchidens</i>	10011-0001	100-1?0021	-110010010	0010010111	1000001000	011000????	??????????	????00
<i>K. massai</i>	10011-0101	1100100021	1200011010	0010110111	1000001000	011010010?	001111?101	001010
<i>K. minheensis</i>	1???1-???1	1100?0????	??00???0??	?0???10111	000000100?	?11010????	?????????12	??????
<i>K. gigas</i>	10011-12?1	11001?????	0100011010	0010110111	0000001000	0110100?0?	001121?112	001010
<i>K. kinzhikebirus</i>	??????????	??????????	???????1010	?0101?0???	?????0?0?0	0110?0????	??????????	??????
<i>Lo. moruoroti</i>	11110-0002	100-???121	-1011100-1	1100010010	000011-121	-001000?0?	00000??000	??????

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the taxa included in the phylogenetic analysis and the corresponding checked material.

Appendix S2. Taxon/character matrix. Reconstructed character states for internal nodes of the strict consensus shown in Figure 8. Character-state optimization = accelerated transformation (ACCTRAN). Length of the consensus = 153; consistency index = 0.55; retention index = 0.77. Letters refer to the nodes of Figure 8.

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