New Listriodontinae (Mammalia, Suidae) from Europe and a review of listriodont evolution, biostratigraphy and biogeography

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ABSTRACT

Newly collected listriodont suid fossils from Spanish deposits assigned to zones MN4, MN5 and MN7 and from France (MN4 to MN7) reveal a great deal about these Suiformes and indicate that a revision of their systematics and phylogeny is necessary. One new species of *Listriodon* von Meyer, 1846, *Listriodon retamaensis* n. sp., is described, and descriptions of craniodental specimens of other species (*Listriodon lockharti* Pomel, 1848 and *Listriodon splendens* von Meyer, 1846) are provided. There are two distinct cranial and postcranial morphotypes among European listriodonts: *Eurolistriodon* Pickford & Moya Sola, 1995, in which the postcranial bones are elongated and gracile and the snout is adorned with large laterally oriented horn-like processes above the canine; and *Listriodon*, in which the postcranial bones are short and robust, and in which the canine flange is not as marked. The dental morphology of primitive listriodonts, including both *Eurolistriodon* and *Listriodon*, suggests that the subfamily was derived from a hyothere similar to *Hyotherium meisneri* von Meyer, 1850 or a similar species. The chronological and geographic distribution of listriodonts in Africa and Eurasia is examined. It is confirmed that Kubanochoerinae do not belong to the same subfamily as listriodonts.

KEY WORDS
Mammalia,
Suidae,
Listriodontinae,
Old World,
biogeography,
biostratigraphy,
new species.

RÉSUMÉ

Un nouveau Listriodontinae (Mammalia, Suidae) d'Europe et revue de l'évolution, de la biostratigraphie et de la biogéographie des listriodontes.

Les découvertes récentes de fossiles de listriodontes dans des dépôts d'Espagne appartenant aux zones MN4, MN5 et MN7 et en France dans les zones MN4 à MN7 posent de nombreuses interrogations qui convergent pour proposer les révisions systématique et phylogénétique de ce groupe de Suidae. La description d'une nouvelle espèce du genre *Listriodon* von Meyer, 1846, *Listriodon retamaensis* n. sp., est donnée, elle est accompagnée par celle de spécimens d'autres espèces (*Listriodon lockharti* Pomel, 1848 et *Listriodon splendens* von Meyer, 1846). Au sein des listriodontes d'Europe, on peut distinguer deux morphotypes à partir des restes crâniens et postcrâniens : *Eurolistriodon* Pickford & Moya Sola, 1995, dont les restes postcrâniens sont allongés et graciles, et dont le museau développe sous les canines des processus latéraux ; et *Listriodon*, dont les restes postcrâniens sont courts et robustes, et dont le rebord de la canine est moins marqué. La morphologie dentaire des listriodontes primitifs, incluant *Eurolistriodon* et *Listriodon*, suggère que la sous-famille était issue d'un hyothère proche de *Hyotherium meisneri* von Meyer, 1850 ou d'une espèce voisine. La répartition chronologique et géographique des listriodontes en Afrique et en Eurasie est analysée. Il apparaît que les Kubanochoerinae n'appartiennent pas à la même sous-famille que celle des listriodontes.

MOTS CLÉS
Mammalia,
Suidae,
Listriodontinae,
Ancien Monde,
biogéographie,
biostratigraphie,
nouvelle espèce.

INTRODUCTION

This note deals with new listriodont fossils found in Spain and France over the past few years. The most interesting material is from Retama (MN4a), Madrid (Estacion Imperial and Acacias, MN4b) and Toril 3 (MN7). Previously described Spanish fossils from La Artesilla, Valdemoros and Terrero are included in this study. Some undescribed fossils from France (La Romieu and Pellecahus, MN4a) are also examined.

Retama, a basal middle Miocene (MN4a) site in Spain, has yielded listriodont remains that throw appreciable light on the relationships between bunodont listriodonts and other suids from the same epoch. The new material also reveals that the listriodonts are not particularly closely related to the kubanochoeres, and that the sole character hitherto used to unite the two subfamilies together – the enlarged upper central incisor – developed by convergence in different suid lineages at different times and in different continents.

Listriodonts are relatively rare in Iberian deposits of MN4b. For this reason it is of interest to report on a few fossils from Madrid (Estacion Imperial and Acacias) that fall into this time span. The recent discovery of an almost complete, though partly crushed, cranium at Toril 3 (MN7 *c.* 12 Ma), Zaragoza, Spain (Daams & Freudenthal 1988; Mein 1990; De Bruijn *et al.* 1992; Van der Made 1996) is of great interest because it reveals a wealth of information about the morphology of the neurocranium and splanchnocranium of listriodonts, and throws light on the systematic and phylogenetic position of these suids. Comparison of the new skull with previously available partial skulls from Sansan (France), Els Casots (Spain), Inönü (Turkey), Ngorora (Kenya) and Tongxin (China) confirms that listriodonts were sexually dimorphic in the canines and peri-canine parts of the skull. The postcanine dentition is basically monomorphic. The Toril cranium evidently belongs to a female individual.

A reassessment of the mandibular and cranial material hitherto assigned to the two genera *Bunolistriodon* Arambourg, 1963, and *Listriodon* von Meyer, 1846, indicate that all the Eurasian material except for *Eurolistriodon adelli* Pickford & Moya Sola, 1995, should be subsumed into a single genus, *Listriodon*, a view already proposed by Leinders (1975) and Pickford (1986). Most of the African material hitherto assigned to *Bunolistriodon* (Arambourg 1963; Van der Made 1996) belongs to the subfamily Kubanochoerinae Gabunia, 1958 (Gabunia 1955, 1958, 1960). Comparison of the new *Listriodon* skull from Toril to those of kubanochoeres from Moruorot (Kenya), Gebel Zelten (Libya), Belometchetskaya (North Caucasus) and Tongxin (China) underlines the fact that there are many fundamental differences between the crania and dentitions of these two groups of suids and strengthens the hypothesis that they belong to distinct evolutionary lineages. The differences are so great that the two groups should be classed as separate subfamilies, Listriodontinae and Kubanochoerinae.

The new fossil material described here provides an opportunity to examine some of the palaeobiological aspects of listriodonts, including any role that geological events of the Miocene may have had on their distribution and evolution.

SYSTEMATICS

Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821

Subfamily LISTRIODONTINAE Simpson, 1945

NOTE ON THE AUTHORSHIP OF LISTRIODONTINAE

Van der Made (1996) has proposed that Gervais (1859) and not Simpson (1945) was the author of the subfamily Listriodontinae on the grounds that the former author referred to a group "tribu de listriodontins". However, resurrecting long forgotten names or authorship for supra-generic categories of zoological groups is not recommended by the latest edition of the *International Code of Zoological Nomenclature* (ICZN 1999). In the introduction (p. XXVIII, paragraph 11) it is clearly explained that "an author will be required (without a ruling by the Commission) not to displace a name which has been used as valid by at least 10 authors in 25 publications during the past 50 years, and encompassing a span of not less than ten years, by an earlier synonym or homonym which has not been used as valid since 1899".

In this case, even though the family name Listriodontidae was erected by Roger (1882) and later by Lydekker (1884), according to the new provisions of the ICZN (1999) this should not be taken to mean that the subfamily Listriodontinae was erected by these authors, their publications appearing prior to the end of 1899. To my knowledge there have been only two papers published during the past 50 years which credit the subfamily Listriodontinae to authors other than Simpson (1945) and these are McKenna & Bell (1997) who give credit to Lydekker (1884) and Van der Made (1996) who gives it to Gervais (1859). Furthermore, there are no papers published during the 20th century that attribute the subfamily name to any of these authors, but there are many that credit Simpson with creating it. For these reasons, we adhere to the latest version of the ICZN and continue to credit Simpson (1945), with the authorship of the subfamily Listriodontinae. This decision accepts the wish of the ICZN "to act in the interests of preserving established usage". Otherwise, I could easily suggest that the subfamily be credited to Roger (1882) who published the name Listriodontidae two years before Lydekker (1884) did, thereby nullifying the decision of McKenna & Bell (1997) to credit the name to Lydekker.

Genus *Listriodon* von Meyer, 1846

Listriodon retamaensis n. sp.

HOLOTYPE. — RET 574 (Fig. 1G), snout of a female individual with left I3, left and right canine roots, left and right P1-P3 (left P3 broken), housed at the Museo Nacional de Ciencias Naturales, Madrid.

ETYMOLOGY. — Named for the type locality.

PARATYPES. — RET 740, right I1 (Fig. 1A); RET 348, left maxilla with P3-M3 and right maxilla with M2-M3 (Fig. 2A); RET 832, upper male canine (Fig. 1B); right p4 (Fig. 1C); RET 2, left mandible fragment with m1-m3 (occludes perfectly with RET 348) (Fig. 2B); RET 338, right mandible fragment with broken m3 (Fig. 2C). Housed at the Museo Nacional de Ciencias Naturales, Madrid.

TYPE LOCALITY. — Retama, Huete, Spain (MN4a).

OTHER LOCALITIES. — Spain: Acacias (MN4b); Casal das Chitas (MN4b); Corcoles (MN4a); Estacion Imperial (MN4b); La Hidroelectrica (MN4b); Tejar Manzanares (MN4b or MN5); Munebrega (MN4b); Olival da Susana (MN4b); Quinta Grande (MN4a); Quinta das Flamengas (MN4b); Quinta de Lobeira (MN4a); Quinta da Raposa (MN4a); Quinta da Silvéria (MN4b); Terrero (MN4a); Torralba (MN4b); Valdemoros (MN4b). France : Bézian (MN4b).

AGE. — This new species of *Listriodon* is known from several middle Miocene localities in Europe ranging in age from MN4a to MN5 (Figs 3; 4) (*c.* 17-15 Ma).

DIAGNOSIS. — A small species of *Listriodon* with moderately elongated snout (diastemata between canine and premolar row shorter than in *Eurolistriodon*), full complement of upper premolars, three lobed I1 with a length-width index of *c.* 177; bunolophodont dentition; metapodials short and robust.

REMARKS

Van der Made (1996) listed material from Echzell and ?Georgensmund as *Bunolistriodon* aff. *latidens* (Biedermann, 1873), but the material falls within the range of variation of *L. latidens* and *L. lockharti* Pomel, 1848 and it is more likely to belong to one or other of these taxa rather than to *L. retamaensis* n. sp. Some specimens from MN4a were also assigned to *Bunolistriodon* aff. *latidens* by Van der Made (1996), but these possess a single lobed upper central incisor, and are here assigned to *Eurolistriodon adelli*. Thus, apart from one locality in France (Bézian) all the known occurrences of *L. retamaensis* n. sp. are from the Iberian Peninsula.

DESCRIPTION

Skull

In palatal view (Fig. 1G) the anterior end of the snout is oval in outline, being widest at the canines. There is a distinct waist behind the P1, beyond which the palate widens gradually to where it is broken behind the P3. The incisive foramina are located immediately behind the I1 and extend backwards as far as the distal margin of the alveolus of I3. The maxillo-palatine sutures run almost parallel to each other distally from the rear of the incisive foramina. On each side of the palate a groove runs backwards from the incisive foramen coursing close to the alveolar processes. The suture between the premaxillae and maxillae is raised into a slight but sharp ridge.

The incisor alveoli form a curved battery, the I1 being the largest and the I3 the smallest of the incisors. A short diastema separates the I3 from the canine, the margin of the palate being curved dorsally, thereby forming a shallow niche for the lower canine. The P1 is a two-rooted tooth separated from the rear of the canine by a very modest gap. Behind it there is a short diastema marked laterally by a depression in the outer surface of the maxilla. The P2 and P3 are in contact with each other.

In lateral view, the anterior margin of the premaxilla sweeps upwards steeply from the alveoli of the central incisors, the hindmost margin of the anterior nares being above the alveolus of I3. The anterior ends of the nasal bones are broken but probably did not extend very far anteriorly.

Inside the nasal cavity of the Retama snout, above and behind the level of the P2 there is a well developed sheet of bone oriented vertically which separates the nasal cavity into two halves. In distal view, a curved sheet of bone is seen to extend into the nasal cavity from about half the height of the snout while a second sheet curves into the cavity from the roof of the snout near the suture between the maxilla and the nasals. In a remnant of limestone that is still lodged in the nasal cavity it is possible to discern portions of thin curved sheets of bone that represent turbinates. These extend as far forwards as the level of the canine alveoli, if not further forwards, from which it is deduced that the sense of smell was well developed in this species.

RET 348 (Fig. 2A) is a fragmented left maxilla containing P3-M3 and part of the right maxilla

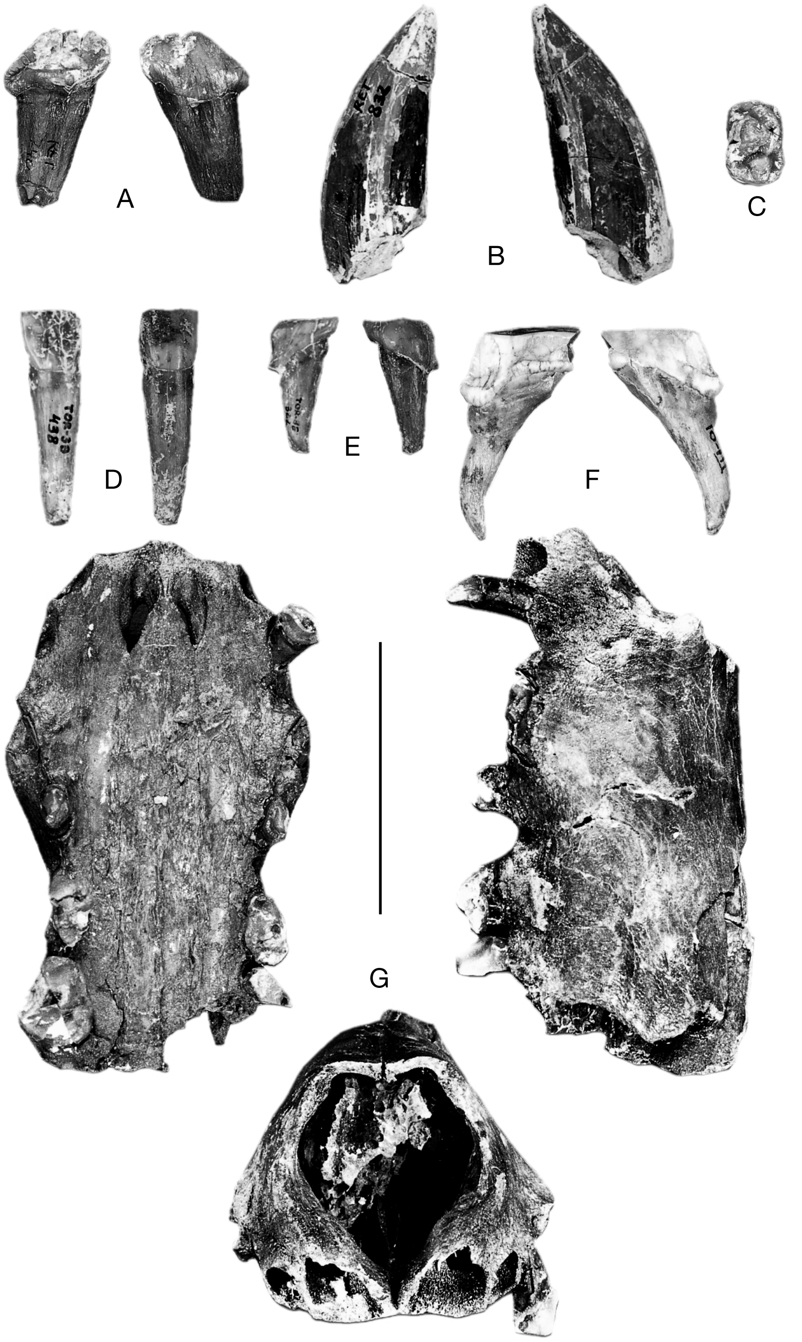


FIG. 1. — **A**-**C**, **G**, *Listriodon retamaensis* n. sp. from Retama, Spain; **A**, RET 740, right I1, lingual and labial views; **B**, RET 832, upper male canine, medial and lateral views; **C**, right p4, occlusal view; **G**, RET 574, holotype, female snout with left I3, left and right canine roots, left and right P1-P3, occlusal, left lateral and anterior views; **D**-**F**, *Listriodon splendens major* Roman, 1907 from Toril, Spain; **D**, TOR 3B 438, right i1, lingual and labial views; **E**, TOR 3B 322, left i3, lingual and labial views; **F**, TOR III (33.234), left i3, lingual and labial views. Scale bar: 5 cm.

with M2-M3. The midline of the maxilla is not preserved, nor is its distal margin. It is not possible to determine the width of the palate, nor its extension behind the molar row. The palatal foramen is located close to the disto-lingual root of the M2. Close behind the M3 there is a well developed tubercle of bone above which is a groove which probably housed a blood vessel which coursed from the palate upwards and outwards behind the M3.

Upper dentition (Table 1)

The upper central incisor, RET 740 (Fig. 1A), is slightly worn on its lingual aspect, but is otherwise well preserved. The tooth is wide mesiodistally and its apical edge is divided into three lobes, the central one being the narrowest. Its length-width index is 177 (for calculation of index, see Van der Made 1996). There is a prominent lingual cingulum which runs the entire length of the tooth. The root is appreciably narrower than the crown and it tapers rapidly towards its apex which has been broken away.

The I3 *in situ* in the snout is a small tooth with a triangular crown in lingual view. The anterior edge is worn flat parallel to the palate while the distal edge is unworn. It has a weakly developed, but sharp, lingual cingulum.

The canine roots are oval and short, indicating that this individual was probably a female. The P1 is a two-rooted tooth, the roots splaying out rapidly so that the length of the premolar alveoli is greater than that of the crown. The crown is bunoid with a central cusplet from which low crests run anteriorly and distally. Lingually there is a low, rounded cingulum. The P2 is more than twice the size of the P1 and its crown is formed of a main centrally positioned cusp behind which is a low shelf and a small distal cusplet. Ridges run anteriorly and distally from the apex of the main cusp. A prominent wear facet caused by abrasion with the lower second premolar scores the anterior crest of the P2. In occlusal view the P3 is a large triangular tooth. The main cusp and its anterior and distal crests are obliquely oriented and the disto-lingual corner of the tooth is formed of a large cusplet which is separated from the main cusp by a valley. Labially, the distal part of the crown is adorned by a cingular ridge. The anterior surface of the tooth is the site of a large flat wear facet caused by abrasion with the p3.

An unworn upper male canine (Fig. 1B) has an almost circular cross section with low pre- and post-crista. The enamel is scored by slightly wavy, shallow, longitudinal grooves. The pulp cavity is visible where part of the root has broken away, revealing that this tooth was not as elongated nor as curved as the upper male canines that typify *Eurolistriodon*, and later species of *Listriodon*.

In the maxilla RET 348, the P4 is moderately worn but it is possible to make out that the buccal cusp was probably formed of a pair of closely appressed cusps. Lingually there is a single cusp bordered by a well developed cingulum which extends along the anterior, lingual and distal margins of the crown and reaches onto the labial surface of the tooth anteriorly and distally. The upper first and second molars in this specimen are so worn that little morphology is preserved. It is possible to determine, however, that both teeth possessed prominent buccal cingula. The M3 possesses four main cusps and a lingually positioned talon. It has well developed but low anterior and median accessory cusplets. The four main cusps and the two accessory cusplets all have dentine exposed at their tips. The dentine exposures of the anterior cusps are joined to that of the anterior accessory cusplet. The buccal margin of the crown possesses a well developed cingulum. The tooth, even though well worn, is evidently of the bunolophodont type.

Mandible

RET 338 and RET 2 (Fig. 2B, C) are parts of the right and left bodies of an individual lower jaw which occlude perfectly with the two maxillae, RET 348. RET 2 is so fragmentary that it reveals little about mandibular morphology except that the root of the ascending ramus sweeps upwards behind the m3 as in other listridonts, and in contrast to the short mandibles of hyotheres. RET 338 in contrast preserves much of the body below the m3 including the angle and part of the

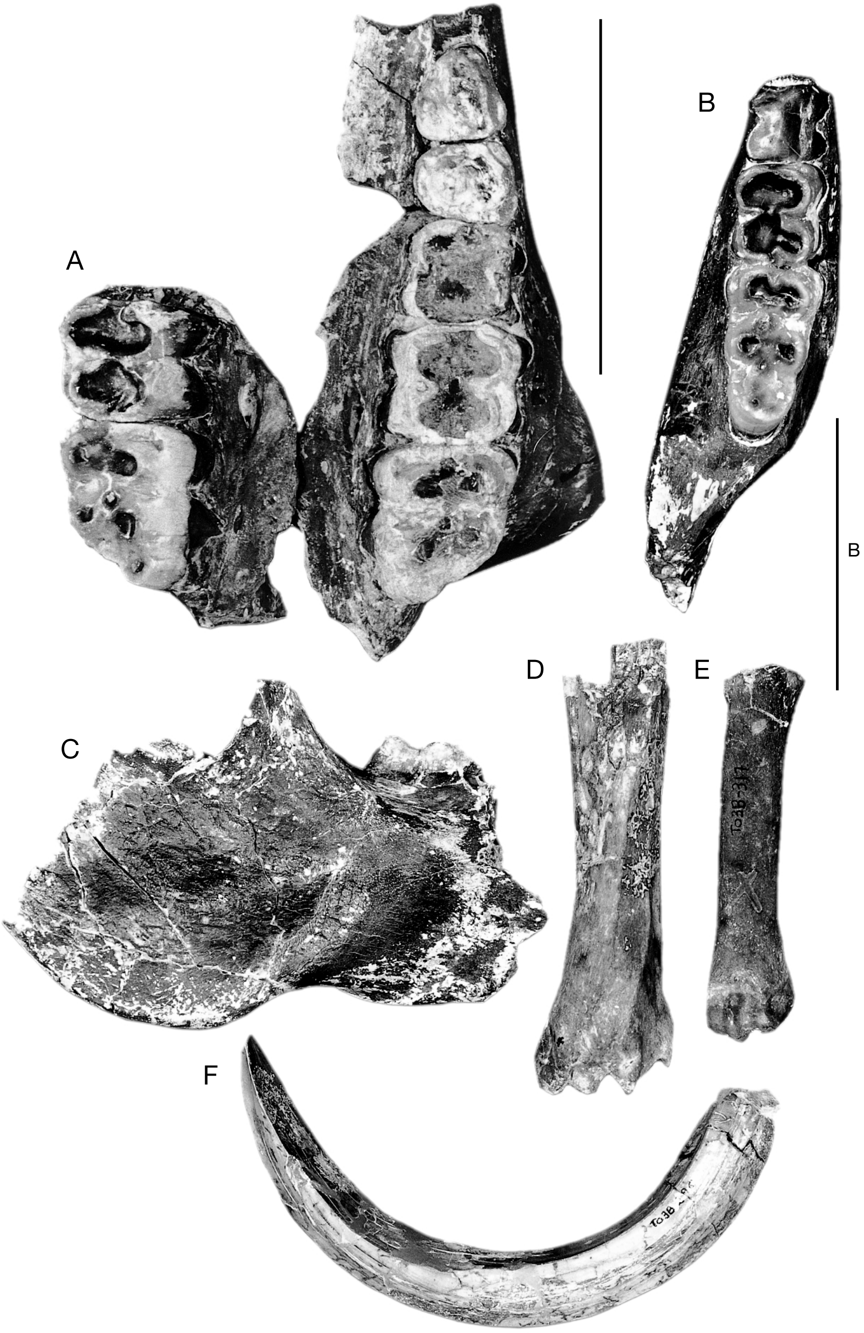


FIG. 2. — **A**-**C**, *Listriodon retamaensis* n. sp. from Retama, Spain; **A**, RET 348, palatal fragments with left P3-M3 and right M2-M3, occlusal view; **B**, RET 2, left mandible with m1-m3, occlusal view; **C**, RET 338, right mandible fragment with broken m3, lateral view; **D**-**F**, *Listriodon splendens major* Roman, 1907 from Toril, Spain; **D**, TOR 3B 333, distal end of tibia, anterior view; **E**, TO 3B, 317, metapodial, superior view; **F**, TO 3B, 295, left male canine, lateral view. Scale bars: A-C, 5 cm; D-F, 10 cm.

TABLE 1. — Dental measurements (in mm) of the teeth of Spanish Listriodontinae from zone MN4.

Listriodon retamaensis n. sp., Retama (three lobed I1)

Upper dentition	Length	Breadth
RET 740 I1 right	19.1	10.8
RET 574 I3 left	12.3	7.1
RET 574 cf root	11.6	10.0
RET 832 cm	23.4	22.2
RET 574 P1 left	8.5	5.6
RET 574 P1 right	8.2	5.9
RET 574 P2 left	15.3	9.3
RET 574 P3 right	18.4	15.8
RET 348 P3 left	14.0	13.8
RET 348 P4 left	12.7	15.6
RET 348 M1 left	16.0	16.4
RET 348 M2 right	18.7	19.7
RET 348 M2 left	18.0	19.5
RET 348 M3 right	24.6	21.3
RET 348 M3 left	25.9	20.0

Lower dentition	Length	Breadth
RE 17 p4 right	16.5	11.4
RE 2 m1 left	14e	13.9e
RE 2 m2 left	19.0	15.9
RE 2 m3 left	31.5	17.9

Listriodon retamaensis n. sp., Acacias (I1 unknown)

Lower dentition	Length	Breadth
AC 166 left i2	10.0	7.6
AC 163 left p2	11.0	5.4
AC 163 left p3	12.6	8.0
AC 163 left p4	15.6	11.0
AC 163 left m3	29.6	17.3

Listriodon retamaensis n. sp., Estacion Imperial (three lobed I1)

Lower dentition	Length	Breadth
EO 167 right i1	9.5	7.0
EO 172 left i2	10.5	7.5
EO 163 left i3	11.2	7.1
EO 169 left i3	11.6	6.1
EO 173 left cm	10.0	8.8
EO 180 left p3	14.5	8.9
EO 161 left dm2	9.6	5.0
EO 161 left dm3	13.0	7.5
EO 162 right dm4	21.7	10.3

Upper dentition	Length	Breadth
EO 165 right I1	16.9	9.7
EO 164 left I1	-	8.1
EO 171 left I2	12.0	6.9
EO 166 left I3	10.2	5.8
EO 168 left I3	10.3	6.3
EO 182 left P3	12.5	9.0
EO 177 right M1	17.0	17.0

Listriodon retamaensis n. sp., Valdemoros

Lower dentition	Length	Breadth
VD 61 left m3	34.0	17.4

Listriodon retamaensis n. sp., Terrero

Upper dentition	Length	Breadth
TE 43 left P3	14.2	14.6
TE 43 left P4	13.0	15.9

Eurolistriodon adelli Pickford & Moya Sola, 1995, Artesilla (one lobed I1)

Lower dentition	Length	Breadth
ART 67 left i1	9.6	8.4
ART 89 right di2	7.4	6.5
AR 264 right i2	11.0	10.5
AR 589 cm	21.0	18.0
AR 254 right cf	11.4	10.4
ART 588 left dm2	13.7	6.3
ART 54 right dm2	12.4	6.0
AR 188 right dm3	15.4	-
ART 588 left dm3	14.0	7.2
AR 367 left dm3	13.3	7.0
ART 54 right dm3	13.3	6.7
ART 58 right dm4	22.7	10.0
ART 54 right dm4	21.3	11.1
AR 57 left p3	17.1	10.0
ART 61 left p3	17.7	11.4
ART 55 right p3	16.0	9.7
AR 274 right p3	16.3	9.6
ART 55 right p4	15.3	11.9
AR 57 left p4	16.0	11.8
AR 590 left p4	17.0	12.5
AR 595 right m1	18.0	12.5
ART 54 right m1	18.2	13.0
ART 61 left m1	17.3	12.4
ART 55 right m2	20.0	16.8
ART 55 right m3	31.0	16.8
AR 11 left m3	36.0	20.4
ART 60 right m3	30.8	16.5

Upper dentition	Length	Breadth
AR 267 right I1	20.0	10.6
AR 269 left I1	18.0	10.3
AR 131 right I1	17.5	10.4
ART 64 right I1	18.0	10.9
AR 593 left I3	13.4	7.4
AR 251 left I3	12.0+	7.5
AR 591 left I3	12.6	6.6
AR 1285 right CM	21.4	22.1
AR 295 right CM	21.6	20.0
AR 261 right CF	12.6	10.0
AR 252 right CF	11.8	9.6
AR 289 left P1	8.6	5.4
AR 600 right P1	7.1	4.0
AR 599 left dM2	12.8	7.9
AR 250 left dM3	16.0	14.1
ART 63 left dM4	15.4	13.0
AR 596 left dM4	15.4	13.3
AR 597 right dM4	14.9	13.7
AR 598 left dM4	15.9	14.6
AR 182 right P2	16.6	11.2
AR 587 right P2	16.2	10.0
AR 587 right P3	16.4	14.5
AR 592 left P3	16.4	14.2

Upper dentition	Length	Breadth
AR 278 left P3	15.1	-
AR 258 left P3	17.0	13.9
ART 56 right P3	16.0	14.5
ART 56 right P4	13.0	15.6
AR 275 left P4	13.0	15.2
AR 289 left P4	13.0	16.0
AR 277 right M1	18.7	16.4
AR 276 right M1	18.1	17.8
AR 289 left M1	18.7	17.2
AR 118 left M1	18.7	16.8
AR 289 left M2	21.0	20.9
AR 289 left M3	25.5	22.0
ART 59 right M3	21.5	19.2

masseteric fossa. The lower border of the jaw below the third molar terminates in a prominent flange and lingual tubercle which is separated from the slightly descending angle by a low crest of bone. The internal and external surfaces of the jaw distal to the third molar are marked by well developed rugosities representing muscle attachments. The lower border of the masseteric fossa is everted to a small extent. The mandibular foramen enters the lingual side of the ascending ramus 30 mm behind the talonid of m3.

Lower dentition (Table 1)

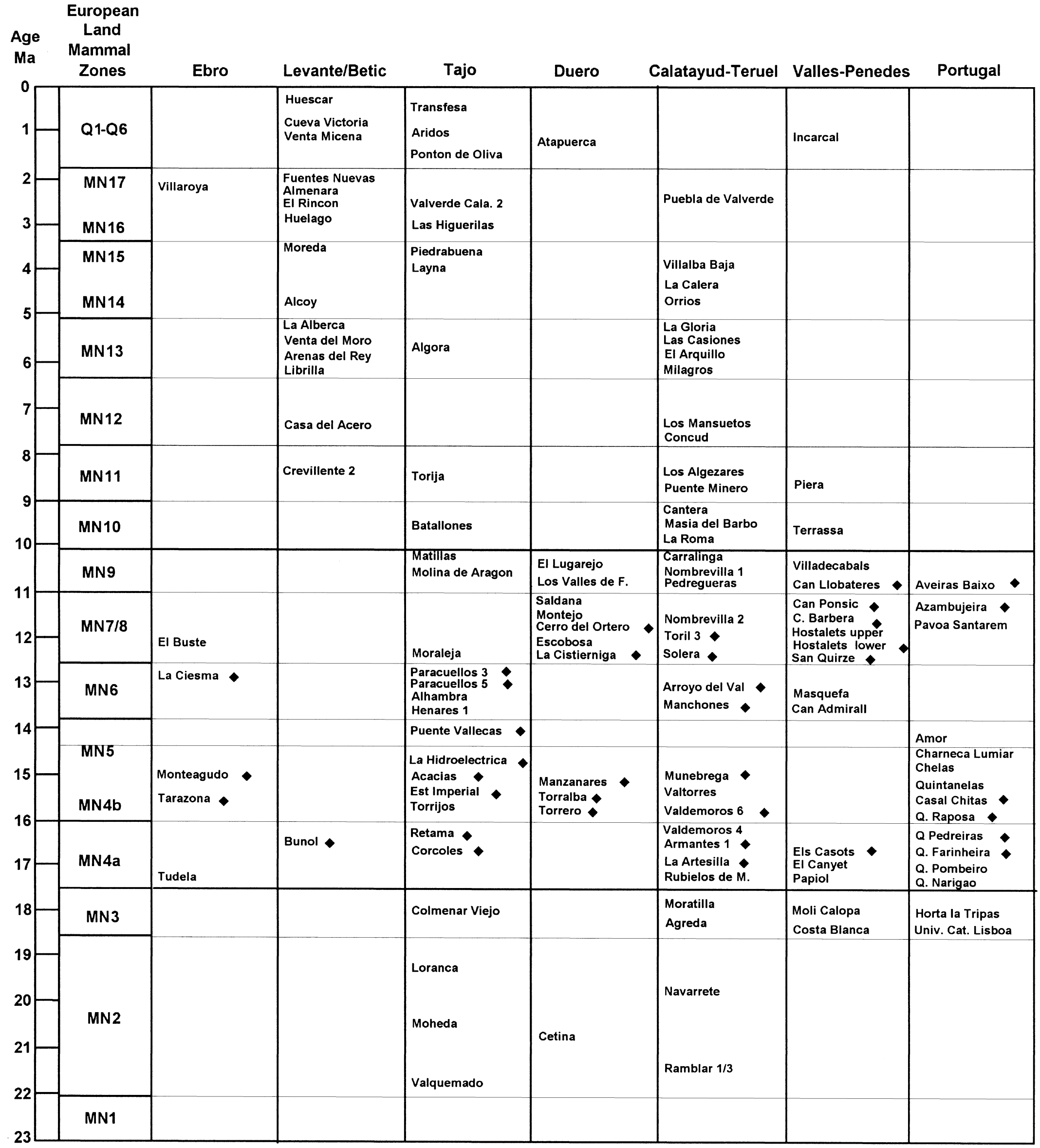
The p4 (Fig. 1C) is rectangular in occlusal outline. Centrally there is a prominent main cusp beside which is a large, offset innenhugel. Anteriorly the anterior crest of the main cusp is swollen and descends rapidly towards a well developed but low anterior cingulum. Distally there is a prominent talonid cusp joined lingually and labially by a swollen cingulum.

The lower first and second molars of RET 2 are deeply worn and the most informative morphological characters have been eradicated. The m3 is also deeply worn but it is possible to make out that it consisted of five main cusps with median and posterior accessory cusplets. The main cusps are arranged in two loph-like pairs with a centrally positioned talonid distally, and there is an anterior cingulum. In lateral view the cervix of the tooth is seen to ascend distally. The five main cusps and the two accessory cusplets all have dentine exposed at their tips, that of the anterior cusp pair forming a loph-like dentine lake. In RET 338 only the talonid and the broken surface of the distal cusp pair of the m3 are preserved.

The dimensions of the Retama teeth fall outside the currently documented range of metric variation of *Listriodon lockharti* (Pomel 1848) and *Listriodon latidens* (Biedermann, 1873) (Van der Made 1996; Van der Made *et al.* 1998), but they are close in size to the teeth of *Eurolistriodon adelli* as noted by Van der Made (1996) (Figs 5-10). However, morphologically they fall well outside the known range of variation of the latter species, their cheek teeth being more lophodont and the upper central incisor possesses three lobes rather than one. It is impossible to determine from metric data alone to which species isolated cheek teeth of small listriodonts may belong, the size distribution of all species (*adelli*, *retamaensis*, *lockharti* and *latidens*) overlapping each other. For this reason, we consider that some of the material previously assigned to *L.* aff. *latidens* (Van der Made 1996) belongs to *E. adelli* while some of it belongs to small individuals of *L. lockharti*. The main differences between the cheek teeth of these listriodonts concern the degree of bunodonty and lophodonty. For example, the molars of *E. adelli* are more bunodont than those assigned to *L. lockharti*, but the distinctions can disappear with moderate wear. The upper central incisors of the two groups are different, as is the morphology of the canine flange and there are important differences in the postcranial skeleton (Pickford & Moya Sola 1995). From the morphological data we conclude that there are two genera of listriodonts in Spanish deposits ranging in age from MN4a to MN5.

COMPARISONS AND DISCUSSION

The Retama snout closely resembles a specimen from Bézian attributed to *Bunolistriodon lockharti* by Ginsburg & Bulot (1987) but identified as *Bunolistriodon* aff. *latidens* by Van der Made (1996). It differs markedly from the species *Eurolistriodon adelli* from Els Cassots, Spain (Pickford & Moya Sola 1995) which is a long snouted listriodont in which the anterior premolars have been suppressed, in which there is a long post-canine diastema and in which the molars are

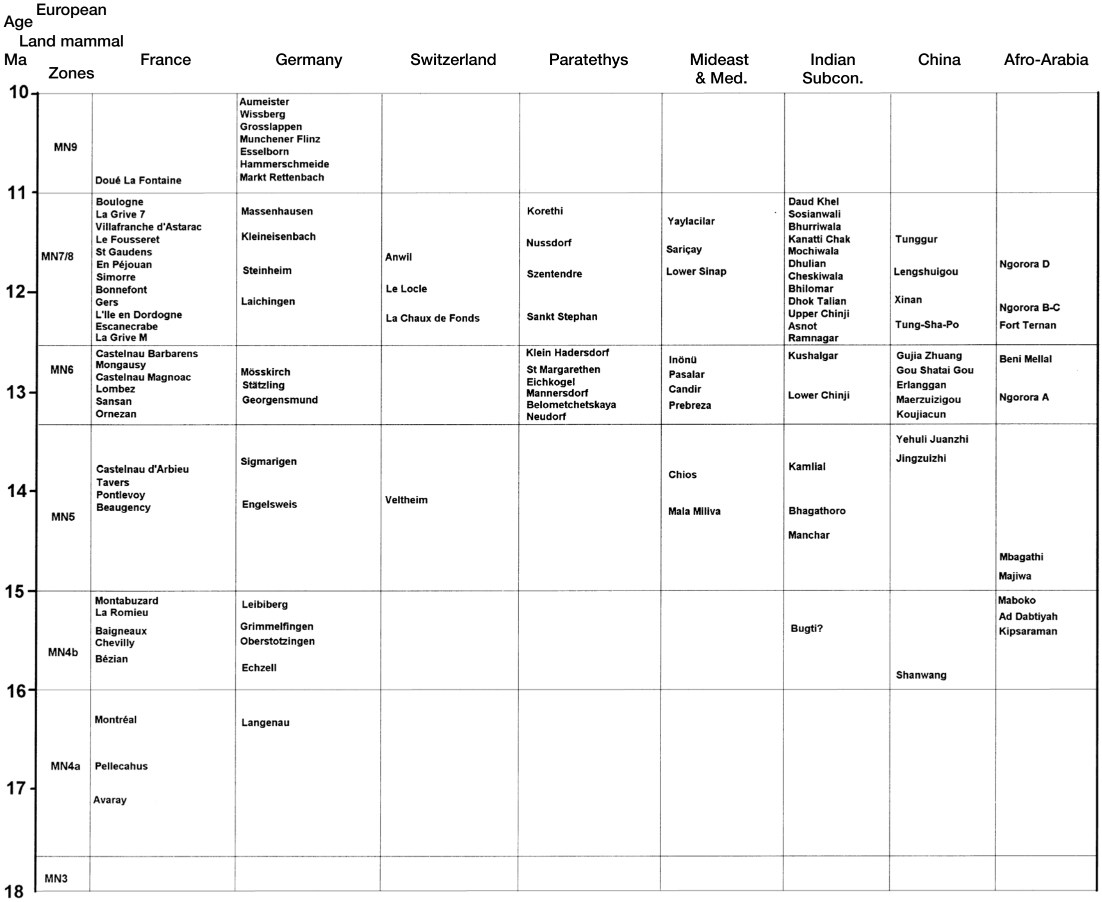


European Land Mammal Zones	Ebro	Levante/Betic	Tajo	Duero	Calatayud-Teruel	Valles-Penedes	Portugal
Q1-Q6		Huescar Cueva Victoria Venta Micena	Transfesa Aridos Ponton de Oliva	Atapuerca		Incarcal	
MN17 MN16	Villaroya	Fuentes Nuevas Almenara El Rincon Huelago	Valverde Cala. 2 Las Higuerilas		Puebla de Valverde		
MN15 MN14		Moreda Alcoy	Piedrabuena Layna		Villalba Baja La Calera Orrios		
MN13		La Alberca Venta del Moro Arenas del Rey Librilla	Algora		La Gloria Las Casiones El Arquillo Milagros		
MN12		Casa del Acero			Los Mansuetos Concud		
MN11		Crevillente 2	Torija		Los Algezares Puente Minero	Piera	
MN10			Batallones		Cantera Masia del Barbo La Roma	Terrassa	
MN9			Matillas Molina de Aragon	El Lugarejo Los Valles de F.	Carralinga Nombrevilla 1 Pedregueras	Villadecabals Can Llobateres ◆	Aveiras Baixo ◆
MN7/8	El Buste		Moraleja	Saldana Montejo Cerro del Ortero ◆ Escobosa La Cistierniga ◆	Nombrevilla 2 Toril 3 ◆ Solera ◆	Can Ponsic ◆ C. Barbera ◆ Hostalets upper Hostalets lower ◆ San Quirze ◆	Azambujeira ◆ Pavoa Santarem
MN6	La Ciesma ◆		Paracuellos 3 ◆ Paracuellos 5 ◆ Alhambra Henares 1		Arroyo del Val ◆ Manchones ◆	Masquefa Can Admirall	
MN5			Puente Vallecas ◆				Amor
MN4b	Monteagudo ◆ Tarazona ◆		La Hidroelectrica ◆ Acacias ◆ Est Imperial ◆ Torrijos	Manzanares ◆ Torralba ◆ Torrero ◆	Munebrega ◆ Valtorres Valdemoros 6 ◆		Charneca Lumiar Chelas Quintanelas Casal Chitas ◆ Q. Raposa ◆
MN4a	Tudela	Bunol ◆	Retama ◆ Corcoles ◆		Valdemoros 4 Armantes 1 ◆ La Artesilla ◆ Rubielos de M.	Els Casots ◆ El Canyet Papiol	Q Pedreiras ◆ Q. Farinheira ◆ Q. Pombeiro Q. Narigao
MN3			Colmenar Viejo		Moratilla Agreda	Moli Calopa Costa Blanca	Horta la Tripas Univ. Cat. Lisboa
MN2			Loranca Moheda Valquemado	Cetina	Navarrete Ramblar 1/3		
MN1							

FIG. 3. — Neogene fossiliferous localities in the Iberian Peninsula arranged by chronological order and by sedimentary basins. Note the distribution of listriodonts from MN4a to MN9. Symbol: ◆, listriodon species.

more bunodont. It is unlikely that these differences are due solely to sexual dimorphism within a single species, even though in listriodonts sexual dimorphism of the snout region is marked (Pickford & Moya Sola 1995).

At the time of their study, Van der Made (1996, 1997a) and Van der Made & Alferez (1988) recognised that localities such as Corcoles and several other Iberian sites of similar age (MN4) possessed two listriodont species, but the avail-



European Land mammal Zones	France	Germany	Switzerland	Paratethys	Mideast & Med.	Indian Subcon.	China	Afro-Arabia
MN9	Doué La Fontaine	Aumeister Wissberg Grosslappen Munchener Flinz Esselborn Hammerschmeide Markt Rettenbach						
MN7/8	Boulogne La Grive 7 Villafranche d'Astarac Le Fousseret St Gaudens En Péjouan Simorre Bonnefont Gers L'Ile en Dordogne Escanecrabe La Grive M	Massenhausen Kleineisenbach Steinheim Laichingen	Anwil Le Locle La Chaux de Fonds	Korethi Nussdorf Szentendre Sankt Stephan	Yaylacilar Sariçay Lower Sinap	Daud Khel Sosianwali Bhurriwala Kanatti Chak Mochiwala Dhulian Cheskiwala Bhilomar Dhok Talian Upper Chinji Asnot Ramnagar	Tunggur Lengshuigou Xinan Tung-Sha-Po	Ngorora D Ngorora B-C Fort Ternan
MN6	Castelnau Barbarens Mongausy Castelnau Magnoac Lombez Sansan Ornezan	Mösskirch Stätzling Georgensmund		Klein Hadersdorf St Margarethen Eichkogel Mannersdorf Belometchetskaya Neudorf	Inönü Pasalar Candir Prebreza	Kushalgar Lower Chinji	Gujia Zhuang Gou Shatai Gou Erlanggan Maerzuizigou Koujiacun	Beni Mellal Ngorora A
MN5	Castelnau d'Arbieu Tavers Pontlevoy Beaugency	Sigmarigen Engelsweis	Veltheim		Chios Mala Miliva	Kamlial Bhagathoro Manchar	Yehuli Juanzhi Jingzuizhi	Mbagathi Majiwa
MN4b	Montabuzard La Romieu Baigneaux Chevilly Bézian	Leibiberg Grimmelfingen Oberstotzingen Echzell				Bugti?	Shanwang	Maboko Ad Dabtiyah Kipsaraman
MN4a	Montréal Pellecahus Avaray	Langenau						
MN3								

FIG. 4. — Neogene fossiliferous localities of Europe, Asia and Afro-Arabia which have yielded Listriodontinae.

able material was not well enough preserved to permit the formal naming of a new taxon. In a note printed at the end of his monograph, Van der Made (1996) suggested that the material assigned by him to *B.* aff. *latidens* belongs to *Bunolistriodon adelli* a species which was published while his monograph was in preparation. The snout from Retama differs markedly from that of *E. adelli*, and reveals that by MN4 there were in fact three distinct listriodonts in Spain: *Eurolistriodon adelli*, *Listriodon retamaensis* n. sp. and *Listriodon lockharti*.

It now appears that by the onset of MN4, there were two genera of listriodont suids in Europe, one which possessed a derived pattern of bunolophodont cheek teeth, trilobed upper central incisors and a canine which emerged from the end of the canine flange, represented by two species (*L. lockharti* and *L. retamaensis* n. sp.), and one which retained a plesiomorphic pattern of bunodont (crystodont) cheek teeth, a single lobed upper central incisor, and upper canines which emerged from the ventral surface of the canine flanges (*Eurolistriodon adelli*). The two genera are further distinguished by their postcranial skeletons – short and robust metapodials in *Listriodon retamaensis* n. sp. and *L. lockharti*, compared with long and gracile ones in *Eurolistriodon adelli*. The two genera share several derived features of the skull and dentition including

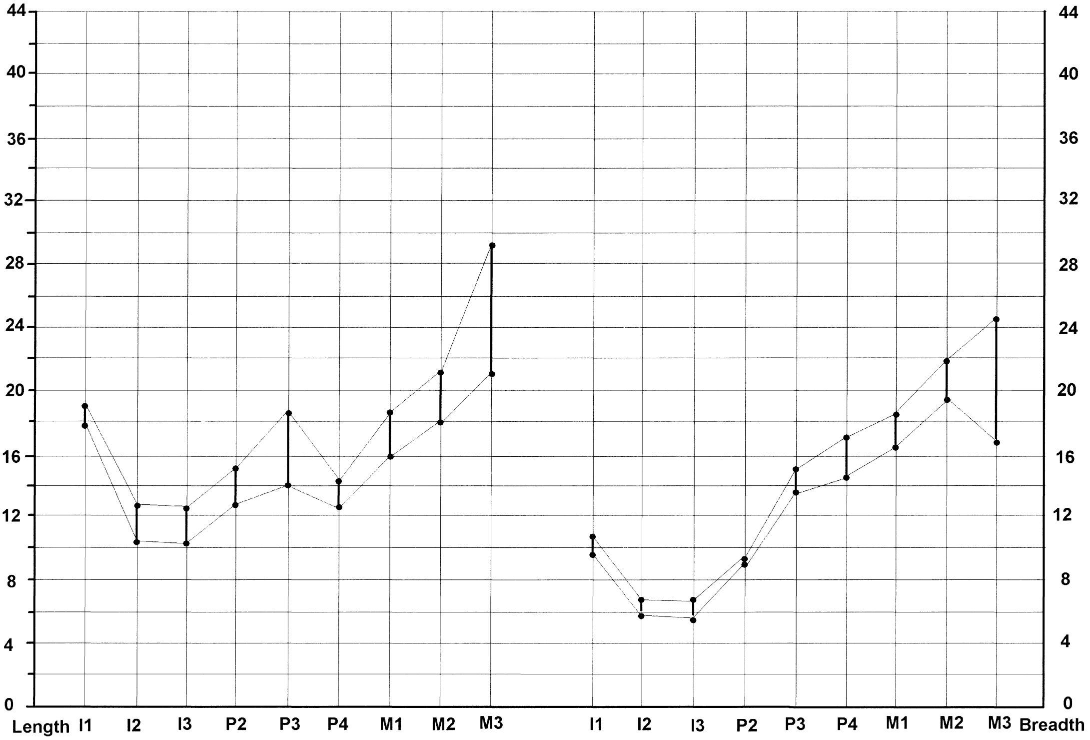


FIG. 5. — Size variation (in mm) of the upper dentition of *Listriodon retamaensis* n. sp. Symbols: ●, maximum and minimum measures, various localities; **|**, range of variation.

distal prolongation of the palatines, elongated snout with diastemata between the canines and premolars, spatulate anterior palate, and mesiodistally elongated upper central incisors, indicating that they diverged from a common stock some time prior to MN4.

The morphology and length/breadth index of the upper central incisors of *L. retamaensis* n. sp. are close to those of *L. lockharti*, and differ from those of *E. adelli* and *L. latidens*, as well as from those of other *Listriodon* species. The Retama cheek teeth are more lophodont than those of *E. adelli*, and resemble those of both *L. latidens* and *L. lockharti*. It would thus appear that the listriodonts from Retama were drawn from an early population of *Listriodon*, the body size of which was smaller than later populations of the genus.

Ginsburg & Bulot (1987) described a snout from Bézian, France, which they identified as *Bunolistriodon lockharti* in which the nasals are complete, extending forwards only as far as the level of the I3 alveolus. The canine jugum is modestly developed, there being no sign of a canine flange, but this may well be because the individual is female. In section, the snout is rounded dorsally with a flat palatal floor. This specimen is here assigned to *Listriodon retamaensis* n. sp.

Sexual dimorphism

It could be argued that the morphological differences between *Eurolistriodon adelli* and *Listriodon retamaensis* n. sp. merely represent sexual differences, the material assigned to *E. adelli* being male and that assigned to *L. retamaensis* n. sp. being female. However, the differences between the two forms are considerably greater than is usually accepted as being due to sexual dimorphism in suids, and they comprise cranio-dental and postcranial parts of the skeleton. It would,

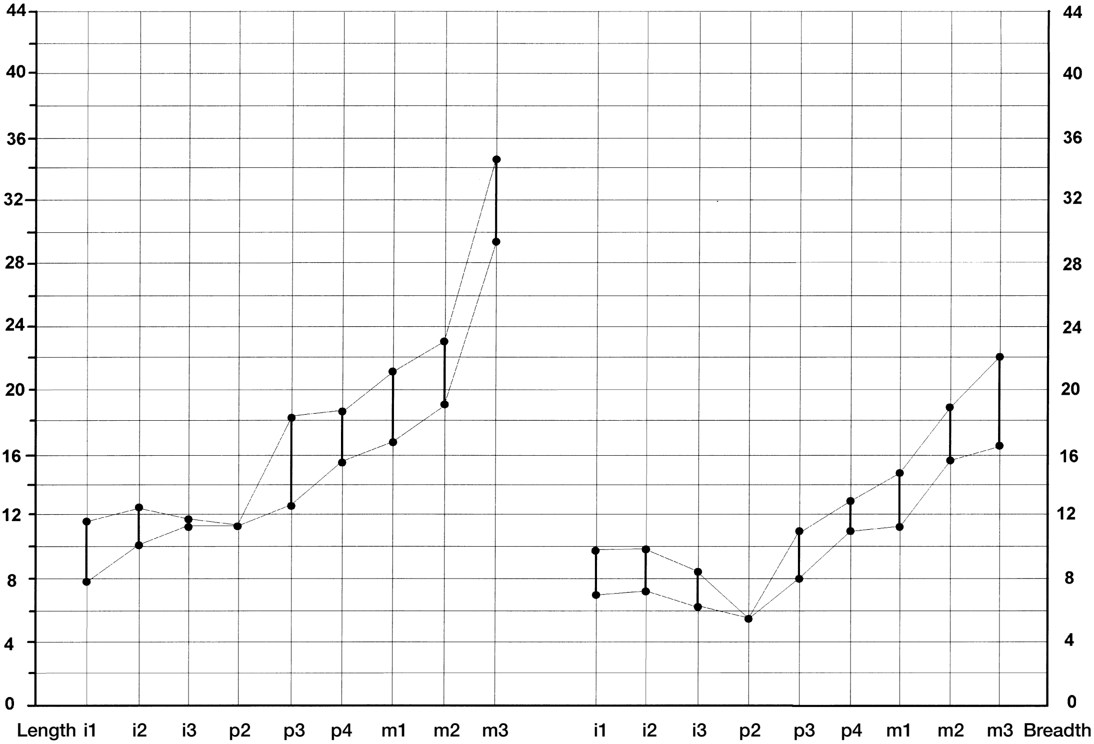


FIG. 6. — Size variation (in mm) of the lower dentition of *Listriodon retamaensis* n. sp. Symbols: ●, maximum and minimum measures, various localities; |, range of variation.

for instance, be extremely doubtful that males would suppress the anterior premolars while females retained them or that males would possess more bunodont cheek teeth than females, or that the upper central incisors of males would have one lobe while those of females had three. The post-canine diastema in *Eurolistriodon* is long (65 mm in the holotype) while that in *L. retamaensis* n. sp. is shorter. Even if we take the homologous measure of the distance between the rear of the canine and the front of P3, it is evident that the Retama snout, with a distance of 38 mm, is considerably shorter than that of *Eurolistriodon adelli* which has a gap of 65 mm. The Inönü, Turkey (MN6), male palate assigned to *L. latidens* (Pickford & Erturk 1979) has a C-P3 measure of about 38 mm, appreciably shorter than that of *E. adelli*. Whilst it is admitted that the length of diastemata can vary appreciably within suid populations (Van der Made 1991, 1997b) it seems excessive to consider such large differences to be due solely to individual variation, especially when they are considered in conjunction with other differences in morphology. If we now move on to take into account the morphology of the canine flange, we notice even more striking differences between *Eurolistriodon* and *Listriodon*. In *E. adelli* the canine flange in the male is extremely wide – it doubles the breadth of the maxilla – and the canine emerges from the ventral aspect of the flange, not at its tip. In all *Listriodon* specimens where this part of the anatomy is preserved, the canines emerge from the ends of the canine flanges. Added to this is the evidence afforded by the postcranial skeleton, in particular the long and slender metapodials of *Eurolistriodon adelli* which contrast with the shorter more robust metapodials of *Listriodon retamaensis* n. sp. and other species of *Listriodon*. For all these reasons, we consider it likely that

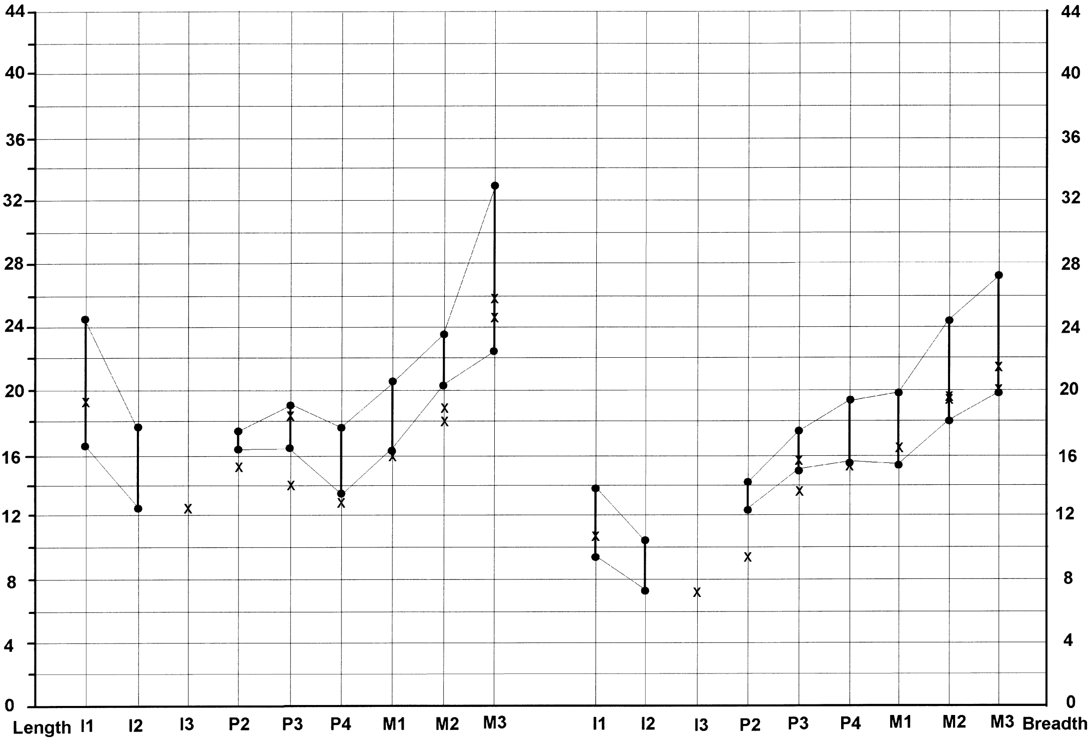


FIG. 7. — Size variation (in mm) of the upper dentition of *Listriodon lockharti* Pomel, 1848. Symbols: ●, maximum and minimum measures; |, range of variation; ✖, Retama fossils.

there are two distinct genera of listriodont suids (*Eurolistriodon* and *Listriodon*) in the basal middle Miocene deposits of Europe.

Listriodon lockharti Pomel, 1848

Listriodonts with bunodont to bunolophodont dentitions are common in European basal middle Miocene deposits such as Pellecahus (MN4a) and La Romieu (MN4b) in the Aquitaine Basin (Fig. 11). The main distinguishing feature of the species is the degree of bunodonty in the cheek teeth, but the mesiodistal expansion of the upper central incisor and the number of subdivisions that it has are additional factors that separate this species from more lophodont forms such as *Listriodon splendens*. Some undescribed material from Pellecahus in the Muséum national d'Histoire naturelle, Paris, is more complete than previously described specimens (Van der Made 1996) and adds considerably to our understanding of the morphology of the lower jaw.

MATERIAL EXAMINED

Lower dentition

LRM 557, i1; LRM 842, i1; LRM 796, i1; LRM 843, i1; LRM 556, i1; LRM 558, i1; LRM 841, left i2; LRM 844, left i2 (unerupted); LRM 555, left i3; LRM 536, mandible with left p4-m3 (m3 broken); LRM 538, right mandible with p2-m3 (m2-m3 broken); LRM 544, p2-p4; LRM 968, right p2; LRM 849, right p3; LRM 550, right p4; LRM 551, left p4; LRM 850, left p4; LRM 965, right m1-m3 (m1 broken); LRM 542, left m1-m2; LRM 1054, right m1; LRM 548, worn m1; LRM 546, right m1 (same individual as LRM 542); LRM 547, left m2; LRM 543, right

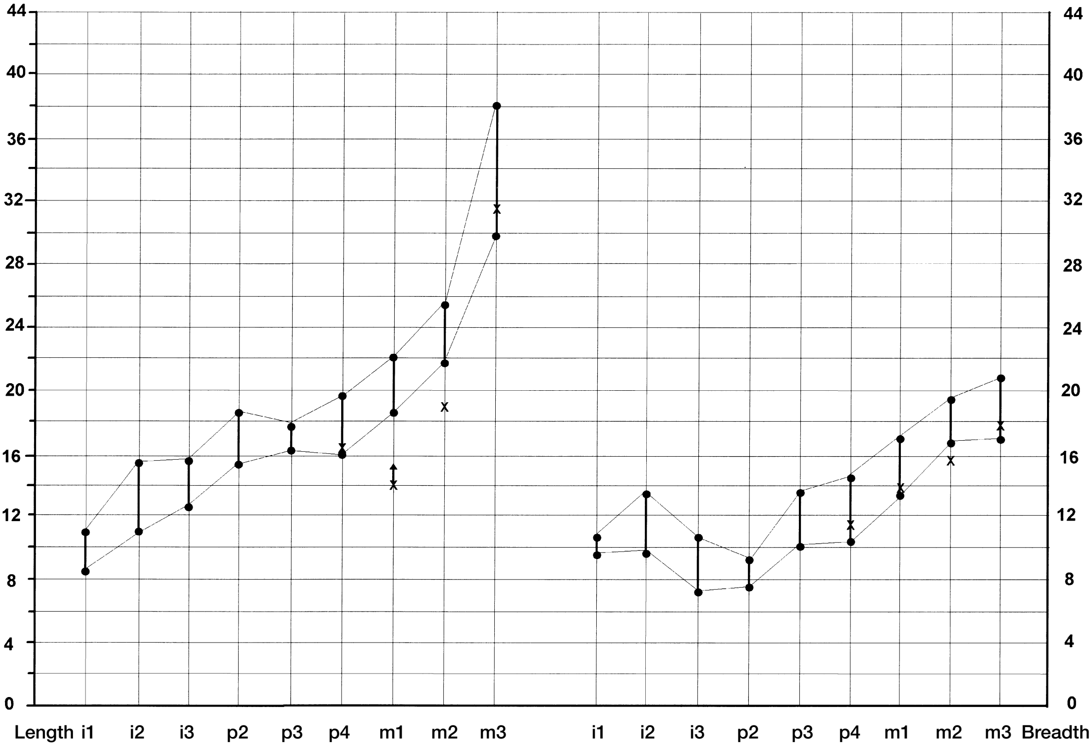


FIG. 8. — Size variation (in mm) of the lower dentition of *Listriodon lockharti* Pomel, 1848. Symbols: ●, maximum and minimum measures; |, range of variation; ✖, Retama fossils; ↑, worn specimens.

m3; LRM 545, left m3; LRM 852, left m3; LRM 568, left di2; LRM 569, left di2; LRM 571, left dm4. All the specimens listed here are housed in the Muséum national d'Histoire naturelle, Paris.

Upper dentition
LRM 845, right I2; LRM 966, left I3; LRM 563, left I3; LRM 851, right upper male canine; LRM 561, left P2; LRM 562, left P3; LRM 549, broken left upper molar; LRM 573, left M1; LRM 554, left M2 (broken); LRM 967, right M3; LRM 572, right dM3.

Postcranial skeleton
LRM 585, distal right humerus (fragmentary); LRM 586, proximal right ulna; LRM 587, proximal left ulna; LRM 853, proximal right radius; LRM 588, proximal right radius (same individual as LRM 586); LRM 537, proximal left third metacarpal; LRM 591, right fourth metacarpal; LRM 854, right fourth metacarpal; LRM 592, proximal left fifth metacarpal; LRM 593, distal left tibia; LRM 594, distal left tibia; LRM 597, right calcaneum (broken); LRM 595, left talus; LRM 596, right talus; LRM 599, left cuboid; LRM 600, right navicular; LRM 603, proximal left third metatarsal; LRM 602, proximal right third metatarsal; LRM 751, right third tarsal bone; LRM 601, right third tarsal bone; LRM 755, right third tarsal bone; LRM 604, distal end first phalanx; LRM 605, second phalanx; LRM 606, second phalanx; LRM 607, second phalanx; LRM 608, third phalanx.

DESCRIPTION

Upper dentition (Table 2)

In labial view the crown of I2 is low and triangular. It possesses a beaded cingulum lingually and

TABLE 2. — Dental measurements (in mm) of the teeth of French Listriodontinae from zone MN4, *Listriodon lockharti* Pomel, 1848, from Pellecahus (Muséum national d'Histoire naturelle, Paris).

Upper dentition	**Length**	**Breadth**
I3	13.8	7.3
I3	15.2	7.8
I3	14.0	7.2
P2	15.6	12.3
P3	17.4	16.3
M1	21.5	20.0
M3	26.0	23.6
M3	22.7	17.3
Lower dentition	**Length**	**Breadth**
i1	10.4	10.3
i1	10.5	10.2
i1	10.2	9.8
i1	10.2	9.7
i1	10.2	10.0
i1	10.6	10.3
i2	12.2	10.7
i3	13.2	8.7
p2	16.9	9.0
p2	16.5	9.1
p2	16.3	8.8
p3	18.4	10.5
p3	18.7	10.5
p3	18.3	11.5
p3	18.9	11.2
p4	17.8	12.6
p4	19.0	13.1
p4	17.0	13.4
p4	17.3	13.1
p4	16.8	12.7
p4	18.2	14.0
m1	20.4	14.2
m1	20.4	15.7
m1	19.8	15.3
m2	23.4	19.0
m2	23.6	18.6
m2	23.2	18.3
m2	22.6	19.1
m2	22.9	18.3
m3	30.5	19.0
m3	31.0	18.6
m3	32.5	19.2
m3	29.4	18.2

the root is short and curves distolingually. Both upper third incisors in the sample from Pellecahus possess triangular crowns in lateral view. In occlusal view the teeth are trenchant. Lingually there is a sharp basal cingulum. Both specimens have long conical roots that curve sharply lingually near their apices.

The upper male canine is almost circular in section, and is strongly curved from root to tip. There is a prominent, almost flat wear facet anteriorly caused by abrasion against the lower canine. A remnant of wrinkled enamel is present ventrally but it does not extend onto the root.

The P2 has an occlusal outline which is triangular with rounded corners. The tip of the main cusp is in the centre of the crown and has ridges that reach the anterolingual and posterolabial corners of the tooth. A cingulum completely surrounds the tooth apart from a small gap in the middle of its buccal surface, and in the distolingual corner there is a small accessory cusplet between the cingulum and the main cusp.

The P3 is basically an enlarged version of the P2. It has three roots.

Upper molars from Pellecahus differ from those of fully lophodont listriodonts by having clear anterior and median accessory cusplets, even if these are small and located between the anterior ends of the main cusps in each loph rather than anterior to the lophs as in other suids. In fully lophodont listriodonts a ridge connects the tips of the main cusps in each loph. In the Pellecahus material, in contrast, ridges descend anteriorly towards the anterior and median accessory cusplets, and it is only in medium wear that a loph-like morphology is expressed. "Furchen" (Hünerman 1968) are present but weakly developed in the upper molars, but in any case are more distinct than they are in fully lophodont listriodonts. In the M3, the talon is located in a lingual position, almost in line with the protocone and hypocone. The Pellecahus upper molars are usually adorned with more or less complete buccal cingula.

Mandible

LRM 536 is the most complete of the mandibles from Pellecahus and it could well belong to the same individual as LRM 538. The anterior part of the symphysis is broken as far back as the right canine alveolus on the right and the middle part of the postcanine diastema on the left side. The symphysis reaches back to the rear of the p2. Judging from the remnant of the canine alveolus preserved the mandible probably represents a male individual. Immediately behind the canine alveolus there is a prominent circular, but not very deep, alveolus for the p1. Between the p1 and the p2 there is a diastema of about 58 mm. An accurate measurement is not possible due to the crushed condition of the specimen, but in any case the diastema is long. The body of the mandible is deep (58 mm below p3 and 65 mm below m3) and it is bucco-lingually relatively narrow, but this may be due to the crushing that the jaw has undergone. There is a mental foramen below the anterior end of p4 positioned about two thirds the height of the body. The overall morphology of the mandible is typical of *Listriodon* species and departs radically from the *Libycochoerus* plan (Pickford 1986) and we see no substantive reason to consider that it should be assigned to a separate genus *Bunolistriodon*. In this respect we are in agreement with Leinders (1975) who studied listriodont mandibles from Torralba 2 and Munebrega 1 in Spain.

Lower dentition (Table 2)

The lower incisors from Pellecahus are generally more robust than those of lophodont listriodonts. The i1s are low crowned with a curved cutting edge, the mesial and distal ends of the cusp curving lingually in unworn specimens. There is a prominent centrally positioned lingual pillar which is large at its base and dies out apically, so that with wear the cutting edge of the crown becomes more and more square in outline. The roots are straight, robust and elongated. The i2 is slightly higher crowned and less symmetrical than the i1, the distal edge protruding slightly to form a shallow scoop-like basin between the central pillar and the distal edge of the crown. Its occlusal edge is almost straight, even in unworn specimens. The root is also slightly bowed, its apex curving mesially. The i3 is even more asymmetrical than the i2 and lower crowned and more spatulate in labial aspect. Its cutting edge is virtually straight when unworn. The mesial height of the crown is appreciably less than the distal height, the central pillar is low but strong, and the root is short and straight.

The p2 is located at the distal end of a diastema. It is a two-rooted tooth with a single main cusp accompanied distally by an enlarged distal accessory cusp which is located slightly to the buccal side of midline. There is a tiny anterior accessory cusplet and a low, sharp, cingulum distally. The distal cusplet is about one third the height of the main cusp.

The p3 is basically a larger version of the p2, except that the distal accessory cusplet is about half the height of the crown and the main cusp has a hint of the development of an "innenhugel" (Hünerman 1968). The p4 is shorter than the p3 and is more rectangular in occlusal outline. The anterior accessory cusplet is more strongly developed than it is in the anterior premolars, and there is a strong crest running from it to the apex of the main cusp. There is a well developed "innenhugel" which is closely fused to the main cusp. In unworn specimens the tips of the main cusp and the "innenhugel" are separated from each other, but even with slight wear they fuse together to form a loph-like structure. The distal accessory cusplet is two thirds the height of the crown, almost forming a separate cusp, which however, is joined to the main cusp by a crest. The distal cingulum fades into the lingual and labial surfaces of the crown.

The lower molars are bunodont with the usual suid layout of four main cusps arranged in two lophs, with anterior, median and posterior accessory cusplets in the midline of the crown. The median accessory cusp is particularly prominent and blocks the median transverse valley to well over half the height of the crown. Several of the teeth retain cingular remnants on their buccal surfaces, but in none of them is the cingulum complete. The "furchen" are present but weakly expressed, and the main cusps in each pair are positioned in close proximity to each other, so that even in the early wear stages, a loph-like structure is developed. The talonid of the third lower molar consists of a dune-shaped cusp with the horns of the dune pointing anteriorly, the buccal horn joining the posterior accessory cusplet which is well developed.

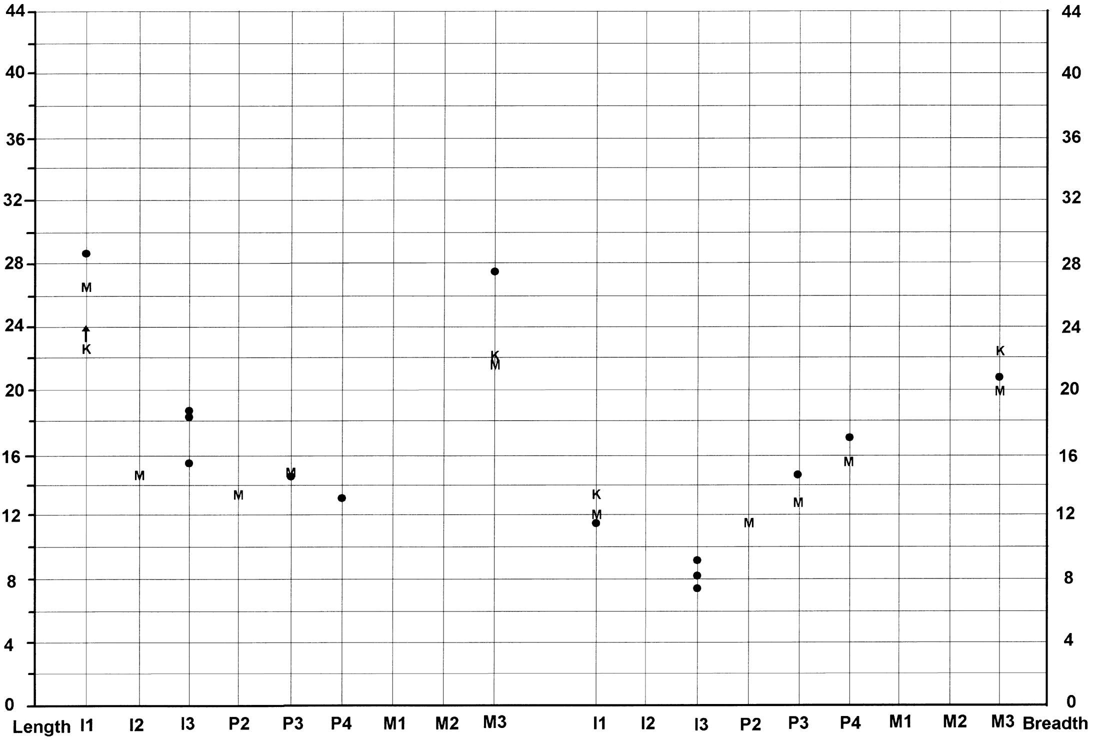


FIG. 9. — Size variation (in mm) of the upper dentition of *Listriodon latidens* (Biedermann, 1873). Symbols and abbreviations: ●, Inönü; **K**, Krusevica; **M**, Mala Miliva; ↑, broken specimen.

Listriodon splendens von Meyer, 1846

The middle Miocene suid, *Listriodon splendens*, has been known for well over a century, and fossils assigned to this species have been recorded from over a hundred localities in Europe, Asia and Africa yet complete skulls are extremely rare. Measurements of the dentition of French *Listriodon splendens* are given in Table 3.

CRANIUM OF *LISTRIODON SPLENDENS* FROM TORIL, SPAIN

The Toril cranium (TO 3B, 129) (Figs 12; 13), presently stored at the Museo Nacional de Ciencias Naturales, Madrid, but belonging to the Museo de Paleontologia, Zaragoza, consists of a virtually complete cranium which has been crushed laterally and slightly obliquely. It lacks the anterior dentition back to and including the P1 but the cheek tooth series (P2-M3) on both sides are present, though the teeth are heavily worn and damaged by cracking and expansion. The premaxillary margins of the external nares are preserved, but the anterior parts of the nasal bones have broken away. Both zygomatic arches have been damaged and much of the squamous part of the occipital bone is missing so that the nuchal crest is not preserved. Interpretation of the basicranium is rendered difficult because of the crushing that it has undergone, but enough is preserved for the major structures to be observed. Cranial sutures are not visible in this specimen which was evidently almost senile when it died, judging from the stage of wear of the dentition.

Palatal view

In palatal view, the anterior part of the snout is spatulate, being narrowest behind the canines

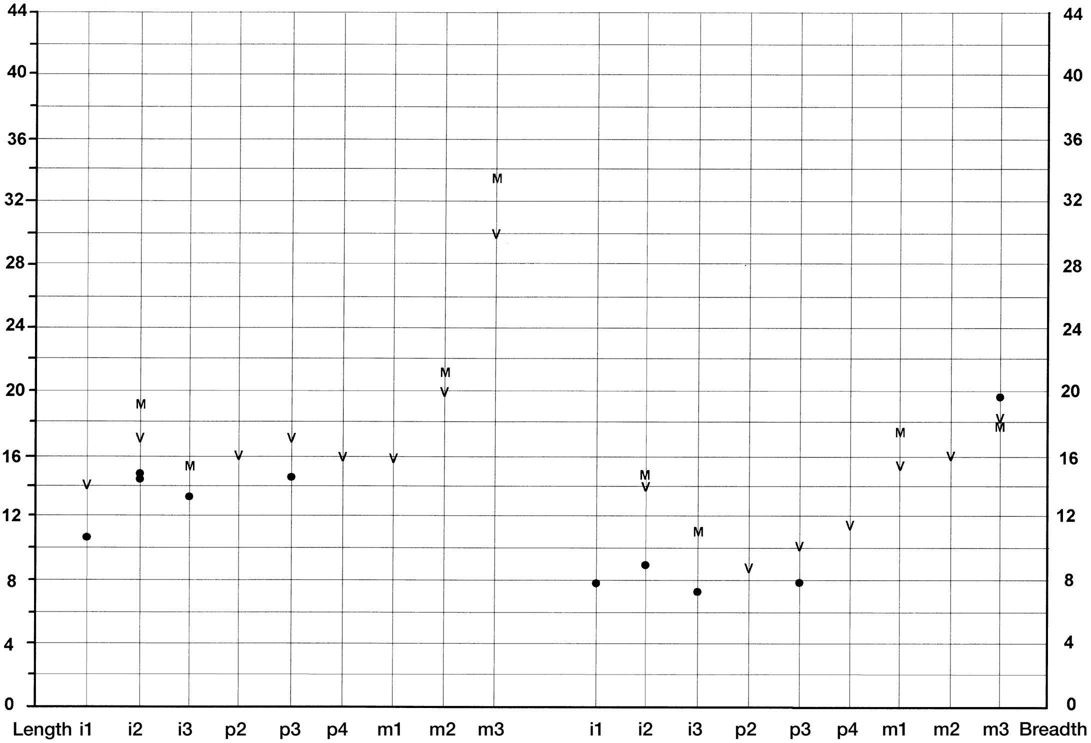


FIG. 10. — Size variation (in mm) of the lower dentition of *Listriodon latidens* (Biedermann, 1873). Symbols and abbreviations: ●, Inönü; **M**, Mala Miliva; **V**, Veltheim (type locality).

and widest between the canine and I3. There is a substantial diastema (*c.* 5 cm) between the posterior margin of the canine alveolus and the anterior edge of the P2 and a shorter diastema (12 mm) between the anterior edge of the canine alveolus and the posterior margin of the alveolus for I3. The edge of the palate between the canine and the P2 is delimited by a narrow crest of bone and there is no sign of alveoli for P1.

The posterior nares are located far back (33 mm) behind the M3. The pterygoid process of the palatine is well developed, as in *Sus* Linnaeus, 1758. The vertical portions of the pterygoid and the pterygoid process of the sphenoid are poorly preserved, but appear to have been similar to those of *Sus*.

In *Sus* there is a substantial space between the pterygoids and the tympanic bullae, but in the Toril cranium, the anterior portion of the bullae terminate close to the pterygoids. This is due partly to a relative increase in the size of the bullae, and partly due to their inclination at a marked angle. Whereas in *Sus* the bullae are oriented almost vertically, such that in lateral view the angle between their distal edge and the paramastoid process is narrow (*c.* 15°), in *Listriodon* the angle is much wider (100°), the bullae pointing towards the palate. In addition, the bullae in *Sus* are ovoid with a low but sharp anterior crest, whereas in *Listriodon* the anterior part of the bullae including the crest are much expanded. The morphology and inclination of the tympanic bullae in *Listriodon* is close to that described for *Lopholistriodon kidogosana* Pickford & Wilkinson, 1975 by Pickford (1986).

The paramastoid process in *Sus* is long and oriented vertically, bending slightly backwards towards their tips, and they thus extend well

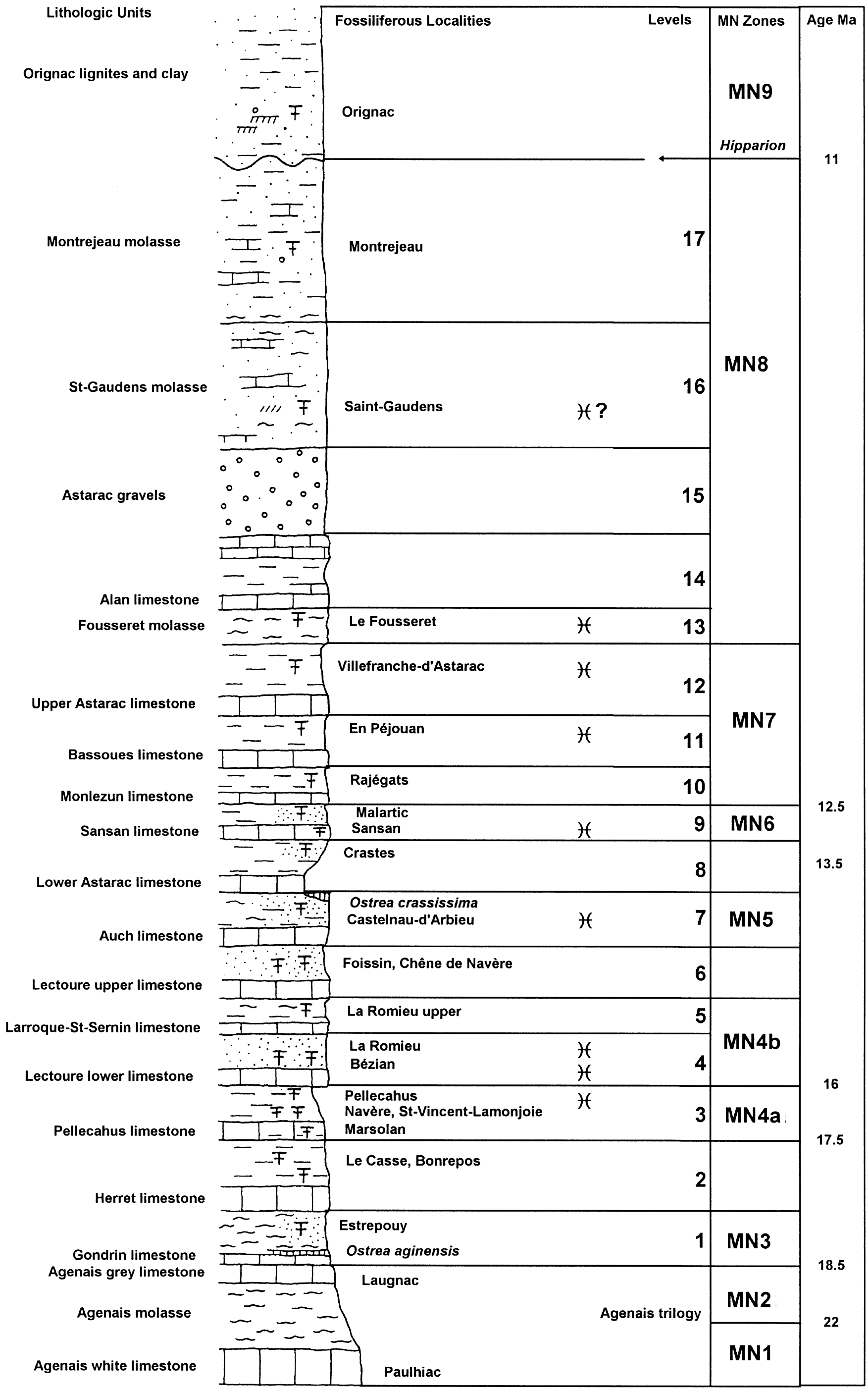


FIG. 11. — Stratigraphic succession in the Aquitaine Basin, Southern France (modified from Ginsburg 2000), showing the distribution of *Listriodon* fossils (✱).

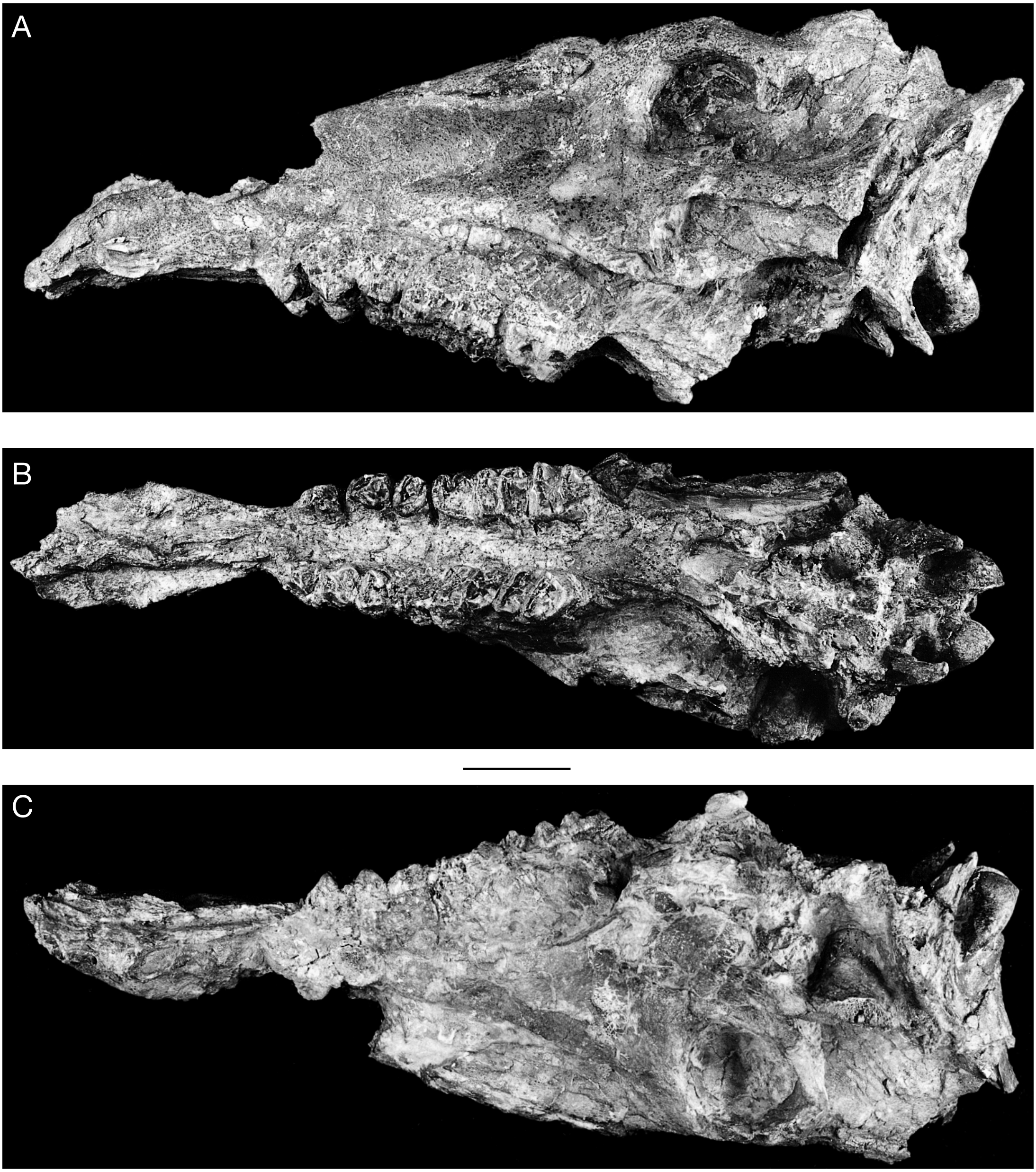


FIG. 12. — TO 3B, 129, female skull with cheek dentition, *Listriodon splendens major* Roman, 1907 from Toril, Spain; **A**, left lateral view; **B**, palatal view; **C**, right lateral view. Scale bar: 5 cm.

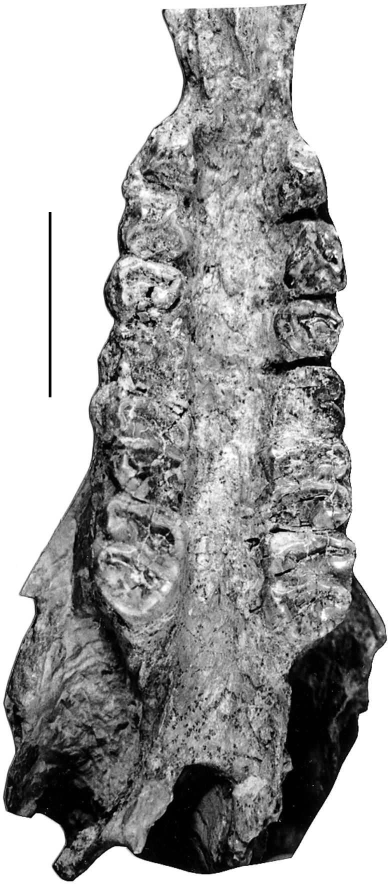


FIG. 13. — TO 3B, 129, female skull with cheek dentition, *Listriodon splendens major* Roman, 1907 from Toril, Spain, occlusal view. Scale bar: 5 cm.

below the occipital condyles, terminating in the same plane as the occlusal surface of the cheek teeth. In *Listriodon* in contrast, the processes are shorter and terminate just below the occipital condyles and well above the occlusal plane of the cheek dentition. They also point more distally. In these features, *Listriodon splendens* resembles *Lopholistriodon kidogosana*.

The temporal condyles are located high above the occlusal plane of the cheek teeth, much as in *Sus*. However, the ventral temporal crest is much closer to the temporal condyle, especially its median end, and in this *Listriodon* and *Lopholistriodon* are similar to each other and both differ from *Sus*.

Lateral view

The anterior nares of the Toril *Listriodon* extend as far back as the anterior margin of the canine, whereas in *Sus* they terminate further forwards, over the I3. The Retama snout of *Listriodon retamaensis* n. sp. has shorter external narial margins, more like the situation in *Sus*.

In the Toril cranium the infraorbital foramen is located above the P3 whereas in *Sus* it is usually located further back over the M1. The anterior end of the crest on the maxilla which separates the fossa for the levator rostri muscles above from the depressor rostri muscles below is located above the P4. The zygomatic arches sweep backwards at a gentle angle with no sign of a pre-zygomatic shelf. The preorbital fossa, which in *Sus* is well developed distally, forming an overhanging ledge in the lachrymal bone and a depression in the malar bone, is poorly developed in *Listriodon*. In the Toril lachrymal, there is a shallow depression with no overhang, and in the malar there is no trace of a fossa. In *Sus* the rhinarial musculature associated with rooting behaviour originates in the preorbital fossa, from which we infer that in *Listriodon*, the rhinarial musculature was probably relatively weakly developed. The rounded profile of the anterior part of the snout in *Listriodon* also indicates that there was not a major muscle mass leading forwards towards the rhinarium. In *Sus*, in contrast, the snout is almost square in profile, with the side of the face possessing a wide groove along which pass the muscles and tendons of the rhinarial musculature which insert into the rostral bone. In *Sus*, above the third molar there is a triangular process projecting ventrally from the base of the prezygomatic crest. This process separates the lower part of the facial aspect of the maxilla (where the depressor rostri musculature originates) from its maxillary recess. In *Listriodon* there does not appear to be an analogous process, there being no clear separation between the maxillary recess and the ventral surface of the root of the zygomatic arch.

In *Listriodon* the zygomatic arch is relatively much deeper than it is in *Sus*. Taking the greatest diameter of the orbit as a reference, the depth of the zygomatic arch taken lateral to the maxillary recess is about 61% of this diameter in *Sus* (26 mm/43 mm), whereas in *Listriodon* the depth of the zygomatic measured in the homologous position is over 100% the orbital diameter (67 mm/53 mm).

There appears to be no lachrymal foramen in *Listriodon*, in contrast to the double foramen located on the margin of the orbit in *Sus*. *Lopholistriodon* likewise has no lachrymal foramina, but *Libycochoerus* Arambourg, 1961 and *Kubanochoerus* Gabunia, 1955, each possess a single foramen. The outline of the orbits in the Toril specimen is more squared off than are the orbits of most suids. In particular the corner of the orbit between the anterior and ventral margins forms almost a right angle on both sides of the skull, but it is not clear whether this angulation has been enhanced by or is due solely to plastic deformation and crushing.

The malar of *Sus* possesses no foramina, but both malars in the Toril *Listriodon* cranium possess a prominent foramen below and anterior to its triangular temporal process. As far as we are aware, such a foramen has not previously been reported to occur in Suidae, and its presence in *Listriodon* may well be a synapomorphy of the subfamily. In *Listriodon* from Toril, the temporal process of the malar forms a prominent spine reaching upwards and backwards towards the supraorbital process, thereby reducing the extent of the post-orbital opening (*c.* 13 mm), which, in *Sus*, is wide open (*c.* 25 mm in a much smaller skull used for comparison). The inferior margin of the zygomatic arch of the Toril cranium has been broken, revealing that it is extensively invaded by sinuses.

The orbits of the Toril cranium lie entirely behind the third molars, their position being close to the condition observed in *Sus scrofa* Linnaeus, 1758.

In *Listriodon* the external accoustic meatus is high, as in *Sus*, opening about half the distance between the base of the occipital condyles and the nuchal crest. The detailed architecture of the bones surrounding the temporal fossa is difficult to make out on account of the crushing and plastic deformation that the Toril specimen has undergone. However, in overall shape, it appears that this part of the cranium was not markedly different from that of *Sus*. The parietal and temporal crests are well developed, but the nuchal crest is missing in the fossil. The frontal contains extensive sinuses as shown by a break above the right orbit.

From the above description it is evident that the Toril cranium is close in general morphology and proportions to that of *Sus scrofa*. Yet there are several important differences between the skulls of the two genera. The preorbital fossa in the lachrymal and malar, which in *Sus* is highly developed, is reduced or absent in *Listriodon*. This suggests that the rooting habit was not important in *Listriodon*. There is no lachrymal foramen outside the orbit in *Listriodon*, whereas in *Sus* there is usually a double foramen outside the orbit. Unique to *Listriodon* is the presence of a large foramen near the temporal process of the malar. This process is well developed and forms a prominent spine which reaches upwards towards the supraorbital process thereby reducing the gap between these two bones. In *Sus scrofa*, the temporal process of the malar barely extends above the zygomatic process of the temporal bone, whereas in *Listriodon* it projects well above it.

TABLE 3. — Dental measurements (in mm) of the teeth of French Listriodontinae from zone MN7, *Listriodon splendens* von Meyer, 1846, from Simorre (Muséum national d'Histoire naturelle, Paris).

Upper dentition	**Length**	**Breadth**
P3	16.9	15.6
P3	15.5	11.5
P4	14.3	16.6
M1	17.4	17.5
M2	19.8	19.7
M3	25.4	20.9
Lower dentition	**Length**	**Breadth**
p2	14.8	8.4
p3	17.0	9.6
p3	15.9	10.1
p4	16.4	13.3
p4	16.7	12.9
m1	16.4	12.5
m1	17.1	13.1
m2	20.8	16.3
m3	31.9	19.6

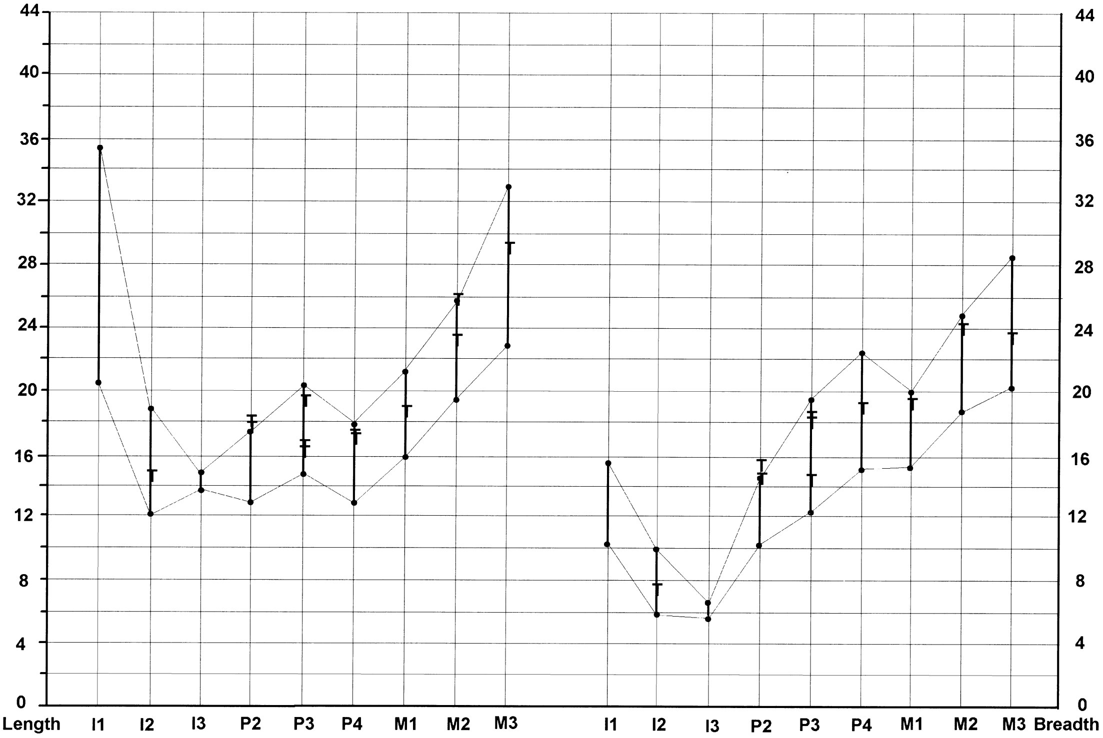


FIG. 14. — Size variation (in mm) of the upper dentition of *Listriodon splendens* von Meyer, 1846. Symbols and abbreviation: ●, maximum and minimum measures; **|**, range of variation; **T**, Toril specimens.

In the neurocranium, the most obvious differences between *Sus* and *Listriodon* are the enlarged tympanic bullae in the latter genus which point more anteriorly than in *Sus* and the short paramastoid processes which terminate well above the occlusal plane of the cheek dentition. In *Sus* the paramastoid processes are long and terminate on a level with the occlusal surface of the cheek teeth. In view of the fact that some of the movements of the mandible are controlled by muscles which originate at the ends of the paramastoid processes, the major differences between these two suids indicate important functional differences in mastication.

In palatal view the most obvious differences between the Toril *Listriodon* and *Sus*, apart from the dentition, are the spatulate anterior part of the snout, the elongated diastemata either side of the canine and the retired posterior nares which open up well behind the third molars.

Upper dentition (Table 4)

In the Toril cranium the three upper incisor alveoli form a closed series separated by a short diastema from the canine alveolus. The canine alveolus is small and opens downwards, forwards and laterally, and is bordered on its dorsal side by a low canine jugum. The size of the alveolus, its orientation and the low, non-projecting jugum indicate that this individual was probably a female. Male listriodonts usually possess large projecting canine juga forming canine flanges and much larger canines that emerge from the end of the canine flange and then flare sideways before curving laterally and upwards. In the Toril cranium there is a long diastema behind the upper canine and there is no sign of alveoli for the first upper premolar which appears either to have been a rudimentary tooth or to have been suppressed altogether. By way of contrast, the Retama female snout of *Listriodon retamaensis*

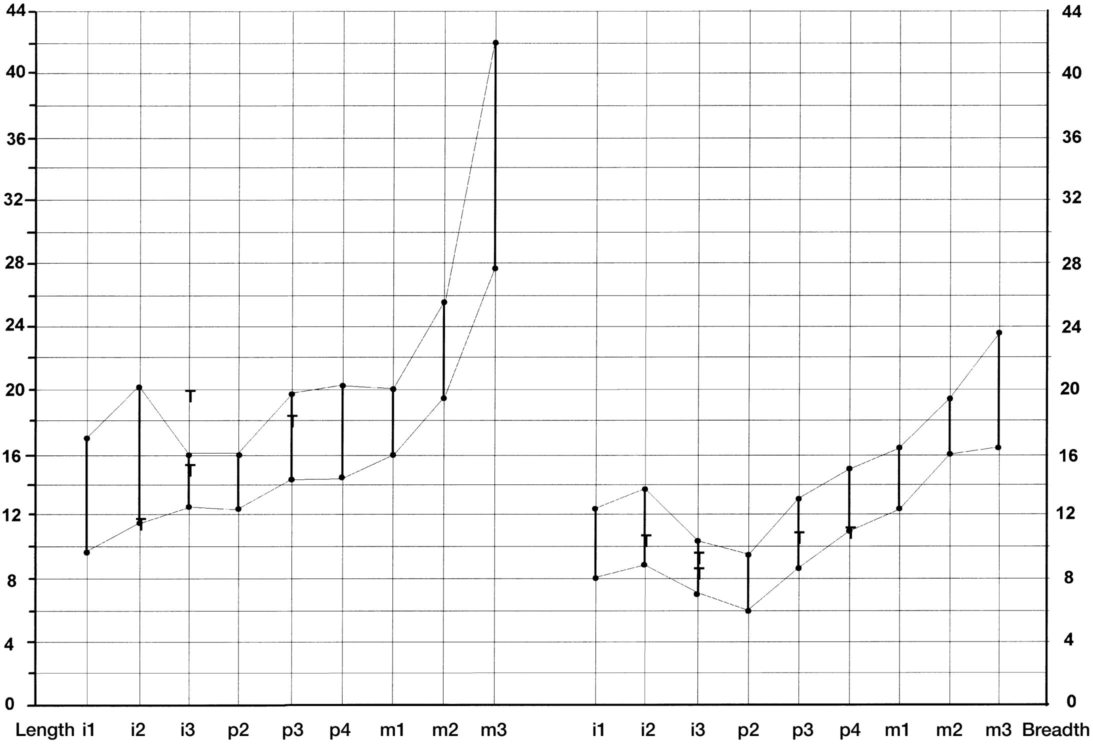


FIG. 15. — Size variation (in mm) of the lower dentition of *Listriodon splendens* von Meyer, 1846. Symbols and abbreviation: ●, maximum and minimum measures; **|**, range of variation; **T**, Toril specimens.

n. sp. has a double rooted P1 situated midway between the canine and the P2. In the Toril cranium the P2-M3 form a closed dental series.

The cheek teeth in the Toril skull are heavily worn and have suffered damage which means that accurate dimensions are difficult to obtain. The measurements given in the table overestimate most dimensions, because the teeth have cracked and "expanded". In lateral view, the occlusal surface of the cheek teeth curves gently ventrally as one progresses from the molars towards the premolars.

OTHER *LISTRIODON SPLENDENS* FOSSILS FROM TORIL (TABLES 4; 5)

In the collection from Toril, there are several isolated listriodont teeth and a few post-cranial bones (Figs 1D-G; 2D-F). There are three upper central incisors in the sample, but they are either broken or extremely worn. TO 3B, 337 and 334 are right I1s, both of which are so worn that only a little enamel remains on the labial surface and tiny patches lingually. Both individuals suffered from heavy abrasion of the root on the labial side indicating that the gingiva had retracted and exposed the cervical part of the root to abrasion from vegetation and also the lips. In TO 3B, 337 the abrasion surface extends for *c.* 5 mm from the crown-root margin, while in specimen 334, the surface extends *c.* 10 mm. In both specimens the abraded surface of the roots is bordered by a series of shallow, rounded, sharp-edged depressions up to 1 mm in diameter, probably caused by a periodontal disease. TO 3B, 13 is the unworn germ of a left I1 with an incompletely formed root which has been crushed buccolingually. It lacks the mesial corner of the crown which has been replaced with plaster of Paris. The occlusal edge of the crown is marked by many small indentations producing a beaded

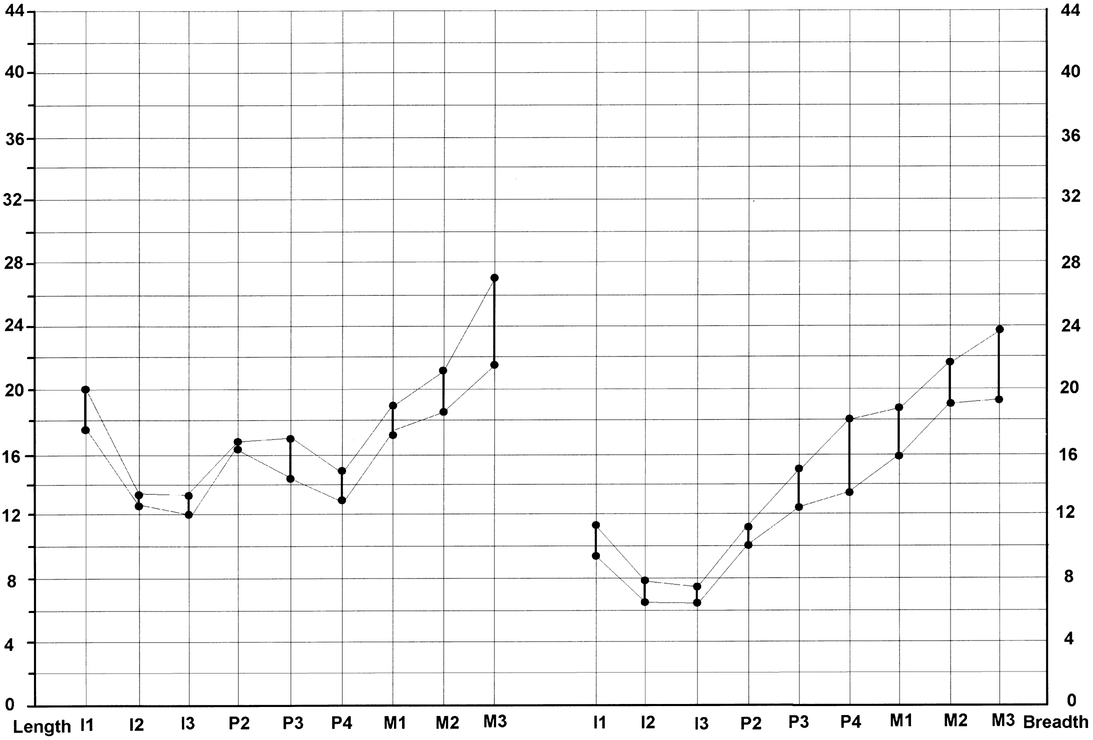


FIG. 16. — Size variation (in mm) of the upper dentition of *Eurolistriodon adelli* Pickford & Moya Sola, 1995. Symbols: ●, maximum and minimum measures; |, range of variation.

effect. The distal margin of the crown overhangs the root, and there is a prominent lingual cingulum. The central lingual pillar is poorly developed.

TOR 3A 223'98 is an unworn right P3. The occlusal outline of the tooth is triangular with rounded corners. The apex of the main cusp lies over the centre of the tooth and it has a prominent crest descending labiodistally towards the cervix. A second shorter crest runs mesiolingually. The anterior surface of the main cusp has a wear facet oriented transversely, caused by its lower antagonist, as described by Leinders (1977). There is a low distolingual cusp separated from the main cusp by a valley which opens distally into a low shelf bordered by the distal cingulum. There is also a low cingulum anteriorly. There are three roots, the distal pair being fused labiolingually into a wall-like structure.

TOR 3A 508'98 is a lightly worn left dM4 with a slightly trapezoidal, almost rectangular occlusal outline. The four main cusps are arranged into two lophs with a continuous crest joining the main cusps to each other located slightly anterior to them. Each of the main cusps has a subsidiary crest running from its tip transversely towards the midline of the tooth. The paracone has a "zygodont" crest running distally from its tip into the median transverse valley. There is a prominent anterior, labial and distal cingulum.

TOR 3B 438 is a right i1. It has an almost bilaterally symmetrical crown with a prominent lingual pillar and low lingual cingular ridges. The root is straight and robust. TO 3B, 201 is a right i2 in light wear. It has a scooped out distal margin, a well developed central lingual pillar with a bulbous base and the lingual mesial margin is raised into a crest. TOR III (33.234) is a left i3 with a prominent wear facet apically. Its root

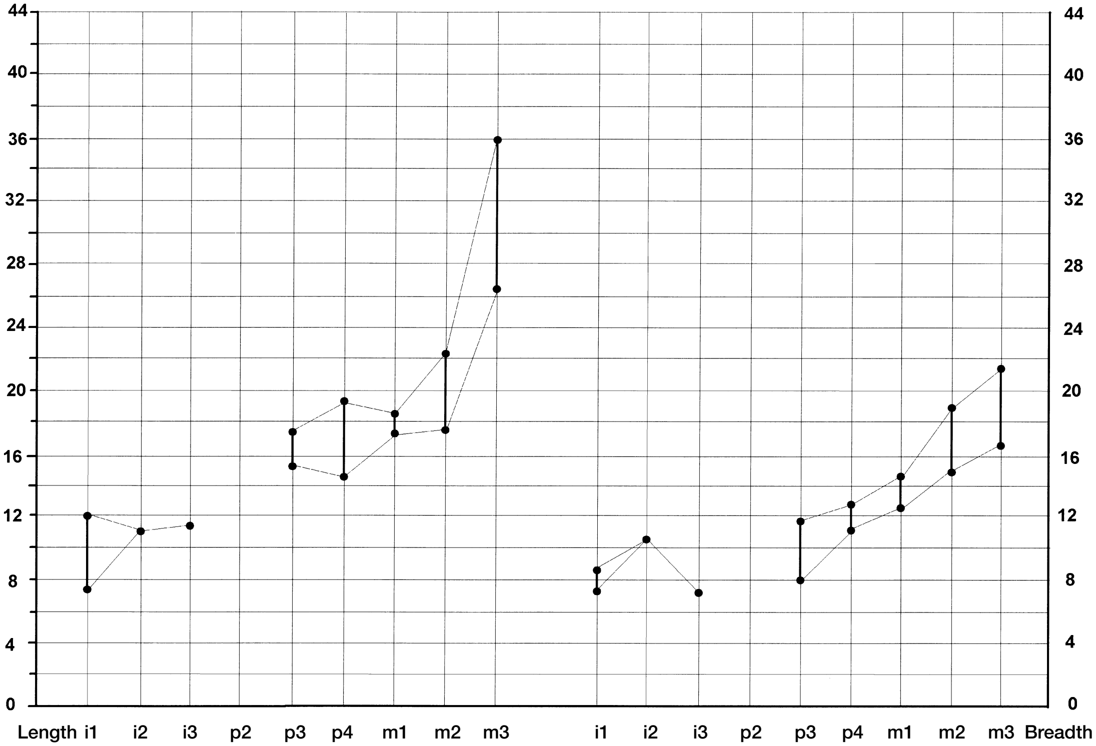


FIG. 17. — Size variation (in mm) of the lower dentition of *Eurolistriodon adelli* Pickford & Moya Sola, 1995. Symbols: ●, maximum and minimum measures; |, range of variation.

narrows rapidly from cervix towards its apex which is curved. The crown is triangular in lingual view and sits obliquely on its root. Mesially it is missing a small part of the crown. It possesses a lingual cingulum and there is a weakly developed lingual pillar. There is also a cingulum on the distal part of the labial surface of the crown. TOR 3B 322 is also a left i3 but it is appreciably smaller than the previous specimen. In RET 338, i3 possesses a triangular crown posed obliquely on its root. The lingual cingulum and pillar are weakly developed and there is no labial cingulum. The distal scoop is well expressed and has a small wear facet cutting its distal margin. The presence of two such different i3s from the same site poses a problem. Either these teeth were extremely variable, or they may be sexually dimorphic.

TOR 3B 290 is a small section of a lower canine of a male individual. TO 3B, 295 is a complete lower canine of a male individual (Fig. 2F). It has enamel on the lingual and labial surfaces but there is none on the distal surface. The distal surface has a broad central ridge, but near the apex of the tusch, this ridge has been abraded away by wear against the upper canine. In section the canine is scrofic, with a slightly larger lingual (23.2 mm) than labial surface (20.8 mm). TOR 3B 197 is a lightly worn but broken right lower molar and TOR III (33.233) is the unerupted crown of a left M2.

TOR 3A 1335'98 is a broken right p4, lacking the buccal and anterior half of the main cusp. The innenhugel is robust and well offset from the main cusp, being joined to it by a transverse crest. Distally there is a low but robustly constructed posterior accessory cusp accompanied by a distal cingulum which fades out labially and lingually as it approaches the main cusp.

TABLE 4. — Measurements (in mm) of the dentition in the Toril *Listriodon splendens* von Meyer, 1846, cranium and other material from the site.

	Left		Right	
	Length	Breadth	Length	Breadth
TO 3B, 337, right I1			22.2+	10.7+
TO 3B, 334, right I1			25+	11.0+
TO 3B, 129, cf alveolus	25.0	15.0	27.0	-
TO 3B, 129, P2	18.6	14.8	18.7	16.0
TO 3B, 129, P3	19.9	18.6	17.2	18.8
TO 3B, 129, P4	17.7	19.5	17.5	22.3
TO 3B, 129, M1	19e	20.0	18.2	18.8
TO 3B, 129, M2	23.5e	24.4	26.0	24.4
TO 3B, 129, M3	28.0	24.7	29.3	23.9
TOR no No. , left I3	15.0	8.0		
TO III (33.323), left M2	23.1	18.9		
TOR 3A 223'98, right P3			17.5	16.5
TOR no No. , left P3	17.0	15.5		
TOR 3A 508'98, left dM4	18.2	15.6		
TOR no No. , left i1	-	10.8		
TOR 3B 438, right i1			12.8	10.4
TO 3B, 201, right i2			15.5	11.6
TO III (33.234), left i3	20+	9.3		
TOR 3B 322, left i3	15.0	8.8		
TO 3B, 295, right cm			22.2	19.0
TOR no No. , right p3			18.2	11.0
TO III (33.233), right m2			23.6	-
TO 3B, 3, right m1 germ			-	12.8

The cheek teeth in the Toril cranium are very large, plotting at the upper end of the range of variation of *Listriodon* teeth, or even falling beyond the known range of variation in the case of the P2 (Figs 14; 15). However, in view of the cracking and expansion that the teeth in the skull have undergone, we should perhaps reduce the measurements by 1 or 2 mm in order to obtain a more accurate estimate of the original dimensions of the teeth. Even if we do this, the material still plots out at the large end of the size range of listriodont teeth (Figs 14; 15). The P3 and P2 have incipient metacones, which, when combined with the large dimensions of the cheek teeth suggests that the Toril species should be identified as *Listriodon splendens major* Roman, 1907. The greatly expanded mesiodistal dimension of one of the i3s confirms this identification.

Postcranial bones (Table 5)

There are several suid postcranial elements from Toril. The left talus TOR 3B 107 is large, plotting in the upper part of the range of distribution of *Listriodon* tali. The measurements of other bones are given in Table 5.

DISCUSSION

There has been a long-running debate (Van der Made 1997b) about the validity of the genus *Bunolistriodon*, which the Toril cranium helps to resolve. There have been two main points of view in the literature. The first is that *Bunolistriodon* is so close to *Listriodon* that the two should not be separated at the generic level (Gabunia 1973; Leinders 1975; Pickford 1986). The other is that the dentition and skulls are widely divergent and that this warrants their generic separation. However, the erroneous view that the skulls of *Bunolistriodon* and *Listriodon* are markedly different is based on a combination of two factors. Firstly there has been a lack of comparative material, the skulls of both supposed genera being rare and often crushed or distorted, and secondly, many of the skull characters claimed to distinguish *Bunolistriodon* from *Listriodon* do not occur in the former genus, but were drawn from a suid skull from Libya (*Libycochoerus massai* Arambourg, 1961) that belongs to a different subfamily, the Kubanochoerinae. The importance of the Toril *Listriodon* cranium is that it reveals that there are no major differences in cranial architecture between the European skulls hitherto assigned to *Bunolistriodon* and those assigned to *Listriodon*. The differences observed are of lesser degree than those that separate two species of the genus *Sus* (*S. scrofa* and *S. verrucosus* Müller, 1840). On this basis one should seriously question whether the continued use of these two genera within Listriodontinae is warranted. The European dentitions assigned variously to *Bunolistriodon* and *Listriodon* form a morphological continuum from buno-lophodont forms such as occur in the species *L. retamaensis* n. sp. and *L. latidens* on the one hand and more lophodont forms such as occur in *L. splendens* on the other. There is no clear separation into two morphometric groups. From this it is concluded that *Bunolistriodon* is not generically separable from *Listriodon* and is therefore a junior synonym of it. In general features the skull of *Eurolistriodon adelli* (Pickford & Moya Sola 1995), even though the only known specimen is badly crushed, is typically listriodont, and were it not for the precocious loss of P1 and P2, the exaggerated development of canine flanges in males which extend like a horn as a separate projection beyond the canine alveolus, together with its bunodont (almost crystodont) dentition, it would also fit within the genus *Listriodon*. The form of the canine flange is so different from that of other *Listriodon* species, however – the canines emerge from the ventral side of the canine flange, not at its end – that when added to the dental and postcranial differences enumerated above, it means that at Els Casots we are in the presence of a genus distinct from *Listriodon*. The cranial differences are reflected in the postcranial skeleton, with *Eurolistriodon* possessing elongated, relatively gracile metapodials and *Listriodon* shorter, more robust ones.

A second area of divergent opinions in suid systematics is whether the kubanochoeres (subfamily Kubanochoerinae) should be subsumed into Listriodontinae as proposed by Van der Made (1996, 1997b) or whether they should not, a position maintained by Pickford (1986, 1993). Van der Made, on the basis of a few characters such as the enlarged I1, considers that these two subfamilies should be united together. However, Pickford (1986, 1993) has pointed out numerous fundamental differences between the skulls and dentitions assigned to these two groups. The Toril cranium, by providing further information that was hitherto not available, serves to underline the fundamental differences between these two suid lineages.

Listriodonts do not possess lachrymal fossae on the orbital margin, whereas the skulls of *Libycochoerus massai* and *Kubanochoerus gigas* (Pearson, 1928) do. The loss of these foramina appears to be a synapomorphy of the Listriodontinae, as they are unknown in any of the

TABLE 5. — Measurements, in mm, of the *Listriodon* postcranial bones from Toril. Abbreviations from Van der Made (1996).

TOR 3B 107, talus	
External length (Lext)	47.3
Internal length (Lint)	43.3
Proximal transverse diameter (DTp)	24.0
Length in the middle (Lm)	38.3
Distal transverse diameter (DTd)	28.8
Width of cuboid facet (d)	12.0
Diameter of tibial pulley (R)	28.3
TO III (33.236), proximal end of a third metacarpal	
Proximal transverse diameter (Dtp)	34.0
Proximal antero-posterior diameter (DAPp)	29.3
TO 3B, 333, distal tibia	
Mesiolateral diameter (Dtd)	35.0
Anteroposterior diameter (DAPd)	32.0
TO 3B, 317, left fourth metatarsal	
Length (L)	104.2
Distal mesiolateral diameter (Dtd)	21.0
Distal anteroposterior diameter (DAPd)	21.8
TO 3B, 30, distal end of a second or third metapodial	
Mesiolateral diameter (Dtd)	23.6
Anteroposterior diameter (DAPd)	23.2
TOR 3B 250, juvenile second phalanx lacking the proximal epiphysis	
Distal breadth (Dtd)	13.5
Distal height (DAPd)	10.2
TOR 3B 108, terminal phalanx	
Length (L)	34.2
Anterior height (DAP)	23.0
Anterior breadth (Dtp)	13.5

available *Listriodon* skulls including those from China and the skull of *Lopholistriodon kidogosana* from Kenya, but are present in all other known lineages of suids. *Listriodon* possesses a prominent foramen on the malar bone, just below the triangular apex of its zygomatic process. Such a foramen is unknown in other suids, and it probably represents a synapomorphy of the subfamily. The tympanic bullae of *Listriodon* and *Lopholistriodon* are enlarged and point forwards rather than ventrally, and in this respect they are markedly different from those of other suids, including *Libycochoerus massai*. The skull of the latter species from Gebel Zelten, Libya, has small, vertically oriented bullae which are located far behind the pterygoid wings of the palatines.

If we add these characters to the others discussed by Pickford (1986, 1993), then it is difficult to escape the conclusion that kubanochoeres differ from listriodonts at least at the subfamily level. The differences in their skulls are as great or greater than those between the skulls of *Listriodon* and *Sus* which most authors readily accept as representing different subfamilies. Furthermore, these differences are present in the earliest members known of each of the subfamilies, from which it is concluded that the two subfamilies evolved from different ancestral groups.

If we include biogeographic evidence with the palaeontological data, then the separate evolution of the two groups becomes even more evident. Kubanochoeres evolved in Africa and then spread to the Middle East and Asia, but apparently never reached Europe. Listriodonts evolved in Eurasia (probably Europe) and then spread to Africa after they had become lophodont.

If we examine the palaeoecology of the two subfamilies, then we cannot fail to be struck by the fact that kubanochoeres evolved from small precursors the size of the pygmy hog (*Sus* (*Porcula*) *salvanius* (Hodgson, 1847)) and that, with the passage of geological time, they experienced a regular and exaggerated increase in size, with the late middle Miocene species *Megalochoerus khinzikebirus* (Wilkinson, 1976) being of gigantic size as large as a hippopotamus, whilst the largest known suid species (*Megalochoerus homungous* Pickford, 1993) was as large as a gomphothere. Thus from about 20 Ma to 12 Ma the kubanochoeres followed a steep but classic Depéret-Cope body size trajectory during their evolution. Listriodonts, in strong contrast, started out being medium sized suids about the same size as *Sus scrofa* and remained virtually the same size throughout their history, except for the middle Miocene African genus *Lopholistriodon* which was smaller than *Listriodon*. Even the largest listriodonts, *L. splendens major*, of which the Toril cranium is a particularly large representative, is barely larger than that of a big wild boar. The main evolutionary trend in listriodonts was the development of lophodont cheek dentition and extremely wide incisors, and in this the subfamily converged functionally on the tapirs (folivorous perissodactyls) (Leinders 1978). Kubanochoeres, in contrast, retained a bunodont cheek dentition, the largest species converging dentally to some extent with bunodont proboscideans. The middle Miocene species of this subfamily even developed cranial appendages on the frontal bone, the only group of suids known to do so.

Thus, morphological, palaeontological, biogeographic and palaeoecological evidence all point to the same conclusion – that Listriodontinae and Kubanochoerinae evolved from different ancestors on different continents and thereafter had quite separate evolutionary histories (Pickford 1986). For all these reasons, it is concluded that the two groups should not be classed within the same subfamily, and we therefore recognise two subfamilies, Listriodontinae and Kubanochoerinae.

THE STATUS OF *BUNOLISTRIODON*

It has previously been argued (Leinders 1975; Pickford 1986; Pickford & Moya Sola 1995) that the genus *Bunolistriodon* was erected in an invalid manner and that in any case the type and other European species assigned to it did not differ enough from *Listriodon splendens* to warrant separation at the generic level. Van der Made (1996, 1997b) has pointed out that even though the erection of the generic name was done in a most peculiar way, it is nevertheless valid according to the *International Code of Zoological Nomenclature* (ICZN 1999).

Re-examination of the fossils assigned to *Bunolistriodon lockharti* (the type species of *Bunolistriodon*) and *Listriodon splendens* (the type species of *Listriodon*) reveals that they are so similar in cranial, mandibular and postcranial anatomy that they are most probably congeneric, in which case *Listriodon* takes precedence over *Bunolistriodon*. The only significant differences between these two species relate to the degree of lophodonty of the cheek teeth and the antero-posterior lengthening of the incisors. With the passage of time the bunodont cheek dentition of *L. lockharti* gradually became more lophodont until the fully lophodont condition observed in *L. splendens* was achieved. There is no marked break in the morphometric continuum, nor is there evidence of two immigration events into Europe, one for *Bunolistriodon* and one for *Listriodon*. Leinders (1975) studied the problem of the affinities of the bunodont listriodonts of Europe, and concluded that the differences between *Listriodon lockharti* and *Listriodon splendens* were relatively unimportant and could not justify the continued generic subdivision between the two species. We fully concur with him. Under the circumstances, the safest and most stable conclusion to reach is that *Bunolistriodon* is a synonym of *Listriodon*.

We have considered whether *Bunolistriodon* should be kept on in the interests of stability of nomenclature, but have concluded that far from promoting stability, its continued use will merely add to the confusion that already exists. One of the reasons for the confusion is that the characters cited by Arambourg (1963) as defining the genus do not occur in it, but rather in the genera *Libycochoerus* and *Kubanochoerus*, both of which belong to a different subfamily, Kubanochoerinae (Gabunia 1960). Because of this, not only Arambourg (1963), but also other scientists (Wilkinson 1976; Van der Made 1996, 1997b) have employed the generic name *Bunolistriodon* for several species of suids which are not listriodonts.

Van der Made (1996) included within *Bunolistriodon* a heterogeneous suite of suids, several species of which we consider to be kubanochoeres while others are listriodonts. *Bunolistriodon affinis* (Pilgrim, 1908), based on a fragmentary maxilla with P4 and M1, from Bugti, Pakistan, could well be a kubanochoere (Pickford 1988), but until better material is collected from the type locality doubt will persist about the status of this species. *Bunolistriodon anchidens* Van der Made, 1996, from Rusinga, Kenya, is a kubanochoere (Pickford 1986) and we consider it to be a junior synonym of *Libycochoerus jeanneli* (Arambourg, 1933) as it does not differ from the latter species either metrically or morphologically. Most of the material assigned by Van der Made (1996) to *Bunolistriodon* aff. *latidens* is equivalent to *Listriodon retamaensis* n. sp. and not to *Eurolistriodon adelli* as thought by Van der Made (1996). *Bunolistriodon meidamon* Fortelius, Van der Made & Bernor, 1996 is similar in many features to *Listriodon latidens* (Biedermann 1873). There can be little doubt that these two species are closely related. They occur within the same relatively restricted geographic area (southeastern Europe) and time period (MN5-6) and share several derived features in the morphology of the incisors (greatly elongated mesiodistally and with a crenulated apical border), canines (greatly enlarged) and cheek dentition (bunolophodont) (Figs 9; 10). In passing we should note that Van der Made (1996: pl. 18, figs 1, 2) gives the holotype of this species as a left upper canine (NSSW 113) and a right and left mandible (NSSW 99) of which the symphysis (Van der Made 1996: pl. 18, fig. 3) is said to be a paratype. This is erroneous, the mandible with the symphysis is the holotype, while the upper canine is the paratype. *Bunolistriodon lockharti* (Pomel, 1848), *Bunolistriodon intermedius* (Liu & Lee, 1963) (Liu & Lee 1963a; Ye *et al.* 1992) and *Bunolistriodon akatikubas* Wilkinson, 1976 (Wilkinson 1976) are all listriodonts of the genus *Listriodon*. Van der Made's (1996) hypodigm of *Bunolistriodon guptai* (Pilgrim, 1926) is, in our opinion, a mixture of kubanochoere and listriodont fossils, but the holotype is a *Listriodon*. In any case, Pickford (1988) considered *L. guptai* to be a synonym of *L. pentapotamiae* (Falconer, 1868).

RELATIONSHIPS BETWEEN LISTRIODONTINAE AND KUBANOCHOERINAE

Van der Made (1996, 1997b) has argued that kubanochoeres represent a tribe within the subfamily Listriodontinae, whereas Pickford (1993) considered that they are a separate subfamily of Suidae. Van der Made (1996: text fig. 58) indicated that his tribe Kubanochoerini consisted of only a single genus *Kubanochoerus* which was derived with doubt from *Bunolistriodon affinis* or from a form more primitive than *Bunolistriodon affinis*.

Van der Made's arrangement of his tribe Listriodontini recognises two genera, *Bunolistriodon* and *Listriodon*. Skulls of some of the species assigned by Van der Made to *Bunolistriodon* are now known. The species *Eurolistriodon adelli* possesses a skull with morphology that is close in several derived features to that of *Listriodon splendens*, the most derived species of the large Listriodontini. The snouts of *Listriodon retamaensis* n. sp. from Bézian and Retama are also typically listriodont, even if shorter than that of *Eurolistriodon*. The male snout of *L. latidens* from Inönü, Turkey, is also typical of Listriodontini, possessing a widely flaring canine flange, and the same morphology occurs in the Chinese sample of *Listriodon* (Chen 1986). In all these forms, the male snout has wide canine flanges and the U-shaped posterior nares are retired a long distance behind the level of the third upper molars.

In the African species assigned to *Bunolistriodon* by Van der Made, however, (i.e. *B. anchidens*, *B. jeanneli*) the skulls and mandibles show no close resemblance to those of European Listriodontini. For example they do not have retired posterior nares (which are in any case V-shaped) among a host of other features enumerated by Pickford (1986). Similarly, none of the species assigned to Kubanochoerini by Van der Made possesses expanded canine flanges in male individuals, and the early species (*Kenyasus rusingensis* Pickford, 1986, *Libycochoerus jeanneli*, *L. massai*) do not have retired posterior nares.

All this suggests that the Listriodontinae as conceptualised by Van der Made comprises at least two suid lineages which have no close phylogenetic relationships to each other. It is likely that the Kubanochoerini of Van der Made is a natural clade, but it should have attached to it the African species put by him, erroneosly in our view, into the genus *Bunolistriodon*. Pickford (1986) previously argued on the basis of cranial, mandibular and dental evidence that the African species *Libycochoerus jeanneli* is a kubanochoere and not a listriodont, and we see no compelling reason to change his conclusions about it. If the species *Libycochoerus anchidens* proves to be separate from *L. jeanneli*, which we doubt, then it too would join the Kubanochoerinae.

ORIGINS OF LISTRIODONTINAE

By the onset of MN4a European listriodonts already comprised two genera, *Eurolistriodon* and *Listriodon*, with significant differences in cranial and postcranial anatomy. It is therefore likely that the initial radiation of the subfamily occurred in MN3 or MN2, but thus far no convincing listriodont ancestor has been identified in these levels. For this reason some authors, including Van der Made (1996) have proposed that listriodonts evolved elsewhere and then migrated into Europe during the faunal turnover that heralded European land mammal zone MN4, a period which saw proboscideans, among other mammals, colonise Eurasia from Africa. The main problem with this suggestion is that listriodonts are unknown anywhere else in the world in deposits of MN3 and MN2.

In a general way it has been suggested that the listriodonts evolved from a species of *Hyotherium* such as *H. meisneri* von Meyer, 1850 or *H. major* (see Fig. 18), but there has never been much conviction in these proposals, even though out of the known suids from MN2 and MN3, the genus *Hyotherium* possesses dental morphology which is closest to that of early listriodonts. What is required to settle the matter is a detailed study of the skulls, because it is now evident that in suids in general and in listriodonts in particular, it was the skull that diversified more rapidly than the dentition. Thus early listriodonts will probably be identifiable as such on the basis of their skull morphology, whereas their dentitions will not be

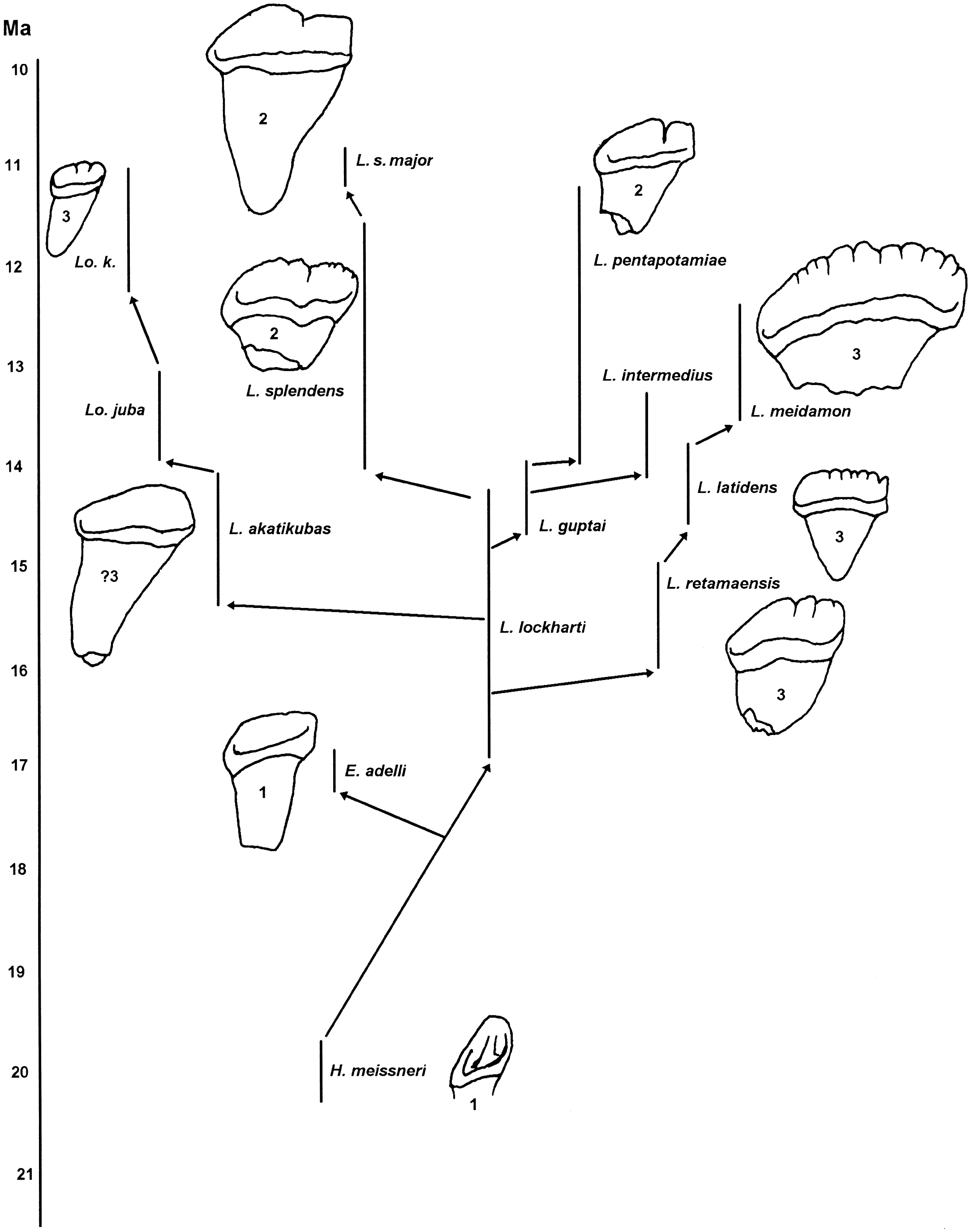


FIG. 18. — Evolution of the central upper incisor in Listriodontinae. Abbreviations: **E.**, *Eurolistriodon*; **H.**, *Hyotherium*; **L.**, *Listriodon*; **Lo.**, *Lopholistriodon.*

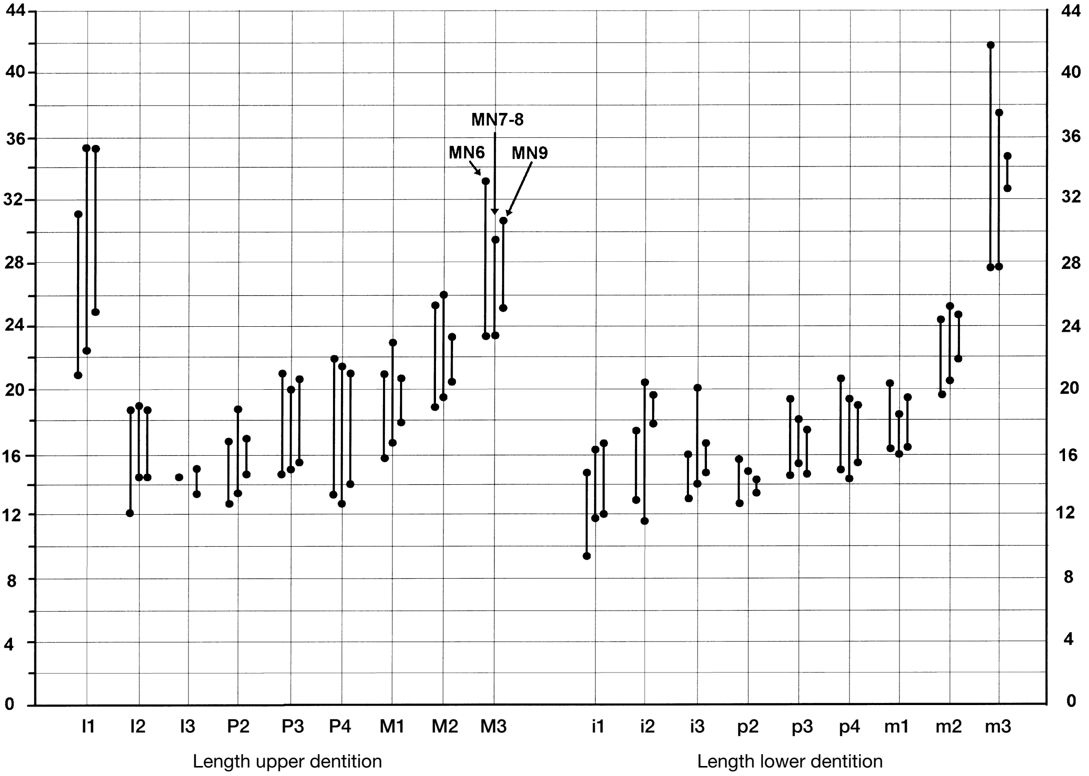


FIG. 19. — Size variation (in mm) of the lengths of the upper (left) and lower (right) teeth of three subspecies of *Listriodon splendens* von Meyer, 1846 from MN6, MN7/8 and MN9, showing significant overlap in measurements. Symbols: ●, maximum and minimum measures; |, range of variation.

markedly different from those of hyotheres. No doubt this is why some isolated teeth of early *Listriodon* have on occasion been identified as *Hyotherium* (Golpe-Posse 1972; Chang 1974). *Eurolistriodon adelli* possesses a skull with all the classic listriodont morphology (Pickford & Moya Sola 1995) yet its cheek dentition is primitive, differing from that of *Hyotherium meisneri* principally by its superior size (Figs 16; 17). Even the upper central incisors of *E. adelli* are weakly elongated, being intermediate in length/breadth index between those of *H. meisneri* and those of *L. lockharti* (Fig. 18).

The dentition of *Aureliachoerus* Ginsburg, 1974 differs in several important respects from those of early listriodonts, and it is unlikely that this genus is closely related to them. The original hypodigm of *Xenohyus venitor* Ginsburg, 1980, a suoid known from MN2 and MN3 of southwestern Europe, originally thought to be a suid (Ginsburg 1980) but later transferred to the Old World Tayassuidae (Pickford & Morales 1989), contains a few teeth that may well be suid, and there remains the possibility that the origin of the listriodonts could be found in the taxon represented by these specimens. However, its fossil record is so fragmentary and poor that, for the time being, very little can be said about it.

BIOSTRATIGRAPHIC IMPLICATIONS OF THE NEW SPANISH AND FRENCH LISTRIODONT MATERIAL

Retama is a basal middle Miocene site (MN4a) containing gomphotheres and *Anchitherium* von

Meyer, 1844 among other taxa. *L. lockharti* is reported to occur at a number of other sites in southern Europe ranging in age from MN4a to MN5 (Van der Made 1996), but the Retama specimens are appreciably smaller than material hitherto assigned to this species. It is possible, though not yet definite, that *L. retamaensis* n. sp. represents an early stage in the evolution of the lineage which underwent a moderate increase in size over time. If so, then Bézian, which is currently positioned in MN4b (Ginsburg & Bulot 1987) could be close in age to Retama (MN4a). The cheek teeth of the Retama listriodont are more derived than those of *E. adelli* from Els Casots (Pickford & Moya Sola 1995) and Artesilla (Azanza *et al.* 1993), which suggests that Retama is somewhat younger than these two localities, both of which have previously been assigned to MN4a. Metrically, however, the ranges of variation of the dentitions of *E. adelli* and *L. retamaensis* n. sp. overlap significantly.

The fauna from Toril is typical of MN7 (Daams & Freudenthal 1988; Mein 1990; De Bruijn *et al.* 1992; Van der Made 1996). Van der Made (1996) recognised three time successive subspecies of *Listriodon splendens*. The earliest of these (*L. s. tapirotherium* Blainville, 1847) was considered by him to be typical of MN6, to the extent that he proposed that Simorre, the type locality, should be placed in the early part of MN6 rather than in MN7/8 which seems to be the prevailing opinion among European biostratigraphers (De Bruijn *et al.* 1992). The second of these subspecies (*L. s. splendens*) was thought to be characteristic of MN7, while the third (*L. s. major*) was considered to typify MN8 and MN9 (Van der Made 1996). However, the ranges of variation of these three subspecies overlap to a considerable extent (Fig. 19) which reduces their utility for fine scale biostratigraphy, and which renders their identity as separate taxa unlikely.

Van der Made (1996) reported that the subspecies *L. s. major* occurs only in MN8 and MN9. The Toril cranium extends its range downwards in time to MN7. It appears that *L. s. major* is a geographic subspecies, rather than a chronosubspecies as thought by Van der Made (1996) all the material having been found in the Iberian Peninsula. *Listriodon splendens* from MN7 to MN9 in the rest of Europe does not follow the same fine scale evolutionary trend as the Iberian one, and all of it is assigned to the subspecies *L. s. splendens.*

EVOLUTIONARY TRENDS IN THE UPPER CENTRAL INCISORS OF LISTRIODONTS

As Van der Made (1996) pointed out, there was a trend for listriodont incisors to increase in mesiodistal length with the passage of time. He also noted the tendency for the apical edge and labial surface of the crown to become subdivided by one or two main grooves (Fig. 18). The lengthening of the crown is reflected to a great degree in the root morphology which becomes strongly triangular in lingual or labial view, tapering sharply towards the apex. Study of the number of grooves and the length/breadth index leads to the suggestion that several lineages of listriodonts can be recognised (Fig. 18).

The I1 of *Listriodon retamaensis* n. sp. has two main grooves whereas its contemporaries *L. lockharti* and *Eurolistriodon adelli* had one and none respectively. The two species *L. latidens* and *L. meidamon* have two main grooves and the cutting edge of the crown is often heavily beaded, suggesting that they may well be descendents of *L. retamaensis* n. sp. *Listriodon splendens*, *L. pentapotamiae*, and *L. intermedius* represent a second lineage in which there was one main groove in the labial surface of the crown. The condition in African *L. akatikubas* (Wilkinson, 1976) is not clear because the only known upper central incisor is heavily worn but its length/breadth index suggests affinities with *L. retamaensis* n. sp.

Species of *Lopholistriodon* have two main grooves in their I1s but they differ from those of other *Listriodon* species by having more cylindrical roots that do not taper so markedly towards their apices, and the crown is less elongated mesiodistally (Fig. 18).

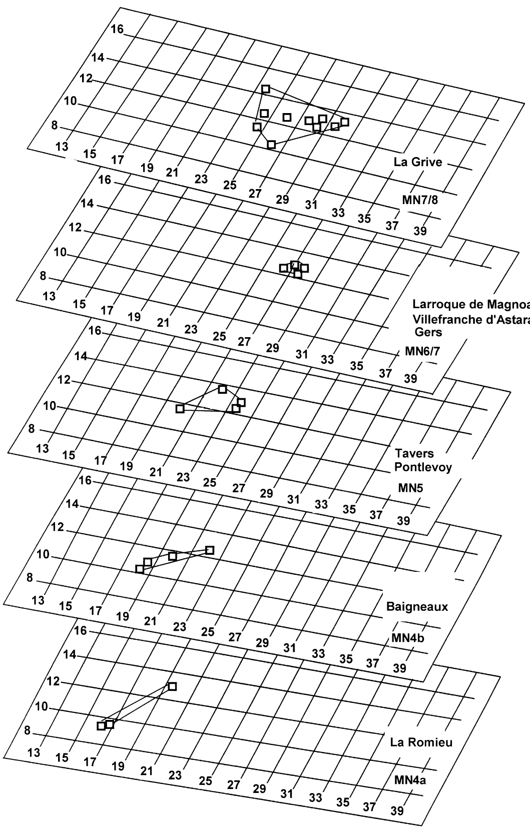


FIG. 20. — Metric changes of *Listriodon* upper first incisors from France. Horizontal axis: mesiodistal length; vertical axis: buccolingual breadth.

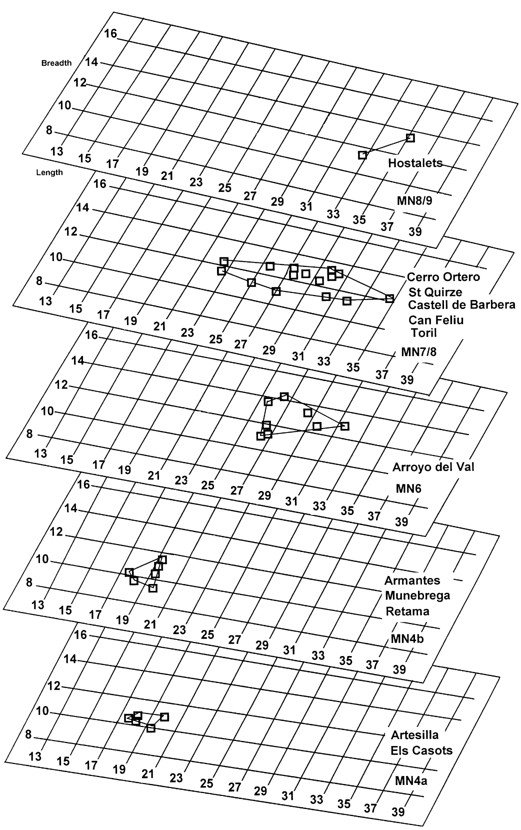


FIG. 21. — Metric changes in *Listriodon* upper first incisors from Spain.

In France there were gradual changes in the length of *Listriodon* I1s from MN4a to MN5, followed by a rather abrupt increase in length in MN6, which was succeeded by a second period of little change (Fig. 20). A similar picture emerges from study of the Spanish record, but the major change seems to be sharper than it probably was because of a lack of evidence from MN5 (Fig. 21). The apparent acceleration in increase of length of I1 occurred in France about 13.5 ± 0.5 Ma but it should be kept in mind that the trends observed are based on relatively few specimens (four specimens in each of MN5 and MN6). As soon as larger samples are obtained, as for example in MN7/8 in France, or MN6 and MN7/8 in Spain, the range of variation increases to the extent of reducing the differences between successive samples.

There remains to explain, however, the relatively abrupt change in central upper incisor length that occurred between MN5 and MN6 in both France and Spain. Is it because there was a brief but potent increase in evolutionary activity within Europe? If so, then it would conform to the concept of punctuated equilibrium. If not, could it then be due to the immigration from elsewhere of a different lineage (*Listriodon splendens*) that had already evolved longer incisors, followed by the extinction of the previously established lineage (*Listriodon lockharti*) – the model preferred by Van der Made (1996: 133)? With presently available information it is difficult to decide, although it should be noted that in other features such as body size and cheek tooth morphology, there does not appear to have been an equivalent burst of change during MN5, but almost no change at all (body size) or a more gradual process of change (cheek tooth morphology).

Furthermore, deriving European *Listriodon splendens* from *Listriodon pentapotamiae* of the Indian subcontinent by immigration (Van der Made 1996: 136, 140) raises several difficulties. Firstly the range of metric variation of the upper central incisors from Pakistan (Figs 22; 23) does not overlap with the range of variation of European fossils, which means that in migrating they would have to have undergone an abrupt size increase. Secondly, the Chinji levels which yielded most of the fossils assigned to *L. pentapotamiae* are usually considered to be equivalent in age to MN7/8 (see Fig. 32), and thus the Indian species is too young to represent the ancestor of *L. splendens* which already occurs in Europe in MN6 (Sansan for example). Thirdly, the observation that *Bunolistriodon guptai*, the putative ancestor of *L. pentapotamiae*, had a single labial groove in the I1, thus making it an ideal ancestor for the later species, appears to be false. This is because one of the upper central incisors assigned to *B. guptai* by Van der Made (1996: pl. 27, fig 7) belongs in our opinion, to *Libycochoerus* – the groove is in a more distal position than is the case in listriodonts and the distal end of the crown curves sharply rootwards to form a distinct hook-like structure. This morphology occurs in some specimens of *Libycochoerus massai* from Gebel Zelten (see for example Van der Made 1996: pl. 8, fig. 10). The other specimen identified by Van der Made (1996: pl. 27, fig. 3) as an upper central incisor of *Bunolistriodon guptai* has no labial groove and is not greatly elongated and in these respects it is closer in morphology to *Eurolistriodon adelli* than to *L. pentapotamiae* or *L. splendens*.

Re-examination of the morphology of listriodont upper central incisors from MN4 and MN5 in Europe, Asia and the Indian subcontinent reveals that the specimens with the closest resemblance to those of *L. splendens* are from Pellecahus and Baigneaux, which belong to *L. lockharti*. In particular, the part of the crown mesial to the labial groove tends to be comprised of two or three, sometimes four small cusplets or beads separated by short, shallow grooves. In *L. retamaensis* n. sp. there are two labial grooves, as in *L. latidens* and *L. meidamon*. In *E. adelli* there is no labial groove in the I1.

BODY WEIGHT IN LISTRIODONTS

Measurements of the cheek teeth of listriodonts reveals that the Eurasian species and one of the African species remained remarkably constant in size throughout their existence from MN4 to MN7/8, a period of some 6.5 million years. There were minor fluctuations in size, *L. retamaensis* n. sp. being slightly smaller than *L. lockharti* and *L. splendens*, but the differences were relatively small. Van der Made (1996) calculated body weights of various suids using the method proposed by Legendre (1986) which is based on the size of the lower first molar. All the body weights calculated for Eurasian *Listriodon* fell into the range 112 to 165 kg which is somewhat less than the mean body weight of females of the Giant Forest Hog (*Hylochoerus*, female mean 180 kg, range 130-204 kg [Kingdon 1979]). *Listriodon akatikubas* from Africa was of similar size (Figs 24; 25), but the *Lopholistriodon* lineage was considerably smaller, the Maboko material weighing in at about 13 kg and the Ngorora species, *Lopholistriodon kidogosana*, at about 26 kg (Van der Made 1996: fig. 59).

As far as the Eurasian listriodonts are concerned, the calculated body weights indicate a remarkable conservatism in body size over a period of *c.* 6.5 million years (Fortelius *et al.* 1996b). During the same period there were important changes in lophodonty of the cheek teeth and the mesiodistal length of the incisors. This history contrasts strongly with that of kubanochoeres (Van der Made 1996; Pickford 2001a) which experienced an enormous increase in body size (from *c.* 40 kg to *c.* 3000 kg) over the same geological time span, but remained bunodont throughout their history.

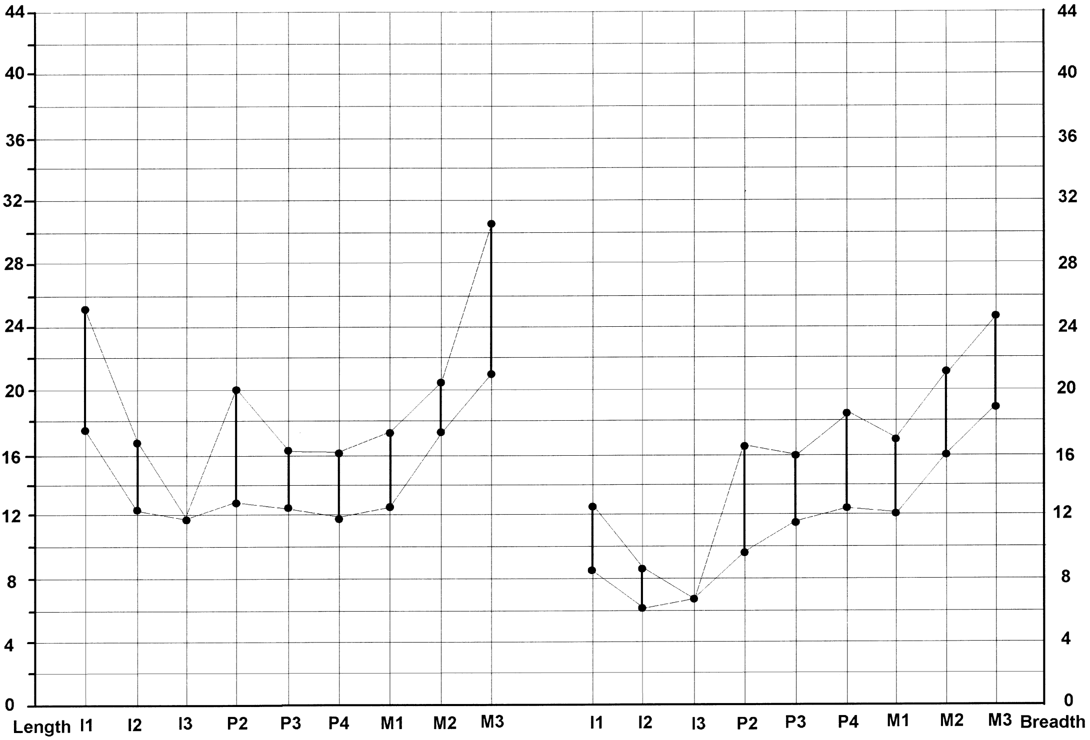


FIG. 22. — Size variation (in mm) of the upper dentition of *Listriodon pentapotamiae* (Falconer, 1868). Symbols: ●, maximum and minimum measures; |, range of variation.

Comparison of listriodont dentitions with those of other medium to large mammals suggests that they may have been browsers, much as tapirs (body weight 225-300 kg) are today. Leinders (1978) was of a similar opinion, that *Listriodon* (lophodont cheek teeth) was a herbivore rather than an omnivore such as *Sus* (bunodont cheek teeth) and Hunter & Fortelius (1994) came to a similar conclusion based on their study of dental microwear.

REPRESENTATION OF LISTRIODONTINAE IN THE FOSSIL RECORD

There are several ways that the representation of listriodonts in the fossil record can be expressed: the number of localities at which they have been found, the quantity of specimens, geographic location of fossil sites and the stratigraphic ranges of the species.

NUMBER OF LOCALITIES BY CHRONOLOGICAL INTERVAL

Listriodonts have been found at over 140 localities in Europe ranging in age from MN4a to MN9 (Van der Made 1996). There are two peaks of locality richness: in MN4b there are 31 localities and in MN7/8 there are 43 (Fig. 26). In MN5 there are only 12 known localities. There is thus a dearth of information about the transition from the more bunodont forms that existed in MN4a and MN4b, and the extremely lophodont forms that occur in MN6 and MN7/8. It is possibly because of this that some authors such as Ginsburg (1977) and Van der Made (1999) have proposed that there were two colonisations of Europe by listridonts, an earlier so-called "*Bunolistriodon*" event at the onset of MN4a, and a subsequent "*Listriodon*" event at the beginning of MN6. It is also for this reason that the same authors support the view

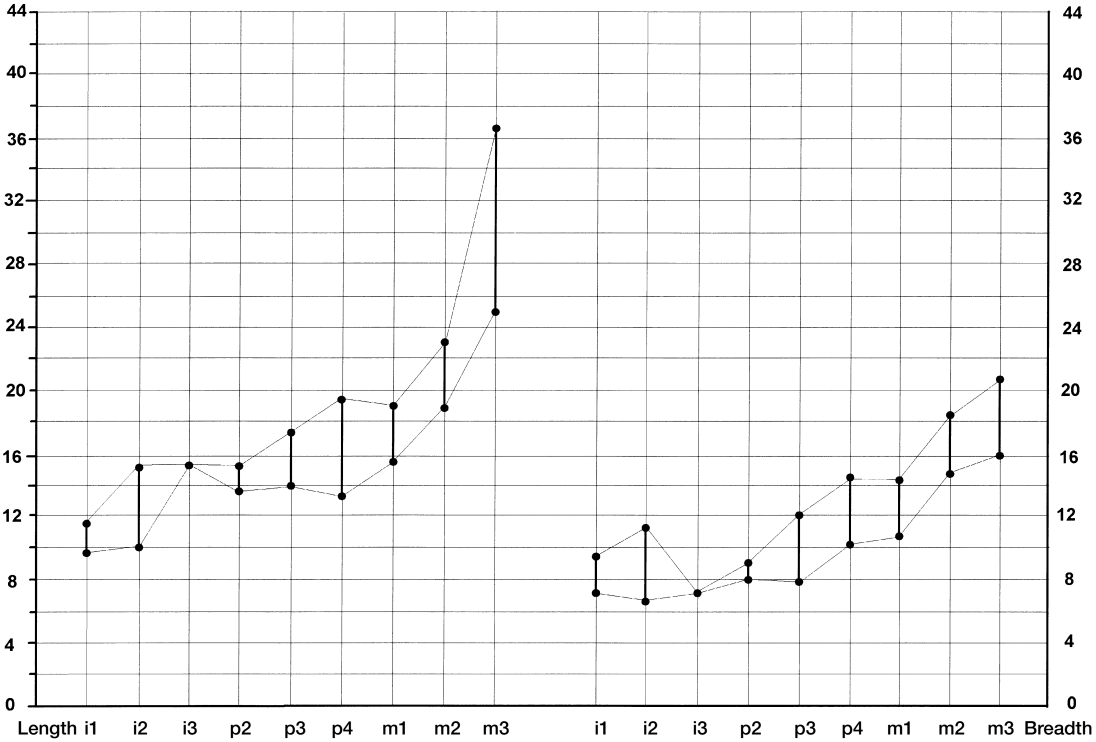


FIG. 23. — Size variation (in mm) of the lower dentition of *Listriodon pentapotamiae* (Falconer, 1868). Symbols: ●, maximum and minimum measures; **|**, range of variation.

that there are two genera of European listriodonts separated by a morphological and chronological gap. However, study of some relatively continuous stratigraphic sequences such as that in the Aquitaine Basin, France (Fig. 11) reveals that there was no major break in the European listriodont fossil record but only a sort of bottleneck during MN5.

Our view is that although there is a relative scarcity of listriodont localities in Europe during MN5, it does not mean that they stopped evolving within the continent – it is just that it is difficult to document the changes. The fact that in MN5 there are 11 listriodont localities known in Spain and other parts of Europe, indicates that the region was probably inhabited continuously by these suids throughout the middle Miocene, and that the impression of allochthonous evolution followed by a separate colonisation during MN6 does not take this into account.

QUANTITY OF LISTRIODONT TEETH IN EUROPE

There are over 2000 listriodont teeth known from Europe (including Anatolia) (Van der Made 1996). By far the greatest number of specimens (928) has been documented from MN6 (of which 672 come from Pasalar), while 508 are known from MN4 (Fig. 27). From MN5 only 92 listriodont teeth have been described or measured, and this relatively poor sample undoubtedly enhances the impression of a morphological gap between the more bunodont forms of MN4 and the more lophodont ones of MN6 and later deposits because it is difficult to document a transitional status using such a restricted sample. This has in turn given rise to the idea that the bunodont and lophodont forms should be classed as separate genera "*Bunolistriodon*" and *Listriodon* rather than as different species within a single evolving lineage of suids. However, by their very existence these few specimens from MN5 indicate

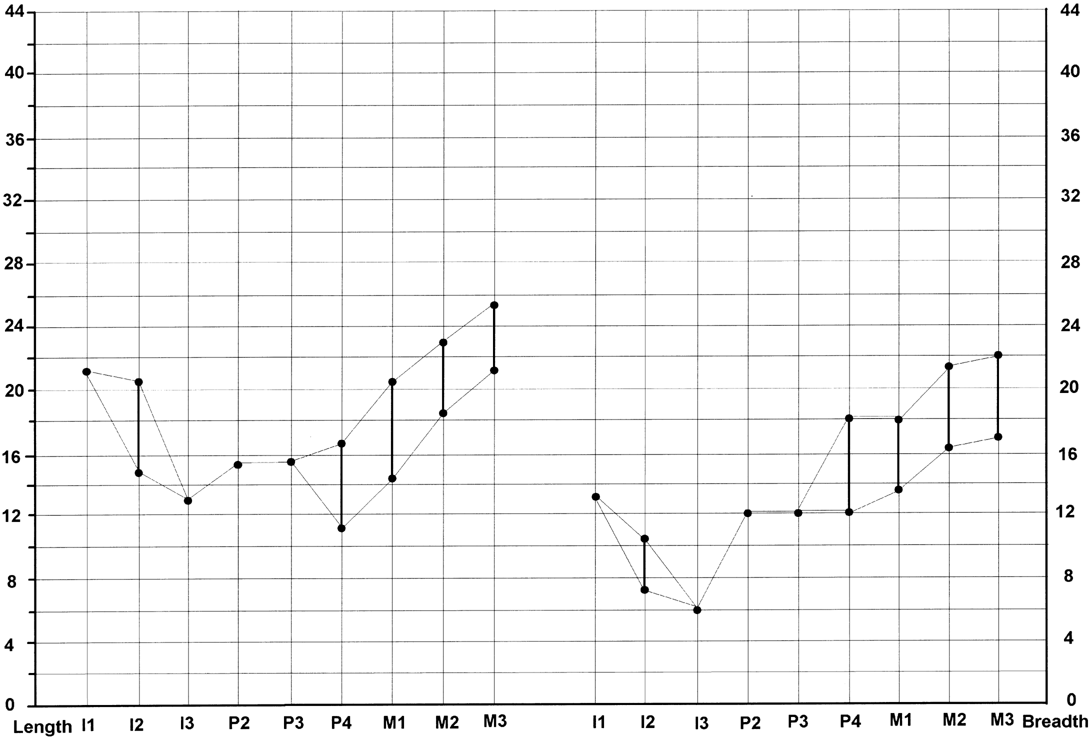


FIG. 24. — Size variation (in mm) of the upper dentition of *Listriodon akatikubas* (Wilkinson, 1976) (fossils from Fort Ternan, Maboko and Mbagathi). Symbols: ●, maximum and minimum measures; |, range of variation.

that listriodonts were not absent from Europe during any part of the middle Miocene (Fig. 27), and thus they weaken the hypothesis of two separate colonisations of the continent during this period as well as the notion that European listriodonts should be classified into two separate genera. From MN7/8 to MN10 there is a decrease in the quantity of teeth (492 in MN7/8, 35 in MN9 and none in MN10).

The transition from bunodonty to lophodonty occurred virtually simultaneously in Europe, China and the Indian subcontinent, and the most likely scenario is one of regional continuity. If this is so, then it is likely that gene flow was relatively unrestricted throughout this area during the middle Miocene. Africa appears to have been somewhat of a separate entity, as it lacks the bunodont listriodonts early on, and was only colonised by relatively lophodont forms about 15.5 Ma. In addition a separate genus with hyperlophodont cheek teeth (*Lopholistriodon*) evolved about 15 Ma and survived until about 11.5 Ma.

BIOGEOGRAPHY AND BIOSTRATIGRAPHY OF *LISTRIODON*

Listriodonts occur over a vast expanse of mid-latitude Eurasia from Portugal in the west to China in the east (Fig. 28). The most northerly localities at which they have been found are in Germany at about 53°N. In China they are documented as far north as 38°N. Their most southerly record is Kenya at the Equator (Fig. 29), but it should be noted that very few middle Miocene localities are known in Africa south of the Equator which poses an important impediment to interpreting their fossil record within the continent. The geographic spread of *Listriodon* fossils

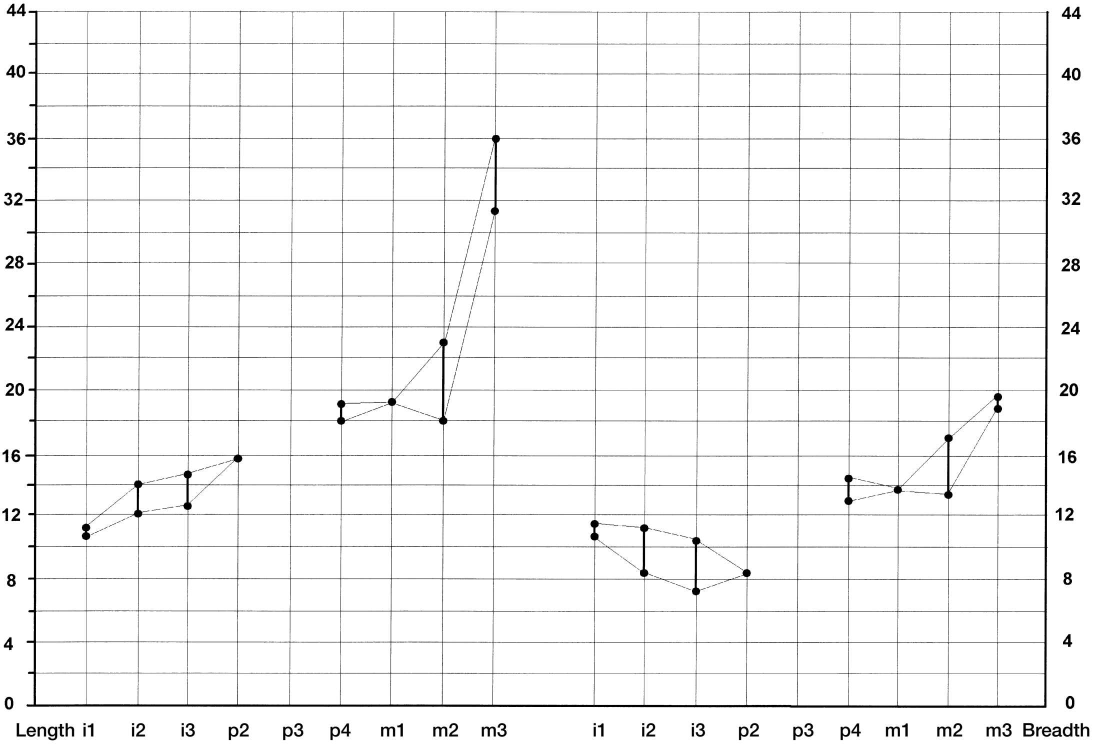


FIG. 25. — Size variation (in mm) of the lower dentition of *Listriodon akatikubas* (Wilkinson, 1976) (fossils from Fort Ternan, Maboko and Mbagathi). Symbols: ●, maximum and minimum measures; |, range of variation.

and the fact that throughout their range in Eurasia they underwent dental changes from bunodont at the base of the middle Miocene (MN4) to lophodont towards its end (MN6), suggests that this huge area comprised a single biogeographic realm with relatively unrestricted gene flow over a time span of some 4 to 5 million years (Figs 30; 37).

Finally, it is noted that listriodonts became extinct in Europe, China, India and Africa over a short period at the end of the middle Miocene and the beginning of the Late Miocene (Fig. 31). In Europe a few specimens have been found in sites which have also yielded the equid *Hipparion* but by the end of MN9 listriodonts were extinct everywhere.

LISTRIODONTS IN CHINA

The Shanwang faunal span (roughly equivalent to European MN4) is the earliest of the Chinese Neogene units to have yielded bunodont listriodonts. Little has been published on the Suiformes from this time span, but Chang (1974) described and figured two species, *Hyotherium penisulus* Chang, 1974 and *Palaeochoerus* cf. *pascoei* Pilgrim, 1926, from the Shanwang Formation at Hsiehchiaho (Xiacaowan) and Li *et al.* (1984) reported the presence of *Pecarichoerus* and Suidae indet. from Sihong.

The type material of *Hyotherium penisulus* is listriodont. The lower third molars have "four equally developed conical main cusps, hypoconid in the tendency of becoming crescentic, talonid long, about one third the entire length of the tooth, cingula almost absent" (Chang 1974: 123). The published photographs of the two specimens described by Chang (the clearest ones are in the *Chinese Handbook of Vertebrate Palaeontology* [Anonymous 1979]) do not yield enough information to allow its precise specific

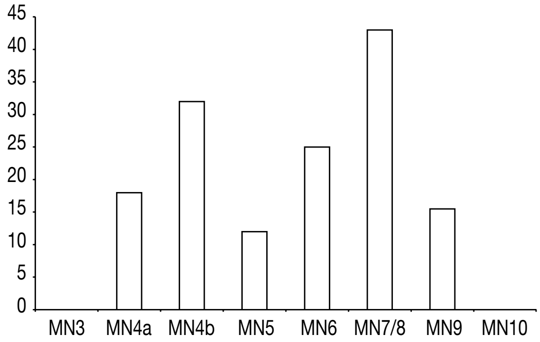


FIG. 26. — Quantity of European listriodont localities arranged by MN Zone.

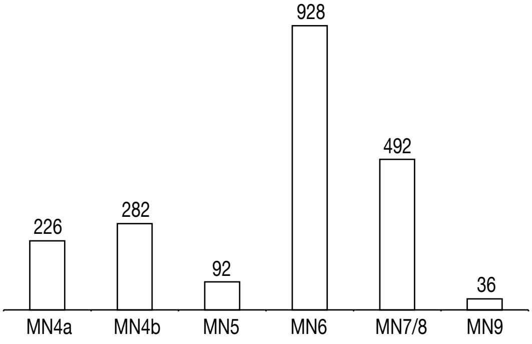


FIG. 27. — Quantity of teeth of Listriodontinae arranged by MN Zone.

identification although it appears to be relatively lophodont. Pending the recovery of better material from the site, we refer to the Shanwang listriodonts as *Listriodon penisulus*, recognising that this name may turn out to be a synonym of an established species from elsewhere in the Old World.

In younger Chinese deposits several species of *Listriodon* have been described over the years. Van der Made (1996) reduced the number of species to two, one each in the genera *Bunolistriodon* and *Listriodon*. *B. intermedius*, into which Van der Made (1996) sunk *Listriodon robustus*, is known from seven localities which he correlated with MN5. *L. splendens* is represented at four localities which he correlated to MN6 and MN6/7. At least one of these localities (Colbert 1934) probably correlates to MN7/8. Into this species he sunk *L. mongoliensis* Colbert, 1934, *L. lishanensis* Lee & Wu, 1978, and *L. xinanensis* Chen, 1986.

Thus, in China, as in Europe, the fossil record of *Listriodon* spans the period MN4 to MN7/8. It begins with relatively bunodont forms, which is one of the reasons why the fossils were originally classified as species of *Hyotherium* (an error also made in Europe, Golpe-Posse 1972), then it passes through a bunolophodont stage (*Listriodon intermedius*) in MN5 before reaching a fully lophodont stage in MN6 and MN7/8. The Chinese history is thus remarkably similar to the European one, despite the less complete nature of the far eastern record. This coincidence suggests that there were genetic links between Europe and China throughout the middle Miocene.

LISTRIODONTS IN THE INDIAN SUBCONTINENT

It has long been suggested that listriodonts occur in early Miocene deposits at Bugti and Sind. Unfortunately, the Bugti specimens are extremely fragmentary and there is debate about their subfamilial status (Pickford 1988; Van der Made 1996). The age of material from Sind is poorly constrained, and for this reason it is difficult to propose a robust scenario about the early evolution of listriodonts in the subcontinent. Nevertheless, there are a few specimens with cheek teeth that are relatively bunodont and in which the upper central incisors are not greatly elongated, corresponding in morphology to European material from MN4. Highly lophodont *Listriodon pentapotamiae*, and its synonym *L. theobaldi*, is abundant in the Chinji succession and deposits of similar age elsewhere in the Potwar Plateau. Biostratigraphy and palaeomagnetic stratigraphy indicate that the Chinji levels correspond to MN6 and MN7/8 (Figs 31; 32).

Thus, the available evidence about the broad tendencies of listriodont evolution in the Indian subcontinent accords with that from Europe and China, which supports the view that for much of the middle Miocene, Europe, Asia and the Indian subcontinent were all part of a single biogeographic region (see Fig. 37).

LISTRIODONTS IN AFRICA

The earliest known listriodonts in Africa have been found at Maboko and Kipsaraman, Kenya, in Faunal Set IIIB, equivalent in age to MN4b or perhaps MN5. Two genera are represented, *Listriodon* and *Lopholistriodon*. The Maboko and Mbagathi *Listriodon* specimens (Wilkinson 1976) are bunolophodont whereas the material assigned to *Lopholistriodon* is hyper-lophodont and belongs to a considerably smaller species.

From Fort Ternan there is a fully lophodont species of *Listriodon* which was assigned to *L. akatikubas* by Pickford (1986) but which is in some features closer to *L. splendens*. We do not concur with Van der Made (1996: 48) that the Fort Ternan fossils should be assigned to *Lopholistriodon akatidogus*, nor should all the material identified as *Listriodon juba* Ginsburg, 1977 from Beni Mellal, Morocco (Ginsburg 1977). Morphologically they are closer to *Listriodon* than to *Lopholistriodon* as was realised by Van der Made (1996). Pickford (2001b) has erected *Listriodon bartulensis* for this species, of which a mandible was recently recovered from Member A of the Ngorora Formation, Kenya, aged *c.* 13 Ma.

Lopholistriodon survived from about 15.5 Ma until the end of the middle Miocene where it is known from sediments at Ngorora, Baringo District, Kenya, aged about 12-11.5 Ma.

LISTRIODONTS IN ASIA MINOR AND THE MIDDLE EAST

The listriodont record in Asia Minor and the Middle East is extremely patchy, although one locality (Pasalar, Turkey) has yielded the most comprehensive sample of listriodont teeth known in the world (Figs 33; 34) (Fortelius *et al.* 1996a). Some undescribed specimens have been reported from deposits at Antonius, Greece, said to be equivalent to MN4 or MN5 (De Bonis & Koufos 1999). Other material from MN5 has been described from Chios, Greece, but it consists of isolated teeth which are difficult to interpret because of the worn aspect of the crowns (Paraskevaidis 1940). *Listriodon latidens* was recorded from Mala Miliva, Bulgaria (Petronijevic 1967) in deposits correlated to MN5. Possibly of similar age are a couple of teeth from Saudi Arabia identified as *Listriodon akatikubas* (Pickford 1987).

The listriodont fossil record of Asia Minor improves in MN6 with important fossils from Turkey (Pickford & Ertürk 1979; Fortelius *et al.* 1996a) and Prebreza, Serbia (Pavlovic 1969) but it is poor again in MN7/8 with a few fossils known from Korethi (Eastern Paratethys) and Turkey (Sariçay, Yaylacilar, Lower Sinap).

With such a poor fossil record for the early parts of listriodont history in Asia Minor and the Middle East, it is difficult to reconstruct a satisfactory scenario. There was evidently some contact or interchange with neighbouring biogeographic regions because similar species are reported from them (*Listriodon latidens*, *L. splendens*) but there are also signs of endemism with the development of forms such as *L. meidamon* in Turkey which have not been reported from elsewhere.

DISPERSAL HISTORY OF LISTRIODONTINAE THROUGH GEOLOGICAL TIME

It has long been suggested that there were two colonisations of Europe by listriodonts (Ginsburg 1977), one at the onset of the middle Miocene with *Bunolistriodon* and a second in MN6 by *Listriodon*.

Van der Made (1999) has recently summarised the arguments by proposing two immigration "events". The first of these he labelled the "*Bunolistriodon*" event (MN4) and the second the "*Listriodon*" event (MN6). Van der Made and his precursors have suggested that both these events represented immigrations of the respective genera into Europe from pre-existing populations in Africa and/or India. In the same paper he also considered that *Bunolistriodon* immigrated into Africa from Eurasia during what he called the "*Brachyodus*" event (21 Ma), which is inconsistent with the above scenario in that it implies the presence of the genus *Bunolistriodon* somewhere

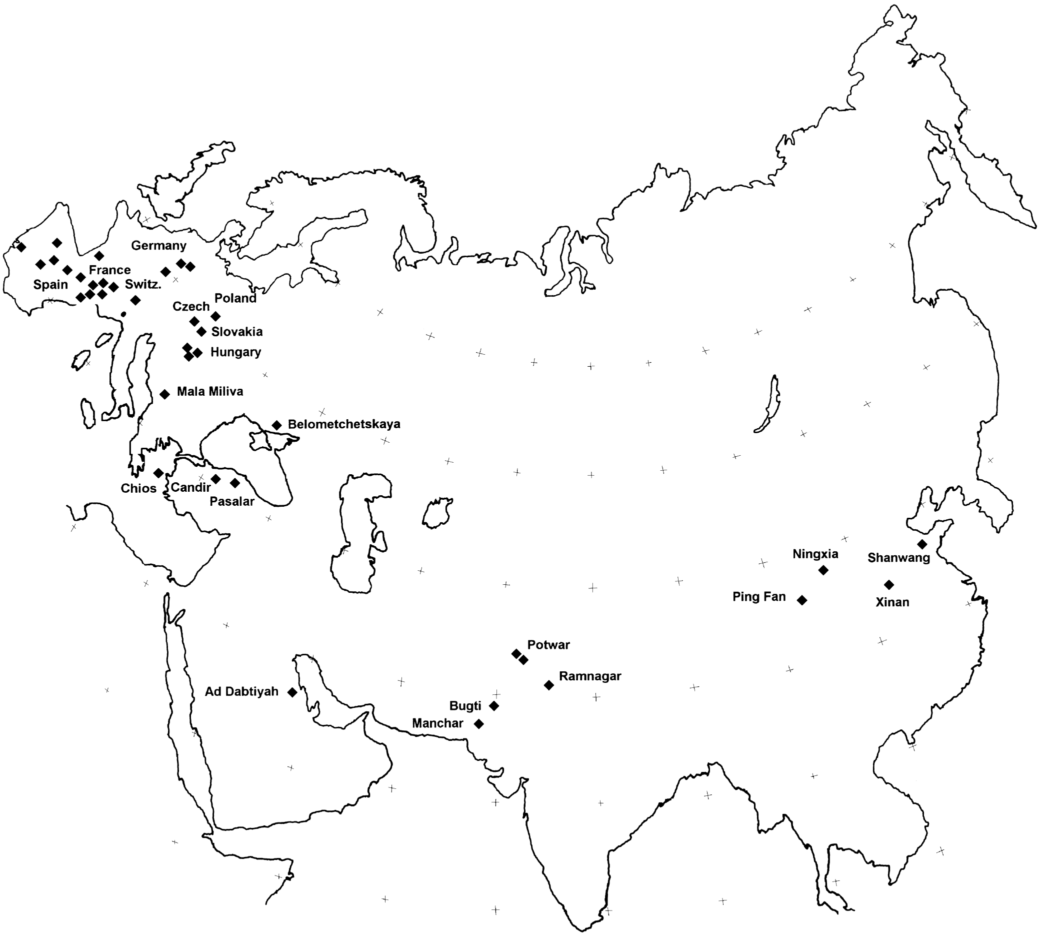


FIG. 28. — Distribution of Listriodontinae in Eurasia.

in Eurasia about 4.5 million years earlier than "*Bunolistriodon*" event.

Whilst it is true that listriodonts are rarer in European deposits of MN5 than in MN4 and MN6, there can be little doubt that the subfamily occurred in Europe throughout the period from MN4 to MN9 (Figs 26; 27). The same can be said of China (Pickford & Liu 2001) where listriodonts are known to occur from the Shanwangian to the Tunggurian in a relatively continuous but spotty record (Fig. 31) (Liu & Lee 1963a, b, 1978). In the Far East they have not been recorded in any strata that yielded *Hipparion*. In Africa, the record is less complete, the earliest genuine listriodonts (as opposed to kubanochoeres misidentified as listriodonts) are aged *c.* 15.5 Ma and the youngest are *c.* 11.5 Ma (Fig. 31). In the Indian subcontinent, listriodonts are commonest in Chinji levels, but are known from older deposits in the Sind, but the earliest known listriodonts from there are in any case younger than the earliest European ones (Figs 31; 32). However, this could be due to the fact that the basal deposits of the Siwaliks have not yielded a great wealth of fossil material and are not well dated.

Thus, far from Africa being the source for intercontinental Listriodontinae migrations, it appears

FIG. 29. — Distribution of Listriodontinae in Africa.

to have been a recipient of such migrations from more northerly parts of the Old World.

In Europe and China the early forms of Listriodontinae are bunodont and the later ones lophodont, whereas in Africa the earliest known listriodonts (Kipsaraman, Maboko; both sites in Kenya) are more derived in cheek tooth lophodonty than the earliest European ones (Pellecahus specimens described herein for example). Thus, if anything, the transition from bunodonty to lophodonty took place in the mid-latitudes of Eurasia and the African forms are probably descendents of lineages that evolved in more northerly settings. Furthermore, some of the fully lophodont African forms equivalent in age to MN6 and MN7 (Ngorora) belong to a different genus, *Lopholistriodon*, which is an African endemic that has so far not been recorded outside the continent.

The evidence available from China and Europe indicates a different scenario from that of Van der Made. The subfamily probably evolved sometime during MN3 most probably from a hyotheriine stock, and became morphologically distinct (cranially but not initially dentally) from other suids by MN4. The geographic location of the evolution of the earliest listriodonts is not known, but their earliest records in Europe and China are almost coeval. It is unlikely that listriodonts originated in Africa, where the dominant subfamily in the early and middle Miocene is the Kubanochoerinae and listriodonts do not make their appearance until about 1.5 million years after their first appearance in Europe. The Indian subcontinent has yielded some evidence, but the age context of the earlier part of the listriodont fossil record in the subcontinent is not clear, and some of the early specimens assigned to *Bunolistriodon* probably represent kubanochoeres rather than listriodonts.

As for the second of Van der Made's events (the "*Listriodon*" event), the continuity of the listriodont record in Europe, India and China, with the occurrence of forms intermediate between bunodont and lophodont types in all three areas, indicates that his scenario is unlikely to be correct. This means that there is no need to postulate a migration event from India to the rest of Eurasia at the beginning of MN6 because biogeographically speaking, all three areas were part of a single bioprovince. In other words, mid-latitude Eurasia was continuously populated by listriodonts from MN4 to MN7/8 and even into MN9, and the transition from bunodont to lophodont took place throughout this wide area. This speaks for relatively unrestricted gene flow from Spain to China and India from about 16.5 to 11 Ma.

COINCIDENCES BETWEEN LISTRIODONT HISTORY AND GEOLOGICAL EVENTS

SEA LEVEL FLUCTUATIONS

During the Neogene there were several periods of exceptionally high sea levels interspersed with periods of "normal" or very low sea levels (Van der Made 1996; Pickford 1998; Pickford & Senut 2000). In various parts of the world, the exceptionally high sea levels are represented on land by marine sediments intercalated in

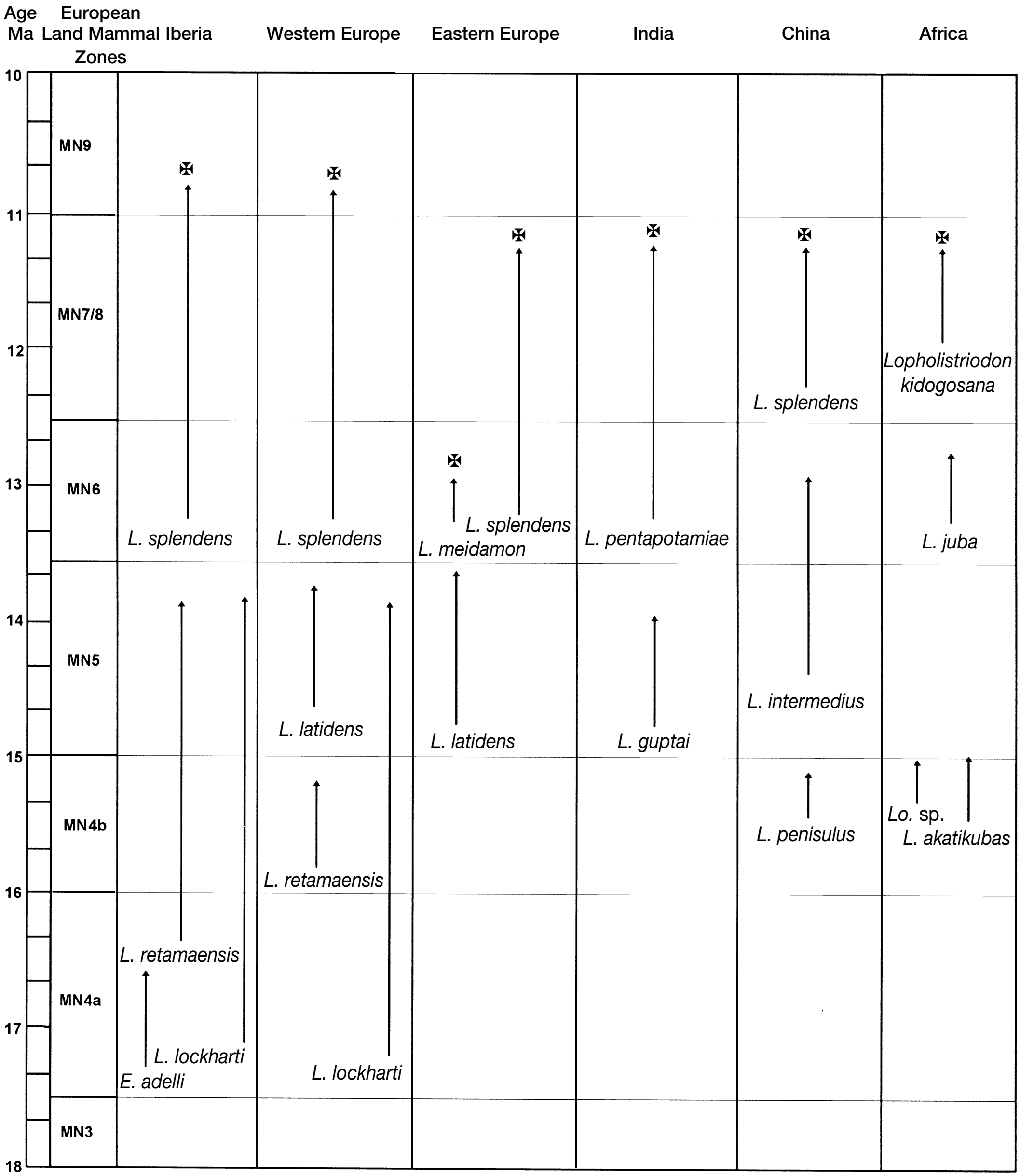


FIG. 30. — Stratigraphic ranges of species of Listriodontinae in various parts of the world. Symbol and abbreviations: ✠, lineage extinction; ***E.***, *Eurolistriodon*; ***L.***, *Listriodon*; ***Lo.***, *Lopholistriodon*.

predominantly terrestrial sedimentary successions. In tectonically quiet areas such as coastal southwestern Africa, such deposits occur today at more or less the same altitude at which they were formed, but in other areas such as parts of Europe where Alpine tectogenesis has occurred, the sediments may have been uplifted or downwarped. Studies of near coast deposits of Miocene age in southern Africa, western Australia, China and Europe reveal that many of these onland marine

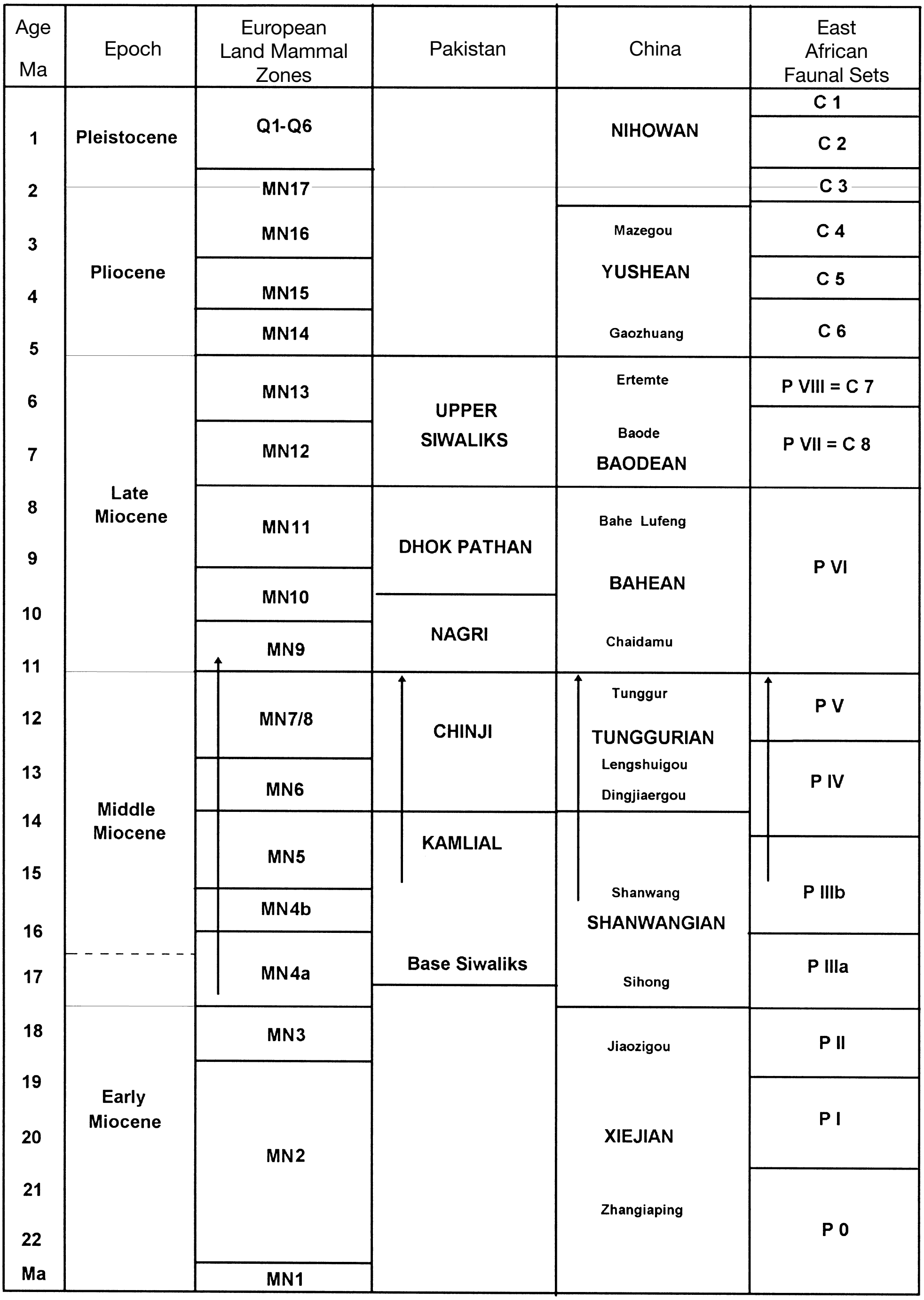


FIG. 31. — Geochronological ranges of listriodonts in the Old World (↑). Abbreviations: **C1-C8**, Coppens 1974 Faunal zones; **P0-PVIII**, Pickford 1981 Faunal Sets. Pakistan data from Johnson *et al.* 1982 and Barry 1986; China data from Tong *et al.* 1996; hatched line in the middle Miocene is the early to middle Miocene boundary according to Berggren *et al.* 1995.

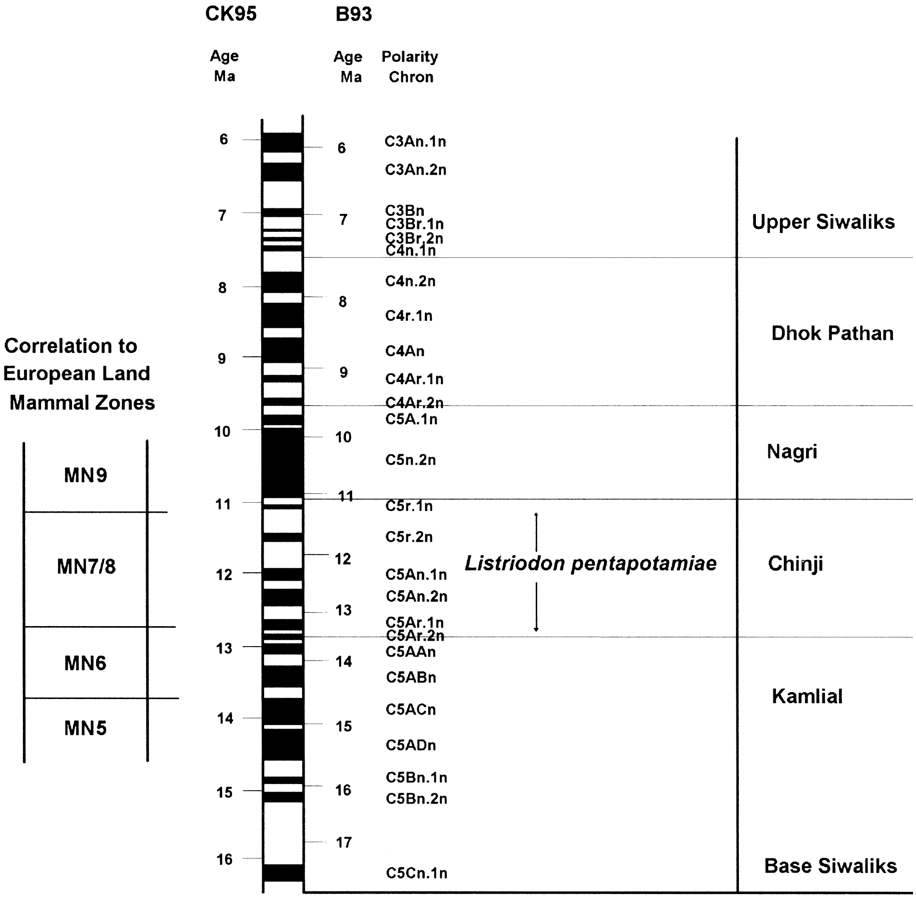


FIG. 32. — Siwaliks geochronology and the distribution of *Listriodon pentapotamiae* (Falconer, 1868). Abbreviations: **CK95**, Cande & Kent 1995; **B93**, Baksi 1993.

deposits resulted from eustatic changes rather than tectonic events, but that tectonic activity has in cases resulted in changes in altitude of the strata. Available evidence indicates that there were major marine transgressions at the end of the early Miocene, during the middle Miocene, at the end of the middle Miocene and at the end of the late Miocene, plus some activity during the Pliocene and Pleistocene which need not concern us here. The fact that the various major transgressions occurred in widely scattered parts of the globe at the same time, means that they were due to global eustacy rather than to localised or regional tectonism. They can thus be used as a basis for intercontinental correlations.

Lithostratigraphic records of transgressions and regressions in various parts of the world may differ from each other in terms of the number of cycles preserved. This is usually due to the location of the particular basin in which the record is preserved, basins proximal to the oceans usually possessing a more complete record than localities further inland. Local and regional tectonics may also have played a role in determining whether transgressions or regressions would occur. For example, the Tagus Basin in Portugal preserves evidence of six Neogene transgressions and regressions (Antunes 1984) whereas the Blésois Basin in France preserves only three of them (Ginsburg 2000) (Fig. 35). The three marine levels in the Blésois correspond to the highest and longest lived transgressions mapped in Portugal. In the Paratethys, the succession of marine sediments is far more complete with fewer unconformities in the sequence and thus fewer intercalations of terrestrial sediments.

In Europe, *Listriodon* fossils have been found in stratigraphic successions which contain evidence of marine transgressions, for example in the Aquitaine Basin (Fig. 11), the Blésois region of France, the Faluns de Touraine, France, the Swiss molasse deposits, the Tagus Basin of Portugal, the Valles-Penedes Basin, Spain, and others (Fig. 35). It is thus possible to examine the relative timing of events in listridont history and marine transgressions by direct observation of field relationships of strata and fossils. This approach yields good evidence of the sequence of events, because the superpositional relationship of each event is known with respect to that of the other. Thus, it is not necessary to infer sequences of events by making correlations that may or may not be valid, which means that the results of such a survey have a better chance of reflecting the true course of events that took place within a particular basin.

The stratigraphic succession in the Aquitaine Basin (Fig. 11) shows that there were exceptionally high sea levels during MN3 and MN5 during which strata rich in oysters and other marine fauna were laid down. The same two transgressive events are represented in the Blésois, and a third transgression occurred there during MN8 or MN9. In the Tagus Basin, Portugal, being closer to sea level, the record of transgressions and regressions is more complete, with six transgressive episodes represented ranging in age from MN2 to MN8.

As far as listriodont history is concerned, it is interesting to note that the subfamily made its appearance in the French fossil record in MN4a soon after the end of the MN3 transgression (Fig. 11). In Portugal they appeared within the local stratigraphic record during the R3 regression (Antunes 1984) which followed a limited, short-lived transgression that is not represented in the Aquitaine or Blésois Basins. Bunodont to bunolophodont listriodont fossils are thereafter abundant throughout MN4 but become scarcer during MN5, just at the time that there was a second marine transgression in the French basins which we take to correlate with the C5 transgression in Portugal. It was during this period of high sea level that there was an important increase in the mesiodistal length of the upper central incisors of *Listriodon* (Fig. 21), suggesting that some kind of change occurred in the diet of listriodonts, possibly in response to a change in vegetation. After the MN5 transgression, all the listriodonts were lophodont, in agreement with the suggestion of a change in listriodont diet. During MN6 and MN7/8, there were relatively minor changes in listriodont morphology indicating that the environment, especially the vegetation that they were eating, did not change fundamentally during this period. Then the subfamily abruptly went extinct just before or early during MN9, when the third major marine transgression occurred in the French basins, equivalent to the C6 transgression in Portugal. It is most likely that this transgression was accompanied by a major change in vegetation and habitat which listriodonts could not exploit, leading to their extinction. The fact that listriodonts went extinct almost simultaneously throughout their former range, from Iberia in the west to China in the far east, as well as the Indian subcontinent and Africa, indicates that the changes that led to their extinction were expressed on the scale of the Old World, if not globally. The spread of *Hipparion* from the New World into the Old World at the time that listriodonts were going extinct supports the view that whatever caused the one may have permitted the other to happen.

OCEAN WATER TEMPERATURES

Oxygen isotope measurements obtained from analyses of benthic foraminiferans reveals that there were major changes in isotope conditions in the world's oceans during the Neogene. It is usually considered that the ratio of oxygen 18 to oxygen 16 in the tests of Foraminifera can be used as a proxy for the water temperature in which the tests grew (Fig. 36). If this is so, then the oxygen

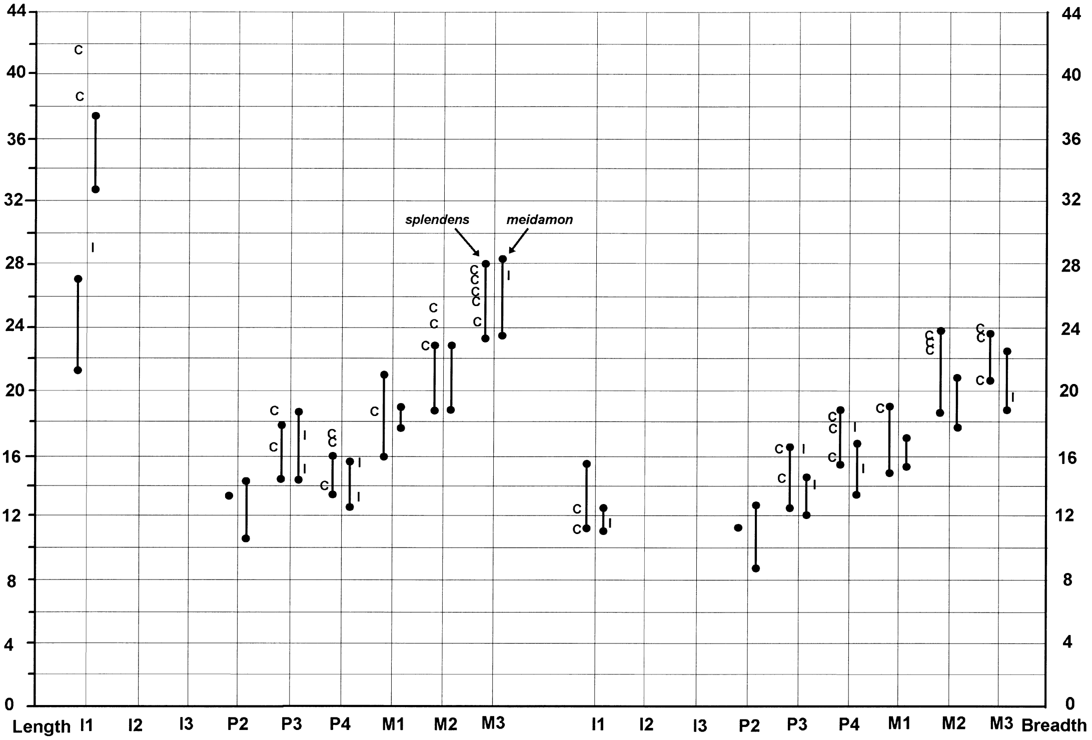


FIG. 33. — Measurements (in mm) of the upper dentition of *Listriodon* species from Pasalar, and other Turkish sites. Symbols and abbreviations: ●, maximum and minimum measures; **|**, range of variation; **C**, Candir; **I**, Inönü.

isotope data can provide a record of ocean water temperatures. A compilation of data, such as that published by Miller & Fairbanks (1985), reveals that there were several major shifts in oxygen isotope ratios during the Miocene which were much greater in magnitude than the background fluctuations that occurred throughout the Neogene. A dramatic plunge in inferred water temperature occurred about 16-15 Ma and a further one took place at the end of the Miocene (Fig. 36).

The major cooling event in the oceans between 16 and 15 Ma is thought to have been caused by expansion of the Antarctic ice sheet to continental proportions with a concomitant huge increase in the quantities of cold water being shed into the southern oceans compared with the amounts that were flowing into the oceans during the late Oligocene and early Miocene.

The growth of the south polar ice sheet during the early to middle Miocene was not accompanied by an equivalent growth of a north polar icecap, and this imbalance led to an asymmetry in the disposition of the world's ecoclimatic belts, which were displaced northwards, the tropical belt coming to lie 15 to 20° north of where it is today (Pickford & Morales 1994). This shift led to the establishment of tropical to sub-tropical conditions over much of mid-latitude Eurasia, and permitted the northwards expansion of the ranges of many plants and animals that had hitherto been confined to Africa and Southeast Asia (Fig. 37). This change is amply recorded in the fossil records of Europe and Asia. In the southern hemisphere it led to the formation of the west coast deserts of the southern continents, including the Namib and Atacama deserts. In southwestern Africa the climate changed from being subtropical with summer rainfall to one in which more temperate conditions with winter rainfall predominated.

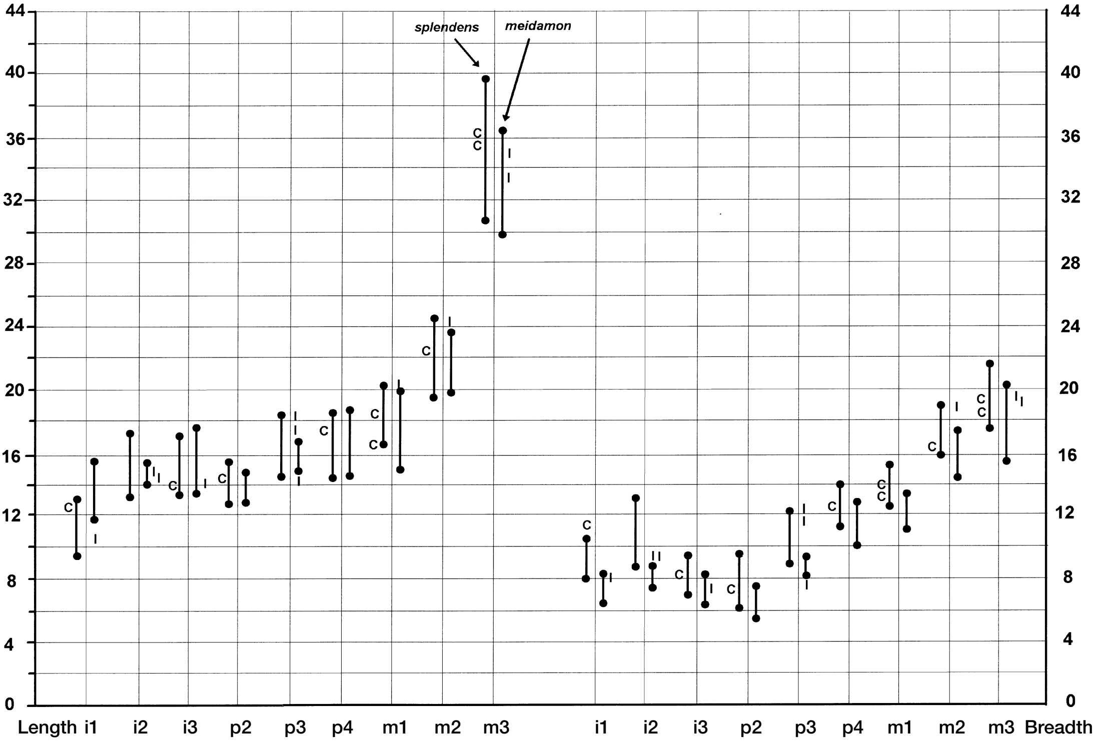


FIG. 34. — Measurements (in mm) of the lower dentition of *Listriodon* species from Pasalar, and other Turkish sites. Symbols and abbreviations: ●, maximum and minimum measures; **|**, range of variation; **C**, Candir; **I**, Inönü.

During the middle and late Miocene, fluctuations in ocean water temperature suggest that the amount of cold water being shed into the southern oceans from Antarctica varied considerably, which in turn suggests that the ice sheet itself may have been fluctuating in size, even though it was always present.

Towards the end of the Miocene, a north polar ice cap began to form, and by about 8-7 Ma it was large enough to force the ecoclimatic zones back towards the south. Thus, as the Arctic and Boreal zones expanded in size, the sub-tropical and tropical zones were squeezed towards the equator and became narrower than they were before. One of the more dramatic results of this shift was the formation of the Sahara Desert and the other mid-latitude arid belts of the northern hemisphere.

As far as listriodonts are concerned, those that existed before the major Neogene cooling event were bunodont whereas those that existed afterwards were lophodont. The cooling event itself corresponds to MN5 which is when listriodonts became relatively rare throughout their range, causing a kind of bottleneck in their population numbers. Although listriodonts continued to exist in various parts of Europe, Africa, the Indian subcontinent and China during MN5, the drop in number of localities at which they occur suggests that their ranges within the overall geographic range were reduced. Such a fragmentation of the population spread could explain why listriodonts are found in fewer localities in MN5, compared with MN4a, MN4b, MN6 and MN7/8.

TECTOGENESIS

The Alpine fold belt, which includes the Himalayas, experienced several tectogenic phases during the Neogene. The Savic phase peaked at

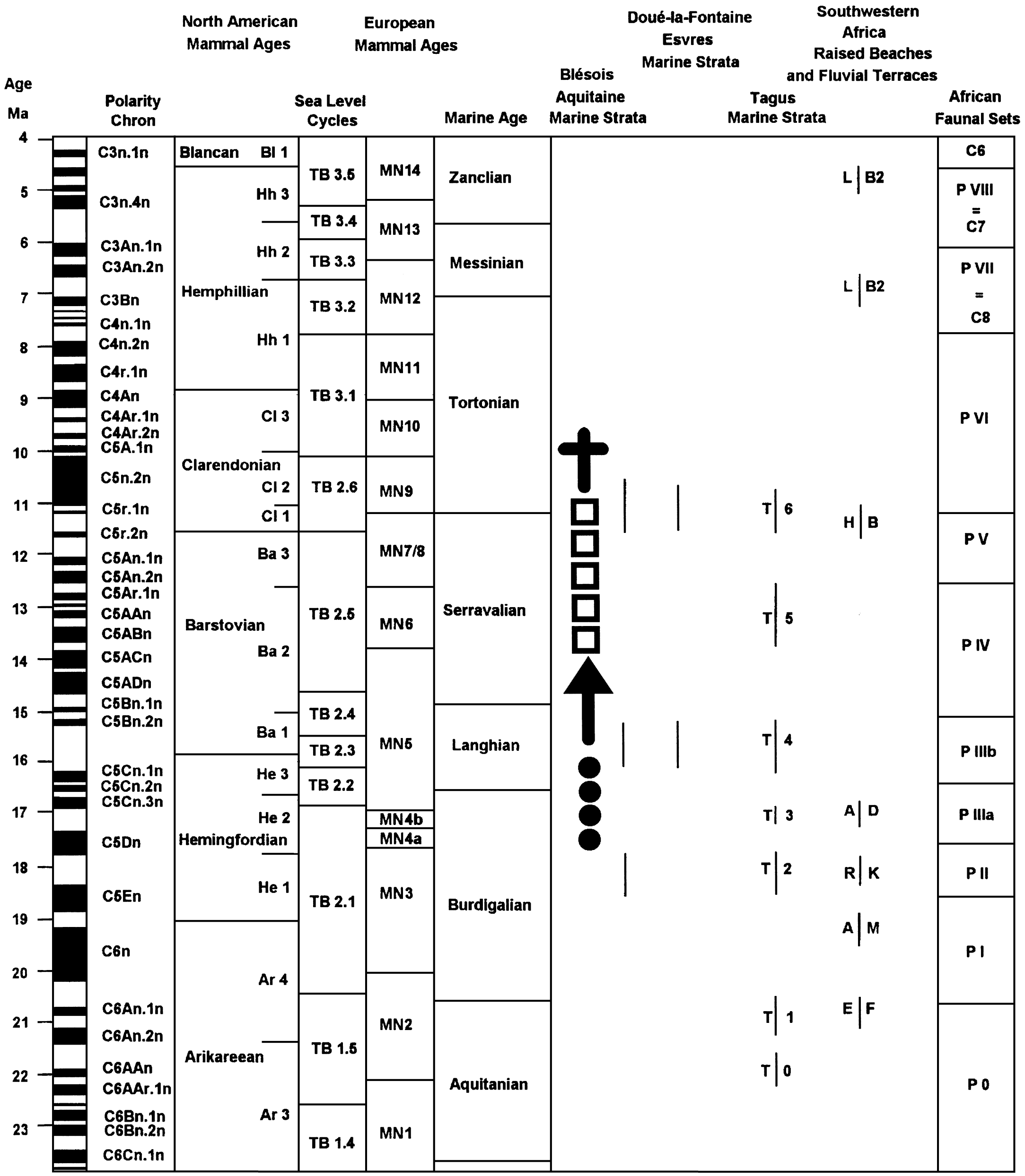


FIG. 35. — Major marine transgressions of the Neogene and listriodont history. Abbreviations: **C6-C8**, Coppens 1974 Faunal zones; **P0-PVIII**, Pickford 1981 Faunal Sets. Symbols: □, lophodont listriodonts; ●, bunodont listriodonts.

about 24 Ma, the Styrian at *c.* 17 Ma, the Attic at *c.* 12 Ma and the Rhodanian at 8 Ma (Pickford 1996). Each tectogenic phase lasted about 2-3 million years and between phases there was relative tectonic calm. Listriodonts appeared in Eurasia during the Styrian tectogenic phase (*c.* 17.5 Ma) and went extinct during the Attic phase (*c.* 11 Ma). The appearance of the subfamily

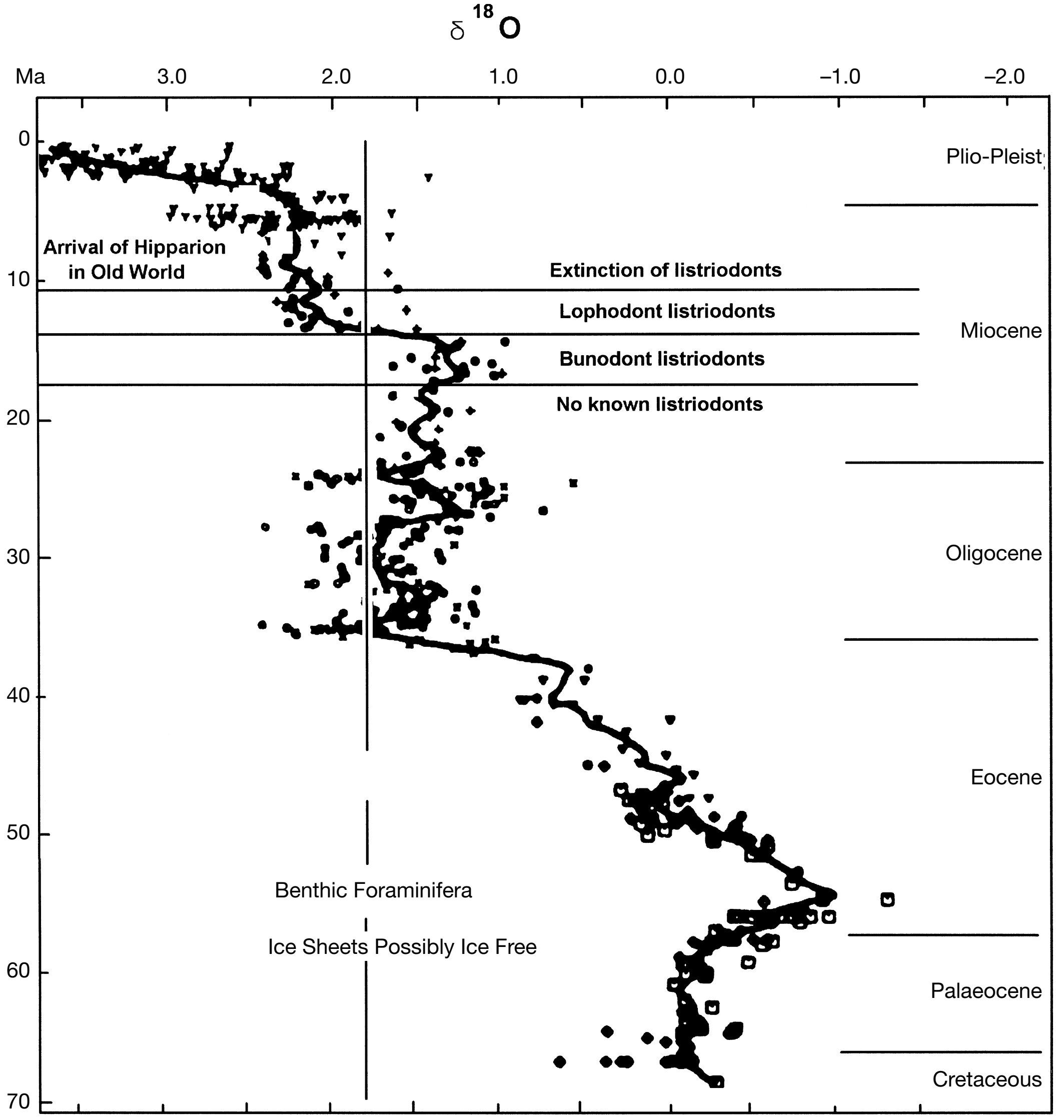


FIG. 36. — Atlantic Ocean water temperature and evolution of Listriodontinae.

Listriodontinae during one such phase and its extinction during the following one could be coincidental, but there might be a link between the two histories, to the extent that tectogenic phases resulted in orogenesis which in turn affected local and regional climate and vegetation. For example, the establishment of the monsoon system likely occurred during the Attic tectogenic phase, which in turn led to marked changes in the weather systems of the mid- and low-latitudes.

Although the details are somewhat hazy, mainly due to imprecisions in correlating events that occurred in different geological and biological systems, the available evidence points to a "cause and effect" relationship between events in the geosphere and changes in the biosphere. Listriodonts yield evidence of changes in the biosphere from about 17.5 to 11-10.5 Ma. Their abrupt appearance in the Eurasian fossil record in MN4a suggests that a major adjustment occurred to the world's biogeographic realms at the end of

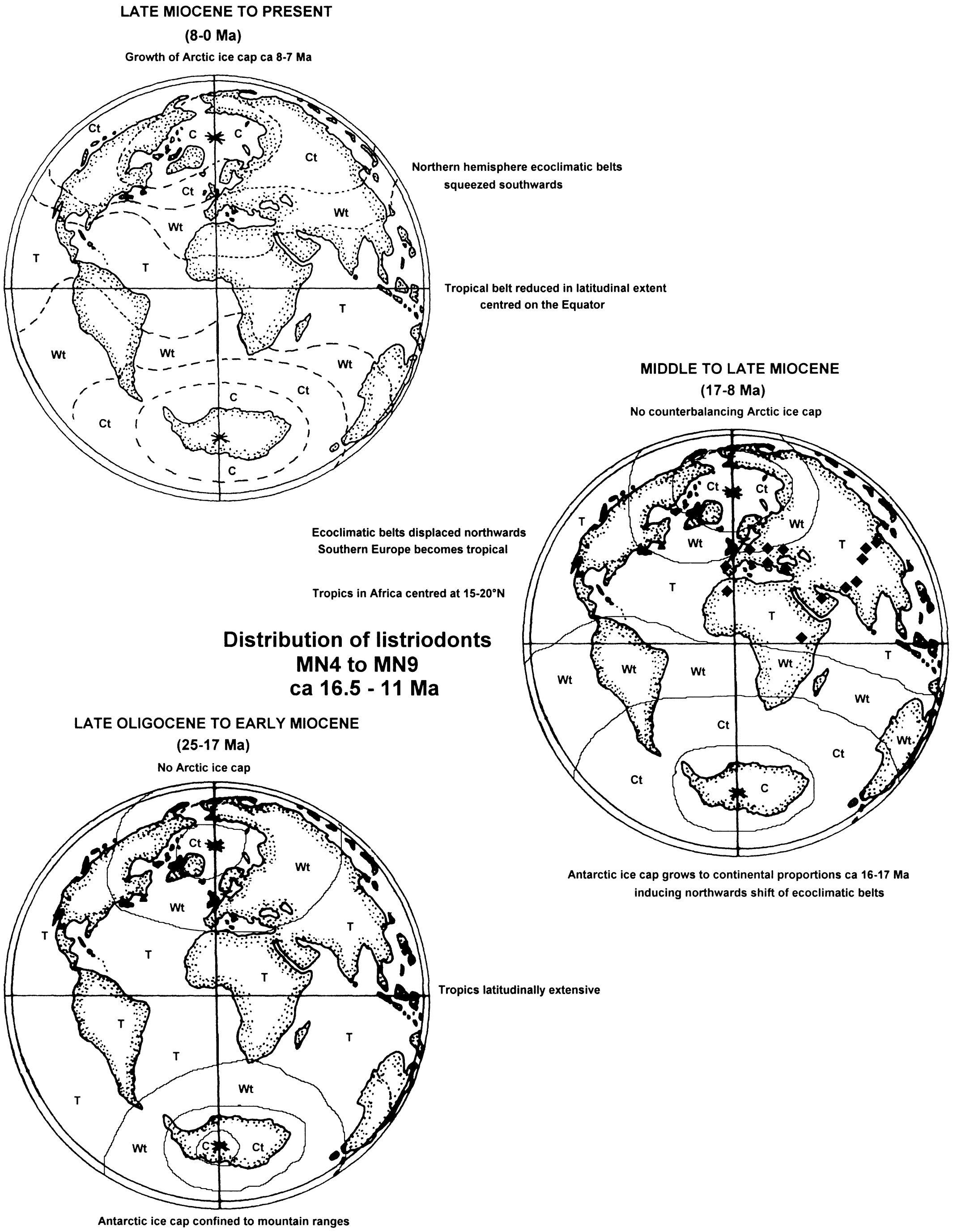


FIG. 37. — Major changes in ecoclimatic belts of the world from Oligocene to Recent times. Note that listriodonts were probably tropical mammals because their known distribution falls within the warm tropical zone. Symbol and abbreviations: ◆, listriodont fossils; **C**, cold; **Ct**, cold temperate; **T**, tropical; **Wt**, warm temperate.

MN3 (*c.* 18-17.5 Ma). Europe became more tropical than it had been before, suggesting a northwards shift in the boundary zone between the proto-Palaearctic, proto-Oriental and proto-Ethiopian Realms, currently at about 23°N but up to 50°N during the middle Miocene (Pickford & Morales 1994). In other words, at the end of MN3, the boundary between the tropics and subtropics appears to have shifted northwards in Eurasia. During the middle Miocene the position of the boundary fluctuated, shifting equatorwards in MN5 and polewards again during MN6. At the end of the middle Miocene, the boundary shifted southwards once again bringing boreal and sub-tropical conditions to much of mid-latitude Eurasia, and the vegetation and climatic changes that resulted may well have spelled the end for listriodonts in the mid-latitudes. This would not explain the demise of listriodonts in Africa, but the fossil record suggests that they also went extinct there at the end of the middle Miocene.

CONCLUSIONS

The remains of *Listriodon retamaensis* n. sp. resolve certain questions concerning the morphology, systematic position and phylogenetic relationships of early listriodonts in Europe. Once again they indicate that among suids, the skull tended to evolve new features before the dentition did. Thus, by MN4a, there were two distinct listriodont skull morphologies in existence represented by the genera *Eurolistriodon* and *Listriodon*. Thanks to discoveries at Corcoles, Artesilla, Els Casots and Retama, it has become clear that there were two separate species of early listriodonts in Spanish deposits of zones MN4a and MN4b, and these were assigned to *Bunolistriodon lockharti* and *B.* aff. *latidens* by Van der Made (1996) or to *L. retamaensis* n. sp. and *E. adelli* in this study (Pickford & Moya Sola 1995). The Spanish fossil record reveals that by the onset of MN4 the listriodonts had already radiated into at least two genera, and that the subfamily must therefore have originated somewhat earlier, probably during MN3 or MN2. Until now, however, no convincing listriodont ancestor has been identified, even though, *faute de mieux*, the genus *Hyotherium* has been proposed to fulfill such a role. After examining *Hyotherium meisneri* from Cetina de Aragon (Van der Made 1994), we consider it plausible that the roots of listriodont origins are more likely to be found somewhere in the early Miocene complex of *Hyotherium* species rather than among *Aureliachoerus* and *Xenohyus* Ginsburg, 1980.

Re-examination of fossils assigned to *Bunolistriodon* by Van der Made (1996) reveals that the material includes two widely divergent cranial morphotypes. European species are all typically listriodont, while the African species are most similar to kubanochoeres. It is therefore concluded that *Bunolistriodon jeanneli* (of which *Bunolistriodon anchidens* is a junior synonym) are Kubanochoerinae and played no role whatsoever in the evolution of the subfamily Listriodontinae. The (very) few derived morphological similarities claimed to be "shared" by the two subfamilies (mainly the mesiodistally elongated incisors) are due to convergent evolution, having developed from different precursors on different continents and at different times.

It is possible that *L. retamaensis* n. sp. (MN4b) represents the beginning of the lineage which culminated in *Listriodon latidens* (MN5) and its close relative *L. meidamon* (MN6).

The Toril 3 listriodont represents a fully lophodont form, *L. splendens major*. It is one of the largest specimens ever found.

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REFERENCES

ANONYMOUS 1979. — *Chinese Handbook of Vertebrate Palaeontology*. Science Press, Beijing.

ANTUNES M. 1984. — Essai de synthèse sur les mammifères du Miocène du Portugal, *in Volume d'hommage au géologue G. Zbyszewski*. Recherche sur les Civilisations, Paris: 301-323.

ARAMBOURG C. 1933. — Mammifères Miocènes du Turkana (Afrique orientale). *Annales de Paléontologie* 22: 123-146.

ARAMBOURG C. 1963. — Le genre *Bunolistriodon* Arambourg, 1933. *Bulletin de la Société géologique de France* 5: 903-911.

AZANZA B., CERDEÑO E., GINSBURG L., VAN DER MADE J., MORALES J. & TASSY P. 1993. — Les grands mammifères du Miocène inférieur d'Artesilla, bassin de Calatayud-Teruel (province de Saragosse, Espagne). *Bulletin du Muséum national d'Histoire naturelle* 4^{e} sér., 15: 105-153.

BAKSI A. K. 1993. — A geomagnetic polarity time scale for the period 0-17 Ma, based on ^{40}Ar/^{39}Ar Plateau ages for selected field reversals. *Geophysics Research Letters* 20: 1607-1610.

BARRY J. 1986. — A review of the chronology of Siwalik hominoids, *in* ELSE J. & LEE P. (eds), *Primate Evolution*. Cambridge University Press, Cambridge: 93-106.

BERGGREN W., KENT D., SWISHER C. & AUBRY M.-P. 1995. — A revised Cenozoic geochronology and chronostratigraphy, *in* BERGGREN W., KENT D., AUBRY M.-P. & HARDENBOL J. (eds), Geochronology, time scales and global stratigraphic correlations. *Special Publication of the Society of Economic Paleontologists and Mineralogists* 54: 17-28.

BIEDERMANN W. 1873. — *Petrefacten aus der Umgegend von Winterthur 4. Reste aus Veltheim*. J. Westfehling, Winterthur: 1-16.

CANDE S. & KENT D. 1995. — Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. *Journal of Geophysics Research* 100: 6093-6095.

CHANG YUPING 1974. — Miocene suids from Kaiyuan, Yunnan and Linchu, Shantung. *Vertebrata PalAsiatica* 12 (2): 118-123.

CHEN GUANFANG 1986. — A new species of *Listriodon* Meyer (Suidae, Artiodactyla, Mammalia) from Xinan, Henan. *Vertebrata PalAsiatica* 24 (4): 295-307.

COLBERT E. H. 1934. — An upper Miocene suid from the Gobi Desert. *American Museum Novitates* 690: 1-7.

COPPENS Y. 1974. — Les faunes de vertébrés du Pliocène et du Pléistocène ancien d'Afrique. *Mémoires du Bureau de Recherches géologiques et minières* 78: 109-119.

DAAMS R. & FREUDENTHAL M. 1988. — Synopsis of the Dutch-Spanish collaboration program in the Aragonian type area, 1975-1986. *Scripta Geologia Special Issue* 1: 3-18.

DE BONIS L. & KOUFOS G. 1999. — The Miocene large mammal succession in Greece, *in* AGUSTI J., ROOK L. & ANDREWS P. (eds), *Hominoid Evolution and Climatic Change in Europe*, Vol. 1, *The Evolution of the Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge: 205-237.

DE BRUIJN H., DAAMS R., DAXNER HÖCK G., FAHLBUSCH V., GINSBURG L. & MORALES J. 1992. — Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsletters of Stratigraphy* 26: 65-118.

FALCONER H. 1868. — *Palaeontological memoirs*, vol. 1. *Fauna antiqua sivalensis*. London.

FORTELIUS M., VAN DER MADE J. & BERNOR R. 1996a. — A new listriodont suid, *Bunolistriodon meidamon* sp. nov., from the Middle Miocene of Anatolia. *Journal of Vertebrate Paleontology* 16: 149-164.

FORTELIUS M., VAN DER MADE J. & BERNOR R. 1996b. — Middle and Late Miocene Suoidea of Central Europe and the eastern Mediterranean: Evolution, biogeography and palaeoecology, *in* BERNOR R., FAHLBUSCH V. & MITTMANN W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 348-377.

GABUNIA L. 1955. — Novia predstaviteli Suidae iz srednego miotsena Beolometchetskaya (Severnia, Caucas) [= New representative of the Suidae from the middle Miocene of Belometchetskaya (Northern Caucasus)]. *Doklady Akademie Nauk SSSR* 102 (6): 1263 (in Russian).

GABUNIA L. 1958. — O cherepe rogatoi iskopaemoi svinia iz srednego miotsena Caucasia [= On a skull of a horned pig from the middle Miocene of Caucasus]. *Doklady Academie Nauk SSSR* 118 (6): 1187 (in Russian).

GABUNIA L. 1960. — Kubanochoerinae, nouvelle sous-famille de porcs du Miocène moyen du Caucase. *Vertebrata PalAsiatica* 4 (2): 87-97.

GABUNIA L. 1973. — *The Fossil Vertebrate Fauna from Belometchetskaya*. Academy of Science Georgia, Institute of Palaeobiology, Metsnierela, Tbilisi, 137 p.

GERVAIS P. 1859. — *Zoologie et paléontologie françaises*. Bertrand, Paris, 2nd ed., 544 p.

GINSBURG L. 1977. — *Listriodon juba*, suidé nouveau du Miocène de Beni Mellal (Maroc). *Géologie méditerranéenne* 4: 221-224.

Ginsburg L. 1980. — *Xenohyus venitor*, Suidé nouveau (Mammalia, Artiodactyla) du Miocène inférieur de France. *Geobios* 13: 861-877.

Ginsburg L. 2000. — Chronologie des dépôts miocènes du Blésois à la Bretagne. *Symbioses* n.s. 2: 3-16.

Ginsburg L. & Bulot C. 1987. — Les Suiformes (Artiodactyla, Mammalia) du Miocène de Bézian (Gers). *Bulletin du Muséum national d'Histoire naturelle* 4^{e} sér., 9: 455-469.

Golpe-Posse J. M. 1972. — Suiformes del Terciario Español y sus yacimientos. *Paleontologia y Evolución* 2: 1-197.

Hünermann K. A. 1968. — Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän: Pont) Rheinhessens (Sudwestdeutschland). *Schweizerische Paläontologische Abhandlungen* 86: 1-96.

Hunter J. P. & Fortelius M. 1994. — Comparative dental occlusal morphology, facet development, and microwear in two sympatric species of *Listriodon* (Mammalia: Suidae) from the Middle Miocene of Anatolia (Turkey). *Journal of Vertebrate Paleontology* 14: 105-126.

ICZN 1999. — *International Code of Zoological Nomenclature*. 4th ed., International Trust for Zoological Nomenclature, London, xxix + 306 p.

Johnson N., Opdyke N., Johnson G., Lindsay E. & Tahirkheli R. 1982. — Magnetic polarity stratigraphy and ages of Siwalik Group rocks of the Potwar Plateau, Pakistan. *Palaeogeography Palaeoclimatology Palaeoecology* 37: 17-42.

Kingdon J. 1979. — *East African Mammals: An Atlas of Evolution in Africa*, vol. 3B *(Large Mammals)*. Academic Press, London, 436 p.

Legendre S. 1986. — Analysis of mammalian communities from the Late Eocene and Oligocene of southern France. *Palaeovertebrata* 16 (4): 191-212.

Leinders J. 1975. — Sur les affinités des Listriodontinae bunodontes de l'Europe et de l'Afrique. *Bulletin du Muséum national d'Histoire naturelle* 341: 197-204.

Leinders J. 1977. — The configuration of the wear facets on the premolars of *Listriodon* (Suidae, Artiodactyla) and its implications. *Proceedings of the Koninklijke Nederlandse Akademie Wetenschappen* B 80: 360-366.

Leinders J. 1978. — A functional interpretation of the dental morphology of *Listriodon* (Suina). *Proceedings of the Koninklijke Nederlandse Akademie voor Wetenschappen* B 81: 61-69.

Li Chuankui, Wu Wenyu & Qiu Zhuding 1984. — Chinese Neogene: Subdivision and correlation. *Vertebrata PalAsiatica* 22 (3): 163-178.

Liu Tungsen & Lee Yuching 1963a. — New species of *Listriodon* from Miocene of Lantien, Shensi, China. *Vertebrata PalAsiatica* 7 (4): 291-304.

Liu Tungshen & Lee Yuching 1963b. — Miocene mammals from Tung-Sha-Po, Loyang, Honan Province. *Vertebrata PalAsiatica* 7 (4): 352-356.

Liu Tungsen & Lee Yuching 1978. — Miocene artiodactyl fossils from Lingtung, Lantien, Shaanxi. *Professional Paper on Stratigraphy and Palaeontology* 7: 127-135.

Lydekker R. 1884. — Indian Tertiary and post-Tertiary Vertebrata. Siwalik and Narbada Bunodont Suina. *Memoirs of the Geological Survey of India, Palaeontologica Indica* (10) 3 (2): 35-104.

McKenna M. C. & Bell S. K. 1997. — *Classification of Mammals above the Species Level*. Columbia University Press, New York, 631 p.

Mein P. 1990. — Updating of MN Zones, *in* Lindsay E., Fahlbusch V. & Mein P. (eds), *European Neogene Mammal Chronology, NATO ASI series A*. Plenum Press, New York; London 180: 73-90.

Miller K. G. & Fairbanks R. G. 1985. — Cainozoic ∂^{18}O record of climate and sea level. *South African Journal of Science* 81: 248-249.

Paraskevaidis L. 1940. — Eine obermiocäne Fauna von Chios. *Neues Jahrbuch fur Mineralogie, Geologie, Paläontologie* 83: 363-442.

Pavlovic M. B. 1969. — Miocene mammals of Toplicka Basin: Palaeontology, stratigraphy, study. *Annales géologiques de la Péninsule des Balkans* 34: 269-394.

Petronijevic Z. M. 1967. — Middle Miocene and lower Sarmatian mammalian fauna of Serbia. *Palaeontologica Jugoslavica* 7: 1-160.

Pickford M. 1981. — Preliminary Miocene Mammalian biostratigraphy for Western Kenya. *Journal of Human Evolution* 10: 73-97.

Pickford M. 1986. — A revision of the Miocene Suidae and Tayassuidae (Artiodactyla, Mammalia) of Africa. *Tertiary Research Special Paper* 7: 1-83.

Pickford M. 1987. — Révision des Suiformes (Artiodactyla, Mammalia) de Bugti (Pakistan). *Annales de Paléontologie* 73: 289-350.

Pickford M. 1988. — Revision of the Miocene Suidae of the Indian Subcontinent. *Münchner Geowissenschaften Abhandlungen* 12: 1-91.

Pickford M. 1993. — Old World suoid systematics, phylogeny, biogeography and biostratigraphy. *Paleontologia y Evolución* 26-27: 237-269.

Pickford M. 1996. — Earth expansion, plate tectonics and Gaia's pulse. *Bulletin du Muséum national d'Histoire naturelle* 4^{e} sér., 18: 451-516.

Pickford M. 1998. — Onland Tertiary marine strata in southwestern Africa: Eustasy, local tectonics and epeirogenesis in a passive continental margin setting. *South African Journal of Science* 94: 5-8.

Pickford M. 2001a. — The biochronological importance of Kubanochoerinae (Mammalia, Suidae) together with a description of new material of *Megalochoerus khinzikebirus* and *Libycochoerus massai* from Kenya. *Comptes Rendus de l'Académie des Sciences* IIa 332 (3): 193-201.

Pickford M. 2001b. — New species of *Listriodon* (Suidae, Mammalia) from Bartule, Member A, Ngorora Formation (*ca* 13 Ma), Tugen Hills, Kenya. *Annales de Paléontologie* 87: 209-223.

PICKFORD M. & ERTÜRK C. 1979. — Suidae and Tayassuidae from Turkey. *Bulletin of the Geological Society of Turkey* 22: 141-154.

PICKFORD M. & LIU LIPING 2001. — Revision of the Miocene Suidae of Xiaolongtan (Kaiyuan), China. *Bollettino della Societa Paleontologica Italiana* 40 (2): 275-283.

PICKFORD M. & MORALES J. 1989. — On the tayassuid affinities of *Xenohyus* Ginsburg, 1980, and the description of new fossils from Spain. *Estudios geologicos* 45: 233-237.

PICKFORD M. & MORALES J. 1994. — Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. *Palaeogeography Palaeoclimatology Palaeoecology* 112: 297-322.

PICKFORD M. & MOYA SOLA S. 1995. — *Eurolistriodon* gen. nov. (Suoidea, Mammalia) from Els Casots, early middle Miocene, Spain. *Proceedings of the Koninklijke Nederlandse Akademie voor Wetenschappen* 98: 343-360.

PICKFORD M. & SENUT B. 2000. — Geology and palaeobiology of the Namib Desert Southwestern Africa. *Memoir of the Geological Survey of Namibia* 18: 1-155.

PILGRIM G. E. 1908. — The Tertiary and post Tertiary deposits of Baluchistan and Sind with notices of new vertebrates. *Records of the Geological Survey of India* 37: 139-168.

PILGRIM G. E. 1926. — The fossil Suidae of India. *Memoirs of the Geological Survey of India* n.s. 8 (4): 1-65.

POMEL A. 1848. — Observations paléontologiques sur les hippopotames et les cochons. *Archives des Sciences physiques et naturelles de Genève* 8: 155-162.

ROGER O. 1882. — *Verzeichnis der bisher bekannten fossilen Säugetiere*. Regensburg, 162 p.

SIMPSON G. G. 1945. — The principals of classification and a classification of Mammals. *Bulletin of the American Museum of Natural History* 85: 1-350.

TONG Y., ZHENG S. & QIU Z. 1996. — Cenozoic Mammal Ages of China. *Vertebrata PalAsiatica* 33 (4): 290-314.

VAN DER MADE J. 1991. — Sexual bimodality in some recent pig populations and application of the findings to the study of fossils. *Zeitschrift für saugetierkunde* 56: 81-87.

VAN DER MADE J. 1994. — Suoidea from the lower Miocene of Cetina de Aragon (Spain). *Revista Española de Paleontologia* 9: 1-23.

VAN DER MADE J. 1996. — Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology* 33: 3-254.

VAN DER MADE J. 1997a. — Los Suoidea de la Peninsula Iberica, *in* CALVO J. P. & MORALES J. (eds), *Avances en el conocimiento del Terciario Ibérico*. Museo Nacional de Ciencias Naturales, Madrid: 109-112.

VAN DER MADE J. 1997b. — On *Bunolistriodon* (= *Eurolistriodon*) and kubanochoeres. *Proceedings of the Koninklijke Nederlandse Akademie voor Wetenschappen* 100: 141-160.

VAN DER MADE J. 1999. — Intercontinental relationship Europe-Africa and the Indian Subcontinent, *in* RÖSSNER G. & HEISSIG K. (eds), *The Miocene Land Mammals of Europe*. Friedrich Pfeil, Munich: 457-472.

VAN DER MADE J. & ALFEREZ F. 1988. — Dos suidos (Listriodontinae) del Mioceno Inferior de Corcoles (Guadalajara, España). *Coloquium homenaje a Rafael Adrover: "Bioeventos y Sucesiones faunistics en el Terciario continental Iberic"*, Sabadell, 14-16 December, 1998, abstracts: 22.

VAN DER MADE J., BELINCHON M. & MONTOYA P. 1998. — Suoidea (Mammalia) from the Lower Miocene locality of Buñol, Valencia, Spain. *Geobios* 31: 99-112.

WILKINSON A. 1976. — The Lower Miocene Suidae of Africa, *in* SAVAGE R. & CORYNDON S. (eds), *Fossil Vertebrates of Africa*. Academic Press, London 4: 173-282.

YE JIE, QIU ZHANGXIAN & ZHANG GUODIAN 1992. — *Bunolistriodon intermedius* (Suidae, Artiodactyla) from Tongxin, Ningxia. *Vertebrata PalAsiatica* 30 (2): 135-145.

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