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LISTRIODONTINAE (SUIDAE, MAMMALIA), THEIR EVOLUTION, SYSTEMATICS AND DISTRIBUTION IN TIME AND SPACE

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Representatives of the pig subfamily Listriodontinae are found in Miocene deposits of Africa and Eurasia. Listriodontinae differ from other suids in morphology and size of the incisors, which may be three times as large as in their suid relatives. Many listriodonts showed a tendency to develop lophodonty and in some species the males developed large median 'horns' on the frontals; smaller protuberances above the orbits are found in both males and females. On account of molar similarity, some listriodonts have previously been described erroneously as tapirs. The oldest representatives of the subfamily occur in strata of Early Miocene, the youngest in strata of early Late Miocene age, documenting a chronostratigraphical range from *c.* 20 to 9 Ma.

Listriodonts from 350 localities in Eurasia and Africa were studied in order to clarify their systematics, study their palaeoecology, unravel phylogenetic relationships, establish a more refined biostratigraphical framework, and better understand migration and dispersal patterns. Problems related to the geographical distribution of species and phylogenetic lineages were focused on in an attempt to improve our knowledge of the evolution of the group, study the potential of lineages for long-distance correlations, and - document the relationship between migration/dispersal events, eustatic sea level changes and alaeogeographical reorganisations resulting from plate tectonics.

Listriodont evolution was marked by major changes in tooth morphology. A comprehensive nomenclature based on the Cope-Osborn terminology is proposed to facilitate discussions and comparisons of dental structures in suids and other groups of Artiodactyla.

Four new species are described, *viz. Lopholistriodon pickfordi, Kubanochoerus marymunnguae, Kubanochoerus mancharensis* and *Bunolistriodon anchidens*. The genera *Nguruwe* (1 species) and *Lopholistriodon* (4 species) are placed in the Lopholistriodontini (new tribe). *Libycochoerus* is included in *Kubanochoerus* (6 species), the sole genus of the Kubanochoerini. Small species often placed in *Libycochoerus* are reassigned to *Bunolistriodon* (10-12 species), which, together with *Listriodon* (2 species), is placed in the Listriodontini. *Kenyasus* is excluded from the Listriodontinae.

The ecological significance of incisor morphology and morphometry, thickness of molar enamel, geographical and temporal distribution and species abundances are discussed. Changes in listriodontine distribution and abundance during the Middle and Late Miocene reflect environmental changes.

The evolutive trends in listridont lineages are used to improve local biostratigraphy and long distance correlations. During the study period, northern Eurasia, a subcontinent comprising SE Europe & Turkey, the Indian Subcontinent and Africa were separate landmasses. Dispersals of listriodonts in thses landmasses coincide with those of other mammals and represent "dispersal events". Such dispersal events occurred simultaneously in the different land masses. Some of those dispersal events are known under the name Proboscidean Datum Event and are widely believed to be allowed for by eustatic sea level low stands. The different dispersal events are related to particular eustatic sea level low stands of Haq *et al.* (1987). Dates as inferred from the the relation between dispersal events and the dated curves of Haq *et al.* agree well with the available radiometric and paleomagnetic dates of mammal localities.

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CONTENTS

INTRODUCTION

In comparison with other mammals, such as primates, carnivores, proboscideans, horses and rodents, fossil Suoidea have received little attention. The Suoidea comprise the Suidae (pigs) and Tayassuidae (peccaries). The former are Eurasian and African, the oldest representatives being known from the earliest Miocene of Europe. Only with the help of man did they reach other parts of the world. A number of fossil Suoidea from Eurasia and Africa currently assigned to the Doliochoerinae or Palaeochoerinae, Tayassuidae or to the Sanitheriidae probably represent a homogeneous group, for which the name Palaeochoerinae has priority. Recently the name Palaeochoeridae was proposed for this group (Van der Made, in press).

The Suidae comprise the Suinae, Hyotheriinae, Tetraconodontinae and Listriodontinae. Some other suids are difficult to assign to one of these subfamilies. The Hyotheriinae occurred in Europe during the early Middle Miocene and in China ranged up to the Late Miocene. They have no undisputed record in Africa or Pakistan and India. Tetraconodontinae are known from Europe and Anatolia and from the Indian Subcontinent from the Middle and Upper Miocene and from Africa from the Upper Miocene and Pliocene. There is no record from China. Living Suinae are known in all these areas and the first record of the group is from the Middle Miocene of Pakistan.

Listriodonts occurred in Africa and the Indian Subcontinent during the Early and Middle Miocene. In Europe and Asia (excluding the Indian Subcontinent), they ranged in age from the very latest Early Miocene to the earliest Late Miocene. The Listriodontinae are characterised by wide incisors, with low crowns and many of them show a tendency towards lophodonty (molars with crests instead of cusps), which is a herbivore adaptation while most pigs are omnivores. Some listriodonts were peculiar in that the males had 'horns' on their frontals and both sexes had smaller protuberances above the orbits. Their estimated body weights range from 8 to over 3,000 kg.

Usually listriodonts are derived from the Hyotheriinae because Tetraconodontinae and Suinae have many derived characters and are later in time. However, the oldest hyotheriines known also have adaptations that might exclude them from the ancestry of the listriodonts. It is clear that a discussion of the origin of the Listriodontinae should involve the archetypal hyotheriines, tetraconodonts and suines, but this is beyond the scope of the present study.

The remains of listriodonts were first found in Europe and on account of the peculiar dentition they were initially believed to belong to tapirs (Nicolet, 1844a). Shortly afterwards they were found in what is now Pakistan and the same assignment was favoured (Falconer, 1868). Much later the first listriodonts in China were recognised (Pearson, 1928). Many listriodont remains may have been sold as 'dragon bones' and may have been ground up to be used as medicine (Guan & Rice, 1990). Finally they were found in Africa (Arambourg, 1933).

Amongst the Suidae, the Listriodontinae have received closer attention. Papers on listriodonts that had more than average impact include those by Stehlin (1899-1900), Gabunia (1960), Arambourg (1933, 1961, 1963), Leinders (1975, 1976, 1977a, b), Wilkinson (1976, 1978) and Pickford (1986b, 1988a). These studies have increased the number of taxa and the main points of discussion are the validity and the contents of the genera *Bunolistriodon* and *Libycochoerus* and the recognition of a separate subfamily Kubanochoerinae. At present, eight genera are included in the Listriodontinae. Of these, *Kenyasus* and *Hemimastodon* are here excluded from the Listriodontinae and the genus *Libycochoerus* is synonymised with *Kubanochoerus*. There is not a single author who studied all listriodont species, but the species that are recognised in at least one recent publication amount to a total of *c.* 25. Some changes are proposed in the present study, but the number of species recognised remains roughly the same.

Listriodonts from one continent have only occasionally been compared to those of another. The result is that species names are geographicalally restricted. The extant wild pigs from a large area including Europe, North Africa, Japan and Indonesia are currently placed in a single species, *Sus scrofa*. The question arises whether the Miocene listriodonts could not have had similar large geographical ranges. If this is the case, listriodont evolution might help in long-distance correlations.

During 'listriodont times', major geographical changes occurred. Due to the northward movement of Africa, Tethys and Paratethys were separated from the Indian Ocean. A large area in the Middle East was turned into an extensive shallow sea that periodically fell dry as a result of global sea level drops. Africa, India and Eurasia north of the Himalayas were separate continental blocks for a long period and as a result very different kinds of mammals evolved in these continents. When the connections were established a stepwise faunal exchange occurred, unequalled subsequently in Old World history. This faunal exchange, or rather its stratigraphical consequence, was termed the 'Proboscidean Datum Event' by Madden & Van Couvering (1976), after the dispersal of the proboscideans into

Eurasia. In fact, several events occurred millions of years apart (Antunes, 1990; Tassy, 1990), involving many taxa and especially the dispersal of various kinds of Hominoidea in Eurasia (Thomas, 1985; Bernor *et al.*, 1988).

Listriodontine evolution in the context of changing geography is studied in the present paper and an attempt is made to determine whether or not this can help understand the complex of events that occurred. This implies that: 1) evolutionary lineages and phylogeny are studied in conjunction with stratigraphy, with the ultimate aim of refining local stratigraphy and long-distance correlations; 2) major attention is paid to geographical ranges of taxa at any moment in their history in order to detect geographical patterns as well as dispersals; 3) listriodont dispersals are compared to known coeval dispersal events; 4) these events are matched to literature data on palaeogeography and eustatic sea level and on the interfingering of terrestrial and marine sediments. Attention is also focused on the ecology of the listriodonts.

METHODS

- Introduction on nomenclature

Cheek teeth or 'molars', which include permanent molars, deciduous molars and premolars are assumed to belong to one tooth class (Osborn, 1978), though this opinion is not shared by everyone. There are two other tooth classes, canines and incisors. Within each class, teeth are assumed to be serially homologous. For different elements of the teeth, there are different gradients in development, resulting in different morphologies (Butler, 1939; Osborn, 1978).

In tooth nomenclature, usually, but not always, it is attempted to name homologous structures. However, 'homology' does not mean the same to everyone. Van Valen (1982) considered homology to be 'resemblance caused by a continuity of information'. Roth (1984) pointed out that there are different types of homology, such as phylogenetic and iterative homology. Iterative homology includes serial homology and may be caused by gene duplications. In palaeontology it is difficult, often impossible, to prove homology. Roth (1984) pointed out that homology and parallelism are often difficult to distinguish. The study of Listriodontinae showed that many characters developed parallel. It is frequently found that a trend in a character starts, a speciation event occurs and both lineages continue the trend in that character. This is not surprising: the animals had nearly the same genes and reacted to the same selection pressures. The later part of development of the character is a parallel, not a homology, at least in Van Valen's sense (1982). However, the resulting structures are some kind of a homologue, having the same genetic basis.

In *Listriodon*, lophodonty developed in molars, but also in the P4. This is no isolated case; the same happened in *Lopholistriodon* and in *Schizochoerus*, a non-listriodont suoid. This indicates that a change may occur in cheek teeth irrespective of the molar-premolar junction. In a later stage, the P_2 and P_3 of *Listriodon* developed lophids. This is serial homology and it is very likely that lophids of the P_2 and P_3 have the same genetic basis as the molars. *Lopholistriodon* also evolved lophodonty, which also led to the development of lophids in the P_2 and P_3. The formation of the lophids in these premolars involved the formation of the cusps here called metaconids, which were not present in the ancestors. If the metaconids in the premolars are homologous to those of the molars, the metaconids in the P_3 of *Listriodon* and *Lopholistriodon* are also homologous. There is, however, no direct 'continuity of information' in the premolars and thus no homology in the sense of Van Valen (1982). Similar examples can be chosen with taxa that are less closely related; there is a continuum. Roth (1984) concluded that in practice one should be willing to tolerate some ambiguity between parallellism and homology.

One should be cautious in interpreting historical homologies from morphological similarities. Van Valen (1982) illustrated a case where in a series of horses, P^4 and P^3, were molarised, but one through the addition of a hypocone and the other through growth of the paraconule. For a palaeontologist, the main way to recognise homology is through the study of gradual changes in lineages.

The homology of elements in teeth has occupied palaeontologists and neontologists for a long time and will continue to do so. Ideally, a nomenclature for teeth should be based on (some kind of) homology, but at present this is possible only to some extent. The molars are usually the most complicated teeth and their homologies are best known. Nomenclature for main features of artiodactyle molars is accepted, but is incomplete and less well accepted for the minor features. For other teeth there are different nomenclatures, none of which is widely accepted, nor comprehensive.

For artiodactyles, as well as for many other groups, the only uniformly accepted nomenclature for the cusps of the molars is the Cope-Osborn nomenclature (Osborn & Gregory, 1907 and references therein; Butler, 1978). For ruminants a very elegant alternative was proposed by Obergfell (1957), who called the first (anterior) lingual cusp $licol_1$, the first labial one $lacol_1$, the second licol$_2$ and so on. For Suidae, Hünermann (1963, 1968) simply used terms like, 'vorderer Innenhügel' (antero-internal cusp). Selected nomenclatures are compared in Table 1.

In ruminants and anthracotheres a number of crests, styles and minor cusps were recognised and named in a nomenclature that is parallel or additional to the Cope-Osborn nomenclature. For instance, Forster Cooper (1924), Obergfell (1957) and Heintz (1970) named the same crest 'ridge 4 of the metaconid', 'postala$_1$' and 'aille postérieur du metaconide', respectively. For Helohyidae, Coombs & Coombs (1977) expanded the Cope-Osborn terminology and this nomenclature was again expanded for the ruminants by Azanza (1989). Azanza called the postala$_1$ 'postmetacrístida' while Coombs & Coombs did not name this element.

The molars of Suidae are usually considered to consist of four main cusps (for M1 and M2) and a chaotic lot of 'accessory' cusplets and folds. Butler (1956) explained the difference between cuspules, wrinkles and crenulations of the enamel on the one hand, which do not involve the dentine-enamel junction and on the other hand, 'true cusps' and folds, which do involve that junction (see Butler, 1956, fig. 2). The small cuspules and wrinkles of the pig molar were considered to be of the first type and to be the result of local thickening of the enamel. However, when small cusplets of suid molars are worn, small dentine islets appear. Only of the very smallest cusplets and crenulations, it can not be seen whether the dentine-enamel junction is involved. Like ruminants and anthracotheres, suoids have not only cusps, but also crests (or rather lobes) and cusplets with a constant position.

Hünermann (1963, 1968) and Pickford (1984, 1986b, 1988a) recognised that the structure of the suoid molar is not chaotic, but very constant and that a great number of folds and cusplets can be recognised. Unfortunately, the structure of the teeth was mainly thought of as pattern of furrows ('Furchenmuster'). Each of the four main cusps of a molar was thought to have three grooves of a constant position, numbered from 1 to 12 and a number of small and variable valleys. Pickford (1984) called a cusp between the second and third furrow 'the 2/3 cusp' on account of its position. Since the nomenclatures applied to ruminants and anthracotheres name mainly the ridges, a comparison is difficult. However, resemblance of the suoid and ruminant molar patterns was hinted at by Pickford (1984), who indicated a 'palaeomeryx-fold', although he apparently meant a groove and not a ridge. Heintz (1970) considered the 'pli-*Palaeomeryx*' to be a ridge.

As indicated by Hünermann (1968), a cusp has three furrows and the areas between the furrows are indicated as front field, hind field and outer field. The outer field comprises an anterior crest, a posterior crest and the flat outer surface between these crests. Thus, there are four crests (or lobes) and these crests are the same as the four ridges that Forster Cooper (1924) recognised in the lingual cusps of the anthracothere lower molars and three of these crests were recognised by Azanza (1989) in ruminants (Table 1). The small 'cristida accesoria interlobular' and the 'postmetacrístida' of Azanza are fused and diverge at some distance of the tip of the metaconid in cervids, but in tragulids they are divergent from the tip of the metaconid. The crests that are not normally represented in ruminants occasionally appear as anomalies in early cervids. In Suidae, three of the four crests of the labial cusps are the same as those in ruminants. It appears that many of the crests found in suids are named in another group, but none of the other groups has all crests. In the following section, these ridges will be named.

For premolars, some authors have applied a nomenclature based on molar nomenclature, while others have used a different nomenclature. The reason for this is that some considered structures homologous and others did not. The former group did so because of serial homology, the latter group pointed to the lack (of evidence for) evolutionary homology. Obergfell (1957), Geraads *et al.* (1987), Azanza (1989) and others used a nomenclature that partially or completely differed from molar nomenclature, reflecting more or less the acceptance of homologies in these elements.

Whereas several nomenclatures were proposed for the molars, next to nothing is available for canines. However, canines are important and are used *e.g.* in separating the Suidae and Tayassuidae. In tayassuids and palaeochoerids canines tend to be vertical and in suids they tend to flare out (Pearson, 1927) and in addition the morphologies of the crowns differ. The presence of sexual bimodality in the canines has been used to transfer *Cainochoerus* from the tayassuids to the suids (Pickford, 1988c). However, sexual bimodality occurs in both Palaeochoeridae and Tayassuidae (Hellmund, 1992; Wright, 1993). Since the canines have a very simple shape, probably no nomenclature has ever been proposed except for the descriptive terms, 'scrofic' for the section of the male lower canine (with the posterior side wider than the labial, as in *Sus scrofa*) and 'verrucosic' (with the labial side wider, as in *Sus verrucosus*). The character itself seems to have been used first by Nehring (1888, as cited by Groves, 1985).

Morphology of suoid incisors was used in taxonomic or functional studies by Leinders (1975, 1977a), Ginsburg (1980), Hürzeler (1982), Pickford (1986b, 1988a), Van der Made (1990d), Fortelius & Bernor (1990), Hellmund (1991, 1992), Guan & Van der Made (1993) and Fortelius *et al.* (1966). Also non-morphological characters, such as relative sizes of incisors, degree of elongation, position, orientation and presence/absence of incisors were used for taxonomic purposes by Hendey (1976), Leinders (1977a), Hürzeler (1982), Van der Made & Moyà-Solà (1989), Van der Made *et al.* (1992), Van der Made (1994a), Van der Made & Han (1994). Whereas this list could easily be extended, no one seems to have introduced a nomenclature for the important elements of suoid incisors. Obergfell (1957) proposed a set of names for ruminant incisors and canines which was an extension of her molar nomenclature (Table 5). However, not all elements seen in the suoid incisors are also found in the ruminant incisors. In addition, a set of names that is derived from the nomenclature for the molars is more consistent.

Nomenclature for the lower molars

As can be seen from Table 1, a great number of names have been proposed, but no comprehensive nomenclature is available yet. The nomenclature of Azanza (1989) is the most complete and can easily be extended to comprise all elements.

The main cusps are called protoconid, metaconid, hypoconid and entoconid; a paraconid is usually not developed. Several lineages of Suoidea add lobes to the last molars at their posterior ends. Whereas an early suid may have an M_3 with three lobes, *Notochoerus* may have an M_3 with more than 8 lobes. The posterior growth of the M_3 follows the same pattern in each new lobe (Text-fig. 1) and in the rare cases when the M_2 is elongated, the same pattern is followed (Text-fig. 2).

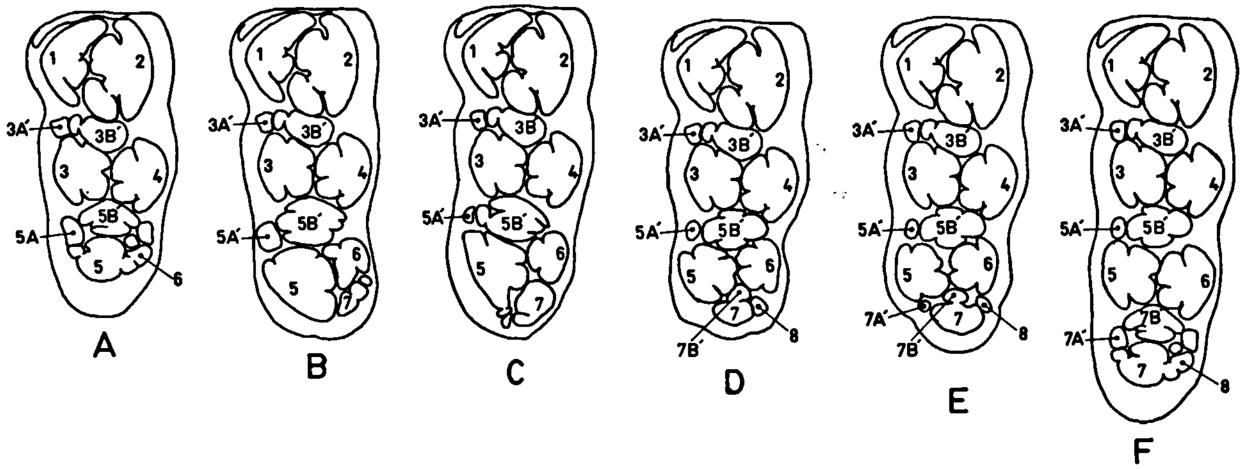


Fig. 1. Elongation of M_3 in Suidae. Composites based on *Propotamochoerus* and *Microstonyx* (A-F). All left M_3. Legend: 1 - protoconid, 2 - metaconid, 3 - hypoconid, 3A' - hypoectoconulid, 3B' - hypopreconulid, 4 - entoconid, 5 - pentaconid, 5A' - pentaectoconulid, 5B'- pentapreconulid, 6 -hexaconid, 7 - heptaconid, 7A' - heptaectoconulid, 7B' - heptapreconulid, 8 - octaconid.

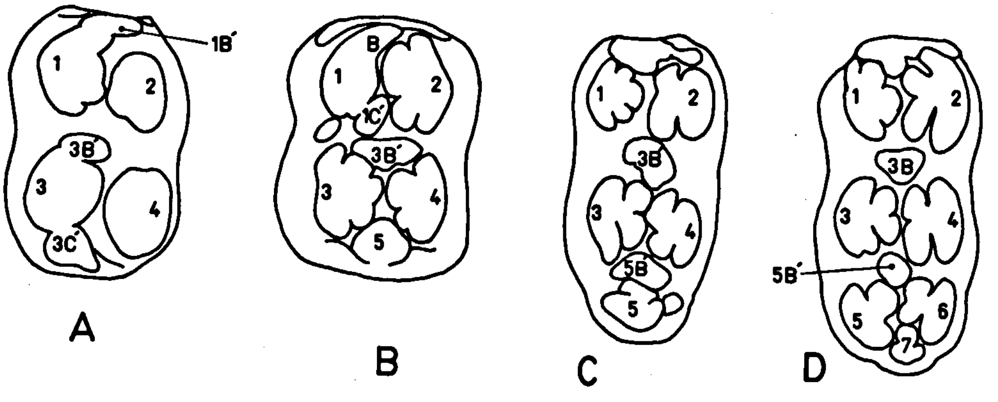


Fig. 2. Elongation of M_2 in Suoidea. From left to right: *Propalaeochoerus* (A), *Hyotherium* (B), *Notochoerus* (C), *Metridiochoerus* (D). All left M_2. Legend: 1 - protoconid, 1B' - protopreconulid, 1C' -protoendoconulid, 2 - metaconid, 3 - hypoconid, 3B' - hypopreconulid, 4 - entoconid, 5 - pentaconid, 5B' - pentapreconulid, 6 - hexaconid, 7 - heptaconid, 8 - precristid.

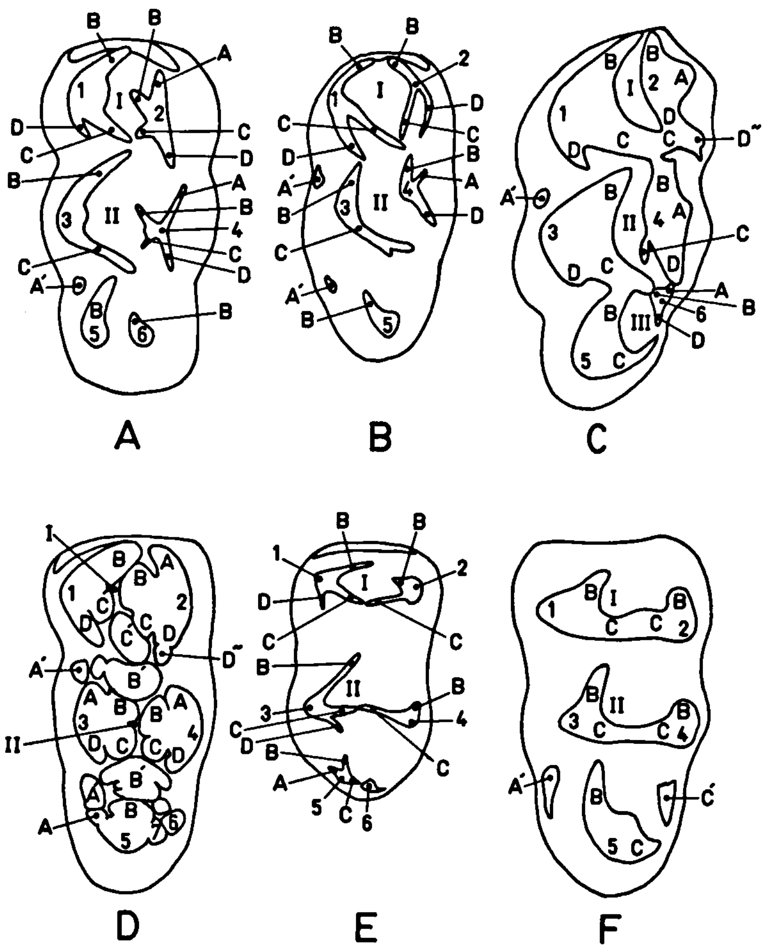


Fig. 3. Nomenclature of the lower molars in some Artiodactyla. Upper row, from left to right: buno-selenodont *Anthracotherium* (A; Anthracotheriidae), selenodont *Dorcabune* (B; Tragulidae), selenodont *Procervulus* (C; Cervidae), lower row, from left to right: bunodont *Microstonyx* (D; Suidae), sublophodont *Schizochoerus* (E; Palaeochoeridae), lophodont *Listriodon* (F; Suidae). All molars left M_3, except for the *Schizochoerus* molar, which is a left M_2. Legend: 1 - protoconid, 2 - metaconid, 3 - hypoconid, 4 - entoconid, 5 - pentaconid, 6 - hexaconid, A - ectocristid, B - precristid, C - endocristid, D - postcristid, A' -ectoconulid, B' - preconulid, C' - endoconulid, D'' - poststylid, I - protofossid, II - hypofossid, III - pentafossid.

This may be deduced from comparing the morphotypes that occur in one stage of development of a species or lineage with those of a more advanced stage. A hypoconulid-like small cusp is detached from the last buccal cusp, grows and moves in posterior direction. When there is some distance to the lobe before this cusp, a smaller cusp is formed in between, and another one is formed lingually of the hypoconulid-like cusp. The hypoconulid-like cusp attains a size and position comparable to the protoconid and hypoconid, the cusp lingual to it becomes comparable to the metaconid and entoconid. The cusp anterior of the hypoconid-like cusp becomes comparable to the 'central cusp', the smaller cusp in the middle between the first and second lobes.

The name hypoconulid is suggestive of a smaller cusp that is a derivative of the hypoconid. In the M_1 and M_2 of primitive suoids, the hypoconulid still is very close to the hypocone (*Propalaeochoerus*, symbol 3C' in Text-fig. 2a). However, if this cusp attains a size and position comparable to the protocone and hypocone (symbol 5 in the *Metridiochoerus* M_2, Text-fig. 3d, and in many M_3, Text-fig. 1), it seems best to give it a name of its own. It is proposed here to give the name pentaconid (the fifth cusp) to a hypoconulid that is not connected to the hypocone. This name was proposed by Röse (1892), but does not seem to have been used often, if at all. The next large cusp to be formed will be a lingual cusp comparable to the metaconid and will be called hexaconid. In longer molars, the next cusps may be termed, heptaconid, octaconid, nonaconid, decaconid etc. (Text-fig. 1).

In suoids, most cusps have four lobes and these lobes are comparable to crests in ruminants and anthracotherioids. They are named cristids here, even if they are inflated and have the shape of a lobe. The crests are named similarly in both lingual and labial cusps: ectocristid (originating at the external or antero-external side of the cusp), precristid (anterior-internal), endocristid (posterior-internal) and postcristid (posterior-external) (Text-fig. 3). Cusps may rotate slightly according to their size and position in a molar. For instance, the pentaconid (Text-fig. 1) is oriented differently in different stages of evolution. The crests rotate accordingly and their identity is not always unambiguous. Ectocristids frequently are rotated a little and if they are directed exactly outward, they are very short. The relation of these crests to a cusp is expressed by the prefix proto-, meta- etc., *e.g.* protoprecristid. An overview of the names used here is given in Table 2.

The translation of the names for the crests into existing nomenclature is not straightforward, since in the different Artiodactyla the lingual and labial cusps did not preserve or evolve the same crests. For instance, cervids reduced the precristids at the lingual sides and the ectocristids at the buccal sides of the molars. Azanza (1989) used preprotocristid for my protoprecristid (buccal side) and premetacristid for my metaectocristid (lingual side). Similarly, in most cervids, the postcristid is reduced at the labial side (a remnant is the pli-*Palaeomeryx*) and the endocristid is reduced at the lingual side (a remnant is Azanza's entoconid fold). As a result there is again a discrepancy between Azanza's nomenclature and the present one: hypoendocristid = posthypocristid and entopostcristid = postentocristid. Azanza's nomenclature is internally logical for the cervids, but not for all artiodactyls. The present nomenclature is applicable to many more groups of artiodactyls.

The proposed nomenclature is aimed to be a logical system, which can easily be remembered. Changing existing names is not a good custom. However, the precristids and postcristids of Azanza do not have comparable positions in the lingual and labial cusps. Maintaining these names would lead to a confusing situation. A minor change is preprotocristid into protoprecristid, which is a more logical sequence, first the main cusp is indicated and then the position of the smaller element relative to that cusp and then the type of element, a crest in this case. For Osborn proto-, meta-, hypo- etc. were prefixes, which could be attached to -cone, -conule, -style, -lophe. The sequence used here is more in the tradition of the old nomenclature. Besides, the postprotocristid of Azanza will not be confused with the protopostcristid as used here.

When at the end of a ridge a smaller cusp is separated it is called conulid. For instance, a cusp separated at the end of the hypoprecristid, is called the hypopreconulid. The 'central cusp', the cusp in the centre of a suid molar is a hypopreconulid. The 2/3 cusp of Pickford (1984) becomes the protoendoconulid and the ectostylid becomes the entoectoconulid.

If the lingual or labial walls of the tooth indicate a vertical structure, it may be indicated as stylid. This will often be a kind of cusp and may or may not be at the end of a cristid. The stylid will be related to a cusp, *e.g.* metapoststylid [the metastylid of Azanza (1989) and Heintz (1970)]. The use of the term stylid is slightly different from its original use, since the name was intended for smaller cusps that arose from the cingulum (Osborn & Gregory, 1907). Here the name is used to stress the vertical aspect at the lingual or labial wall of a tooth, rather than its supposed origin. And in this sense the name stylid was already used by Azanza, Heintz and many others: their metastylid, for instance, did not arise from a cingulum. None of the names of styles as used here will be confused with existing names, that may not have the same meaning. The names protoconid, metaconid etc. are applied to the cusps and not to the cristids associated with the cusps. If one intends to include all crests, styles and cusplets that are associated with a cusp one might call this a complexid: protocomplexid, metacomplexid etc.

If the endocristids of two cusps are fused to form a lophe this is indicated as lophid: protolophid, hypolophid, pentalophid etc.

The valley between two cristids may be named after the cresta in front of it: between the ectocristid and precristid, the ectofossid, between the precristid and endocristid, the prefossid; between the endocristid and postcristid, the endofossid; between the postcristid and ectocristid, the postfossid. The large fossid between the protoprecristid and protoendocristid in selenodont molars may simply be called protofossid.

These names may seem an exercise in dog Latin. However, in view of the number of names that have been proposed in the past (Table 1), it seems that names for details of the teeth are needed. Butler (1978) argued for not introducing new names or nomenclatures. Here a great number of elements is named by a combination of the parts: proto-, para-, meta- etc., -ecto-, -pre-, -endo-, -post- and -conid, -conulid, -stylid and -fossid. This is not going to be a burden to the memory.

The proposed system of naming is not the only possibility. Another simpler system would be a combination of the systems of Forster Cooper (1924) and Obergfell (1957): Licol$_1$, Licol$_2$ and so on for the lingual cusps, Lacol for the labial cusps, and the cristids, conulids and stylids, *e.g.* cristid 4 of licol$_3$. However, various authors have gradually expanded the Cope-Osborn nomenclature and this was picked up (Van Valen, 1966; Coombs & Coombs, 1977; Azanza, 1989), whereas the nomenclature of Obergfell was not used by others. For this reason, the nomenclature by Azanza is expanded further.

It should be borne in mind, that the aim of this nomenclature is in the first place description and the names are topographical. However, it might be argued that the names also suggest homologies, although this remains to be proved.

Nomenclature for the lower premolars and deciduous molars

Azanza (1989) did not use the Cope-Osborn nomenclature for the premolars. Obergfell (1957) also applied different names to the crests of the molars and premolars, as did Geraads *et al.* (1987). Butler (1941) argued for homology of the elements of molars and premolars. Heintz (1970) applied the same names for elements of the premolars and molars. Here the same terminology is applied to molars, premolars and milk molars (Text-figs 4, 6).

In the suoid P_4 development into a molariform tooth occurs rarely beyond the first steps in that direction. If it does take place, the talonid cusp (hypoconid) becomes extended lingually and eventually a separate lingual cusp is formed (entoconid) and a small hypopreconulid is formed (Text-fig. 4).

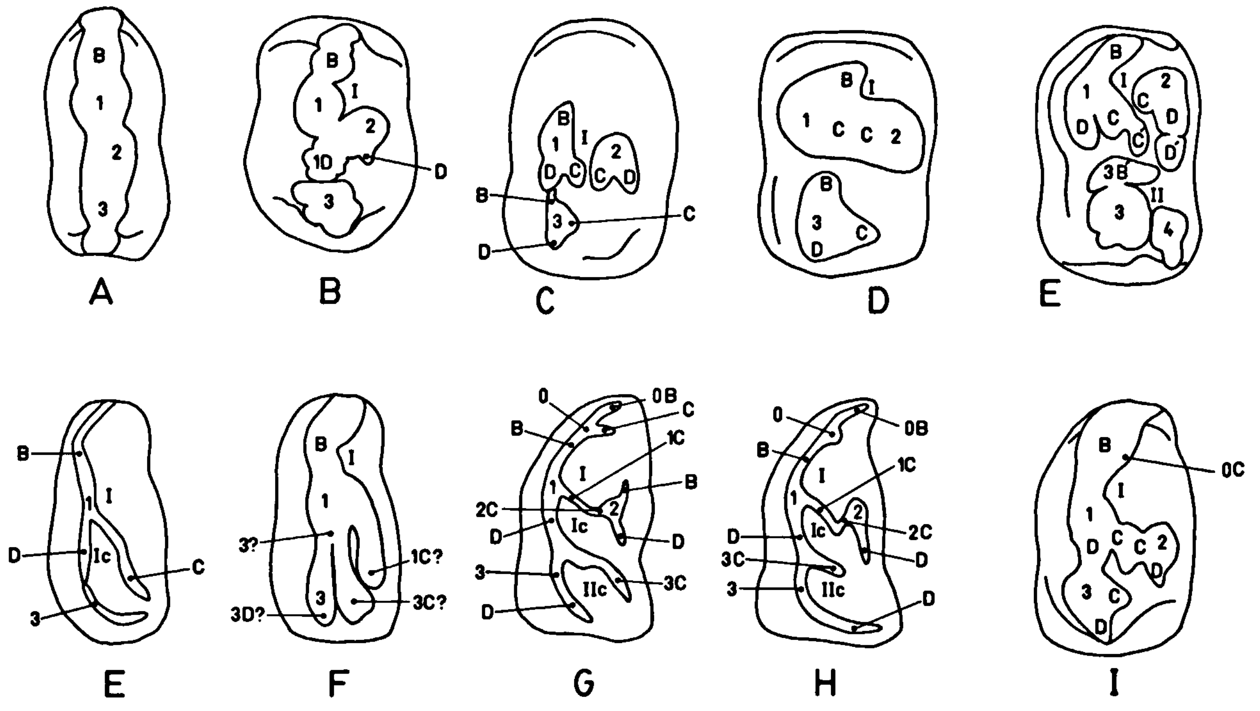


Fig. 4. Nomenclature of the lower premolars in some Artiodactyla. Upper row, from left to right: cutting-edge type *Sus* (A), Dicoryphochoerini type *Hippopotamodon* (B), sublophodont *Bunolistriodon* (C), lophodont *Listriodon* (D) (all Suidae), submolarised bunodont *Sanitherium* (E; Palaeochoeridae), lower row, from left to right: two types of *Dorcabune* (E, F; Tragulidae), two types of cervids (G, H) and bovids, buno-selenodont *Anthracotherium* (I; Anthracotheriidae). All premolars left P_4. Legend: 0 - paraconid, 0B - paraprecristid, 0C - paraendocristid, 1 - protoconid, 1C - protoendocristid, 1D - protopostcristid, 2 - metaconid, 2C - metaendocristid, 3 - hypoconid, 3B' - hypopreconulid, 3C - hypoendocristid, 4 - entoconid, B - precristid, C - endocristid, C' - endoconulid, D - postcristid, D' - postconulid, I - protofossid, Ia - protopostfossid, IIa - hypopostfossid.

Similar morphologies in premolars and molars have been interpreted as parallels and as homologies (Butler, 1941). The similarity of processes of molarisation of the talon of the P_4 and the posterior extension of the M_3 is striking, even in details such as the metapoststylid, protoendocristid and protopostcristid in the P_4.

In the lower premolars, the metaconids split off from the lingual sides of the protoconids near the tips. In the M_3 that add new lobes, the lingual cusps (hexaconid, octaconid) split off the labial cusps (pentaconid, heptaconid) near the tips. This is the same situation, but rotated 180°. The paraconid in the premolars is formed at the end of the protoprecristid, in the new lobes of the M_3 the preconulid is split off at the end of the precristid of a labial cusp. Formation of new cusps seems to occur in two ways, new cusps in the same lobe split off near the tip and cusps that will end up in another lobe usually split off at the end of a cristid.

Fig. 5. Nomenclature of the lower suoid premolar. A, B: two *Listriodon* P_3, occlusal view. Both right P_3. Legend: 1 - protoconid, 3 - hypoconid, B - precristid, C - endocristid, D - postcristid.

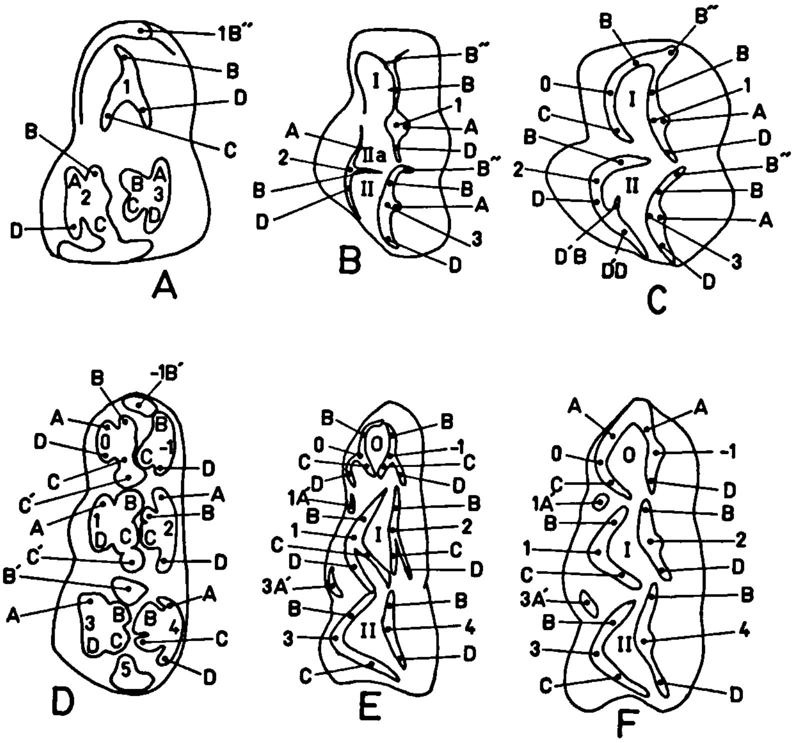


Fig. 6. Nomenclature of D^3 and D_4. Upper row, left D^3, from left to right: *Parachleuastochoerus* (A; bunodont suid), *Bachitherium*? (B; primitive ruminant), *Eucladoceros* (C; Cervidae). Legend as in Fig. 8, in addition: O - primofossa, Ia - protoprefossa. Lower row, left D_4, from left to right: *Propotamochoerus* (A; bunodont suid), *Dorcatherium* (B; Tragulidae), *Eucladoceros* (C; Cervidae). Legend as in Figure 3, in addition: 0 - paraconid, 0B' - parapreconulid, 1 - primonid, O - primofossid.

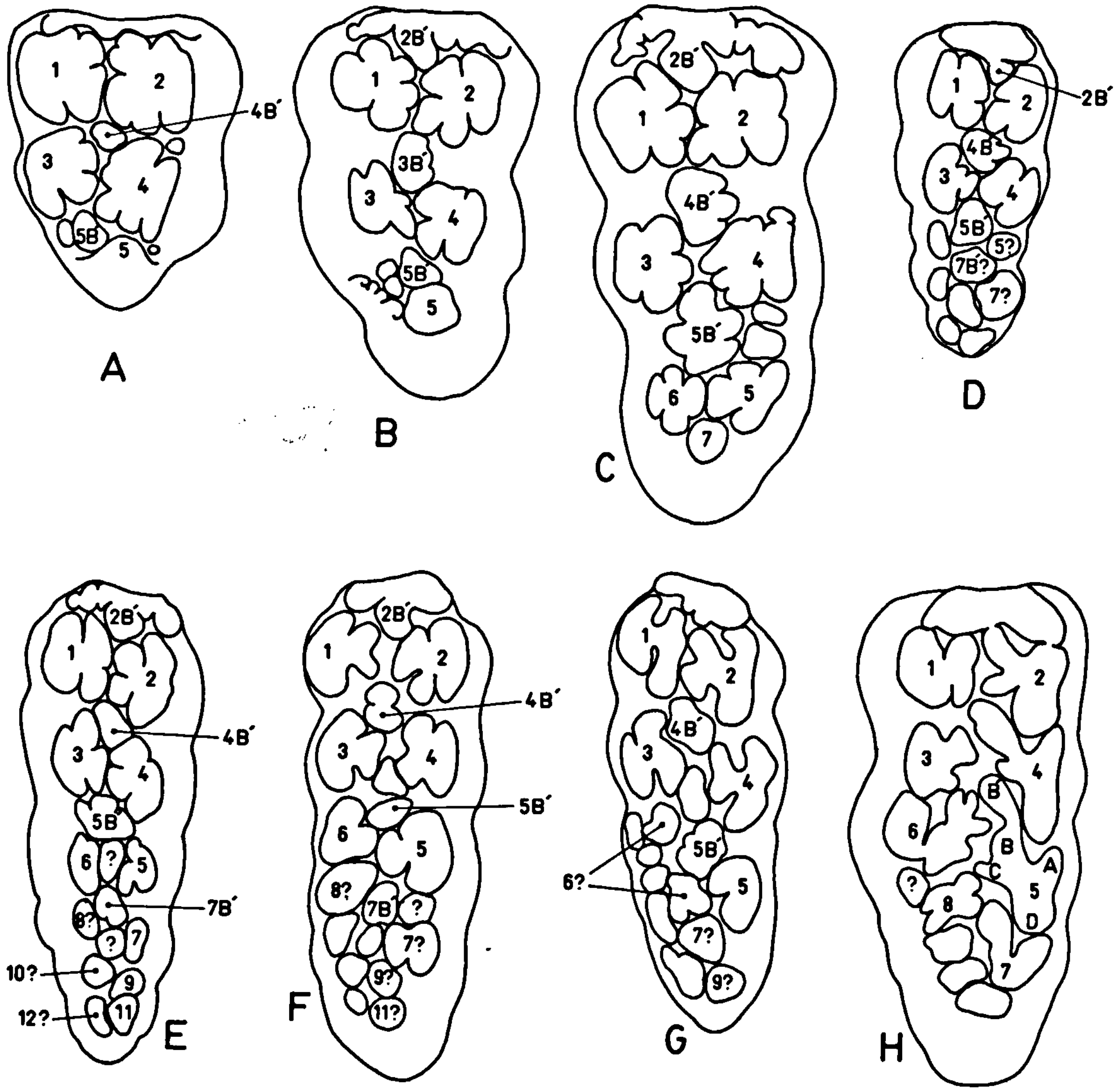


Fig. 7. Elongation of M^3 in Suidae. From left to right, upper row: *Nyanzachoerus tulotos* (A), *Nyanzachoerus kanamensis* (B), *Nyanzachoerus jaegeri* (C), *Kolpochoerus limnetes* (D) and lower row: *Kolpochoerus olduvaiensis* (E), *K. olduvaiensis* (F), *Metridiochoerus jacksoni* (G), *M. jacksoni* (H). All right M^3. Legend: 1 - paracone, 2 - protocone, 2B' - protopreconule, 3 - metacone, 4 - tetracone, 4B' - tetrapreconule, 5 - pentacone, 5B' - pentapreconule, 6 - hexacone, 7 - heptacone, 7B' - heptapreconule, 8 - octacone, 9 - nonacone, 10 - decacone, 11 - undecacone, 12 - dodecacone, A - ectocrista, B - precrista, B' - preconule, C - endocrista, D - postcrista.

The artiodactyle D_4 seems to have added an anterior lobe, the lingual cusp of that lobe is named paraconid (Heintz, 1970). Ruminant P_4 and D_4 of *Choeropotamus* have a very similar shape where the anterior lobe is concerned. The anterior lobe of the *Choeropotamus* D_4 has a paraconid, like in ruminant premolars, but no selenodont structure. This might, but need not, indicate that the ruminant D_4 really have a paraconid. No name was proposed for the anterolabial cusp; it might be called primoconid (if the paraconid is considered as zero, this is the first one negative).

In the D_3 of many suids, but also in some P_4 of tragulids (Text-fig. 4f, g), there seem to be three posterior ridges departing from the protocone. As the anterior crest is the precristid, naming these three crests presents problems. Probably a hypocone should be assumed directly behind the protocone and the crests are: protoendocristid, hypoendocristid and hypopostcristid. *Listriodon* P_3 are also suggestive of such a configuration (Text-fig. 5).

Nomenclature for the upper molars

The nomenclature for the upper molars is given in Text-fig. 8 and Table 3 and it is compared to other nomenclatures in Table 4. An expanded Cope-Osborn terminology is proposed, like in the lower molars.

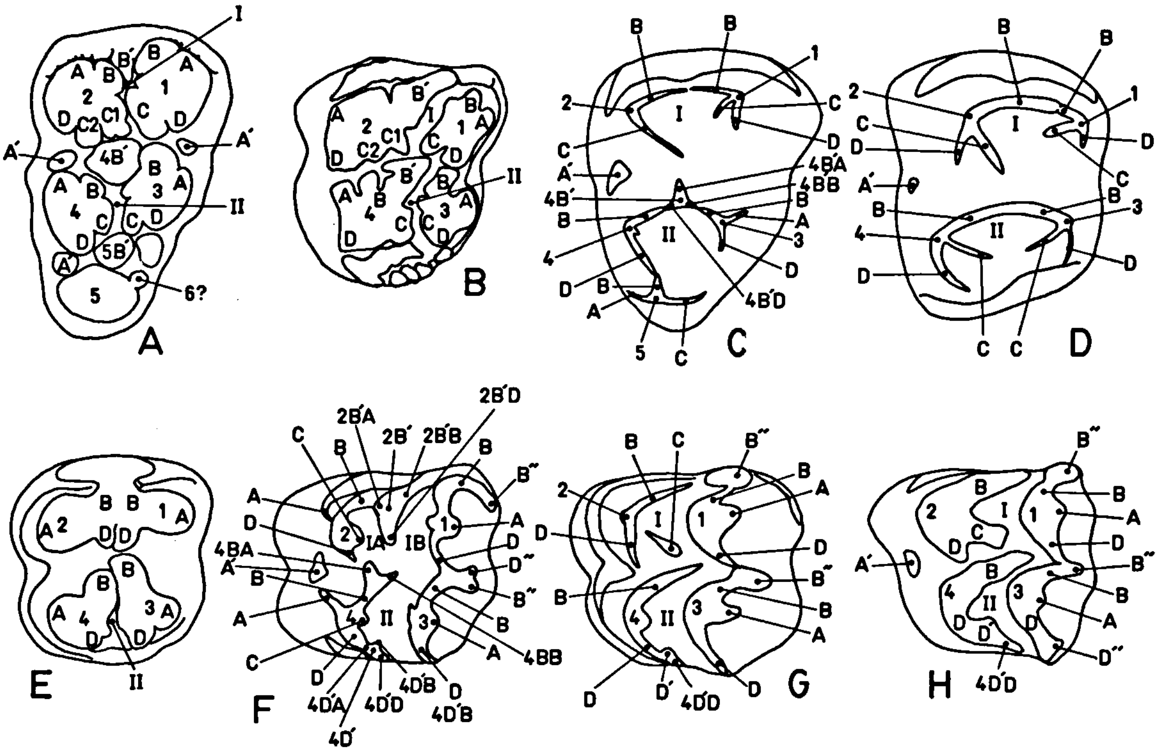


Fig. 8. Nomenclature of upper molars in some Artiodactyla. Upper row, from left to right: bunodont *Microstonyx* (A; Suidae), *Sanitherium* (B; Palaeochoeridae), sublophodont *Schizochoerus* (C; Palaeochoeridae), lophodont *Listriodon* (D; Suidae). Lower row, from left to right: bunodont *Hippopotamus* (E; Hippopotamidae), buno-selenodont *Anthracotherium* (F; Anthracotheriidae), selenodont *Dorcabune* (G; Tragulidae), selenodont *Procervulus* (H; Cervidae). All left M^1. Legend: 1 - paracone, 2 - protocone, 2B' - protopreconule, 2B'A - ectocrista of protopreconule, 2B'B - precrista of protopreconule, 2B'D - postcrista of protopreconule, 3 - metacone, 4 - tetracone, 4b - tetrapreconule, 5 - pentacone, 5b - pentapreconule, 6 - hexacone, A - ectocrista, A' - ectoconule, B - precrista, B' - preconule, B'' - prestyle, C - endocrista, C1 - internal endocrista, C2 - external endocrista, D - postcrista, D' - postconule, D'' - poststyle, I - protofossa, II - hypofossa, IA - lingual protofossa, IB - labial protofossa.

In a common upper molar there are four main cusps, the paracone (antero-buccal), metacone (postero-buccal), protocone (antero-lingual) and hypocone or metaconule (postero-lingual). For the last cusp, the name tetracone is proposed. The hypocone is a cusp formed out of the cingulum. In the premolars, nearly every lingual cusp is formed out of the cingulum (Text-fig. 10). The metaconule is a small cusp at a posterior ridge of the protocone. In the M^3, a similar cusp is each time the germ of a new lobe. It seems only proper to give this cusp its own name, when it reaches the size of a main cusp. Here, the name hypocone is reserved for an additional cusp formed out of the cingulum lingual to the tetracone (Text-fig. 10).

In some taxa, the third upper molar becomes longer during evolution. Whenever a new lobe is added, first a lingual cusp is added, and near the axis of the tooth, a preconule (Text-fig. 7). These cusps are named pentacone and pentapreconule, hexacone and hexapreconule, nonacone etc. In a later stage, cusplets are separated at the labial side and the cycle starts again. These labial cusps are not always regular and often it is not possible to recognise a hexacone, octacone, decacone etc. In many taxa a cusp invariably seems to be lacking, or there is one too many or the size is not right and the cusp might be confused with a preconule etc. (Text-fig. 7). This seems to occur especially in hypsodont suids.

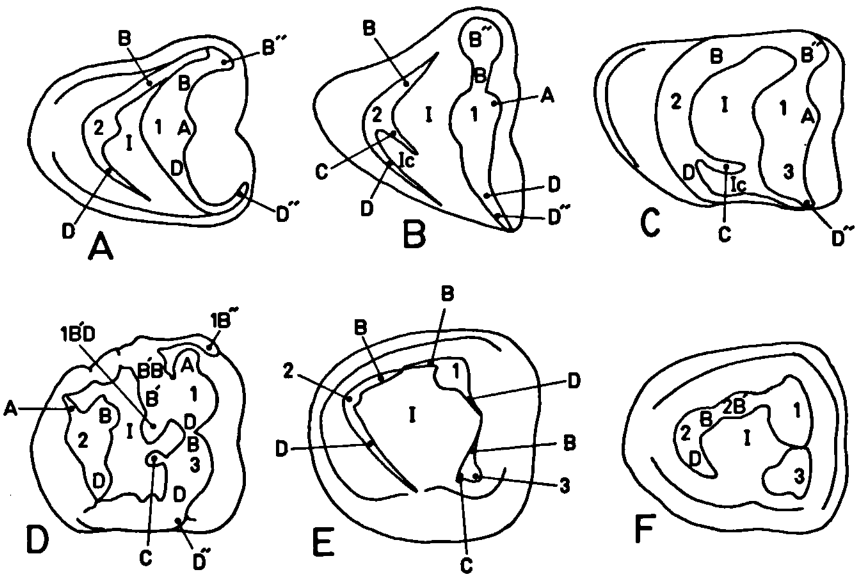


Fig. 9. Nomenclature of P^4 in Artiodactyla. From left to right, upper row: ***Anthracotherium*** (A; Anthracotheriidae), ***Dorcatherium*** (B; Tragulidae), ***Procervulus*** (C; Cervidae). Lower row: ***Sus*** (D; bunodont, Suidae), ***Schizochoerus*** (E; lophodont, Palaeochoeridae), *Listriodon* (F; lophodont, Suidae). Legend as in Fig. 8, in addition to: 1B'' - protoprestyle, 1B'D - postcrista of the protopreconule, Ic - protopostfossa.

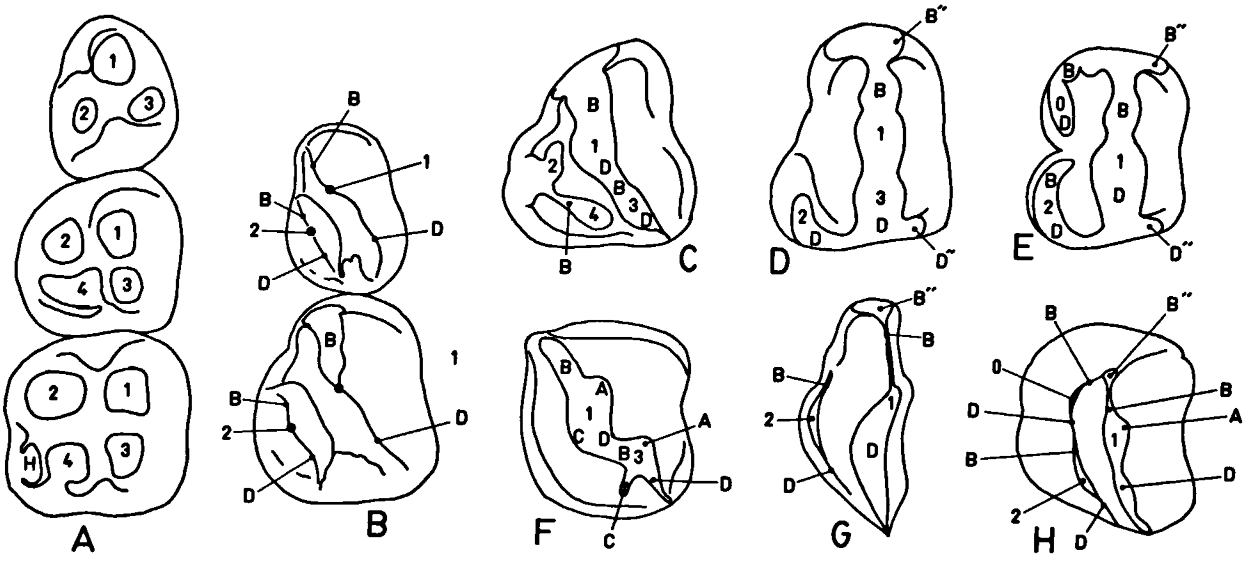


Fig. 10. Nomenclature of upper premolars in some Artiodactyla. Upper row left to right, lower row left to right and left P^2 - P^4 of *Tayassu* (A; Tayassuidae), left P^2 - P^3 of ***Bunolistriodon*** (B; Suidae), left P^3 of *Listriodon* (C), *Sus* (type 1; D), *Sus* (type 2; E) (all Suidae), ***Merycopotamus*** (F; Anthracotheriidae), ***Dorcatherium*** (G; Tragulidae) and *Tethytragus* (H; Bovidae). Legend as in Fig. 8, in addition to: 0 - primocone, H - hypocone.

Most brachyodont taxa seem to be more regular (compare *Nyanzachoerus* with other taxa in Text-fig. 7). In the M$_3$ some taxa are irregular, but most are regular; in the upper molars most are irregular. With wear cusps fuse and the pattern sends to become clearer.

The ridges that start from the cusps are named as in the lower molars, ectocrista (antero-external), precrista (antero-internal), endocrista (postero-internal) and postcrista (postero-external). In the molars of certain suids, the endocrista is a lobe that seems to divide itself into two. That is a very typical feature in some Suinae and in such a case the lobes are named internal endocrista and external endocrista. Styles and conules are named following the same system as in the lower molars, ectoconule and ectostyle, preconule etc. The names of the crests of the conules are similarly according to direction and relative position as in the main cusps, *e.g.* precrista of the preconule.

In M^1 and M^2 the tetrapostcrista forms a small cusp, the tetrapostconule (Text-fig. 8f-h). In some taxa, this cusp becomes larger and independent: the pentacone. This reflects the formation of a pentaconid in the lower molars, but does not happen synchronously. Many Suidae, including listriodonts, have pentaconids and simple tetrapostcristas. The tetrapostconule mirrors the protopreconule, but the protopreconule is disconnected from the protocone in taxa, where there is (still) a tetrapostcrista.

The protopostcrista (Text-fig. 8g, h) is replaced by the tetraendotcrista (or pli-protoconal). This seems to occur in several different ruminants independently. In the lower molars, the protopostcristid (pli-*Palaeomeryx*) is reduced. This is a similar development as in the upper molars, but it happened much earlier in evolution. This is a superficial similarity, since in the lower teeth it happens between the trigonid and talonid; and in the uppers, within the trigon.

The fossae are named as in the lower teeth, the prefossa between precrista and endocrista and so on. The large fossae in the selenodont teeth are not always between the same crests, when the endocrista is not developed, the fossa is between the precrista and postcrista. Such fossae are important and are named irrespective of the crests that form the fossae. These fossae are named after the lingual cusps, protofossa, tetrafossa etc. If a preconule splits the fossa, the names are lingual fossa and labial fossa, for instance lingual protofossa (Text-fig. 8).

Transverse lophs are named after the lingual cusps, protoloph, tetraloph, pentaloph etc.

The 'irregular' third molars, mentioned above, may prove to be less irregular, when studied in more detail. Unworn molars tend to be more irregular. With little wear, some of the many small cusps fuse and the normal cusp and crest pattern can be recognised. In some taxa, such as *Metridiochoerus* (Text-fig. 7g, h), there seems to be a tendency for cusps to be split into two elongate units. The ecto- and postcristas form a longitudinal crest and the pre- and endocristas from a longitudinal crest. What possibly happens in such hypsodont molars, is that one cusp starts to be formed from two or four points, instead of one. Such cusps would then be *e.g.* the tetraectoconule, tetraendoconule, tetrapostconule and a cusp between the tetrapreconule and the others. The tetrapreconule is a cusp that was separated already before and seems to be nearly independent and a new cuspule is formed between this cusp and the tetracone. These four cusps fuse at some distance from their tips, first forming two elongate cusps, later forming one cusp. In a later stage of wear, the tetrapreconule fuses also to this unit. In the more hypsodont species, this fusion is retarded. Besides, all kind of intermediate steps in the process are to be expected. This is a hypothetical explanation for 'irregular' M3, which still needs further study.

Nomenclature for the upper premolars and deciduous molars

For the premolars and deciduous molars, a terminology is used which resembles that of the molars (Text-figs 6, 9, 10; Table 3). However, there is a problem: cusps may be added at the anterior side, like in the D_4.

A simple upper premolar has one main cusp (paracone) and a lingual cingulum or posterolingual cingulum. If a cusp is formed from that cingulum, it is the protocone. If a cusp is formed posterior of the paracone, it is the metacone. The protocone is not always separate from the cingulum, and this cingulum may be a high crest. This is the case in many ruminants (Text-fig. 10). In *Bunolistriodon* and *Listriodon* the protocone is initially formed as a cusp in the cingulum, but in the course of evolution, the protocone moves into the fossa and separates from the cingulum (Text-fig. 10).

In some P^3, a new cusp is separated from the posterior side of the protocone (as in *Listriodon*, Text-fig. 10). That cusp is the tetracone (metaconule in the old terminology). In others, a fourth cusp seems to be separated from the cingulum behind the protocone (as in *Tayassu*, Text-fig. 10). That cusp is also, in topographical terms, tetracone. Lingually of the tetracone, still another cusp may be formed from the cingulum and that cusp is termed here hypocone (*Tayassu*, Text-fig. 10). If a tetracone is formed, the protocone and the root below it usually move forward. This is also the case in *Cervus*.

In other P^3, a new cusp is formed anterior of the protocone. Again this may happen in two ways. It may be formed on the protoprecrista (as in *Tethytragus*, Text-fig. 10). In a rare case, even a new root is formed below that anterior cusp. That cusp is here called primocone if it is large and protopreconule if it is small (in the old terminology it would be called protoconule or paraconule). The primocone may also be formed as an outgrowth of the antero-lingual cingulum (as in *Sus*, Text-fig. 10). The position of the protocone opposite the metacone is analogous to the molars in *Cainotherium*. It is strange, however, that in a group of suids or ruminants, where in the molars the protocone moved forward, this is not automatically the case in the premolars. A similar case for horses was recorded by Van Valen (1982).

The D^3 (and some D^2) often have one anterior and two posterior cusps. The posterior half looks like the posterior half of a molar, but often also as a P^4 and the tooth also resembles the P^3. In D^3 with three cusps, the lingual cusp seems to be the protocone. Comparison to the P^3 suggests that the antero-buccal cusp is the paracone and the postero-buccal cusp the metacone. In that case, the posterior lobe would consist of protocone and metacone. However, it is also possible that the posterior lobe is like the P^4 and that anterior cusps are added, labially a secundocone as it would be termed here, and lingually a primocone in the case of molarisation. At present it is impossible to choose between the possibilities and the cusps will be termed topographically: paracone (antero-buccal), metacone (postero-buccal), protocone (postero-lingual) and, if present, primocone (antero-lingual). This also conforms to the probable situation in *Cainotherium*, where there is a first lobe with two cusps, and a second lobe with three cusps as in the molars (Heizmann, 1983). In that case, the first two cusps are the paracone and primocone (paraconule) and metacone, protopostconulid (metaconule) and protocone.

In a D^3 (Text-fig. 6) a fossa between the precrista and endocrista occurs. It is called prefossa.

The D^4 is a copy of the M^1, except that in some taxa the anterobuccal corner protrudes more. The D^4 is considered to be a 'stem progenitor' for all 'molar teeth', which includes molars, premolars and deciduous molars (Osborn, 1978). For that reason it is not even certain that the cusps should bear the same name as in the molars, where the protocone is the anterolingual cusp or as in the D^3, where the protocone might be the postero-lingual cusp. In *Cainotherium*, the D^4 has the shape of the M^1 (Heizmann, 1983), with a posterior lobe with three cusps, which are probably the metacone, metaconule and protocone. This suggests that the D^4 has indeed the same cusps as the M^1. However, what seems to be the case in *Cainotherium* need not be the case in suoids, anthracotherioids and ruminants.

Bunodont, selenodont and lophodont cheek teeth

The present nomenclature makes it possible to define in a more precise way tooth categories such as bunodont, selenodont and lophodont.

Teeth where the crests are short and take the form of lobes, or where the crests are (nearly) lost, have only or mainly cusps and are called bunodont.

Selenodont lower molars, like those of ruminants, have well- developed precristids and endocristids at the labial side. These cristids form crescents. At the lingual sides the precristids and postcristids are well developed. In the upper molars, the precristas and the postcristas are well developed, but in some cases the lingual endocristas take over in importance from the postcristas. The lingual precristas and postcristas or endocristas form cresents. Often selenodonty is much less well developed or not at all in anterior premolars and anterior deciduous teeth.

The name buno-selenodont might be applied to intermediate morphologies, such as in *Anthracotherium*.

The formation of lophs is a gradual process and for teeth that are not yet fully lophodont the term sublophodont has been applied (Fortelius & Bernor, 1990). In lower molars, premolars and deciduous molars that develop lophodonty, the first loph tends to be more advanced than the second. Teeth with a protolophid and where the endocristids of the hypolophid touch, but are not fully fused, as in *Schizochoerus* (Text-fig. 3), are here called sublophodont. When the lophs of the hypolophid are completely fused, as in *Listriodon* (Text-fig. 3), they are called lophodont. In the upper cheek teeth that develop lophodonty, precristas form a loph. Again the protoloph forms before the second loph, the tetraloph. When the tetraloph is fully developed, with a complete fusion of both precristas, the tooth is lophodont.

Nomenclature of the lower limit of the crown in all teeth

In the incisors and canines, it is of interest to describe the lower limit of the crown. The same nomenclature can be applied to the premolars. In molars the lower limit of the crown is more difficult to describe and its detailed course is probably less relevant.

The lower limit of the crown is at some places close to the apex or occlusal surface of the crown, which is called an anticline (anticlinid) here (Text-figs 5, 13, 14). Between the anticlines, the lower limit of the crown is further away from the apex, these are the synclines (synclinids). In a simple tooth like the first lower incisor of *Microstonyx* (Text-fig. 13), there are two synclinids, the ectosynclinid at the labial or outer side and the endosynclinid at the lingual side. The anticlinids in between, are the presynclinid and the postsynclinid, mesially and distally, respectively. In the I_3, there is only one well-developed anticlinid, the preanticlinid, consequently the synclinids are not really well developed. In the *Listriodon* I_2, the endosynclinid starts to subdivide: anteriorly the presynclinid is formed as well as the endoanticlinid (Text-fig. 13). This division is still clearer in teeth with two roots like premolars (Text-fig. 5) and in those teeth there is also an ectoanticlinid and postsynclinid.

Nomenclature for the lower canines

The Suoidea tend to be sexually dimorphic in canines, that is, the shape is different. In addition, size differs (sexual bimodality). The male canines grow continuously and no root is formed in most of the male suids, or it is formed late in life. In most of the female suids and most of the peccaries, the canines have a distinct crown and root already early in life.

The horizontal section of female and male canines is triangular. The lingual side is called endofacet, the labial side ectofacet and the posterior side postfacet (Text-fig. 11a, b). The angles between the facets are crests and are called precristid, ectocristid and postcristid.

Usually the male canines do not have enamel at the posterior side. This is a large postanticlinid. When the lower limit of the crown is formed there are an endoanticlinid and an preanticlinid. The synclinids are: ectosynclinid, presynclinid and postsynclinid (Text-fig. 11c). Nomenclature is similar for female canines (Text-fig. 11d).

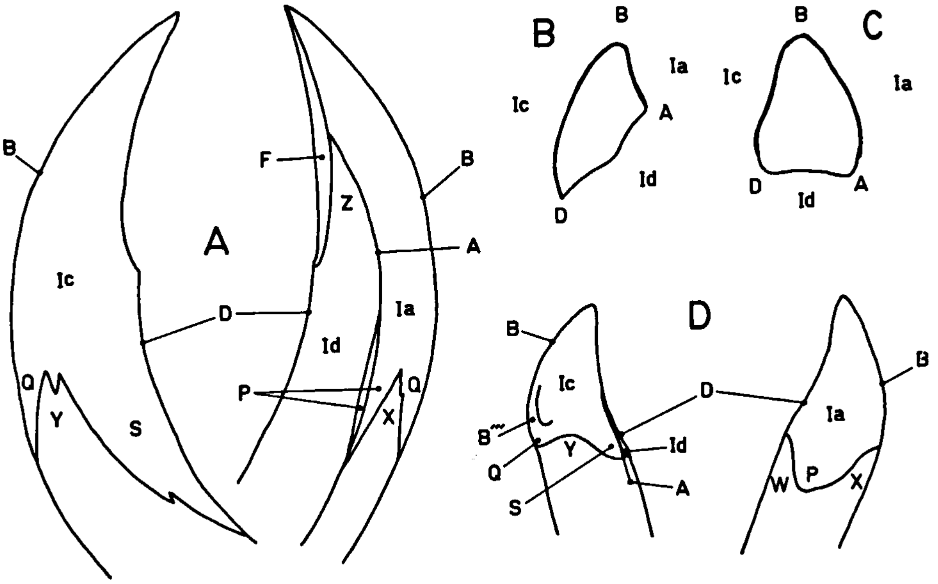


Fig. 11. Nomenclature of lower canines in Suoidea. Left: right male canine, lingual side and labial side (A), right upper row: section of the right canines of *Sus scrofa* ('scrofic type'; B) and *Sus strozzii* ('verrucosic type'; C), right lower row: right female canine (D), lingual and labial views. Legend: A - ectocristid, B -precristid, B''' - lingual prestylid, D - postcristid, F - wear facet caused by upper canine, P - ectosynclinid, Q - presynclinid, S - postsynclinid, Z - postanticlinid, X - preanticlinid, Y - endoanticlinid, Ia - ectofacet, Ic - endofacet, Id - postfacet.

Nomenclature for the upper canines

The upper canines tend to have an oval, rounded-triangular, round or kidney-shaped section. In the males of many species and in the females of some species, there is a rounded lingual crest, the endocrista (Text-fig. 12a, e). In the canines with kidney-shaped section (as in *Sus scrofa*), there is a groove at the external side, which is probably a remnant of the division of two roots. In the males, the synclines tend to be very deep, forming long enamel bands (Text-fig. 12h). In most suid species, there are three enamel bands, the presyncline, postsyncline and the wide endosyncline. The anticlines are called ectoanticline, preanticline and endoanticline. In

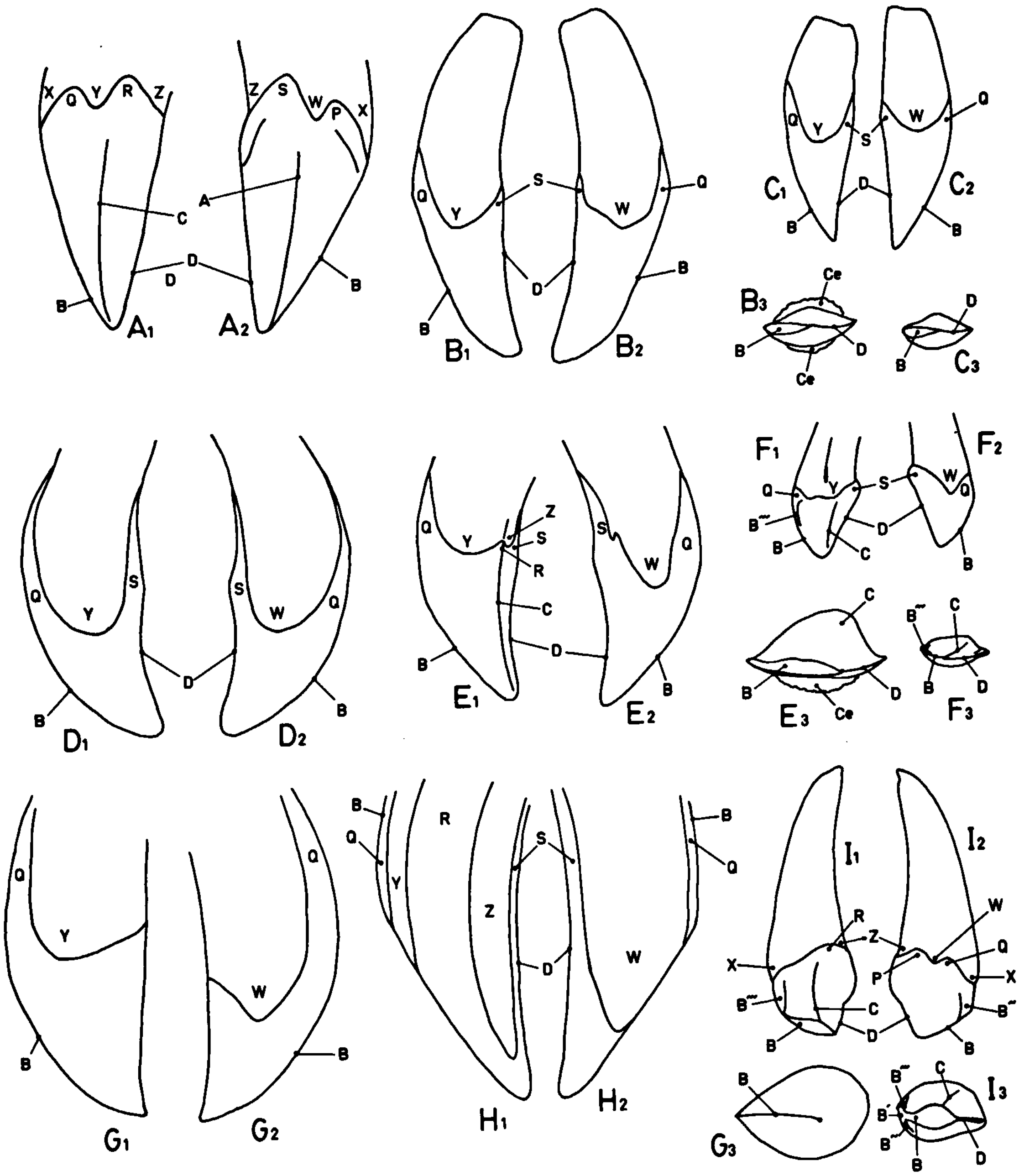


Fig. 12. Nomenclature of upper canines in Suoidea. *Tayassu pecari* (sex unknown; A), *Propalaeochoerus* sp. (♂; B), *Propalaeochoerus* sp. (♀; C), *Taucanamo* aff. *sansaniense* (probably ♂; D), *Hyotherium* sp. (♂; E), *Hyotherium* same sp. (♀; F), *Hyotherium meisneri* (♂; G), *Propotamochoerus* sp. (♂; H), *Microstonyx major* (♀; I) and apical views of *H. meisneri* and *M. major*. All right canines; A1, B1 etc. - lingual views; A2, B2 - labial views; B3, C3 - apical views. Legend: A - ectocrista, B - precrista, B' - preconulid, B''' - lingual prestyle, C - endocrista, Ce - cementum, D - postcrista, P - ectosyncline, Q - presyncline, R - endosyncline, S - postsyncline, W - ectoanticline, X -preanticline, Y - endoanticline, Z - postanticline.

palaeochoerids, there seem to be two (Text-fig. 12b-d) and in tayassuids four anticlines (Text-fig. 12a), which are named as in the premolars.

Nomenclature for the lower incisors

There is one cusp. From this cusp, three ridges may radiate, a mesial, a lingual and a posterior ridge (Text-fig. 13a, b). In analogy to the cusps of the molars, these ridges are called precristid, endocristid and postcristid. If a section of the cristids is separated from the cusp by a groove, they are called conulids, *e.g.* the preconulid.

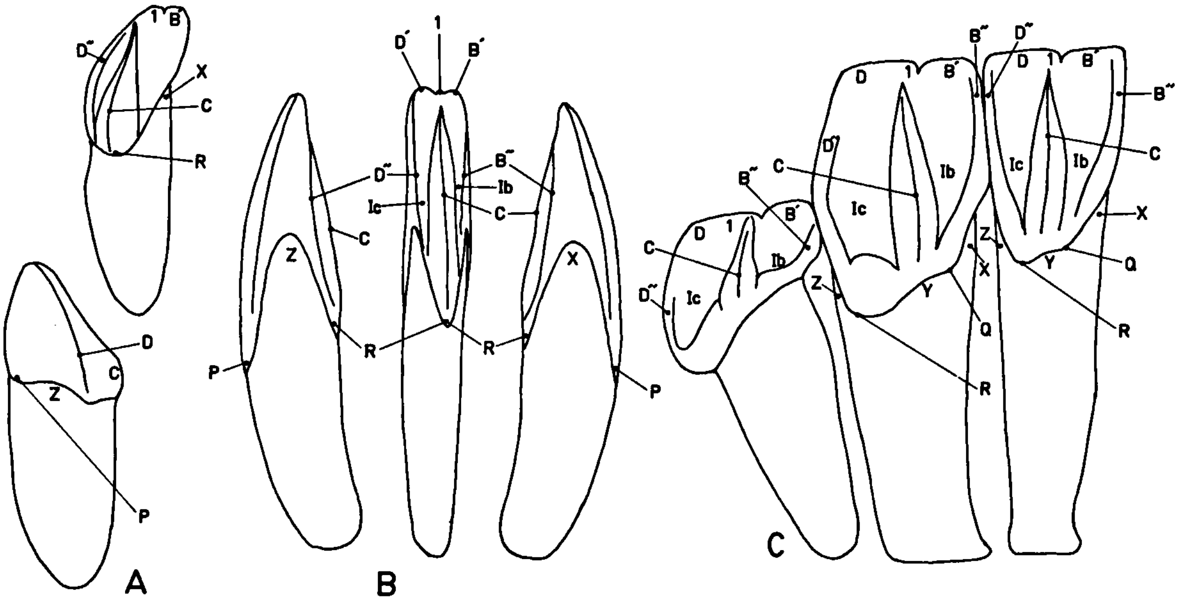


Fig. 13. Nomenclature of lower incisors. From left to right: I_3 of *Propotamochoerus* (lingual view top, distal view bottom; A), I_1 of *Microstonyx*, distal, lingual and mesial views (B), *Listriodon* I_1 - I_3 (C) (all Suidae, all left teeth). Legend: 1 - protoconid, B' - preconulid, B'' - prestylid, C - endocristid, D - postcristid, D' - postconulid, D'' - poststylid, X - preanticlinid, Y - endoanticlinid, Z - postanticlinid, P - ectosynclinid, Q - presynclinid, R - endosynclinid, Ib - prefossid, Ic - endofossid.

At the lingual side, the precristid and postcristid tend to form stylids, the prestylid and poststylid. In a very rare case a similar stylid is formed at the labial side, which might be called labial prestylid. However, such a stylid is an abnormality. Between the prestylid and endocristid, there is a valley, the prefossid and between the endocristid and the poststylid there is another valley, the postfossid. There may be something like a lingual cingulum or cusp in Listriodontinae, a thickening near the base of the posterocristid in the I_2 (Text-fig. 13c).

Nomenclature for the upper incisors

The I^1 and DI^1 are very much the same, although the deciduous tooth tends to be simpler. The milk tooth may lack a cingulum. The I^2, I^3 and DI^2, are very similar, although the I^2 tends to be more complex than the others. The first incisors have a different overall shape, in many taxa they are less elongate and more curved, but they have the same morphological elements as the other incisors. And even part of the elements have homologies in the lower incisors.

There is one main cusp which is here called paracone. This does not mean that it is assumed that the cusp is homologous to the paracone of the molars, but rather that it has some similarities in that it is the first cusp to develop and that it is anterior to a second cusp, if that is present. And such a second cusp is called metacone, for similar reasons. Three crests may radiate from the paracone, the paraprecrista, paraendocrista and the parapostcrista (Text-figs 14, 15). The paraendocrista usually is not well marked; it is a gentle elevation and in the I^1 it may become clearly visible, when a wear facet develops over it. The metacone may also have its crests, the metaendocrista and metapostcrista. In the majority of species, the precrista and postcrista of the I^1 and DI^1 form styles at the lingual side, the prestyle and poststyle. Occasionally a style is formed at the labial side; it may be called labial prestyle. As in the lower incisors, such a style is an abnormality. In the second and third incisors, cusplets may be formed near the main cusp, when small grooves divide the crests: the preconules and postconules. In the Listriodontinae, this occurs in the I^1 as well. There is a lingual cingulum, which may consist of a couple of small cusps, but is often smooth. In the I^1 or I^2 of some species there is one really large cusp on this cingulum. Such a cusp is here called protocone, but again, the name is given because of the similarity in position in premolars, and it is not argued here that it is homologous to that cusp.

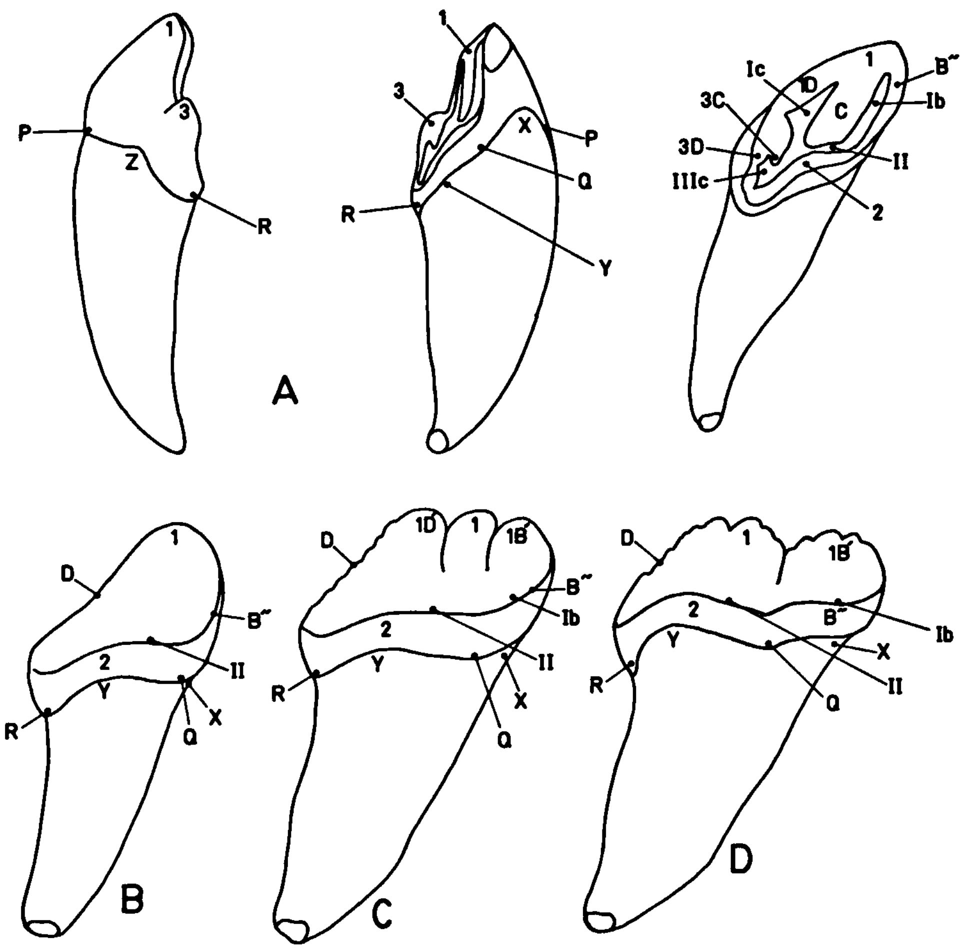


Fig. 14. Nomenclature of first upper incisors. From left to right, upper row: *Hyotherium soemmeringi* (A), labio-distal view, meso-lingual view, lingual view, lower row: primitive *Bunolistriodon* (B), advanced *Bunolistriodon* (C), *Listriodon* (D). All right I^1, all lingual views, all Suidae. Legend: 1 - paracone, 1B' -parapreconule, 1B" - paraprestyle, 1D - parapostcrista, 1D' - parapreconule, 1D" - paraprestyle, 2 - lingual cingulum and/or protocone, 2A - anterior lingual cingulum, 2D - posterior lingual cingulum, 3 - metacone, 3C - metaendocrista, 3D - metapostcrista, B - precrista, B' - preconule, B" - prestyle, C - endocrista, D - postcrista, D' - postconule, X - preanticline, Y - endoanticline, Z - postanticline, P - ectosyncline, Q - presyncline, R - endosyncline, Ib - (proto)prefossa, Ic - (proto)endofossa, II - basal fossa, IIIc - metapostfossa.

It should be noted however, that Butler (1941, p. 435) seemed to homologise such a cusp with the protocone of the molars. Here, these three names are applied topographically, rather than introducing new names and the question of homology is simply not addressed. It is not likely that this will lead to confusion.

A comparison of the listriodont I^1 and even more the I^2 of *Propotamochoerus* and *Sus strozzi* with the *Listriodon* I_3 will make the homologies within the category of the incisors clear (Text-figs 14, 15).

Abbreviations and definitions of measurements and ratios

All measurements in this paper are in mm. The way of measuring is indicated in Text-figs 16-21, where a number of representative teeth and bones are shown. Similar teeth or bones should be measured in a similar way. As a general rule it can be said that measurements are taken in such a way, that the callipers feel 'right'. This is the case when a distance between a point and a line or plane is measured. At one side of the bone or tooth, the beak of the callipers touches in two (line) or three (plane) points and at the other side at one point. The callipers also feel 'right' when the distance is taken between two points that are at opposing sides of a bone or tooth, and where the surface of the bone is perpendicular to the line connecting the two points.

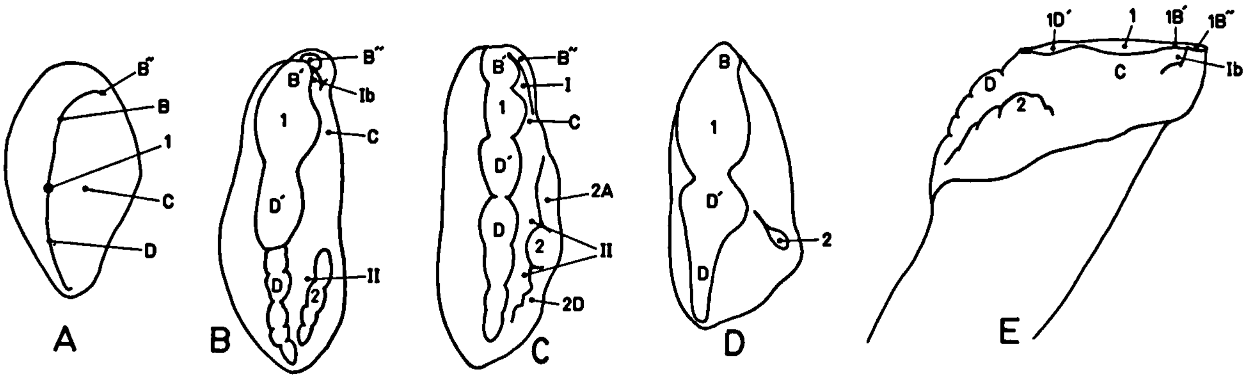


Fig. 15. Nomenclature of second and third upper incisors. From left to right *Hyotherium* (A), *Propotamochoerus* (B), *Sus strozzii* (C), *Potamochoerus* (D), all apical views and *Propotamochoerus*, lingual view (E). All Suidae, all right I^2, nomenclature of I^3 is identical. Legend: 1 - paracone, 2 - lingual cingulum and/or protocone, 2A - anterior lingual cingulum, 2D - posterior lingual cingulum, B - precrista, B' - preconule, B'' - prestyle, C - endocrista, D - postcrista, D' - postconule, Ib - prefossa, II - basal fossa.

d	Width of the facet for the cuboid in the astragalus (Text-fig. 21).
DAP	Antero-posterior diameter in cheek teeth (Text-figs 16, 17) or bones (Text-figs 19, 20, 21) ('length' in teeth, but not in limb bones). In cheek teeth and C_p DAP is measured parallel to the occlusal plane. The most anterior and most posterior points are not necessarily at the same level, compared to the occlusal plane or compared to the base of the crown. In M^x the DAP is measured perpendicular to the anterior side of the tooth. In skewed molars, this is not the connection between the middle of the anterior and the middle of the posterior sides. In M^3, this is not the connection between the middle of the anterior side and the most distal point of the talon. Since in D^4 the anterior side of the tooth is oblique, DAP is measured along the (supposed) axis of the tooth row. DAP in cheek teeth, especially in M2 and M3, is affected by wear. The DAP of the symphysis of the mandible is measured from the rim of the alveolus of the I_1 to the posterior end in the middle.
DAP'	Length of a tooth expressed as a percentage of the length of the first molar DAP' = (DAP/DAP M1) x 100% (for upper teeth the length of the M^1 is used as a standard, for lower teeth the M_1). An indication of the variation of this value in a large sample of Recent *Sus scrofa vittatus* from Deli (Sumatra) is given by Guan & Van der Made (1993, fig. 8).
DAP''	Antero-posterior diameter of a Cm expressed as a percentage of the width of the second molar DAP'' = (DAP Cm/DAP M2) x 100%. Van der Made & Han (1994, fig. 12) gave an indication of the variation of this index in a sample of Recent *Sus scrofa vittatus* from Deli (Sumatra).
DAP*	Length of a Cm expressed as a percentage of the length of the second molar DAP* = (DAP Cm/DAP M2) x 100%. Van der Made & Han (1994, fig. 12) gave an indication of the variation of this index in a sample of Recent *Sus scrofa vittatus* from Deli (Sumatra).
DAPd	Distal antero-posterior diameter in a bone (Text-figs 19, 20, 21).
DAPdf	Antero-posterior diameter of a facet at the distal side of a bone (Text-fig. 19).
DAPn	Anteroposterior diameter at the 'neck' of a bone (Text-fig. 19).
DAPp	Proximal antero-posterior diameter in a bone (Text-figs 19, 20, 21).
DAPpf	Antero-posterior diameter of a facet at the proximal side of a bone (Text-fig. 19).
DAPps	Maximum diameter of a bone at the proximal side (Text-fig. 19).
DLL	Linguo-labial diameter in incisors (Text-figs 16, 17).
DLL'	Linguo-labial diameter expressed as a percentage of the width (DT or, preferentially, DTp in lowers and DTa in uppers) of the first molar DMD' = (DLL Ix/DT M1) x 100 %.
DLL''	Linguo-labial diameter expressed as a percentage of the width (DT or, preferentially, DTp in lowers and DTa in uppers) of the second molar DMD'' = (DLL Ix/DT M2) x 100 %.
Dmax	Maximum diameter of the crown in I_3 (Text-fig. 16) or maximum diameter in a bone (Text-fig. 19).
DMD	Meso-distal diameter in incisors (Text-figs 16, 17).
DMD'	Meso-distal diameter expressed as a percentage of the width (DT or, preferentially, DTp in lowers and DTa in uppers; not DAP, as by Van der Made,

	1994a, fig. 3) of the first molar DMD' = (DMD Ix/DT M1) x 100 %.
DMD''	Meso-distal diameter expressed as a percentage of the width (DT or, preferentially, DTp in lowers and DTa in uppers) of the second molar DMD'' = (DMD Ix/DT M2) x 100 %.
DMDo	Meso-distal diameter of I^1, measured along the occlusal surface either as a total length of the crown or of the occlusal surface (Van der Made & Han, 1994, fig. 2).
DT	Transverse diameter ('width') of a cheek tooth or bone. If nothing else (DTa, DTp etc.) is indicated, usually maximum width. In cheek teeth, it is measured as the greatest distance between lingual and labial sides of the tooth, usually, but not necessarily close to the base of the crown. This measurement is usually not affected by wear of the teeth, until nearly all of the crown is worn away.
DT'	Width of a tooth expressed as a percentage of the width of the first molar DT' = (DT/DT M1) x 100% An indication of the variation of this value in a large sample of Recent *Sus scrofa vittatus* from Deli (Sumatra) is given by Guan & Van der Made (1993, fig. 8).
DT''	Width of a Cm expressed as a percentage of the width of the second molar DT'' = (DT Cm/DT M2) x 100%. Van der Made & Han (1994, fig. 12) gave an indication of the variation of this index in a sample of Recent *Sus scrofa vittatus* from Deli (Sumatra).
DT*	Width of a Cm expressed as a percentage of the length of the second molar DT* = (DT Cm/DAP M2) x 100%. Van der Made & Han (1994, fig. 12) gave an indication of the variation of this index in a sample of Recent *Sus scrofa vittatus* from Deli (Sumatra).
DTa	Width of anterior lobe of a cheek tooth (Text-figs 16, 17). In the P^2 and P^3 of the listriodonts, this measurement is difficult to take in a consistent way and thus less reliable.
DTd	Transverse diameter ('width') of a bone at the distal side (Text-figs 19-21).
DTdf	Transverse diameter ('width') of a facet at the distal side of a bone (Text-fig. 19).
DTm	Width of the middle lobe in D_4.
Dtmax	Maximum transverse diameter ('width') of a bone (Text-fig. 19).
DTp	Transverse diameter ('width') of the second lobe of a cheek tooth (Text-figs 16, 17), or in a bone, the proximal 'width'.
DTpf	Transverse diameter ('width') of a facet at the proximal side of a bone (Text-fig. 19).
DTpp	Width of third lobe (Text-figs 16, 17). In M^3 with small talons, this measurement is difficult or impossible to take in a consistent way.
Flun	Width of the facet for the (semi)lunar (Text-fig. 19).
Fma	Width of the facet for the magnum (Text-fig. 19).
Fsca	Width of the facet for the scaphoid (Text-fig. 19).
Fun	Width of the facet for the unciform (Text-fig. 19).
H	Height of a bone (Text-figs 18, 19, 21).
Ha	Height of a molar at the anterior lobe at the lingual side in M_x (Text-fig. 16) and at the buccal side in M^x (Text-fig. 17). Height of a bone at the anterior side (Text-figs 19, 21).
Hdist	Height of an incisor at the distal side (Text-fig. 16).
Hla	Height of an incisor at the labial side (Text-figs 16, 17), or of a premolar at the buccal side. In premolars, the measurement is between a line through the two lowest points of the crown and the tip of the crown.
Hli	Height of an incisor or premolar at the lingual side (Text-figs 16, 17). In premolars, the measurement is between a line through the two lowest points of the crown and the tip of the crown.
Hmes	Height of an incisor at the mesial side (Text-figs 16, 17).
Hp	Height of a molar at the posterior lobe at the lingual side in M_x (Text-fig. 16) and at the buccal side in M^x (Text-fig. 17).
I	Index (DAP/DT) x 100% or (DMD/DLL) x 100%.
L	Length of a bone in proximo-distal direction (Text-figs 19-21). The extremes of the bone are often not two points on one line of this direction.
l	Alternative length of a bone, usually excluding fragile projections (Text-figs 19-21).
La	Width of the labial side of the C_m (Text-fig. 16). The limit of the enamel is not necessarily the limit of the labial side.
La''	Width of the labial side of the C_m as a percentage of the width of the M_2.
Ld	Length of the lower part of a bone (Text-fig. 21).
Lext	Length of a bone at the external side (Text-fig. 21).
Li	Width of the lingual side of the C_m (Text-fig. 16). The limit of the enamel is not necessarily the limit of the lingual side.
Li''	Width of the lingual side of the C_m as a percentage of the width of the M_2.
Lint	Length of a bone at the internal side (Text-fig. 21).
Lm	Length of a bone in the middle (Text-fig. 21).
Lu	Length of the upper part of a bone (Text-figs 19, 21).
Po	Width of the posterior side of the C_m (Text-fig. 16). The limit of the enamel is not necessarily the limit of the posterior side.
Po''	Width of the posterior side of the C_m as a percentage of the width of the M_2.
R	Diameter in an astragalus (Text-fig. 21).
R1	Diameter in the humerus (Text-fig. 19).
R2	Diameter in the humerus (Text-fig. 19).
R3	Diameter in the humerus (Text-fig. 19).
R4	Diameter in the humerus (Text-fig. 19).

Ri	Radius of curvature in male canines measured from the inner side (Text-fig. 17). The canines are in reality spirals; when growing, the upper canines become usually tighter and the lower canines more open. A section that is not close to the tip of a canine may resemble a circle. Measurements further from the tip are preferred here.
Ro	Radius of curvature in male canines measured from the outer side (Text-fig. 17). See remarks with Ri.
SD	Standard deviation.
Ta	Thickness of enamel measured at the metaconid (Text-fig. 16).
Tp	Thickness of enamel measured at the entoconid (Text-fig. 16).
V'	Measure of variability (Freudenthal & Cuenca Bescos, 1984):

$$V' = \frac{200 \text{ x } (\text{maximum-minimum})}{(\text{maximum+minimum})}$$

Lengths, widths of the skull, mandible, atlas and axis are indicated in Text-fig. 18 as are lengths of diastemata and depth of mandible.

Abbreviations

AVP	Accademia Valdarnese del Poggio (Montevarchi).
BMNH	Natural History Museum (London).
BNHM	Beijing Natural History Museum.
BSPHGM	Bayerische Staatssammlung für Paläontologie und historische Geologie (München).
CCL	Collection Carlos Langa (Daroca).
CEPUNL	Centro de Estratigrafia e Paleobiologia da Universidade Nove de Lisboa.
CFE	François Escuillé Collection (Lyon).
CJFV	J.F. de Villalta Collection (Barcelona).
COBO	Olivier Bardot Collection (Orléans).
CTMO	Thierry Mulder Collection (Orléans).
DSTT	Dipartimento di Scienze della Terra, Università degli Studi di Torino.
FISF	Forschungsinstitut Senckenberg (Frankfurt am Main).
FMNH	Finnish Museum of Natural History (Helsinki).
GSP	Geological Survey of Pakistan (Islamabad).
HGSB	Hungarian Geological Survey (Budapest).
HGSP	Howard-Geological Survey of Pakistan Project, material will be stored in GSP.
HLD	Hessisches Landesmuseum (Darmstadt).
IGF	Istituto di Geologia (Firenze).
IM	Indian Museum (Calcutta).
IMGURP	Istituto e Museo di Geologia della R. Università di Padova.
IPS	Institut Paleontològic Dr. M. Crusafont (Sabadell).
IPUW	Institut für Paläontologie der Universität (Wien).
ITGE	Instituto Technológico y Geominero de España (Madrid).
IVAU	Instituut voor Aardwetenschappen (Utrecht).
IVPP	Institute for Vertebrate Paleontology and Paleoanthopology, Academia Sinica (Beijing).
KNM	Kenya National Museums (Nairobi).
MGL	Museum Guimet (Lyon).
MGSP	Museum of the Geological Service of Portugal (Lisbon).
MHNCHF	Musée d'Histoire naturelle (La Chaux-de-Fonds).
MHNT	Muséum d'Histoire naturelle Toulouse.
MLGSB	Museu i Laboratori de Geologia del Seminari (Barcelona).
MNCN	Museo Nacional de Ciencias Naturales (Madrid).
MNHN	Muséum national d'Histoire naturelle (Paris).
MPV	Museo Paleontológico de Valencia.
MPZ	Museo Paleontológico de la Universidad de Zaragoza.
MSNO	Muséum des Sciences naturelles (Orléans).
MTA	Maden Tetkik ve Arama (Ankara).
NMB	Naturhistorisches Museum Basel.
NMBe	Naturhistorisches Museum Bern.
NMM	Naturhistorisches Museum Mainz.
NMW	Naturhistorisches Museum Wien.
NNML	Nationaal Natuurhistorisch Museum (Leiden).
NSSW	Naturwissenschaftliche Sammlungen der Stadt Winterthur.
PIMUZ	Paläontologisches Institut und Museum der Universität (Zürich).
PDTFAU	Paleoantropoloii, Dil ve Tarih Cografya Faccultesi, Ankara Universitesi.
PMNH	Pakistan Natural History Museum (Islamabad).
RGM	Rijksmuseum voor Geologie en Mineralogie, now Nationaal Natuurhistorisch Museum (Leiden).
RMNHL	Rijksmuseum voor Natuurlijke Historie, now Nationaal Natuurhistorisch Museum (Leiden).
SMNS	Staatliches Museum für Naturkunde (Stuttgart).
UCBL	Université Claude Bernard (Lyon).
UCM	Universidad Complutense (Madrid).
UN	Université de Neuchâtel.
UPM	Laboratoire de Sédimentologie et Paléontologie, Université de Provence (Marseille).
UPVB	Departamento de Geología, Facultad de Ciencias, Universidad del País Vasco (Bilbao).
ZMA	Zoologisch Museum (Amsterdam).

STRATIGRAPHY

The Listriodontinae have a fossil record from about 20 to 9 Ma, *i.e.* early, middle and early Late Miocene, or the Ramblian, Aragonian and Vallesian stages.

In the following sections, local stratigraphy is reviewed. Special attention will be paid to details of lithostratigraphy and biostratigraphy that yield more precise data on the ages of listriodont localities relative to each other, than do the current schemes.

Radiometric dates are valuable information.

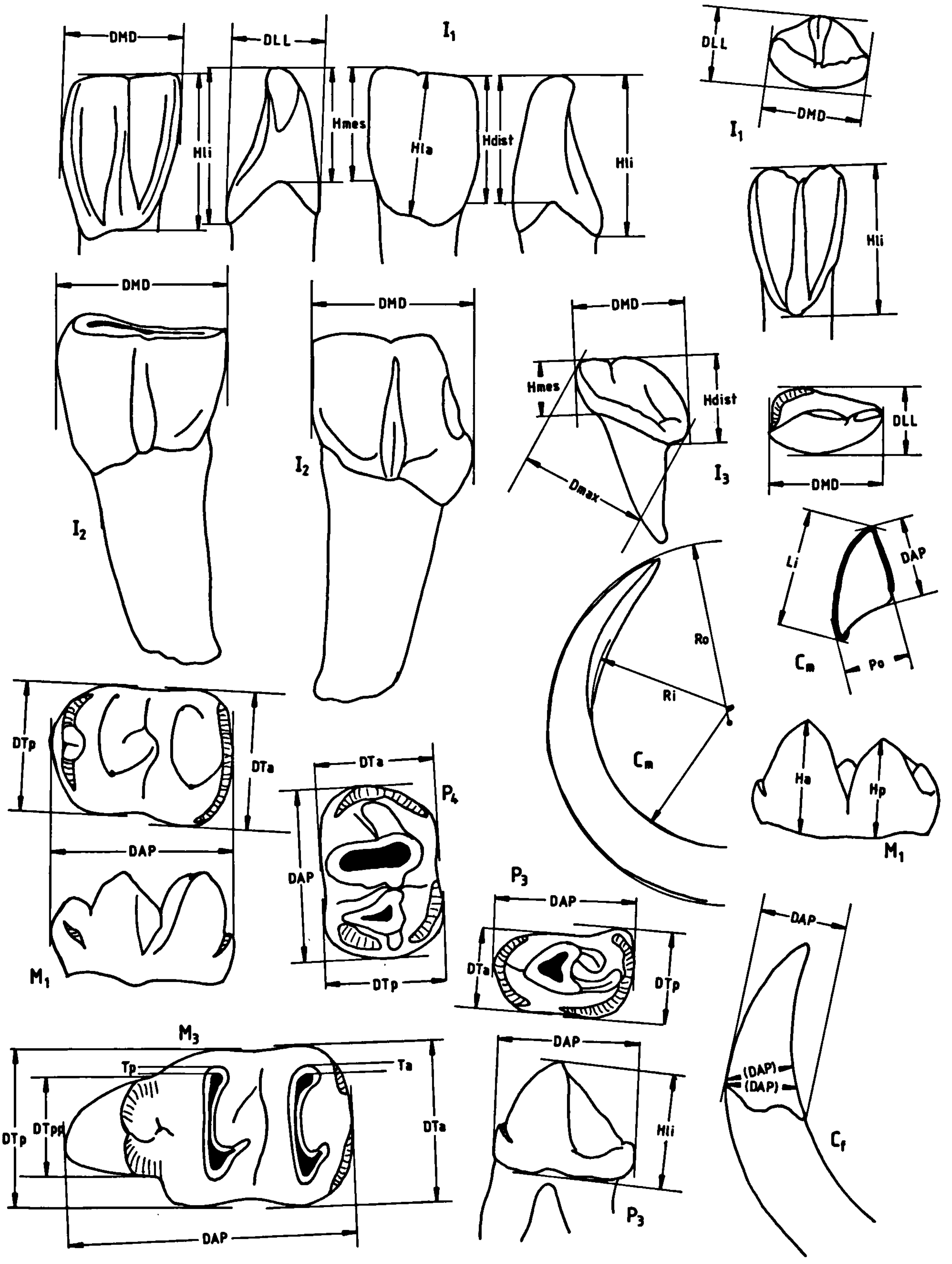


Fig. 16. Measurements of lower teeth. P_3 is also representative of P_1, P_2, D_2 and D_3, M_1 of M_2 etc. See section on abbreviations and definitions of measurements.

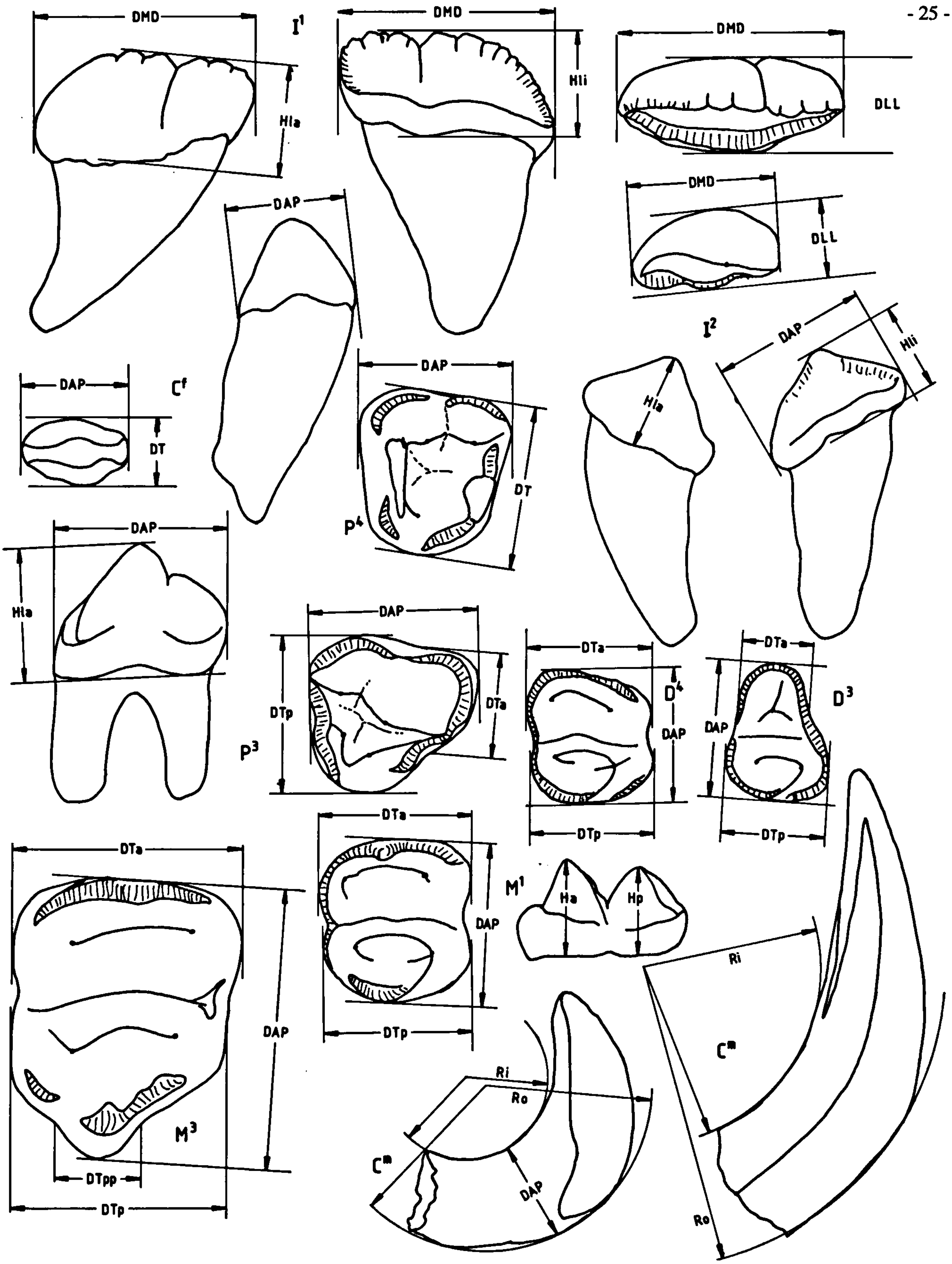


Fig. 17. Measurements of upper teeth. I¹ is also representative of DI¹, I² of I³, DI² and DI³ etc. See section on abbreviations and definitions of measurements.

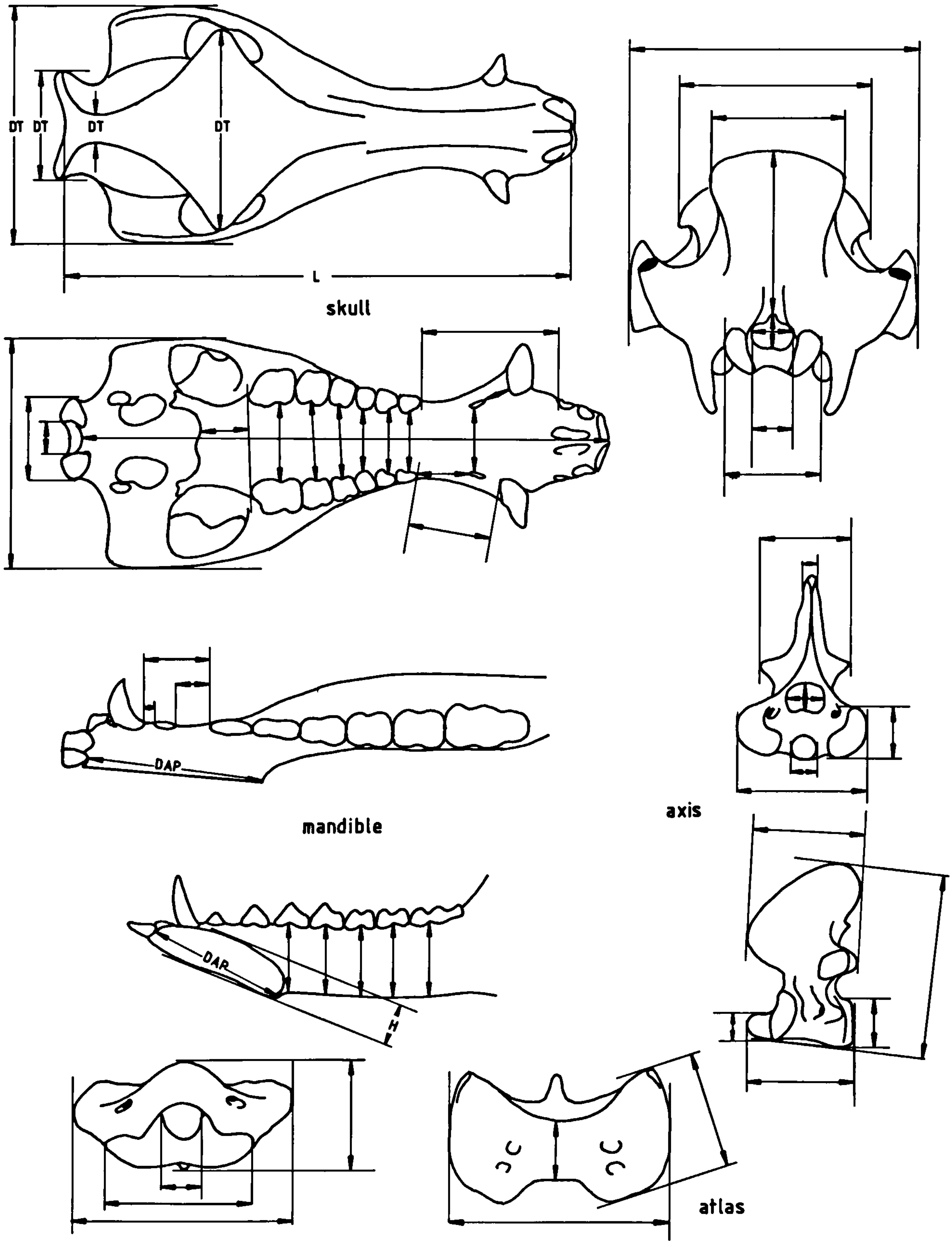


Fig. 18. Measurements of skull, mandible, atlas and axis. See section on abbreviations and definitions of measurements.

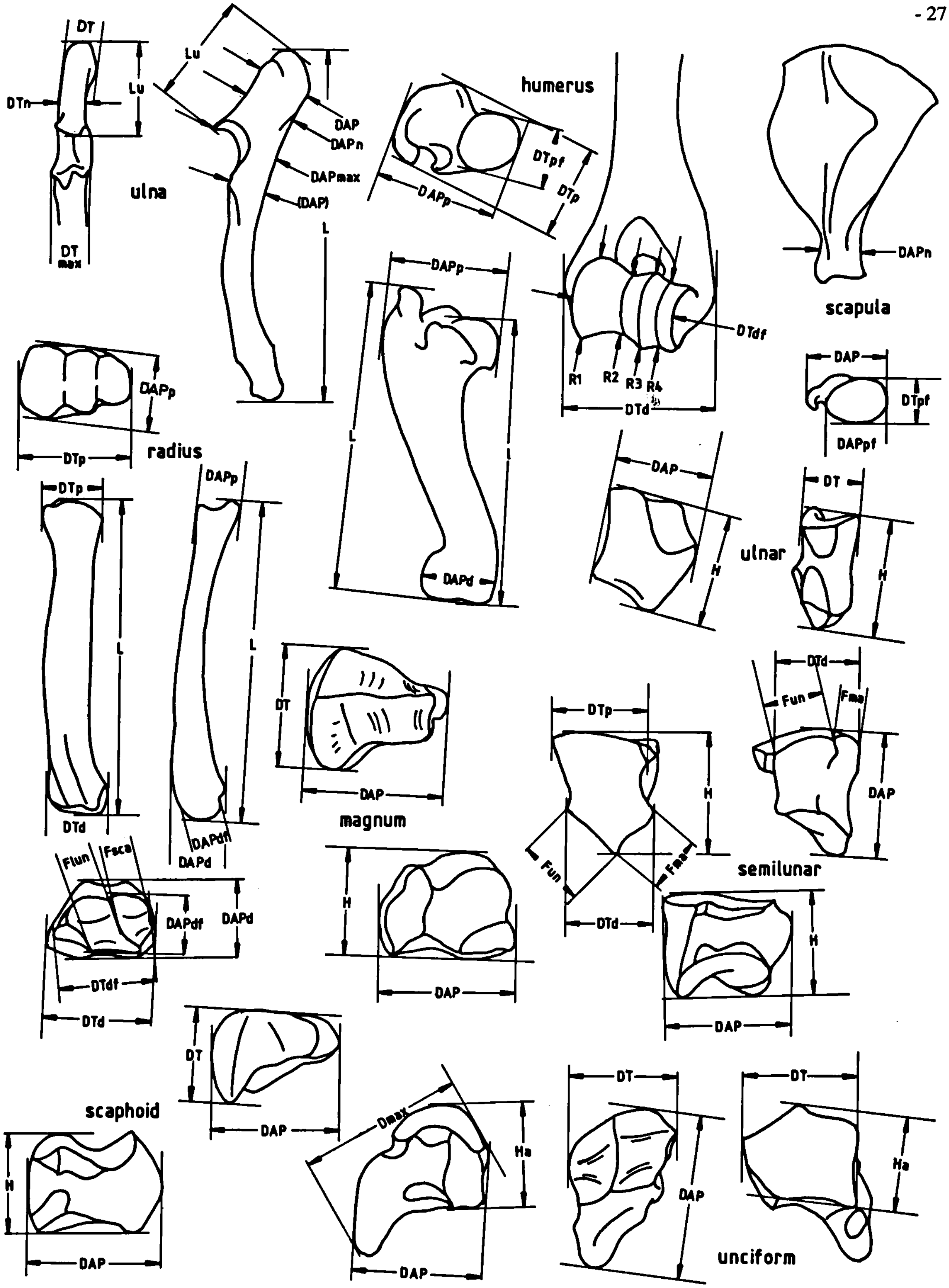


Fig. 19. Measurements of long bones of fore limb and of carpals. See section on abbreviations and definitions of measurements.

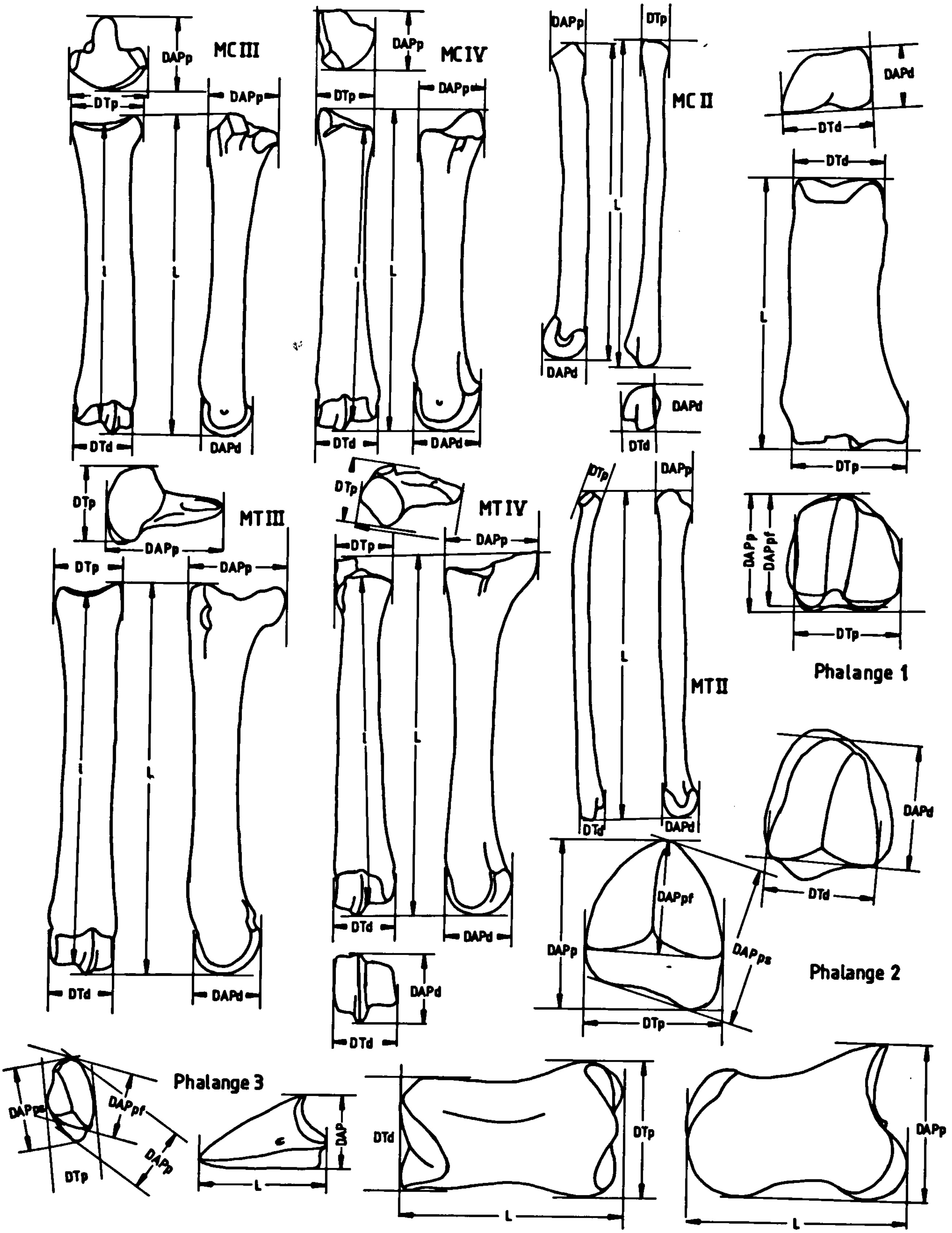


Fig. 20. Measurements of metapodials and phalanges. See section on abbreviations and definitions of measurements.

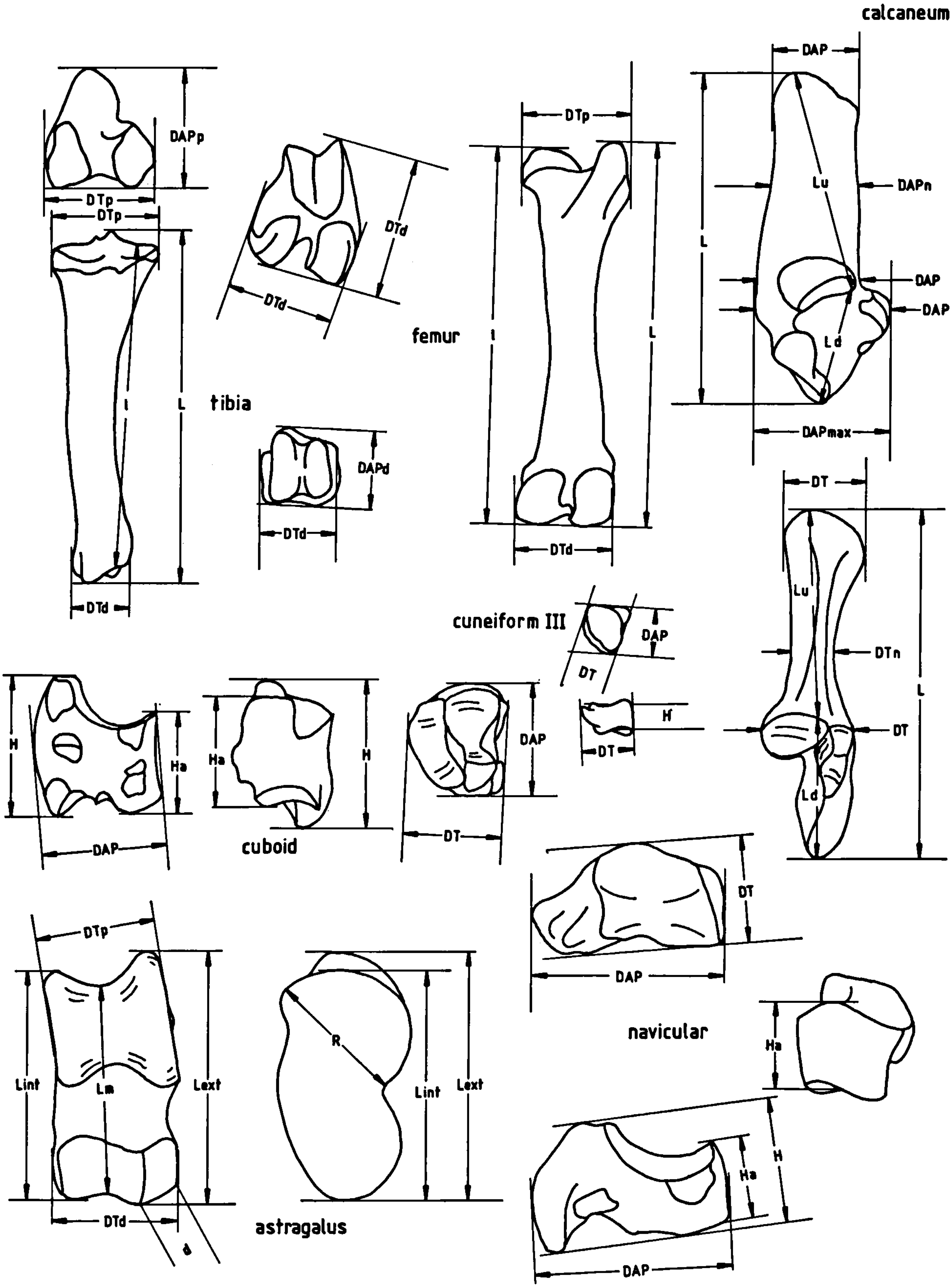


Fig. 21. Measurements of long bones of hind leg and of tarsals. See section on abbreviations and definitions of measurements.

If such information is available for a locality, it is given in the tables of localities in the section 'Systematic descriptions'. It should be borne in mind that occasionally the connection between the fossils and the dated rock or mineral is a source of errors. In addition important information tends to get lost: an overlying rock gives an age of 15 Ma, the fossils are >15 Ma old and what is often repeated in the literature is just the age of 15 Ma. Here, radiometric or palaeomagnetic dates are given, but are used only after the biostratigraphy section. If radiometric dates are used in phylogeny or biostratigraphy, this may lead in the final synthesis to a way of circular reasoning, difficult to detect.

MN Units

The MN units (MN for Mammal and Neogene) were first proposed as biozones (Mein, 1975a). The system evolved (Mein, 1975b, 1977, 1979, 1990; De Bruijn *et al.*, 1992) and was subsequently applied not as true biozones but as time units. The units are thought of as a continuum, without sharp limits, though limits are usually indicated in the graphs and the position of a locality seems to be changed more easily within a unit than to a next unit.

Each unit has its reference locality, which does not need to be in the centre of the unit, but may be closer to the transition to the following or preceding unit (as in the case of Sansan, MN 6). Reference localities have been changed several times and now most of the original reference localities are used again. This does not affect the system much, since its most stable part seems to be the part of the chart with the localities arranged to MN unit, and this seems to define the MN units truly. Many units were later subdivided, but most subdivisions have been suppressed and MN 7 and MN 8 have even been combined. Here, indications are used such as MN 4l or MN 4 late, if such an indication seems appropriate and MN 8 is used instead of MN 7+8 late. Such use is meant to be informal. Indications like MN 4a, MN 5a, which are cited, are given as such.

The definitions of MN 3 and 4 were changed for a brief period. Artenay was placed originally in MN 4a. Later (Mein, 1979), it was transferred to the newly created MN 3b (Text-fig. 61). At that time, the earlier part of MN 4 was marked by a number of entries including that of *Bunolistriodon*. Now Artenay is placed again in MN 4.

Besides the temporal use of *Bunolistriodon* in recognition of the beginning of MN 4, it was used to mark the end of MN 5. Along with only a few other criteria, Mein (1979) used the extinction of *Bunolistriodon* to define the passage from MN 5 to MN 6. In MN 6, it is replaced by *Listriodon splendens*. Some localities in SE Europe and Anatolia have yielded a specialised *Bunolistriodon* along with *Listriodon*. This *Bunolistriodon* belongs to another lineage than the typical *B. lockharti*. These localities are placed in MN 6.

Agustí & Moyà-Solà (1991) proposed to divide MN 6 and combine the later part (including the localities Manchones, Arroyo del Val and Paracuellos 3) in MN 7. Indeed there seem to be more important faunal changes within MN 6 than between MN 6 and MN 7. But for the sake of stability, Agustí & Moyà-Solà's scheme is not adopted here.

The MN units have been used in close connection to the Agenian stage (MN 1 + 2), the Aragonian superstage with the Orleanian (MN 3-5) and Astaracian (MN 6-8) stages and the Catalanian superstage with the Vallesian (MN 9-10) and Turolian stages and the Ruscinian and Villafranchian and the entries of *Anchitherium* (MN 3) and *Hipparion* (MN 9) (Mein, 1977). Several of these stages have never been well defined. The Aragonian is discussed in the next section.

The MN units have originally been defined for Europe and North Africa, though they are applied to localities in Pakistan (Wessels *et al.*, 1982, 1987) and China (Qiu, 1990).

There have been many attempts to correlate MN units to the marine scales and to localities or sequences with radiometric or palaeomagnetic control. Recent overviews are by Steininger *et al.* (1990) and Berger (1992).

Spain and Portugal

Several continental stages were defined in Spain. The Ramblian (Early Miocene; defined near Navarrete del Rio, Teruel), the Aragonian (Early and Middle Miocene; near Daroca, Aragon) and the Vallesian (early Late Miocene; Valles Penedes) cover the study period.

The **Aragonian** was first meant to be a superstage comprising the stages Orleanian and Astaracian, but when it was formally published, it was done so as a stage (Daams *et al.*, 1977). The localities of **Arroyo del Val** (I-VI) and **Murrero** (= Paridera de Venacecquia) near Daroca can be lithostratigraphically correlated to the type section. The localities of **Munébrega I & III** and **Armantes I** in the Calatayud area were used to define the lower part of the Aragonian. Daams *et al.* (1987) introduced the **Ramblian**, which comprises part of what formerly was the Aragonian. In the process, they redefined the lower limit of the Aragonian as well as the lower limit of the middle Aragonian. By now, the Calatayud-Daroca area is one of the richest in Aragonian localities (Freudenthal, 1988).

Daams & Freudenthal (1981) introduced a biozonation of the Aragonian and part of the Vallesian (zones A-I). This biozonation was extended to the Ramblian (zone Z; Daams *et al.*, 1987) and current work extends it to the Oligocene.

In Spain, this zonation reflects better the evolution of the faunas than do the MN units. Outside Spain, MN units are usually applied.

An introduction to the localities of the Madrid area may be found in Alberdi *et al.* (1985a, b). The cervid *Heteroprox* from **Puente de Vallecas** and **Paracuellos 5** (Madrid area) is replaced by a different species in **Paracuellos 3, Manchones** and **Arroyo del Val** (Azanza, 1989). This suggests that the former group of localities are older than the latter group.

The Lisbon area has interfingering marine (prefix C) and terrestrial (prefix R) sediments ranging from the earliest Miocene (21 Ma) to the Vallesian (Antunes, 1984). The different biostratigraphical units are numbered (Roman numeral). In sequence (with only the biostratigraphical units with terrestrial mammals): C0 marine, 21 Ma — Lisbon I (R0) terrestrial — C1 marine — **Lisbon II** (R1) is terrestrial and has localities that are placed in MN 3a — Lisbon III and IVa (C2) marine with foraminifera of Blow zones N5 to 7 — **Lisbon IVb** (R2) MN 3b — Lisbon Va1 (C3) with forams of N8 — **Lisbon Va2** (R3) MN 4a — Lisbon Va3 (C4) with N8 forams — **Lisbon Vb** (R4) MN 4b/5 — above this there are mammal localities at any level and foraminifera of zones N9 to N15 or N16.

A synopsis of the litho- and biostratigraphy of the Valles Penedes was given by Agustí *et al.* (1984). The localities of **Can Julià, Sant Mamet** and **Martí Vell** are reported to be overlain by transgressive sediments with N7-8 foraminifera, though in the original study of the foraminifera only N8 was indicated (Anglada & Martín, 1971). **El Canyet** is reported to be of the same age. The localities of **Sant Quirze** (lower) and **Can Ponsic** (upper) are in superposition. The same is the case with **Castell de Barberá, Santiga** and **Can Llobateres**. The **Vallesian** was defined in this area.

The earliest collections at Hostalets (or Hostalets de Pierola) were from a large area. Later it was recognised that there are two different levels in this area, one with *Hipparion* and one without. Now more precise locality names, such as Can Mata, are used (Agustí, pers. comm.). The older collections are thus a mixed sample. **'Hostalets'** is here placed in text-figures at the MN 8/9 transition, but may hold specimens older or younger than that position.

Moyà-Solà & Agustí (1990) grouped localities using artiodactyls and rodents and placed **Sant Quirze** below **Castell de Barberà**.

France

Richard (1946) presented an extensive overview of localities in the Aquitaine Basin, their fauna and lithostratigraphy and the literature, as well as a synthesis of trans- and regressions in the area and the changing coast lines as indicated by sediments and mammal localities. In this basin, the marine stages Aquitanian and Burdigalian were defined. Hugueney & Ringeade (1990) correlated a number of mammal localities of MN 2 to the type Aquitanian. Ginsburg (1971) and Bulot (1986) supplied additional data on faunas of the Aquitaine Basin. There is a very detailed lithostratigraphy giving a series of localities in superposition. Localities with listriodonts from old to young are: **Pellecahus, Bézian, La Romieu** (Sablière Pujos = Soucaret, Depéret's first excavation, Freudenthal's sample), La Romieu (Labadie & Sablière Cecile, Depéret's classic locality, Collier's excavation), **Castelnau-d'Arbieu** (= Le Mouné + Birosse), **Sansan**, Rajegats, **Castelnau-Barbarens** and **Simorre** and **Villefranche d'Astarac**. Richard (1946) also noted the geographical heights of the localities: since strata are essentially horizontal, it is used as an indication of age. This gives the following sequence: **L'Isle-en-Dodon, Boulogne-sur-Gesse** and **Escanecrabe** in Bas-Comminges.

Ginsburg (1992) presented the stratigraphy of the Orelanian of the Loire basin. The localities are placed in order: **Artenay**, Aérotrain, **Baigneaux-en-Beauce, Beaugency-Tavers, Pontlevoy-Thenay** and Faluns de Touraine et de l'Anjou. Ginsburg & Morales (1992) studied the mustelids and derived *Iberictis azanzae* Ginsburg & Morales, 1992 at Bézian and Baigneaux in France and **La Artesilla** in Spain) from *Iberictis buloti* Ginsburg & Morales, 1992 (at Pellecahus).

At La Grive there are several fissures in the Carrière Peyre et Beau, Carrière Milliet (La Grive M) and in the Carrière Lechartier (La Grive L, various localities). They range from MN 6 and are slightly older than Sansan (Peyre et Beau), MN 7 (La Grive M) and MN 8 (**La Grive** L3, **L7**) (Guérin & Mein, 1971). Of specimens in old collections (here called **La Grive oc**) the exact provenance is not known, but most appear to be of MN 7 age.

Central Europe

Heizmann (1992) presented a review of the lithostratigraphy of the SW German Molasse and its most important fossil localities. A summary is given here. The Untere Süsswassermolasse (USM) and Obere Meeresmolasse (OMM) are unconformably overlain by the Süssbrackwassermolasse (SBM) and Obere

Süsswassermolasse (OSM). The SBM comprises the basal Grimmelfinger Schichten and the Kirchberger Schichten. The OSM is divided into an older, middle and younger series. The localities of **Grimmelfingen, Gerlenhofen** and **Langenenschlingen** are in the Grimmelfinger Schichten. This unit locally has the oldest *Deinotherium*. **Langenau 1 & 2** are two localities in the same bed, but on opposite sides of a valley (Heizmann, pers. comm.). The locality is in the Kirchberger Schichten. The locality of **Engelswies** is in the transition of the Kirchberger Schichten to the lower unit of the OSM and is still younger than Langenau. **Ravensburg** is in the middle unit of the OSM, and as it still has *Bunolistriodon lockharti*, it is MN 5.

An overview of localities and the stratigraphy of the Obere Süsswassermolasse in Bayern is given by Heissig (1989). There are a great number of localities with micromammals and some with large mammals, including **Stätzling**. In this area, the 'Brockhorizonte' is found, a lithostratigraphical marker, with MN 6 localities above and below. Stätzling is above the marker.

Stehlin (1937) reviewed localities near **La Chaux-de-Fonds** and **Locle** (Switzerland). At Crêt-du-Locle, an isolated horn core of *Tethytragus* was found. This is not the same locality near Locle that yielded *Listriodon*. De Bruijn *et al.* (1992) probably applied the name Crêt-du-Locle for the locality La Chaux-de-Fonds, which is the richest locality in the area.

Klein Hadersdorf (Austria) was placed in MN 8 on the basis of the presence of *Tethytragus stehlini* (Mein, 1986), represented at this locality only by horn cores. *Tethytragus* Azanza & Morales, 1994 (a new name for *Caprotragoides*) from Paşalar, Çandir and La Grive are brachyodont, those from Arroyo del Val and Manchones are more hypsodont. Moreover, there are size differences (Van der Made, 1994b). There are probably two lineages and it is not clear to which the horn cores from Klein Hadersdorf belong. In any case, the genus seems to be restricted to MN 6 and MN 7.

There are two localities in **Eichkogel** (Höck, pers. comm.), the MN 11 locality being well known. In addition there is an MN 6 locality, with *Listriodon* and *Dicrocerus*. Vacek (1900) described material from both localities as if it were a single fauna.

Mottl (1970) reviewed Styrian fossil localities, their fauna, literature references and geology.

Steininger & Rögl (1985), Steininger *et al.* (1985) and Steininger (1986) presented correlations of marine and terrestrial deposits of the Mediterranean and Paratethys as well as palaeogeographical reconstructions. In this area, the same transgressions are found as in the Aquitaine Basin and some of them also in the southern German Molasse Basin. In these sediments, a number of stages were defined, in ascending order: Eggenburgian, Ottnangian, Karpatian, Badenian, Sarmatian and Pannonian, which cover the time interval studied.

Turkey

A comprehensive overview of Turkish fossil localities, their stratigraphy and mammalian faunas is given by Sickenberg (1975). The localities are placed in 'Faunengruppen' (faunal units), which were correlated to the MN units: Paşalar(MN 6), **Çandir** (MN 6), Sofça (MN 7), Yeni Eskihisar (MN 8), Eşme-Akçaköy (MN 9). The pollen record of the area was studied in detail, in some cases from the same localities as the mammals (Sickenberg, 1975; Benda & Meulenkamp, 1990).

China

A subdivision and tentative correlation of the Chinese Neogene was documented by Li *et al.* (1984), who recognised the Xiejian, Shanwangian, Tunggurian and Bahean, which were correlated with the Agenian, Orleanian, Astaracian and Vallesian, respectively. They placed Dongshapo (**Tung Sha-po**) and **Lengshuigou** (= Lishan?) (both with *Listriodon*) in the Shanwangian and **Erlanggang** (with *Bunolistriodon*), Lierbao, **Tung Gur** (with *Listriodon*), Tongxin (with *Bunolistriodon* and *Kubanochoerus gigas lii*) and **Koujiacun** (with *Bunolistriodon* and *Kubanochoerus g. gigas*) in the Tunggurian. In the section on stratigraphical results below, some changes in the relative ages of these localities will be proposed.

At **Tongxin**, there are several fossiliferous levels and many localities (Guan, 1988; Guan *et al.*, 1981). Wherever Tongxin, Dingjiaergou or Maerzuizigou is mentioned in the present paper, the level with *Kubanochoerus gigas* is referred to (Guan & Van der Made, 1993).

Qiu (1990) correlated the Chinese localities with the MN scale. Tongxin, Koujiacun, and Quantougou (Chuan Tou Kou, type locality of *K. gigas*) were placed in the Tunggurian and correlated with Belometchetskaia, which was believed to be MN 6 (or 5). Lengshuigou (with *Listriodon*) was thought to be slightly younger than Tongxin. Halamagai and Erlanggang were assumed to be still younger, but not yet of Bahean (Vallesian) age.

At **Halamagai** there are two fossiliferous levels (Tong *et al.*, 1990), a lower with *'Eotragus' halamagaiensis* Ye, 1989 and an upper with *Kubanochoerus*. The bovid is no *Eotragus*, but probably represents a primitive *Turcocerus* (Van der Made, submitted), more primitive than *Turcocerus* from Çandir and suggesting a greater age for these specimens.

Guan & Van der Made (1993) held Koujiacun, Erlangang and Dingjiaergou to be MN 5 on the occurrence of the *Bunolistriodon* at these localities and assumed Gujiazhuang, Quantougou, as well as Belometchetskaia to be older than Dingjiaergou (Tongxin) on the basis of the evolutionary stage of *Kubanochoerus*. Nanhawangou and Halamagai were tentatively placed in MN 5.

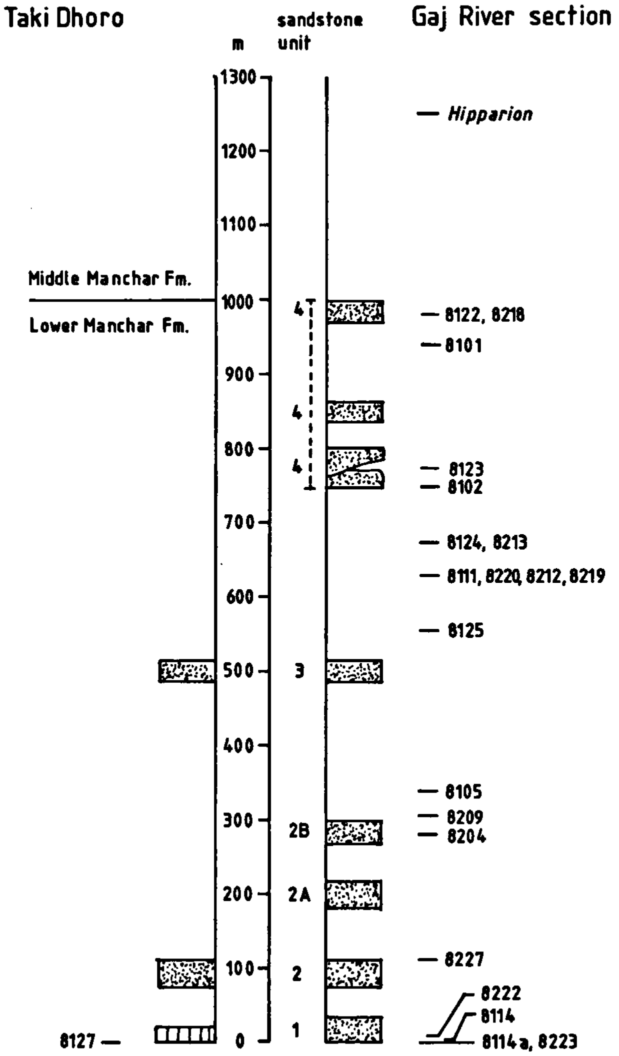


Fig. 22. Stratigraphical position of some of the HGSP localities. Sandstone units 1-4 are indicated, as is the subdivision of the Manchar Formation and the local first appearance of *Hipparion* (after HGSP catalogue). Only 1981 and 1982 localities yielding suoids are indicated.

Pakistan and India

The Miocene fossil mammalian faunas in North Pakistan have been described as **Murree, Kamlial, Chinji,** Nagri and Dhok Pathan zones. The names have subsequently been applied to the formations that yielded these faunas and even to 'stages' (Shah, 1984). Despite the fact that there is some discussion as to the formations being diachronous, these names are used here both for the formations as well as for the faunas. These formations have been studied over a long period (Pilbeam *et al.*, 1979; Badgley, 1984; Flynn *et al.*, 1990; and many others). The material included in the present study is mainly from the IVAU, BSPHGM and FISF collections. The collection catalogue in the IVAU was used to determine the relative position of the IVAU and FISF localities. Heissig (1972) indicated the stratigraphical position of the localities from which there are fossils in BSPHGM. In a few cases, it is not clear whether the IVAU and BSPHGM samples really come from the same locality, though they are indicated with the same name. In order to avoid mistakes, they are here treated as separate localities. In the case of the **Kanatti**, BSPHGM collection includes fossils from different localities of different ages. All the material in the IVAU collections is referred to simply as 'Kanatti', which is treated here as a single locality, though I am not absolutely sure that the material really is from one locality. Part of the IVAU collection consists of specimens bought from local people. These specimens have prefix 'CH' without an addition for the locality (like 'CHH' for Bhilomar) and are assumed to be from the Chinji Formation, but the exact provenance is not recorded. Such specimens are used only when they are the only indication of a certain species, stage of evolution or morphology.

The name **Bugti** is here applied to the 'locality' Bugti in Baluchistan, the fauna and the formation. The oldest fossils from Bugti are older than those from the Murree Formation, and are of Early Miocene age. Bugti also yielded fossils of Middle Miocene age (Pickford, 1987a, 1988b). It is quite possible that the old collections from Bugti include fossils from many levels of Early to Middle Miocene age, like the Lower Manchar Formation. More precise locality indications, such as Chur Lando, Dera Bugti, Gandoi and Khumbi indicate geography, not stratigraphy. Fossils from the Bugti area which are held to be younger than the typical Bugti fauna, are here indicated as **Bugti II**, to mark the difference.

The Bugti microfauna is dominated by descendants of the Chapatimyidae, a group of rodents of Indian origin (Jacobs *et al.*, 1981; De Bruijn & Hussain, 1984). However, doubts have been expressed over whether the micromammals came from different (older) beds than the large mammals (Bernor *et al.*, 1987).

De Bruijn & Hussain (1984) furnished a condensed, clear account of the stratigraphy of deposits in Pakistan, covering the time interval studied here and emphasising the **Manchar Formation**. There are a number of HGSP localities in the Manchar Formation that have yielded listriodonts which are studied here (Text-fig. 22). HGSP stands for Howard-Geological Survey of Pakistan and the localities are numbered according to year (81-84 for 1981 to 1984) together with a number. HGSP 8114 at the base of the Manchar Formation yielded the primate *Dionysopithecus* (Bernor *et al.*, 1988), but suids as well, which will be described separately. An overview of the Manchar Formation and its fauna was presented by Raza *et al.* (1984).

Locality HGSP 8106 (Gaj) was correlated with the Murree Formation, HGSP 8114a at the very base of this formation in Sehwan with the Kamlial Formation and higher parts of the Lower Manchar Formation with the Chinji Formation (De Bruijn & Hussain, 1984). HGSP 8224, 25 m above HGSP 8227, yielded rodents with affinities to those of the Chinji Formation. Wessels *et al.* (1987) correlated HGSP 8214 and HGSP 8224 with Beni Mellal and Yeni Eskihisar and thus MN 7+8. These HGSP localities are in the Manchar Formation, but do not have Suidae (Text-fig. 22). HGSP 8214 is 36 m below sandstone unit 4 (HGSP catalogue) at over 700 m in the section and thus above most of the *Listriodon* localities (Text-fig. 22). HGSP 8224 is between the *Bunolistriodon* and *Listriodon* localities and is 116 m above the base of the Manchar Formation. It is surprising that this locality should be that young: the basis of the formation should be dated at about 16 Ma and the entry of *Hipparion* is between 1200 and 1300 m; below the locality there is twice as much time and ten times less stratigraphical section than above. De Bruijn *et al.* (1989) recorded a *Sayimys* lineage. The older *Sayimys intermedius* Sen & Thomas, 1979 was found at HGSP 8114a, an intermediate *Sayimys* at HGSP 8114 and *Sayimys sivalensis* Hinton, 1933 at HGSP 8227 and HGSP 8224.

In the Gaj River section 63 palaeomagnetic samples were collected from a 1700 m thick section. The base of the Manchar Formation was estimated at 15.3 Ma (Khan *et al.*, 1984). This estimate appears rather young and was not adopted by Bernor *et al.* (1988).

No material from the **Ramnagar** Formation in India is included in the present study, though the formation has yielded *L. pentapotamiae*. The Ramnagar Formation is considered to be the time equivalent of the Chinji Formation (Thomas *et al.*, 1980).

Arabia

Miocene animal migrations between Africa and Eurasia must have passed via Arabia, which at that time was connected to Africa. For this reason, Arabian mammal localities have received much attention, but also the marine strata have been studied to date such migrations (Adams *et al.*, 1983).

Whybrow (1984) and Whybrow & Bassiouni (1986) summarised the relevant geology of the northeastern edge of the Arabian landmass. The terrestrial Hadrukh Formation is overlain by the marine Dam Formation, which extends about 120 km inland and which, in turn, is overlain by the terrestrial Hofuf Formation. The Dam Formation is of Burdigalian age (Adams *et al.*, 1983). The Al Jadidah locality is in the Hofuf Formation and was placed in MN 6 (Sen & Thomas, 1979). **Ad Dabtiyah** is in a terrestrial equivalent of the transgressive Dam Formation. Gentry (1987) assumed an age for Al Jadidah between Bugti and Maboko on the basis of proboscideans.

Africa

A biostratigraphy for the Miocene mammal localities in western Kenya was proposed by Pickford (1981): Faunal Sets I-VII. Seven 'Core Faunas' were selected: **Songhor**, Hiwegi (Hiwegi Formation at **Rusinga**), Maboko, Ngorora, Ngerigerowa and Lukeino. Other faunas were added to the Core Faunas on the basis of faunal distance (expressed as a percentage) and (litho)-stratigraphical position. Together these faunas constitute the Faunal Sets. Faunas outside the Nyanza area were assigned to a set on the basis of species' ranges and radiometric ages.

From the start, this system was applied also to other African localities. Later, a Set 0 or pre-Set I was added for Meswa Bridge, some localities changed position and a subdivision of Set III into Set IIIA and Set IIIB was introduced (Pickford, 1986a-c; Pickford *et al.*, 1986a). An example of a locality that changed position is **Kirimun**, which was originally placed in Set II, in a note in the same paper it was placed in Set III (Pickford, 1981) and later it was either placed in Set IIIA or Set IIIB (Pickford, 1986c, tab. 1 versus tab. 3). Pickford *et al.* (1986a) used a zonation based on anthracotheres and hippos alongside the Faunal Sets and used this zonation to place Kirimun in Set IIIB.

For an overview of Kenyan lithostratigraphy reference is made to Pickford (1981), for the most complete picture of West Kenyan localities, their faunas and lithostratigraphy to Pickford (1986a) and for a compilation of radiometric dates of Kenyan (primate) localities to Pickford (1986c). Some of the listriodont-yielding localities have been dated subsequently. Boschetto *et al.* (1992) gave a minimum age for the localities at **Moruorot**, including the exact locality which yielded the type of *Bunolistriodon jeanneli* (16.8 ± 0.2 Ma). A sequence of 50 m at **Maboko** yields fossils at various levels, though most come from the lower half. The phonolite overlying this sequence is dated at 13.8 Ma, whereas Bed 8, overlying the richest fossil-bearing beds is dated at 14.71 ± 0.16 Ma (Feibel & Brown, 1991). **Majiwa** can be correlated lithostratigraphically with the top of the Maboko section (Pickford, 1986a).

An introduction to the Libyan locality of **Gebel Zelten** was presented by Savage & Hamilton (1973). Gebel Zelten is in the Marada Formation, which is a terrestrial intercalation between marine beds. A similar sequence is found in a large area in Libya and is believed to be a continuation of the Moghara Formation in Egypt of comparable age (Savage, 1990).

Savage & Hamilton (1973) indicated that Arambourg spent several days collecting surface finds at Gebel Zelten. However, most of the fossils are fragile and show few or no signs of weathering, which suggests that they were excavated. The matrix consists of a bluish marl. The holotype of *Kubanochoerus massai* is much weathered and was described two years before the large collection, and obviously without knowledge of that later collection. The skull of *K. massai* has a matrix of sandstone and a different fossilisation from the bulk of the other fossils. Listriodonts commonly show an increase in incisor size. The incisors of the skull are much larger than the other incisors. This suggests that most of the fossils actually came from a single excavation and that the holotype and skull from one or two other localities. The skull might be from a younger locality.

SYSTEMATIC DESCRIPTIONS

In the descriptions below, to a certain extent, interpretations cannot be avoided. Evolution is treated only as changes within a single species. Only occasionally is reference made to evolution from one species to another.

There are some 25 species which each have up to 32 different types of teeth (including male and female canines and deciduous teeth) and over 50 foot bones (counting the different phalanges) as well as cranial remains and vertebrae. Although a species may be represented at a locality by a single bone or tooth only, recognition of this single fossil may be important. Attention is paid to all elements. However, a selection is made in the descriptions. Described and compared are characters which separate one species from the other, and characters which will be referred to in the sections on phylogeny and palaeoecology. Comparisons for the sake of taxonomy are made to highlight: 1) differences between type species; 2) similarities between species and the type species of the genus to which they belong; and 3) differences between a species and a similar species which has priority.

Figures which are referred to in this section serve two ends: they compare taxa and they may illustrate characters or phenomena that will be referred to in later sections. As a consequence, the figure captions may hold references to lineages, which will only be explained in the section on phylogeny. Similarly, the symbols are chosen in such a way that certain taxa are grouped for reasons which will become clear in later sections. In the text, no lists of specimens are given; however, lists of localities with references to listriodonts and their ages, are. All specimens are listed in Tables 6-19 (microfiche).

Superfamily Suoidea Gray, 1821

Diagnosis — Artiodactyla with snout disc and rostral bone, and with long external auditory meatus directed upwards and outwards and the posterior end of the zygoma forming upward-projecting protuberances.

Family Suidae Gray, 1821

Diagnosis — Suoidea with canines that have a tendency to flare out, especially in the males. The mandibular condyle is well elevated above the plane of occlusion of the cheek teeth and the glenoid is in an elevated and posterior position. The postglenoid process tends to be small. The jugular process tends to be large and directed downwards and forwards or only slightly backwards. The upper molars have two separate lingual roots and the lower first and second molar have four roots, one beneath each major cusp.

Subfamily Listriodontinae Gervais, 1859

1859	Tribu des Listriodontins; Gervais, p. 200.
1882	Listriodontidae; Roger, p. 94;
1884	Listriodontidae; Lydekker, p. 100
1887	Listriodontoïdea; Cope, p. 379
1887	Listriodontidae; Cope, pp. 379, 386.
1945	Listriodontinae, new from; Simpson, 145.

Remark — The oldest use of a family group taxon, based on *Listriodon* is, as far as I know, that by Gervais (1859, p. 200). Gervais listed it as 'Tribu des Listriodontins'.

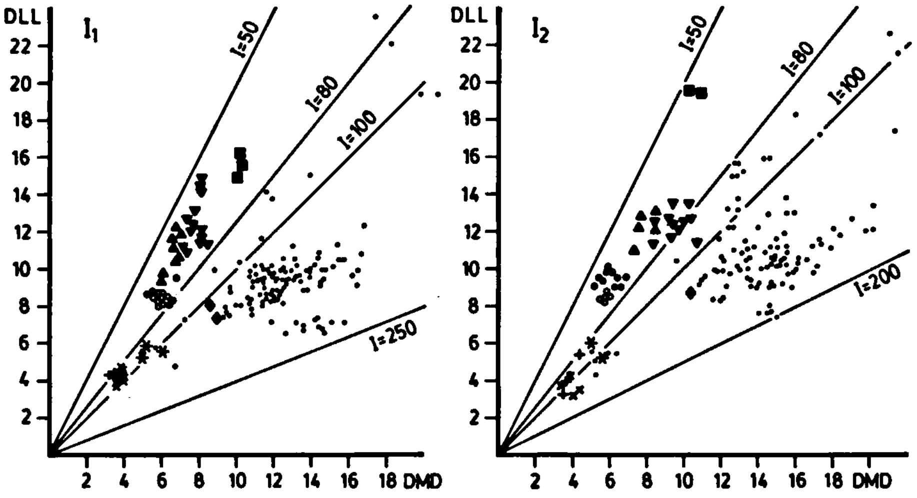


Fig. 23. Bivariate plots of the I_1 and I_2 of Listriodontinae compared to selected other Suidae. Legend: small dots - Listriodontinae; crosses - *Albanohyus*; oblique crosses - *Cainochoerus*; asterisks - *Kenyasus rusingensis*; large dots - *Hyotherium soemmeringi*; circles - *Hyotherium* aff. *major*; triangles with points upward - *Parachleuastochoerus steinheimensis*; triangles with points downward - *Sus strozzii*; squares - *Microstonyx antiquus*; diamonds - *Celebochoerus*. The lines indicate values of index I. *Celebochoerus* has wide (DMD, I) incisors, but, like *Kolpochoerus* and *Hylochoerus*, it differs from the Listriodontinae in having more hypsodont incisors.

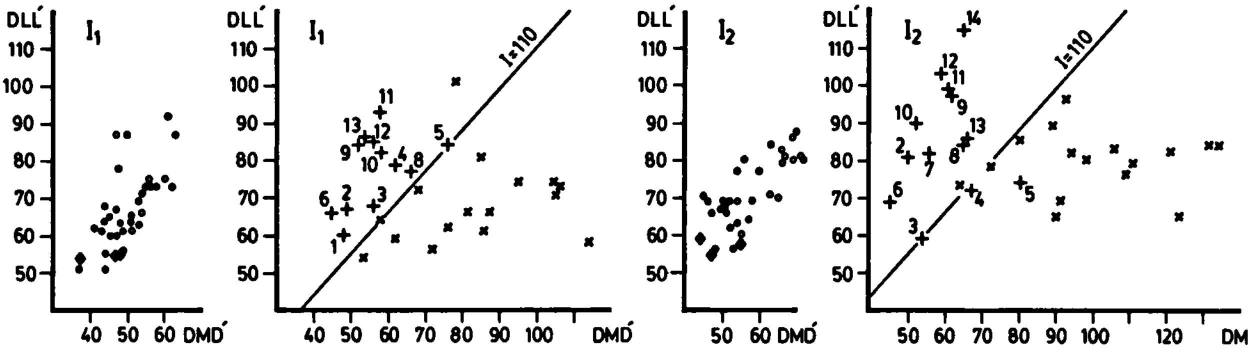


Fig. 24. Bivariate plots of DMD' and DLL' of Listriodontinae and other selected Suoidea. Legend: diamonds - Recent *Tayassu peccari* (ZMA); dots - Recent *Tayassu tayacu* (ZMA); circles - Recent *Sus scrofa* from Europe (NNML, MNCN, UCM, UPVB, ZMA); oblique crosses - Listriodontinae; crosses 1 - *Palaeochoerus typus* (St.-Gérand, individual, MGL); 2 - *Palaeochoerus aquensis* (Quercy, individual, MNHNP); 3 - *Kenyasus rusingensis* (Songor, sample, KNM); 4 - *Albanohyus castellensis* (Castell de Barberà, sample, IPS); 5 - *Cainochoerus africanus* (Langebaanweg sample, Pickford, 1988c); 6 - *Hyotherium soemmeringi* (Sandelzhausen, sample, BSPHGM); 7 - *Hyotherium* aff. *major* (Ulm West-Tangente, sample, SMNS); 8 - *Hyotherium meisneri* (Cetina, sample, Van der Made, 1994a); 9 - *Parachleuastochoerus steinheimensis* (La Grive, sample, MGL, UCBL); 10 - *Propotamochoerus wui* (Lufeng, sample, Van der Made & Han, 1994); 11 - *Microstonyx major* (Spain, sample, Van der Made *et al.*, 1992); 12 - *Microstonyx erymanthius* (Dorn Dürkheim, sample, Van der Made in press); 13 - *Sus strozzii* (Valdarno, sample, AVP, IGF); 14 - *Xenohyus venitor* (Les Beilleaux, sample, Ginsburg *et al.*, 1987). The lines indicate values for index I. The diagrams on Recent species show one point for one individual. These diagrams give an indication of the variability of the DMD' and DLL' values within one species. The values for the Listriodontinae are taken from table 16 and mostly concern (small) samples. Using DMD' and DLL', this figure is intended to show the size of the incisors irrespective of absolute size of a species. For the non-listriodont suids, it appears that the index is not affected by relative size of the incisors. The relatively smallest incisors occur in *Palaeochoerus* and *Hyotherium*, the stratigraphically oldest and most primitive suoids. Small incisors appear to be primitive. The greatest DMD' and indices I occur in the I_2. This tooth seems to be more progressive in increasing its DMD' than the I_1. The incisors of *Kenyasus*, *Albanohyus* and *Cainochoerus* are in the range of variation of the Listriodontinae, but tend to be small, especially in DLL'.

No indication is given as to authorship and date, which was common practice at that time. Roger (1882, p. 94) and Lydekker (1884, p. 100) applied the name Listriodontidae at the family level, but they too did not indicate author nor date. On the same page, Lydekker cited Gervais (1859) in connection with theclassification of *Listriodon*. Simpson (1945, p. 145) seems to have used Listriodontinae for the first time as a subfamily.

Most subsequent authors considered Simpson to be the author of the subfamily. However, if a taxon is changed in rank within its group (family group in this case) it keeps the original author and date (International Code of Zoological Nomenclature; ICZN; Ride *et al.*, 1985). Although Gervais (1859) did not correctly latinise the name, this does not impair validity of the taxon, being amended and recognised subsequently by other scientists (ICZN). Unless an older citation is found, Gervais should be considered the author of this name and 1859 the year of publication.

Kubanochoerinae is included here in the Listriodontinae, but recognised as a separate tribe.

Diagnosis — Suidae with I^1, I_1 and I_2 with wide and low crowns. The right and left first upper incisors form a transverse ridge; the long axes of both crowns are in an even line with each other, whereas in many other suids they form a V-shape. See Text-figs 23 and 24 for morphometry of the I_1 and I_2 and Text-fig. 25 for the morphology of I^1 of Listriodontinae compared to those of other Suoidea.

Tribus Lopholistriodontini n. trib.

Diagnosis — Small Listriodontinae without cranial appendages, but with short C^m that are nearly straight and oriented downwards and slightly outwards and with relatively small incisors that are not much extended in meso-distal direction. (For a comparison of the sizes of the incisors in the listriodont tribes, see Text-fig. 27 and Text-figs 26 & 27 for the relative sizes and mesodistal elongation.)

Genus *Nguruwe* Pickford, 1986b

Type species — *Hyotherium kijivium* Wilkinson, 1976.
Diagnosis — Bunodont or nearly sublophodont Lopholistriodontini.

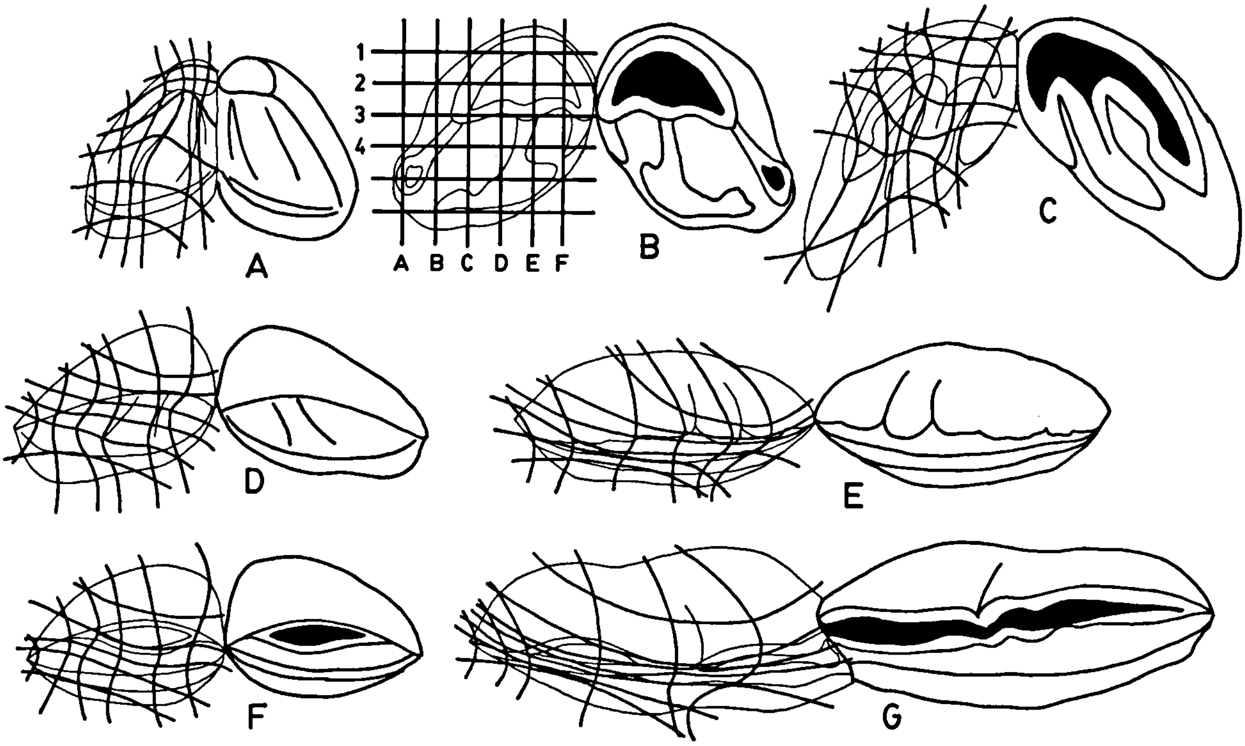


Fig. 25. Morphology of I^1 of Suoidea compared using the 'Method of Co-ordinates' (d'Arcy Wentworth-Thompson, 1961). The grids are fitted by hand. Upper row from left to right: *Tayassu tayacu*, *Conohyus simorrensis* and *Propotamochoerus* sp. Middle row: *Nguruwe kijivium* and *Bunolistriodon lockharti*. Lower row: *Lopholistriodon moruoroti* and *Listriodon splendens*. The teeth are shown in the approximate orientation when in the premaxilla, with the palate parallel to the page. Not to scale. The *Conohyus* incisor is closest to the supposed primitive suoid morphology. Most suid incisors resemble those of *Propotamochoerus* in that two of them have a 'V-shape', which is brought about by an inflation of the distal part (around A,B - 5,6). Listriodont incisors form a transverse ridge, which is brought about by shrinking the same area that is inflated in other suids and by extending the mesial part (C to F). *Tayassu* has a nearly continuous occlusal surface like the listriodonts. This is done by filling in the space in the 'V' (squares E,G - 3,5 are extended in antero-posterior direction).

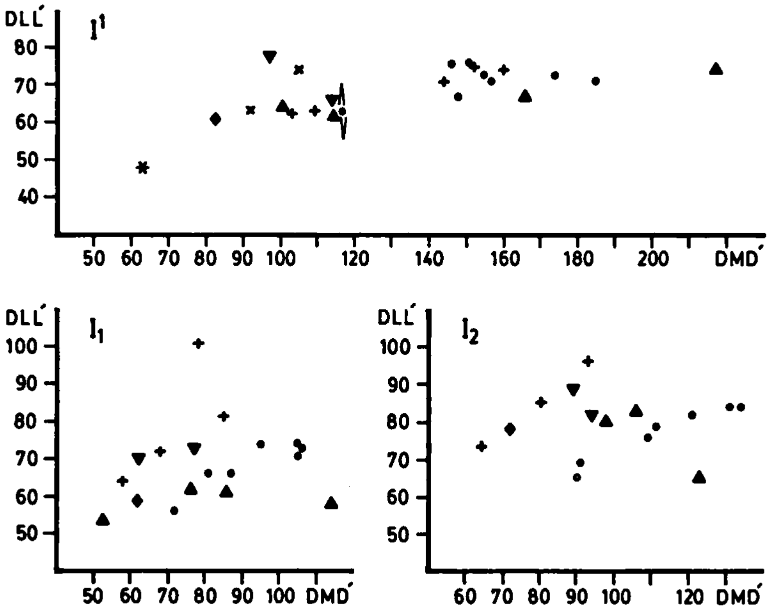


Fig. 26. Bivariate plots of the central incisors of Listriodontinae. Legend: asterisk - *Nguruwe*; oblique crosses - *Lopholistriodon*; crosses - *Kubanochoerus*; diamonds - *B. anchidens*; triangles with points downward - *Bunolistriodon lockharti*; triangles with points upward - *Bunolistriodon latidens*-lineage (*Bunolistriodon* aff. *latidens*, *B. latidens* and *B. meidamon*); circles - *Listriodon pentapotamiae*; dots - *Listriodon splendens* (including Chinese *Listriodon* - the smallest value); arrows indicate an approximate value. Using DMD' and DLL' this figure intends to compare relative incisor size and to eliminate differences in body size. This figure shows differences in size of the incisors relative to the M1. The figure shows that for most listriodonts, DLL' values are similar, but DMD' values vary greatly. This is especially true for the I^1. For the lower incisors, *Kubanochoerus* tends to have a positive correlation for DMD' and DLL' and the *B. latidens* lineage a negative correlation.

Nguruwe kijivium (Wilkinson, 1976)

Pl. 1, Figs 1-22; Pl. 2, Figs 8-11, 13, 17, 18?;
Pl. 3, Figs 9, 10, 12?, 13, 14

1976 *Hyotherium kijivium* n. sp. — Wilkinson, pp. 201-203, pl. 2, figs f-h; pl. 3, figs d, e.

1986b *Nguruwe kijivium* (Wilkinson, 1976) — Pickford, pp. 15-24, figs 4-22.

Holotype — NAP 1'64, left maxilla with M^1-M^3, illustrated by Wilkinson (1976, pl. 2, fig. g).

Type locality — Napak I, Uganda.

Age of the type locality — Early Miocene, Set I, approximately 19 Ma.

Diagnosis — As for genus.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Songhor	KNM	Pickford 1986b	Set I	Pickford 1986c
			19.6 Ma	Pickford 1986c
Mteitei-32	KNM	Pickford 1986b	Set I	Pickford 1986c
Koru-25	KNM	Pickford 1986b	Set I	Pickford 1986b
Legetet-10		Pickford 1986b	Set I	Pickford 1986b
Legetet-14	KNM (casts)	Pickford 1986b	Set I	Pickford 1986b
Napak I		Wilkinson 1976	Set I	Pickford 1986b
		Pickford 1986b	19 Ma	Pickford 1981
Napak IV		Pickford 1986b	Set I	Pickford 1986b
Napak V		Pickford 1986b	Set I	Pickford 1986b
Napak loc.?	KNM (casts)		19 Ma	Pickford 1986c
Loncherangan	KNM		Set I/II	(based on suoids)
Mfwangano-A3	KNM	Pickford 1986b	Set II	Pickford 1981
Mfwangano-AS	KNM	Pickford 1986b	Set II	Pickford 1981
Mfwangano-B	KNM	Pickford 1986b	Set II	Pickford 1981
Mfwangano-L	KNM	Pickford 1986b	Set II	Pickford 1981
Mfwangano-N	KNM	Pickford 1986b	Set II	Pickford 1981
Mfwangano-O	KNM	Pickford 1986b	Set II	Pickford 1981
Rusinga-R1a	KNM	Pickford 1986b	Set II	Pickford 1986b
Rusinga-R3	KNM	Pickford 1986b	Set II	Pickford 1986b
Rusinga-R3a	KNM	Pickford 1986b	Set II	Pickford 1986b
Rusinga-R30	KNM	Pickford 1986b	Set II	Pickford 1986b
Rusinga-R106	KNM	Pickford 1986b	Set II	Pickford 1986b
Rusinga-Gumba	KNM	Pickford 1986b	Set II	Pickford 1981, 1986b
			17.9 Ma	Pickford 1986b
Rusinga-Kathwanga	KNM	Pickford 1986b	Set II	Pickford 1981, 1986b
Rusinga-Wayondo	KNM	Pickford 1986b	Set II	Pickford 1981, 1986b
Kirimun	KNM		Set IIIA	Pickford 1986b
			Set II	Pickford 1981
			Set IIIB	Pickford *et al.* 1986b
			> 15 Ma	Matsuda *et al.* 1986
?HGSP 8412	HGSP			
?Chharat	IM	Pilgrim 1926	Murree	Pilgrim 1926

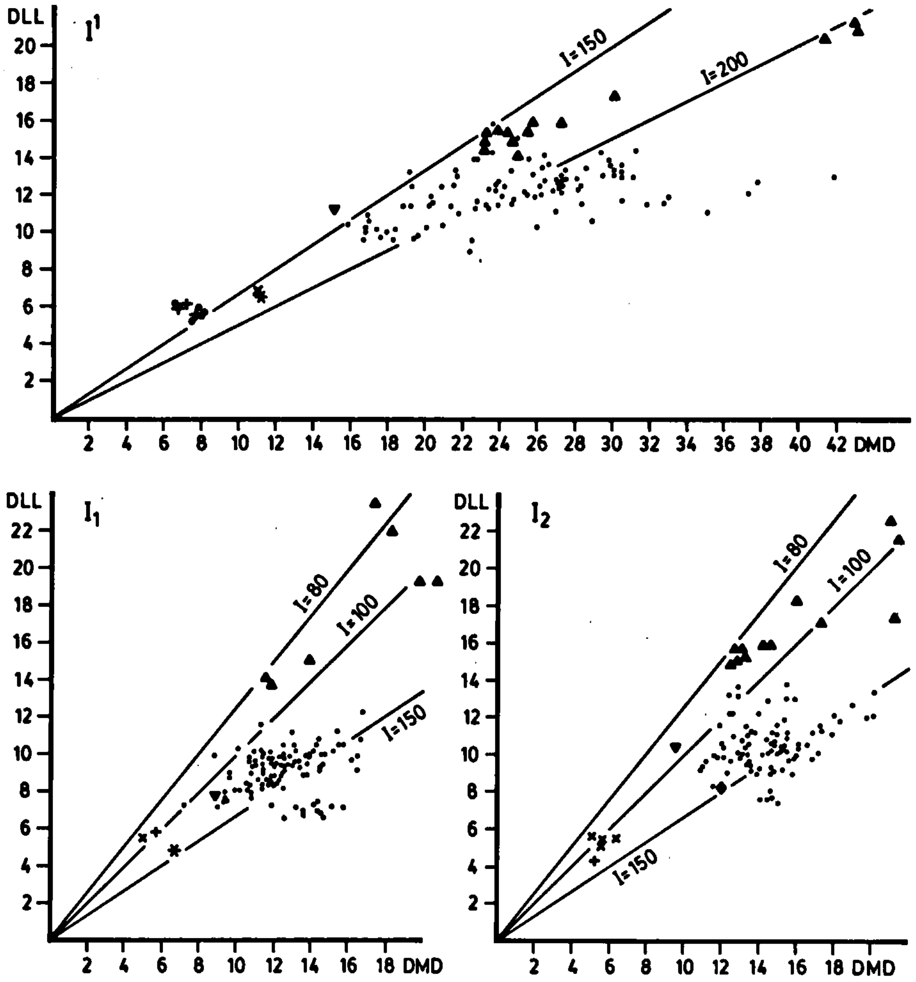


Fig. 27. Bivariate plots of the central incisors of the Lopholistriodontini and Kubanochoerini, as well as *Bunolistriodon anchidens*. Legend: crosses - *Nguruwe kijivium*; large dots - *Lopholistriodon moruoroti*; oblique cross - *Lopholistriodon pickfordi*; asterisks - *Lopholistriodon kidogosana*; diamond - *Lopholistriodon akatidogus*; triangle with point downward - *B. anchidens*; triangles with point upward - *Kubanochoerus;* small dots - other *Listridontinae*. The lines indicate various values for the index I.

Description and comparison — Nguruwe kijivium co-occurs with *Kenyasus rusingensis*, another suoid (see Pickford, 1986b), but is smaller (Text-fig. 28). It is the only species of its genus and differs from the related genus *Lopholistriodon* (type species *L. kidogosana*) in particular in incisor, premolar and molar morphology.

The I_1 (Pl. 2, Fig. 17) has a high crown for a listriodont and does not have a clear endocristid. The homologue in *L. kidogosana* has a wide and low crown (Pl. 5, Fig. 1).

The C_f shows a sign of a division of the root, although there are no two separate roots.

The C_m (Pl. 2, Fig. 8) has a scrofic section. The crown is high and the tooth appears to have grown during all, or the major part of, individual's lifespan.

The P_1 (Pl. 2, Fig. 13) has two well-separated roots, of which the anterior one is curved backwards.

The P_2 has a simple crown with pre- and postcristid and anterior and posterior cingulum. The crown is high for a suid.

The P_3 is represented by a single tooth from Songhor (Pl. 1, Fig. 10) and one from Kirimun (Pl. 2, Fig. 9). Pickford (1986b) used the wide talonid in the diagnosis of the species. However, the Kirimun specimen does not have a wide talonid and occasionally a wide talonid occurs in *B. lockharti* (Pl. 29, Fig. 5). The specimen from Songhor is probably not representative.

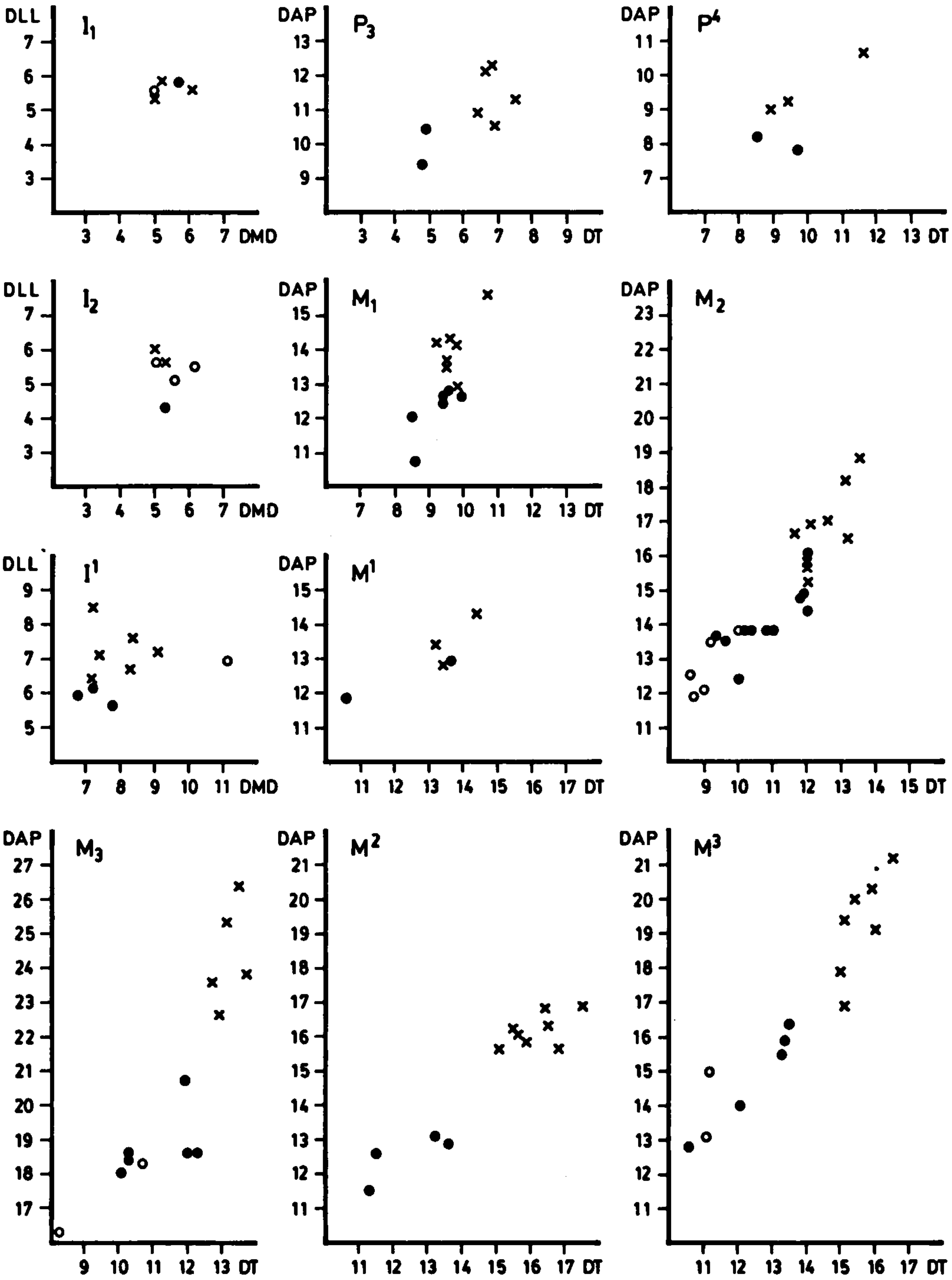


Fig. 28. Bivariate plots of *Kenyasus rusingensis* (crosses) and the listriodonts *Nguruwe kijivium* (dots) and *Lopholistriodon pickfordi* (circles).

The P_4 (Pl. 1, Fig. 8) has a protoconid and a low hypoconid; there is no sign of a metaconid. The anterior cingulum is elevated in the centre, but no paraconid is developed at this place. The protoprecristid is a sharp ridge. There is no depression that might be called the protoprefossid. There is a clear protopostcristid and the hypoconulid is well separated from it. The hypoconulid is not expanded lingually. The premolars of *L. kidogosana* have metaconids, as shown by its P_3.

The D_2, D_3 (Pl. 3, Fig. 13) and D_4 (Pl. 3, Fig. 13) are found associated in a mandible with a D_4. Both D_2 and D_3 have simple postcristids and no posterior-directed endocristid or other structures in the posterior part, except for a cingulum in the D_3.

The **M_1**, **M_2** (Pl.1, Fig. 21) and **M_3** (Pl. 1, Figs 12, 19, 20) have narrow transverse valleys, which are filled in by large hypopreconulids. In the Songhor specimen the protoendocristid and metaendocristid are not connected to each other, nor are the hypoendocristid and entoendocristid. There is a tendency of the wear facets to be oriented transversely. In the Kirimun specimens (Pl. 3, Figs 9, 10, 14) the endocristids touch and wear facets tend to be more transversely oriented and the hypopreconulid is smaller and is more like a hypoprecristid than like a separate structure. The Kirimun molars approach a sublophodont condition, though a protolophid is still not well formed. The *Lopholistriodon* molars are still more (sub)lophodont than the molars from Kirimun. The molars have four roots (Pl. 1, Fig. 21b, d).

The **DI^2** is represented by a small incisor with low and wide crown from Songhor. As there is no other suoid, it is likely to belong to *Nguruwe.*

The **I^1** (Pl. 1, Figs 1, 3; Pl. 2, Figs 10, 24) has a wide crown. The wear facet over the lingual side is parallel to the precrista and postcrista. The long axis (DMD) of the crown is transverse with respect to the skull; the right and left incisors formed a transverse ridge as is typical in Listriodontinae. A basal cingulum is not developed or in some specimens only faintly in the distal half. Since the tooth is still rather narrow for a listriodont, the protoendocrista is clearly visible. The protoprestyle and protopoststyle are well developed. The incisor of *L. pickfordi* is more extended in meso-distal direction (Text-fig. 28). In the listriodonts, the I^1 of *N. kijivium* is the smallest relative to the M^1 (Text-fig. 26) and has the lowest index I together with the incisor of *L. moruoroti* (Text-fig. 27). The I^1 has two lobes in *L. kidogosana* but only one in *N. kijivium.*

One tooth (KNM-SO 49977) might be an **I^2** (Pl. 1, Fig. 5; as seen here, the tooth is erroneously labelled KNM-RU). The sole root is long and curved and the crown is high and not much elongated.

Another tooth (KNM-MW 560) might be the **I^3** (Pl. 1, Fig. 4). The root is not so strongly curved and shorter than in the supposed I^2. The index I is 184 versus 161 in the supposed I^2. In many suoids, the I^2 are more elongate than the I^3.

The **C^m** (Pl. 1, Figs 6, 7) is curved slightly inwards (Pl. 1, Fig. 6d) instead of outwards, which is the more normal condition in suids. The presyncline and postsyncline are narrow and deep, the mesosyncline is wider but very shallow. There is no important cementum. Labially there is a shallow groove that seems to mark a (former) separation between two roots.

The **C^f** has a crown that is much lower than in the males. A large part of the root is exposed and the anterior facet extends even over the root. The root shows signs of division at the lingual and labial sides. It is possible that distally the root divides into two, but this cannot be seen as the tooth is still in the maxilla. There is only a presyncline and postsyncline. There is a large anterior facet that extends over the root.

The **P^1** is found in connection with the C^f in one case, another specimen is isolated (Pl. 1, Fig. 17). It has two divergent roots and there is a large posterior facet.

The **P^4** (Pl. 1, Figs 9, 13, 14) has a long and well-developed protoprecrista as well as protopostcrista. With wear both cristas fuse to the cingulum. The protoprecrista is not fused to the paracone and its labial end is low. The surface of the paracone shows an angle at the place where a paraprecrista might be developed. There is, however, no such a crista. In some P^4 (Pl. 1, Fig. 13), but not in all (Pl. 1, Figs 9, 14), a metacone may be faintly separated from the paracone. The P^4 of *Lopholistriodon* have protolophs.

The **D^2** (Pl. 1, Fig. 2) resembles the P^1, but is longer and more elongate. A D^3 and D^4 are found in connection.

The **M^1** and **M^2** (Pl.1, Figs 18, 22) from Songhor tend to have the protopreconule fused to the protocone and not to the cingulum. Specimens from Koru have the protopreconule fused to the cingulum and not to the protocone. The protopreconules are not yet connected to the paracones. Labial cingula are not formed along the labial cusps, but there is a piece of cingulum at the end of the transverse valley. There are two lingual roots.

The **M^3** (Pl. 1, Figs 11, 15, 16) have posterior cingula that are wide lingually; no pentacone is formed. A specimen from Songhor has the protopreconule fused to the cingulum and not to the protocone (Pl. 1, Fig. 16), in most others this is not the case (Pl. 1, Fig. 11); KNM-SO 1056 (Pl. 1, Fig. 15) is intermediate. In Koru the protopreconule is fused to the cingulum and this also seems to be the case in the holotype from Napak (Wilkinson, 1976, pl. 2, fig. g). *Listriodon pickfordi* has a sublophodont M^3 (Pl. 4, Fig. 7) with a complete protoloph and flat transverse wear facet. The upper molars in *L. kidogosana* are fully lophodont.

The morphology of the **postcranial skeleton** is close to that of Recent suids. Distal humeri, astragali, an MC IV, an MT III, a distal MP and a first phalange are assigned to *Nguruwe* on the basis of their small size. Bones of *Sanitherium* are expected to be similar to those of other Palaeochoeridae, which differ in many characters from bones of Suidae.

The astragali have sustentacular facets that are slightly convex in transverse section and there are no well-developed lateral ridges (or none at all) along those facets. Leinders (1976) assumed the loss of such a ridge to occur in the lineage '*Listriodon*' *lockharti*-*Listriodon splendens*. However, the astragalus that Leiders believed to be *B. lockharti* seems to belong to *Hyotherium soemmeringi* (Van der Made, 1990a). The *Nguruwe* astragali show that the shape of the sustentacular facet was already *Listriodon*-like in an early stage of evolution of the subfamily. The distal articulation of the humerus consists of three ridges divided by two valleys. The surface between the large external ridge and external valley is concave in transverse section; in *Sus* and *Bunolistriodon* this is not so clear (Pl. 25, Fig. 1). This is a general primitive trait found in early suids. The humeri might belong to *Sanitherium*, though this genus is not represented by teeth at Mteitei.

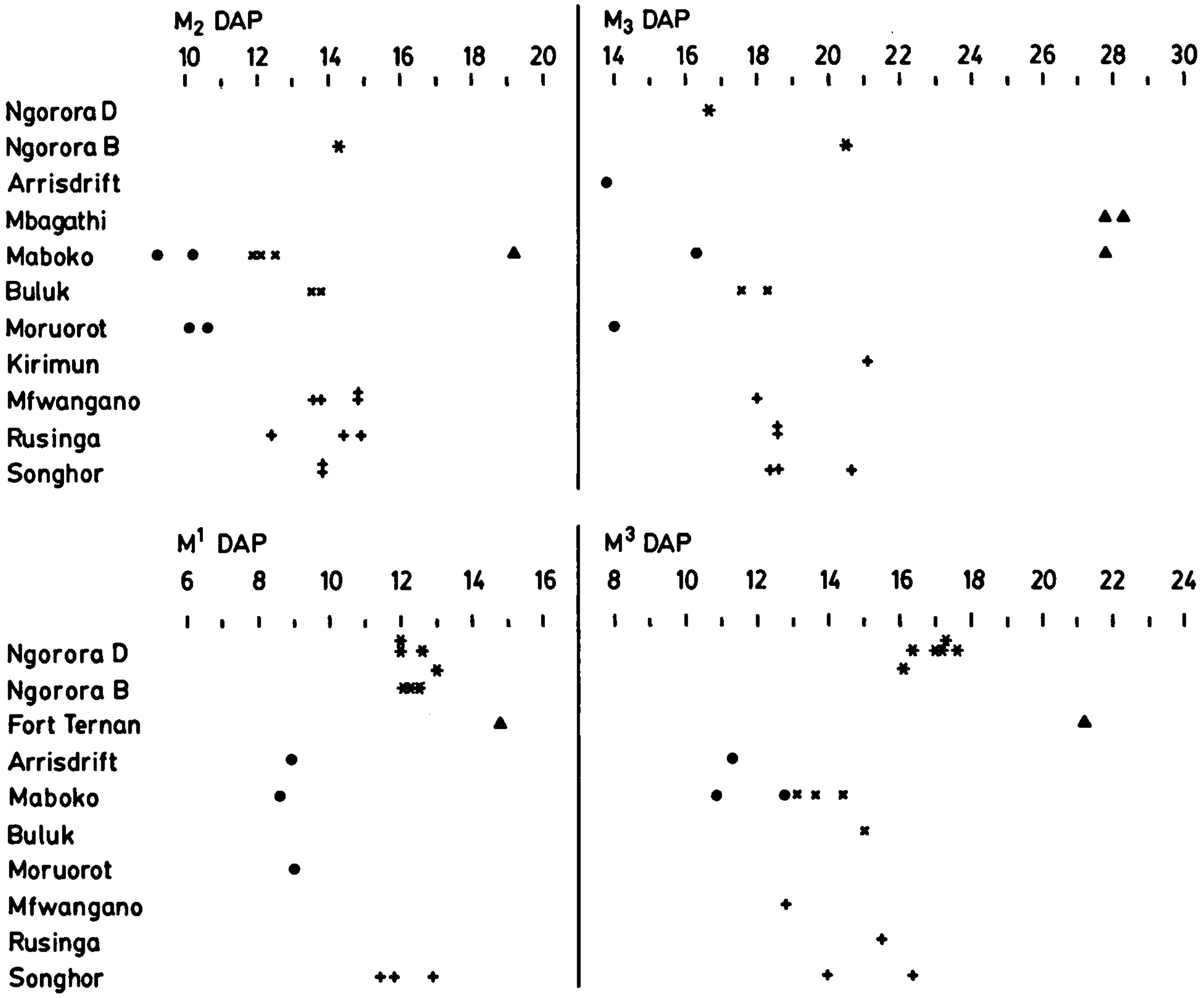


Fig. 29. Size increase in various cheek teeth of Lopholistriodontini. The localities are in approximate stratigraphical order. Legend: crosses - *Nguruwe kijivium*; oblique crosses - *Lopholistriodon pickfordi*; asterisks - *Lopholistriodon kidogosana*; dots - *Lopholistriodon moruoroti*; triangles - *Lopholistriodon akatidogus*. Some of the material of the Ngorora Formation is of unknown exact provenance and is placed between member B and D.

The size of *N. kijivium* is close to that of *Lopholistriodon pickfordi* and inferior to that of *Kenyasus rusingensis* (Text-figs 28, 29).

Discussion — Hooijer (1963) described a molar from Malembe (Cabinda, Angola) as *Hyotherium dartevellei*. Wilkinson (1976) referred a large collection of suids to *H. dartevellei* and described a smaller collection of a smaller suid as *Hyotherium kijivium*. Wilkinson did not state clearly why this smaller species was assigned to *Hyotherium*; the limited material he studied did not really indicate another genus than the larger species. Pickford (1986b) showed the tooth from Malembe to belong to an anthracothere and introduced the new generic name *Nguruwe* for the small suid and the new specific and generic names *Kenyasus rusingensis* for the larger suid. Pickford (1986b) placed *Nguruwe kijivium* in the Kubanochoerinae, a subfamily that is included here in the Listriodontinae.

The material described here shows quite some morphological variation from clearly bunodont to nearly sublophodont with the type of *N. kijivium* from Napak at the 'bunodont' end of the range. Since the variation is gradual, it is preferred here to assign it to one species, rather than create new taxa. There is more than enough difference in morphology between *N. kijivium* and *L. kidogosana* to maintain two genera.

The Set I localities seem to have yielded only or mainly molars with the protopreconule fused to the cingulum. In Songhor (Set II) the protopreconule is fused to the protocone in most of the molars. There seems to be a shift in the connections of the protopreconule towards (sub)lophodonty. Similarly, the lower molars from Kirimun are more (sub)lophodont than those from Songhor and other Set I and Set II localities. Kirimun has been assigned various ages (Pickford, 1981, 1986c), but in any case seems to be younger than most Set II localities.

A small bunodont suid from Arrisdrift was tentatively placed in *N. kijivium* (Pickford, 1986b, p. 21). The upper molar has the protopreconule fused to the cingulum, a primitive feature for *Nguruwe*. This would suggest that Arrisdrift should be placed in Set I or early Set II. However, *L. moruoroti* from Arrisdrift is more advanced in its lophodonty than the one from Moruorot and this would suggest that Arrisdrift is late Set II or Set III. It seems likely that the small bunodont suid from Arrisdrift does not belong to *N. kijivium*.

Palaeochoerus pascoi Pilgrim, 1926 from the base of the Murree Formation in Pakistan is based on an M^3 only (Pl. 3, Fig. 11). This tooth resembles *Nguruwe* molars in size and general morphology and in particular in its protopreconule which is small and fused to the protocone. The only Suidae with a protopreconule (or protoconule) fused to the protocone and not to the cingulum are some of the Listriodontinae, but this is also found in Palaeochoeridae (Van der Made, 1994a, in press), where the protopreconule tends to be larger.

Two specimens from the base of the Lower Manchar Formation (Pl. 2, Fig. 18; Pl. 3, Fig. 12) are of the size and morphology of *P. pascoi* and *N. kijivium*. The specimens are of approximately the same age as *P. pascoi*. The P$_4$ has a blunt protoconid and no metaconid and no large paraconid. This morphology is comparable to *N. kijivium* and differs from *Palaeochoerus* and *Propalaeochoerus*. These genera have P$_4$ with well-developed metaconids and paraconids and P$_3$ with much more slender protoconids. These specimens suggest that *'Palaeochoerus' pascoi* belongs to the Suidae and not to *Palaeochoerus* or *Propalaeochoerus*. *P. pascoi* seems to be too young to be synonymous with *N. kijivium* (see section on stratigraphical results), which is supposed to have evolved into *Lopholistriodon*, but might well be related. Should more material from Pakistan become available, a comparison with *Nguruwe* is called for.

Genus *Lopholistriodon* Pickford & Wilkinson, 1975

Type species — *Lopholistriodon kidogosana* Pickford & Wilkinson, 1975.
Diagnosis — Lopholistriodontini with sublophodont or lophodont molars.

Lopholistriodon moruoroti Wilkinson, 1976

Pl. 2, Figs 1-6, 12; Pl. 3, Figs 1, 2, 4-6, 8;
Pl. 4, Figs 8, 9; Pl. 34, Figs 4, 5

1972 *Listriodon* sp. indet. [small sp.] — Madden, p. 6.
1975 *Lopholistriodon* sp. D — Pickford & Wilkinson, pp. 133, 134, 139.
1976 *Lopholistriodon moruoroti* (Wilkinson) — Wilkinson, pp. 244-245, pl. 9, fig. b.
1978 *Lopholistriodon moruoroti* (Wilkinson) 1976 — Wilkinson, p. 446.
1978 *Lopholistriodon moruoroti* Wilkinson, 1976 — Hendey, p. 23, fig. 9.
1981 *Lopholistriodon* sp. — Andrews *et al.*, p. 45 (*partim*).
? 1981 Tayassuidae indet. — Andrews *et al.*, p. 45 (*partim*).
1986b *Lopholistriodon moruoroti* Wilkinson, 1976 — Pickford, p. 56-58 (*partim*), fig. 61.
? 1986b Genus indet. cf. *Schizochoerus* Crusafont and Lavocat, 1954 Species nov. small — Pickford, p. 74 (KNM MY 25 and 68).
1992b *Lopholistriodon moruoroti* — Van der Made, pp. 91, 97.

Holotype — KNM-MO 5 (field no. MT 90:51), mandible with left M$_1$-M$_3$ and roots of P$_3$, P$_4$ and I$_1$-I$_3$ and right I$_1$-I$_2$, C$_1$, P$_2$-M$_3$ and the root of I$_3$ (Pl. 3, Fig. 4; Pl. 4, Fig. 9), in KNM collections, illustrated by Wilkinson (1976, pl. 9, fig. b.
Type locality — Moruorot, Kenya.
Age of type locality — Early Miocene, Set II.
Diagnosis — Sublophodont *Lopholistriodon* of small size with central incisors with small meso-distal diameter.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Moruorot	KNM	Wilkinson 1976	Set III	Pickford 1986b
		Pickford 1986b	(Set II	Pickford 1981)
Maboko	KNM	Pickford 1986b	Set IIIB	Pickford 1986b
Majiwa	KNM		Set IIIB	Pickford 1986b
Arrisdrift	KNM	Hendey 1978		
	(cast)	Pickford 1986b		
Muruyur	KNM	Pickford 1986b	Set IV	Pickford 1981

Description and comparison — Lopholistriodon moruoroti is morphologically intermediate between *Nguruwe kijivium* and *L. kidogosana* and is compared primarily with these two species. *L. pickfordi* is slightly larger than *L. moruoroti* and contemporaneous specimens are assigned to either one of these mainly on the basis of size (Text-fig. 29).

The $\mathbf{I_1}$ and $\mathbf{I_2}$ are only known from the holotype, where they are in a poor state of preservation. The remains suggest that in both teeth, DLL exceeds DMD. This is a general primitive character in listriodonts and it thus resembles *Nguruwe* more closely than *L. kidogosana.*

The $\mathbf{C_m}$ (Pl. 3, Fig. 2) has a scrofic section. The C_f is a relatively large tooth.

The $\mathbf{P_2}$ (Pl. 4, Fig. 9) and $\mathbf{P_3}$ (Pl. 4, Fig. 9) are known from the holotype only. They have extensive wear facets over the posterior sides and the morphology of the talonid cannot be studied. There is no metaconid. In the P_2 both roots curve backwards and are somewhat convergent, but still separate. *L. moruoroti* seems to resemble *L. kidogosana* in the reduction of the size of the P_2.

The $\mathbf{P_4}$ (Pl. 2, Fig. 11; Pl. 3, Fig. 5; Pl. 4, Fig. 9) has a metaconid not very close to the protoconid. In Maboko (Pl. 2, Fig. 1), these cusps are placed wider apart than in Moruorot (Pl. 4, Fig. 9). There is a well-developed protopostcristid passing smoothly into the hypoconid, which is indicated as a mere swelling in this ridge. *Nguruwe* does not have a metaconid (Pl. 1, Fig. 8), *L. kidogosana* probably does.

The $\mathbf{M_1}$ and $\mathbf{M_2}$ (Pl. 3, Figs 4, 5, 8; Pl. 4, Fig. 9) from Maboko always have protolophids, but only in some specimens a hypolophid whereas in others the endocristids of the second lobe touch, but are not fused. So some teeth are lophodont and others sublophodont. The M_3 from Moruorot (Pl. 3, Fig. 4; Pl. 4, Fig. 9) does not have a hypolophid. The dentine islets of the endocristids are still well separated, even if the tooth is much worn. The hypoprecristid is large and nearly touches the protolophid, but does not have transverse extensions; it is clearly no hypopreconulid. Moruorot is less advanced in the direction of lophodonty than Maboko, which seems to represent the time when full lophodonty was about to be attained. *L. moruoroti* is intermediate between the bunodont *Nguruwe* and the lophodont *L. kidogosana.*

The $\mathbf{M_3}$ (Pl. 3, Fig. 4; Pl. 4, Figs 8, 9) has a long but narrow third lobe as in *L. kidogosana.* An unworn specimen from Arrisdrift has a perfect protolophid, but the endocristids of the second lobe fuse only at half their height. Seen from behind, the ends of the endocristids are convex up and where they meet there is a deep and narrow valley. Seen from behind, the protolophid is also lower in the middle, but endocristids are concave up and the valley in the middle is wide and shallow. The molars are smaller than those of *N. kijivium* and other species of *Lopholistriodon* (Text-fig. 29).

The $\mathbf{I^1}$ (Pl. 2, Figs 3, 5, 6) has only one lobe as in *Nguruwe* and is of equal size (Text-fig. 27). The crown is high compared to the other dimensions. DMD' and DLL' are small (Text-fig. 26) and intermediate between *Nguruwe* and *L. kidogosana.* A specimen from Muruyur that was assigned to cf. *Schizochoerus* (Pickford, 1986b) is similar to the other I^1 (Pl. 34, Fig. 4).

The $\mathbf{I^2}$ has a high crown.

The $\mathbf{C^m}$ (Pl. 2, Fig. 1; Pl. 3, Fig. 1) have three short enamel bands; the pre-, post- and endosinclines. In some specimens, all enamel is worn away. Labially, there is a groove which seems to be a vestige of the separation between two toots. The teeth must have been curved backwards a little, and nearly undetectably outwards. There is one huge oblique apical facet. In the few known specimens, the endosyncline is deeper than in *Nguruwe*, but variation of the character is not known.

The $\mathbf{P^3}$ (Pl. 2, Fig. 2) is known in a single worn specimen. The tooth is not very wide and the cingula are not so prominent as in *L. kidogosana.*

The $\mathbf{P^4}$ (Pl. 2, Figs 2, 12) has a large protocone and well-developed protoloph. The metacone is not very well separated and smaller than the paracone. *Nguruwe* does not have a protoloph, *L. kidogosana* does.

The $\mathbf{M^1}$, $\mathbf{M^2}$ and $\mathbf{M^3}$ (Pl. 2, Fig. 4) have a well-formed protoloph. There may be a fairly high and straight tetraloph, but fusion may also be less complete and a tetraprecrista extends into the transverse valley. The morphology is intermediate between the bunodont *Nguruwe* and the fully lophodont *L. kidogosana,* but closer to the latter. An M^3 which was believed to be an M^2 of cf. *Schizochoerus* (Pickford, 1986b) is similar in morphology to a specimen from Arrisdrift (Pl. 34, Fig. 5). The size of the molars is inferior to those of other Lopholistriodontini (Text-fig. 29).

There are few elements of the **postcranial skeleton,** of general suoid morphology; their most important information is their size.

Discussion — The material described here includes the holotype (from Set II) of *Lopholistriodon moruoroti,* which is among the specimens with least developed lophs.. Some specimens from Maboko (Set III) have full lophodonty. Despite morphological variation, all material is assigned to *L. moruoroti.* Morphologically, the species is intermediate between *N. kijivium* and *L. kidogosana* and there are arguments for placing the species in *Nguruwe* as well as in *Lopholistriodon.* It is here retained in the latter genus. It is not considered advantageous to create a genus for the sublophodont state in this tribe.

Lopholistriodon pickfordi n. sp.

Pl. 2, Fig. 7; Pl. 3, Figs 3, 7; Pl. 4, Figs 6, 7;
Pl. 5, Fig. 13

1974 *Listriodon* sp. — Harris & Watkins, p. 576.
1981 *Lopholistriodon* sp. — Andrews *et al.*, p. 45 (*partim*).
1981 Tayassuidae indet. — Andrews *et al.*, p. 45 (*partim?*).
1985 *Lopholistriodon* cf. *moruoroti* — Leakey & Walker, p. 174.
1986b *Lopholistriodon moruoroti* Wilkinson, 1976 — Pickford, p. 56-58 (*partim*).
1986b Genus indet cf. *Schizochoerus* Crusafont and Lavocat, 1954, species nov. small — Pickford, p. 74-76 (only KNM MB 406).

Holotype — KNM-WS 115, a right mandible with M_2 and M_3 and a left mandible of the same individual also with M_2 and M_3 (Pl. 4, Fig. 6), in the Kenya National Museums collections. Paratypes are KNM-WS 14478, left M^3 from West Stephanie; Majiwa: KNM-MJ 9778 right I^1 and I^2, KNM-MJ 9779 C^{m}; Nyakach-Kaimoroon: KNM-NC 9802 M_3, KNM-NC 9808 M_3; Maboko: KNM-MB 25 I_1, KNM-MB 26 I_2, KNM-MB 14446 I_2, KNM-MB 14448 I_2, KNM-MB 10289 M_2, KNM-MB 10333+144 M_2, KNM-MB 14479 M_2, KNM-MB 14480 M_2, KNM-MB 15118 M_2, KNM-MB; KNM-MB 406 M^3, KNM-MB 611 M^3, KNM-MB 14478 M^3. All specimens in KNM.
Type locality — West Stephanie-Buluk, Kenya.
Age of type locality — Early Miocene, Set III.
Diagnosis — Sublophodont *Lopholistriodon* with I^1 with one lobe, but with tendency to increase the DMD and index I; slightly larger than *L. moruoroti.*
Derivatio nominis — Named in honour of Martin Pickford, in recognition of his work on fossil Suoidea.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Maboko	KNM	Pickford 1986b	Set IIIB	Pickford 1986c
Majiwa	KNM		Set IIIB	Pickford 1986c
West Stephanie-Buluk	KNM		Set IIIA <17.3 Ma >17.2 Ma	Pickford 1986c Harris & Watkins 1974 McDougall & Watkins 1985
Nyakach-Kaimoroon	KNM		Set IIIC	Pickford 1986c

Description and comparison — Lopholistriodon pickfordi is very similar to *L. moruoroti* in morphology and is only slightly larger.

The I_1 and I_2 (Pl. 3, Figs 3, 7) have high crowns. The endocristid is not as pronounced as in suids of other subfamilies. The I_1 has an index of <100 and the I_2 of around that value (Text-fig. 27). The teeth are still close to the primitive suid type and resemble the incisors of *Nguruwe.* Later incisors of *L. pickfordi* are expected to be wider (see description I^1). The crowns of the incisors of *L. kidogosana* are much lower and wider.

No M_1 are known from West Stephanie or Nyakach. In Maboko, *L. pickfordi* co-occurs with *L. moruoroti.* In the case of isolated teeth it is difficult or impossible to know the difference between an M_2 of the small species and an M_1 of the larger species.

The M_2 (Pl. 4, Fig. 6) is known from West Stephanie from mandibles where their position is known. The endocristids in the second lobe are not yet completely fused. The teeth are sublophodont.

The M_3 (Pl. 4, Fig. 6) is larger than in *L. moruoroti.* The protolophid is well formed. In Nyakach, one of the specimens has a hypolophid and thus is fully lophodont. The other specimen from Nyakach, as well as those from West Stephanie (Pl. 4, Fig. 6b) and Maboko have second lobes with high and slender endocristids that have the dentine in contact, but that do not fuse, *e.g.* the dentine remains separate. These teeth are still sublophodont. The third lobe is wide and long with one main cusp. The third lobe does not have a fossid as described in *L. kidogosana*, but is of a normal listriodont morphology.

The I^1 (Pl. 5, Fig. 13) is known only from Majiwa. It is elongated compared to the incisor of *L. moruoroti*, which is also found in Majiwa (Pl. 2, Fig. 5). It is assigned to *L. pickfordi* because it has the right size (DLL) and there is no other listriodont known from localities of this age, to which it might have belonged. It is certainly too small for *L. akatidogus.* The I_1 and I_2 from Maboko seem too narrow for the I^1 from Majiwa. This might indicate an increase in DMD and I of the incisors (Maboko has a section of 50 m yielding fossils, the upper part is equivalent to Majiwa). The tooth has one lobe, unlike the I^1 of *L. kidogosana*, which is bilobed. The I^1 of *L. pickfordi* and *L. kidogosana* are of similar size, like the cheek teeth of these species. Distally, there is a low extension, which is lacking in *L. moruoroti* and in *Nguruwe.* This part is much higher in

L. kidogosana. The tooth of *L. pickfordi* is intermediate.

The **I^2** (Pl. 5, Fig. 13) is known from Majiwa, where it is found in a premaxilla with I^1. It is close in size to the I^2 of *L. kidogosana*.

There is one **C^m** from Majiwa, which is heavily abraded. It is short and not much curved.

One **M^2** (or M^1?; Pl. 3, Fig. 6) from Maboko is assigned to *L. pickfordi*. It is much smaller than the M^2 of *L. akatidogus* and slightly larger than the M^2 of *L. moruoroti* and might also belong to that species. The protoloph is well formed. The tetraprecrista is directed anteriorly of the metacone and is not well fused to that cusp. There is, however, no tetrapreconule. The molar is still sublophodont.

The **M^3** is either sublophodont, as in West Stephanie (Pl. 4, Fig. 7), or fully lophodont as in a specimen from Maboko, where the tetraloph is even fairly straight. The specimens are clearly larger than the molars of *L. moruoroti*, but smaller than *L. kidogosana*.

Discussion — *L. pickfordi* resembles *L. moruoroti*, but the known parts differ in two characters. The I^1 of both *L. moruoroti* and *L. pickfordi* are known from Majiwa (Pl. 5, Fig. 13; Pl. 2, Fig. 5) and they are clearly different. *L. moruoroti* has the I^1 identical to *Nguruwe*, but relatively larger. There is no tendency in *L. moruoroti* to increase the index I, not even in Muruyur, which is generally placed in Set IV. The I^1 of *L. pickfordi* increased the index I and DMD, the distal side clearly shows a low extension (Pl. 5, Fig. 13).

The second difference is one of size. For the M_2, there are small samples from Maboko of *L. moruoroti* and *L. pickfordi*. *L. moruoroti* from Maboko is known by several mandibles which preserve the M_2 (Pl. 3, Figs 5, 8). Some isolated specimens from Maboko are much larger than these M_2 and are assigned to *L. pickfordi* on account of size. The coefficient of variation of the lengths of the large isolated specimens and the M_2 from mandibles together is 10.9 and the V' is 30. For the maximum width CV is 7.7 and V' is 37. The variation of V' is dependent of sample size, high values being rare in small samples (Freudenthal & Cuenca Bescos, 1984). A V' of 37 for only 6 measurements would be extreme in Suoidea. For 48 M_2 of Recent *Sus scrofa vittatus* from Deli (Sumatra), V' for the DT is 23. Other large samples, mainly of fossils, never are over 30.

L. pickfordi has larger molars (and canines) than *L. moruoroti* and has an elongate I^1. These characters are considered sufficient proof that *L. pickfordi* is a different species.

L. pickfordi is placed in *Lopholistriodon* because of its resemblance to *L. moruoroti* in molar structure and because of its C^m, which is not curved outwards.

Lopholistriodon kidogosana

Pickford & Wilkinson 1975

Pl. 2, Figs 14-16; Pl. 4, Fig. 2; Pl. 5, Figs 1-12, 14-16

? 1974 *Schizochoerus* sp. n. — Aguirre & Leakey, p. 224-225, fig. 9?
1975 *Lopholistriodon kidogosana* sp. nov. — Pickford & Wilkinson, p. 132-139, pl. 1.
1978 *Lopholistriodon kidogosana* Pickford and Wilkinson 1975 — Wilkinson, p. 446.
1986b *Lopholistriodon kidogosana* Pickford and Wilkinson, 1975 — Pickford, pp. 58-69, figs 62-69.
1992b *Lopholistriodon kidogosana* — Van der Made, pp. 92, 95, 97.
1992b *Lopholistriodon* aff. *kidogosana* — Van der Made, pp. 95, 97.

Holotype — KNM BN-992, a male skull with right and left C^m, P^2-M^3 (Pl. 5, Figs 14, 15), in the Kenya National Museums collections and figured by Pickford & Wilkinson (1975, pl. 1) and Pickford (1986b, figs 62-69).
Type locality — Locality 2/10 in the Ngorora Formation, Member D, Kenya.
Age of the type locality — Middle Miocene, approximately equivalent to MN 8.

Diagnosis — Lophodont *Lopholistriodon*, with bilobed I^1.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
2/1 Ngorora Fm, Member B	KNM	Pickford 1986b	11.94-12.31 Ma	Bishop & Pickford 1975
2/56 Ngorora Fm, Member B	KNM	Pickford 1986b	11.94-12.31 Ma	Bishop & Pickford 1975
2/71 Ngorora Fm, Member C	KNM	Pickford 1986b	11.94-9.82 Ma	Bishop & Pickford 1975
2/73 Ngorora Fm, Member C	KNM	Pickford 1986b	11.94-9.82 Ma	Bishop & Pickford 1975
2/10 Ngorora Fm, Member D	KNM	Pickford & Wilkinson 1975; Pickford 1986b	9.82-9.68 Ma	Bishop & Pickford 1975
2/11 Ngorora Fm, Member D	KNM	Pickford 1986b	9.82-9.68 Ma	Bishop & Pickford 1975

Description and comparison — *L. kidogosana* is the type and first species of the genus to have been described. It resembles *Listriodon* in the lophodont molars. Comparisons are made with *L. splendens*, the type of *Listriodon*, and with *L. pentapotamiae*, the most primitive *Listriodon*.

The **I_1** (Pl. 2, Fig. 16) has an index I (Text-fig. 27) and crown height resembling the incisors of *L. pentapotamiae* and early *L. splendens*.

The **C_m** has clearly a scrofic section.

The **P_3** (Pl. 5, Fig. 7) has a large protoconid, metaconid and paraconid. The protoconid and metaconid form a wide lophid. The back of this lophid is flat, but a low protopostcristid originates at midheight of the protolophid. It is straight and does not show any swelling or indication of a hypoconid. The posterior lobe is much wider than the anterior lobe and is made up of the buccal protopostcristid and a large central and lingual basin. The absence of a hypoconid and hypoendocristid suggests that this tooth is not a P_4. The protolophid is wider with a much flatter and more vertical posterior side than in *Listriodon.*

The **D_4** and **M_1** are only represented by fragments.

The **M_2** (Pl. 4, Fig. 2) is fully lophodont, with high and slender lophids a wide transverse valley and a low and reduced hypoprecristid. In *Listriodon* the sides of the molars slope, so that the DT of a loph is much less near the top than near the base. This is not the case in *L. kidogosana* (Pl. 4, Fig. 2a, c).

The **M_3** has a large third lobe in two older specimens from the B member (Pl. 2, Figs 14, 15) with a high pentaconid with clear pentaendocristid and pentaprecristid and closing a shallow pentafossid. In two specimens from Member D (Pl. 5, Fig. 9) the third lobe is very short and low and extends only slightly more distally than the posterior cingulum of an M_1 or M_2. In *Listriodon* the third lobe is narrower relative to the second lobe, the anterior end of the pentaprecristid is higher, placed nearer to the axis of the tooth and often there is a pentapreconulid. In *Listriodon* there is never such a clear pentafossid as in the older *L. kidogosana.*

The **I^1** (Pl. 5, Fig. 1) has two lobes as in *Listriodon.* The index I is 172, which is less than all *L. splendens,* but two (151, 166) and all *L. pentapotamiae,* but one (156), which in both cases are values far beyond the normal range (Text-fig. 27). The DMD' value is lower than in *L. splendens* (Text-fig. 26).

The **I^2** (Pl. 5, Figs 2, 4) has an elongate 'talon' and a low crown. In lateral view, the anterior edge of the root is convex and curved backwards.

The teeth that are interpreted as **I^3** (Pl. 5, Fig. 3) have slightly higher and shorter crowns than the I^2 with a shorter 'talon'. The root has a concavo-convex anterior edge.

The **C^m** (Pickford, 1986b, figs 62-65) are known from the holotype skull only. Therefore, only their tips can be studied. They are short and have three enamel bands. The canines are rotated 40-45° outwards, but are not curved outwards. In *Listriodon* the canines are much longer and very clearly curved outwards.

Both **P^2** and **P^3** (Pl. 5, Figs 5, 8, 15) have a large, but low, protocone and wide labial and lingual cingula. Although the teeth look very wide, their index I is not lower than that of *Listriodon.* The paracone is very narrow, so that the cingula and protocone occupy a lot of space compared to the paracone; this probably gives the impression that the *Lopholistriodon* premolars are very wide. The DAP' and DT' values of the P^3 are low compared to *Listriodon.*

The **P^4** (Pl. 5, Fig. 6) tends to have the paracone and the large metacone well separated. However, in the P^4 (Pl. 5, Fig. 15) of the skull, the metacone is small. It is not clear whether this difference is just variation or reflects a change in time. The protoloph is well developed and high. The protopostcristid may be high and connected to the metacone or low and short, leaving the protofossid open from behind. The anterior and posterior cingula are wide, wider than in *Listriodon.*

The **M^1** and **M^2** (Pl. 5, Figs 10-12, 14) are perfectly lophodont with high and slender lophids, wide transverse valleys and low protopostcristid and tetrapostcristid. As in the lower molars, the tips of the cusps are wide apart, resulting in wide lophs.

The **M^3** (Pl. 5, Figs 14, 16) have small talons. The reduction of the third lobe in the younger M_3 (from Member D) apparently does not affect the morphology of the M^3. There is one aberrant specimen with a complete lingual cingulum. Such a character does not normally occur in Suidae.

The **mandible** is known from a fragmentary symphysis.

The **skull** (Pickford & Wilkinson, 1975, pl. 1; Pickford, 1986b, figs 62-64) was described in great detail and the function of its morphology was interpreted by Pickford (1986b). Some of characters of importance are mentioned here. The frontals do not show any protuberances, but the orbits project a little above the plane of the frontals. The transverse section through the snout is rounded, not angular as in *e.g. Sus.* There are no lacrimal foramina. There is no preorbital fossa, in this area the bone is flat. The zygomatic arcs do not depart at a great angle from the side of the skull and there is no indication of inflation of these bones. There is a small crista alveolaris over the C^m. It is not an elongate structure as in *e.g. Potamochoerus,* but a structure with a flat and transverse anterior side, much like in Recent tayassuids, but placed more externally and free from the side of the snout. The diastemata are long. The palate extends far behind the M^3. The palatine foramen is at the level of the first lobe of the M^3. The glenoid is 'saddle' shaped as in suids and not cylindrical as in Recent tayassuids. Its position is high above the occlusal plane and far to the back of the skull, at the end of the zygomatic arcs. The jugular process has a massive base (the rest is broken off) and is directed slightly backwards.

Discussion — Lopholistriodon kidogosana is very similar to *Listriodon pentapotamiae* and to the more primitive *L. splendens,* especially in incisor, molar and skull morphology. There are differences in premolar, canine and M_3 morphology. Superficially, the resemblances are such that all three might be included in a single genus. However, the C^m of *L. kidogosana* are short and not much curved outwards which is also the case in *L. moruoroti* and *Nguruwe*. *Listriodon* has longer canines which are always curved much as in *Bunolistriodon*. The transition from sublophodonty towards lophodonty is observed in *Lopholistriodon moruoroti* and in *Bunolistriodon-Listriodon* (see chapter on phylogeny). If the latter observations are right, than the resemblances in incisor and molar morphology between *L. kidogosana* and *Listriodon* must represent convergence and part of the skull morphology too (the incisor area and diastemata). Thus, *Lopholistriodon* is a genus distinct from *Listriodon*.

Lopholistriodon kidogosana is represented by only few elements from Members B and D. So comparisons are restricted to those elements. The M_3 are the only teeth that really do show differences. The difference in width of the second lobe still might be variation as encountered in a population, but the variation in size of the third lobe exceeds that found in all material assigned to the genus *Listriodon*. There are two specimens of two individuals each (as indicated by side or wear) from Member B and two from Member D, so the variation is probably not due to some abnormality, but to a real difference. The reduction of the third lobe may prove to be a useful stratigraphical tool, but more material is needed.

Lopholistriodon akatidogus (Wilkinson, 1976)
Pl. 6, Figs 1-11

? 1963 *Listriodon* cf. *jeanneli* Arambourg — Hooijer, p. 52, pl. 9, figs 4, 8-10, excluding the premolar of pp. 52-53 and pl. 9, figs 5-7.
? 1975 *Listriodon* sp. C — Pickford & Wilkinson, p. 133-134 (Fort Ternan specimens).
? 1975 *Lopholistriodon kidogosana* sp. nov. — Pickford & Wilkinson (Fort Ternan material only).
1976 *Listriodon akatidogus* sp. nov. — Wilkinson, pp. 240-243 (except the specimen from Rusinga, and the P^3), pl. 7, fig. D.
1977 *Listriodon juba* nov. sp. — Ginsburg, pp. 221-224, figs 1-3.
1978 *Listriodon akatidogus* Wilkinson 1976 — Wilkinson, p. 445.
? 1981 *Bunolistriodon kidogosana* — Shipman *et al.*, p. 67.
? 1986 *Bunolistriodon kidogosana* — Shipman, p. 196.
1986b *Listriodon akatikubas* Wilkinson, 1976 — Pickford, pp. 49-52 (material from Fort Ternan, figs 52-54, 58 and an incisor from Majiwa).
1986b ?*Listriodon akatidogus* Wilkinson, 1976 — Pickford, pp. 54-55, fig. 60.
1986b *Listriodon juba* Ginsburg, 1977 — Pickford, p. 55.
1992b *Lopholistriodon akatidogus* — Van der Made, pp. 92, 95, 97.
1992b *Lopholistriodon juba* — Van der Made, pp. 92, 95, 97.

Holotype — KNM-MG 9, left M_3 (Pl. 6, Fig. 3), in the Kenya National Museums collections, figured by Wilkinson (1976, pl. 7, fig. D).
Type locality — Mbagathi, Kenya.
Age of the type locality — Early Miocene, Set III.
Diagnosis — A sublophodont species of *Lopholistriodon* with wide incisors, approximately 130 % the size of *L. kidogosana*.

Loc.	**Coll.**	**Ref./Descr.**	**Stratigr.**	**Ref.**
?Sinda 2		Hooijer 1963	Set III?	
?Sinda 10		Hooijer 1963	Set III?	
?Gebel Zelten		Wilkinson 1976	Set III	Pickford 1981
Mbagathi	KNM	Wilkinson 1976, Pickford 1986b	Set III	Pickford 1986a
Maboko	KNM		Set IIIB	Pickford 1986c
Majiwa	KNM		Set IIIB	Pickford 1986c
Beni Mellal	MNHN (casts)	Ginsburg 1977	MN 7	Mein 1990
Fort Ternan	KNM	Wilkinson 1976	Set IV	Pickford 1981

Description and comparison — Comparisons with *Lopholistriodon kidogosana* and *L. moruoroti* are made, because these species were described earlier. Since the present species was initially placed in *Listriodon*, it is compared with *L. splendens* as well.

The **I_2** (Pl. 6, Fig. 1) has a low and wide crown (index I = 145) and is comparable to early *L. splendens* and advanced *L. pentapotamiae*. In this respect it is as advanced as the I_1 of *L. kidogosana*. The endocristid is clear.

A small incisor is assumed to represent a **DI_2** because of its small size and association, being from Maboko.

The **I_3** (Ginsburg, 1977, fig. 3) has a wide and low crown. The root is broken and it can be seen that there are two pulp cavities just below the crown, which only occurs in very wide incisors. A specimen from Sinda 2, figured by Hooijer (1963, pl. 9, figs 9, 10) is similar in size and morphology. The degree of flattening is as in early *L. splendens*.

One tooth was assumed to be a P_3 (Ginsburg, 1977, fig. 1) However, because of its size relative to the P^3, it seems more likely to be a **P_2**. A small metaconid is present, but it is not well separated from the protoconid. The protopostcristid is low and a hypoconid is not really developed as a cusp, though there is a low continuation of the protopostcristid at that place. The major part of the talonid is occupied by a basin. The shape of the talonid resembles that of the P_3 of *L. kidogosana*, but differs from that in *Listriodon*, where the protopostcristid is much higher. There are two roots, but they are fused for most of their length, which fact might be another indication that the tooth is a P_2.

The M_2 (Pl. 6, Figs 10, 11) has a real protolophid. The endocristids of the second lobe touch, but are not fused, at least for most of their height. There are sharp grooves at the anterior and posterior sides of the structure, marking the ends of the endocristids. The M_2 is sublophodont. However, the protolophid and pseudohypolophid are slender and high structures. In the earliest *Listriodon*, full lophodonty is attained when these structures seem much lower and only in later forms do the lophids seem higher. It is not clear, whether the lophids in these forms really become a little higher, or that they become more slender and the transverse valley wider, so that they seem higher. The hypoprecristid is high and ends in a hypopreconulid. Seen from the buccal side, the hypoprecristid may be smooth, or the hypopreconulid may be visible as a bulge. At the lingual side, the hypopreconulid is always visible as a separate cusp. The protoprecristid is a real crest, enclosing a protofossid. It is not such a gentle fold in the enamel as in *Listriodon*.

The M_3 (Pl. 6, Figs 3, 11) has a variable third lobe, which may be short with a steep posterior side or long, with a gently sloping posterior side. There is a clear hypopostcristid running towards the pentapreconulid.

The I^2 (Pl. 6, Fig. 4) has an elongate and low crown. Its index I is 218, which is more than in *L. kidogosana* ($174 \leq I \leq 200$) and *L. moruoroti* (149).

The I^3 (Pl. 6, Fig. 5) is elongate (index I = 227). The end of the root is absorbed, probably because it touched the root of the I^2.

The C^m (Pl. 6, Fig. 6) is a short tooth which is not much curved outwards. In *Listriodon* the C^m is long and much curved outwards, but in *L. kidogosana* and *L. moruoroti* the canine is short and not much curved.

A canine from Sinda 2 (Hooijer, 1963, pl. 9, fig. 4) probably represents a C^f of this species. The crown is low and there is a clear endosyncline.

The D^4 (Pl. 6, Fig. 9) has the anterolabial angle protruding, as is normal for this tooth. The precristas of the labial and lingual cusps meet, but are low where they meet. The transverse valley is wide and there is no tetrapreconule nor large tetraprecrista.

The P^3 (Ginsburg, 1977, fig. 2) has a clear labial cingulum, but not as clear as in *L. kidogosana* (Pl. 5, Figs 8, 15). The protocone is well developed (but not as well as in *L. kidogosana*) and surrounded by a wide lingual cingulum. The tooth is not as wide as in *L. kidogosana*, but resembles that of *L. moruoroti* and *Listriodon*.

There is one P^4 with a metacone and one without (Pl. 6, Fig. 8). Both paracone and protocone have a simple postcrista and precrista. There is a wide anterior, lingual and posterior cingulum; at the labial side it is not continuous. In *L. moruoroti* there is no metacone either and the cingulum is less developed. In *L. kidogosana*, the cingulum is also well developed at the labial side and a small metacone is formed. The *L. akatidogus* premolars have an intermediate morphology. *L. splendens* has a large metacone.

The only M^1 and M^2 from Fort Ternan are worn and damaged and not much can be said about their morphology. The M^2 from Maboko (Pickford, 1986b, fig. 60) has a protoloph, that is low near to the paracone. The protopostcrista is a clear crest. The tetraloph is low in the middle and has a V-shaped facet over it. It is still an imperfect tetraloph.

The M^3 from Fort Ternan (Pl. 6, Fig. 2) is sublophodont; the metaprecrista and tetraprecrista meet, but are not fused. The tooth is worn and the dentine islands of the metacone and tetracone are large already, still the two dentine islands do not meet. There is no tetrapreconule nor a large tetraprecrista; the transverse valley is wide. The specimen from Maboko (Pl. 6, Fig. 7) has a large tetraprecrista that remains well separated from the metacone. There is an upper molar from Sinda 10 (Hooijer, 1963, pl. 9, fig. 8), that should be an M^3 (and no M^1) on account of its skewed outline. It has a protoloph, but from the plate it appears that the second lobe is not yet lophodont like in the specimen from Maboko. In size this tooth agrees well with the Fort Ternan and Maboko specimens. The upper molars have better developed lophodonty (with the precristas fused better) in *L. kidogosana* and *L. splendens*. In *L. moruoroti* the molars are in some cases more lophodont and in other cases more sublophodont.

A **distal metapodial** is assigned to this species on account of its size.

Discussion — All specimens described here resemble some species of *Lopholistriodon*, but are larger and all indicate the same size of animal. The material seems to be homogeneous and to have belonged to a single species.

The fossils from Mbagathi include the type of *L. akatidogus*, teeth from Beni Mellal are the types of *L. juba* and those from Fort Ternan have been assigned to *'Listriodon' akatikubas* (Pickford, 1986b). The latter species is here considered to belong in *Bunolistriodon*.

The sizes of the teeth from Beni Mellal and Fort

Ternan and the type of *B. akatikubas* cannot be compared directly. Compared with the type of *L. kidogosana*, the length of the P^3 from Beni Mellal is 130 % and the lengths of the P^4, M^1 and M^3 of the maxilla from Fort Ternan are 123, 123 and 125%. The type of *B. akatikubas* is an M_3 and compared to the larger M_3 of *L. kidogosana* (which do not have a reduced third lobe), it has a length of 161 %. There are more specimens of the small listriodont from Fort Ternan and of *B. akatikubas*, which show that the sizes of the specimens compared are representative of the sample. It is likely that the teeth of the small listriodont from Fort Ternan do not belong to *B. akatikubas*. On the basis of size, the teeth from Fort Ternan and Beni Mellal cannot be assigned to different species.

Similarly, the sizes of these teeth can be compared indirectly to *L. kidogosana*. The holotype M_3 of *L. akatidogus* has 140 % the size of a specimen of *L. kidogosana*, but an M_2 and M^2 only 134 and 130 %, respectively. These fossils from Mbagathi, Maboko, Sinda, Beni Mellal and Fort Ternan must all have belonged to individuals of approximately the same size. All these molars are sublophodont. Those from the younger localities approach more closely the lophodont condition. If they really are typical of their populations, this indicates a small evolutionary advance, but the difference is so small that the variation in morphology is expected to overlap in these populations. All samples with lower molars show a tendency for slender and high lophids before full lophodonty is attained, contrary to *Listriodon* where first lophodonty is attained and then the lophs become higher and/or more slender. All material is here assigned to the same species, *viz. L. akatidogus*. If in future there should appear to be significant differences in the development of the lophs, which in any case are expected to be very small differences, a subspecies *L. akatidogus juba* might be recognised.

Lopholistriodon akatidogus was first assigned to *Listriodon*. *Listriodon* attained full lophodonty before it entered Europe in MN 6. The oldest *Listriodon pentapotamiae* is probably older than that. *Listriodon* was already lophodont when *L. akatidogus* remained still sublophodont. Thus lophodonty is not a shared derived character of *Listriodon* and *L. akatidogus* and cannot be used to place this species in that genus. The talonid basin of the P_2 is like in *L. kidogosana* and unlike *Listriodon*, where there is a cusp at that place. The C^m is short and not curved outward as in *Lopholistriodon* and unlike *Listriodon*. Thus *L. akatidogus* should be placed in the former genus.

Wilkinson (1976) doubtfully assigned a mandible from Gebel Zelten to *L. akatidogus*, on the basis of size, since the morphology of the teeth could not be studied any more on account of poor preservation. The molars agree in size with *L. akatidogus*, but the premolars are much larger. *Lopholistriodon* shows a tendency to reduce size (and number) of the premolars, this is not or not so much the case in *Bunolistriodon* and the specimen might belong to that genus. The specimen will be discussed later on in the section on *Bunolistriodon*? sp.

Tribus Kubanochoerini Gabunia, 1958
(nom. trans. ex Kubanochoerinae Gabunia, 1958)

Diagnosis — Large bunodont Listriodontinae with cranial appendages. (A description of the cranial appendages is given under *K. gigas* and *K. massai*, these parts are not known from all Kubanochoerini.)

Genus *Kubanochoerus* Gabunia, 1955
(including *Libycochoerus* Arambourg, 1961)

Type species — *Kubanochoerus robustus* Gabunia, 1955 = *K. gigas* (Pearson, 1928).
Diagnosis — As for tribe.

Kubanochoerus marymunnguae n. sp.
Pl. 7, Figs 1, 2, 5, 7-9, 11-15

1981 *Libycochoerus khinzikebirus* — Pickford, p. 89.
1985 *Libycochoerus massai* — Leakey & Walker, p. 174.
1992b *Kubanochoerus* sp. — Van der Made, pp. 91, 97.
1993 *Kubanochoerus* sp. — Guan & Van der Made, p. 176.
1993 *Kubanochoerus khinzkebirus* — Guan & Van der Made, fig. 9 (Karungu and Mfwangano).

Holotype — Holotype is KNM-WS 12595, right and left P_2-M_3 (Pl. 7, Figs 7-9, 11, 15), in the Kenya National Museums collections.
Paratypes — West Stephanie-Buluk: KNM-WS 12588 P^2, KNM-WS 12590 M^3, KNM-WS 12656 P^3, KNM-WS 12656 M^3, KNM-WS 125149A I_2, KNM-WS 12549B I_3, KNM-WS 125 KNM-WS 12594 M^3, KNM-WS 12586 P_4, KNM-WS 12587 P_4; Baragoi: KNM-BG 18014 I^2 or I^3, KNM-BG 18012 P_2, KNM-BG 17868 D^2, KNM-BG 17970 astragalus, KNM-BG 16903 astragalus, KNM-BG 169 16916 astragalus, KNM-BG 17861 distal tibia. All specimens in the KNM.
Type locality — West Stephanie-Buluk, Kenya.
Age of the type locality — Early Miocene, Set III.
Diagnosis — *Kubanochoerus* with molars as long as in *K. massai*, but much wider and relatively large premolars (DAP' and DT'); the lower premolars are relatively wide (I).

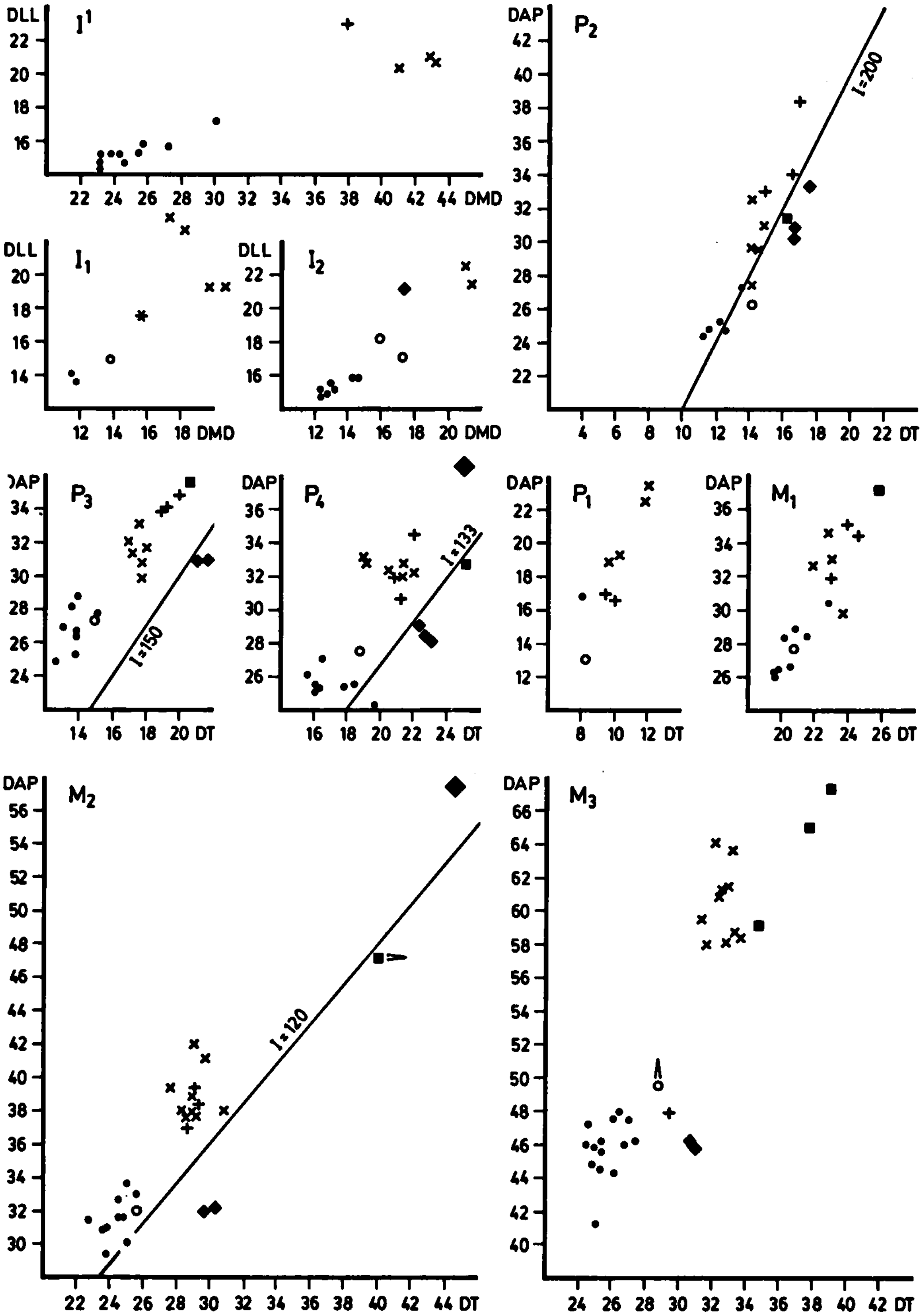


Fig. 30. Bivariate plots of *Kubanochoerus* central incisors and lower cheek teeth. Legend: dots - *Kubanochoerus massai*; circles - *Kubanochoerus minheensis*; crosses - *Kubanochoerus g. gigas* (data from Gabunia, 1960 and Liu & Lee, 1963a); asterisks - type material of *K. g. gigas* (data from Pearson, 1928); oblique crosses - *Kubanochoerus g. lii*; small diamonds - *Kubanochoerus marymunnguae*; squares - *Kubanochoerus khinzikebirus*; large diamonds - *Kubanochoerus mancharensis* (data on P_4 from Pickford, 1986b); arrows indicate that a tooth is damaged and is larger than indicated. The lines represent values of the index I.

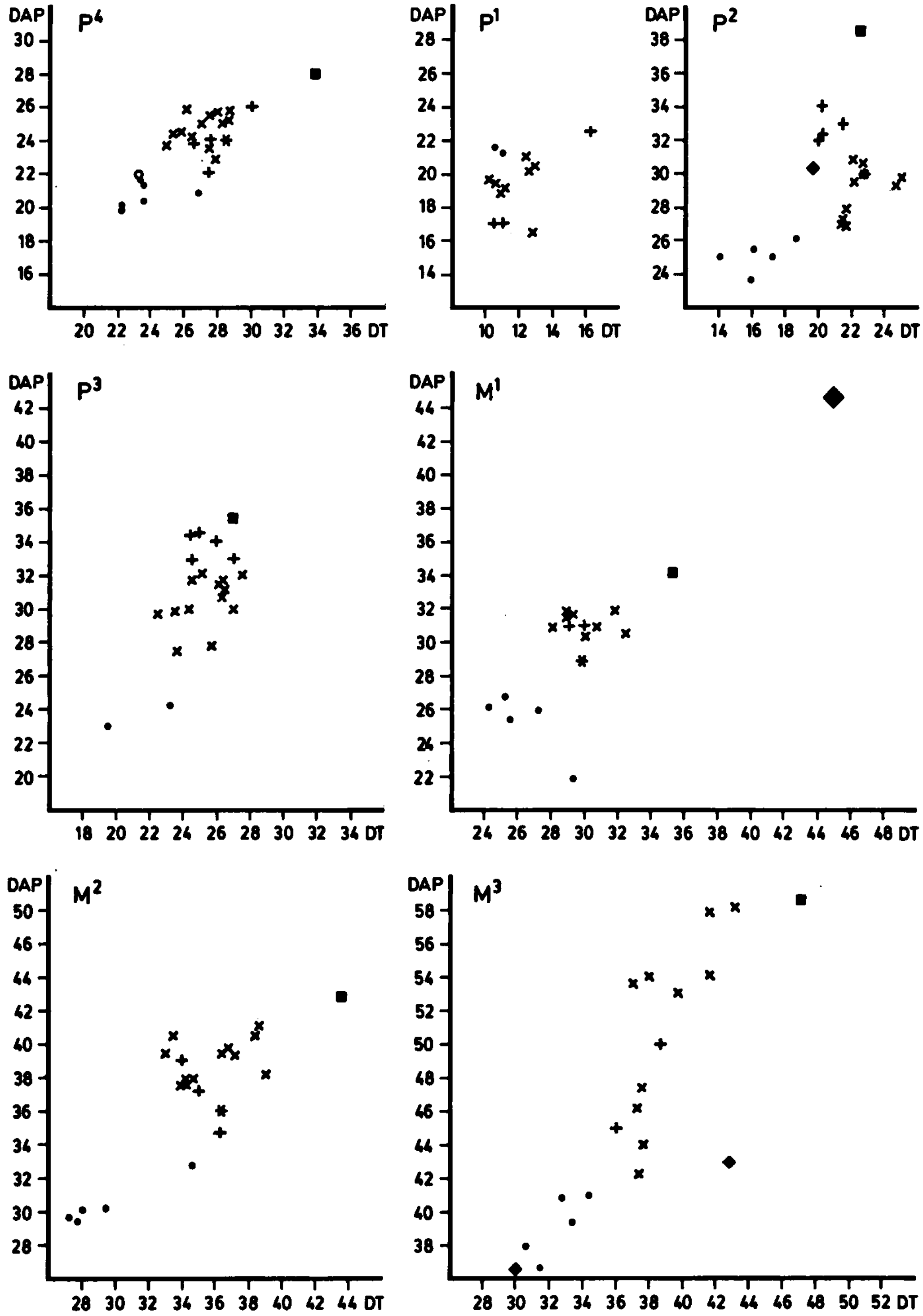


Fig. 31. Bivariate plots of *Kubanochoerus* upper cheek teeth. Legend as in Fig. 30.

Derivatio nominis — Named in honour of Mary Mungu, who assisted me during my work in the KNM.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
West Stephanie-Buluk	KNM		Set IIIA <17.3 Ma >17.2 Ma	Pickford 1986c Harris & Watkins 1974 McDougall & Watkins 1985
Baragoi	KNM		Set III	Pickford pers. com.
?Mfwangano	KNM		Set II	
?Karungu	KNM		Set II	Pickford et al. 1986b

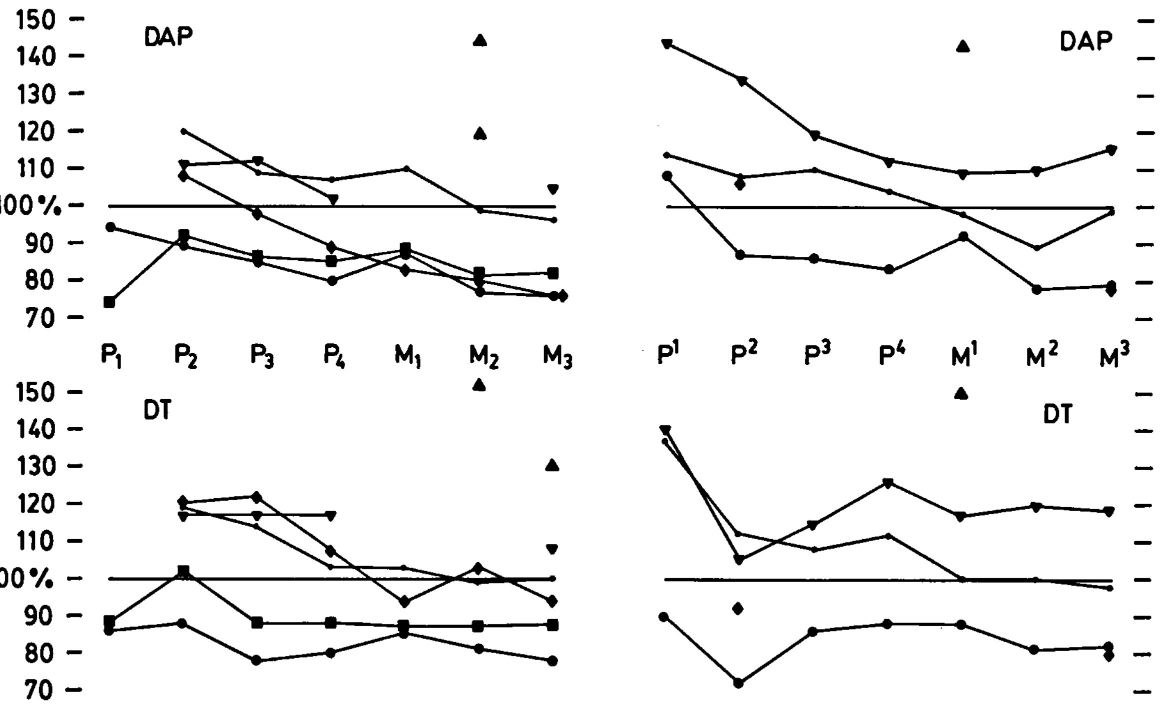


Fig. 32. Size of cheek teeth of *Kubanochoerus* species compared. The mean of *K. g. lii* from Tongxin is 100 % (data from Guan & Van der Made, 1993). Legend: diamonds - *K. marymunnguae* from Buluk (holotype for lower, average for M^3); triangles with points downward - *K. khinzikebirus* from Gebel Zelten (data from Wilkinson, 1978); triangles with points upward - *K. mancharensis* from Nyakach, Bugti (data from Pickford, 1987a) and Inönü I (data from Pickford & Ertürk, 1979); large dots - mean of *K. massai* from Gebel Zelten (from Guan & Van der Made, 1993); squares - *K. minheensis* from Nanhawangou; small dots - *K. g. gigas* from Belometchetskaia (data from Gabunia, 1960). Apart from the size differences, the figure illustrates that *K. gigas* has an enlarged M_3 and slightly reduced premolars (best seen in P2; reduction starts with the mesial premolars) and a tendency in the upper premolars to have larger protocones (best seen in DT of P^2). It can also be observed that *K. marymunnguae* and *K. khinzikebirus* share relatively wide molars (compare uppers and lowers) and very long premolar rows.

Description and comparison — Kubanochoerus marymunnguae is of approximately the size of *K. massai* and shares certain characters with *K. khinzikebirus*. Comparisons are made primarily with these taxa.

The I_2 and I_3 (Pl. 7, Figs 13, 14) have low indices I (Text-fig. 27) and are large compared to the molars (in terms of DMD' and DLL', though no good M_1 is preserved; Text-fig. 30).

The P_2 and P_3 (Pl. 7, Figs 7, 8) are relatively large compared to the molars (Text-fig. 32) and they have greater DAP and smaller index I than in *K. massai* (Text-fig. 30).

The P_4 (Pl. 7, Figs 5, 9) is slightly longer, but much wider than in *K. massai*. There are specimens of three individuals and all have the same proportions. In the unworn specimen, there is a protoconid, protoprecristid, protopostcristid and a protoendocristid or faint indication of a beginning of a metaconid. In *K. massai*, the metaconid is always better developed. The trigonid morphology is simpler than in *K. massai*, *K. gigas* and *K. minheensis*; in the remaining *Kubanochoerus*, no P_4 with little wear are known.

The **M_1** and **M_2** (Pl. 7, Fig. 11) have short and wide crowns. The M_2 is as long as in *K. massai*, but much wider (Text-fig. 30).

The **M_3** (Pl. 7, Fig. 15) has narrow second and third lobes. The tooth is wide and short, its length comparable to that in *K. massai*, but its width much greater (Text-fig. 30). Whereas the M_2 might be relatively wide because of wear, this effect is much less on the M_3 and the difference seems to be real.

Like the lower incisors, the **I^2** is relatively large.

The **P^2** (Pl. 7, Fig. 12) has an extremely small protocone and consequently the second lobe, and the tooth as a whole, are rather narrow. Unlike the lower premolars, the P^2 is not relatively wider (I) than in *K. massai* (Text-fig. 31).

The **M^3** (Pl. 7, Figs 1, 2) has the protopreconule connected to the cingulum. The tooth is slightly shorter than in *K. massai*, but has the same index I (Text-fig. 31).

A fragment of an upper molar from Mfwangano cannot be measured, but belonged to a suid of the size of *K. khinzikebirus*.

The **astragali** and the **tibia** are only slightly larger than in *K. massai*. The sustentacular facet is rather flat, as is common in Listriodontinae, but a low lateral ridge is present. A **first lateral phalange** (phalange II/IV 1) from Karungu has the right size for a large *Kubanochoerus* and might well belong to this species.

Discussion — In *K. marymunnguae*, the incisors and premolars (Text-fig. 32) are relatively larger, compared to the molars, than in any other *Kubanochoerus*, where these elements are known. The lower cheek teeth are relatively wider (index I) than in *K. massai*, *K. minheensis* and *K. gigas* and the P_4 has a simpler structure than in those species. *K. marymunnguae* is smaller than *K. khinzikebirus* and *K. mancharensis*, and thus is a different species.

Kubanochoerus khinzikebirus (Wilkinson, 1976)

1975 *Bunolistriodon* sp. nov. A — Pickford & Wilkinson, pp. 133-135.

1976 *Bunolistriodon* aff. *B. gigas* Pearson — Van Couvering & Van Couvering, p. 203 (Gebel Zelten).

1976 *Bunolistriodon khinzikebirus* sp. nov. — Wilkinson, pp. 230-236, pl. 6, figs a-c, non d (=? *K. massai*).

1978 *Kubanochoerus khinzikebirus* (Wilkinson 1976) — Wilkinson, p. 446.

1986b *Libycochoerus khinzikebirus* (Wilkinson) 1976 — Pickford, pp. 45, 48 (material from Gebel Zelten).

1993 *Kubanochoerus khinzikebirus* (Wilkinson, 1976) — Guan & Van der Made, p. 176 (*partim*).

Holotype — BU 6416-82 a-e, right $P_{2\text{-}4}$ and $M_{2\text{-}3}$; in the Bristol University, Geology Department collections, cast in the KNM; figured by Wilkinson (1976, pl. 6, fig. a).

Type locality — Gebel Zelten, Libya.

Age of the type locality — Early Miocene, probably equivalent to MN 4.

Diagnosis — Large *Kubanochoerus*, cheek teeth approximately 117 % the size of those of *K. gigas* and comparatively wide.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Gebel Zelten	KNM (cast)	Wilkinson 1976	Set III (lower)	Pickford 1981

Description and comparison — This species is close in size to the type species, *K. g. gigas*. Comparisons will primarily be made with that species.

The **P_2**, **P_3** and **P_4** (Wilkinson, 1976, pl. 6, fig. b) are as long as in *K. gigas* or slightly longer, whereas in the upper dentition the premolars are clearly longer (Text-fig. 32). This indicates that the lower dentition (P_2-P_4 and M_2-M_3 of one individual) belonged to a small individual and the upper teeth to a large individual. The P_4 is relatively wide (index I).

The **M_2** (Wilkinson, 1976, pl. 6, fig. b) is bunodont, at least the second lobe (the first lobe is not preserved).

The **M_3** (Wilkinson, 1976, pl. 6, fig. b) is fully bunodont. The length is about as in *K. gigas*, but the width is slightly greater (Text-fig. 30).

The **C^m** figured by Wilkinson (1976, pl. 6, fig. d) is small for such a large pig and might belong to *K. massai*.

The **P^1**, **P^2** and **P^3** (Wilkinson, 1976, pl. 6, fig. b) have a straight parapostcrista. The first premolar has only a postero-lingual cingulum, the third premolar has a protocone and is considerably wider. Compared to their homologues in *K. massai* and *K. gigas*, these premolars are not particularly wide for their length (Text-fig. 31). The premolars are much larger (also longer) than in *K. gigas*, whereas the molars of the same specimen (one maxilla with P^1-M^3) are only slightly longer, though much wider.

The **P^4** (Wilkinson, 1976, pl. 6, fig. d) is relatively wide (Text-fig. 31).

The **M^1** and **M^2** (Wilkinson, 1976, pl. 6, fig. d) have the parapreconule connected to the cingulum and are thus fully bunodont. They are slightly larger than the molars of *K. gigas* (Text-fig. 31).

The **M^3** (Wilkinson, 1976, pl. 6, fig. d) has a small pentacone.

Discussion — *Kubanochoerus khinzikebirus* differs from *K. gigas* in having relatively wide (upper) molars, which tend to be slightly longer. The premolars are relatively larger than in *K. gigas* and the P_4 is also relatively wide.

Kubanochoerus mancharensis n. sp.

Pl. 11, Figs 7, 9, 10; Pl. 12, Fig. 12

1924 *Anthracotherium*? sp.? — Forster Cooper, p. 17, fig. 14.
1976 *Bunolistriodon* aff. *B. gigas* Pearson — Van Couvering & Van Couvering, p. 203 (Maboko).
1979 *Libycochoerus khinzikebirus* (Wilkinson, 1976) — Pickford & Ertürk, p. 145, fig. 4.
1981 *Libycochoerus khinzikebirus* — Andrews *et al.*, p. 45 (Majiwa?).
1986b *Libycochoerus khinzikebirus* (Wilkinson) 1976 — Pickford, pp. 45, 48, figs 49a, b, 50a, b?.
1987a *Hemimastodon crepusculi* (Pilgrim), 1908 — Pickford, pp. 298-304 (*partim*), pl. 2, fig. 3.
1988a *Hemimastodon crepusculi* — Pickford, p. 947 (material from Nyakach and Maboko, only part of the material from Bugti).
1989 *Libycochoerus* cf. *khinzikebirus* (Vilkinson) — Tekkaya, p. 157.
1993 *Kubanochoerus khinzikebirus* (Wilkinson, 1976) — Guan & Van der Made, p. 176 (*partim*).

Holotype — Holotype is HGSP 8425/3557, a right astragalus (Pl. 11, Fig. 7), to be deposited in the collections of the Geological Survey of Pakistan. Paratypes are: Manchar Formation: HGSP 8213/450 phalange 1, HGSP 8219/1032 distal metapodial, HGSP 8311/1556 lateral phalange 1, all material in HGSP collections; Bugti: M 12700 M_2 in BMNH (figured by Pickford, 1987a, pl. 2, fig. 3); Inönü I: AKI-3/779 M^1 (figured by Pickford & Ertürk, 1979, fig. 4).

Type locality — HGSP 8425, a locality in the lower Manchar Formation.

Age of the type locality — HGSP 8425 yielded also *Listriodon pentapotamiae*, and therefore has the same age as the Chinji Formation in its type area; Middle Miocene.

Diagnosis — Very large *Kubanochoerus* (larger than *K. khinzikebirus*), with comparatively wide cheek teeth.

Derivatio nominis — Named after the Manchar Formation, the provenance of most of the type material.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Maboko	KNM	Pickford 1986b	Set IIIB	Pickford 1986c
Nyakach Kaimogool East	KNM		Set IIIB	Pickford 1986c
Nyakach Kadianga West	KNM		Set IIIB	Pickford 1986c
HGSP 8127	HGSP		Manchar ssu 1	
Inönü I		Pickford & Ertürk 1979	MN 6	Van der Made 1993
HGSP 8213	HGSP		Manchar ssu 3-4	HGSP catalogue
HGSP 8219	HGSP		Manchar ssu 3-4	HGSP catalogue
HGSP 8405	HGSP		L. Manchar	
HGSP 8425	HGSP		L. Manchar	
Chur Lando (Bugti)		Forster-Cooper 1924 Pickford 1987a		

Description and comparison — This species is very large and is approached in size by *K. khinzikebirus*. It is found together with large-sized anthracotheres and their foot bones could be confused. Comparisons are made primarily with those taxa.

An I_2 (Pickford, 1986b, fig. 49a) is not very wide and has a width comparable to the incisors of *K. gigas*. It may have had a much greater linguo-labial diameter.

A P_4 from Maboko is much wider than in *K. gigas* and comparable to *K. khinzikebirus*. Another specimen figured by Pickford (1986b, fig. 50b) is very large (Text-fig. 30).

The M_2 from Nyakach-Kaimogool East is huge and much exceeds the upper molar from Inönü I in length. The specimen is also very wide (index I $\leq$ 118). BMNH M 12700 from Chur Lando (Bugti), which was first described and figured by Forster-Cooper (1924, p. 17, fig. 14) as '*Anthracotherium*? sp.?' might well represent this species. Pickford (1987a, p. 11, pl. 2, fig. 3) assigned this specimen to *Hemimastodon crepusculi*, a suid in his opinion.

Two fragments of M_3 from Maboko (Pickford, 1986b, fig. 50a) are larger than the holotype of *K. khinzikebirus*. The largest specimen measures 124 % of the holotype of the latter species. The first lobe of a specimen from Nyakach is much wider than the holotype of *K. khinzikebirus* (122 %).

The I^3 (Pickford, 1986b, fig. 49b) is very wide. It is probably an I^3 and not an I^2 because of its very large posterior wear facet, which is caused by contact with the lower canine. I^2 have facets there that are caused by the I_3, but these facets tend to be smaller compared to the apical and anterior facets in the same tooth.

The M^1 (Pickford & Ertürk, 1979, fig. 4) has the protopreconule fused to the cingulum and is fully bunodont. The tooth was assumed to be an M^2 (Pickford & Ertürk, 1979) and is close in size to the M^2 of *K. khinzikebirus*. However, *K. khinzikebirus* is an older species and localities of the age of Inönü I yield the large *K. mancharensis*, so the tooth from Inönü may well be a first molar.

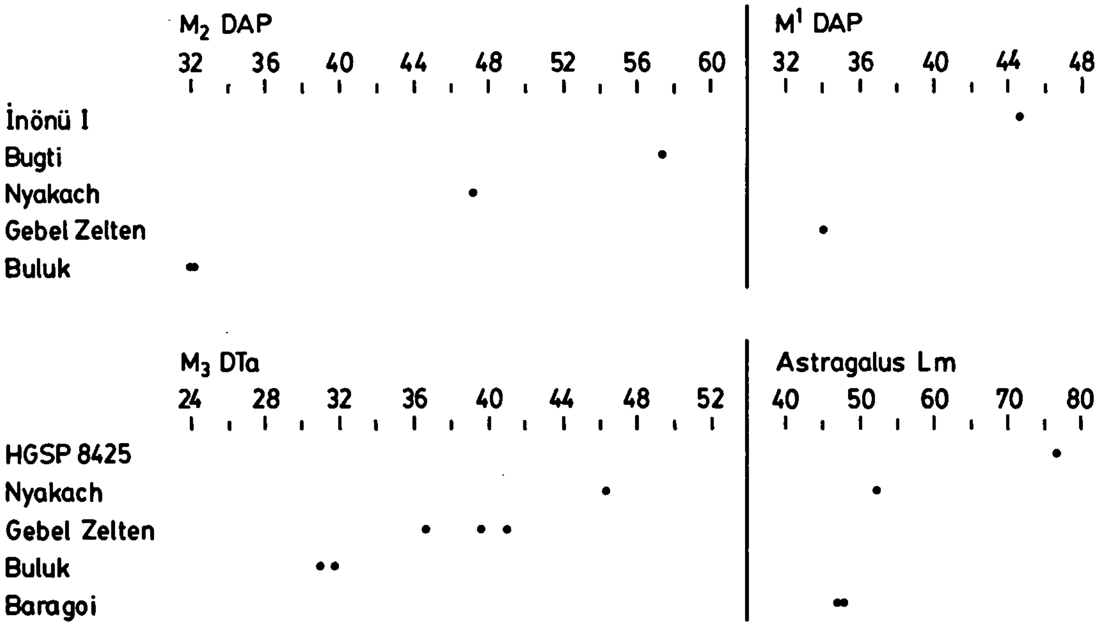


Fig. 33. Size changes in *Kubanochoerus khinzikebirus*-lineage: *K. marymunnguae* (Buluk, Baragoi), *K. khinzikebirus* (Gebel Zelten) and *K. mancharensis* (Nyakach, Bugti, Inönü I, HGSP 8425). The localities are in approximate stratigraphical order.

A fragment of M^3 from Nyakach is referred to this species.

The **astragalus** from HGSP 8425 (Pl. 11, Fig. 7) is by far the largest suid astragalus known to me. The sustentacular facet is slightly convex in transverse direction. This is typical of listriodonts, whereas in other suids this facet may be more convex. In anthracotheres there is a wide ridge next to this facet, giving the whole a concave transverse section. Anthracothere astragali of this size (and even larger) have been found in the Lower Manchar Formation, but those are clearly different. An astragalus from Nyakach-Kaimogool East is much smaller and measures about 60 % of the astragalus from HGSP 8425. It either indicates the presence of a second species in Nyakach or indicates that the individuals from Nyakach were smaller than in HGSP 8425. This astragalus is from the same site at Nyakach as the large M_2.

A distal part of a **central metapodial** (MP III/IV) has a ridge on the distal facet that continues dorsally. In anthracotheres this area is flat.

The **first central phalange** (phalange III/IV 1) has a proximal facet that matches the distal facet of the metapodials; there is a continuous dorso-plantar groove. The phalange is short relative to its DAP and DT measurements. For instance in all other phalanges length exceeds twice the DAPp value, not so in HGSP 8213. There is a second phalange of a juvenile (Pl. 11, Fig. 10). The phalange from HGSP 8405 is much smaller than the one from HGSP 8213 and it fits a second phalange from HGSP 8127. The large first phalange fits the metapodial from HGSP 8219.

The **second lateral phalange** (phalange II/IV 2; Pl. 12, Fig. 12) and **second central phalange** (phalange III/IV 2; Pl. 11, Fig. 9) are very large. The central phalange differs from anthracothere phalanges in being less flat in dorso-plantar direction. It is however, flat compared to most suid phalanges and this probably is an adaptation to the large body weight of the animal. The 'tuberosité interne' and 'tuberosité externe' (*sensu* Heintz, 1970) are not well developed. In general suids have those parts well developed (contrary to anthracotheres) and especially the external one. The proximal and distal facets are flatter than in other suids. These two characters might indicate a more restricted movement along the phalangeal joints than is common in Suidae.

Discussion — The lower cheek teeth from Nyakach, Maboko and Bugti have in common that they tend to be wide (index I) as in *K. marymunnguae* and *K. khinzikebirus*, but they are all larger than teeth assigned to those species (Text-fig. 33). They are so large, that they may represent the largest suid species ever. Similarly, foot bones from the Lower Manchar Formation are by far the largest known suid bones (Text-fig. 33). In addition, these remains are of approximately the same age. *Kubanochoerus* is the only gigantic suid of this period.

Nyakach and Maboko are probably younger than Gebel Zelten (Pickford, 1981), the collections from Bugti seem to represent more than one level and may include Middle Miocene forms (Pickford, 1988b), the HGSP localities are around the local entry of *Listriodon*. All these localities are younger than the typical *K. khinzikebirus* and have a still larger species of *Kubanochoerus*. It is a small step to assume that the largest species descended from the next largest and slightly older species.

The astragalus from Nyakach is much smaller than the astragalus from HGSP 8405. The small second phalange is from HGSP 8127, a locality with *B. guptai*, which is at the very base of the Manchar Formation. Higher in the Manchar Formation, with *L. pentapotamiae* (a descendant of *B. guptai*, see section on phylogeny) the larger foot bones are found. All available data indicate that the remains represent a lineage of *Kubanochoerus* which greatly increased its size. If this really is the case, the upper molar from Inönü I (MN 6) is more probably an M^1 than an M^2, since the M^2 of this species should be still larger to occlude with the M_2 from Bugti or to match the huge bones from the HGSP localities, which are closer in age than Gebel Zelten.

Pickford (1987a) assigned the kubanochoere molar from Bugti as well as several other specimens from Bugti to *Hemimastodon crepusculi*, in his opinion a suid related to *Kubanochoerus*. The affinities of this monospecific genus have often been discussed, proboscidean or suid. The species is based on an M^3 and besides there is a similar M^3 which both are maintained in the Proboscidea by Tassy (1988). Tassy's arguments in favour of proboscidean affinities seem to be valid. Two of the arguments used by Tassy are of particular interest and are rephrased and extended here. *Kubanochoerus* has well-developed protopreconules and tetrapreconules. These are not visible as individual structures in *Hemimastodon* (but are 'V-shaped' lophs). No species of *Kubanochoerus* shows a tendency to develop longer M^3; no large hexacones are found. Besides, it can be argued that the two *Hemimastodon* M^3 seem too large for the rest of the hypodigm, as given by Pickford.

Of the lower molars assigned by Pickford to *Hemimastodon* there are two types. In type 1, the cusps have several cristids, but apart from that the enamel is smooth (Pickford, 1987a, pl. 1; pl. 2, figs 1, 2). This morphotype includes part of the syntypes of *Anthracotherium ingens*. In morphotype 2, there are also cristids, but in addition there are furrows in the enamel (Pickford, 1987, pl. 2, fig. 3). In the first type, the hypoprecristid is well connected to the hypoconid; there is no anterior furrow in the enamel, however shallow, separating the structure into two cusps. With wear, dentine islands are formed at these cusps and these islands rapidly fuse. In the second type, the hypopreconulid is fully separated from the hypoconid and is placed exactly in the middle of the transverse valley, as is the case in *Kubanochoerus*. In the more heavily worn specimens of *Kubanochoerus*, the dentine island that forms on the hypopreconulid has a different shape as the one formed on the teeth of type 1. However, exactly this morphology is found in the various species of *Anthracotherium*, such as *A. magnum* Cuvier, 1822 from Cadibona (DSTT) and *A. monsvialense* De Zigno, 1888 from Monteviale (IMGURP). The same is true for the pentapreconulids in the M_3 of the first type. Besides, the M_3 of type 1 have third lobes with two large cusps; the pentaconid and hexaconid are of equal size. These molars do not have the additional structures such as a pentaectoconulid, which certainly would be there in a suid like *Kubanochoerus*. In addition, type 1 molars are associated with small P_4. In GSI B450, the DAP' of the P_4 would be 73 (measurements from Pickford, 1987a, table 3). This value is far lower than in any listriodont, where values range between 86 and 106. In addition, the P_4 has a protopostcristid, but no separate cusp on the talonid (the hypoconid) and there is no trace of a metaconid. The type 1 molars and associated premolars share many characters with anthracotheres and here Forster-Cooper (1924) is followed in placing them in *Anthracotherium*.

Some P^4 were suggested by Forster-Cooper (1924) to belong to 'some Entelodont animals', but were included in the *Hemimastodon crepusculi* hypodigm by Pickford (1987a). They might be entelodont or *Kubanochoerus*. If entelodont, they would be late survivors of this group.

Carroll (1988, p. 640) placed *Bugtitherium* in the Suidae. Pilgrim (1908) erected the genus and species *Bugtitherium grandincisivum* for two anterior fragments of a palate, of what he believed to be an anthracothere. The morphology and size is much like that of a large species of *Kubanochoerus* and in the case of synonymy, *Bugtitherium* would be the senior synonym. However, Pickford (1987a) showed already that these fossils belong to *Anthracotherium bugtiense*. Especially the position of the foramina palatina at the level of the P^3 is different from the Suidae, where these foramina are at the level of the M^2 or M^3.

The foot bones from the Lower Manchar Formation, and teeth and some bones from Inönü I, Maboko, Nyakach and the one molar from Bugti do thus not belong to *H. crepusculi*, nor to *Bugtitherium grandincisivum.* These fossils indicate a *Kubanochoerus* 30 to nearly 50 % larger than the next largest *Kubanochoerus* (linear measurements). Such differences in size justify the introduction of a new species name (see discussion on *L. pickfordi*).

The material assigned here to *K. mancharensis* represents a great size increase and by now it is already clear that two chrono-'species' could be recognised. It is possible that in the future a second name will be introduced. Now, provisionally all material is assigned to one species. The holotype of this species is chosen from the larger (and younger) specimens. The molar from Inönü I is not selected because its position might be disputed. The age of the molar from Bugti might be disputed as well. For this reason the astragalus is designated holotype. Astragali are the most frequently encountered foot bones and therefore are useful indicators of size, the distinctive character of this species.

Kubanochoerus massai (Arambourg, 1961)

Pl. 8, Figs 1-19; Pl. 9, Figs 1-15, 18; Pl. 10, Figs 1-3, 5-18; Pl. 11, Figs 1-6, 8

1961 'un grand suidé voisin des genres indiens *Tetraconodon* ou *Conohyus*' — Arambourg & Magnier, p. 1182.
1961 *Libycochoerus massai* nov. gen. nov. sp. — Arambourg, p. 108, fig. b.
1963a *Libycochoerus Massai* — Arambourg, p. 61.
1963b *Bunolistriodon massai* (Arambourg) — Arambourg, pp. 903-911, figs 1-3; text-pls 1-3; pl. 24.
1973 *Bunolistriodon massai* Arambourg — Savage & Hamilton, p. 521.
1976 *Bunolistriodon massai* Arambourg — Van Couvering & Van Couvering, p. 203.
1975 *Bunolistriodon massai* (Arambourg) — Pickford & Wilkinson, pp. 133-134.
1975 *Libycochoerus massai* Arambourg — Leinders, pp. 199-203, fig. 1 (no. 7).
1976 *Bunolistriodon massai* (Arambourg) — Wilkinson, pp. 226-229, plate 5, figs d-g.
1978 *Kubanochoerus massai* (Arambourg 1961) — Wilkinson, p. 446.
1986b *Libycochoerus massai* Arambourg, 1961 — Pickford, pp. 40, 45, 46, figs 47-49.
1993 *Kubanochoerus massai* (Arambourg, 1961) — Guan & Van der Made, p. 175.

Holotype — 1961-5-8, a left mandible with P_2-M_3, in the MNHN collections, figured by Arambourg (1961, fig. b).

Type locality — Gebel Zelten, Libya.
Age of the type locality — Early Miocene, approximately equivalent to MN 4.
Diagnosis — Small *Kubanochoerus* (cheek teeth approximately 85 % linear size of *K. gigas*) with relatively small M3 and the palate not extending much behind the M^3.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Gebel Zelten	MNHN	Arambourg 1963b	Set III (lower)	Pickford 1981

Description and comparison — *Kubanochoerus massai* has been placed in *Bunolistriodon* and *Kubanochoerus* and is the type of *Libycochoerus*. *B. jeanneli* (including what is here called *B. anchidens*) from Rusinga have been brought in connection with *K. massai* by placing them together in the genus *Libycochoerus*. Comparisons are thus made with type species *Bunolistriodon lockharti* and *Kubanochoerus gigas*, and with *B. jeanneli* and *B. anchidens*.

The I_1 (Pl. 8, Fig. 7) has a wide and low endocristid. The index I ranges between 83 and 87 (Text-fig. 27). In *K. gigas* this is 74-108 and in *B. lockharti* 89-117. DMD' in *B. anchidens* and early *B. lockharti* is comparable, in *K. gigas* it is much greater. The DLL' is small but not exceptionally so (Text-fig. 26).

The I_2 (Pl. 8, Figs 6, 14, 15, 17) is nearly symmetrical, and differs from the I_1 in having a small curve in the postcristid and in developing a facet with the I^2 over this cristid. It also has a clearer endocristid and a lower postanticlinid. The distal area is much more like in the I_1 than in *K. gigas*, *B. lockharti* and *B. anchidens*, except for the postanticlinid which is higher in *B. anchidens*. The index I ranges between 82 and 92 (Text-fig. 27). In *K. gigas* this is 93-100 and in *B. lockharti* 94-127. DMD' and DLL' values are comparatively low (Text-fig. 26). The tooth is bilobate and has a protocone and protopreconule.

The I_3 (Pl. 8, Figs 11, 16, 18) is like in *K. gigas*, and not yet so distally extended as in *B. lockharti*. It is a bilobate tooth, with protocone and protopostconulid as in *K. gigas*. *B. lockharti* has a trilobate I_3.

The C_m (Pl. 8, Fig. 19) has the posterior and labial sides about as wide. It is thus in some cases 'scrofic' and in others 'verrucosic'. It is a hypsodont tooth and the lower rim of the crown is not formed.

The P_1 (Pl. 9, Figs 11, 14) is a small tooth with the protopostcristid placed slightly labial. It is relatively larger than in *B. lockharti* (DAP' 62 versus 43 for Baigneaux and DT' 39 and 38, respectively) but about equal in relative size in *K. gigas* (where the values range 58-74 and 36-54). The anterior root is curved backwards (Pl. 9, Fig. 11) and might be even fused with the posterior root (Pl. 9, Fig. 14?).

The **P_2** (Pl. 9, Figs 8, 13) and **P_3** (Pl. 9, Figs 7, 10, 12) differ in that the P_2 has a straight protopostcristid and the P_3 has small cusps in this crest, the protopostconulid and a still not well-individualised hypoconid.

The **D_2** (Pl. 9, Fig. 18) and **D_3** (Pl. 9, Figs 9, 15) have divergent roots and are much smaller than the P_2 and P_3.

The **P_4** usually has a large metaconid that is placed at the same level as the protoconid (Pl. 9, Figs 5, 6). Occasionally there is no clear metaconid (Pl. 9, Fig. 2). There is a short protopostcristid; in *K. gigas* this tends to be a protopostconulid (Pl. 12, Figs 1, 2). There is usually a protopreconulid (Pl. 9, Fig. 4). The hypoconid is large and individualised (Pl. 9, Fig. 3) or incorporated into the protopostcristid and does not show in profile in a slightly worn tooth (Pl. 9, Fig. 1). In *B. lockharti* the protoprecristid does not have a conulid and is shorter.

The **D_4** is fully bunodont.

The **M_1** and **M_2** (Pl. 10, Fig. 5) do not have the endocristids of the lingual and labial cusps fused and have large hypopreconulids. The teeth are fully bunodont, as in *K. gigas*, *B. anchidens* and *B. jeanneli*. In *B. lockharti*, the endocristids in the first lobe may touch and even be connected.

The **M_3** (Pl. 10, Figs 1, 2, 3, 6) is relatively small (DAP' and DT') and has a simple third lobe with a pentaconid in the middle.

The **I^1** (Pl. 8, Figs 3, 5, 9, 10) has two lobes, one consisting of the paracone and parapostcrista and the other consisting of the parapreconule. The same configuration is found in *K. gigas*, but *B. lockharti* has three lobes; the parapostconule, paracone and the parapreconule and *B. anchidens* has only one lobe, the paracone (Pl. 4, Fig. 1). The tooth is larger (DMD' and DLL') than in *B. anchidens* (Text-fig. 26) and more elongate (index I 152-177 *vs* 139; Text-fig. 27), but smaller and less elongate than in the other two species (201-215 in *K. gigas* and 145-200 in *B. lockharti*). Seen from the lingual side, the crown appears to be high (in particular Pl. 8, Fig. 9).

The **DI^1** (Pl. 8, Fig. 8) resembles the I^1, but is flatter and has only one lobe.

The **I^2** (Pl. 8, Figs 1, 12) is a simple tooth with a more or less central paracone and straight proto- and postcristas. There is a continuous lingual cingulum. The index I has high values (146-170) compared to the indices in *K. gigas* (131-150) and *B. anchidens* (139-148), but low values compared to the index in *B. lockharti* (173-221).

The **I^3** differs from the I^2 in being bilobate (Pl. 8, Fig. 4). In analogy to the I^1, the extra cusp might be a parapreconule, but this is not certain. The anterior cusp may disappear early due to wear (Pl. 8, Fig. 2). The crown is higher and flatter than in the I^2.

The **C^m** (Pl. 8, Fig. 13) has three enamel bands; the presyncline, endosyncline and postsyncline. Only very near to the tip is there enamel all around. The endosyncline is wide and extends 6 cm 'downwards'; the other synclines are less deep. In *B. lockharti* and *K. gigas* the synclines are deeper. Maybe this is because the C^m kept growing in the latter two species and not in *K. massai*. Alternatively, the *K. massai* tooth might just be an ontogenetically young specimen. The tooth is curved (Pl. 8, Fig. 13c), suggesting that it was oriented externally.

A **C^f** is only known from the skull. It is oriented outwards, but little can be said about the morphology, due to its state of preservation.

The **P^1, P^2** (Pl. 10, Figs 14, 15) and **P^3** (Pl. 10, Figs 16, 18) have similar shapes, but differ in the development of the protocone. In the P^3 it is large and often (Pl. 10, Fig. 18), but not always (Pl. 10, Fig. 16) separate from the lingual cingulum, making the tooth wide at the second lobe, wider than the P^2 and much wider than the P^1. The parapostrista is straight and no metacone is developed. The sole posterior root of the P^2 is curved lingually (Pl. 10, Fig. 15e).

The **D^2** (Pl. 10, Fig. 17) is smaller, lower and more elongate than the P^2 and its roots are divergent. The protocone is very small and fused to the cingulum.

The **P^4** (Pl. 10, Figs 11-13) has the paracone and metacone usually separated (Pl. 10, Fig. 11a). The separation is best seen as a groove lingually of the parametacone structure. There is often, but not always (Pl. 10, Fig. 13a) a continuous wide lingual cingulum. The protoprecristid is of variable length and may extend to the middle of the anterior side of the paracone where it may fuse, or seem to fuse, to the cingulum (Pl. 10, Fig. 13a). At this place the cingulum may be higher (Pl. 10, Fig. 12b), or not (Pl. 10, Fig. 11b). There is no paraendoconule.

The **D^3** and **D^4** (Pl. 10, Fig. 10) are fully bunodont.

The **M^1** and **M^2** (Pl. 10, Fig. 9) tend to have the protopreconule fused to the cingulum, but occasionally, it may be fused to the protocone. The precristas of the lingual and labial cusps do not fuse and the teeth are fully bunodont. The tetrapostcrista is connected to the cingulum. *K. gigas*, *B. anchidens* and *B. jeanneli* are also fully bunodont, but *B. lockharti* has the protopreconule generally connected to the protocone and often connected to a paraprecrista, forming a V-shaped loph.

The **M^3** (Pl. 10, Figs 7, 8) is like the first two molars, but with a small talon, which ranges from a mere wide cingulum which is postero-lingually extra wide to having a large pentacone at that place.

The **mandible** has relatively short diastemata and a not very massive symphysis, though these values are very variable (Van der Made, 1991a).

The **skull** of a female (Arambourg, 1963b, pl. 24) has a long snout and there are diastemata between the canine and the teeth before and behind it and between the P^1 and P^2. The area of the brain case is relatively short, narrow and presumably low (there is some damage in this area). The zygomatic arcs are not much inflated and do not stand out much. The glenoid has the typical suid shape (convex in antero-posterior direction) and position (far to the back of the skull and relatively high). The palate extends only a short distance behind the M^3. The most peculiar characters are the small protuberances of the frontals, there is one above each orbit, pointing up. Their bases are wide, but the protuberances diminish in diameter rapidly and change into notches with more or less circular sections of only a few millimetres diameter. The whole of these structures is only two or three centimetres high. In the male *K. gigas* skulls, these protuberances are also present (though oriented outwards), but there is an additional and much larger protuberance (Qiu *et al.*, 1988). Such structures are not known in *Bunolistriodon* skulls, though none of *B. lockharti* have yet been described.

There are many elements of the **postcranial skeleton** (Pl. 11, Figs 1-6, 8). They do not present many special morphological characters. In proportions, the phalanges seem to be relatively wide and the metapodials relatively long. Especially the lateral metapodials are long and slender (Pl. 11, Figs 3, 6), in comparison to Recent *Sus scrofa*. The sustentacular facet of the astragalus (not figured) is flat, but not as flat as in *Listriodon* (Pl. 25, Fig. 8) and *B. lockharti* (Pl. 25, Fig. 9).

Discussion — Arambourg (1961) erected the genus and species *Libycochoerus massai* for a mandible from Gebel Zelten. Later (Arambourg, 1963b), when more material had become available, its listriodont affinities became clear and the material was included in the genus *Bunolistriodon*, which Arambourg had conditionally introduced in 1933.

Leinders (1975) placed *B. lockharti*, type species of *Bunolistriodon*, in *Listriodon* and maintained the genus *Libycochoerus* for *L. massai.* Pickford (1986b) extensively compared *Listriodon pentapotamiae* and '*L. jeanneli*' (*B. anchidens*) and placed *K. massai* and *B. jeanneli* in *Libycochoerus.* No direct comparisons between *K. massai* (the type species of *Libycochoerus*) and *Kubanochoerus gigas* (= *K. robustus*, the type species) were made.

Qiu *et al.* (1988) compared a skull from Tongxin of *Kubanochoerus 'lantienensis'* (= *K. gigas*) and *Libycochoerus* (including the material from Rusinga - *B. anchidens* - and *K. massai*) and concluded the latter genus to be valid. They used seven characters for separating the genera. These characters are here discussed, but using only their state in *K. massai* and not the information from the Rusinga material:

1 - The posterior border of the palate in *K. massai* is V-shaped and near the M^3 and in *K. gigas* U-shaped and far behind the M^3. The shape and position of the border is very variable in a large sample of *Sus scrofa vittatus* from Sumatra (ZMA) and is age and sex dependent. Although the difference in position of this border is greater in the two listriodonts than the intraspecific variation in *S. scrofa vittatus*, it is comparable to the difference between *Sus scrofa vittatus* and *Sus barbatus* (ZMA).

2 - The I^x in *K. massai* form a V-shaped arc and the I^1 are not much larger than the I^2; in *K. gigas* the arc is U-shaped and the I^1 are much wider. The size of the I^1 influence the shape of the arc, the wider the incisors, the clearer the U-shape will be. Increase in size of the central incisors is a common trend in Listriodontinae and in *Listriodon splendens* the same differences are seen, yet the forms are of no more than subspecies status.

3 - The supraorbital protuberances are larger in *Kubanochoerus* and this genus has in addition a frontal 'horn'. The skull with the small protuberances is a female, the skulls with the large protuberances and 'horns' are males, as indicated by the canines. Animals with cranial appendages are more often sexually dimorphic than not.

4 - The shape of the upper border of the nasals is steeper in *K. massai.* Such a character may well be related to the length of the diastemata, which in turn is sex dependent. A study of variation should be made before the character can be shown to be useful and even then it may be only of specific value.

5 - P1 less reduced, diastema P1-P2 shorter. The length of diastemata is very variable (Van der Made, 1993) and reduction of the anterior premolars is very common in suid lineages and large differences may be found in one genus or even a single species (Van der Made, 1989a, b).

6 - The P^4-M^2 are wider compared to their lengths than in *K. massai.* This is contradicted by data from Text-fig. 31.

7 - M_1 and M_2 are square in *K. massai* and elongate in

K. gigas. Text-fig. 30 shows they are all about as elongate.

The differences between *Kubanochoerus gigas* and *'Libycochoerus' massai* are either not real, probably sexually dimorphic, subject to intraspecific variability or comparable to specific or subspecific differences in other widely accepted suid taxa. The characters of this last category are of taxonomical value, but because of their small number do not allow for the maintenance of a separate genus.

There are several localities in the Gebel Zelten area (Savage & Hamilton, 1973). Arambourg (1961, 1963b) did not exactly indicate the provenance of the specimens of *K. massai*. The holotype and the skull show a different fossilisation. They seem to come from ferruginous sands. Most of the remaining material looks as if it came from clays or marls. The I^1 of the skull are much larger than all others and a trend towards larger or more elongate I^1 is expected. It would not be surprising if the skull and maybe also the holotype came from a slightly younger locality.

Kubanochoerus minheensis (Qiu, Li & Wang, 1981)
Pl. 9, Figs 16, 17, 19; Pl. 10, Fig. 4;
Pl. 12, Figs 8, 10, 11

? 1928 *Listriodon gigas* sp. nov. — Pearson, p. 11 (*partim*), fig. 4a-d.
1981 *Bunolistriodon minheensis* sp. nov. — Qiu *et al.*, pp. 164-166, 172, pl. 2, figs 3, 4.
1993 *Kubanochoerus minheensis* (Qiu, Li & Wang, 1981) — Guan & Van der Made, p. 175-176.

Holotype — V6021, a mandible with all teeth except for the right I_3 and canine and the left P_1 (Pl. 9, Figs 16, 17, 19; Pl. 10, Fig. 4; Pl. 12, Fig. 11), in the IVPP collections, figured by Qiu *et al.* (1981, pl. 2, fig. 3).
Type locality — Nanhawangou, Lierbao, Minhe county, China.
Age of the type locality — Middle Miocene.
Diagnosis — Small *Kubanochoerus*, cheek teeth approximately 85 % of those of *K. gigas*, with elongated M3, enlarged incisors and with a palate that extends far behind the M^3.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
?Quantougou (=Quan Tou Kou)		Pearson 1928	MN 5	Guan & Van der Made 1993
Nanhawangou	IVPP	Qiu *et al.* 1981	MN 5	Guan & Van der Made 1993
Guanghe 2	BNHM		MN 6-8	Guan & Van der Made 1993

Description and comparison — *Kubanochoerus minheensis* resembles *K. gigas*, which is found in the same area, and *K. massai*. Comparisons are primarily with those species.

The **I_1** and **I_2** (Pl. 12, Fig. 11) have well-developed endocristids. The incisors are large compared to those of *K. massai*, but still small compared to those of *K. gigas* (Text-fig. 30).

The **I_3** (Pl. 12, Fig. 11) is smaller than in *K. massai*, in contrast to the central incisors which are larger than in that species.

The **C_m** has a verrucosic section, which is common in all more derived listriodonts, but not in *e.g. B. jeanneli*.

The **P_1** (Pl. 9, Fig. 16) is small with a small individual hypoconid.

The **P_2** (Pl. 9, Fig. 17) and **P_3** (Pl. 9, Fig. 19) have both small cusps immediately anterior and posterior of the protoconid, which might be termed protopreconulids and protopostconulids. Such cusps are not or much less developed in *K. massai* and *K. gigas*. The P_3 has a well-developed hypoconid, which is seen in profile as a clear elevation at the end of the protopostcristid (Pl. 9, Fig. 19b, c). In *K. massai*, it looks more like a swelling in the gently sloping protopostcristid (Pl. 9, Figs 7, 10, 12). *K. gigas* is intermediate in this character (Pl. 12, Figs 3, 13).

The **P_4** (Pl. 9, Fig. 19) has a large metaconid, a clear protopreconulid and small protopostcristid. The latter crest is small, because the hypoconid became a large cusp, which is placed on the axis of the tooth. The P_4 is relatively large (DAP' and DT') compared to those of *K. massai* (Text-fig. 30).

The **M_1** and **M_2** are fully bunodont and have the size of their homologues in *K. massai* (Text-fig. 30). They are elongate like in *K. massai* and *K. gigas*, but not as in *K. marymunnguae*.

The **M_3** (Pl. 10, Fig. 4) does not have the endocristids of the lingual cusps fused to those of the labial cusps and thus it is fully bunodont. Its absolute (Text-fig. 30) and relative size (DAP' and DT') is larger than in *K. massai*.

The **I^2** (Pl. 12, Fig. 10) is small in comparison to the same tooth in *K. massai*. This is odd, in view of the fact that the I_1 and I_3 are larger. But then the I_3 is also smaller. This might indicate an increase in size of the central incisors, whereas the lateral incisors are being reduced.

The **P^4** (Pl. 12, Fig. 8) has a well-separated metacone and has a separate tetracone, which is only slightly smaller than the protocone. Thus the tooth is quadricuspid. This may well be related to the trend in the lower premolars for large hypoconids ('molarisation of the premolars').

The **mandible** shows the development of long diastemata between the P_2 and P_1 and to a lesser extent between the P_1 and C_m. These diastemata seem to be large compared to other species of *Kubanochoerus*, though it should be borne in mind that the size of diastemata is extremely variable (Van der Made, 1991a).

A **skull** on display in the BNHM from the Tongxin area shows that the palate extends far behind the M^3, like in *K. gigas*. In *K. massai* the palate extends only little behind the M^3.

Discussion — *Kubanochoerus minheensis* is much smaller than *K. gigas* and has the size of *K. massai*, but differs from that species in a number of characters: larger central incisors (I^1, I_1 and I_2) and smaller lateral incisors, larger M_3, 'molarised premolars' and large P_4 as well as a palate that extends far behind the M^3 and probably longer diastemata.

Kubanochoerus gigas (Pearson, 1928)

Pl. 7, Figs 3, 4, 6, 10; Pl. 12, Figs 1-7, 9, 13-16

1928 *Listriodon gigas* sp. nov. — Pearson, pp. 8-12 (*partim*), figs 1-3, 4e, 5.
1960 *Kubanochoerus robustus* Gabunia, 1955 — Gabunia, pp. 87-97, pls 1-4.
1963a *Listriodon lantienensis* sp. nov. — Liu & Lee, pp. 293-296, 301-302, figs 2, 3; pls 2-4.
1963a *Listriodon gigas* Pearson — Liu & Lee, pp. 292-293, 300-301, pl. 1.
? 1963a *?Listriodon* sp. — Liu & Lee, pp. 297-299, 303; pl. 5, figs 2-8.
1968 *Kubanochoerus robustus* Gabunia — Godina *et al.*, p. 487, fig. 458d.
1973 *Kubanochoerus robustus* Gabunia — Gabunia, pp. 76-94, figs 18-20, 22b; pl. 6, figs 3-6; pl. 7, figs 1-4.
? 1981 *Kubanochoerus robustus* — Gabunia, p. 197.
? 1988 *Kubanochoerus lantienensis* (Liu et Lee, 1963) — Qiu *et al.*, p. 1, text-figs 1-5, pls 1-3.
1988 *Kubanochoerus lantianensis* — Guan, pp. 3, 15, 20.
1989 *Kubanochoerus* sp. — Ye, pp. 37, 38, 50.
1990 *Kubanochoerus* sp. — Tong *et al.*, p. 70.
1993 *Kubanochoerus gigas gigas* (Pearson, 1928) — Guan & Van der Made, p. 174.
1993 *Kubanochoerus gigas lii* subsp. nov. — Guan & Van der Made, pp. 159-169, 175, pls 1, 2; pl. 3, fig. 3.

Lectotype — A left maxilla with P^2-M^3, figured by Pearson (1928, fig. 1), in the Uppsala collections, cast in IVPP.
Type locality — Quantougou (= Chuan Tou Kou), Ping Fan Hsien, Gansu, China.
Age of the type locality — Middle Miocene, approximately MN 5.
Diagnosis — *Kubanochoerus* of intermediate size, with relatively large incisors (DMD', I) and the palate extending far behind the M^3. There are two subspecies.

Kubanochoerus gigas gigas (Pearson, 1928)

Diagnosis — *Kubanochoerus gigas* with relatively large premolars and small M3.

Kubanochoerus gigas lii Guan & Van der Made, 1993

Holotype — BPV-909, male skull, in the Beijing Natural History Museum and figured by Guan & Van der Made (1993, pl. 1, figs 2, 4; pl. 3, fig. 3).
Type locality — Maerzuizigou, near Dingjiaergou, Tongxin county, Ningxia, China in Tongxin fossiliferous level 2.
Age of the type locality — Middle Miocene, MN 5.
Diagnosis — *Kubanochoerus gigas* with relatively small premolars and relatively large M3, and with I^1 with great meso-distal diameter.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Quantougou (= Quan Tou Kou)	IVPP cast	Pearson 1928	MN 5	Guan & Van der Made 1993
Koujiacun		Liu & Lee 1963	MN 5	Guan & Van der Made 1993
Belometchetskaia		Gabunia 1960, 1973	MN 5	Guan & Van der Made 1993
Maerzuizigou	IVPP, BNHM	Qiu, Ye & Huo 1988, Guan & Van der Made 1993	MN 5	Guan & Van der Made 1993
Hamalagai	IVPP		MN 5	Guan & Van der Made 1993
Kundal Nali	IVAU		U Chinji	IVAU catalogue

Description and comparison — *Kubanochoerus gigas* is the first species of this genus to have been named and thus has priority. Two other species names were introduced, which Guan & Van der Made (1993) synonymised with *K. gigas*, *viz. K. lantienensis* and the type species, *K. robustus*. Species of this genus have been placed in *Bunolistriodon* (which would have priority), so it would be useful to compare both types, but the comparison between *B. lockharti* and *K. massai* reveals already essential points. Since *K. gigas* comprises two subspecies, these are compared in the description.

The I_1 and I_2 (Qiu *et al.*, 1988, pl. 3, fig. 2) have clear endocristids. The DLL' values of both teeth are very high.

The $\mathbf{I_3}$ (Qiu *et al.*, 1988, pl. 3, fig. 2) has very low meso-distal elongation.

The $\mathbf{C_m}$ (Qiu *et al.*, 1988, fig. 5) is clearly verrucosic. The lingual side is convex without any longitudinal grooves.

The $\mathbf{P_1}$ (Pl. 12, Fig. 5) has a narrow talonid with very low hypoconid. The average DAP' and DT' are 57 and 39.

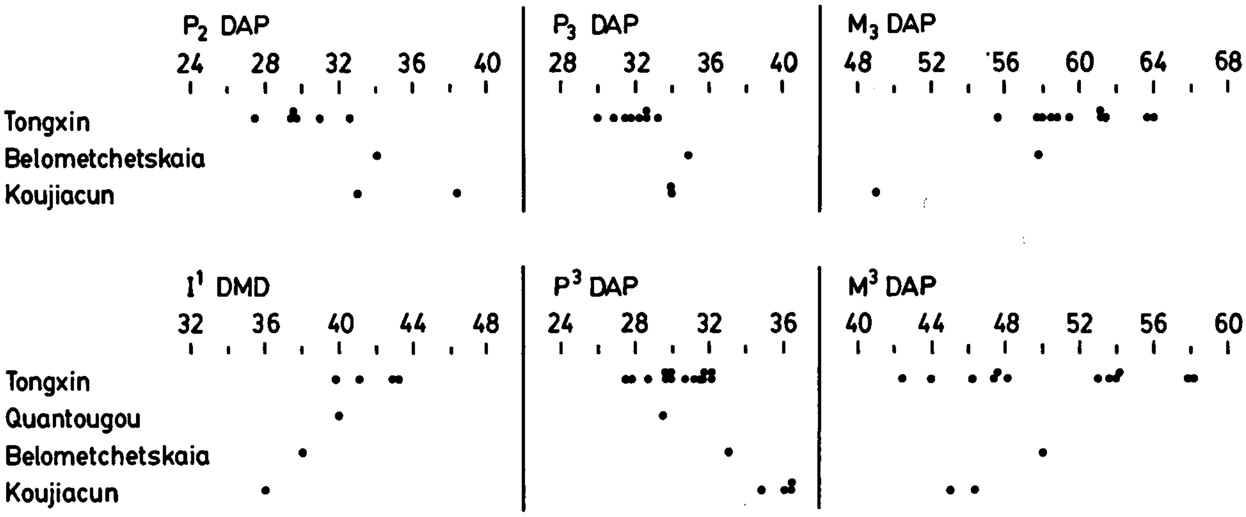


Fig. 34. Size changes in *Kubanochoerus gigas*. The localities are in approximate stratigraphical order. Data for *K. g. gigas* from Koujiacun from Pearson (1928), from Belometchetskaia from Gabunia (1960) and from Quantougou from Liu & Lee (1963) and *K. g. lii* from Tongxin from Guan & Van der Made (1993).

The $\mathbf{P_2}$ (Pl. 12, Fig. 4) and $\mathbf{P_3}$ (Pl. 12, Figs 3, 13) have small, but independent hypoconids. These teeth tend to be larger in *K. g. gigas* than in *K. g. lii* (Text-figs 30, 34).

The $\mathbf{P_4}$ (Pl. 12, Figs 1, 2) has a trigonid with three cusps close together, they are placed in an antero-posterior row. They might represent protopreconulid, protoconid and protopostconulid. Besides there is a small lingual extension that might be the protoendocristid. Alternatively, the cusps could represent a paraconid, protoconid and metaconid. The first name is a question of grade (is the cusp large or independent enough to be called paraconid) the second is a question of quality: the structure seems to originate at the back of the protoconid and then extend lingually; could it be a paraconid that moved backwards? The hypoconid is a large and individual cusp.

The $\mathbf{M_1}$, $\mathbf{M_2}$ and $\mathbf{M_3}$ (Pl. 12, Fig. 9) are fully bunodont; the endocristids of the lingual and labial cusps do not fuse and the hypopreconulid is large and independent. The M_3 of *K. g. gigas* tends to be smaller than that of *K. g. lii* (Text-figs 30, 34).

The $\mathbf{I^1}$ (Gabunia, 1960, pl. 1) is bilobate. The tooth is slightly enlarged (Text-fig. 26) and elongated (I ranges 201-215; Text-fig. 27) compared to its homologue in *K. massai*. The I^1 of *K. g. gigas* is smaller than that of *K. g. lii* (Text-fig. 34).

The $\mathbf{I^2}$ and $\mathbf{I^3}$ (Qiu *et al.*, 1988, pl. 3, fig. 1) are larger than in *K. massai*, but the I^2 is less elongate than in *K. massai*. The I^3 has about the same size as the I^2. There is an upper incisor from the Chinji Formation, but no exact provenance is known (Pl. 7, Fig. 6). The specimen has the morphology of an I^2 or I^3. In size it perfectly matches these teeth in *K. gigas*.

The $\mathbf{C^m}$ (Qiu *et al.*, 1988, pl. 3, fig. 1) is large and curved and has a deep endosyncline.

The $\mathbf{P^1}$ (Pl. 12, Figs 6, 7) has two widely diverging roots and a wide posterolingual cingulum, but no protocone. It is a small tooth (the average DAP' is 63 and DT' is 40).

The $\mathbf{P^2}$ (Pl. 12, Fig. 14) and $\mathbf{P^3}$ (Pl. 12, Fig. 15) have straight parapostcristas. The protocone is surrounded by a lingual cingulum, making the second lobe the widest part of the tooth, even in the P^2. The P^2 and P^3 of *K. g.*

lii are shorter and (relatively) wider than those of the supposedly older *K. g. gigas*, indicating a tendency of size reduction of the premolars combined with molarisation (Text-fig. 34). A tooth from the Chinji Formation, but of unknown exact provenance (Pl. 7, Fig. 3) probably represents a P^2. The tooth is very large, but the paracone is not inflated as in the Tetraconodontinae. The parapostcrista is straight and there is no metacone. In morphology and size the tooth fits *Kubanochoerus* well. The protocone is relatively small as in a P^2. The tooth is slightly larger than in the Tongxin sample, but comparable in size to the specimen from Belometchetskaia and thus probably represents *K. gigas* and most likely even *K. g. gigas*.

The $\mathbf{D^2}$ (Pl. 12, Fig. 4) is represented by a specimen from Kundal Nali in the Chinji Formation. Only the posterior part of the tooth is preserved. The posterior root is directed much posteriorly. The protocone is placed far posteriorly. Although the protocone is not very large and still partially connected to the cingulum, the posterior lobe clearly was the wider part of the tooth. This is due to the narrow paracone. In these characters the tooth resembles the D^2 of *K. massai* (Pl. 10, Fig. 17), but is larger; 128 %). The paracone is higher than would be the case in the P^1 of *K. gigas*. The DTp is too small for a P^2 of *K. gigas* and *K. massai* and a P^1 of *K. khinzikebirus*. A phalange from the same locality fits *K. gigas* well.

The $\mathbf{P^4}$ (Pl. 12, Fig. 16) has a separate metacone.

The $\mathbf{M^1}$, $\mathbf{M^2}$ and $\mathbf{M^3}$ (Qiu *et al.*, 1988, pl. 2, fig. 2) are fully bunodont. The M^3 of *K. g. lii* show a tendency to become larger than those of *K. g. gigas* (Text-fig. 34).

The **mandible** (Gabunia, 1960, pl. 3) shows the presence of long diastemata.

A **skull** from Belometchetskaia (Gabunia, 1960, pl. 2) and one from Tongxin (Qiu *et al.*, 1988, figs 1-4, pls 1, 2) and a small series of skulls from Tongxin (Guan & Van der Made, 1993), all males, have been described and figured. Here, only the most striking and most important characters are mentioned.

The skulls are long (some 70 cm), narrow and low. There are long diastemata between the canines and premolars.

In the middle of the skull there is a 'horn' originating from the frontals and pointing forwards. In one specimen the length is 18 cm. The section is either round or dorso-ventrally flattened with a width of up to 6 cm in the middle part. Qiu *et al.* (1988) supposed that the structure consisted of a 'pedicle' that is a formation of the frontals and a separate bone that later in ontogeny became fused with the pedicle. Guan & Van der Made (1993) argued that this may not have been the case and that these authors may have been misled by a suggestively eroded post-mortem fracture of the 'horn'. A skull of a not fully adult individual, has only the most basal parts of the 'horn' (Guan & Van der Made, 1993). Above each orbit, there is a small protuberance, pointing outward and not upwards as in the female *K. massai* skull.

There is a pronounced sagittal crest. The occipital area is lower than the frontal area, even if the 'horn' is not taken into account. In (all?) other suids, the occipitals form the highest part of the skull. In *K. gigas*, the occipitals are not wide, but the occipital condyles are very large relative to other parts of the posterior part of the skull.

There is no lacrimal fossa, nor a deep preorbital fossa. The zygomatic arc below and in front of the orbit has a flat surface. There is no inflation of the zygomatic arcs. There is no alveolar crest above the canines.

The palate extends over 10 cm behind the M^3. At the level of the incisors, the premaxillaries are twice as wide as the maxillaries between the molars.

The **astragalus** has a ridge next to the sustentacular facet, as in most suids, but unlike *Listriodon* (Leinders, 1976). In the *K. massai* sample, this character is variable. The astragalus is much larger than in *K. massai*, it is about 160 % the size of that species.

The **calcaneum** has a deep groove over the back of the head as in *Listriodon* (Leinders, 1976). Like the astragalus, it is large compared to the homologue of *K. massai*.

The **third metatarsal** is large, but not as large as the tarsals (about 135 % of *K. massai*).

A **first central phalange** (phalange III/IV 1) from Kundal Nali in the Chinji Formation (Pl. 7, Fig. 10) is very large. It is a relatively wide and short phalange. The facet for articulation with the metapodial shows a dorso-plantar groove that is deep at the dorsal side; this would not be the case in an anthracothere phalange. The specimen is intermediate in size to the specimens attributed to *K. massai* and *K. mancharensis* and thus has the right size for *K. gigas*, which in dentition is intermediate between the two. *K. minheensis* is supposed to be of the same size as *K. massai*. The presence of a D^2 of listriodontine habitus and the size of both D^2 and phalange indicate the presence of *K. gigas* in Kundal Nali.

Discussion — The *Kubanochoerus* from Quantougou (type of *K. gigas*), Belometchetskaia (type of *K. robustus*) and Koujiacun (type of *K. lantienensis*) are of equal size (Text-figs 30, 31) and morphology of the common preserved parts. There is no reason to consider them to be different species (Guan & Van der Made, 1993). The collection of *Kubanochoerus* from Tongxin is very similar to these specimens of *K. gigas*, but differs in having central incisors with great meso-distal diameters and smaller premolars and in having a tendency for larger M3. These differences are taxonomically expressed in the subspecies name *K. g. lii.*

Kubanochoerus gigas is different from *B. lockharti*, type species of *Bunolistriodon*, in being fully bunodont, having longer premolars, in the lack of a real metaconid in the P_4 and in having cranial appendages (observations on not yet published cranial material of *B. lockharti*).

Tribus Listriodontini Gervais, 1859

Diagnosis — Medium-sized Listriodontinae, with no cranial appendages, but with a tendency towards outward flaring C^m.

Genus *Bunolistriodon* Arambourg, 1963

Type species — *Bunolistriodon lockharti* (Pomel, 1848).
Diagnosis — Bunodont or sublophodont Listriodontinae, (supposedly) without cranial protuberances, with C^m that tend to have deep synclines and 'high' anticlines and tend to curve outward.
Remarks — When describing *B. jeanneli*, Arambourg (1933) conditionally made the genus *Bunolistriodon* for the 'bunodont' listriodonts, including what are here called sublophodont *Bunolistriodon*. Several species were to be included, but no type species was indicated. Arambourg (1961) introduced the specific and generic names *Libycochoerus massai* for a mandible from Gebel Zelten. Later (Arambourg, 1963b), more material became available, the listriodont affinities became clear and '*L.*' *massai* was included in the genus *Bunolistriodon*. According to the ICZN (Ride *et al.*, 1985) it is possible to introduce a name conditionally, but after 1930 a type species should be indicated even for a conditional introduction of a genus. *Bunolistriodon* Arambourg, 1933 is thus a *nomen nudum*. A *nomen nudum* can be made available later. Arambourg (1963b) indicated *B. lockharti* as type species of *Bunolistriodon* and gave and indication of what he believed to be *Bunolistriodon* and met all requirements of the ICZN for the description of a genus. The diagnosis for *Bunolistriodon* that was given in 1963, was partially based on *K. massai.* It is claimed that the genus is not valid for that reason, but a poor diagnosis does not affect the validity of the genus *Bunolistriodon*, in fact the word 'diagnosis' does not even occur in the ICZN.

In the opinion of Leinders (1975), *Bunolistriodon* is valid from 1963, *B. lockharti* should be placed in *Listriodon* and both differ from *K. massai* from Gebel Zelten, which was retained in *Libycochoerus* Arambourg, 1961. Several authors have followed this classification. However, here *B. lockharti* is not placed in *Listriodon*, but in its own genus and *K. massai* is placed in *Kubanochoerus*, which has priority over *Libycochoerus*. See also discussions on *B. lockharti* and *K. massai.*

Bunolistriodon affinis (Pilgrim, 1908)
Pl. 13, Fig. 1

1908 *Palaeochoerus affinis* n. sp. — Pilgrim, pp. 148, 155.
1912 *Palaeochoerus affinis*, Pilgrim — Pilgrim, pp. 37-39, pl. 12, fig. 7.
1913a *Listriodon affinis* — Pilgrim, pp. 74-75
1913b *Listriodon affinis* — Pilgrim, p. 317.
1926 *Listriodon affinis* Pilgrim — Pilgrim, pp. 36-37, pl. 11, fig. 1.
1950 *Listriodon affinis* (Pilgrim) — Eames, p. 56.
1963 *B. affinis* (Pilgrim) — Arambourg, p. 910.
? 1976 *Bunolistriodon jeanneli* (Arambourg) — Van Couvering & Van Couvering, p. 203 (Songhor).
1976 *Bunolistriodon jeanneli* Arambourg 1933 — Wilkinson, p. 218 (Songhor).
1976 *B. affinis* — Wilkinson, pp. 225, 247-248.
1984 *Listriodon affinis* — Raza & Meyer, pp. 49, 51.
1987a *Libycochoerus affinis* (Pilgrim), 1908 — Pickford, p. 305 (only GSI B 528).
1988a *Libycochoerus affinis* (Pilgrim) — Pickford, p. 36.
1988b *Libycochoerus affinis* — Pickford, pp. 947-948 (the specimen from Bugti).

Holotype — B 528, a right maxilla with P^4 and M^1 (Pl. 13, Fig. 1), in the Indian Museum (Calcutta), figured by Pilgrim (1926, pl. 12, fig. 1).
Type locality — Kumbhi, Bugti Beds, Pakistan.
Age of the type locality — Early Miocene, MN 3 or Set I.
Diagnosis — Very small (as indicated by molar size) *Bunolistriodon*, with relatively large P^4.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Bugti	IM	Pilgrim 1926	'Bugti'	
Songhor	KNM	Wilkinson 1976	Set I	Pickford 1981

Description and comparison — *B. affinis* has been placed in *Libycochoerus* (= *Kubanochoerus*). Comparisons are primarily made with the type species of *Bunolistriodon* and *Kubanochoerus*.

The P^4 (Pl. 13, Fig. 1) has the paracone and metacone close together. The protoprecrista is not connected to the cingulum and extends much buccally, but it remains well separated from the paracone. The P^4 has higher DAP' and DT' values than other *Bunolistriodon*, though *Listriodon* and *Kubanochoerus* may have values as large or larger.

The M^1 (Pl. 13, Fig. 1) has a protopreconule that is placed much posteriorly. It is not connected to the paracone. Likewise the tetrapreconule is placed well posterior of median valley, it remains separate from the tetracone, though it is placed very close to the tetracone and is not connected at all to the metacone. A molar with no loph is termed here bunodont, though it should be noted, that the arrangements of the cusps indicates a tendency towards lophodonty and thus is not purely bunodont. Within the Listriodontinae, bunodont molars are found in early *Bunolistriodon* and in *Nguruwe* and *Kubanochoerus*.

A C_m from Songhor is tentatively referred to *B. affinis*. It is too large for *Nguruwe*, *Kenyasus* and *Sanitherium*, the only other suoids of Sets I and II. It has a scrofic section like the canine of *Bunolistriodon anchidens*, but is smaller.

Discussion — The genus *Bunolistriodon* Arambourg, 1963 was meant to include *B. affinis* as well as what is here called *Kubanochoerus*.

Wilkinson (1976) placed *B. affinis* in *Bunolistriodon*, but then he considered *Kubanochoerus* to be a junior synonym of *Bunolistriodon*. However, in his fig. 11, he grouped *B. affinis* with *B. lockharti* and other species which are placed here in *Bunolistriodon*. Later, Wilkinson (1978) recognised *Kubanochoerus* (including in it *B. jeanneli*) and *Bunolistriodon*; it is not clear where he would have placed *B. affinis*.

Pickford (1987a, 1988a) placed *B. affinis* together with *K. massai* in *Libycochoerus*, a genus that is here considered synonymous with *Kubanochoerus*, but did not really discuss the generic affinities of *B. affinis*.

B. affinis, *B. anchidens* and *B. jeanneli* are all bunodont species, which have very similar morphologies in the premolars. The generic identity of this group will be discussed with *B. anchidens*, since that is the species with the best material. In this group of bunodont species, *B. affinis* is the oldest name and thus is a valid species in any case.

Bunolistriodon anchidens sp. nov.

Pl. 4, Fig. 1; Pl. 13, Figs 2, 4-7, 10; Pl. 14, Figs 1-4, 7-9, 11, 13

? 1961 *?Lystriodon jeanneli* Arambourg — Walker, p 592.
1976 *Bunolistriodon jeanneli* (Arambourg) — Van Couvering & Van Couvering, p. 203 (only Rusinga).
1976 *Bunolistriodon jeanneli* Arambourg 1933 — Wilkinson, pp. 217-225 (Rusinga only), pl. 5, figs a-c.
1978 *Kubanochoerus jeanneli* (Arambourg) 1933 — Wilkinson, pp. 445-446, fig. 22.5.
? 1984 *Listriodon* cf. *L. mongoliensis* Colbert, 1934 — Barry & Cheema, pp. 1516.
1986b *Libycochoerus jeanelli* (Arambourg, 1933) — Pickford, p. 36, figs 34-46.
1988 *Libycochoerus jeanneli* — Qiu *et al.*, p. 16, the material from Rusinga.

Holotype — KNM-RU 2785, a mandible with left I_1, the inferior part of C_m, P_1-M_3 and right I_1-I_2, inferior part of C_m and P_1-P_3 (Pl. 13, Fig. 5; Pl. 14, Figs 1, 2, 9, 13), in the KNM collections, figured by Wilkinson (1976, pl. 5, fig. C; 1978, fig. 22.5) and Pickford (1986b, figs 39-46).

Paratypes — The other specimens from Rusinga, assigned to *B. anchidens* in the plates and tables. Wilkinson (1976, p. 217) listed KNM-RU 2785 to be the syntype of *B. jeanneli*. A syntype is a specimen of a type series of which no specimen was indicated as holotype. A type series consists of all specimens, on which the author of the species based the species (ICZN; Ride *et al.*, 1985). KNM-RU 2785 was not mentioned by Arambourg (1933), thus it cannot be a syntype of *B. jeanneli* for technical reasons. Besides, it represents a different species.

Type locality — Rusinga R1, in the Hiwegi Formation.

Age of the type locality — Early Miocene, Set II.

Derivatio nominis — In allusion to the narrow incisors, as opposed to *B. latidens*, a species with very wide incisors.

Diagnosis — bunodont *Bunolistriodon* with a size that is intermediate between *B. affinis* and *B. jeanneli*.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Rusinga loc.?	KNM	Pickford 1986b Wilkinson 1978	Set II	Pickford 1981
Rusinga R1	KNM	Pickford 1986b Wilkinson 1976	Set II	Pickford 1981
Rusinga R2-4	KNM	Pickford 1986b	Set II	Pickford 1981
Rusinga R3	KNM	Pickford 1986b Wilkinson 1976	Set II	Pickford 1981
Rusinga R3a	KNM	Pickford 1986b	Set II	Pickford 1981
Rusinga R113	KNM	Pickford 1986b Wilkinson 1976	Set II	Pickford 1981
Rusinga Rs III	KNM	Pickford 1986b Wilkinson 1976	Set II	Pickford 1981
Rusinga AW126	KNM	Pickford 1986b	Set II	Pickford 1981
Rusinga-Gumba	KNM	Pickford 1986b Wilkinson 1976	Set II	Pickford 1981
Rusinga-Kathwanga	KNM	Pickford 1986b Wilkinson 1976	Set II	Pickford 1981
Karungu	KNM	Pickford 1986b	Set II	Pickford 1981
?Bukwa		Walker 1969	Set II	Pickford 1981

?Gali Jagir	Barry & Cheema 1984	Murree	Barry & Cheema 1984

Description and comparison — This material was assigned to the genera *Bunolistriodon* and *Kubanochoerus* (or '*Libycochoerus*'). *Bunolistriodon anchidens* is very similar in morphology to *Nguruwe*, but is larger. Comparisons are primarily made with those taxa.

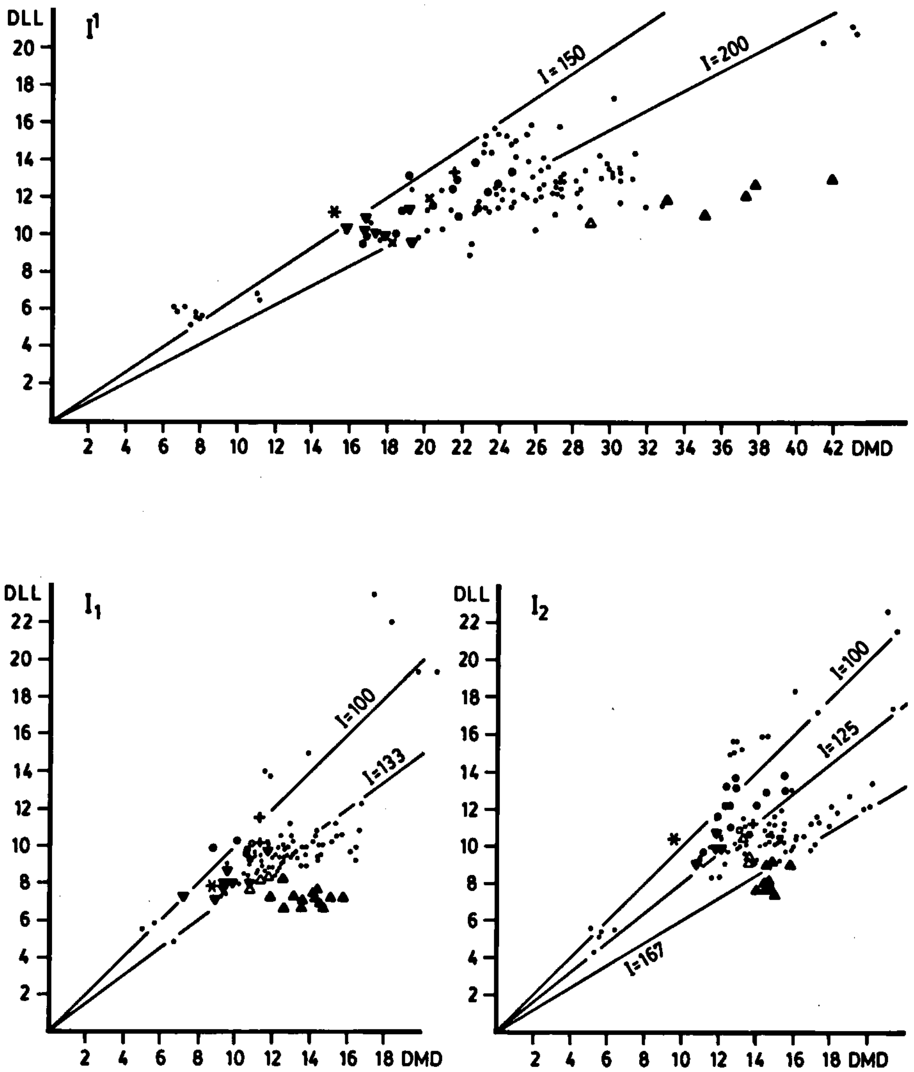


Fig. 35. Bivariate plots of central incisors of *Bunolistriodon*. Legend: asterisk - *B. anchidens*; triangles with points downward - *Bunolistriodon* aff. *latidens*; open triangles with point upward - *B. latidens*; black triangles with points upward -B. meidamon; oblique crosses - *B. guptai*; crosses - *B. akatikubas*; large dots - *B. lockharti*; small dots - remaining Listriodontinae. The lines indicate various values for the index I. The figure illustrates that wider incisors (DMD) in *B. lockharti* tend to have larger DLL and both wide and narrow incisors have the same indices. In the *B. latidens*-lineage, wider incisors tend to have higher indices. In the I^1, DMD and DLL tend to be positively correlated, in the lower incisors negatively. This is the other way around in *L. splendens* (Fig. 44).

The I_1 and I_2 (Pl. 14, Fig. 1) have small DMD and index I (Text-fig. 35). The I_2 has a lingual crown height of over 20 mm and the index 100 x Hli/DLL exceeds 192. The preanticlinids and postanticlinids of both incisors are deep. In species with a relatively lesser DLL or lower crown, the anticlinids tend to be less deep.

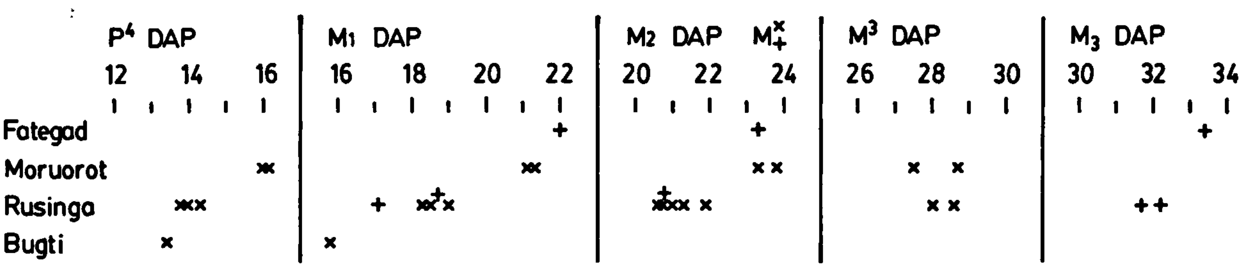


Fig. 36. Size changes in *Bunolistriodon jeanneli*-lineage: *B. affinis* (Bugti)-*B. anchidens* (Rusinga)-*B. jeanneli* (Moruorot and Fategad). Lower cheek teeth indicated with crosses, uppers with oblique crosses. Since they occlude, upper and lower M1 tend to have about the same length and the same is the case for the upper and lower M2. The localities are in tentative stratigraphical order.

The C_m has a scrofic section (with posterior side much larger than the labial side), like in *Nguruwe*. In *Kubanochoerus* and *Bunolistriodon* the section tends to be verrucosic (labial side wider than posterior side).

The P_1 (Pl. 13, Fig. 5) is a large tooth with two roots. Its DAP' and DT' values (54 and 43) are like in *Kubanochoerus* (47-62 and 39-40) and *Nguruwe* (60 and 40) and greater than in *Bunolistriodon* (43 and 38).

The P_2 (Pl. 13, Fig. 6) and P_3 have simple and straight protopostcristids and no hypoconids. In the figured P_2, the tooth is narrower at the talonid than at the trigonid. This is not the case in another P_2 and in the P_3.

The P_4 (Pl. 14, Fig. 2) does not have the metaconid well separated from the protoconid (though much better than in most species of *Kubanochoerus*). Anteriorly, the tooth is rounded and there is no clear protoprecristid. The hypoconulid is circular and positioned in the middle of the talonid, this is still more or less the case in *B. jeanneli*. In later *Bunolistriodon*, it is displaced buccally and has an endocristid. In *K. gigas*, there is a tendency for this tooth to be elongate; the cusps of the trigonid are placed closely together and tend to be positioned in an antero-posterior line (Pl. 12, Figs 1, 2). *K. marymunnguae* is one of the most primitive *Kubanochoerus, and its* P_4 has only the faintest indication of a metaconid (Pl. 7, Fig. 5). *Nguruwe* has a P_4 with only a single main cusp (Pl. 1, Fig. 8).

The M_1, M_2 (Pl. 14, Fig. 9) and M_3 (Pl. 14, Fig. 13) are fully bunodont, the labial and lingual cusps are well separated and the endocristids are not well developed. The pentaconids are large and are placed much anteriorly, so that they do not project posteriorly like in later *Bunolistriodon*, but extend between the hypoconid and entoconid. *Kubanochoerus*, *Nguruwe* and *B. jeanneli* have also bunodont molars.

The I^1 (Pl. 4, Fig. 1) has only one lobe. Other listriodonts have one lobe (in *Nguruwe*, Pl. 1, Fig. 1, in some early European *Bunolistriodon*, where forms with one and three lobes may occur in one sample and in *B. guptai*, Pl. 27, Fig. 3) or there are two (as in *Kubanochoerus* and possibly *B. guptai*, Pl. 27, Fig. 7), or three lobes (as in later *Bunolistriodon* from Europe). The tooth is not much enlarged in meso-distal direction; the I and DMD' values are small. In this character, the tooth resembles the incisors of *Nguruwe*.

The I^2 (Pl. 13, Fig. 2; Pl. 14, Fig. 3) has a very low index I, and in this character it is the most primitive listriodont I^2 known.

The C^m (Pl. 14, Fig. 7) has still a large portion of the tip covered with enamel all around. In *Kubanochoerus* and sublophodont *Bunolistriodon*, the part that is completely covered with enamel is much smaller and the synclines and anticlines have a much greater amplitude than in *B. anchidens*. The tooth resembles the canine of *Nguruwe*.

The P^1 (Pl. 14, Fig. 11) and P^2 (Pl. 14, Fig. 4) have elongate low crowns with narrow posterolingual cingula as in *Kubanochoerus*. These teeth are much smaller, but relatively wider (index I) in sublophodont *Bunolistriodon*.

The P^3 (Pl. 14, Fig. 8) has a posterolingual cingulum that does not extend much lingually and the protocone is a small inflation of this cingulum, like in *B. jeanneli*. In *Kubanochoerus* the cingulum extends more lingually and the protocone is a separate cusp surrounded by the cingulum. In European *Bunolistriodon* this structure may be still better developed.

The P^4 has a small metacone. The protoprecrista is an elongate and elevated structure, but is not fused to the paracone. It is similar in morphology to the teeth of

B. affinis and *B. jeanneli.*

The M^1, M^2 (Pl. 13, Fig. 7) and M^3 (Pl. 13, Fig. 4) are bunodont with the protopreconule separate from the protocone. The tetrapreconule is separate from, but close to the tetracone and posterior of the transverse valley. The same morphology is found in *Kubanochoerus*, early *Nguruwe*, *B. affinis* and *B. jeanneli.* In size the M^1 from Rusinga are intermediate between the last two species (Text-fig. 36).

The **mandible** (Wilkinson, 1976, pl. 5, fig. C; 1978, fig. 22.5 and Pickford, 1986b, figs 39-46) is narrow in the area of the symphysis. This reflects the narrow incisors. In listriodont species with incisors that are enlarged in meso-distal direction, this part of the mandible tends to become wider. The mandible from Fategad that is assigned to *B. jeanneli* is also narrow in its anterior part. In the male *B. anchidens* from Rusinga (Pickford, 1986b, fig. 41) the canines dip more than 45°. This character is related to the orientation of the upper canines and in the males also to the curvature of the canines. In the later forms the C^m are oriented and curved in such a manner that they are horizontal at the place of occlusion. This is also apparent from the wear striae. In *B. anchidens*, the upper canines were directed downward and less outward and were not much curved. Although there are no good mandibles of later *Bunolistriodon*, it seems likely from the curved canines that these forms had the lower canines dipping less than 45°. This change is probably related to an increased lateral strike in mastication and in this way it is probably related to the development of lophodonty.

The **postcranial skeleton** does not present many interesting characters, except for the astragalus. The astragalus has a clear ridge along the sustentacular facet. In *B. lockharti* and *Listriodon*, such a ridge is not clearly developed. An unciform from Karungu seems to represent *B. anchidens* because of its size and elongate posterior process, which is typical for listriodonts.

Discussion — This material was invariably referred to the species *B. jeanneli.* From the descriptions it appears that it is similar in morphology, but is much smaller (Text-fig. 36). Similarly, the material is morphologically similar to (few) material that is known from *B. affinis*, but it is larger (Text-fig. 36). For this reason a new species is named.

The three species *B. affinis*, *B. anchidens* and *B. jeanneli* are similar in morphology of all known parts. *B. anchidens* is represented by the best material. For this reason, the generic affinities of this group of species are discussed here.

Following Arambourg (1963b), Wilkinson (1976) placed *B. affinis*, *B. jeanneli*, the material from Rusinga and what is here named *Kubanochoerus* in *Bunolistriodon*. Leinders (1975) placed *B. lockharti* in *Listriodon*, thus synonymising *Bunolistriodon* with *Listriodon* and recognised *Libycochoerus*, but did not indicate the status of *B. jeanneli.* Wilkinson (1978) assigned all material of '*Libycochoerus*' and *B. jeanneli* to *Kubanochoerus*, but did not discuss the possibility that *K. massai* and *B. jeanneli* belonged to different genera.

Pickford (1986b) recognised both *Libycochoerus* and *Kubanochoerus* but not *Bunolistriodon* and placed *B. jeanneli* in *Libycochoerus.* He compared the jaw from Rusinga to a jaw of *L. pentapotamiae* (p. 40 and especially text with figs 40-43) and because the material from Rusinga resembles the material of '*Libycochoerus*' *massai* more closely than *L. pentapotamiae*, he concluded that *B. jeanneli*, including the fossils from Rusinga, should be placed in *Libychochoerus.* Following Leinders (1975), Pickford considered *B. lockharti* to belong to *Listriodon*, which may explain the comparison with a species of that genus. The differences mentioned are either primitive characters in *B. jeanneli* and derived characters in *L. pentapotamiae*, or they are difficult to interpret. Characters like the length of a diastema are extremely variable in one large sample of Recent *Sus* and several smaller ones (Van der Made, 1991a), length and thickness of the symphysis of the same samples was also measured and showed a very great variation as well as the shape and extension of the palate behind the M^3.

For a correct assignation of this material to genus, a comparison with *B. lockharti* and *K. gigas* (= *K. robustus*, type species of *Kubanochoerus*) should be made. In *Kubanochoerus*, the males have a large 'horn' in the middle of the frontals and a small protuberance above each eye (known from several skulls of *K. gigas*) and the females have only the two smaller protuberances (known in one skull of *K. massai*). All *Kubanochoerus* are of gigantic size and the protuberances may have developed after these suids became so large or earlier. *B. affinis*, *B. anchidens* and *B. jeanneli* are small and their skulls are not described. For all known characters of the material, but one, *B. anchidens* is primitive compared to *K. gigas* and *B. lockharti.* The P_4 of *B. anchidens* is more derived in having a larger metaconid, than the P_4 of *K. gigas* and especially the more primitive P_4 of *K. marymunnguae.* Whereas *B. anchidens* might be an ancestor to *B. lockharti*, it seems less likely to be the ancestor to *K. gigas.*

Comparisons of other characters with other species than the type species does not lead to an indication of generic identity. The bunodont molar pattern is shared by *B. affinis*, *B. anchidens*, *B. jeanneli*, early *Nguruwe* and *Kubanochoerus*. An I^1 with one lobe only is shared by *B. anchidens* and *Nguruwe*; *Kubanochoerus* has a bilobed incisor. The I^2 of *B. anchidens* is more primitive than in *Kubanochoerus* and *Nguruwe*. The short and rather vertically implanted C^m is shared by *Nguruwe* and *Bunolistriodon anchidens*; where the canine of *Kubanochoerus* is known, it is curved outward. Apparently, all similarities of *B. affinis*, *B. anchidens* and *B. jeanneli* with *Nguruwe* and *Kubanochoerus* are primitive characters.

It appears possible that *B. affinis* evolved into *B. anchidens* and later into *B. jeanneli* and these species are the most likely ancestors of other *Bunolistriodon*, such as *B. lockharti* (see section on phylogeny). Therefore, Arambourg's original suggestion is followed to place these species in *Bunolistriodon*.

A P^3 from the Murree Formation at Gali Jagir was described by Barry & Cheema (1984) as *Listriodon* cf. *L. mongoliensis*. Because of the age, the locality was supposed to be equal in age to Bugti, it does not seem likely that the premolar belongs the latter species, but rather to a *Bunolistriodon* of the *B. affinis* - *jeanneli* group. The size ('much larger than *L. pentapotamiae* and somewhat smaller than the type of *L. mongoliensis*', p. 16) seems to be similar to *B. anchidens*.

Bunolistriodon jeanneli (Arambourg, 1933)

Pl. 13, Figs 3, 8, 9, 11; Pl. 14, Figs 5, 6, 10, 12

1933 *Listriodon jeanneli* nov. sp. — Arambourg, pp. 134-137, pl. 13, figs 1-3.
1933 Suidé indeterminé — Arambourg, pl. 12, fig. 8.
1963 *B. jeanneli* (Aramb.) — Arambourg, p. 910.
1967 *Dicoryphochoerus fategadensis* sp. nov. — Prasad, p. 11, fig. 2.
1972 *Bunolistriodon jeanneli* (Arambourg) — Madden, pp. 2, 6.
1976 *Bunolistriodon jeanneli* (Arambourg) — Van Couvering & Van Couvering, p. 203 (only Moruorot).
1976 *Bunolistriodon jeanneli* Arambourg 1933 — Wilkinson, pp. 217-225 (only the material from Moruorot).
1986b *Libycochoerus jeanelli* (Arambourg, 1933) — Pickford, p. 36-37 (Moruorot only).
1987a *Libycochoerus affinis* (Pilgrim), 1908 — Pickford, p. 305 (only GSI 18098).
1988a *Libycochoerus fategadensis* (Prasad 1967) — Pickford, p. 35, fig. 64.
1988b *Libycochoerus affinis* — Pickford, pp. 947-948 (the specimen from Cutch).
1988 *Libycochoerus jeanneli* — Qiu *et al.*, pp. 16-18 (the material from Moruorot).

Holotype — 1933-9, a palate with right and left P^3-M^3 (Pl. 14, Figs 5, 6, 10, 12). A C^f was believed to be of the same individual. The specimens are in the MNHN collections, and were figured by Arambourg (1933, pl. 13, figs 1-3).

Type locality — Moruorot. Also known as Muruarot, Moruaret, Losodok etc. The University of California Museum of Paleontology named the original locality of Arambourg Moruarot 2 and another locality in the same fossiliferous bed Moruarot 1 (Madden, 1972).

Age of the type locality — Early Miocene, Set II (Pickford, 1986b), more than 16.8 ± 0.2 and probably less than 17.5 Ma (Boschetto *et al.*, 1992).

Diagnosis — Large bunodont *Bunolistriodon*, with relatively large premolars and relatively small M3.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Moruorot	MNHN, KNM	Arambourg 1933	Set IIIB	Pickford 1986c
			(Set II	Pickford 1981)
Fategad	IM	Prasad 1967 Pickford 1988a		

Description and comparison — The species was placed in *Kubanochoerus* (including *Libycochoerus*) and *Bunolistriodon*. Comparisons with the type species *K. gigas* and *B. lockharti* are especially relevant.

The P_4 (Pl. 13, Fig. 3) has the protoconid and metaconid close together. Like in *B. anchidens*, the metaconid is larger and better separated from the protoconid than in *K. gigas* and *K. marymunnguae*, but less so than in *B. lockharti*. The hypoconid is placed in the middle and there is no clear hypoendocristid. In this respect the tooth resembles *B. anchidens*. The tooth is relatively wide (small I), like in *Bunolistriodon*.

The M_1 (Pl. 13, Fig. 3), M_2 (Pl. 13, Fig. 9) and M_3 (Pl. 13, Fig. 11) have the lingual and buccal cusps well separated. Transverse facets are well developed (Pl. 13, Fig. 9), which seems to herald lophodonty.

The **mandible** is narrow in the area of the canines and incisors. For this character, it is like *Kubanochoerus* intermediate between *Sus* and *Potamochoerus* on the one hand and *Listriodon*, *B. lockharti* and *B. latidens* on the other. This reflects the (supposed) shape of the incisors; in the former taxa they have a small DMD and in the latter the DMD is greatly increased.

The **DI^1** (Pl. 13, Fig. 8) can be recognised because of its small size, relatively thin enamel and the lack of a well-developed lingual cingulum. There is a well-developed endocrista, which usually is very wide and low in the permanent incisors.

The **P^3** (Pl. 14, Figs 5, 10) has a small protocone, which is not more than a swelling in the posterolingual cingulum. This structure is smaller than in later species of *Bunolistriodon*, where the protocone is more widely separated from the cingulum. Apparently, when the talon increases in size, the cingulum expands lingually and the protocone remains at the same place and thus becomes separate from the cingulum. Although there are few specimens from *B. anchidens*, this species seems to have an even smaller talon (Pl. 14, Fig. 8). The P^3 has large DAP' values.

The P^4 (Pl. 14, Figs 5, 10) has a small metacone, that is not well separated from the paracone. The protopreconule is a separate cusp. *B. affinis* and *Nguruwe* tend to have a low protoprecrista. If lophodonty is attained, as in *Listriodon*, the protopreconule, merges into the protoloph.

The M^1, M^2 (Pl. 14, Fig. 6) and M^3 (Pl. 14, Fig. 12) have protopreconules that are fused to the cingulum. The M^3 has low DAP' and DT' values.

The **palate** extends only slightly behind the M^3 (Arambourg, 1933, pl. 2, fig. 1a).

Discussion — Apart from the holotype from Moruorot, a mandible from Fategad in India is placed in this species. This mandible is the holotype of *Dicoryphochoerus fategadensis* Prasad, 1967. The latter specimen was recognised by Pickford (1987a, 1988a) as (what is here called) a listriodont and placed in the genus *Libycochoerus*. Pickford hinted already at a possible close relationship with *B. jeanneli* and tentatively placed the mandible in *B. affinis*. The DAP of the M^1 of *B. affinis* is 15.8, and of the M_1 of '*D. fategadensis*' is 22.0, which makes it unlikely that they belong to the same species.

Although some material has been assigned to *B. jeanneli* and *B. affinis*, these species are mainly known by their holotypes, which are upper dentitions. This makes a direct comparison with the mandible from Fategad difficult. The material from Rusinga (which was ascribed to *B. jeanneli*) is helpful, since it comprises upper and lower dentitions. The species from Rusinga resembles *B. jeanneli* and *B. affinis* in having bunodont upper molars (protoconule fused to the cingulum; no protoloph) and premolars with not too well-developed protocone and it resembles the specimen from Fategad in having bunodont lower molars (no protolophid). Besides, the narrow symphyseal area of the mandible from Fategad indicates that incisors had probably small DMD and were like the incisors from Rusinga, which have small DMD. This is corroborated by the deciduous incisor from Moruorot (Pl. 13, Fig. 8). Generally, the upper first and second upper molars are about as long the first and second lower molars, respectively. The specimen from Moruorot and Fategad have similar sizes (Text-fig. 36). There is no morphological or biometrical reason why the holotypes of *B. jeanneli* and *D. fategadensis* may not have belonged to the same species. In a later section the biogeographical implications of this assumption will be discussed.

Bunolistriodon aff. latidens

Pl. 15, Figs 1, 3-16; Pl. 16, Figs 1-12; Pl. 17, Figs 1-7

? 1848 *S. antiquus* — Pomel, p. 157 (Montabuzard).
? 1848-1852 Sus belsiacus — Gervais, p. 101, pl. 33, fig. 7.
? 1850 *Sus antediluvianus* — De Blainville, Tome quatrième, AA Sur les Hippopotames et les Cochons, p. 206 (the mandible with the premolars still in the alveoles) (this volume 1850?).
? 1850 *Sus antiquus* De Blainville, Tome quatrième, AA Sur les Hippopotames et les Cochons, p. 217 (Montabuzard).
? 1853 *Sus belsiacus*, Gervais — Pictet, p. 324.
? 1857 *Sus belsiacus* Gerv. — Rütimeyer, p. 543.
? 1859 *Sus belsiacus* — Gervais, p. 179, pl. 33, fig. 7.
? 1907 *Listriodon* cf. *latidens* et *Lockharti* — Stehlin, p. 543.
? 1908 *Listriodon Lockharti* Pomel — Mayet, pp. 31, 164 (Montabuzard), fig. 57.
1958 *Listriodon lockharti* Pomel — Bergounioux & Crouzel, p. 273.
1965 *Listriodon* sp. — De Bruijn, pp. 15-17.
? 1971 *Bunolistriodon lockharti* (Pomel) — Ginsburg, p. 157.
1975 *Listriodon lockharti* (Pomel) Stehlin 1899 — Leinders, pp. 197-203 (the Spanish material), tabs 1, 2 (not 'Orléanais'), pl. 1, figs 1, 2; pl. 2, figs 4, 7 (*non* fig. 3), text-fig. 1/1, 2 (*non* 3).
1977a *Listriodon lockharti* — Leinders, pp. 61-68, figs 6b, 7b.
1977b *Listriodon lockharti* — Leinders, pp. 360-366 (the Spanish material), fig. 3a.
1982 *Listriodon lockharti* Pomel — Alférez *et al.*, pp. 262-272 (*partim*).
1984 *Bunolistriodon lockharti* (Pomel) — Antunes, pp. 306, 310-311, tab. 1 (*partim*).
1984 *Bunolistriodon lockharti* (Pomel) — Astibia *et al.*, p. 387.
1984 *Bunolistriodon lockharti* — Alberdi *et al.*, pp. 59-60.
1985 *Bunolistriodon lockharti* Pomel 1848 — Morales & Soria, pp. 82-83 (*partim*), pl. 3, figs 2, 3 (*non* fig. 4).
1987 Suidae indet. aff. *Conohyus simorrensis* (Lartet, 1851) — Astibia, pp. 22-23 (not the M_3, the M_1 with doubt), fig. 10a, b (?), 10e, f; pl. 3, figs 5?, 7, 8.
1987 *Bunolistriodon lockharti* (Pomel, 1848) — Ginsburg & Bulot, pp. 455-463, pl. 1, figs 1-9; pl. 2,

figs 1-17; pl. 3, figs 1-9.

1988 *Bunolistriodon latidens* (Biedermann) — Van der Made & Alférez, p. 22.

1990a *Bunolistriodon latidens* (Biedermann, 1873) — Van der Made, p. 86, fig. 3 (*partim*).

1990b *Bunolistriodon latidens* — Van der Made, pp. 100, 104 (*partim*).

1993 *Bunolistriodon* aff. *latidens* (Biedermann, 1873) — Azanza *et al.*, pp. 125-131, pl. 4, figs 1-7.

1996 *Bunolistriodon* aff. *latidens* — Fortelius et al., pp. 150-161, fig. 1, 6.

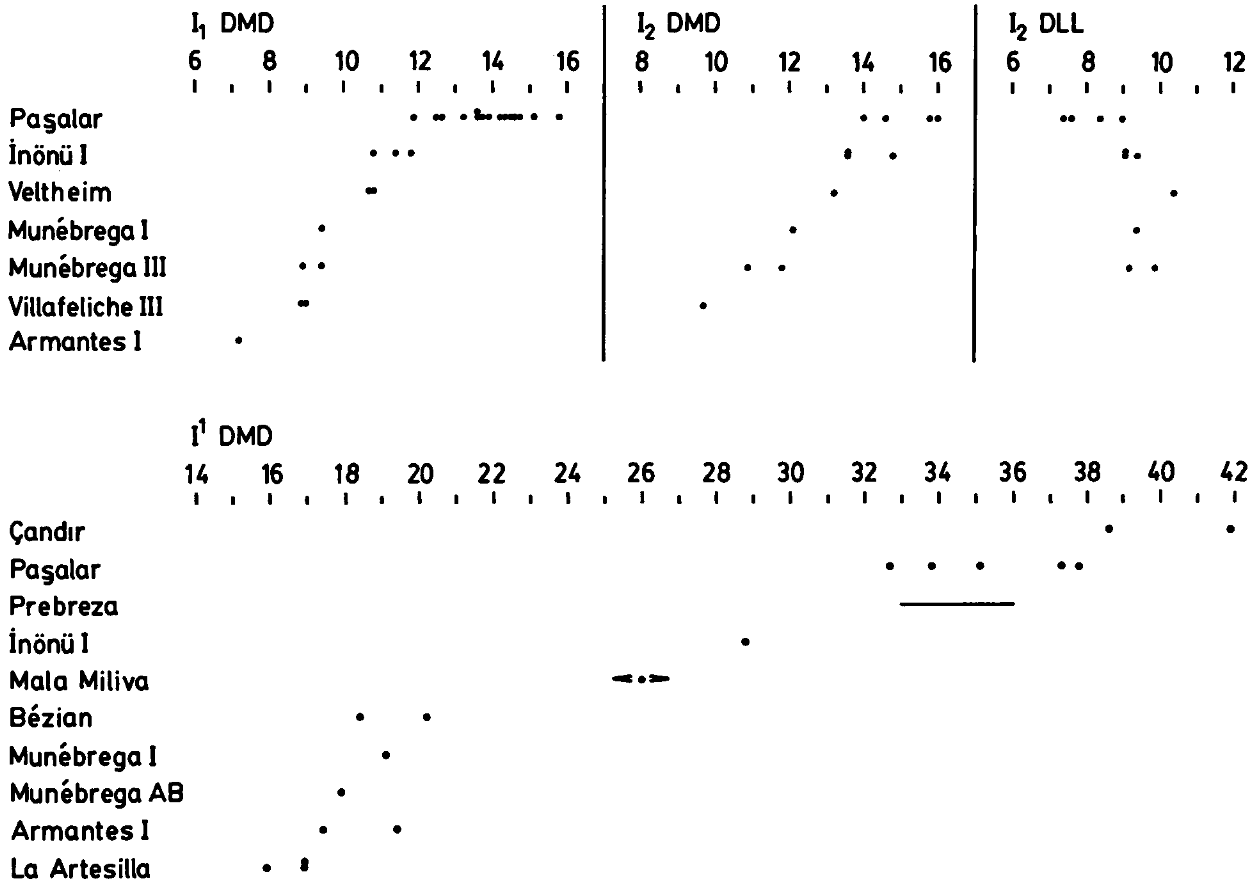


Fig. 37. Size changes in central incisors of *Bunolistriodon latidens*-lineage: *Bunolistriodon* aff. *latidens* (La Artesilla-Bézian), *B. latidens* (Mala Miliva, Veltheim & Inönü I) and *B. meidamon* (Prebreza-Çandir). The localities are in approximate stratigraphical order. Data from Mala Miliva from Petronijević (1967) and from Prebreza from Pavlović (1969). The bar for Prebreza indicates the range of sizes measured from different figures. The arrows for Mala Miliva indicate approximate size.

Diagnosis — *Bunolistriodon* similar to *B. lockharti*, but smaller, the size difference being very clear in the post-cranial skeleton.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Quinta da Raposa	MGSP, CEPUNL	Antunes & Estravís 1986	L Vb MN 4	Antunes 1984
Quinta da Farinheira	MGSP, CEPUNL	Antunes & Estravís 1986	L Vb MN 4b	Antunes 1984
Casal das Chitas	MGSP, CEPUNL	Antunes & Estravís 1986	L Vb MN 4b	Antunes 1984
Courelas do Covao	MGSP	Antunes & Estravís 1986	L Vb MN 4	Antunes 1984
Olival da Susana	CEPUNL	Antunes & Estravís 1986	L Vb MN 4b	Antunes 1984
Quinta das Flamengas	CEPUNL	Antunes & Estravís 1986	L Vb MN 4b	Antunes 1984
Quinta da Silvéria	CEPUNL	Antunes & Estravís 1986	L Vb MN 4b	Antunes 1984
Quinta Grande	MGSP, CEPUNL	Antunes & Estravís 1986	L Vb MN 4	Antunes 1984
Quinta da Lobeira	CEPUNL	Antunes & Estravís 1986	L VB	Antunes 1984
La Artesilla	MPUZ	Azanza *et al.* 1993	MN 4a/C	Azanza 1989
Bézian		Ginsburg & Bulot 1987	MN 4b	Ginsburg & Bulot 1987
Tarazona	UPVB	Astibia 1987	MN 4/D	Astibia *et al.*

				1984
La Hidro-electrica	MNCN, IPS		MN 4	Alberdi *et al.* 1985
Echzell	HLD			
?Montabuzard	MNHN	Gervais 1848-1852, 1859	MN 4b	Abusch Siewert 1983
Córcoles	UCM	Van der Made & Alférez 1988; in prep.	MN 4a/C	Azanza 1989
Armantes I	IVAU		MN 4b	Antunes 1984
Munébrega I	IVAU		MN 4b/D	Azanza 1989
Munébrega II	IVAU			
Munébrega III	IVAU		MN 4b/D	Azanza 1989
Munébrega AB	IVAU	Leinders 1975		
Torralba II	IVAU			
Villafeliche III	IVAU			
Moratines	IPS, MNCN		MN 4	Alberdi *et al.* 1985
Tejar Manzanares	IPS		MN 4b	Antunes 1984
?Georgensgmünd	NMB		MN 4/5	this paper

Description and comparison — Bunolistriodon aff. *latidens* is morphologically closely similar to *B. lockharti* and material of the former species has often been assigned to the latter. More recently the material has been recognised as different and assigned to *B. latidens.*

The **I$_1$** (Pl. 15, Fig. 1; Pl. 16, Fig. 2; Pl. 17, Fig. 2) does not have a clear endocristid. Its DLL is smaller than in *B. lockharti,* except for the earliest samples. The DMD is smaller than in both *B. lockharti* and *B. latidens* (Text-figs 35, 37). The DMD' (53-76) and I (99-125) are less than in *B. latidens* (86 and 137-142, respectively) and are comparable to the values of *B. lockharti* (62-77 and 89-111).

The **I$_2$** (Pl. 16, Figs 2, 3) may have a clear endocristid. DLL of the earlier *B.* aff. *latidens* are comparable to the earlier *B. lockharti*; the later *B.* aff. *latidens* has smaller DLL and the later *B. lockharti* larger. The values for DMD' (98) and index I (113-122) are less than in *B. latidens* (106 and 128-149 respectively) and similar to those of *B. lockharti* (89-94 and 94-127) (Fig. 35). DMD is much smaller than in *B. latidens* (Text-figs 35, 37).

The **I$_3$** (Pl. 15, Fig. 5; Pl. 16, Fig. 9; Pl. 17, Fig. 3) has a smaller DLL than in *B. lockharti,* except in the earliest samples.

The **DI$_2$** (Pl. 15, Fig. 10) does not have a clear endocristid.

The **C$_m$** (Pl. 16, Fig. 8) is 'scrofic' in an early sample and 'verrucosic' in a later sample. The size seems to diminish.

The **C$_f$** (Pl. 17, Fig. 1) is a large tooth and is not as small compared to the C$_m$ as might be expected. It lacks posterior enamel.

The **P$_1$** is a small tooth with only one root (alveolus Pl. 16, Fig. 8).

The **P$_2$** (Pl. 16, Fig. 11) and **P$_3$** (Pl. 16, Fig. 11) have simple morphologies; there are not many posterior crests or cusps additional to the protopostcristid. The P$_3$ is smaller than in *B. lockharti* and tends to be relatively wide compared to *B. latidens.*

The **D$_2$** and **D$_3$** have low crowns, relative to their widths and divergent roots. There are two or three posterior crests.

The **P$_4$** (Pl. 16, Figs 10, 11; Pl. 17, Fig. 6) has a large metaconid, which is well separated from the protoconid. The hypoconid is not always a structure that is separate from the protopostcristid. It is placed labially of the axis of the tooth. It is on average smaller than in *B. lockharti,* but overlap occurs (Text-fig. 38). The width and index I tend to be less than in *B. latidens.*

The **D$_4$** is sublophodont and tends to be smaller than in *B. lockharti.*

The **M$_1$** (Pl. 15, Fig. 14), **M$_2$** and **M$_3$** (Pl. 16, Figs 7, 12) are sublophodont or bunodont. In the bunodont molars, the protoendocristid and metaendocristid (nearly) touch, but are not fused; a clear furrow is seen to separate the structures (Pl. 16, Fig. 7a, b). A hypolophid is not formed. There is a large and high hypopreconulid. The most primitive (bunodont) molars of *B.* aff. *latidens* seem to be more primitive than those of *B. lockharti.* The bunodont type does not occur in *B. latidens.* The molars are on average smaller than those of *B. lockharti,* but overlap occurs (Text-fig. 38), certainly in the earlier samples.

The **I^1** (Pl. 15, Figs 3, 4, 16; Pl. 17, Fig. 5) may have one lobe or three lobes. In the latter case (Pl. 15, Fig. 3), the separation into lobes is not so clear as in *B. lockharti* (Pl. 24, Fig. 3). After some wear any separation of the lobes disappears (Pl. 17, Fig. 5). The values for the index I (152-202) and DMD' (101-115) are much less than in *B. latidens* (249 and 166 respectively), but comparable to *B. lockharti* (Text-fig. 35). The DLL values tend to be lower than in *B. lockharti* and the DMD values lower than in *B. latidens* (Text-fig. 37).

The **DI^1** (Pl. 17, Fig. 4) is a flat tooth and, like the permanent incisors, has three weakly developed lobes.

The **I^2** and **I^3** (Pl. 15, Fig. 11; Pl. 16, Fig. 4) are difficult to distinguish. All specimens are thought to be I^2, which assumption may prove to be a wrong. Their DLL is less than in *B. lockharti,* except for in the very earliest forms.

The **C^m** is possibly not curved outwards very much in the earliest forms, as in La Artesilla. Probably, the tooth increased in size and outward orientation with time. The 100Ri/DT value ranges 202-245 in the specimens measured. This is more than in the majority, but not the extremes of *B. lockharti.* In *B. meidamon,* the values are still higher.

The C^f (Pl. 15, Fig. 7) has a high crown.

The P^2 and P^3 (Pl. 15, Fig. 6) have variable lingual cingula, which may be wide.

The P^4 (Pl. 15, Figs 9, 15) does not have a (clear) metacone, like in *B. lockharti*, but unlike *B. latidens*.

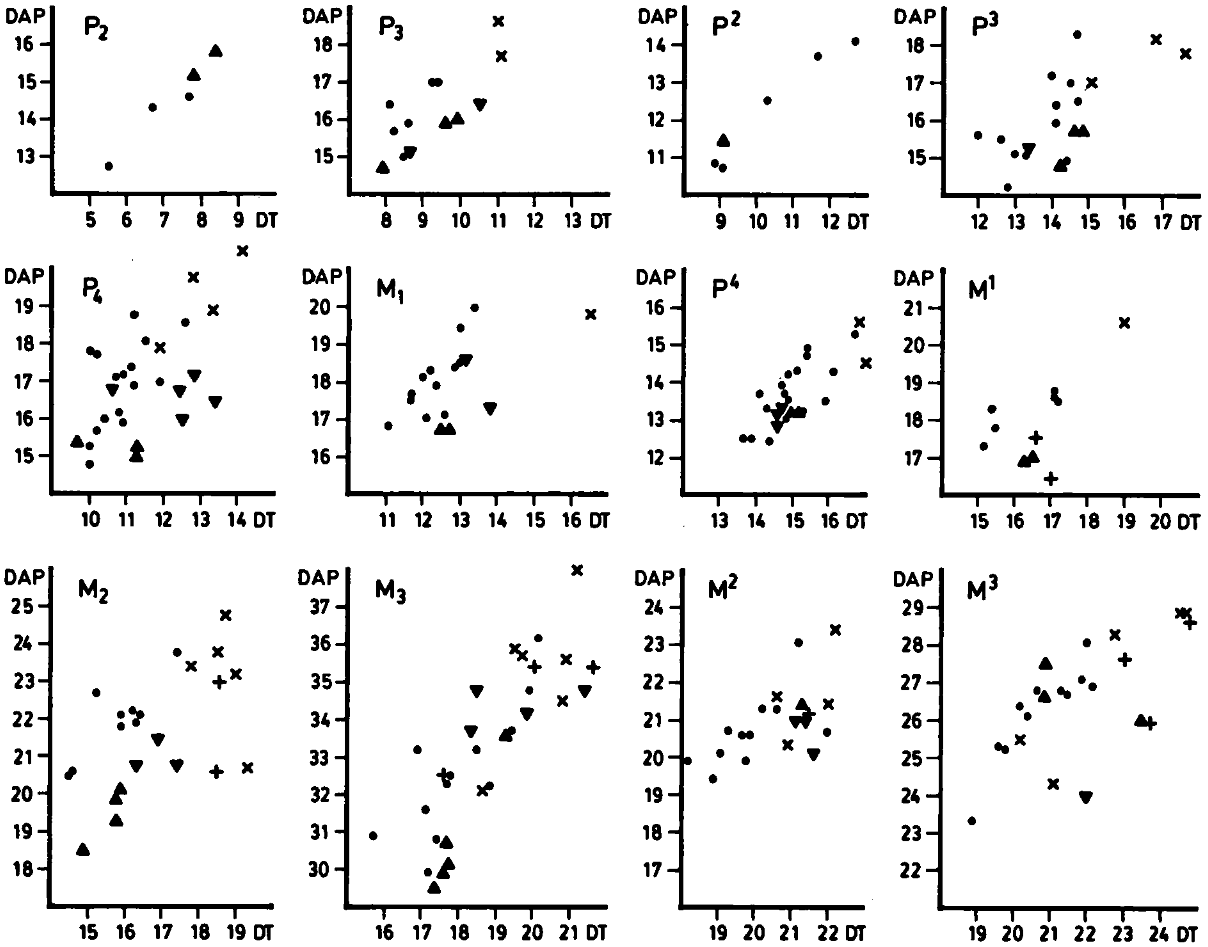


Fig. 38. Bivariate plots of cheek teeth of the *Bunolistriodon latidens*-lineage and of *B. lockharti* from type locality Chevilly and from MN 5 localities. Legend: triangles points downward - *Bunolistriodon* aff. *latidens* (Armantes I, Munébrega I & II, Torralba II); triangles points upward - *Bunolistriodon latidens* (Inönü I, Veltheim); dots - *B. meidamon* (Paşalar); crosses - *B. lockharti* from Chevilly; oblique crosses - *B. lockharti* (Engelswies, Pontlevoy, Beagency, Tavers, Ravensburg).

The lingual cingulum, if present, is not yet very wide. The protocone is a rounded cusp; there is no large protoprecrista, nor a protopreconule. Both other species have such structures.

The D^4 is sublophodont.

The M^1, M^2 (Pl. 15, Fig. 13; Pl. 16, Fig. 1) and M^3 (Pl. 15, Figs 8, 12; Pl. 16, Fig. 6) are sublophodont (Pl. 15, Fig. 13) or even still bunodont (Pl. 15, Fig. 12). In the sublophodont type, the protoprecrista is fused to the paracone. At the place of this fusion, the loph is very low and positioned far anteriorly. The resulting loph is not well formed: high and straight. In the bunodont form, there is a protopreconule, that is not fused to the paracone, it is close to the protocone, but still separated by a furrow and it is either free from the cingulum or faintly connected to it, though placed much posteriorly. In both types, the tetrapreconule, is placed close to the tetracone and well behind the middle of the transverse valley. The bunodont type is more advanced in the direction of lophodonty than in bunodont *Bunolistriodon*, such as *B. anchidens* (Pl. 13, Fig. 4) and *B. jeanneli* (Pl. 14, Fig. 12), where the protopreconule is well fused to the cingulum and well separated from the protocone. It seems that this 'bunodont-sublophodont' morphology does not occur or is much rarer in *B. lockharti* (Pl. 24, Figs 7-13), even in the earliest samples. In the M^3 there is a talon, that is either like a wide cingulum or has a pentacone. In the other molars, the tetrapostcrista forms a continuous structure with the postero-labial cingulum.

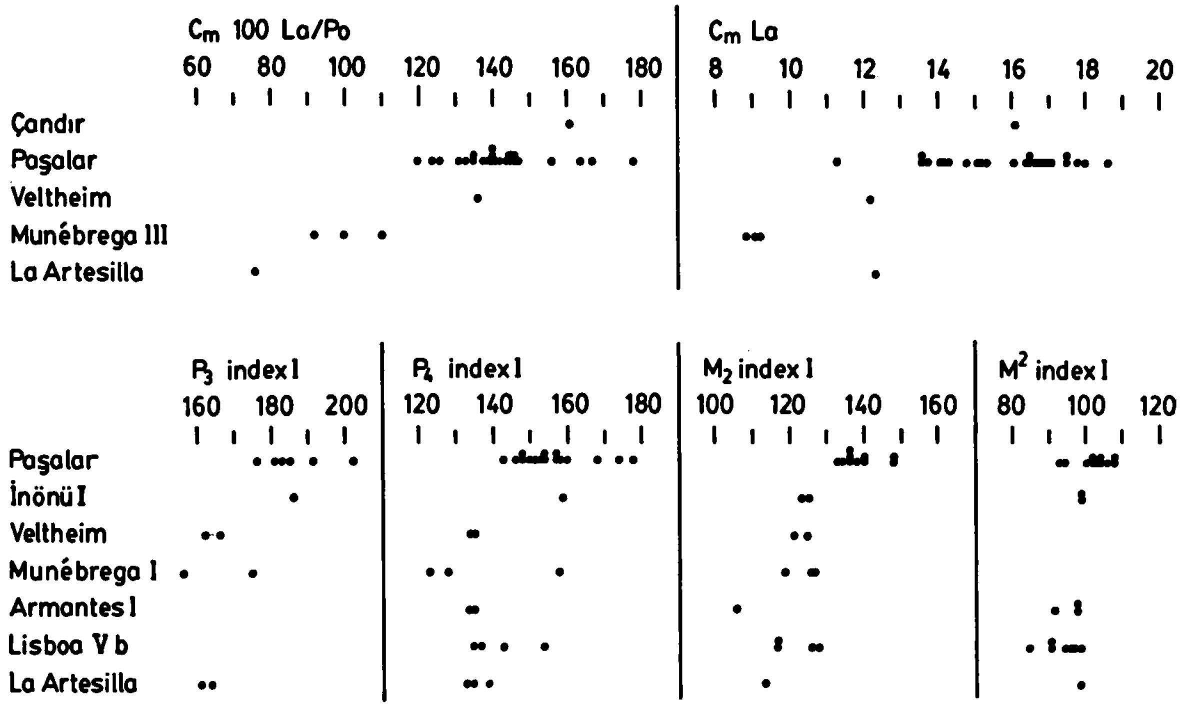


Fig. 39. Changes in canines and cheek teeth through time in the *Bunolistriodon latidens*-lineage: *B.* aff. *latidens* (La Artesilla-Munébrega I/III) — *B. latidens* (Veltheim & Inönü I) — *B. meidamon* (Paşalar & Çandir). The oldest *B.* aff. *latidens* (La Artesilla) are still large, which is reflected in a large canine (La). The increase of the index of the labial and posterior sides of the canine is gradual and unites Veltheim with the younger localities. The increase in index I of the cheek teeth seems to occur mainly between Veltheim and Paşalar and unites Veltheim still with the older localities.

The **mandible** has a wide anterior part where the incisors are implanted. Although there are no undeformed specimens, as it is clear that this area was wider than in bunodont *Bunolistriodon*, such as *B. anchidens* and *B. jeanneli*. The diastemata are long.

A partial **skull** was figured by Ginsburg & Bulot (1987). It has a wide snout, which is rounded dorsally. The alveoles of the C^m indicate that these teeth are directed outward. The bases of the canines are covered by a smooth bone cover, not a crista alveolaris in the sense of Thenius (1972). The parietal crests came very close to forming a sagittal crest. There is a single lacrimal foramen on the anterior rim of the orbit. This is the only mention of such a foramen in Listriodontinae. *Lopholistriodon*, *Kubanochoerus* and *Listriodon* lack lacrimal formanina. There is no 'horn' or other type of cranial appendage.

The **postcranial skeleton** is of particular interest. In the large collection from Córcoles, two separate sizes of bones are present (Text-fig. 40), whereas the cheek teeth are more difficult to separate (Van der Made & Alférez, 1988). It is absolutely impossible to assign the two sizes of astragalus to one species, the variation would be much too large compared to many other samples of suoids and other artiodactyls. The separate size groups have normal variation in size. The size of the larger specimens is comparable to *L. splendens*. *B. lockharti* cheek teeth are also of a size comparable to *L. splendens*. The smaller astragali obviously go with the smaller cheek teeth, which are smaller than those of *L. splendens*. Text-figure 40 shows the size of the astragalus of *Bunolistriodon* aff. *latidens* and *B. lockharti* from a number of localities, which are roughly arranged according to age. *B. lockharti* shows some variation in size, but is always large. Córcoles has both species and they are well separated. Other localities have intermediate sizes. This is interpreted as *B.* aff. *latidens* decreasing in size, until it reached the size of Córcoles. An astragalus from La Hidroélectrica is small, but is not plotted, since its stratigraphical position is not clear to me.

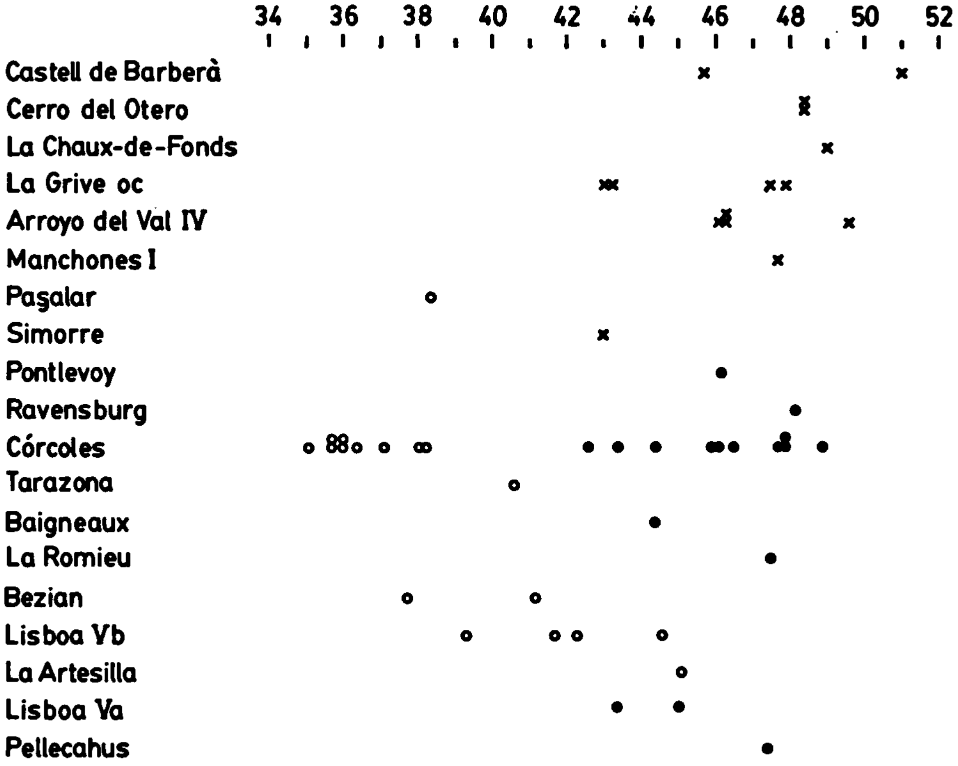


Fig. 40. Size change in astragalus of European *Bunolistriodon* and *Listriodon*. The size indicated is the Lext of the astragalus. The localities are in approximate stratigraphical order. Legend: dots - *B. lockharti*; circles - *B. latidens*-lineage (*B.* aff. *latidens*, La Artesilla-Córcoles, and *B. meidamon*, Paşalar); oblique crosses - *L. splendens*. The figure shows that there are two sizes of *Bunolistriodon* in Córcoles, *B. lockharti* and *Bunolistriodon* aff. *latidens* and that there are a number of localities which are older than Córcoles with sizes intermediate between *B. lockharti* and *B.* aff. *latidens*, suggesting that the latter species decreased in size during its early history. Córcoles is placed here as indicated by the size of the astragali. This may not be its exact stratigraphical position; see discussion on the biostratigraphical results of Europe and Anatolia.

Morphologically there is little variation in the **postcranial skeleton** of the listriodonts (**magnum** Pl. 17, Fig. 7), except for the facet for the second cuneiform, on the **navicular** which may be lacking in some forms, including *Bunolistriodon* aff. *latidens*.

Discussion — The size, especially of the postcranial skeleton (Text-fig. 40), indicates the presence of a species smaller than *B. lockharti*. What are believed to be the younger samples have smaller sizes and are more easily separated from *B. lockharti*, for instance by DLL values of the incisors. In the older samples, bunodont molars occur and P^4 with no protopreconule or large protoprecrista and P_4 with the hypoconid not well separated from the protopostcristid. Such morphologies are rare or do not occur in *B. lockharti*.

For European *Bunolistriodon*, several species have been proposed of which *B. latidens* and *B. belsiacus* are of interest here. The material described here differs from *Bunolistriodon latidens* in the much lesser mesiodistal diameters of the incisors.

Sus belsiacus Gervais, 1848-1852 might as well have been treated with *B. lockharti*. However, *B. lockharti* seems to be the older name and would have priority in case of synonymy. That is why *B. belsiacus* is treated here. The species is based on a mandible from Montabuzard with the premolars in the alveoles and the first two molars functioning. The specimen was figured by Gervais (1848-52, 1859) and Mayet (1908); it is stored in the MNHN. One of the molars is lost now. The morphology is that of *Bunolistriodon*. The molar is bunodont; the protoendocristid and metaendocristid are directed towards each other, but are not fused into one structure (Pl. 22, Fig. 11). This might indicate that the specimen belongs to what is termed here *B.* aff. *latidens*. The size is more or less in the overlap zone between *B.* aff. *latidens* and *B. lockharti*. No other *Bunolistriodon* is known from Montabuzard and the locality is no longer worked. Other localities in the Orléans area have *B. lockharti*. There is no reliable way to assign this mandible to either the large or the small *Bunolistriodon*. This, however, is no real problem, since the name has not been applied for over a century and may thus be forgotten. Obviously, the small *Bunolistriodon* should be named from a collection with good postcranial material, such as Córcoles. A description of that collection is in preparation (Van der Made & Alférez, in prep.).

Bunolistriodon latidens (Biedermann, 1873)

Pl. 4, Fig. 4; Pl. 18, Figs 1-9

1873 *Sus latidens* m. — Biedermann, p. 11, pl. 7.
1899-1900 *Listriodon latidens* Biederm. — Stehlin, pp. 13, 85, 173, 285, 327, 426, 462, pl. 1, fig. 15; pl. 3, figs 31-33.
1914 *Listriodon latidens* Biedermann — Stehlin, p. 192.
1925 *Listriodon latidens* Biedermann — Stehlin, p. 68.
? 1940 *Listriodon* (n. sp.?) *lockharti* Pomel var. *Michali* n. var. — Paraskevaidis, pp. 394-399, pl. 12, fig. 6.
1967 *Listriodon lockharti* (Pomel) — Petronijevic, pp. 70, 141 (not Krusevica - ?), tab. 19, pl. 10, figs 1, 2; pl. 11, figs 1-10.
1967 "*Listriodon latidens*" — Nikolov & Thenius, p. 335.
1967 *Listriodon lockharti michali* — Nikolov & Thenius, p. 338.
1979 *Listriodon* cf. *lockharti* (Pomel, 1848) — Pickford & Ertürk, pp. 144-145 (the material from Inönü), pl. 1, fig. 9; pl. 2, figs 1, 2.
1985 *Bunolistriodon lockharti* Pomel 1848 — Morales & Soria, p. 82-83 (Puente de Vallecas).
1989 *Listriodon* cf. *lockharti* (Pomel) — Tekkaya, p. 157.
1990 *Listriodon lockharti* — Fortelius & Bernor, tab. 1 (*partim*).
1990a *Bunolistriodon latidens* (Biedermann, 1873) — Van der Made, p. 86, fig. 3 (*partim*).
1990b *Bunolistriodon latidens* — Van der Made, pp. 100, 104 (*partim*).
1996 *Bunolistriodon latidens* (Biedermann, 1873) — Fortelius, Van der Made & Bernor, pp. 150-162, figs 1, 4, 6

Holotype — No. 99, a mandible with right and left P_2-M_3, C_m and I_1 and left I_2 (Pl. 18, Fig. 2), in the Naturwissen-schaftliche Sammlungen der Stadt Winterthur, figured by Biedermann (1873, pl. 7) and Stehlin (1899-1900, pl. 1, fig. 15; pl. 3, figs 31-33).
Type locality — Veltheim, Switzerland.
Age of the type locality — Miocene, Aragonian, probably MN 5, or else early MN 6.
Diagnosis — *Bunolistriodon* smaller than *B. lockharti*, with I^1, I_1 and I_2 with relatively greater meso-distal diameters, but not with extreme diameters.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Puente de Vallecas	IPS	Morales & Soria 1985	MN 5	Alberdi *et al.* 1985
Veltheim	NSSW	Biedermann 1873, Stehlin 1899/1900	MN 5	
Mala Miliva		Petronijevic 1967	MN 5	Mein 1990
Inönü I	MTA	Pickford & Ertürk 1979	MN 6	
Schlatt	NMB			
Sigmaringen	PIMUZ, NMB			

Description and comparison — *Bunolistriodon latidens* has often been synonymised with *B. lockharti*. For this reason, comparisons are primarily made with that species.

The I_1 (Pl. 18, Figs 3-5) and I_2 (Pl. 18, Figs 3-5) do not have a very clear endocristid. Index I and DLL differ from *B. lockharti* (Text-fig. 35). For the I_1, the index I ranges 137-142; in *B. lockharti* this is 89-122. DMD' is 86 versus 62-77. For the I_2 the I ranges 128-162 for *B. latidens* and for *B. lockharti* 94-127. DMD' is 106 and 89-94, respectively.

In the older literature, the I_3 (Pl. 18, Figs 4, 5) was claimed to be absent in this species. However, it is present in two specimens from Inönü I. In the type, the tooth is simply lost because of damage.

The C_m is a slender tooth. The labial side is wider than the lingual side and the posterior side is very narrow. These typical proportions are also found in the *Bunolistriodon* from Paşalar. *B. lockharti* has canines with a 'verrucosic' section; the width of the labial and posterior sides are about equal.

The P_2 (Pl. 18, Fig. 2) and P_3 (Pl. 18, Figs 2, 7) tend to have simple protopostcristids and very little additional structures in the posterior part of the tooth.

The P_4 (Pl. 18, Fig. 2) has the metaconid separated from the protoconid, though it may be placed slightly posteriorly of the protoconid. A protoposcristid connects hypoconid and protoconid. The hypoconid is placed labially and has a large hypoendocristid. The D_4 is sublophodont.

The M_1 (Pl. 18, Fig. 2), M_2 (Pl. 18, Fig. 2) and M_3 (Pl. 18, Fig. 2) are sublophodont. The point where protoendocristid fuses with the metaendocristid is posterior of the line through the protoconid and metaconid. The protoprecristid and protoloph enclose a large protofossid. The hypoendocristid and entoendocristid touch but do not yet form a straight loph. The hypopreconulid is large and in the middle of the transverse valley.

The I^1 (Pl. 18, Fig. 6) has three lobes. It is much more flattened than in *B. lockharti*: the value I is 249 versus 145-200. The DMD' values are 166 for *B. latidens* and 97-114 for *B. lockharti.*

Some of the larger I^2 from Inönü I are assigned to *B. latidens* because they are larger than most of the incisors of *L. splendens* from other localities. The latter species is also found in Inönü I. However, there is no reliable way to separate I^2, I^3 and DI^2 (and DI^3) of the two species, there are too many and too similar types.

One C^m (Pl. 18, Fig. 1) is known from Veltheim. Its length is over 20 cm. The section is slightly larger than in *B. lockharti.* The radius of curvature is large. 100Ri/DT is 202.

The P^2 (Pl. 4, Fig. 4) and P^3 (Pl. 4, Fig. 4; Pl. 18, Fig. 8) have a wide lingual cingulum and the protocone is much better separated from that cingulum than in *B. lockharti* (Pl. 22, Fig. 6; Pl. 24, Fig. 2).

The P^4 (Pl. 4, Fig. 4; Pl. 18, Fig. 9) has a large metacone, which is well separated from the paracone. There is a large and high protopreconule, virtually forming a protoloph, but still recognisable as a separate element. In the available specimens, the lingual cingulum is continuous and wide.

The M^1 (Pl. 4, Fig. 4), M^2 and M^3 are sublophodont.

The size of all cheek teeth is on average smaller than those of *B. lockharti,* though overlap does occur (Text-fig. 38).

The anterior part of the **mandible** is wide, in accordance with the wide incisors.

The **skull** (Pl. 4, Fig. 4) is really massive in the area of the (male) canines. The maxilla extends very much laterally at the place of the canines and extends over the base of the canines as a relatively thin smooth bone, not like the 'crista alveolaris' (*sensu* Thenius, 1972) in *Potamochoerus* or *Microstonyx.* The snout is wide and the dorsal side is round in transverse section. The impression of the palate is that it is wide, relative to the other measurements.

Discussion — The fossils differ from *B. lockharti* in a number of characters: the incisors (I^1, I_1 and I_2) are much wider, the C_m have wide labial sides, the C^m tend to be larger, the P^4 have a well-individualised metacone and the cheek teeth tend to be smaller, though overlap does occur.

The material includes the holotype of *Bunolistriodon latidens* (Biedermann, 1873). *'Listriodon* (n. sp.?) *lockharti* Pomel var. *Michali* n. var.' Paraskevaidis, 1940 is based exclusively on a worn M^3 from Chios. The specimen is small and for that reason, probably does not belong to *B. lockharti.* It may belong to what is considered here as a single lineage: *B.* aff. *latidens-B. latidens-B. meidamon.* The species of this lineage differs mainly in characters that cannot be studied in the M^3. The imprecise datation of Chios compared to the rapid evolution of the *B. latidens* lineage does not allow assignment of this type to any stage of evolution.

Bunolistriodon meidamon

Fortelius, Van der Made & Bernor, 1996
Pl. 4, Figs 3, 5; Pl. 17, Fig. 8; Pl. 19, Figs 1-23;
Pl. 20, Figs 1-10

1959 *Listriodon michali* Parask. — Pavlović & Thenius, p. 216.
1960 *Listriodon splendens michali* Parask. — Ćirić, p. 128, pl. 2, figs 4, 5.
1969 *Listriodon michali* (Parask.) — Pavlović, pp. 389-390, pl. 9, figs 1-5; pl. 10, figs 1, 2; pl. 11, figs 1-4.
? 1972 *'Listriodon' michali* — Thenius, p. 578.
1975 *Schizochoerus* sp. — Hünermann, pp. 153-154.
1975 *Listriodon splendens* Meyer — Hünermann, p. 154 (the canine).
1979 *Listriodon splendens* H. von Meyer 1846 — Pickford & Ertürk, p. 142 (the 'form with huge upper canines and very large I^1'), pl. 1, figs 1, 6, 7 (*partim*).
1990 *Listriodon* sp. nov. Fortelius & Bernor, pp. 512-519, figs 2a-d, 3, 4, 5a, b.
1994 *Listriodon* aff. *L. latidens* — Hunter & Fortelius, pp. 105-124.
1996 *Bunolistriodon meidamon* — Fortelius, Van der Made & Bernor, pp. 149-162, figs 1-13.

Holotype — B609.1, right I_1, B35.13, left I_1 and B601.1, left I_2 of the same individual (Pl. 20, Fig. 4), in the PDTFAU collections.

Type locality — Paşalar, Turkey.

Age of the type locality — Middle Miocene, Aragonian, Astaracian, MN 6.

Loc.	**Coll.**	**Ref./Descr.**	**Stratigraphy**	**Reference**
Prebreza		Pavlović 1969	MN 6	Mein 1990
Paşalar	MTA, PIMUZ	Fortelius & Bernor 1990 Fortelius et al. 1996	MN 6	Mein 1990
Çandir	MTA, PIMUZ		MN 6	Mein 1990

Description and comparison — This species belongs to the *B. latidens*-lineage. *B. latidens* is an older species. For this reason, comparisons are mainly made with this species. Since this species has all characters involving incisor and canine size and morphology of *B. latidens* in an exaggerated form, a comparison with *B. lockharti* is superfluous and the reader is referred to the description of *B. latidens*. Since the species co-occurs with *L. splendens* comparisons with that species are made for some of the teeth.

The **I_1** (Pl. 19, Figs 15, 16, 18; Pl. 20, Figs 4-6) and **I^2** (Pl. 19, Fig. 19; Pl. 20, Fig. 4) do not have clear endocristids. If such a structure is visible, it departs from a clearly separate cusplet at the cutting edge of the tooth, leaving this edge divided into three elements: the protopreconulid, protoconid and protopostconulid. In *L. splendens* the protoconid is not so well separated, and there are two elements: the protoconid + protopostcristid and the protopreconulid. For both species similar arrangements as in the I_1 and I_2 are found in the I^1 and I_3. The teeth have greatly increased DMD, which is reflected in high values for the index I (I_1: 152-223, I_2: 176-188, F35) and DMD' (I_1: 114, I_2: 123). The DLL has very low values and probably for this reason the preanticlinid and postanticlinid nearly disappeared (Pl. 19, Fig. 15b, d; Pl. 19, Fig. 19c), leaving the lower limit of the crown nearly straight. Values for DMD, DMD' (I_1: 86, I_2: 106) and I (I_1: 137-142, I_2: 128-162) for *B. latidens* are lower.

The **I_3** (Pl. 19, Fig. 20) has a protopreconulid, protoconid and protopostconulid. It has very low values for DLL.

The **DI_1** (Pl. 20, Fig. 2) and **DI^2** (Pl. 19, Fig. 22) are small with relatively thin enamel. They resemble the permanent incisors, except for the DI_1 being less symmetrical.

The **C_m** (Pl. 4, Figs 3, 5) has a section with the labial side as wide as the lingual side and much wider than the posterior side. This is also the case in *B. latidens*, but not in *B. lockharti* and *L. splendens*, where the labial and posterior sides have the same width and the lingual side is much wider (Text-fig. 49).

The **C_f** has enamel at the posterior side. This is not the case in specimens of *L. splendens* known.

The **P_2** (Pl. 19, Figs 6, 10) and **P_3** have a simple protoconid, with only a protoprecristid and protopostcristid. In some specimens, a low hypoconid is indicated. The anterior cingulum is high and slightly elevated in the middle. The protoprecristid is concave in lateral view. In *B. latidens* it tends to be convex. In many specimens, the protopostcristid reaches a low point far before the posterior end of the tooth. In lateral view, the protocone seems a much more slender cusp than in most other listriodonts, because of the structures at the ends of the protoprecristid and protopostcristid. The teeth have higher indices I (P_2 190-231; P_3 176-202) than most *B. latidens* (P_2 188-195; P_3 162-166) and *Listriodon* (P_2 146-204; P_3 124-173); the teeth are more elongate.

Except for the smaller size, thinner enamel and divergent roots, the **D_2** (Pl. 19, Fig. 2) and **D_3** (Pl. 19, Fig. 11) resemble the permanent premolars.

The **P_4** (Pl. 19, Figs 1, 3, 5, 7) has usually a large metaconid that is well separated from the protoconid. The cusps are not as wide apart as in *Listriodon*. The anterior cingulum has usually a cusp in the middle that may be really large. This is not the case in *Listriodon* and *B. latidens*. There is a large protopostcristid linking protoconid and hypoconid. The hypoconid is placed buccally of the axis of the tooth, but there is no hypoendocristid. The I value (143-178) is higher than in most *Listriodon* (118-152) and *B. latidens* (134-159).

The **D_4** is sublophodont.

The **M_1** and **M_2** (Pl. 20, Fig. 7) are sublophodont. The protoendocristid and metaendocristid are fused into one protolophid, which is not fully straight. The hypoendocristid and entoendocristid touch but are not yet fused into one structure. The hypopreconulid is still a separate cusp in the middle of the transverse valley. The molars are considerably more elongate than in *Listriodon* and *B. latidens*.

The **M_3** (Pl. 20, Fig. 8) is also sublophodont. It is not more elongate than in *B. latidens*.

The **I^1** (Pl. 17, Fig. 8; Pl. 20, Figs 3, 9) has three lobes, which are best seen from the labial side. The tooth is extremely elongated in mesodistal direction. No other listriodont has such high values for I (277-322) and DMD' (217) (Text-fig. 26). For *B. latidens* the values are 249 and 166, respectively. For *L. splendens*, which has a bilobed I^1, the values are 151-283 for I and 146-185 for DMD'.

The **DI^1** (Pl. 19, Fig. 23) seems to have two lobes, where three lobes are expected. However, these are the most elongate specimens in Paşalar.

No reliable way was found to separate **I^2**, **DI^2** and **I^3** (and DI^3?) of *B. meidamon* and *L. splendens* from Paşalar and measurements are not given in the tables.

The **C^m** is large and has a large radius of curvature.

The **C^f** (Pl. 19, Fig. 17) has a high crown, higher than in *L. splendens* (Pl. 35, Fig. 1), though DAP and DT are smaller.

The **P^1** does not have a protocone. There is a lingual cingulum. There are two roots.

The **P^2** (Pl. 19, Figs 13, 14) and **P^3** (Pl. 19, Fig. 12) have protocones that are well separated from the wide lingual cingulum. There is no large metacone, there may, however, be a small cusp in the parapostcrista, which might be called parapostconule.

The **D^2** has a low posterior part, where there are both a parapostcrista and paraendocrista that is turned posteriorly. The latter might be termed a protocone, if it were a larger structure.

The **P^4** (Pl. 19, Figs 4, 8, 9) has a metacone that is well separated from the paracone; often it is nearly as large as the paracone (Pl. 19, Fig. 9), but it may be low (Pl. 19, Fig. 4). In many cases there is a perfect protoloph, but in other instances, the protoendocrista stops short of fusing to the paracone. In nearly all cases there is a wide lingual cingulum.

The **D^3** and **D^4** are sublophodont; the posterior lobe does not have a well-formed loph.

The **M^1**, **M^2** and **M^3** (Pl. 20, Fig. 10) are sublophodont. There is usually a protoloph, but the tetraendocrista is not fused to the metacone. There is no large tetrapreconule, blocking the transverse valley.

Some elements of the **postcranial skeleton** from Paşalar are assigned to *B. meidamon* on the basis of their size, which is too small for *L. splendens*, also found at that locality.

Discussion — *Bunolistriodon meidamon* is a sublophodont listriodont with incisors with greater DMD, DMD' and I than any other listriodont. The most similar suid is *B. latidens*, from which it differs in narrower (I) lower cheek teeth and larger and more elongate (DMD, DMD' and I) incisors. It differs in a great number of characters from *L. splendens*: sublophodonty, narrower (I) cheek teeth, smaller size, three-lobed incisors, and much greater values for DMD, DMD' and I of the incisors.

Part of the material was ascribed to *B. michali*. This species, however, is based on a single M^3. It does not show any of the important characters, which separate *B. meidamon*, *B. latidens* and *B. lockharti*. In view of the approximate age of the locality and the size of the tooth, the M^3 might belong to one of these three species.

Bunolistriodon lockharti (Pomel, 1848)

Pl. 15, Fig. 2; Pl. 21, Figs 1-9; Pl. 22, Figs 1-9, 12;
Pl. 23, Figs 1-13; Pl. 24, Figs 1-11;
Pl. 25, Figs 1-6, 9, 10

1839 *Hyotherium sidero molassicum minus* — Jäger, p. 76, pl. 10, figs 55-57.
1839 *Hyotherium sidero molassicum majus* — Jäger, p. 76, pl. 10, figs 23-27, 58.
1847 *Choeropotamus*? sp. de l'Orléanais — De Blainville, Tome Quatrième. Y Des Palaeotheriums, Lophio-donts, Anthracotheriums, Choeropotames, p. 147, Genre *Choeropotamus*, pl. 1 (not the canine).
1847 *Sus antiquus* — De Blainville, Tome Quatrième. Y Des Palaeotheriums, Lophiodonts, Anthracotheriums, Choeropotames, pp. 154, 176 (Avaray).
1848 *Sus Lockharti* (Pom.) — Pomel, p. 159.
1848-1852 *Sus lockharti* — Gervais, p. 101.
1850 *Sus antediluvianus* — De Blainville, Tome Quatrième. AA Sur les Hippopotames et les Cochons, pp. 205-206 (material from the Orléanais, but not the mandible with the premolars still in the alveoles), Genre *Sus*, pl. 8.
1850 *Sus larvatus*? — De Blainville, Tome Quatrième. AA Sur les Hippopotames et les Cochons, p. 217, Genre *Sus*, pl. 9 (the larger two specimens from Anjou).
1853 *Sus Lockharti*, Pomel — Pictet, p. 324.
? 1853 *H. sideromolassicum*, Jaeger — Pictet, p. 330.
1857 *Sus lockharti* Pomel — Rütimeyer, p. 542.
1859 *Sus lockharti* — Gervais, p. 178.
1878 *Sus Lockharti* — Gaudry, p. 70.
1899/1900 *Listriodon Lockharti* Pomel — Stehlin, pp. 13, 85, 172, 175, 283, 286, 333, pl. 1, figs 16?, 17?; pl. 5, figs 17, 24; pl. 6, fig. 17; not the canine of p. 284 and pl. 5, fig. 5 (*Hyotherium soemmeringi*?).
1907 *Listriodon lockharti* — Stehlin, pp. 531-532.
1908 *Palaeochoerus aurelianensis* Stehlin — Mayet, p. 294 (where the specimen of pl. 10, fig. 11 is meant), pl. 10, fig. 11.
1908 *Listriodon Lockharti* Pomel — Mayet, pp. 78, 81-82 (*partim*), 84, 162-172 (*partim*), 294-295, figs 56-58, 99b, c; pl. 5, figs 17-20, 23-25, *non* figs 21, 22, pl. 10, fig. 12.
1908 *Listriodon latidens* Biedermann — Mayet, p. 296, pl. 11, fig. 1.
1914 *Listriodon lockharti* Pomel (?) — Hernandez-Pacheco, pp. 458-459.
1925 *Listriodon Lockharti* Pomel — Stehlin, pp. 67-70.
1928 *Listriodon latidens* Biederman — Depéret & Viret, p. 580.
1934 *Listriodon lockharti* (Pomel) — Dehm, pp. 522-524 (not material from Stätzling; material from Biberach possibly not either), figs 10-13, 17.
1934 *Listriodon Lockharti* Pomel — Roman & Viret, pp. 38-43 (not the material from Veltheim), figs 15, 16; pl. 3, figs 1-18; pl. 4, figs 1-5.
1940 *Listriodon lockharti* Pomel — Paraskevaidis, text-fig. 8/1- 2; pl. 12, figs 7, 8.
1946 *Listriodon Lockharti* Pomel — Richard, pp. 244, 246, 254.
1958 *Listriodon splendens* Meyer — Bergounioux & Crouzel, p. 296.
1968 *Listriodon lockharti* — Hünermann, figs 26-31.
1971 *Bunolistriodon lockharti* (Pomel) — Ginsburg, pp.

156, 158-160.
1972 *Palaeochoerus giganteus* n. sp. — Golpe-Posse, pp. 118, 155, pl. 1, fig. 1c.
1972 *Listriodon (Bunolistriodon) lockharti* (Pom., 1848) — Golpe-Posse, pp. 134-137 (*partim*).
1975 *Listriodon lockharti* (Pomel) Stehlin, 1899 — Leinders, tab. 2 'Orléanais'?, figs 1, 3.
1977 *Listriodon lockharti* — Leinders, fig. 3b?
1977 *Listriodon lockharti* (Pomel) — Collier & Guex, p. 470.
? 1981 *Bunolistriodon* cf. *lockharti* — Gabunia, p. 197.
1982 *Listriodon lockharti* Pomel — Alférez *et al.*, p. 262-272 (*partim*), pl. 2, figs 9, 10; pl. 3, figs 3, 11.
1984 *Bunolistriodon lockharti* (Pomel) — Antunes, pp. 306, 310-311, tab. 1 (*partim*).
1985 *Bunolistriodon lockharti* Pomel 1848 — Morales & Soria, pp. 82-83 (*partim*).
1986 *Bunolistriodon lockharti* (Pomel, 1848) — Antunes & Estravís, pp. 141, 149-161 (material of Lisbon Va), pl. 3, figs 21, 28, 30; pl. 4, figs 36, 37; pl. 5, fig. 41; pl. 6, figs 43, 45.
1987 *Bunolistriodon lockharti* (Pomel, 1848) — Astibia *et al.*, pp. 425-430, pl. 1, figs 3-5.
? 1988 *Bunolistriodon lockharti* (Pomel) — Agustí *et al.*, p. 95, pl. 2, figs 1-4.
1988 *Bunolistriodon lockharti* (Pomel) — Van der Made & Alférez, p. 22.
1988 *Bunolistriodon lockharti* (Pomel, 1848) — Crouzel *et al.*, p. 102.
1990 *Listriodon lockharti* — Fortelius & Bernor, tab. 1 (*partim*).
1990a *Bunolistriodon lockharti* (Pomel, 1848) — Van der Made, pp. 85-86, fig. 3.
1990b *Bunolistriodon lockharti* — Van der Made, pp. 100, 104.
1990 *Bunolistriodon lockharti* (Pomel, 1848) — Ginsburg, pp. 164-166.
? 1991 *Listriodon* aff. *lockharti* (Pomel), 1848 — Codrea *et al.*, pp. 93-102, fig. 3; pl. 1, figs 1-3.

Type and type locality — In a short note, Pomel (1848) did not indicate a holotype nor paratypes for '*Sus*' *lockharti*. He gave a short description and comparison to '*Sus antediluvianus*', a species by Kaup, and indicated that his species was from the Orléannais. Contemporary literature might give a clue as to what material was studied by Pomel, when he erected the species.

Pictet (1853) included the 'choeropotame d'Avaray Lock(h)art' as well as '*Sus antediluvianus* de l'Orléanais' in this species. Gervais (1848-1852, 1859) also included 'Choeropotame d'Avaray Lockhart' in the species and cited it from Avaray and Chevilly, but named a new species for material from Montabuzard previously placed in '*Sus antediluvianus*'.

Lockhart (various papers, which are summarised by Mayet, 1908, pp. 81, 82) described fossils from Avaray as a 'choeropotame'. Lockhart was the founder of the Musée d'Histoire naturelle d'Orléans, but the fossils are not in the present MSNO, nor in the MNHN and appear to be lost. The summary of the descriptions as given by Mayet do not recall *B. lockharti*. There is a lower molar of *B. lockharti* in the MSNO (Mayet, 1908, pl. 5, fig. 25), but this was probably found at a later date.

De Blainville (1839-1864; this volume 1847?) figured a right upper third molar, a right mandible fragment with the last two molars and an upper canine as '*Choeropotamus*? de l'Orléanais'. Later, De Blainville (1850?) figured the molar and mandible again, together with a left upper M^3, but now as *Sus antediluvianus* from the Orléanais. Besides these specimens a mandible with the premolars still in the alveoles was described as *Sus antediluvianus*. These specimens were presented to him by Lokart (as he wrote the name) and Thion. Both collected in the Orléans area.

The mandible with the premolars still in the alveoles is the type of *Sus belsiacus* Gervais, 1848-52, which is from Montabuzard. Strangely enough, Pomel (1848) cited the large '*Sus*' *antiquus* from Montabuzard; as no larger suid is known from there (Mayet, 1908), Pomel seems to have meant this, not so very large, specimen. This mandible is now in the MNHN and belongs to *Bunolistriodon*, possibly to a smaller species. It is clear that both Pomel and Gervais did not consider this mandible to represent *B. lockharti*.

The canine that was figured by De Blainville is probably the same as the one figured by Mayet (1908, pl. 5, fig. 22), which might be from Beagency-Tavers and possibly belonged to a female *Hyotherium soemmeringi*.

The mandible figured by De Blainville was assumed lost (Mayet, 1908) but is actually present in the MNHN and bears the number CHE 30 (old number 434). It is a left mandible from Chevilly, which was figured by De Blainville in reverse. It is figured here (Pl. 22, Fig. 9).

The right M^3 figured by De Blainville (in reverse) is from the quarry Cassegrain at Chevilly (Mayet, 1908, p. 166, pl. 5, fig. 19). It bears number 233 in the MSNO.

The left M^3 which was figured by De Blainville (in reverse), might be the same specimen as that figured by Mayet (1908, pl. 5, fig. 17) the provenance of which is not exactly known, but of which Mayet supposed that it might be the type of the 'Chéropotame d'Avaray, de Lockhart'. However, he did not indicate this specimen as lectotype. I have not seen this specimen in the MNHN, nor in the MSNO.

Of the specimens that were probably known to Pomel (and which are thus probably syntypes), mandible CHE 30 is the best specimen and should be designated lectotype and the M^3 no. 233 paralectotype. Other possible syntypes belong or may belong, to species which are different to what is now considered as *B. lockharti* or are lost.

Type locality — Chevilly.

Age of the type locality — Early Miocene, Aragonian, MN 4.

Diagnosis — Large *Bunolistriodon* with I^1 with one or three lobes and with incisors of moderate meso-distal diameters and C^m with a relatively short radius of curvature compared to its section.

Loc.	**Coll.**	**Descr.**	**Strat.**	**Ref.**
Quinta das Pedreiras	CEPUNL	Antunes & Estravís 1986	L Va MN 4a	Antunes 1984
Quinta la Barbacena	CEPUNL	Antunes & Estravís 1986	L Va MN 4a	Antunes 1984
Quinta da Conce çao	CEPUNL	Antunes & Estravís 1986	L Va MN 4a	Antunes 1984
Pellecahus	UCBL, NMB	Roman & Viret 1934	MN 4	De Bruijn *et al.* 1992
La Romieu	UCBL, NMB	Roman & Viret 1934	MN 4a	Mein 1977
Baigneaux	NMB, MSNO, COBO		MN 4b	Mein 1977
?Mas Antolino 3	MNHN	Agustí *et al.* 1988	MN 4	Agustí *et al.* 1988
Córcoles	UCM, IPS, MNCN	Van der Made & Alférez (in prep.)	MN 4a/C	Azanza 1989
?Puente de Toledo	ITGE	Morales & Soria 1985	MN 4	Alberdi *et al.* 1985
Buñol	IVAU, IPS, MPV	Belinchón 1987	MN 4a/C	Azanza 1989
Montréal	MHNT	Crouzel *et al.* 1988	MN 4	Crouzel *et al.* 1988
Can Canals	IPS		MN 4	Agustí *et al.* 1984
Avaray	MSNO	Mayet 1908	MN 4	(Mayet 1908)
Chevilly	MSNO,, MNHN, NMB	Mayet 1908	MN 4b	Ginsburg 1992
'Graviers de l'Orléanais'	MSNO	Mayet 1908		
Grimmelfingen	SMNS	Stehlin 1899-1900	SBM	Heizmann 1992
Leibiberg		Dehm 1934		
Langenau 1	SMNS		MN 4	De Bruijn *et al.* 1992
Langenen-schlingen	NMB	Jäger 1839	SBM	Heizmann 1992
Gerlenhofen	BSPHGM	Dehm 1934	SBM	Heizmann 1992
Oberstotzingen		Dehm 1934, Paraskevaidis 1940		
Monteagudo	IPS	Astibia *et al.* 1987	MN 4/5	Astibia *et al.* 1987
Beaugency	MNHN casts	Mayet 1908	MN 5a	Ginsburg 1992
Tavers	COBO, CTMO		MN 5	
Castelnau (d'Arbieu?)	NMB		MN 5	Bulot *et al.* 1992
Ravensburg	NMB		MN 5	this paper
Pontlevoy	MNHN, NMB	Stehlin 1925	MN 5	Mein 1990
Engelswies	NMB	Stehlin 1899-1900	MN 5	Abusch Siewert 1983
?Szentendre (old coll.)	HGSB cast			

Description and comparison — *Bunolistriodon lockharti* is the first species to have been described of this genus. Thus for taxonomic reasons, no comparisons with the other species are needed here. It has been suggested that *B. lockharti* evolved into *Listriodon* (*e.g.* Leinders, 1976, 1977b). Wherever relevant, comparisons with that genus are made. Much material is assigned to *B. lockharti* and evolutionary trends can be recognised.

The $\mathbf{I_1}$ (Pl. 21, Fig. 2; Pl. 22, Fig. 2) does not have a well-developed endocristid and has a great DLL' (77 for La Romieu) and small DMD' (73 for La Romieu) and index I (ranging 98-117). The latter value ranges 107-145 for the early *L. splendens* from Paşalar and 117-139 for *L. pentapotamiae.*

The $\mathbf{I^2}$ (Pl. 21, Fig. 1; Pl. 22, Fig. 1; Pl. 23, Fig. 6) has a weakly developed endocristid. The index I ranges 94-127 and does not seem to increase with time. For *L. pentapotamiae* the lowest value is 117 and for *L. splendens* 131. The size increases from stratigraphically older to younger specimens. For La Romieu and for Baigneaux, DMD' is 94 and 89 respectively and DLL' is 82 and 89.

The $\mathbf{I_3}$ (Pl. 22, Fig. 3) is a three-lobed tooth, like the I^1. It does not have a clear endocristid. In *Listriodon* it has two lobes and an endocristid is slightly better developed. The dimensions seem to increase in the younger specimens.

The $\mathbf{DI_1}$ and $\mathbf{DI^2}$ (Pl. 21, Fig. 6) are small, have thin enamel and the lower limit of the crown is formed by very gradually thinning enamel. The index I is on average greater than in the permanent teeth (132 for a DI_1 and 118-132 for two DI_2). This would indicate that listriodont specialisation is better developed in the deciduous teeth. The DI_2 from Pellecahus is 70-80 % of the size of the I_2.

The $\mathbf{C_m}$ have a 'verrucosic section', with the posterior and labial sides about as large.

The $\mathbf{C_f}$ (Pl. 21, Fig. 4) do not have posterior enamel, which is common in Listriodontinae, but not in Hyotheriinae and Tetraconodontinae.

The $\mathbf{P_1}$ (Pl. 22, Fig. 7) is a small tooth with one thick root that is curved backwards. It is reduced in size compared to older or more primitive listriodonts.

The $\mathbf{P_2}$ (Pl. 23, Fig. 8) and $\mathbf{P_3}$ (Pl. 23, Figs 3, 5) tend to have simple protopostcristas, that are situated buccally. There may be some, but generally not much, complication of the pattern. Lingually, the talonid may be wide (Pl. 23, Fig. 5a), but this is not common.

The $\mathbf{P_4}$ (Pl. 23, Figs 4, 9) has a protoconid and a paraconid, that are well separated, but not as far apart as in *Listriodon*. The protoendocristid and paraendocristid are directed slightly posteriorly; the posterior side of this structure is not straight and smooth as in *Listriodon*. The protopostcristid is large and is directed towards the hypoconid. In the earliest *Listriodon*, there may be a protopostcristid, but it is not large. The hypoconid is placed buccally of the axis of the tooth, but does not have a long hypoendocristid as in *Listriodon*.

The D_4, M_1 and M_2 (Pl. 23, Fig. 1) are sublophodont. The endocristids in the anterior lobe of the permanent molars are directed slightly posteriorly and come close to fusing or are fused. There is a protofossid that is slightly larger and extends more posteriorly than in *Listriodon*. The hypopreconulid is still a large cusp in the middle of the transverse valley. The hypoendocristid and entoendocristid touch but do not fuse. They are still separated by a groove and they are still more forward than in *Listriodon*.

The M_3 (Pl. 23, Figs 7, 10, 11) has a large third lobe, which may have a well-developed buccal cingulum (Pl. 23, Fig. 10a) and even a low cusp behind the pentaconid (Pl. 23, Fig. 7). The third lobe is clearly larger than in *Listriodon*. Because the talon of the M^3 may be large too, there may be a posterior dipping facet on the pentaconid (Pl. 23, Fig. 10b), which is caused by the pentacone. Such a facet does not normally occur in *Listriodon*.

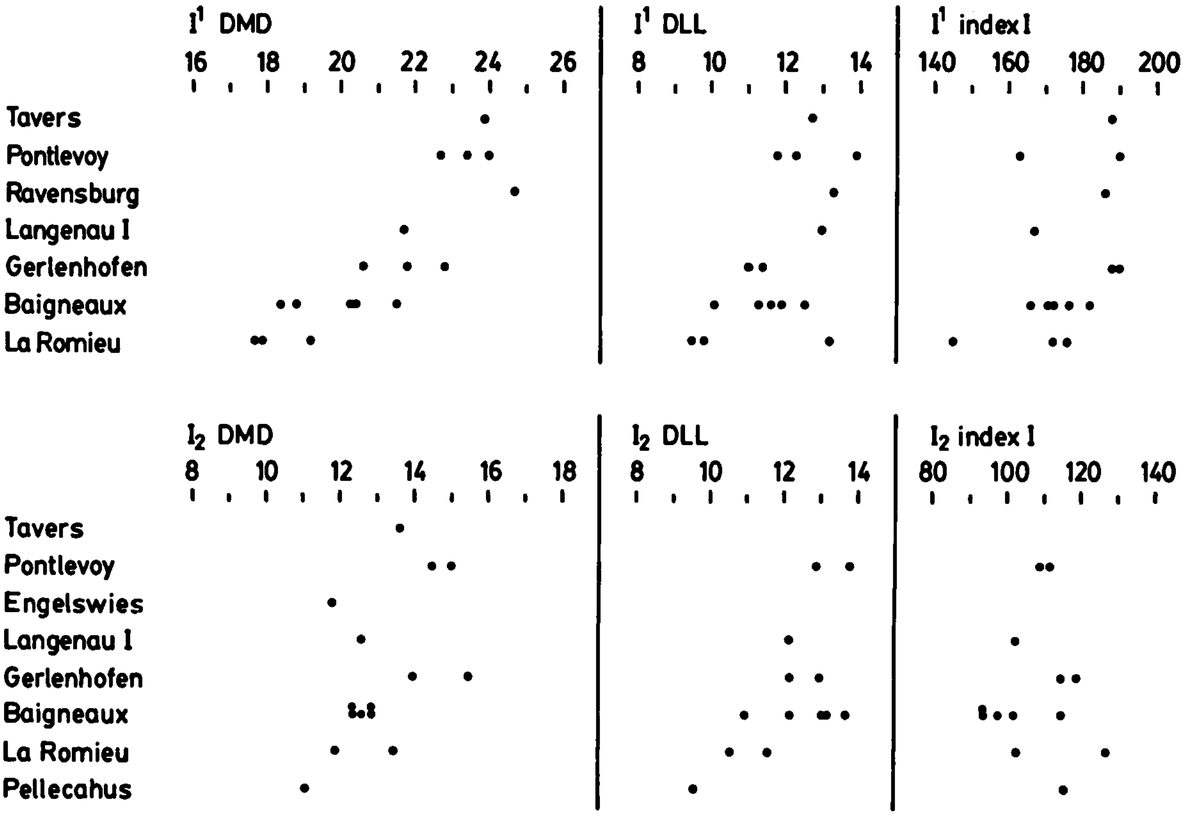


Fig. 41. Size increase in incisors of *Bunolistriodon lockharti*. The index I is also indicated. The localities are in approximate stratigraphical order. One value for Pontlevoy (I^1, 24 mm) is from Stehlin (1925).

The I^1 that can be assigned to this species with certainty have three lobes (Pl. 22, Figs 4, 5, 12; Pl. 23, Fig. 2; Pl. 24, Fig. 3). With wear, the separation into three lobes may disappear. In *Listriodon*, there are two lobes (Pl. 30, Fig. 11; Pl. 36, Fig. 2). This incisor increases its DMD from a maximum of around 19 mm in the oldest localities to nearly 25 mm in the younger localities (Fig. 41). The DLL (9.5-13.2 vs 11.8-13.9) and index I (145-176 vs 163-190) increase only slightly; the incisor becomes larger and more elongate.

Some of the I^2 (Pl. 21, Fig. 3; Pl. 22, Fig. 8) have a small postconule (Pl. 22, Fig. 8) and thus appear bilobed. The paracone is placed more mesially than in *L. splendens*. In the younger localities the tooth tends to be larger.

The I^3 might be smaller with a relatively higher crown than the I^2, though this is not certain. It is well possible that some I^3 are listed as I^2.

The **C^m** (Pl. 21, Fig. 7) has a nearly circular section; at the labial side there is a very shallow groove. The pre- and postsynclines are narrow; the endosyncline is wider and longer or 'deeper'. The radius of curvature is small, but because the DT is not much, the value for 100Ri/DT is high. Besides, the teeth are not so high or 'long' and the curvature of the canines does not cover a great section of an arc. Consequently, the teeth appear less curved than in early *Listriodon*. No tendencies are apparent.

The **C^f** has a high crown compared to *Listriodon*.

One tooth is believed to be a **DC^x** (Pl. 21, Fig. 5). Since suids change their canines early and since the deciduous canine is small, they are rare as fossils.

There is no **P^1** among the material studied, but since there is a P$_1$, it seems likely that there was also a P^1.

The **P^2** (Pl. 24, Fig. 1) and **P^3** (Pl. 22, Fig. 6; Pl. 24, Figs 2, 4) differ in the size of the protocone, which usually is separate from the cingulum (Pl. 24, Fig. 4), but not always (Pl. 22, Fig. 6).

The **P^4** (Pl. 24, Figs 5, 6) usually has a paracone and metacone close together, the separation mainly being seen lingually. In some cases there is no separation at all. Most P^4 have low and individual protopreconules, but presumably the stratigraphically younger P^4 may have a protoprecrista that is low and fused to the paracone. The protocone is usually placed slightly forward. This seems a step in the direction of lophodonty. In the truly lophodont *Listriodon*, there is a protoloph (Pl. 32, Fig. 8a; Pl.39, Fig. 2a), though it may be low near the paracone.

The **D^2** has a low crown, no protocone, but only a posterolingual cingulum and it has the roots wide apart. Besides this it looks like a small P^2.

The **D^3** resembles the one of *Listriodon*; in both, the posterior lobe does not have a loph.

The **D^4** differs from the molars in its anterior projecting anterolabial corner.

The **M^1** (Pl. 24, Fig. 7) and **M^2** (Pl. 24, Figs 7-10) are sublophodont. The morphology of the anterior lobe ranges between two extremes. There may be a protoloph. The protoprecrista meets the paracone, though it is very low at this place (Pl. 24, Figs 7a, c, 12a, e). In such a case, there may be a small swelling in the protoprecrista, the protopreconule, but it is not well individualised (Pl. 24, Fig. 10). The protopreconule is an individual cusp, which is not connected to the paracone, neither well connected to the cingulum either, or may appear like connected to both. With wear, it forms a dentine island that remains long separate from the dentine island of the protocone (Pl. 24, Fig. 8a). The protoendocrista and paraendocrista are always developed to some extent and form together with the protoloph a shallow protofossa. In *Listriodon*, these crests are reduced and an enclosed fossa is not formed. There is always a tetrapreconule that remains separate from the metacone. The tetrapostcrista forms a continuum with the posterolabial cingulum.

The **M^3** may have a talon that is a mere cingulum (Pl. 24, Fig. 13), or one with a well-developed cusp, placed lingually (Pl. 24, Fig. 11).

There are many elements of the **postcranial skeleton**. The astragalus (Pl. 25, Fig. 9) has a flat sustentacular facet, with no lateral ridge (Pl. 25, Fig. 9a, f). The navicular (Pl. 25, Fig. 10) tends to reduce the facet for the second cuneiform. It is not clear whether this bone disappeared or became fused to the third cuneiform, or whether it simply lost contact with the navicular (through another system of articulation). The MC III (Pl. 25, Fig. 2) has a facet for the trapezium. The unciform (Pl. 25, Fig. 4) has a very long posterior extension, which is not common in other Suidae. The distal articulation surface of the humerus has a concave transverse profile at the internal side (Pl. 25, Fig. 1). The MT III (Pl. 21, Fig. 9), tibia (Pl. 25, Fig. 3), first phalange (Pl. 25, Fig. 6) and most of the other bones are very much like their counterparts in *Sus*.

Discussion — The material described as *B. lockharti* seems homogeneous, except for increase in size of the incisors with time (Text-fig. 41). There are two lineages in Europe, the *B. lockharti*- and *B. latidens*-lineages. These are best recognised in the sizes of the postcranial skeleton, like the astragalus (Text-fig. 40). There is overlap in size of the dentitions (Text-fig. 38). In the descriptions, no special attention was paid to the material from Chevilly, but these teeth (C$_m$, C^m, M$_2$, M$_3$, M^2 and M^3) match the other teeth in morphology and size. They are large compared to teeth of the *B. latidens*-lineage, especially the M^3 is outside the range for that species. It seems thus justified to assign the material to *B. lockharti* as defined by the fossils from Chevilly.

Palaeochoerus giganteus Golpe-Posse, 1972 is based on a deformed molar from Can Canals (Pl. 15, Fig. 2). The molar is sublophodont and much larger and stratigraphically much younger than any *Palaeochoerus*. Possibly, Golpe-Posse separated it from *B. lockharti*, which also is found in Can Canals because of the trapezoidal shape that resulted after deformation. Because of its morphology, it is clear that the tooth belongs to *Bunolistriodon* and the postcranial skeleton from that locality indicates *B. lockharti*. Because of its size, the tooth must be an M^1, not an M^2. It was claimed that *B. lockharti* evolved into *Listriodon splendens* and therefore should be included in the genus *Listriodon* (Leinders, 1975, 1977b). This claim was cited several times in relation to the validity of the genus *Bunolistriodon* (Wilkinson, 1978; Pickford, 1986b). The three-lobed I^1 and I_3 and the tendency for the facet for the second cuneiform on the cuboid to disappear are derived characters of *B. lockharti* that do not occur in *Listriodon* at all. Besides, *L. pentapotamiae* is more primitive than *L. splendens* and therefore, a sublophodont species from which *Listriodon* evolved is expected to lack any characters that are more derived than in *L. pentapotamiae*. *B. lockharti* is too derived in the size of its incisors, which increased in size until they were larger than in *L. pentapotamiae*. It would be strange that they increased in size in *B. lockharti*, decreased when evolving into *L. pentapotamiae* and increased again in *L. splendens*. Besides, *B. lockharti* is probably contemporaneous with the earliest *L. pentapotamiae* (see section on stratigraphy).

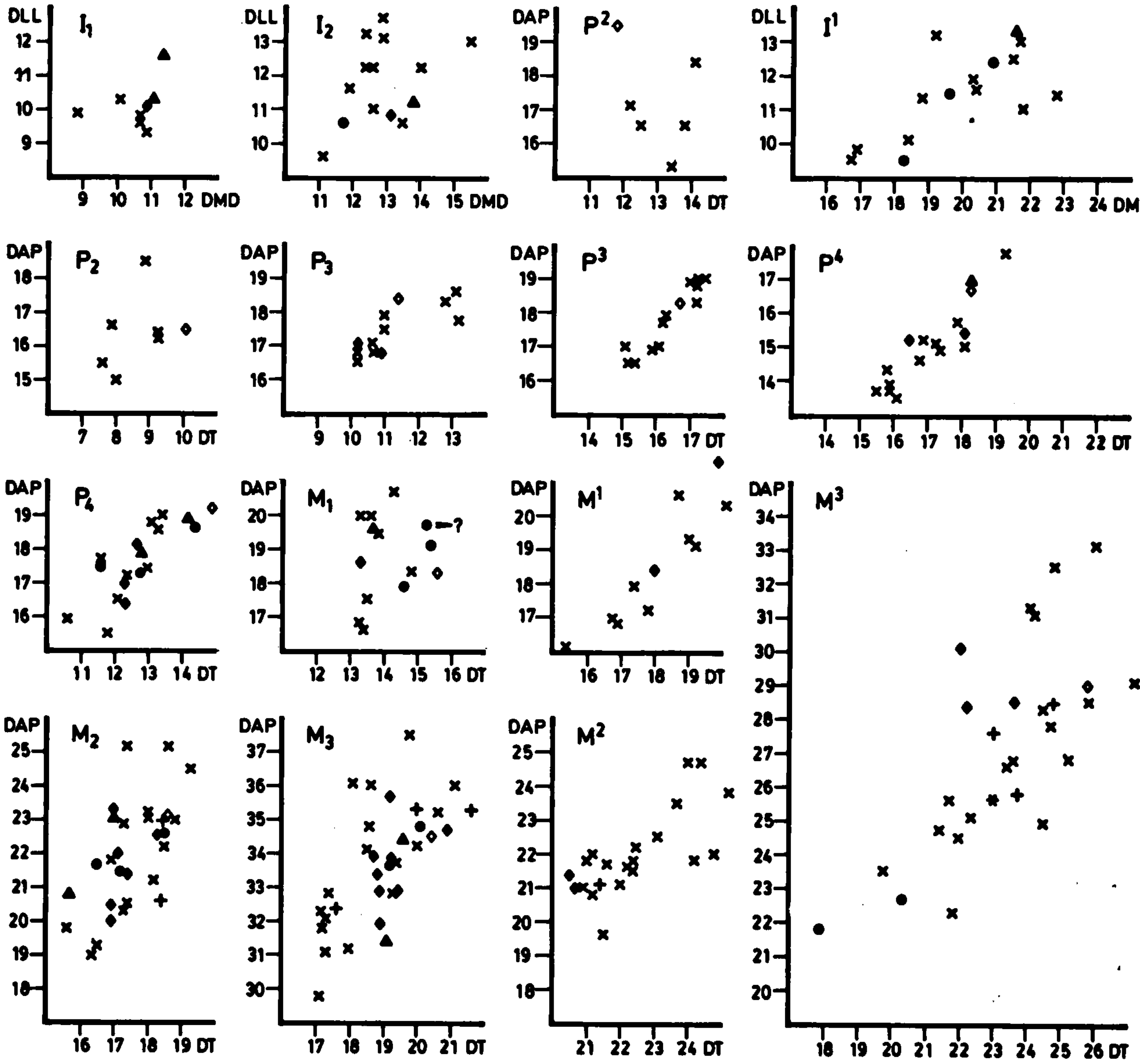


Fig. 42. Bivariate plots of large sublophodont species of *Bunolistriodon*. Legend: crosses - *B. lockharti* from type locality Chevilly; oblique crosses - *B. lockharti* from MN 4 localities (Pellecahus, Quinta la Barbacena, La Romieu, Baigneaux, 'Orléans', Buñol, Gerlenhofen, Grimmelfingen, Langenau 1 & Langenenschlingen); triangles - *B. akatikubas*; black diamonds - *B. intermedius*; open diamonds - *B. intermedius* from Erlanggang (type material of *B. robustus*; data from Yan, 1979); dots - *B. guptai*; asterisk - *Bunolistriodon* sp. from Ad Dabtiyah. An arrow and question mark indicate " ≥".

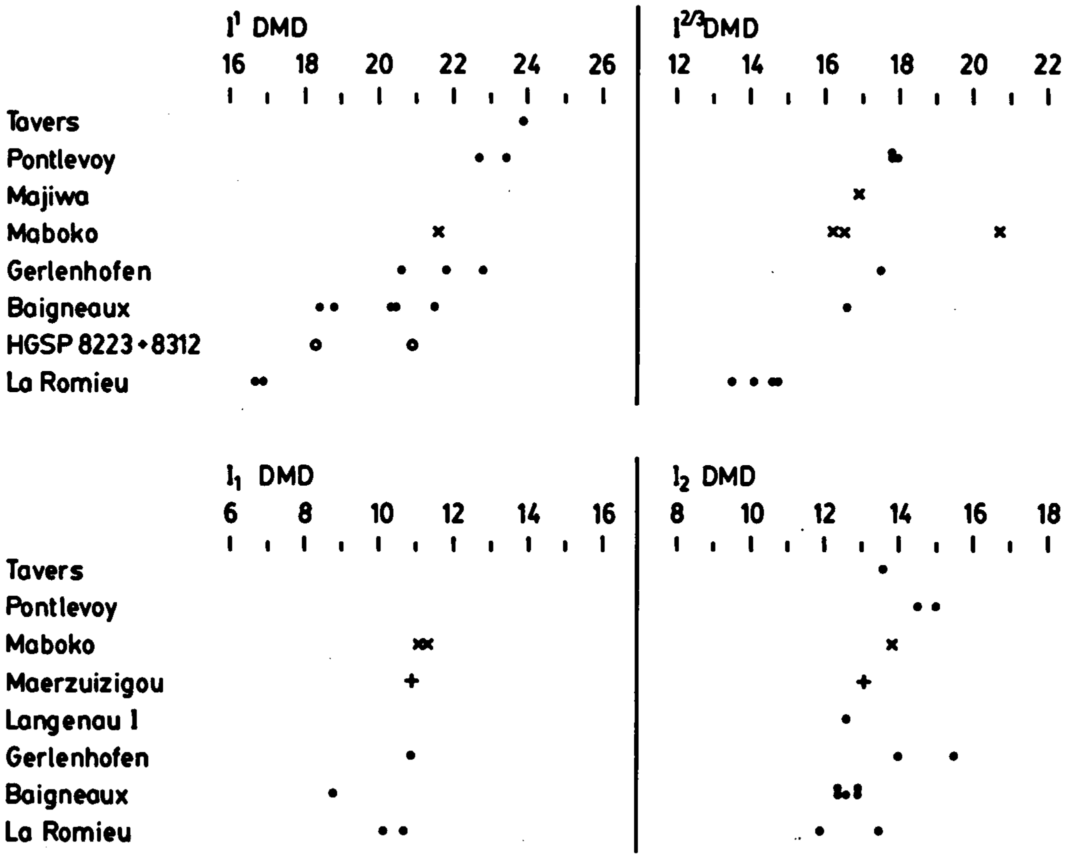


Fig. 43. Size increase in incisors of *Bunolistriodon lockharti* compared with those of *Bunolistriodon akatikubas* (Majiwa, Maboko), *Bunolistriodon intermedius* (Maerzuizigou near Tongxin) and *Bunolistriodon guptai* (HGSP 8223, HGSP 8312). This figure shows that the level of evolution of the available incisors of *B. akatikubas* and *B. intermedius* is comparable to that of *B. lockharti* of late MN 4 or MN 5, and of *B. guptai* comparable to that of *B. lockharti* of early or middle MN 4. This figure is not meant to suggest that all four species really belonged to a single lineage.

Therefore, it seems unlikely that *B. lockharti* had a direct relation with *L. splendens* and there is no reason to include it in the genus *Listriodon.*

Bunolistriodon intermedius (Liu & Lee, 1963)

Pl. 28, Fig. 12

1963a *Listriodon intermedius* sp. nov. — Liu Tung-sen & Lee Yu-ching, pp. 296-297, 302-303, pl. 5, fig. 1.
1979 *Listriodon robustus* sp. nov. — Yan De-fa, pp. 196-197, 199, pl. 1, fig. 1; pl. 3, figs 5-10.
1990 *Listriodon robustus* — Qiu, p. 543.
1992 *Bunolistriodon intermedius* Liu et Lee, 1963 — Ye *et al.*, pp. 135-145, figs 1, 2; pl. 1, figs 1-3; pl. 2, figs 1-10.
1993 *Bunolistriodon intermedius*? — Guan & Van der Made, pp. 156-158, pl. 3, figs 1, 2.

Holotype — Cat. no. 59003, the posterior half of a right M_1 or M_2, figured by Liu & Lee (1963a, pl. 5, fig. 1).
Type locality — Koujiacun (= Kou Chia Tsun), Lantien Hsien, Shensi, in the Kou Chia Tsun Formation.
Age of the type locality — Early Miocene, probably MN 5 and older than Maerzuizigou.
Diagnosis — *Bunolistriodon* equal in size to *B. lockharti* with not very large incisors. On the available evidence, it is difficult or even impossible to separate the species from *B. lockharti* or *B. guptai.*

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Koujiacun		Liu & Lee 1963	MN 5	Guan & Van der Made 1993
Maerzuizi Gou	IVPP	Ye *et al.* 1992 Guan & Van der Made 1993	MN 5	Guan & Van der Made 1993
Yehuli Juanzhi	IVPP	Ye *et al.* 1992	MN 5	Guan & Van der Made 1993
Jingzuizhi	IVPP	Ye *et al.* 1992	MN 5	Guan & Van

Gou				der Made 1993
Shatai Gou	IVPP	Ye *et al.* 1992	MN 5	Guan & Van der Made 1993
Gujia Zhuang	IVPP	Ye *et al.* 1992	MN 5	Guan & Van der Made 1993
Erlanggang		Yan 1979	MN 5	Guan & Van der Made 1993

Description and comparison — *B. intermedius* was considered to be an intermediate form between the bunodont listriodonts (or sublophodont as they are called here) and the truly lophodont ones (Liu & Lee, 1963; Ye *et al.*, 1992). The species is large with not very wide incisors. For these reasons, the comparison is mainly with *B. lockharti*, *B. guptai*, *B. akatikubas* and *L. pentapotamiae.*

The **I_1** and **I_2** have measurements like *B. lockharti* of MN 4 and are smaller than those of MN 5 and close to, but smaller than those of *B. akatikubas* (Text-fig. 43). The indices I of the I_1 of all *Bunolistriodon* are similar, but less than for *L. pentapotamiae*. For the I_2, all species are close.

The **DI_1** is larger than the sole homologue of *B. lockharti* that was measured, which is an early specimen.

The **C_m** has a verrucosic section; the labial side is wider than the posterior side.

The **P_3** is close in size to *B. lockharti* and slightly smaller than early *B. guptai* (Text-fig. 42). The protopostcristid is still of a simple, but not entirely straight type. It is not labially displaced.

The **P_4** has the protoconid and metaconid placed far apart, forming a protoloph. The protopostcristid is still a large crest touching the hypoconid. At the back of the protoloph the ends of the protoendocristid, metaendocristid and metapostcristid are still indicated, but small. In *L. pentapotamiae* the back of the protoloph tends to be smooth. The protofossid is still sharp and deep, not shallow and wide as in *L. pentapotamiae.*

The **M_1**, **M_2** (Pl. 28, Fig. 12) and **M_3** (Pl. 28, Fig. 12) are sublophodont; the hypoendocristid and entoendocristid are not fused and the hypopreconulid is still a large individual cusp. The holotype of *B. intermedius* is the posterior half of an M_1 or M_2. The hypoendocristid and metaendocristid are not fused, but touch and form a high and straight crest. The place where the cristids touch is only slightly lower than the tips of the cusps. The pentaconid or hypopostconulid is still close to the hypoconid and the hypopreconulid is still a separate cusp. This morphology is close to lophodonty, but is not yet fully lophodont. The size is close to *B. lockharti*, *B. guptai*, *B. akatikubas* (Text-fig. 42) and *L. pentapotamiae.*

The **P^4** has a large paracone; the metacone is only indicated as a swelling in the parapostcrista. This is a morphology which occurs in *B. akatikubas* and *L. pentapotamiae*. *B. lockharti* tends to have either two cusps close to each other or one cusp, but not with a long postcrista.

The **M^1**, **M^2** and **M^3** are sublophodont; there is still a tetrapreconule that is not fused to the metaprecrista. The M^3 has a large talon.

A **skull** was described by Guan & Van der Made (1993). It has a parietal crest. The frontals are flat and there is no indication of cranial appendages. The zygomatic arc is thin and not inflated.

Discussion — The material from the Tongxin area, which is studied here, resembles that which was described from Erlanggang as *Listriodon robustus* (Yan, 1979). This was noted already by Ye *et al.* (1992), who assigned both collections to *B. intermedius*. Apart from the holotype, no other material from the type locality is known to me. On the basis of the available data, both species must be considered synonymous. However, if more material becomes available, there may prove to be more species, contemporary or not.

The molars are sublophodont, the species should be placed in *Bunolistriodon* and not in *Listriodon*. There are four *Bunolistriodon* species of similar size, *B. lockharti* (Europe), *B. guptai* (Indian Subcontinent), *B. intermedius* (China) and *B. akatidogus* (Africa). Could *B. intermedius* be identical to one of the others?

B. intermedius differs from early *B. lockharti*, in its slightly 'more lophodont' P_4 and molars and in the morphology of the metacone of the P^4. However, localities with *B. intermedius* are probably MN 5 (Guan & Van der Made, 1993) and also late *B. lockharti* tends to be 'more lophodont'.

B. intermedius is close to *B. guptai* and *B. akatikubas* in all known teeth. *B. akatikubas* has large I^2, like *B. lockharti*, whereas *B. guptai* has small I^2. This tooth is not known in *B. intermedius*. *B. guptai* probably has a bilobed I^1. Again this tooth is not known in *B. intermedius*. It seems unlikely that *B. intermedius* is identical to *B. akatikubas*, since this would mean that the area of the species is disjunct with *B. guptai* and *B. lockharti* in between.

On the material available, *B. intermedius* cannot be proved to be different from late *B. lockharti* and *B. guptai* (one of which might be a senior synonym) or *B. akatikubas* (which might be a junior synonym). Important data are (still) missing.

Bunolistriodon akatikubas (Wilkinson, 1976)
Pl. 26, Figs 1-16; Pl. 28, Figs 10, 11?

1976 *Bunolistriodon jeanneli* (Arambourg) — Van Couvering & Van Couvering, p. 203 (only Maboko).
1976 *Listriodon akatikubas* sp. nov. — Wilkinson, pp. 236-240, pl. 7, figs A-C.
1978 *Listriodon akatikubas* Wilkinson 1976 — Wilkinson, p. 445.
1981 *Listriodon akatikubas* — Andrews *et al.*, p. 45 (Majiwa & Kaloma?).
1986b *Listriodon akatikubas* Wilkinson, 1976 — Pickford, pp. 49-52 but not the material from Fort Ternan, figs 55-57, 59.
1986b indeterminate suid — Pickford, fig. 74.
1987b *Listriodon* cf. *lockharti* (Pomel, 1848) — Pickford, pp. 441-443, figs 49, 50.

Holotype — KNM-MG 2, left M_3 (Pl. 26, Fig. 6) in the KNM collections, figured by Wilkinson (1976, pl. 7, fig. A).
Type locality — Mbagathi, Kenya.
Age of the type locality — late Early Miocene, faunal Set III or IV.
Diagnosis — *Bunolistriodon* of the same size as *B. lockharti*. with large incisors, particularly the I^2. On the basis of the known material. this species cannot well be separated from *B. lockharti.*

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Mbagathi	KNM	Wilkinson 1976 Pickford 1986b	Set III/IV	Pickford 1981
Majiwa	KNM	Pickford 1986b	Set IIIB	Pickford 1986c
Maboko	KNM	Wilkinson 1976 Pickford 1986b	Set IIIB	Pickford 1986c
Ad Dabtiyah	BMNH	Pickford 1987b	Set IIIB	this paper

Description and comparison — This species was placed in *Listriodon* (Wilkinson, 1976; Pickford, 1986b) and is of a size similar to that of *B. lockharti*, *B. guptai* and *B. intermedius*. This species follows in Africa *B. jeanneli* and *B. anchidens*. Therefore, comparisons with those taxa are made.

The **I_1** (Pl. 26, Fig. 15) have an index I (97-108) which is more or less like that in *B. lockharti* (88-117) and *B. intermedius* (108) and less than in *L. pentapotamiae* (117-139). The root has a much greater DLL than DMD (Pl. 26, Fig. 15), which is like in most *Bunolistriodon*, excluding *B. latidens* and *B. meidamon* (Pl. 17, Fig. 2; Pl. 21, Fig. 2; Pl. 22, Fig. 2) and unlike *Listriodon* (Pl. 30, Fig. 4; Pl. 31, Fig. 1; Pl. 35, Fig. 13; Pl. 36, Fig. 4; Pl. 41, Fig. 12). They are large, but not larger than expected for later *B. lockharti* (Text-fig. 43).

The **DI_1** (Pl. 26, Fig. 4) has a low index I and is comparable to *B. lockharti.*

The **I_2** (Pl. 26, Fig. 3) is more flattened than in most, but not all *B. lockharti* (index I 123 versus 94-127), but less flattened than in *L. pentapotamiae* (I is 129-145). The specimen has the size of late MN 4 or MN 5 *B. lockharti* I_2 (Text-fig. 43). Like in the I_1, the root has a large DLL.

The **I_3** (Pl. 26, Fig. 5) is extremely thick, thicker than in early *B. lockharti* and all *Listriodon.*

The **C_m** has a slightly scrofic section, which means that the posterior side is a little wider than the labial side. In the earliest *Bunolistriodon*, the section is clearly scrofic and in *B. lockharti* and *Listriodon* the section may be even verrucosic (with posterior side wider than the labial side). It should be borne in mind that the section may be different near the tip; one of the specimens is only preserved near the tip.

There is one fragmentary **P_2** (Pl. 26, Fig. 11). Because of its relatively small size it is assumed to be a P_2. The talonid is wider than the trigonid and the protopostcristid has small additional crests. This is a more progressive structure than found in *B. anchidens.* The posterior crests are not common in MN 4 *B. lockharti.*

The **P_3** has a number of posterior crests (Pickford, 1986b, fig. 74). This morphology is unusually complex for *Bunolistriodon.*

There are two **P_4**. One has the protoconid and metaconid placed fairly close together, with a deep sharp protofossid (Pl. 26, Fig. 13) and with a sharp furrow at the back of the 'protolophid' separating protoconid and metaconid. This is never seen in *Listriodon.* The other P_4 (Pl. 26, Fig. 10) has the cusps wider apart and the protofossid is shallower and not sharp, the back of the structure is without a furrow; this is more of a loph. It is also the former tooth that has a clear protopostcristid towards the hypoconid, whereas it is much less developed in the latter tooth. The first tooth has much in common with typical *Bunolistriodon* premolars. The second one is reminiscent of *Listriodon.* Both teeth have the protoconid and metaconid placed further apart than in *B. jeanneli* from Fategad. The hypoendocristid is better developed than in most *Bunolistriodon* and resembles the structure in *Listriodon.*

The **M_1**, **M_2** (Pl. 26, Figs 7, 8) and **M_3** (Pl. 26, Figs 6, 8, 9) are sublophodont. There is a protolophid, though it is low in the middle. There is no complete hypolophid. The hypoendocristid and entoendocristid do not fuse and when seen from behind, a sharp furrow is seen in the middle (Pl. 26, Fig. 6b), like in *B. lockharti* (Pl. 23, Fig. 11d). The formation of lophids in *Listriodon* is accompanied by the formation of dominant transverse wear facets (Hunter & Fortelius, 1994). In *Listriodon*, facets 7 and 8 (terminology of Butler, 1952) on the hypolophid fuse in a very early stage to one flat facet (Pl. 41, Fig. 9e; Pl. 28, Fig. 3b). In *B. lockharti* (Pl. 23, Fig. 10b) these facets remain separate for a long time and are not exactly parallel. In about the same stage of wear in *B. akatikubas*, the facets remain separate (Pl. 26, Fig. 6b). Much wear is needed for the dentine islands of the hypoconid and entoconid to unite (Pl. 26, Fig. 8), whereas, in a lophodont molar, a narrow dentine connection is rapidly formed (Pl. 29, Fig. 1). The hypopreconulid is a large individual cusp, which extends far lingually (Pl. 26, Figs 6a, 7b, 9a). In some molars from Majiwa (Pl. 26, Fig. 8), there is a hypoprecristid, rather than a hypopreconulid. *Listriodon* has a hypoprecristid. The holotype of *B. akatikubas* is an M_3 (Pl. 6, Fig. 6), which is clearly sublophodont and not lophodont.

The M^3 from Ad Dabtiyah (Pl. 28, Fig. 11) is a sublophodont tooth with a protolophid that is low in the middle. The hypoendocristid and entoendocristid are not fused. The pentaconid has a posteriorly dipping facet on the back.

The only I^1 (Pl. 26, Fig. 1) is worn and it cannot be judged whether the tooth had one (primitive), two (as in *Listriodon*) or three lobes (as in *B. lockharti*- and *B. latidens*-lineages). The index I is within the range for *B. lockharti*, as is the absolute size. The incisors of *B. anchidens* have one lobe, but have a much lower value for I.

The I^2 (Pl. 26, Fig. 14) are large and the largest specimen is larger than any *Listriodon* or *Bunolistriodon* specimen. However, the other specimens are slightly smaller than *B. lockharti* incisors of MN 5. They are much larger than a specimen referred to *B. guptai* and any *L. pentapotamiae*; the most primitive *Listriodon*.

One C^f is preserved (Pl. 26, Fig. 2) It is large (DAP and DT) compared to *Listriodon*. It has a very high crown, like in *Bunolistriodon* (Pl. 15, Fig. 7; Pl. 19, Fig. 17); *Listriodon* canines have lower crowns (Pl. 35, Fig. 1).

The P^2 (Pl. 26, Fig. 12) does not have a well-developed protocone yet. The protocone is smaller than in *L. pentapotamiae* (Pl. 32, Fig. 7) and many *B. lockharti* (Pl. 24, Fig. 1), but much better developed than in *B. anchidens* (Pl. 14, Fig. 4).

The P^4 (Pl. 26, Fig. 16) has only a parapostcrista and no separate metacone. This is often also the case in (later?) *L. pentapotamiae*, later *B. lockharti* tend to form a small metacone. The protoprecrista is connected to the protocone and forms a smooth loph as in *L. pentapotamiae*. In *B. lockharti*, either the protoprecrista becomes very low near the protocone or a protopreconule is formed which fills in the space.

The M^1, M^2 and M^3 are sublophodont. The protoloph is well developed. The tetraprecrista and metaprecrista are directed forward into the median valley and do not completely meet. With wear two dentine islands are formed, which remain separate until a very advanced stage of wear (KNM-MG 4). An M^3 from Maboko has the posterior cusps well separated.

The M^3 from Ad Dabtiyah (Pl. 28, Fig. 10) has the protoprecrista fused to the anterior side of the paracone. There is a large tetrapreconule, which is not fused to the metacone. The tooth is sublophodont.

Discussion — *B. akatikubas* was placed in *Listriodon* (Wilkinson, 1976, 1978; Pickford, 1986b). However, that genus is lophodont and this species is sublophodont. In addition the high crown of the C^m is like in *Bunolistriodon*. The incisors are large as in *B. lockharti*, and the most primitive true *Listriodon*, *L. pentapotamiae*, has much smaller incisors. The crowns and roots of the lower incisors in *B. akatikubas* have greater DLL relative to the DMD than in *Listriodon*. *B. akatikubas* differs from *Listriodon* and is too advanced in certain characters to be a likely ancestor for that genus and resembles *Bunolistriodon* in nearly all its known characters. Therefore, it is placed in *Bunolistriodon*. One of the P_4 has the protolophid flat at the posterior side and a wide protofossid. This is not common in *B. lockharti*. The P_3 has a wide talonid. These are the main differences with *B. lockharti*.

There are three other *Bunolistriodon* species of the size of *B. akatikubas*: *B. lockharti*, *B. guptai* and *B. intermedius*. Each of these species would have priority over *B. akatikubas*, if they were synonymous.

B. guptai probably differs from *B. akatikubas* in having much smaller I^2, though trends in any of the species are not known. *B. intermedius* resembles *B. akatikubas* in all known characters. *B. lockharti* is best known and has an increase in the size of the incisors with time. The incisors of *B. akatikubas* are as large as those of *B. lockharti* of late MN 4 or MN 5. On the whole, the development of lophodonty of the molars seems to be advanced over the early *B. lockharti*. With the present material, *B. akatikubas* cannot be differentiated from the other large sublophodont species of *Bunolistriodon* and *B. lockharti* in particular.

The two molars from Ad Dabtiyah are sublophodont and might represent *B. lockharti*, *B. akatikubas*, *B. guptai*, *B. intermedius* or *B.* aff. *latidens*. On the basis of geography it seems probable that they belonged to *B. akatikubas*, if this is accepted as a separate species, of course.

Two molar fragments from Ad Dabtiyah were assigned to ?Kubanochoerinae, genus indet. and might belong to *Kenyasus rusingensis* (Pickford, 1987b). Such an assignment would lend support to the view that the *Bunolistriodon* is *B. akatikubas*. However, the material is too fragmentary for a reliable identification.

Bunolistriodon guptai (Pilgrim, 1926)

Pl. 27, Figs 1-14; Pl. 28, Fig. 9; Pl. 29, Fig. 10

1913b *Listriodon* sp. — Pilgrim, p. 317.
1926 *Listriodon guptai* sp. nov. — Pilgrim, pp. 34-36 (excluding B 705, which is probably anthracothere), pl. 11, figs 2-4, 5? (*non* fig. 6).
1935a *Listriodon guptai* — Colbert, p. 237.
1984 *Listriodon guptai* (Pilgrim, 1926) — Raza *et al.*, p. 593.
? 1987a *Libycochoerus affinis* (Pilgrim), 1908 — Pickford (the material described by Raza & Meyer, 1984).
1988a *Listriodon pentapotamiae* Falconer 1868 — Pickford, p. 28 ('*L. guptai*').

Holotype — B 701, a right M^3 (Pl. 27, Fig. 1) in the IM collections; figured by Pilgrim (1926, pl. 11, fig. 2).
Type locality — 'The basal beds of the Lower Manchars of Sind at Bhagothoro' (Pilgrim, 1926, p. 34). There are many localities in these levels in this area and the exact locality probably can no longer be determined.
Age of the type locality — The 'basal beds of the Lower Manchars' corresponding to the 'Kamlial horizon' (Pilgrim, 1926, p. 35). Early Miocene.
Diagnosis — *Bunolistriodon* with tendency to develop lophodonty in the younger specimens, and with relatively large premolars in the older specimens, otherwise very similar to *B. lockharti*, but slightly smaller.

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Bhagothoro	IM	Pilgrim 1926	'Kamlial'	
?Shali Nala	IM	Pilgrim 1926	'Kamlial'	
?HGSP 8105	HGSP			
HGSP 8127	HGSP		Manchar ssu 1	HGSP cat.
HGSP 8222	HGSP		Manchar ssu 1	HGSP cat.
HGSP 8223	HGSP		Manchar ssu 1	HGSP cat.
?HGSP 8227	HGSP		Manchar ssu 1?	HGSP cat.
HGSP 8311	HGSP		'Kamlial'	
?HGSP 8312	HGSP		'Kamlial'	
HGSP 8320	HGSP		'Kamlial'	
HGSP 8321	HGSP		'Kamlial'	
HGSP 8412	HGSP		'Kamlial'	
HGSP 8418	HGSP		'Kamlial'	
HGSP 8420	HGSP		'Kamlial'	

Description and comparison — *B. guptai* is known from the same area where in younger deposits also the most primitive *Listriodon*, *L. pentapotamiae* is found. It is similar in size to the sublophodont *B. lockharti*, *B. akatikubas* and *B. intermedius*. Comparisons are primarily made with those taxa.

The P_2 has a talonid that is wider than the trigonid.

The P_3 (Pl. 28, Fig. 9) has a straight protopostcristid, which is a common morphology in *Bunolistriodon*. This P_3, from HGSP 8127, which is one of the oldest specimens of this species, is a huge tooth and much longer than a P_4 in the same mandible.

The P_4 (Pl. 27, Fig. 4; Pl. 28, Fig. 9; Pl. 29, Fig. 10) has the protoconid and metaconid placed far apart; in *B. jeanneli* from Fategad they are close together. The hypoconid is still connected to the protoconid by the protopostcristid and hypoprecristid. In the specimen from HGSP 8127 (Pl. 28, Fig. 9), the hypoconid is still placed in the middle, like in *B. jeanneli* from Fategad, but at the same levels (the very base of the Manchar Formation), sublophodont molars are found, so it is likely that the specimen does not present that species, but an early morph of *B. guptai*. The P_4 from HGSP 8311 (Pl. 29, Fig. 10) is more advanced in the position of the hypoconid and the beginning development of a hypoendocristid.

The M_1 (Pl. 27, Fig. 5; Pl. 29, Fig. 10), M_2 (Pl. 27, Figs 6, 10, 12, 13; Pl. 29, Fig. 10) and M_3 (Pl. 27, Figs 2, 8; Pl. 29, Fig. 10) are sublophodont. This species may well have evolved into the lophodont *Listriodon*, and detailed description of the important structures is given here. The protoendocristid and metaendocristid form a lophid that is still low where the two cristids meet, which is close to the metaconid, and develop one flat posterior dipping facet over the whole lophid. In *B. jeanneli* from Fategad the cusps remain isolate. In *B. guptai*, the endocristids of the posterior lobe do not fuse, which is seen in the maintenance of two separate dentine islands in a late stage of wear (Pl. 29, Fig. 10a) and in unworn specimens as a groove separating the two cristids (Pl. 27, Figs 5b, 6d). In *Listriodon*, the posterior cristids are fused. There may be a furrow, but this disappears with little wear. If there are separate dentine islands, they are small and placed at the tips of the cusps, with very narrow extensions over the cristids and with a little more wear, one dentine island is formed (Pl. 29, Fig. 1a).

In most suids, the transverse movement of the jaw causes occlusion of the hypopreconulid and paracone. In lophodont listriodonts, the hypopreconulid is reduced and there is no more, or at least less, occlusion between the hypopreconulid and the paraconid; consequently, the corresponding wear facets tend to disappear.

The reduction of the central cusps (incl. the hypopreconulids) and formation of lophs is functionally correlated (Hunter & Fortelius, 1994). In most specimens of *B. guptai*, the hypoprecristid ends with a swelling that extends in transverse direction; the hypopreconulid. With wear, a dentine island is formed on the hypopreconulid that is not connected to the dentine island of the hypoconid (Pl. 29, Fig. 10). In the specimens that reduced the hypopreconulid and have only a hypoprecristid, dentine is exposed as an extension of the hypoconid dentine island (Pl. 29, Fig. 1). If the hypoprecristid becomes lower, no dentine is exposed there, even in an advanced stage of wear (Pl. 35, Fig. 18). In *B. guptai*, hypopreconulids that form large dentine islands (Pl. 29, Fig. 10) and hypoprecristids/conulids that are connected to the hypoconid dentine island in an early stage of wear (Pl. 27, Fig. 13) are found.

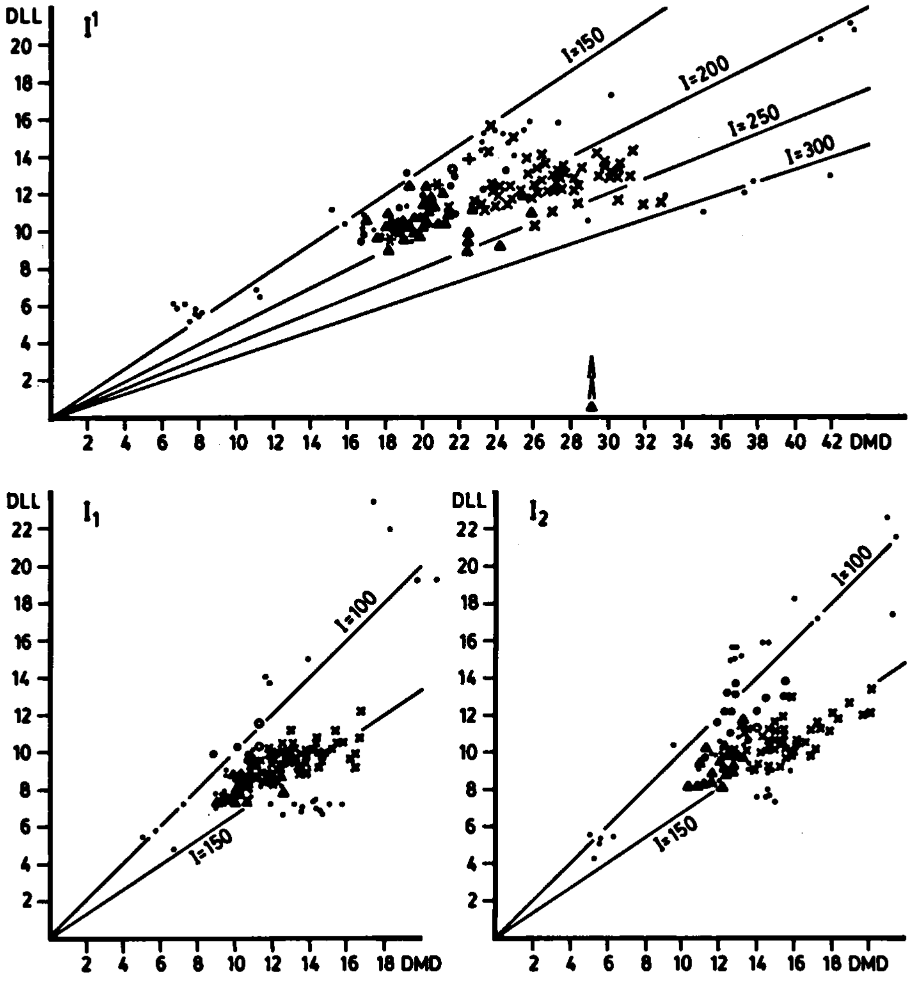


Fig. 44. Bivariate plots of central incisors of *Listriodon* and selected species of *Bunolistriodon*. Legend: crosses - Chinese *Listriodon splendens*; oblique crosses - European and Anatolian *L. splendens*; asterisks - *B. guptai*; circles - *B. akatikubas*; large dots - *B. lockharti*; small dots - remaining Listriodontinae. The lines indicate various values for the index I. The arrows indicate the position of one I^1 of which the DLL could not be measured. For *L. pentapotamiae*, specimens from the GSP and IM are plotted which are not listed in the tables, since their (stratigraphical) provenance is not known to me. The diagram illustrates the following points. 1) The wider (DMD) I^1 of *L. splendens* and *L. pentapotamiae* tend to have smaller DLL and thus higher values for I, whereas for *B. lockharti*, the wider incisors tend to have also higher values for DLL. For the lower incisors, the wider specimens (DMD) have also larger DLL, for *L. splendens*, the index increases with DMD, for *L. pentapotamiae* and *B. lockharti* it does not. 2) The I^1 of *L. pentapotamiae* are smaller than those of *L. splendens*, but may have similar indices. 3) The Chinese incisor is within the ranges for *L. splendens* and outside the ranges for *L. pentapotamiae*. For *L. splendens* it has low (= primitive) values for DMD and I. 4) The I^1 of *B. guptai* are within the ranges for *L. pentapotamiae* (The species singled out in this graph have all cheek teeth of approximately the same size).

The change from sublophodonty to lophodonty is gradual, variation in one population is to be expected, and moreover, teeth with a progressive hypopreconulid may be more conservative in hypolophid morphology and vice versa.

One **I^1** has one lobe (Pl. 27, Fig. 3) and a postcrista that becomes lower very rapidly. Its appearance is very primitive, resembling the tooth of *B. anchidens* (Pl. 4, Fig. 1), but it is a very flat tooth, the index I is 193 (136 for the latter species). This value is higher than in most of the latest (MN 5) and most elongated incisors of *B. lockharti*. Another specimen (Pl. 27, Fig. 7) is tentatively referred to this species because it has a very low index I. The separation into two lobes in this specimen, is only to be seen near the tip, and the endosyncline is very deep. For this specimen the index I is 169 although it is unworn. For *L. pentapotamiae* the index is 156-252, the lower value is from a specimen much shortened by wear. In lingual view (Pl. 27, Fig. 7), the crown looks like very high, much higher than in any *P. pentapotamiae* (Pl. 28, Fig. 2; Pl. 30, Fig. 11; Pl. 32, Figs 2-5; Pl. 33, Fig. 3). This specimen has two lobes as in *Listriodon*. Both incisors are within the range for *L. pentapotamiae* (Text-fig. 44).

Two **I^2** in the IM are referred to this species. Their exact provenance is unknown to me. They are small and have a low value for the index I even for early *B. lockharti* and *L. pentapotamiae*. They are much smaller than in *B. akatikubas* and later *B. lockharti*.

The **D^4** (Pl. 27, Fig. 9) is sublophodont, like the molars.

The **M^2** (Pl. 27, Fig. 11) and **M^3** (Pl. 27, Figs 1, 14) are sublophodont. The protoprecrista is fused to the paracone and forms a protoloph, or is just very long, but not even well fused to the paracone. There is still a tetrapreconule or a tetraprecrista that is not connected to the metaprecrista. In the most primitive lophodont molars, the precristas are directed still a little anteriorly, but have a flat facet over the tetraloph.

Seeing that this species was synonymised with *L. pentapotamiae* (Pickford, 1988a), it should be pointed out here that the holotype (Pl. 27, Fig. 1) is sublophodont. The tetraprecrista is clearly not connected to the metacone and is directed into the median valley. Clear furrows separate the tetraprecrista from the metacone.

Only a few **bones** are assigned to this species. They are slightly smaller than in *B. lockharti*, but comparable in size to the bones of *L. pentapotamiae*.

Discussion — The holotype of *B. guptai* comes from the 'the basal beds of the Lower Manchars' (Pilgrim, 1926). Most of the other fossils assigned here to that species come from the same area and same level. In the higher part of the Lower Manchar Formation, *L. pentapotamiae* is found. From the descriptions, it is clear that all the material from the basal levels is sublophodont and differs from the lophodont *Listriodon*. The holotype of the species is not a conservative morphology in an otherwise lophodont population. *B. guptai* was synonymised with *L. pentapotamiae* by Pickford (1988a, pp. 24, 87), who referred to new material from Bhagothoro as evidence that *B. guptai* is identical with *L. pentapotamiae*. This material was not described, nor mentioned in the hypodigm. The fossils described here clearly indicate that these species are different.

B. guptai differs from *B. akatikubas* in incisor size. The material known of both *B. guptai* and *B. intermedius* is not sufficient to demonstrate differences between these species. Should they turn out to be synonymous, *B. guptai* is the senior synonym.

B. guptai is fairly easily distinguished from the later *B. lockharti*; the latter has a three-lobed I^1 and the former has an incisor with one or two lobes. Moreover, *B. lockharti* tends to reduce the facet for the cuneiform II on the navicular, which is not the case in *B. guptai*, if this species evolved into *L. pentapotamiae*. Early *B. lockharti* has (relatively) smaller premolars than early *B. guptai*. All differences become less clear comparing early *B. lockharti* with later *B. guptai*, though in that case *B. guptai* tends to be 'more lophodont' and probably still has smaller incisors.

Bunolistriodon? sp.

Pl. 17, Figs 9-11; Pl. 22, Figs 10, 11

? 1976 *?Listriodon akatidogus* sp. nov. — Wilkinson, pp. 241-242 (the mandible from Gebel Zelten).

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Baragoi	KNM			
?Gebel Zelten		Wilkinson 1976	Set III	Pickford 1981

Description and comparison — The crown of the **I_2** (Pl. 17, Fig. 10) is not very low and not meso-distally widened. Its index I (117) is comparable to that of *B. lockharti*. It is as large as the smaller specimens of *B. lockharti*, though the cheek teeth are smaller than in any other *Bunolistriodon*.

The **P^4** (Pl. 17, Fig. 9) has a metacone which is not very large, but well separated from the paracone as indicated by grooves at the lingual and labial sides of this structure. There is no tendency for the formation of a protoloph and the valley between the lingual and labial cusps is wide open anteriorly and posteriorly.

A fragment of a maxilla (Pl. 17, Fig. 11) has remains of two molars probably representing M^1 and M^2. The teeth are much worn and broken. What still can be seen of the morphology indicates that the teeth may have been sublophodont or bunodont. The second tooth shows a large isolated tetrapreconule.

A mandible from Gebel Zelten was doubtfully assigned by Wilkinson (1976) to *L. akatidogus*. The sizes of the molars are similar to that species, but the premolars are rather long; the DAP' of the P$_3$ and P$_4$ are 112 and 103. Such values are far too high for *Listriodon* or *Lopholistriodon*, but may occur in *Bunolistriodon anchidens*. However, the latter species is larger. The molar lengths of the mandible from Gebel Zelten are close to those of the maxilla from Baragoi and it cannot be ruled out that both specimens belong to the same species.

Discussion — The bunodont or sublophodont condition and the incisor indicate that the species belongs to a genus similar to *Bunolistriodon*.

The incisor is relatively larger than in most *Bunolistriodon*, certainly its DLL. The large premolars of the mandible from Gebel Zelten resemble those of bunodont *Bunolistriodon* and are relatively larger than in any *Bunolistriodon*. The mandible is closest in size to *B. affinis*, but seems stratigraphically much too young. In any case, a direct study is needed to assign the specimen properly.

Whether the fossils from Gebel Zelten and Baragoi represent one species or not, the combination of characters in each locality makes the fossils difficult to relate to any known taxon.

Genus *Listriodon* Von Meyer, 1846
(= *Calydonius* Von Meyer, 1846, *Tapirotherium* De Blainville, 1847 (?), *Lophiochoerus* Bayle, 1856)

Diagnosis — lophodont Listriodontinae with high crowned C^m that curve outwards and upwards.
Type species — *Listriodon splendens* Von Meyer, 1846.

Listriodon pentapotamiae (Falconer, 1868)
Pl. 28, Figs 1-8; Pl. 29, Figs 1-9, 11; Pl. 30, Figs 1-11; Pl. 31, Figs 1-17; Pl. 32, Figs 1-18; Pl. 33, Figs 1-4; Pl. 35, Figs 1-3

1868 *Tapirus Pentapotamiae* (Falc.) — Falconer, p. 145.
1876 *Listriodon pentapotamiae* Falc. sp. — Lydekker, pp. 52-54, pl. 8, figs 8, 9.
? 1876 *Listriodon* sp. — Lydekker, pp. 90, 91, 93, 95.
? 1876 *Tapirus*, Clift — Lydekker, p. 91.
? 1876 *Listriodon pentapotamiae*, Falc. — Lydekker, pp. 92, 94.
1878 *Listriodon theobaldi* Lydekker, p. 98.
1883 *Listriodon pentapotamiae*, Falc. — Lydekker, pp. 83, 91.
1883 *Listriodon theobaldi*, Lyd. — Lydekker, pp. 83, 91.
1884 *Listriodon pentapotamiae* (Falconer) — Lydekker, pp. 101-102, pl. 8, figs 13-17.
1884 *Listriodon theobaldi*, nobis — Lydekker, p. 102, pl. 8, fig. 12.
? 1884 (?)*Hyotherium* sp. — Lydekker, p. 96, pl. 12, fig. 9.
? 1884 (?)*Hyotherium sindiense*, Lyd. — Lydekker, p. 96, pl. 12, fig. 15.
1885 *Listriodon theobaldi*, Lyd. — Lydekker, p. 53.
1885 *Listriodon pentapotamiae*, Falc. — Lydekker, p. 53.
1885 *Listriodon pentapotamiae* (Falconer) — Lydekker, pp. 276-277.
1899-1900 *Listriodon pentapotamiae* Falc. — Stehlin, pp. 14, 86, 238.
1899-1900 *Listriodon Theobaldi* Lyd. — Stehlin, pp. 13, 86.
? 1908 *Listriodon* sp. — Pilgrim, pp. 162-163.
1910 *Listriodon pentapotamiae*, Falc. — Pilgrim, pp. 189-190, 202.
1910 *Listriodon theobaldi*, Lyd. — Pilgrim, p. 202.
1913b *Listriodon pentapotamiae* — Pilgrim, pp. 285, 299?, 308, 310, 313, 317.
1926 *Listriodon pentapotamiae* (Falconer) — Pilgrim, pp. 31-34, pl. 1; pl. 11, figs 13, 14; pl. 12; pl. 20, fig. 3.
1926 *Listriodon* cf. *pentapotamiae* (Falconer) — Pilgrim, pl. 11, figs 11, 12.
1926 *Listriodont theobaldi* Lydekker — Pilgrim, p. 34, pl. 1; pl. 11, figs 7, 8.
1926 *Listriodont* cf. *theobaldi* Lydekker — Pilgrim, pl. 11, figs 9, 10.
1935a *Listriodon pentapotamiae* (Falconer) — Colbert, pp. 231-237, figs 108, 109.
1935b *Listriodon pentapotamiae* — Colbert, pp. 3-4, fig. 1.
1976 *Listriodon pentapotamiae* — Wilkinson, pp. 245-246, fig. 11.
1976 *Listriodon theobaldi* — Wilkinson, p. 246, fig. 11.
1977 *Listriodon pentapotamiae* — Hussain *et al.*, p. 15.
1978 *Listriodon pentapotamiae* Lydekker 1876 — Wilkinson, pp. 444-445.
1978 *Listriodon theobaldi* Lydekker 1878 — Wilkinson, p. 444.
1978 *Listriodon pentapotamiae* — Pickford, p. 36.
1979 *Listriodon pentapotamiae* — Hussain *et al.*, p. 9, fig. 9C.
1983 *Listriodon pentapotamiae* — Hussain *et al.*, pl. 3, figs 5, 6; pl. 7, fig. 13.

? 1983 *Listriodon* spec. — Hussain *et al.*, pl. 3, figs 7, 8; pl. 7, fig. 7.

1984 *Listriodon pentapotamiae* — Barry, pp. 11-12.

? 1984 *Listriodon* cf. *pentapotamiae* — Raza *et al.*, p. 591, 593, not S-309.

1986b *Listriodon pentapotamiae* — Pickford, figs 40-43.

1988a *Listriodon pentapotamiae* Falconer 1868 — Pickford, p. 24, but not including *B. guptai* (B 701-703) and not B 705, which is anthracothere, figs 8-63.

1990 *Listriodon pentapotamiae* — Fortelius & Bernor, tab. 1.

1996 *Listriodon pentapotamiae* — Fortelius, Van der Made & Bernor, 151-162, tab. 2.

Holotype — B 107, right M^2 and part of M^3, in the IM collections. Lydekker (1876, pl. 8, fig. 8) claimed to have figured Falconer's specimen. However, the specimen bears a different number (no. 499).
Type locality — Kushalghar, Attock.
Age of the type locality — Middle Miocene.
Diagnosis — *Listriodon* with incisors that are relatively small and P^4 with not well separated metacone.

There are two chronosubspecies which grade into each other.

Listriodon p. pentapotamiae (Falconer, 1868)

Diagnosis — Large *L. pentapotamiae* with low, not always well-developed lophs and large hypoprecristids; the P_2 and P_3 do not have well-developed metaconids.

Listriodon p. theobaldi Lydekker, 1878

Holotype — B 109, a right M^1 or M^2, in the Indian Museum collections.
Type locality — Jabi, Punjab.
Diagnosis — Small *L. pentapotamiae* with molars with high slender lophs and wide transverse valleys and with P_3 and P_2 that tend to develop metaconules.

Material of *Listriodon pentapotamiae*

Loc.	Coll.	Ref./Descr.	Strat.	Ref.
Kushalgar		Lydekker 1876		
Asnot		Lydekker 1876		
'Chinji'	IM	Pilgrim 1926		
N Maliar Dhok	IM	Pilgrim 1926		
S Bhilomar	IM	Pilgrim 1926		
Bhilomar	IM			
W-Marianwala	BSPHGM		L Chinji	Van der Made & Hussain 1994
Cheskewala	BSPHGM		L Chinji	Heissig 1972
Mochiwala	BSPHGM		L Chinji	Heissig 1972
Kanatti Chak 9	BSPHGM		L Chinji	Heissig 1972
Marianwala Kas	BSPHGM		L? Chinji	Heissig 1972
SSO Bhilomar	BSPHGM		lM Chinji	Heissig 1972
Bhurriwala	BSPHGM		lM Chinji	Heissig 1972
Kanatti Chak 5	BSPHGM		lM Chinji	Heissig 1972
Kanatti Chak 8	BSPHGM		lM Chinji	Heissig 1972
Chari Gambhir	BSPHGM		lM Chinji	Heissig 1972
Bhurriwala 2	BSPHGM		lM Chinji	Heissig 1972
Sosianwali	BSPHGM		M Chinji	Heissig 1972
Kanatti Chak 6	BSPHGM		uM Chinji	Heissig 1972
Kanatti Chak 7	BSPHGM		uM Chinji	Heissig 1972
Kagdawala	BSPHGM		uM Chinji	Heissig 1972
Chhoinjawala	BSPHGM		uM Chinji	Heissig 1972
Hessuwala	BSPHGM		uM Chinji	Heissig 1972
Jandawala	BSPHGM		uM Chinji	Heissig 1972
Kali Nal	BSPHGM		uM Chinji	Heissig 1972
Pirawalaban 1	BSPHGMU		Chinji	Heissig 1972
Kundalnala 1	BSPHGMU		Chinji	Heissig 1972
Kundalnala 2	BSPHGMU		Chinji	Heissig 1972
Kadirpur	BSPHGMU		Chinji	Heissig 1972
Kanatti Chak 3	BSPHGM		Chinji	
Kund Nala	BSPHGM		Chinji	
Dhulian	BSPHGM		Chinji	Heissig 1972
Djuguwala	BSPHGM		Chinji	
Pirawalaban 3	BSPHGM		Chinji	
Chattuwala	BSPHGM		Chinji	
Parrewali	BSPHGM		Chinji	
Kotli (=Katli?)	BSPHGM		Chinji	Heissig 1972
Mochi Wala	IVAU		L Chinji	Van der Made & Hussain 1994
Kanetti	IVAU		L Chinji	Van der Made & Hussain 1994
Tekunja	IVAU		L Chinji	cat. IVAU
Burri Wala	IVAU		M Chinji	cat. IVAU
Parriwala	FISFM		Chinji	cat. IVAU
Cheski Wala	IVAU		M Chinji	cat. IVAU
Achora	FISF,IVAU		M Chinji	cat. IVAU
Kundal Nali	FISF,IVAU		U Chinji	cat. IVAU
Bilomar	IVAU		U Chinji	cat. IVAU
Kali Nachi	IVAU		Chinji	cat. IVAU
Chinji Fm.	FISF,IVAU		Chinji	cat. IVAU
bought specimens				
HGSP 8101	HGSP		ssu 3-4	HGSP cat.
HGSP 8102	HGSP		ssu 4	HGSP cat.
HGSP 8111	HGSP		ssu 3-4	HGSP cat.
HGSP 8122	HGSP		ssu 4	HGSP cat.
HGSP 8124	HGSP		ssu 3-4	HGSP cat.
HGSP 8125	HGSP		ssu 3-4	HGSP cat.
?HGSP 8128	HGSP	Hussain *et al.* 1983.		
HGSP 8212	HGSP		ssu 3-4	HGSP cat.
HGSP 8218	HGSP		ssu 4	HGSP cat.
HGSP 8220	HGSP		ssu 3-4	HGSP cat.
HGSP 8304	HGSP			
HGSP 8415	HGSP		L Chinji	Van der Made & Hussain 1994
HGSP 8425	HGSP			
HGSP 8427	HGSP			
Daud Khel 17		Hussain *et al.* 1977	with *Hipparion*	Hussain *et al.* 1977
Dhok Talian 189	GSP	Pickford 1988a	Chinji	
Dhulian 302	GSP	Pickford 1988a	Chinji	
Dhulian 304	GSP	Pickford 1988a	Chinji	
Dhulian 305	GSP	Pickford 1988a	Chinji	
Chinji 26	GSP	Pickford 1988a	Chinji	
Chinji 38	GSP	Pickford 1988a	Chinji	
Chinji 39	GSP	Pickford 1988a	Chinji	
Chinji 40	GSP	Pickford 1988a	Chinji	
Chinji 51	GSP	Pickford 1988a	Chinji	
Chinji 53	GSP	Pickford 1988a	Chinji	
Chinji 54	GSP	Pickford 1988a	Chinji	
Chinji 56	GSP	Pickford 1988a	Chinji	
Chinji 62	GSP	Pickford 1988a	Chinji	
Chinji 64	GSP	Pickford 1988a	Chinji	

Chinji 67	GSP	Pickford 1988a	Chinji
Chinji 76	GSP	Pickford 1988a	Chinji
Chinji 83	GSP	Pickford 1988a	Chinji
locality?	IM	Pickford 1988a	Chinji
Ramnagar Fm.		Thomas *et al.* 1980	Chinji equivalent

Description and comparison — Bunolistriodon guptai is close in size and morphology to *L. pentapotamiae* and is found in older strata in the same area. *L. splendens* is the only other species of the genus *Listriodon* recognised here. Comparisons are made primarily with these species. A great deal of material, of which the provenance is not or only very imprecisely known was studied in various collections. These specimens are generally not figured and not mentioned in the tables. These specimens are used only when they provide information that is rare, but valuable, even when exact (stratigraphical) provenance is not known.

The I_1 (Pl. 30, Fig. 4; Pl. 31, Figs 1, 3) and I_2 (Pl. 31, Figs 3, 5-7) are similar in size and morphology to the incisors of early *L. splendens*, including index I (ranging 117-139 and 117-145 respectively for *L. pentapotamiae*). Later *L. splendens* incisors are larger and have much greater DMD and thus also I (up to 167 and up to 172, respectively). There are not enough specimens and not enough data on stratigraphical provenance to determine whether *L. pentapotamiae* also increased the DMD greatly. However, all incisors (irrespective of provenance data) have similar (low) index values and variation is mainly in size (Text-fig. 44). This is quite unlike *L. splendens*, where index I and DMD increase with decreasing geological age.

The I_3 (Pl. 31, Fig. 2) resembles its homologue in *L. splendens*.

There are no good C_m and few C_f with stratigraphical provenance known to me. In general they are small compared to *L. splendens*.

The P_1 (Pl. 34, Fig. 2) is a small tooth with a single root and a high crown. In the sole specimen having this tooth it is not oriented upright, but inclined. It is not known whether the younger forms of this species maintain the tooth. *L. splendens* lost the P_1.

The P_2 and P_3 (Pl. 31, Figs 9, 14; Pl. 32, Fig. 6) have a posterior-directed protoendocristid and a protopostcristid that is often bifurcated. In later forms (Pl. 32, Fig. 6) a metaconid develops and a hypoconid is separated from the protopostcrista. The first morphology tends to occur in larger specimens, which often are assigned to *L. pentapotamiae*. The premolars with metaconids and hypoconids tend to be assigned to *L. theobaldi* by authors who accept that species (Pilgrim, 1926). The morphology is similar to that in *L. splendens* and moreover must have evolved parallel, since in both species it is typical of the later forms. The talonid structure is more complex than in *B. guptai*.

The P_4 may have the protoconid and metaconid still fairly close together (Pl. 30, Fig. 9; Pl. 32, Fig. 11) or wide apart (Pl. 31, Fig. 11), may have a clear protopostcrista (Pl. 29, Fig. 6) or not (Pl. 29, Fig. 1) and the protoprecristid may be clear and the protofossid shallow (Pl. 30, Fig. 9; Pl. 32, Fig. 11) or clear and sharp and the protofossid with a sharp axis (Pl. 30, Fig. 6). In each case, the first structure is the more primitive and the more common in *B. guptai* and the second more derived and more common in *L. splendens*.

There are few specimen of D_2, D_3 and D_4. They resemble the same teeth in *L. splendens*.

The M_1 (Pl. 29, Fig. 1), M_2 (Pl. 29, Figs 1, 2) and M_3 (Pl. 28, Figs 3, 5, 6; Pl. 31, Fig. 10; Pl. 32, Fig. 18) are found in various degrees of development of lophodonty. The older specimens (Pl. 29, Figs 3, 8; Pl. 32, Fig. 18) have lophids that look low and the hypoprecristids are still bulky. These specimens tend to be large. These morphologies show a gradual transition to the, often smaller, molars with lophs which look higher and with hypoprecristids that are slender crests (Pl. 29, Fig. 1; Pl. 31, Fig. 10). There is little evidence that the crowns of the later molars are higher (relative to their width). The fact that the lophids appear higher is possibly caused by a decrease of the antero-posterior diameter at the base of the lophid, resulting in wider transverse valleys with steeper slopes and by an increase of the DT at the top of the lophid. In addition, the reduction of the hypoprecristid makes the transverse valley appear deeper and thus the lophids higher. In the former type the dentine islands that are formed by wear remain longer separate. The molars show a development from large and primitive lophodonty to, on average, smaller and with perfect lophodonty. This is found in the Manchar Formation and in the Chinji Formation. Authors who accept two species (*e.g.* Pilgrim, 1926) assign the large primitive molars to *L. pentapotamiae* and the smaller and more developed molars to *L. theobaldi*. In *L. splendens* the molars are always 'more lophodont' than in the very oldest *L. pentapotamiae*. The known specimens of *B. guptai* are always sublophodont, and present a stage of development that is more primitive than the earliest *L. pentapotamiae*.

The I^1 (Pl. 28, Fig. 2; Pl. 29, Fig. 9; Pl. 30, Fig. 11; Pl. 32, Figs 2-5; Pl. 33, Fig. 3, Text-fig. 44) have two lobes, like in *L. splendens*, but are much smaller in DLL (Text-fig. 44) and tend to have small DMD. Index I ranges 156-252. In *L. splendens* the range is 151-283 (Paşalar: 151-224) and increases with decreasing geological age of the fossils. In *L. pentapotamiae*, there is considerable variation in the DMD, as well as in I

(Text-fig. 44), and there might be an increase in these values. However, most of the larger specimens measured are of unknown stratigraphical provenance and none were measured from the upper Chinji Formation. It is strange that no increase in index I in the lower incisors was detected. Possibly, lower incisors increase in size and uppers in index and DMD, but not in DLL, so that occlusion remains complete.

The **I^2** (Pl. 32, Figs 13, 14, 16, 17) and **I^3** are difficult to separate and specimens listed as I^2 might be I^3. The teeth have high values for I as in *L. splendens* but tend to be slightly smaller. In lateral view, the precrista and postcrista are convex. In *L. splendens* they are concave.

One incisor might be a **DI^2** (Pl. 31, Fig. 4) because of its small size and the not clearly defined rim of the enamel.

The **C^m** (Pl. 32, Fig. 1) is small with a small radius of curvature. There seems to be a very moderate increase in size from the lower Middle to Upper Chinji Formation. Only the younger specimens have a size comparable to that of *L. splendens*. In *L. pentapotamiae*, the canine has a lesser radius of curvature, compared to its diameter (expressed as 100 Ri/DT), than in *L. splendens* (75 versus 93-438).

There is still a **P^1** (Pl. 31, Fig. 15). It is a small tooth, the crown is relatively lower than in the P^2 and there is no protocone, but only a cingulum at that place.

The **P^2** (Pl. 30, Fig. 10; Pl. 32, Fig. 7; Pl. 33, Figs 1, 4) and **P^3** (Pl. 32, Fig. 15; Pl. 33, Figs 1, 4) differ mainly in the size of the protocone and the height of the paracone. The geologically younger premolars tend to be wider and have larger protocones. The younger *L. splendens* occasionally has a large metacone (Pl. 42, Fig. 1), but this is not found in *L. pentapotamiae*. When the protocones are large, a transverse wear facet over the protocone and parapostcrista tends to develop which dips posteriorly (Pl. 33, Figs 1, 4). This facet results from occlusion with the protoloph of the P$_4$. In *L. splendens*, the facet on the parapostcrista tends to dip more lingually, indicating more of a 'scissor-type' of occlusion of this part of the tooth with the lower premolar.

The **P^4** has a great variety of morphologies. There are two extreme types; most of the teeth have an intermediate morphology (Pl. 30, Fig. 5; Pl. 32, Figs 9, 10; Pl. 33, Figs 1, 4). One extreme type has a small metacone, the paracone is placed anteriorly, the protocone is placed in the middle of the lingual side, there is a clear protopostcrista and the protoloph is low (Pl. 30, Fig. 1). The other type has only a parapostcrista, the paracone is shifted backwards and the protocone forwards, so that the protoloph is transverse and not oblique, the protoloph is higher or at least has a straight crest and the protopostcrista is reduced (Pl. 32, Figs 8, 12). Presumably, the latter morphology is on average the younger, though there is probably a lot of variation at any level. In *L. splendens*, the protoloph is never so dominant and the metacone and protopostcrista are better developed than in *L. pentapotamiae*.

The **D^2**, **D^3** and **D^4** resemble their homologues in *L. splendens*.

The **M^1** (Pl. 29, Fig. 5; Pl. 30, Fig. 2), **M^2** (Pl. 28, Fig. 1; Pl. 29, Fig. 11; Pl. 30, Figs 1, 2) and **M^3** (Pl. 28, Figs 4, 7; Pl. 31, Figs 12, 16, 17) are generally lophodont, though in the oldest samples still sublophodont morphologies may occur. In a heavily worn M^1 from Kanatti (Pl. 29, Fig. 5), there are still separate dentine islands at the metacone and tetracone-tetrapreconule. An unworn M^2 from Mochiwala (Pl. 31, Fig. 8) has the metaendocrista and tetraendocrista unfused, which is seen very clearly from behind (Pl. 31, Fig. 8b; see also Pl. 31, Fig. 8e). The most primitive lophodont molars, have the metaendocrista and tetraendocrista directed slightly anterior and a facet develops that has a 'V-shape', with the lower point of the 'V' nearly reaching the bottom of the transverse valleys (Pl. 29, Fig. 11), even in an early stage of wear. An M^3 (Pl. 28, Fig. 7) even has the protoloph not straight, but low near the paracone and fused to the anterior side of the paracone. The lophodont molars grade from a type with 'low' lophs to a type with 'higher' and straighter lophs, with wider and deeper transverse valleys (Pl. 30, Figs 1, 2). The specimens with most perfect lophodonty tend to be smaller and geologically younger and are placed in *L. theobaldi*, by those who accept that species. M^3 may have large talons or small talons in one locality (Pl. 31, Figs 16, 17); in the younger M^3, they reduce to a mere cingulum (Pl. 34, Fig. 1). The sublophodont molars are exactly the same as *B. guptai* molars, but are primitive morphologies in a sample, that is otherwise lophodont. The most primitive lophodont morphologies have less perfect lophodonty than in any *L. splendens*.

A well-preserved **mandible** of a female from Dhok Talian was described by Pickford (1986b, figs 40-43; 1988a, figs 50-55) and contrasted with a *Bunolistriodon* mandible from Rusinga. The incisor area is wide, but not as wide as in later *L. splendens* (Kittl, 1889, pl. 14) and comparable to the mandible of *Bunolistriodon* aff. *latidens* from Torralba 2. Apparently, the incisor area of the mandible becomes wider when the incisors become wider. As the incisors become wider, they tend to form a straight ridge and their implantation in the mandible changes from an arc into a straight line. The canines flare out much and dip less than 45°.

The symphysis and diastemata are long. However, these are extremely variable measurements, subject to sex, age and individual variation (Van der Made, 1991a). However, the increase in length of the diastema and symphysis from *Bunolistriodon* to *Listriodon* is probably real.

The **skull** (Pl. 33, Fig. 2; Pl. 33, Fig. 1) has a low occiput. The orbit is but slightly elevated above the plane of occlusion and therefore, the root of the zygomatic arc is not extensive in vertical direction. The slope of the occipital-parietal-frontal area is such that the profile of the skull must have been concave, with a less sloping nasal region. This part however, is not preserved. The European skulls of *L. splendens* that were studied are all deformed and broken. However, the wide flat area of bone below the orbit on the zygomatic arc suggests that the orbit was elevated in *L. splendens*. If this really is the case, the occiput must have been elevated too and the profile must have been more convex than in *L. pentapotamiae*, as may be seen in a Chinese specimen that is assigned here to *L. splendens* (Pl. 44, Fig. 1).

In transverse section the occipital and frontal areas are convex. There were sinuses between the brain case and the surface of the frontals, parietals and occipitals. In primitive pigs like *Hyotherium*, there are no such sinuses in the parietal area.

The zygomatic arc is not inflated and does not stand out wide. Its base is just above the molars. There is no lacrimal foramen. There is a small incisura infraorbitalis (*sensu* Thenius, 1972). There is no fossa infraorbitale. In such a fossa, the levator rostri muscle originates. This is one of the muscles that move the nasal disc. A shallow groove or no groove at all indicates that this muscle was not well developed and that the nasal disc and thus rooting was less important (Ewer, 1958).

The preserved foramen palatinum is placed next to the anterior lobe of the M^2. The tooth rows seem to converge anteriorly, but this might be an artifact of deformation and/or reconstruction.

The shape of the glenoid is convex in anteroposterior direction and its position is well elevated above the plane of occlusion and at the posterior end of the zygomatic arc as is common in Suidae. The external auditory meatus is long and oriented upwards and outwards.

There are few elements of the **postcranial skeleton** and they are difficult to assign to this species. Assignation mainly on the basis of size; larger than *Conohyus*, smaller than *Kubanochoerus*. However, there may be a size increase in *Conohyus* in the Chinji Formation and the size of *Propotamochoerus* is not quite clear. The listriodont **astragalus** has a sustentacular facet with no lateral ridge (Leinders, 1976). This ridge is well developed in Suinae, but *Conohyus* probably did not have a clear ridge either. Combining morphological and metrical data, a group of astragali may be assigned to *L. pentapotamiae* with some confidence. These astragali are smaller than those of *L. splendens*. An **unciform** has the typical long posterior process that is also found in other Listriodontinae. The **navicular** shows a clear facet for the second cuneiform, which is well separated from the facet for the third cuneiform. In *B. lockharti* and the *B. latidens* lineage, there seems to be a tendency for this facet to disappear.

Discussion — The material described here resembles *L. splendens* in having both lophodont molars and curved canines in the males. In *Lopholistriodon*, the molars may be lophodont, but the canines are short and not strongly curved (*i.e.* they do not form a long section of an arc, and the radius of curvature is long). Yet from the descriptions it is clear that there are numerous small differences with *Listriodon splendens*.

Two species were erected on the basis of material from the Indian Subcontinent, *L. pentapotamiae* (Falconer, 1868) and *L. theobaldi* Lydekker, 1878. Pilgrim (1926) still recognised the two species on the basis of size and a number of morphological differences, most of which are mentioned here in the description. He assumed the species to belong to different lineages, with *L. theobaldi* more closely related to *L. splendens* and slightly older than *L. pentapotamiae*.

Colbert (1935a) noted that there is a continuous range in size and that a large size variation exists in material from all levels of the Chinji Formation. He recognised only one species, *L. pentapotamiae*, and even stated that the main reason for separating *L. pentapotamiae* from *L. splendens* is geographical separation (Colbert, 1935a, p. 233). In view of the many differences, the latter statement is more indicative of the way of splitting according to biogeography that was common in that period.

For Pickford (1988a), *L. theobaldi* was just based on small specimens of *L. pentapotamiae*.

In the descriptive part, for most teeth two morphologies are described. In all cases, the morphology that is most conservative (resembling *Bunolistriodon*), is more frequently found in the slightly larger and usually older cheek teeth. There is much variation at any level, but this seems to be a general trend. If material of all levels is lumped, variation is higher. There are two forms. However, changes are so gradual compared to the level of variation, that it is often impossible to assign material from one locality to one of the two forms. This is even worse in view of the small sample sizes that are generally known from localities in India and Pakistan. For this reason, it is very impractical to give the two forms taxonomic status at the species level. If lineages are separated in chronospecies, it is most practical and accepted practice to take specific breaks at the gaps in the geological record. Still it is useful to give the two forms a taxonomic status, and this is done here at the subspecific level.

Listriodon splendens Von Meyer, 1846

Pl. 25, Figs 7, 8; Pl. 35, Figs 1-18; Pl. 36, Figs 1-14; Pl. 37, Figs 1-9; Pl. 38, Figs 1-15; Pl. 39, Figs 1-10; Pl. 40, Figs 1-6; Pl. 41, Figs 1-14; Pl. 43, Figs 1-5; Pl. 44, Figs 1, 2

1844a *Lophiodon* — Nicolet, p. 34.
1844b *Lophiodon* — Nicolet, pp. 124-126.
1846 *Listriodon splendens* — Von Meyer, pp. 465-466.
1846 *Calydonius trux* — Von Meyer, p. 467.
1846 *Calydonius tener* — Von Meyer, p. 467.
1847? *Lophiodon* — De Blainville, Tome Quatrième, Y Des Palaeotheriums, Lophiodons, Anthracotheriums, Choeropotames. Genre *Tapirus*, pl. 6: *Lophiodon* from Sansan. (Hünermann, 1968 cited this volume as 1847. The dates for the complete work are 1839-1864).
1847? *Tapirotherium* — De Blainville, Tome Quatrième, AA Sur les Hippopotames et les Cochons, Genre *Choeropotamus*, pl. 1.
1847? *Sus antediluvianus* — De Blainville, Tome Quatrième, AA Sur les Hippopotames et les Cochons, p. 206 (Simorre). (Hünermann, 1968 cited this volume as 1847. The dates for the complete work are 1839-1864).
1847? *Sus tapirotherium* — De Blainville, Tome Quatrième, AA Sur les Hippopotames et les Cochons, p. 217.
1847? *Sus scrofa*? — De Blainville, Tome Quatrième, AA Sur les Hippopotames et les Cochons, p. 191, Genre *Sus* , pl. 8 (Simorre).
1848 *S. tapirotherium* — Pomel, p. 157.
1848-1852 *Listriodon Lartetii* — Gervais, pp. 50-51, pl. 20, figs 2-4.
1851 *Tapirotherium Blainvilleanum* — Lartet, pp. 31-32.
1856 *Lophiochoerus Blainvillei* (Lartet) — Bayle, pp. 24-30.
1881 *Listriodon splendens* — Kittl, pp. 103-104 (probably not the material from Zsylthal).
1853 *Listriodon splendens* H. de Meyer — Pictet, p. 308, pl. 11, figs 6, 7.
1853 *Calydonius trux* H. de Meyer — Pictet, p. 327.
1853 *Calydonius tener*, H. de Meyer — Pictet, p. 327.
1857 *Calydonius trux* H. v. M. — Rütimeyer, p. 542.
1857 *Calydonius tener* H. v. M. — Rütimeyer, p. 542.
1857 *Sus Tapirotherium* Blainv. — Rütimeyer, p. 542.
1859 *Listriodon splendens* H. v. Mey. — Suess, p. 53.
1859 *Listriodon splendens* H. de Meyer — Gervais, p. 201.
1859 *Listriodon Lartetii* — Gervais, p. 201, pl. 20, figs 2-4, *non* fig. 1.
1870 *Listriodon splendens* Mey. — Suess, p. 28.
1870 *Listriodon splendens* H. v. Meyer — Fraas, pp. 24-25.
1870 *Chaeropotamus Steinheimensis* — Fraas, pl. 5, fig. 4.
1870 *Tapirus suevicus* — Fraas, p. 21, pl. 5, fig. 9.
1873 *Listriodon splendens* H. v. M. — Kowalewsky, pp. 258-261, pl. 8, figs 71, 72.
1879 *Listriodon* — Fuchs, p. 59.
1885 *Listriodon splendens*, H. v. Meyer — Lydekker, pp. 275-276.
1887 *Listriodon* — Neumayr, pp. 302-303.
1887 *Listriodon splendens*, H. v. Meyer — Depéret, pp. 230-234, figs 2-4.
1889 *Listriodon splendens* H. v. Meyer — Kittl, pp. 232-249, pl. 14, figs 1-3; pl. 15, figs 1-9.
1891 *Listriodon splendens* (H. de Mey.) — Filhol, pp. 205-219, pls 17, 18.
1891-1893 *Listriodon splendens* Meyer — von Zittel *et al.*, p. 343, fig. 281.
1892 *Listriodon splendens*, v. Meyer — Depéret, pp. 83-84.
1895 *Listriodon splendens* Meyer — von Zittel, p. 889, fig. 1979.
1897 *Listriodon splendens* H. v. M. — Roger, pp. 29-32, pl. 2, fig. 9.
1899-1900 *Listriodon splendens* H. v. Meyer — Stehlin, pp. 83-89, 171-176, 210-212, 281-286, 324-328, 423-426, 455-456, 462, 491, 496, pl. 1, fig. 14; pl. 5, figs 1, 2, 14-16, 22, 23; pl. 6, figs 18, 19, 28-31, 37.
1900 *L. latidens* Bied. — Roger, p. 59.
1900 *L. splendens* H. v. M. — Roger, p. 59.
1900 ?*Helladotherium* — Vacek, pp. 14-15, pl. 7, fig. 3.
1902 *Listriodon* cfr. *Lockharti* Pomel — Schlosser, p. 59 (material from Mösskirch and Stätzling).
1902 *Listriodon splendens* H. v. Meyer — Schlosser, pl. 3, figs 34, 41.
1907 *L. splendens* Lartet — Stehlin, p. 528.
1907 *Listriodon splendens* H. von Meyer var. *major* — Roman, pp. 57-58, pl. 3, fig. 4.
1908 *Listriodon splendens* H. v. M. — Bach, pp. 117-118.
1909 *Listriodon splendens* H. v. M. — Bach, p. 73.
1911 *Listriodon splendens* v. Meyer — von Zittel et al., p. 474, fig. 658.
1914 *Listriodon splendens* H. von Meyer, var. *major* Roman — Hernández-Pacheco, p. 459.
1914 *Listriodon splendens* Myr. — Stehlin, p. 192.
1915 *Listriodon splendens* H. von Meyer, subesp. *major* Roman — Hernández-Pacheco & Dantín Cereceda, pp. 112-135, figs 21-34; pl. 47, figs 1-3; pl.

48, figs 1-14; pls 49, 50 (not the figure of the phalange of *Dorcatherium*).

1915 Artiodactilo indeterminado (género nuevo?) — Hernández-Pacheco & Dantín, pp. 135-138, figs 35-36; pl. 51, figs 1-3.

1918 *Listriodon splendens* v. Meyer — von Zittel, pp. 535-536, fig. 684.

1921 *Listriodon splendens* Mey. sub. *major* Roman — Schlosser, pp. 443, 474, 495.

1921 *Listriodon splendens* — Schlosser, p. 479.

1922 *Listriodon splendens* H. von Meyer — Abel, pp. 195-196, fig. 161.

1923 *Listriodon splendens* v. Meyer — von Zittel, p. 562, fig. 697.

1924 *Listriodon splendens* H. v. Meyer var. nova — Bataller, p. 17, pl. 5, figs 1-7, 9, 10, 12-14.

1925 *Listriodon splendens* v. M. — Klähn, p. 202.

1925 *Listriodon splendens* Lartet — Stehlin, p. 68.

1926 *Listriodon splendens* — Pilgrim, pp. 29-37, pl. 1.

1928 *Listriodon splendens* — Pearson, p. 405.

1928 *Listriodon splendens* H. v. Meyer — Stromer, pp. 31-33, pl. 1, figs 13-16.

1929 *Listriodon splendens* H. v. Meyer — Sickenberg, p. 74.

1934 *Listriodon splendens* H. v. Meyer — Dehm, pp. 513-522, figs 1-9, 14-16a.

1934 *Listriodon mongoliensis* Colbert, pp. 1-6, figs 1, 2.

1935b *Listriodon mongoliensis* — Colbert, p. 3.

1935 *Listriodon splendens* — Boule & Piveteau, p. 678, fig. 1096.

1940 *Listriodon splendens* H. v. M. — Paraskevaidis, pp. 395-399, fig. 9/2.

1946 *Listriodon splendens* Von Meyer — Richard, pp. 274, 277, 280, 282, 284-286, 297, 305, 306, 308, 312, 317.

1946 *Listriodon* cf. *Theobaldi* Lydekker — Richard, pp. 284, 297.

1952 *Listriodon splendens* Meyer — Crusafont, p. 29.

1952 *Listriodon lockharti* (Pomel) — Thenius, pp. 73-75, figs 34-37.

1956 *Listriodon splendens* H. v. Meyer — Thenius, pp. 365-366, fig. 25.

1957 *Listriodon splendens* H. v. Meyer — Mottl, pp. 41, 72, 78-79.

1958 *Listriodon splendens* — Mottl, p. 46.

1958 *Listriodon splendens* Meyer — Bergounioux & Crouzel, p. 313.

1963 *Listriodon splendens* Meyer — Ginsburg, p. 11.

1963b *Listriodon* cf. *lockharti* (Pomel) — Liu & Lee, pp. 352-356, fig. 1.

1965 *Listriodon piveteaui* nov. sp. — Ozansoy, p. 16.

1967a *Listriodon splendens* Von Meyer — Bergounioux & Crouzel, pp. 525-526.

1967b *Listriodon splendens* Von Meyer, 1846 — Bergounioux & Crouzel, pp. 17-23, figs 12, 13.

1968 *Listriodon splendens* Meyer, 1846 — Godina *et al.*, p. 485, fig. 457.

1968 *Listriodon splendens* Meyer, 1846 — Hünermann, pp. 33-37, 60, 62, 66, figs 19-25, 37-41, 55, 63; pl. 1, figs 22, 23, 28, 29, 36, tabs, 1, 2, 9, 17.

1970 *Listriodon splendens* H. v. M. — Mottl, pp. 122-123.

1971 *Listriodon splendens* Meyer — Ginsburg, pp. 162-163.

1972 *Listriodon splendens* H. von Meyer 1846 — Engesser, pp. 318-319.

1972 Suide gen. et spec. indet. — Engesser, pp. 319-320, fig. 131.

1972 *Listriodon splendens* Mey. 1846 — Golpe-Posse, pp. 137-144 (*partim*).

1972 *Listriodon splendens* Mey. var. *aragonensis* nva. var. — Golpe-Posse, p. 145.

1972 *Listriodon splendens* — Thenius, p. 578.

1975 *Listriodon splendens* Von Meyer, 1846 — Leinders, pp. 197-203, pl. 2, figs 1, 2, 5, 6; text-fig. 1/4-6.

1975 *Listriodon splendens* Meyer — Hünermann, pp. 153-154 (not the canine described on p. 154).

1976 *Listriodon splendens* — Leinders, pp. 45-53, pl. 2, figs 5, 6.

1977 *Listriodon splendens* — Ginsburg & Tassy, p. 25.

1977a *Listriodon splendens* — Leinders, pp. 61-68, figs 1, 6a, 7a.

1977b *Listriodon splendens* — Leinders, pp. 360-366, fig. 4.

1978 *Listriodon lishanensis* sp. nov. — Lee Yu-qing & Wu Wen-yu, pp. 127-129, fig. 47; pl. 15, figs 1-7; pl. 16, fig. 1.

1978 *Listriodon* sp. — Lee Yu-qing & Wu Wen-yu, pp. 129-130, pl. 16, fig. 2.

1979 *Listriodon splendens* Meyer — Ginsburg *et al.*, pp. 224-225.

1979 *Listriodon splendens* H. von Meyer 1846 — Pickford & Ertürk, pp. 142, 144 (the 'second form with smaller canines and less elongated upper central incisors'), figs 1-3; pl. 1, figs 2-5, 8, text-figs 1, 6, 7 (*partim*).

1979 *Listriodon* cf. *lockharti* (Pomel, 1848) — Pickford & Ertürk, pp. 144-145 (the material from Sariçay).

? 1982 Suidae indet. (? *Listriodon*) — Kordos, p. 384.

1983 *Listriodon splendens* Von Meyer, 1846 — Antunes *et al.*, p. 167, pl. 1, fig. 4.

1983 *Listriodon splendens* — Hussain *et al.*, pl. 3, figs 1-4; pl. 7, fig. 8.

1983 *Listriodon splendens* (Meyer) — Cuesta *et al.*, pp. 165-166, fig. 2.

1984 *Listriodon splendens* v. Meyer 1846 — Chen, pp. 80-83, pl. 1, figs 1-9, but not the phalange.

1984 *Listriodon splendens* — Alberdi *et al.*, pp. 59-60.

1985 *Listriodon splendens* Meyer 1846 — Morales & Soria, p. 83, pl. 1, figs 5, 6.

1986 *Listriodon splendens* Von Meyer, 1846 — Azanza

Asensio, pp. 105-112, pl. 3, fig. a-c.
1986 *Listriodon xinanensis* sp. nov. — Chen Guanfang, pp. 295-307, pls 1-3.
1986 *Bunolistriodon lockharti* — Mein, p. 65.
1989 *Listriodon* sp. — Tekkaya, p. 157.
1990 *Listriodon* cf. *splendens* — Fortelius & Bernor, pp. 510-511, figs 1, 2e-h, 5c-d.
1990 *Listriodon splendens* — Fortelius & Bernor, tab. 1.
1990a *Listriodon splendens* Von Meyer, 1846 — Van der Made, p. 86, fig. 3.
1990b *Listriodon splendens* — Van der Made, pp. 100, 104.
1990 *Listriodon lishanensis* Li et Wu, 1978 — Qiu, p. 542.
1990 *Listriodon mongoliensis* Colbert, 1934 — Qiu, p. 543.
1991 *Listriodon piveteaui* n. sp. (Ozansoy, 1965; 16, *nomen nudum*) — Sen, p. 250.
1994 *Listriodon* aff. *L. splendens* — Hunter & Fortelius, pp. 105-125.
1996 *Listriodon splendens* — Fortelius, Van der Made & Bernor, 149-162, figs 1, 3, 6, tabs 1-3.

Lectotype — right I^1 (Pl. 41, Fig. 1) in the Natural History Museum of La Chaux-de-Fonds and figured by Stehlin (1899-1900, pl. 5, fig. 22).

H. von Meyer (1846) based the species on material from La Chaux-de-Fonds Place Neuve, collected by Nicolet. He did not select a holotype, nor did he indicate precisely what material he studied. He seems to have prepared drawings, some of which were copied and then reproduced by Stehlin (1899-1900). Stehlin mentioned that the drawings were in München. Manuscripts and drawings by Von Meyer seem to have been destroyed there during World War II (H. Mayr, pers. comm.). Probably all material from this locality which is now preserved at La Chaux-de-Fonds was collected by Nicolet and probably all was studied by Von Meyer, and consequently may be considered syntypes. One of the figured specimens, the I^1, is here selected **lectotype**. When I was in La Chaux-de-Fonds, not all original material was there, *e.g.* an M^3 that was figured by Stehlin. Casts, including one of the latter specimen, are kept in the NMBe.

Type locality — La Chaux-de-Fonds, Switzerland.

Age of the type locality — Middle Miocene, Late Aragonian, Astaracian, MN 7+8.

Diagnosis — *Listriodon* with large incisors and P^4 with a metacone that is well developed and well separated from the paracone.

In Europe, three stages of evolution can be recognised, which grade into each other. They might be considered as subspecies.

A - *Listriodon s. tapirotherium* (De Blainville, 1847)

Holotype — Skull Si 156 and mandible Si 155 of a female, figured by De Blainville (1847?; Vol. 4, Pl. Genre *Cheoropotamus*) and Godina *et al.* (1968, fig. 457a).

Type locality — Simorre-le Seignou.

Age of the type locality — Middle Miocene, Aragonian, Astaracian, supposedly MN 7, but probably the earlier part of MN 6.

Diagnosis — Small to normal-sized *Listriodon splendens* with incisors with very little increase in DMD and small canines in the males.

B - *Listriodon s. splendens* Von Meyer, 1846

Diagnosis — *Listriodon splendens* with incisors with a moderate increase in DMD and a tendency to increase the size of the canines in the males.

C - *Listriodon s. major* Roman, 1907

Holotype — No. 5742, a right M^3, in the MGSP collections; figured by Roman (1907, pl. 3, fig. 4).

Type locality — Aveiras de Baixo, Portugal.

Age of the type locality — Late Miocene, Vallesian, MN 9.

Diagnosis — *Listriodon splendens* with incisors with much increased DMD and P_2 and P_3 with well-developed metaconids and P^2 and P^3 with tendency to develop separate metacones and large canines in the males.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Mösskirch		Schlosser 1902	mixed/MN 6	(Klähn 1925)
Sansan	MNHN, NMB, MGL	De Blainville 1847, Filhol 1891	MN 6	Mein 1990
Gers (Simorre and/or Villefranche)	MNHN		(MN 6)	
Ornezan		Stehlin 1899-1900	MN 6	(Richard 1946)
Klein Hadersdorf (Mattner)	IPUW		MN 6/7	(Thenius 1960)
Klein Hadersdorf (Frank)	IPUW			
St. Margarethen	NMW	Kittl 1889	MN 6	(Thenius 1960)
Stätzling	BSPHGM cast	Roger 1897	MN 6	Abusch Siewert 1983
Inönü 1	MTA		MN 6	Van der Made 1993
Eichkogel	NMW	Vacek 1900	MN 6	(Thenius 1960)
Paşalar	MTA, PIMUZ	Fortelius & Bernor 1990	MN 6	Mein 1990
Çandir	MTA	Pickford & Ertürk 1979	MN 6	Mein 1990
Paracuellos V	MNCN	Morales & Soria 1985	MN 6/F	Azanza 1989
Neudorf Sandberg	NMW	Thenius 1952	MN 6	Mein 1990
Paracuellos 3	MNCN	Morales & Soria 1985	MN 6/G	Azanza 1989

Manchones I	IVAU, IPS		MN 6	Mein 1990
Arroyo del Val IV	IVAU, RGM, MPUZ, MNCN, IPS	Leinders 1975, 1976, 1977	MN 6	Mein 1975
Arroyo del Val I	IVAU	Leinders 1975	MN 6	(Freudenthal *et al.* 1977)
Arroyo del	IVAU		MN 6	(Freudenthal *et al.* 1977)
Manchones II	IVAU			
Murrero	IVAU			
Lombez		Stehlin 1899-1900	MN 6	(Richard 1946)
Péjouan		Ginsburg& Tassy 1977	MN 6?	(Ginsburg & Tassy 1977)
Mannersdorf	NMW	Kittl 1889	MN 6/7	(Thenius, 1960)
?Szentendre (Cseresznyésárok)	HGSB	Kordos 1982	MN 6/7	Kordos 1982
Castelnau de Barbarens	CFE (cast)		MN 6/7	(Richard 1946)
Castelnau-Magnoac	MSNO		MN 6/7	(Richard 1946)
Laroque de Magnoac	MNHN		MN 6/7	(Richard 1946)
Mongausy		Stehlin 1899-1900	MN 6/7	(Richard 1946)
Villefranche	MNHN, NMB	Stehlin 1899-1900	MN 6/7	(Richard 1946)
Simorre	MNHN, UPM, CFE cast	De Blainville 1847, Pictet 1853	MN 7	Mein 1990
Locle	UN	Stehlin 1899-1900, 1914	MN 7	Mein 1990 1914
Yaylacilar	PIMUZ		MN 7	Steininger *et al.* 1989
			11.6 Ma	Sen 1989
Sari Çay	MTA		MN 7	Mein 1990
Korethi		Gabunia 1981	MN 7	Mein 1990
Steinheim	SMNS, NMB	Fraas 1870, Stehlin 1899-1900, Chen 1984	MN 7	Mein 1990
Laichingen		Hünermann 1968	MN 7	Abusch-Siewert 1983
Toril III	CCL		MN 7	Mein 1990
La Grive M	CFE		MN 7	Mein 1990
Cerro del Otero (= Palencia)	MNCN	Hernandez Pacheco 1914	MN 7	Mein 1990
Boulogne	NMB (cast)	Stehlin 1899-1900	MN 7+8	(Richard 1946)
Coca		Cuesta *et al.* 1983	MN 7+8	Cuesta *et al.* 1983
L'Ile en Dodon	FMNH (cast)		MN 7+8	(Richard 1946)
Solera	IVAU		MN 7+8, G	Daams & Freudenthal 1988
Le Fousseret		Richard 1946	MN 7+8	(Richard 1946)
La Chaux-de-Fonds	MHN-CHF	Stehlin 1899-1900	MN 7+8	(De Bruijn *et al.* 1992)
La Grive	MGL, UCBL, IGF, NMB		MN 7+8	
Escanecrabe	MNHN		MN 7+8	(Richard 1946)
Bonnefont	MNHN		MN 7+8	(Richard 1946)
La Grive L7	UCBL		MN 8	Mein 1990
La Ciesma	MPUZ	Azanza 1986	MN 8	Van der Made 1990
Mas del Olmo	ITGE		MN 8	(Golpe-Posse 1972)
La Cisterniga	MNCN, IPS		MN 8	Mein 1990
St. Gaudens?	MNHN	Stehlin 1899-1900	MN 8	Mein 1990
Kleineisenbach	BSPHGM		MN 8	Mein 1990
Friedberg	BSPHGM		MN 8?	Abusch-Siewert 1983
Lower Sinap	MNHN, MTA		MN 8	Sen 1990
St. Stephan		Mottl 1957	MN 8	Mein 1990
Anwill		Engesser 1972	MN 8	Mein 1990
Massenhausen	BSPHGM		MN 8	Heissig 1989
Nombrevilla II	MNCN		MN 8	Van der Made 1990
Can Feliu	IPS		MN 8	Agustí *et al.* 1984
Castell de Barberá	IPS		MN 8	Mein 1975
S. Quirze (= Trinchera de Ferrocaril)	IPS, MLGSB CJFV	Bataller 1924	MN 8	Mein 1975
Can Mata	MLGSB		MN 8	Agustí *et al.* 1984
Atzgersdorf		Kittl 1889	MN 8	(Thenius, 1960)
Loretto	NMW	Kittl 1889	MN 8	(Thenius, 1960)
Nussdorf = Wien-Heiligenstadt	NMW	Kittl 1881, 1889, von Zittel 1891-1893	MN 8	(Thenius 1960)
Oberhollabrunn		Sickenberg 1929	MN 8	(Sickenberg 1929)
Wartenberg	IVAU, BSPHGM		MN 8/9	Abusch-Siewert 1983
Löffelbach		Bach 1908	MN 8/9	this paper
Hostalets	IPS, MLGSB, CJFV, NMB		MN 8 + 9	Agustí *et al.* 1984
Markt Rettenbach	BSPHGM	Dehm 1934	MN 9?	
Aveiras de Baixo	LM	Roman 1907	MN 9a	Antunes *et al.* 1983
Doué-la- Fontaine	MNHN	Ginsburg *et al.* 1979	MN 9	Ginsburg *et al.* 1979
Aumeister		Stromer 1928	MN 9	Mein 1990
Grosslappen		Stromer 1928	MN 9	Mein 1990
Hammerschmiede	BSPHGM		MN 9	Mayr 1979
Wissberg	NMM	Hünermann 1968	MN 9	Abusch-Siewert 1983
Esselborn	HLD	Hünermann 1968	MN 9	Abusch-Siewert 1983
Azambujeira inf.		Antunes *et al.* 1983	MN 9a	Antunes *et al.* 1983
Santiga	IPS		MN 9/H	Azanza 1989
Can Ponsic I	IPS		MN 9/H	Azanza 1989
Can Llobateres	IPS		MN 9/I	Azanza 1989
Haselbach		Thenius 1956		
Stützenhofen (Schodel Sandgrube)	IPUW			
Mering	NMB, BSPHGM casts	Roger 1900 Dehm 1934		
Morsingen	NMB			
Lac Morat	MHNCHF			
St. Georgen	BSPHGM	Dehm 1934		
Prittlbach	BSPHGM			
Fünfkirchen		Suess 1859		
Soóskut	NMW	Kittl 1889		
Kaiserstein-bruch	NMW	Kittl 1889		
Mauer	NMW	Kittl 1889		
'Leithagebirge'	NMW			
Can Cunilé	IPS			
Gyala Mendru		Suess 1870		
Krivádia railway station (Merisor)	HGSB	Suess 1870		
Merisor west slope Mendru	HGSB			
Jablonica	HGSB			
Guanghe	BNHM			
Tri-sur-Brise	MNHN cast			
Espinau		Stehlin 1899-1900		

Saverdun		Stehlin 1899-1900		
Mantelan		Stehlin 1899-1900		
Las Gruas	NMB		MN 6	this paper
Wolf Camp		Colbert 1934	MN 6/7	this paper
Quarry (Tung Gur)				
Lengshuigou		Lee & Wu 1978	MN 6	this paper
Xinan	IVPP	Chen 1986	MN 6	this paper
Tung-Sha-Po		Liu & Lee 1963	MN 6	this paper

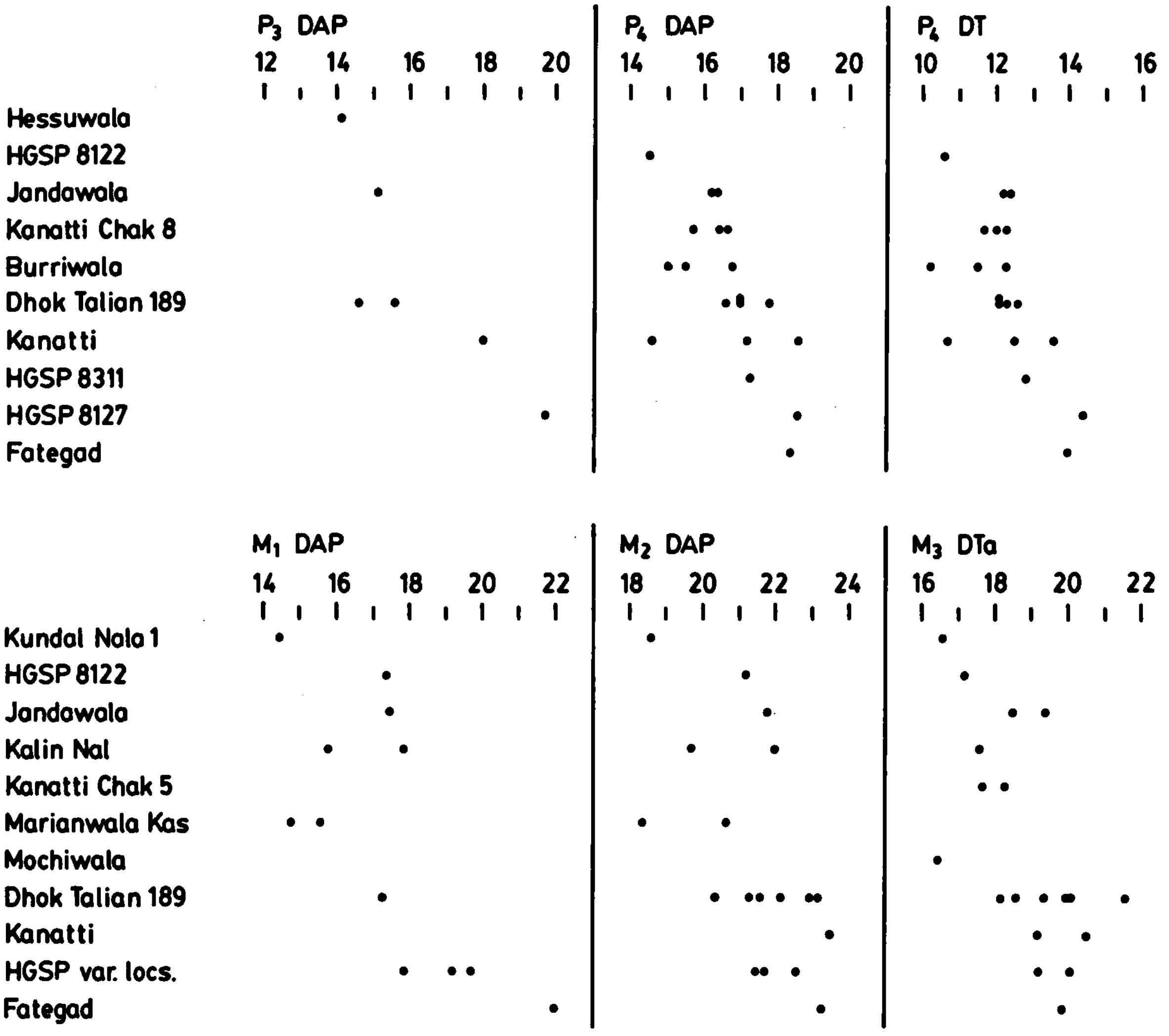


Fig. 45. Size changes in listriodonts from Pakistan and India: *Bunolistriodon jeanneli* (Fategad), *B. guptai* (HGSP localities, except HGSP 8122) and *Listriodon pentapotamiae* (Kanatti to Hessuwala/Kundal Nala 1, including HGSP 8122). The localities are in approximate stratigraphical order. 'Kanatti' represents material from the IVAU collection and is placed low, according to the IVAU catalogue. The position of Dhok Talian is not known to me, but the characters of the fossils suggest it is low in the Chinji Formation. The figure suggests a slight size decrease in *L. pentapotamiae*. Most of the localities with this species are from the Lower and lower Middle Chinji Formation. Very small material in the IM and GSP might be from the upper Chinji Formation.

Description and comparison — *Listriodon splendens* is the first validly named listriodont and thus no comparisons with other taxa are necessary for taxonomic reasons. However, several species are synonymised here with *L. splendens* and comparisons will be made with material assigned to those species. In addition, attention will be paid to the evolutionary changes affecting many of the teeth.

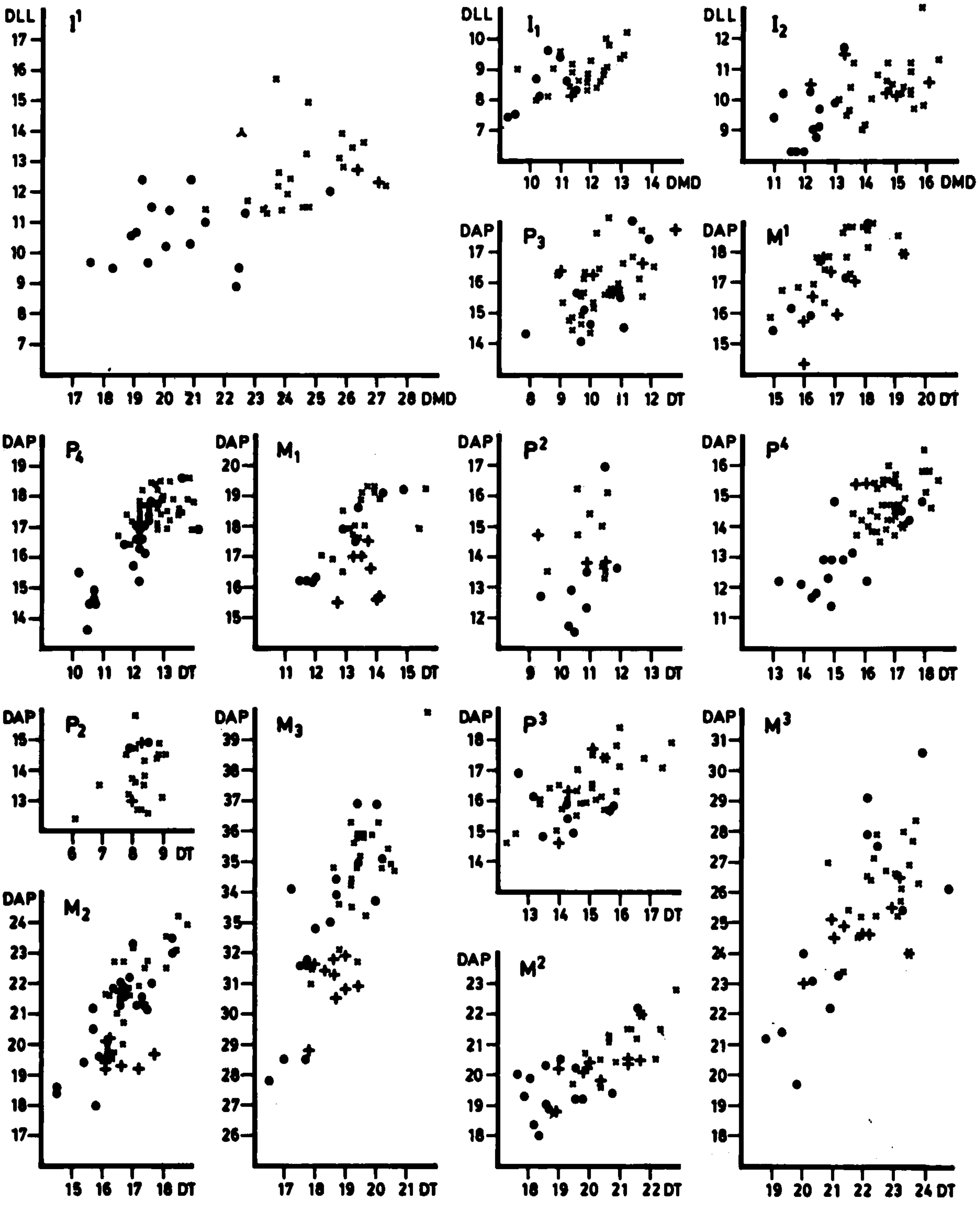


Fig. 46. Bivariate plots of incisors and cheek teeth of *Listriodon*. Legend: crosses - early European *L. splendens* (Sansan, Simorre, Castelnau-Barbarens, Isle-en-Dodon & Villefranche); oblique crosses - *Listriodon splendens* from Paşalar; asterisks - *Listriodon splendens* from Lishan (type of *Listriodon lishanensis*; data from Lee & Wu, 1978); three pointed star - *Listriodon splendens* from Xinan (type material of *L. xinanensis*; I^1 only); dots - *L. pentapotamiae*; circles - *Bunolistriodon guptai* (I^1 only).

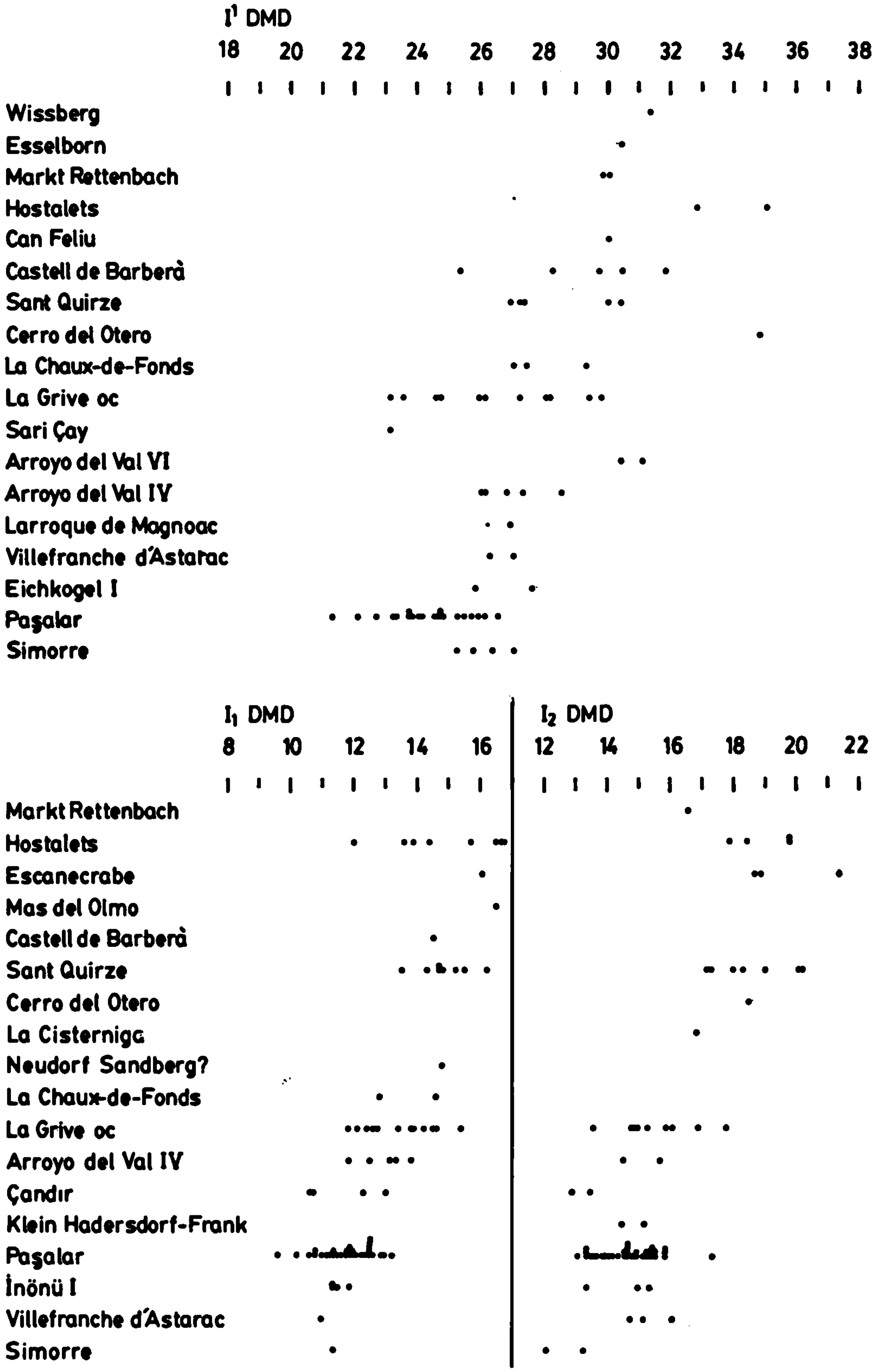


Fig. 47. Increase of 'width' (DMD) of I^1, I$_1$ and I$_2$ in European *Listriodon splendens*. The localities are in approximate order.

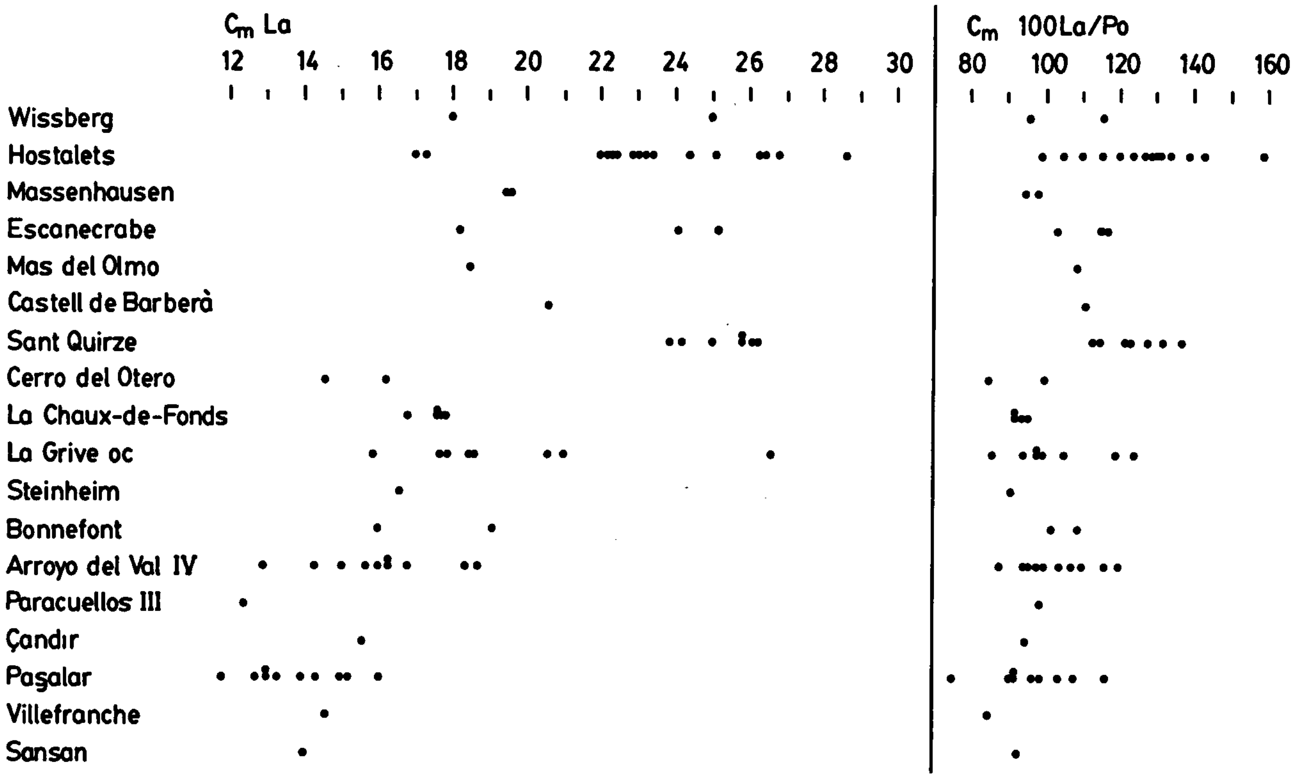


Fig. 48. Increase in width of labial side of C_m in *Listriodon splendens*: as an absolute value (La) and as a relative value (100 La/Po). The localities are in approximate stratigraphical order. Hostalets and La Grive oc (old collections) are mixed faunas and show greater variability. All three sides of the canine of *L. splendens* increase in width with decreasing geological age and the labial side increases most rapidly. This changes the shape of the section, as can be seen, from 'scrofic' (100 La/Po < 100) to 'verrucosic'.

Description and comparison of European and Turkish material — Most of the I_1 (Pl. 35, Figs 4, 8; Pl. 36, Fig. 4; Text-fig. 44) except for some of the very earliest (Pl. 35, Figs 13,14) and all I_2 (Pl. 35, Figs 4, 8; Pl. 42, Figs 5, 7, 8; Text-fig. 44) have clear endocristids. The DMD, DLL, DMD', DLL' and I (extremes 107-179) increase with decreasing geological age (Text-fig. 47). The available data suggest that there is a slight decrease in height of the crown, both absolutely and relative to DMD and DLL.

The DI_1 and DI_2 (Pl. 35, Fig. 15) are much like the permanent incisors, though they are smaller, flatter (higher I) and have slightly higher crowns, relative to DMD and DLL.

The I_3 is a bilobed tooth with either no (Pl. 35, Fig. 17; Pl. 40, Fig. 3; Pl. 41, Fig. 8) or a clear endocristid (Pl. 36, Figs 7, 11; Pl. 41, Figs 4, 11). The size increases with time.

The C_m has a verrucosic section (Text-fig. 49). From Arroyo del Val IV there are tips, with very little wear. These are 'pyramidal' in that the diameters (Li, La, Po) increase (Pl. 37, Fig. 4). The tooth is slightly curved and does not show a strong increase in the Ro and Ri giving the tooth a spiral shape, as in *Sus scrofa* and *Babyrousa*. In nearly all preserved canines, there is a big wear facet and the original tip is not preserved (Pl. 37, Figs 1-3). This suggests that wear of this tooth is very strong. The younger the localities, the larger the teeth. This size increase is seen most clearly in an increase in the width of the labial side, which increases also with respect to the width of the other sides (Text-fig. 48); the canine passes from scrofic to verrucosic.

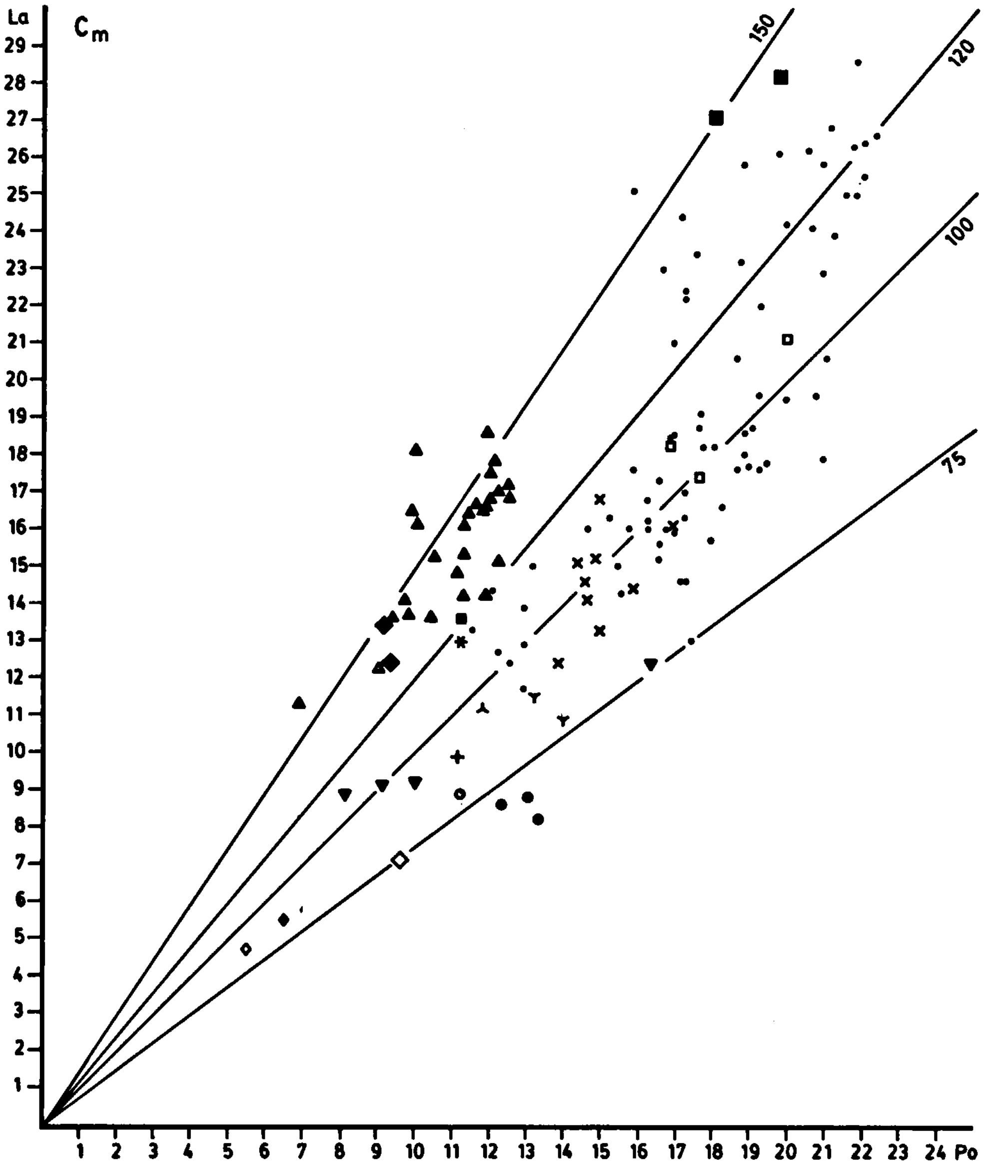


Fig. 49. Bivariate plot of C_m. Legend: small black diamond - *Nguruwe kijivium*; small open diamond - *Lopholistriodon moruoroti*; large black diamonds - *Lopholistriodon akatidogus*; large open diamond - *Lopholistriodon kidogosana*; small black square - *Kubanochoerus minheensis*; small open squares - *Kubanochoerus massai*; large black squares - *Kubanochoerus gigas*; circle - *Bunolistriodon affinis*; large dots - *Bunolistriodon anchidens*; black triangles points downward - *Bunolistriodon* aff. *latidens*; open triangle point upward - *Bunolistriodon latidens*; black triangles points upward - *Bunolistriodon meidamon*; oblique crosses - *Bunolistriodon lockharti*; crosses - *Bunolistriodon akatikubas*; asterisk - *Bunolistriodon intermedius*; three pointed star point up - *Bunolistriodon guptai*; three pointed stars points down - *Listriodon pentapotamiae* (IM); small dots - *Listriodon splendens*. The lines indicate values for the index 100 La/Po. There is a general tendency for the larger canines to have relatively wider labial sides. Since the smaller canines of *B. meidamon* have indices as high as or higher than those of the large *L. splendens* and *K. gigas*, this tendency does not seem to be caused by allometric scaling.

Radius of curvature increases also in the geologically younger specimens, even in comparison to the size of the canines (Text-fig. 50); the canines become 'straighter'. There are specimens (Pl. 37, Fig. 1) with alternating bands with and without enamel. Possibly, these are canines of senile individuals; in old age the whole lingual and labial sides of the canine have such bands. If this is the case, the length of the bands without enamel indicates that huge amounts of canine are worn away.

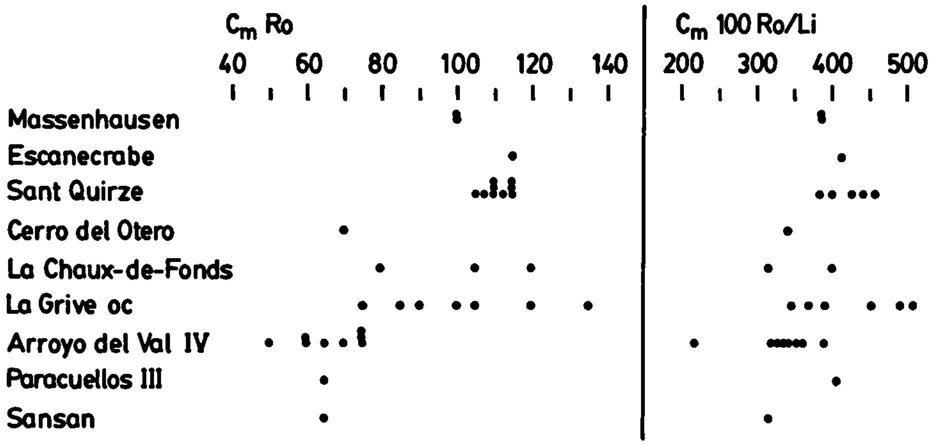


Fig. 50. Increase in radius of curvature (Ro) of C_m in *Listriodon splendens* and increase in radius of curvature relative to width of lingual side (100 Ro/Li). The localities are in approximate stratigraphical order. This figure shows that the radius of curvature is longer in the geologically younger specimens. The size of the canines as a whole increases also, but less than the radius of curvature (100 Ro/Li graph). The effect is that a given length of canine appears 'less curved' or that canines can be longer, before they curve back to the skull. The latter effect may give rise to larger and more impressive canines.

The C_f (Pl. 38, Figs 6, 12) are large but not hypsodont. They lack enamel at the posterior side. Worn specimens have round facets at the labial side. This kind of wear is not caused by occlusion between upper and lower canines and indicates that the canines are intensively used as some kind of 'tool'. Male canines probably wear off too rapidly for such facets to be preserved.

The P_2 (Pl. 38, Figs 5, 15; Pl. 42, Fig. 2) and P_3 (Pl. 38, Figs 4, 10, 11; Pl. 42, Fig. 2) are similar, but the P_3 is always more progressive in the development of additional cusps or crests. In the more primitive and stratigraphically older premolars, there is a protoconid, protopostcristid, a posteriorly directed protoendocristid and usually an additional crest (Pl. 38, Figs 4, 10, 11). If the hypoconid is interpreted as being at the verge of separating from the protoconid, this ridge should be named hypoendocristid. In the more progressive premolars (Pl. 42, Fig. 2), the protoendocristid forms a cusp at its end; the metaconid, which eventually may become as large as the protoconid and form a protoloph. The hypoconid becomes an individual cusp and the hypoendocristid becomes oriented transversely. One tooth from Manchones I (Pl. 38, Fig. 7) has a simple morphology, like a P_2, but a gigantic size and is larger than any P_3 (Text-fig. 51).

The D_2 and D_3 (Pl. 38, Fig. 14; Pl. 35, Fig. 12) are small teeth with low crowns. The D_3 can be separated from the P_2 and P_3 because of the long protoendocristid that reaches very far posteriorly.

The earlier P_4 tend to have some connection of the hypoconid with the protolophid. The connection is very low. In the geologically older specimens, a very small protopostcristid can be seen at the back of the protolophid (Pl. 38, Fig. 2). With much wear a connection of the dentine may develop (Pl. 38, Fig. 8). Most of this connection, however is made up of the hypoprecristid. As with any character, there tends to be some variation in this morphology in any population (Pl. 38, Figs 3, 8). In all P_4, the upper part of the protolophid has a flat back (Pl. 42, Fig. 2) and there is no posterior groove in the protolophid between the protoconid and metacristid. There is a very sharp protoprecristid (Pl. 38, Fig. 3), which tends to be worn away completely (Pl. 38, Fig. 1). The hypoconid tends to have three clear crests, the hypoprecristid, hypoendocristid and hypopostcristid. The older localities always yield small sized teeth (Text-fig. 51).

The D_4 tends to have the lophs less well developed than the molars.

The M_1 (Pl. 38, Fig. 9), M_2 (Pl. 35, Fig. 3) and M_3 (Pl. 35, Figs 2, 18; Pl. 40, Figs 2, 4, 6; Pl. 41, Fig. 9) have well-developed lophodonty. Only in the oldest specimens do the hypoendocristids and entoendocristids have crests that are each straight and sloping towards the point where they meet, forming an open 'V-shape' (Pl. 35, Fig. 3). In the more advanced specimens, this point is not recognisable and there is an open 'U-shape' (Pl. 40, Figs 2, 6). The hypoprecristids tend to be larger in the geologically older specimens (Pl. 35, Figs 2, 3), than in only slightly younger specimens (Pl. 40, Fig. 6).

However, even with wear, never is a dentine island or elongate extension (as in Pl. 29, Fig. 1) exposed (Pl. 35, Fig. 18). The very early specimens are always small (Text-figs 51, 52); later there seems to be a more or less constant size, though specimens from Manchones I, Arroyo del Val I and Cerro del Otero are suggestive of the presence of a distinctly larger species.

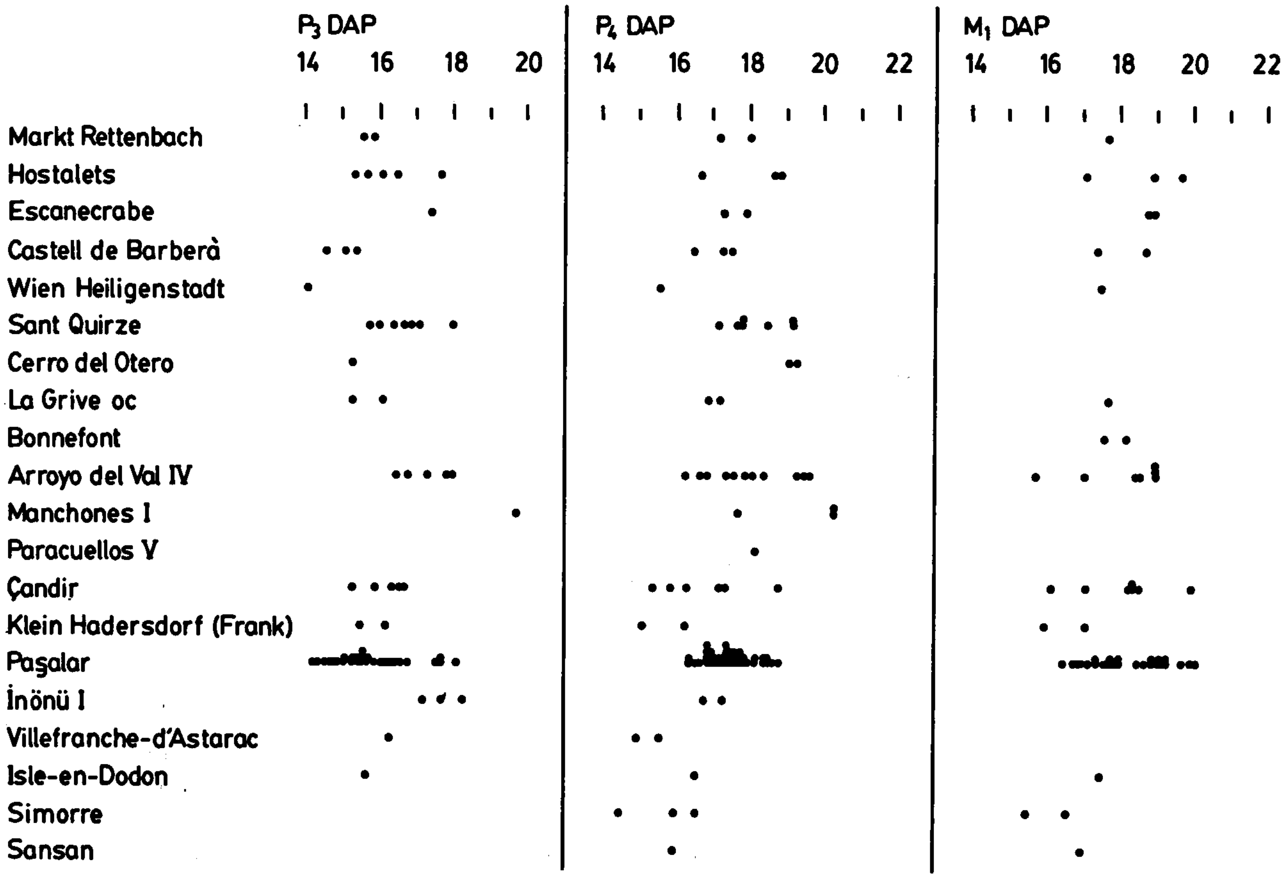


Fig. 51. Sizes of P_3, P_4 and M_1 of *Listriodon splendens* through time. The localities are in approximate stratigraphical order. There is a tendency of the teeth of the older localities (Sansan to Villefranche) to be small. There is one exceptionally large P_3 (the simple morphology would even suggest P_2) in Manchones I.

The I^1 (Pl. 35, Fig. 11; Pl. 36, Figs 1, 2; Pl. 41, Figs 1, 2, 6; Pl. 42, Figs 3, 4; Text-figs 44, 46) has two lobes, separated with a deep groove that usually extends over much of the labial surface. The indices I, DMD, DLL, DMD' and DLL' increase with decreasing geological age. Two specimens from Arroyo del Val I (Pl. 36, Fig. 12) are much too large for their supposed geological age (Text-fig. 47).

The DI^1 (Pl. 35, Fig. 16) is bilobed, like the permanent incisor. Similarly it increases in size and index I.

The I^2 (Pl. 36, Figs 9, 10, 13), DI^2 and I^3 (Pl. 36, Fig. 5) are similar in shape and not easy to separate. The deciduous incisor is smaller, with thinner enamel. The I^2 has a posterior facet with the I_3 and the I^3 one with the C_x. It is not clear whether the shape of these facets is helpful or not in separating the teeth. It is likely that I^3 are included in the tables as I^2. There is no absolute evidence that the teeth become larger or more elongate (larger I) with time.

The C^m (Pl. 36, Fig. 14; Pl. 37, Figs 5-9) are rather variable in size and in radius of curvature and no reliable trends can be observed (Text-figs 53, 54). The variation is great even in a single sample (Pl. 36, Fig. 14; Pl. 37, Fig. 7) and has led to the erection of *Calydonius trux* (Pl. 41, Fig. 14) and *Calydonius tener* (Pl. 41, Fig. 7) from one locality.

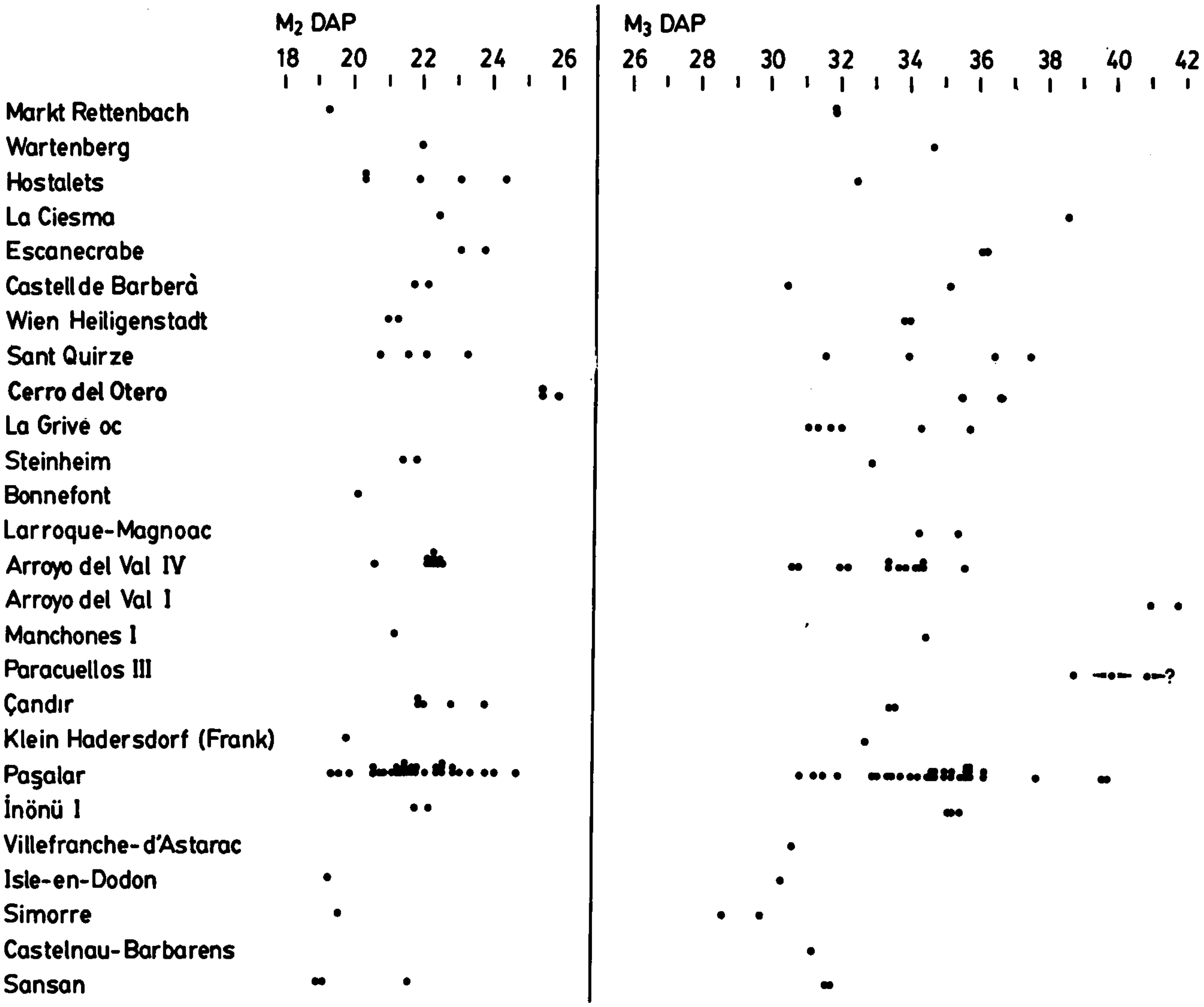


Fig. 52. Sizes of M_2 and M_3 of *Listriodon splendens* through time. The localities are in approximate stratigraphical order. Arrows indicate approximate values and an arrow and question mark means '≥'. There is a tendency of the teeth of the older localities (Sansan to Villefranche) to be small. A number of localities yield exceptionally large specimens (La Ciesma, Cerro del Otero, Arroyo del Val I and Paracuellos III).

Specimens from Sant Quirze appear to have a great radius of curvature compared to the diameter of the section of the tooth. A small section, a small radius but with the radius small compared to the section (100 Ri/DT) is expected for the first *L. splendens*. These values are small in the earliest samples, but within the range of much later samples. The canines are spirals and the apical part has often a clearly greater radius of curvature (Pl. 37, Fig. 8). This means that the teeth become more curved when they grow. This is the opposite of *Babyrousa*, where the apical part has greatest curvature. The smaller specimens of *Listriodon* (Pl. 36, Fig. 14) tend to have a small radius of curvature and thus are not parts that are near the apex; they are just smaller in all dimensions. Large specimens reach a large diameter not very far from the tip and do not become small near the base (Pl. 37, Fig. 8), so the small specimens with a small radius of curvature cannot be the basal parts of large canines. Pl. 37, Fig. 7 and Pl. 37, Fig. 9 suggest that in old age parts of the tooth may break off because the part below the tip is worn off too much. The enamel is present as three bands and only near the tip is there enamel all around (Pl. 37, Fig. 5), this apical part is often completely worn away.

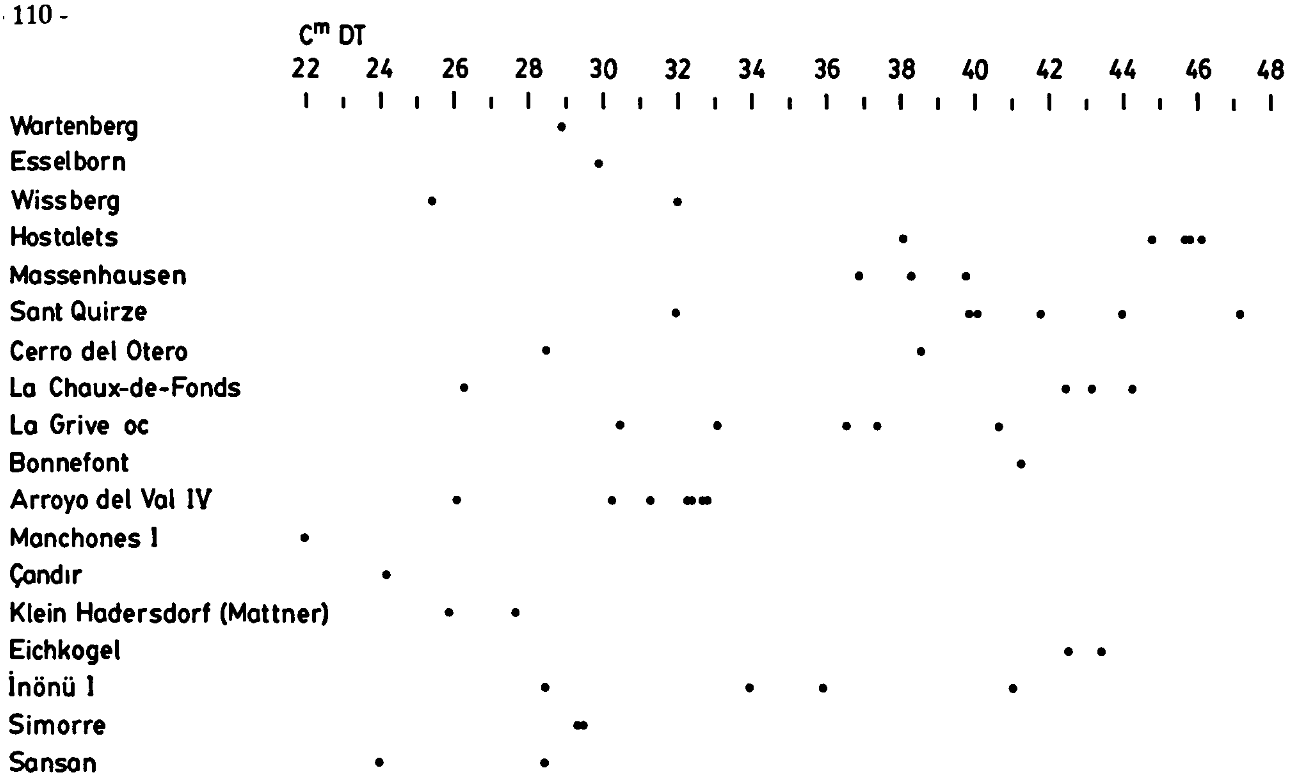


Fig. 53. Variability in size of C^m in *Listriodon splendens*. The DT is indicated, the DAP gives similar results. The localities are in approximate stratigraphical order. The sample from La Chaux-de-Fonds includes the type material of *Calydonius trux* and *C. tener*. Variability in size of C^m is extreme and even in very early localities large specimens are found. The size of this tooth does not seem to be useful for stratigraphy.

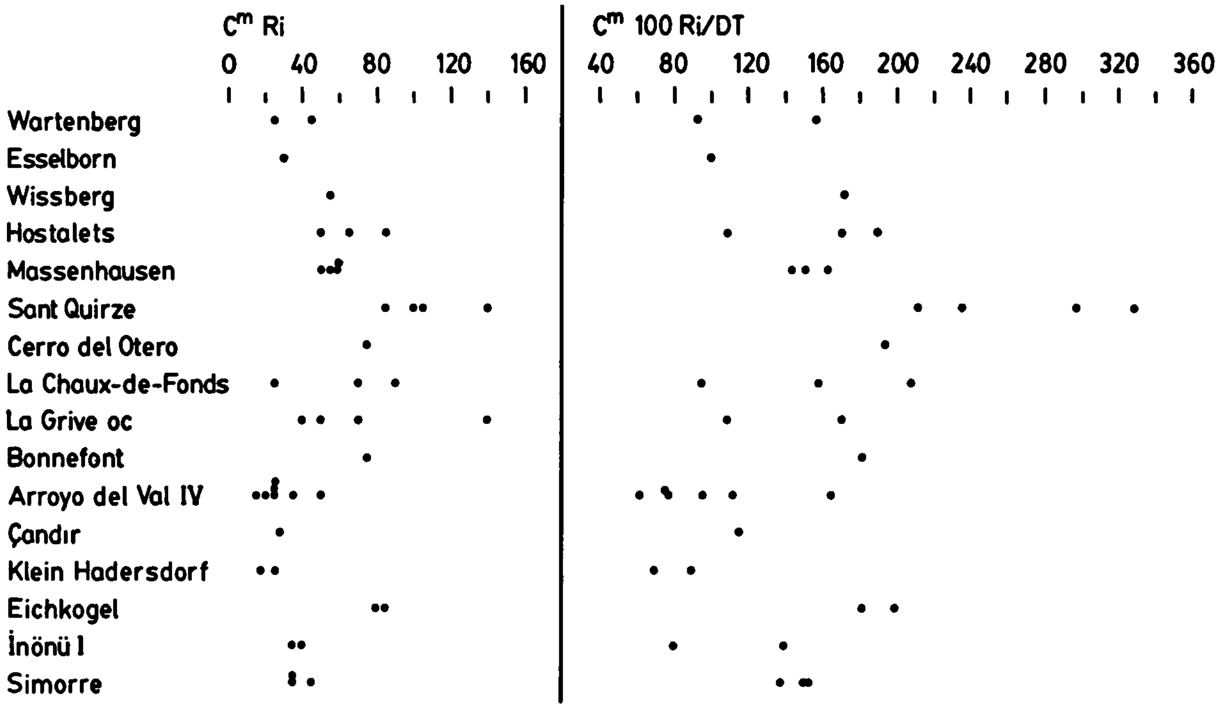


Fig. 54. Radius of curvature of C^m (Ri) as well as radius compared to diameter (100 Ri/DT). The sample from La Chaux-de-Fonds includes the type material of *Calydonius trux* and *C. tener*. The 100 Ri/DT values seem to be limited between 60 and 200, except for the sample from Sant Quirze, which is far outside this range. This would make the S. Quirze canines appear 'less curved'.

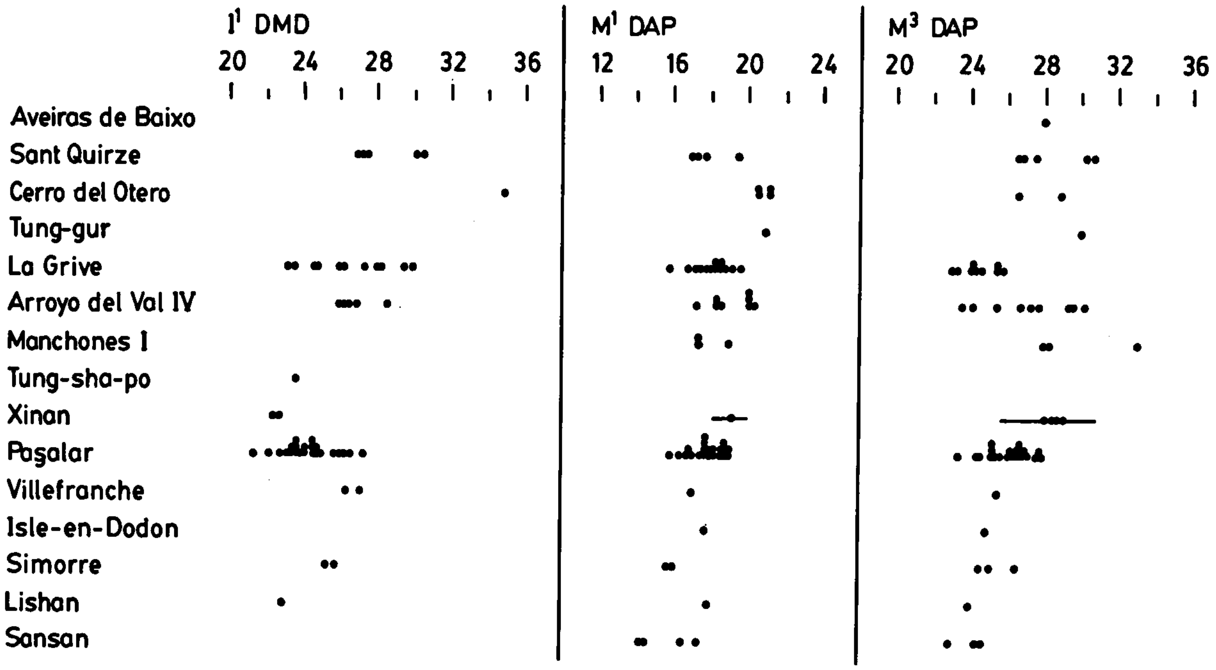


Fig. 55. Sizes of selected teeth of European/Anatolian and Chinese *Listriodon* compared. The European localities are in approximate order, the Chinese localities are fitted in this sequence at very approximate and very tentative positions. Data for Lishan from Lee & Wu (1978), for Tung-sha-po from Liu & Lee (1963) from Tung-gur (Wolf Camp quarry) from Colbert (1934) and the bars represent the ranges for Xinan as indicated by Chen (1986). The dots for Xinan represent my own measurements. My own measurements for (a part of the) Xinan sample do not always agree with those by Chen. The values given by Colbert for the premolars do not agree with the figures, whereas for the molars, there is no discrepancy. Apparently, my way of measuring differs from the ways of those authors. Three species names were introduced for the Chinese *Listriodon* (for the Tung-gur, Xinan and Lishan samples). Size played an important role. *Listriodon lishanensis* from China is comparable to the smaller and older European fossils, such as those from Sansan. The cheek teeth of the intermediate *L. xinanensis* are comparable in size to most European specimens, though the small size of the incisors is comparable to the earlier samples, such as Paşalar. *L. mongoliensis* is comparable to the larger European specimens such as those from Manchones I. The specimen from Aveiras de Baixo is the type of *L. splendens major* and is not a particularly large specimen, and does not indicate that this subspecies is larger than *L. s. splendens* (contrary to what has often been suggested).

The C^f (Pl. 35, Fig. 1; Pl. 38, Fig. 13) has a low crown compared to the canines in other listriodont genera. There are not enough specimens to detect any size changes.

The P^2 (Pl. 35, Fig. 7; Pl. 41, Fig. 10; Pl. 42, Fig. 1; Pl. 43, Fig. 3) and P^3 (Pl. 39, Figs 1, 4; Pl. 42, Figs 1, 6; Pl. 43, Fig. 3) differ mainly in the size of the protocone; in the P^2 it is smaller. With decreasing geological age the size of the protocones increase and old P^3 are difficult to separate from young P^2. As a result the teeth become wider and get a lower index I (Text-fig. 56). This process is often referred to as 'molarisation' and its effects are best noted in the P^2. In the narrower specimens, the protocone is still connected to the cingulum (Pl. 35, Fig. 7; Pl. 39, Fig. 1), in the wider specimens, it is free from the cingulum (Pl. 42, Figs 1, 6). The protocone may have a large protopostcrista that curves labially (Pl. 39, Fig. 1c, e). This large protopostcrista (or even beginning tetracone?) occludes with the hypoconid and develops a dentine island (Pl. 39, Fig. 4d). In the geologically younger forms a metacone may develop (Pl. 42, Fig. 1), but in other cases the parapostcrista remains smooth, without any indication of a developing cusp (Pl. 42, Fig. 6).

The D^2 (Pl. 35, Figs 6, 9, 10; Pl. 39, Fig. 7) is a narrow tooth and the protocone is barely more than a paraendocrista that is directed posteriorly and that comes very close to fusing with the cingulum. The crown is very low compared to its height.

The P^4 (Pl. 39, Fig. 2; Pl. 41, Fig. 5; Pl. 42, Fig. 1) has always a very individual metacone that is nearly as high as the paracone and there is a deep separation between the two. There is always a protoloph, though it may be low near the paracone. The protopostcrista is always present, but usually low; it never fuses to the cingulum. The cingulum is usually not continuous at the lingual side.

The D^3 (Pl. 39, Fig. 7) and D^4 (Pl. 39, Fig. 7) have similar posterior lobes. However, the D^4 is fully lophodont, but the protopostcrista of the D^3 is not fused to the metacone, the cusp that is opposite of it. The D^3 has a continuous lingual cingulum, like the P^2 and P^3.

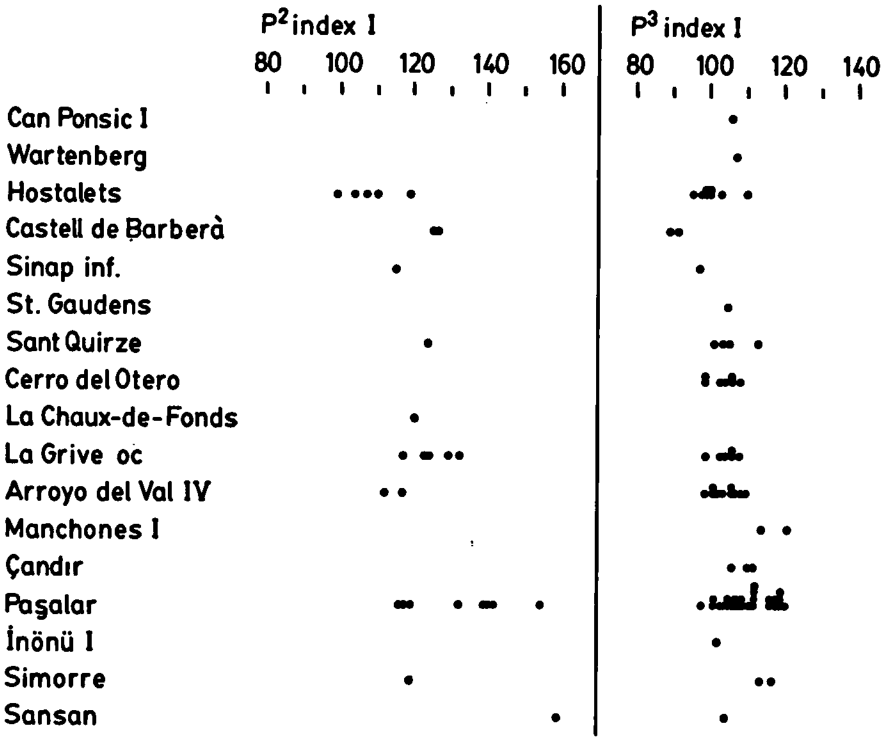


Fig. 56. Increase in width of P^2 and P^3 of European and Anatolian *Listriodon splendens* as a result of the increase in size of the protocone and its lingual translation. The localities are in approximate stratigraphical order.

The M^1 (Pl. 39, Figs 3, 7), M^2 (Pl. 40, Fig. 5) and M^3 (Pl. 35, Fig. 5; Pl. 40, Figs 1, 7) are fully lophodont. In the later specimens, the tetraloph is perfectly developed. In the very earliest *L. splendens*, the point where the tetraendocrista meets the metaendocrista may be low and marked with a small groove in unworn specimens (Pl. 35, Fig. 5a-d). When these primitive forms are worn, the wear facet is 'V-shaped', with the point near the bottom of the transverse valley. In later specimens the tetraloph has a nearly straight crest (Pl. 39, Fig. 3c-e). The tetrapostcrista forms one continuity with the postero-buccal cingulum. The earlier M^3 have a talon (Pl. 35, Fig. 5). The younger M^3 are sometimes difficult to separate from an M^2 and differ mainly by the posterior cingulum, extending more posteriorly just lingually of the axis of the tooth instead of exactly in the middle. A specimen from Manchones (Pl. 40, Fig. 1) is huge (Text-fig. 55).

The **sequence of eruption of the teeth** is shown by some mandibles from Arroyo del Val IV, which have D$_4$ or remains of this tooth and which have the M$_3$ in use. The same sequence is suggested by a maxilla of *B. lockharti* from Langenau. In most Suidae, the P$_4$ erupts before the M$_3$. In Tayassuidae and Palaeochoeridae, the P$_4$ erupts also later than the M$_3$.

The **mandible** is characterised by the wide anterior part where the incisors are implanted. The wider the incisors, the wider the anterior part of the mandible. The size of the symphysis is very variable and the size is subject to age, sex and individual variation. The same is true for the diastemata (Van der Made, 1991a). None of the mandibles have P$_1$ or alveoles for P$_1$.

There are several **skulls** from Europe, but all are deformed. Seen from behind the occipitals form a rounded structure. There is no sagittal crest, but the parietal crests come very near to fusing. A skull fragment from Turkey indicates a concave profile (Pl. 43, Fig. 2).

The skulls from Sansan (♂), Simorre (♀) and Arroyo del Val IV (sex unknown) have zygomatic arcs that are not greatly inflated and that do not stand out at a great angle. These are all skulls from MN 6. The skull from Sinap, Turkey (sex unknown) is younger. The bases of the zygomatic arcs are preserved. They are inflated and stand out approximately perpendicularly. It is possible that the geologically younger males developed more robust zygomatic arcs. The zygomatic arcs form a wide and flat area before and below the orbits. There is no fossa infraorbitalis, where a strong levator rostri muscle may have originated. This muscle moves the nasal disc. There are no indications that the other muscles involved in moving the nasal disc were well developed. The snout is wide and rounded.

All skulls are damaged in the area where in other suids the foramina lacrimalia are found. What is preserved indicates that there were no such foramina.

A skull from Sansan shows a possible alveolus of a P^1, indicating that the tooth still was present. Although it may have been lost early in life. The palate extends quite some distance behind the M^3 (Pl. 43, Fig. 4).

The remains of the bullae have an antero-posterior diameter that is much greater than the transverse diameter. The long axis of the bullae may have been vertical. The bone is spongy. The glenoids are positioned high and far posterior. They are convex in antero-posterior direction. The external auditory meatus is oriented outwards and upwards, and ends at the postero-external part of the zygomatic arc. The basicranium is typically suid like.

The **postcranial skeleton** is preserved by many parts, but there is not a single complete long bone. There are few differences with *Sus scrofa*, though differences in proportions cannot be ruled out. The radius (Pl. 39, Fig. 10) has a proximal facet that is rectangular. The magnum (Pl. 43, Fig. 5) has a facet for the unciform at the anterior side. The unciform has a long posterior extension like in *B. lockharti* (Pl. 25, Fig. 4). The MC III (Pl. 25, Fig. 7) has a well-developed facet for the trapezoid. Phalanges are as in most suids (Pl. 39, Figs 5, 6, 8, 9). The astragalus (Pl. 25, Fig. 8) has a sustentacular facet without a lateral ridge, which makes it a flat facet in transverse direction (see Leinders, 1976). The navicular has a facet for the second cuneiform that is always well visible as a large and individual facet.

Description and comparison of the Chinese material — Comparisons are made with *Listriodon splendens* from Europe and with *L. pentapotamiae*.

The I^1 (Pl. 44, Figs 1d, 2b) have two lobes. The DLL is clearly larger than the DLL of the *L. pentapotamiae* incisors. The DMD of the specimens known is up to 24.5 mm (Li & Wu, 1978, fig. 47), which is more than in most *L. pentapotamiae*. The size and index I are within the ranges of *L. splendens* from Paşalar (Text-fig. 55). DMD' and DLL' values are clearly less than in *L. splendens* from Europe (Text-fig. 26, the smallest value for *L. splendens*), though these values could not be calculated for the very earliest samples (such as Sansan). Either the I^1 of the Chinese *Listriodon* did not increase in size as in *L. splendens* from Europe, or Tung-Sha-Po, Xinan and Lengshuigou are all old localities.

The C^m (Pl. 34, Fig. 1) is larger than in any *L. pentapotamiae*. The radius of curvature and DT can be measured from a specimen figured by Li & Wu (1978). The value 100Ri/DT is 86, which is lower than in any *L. splendens* and comparable to *L. pentapotamiae*.

In the skull remains, there is evidence that the P^1 was lost.

The P^2 (Pl. 44, Fig. 2e, f) and P^3 (Pl. 44, Fig. 2e, f) are in the ranges of the sample from Paşalar. There is no indication of a metacone.

The P^4 (Pl. 44, Fig. 2e, f) has a metacone that is large and well separated from the paracone, like in *L. splendens* and unlike in *L. pentapotamiae*. The fossa is large, like in *L. splendens*.

The M^1, M^2 and M^3 (Pl. 44, Fig. 2e, f) are fully lophodont. All cheek teeth from Xinan and Tung-gur are large compared to *L. splendens* and *L. pentapotamiae* (Text-fig. 55).

The **skull** has a concave profile, like in *L. splendens*. This is very clear in a male (Pl. 44, Fig. 1), less so in a female (Pl. 44, Fig. 2).

The orbits are elevated much above the plane of occlusion. The zygomatic arc is 'high', and there is a large flat area in front of and below the orbit. There are no fossae that indicate the presence of strong muscles that move the nasal disc. The zygomatic arcs depart from the skull under a gentle angle, they do not project under an angle of 90°, not even in the males. The thickness of the zygomatic arc is moderate, even in males. None of the skulls has foramina lacrimalia.

The transverse section of the snout is rounded. The frontal area, in frontal view, is also rounded. It is not flat as in *e.g. Sus scrofa*. The parietal crests are close to each other, but do not form one sagittal crest.

The distance of the palate behind the M^3 and its morphology are very variable in Recent suids. However, it seems that the more the palate may extend in a species, the more the variability of the distance increases. Taking M^3 size as a standard, it seems that the later listriodonts, including *Listriodon* have a palate that extends further posteriorly than in the earlier listriodonts.

The bases of the canines of the males are covered by a thin and smooth extension of the maxillary. This bone does not form a cresta alveolaris (*sensu* Thenius, 1972), which tends to be rugose at the external or superior surfaces as in *e.g. Potamochoerus*.

Discussion — In Europe, other names have been introduced for material that belongs to *L. splendens.* But since 1859 none of these has been used and all material was assigned to *L. splendens* (see synonymy list). However, the material is not entirely homogeneous. Several stages of evolution can be recognised and names are available for these stages. There are two possibilities: 1) to name the stages as species, and b) to name the stages as subspecies. Naming the stages as species would imply breaking with accepted nomenclature. Besides, there is a vast quantity of material that is either not complete enough to assign to one of the stages of this lineage or that is intermediate. When the three stages of evolution are given species status, this material would be named *Listriodon* sp., despite that it is known that the material belongs to the *L. splendens*-lineage and not to *L. pentapotamiae.* In such a situation, nomenclature would obscure the situation, rather than help us. For practical reasons, the three stages of evolution are given here subspecific names. It is good to bear in mind, that evolution in *L. splendens* is slow, whereas it is rapid in *e.g.* the *B. latidens*-lineage.

The very earliest material (MN 6, especially earliest part) tends to be small and the second loph is not always straight. The premolars are simple with besides the protocon(id) small and few additional crests and cusps. The incisors are not very large and not elongated in meso-distal direction. The male canines are small. This material includes the types of some of the species that were named only few years after *L. splendens. Tapirotherium Lartetii* Gervais, 1849 is based on material from Simorre (?). *Tapirotherium Blainvilleanum* Lartet, 1851 was based on material from Simorre, Villefranche and Castelnau-Magnoac. *Sus tapirotherium* is probably a species by De Blainville (1847), though it is not indicated in the text as a new species and the year of this volume is not indicated in the volume itself. Hünermann (1968) considered De Blainville to be the author and 1847 the date of publication. De Blainville indicated in the text that the species was from 'Sansans', but the material figured is from Simorre, a group of nearby localities. The exact locality is Simorre-le Seignou (Richard, 1946). The earlier stage of evolution is here called *L. s. tapirotherium* (De Blainville, 1847).

A following stage of evolution (MN 6, later part and MN 7) is large with perfect lophodonty and slightly more complex premolars and larger and more elongate incisors. This material includes the type material of *L. splendens. Calydonius trux* Von Meyer, 1846 and *C. tener* Von Meyer, 1846 are based on the canines of *L. splendens* from La Chaux-de-Fonds.

The last stage (MN 8 and 9) is large and has much enlarged and elongated incisors. The premolars are more complex. This material includes the holotype of *L. s. major* Roman, 1907. But also a possible syntype of *Sus? doati* Lartet, 1851. No holotype for this species was indicated. In the collections of the MNHN, there are a bunodont molar and a huge canine that belongs to *Listriodon.* Lartet (1851, p. 33) apparently had the canine in mind when he stated that '*Sus? Doati*' was larger than '*Sus Simorrenis*'. The canine is accompanied by a label that states it belongs to the former species. Since most authors agreed in using the name '*doati*' for material of the bunodont *Conohyus*, the molar is here designated **lectotype**. Consequently, the name for the later stage of *L. splendens* is *L. s. major* Roman, 1907.

Several species of *Listriodon* have been erected for Chinese and Mongolian material: *L. mongoliensis* Colbert, 1934, *L. lishanensis* Li & Wu, 1978 and *L. xinanensis* Chen, 1986.

L. mongoliensis has a very large holotype, larger than most *L. splendens.* However the paratype is a lot smaller, suggesting that the holotype is just a large individual of a population of individuals of lesser average size. Colbert (1934) considered the only differences with *L. splendens* to be the narrow P^2 and a P^4 with a large and separate metacone. The measurements for the P^2 (16 x 11.5 mm) are comparable to those of the larger P^2 from Paşalar (for instance 16.3 x 10.6 mm). Later P^2 from Europe and Anatolia are relatively wider. Comparison to a large sample of *L. splendens* P^4 reveals that the separation of the metacone and paracone are not exceptional in the Mongolian fossils. In the absence of incisors, the Mongolian specimens seem closest to the late MN 6 *L. splendens*, such as from Paşalar, although Tung-gur is usually considered to be younger.

L. lishanenensis is based on very small type material and in size it is comparable to the very early MN 6 *L. splendens* from Europe (Text-fig. 55). The I^1 has a DMD of about 24.5 mm (taken from Li & Wu, 1978, fig. 47). This is more than in most *L. pentapotamiae* and comparable to the earlier *L. splendens.* The C^m has a large DT (35 mm), more than *L. pentapotamiae* and well within the range of *L. splendens.* Its value for 100Ri/DT is 86, which is lower than any *L. splendens* measured, but coincides very well with what is expected for the earliest individuals of that species. The P^4 has two well-separated labial cusps, as in *L. splendens.* On the present evidence, *L. lishanensis* cannot be separated from the very earliest *L. splendens.*

There is very good material from Xinan, part of which is described above in more detail. It is the type material of *L. xinanensis* (holotype V 8283; Pl. 44, Figs 1, 2). *L. xinanensis* was supposed to differ from *L. splendens* in its large size, narrow palate, the large size or position of its infraorbital foramen above P^2-P^3, backward curvature of the C^m, absence of P1, P^2 and P^3 having a well-developed protocone (?) and P_2 and P_3 a hypoendocristid (? - my terminology) and the I^1 being more high crowned. The size of the cheek teeth is well within the range of *L. splendens* (Text-fig. 55). The width of the palate is very close to that in *L. splendens.* Comparison of different sizes of skulls is possible taking the width of a molar as standard: 100Wi/DTa, where Wi is the width of the palate at a certain molar position and DTa the size of that molar. For the M^3 this is 166, 160, 173 and 180 for *K. gigas*, *B. jeanneli*, *L. splendens* and *L. xinanensis* respectively. The latter has the widest palate. *L. kidogosana* has a really wider palate with value 234. Skull Sa 10141 from Sansan has a C^m with a tip that is turned backwards. In *L. splendens*, the P_1 is totally lost and only in the Sansan skull is there a possible alveole for the P^1, the only possible P^1 is from Paşalar, besides that specimen there is no trace of the tooth. The P^1 was probably lost in all but some of the earliest *L. splendens.* Development of the protocone and hypoendocristid of the premolars is subject to evolution within *L. splendens.* In frontal view, in the skull of *L. xinanensis* the height of the I^1 appears to be great compared to the DMD. This does not so much indicate crown height, but small DMD, a generally primitive trait. *L. xinanensis* is characterised by small I^1 and C^m that are less curved (100Ri/DT in one case over 200) than in *L. lishanensis.* In the characters that were studied, it seems more progressive than *L. lishanensis* and similar to *L. mongoliensis* and cannot be separated from *L. splendens.*

All Chinese material is very similar to *L. s. tapirotherium* (Lengshuigou) and early *L. s. splendens* (Xinan and Wolf Camp Quarry = Tung-gur). The fact that various stages of evolution are found both in China and in Europe, shows that the populations were not only similar, but also evolved in the same direction. This suggests that the Chinese *Listriodon* belonged to the same species as the European *Listriodon*, and is therefore referred to *L. splendens.*

Material from some localities is characterised by very large size. These localities include Arroyo del Val I, Paracuellos 3, La Ciesma, Boulogne, Coca and Doué-la-Fontaine. Usually, listriodont fossils are rare in these localities, but occasionally, there is evidence of two extremely large individuals. The fact that the extreme values are found in the smaller samples and not in the larger samples, where they would have more chance to be recorded, suggests that there is a rare larger species. However, in Manchones I, Cerro del Otero and Wolf Camp Quarry there are smaller and some large individuals in one sample. With some reservation, all the material is placed in *L. splendens*, but if the material really proves to be a different larger species, the European and Mongolian material might well belong to the same species (*L. mongoliensis*).

Listriodontinae indet.

? 1981 *Listriodon* sp. — Shipman *et al.*, p. 67.
? 1986 *Listriodon* sp. — Shipman, p. 196.

Loc.	**Coll.**	**Ref./Descr.**	**Strat.**	**Ref.**
Fort Ternan	KNM		Set IV	Pickford 1981

Description and comparison — A D_4 which has the two anterior lobes buccally damaged, does not have lophs. The third lobe seems to come closest to this condition as the endocristids touch, but are not really fused.

A P^2 and P^3 of one individual are poorly preserved and the only thing that really can be seen is that they have a listriodont morphology. All these specimens are too large for *L. akatidogus*, which is also found in this locality.

Discussion — There is only limited material and it is poorly preserved. The specimens reach the size of *L. pentapotamiae*, *L. splendens* and *B. akatikubas.* The last-named species is known from Mbagathi and Maboko, which are older localities. The D_4 seems to indicate a sublophodont species, such as *B. akatikubas.* However, the D_4, D^4 and especially the D^3 of the earliest *Listriodon* sometimes still have a sublophodont morphology and it seems that the development of lophodonty lags behind in these teeth.

Thus it is not known whether the larger listriodont from Fort Ternan belonged to *Listriodon* or to *Bunolistriodon.* In the former case these teeth would be the only indication of the presence of this genus in Africa and in the latter case, they would represent the last surviving *Bunolistriodon* known.

PALAEOECOLOGY

Aspects of the palaeoecology of listriodonts may be studied in a number of ways. Incisor and cheek tooth morphology, morphometrics and wear, as well as enamel thickness yield information on the diet of listriodonts. The postcranial skeleton may give information on locomotion. Species abundance, estimates of body size and geographical and temporal distribution supply additional data.

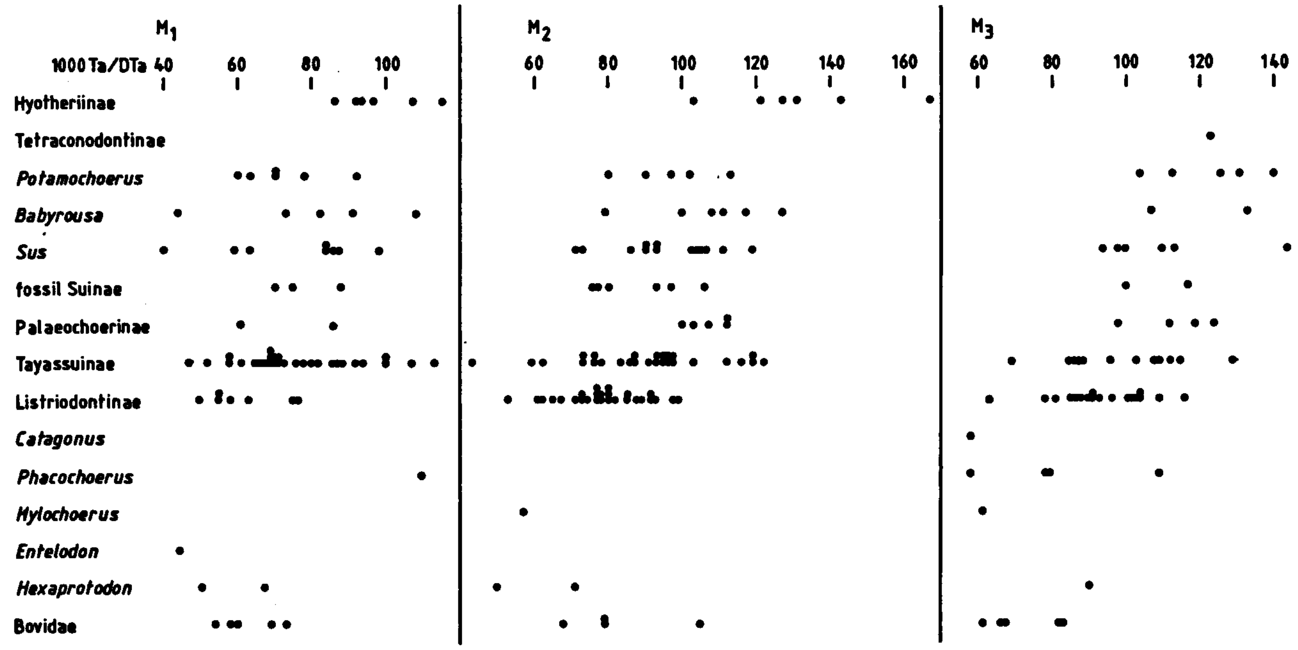


Fig. 57. Relative thickness of molar enamel. Thickness of enamel (Ta) measured at the metaconid as a promillage of width of the molar (DTa).

Incisor morphology, morphometrics and wear

The incisors are used to grasp and bite off food items. Pigs use them in rooting, digging for food. Thus incisors hold information on part of the food gathering habits of pigs.

Incisor morphology of listriodonts was studied by Leinders (1977a), who compared it to that of ruminants, tapirs and *Sus* and concluded that *Listriodon* was adapted to feeding on herbs. In this comparison, few other listriodonts and few other pigs were taken into account. The high-crowned incisors of *Sus* are an extreme adaptation and there is great variation in the degree of adaptation in listriodonts.

Fairly low-crowned incisors are probably primitive to suoids (Table 18) and an increase in height of the crown is an adaptation, very probably to rooting. Most suoids root and have incisors with very low index I and high DLL' values. This can be explained as an adaptation to forces that work on the incisors in linguo-labial direction, which may occur when teeth are used to dig up some resisting root. That teeth are used in such a way is indicated by lingual wear facets on the lower incisors and apical wear facets in the uppers. These facets are not formed by occlusion of the upper and lower incisors (occlusion of listriodont incisors is explained by Leinders, 1977a).

Listriodonts have decreased the height of the crown of the I_1 and I_2 (Text-fig. 59) and I^1 and have increased the DMD' and index I of these incisors. The lesser increase or even decrease of the DLL' in listriodonts suggests that there were no strong forces in linguo-labial direction. In *Lopholistriodon moruoroti*, an apical facet in the I^1 is found (Pl. 2, Figs 5, 10). This suggests that only some of the earliest listriodonts occasionally rooted.

Ewer (1958) studied suid musculature and found that the size of the muscles that move the rhinarium and the size of the depressions on the snout where these muscles originate are indicative of rooting habits. Pickford (1986b) applied these findings to the holotype skull of *Lopholistriodon kidogosana* and concluded that that species did not dig or root as much as did *Potamochoerus*, but may have resembled *Phacochoerus* in the frequency and way of digging. Skulls of *Listriodon splendens*, *L. pentapotamiae*, *Kubanochoerus massai* and *K. gigas* have the same shallow fossae for the origin of the muscles for the rhinarium. In all three tribes of the listriodonts, the places of origin of the muscles for the rhinarium indicate little or no rooting. This corroborates the findings on the incisors.

Solounias *et al.* (1988) studied the width of the snout in ruminants as indicated by premaxilla width and found that grazers have wide snouts and browsers narrower snouts. This reflects the large amount of food ingested by the first group and the selectivity of the second. Species with wide snouts tend to have wide incisors.

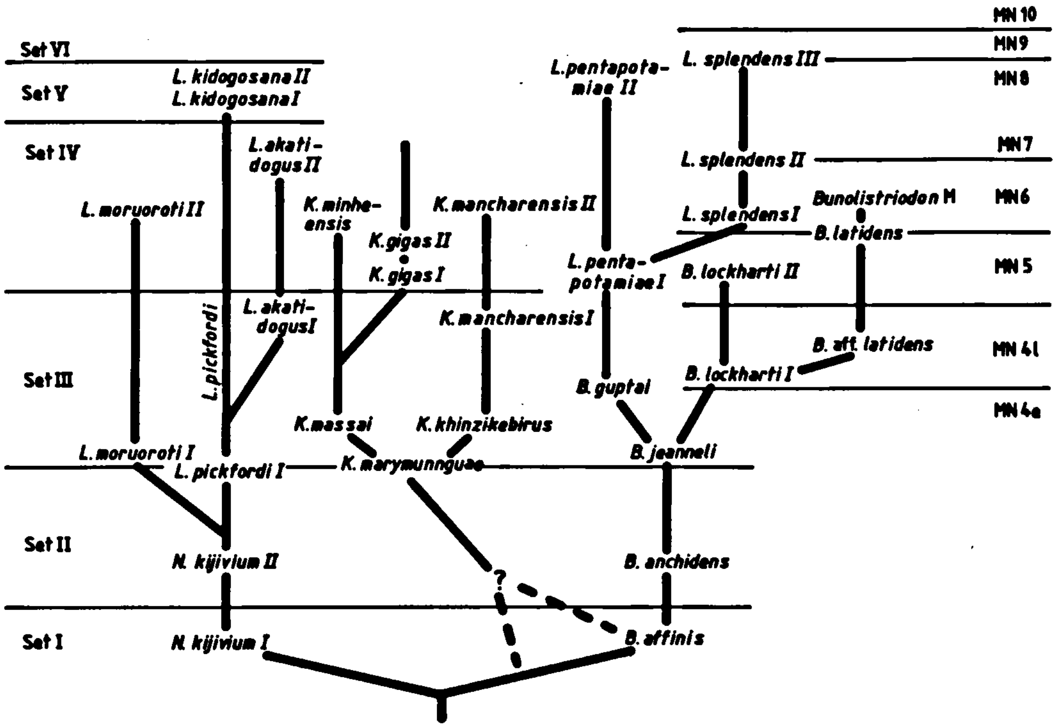


Fig. 58. Phylogenetic tree of the Listriodontinae. The most probable or most favoured relations are indicated (see text). The species are indicated at their approximate stratigraphical levels. Left, the African Sets I-VI (Pickford, 1981) are indicated and to the right, the European MN units (Mein, 1990). *Bunolistriodon akatikubas*, *B. intermedius* and *Bunolistriodon*? sp. from Baragoi are not indicated, because not enough is known about them, or because it is uncertain whether they are distinct species. Some species are followed by roman numerals. These generally indicate different stages of evolution. In some cases, subspecies names are available for these stages, as in the case for *K. gigas*: I - *K. g. gigas* and II - *K. g. lii* and for European *L. splendens*: I - *L. s. tapirotherium*, II - *L. s. splendens* and III - *L. s. major*. In other cases, the stages are informal. *Bunolistriodon* M stands for *B. meidamon*.

The parallel with listriodonts is obvious; may they have been grazers of some sort?

Grass contains silica particles. Grazing animals also ingest sand grains. Both increase wear to the molars and incisors. Grazers have molars and often incisors with high crowns. Listriodonts do not have molars or incisors with high crowns and it does not seem likely that they fed on large amounts of grasses. A solution that fits all these data would be that listriodonts ingested large quantities of some kind of food which was not grass. This is in line with Leinders' (1977a) conclusion that *Listriodon* was adapted to eating herbs.

Cheek tooth morphology and wear

Molar and premolar morphology are indicative of the kind of food taken and of the way how it is digested. Premolars usually cut and molars grind food items.

The similarity of the lophodont molars of *Listriodon* to those of tapirs is often cited in relation to the diet of *Listriodon* (Dehm, 1934; Leinders, 1977a). Tapirs have premolars that are 'molarised', they resemble molars to some extent in morphology and in function. *Listriodon* premolars tend to form lophids and become more like molars in shape and function.

Leinders (1977b) pointed out that wear facets on premolars of *Listriodon* and *Bunolistriodon* ('*Listriodon lockharti*') are predominantly transverse in contrast to those in *Sus*. Although *Bunolistriodon* premolars did not yet have lophids, their use was already like in premolars with a more marked lophodont morphology. Use preceded morphology.

Hunter & Fortelius (1994) studied wear facets on molars of *Listriodon splendens* and *Bunolistriodon meidamon* ('*L.* cf. *L. latidens*'). Wear facets reflect the chewing movement. Lophodonty is accompanied by an increased importance of the lateral movements during mastication.

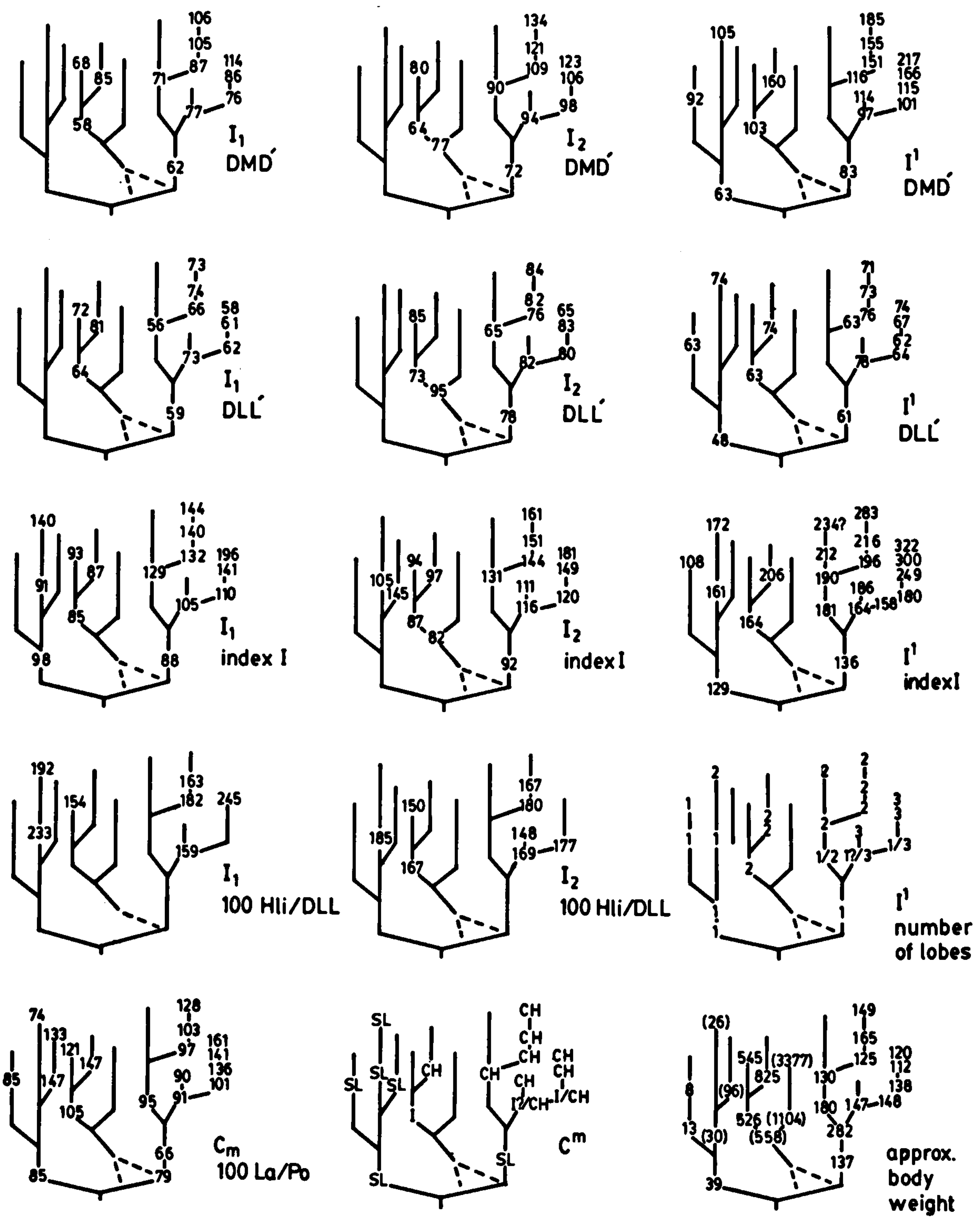


Fig. 59. Changes in morphometrical, metrical and morphological characters in the Listriodontinae. The trees are the same as in Fig. 57. For I_1 and I_2, changes in DMD', DLL', index I and the hypsodonty index 100 Hli/DLL are indicated. For I^1, DMD', DLL', index I and the number of lobes is indicated. For the C_m, the index 100 Li/Po and for the C^m the state, low crowned and straight (LS), intermediate (I) and curved and high crowned (CH) are indicated. An estimation of the body weight (in kg) is given following the method of Legendre (1986). This method uses M_1 size. When M_1 size is estimated from the size of other teeth, the estimated body weight is given between brackets.

This is reflected in a stronger development of transverse facets. Although still sublophodont, *Bunolistriodon* wear facets already indicate an increased lateral movement of the jaw. Hunter & Fortelius (1994) also studied microwear of *Bunolistriodon* and *Listriodon* molars. On the basis of macro- and micro-wear, they interpreted *L. splendens* as a more specialised folivore than *Bunolistriodon* and listriodonts with lesser developed lophodonty.

The combined data on cheek tooth morphology and wear indicate various degrees of folivory for the (sub)lophodont listriodonts.

Enamel thickness

Enamel thickness is used in the study of fossil primates and hominoids in particular. Kay (1981) concluded that frugivorous primates had thicker enamel than folivorous primates and investigated allometry of enamel thickness. Macho & Berner (1993) found that enamel thickness increased from the M^1 to the M^3 and related this to the mechanics of chewing. Here enamel thickness (Ta, Tp; Text-fig. 16) of lower molars of the listriodonts is studied.

Kay (1981) measured enamel thickness at the hypoconid of the M_2 and related that value to molar length. The regression line was calculated over the logarithms of these values for a sample of primates, ranging from small to large, in order to investigate allometry. The relation $E = 0.086 \times M^{0.99}$ was found, where E = enamel thickness and M is molar length. This is approximately a linear relationship within the size ranges studied. For suoids, which have a much greater size range, no indication of allometry is found. There is no clear difference between enamel thickness relative to molar size in related suids of small or large size; not between *Listriodon splendens* and *Kubanochoerus massai*, nor between the very small *Sus salvanius* (Hodgson, 1847) and the normal *S. scrofa*. In contrast, there are great differences from one subfamily of suoids to another and between groups with different diets. This is strange. One would expect enamel thickness to be related to diet. Hard nuts, for instance, need the same power to be crushed, whatever the size of the animal that eats them. Since no important allometry is found for the range of sizes studied, it is ignored for the time being.

Macho & Bernor (1993) sectioned upper molars and measured enamel thickness. Upper molars tend to have lower crowns. As enamel thickness decreases from the tip of a cusp to the base of the crown, the gradient is steeper in upper molars than in lowers. Here lower molars are used, because in these teeth it is easier to obtain constant results, without sectioning. Near the tip of the cusp enamel thickness is great and it is more difficult to decide what is perpendicular to the surface of the enamel. Near the base of the crown, enamel thickness decreases rapidly. The relation between remaining crown height and molar size might be used to limit variability of the enamel thickness measured, within a group of species with a similar grade of hypsodonty. Another possibility is to limit variability by relating remaining crown height to maximum crown height and determine where variability increases. In this provisional study, lower molars are measured and those which are heavily worn are omitted. Since all taxa are treated in the same way, there is probably no bias, but only increased variability.

Since it is the intention here to study also the gradient of enamel thickness in the lower molars and since the M_3 is much more elongate, molar length is not used as a measure for size, but molar width. Many suids evolved more elongate molars, and in many cases it does make a difference whether length or width is taken as a standard. In listriodonts, there are only few changes in elongation of the molars. Moreover, if enamel thickness is measured at the lateral side of a cusp, a relation to molar width seems more likely than to molar length. Here the enamel thickness is measured at the lingual side of the lower molars. This is done because the surface of the tooth is nearly vertical here, while it slopes at the buccal side. It might be argued that buccal enamel thickness is more critical and thus more indicative. Enamel thickness was not among the standard measurements in this study. As a consequence, there are few measurements and therefore comparisons are made at subfamily level and not at species level.

Enamel thickness in suoids has a strong gradient from M_1 to M_3, there seems to be less overlap than in the upper molars of man (Macho & Berner, 1993). Expressing enamel thickness as a promillage of the width reduces the gradient. Within the studied suoids (Text-fig. 57), Hyotheriinae have thickest enamel, which is thick even in the M_1, and seem to have a great gradient (though no M_3 could be measured in the samples studied for enamel thickness). Unfortunately nearly no Tetraconondontinae were measured. They are said to have very thick enamel (Pickford, 1988a). Most other suoids form a group with less enamel thickness and a lesser gradient. Listriodonts, the lophodont peccary *Catagonus* and *Phacochoerus* and *Hylochoerus* tend to have a lesser enamel thickness and a lesser gradient (Text-fig. 57). The latter two suids have hypsodont teeth and cementum. Bovids, hippos and *Entelodon* have also thin enamel and a small gradient (Text-fig. 57). *Entelodon* is a fossil bunodont suiform of enormous size.

Bovids and hippos (*Hexaprotodon*) are folivorous.

Phacochoerus and *Hylochoerus* mainly feed on grasses, of which the former also may eat the roots (D'Huart, 1991; Radke, 1991). *Catagonus* does eat fruit of cactus, but also herbs and it roots much less than other peccaries (Taber, 1991). *Potamochoerus*, *Babyrousa* and *Sus* are omnivores which root and eat fruits and nuts (MacDonald, 1991; Seydak, 1991). The results suggest that listriodonts were adapted folivores and that hyotheres and tetraconodonts may have fed on fruit, nuts, roots and other hard food items. Since most suoids, including the early *Palaeochoerus*, have thick enamel, thick enamel seems to be primitive within Suoidea. Thus, thin enamel is probably a later adaptation in Listriodontinae. This adaptation is independent of tooth morphology, since it is found in selenodont bovids, brachyodont bunodont to lophodont listriodonts and hypsodont bunodont *Phacochoerus*. In Listriodontinae, the decrease of enamel thickness preceded lophodonty, which is also an adaptation to folivory.

There is a peculiar parallel between suids and bovids. Bovids increase the durability of their molars with a strong gradient in hypsodonty from the first to the last molar. Suids do the same, though generally not with crown height, but with enamel thickness.

Diet

The available evidence suggests that all listriodonts were specialised folivores, but that this specialisation was more marked in the later forms than in the earlier. Incisor size suggests that somehow there was a 'grazing' habit, but absence of hypsodonty indicates that the food ingested was not grass. Possibly listriodonts ate large amounts of herbs, but not grass.

Locomotion

Leinders (1976) studied the ankle joint of *Listriodon splendens* and compared it to Recent cursorially adapted species (*Cervus elaphus* Linnaeus, 1758) and a Recent pig (*Sus scrofa* Linnaeus, 1758). A comparison of foot bones from Munébrega I, which were assigned to '*L*'. *lockharti* with foot bones of *L. splendens* was made and the evolution of a cursorial adaptation in *Listriodon* deduced.

However, the foot bones from Munébrega I are too small for *B. lockharti*. Astragali of *B. lockharti* and *B. latidens* resemble those of *L. splendens*. The foot bones from Munébrega I may have belonged to *Hyotherium soemmeringi*, which is also found in this locality. Several of the resemblances of *Listriodon* to *Cervus* are also resemblances to anthracotheres, such as the shape of the head of the calcaneum and the shape of the proximal side of the sustentaculum tali. Other characters, such as the flat sustentacular facet of the astragalus, occur to some extent in other early suids. The ridge next to this facet is small or absent in *Listriodon*, but large in *Sus*. However, in *Sus* there is a ridge between the internal side of the proximal condyle and the side of the sustentacular facet. The proximal part of the sustentacular facet covers part of this ridge. Such a structure is common in Suinae, but not common or absent in other subfamilies.

Animals that are cursorially adapted tend to have the distal elements of the legs lengthened: humerus and femur are still short, but metapodials have increased length. Reduction of length, robustness, or number of the lateral metapodials is also a common cursorial adaptation. Metapodials of *Kubanochoerus massai* have an elongate appearance, in comparison to *e.g. Sus scrofa*. But there are many more primitive suiforms with elongate metapodials. These suiforms tend to be plantigrade (Golpe-Posse, 1972) and a cursorial adaptation is questionable. There are nearly no complete humeri, radii etc. A reconstruction of a complete leg, or at least its basic proportions is not possible on the basis of the material studied.

The analysis of the locomotory system of the listriodonts is not an easy subject and a straightforward comparison between a limited number of taxa might be an oversimplification. A functional interpretation of the morphology of the foot bones of Listriodontinae should ideally involve at least some phylogeny and some comparisons to primitive artiodactyls. The claim of a cursorial adaptation is considered here with some reservation.

Body size

Body size is considered an important variable in ecology and is usually applied to fossils by estimations on the basis of tooth size. Legendre (1986) estimated body weight on the basis of M_1 surface. Fortelius (1990) indicated that molar width might be influenced by diet and that molar length is probably a more reliable estimator of body size and Fortelius *et al.* (in press) give body sizes estimated on M^2 length. It should be noted that in Suoidea, changes in indices I of the molars are more marked in the uppers, so that body size estimates based on M_1 size are less affected. In Suidae, M2 length increases in many instances relative to M1 length, as an adaptation to diet (Van der Made, 1989b). Here, body weight estimations according to Legendre (1986) are applied (Text-fig. 59) and a possible lesser reliability is accepted.

Both increases and decreases in body weight are found in the evolution of listriodonts. Sympatric species tend to have large size differences. The *B. latidens*-lineage is sympatric with species that are comparable in size. It is found in Córcoles together with *B. lockharti* and in Paşalar and Çandir with *L. splendens*. In the first case, the differences with *B. lockharti* are very small and are mainly in size (Van der Made & Alférez, 1988).

Body size is important in ecology in terms of reproductive rates, home range size and resulting biomass per surface etc. In palaeontology the use of body size is far more pedestrian and here, it is used for a tentative estimate whether a species might be an indicator of an open (few large plants) or closed (forest) habitat.

The ungulate response to predators includes: to outrun the predator, to hide and to attack. For the first response cursorial adaptation is a prerequisite. The last named response is mainly found in large ungulates, especially when living in herds. The large *Kubanochoerus mancharensis* probably could defend itself equally well as a hippopotamus or a rhino. And if *L. splendens* with huge canines lived in larger groups it may well have stood its ground. Most listriodonts would run and hide, as do their modern counterparts. The size of the vegetation would then, from a defensive point of view, have to match body size. That is, a small animal can hide in moderately tall grass or low bushes, but a larger one cannot. If then the size of the vegetation was an important factor in the distribution of listriodonts, this would indicate that most of the Lopholistriodontini could live in an environment with low vegetation, which to taller animals might appear as an open landscape. Most of the Listriodontini would then be confined to the vicinity of larger vegetation. At least some of the Kubanochoerini may have lived in open landscapes.

Geographical and temporal distribution

Listriodon molars, the lower ones in particular, resemble those of tapirs and suggest dependence on similar vegetation for food. However, *L. splendens* was common in Europe in MN 6-9, but tapirs were rare during MN 6-7, and more abundant during MN 8-9. Tapiridae never reached Pakistan, nor Africa. This suggest that tapirs and listriodonts had different ecologies.

Tapir fossils tend to be associated with peats, whereas listriodont fossils are never abundant in peats. Peats are believed to have formed in wet environments and to be indicative of a more humid climate. In some cases, listriodonts are associated with gypsiferous sediments (Guan & Van der Made, 1993). If the gypsum is not reworked, it indicates that evaporation was high and at least during a large part of the year exceeded precipitation. This suggests that listriodonts could survive in a drier climate than tapirs.

The presence of listriodonts in Turkey coincides with the Eskihisar ad Yeni Eskihisar pollen spectra. The Eskihisar pollen spectrum represents an 'open bush' landscape (Benda & Meulenkamp, 1990).

Species abundance and extinction

A large number of related and similarly adapted species in a certain habitat indicate obviously that the habitat was favourable to that kind of animals. An optimum in species abundance might, but need not, coincide with a biomass optimum. In Artiodactyla, several examples are known that the geographical positions of such optima in species abundance migrate, apparently due to climatic changes (Van der Made, 1992a). The same principle, but presumably with less resolution, is found in species diversity of higher order taxa, involving more morphological and ecological diversity (Van der Made, 1991b).

In the Lower Miocene of Africa two or three listriodonts in one locality are common, but four (Majiwa) or five (Maboko) may be found. The section at Maboko represents a longer period, but in view of the presence of all of these lineages in younger and older localities, the presence of five sympatric contemporaneous species is well possible. Outside Africa listriodont diversity was lower and three species are found only in Inönü I and two species in few other localities. This suggests that Africa had the most favourable environment for listriodonts.

In Africa species abundance dropped somewhere between about 13.4 and 12.3 Ma from about 5 to 1. In Europe, listriodont diversity dropped from 2 to 1 at the beginning of MN 6; the known area of the *B. latidens*-lineage retracted to Anatolia, where it disappeared later in MN 6 (no MN 6 localities in west and central Europe, but presence in Inönü I, Prebreza, Paşalar and Çandir). The latter event is assumed to coincide with the decrease in tragulid species diversity in Europe from 4 to 1 and the disappearance of crocodiles from central Europe (Van der Made, 1992a, 1993). These events are assumed to have taken place during MN 6. Two more analyses indicate major faunal events at about this time, but are at the scale of MN units and thus do not detect changes as within an MN unit. Between MN 6 and 7, there was a great drop in overall suid diversity in Anatolia (Fortelius *et al.*, in press) and a similar analysis for the primates, rhinos, suoids and carnivores together indicated a similar drop for Europe and Anatolia (Fortelius *et al.*, 1994). The progressive contraction of the areas of geographicalal distribution of crocodiles, tragulids and the *B. latidens*-lineage to the south suggests that a drop in temperature was involved. The distribution of crocodiles is known to be limited by temperature. Benda & Meulenkamp (1990) reported on a drop in temperature between 15 and 13 Ma BP, as indicated by pollen, foraminifera, clay minerals and stable isotopes.

However, it remains unresolved why African listriodont diversity dropped at the same time; equatorial temperatures are bound to have remained high.

Listriodonts disappeared more or less simultaneously everywhere, around the arrival of *Hipparion*. In Europe, the last *Listriodon splendens* is known from Can Llobateres, near the MN 9/10 transition. In Pakistan, *L. pentapotamiae* is known to co-occur with *Hipparion* (Hussain *et al.*, 1977). In Africa, *Lopholistriodon kidogosana* is found in Member D of the Ngorora Formation, which is dated between 9.7 and 9.8 Ma and which has locally the first *Hipparion*. In Europe, the density of data is greatest and indicate that *L. splendens* became extinct a considerable period after the entry of *Hipparion* (the whole of MN 9). At about this time, there was a marked drop in suoid diversity in Europe, but not in Pakistan (Van der Made, 1990a, 1991b). This event has been termed the 'mid-Vallesian crisis'. Fortelius *et al.* (1994) found an MN 9/10 event for the primates, hipparions, rhinos, suoids and carnivores in western Europe, but not in southeast Europe and Anatolia.

In a peculiar way, listriodont diversity reacted more or less simultaneously to not yet understood climatic or maybe predominantly vegetational (?) changes in such very different areas as Europe, Pakistan and Kenya.

PHYLOGENY

Before discussing the phylogeny of the Listriodontinae, I would like to draw attention to some general problems in the reconstruction of phylogenies.

In earlier literature, phylogenetic trees are given without a detailed justification (for suids: Pilgrim, 1926; Colbert, 1935b). Such trees tend to be highly subjective, but we do not want subjective trees. There are several methods that try to minimise subjectivity, cladistics being one of them. The starting point in these methods is the preparation of a data matrix. This involves some decisions that may greatly influence the final results.

One of the decisions is how to treat characters that may be split up or lumped together. For instance, listriodonts evolved lophodonty. This is probably part of a larger set of adaptations, which involved changes in myology and in the structure of the skull, the position of the mandibular condyle and the glenoid etc. However, for the sake of this discussion, a description of the teeth will do. First the anterior lobes of the upper and lower molars and P4 form lophs, then the posterior or second lobes of the upper and lower molars form lophs and in a last stage, the anterior lobes of the P_2 and P_3 form lophs. There are several possibilities to treat this: 1) Each tooth and each step are treated separately. In this case, there are 16 characters; 2) Since the molars seem to do the same thing at the same time, they are treated as a whole; 6 characters; 3) In addition P_4 and P^4 become lophodont at the same time as the anterior lobes of the molars; 4 characters; 4) P_3 and P_2 are synchronous; 3 characters; 5) The animal is lophodont, sublophodont or bunodont; 1 character. The number of characters might be increased easily by increased detail of description of the structures involved. If we choose to treat each character separately or lump related characters, we are giving a weight to complex character of lophodonty, compared to other characters. The consequences of such choices are usually not discussed in the cladistic or morphometric analyses I am familiar with. Although these analyses treat a data matrix in an objective way, subjectivity enters the analysis before this stage.

After preparing a data matrix, all characters are treated as if they are of the same value. This may be a good method when large amounts of data are available which are of equal value (or at least seem to be so to the scientist). But in many cases, some characters could be considered to be of higher value because they are complex structures and unlikely to have evolved in parallel, or because their function is well known and their evolutionary history are well documented. In a data matrix, such characters are easily swamped by others: 1) that are very real but that may have evolved more than once, 2) that are very variable and therefore need larger samples than usually available, 3) that are known in few species only, 4) of which the polarity is debatable, or 5) characters which may be functionally related to other characters, etc. It is of course possible to give more weight to certain characters in a data matrix, but if we start doing that, the objectivity of the method is lost.

In an analysis of higher order taxa, parallels and convergencies are easily recognised, but in closely related species with very similar genes which are subject to similar selection pressures, parallels are expected to be multiple and more difficult to detect. Additional information, such as the age of the remains, observed changes in a species in a sequence of localities etc., frequently are indispensable to detect parallels. Within the Listriodontinae, incisors evolved lower crowns, incisors became wider, the I^1 became bilobed, C_m got a verrucosic section, C^m became more hypsodont, premolars were reduced in size or number, diastemata grew and molars became lophodont more than once. Several of these characters are very useful to recognise stages of evolution or relationships within one tribe or lineage, but if all listriodonts are taken together, there are so many parallels, that they well outnumber unique characters. For instance, if we observe the evolution of lophodonty in two sequences of fossils, one of small species and one of large species, which are found in two different places and in deposits of different ages, we know that the character evolved parallel. In such a case, we would like to use lophodonty to unite certain taxa to each other, but not to others. Such information cannot be put into a common data matrix, but is valuable.

What is rare in neontology, but common in palaeontology: one may observe how evolution proceeds. It can be seen as a gradual change of a character in a sequence of remains of different ages of a single species. This is possible when there is much material of a species; when material is rare, gaps between the various stages of evolution increase and reliability decreases. There are several examples of well-documented lineages in the Listriodontinae. The notion that the polarity of a character determined by using the stratigraphical record, is always suspect (Forey *in* Forey *et al.*, 1992, p. 136) is probably based on examples with many gaps in the record. Trends like the size increase of the incisor in *Listriodon splendens* (Text-fig. 47) seem to me beyond suspicion.

It appears that most well-documented sequences are limited in length, because the species lived in that area only for a limited period, or it became very rare, or because the fossil record of the area is limited. For instance, Lower Miocene localities with large mammals are rare in Turkey, but very common in Africa, for the Middle and Upper Miocene, this is the other way around. Thus it is relatively easy to recognise short pieces of lineage. Here such short pieces of lineage are put together using all available additional data, including data on stratigraphy. This method may seem to be less reliable and to give no lasting or stable results, since any new find may change the picture. But so may inclusion of new species in cladistic analysis (Forey *in* Forey *et al.*, 1992). The main thing that is done here to increase reliability of the phylogenetic analysis is to study as much material as possible and to present and discuss all data used. Where there are few data, it is accepted that reliability decreases, though in any case the most favoured solution is presented.

Justification of the tree

An important part of the phylogenetic analysis appeared in the chapter on systematics. Trends within species were described there, resulting in the recognition of a number of short lineages or sections of lineages. In fact, several lineages were initially recognised as such and only later divided into stages that are described here as species. This is the case with the *B. latidens*- lineage, of which the earlier stage was described as *B. latidens* (Van der Made & Alférez, 1988), but which here is recognised as a different species (*B.* aff. *latidens*). The presentation of data in the figures of the systematic descriptions reflects the recognition of lineages with more than one species (Text-figs 29, 33, 36-39, 40). In this section, these lineages are put together in a tree (Text-fig. 58). Since the tree is a best fit for the available data and since data are not equally available for all taxa, some sections are less reliable.

Some morphometric characters are very important in the evolution of the Listriodontinae, but evolve parallel in different lineages. Text-figure 59 presents a selection of available or representative morphometric values for the incisors and canines, morphological changes in incisors and canines as well as changes in estimated body weight. It can be observed that most characters in the descendance of most species change unidirectionally. This illustrates that these data are useful in assigning a species to a position in a lineage, but that generally these data cannot be used to assign a species to one lineage or another. The tree (Text-fig. 58) is justified in the four following sections, discussing the unity of the listriodonts and each of the three tribes.

Unity of the Listriodontinae

The first assumption in the analysis of the phylogeny of the Listriodontinae is that this group, as it is treated here, is monophyletic. *Kenyasus rusingensis* and *Schizochoerus*, taxa which have been included in Listriodontinae or Kubanochoerinae, are excluded here from the Listriodontinae.

The Listriodontinae share incisors with increased meso-distal diameters and with low crowns (Text-figs 23, 24) and with I^1 that form a straight transverse ridge (Text-fig. 25). This is believed to be a complex of common derived characters uniting the Listriodontinae. Other suids with incisors with increased DMD have incisors with higher crowns and the I^1 are placed in a 'V-shape'.

Gabunia (1960) introduced the subfamily Kubanochoerinae. Because of the protuberances of the skull of *Kubanochoerus*; comparisons were made with Tetraconodontinae. Pickford (1986b, 1988a) separated the Kubanochoerinae and Listriodontinae, but gave no diagnoses of the subfamilies. Pickford (1986b, fig. 81) derived Listriodontinae from Kubanochoerinae, whereas Pickford (1988a, fig. 87) apparently considered them to be of different origin. Pickford (1986) indicated lophodonty as a difference between Listriodontinae and Kubanochoerinae. *Kubanochoerus* shares derived characters with other Listriodontinae and is therefore included in this subfamily. *Kubanochoerus* differs from other listriodonts in a number of derived characters ('horns' in *Kubanochoerus*, lophodonty in *Listriodon* etc.). There is no evidence that indicates that these different derived characters evolved earlier than the derived characters (incisor morphology and morphometry) that are similar in *Kubanochoerus* and other listriodonts. Where evidence is available (*e.g.* in the case of lophodonty), it indicates that derived characters that separate *Kubanochoerus* and listriodonts evolved later than the similar derived characters. Therefore, the derived characters that are similar in *Kubanochoerus* and listriodonts are considered to be common derived characters and as a consequence, Kubanochoerinae are included in the Listriodontinae.

The absence of the foramina lacrimalia is unique or predominant (within Suidae) in the Listriodontinae, though not universal in this group. In skulls of *Kubanochoerus*, *Lopholistriodon* and *Listriodon* such foramina are lacking. However, one skull of *Bunolistriodon* is reported to have one foramen lacrimale (Ginsburg & Bulot, 1987). In Tayassuinae, foramina lacrimalia were present in the Oligocene (Pearson, 1932), but are lost in Recent peccaries. The presence of these foramina may have been variable during the process of reduction, which would explain their presence in this skull of *Bunolistriodon*. In *Hyotherium* there is one foramen lacrimale per orbit. In the Late Miocene hyotheriine *Chleuastochoerus*, there is usually one foramen. However, out of 16 observations in 10 skulls, there are two cases with two foramina on one side and one on the other and two cases with no foramen, one of which is in a skull with one foramen at the other side (Stuenes, pers. comm.). Recent suids usually have two foramina lacrimalia per orbit.

Pickford (1986b) included *Kenyasus* in the Kubanochoerinae on the basis of a number of characters which exclude one subfamily or another. Characters which were cited as uniquely (within Suidae) or predominantly kubanochoerine are: 1) the absence of 'interproximal' wear facets in the I^1 and 2) the shape and orientation of I^2 and I^3. Incisors of early species of the Hyotheriinae (Hellmund, 1991, pl. 7, fig. 1b; Van der Made, 1994, pl. 2, fig. 4c, d), *Conohyus simorrensis* (Lartet, 1851), *Albanohyus*, *Cainochoerus* as well as Palaeochoeridae lack mesial facets and the character is very probably just primitive. The I^2 and I^3 are typically primitive within Suidae and resemble the incisors of early species of *Hyotherium* (Van der Made, 1994a, pl. 1, figs 10, 14; pl. 2, figs 4, 5).

The incisors of *Kenyasus* resemble those of *Albanohyus* and *Cainochoerus* in morphology and in morphometric characters such as index I (Text-fig. 23), DMD' and DLL' (Text-fig. 24) and in being slightly more hypsodont than in Listriodontinae. The premolars of *Kenyasus*, *Albanohyus* and *Cainochoerus* are small relative to the molars. In the most primitive listriodonts, the premolars are large. *Nguruwe*, *Albanohyus* and *Cainochoerus* may well be related to each other.

A skull from the Ngorora Formation (KNM BN 1731) is not a 'tayassuid' (as assumed by Pickford, 1986b) or palaeochoerid, because of the presence of alveoles for two lingual roots per molar and probably belongs to *Albanohyus* (Van der Made, in press). This skull has one foramen lacrimale per orbit. The skull of *Kenyasus* is slightly damaged at the lacrimal, but seems to have a foramen lacrimale. As an isolated case, the presence of such a foramen in this skull is not a strong argument against placing *Kenyasus* in the Listriodontinae, since such a foramen is found in a skull of *Bunolistriodon*. However, the two skulls with foramina lacrimalia of *Albanohyus* and *Kenyasus* somewhat lend support to the idea, that these suids are related to each other and different from listriodonts.

Cainochoerus and *Albanohyus* have never been brought in connection with Listriodontinae (Pickford, 1988a; Van der Made, in press), and are here excluded from that subfamily. There is a certain degree of resemblance between the listriodont incisors and those of this group, but further study has to reveal whether this is a parallel or a common derived character. The possible persistence of foramina lacrimalia would be a difference from the Listriodontinae.

The sublophodont *Schizochoerus* was believed to be a listriodont (Thenius, 1970; Wilkinson, 1976), until Pickford (1978) transferred it to the Tayassuidae, now I place such forms in the Palaeochoeridae.

Lopholistriodontini

The Lopholistriodontini contain two genera with five species (Text-fig. 58), which maintain straight, low crowned C^m (Pl. 1, Fig. 1; Pl. 2, Fig. 1; Pl. 6, Fig. 6), or at least low crowned compared to the C^m of the other listriodonts. *B. anchidens* is the only other listriodont in which a straight low crowned C^m is known. Since outward-curved canines are found in Suidae only, they have to be derived and suids with straight low crowned canines should be primitive suids. The lopholistriodonts retain a small body size, which again is primitive, though of very limited value in phylogenetic reconstructions. The fossils show no unique common derived characters uniting all species. The maintenance of primitive canines, makes it less likely that the younger forms are related to other listriodonts which nearly all have more derived canine morphologies.

Nguruwe kijivium, Lopholistriodon pickfordi and *Lopholistriodon kidogosana* are of the same size (Text-fig. 29) and are found in the same area in successive deposits. They represent a morphological continuum from bunodont to lophodont (see description of the species). Morphological changes are found between and within the species. *N. kijivium* moved towards sublophodonty, *L. pickfordi* towards lophodonty and increased incisor width (informal stages I and II in Text-fig. 58) and *L. kidogosana* reduced the size of the third lobe in the M_3 (stages I and II in Text-fig. 58). Overall, the lineage increased the absolute (DMD, DLL) and relative (DMD', DLL') size as well as the index I of the I^1 (Pl. 1, Fig. 1; Pl. 5, Fig. 13; Text-fig. 59).

L. moruoroti is believed to be an offshoot of this lineage, it is similar in most known characters to *L. pickfordi*, except for its smaller size (Text-fig. 29) and I^1 without distal extension (Pl. 2, Fig. 10). The I^1 remained the same, even in the very youngest locality with the species. The index I of the I^1 remained the same as in *N. kijivium*, but the relative size of the I^1 (DMD', DLL') increased (Text-fig. 59). In both *L. pickfordi* and *L. moruoroti*, the younger samples seem to be 'more lophodont' (stages I and II in Text-fig. 58).

L. akatidogus is nearly lophodont, it has wide incisors like *L. kidogosana* (Pl. 6, Fig. 1) and they share P_2 (Ginsburg, 1977, fig. 1) and P_3 (Pl. 5, Fig. 7) with large metaconid, hypoconid without lingual extension and a deep talonid basin (in Listriodontinae, the P_2 and P_3 tend to have similar morphologies). This premolar morphology is unique in Listriodontinae. *L. akatidogus* is believed to be an offshoot of *L. pickfordi* after the typical incisor and premolar morphologies evolved, or started to evolve, and nearly lophodont molars were attained. First, it became larger than *L. pickfordi* (Text-fig. 29), later it seems to have increased incisor width (Stages I and II in Text-fig. 58).

The Lopholistriodontini are recognised here for the first time as a distinct and monophyletic group. In earlier classifications and phylogenies, some lopholistriodonts have been placed in different positions.

Nguruwe has been placed in the Kubanochoerinae, along with species as *B. affinis* and *B. jeanneli* (Pickford, 1986). *B. affinis* is rather poorly known, but it is only slightly larger than *N. kijivium* and might represent an alternative ancestor to *L. pickfordi*. The still larger, but probably morphologically similar *B. anchidens* shares with Nguruwe the low crowned and straight C^m (Pl. 14, Fig. 7). The incisors of *B. anchidens* are close to those of *Nguruwe* and *L. pickfordi* in their hypsodonty and index I and in that the I^1 has only one lobe (Pl. 4, Fig. 1); these characters are primitive for Listriodontinae. The tendency in *B. affinis-B. anchidens-B. jeanneli* is size increase, rather than decrease. In this lineage, lophodonty developed only after *B. jeanneli* and thus later than in the Lopholistriodontini.

Like *B. affinis*, the small and early *Bunolistriodon*? sp. from Baragoi might be considered a possible ancestor to *Lopholistriodon*. However, it has fully bunodont molars and no wide incisors, and therefore, such a relation seems unlikely.

Wilkinson (1978, fig. 11) placed *'Listriodon' akatidogus* at the root of *Listriodon*, believed *Lopholistriodon* to be closely related to *L. akatidogus* and derived both genera from *Bunolistriodon*. Pickford (1986b) placed *Lopholistriodon* and *Listriodon* in the Listriodontinae and placed *Nguruwe* and what is called here *B. anchidens* in the Kubanochoerinae, but indicated that some of the similarities between *Listriodon* and *Lopholistriodon* might be due to parallel evolution (p. 69). Since lophodonty was attained by *Lopholistriodon* and by *Listriodon* at different times and different places, this important character cannot be used to relate them. Besides, all *Listriodon* and sublophodont *Bunolistriodon* in which the canine is known have a C^m that is hypsodont and curved outwards, in the Lopholistriodontini it is always less hypsodont and (nearly) straight.

The protopreconule is fused to the protocone in Palaeochoeridae, in some Hyotheriinae it is found fused to both cingulum and protocone, and it is fused to the cingulum in all Suidae, except for the Listriodontinae (Van der Made, 1994a). In the Listriodontinae, the protopreconule is fused to the cingulum in bunodont and sublophodont species and to the protocone in sublophodont and lophodont species. Lophodonty is typically attained by forming a crest out of protocone, protopreconule and paracone in a first stage (sublophodonty). In a later stage the same occurs with the tetracone, tetrapreconule and metacone (lophodonty). The molars of *Nguruwe* seem to pass from fully bunodont to nearly sublophodont. This suggests that the lineage was in the process of evolving lophodonty and that the primitive state for the Listriodontinae was fully bunodont. The fact that in *Nguruwe kijivium* the protopreconule became connected to the protocone, suggests that the species is not ancestral to *Bunolistriodon* and *Kubanochoerus*, which either maintain the protopreconule fused to the cingulum or started their evolution with that stage of development.

Kubanochoerini

The Kubanochoerini consist of a single genus and 6 species (Text-fig. 58) which share a gigantic size and C^m that (where they are known) are curved and oriented outward (both are derived) and all species maintain bunodonty (primitive in Listriodontinae). Skulls are known of *K. massai* and *K. gigas* and both have protuberances on the frontals, which is unique in Suoidea. Their premolar rows are very long, which probably is shared also by *Nguruwe* and the bunodont *Bunolistriodon* (*B. affinis-B. jeanneli*) and which appears to be a primitive character in the Listriodontinae. Possible relations with these taxa are discussed later.

K. massai, K. minheensis and *K. gigas* tend to have narrow molars and P_x (Text-figs 30, 31) but P^2 with large protocones (which are thus relatively wide) and short premolars rows compared to *K. marymunnguae* and *K. khinzikebiurus* (Text-fig. 32). Primitive suoids tend to have 'normal' sized premolars and no diastemata. Premolars may become large, as in *Kubanochoerus*. When later premolar size is reduced, diastemata start to develop (Van der Made, 1989b). *K. massai, K. minheensis* and *K. gigas* have long diastemata, in the other species of *Kubanochoerus*, the character is not known. The shorter premolar rows in the former species are probably due to reduction, a trend which can be observed in successive *K. gigas* subspecies: *K. g. gigas* and *K. g. lii* (stages I and II in Text-fig. 58; Text-figs 32, 34).

K. minheensis and *K. gigas* have a palate that extends far behind the M^3, this is not the case in *K. massai*, but it is in *L. kidogosana* and *Listriodon*. The character must have evolved more than once. *K. gigas* resembles *K. minheensis* in most known characters, including larger and wider incisors than in *K. massai* (Tables 11, 12), but it is larger than *K. minheensis* (Text-fig. 30). Within *K. gigas* incisor size increased, M3 increased and premolars became reduced in size (Text-fig. 34). The lack of a real metaconid in the P_4 of *K. gigas* (Pl. 12, Fig. 2) and the presence (though variable) in *K. massai* (Pl. 9, Fig. 5) and *K. minheensis* (Pl. 9, Fig. 19) might indicate that *K. gigas* did not evolve from *K. massai* and that palate morphology and wide incisors evolved parallel to *K. minheensis* and narrow molars parallel to the latter species and to *K. massai.*

K. marymunnguae and *K. khinzikebirus* resemble each other in the maintenance of narrow P^2 and wide P_x and M_x (Text-fig. 32). There is a trend of size increase *K. marymunnguae-K. khinzikebirus-K. mancharensis* (Text-figs 32, 33). Within the last species there is even a marked increase in size (between Nyakach and HGSP 8425; Text-fig. 33); this is indicated as the informal stages I and II in Text-fig. 58. Size increase occurred also in the lineage leading to *K. gigas*, but this species is no likely ancestor for *K. mancharensis* or *K. khinzikebirus* since it is much too late. *K. khinzikebirus* was already large in Gebel Zelten, where *K. massai* is found, *K. gigas* probably evolved from the latter species. Similarly the oldest occurrence of *K. mancharensis* is probably earlier than the appearance of *K. gigas*. *K. marymunnguae* might be the ancestor to both *K. massai* (reduction of premolar size, narrower molars) and to *K. khinzikebirus* (size increase). Alternatively, one of these species might be contemporary with *K. marymunnguae* and the separation of the *K. massai-minheensis-gigas* and *K. khinzikebirus-mancharensis* groups might be older. Early material from Karungu and Mfwangano is very incomplete, but additional collections from these localities might elucidate this part of *Kubanochoerus* phylogeny.

A number of different phylogenies or classifications which imply relations were proposed. Wilkinson (1976) placed all *Kubanochoerus* in *Bunolistriodon*, and supposed the following two lineages *K. khinzikebirus-K. lantienensis-K. gigas* and *K. massai-K. robustus. K. lantienensis* and *K. robustus* are here considered synonyms of *K. gigas* and it is not clear why Wilkinson believed them to belong to different lineages, except for, possibly, the geographical separation. Wilkinson (1978) transferred these species and *B. jeanneli* (including *B. anchidens*) to *Kubanochoerus* and placed all in the Listriodontinae. Pickford (1986b, 1987, 1988a) placed *K. massai, K. khinzikebirus, B. jeanneli* (including what is here called *B. anchidens*) and *B. affinis* in *Libycochoerus* (= *Kubanochoerus*) and included these taxa and *Nguruwe* in the Kubanochoerinae. Pickford (1986b) derived the Listriodontinae from the Kubanochoerinae, but Pickford (1988a) seemed of the opinion that they evolved separately. Qiu *et al.* (1988) placed *B. jeanneli* in *Kubanochoerus* and this genus in the Listriodontinae. The opinion most different from the scheme proposed here is thus: *Kubanochoerus* is related to *Nguruwe* and *B. jeanneli* and these are not closely related to the Listriodontinae. This implies that *B. jeanneli* (or rather *B. anchidens*) might be an ancestor of the large *Kubanochoerus* species.

Pickford (1986b) did not give a diagnosis of Kubanochoerinae (nor of Listriodontinae), but it seems that the flat shape of the I^1 and the absence of mesial wear facets characterises what he sees as Kubanochoerinae. These characters can be seen without problem as primitive characters in the Listriodontinae. *Nguruwe* evolved towards sublophodonty and thus diverged from *Kubanochoerus*. The metaconid of the P_4 in *B. anchidens* suggests that this species evolved towards the sublophodont *Bunolistriodon*, where this cusp is well developed. *K. marymunnguae* did not yet have a metaconid in the P_4, which suggests that an ancestor to *Kubanochoerus* should not have a metaconid. *B. affinis* may have had a P_4 with only a protoconid and might be ancestral to the Kubanochoerinae, though there may as well be an unknown ancestor, *B. affinis* being already on the line towards the Listriodontinae. Evolutionary trends connect the bunodont species of *Bunolistriodon* clearly to other Listriodontinae and the link between the earliest *Kubanochoerus* and other Listriodontinae is still missing.

Listriodontini

The Listriodontini are a large group, consisting of 2 genera and 10 to 12 species. There seems to have been one lineage in *Bunolistriodon* until a radiation occurred. At about the time of this radiation, sublophodonty appeared. *Listriodon* evolved from one of the sublophodont species of *Bunolistriodon*. The sublophodont *Bunolistriodon* (all species younger than *B. jeanneli*) and *Listriodon* share C^m that are hypsodont and that curve outward (Text-fig. 59) and have P^2 and P^3 with lower indices and larger protocones. The bunodont *Bunolistriodon* are connected to sublophodont *Bunolistriodon*, because of general resemblance and because sublophodont species start their development with resemblances to the bunodont species.

B. affinis, *B. anchidens* and *B. jeanneli* are bunodont, have (where known) P_4 with the metaconid close to the protoconid (Pl. 13, Fig. 3; Pl. 14, Fig. 2), long premolars and P^3 with very small protocones or just a wide cingulum at that place (Pl. 14, Figs 8, 10). *B. anchidens* has narrow incisors and, related to that, a narrow symphysis. *B. jeanneli* has also a narrow symphysis. The species show a size increase with decreasing geological age (Text-fig. 36) and seem to be a lineage. No derived character is known from these species that would exclude them as ancestors of the later Listriodontini. In slightly younger strata *B.* aff. *latidens*, *B. lockharti*, *B. akatidogus*, *B. intermedius* and *B. guptai* are found and may be descendants of the *B. jeanneli*-lineage.

Alternatively, (some of) these species might be derived from early *Lopholistriodon*, such as *L. pickfordi* and *L. akatidogus* or from the small *Bunolistriodon*? from Baragoi. However, *B. guptai* seems to be connected to *B. jeanneli* with intermediate fossils. Besides, *L. akatidogus* has an I_2 with too high an index for most species of *Bunolistriodon* and in *Lopholistriodon*, the 'sub-lophs' seem to have become high before lophodonty was attained, whereas in *Bunolistriodon*, they are lower.

The *B. latidens*-lineage, consisting of *Bunolistriodon* aff. *latidens*-*B. latidens*-*B. mediamon* (Text-fig. 58) is fairly well documented. The earliest *B.* aff. *latidens* resembled *B. lockharti* but decreased in size (Text-fig. 40) and increased index 100 La/Po of the C_m (Text-fig. 39), the DMD, DMD' and index I of the incisors (Text-figs 35, 37). In these characters the species evolved towards *B. latidens*, which then continued the trend and started to increase the index I of the cheek teeth (Text-fig. 39). *B. meidamon* formed the culmination of the trend. The changes are gradual (Text-fig. 59), even within one species and there are no indications that this might not represent a single lineage. The earliest *B.* aff. *latidens* may still have bunodont molars (Pl. 16, Fig. 7; Pl. 15, Fig. 8), though in the same sample also sublophodont molars are found (Pl. 16, Fig. 1) and the I^1 is not or not clearly three lobed (Pl. 15, Fig. 16), certainly after some wear (Pl. 17, Fig. 5). In later samples, the molars are sublophodont and the I^3 clearly three lobed. Sublophodont molars and three lobed I^1 were thus not (completely) acquired before *B. lockharti* and the *B. latidens*-lineage diverged. The occasional occurrence of bunodont molars, low index I of the incisors and not very clear separation into three lobes of the I^1 in the earliest samples, links the lineage to the *B. jeanneli*-lineage.

B. lockharti gradually increased the size of its incisors, but the index only very slightly or not at all (Text-fig. 41). This increase in incisor size is indicated as stages I and II in Text-fig. 58, but is not reflected in formal taxonomy. Size and incisor morphometry of the oldest *B. lockharti* samples link this species to the *B. jeanneli*-lineage (Text-fig. 59).

B. akatikubas is very difficult to separate from *B. lockharti*, if at all different. Because of the doubts whether it is really a different species, it is not indicated in Text-fig. 58. It seems to approach slightly more a lophodont condition (Pl. 26, Figs 10, 16), without really acquiring lophodonty (Pl. 16, Figs 6-9, 13). Since the development towards lophodonty is found in so many listriodont lineages, this does not mean that the species is very closely related to the really lophodont *Listriodon*. Since a gradual transition from *B. guptai* into *Listriodon pentapotamiae* is found, and since *B. akatikubas* has I^2 that are larger (more progressive) than those of *B. guptai* and *L. pentapotamiae*, it does not seem likely that *B. akatikubas* has anything to do with the origin of *Listriodon*. If it is different from *B. lockharti*, it must be a local (African) descendant of *B. jeanneli*.

B. intermedius is also a species that, on the basis of available material, is difficult to separate from *B. lockharti*, but additionally its separation from *B. guptai* is not clear. Therefore, it is not indicated in Text-fig. 58. It might be a local descendant which should be traced back either independently or through one of the other sublophodont species to bunodont *Bunolistriodon*.

At the base of the Lower Manchar Formation, huge premolars are found (Pl. 28, Fig. 9) like those of *B. jeanneli*, but the molars in the same strata are sublophodont in an other specimen (Pl. 29, Fig. 10), the P_4 is much smaller and has a morphology that is common in sublophodont *Bunolistriodon*. These specimens, together with the one from Fategad (Pl. 13, Fig. 3) form a gradual transition and indicate a transition from *B. jeanneli* to *B. guptai*. Within the Lower Manchar Formation, the transition from *B. guptai* to *L. pentapotamiae* occurs between HGSP 8222 and HGSP 8125. The lithostratigraphical positions of the HGSP 83 and HGSP 84 localities are not known to me, but they have morphologies that are intermediate between the HGSP 81 and HGSP 82 localities with *Bunolistriodon* and *Listriodon*. The fossils from these localities suggest a gradual transition. Higher in the Lower Manchar Formation the lophs become higher and straighter. Similarly, Kanatti and Mochi Wala in the lower Chinji Formation have some sublophodont specimens (Pl. 29, Fig. 5; Pl. 31, Fig. 8) in samples with mainly lophodont molars. The incisor of *B. guptai* may have been bilobate (Pl. 27, Fig. 7), like in *Listriodon*, but unlike in other *Bunolistriodon*. A transition from the sublophodont *B. guptai* to the lophodont *L. pentapotamiae* seems likely.

The origin of *Listriodon* has attracted much attention and a number of models have been proposed that differ from the model presented here.

One alternative would be to derive *Listriodon* from *Lopholistriodon*, since that genus was on its way to lophodonty long before the transition from *B. guptai* to *L. pentapotamiae*. As a matter of fact, *Lopholistriodon akatidogus* was placed in *Listriodon* (Wilkinson, 1976; Pickford, 1986). *L. akatidogus* is more advanced in I_2 morphometrics than the earliest *L. pentapotamiae* (Text-fig. 59). Since *L. akatidogus* shares its premolar morphology with *L. kidogosana*, this character must be older than the first *L. akatidogus* known and thus must have been present also in later *L. pickfordi*. This implies that both larger *Lopholistriodon* species are no likely ancestors for *Listriodon*. There is quite a stratigraphical and geographical gap between the earliest *Listriodon* on the one hand and *L. moruoroti* and the earlier *L. pickfordi* on the other, as well as a morphological gap (P_4 and incisors).

Leinders (1975, 1976) considered *L. splendens* to be a direct descendant of '*Listriodon*' *lockharti*, which for that reason was placed in the genus *Listriodon*. Part of the material on which that conclusion was based, is placed here in *Bunolistriodon* aff. *latidens* (and the foot bones and a P^4 in *Hyotherium soemmeringi*). Leinders compared only European *Bunolistriodon*, *L. splendens* and *K. massai*. *B. lockharti* and *B.* aff. *latidens* have a tendency to reduce the facet for the second cuneiform on the distal side of the navicular. Or else, the separation of the facets for the second and third cuneiforms becomes invisible. A separate facet for the second cuneiform is very clear in *Listriodon splendens*. These species have three-lobed I^1, which is a derived character, different from the bilobed incisor of *L. splendens*, which is also a derived character. The European species of *Bunolistriodon* resemble European *Listriodon*, but *B. guptai* more closely resembles *L. pentapotamiae*.

L. splendens and *L. pentapotamiae* share a number of characters: lophodonty, a bilobed I^1 (Pl. 30, Fig. 11; Pl. 36, Fig. 1) and I^1, I_1 and I_2 with high values for index I (Text-fig. 44). Since the transition of sublophodont to lophodont occurred in *L. pentapotamiae* and since it tends to be more primitive than *L. splendens* in its smaller incisors and Cm, it is to be expected that *L. splendens* is an offshoot of *L. pentapotamiae*. The earliest *L. splendens* are small (Text-figs 51, 52) and have small incisors (Text-fig. 47) and Cm (Text-fig. 48) and resemble thus (early) *L. pentapotamiae*. Chinese *Listriodon* have small incisors (Text-fig. 55), but with greater DLL than those of *L. pentapotamiae* (Text-fig. 46) and are like early *L. splendens* from Europe. The species seems to be a palaearctic species and its geographical range extended from Europe through central Asia to China and occurred north of the range of *L. pentapotamiae*. *L. splendens* increases the size and index of its incisors (Text-figs 47, 59) and the size and 100 La/Po index of the C_m (Text-figs 48, 59) as well as the width of the upper premolars (Text-fig. 56). In Europe three subspecies are recognised to reflect these stages (stages I-III in Text-fig. 58): *L. s. tapirotherium*, *L. s. splendens* and *L. s. major*. *L. pentapotamiae* decreased in size (Text-fig. 45), developed very high lophs and possibly increased the size of the incisors and index of the I^1. Taxonomically this is reflected in two subspecies (*L. p. pentapotamiae* and *L. p. theobaldi*; stages I and II in Text-fig. 58).

BIOSTRATIGRAPHICAL RESULTS

The biostratigraphy within each area that yielded listriodont remains will be discussed separately. Correlations between these areas will be suggested at the end of the chapter.

Africa and Arabia

The distribution of the African Early and Middle Miocene Suoidea is shown in Text-fig. 60. Three lineages are useful for biostratigraphy: one in *Kubanochoerus*, one in *Bunolistriodon* and one in *Lopholistriodon*.

Kubanochoerus marymunnguae is believed to be ancestral both to *K. massai* and *K. khinzikebirus*. This implies that Gebel Zelten is younger than Buluk and Baragoi, even if *K. marymunnguae* were ancestral to only one of the two. *Kubanochoerus* from Maboko and Nyakach is a descendant of *K. khinzikebirus*, which places these localities above Gebel Zelten. This (Text-fig. 60) corroborates the arrangement of the localities as given by Pickford (1981, 1986b, 1988a).

African ***Bunolistriodon*** has four stages of evolution: *B. affinis* is known from Set I, *B. anchidens* from Set II, *B. jeanneli* from Set IIIA and *B. akatikubas* from Set IIIB and Set IV (Text-fig. 60). Although the changes are probably gradual, the stages of evolution of this lineage are in accordance with the arrangement of the localities in faunal Sets, as based on faunal resemblance (Pickford, 1981). The *Bunolistriodon* from Ad Dabtiyah is sublophodont, suggesting that Ad Dabtiyah is younger than localities with *B. jeanneli*, such as Moruorot, that is Set IIIB or IV.

The succession of localities as based on the ***Nguruwe-Lopholistriodon*** **lineage** is controversial. *Lopholistriodon* is thought to be a descendant of *Nguruwe* and the locality of Kirimun yields a stage between typical *Nguruwe* and the *Lopholistriodon*. Therefore Kirimun should be older than the earliest *Lopholistriodon*, which is probably from Buluk or from Moruorot (Text-fig. 60). Pickford (1981) initially placed Kirimun in Set II, in a 'note added in proof', he changed this into Set III. Matsuda *et al.* (1986) dated a tuff overlying the Kirimun Formation at 15 ± 2 Ma, which is thus a minimum age. Pickford (1986c, tabs 1, 3) placed the locality either in Set IIIA or IIIB. Pickford *et al.* (1986b) placed Kirimun high in Set IIIB. This correlation seems to be based on a series of biozones, the *Brachyodus*, *Hemimeryx*, *Kenyapotamus* and *Hippopotamus* zones, which were used alongside the faunal sets. Each zone comprised the supposed range of a genus, with nearly no overlap in the ranges of the genera. In this scheme, Kirimun, with *Kenyapotamus*, was placed above Maboko, with *Hemimeryx*.

There are three reasons why the presence of *Kenyapotamus* in Kirimun cannot be used to place the locality so high:

1) *Kenyapotamus* is found in older localities. Pickford (1983) mentioned the possible presence of *Kenyapotamus* in Maboko, I have seen specimens from Maboko in the KNM and there cannot be any doubt about their identity, moreover the genus is present in Baragoi.

2) Pickford (1989) derived the primitive hippopotamus *Kenyapotamus* from *Doliochoerus* (a 'tayassuid') via *Xenohyus* (a suid in my opinion, which is known from Europe only). *Xenohyus* is not known from deposits later than MN 3 so there is quite a time gap between the last occurrence of *Xenohyus* and the supposed first occurrence of *Kenyapotamus* (Set IIIB). If one accepts a lineage *Xenohyus-Kenyapotamus*, the presence of *Kenyapotamus* in Kirimun cannot be used to assign this locality an age that is much younger than the last record of *Xenohyus*.

3) Coryndon (1978) described a hippopotamid tooth from Rusinga, which is very similar to *Kenyapotamus*. Pickford (1983) mentioned the specimen, but believed it a to be a bunodont anthracothere. However, the specimen has resembles both *Kenyapotamus* and anthracotheres and seems a real link between the two groups. Pickford (1983, 1989) used the absence of morphologies intermediate between anthracotheres and hippos as an argument against the descendance of hippos from anthracotheres.

The only indication for a maximum age of Kirimun remains the intermediate *Nguruwe*, which seems to be the ancestor of *Lopholistriodon*. This would place Kirimun above Mfwangano and Rusinga but below Buluk and Moruorot (Text-fig. 60).

The stratigraphical arrangement of localities as suggested by later stages of the *Nguruwe-L. pickfordi-L. kidogosana* lineage is conform to the succession based on other criteria (Pickford, 1986c). Probably there is an increase in incisor width (DMD) from Maboko to Majiwa and certainly to the Ngorora Formation. This observation has potential for biostratigraphy. The transition of *L. pickfordi* to *L. kidogosana* is gradual and occurs at the transition of Set IV to V (Text-fig. 60). Reduction of the third lobe of the M_3 in *L. kidogosana* occurs between the members B and D of the Ngorora Formation.

Pakistan and India

Representatives of three listriodont lineages are known from Pakistan and India, *viz.* of the *Kubanochoerus mancharensis*, the *K. gigas* and *Bunolistriodon-Listriodon* lineages.

The ***Bunolistriodon-Listriodon*** **lineage** (Text-figs 36, 45) is represented by several stages. *B. affinis* is found in Bugti and *B. jeanneli* in Fategad. Fategad must be considerably younger than Bugti. At the base of the Lower Manchar Formation, *B. guptai* has been found.

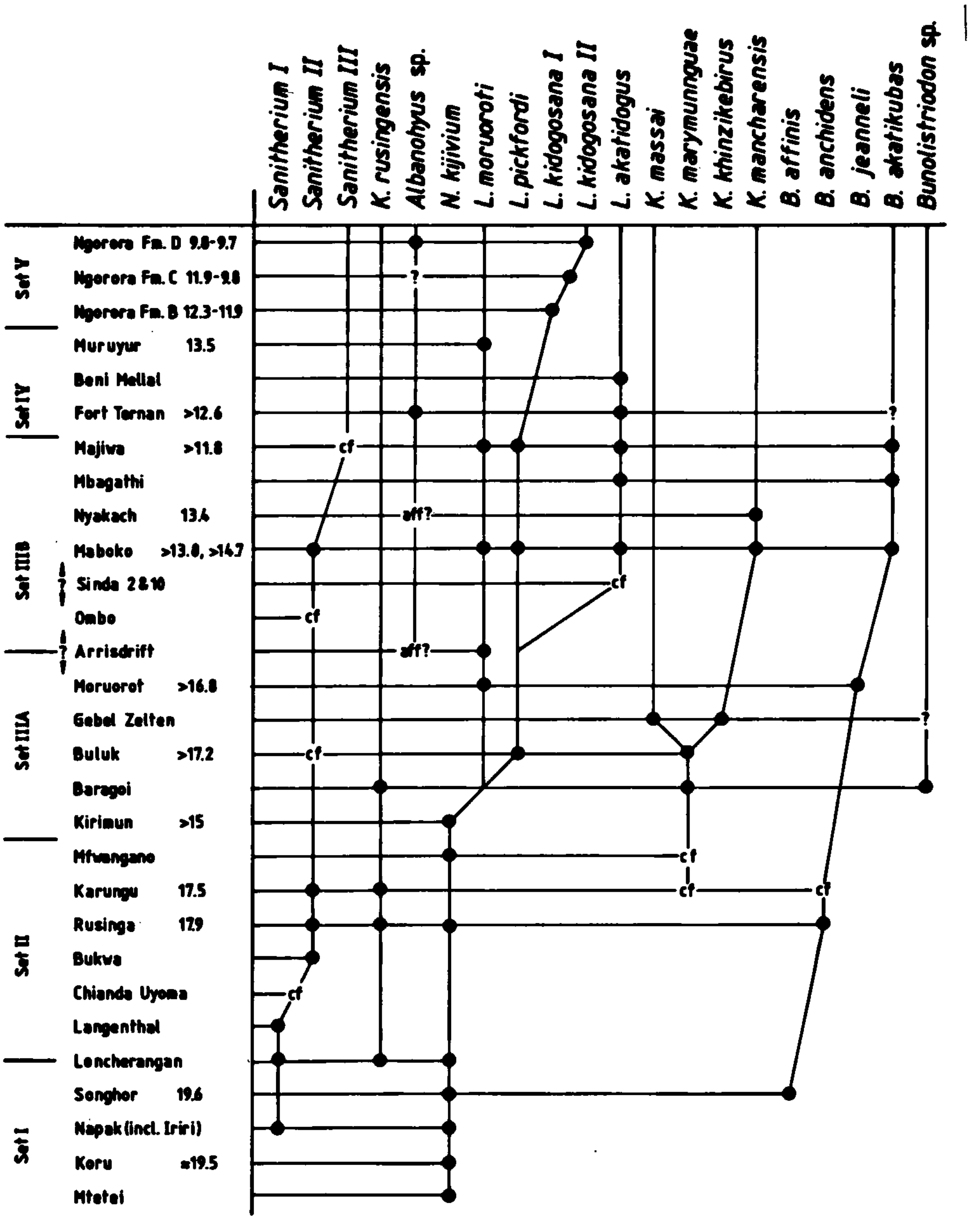


Fig. 60. Stratigraphical distribution of early and middle Miocene African Suoidea, including *Sanitherium*, *Kenyasus rusingensis* and *Albanohyus*, which are no Listriodontinae, but excluding *Kenyasus namibensis*. I have not had the opportunity to examine specimens of this (rare) species. Faunal sets according to Pickford (1981, 1986a, b) and Pickford *et al.* (1986a), except for Beni Mellal, Sinda, Arrisdrift and Loncherangan. Behind the localities, radiometric dates are given (after Pickford, 1986c; Feibel & Brown, 1991; Boschetto *et al.*, 1992). Sequences within faunal sets are in some cases adopted from Pickford (op. cit.), as in the case for Muruyur and Fort Ternan. 'Napak (incl. Iriri)' stands for the Iriri Member at Napak with a sanithere and the overlying Napak Member with *N. kijivium* (Pickford *et al.*, 1986a). Oblique lines indicate presumed ancestor-descendant relations between the taxa. *Sanitherium* I-III refers to evolutionary stages of Van der Made & Hussain (1992) and Van der Made (1992b).

The morphology of these specimens is still close to *B. jeanneli*. The base of the Manchar Formation should therefore be younger than, but close to, Fategad. Higher in the Lower Manchar Formation (between Sandstone Units 3 and 4), the transition to *Listriodon pentapotamiae* occurs. The localities of Kanatti and Mochi Wala near the base of the Chinji Formation near Chinji have still sublophodont specimens in otherwise primitive lophodont *Listriodon* samples. *B. guptai* is not known from the Chinji Formation. The appearance, by evolution, of *Listriodon* thus coincides with the base of the Chinji Formation, which can be correlated to a level in the Manchar Formation between Sandstone Units 1 and 3, where the *Bunolistriodon-Listriodon* transition is found. According to Barry & Flynn (1990), the entry of a number of bovids including *Sivoreas* occurred at 13.8 Ma. Kanatti and Mochi Wala have very primitive *Sivoreas* (Van der Made & Hussain, 1994). The transition from *Bunolistriodon* to *Listriodon* should thus be close to 13.8 Ma.

Two stages of evolution of *K. mancharensis* are found in the Gaj River section of the Lower Manchar Formation and increase in size from unit 1 to localities above unit 3, where *K. mancharensis* is associated with *Listriodon*. The largest suid molar known is from the old collections from Bugti and it represents the later stage of evolution of *K. mancharensis*. This corroborates Pickford's (1988a, b) conclusion that fossils of Chinji age are present in the old Bugti collections.

K. g. gigas is known from the Chinji Formation, but without locality data. In the Upper Chinji of Kundal Nali *K. gigas* has been found, but the stage of evolution can be assessed on the basis of age only and should be *K. g. lii*, since Kundal Nali is in the Upper Chinji Formation and younger than Chinese localities with *K. g. lii*. The transition from one subspecies to the other should thus occur in the Chinji Formation.

Europe and Anatolia

In Europe the entries of *Bunolistriodon lockharti* and *Listriodon splendens* have been considered to be of stratigraphical importance. During the period that Artenay was placed in MN 3, the base of MN 4a was taken as the entry of *Deinotherium*, *Bunolistriodon*, *Dorcatherium*, *Schlossericyon*, *Megacricetodon*, *Democricetodon*, *Fahlbuschia*, *Eumyarion*, *Neocometes* and *Spermophilinus* (Mein, 1979). Now Artenay is again placed in MN 4 and the first appearance in West and central Europe of most of these species is within MN 4 (Mein, 1990; De Bruijn *et al.*, 1992). Mein (1979) considered the transition from MN 5 to MN 6, or from Orleanian to Astaracian, to be indicated by the extinctions of *Cynelos*, *Bunolistriodon* and *Cainotherium*. The latter genus, is now known to have ranged into MN 6 in Germany (Heizmann, 1983). *Listriodon* replaced *Bunolistriodon*. *Listriodon* is the only genus listed by De Bruijn *et al.* (1992) that appeared simultaneously in France and Spain and in central Europe in MN 6. For that reason it would be an useful indicator for MN 6 in these areas.

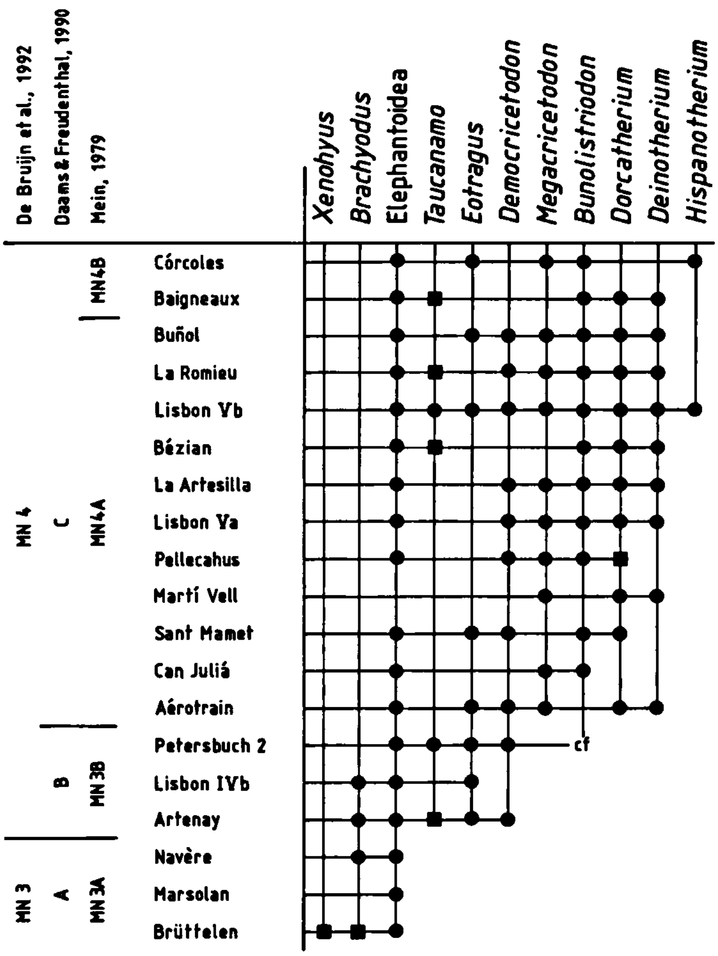
In this section the topics to be treated are: the precise entries and exits of the species of *Bunolistriodon* and *Listriodon* in Europe and Anatolia; whether these are isolated events or whether they are associated with other dispersals; the biostratigraphical value of listriodonts in some particular localities.

It is not clear whether the **entry of *Bunolistriodon*** involved one or two species. However, from localities that are only slightly younger than the entry it is known that there are two *Bunolistriodon* lineages (for instance different species in La Artesilla and Pellecahus). Initially both lineages were very similar in size (Text-fig. 40) and morphology and it is (at present) impossible to recognise whether there was one entry and subsequent speciation or two separate entries. Trends in the evolution of *Bunolistriodon* (Text-figs 37, 39-41) suggest that La Artesilla, Lisboa Va and Pellecahus are among the earliest localities with *Bunolistriodon*. Localities with large mammals that are placed in MN 4, which could be older are Quinta do Narigao (Lisbon IVb), Can Julià, Sant Mamet, Rubielos de Mora, Villafeliche 2A, Artenay, Aérotrain and Petersbuch 2. In the following paragraphs, the stratigraphical position of these localities, relative to La Artesilla, Lisboa Va and Pellecahus will be discussed, with the aim of obtaining a more precise indication of the entry of *Bunolistriodon* and the accompanying fauna.

Ginsburg (1990) proposed a subdivision of MN 4 in three units for the Loire Basin: the Artenay Group (with the entries of: Elephantoidea, *Eotragus*, '*Albanohyus*' — here called *Taucanamo* — and other taxa), the Aérotrain Group (with the entries of *Deinotherium*, *Dorcatherium* and others) and the Baigneaux Group (with the entries of *Bunolistriodon* and others).

Daams & Freudenthal (1990) discussed the 'cricetid vacuum'. In zone Z of the Ramblian or MN 3a the cricetids became rare in Spain, but also in other parts of Europe, the last cricetids being *Eucricetodon* and *Melissiodon*. During MN 3b or zone A, there were nearly no cricetids in southwest and central Europe. Zone B has the entry of *Democricetodon* and zone C of *Megacricetodon*, *Fahlbuschia* and *Eumyarion* (Daams & Freudenthal, 1988). The Spanish localities of zone B have few or no large mammals. The locality of Petersbuch 2 was placed in zone B.

The distribution of *Democricetodon* and *Megacricetodon* (indicators for zones B and C) and various large mammals (Text-fig. 61) show that in many places the record is still incomplete as already noted by Daams & Freudenthal (1990).



De Bruijn et al., 1992	Daams & Freudenthal, 1990	Mein, 1979		*Xenohyus*	*Brachyodus*	Elephantoidea	*Taucanamo*	*Eotragus*	*Democricetodon*	*Megacricetodon*	*Bunolistriodon*	*Dorcatherium*	*Deinotherium*	*Hispanotherium*
MN 4	C	MN4B	Córcoles			●		●		●	●			●
			Baigneaux			●	■				●	●	●	
		MN4A	Buñol			●		●	●	●	●	●	●	
			La Romieu			●	■		●	●	●	●	●	
			Lisbon Vb			●	●	●	●	●	●	●	●	●
			Bézian			●	■				●	●	●	
			La Artesilla			●			●	●	●	●	●	
			Lisbon Va			●			●	●	●	●	●	
			Pellecahus			●			●	●	●	■		
			Martí Vell							●		●	●	
			Sant Mamet			●		●	●		●	●		
			Can Julià			●				●	●			
			Aérotrain			●		●	●	●		●	●	
	B	MN3B	Petersbuch 2			●	●	●	●		cf			
			Lisbon IVb		●	●		●						
			Artenay		●	●	■	●	●					
MN 3	A	MN3A	Navère		●	●								
			Marsolan			●								
			Brüttelen	■	■	●								

Fig. 61. The distribution of various taxa in European localities of about the age of the entry of *Bunolistriodon*. Data from: Agustí *et al.* (1984): Can Julià, Sant Mamet, Marti Vell; Alférez *et al.* (1982): Córcoles; Antunes (1984): Lisbon IVb, Va, Vb; Bulot & Ginsburg (1993): Marsolan, Navère, Artenay, Pellecahus, Bézian, La Romieu; Ginsburg (1990): Artenay, Aérotrain, Baigneaux; Heissig (1978): Petersbuch 2; Studer (1896): Brüttelen. The squares represent changes and additions based on other literature sources and personal observations. Biozones and MN units as approximately intended by those authors. Not all localities are named by all authors and some would be placed in other positions. This is in particular the case with Córcoles (see discussion at the end of the section on biostratigraphical results from Europe and Anatolia).

The presence of *Megacricetodon*, *Deinotherium* and *Dorcatherium* indicate that Aérotrain is younger than Petersbuch 2, whereas the possible presence of *Bunolistriodon* would make Petersbuch 2 younger (Heissig, 1978, listed a cf. *B. lockharti*; other large suids of approximately this age are *H. soemmeringi* and *Xenohyus*).

If either *Deinotherium*, *Dorcatherium* or *Bunolis-*

triodon is absent or present in a much greater number of localities of this approximate age, the bias might be caused by different stratigraphical distributions (or by ecology or taphonomy). At present there is little indication for such a bias: they seem to co-occur quite often (Text-fig. 61, localities older than Pellecahus were not selected on the presence of *Bunolistriodon*, but on being older than Pellecahus but still MN 4).

Lisbon IVb has the first local record of Elephantoidea but does not have *Democricetodon*, *Megacricetodon*, *Bunolistriodon* and *Deinotherium*, which are present in Lisbon Va (Text-fig. 64). Lisbon IVb overlies marine sediments with N7 foraminifera and is overlain by sediments with N8 fauna (Blow zonation). Lisbon Va is in continental sediments within the N8 zone (Text-fig. 64). Haq *et al.* (1987) indicated the global sequence: N7 fauna — regression — N8 — regression — N9. So there is no global regression within N8. A possible explanation is that the extra local regression with the Lisbon Va fauna is caused by the interplay of subsidence and sedimentation. There are foraminifera of zone N7 below Lisbon IVB and of N 8 above (Antunes, 1984, 1990). Can Martí Vell, Sant Mamet and Can Julià have (composite list) *Democricetodon*, *Megacricetodon*, *Deinotherium* and *Bunolistriodon* and are overlain by marine sediments with N 8 foraminifera (Anglada & Martín, 1971; though cited as N7-8 by Agustí *et al.*, 1984). The marine sediments overlying Lisbon IVb and Can Martí Vell, Sant Mamet and Can Julià probably belong to the same transgression and as a consequence, these mammal localities have the same minimum age. If this is the case, the record in the Lisbon IVb localities is incomplete.

There is one citation of a very old *Dorcatherium* from Molí Calopa, MN 3 (Agustí *et al.*, 1984). However, the large mammals are indicative of a more recent age and the list of rodent species is short (3) which may explain the lack of modern cricetids.

In the Aragonian type area, there are few localities belonging to zone B, and in general there are few localities with large mammals of zone B, suggesting that the time represented by this zone is short. The available data (Text-fig. 61) suggest that *Democricetodon*, *Taucanamo* and *Eotragus* entered western Europe simultaneously (zone B, transition MN 3-MN 4) and a little later, *Megacricetodon*, *Bunolistriodon*, *Dorcatherium* and *Deinotherium* also appeared simultaneously (zone C).

The last *Bunolistriodon* is of the *B. latidens*-lineage. The relative ages of the localities follow from the evolutionary trends in *Bunolistriodon* (Text-figs 37, 39) and for the earlier part of this lineage (Text-fig. 40) as well as trends in other species in the same localities (Van der Made, 1993). *B. latidens* disappeared from west and central Europe after MN 5, but persisted in southeastern Europe and Anatolia. The last *Bunolistriodon* is from Çandir (MN 6) and is found together with *Listriodon splendens*. The *B. latidens*-lineage was highly specialised and smaller than *L. splendens*, suggesting that there was no direct competition and the extinction of the former is not related to the entry of the latter. The localities of Çandir and Paşalar have both hominoids and have therefore received much attention. Çandir is believed to be the younger locality, yet few arguments have been put forward for this relative age. The trends in the *B. latidens*-lineage (Text-figs 37, 39) indicate that Çandir is really the younger locality.

The last *Bunolistriodon lockharti* is from MN 5 (Pontlevoy, Tavers, Ravensburg). *B. lockharti* is of the size of *L. splendens* and close in degree of lophodonty. The incisors and canines of the last *B. lockharti* are comparable in size to those of the earliest *L. splendens*. It seems plausible, that these two species are ecologically exclusive: the entry of *L. splendens* meant probably the (geologically speaking) immediate extinction of *B. lockharti*. There are two possible cases of *B. lockharti* in MN 6, which will be discussed below.

For **the age of Neudorf-Sandberg** (Dvinská Nová Ves) two taxa have predominantly been cited: *Bunolistriodon lockharti* and *Protragocerus* (Mein, 1986; Thenius, 1952). *Bunolistriodon* would place the locality in MN 5 or 4, *Protragocerus* would place it in MN 7 or younger. The locality was first placed in MN 6 as a compromise. The locality is in marine sands which overlie the three nearby fissures of Neudorf-Spalte. These localities have attracted much attention because they have hominoids and because of the possibility to correlate continental and marine stratigraphical scales.

The Neudorf sands are said to have yielded foraminifera of N9/13 and nannofossils of NN6/7 (Mein, 1986). This would favour placing the locality in MN 7+8 rather than in MN 5. However, Bernor *et al.* (1990) and Chica *et al.* (1972) did neither mention N9/13 foraminifera, nor nannoplankton, but *Bulimina-Bolivina* Zone. Chica *et al.* (1972) correlated a transgressive event to this foram zone and indicated that the mammal locality is in sands produced by the same transgression, but did not indicate that the forams are from the same locality as the mammals. Before forams can be used in dating Neudorf, it has to be clear what forams there are and where they come from.

The bovid teeth from Neudorf-Sandberg are very fragmentary and are not very useful in a discussion on the age of the locality. Bovids with teeth of same approximate size include *Tethytragus* (formerly *Caprotragoides*; Azanza & Morales, 1994) from Arroyo del Val VI and Manchones I (MN 6).

In any case, Neudorf-Sandberg is usually placed in MN 6 or later, too late for *B. lockharti*. To solve the problematic presence of *B. lockharti*, it has been proposed that the specimens are reworked. However, the solution is much simpler, the suid is *Listriodon splendens.*

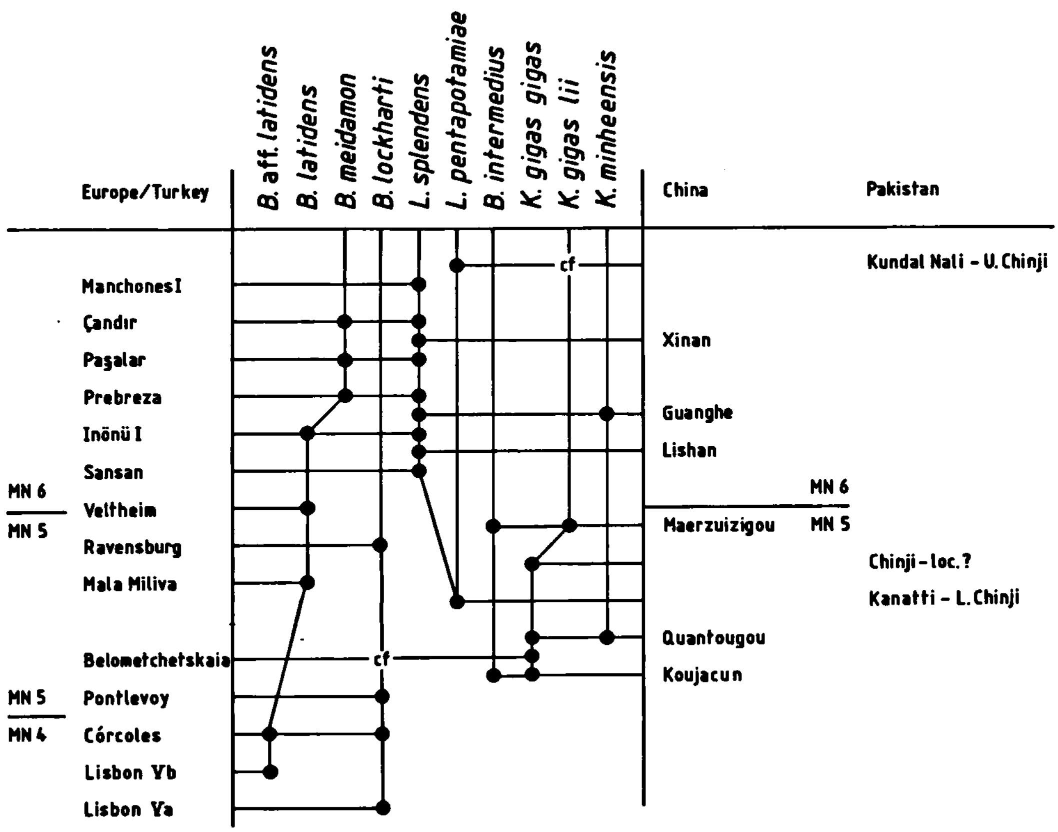


Fig. 62. Stratigraphical positions of listriodonts that illustrate correlations between Europe and Turkey and between these two as a whole, China and Pakistan. The selected localities are in sequence after their placement in MN units (Europe) or lithostratigraphy (Pakistan-IVAU catalogue) and the evolutionary stage of listriodonts (Europe, Pakistan and China). Guanghe is added to illustrate that *Listriodon* and *K. minheensis* had overlapping ranges. The position of Guanghe relative to Xinan and Lishan is not known to me.

An I_1 in the NMW labelled 'A. d. alten Sammlung - Mioc? - ?Neudorf?' is clearly larger than those from Paşalar and Çandir and most of those from La Grive, suggesting a younger age (Text-fig. 47).

In **Georgensgmünd**, *Bunolistriodon* sp. has been found (Pl. 22, Fig. 10) and the locality is usually placed in MN 6 (Mein, 1990; De Bruijn *et al.*, 1992). Ginsburg & Heintz (1966) have shown that there is a size increase in *Palaeomeryx* from MN 4 to MN 6 and that all material from Georgensgmünd (the type material of *P. kaupi* Von Meyer, 1834 and *P. bojani* Von Meyer, 1834) is within the range of variation of the samples from Artenay, Bézian and Baigneaux (MN 4) and smaller than those from Pontlevoy (MN 5), Göriach and Sansan (MN 6). *P. kaupi* was taken as representative of the Burdigalian. Since then, more *Palaeomeryx*-like fossils have been found (Astibia, 1987), but small specimens remain restricted to older deposits. These data are certainly not in support of placing Georgensgmünd in MN 6, but suggest MN 4 or early MN 5.

The oldest locality with *L. splendens*. As indicated by lithostratigraphy (Ginsburg, 1971), Sansan is the oldest of a series of localities with *Listriodon splendens* in that area. Evolutionary trends show it to be one of the most primitive European *Listriodon* (Text-figs 48, 50-52, 55, 56). This would mean that Sansan is one of the oldest localities in MN 6. This is substantiated by trends in *Taucanamo* and *Eotragus* and comparisons with localities that have also representatives of the *Conohyus*, *Tethytragus* (was: *Caprotragoides*) and *B. latidens*-lineages (Van der Made, 1993).

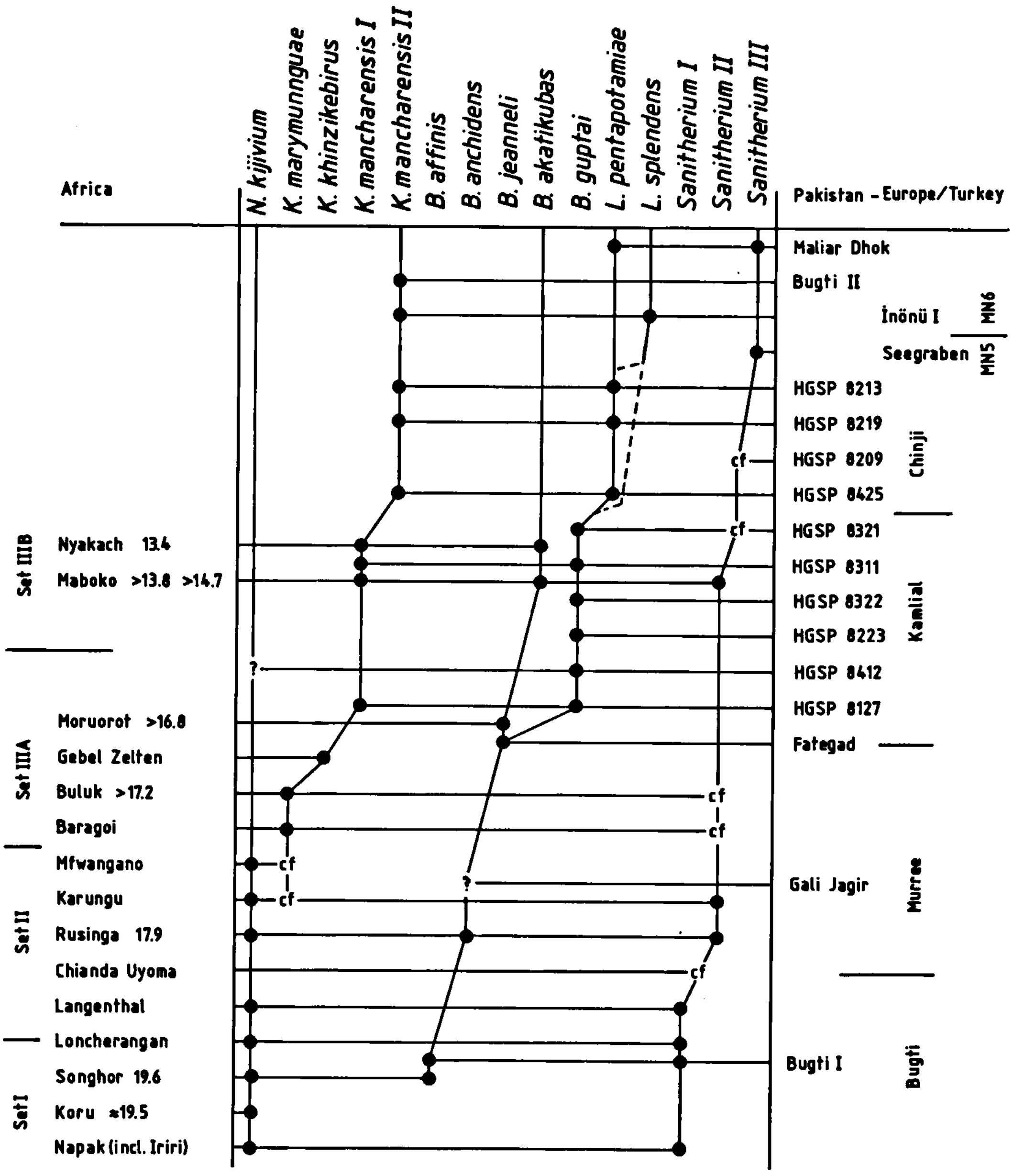


Fig. 63. Stratigraphical distribution of the Listriodontinae which have a bearing on correlation from Africa to Pakistan and India as well as of three stages of evolution of *Sanitherium* (according to Van der Made & Hussain, 1992 and Van der Made, 1992b). Faunal sets as in Figure 4.1. Stages or time equivalent formations for the localities of Pakistan and India are largely as indicated by the suoids. Bugti II refers to material from old collections from the Bugti area, of which the exact provenance is not known, but which is assumed to be much younger than the typical Bugti fauna. Oblique lines indicate presumed ancestor-descendant relations between the taxa. *K. mancharensis* I and II represent subsequent stages of evolution. The positions of the HGSP 81 and 82 localities according to lithostratigraphy; the positions of the 83 and 84 localities on the basis of evolutive stage of the listriodonts. Two localities in Europe and Turkey are included to indicate the age significance of taxa relative to the MN scale. Their positions relative to the upper part of the HGSP sequence, which is kept together, are probably too high in the figure, but their exact positions are not known. The same is the case with the 'Bugti II' and Maliar Dhok localities. Inönü I, Maliar Dhok and Bugti II should be above the HGSP localities with *B. guptai* and Seegraben above Maboko.

The last occurrence of ***Listriodon splendens*** is in MN 9. Agustí *et al.* (1984) divided MN 9 in two parts, with Can Ponsic and Can Llobateres (with *Listriodon*) in the upper part, the *Cricetulodon* Zone. In the Valles Penedes, *Parachleuastochoerus huenermanni* (Heissig, 1989), a small suid found in Can Ponsic and MN 8 localities, is followed by the still smaller *P. crusafonti* Golpe Posse, 1972, which is found in Can Llobateres and La Tarumba, which is placed in MN 10 (Van der Made, 1990a). Several MN 9 localities with *Listriodon* have *P. huenermanni* (Wissberg, Santiga, Hostalets, Can Ponsic), whereas others have *Anchitherium* (Antunes *et al.*, 1983), which is often taken as indicative of only the earlier part of MN 9. The locality of Can Llobateres, must be one of the youngest with *Listriodon*. It seems to be very close to the MN 9-MN 10 transition. *Listriodon* thus became extinct at the MN 9-10 transition.

At **St. Stefan** in Austria, *Dryopithecus* was found along with some other mammalian remains. The fauna seems to have been dated largely on the size of its *Anchitherium* and indirect correlations with marine sediments (Mein, 1986). Mottl (1957) gave the sizes of the C_m: Li = 24 mm, La = 20 mm, Po = 18 mm and the I_2, DMD = 15 mm ('lang'), DLL = 12 mm ('dick') of the *Listriodon* from St. Stephan. These values do not seem to be in support of an age as young as or younger than Sant Quirze (compare Text-figs 47 and 48) and therefore, the *Dryopithecus* from St. Stefan might be one of the older representatives of the genus in Europe.

Bach (1908) gave the sizes of a *Listriodon* C_m from **Löffelbach**: Li = 29 mm, La = 24, Po = 22. These measurements indicate an age comparable to Sant Quirze or younger (Text-fig. 24), that is MN 8.

Córcoles is treated here as considerably younger than La Artesilla (Text-figs 40, 61). However, the whole rodent faunas indicate that Córcoles belongs to zone C and Tarazona to zone D (Daams, pers. comm.). The position of Córcoles in this study is tentatively based on trends in the size of the postcranial skeleton, relative size and index I of the incisors and the index 100 La/Po. If allowance is made for a greater variability in the characters, the position of the locality can be shifted. It seems likely that Córcoles is older than Tarazona, but its exact position relative to other localities in this study can only be discussed when the abundant *Bunolistriodon* material from Córcoles is published.

Correlations Europe/Anatolia-China

The Chinese *Bunolistriodon intermedius* is very similar to and possibly conspecific with *B. lockharti*. *Listriodon* from China is very similar to European *Listriodon splendens* and is believed to belong to the same species. It has been argued above, that *B. lockharti* and *L. splendens* were never found in the same locality and that they were very probably ecologically exclusive. This applies also to the Chinese situation. Localities with *Listriodon* are believed to be younger than those with *B. intermedius* (Text-fig. 62). This implies that the locality of Erlanggang is older than previously assumed (Qiu, 1990).

L. splendens, which has incisors and canines that increased in size, is believed to be an offshoot of *L. pentapotamiae*, which has smaller incisors and canines. Therefore, the earliest *L. splendens* is expected to have had very small incisors and canines. *Listriodon* from Lishan, Tung Sha-po and Xinan have small incisors (Text-fig. 55) and a canine from Lishan is very small. These localities have probably very early *L. splendens*.

It has been proposed that *B. intermedius* was an intermediate form between *Bunolistriodon* and *Listriodon*. This and the presence of very primitive *Listriodon splendens* in China, raises the question, whether the entry of *Listriodon* might not be earlier in China than in Europe. *Kubanochoerus* may help to answer this question.

Kubanochoerus g. gigas evolved into *K. g. lii*. At Maerzuizigou (Tongxin), the latter subspecies is found along with *B. intermedius* (Text-fig. 62). Belometchetskaia is usually placed in MN 6 and has *K. g. gigas* and thus should be older than Maerzuizigou. Either the age of Belometchetskaia must be greater than previously thought or it has to be assumed that *Listriodon* entered later in China than in Europe. It is assumed here that the entry of *Listriodon* was synchronous and that Belometchetskaia should be placed in MN 5 (Text-fig. 62).

In large mammals, the MN 5-MN 6 transition is mainly recognised by the entry of *Listriodon splendens* and in small mammals by stage of evolution of lineages. If the dispersal of *Listriodon splendens* is synchronous, it is a good marker for correlation over long distances in Eurasia for the MN 5-6 or Orleanean-Astaracian transitions.

The correlation of the replacement of *Bunolistriodon* by *Listriodon* in Europe and China implies that Maerzuizigou (Tongxin), which has *Bunolistriodon*, is older than previously thought. In Maerzuizigou *Pliopithecus* was found (Harrison *et al.*, 1991) and it was believed to be as old as MN 6 and younger than the pliopithecids from Elgg, Trimmelkam, the Faluns de Touraine et de l'Anjou, Pontlevoy and Neudorf Spalte. Elgg has a *Conohyus* that is more progressive than that of Göriach, which is commonly placed in MN 6 (Van der Made, 1993). Ginsburg (1986) placed Trimmelkam in MN 6 and Ginsburg (1990) subdivided MN 5 into three levels, Pontlevoy and the Faluns being placed above Tavers. All this would imply that *Pliopithecus* from Maerzuizigou is one of the oldest pliopithecids known.

Correlations Africa-Pakistan/India-Europe/Anatolia

For the correlations between these areas, the stages of evolution of *Sanitherium* are used in addition to the listriodonts (Text-fig. 63). Basically, the three stages of evolution of *Sanitherium* used are those recognised by Van der Made & Hussain (1992), which scheme was modified after Pickford (1984). There is an important exception; the *Sanitherium* from Maboko has been recognised as belonging to the second stage of evolution in stead of the third (Van der Made, 1992b). There are still nomenclatorial problems, thus the stages are numbered and no species names are applied.

Bunolistriodon affinis (Bugti and Songhor, Set I) evolved into *B. anchidens* (Rusinga, Set II). *Sanitherium* I is found in Bugti and in Set I and in the oldest localities of Set II (Text-fig. 63), it is replaced by the next evolutionary stage in Sets II and III. Both observations coincide in that Bugti should be older than Rusinga.

B. jeanneli, found in Moruorot and Fategad, is derived from *B. anchidens*, which is found in Rusinga (17.9 Ma old), implying that Fategad should be younger than Rusinga (Text-fig. 63).

B. jeanneli is believed to be ancestral to *B. guptai* in the Indian Subcontinent, the transition is found at the base of the Manchar Formation, and to *B. akatikubas* in Africa, found in Maboko. This suggests that the Manchar Formation and Maboko are younger than Moruorot and Fategad (though the transition need not be synchronous in both areas).

K. khinzikebirus, which is found in Gebel Zelten, is believed to have evolved into *K. mancharensis*, which is present in Maboko, Nyakach and the base of the Lower Manchar Formation. This implies that Gebel Zelten should be older than Maboko, Nyakach and the Lower Manchar Formation (Text-fig. 63).

K. mancharensis increased greatly in size. At the base of the Manchar Formation and in Maboko and Nyakach it is still small, but it is much larger ar higher levels in the Manchar Formation, where it co-occurs with *L. pentapotamiae*, and in Inönü I, where it is found with one of the earlier *L. splendens*. This indicates that Maboko, and probably Nyakach, are older than MN 6. *L. splendens* is believed to be an offshoot of early *L. pentapotamiae*, therefore MN 6 should be younger than beds of the Manchar Formation with *L. pentapotamiae* and thus the base of the Chinji Formation and Nyakach and much younger than Maboko. Maboko has a stage II and Seegraben (MN 5) a stage III *Sanitherium* (Text-fig. 63), indicating that Maboko is even older than at least a part of MN 5.

The occurrence of *K. g. gigas* in the Chinji Formation (which is however only indicated by a specimen bought from locals), where *L. pentapotamiae* replaced *B. guptai*, and the transition of this subspecies to *K. g. lii* in strata predating the entry of *Listriodon splendens* (Maerzuizigou, Tongxin) supports the view that the earliest *L. pentapotamiae* is older than the first *L. splendens* and that the latter species evolved from an early population of the former. For these reasons, the base of the Chinji Formation should be older than the MN 5-MN 6 transition (Text-fig. 62).

PALAEOBIOGEOGRAPHY AND DISPERSAL EVENTS

Extant mammal communities are grouped as the Palaearctic fauna province (the major parts of Eurasia and North Africa), the Ethiopian province (Africa south of the Sahara and part of the Arabian peninsula) and the Oriental province (Pakistan, India and southeast Asia). This configuration had not yet fully developed during the Miocene. Palaeogeographical reconstructions, such as those by Rögl & Steininger (1983), Steininger & Rögl (1985) and Steininger *et al.* (1985) show that there were several areas or subcontinents that were separated by sea during periods of a high eustatic sea level and connected when the sea level was low. Through tectonics and sedimentation, landmasses became connected when time proceeded. The limits of the bioprovinces probably were different, certainly during periods of high sea level. Africa and Arabia, south eastern Europe and Anatola, and northern Eurasia were separate blocks during the Early Miocene (Rögl & Steininger, 1983).

The SE European and Anatolian subcontinent was intermittently connected to central Europe to the north, to Africa through an area that now includes the Lebanon and Israel, to the south, or to Pakistan and India through what is now Iran, to the east (Text-fig. 65a-d).

Iran, Afghanistan, Pakistan and India probably formed one block, but the fossil record is mainly from Pakistan, so this remains an assumption. This block seems to have been isolated from central Asia by the Himalayas and the Paratethys in the north. There may have been a migration route from the east of India to Asia. However, the record of large mammals suggests that there was few or no limited direct faunal exchange between these areas. Chinese Miocene localities, for instance, yield many cervids, *Palaeomeryx*, the horse

Anchitherium and tapirs, but these are not known from the Miocene of India and Pakistan. *Deinotherium* and the suid *Conohyus* are common in Pakistan, but are not known from China. The area between the Paratethys and the Himalayas may have functioned as a route for faunal exchange (Text-fig. 65).

Dispersal of land mammals between parts of the (palaeo-) Palaearctic are expected to be controlled by climate rather than sea level changes from MN 3 onwards (Rögl & Steininger, 1983). Curves on humidity and temperature, that are based on mammal localities in Spain are given by Van der Meulen & Daams (1992). The temperature curve resembles curves based on the marine record. A disadvantage of these curves is that they may not reflect climate in the areas that control the dispersal of species. For instance, a change in climate in central Asia may allow the dispersal of a Chinese species to Europe, but a different or no change in climate may be recorded in Spain.

There is a good palynological record of the Miocene from Turkey (Benda & Meulenkamp, 1990). This record is tied to the MN units and has a potential in resolving questions of why mammals migrated to/through this area or not. Unfortunately, the southeast European-Turkish block has few Early Miocene large mammal localities and no listriodont record older than MN 5. Like in Pakistan/India, the Early Miocene record is very incomplete. This poses a problem to the analysis.

Africa and the Indian Subcontinent had at least partially the same listriodonts (and sanitheres) during the Early Miocene. These listriodonts are represented by subsequent evolutionary stages in both areas. These areas probably were frequently disconnected during the Early Miocene. The apparent presence of the same lineage in both areas may be explained in two ways:

— The periods of separation were short in comparison to the rate of evolution of the listriodonts and sanitheres and had little effect on the evolution. After separation, the geographical ranges of the species became continuous again, without a speciation event;
— Dispersals were frequent. For instance, species A, which occurred in Africa and Pakistan, evolved in Africa into species B during separation. Later species B dispersed to Pakistan and replaced species A. Such a process must then have been repeated several times in *Bunolistriodon*, *Kubanochoerus* and *Sanitherium*.

As a working hypothesis, it is assumed that there were no migrations when the same subsequent stages of evolution are found in two areas, and it is assumed that the evolution occurred in one large area.

Listriodont dispersals

The origin of the Listriodontinae is unknown. The oldest Suoidea known are the Tayassuidae from the Oligocene of North America (Pearson, 1932), the Palaeochoeridae from the Oligocene of Europe (Ginsburg, 1974; Van der Made, 1994a) and the palaeochoerid *Odoichoerus* from the Eocene (?) of China (Tong & Zhao, 1986). The first suids appear in Europe in MN 1 as immigrants. This indicates that Suidae probably originated in Asia. The first record of Listriodontinae is from Africa in Set I (Faunal Sets: Pickford, 1981) and in Bugti, Pakistan. They are absent in Meswa Bridge (Set O) and in Pakistan, there is no earliest Miocene or Oligocene record of mammals. Later members of the subfamily are found in Europe and China, suggesting that the earliest listriodonts evolved somewhere south of the Himalayas.

The phylogeny (Text-fig. 58) and the geographical distribution of the Listriodontinae suggest that there have been only few dispersals, or 'migrations' of listriodonts.

Lopholistriodontini are known from Africa only, with the possible exception of some specimens of *Nguruwe* from Pakistan. They appeared first in Set I, probably as immigrants.

The origin of *Kubanochoerus* is not known. The first *Kubanochoerus* is known from Set II in Africa. The geographical distribution of the different stages of the *K. mancharensis*- lineage suggest that this lineage evolved in an area comprising Africa, Pakistan and possibly Turkey. It is not known whether or not the lineage originated in Africa in Set II or had an earlier origin in a larger area (including the Indian Subcontinent). *K. gigas* (southern Russia, Pakistan, China) and *K. minheensis* (China) evolved from *K. massai* (Africa). This species is a possible descendant of *K. marymunnguae* (Africa). The distribution of *K. massai*, *K. minheensis* and *K. gigas* can be explained by one dispersal of *K. marymunnguae* followed by evolution to *K. massai* and subsequent local diversification. This model may be too simple, but there are no grounds for a more complicated model.

Bunolistriodon affinis seems to have evolved in both Africa and Pakistan into *B. jeanneli*. A scenario with an extra migration is possible, with *B. affinis* entering Africa, subsequently evolving into *B. anchidens* and into *B. jeanneli* and then migrating to Pakistan and India. The alternative does not affect correlations based on this lineage.

Bunolistriodon entered Europe in MN 4 and possibly more or less synchronously in China, though there is no MN 4 record to confirm this (Rögl & Steininger, 1983 assumed that there were no barriers to migration in this period). It is not clear whether or not the large *Bunolistriodon* from Europe, China and Africa are really different species. The *B. latidens*-lineage, of small size, may have evolved in Europe from *B. lockharti*, or may have entered Europe as a distinct species that subsequently became smaller.

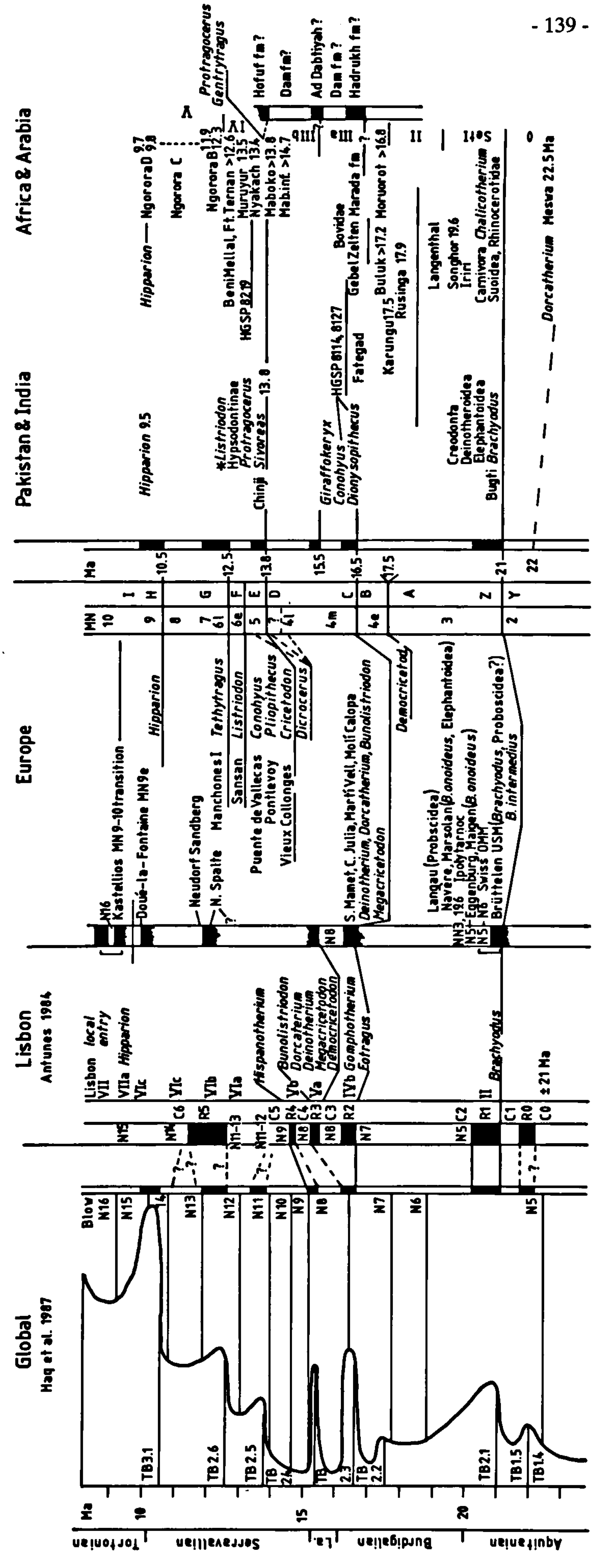


Fig. 64. Eustatic sea level changes, dispersals of land mammals and fossil mammal localities. The left column ('global') gives eustatic sea level, cycle number, millions of years and Blow's foraminifera zonation, all according to Haq *et al.* (1987). The next column ('Lisbon') gives transgressions (white) with their foraminifera zones, the regressions (black), the transgression (C number) and regression code (R number), the mammalian faunal level (Roman numeral), some local entries and a K/Ar date according to Antunes (1984, 1990). The following column ('Europe') gives selected localities with correlations to marine zonations, absolute dates, MN units and the units of the Ramblian and Aragonian. Generic names refer to first appearances, except when between brackets, in that case mere presence is indicated. The forth column (Pakistan & India and Africa & Arabia) gives selected localities and formations in India, Pakistan, Africa and Arabia, their radiometric or palaeomagnetic ages, the entries of selected taxa and Faunal Sets.

* indicates the first appearance of a genus by local evolution.

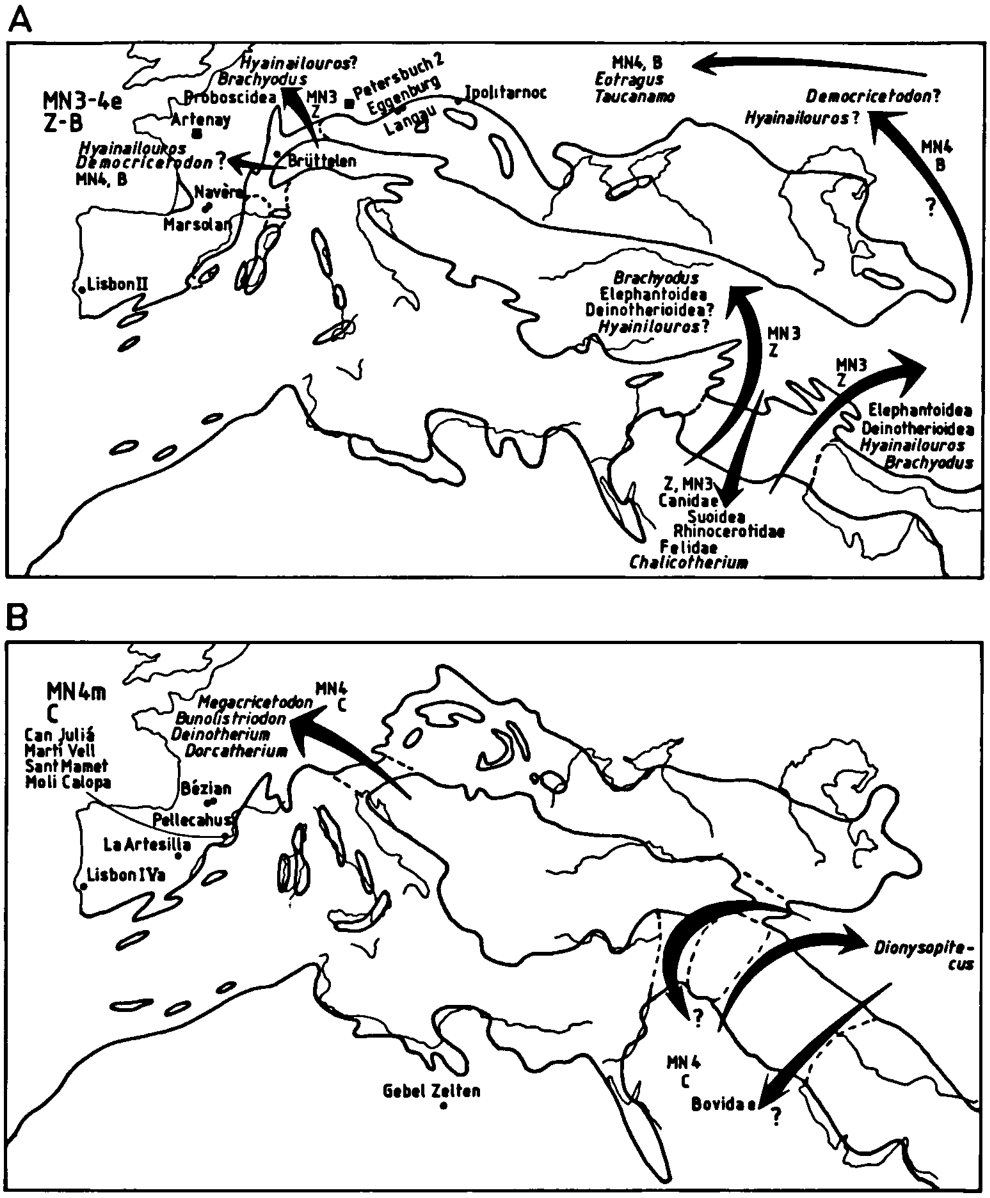


Fig. 65. Palaeogeographical maps according to Rögl & Steininger (1983), selected localities and dispersals of mammals. The Langhian-Serravallian transition is placed at different positions by Haq *et al.* (1987) and Rögl & Steininger (1983). The maps are taken as a rough indication of palaeogeography. A - The middle and late Burdigalian configuration (MN3l and MN 4e; zones A and B). Possible early Burdigalian 'land bridges' during the low sea level stand are stippled (MN 3e; zone Z). Dots MN 3 localities, squares MN 4 localities. B -The Langhian configuration (MN 4m; zone C). Possible early Langhian 'land bridges' are stippled. C - The early middle Serravallian map, to illustrate the migration of the rhino *Hispanotherium* (MN 4l; zone C). D - The late middle Serravallian configuration (MN 5-MN 6e). Possible 'land bridges' (early MN 5) are stippled. Dots MN 5 localities, squares MN 6 localities.

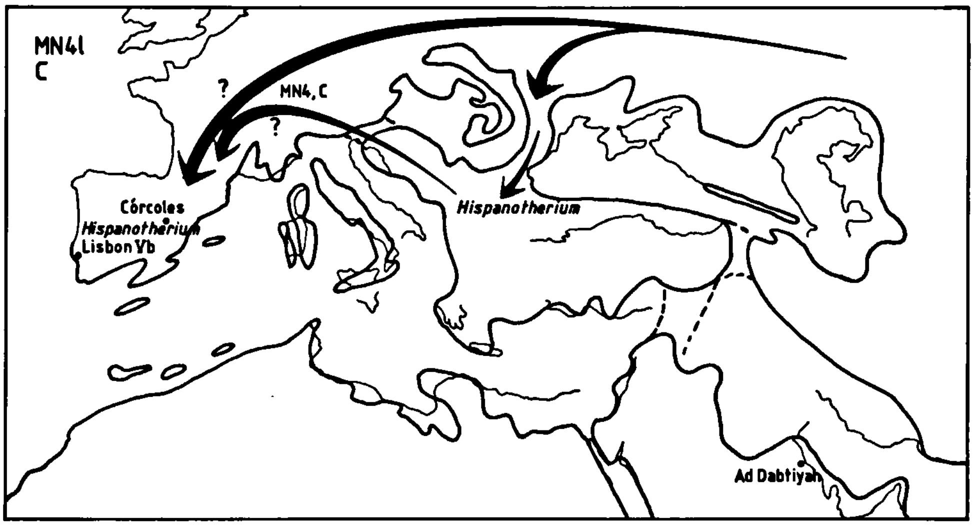
Listriodon pentapotamiae evolved from *Bunolistriodon guptai. Listriodon splendens* is derived from early *L. pentapotamiae.* The dispersal of *L. splendens* is early in MN 6 in Europe and China and is probably synchronous.

There is thus evidence for the following dispersals of listriodonts:

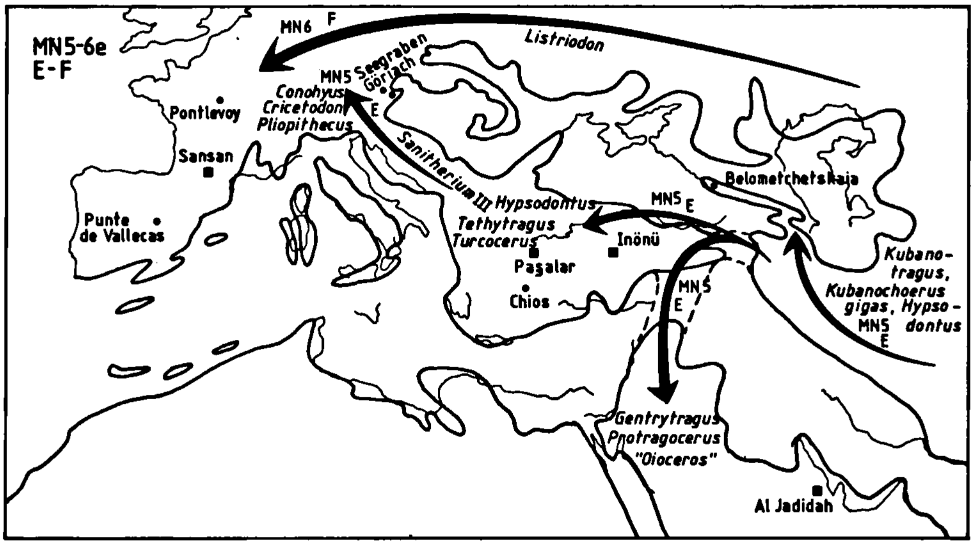
— Listriodontinae (*Nguruwe* and *Bunolistriodon*) enter Africa (Set I);

— *Kubanochoerus* may have entered Africa later (Set II);

C



D



— *Bunolistriodon* entered Europe and possibly the whole Palaearctic (MN4);

— *Listriodon splendens* dispersal in the Palaearctic (MN 6).

The dispersal of some *Kubanochoerus* species to China and Turkey cannot be sufficiently dated.

In the following sections a series of mammal dispersals is discussed that either are supposed here to be synchronous to listriodont dispersals or that have been claimed elsewhere to be simultaneous to listriodont dispersals. Some intermediate dispersals are also discussed, since they have a bearing on the subject.

The dispersal of *Dorcatherium* in Africa

Dorcatherium is found in Meswa Bridge, Kenya (Pickford, 1986a), which is placed in Set 0 (= pre-Set I; Faunal Sets of Pickford, 1981) and is the oldest known representative of this genus. No ruminant is known from the Eocene and Oligocene of Africa (Maglio, 1978) and *Dorcatherium* or its ancestor must have entered Africa later than the well-known Palaeogene Fayum faunas. The fauna from Meswa Bridge other than *Dorcatherium* has African origins. The dispersal of *Dorcatherium* was claimed to be part of the main African Early Miocene dispersal event (NDP 1 of Thomas, 1985).

The main African Early Miocene dispersal event

This event is best known from Africa. In addition, it had important effects in the Indian Subcontinent and some effects in Europe (Text-figs 64, 65a). It involved a great number of taxa, including the listriodonts *Nguruwe* and *Bunolistriodon.*

The major dispersal event for the African Miocene involves many taxa. Thomas (1985) gives a long list for his NDP 1 dispersal towards Africa, all except the bovids, Hyotheriinae (*Kenyasus* may be meant, but is probably not hyotheriine) and the tragulids belong to this dispersal event. The *Nguruwe* and *Bunolistriodon* and an other suoid, *Sanitherium,* entered during this event as well as the first Felidae, Canidae, Mustelidae, Rhinocerotidae and Chalicotheriidae (Text-fig. 65a). This event marks the start of the Set I faunal association.

The oldest known *Kubanochoerus* is from Set II. As pointed out above, it is not known where and when this genus originated; it may have entered Africa during or after the main Early Miocene dispersal event, or have originated later in Africa.

The dispersal event in Africa is widely believed to be synchronous to dispersals in the Indian Subcontinent and in Europe. Dispersals into these areas are discussed per taxon.

Brachyodus is often said to be related to or identical with *Masritherium* which evolved from the anthracotheres that were already present in the Fayum in Egypt in Oligocene times (Black, 1978).

The first record of *Brachyodus* in the Indian Subcontinent is in the Bugti Fauna. The old collection from Bugti probably holds fossils from various ages, but includes mainly Early Miocene fossils. A more recent collection of fossils of largely endemic rodents from the Bugti area (Jacobs *et al.*, 1981), may represent a time prior to this faunal exchange.

European *Brachyodus* increased in size; *B. intermedius* Mayet, 1908 is found in the earlier part of MN 3 and it descendant *B. onoideus* (Gervais, 1869) in the later part of MN 3 and in the earlier part of MN 4 (Dineur & Ginsburg, 1986; Text-fig. 64, third column). Brüttelen 1 has *B. intermedius* and *Xenohyus venitor* (Ginsburg, 1980). The range of the latter species being MN 2b-3a (Ginsburg *et al.*, 1987), the combination of both species place the locality in early MN 3. *B. intermedius* is also found in Lisbon II (Text-fig. 64, column 2).

Elephantoidea and Deinotherioidea are known to have originated in Africa (Tassy, 1990). The first Elephantoidea and Deinotherioidea in the Indian Subcontinent are from the Early Miocene Bugti Fauna. In Europe no deinotheres are found in MN 3. Elephantoids are found in Marsolan and Navère (MN 3; Bulot & Ginsburg 1993), Langau (MN 3; Text-fig. 64, third column) in Europe. Some footprints from Ipolitarnoc may represent proboscideans. A proboscidean is reported from Brüttelen 1 (Studer, 1896). There are two specimens, one of which is figured and seems questionable to me (the enamel seems too thin). I have seen neither of these two specimens. In Lisbon IVb an elephantoid is found along with the large *B. onoideus* (Text-fig. 64, column 2). There is not sufficient evidence to assume that the earliest European proboscidea entered early in MN 3, though this cannot be excluded either.

Creodonts are known of the Palaeogene from Eurasia, but not from the earliest Miocene. In Africa their record is uninterrupted. The creodont *Hyainalouros* is found in the Bugti fauna and is believed to be an immigrant from Africa (Ginsburg, 1979).

The earliest African *Bunolistriodon* and *Sanitherium* are similar to those from Bugti, suggesting similar ages for Bugti and Set I. The Bugti and Set I and II faunas are comparable to the MN 3 faunas in Europe in the absence of bovids and seem to be older than MN 4 faunas because of their primitive *Bunolistriodon.* The Bugti and MN 3 faunas share a number of new elements of African origin, including *Brachyodus* and Elephantoidea.

Hyainalouros and *Democricetodon*

The creodont *Hyainalouros* (first in Artenay, earliest MN 4) and the rodent *Democricetodon* (Zone B in the Aragonian type area, Artenay, Petersbuch 2; Text-fig. 64, third column, Text-fig. 65a) may have entered Europe at the same time. *Democricetodon* evolved in an area including Anatolia (De Bruijn, pers. comm.). The creodont is of African origin (Ginsburg, 1979) and is found also in the Bugti fauna, along with the earliest Asian Elephantoidea and deinotheres.

I do not know how common *Hyainalouros* is. If the animal is rare, it may well have entered Europe along with *Brachyodus* and have been overlooked. *Democricetodon* is now known from Spain from Loranca (MN 2b) and another locality in MN 3 (Daams, pers. comm.). It is not certain whether the dispersal of both taxa is simultaneous.

The first occurrences of *Eotragus* (Bovidae) and *Taucanamo* (Palaeochoeridae) are in Artenay. These genera probably had their origin in northern Asia, since the origin of Suoidea and of Pecora seems to be in the northern continents.

The entry of *Hyainalouros* (and *Democricetodon*?) together with *Taucanamo* and *Eotragus,* suggests that they came through northern Asia and must initially have come through the route between the Paratethys and Himalayas. In that case, the entry may have been controlled by climate.

The *Bunolistriodon* dispersal in Europe

Bunolistriodon, *Dorcatherium*, *Deinotherium*, *Megacricetodon* and *Eumyarion* are believed to have entered western Europe simultaneously. This is the major Miocene dispersal event of Europe (Text-fig. 64, third column, Text-fig. 65b). Dispersals in Africa and the Indian subcontinent are thought to be of the same age.

As pointed out above, *Bunolistriodon* is known from older deposits in Pakistan and Africa than Europe, deinotheres are of African origin and the oldest known *Dorcatherium* is from Africa also. *Eumyarion* was present in Turkey in MN 1 or 2 (De Bruijn & Saraç, 1991) and also *Megacricetodon* was present in Turkey at a very early date (De Bruijn, pers. comm.).

The first African bovids are from Gebel Zelten (Set IIIA). There is no previous bovid record in Africa and the bovids are small and with simple horn cores as is the case with the earliest European bovids.

The first *Conohyus* and *Dionysopithecus* are from the base of the Manchar Formation (Bernor *et al.*, 1988). The primate is of African origin, but *Conohyus* is certainly not of African origin, because it is not known from any of the rich lower Miocene localities of Africa, nor from Europe. *Conohyus* is a suid and suids have their origins in Asia, thus *Conohyus* probably originated there.

Dionysopithecus is also found in Shihong, China, along with *Platodontopithecus*, *Dorcatherium* and *Megacricetodon* and this fauna is correlated with MN 4 (Qiu, 1990). The time of entry of *Bunolistriodon* in China is poorly known and it is not clear whether or not the Chinese *B. intermedius* and European *B. lockharti* differ.

On the basis of a lineage in *Kubanochoerus*, the base of the Manchar Formation is believed to be younger than the Set II-III transition. The presence of a sublophodont *Bunolistriodon* at the base of the Manchar Formation suggests an age comparable to the earliest representatives of that genus in Europe. The bovids from Gebel Zelten are as simple as the earliest bovids from Europe. There are a number of taxa that first appear in China, that also have their first appearance in Europe or Pakistan. All this suggests that the dispersals in Europe, China, Africa and the Indian Subcontinent were approximately coeval.

'Overdue' dispersals in western and central Europe

Brachyodus, deinotheres and elephantoids dispersed from Africa during Set I. The three taxa are found together in Pakistan. *Bunolistriodon* and tragulids were present in Pakistan in Bugti (Set I, MN 3 equivalent). *Bunolistriodon*, *Dorcatherium* and deinotheres appeared much later in Europe (MN 4), though they might have migrated along with the elephantoids and *Brachyodus*. This needs an explanation.

These taxa are believed to have migrated through Turkey and southeastern Europe. The pollen record in the eastern Mediterranean is well studied and well correlated to marine zonations and MN units (Benda & Meulenkamp, 1990). There are a number of sporomorph associations ('Pollenbilder'), each of which lasts as long as two to five MN units. This indicates that the vegetation was stable compared to the faunas. The change of one pollen association to another, must then reflect a major change, probably a climatic change, and not a minor fluctuation. The transition of the Kale to Eskihisar pollen associations is during the Burdigalian. The environment that produced the Kale pollen association may have acted as a filter. This may explain why *Deinotherium*, *Dorcatherium* and *Bunolistriodon* arrived late in Europe. The late arrival in Europe of *Megacricetodon* and *Eumyarion*, which were present in Turkey at a very early date, may also be due to environmental changes caused by a change in climate.

Hispanotherium dispersal in Europe

Hispanotherium does not have ancestors in Spain and Portugal. It has a relatively long stratigraphical range in Turkey and is assumed to be an immigrant of Asian origin (Antunes, 1979, 1990). This rhino first occurs in Córcoles (Alférez *et al.*, 1982), zone C and in the Lisbon Vb fauna and is more abundant in zone D (Text-fig. 64, second column, Text-fig. 65c). The occurrence of *Hispanotherium* is related a to drier climate in Spain, as indicated by rodent faunas (Van der Meulen & Daams, 1992). *Hispanotherium* seems to be adapted to a drier environment and its dispersal may have been caused by a change in climate. There seem to be no simultaneous dispersals of other taxa.

The *Conohyus*/*Cricetodon* dispersals in Europe

This group of dispersals in Europe may or may not be contemporaneous to dispersals in Africa and the Indian Subcontinent (Text-fig. 64, third and fourth column, Text-fig. 65d).

Conohyus is characterised by size increase through time. In Europe its oldest record is from Puente de Vallecas (Van der Made, 1989a). Older and smaller *Conohyus* is found in Pakistan. Gabunia (1981) recorded the presence of *Conohyus* and *Cricetodon* in Kzylbulak, a locality between the Aral Lake and Caspian Sea. This locality is in sediments that overly marine sediments of Tarkhanian age. The locality is placed in MN 4b or 5.

Pliopithecus and the related *Crouzelia* are probably of African origins, though they have not been found in Africa; they may have evolved outside Africa from a primate of African origin. Both pliopithecines are found in Europe in MN 5 (Ginsburg, 1986). *Pliopithecus* is also found in in Tongxin, China (Harrison *et al.*, 1991), which probably is of MN 5 age.

Cricetodon was already present in Turkey in MN 1 and in Greece at least in MN4, but did not migrate to western Europe until MN 5 (De Bruijn *et al.*, 1993).

In Seegraben near Leoben, a *Sanitherium* is found of the third evolutionary stage (see section 'Correlations Africa-Pakistan-Europe/Turkey'). Seegraben is on the northwest European block. Although *Sanitherium* is not known from any other locality in western and central Europe, it should form part of the same group of dispersals. The third stage of evolution of *Sanitherium* is also known from Chios and Pakistan.

The first appearance of a variety of bovids occurred at approximately the same time in a number of areas.

Paratragocerus and *Protragocerus* are closely related or synonymous (Köhler, 1987). The genus is an immigrant in Pakistan and Africa. The first appearance of *Protragocerus* in Europe is not quite clear, but the genus does not have its origin there. The genus is assumed to have its origin somewhere in Asia.

Kubanotragus, *Hypsodontus*, '*Oioceros*' *tanycerus* and *Turcocerus* are Hypsodontinae. *Turcocerus* is found in Çandir and *Hypsodontus* in Paşalar and Çandir (Köhler, 1987). The Hypsodontinae is a group with a previous record (Shanwangian) and with a great diversity in China (Köhler, 1987; Chen, 1988; Qiu, 1990).

Gentrytragus and *Tethytragus* were formerly placed in *Caprotragoides* (Azanza & Morales, 1994). They have probably a common origin. *Tethytragus* is known from Paşalar and Çandir, which are MN 6. There is however no good MN 5 record in Turkey. These taxa have, in my opinion, no ancestors in Europe or Africa and an Asian origin seems likely.

Belometchetskaia has *Kubanochoerus g. gigas* and the bovids *Kubanotragus*, *Hypsodontus* and *Paratragocerus*. Belometchetskaia is placed in MN 5.

The entry of *Protragocerus* (or *Kipsigicerus*, see Van der Made & Hussain, 1994), *Gentrytragus* (= '*Caprotragoides*', see Azanza & Morales, 1994) and possibly '*Oioceros*' *tanyceras* (Text-fig. 64, column 4, right, Text-fig. 65b) marks an important event in Africa. These are found in Nyakach (13.4 Ma), Muruyur (13.5 Ma), Fort Ternan (> 12.6 Ma) and Al Jadidah, but not in Maboko (> 13.8 Ma). Nyakach and Maboko are placed in Set III and the other localities in Set IV (Pickford, 1981, 1984, 1986c, 1988a). Thomas (1985) assumed, on the basis of the presence of these bovids in Nyakach, that the locality was younger than Maboko. In view of this important addition to the African fauna and in view of its radiometric age (younger than Muruyur, which is placed in Set IV), it is difficult to understand that Nyakach is placed in Set III. It seems reasonable to transfer Nyakach to Set IV and consider the entry of *Tethytragus* ('*Caprotragoides*') and *Protragocerus* to indicate Set III-IV transition. Maboko has a stage II *Sanitherium*, Leoben (MN 5) and Chios have stage III. If this bovid dispersal is after Maboko, it is likely to be as old as MN 5.

Barry & Flynn (1990) indicated a major faunal turnover in Pakistan at about 14 Ma. The entry of the bovids *Protragocerus*, *Sivoreas*, *Kubanotragus* and *Sivaceros* is given at 13.8 Ma. *Protragocerus* and *Sivoreas* show an evolution in horn core morphology and primitive representatives are found in Mochi Wala and Kanatti low in the Chinji Formation (Van der Made & Hussain, 1994). Two species help to correlate this entry to the MN scale. Mochi Wala and Kanatti are in the lower part of the Chinji Formation and have the most primitive *Listriodon pentapotamiae* yet recorded. The entry of these bovids and the local appearance by evolution of *Listriodon* are probably at about the same time. The first appearance of *Listriodon* is believed to be close to the MN 4-5 transition and younger than Maboko.

The giraffid *Giraffokeryx* is found in Prebreza (Pavlović, 1969; MN 6) and Mala Miliva ('*Palaeomeryx*' by Petronievič, 1967; MN 5). It is cited from the Siwaliks from 16 Ma onward (Barry & Flynn, 1990). *Giraffokeryx* may have migrated to the SE European-Anatolian landmass in MN 5, but may also have been present earlier. Data in the SE European-Anatolian area are lacking.

There are thus a great number of dispersals during MN 5, to west and central Europe, to the SE European-Anatolian land mass and to various parts of the eastern Paratethys domain.

The cervid *Dicrocerus* (of north Asiatic or Chinese origin) entered Europe in early MN 5. The dispersal of this species is not controlled by trans- or regressions, but probably by climate. The dispersal of *Dicrocerus* might be triggered by the mid Miocene cooling event indicated by Van der Meulen & Daams (1992). It is of importance for the understanding of the MN 4-5 transition, whether the north Asiatic migrants (controlled by climate) or the SE European and Turkish migrants (possibly controlled by sea level) entered western and central Europe first.

Listriodon splendens dispersal

The dispersal of *Listriodon splendens* is an isolated event in Europe (Text-fig. 64, third column, Text-fig. 65d) and in China. The species descended from an early *Listriodon pentapotamiae*, which is known from Pakistan and India. The dispersal of *Listriodon* in the Palaearctic is an isolated event.

Matching the mammal record and marine regressions

The 'Proboscidean Datum Event' was believed to be a synchronous migration of elephants and other mammals, including listriodonts, from Africa to Eurasia as a result of the closing of the eastern Tethys during the Early Miocene (Madden & Van Couvering, 1976). Therefore, the dispersal of the proboscideans was controlled by eustatic sea level changes and by tectonics. Later, the 'event' was shown to have involved several dispersals of different Proboscidea, which did not reach Europe simultaneously (Antunes, 1990; Tassy, 1990).

The same marine regressions that allowed the proboscideans to disperse, allowed a large number of other mammals to do the same. The taxa involved in each of the dispersals and in particular the exact timing of the dispersals have attracted much discussion (Adams *et al.*, 1983; Bernor *et al.*, 1987, 1988; Ginsburg, 1979; Savage, 1990; Thomas, 1985). The correlation of these dispersals to regressions has stratigraphical value because:

— it implies that the dispersals discussed above were synchronous in Europe, the Indian Subcontinent and Africa;
— it relates these events to marine events and thus marine and continental stratigraphy.

Although there are difficulties in correlation of marine and continental sediments, it is attempted here to relate the dispersals of the previous sections to periods of low eustatic sea levels.

On a large scale, the correlation of continental faunas and transgressive events does not present great problems. In the Aquitanian Basin, the transgressive type Aquitanian is followed by a regression, and the transgressive type Burdigalian. The relation of marine deposits and the continental faunas is indicated by numerous fossil localities (Richard, 1946; Hugueney & Ringeade, 1990). The same alternation is found in the Touraine and Anjou with numerous fossil mammal localities in the continental and nearshore deposits (Ginsburg & Mornand, 1986). The extent of subsequent transgressions in the Atlantic coast of Morocco, Portugal, Spain, France and southern England is indicated by Cahuzac *et al.* (1992). A similar and time-equivalent sequence is formed by the Lower Marine Molasse (UMM), Lower Fresh Water Molasse (USM), Upper Marine Molasse (OMM) and Upper Fresh Water Molasse (OSM) north of the Alps (Berger, 1992; Heizmann, 1992). In the Swiss area magnetostratigraphy, palaeontology and the interaction of subsidence and sedimentation were studied (Burbank *et al.*, 1992); subsidence rates decreased before and during the early part of the period studied here. Thus sea level fluctuations in this area do not seem to be greatly influenced by local subsidence. These data indicate a similar history for several areas, all having an important regressive event during the late Aquitanian and/or early Burdigalian. The position of the oldest localities with *Brachyodus* in the Lisbon area and in Switzerland suggest that the dispersal of that taxon in Europe and the supposedly coeval main Early Miocene African dispersal event happened during the Aquitanian and early Burdigalian regression.

There are, however, more dispersal events. In order to correlate these to global eustatic sea level changes, greater detail is needed. In the following analysis, the sea level curve and accompanying zonations for foraminifera (Blow) and in some cases nannoplankton and their ages by Haq *et al.* (1987) are used, as well as the Lisbon section where marine and continental deposits interfinger (Antunes, 1984). There seem to be certain problems with the curve given by Haq *et al.* (Meulenkamp, pers. comm.) and therefore the use of this curve is tentative.

Palaeogeographical reconstructions by Rögl & Steininger (1983) and Steininger & Rögl (1985) are used in Text-fig. 64. These maps are used here as an approximate indication of palaeogeography. The main aim is to visualise dispersals of taxa, not minor details of palaeogeography.

There are discrepancies in the correlation of Blow zones to stages. For instance N9 is included in the Langhian by Steininger & Rögl (1985), Steininger *et al.* (1985) and Steininger (1986), but N9 is included in the Serravallian by Haq *et al.* (1987). There are also discrepancies between the ages assigned to foram zones and correlations to nanno zones according to Haq *et al.* and according to the various papers by Steininger *et al.* In general, the ages given by Steininger *et al.* are slightly older. Steininger *et al.* (1990) give in some cases younger ages than in the previous papers and N9 straddles the Langhian-Serravallian boundary. All this does not pose a real problem to the analysis, if the number and approximate amplitude of the sea level changes as given by Haq are correct. No updated eustatic sea level curves are available at present. Therefore, the curve by Haq *et al.* (1987) is used (Text-fig. 64), despite possible problems.

It seems unlikely that the dispersal of *Dorcatherium* in Africa occurred during a period of high eustatic sea level, but it seems also unlikely that it occurred when there were good connections between Africa and the Indian Subcontinent or the SE European and Anatolian block because it is an isolated dispersal. This is not understood. The *Dorcatherium* dispersal preceeded the main African Early Miocene dispersal event (Text-fig. 65). The latter event is related to the TB2.1 regression at 21 Ma. *Dorcatherium* is present at Meswa Bridge. This locality is dated at 22.5 Ma. A tentative interpretation is that the sea level low at the onset of the TB1.5 cycle at 22 Ma might have allowed *Dorcatherium* to reach Africa. The next older period of low sea level is during the Oligocene (25-30 Ma; Haq *et al.*, 1987).

The main African Early Miocene dispersal event is supposed to have involved a massive dispersal in Africa marking the transition of Set 0-I, the installment of the Bugti Fauna in Africa and the dispersal of *Brachyodus* and possibly Elephantoidea in Europe (Text-figs 64, 65a).

Early European *Brachyodus* is found in Brüttelen and in Lisbon II. Brüttelen is at the base of the Upper Freshwater Molasse (OMM) (Engesser, 1990). In the Swiss area N5 and N6 fauna and NN2-NN5 flora are found in the OMM (Berger, 1992). Lisbon II is overlain by marine sediments with N5 forams (Antunes, 1984). Later *Brachyodus* is found in Maigen and Eggenburg and are said to be associated with NN2 flora and N5 fauna (Steininger *et al.*, 1990). Early European elephantoids, associated with marine sediments are more problematic. Some footprints from Ipolitarnoc might represent proboscideans. These are above marine sediments with NN3 flora and below rhyolite tuffs dated as older than 19.6 ± 1.4 Ma (Rögl & Steininger, 1983). This date is incompatible with the upper limit of 17.8 Ma for the NN 3 zone, as given by Haq *et al.*, 1987. The Lisbon IVb fauna has the first local elephantoids, but may not be the first European record of elephantoids. Lisbon IVb is from terrestrial sediments, overlying marine sediments with N7 forams.

These data on the entry of *Brachyodus* fit the sea level low at the beginning of the TB2.1 cycle of Haq *et al.* (1987) (Text-fig. 64), which is within N5 and dated at 21 Ma.

In Africa this event is at the Set 0-I transition. The oldest Set I localities are 19 to 20 Ma old and there is a gap between the oldest localities of Set I and Meswa Bridge of pre-Set I, which is 22.5 Ma. The dispersal occurred in this time interval. The TB2.1 regression is dated at 22 Ma and fits well in this time range (Text-fig. 64).

The ages of the dispersals of *Hyainalouros* and *Democricetodon* in Europe are uncertain but do not seem to match eustatic sea level changes.

The *Bunolistriodon* dispersal in Europe is believed to be coeval with the first occurrance of bovids in Africa and the dispersal of *Conohyus* and *Dionysopithecus* in the Indian Subcontinent.

As discussed above, the *Bunolistriodon* dispersal in Europe is part of a group of dispersals, including those of deinotheres, *Dorcatherium*, *Megacricetodon* and *Eumyarion*. These taxa are present in the localities of Sant Mamet, Can Julià, Martí Vell and Molí Calopa (Text-fig. 60). These localities are in continental sediments below a transgressive sediments with N8 fauna (Anglada & Martín, 1971), though Agustí *et al.* (1984) cited it as an N7 to N8 fauna. Compared to the curve given by Haq *et al.* (1987) these data fit the sea level low at the beginning of the TB2.3 cycle (Text-fig. 64). This is the first major sea leavel drop after the one of the TB2.1 cycle.

In the Lisbon area the taxa are first present in the Va fauna, which is in the R3 continental sediments between the C3 and C4 marine sediments (Text-fig. 64). C3 and C4 have N8 foraminifera. The R4 regression on top of the C4 transgression is covered by N9 foraminifera. The R2 continental sediments with the Lisbon IVb fauna do not yet contain deinotheres, *Dorcatherium*, *Megacricetodon* nor *Eumyarion* and overlie sediments with N7 fauna and are overlaid by deposits with N8 fauna. Haq *et al.* (1987) do not indicate a regression within N8. Compared to the chart by Haq *et al.* there is one cycle too many in Lisbon (Text-fig. 64). It is assumed here that the R3 local regression was caused by a change in the balance between sedimentation and subsidence in the Lisbon area. By comparison with the Catalonian fauna, it seems that the Lisbon IVb fauna is incomplete.

In Africa, the first bovids are known from Set III. Gebel Zelten has bovids and is an early Set III locality. Gebel Zelten is in the Marada Formation, which is a terrestrial unit between marine formations (Savage & Hamilton, 1973) and it seems likely that the regression caused the faunal change that marks the Set II-III transition. This does not mean that it is assumed here that the Marada Formation represents in all its geographical range this regression. That needs to be checked.

The TB2.3 sea level low is believed to have occurred 16.5 Ma ago and is younger than the tentative dates that have been mentioned for the Proboscidean Datum Event, even though it is clear that this 'event' involved at least two different dispersals in Europe at different times. There are however few radiometric or palaeomagnetic dates of this event in Europe.

Gomphotherium, *Eumyarion* and *Democricetodon* are found in Bełchatów C, a locality below beds that are radiometrically dated 18.1 ± 1.7 Ma and above NN3 flora (Kowalski & Kubiak, 1993). Although no *Bunolistriodon*, *Megacricetodon* and *Deinotherium* were found in Bełchatów, the presence of *Eumyarion* suggests that the fauna is younger than the dispersal of the former genera in Europe. Either the dates by Haq *et al.* (1987), 16.5 Ma for the sea level low and 17.8 for the top of NN 3, are too young or the Bełchatów date should be interpreted as as younger than 16.5 Ma.

The *Hispanotherium* dispersal in Europe may have been caused by climatic rather than eustatic sea level changes. It is however important in that it is found below marine sediments with N9 fauna and above sediments with N8 fauna. In Spain, *Hispanotherium* is typical of MN4, though it is claimed that it is typical of MN 5 in Portugal (Antunes, 1979).

The *Conohyus/Cricetodon* dispersals in Europe in MN 5 as well as those of *Pliopithecus* and *Crouzelia* are believed to be coeval with dispersals of a variety of bovids in Africa and the Indian Subcontinent and in the Paratethys area.

After the R4 local regression with the Vb fauna, the record becomes less clear in the Lisbon area; no clear regressions are indicated (Text-fig. 64; Antunes, 1984). Krijgsman *et al.* (1994) indicate an age of 14.1 Ma for the MN4-5 transition. The date given by Barry & Flynn (1990) for the dispersal of a number of bovids in Pakistan is 13.8 Ma. The dispersal of bovids in Africa at the Set III-IV transition should be later than Maboko (> 13.8 Ma) and before Nyakach (13.4 Ma). These data fit the sea level low at the beginning of the TB2.5 cycle of Haq *et al.* (1987), which is dated at 13.8 Ma (Text-fig. 64).

Al Jadidah is in the terrestrial Hofuf Formation, which overlies the transgressive Dam Formation. Bovids from Al Jadidah are comparable to those from Nyakach, but more primitive than those of the Ngorora Formation, which would place Al Jadidah in Set IV. It seems that at least part of the Hofuf Formation may be time equivalent to the TB2.5 cycle. The Arabian situation is probably more complex than it seems and the Dam Formation may not represent a single transgressive event. In this context it is of interest that the locality of Ad Dabtiyah is said to be in a continental equivalent of the Dam Formation. It might be in sediments representing the regression at the base of the TB2.4 cycle (Text-fig. 64, column 4, right). This would agree well with the age of Ad Dabtiyah as indicated by *Bunolistriodon akatikubas* (Set IIIa).

The *Listriodon splendens* dispersal was an isolated event and does not seem to be related to eustatic sea level changes.

Conclusions

Several important dispersal events were caused by eustatic sea level drops.

The main African Early Miocene dispersal event marks the Set 0-I transition in Africa and is coeval with the instalment of the Bugti Fauna on the Indian Subcontinent and with the entry of *Brachyodus* in Europe early in MN 3. This event had its major impact in Africa and the Indian Subcontinent and brought listriodonts, rhinos, carnivores and many other taxa to Africa, the deinotheres to the Indian subcontinent and *Brachyodus* and elephantoids to Eurasia including the Indian Subcontinent. This event may have been caused by the sea level low of the TB2.1 cycle of Haq *et al.* (1987), dated at 22 Ma.

The *Bunolistriodon* dispersal in Europe is coeval with the dispersal of deinotheres, *Dorcatherium* and *Megacricetodon* in Europe, the dispersals of *Dionysopithecus* in the Indian Subcontinent and the dispersals of the first bovids in Africa. It marks the zone B-C transition, is early in MN 4 in Europe and marks the Set II-III transitions in Africa. This event had its major impact in western and central Europe and possibly in Asia north of the Himalayas. This event may have been caused by the TB2.3 regression at 16.5 Ma.

The *Conohyus*, *Cricetodon*, *Pliopithecus* and *Crouzelia* dispersals in Europe are coeval with the dispersals of a great number of bovids in Africa and the Indian subcontinent. The event marks the Set III-IV transition in Africa, is around the MN 4-5 transition in Europe and caused the instalment of the Chinji fauna in the Indian Subcontinent. The event had its major impact in the latter area. It may have been caused by the TB2.5 eustatic sea level drop dated at 13.8 Ma.

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NOTE

When this paper was in press, several papers appeared that treated the taxonomy of the Listriodontinae.

Pickford (1995) introduced the specific and generic names *Megalochoerus homungus* for a group of fossils from Bugti, which he before placed in *Hemimastodon crepusculi* (Pickford, 1987) and for some specimens from Nyakach. This material is discussed here under *K. mancharensis* and it is concluded that most of the material is anthracothere and that the only figured specimen is very probably a suid. The type of *M. homungus* is one of the specimens that is believed here to be anthracothere. As a consequence, the only name introduced for the large suid from the Manchar Formation, Bugti, Nyakach, Maboko and Inönü I is *K. mancharensis.*

Pickford (1986b) placed *Kenyasus* in the Kubanochoerinae and Pickford (1995) introduced the subfamily name Cainochoerinae for the small suid *Cainochoerus* Pickford, 1988, which he considered as mysterious. Here (chapter on phylogeny), *Cainochoerus*, *Albanohyus* and *Kenyasus* are believed to be related; they should all be placed in the Cainochoerinae.

Pickford (1986) placed the species *L. moruoroti* in *Lopholistriodon* and believed this genus to be closely related to *Listriodon*. For the appearent problem that *L. moruoroti* seems to have evolved into the fully lophodont *L. kidogosana* and that it is known from localities that are older than the first lophodont *Listriodon* (p. 69) two possible solutions were presented. The first was doubting the "Burdigalian" age of Moruorot and assuming all localities with *L. moruoroti* to be of Middle Miocene age (pp. 57-58), apparently assuming them to be younger than the first lophodont *Listriodon*, that is MN 6 or younger. The second was admitting the possibility of parallel evolution (p. 69). Pickford (1995) "solved" this "enigma" by creating a new genus *Namachoerus* for the species *L. moruoroti* and placing it in the new subfamily Namachoerinae.

Thus Pickford (1995) admitted parallel evolution of lophodonty in two lineages. A possible relation to the "Kubanochoerinae" (or with any other suids) was not discussed. No formal diagnosis was given, but appearently the characters "precociously lophodont" and "short-snouted" are considered the ones defining the Namachoerinae. Parallel evolution of lophodonty in a new subfamily is apparently accepted, but why can it not be accepted within the subfamily of the Listriodontinae? This question is not asked by Pickford (1995). My answere to this question is given in the systematics and phylogeny chapters. A short snout is the primitive state for suids and apparently is no good foundation for erecting a new subfamily either.

L. moruoroti is placed here in the Lopholistriodontini new tribe in the Listriodontinae. Namachoerinae have thus priority above the Listriodontini. The Namachoerini are here believed to be a tribe of the Listriodontinae.

Pickford (1986, p. 69): "... the species *kidogosana* has a perfectly reasonable progenitor in *Lopholistriodon moruoroti* ...". Pickford (1995) apparently changed his mind completely. However, none of the characters mentioned in the diagnosis of *Namachoerus* are derived characters that contradict a derivation of *L. kidogosana* from a suid like *L. moruoroti* or *L. pickfordi* (which is of the same evolutionary level in all characters known).

The character "molars and posterior premolars highly lophodont" in the diagnosis of *Namachoerus* (p. 321) excludes the sublophodont holotype of *L. moruoroti*, type species of *Namachoerus*. It could be argued that a generic name for the sublophodont stage of what in this study is called *Lopholistriodon* is usefull. However, it appears that lophodonty appeared in some specimens of the later *L. moruoroti* and appeared in the lineage leading to *L. kidogosana*. The character appeared thus parallel in both lineages. Recognizing the genus *Namachoerus* for the species *L. moruoroti* alone obscures its affinities and would separate it from very similar suids, such as *L. pickfordi.*

Pickford & Moyà Solà (1995) stated that *Bunolistriodon* is a nomen nudum and introduced the name *Eurolistriodon* as a replacement. *B. lockharti,* type species of *Bunolistriodon* is included in the new genus. Above it is argued that *Bunolistriodon* Arambourg, 1963 is valid and thus *Eurolistriodon* is a junior synonym. The same authors introduced the specific name *E. adelli.* The type of this species is of small size and shares a number of morphological characters with the material assigned here to *Bunolistriodon* aff. *latidens.* It differs in lacking the P2. If this character is pathological, the name *B. adelli* might be the valid name for *B.* aff. *latidens.*

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Pickford, M. & S. Moyà Solà, 1995. *Eurolistriodon* gen nov., (Suoidea, Mammalia) from Els Casots, early middle Miocene, Spain. — Proc. Kon. Ned. Akad v. Wetensch. 98(48): 343-360.

PLATE 1

Figs 1-22. *Nguruwe kijivium* from Songhor, Mfwanganu and Rusinga.

1 - KNM-SO 4976, right I^1 (ap-li-mes-la-dist) from Songhor;
2 - KNM-SO 5408, left D^2 (oc-buc-li) from Songhor;
3 - KNM-SO 4980, left I^1 (oc-li) from Songhor;
4 - KNM-MW 560, right I^3 (ap-la-li) from Mfwanganu;
5 - KNM-SO 4977, right I^2 (la-oc-li) from Songhor;
6 - KNM-SO 1052, right C^m (ap-ant-la-po-li) from Songhor;
7 - KNM-SO 4974, left C^m (po) from Songhor;
8 - KNM-SO 4979, left P_4 (oc-buc-ant-po-li) from Songhor;
9 - KNM-RU 3030, left P^4 (po-buc-ant-oc) from Rusinga;
10 - KNM-SO 4978, right P_3 (oc-la-li) from Songhor;
11 - KNM-RU 2771, left M^3 (oc) from Rusinga;
12 - KNM-RU 2773, left M_3 (oc) from Rusinga;
13 - KNM-SO 1131, right P^4 (ant-buc-po-oc) from Songhor;
14 - KNM-SO 1118, left P^4 (oc-ant-po) from Songhor;
15 - KNM-SO 1056, left M^3 (oc-ant) from Songhor;
16 - KNM-SO 1055, left M^3 (oc-ant) from Songhor;
17 - KNM-SO 4975, right P^1 (oc-li) from Songhor;
18 - KNM-SO 1118, left M^1 - M^2 (oc) from Songhor;
19 - KNM-SO 1121, right M^3 (oc-li) from Songhor;
20 - KNM-SO 1138, right M_3 (oc-li) from Songhor;
21 - KNM-MW 173, right M_2 (oc-ant-li-po) from Mfwanganu;
22 - KNM-SO 1057, right M^1 (oc) from Songhor.

Scale bar equals 5 cm (photographs by the author, copyright Kenya National Museums).

PLATE 1

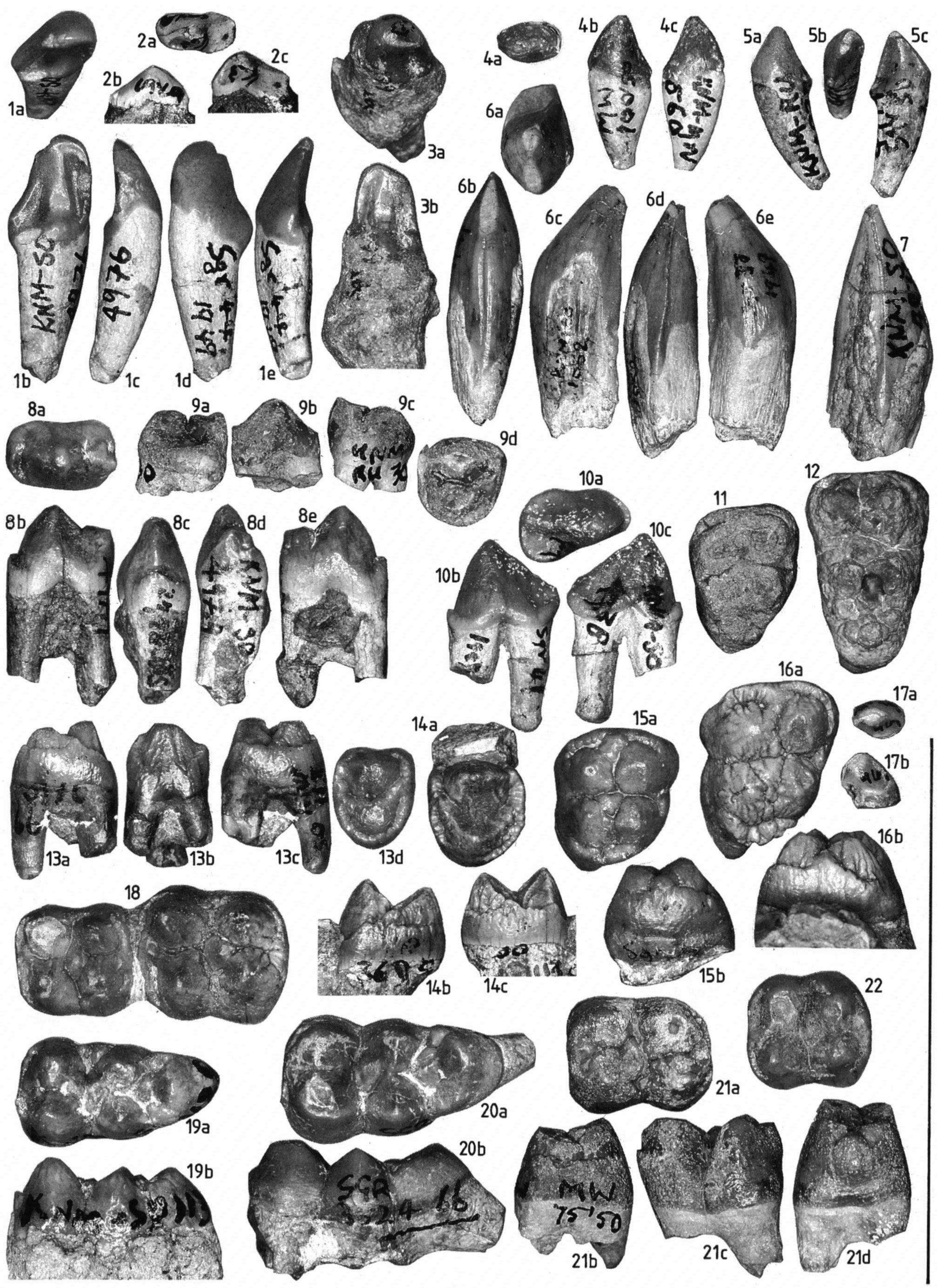
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PLATE 2

Figs 1-6, 12. *Lopholistriodon moruoroti*; **1** - KNM-MB 142, left C^m (la-ap-li-ant) from Maboko; **2** - KNM-MO 9, left P^3 - P^4 (oc-buc) from Moruorot; **3** - KNM-MB 14490, left I^1 (ap-la-li) from Maboko; **4** - KNM-MB 15114, left M^3 (oc) from Maboko; **5** -KNM-MJ 9775, left I^1 (la-dist-oc-li) from Majiwa; **6** - KNM-MB 15116, left I^1 (ap-li) from Maboko; **12** - KNM-MB 14485, right P^4 (buc-oc-po) from Maboko.

Fig. 7. *Lopholistriodon pickfordi* n. sp. KNM-MB 14447, left I_1 (dist-li) from Maboko.

Figs 8-11, 13, 17. *Nguruwe kijivium*; **8** - KNM-KI 18034, left C_m (la) from Kirimun; **9** - KNM-KI 18048, right P_3 (li-oc-buc) from Kirimun; **10** - KNM-MW 384, left I^1 (ap-li-dist-la) from Mfwangano; **11** - KNM-MB 14487, posterior half of a right P_4 (oc-po) from Maboko; **13** - KNM-KI 18039, left P_1 (oc-buc-li) from Kirimun; **17** - KNM-KI 18037, left I_1 (dist-li-mes) from Kirimun.

Figs 14-16. *Lopholistriodon kidogosana*; **14** - KNM-BN 1727, left M_3 (po-ant-oc-li) from the Ngrora Formation; **15** - KNM-BN 1723, second and third lobes of left M_3 (buc-oc-li-po) from the Ngrora Formation; **16** - KNM-BN 548, right I_1 (ap-li-me) from the Ngrora Formation.

Fig. 18. *Nguruwe kijivium* or *Palaeochoerus* ? *pascoi*; HGSP 8412/3152, anterior half of a right P_4 (li-oc-la) from the Manchar Formation.

Scale bar equals 5 cm, except for Fig. 2, where it equals 2.5 cm (Photographs by the author, copyright of Figs 1-17 Kenya National Museums).

PLATE 2


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KNM-KI 18037
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PLATE 3

Figs 1, 2, 4-6, 8. *Lopholistriodon moruoroti*; **1** - KNM-MB 877, right C^m (ap-ant-la) from Maboko; **2** - KNM-MB 102, right C_m (po-la) from Maboko; **4** - KNM-MO 5B, right M_2-M_3 (oc-li), part of **holotype**, from Moruorot; **5** - KNM-MB 10332, left P_4-M_2 (oc-la) from Maboko; **6** - KNM-MB 15115, right M^2 (po-buc-oc-ant/oc-ant) from Maboko; **8** - KNM-MB 10318, left M_1-M_2 (oc-po-buc-li) from Maboko.

Figs 3, 7. *Lopholistriodon pickfordi* n. sp.; **3** - KNM-MB 14448, left I_2 (ap-dist, li-mes); **7** - KNM-MB 26, left I_2 (ap-dist-li-mes) from Maboko.

Figs 9, 10, 13, 14. *Nguruwe kijivium*; **9** - KNM-KI 18050, left M_3 (oc-la-po) from Kirimun; **10** - KNM-KI 18032, right M_3 (ant-oc-buc-po) from Kirimun; **13** - KNM-SO 1062, left D_2-D_4 (oc-li-buc) from Songhor; **14** - KNM-KI 18047, left M_1 (oc-ant: stereo pair) from Kirimun.

Fig. 11. *Palaeochoerus ? pascoi*; IM B 717, right M^3 (oc-ant), **holotype** from Chharat.

Fig. 12. *P. ? pascoi* or *N. kijivium*; HGSP 8412/3133, posterior half of a right M^3 (oc) from HGSP 8412, Lower Manchar Formation.

Scale bar represents 5 cm (photographs by the author, copyright for Figs 1-11, 13, 14 Kenya National Museums).

PLATE 3

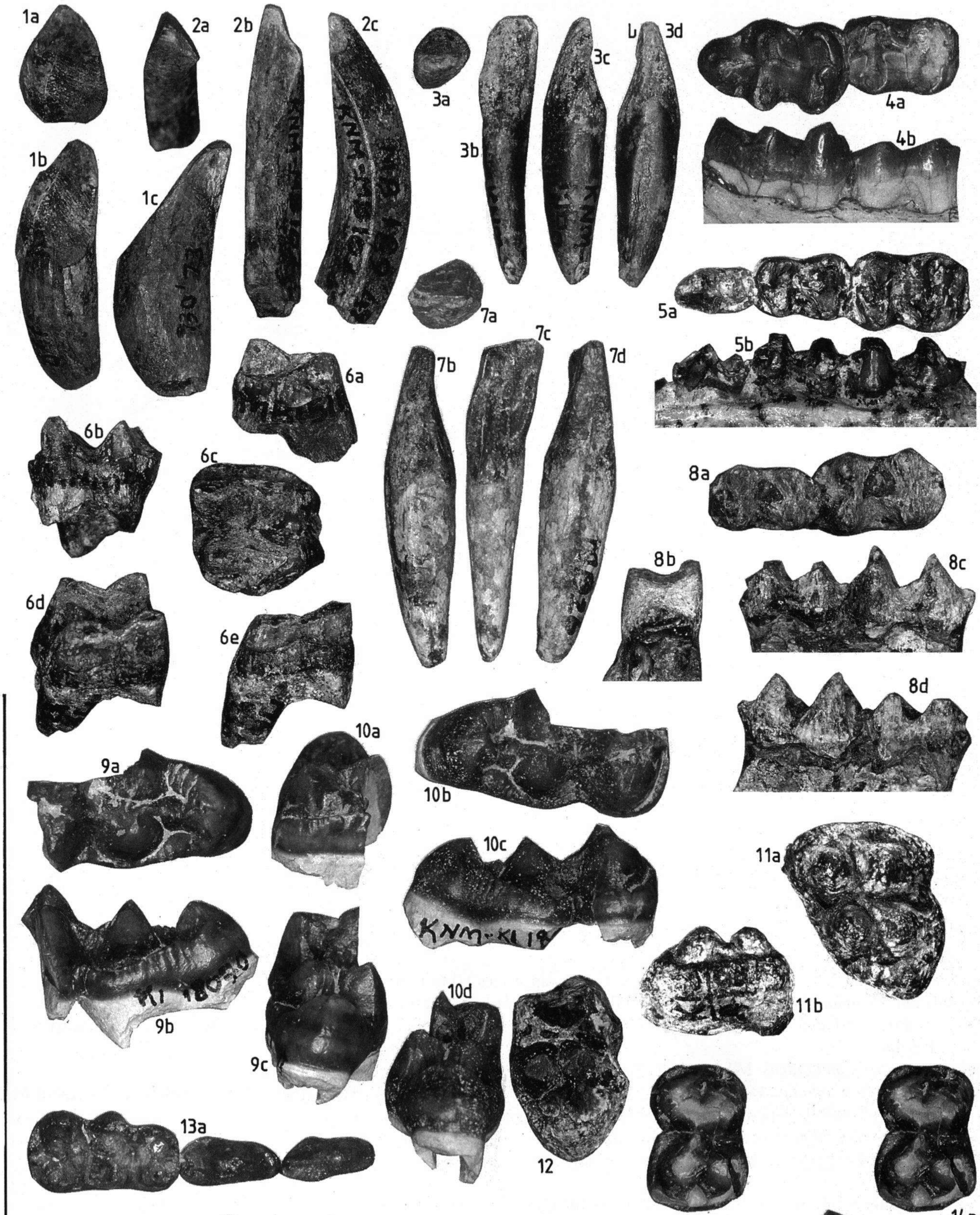
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PLATE 4

Fig. 1. *Bunolistriodon anchidens*; KNM-RU 8322, right I^1 (ap-li-mes-la) from Rusinga.

Fig. 2. *Lopholistriodon kidogosana*; KNM-BN 2084, right M_2 (ant-li-po-oc) from the Ngorora Formation.

Figs 3, 5. *Bunolistriodon meidamon*; **3** - PIMUZ BP 87, right C_m (li-la) from Paşalar; **5** - PIMUZ BP 85, right C_m (la-li) from Paşalar.

Fig. 4. *Bunolistriodon latidens*; MTA AKI-3/780, skull (oc) from Inönü I.

Figs 6, 7. *Lopholistriodon pickfordi* n. sp.; **6** - KNM-WS 115, right mandible with M_2-M_3 (oc-po-li-buc), **holotype**; **7** - KNM-WS 12582, left M^3 (li-oc-po-ant), **paratype**, from West Stephanie-Buluk.

Figs 8, 9. *Lopholistriodon moruoroti*; **8** - KNM-MB 14482, left M_3 (ant-oc-buc-li) from Maboko; **9** - KNM-MO 5A, left mandible with P_2-M_3 (oc), part of **holotype**, from Moruorot.

Scale bar equals 5 cm for Figs 1, 2, 6-9, and 20 cm for Figs 3-5 (photographs by the author, copyright for Figs 1, 2, 6-9 Kenya National Museums).

PLATE 4

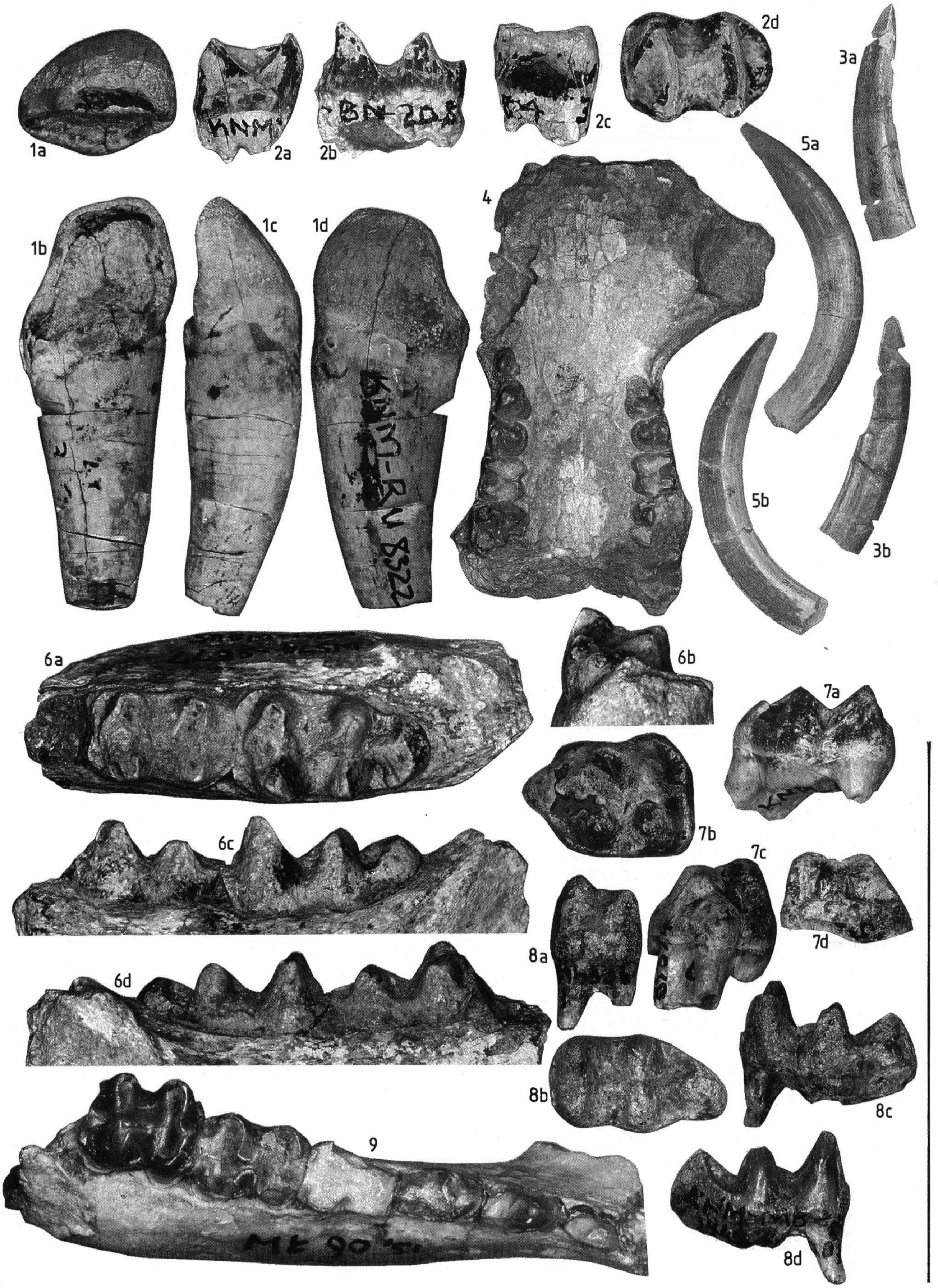
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PLATE 5

Figs 1-12, 14-16. *Lopholistriodon kidogosana*; Ngorora Formation, member B (locality 2/56) and member D (localities 2/10 and 2/11).

1 - KNM-BN 190, left I^1 (ap-li-la) from locality 2/11;
2 - KNM-BN 726, left I^2 (ap-la-li) from locality 2/56;
3 - KNM-BN 842, left I^3 (ap-li) from locality 2/56;
4 - KNM-BN 1728, right I^2 (ap-li) from locality 2/56;
5 - KNM-BN 1712, left P^3 (oc-buc) from locality 2/56;
6 - KNM-BN 1473, left P^4 (oc-buc-ant-po-li) from locality 2/56;
7 - KNM-BN 1729, left P$_4$ (oc-po-li-ant-buc) from locality 2/56;
8 - KNM-BN 1475, right P^3 (oc-buc) from locality 2/56;
9 - KNM-BN 188, left M$_3$ (oc-ant-buc-po-li) from locality 2/11;
10 - KNM-BN 1744, right M^2 (oc-po-buc-ant) from locality 2/56;
11 - KNM-BN 1471, right M^2 (buc-ant-po-oc) from locality 2/56;
12 - KNM-BN 2027, left M^2 (oc-ant-buc-po) of unknown exact provenance;
14 - KNM-BN 992, left M^2 and M^3 (oc), locality 2/10, part of **holotype**;
15 - KNM-BN 992, right P^2-P^4 (oc-buc), locality 2/10, part of **holotype**;
16 - KNM-BN 385, left M^3 (oc-buc-ant), locality 2/11;

Fig. 13. *Lopholistriodon pickfordi* n. sp.; KNM-MJ 9778, left I^1 and I^2 (ap-li-la) from Majiwa

Scale bar represents 5 cm (photographs by the author, copyright for all figures Kenya National Museums).

PLATE 5

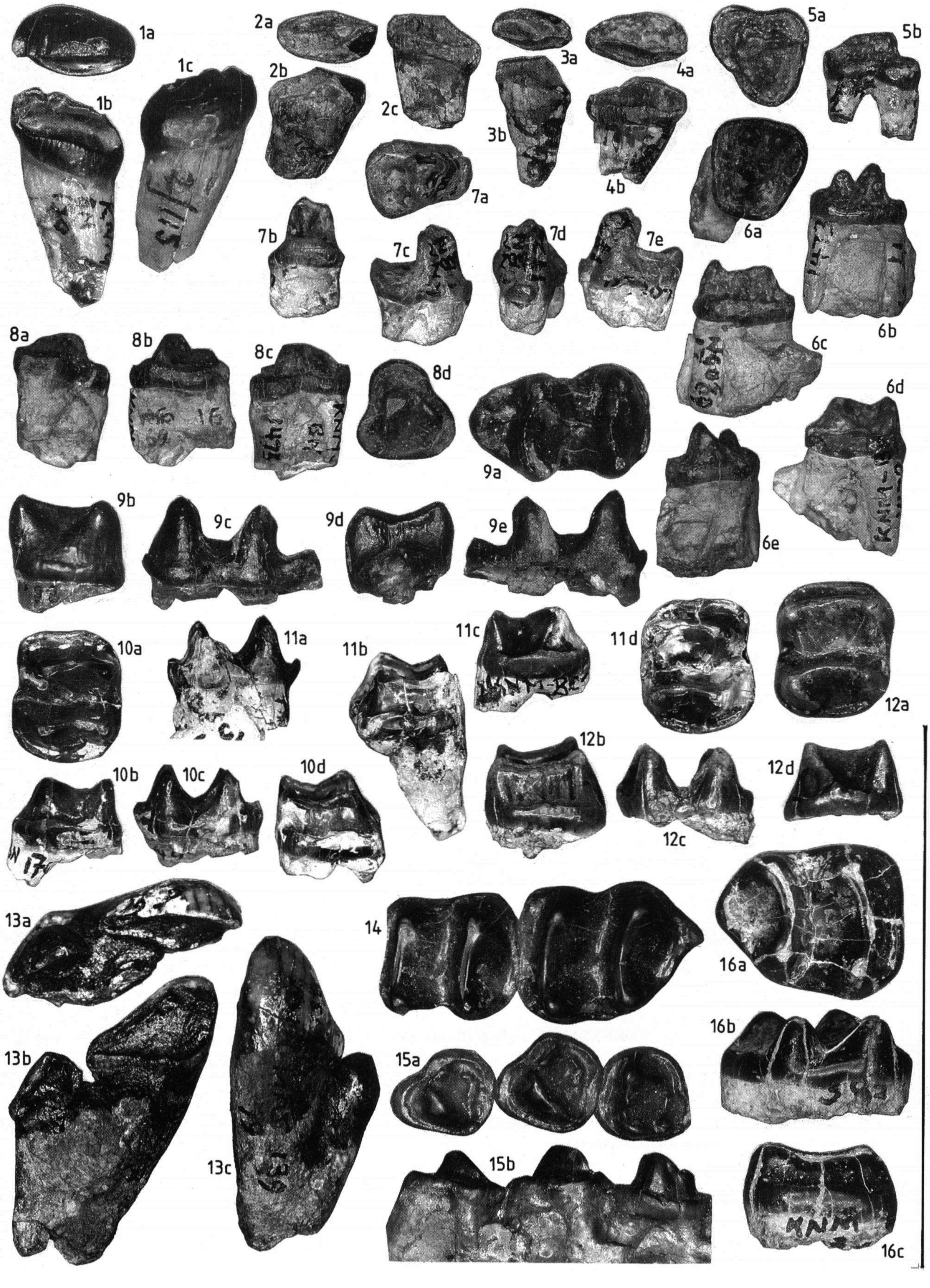
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PLATE 6

Figs 1-11. *Lopholistriodon akatidogus*; **1** - KNM-MG 7, right I_2 (li-dist-ap) from Mbagathi; **2** - KNM-FT 3319, right M^1 (oc) from Fort Ternan; **3** - KNM-MG 9, left M_3 (oc-buc-li-po-ant), **holotype** from Mbagathi; **4** - KNM-FT 3790, left I^2 (ap-la-li) from Fort Ternan; **5** - KNM-MJ 9777, right I^3 (ap-li-la) from Majiwa; **6** - KNM-MB 19518, right C^m (li) from Maboko; **7** - KNM-MB 862, right M^3 (po-oc-ant) from Maboko; **8** - KNM-FT 3319, right P^4 (oc-ant-buc) from Fort Ternan; **9** - KNM-FT 3325, left D^4 (oc-buc-ant/oc) from Fort Ternan; **10** -KNM-MB 10370, right M_2 (po-oc-buc-ant) from Maboko; **11** - KNM-X 208, right M_2-M_3 (oc-li) of unknown provenance.

Scale bar represents 5 cm, except for Fig. 6, where it equals 10 cm (photographs by the author, copyright for all figures Kenya National Museums).

PLATE 6

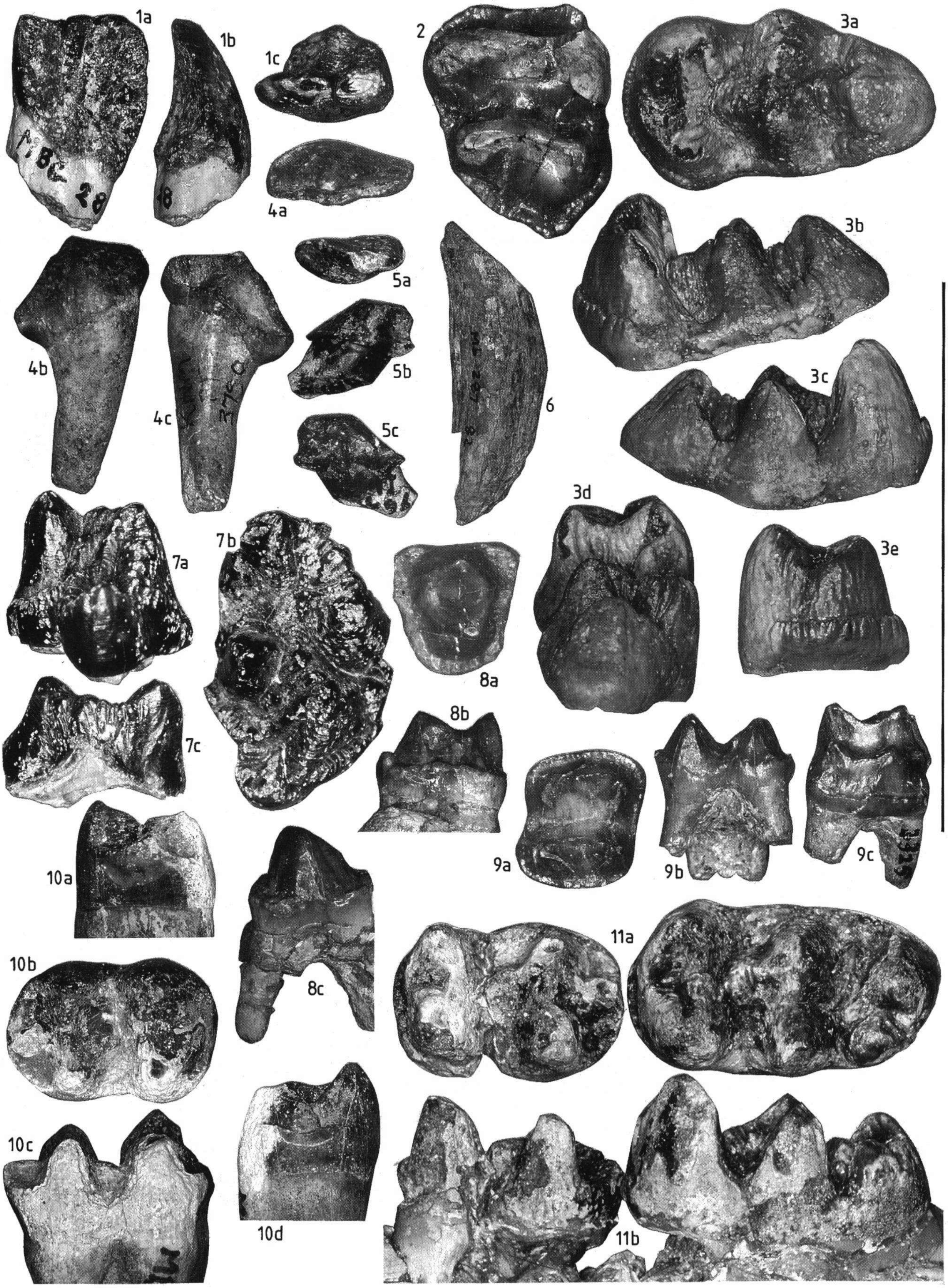
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PLATE 7

Figs 1, 2, 5, 7-9, 11-15. *Kubanochoerus marymunnguae* n. sp.; **1** - KNM-WS 12590, left M^3 (oc); **2** - KNM-WS 12594, right M^3 (oc-buc); **5** - KNM-WS 149B, right P$_4$ (oc-buc-ant-li-po); **7** - KNM-WS 12595, left P$_2$ (li-oc-buc) (**holotype**); **8** - KNM-WS 12595, left P$_3$ (li-oc-buc) (**holotype**); **9** - KNM-WS 12595, left P$_4$ (li-oc-buc) (**holotype**); **11** - KNM-WS 12595, left M$_2$ (oc) (**holotype**); **12** - KNM-WS 12588, right P^2 (oc-po-li-ant-la); **13** - KNM-WS 149A, right I$_2$ (ap-li-mes-dist); **14** - KNM-WS 149B, left I$_3$ (dist-li-mes-ap); **15** - KNM-WS 12595, left M$_3$ (oc) (**holotype**), all from West Stephanie-Buluk.

Figs 3, 4, 6, 10. *Kubanochoerus gigas*; **3** - FISF SMF/PA/F 6168, right P^2 (oc-buc-po-li-ant) of unknown exact provenance, from Chinji Formation; **4** - IVAU CHK 120, left D^2 (buc-oc-li) from Kundal Nali; **6** - IVAU CH 262, left I^2 (ap-li-la) from Kundal Nali; **10** - IVAU CHK 168, first phalange, left of axis of foot (dors-prox) from Kundal Nali, Chinji Formation.

Scale bar equals 10 cm, except for Fig. 10 where it represents 20 cm (photographs by the author, copyright for Figs 1, 2, 5, 7-9, 11-15 Kenya National Museums).

PLATE 7

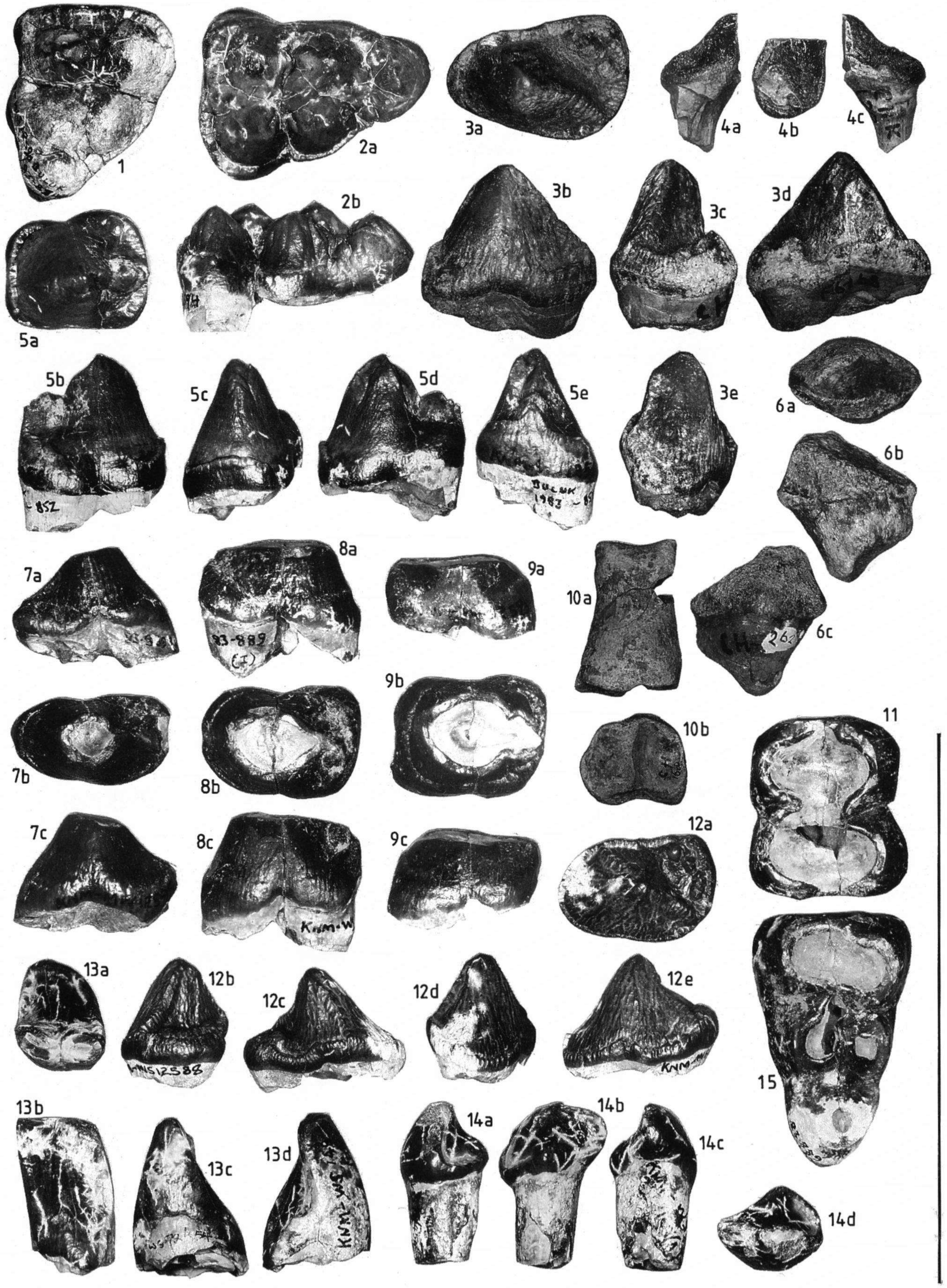
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PLATE 8

Figs 1-19. *Kubanochoerus massai* from Gebel Zelten;

1 - MNHNP Z-1961, right I^2 (ap-li-la);
2 - MNHNP Z-1961, left I^3 (la-ant-li-ap);
3 - MNHNP Z-1961, right I^1 (ap-li-mes-la-dist);
4 - MNHNP Z-1961, left I^3 (ap-li-mes-la);
5 - MNHNP Z-1961, right I^1 (li);
6 - MNHNP Z-1961, right I_2 (mes-li-dist-la-ap);
7 - MNHNP Z-1961, right I_1 (ap-mes-li-dist-la);
8 - MNHNP Z-1961, right DI^1 (ap-li-mes-la);
9 - MNHNP Z-1961, right I^1 (li);
10 - MNHNP Z-1961, right I^1 (li);
11 - MNHNP Z-1961, left I_3 (ap-la-dist-li-mes);
12 - MNHNP Z-1961, left I^2 (ap-la-mes-li);
13 - MNHNP Z-1961, right C^m (ap-la-po-li);
14 - MNHNP Z-1961, left I_2 (li-ap);
15 - MNHNP Z-1961, right I_2 (li-dist-ap);
16 - MNHNP Z-1961, left I_3 (li);
17 - MNHNP Z-1961, right I_2 (li);
18 - MNHNP Z-1961, left I_3 (li);
19 - MNHNP Z-1961, left C_m (li);

Scale bar equals 10 cm.

PLATE 8

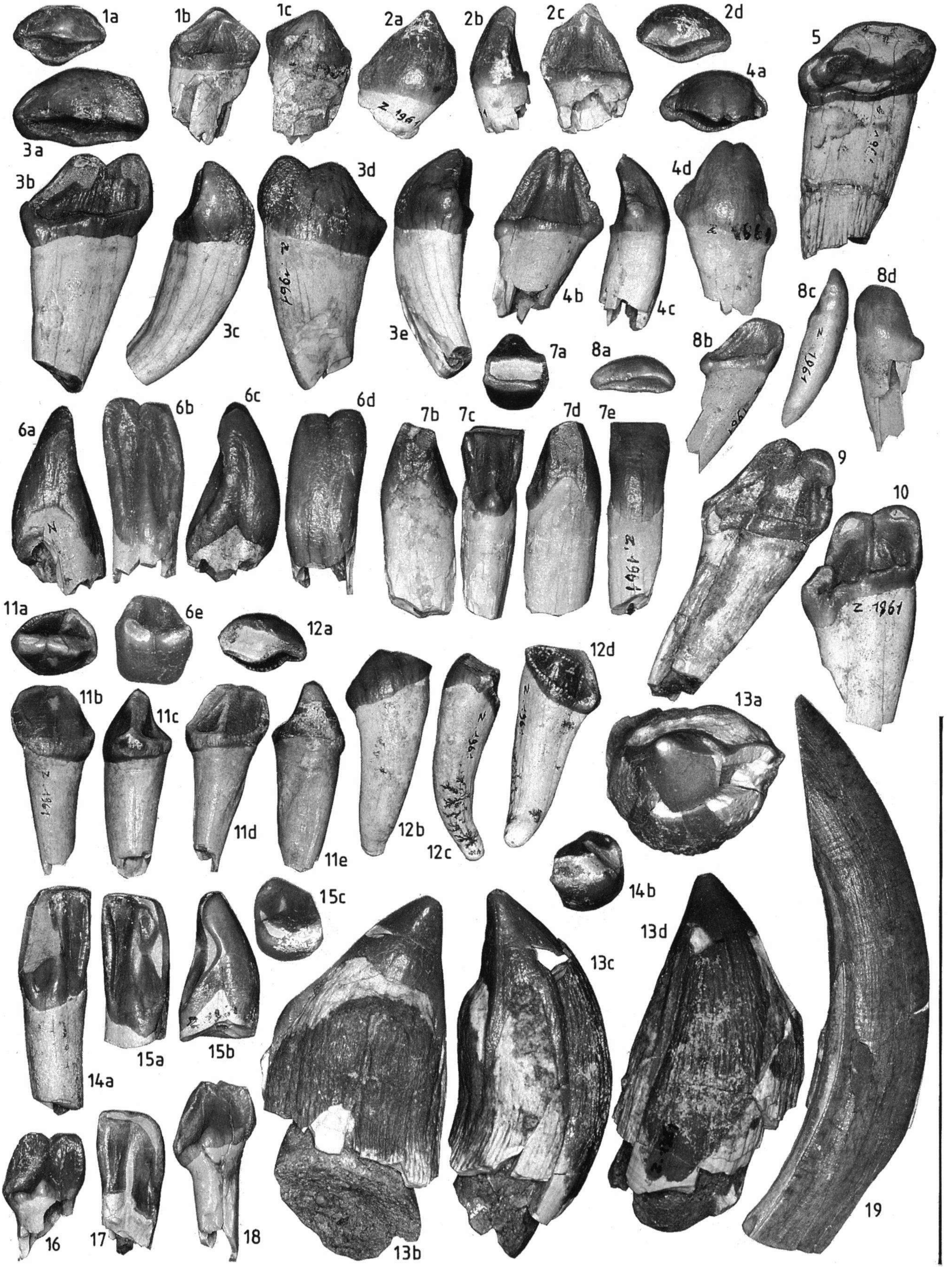
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PLATE 9

Figs 1-15, 18. *Kubanochoerus massai* from Gebel Zelten; **1** - MNHNP Z-1961, right P_4 (li-buc-oc); **2** - MNHNP Z-1961, left P_4 (oc-buc-li); **3** - MNHNP Z-1961, right P_4 (oc-buc-li); **4** - MNHNP Z-1961, left P_4 (oc-li); **5** - MNHNP Z-1961, right P_4 (oc); **6** - MNHNP Z-1961, left P_4 (oc); **7** - MNHNP Z-1961, left P_3 (oc-li-buc); **8** - MNHNP Z-1961, right P_2 (oc-buc-li); **9** - MNHNP Z-1961, left D_3 (oc-li-buc); **10** - MNHNP Z-1961, right P_3 (oc-buc-li); **11** - MNHNP Z-1961, right P_1 (oc-buc-li); **12** - MNHNP Z-1961, left P_3 (oc-li-buc); **13** - MNHNP Z-1961, right P_2 (li-buc-oc); **14** - MNHNP Z-1961, right P_1 (li-oc-buc); **15** - MNHNP Z-1961, right D_3 (oc-li); **18** - MNHNP Z-1961, left D_2 and half of the D_3 (oc-li).

Figs 16, 17, 19. *Kubanochoerus minheensis* from Nanhawangou, parts of **holotype**; **16** - IVPP V 6021, left P_1 (buc-oc); **17** - IVPP V 6021, left P_2 (oc-li-buc); **19** - IVPP V 6021, left P_3 and P_4 (oc-li-buc).

Scale bar equals 10 cm.

PLATE 9

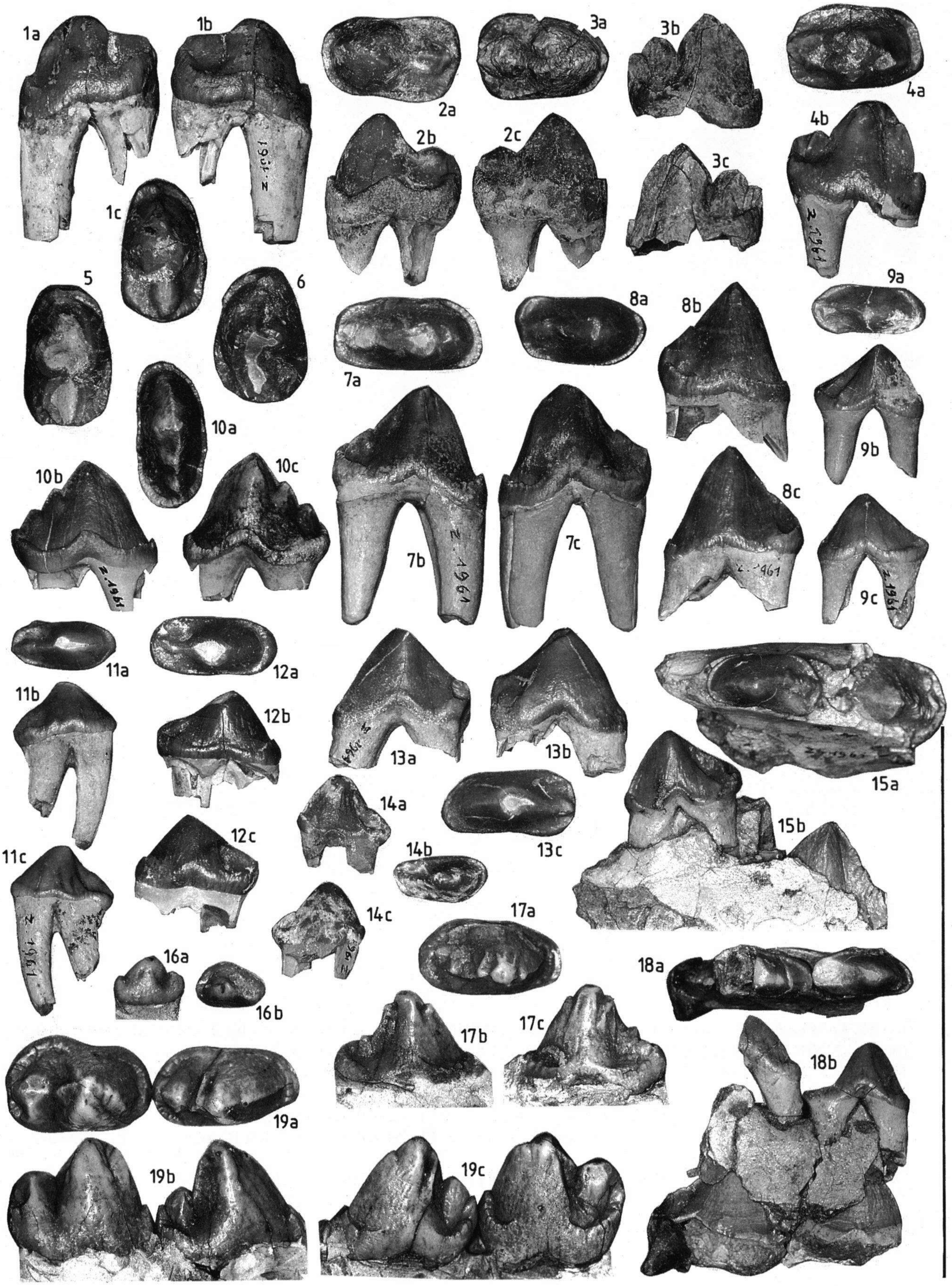
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PLATE 10

Figs 1-3, 5-18. *Kubanochoerus massai* from Gebel Zelten; **1** - MNHNP Z-1961, left M_3 (oc-buc-li); **2** - MNHNP Z-1961, left M_3 (oc); **3** - MNHNP Z-1961, left M_3 (oc); **5** - MNHNP Z-1961, right M_2 (oc-la-ant); **6** - MNHNP Z-1961, right M_3 (oc); **7** - MNHNP Z-1961, left M^3 (oc); **8** - MNHNP Z-1961, right M^3 (oc); **9** - MNHNP Z-1961, right M^2 (ant-buc-li-oc); **10** - MNHNP Z-1961, right D^4 (oc); **11** - MNHNP Z-1961, right P^4 (oc-ant-buc-po); **12** - MNHNP Z-1961, left P^4 (oc-po-buc); **13** - MNHNP Z-1961, right P^4 (oc-buc-ant); **14** - MNHNP Z-1961, right P^2 (oc-buc-li); **15** - MNHNP Z-1961, left P^2 (oc-buc-ant-li-po); **16** - MNHNP Z-1961, left P^3 (oc-li-po-buc-ant); **17** - MNHNP Z-1961, left D^2 (oc-buc-li); **18** - MNHNP Z-1961, right P^3 (oc-li-buc).

Fig. 4. *Kubanochoerus minheensis* from Nanhawangou, part of **holotype**; IVPP V 6021, left M_3 (oc-buc-la).

Scale bar represents 10 cm.

PLATE 10

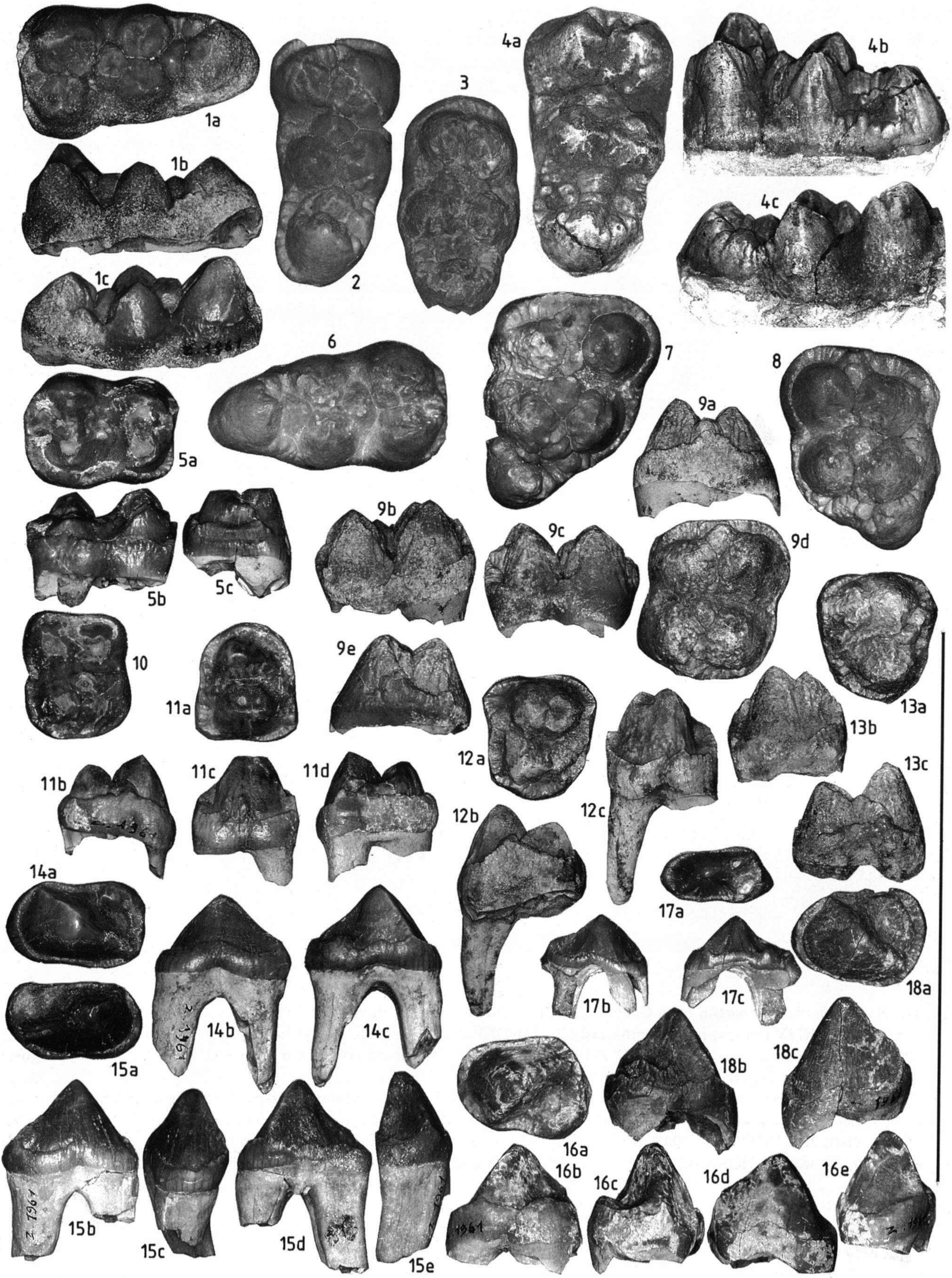
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PLATE 11

Figs 1-6, 8. *Kubanochoerus massai* from Gebel Zelten; **1** - MNHNP Z-1961, right MC III (ant-int-post-ext-prox); **2** - MNHNP Z-1961, left MC IV (ant-ext-post-int-prox-dist); **3** - MNHNP Z-1961, left MC II (ext-int-post-dist); **4** - MNHNP Z-1961, left MT III (prox-ant-int-post); **5** - MNHNP Z-1961, left MT IV (prox-ant-ext-post-int); **6** - MNHNP Z-1961, right MT II (post-ext-ant-int-prox-dist); **8** - MNHNP Z-1961, right MC III (ant).

Figs 7, 9, 10. *Kubanochoerus mancharensis* n. sp.; **7** - HGSP 8425/3557, right astragalus (prox-po) from locality HGSP 8425 in the Manchar Formation (**holotype**); **9** - HGSP 8127/432, second phalange of central toe, left of axis of foot (dors-int-plant-ext-prox-dist); **10** - HGSP 8405/3047, first phalange of central toe, left of axis of foot, juvenile, proximal part lacking (dors-dist) from localities HGSP 8127 and HGSP 8405 in the Manchar Formation.

Scale bar equals 10 cm, except for Figs 7 and 10, where it represents 20 cm.

PLATE 11

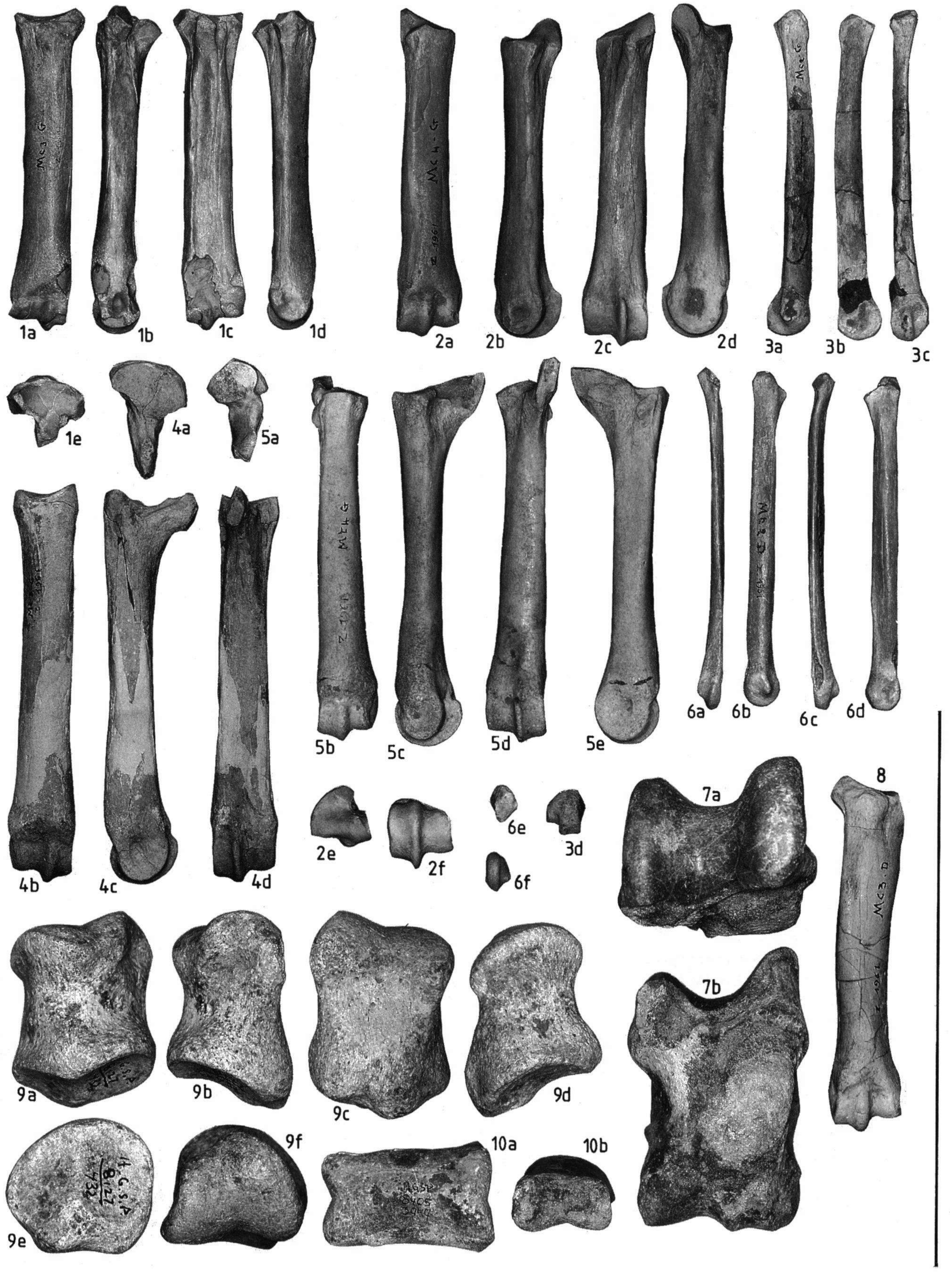
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PLATE 12

Figs 1-7, 9, 13-16. *Kubanochoerus gigas* from Maerzuizigou, Tongxin; **1** - BNHM BPV-905, left P_4 (oc-buc); **2** - BNHM BPV-905, right P_4 (oc-buc); **3** - BNHM BPV-905, left P_3 (oc-buc); **4** - BNHM BPV-905, right P_2 (oc-buc); **5** - BNHM BPV-905, left P_1 (oc-li-buc); **6** - BNHM BPV-909, left P^1 (oc); **7** - BNHM BPV-909, right P^1 (buc-oc-li); **9** - BNHM BPV-905, right M_3 (oc-li-buc); **13** - BNHM BPV-905, right P_3 (buc-oc); **14** - BNHM BPV-909, left P^2 (oc); **15** - BNHM BPV-909, left P^3 (oc); **16** - BNHM BPV-909, left P^4 (oc).

Figs 8, 10, 11. *Kubanochoerus minheensis*; **8** - BNHM BPV—, right P^4 (oc-li-ant-buc-po) from Guanghe; **10** - BNHM BPV—, right I^2 (li-oc-la) from Guanghe; **11** - IVPP V 6021, symphysis with left I_1 - I_2 and right I_1-I_3 (li) from Nanhawangou, part of **holotype**.

Fig. 12. *Kubanochoerus mancharensis* from locality HGSP 8311, Manchar Formation; HGSP 8311/1556, second phalange of side toe, right of axis of foot (int-dors-ext-plant-dist-prox).

Scale bar represents 10 cm.

PLATE 12

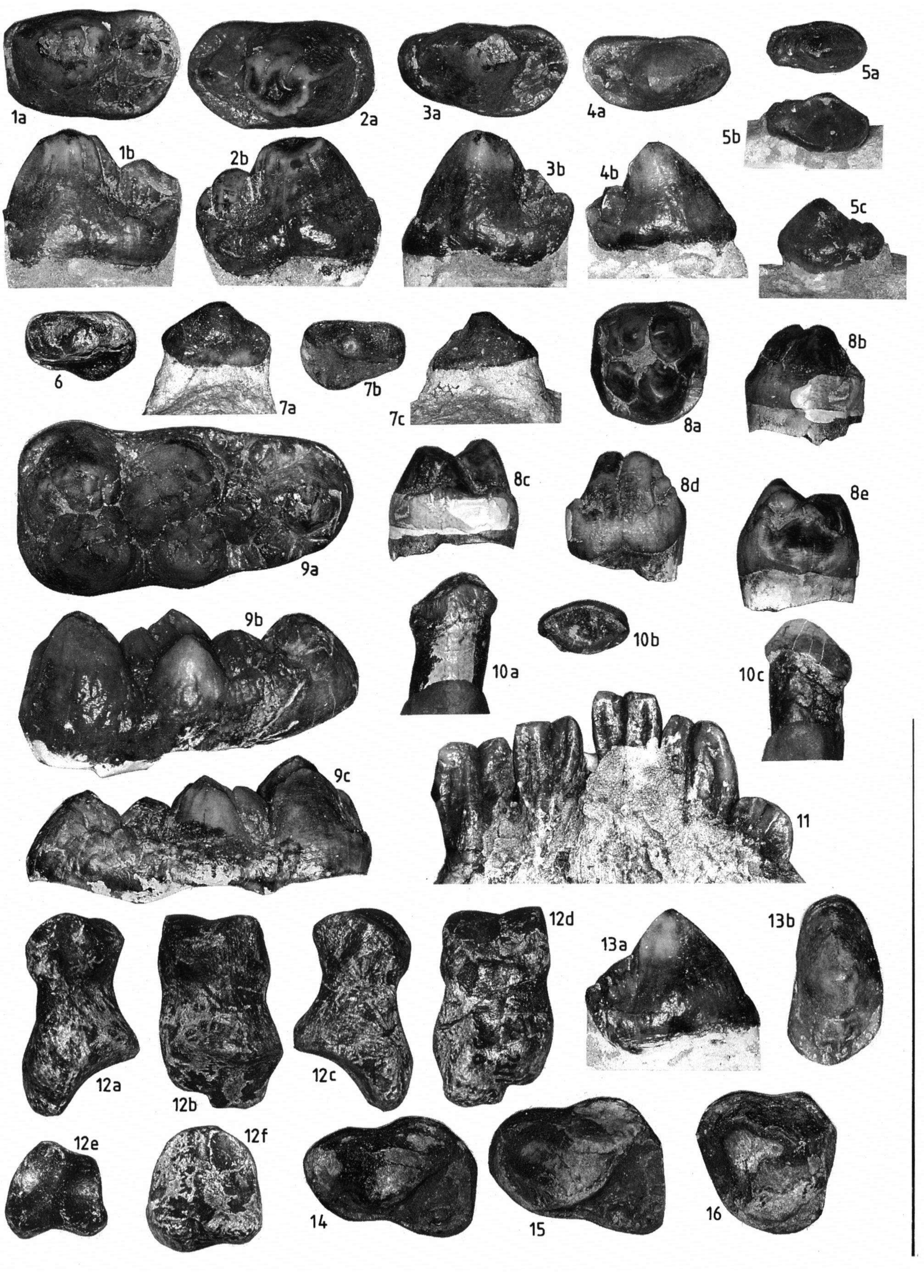
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PLATE 13

Fig. 1. *Bunolistriodon affinis* from Bugti (**holotype**); IM B 528, right P^4 and M^1 (oc-li-buc-po).

Figs 2, 4-7, 10.*Bunolistriodon anchidens* from Rusinga; **2** - KNM-RU 5847, left I^2 (ap-la-li) from Rusinga R3; **4** - KNM-RU 2780, left M^3 (oc) from Rusinga R1; **5** - KNM-RU 2785, right P_1 (ap-buc) from Rusinga R1, part of **holotype**; **6** - KNM-RU 4415, left P_2 (oc-buc-li), exact provenance unknown; **7** - KNM-RU 2781b, right M^2 (oc) from Rusinga R1; **10** - KNM-RU 9785, right P^1 (buc-oc-li).

Figs 3, 8, 9, 11. *Bunolistriodon jeanneli*; **3** - IM GSI 18098, left P_4-M_1 (oc-li-buc) from Fategad (part of **holotype** of *B. fatehgadensis*); **8** - KNM-MO 10, right DI^1 (ap-dist-li) from Moruorot; **9** - IM GSI 18098, left M_2 (oc) from Fategad (part of **holotype** of *B. fatehgadensis*); **11** - IM GSI 18098, left M_3 (oc) from Fategad (part of **holotype** of *B. fatehgadensis*).

Scale bar equals 5 cm for all figures, except for Fig. 7 where it represents 10 cm (photographs by the author, copyright for Figs 2, 4-8, 10 Kenya National Museums).

PLATE 13

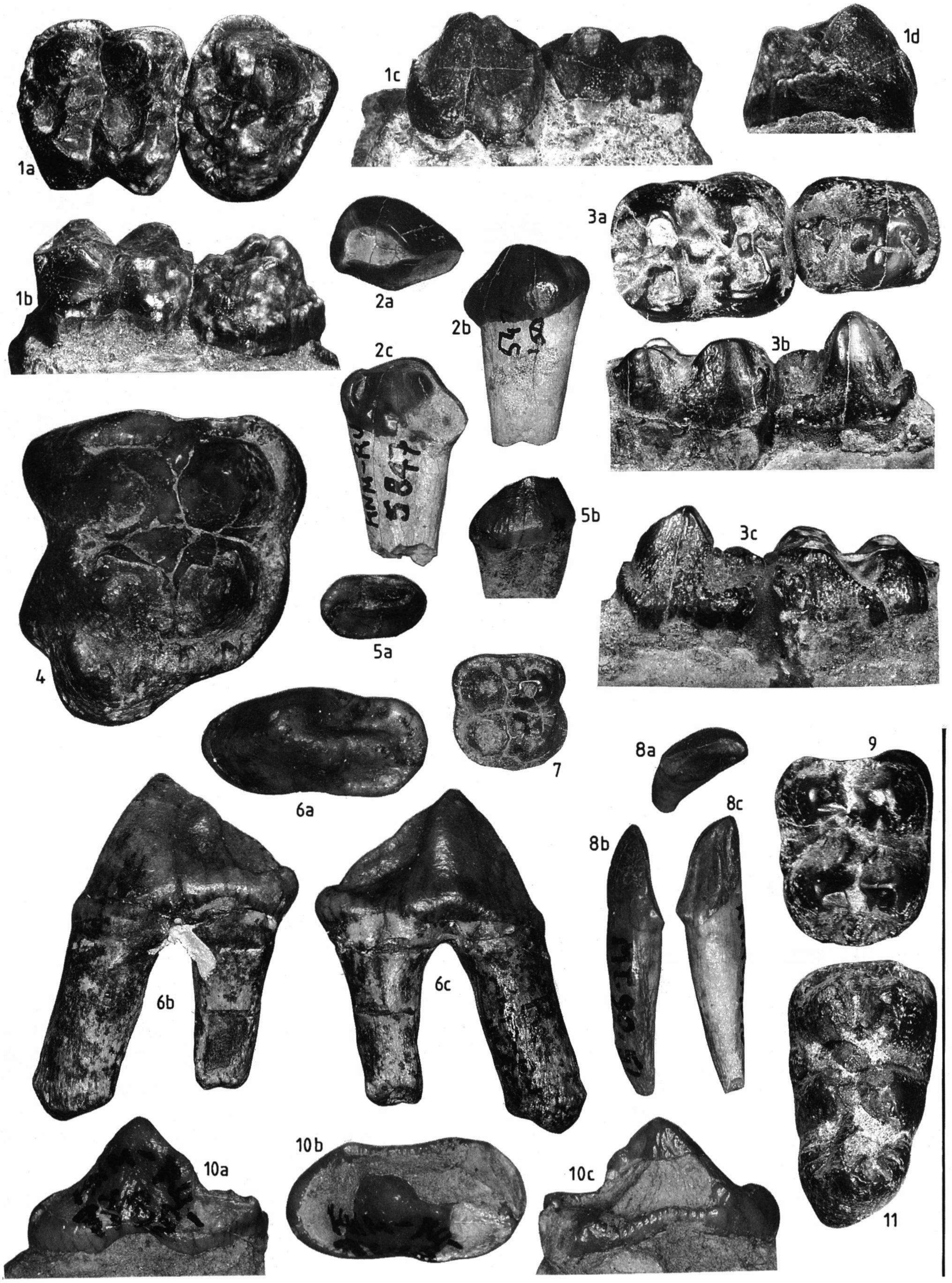
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PLATE 14

Figs 1-4, 7-9, 11, 13. *Bunolistriodon anchidens*; **1** - KNM-RU 2785, right I_2 (mes-li-dist-ap) from Rusinga R1, part of the **holotype**; **2** - KNM-RU 2785, left P_4 (oc-buc-li) from Rusinga R1, part of the **holotype**; **3** - KNM-RU 5846, right I^2 (ap-li-la) from Rusinga 3a; **4** - KNM-RU 2780, left P^2 (buc-oc-li) from Rusinga R1; **7** - KNM-RU 952, left C^m (la) from Rusinga without exact provenance data; **8** - KNM-RU 977, right P^3 (oc-buc-li) from Rusinga Gumba; **9** - KNM-RU 2785, left M_2 (oc) from Rusinga R1, part of the **holotype**; **11** - KNM-RU 5844, left P^1 (oc-li-buc) from Rusinga R1; **13** - KNM-RU 2785, left M_3 (oc) from Rusinga R1, part of the **holotype**.

Figs 5, 6, 10, 12. *Bunolistriodon jeanneli* from Moruorot parts of **holotype**; **5** - MNHNP 1933-9, left P^3-P^4 (oc-li-buc); **6** - MNHNP 1933-9, left M^2 (oc); **10** - MNHNP 1933-9, right P^3-P^4 (oc-li-buc); **12** - MNHNP 1933-9, left M^3 (oc).

Scale bar represents 5 cm for Figs 1-4, 8, 9 and 11-13 and 10 cm for Figs 5-7 and 10 (photographs by the author, copyright for Figs 1-4, 7-9, 11 and 13 Kenya National Museums).

PLATE 14

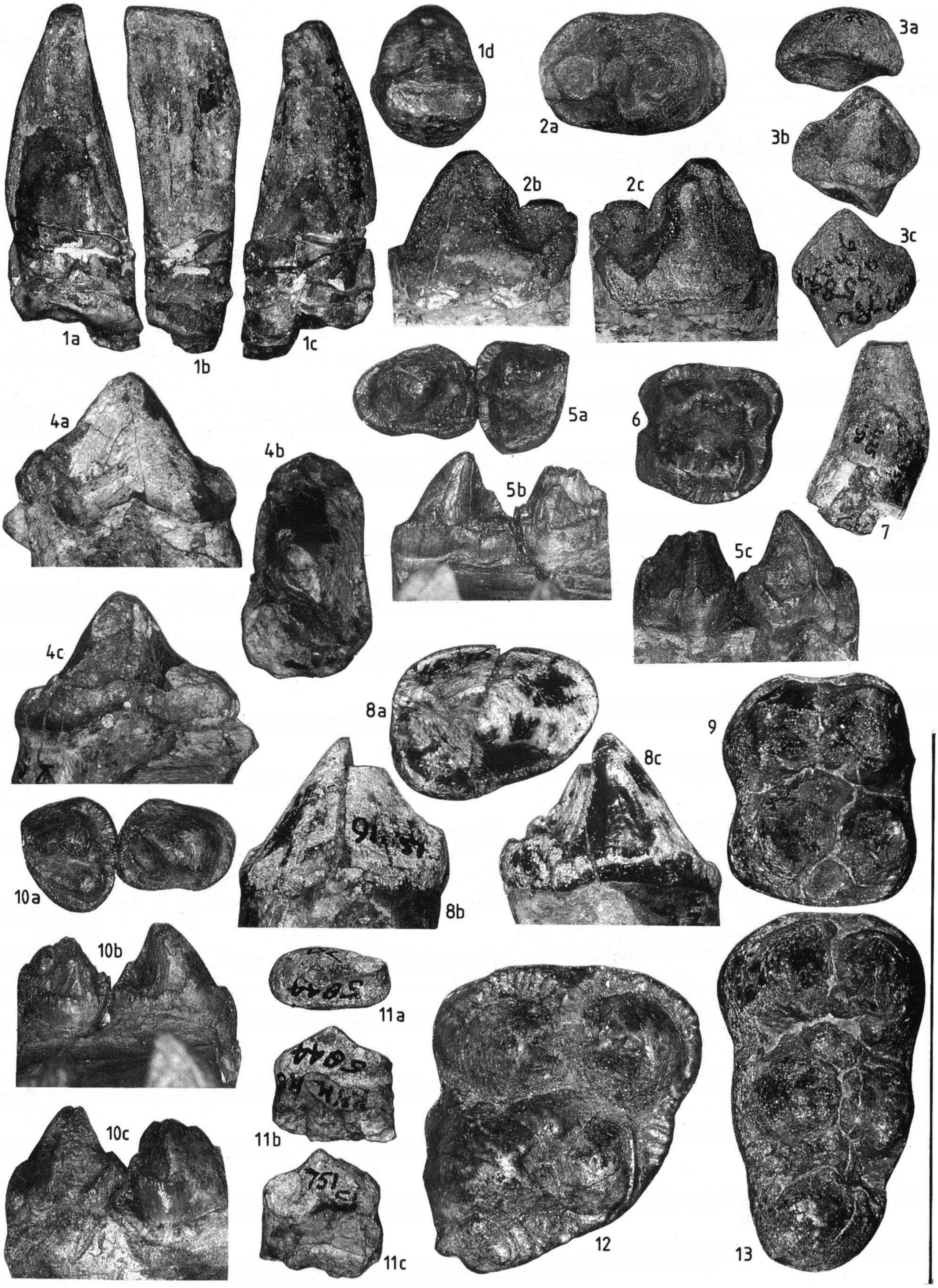
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PLATE 15

Figs 1, 3-16. *Bunolistriodon* aff. *latidens*

1 - IVAU VL3/6, right I_1 (li-ap) from Villafeliche III;
3 - IVAU 55/1055, left I^1 (ap-la-mes-li) Munebrega I;
4 - IVAU Mun 3, right I^1 (ap-li-la) Munebrega AB;
5 - IVAU 41/425, left I_3 (ap-la-li) from Armantes I;
6 - IVAU 41/519, right P^3 (ant-la-li-oc-po) from Armantes I;
7 - IVAU 55/1094, left C^f (buc-ant-li-po) from Munebrega I;
8 - IVAU 41/511, right M^3 (oc-ant) from Armantes I;
9 - IVAU 18/201, left P^4 (po-oc-buc-ant) from Torralba II;
10 - IVAU 41/560, right DI_2 (ap-li-dist-la-mes) from Armantes I;
11 - IVAU 55/59, left I^3 (ap-la-li) from Munebrega I;
12 - IVAU 41/510, right M^3 (oc) from Armantes I;
13 - IVAU 41/522, right M^2 (oc) from Armantes I;
14 - IVAU 41/543, left M_1 (oc-buc-po-li-ant) from Armantes I;
15 - IVAU 41/529, right P^4 (ant-buc-po-oc) from Armantes I;
16 - IVAU 41/527, left I^1 (ap-li) from Armantes I;

Fig. 2. *Bunolistriodon lockharti* from Can Canals, IPS 1184, right M^1 (oc), **holotype** of *Palaeochoerus giganteus*.

Scale bar represents 6.7 cm for all figures, except for Fig. 2, where it equals 10 cm.

PLATE 15

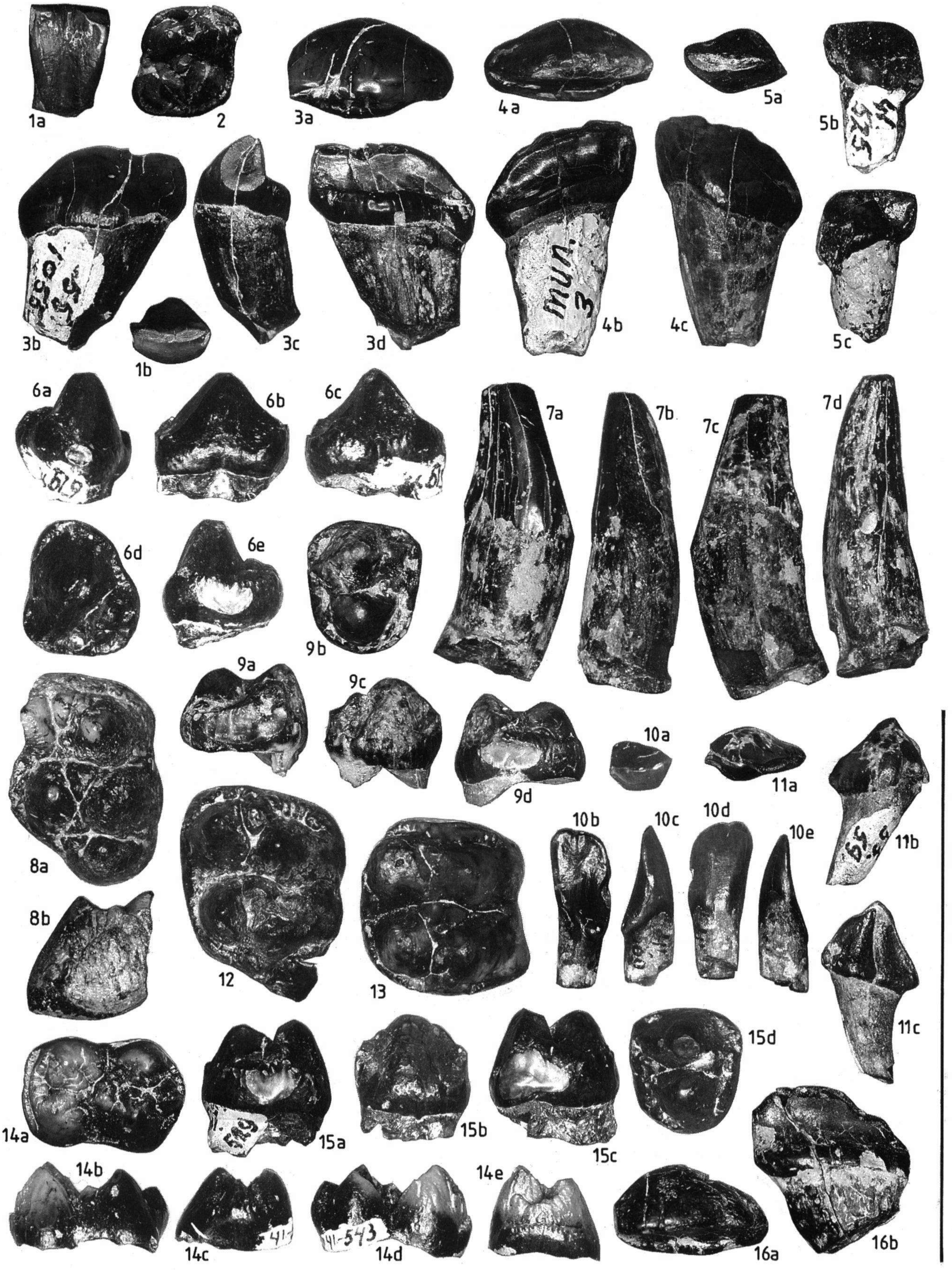
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PLATE 16

Bunolistriodon aff. *latidens*

1 - IVAU 41/521, left M^2 (oc-li-po-la-ant) from Armantes I;
2 - IVAU 55/1054, left I_2 & 55/1061, left I_1 of a single individual (li) from Munebrega I;
3 - IVAU 53/54, left I_2 (dist-li-mes-ap) from Munebrega III;
4 - IVAU 41/537, right I^2 (ap-la-li) from Armantes I;
5a - IVAU VL3/6, right I_1 (mes) from Villafeliche III;
5b - IVAU 53/55, right I_1 (ap) from Munebrega III;
6 - IVAU 41/509, right M^3 from Armantes I;
7 - IVAU 55/1049, left M_3 (po-ant-oc-buc-li) from Munebrega I;
8 - IVAU 53/50, right mandible with C_m and alveolus of P_1 (buc-li) from Munebrega III;
9 - IVAU 53/58, right I_3 (la-ap-li) from Munebrega III;
10 - IVAU 55/1050, right P_4 (oc-buc-li) from Munebrega I;
11 - IVAU 55/1049, left P_3-P_4 and partial P_2 (oc-buc-li) from Munebrega I;
12 - IVAU 41/507, right M_3 (oc) from Armantes I;

Scale bar equals 6.7 cm.

PLATE 16

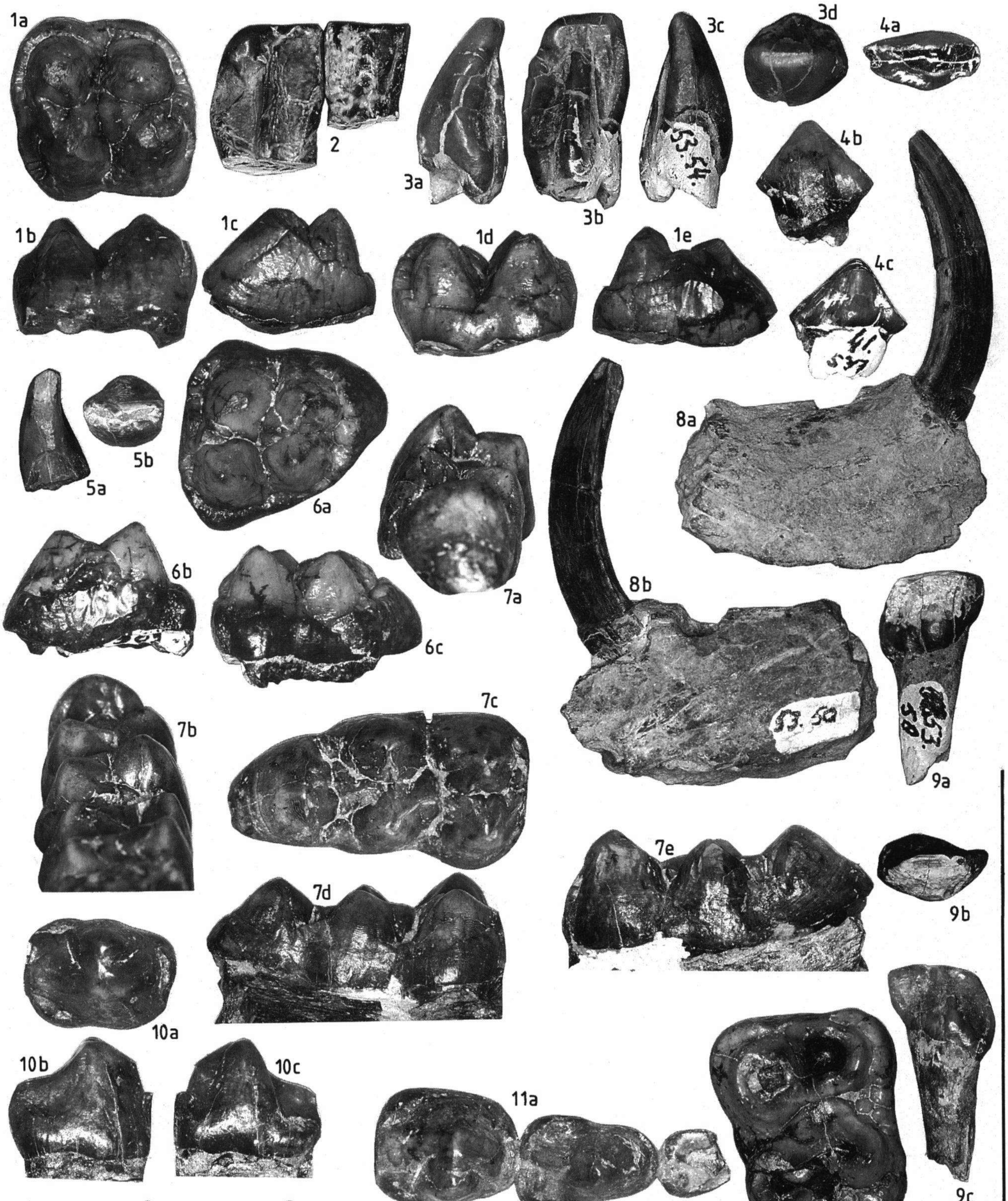
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PLATE 17

Figs 1-7. ***Bunolistriodon*** aff. ***latidens***; **1** - IVAU 55/1053, left C_f (li-po-la) from Munebrega I; **2** - IVAU 53/55, right I_1 (li-dist-la-dist) from Munebrega III; **3** - IVAU 55/1060, left I_3 (li-la) from Munebrega I; **4** - IVAU 41/539, right DI^1 (ap-li-mes-la) from Armantes I; **5** - IVAU 41/526, left I^1 (ap-li-la) from Armantes I; **6** - IVAU 41/516, left P_4 (oc-buc-li) from Armantes I; **7** - IVAU 41/603, left magnum (prox-int-dist-ext) from Armantes I.

Fig. 8. ***Bunolistriodon meidamon*** from Çandir, PIMUZ CA I, left I^1 (ap-li-la).

Figs 9-11. ***Bunolistriodon*** sp. from Baragoi; **9** - KNM-BG 15393, left P^4 (po-buc-ant-oc); **10** - KNM-BG 14786, right I_2 (ap-dist-mes-li); **11** - KNM-BG 14778, left M^1-M^2 (oc).

Scale bar equals 5 cm for Figs 9-11, 6.7 cm for Figs 1-7 and 10 cm for Fig. 8 (photographs by the author, copyright for Figs 9-11 Kenya National Museums).

PLATE 17

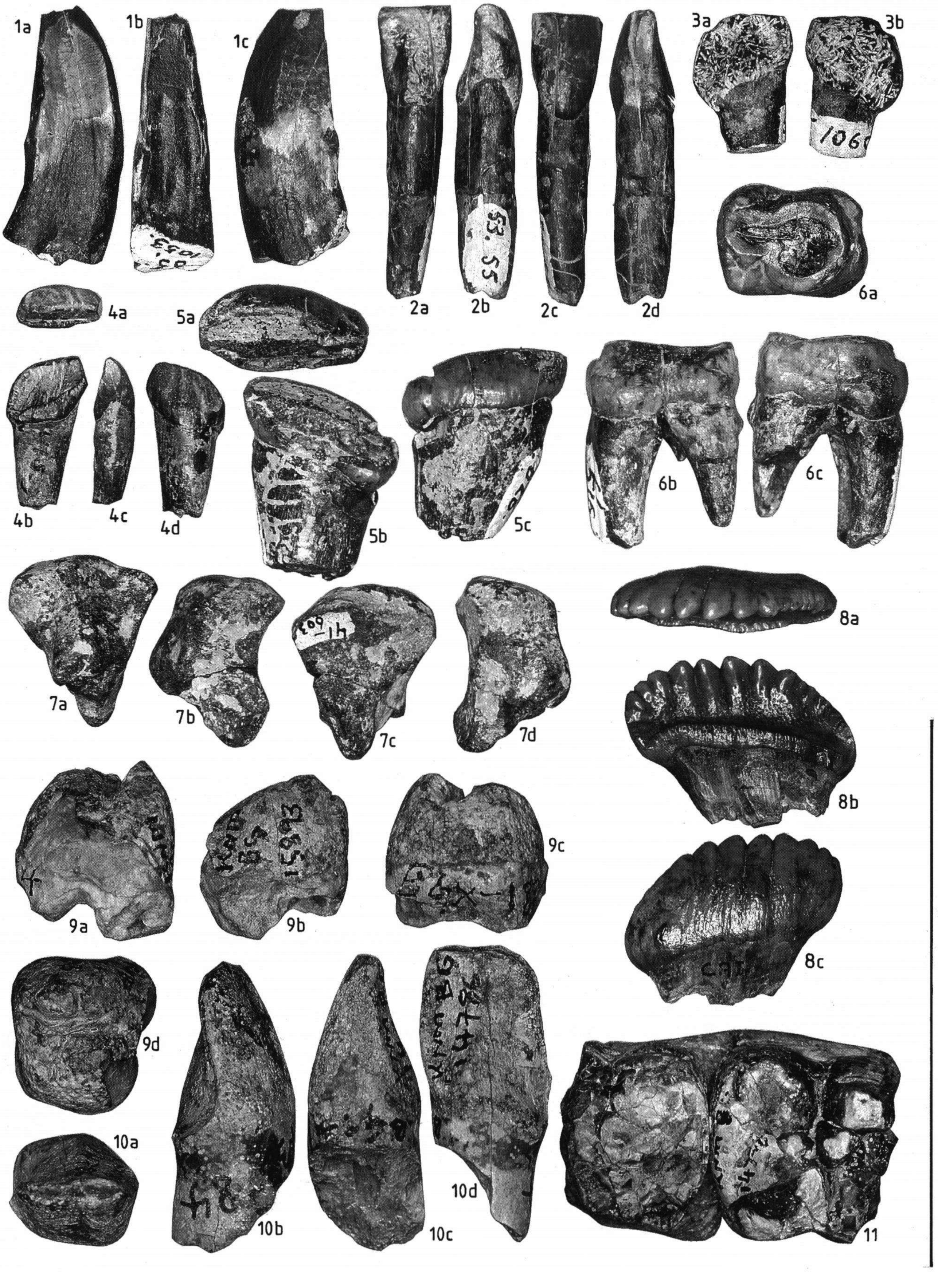
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PLATE 18

Bunolistriodon latidens

1 - NSSW 113, left C^m (li) from Veltheim (**holotype**);
2 - NSSW 99, right (a, b) and left (c) mandible with P_2-M_3 (oc-buc-li) from Veltheim (**holotype**);
3 - NSSW 99, symphysis with left I_1 and I_2 and right I_1 (li) from Veltheim (**paratype**);
4 - MTA AKI 3/7, symphysis with left I_1-I_3 and right I_1-I_2 (ap-la-li) from Inönü I;
5 - MTA AKI 3/777, symphysis with left I_1 and right I_1-I_3 (li) from Inönü I;
6 - MTA AKI 3/571, left I^1 (ap-la-li) from Inönü I;
7 - MTA AKI 3/575, left P_3 (oc-buc-li) from Inönü I;
8 - MTA AKI 3/577, right P^3 (oc-buc-li) from Inönü I;
9 - MTA AKI 3/576, right P^4 (ant-oc-buc-po) from Inönü I.

Scale bar equals 6.7 cm for Figs 7-9, 10 cm for Figs 2-6 and 20 cm for Fig. 1.

PLATE 18

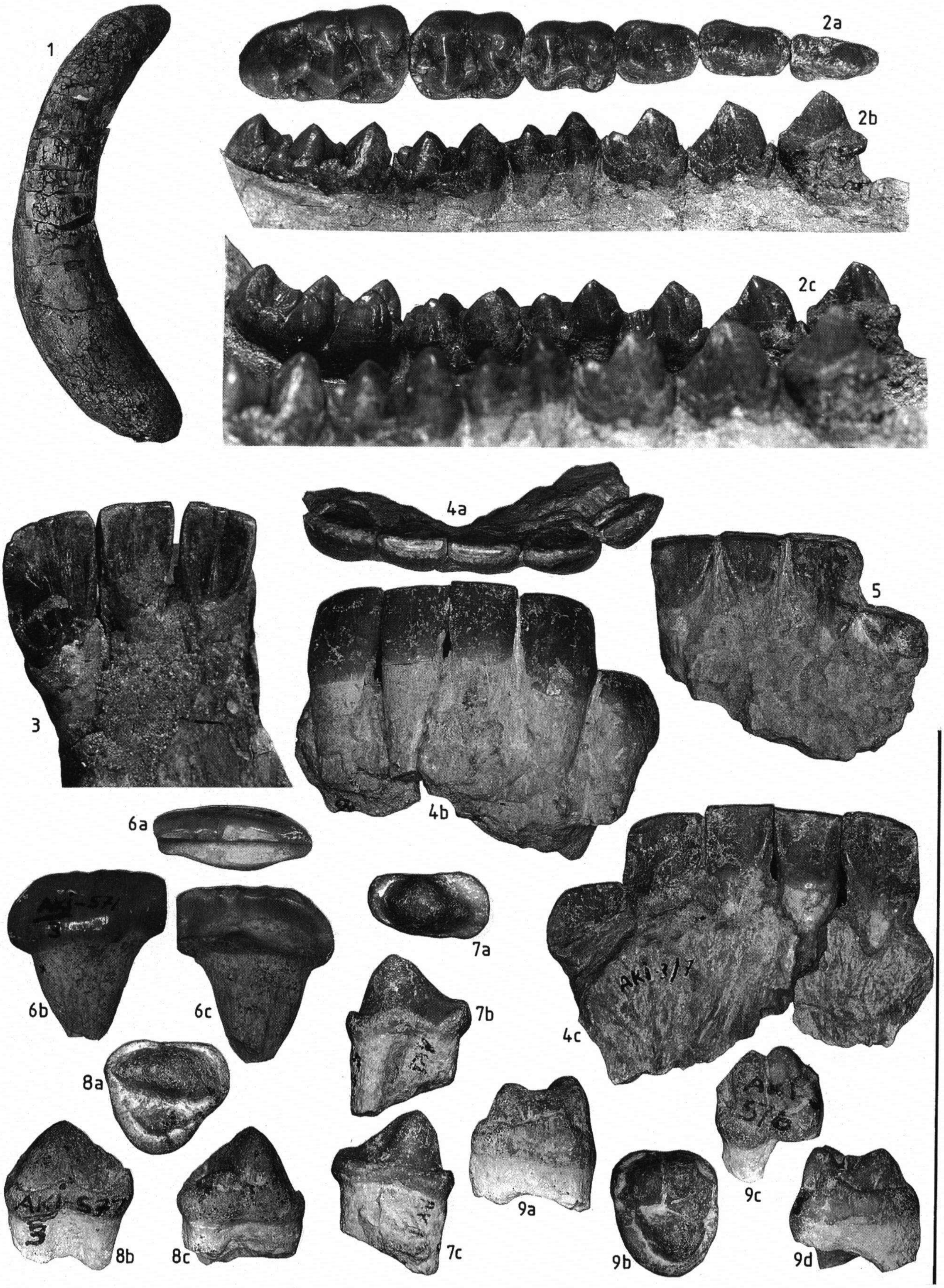
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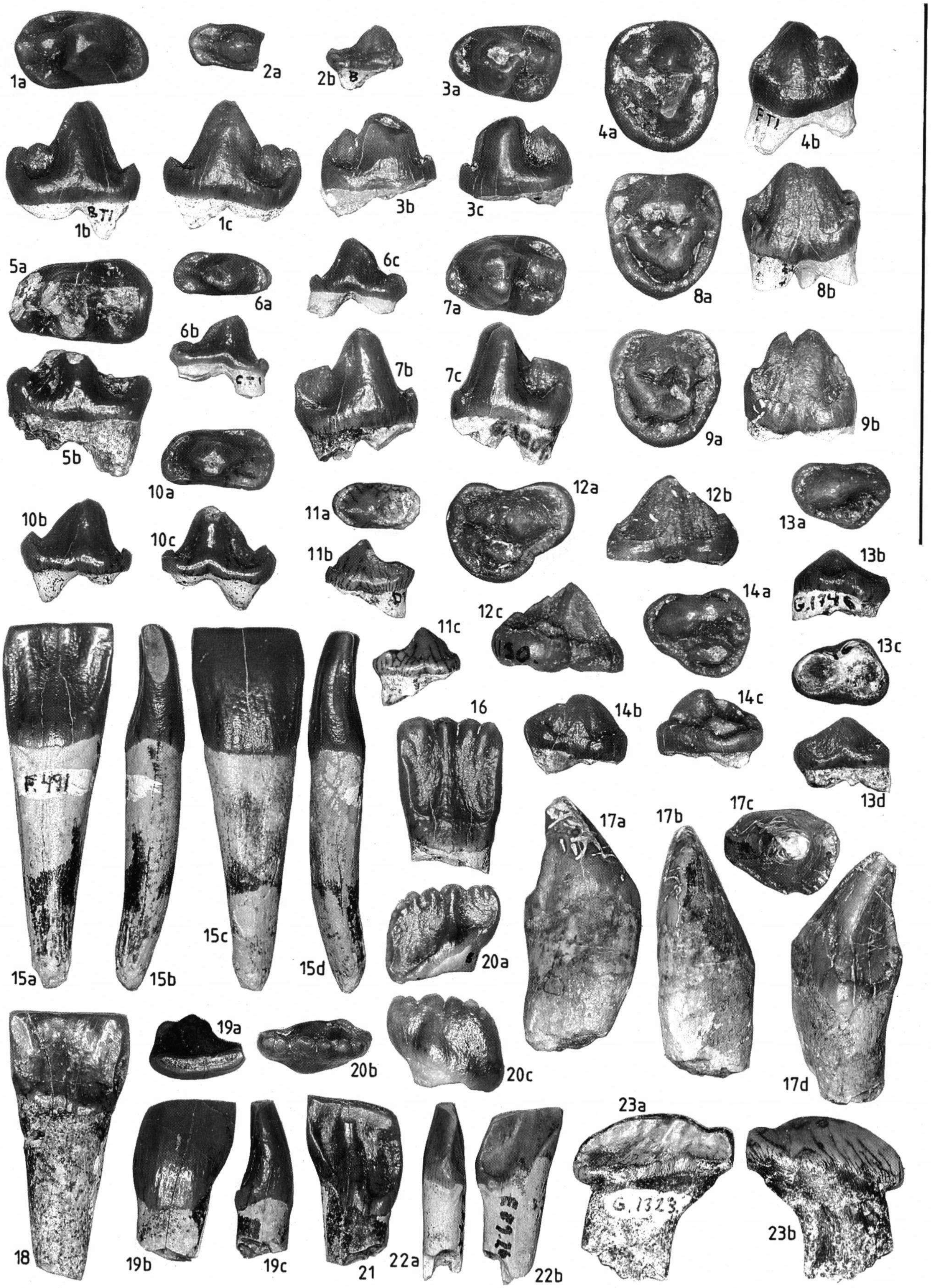
PLATE 19

Bunolistriodon meidamon from Paşalar.

1 - PDTFAU BTI, left P_4 (oc-li-buc);
2 - PDTFAU B, right D_2 (oc-li);
3 - PDTFAU F930, right P_4 (oc-la-li);
4 - PDTFAU ETI, right P^4 (oc-buc);
5 - PDTFAU ETI, right P_4 (oc-li);
6 - PDTFAU ETI, right P_2 (oc-li-buc);
7 - PDTFAU B1907, right P_4 (oc-buc-li);
8 - PDTFAU CTI, right P^4 (oc-buc);
9 - PDTFAU G995, left P^4 (oc-buc);
10 - PDTFAU ETI, right P_2 (oc-buc-li);
11 - PDTFAU DTI, left D_3 (oc-buc-li);
12 - PDTFAU CTI, right P^3 (oc-buc-li);
13 - PDTFAU G1746, left P^2/P^1 (oc-li-roots-la);
14 - PDTFAU —, left P^2 (oc-la-li);
15 - PDTFAU F491, left I_1 (li-mes-la-dist);
16 - PDTFAU G1718, right I_1 (li);
17 - PDTFAU D37, left C^f (la-ant-ap-li);
18 - PDTFAU G1778, right I_1 (li);
19 - PDTFAU G997, right I_2 (ap-la-mes-li);
20 - PDTFAU B592.5, left I_3 (li-ap-la);
22 - PDTFAU E89.26, left DI_2 (dist-li);
23 - PDTFAU G1323, right DI^1 (li-la).

Scale bar represents 6.7 cm.

PLATE 19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F.491
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G.1323

PLATE 20

Figs 1-10. *Bunolistriodon meidamon* from Çandir (Fig. 1) and Paşalar (Figs 2-10); **1** - PIMUZ CA V I/21 right C^m (la); **2** - PDTFAU F278.16, left DI_1 (li); **3** - PDTFAU D210.23, right I^1 (ap-li-la); **4** - PDTFAU B609.1, right I_1, B35.13, left I_1 and B601.1 left I_2 of one individual (**holotype**); **5** - PDTFAU F379, left I_1 (li); **6** - PIMUZ BP-311, left I_1 (ap-li-mes-la); **7** - PIMUZ BP-145, right M_2 (oc-po-li-buc-ant); **8** - PIMUZ BP-118, right M_3 (buc-oc); **9** - PDTFAU D210/1, right I^1 (ap-li-la); **10** - PIMUZ BP-128, right M^3 (ant-oc-po-buc).

Scale bar represents 5 cm for Fig. 1, 6.7 cm for Figs 2, 3, 5-10 and 10 cm for Fig. 4.

PLATE 20

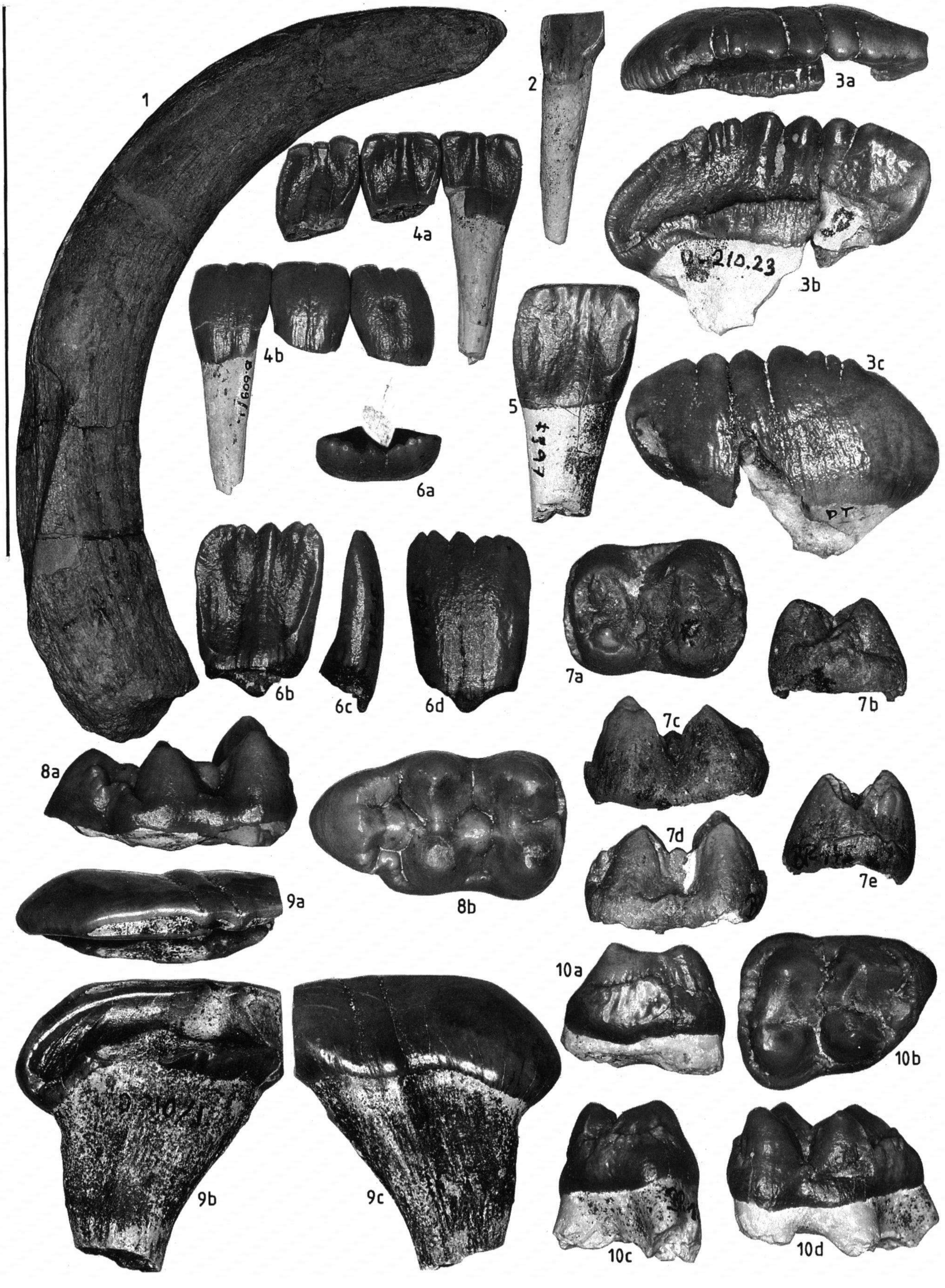
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PLATE 21

Figs 1-9. *Bunolistriodon lockharti* from Pellecahus; **1** - NMB GB 1386, left I_2 (li-mes-la-dist-ap); **2** - NMB GB 1387, right I_1 (ap-li-mes-la-dist); **3** - NMB GB 2456, left I^2 (ap-li-la); **4** - NMB GB 2458, left C_f (la-po-li); **5** - NMB GB 1395, left DC^x (?) (ap-la-li); **6** - NMB GB 1388, right DI_2 (ap-li-dist-la-mes); **7** - NMB GB 1381, left C^m (ap-la-ant-li-po); **8** - NMB GB 1389, right I_3 (li-ap); **9** - NMB GB 1390, right MT IV (prox-ext-po-int-ant).

Scale bar equals 6.7 cm.

PLATE 21

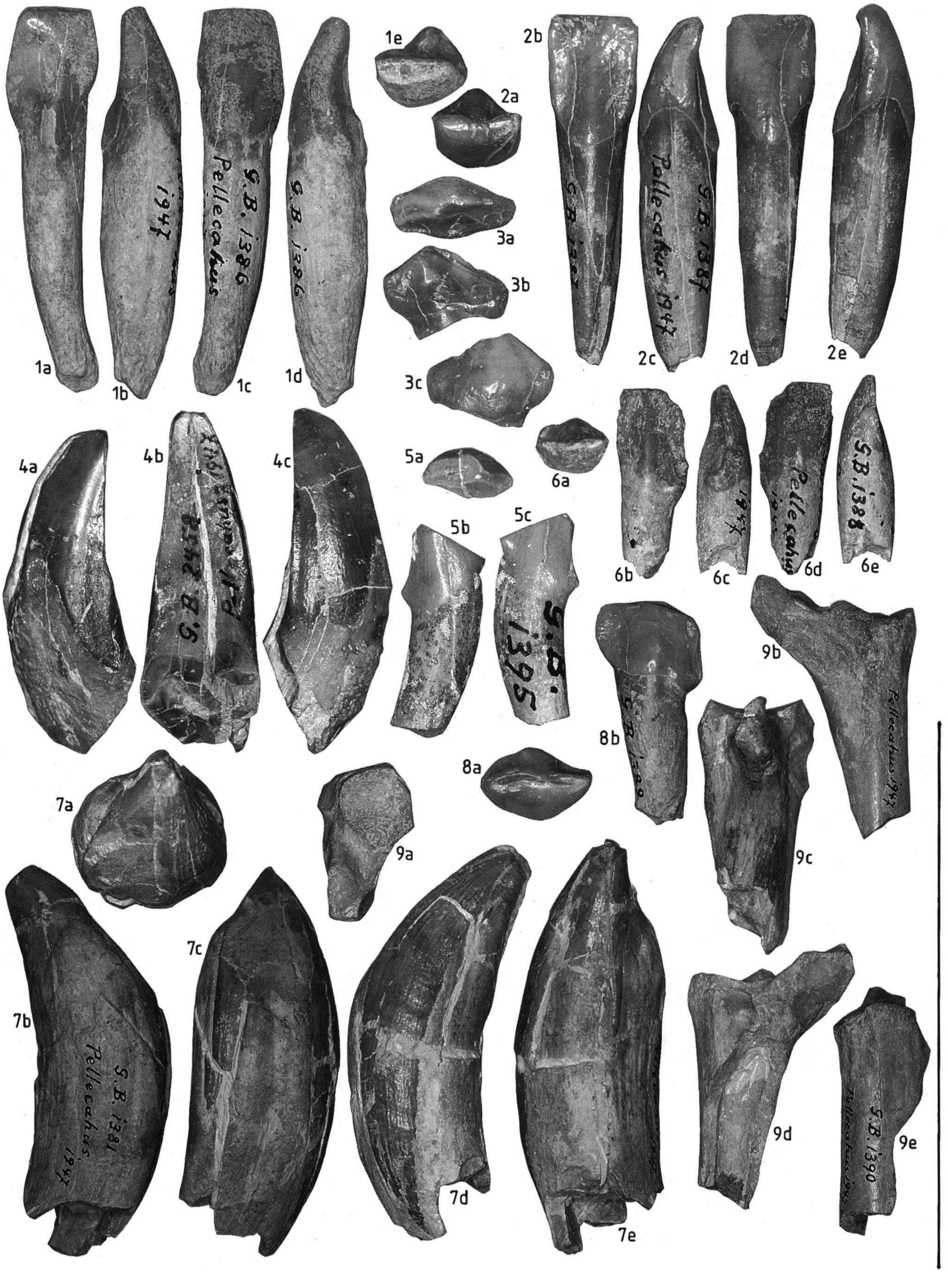
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PLATE 22

Figs 1-9, 12. ***Bunolistriodon lockharti***; **1** - NMB SO 6427, left I_2 (dist-li-mes-la-ap) from Baigneaux-en-Beauce; **2** - NMB SO 3020, left I_1 (ap-dist-li-mes-la) from Baigneaux-en-Beauce; **3** - NMB SO 6593, right I_3 (ap-li-dist-la-mes) from Baigneaux-en-Beauce; **4** - NMB SO 751, left I^1 (ap-la-li); **5** - NMB SO 5632, left I^1 (li); **6** - NMB GB 2451, left P^3 (li-oc-la) from Pellecahus; **7** - NMB SO 6495, right P_1 (li-ap-la) from Baigneaux-en-Beauce; **8** - NMB SO 6105, right I^2 from Baigneaux-en-Beauce; **9** - MNHNP CHE 30, left mandible with M_2 and M_3 (buc-oc-li) Chevilly (**lectotype**); **12** - NMB TD 547, right I^1 (li-la-ap) from Ravensburg.

Figs 10, 11. ***Bunolistriodon*** sp.; **10** - NMB TD 622, right M^1 or M^2 (oc-po-li) from Georgensgmünd; **11** - MNHNP Or 68, right M_2 (li-oc) from Montabuzard, **holotype** of *Sus belsiacus* (nomen dubium).

Scale bar represents 6.7 cm for Figs 1-8 and 10 cm for Figs 9-12.

PLATE 22

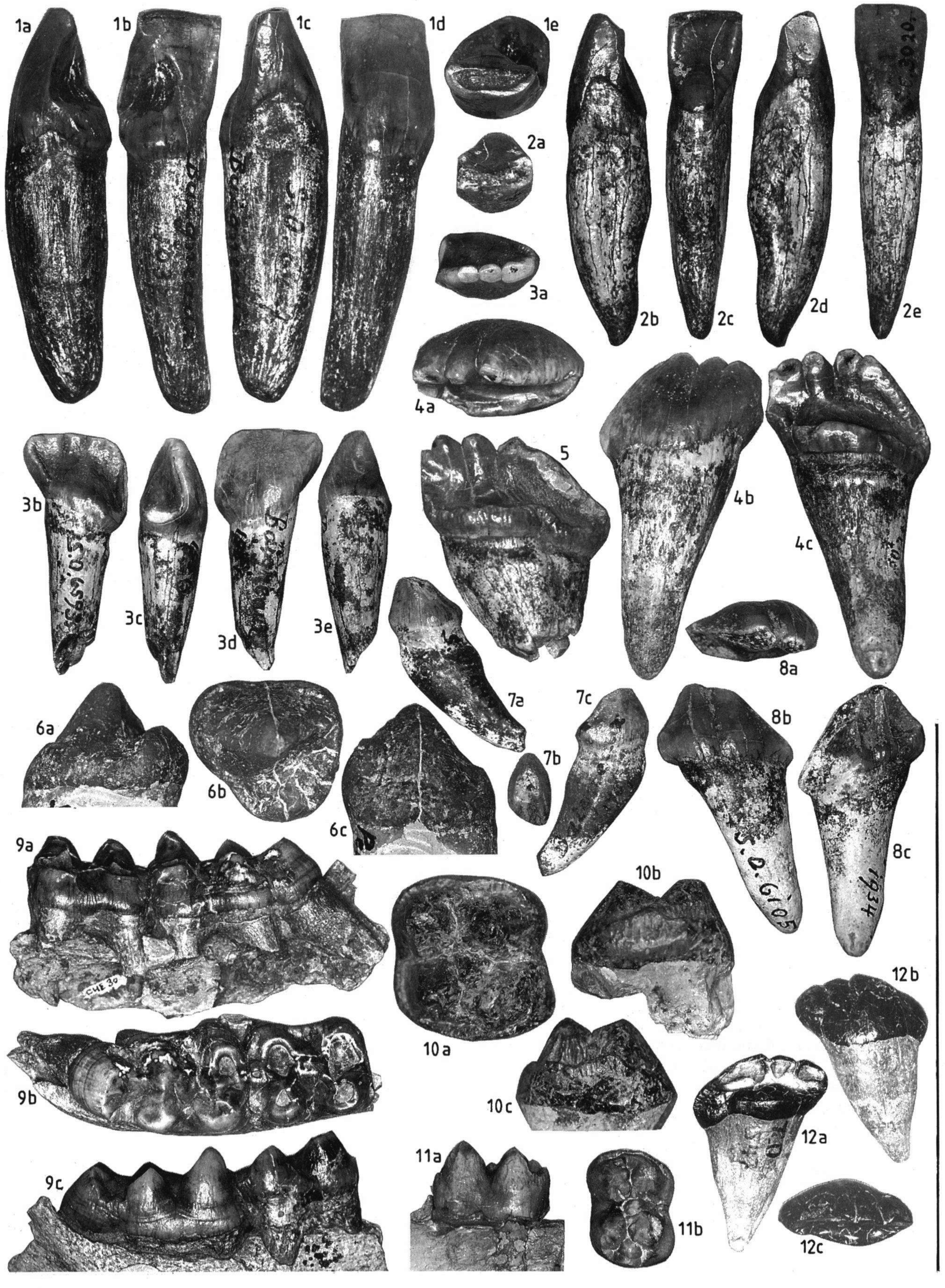
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PLATE 23

Bunolistriodon lockharti **from Pellecahus (Fig. 1) and Baigneaux-en-Beauce (Figs 2-13);**

1 - NMB GB 1380, right P^2 (buc-li-oc);
2 - NMB —, right P^3 (li-oc);
3 - NMB SO 3613, right I^1 (ap-li-la);
4 - NMB SO 5992, left P^3 (oc-la-li);
5 - NMB SO 3021, right P^4 (ant-buc-po-oc);
6 - NMB SO 6428, right P^4 (ant-buc-po-oc);
7 - NMB SO 716, left M^2 (oc-li-ant-la-po-po/oc);
8 - NMB SO 2188, left M^2 (oc-po-ant);
9 - NMB SO 2495, right M^2 (oc-ant-po);
10 - NMB SO 6592, left M^2 (oc);
11 - NMB SO 2189, right M^3 (oc);
12 - NMB SO 1161, right M^1 (oc-la-ant-li-po);
13 - NMB SO 3228, left M^3 (li).

Scale bar equals 6.7 cm.

PLATE 23

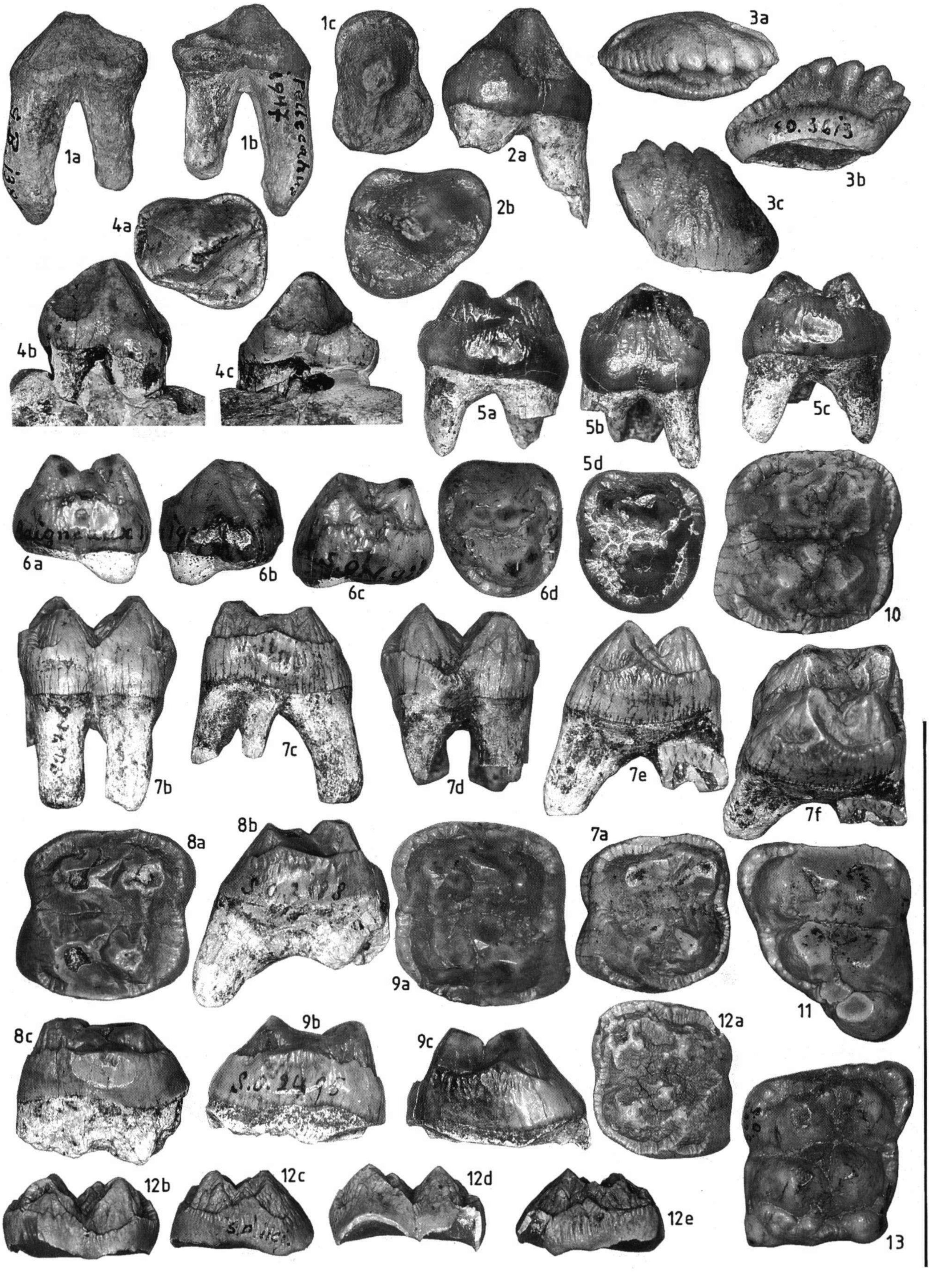
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PLATE 24

Bunolistriodon lockharti from Baigneaux-en-Beauce (Figs 1-3, 5-11) and Pellecahus (Fig. 4);

1 - NMB SO 2190, left M_2 (oc-li-po-buc-ant);
2 - NMB SO 752, right I^1 (li-la-ap);
3 - NMB SO 392, left P_3 (oc-li-buc);
4 - NMB GB 2452, left P_4 (oc-buc-li);
5 - NMB SO 3227, right P_3 (oc-li-buc);
6 - NMB SO 928, left I_2 (li-mes-la-dist);
7 - NMB SO 2814, left M_3 (oc-po/oc);
8 - NMB SO 3227, right P_2 (li-oc-buc);
9 - NMB SO 392, right P_4 (li-oc-la);
10 - NMB SO 2002, right M_3 (oc-po-li);
11 - NMB SO 4926, right M_3 (oc-li-buc-po-ant).

Scale bar represents 6.7 cm.

PLATE 24

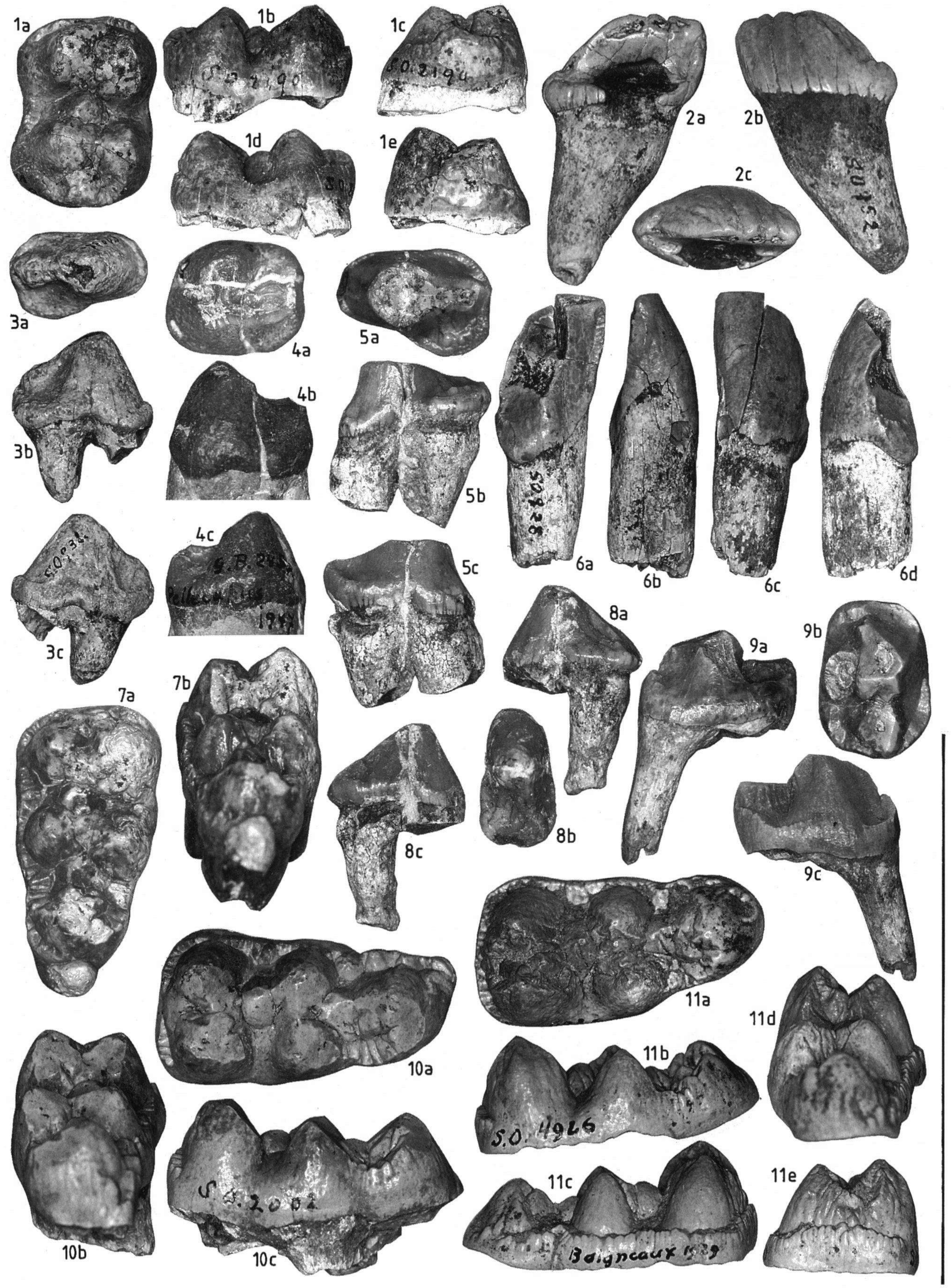
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PLATE 25

Figs 1-6, 9, 10. ***Bunolistriodon lockharti***; **1** - SMNS 41231, left humerus (ant-po) from Langenau I; **2** - SMNS 41234, left MC III (ext-int-prox-ant-po) from Langenau I; **3** - SMNS 41232, right tibia (prox-po-ext-dist) from Langenau I; **4** - SMNS 40680, left unciform (ext-ant-po-dist-prox) from Langenau I; **5** - NMB GB 1392, right MT III (ant-int-prox-ext) from Pellecahus; **6** - NMB GB 1457, left phalange IV 1 or right phalange III 1 (dors-plant-ext-prox-dist) from Pellecahus; **9** - NMB SO 5746, left astragalus (prox-post-int-ant-ext-dist) from Baigneaux-en-Beauce; **10** - NMB GB 1394, right navivular (dist-prox-ant-int-post-ext) from Pellecahus.

Figs 7, 8. ***Listriodon splendens***; **7** - IVAU MR 10, right MC III (prox-int-ant-ext-dist) from Murrero; **8** - IVAU AR IV 95, right astragalus (prox-post) from Arroyo del Val IV.

Scale bar represents 10 cm for Figs 2-6 and 8-10 and 20 cm for Figs 1 and 7; Fig. 3d is not to scale.

PLATE 25


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PLATE 26

Figs 1-16. ***Bunolistriodon akatikubas***; **1** - KNM-MB 409, left I^1 (ap-li-la) from Maboko; **2** - KNM-MB 126, right C^f (ap-ant-la) from Maboko; **3** - KNM-MB 19414, left I_2 (dist-li-ap) from Maboko; **4** - KNM-MB 14447, right DI_1 (ap-li-mes) from Maboko; **5** - KNM-MB 10367, left I_3 (li-ap) from Maboko; **6** - KNM-MG 2, left M_3 (oc-po-buc-ant) from Mbgathi (**holotype**); **7** - KNM-MB 9781, left M_2 (li-oc-po) from Maboko; **8** - KNM-MJ 9773, right mandible with two molars, probably M_2 and M_3 (oc) from Majiwa; **9** - KNM-MB 132, left M_3 (oc-li) from Maboko; **10** - KNM-MB 14424, right P_4 (oc-li-buc) from Maboko; **11** - KNM-MB 14449, right P_2 (li-oc-buc) from Maboko; **12** - KNM-MG 41, left P^2 (buc-oc) from Mbgathi; **13** - KNM-MB 872, left P_4 (buc-oc) from Mbgathi; **14** - KNM-MB 19416, left I^2 (ap-li); **15** - KNM-MB 19418, right I_1 (mes-li-ap) from Maboko; **16** - KNM-MG 5, right P^4 (ant-oc-la) from Mbgathi.

Scale bar represents 5 cm for Figs 4, 10-16, 6.7 cm for Fig. 6, and 10 cm for Figs 1-3, 5, 7-9.

PLATE 26

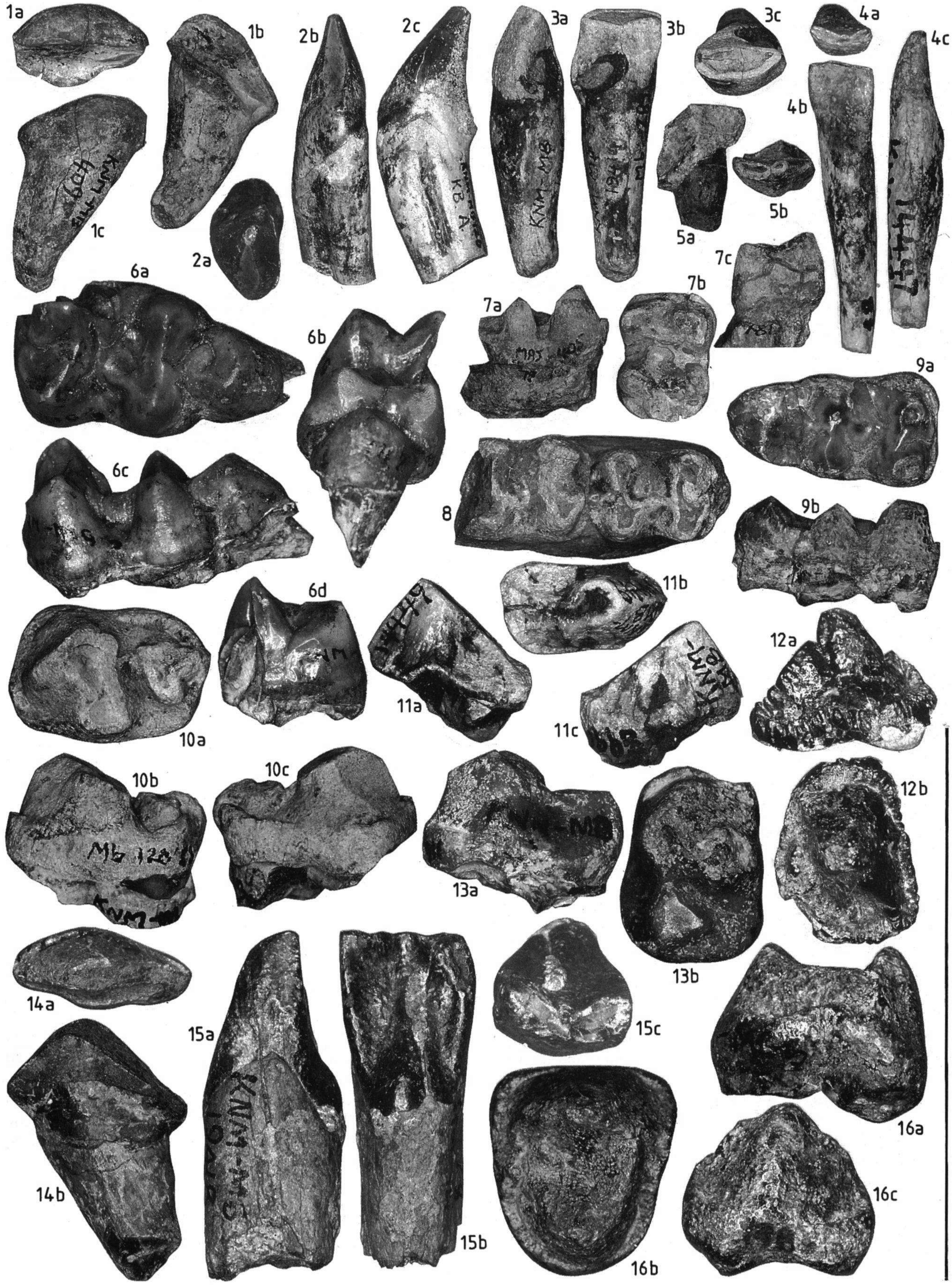
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PLATE 27

Figs 1-14. ***Bunolistriodon guptai*** from Bhagothoro and the various HGSP localities in the Lower Manchar Formation; **1** - IM B 701, right M^3 (oc-buc) from Bhagothoro (**holotype**); **2** - HGSP 8320/2016, left M_3 (oc-buc-ant-po-li); **3** - HGSP 8223/1215, right I^1 (ap-li-la); **4** - HGSP 8412/3123, left P_4 (oc-buc-li); **5** - HGSP 8427/3646, left M_1 (oc-po-li-buc-ant); **6** - HGSP 8424/3686, left M_2 (ant-oc-li-po); **7** - HGSP 8312/1402, right I^1 (li-la-ap); **8** - HGSP 8321/2072, left M_3 (oc); **9** - HGSP 8311/1526, left D^4 (oc-ant-po); **10** - HGSP 8222/1217, right M_2 (oc-li-buc-ant-po); **11** - HGSP 8412/3320, left M^2 (oc-ant-po); **12** - HGSP 8222/1218, right M_2 (oc); **13** - HGSP 8412/3155, right M_2 (oc); **14** - HGSP 8420/3441, right M^3 (oc).

Scale bar represents 6.7 cm.

PLATE 27

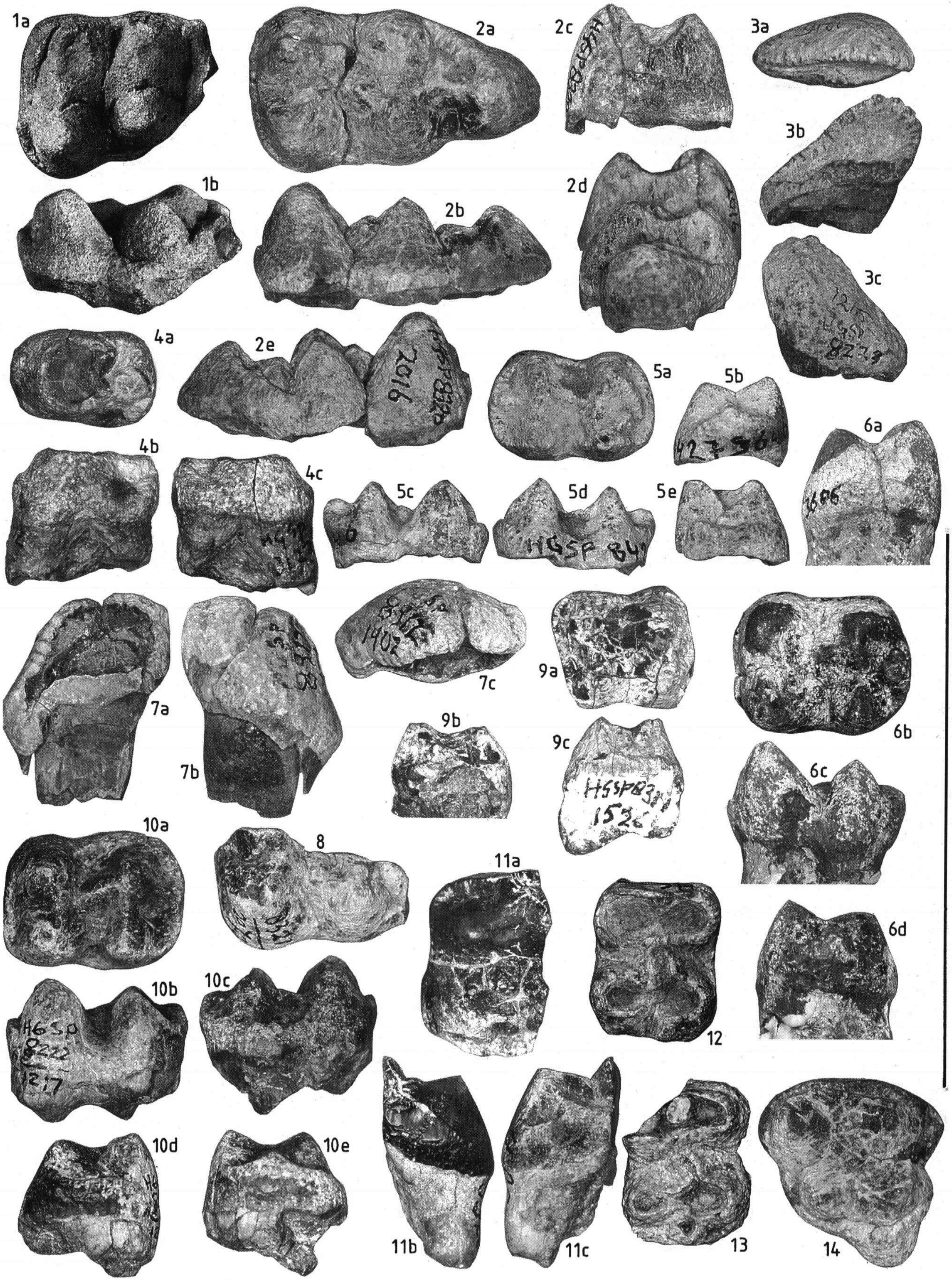
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PLATE 28

Figs 1-8. *Listriodon pentapotamiae*; **1** - IVAU CHH 24, right M^2 (oc-li-ant-po-buc) from Bhilomar; **2** - HGSP 8415/320, left I^1 (la-li-ap) from the Lower Manchar Formation; **3** - IVAU CH 16, posterior part of left M_3 (oc-po) from the Chinji Formation, of unknown exact provenance; **4** - IVAU CH 21, left M^3 (oc) from the Chinji Formation, of unknown exact provenance; **5** - IVAU CH 26, posterior part of left M_3 (ant-po-oc-buc) from the Chinji Formation, of unknown exact provenance; **6** - HGSP 8304/1333, right M_3 (po-li-oc) from the Manchar Formation; **7** - HGSP 8111/130, left M^3 (oc-po-ant) from the Manchar Formation; **8** - IVAU KA 84, right M^1 (oc) from Kanatti.

Fig. 9. ***Bunolistriodon guptai*** from the Lower Manchar Formation, HGSP 8127/1436, right P_3 and P_4 (oc-li-buc).

Figs 10, 11. ***Bunolistriodon akatikubas*** from Ad Dabtiyah; **10** - BMNH M 42950, right M^3 (ant-oc-po); **11** - BMNH M 42949, right M_3 (po-oc-li).

Fig. 12. ***Bunolistriodon intermedius*** from Maerzuizigou, Tongxin, BNHM BPV 1670, left M_2 and M_3 (oc).

Scale bar equals 6.7 cm for Figs 1-11 and 10 cm for Fig. 12.

PLATE 28

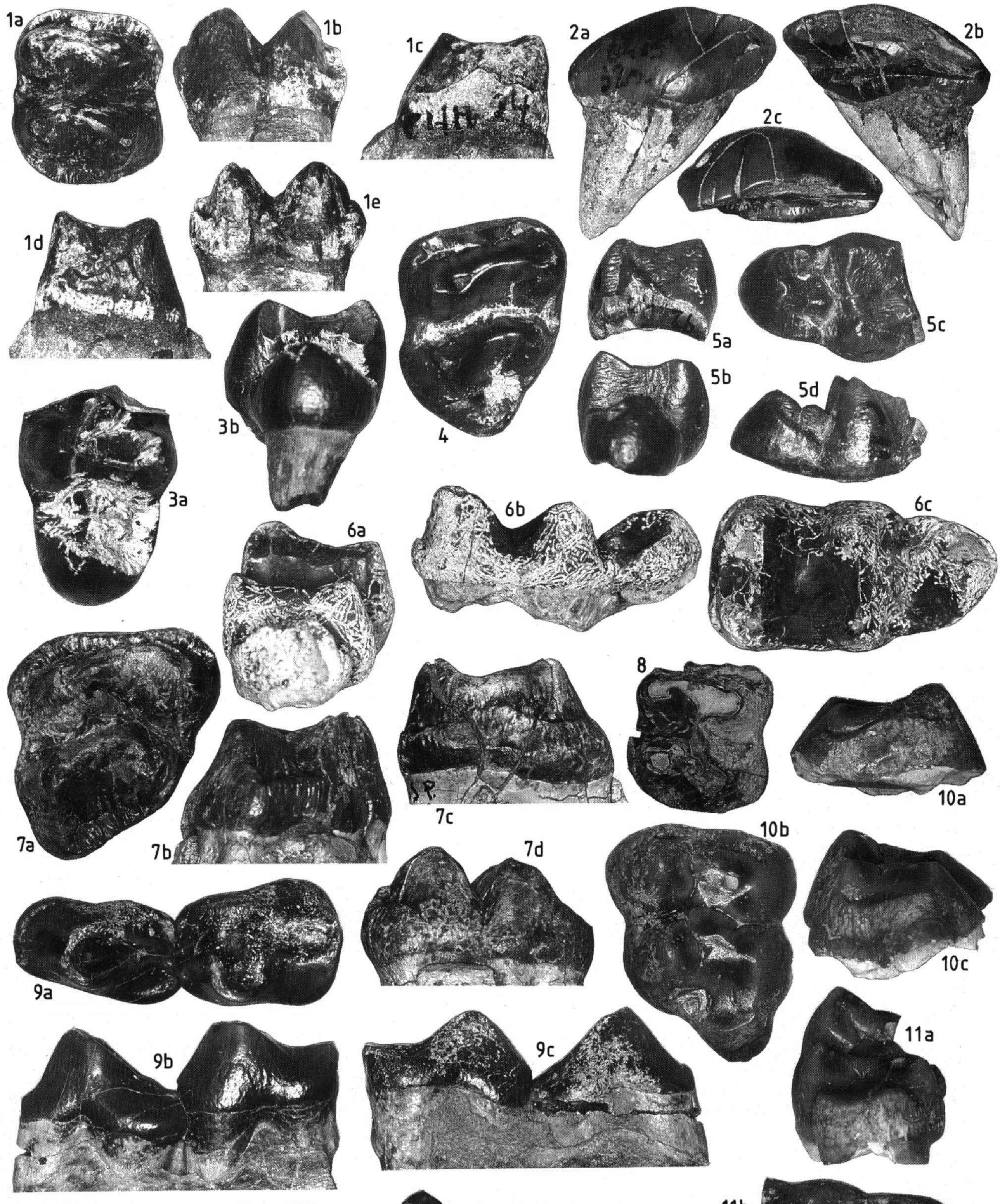
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PLATE 29

Figs 1-9, 11. ***Listriodon pentapotamiae***; **1** - HGSP 8122/257, right mandible with P_4-M_3 (oc-li-buc) from the Lower Manchar Formation; **2** - HGSP 8124/3721, right M_2 (po-oc-li) from the Lower Manchar Formation; **3** - HGSP 8220/1037, right M_3 (oc-li-po) from the Lower Manchar Formation; **4** - HGSP 8427/3648, left M_3 (oc-li-po) from the Lower Manchar Formation; **5** - IVAU KA 84, right M^1 (oc) from Kanatti; **6** - IVAU CH 25, left P_4 (oc-buc) from the Chinji Formation, of unknown exact provenance; **7** - IVAU CHC 86, posteror half of left M^3 (oc-ant) from Cheski Wala; **8** - IVAU KA 81, right M_3 (po-oc) from Kanatti; **9** - IVAU CHH 35, right I^1 (li-ap-la) from Bhilomar; **11** - HGSP 8125/381, right M^2 (oc-ant-po-buc) from the Lower Manchar Formation.

Fig. 10. ***Bunolistriodon guptai*** from HGSP 8311 in the Manchar Formation, HGSP 8311/1406, left mandible with M_1-M_3 and HGSP 8311/1550, left P_4 (oc-buc-li) from the Lower Manchar Formation.

Scale bar represents 6.7 cm for Figs 2-9, 11 and 10 cm for Figs 1 and 10.

PLATE 29

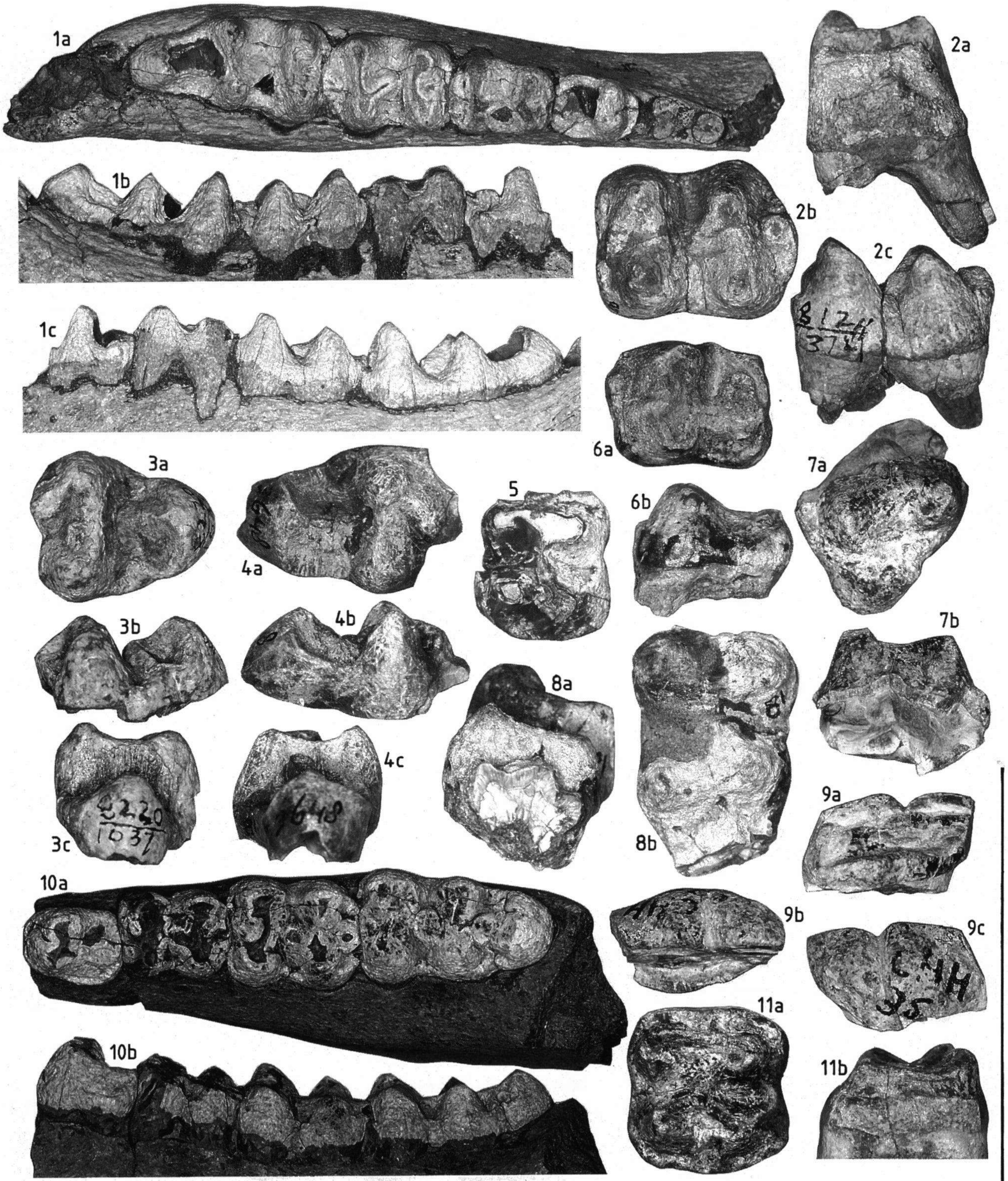
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PLATE 30

Figs 1-11. *Listriodon pentapotamiae*; **1** - BSPHGM 1956 II 106b, left M^4 (oc-po-ant-buc) from Kadirpur; **2** - BSPHGM 1956 II 112, left M^1 & M^2 (oc-buc-li-po-ant) from Kanatti Chak 8; **3** - IVAU KA 82, left P^4 (buc-oc-ant) from Kanatti; **4** - IVAU CHC 39, left I_1 (ap-la-dist-li-mes) from Cheksi Wala; **5** - IVAU CHA 62, left P^4 (ant-buc-oc) from Achora; **6** - IVAU CHB 21, left P_4 (oc-buc-ant-li) from Burri Wala; **7** - IVAU KA 83, left P_4 (ant-oc-li-buc) from Kanatti; **8** - IVAU KA 86, right P_4 (ant-oc-li-buc) from Kanatti; **9** - IVAU KA 87, anterior half of left P_4 (ant-oc) from Kanatti; **10** - IVAU CHC 45, right P^2 (buc-li-oc) from Cheksi Wala; **11** - IVAU CH 201, right I^1 (ap-li-la) from the Chinji Formation, of unknown exact provenance.

Scale bar equals 6.7 cm.

PLATE 30

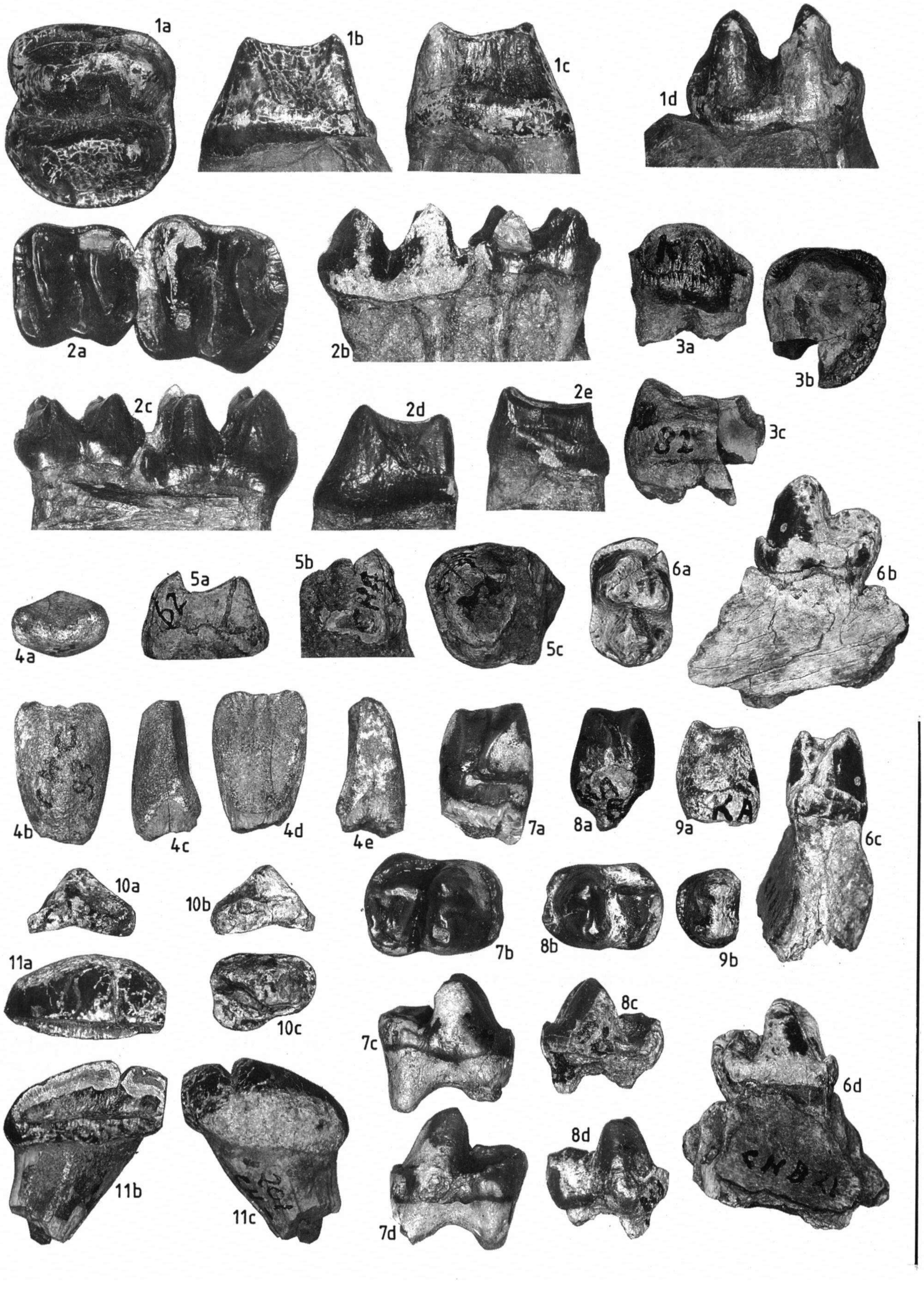
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PLATE 31

Figs 1-17. *Listriodon pentapotamiae* from the Chinji Formation; **1** - BSPHGM 1956 II 101, right I_1 (la-mes-li-ap) from Chari Gambhir; **2** - BSPHGM 1956 II 99, left I_3 (dist-li); **3** - BSPHGM 1956 II 103, left I_1-I_2 and right I_1 (li) from Kanatti Chak 5; **4** - BSPHGM 1956 II 98, left DI^2 (li-oc-la) from Kadirpur; **5** - BSPHGM —, right I_2 (li-dist) from Kanatti Chak 3; **6** - BSPHGM 1936 X 596, right I_2 (li-dist-ap-la) from Kund Nala; **7** - BSPHGM 1956 II 102, right I_2 (mes-li-dist-ap) from Pirawalaban 1; **8** - BSPHGM 1341, left M^1 or M^2 (buc-po-ant-oc-oc) from Mochiwala, 8e under low-angle illumination; **9** - BSPHGM 1956 II 45, right P_3-P_4 (oc-buc-li) from Katli; **10** - BSPHGM 1956 II 48, left M_3 (oc-li-po-buc) from Kanatti Chak 5; **11** - BSPHGM 1956 II 57, left P_4 (oc-buc) from Jandawala; **12** - BSPHGM 1956 II 119, left M^3 (oc-po) from Kanatti Chak 6; **13** - BSPHGM 1956 II 115, left M^3 (oc-ant) from West Marianwala; **14** - BSPHGM 1956 II 107, left P_3 (oc-po-li) from Pirawalaban; **15** - BSPHGM 750 - 753, right P^1 (oc-buc-li) from Kadirpur; **16** - BSPHGM 1956 II 114, left M^3 (po-oc-ant-buc) from Kanatti Chak 8; **17** - BSPHGM 1956 II 110, right M^3 (oc-ant-po) from Kanatti Chak 8.

Scale bar represents 6.7 cm for Figs 1-14, 16, 17 and 2.8 cm for Fig. 15.

PLATE 31

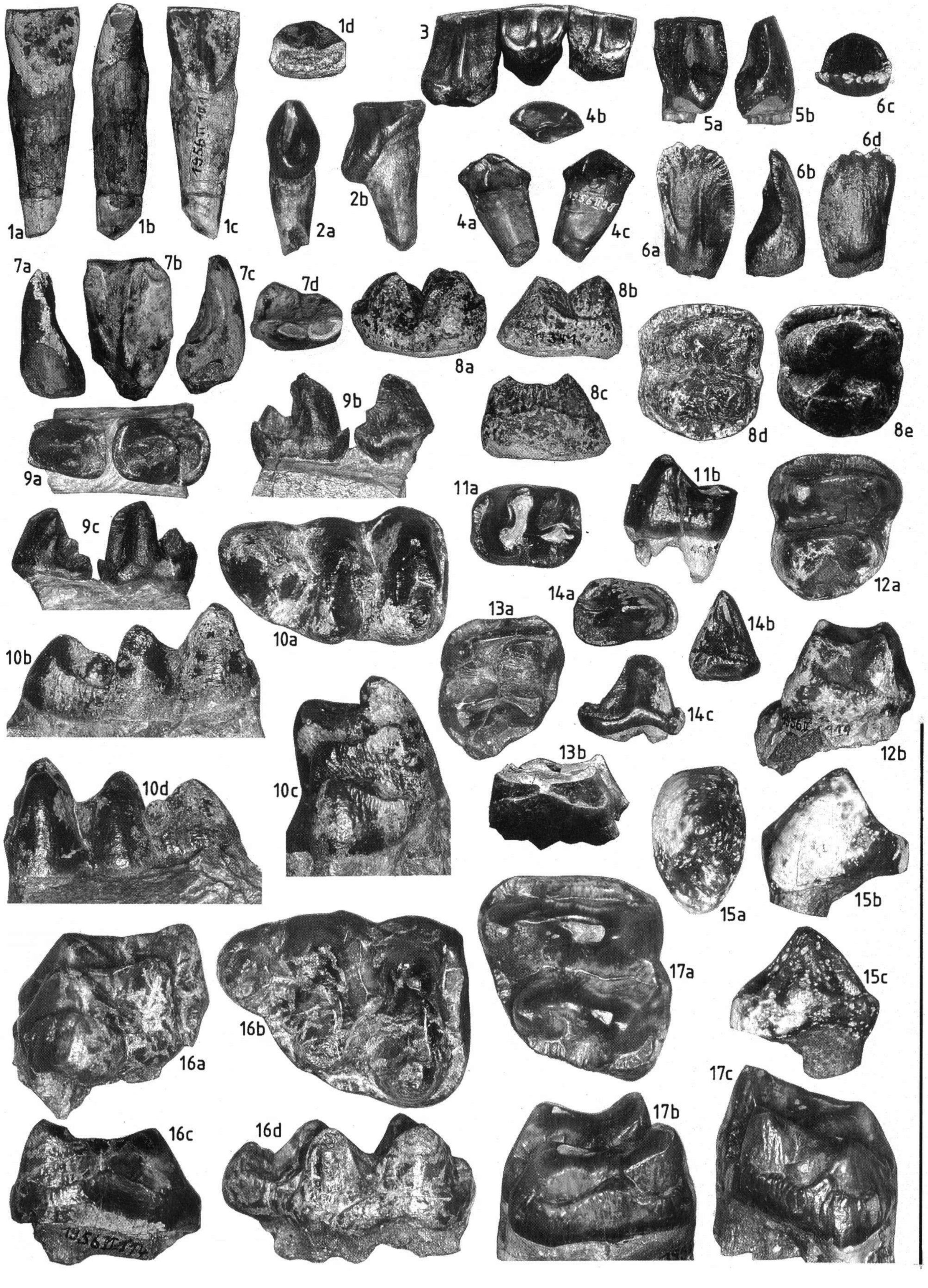
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PLATE 32

Figs 1-18. *Listriodon pentapotamiae* from the Chinji Formation; **1** - BSPHGM 1956 II 79, left C^m from Kanatti Chak 7 (ant-po); **2** - BSPHGM 1939 X, left I^1 from Dhulian (ap-li); **3** - BSPHGM 205, right M_3 from Burriwala (ap-li-la); **4** - BSPHGM 1956 II 89, right I^1 from Chattuwala (ap-li-la); **5** - BSPHGM 1956 II 91, left I^1 from Kadirpur (ap-li-la); **6** - BSPHGM 1956 II 60, left P_3 from Hessuwala (po-oc-li-buc); **7** - BSPHGM 1674, right P^2 from Marianwala-Kas (oc-li-buc); **8** - BSPHGM 1956 II 110, right P^4 from Marianwala-Kas (oc-oc-ant-buc), 8a under low-angle illumination; **9** - BSPHGM 1956 II 115, left P^4 from Kanatti Chak 5 (oc-ant-buc); **10** - BSPHGM 1956 II 116, right P^4 from Kanatti Chak 8 (buc-ant-oc); **11** -BSPHGM 3275-84, right P_4 from Kanatti Chak 8 (oc-ant-li-buc); **12** - BSPHGM 1956 II 114, left P^4 from Kanatti Chak 8 (oc-buc-po-ant); **13** - BSPHGM 1378-81, left I^2 from Chari Gambhir (la-ap-li); **14** - BSPHGM 1378-81, left I^2 from Chari Gambhir (ap-li-la); **15** - BSPHGM 1956 II 119, left P^3 from Sosianwali (oc-po-buc-li); **16** - BSPHGM 1378-81, left I^2 from Chari Gambhir (la-ap-li); **17** - BSPHGM 1378-81, left I^2 from Chari Gambhir (ap-li-la); **18** -BSPHGM 1956 II 85, right M_3 from Kanatti Chak 9 (oc-ant-buc-li-po).

Scale bar equals 6.7 cm.

PLATE 32

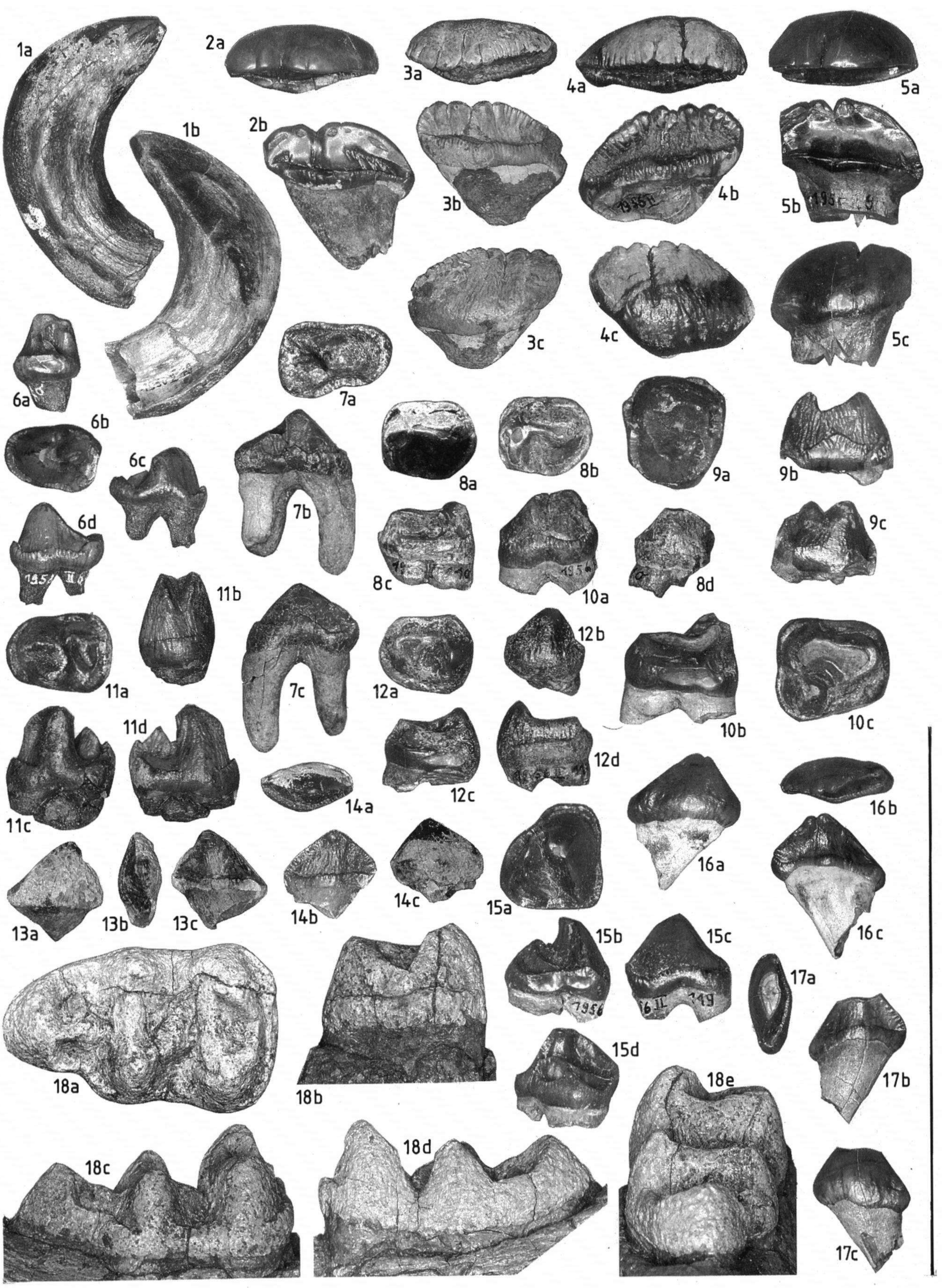
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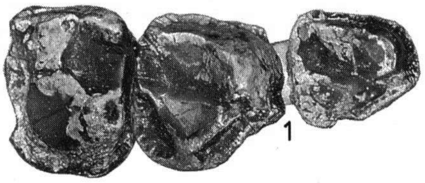
PLATE 33

Figs 1-4. *Listriodon pentapomiae* from Kundal Nala 2, Chinji Formation; **1** - BSPHGM 1956 II 37, right P^2-M^3, detail of skull (oc); **2** - BSPHGM 1956 II 37, skull (ant-dors-po); **3** - BSPHGM 1965 II 93, right I^1 (li-la-ap); **4** - BSPHGM 1956 II 37, left P^2-P^4, detail of of skull (oc).

Scale bar represents 6.7 cm for Figs 1, 3 and 4 and approximately 13 cm for Fig. 2.

PLATE 33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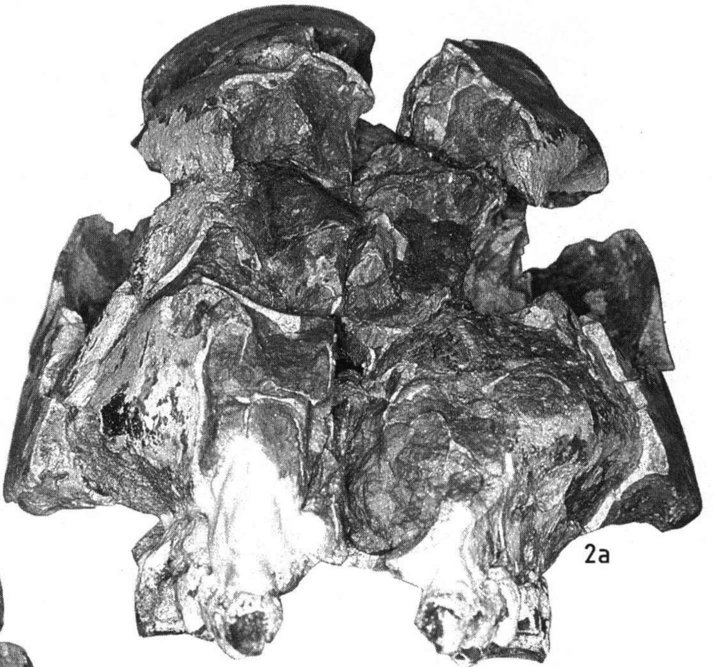
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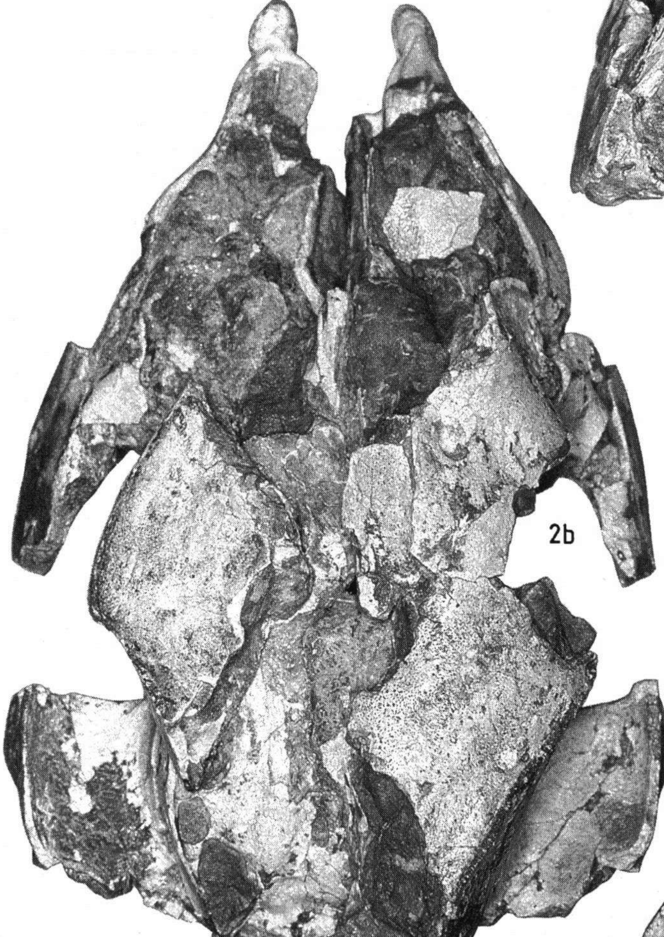
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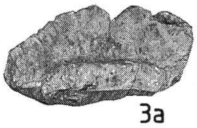
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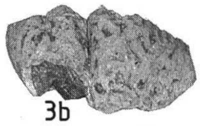
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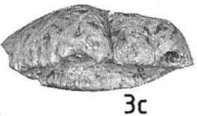
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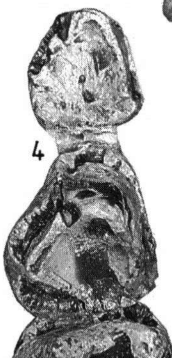
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PLATE 34

Figs 1-3. *Listriodon pentapomiae*; **1** - BSPHGM 1956 II 37, skull (oc-lat/right) from Kundal Nala 2; **2** - Mus 31 (= GSP 4527?), left P_1 of complete mandible (li-buc) from Dhok Talian 189; **3** - Mus 31 (= GSP 4527 ?), right and left I_1 and I_2 of complete mandible (li) from Dhok Talian 189.

Figs 4, 5. *Lopholistriodon moruoroti* from Muruyur; **4** - KNM-MU 25, left I^1 (li-dist-la-mes-ap); **5** - KNM-MY 68, left M^3 (oc-ant-po).

Scale bar represents 5.6 cm for Fig. 2, 10 cm for Fig. 3 and approximately 13 cm for Fig. 1, and 5 cm for Figs 4 and 5.

PLATE 34

PLATE 35

Figs 1-18. *Listriodon splendens* from Paşalar (Figs 1-17) and Inönü 1 (Fig. 18); **1** - PIMUZ —, left C^f (ap-li-la); **2** - PIMUZ BP 123, right M_3 (oc-buc); **3** - PIMUZ BP 235, right M_2 (oc-po-buc-li-ant); **4** - PIMUZ BP 89, left I_2, BP —, left I_1 and BP 165, right I_1 of a single individual (ap-li-la); **5** - PIMUZ BP 127, right M^3 (oc-ant-buc-po); **6** - PDTFAU F450, left D^2 (oc-li-buc); **7** - PDTFAU D995, right P^2 (oc-buc-li); **8** - PIMUZ BP —, right I_1 and I_2 (li); **9** - PDTFAU G1570, left D^2 (oc-buc-li); **10** - PDTFAU F450.1, right D^2 (buc-oc-li); **11** - PDTFAU G273, right I^1 (ap-li-la); **12** - PDTFAU F9.9, left D_3 (oc-buc-li); **13** - PDTFAU G44.9, left I_1 (ap-la-mes-li); **14** - PDTFAU F353, left I_1 (li); **15** - PDTFAU D86A, left DI_2 (li-dist); **16** - PDTFAU G113, right DI^1 (li-la); **17** - PDTFAU G1050.O, right I_3 (ap-la-li); **18** - MTA AKI 3/41, right mandible with P_3-M_3 (oc).

Scale bar represents 6.7 cm for Figs 1-3, 5-7 and 9-17 and 10 cm for Figs 4, 8 and 18.

PLATE 35

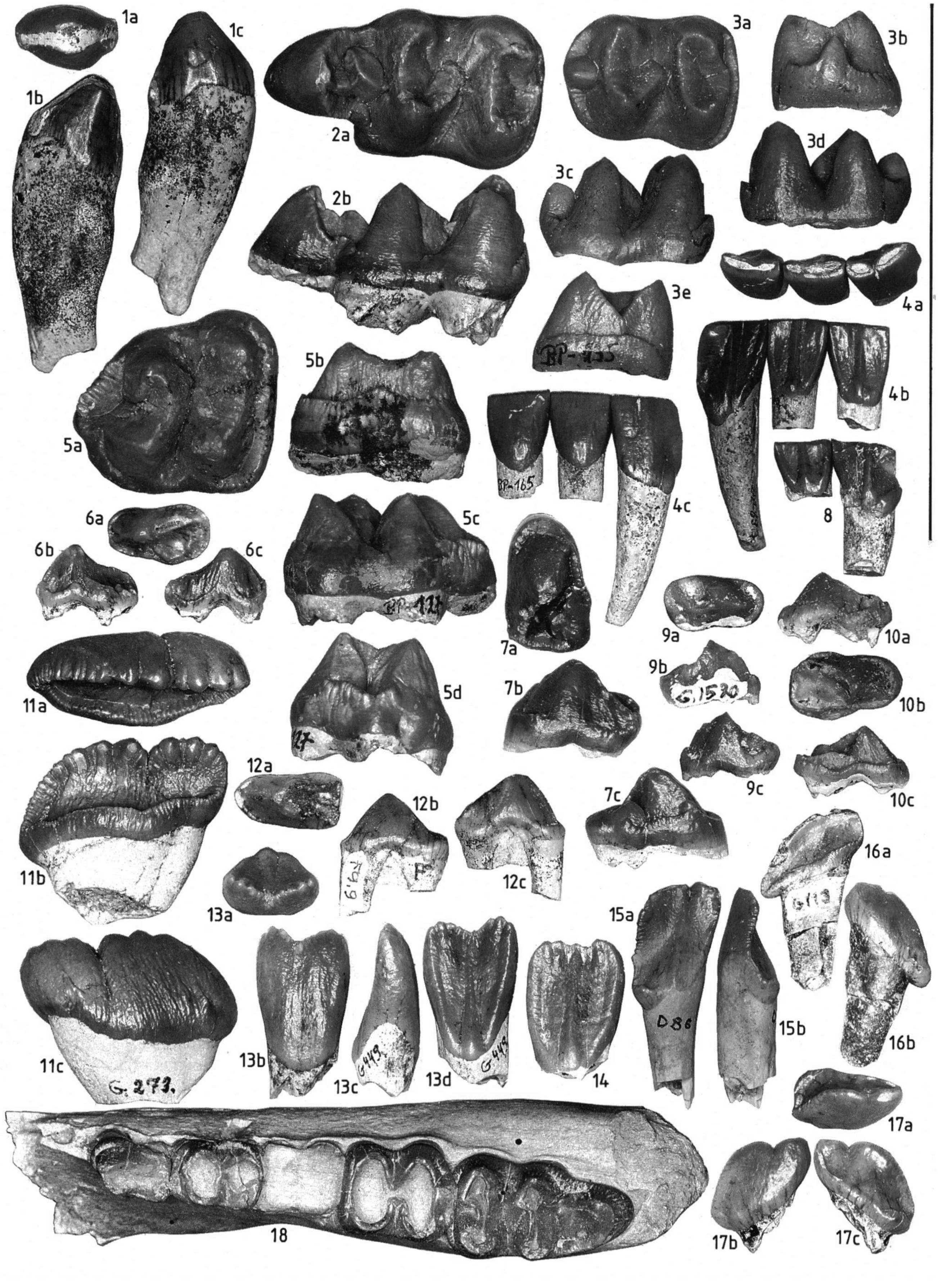
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PLATE 36

Figs 1-14. *Listriodon splendens* from Arroyo del Val IV (Figs 1-11 and 14) and Arroyo del Val VI (Figs 12, 13); **1** - RGM 263.009, left I^1 (ap-li-la); **2** - IVAU AR IV 80, right I^1 (ap-li-la-mes); **3** - IVAU AR IV 91, right I$_2$ (la-ap-mes-li-dist); **4** - IVAU AR IV 92, left I$_1$ (ap-li-mes-la-dist); **5** - IVAU AR IV 15, right I^3 (ap-li-la); **6** - IVAU AR IV 413, totally worn off left I^1 (li); **7** - IVAU AR IV 45, right I$_3$ (ap-la-li); **8** - IVAU AR IV 94, left I$_1$ (li); **9** - IVAU AR IV 83, left I^2 (li); **10** - IVAU AR IV 78, right I^2 (ap-li-la); **11** - IVAU AR IV 48, right I$_3$ (li); **12** - IVAU AR VI 1 & AR VI 2, right and left I^1 of a single individual (la-ap-li); **13** - IVAU AR VI 14, left I^2 (ap-la-li); **14** - IVAU AR IV 63, right C^m (ant).

Scale bar equals 6.7 cm for Figs 1-11, 13, 14 and 10 cm for Fig. 12.

PLATE 36

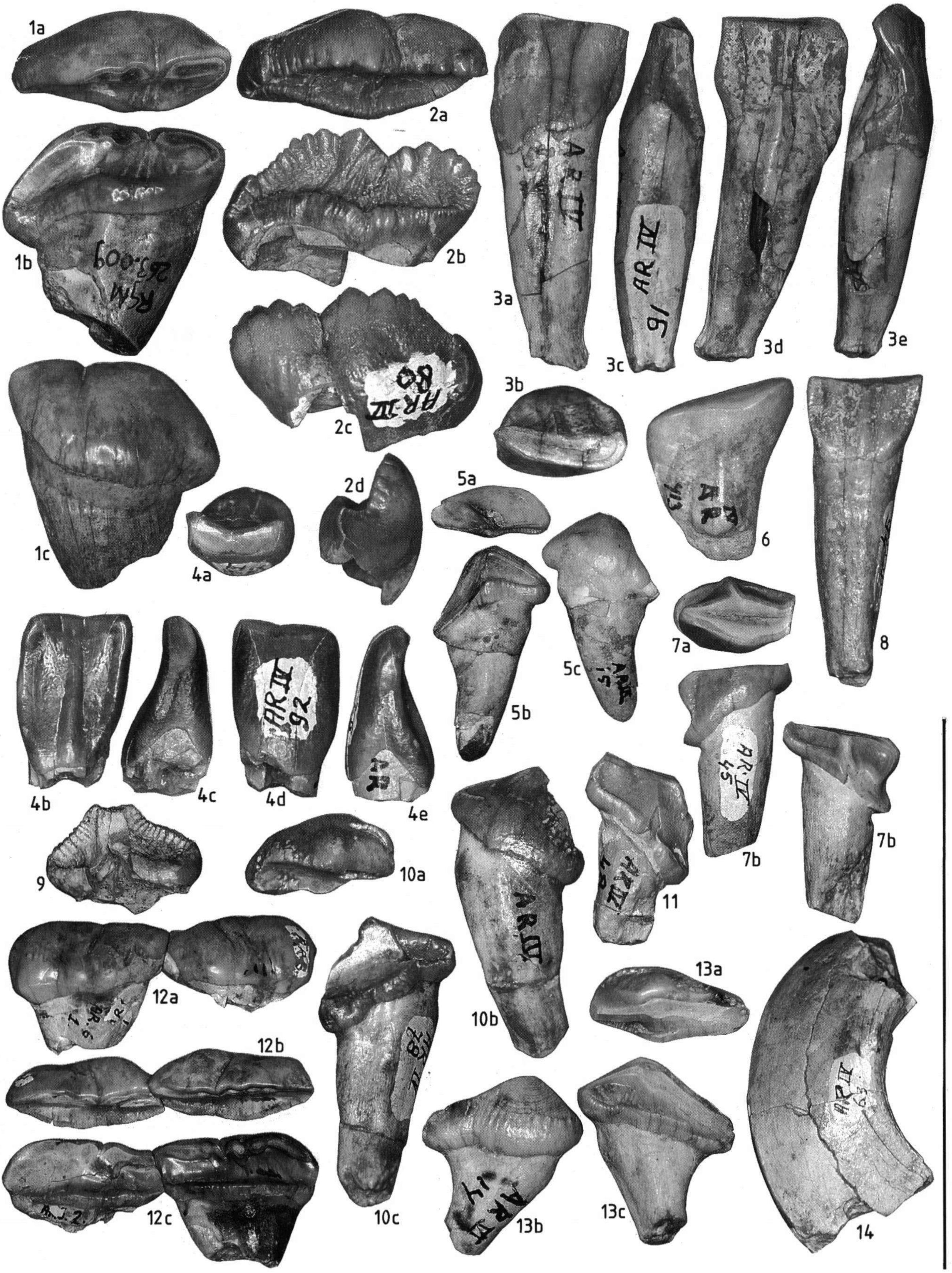
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PLATE 37

Figs 1-9. *Listriodon splendens*; **1** - MLGSB 48571, left C_m (la-li) from Sant Quirze; **2** - MLGSB 48575, left C_m (la-li) from Sant Quirze; **3** - IVAU AR IV 53, right C_m (li-la) from Arroyo del Val IV; **4** - IVAU AR IV 56, left C_m (la-po-li) from Arroyo del Val IV; **5** - RGM 263.016, right C^m (po-ap-la-ant); **6** - MLGSB 48582, right C^m (ant-po) from Sant Quirze; **7** - IVAU AR IV 60, left C^m (po-ant) from Arroyo del Val IV; **8** - MLGSB 48581, right C^m (ant-po) from Sant Quirze; **9** -PIMUZ CA I/2, right C^m (ant) from Çandir.

Scale bar represents 10 cm for Figs 4 and 5 and 20 cm for Figs 1-3 and 6-9.

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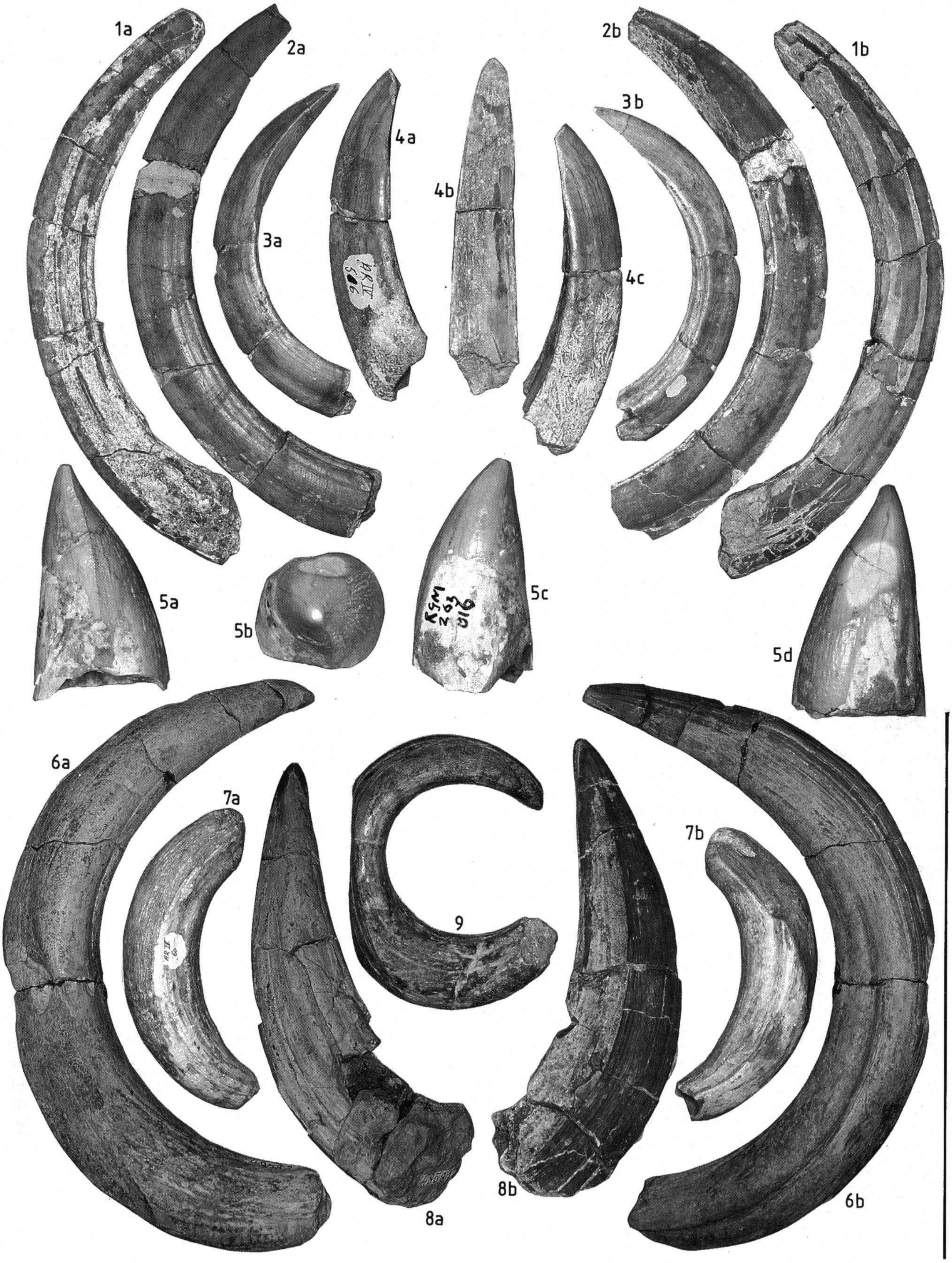

PLATE 38

Figs 1-15. *Listriodon splendens*; **1** - IVAU MA I 107, left P_4 (oc-li-buc-ant) from Manchones I; **2** - IVAU AR VI 18, right P_4 (oc-li-buc-po) from Arroyo del Val VI; **3** - IVAU AR IV 19, right P_4 (oc-li-buc-ant-po) from Arroyo del Val IV; **4** - RGM 263.037, left P_3 (oc-li-buc-po), RGM 263.037, RGM 263.039 and RGM 263.038 belong to the same individual from Arroyo del Val IV; **5** - RGM 263.039, left P_2 (oc-li-buc-po) from Arroyo del Val IV; **6** - IVAU AR IV 437, left C_f (li-la) from Arroyo del Val IV; **7** - IVAU MA 108, right P_3 (po-li-la-oc) from Manchones I; **8** - RGM 263.038 left P_4 (oc) from Arroyo del Val IV; **9** - IVAU AR IV 42, right M_1 (po-oc-li-buc-ant) from Arroyo del Val IV; **10** - IVAU AR IV 4, right P_4 (oc) from Arroyo del Val IV; **11** - IVAU AR IV 88, left P_3 (oc) from Arroyo del Val IV; **12** - IVAU AR IV 54, right C_f (li-la) from Arroyo del Val IV; **13** - IVAU AR IV 440, right C^f (ap-li-la) from Arroyo del Val IV; **14** - IVAU MR 29, left D_3 (oc-buc-li) from Murrero; **15** - IVAU MA I 109, left P_2 (oc-li-buc) from Manchones I.

Scale bar represents 6.7 cm for Figs 1-5, 7-11 and 13-15 and 10 cm for Figs 6 and 12.

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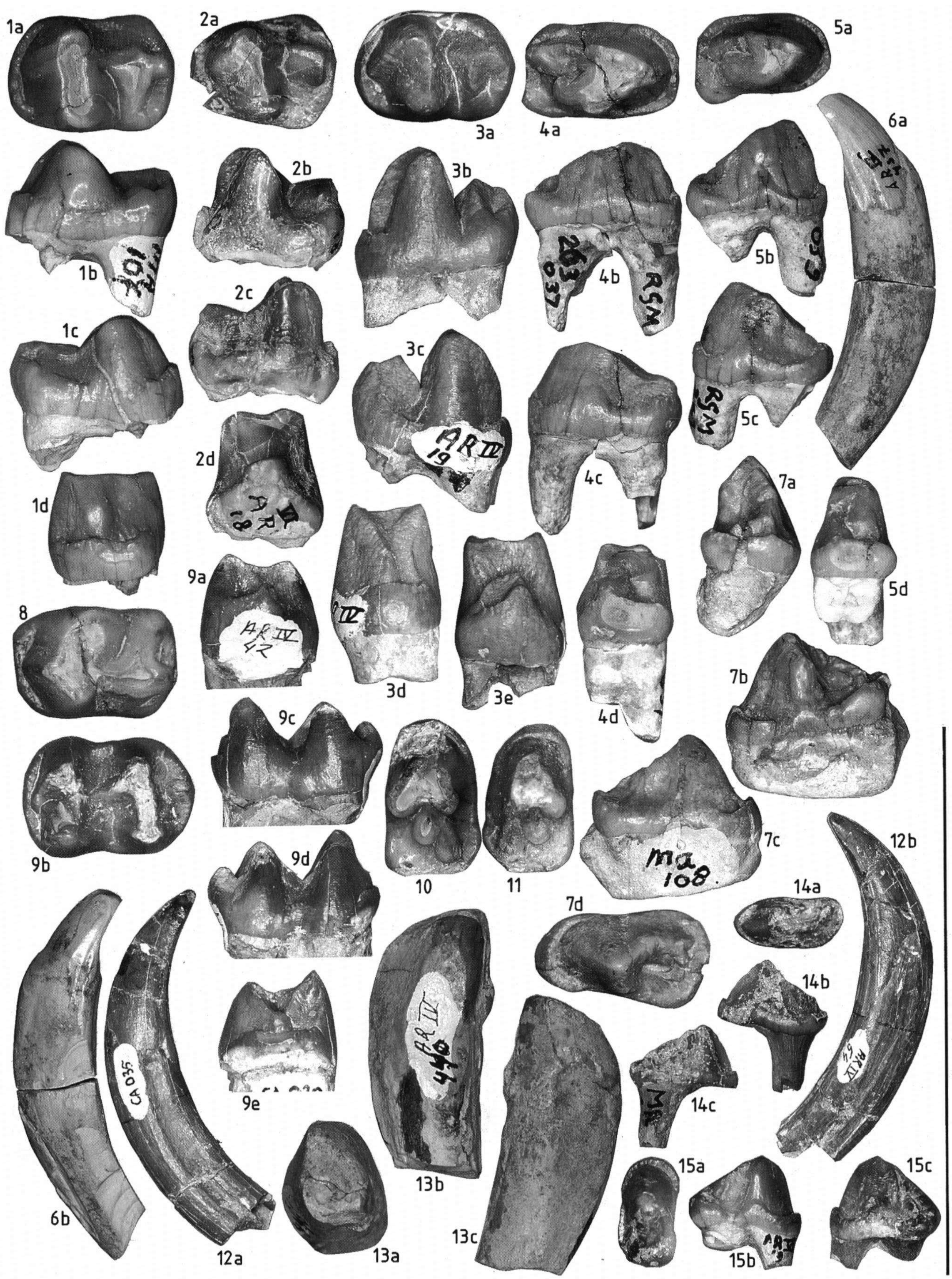
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PLATE 39

Figs 1-10. *Listriodon splendens*; **1** - IVAU AR IV 29, right P^3 (ant-buc-po-li-oc) from Arroyo del Val IV; **2** - IVAU AR IV 39, left P^4 (ant-li-buc-oc) from Arroyo del Val IV; **3** - IVAU AR IV 18, right M^1 (ant-la-po-li-oc) from Arroyo del Val IV; **4** - IVAU AR IV 37, right P^3 (buc-po-li-oc) from Arroyo del Val IV; **5** - IVAU MA I 261, left phalange II 2 or right phalange V 1, probably of pes (lat-dors-prox) from Manchones I; **6** - IVAU AR IV 98, left phalange III 2 or right phalange IV 2 (dors-dist-lat-prox) from Arroyo del Val IV; **7** - IVAU MA I 102, right D^2 - M^1 (buc-oc-li) from Manchones I; **8** - IVAU MA I 259, left phalange II 2 or right phalange V 1, probably of manus (lat-dors-prox); **9** - IVAU MAI 243, left phalange II 2 or right phalange V 2 (dors-lat-prox) from Manchones I; **10** - AR IV 400, left radius (prox) from Arroyo del Val IV.

Scale bar equals 6.7 cm.

PLATE 39

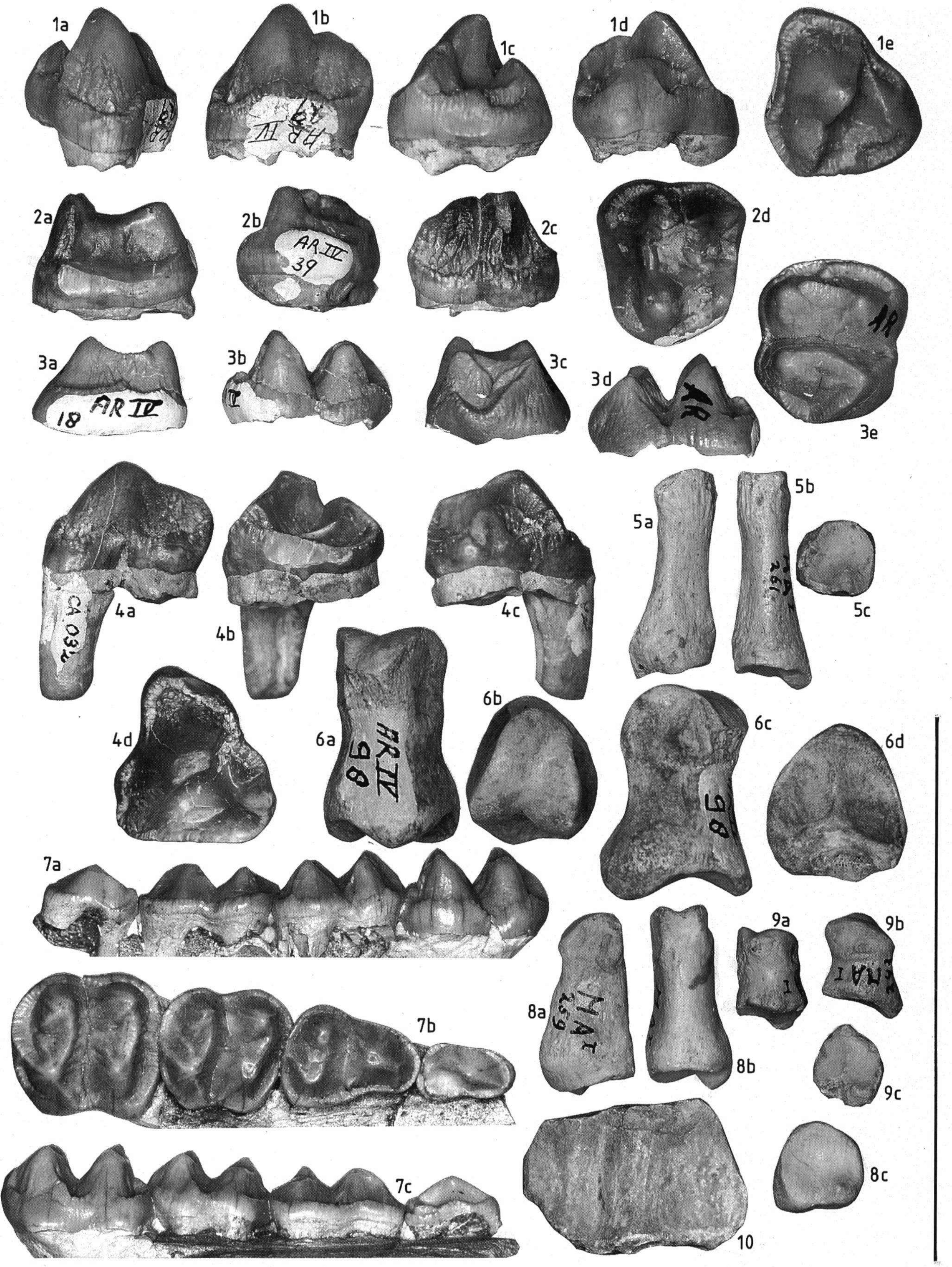

1a
1b
1c
1d
1e
2a
2b
AR IV
39
2c
2d
3a
18 AR IV
3b
3c
3d
AR
3e
AR
4a
CA 032
4b
4c
4d
5a
5b
5c
6a
AR IV
98
6b
6c
6d
7a
7b
7c
8a
8b
8c
9a
9b
9c
10

PLATE 40

Figs 1-6. *Listriodon splendens*; **1** - IVAU MA I 100, left M^3 (buc-ant-li-oc-po) from Manchones I; **2** - IVAU AR IV 10, right M_3 (ant-po-oc-li) from Arroyo del Val IV; **3** - IVAU MA I 101, right I_3 (ap-la-li) from Manchones I; **4** - IVAU AR IV 5, left M_3 (oc-po-li) from Arroyo del Val IV; **5** - IVAU AR VI 7, left M^2 (oc) from Arroyo del Val VI; **6** - IVAU AR I 2, left M_3 (oc-li-ant-po-buc) from Arroyo del Val I.

Scale bar represents 6.7 cm.

PLATE 40

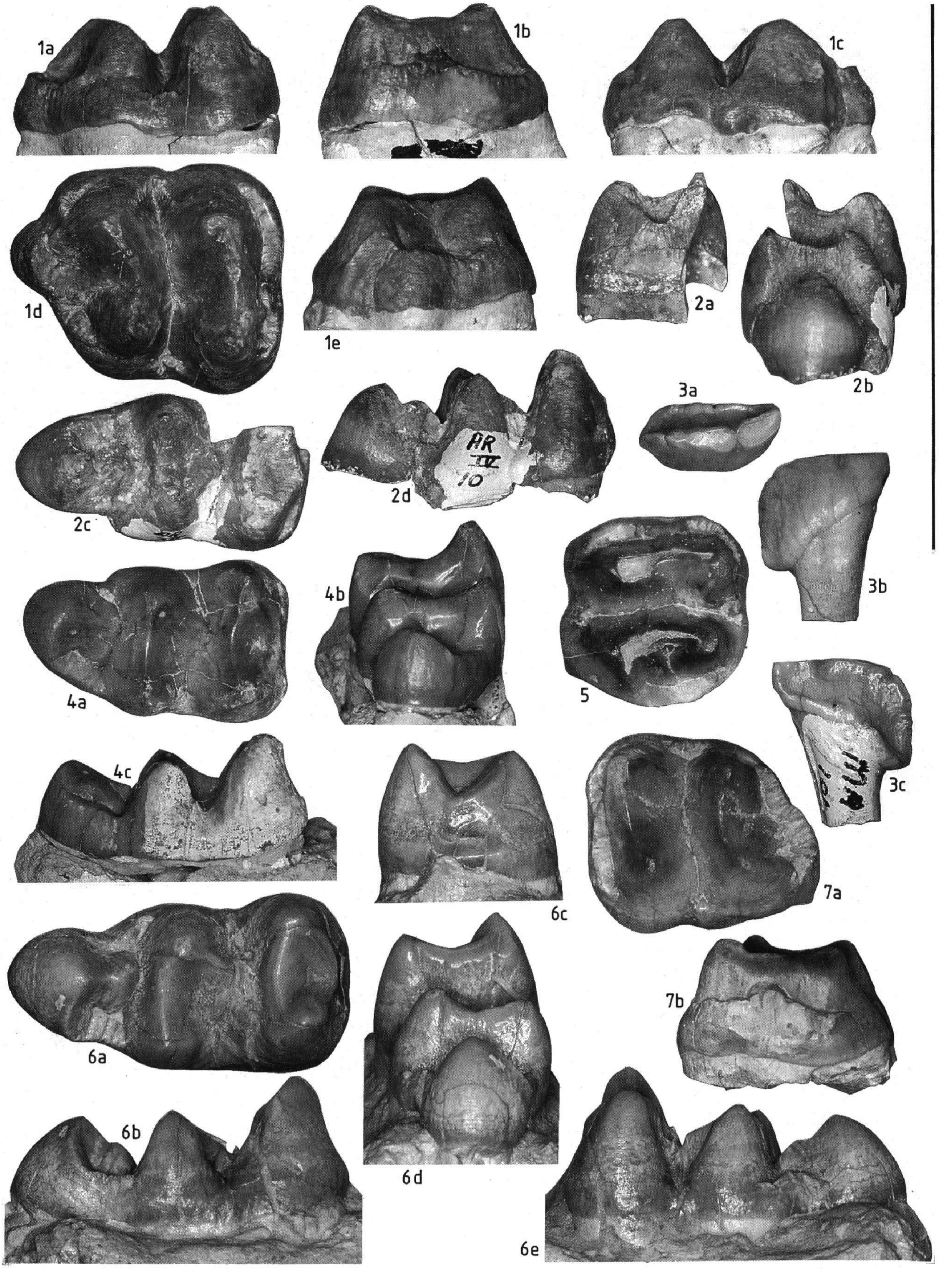

1a
1b
1c
1d
1e
2a
2b
2c
2d
AR
IV
10
3a
3b
3c
4a
4b
4c
5
6a
6b
6c
6d
6e
7a
7b

PLATE 41

Lectotype (Fig. 1) and **paratypes** (Figs 2-14) of *Listriodon splendens* from La Chaux-de-Fonds, Fig. 7 representing the **holotype** of *Calydonius tener* Von Meyer, 1846 and Fig. 14 probably one of the **paratypes** of *Calydonius trux* Von Meyer, 1846.

1 - MHNCHF 8, right I^1 (ap-li-mes);
2 - MHNCHF 8', left I^1 (li-ap-la);
3 - MHNCHF 56b, left C_m (li-la);
4 - MHNCHF 10, left I_3 (ap-mes-la-dist-li);
5 - MHNCHF 4, left P^4 (buc-ant-oc-po);
6 - MHNCHF 9 aua, left I^1 (li);
7 - MHNCHF 48, right C^m (ant);
8 - MHNCHF 10x, left I_3 (li);
9 - MHNCHF 2, right M_3 (ant-li-oc-buc-po);
10 - MHNCHF 4, left P^2 (buc-oc-li);
11 - MHNCHF 10, right I_3 (li);
12 - MHNCHF 6, left I_1 (ap-li-mes-la-dist);
13 - MHNCHF 6, right I_1 (li);
14 - MHNCHF 45, right C^m (ant).

Scale bar equals 6.7 cm.

PLATE 41

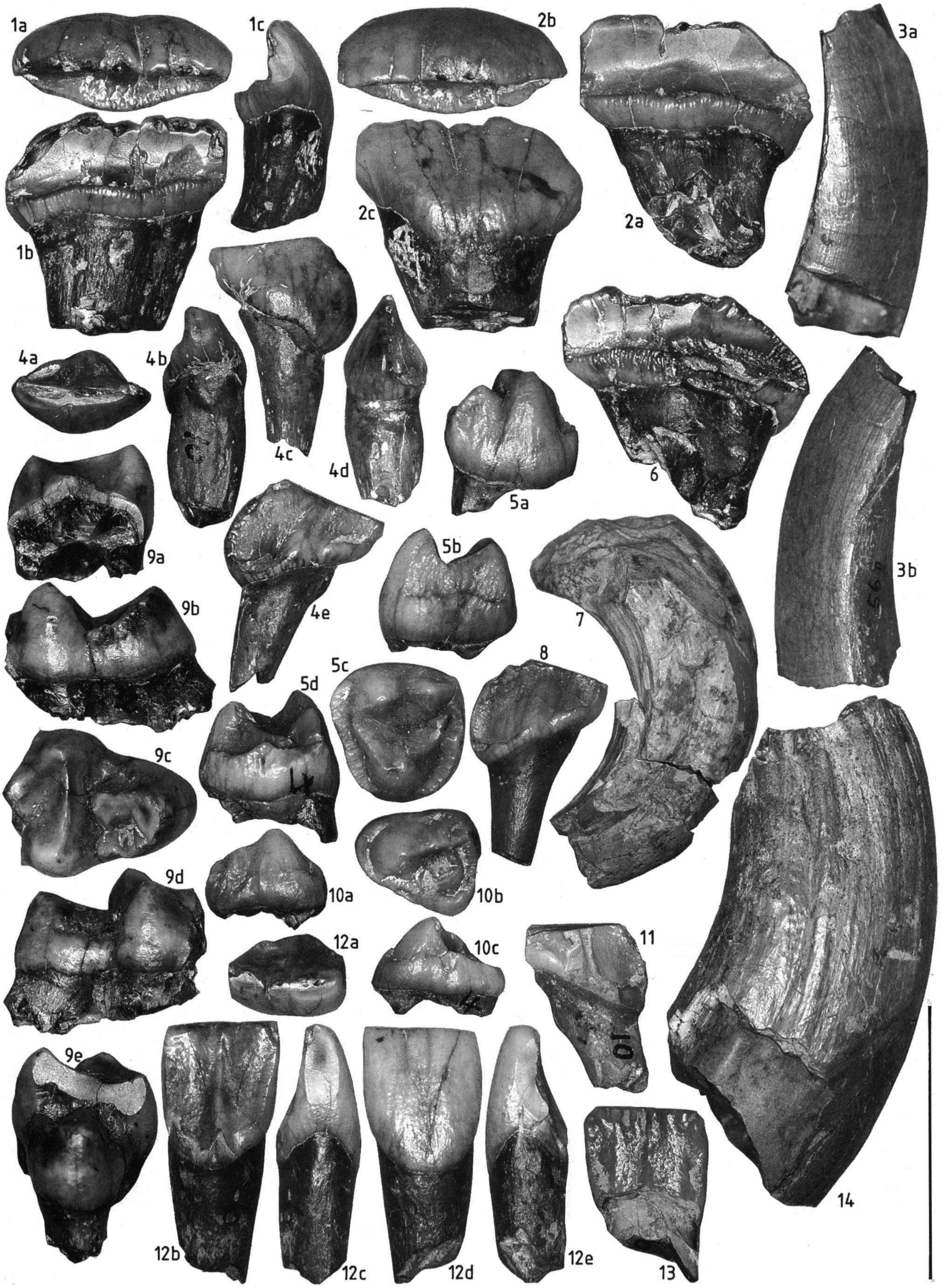
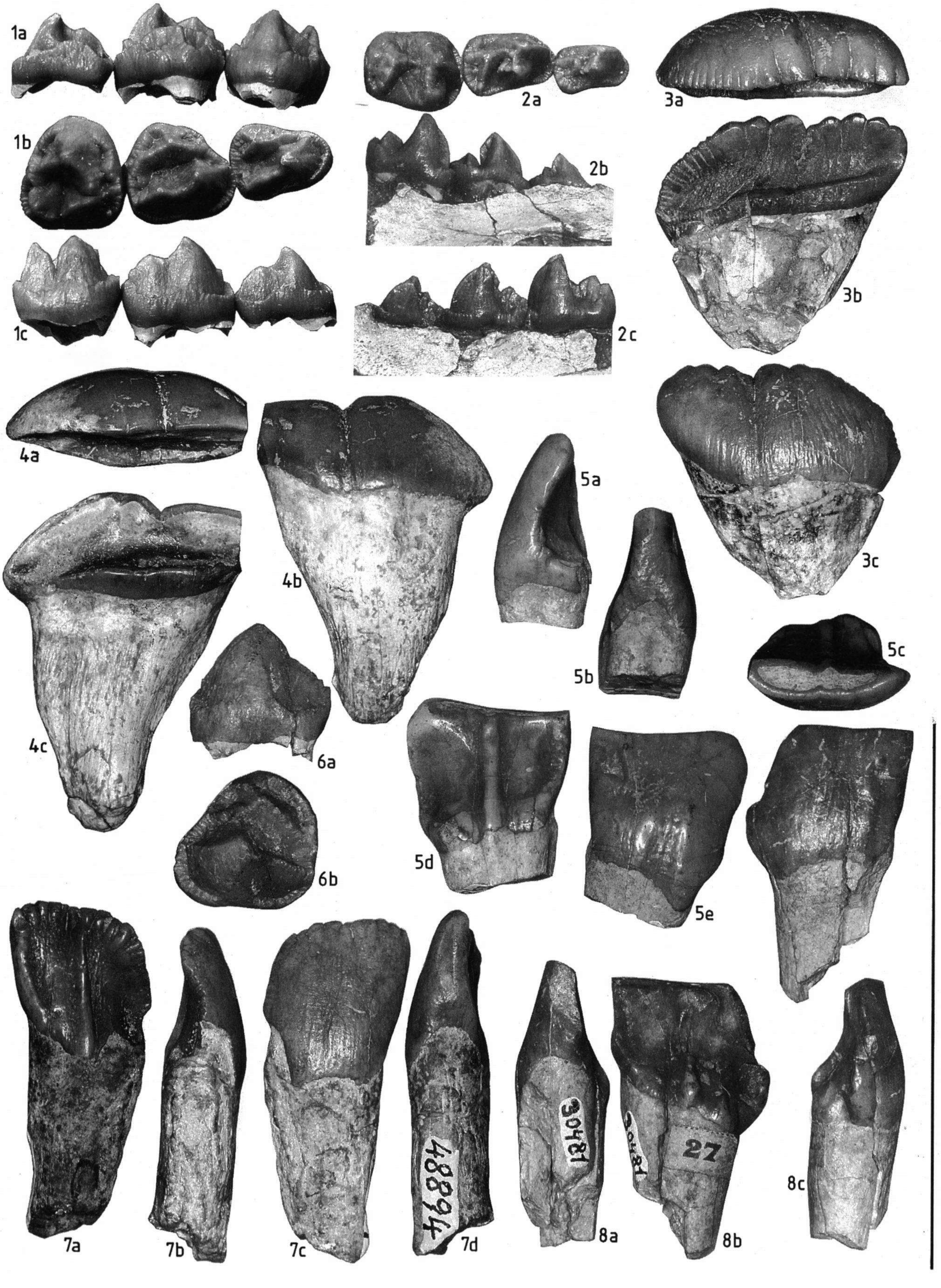

1a
1c
2b
3a
1b
2c
2a
4a
4b
4c
4d
6
5a
9a
5b
3b
9b
4e
7
5c
5d
8
9c
10a
10b
9d
12a
10c
11
9e
12b
12c
12d
12e
13
14

PLATE 42

Figs 1-8. *Listriodon splendens major*; **1** - IPS —, left P^2-P^4 from a series P^2-M^3 (li-oc-buc) from Castell de Barberà; **2** - IPS —, left P_2-P_4 from a mandible P_2-M_3 (oc-li-buc) from Castell de Barberà; **3** - IPS —, right I^1 (ap-li-la) from Castell de Barberà; **4** - IPS —, right I^1 (ap-la-li) from Castell de Barberà; **5** -MLGSB 48498, left I_2 (dist-mes-ap-li-la) from Sant Quirze; **6** - MLGSB 48925, right P^3 (buc-oc) from Sant Quirze; **7** - MLGSB 48894, right I_2 (li-dist-la-mes) from Sant Quirze; **8** - MLGSB 30481, right I_2 (mes-li-dist) from Sant Quirze.

Scale bar equals 6.7 cm.

PLATE 42


1a
2a
3a
1b
2b
3b
1c
2c
3c
4a
5a
4b
5b
5c
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6a
6b
5d
5e
7a
7b
7c
7d
8a
8b
8c
48894
30481
30481
27

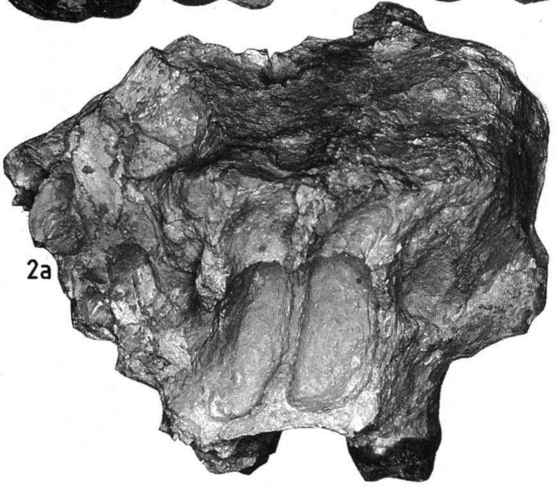
PLATE 43

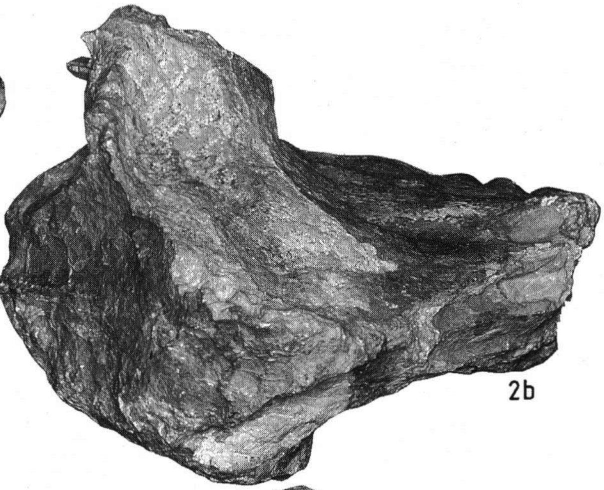
Figs 1-5. *Listriodon splendens*; **1** - MNHNP —, right P^3-M^3 of skull (oc) from Sinap; **2** - MNHNP —, skull (po-dors-lat/right-inf) from Sinap; **3** - MNHNP —, left P^2-P^4 of skull (oc) from Sinap; **4** - IVAU AR IV 82, skull (inf) from Arroyo del Val IV; **5** - IVAU AR IV 116, left magnum (dist-ext-prox) from Arroyo del Val IV.

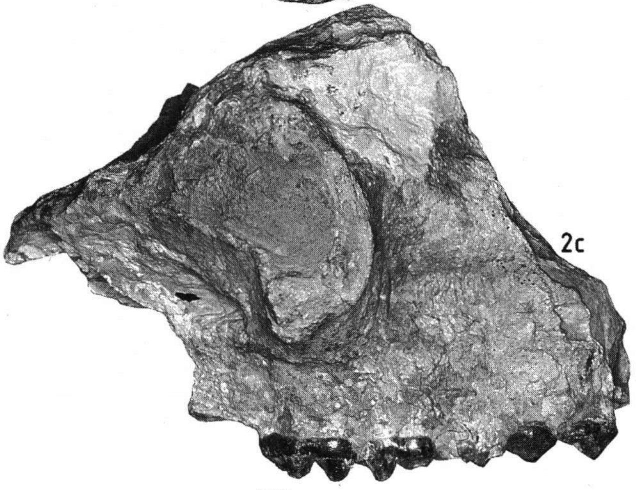
Scale bar represents 6.7 cm for Figs 3 and 5, 10 cm for Fig. 1 and 16 cm for Fig. 2.

PLATE 43

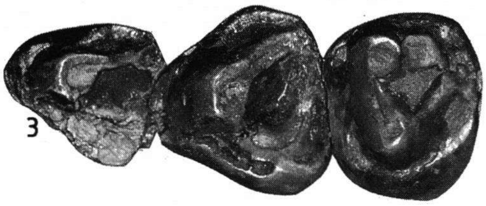

1

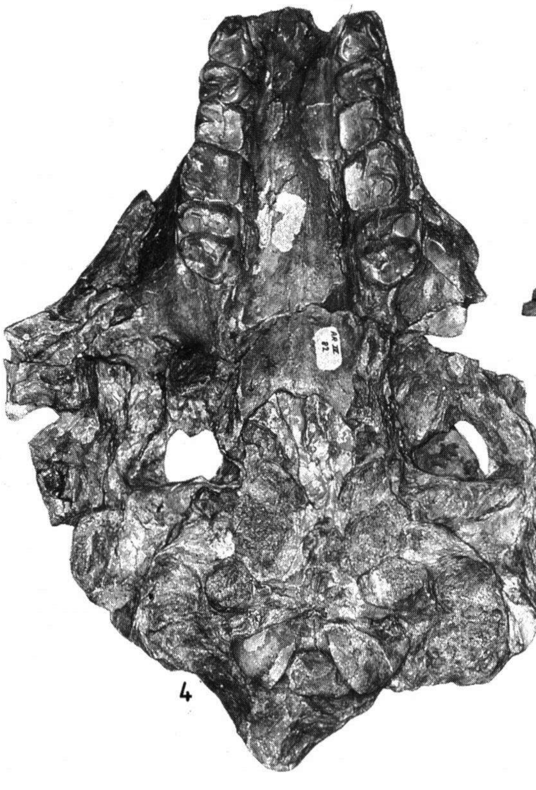

2a

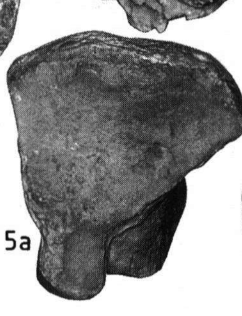

2b

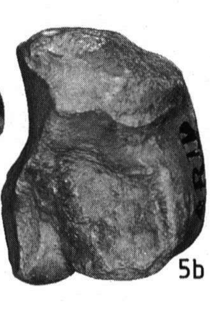

2c


2d


3


4


5a


5b

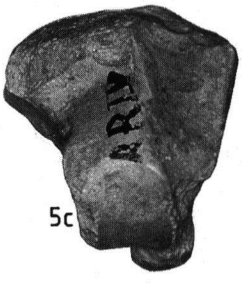

5c

PLATE 44

Figs 1, 2. ***Listriodon splendens*** from Xinan; **1** - IVPP V 8283, - skull, **holotype** of *Listriodon xinanensis* Chen, 1986 (dors-ant-lat/right-oc-oc); **2** - IVPP V 8285, - skull (lat/right-oc-dors-oc-oc-buc).

Scale bar equals *c*. 10 cm for Fig. 2b, 2e and 2f, 18 cm for Fig. 1d, 26 cm for Fig. 1a-1c, 1e and 1f and 40 cm for Fig. 2a, 2c and 2d.

PLATE 44

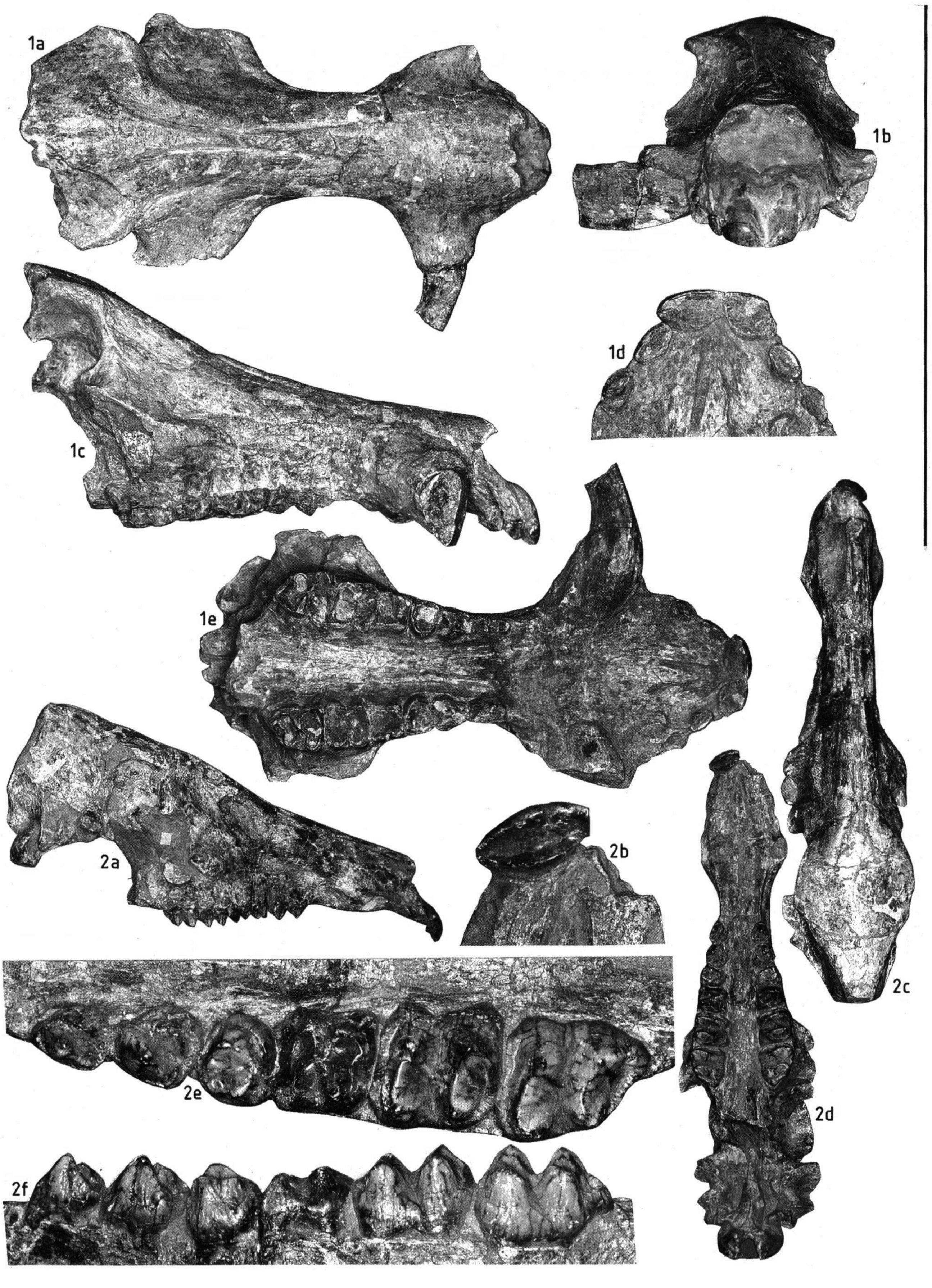


TABLE 1

The nomenclature for the elements of the lower cheek teeth, as used in the present paper, compared with terms for the lower molars as used by previous authors. The first three columns on the left-hand side show a progressive expansion of the Cope-Osborn nomenclature. The remaining columns list various adaptations of this nomenclature or entirely different terminology. Obergfell (1957) and Azanza (1989) employed different names for the premolars.

Coombs & Coombs 1977	Azanza 1989	Present study	Forster Cooper 1924	Pickford 1984	Hünermann 1963&1968	Obergfell 1957
		anterior lobe				
		primoconid				
paraconid		paraconid				
		anterior transverse valley				
		first lobe				
protoconid	protocónido	protoconid	protoconid	protoconid	Vorderer Ausenhügel	Lacol$_1$
		protoectocristid			Aussenfeld	
paracristid	preprotocrístida	protoprecristid		paraconid	Vorderfeld	Praespina$_1$
	foseta anterior	protofossid				
protocristid	postprotocrístida	protoendocristid			Hinterfeld	Postspina$_1$
		protoendoconulid		2/3 cusplet		
		protolophid				
	pliegue palaeomerícido	protopostcristid	accessory ridge		Aussenfeld	Palaeomeryxfalte I
		protopostfossid		palaeomeryx-fold		
	ectostílido	protopoststylid				Medianstyl$_1$
metaconid	metacónido	metaconid	metaconid		Vorderer Innenhügel	Licol$_1$
		metaectocristid	ridge 1 of the metaconid		Aussenfeld	
		metaectostylid				
	premetacrístida	metaprecristid	ridge 2		Vorderfeld	Praeala$_1$
protocristid	cristida accesoria interlobular	metaendocristid	ridge 3		Hinterfeld	
	postmetacrístida	metapostcristid	ridge 4		Aussenfeld	Postala$_1$
	metastílido	metapoststylid		metastylid		Mesostylid
		metapostconulid				
		(first) transverse valley			Quertal	
		second lobe				
hypoconid	hipocónido	hypoconid	hypoconid	hypoconid	Hinterer Ausenhügel	Lacol$_2$
		hypoectocristid			Aussenfeld	
cristid obliqua	prehipocrístida	hypoprecristid			Vorderfeld	Praespina$_2$
		hypopreconulid		median accessory cusplet	Zentralhügel	
	foseta medial	hypofossa				
hypolophid		hypolophid				
hypolophid	posthypocrístida	hypoendocristid			Hinterfeld	Postspina$_1$
postcristid		hypopostcristid			Aussenfeld	Postspina-Leiste
		hypopostconulid				
		hypopoststylid	accessory cusp			Medianstyl$_2$
entoconid	entocónido	entoconid	entoconid	entoconid	Hinterer Innenhügel	Licol$_2$
		entoectocristid	ridge 1		Aussenfeld	
	preentocrístida	entoprecristid	ridge 2		Vorderfeld	Praeala$_2$
hypolophid	pliegue del entocónido	entoendocristid	ridge 3		Hinterfeld	
	postentocrístida	entopostcristid	ridge 4		Aussenfeld	Postala$_2$
		entopoststylid		entostylid		
	valle posterior	second transverse valley				
		third lobe				
hypoconulid	hipoconúlido	pentaconid		hypoconulid		Lacol$_3$
	prehipoconulidocristída	pentaprecristid				
		pentapreconulid			Verbindungshügel	
	foseta posterior	pentafossa				
	posthipoconulidocristída	pentapostcristid				
	entoconúlido	hexaconid				
	postentoconulidocrístida	hexapostcristid				

TABLE 2

Nomenclature for the lower cheek teeth by type of element.

lobes, valleys & fossas	main cusps	crests	minor cusps	styles
anterior lobe	primoconid			
	paraconid			
anterior transverse valley				
first lobe				
protofossid	protoconid	protoectocristid	protoectoconulid	protoectostylid
protopostfossid		protoprecristid	protopreconulid	
		protoendocristid	protoendoconulid	
		protolophid		
		protopostcristid	protopostconulid	protopoststylid
	metaconid	metaectocristid	metaectoconulid	
		metaprecristid	metapreconulid	metaprestylid
		metaendocristid	metaendoconulid	
		metapostcristid	metapostconulid	metapoststylid
(first) transverse valley				
second lobe				
hypofossid	hypoconid	hypoectocristid	hypoectoconulid	hypoectostylid
hypopostfossid		hypoprecristid	hypopreconulid	
		hypoendocristid	hypoendoconulid	
		hypolophid		
		hypopostcristid	hypopostconulid	hypopoststylid
	entoconid	entoectocristid	entoectoconulid	entoectostylid
		entoprecristid	entopreconulid	entoprestylid
		entoendocristid	entoendoconulid	
		entopostcristid	entopostconulid	entopoststylid
second transverse valley				
third lobe				
	pentaconid			
	hexaconid			
forth lobe				
	heptaconid			
	octaconid			
fifth lobe				
	nonaconid			
	decaconid			

TABLE 3

Nomenclature for the upper cheek teeth by type of element.

lobes, valleys & fossas	main cusps	crests	styles	minor cusps	crests of minor cusps
first lobe					
protofossa	protocone	protoectocrista	protoectostyle		
lingual protofossa		protoprecrista		protopreconule	ectocrista of protopreconule
labial protofossa					precrista of protopreconule
					postcrista of protopreconule
		protoendocrista			
		internal protoendocrista			
		external protoendocrista			
		protolophe			
		protopostcrista	protopoststyle		
	paracone	paraectocrista			
		paraprecrista	paraprestyle		
		paraendocrista			
		parapostcrista	parapoststyle		
(first) transverse valley					
second lobe					
tetrafossa	tetracone	tetraectocrista	tetraectostyle	tetraectoconule	
		tetraprecrista		tetrapreconule	ectocrista of tetrapreconule
					precrista of tetrapreconule

					postcrista of tetrapreconule
		tetraendocrista			
		tetralophe			
		tetrapostcrista	tetrapoststyle		postcrista of tetrapostconule
	metacone	metaectocrista		metaectoconule	
		metaprecrista	metaprestyle		
		metaendocrista			
		metapostcrista	metapoststyle		
	hypocone				
second transverse valley					
third lobe					
	pentacone				
	hexacone				
forth lobe					
	heptacone				
	octacone				
fifth lobe					
	nonacone				
	decacone				

TABLE 4

Nomenclature for the upper cheek teeth as used in the present paper compared with the terminologies of previous authors for the upper molars. Azanza (1989) used a different set of names for the premolars.

Coombs & Coombs 1977	Azanza 1989	Present study	Forster Cooper 1924	Pickford 1984	Hünermann 1963&1968
		first lobe			Vorderhügelpaar
		protocomplex			
protocone	protocono	protocone	protocone	protocone	vorderer Innenhügel
		protoectocrista		parastyle	Aussenfeld
preprotocrista	preprotocrista	protoprecrista			Vorderfeld
paraconule		protopreconule	protoconule	protoconule	
		ectocrista of protopreconule			
preparaconule crista		precrista of protopreconule			
postparaconule crista		postcrista of protopreconule			
	foseta anterior	protofossa			
		lingual protofossa			
		labial protofossa	transverse valley		
	pliegue central	protoendocrista			Hinterfeld
		internal protoendocrista			
		external protoendocrista			
		protolophe			
postprotocrista	postprotocrista	protopostcrista			Aussenfeld
		protopoststyle			
		paracomplex			
paracone	paracono	paracone	paracone	paracone	vorderer Aussenhügel
		paraectocrista	barrel of paracone		Aussenfeld
paracrista	preparacrista	paraprecrista			Vorderfeld
parastyle	parastilo	paraprestyle	parastyle		
		paraendocrista			Hinterfeld
		paraendofossa		palaeomeryx-fold	Hauptfurche 6
centrocrista	postparacrista	parapostcrista			Aussenfeld
		parapoststyle			
	valle medial	(first) transverse valley	median alley		
		second lobe			Hinterhügelpaar
		tetracomplex			
metaconule	metaconúlo	tetracone	metaconule	hypocone/ metaconule	hinterer Innenhügel
		tetraectocrista		hypocone crest	Aussenfeld
		tetraectostyle			
	entostylo	tetraectoconule			
premetaconule crista	premetaconúlocrista	tetraprecrista			Vorderfeld
		tetrapreconule			
		ectocrista of tetrapreconule			
		precrista of tetrapreconule			
		postcrista of tetrapreconule			
	foseta posterior	tetrafossa	transverse valley		
		tetraendocrista			Hinterfeld

		internal tetraendocrista			
		external tetraendocrista			
		tetralophe			
postmetaconule crista	postmetaconúlocrista	tetrapostcrista			Aussenfeld
		tetrapoststyle			
		tetrapostconule	accessory cusp		
		ectocrista of tetrapostconule			
	pliegue del metaconúlo	precrista of tetrapostconule			
		postcrista of tetrapostconule			
hypocone		hypocone		hypocone	
		metacomplex			
metacone	metacono	metacone	metacone	metacone	hinterer Aussenhügel
		metaectocrista	barrel of metacone	mesostyle	Aussenfeld
		metaectostyle			
		metaectoconule			
	premetacrista	metaprecrista			Vorderfeld
mesostyle	mesostylo	metaprestyle	mesostyle		
		metaendocrista			Hinterfeld
metacrista	postmetacrista	metapostcrista		metastyle	Aussenfeld
metastyle	metastylo	metapoststyle	metastyle		
		second transverse valley			
		third lobe			
		pentacone			
		hexacone			
		forth lobe			
		heptacone			
		octacone			
		fifthlobe			
		nonacone			
		decacone			

TABLE 5

Nomenclature for the incisors and canines used in the present paper compared with Obergfell's (1957) nomenclature.

Present study	Obergfell (1957)
Lower incisors	
protoconid	Licol = Hauptleiste
(proto)precristid	Praeala = mesialer Flügel
(proto)preconulid	
(proto)prestylid	Praemargo = Vorderrand
(proto)prefossid	
labial (proto)prestylid	
(proto)endocristid	
(proto)endofossid	Fornix = Wölbung
(proto)postcristid	Postala = distaler Flügel
(proto)postconulid	
(proto)poststylid	Postmargo = Hinterrand
lingual cingulum	Cingulum
Upper incisors	
paracone	
paraprecrista	
parapreconule	
paraprestyle	
paraprefossa	
labial paraprestyle	
paraendocrista	
paraendofossa	
parapostcrista	
parapostconule	
parapoststyle	
metacone	
metaprecrista	
metaendocrista	
metaendofossa	
metapostcrista	
basal fossa	
lingual cingulum	

protocone
anterior lingual cingulum
posterior lingual cingulum

Lower canines
precrista
endofacet
postcrista
postfacet
ectocrista
ectofacet

Upper Canines

precrista	Vorderkande, Praemargo
prefossa	
endocrista	lingual Wölbung
endofossa	
postcrista	Klinge, Schneide, Postmargo
ectofossa	

Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space.

J. van der Made

Tables 6-19.

Contributions to Tertiary and Quaternary Geology, 33(1-4), 1996. Leiden.

TABLE 6 Measurements in mm of isolated teeth. "--" indicates that a measurment was not taken due to damage, ".." means that it was not taken for another reason (covered by sediment, simply not taken, etc.).

I_1		DMD	DLL	HLi	HLa	Hme	Hdi
Nguruwe kijivium							
Kirimon							
KNM-KI 18037	l	5.7	5.8	>11.2	>11.6	>8.7	>8.0
Lopholistriodon pickfordi							
Maboko							
KNM-MB 25	l	5.0	5.5	12.8	13.3	8.7	8.4
Lopholistriodon kidogosana							
Ngorora B5, 2/1							
KNM-BN 1254	r	6.4	≥5.5				
Ngorora B5, 2/56							
KNM-BN 548	l	6.7	4.8	9.2	±10.8	7.0	6.8
KNM-BN 1743	l?	>5.5	5.6	10.3	11.0	—	7.4
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	l	12.2	>14.6	..	..	≥16.6	≥24.6
MNHNP Z 1961	r	11.6	14.0				
MNHNP Z 1961	r	11.9	13.7				
MNHNP Z 1961	r	—	12.2				
MNHNP —	r	11.5	—				
MNHNP —	r	12.6	—				
Bunolistriodon anchidens							
Rusinga Rl							
KNM-RU 15129	l	8.9	7.8				
Bunolistriodon aff. *latidens*							
Olival da Suzana							
CEPUNL —	r	11.8	9.7	..	17.6	12.0	12.4
La Artesilla							
MPZ 6414	r	9.6	8.7				
Armantes I							
IVAU 41/559	r	7.2	7.3				
Munébrega I							
IVAU 55/1061	l	9.4	7.6				
Munébrega III							
IVAU 53/55	r	8.9	8.0	>12.5			
IVAU 53/56	l	9.4	7.9				
Bunolistriodon latidens							
Inönü I							
MTA AKI-3/573	r	10.8	7.9				
Bunolistriodon M							
Paşalar							
PIMUZ BP-311	l	14.6	6.8	16.7	18.8	15.8	15.8
PDTFAU B609	l	13.7	—				
PDTFAU B609/1	r	14.4	6.9				
PDTFAU CT1 B 35.13	l		14.3	>6.7			
PDTFAU DT	l	14.5	—				
PDTFAU E8229	l	11.9	7.2				
PDTFAU ET	l	—	—				
PDTFAU F278.17	l	12.5	8.2				
PDTFAU F278.19	l	—	7.1				
PDTFAU F278.22	r	12.6	6.6				
PDTFAU F355	r	14.3	7.4				
PDTFAU F397	l	15.8	7.2				
PDTFAU F491	l	14.2	7.3				
PDTFAU G21.a	l	14.7	6.6	—	≥17.4	15.1	14.9
PDTFAU G210.24	r	13.9	≥7.6				
PDTFAU G223	l	13.2	7.2				
PDTFAU G1094	r	13.6	7.0				
PDTFAU G1718	r	13.6	6.9	16.8	18.7	14.7	15.2
PDTFAU G1778	r	15.1	7.2				
Bunolistriodon lockharti							
Pellecahus							
NMB GB 1387	r	10.7	9.8	15.6	16.8	10.7	10.7
La Romieu							
UCBL 320270	l	10.7	9.6				
UCBL 320270	r	10.1	10.3				
Baigneaux							
NMB SO-3020	l	8.8	9.9				
Gerlenhofen							
SMNS — cast	l	10.9	9.3				
Bunolistriodon akatikubas							
Maboko							
KNM-MB 19418	r	11.3	11.6	>15.1	>16.2	>10.0	>11.3
KNM-MB 19710	l	11.1	10.3				
Bunolistriodon intermedius							
Maerzuizigou							
IVPP V 9522.8	r	10.9	10.1				
Listriodon							
Listriodon pentapotamiae							
Chinji 38							
GSP 2296	l	10.6	9.6				
Dhulian 302							
GSP 10021	l	10.3	8.7				
Cheski Wala							
IVAU CHC 93	l	11.5	8.3	14.7	16.3	11.2	11.8
Chari Gambhir							
BSPHGM 1956II101	r	11.2	8.6				
Kanatti Chak 3							
BSPHGM 1956II96	r	11.0	9.4				
Listriodon splendens							
Paşalar							
PDTFAU C187.15	l	10.2	8.0				
PDTFAU C324	r	11.4	8.8				
PDTFAU C369	r	12.5	10.0	17.4	18.2	13.5	13.7
PDTFAU D86.8	r	9.6	9.0				
PDTFAU D568	r	11.4	9.2				
PDTFAU D1031	l	11.9	8.7	16.5	17.0	13.6	14.1
PDTFAU D1031	r	11.9	8.6	16.6	17.1	13.6	14.1
PDTFAU D1039	r	11.3	8.4				
PDTFAU DT 8.6	l	13.0	9.4	16.1	17.7	11.6	12.0
PDTFAU DT 8.7	l	12.2	8.4				
PDTFAU DT 8.8	l	12.0	9.3				
PDTFAU DT 8.9	r	13.0	9.4	16.0	17.3	11.5	11.8
PDTFAU DT 8.10	r	11.0	9.6	17.6	19.1	12.2	12.6
PDTFAU DT 8.11	r	10.6	8.1				
PDTFAU DT 8.12	r	11.8	—				
PDTFAU DT 8.13	r	12.5	—				
PDTFAU DT 8.14.8	r	12.5	—				
PDTFAU E773	l	11.9	8.3				
PDTFAU E917	l	11.2	—				
PDTFAU F9.1	l	—	8.8				
PDTFAU F9.4	l	12.1	—	—	—	—	—
PDTFAU F9.8	l	10.8	9.0				
PDTFAU F9.15	r	11.5	—				
PDTFAU F353	l	12.5	9.0	16.8	17.3	12.6	12.3
PDTFAU F354	l	10.8	—				
PDTFAU F409	l	12.5	9.0	—	18.2	11.8	12.3
PDTFAU G248	r	13.2	10.2				
PDTFAU G449	l	12.3	8.6	16.8	15.9	12.1	12.0
PDTFAU G582.a	l	11.8	—	—	18.5	12.0	12.2
PDTFAU G1129	l	12.6	9.8	16.3	16.8	12.5	13.0
PDTFAU G1138	l	12.9	—				
PDTFAU G1738.1	l	12.4	8.8				
PDTFAU G1833.1	l	11.6	8.6	16.8	18.3	11.3	11.7
PDTFAU G2080	l	11.9	8.8				
Çandir							
MTA AÇH 588	l	13.0	11.2				
Mörsingen							
NMB TD 692	l	13.6	8.9				
Manchones I							
IVAU MA 5208	r	—	—				
Arroyo d. Val IV							
IVAU AR IV 49	l	13.1	10.5				
IVAU AR IV 92	l	12.5	10.5	18.1	17.9	12.8	14.2
IVAU AR IV 94	l	13.8	9.5				
IVAU AR IV 391	l	11.8	10.1				
MPZ AV-23	r	13.3	9.6				
La Grive oc							
IGF 299	l	14.5	9.3	16.0	17.2		
IGF 299	l	12.7	9.4	>14.6	>15.3		
IGF 299	r	12.1	9.5				
UCBL —	r	14.6	10.0				
MGL LGr 1577	r	13.4	9.3				
MGL LGr 6004	l	13.8	8.9				
MGL LGr 6004	l	14.2	10.2				
MGL LGr 6004	l	13.9	10.0	15.3	16.6	10.9	10.8
MGL LGr 6004	r	15.4	11.2				
MGL LGr 6004	r	12.6	9.3				
MGL LGr 6004	r	12.4	9.4				
MGL LGr 6004	r	11.8	8.6	14.2	14.6	9.8	10.8
Neudorf Sandberg?							
NMW —	r	14.8	9.7	17.3	18.2	12.3	13.2
La Chaux-de-Fonds							
MHNCF 6	r	14.6	—	—	17.9	—	13.1
MHNCF 6	l	12.8	>10.0				
Mas del Olmo							
ITGE 409M	r	16.5	9.2				
Cerro del Otero							
MNCN NM 18030	l?	≥16.4	9.3				
Sant Quirze							
MGSCB 48930	r	14.7	10.0				
MGSCB 48931	l	14.7	9.5				
MGSCB 48932	r	16.2	9.7				
MGSCB 48933	l	15.2	10.2				
Castell de Barberà							
IPS 1959	r	14.5	9.2				
Hostalets							
MGSCB 48496	r	13.9	9.9				
MGSCB 48497	l	>13.4	9.8				
IPS 1020	r	16.7	10.8				
IPS 1021	r	16.5	9.9				
IPS 1022	r	15.7	>10.3				
IPS 1023	r	16.8	12.3				
IPS 1024	l	13.7	9.9				
IPS VP 761	l	12.0	8.8				

CJFV —	r	14.4	10.8					

DI$_1$			DMD	DLL			
Bunolistriodon M							
Paşalar							
PDTFAU F278.15	r	8.3	4.2				
PDTFAU F278.16	1	8.2	4.1	≥10.2	≥10.0	≥8.2	≥6.8
Bunolistriodon lockharti							
Buñol							
IVAU —	1	6.6	5.0				
Bunolistriodon akatikubas							
Maboko							
KNM-MB 14447	r	5.4	4.5				
Bunolistriodon intermedius							
Shatai Gou							
IVPP V 9523	r	8.8	6.6				
Listriodon splendens							
Paşalar							
PDTFAU C187.8	1	7.7	4.7				
PDTFAU C187.9	r	7.2	3.9				
PDTFAU D210.21	r	7.4	4.4				
PDTFAU F418	r	7.0	3.9				
PDTFAU G1022	r	6.3	4.1				
PDTFAU —	r	7.6	—				
Murrero							
IPS —	1	9.4	4.6				
La Grive oc							
IGF 299	1	14.4	5.6				

I$_2$			DMD	DLL	Hli	Hla	Hme	Hdi
Nguruwe kijivium								
Rusinga Rl								
?KNM-RU 5838	1	5.3	4.3					
Lopholistriodon pickfordi								
Maboko								
KNM-MB 26	1	6.2	5.5	10.9	12.8	7.7	8.9	
KNM-MB 14446	r	5.6	5.1	—	13.2?	7.9	8.5	
KNM-MB 14448	1	5.1	5.6	9.9	12.2	6.4	8.7	
Lopholistriodon akatidogus								
Mbagathi								
KNM-MG 7	r	12.0	8.3	>12.2	13.5	>6.7	>13.0	
Kubanochoerus marymunngui								
Buluk								
KNM-WS 149a	r	17.4	21.3	>27.8	—	>17.5	>21.9	
Kubanochoerus khinzikebirus								
Maboko								
KNM-MB 612	r	>19.8	..					
Kubanochoerus massai								
Gebel Zelten								
MNHNP Z 1961	r	13.1	>12.1	—	≥26.1	>16.8	>19.8	
MNHNP Z 1961	r	12.8	15.0	>24.2	>24.4	>14.3	>15.6	
MNHNP Z 1961	1	12.9	15.6					
MNHNP Z 1961	r	12.8	15.6	>24.6	>24.3	>14.3	>16.2	
MNHNP Z 1961	r	14.6	15.9					
MNHNP Z 1961	r	13.5	—					
MNHNP Z 1961	1	12.2	—					
MNHNP Z 1961	1	13.2	15.2	>21.2	>23.0	>12.6	>17.8	
MNHNP Z 1961	r	—	13.1					
MNHNP Z 1961	1	—	>15.9					
MNHNP Z —	r	14.3	15.9	26.6	27.2	18.7	21.7	
MNHNP Z 1961	r	12.6	14.9	>24.1	>25.5	>15.4	>17.7	
Bunolistriodon? sp.								
Baragoi								
KNM-BG 14786	r	11.6	9.9	>14.2	>14.2	>10.2	>13.4	
Bunolistriodon aff. latidens								
La Artesilla								
MPZ 6416	r	12.0	10.6					
Munébrega I								
IVAU 55/1054	1	12.1	9.9					
Munébrega III								
IVAU 53/53	r	10.9	9.2	17.7	..	..	..	
IVAU 53/54	1	11.8	9.9	>18.3				
Bunolistriodon latidens								
Inönü I								
MTA AKI-3/572	1	14.6	9.0					
MTA AKI-3/574	r	14.8	9.1					
Bunolistriodon M								
PDTFAU B609/3	1	15.0	7.4					
PDTFAU E7.14	1	14.5	7.7					
PDTFAU G629	1	±16.1	—					
PDTFAU G692.6	1	16.0	—					
PDTFAU G997	r	15.8	9.0					
PDTFAU G1786	1	14.6	8.0					
PDTFAU G1912	r	14.0	7.6					
Bunolistriodon lockharti								
Pellecahus								
NMB GB 1386	1	11.1	9.6	>16.8	>15.4			
La Romieu								
UCBL 320270	r	13.5	10.6	..	≥23.5			
UCBL 320270	1	11.9	11.6					
Baigneaux								
NMB SO-928	1	12.6	11.0					
NMB SO-3022	1	12.9	13.7					
NMB SO-6427	1	12.4	13.2					
MSNO 904	r	12.4	12.2	20.6	21.4	12.7	19.6	
COBO —	r	12.9	13.1	20.3	21.4	10.9	18.1	
Gerlenhofen								
SMNS — cast	1	14.0	12.2					
SMNS — cast	r	15.5	13.0					
Langenau 1								
SMNS 41417	1	12.6	12.2					
Engelswies								
NMB TD 819 cast	1	11.8	≥11.5					
Pontlevoy								
MNHNP FP 1029	r	15.0	13.8	>20			>20	
Pontlevoy?								
MNHNP cast	1	14.5	12.9	19.4	19.1	12.8	18.0	
Tavers								
COBO —	r	13.6	—					
COBO —	1	—	≥12.1					
Bunolistriodon akatikubas								
Maboko								
KNM-MB 19414	1	13.8	11.2					
Bunolistriodon intermedius								
Maerzuizigou								
IVPP V 9522.7	1	13.1	10.8	±21.5				
Bunolistriodon guptai								
Loc.?								
IM K 13/57	r	11.7	10.6	>18.3	>19.5	>9.2	>17.5	
Listriodon pentapotamiae								
Dhok Talian 189								
GSP 4416	1	12.2	10.3	19.1	18.5	10.6	15.3	
GSP 4417	1	11.3	10.2					
GSP 4461	r	12.4	8.8					
GSP 4462	r	13.3	11.7	20.5	19.9	11.9	18.6	
Dhulian 304								
GSP 10031	1	11.7	8.3					
Kanatti Chak 3								
BSPHGM 1956II96	r	11.0	9.4					
Kund Nala								
BSPHGM 1939X596	r	12.5	9.7					
Pirawalaban 1								
BSPHGM 1956II102	r	13.0	9.9					
Dhulian								
BSPHGM —	r	12.0	8.3					
Chinji bought specimen								
IVAU CH 292	1	≥12.2	10.2					
Listriodon splendens								
Paşalar								
PIMUZ BP-89b	1	13.1	10.0					
PIMUZ BP-282	r	15.6	9.7					
PIMUZ BP-384	1	15.3	10.3					
PDTFAU A178	1	14.0	9.2					
?PDTFAU B539	1	15.9	9.8					
PDTFAU B592.6	1	15.0	—					
PDTFAU B608	1	13.4	9.5					
PDTFAU B609	r	14.1	≥10.6					
?PDTFAU B935	r	14.7	9.2					
PDTFAU C8.10	r	15.0	10.1					
PDTFAU C8.11	r	17.4	11.3	20.2	—	15.2	>18.3	
PDTFAU C8.12	r	13.4	9.5					
PDTFAU C8.13	r	13.5	10.4					
PDTFAU C224	1	14.7	10.2	17.6	18.5	—	17.6	
PDTFAU D8.16	r	14.7	11.2					
PDTFAU D8.17	r	14.7	10.6					
PDTFAU D8.18	r	—	>8.2					
PDTFAU D8.19	1	14.6	≥9.7	—	—	12.5	—	
PDTFAU D8.20	1	14.4	10.8					
PDTFAU D9.4	1	14.8	≥10.8	>18.8	—	14.7	—	
PDTFAU D9.5	1	>14.2	—					
PDTFAU D9.6	1	15.4	—	—	—	13.5	—	
PDTFAU D177	r	15.5	10.3					
PDTFAU D1079	r	15.3	10.4	—	18.6	12.2	16.4	
PDTFAU DT 9.1	1	15.5	10.9	19.3	19.5	12.2	17.2	
PDTFAU DT 9.2	1	13.6	11.2					
PDTFAU DT 9.3	1	15.5	11.2					
PDTFAU E7.11	r	15.9	—					
PDTFAU E7.12	1	15.4	>10.7					
PDTFAU E7.13	1	15.5	10.2					
PDTFAU F9.5	1	13.4	—					
PDTFAU F9.7	1	14.6	≥9.2					
PDTFAU F278.29	1	14.2	10.0					
PDTFAU F398	1	13.7	>9.4					
PDTFAU G202	r	14.9	10.5					
PDTFAU G330	r	15.2	10.2					

PDTFAU G1667	r	—	—				
PDTFAU G1688	1	15.9	13.0				
PDTFAU G1688.1	1	13.9	9.0				
Villefranche d´Astarac							
MNHNP VAS 29	r	16.1	10.5				
Arroyo del Val IV							
IVAU AR IV 47	1	—	11.1				
IVAU AR IV 91	r	15.7	>10.0				
IVAU AR IV 93	1	14.5	10.1				
MPZ AV-24	r	≥14.2	11.0				
Torril							
OCL —	1	>11.4	10.7				
La Grive oc							
IGF 299	1	14.9	>9.2	15.7	—		
IGF 299	1	14.8	10.6	18.1	17.3		
IGF 299	r	17.8	>10.7	>16.8	>16.9		
UCBL 65616	1	..	11.5	>20.3			
UCBL —	r	15.0	11.1				
UCBL —	r	>15.9	10.8				
MGL LGr 1444	1	>17.2	>10.8				
MGL LGr 6003	1	15.3	9.2	15.2	15.7	12.4	16.8
MGL LGr 6003	1	13.6	>9.8				
MGL LGr 6004	1	15.9	9.8				
MGL LGr 6004	1	16.9	11.2				
MGL LGr 6004	1	16.1	10.4				
MGL LGr 6004	r	>14.5	—				
Prittlbach							
BSPHGM 1951 I 49	r	15.7	>10.3				
La Cisterniga							
MNCN NM 14014	r	16.9	9.8				
Cerro del Otero							
MNCN NM 18024	1	≥20.6	—				
MNCN NM 18025	1	18.5	≥10.0				
Sant Quirze							
IPS VP 1020	1	17.3	11.6				
MGSCB 30486	r	18.3	—				
MGSCB 48894	r	17.2	10.1	>18.8	>19.7	13.8	—
MGSCB 48929	1	—	11.6				
CJFV SQu 5457	r	20.2	13.4				
Masquefa							
CJFV —	r	17.9	11.1				
Can Mata							
MGSCB 48565	r	—	11.6				
Hostalets							
MGSCB 48498	1	19.8	12.0				
MGSCB 48499	r	—	>12.0				
IPS 1025	1	—	10.4				
IPS 1105	1	>18.1	>9.7				
IPS 1106	1	19.8	>12.3				
IPS 1107	1	17.9	±13.5				
CJFV —	1	—	13.1				
CJFV —	r	18.4	11.8	>21.0			

DI$_2$		**DMD**	**DLL**	**Hli**	**Hla**	**Hme**	**Hdi**
Nguruwe kijivium							
Songhor							
KNM-SO 5470		3.2	3.0				
Lopholistriodon akatidogus							
Maboko							
KNM-MB 10337	r	5.7	5.4				
Bunolistriodon aff. latidens							
La Artesilla							
MPZ 6415	r	7.5	6.5				
Armantes I							
IVAU 41/560	r	6.7	6.4	10.7	10.8	6.4	8.8
Bunolistriodon M							
Paşalar							
PDTFAU E89.26	1	10.0	5.1				
PDTFAU G1833	r	9.9	5.7	11.9	14.6	8.4	12.5
Çandir							
PIMUZ CA I 44	r	8.5	4.6	10.7	9.8	..	..
Bunolistriodon lockharti							
Pellecahus							
NMB GB 1388	r	9.0	6.8	11.2	12.6	9.3	13.9
Gerlenhofen							
SMNS — cast	1	8.4	7.1	>11.7	>12.3		
Listriodon pentapotamiae							
Chinji 76							
GSP 1421	1	7.2	4.5				
Listriodon splendens							
Paşalar							
PDTFAU C	r	9.7	—	11.6	—	—	—
PDTFAU D86A	1	9.6	6.9	>13.3	>13.2	>7.7	>11.4
PDTFAU D629	r	9.8	6.1	13.8	12.9	8.7	12.7
PDTFAU D629.1	r	9.5	5.6				
PDTFAU DT	1	10.1	—	11.7	≥12.5	≥6.3	—
PDTFAU F	1	>7.7	—	—	—	—	—
Manchones I?							
IVAU —	1	11.0	3.6				
La Grive oc							
MGL 1493	r	11.7	±8.9				
Sant Quirze							
MGSCB 48847	r	≥12.2	>7.3				
Castell de Barberà							
IPS —	1	±11.1	6.8	12.3	12.6		

I$_3$		**DMD**	**DLL**	**Dmax**	**Hli**	**Hme**	**Hdi**
Kubanochoerus marymunngui							
Buluk							
KNM-WS 149b	1	19.2	16.6	..	>14.9	>14.9	>16.9
Kubanochoerus massai							
Gebel Zelten							
MNHNP —	1	16.3	14.8	..	12.1	16.0	16.9
MNHNP Z 1961	1	±16.1	—	..	—	—	15.1
MNHNP Z 1961	1	15.3	13.8	..	11.0	12.9	15.2
MNHNP Z 1961	r	15.6	12.5	..	—	>13.4	>14.1
MNHNP Z 1961	1	16.3	14.9	..	12.5	14.7	17.1
MNHNP Z 1961	1	16.3	±12.5				
MNHNP Z 1961	1	15.2	10.9	..	13.1	9.8	15.3
Lopholistriodon akatidogus							
Beni Mellal							
KNM-ZP 1398 cast	r	12.4	7.4	..	8.8	6.8	10.3
Bunolistriodon aff. latidens							
Tejar Manzanares							
IPS 1139	r	—		5.3			
Armantes I							
IVAU 41/525	1	11.4	7.4	12.8			
Munébrega I							
IVAU 55/1060	1	11.3	8.3	13.3			
Munébrega III							
IVAU 53/58	r	11.2	7.3	13.3			
Bunolistriodon latidens							
Inönü I							
MTA AKI-3/578	r	>13.4	7.3	16.2			
Bunolistriodon M							
Paşalar							
PDTFAU B592.5	1	15.2	6.8	17.2	9.2	7.6	>11.0
PDTFAU C8.14	1	—	6.6	—			
PDTFAU C8.15	1	—	6.8	—			
PDTFAU C187.10	1	16.0	—	17.0	—	9.2	12.1
PDTFAU C187.11	r	16.3	8.0	17.2			
PDTFAU D27	r	14.3	6.8	16.3	10.1	8.5	12.3
PDTFAU D167	r	14.3	7.3	15.4			
PDTFAU D210.28	1	14.5	7.0	16.3			
PDTFAU D210.36	1	14.5	7.0	16.3	10.4	9.3	11.6
PDTFAU D480	1	>13.9	6.7	>14.8			
PDTFAU F9.2	r	14.7	6.8	16.1			
PDTFAU F356	1	14.9	7.6	15.2			
PDTFAU F394	r	14.5	7.3	16.7			
PDTFAU F399	1	14.0	—	14.7			
PDTFAU F399	r	13.4	6.7	14.5			
PDTFAU F399	r	—	6.7	—			
PDTFAU G543	r	15.0	7.4	16.5			
PDTFAU G1021	r	16.6	7.2	17.7	10.4	9.1	12.3
PDTFAU G1031	1	14.4	6.4	16.1			
PDTFAU G1058.3	r	15.0	6.4	16.0	8.8	8.1	11.0
PDTFAU G1090	1	17.3	8.1	19.3			
PDTFAU G1738.6	r	13.4	6.2	14.4			
PDTFAU G1960.1	r	14.5	7.3	15.7			
PDTFAU G2054.1	r	14.5	7.3	15.7			
PDTFAU G2107	1	—	—	—			
PDTFAU G6595	1	—	5.3	—			
Bunolistriodon lockharti							
Pellecahus							
NMB GB 1389	r	12.8	9.2	14.9			
La Romieu							
UCBL 320268	1	14.8	8.0	..			
Baigneaux							
NMB SO-6593	r	12.5	8.5	14.8			
Gerlenhofen							
SMNS — cast	r	15.3	10.6	16.9			
SMNS — cast	1	—	9.3	17.8			
Buñol							
—	r	13.1	7.1	14.4			
IVAU —	1	13.6	..	14.2			
IVAU —	r	—	7.2	—			
Pontlevoy							
MNHNP FP 1030	r	14.2	9.5	17.2			
Bunolistriodon akatikubas							
Maboko							
KNM-MB 10367	1	14.5	10.2	..	>10.8	>7.0	>15.6
KNM-MB 14418	r	13.4	10.3	..	>10.6	>7.1	>11.0
Bunolistriodon guptai							
Loc.?							
IM K 13/536	1	9.8	7.2	12.7	9.2	4.6	..
Listriodon splendens							

Paşalar					
PDTFAU B592.7	l	14.6	7.7	16.5	
PDTFAU C9.1	r	14.6	7.6	16.5	
PDTFAU C9.3	r	14.0	8.1	16.6	
PDTFAU C144	r	14.3	8.7	16.1	
PDTFAU D8.20	r	15.1	8.6	17.6	
PDTFAU D9.12	l	14.1	—	16.8	
PDTFAU D9.13	r	13.7	7.1	14.8	
PDTFAU D9.15	r	14.0	9.2	15.4	
PDTFAU D9.16	r	—	—	—	
PDTFAU E7.16	l	13.6	8.6	15.1	
PDTFAU G7.17	r	13.5	8.5	16.0	
PDTFAU . 8.16	l	13.3	8.3	15.8	
PIMUZ BP-181	l	14.5	8.2	16.8	
PIMUZ BP-197	l	14.2	8.5	16.7	
PIMUZ BP-294	r	13.2	7.8	16.0	
PIMUZ BP—	r	13.2	9.3	14.7	
Çandir					
MTA AÇH 592	l	14.0	8.1	17.9	
Manchones I					
IVAU MA 101	r	16.0	8.2	19.7	
IVAU MA 112	r	>14.4	8.9	>13.6	
IVAU MA 113	l	14.8	≥8.7	14.3	
Arroyo del Val IV					
IVAU AR IV 45	r	13.6	8.6	15.2	
IVAU AR IV 48	r	13.8	9.3	17.2	
IVAU AR IV 100	l	≥13.1	≥9.3	≥14.9	
IVAU AR IV 473	l	13.4	8.6	16.2	
RGM 263.122	r	—	—	—	
Steinheim					
SNMS 4777b	l	17.5	8.9	..	
SMNS 4777b	l	17.2	9.3	..	
La Grive oc					
IGF 299	l	14.9	8.7	18.9	11.6
IGF 299	l	15.8	8.5	19.1	
IGF 299	r	14.5	7.9	16.6	
MGL LGr 6004	r	15.7	9.3	..	
La Chaux-de-Fonds					
MHNCF 10	l	17.4	10.0	..	
MHNCF 10	r	>14.0	>9.7	..	
MHNCF 10x	l	14.0	9.1	..	
Castell de Barberà					
IPS 1962	l	17.2	8.1	..	
IPS —	l	14.4	8.6	..	
Sant Quirze					
IPS VP 1033	r	..	9.4	21.8	
IPS VP 1034	r	..	8.9	20.7	
MGSCB 48846	r	—	9.2	..	
MGSCB 48906	l	16.1	8.8	..	
Can Mata I					
IPS 1676	l	..	8.7	>19.6	
Hostalets					
ITGE 410 M	r	16.6	10.3	18.8	
MGSCB 48509	r	>14.8	8.7	—	
IPS 169	l	..	8.6	>17.8	
IPS 1073	r	..	+10.8	±18.1	
IPS VP 302	l	..	8.7	21.1	
CJFV —	l	..	9.6	21.2	
CJFV —	r	..	—	17.4	
CJFV —	l	16.0	10.3	19.7	

C_m		Li	La	Po	Ri	Ro
Nguruwe kijivium						
Napak (loc. ?)						
KNM-ZP 1383 cast	l	8.3	5.5	6.5		
Kirimon						
KNM-KI 18034	l	8.5	5.1	≤6.8	20	25-30
Lopholistriodon moruoroti						
Maboko						
KNM-MB 102	r	6.8	4.7	5.5		
Lopholistriodon akatidogus						
Fort Ternan						
KNM-FT 3653	l	12.0	12.4	9.3	(tip)	
Lopholistriodon kidogosana						
Ngorora						
KNM-BN 1466	r	13.1	7.1	9.6		
Ngorora D, 2/10						
KNM-BN 969	..	>7.5 (alveolus)				
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	l?	18.6	—	—		
MNHNP Z 1961	r	19.3	17.4	17.6		
MNHNP Z 1961	l	22.7	21.1	19.9		
MNHNP Z1961	r	15.2	13.6	12.9	(juv.)	
Bunolistriodon affinis						
Songhor						
KNM-SO 1061	l	12.3	8.9	11.2		
Bunolistriodon anchidens						
Rusinga R1						
KNM-RU 9784	l	14.5	8.2	13.3		
Bunolistriodon aff. latidens						
La Artesilla						
MPZ 6418	r	18.0	12.4	16.3		
Munébrega III						
IVAU 53/50	l	10.7	9.1	9.1		
IVAU 53/51	..	9.6	8.9	8.1		
IVAU 53/52	..	11.0	9.2	10.0		
Bunolistriodon M						
Paşalar						
PDTFAU BT1	l	13.9	14.1	9.7		
PDTFAU BT1	l	16.7	16.4	11.4		
PDTFAU BT1	l	16.7	16.8	12.0		
PDTFAU B457	r	16.9	16.5	11.8		
PDTFAU C152	r	16.3	16.1	11.3		
PDTFAU CT 5	r	17.7	17.5	12.0		
PDTFAU CT1	l	17.4	17.1	12.4		
PDTFAU CT1	l	17.5	17.0	12.2		
PDTFAU DT1	l	18.5	18.0	10.1		
PDTFAU DT1	l	18.6	14.3	11.9		
PDTFAU E	l	14.7	13.6	10.4		
PDTFAU G212	r	10.5	11.3	6.9		
PDTFAU G492	l	15.3	15.3	11.3		
PDTFAU G1813	r	16.7	16.9	12.5		
PDTFAU G1841	r	—	—	—		
PDTFAU —	l	15.4	14.2	11.3		
PDTFAU —	r	18.4	17.8	12.1		
PDTFAU —	l	16.4	14.8	11.1		
PDTFAU —	l	13.8	13.6	9.3		
PDTFAU —	r	16.6	15.2	10.5		
PDTFAU —	r	14.3	13.7	9.8		
PDTFAU —	l	17.9	15.1	12.2		
PIMUZ BP-83	l	15.8	18.6	11.9		
PIMUZ BP-84	l	16.9	16.6	11.8		
PIMUZ BP-85	r	16.7	16.5	9.9		
PIMUZ BP-87	r	17.4	16.7	11.6		
Çandir						
MTA UÇHÜ 322	l	17.8	16.1	10.0		
Bunolistriodon lockharti						
Pellecahus						
UCBL 320293	..	17.3	..	..		
NMB GB 2459	l	18.5	14.4	15.8		
La Romieu						
UCBL 320313	..	18.5	14.1	14.6		
UCBL 320294	r	17.0	14.6	14.5		
UCBL 320294	..	18.7	15.2	14.8		
NMB GB 1263	r	16.6	13.3	14.9		
Chevilly						
MNHNP cast	r	17.6	16.8	14.9	50	65
Buñol	—	r	17.6	15.1	14.3	
Langenau 1						
SMNS 40678	..	19.8	16.1	16.9		
Tavers						
COBO —	l	>19.2	—	—		
CIMO —	l	15.1	12.4	13.8	40	60
Bunolistriodon akatikubas						
Mbagathi						
KNM-MG 33	l	16.7	9.9	11.1		
Maboko						
KNM-MB 16713	r	13.6	13.5	9.2	(tip)	
KNM-MB 10364	r?	17.9	±13.5	±14.0		
Bunolistriodon intermedius						
Yehuli Juanzhi						
IVPP V 9519	r	15.0	13.0	11.2		
Bunolistriodon guptai						
HGSP 8418						
HGSP 8418/3387	r	14.2	11.2	11.8	40	45
Listriodon pentapotamiae						
Chinji 76						
GSP 9358	l	17.2	≥12	13.8		
Kanatti Chak 8						
BSPHGM 3275 - 84	l	—	—	—		
Listriodon splendens						
Sansan						
MGL Ss 162	l	20.6	14.0	15.1	50	65
Inönü I						
MTA AKI 3/252	r?	tip				
MTA AKI 3/424	r	tip				
Paşalar						
PDTFAU D920	r	20.2	13.0	17.4		
PDTFAU DT	r	16.5	13.3	11.5		
PDTFAU E309	r	20.0	15.2	16.5		
PDTFAU E309	l	19.1	14.3	15.5		
PDTFAU F1	l	20.4	15.0	15.4		
PDTFAU G1905	l	16.7	13.9	12.9		
PDTFAU —	r	15.5	11.8	12.9		
PDTFAU —	r	>19.7	16.0	16.2		

PIMUZ BP-86	r	19.1	12.7	12.2			
Villefranche d´Astarac							
MNHNP VAS 32	?	>21.1	14.6	17.1			
MNHNP VAS 33	..	—	—	—			
Paracuellos III							
MNCN PA 1621	r	15.9	12.4	12.5	50	65	
Manchones I							
IVAU MA I 111	1	18.3	16.0	14.6	50	70	
Arroyo del Val IV							
IVAU AR IV 51	1	20.6	16.3	15.2	55	75	
IVAU AR IV 53	r	20.7	16.0	16.7	50	70	
IVAU AR IV 55	r	18.1	14.3	11.9	50	60	(tip)
IVAU AR IV 56	r	15.3	12.9	12.9	55	60	(tip)
IVAU AR IV 62	r	19.7	15.0	13.1	50	40-50	(tip)
RGM 262.974	r	21.8	18.7	19.0	55	75	
RGM 263.060	1	—	—	—			
RGM 263.066	1	19.9	16.8	16.2	40	65	
RGM 263.072	r	21.1	15.7	17.9	65	75	
RGM 263.229	1	21.0	16.3	17.2			
MPZ AV-36	1	22.3	18.4	16.8			
Bonnefont							
MNHNP HGP 61	1	18.6	≥16.0	—			
MNHNP HGP 62	r?	—	—	—			
MNHNP HGP 63	1	19.7	16.0	15.7			
MNHNP HGP 65	r	24.7	19.1	17.6			
MNHNP HGP 67	?	—	—	—			
Steinheim							
SMNS 20221	r	21.4	16.6	18.2			
Mauer							
NMW 1886XVII219	r	≥22.6	24.6	22.1	—	105	
La Grive oc							
UCBL —	r	21.9	17.7	18.0			
UCBL —	r	26.5	20.6	21.0			
MGL LGr 720	r	23.6	21.0	16.9	95	120	
MGL LGr 723	r	23.2	18.5	17.6	80	105	
MGL LGr 724	1	24.4	18.6	18.8	65	90	
MGL LGr 725	1	25.5	17.9	20.9	90	100	
MGL LGr 726	r	21.6	15.9	16.9	65	75	
MGL LGr 727	r	>18.8	>17.1	13.5	70	85	
MGL LGr 1402	r	27.4	26.6	22.3	110	135	
La Chaux-de-Fonds							
MHNCF 56	r	24.5	17.6	18.6	80	50	
MHNCF 56a	r	24.6	17.7	18.9			
MHNCF 56b	1	>24.2	16.8	±18.7	—	120	
MHNCF 57	1	26.0	17.8	19.4	80	105	
MHNCF 59	1	>22	—	—			
MHNCF 59a	r	19.6	—	—			
MHNCF 60	r	23.8	17.6	19.2			
MHNCF — 5 fragments				—	—	—	
Prittlbach							
BSPHGM 1953 I 73	r	22.3	18.7	17.6	75	90	
Santiga							
IPS —	r	>22.6	>21.0	>21.8			
Cerro del Otero							
MNCN NM 18015	1	20.4	16.2	16.2	60	70	
MNCN NM 18016	1	22.8	14.6	17.2			
Sant Quirze							
IPS VP 1036	1	26.3	26.2	20.5			
IPS 1112	r	27.0	25.0	21.8			
MGSCB 48571	1	28.6	25.8	20.9	85	110	
MGSCB 48572	r	26.0	25.8	18.8	85	115	
MGSCB 48573	r	26.1	19.3	<27.6			
MGSCB 48574	1	27.0	26.1	19.7	90	115	
MGSCB 48575	r	26.3	24.2	19.9	75	105	
MGSCB 48576	r	25.1	23.9	21.2	90	115	
MGSCB 48577	?	tip					
Escanecrabe							
MNHNP HGP 21	r?	28.0	22.0	25.5	90	115	
MNHNP HGP 22	1	26.4	24.1	20.6			
MNHNP HGP 23	1	21.8	18.2	17.7			
Massenhausen							
BSPHGM 1951 I 21	1	25.8	19.6	20.7	—	100	
BSPHGM 1963 I 45	r	25.7	19.5	19.9	100	100	
Mas del Olmo							
ITGE 73 (408M)	r	24.5	18.5	16.9			
Castell de Barberà							
IPS —	..	23.3	20.6	18.6			
Hostalets							
MGSCB 48515	r	26.5	23.4	17.5			
MGSCB 48516 tip	r	—	11.9	—			
MGSCB 48557	r	26.1	23.0	16.6			
MGSCB 48558	1	24.1	22.2	17.2			
IPS 1026	..	tip					
IPS 1028	r	25.7	26.3	21.7			
IPS 1030	..	29.1	28.6	21.8			
IPS 1031	1	22.5	22.9	20.9			
IPS 1034	r	20.1	22.4	17.2			
IPS 1035	r	26.1	24.4	17.1			
IPS 1037	..	tip					
IPS VP 307	r	28.7	26.4	22.0			
IPS —	..	>27.1	23.2	18.7			
CJFV 4226	1	25.6	26.8	21.1			
CJFV 4329	1	—	—	—			
CJFV —	1	—	22.3	—			
CJFV —	1	25.6	—	—			
CJFV —	1	21.9	25.1	15.8			
CJFV —	1	20.7	17.3	16.5			
CJFV —	r	26.5	22.0	19.2			
Wissberg							
HLD 1933/896	1	27.3	25.0	21.5			
HLD 1933/897	1	23.2	18.0	18.8			

C_f		DAP	DT
Nguruwe kijivium			
Songhor			
KNM-SO 9913	1	±6.7	4.4
Bunolistriodon aff. latidens			
La Artesilla			
MPZ 6419	r	12.7	10.0
Munébrega I			
IVAU 55/1053	1	11.1	8.8
IVAU 55/1057	1	—	≥8.2
Bunolistriodon M			
Paşalar			
PDTFAU F351	1	12.9/12.0	8.2
PDTFAU F370	r	>12.3	7.5
PDTFAU G1746	r	12.8/11.4	7.1
Bunolistriodon lockharti			
Pellecahus			
UCBL 32028	1	10.3/11.7	10.2
Pontlevoy			
NMHNP FP 1028	1	14.6	12.7
Listriodon splendens			
Paşalar			
PDTFAU			
PDTFAU F174	r	14.7	8.3
PDTFAU F360	1	15.0/13.6	9.0
PIMUZ BP-95	r	14.1/..	8.4
PIMUZ BP-104cast	1?	11.2/..	9.1
Arroyo del Val IV			
IVAU AR IV 54	1	12.1	9.2
IVAU AR IV 127	1	—	—
IVAU AR IV 437	1	12.6	9.5
IVAU AR IV 438	r	14.0	9.8
IVAU AR IV 439	1	14.1	10.3
RGM 263.220	r	10.8	8.4
RGM 263.023	r	>13.8	≥10.8
MPZ AV-46 (2)	1	12.0	8.7
Arroyo del Val VI			
IVAU AR VI 44	r	13.4	9.8
IVAU AR VI 86	1	12.1	9.1
La Grive oc			
MGL LGr 733	1	13.1	8.4
MGL LGr 1534	r	tip	
MGL LGr 1542	r	tip	
MGL LGr 1543	1	tip	
La Cisterniga			
MNCN NM —	1	≥12.9	—
MNCN NM —	1	≥13.1	—
Sant Quirze			
MGSCB 48841	r	15.8	10.4
CJFV SQu 5443	1	—	11.6
Hostalets			
IPS 1046	1	>15.9	12.8
IPS 1047	..	16.0	10.6
CJFV 4230	1	17.7	10.4

P_1		DAP	DTa	DTp	Hli	Hla
Nguruwe kijivium						
Songhor						
KNM-SO 8451	r	7.2	3.6	3.6		
Kirimon						
KNM-KI 18039	1	6.6	3.4	3.4	4.8	4.6
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	r	16.8	8.1	7.4	11.8	12.2
Bunolistriodon lockharti						
Pellecahus						
NMB GB 1385	r	8.6	..	4.4	..	>6.9
Baigneaux						
NMB SO-6495	r	8.8	..	5.3		
MGL Or 3109	1	8.6	..	5.5	..	7.9

P_2		DAP	DTa	DTp	Hli	Hla
Nguruwe kijivium						
Kirimon						

KNM-KI 18064	1	—	3.9	—		
Lopholistriodon akatidogus						
Beni Mellal						
KNM-ZP 1398	r	8.8	5.6	6.0	7.4	7.8
Kubanochoerus marymunngui						
Baragoi BX						
KNM-BG 18012	1	33.4	>15.9	17.6		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	1	24.8	10.8	11.6		
MNHNP Z 1961	1	—	11.6	—		
MNHNP Z 1961	1	24.8	11.5	12.6		
MNHNP Z 1961	r	—	11.0	—		
MNHNP Z 1961	r	25.3	11.1	12.3		
Bunolistriodon anchidens						
Rusinga						
KNM-RU 4415	1	19.7	8.6	7.4	12.2	13.1
Bunolistriodon M						
Paşalar						
PDTFAU B	r	—	—	5.5	—	±6.1
PDTFAU C	1	14.3	6.5	6.7		
PDTFAU CT1	1	12.7	5.0	5.5		
PDTFAU ET1	r	14.6	6.9	7.7		
PDTFAU ET1	1	≥13.9	6.8	7.0		
PDTFAU G508b	1	—	5.3	—	6.6	7.1
PDTFAU G1924	1	—	6.5	—		
Bunolistriodon lockharti						
Pellecahus						
UCBL 320293	r	16.6	7.9	7.9		
Quinta la Barbacena						
CEPUNL 63	r	18.5	..	8.9		
Baigneaux						
NMB SO-6491	1	15.5	6.6	7.6	10.5	11.1
Pontlevoy						
MNHNP FP 1033	r	—	—	9.9		
Bunolistriodon akatikubas						
Maboko						
KNM-MB 14449	r	>15.8	≥8.3	8.8		
Bunolistriodon guptai						
HGSP 8321						
HGSP 8321/2075	1	—	—	9.0		
Listriodon splendens						
"Gers"						
MNHNP Ger 51	r	14.6	7.1	8.4		
Paşalar						
PDTFAU BT1	1	14.5	7.3	9.1		
PDTFAU BT1	1	14.5	7.5	8.9		
PDTFAU C464	1	14.4	7.9	>8.9		
PDTFAU C604	r	13.6	7.5	8.1		
PDTFAU CT1	r	13.2	7.0	7.9		
PDTFAU E118	1	14.9	7.9	8.9		
PDTFAU E742	1	12.7	7.4	8.3		
PDTFAU E853	r	14.6	7.7	8.2		
PDTFAU ET1	1	12.4	6.0	6.1		
PDTFAU ET1	r	13.5	7.3	8.4		
PDTFAU ET1	1	13.5	6.9	6.9		
PDTFAU ET1	r	—	—	—		
PDTFAU ET1	1	13.7	—	8.0		
PDTFAU ET1	1	14.3	7.7	8.4		
PDTFAU F386	r	12.6	7.0	8.5		
PDTFAU F387	r	13.1	7.2	9.0		
PDTFAU F2783	r	14.5	7.8	7.1		
PDTFAU G438h	1	—	—	6.7		
PDTFAU G1058.8	r	—	—	7.0		
PDTFAU G1100	1	13.8	7.8	8.4		
PDTFAU G1741.1	r	14.4	8.1	8.8		
PDTFAU G1748.3	1	12.7	7.5	8.2		
PDTFAU —	r	15.8	7.2	8.1		
PIMUZ BP-230	1	13.2	6.8	≥9.2		
Çandir						
MTA CA —	r	14.5	7.7	7.1		
Manchones I						
IVAU MA 109	r	15.4	7.1	7.7	10.0	10.5
Arroyo del Val IV						
IVAU AR IV 26	r	15.9	8.1	9.0		
IVAU AR IV 485	r	—	—	9.4		
Arroyo del Val VI						
IVAU AR VI 19	r	13.1	6.8	6.8		
Sant Quirze						
MGSCB 48895	1	13.8	7.4	8.4		
MGSCB 48898	r	13.7	7.8	8.3		
CJFV SQu 5449	r	14.3	7.5	9.3		
CJFV SQu 5453	r	14.6	7.3	8.7		
Escanecrabe						
MNHNP HGP 28	1	14.9	7.7	9.3		
Castell de Barberà						
IPS 1968	1	14.7	8.9	9.1		
IPS 1970	1	14.7	8.9	9.1		
Hostalets						
IPS —	1	13.5	7.4	8.0		

D_2		DAP	DTa	DTp	Hli	Hla
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	1	20.3	8.3	8.8	12.7	13.2
MNHNP Z 1961	r	21.7	9.5	10.4	14.6	14.9
MNHNP Z 1961	r	19.8	9.2	10.1	13.1	12.7
MNHNP Z 1961	r	18.7	8.7	8.4	10.8	11.3
Bunolistriodon aff. latidens						
Moratines						
MNCN —	1	10.0	..	4.9		
Listriodon splendens						
Paşalar						
PDTFAU DT1	r	—	5.5	—		
PDTFAU ET1	1	—	—	5.8		
PDTFAU F4?3	r	>10.6	4.7	4.9	6.1	7.2
PDTFAU G637	r	—	—	6.8		
PDTFAU G1570	r	11.7	5.7	6.6	7.7	8.0
Cerro del Otero						
MNCN NM 18022	1	13.6	5.1	6.8		

P_3		DAP	DTa	DTp	Hli	Hla
Nguruwe kijivium						
Songhor						
KNM-SO 9916	1	9.4	4.0	4.8	7.3	7.5
Kirimon						
KNM-KI 18048	r	10.4	4.6	4.9	6.9	7.2
Lopholistriodon kidogosana						
Ngorora B						
KNM-BN 1729	1	9.8	5.2	6.9		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	1	27.8	13.5	15.1	21.6	22.8
MNHNP Z 1961	1	28.3	13.6	13.6		
MNHNP Z 1961	r	27.0	12.2	13.1	20.3	20.4
MNHNP Z 1961	r	>26.5	14.1	14.9	±21.3	±21.5
MNHNP Z 1961	r	25.0	12.7	12.4	20.4	21.8
MNHNP Z 1961	r	—	13.4	—		
MNHNP Z 1961	1	—	14.0	—		
MNHNP Z 1961	1	—	12.2	—		
MNHNP Z 1961	r	26.5	12.4	13.9		
MNHNP Z 1961	r	..	..	17.1	..	23.2
Bunolistriodon anchidens						
Rusinga-Kamasengere						
KNM-RU 907	r	—	—	12.8		
Rusinga						
KNM-RU 949	1	—	—	13.5		
MNHNP 3903 cast	r	18.6	9.6	11.0		
Bunolistriodon aff. latidens						
Quinta Pedreiras						
CEPUNL 59	1	≥18.1	..	11.1		
La Artesilla						
MPZ 6437	r	16.4	9.0	9.5		
Echzell						
HLD Ez 6	1	17.0	9.8	11.9		
?T. Manzanares						
IPS 1069	r	15.7	..	9.4		
Bunolistriodon latidens						
Inönü I						
MTA AKI-3/575	1	14.7	7.0	7.9	10.4	10.6
Bunolistriodon M						
Paşalar						
PDTFAU BT1 592/1	1	16.6	7.3	—		
PDTFAU C464/1	r	15.7	7.1	8.2		
PDTFAU C508	1	15.9	7.6	8.6	12.1	12.2
PDTFAU CT1	1	15.0	7.1	8.5		
PDTFAU E253	1	16.4	7.6	8.1		
PDTFAU F286	r	17.0	7.9	9.4		
PDTFAU F785	r	17.0	7.6	9.3	11.5	11.7
Bunolistriodon lockharti						
Pellecahus						
UCBL 320269	r	17.7	13.8	13.2		
NMB GB 1384	r	—	8.8	10.3		
La Romieu						
UCBL 320268	1	16.5	9.0	10.2		
Baigneaux						
NMB SO-931	1	17.1	8.5	10.6		
NMB SO-1151	1	—	—	10.1		
Buñol—	1	—	8.7	—		
Gerlenhofen						
SMNS 14953c	1	17.9	..	11.0		
Pontlevoy						
NMB Fa 156	r	17.7	9.4	11.1		
Beaugency						
Bunolistriodon akatikubas						
Maboko						

KNM-MB 129	r	—	—	11.8
Bunolistriodon guptai				
HGSP 8321				
HGSP 8321/2075	1	—	—	9.0
Listriodon pentapotamiae				
Chinji 38				
GSP 2065	1	14.3	7.2	7.9
Kali Nachi				
IVAU CHN 37	r	—	7.8	—
Hessuwala				
BSPHGM 1956II60	1	14.0	8.3	9.7
Kundal Nali				
IVAU CHK 110	1	—	9.6	—
Chhonjawala				
BSPHGM 1956II106	1	15.5	9.1	11.0
HGSP 8425				
HGSP 8425/3530	r	17.4	9.5	11.9
Kalin Nal				
BSPHGM 3414-22	r	—	9.3	—
Pirawalaban 1				
BSPHGM 1956II107	1	15.7	8.8	10.8
Listriodon splendens				
Inönü I				
MTA AKI-3/357	r	18.3	10.8	12.4
MTA AKI-3/384	r	17.7	10.1	11.5
Paşalar				
PDTFAU CT1	r	16.6	9.0	11.1
PDTFAU CT1	1	15.6	9.2	9.8
PDTFAU D3	r	17.6	9.7	10.2
PDTFAU D591	1	15.7	8.8	10.9
PDTFAU D731	r	16.1	9.1	9.8
PDTFAU D1026	1	14.8	8.1	9.4
PDTFAU DT1	1	16.1	9.2	11.6
PDTFAU DT1	r	>16.6	9.2	≥11.3
PDTFAU E66	1	14.3	7.7	10.0
PDTFAU E66/1	r	18.1	9.6	10.6
PDTFAU E757	r	17.7	9.9	11.7
PDTFAU ET1	1	15.5	8.8	11.7
PDTFAU ET1	1	17.7	99	—
PDTFAU ET1	r	—	—	—
PDTFAU ET1	1	15.7	8.2	10.8
PDTFAU ET1	1	15.9	10.0	10.9
PDTFAU ET1	r	15.1	8.6	10.1
PDTFAU ET1	r	16.3	8.8	9.8
PDTFAU ET1	r	16.8	9.6	11.4
PDTFAU ET1	1	—	—	8.9
PDTFAU ET1	r	—	8.1	—
PDTFAU ET1	1	14.6	9.0	9.7
PDTFAU ET1	1	>16.0	—	10.8
PDTFAU F287	1	15.6	9.6	10.5
PDTFAU F389	r	15.5	8.8	9.7
PDTFAU G408	1	16.2	7.6	8.9
PDTFAU G666.6	r	15.1	≥7.5	10.1
PDTFAU G669.c	r	15.3	8.8	9.1
PDTFAU G722	r	14.4	8.5	9.4
PDTFAU G1248	1	15.3	8.8	10.1
PDTFAU G1666	r	16.5	9.5	12.1
PDTFAU G1748cd	1	15.6	8.3	10.7
PDTFAU —	r	—	—	9.9
PIMUZ BP-196	r	14.9	8.4	9.7
PIMUZ BP-215	r	16.4	9.0	10.3
PIMUZ BP-375	1	14.7	7.5	9.3
Villefranche d'Astarac				
MNHNP VAS 26	r	15.6	≥8.1	—
Manchones I				
IVAU MA 108	r	19.7	9.5	11.6
Arroyo del Val IV				
IVAU AR IV 15	1	17.3	10.8	11.8
IVAU AR IV 485	r	—	≥9.3	—
Torril				
CCL —	r	17.4	10.4	11.0
La Grive oc				
UCBL 65621	r	15.3	..	10.8
Cerro del Otero				
MNCN NM 18034	r	15.3	8.4	9.8
Sant Quirze				
MGSCB 48887	r	18.0	11.1	13.1
MGSCB 48888	r	16.7	9.9	12.0
MGSCB 48896	1	16.4	9.2	10.7
MGSCB 48897	r	15.8	9.3	10.5
CJFV SQu 5454	r	16.9	9.6	11.5
CJFV SQu 5456	1	17.1	9.8	12.0
Escanecrabe				
MNHNP HGP 29	r	17.4	9.8	11.6
Castell de Barberà				
IPS 1967	1	14.6	10.8	11.8
IPS 1969	r	15.1	10.5	12.0
Hostalets				
IPS VP 320	1	16.1	..	10.6
IPS VP 321	1	15.7	..	10.9
CJFV4235 = HP196	1	17.7	10.6	10.8

D_3		DAP	DTa	DTp		
Nguruwe kijivium						
Mfwanganu						
KNM-MW 391	1	—	—	4.6		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	1	23.0	10.4	10.8		
Bunolistriodon aff. *latidens*						
La Artesilla						
MPZ 6433	1	13.3	6.1	6.9		
Munébrega I						
IVAU 55/1087	r	13.5	4.2	6.2		
Bunolistriodon M						
Paşalar						
PDTFAU BT 1	1	—	—	6.7		
PDTFAU DIT	r	12.4	5.3	6.1		
PDTFAU G1770.6	1	11.4	4.6	5.9		
Bunolistriodon guptai						
HGSP 8418						
HGSP 8418/3372	1	—	—	6.7		
Listriodon pentapotamiae						
Jandawala						
BSPHGM 163	1	12.3	5.6	6.6		
Listriodon splendens						
Paşalar						
PDTFAU D937	r	—	5.6	—		
PDTFAU DT1	1	—	—	7.2		
PDTFAU DT1	r	—	6.7	7.9		
PDTFAU DT	r	—	6.0	6.6	>7.9	
PDTFAU ET1	1	13.3	6.3	7.2		
PDTFAU ET1	1	13.0	6.0	6.7		
PDTFAU ET1	1	—	5.9	6.5	7.7	
PDTFAU ET1	r	—	5.1	—		
PDTFAU F9.9	1	12.9	5.9	6.8	>6.9	
PDTFAU F450	r	—	6.4	7.6		
PDTFAU G51	r	—	6.1	—		
Murrero						
IVAU MR 29	1	12.7	6.0	6.0	8.3	6.9
La Grive oc						
MGL —	1	12.8	5.7	6.4		
Cerro del Otero						
MNCN NM 18012	1	14.2	7.1	7.5	9.1	9.2
MNCN NM 18033	1	14.6	8.3	8.2		
Castell de Barberà						
IPS —	1	—	—	6.4		
IPS —	r	12.0	..	6.7		
Hostalets						
CJFV IPS 1982	r	14.0	..	8.1		
CJFV IPS 1975	..	13.0	..	7.5		

P_4		DAP	DTa	DTp
Nguruwe kijivium				
Rusinga R106				
KNM-RU 5854	r	10.9	6.9	7.4
Songhor				
KNM-SO 4979	1	10.0	6.2	6.6
KNM-ZP 1369 (cast M32661)	r	10.7	6.6	6.8
HGSP 8412				
HGSP 8412/3152	r	—	6.2	..
Lopholistriodon moruoroti				
Maboko				
KNM-MB 14487	r	—	4.8	—
Kubanochoerus marymunngui				
Buluk				
KNM-WS 12587	r	27.3	20.9	22.8
KNM-WS 12594	r	>28.0	>20.5	>21.5
Kubanochoerus khinzikebirus				
Maboko				
KNM-MB 14427	r	—	—	>25.1
Kubanochoerus massai				
Gebel Zelten				
MNHNP Z 1961	r	26.1	14.2	15.7
MNHNP Z 1961	r	±26.9	—	—
MNHNP Z 1961	r	27.1	16.0	≥16.7
MNHNP Z 1961	r	25.3	14.9	16.4
MNHNP Z 1961	r	≥26.5	15.9	—
MNHNP Z 1961	1	25.5	15.1	16.2
MNHNP Z 1961	1	25.1	14.9	16.2
MNHNP Z 1961	1	25.4	15.6	17.9
MNHNP Z 1961	r	25.3	≤16.8	—
MNHNP Z 1961	1	27.1	16.1	16.6
MNHNP Z 1961	r	—	—	±15.3

MNHNP Z 1961	r	—	—	16.1
MNHNP Z 1961	r	25.4	≥14.4	≥16.4
Bunolistriodon anchidens				
Rusinga R113				
KNM-RU 15163	r	±16.6	12.7	13.5
Bunolistriodon aff. latidens				
Olival da Suzana				
CEPUNL 23	r	18.4	..	12.9
Quinta da Conceição				
CEPUNL 54	1	19.3	..	12.5
Quinta da Fariheira				
CEPUNL 14	1	16.0	..	11.7
La Artesilla				
MPZ 6439	r	17.1	11.7	12.3
Armantes I				
IVAU 41/516	1	17.2	12.6	12.8
IVAU 41/517	r	16.8	12.4	12.4
Bunolistriodon M				
Paşalar				
PDTFAU B592/2	r	17.8	9.4	10.0
PDTFAU BT1	1	17.7	8.9	10.2
PDTFAU C438.c	r	17.4	9.5	11.1
PDTFAU C469.3	r	17.2	9.7	10.9
PDTFAU CT 5	1	18.1	9.9	11.5
PDTFAU CT1	r	17.1	9.7	10.7
PDTFAU CT1	r	15.3	9.7	10.0
PDTFAU CT1	r	>17.0	10.3	11.0
PDTFAU CT1	1	16.2	10.4	10.8
PDTFAU CT1	1	18.6	11.5	12.6
PDTFAU D639	r	17.0	11.4	11.9
PDTFAU ET1	r	15.9	10.5	10.9
PDTFAU ET1	r	18.8	10.0	11.2
PDTFAU ET1	1	—	—	—
PDTFAU ET1	r	—	—	—
PDTFAU F390	r	14.8	9.1	10.0
PDTFAU G371	1	..	..	..
PDTFAU G1748.9	1	16.9	10.4	11.2
PDTFAU G1924.5	1	15.7	9.3	10.2
PDTFAU G1970	r	16.0	9.6	10.4
Bunolistriodon lockharti				
Pellecahus				
NMB GB 2453	1	—	≥13.0	—
NMB GB 2459	1	17.4	13.5	13.0
La Romieu				
UCBL 320273	1	15.9	10.6	10.6
UCBL 320275	r	18.6	12.0	13.3
Buñol				
MPV PAN-148	r	>16.8	12.6	14.2
Baigneaux				
NMB —	r	19.0	12.6	13.4
FMNH cast	1	18.8	12.0	13.1
Engelswies				
NMB TD 679	r	18.3	>11.9	>12.4
Pontlevoy				
MNHNP FP 226	r	17.9	11.9	10.6
NMHNP FP 1035	r	19.8	12.8	12.7
Beaugency				
MNHNP 3903 cast	1	18.9	12.6	13.3
Tavers				
COBO —	r	20.5	12.6	14.1
Bunolistriodon akatikubas				
Maboko				
KNM-MB 14424	r	17.9	12.7	12.8
KNM-MB 872	1	18.9	12.4	14.2
Bunolistriodon intermedius				
Maerzuizigou				
IVPP V 9525	1	17.0	10.2	12.3
Bunolistriodon guptai				
HGSP 8412				
HGSP 8412/3123	1	17.5	10.9	11.6
Listriodon pentapotamiae				
Chinji 38				
GSP 751	r	—	—	>15.3
Chinji 76				
GSP 5340	r	—	10.1	—
GSP 9662	r	—	—	>9.2
GSP 14163	1	13.6	10.5	10.4
Dhok Talian 189				
GSP 4422	1	17.8	12.5	12.6
GSP 4528	r	16.6	11.3	12.1
Kanatti				
IVAU KA 83	1	17.2	11.5	12.5
IVAU KA 86	r	14.6	10.4	10.7
IVAU KA 87	1	—	≥9.9	—
Burri Wala				
IVAU CHB 21	1	15.5	9.7	10.2
Tekunja				
IVAU CHT 66	r	—	10.3	—
Cheski Wala				
IVAU CHC 87	r	≥16.8	≤14.3	≤14.2
Achora				
FISF CHA F6132	1	16.9	12.1	14.1
Kanatti Chak 8				
BSPHGM 1956II105	1	16.4	11.7	11.7
BSPHGM 3275-84	1	15.7	10.8	12.0
BSPHGM 3275-84	r	16.6	10.9	12.3
Kundal Nali				
IVAU CHK 104	1	—	12.3	—
HGSP 8415				
HGSP 8415/3584	r	17.0	—	—
Bhurriwala				
BSPHGM 1956II59	1	16.9	11.5	12.3
Jandawala				
BSPHGM 1956II57	..	16.1	12.2	12.4
Chinji Fm. bought specimens				
IVAU CH-25	1	18.1	13.8	>14.6
IVAU CH-27	1	—	11.0	—
IVAU CH-29	r	14.9	10.1	10.7
IVAU CH-32	r	—	—	—
IVAU CH-42	1	14.9	>11.5	10.8
Listriodon splendens				
Simorre				
NMB DG 55	1	14.5	10.9	10.8
"Gers"				
MNHNP Ger 1	1	18.5	11.5	12.8
Paşalar				
PDTFAU A54	r	17.6	12.5	12.4
PDTFAU A169	1	17.8	12.4	14.0
PDTFAU BT1	r	17.6	12.2	11.9
PDTFAU B	r	17.1	12.2	12.8
PDTFAU CT1	r	16.7	11.5	11.3
PDTFAU CT1	1	17.4	12.1	13.5
PDTFAU CT1	r	>15.2	11.0	11.2
PDTFAU CT1	r	—	—	13.0
PDTFAU CT1	1	16.9	12.0	13.1
PDTFAU CT1	r	17.2	12.3	13.2
PDTFAU D123	1	17.9	12.2	13.8
PDTFAU D656	r	18.4	12.2	12.6
PDTFAU D889	r	>17.9	>12.5	>11.8
PDTFAU E305	1	—	—	12.7
PDTFAU E467	1	17.5	12.4	13.1
PDTFAU E588	r	17.4	11.0	11.8
PDTFAU E852	1	17.8	10.9	12.7
PDTFAU ET1	r	—	—	—
PDTFAU ET1	r	18.2	12.3	11.9
PDTFAU ET1	r	17.1	12.0	11.3
PDTFAU ET1	r	17.6	11.7	12.8
PDTFAU ET1	1	18.4	12.7	12.2
PDTFAU ET1	1	17.7	11.9	12.2
PDTFAU ET1	r	—	—	12.9
PDTFAU F278.6	1	16.9	11.8	12.3
PDTFAU F278.7	r	17.8	12.2	11.6
PDTFAU F281	1	16.9	12.3	14.0
PDTFAU F486	r	18.5	13.2	12.4
PDTFAU F509	r	16.9	11.5	12.8
PDTFAU F2784	r	17.3	11.0	12.2
PDTFAU G172	r	17.9	13.3	12.7
PDTFAU G408.c	r	18.0	12.9	13.0
PDTFAU G692.1	1	17.3	—	—
PDTFAU G870	r	17.0	12.1	12.3
PDTFAU G1598	1	18.6	12.5	13.8
PDTFAU G1599.1	1	17.3	12.2	11.6
PDTFAU G1646	1	16.4	10.5	11.9
PDTFAU G2032.1	1	17.4	12.0	12.9
PDTFAU —	1	18.2	12.3	12.8
PDTFAU —	r	18.5	12.8	12.9
PDTFAU —	1	—	12.0	—
PIMUZ BP-312	r	17.5	11.9	13.5
PIMUZ BP-—	r	17.7	12.4	12.4
Çandir				
MTA CA —	r	17.4	12.3	12.6
Villefranche d'Astarac				
MNHNP VAS 19	1	17.8	11.8	12.8
MNHNP VAS 20	r	>16.4	12.0	13.2
Krivádia railway station				
HGSB Ob-19	1	18.8	13.7	14.5
St. Margarethen				
NMW SK 3607	r	17.6	12.9	12.9
Paracuellos V				
MNCN PA V 553	r	18.2	—	—
Manchones I				
IVAU MA 107	r	20.3	13.7	13.6
IPS MA 260	1	17.7	11.5	12.9
IPS MA 263	1	20.3	11.5	13.1

Arroyo del Val IV						
IVAU AR IV 19	r	19.6	13.1	12.5	9.1	10.0
IVAU AR IV 20	l	19.4	12.6	12.6		
IVAU AR IV 392	l	—	—	>12.8		
IVAU AR IV 485	r	—	—	14.0		
IVAU AR IV 485	l	—	—	—		
IPS 1262	r	18.4	..	12.4		
MNCN —	r	16.7	..	11.5		
Arroyo del Val VI						
IVAU AR VI 18	r	17.9	12.1	13.6		
La Grive oc						
UCBL 65619	l	16.9	..	12.0		
Castelnau Magnoac						
MSNO —	r	17.3	11.3	12.3		
Can Cunillé						
IPS 1056	l	18.4	11.8	14.0		
Arroyo del Val I						
IVAU AR I —	l	—	—	±16		
Cerro del Otero						
MNCN NM 18017	r	19.3	13.1	12.6		
MNCN NM 18018	r	19.1	12.7	13.8		
Sant Quirze						
IPS ..	r	17.7	..	15.0		
MGSCB 48882	r	—	≥15.4	14.9		
MGSCB 48884	r	18.5	14.6	15.2		
MGSCB 48885	r	17.8	13.6	13.8		
MGSCB 48886	l	17.8	≥14.4	15.1		
CJFV SQu 545	r	19.2	14.1	14.7		
CJFV SQu 5448	l	19.2	13.9	14.6		
Castell de Barberà						
IPS 1964	l	17.5	14.0	13.3		
IPS 1968	r	17.3	13.7	13.5		
IPS —	l	≥15.7	12.0	11.1		
Hostalets						
IPS 1104	r	18.8	12.8	13.8		
CJFV —	l	..	..	..		

D_4		DAP	DTa	DTm	DTp
Nguruwe kijivium					
Napak (loc. ?)					
KNM-ZP 1383bcast	l	13.5	5.0	6.2	7.2
Songhor					
KNM-SO 951	l	—	—	—	6.8
KNM-SO 1129	l	—	—	—	7.6
KNM-SO 1129	r	—	—	6.6	—
Mfwangamu					
KNM-MW 175	r	≥15.8	5.6	7.3	7.8
Lopholistriodon moruoroti					
Maboko					
KNM-MB 10291	r	—	—	—	4.9
Lopholistriodon kidogosana					
Ngorora					
KNM-BN 1725	l	—	—	—	5.5
Bunolistriodon aff. *latidens*					
La Artesilla					
MPZ 6432	r	22.6	7.6	9.3	10.0
MPZ 6434	l	—	—	—	11.0
Bunolistriodon M					
Paşalar					
PDTFAU C187.2	l	—	—	—	9.3
PDTFAU C187.3	l	—	—	9.0	—
PDTFAU C280.29	r	21.9	8.6	9.2	10.8
PDTFAU C280.30	r	—	8.8	—	—
PDTFAU CT 5	r	—	—	—	10.6
PDTFAU CT1	r	—	—	—	10.4
PDTFAU D1186.b	l	—	—	—	9.8
PDTFAU E89.23	l	—	—	—	—
PDTFAU ET1	r	—	8.6	—	—
PDTFAU G1334	r	—	8.5	9.8	—
Bunolistriodon lockharti					
Pellecahus					
UCBL 320293	l	24.8	9.0	10.6	11.6
La Romieu					
UCBL 320268	r	21.7	8.5	9.6	11.0
Baigneaux					
NMB SO-3229	l	22.0	8.3	9.9	10.8
Buñol					
—	l	—	—	—	11.6
Reisensburg					
NMB TD 844 cast	l	>20.6	8.6	10.9	12.0
Listriodon pentapotamiae					
Cheski Wala					
IVAU CHC 37	l	—	—	—	11.8
Listriodon splendens					
Paşalar					
PDTFAU B592.4	l	—	—	—	10.6
PDTFAU C187.4	l	22.5	9.3	10.3	11.2
PDTFAU C187.5	r	21.8	8.9	10.1	10.8
PDTFAU C187.6	r	—	—	—	11.6
PDTFAU C187.6	l	—	—	9.5	10.4
PDTFAU C187.7	r	—	8.5	—	—
PDTFAU D210.13	l	—	—	—	11.7
PDTFAU D210.16	r	—	—	11.0	11.6
PDTFAU D210.17	l	—	—	—	10.4
PDTFAU D210.18	l	—	—	—	12.0
PDTFAU D210.20	r	—	—	9.3	—
PDTFAU E143	l	—	—	—	12.0
PDTFAU E838	r	—	—	9.4	11.0
PDTFAU E838.1	r	—	—	—	10.8
PDTFAU E838.2	r	—	—	—	11.2
PDTFAU F40	l	—	—	10.3	11.5
PDTFAU F401	l	—	—	—	10.9
PDTFAU G190	r	—	—	9.6	10.7
Çandir					
MTA AÇH 574	r	23.2	8.7	10.1	11.4
La Grive oc					
NMB GA 2826	..	—	—	—	10.8
NMB GA 3767	r	—	—	10.4	—
Arroyo del Val IV					
IVAU AR IV 395	l	—	8.4	>9.4	—
RGM 263.220	r	23.3	—	11.1	12.2
La Grive oc					
MGL LGr 750	r	23.3	9.1	10.3	11.1
Sant Quirze					
MGSCB 48837	r	—	—	—	12.3
Castell de Barberà					
IPS —	r	21.1	8.4	9.6	10.4
IPS —	l	—	8.8	—	—
Hostalets					
CJFV IPS 1053	l	22.9	8.7	10.4	11.3
Can Ponsic					
IPS 1973	r	—	—	12.0	>12.5
Listriodontinae indet.					
Fort Ternan					
KNM-FT 3323	l	17.1	—	—	9.6

M_1		DAP	DTa	DTp	Ha	Hp
Nguruwe kijivium						
Rusinga R1-3						
KNM-RU 3040	l	12.4	9.4	8.9		
Songhor						
KNM-SO 1127	l	12.6	9.3	9.9		
KNM-SO 1128	l	12.0	8.5	8.4		
KNM-SO 1139	r	10.4	>7.8	7.9		
KNM-SO 1651	l	12.6	9.3	9.4		
Lopholistriodon kidogosana						
Ngorora B5, 2/56						
KNM-BN 1724	l	—	—	7.8		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	r	28.5	20.2	21.6		
MNHNP Z 1961	l	26.3	18.3	19.6		
MNHNP Z 1961	l	28.4	19.2	20.2	>16.1	>14.9
MNHNP Z 1961	l	—	—	≥21.1		
MNHNP Z 1961	r	28.9	19.5	20.9		
MNHNP Z 1961	l	—	—	22.6		
Bunolistriodon anchidens						
Rusinga-Gumba						
KNM-RU 15076	l	17.1	12.9	12.5		
Bunolistriodon aff. *latidens*						
Quinta da Farinheira						
CEPUNL 12	r	16.8	≥13.2	13.4		
La Artesilla						
MPZ 6441	l	17.7	12.0	12.0		
MPZ 6440	r	17.9	11.6	12.4		
Tarazona						
UPV T56.23	r	—	11.6	—		
Armantes I						
IVAU 41/512	r	>15.0	—	13.7		
IVAU 41/543	l	18.6	12.7	13.1	≥10.1	>8.6
Munébrega I						
IVAU 55/1066	r	—	12.4	—		
IVAU 55/1067	r	±18.2	11.2	10.9		
Valdemoros IA						
IVAU VaIA500-501	..	±21.1	14.6	14.7		
Bunolistriodon M						
Paşalar						
PDTFAU C8.1	r	17.0	12.1	11.7		
PDTFAU C8.2	l	—	—	12.9		
PDTFAU C280.10	l	18.1	12.0	11.9		
PDTFAU C280.11	r	16.8	11.1	10.9		
PDTFAU D210.8	l	—	—	12.6		
PDTFAU D301	r	19.4	13.0	12.3		
PDTFAU E7.5	l	—	—	13.2		
PDTFAU E7.6	l	—	12.8	—		
PDTFAU E7.7	l	—	12.8	—		

PDTFAU E89.11	r	17.5	11.4	11.7		
PDTFAU E297	r	—	—	—		
PDTFAU F9.2	r	—	—	12.3		
PDTFAU F377	r	18.5	13.0	13.0		
PDTFAU F382	r	—	11.1	—		
PDTFAU G240	l	—	>13.1	>12.1		
PDTFAU G408.6	r	18.5	13.0	12.9		
PDTFAU G915	l	17.6	11.7	11.6		
PDTFAU G1232	l	20.0	13.4	>12.4		
PDTFAU G1557	l	17.9	11.9	12.4		
PDTFAU G1645	r	17.1	12.6	12.1		
PDTFAU G1868	l	18.3	11.6	12.2		
PDTFAU G2023	l	>15.3	11.4	11.4		
Bunolistriodon lockharti						
Pellecahus						
NMB GB 2454	r	—	14.2	—		
La• Romieu						
UCBL 320288	l	20.0	12.7	13.3		
Baigneaux						
NMB SO-929	l	20.0	13.6	13.6		
NMB SO-1694	r	21.9	17.1	—		
NMB SO-6737	r	18.3	14.4	14.8		
Avaray						
MSNO —	r	19.1	13.9	14.6		
Buñol						
—	l	—	—	>14.1		
FMNH cast	r	19.5	13.2	13.8		
Bunolistriodon akatikubas						
Majiwa						
KNM-MJ 9776	r	19.4	13.0	13.7		
Bunolistriodon guptai						
HGSP 8222						
HGSP 8222/1218	r	19.1	15.2	15.4		
HGSP 8412						
HGSP 8412/3135	r	19.7	≥15.3	15.3		
Listriodon pentapotamiae						
Dhok Talian 189						
GSP 4419	l	—	—	14.8		
Tekunja						
IVAU CHT 14	r	—	—	14.4		
HGSP 8427						
HGSP 8427/3646	l	18.6	13.4	13.2		
Chinji Fm. bought spec.						
IVAU CH-28	l	16.3	≥11.7	12.0		
IVAU CH-35	..	—	—	11.8		
Listriodon splendens						
"Gers"						
MNHNP Ger 44	l	18.7	16.3	15.7		
Paşalar						
PDTFAU B593	r	—	13.3	—		
PDTFAU B593/1	l	19.3	13.7	13.7		
PDTFAU C280.5	r	—	—	14.6		
PDTFAU CT1 93	l	18.9	13.5	13.5		
PDTFAU CT1	l	18.0	12.9	13.3		
PDTFAU CT1	r	—	12.9	—		
PDTFAU CT1	r	—	13.1	—		
PDTFAU CT1	l	—	13.7	—		
PDTFAU CT5	r	>16.3	≥13.3	13.5		
PDTFAU D5	l	16.9	12.0	12.6		
PDTFAU D9.43	l	≤18.3	13.6	14.0		
PDTFAU D210.11	l	—	—	13.2		
PDTFAU DT1	r	19.1	13.9	13.8		
PDTFAU E89.2	l	18.9	13.2	14.1		
PDTFAU E118	r	19.3	13.9	13.8		
PDTFAU E251	l	19.2	14.5	15.6		
PDTFAU E532	r	19.1	12.6	13.5		
PDTFAU ET1	r	17.7	13.2	13.2		
PDTFAU ET1	l	—	13.2	—		
PDTFAU ET1	r	—	14.8	—		
PDTFAU ET1	r	—	13.1	—		
PDTFAU ET1	r	—	11.8	—		
PDTFAU ET	r	17.6	13.0	13.4		
PDTFAU F278.8	r	19.7	14.6	15.4		
PDTFAU F278.9	l	18.0	13.6	13.6		
PDTFAU F278.13	r	—	12.4	—		
PDTFAU F384	l	—	—	13.7		
PDTFAU G458	l	—	—	13.4		
DTFAU G704	r	18.5	12.9	12.3		
PDTFAU G1548	r	16.5	12.5	12.9		
PDTFAU G1598.1	r	20.1	—	14.8		
PDTFAU -583	r	17.0	12.2	11.9		
PIMUZ BP-307	l	17.9	12.8	13.1		
Çandir						
MTA CA —	r	18.3	13.2	14.0		
MTA AÇH 910	l	16.2	≥13.2	13.4		
Villefranche d'Astarac						
MNHNP VAS 21	l	17.0	—	12.9		
MNHNP VAS 23	l	17.0	13.4	13.3		
Arroyo del Val IV						
IVAU AR IV 42	r	20.0	13.9	13.6	12.1	10.7
IVAU AR IV 43	r	19.5	14.5	14.0		
RGM 263.103	r	—	—	13.5		
MPZ AV-42	l	19.6	14.4	13.5		
Murrero						
IVAU MR 28	r	—	≥15.7	—		
Arroyo del Val I						
IVAU AR I —	.	—	—	18.0		
Bonnefont						
MNHNP HGP 69	r	18.2	13.3	13.7		
MNHNP HGP 70	r	17.6	12.6	12.4		
La Grive oc						
NMB GA 4706	..	—	12.8	—		
MGL LGr 715	l	15.9	12.5	12.4		
Sant Quirze						
MGSCB 48910	..	—	—	14.0		
MGSCB 48911	..	—	—	>13.9		
CJFV SQu 5451	l	>16.5	14.2	14.3		
Castell de Barberà						
IPS —	l	17.4	13.3	12.4		
Hostalets						
IPS 1075	r	20.4	—	—		
IPS H 213	r	18.2	—	14.3		
CJFV4223 = HP194	r	19.7	15.4	14.0		
M_2		**DAP**	**DTa**	**DTp**		
Nguruwe kijivium						
Mteitei						
KNM-MV 19	r	13.8	10.8	10.5		
Koru 25						
KNM-KO 51	..	—	—	>9.8		
Napak (loc. ?)						
KNM-ZP1383a cast	r	13.5	9.5	9.6		
Rusinga R106						
KNM-RU 2776	l	12.4	9.9	10.0		
Mfwanganu						
KNM-MW 169	r	13.6	9.3	9.8		
KNM-MW 173	l	13.8	10.8	11.0		
KNM-MW 174	l	14.8	11.9	11.2		
KNM-MW 390	l	14.8	11.4	11.9		
Lopholistriodon moruoroti						
Maboko						
KNM-MB 145	r	—	—	6.5		
KNM-MB 881	r	—	—	6.4		
KNM-MB 10288	r	—	7.7	7.3	6.8	—
KNM-MB 10331	r	10.6	6.9	7.4		
KNM-MB 14488	l	—	—	6.0		
Lopholistriodon pickfordi						
Maboko						
KNM-MB 10289	r	—	8.0	—		
KNM-MB 10333+144	r	12.5	8.6	8.6	8.1	..
KNM-MB 14479	r	12.1	8.1	9.0		
KNM-MB 14480	l	11.9	8.2	8.7		
KNM-MB 15118	l	—	—	8.8		
Lopholistriodon akatidogus						
Maboko						
KNM-MB 10370	r	19.2	13.0	12.9	9.9	9.9
Lopholistriodon kidogosana						
Ngorora B5, 2/56						
KNM-BN 2084	r	14.3	9.6	9.6	>7.0	
Ngorora B						
KNM-BN 1711	l	—	10.0	—		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	l	—	—	22.6		
MNHNP Z 1961	l	31.4	22.5	22.8		
MNHNP Z 1961	..	≥30.7	—	—		
MNHNP Z 1961	r	30.1	23.5	≥22.8		
MNHNP Z 1961	l	33.0	25.0	25.6	±21.7	18.0
MNHNP Z 1961	l	30.9	23.6	23.2		
MNHNP Z 1961	l	32.7	24.3	24.5		
MNHNP Z 1961	l	33.6	24.4	25.0		
Bunolistriodon aff. latidens						
Quinta da Farinheira						
ML 5545	r	22.0	15.6	14.6		
CEPUNL 9	r	22.1	18.1	18.6		
CEPUNL 10	l	22.1	18.8	17.7		
CEPUNL 13	r	17.5	14.3	15.0		
Casal das Chitas						
ML 5542	l	23.1	18.7	16.5		
Olival da Suzana						
CEPUNL 22	r	21.5	17.1	15.3		
Echzell						
HLD Ez 323	r	20.9	15.9	16.4		
Bunolistriodon aff. latidens						
Armantes I						

IVAU 41/514	1	21.5	18.1	≥18.2			
IVAU 41/575	..	—	≥16.4				
Munébrega III							
IVAU 53/57	1	22.5	±16.5	—			
Bunolistriodon M							
Paşalar							
PIMUZ BP-145	r	22.1	15.6	16.4			
PIMUZ BP-272 cast		1	21.8	15.5	15.9		
PDTFAU A134	1	—	—	>16.5			
PDTFAU A169	1	—	—	>14.2			
PDTFAU C8.3	r	—	—	14.6			
PDTFAU C8.4	r	—	—	15.9			
PDTFAU C8.5	1	—	—	15.8			
PDTFAU C280.16	1	—	—	16.7			
PDTFAU D870	1	≥19.8	14.7	14.4			
PDTFAU E7.8	r	20.6	14.6	14.2			
PDTFAU F9	1	22.1	15.9	15.7			
PDTFAU F9.3	1	≥22.2	—	15.9			
PDTFAU F145	r	—	16.1	—			
PDTFAU F410	r	22.2	15.6	16.2			
PDTFAU G270	1	23.8	17.3	17.4			
PDTFAU G1248	r	21.9	16.3	16.3			
PDTFAU G1574	1	20.5	14.5	14.4			
PDTFAU G1660	r	—		—	14.9		
PDTFAU G1665.2	1	≥21.5	—	15.3			
PDTFAU G1748.1	1	—	—	16.3			
PDTFAU G1840	1	22.7	15.2	15.0			
Bunolistriodon lockharti							
Chevilly							
MSNO —	r	22.2	18.0	18.8			
La Romieu							
UCBL 320268	1	21.8	16.6	16.9			
UCBL 320288	1	23.0	18.5	18.7			
Baigneaux							
NMB SO-2190	1	22.9	17.3	17.3			
Buñol							
L 307	r	25.2	18.2	18.6			
MPV FBS4	r	24.5	19.0	19.3			
MPV FBB 215	1	25.2	17.2	17.4			
Gerlenhofen							
SMNS 14953h	1	23.1	..	18.0			
FMNH cast	1	22.2	17.8	18.5			
Langenau 1							
SMNS 41229	r	..	..	..			
Monteagudo							
IPS 1146	r	±24.1	18.9	±19.0			
Beagency							
MNHNP 3903 cast	r	24.8	17.6	18.7			
Ravensburg							
NMB TD 551	r	23.8	17.0	18.5			
NMB TD 552	r	23.4	16.6	17.8			
Bunolistriodon akatikubas							
Mbagathi							
KNM-MG 40	1	>18.1	—	>13.4			
Majiwa							
KNM-MJ 9781	1	23.1	17.0	16.5			
Bunolistriodon intermedius							
Maerzuizigou							
IVPP V 9522.6	r	22.6	17.5	18.3			
Bunolistriodon guptai							
HGSP 8222							
HGSP 8222/1217	r	21.5	16.5	17.2			
HGSP 8424							
HGSP 8424/3606	r	21.7	16.4	16.5			
Listriodon pentapotamiae							
Dhok Talian 189							
GSP 4423	r	23.2	17.0	16.4			
Achora							
IVAU CHA-68	r	±19.2	—	—			
Cheskewala							
BSPHGM 1956II56	1	19.6	15.9	15.9			
Bhurriwala							
BSPHGM 1956II58	1	19.4	15.4	≥15.3			
Kanatti Chak 5							
BSPHGM 3028	1	—	—	12.6			
Bhilomar							
IVAU CHH 28	r	—	—	16.5			
IVAU CHH 30	1	—	14.6	—			
IVAU CHH	1	—	—	14.8			
IVAU CHH 32	r	—	—	≥14.5			
Chinji Fm. bought spec.							
IVAU CH-22	1	>19.0	14.9	≥14.9			
IVAU CH-23	1	—	—	15.3			
HGSP 8124							
HGSP 8124/3727	r	23.0	17.6	18.3			
Listriodon splendens							
"Gers"							
MNHNP Ger 42	r	21.5	16.9	17.3			
MNHNP Ger 49	1	21.3	17.0	17.2			
Inönü I							
MTA AKI 3/514	1	24.2	19.1	18.7			
Paşalar							
PDTFAU B593	r	21.7	17.1	16.7			
PDTFAU BT1	r	23.0	17.1	—			
PDTFAU C150	r	—	—	18.4			
PDTFAU C336	r	24.2	18.5	18.4	15.7	13.7	
PDTFAU CP1	r	21.5	17.9	18.1			
PDTFAU CT1	1	20.0	15.9	16.7			
PDTFAU CT1	r	19.5	16.3	16.0			
PDTFAU CT1	1	—	15.6	—			
PDTFAU CT1	1	—	—	16.1	—	≥13.1	
PDTFAU CT1	r	—	—	16.2			
PDTFAU D210.c	1	22.7	16.7	16.1			
PDTFAU D284	r	22.5	17.0	17.4	14.1	12.1	
PDTFAU D406	r	21.8	16.8	16.8			
PDTFAU D614	r	—	—	17.7			
PDTFAU D951	1	—	—	17.6			
PDTFAU E64	r	22.7	16.9	17.5			
PDTFAU E178	r	22.5	18.1	18.0			
PDTFAU E260	1	21.9	17.2	16.7	13.3	—	
PDTFAU E705	1	>19.7	—	16.7			
PDTFAU ET1	1	21.8	16.8	16.5	≥13.1	≥12.3	
PDTFAU ET1 5	1	20.7	16.7	16.4			
PDTFAU ET	r	23.2	16.0	17.0	13.0	12.7	
PDTFAU ET	r	—	—	16.2			
PDTFAU F97	1	19.7	16.3	16.4			
PDTFAU F279	1	23.9	18.8	18.3	>14.4	>12.4	
PDTFAU F280	1	21.6	16.2	15.7	13.9	12.1	
PDTFAU F378	r	22.7	16.4	>15.9	13.7	12.9	
PDTFAU F379	1	23.0	17.8	18.4	14.1	12.6	
PDTFAU G34	r	19.9	16.1	16.2			
PDTFAU G438.2	1	—	—	16.7			
PDTFAU G1131	r	21.6	16.9	16.4	13.3	12.0	
PDTFAU G1597	1	22.0	—	—			
PDTFAU G1740	r	23.5	17.8	18.1	14.3	12.4	
PDTFAU G1924	r	21.9	16.2	16.7	≥13.5	≥11.5	
PIMUZ BP-235	r	21.0	16.5	15.4			
Çandir							
MTA UÇHÜ 640	r	22.9	16.7	15.8			
Villefranche d'Astarac							
MNHNP VAS 24	1	19.7	—	16.0			
Krivâdia railway station							
HGSB Ob-18	..	—	—	—			
Arroyo del Val IV							
IVAU AR IV 7	r	—	19.3	≥18.6			
IVAU AR IV 13	1	22.4	18.1	—			
IVAU AR IV 85	r	22.6	17.8	≥17.9			
IVAU AR IV 485	1	>22.0	—	—			
IVAU AR IV 485	1	—	—	17.2			
IVAU AR IV —	r	—	20.3	—			
Bonnefont							
MNHNP HGP 68	1	20.2	16.4	15.8			
Steinheim							
SMNS 5811	1	21.5	..	17.3			
SMNS 10419	r	21.9	..	17.0			
La Grive oc							
MGL LGr 713	r	>21.4	>17.3	—			
MGL LGr 736	r	21.0	16.6	16.7			
MGL LGr 736	r	21.8	17.3	17.6			
MGL —	r	—	—	16.5			
Cerro del Otero							
MNCN —	1	25.4	18.1	17.9	14.8	13.7	
Sant Quirze							
MGSCB 48907	1	22.1	≥17.9	17.9			
CJFV SQu 5450	r	21.6	—	—			
Massenhausen							
BSPHGM 19I 3e	1	23.0	18.4	17.8			
St. Gaudens?							
MNHNP —	r	—	18.5	—			
Hostalets							
MGSCB 48505	1	23.3	19.1	18.1			
CJFV HP 4219	1	24.3	19.4	17.9			
CJFV —	1	21.9	17.5	17.3			
Can Feliu							
IPS 1675	1	22.6	17.5	17.0			
Wartenberg							
IVAU P25-1963	r	22.0	18.1	18.5			

M_3		DAP	DTa	DTp	DTpp	Ha	Hp
Nguruwe kijivium							
Legetet 14							
KNM-ZP 1372 cast BMNH M14286	r	—	—	>9.6	8.2		
Rusinga R106							

KNM-RU 2773	r	18.6	12.0	9.7	7.4		
KNM-RU 15162	r	>22.8	±13.1	±11.3	—		
Rusinga R3							
KNM-RU 2777	r	—	11.3	9.6	—		
Songhor							
KNM-SO 1054	l	—	—	9.7	7.7		
KNM-SO 1121	r	20.7	11.9	11.1	8.3		
KNM-SO 1138	r	18.4	10.3	9.1	7.0		
KNM-ZP 1381 cast							
BMNH M32660	l	18.6	10.3	8.4	7.2		
Mfwanganu							
KNM-MW 172	r	18.0	10.1	9.0	6.7		
KNM-MW 502	l	—	—	—	—		
Kirimon							
KNM-KI 18040	l	—	—	10.3	7.6		
KNM-KI 18032	r	21.1	—	≥10.4	7.5		
Lopholistriodon moruoroti							
Maboko							
KNM-MB 14482	l	16.3	8.3	8.9	5.7	7.3	6.9
Arrisdrift							
KNM-ZP 1390 casts							
AD 135	l	13.8	7.6	7.4	5.4	7.6	≥6.0
AD 636	l	≥12.0	7.9	7.2	4.5		
Lopholistriodon pickfordi							
Nyakach-Kaimoroon							
KNM-NC 9802	l	—	—	12.3	8.1		
KNM-NC 9808	l	>19.0	—	11.3	7.8		
Lopholistriodon akatidogus							
Mbagathi							
KNM-MG 9	l	28.8	15.5	14.7	11.7	13.6	11.3
KNM-MG 11	r	29.3	14.8	14.4	12.6		
?Maboko							
KNM-MB 10363	r	>27.1	—	>14.6	12.6		
KNM-MB 613 + 869	r	28.8	17.9	16.4	12.9		
Lopholistriodon kidogosana							
Ngorora B5, 2/56							
KNM-BN 1723	l	—	—	11.3	7.4		
KNM-BN 1727	l	20.5	—	>10.0	7.6		
Ngorora D, 2/11							
KNM-BN 188	l	16.7	10.3	10.0	6.8	7.6	>6.2
Ngorora D							
KNM-BN 847	l	—	—	8.3	5.0		
Kubanochoerus khinzikebirus							
Gebel Zelten							
KNM-ZP 1394 cast	r	59.1	34.7	31.5	22.8		
Kubanochoerus hussaini							
Maboko							
KNM-MB 130	l	—	—	>28.3	23.7		
KNM-MB 131	l	—	—	—	28.3		
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	r	≥45.7	—	21.0	16.7		
MNHNP Z 1961	r	>46.6	>23.8	>21.7	>16.3		
MNHNP Z 1961	r	>41.9	>22.7	—	—		
MNHNP Z 1961	l	≥45.9	≥25.2	21.7	17.9		
MNHNP Z 1961	l	≥41.9	≥25.0	21.7	17.9		
MNHNP Z 1961	r	≥45.4	—	21.1	16.8		
MNHNP Z 1961	r	—	—	≥21.5	—		
MNHNP Z 1961	l	—	—	22.5	16.6		
MNHNP Z 1961	l	—	—	≥20.9	17.8		
MNHNP Z 1961	l	44.8	24.9	22.1	17.3	>18.3	>15.6
MNHNP Z 1961	l	48.1	>25.2	>22.4	17.1	>17.7	—
MNHNP Z 1961	l	45.6	25.4	22.3	17.6	18.3	15.1
MNHNP Z 1961	l	46.2	25.4	22.3	17.6	>19.9	—
MNHNP Z 1961	l	44.3	26.1	22.5	18.9		
MNHNP Z 1961	r	47.6	26.1	23.2	18.4	18.1	14.8
MNHNP Z 1961	r	44.5	25.3	22.6	18.6		
MNHNP Z 1961	r	>46.6	>26.8	25.0	19.4		
MNHNP Z 1961	r	45.2	≥25.4	22.3	15.5	..	>16.0
MNHNP Z 1961	l	>42.1	21.9	23.3	16.4	20.3	16.2
MNHNP Z 1961	r	—	—	24.9	20.7		
MNHNP Z 1961	l	—	—	—	16.7		
MNHNP Z 1961	l	—	—	23.6	18.2		
MNHNP Z 1961	l	—	—	24.1	18.4		
MNHNP Z 1961	r	—	—	24.2	17.6		
MNHNP Z 1961	l	41.3	25.1	21.6	17.6	>17.8	>15.0
MNHNP Z 1961	r	46.2	27.4	23.3	17.1		
MNHNP Z 1961	l	47.9	—	22.4	18.3		
MNHNP Z 1961	r	45.6	—	21.2	16.6		
MNHNP Z 1961	l	±42.4	—	—	18.4		
MNHNP Z 1961	l	46.0	24.5	21.6	15.3		
Bunolistriodon anchidens							
Rusinga R113?							
KNM-RU 15164	l	32.2	18.8	>16.0	11.9		
Karungu	?						
KNM-KA 51	l	—	18.6	16.3	—		
Bunolistriodon aff. latidens							
Olival da Suzana							

CEPUNL 20	r	—	—	—	12.9		
CEPUNL 17	r	35.0	—	—	15.0		
Quinta Flamengas							
CEPUNL 36	r	34.4	22.0	19.7	15.8		
Quinta da Silvéria							
CEPUNL 42	r	34.5	—	18.4	14.4		
Quinta Grande							
CEPUNL 31	l	33.3	—	14.5	13.3		
CEPUNL 32	l	—	—	≥16.0	>11.8		
Quinta da Conceição							
CEPUNL 50	l	≥36.2	—	18.9	14.7		
Quinta da Lobeira							
CEPUNL 44	r	≥27.9	18.8	16.2	11.3		
La Artesilla							
MPZ 6442	r	30.5	16.0	15.1	11.5		
MPZ 6443	l	—	17.7	—	—		
MPZ 6444	r	35.3	19.9	19.4	13.7		
Armantes I							
IVAU 41/506	l	34.2	19.8	18.3	13.3		
IVAU 41/507	r	34.7	21.4	18.9	13.4		
IVAU 41/508	r	—	—	—	—		
Munébrega III							
IVAU 53/73	r	—	—	—	—		
Munébrega AB							
IVAU Mun 1	l	32.7	≥17.4	17.4	13.0		
IVAU Mun 2	r	—	—	16.7	14.1		
Bunolistriodon latidens							
Inönü I							
MTA AKI-3/162	r	33.6	19.3	17.3	12.5		
Bunolistriodon sp.							
Ad Dabtiyah							
BMNH M 42949	r	32.6	—	16.8	12.3		
Bunolistriodon M							
Paşalar							
PIMUZ BP-118	r	30.8	17.4	16.9	12.2	13.2	10.7
PDTFAU B593	l	—	—	18.1	13.8		
PDTFAU C8.5	l	32.3	17.7	16.2	12.8		
PDTFAU C8.7	r	—	—	17.2	12.1		
PDTFAU C8.8	l	—	19.0	—	—		
PDTFAU C8.9	l	—	18.4	—	—		
PDTFAU C279	r	—	—	17.1	13.6		
PDTFAU C280/1	l	31.6	17.1	16.1	11.6		
PDTFAU C280/2	l	33.7	19.4	17.5	13.5		
PDTFAU C280/3	l	33.2	18.5	17.1	13.7		
PDTFAU C374	r	—	—	16.9	12.4		
PDTFAU CT1	r	—	—	18.0	12.2		
PDTFAU D8.14	r	—	—	15.7	12.7		
PDTFAU D8.15	l	—	—	17.5	12.4		
PDTFAU D62	l	33.2	16.9	16.2	12.4		
PDTFAU D210/3	r	32.5	17.8	16.5	12.6		
PDTFAU D210/4	l	34.8	19.9	18.1	12.8		
PDTFAU D813	r	32.2	18.8	17.1	12.5		
PDTFAU E7.9	r	—	—	15.8	12.0		
PDTFAU E7.18	l	—	—	—	13.3		
PDTFAU E89.1	r	—	17.1	16.2	—		
PDTFAU E662	l	—	—	16.3	11.7		
PDTFAU E805+807	l	—	17.1	15.8	—		
PDTFAU G652a	l	36.2	20.1	18.0	12.7		
PDTFAU G1248	l	30.9	15.7	15.2	11.6		
PDTFAU G1286	r	29.9	17.2	15.7	10.1		
Çandir							
FMNH cast	r	35.9	≥18.4	17.6	13.2		
Bunolistriodon lockharti							
Pellecahus							
UCBL 320293	l	32.4	17.2	17.4	..		
La Romieu							
UCBL 320275	r	31.3	18.0	16.5	12.8		
UCBL 320288	r	≥34.9	19.2	17.1	12.2		
UCBL 320288	l	35.3	20.6	17.7	13.6		
UCBL 320299	r	29.9	17.1	16.4	10.7		
UCBL 320311	r	—	20.8	18.6	—		
Baigneaux							
NMB SO-2002	r	34.9	18.6	16.8	13.6		
NMB SO-2814	l	31.2	17.3	15.9	12.2		
NMB SO-4926	r	34.2	18.5	16.9	13.1		
NMB SO-5633	r	—	—	15.6	12.9		
Chevilly							
MNHNP CHE 43	r	35.4	21.6	18.8	13.0		
MNHNP CHE 44	..	35.1	—	18.2	12.3	16.0	13.4
"Orléans"							
MSNO 266	r	36.6	21.1	18.9	13.6	16.5	13.3
Buñol							
IPS 1147	l	—	>20.6	20.1	14.6		
Gerlenhofen							
SMNS — cast	r	37.6	19.8	..	..		
SMNS — cast	r	±32.4	≥18.0	..	..		
SMNS — cast	l	34.3	20.0	..	..		
Pontlevoy							

MNHNP FP 1807	r	34.5	20.8	18.9	13.0			
MNHNP FP 1808	l	38.0	21.2	19.3	14.7	16.9	13.6	
Tavers								
COBO —	l	35.9	19.5	18.2	13.6			
COBO —	r	32.2	18.7	16.9	12.8	14.8	11.8	
Ravensburg								
NMB TD 549	r	35.7	19.7	19.7	13.6			
NMB TD 550	l	35.6	20.9	19.1	12.8			
Szentendre								
HGSB V60614 cast	r	33.1	19.3	17.3	12.2			
Bunolistriodon akatikubas								
Mbagathi								
KNM-MG 2	l	33.1	—	18.1	12.0	—	11.6	
Maboko								
KNM-MB 132	l	34.5	19.6	16.9	13.6			
KNM-MB 614	r	—	18.4	16.3	—			
KNM-MB 16712	l	—	>19.8	—	—			
KNM-MB 19424	l	31.5	19.1	16.6	10.8			
KNM-MB 19524	l	—	—	—	10.9			
Bunolistriodon guptai								
HGSP 8320								
HGSP 8320/2016	l	34.9	20.1	19.0	12.1			
HGSP 8321								
HGSP 8321/2072	l	—	—	—	—			
Listriodon pentapotamiae								
Chinji 38								
GSP 1360	r	31.6	17.7	16.4	11.1			
Dhok Talian 189								
GSP 4532	l	—	21.7	—	—	—	16.0	—
Kanatti								
IVAU KA 81	r	—	19.3	18.0	12.2			
HGSP 8427								
HGSP 8427/3646	l	—	—	16.7	12.6			
Achora								
IVAU CHA-60	r	—	17.0	—	—			
Mochiwala								
BSPHGM 1294	l	—	—	16.8	12.0			
Mochi Wala								
IVAU CHO 33	r	—	—	—	—			
IVAU CHO 126	r	32.2	≥17.9	16.7	9.3			
IVAU CHO 127	l	27.8	16.5	>13.6	9.9			
HGSP 8304								
HGSP 8304/1333	r	32.8	18.0	17.4	13.3			
HGSP 8220								
HGSP 8220/1037	r	—	—	>17.0	11.8			
Kanatti Chak 5								
BSPHGM 1956II48	l	28.5	17.7	15.8	12.0			
Kanatti Chak 9								
BSPHGM 1956II85	r	33.7	20.0	18.6	12.8			
Sosianwali								
BSPHGM 1956II49	r	—	16.5	15.8	—			
Bhurriwala								
BSPHGM 205	r	—	—	—	—			
Bhilomar								
IVAU CHH 25	l	—	—	—	11.5			
Marianwala Kas								
BSPHGM 1672	r	—	—	16.3	11.2			
Kundal Nali								
IVAU CHK 105	r	—	—	15.0	..	—	>10.5	
IVAU CHK 118	r	—	—	—	—			
Kalin Nal								
BSPHGM 1956II50	r	31.6	17.6	16.2	11.0			
SSO Bhilomar								
BSPHGM 1956II107	l	34.4	18.7	17.9	11.4			
Djuguwala								
BSPHGM 2613	r	—	—	≥18.0	12.9			
Chinji Fm. bought spec.								
IVAU CH-16	l	—	—	18.1	14.6	—	12.2	
IVAU CH-26	r	—	—	14.9	10.8	—	10.0	
IVAU CH-43	l	—	—	—	11.8			
Listriodon splendens								
La Gruas								
NMB DG 34	r	27.8	16.5	15.4	8.2			
Simorre								
CFE cast ICT	r	28.8	17.8	16.7	10.2			
Castelnau de Barbarens								
CFE cast ICT	r	31.4	18.3	17.2	10.8			
"Gers"								
MNHNP Ger 37	r	33.8	—	17.6	12.7			
Inönü I								
MTA AKI 3/778	r	35.3	19.7	18.6	13.6			
Stätzling								
BSPHGM — cast	l	33.9	19.7	18.0	13.1	15.2	10.4	
Paşalar								
PDTFAU A167	l	—	17.9	—	—			
PDTFAU B592	r	36.3	19.2	17.2	11.8			
PDTFAU B593	r	—	—	16.8	12.4			
PDTFAU B593	r	—	—	≥18.3	—			
PDTFAU BT	l	—	20.4	19.1	—	14.3	12.4	
PDTFAU C280	l	35.9	19.6	19.1	12.6			
PDTFAU C280/4	l	35.9	19.9	18.1	12.6			
PDTFAU C396	r	35.8	19.6	18.4	12.2			
PDTFAU C663	l	33.5	19.2	17.7	12.1			
PDTFAU CT1	r	35.9	19.4	19.2	12.7			
PDTFAU CT1	r	—	—	19.0	14.2			
PDTFAU CT1	r	—	>19.2	—	—			
PDTFAU CT1	l	—	—	—	11.8			
PDTFAU CT5	r	—	18.3	—	—			
PDTFAU CT5	r	—	—	—	12.7			
PDTFAU D188	l	—	—	17.4	12.0	—	11.7	
PDTFAU D210.5	l	35.8	19.4	18.2	13.3			
PDTFAU D381	r	—	—	—	18.1			
PDTFAU D593	r	—	—	16.8	12.4			
PDTFAU D728	r	—	—	17.2	11.2	—	12.8	
PDTFAU D993	l	—	—	18.1	12.7			
PDTFAU D1064	r	31.0	17.9	16.6	11.2			
PDTFAU D1140	r	35.2	19.5	17.9	13.8			
PDTFAU D1190/1	l	34.8	19.4	18.0	12.1	15.1	13.4	
PDTFAU DT1	r	—	—	17.7	12.0	—	13.0	
PDTFAU DT1	r	—	—	—	≥11.6			
PDTFAU DT1	r	—	—	—	>11.9			
PDTFAU E89	r	31.7	19.4	18.0	12.2			
PDTFAU E470	r	35.8	20.2	18.3	12.8			
PDTFAU E541	l	—	—	17.1	11.7	—	12.1	
PDTFAU E546	l	34.8	18.6	18.0	13.2	14.8	13.9	
PDTFAU E955	r	—	17.4	—	—			
PDTFAU ET1	r	34.4	19.2	18.0	11.1			
PDTFAU ET1	l	32.1	18.8	17.9	10.4	13.9	12.6	
PDTFAU ET	r	—	18.5	18.2	—			
PDTFAU ET	l	—	—	—	13.7			
PDTFAU F7	r	34.2	19.2	18.0	12.2			
PDTFAU F289	r	37.8	21.7	19.7	14.2	15.9	14.2	
PDTFAU F380	r	—	—	18.6	12.4	—	13.8	
PDTFAU F404	l	—	—	19.5	14.0			
PDTFAU F445	l	31.5	17.9	17.1	11.3			
PDTFAU F765	r	34.9	20.5	18.1	12.3	15.3	13.1	
PDTFAU G370	l	39.9	21.7	19.1	12.2			
PDTFAU G402	l	34.9	19.4	≥17.6	12.6	14.0	—	
PDTFAU G408	r	—	—	19.3	13.9			
PDTFAU G774	l	—	19.9	18.2	—			
PDTFAU G1091	r	34.7	20.6	19.2	12.8			
PDTFAU G1371	r	33.2	19.7	18.3	12.1			
PDTFAU G1665.4	r	—	19.4	—	—			
PDTFAU G1690	r	35.4	20.4	18.6	12.7			
PDTFAU —	l	36.3	20.1	19.5	14.2	15.0	12.7	
PIMUZ BP-117	r	35.6	19.3	17.8	12.6	14.1	12.0	
PIMUZ BP-123	r	33.6	18.8	17.7	11.0	13.9	12.6	
Çandir								
PIMUZ CA I/61	l	36.0	19.7	17.6	11.4			
Villefranche d'Astarac								
MNHNP VAS 14	r	31.6	17.9	16.3	10.9			
MNHNP VAS 22	r	—	19.3	—	—			
MNHNP VAS 25	l	>30.1	—	—	—			
Paracuellos III								
MNCN PA 450	r	≥41.0	—	20.9	12.1			
MNCN PA 619	l	38.9	21.6	>19.2	12.2	±18	13.4	
Manchones I								
IVAU MA 104	r	—	21.1	18.7	—			
Arroyo del Val IV								
IVAU AR IV 5	l	32.3	19.9	18.0	11.9			
IVAU AR IV 8	r	33.5	≥20.4	19.0	13.1			
IVAU AR IV 10	r	35.7	—	18.1	12.6	—	13.6	
IVAU AR IV 11	r	≥32.1	—	18.4	13.7			
IVAU AR IV 84	l	34.0	20.4	18.9	13.7			
IVAU AR IV 86	r	—	20.5	18.7	—			
MPZ AV-33	l	34.5	20.6	18.4	12.3			
Arroyo del Val I								
IVAU AR I 1	r	41.1	22.8	20.4	12.3			
IVAU AR I 2	l	41.9	21.4	20.0	12.6			
IVAU AR I 3	l	—	—	22.8	—			
Larroque de Magnoac								
MNHNP HGP 31	l	35.5	21.0	19.2	10.4			
MNHNP HGP 32	r	33.4	17.2	16.3	11.4			
Yaylacilar								
PIMUZ AY 1/7	r	33.2	18.6	18.1	10.0	14.5	12.0	
Kaisersteinbruch								
NMW 1866II14	l	31.7	18.9	18.3	10.9			
Sooskút								
NMW 1865XXX21	l	33.7	19.8	18.3	12.4			
Steinheim								
SMNS 5811	r	33.0	19.1	..	..			
SMNS —	r	—	—	..	..			
La Grive oc								
IGF 295	l	—	—	15.9	—			

IGF 295	r	31.8	17.3	15.6	10.7	13.8	..
UCBL 65618	l	32.1	18.5	16.6	11.4	14.8	..
UCBL 65618	l	31.1	18.4	16.9	11.1		
UCBL 65618	l	31.4	17.5	16.2	9.5	14.1	..
UCBL 65618	r	34.4	19.9	18.1	11.0		
UCBL 65618	r	—	—	17.2	11.2		
La Chaux-de-Fonds							
MHNCF 2	r	—	—	17.8	11.6		
Solera							
IVAU —	l	36.9	21.7	19.9	11.9		
Sant Quirze							
MGSCB 30485	r	>36.4	—	21.2	13.4		
MGSCB 30501	l	±36.2	23.5	20.3	10.9		
MGSCB 48883	r	—	—	18.4	..		
MGSCB 48899	l	—	—	≥19.8	—		
MGSCB 48908	r	—	19.1	—	—		
MGSCB 48909	l	—	>18.7	—	—		
MGSCB 48924	r	36.5	>20.7	20.1	12.8		
ITGE 69 (411M)	l	31.6	≥20.0	±17.6	8.6		
CJFV SQu 5452	r	37.5	21.4	19.3	12.2		
Wartenberg							
IVAU P25-1963	r	34.7	19.9	19.1	14.7		
Hostalets							
MGSCB 48504	l	—	—	18.2	10.7		
MGSCB 48507	l	—	—	≥18.7	..		
CJFV 4221	l	>32.9	±20.5	—	12.4		
CJFV 4229	r	—	—	—	12.9		
CJFV —	r	32.5	18.2	16.8	10.8		
Mering							
NMB TD 838 cast	r	33.5	18.9	18.0	12.1		
Doué la Fontaine							
MNHNP cast	r	—	—	19.6	12.4		

I^1		DMD	DLL	Hli	Hla
Nguruwe kijivium					
Songhor					
KNM-SO 4976	r	7.8	5.6	9.9	8.3
KNM-SO 4980	l	7.2	6.1		
Mfwanganu					
KNM-MW 384	l	6.8	5.9	7.2	8.5
Lopholistriodon moruoroti					
Maboko					
KNM-MB 14486	l	8.1	5.6		
KNM-MB 14490	l	8.0	5.5		
KNM-MB 15116	l	7.5	5.2	8.6	9.5
Majiwa					
KNM-MJ 9775	l	7.8	5.8		
Muryur					
KNM-MY 25	l	6.6	6.1	10.3	11.5
Lopholistriodon kidogosana					
Ngorora B5, 2/56					
KNM-BN 2086	l	—	—		
Ngorora D, 2/11					
KNM-BN 190	l	11.2	6.5	6.5	8.1
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	24.9	14.1	16.4	20.4
MNHNP Z 1961	l	23.2	14.8	17.1	20.0
MNHNP Z 1961	r	24.7	14.8	≥15.8	19.2
MNHNP Z 1961	r	24.4	15.3	17.8	20.7
MNHNP Z 1961	l	23.9	15.4	>18.2	>19.4
MNHNP Z 1961	r	23.2	14.4	>15.3	>18.7
MNHNP Z 1961	l	27.3	15.8	17.7	18.6
MNHNP Z 1961	l	25.8	15.9	16.4	18.8
MNHNP Z 1961	r	23.3	15.3	>16.3	>18.3
MNHNP Z 1961	l	24.6	>14.9		
MNHNP Z 1961	r	25.5	15.4		
MNHNP Z 1961	l	≥23.3	>14.3		
MNHNP Z 1961	r	—	—		
MNHNP Z 1961	l	—	—		
Bunolistriodon anchidens					
Rusinga					
KNM-RU 8322	r	15.2	11.2	>14.0	>12.8
Rusinga R1					
KNM-RU 15166	r	>15.5	±11.6	±14.6	±15.3
Bunolistriodon aff. latidens					
La Artesilla					
MPZ 6420	r	15.9	10.4		
MPZ 6421	l	16.9	10.2		
MPZ 6422	r	>17.4	10.7		
MPZ 6423	r	16.9	10.9		
Munêbrega AB					
IVAU Mun 3	r	17.9	9.9		
Armantes I					
IVAU 41/526	r	19.4	9.6		
IVAU 41/527	l	17.4	10.1		
Munêbrega I					
IVAU 55/1055	l	19.1	11.4		
IVAU 55/1056	r	—	11.2		
Bunolistriodon latidens					
Inönü I					
MTA AKI-3/571	l	28.9	11.6		
Bunolistriodon M					
Paşalar					
PIMUZ BP268 cast	l	—	—		
PIMUZ BP143 cast	l	35.1	11.1		
PDTFAU A173	r	—	—		
PDTFAU D210/1	r	33.0	11.9		
PDTFAU D210/2	l	32.7	>11.3		
PDTFAU D210.23	r	37.8	12.7		
PDTFAU DT 210.30	l	—	—		
PDTFAU E89.28	l	—	≥11.5		
PDTFAU E189	l	37.3	12.1		
PDTFAU E934	l	—	—		
PDTFAU F278.21	r	—	—		
PDTFAU F278.26	l	—	—		
PDTFAU G631.3	l	—	—		
Çandir					
MTA AÇH-1334	r	38.6	≥11.2		
PIMUZ CA I	l	41.9	13.0		
Bunolistriodon lockharti					
La Romieu					
UCBL 320268	r	16.7	9.5		
UCBL 320270	l	19.2	13.2		
UCBL 320270	r	16.9	9.8		
Baigneaux					
NMB SO-571	l	20.3	11.9		
NMB SO-752	r	18.4	10.1		
NMB SO-3019	r	18.8	11.3		
NMB SO-3613	r	20.4	11.6		
NMB SO-5632	l	21.5	12.5		
Gerlenhofen					
SMNS — cast	l	22.8	11.4		
SMNS — cast	r	20.6	≥10.9		
SMNS — cast	l	21.8	11.0		
Langenau 1					
SMNS 40965	l	21.7	13.0		
Ravensburg					
NMB TD 547	r	24.7	13.3		
Pontlevoy					
MNHNP FP 220	r	22.7	13.9		
MNHNP FP 1027	l	>20.0	11.8		
MNHNP FP 1037	r	23.4	12.3	11.4	16.0
Tavers					
COBO —	l	23.9	12.7		
Bunolistriodon akatikubas					
Maboko					
KNM-MB 409	l	21.6	13.3		
Bunolistriodon guptai					
HGSP 8223					
HGSP 8223/1215	r	18.3	9.5	11.0	16.0
?HGSP 8312					
HGSP 8312/1402	r	20.9	12.4	13.2	12.4
Loc.?					
IM K 13/768	l	19.6	11.5	10.7	12.2
Listriodon pentapotamiae					
Chinji 38					
GSP 811	l	19.0	10.6		
Chinji 67					
GSP 1424	l	21.4	11.0		
Dhulian 305					
GSP 10050	l	—	—		
Marianwala-Kas					
BSPHGM 1956II100	l	19.0	10.6		
Bhurriwala					
BSPHGM 2637	r	—	—		
Bhurriwala 2					
BSPHGM 1956II94	r	—	13.4		
BSPHGM 1956II97	r	—	11.4		
Kanatti Chak 5					
BSPHGM 1956II95	l	—	11.9		
Kanatti Chak 6					
BSPHGM 1956II90	r	17.6	9.7		
Dhulian W. Khaur					
BSPHGM 1939X	l	20.9	10.3		
Kadirpur					
BSPHGM 1956II91	l	20.2	11.4		
Kundal Nali					
FISF CHK - F6114	l	—	11.8		
IVAU CHK 31	l	—	>8.8		
Kundal Nala 2					
BSPHGM 1956II93	r	>19.3	9.2		
Pirawalaban 3					
BSPHGM 1956II92	r	±18.5	8.4		
Chattuwala					
BSPHGM 1956II89	r	25.5	12.0		

Parrewali					
BSPHGM 1939X	l	22.5	9.5		
Bhilomar					
IM B 698	r	22.4	8.9		
Bhilomar					
IVAU CHH 35	r	—	12.5		
HGSP 8415					
HGSP 8415/3202	l	22.7	11.3		
Chinji Formation bought spec.					
FISF CH – F 6114	r	19.3	12.4		
IVAU CH 200	r	19.5	9.7	10.2	12.9
IVAU CH 201	r	20.1	10.2		
Listriodon splendens					
"Gers"					
MNHNP Ger 52	l	27.5	13.3	12.0	17.4
Paşalar					
PDTFAU A173/1	l	23.8	12.2		
PDTFAU A173/2	r	22.8	11.7		
PDTFAU C133	r	25.8	13.1		
PDTFAU C187.12	l	24.8	11.5		
PDTFAU C187.13	l	≥26.7	±13.4		
PDTFAU C323	l	23.7	15.7		
PDTFAU CT 5	r	—	—		
PDTFAU D8.4	l	21.4	11.4		
PDTFAU D400	r	24.8	14.9		
PDTFAU D878	r	24.7	13.2		
PDTFAU DT 8.1	r	23.4	11.3		
PDTFAU DT 8.2	r	22.2	—		
PDTFAU DT 8.6	l	—	12.8		
PDTFAU DT 8.7	l	—	>12.4		
PDTFAU DT 210.20	l	23.9	11.4		
PDTFAU DT 210.28	r	24.6	11.5		
PDTFAU DT 210.30	r	23.3	11.4		
PDTFAU E89.30	l	—	—		
PDTFAU E319	l	—	—		
PDTFAU F111	r	25.9	12.8		
PDTFAU F278.28	l	—	13.1		
PDTFAU F396	r	24.2	12.4		
PDTFAU F511	l	26.6	13.6		
PDTFAU F522	r	—	12.5		
PDTFAU G239	r	24.6	>12.1		
PDTFAU G273	r	27.3	12.2		
PDTFAU G323	r	>23.4	—		
PDTFAU G1310	l	>26.4	13.5		
PDTFAU G1596	l	26.2	13.4		
PDTFAU G1897	l	23.8	12.6		
PDTFAU G1924.1	l	—	≥12.3		
PDTFAU 1988 surface	r	26.0	—		
PIMUZ BP-150	l	25.6	13.9		
PIMUZ BP-277	r	24.1	11.9		
Eichkogel					
NMW 1954/74	r	27.7	13.5		
NMW SK 1614	l	25.9	..		
Villefranche d'Astarac					
MNHNP VAS 27	l	26.4	12.7		
MNHNP VAS 28	r	27.1	12.3		
Larroque de Magnoac					
MNHNP HGP 33	l	27.0	13.0	±10.9	±13.5
MNHNP HGP 34	l	—	≥12.1		
Manchones I					
IVAU MA 103	r	>25.4	—		
IVAU MA I 5212	r	—	—		
Arroyo del Val IV					
IVAU AR IV 80	r	28.6	13.4	15.1	≥19.9
IVAU AR IV 413	r	—	—		
IPS 1292	l	26.1	12.0		
RGM 262.757	l	—	14.0		
RGM 263.009	r	26.9	11.2		
RGM 263.010	l	26.2	±11.0		
RGM 263.021	l	>16.7	9.2		
RGM 263.159	r	—	—		
MPZ AV-38	l	26.4	14.1		
Arroyo del Val VI					
IVAU AR VI 1	l	31.2	13.0		
IVAU AR VI 2	r	30.5	12.9		
IVAU AR VI 34	l	>25.6	≥13.9		
Sariçay					
MTA —	l	>22.9	≥10.7		
MTA —	r	23.2	11.4		
La Grive oc					
IGF 299	l	24.8	11.7	11.0	14.3
IGF 299	r	26.0	10.3	12.0	14.0
MGL LGr 701	r	28.1	12.9		
MGL LGr 702	r	24.7	12.4		
MGL LGr 704	r	29.9	13.5		
MGL LGr 705	r	28.2	12.2		
MGL LGr 706	r	27.3	12.4		
MGL LGr 707+711	r	23.6	14.3		
MGL LGr 708	l	23.2	—		
MGL LGr 709	r	26.2	12.5		
MGL LGr 710	r	29.5	13.0	13.8	17.0
Stützenhofen (Schodel Sandgrube)					
IPUW 10 X 1937	r	28.9	12.4		
La Chaux-de-Fonds					
MHNCF 8	r	27.1	12.5		
MHNCF 8'	l	29.4	14.2		
MHNCF 9	l	27.5	12.8		
Can Feliu					
IPS —	l	30.1	13.2		
Cerro del Otero					
MNCN NM 18029	r	34.9	≥12.1		
MNCN NM 18028	l	≥29.5	≥12.5		
Sant Quirze					
IPS VP 1019	l	30.5	13.3		
IPS VP 1026	l	27.0	11.1		
IPS VP 1027	l	30.1	13.6		
MGSCB 48901	l	≥22.5	≥12.1		
MGSCB 48902	l	27.3	13.0		
MGSCB 48903	l	—	>11.4		
MGSCB 48904	l	—	13.1		
CJFV SQu 478	r	27.4	12.7		
Castell de Barberà					
IPS 1956	l	28.3	12.4		
IPS 1957	l	25.4	≥12.8		
IPS —	l	30.5	11.7		
IPS —	r	31.9	11.5		
IPS —	r	29.8	13.8		
Hostalets					
MGSCB 48501	l	35.1	>13.2		
IPS 1054	l	32.9	11.6		
CJFV —	r	—	±14.4		
CJFV 4234	..	—	14.6		
Esselborn					
HLD Din 34	l	30.5	13.5		
Wissberg					
HLD 1933/362	r	31.4	14.3	15.4	..
HLD 1933/879	l	—	>9.9		

DI^1		**DMD**	**DLL**	**Hli**	**Hla**
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	13.2	6.6	9.6	10.1
Bunolistriodon aff. latidens					
Armantes I					
IVAU 41/539	r	9.9	4.8		
Bunolistriodon M					
Paşalar					
PDTFAU E89.27	l	—	6.3		
PDTFAU G968	r	20.6	5.7		
PDTFAU G1323	r	20.8	6.1		
Listriodon splendens					
Paşalar					
PDTFAU A...	r	15.0	5.7	8.3	7.9
PDTFAU D161.1	r	13.7	5.2		
PDTFAU D161.2	l	—	5.1		
PDTFAU D161.2	l	—	—		
PDTFAU E89.25	l	15.6	5.1		
PDTFAU G113	r	14.4	5.0		
PDTFAU G629	l	—	4.8		
Murrero					
IPS 1072	r	±20.1	±6.1		
Hostalets					
IPS 1091	r	22.0	6.3		
IPS VP 760	l	19.7	6.8		
CJFV 4337	r	>19.2	>7.1		
CJFV —	r	22.0	7.5	9.7	..

I^2		**DMD**	**DLL**	**Hli**	**Hla**	**Hme**	**Hdi**
Nguruwe kijivium							
Songhor							
KNM-SO 4977	r	5.9	3.2	5.8	5.4		
Lopholistriodon moruoroti							
Maboko							
KNM-MB 10316	l	7.8	—				
KNM-MB 10335	r	5.8	3.9	5.2	5.7		
KNM-MB 10336	r	5.4	3.5	>4.4	>5.0		
Lopholistriodon akatidogus							
Fort Ternan							
KNM-FT 3790	l	13.3	6.1	6.5	8.9		
Lopholistriodon kidogosana							
Ngorora B5, 2/56							
KNM-BN 1726	l	9.1	4.8				

KNM-BN 1728	1	9.2	4.9		
Kubanochoerus marymunngui					
Baragoi BGX					
KNM-BG 18012	1	>19.5	>13.4		
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	17.0	10.6	>12.5	>13.2
MNHNP Z 1961	1	15.8	10.8		
MNHNP Z 1961	1	18.0	10.6		
MNHNP Z 1961	1	17.1	10.9		
MNHNP Z 1961	r	17.3	11.6		
MNHNP Z 1961	r	>18.4	8.9	>11.6	>11.4
MNHNP Z 1961	1	—	±12.3		
MNHNP —	r	—	10.5		
Kubanochoerus minheensis					
Guanghe					
BMNH —	r	16.9	9.9		
Kubanochoerus gigas					
Chinji Fm bought material					
IVAU CH 262	1	25.6	15.1		
Bunolistriodon anchidens					
Rusinga R3					
KNM-RU 5847	1	12.2	8.8		
Rusinga R3a					
KNM-RU 5846	r	11.7	7.9	9.4	10.5
Rusinga					
KNM-RU 8318	r	12.5	8.8		
KNM-RU 4363	1	12.2	8.7	>9.7	>10.2
Rusinga? R1?					
KNM-X 119	1	>10	8.1		
Bunolistriodon aff. latidens					
La Artesilla					
MPZ 6424	1	13.1	7.5		
MPZ 6425	1	12.6	6.6		
Moratines					
MNCN —	r	>12.3	6.3		
Armantes I					
IVAU 41/537	r	>12.6	6.6		
Munébrega III					
IVAU 53/59	1	10.3	5.9	..	10.4
Bunolistriodon lockharti					
Pellecahus					
NMB GB 2456	1	15.1	7.6		
La Romieu					
UCBL 320270	r	14.7	8.2		
UCBL 320270	1	14.6	8.3		
UCBL 320270	r	13.5	7.8		
UCBL 320270	1	14.1	>7.8		
Baigneaux					
NMB SO-6105	r	16.6	7.5		
Gerlenhofen					
SMNS — cast	1	17.5	8.8		
Engelswies					
NMB TD 1102	1	13.0	7.6		
Pontelevoy					
NMHNP FP 222	r	17.8	10.2		
NMHNP FP 223	r	17.9	9.6	11.7	≥14.9
NMHNP FP 1031	r	>15.1	8.5		
NMHNP FP 1032	1	17.8	10.2		
Bunolistriodon akatikubas					
Majiwa					
KNM-MJ 9774	r	16.9	9.2	>9.6	>9.7
Maboko					
KNM-MB 10366	1	16.2	8.6	>10.2	>11.3
KNM-MB 19416	1	16.5	7.3		
KNM-MB 14419	r	>15.1	>8.0		
KNM-MB 19713	r	20.7	10.5	11.5	14.4
Bunolistriodon guptai					
?Shali Nala					
IM B 704	r	16.1	8.7	10.3	11.8
Loc.?					
IM K 13/774	1	13.4	8.5	10.1	12.7
IM K 13/768	1	12.4	6.8	>8.4	>10.1
Listriodon pentapotamiae					
Dhok Talian 189					
GSP 4530	1	14.6	7.8		
GSP 4472	r	15.8	7.1		
GSP 4474	r	—	—		
Chari Gambhir					
BSPHGM 1378-81	1	14.4	6.8		
BSPHGM 1379-81	1	17.0	7.2		
BSPHGM 1379-81	r	14.7	6.5		
BSPHGM 1379-81	r	13.9	7.4		
Kalinal					
BSPHGM 3611 - 12	1	—	6.3		
Son Nala					
IVAU CHS —	r	12.3	7.1	7.2	9.5
Listriodon splendens					
Inönü I					
MTA AKI 3/579	r	12.2	6.1		
MTA AKI 3/580	r	13.3	7.1		
Eichkogel					
NMW SK 1614	r	18.4	8.6		
Çandir					
MTA AÇHÜ 838	1	15.4	7.0		
MTA UÇHÜ 1108	1	17.4	8.6	10.2	12.6
Arroyo del Val IV					
IVAU AR IV 78	r	18.4	8.8	10.6	12.4
IVAU AR IV 79	r	15.6	8.5		
IVAU AR IV 83	1	17.9	>8.5		
IVAU AR IV 394	r	—	—		
IVAU AR IV 485	1	—	—		
IPS 1293	1	>16.6	8.3		
MPZ AV-35	1	12.0	7.0		
MPZ AV-43 (2)	r	16.8	9.9		
MPZ AV-46 (1)	1	16.6	8.0	8.6	10.9
MPZ AV-47	r	15.0	7.3		
Arroyo del Val VI					
IVAU AR VI 14	1	18.5	8.5		
IVAU AR VI 16	r	18.1	8.3		
Sariçay					
MTA —	r	—	≥8.2		
Torril					
CCL —	1	15.0	7.9		
La Grive oc					
NMB GA 468	r	>16.8	7.8		
NMB GA 469	r	14.4	7.1		
NMB GA 470	r	>16.1	7.1		
Cerro del Otero					
MNCN NM 18026	r	19.1	≥9.1		
MNCN NM 18027	1	18.5	9.5	10.1	13.7
Sant Quirze					
IPS VP 1021	1	17.1	8.8		
Castell de Barberà					
IPS 1960	1	16.6	7.7		
IPS 1963	1	>16.3	7.5		
IPS —	r	>14.2	7.9		
Hostalets					
MGSCB 48510	r	15.7	7.6		
IPS 1076	1	—	—		
IPS VP 314	r	16.5	7.0		
CJFV —	r	18.3	8.6	10.5	14.6

DI^2		DMD	DLL	Hli	Hla
Bunolistriodon M					
?Paşalar					
PDTFAU DT	r	8.1	3.5		
Listriodon pentapotamiae					
Kadirpur					
BSPHGM 1956II98	1	10.9	6.4		
Listriodon splendens					
?Paşalar					
PDTFAU C323	1	10.2	4.5	>5.9	>6.4
PDTFAU CT5	r	10.1	4.2		
PDTFAU CT5	r	10.4	4.5		
PDTFAU ET	1	9.9	4.4		
La Grive oc					
MGL LGr 1493	r	11.7	±8.9		
Sant Quirze					
CJFV SQu 4291	r	11.2	5.1	5.8	5.1

I^3		DMD	DLL	Hli	Hla
Nguruwe kijivium					
Mfwanganu					
KNM-MW 560	1	5.8	3.6	6.1	6.1
Lopholistriodon akatidogus					
Majiwa					
KNM-MJ 9777	r	10.0	4.4		
Lopholistriodon kidogosana					
Ngorora B5, 2/1					
KNM-BN 1162	r	7.5	4.3		
Ngorora B5, 2/56					
KNM-BN 842	1	7.4	3.7		
Kubanochoerus khinzikebirus					
Maboko					
KNM-MB 932	1	>24.3	17.4		
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	20.1	11.5	15.3	18.1
MNHNP Z 1961	1	20.7	10.8	>15.1	>17.2
MNHNP Z 1961	1	≥16.0	9.4		
Bunolistriodon latidens					
Inönü I					
MTA AKI-3/49	1	18.5	9.2		
MTA AKI-3/50	r	18.3	8.1		

MTA AKI-3/162	r	15.8	7.6
Listriodon splendens			
Arroyo del Val VI			
IVAU AR VI 15	r	14.5	6.1
Castell de Barberà			
IPS —	1	≥13.8	6.3
IPS —	1	15.1	5.8
Hostalets			
IPS VP 764	1	14.6	6.6

C^m		DAP	DT	Ri	Ro
Nguruwe kijivium					
Songhor					
KNM-SO 1052	r	11.7	9.7		
KNM-SO 4974	1	—	9.6		
Lopholistriodon moruoroti					
Maboko					
KNM-MB 141	r	10.8	9.7		
KNM-MB 142	1	9.4	6.9		
KNM-MB 143	r	..	..		
KNM-MB 877	r	11.6	9.8		
Lopholistriodon pickfordi					
Majiwa					
KNM-MJ 9779	r?	12.5	11.1		
Lopholistriodon akatidogus					
Maboko					
KNM-MB 19518	r	18.0	14.2		
Majiwa					
KNM-MJ 9788	r?	16.7	14.9		
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	±31.7	±33.0	35	55
MNHNP Z 1961	r	34.7	29.9		
Kubanochoerus gigas					
Quantougou					
IVPP cast type	1	±29.0	±25.4		
Maerzuizigou					
BMNH BPV-921	r	38.6	39.1	130	150
Bunolistriodon anchidens					
Rusinga					
KNM-RU 952	r	18.1	16.2		
Bunolistriodon aff. latidens					
Quinta da Raposa					
ML 5547	..	29.8	35.6		
C. do Covão					
ML —	..	30.0	33.5		
Quinta Grande					
ML 5544	..	26.1	28.2		
Olival da Suzana					
CEPUNL 25	1	26.7	31.7	65	90
CEPUNL 26	r	21.6	26.5	65	70
C. da Conceição					
ML 5549	r	28.0	33.0		
Quinta da Farinheira					
CEPUNL —	r	24.6	30.5		
La Artesilla					
MPZ 6427	1	20.5	22.0		
Bunolistriodon latidens					
Veltheim					
NSSW 113	1	31.5	34.7	70	80
Bunolistriodon M					
Paşalar					
PDTFAU G114	r	30.7	36.6		
PDTFAU G987	1	32.2	40.4		
Çandir					
PIMUZ CA V/21	r	49.3	40.6	120-130	165
Bunolistriodon lockharti					
Chevilly					
MNHNP CHE 31	1	—	29.1	30	±50
MNHNP CHE 32	r	31.6	26.6	25	50
MNHNP CHE 68	r	27.2	27.9	25	50
Chevilly?					
MSNO 231	r	24.0	26.5	35	50
La Romieu					
UCBL 320281	r	26.1	26.3		
UCBL 320303	r	25.0	22.1		
UCBL 320303	r	≥23.3	≥28.0		
Pellechaus					
NMB GB 1381	1	24.8	26.8	80	60
Baigneaux					
NMB SO-3022	r	25.9	27.2	50	60
Buñol					
IVAU —	r	26.1	31.0		
MPV FBB-217	r	>25.2	>18.9		
IPS 1148	1	31.4	30.6		
—	1	32.5	29.8		
MPV FB 52	1	30.7	29.8		
MPV FB 53	1	—	28.2		
Langenau 1					
SMNS 41228	1	..	..		
Pontlevoy					
MNHNP FP 224	?	—	—		
MNHNP FP 225	1	29.2	32.0		
MNHNP FP 739	r	30.7	31.7	40	60
MNHNP FP 1155	1	—	≥30.1		
MNHNP FP 1156	r	—	≥32.4		
Ravensburg					
NMB TD 545	r	28.2	32.4	35-50	60-70
HLD TD 546 cast	1	>24.5	30.5	70	90
Tavers					
COBO —	r	25.9	29.1	50	60
Listriodon pentapotamiae					
Chinji 26					
GSP 431	r	18.4	24.6		
Chinji 40					
GSP 860	..	—	—		
Chinji 54					
GSP 979	1	21.3	20.4		
Chinji 83					
GSP 2022	1	19.6	21.9		
Kanatti Chak 8					
BSPHGM 1956II82	r	22.5	18.5		
Chari Gambhir					
BSPHGM 1956II80	r	—	23.5		
Bhurriwala					
BSPHGM 1956II84	r	19.8	22.8		
Kanatti Chak 7					
BSPHGM 1956II79	1	19.7	19.9	15	30
Kagdawala					
BSPHGM 1956II83	r	22.5	≥19.3		
BSPHGM 1956II85	1	—	>22.0		
Kalinal					
BSPHGM 1956II81	1	17.9	19.6		
Kadirpur					
BSPHGM 1956II78	1	24.8	24.6		
IVAU CHD 26	1	—	—		
Chinji					
IM B 549	1	24.5	23.5		
HGSP 8218					
HGSP 8218/....	..	26.3	26.9	30	60
HGSP 8415					
HGSP 8415/3269	r	—	—		
HGSP 8427					
HGSP 8427/3632	1	30.0	31.5	20	40
HGSP 8427/3692	r	24.9	26.6	40	70
Listriodon splendens					
Sansan					
MNHNP Sa 4317	..	21.0	28.5		
Klein Hadersdorf (Mattner)					
IPUW 18 IX 15	1	26.8	27.7	25	40
IPUW 18 IX 15	1	24.2	25.9	18	40
Simorre					
MNHNP Si 157	1	25.7	25.3	35	55
MNHNP Si 158	1	≥17.4	≥22.3		
MNHNP Si 159	1	—	29.5	45	80
MNHNP Si 160	r	—	29.4	35	—
Eichkogel					
NMW SK 1614	1	37.2	42.6	85	100
NMW SK 1614	r	38.1	43.5	80	100
Çandir					
MTA CA 1/2	r	28.2	24.2	28	55
MTA AÇH 989	..	—	—		
Inönü I					
MTA AKI-3/325	r	32.6	41.1	30-35	80
MTA AKI-3/327	r	31.9	36.0		
MTA AKI-3/332	r	27.7	34.0		
MTA AKI-3/588	1	31.2	28.5	40	55
MTA AKI-3/772	r	—	—		
Manchones I					
IPS 1101	1	24.4	22.0		
Manchones II					
IVAU MA II —	r	..	..		
Arroyo del Val IV					
IVAU AR IV 57	1	—	26.1	25	—
IVAU AR IV 60	1	26.2	30.3	50	65
IVAU AR IV 63	1	..	..	15	>40
IVAU AR IV 64	r	30.5	32.3	25	50
IVAU AR IV 77	1	—	32.4	20	—
IVAU AR IV 119	1	—	—		
IVAU AR IV 120	1	—	—		
IVAU AR IV 398	r	30.4	27.4		
RGM 262.972	r	30.0	32.7	25	55
RGM 263.016	r	>21.0	>24.2		
RGM 263.162	1	31.0	31.3	35	60
MPZ AV-21	1	29.7	33.2		

MPZ AV-35	1	—	32.9		
Steinheim					
SMNS 20222	r	—	—		
Jablonica					
HGSB Ob-868	.	—	37.3		
Mauer					
NMW SK 1776	1	35.7	37.9	55	—
Bonnefont					
MNHNP HGP 46	1	43.3	41.3	70-80	120
MNHNP HGP 64	1	—	—	—	—
La Grive oc					
UCBL —	1	26.7	30.5		
MGL LGr 716	1	42.6	40.7	70	100
MGL LGr 717	1	32.5	36.6	40	65
MGL LGr 728	1	38.7	37.4	130	..
MGL LGr 729	1	—	—		
MGL LGr 730	?	—	—		
MGL LGr 1660	r	34.0	33.1	50	85
La Chaux-de-Fonds					
MHNCF 14	r	41.9	44.3	70	80
MHNCF 45	r	42.3	43.2	90?	100
MHNCF 48	1	24.2	26.3	25	45
MHNCF —	r	—	42.5		
MHNCF — 21 fragments			—	—	
Locle					
UN —	r	38.8	36.9	60	100
Lac Morat					
MHNCF —	r	≥41.1	—		
Massenhausen					
BSPHGM 1950I34b	r	≥35.9	36.9	60	—
BSPHGM 1951 I 3d	r	37.6	39.8	60	80
BSPHGM 1956I135	r	39.4	38.3	55	65
BSPHGM 1957I218	r	36.4	≥43.2	50	75
Wartenberg					
BSPHGM 1953I555	r	—	—		
BSPHGM 1957I194	1	24.4	27.0	25	55
BSPHGM 1958I34	r	25.4	28.9	45	70
Kleineisenach					
BSPHGM —	r	>31.5	—	50	—
Esselborn					
HLD Din 40	1	26.3	29.9	30	55
Wissberg					
HLD Din 39	r	—	25.4		
NMM 1930/375	1	37.4	32.0	40-70	70
Tri sur Brise					
MNHNP cast	1	35.7	34.4	100	130
Cerro del Otero					
MNCN NM 18004	r	29.3	28.5		
MNCN NM 18005	r	—	—		
MNCN NM 18009	1	39.2	38.6	75	110
Sant Quirze					
IPS 1674	..	54.0	44.0		
MGSCB 48578	1	37.9	39.9		
MGSCB 48579	1	>37.5	40.1	85	110
MGSCB 48580	1	45.7	47.2	140	80-120
MGSCB 48581	r	40.3	41.8	80-120	120-160
MGSCB 48582	r	41.0	32.0	70-140	90-130
ITGE 407M	1	tip			
Hostalets					
MGSCB 48511	1	49.7	45.8	..	±125
MGSCB 48512	1	41.4	45.7	50	85
MGSCB 48513	1	45.1	44.8	85	100
MGSCB 48514	r	37.9	38.1	65	105
MGSCB 48517 tip	r	>20.3	>19.6		
MGSCB 48518	r	tip			
IPS 1035	..	>46	..		
IPS 1041	..	>39.7	..		
IPS 1043	..	—	46.1		
"Leithagebirge"					
NMW 1862III14	r	37.5	41.3	70	90

c^f		DAP	DT	Hli	Hla
Nguruwe kijivium					
Songhor					
KNM-SO 9912	r	>8.0	5.9		
Bunolistriodon anchidens					
Rusinga					
Kathwanga					
KNM-RU 1911	r	±12.3	±9.1		
Bunolistriodon aff. latidens					
La Artesilla					
MPZ 6428	1	13.5	9.5		
MPZ 6429	1	12.9	9.2		
Munébrega I					
IVAU 55/1094	r	13.4	10.4		
Bunolistriodon M					
Paşalar					
PDTFAU D37	1	15.2	12.1	22.0	..
PDTFAU D37	1	±15.5	±12.0		
PDTFAU D1131	r	14.8	12.1	22.8	..
PDTFAU G319	r	14.2	10.2	14.6	..
Bunolistriodon lockharti					
Buñol					
MPV FBB-218	1	>14.0	10.0		
Bunolistriodon akatikubas					
Maboko					
KNM-MB 126	r	16.8	11.0		
Listriodon splendens					
Paşalar					
PIMUZ —	1	12.8	7.9		
Arroyo del Val IV					
IVAU AR IV 470	r	14.4	≥9.8		

DC^x		DAP	DT
Bunolistriodon lockharti			
Pellecahus			
?NMB GB 1395	r	6.0	3.3

p^1		DAP	DTa	DTp	Hla
Nguruwe kijivium					
Songhor					
KNM-SO 4975	r	>4.8	—	3.6	
KNM-SO 8289	1	6.1	3.8	3.8	>4.3
KNM-SO 9912	r	5.1	3.6	4.0	
Bunolistriodon anchidens					
Rusinga R1					
KNM-RU 5843	r	12.8	6.4	6.8	6.3
KNM-RU 5844	1	11.2	5.7	5.4	6.5
Bunolistriodon aff. latidens					
La Artesilla					
MPZ 6463	1	7.2	3.8	3.7	4.9
Listriodon splendens/Bunolistriodon M					
Paşalar					
PDTFAU G1746	1	11.5	6.6	7.9	6.2
Listriodon pentapotamiae					
Kadirpur					
BSPHGM 750-753	r	8.9	5.7	4.6	

p^2		DAP	DTa	DTp	Hla
Nguruwe kijivium					
Songhor					
KNM-SO 4978	r	10.6	4.8	6.6	8.8
Kubanochoerus marymunngui					
Buluk					
KNM-WS 12588	r	30.3	18.6	19.7	21.2
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	25.4	15.3	16.1	17.7
MNHNP Z 1961	1	>23.2	13.5	15.9	
MNHNP Z 1961	r	25.0	13.2	17.3	16.5
MNHNP Z 1961	1	23.6	13.1	16.0	18.5
MNHNP Z 1961	1	25.0	13.8	14.1	18.2
Kubanochoerus gigas					
Chinji Fm.					
bought spec.					
FISFSMF/PA/F6168	r	32.0	16.6	22.8	24.6
Bunolistriodon anchidens					
Rusinga AWI26					
KNM-RU 5870	r	>17.4	9.3	11.9	
Bunolistriodon aff. latidens					
La Artesilla					
MPZ 6462	r	15.8	10.0	11.3	10.3
MPZ 6464	1	15.3	8.8	—	
Bunolistriodon M					
Paşalar					
PDTFAU BT1	r	—	8.5	10.4	±8.4
PDTFAU C	r	13.6	7.6	—	
PDTFAU CT1	1	12.5	7.6	10.3	7.8
PDTFAU CT1	r	14.1	7.9	12.7	9.4
PDTFAU F514	r	10.7	6.2	9.1	7.2
PDTFAU G613	1	10.8	6.3	8.9	7.1
PDTFAU G1063.1	r	11.7	6.9	≥9.8	7.0
PDTFAU G1200	r	13.7	7.9	11.7	9.2
Bunolistriodon lockharti					
Pellecahus					
NMB GB 1380	r	17.1	10.2	12.3	
La Romieu					
UCBL 320269	1	16.5	9.4	12.5	
Baigneaux					
NMB SO-5992	1	16.5	10.7	13.8	
Langenenschlingen					
NMB TD 821 cast	r	18.4	11.3	14.1	
NMB TD 824 cast	1	17.2	≥11.1	≥13.9	
Bunolistriodon akatikubas					
Mbagathi					
KNM-MG 41	1	15.9	10.4	≥12.0	12.1

Listriodon pentapotamiae					
Dhulian 302					
GSP 10018	l	>12.2	7.9	10.3	
Mochi Wala					
IVAU CHO 95	l	13.5	8.6	10.9	11.1
Marianwala Kas					
BSPHGM 1674	r	16.9	9.2	11.5	
Kanatti Chak 8					
BSPHGM 1956II120	r	12.9	7.6	10.4	
Chinji Fm.					
bought spec.					
IVAU CH-45	r	12.7	7.6	9.4	8.8
Listriodon splendens					
Paşalar					
PDTFAU A133	r	16.3	8.7	10.6	11.3
PDTFAU C284	r	13.5	7.4	9.6	10.2
PDTFAU CT193	l	—	8.8	11.6	
PDTFAU CT1	l	15.0	9.6	11.4	10.9
PDTFAU CT1	l	—	8.5	11.3	
PDTFAU CT1	l	—	8.9	11.3	
PDTFAU CT1	r	—	7.9	—	
PDTFAU CT1	l	13.9	9.0	—	
PDTFAU D995	r	13.3	8.3	11.5	10.6
PDTFAU E392	r	14.7	8.7	10.6	10.4
PDTFAU ET1	l	≥14.1	9.5	11.0	
PDTFAU ET1	r	—	9.1	9.7	
PDTFAU ET1	l	13.5	8.1	11.5	
PDTFAU F392	l	—	—	11.7	
PDTFAU G1740	r	16.1	9.5	11.6	
PDTFAU G1741.2	r	15.4	9.3	11.0	
PDTFAU G1955	l	—	8.0	11.4	
PDTFAU G2065	l	13.7	9.5	11.5	
PIMUZ BP-217 cast	l	≥17.3	8.6	9.6	
Manchones I					
IVAU MA I —	l	—	8.9	>9.4	
Arroyo del Val IV					
IVAU AR IV 33	r	16.8	10.2	14.4	
IVAU AR IV 41	l	15.9	10.0	14.2	
La Grive oc					
UCBL 65620	l	15.6	..	13.3	
MGL LGr 722	l	13.2	7.8	10.2	
MGL LGr 1608	l	17.4	8.6	13.2	
MGL —	r	13.0	7.8	10.5	8.1
La Chaux-de-Fonds					
MHNCF 4	l	15.1	8.8	12.6	9.8
Neudorf Sandberg					
NMW 1945/75	l	>12.8	8.9	11.3	
Lower Sinap					
MTA —	l	15.3	9.3	13.3	
Cerro del Otero					
MNCN NM 18023	r	>15.3	10.0	13.9	
Sant Quirze					
CJFV SQu 5435	l	15.8	9.8	12.7	
Hostalets					
IPS 1092	r	16.0	..	14.5	±10.0
IPS 1093	l	16.0	..	≥13.1	10.8
IPS 1094	l	14.6	..	14.0	
IPS 1109	r	14.5	..	13.5	>9.3
IPS —	l	17.0	..	14.3	
CJFV —	l	14.5	..	14.6	

D^2		DAP	DTa	DTp	HIa
Nguruwe kijivium					
Songhor					
KNM-SO 5408	l	7.5	3.4	3.8	
Kirimon					
KNM-KI 18065	r	8.6	3.2	3.6	
Kubanochoerus marymunngui					
Baragoi					
KNM-BG 17868	l	—	—	13.2	
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	l	21.0	9.0	10.6	11.0
Kubanochoerus gigas					
Kundal Nali					
IVAU CHK 120	l	—	—	13.6	
Bunolistriodon anchidens					
Rusinga R1					
KNM-RU 9785	r	≥15.0	7.5	8.0	8.7
Bunolistriodon aff. *latidens*					
La Artesilla					
MPZ 6446	l	12.9	6.6	7.9	8.0
Bunolistriodon M					
Paşalar					
PDTFAU DT1	r	10.4	5.1	5.3	
PDTFAU ET1	r	—	5.2	6.1	
PDTFAU F450	l	≥ 12.0	5.8	7.3	
PDTFAU G687	l	>10.3	5.2	6.2	
Bunolistriodon lockharti					
Pellecahus					
UCBL 320293	r	12.5	5.8	6.3	
Listriodon splendens					
Paşalar					
PDTFAU D450	l	>13.3	6.9	9.0	
PDTFAU E89.21	r	11.8	5.9	6.8	6.9
PDTFAU E89.22	l	—	6.5	—	
PDTFAU F361	l	13.4	6.6	7.5	
PDTFAU F450.1	r	13.5	6.5	8.2	7.6
PDTFAU G16	l	>13.0	7.7	9.4	
PDTFAU G181	r	11.6	6.1	7.2	6.4
PDTFAU G185	r	12.5	6.1	7.6	>6.6
PDTFAU G195.1	l	—	6.4	7.6	
PDTFAU G637	l	—	6.9	7.2	
PDTFAU G1067	l	>13.7	6.8	7.6	7.8
PDTFAU G1770.5	r	14.0	5.8	8.2	
Arroyo del Val IV					
IVAU AR IV 14	l	—	—	8.1	
IVAU AR IV 364	r	12.8	6.7	8.4	
Castell de Barberà					
IPS —	l	>11.4	5.3	6.9	
Hostalets					
CJFV —	l	14.4	7.0	9.4	7.8
CJFV —	r	14.0	7.0	≤10.2	

P^3		DAP	DTa	DTp	HIa
Lopholistriodon akatidogus					
Beni Mellal					
KNM-ZP 1398 cast	l	12.5	7.2	10.6	
Lopholistriodon kidogosana					
Ngorora					
KNM-BN 1475	r	9.2	5.7	>9.1	
KNM-BN 12892	l	9.4	6.7	9.6	
Ngorora B					
KNM-BN 1712	l	9.3	5.8	9.1	
Kubanochoerus marymunngui					
Buluk					
KNM-WS 12656	l	—	19.5	—	
Kubanochoerus massai					
Gebel Zelten					
MNHNP Z 1961	r	26.2	15.6	≥18.5	22.0
MNHNP Z 1961	l	25.0	16.9	19.5	21.6
MNHNP Z 1961	l	—	—	—	—
Bunolistriodon anchidens					
Rusinga-Gumba					
KNM-RU 977	r	18.9	10.9	13.4	15.7
Rusinga					
KNM-RU 8303	l	18.3	11.2	13.8	16.3
Bunolistriodon aff. *latidens*					
La Artesilla					
MPZ 6455	l	>15.6	..	>12.1	
MPZ 6456	l	16.4	..	13.9	
MPZ 6458	l	16.8	10.8	13.9	
Armantes I					
IVAU 41/518	r	16.4	9.5	≥15.1	
IVAU 41/519	r	15.2	10.2	13.3	
Munébrega II					
IVAU 52/103	l	—	—	≥13.7	
Bunolistriodon latidens					
Inönü I					
MTA AKI-3/577	r	14.8	9.4	14.3	
Bunolistriodon M					
Paşalar					
PIMUZ BP-176	r	18.3	10.7	14.7	
PDTFAU CT1	r	15.9	9.4	14.1	11.6
PDTFAU CT1	r	16.4	9.7	14.1	11.6
PDTFAU E396	r	17.0	9.0	14.5	12.2
PDTFAU ET1	l	16.5	9.5	14.7	±12.3
PDTFAU ET1	l	15.1	8.8	13.3	
PDTFAU ET1	l	14.2	8.2	12.8	10.5
PDTFAU F80	l	17.2	10.0	14.0	11.6
PDTFAU F403	r	15.1	9.4	13.0	
PDTFAU F410.1	r	—	9.7	—	
PDTFAU F417	r	14.7	8.3	—	
PDTFAU F27823	l	—	—	13.1	
PDTFAU G90	l	16.7	9.1	>12.1	9.8
PDTFAU G312	r	15.6	8.6	12.0	
PDTFAU G1130	r	15.5	8.4	12.6	10.6
PDTFAU G1368	l	14.8	8.3	14.3	
Bunolistriodon lockharti					
Pellecahus					
NMB GB 2451	l	19.0	12.6	17.3	
NMB GB 1376	r	18.9	12.4	17.0	
NMB GB 1379	l	—	—	—	
La Romieu					
UCBL 320299	r	17.0	..	16.2	
Baigneaux					

NMB SO-6489	l	16.5	11.8	15.3	
NMB SO-6738	r	16.5	11.3	15.2	
NMB —	r	16.9	12.6	15.9	
Gerlenhofen					
SMNS 14953d	l	19.0	..	17.4	
FMNH cast	l	17.7	12.0	16.2	
Engelswies					
NMB TD 819 cast	r	17.0	11.2	15.1	
Pontlevoy					
MNHNP FP 1034	r	18.2	11.9	16.8	15.4
Tavers					
COBO —	l	17.8	12.3	17.6	
Ravensburg					
NMB TD 1074	r	>17.2	12.2	15.0	
Listriodon pentapotamiae					
Dhok Talian 189					
GSP 4415	r	16.1	10.1	13.4	
GSP 4429	l	16.9	9.6	12.7	12.4
Cheskewala					
BSPHGM 1956II117	r	16.1	10.7	13.2	
Burriwala					
IVAU CHB 65	l	17.1	—	—	11.7
Bhurriwala					
BSPHGM 1956I174	r	15.4	9.8	14.3	
BSPHGM 2627	r	>17.6	11.3	—	
Bhurriwala 2					
BSPHGM 1956II118	r	15.9	10.2	14.3	
BSPHGM 235	r	15.7	10.9	15.7	
Marianwala Kas					
BSPHGM 1956I173	r	≥13.7	8.6	13.0	
Sosianwali					
BSPHGM 1956II119	l	15.8	10.7	15.8	
Kundal Nala 1					
BSPHGM 412	l	13.0	9.4	12.1	
Listriodon splendens					
Simorre					
MNHNP Si 163	l	17.6	11.3	15.1	
Inönü I					
MTA AKI 3/454	r	17.1	10.9	16.7	
Paşalar					
PDTFAU BT1	r	17.9	11.6	17.7	15.1
PDTFAU BT1	r	15.5	10.2	14.6	12.2
PDTFAU BT1	l	16.4	10.3	15.1	
PDTFAU CT1	l	16.5	10.0	14.0	11.8
PDTFAU CT1	l	15.9	10.4	13.4	
PDTFAU CT1	r	16.0	10.4	13.4	
PDTFAU CT1	r	—	9.8	15.0	
PDTFAU D601	l	17.5	11.5	15.1	13.9
PDTFAU D680	r	14.9	10.9	12.6	
PDTFAU E122	l	15.7	11.7	15.5	
PDTFAU E767	r	17.2	11.6	>15.9	
PDTFAU ET1	r	15.0	10.3	13.9	12.3
PDTFAU ET1	l	17.1	10.2	16.0	14.6
PDTFAU ET1	r	14.6	9.5	12.3	
PDTFAU ET1	r	15.9	10.9	14.7	13.1
PDTFAU F507	l	17.1	12.7	17.4	
PDTFAU G147	r	—	—	—	
PDTFAU G438.6	l	17.0	10.9	14.6	
PDTFAU G448	r	16.5	11.5	15.1	
PDTFAU G929	r	16.3	10.3	14.6	12.2
PDTFAU G959	l	>15.2	>10.7	>12.4	
PDTFAU G1666	r	16.3	11.5	15.9	14.8
PDTFAU G1689.1	l	17.8	12.1	15.9	
PDTFAU G1689.3	l	15.7	9.2	14.1	
PDTFAU G1741.2	r	—	—	14.1	
PDTFAU G1748.7	r	16.2	—	—	
PDTFAU G1924.1	r	17.4	11.7	16.8	
PDTFAU G1924.2	r	16.1	11.4	15.4	
PDTFAU G6601	r	16.0	9.7	15.2	
PDTFAU —	l	15.9	10.1	14.9	12.1
PIMUZ BP156 cast	r	16.4	10.1	13.7	
PIMUZ BP388 cast	r	16.0	10.3	14.3	
Çandir					
MTA AÇH 594	l	16.5	10.9	14.7	
MTA UÇHÜ 749	l	18.8	11.9	16.7	
Manchones I					
IVAU MA 114	l	17.1	11.1	15.0	
IVAU MA 116	l	16.9	10.3	—	
Arroyo del Val IV					
IVAU AR IV 29	r	20.3	12.0	19.1	
IVAU AR IV 32	r	17.5	11.1	16.1	
IVAU AR IV 37	r	21.0	11.7	19.5	
IVAU AR IV 38	r	19.6	11.7	19.1	
IVAU AR IV 59	l	18.4	11.6	18.3	
IVAU AR IV 69	r	≥15.9	—	13.7	
IVAU AR IV 124	r	≥17.0	—	>14.6	
IVAU AR IV 126	r	16.2	10.1	—	
IVAU AR IV 485	..	—	—	—	
IVAU AR IV 485	l	—	—	—	
IVAU AR IV 485	l	—	—	—	
IPS AR IV 28	l	20.4	..	19.3	
IPS AR IV 31	l	16.6	..	16.5	
Sariçay					
MTA —	r	18.2	11.8	15.9	
Lower Sinap					
MTA —	l	17.9	10.7	16.8	
Torril					
CCL —	l	>16.4	..	>15.0	
La Grive oc					
IGF 296	l	15.5	..	14.9	
IGF 296	r	15.1	..	14.6	
UCBL 65620	l	16.1	..	15.2	
UCBL 65620	r	17.0	..	16.0	
MGL LGr 746	r	19.3	10.8	17.8	
MGL LGr 1609	l	16.0	9.1	16.2	
Neudorf Sandberg					
NMW 1909/14	r	18.0	11.8	15.9	
Sant Quirze					
MGSCB 48845	r	17.9	10.3	17.2	
MGSCB 48925	r	17.2	11.6	17.1	
MGSCB 48927	r	—	—	—	
MGSCB 48928	l	—	—	±18.2	
MGSCB —	l	17.2	9.9	>15.3	
CJFV SQu 5436	r	18.2	11.4	17.4	
St. Gaudens?					
MNHNP —	l	16.0	11.7	15.3	
Hostalets					
MGSCB 48491	r	>15.7	10.0	15.7	
IPS 1089	r	15.6	..	16.2	
IPS 1090	l	15.7	..	16.0	
IPS 1095	r	18.0	..	17.5	16.3
IPS H 215	r	16.5	..	16.5	
IPS —	l	17.9	..	18.1	
CJFV 4331	l	16.7	10.7	16.7	
CJFV —	l	16.4	..	16.6	
CJFV —	r	20.2	13.4	18.4	
Wartenberg					
BSPHGM 1953I388	r	17.1	10.5	16.0	

D^3		DAP	DTa	DTp
Nguruwe kijivium				
Songhor				
KNM-SO 1120	r	—	5.1	7.1
Bunolistriodon M				
Paşalar				
PDTFAU D210.14	l	—	—	11.3
PDTFAU G249	l	16.1	8.0	11.9
PDTFAU G758	l	15.8	6.7	11.1
Listriodon pentapotamiae				
Kali Nachi				
IVAU CN 44	l	15.3	7.9	11.9
Listriodon splendens				
Paşalar				
PDTFAU C280.26	l	16.5	9.0	12.8
PDTFAU C280.28	r	—	—	13.0
PDTFAU C280.37	r	14.9	8.9	12.1
PDTFAU D210.15	r	—	—	12.2
PDTFAU E89.20	r	—	—	12.8
PDTFAU E217	r	16.2	8.4	12.5
PDTFAU E653	r	16.4	8.7	13.7
PDTFAU G621.3	l	—	—	13.0
PDTFAU —	l	—	8.6	13.1
PDTFAU —	r	—	8.1	—
PIMUZ BP-343	r	15.7	8.3	12.3
La Grive oc				
MGL LGr 1619	l	15.9	8.5	11.9
MGL LGr 1621	l	16.1	8.8	12.5
IPS —	l	16.0	8.9	12.9
IPS —	l	—	—	11.8
NMB GA 2825	l	—	—	>12.5
Sant Quirze				
CJFV —	r	—	9.3	—

P^4		DAP	DT	Hla
Nguruwe kijivium				
Rusinga (loc. ?)				
KNM-RU 3030	l	8.2	8.5	
Songhor				
KNM-SO 1131	r	7.8	9.7	
Lopholistriodon moruoroti				
Maboko				
KNM-MB 14485	l	6.6	7.3	
Lopholistriodon akatidogus				
Fort Ternan				
KNM-Ft 3320	l	13.1	13.6	>8.5
Lopholistriodon kidogosana				

Ngorora B, 2/56				
KNM-BN 1473	l	9.0	9.6	5.6
KNM-BN 1474	r	9.9	10.5	
KNM-BN 1708	r	9.3	9.7	
KNM-BN 1710	r	9.0	9.3	
Kubanochoerus massai				
Gebel Zelten				
MNHNP Z 1961	l	20.4	23.6	20.2
MNHNP Z 1961	r	20.0	22.3	
MNHNP Z 1961	r	19.8	22.3	
MNHNP Z 1961	l	≥19.6	—	
MNHNP Z 1961	r	21.6	23.4	19.7
MNHNP Z 1961	l	21.4	23.6	
MNHNP Z 1961	l	≥19.6	—	
Kubanochoerus minheensis				
Guanghe				
BMNH	r	21.7	23.3	
Bunolistriodon? sp.				
Baragoi BGX				
KNM-BG 15893	l	—	13.8	
Bunolistriodon aff. latidens				
Olival da Suzana				
CEPUNL 24	l	14.2	17.2	
Quinta Flamengas				
CEPUNL 40	l	12.5	16.2	
Quinta Pedreiras				
CEPUNL 58	l	14.9	18.0	
Quinta da Conceição				
CEPUNL 53	l	14.0	15.7	
Quinta da Farinheira				
CEPUNL —	l	13.8	14.7	
La Artesilla				
MPZ 6460	l	12.5	15.3	
Armantes I				
IVAU 41/529	r	12.9	14.6	
Munébrega II				
IVAU 52/101	l	13.3	14.8	
Torralba II				
IVAU 18/201	l	13.2	14.8	
Bunolistriodon latidens				
Inönü I				
MTA AKI-3/576	r	13.2	15.1	
Bunolistriodon M				
Paşalar				
PIMUZ BP-166	l	14.3	16.1	
PDTFAU C1587	l	12.5	13.7	
PDTFAU C1784	l	13.7	14.8	
PDTFAU CT 5	l	12.4	14.4	
PDTFAU CT1	l	13.5	14.9	
PDTFAU CT1	r	13.7	14.1	
PDTFAU CT1	r	13.9	14.7	
?PDTFAU CT1	r	15.3	16.7	
?PDTFAU CT1	l	16.1	—	
PDTFAU D111a	l	13.2	>13.8	
PDTFAU D210	r	14.3	15.1	
PDTFAU ET1	l	≥12.5	14.6	
PDTFAU ET1	r	14.2	14.9	
PDTFAU ET1	r	14.2	—	
?PDTFAU F182	r	14.9	15.4	
PDTFAU F226	r	12.5	13.9	
PDTFAU F278.12	r	13.5	15.9	
PDTFAU G104.2	r	13.3	14.9	
PDTFAU G142	r	13.3	14.3	
PDTFAU G692	l	—	—	
?PDTFAU G995	l	14.8	15.4	
PDTFAU G1924.3	l	14.2	—	
PDTFAU G1943	l	13.1	14.8	
PDTFAU GT1 1	l	13.2	15.2	
Bunolistriodon lockharti				
Pellecahus				
UCBL 320269	r	13.5	16.1	
La Romieu				
UCBL 320273	r	13.7	15.5	
UCBL 320273	l	13.9	15.9	
Baigneaux				
NMB SO-3021	r	15.7	17.9	
SO-6428	r	15.2	16.9	
Buñol				
IPS? R-BS6	l	14.5	16.8	
MPV FBB-223	r	15.1	17.3	
Gerlenhofen				
SMNS — cast	l	17.7	19.3	
SMNS — cast	l	14.9	17.4	
Engelswies				
NMB TD 819 cast	l	14.5	17.0	
NMB TD 819 cast	r	15.1	17.6	
Tavers				
CTMO —	l	15.6	16.8	

Bunolistriodon intermedius				
Gujia Zhuang				
IVPP V 9524	r	15.4	18.1	
Bunolistriodon akatikubas				
Mbagathi				
KNM-MG 5	r	16.9	18.3	13.8
Listriodon pentapotamiae				
N Maliar Dhok				
IM B 699	l	12.9	15.3	10.1
Kanatti				
IVAU KA 82	l	14.5	17.2	
Achora				
IVAU CHA-62	l	11.4	14.9	
FISF CHA F6113	r	13.1	15.6	
Chari Gambhir				
BSPHGM 1376	l	15.3	—	
Mochiwala				
BSPHGM 1360	r	15.8	>18.7	
Kanatti Chak 5				
BSPHGM 1956II115	l	≥15.6	>16.2	
Kanatti Chak 8				
BSPHGM 1956II113	r	12.1	13.9	
BSPHGM 1956II114	l	11.7	14.3	
BSPHGM 1956II116	r	15.4	17.0	
Marianwala Kas				
BSPHGM 1956II77	l	14.8	17.9	
BSPHGM 1956II110	r	11.7	14.3	
BSPHGM 2633	r	±13.8	—	
Kalin Nal				
BSPHGM 1956II112	l	12.9	14.9	
Bhilomar				
IVAU CHH 37	r	12.2	13.2	10.1
Marian Wala				
IVAU CHM 26	r	13.7	—	10.2
Listriodon splendens				
"Gers"				
MNHNP Ger 47	r	15.9	17.9	13.5
Inönü I				
MTA AKI 3/452	l	15.5	17.9	
MTA AKI 3/—	l	—	≥17.7	
Paşalar				
PDTFAU B593	l	14.2	16.8	
PDTFAU BT1	r	13.8	16.4	
PDTFAU C323	l	14.9	17.3	
PDTFAU CT1	l	15.2	16.4	
PDTFAU CT1	l	15.8	18.1	
PDTFAU CT1	l	>15.8	—	
PDTFAU CT1	l	13.7	17.0	
PDTFAU CT1	r	13.5	16.5	
PDTFAU CT1	l	13.7	15.7	
PDTFAU CT1	r	14.3	17.0	
PDTFAU CT5	r	14.3	16.4	
PDTFAU D500	l	15.8	17.9	
PDTFAU E209	r	16.0	16.8	
PDTFAU E225	l	15.4	16.6	
PDTFAU E439	l	15.7	17.0	
PDTFAU E636	l	—	—	
PDTFAU ET1	r	15.1	18.0	
PDTFAU ET1	r	14.7	17.0	
PDTFAU ET1	l	14.4	15.6	
PDTFAU ET1	r	14.7	17.1	
PDTFAU ET1	l	13.9	16.7	
PDTFAU ET1	r	15.4	16.3	
PDTFAU ET1	r	14.7	16.6	
PDTFAU ET1	r	15.3	17.1	
PDTFAU ET1	r	14.5	17.0	
PDTFAU ET1	l	13.8	16.2	
PDTFAU ET1	r	>13.7	—	
PDTFAU F51	l	14.7	16.7	
PDTFAU F77	r	14.2	15.9	
PDTFAU F282	r	14.5	16.2	
PDTFAU F283	r	15.5	16.7	
PDTFAU G231	l	14.2	16.9	
PDTFAU G438.3	r	≥13.4	—	
PDTFAU G438.9	l	15.5	16.6	
PDTFAU G1599.2	r	15.5	18.4	
PDTFAU G1669.2	l	14.0	16.1	
PDTFAU G1924.4	r	≥14.3	—	
PIMUZ BP—	l	14.6	18.2	
Çandir				
MTA AÇH 593	l	14.0	16.0	
MTA UÇHÜ 642	r	16.4	17.9	
MTA UÇHÜ 793	l	16.6	17.8	
Villafeliche IX				
MNCN —	r	≥16.0	>18.0	
Arroyo del Val IV				
IVAU AR IV 27	l	17.2	19.9	
IVAU AR IV 35	r	>14.9	20.6	

IVAU AR IV 39	l	17.9	19.7	
IVAU AR IV 362	r	—	>21.0	
RGM 262.979	r	±14	17.3	
Mannersdorf				
NMW 1850XXVI9	r	14.4	16.7	
Steinheim				
SMNS 4811	l	15.6	17.1	
La Grive oc				
IGF 296	l	13.6	15.6	
IGF 296	l	12.7	15.8	
IGF 296	r	14.6	15.7	
IGF 296	r	13.5	15.4	
UCBL 65615	r	15.4	16.6	
MGL LGr 688	l	12.8	15.1	
MGL LGr 1626	r	≥13.2	≥14.4	
MGL —	r	14.0	15.2	
La Chaux-de-Fonds				
MHNCF 4	l	15.8	16.7	13.6
Friedberg				
BSPHGM 1962XII32	r	>13.9	—	
Cerro del Otero				
MNCN NM 18021	l	14.5	18.6	
Sant Quirze				
MGSCB 30484	l	17.3	18.5	
CJFV SQu 5437	r	16.6	19.1	
Castell de Barberà				
IPS —	l	14.0	16.4	
Hostalets				
MGSCB 48502	r	15.1	17.7	
IPS 1088	r	15.0	16.9	
IPS 1115	r	15.8	16.9	
IPS H 218	l	15.0	17.3	
CJFV —	l	17.4	19.0	
CJFV IPS 1953	r	15.7	17.6	
CJFV HP 197	r	15.1	16.5	≥13.0

D^4		DAP	DTa	DTp
Nguruwe kijivium				
Songhor				
KNM-SO 1140	l	10.0	9.0	8.6
Lopholistriodon akatidogus				
Fort Ternan				
KNM-FT 3325	l	13.0	11.1	11.0
Kubanochoerus massai				
Gebel Zelten				
MNHNP Z 1961	r	23.6	19.3	19.9
MNHNP Z 1961	r	—	—	18.7
Bunolistriodon aff. latidens				
La Artesilla				
MPZ 6447	r	16.0	12.7	12.6
MPZ 6448	l	14.7	13.9	13.2
MPZ 6449	r	>16.3	—	13.3
Armantes I				
IVAU 41/544	l	15.3	13.4	13.3
Bunolistriodon M				
Paşalar				
PDTFAU B592.3	r	—	—	13.8
PDTFAU B881	l	14.8	13.3	13.8
PDTFAU C187	r	—	—	13.9
PDTFAU C280.19	r	—	—	14.1
PDTFAU C280.21	r	—	—	14.0
PDTFAU C280.70	l	—	—	14.1
PDTFAU D210.12	l	16.7	13.7	13.5
PDTFAU E543	l	15.7	14.4	15.0
PDTFAU F278.14	l	—	—	—
PDTFAU G537	l	—	—	—
Bunolistriodon lockharti				
Pellecahus				
NMB GB 1378	r	17.9	15.7	15.1
La Romieu				
UCBL 320311	r	16.3	15.7	15.1
Buñol				
IVAU US 1	l	17.4	14.7	14.6
Bunolistriodon akatikubas				
Maboko				
KNM-MB 14421	l	>16.3	—	—
Bunolistriodon guptai				
HGSP 8311				
HGSP 8311/1526	l	16.7	13.7	14.1
Listriodon pentapotamiae				
Kali Nachi				
IVAU CHN 36	r	—	13.8	—
Listriodon splendens				
Paşalar				
PDTFAU B593	l	15.2	14.2	14.1
PDTFAU C280.23	l	15.4	14.1	13.8
PDTFAU C280.24	r	—	—	—
PDTFAU C280.25	l	—	—	>13.6
PDTFAU D210.18	l	16.4	14.7	14.2
PDTFAU E19.18	l	—	—	>14.9
PDTFAU E89.15	l	16.2	14.7	14.8
PDTFAU E89.16	l	—	—	13.3
PDTFAU E89.17	l	—	—	13.8
PDTFAU E89.19	r	—	—	—
PDTFAU F353	r	15.3	14.1	14.0
PDTFAU G280.23	l	15.4	14.1	13.8
PDTFAU G280.25	l	—	—	>13.6
PDTFAU G363	l	16.2	14.2	14.5
PDTFAU G652.b	l	14.4	13.9	13.4
PDTFAU G1597	l	—	—	≥13.9
Arroyo del Val IV				
IVAU AR IV 72	r	15.8	16.0	16.1
La Grive oc				
UCBL 65617	l	>14.9	15.6	..
UCBL 65617	l	16.1	16.9	..
Castell de Barberà				
IPS —	l	14.9	13.7	13.0
Hostalets				
IPS VP 762	l	16.0	≥15.6	≥14.1
Can Llobateres				
IPS —	r	14.3	6.9	8.9

M^1		DAP	DTa	DTp	Ha	Hp
Nguruwe kijivium						
Songhor						
KNM-SO 1057	r	11.8	10.6	10.6		
KNM-SO 1125	l	12.9	13.6	11.9		
Lopholistriodon moruoroti						
Maboko						
KNM-MB 617	l	8.6	8.6	8.9		
Lopholistriodon kidogosana						
Ngorora B5, 2/56						
KNM-BN 843	r	12.3	9.9	10.5		
KNM-BN 1707	l	—	—	10.7		
KNM-BM 1744	l	12.2	9.5	10.4		
KNM-BN 2085	r	12.5	9.8	10.5		
Ngorora D, 2/11						
KNM-BN 189	l	12.6	—	—		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	r	26.7	23.6	25.3		
MNHNP Z 1961	r	27.2	24.6	—		
MNHNP Z 1961	l	25.4	22.6	25.6		
MNHNP Z 1961	l	—	—	23.6		
MNHNP Z 1961	l	25.9	24.3	27.3		
Bunolistriodon anchidens						
Rusinga R3						
KNM-RU 5851	r	—	—	—		
Bunolistriodon aff. latidens						
Quinta das Flamengas						
CEPUNL 39	l	18.4	17.8	18.5		
Casal das Chitas						
CEPUNL 47	r	18.4	18.2	18.1		
Quinta da Conceição						
CEPUNL 51	l	19.1	≥18.1	18.7		
La Artesilla						
MPZ 6465	r	18.1	17.7	17.5		
MPZ 6466	r	18.6	16.1	16.4		
Echzell						
HLD Ez 324	l	≥17.0	—	>15.2		
Tarazona						
UPV T56.10	r	—	>14.0	—		
Armantes I						
IVAU 41/515	l	17.3	16.2	16.3		
IVAU 41/532	l	17.4	15.8	15.9		
IVAU 41/576	..	—	—	≥17.9		
Bunolistriodon M						
Paşalar						
PIMUZ BP-271 cast	r		17.3	15.2	14.5	
PDTFAU C587	l	—	16.4	—		
PDTFAU CT 5	r	—	—	14.6		
PDTFAU E236	r	18.7	17.1	16.7		
PDTFAU D273	r	17.8	—	—		
PDTFAU E410	l	18.6	17.1	16.3		
PDTFAU E894	l	>18.3	—	—		
PDTFAU F278-4	r	17.7	—	—		
PDTFAU G86	l	18.5	16.9	17.2		
PDTFAU G538	l	—	—	15.5		
PDTFAU G1041-1	r	16.5	—	16.2		
PDTFAU G1311	l	17.8	15.5	15.5		
PDTFAU G1698	r	18.3	15.4	14.7		
Bunolistriodon lockharti						
Pellecahus						
NMB GB 1377	r	≥20.5	19.9	19.9		
NMB GB 2449	r	16.1	15.1	15.4		
La Romieu						

UCBL 320311	r	20.6	18.1	18.7		
Baigneaux						
NMB SO-716	1	19.3	18.4	19.0		
NMB SO-746	1	17.4	—	17.8		
NMB SO-1142	.	17.6	—	—		
NMB SO-1161	r	19.0	>17.6	>17.3		
NMB SO-2815	1	16.9	16.8	16.7		
NMB SO-6490	r	17.2	17.3	17.8		
Buñol						
MPV FB 55	r	>17.9	—	>16.5		
Engelswies						
NMB TD 818 cast	1	17.5	15.7	16.6		
NMB TD 819 cast	r	16.4	17.0	16.3		
Pontlevoy						
MNHNP FP 221	1	20.6	19.0	18.9		
Puente de Toledo						
ITGE 412M	r	16.9	15.8	15.1		
Bunolistriodon akatikubas						
Maboko						
KNM-MB 19707	1	18.7	17.6	18.0		
Bunolistriodon intermedius						
Maerzuizigou						
IVPP V 9522.1	1	21.6	19.7	19.9		
IVPP V 9522.2	r	20.7	19.5	—		
Listriodon pentapotamiae						
Achora						
IVAU CHA-59	1	19.3	—	—		
Kanatti						
IVAU KA 84	r	≥17.0	—	15.6		
Kanatti Chak 7						
BSPHGM 1956II67	r	16.2	15.5	15.6		
Listriodon splendens						
"Gers"						
MNHNP Ger 43	1	17.7	17.1	17.7		
Inönü I						
MTA AKI 3/—	r	—	18.2	—		
Paşalar						
PDTFAU A22.2	1	19.0	17.6	18.2		
PDTFAU A55	r	17.0	16.2	16.3		
PDTFAU B593	1	—	—	16.8		
PDTFAU C323	r	—	16.2	—		
PDTFAU CT1	r	18.9	18.0	17.2		
PDTFAU CT1	1	—	16.5	—		
PDTFAU CT1	r	16.8	15.0	15.3		
PDTFAU CT1	r	—	—	16.9		
PDTFAU CT5	1	16.4	16.7	16.7		
PDTFAU CT5	r	18.2	17.2	18.1		
PDTFAU D408	r	17.8	16.5	14.9		
PDTFAU D413	1	18.1	16.2	—		
PDTFAU D518	r	18.8	18.1	18.0		
PDTFAU D806	r	>18.5	—	—		
PDTFAU D992	r	18.9	17.4	17.2		
PDTFAU E83.4	1	17.9	16.8	16.5		
PDTFAU E89.3	1	18.9	17.3	17.6		
PDTFAU ET1	r	18.7	17.1	17.3		
PDTFAU F287.10	1	17.8	16.6	16.0		
PDTFAU F376	r	17.9	16.9	17.4		
PDTFAU F412	r	18.6	18.8	19.1		
PDTFAU F801	r	16.9	15.8	15.8		
PDTFAU G339	r	15.9	14.6	14.9		
PDTFAU G390	r	17.8	16.6	16.4		
PDTFAU G445	1	18.6	17.0	16.6		
PDTFAU G1598	r	17.8	>16.1	16.5		
PIMUZ BP-136	1	17.5	16.5	16.7		
Çandir						
MTA AÇH 970	r	—	—	≥19.6		
MTA —	r	19.6	18.4	19.3		
Manchones I						
IVAU MA 123	1	—	—	≥18.7		
Arroyo del Val IV						
IVAU AR IV 12	r	20.3	18.5	18.1		
IVAU AR IV 18	r	20.2	18.4	18.3		
IVAU AR IV 30	r	20.2	18.4	18.3		
IVAU AR IV 125	r	—	—	17.2		
IVAU AR IV 393	1	—	—	—		
RGM 263.098	r	20.2	..	18.1		
Sariçay						
MTA—	1	>18.4	≥18.4	19.0		
La Grive oc						
IGF 295	1	18.6	17.0	17.6		
IGF 295	1	18.6	17.0	17.9		
UCBL 65623	r	18.3	16.9	18.0		
NMB GA 2839	r	—	—	16.5		
NMB GA 7	1	18.1	18.0	17.0		
NMB GA 8	1	19.6	19.4	19.7		
MGL LGr 737	1	19.2	16.0	15.9		
MGL LGr 738	1	17.5	15.8	16.8		
MGL LGr 744	r	18.7	19.1	19.8		
MGL LGr 747	r	18.3	15.8	16.7		
MGL LGr 748	1	17.3	15.9	15.9		
MGL LGr 1614	r	16.8	16.7	17.6		
Neudorf Sandberg						
NMW 1954/75	1	—	—	18.7	—	12.7
Cerro del Otero						
MNCN NM 18013	r	20.6	19.3	19.2		
MNCN NM 18031	1	21.2	19.2	19.6		
MNCN NM 18032	1	21.2	19.0	20.1		
MNCN —	r	20.6	18.9	19.7		
Sant Quirze						
MGSCB 48893	r	17.7	16.3	16.6		
MGSCB 48881	1	19.5	19.1	18.6		
CJFV SQu 5516	1	17.0	19.0	18.2		
Castell de Barberà						
IPS —	1	18.0	15.9	16.4		
Hostalets						
IPS 1050	1	18.1	18.5	19.4		
CJFV IPS 1952	r	17.2	18.2	18.3		
CJFV 4328	1	19.7	—	—		

M^2		DAP	DTa	DTp	Ha	Hp
Nguruwe kijivium						
Koru 25						
KNM-KO 45	r	≥11.7	11.0	11.3		
Koru 25?						
KNM-KO 32	r	12.6	11.5	11.5		
Rusinga R3a						
KNM-RU 2272	1	13.1	13.1	13.2		
Songhor						
KNM-SO 1060	r	11.5	11.3	10.5		
KNM-SO 1125	1	12.9	13.6	11.9		
Lopholistriodon moruoroti						
Moruorot						
KNM-MO 8	r	10.4	>10.2	>9.6		
Maboko						
KNM-MB 10287	r	9.0	≥8.3	8.3		
KNM-MB 14489	1	9.3	≥8.1	8.4		
Maboko						
KNM-MB 15115	r	11.4	10.5	11.1		
Lopholistriodon akatidogus						
Mbagathi						
KNM-MG 10	r	19.4	>16.9	18.0		
Lopholistriodon kidogosana						
Ngorora						
KNM-BN 2027	1	13.0	11.2	11.0		
Ngorora B5, 2/1						
KNM-BN 1782	r	—	>13.4	—		
Ngorora B5, 2/56						
KNM-BN 844 + 845	r	14.3	12.1	12.0		
KNM-BN 1471	1	≥14.3	—	12.4		
Kubanochoerus khinzikebirus						
Mfwangano						
KNM-MW 13145	1	—	—	—		
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	1	29.4	27.8	27.2		
MNHNP Z 1961	1	29.7	27.3	26.4		
MNHNP Z 1961	1	30.2	29.5	28.1	18.7	19.2
MNHNP Z 1961	r	30.1	28.1	27.5		
MNHNP Z 1961	1	≥30.6	—	≥29.7		
Bunolistriodon anchidens						
Rusinga R1						
KNM-RU 2786	r	21.9	—	—		
Rusinga R 2-4						
KNM-RU 2784	..	≤21.3	—	≤20.5		
Rusinga Rs III						
KNM-RU 2783	1	20.6	—	22.2		
Bunolistriodon aff. latidens						
Quinta Grande						
CEPUNL 33	1	21.4	21.9	21.1		
Quinta Pedreiras						
CEPUNL 56	1	21.1	21.8	20.2		
CEPUNL 57	r	18.4	19.1	18.4		
Armantes I						
IVAU 41/520	r	20.1	21.6	19.2		
IVAU 41/521	1	21.0	21.3	20.3		
IVAU 41/522	r	21.2	—	19.7		
IVAU 41/523	..	>18.4	—	—		
IVAU 41/524	r	21.0	21.2	20.8		
Georgensgmünd						
NMB TD 661	r	19.8	18.9	19.9		
NMB TD 808 cast	r	20.1	19.0	20.0		
Bunolistriodon M						
Paşalar						
PDTFAU BT1 608	r	19.9	19.8	19.0		
PDTFAU C187.17	r	22.1	—	—		
PDTFAU C187.18	r	—	—	18.8		

PDTFAU C187.19	1	—	—	19.0			
PDTFAU C280.9	1	20.6	19.7	19.1			
PDTFAU D8.9	1	20.2	21.3	19.8			
PDTFAU D407	1	19.9	18.2	16.9			
PDTFAU E71	r	—	20.3	17.8			
PDTFAU E448	1	21.3	20.6	19.4			
PDTFAU E738	r	20.6	19.9	≥18.6			
PDTFAU E835	r	20.1	19.1	17.9			
PDTFAU F182	1	19.4	18.9	17.6			
PDTFAU G71	1	23.1	21.2	20.9			
PDTFAU G565	r	20.7	22.0	20.7			
PDTFAU G1041-2	r	18.8	—	18.3			
PDTFAU G1047	1	20.7	19.3	17.9			
PDTFAU G1649	1	19.5	—	18.8			
PDTFAU G1746	1	—	—	17.8			
Bunolistriodon lockharti							
Pellecahus							
NMB GB 1374	1	23.7	24.4	23.6			
NMB GB 1375	r	23.7	23.9	24.0			
UCBL 320289	r	22.0	21.2	20.6			
La Romieu							
UCBL 320305	r	23.5	23.5	23.7			
UCBL 320305	r	21.6	22.1	22.2			
Baigneaux							
NMB SO-759	1	21.7	21.3	21.6			
NMB SO-2188	1	20.8	21.0	21.2			
NMB SO-2495	r	22.1	21.8	22.0			
NMB SO-6592	1	22.2	22.3	22.5			
Chevilly							
MNHNP CHE 42	r	23.3	21.8	—			
NMB SO 4907	r	21.1	20.0	21.4			
Gerlenhofen							
SMNS 14953e	r	21.0	..	20.9			
FMNH cast	r	21.5	22.4	21.2			
FMNH cast	1	22.5	—	21.7			
Can Canals							
IPS 1184	1	±19.4	≥17.2	≥18.6			
Tavers							
COBO —	1	20.2	≥21.5	≥19.7			
CIMO —	r	21.4	22.0	21.9			
CIMO —	r	21.6	20.6	20.3			
Ravensburg							
NMB TD 1073	1	23.4	22.2	22.1			
Bunolistriodon akatikubas							
Mbagathi							
KNM-MG 4	r	23.2	≥23.3	≥23.4			
KNM-MG 9922	r	—	—	—			
Maboko							
KNM-MB 556	r	—	23.1	—			
Bunolistriodon guptai							
HGSP 8412							
HGSP 8412/3320	1	22.3	—	—			
Listriodon pentapotamiae							
Cheskewala							
BSPHGM 1956II108	r	17.3	17.0	17.5			
Mochiwala							
BSPHGM 1341	1	20.2	19.1	19.6			
Mochi Wala							
IVAU CHO 128	r	19.3	17.7	17.9			
HGSP 8125							
HGSP 8125/381	r	18.9	18.6	18.7			
Burriwala							
BSPHGM 1956II116	r	19.4	19.6	20.8			
Kanatti Chak 5							
BSPHGM 1956II118	1	19.0	18.6	18.4			
SSO Bhilomar							
BSPHGM 1956II117	1	20.3	18.4	18.6			
Bhilomar							
IVAU CHH 24	1	20.0	17.0	17.7	11.4	..	
Kundal Nali							
IVAU CHK 122	r	—	—	—			
HGSP 8415							
HGSP 8415/3202	r	20.5	19.0	19.1			
Chinji Fm. bought spec.							
IVAU CH-24	r	19.2	19.6	19.0			
Listriodon splendens							
"Environs de Simorre"							
UPM —	1	20.5	—	—			
"Gers"							
MNHNP Ger 40	r	20.7	21.0	21.4	12.6	12.7	
MNHNP Ger 41	r	20.7	20.3	21.0			
Paşalar							
PDTFAU A31	r	≥23.1	—	22.0			
PDTFAU B594	1	20.7	19.9	19.8			
PDTFAU C280.88	1	21.3	20.7	20.6			
PDTFAU CT1	1	19.6	20.4	20.0			
PDTFAU CT1	1	20.5	—	—			
PDTFAU CT1	r	—	19.6	—			
PDTFAU D1022	r	—	22.0	—			
PDTFAU D1106	1	21.5	22.4	21.1			
PDTFAU E89.6	1	—	20.5	—			
PDTFAU E90	r	20.5	19.6	>19.4			
PDTFAU E357	1	21.2	21.6	20.9			
PDTFAU ET1	r	21.1	20.7	19.9			
PDTFAU ET1	1	—	20.7	—			
PDTFAU ET1	r	—	—	19.9			
PDTFAU ET	r	—	>21.6	—			
PDTFAU F72	r	20.5	20.4	20.3			
PDTFAU F278.11	r	22.9	—	—			
PDTFAU F374	r	21.5	20.8	21.4			
PDTFAU G501	r	19.7	19.5	18.2			
PDTFAU F502	r	20.1	20.5	—			
PDTFAU F508	1	20.4	20.9	20.7			
PDTFAU G540	r	20.1	20.5	—			
PDTFAU G1691.3	r	..	..	19.0			
PDTFAU G1740	r	20.5	21.4	22.2			
PDTFAU G1746	1	18.9	—	≥18.8			
PIMUZ BP-272	r	22.8	22.9	21.7			
Eichkogel							
NMW SK 1614	1	21.8	—	—			
NMW SK 1614	r	22.2	23.2	22.3			
Çandir							
MTA CA I 44	r	23.2	21.6	22.8			
MTA —	r	24.1	22.5	23.4			
MTA AÇH-591	1	25.7	22.9	20.2			
Villefranche d'Astarac							
MNHNP VAS 15	r	19.9	20.4	19.5			
Arroyo del Val IV							
IVAU AR IV 9	1	22.5	>21.2	22.5			
IVAU AR IV 25	r	23.8	21.3	21.5			
IVAU AR IV 71	1	21.9	21.1	21.1			
IVAU AR IV 76	1	24.6	22.2	—			
IVAU AR IV 121	r	—	—	—			
RGM 263.151	1	23.2		23.1			
AV-32	r	22.1	—	21.9			
IVAU AR IV 485	1	—	—	>21.3			
IVAU AR IV 485	1	—	≥21.3	—			
Arroyo del Val VI							
IVAU AR VI 6	r	23.4	22.9	22.8			
IVAU AR VI 7	1	23.2	21.9	22.1			
Sariçay							
MTA —	1	21.6	22.4	≥22.8			
Steinheim							
SMNS —	r	≥19.5	..	22.4			
La Grive oc							
UCBL 65623	1	21.1	19.3	20.1			
UCBL 65623	r	19.4	18.7	19.4			
MGL LGr 714	1	22.9	—	—			
MGL LGr 734	r	21.4	22.6	21.9			
MGL LGr 743	r	21.7	21.3	21.2			
MGL LGr 745	r	—	21.0	≥21.0			
MGL LGr ...	1	21.0	21.0	20.7			
Cerro del Otero							
MNCN NM 18014	r	25.0	25.0	24.9			
MNCN —	1	21.4	25.3	25.1			
Sant Quirze							
IPS VP1016	..	23.0	..	23.4			
MGSCB 48891	1	24.1	±22.6	±22.4			
MGSCB 48892	r	24.1	23.8	23.8			
MGSCB 48926	1	21.5	18.8	19.8			
CJFV SQu 5433	1	22.7	23.4	22.5			
CJFV SQu 5446	r	±22.9	—	22.6			
Hostalets							
MGSCB 48508	r	21.4	20.5	20.4			
IPS 1051	r	23.2	22.9	≥22.8			
CJFV —	1	—	—	20.2			
CJFV —	r	—	20.7	—			
Wartenberg							
IVAU P25-1963	1	20.6	20.3	21.0			
BSPHGM —	1	21.4	20.2	20.1			
"Leithagebirge"							
NMW 1841XIII9	1	21.9	20.8	22.4			

M^3		DAP	DTa	DTp	DTpp	Ha	Hp
Nguruwe kijivium							
Legetet 14							
KNM-ZP 1373 (M14286)	1	15.9	13.4	12.2			
Rusinga R3							
KNM-RU 2771	1	15.5	13.3	12.0			
Songhor							
KNM-SO 1055	1	16.4	13.5	11.6	8.6	7.7	
KNM-SO 1056	1	14.0	12.1	10.8			
Mfwanganu							
KNM-MW 176	r	12.8	10.6	10.2	4.7		

HGSP 8412							
HGSP 8412/3133	r	—		—	10.0	..	
Lopholistriodon moruoroti							
Moruorot							
KNM-MO 6	r	>11.2	10.2	8.9	—		
Maboko							
KNM-MB 10320	r	>7.0	≥6.8	5.3	..		
KNM-MB 14481	r	12.8	—	8.7	..		
KNM-MB 15114	1	10.9	7.8	7.3	2.8		
Muryur							
KNM-MY 68	1	—	—	9.6	..		
Lopholistriodon pickfordi							
Maboko							
KNM-MB 406	1	13.6	—	10.2	4.2		
KNM-MB 611	r	14.4	≥12.7	11.2	..		
KNM-MB 14478	r	13.1	11.1	10.1	..	≥6.0	>7.4
Buluk							
KNM-WS 12582	1	15.0	11.2	10.4	4.5		
Lopholistriodon akatidogus							
Maboko							
KNM-MB 862	r	—	—	—	..		
Lopholistriodon kidogosana							
Ngorora B, 2/56							
KNM-BN 1470	1	17.3	13.4	±12.4	..		
KNM-BN 1472	r	17.1	—	11.9	3.9		
Ngorora D3, 2/11							
KNM-BN 385	1	17.3	14.4	12.3			
Ngorora							
KNM-BN 669	r?	—	—	—	..		
KNM-BN 2025	r	16.1	14.2	13.1	..		
Kubanochoerus marymunngui							
Buluk							
KNM-WS 12656	r	—	—	29.5	12.3		
KNM-WS 12590	1	36.2	30.0	27.1	14.2		
KNM_Ws 12594	r	42.6	32.9	26.9	16.4		
Kubanochoerus khinzikebirus							
Nyakach-							
KNM-NC 9806	r	—	—	—	—		
Kadianga W							
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	1	40.8	32.8	30.2	≥17.3	19.1	18.4
MNHNP Z 1961	1	41.9	—	—	17.5		
MNHNP Z 1961	r	—	>32.5	>29.4	—		
MNHNP Z 1961	r	—	—	27.7	—		
MNHNP Z 1961	r	>34.5	>28.3	>22.5	..		
MNHNP Z 1961	1	36.7	31.5	27.0	14.5		
MNHNP Z 1961	r	..	>26.7	>23.0	..		
MNHNP Z 1961	r	>36.4	28.8	24.4	..		
MNHNP Z 1961	r	36.8	—	23.2	11.7		
MNHNP Z 1961	r	32.3	>26.1	>23.1	—		
MNHNP Z 1961	r	+37.4	—	26.5	12.9		
MNHNP Z 1961	r	—	—	—	—		
MNHNP Z 1961	r	—	>29.4	—	—		
MNHNP Z 1961	r	—	±30.8	26.9	—		
MNHNP Z 1961	1	39.4	33.4	≥28.5	13.0	19.2	18.3
MNHNP Z 1961	r	>38.7	>31.0	28.9	12.9		
MNHNP Z 1961	r	—	—	27.9	16.2		
MNHNP Z 1961	1	>33.0	>26.9	>22.9	≥10.4		
MNHNP Z 1961	r	36.5	±29.6	27.3	13.6	17.8	17.4
MNHNP Z 1961	r	38.0	30.6	28.7	12.8	17.7	18.4
Bunolistriodon anchidens							
Rusinga R1							
KNM-RU 2786	1	—	—	—	—		
Maboko	?						
KNM-MB 867	r	—	—	17.2	—		
Bunolistriodon aff. latidens							
Olival da Suzana							
CEPUNL 18	r	26.8	22.3	20.9	..		
CEPUNL 19	1	24.3	22.4	18.9	..		
Quinta Flamengas							
CEPUNL 38	1	24.6	20.2	18.1	..		
Quinta da Raposa							
CEPUNL 37	1	24.4	24.5	20.0	..		
Quinta da Silvéria							
CEPUNL 43	r	24.7	21.8	17.6	±10.2		
Quinta Grande							
CEPUNL 30	1	25.3	21.6	18.9	9.0		
CEPUNL 938	1	29.3	24.6	19.3	12.4		
Quinta da Farinheira							
CEPUNL 7	r	27.1	≥22.8	20.6	..		
CEPUNL 8	1	25.1	22.1	18.6	..		
La Artesilla							
MPZ 6454	r	>21.2	18.8	15.0	..		
Armantes I							
IVAU 41/509	r	24.0	22.0	18.3	9.5		
IVAU 41/510	r	—	>21.7	19.1	—		
IVAU 41/511	r	25.8	—	19.0	11.5		
Munébrega II							
IVAU 52/100	r	27.1	22.4	17.3	9.7		
Munébrega AB							
IVAU Mun 4	r	≥23.0	≥19.8	≥15.3	≥7.6		
IVAU Mun 7	r	≥21.2	≥16.8	≥14.3	≥9.2		
IVAU Mun 34	r	—	—	≥18.6	11.1		
Bunolistriodon latidens							
Puente de Vallecas							
IPS 1065	1	26.5	21.7	19.3	..		
Inönü I							
MTA AKI-3/575	r	27.5	20.9	18.4	9.4		
Bunolistriodon M							
Paşalar							
PIMUZ BP-128	r	23.3	18.9	16.4	..		
PDTFAU C187.20	r	28.1	22.0	17.9	9.6		
PDTFAU D8.10	r	—	—	19.2	9.3		
PDTFAU D8.11	r	—	—	18.3	9.1		
PDTFAU D8.12	r	—	—	—	10.8		
PDTFAU D210.3	1	27.1	21.9	20.1	..		
PDTFAU D987	r	25.8	—	17.7	9.9		
PDTFAU E7.2	1	26.8	20.7	19.3	9.9		
PDTFAU E7.3	1	—	—	18.7	11.3		
PDTFAU E7.4	r	26.7	21.5	19.9	±10.0		
PDTFAU E89.8	1	25.3	19.6	18.4	9.3		
PDTFAU E91	r	26.8	21.3	18.8	8.8		
PDTFAU F504	r	26.9	22.2	18.5	9.1		
PDTFAU F381	r	—	—	19.2	14.1		
PDTFAU G561	r	25.2	19.8	17.7	8.5		
PDTFAU G652	r	—	19.1	18.1	—		
PDTFAU G1132	1	—	18.9	16.1	—		
PDTFAU G1193	r	—	22.1	19.1	—		
PDTFAU G1657	r	26.4	20.2	18.1	9.6		
PDTFAU G1801	1	26.1	20.4	19.2	9.5		
Çandir							
MTA —	r	>24.4	20.9	—	—		
Bunolistriodon sp.							
Ad Dabtiyah							
BMNH 42950	r	25.6	22.0	19.6	8.8		
Bunolistriodon lockharti							
Quinta la Barbacena							
CEPUNL 61	r	33.1	26.0	23.9	12.3		
CEPUNL 62	1	32.5	24.8	22.4	12.4		
Pellecahus							
UCBL 320271	1	28.5	25.8	21.7	11.8		
UCBL 320293	1	28.3	24.5	20.1	..		
NMB GB 1373	1	26.8	25.2	20.5	..		
NMB GB 2445	r	27.8	24.7	19.2	8.3		
NMB GB 2446	1	23.9	24.5	18.1	..		
NMB GB 2447	r	24.2	—	—	—		
La Romieu							
UCBL 320272	r	26.7	23.6	21.0	10.3		
UCBL 320305	r	26.6	23.4	19.8	10.5		
NMB GB 1262	r	23.5	19.8	16.5	..		
Baigneaux							
NMB SO-2189	r	24.7	21.4	18.6	11.2		
NMB SO-2612	r	24.5	22.0	19.1	8.5		
NMB SO-3228	1	22.3	21.8	19.0	..		
NMB SO-3611	1	>22.5	23.3	20.7	11.9		
Chevilly							
MNHNP CHE 47	r	28.6	24.8	21.6	10.4		
MSNO 233	r	27.6	23.0	21.3	8.7		
NMB SO 2	1	25.9	23.7	21.1	..		
Gerlenhofen							
SMNS 14953g	r	31.2	24.1	..	..		
FMNH cast	r	25.6	21.7	20.1	7.5		
Buñol							
??—	r	±32.5	≥22.7	20.7	12.6		
MPV PAN-288	r	29.7	—	≥21.5	9.8		
IVAU BU-S2	1	29.1	27.2	23.7	11.2		
MPV FB 51	1	31.8	—	22.3	11.5		
Monteagudo							
IPS 1513	r	—		—	23.9	..	
Pontlevoy							
MNHNP FP 219	r	—	24.8	—	—		
MNHNP FP 1061	1	24.3	21.1	20.5	6.2		
Beaugency							
MNHNP 3903 cast	1	25.5	20.2	18.8	17.1		
Tavers							
COBO —	1	28.9	23.5	20.0	10.8		
Ravensburg							
NMB TD 544	1	28.9	23.6	21.9	11.4		
Langenenschlingen							
NMB TD 823 cast	1	28.4	21.4	17.4	11.8		
Puente de Toledo							
ITGE 412M	r	30.0	21.3	19.2	10.3		
Bunolistriodon intermedius							
Maerzuizigou							
IVPP V 9522.4	1	28.1	≥23.0	21.5	10.0		

IVPP V 9522.5	r	28.5	23.6	19.9	9.8		
Bunolistriodon akatikubas							
Mbagathi							
KNM-MG 3	r	—	—	—	..		
KNM-MG 8	l	—	—	16.2	6.6		
KNM-MG 9922	r	—	—	—	—		
Maboko							
KNM-MB 863	r	—	—	—	10.3		
Bunolistriodon guptai							
Bhagothoro							
IM B 701	r	—	19.8	18.1	—		
HGSP 8412							
HGSP 8412/3317	r	21.8	17.9	15.3	8.0		
HGSP 8318							
HGSP 8318/3308	l	>23.8	20.0	16.8	—		
HGSP 8420							
HGSP 8420/3441	r	22.7	20.3	17.8	..		
HGSP 8420/3443	r	±23.7	—	—			
Listriodon pentapotamiae							
S Bhilomar							
IM B 696	r	29.1	22.1	20.6	10.4		
Chinji 38							
GSP 774	l	23.1	20.3	19.5	..		
Chinji 56							
GSP 1005	r	—	—	18.7	..		
Chinji 76							
GSP 1606	l	21.3	>19.4	17.3	..		
Dhok Talian 189							
GSP 4456	l	—	—	—	—		
HGSP 8111							
HGSP 8111/136	l	26.1	24.8	19.2	..		
HGSP 8212							
HGSP 8212/971	r	27.9	22.1	19.3	8.5		
Burri Wala							
IVAU CHB 20	l	27.5	22.4	±20.6	..		
W-Marianwala							
BSPHGM 1956II115	l	21.2	18.8	17.1	..		
Kanatti Chak 6							
BSPHGM 1956II119	l	22.2	20.9	18.2	..		
Kanatti Chak 8							
BSPHGM 1956II110	r	25.4	23.3	21.5	..		
BSPHGM 1956II114	l	30.6	23.9	20.0	11.9		
Parriwala							
FISF CHP F6108	r	21.4	19.3	18.4	..	13.8	12.9
Cheski Wala							
IVAU CHC 86	l	—	—	>20.3	10.7		
HGSP 8125							
HGSP 8125/382	r	—	—	19.3	..		
Kalin Nal							
BSPHGM 1956II111	l	—	22.6	20.4	—		
Kundal Nala 2							
BSPHGM 1956II113	l	22.4	>19.1	>17.6	..		
Chinji Fm.							
bought spec.							
IVAU CH-21	l	24.0	20.0	17.9	..		
Listriodon splendens							
Simorre							
MNHNP Si 100	r	26.5	23.1	22.5	8.0		
"Environs de Simorre"							
MNHNP Si 164	l	26.4	22.4	20.4	9.4		
"Gers"							
MNHNP Ger 39	r	25.1	22.4	19.8	..		
MNHNP Ger 45	r	23.9	21.5	20.5	..	12.9	11.7
MNHNP Ger 46	l	25.6	22.9	20.8	9.5		
Inönü I							
MTA AKI 3/450	l	27.9	23.8	22.2	..		
MTA AKI 3/451	r	27.5	24.0	22.5	..		
Paşalar							
PDTFAU B576	l	26.9	23.5	21.0	..		
PDTFAU B593	r	26.8	—	—	..		
PDTFAU C228	r	24.6	—	—	..		
PDTFAU C280.5	r	28.0	23.3	20.3	..		
PDTFAU C280.8	l	25.7	23.2	21.7	..		
PDTFAU C324	r	—	—	—	—		
PDTFAU CT1	l	—	≥22.4	21.5	10.2		
PDTFAU CT1	l	25.2	23.1	20.3	..		
PDTFAU CT1	r	—	—	—	11.2		
PDTFAU CT5	l	—	—	22.5	..		
PDTFAU D571	r	26.4	22.2	20.1	8.7		
PDTFAU D842	r	26.5	22.1	21.2	..		
PDTFAU DT1	r	—	—	—	—		
PDTFAU E89.7	l	—	22.1	—	—		
PDTFAU E273	l	27.7	23.6	21.9	—		
PDTFAU E521	l	26.3	23.8	21.1	..		
PDTFAU ET1	r	—	24.3	—	—		
PDTFAU ET	r	—	—	—	—		
PDTFAU F99.9	r	27.0	20.8	19.5	9.3		
PDTFAU F278	r	25.2	21.9	19.5	..		
PDTFAU F373	r	—	—	—	—		
PDTFAU F375	r	26.6	23.0	21.5	..		
PDTFAU G170	l	26.1	23.2	21.2	..		
PDTFAU G276	l	27.1	22.3	19.6	10.6		
PDTFAU G361	l	25.4	21.5	19.0	..		
PDTFAU G657	r	27.9	22.4	19.4	6.7		
PDTFAU G1712.1	r	—	—	22.7	..		
PDTFAU G1740	l	26.7	22.7	20.5	..		
PDTFAU G18??	l	23.4	21.3	20.9	..		
PIMUZ BP115 cast	r	25.2	22.4	19.8	..		
PIMUZ BP-127	r	24.5	21.8	19.7			
Çandir							
MTA AÇH 589	r	—	—	≥21.6	..		
MTA AÇH-591	l	25.7	22.9	20.2	..		
MTA UÇHÜ 639	r	26.0	22.4	20.2	..		
MTA UÇHÜ 641	r	29.5	22.4	20.6	9.2		
Villefranche d'Astarac							
MNHNP VAS 17	l	≥24.1	≥21.4	20.5			
MNHNP VAS 18	r	≥23.0	≥20.7	18.8	..		
Manchones I							
IVAU MA 100	l	33.1	28.5	26.7	..		
Arroyo del Val IV							
IVAU AR IV 22	l	—	—	20.5	..		
IVAU AR IV 24	r	26.7	—	—	—		
IVAU AR IV 275	l	—	—	>23.4	..		
IVAU AR IV 485	..	—	—	≥19.4	—		
IPS AR IV 23	l	23.6	24.3	23.1	..		
RGM 263.114	l	—	—	—	—		
RGM 263.179	r	25.4	—	22.2	..		
MPZ AV-29	l	27.3	24.0	22.2	..		
Arroyo del Val VI							
IVAU AR VI 3	l	28.5	25.2	24.0	..		
IVAU AR VI 5	r	>24.6	22.5	—	—		
Sariçay							
MTA 98	l	26.2	22.4	20.8	..		
MTA 99	r	26.4	23.2	21.0	..		
Mannersdorf							
NMW 1843XXXII9	l	26.2	21.4	21.3	..		
Steinheim							
SMNS 4994	r	26.9	22.7	..	..		
SMNS 11380	r	24.0	21.9	..	..		
NMB Sth 684	r	26.4	22.1	21.2	..		
La Grive oc							
IGF 295	l	24.2	22.0	19.5	..		
UCBL 65623	l	23.1	20.8	19.4	..		
UCBL 65623	l	25.8	21.9	21.5	..		
UCBL 65623	l	24.6	20.8	19.8	..		
UCBL 65623	r	23.3	20.6	—	..		
MGL LGr 715	l	25.5	21.4	19.8	..		
MGL LGr 739	r	25.5	>21.8	20.3	..		
MGL LGr 746	r	24.3	21.1	20.2	..		
Wartenberg							
BSPHGM 1953I488	l	25.9	>20.2	>19.1	..		
Cerro del Otero							
MNCN NM 18019	l	28.9	23.1	21.5	10.3		
MNCN NM 18028	l	>28.7	25.3	23.6	..		
MNCN —	r	26.6	23.1	19.8	..		
Sant Quirze							
IPS VP 1040	..	27.5	24.3	..	..		
MGSCB 48889	l	30.2	26.1	23.2	..		
MGSCB 48890	r	30.7	26.2	23.2	..		
CJFV SQu 5434	l	26.7	24.5	20.6	..		
CJFV SQu 5445	r	26.8	23.4	21.0	..		
Castell de Barberà							
IPS —	l	25.3	23.6	20.2	..		
Hostalets							
NMB Spa 163	r	28.0	24.0	21.0	..		
MGSCB 48500	r	28.7	≥24.6	23.3	..		
IPS 1052	r	21.4	—	21.6	..		
Aveiras de Baixo							
ML 5742	r	28.0	25.7	22.7	..		
"Leithagebirge"							
NMW 1850XXVI8	r	—	—	>18.0	..		

TABLE 7 Measurements in mm of associated lower incisors and canines.

		I_1						I_2						I_3			C_m			C_f	
		DMD	DLL	Hli	Hla	Hme	Hdi	DMD	DLL	Hli	Hla	Hme	Hdi	DMD	DLL	Dmax	li	la	po	DAP	DT
Lopholistriodon																					
L. moruoroti																					
Moruorot																					
KNM-MO 5	l	—	—					—	—				4.1	—	—						
	r	≥3.8	≥4.1					±3.8	4.9				—	—	—					7.0	5.0
Kubanochoerus																					
K. massai																					
Gebel Želten																					
MNHNP Z 1961	r																20.5	18.3	16.8		
K. minheensis																					
IVPP V 6021	l	13.9	15.0	23.1	>23.5	..	..	17.3	17.2	25.8	>28.0						15.1	13.6	11.2		
	r	14.4	—	—	—	..	..	16.0	18.3	—	>28.0	—	—	13.3	11.1						
K. gigas																					
Maerzuizigou																					
IVPP V 8502	l	18.3	22.7	>23.1	>27.9	..	..	21.1	22.6	>24.2	>28.6	..	..				35.0	27.1	18.0		
	r	17.4	23.5	>22.1	>26.5	..	..	21.5	21.5	>25.0	>28.7	..	>17.1	20.6	15.8	..	34.8	28.2	19.7		
BMNH BPV-907	l	19.3	20.8											18.2	+13.7	22.5	30.6	22.7	28.1		
	r	19.7	19.8											18.7	14.6	+21.0	33.5	22.6	28.3		
Bunolistriodon																					
B. anchidens																					
Rusinga R1																					
KNM-RU 2785	l	7.9	>8.0	—	—	—	—										15.2	8.8	13.0		
	r	8.0	>8.8	—	>14.7	>9.1	>10.2	9.6	10.4	>20.0	>18.3	>10.2	>12.1				13.8	8.6	12.3		
B. aff. latidens																					
Munebrega I																					
IVAU 55/1051	r	..	..					..	..								..	..	..		
Torralba II																					
IVAU 18/200	l	—	—					—	—					—	—	—				12.7	9.4
	r	—	—					—	—					—	—	—				12.5	8.4
Villafeliche 3																					
IVAU VL3/6	l	9.0	7.2					9.7	..												
	r	8.9	—																		
B. latidens																					
Veltheim																					
NSSW 99	l	10.7	±8.3	—	—	—	—	13.3	10.4	17.2	..	..	..				11.2	12.2	9.0		
	r	10.8	7.6	14.4	..	..	..										±11.8	±11.6	8.3		
Inönü I																					
MTA AKI-3/7	l	11.8	8.3					13.6	9.1					13.5	7.7	17.3					
	r	11.4	8.1					13.6	9.4	>16.6	>16.9	..	..								
MTA AKI-3/8	r	—	—					—	—					—	—	—	—	—	—		
Listriodon																					
L. pentapotamiae																					
Dhok Talian 189																					
PMNH MV 31, 527	l	9.5	7.5					11.6	8.3												
	r	9.3	7.4					12.3	9.0											13.5	8.4
Kanatti Chak 5																					
BSPHGM 1956	l	10.3	8.1					12.5	9.1												
II 103	r	10.2	≥8.0																		
Chinji																					
IM B 697	r																			11.0	6.9
L. splendens																					
Simorre																					
MNHNP Si 155	l	11.4	8.2					12.1	10.4					..	10.3	18.3					
	r	>11.0	8.3					13.3	11.5					13.5	9.5	18.5				16.3	10.2
Villefranche																					
MNHNP 4321	l							15.2	..												
	r	11.0	..					14.8	..					..	..	18.1				20.0	16.5
Inönü I																					
MTA AKI 3/333	l	11.4	9.5					15.0	11.6	20.1	22.0	..	18.1								
	r	11.9	9.7					15.4	11.9	21.0	22.2	..	17.0								
MTA AKI 3/777	l	11.4	10.0																		
	r	11.5	10.0					13.4	11.1					±11.8	±9.5	..					
Klein Hadersdorf (Frank)																					
NMW 8X1944	l							15.2	10.7												
	r							14.5	10.8												
Çandir																					
PIMUZ CA I/22	l	10.7	8.3					13.5	10.0											12.0	7.6
	r	10.6	8.4					12.9	10.1					12.1	7.9	16.2				12.7	7.7
MTA —	l	12.3	9.9																		
	r																18.9	15.6	16.5		
Locle																					
UN —	l																23.8	19.6	19.2		
	r	12.9	9.9					>15.4	11.5												
S. Quirze																					
MGSCB 30481	r	13.5	≥9.4					20.1	12.1												
MGSCB 48900	l	≥14.0	10.1																		
	r	14.3	10.5																		
CJFV SQu 5438-	l	15.5	10.5					19.0	12.7					≥16.6	9.0	>20.1					
5442	r	14.8	10.5					18.0	12.1					17.0	9.0	20.1					
Hostalets																					
CJFV —	r																22.5	17.0	17.2		
Markt Rettenbach																					
BSPHGM	l													16.2	8.2	..				18.1	11.2
1929 II ´47	r							16.6	10.5					16.0	8.3	..				18.2	12.1

TABLE 8 Measurements in mm of associated lower deciduous molars and associated permanent molars.

		D_2			D_3			D_4				M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTm	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Nguruwe kijivium																					
Loncherangan 1																					
KNM-LC 17394	1				—	—	>4.2	14.0	5.4	6.1	7.3	10.7	8.5	8.6	>13.5	—	>8.4				
Songhor																					
KNM-SO 1062	1	8.5	3.1	3.8	8.9	3.5	4.5	14.0	6.0	7.0	7.5										
Kubanochoerus																					
K. massai																					
Gebel Zelten																					
MNHNP Z 1961	1	18.9	7.3	8.0	21.6	7.7	9.1														
Bunolistriodon																					
B. aff. latidens																					
La Artesilla																					
MPZ 6430	r	12.8	4.6	5.9	12.8	5.5	6.6	21.4	—	9.8	11.0	18.4	11.7	13.0							
MPZ 6431	1	13.7	5.0	6.0	13.5	5.7	7.3														
Moratines																					
MNCN —	1							21.0	..	..	10.1	17.5	..	>11.4							
La Hidroélectrica																					
IPS 1143	r				—	..	—	±21.5	..	..	±11.8	19.0	12.6	12.1	—	14.4	—				
B. latidens																					
Inönü I																					
MTA AKI-3/586	1							20.6	8.9	11.3	11.0	16.4	13.1	12.1	20.3	16.6	15.9				
B. lockharti																					
Pellecahus																					
NMB GB 1382	1							—	—	—	11.0	±20.7	14.1	±14							
La Romieu																					
UCBL 320268	1				14.3	5.8	6.9	>20.4	8.7	9.8	11.1										
Langenau 1																					
SMNS 40684	1				13.2	..	6.6	23.3	..	..	11.2	±19.1	..	..							
Pontlevoy																					
MNHNP FP 1015	1				13.0	5.6	6.5	22.3	8.9	10.6	11.3										
Listriodon																					
L. pentapotamiae																					
Kalinal																					
BSPHGM 1956 II 44	r							—	—	—	10.1	15.8	—	11.9	19.7	—	15.2	—	17.7	16.1	—
L. splendens																					
Çandir																					
MTA —	1				13.2	6.8	7.4	22.9	9.9	11.2	12.7	20.0	14.0	14.6	23.6	—	17.8				

TABLE 9 Measurements in mm of associated lower molars and premolars.

		P_1 DAP	DTa	DTp	P_2 DAP	DTa	DTp	P_3 DAP	DTa	DTp	P_4 DAP	DTa	DTp	M_1 DAP	DTa	DTp	M_2 DAP	DTa	DTp	M_3 DAP	DTa	DTp	DTpp
Nguruwe kijivium																							
Rusinga																							
KNM-RU 2770	r													12.6	9.7	9.9	14.4	12.0	11.5	18.6	12.3	9.9	7.8
Rusinga-R1A																							
KNM-RU 2774	l																15.9	12.0	11.6	—	12.1	10.8	—
Songhor																							
KNM-SO1059/1123	r																13.8	10.2	9.7	—	10.3	—	—
KNM-SO1126/1122	l																13.8	10.3	9.7	—	11.5	9.9	—
Lopholistriodon																							
L. moruoroti																							
Moruorot																							
KNM-MO 5A	r				4.9	2.4	2.7	6.9	2.9	3.5	7.7	4.6	>4.0	8.6	—	6.1	10.1	—	>6.8	—	7.8	7.7	—
KNM-MO 5B	l													—	—	6.1	10.6	6.9	7.4	14.0	8.0	7.8	5.8
Maboko																							
KNM-MB 10318	l													8.4	5.0	5.0	10.2	6.5	6.2				
KNM-MB 10332	l										6.4	≥3.4	3.6	7.4	4.7	5.1	9.2	6.2	6.2				
L. pickfordi																							
West Stephanie-Buluk																							
KNM-WS 115	l																13.8	8.9	9.0	17.7	>10.0	>8.8	>6.8
KNM-WS 115	r																13.5	8.6	9.2	18.3	10.7	9.5	6.8
L. kidogosana																							
Ngorora																							
KNM-BN 1714	l													—	8.0	—	—	±8.0	—				
L. akatidogus																							
Loc. ?																							
KNM-X 208	r																19.9	>12.9	13.8	27.6	14.8	14.4	13.1
Kubanochoerus																							
K. marymunngui																							
Buluk																							
KNM-WS 12595	l				30.4	15.0	16.6	31.0	20.5	21.1	28.3	22.5	22.9	±26	±20.5	—	32.2	30.3	27.8	46.1	30.8	24.4	18.3
	r				31.0	15.2	16.7	31.1	21.0	21.7	28.9	22.9	22.4	—	—	>22.5	32.0	29.7	27.5	45.9	30.9	24.6	18.7
K. mancharensis																							
Nyakach-Kaimogool E																							
KNM-NC 9807	r																47.2	≥40.0	37.5	—	42.4	—	—
K. massai																							
Gebel Zelten																							
MNHNP Z 1961 holotype	l				26.4	11.8	>10.7	28.9	14.0	13.6	27.8	14.8	>15.5	23.0	—	—	29.6	>22.0	>21.7	47.2	24.6	22.0	18.5
MNHNP Z 1961	l																±30.3	<24.8	±23.6	45.8	25.0	21.8	17.6
MNHNP Z 1961					24.4	11.2	11.3	25.4	13.8	13.4													
MNHNP Z 1961	l																27.6	—	22.5	≥43.0	23.8	21.9	—
MNHNP Z 1961	l													26.5	19.8	19.9	30.1	24.3	25.0				
MNHNP Z 1961	r				27.3	13.6	12.9	28.9	16.2	±16.9	26.8	±18.3	—	—	—	—				±48.9	—	24.4	—
MNHNP Z 1961	r										—	—	—	—	—	—	31.6	24.6	24.2	46.0	26.8	22.7	17.9
MNHNP Z 1961	r													—	—	19.2	29.4	22.3	23.8	48.0	26.5	23.3	18.8
MNHNP Z 1961	l				<26.5	11.0	12.5	26.7	13.2	13.9													
MNHNP Z 1961	l				—	9.6	>7.8	≥22.3	11.6	—	24.3	14.8	19.7	26.1	18.0	19.7	31.0	22.3	23.9				
MNHNP Z 1961	l																30.7	≥23.2	≥24.6	47.5	27.0	24.0	17.0
MNHNP Z 1961	l													26.7	19.3	20.6	31.6	24.8	24.3	—	25.5	—	—
MNHNP Z 1961	r										25.5	18.4	18.5	30.5	22.6	22.8							
K. minheensis																							
Nanhawangou																							
IVPP V 6021	l	13.1	8.3	5.4	26.3	13.5	14.2	27.5	13.9	15.5	27.5	16.2	18.8	27.7	19.8	20.8	32.0	25.5	25.7	>49.6	28.8	24.4	20.6
	r				27.0	12.9	≥13.8																
K. gigas																							
Maerzuizigou																							
IVPP V 8502	l	19.3	10.3	8.4	29.7	12.8	14.3				>23.5	—	21.9	>29.9	>20.8	22.9	37.8	28.8	28.2	61.1	32.4	29.4	23.5
	r	—	—	—	29.6	13.0	14.7				>31.9	19.2	21.8	>29.9	>20.8	22.9	37.8	28.8	28.2	61.1	32.4	29.4	23.5
BMNH BPV-...	r													32.7	20.7	21.9	39.4	27.2	27.6	59.5	31.3	28.6	23.3
BMNH BPV-900	l	≥17.0	..	..	29.5	..	13.6	32.6	..	..	32.2	..	..	31.4	..	..	39.3	..	..	..	..	..	..
	r	±15.6	..	..	—	—	—	32.6	..	..	32.1	..	..	—	..	..	40.0	..	..	55.6	..	..	..
BMNH BPV-907	l	17.9	≥8.7	9.2	≥26.2	12.7	14.0	33.2	15.5	17.6	32.2	19.1	22.0	—	—	—	42.5	30.7	≥29.6	61.4	32.9	29.4	24.8
	r	16.7	9.2	≥8.5	>27.5	12.6	14.0	30.0	14.4	16.8	32.8	18.8	21.4	31.3	≥21.8	23.8	41.2	29.7	29.3	63.7	33.2	29.2	24.9
BMNH BPV-905	l	18.9	9.6	7.4				30.9	15.6	17.8	32.0	19.3	21.2	29.9	22.1	23.7	37.8	27.9	28.9				
	r				27.5	13.0	14.1	31.8	15.3	18.1	32.4	19.4	20.5	—	—	—	41.0	28.6	29.0	64.1	32.2	29.7	24.3
BMNH BPV-906	r													—	—	25.2	38.0	30.6	30.8	58.8	33.3	30.3	25.2
BMNH BPV-908	l													—	—	25.2	38.2	>29.7	31.0	58.5	33.5	29.9	24.1
BMNH BPV-911	l	22.5	10.0	11.8	31.0	13.0	14.9	31.5	14.5	17.2	33.2	16.5	19.0	33.1	21.2	23.0	38.9	29.0	27.9	57.8	32.5	28.9	24.2
	r	23.4	9.5	12.0	32.6	14.0	14.2	32.2	15.0	17.0	32.9	17.8	19.1	34.7	22.2	22.8	37.9	28.0	28.5	58.0	31.7	29.0	24.0
Hamalagai																							
IVPP —	r													30.1	20.6	21.6	37.4	26.9	25.8				
Bunolistriodon																							
B. anchidens																							
Rusinga R1																							
KNM-RU 2785	l	>9.4	—	5.5	>16.3	≥7.3	8.0	18.6	—	—	17.8	11.4	11.3	18.6	14.7	14.1	20.8	>17.1	16.5	31.7	19.1	16.6	12.4
	r	10.1	5.8	6.1	17.9	..	..	19.2	..	11.3													
B. jeanneli																							

2		P_1			P_2			P_3			P_4			M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Fategad																							
IM 18098	l										18.4	13.0	14.0	22.0	17.2	16.5	23.3	20.6	18.8	33.4	19.9	17.5	13.5
B. aff. latidens																							
Quinta da Farinheira																							
CEPUNL 1	l													17.9	≥13.2	13.8	20.6	17.5	16.3	32.9	19.1	16.8	12.6
CEPUNL 2	l													18.3	14.1	14.4	21.1	17.8	17.7	32.9	20.0	17.3	12.9
CEPUNL 3	r										—	—	—	—	—	—	—	—	—	—	—	—	—
Quinta Grande																							
CEPUNL 938	l													15.8	>13.6	>14.5	20.4	17.6	>18.2	31.2	19.5	17.6	13.6
Olival da Suzana																							
CEPUNL 16	r							≥16.5	..	>9.8	18.0	..	13.3	—	—	—	22.2	>17.8	17.5	32.9	21.2	18.1	13.9
Casal das Chitas																							
CEPUNL 46	r																22.2	17.5	16.9	32.3	22.2	18.8	14.4
Quinta da Silvéria																							
CEPUNL 41	r										≥16.2	..	10.7	<18.2	—	13.6	21.1	16.3	16.4				
La Artesilla																							
MPZ 6435	l							16.1	..	9.8	15.4	..	11.4	>14.5	>11.6	>12.3							
MPZ 6436	r							15.7	..	9.7	15.7	..	11.8	—	—	—	19.3	16.3	16.8	30.5	15.5	15.7	13.3
Armantes I																							
IVAU 41/513	l													>14.5	12.8	13.7	18.8	17.3	17.5				
Munebrega I																							
IVAU 55/1049	l				—	—	7.7	16.4	8.3	10.5	16.5	11.9	13.4	17.7	13.5	>13.5	20.8	16.9	17.4	34.8	18.5	17.3	12.9
IVAU 55/1050	r							—	—	≥10.4	16.0	11.6	12.5	17.3	13.4	13.8	21.5	16.5	16.9	33.7	18.3	16.3	12.7
IVAU 55/1051	l	—	—	—	—	—	—	15.1	..	8.6	16.8	..	10.6	—	—	—	20.8	..	16.3	—	19.5	—	—
	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21.6	—	—	—	—	—	—
Torralba II																							
IVAU 18/200	l	—	—	—	—	—	—	±16.6	..	9.2	—	—	—	—	—	—	—	—	—	—	—	—	—
	r	8.3	..	5.0	—	—	—	—	—	—	>16.6	11.6	11.0	±17.5	≤14.8	≤15.1	≤19.8	17.0	17.5	±31.2	18.8	<17.2	13.4
La Hidroélectrica																							
IPS 1142	r																22.8	16.5	18.1	34.7	19.3	18.3	..
?Montabuzard																							
MNHNP Or 68	l				..	..	..	15.2	..	..	16.8	..	..	—	—	—	20.8	16.3	15.5	—	..	..	—
B. latidens																							
Veltheim																							
NSSW 99	l				15.2	6.8	7.8	16.0	8.8	9.9	15.2	9.9	11.3	16.7	12.6	12.7	20.1	15.9	15.8	30.1	17.7	15.1	12.9
	r				15.8	5.9	8.4	15.9	8.6	9.6	15.1	10.3	11.3	16.7	12.6	12.4	19.3	14.4	15.8	29.5	17.4	15.3	12.8
Inönü I																							
MTA AKI-3/6	l										15.4	..	9.7	—	12.5	—	18.5	14.8	14.9	30.7	17.7	15.8	12.5
MTA AKI-3/8	r				—	—	—	—	—	—													
MTA AKI-3/11	r													16.0	12.1	—	19.9	15.8	15.1	29.9	17.6	16.1	12.8
B. lockharti																							
Pellecahus																							
UCBL 320302	l																19.8	15.5	15.6	32.2	17.3	15.5	12.1
UCBL 320309	l																21.9	—	16.8	—	17.4	16.2	—
La Romieu																							
UCBL 320292	l							16.8	8.8	10.7	16.6	11.0	12.1	16.6	>12.4	13.4	19.0	15.2	16.3	31.9	17.2	15.9	12.2
UCBL 320292	r							17.5	8.7	11.0	17.2	11.2	12.4	16.8	12.6	13.3	19.3	15.5	16.5	32.8	17.4	16.3	12.3
UCBL 320291	r				15.0	6.6	8.0	16.8	7.7	10.2	17.7	11.2	11.6										
UCBL 320299	r																21.8	±18.0	17.9	36.2	18.1	17.7	12.9
UCBL 320299	l																20.3	17.3	17.1	—	19.8	16.9	—
UCBL 320275	l													17.5	12.6	13.5	20.5	16.2	17.4	36.1	18.6	16.8	13.8
UCBL 320275	l										15.5	..	11.8	>14.2	—	—	18.2	≥14.9	15.1				
UCBL 320275	l													20.7	13.7	14.3	23.2	18.0	17.6				
Baigneaux																							
NMB SO-3022	l				16.4	7.7	9.3	18.3	9.5	12.8	—	—	—	—	—	—	—	18.3	—	32.9/	19.3	17.5	13.1
	r				16.3	8.0	9.3	18.6	9.4	13.1	—	—	13.8	—	—	—	21.2	18.2	18.1	33.8/	19.4	17.4	13.6
Chevilly																							
MNHNP CHE 30	l																20.6	17.5	18.4	32.5	16.6	17.6	13.2
MSNO 260 + —	r																23.0	17.4	18.5	35.4	20.0	18.6	13.8
Arraya																							
MNHNP —	l				17.1	8.1	≥9.3	17.8	10.3	11.5	17.0	12.4	13.3				21.3	18.2	17.7	32.8	19.3	17.8	12.2
Pontlevoy																							
MNHNP FP 288	..																23.2	..	19.0	33.2	21.2	..	..
MNHNP FP 1062	r													19.6	—	15.4	21.1	17.9	18.8				
Tavers																							
CIMO —	l										18.8	12.1	13.1				22.3	18.5	19.1	35.9	21.0	19.2	14.4
B. akatikubas																							
Majiwa																							
KNM-MJ 9773	r																20.8	15.6	15.7	—	17.6	16.9	—
B. intermedius																							
Yehuli Juanzhi																							
IVPP V 9519	l																20.0	16.9	16.5	33.5	18.8	17.0	13.9
	r													—	—	13.6	22.0	17.1	16.8	32.0	18.9	17.0	13.2
Jinzuizhigou																							
IVPP V 9520	r																>21.6	16.8	16.4	35.8	19.2	18.2	13.7
Maerzuizigou																							
IVPP V 9521	r							17.0	7.7	10.2	16.4	11.2	12.3	18.6	13.5	13.3	23.2	17.0	16.5	34.0	18.7	17.2	14.3
BMNH BPV-928a	r																—	16.5	—	33.9	19.2	17.4	13.8
BMNH BPV-928b	l																—	16.2	16.9	33.0	19.4	17.3	14.0
BMNH BPV-929	r							16.8	7.2	10.8	18.1	10.6	12.7	16.2	—	—	20.5	16.8	16.9	33.0	18.9	16.3	13.2
BMNH BPV-1670	l										18.7	—	±13.5	17.6	—	≤14.3	21.4	17.4	16.4	34.8	20.9	17.6	15.0
B. guptai																							
HGSP 8127																							
HGSP 8127/436	r							19.7	9.8	11.7	18.6	12.9	14.4										
HGSP 8311																							

3		P_1			P_2			P_3			P_4			M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
HGSP 8311/1550 & 1406	l										17.3	11.5	12.8	17.9	14.1	14.6	22.6	18.3	18.4	33.8	19.2	17.0	12.7
Listriodon																							
L. pentapotamiae																							
Kanetti																							
IVAU KA 79	r							18.0	10.8	11.4	18.6	12.4	13.6	—	—	—	23.5	17.6	18.3	—	20.6	19.2	—
Dhok Talian 189																							
GSP 4413	l													—	—	>14.3	21.3	16.6	16.6	±33	18.2	16.1	12.8
GSP 4413	r																20.4	≥16.5	16.7	33.9	18.6	16.4	12.8
GSP 4478	r																23.0	18.3	>16.6	—	20.1	17.9	—
PMNH Mus. 31/	l	7.2/4.6		3.8	14.0	7.0	7.9	14.6	8.7	10.0	17.0	11.4	12.1	17.3	>12.9	13.3	21.6	16.5	16.7	36.9	19.4	17.9	12.6
MV 31/527	r	7.6/4.4		3.4	13.7	—	≥7.5	15.6	8.9	9.6	17.0	11.7	12.3	±16.8	>13.4	>13.9	22.2	16.9	16.6	36.9	20.0	18.1	12.5
Mochi Wala																							
IVAU CHO 125	l							14.1	7.5	>9.4	14.1	10.2	>10.6										
Marianwala-Kas																							
BSPHGM 1956 II 42	r													—	—	—	20.3	—	—	±27.5	—	14.8	10.6
BSPHGM 1956 II 43	l													—	≥12.1	13.1	—	16.6	—				
BSPHGM 1956 II 109	r													14.8	—	11.8	18.4	14.3	14.5				
Burriwala																							
BSPHGM 1956 II 104	l										15.0	—	11.5	15.6	—	—	20.7	16.4	—				
Kanatti Chak 5																							
BSPHGM 1956 II 40	l													≥14.9	—	13.2	19.8	16.2	15.6	±31.5	18.3	16.9	—
BSPHGM 1956 II 41	r							14.5	9.1	11.1	15.2	10.6	12.2										
Hessuwala																							
BSPHGM 1956 II 46	r																20.5	15.7	15.2	31.7	17.7	15.7	11.4
Janda Wala																							
BSPHGM 1956 II 41	r							15.1	9.1	9.8	16.3	11.0	12.2	17.5	13.3	13.3	21.8	16.4	16.4	33.0	18.5	17.1	12.6
BSPHGM 1956 II 43	l																—	—	17.5	34.9	19.4	17.8	12.2
Kalinal																							
BSPHGM 1956 II 47	r													17.9	12.9	12.8	22.0	15.0	16.6				
BSPHGM 1956 II 108	l													>12.5	—	>11.5	±19.6	15.2	15.0				
Kundal Nala 1																							
BSPHGM 1956 II 87	l													14.5	>10.9	11.8	18.6	14.2	14.5	—	16.6	15.8	—
Katli																							
BSPHGM 1956 II 45	r							>11.3	7.7	9.0	14.5	9.8	10.8	16.2	11.3	11.7	20.7	—	15.2				
Chinji loc. 76																							
GSP 9663																	18.0	15.8	15.0	28.5	17.0	15.7	9.8
Chinji																							
IM B 697	l							>15.1	10.3	10.8	17.3	10.4	12.5	19.1	14.2	14.0	22.0	17.6	17.0	35.1	20.2	±16.2	13.0
	r				14.9	8.5	8.2	—	9.9	—	—	—	—	19.2	13.9	14.9	21.2	17.4	17.1	—	20.2	—	—
HGSP 8122																							
HGSP 8122/257	r							≤16			14.5	10.1	10.6	17.4	≥11.6	>12.9	21.2	15.1	15.7	34.1	17.2	15.7	10.0
L. splendens																							
Simorre																							
MNHNP Si 155	l				13.0	..	8.0	—	..	9.8	16.8	..	13.1	15.6	..	14.0	19.3	..	16.6	31.3	18.6	..	..
	r				12.7	7.4	8.4	≥14.0	>9.4	—	15.8	12.1	12.8	16.6	—	13.8	19.7	16.4	17.7	30.9	19.4	17.4	10.5
MNHNP SI 162	r				14.9	7.3	8.4	16.2	9.3	10.1													
Villefranche d´Astarac																							
MNHNP 4321	l				—	—	—	16.3	..	9.0	16.0	..	11.6	15.5	..	12.7	—	—	—	—	—	—	—
	r				±14.0	..	8.0	—	..	9.0	16.6	..	11.9	15.6	..	14.0	—	..	±15.1	30.8	19.0	..	..
MNHNP VAS 11	l										16.3	10.8	11.5	—	—	12.6	20.1	15.8	16.2				
MNHNP VAS 12	r							16.6	8.5	9.7	17.7	11.5	12.8										
MNHNP VAS 30	r				—	—	8.7	15.9	8.4	9.6													
l´Ile-en-Dodon																							
QMF cast BMNH 33577	..							15.7	8.8	9.8	16.6	11.1	11.7	17.5	13.4	13.7	19.4	15.7	16.1	30.5	18.7	16.8	10.7
Sansan																							
MNHNP Sa 4314	l										16.0	..	—	17.0	..	13.3	19.2	..	12.2				
MGL Ss 163	l																21.7	16.6	16.3	31.9	19.0	16.5	11.0
NMB Ss 157	r																19.2	16.1	15.5	31.8	18.6	16.6	11.3
La Gruas																							
NMB DG 33+34	l																21.3	16.8	17.3	33.5	20.2	18.3	11.5
Inönü I																							
MTA AKI 3/41	r							17.2	9.6	10.1	17.3	12.8	13.7	—	—	—	22.3	18.6	20.0	35.4	21.4	19.7	14.0
MTA AKI 3/42	l										16.8	12.6	13.8	—	—	±14.9	21.9	18.6	20.3	35.6	21.2	19.6	14.0
Paşalar																							
PDTFAU D920	l																21.6	16.8	16.6	35.4	19.3	17.3	11.8
PDTFAU E89.10	..																21.3	17.0	16.5	35.2	19.9	17.7	13.1
PDTFAU E614	r													17.4	13.4	13.3	21.4	17.2	16.7	33.1	19.9	17.9	12.3
PDTFAU G589	l							14.5	7.8	9.0	18.8	12.2	13.3	17.8	13.1	13.4							
PDTFAU G775	l																24.8	19.4	18.7	39.7	21.5	—	12.0

4		P_1			P_2			P_3			P_4			M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Klein Hadersdorf (Frank)																							
NMW 8X1944	l							16.2	8.9	9.3	16.3	11.4	12.5	16.0	12.6	13.3	19.9	16.2	15.8	32.9	18.6	16.5	10.7
	r				12.9	7.4	7.9	15.5	9.0	9.2	15.1	11.4	12.3	17.1	12.6	12.9							
Çandir																							
PIMUZ CA I/22	l				13.4	7.0	7.8	16.4	8.6	10.2	15.4	11.4	13.6	18.5	13.7	15.0	22.0	17.8	19.0	33.6	20.5	19.8	13.5
	r				14.0	7.2	7.9	16.7	8.8	10.8	16.3	11.0	13.8	18.4	13.7	15.0	22.0	17.8	19.1	33.7	20.5	19.7	12.8
MTA —	l				12.8	7.6	7.2	15.3	9.5	10.2	17.2	12.6	13.2										
	r				13.1	7.8	8.1	15.9	7.8	10.6	—	12.4	—	17.1	13.8	15.0	22.1	18.5	18.1	—	19.6	18.4	—
MTA —	r				14.0	7.8	8.7	16.6	9.6	11.6	18.8	13.5	—										
MTA —	l										15.9	11.0	12.5	18.4	13.7	14.5	22.4	17.3	16.7				
Mörsingen																							
NMB TD 691	l																—	16.8	—	32.6	18.7	16.9	11.9
Paracuellos V																							
MNCN PA V569	l							16.9	9.2	10.1	18.5	≥12.3	—				22.6	17.6	17.5				
Manchones I																							
IVAU MA 105	r										—	—	—	21.3	18.0	17.7							
IVAU MA 120	r							—	9.0	8.8	≥17.0	11.5	≥12.8										
IPS 1100	l																21.3	18.1	17.8	34.6	—	18.4	12.8
Arroyo del Val IV																							
IVAU AR IV 2	r							—	10.1	≥10.6	17.4	12.0	12.5				—	—	—	32.1	18.5	17.7	12.5
IVAU AR IV 3	l							—	—	11.6	18.1	12.3	14.2	—	—	—	—	—	16.8	34.5	19.3	16.9	14.6
IVAU AR IV 4	r							18.0	10.4	11.4	17.9	12.8	14.0	—	—	—	22.4	17.6	16.8	34.3	19.7	17.7	14.0
IVAU AR IV 6	r										17.6	12.5	12.2	—	—	>13.0							
IVAU AR IV 87	l													—	—	—	22.3	—	18.0	33.5	—	—	14.2
IVAU AR IV 88	l							16.8	9.5	10.7	16.9	11.9	12.3	16.8	—	13.4	20.7	≥17.1	16.8	30.7	18.4	17.5	13.0
IVAU AR IV 89	r													—	—	—	22.7	18.8	18.1	—	—	—	—
MPUZ AV-57	l													20.0	13.2	13.5	22.4	16.4	16.5	—	18.2	—	—
RGM 263.035 - 263.040	l				16.6	9.2	9.9	17.9	11.1	11.2	19.3	12.9	13.4	—	—	13.7	22.2	18.5	17.5	33.8	20.6	19.0	14.3
RGM 263.103	r													—	—	13.5							
RGM 263.220	r										±16.0	—	≥9.7	20.0	13.4	13.4	22.2	16.2	16.5	30.9	—	17.5	±13.3
MNCN —	.							16.5	..	10.5	16.3	..	12.2	18.1	..	14.2	22.5	..	17.2	34.4	20.1	..	..
Merisor (west slope Mendru)																							
HGSB Ob 14	l										17.2	13.8	13.6	>17.5	—	13.6	23.6	18.3	17.6	—	—	—	12.4
	r							17.0	10.5	12.2	18.0	14.2	13.4							37.0	20.5	18.7	13.0
Loretto																							
NMW SK 1072	l				≤17.7	..	..	..	..	..	±16.7	..	..	±19.0	..	..	±22.7	..	±19.2	36.5	..	19.6	12.7
	r				16.0	..	..	18.2	9.9	10.6	18.4	14.9	14.2	—	—	—	23.8	19.6	18.7	34.7	21.3	20.1	12.8
La Grive																							
MGL LGr 712	l																21.1	16.9	17.1	30.9	—	17.3	10.2
MGL LGr 722 (composite)	r							16.1	9.1	11.2	17.2	12.7	11.6	17.7	14.0	13.4				—	19.3	17.1	—
MGL LGr 735	r																—	—	19.1	35.8	21.4	20.6	11.7
Cerro del Otero																							
MNCN NM 18001	r																25.4	19.1	19.8	35.4	21.9	19.3	14.2
MNCN NM 18002	l																25.8	19.5	19.6	36.5	21.0	19.2	14.0
S. Quirze																							
IPS VP 1025	l				14.2	..	7.2	16.0	..	10.0	17.2	..	13.0	—	—	—	20.8	..	18.6	34.0	19.5	..	..
Escanecrabe																							
MNHNP HGP 18	l										17.9	13.0	14.1	18.8	14.6	14.5	23.8	19.6	19.2	36.2	21.9	19.0	10.9
MNHNP HGP 19	r										17.3	12.9	14.0	18.9	14.6	14.2	23.1	19.5	19.1	36.1	21.9	19.3	10.6
Wien Heiligenstadt																							
NMW SK 1666a	l							14.1	9.2	9.1	15.6	12.6	12.3	17.5	13.7	13.6	21.0	17.7	16.9	33.9	19.3	18.1	11.1
	r																21.3	17.7	16.8	34.0	19.5	17.6	10.6
Castell de Barberà																							
IPS 1955	l																22.2	17.9	17.2	35.2	19.9	17.9	10.4
IPS —	l				12.7	..	8.0	15.4	..	10.3	16.5	13.0	11.2	18.7	14.4	12.5	21.8	18.3	17.3	30.5	20.4	17.8	..
Hostalets																							
CJFV —	r				13.7	7.5	8.0	16.5	9.1	10.3													
CJFV —	l										—	—	—	>15.4	—	—	20.4	—	—	—	—	17.5	10.6
CJFV —	l							15.4	..	..	16.7	..	..	17.1	..	..							
MGSCB 48506	r										18.7	13.0	14.3	18.9	≥13.5	≥13.9	23.1	18.8	17.9				
Markt Rettenbach																							
BSPHGM	l				13.2	7.6	8.5	15.6	9.5	11.6	17.2	13.5	13.5	≥17.4	—	13.1	19.3	11.8	11.9	31.9	19.1	18.2	12.2
1929 I ´47	r				13.6	7.5	8.8	15.9	9.6	11.3	18.0	13.6	13.9	17.7	—	13.2	21.8	16.8	17.1	31.9	19.2	18.6	12.3

TABLE 10 Measurements in mm of associated upper incisors and canines as well as lengths of diastemata.

		I^1				I^2				I^3		C^f		C^m		Diastema			
		DMD	DLL	Hli	Hla	DMD	DLL	Hli	Hla	DMD	DLL	DAP	DT	DAP	DT	I^3-C^x	C^x-p^1	C^x-p^2	p^1-p^2
Lopholistriodon																			
L. pickfordi																			
Majiwa																			
KNM-MJ 9778	r	11.1	6.9	8.9	9.8	8.1	4.6	4.9	±6.3										
L. kidogosana																			
Ngorora Dl, 2/10																			
KNM-BN 992	l													..	..	—	—	—	—
	r													..	..	..	..	34.7	..
Kubanochoerus																			
K. massai																			
Gebel Zelten																			
MNHNP Z 1961	l	±29.4	±15.8			18.9	11.7			20.5	≥11.0								
	r	30.1	17.3									±20.7	±15.2			—	..	..	10.5
MNHNP Z 1961	l											alveolus				±18.7	±10.2		
	r											alveolus				16.4	8.6	28.8	8.9
K. gigas																			
Maerzuizigou																			
IVPP V 8501	l	43.0	21.2			24.4	16.3			24.3	14.2			alveolus		..	3.1	..	13.5
	r	41.1	20.4			21.7	16.6			—	—			alveolus		..	4.7	..	8.0
BNHM BPV 900	l	39.9	..			..	..			24.8	..			31.0	31.0				
	r	±39.0	..											..	—				
BNHM BPV 901	l													29.3	31.6				
	r	43.2	20.8											30.5	31.2				
Bunolistriodon																			
B. anchidens																			
Rusinga AWI26																			
KNM-RU 5870	r																		>6.0
Listriodon																			
L. splendens																			
Sansan																			
MNHNP Sa 10.141	l					16.4	8.0			—	—			24	28	±19.0		±40.0	
Simorre																			
MNHNP Si 156	l	25.3	12.9									15.6	±10.5						
	r	25.8	≥13.9																
Xinan																			
IVPP V8283	l	22.7	±12.3			15.7	9.1			±14.3	≥8.1			32.2	35.9	..		33.3	
	r													33.8	36.2	..		32.0	
IVPP V8285	l															..		45.4	
	r	22.6	13.9															45.7	
Markt Rettenbach																			
BSPHGM	l	30.1	12.6			16.9	7.6			>15.3	—								
1929 II ´47	r	29.9	12.8			16.4	8.1												

TABLE 11 Measurements in mm of associated upper deciduous molars and associated permanent molars.

		D^2			D^3			D^4			M^1			M^2			M^3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Nguruwe kijivium																				
Songhor																				
KNM-SO 1119	r	11.1	5.3	8.2	10.6	9.7	10.2													
Bunolistriodon																				
B. aff. jeanneli																				
Rusinga R1																				
KNM-RU 9786	r				16.9	8.9	12.4	16.5	15.2	15.7	..	16.5	..							
Rusinga R113?																				
KNM-X 114	r				17.1	9.2	12.5	16.4	15.0	15.6										
B. aff. latidens																				
La Artesilla																				
MPZ 6445	1				16.0	7.3	11.1	15.5	13.8	13.1										
B. lockharti																				
La Romieu																				
UCBL 320296	r				16.8	8.7	13.3	17.3	17.0	15.6										
Langenau 1																				
SMNS 41630	1				16.7	..	11.4	16.1	..	13.9	..	..	..							
	r				16.0	..	11.4	15.9	..	14.3	..	..	..							
Grimmelfingen																				
SMNS 20250a	1							15.8	..	14.6	17.9	..	17.4	19.6	..	21.5	±24.0	±20.5	..	..
Puente de Toledo																				
ITGE 412M	1							15.4	13.1	13.5	17.6	15.8	17.5							
Castelnau (d'Arbieu?)																				
NMB D964	r	≥11.2	..	..	16.7	..	..	±15.8	..	..	18.4	..	..							
Listriodon																				
L. pentapotamiae																				
Bhilomar																				
IVAU CHH —	1							—	7.8	—	9.8	16.2	11.5	11.5						
	r											16.2	11.5	11.9						
"Chinji"																				
IM B 543	1				17.2	8.8	13.3	16.6	15.9	≥14.3										
L. splendens																				
Çandir																				
MTA —	1										20.1	18.4	18.6	22.3	22.0	21.6				
	r				16.9	8.9	12.9	16.7	15.5	15.9	19.8	18.5	19.0	22.3	22.0	21.3				
MTA Çan-V-1/73	1				16.5	9.1	12.3	15.6	15.2	14.7	18.9	18.9	17.8	21.6	21.6	21.4				
	r				16.4	9.2	12.6				19.5	18.1	17.8	21.8	22.0	22.1				
Manchones I																				
IVAU MA 102	1				17.4	8.6	12.9	16.0	15.3	15.2										
IVAU MA 102	r	12.2	6.1	7.1	17.4	8.5	13.0	16.8	15.3	15.1	19.0	18.3	17.9							
Arroyo del Val IV																				
IVAU AR IV 81	r				16.9	9.4	12.8	17.2	14.5	14.4										
Yaylacilar																				
PIMUZ AY 1/7	1	12.1	6.6	8.5	16.3	8.9	12.4													
Hostalets																				
IPS —	r				17.1	—	12.4	16.0	15.1	15.2										
Can Llobateres																				
IPS 1092	1	13.3	6.9	8.8	17.4	9.5	12.9	17.0	14.4	14.7										

TABLE 12 Measurements in mm of associated upper molars and premolars.

		P^1			P^2			P^3			P^4		M^1			M^2			M^3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Nguruwe kijivium																						
Songhor																						
KNM-SO 1118	1										9.2	10.3	11.4	10.5	10.6	14.2	12.7	12.3				
Lopholistriodon																						
L. moruoroti																						
Moruorot																						
KNM-MO 9	1							6.9	4.6	6.4	6.7	7.8	9.0	8.8	9.1	10.4	10.5	>9.8				
Arrisdrift																						
KNM-ZP 1390 cast																						
SAM-PQ AD 136	1										6.4	8.3	8.9	≥8.9	9.2	10.8	10.5	10.2	11.3	10.3	8.2	..
L. akatidogus																						
Fort Ternan																						
KNM-FT 3319	r										11.2	12.1	14.8	13.4	13.5	±17.7	—	—	21.2	>17.2	15.3	..
L. kidogosana																						
Ngorora D, 2/10																						
KNM-BN 992	1							9.3	5.9	9.0	9.4	9.1	12.0	8.8	9.9	14.8	11.4	11.9	16.4	—	12.0	..
	r				9.5	5.3	8.2	9.9	5.9	9.2	8.8	8.7	12.0	8.8	10.2	15.0	≥11.5	12.0	17.6	12.8	11.8	..
Kubanochoerus																						
K. khinzikebirus																						
Gebel Zelten 6424/92																						
KNM-ZP-1389 cast	1	>28.6	—	16.7	38.5	22.6	22.3	35.4	24.9	26.9	27.9	33.8	34.1	32.0	35.3	42.9	43.5	41.8	58.6	47.1	44.5	20.1
K. massai																						
Gebel Zelten																						
MNHNP Z 1961	1	21.2	11.0	9.7																		
	r	21.6	10.5	9.4	26.1	13.8	18.7	26.2	17.1	23.2	20.9	26.9	21.8	27.6	29.4	32.8	34.7	33.0	41.0	34.4	29.4	13.7
MNHNP Z 1961	r												26.1	22.9	24.3	29.2	≥26.2	27.4				
MNHNP Z 1961	r												25.9	±24.7	≤25.6	31.5	>30.4	>28.3				
K. gigas																						
Quantougou																						
IVPP cast type	1				31.4	18.9	>22	29.5	22.3	—	24.0	28.5	28.8	26.9	29.9	36.0	36.2	36.4	—	36.9	—	—
Maerzuizigou																						
IVPP V 8501	1	≥17.5	9.9	12.5	29.7	17.2	25.0	32.0	20.8	27.5	22.9	27.9	30.9	28.3	30.7	39.6	36.7	35.6	48.1	37.5	36.7	±23.2
	r	17.4	10.1	12.8	29.2	16.6	24.7	31.7	21.4	24.5	25.8	28.7	30.5	28.6	30.0	39.5	36.4	36.0	47.5	38.0	34.9	±21.6
BNHM BPV-900	1	≥18.0	..	..	29.5	16.3	22.1	28.7	±19.5	26.2	25.2	28.7	28.1	..	..	40.1	..	..	..	..	..	..
	r	—	—	—	..	..	..	29.7	16.5	22.5	25.3	..	±29.2	..	..	40.5	..	..	..	..	..	..
BNHM BPV-901	1	18.9	9.1	11.0	—	—	—	29.9	19.0	24.3	24.4	25.3	31.5	28.0	28.9	37.9	34.6	34.3	47.4	37.6	36.9	24.8
	r	19.4	10.6	9.2	—	—	—	29.8	19.2	23.5	23.7	24.9	31.6	27.0	29.3	37.9	34.2	33.5	46.2	37.1	37.3	20.6
BNHM BPV-902	1				26.9	16.1	21.6	27.8	19.0	25.7	24.5	25.8	30.6	27.5	28.9	37.7	34.1	34.3	42.2	37.4	33.1	..
	r	18.9	<10.3	10.7	27.2	16.9	21.5	27.5	20.7	23.6	24.2	26.5	30.9	26.9	28.1	37.6	34.0	33.9	44.0	37.7	33.9	..
BNHM BPV-903	1	21.0	10.1	12.4	27.2	15.8	>22.7	31.7	19.2	26.3	25.7	28.0	±34.2	29.5	≤32.4	38.2	39.0	37.5	57.8	41.6	37.6	22.7
	r	>20.3	10.4	14.6	≥29.8	15.9	21.4	31.5	19.0	26.1	25.5	27.5	33.2	±30.7	32.0	41.1	38.6	38.1	58.2	43.1	38.2	25.4
BNHM BPV-909	1	20.4	10.9	12.9	30.6	17.0	22.7	32.1	20.3	25.1	25.9	26.1	32.2	—	31.6	40.5	38.4	37.2	54.1	41.6	35.3	18.7
	r	20.2	10.1	12.8	30.8	17.1	22.1	30.7	20.0	26.3	25.0	28.3	31.9	30.4	31.8	39.4	37.0	37.1	53.0	39.7	35.0	21.0
BNHM BPV-910	1	19.7	10.2	9.1	27.1	16.5	21.5	31.2	21.8	26.5	25.0	27.0	31.5	34.5	—	40.5	33.0	33.5	53.6	37.0	31.0	..
	r	19.0	11.0	9.5	27.8	18.0	21.7	30.0	20.0	27.0	23.6	27.5	30.5	34.0	32.5	39.5	33.0	33.0	54.0	38.0	32.0	..
Bunolistriodon																						
B. affinis																						
Bugti																						
IM B 528	r										13.5	16.2	15.8	15.5	16.3							
B. anchidens																						
Rusinga R1																						
KNM-RU 2780	1				19.7	9.7	11.6				14.3	17.7	19.0	18.3	20.3	21.3	—	22.1	28.6	25.3	23.2	9.7
KNM-RU 2781	r										13.9	16.3	18.3	18.2	19.3	21.0	21.6	±22.0	28.0	25.2	23.3	9.4
KNM-RU 2782	1							—	—	15.1	13.8	16.0	18.5	18.2	19.4	20.7	21.7	≥21.8				
B. jeanneli																						
Moruorot																						
MNHNP 1933-9	1							21.0	14.3	≤16.7	16.1	19.7	21.1	21.1	20.6	23.3	25.0	22.9	27.5	23.8	20.5	..
(holotype)	r							20.8	14.6	16.8	16.0	19.6	21.3	20.1	20.1	23.8	24.2	23.2	28.7	23.6	20.6	..
B. sp.																						
Baragoi BAR																						
KNM-BG 14778	1												—	—	15.3	—	16.3	—				
B. aff. latidens																						
Quinta da Farinheira																						
CEPUNL 4	r										13.8	16.9	16.7	17.7	17.9	20.3	23.7	22.4	29.5	24.9	21.3	..
CEPUNL 6	r				14.9	..	10.7	16.4	..	14.4												
Quinta da Raposa																						
CEPUNL 35	..												—	—	—	20.7	22.3	22.6	26.1	22.5	20.7	..
Quinta Grande																						
CEPUNL 29	r															20.9	22.7	21.5	27.9	23.8	21.3	..
Quinta das Pedreiras																						
CEPUNL 55	r															20.8	20.8	19.9	24.0	22.1	17.7	..
La Artesilla																						
MPZ 6450	1										12.5	15.0	16.3	15.7	15.6							
MPZ 6451	r															>18.8	>16.5	19.1	>24.4	21.6	18.5	
MPZ 6452	1															20.0	—	19.4	±25.2	20.9	15.3	
MPZ 6453	r							16.0	..	15.4	12.7	15.4										
MPZ 6457	1	8.6	5.1	5.2							13.9	15.9	18.4	17.2	17.1	21.3	20.9	21.3	26.2	21.9	19.0	11.6
MPZ 6459	r				16.0	9.8	—	16.5	11.1	—												
B. latidens																						

		P^1			P^2			P^3			P^4		M^1			M^2			M^3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Sigmaringen																						
PIMUZ A/V 115	r												16.8	16.3	16.1	20.3	19.1	19.4				
Inönü I																						
MTA AKI-3/9	1										13.2	15.0	—	—	—	21.4	19.6	21.3	±26.1	<23.7	—	—
MTA AKI-3/166	r															21.4	21.3	21.1	26.0	23.5	18.4	—
MTA AKI-3/780	1							15.7	9.0	14.8	13.6	14.4	16.9	16.3	16.3	—	—	—	26.6	20.9	18.9	10.8
	r				11.4	6.5	9.1	15.7	9.0	14.6	13.3	13.5	17.0	16.2	16.5	—	20.9	—				
Schlatt																						
NMB OSM 1060 cast	r												±18.2	—	16.4	18.5	19.3	≥19.1	22.8	20.5	17.9	..
B. lockharti																						
Pellecahus																						
UCBL 320293	1															21.8	22.8	22.4	—	—	—	—
La Romieu																						
UCBL 320272	1															20.8	20.9	21.0	25.1	22.4	19.2	..
UCBL 320305	1												19.1	19.1	19.2	22.0	24.8	24.3				
UCBL 320288	r							17.9	11.8	16.3	14.3	15.8	20.3	20.1	19.7	23.8	24.2	25.2				
UCBL 320295	1							18.3	11.9	17.2	13.7	15.9	18.7	>17.7	19.0	22.5	22.2	23.1				
Langenau 1																						
SMNS 41631	r				15.3	..	13.4	18.8	..	17.2	15.0	18.1	16.8	..	19.9	21.8	..	24.2	31.3	24.1	..	..
Ravensburg																						
NMB TD 543	r															20.3	20.9	20.8	28.3	22.8	19.4	9.2
B. intermedius																						
Maerzuizigou																						
BNHM BPV-930	1							17.8	10.0	13.1	—	—	—	—	—	21.0	20.0	20.8	28.4	22.2	20.0	10.0
	r										15.2	16.5	18.4	18.0	18.0	21.4	20.5	19.4	30.1	22.0	18.9	9.8
BNHM BPV-952	1																		—	—	..	..
Listriodon																						
L. pentapotamiae																						
Marianwala Kas																						
BSPHGM 1956 II 109	r										14.8	15.0	—	16.1	—							
BSPHGM 1956 II 77	r															—	—	—	—	24.2	23.2	—
Sosianwali																						
BSPHGM 1956 II 76	1				13.6	—	11.9	16.3	10.5	≥15.6	14.0	17.3	17.2	—	17.2							
BSPHGM 1956 II 88	r															18.0	18.4	18.0	19.7	19.8	17.8	..
Kanatti Chak 7																						
BSPHGM 1956 II 112	1												15.5	15.0	14.8	18.4	17.9	18.2				
Kadirpur																						
BSPHGM 1956 II 106 a, b	1												19.0	17.2	18.1	22.2	20.0	21.6				
Kundal Nala 2																						
BSPHGM 1956 II 37	1				11.5	7.5	10.5	14.8	9.3	13.5	12.3	14.8	>14.3	—	15.6	19.9	17.7	18.1	—	19.8	—	..
	r				11.7	8.1	10.3	>12.6	8.8	13.5	12.9	14.7	—	—	—	—	—	—	>21.7	19.3	17.9	..
Chinji																						
IM B 541	r				12.3	8.2	10.9	14.9	10.4	14.5	12.2	16.1	16.0	15.2	16.2	19.2	18.4	19.8	23.3	21.2	18.9	13.4
L. splendens																						
Sansan																						
MNHNP Sa 4298	r										15.4	15.7	17.4	..	16.9	20.3	..	20.0	24.5	21.0	..	..
MNHNP Sa 4299	r												16.6	..	16.3	20.2	..	19.0	24.6	21.9	..	..
MNHNP Sa 10.141	1												14.5	—	—	18.8	..	18.9	±22.0	±21.0	..	..
	r				14.8	..	9.3	14.6	..	14.0	—	—	14.4	..	16.0	—	..	±19.0	23.0	20.0	..	..
Paşalar																						
PDTFAU F402	r							18.4	11.3	16.0	16.5	18.0	>17.6	>16.6	17.0	21.5	21.2	21.3	28.4	23.7	19.9	11.4
Simorre																						
MNHNP Si 156	1				—	—	—	—	—	—			15.8	..	16.0	20.1	..	19.8	25.1	20.9	..	..
	r				13.7	9.1	11.5	16.3	10.9	14.3			16.0	16.9	17.1	19.8	20.2	20.4	24.6	22.1	18.9	..
Villefranche d´Astarac																						
MNHNP 4298	1										15.4	16.1	17.1	16.6	17.7	20.5	21.7	21.7	25.5	22.9	19.5	..
MNHNP VAS 13	r												—	—	>16.7	20.4	20.5	21.3				
L´Île-en-Dodon																						
FMNH cast of BMNH 33577	..				13.8	8.3	10.9	16.2	≥9.8	≥13.3	12.6	≥15.2	17.8	16.5	16.6	20.2	19.9	19.8	24.9	21.3	18.5	..
Xinan																						
IVPP V8283	1				—	—	—	18.7	—	—	15.3	19.4	—	19.6	—	22.5	24.8	≥24.0	28.7	25.3	22.5	..
	r				—	—	—	19.1	12.1	17.8	15.8	19.4	—	—	—	≥21.4	—	—	28.5	—	23.8	..
IVPP V8285	1				14.8	8.7	12.8	19.5	10.3	16.1	17.2	17.7	—	—	19.9	22.9	23.5	22.6	29.1	24.3	20.4	..
	r				14.6	8.2	12.3	17.3	10.9	16.4	15.1	17.7	19.2	≥19.6	19.8	23.0	23.6	23.6	28.1	24.2	21.1	..
Çandir																						
PIMUZ CA —	r				14.7	9.3	≥11.9	17.2	11.7	16.3	14.9	17.8	18.5	17.6	18.0	21.9	21.6	21.3				
MTA —	1							18.5	12.7	16.8	15.3	19.4	20.7	20.8	20.6	24.1	24.8	24.9	29.5	27.1	25.3	..
	r							18.4	12.9	16.5	15.7	18.3	19.5	20.0	20.4	23.9	24.7	24.6	30.6	27.1	25.0	..
Manchones I																						
IVAU MA 115	r				>13.8	9.8	11.2	17.2	10.5	14.2												
IPS 1097	1										15.0	17.0	17.4	19.0	19.2	22.2	23.0	22.8	28.3	25.0	21.3	..
IPS 1098	r										15.4	17.0	17.4	19.0	19.3	21.4	23.0	22.8	28.0	24.9	21.8	..
Arroyo del Val IV																						
IVAU AR IV 21	r															21.8	22.0	—	29.7	24.2	22.8	..
IVAU AR IV 44	1							18.3	10.7	18.4	≥16.8	—										
IVAU AR IV 73	r															23.4	21.1	21.9	27.7	23.1	21.3	..
IVAU AR IV 74	r							18.1	13.2	—	15.8	±18.2	18.6	17.9	18.5							
IVAU AR IV 75	1										16.7	18.3	18.4	17.8	18.5							
IVAU AR IV 82	1							18.8	11.9	18.5	17.3	≥19.3	17.4	18.5	19.2	23.8	24.3	23.7	29.4	25.6	23.9	..

		p^1			p^2			p^3			p^4		M^1			M^2			M^3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
	r							18.7	12.4	18.8	17.2	19.7	15.9	18.5	19.0	21.5	23.0	23.4	30.2	25.2	23.8	..
IPS AR IV 40	1										17.8	20.2	—	—	—							
MPZ AV-19	1							18.4	10.8	17.4	15.5	17.4	17.7	17.5	18.0	20.7	20.5	21.0	24.1	21.5	20.4	..
Arroyo del Val VI																						
IVAU AR VI 13	r												18.5	17.4	17.4	21.8	20.9	21.2				
La Grive																						
MGL LGr 721 (composite)	r				14.0	9.7	11.4	15.2	10.9	15.3	13.1	16.5	17.8	17.6	17.9	20.6	20.8	20.4	24.1	21.9	18.5	..
MGL LGr 742	1										14.5	17.1	15.8	15.8	16.7	19.2	19.0	20.1				
Cerro del Otero																						
MNCN NM 18006	1				>13.6	9.0	13.7	>18.1	10.5	16.7	≥13.0	—	>18.5	—	—	22.8	23.8	—	28.5	24.2	20.8	..
	r							≥17.5	—	17.1	14.4	18.3	>18.3	20.5	—	>22.5	—	—	28.8	24.2	22.2	..
MNCN NM 18007	r										15.6	19.2	18.0	20.0	20.7	21.8	25.3	25.4				
MNCN NM 18011	r							—	—	15.9	14.3	17.1	≥17.9	—	21.0							
Sinap																						
MNHNP —	1				≥13.4	—	—	15.6	±10.7	16.0	13.2	16.3	—	—	—							
	r							16.0	11.2	16.5	13.1	16.6	15.7	—	—	19.8	—	19.4	23.1	21.0	20.0	..
Sant Quirze																						
IPS VP 1037	1							19.0	..	16.8	15.8	18.3	17.3	..	18.7	20.3	..	..				
Wien Heiligenstadt																						
NMW SK 1613	1				14.9	8.8	12.2	17.4	11.6	14.9	14.5	18.3	18.9	17.4	17.3	—	—	—	25.4	23.3	20.6	
	r				14.8	9.8	12.0	16.8	11.8	15.6	14.5	18.3										
Castell de Barberà																						
IPS —	1				14.4	..	11.5	14.7	..	16.2						22.3	21.5	21.0	25.3	22.5	19.7	..
	r				14.4	..	11.4	14.7	..	16.6	15.0	16.8	17.4	16.7	17.1	22.1	21.5	21.5	25.2	23.1	20.8	..
Hostalets																						
IPS —	r															20.3	21.6	21.8	25.8	21.8	19.8	..
Can Ponsic																						
IPS 1981/1979/1980 /1977/1976/1975	1				≥15.0	..	>11.0	16.7	..	15.7	14.8	16.4	18.5	18.2	18.5	23.9	21.4	20.9	25.0	22.0	20.2	..
Listriodontinae indet.																						
Fort Ternan																						
KNM-FT 3321	1				±17.5	10.2	—	17.4	10.4	>13.4												

TABLE 13 Measurements in mm of the mandible. Depth below a certain tooth and width of that tooth, length of diastemata and size of the symphysis.

	m/f		P_2		P_3		P_4		M_1		M_2		M_3		Diastemae			symhysis	
			DT	D	DT	D	DT	D	DT	D	DT	D	DT	D	C_x-P_1	C_x-P_2	P_1-P_2	DAP	H
Lopholistriodon																			
L. moruoroti																			
Moruorot																			
KNM-MO 5	f	l							≥6.1	±19.0	7.4	20.0	8.0	20.8					
		r					≥4.6	20.2											
Maboko																			
KNM-MB 10332	?	r			—	20.6	3.6	21.5	5.1	21.9	6.2	21.6							
L. kidogosana																			
Ngorora D, 2/10																			
KNM-BN 969	m																	>29	10.0
Kubanochoerus																			
K. massai																			
Gebel Zelten																			
MNHNP Z 1961	f	l			—	51.9	—	50.6					±42.4	61.8				—	>22.7
MNHNP Z 1961	?	r									24.6	60.3	26.8	71.4					
MNHNP Z 1961	?	r									23.8	50.5	26.5	58.4					
MNHNP Z 1961	f	r	13.6	±61.1	±16.9	±60.8							>24.4	±63.7					
MNHNP Z 1961	m	r													7.6	..	±23.4	129.5	26.9
MNHNP Z 1961	m	r													—	—	>12.0		
K. minheensis																			
Nanhawangou																			
IVPP V 6021	m	l													—	—	±32	—	—
		r													—	±57	—	—	—
K. gigas																			
Maerzuizigou																			
IVPP V 8502	m	l													13.0	60.6	29.0	>120	34.3
		r													7.9	58.2	31.0		
BMNH BPV 905	m?	l													—	—	26.7	145.5	±30.4
		r													5.8	57.4	33.5		
Bunolistriodon																			
B. anchidens																			
Rusinga Rl																			
KNM-RU 2785	m	l	8.0	39.1	—	35.2	11.4	33.7	14.7	38.3	>17.1	41.2	19.1	43.7	2.4	—	14.6	74.3	22.1
		r													±3.6	±26.5	14.4		
B. fategadensis																			
IM 18098 (K50/952)	f	l		46		44	14.0	43	17.2	43	20.6	±46	19.9	48					
B. aff. latidens																			
Olival da Suzana																			
CEPUNL 16	?	r			>9.8	39.5	13.3	37.0	—	38.5	>17.8	40.9	21.2	44.8					
La Artesilla																			
MPZ 6442	?	r											16.0	51.0					
B. lockharti																			
Pellecahus																			
NMB BG 2459	m	l													±7.6	±54.5	39.8		
B. intermedius																			
Yehuli Juanzhi																			
IVPP V 9520	m	l									16.9	47.5	18.8	45.7					
		r							≥13.6	±44	17.1	47.2	18.9	—					
Listriodon																			
L. pentapotamiae																			
Dhok Talian loc. 189																			
PMNH MV 31, 527	f	l	7.9	49.4	10.0	48.7	12.1	51.2	13.3	49.8	16.7	53.2	19.4	56.6	11.4	58.1	42.7	98.1	±19.2
		r													10.4	61.2	45.4		
Jandawala SO Kotchra																			
BSPHGM 1956 II 41	f?	r			9.8	47.7	12.2	47.1	13.3	47.3	16.4	48.3	18.5	49.0					
Kanatti Chak 5																			
BSPHGM 1956 II 40	?	l			—	41.4	—	41.1	13.2	41.6	15.6	39.9	18.3	41.7					
L. splendens																			
Simorre																			
MNHNP Si 155	f	l											18.6	48.5		67			
		r											18.0	47.0		52			
Çandir																			
PIMUZ CA I/22	f	l														71.5		107.5	18.4
		r														>64.8			
Arroyo del Val IV																			
IVAU AR IV 2	?	r														>30			
IVAU AR IV 87	?	l							—	51.0	≥18.0	55.8	—	57.9					
MPZ AV-57	m	l							13.5	41.2	16.5	41.4	18.2	45.1					
Manchones I																			
IVAU MA 5216	?	l	—	≥44.4	—	≥43.9	—	>46.2	—	>53.0									
Arroyo del Val VI																			
IVAU AR VI 46	f?	l	—	≥46.5	—	≥43.6	—	—											
Cerro del Otero																			
MNCN NM 18060	f	l																—	12.1
Hostalets																			
CJFV —	m	r					10.3	56								>54			
CJFV —	?	l									—	55	—	55					
Markt Rettenbach																			
BSPHGM 1929 I ´47	f	l														71.5			
		r														71			

TABLE 14 Measurements of the skull in mm. Width of the palate between certain cheek teeth, the length of the palate posterior to M^3, width of the frontals, parietals and occipitals, height foramen magnum-occipital, length and width of the skull, width of the occipital condyles and height and width of the foramen magnum.

		width of palate at							palate	Width			Height	total	total	occ.	For.	magn.
	mf	P^1	P^2	P^3	P^4	M^1	M^2	M^3	p. M^3	front.	par.	occ.	occ.	length	width	c. DT	H	DT
Kubanochoerus																		
K. massai																		
Gebel Zelten																		
MNHNP Z 1961	f	—	—	—	—	—	—	—	11	..	..	..	..	±490	±231.8	..	..	..
K. gigas																		
Maerzuizigou																		
IVPP V 8501	m	68.6	54.2	44.9	49.6	61.6	62.6	62.9	94.9	..	4.4	>97	±115	675	..	103.7	40.3	±53
Lopholistriodon																		
L. kidogosana																		
Ngorora D1, 2/10																		
KNM-BN 992	m			21.7	25.3	28.6	29.4	29.9	>20							36.1	..	18.4
Bunolistriodon																		
B. jeanneli																		
Moruorot																		
MNHNP 1933-9	?			±39.9	±34.2	39.7	39.7	38.0	10.0									
Listriodon																		
L. pentapotamiae																		
Kundal Nala 2																		
BSPHGM 1956 II 37	?			±24.0	±28.2	±41.6	40.8	35.2	—	±92	±40	±41.8	69.6	—	131.6	±48.8	—	—
L. splendens																		
Sansan																		
MNHNP Sa 10.141	m											≤73				50	—	±20.5
Xinan																		
IVPP V8283	m			34.6	31.2	—	±42.7	±45.6										
IVPP V8285	f								>23	>80.9	±19.8	—	≥95					
Arroyo del Val IV																		
IVAU AR IV 82	?							44.0	36.7									
MPZ AV-19	?			(37.4)	(42.0)	(43.4)	(45.0)	—										
Wien Heiligenstadt																		
NMW SK 1613	?	33.0	34.0	±33.0														

TABLE 15a Measurements of the postcranial skeleton in mm.

Axis		**Body** **DAP**	**DTp**	**Hp**	**Total** **H**	**Vertebral Foramen** **H**	**DT**	**Craneal artic.** **DT**	**Caudal artic.** **DT**
Kubanochoerus massai									
Gebel Zelten									
MNHNP Z 1961		62.6	38.8	34.8	--	15.1	21.3	66.4	44.7
MNHNP Z 1961		61.0	--	--	--	--	--	58.8	--
MNHNP Z 1961		56.1	38.2	32.6	--	--	--	65.2	--

Humerus distal		**DAPd**	**DTd**	**DTdf**	**R1**	**R2**	**R3**	**R4**
Nguruwe kijivium								
Mteitei 32								
KNM-MV 18	l	..	24.4	16.7	15.4	11.4	13.4	11.1
Rusinga R30								
KNM-RU 5343	r	--	--	16.5	14.5	9.5	10.6	9.4
Kubanochoerus massai								
Gebel Zelten								
MNHNP Z 1961	..	62.3	54.3	41.0	40.4	28.3	33.5	27.6
MNHNP Z 1961	..	57.4	51.6	39.2	36.8	26.6	31.8	27.5
Bunolistriodon								
B. anchidens								
Rusinga R1								
KNM-RU 3342	l	--	43.6	31.4	>24.4	19.8	20.9	>17
B. lockharti								
Langenau 1								
SMNS 41231	l	..	..	37.4	--	--	--	26.0
SMNS 41418	..	..	..	34.5	32.0	--	--	28.2
Listriodon splendens								
Paşalar								
PDTFAU G 932	l	--	--	33.2	31.6	22.1	25.4	24.6
La Grive								
MGL LGr 718	r	--	>55.5	42.2	30.6	29.4	30.0	26.0
MGL LGr 2644	l	--	≥42.3	34.3	--	22.9	27.7	24.0
La Chaux-de-Fonds								
MHNCF --	r	--	--	34.8	--	--	--	--
La Cisterniga								
MNCN NM 1292	l	--	--	38.5	≥38.0	27.1	31.3	27.5
MNCN NM 1292	l	--	--	>37.1	>35.9	25.9	29.9	25.1
MNCN NM 1421	r	>45.7	52.8	36.6	33.5	25.7	31.8	27.3

Radius		**DAPp**	**DTp**	**L**	**DAPd**	**DAPdf**	**DTd**	**DTdf**	**Fsca**	**Flun**
Kubanochoerus massai										
Gebel Zelten										
MNHNP Z 1961	r	..	31.9							
Bunolistriodon										
B. anchidens										
Rusinga R1										
KNM-RU 5853	l	20.9	30.8							
Listriodon splendens										
Paşalar										
PDTFAU G 305	l	21.1	32.8							
PDTFAU G 1808	r	--	35.4							
PDTFAU G 1885	l	22.7	37.9							
Arroyo del Val IV										
AR IV 400	l	27.9	42.3							
La Grive										
MGL LGr 607	l	--	--	--	25.2	18.5	33.7	29.1	15.5	14.7
La Ciesma										
DPZ 2009	..	--	--	--	..	19.9	..	28.9		

Ulna		**head** **DAP**	**DT**	**..** **DAP**	**DT**	**max** **DAP**	**DT**	**Olecranon** **La**
Kubanochoerus massai								
Gebel Zelten								
MNHNP Z 1961	r	--	--	--	--	41.9	..	--
MNHNP Z 1961	r	--	--	--	--	--	24.9	--
Listriodon splendens								
Arroyo del Val IV								
IVAU AR IV 186	l	--	--	39.4	--	--	31.5	--

MC III		**DAPp**	**DTp**	**L**	**l**	**DAPd**	**DTd**
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	l	>26.5	29.7	±126.2	120.5	--	24.2
MNHNP Z 1961	r	≥28.7	--	116.3	110.5	--	25.3
MNHNP Z 1961	r	--	34.9	--	--	--	--
MNHNP Z 1961	r	--	>27.1	--	--	--	--
Bunolistriodon							
B. aff. latidens							
La Artesilla							
MPZ-6473	r	20.6	20.4				
B. lockharti							
Buñol							
FBS 13	l	--	>23.9				

MC III		**DAPp**	**DTp**	**L**	**1**	**DAPd**	**DTd**
Pellecahus							
UCBL 320282	r	25.0	..				
La Romieu							
NMB GB 1265	r	21.7	22.1				
Langenau 1							
SMNS 41234	1	27.1	26.0				
Szentendre							
HGSB V 13077	r	--	≥24.6				
B. guptai							
?HGSP 8316							
HGSP 8316/1982	1	21.8	25.8				
Listriodon splendens							
Arroyo del Val IV							
IVAU AR IV 114	1	--	28.5				
MNCN --	1	>23	26.8				
Murrero							
IVAU MR 10	1	--	29.8	99.2	..	22.1	24.1
La Grive							
MGL LGr 755	r	>27.0	30.3	--	109.6	--	25.6
MGL LGr 756	r	>22.4	>25.2	105.7	97.3	22.1	22.0
MGL LGr 1675	r	>21.7	>23.1				
MGL LGr 1679	r	>19.6	23.7				
La Cisterniga							
IPS 1133	r	28.2	25.4				

MC IV		**DAPp**	**DTp**	**L**	**1**	**DAPd**	**DTd**
Nguruwe kijivium							
Mfwanganu							
KNM-MW 516	1	9.0	10.7	--	--	--	
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	1	20.8	19.1	110.8	99.2	23.6	21.3
MNHNP Z 1961	1	20.3	20.2	--	--	--	--
Bunolistriodon							
B. aff. latidens							
La Artesilla							
MPZ-6474	1	16.2	20.2				
B. lockharti							
Pellecahus							
NMB GB 2460	r	≥17.9	±17.8				
UCBL 320282	r	18.9	20.5				
UCBL 320282	r	18.1	19.9				
Buñol							
PAN 681	r	18.2	19.9	103.0	..	21.0	>19.5
FBS 11	r	19.0	22.0				
Can Canals							
IPS 1177	1	--	--				
Listriodon splendens							
Paşalar							
PDTFAU G 742	1	17.6	17.7				
PDTFAU G 879	1	≥17.6	19.9				
La Grive							
MGL LGr 752	r	18.9	21.7	106.0	96.5	22.0	20.6
MGL LGr 754	1	>17.1	>17.9	>96.8	90.6	>19.5	19.8
MGL LGr 1749	1	16.6	19.4	96.1	87.3	19.6	19.5
MGL LGr 1753	r	>18.4	>20.9				
S. Quirze							
MGSCB 48562	r	16.1	18.3				

Phalange 1, III/IV		**DAPp**	**DAPpf**	**DTp**	**L**	**DAPd**	**DTd**
Nguruwe kijivium							
Mfwanganu							
KNM-MW 517	r	9.6	..	10.8	--	--	--
Kubanochoerus							
K. hussaini							
HGSP 8213							
HGSP 8213/450	r	43.2	..	55.7	77.8	27.1	42.3
HGSP 8405							
HGSP 8405/3047	1	--	--	--	>58.5	20.1	32.9
K. massai							
Gebel Zelten							
MNHNP Z 1961	r	19.7	..	23.4	48.2	≥12.9	20.0
K. gigas							
Kundal Nali							
IVAU CHK 168	1	32.3	..	32.3	60.3	31.7	21.7
Bunolistriodon							
B. lockharti							
La Romieu							
UCBL 320298	1	19.9	..	--	--	--	--
Pellecahus							
UCBL 320310 pes, IV	1	19.6	..	22.6	±43.5	±13.0	--
NMB GB 1457	r	20.7	20.1	22.5	49.6	12.2	≥15.8
Langenau 1							
SMNS 40681	r	19.0	..	18.5	--	13.1	15.5
Buñol							
FBS 17	1	20.6	..	22.8	--	--	--
FBS 21	1	--	--	--	--	13.2	17.0

Phalange 1, III/IV		**DAPp**	**DAPpf**	**DTp**	**L**	**DAPd**	**DTd**
FBS 22	r	--	--	--	--	14.3	17.6
PAN 23	r	>18.2	..	21.8	--	--	
PAN 209	r	--	--	17.6	--	--	--
IVAU BU 53	r	22.3	..	22.9	45.3	12.8	16.5
Monteagudo							
IPS 1511	r	±20.6	19.5	..	>49.0	12.0	14.6
Pontlevoy							
NMB Fa 209	r	17.0	14.7	17.5	43.1	11.3	13.5
B. aff. *latidens* I							
Tarazona							
UPV T2.49	1	--	--	--	--	11.5	15.4
Listriodon splendens							
Paşalar							
PDTFAU G 43	r	20.2	..	22.8	--	--	--
PDTFAU G 1341	r	--	--	--	--	13.4	15.8
PDTFAU G 2114	1	19.3	..	21.3	47.4	12.8	15.7
Manchones I							
IPS 1865	r	21.7	..	23.2	51.6	14.4	17.7
La Grive							
UCBL --	1	18.1	..	19.3	46.5	13.1	15.4
UCBL --	1	21.2	..	19.8	48.4	13.5	17.0
UCBL --	1	18.6	..	19.4	47.5	12.0	15.3
UCBL --	1	19.6	..	22.1	44.1	14.1	17.8
UCBL --	r	20.2	..	20.2	45.5	12.8	16.3
MGL LGr 1743	1	juvenile				13.3	17.6
MGL LGr 1862	1	18.0	17.2	19.2	46.3	11.8	14.6
MGL LGr 1863/1685	1	19.6	16.7	18.4	45.9	12.3	15.9
MGL LGr 1864	1	21.0	17.5	20.4	48.7	12.3	17.4
MGL LGr 2639	r	22.2	19.7	23.6	52.6	15.7	18.6
La Chaux-de-Fonds							
MHNCF --	1	19.3	17.9	19.9	47.8	12.5	16.3
La Cisterniga							
MNCN M 610	1	18.8	20.1	20.1	48.2	12.4	16.2

Phalange 2, III/IV		**DAPp**	**DAPps**	**DTp**	**L**	**DAPd**	**DTd**
Lopholistriodon							
L. moruoroti/pickfordi							
Maboko							
KNM-MB 10304	1	5.5	5.1	5.1	9.2	4.3	4.3
KNM-MB 14458	1	6.6	..	6.5	8.8	5.8	6.2
Kubanochoerus							
K. hussaini							
HGSP 8127							
HGSP 8127/432	r	27.1	..	30.1	41.4	22.7	29.7
K. massai							
Gebel Zelten							
MNHNP Z 1961	r	20.9	19.4	18.2	29.6	16.6	19.0
Bunolistriodon							
B. aff. *latidens*							
La Artesilla							
MPZ-6482	1	17.2	..	15.0	25.9	13.5	14.3
MPZ-6483	r	18.9	..	15.8	25.8	13.8	13.9
B. lockharti							
La Romieu							
UCBL 320308	r	17.3	..	14.6	24.6	12.0	14.6
UCBL 320308	r	17.0	..	14.5	23.8	12.9	14.4
UCBL 320308	1	17.8	..	15.1	26.3	12.1	12.9
Pellecahus							
UCBL 320310 pes IV	1	19.2	..	16.2	26.4	14.4	16.0
Buñol							
IPS 1145	1	--	--	>16.9	25.8	--	>16.9
BUS 4	r	20.1	18.8	16.5	27.6	>13.5	13.9
FBS 16	1	20.8	19.9	18.5	29.3	17.3	19.7
FBS 19	r	18.3	17.5	16.4	26.4	13.3	13.6
FBS 20	r	>17.8	>17.6	15.7	±28.6	--	--
PAN 37	1	--	--	--	--	>15.2	18.0
Szentendre							
HGSB V 13077	r	21.1	19.0	23.0	--	--	--
B. aff. *latidens* I							
Valdemoros IA							
IVAU VA IA --	r	--	--	--	--	10.2	12.3
Listriodon							
L. pentapotamiae							
Kanetti							
IVAU KA 54	1	--	..	14.6	24.1	13.9	14.1
Cheski Wala							
IVAU CHC 133	r	20.4	..	15.7	28.5	15.4	15.1
IVAU CHC 134	r	--	..	15.4	17.8	--	14.1
IVAU CHC 137	1	>18.4	..	15.1	26.9	13.9	13.5
Mochi Wala							
IVAU CHO 90	r	19.9	..	15.2	28.1	12.3	13.7
L. splendens							
Paşalar							
PIMUZ --	1	19.8	18.4	15.5	28.6	15.2	14.4
PIMUZ --	1	20.1	18.9	16.3	≥29.8	14.6	15.7
PDTFAU F 89	r	19.3	19.3	17.9	28.9	--	17.9
PDTFAU F 348/1	r	19.2	18.4	17.2	--	--	15.1

Phalange 2, III/IV		**DAPp**	**DAPps**	**DTp**	**L**	**DAPd**	**DTd**
PDTFAU F 348/2	l	--	--	--	±28	--	--
PDTFAU F 590/9	r	21.0	19.5	16.8	--	--	--
PDTFAU G 348	r	20.9	20.0	18.3	30.2	16.6	17.1
PDTFAU G 428	l	20.6	19.5	16.1	30.3	15.4	14.7
PDTFAU G 1016	r	20.6	20.0	16.7	29.2	14.7	14.5
Manchones I							
MA I 136	r	20.2	19.6	16.0	19.6	15.8	>13.5
Arroyo del Val IV							
IVAU AR IV 98	r	>19.7	>18.7	16.8	28.7	15.3	13.7
IVAU AR IV 113	l	23.7	22.4	20.5	≥32.9	17.6	18.8
Arroyo del Val I							
IVAU AR I --	l	23.3	21.5	19.7	--	--	--
Murrero							
IPS 1070	l	18.0	..	16.8	24.8	15.9	13.9
La Grive							
UCBL --	l	17.6	..	15.6	24.3	13.9	13.7
UCBL --	r	19.7	..	15.4	28.2	>14.2	14.4
UCBL --	r	19.3	..	15.5	29.1	15.0	14.0
UCBL -- (juvenile)	r	--	--	--	--	17.3	12.9
MGL LGr 2240	l	17.6	16.8	15.1	27.4	12.5	11.7
MGL LGr 1693	r	22.1	20.9	19.0	32.8	≥16.0	--
MGL LGr 1695	r	20.3	19.6	17.0	31.3	15.0	15.2
MGL LGr 1697	l	20.5	20.0	16.1	30.8	14.7	13.9
MGL LGr 1704	r	--	--	17.2	28.4	17.4	≥15.3
MGL LGr 1723	r	22.8	21.2	17.8	31.2	15.8	17.0
La Chaux-de-Fonds							
MHNCF --	l	--	--	18.9	35.8	17.3	18.5
La Cisterniga							
MNCN NM 1396	l	23.8	22.2	19.9	33.8	18.3	20.5
Hostalets							
MGSCB 48555	r	21.8	20.5	17.1	31.2	16.6	14.9

Tibia		**DAPp**	**DTp**	**L**	**l**	**DAPd**	**DTd**
Kubanochoerus							
K. marymunngui							
Baragoi							
MNHNP Z 1961	l	--	--	--	--	34.5	47.7
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	l	35.7	39.4				
Bunolistriodon							
B. lòckharti							
Langenau 1							
SMNS 41232	r	--	--	--	--	29.0	27.5
SMNS 41233	l	--	--	--	--	..	..
SMNS 41236	r	38.3	37.8	±151	..	19.6	24.4
Szentendre							
HGSB V 13077	r	--	--	--	--	--	--
Listriodon							
L. pentapotamiae							
Cheski Wala							
IVAU ..	r	--	--	--	--	22.1	22.5
L. splendens							
MGL LGr 1659	r	--	--	--	--	26.1	29.9
Cerro del Otero							
MNCN 201	l	..	..	>233.0	..	31.4	36.8
MNCN 201	l	..	..	--	--	±33.0	--
MNCN 201	r	..	..	235.4	..	33.3	29.0

Calcanaeum		**L**	**Lup**	**Llow**	**head**		**tuber**		**facet**		**max**
					DAP	**DT**	**DAP**	**DT**	**DAP**	**DT**	**DAP**
Kubanochoerus											
K. massai											
Gebel Zelten											
MNHNP Z 1961	l	107.6	67.7	±42.9	27.8	21.1	26.2	12.1	31.0	--	43.2
MNHNP Z 1961	r	101.1	62.2	42.8	27.5	21.8	24.5	13.2	29.4	23.7	39.3
K. gigas											
Maerzuizigou											
BMNH	l	±170	±99	±65	±39.6	--	41.5	17.3	46.2	40.2	±63
Bunolistriodon											
B. lockharti											
La Romieu											
UCBL 320301	r	--	61.3	--	26.7	23.8	26.4	15.5	..	26.4	--
Pellecahus											
UCBL 320310	l	>88	59.5	30.8	22.8	21.6	24.1	12.7	..	..	36.1
Buñol											
FBB-206	r	--	--	--	--	--	26.6	14.0	29.0	..	--
Szentendre											
HGSB V 13077	r	--	--	41.5	--	24.2	--	--	30.8	26.2	41.5
B. guptai											
HGSP 8412											
HGSP 8412/3128	r	--	--	--	--	--	--	--	28.5	20.7	--
Listriodon											
L. pentapotamiae											
Burri Wala											
IVAU CHB 26	..	--	--	--	--	--	18.7	9.7	23.3	18.3	--

Calcanaeum		**L**	**Lup**	**Llow**	**head**		**tuber**		**facet**		**max**
					DAP	**DT**	**DAP**	**DT**	**DAP**	**DT**	**DAP**
HGSP 8220											
HGSP 8220/1040	l	--	--	--	--	--	22.5	..	25.1	18.6	--
?HGSP 8302											
HGSP 8302/1305	l	--	--	--	--	--	--	≥12.1	--	--	--
L. splendens											
Arroyo del Val IV											
MPZ DPZ/AV-55	r	--	--	32.9	--	--	--	--	27.5	24.6	37.3
La Grive											
MGL LGr 1901	l	--	--	--	--	--	20.6	10.6	22.9	≥17.3	--
MGL LGr 1908	l	--	--	--	juvenile		22.3	12.2	25.7	--	--
MGL LGr 1910	r	--	--	37.5	--	--	23.5	12.1	28.1	20.9	35.0
MGL LGr 2619	l	82.8	50.1	36.0	19.8	18.4	20.8	11.6	24.5	19.8	31.2
La Chaux-de-Fonds											
MHNCF --	l	--	--	38.7	--	--	--	--	27.8	24.0	35.4
Cerro del Otero											
MNCN 190	r	>91.3	>57.6	33.6	23.2	20.6	23.9	14.3	28.6	22.4	36.5
MNCN 190	r	--	--	34.4	--	--	--	13.5	22.1	20.0	>33.4
La Cisterniga											
MNCN NM 1422	l	--	66.7	--	27.6	23.0	26.8	14.1	31.0	24.8	--
S. Quirze											
MGSCB	l?	--	--	--	≥25.6	≥19.7					

Astragalus		**Lext**	**Lm**	**Lint**	**DTp**	**DTd**	**R**	**d**
Nguruwe kijivium								
Rusinga Kathwanga								
KNM-RU 3036	l	24.1	20.0	21.4	10.5	12.3	13.7	3.5
Rusinga (loc.?)								
KNM-RU 5868	l	25.6	21.1	23.3	11.2	12.2	13.1	4.7
Songhor								
KNM-SO 249	l	25.4	20.7	22.7	12.1	12.4	14.8	4.7
Mfwanganu								
KNM-MW 439	l	>28.5	23.7	26.6	13.4	15.3	16.2	5.8
KNM-MW 543	l	--	--	--	14.2	--	15.7	--
Kubanochoerus								
K. marymunngui								
Baragoi BGX								
KNM-Bg 17970	l	59.9	47.3	54.7	30.3	36.3	34.4	10.7
Baragoi loc.?								
KNM-BG 16903	r	61.4	47.0	≥54.0	28.3	34.1	--	10.7
KNM-BG 16916	l	--	--	--	--	38.0	--	13.1
K. hussaini								
Nyakach-Kaimogool E								
KNM-NC 9797	r	≥65.2	52.5	>61.2	32.3	>37.5	>34.5	--
HGSP 8425								
HGSP 8425/3557	r	102.4	77.2	89.5	55.3	59.0	54.5	20.7
K. massai								
Gebel Zelten								
MNHNP Z 1961	l	--	40.9	46.7	--	29.2	26.6	9.7
MNHNP Z 1961	l	>57.5	±48.2	--	≥26.2	±26.7	--	11.8
MNHNP Z 1961	r	57.6	45.3	53.3	26.3	29.3	28.4	9.8
MNHNP Z 1961	r	56.3	43.8	50.6	27.1	30.8	28.8	10.2
K. gigas								
Maerzuizigou								
BNHM --	l	82.2	62.6	71.5	46.0	52.0	44.7	19.9
Bunolistriodon								
B. anchidens								
Rusinga Rl								
KNM-RU 5089	r	42.7	34.4	39.0	20.4	22.1	22.1	6.3
Rusinga-Kulu								
KNM-RU 5090	r	38.8	31.4	35.0	17.4	19.7	19.6	6.9
B. aff. latidens								
Olival da Suzana								
CEPUNL 27	l	41.7	..	..	22.3	24.4	23.8	8.3
Quinta da Silvéria								
CEPUNL 48	l	42.3	..	..	20.1	23.6	22.8	8.8
Quinta Grande								
CEPUNL 34	l	44.6	..	..	22.4	25.0	24.7	±7.8
Quinta da Lobeira								
CEPUNL 45	l	39.3	..	..	19.4	22.1	22.1	7.9
La Artesilla								
MPZ-6470	l	≥42.1	..	..	20.6	22.1	--	9.2
MPZ-6471	l	45.1	31.4	41.3	22.1	25.3	26.5	9.8
MPZ-6472	r	--	32.9	38.2	20.4	23.4	21.1	±7.6
Tarazona								
UPV T5.1	l	40.6	32.5	--	--	21.4	--	8.3
UPV T6.35	r	>39.5	--	--	20.3	23.4	21.8	7.5
La Hidroélectrica								
IPS 1143	l	40.7	..	..	20.9	>20.3	24.2	7.3
B. M								
Paşalar								
PDTFAU G 790	r	38.4	30.7	35.2	18.1	19.9	21.3	6.9
PDTFAU G 1661	l	--	--	38.9	--	±22.8	--	7.7
B. lockharti								
La Romieu								
UCBL 320301	l	47.5	..	..	>23.3	26.2	28.2	9.8
UCBL 320301	r	52.0	..	..	25.3	27.8	27.6	10.4

Astragalus		**Lext**	**Lm**	**Lint**	**DTp**	**DTd**	**R**	**d**
UCBL 320301	r	51.3	..	..	23.4	26.5	26.8	9.8
Pellecahus								
UCBL 320310	l	47.4	..	..	22.8	27.4	23.9	9.3
Baigneaux-en-Beauce								
NMB SO 1856	r	--	33.5	--	--	22.3	--	7.3
NMB SO 5746	l	44.4	36.2	>40.5	21.2	22.8	24.2	7.5
Buñol								
IPS 1144	l	47.3	..	44.2	±24.3	26.4	25.8	9.5
FBS 7	r	46.4	37.2	42.7	23.8	25.7	24.8	8.4
FBS 8	r	47.4	38.1	43.6	23.5	27.5	26.5	10.0
PAN 915	r	49.5	39.3	45.0	25.5	28.1	27.6	10.3
--	r	47.4	38.2	--	22.1	25.2	--	9.5
Gerlenhofen								
SMNS cast	r	--	--	--	--	23.8	26.5	9.7
Ravensburg								
NMB TD 554	r	48.2	38.5	44.1	23.6	26.0	25.9	8.6
NMB TD 554	l	≥46.0	37.1	>41.7	21.7	23.5	23.7	--
Monteagudo								
IPS 1510	l	47.6	..	42.4	22.1	24.0	26.4	8.2
Pontlevoy								
MNHNP FP 727	r	46.3	36.8	41.9	22.9	25.9	26.1	9.3
Szentendre								
HGSB V 13077	r	51.0	39.0	45.5	25.9	30.5	27.3	10.7
Can Canals								
IPS 1176	l	--	--	--	--	27.2	--	10.4
IPS 1179	l	--	--	--	--	21.8	--	8.5
Quinta Pedreiras								
CEPUNL 60	l	43.4	..	..	20.4	>20.8	23.0	7.9
Quinta da Conceição								
CEPUNL 54	l	45.0	..	..	21.7	23.1	24.2	2.7
B. guptai								
?HGSP 8227								
HGSP 8227/1248	l	--	27.8	30.2	28.0	--	--	--
Listriodon								
L. pentapotamiae								
Dhok Talian loc. 189								
GSP 4484	l	40.2	36.8	44.5	21.8	24.6	..	9.0
Tekunja								
IVAU CHT 89	l	40.0	32.2	36.6	18.2	≥22.3	20.9	±7.7
Mochi Wala								
IVAU CHO 76	r	42.5	34.3	39.6	19.9	>21.6	23.7	±7.0
HGSP 8102								
HGSP 8102/898	r	34.9	28.5	31.0	14.6	17.3	19.0	6.3
?HGSP 8105								
HGSP 8105/52	r	--	--	--	--	--	--	--
L. splendens								
Simorre								
MNHNP Si 170	l	43.0	..	..	20.9	25.8	22.1	9.6
Paşalar								
PDTFAU C 2071	r	--	--	--	26.8	--	--	--
PDTFAU F 347	r	--	--	--	--	--	--	9.6
PDTFAU F 494/8	l	--	--	--	--	27.2	--	9.4
PDTFAU G 447	r	--	--	--	--	27.9	--	9.6
Çandir								
MTA --	r	--	--	--	--	29.3	--	10.9
Manchones I								
MA 119 = MA 271	l	47.7	36.6	41.5	23.4	>23.4	>23.3	11.5
IPS 1867	r	--	--	--	--	30.0	--	9.5
Arroyo del Val IV								
IVAU AR IV 35	r	49.6	39.3	44.8	25.0	28.1	27.9	8.7
IVAU AR IV 65	l	46.2	36.2	42.8	24.3	25.3	25.5	9.1
IVAU AR IV 66	r	46.3	36.7	42.4	23.8	27.6	25.5	8.1
MPZ DPZ/AV-54	l	46.3	..	..	24.2	27.2	25.8	8.5
La Grive								
MGL LGr 757	r	43.1	34.5	38.9	21.7	23.9	23.2	--
MGL LGr 758	l	--	37.9	44.2	24.1	28.3	26.8	±8.6
MGL LGr 759	r	≥43.3	34.5	≥39.3	23.5	26.1	>24.3	9.6
MGL LGr 1532	l	47.9	37.8	42.3	23.3	24.8	25.1	±8.5
MGL LGr 1548	l	40.9	32.4	38.1	22.4	23.7	22.3	6.9
MGL LGr 1549	r	47.5	37.3	42.3	24.6	26.4	26.5	8.0
MGL LGr 1550	l	43.2	34.2	38.3	19.5	23.4	22.3	9.0
MGL LGr 1551	l	>42.4	33.8	38.4	19.6	21.7	24.1	--
MGL LGr 1552	l	38.9	31.1	34.2	17.5	20.8	20.8	9.1
MGL LGr 1745	r	--	35.1	38.9	--	24.0	24.0	8.2
MGL LGr 2491	r	--	33.2	37.7	--	--	23.2	--
La Chaux-de-Fonds								
MHNCF --	l	--	41.1	47.3	--	28.8	--	9.7
MHNCF --	r	--	38.7	45.7	≥25.3	28.1	27.7	10.4
MHNCF --	r	49.0	38.9	43.0	24.7	28.7	26.4	9.4
MHNCF --	r	--	≥37.8	42.5	23.6	26.7	25.3	9.5
Cerro del Otero								
MNCN 191	l	48.4	--	--	24.8	--	--	--
MNCN 191	r	≥51.5	42.6	≥47.4	25.8	28.6	26.4	9.6
MNCN 191	r	>45.6	>39.0	>44.9	--	--	--	--
MNCN 191	r	48.4	--	--	24.8	--	--	--
Castell de Barberà								
IPS 1569	l	45.7	..	41.6	21.8	23.3	26.1	9.4

Astragalus		**Lext**	**Lm**	**Lint**	**DTp**	**DTd**	**R**	**d**
IPS --	l	51.0	..	47.0	25.6	29.3	28.6	8.7
S. Quirze								
MGSCB 48583	r	--	--	--	--	--	--	--
Hostalets								
IPS 1032	l	--	..	46.0	>27.1	29.7	27.2	9.9

MT III		**DAPp**	**DTp**	**L**	**l**	**DAPd**	**DTd**
Nguruwe kijivium							
Mfwanganu							
KNM-MW 71	r	--	11.3	>63.8	61.7	>10.1	10.5
Lopholistriodon							
L. moruoroti							
Moruorot							
KNM-MO 50	l	10.1	6.6				
Kubanochoerus							
K. massai							
Gebel Zelten							
MNHNP Z 1961	l	33.5	25.0	<142.0	<135.4	24.2	22.2
MNHNP Z 1961	l	--	24.6	--	--	--	--
K. gigas							
Maerzuizigou							
BMNH --	l	--	36.1	142.9	138.5	--	29.0
Bunolistriodon							
B. anchidens							
Rusinga R1							
KNM-RU 5151	r	25.0	16.0				
B. lockharti							
Pellecahus							
NMB GB 1392	l	27.8	22.3				
UCBL 320278	r	>23.3	19.6				
UCBL 320278	l	27.0	20.4				
UCBL 320278	l	27.8	21.7				
UCBL 320310	l	27.8	22.1	109.8	..	19.0	21.3
Buñol							
FBS 82	r	25.1	21.0				
Can Canals							
IPS 1178	l	26.4	21.1				
Listriodon splendens							
Simorre							
MNHNP ..	r	25.9	19.5	95.8	..	19.0	16.1
Paşalar							
PDTFAU G 1385	r	24.5	>19.9				
Çandir							
MTA --	l	--	20.9	106.3	99.3	22.2	20.4
MTA --	r	--	22.5	109.5	101.5	±22.5	>20
Paracuellos III							
MNCN PA 626	r	≥27.0	21.0				
Arroyo del Val IV							
MPZ AV-37	l	28.1	--	>102.9	..	>19.0	18.5
La Grive							
MGL LGr 6007	l	24.5	20.0				

MT IV		**DAPp**	**DTp**	**L**	**l**	**DAPd**	**DTd**
Kubanochoerus massai							
Gebel Zelten							
MNHNP Z 1961	l	--	≥17.1	--	--	--	--
MNHNP Z 1961	l	36.1	21.3	131.4	119.2	24.5	21.0
MNHNP Z 1961	l	--	20.6	--	--	--	--
Bunolistriodon							
B. aff. latidens							
La Artesilla							
MPZ-6475	r	--	14.4				
B. lockharti							
Pellecahus							
UCBL 320310	l	28.4	18.0	115.4	..	19.3	18.9
UCBL 320278	r	--	--	>111	..	--	--
NMB GB 1390	r	29.3	18.3				
NMB GB 1391	r	≥30.5	18.1				
Listriodon splendens							
Çandir							
MTA --	r	--	19.6	±108.4	104.8	22.9	>20.4
La Grive							
MGL LGr 753	r	27.6	19.6	115.8	104.9	21.5	19.6
La Grive M							
CFE --	r	--	17.8	--	98.3	>19.7	≥17.4
Castell de Barberà							
IPS --	l	--	21.7	--	--	--	--

TABLE 15b Measurements of the postcranial skeleton in mm.

Atlas		Total DAP	DT	prox. fac. DT	dist. fac. DT
Listriodon					
L. splendens					
Cerro del Otero					
MNCN 187		—	—	67.5	±72.1
MNCN 187		—	—	—	68.9

Scapula		DAPd	DAPf	DTd	DAPn	DTn
Lopholistriodon						
L. moruoroti						
Moruorot						
KNM-MO 48	1	19.7	13.7	13.8		
Bunolistriodon						
B. lockharti						
Langenau 1						
SMNS 41230	1	—	28.5	31.0	16.5	
Listriodon splendens						
La Cisterniga						
MNCN NM 662	1	46.5	39.3	34.2	32.1	15.3

Humerus proximal		DAPp	DTp	L	1
Bunolistriodon					
B. anchidens					
Rusinga R1					
KNM-RU 3342	1	62.6	53.5	>206	>196

Scaphoid		DAP	DT	H
Kubanochoerus				
K. massai				
Gebel Zelten				
MNHNP Z 1961	1	29.9	18.4	21.6
Bunolistriodon				
B. aff. latidens				
Armantes I				
IVAU 41/535	r	>16.6	12.9	±12.8
Listriodon				
L. splendens				
Arroyo del Val IV				
MNCN —	r	30.0	20.7	21.5
La Grive				
MGL LGr 6002	1	>29.5	≥15.5	25.2
MGL LGr 6002	r	30.5	16.7	22.4
Castell de Barberà				
IPS —	1	>23.5	14.9	20.1

Semilunar		DAP	DTp	DTd	H
Bunolistriodon					
B. lockharti					
Pellecahus					
NMB GB 1432	1	24.3	16.7	15.5	16.7
UCBL 320276	r	30.0	19.2	17.3	19.1
Listriodon					
L. splendens					
Arroyo del Val IV					
RGM 263.106	1	>25.8	>14.0	..	21.6
La Grive					
MGL LGr 6002	r	25.9	20.2	18.4	18.4

Ulnar		DAP	DT	H
Bunolistriodon				
B. lockharti				
Pellecahus				
UCBL 320287	1	20.8	12.7	..
B. M				
Paşalar				
PDTFAU F 506	1	18.5	12.1	21.0
Listriodon				
L. splendens				
Arroyo del Val I				
IVAU AR I —	r	20.8	11.2	22.3
La Grive				
MGL LGr 1730	1	19.0	11.3	20.9
MGL LGr 6002	1	21.9	13.3	25.6
La Chaux-de-Fonds				
MHNCF —	1	22.3	10.5	26.2
Cerro del Otero				
MNCN 202	1	20.9	..	24.9
Castell de Barberà				
IPS —	r	19.8	11.4	22.7

Magnum		DAP	DT	H
Bunolistriodon				
B. aff. latidens				
La Artesilla				
MPZ 6468	r	±21.6	20.0	—
MPZ 6469	1	>18.4	18.3	17.3
La Hidroélectrica				
MNCN —	1	21.1	15.8	15.6

Magnum		DAP	DT	H
Armantes I				
IVAU 41/606	1	—	—	—
IVAU 41/603	1	20.0	16.3	14.2
B. lockharti				
Pellecahus				
UCBL 320277	r	..	20.0	18.0
UCBL 320277	1	..	20.6	17.6
Listriodon				
L. splendens				
Paşalar				
PDTFAU F 494/10	r	23.5	—	17.9
PDTFAU G 467	r	23.8	19.8	20.8
Arroyo del Val IV				
IVAU AR IV 116	1	23.6	20.9	18.3
RGM 263.004	r	..	..	..
MPZ DPZ/AV-57	1	26.0	22.9	19.6
MPZ DPZ/AV-61	r	23.2	20.7	19.9
La Grive				
MGL LGr 6002	r	23.9	21.6	20.4
MGL LGr 6002	r	22.5	22.1	19.6
MGL —	..	23.3	17.7	18.9
La Chaux-de-Fonds				
MHNCF —	r	23.2	19.8	18.9
Castell de Barberà				
IPS —	1	22.7	20.0	18.8
Sant Quirze				
MGSCB 48584	r	21.8	18.2	18.9

Unciform		DAP	Dmax	DT	Ha
Bunolistriodon					
B. anchidens					
Rusinga R1					
KNM-RU 5550	1	23.9	27.2	17.9	17.5
Karungu					
KNM-KA 459	1	21.9	28.0	15.2	16.8
B. aff. latidens					
Armantes I					
IVAU 41/594	1	—	—	17.2	15.1
B. lockharti					
Langenau 1					
SMNS 40680	1	..	36.6	20.3	21.4
SMNS 41235	1	—	—	18.8	18.6
Buñol					
IVAU —	1	—	—	±19.1	—
—	1	..	31.3	18.3	..
Listriodon					
L. pentapotamiae					
Cheski Wala					
IVAU CHC —	1	26.1	≥30.3	15.1	20.6
L. splendens					
Arroyo del Val IV					
RGM 263.065	r	—	—	19.8	21.1
Castell de Barberà					
IPS —	1	30.4	..	16.5	20.4

MC II		DAPp	DTp	L	DAPd	DTd
Kubanochoerus						
K. massai						
Gebel Zelten						
MNHNP —	1	12.9	8.5	115.9	16.2	12.7
Listriodon						
L. splendens						
Santiga (?)						
IPS 1950	r	10.4	7.8			

MC V		DAPp	DTp	L	DAPd	DTd
Bunolistriodon						
B. lockharti						
Buñol						
IVAU —	1	—	5.9	—	—	—
Listriodon						
L. splendens						
Santiga (?)						
IPS 1450	r	10.8	7.4			

MP II/V distal		DAPd	DTd
Lopholistriodon			
L. sp.			
Maboko			
KNM-MB 567	r	8.2	5.7
KNM-MB 611	r	4.9	3.7
Bunolistriodon			
B. anchidens			
Rusinga R 114			
KNM-RU 3622	r	9.5	8.1
B. aff. latidens			
Paşalar			
PDTFAU F 350	1	11.7	7.0
PDTFAU F 387/13	1	10.2	6.7

MP II/V distal		**DAPd**	**DTd**
B. lockharti			
Buñol			
IVAU —		14.9	10.5
B. akatikubas			
Mbagathi			
KNM-MG 29	..	15.2	10.0
Listriodon			
L. pentapotamiae			
Chinji Formation			
bought specimens			
IVAU CH —	1	—	8.5
IVAU CH —	r	12.4	10.5
L. splendens			
Paşalar			
PDTFAU D 1191	r	13.4	7.8
PDTFAU G 1512	r	12.6	9.3
Arroyo del Val IV			
IVAU AR 257	..	12.9	8.7
Sant Quirze			
MGSCB 48561	1	15.9	11.7

MP III/IV distal		**DAPd**	**DTd**
Nguruwe kijivium			
Songhor			
KNM-SO 1973	r	9.2	8.8
Lopholistriodon			
L. moruoroti			
Moruorot			
KNM-MO 49	r	8.6	7.5
Kubanochoerus			
K. hussaini			
HGSP 8219			
HGSP 8219/1032	1	26.8	40.4
K. massai			
Gebel Zelten			
MNHNP Z 1961	1	23.9	22.9
MNHNP Z 1961	r	>21.6	>20.0
MNHNP Z 1961	r	25.6	22.7
MNHNP Z 1961	1	22.9	24.6
MNHNP Z 1961	1	24.3	22.3
Bunolistriodon			
B. anchidens			
Rusinga R1a			
KNM-RU 5852	r	17.6	16.3
Rusinga R12			
KNM-RU 3294	1	17.3	≥15.6
KNM-RU 3294	r	>16.6	>15.6
Rusinga loc. ?			
KNM-RU 4426	1	>14.0	14.3
B. aff. latidens			
La Artesilla			
MPZ-6476	1	15.7	20.7
MPZ-6477	r	15.9	—
MPZ-6478	1	17.4	16.6
MPZ-6479	1	>14.7	16.7
B. M			
Paşalar			
PDTFAU F 349/2	1	18.7	18.4
B. lockharti			
Buñol			
FBS 14	r	21.5	20.6
FBS 15	r	21.3	19.0
IVAU —	r	21.6	20.8
Monteagudo			
IPS 1508	1	—	16.8
Can Canals			
IPS 1180	r	>19.2	20.3
IPS 1181	1	21.2	19.3
Szentendre			
HGSB V 13077	1	22.8	—
HGSB V 13077	r	—	21.3
Bunolistriodon guptai			
HGSP 8311			
HGSP 8311/1744	1	>17.2	16.7
Listriodon			
L. pentapotamiae			
Cheski Wala			
IVAU CHC 231	r	21.9	19.5
IVAU CHC 232	r	19.7	16.6
IVAU CHC 233	r	19.5	19.0
?HGSP 8129			
HGSP 8129/540	1	>17.2	15.5
L. splendens			
Inönü I			
MTA AKI-3/122	..	22.5	22.7
Paşalar			
PDTFAU F 349	r	—	19.9
PDTFAU F 349/2	1	18.7	18.4
PDTFAU G 1205	1	—	19.5
PDTFAU G 1528	1	20.7	18.0
PDTFAU G 1780	1	19.7	18.6
Çandir			
MTA ÇBH1/142	1	—	23.4
Arroyo del Val IV			
IVAU AR IV 99	1	21.8	19.6
IVAU AR IV 115	r	—	≥26.6
RGM ...	1	±20.0	18.0
MPZ AV-37	1	21.0	19.8
MPZ DPZ/AV-45	1	18.6	15.0
La Grive			
MGL LGr 1676	r	>18.2	17.9
MGL LGr 1677	1	>18.4	≥17.8
MGL LGr 1678	r	>19.0	≥21.3
MGL LGr 1751	r	19.8	19.9
MGL LGr 1755	r	19.7	17.9
MGL LGr 1758	1	21.7	>18.0
MGL LGr 1759	r	>19.2	≥18.5
MGL LGr 1762	r	—	19.5
La Chaux-de-Fonds			
MHNCF — juvenile	1	21.5	19.5
MHNCF —	1	≥21.1	21.8
La Cisterniga			
MNCN NM 1432	r	23.6	20.4
Sant Quirze			
MGSCB 48560	1	19.3	19.7
MGSCB —	1	>21.4	>22.5
Hostalets			
CJFV 4447		23.3	21.2
CJFV —		22.6	21.1

Phalange 1, II/V		**DAPp**	**DTp**	**L**	**DAPd**	**DTd**
Kubanochoerus						
K. khinzikebirus						
Karungu						
KNM-KA 13180	1	12.7	12.9	34.9	±8.5	>8.5
Bunolistriodon						
B. lockharti						
Langenau 1						
SMNS 41240	r	9.5	8.7	20.6	6.0	8.3
Listriodon						
L. splendens						
Paşalar						
PDTFAU F 494/5	r	11.9	10.9	29.1	8.5	7.8
PDTFAU F 587/5	r	—	—	—	8.5	7.8
PDTFAU G 2038	1	9.7	8.5	23.3	7.0	6.2

Phalange 2, II/V		**DAPp**	**DTp**	**L**	**DAPd**	**DTd**
Kubanochoerus						
K. hussaini						
HGSP 8311						
HGSP 8311/1556	r	14.8	14.1	25.1	12.1	12.7
Bunolistriodon						
B. anchidens						
Rusinga Wayondo Fm.						
KNM-RU 5530	r	11.9	11.0	16.9	9.2	9.7
B. aff. latidens						
Tarazona						
UPV T2.90	..	9.7	10.2	14.5	8.6	9.8
B. M						
Paşalar						
G 103	..	8.5	6.5	11.2	6.9	6.6
G 1166	..	8.7	7.4	10.7	7.3	6.8
Listriodon						
L. splendens						
Paşalar						
PDTFAU F 494/6	r	10.3	8.2	13.9	9.2	7.7

Phalange 3, II/V		**DAPp**	**DAPps**	**DTp**	**L**
Listriodon					
L. splendens					
Paşalar					
PDTFAU G 40	r	9.1	12.4	7.0	16.1

Phalange 3, III/IV		**DAPp**	**DAPps**	**DAPf**	**DTp**	**L**
Kubanochoerus						
K. massai						
Gebel Zelten						
MNHNP Z 1961	r	26.1	..	17.1	15.2	36.9
Lopholistriodon						
L. moruoroti/pickfordi						
Maboko						
KNM-MB 10303	r	5.5	6.2	4.4	..	
Bunolistriodon						
B. aff. latidens						
Tarazona						
UPV T2.303	1	..	>22.3	14.7	14.4	—
UPV T 5.20	1	..	21.2	14.8	13.6	28.1
B. lockharti						
Langenau 1						
SMNS 40682	r	23.0	..	..	15.0	32.9

Phalange 3, III/IV		**DAPp**	**DAPps**	**DAPf**	**DTp**	**L**
Listriodon						
L. splendens						
Paşalar						
PDTFAU F 150	r	..	23.0	13.7	—	37.9
PDTFAUG 1281	r	..	20.9	13.2	13.5	37.3
La Grive						
MGL LGr 470	1	21.9	22.9	17.1	13.8	>32.3
MGL LGr 1763	r	21.2	22.4	21.2	13.6	33.0
MGL LGr 1764	1	20.4	22.2	15.0	14.0	33.1
La Chaux-de-Fonds						
MHNCF —	1	25.8	20.7	18.8	14.9	39.3
MHNCF —	1	21.7	16.7	16.4	13.2	33.6

Fibula, distal part		**DAPd**	**DTd**
Bunolistriodon			
B. lockharti			
Buñol			
—	r	20.2	13.0
BE 9	1	19.6	12.6

Navicular		**DAP**	**DT**	**Ha**	**H**
Bunolistriodon					
B. lockharti					
Pellecahus					
UCBL 320310	1	32.8	20.1	16.1	..
UCBL 320285	r	32.8	17.6	14.7	..
UCBL 320293	r	>28.2	16.5	13.4	..
NMB GB 1394	r	34.5	20.0	13.2	21.8
Grimmelfingen					
NMB TD 718	r	30.0	17.2	11.1	≥17.8
Buñol					
FBB 1.98	1	>33.7	21.8	18.9	..
FBS 90	1	—	18.7	15.7	—
—	1	≥31.5	20.8	19.6	..
Listriodon					
L. pentapotamiae					
Kali Nachi					
IVAU CHN 56	r	—	15.0	10.6	—
Chinji Fm. bought specimen					
IVAU CH 346	r	28.4	16.9	≥10.8	—
L. splendens					
Paşalar					
PDTFAU F 494/9	r	—	18.7	11.6	—
PDTFAU G 1062	r	—	19.5	12.3	—
PDTFAU G 1194	r	—	±19	10.8	—
PDTFAU G 1527	r	—	≥16.7	10.8	—
Çandir					
MTA —	r	34.7	22.0	12.1	25.4
Arroyo del Val IV					
MNCN —	r	—	19.9	11.3	—
La Cisterniga					
MNCN NM 1430	r	>29.1	>16.2	11.3	—
La Grive					
NMB 2837	1	36.7	24.3	12.3	20.0
MGL LGr 6008	r	34.3	22.1	12.9	21.6
MGL LGr 6008	r	37.8	23.9	13.1	25.1
MGL —	1	33.5	20.1	13.1	20.9
La Chaux-de-Fonds					
MHNCF —	1	>32.6	≥21.0	11.1	—
MHNCF —	1	—	≥19.4	12.0	—

Cuneiforme III		**DAP**	**DT**
Bunolistriodon			
B. lockharti			
Pellecahus			
UCBL 320310	1	18.1	16.1
Listriodon			
L. splendens			
Paşalar			
PDTFAU F 494/3	r	21.2	≥13.9
Çandir			
MTA —	r	18.2	15.7
Paracuellos III			
MNCN PA 878	r	17.3	20.8
Arroyo del Val IV			
IVAU AR IV 27	r	17.6	15.2

Cuboid		**DAP**	**DT**	**Ha**	**H**
Kubanochoerus					
K. massai					
Gebel Zelten					
MNHNP Z 1961	r	33.9	21.6	30.0	45.0
Bunolistriodon					
B. aff. latidens					
La Artesilla					
MPZ-6467	r	>23.9	>17.5	22.5	—
Villafeliche "bocht"					
IVAU VLB/1	1	—	20.4	22.0	—

Cuboid		**DAP**	**DT**	**Ha**	**H**
B. lockharti					
La Romieu					
UCBL 320312	1	29.4	21.8	≥23.6	35.8
Pellecahus					
UCBL 320310	1	28.9	19.7	23.6	34.0
Buñol					
PAN 54	r	—	26.4	22.5	—
Listriodon					
L. pentapotamiae					
Kundal Nali					
IVAU CHK 205	r	22.1	20.1	21.2	≥30.7
HGSP 8204					
HGSP 8204/694	r	23.6	>16.0	17.5	28.0
L. splendens					
Paşalar					
PDTFAU G 103	r	—	21.0	20.0	—
Çandir					
MTA —	r	32.2	26.4	24.5	39.0
Arroyo del Val IV					
IVAU AR IV 112	1	≥27.2	≥21.4	21.3	—
IVAU AR IV 154	1	—	≥19.2	22.9	—
RGM 263.058	1	30.1	21.1	—	—
RGM 263.133	r	32.5	22.9	±23	—
La Chaux-de-Fonds					
MHNCF —	1	≥28.9	23.6	19.2	—
MHNCF —	r	30.0	24.3	18.8	35.2
MHNCF —	r	29.9	24.6	18.3	—

MT II		**DAPp**	**DTp**	**L**	**DAPd**	**DTd**
Kubanochoerus						
K. massai						
Gebel Zelten						
MNHNP Z 1961	r	≥13.2	≥7.3	≥117.2	12.8	8.5
Listriodon						
L. splendens						
Çandir						
MTA —	r	11.3	±5.8	78.9	15.3	±7.5

MT V		**DAPp**	**DTp**	**L**	**DAPd**	**DTd**
Listriodon						
L. splendens						
Çandir						
MTA —	r	15.6	7.2	80.2	15.4	9.9
La Grive						
MGL LGr 1757	1	—	6.7	75.7	15.4	9.9

TABLE 16 DMD' and DLL' values of the first and second lower incisors, as well as numbers of specimens, of Listriodontinae and selected other Suoidea. The values are calculated either from samples or from individuals.

	M_1	I_1				I_2			
	n	n	DMD´	n	DLL´	n	DMD´	n	DLL´
Kubanochoerus marymunngui									
West Stephanie - Buluk	2					1	±77	1	±95
Kubanochoerus massai									
Gebel Zelten	10	5	58	3	64	10	64	8	73
Kubanochoerus minheensis									
Minhee IVPP V 6021	1	2	68	1	72	2	80	2	85
Kubanochoerus gigas									
Maerzuizigou BNHM BPV907	1	2	85	2	81	0	--	0	--
Bunolistriodon anchidens									
Rusinga	2	3	62	1	59	1	72	1	78
Bunolistriodon C									
Munébrega I	2	1	76	1	62	1	98	1	80
Armantes I	3	1	53	1	54	0	--	0	--
Bunolistriodon latidens									
Veltheim NSSW 99	2	2	86	1	61	1	106	1	83
Bunolistriodon M									
Paşalar	16	17	114	14	58	6	123	5	65
Bunolistriodon lockharti									
La Romieu	5	2	77	2	73	2	94	2	82
Baigneaux	2	1	62	1	70	5	89	5	89
Listriodon pentapotamiae									
Dhok Talian 189									
PMNH MV 31, 527	1	2	71	2	56	2	90	2	65
Listriodon splendens									
Paşalar	24	33	87	25	66	36	109	26	76
Çandir	7	4	81	4	66	2	91	2	69
Arroyo del Val IV	10	5	95	5	74	2	111	3	79
La Grive oc (mixed)	2	12	105	12	74	9	121	8	82
S. Quirze	2	8	105	8	71	7	131	7	84
Hostalets (mixed)	2	8	106	8	73	4	134	4	84
T. tayacu									
ZMA 470	1	1	47	1	60	1	51	1	66
ZMA 471	1	1	43	1	61	1	50	1	67
ZMA 472	1	1	49	1	56	1	50	1	67
ZMA 1838	1	1	46	1	60	1	57	1	64
ZMA 9377	1	1	48	1	63	1	54	1	63
ZMA 9380	1	1	44	1	64	1	52	1	62
ZMA 9393	1	1	51	1	64	1	56	1	80
ZMA 9382	1	1	53	1	63	1	58	1	69
ZMA 9384	1	1	47	1	67	1	46	1	69
ZMA 9387	1	1	44	1	68	1	50	1	69
ZMA 9388	1	1	45	1	65	1	52	1	69
ZMA 9394	1	1	49	1	61		--		--
ZMA 9539	1	1	41	1	62	1	53	1	65
ZMA 9541	1	1	51	1	65	1	47	1	66
ZMA 9604	1	1	44	1	55	1	45	1	70
ZMA 10512	1	1	44	1	51	1	48	1	55
ZMA 10513	1	1	37	1	51	1	--		--
T. pecari									
ZMA 476	1	1	47	1	55	1	44	1	59
ZMA 1835	1	0	--	1	55	1	47	1	55
ZMA 1836	1	1	37	1	54	1	55	1	58
ZMA 9391	1	1	49	1	56	0	--	0	--
Palaeochoerus aquensis									
Quercy	2	2	49	2	56	2	50	2	81
Palaeochoerus typus									
St.-Gérand-le-Puy									
MGL StG 690-691	2	1	48	1	60	0	--	0	--
Kenyasus rusingensis									
Rusinga	8	4	56	3	58	3	54	2	59
Albanohyus castellensis									
Castell de Barberà	4	4	62	4	79	3	67	3	72
Hyotherium meisneri									
Cetina	10	3	66	3	77	7	65	4	84
Parachleuastochoerus steinheimensis									
La Grive	7	14	52	12	84	6	62	5	97
Propotamochoerus wui									
Lufeng	19	12	52	6	81	9	52	8	90
Microstonyx major									
Spain	15	8	58	5	93	5	61	2	99
Microstonyx erymanthius									
Dorn Dürkheim	12	14	56	2	85	25	59	8	103
Sus strozzii									
Valdarno	21	15	54	13	86	12	66	12	86

TABLE 17 DMD' and DLL' values of the first and second upper incisors, as well as number of specimens. The values are calculated either from samples or from individuals.

	M^1	I^1				I^2			
	n	n	DMD'	n	DLL'	n	DMD'	n	DLL'
Kubanochoerus massai									
Gebel Zelten	6	12	103	11	63	6	71	8	44
Gebel Zelten skull	1	1	109	1	63	1	64	1	40
Kubanochoerus gigas									
Maerzuizigou									
BNHM BPV-900	1	1	160	1	74				
BNHM BPV-910 1	1	1	166	1	..				
r	1	1	159	1	..				
Nguruwe kijivium									
Songhor	2	2	63	2	48	1	49	1	26
Lopholistriodon moruoroti									
Maboko	1	3	92	3	63	3	74	2	43
Lopholistriodon kidogosana									
Ngorora D	2	1	105	1	74				
Ngorora B5, 2/56	3					3	88	3	46
Bunolistriodon anchidens									
Rusinga	3	1	83	1	61	4	67	4	47
Bunolistriodon aff. *latidens*									
La Artesilla	2	3	101	4	64				
Armantes I	2	2	115	2	62				
Bunolistriodon latidens									
Inönü I	3	1	166	1	67				
Bunolistriodon M									
Paşalar	7	5	217	4	74				
Bunolistriodon lockharti									
La Romieu	3	3	97	3	78				
Baigneaux en Beauce	3	5	114	5	66				
Listriodon splendens									
Simorre MNHNP Si 156	1	2	151	1	76				
Paşalar	23	23	146	24	76				
Xinan IVPP V8283	1	1	116	1	±63	1	80	1	46
Arroyo del Val IV	8	5	148	6	68				
La Grive	11	11	155	10	73				
St. Quirze	3	5	157	6	71				
Castell de Barberà	2	5	174	4	73				
Hostalets	2	2	185	2	71				

TABLE 18 Indices of hypsodonty of the lower incisors, as well as index I of each tooth for Listiodontinae and selected other Suoidea.

I_1		100x Hli/DMD	100x Hla/DMD	100x Hli/DLL	100x Hla/DLL	I
Propaleochoerus sp.						
Tomerdingen						
SMNS 45070	r	259	286	200	221	77
Tayassu pecari						
Recent ZMA 9321	r	234	267	203	231	87
Tayassu tayacu						
Recent ZMA 472	1	216	216	190	190	88
ZMA 9380	1	240	245	166	169	69
ZMA 9394	1	..	245	..	196	80
ZMA 10513	1	±241	282	±173	203	72
Hyotherium meisneri						
Cetina de Aragon						
CT —	r	195	221	184	207	94
IPS 1401	1	—	234	—	<231	<98
Xenohyus venitor						
Faluns d´Anjou						
MNHNP cast	r	>130	>184	>220	>310	59
Kenyasus rusingensis						
Rusinga R114						
KNM-Ru2745	r	284	278	268	262	94
Lopholistriodon pickfordi						
Maboko KNM-MB25	1	256	266	233	242	91
Lopholistriodon kidogosana						
Ngorora 2/56						
KNM-BN 548	1	137	±161	192	±225	140
Kubanochoerus minheensis						
Nanhawangou						
IVPP V 6021	1	166	—	154	—	93
Bunolistriodon aff. latidens						
Olival da Suzana						
CEPUNL —	r	..	149	..	181	122
Bunolistriodon M						
Paşalar						
PDTFAU G1718	r	124	138	243	271	215
PIMUZ BP-311	1	144	129	246	276	197
Bunolistriodon lockharti						
Pellecahus						
NMB GB 1387	r	146	171	159	171	109
Listriodon pentapotamiae						
Cheski Wala						
IVAU CHC 93	1	128	142	177	196	139
Listriodon splendens						
Paşalar						
PDTFAU C361	r	139	146	174	182	125
PDTFAU D1031	1	139	143	190	195	137
PDTFAU D1031	r	139	144	193	199	138
PDTFAU DT8.6	1	124	136	171	188	138
PDTFAU DT8.9	r	123	133	170	184	138
PDTFAU DT8.10	r	160	174	183	199	115
PDTFAU F353	1	134	192	187	192	139
PDTFAU F409	1	—	146	—	202	139
PDTFAU G449	1	137	129	195	202	143
PDTFAU G582.a	1	—	157	—	—	—
PDTFAU G1129	1	129	133	166	171	129
PDTFAU G1833.1	1	145	158	195	213	135
Arroyo del Val IV						
IVAU AR IV 92	1	145	143	172	170	119
La Grive						
IGF 299	1	110	118	172	185	156
MGL LGr 6004	1	110	119	153	166	139
MGL LGr 6004	r	120	123	165	170	137
La Chaux-de-Fonds						
MHNCF 6	r	—	123	—	—	—

I_2		100x Hli/DMD	100x Hla/DMD	100x Hli/DLL	100x Hla/DLL	I I
Propalaeochoerus sp.						
Tomerdingen						
SMNS 45049	r	237	253	199	209	83
SMNS 45050	1	238	257	191	207	80
SMNS 45051	1	235	265	174	196	74
SMNS 45051	1	222	200	174	200	78
Tayassu pecari						
Recent ZMA 1835	1	243	248	209	213	86
Tayassu tayacu						
Recent ZMA 472	1	264	260	198	195	75
ZMA 9380	1	274	264	230	207	84
ZMA 9383	1	273	263	189	182	69
ZMA 9540	1	254	271	183	195	82
Hyotherium meisneri						
Cetina						
MNCN CT 469	1	249	293	187	220	75
MNCN CT 469	r	±249	275	±184	204	74
MNCN CT —	1	230	254	182	201	79
MNCN CT —	r	—	241	—	—	—
Xenohyus venitor						
Faluns d´Anjou						
MNHNP Fs 678	r	>217	>248	>165	>217	66
Kenyasus rusingensis						
Rusinga R114						
KNM-Ru 2744	r	272	270	227	225	83
Kubanochoerus massai						
Gebel Zelten						
MNHNP Z 1961	1	..	210	..	195	93
MNHNP Z 1961	r	186	190	167	171	90
Lopholistriodon pickfordi						
Maboko						
KNM-MB 26	1	176	206	198	233	113
KNM-MB 14446	r	—	259?	—	236?	110
KNM-MB 14448	1	194	239	177	218	91
Lopholistriodon akatidogus						
Mbagathi						
KNM-MG 7	r	>102	113	>147	163	145
Kubanochoerus minheensis						
Nanhawangou						
IVPP V6021	1	149	—	150	—	101
Bunolistriodon aff. latidens						
Munébrega III						
IVAU 53/53	r	162	..	17.7	..	118
Bunolistriodon lockharti						
Baigneaux						
MSNO 904	r	166	172	169	175	102
COBO —	r	157	163	155	163	98
Pontlevoy?						
MNHNP cast	1	133	132	150	148	112
Bunolistriodon intermedius						
Maerzuizigou						
IVPP V 9522.7	1	±164	..	±199	..	121
Listriodon splendens						
Paşalar						
PDTFAU C8.11	r	116	—	178	—	154
PDTFAU C224	1	120	126	173	181	144
PDTFAU D1079	r	—	122	—	179	147
PDTFAU DT9.1	1	125	126	177	179	142
La Grive						
IGF 299	1	122	117	171	163	140
MGL LGr 6003	1	99	103	165	171	166

TABLE 19 Enamel thickness Ta andTp and ratios 1000 Ta/DTa and 1000 Tp/DTp in Listriodontinae.

			P_4 DTa	Ta	1000 x Ta/DTa	DTp	Tp	1000 x Tp/DTp
B. aff. latidens								
Armantes I	IVAU 41/516	l	12.6	1.7	134			
	IVAU 41/517	r	12.4	1.6	129			
B. guptai								
HGSP 8311	HGSP 8311/150	l	11.5	0.7	61			
L. splendens								
Arroyo del Val IV	IVAU AR IV 6	r	12.5	1.3	104			
	IVAU AR IV 16	.	..	1.2	..			
	RGM 263.040	l	12.9	1.4	109			
Arroyo del Val VI	IVAU AR VI 18	r	12.1	1.2	99			
Manchones I	IVAU MA 107	r	13.7	1.2	88			

			M_1 DTa	Ta	1000 x Ta/DTa	DTp	Tp	1000 x Tp/DTp	
K. massai									
Gebel Zelten	MNHNP Z 1961	r	--	--	--	19.2	1.3	67	
	MNHNP Z 1961	r	18.4	0.6	33	18.5	0.8	43	
B. aff. latidens									
Armantes I	IVAU 41/513	l	12.8	0.8	63	13.7	0.8	58	
Munebrega I	IVAU 55/1049	l	13.5	±1.0	±74	>13.5		--	--
	IVAU 55/1050	r	13.4	1.0	75	13.8	1.2	87	
B. lockharti									
Avaray	MSNO 262	r	13.9	0.8	58	14.6	0.8	55	
Pontlevoy	MNHNP FP 1062	r	--	1.0	--	15.4	--	--	
B. guptai									
HGSP 8311	HGSP 8311/1406	l	14.1	0.7	50	14.6	1.0	68	
HGSP 8412	HGSP 8412/3135	r	≥15.3	--	--	15.3	1.2	56	
L. pentapotamiae									
HGSP 8122	HGSP 8122/257	r	15.1	1.1	73	15.7	0.9	57	
Kanatti	IVAU KA 79	r	--	--	--	--	0.7	--	
Chinji Fm.	IVAU CH 28	l	--	--	--	12.0	0.9	75	
L. splendens									
Arroyo del Val IV	IVAU AR IV 3	l	--	0.6	--	--	0.8	--	
	IVAU AR IV 43	r	14.5	1.1	76	14.0	0.9	64	
	IVAU AR IV 87	l	--	--	--	--	0.9	--	
	IVAU AR IV 89	r	--	--	--	--	0.9	--	
	RGM 263.036	l	--	--	--	13.7	0.9	66	
Wien Heiligenstadt	NHMW SK 1666a	l	13.7	0.9	66	13.6	0.9	66	
Escancrabe	MNHNP HGP 18	l	14.6	0.8	55	14.5	1.0	69	
	MNHNP HGP 19	r	14.6	0.8	55	14.2	1.0	70	

			M_2 DTa	Ta	1000 x Ta/DTa	DTp	Tp	1000 x Tp/DTp
K. hussaini								
Nyakach-Kaimogool E	KNM-NC 9807	r	--	--	--	37.5	2.1	56
K. massai								
Gebel Zelten	MNHNP Z 1961	l	--	1.2	--	22.5	1.7	76
	MNHNP Z 1961	l	24.3	2.0	82	25.0	2.2	88
	MNHNP Z 1961	r	24.6	1.6	65	24.2	1.8	74
	MNHNP Z 1961	r	22.3	2.2	99	23.8	2.2	92
	MNHNP Z 1961	r	22.6	1.8	80	22.8	1.9	83
	MNHNP Z 1961	l	24.3	1.9	78	24.5	2.0	82
	MNHNP Z 1961	l	22.5	1.8	80	22.8	2.0	88
B. aff. latidens I								
Armantes I	IVAU 41/513	l	17.3	1.7	98	17.5	1.8	103
	IVAU 41/514	l	18.1	1.4	77	≥18.2	--	--
Munebrega I	IVAU 55/1049	l	16.9	--	--	17.4	1.8	103
	IVAU 55/1050	r	16.5	1.4	85	16.9	1.7	101
B. lockharti								
Chevilly	MSNO --	r	17.4	1.4	80	18.5	1.3	70
"Orléans"	MSNO --	r	18.0	1.1	61	18.8	1.2	64
Araya	MNHNP --	l	18.2	1.7	93	17.7	1.4	79
Pontlevoy	MNHNP FP 1062	r	17.9	1.4	78	18.8	..	..
B. guptai								
HGSP 8311	HGSP 8311/1406	l	18.3	1.6	87	18.4	1.2	65
HGSP 8222	HGSP 8222/1218	r	15.2	0.8	53	15.4	0.9	58
L. pentapotamiae								
HGSP 8122	HGSP 8122/257	r	15.1	1.1	74	18.3	1.1	60
Kanatti	IVAU KA 79	r	17.6	1.3	74	18.3	1.1	60
L. splendens								
Gers	MNHNP Ger 44	l	16.3	1.5	92	15.7	1.6	102
Villefranche d´Astarac	MNHNP VAS 11	l	15.8	1.4	89	16.2	1.3	80
Paracuellos III	MNCN PA 450	r	--	1.7	--	20.9	..	..
	MNCN PA 619	l	21.6	1.6	74	>19.2	..	..
Paracuellos V	MNCN PA V 569	l	17.6	1.4	80	17.5	1.6	91
Arroyo del Val IV	IVAU AR IV 1	.	..	1.4	..	..	1.5	..
	IVAU AR IV 2	r	--	1.1	--	--	1.5	--
	IVAU AR IV 3	l	--	1.1	--	16.8	1.5	89
	IVAU AR IV 4	r	17.6	1.3	74	16.8	1.5	89
	IVAU AR IV 7	r	19.3	--	--	≥18.3	2.0	≤109
	IVAU AR IV 13	l	18.1	1.4	77	--	--	--
	IVAU AR IV 85	r	17.8	1.3	73	≥17.9	1.1	≤61

	IVAU AR IV 87	l	--	--	--	18.0	1.8	100
	IVAU AR IV 89	r	18.8	1.6	85	18.1	1.7	94
	RGM 263.040	l	18.5	1.7	92	17.5	1.4	80
Manchones I	IVAU MA I 105	r	18.0	1.2	67	17.7	1.3	73
Escancrabe	MNHNP HGP 18	l	19.6	1.5	77	19.2	..	..
Wartenberg	IVAU P25-1963	r	18.1	1.6	88	18.5	1.6	86
Merisor	HGSB Ob 14	l	18.3	1.3	71	17.6	1.3	74
			M_3 **DTa**	**Ta**	**1000 x Ta/DTa**	**DTp**	**Tp**	**1000 x Tp/DTp**
K. massai								
Gebel Zelten	MNHNP Z 1961	l	26.1	2.7	103	22.5	2.2	98
	MNHNP Z 1961	r	--	--	--	24.9	3.1	124
	MNHNP Z 1961	r	--	--	--	21.2	2.9	138
	MNHNP Z 1961	l	--	2.5	--	22.4	2.2	98
	MNHNP Z 1961	l	23.8	2.4	101	21.9	2.7	123
	MNHNP Z 1961	r	--	2.6	--	24.4	..	..
	MNHNP Z 1961	r	26.5	2.4	91	..	..	..
	MNHNP Z 1961	l	24.5	..	..	21.6	2.7	125
B. aff. *latidens* I								
Armantes I	IVAU 41/506	l	19.8	2.3	116	18.3	..	..
	IVAU 41/507	r	21.4	2.0	93	18.9	2.0	106
B. lockharti								
"Orléans"	MSNO 260	r	20.0	1.7	85	18.6	..	..
Araya	MNHNP --	l	19.3	2.1	109	17.8	2.1	118
L. pentapotamiae								
Kanatti	IVAU KA 79	r	20.6	1.8	87	19.2	1.7	89
Mochi Wala	IVAU CHO 126	r	--	--	--	16.7	1.7	102
	IVAU CHO 127	r	16.5	1.5	9.1	--	--	--
HGSP 8304	HGSP 8304/1333	r	18.0	1.4	78	17.4	1.3	75
L. splendens								
Arroyo del Val I	IVAU AR I 3	.	--	1.7	--	--	1.9	--
Arroyo del Val IV	IVAU AR IV 1	.	..	2.0	..	..	2.1	..
	IVAU AR IV 2	r	18.5	..	..	17.7	2.2	124
	IVAU AR IV 3	l	19.3	2.0	104	16.9	1.9	112
	IVAU AR IV 4	r	19.7	2.0	102	17.7	1.8	102
	IVAU AR IV 8	r	≥20.4	2.0	≤98	19.0	2.0	105
	IVAU AR IV 84	l	20.4	1.8	88	18.9	2.0	106
	IVAU AR IV 86	r	20.5	1.3	63	18.7	1.8	96
	RGM 263.035	l	--	..	--	17.5	2.3	131
Manchones I	IVAU MA I 104	r	21.1	2.2	104	18.7	2.1	112
Solera	IVAU --			2.2			2.1	
Larroque de Magnoac	MNHNP HGP 31	l	21.0	1.7	81	19.2	1.4	73
Wartenberg	IVAU P25-1963	r	19.9	1.8	90	19.1	..	..
Sooskút	NMW SK 1770a	l	19.8	1.9	96	18.3	1.6	8.7
			M^3 **DTa**	**Ta**	**1000 x Ta/DTa**	**DTp**	**Tp**	**1000 x Tp/DTp**
Kubanochoerus								
K. massai								
Gebel Zelten	MNHNP Z 1961	r	--	1.9	--	23.2	1.4	60
	MNHNP Z 1961	r	±30.8	2.4	±78	26.9	2.2	82