

LISTRIODON SKULL FROM THE LATE MIDDLE MIOCENE OF NEBISUYU (ÇANAKKALE – MN 8) TURKEY

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Pickford, M., Kaya, T., Mayda, S. (2020): *Listriodon* skull from the late middle Miocene of Nebisuyu (Çanakkale – MN 8) Turkey. – Fossil Imprint, 76(2): 252–269, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: The late middle Miocene (MN 8) sediments at Nebisuyu, in the southwestern extremity of the Gelibolu Peninsula, Turkey, yielded remains of a large individual of *Listriodon splendens*: a skull lacking the premaxillae but containing both cheek tooth rows, and a detached left maxilla fragment containing a canine. The material evidently represents a male individual on the basis of the large dimensions of the canine, an inference borne out by the presence of a horn-like protuberance on the thickened frontal bones. The dentition is typical of the large “subspecies” *Listriodon splendens major* ROMAN, 1907. The presence of an ossicone suggests that head-to-head combat was an aspect of the behaviour of *Listriodon*, just as it is in several extant suid taxa. The Nebisuyu discovery extends the geographic distribution of the subspecies well to the east of its previously known range.

Key words: Listriodontinae, biogeography, behaviour, sexual selection, ossicone

Received: June 14, 2020 | Accepted: August 20, 2020 | Issued: December 30, 2020

Introduction

Neogene deposits in Çanakkale, Turkey, have long been known to yield fossils of various ages (Newton 1904). A skull of *Listriodon splendens* lacking the premaxillae was recovered at Nebisuyu in the Alçıtepe area, in the southwestern part of the Galipoli Peninsula (Kaya 1989, Sen 2016). The skull was associated with a maxilla fragment of a suid containing a large canine, possibly representing the same individual. The strata that yielded the fossils are correlated to MN 8 on the basis of the macro- and micro-faunas that have been collected from the Alçıtepe Formation (Sen 2016).

The aim of this paper is to describe and interpret the Nebisuyu suid specimens and to discuss their implications for phylogeny, palaeoecology and palaeobiogeography.

Geological and faunal context

Nebisuyu is located in the southwestern end of the Galipoli (Gelibolu) Peninsula, Turkey (Kaya 1989, Sen 2016) (Text-fig. 1).

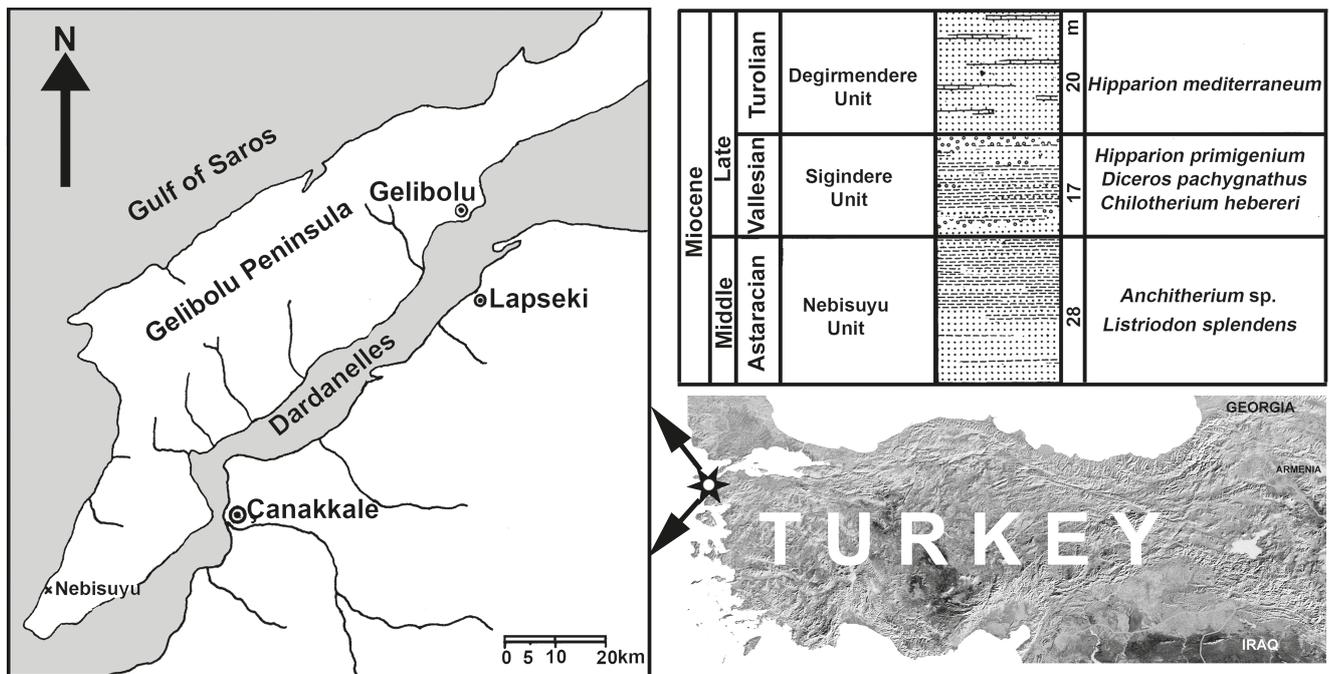
The Neogene deposits of the Dardanelles region (Turkey) comprise sedimentary successions (Kirazlı and Alçıtepe formations) that yield abundant fossil mammalian

remains (Sümengen et al. 1987, Çağatay et al. 1999, 2006), but most of the localities have never been the subject of detailed studies. Previous studies have correlated the Kirazlı Formation to MN 9–12. In this study, the Nebisuyu locality is considered to correlate more precisely to MN 8 which is earlier than the Kirazlı Formation.

Among these localities, Nebisuyu has yielded fossils of a huge ursid (*Hemicyon*), a robust anchitherid (*Sinhippus*), a medium-sized aceratherid “*Hoploaceratherium cf. tetradactylum*”, a chalicotherid “*Chalicotherium grande*”, and a medium-sized tragulid “*Dorcatherium nauï*” all of which were found in the lowermost part of the Kirazlı Formation (Kaya and Mayda 2012). Kaya (1989) described an anchitherid from the locality of Nebisuyu, Ünay and de Bruijn (1984) discussed the micromammals from the broader region on both sides of the Dardanelles, while Kayseri et al. (2014) discussed its palaeobotanic and ecological aspects.

Material and methods

The fossil skull described herein is curated at the EUNHM. It has been compared with other cranial material of *Listriodon* from Spain, France, Germany and Switzerland. Measurements of the teeth were made following the method outlined by Van der Made (1996). Upper teeth are given in



Text-fig. 1. Location and stratigraphy of Nebisuyu, Gelibolu Peninsula, Turkey (figure modified from Kaya 1989).

upper case letters (I, C, P, M – incisor, canine, premolar, molar) and lower case teeth in lower case letters (i, c, p, m). The biochronological scale used in this paper is the European Land Mammal Zonation (Mein 1989). The catalogue number PV refers to Palaeontology, Vertebrates, followed by a unique number, in this case PV 3075.

Institution abbreviations

BSPG	Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
CEPUNL	Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa, Portugal
COBO	Collection Olivier Bardot, Orléans, France
EUNHM	Ege University Natural History Museum, Izmir, Turkey
HLD	Hessisches Landesmuseum, Darmstadt, Germany
IPS	Institut Català de Paleontologia Miquel Crusafont, Campus de la UAB, Cerdanyola del Vallès, Barcelona, Spain (previously Institut Paleontològic Dr. M. Crusafont, Sabadell)
IPUW	Institut für Paläontologie der Universität Wien, Vienna, Austria
IVAU	Instituut voor Aardwetenschappen, Utrecht, the Netherlands
MGL	Le Musée des Confluences (previously Muséum Guimet), Lyon, France
MGM	Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain
MGSCB	Museu i Laboratori de Geologia del Seminari, Barcelona, Spain
MHNC	Musée d'Histoire naturelle, La Chaux-de-Fonds, Switzerland
MHNCHF	Musée d'Histoire naturelle, La Chaux-de-Fonds, Switzerland
ML	Museu Nacional de História Natural, Lisbon, Portugal

MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
MPV	Museo Paleontológico de Valencia, Valencia, Spain
MPZ	Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain
MNSO	Muséum de Sciences naturelles, Orléans, France
MTA	Maden Tetkik ve Arama, Ankara, Turkey
NMB	Naturhistorisches Museum, Basle, Switzerland
NMM	Naturhistorisches Museum Mainz, Mainz, Germany
NSSW	Naturmuseum Winterthur (previously Naturwissenschaftliches Sammlungen der Stadt, Winterthur), Switzerland
PIMUZ	Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland
PDTFAU	Paleoantropologii, Dil ve Tarih Cografya Facultesi, Ankara Universitesi, Ankara, Turkey
RGM	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum voor Geologie en Mineralogie), Leiden, the Netherlands
UCBL	Université Claude Bernard, Lyon, France
UN	Université de Neuchâtel, Neuchâtel, Switzerland

Systematic palaeontology

Order Artiodactyla OWEN, 1848
Superfamily Suoidea GRAY, 1821
Family Suidae GRAY, 1821
Subfamily Listriodontinae GERVAIS, 1859

Genus *Listriodon* VON MEYER, 1846

Type species. *Listriodon splendens* VON MEYER, 1846.

Note. Ameghino (1904) erected two species of *Listriodon* (*Listriodon bonaerensis*, *Listriodon tarijensis*) on the basis of suiform fossils from South America. There are some morphological resemblances between the specimens and *Listriodon* from Europe, but these are due to convergent evolution. The South American fossils belong to *Platygonus*, a Tayassuidae (Gasparini et al. 2010).

Listriodon splendens VON MEYER, 1846

Lectotype. MHNCHF 8, right I1/ in the Natural History Museum, La Chaux-de-Fonds, figured by Stehlin (1900: pl. 5, fig. 22). Lectotype designated by Van der Made (1996: 100, pl. 41, fig. 1a, b, c and 2c – the latter is mislabelled as MHNCHF 8' left I1/). The specimen has lost part of the root since being figured by Stehlin (see also Bayle 1856).

Paralectotypes. According to Van der Made (1996): MHNCHF 8', left I1/; MHNCHF 56b, left c/1m; MHNCHF 10, left i/3; MHNCHF 4, left P4/; MHNCHF 9aua, left I1/; MHNCHF 48, right C1/m (*Calydonius tener* VON MEYER, 1846); MHNCHF 10x, left i/3; MHNCHF 2, right m/3; MHNCHF 4, left P2/; MHNCHF 10, right i/3; MHNCHF 6, left i/1; MHNCHF 6, right i/1; MHNCHF 45, right C1/m (one of the syntypes of *Calydonius trux* VON MEYER, 1846).

Material associated with the lectotype. According to Van der Made (1998), plate 1: MHNC 48, left C1/m (contradiction of side with Van der Made 1996); MHNC 9aua, left I1/; MHNC, right cuboid; MHNC 6, right i/1; MHNC 10x, left i/3; MHNC, left calcaneum; plate 2: MHNC, right astragalus; MHNC, left navicular; MHNC, right magnum.

A note on the subdivision of the species *Listriodon splendens*. Van der Made (1996) proposed a tripartite subdivision of *Listriodon splendens* with chronological connotations, the lineage being interpreted as increasing in dimensions over geological time from small *Listriodon splendens tapirotherium* (DE BLAINVILLE, 1847) to medium-sized *Listriodon splendens splendens* VON MEYER, 1848, and thence to large *Listriodon splendens major* ROMAN, 1907. He also referred to this sequence as evolutionary stages I, II and III. Stage I was considered to be typical of early MN 6, stage II characteristic of the transition MN 6–7, whereas stage III was reported to occur at the transition MN 8–9. Pickford and Morales (2003) reported the presence of a huge specimen from Toril, Spain, that challenged this scheme because Toril is correlated to MN 7, but in general, the sequence appears to be sound.

The naming of the large subspecies of *Listriodon splendens* is problematic in that some of the material from La Chaux-de-Fonds is large, falling into the range of variation of *L. s. major*, yet it has a prior name *trux* VON MEYER, 1846. The available evidence suggests that *trux* rather than *major* is likely to be the valid name for this subspecies. The differences in dimensions of the sample from La Chaux-de-Fonds could reflect sexual bimodality rather than the presence of two species or subspecies, but the available material is too restricted to resolve the issue. In essence, the problem is one of nomenclature. Should *L. s. major* be called *L. s. trux*?

Material from Nebisuyu. EUNHM PV 3075, skull lacking the premaxillae, and left maxilla fragment containing the canine.

Description. Skull. In dorsal view (Text-fig. 2), the frontal bone dominates the skull, not only by its relatively great breadth, but also by its massiveness, its somewhat rugose surface and the thickness of the bone, extending even onto the post-orbital process. The anterior parts of the frontal bones narrow markedly and descend towards the nasals at a steep angle, and are scored by two deep, parallel, grooves that link distally to the supra-orbital foramina. The supra-orbital foramina are poorly exposed but lie about half way down the steeply sloping anterior surface of the frontal. The frontals are domed upwards between the lachrymals, and are so swollen that they overhang the latter bones to a small extent. Careful scrutiny of the frontal dome reveals the presence of a suture all around the top of the frontal, on top of which is a bony apophysis, the apex of which has broken off. The broken base of the apex is oval and measures 50 mm antero-posteriorly by 31 mm bilaterally. This bony apophysis resembles an ossicone rather than a horn, since its origin appears to have been dermal. The lachrymal foramina are not preserved.

The parietals posterior to the frontals are not swollen and the surface of the bones is smooth. The temporal crests are far apart, but because the skull is slightly crushed, there is an irregular ridge running along the midline, but this should not be confused with a sagittal crest, although it could represent a distal extension of the suprafrontal structure or ossicone. The posterior margin of the neurocranium is incurved rather than rectilinear.

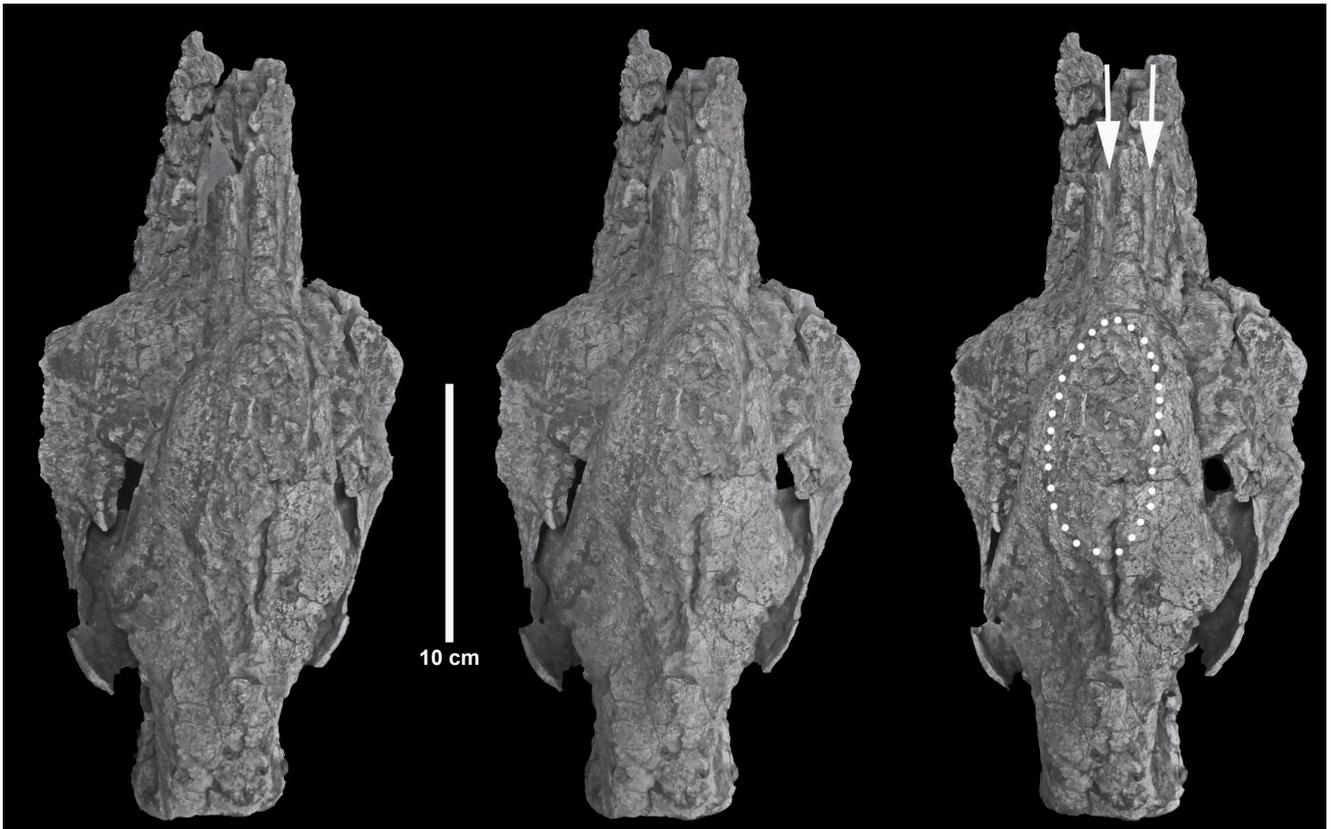
The distal extremities of the zygomatic arches are visible in dorsal view, and they terminate about half way between the posterior margin of the orbit and the nuchal ridge at the rear of the skull.

Finally, in dorsal view, it is possible to make out that the zygomatic arches slope laterally and ventrally to a marked extent, but because the lateral edges of the structures are broken off on both sides it is not possible to determine the diameter of the skull at this point, nor whether the zygoma possessed laterally projecting apophyses. They do, however, have a rugose upper surface and are dorso-ventrally thickened, which is rather unusual in a suid context.

In lateral view (Text-figs 3, 4), it is once again the frontal bones that dominate the skull. They comprise a solid dome-like structure above the lachrymals, the swollen and somewhat rugose bone surface extending posteriorly onto the post-orbital processes, which are themselves enlarged antero-posteriorly and thicker than is usual in suid skulls. The suture between the frontal and the lachrymal is well exposed on both sides. The anterior parts of the frontals descend steeply towards the nasals before curving anteriorly. The nasals are broken off.

The anterior margin of the orbits is about 13 mm behind the distal extremity of the M3/ and are positioned high in the skull. Distortion makes it difficult to estimate the original dimensions of the orbits.

Posteriorly, the temporal fossae are clear and deeply excavated. The zygomatic arches are large and form a massive base to the orbits. However, their lateral extremities



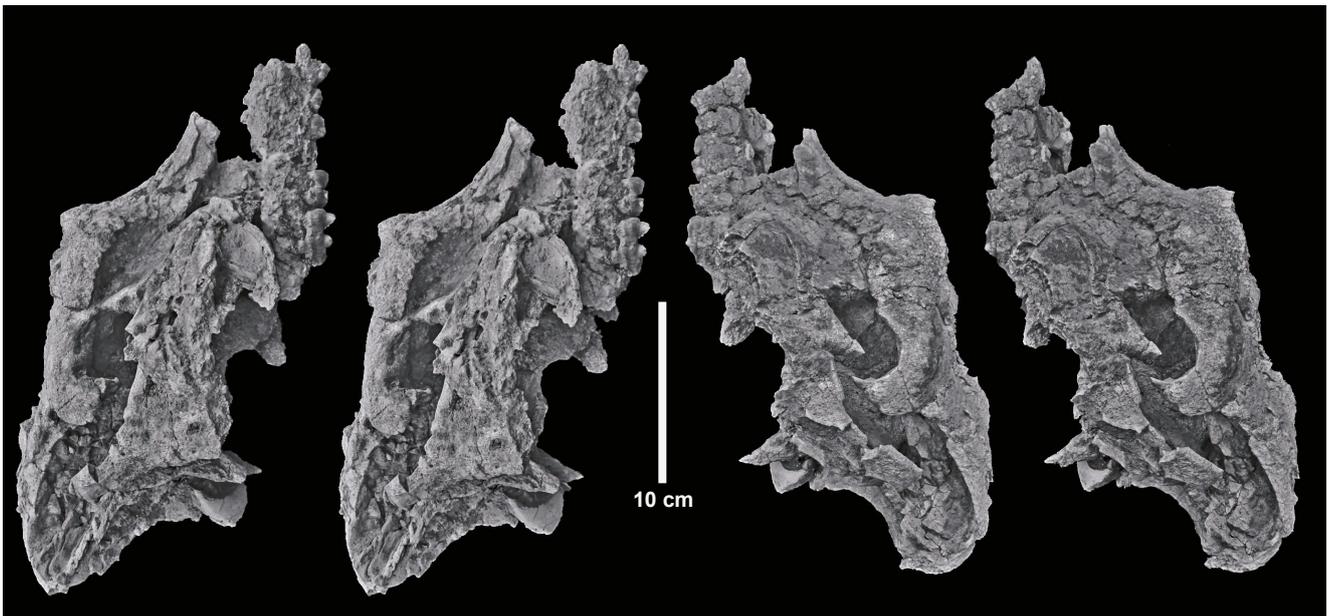
Text-fig. 2. Stereo dorsal views of the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075). Arrows show the two grooves associated with the supraorbital foramina.

have been broken off, so it is not possible to ascertain their original extent.

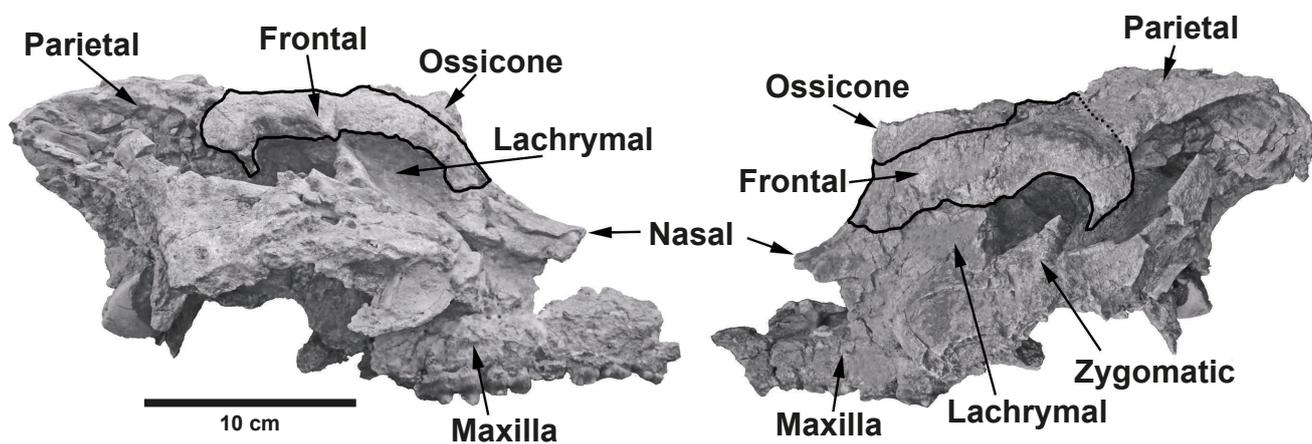
The occipital condyles are small and lie only slightly above the level of the plane of the cheek teeth and well beneath the level of the orbits. The paroccipital processes are short and are directed ventro-distally.

In ventral view (Text-fig. 5), the palate is observed to extend beyond the distal ends of the M3/s by about 22 mm

(estimated due to damage). The zygomatic arches more than double the breadth of the skull, but to what extent is difficult to estimate due to the fact that the lateral parts of both zygoma are broken off. The root of the zygomatic process of the maxilla is far back, opposite the front of M3/. The tooth rows diverge gently from fore to aft, but the skull is slightly crushed and the palate has been partly reconstructed so this divergence may be somewhat altered by post-mortem



Text-fig. 3. Stereo lateral views of the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075).



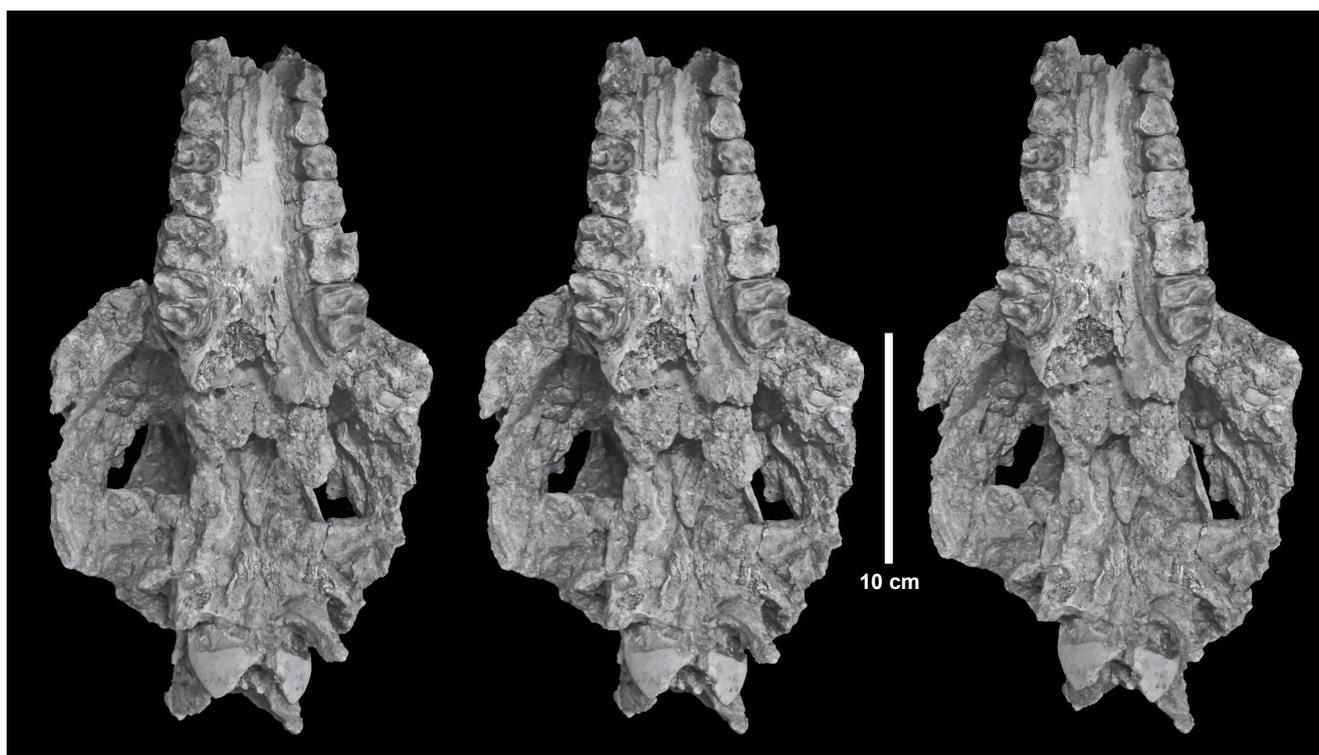
Text-fig. 4. Lateral views of the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075), with interpretation of the bony structures surrounding the thickened frontal bones outlined in black.

distortion. The occipital condyles appear to be small for such a massive skull, and the paroccipital processes are short and are oriented ventro-distally. Much of the basicranium is preserved, but the state of preservation does not permit accurate description or interpretation.

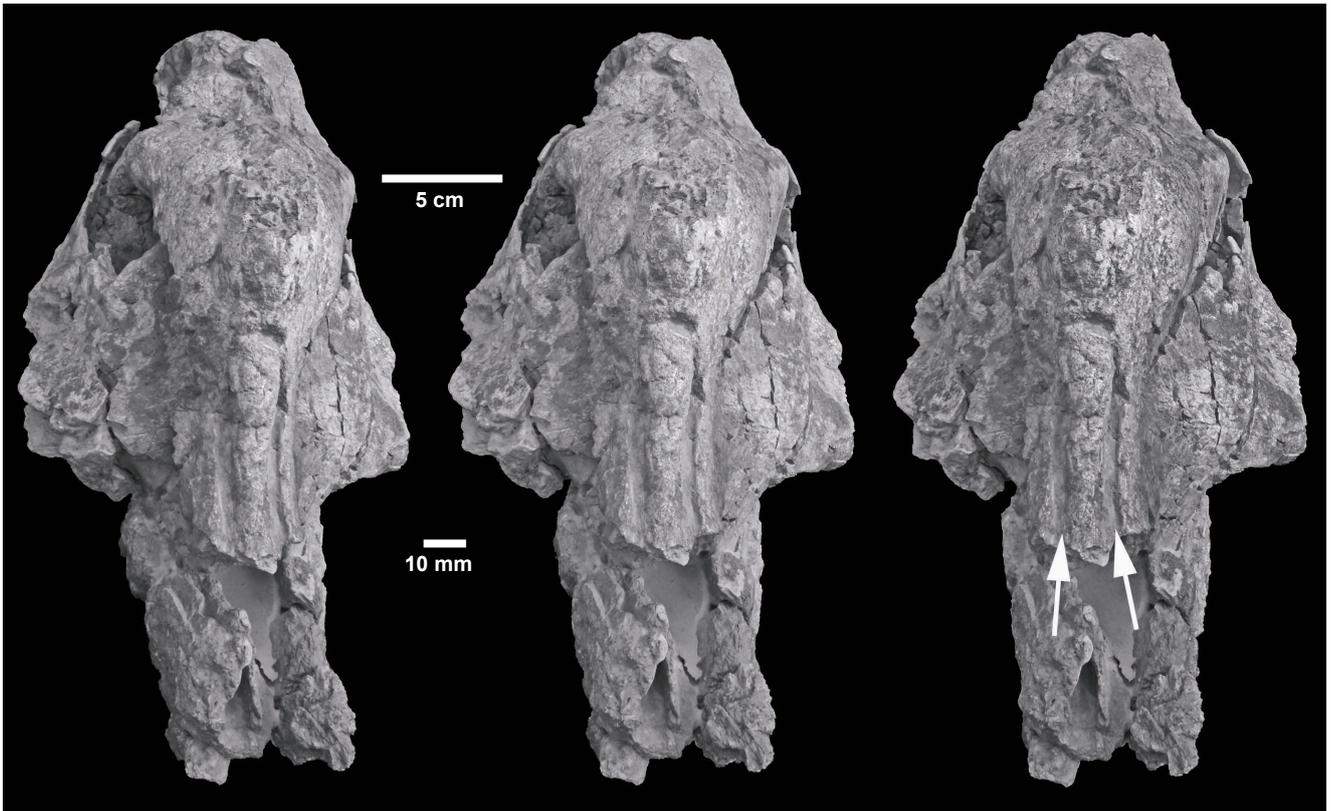
In supero-anterior view (Text-fig. 6), there are two aspects of the skull which are striking to the eye. The first is the narrowness of the snout, the second is the massiveness of the frontal zone which dominates the area above the orbits. The two grooves linked to the supraorbital foramina are deep and subparallel, coursing along the dorsal part of the frontals. The foramina from which they emerge are poorly preserved, partly due to damage, but partly due to thickening of the frontal bone which has a distinctly rugose surface which contrasts vividly with the smooth bone of the lachrymals beneath them.

In supero-anterior view the base of the ossicone structure is clearly visible, forming an apophysis above the thickened and domed frontal bone and marked by a suture (subtle but clearly visible in glancing light). This ossicone is located above and anterior to the orbits in the anterior part of the frontal dome, the main part of which lies between the orbits. In this view, the thickening of the post-orbital processes is clearly evident, the bones forming a massive margin at the rear of each orbit. This contrasts with the sharp edges of the rear extremities of the zygomatic arches which form the margins of the temporal fossae.

In distal view, the point that leaps to the attention is the deeply concave nuchal area of the neurocranium. The upper margins of the depression are thickened laterally and dorsally, and gradually diminish in thickness as they



Text-fig. 5. Stereo palatal views of the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075).



Text-fig. 6. Stereo supero-anterior views of the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075). Arrows show the two grooves associated with the supraorbital foramina (scales are 10 mm for the anterior part of the frontal bones, and 5 cm for the parietals).

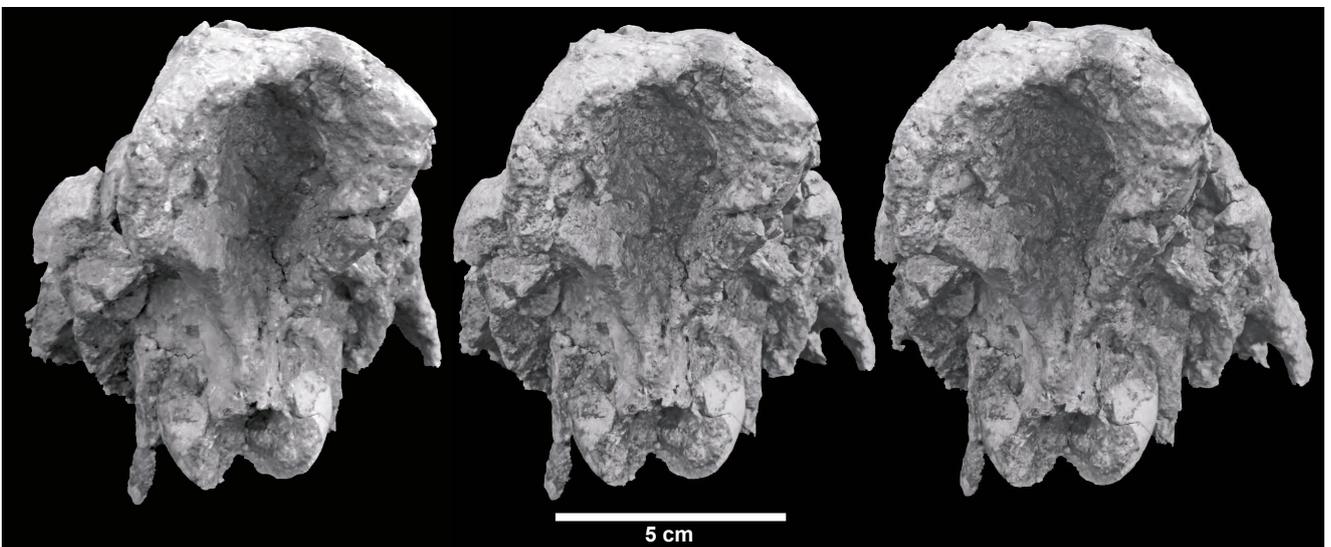
approach the occipital condyles, where they form a V-shaped junction in the mid-line of the skull.

In posterior view (Text-fig. 7) the paroccipital processes are short and oriented vertically just to the lateral side of the occipital condyles. They extend barely a cm beyond the lowest point of the condyles.

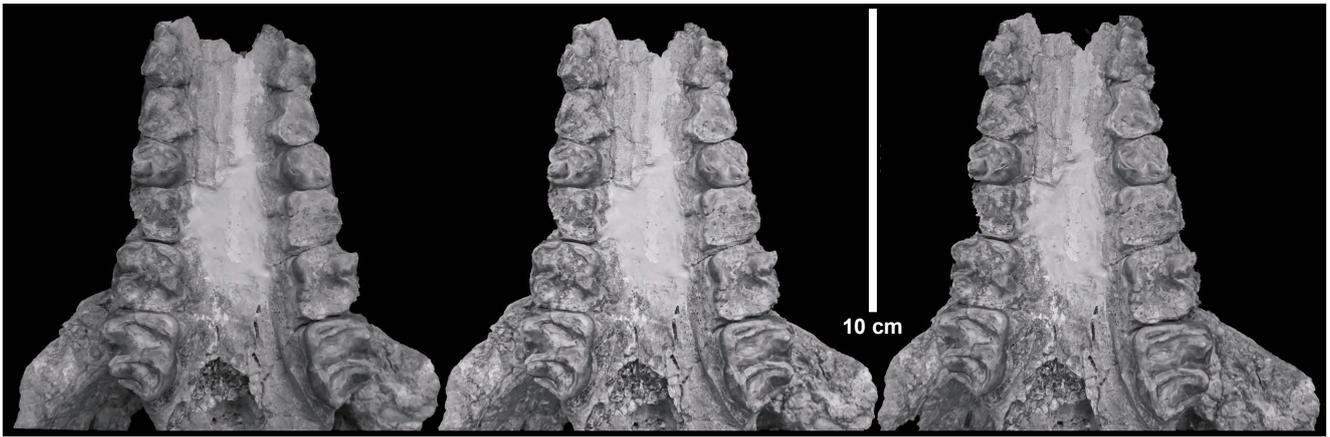
Dentition. The palate retains heavily worn P2/–M3/ on both sides (Text-fig. 8).

The P2/ and P3/ are worn to stubs revealing little about their occlusal cusp morphology. On the buccal sides of both

the P2/ and the P3/, there is a low, beaded cingulum, while a depression on the lateral surface of each tooth indicates that there was likely a metacone in these two teeth, now largely eliminated by wear. The occlusal outline of each tooth is triangular with rounded corners. P4/ is heavily worn but shows three cusps, the protocone and paracone forming an anterior loph, and the metacone somewhat isolated in the disto-buccal corner of the crown. There are remnants of mesial and distal cingula. M1/ and M2/ are reduced to stubs with no cuspal morphology discernible. The M3/ in contrast, even though



Text-fig. 7. Stereo posterior views of the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075).

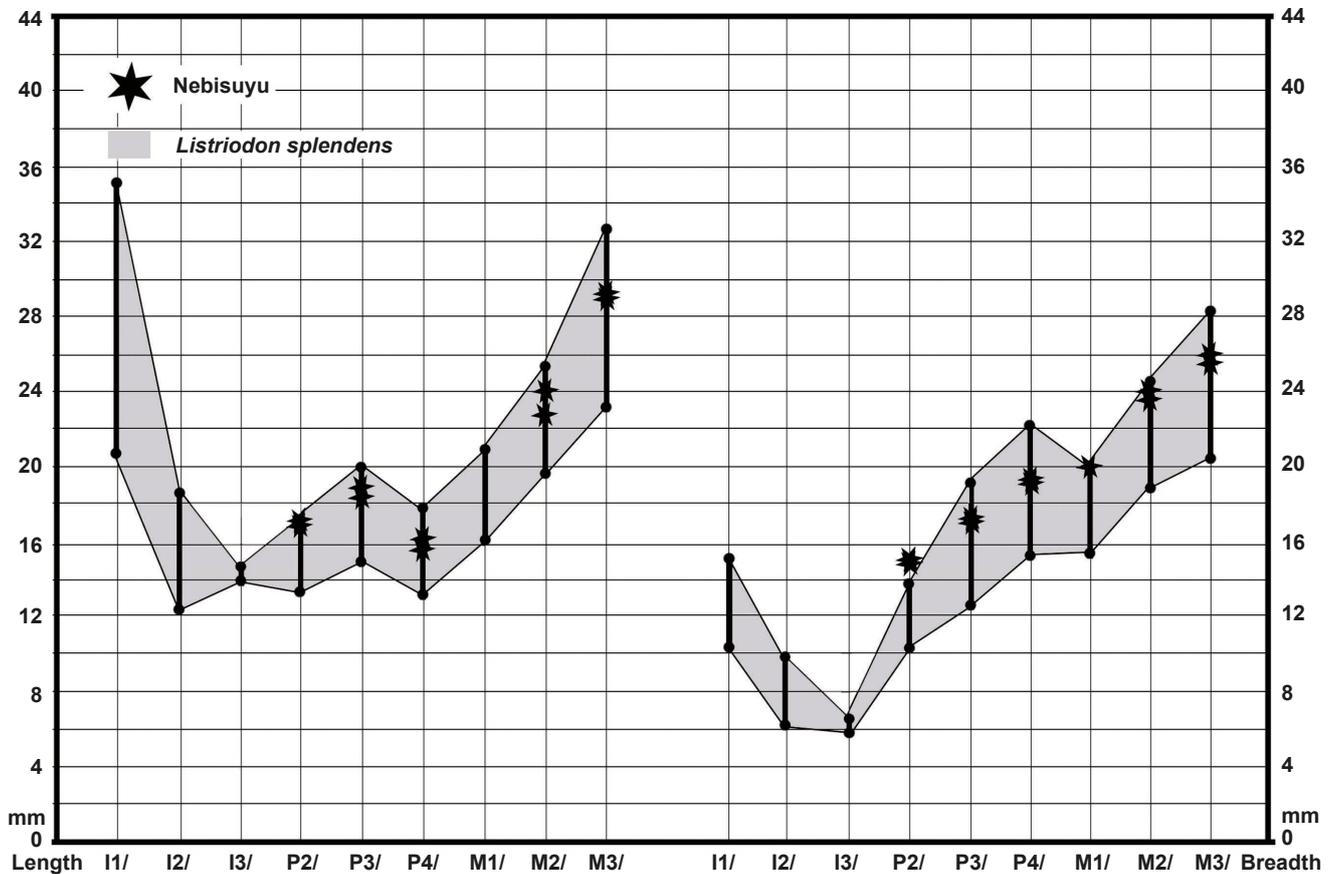


Text-fig. 8. Stereo palatal views of maxillae of *Listriodon splendens* from Nebisuyu, Çanakkale, Turkey (EUNHM PV 3075).

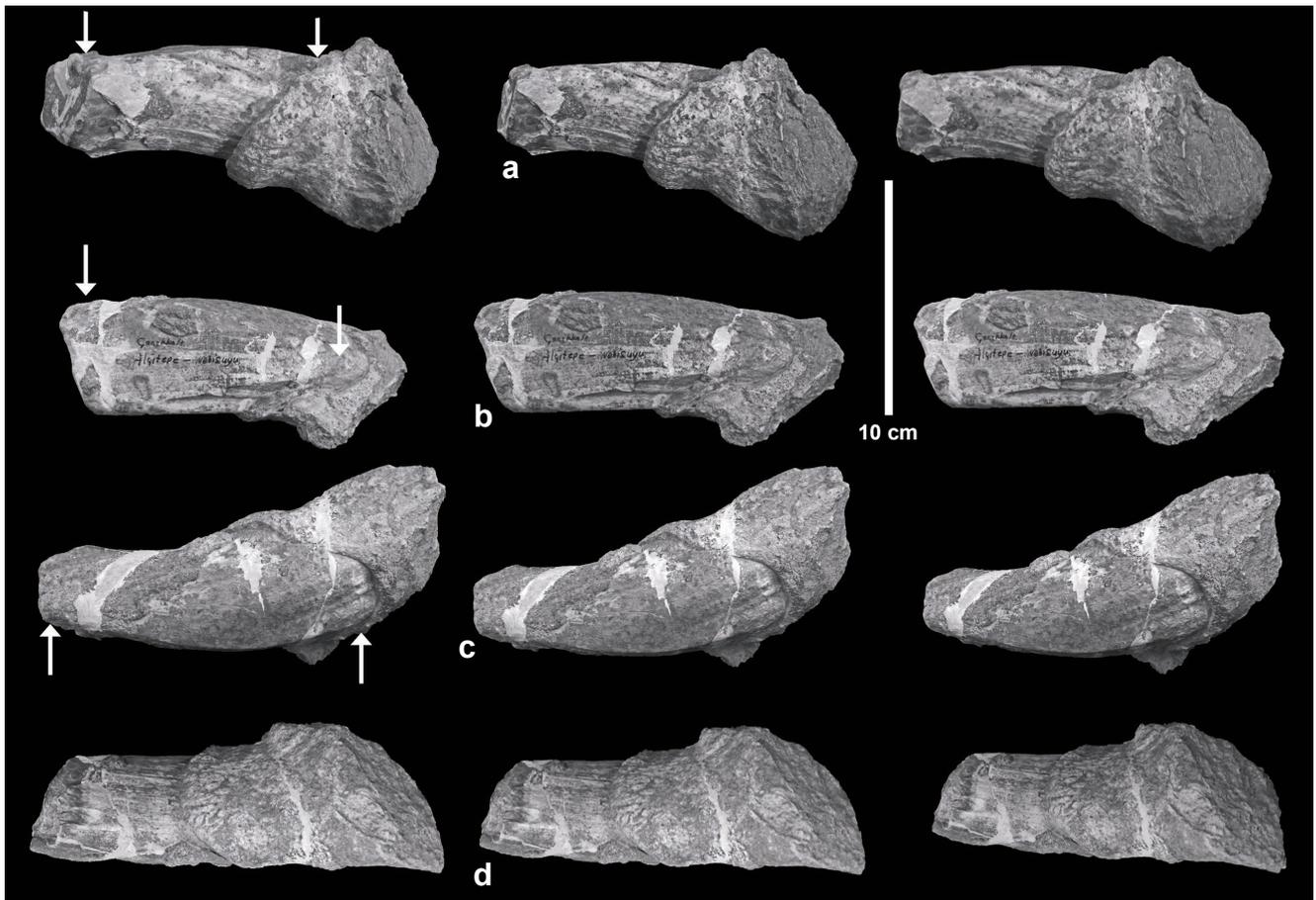
heavily worn shows two clear transverse lophs separated by a transverse valley which is not blocked by a median accessory cusplet. There is a mesial cingulum, especially evident in the mesio-lingual half of the crown, and there is a distal cingulum between the metacone and hypoconule. Wear has advanced to the stage where the protocone and paracone are joined together thereby forming a strong, slightly oblique transverse loph, and the metacone, hypocone and hypoconule are joined together, forming an obliquely oriented distal loph.

The overall aspect of the dentition of the Nebisuyu suid skull is that it is of a highly lophodont listriodont such as

Listriodon splendens, but it is not as finely lophodont as *Lopholistriodon kidogosana* PICKFORD et WILKINSON, 1975, which is in any case a much smaller animal (Pickford 1986). Metrically, the teeth of the Nebisuyu fossil plot into the upper part of the range of variation of dentitions of *Listriodon splendens* from Europe (Text-fig. 9), with the sole exception that the breadth of the P2/ slightly surpasses that of any other known specimen. However, considering its extremely worn status, measurement of the P2/ had to be estimated from the roots which are known to be larger than the crown. Therefore, the seemingly very broad P2/ does not comprise



Text-fig. 9. Length and breadth diagram of upper teeth *Listriodon splendens* from Europe (after Pickford and Morales 2003). The cheek teeth of the Nebisuyu fossil plot into the upper part of the range of variation, close to specimens attributed to the subspecies *Listriodon splendens major*.



Text-fig. 10. Stereoscopic views of EUNHM PV 3075, upper left male canine in maxilla fragment from Nebisuyu, Turkey, attributed to *Listriodon splendens*. Radicular end is to the right. Arrows indicate extent of wear facet caused by abrasion against the lower canine. a: antero-dorsal, b: oblique anterior view, c: ventral, d: dorsal views.

a substantive argument against attributing the specimen to *Listriodon splendens*.

If one accepts the presence of diverse subspecies of *Listriodon splendens*, as was the position of Van der Made (1996) then, on the basis of its large cheek teeth with a suggestion that P2/ and P3/ possessed distinct metacones, one would conclude that the Nebisuyu skull should be classified as *Listriodon splendens major* ROMAN, 1907, or as *Listriodon splendens* Evolutionary Stage III of Van der

Made (1996). Given, however, that the type specimen of *Calydonius trux* VON MEYER, 1846, is a large upper canine from the same locality as the upper central incisor which is the lectotype of *Listriodon splendens*, the possibility exists that evolutionary stage III should be called either *splendens* or *trux*, both names having priority over *major*. The question is delicate in that the lectotype incisor, even though large within the context of *Listriodon*, could represent evolutionary stage II as thought by Van der Made (1996) whereas the canine attributed to *Calydonius trux* is rather too large to belong to this evolutionary stage, and more likely represents evolutionary stage III.

Table 1. Measurements (in mm) of the cheek teeth in the skull of *Listriodon splendens* from Nebisuyu, Turkey (EUNHM PV 3075). lt – left, rt – right.

Tooth	Mesio-distal length	Bucco-lingual breadth
P2/lt	17.0	15.0
P2/rt	17.4	15.2
P3/lt	18.3	17.2
P3/rt	19.0	17.4
P4/lt	16.3	19.5
P4/rt	15.8	19.6
M1/lt	–	20.0
M1/rt	–	–
M2/lt	24.0	24.0
M2/rt	23.0	23.6
M3/lt	28.7	25.8
M3/rt	28.1	26.0

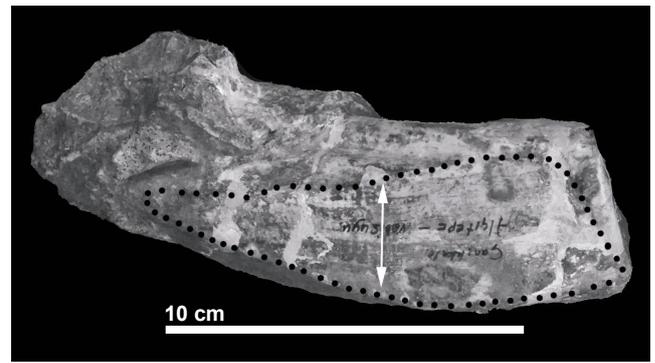
Metric analysis of the dentition. Comparisons of the dimensions of the cheek teeth of the Nebisuyu specimen with other listriodonts from Eurasia, indicates that they fall into the known range of variation of *Listriodon splendens* (Tab. 1). In detail the specimen corresponds closely in dimensions with material often attributed to the subspecies *Listriodon splendens major* ROMAN, 1907, or *Listriodon splendens* evolutionary stage III of Van der Made (1996) which ranges in age from the end of MN 7 to the beginning of MN 9. This subspecies was defined in the Iberian Peninsula (Aveiras de Baixo, Portugal) (Roman 1907) and has been reported from several localities in Spain (Hernandez-Pacego and Dantin Cereceda 1915, Van der Made 1996, Pickford and Morales 2003) and may occur at the type locality of *Listriodon splendens*, La Chaux-

de-Fonds, Switzerland, where it is known under the name *Calydonius trux* VON MEYER, 1846.

Huge suid canine from Nebisuyu. The locality at Nebisuyu from which the large skull of *Listriodon splendens* was collected also yielded a left upper male canine in a fragment of maxilla (EUNHM PV 3075) (Text-figs 10, 11). The specimen is large within the context of *Listriodon*, and it is possible that it represents the same individual as the skull. Large canines of *Listriodon splendens* are known from St Quirze and Hostalets, Spain, Bonnefont (Text-fig. 14) and La Grive, France, and La Chaux-de-Fonds, Switzerland, the last being the type specimen of *Calydonius trux* VON MEYER, 1846 (Van der Made 1996). The specimen from St Quirze, in particular, has almost the same antero-posterior diameter as the Nebisuyu tooth (54 mm versus 55 mm for the Turkish specimen) (Text-fig. 15).

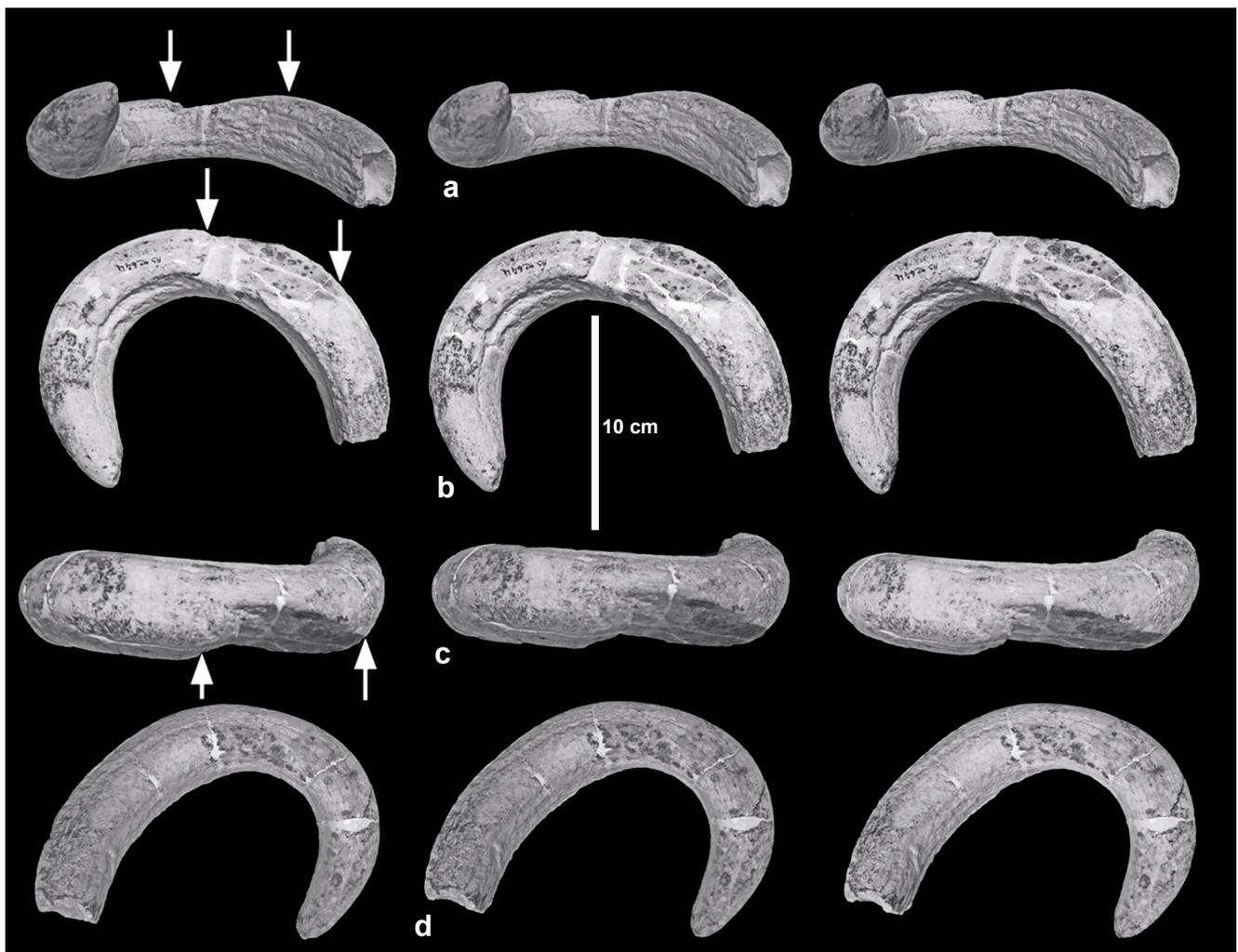
The radicular part of the Nebisuyu canine is short, about 25 mm on the ventral side and ca. 73 mm dorsally where the root is covered by the canine flange. This measurement is of the same order of magnitude as that of the canine in the skull of *Listriodon xinanensis* CHEN, 1986 from China (Chen 1986, Van der Made 1996).

Even though the Nebisuyu canine lacks the apex (broken off or worn away, so no enamel bands are preserved) what

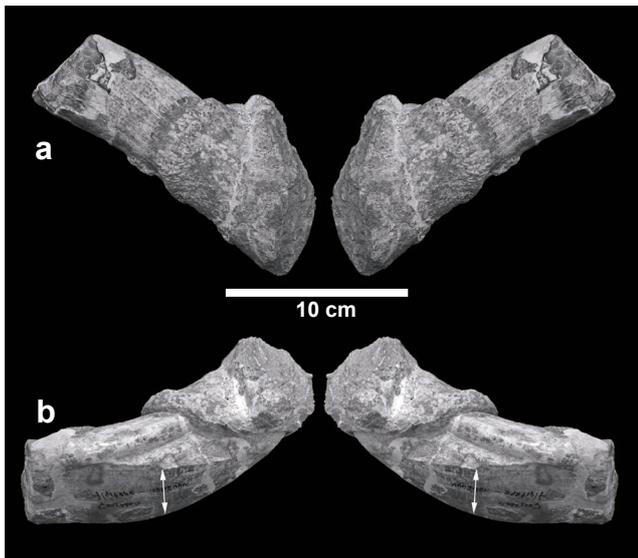


Text-fig. 11. Slightly oblique anterior view of the Nebisuyu suid canine (EUNHM PV 3075) to show the extent of the wear facet caused by thegosis against the lower canine. The double-headed arrow shows the orientation of scratches on the wear facet.

remains accords closely in morphology with a specimen of *Listriodon splendens* from Sinap, Turkey, but it is substantially larger. There is a prominent dorsal gutter backed by a ridge as in the specimen from Sinap (EUNHM AS 92.644) (Text-fig. 12) and the anterior gutter is weakly expressed. The almost planar wear facet caused by abrasion against the lower



Text-fig. 12. Stereoscopic views of EUNHM AS 92-644, left upper male canine of *Listriodon splendens* from Sinap, Turkey. a: oblique posterior, b: oblique ventral, c: oblique anterior, d: oblique superior views. The radicular end is towards to the right except in (d) where it is to the left. Arrows indicate the extent of the wear facet caused by abrasion against the lower canine.



Text-fig. 13. Reconstruction of the upper canines of the Nebisuyu listriodont (EUNHM PV 3075). a: dorsal view (anterior towards top of page), b: anterior view. The two-headed arrows show the orientation of the scratches on the wear facet caused during thegosis with the lower canine. These orientations are approximate.

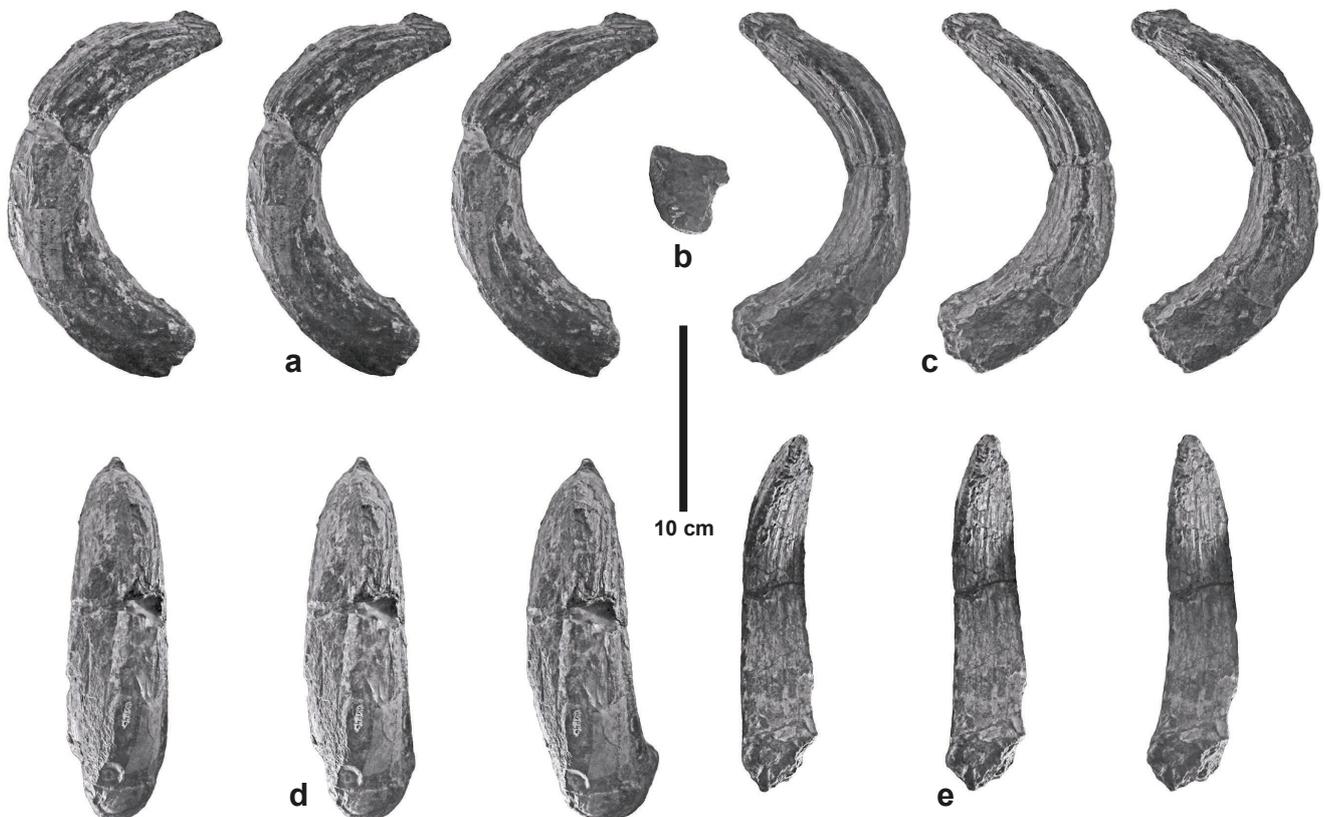
canine is similar in the two specimens, with a notched outer edge which makes a prominent step on the anterior surface of the tooth. The wear facet narrows towards the root, its inner end being close to the edge of the alveolus (21 mm in the Nebisuyu specimen, 14 mm in the Sinap tooth).

Measured from the medial end to the outer notch, the wear facet is 64 mm long in the Sinap specimen and 112 mm in the specimen from Nebisuyu. This measurement corresponds to the length of that part of the lower canine that contacts the upper canine during thegosis (Text-fig. 13).

Other unpublished material of the large variant of *Listriodon splendens* is known from the locality of Helsighausen, Switzerland (Text-fig. 16, Tab. 3). An upper central incisor and a right mandible with cheek teeth from fine sandstone deposits in the area falls into the upper part of the range of metric variation of the species (Tab. 2).

Some unpublished specimens of large *Listriodon splendens* from Hostalet, Spain, curated in other institutions, are included in order to fill out the fossil record of the taxon (Text-fig. 17).

Hernandez-Pacego and Dantin Cereceda (1915) published detailed descriptions of teeth, jaws and post-cranial elements of *Listriodon splendens* from Cerro del Ortero, Spain, attributing the fossils to the large subspecies *major*. The authors also discussed and illustrated what they considered to be an unknown artiodactyl. Stehlin (in Hernandez-Pacego and Dantin Cereceda 1915: 137–138, 260–261) in a written communication to the authors commented that, after examining casts of the latter specimens, they show affinities to *Hyopotamus* and more particularly to a specimen from Monte Massi, Italy, that he had identified as *Anthracotheium? meneghinii*, but probably representing a new genus of anthracothere. In fact all the Spanish fossils concerned are juveniles of *Listriodon splendens major* and are not in any way related to anthracotheres.



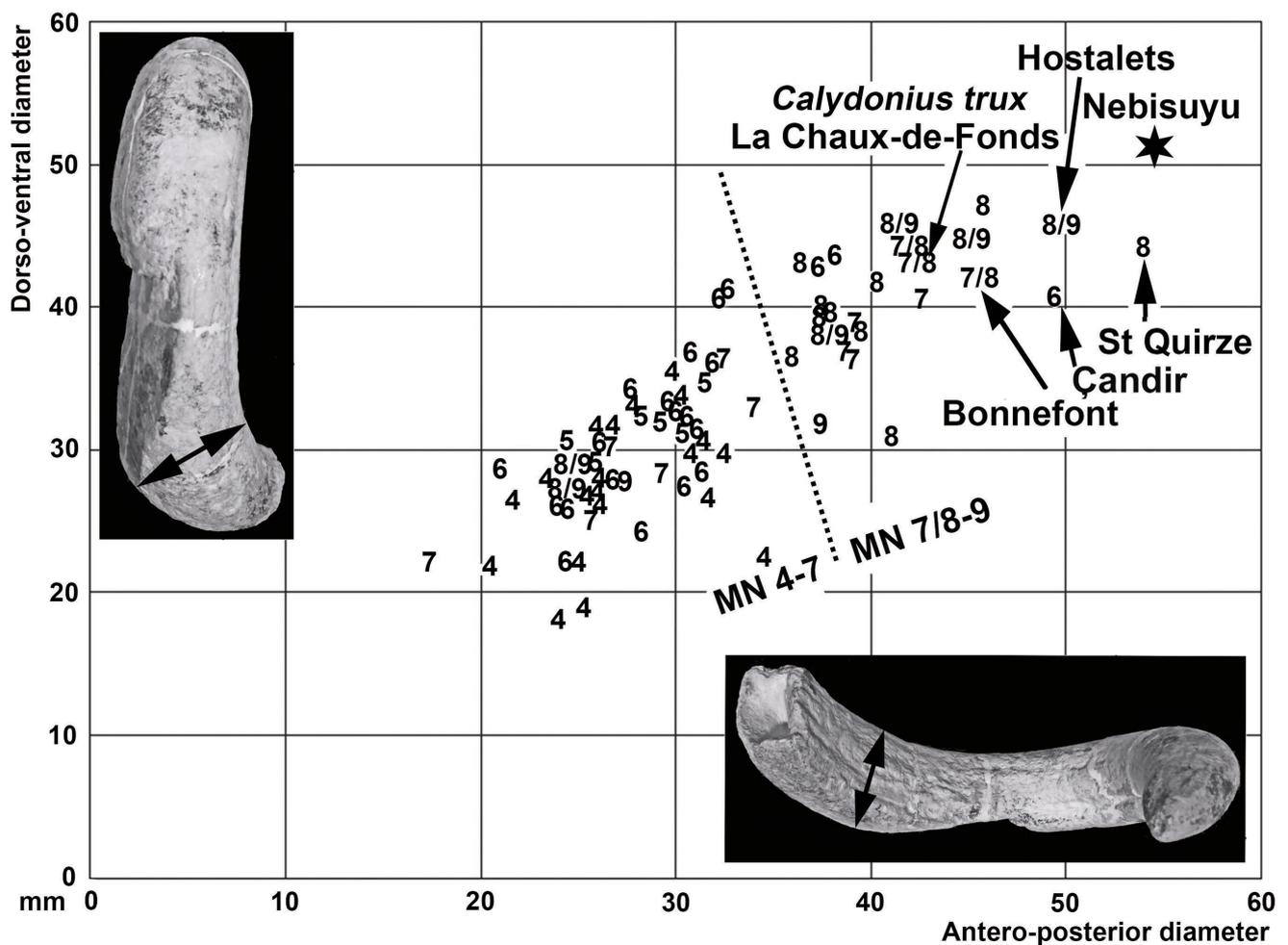
Text-fig. 14. Stereo images of MNHN HGP 46, left upper male canine of *Listriodon splendens* from Bonnefont, France, first published by Crouzel (1980) as *Sus (?) doati*. a: ventral view, b: radicular section, c: dorsal view, d: oblique lateral view, e: oblique medial view.

Table 2. Measurements (in mm) of upper male canines of Listriodontinae from Europe and Turkey arranged by MN Zones. Dap – antero-posterior diameter, Dvd – dorso-ventral diameter, lt – left, rt – right, VDM – Van der Made.

Catalogue no.	Tooth	Dap	Dvd	Locality	Data source and comments	Correlation
ML 5547	C1/	29.8	35.6	Quinta da Raposa, Portugal	VDM 1996	MN 4
MNCN HOT-SI 072	C1/lt	24.0	18.0	Hidroelectrica, Spain	Own, 2015	MN 4
MNCN 193	C1/lt	25.5	27.0	Los Nogales, Spain	Own, 2015	MN 4
MNCN 33	C1/rt	27.0	28.0	Los Nogales, Spain	Own, 2015	MN 4
MNCN FMH'14 4075	C1/rt	34.5	22.4	Mahou, Spain	Own, 2015	MN 4
MNHN LRM 851	C/lt	25.5	21.0	Pellecahus, France	Own, 2019	MN 4
MPZ 6427	C1/lt	20.5	22.0	Artesilla, Spain	VDM 1996	MN 4a
MPV FB 52	C1/lt	30.7	29.8	Buñol, Spain	VDM 1996	MN 4a
IPS 1148	C1/lt	31.4	30.6	Buñol, Spain	VDM 1996	MN 4a
IPS	C1/lt	32.5	29.8	Buñol, Spain	VDM 1996	MN 4a
MPV FBB 217	C1/rt	25.2	18.9	Buñol, Spain	VDM 1996	MN 4a
IVAU	C1/rt	26.1	31.0	Buñol, Spain	VDM 1996	MN 4a
ML	C1/	30.0	33.5	Curelos de Cavao, Portugal	VDM 1996	MN 4a
CEPUNL	C1/rt	24.6	30.5	Quinta da Farinheira, Portugal	VDM 1996	MN 4a
ML 5549	C1/rt	28.0	33.0	Quinta de Conceição, Portugal	VDM 1996	MN 4a
NMB SO 3022	C1/rt	25.9	27.2	Baigneaux, France	VDM 1996	MN 4b
MNHN CHE 68	C1/rt	27.2	27.9	Chevilly, France	VDM 1996	MN 4b
MNHN CHE 32	C1/rt	31.6	26.6	Chevilly, France	VDM 1996	MN 4b
MSNO 231	C1/rt	24.0	26.5	Chevilly?, France	VDM 1996	MN 4b
UCBL 320303	C1/rt	23.3	28.0	La Romieu, France	VDM 1996	MN 4b
UCBL 320303	C1/rt	25.0	22.1	La Romieu, France	VDM 1996	MN 4b
UCBL 320281	C1/rt	26.1	26.3	La Romieu, France	VDM 1996	MN 4b
CEPUNL 25	C1/lt	26.7	31.7	Olival da Susana, Portugal	VDM 1996	MN 4b
CEPUNL 26	C1/rt	21.6	26.5	Olival da Susana, Portugal	VDM 1996	MN 4b
ML 5544	C1/	26.1	28.2	Quinta Grande, Portugal	VDM 1996	MN 4b
MNHN FP 225	C1/lt	29.2	32.0	Pontlevoy, France	VDM 1996	MN 5
MNHN FP 739	C1/rt	30.7	31.7	Pontlevoy, France	VDM 1996	MN 5
NMB 546 cast	C1/lt	24.5	30.5	Ravensberg, Germany	VDM 1996	MN 5
NMB TD 545	C1/rt	28.2	32.4	Ravensberg, Germany	VDM 1996	MN 5
COBO	C1/rt	25.9	29.1	Tavers, France	VDM 1996	MN 5
NSSW 113	C1/lt	31.5	34.7	Veltheim, Austria	VDM 1996	MN 5
MTA CA 1/2	C1/rt	28.2	24.2	Çandır, Turkey	VDM 1996	MN 6
PIMUZ CA V/21	C1/rt	49.3	40.6	Çandır, Turkey	VDM 1996	MN 6
MTA AKI 3/588	C1/lt	31.2	28.5	Inönü, Turkey	VDM 1996	MN 6
MTA AKI 3/332	C1/rt	27.7	34.0	Inönü, Turkey	VDM 1996	MN 6
MTA AKI 3/327	C1/rt	31.9	36.0	Inönü, Turkey	VDM 1996	MN 6
MTA AKI 3/325	C1/rt	32.6	41.1	Inönü, Turkey	VDM 1996	MN 6
IPUW 18 IX 15	C1/lt	24.2	25.9	Klein Hadersdorf, Austria	VDM 1996	MN 6
IPUW 18 IX 15	C1/lt	26.8	27.7	Klein Hadersdorf, Austria	VDM 1996	MN 6
IPS 1101	C1/lt	24.4	22.0	Manchones 1, Spain	VDM 1996	MN 6
IVAU AR IV 60	C1/lt	26.2	30.3	Manchones 2, Spain	VDM 1996	MN 6
MPZ AV-21	C1/lt	29.7	33.2	Manchones 2, Spain	VDM 1996	MN 6
RGM 263.162	C1/lt	31.0	31.3	Manchones 2, Spain	VDM 1996	MN 6
RGM 262.972	C1/rt	30.0	32.7	Manchones 2, Spain	VDM 1996	MN 6
IVAU ARIV 398	C1/rt	30.4	27.4	Manchones 2, Spain	VDM 1996	MN 6
IVAU AR IV 64	C1/rt	30.5	32.3	Manchones 2, Spain	VDM 1996	MN 6
PDTEFAU G987	C1/lt	32.2	40.4	Pasalar, Turkey	VDM 1996	MN 6
PDTEFAU G114	C1/rt	30.7	36.6	Pasalar, Turkey	VDM 1996	MN 6
MNHN Sa 4317	C1/	21.0	28.5	Sansan, France	VDM 1996	MN 6
BSPG 1957 I 194	C1/lt	24.4	27.0	Wartenberg, Germany	VDM 1996 as MN 8/9	MN 6
BSPG 1958 I 34	C1/rt	25.4	28.9	Wartenberg, Germany	VDM 1996 as MN 8/9	MN 6
HLD Din 40	C1/lt	26.3	29.9	Esselborn, Germany	VDM 1996 as MN 9	MN 6
NMM 1930/375	C1/lt	37.4	32.0	Wissberg, Germany	VDM 1996 as MN 9	MN 6
MNCN NM 18004	C1/rt	29.3	28.5	Cerro del Ortero, Spain	VDM 1996	MN 7
UCBL sans n°	C1/lt	26.7	30.5	La Grive St-Alban, France	VDM 1996	MN 7
MGL LGr 717	C1/lt	32.5	36.6	La Grive St-Alban, France	VDM 1996	MN 7
MGL LGr 1660	C1/rt	34.0	33.1	La Grive St-Alban, France	VDM 1996	MN 7
MNHN Si 158	C1/lt	17.4	22.3	Simorre, France	VDM 1996	MN 7
MNHN Si 157	C1/lt	25.7	25.3	Simorre, France	VDM 1996	MN 7
NMW SK 1614	C1/lt	37.2	42.6	Eichkogel, Austria	VDM 1996 as MN 6	MN 7/8
NMW SK 1614	C1/rt	38.1	43.5	Eichkogel, Austria	VDM 1996 as MN 6	MN 7/8
MNHN HGP 46	C1/lt	45.5	42.0	Bonnefont, France	Own, 2019; VDM 1996 as 43.3 × 41.3	MN 7/8

Table 2. continued.

Catalogue no.	Tooth	Dap	Dvd	Locality	Data source and comments	Correlation
MHNCF 48	C1/ lt	24.2	26.3	La Chaux-de-Fonds, Switzerland	VDM 1996	MN 7/8
MHNCF 14	C1/ rt	41.9	44.3	La Chaux-de-Fonds, Switzerland	VDM 1996	MN 7/8
MHNCF 45	C1/ rt	42.3	43.2	La Chaux-de-Fonds, Switzerland	VDM 1996	MN 7/8
MNCN NM 18009	C1/ lt	39.2	38.6	Cerro del Ortero, Spain	VDM 1996 as MN 7	MN 8
MGL LGr 728	C1/ lt	38.7	37.4	La Grive St-Alban, France	VDM 1996 as MN 7	MN 8
MGL LGr 716	C1/ lt	42.6	40.7	La Grive St-Alban, France	VDM 1996 as MN 7	MN 8
UN	C1/ rt	38.8	36.9	Le Locle, Switzerland	VDM 1996 as MN 7	MN 8
BSPG 1950 I 34b	C1/ rt	35.9	36.9	Massenhausen, Germany	VDM 1996	MN 8
BSPG 1957 I 218	C1/ rt	36.4	43.2	Massenhausen, Germany	VDM 1996	MN 8
BSPG 1951 I 34	C1/ rt	37.6	39.8	Massenhausen, Germany	VDM 1996	MN 8
BSPG 1956 I 135	C1/ rt	39.4	38.3	Massenhausen, Germany	VDM 1996	MN 8
MGSCB 48579	C1/ lt	37.5	40.1	St Quirze, Spain	VDM 1996	MN 8
MGSCB 48578	C1/ lt	37.9	39.9	St Quirze, Spain	VDM 1996	MN 8
MGSCB 48580	C1/ lt	45.7	47.2	St Quirze, Spain	VDM 1996	MN 8
IPS 1674	C1/	54.0	44.0	St Quirze, Spain	VDM 1996	MN 8
MGSCB 48581	C1/ rt	40.3	41.8	St Quirze, Spain	VDM 1996	MN 8
MGSCB 48582	C1/ rt	41.0	31.0	St Quirze, Spain	VDM 1996	MN 8
MGSCB 48512	C1/ lt	41.4	45.7	Hostalets, Spain	VDM 1996	MN 8/9
MGSCB 48513	C1/ lt	45.1	44.8	Hostalets, Spain	VDM 1996	MN 8/9
MGSCB 48511	C1/ lt	49.7	45.8	Hostalets, Spain	VDM 1996	MN 8/9
MGSCB 48514	C1/ rt	37.9	38.1	Hostalets, Spain	VDM 1996	MN 8/9
EUNHM PV 3075	C1/ lt	54.4	51.4	Nebisuyu, Turkey	Own, 2019	MN 8



Text-fig. 15. Bivariate plots of antero-posterior diameter and dorso-ventral diameter of upper male canines of European Listriodontinae arranged by MN zonation (MN 4 – MN 9). Nebisuyu (star) and other large specimens are highlighted. There are some small individuals which have been correlated to MN 8/9 which could be mis-correlated (probably from MN 6), just as there are some large specimens reported to be from MN 7 but which are more likely to be from MN 7/8 or MN 8. Large specimens correlated to MN 6 are from Çandir, Turkey, and Eichkogel, Austria, suggesting a possible mis-correlation of the age of these specimens, at least for the material from the latter locality.

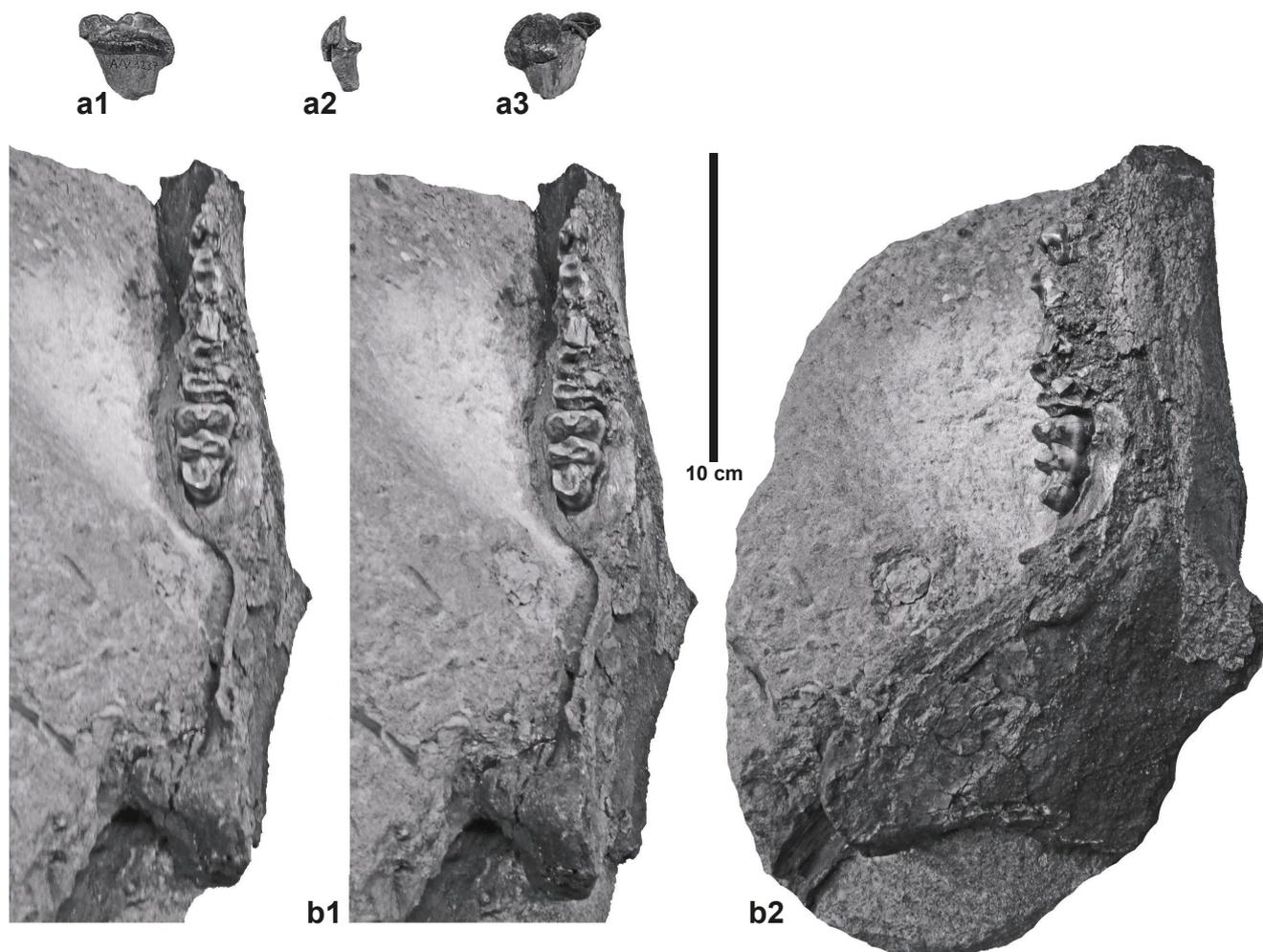
Table 3. Measurements (in mm) of teeth of *Listriodon splendens* from Helsinghausen, Switzerland and Hostalets de Pierola, Spain. BLB – bucco-lingual breadth, lt – left, MDL – mesio-distal length, rt – right.

Catalogue no.	Tooth	MDL	BLB	Locality
PIMUZ A/V 1237	l1/lt	30.0	14.0	Helsinghausen
PIMUZ A/V 1236	m/2 rt	21.0	18.0	Helsinghausen
PIMUZ A/V 1236	m/3 rt	33.0	21.1	Helsinghausen
PIMUZ A/V 1236	p/3 rt	16.7	11.3	Helsinghausen
PIMUZ A/V 1236	p/4 rt	17.0	14.0	Helsinghausen
MNHN 1952-3	m/2 lt	23.0	19.3	Hostalets de Pierola
MNHN 1952-3	m/3 lt	35.0	22.7	Hostalets de Pierola

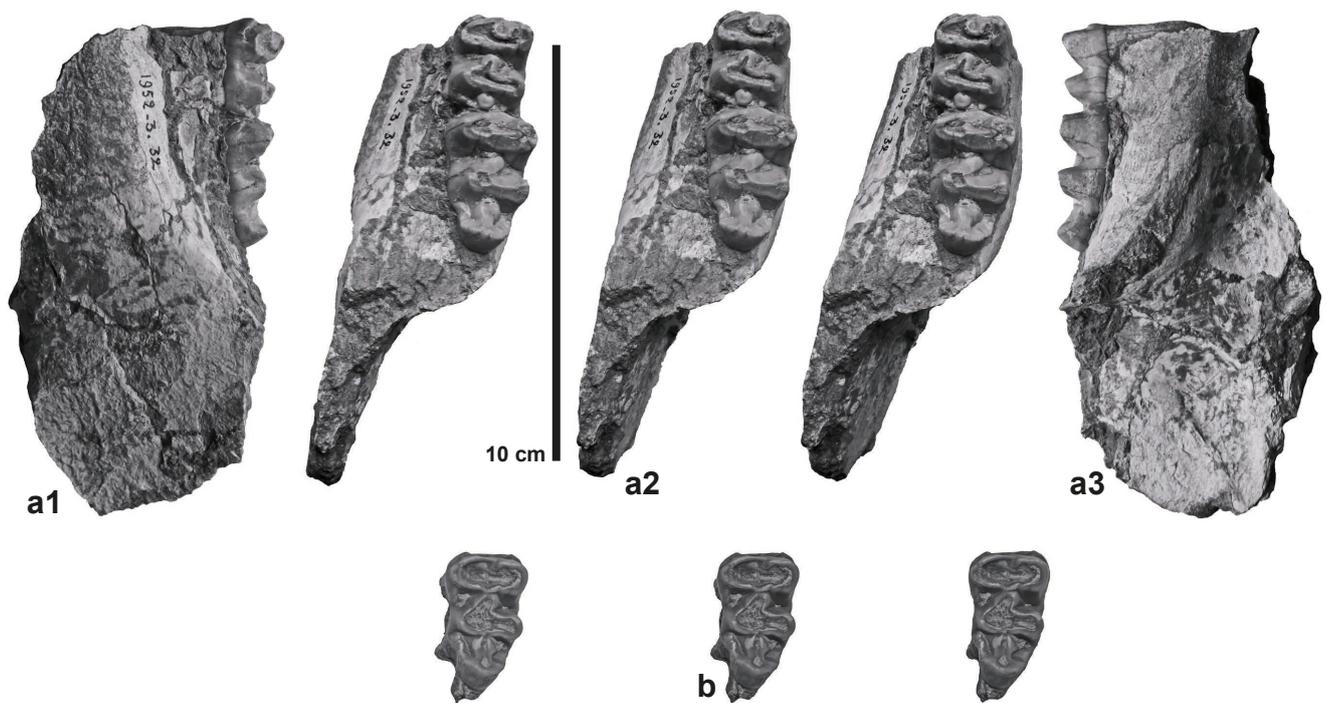
Discussion. The skull of *Listriodon* from Nebisuyu is of an old individual – the M3/s are heavily worn and all that remains of the M1/s are stubs with small remnants of enamel at the bases of the paracone and protocone. The premaxillae and parts of the nasals are broken off and the skull has suffered slight lateral compression and diverse fractures affect much of the surface of the specimen. Of the dentition, only the P2/–M3/ are preserved on both sides, but from the same locality there is a left upper canine in a fragment of maxilla which could well be from the same

individual. The neurocranium is almost complete but has been slightly compressed from side to side and has suffered soft-sediment distortion and some displacement of bony parts. The sutures are difficult to make out due to the advanced age of the individual, but the contact between the lachrymal and frontal can be made out on both sides, the surface of the lachrymal being smooth, whereas that of the frontal above it is thickened and rugose.

What is remarkable about the Nebisuyu specimen is the fact that it preserves the frontals, which are rarely represented in the fossil record of the genus, the few specimens retaining this part of the skull being a large female of *Listriodon splendens* from Toril, Spain (Pickford and Morales 2003), a fossil of *Listriodon xinanensis* from Xinan, China (Chen, 1986) and a specimen from Bézian, France, attributed to *Bunolistriodon lockharti* (POMEL, 1848) by Ginsburg and Bulot (1987). *Lopholistriodon kidogosana* from Ngorora, Kenya (Pickford 1986) also preserves the frontals, but, as its name implies, it is a considerably smaller animal than *Listriodon splendens*. Specimens of *Eurolistriodon adelli* PICKFORD et MOYA-SOLA, 1995, from Els Casots, Spain and *Eurolistriodon tenarezensis* ORLIAC, 2006, from Montréal-du-Gers, France preserve the frontals but the fossils are highly compressed and yield little information about their morphology. A partial skull from Chinji, Pakistan, also



Text-fig. 16. *Listriodon splendens* from Helsinghausen, Switzerland. a: PIMUZ A/V 1237, left I1/ (a1 – lingual, a2 – mesial, a3 – labial views); b: PIMUZ A/V 1236, right mandible containing p/3–m/3 (b1 – stereo occlusal view, b2 – buccal view).



Text-fig. 17. *Listriodon splendens* from Hostalets de Pierola, Spain. a: MNHN 1952-3, left mandible of containing m/2 and m/3 (a1 – buccal view, a2 – stereo occlusal view, a3 – lingual view); b: MGM, left m/3, stereo occlusal view.

preserves part of the frontal bones (Van der Made 1996). Thus, despite its crushed and distorted morphology, the Nebisuyu fossil is of great interest in revealing aspects of the morphology of part of the skull that is rarely represented in the palaeontological record.

Furthermore, the Nebisuyu skull is unusual among Suidae in showing thickened and inflated frontals which rise abruptly just distal to the naso-frontal zone, well in front of the orbits, thereby forming a solid base for a single sagittal horn-like protuberance, the ossicone. The apex of the ossicone itself is missing but its broken base measures about 50 mm antero-posteriorly by ca. 31 mm from side to side. Lower down, the solid base of the horn-like structure measures 65 mm across and it overhangs the lachrymals on both sides (7 mm on the left and 25 mm on the right, the latter measurement possibly exaggerated by inward, post-mortem displacement of the lachrymal). The swollen, inflated and somewhat rugose appearance of the surface of the frontals extends distally from this horn base and affects the post-orbital processes which are enlarged and show a rugose outer surface. Distal to the post-orbital processes the frontals display a more usual suid-like appearance of the fronto-parietal parts, the temporal ridges lying well apart from each other (i.e., no sagittal crest is present). However, the nuchal area is deeply excavated and the distal margin of the temporo-nuchal crest invaginates anteriorly rather than being almost straight and transversely oriented as in many suids (Stehlin 1899, 1900).

The only other suids that are known to have possessed frontal protuberances are Kubanochoerinae GABUNIA, 1958 (Gabunia 1958, 1960) but the position and structure of the horns in this subfamily are different in the Nebisuyu specimen, the base of the horn being more distally positioned (above the orbits) and the frontal bones on which

it is posed are not raised dorsally, nor are they thickened to any great extent. Some nyanzachoeres possess horn-like protuberances on the zygomatic arches (Gebreyesus 2011, Reda et al. 2017) but these are radically different from the horns of listriodonts and kubanochoeres, not only by their positions, but also by the fact that they are present on both sides of the skull.

General discussion and comparisons

Were it not for the swollen, domed frontal bone and the presence of an ossicone on this skull, it would readily fit into the definition of *Listriodon splendens* as a large, old, male individual, and in particular it would accord with current concepts of the subspecies *Listriodon splendens major*. The latter subspecies is known from MN 7, MN 8 and MN 8/9 in Spain and Portugal, which agrees with the estimated correlation of Nebisuyu to MN 8. As such the skull would not attract undue attention, representing a discovery mainly of biogeographic interest, extending, as it does, the known range of the taxon well to the east of its previously documented range (Text-fig. 18).

However, the presence of a thickened, domed frontal bone with a rugose surface, apparently topped by an ossicone, raises a series of questions regarding the taxonomy and ecology of the lineage that it represents. Can the specimen be attributed to an existing taxon? Does the presence of a frontal protuberance indicate affinities with other suids, notably Kubanochoerinae, which possess frontal horns? What selective pressures led to the development of such a cranial structure?

Concerning the taxonomic affinities of the Nebisuyu skull, we have little hesitation in attributing it to *Listriodon splendens*. The dental evidence is striking in this regard, the

M3/, which is the only molar retaining reliable indications of the crown morphology, is clearly that of a highly lophodont species of *Listriodon* in which the median accessory cusplet does not block the median transverse valley (see for example Stehlin 1900: pl. 6, fig. 19, for a figure of an M3/ from La Chaux-de-Fonds, Switzerland). What remains of the P4/ underlines this identification, as do the dimensions of the cheek teeth.

If one accepts the notion of subspecies (or evolutionary stages of Van der Made 1996) then the Nebisuyu skull would be attributed to *Listriodon splendens major* (or to *Listriodon splendens* evolutionary stage III). The only other known skull of this subspecies is from Toril, Spain (MN 7), but it does not possess a thickened frontal bone, nor any sign of an ossicone, probably because it is female (Pickford and Morales 2003).

As for any possibility of a close relationship between the Nebisuyu specimen and *kubanochoeres*, this can be discounted because the form of the frontal bone, the way it is thickened and domed, and the positioning of the ossicone on its top is radically different from the situation in *Kubanochoerus gigas* (PEARSON, 1928) and other species of the genus (GABUNIA 1958, 1960). It is also divergent from the frontal swelling in the genus *Libycochoerus* (only known in *Libycochoerus massai* ARAMBOURG, 1961; Arambourg 1961, 1963).

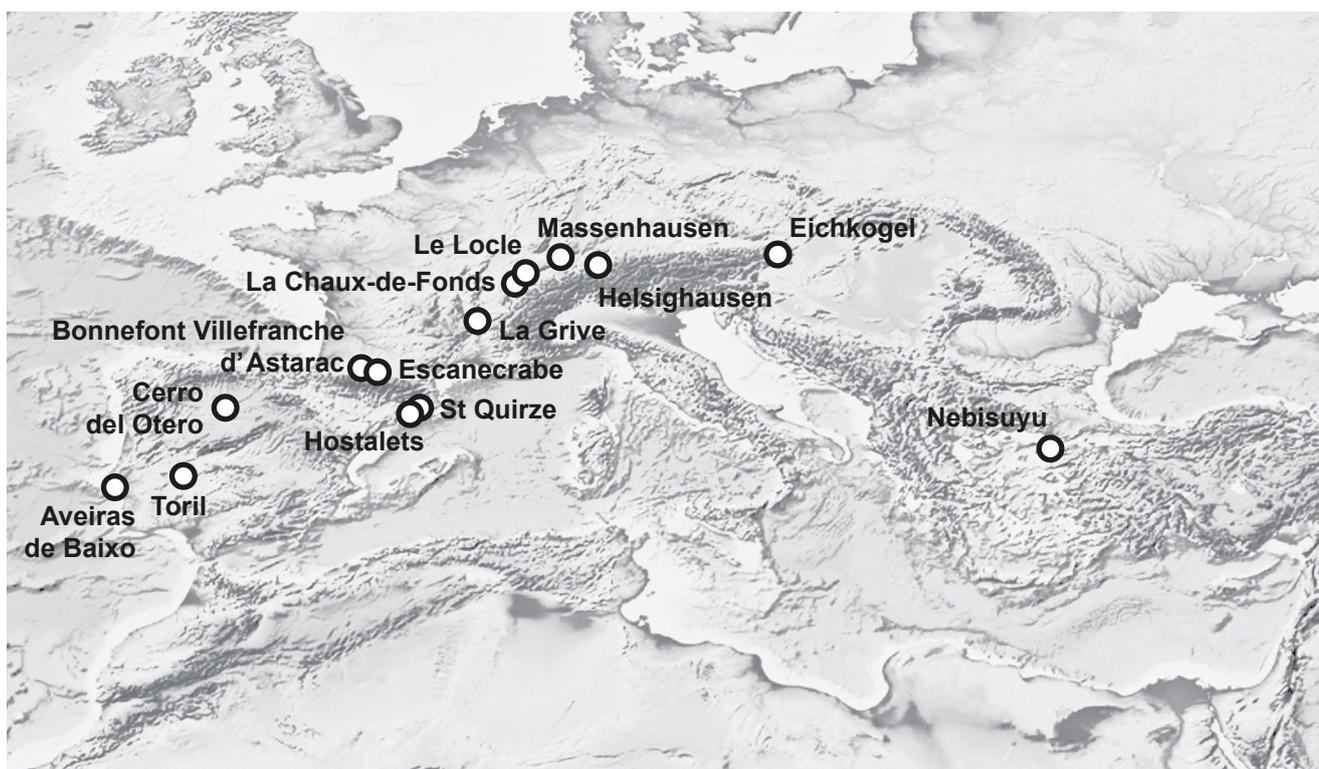
In *Kubanochoerus* GABUNIA, 1955, the base of the frontal horn is located well behind the anterior root of the zygomatic arch: in the Nebisuyu skull it is above the root of the zygomatic arch, and is thus in a forward position. In the Nebisuyu specimen, the vertical part of the frontal containing the supra-orbital grooves lies 92 mm antero-dorsally from the anterior edge of the orbit whereas, in *Kubanochoerus*, the corresponding part is close to the

orbit and almost directly above it. The posterior part of the ossicone base is positioned in front of the orbit in the Nebisuyu skull, but in *Kubanochoerus* the posterior margin of the base of the frontal protuberance is well behind the orbit. In the Nebisuyu individual the post-orbital process is thickened, antero-posteriorly enlarged, and possesses a rugose surface, whereas in *Kubanochoerus* it is gracile, smooth and descends only a short way as in suids in general.

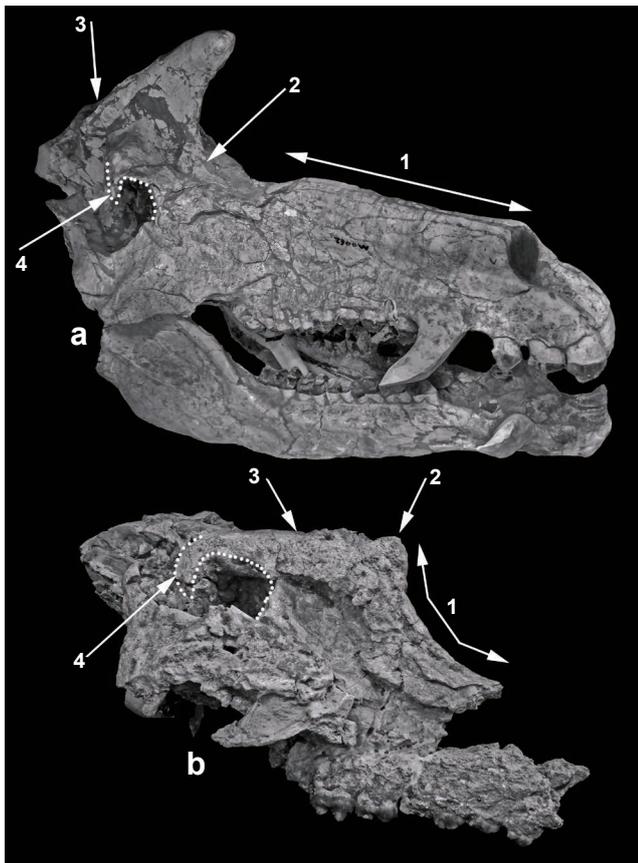
A further striking difference between the Nebisuyu skull and those of *Kubanochoerus* concerns the snout. In the Nebisuyu specimen the anterior part of the face is relatively short, the dorsal profile curving sharply upwards at the naso-frontal suture, whereas in *Kubanochoerus gigas*, the frontal bone anterior to the horn base does not rise significantly above the level of the nasals (Text-fig. 19). Thus in *Kubanochoerus* the snout appears distinctly elongated when compared to the foreshortened facial profile in the Nebisuyu individual (even taking into account the absence of the premaxilla in the Turkish skull). The Toril skull from Spain confirms this inference (Pickford and Morales 2003).

Ecological considerations

In animals in general, the presence of horns on the head has been the subject of much research, several scenarios having been proposed to explain the agencies of natural selection that resulted in their evolution. These fall broadly into two categories which can be called, for the sake of simplicity, exogenic and endogenic. Exogenic selective pressures arise from interactions between the species concerned and other elements in the biosphere and the environment, such as predator-prey interactions or climate parameters, vegetation categories etc. Endogenic selective pressures concern interactions between members of the same



Text-fig. 18. Distribution of large specimens of *Listriodon splendens* from MN 7, MN 8 and MN 8/9.



Text-fig. 19. Comparison between the skulls of (a) *Kubanochoerus gigas* from China (Hezheng Museum, M0062) and (b) *Listriodon splendens* (EUNHM PV 3075). 1 – profile of dorsal edge of nasals and frontal bones, 2 – anterior base of frontal protuberance, 3 – posterior base of frontal protuberance, 4 – post-orbital process. The superior and posterior margins of the orbits are outlined for ease of reference (not to scale).

species, such as male-to-male combat and male dominance over females and youngsters.

Large, easily visible canines occur in many lineages of suids, and it is likely that a major selective pressure was predator deterrence, but there could also have been an element of sexual selection involved, because a goodly sample of suid taxa is dimorphic in canine dimensions and morphology, males often possessing large, laterally flaring canines, while females may have small, more vertically inserted canines (Stehlin 1899, 1900). In some suids, such as the Wart Hog (*Phacochoerus*) both males and females possess large canines, probably as a result of exogenic selection involving predators.

The fact that most Neogene suids possessed large canines suggests that these sufficed for generally discouraging predator attention. If this is so, then one needs to search for an endogenic explanation of the presence of frontal protuberances in *Kubanochoerus* (and now *Listriodon*) because both these genera possessed relatively large laterally projecting canines.

Many suids (*Sus*, *Dasychoerus*, *Phacochoerus*, *Hylochoerus*) indulge in male-to-male combat during the rut season. Males engaging in such behaviour typically push their heads together and use brute force to vanquish an opponent (Ewer 1958) and often also use side swipes of

the head and canines. The presence of thickened skin and warts on the heads in some of these taxa has usually been explained in terms of male-to-male combat, with the warty pads protecting the individuals from serious injury.

Given the propensity for head-to-head contact during male-to-male combat in several extant suids, it is possible that *Listriodon* indulged in much the same form of combat, and this could account for the thickened frontal bone that aged individuals such as the Nebisuyu individual possessed. The female cranium from Toril, Spain, is also of an aged individual, perhaps even more dentally aged than the Nebisuyu specimen, but as would be expected for a female, it shows no signs of frontal bone thickening. If these two specimens belong to the same taxon, as is suggested by the overall similarities in their morphology and dental characteristics, then it is likely that thickening of the frontal bone in the Nebisuyu male specimen was related to sexual selection. The development of an ossicone atop the thickened frontal bone would then represent an endogenic feature related to male-on-male combat in the species.

A comparable set of circumstances could explain the presence of frontal protuberances in *Kubanochoerus*, but there is a significant difference from *Listriodon*, in that the frontal bone does not appear to be thickened in *kubanochoeres*, the horn atop the frontal being highly visible and impressive, but not well-supported on a solid bony foundation. The fragility of the frontal bone in *Kubanochoerus* suggests instead that the male-on-male interaction in this genus did not imply serious head-to-head contact, but was more along the lines of a highly visible combat deterrent. *Listriodon*, in contrast, appears to have indulged in serious head-banging between males, implicating not just the frontal zone, but also the post-orbital processes as well as the zygomatic arches, the lateral surfaces of which are thickened and rugose. The latter observations indicate an important element of head side-swiping in *Listriodon*.

Thickening of the frontal bone could increase during ontogeny, such that older males would possess thicker frontal bones than younger individuals. The Nebisuyu specimen, representing an aged (senile) member of the species, could have experienced many head-to-head encounters during its lifetime, with the concomitant result that its frontal and zygomatic bones became exceptionally thick. The presence of dermal bone fused to the frontal (the ossicone) indicates that the head-to-head contact in this genus was not a gentle affair.

The deeply concave nuchal area of the Nebisuyu skull and the thickened bony margins of the nuchal depression indicate that the nuchal musculature was strongly developed, much more so than would be required for activities related predominantly to acquisition of food, which suggests an alternative possibility: the role of forceful head-to-head contact and cranial side-swiping between individuals of this taxon during dominance encounters, likely during the rut season.

Acknowledgements

M. P. thanks the Muséum National d'Histoire Naturelle, Paris, for support and Ege University Natural History Museum for providing access to the fossils described

herein. Serdar Mayda and Tanju Kaya were funded by EGE University Research Grants TTM/2009/001, TTM/2013/001 and TTM/2015/001.

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