



Anatomy and phylogenetic value of the mandibular and coronoid canals and their associated foramina in proboscideans (Mammalia)

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Characters associated with the mandibular canal are differently distributed amongst proboscidean lineages and provide useful information on the systematics and relationships of proboscideans. The aim of this paper is to describe the pattern of the mandibular canal and its associated foramina in proboscideans in order to fully appreciate the extent of interspecific variation of these structures within the group and to discuss its systematic and phylogenetic value. Outgroup comparison indicates that the condition presented by the basal proboscidean *Phosphatherium* is morphotypic for proboscideans. Primitive proboscidean characters are: the low position of the mandibular foramen, and its crescent-shaped outline, the occurrence of a coronoid foramen (canal), the occurrence of two lateral mental foramina, the posterior one at the level of (or slightly behind) the posterior margin of the symphysis, the anterior one in a more distal position, the absence of a medial mental foramen (MMF), the mandibular canal set just below the tooth row. The occurrence of a single lateral mental foramen may represent a shared derived character of *Daouitherium*, *Numidotherium*, and *Barytherium*. A unique derived feature of the Elephantinae mandible is the occurrence of a medial mental foramen on the medial side of the incisive part of the mandible. MMFs have never been observed in other proboscideans excluding elephantines. The very high frequency of MMFs observed in *Mammuthus meridionalis*–*Mammuthus trogontherii*–*Mammuthus primigenius* (>93 per cent of the studied specimens) could be considered a synapomorphy of this group.

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INTRODUCTION

In mammals, the dentary is traversed by a bony canal (the mandibular canal) in the mesiodistal direction for the passage of the inferior alveolar nerve and artery (Fig. 1). The mandibular canal runs downward and forward in the ramus and then horizontally forward, near the ventral margin of the mandibular body. The caudal opening of the canal, the mandibular foramen, is located on the medial side of the

ascending ramus. Over their course, the alveolar artery and nerve give off a series of branches, which supply the pulp cavities of each tooth. Anteriorly, the canal leads to one or more mental foramina present on the lateral side of the mandibular body, from which exit the mental nerve and artery, supplying the lower lip and mental region (Mariappa, 1986; Williams *et al.*, 1989; Barone, 1996). In proboscideans and in some other mammalian groups, another smaller and shorter canal is present: the coronoid canal, running through the ramus just above the mandibular canal (Fig. 1B). The coronoid canal opens anteriorly in the

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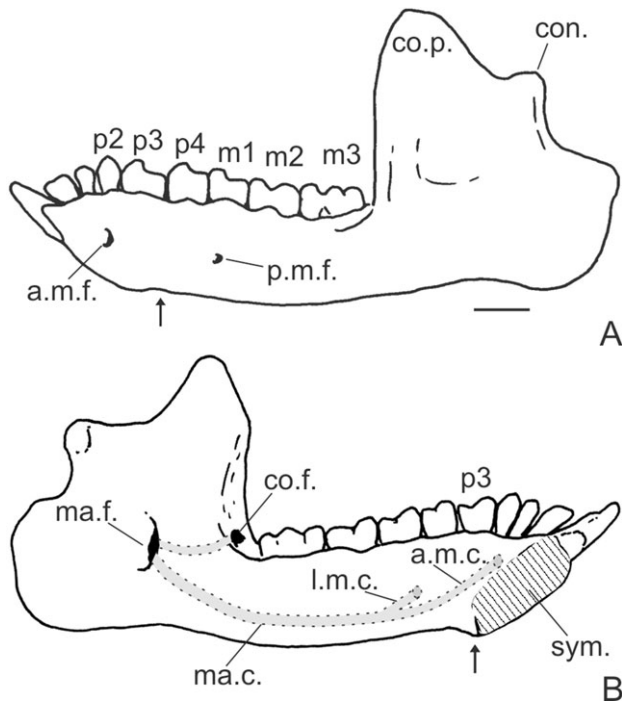


Figure 1. Schematic representation of the mandible of the basal proboscidean *Phosphatherium escuillei* depicting the principal anatomical characters of the coronoid and mandibular canals and their associated foramina in proboscideans (modified from Gheerbrant *et al.*, 2005b). A, labial view; B, lingual view. The courses of the mandibular and coronoid canals in *P. escuillei* are hypothetical and were reconstructed based on the position of the external foramina and by comparison with *Moeritherium*. Abbreviations: a.m.c., anterior mental canal; a.m.f., anterior mental foramen; con., condyle; co.f., coronoid foramen; co.p., coronoid process; l.m.c., lateral mental canal; ma.c., mandibular canal; ma.f., mandibular foramen; p.m.f., posterior mental foramen; sym., symphysis (section). Arrow indicates the position of the posterior border of the symphysis. Scale bar = 1 cm.

coronoid foramen, located medially at the base of the coronoid process, possibly representing the exit of a branch of the inferior alveolar nerve and artery (Laub, 1996).

Some characters associated with the mandibular and coronoid canals, such as the configuration of the mandibular foramen and the occurrence of a coronoid foramen, have been used in the analysis of the phylogeny of proboscideans (Tassy & Shoshani, 1988; Tassy, 1990; Shoshani, 1996). However, a number of other characters associated with these structures have received less attention, although differences amongst taxa have been observed between modern and extinct taxa (Ferretti, 1998; Debruyne, 2003). A unique feature of the elephant mandible is the occur-

rence of a medial mental foramen (MMF) on the medial side of the incisive part of the mandible (Adams, 1881; Van der Merwe, Bezuidenhout & Seegers, 1995; Ferretti, 1998; Maschenko, 2002; Debruyne, 2003). A preliminary analysis (Ferretti & Debruyne, 2005) showed that the MMF and other characters associated with the mandibular canal are differently distributed amongst certain proboscidean lineages and may thus provide useful information on the systematics and relationships of proboscideans.

The aim of this paper is to describe the pattern of the mandibular canal and its associated foramina in proboscideans in order to appreciate fully the extent of interspecific variation of these structures within the group and to discuss its systematic and phylogenetic value, with a special focus on the Elephantinae.

MATERIAL AND METHODS

To describe the anatomy and course of the two main bony canals present in the proboscidean mandible (mandibular and coronoid canals) and to determine the position, anatomy, and frequency of occurrence of the lateral and medial mental foramina amongst proboscideans, 42 taxa (Appendix 1), representing all major groups within the order, were investigated. Taxonomic sampling within Elephantinae is especially dense. Whenever possible, for each species, samples from different geographical areas and from individuals at different ontogenetic stages (from newborn to senile) were analysed. Data were primarily obtained from direct observation of fossil and Recent osteological samples (Appendix 1). We also relied on published sources (Appendix 1) to provide a more exhaustive survey of proboscidean taxa.

The course of the mandibular canal was reconstructed using both cut/broken mandibles, where the canal was exposed, and X-ray computed tomography (CT) images of a mandible of *Elephas maximus* available from www.digimorph.org (Balanoff, 2003). The position of the lateral mental foramina was characterized relative to (1) the cheek teeth and (2) the posterior border of the symphysis. It should be noted that the loss of permanent premolars and the mesial drift and continuous shedding of the mesialmost cheek teeth during life, hamper a direct comparison of the position of the lateral mental foramen relative to the tooth row between elephantoids and other more primitive proboscideans. The only exception is represented by the mandibles of calves, in which the alveolus for the mesialmost deciduous premolar (dp2) can be used as a consistent mandibular landmark in assessing the relative position of the mental foramen in elephantoid taxa (e.g. Gomphotheriidae, Elephantidae).

In order to evaluate the phylogenetic relevance of our observations on the mandibles, we defined ten characters (Appendix 2), scored in 16 representative taxa (Appendix 3), that we subsequently mapped onto a consensual cladistic analysis of the order Proboscidea (Tassy, 1996). All the original taxa not represented in our sample have been preserved but are shaded in Figure 10, allowing for the evaluation of our sample compared with the fossil diversity of the group. Nine characters are qualitative (morphological), one (character 9: frequency of occurrence of a medial mental foramen) is quantitative. Character 9, relative to the increasing frequency of presence of a MMF, is regarded as a quantitative character coded according to the gap weighting system of Thiele, 1993 (see also Schols *et al.*, 2004, and Shoshani *et al.*, 2007, for a discussion of the method). Polarity was defined by outgroup comparison using Perissodactyla, Hyracoidea, Embrithopoda, Sirenia, and Desmostylia.

Institutions housing proboscidean samples (both fossil and extant) studied in this work are numerous. The principal ones are listed in the Abbreviations section. Osteological collections at ACM, AMNH, MCZR, MNHN, and NHM were used to survey the pattern and variability of the mandibular canal and associated foramina amongst living mammalian orders.

ABBREVIATIONS

Anatomy

AMF, anterior mental foramen; dp, deciduous lower premolar; i, lower incisor; LPR, linguoid process of the mandibular foramen; m, lower molar; MMF, medial mental foramen (following the terminology of Van der Merwe *et al.*, 1995); p, lower premolar; PMF, posterior mental foramen.

Institutions

ACM, Museo di Anatomia Comparata, Bologna; AMNH, American Museum of Natural History, New York; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; CER, Cerpolex collection, frozen ice cave, Khatanga, Siberia; CET, ENEL Power plant, Pietrafitta, Perugia; EGM, Egyptian Geological Museum, Cairo; EMB, Museum of the Department of Geology, University of Bristol; GIN, Geological Institute of the Russian Academy of Science, Moscow; GM, Grant Museum of Zoology and Comparative Anatomy (UCL), London; IAM, Ice Age Museum, Moscow; IGF, Museo di Storia Naturale – Sezione di Geologia e Paleontologia, University of Firenze; IGT, Museo di Geologia e Paleontologia, University of Torino; IQW, Forschungstation für Quartärpaläontologie Senckenberg, Weimar; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MCB, Museo di Paleontologia G. Capellini, Bologna; MCZR,

Museo Civico di Zoologia, Roma; MECN, Museo Ecuatoriano de Ciencias Naturales, Quito; MLP, Museo de La Plata, La Plata; MNE, National Museum of Eritrea; MNHN, Museum National d'Histoire Naturelle, Paris; MPG, Museo di Paleontologia 'G. Gemmellaro', Palermo; MPR, Museo di Paleontologia, Roma; MSNC, Museo di Storia Naturale, Calci (Pisa); MUT, Museo Nacional Paleontologico-Arqueologico, Tarija; MZF, Museo di Storia Naturale – Sezione di Zoologia, University of Firenze; NHM, Natural History Museum, London; NHMB, Naturhistorisches Museum, Basel; NMENH, National Museum of Ethnography and Natural History, Kishinau; NMK, National Museums of Kenya, Nairobi; NNM, Nationaal Natuurhistorisch Museum (Naturalis), Leiden; PIN, Paleontological Museum of the Russian Academy of Science, Moscow; RBINS, Royal Belgian Institute of Natural Sciences, Brussels; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; SAM, South African Museum, Cape Town; SMNS, Staatliches Museum Naturkunde, Stuttgart; TMM, Texas Memorial Museum, Austin; ZIN, Zoological Institute of the Russian Academy of Science, S. Petersburg; ZMB, Museum für Naturkunde (Zoology) der Humboldt-Universität Berlin.

RESULTS

MANDIBULAR CANAL AND FORAMINA OF PROBOSCIDEANS

Position and course of the mandibular canal

For the purpose of the present description, the mandibular canal was divided into three portions (Fig. 1): (1) a posterior segment, from the mandibular foramen to the angulus mandibulae, (2) a middle segment, from the angulus to the level of the posterior mental foramen, and (3) an anterior segment, corresponding to the mental canal(s), leading to the mental foramina.

In elephants (Elephantinae), the posterior segment runs near the posteroventral margin of the ramus. In those specimens with developing teeth (Figs 2G, 3), the mandibular canal runs posterior and then ventral to the tooth chamber. The middle segment runs through the mandibular body and opens within a thick pars spongiosa (Figs 2G, 4, 5B). The high-crowned cheek teeth of elephants occupy most of the depth of the mandibular body, often causing the lateral displacement of the mandibular canal with respect to the tooth row. However, the position of the mandibular canal, relative to the teeth, is variable in elephant taxa: it can run either labially or lingually (Figs 5B, C, 6B) but almost never strictly ventrally to the tooth. In *Loxodonta*, *Elephas*, and *Palaeoloxodon*, the canal is more frequently found labially to the cheek teeth (Fig. 5C). A similar condition was also observed in *Mammot americanum* (Fig. 6A). In con-

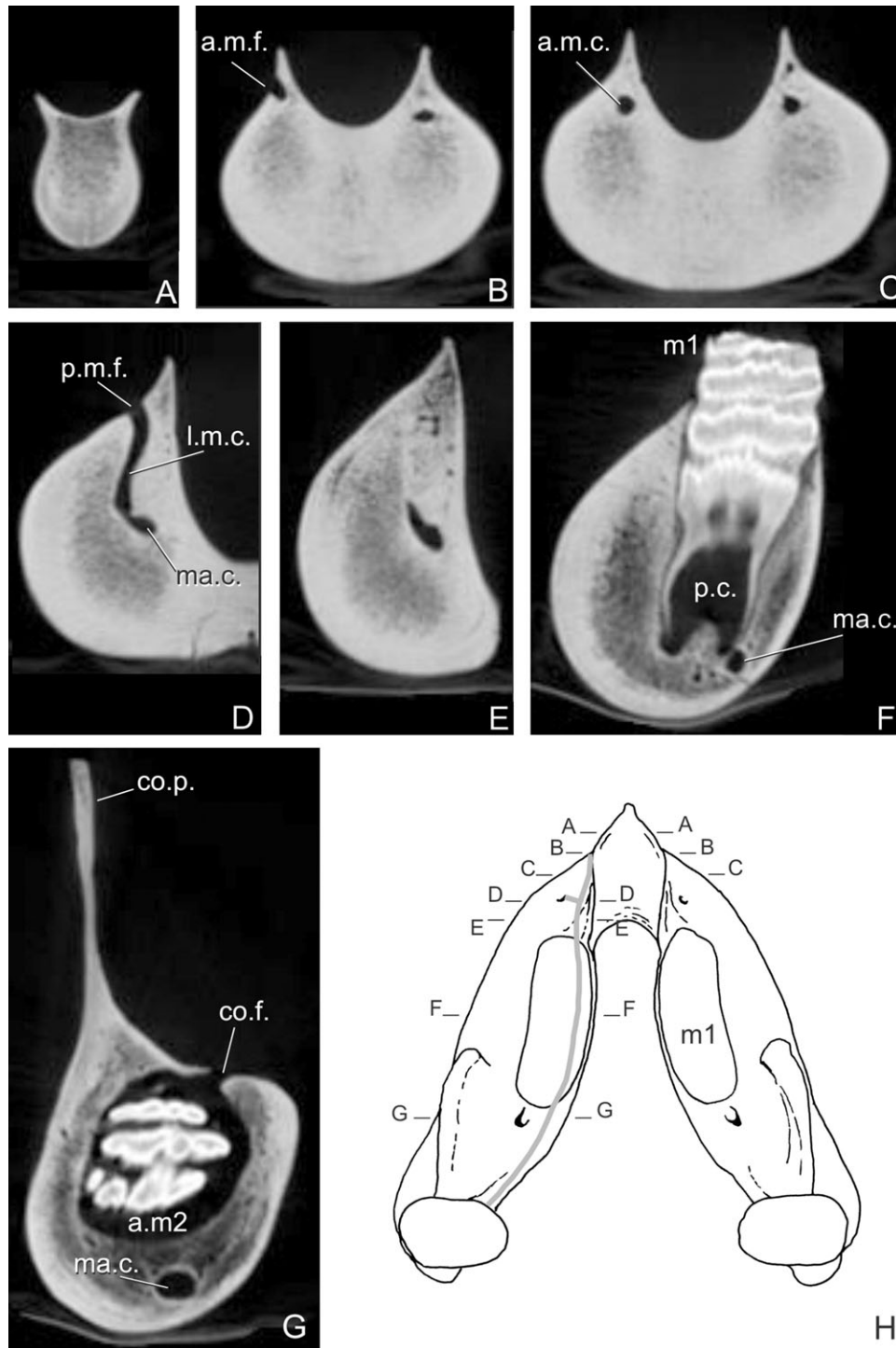


Figure 2. A–G, transversal (coronal) computed tomography (CT) slices of a mandible of *Elephas maximus* (TMM M-6445) showing the position and path of the mandibular canal and its associated foramina. H, diagrammatic representation of the mandible in occlusal view, illustrating the position of the CT slices depicted in A–G. Abbreviations: a.m2, second molar alveolus; a.m.c., anterior mental canal; a.m.f., anterior mental foramen; co.f., coronoid foramen; co.p., coronoid process; l.m.c., lateral mental canal; m1, first lower molar; ma.c., mandibular canal; p.c., pulpar chamber of m1; p.m.f., posterior mental foramen.

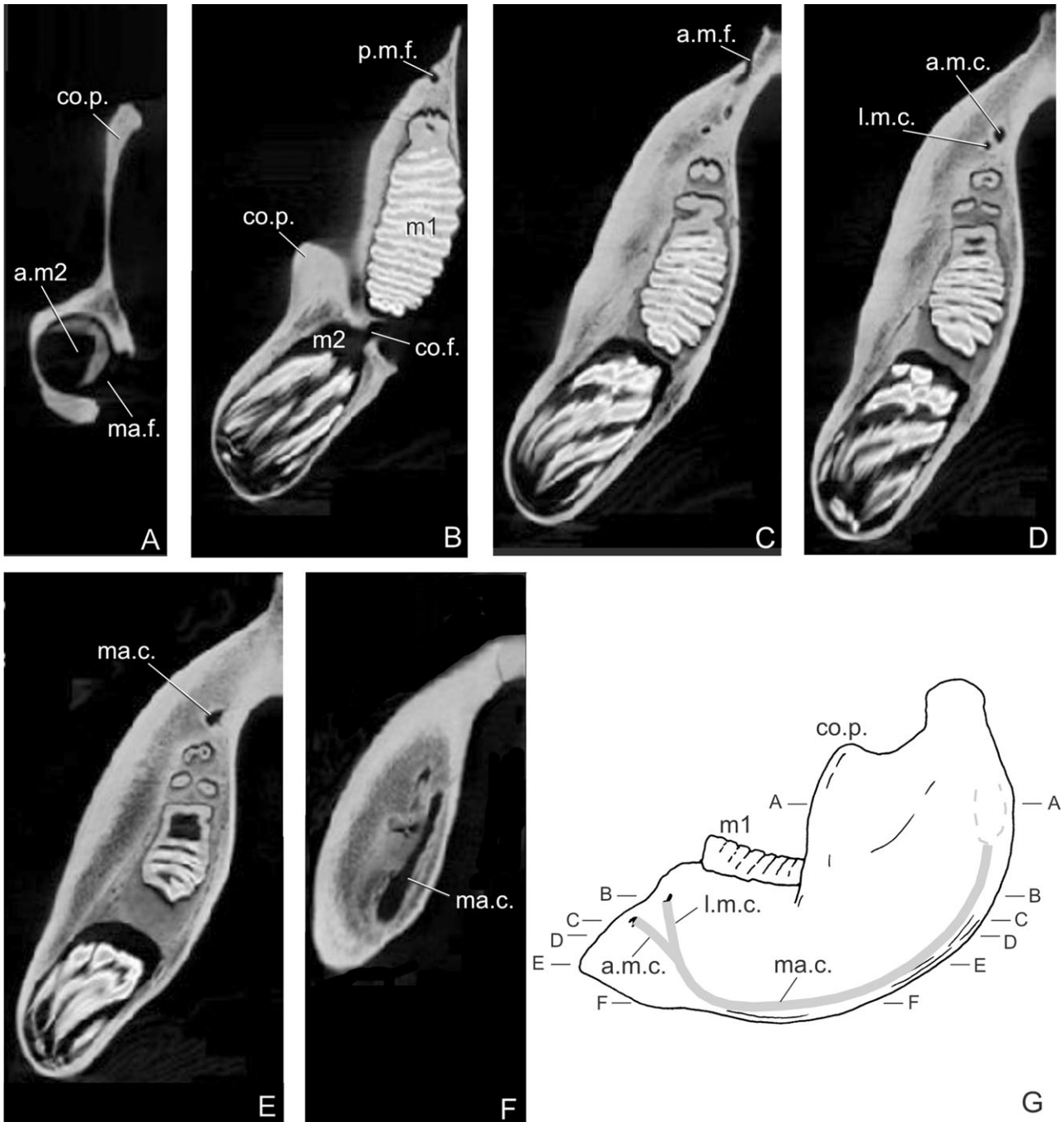


Figure 3. A–F, horizontal computed tomography (CT) slices of a mandible of *Elephas maximus* (TMM M-6445) showing the position and path of the mandibular canal and its associated foramina. G, diagrammatic representation of the mandible in left lateral view, illustrating the position of the CT slices depicted in A–F. The course of the mandibular canal is outlined. Abbreviations: a.m2, second molar alveolus; a.m.c., anterior mental canal; a.m.f., anterior mental foramen; co.f., coronoid foramen; co.p., coronoid process; l.m.c., lateral mental canal; m1, first lower molar; ma.c., mandibular canal; ma.f., mandibular foramen; p.m.f., posterior mental foramen.

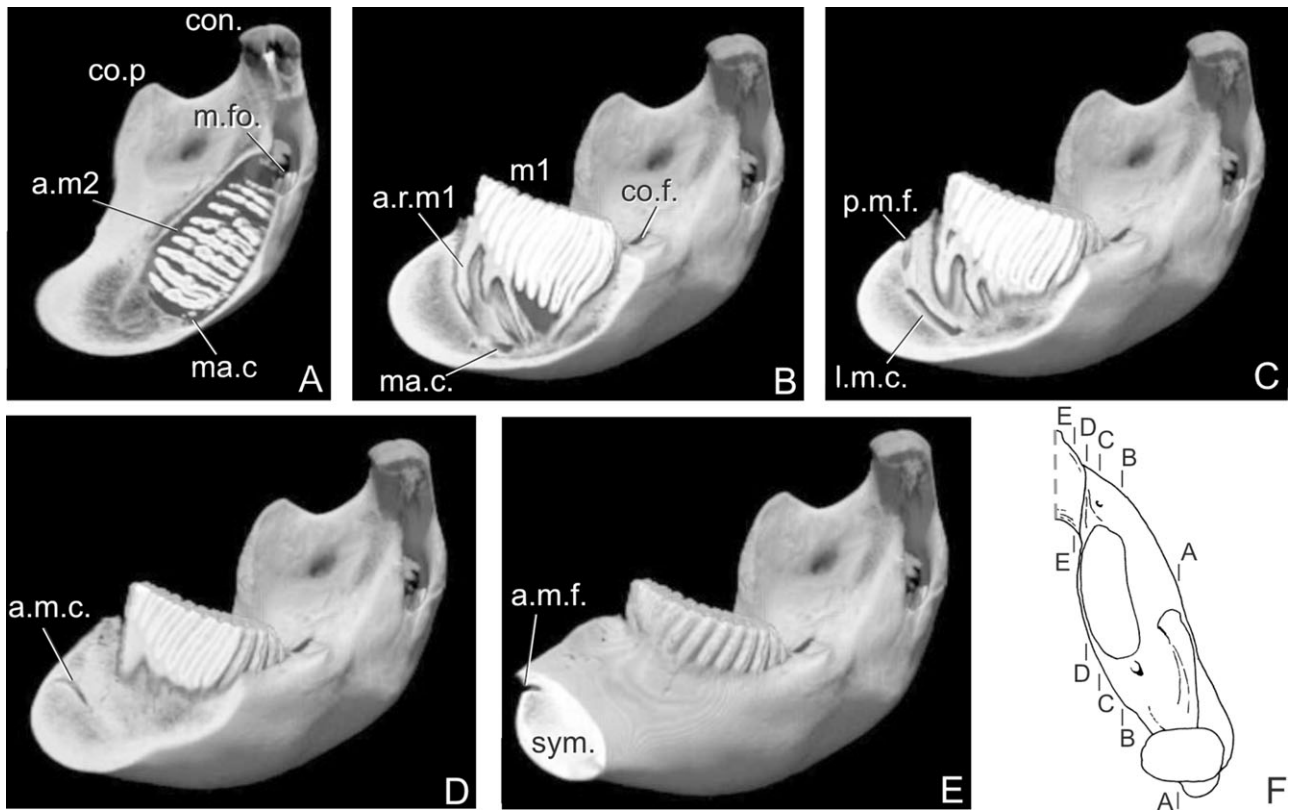


Figure 4. A–E, sagittal computed tomography (CT) slices of a mandible of *Elephas maximus* (TMM M-6445) illustrating the position and path of the mandibular canal and its associated foramina. F, diagrammatic representation of the right hemimandible in occlusal view, showing the position of the serial CT slices shown in A–E. Abbreviations: a.m2, second molar alveolus; a.m.c., anterior mental canal; a.m.f., anterior mental foramen; a.r.m1, anterior root of m1; co.f., coronoid foramen; con., condyle; co.p., coronoid process; l.m.c., lateral mental canal; ma.c., mandibular canal; m.fo., mandibular foramen; m1, first lower molar; p.m.f., posterior mental foramen; sym., symphysis.

trast, in *Mammuthus primigenius* the mandibular canal is always located medially to the teeth (Figs 5B, 6B).

In primitive brachydont proboscideans (e.g. *Moeritherium* and *Palaeomastodon*), the middle segment of the mandibular canal runs ventrally to the teeth (or their roots), near to the ventral border of the mandible. The diameter of the mandibular canal in these taxa is relatively larger than in elephants and the canal is surrounded by a poorly developed pars spongiosa (Fig. 5A). A similar condition was observed in *Mammot americanum* (NHM M17347).

In elephants, at the level of the anteriormost cheek teeth, or just in front of them, the mandibular canal splits into two branches: a lateral branch (lateral mental canal) leading to the posterior mental foramen and an anterior branch (anterior mental canal) leading to the anterior mental foramen (Figs 2–4). The same pattern was observed in *Palaeomastodon* (EMB 22300). In elephants, however, the posterior mental foramen is set in a more superior position

with respect to the level of the mandibular canal, so that the lateral mental canal is relatively long and anterosuperiorly directed (Fig. 4C). In contrast, in *Palaeomastodon*, *Phiomita*, and other primitive proboscideans (e.g. *Moeritherium*) characterized by a relatively shallow mandible, the posterior mental foramen opens at or slightly above the level of the mandibular canal so that the lateral mental canal is relatively short, nearly horizontal, and anteriorly directed. Although we do not have direct evidence concerning the pattern and course of the anterior segment of the mandibular canal in the basal proboscideans *Phosphatherium*, we argue for a condition similar to that of *Moeritherium*, based on the number and position of lateral mental foramina (see below).

Mandibular and coronoid foramina

In *Phosphatherium*, *Daouitherium*, *Moeritherium*, and *Phiomita*, the mandibular foramen is located at the level of the tooth row, almost at the same distance

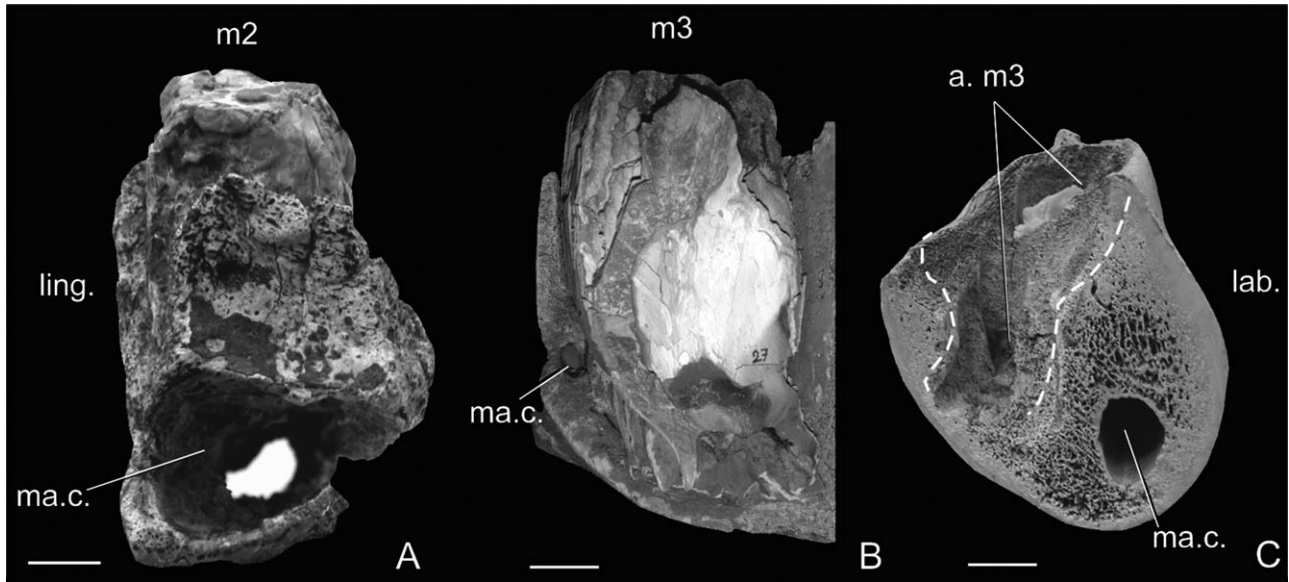


Figure 5. Cross-sections of the right mandibular body of three proboscideans, illustrating the size and location of the mandibular canal relative to the teeth. A, *Palaeomastodon* sp. (EMB 22300); B, *Mammuthus primigenius* (IAM 21); C, *Loxodonta africana cyclotis* (RBINS-1442). In elephants (B, C), the mandibular canal is relatively smaller and displaced laterally compared to the condition in primitive proboscideans (A). Abbreviations: a.m3, third molar, alveolus; lab., labial side; ling., lingual side; ma.c., mandibular canal; m2, second lower molar; m3, third lower molar.

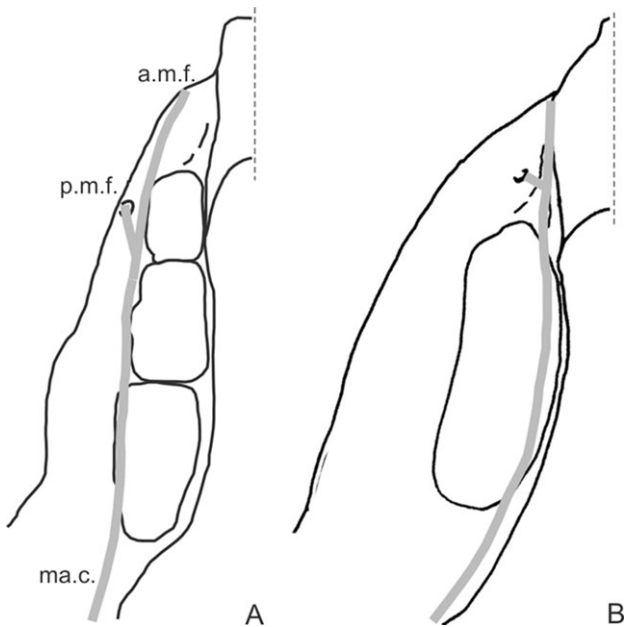


Figure 6. Outline of the path of the mandibular canal in A, *Mammuthus americanum* (Mammutidae) and B, *Mammuthus primigenius* (Elephantidae). The American mastodon exemplifies the primitive condition for elephantoids, with the mandibular canal running labially to the tooth row. In mammoths the mandibular canal is most frequently found lingual to the teeth. Abbreviations: a.m.f., anterior mental foramen; ma.c., mandibular canal; p.m.f., posterior mental canal.

from both the anterior and posterior borders of the mandibular ramus (Fig. 7B). The foramen is relatively small, has a crescentic outline, and opens in a posterosuperior direction. Deinotheres possess a similar configuration of the mandibular foramen, although the foramen is set at a higher position relative to the level of the occlusal plane (Fig. 7A). In elephantoids, the mandibular foramen is much higher than the level of the occlusal plane and closer to the posterior border of the mandibular ramus. It opens in a superior direction and has a V-shaped outline (Fig. 7C–G). In *Mammuthus*, *Gomphotherium*, South American gomphotheres (e.g. ‘*Stegomastodon*’ *platenensis*), and *Anancus*, the mandibular foramen is relatively small (Fig. 7C, D), whereas in elephants the foramen is very large and very close to the posterior border of the mandibular ramus (Fig. 7E–G). Elephantoids differ from more primitive proboscideans in the occurrence of a linguoid process (LPR) on the anterior border of the mandibular foramen (Fig. 7D, F–G). The LPR shows great variability in terms of size and shape both within and across species. The LPR is usually poorly developed amongst gomphotheres (e.g. *Gomphotherium*, *Cuvieronius*, *Anancus*; Fig. 7D), whereas in elephants the LPR frequently develops an extremely large and medially protruding spine (Fig. 7F, G). This latter feature has been observed in specimens of *Loxodonta africana*, *Elephas maximus*, and *Mammuthus primigenius*. Although the frequency of the occurrence of a LPR

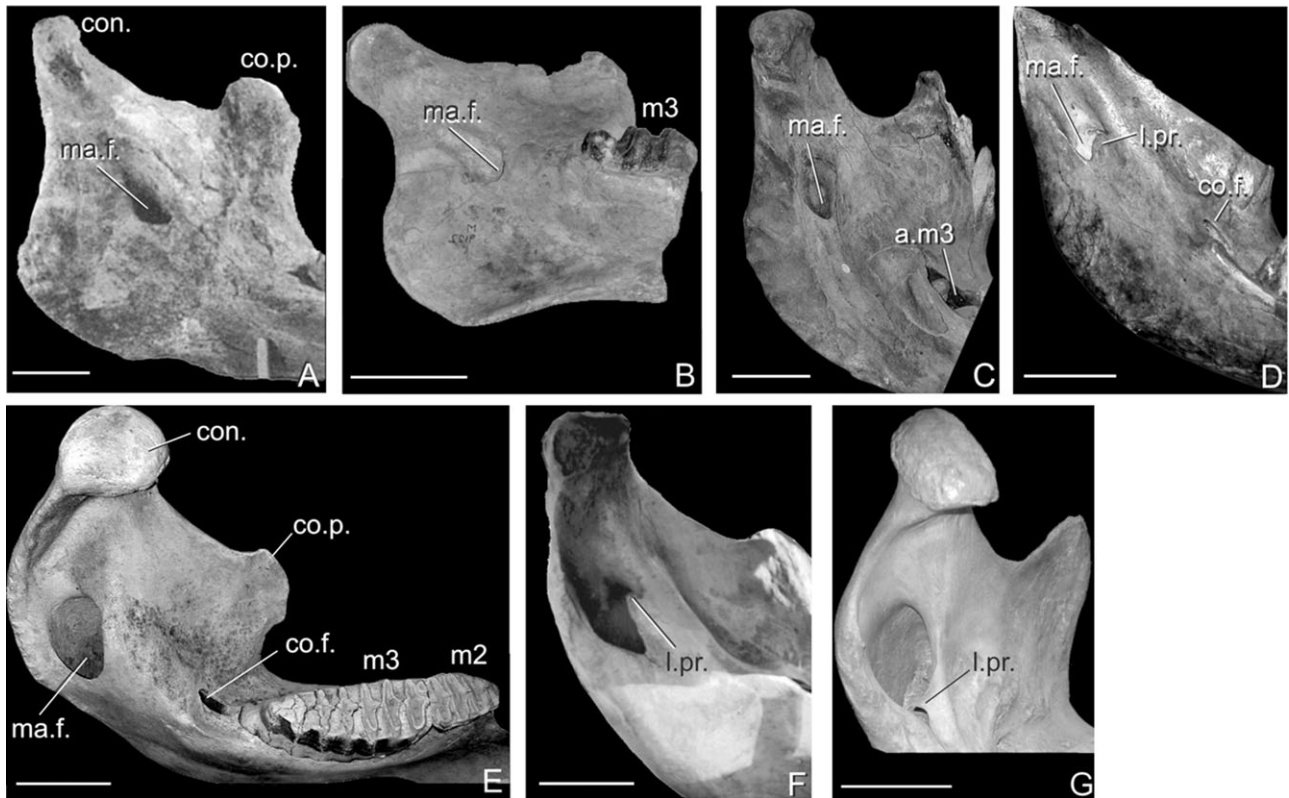


Figure 7. Mandibular rami in medial view illustrating the shape and position of the mandibular foramen amongst various proboscidean taxa. A, *Prodeinotherium bavaricum* (BSP 1977 I 229; from Huttunen & Göhlich, 2002); B, *Phiomyia serridens* (NHM M9122); C, *Mammuth americanum* (NHM M17187); D, '*Stegomastodon*' *platensis* (MNHN PAM187); E, *Loxodonta africana* (MZP); F, *Elephas maximus* (MZP 8065); G, *Mammuthus primigenius* (IAM 6). Abbreviations: a.m3, alveolus of m3; con., condyle; co.f., coronoid foramen; co.p., coronoid process; l.pr., linguoid process; ma.f., mandibular foramen; m2, second lower molar; m3, third lower molar.

forming a large and medially protruding spine appears to differ across elephantine taxa, the data at hand are not sufficient to draw any definite conclusions about the systematic value of this trait.

In all proboscideans considered, with the exception of *Moeritherium* (but including *Phosphatherium*, the oldest and most primitive taxon examined; Gheerbrant *et al.*, 2005b) the mandible shows a coronoid foramen, representing the anterior termination of the coronoid canal. The coronoid foramen is located on the medial side of the ramus, below the coronoid process, just behind the distal margin of the alveolus of the distal-most tooth in use (Figs 2G, 2E, 3B, 4B, 7F). In some specimens (especially amongst elephantines) the coronoid foramen is merged with the alveolus of the distal-most erupting molar. Amongst the elephants checked, the coronoid canal opens posteriorly within the mandibular foramen, where it is separated from the initial tract of the mandibular canal by a thin bony lamina that is probably not preserved in most fossil specimens.

Configuration, position, and variations of the lateral mental foramina

The number of lateral mental foramina shows a high degree of individual variability, even from side to side. Nevertheless, in proboscideans there are usually two principal lateral mental foramina: a posterior one, here called the posterior mental foramen (PMF), located either behind or just at the level of the posterior border of the symphysis, and an anterior mental foramen (AMF), anterior to the posterior border of the symphysis (Figs 1, 3, 8). Both the PMF and AMF may be split into two or more accessory foramina.

In *Phosphatherium*, the PMF is either below the distal root of p4 or the mesial root of m1, whereas the larger AMF is located below the canine (Gheerbrant *et al.*, 2005b; Fig. 1). In this taxon the posterior border of the symphysis reaches the level of the mesial root of p3.

In the type mandible of *Daouitherium*, a single lateral mental foramen occurs below the alveolus for

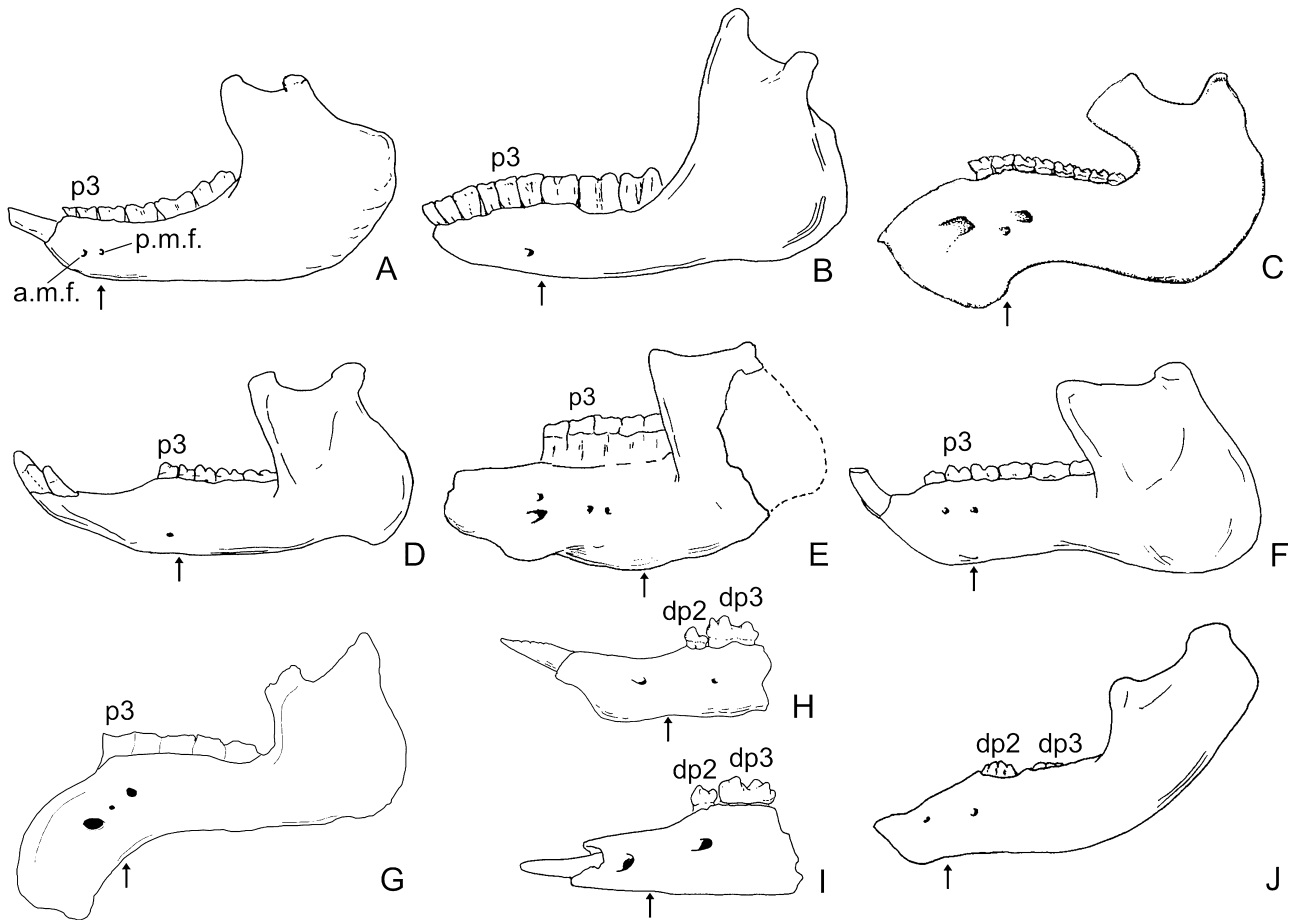


Figure 8. Outline drawings of the mandible of various extant and fossil proboscideans and some related taxa, showing the number and position of lateral mental foramina relative to the dentition (p3, dp2, and dp3 are used as reference) and the posterior border of the symphysis (arrow). All mandibles are depicted in left lateral view. Not to scale. A, *Procavia capensis* (Hyracoidea); B, *Arsinoitherium zitteli* (Embrithopoda; based on NHM M8463); C, *Trichechus manatus* (Sirenia; Proboscidea); D, *Numidotherium koholense* (DGO KAX-11; redrawn from Mahboubi *et al.*, 1986); E, *Barytherium grave* (EGM C10012; redrawn from Andrews, 1906); F, *Moeritherium trigodon* (AMNH 13436; redrawn from Osborn, 1936); G, *Prodeinotherium hobley* (EMB 6412; redrawn from Harris, 1973); H, *Phiomia serridens* (EGM C10007; redrawn from Andrews, 1906); I, *Gomphotherium* (BSM 2711; redrawn from Tassy, 1985); J, *Loxodonta africana* (NHMB). Abbreviations: a.m.f., anterior mental foramen; dp2, second deciduous lower premolar; dp3, third deciduous lower premolar; p3, third lower premolar; p.m.f., posterior mental foramen.

the tooth mesial to p2 (representing either p1 or c; Gheerbrant *et al.*, 2002). *Numidotherium koholense* possesses a single lateral mental foramen below either p3 or p4, located near the ventral border of the corpus (Mahboubi *et al.*, 1986; Fig. 8D). The posterior border of the symphysis in *N. koholense* extends backward to the level of p4.

In *Barytherium grave* there are two lateral mental foramina, one over the other, in front of the mesial root of p2 (Andrews, 1906; C. Delmer, 2008, pers. comm.; Fig. 8E). The symphysis extends back to the distal root of m1. In *Moeritherium* the PMF is located below p3, near the ventral border of the mandible (AMNH 13436; Fig. 8F). The AMF is lacking in some

specimens (e.g. EGM C1000). The posterior border of the symphysis reaches p2 in this taxon.

In deinotheres, the PMF is located mesially to the mesial root of p3 (Harris, 1973; M. P. Ferretti, unpubl. data, SMNS and NHM samples); the AMF is on the down-curved incisive portion, near the distal end of the alveolus of the lower tusk. In some specimens, one or two intermediate mental foramina are present (Fig. 8G).

In the type mandible of *Palaeomastodon beadnelli* (EGM C10014) only the PMF is preserved, set below the mesial root of p3 and well behind the posterior border of the symphysis (Andrews, 1906). In several adult mandibles of *Phiomia serridens* (NHM sample;

Andrews, 1906) there are two lateral mental foramina: the PMF is below the anterior premolars (p2–p3), at some distance behind the posterior border of the symphysis, whereas the AMF is on the incisive portion, opening at the level of the posterior end of the alveolus of the lower tusk. In a juvenile mandible of *P. serridens* (EGM C10007) with dp2 in place, the PMF is located between dp2 and dp3 (Fig. 8H). In *Eritreum melakeghebrekristosi* (Shoshani *et al.*, 2006) there is a large PMF positioned in front of the cheek teeth. The symphyseal portion is broken.

In elephantoids, the posterior border of the symphysis is always anterior to the cheek teeth. In non-elephantid elephantoids (mammutids, tri-, and tetralophodont gomphotheres) both the PMF and the AMF are usually well developed. In adults, the PMF, sometimes doubled, opens below the anterior premolars (or the mesialmost tooth in function). The AMF is significantly larger than the PMF in longirostrine forms (e.g. *Gomphotherium*) and is set slightly anterior to the posterior border of the symphysis (Tassy, 1985), near the posterior end of the tusk alveolus. In a juvenile mandible of *Gomphotherium* (BSM 2711) with dp2 in use, the PMF is positioned at the mesial root of dp2 (Fig. 8I). In those taxa with secondarily brevirostrine mandibles, the AMF is usually smaller than the posterior one. Notice that in choerolophodontines, which possess a mandible without a lower tusk, but with a relatively long symphyseal portion, the AMF is larger than the PMF as in *Gomphotherium*. In stegodontids and elephantids, the AMF is reduced or, less frequently, absent, but the PMF is always well developed. The PMF is sometimes split into several accessory foramina, with the posterior one generally located at the anterior edge of the mesial tooth in use. Amongst stegodontids, the number of lateral mental foramina has modal values between two and three. More variable is the condition amongst elephantids. The holotype of *Stegotetrabelodon orbus* possesses only a single PMF (Maglio & Ricca, 1978). In *Stegotetrabelodon syrticus* there are from two (PMF and AMF) to five mental foramina (Petrocchi, 1954; Ferretti, Rook & Torre 2003). In the type mandible of *Stegodibelodon schneideri* (MNHN), only the PMF is present. The holotype mandible of *Primelephas gomphotherioides* possesses two small lateral mental foramina (Maglio & Ricca, 1978). In primitive representatives of *Loxodonta* (*Loxodonta adaurora*) and *Elephas* (*Elephas nawa-taensis*) there are two lateral mental foramina, the posterior one at the rear end of the symphysis, the anterior one near the interalveolar crest (Maglio & Ricca, 1978; Tassy, 2003). In a mandible of *Mammuthus subplanifrons* from Langebaanweg (SAM PQ-L12723A) there are the two principal lateral mental foramina plus two accessory foramina in between. Owing to the medial path of the canal, the

PMF of *Mammuthus primigenius* is rarely split into several foramina. In foetal specimens of *Elephas maximus*, *Loxodonta africana*, and *Mammuthus primigenius* there are from one to three lateral mental foramina (Eales, 1928; Mariappa, 1986; Maschenko, 2002). In newborns of the same species the PMF opens below or slightly anterior to dp2 (Fig. 8J).

A comparison of the frequencies of the number of lateral mental foramina amongst *Mammuthus meridionalis*, *Mammuthus primigenius*, *Palaeoloxodon mnaidriensis*, *Loxodonta africana*, and *Elephas maximus* indicates a modal value of two to three, although some individuals show as many as seven mental foramina (Debruyne, 2003). The frequencies of occurrence of lateral mental foramina are presented in Table 1. *Mammuthus primigenius* shows a higher frequency of specimens with three mental foramina with respect to *Mammuthus meridionalis*, in which most of the specimens have two mental foramina (AMF and PMF). By separating the various *Mammuthus primigenius* samples by localities, it can be seen that there is a certain variability amongst samples (Table 1). In particular, the Siberian sample shows a lower frequency of mandibles with more than three lateral mental foramina than the north European one.

Anatomy and incidence of the MMF in the Elephantinae

A medial mental foramen (MMF) has been observed in proboscideans only amongst modern-type elephantines (i.e. *Loxodonta*, *Elephas*, *Palaeoloxodon*, and *Mammuthus*; Table 2). Next, the anatomy, variability, and incidence within each genus are described, focusing on *Mammuthus*.

The medial foramen is close to the interalveolar crest, more or less at the same level of the AMF (Fig. 9). The foramen can be either rather large (as large as the PMF; Fig. 9C) or extremely small, sometimes barely noticeable (Fig. 9G). In a sample of *M. primigenius* mandibles ($N = 25$) from various Eurasian localities, 17 mandibles (68 per cent) showed a single MMF, seven (28 per cent) possessed a double MMF (Fig. 9E), and one (4 per cent) a triple MMF. Asymmetry in size between left and right MMF is frequent. The MMF communicates with the mandibular canal and, when present, with the AMF (Fig. 9D). It is present both in newborn specimens (Fig. 9F) and in very old individuals.

Amongst *Mammuthus* species, it has been observed only in *Mammuthus meridionalis*, *Mammuthus trogontherii*, *Mammuthus primigenius*, and *Mammuthus columbi*, all Holarctic *Mammuthus* species. Amongst *Mammuthus meridionalis*, a MMF is present also in the Late Pliocene sample from Kaphry, considered by some authors to represent a distinct,

Table 1. Frequency of lateral mental foramina (LMF) in various elephant species

Number of LMF	<i>Loxodonta cyclotis</i>		<i>Loxodonta africana africana</i>		<i>Loxodonta adaurora</i>	<i>Mammuthus meridionalis</i>		<i>Mammuthus primigenius</i>		<i>Elephas maximus</i>		<i>Elephas rechi</i>		<i>Elephas ekorensis</i>		<i>Palaeoloxodon mnaidriensis</i>	
	N	%	N	%	N	N	%	N	%	N	%	N	%	N	%	N	%
1-2	59	(46.5%)	87	(55.5%)	4	19	(86.4%)	24	(44.4%)	10	(34.5%)	8	(75%)	3	(75%)	5	(45%)
3-4	61	(48%)	66	(42%)	-	3	(13.6%)	30	(55.6%)	19	(65.5%)	4	(25%)	1	(25%)	6	(55%)
> 4	7	(5.5%)	4	(2.5%)	-	-	-	-	-	-	-	-	-	-	-	-	-

more primitive taxon, *Mammuthus gromovi* (Alexeeva & Garutt, 1965; Azzaroli, 1977). Mandibles of the primitive species *Mammuthus subplanifrons* and *Mammuthus rumanus* are few, but the known material does not show a MMF (H. Saegusa, 2005, pers. comm. on *Mammuthus subplanifrons*; Lister & van Essen, 2003; Markov & Spassov, 2003; N. Spassov, 2005, pers. comm. on *Mammuthus rumanus* from Bossilkovtsi; M. P. Ferretti, unpubl. data on *Mammuthus rumanus* from Laiatico). The various species of the genus show a different incidence of the MMF (Table 2). The frequency increases from *Mammuthus meridionalis* (71 per cent) to Late Pleistocene *Mammuthus primigenius* (100 per cent). Note that the Ilford mammoth sample, dated to the late Middle Pleistocene (Schreve, 1997), shows an incidence of MMF similar to that of *M. meridionalis* and *M. trogontherii*, and significantly lower than that of typical woolly mammoths.

In *Elephas*, a consistent MMF has been observed only in the extant species *E. maximus*, with a morphology similar to that described in *Mammuthus* (Fig. 9B, C). The incidence in the *Elephas maximus* is however, significantly lower than in *Mammuthus*, being about 30 per cent.

In contrast, a MMF remains unknown in primitive species of *Elephas* (e.g. *Elephas ekorensis*, *Elephas nawataensis*, *Elephas planifrons*) (Table 2; Maglio & Ricca, 1978; Tassy, 2003; M. P. F. & R. D. pers. observ. 2005, NMK and NHM collections). None of the full-sized *Palaeoloxodon* species here considered possesses a MMF. In this genus a MMF has been observed, with different incidences, only in two small-sized insular species: *Palaeoloxodon mnaidriensis* from Sicily ($N = 38$; frequency of MMF = 5 per cent) and *Palaeoloxodon cyprites* from Cyprus ($N = 9$; frequency of MMF = 56 per cent).

In *Loxodonta* a MMF occurs only in 1 per cent of the examined mandibles ($N = 260$). When present, the foramen is very small and oval in shape (Fig. 9G). A MMF is apparently absent also in fossil *Loxodonta* species, such as *Loxodonta adaurora* and *Loxodonta atlantica*. Note that Van der Merwe *et al.* (1995) indicated that a MMF is present in the *Loxodonta africana* sample from South Africa that they studied. Van der Merwe *et al.* (1995) provided neither a picture of the original specimen nor a description of the morphology of the MMF in the text, but it is schematically depicted in their figure 6 as a relatively large, rounded foramen.

MENTAL AND LINGUAL FORAMINA IN OTHER MAMMALIAN GROUPS

The number and position of lateral mental foramina in members of a number of mammalian orders con-

Table 2. Frequency of occurrence of medial mental foramina (MMF) in Elephantidae and other selected proboscideans

Taxon/sample	Sample	Mandibles	Frequency	Source
	size	with MMF	(%)	
<i>Phosphatherium escuilliei</i>	4	0	0	E. Gheerbrant, pers. comm.
<i>Palaeomastodon/Phiomia</i>	6	0	0	This study
<i>Gomphotherium angustidens</i>	10	0	0	This study
<i>Cuvieronius hyodon</i>	34	0	0	This study
<i>Stegomastodon platensis</i>	15	0	0	This study
<i>Haplomastodon chimborazi</i>	9	0	0	This study
<i>Anancus arvernensis</i>	28	0	0	This study
<i>Stegodon bombifrons</i>	3	0	0	This study
<i>Stegodon insignis</i>	8	0	0	This study
<i>Stegotetrabelodon syrticus</i>	1	0	0	H. Saegusa, pers. comm.
<i>Stegotetrabelodon orbus</i>	1	0	0	This study
<i>Stegodibelodon schneidieri</i>	1	0	0	This study
<i>Mammuthus subplanifrons</i>	1	0	0	H. Saegusa, pers. comm.
<i>Mammuthus rumanus</i>	2	0	0	This study; N. Spassov, pers. comm.
<i>Mammuthus meridionalis</i> (Khapry)	3	2	67	This study
<i>Mammuthus meridionalis</i> (Upper Valdarno)	24	17	71	This study
<i>Mammuthus meridionalis</i> (Pietrafitta)	3	3	100	This study
<i>Mammuthus trogontherii</i>	6	4	67	This study
<i>Mammuthus primigenius</i> (Siberia)	10	10	100	This study
<i>Mammuthus primigenius</i> (Alaska)	45	45	100	This study
<i>Mammuthus primigenius</i> (Taimyr)	32	32	100	This study
<i>Mammuthus primigenius</i> (Netherlands)	86	86	100	This study
<i>Mammuthus primigenius</i> (Ilford)	12	7–10?	70	This study
<i>Mammuthus columbi</i>	5	5	100	This study
<i>Elephas nawataensis</i>	1	0	0	This study
<i>Elephas recki</i> ssp.	32	0	0	This study
<i>Elephas ekorensis</i>	6	0	0	This study
<i>Palaeoloxodon namadicus</i>	4	0	0	This study
<i>Palaeoloxodon antiquus</i>	19	0	0	This study
<i>Palaeoloxodon</i> cf. <i>creutzburgi</i>	1	0	0	This study
<i>Palaeoloxodon</i> cf. <i>cypristes</i>	9	5	56	This study
<i>Palaeoloxodon falconeri</i>	4	0	0	This study
<i>Palaeoloxodon mnaidriensis</i>	38	2	5	This study
<i>Elephas</i> cf. <i>planifrons</i>	1	0	0	This study
<i>Elephas planifrons</i>	5	0	0	This study
' <i>Elephas</i> ' <i>celebensis</i>	2	0	0	This study
<i>Elephas hysudricus</i>	2	0	0	This study
<i>Elephas hysudrindicus</i>	1	0	0	This study
<i>Elephas maximus</i>	36	10	28	This study
<i>Loxodonta adaurora</i>	4	0	0	This study
<i>Loxodonta africana</i>	260	3	1	This study

sidered related to proboscideans (see Gheerbrant, Domning & Tassy, 2005a) are here reported. In perisodactyls there is a large lateral mental foramen behind/below the root of the canine, opening near the posterior border of the symphysis. In hyracoids there are usually two lateral mental foramina (Fig. 8A). The posterior one is below the interdental margin p3/p4 that is at the posterior border of the symphysis.

The anterior lateral mental foramen is below p2/p3, behind the incisor.

Arsinoitherium zitteli (Embrithopoda) possesses a single lateral mental foramen, set below p3 (Fig. 8C), whereas the posterior border of the symphysis extends backward as far as p4 (Andrews, 1906).

Sirenians (Sirenia) typically have a large lateral mental foramen in the incisive portion of the man-

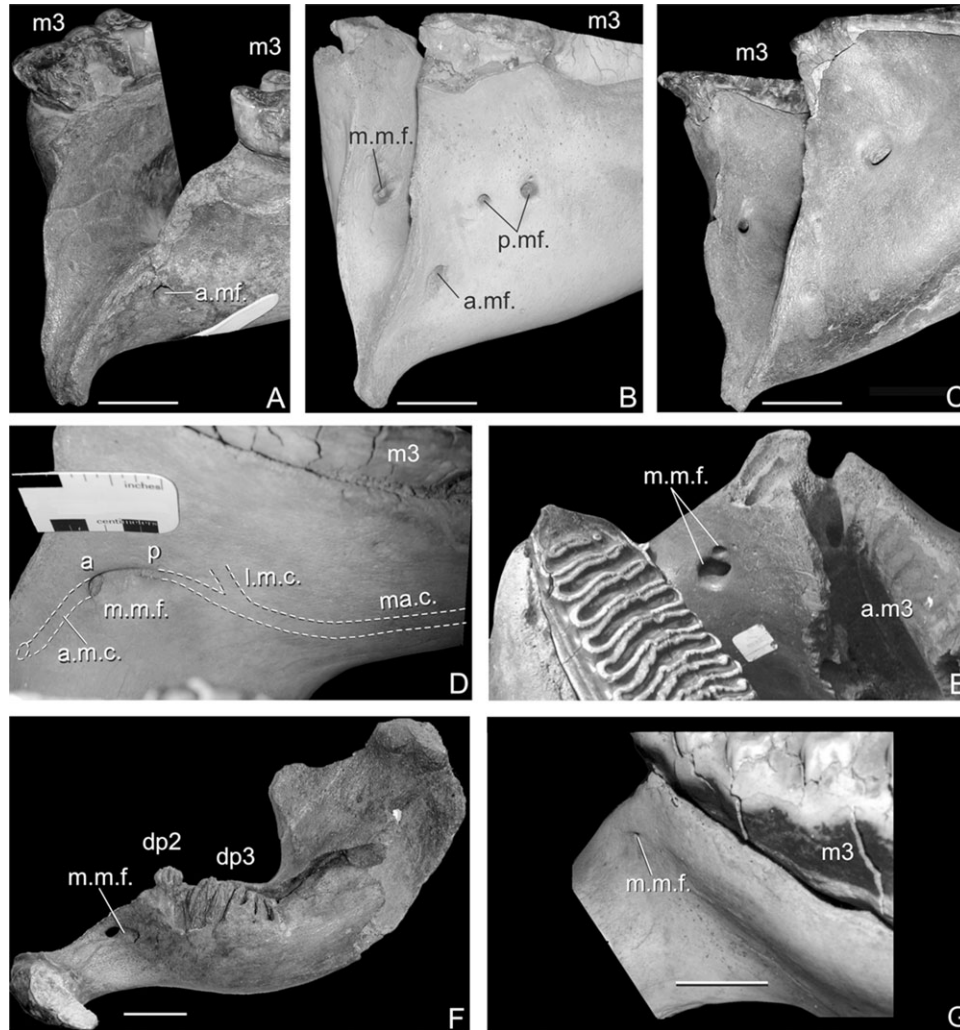


Figure 9. Mandibles of selected proboscidean taxa illustrating the principal anatomical features of the mental and symphyseal regions related to the mandibular canal. A, *Anancus arvernensis* (IGF 1070). Non-elephantine proboscideans never show a medial mental foramen (MMF); B, *Elephas maximus* (MZF 8065). In elephantids, a MMF may occur on the lingual side of the mental region. C, *Mammuthus primigenius* (NNM); D, *M. primigenius* (IAM 20). The path of the mandibular canal, illustrating the connection to the MMF, is outlined. The mandibular canal opens into the MMF through a posterior rounded foramen (p). An anterior opening (a) leads to the anterior mental canal. E, *M. primigenius* (NNM 445377). Specimen with a double MMF. F, *M. primigenius* (PIN 4353-2615). The mandible of this newborn individual shows a well-developed MMF. G, *Loxodonta africana* (NHM). Individual possessing a very small MMF. Abbreviations: a.m3, alveolus of m3; a.m.c., anterior mental canal; a.m.f., anterior mental foramen; dp2, second deciduous lower premolar; dp3, third deciduous lower premolar; l.m.c., lateral mental canal; m3, third lower molar; ma.c., mandibular canal; m.m.f., medial mental foramen; p.m.f., posterior mental foramen.

dible, anterior to the posterior margin of the symphysis. In protosirenids (e.g. *Protosiren*), early dugongids (e.g. *Halitherium*), and extant trichaechids, there are also one or more smaller foramina posterior to the larger anterior one (D. Domning, 2008 pers. comm.). In manatees (e.g. *Trichaechus manatus*) the most posterior foramen is set below the anterior cheek teeth (usually the second or third anteriormost tooth), well behind the posterior margin of the symphysis

(Fig. 8C). In the modern dugong (*Dugong dugong*) there is a single large lateral mental foramen that opens anterior to the cheek teeth in the downward-pointing incisive portion.

In primitive Desmostylia (e.g. *Behemotops proteus*, *Cornwallius sookensis*) there are several small lateral mental foramina in juveniles and a single larger one in adults (Domning, Ray & Mckenna, 1986). The posteriormost lateral mental foramen is below either

p2 or p3, laterally to the alveolus of the large canine. In an adult of *Paleoparadoxia repenningi* there are two lateral mental foramina (Domning, Ray & McKenna, 1986). In all these taxa, the lateral mental foramina are anterior to the posterior margin of the symphysis (D. Domning, 2008 pers. comm.). A young specimen of the derived desmostyloid *Desmostylus hesperus* from Japan (Uno & Kimura, 2004) reportedly has two foramina, one anterior and the other posterior to the rear end of the symphysis.

In our survey of mammalian mandibles (including representatives of all extant orders) we observed paired foramina on the lingual side of the incisive and symphyseal portion of the dentary only in tayassuids and suids (Suoidea), excluding elephants. In suoids, however, the foramina are located just lateral to the symphysis, close to the ventral margin of the symphysis (Barone, 1996; M. P. Ferretti & J. Van Der Made, unpubl. data).

A sagittal lingual foramen is described in primates (mandibular lingual foramen). Two distinct foramina occur at the midline lingual portion of the human mandible: a suprascapular foramen for the lingual nerve and artery, and a subscapular foramen for the sublingual and/or submental artery and a branch of the mylohyoid nerve (Jacobs *et al.*, 2007; Liang *et al.*, 2007). In some individuals, double or triple mandibular lingual foramina have been observed (Liang *et al.*, 2007).

CHARACTER MAPPING

In order to evaluate the phylogenetic relevance of our observations on the mandibles, we defined ten characters that we subsequently mapped onto a consensual cladistic analysis of the order Proboscidea (Tassy, 1996). All the original taxa not represented in our sample have been preserved but are shaded in Figure 10, allowing for the evaluation of our sample compared with the fossil diversity of the group. The tree onto which we mapped our mandibular characters differs slightly from the original tree by Tassy (1996). (1) In order to accommodate our taxonomic sampling, the clade Elephantinae was divided into the two tribes Loxodontini and Elephantini, with the latter being subdivided into three genera: *Palaeoloxodon*, *Elephas*, and *Mammuthus* (the two latter being represented by two species in our analysis), as acknowledged by Shoshani & Tassy (2005) in a recent update on the taxonomy of the family Elephantidae. At the other extremity of the tree (2), the phylogenetic status of *Moeritherium* within early proboscidean taxa remains enigmatic (Shoshani & Tassy, 2005) and although Tassy (1996) could place it at the base of the Proboscidea, the recent advances in the palaeontology of the Palaeocene/Eocene and the phylogenetic analy-

ses of the group (Gheerbrant, 2009, Delmer, 2009) instead support that *Moeritherium* might be the sister taxon to the clade formed by Elephantiformes and Deinotheriidae. Therefore, in our tree *Moeritherium* is placed at a multifurcation with Barytherioid taxa and Deinotheriidae + Elephantiformes.

Based on the mapping analysis with this topology, our ten new characters require 17 evolutionary steps when their complete parsimonious treatment would have involved only 16 steps. In detail, eight of the nine parsimony informative characters are optimized parsimoniously, the tenth character being autapomorphic in *Moeritherium*: loss of the coronoid canal (character 10-1). The only homoplastic character in this optimization is character 2: position of the mandibular foramen relative to the occlusal plane, either convergent in deinotheres and elephantoids, or reversed to the primitive stage in *Phiomia* (we present only the ACCTRAN optimization of the character changes in Figure 10, although both explanations might be as likely). Character 7(1) (i.e. posterior mental foramen between p2 and p3) supports the concept of Elephantiformes with *Phiomia* grouped with elephantoids. One should notice that an alternative grouping of Elephantoida with *Prodeinotherium* would be as parsimonious for the mandibular characters: character 2(1) would be a synapomorphy of this node whereas character 7(1) would become homoplastic between *Phiomia* and the Elephantoida.

Character 6(1) (loss of the PMF) is a putative new synapomorphy of the barytherioid taxa (i.e. a situation where *Numidotherium* and *Barytherium* are sister taxa). However, if *Numidotherium* and *Barytherium* are not sister groups, as suggested by Tassy (1996) and retrieved more recently by Delmer (2009), then character 6 would become a homoplastic feature of these genera, forcing a less parsimonious explanation of our mandibular characters (two steps instead of one in our analysis). Conversely, no character associated to the mandibular canal suggests a closer affinity of *Moeritherium* to either primitive or derived proboscidean lineages.

A majority of the character changes is clustered at two nodes: the clade Elephantoida (four or five changes, relative to the optimization applied), which groups mammutids with elephantid and gomphotheriid taxa, and the clade Elephantinae (four changes), both characterized by drastic changes in the morphology of the mandible. Four changes are non-ambiguous at the node Elephantoida: 1(1) (lateral course of the mandibular canal); 3(1) (posterior position of the mandibular foramen); 4(1) (large, V-shaped mandibular foramen); and 5(1) (occurrence of a linguoid process). The interrelationships of elephantoids are poorly resolved. All four synapomorphies supporting the Elephantinae clade are non-ambiguous:

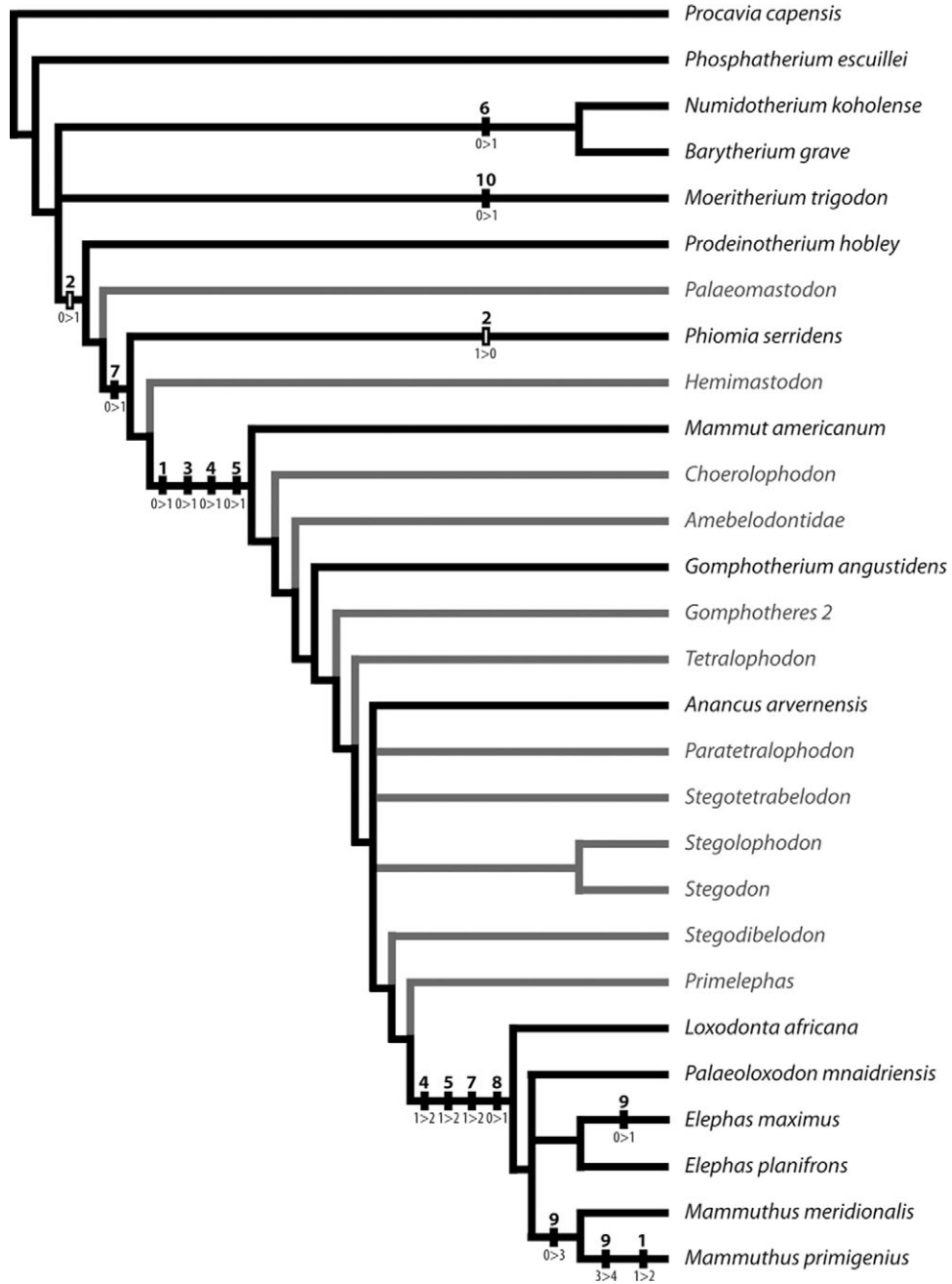


Figure 10. Character mapping analysis of ten mandibular characters on a cladogram of main proboscidean taxa. The original tree by Tassy (1996) was modified (see text for details). Taxa absent from our analysis are shaded. Character changes are displayed by bar with character number over the bar, and evolutionary change below. The changes of the homoplastic character (character 2) are displayed by unfilled bars.

characters 4(2), 5(2), 7(2), and 8(1) (occurrence of a medial mental foramen).

Finally, character 9 underlines the parallelism between the mandibular changes in *Elephas* and *Mammuthus*, with the latter being the only elephantine taxa represented by a high frequency of the MMF, although the strict absence/presence of a MMF

in a single sample is not diagnostic within Elephantinae.

DISCUSSION

MANDIBULAR CANAL

In primitive proboscideans (e.g. *Phosphatherium*, *Moeritherium*), characterized by a shallow and

narrow mandibular body, the mandibular canal is relatively large and positioned just below the tooth alveoli. In contrast, in those species possessing a deep mandibular corpus, the mandibular canal is often pushed laterally to the large tooth roots. In elephants, the mandibular canal is frequently found labially to the tooth roots. However, in *Mammuthus primigenius* the mandibular canal was always found lingually, a derived condition. In its anterior tract, the mandibular canal usually splits into two mental canals, leading to the PMF and AMF. In longirostrine elephantoids (e.g. *Gomphotherium*) the AMF opens at the level of the posterior border of the alveolus for the lower tusk. In the longirostrine proboscidean sample that we studied, there are no specimens with an AMF set near the anterior border of the tusk alveolus as in the *Stegotrabelodon* mandible depicted by Maglio (1973: fig. 10). Furthermore, Maglio (1973) interpreted the large canal present between the PMF and the AMF in the type mandible of *Loxodonta adaurora* as a vestigial incisive canal. Based on our study, however, the canal described by Maglio (1973) should actually correspond to the anterior mental canal. In modern-type elephantines lacking mandibular tusks there are no traces of any vestigial incisive canal, although this was probably present in more primitive species with functional incisors.

MANDIBULAR FORAMEN

Primitively, as seen in basal proboscideans such as *Phosphatherium*, the mandibular foramen is a small, crescent-shaped opening set at the level of the occlusal plane, halfway between the anterior and posterior margins of the ascending ramus. In elephantoids the mandibular foramen lies well above the level of the occlusal plane and closer to the posterior border of the ramus (below the condyle). The relatively high position of the mandibular foramen in deinotheres is a probable convergence with elephantoids, considering that *Phiomia*, the sister taxon of Elephantoida, presents the plesiomorphic condition. The occurrence of a bony lamina and/or protuberance on the anterior margin of the mandibular foramen has been used to distinguish *Elephas* and *Mammuthus* versus more primitive proboscideans (Shoshani, 1996; Tassy, 1996). A well-developed linguoid process appears to be more frequent in the former two genera than in other taxa (J. Shoshani, 2007, pers. comm.). However, Laub (1996) describes a lingula in *Mammuth americanum* and we observed a large linguoid process in a number of *Loxodonta africana* mandibles. Amongst South American *Cuvieronius hyodon*, a short-jawed gomphothere, the linguoid process is variously developed, from a small, barely notable prominence, to a well-individualized spine. By

contrast, basal elephantiforms possess no such structure, and the mandibular foramen has a crescentic shape, in contrast to the V-shaped outline of elephantoids. This would suggest that a linguoid process is a synapomorphy of elephantoids, even though the development of a strong tuberculum is a more derived character present with high frequency in elephantines and possibly in *Elephas* and *Mammuthus* in particular.

In humans, the lingula (linguoid process) gives attachment to the sphenomandibular ligament, connecting the mandibular ramus to the skull base (Williams *et al.*, 1989). A similar function was suggested by Laub (1996) for the linguoid process of the proboscidean mandible.

LATERAL MENTAL FORAMINA

In proboscideans, two main lateral mental foramina can be recognized based on their position relative to the distal border of the symphysis: a PMF located at the posterior border of the symphysis or further back, and an AMF located in front of the posterior border of the symphysis. In *Phosphatherium* the AMF is sensibly larger than the PMF, whereas in *Moeritherium* the two foramina are of subequal size. In longirostrine elephantiforms (e.g. *Phiomia*, *Gomphotherium*) the AMF becomes markedly larger than the PMF. In contrast, in taxa with secondarily brevirostrine mandibles (e.g. stegodonts and elephants), the AMF becomes smaller and is sometimes absent.

The occurrence and frequency of accessory lateral mental foramina vary amongst samples and taxa. This has also been observed in *Homo*, where a correlation with sex has been suggested (Sawyer, Kiely & Pyle, 1998; Agthong *et al.*, 2005). We have no definitive evidence that the number of accessory lateral mental foramina tends to increase from prenatal to neonatal times, although Maschenko (2002) indicated that this occurs in *Mammuthus primigenius*.

In the character mapping analysis, a double lateral mental foramen (PMF and AMF) appears as a primitive condition for proboscideans: it is known in *Phosphatherium*, *Moeritherium* and, amongst the outgroups, in hyracoids. A double lateral mental foramen pattern is also known amongst sirenians (e.g. *T. manatus*) and desmostylians (e.g. *D. hesperus*). We cannot rule out, however, the possibility that these represent convergences. Primitive sirenians and desmostylians (not included in our character mapping analysis) in fact possess several small lateral mental foramina, all set anterior to the rear end of the symphysis. Further investigation is needed to solve this issue.

Differently from all other proboscideans, in *Daouitherium*, *Numidotherium koholense*, and

Barytherium there seems to be a single lateral mental foramen, positioned in front of the posterior border of the symphysis (the position of the lateral mental foramen relative to the symphysis in *Daouitherium* is actually unknown), thus corresponding to the AMF of other proboscideans. This might represent a shared derived character of this group of lophodont proboscideans, as suggested by the results of the character mapping analysis. Deinotheres, however, present the typical proboscidean pattern with two main lateral mental foramina.

The position of the PMF relative to the tooth row, although variable within taxa, appears to be of systematic and phylogenetic value. In all proboscideans examined, the lateral mental foramina are always anterior to m1. In those taxa possessing a double lateral mental foramen, the PMF is anterior to p4 (Fig. 8). In *Phosphatherium* and *Moeritherium*, the PMF is set either below p4, p3, or between the two teeth (Figs 1A, 9F). Amongst the outgroups, a similar position of the PMF is seen in hyracoids, suggesting that this is the primitive condition for proboscideans. In basal elephantiforms (e.g. *Phiomia*), the PMF is positioned below or in front of (dp3)–p3. The PMF is set relatively more anteriorly in elephantoids, opening below dp2–(p2). The most forward position of the PMF relative to the tooth row is observed in elephants, in which the PMF opens below the mesial root of dp2 or anterior to that tooth (Fig. 9J). The character mapping analysis here presented suggests that the more anterior position of the PMF (below or anterior to dp2 in newborns) is a synapomorphy of the Elephantoidae.

The position of the PMF was formerly used in the relative dental age scale of the African elephant by Sikes (1966). According to Sikes, absorption of the mesial root begins at the level of the PMF.

Matsumoto (1924) used the position of the lateral mental foramen as one of the characters distinguishing *Palaeomastodon* from *Phiomia*: according to that author, in the former genus the larger foramen is behind the symphysis, whereas in the latter it is anterior to it. However, Matsumoto evidently did not distinguish between the anterior and posterior lateral mental foramen. Observation of specimens of the two taxa stored at the NHM and AMNH, and the figures provided by Andrews (1906), clearly indicate a similar pattern in the two taxa.

MEDIAL MENTAL FORAMEN

A MMF has never been observed in proboscideans other than elephantines. Indeed, the occurrence of a MMF is one of the four synapomorphies that defined the elephantine clade in our character mapping analysis.

No other mammalian group, except suoids and primates (where the morphology and location of the medial foramina indicate nonhomology with proboscideans), shows this feature. In *Homo*, the lingual mandibular foramen appears not to be linked to the mandibular canal. Furthermore, the foramen is entered by a vascular complex (Jacobs *et al.*, 2007), whereas the MMF of proboscideans probably represents the exit of a branch of the mental nerve and artery. At present, we can not specify which structure is supplied by the nerve and vessel leaving the MMF, pending a dissection of a mandible of an extant elephant presenting a medial foramen (which is outside the scope of the present paper). It is possible, however, that the MMF distributes nerves and vessels to the chin and lower lip, similar to the lateral mental foramen.

MMF have been observed in all derived elephantine genera (*Loxodonta*, *Elephas*, *Palaeoloxodon*, and *Mammuthus*), even though they occur in the various species of each genus with different frequency and configuration. Within each taxon, occurrence of MMF is not dependent on individual age, as MMF have been observed in newborn, young adult and senile individuals. MMF are usually present on both the right and left dentaries. However, specimens with asymmetrically developed MMF, or even with just one MMF, have been observed.

The distribution of this character within the Proboscidea in general suggests that a MMF is a derived character, and that its frequency increased with time in certain lineages (e.g. Asian elephant, mammoths). The very high frequency of MMF observed in *M. meridionalis*–*M. trogontherii*–*M. primigenius* (from about 70–100 per cent) could be considered to be a synapomorphy of this group, with the exclusion of the older and more primitive species *M. subplanifrons* and *M. rumanus*. Within *Mammuthus*, the presence of a MMF in virtually all individuals of Late Pleistocene *M. primigenius* is suggested as an autapomorphy of this taxon. The mammoth sample from Ilford, dated to Marine Isotope Stage, MIS 7 (late Middle Pleistocene; c. 200 thousand years ago), shows a slightly lower frequency of MMF, suggesting a more primitive condition than 'typical' late Pleistocene woolly mammoth populations. The observed frequency of MMF in the Ilford sample would be consistent with an attribution to a derived form of *M. trogontherii* rather than to *M. primigenius*, as suggested by Lister & Sher (2001), based on dental characters.

By contrast, the occurrence of a MMF in roughly 30 per cent of the individuals of *E. maximus*, in light of its virtual absence in primitive species of the *Elephas* clade (*E. nawataensis*, *E. planifrons*, *E. hysudricus*), seems to represent an autapomorphy of

this species, excluding a special relationship with *Mammuthus*. The alternative hypothesis is that *E. maximus* is more closely related to *Mammuthus* than to the other species currently included within *Elephas*, such as *E. hysudricus* and *E. planifrons*. As for *Loxodonta*, a well-rounded MMF, comparable with that of *Mammuthus*, has not been seen in any of the 260 mandibles checked of both *africana* and *cyclotis* forms.

Our results suggest that there is a link between the occurrence of MMF (i.e. of an accessory mental foramen that opens on the lingual side), and the path (lingual to the teeth) of the mandibular canal in *Mammuthus*.

CORONOID FORAMEN

A coronoid foramen is present in all proboscideans checked, excluding *Moeritherium*. *Phosphatherium*, the oldest and most primitive bona fide proboscidean, possesses a coronoid foramen. The occurrence of a coronoid foramen was considered by Gheerbrant *et al.* (2005a, b) to be a shared primitive proboscidean character, implying a reversal in *Moeritherium*. Amongst tethytheres, a coronoid foramen occurs in sirenians and desmostylians. According to Tassy & Shoshani (1988), the occurrence of a coronoid foramen in hyracoids indicates that this is a paenungulate synapomorphy (absent in basal eutherians and perisodactyls).

CONCLUSIONS

Outgroup comparison and the results of the character mapping analysis indicate that the condition presented by the basal proboscidean *Phosphatherium* is morphotypic for proboscideans. Primitive proboscidean mandibular characters are: the low position of the mandibular foramen, and its crescent-shaped outline; the occurrence of a coronoid foramen (canal); the occurrence of two lateral mental foramina, the posterior one at the level of (or slightly behind) the posterior margin of the symphysis, the anterior one in a more anterior position; the absence of a MMF; and the mandibular canal set just below the tooth-row. Most of these characters are primitive eutherian features (e.g. the low mandibular foramen), whereas others are possible tethythere or even paenungulate synapomorphies (e.g. the occurrence of a coronoid canal). The mandibular canal ancestral morphotype of proboscideans lacks any distinctive proboscidean character.

The coronoid canal is lost in *Moeritherium* (reversal to the primitive eutherian condition). The genera *Daouitherium*, *Numidotherium*, and *Barytherium* are

characterized by a single (anterior) lateral mental foramen, although the homology of the foramen in *Barytherium* is uncertain. Further investigation and more specimens are needed to ascertain whether this actually represents a synapomorphy of this group of lophodont proboscideans. The anterior lateral mental foramen is primitively larger than the posterior one. It became even larger in longirostrine proboscideans (e.g. *Gomphotherium*). In contrast, in those taxa with secondarily shortened symphyses (brevirostrine), lacking all anterior teeth, the AMF is smaller or sometimes absent. A linguoid process of the mandibular foramen has been observed only amongst elephantoids, and may represent an elephantoid synapomorphy. The linguoid tuberculum is poorly developed in basal elephantoids whereas it is very prominent amongst elephantines, particularly in *M. primigenius* and *E. maximus*. In the character mapping analysis, a medial mental foramen appears as a synapomorphy of the clade including all modern-type elephantines (*Loxodonta*, *Elephas*, *Palaeoloxodon*, *Mammuthus*), to the exclusion of *Stegodibelodon* and *Primelephas*. The grouping of the Holarctic mammoth species *M. meridionalis*, *M. trogontherii*, *M. columbi*, and *M. primigenius* is supported by the sharing of a very high incidence of MMF. The slightly lower frequency of MMF in late Middle Pleistocene mammoth samples from Ilford (UK), with respect to late Pleistocene woolly mammoth populations, supports the hypothesis, based on dental characters, that the Ilford mammoth represents a more primitive taxon than typical *M. primigenius*.

Mammuthus primigenius and *Elephas maximus* are characterized by a higher frequency of MMF compared to that observed in *Loxodonta africana*. This might indeed be a derived character shared by the woolly mammoth and the extant Asian elephant, which would further support their closer affinity as indicated by molecular data (Yang, Golenberg & Shoshani, 1996; Krause *et al.*, 2006; Rogaev *et al.*, 2006; Rohland *et al.*, 2007). However, the very low incidence of MMF in primitive species of both lineages (e.g. *M. rumanus* and *E. planifrons*), suggests that the high MMF frequency in *M. primigenius* and *E. maximus* is more likely a convergence.

The results of this study thus highlight the phylogenetic and systematic value of the characters associated with the mandibular canal and foramina in proboscideans. Our findings are generally consistent with previous phylogenetic hypotheses based on other dental-skeletal characters (e.g. Tassy, 1990, 1996; Shoshani, 1996; Gheerbrant *et al.*, 2005b; Shoshani *et al.*, 2007) and also provide new character support to clarify the relationships amongst barytherioids and within elephantids.

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APPENDIX 1

SUMMARY LIST OF STUDIED TAXA

Taxon	Locality	Age	Collection/Source
Phosphateriidae			
<i>Phosphatherium escuillei</i>	Ouled Abdoun Basin, Morocco	Early Eocene	Gheerbrant <i>et al.</i> , 2005b
Incertae sedis			
<i>Daouitherium rebouli</i>	Ouled Abdoun Basin, Morocco	Early Eocene	Gheerbrant <i>et al.</i> , 2002
Numidotheriidae			
<i>Numidotherium koholense</i>	El Kohol, Algeria	Middle Eocene	Mahboubi <i>et al.</i> , 1986
Barytheriidae			
<i>Barytherium grave</i>	El Fayum, Egypt		Andrews, 1906
Moeritheridae			
<i>Moeritherium lyonsi</i>	El Fayum, Egypt	Eo-Oligocene	Andrews, 1906
<i>Moeritherium trigodon</i>	El Fayum, Egypt	Eo-Oligocene	NHM, AMNH
<i>Moeritherium</i> sp.	Dor El Talha, Lybia	Eo-Oligocene	EMB
Deinotheriidae			
<i>Prodeinotherium hobleyi</i>	Jabal Zaltan, Lybia	Early Miocene	Harris, 1973
<i>Prodeinotherium bavaricum</i>	Unterzolling, Germany	Early Miocene	Huttunen & Göhlich, 2002
<i>Prodeinotherium</i> cf. <i>bavaricum</i>	Langenau, Germany	Early Miocene	SMNS
<i>Deinotherium giganteum</i>	Eppelsheim, Germany	Late Miocene	NHM
<i>Deinotherium gigantissimus</i>	Pripiceni, Moldova	Early Pliocene	NMNH
Palaemastodontidae			
<i>Palaemastodon beadnelli</i>	El Fayum, Egypt	Eo-Oligocene	NHM, AMNH; Andrews, 1906
Phiomidae			
<i>Phiomia serridens</i>	El Fayum, Egypt	Eo-Oligocene	NHM; Andrews, 1906
Mammutidae			
<i>Mammot americanum</i>	North America (various sites)	Late Pleistocene	NHM, AMNH
Gomphotheriidae			
<i>Choerolophodon penteleci</i>	Turkey (various sites)	Late Miocene	Tassy, 1985; MNHN
<i>Gomphotherium angustidens</i>	France (various sites)	Middle-Late Miocene	MNHN
<i>Gomphotherium productum</i>	Clarendon, Texas, USA	Late Miocene	AMNH
<i>Gomphotherium</i> aff. <i>steinheimensis</i>	Gweng, Muhldorf, Germany	Late Miocene	NHMB (cast); Göhlich, 1998
<i>Cuvieronius hyodon</i>	Tarija, Bolivia	Late Pleistocene	MUT
<i>Stegomastodon platensis</i>	Buenos Aires, Argentina	Late Pleistocene	MLP; MACN
<i>Haplomastodon chimborazi</i>	Bolivar, Ecuador	Late Pleistocene	MECN
<i>Archaeobelodon filholi</i>	Sansan, France	Early Miocene	MNHN
'Tetralophodont gomphotheres'			
<i>Anancus arvernensis</i>	Italy (various sites)	Pliocene	IGT, IGF, MCB
<i>Anancus sivalensis</i>	Siwaliks, India	Late Miocene–Pliocene	NHM
Stegodontidae			
<i>Stegodon bombifrons</i>	Upper Siwaliks, India	Pliocene	NHM
<i>Stegodon insignis</i>	Upper Siwaliks, India	Plio-Pleistocene	NHM
<i>Stegodon ganesa</i>	Upper Siwaliks, India	Plio-Pleistocene	NHM

APPENDIX 1 *Continued*

Taxon	Locality	Age	Collection/Source
Elephantidae			
<i>Stegotrabelodon syrticus</i>	As Sahabi, Lybia	Late Miocene	Petrocchi, 1954
<i>Stegotrabelodon orbus</i>	Kanam East, Kenya	Late Miocene	NMK
<i>Stegodibelodon schneidieri</i>	Menalla, Tchad	Early Pliocene	MNHN
<i>Elephas nawataensis</i>	Lothagam	Late Miocene	NMK
<i>Elephas ekorensis</i>	Kanapoi	Early Pliocene	NMK
<i>Elephas cf. planifrons</i>	Bethlehem, Israel	Early Pliocene	NHM
<i>Elephas planifrons</i>	Upper Siwaliks, India	Early to Middle Pliocene	NHM
<i>Elephas celebensis</i>	Tjeleko, Sulawesi	Pleistocene	NNM
<i>Elephas hysudricus</i>	Upper Siwaliks, India	Plio-Pleistocene	NHM
<i>Elephas hysudrindicus</i>	Kedong, Java	Middle Pleistocene	NNM
<i>Elephas maximus</i>	Various localities	Recent	ACM, GM, MCZR, MNHN, MZF, NHM, NHMB, ZIN, ZMB
<i>Palaeoloxodon recki</i> ssp.	East Africa (various sites)	Plio-Pleistocene	MNE, MNHN, NHM, NMK
<i>Palaeoloxodon antiquus</i>	Italy and UK (various sites)	Middle to Late Pleistocene	MPR, NHM
<i>Palaeoloxodon namadicus</i>	Narbada Valley, India	Middle to Late Pleistocene	NHM
<i>Palaeoloxodon cf. creutzburgi</i>	Crete	Pleistocene	NHM
<i>Palaeoloxodon cf. cipriotes</i>	Kerynia Hills, Cyprus	Pleistocene	NHM
<i>Palaeoloxodon falconeri</i>	Spinagallo, Sicily, Italy	Middle Pleistocene	Ambrosetti, 1968
<i>Palaeoloxodon mnaidriensis</i>	Sicily (various sites), Italy	Late Pleistocene	MPG; Ferretti, 2008
<i>Mammuthus subplanifrons</i>	Kanam East, Kenya	Early Pliocene	SAM; H. Saegusa, pers. comm.
<i>Mammuthus rumanus</i>	Laiatico, Italy	Middle Pliocene	MSNC
<i>Mammuthus rumanus</i>	Bossilkovtsi, Bulgaria	Middle Pliocene	Markov & Spassov, 2003
<i>Mammuthus meridionalis</i>	Upper Valdarno, Italy	Plio-Pleistocene	IGF, NHMB
<i>Mammuthus meridionalis</i>	Pietrafitta, Italy	late Early Pleistocene	CET
<i>Mammuthus columbi</i>	USA and Mexico	Middle to Late Pleistocene	AMNH
<i>Mammuthus trogontherii</i>	Süssenborn, Germany	early Middle Pleistocene	IQW
<i>Mammuthus trogontherii</i>	Mosbach, Germany	early Middle Pleistocene	NHMB
<i>Mammuthus trogontherii</i>	Tiraspol, Georgia	Middle Pleistocene	Dubrovo, 1975
<i>Mammuthus cf. trogontherii</i>	Ilford, UK	late Middle Pleistocene	NHM
<i>Mammuthus primigenius</i>	Siberia (various sites), Russia	Late Pleistocene	IAM, IGF, MNHN, NHM, PIN, ZIN
<i>Mammuthus primigenius</i>	Taimyr Peninsula, Russia	Late Pleistocene	CER
<i>Mammuthus primigenius</i>	Fairbanks, Alaska, USA	Late Pleistocene	AMNH
<i>Mammuthus primigenius</i>	Benelux (various sites)	Late Pleistocene	NNM, RBINS
<i>Loxodonta adaurora</i>	Kanapoi, Kenya	Early Pliocene	NMK
<i>Loxodonta africana africana</i>	Africa (various sites)	Recent	MZF, GM, MCZR, MNHN, NHM, NHMB, RMCA, ZMB
<i>Loxodonta africana cyclotis</i>	Africa (various sites)	Recent	GM, MZF, RMCA, RBINS, ZMB

ACM, Museo di Anatomia Comparata, Bologna; AMNH, American Museum of Natural History, New York; CER, Cerpolex collection, frozen ice cave, Khatanga, Siberia; CET, ENEL Power plant, Pietrafitta, Perugia; EMB, Museum of the Department of Geology, University of Bristol; GM, Grant Museum of Zoology and Comparative Anatomy (UCL), London; IAM, Ice Age Museum, Moscow; IGF, Museo di Storia Naturale – Sezione di Geologia e Paleontologia, University of Firenze; IGT, Museo di Geologia e Paleontologia, University of Torino; IQW, Forschungstation für Quartärpalaeontologie Senckenberg, Weimar; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MCB, Museo di Paleontologia G. Capellini, Bologna; MCZR, Museo Civico di Zoologia, Roma; MECN, Museo Ecuatoriano de Ciencias Naturales, Quito; MLP, Museo de La Plata, La Plata; MNE, National Museum of Eritrea; MNHN, Museum National d'Histoire Naturelle, Paris; MPG, Museo di Paleontologia 'G. Gemmellaro', Palermo; MPR, Museo di Paleontologia, Roma; MSNC, Museo di Storia Naturale, Calci (Pisa); MUT, Museo Nacional Paleontologico-Arqueologico, Tarija; MZF, Museo di Storia Naturale – Sezione di Zoologia, University of Firenze; NHM, Natural History Museum, London; NHMB, Naturhistorisches Museum, Basel; NMENH, National Museum of Ethnography and Natural History, Kishinau; NMK, National Museums of Kenya, Nairobi; PIN, Paleontological Museum of the Russian Academy of Science, Moscow; RBINS, Royal Belgian Institute of Natural Sciences, Brussels; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; SAM, South African Museum, Cape Town; SMNS, Staatliches Museum Naturkunde, Stuttgart; ZIN, Zoological Institute of the Russian Academy of Science, S. Petersburg; ZMB, Museum für Naturkunde (Zoology) der Humboldt-Universität Berlin.

APPENDIX 2

ANALYSIS OF THE PRINCIPAL CHARACTERS
ASSOCIATED TO THE MANDIBULAR AND
CORONOID CANALS

Mandibular canal

1. Course of the mandibular canal relative to the tooth row
 - (0) Beneath the toothrow.
 - (1) Lateral to the toothrow (either labial or, less frequently, lingual).
 - (2) Always lingual to the toothrow.

Mandibular foramen

2. Position of the mandibular foramen relative to the occlusal plane
 - (0) Same level or lower.
 - (1) Higher.
3. Position of the mandibular foramen on the medial side of the ascending ramus
 - (0) Half-way from the anterior and posterior margins of the ramus (laying anteriorly to the condyle).
 - (1) Near the posterior margin (lying below the condyle).
4. Configuration of the mandibular foramen
 - (0) Crescent-shaped, small.
 - (1) V-shaped, small.
 - (2) V-shaped, large.
5. Linguoid tubercle on the anterior margin of the mandibular foramen
 - (0) None.
 - (1) Small tubercle.
 - (2) Large, medially protruding tubercle.

Lateral mental foramen

6. Number of lateral mental foramina
 - (0) Anterior and posterior lateral mental foramina present.
 - (1) Posterior lateral mental foramen absent.
7. Position of the posterior mental foramen (PMF) relative to the dentition
 - (0) Below or posterior to p3(dp3).
 - (1) Between p2(dp2) and p3(dp3).
 - (2) Below or anterior to p2(dp2).

Medial mental foramen (MMF)

8. MMF
 - (0) Absent.
 - (1) Present (at least in some individuals).
9. Frequency (f)* of occurrence of MMF
 - (0) 0% < f < 15%.
 - (1) 15 ≤ f < 40.
 - (2) 40% ≤ f < 65%.
 - (3) 65% ≤ f < 100%.
 - (4) f = 100%.

*Codings (0 to 4) assigned using the gap weighting method (Thiele, 1993; Schols *et al.*, 2004).

Coronoid canal

10. Coronoid foramen
 - (0) Present.
 - (1) Absent.

APPENDIX 3

DATA MATRIX FOR MANDIBULAR CHARACTERS (SEE APPENDIX 2)

Taxon	Characters									
	1	2	3	4	5	6	7	8	9	10
<i>Procavia capensis</i>	0	0	0	0	0	0	0	0	0	0
<i>Phopatherium escuillei</i>	0	0	0	0	0	0	0	0	0	0
<i>Numidotherium koholense</i>	0	0	0	0	0	1	0	0	0	0
<i>Barytherium grave</i>	0	0	0	0	0	1	0	0	0	0
<i>Moeritherium trigodon</i>	0	0	0	0	0	0	0	0	0	1
<i>Prodeinotherium hobley</i>	0	1	0	0	0	0	0	0	0	0
<i>Phiomia serridens</i>	0	0	0	0	0	0	1	0	0	0
<i>Mammuth americanum</i>	1	1	1	1	1	0	1	0	0	0
<i>Gomphotherium angustidens</i>	1	1	1	1	1	0	1	0	0	0
<i>Anancus arvernensis</i>	1	1	1	1	1	0	1	0	0	0
<i>Loxodonta africana</i>	1	1	1	2	2	0	2	1	0	0
<i>Elephas planifrons</i>	1	1	1	2	2	0	2	1	0	0
<i>Elephas maximus</i>	1	1	1	2	2	0	2	1	1	0
<i>Palaeoloxodon mnaidriensis</i>	1	1	1	2	2	0	2	1	0	0
<i>Mammuthus meridionalis</i>	1	1	1	2	2	0	2	1	3	0
<i>Mammuthus primigenius</i>	2	1	1	2	2	0	2	1	4	0