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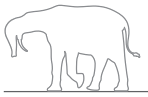
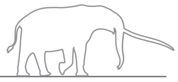
MISCELLANEOUS





vertebral columns are rare among fossils, observation of both extant and fossil species clearly shows that this character is variable among species, and is, thus, of systematic value. At the posterior end of the vertebral column, the sacral vertebrae (from 3 to 6) articulate with the pelvis. These vertebrae tend to fuse together, forming a single functional unit. The spine terminates with the caudal vertebrae that also vary according to species but also individually. The minimum and maximum observed number of vertebrae in proboscidean (complete) caudal series is 19 and 34, respectively. The sternum of the African elephant consists of five sternebrae that tend to fuse with each other. The sternum and its cartilaginous processes are divided into three separate, approximately equal, segments. The first segment is called the manubrium, the second consists of sternebrae 2 to 4 and the third posterior segment is the xiphoid process. Both the vertebral spine and the thoracic cage of elephants form a very rigid structure.

APPENDICULAR SKELETON

In order to support their enormous weight, large proboscideans possess a graviportal skeletal structure, where the limb bones are held in an almost vertical, pillar-like position under the body. In elephants, the bones of the anterior limb (scapula, humerus, ulna, and radius) are very robust, and bear 55–60% of the animal's weight, including the massive head. There is no clavicle, so that the movement of the anterior limb is limited to an antero-posterior swinging. The humerus is the wider and heavier of the limb bones. The ulna is larger than the radius, and these two bones are held fixed in a pronated position. The carpal bones (wrist bones) are 8 in number and are arranged in two rows. The hand consists of 5 rays, each formed by a robust metapodial and one to three phalanges. The 3rd, central ray is the best developed and is the main weight bearer. A cartilage rod (prepollux) forms a sort of sixth digit, reaching from the wrist to the foot pad, probably to stabilize the carpus over the digital cushion. Digits 2, 3 and 4 have three phalanges each. Digit 1 has only one phalanx, while digit 5 consists of 2 phalanges. The digits rest on an extensive cushion of elastic connective tissue and fat, and they are placed in a fairly upright position (digitigrade). The pelvis connects the vertebral column to the posterior limbs and is formed by the fusion of three bones: the ilium, which is the larger, the ischium, and the pubis. As in most mammals, the shape and proportion of the pelvis allows us to discriminate between male and female individuals. The posterior limb consists of the femur, which is the longest of the limb bones, the patella (knee cap), tibia, and fibula. There are seven tarsal bones (ankle bones), arranged in three rows. The pes is also pentadactyl. Of the five metatarsal bones, the largest are the 3rd and 4th. The third and fourth digits have three phalanges each; the first digit is represented by a single, proximal sesamoid bone, while digits 2 and 5 consist of two phalanges each. A large cushion of elastic connective tissue and fat is also present at the base of the pes. Similarly to the hand, a cartilagineous rod (prehallux) is also present in the pes.

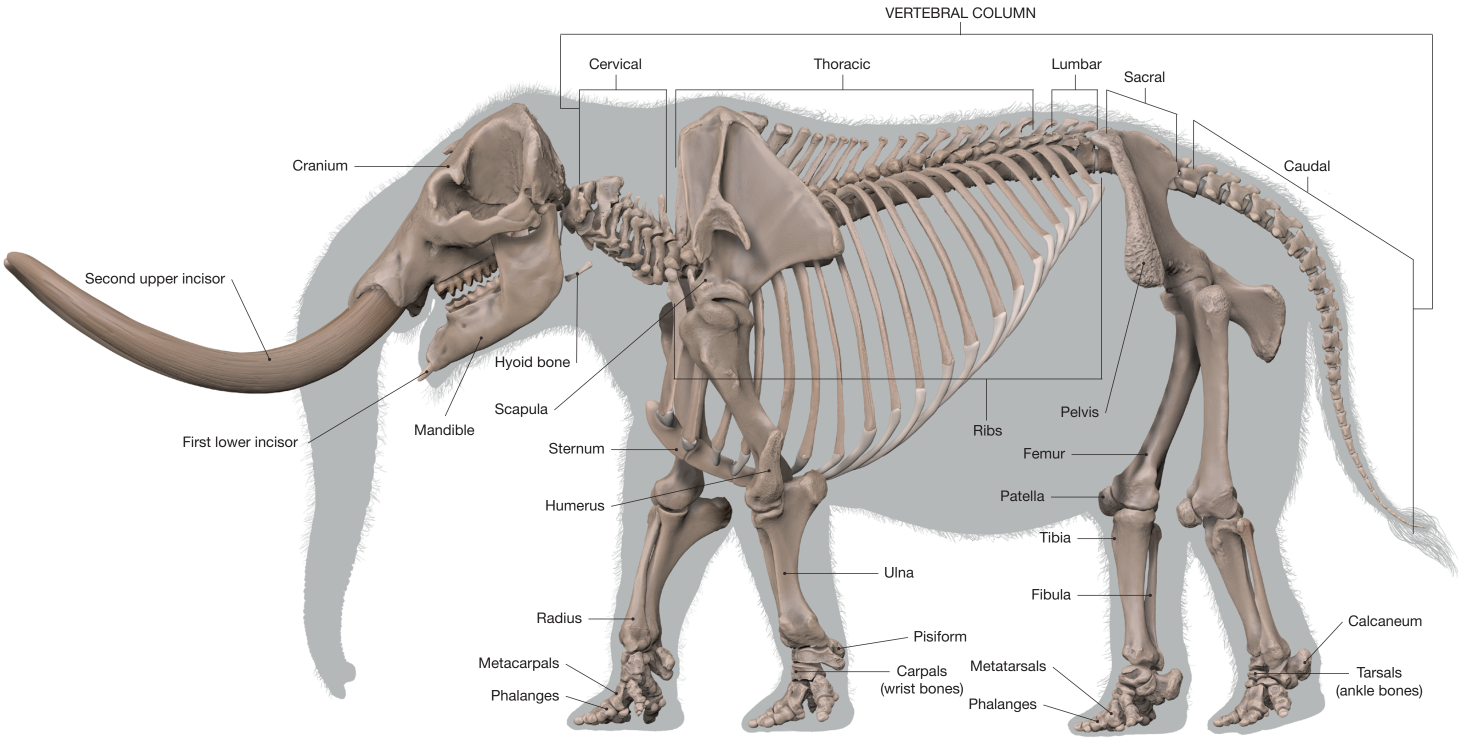


Figure 13. Proboscidean skeletal system

Skeleton of a male American mastodon (*Mammut americanum*) in lateral view showing major bones. The skeleton is very similar to that of living elephants, although the American mastodon has a substantially more robustly built appendicular skeleton and features a more elongated body and trunk. Most proboscideans, regardless of their taxonomy, have a very similar skeletal structure, featuring an elongated vertebral column, a long tail, and elongated limbs where the radius and tibia are always shorter than the humerus and femur, respectively. They also have very short manus and pes (anterior and posterior feet), a columnar posture, and extraordinarily developed second incisors, particularly from euproboscideans onward.

TEETH (DENTITION AND STRUCTURE)

DENTITION

The teeth of living elephants are extremely modified with respect to the basal mammalian pattern. If one takes into consideration also the extinct forms, proboscideans appear quite diverse in terms of the number of teeth present in their dentition, tooth succession, and tooth morphology. This reflects adaptations to cope with different kinds of plant food, but also different feeding strategies linked to the evolution of gigantisms. Primitive proboscideans (plesielephantiformes) possessed a full set of teeth, consisting of incisors (2 or 3), canines (1), premolars (3 or 4) and molars (3). Permanent anterior teeth (incisors and canines) and premolars were preceded by deciduous teeth. Tooth replacement occurred by vertical substitution of the deciduous teeth by the permanent ones, as is typical for mammals. More derived species are characterized by a progressive reduction of the more anterior teeth (incisors, canines, and permanent premolars). In elephants, for instance, all anterior teeth are lost except for a pair of upper incisors forming the tusks. In addition to the tusks, elephants possess six grinding teeth, three deciduous premolars (the permanent premolar being lost), and three permanent molars. These teeth succeed one another in a one-by-one progression, coming into function by horizontal succession. New teeth appear at the back of the tooth row and are shed from the front. Moreover, each tooth is so large that no more than two teeth per each jaw quadrant can be in use simultaneously. Each tooth is commonly formed by a crown, the structure that emerges from the gum and gets into contact with food, and a root which firmly implants the tooth in the jawbone. The crown is composed of two types of mineralized hard tissues: enamel, the hardest material produced by vertebrates, forming a relatively thin layer covering the crown, and dentine, a softer tissue forming the bulk of the tooth. In some species, the crown is covered by a third type of dental tissue called cement. The tooth root is made of dentine and a thin outer layer of cement. These mineralized tissues are 3 component composite materials, consisting of organic material (collagen, a fibrous protein), mineral material (hydroxyapatite, a mineral composed of calcium phosphate) and fluids (water).

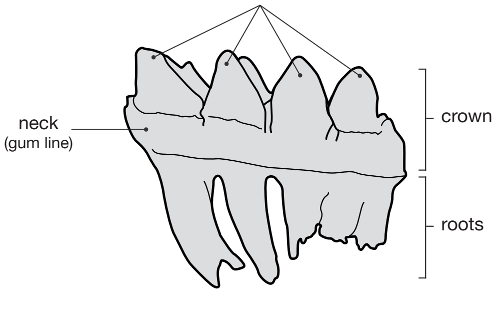


Figure 14. Proboscidean tooth anatomy

A third molar of an American mastodon illustrates the main anatomical parts of a proboscidean tooth, which are the same as in a human tooth.

TUSKS

Proboscidean tusks are ever-growing incisors. As such, they are present only in elephantimorphs. Basal proboscideans display instead a pair of enlarged upper and lower incisors with definite growth. In this case, the incisors possess a crown, usually spatulated, covered by enamel, and a root. Elephantimorph tusks, on the other hand, do not possess a crown/root separation, with enamel reduced to a lateral band or completely absent in the tusks of adults.

The tusks of elephantimorphs are the longest teeth of any living or extinct mammals, with records of 5 meters in "*Mammut*" *borsoni* and in giant mammoth species. They are mostly made by a special kind of dentine (called ivory) covered by cement. The presence of an external enamel layer is extremely variable among taxa. In some groups upper tusks possess a lateral enamel band; in others, an enamel cap is present only on the tip of juvenile tusks (both upper and lower) and is worn away during use. The ivory of elephantimorphs exhibit a unique and complex pattern of criss-crossing microscopic lines called Schreger pattern, also known as "engine turning" or "guillochage." This structure, which is also present in the dentine of cheek teeth, reinforces the ivory, reducing the risk of crack propagation when the tusks are heavily loaded during use. Growth of tusks occurs as dentine-forming cells (odontoblasts) that line the surface of the conically shaped pulp cavity deposit a new layer of dentine inward, displacing the tusk forward. Tusk dentine is thus added within the pulp cavity as a series of conical layers. Because tusk growth is continuous, tusks of older proboscideans are generally longer than tusks of younger proboscideans. Abrasion and breakage of the tip, however, can reduce tusk length, so the oldest individuals occasionally have tusks that are shorter than those of middle-aged adults, though markedly thicker.

The permanent tusks of elephantimorphs are considered homologous to the second upper (I2) and first lower (i1) incisors of primitive proboscideans. Both are preceded by a pair of small deciduous tusks, called "tushes." Differently from the permanent tusks, tushes consist of a crown and a root. Although tushes have no apparent function, they might provide the foundation for the development of the permanent tusks. In living elephants, permanent tusks grow approximately 11 cm per year and continue to grow throughout the life of the elephant. Male tusks can grow six times faster than female tusks. This leads to a high degree of sexual dimorphisms, with females possessing much smaller tusks or no tusks at all.

The relative maximum length of tusks, with respect to body size, curvature, and cross-section outline, varies across taxa and represent characters used in the systematics of proboscideans. The difference in the degree of wear often observed between the left and right upper tusks of an individual suggest it had a dominant (working) tusk. Tusks are used for defense, offense, display, and feeding. In the evolution of elephantimorphs, there is a general trend to increase the size of the upper tusks, accompanied by a change of curvature: from a marked downward curvature, as observed in gomphotheriids, to straight or upward-curved tusks in elephants. The lower tusks tend, on the contrary, to reduce in size, eventually being lost, though in some lineages, lower tusks become extremely specialized and/or very large.

SIZES

Because of the selective poaching and trophy hunting on big tuskers that has occurred in the recent past – especially during much of the 20th century – today's elephants usually exhibit a reduced tusk size in comparison to their recent progenitors, where big tuskers (with tusks weighing more than 100 pounds [45 kg] per side in the case of the African savanna elephant) were probably common. This catastrophic human interaction has also resulted in more and more tuskless elephant births. Nowadays, African savanna mature male elephants (> 40 years) may develop, on average, around 200 cm long tusks, weighing up to 35 kg each, while those of females are much shorter and thinner, and rarely exceed 7 kg. In Asian adult bull elephants, tusks over 150 cm in length are not common, while females are tuskless. The data on the African forest elephant is much scarcer because until recently it was considered a subspecies of the savanna elephant, so data pertaining to the forest elephant were lumped with that of its larger relative. Nevertheless, adult males appear to bear tusks with a length typically around 160 cm and occasionally as much as 180 cm or more, whereas females usually develop tusks half these lengths.

Big tuskers today are very rare, but as recently as a century ago they were probably the norm. In optimal conditions, it has been estimated that the African savanna elephant developed, on average, tusks around 250 cm in length and 50 kg in mass, while the Asian elephant likely had tusks with a mean length over 200 cm and 30 kg in weight. However, world record specimens greatly surpass these numbers. The heaviest African savanna elephant tusk ever reliably recorded had a weigh of 107 kg and a length of 311 cm, and that of the Asian elephant was 73 kg and 267 cm long. However, these weights are truly exceptional, and they are a result of the unusually extreme thickness of these tusks. The record tusk length for the African savanna elephant is 349 cm but with a weight only about two-thirds of the heaviest tusk reported above. The longest Asian elephant tusk measures 326 cm, and it is also around two-thirds as heavy as the most massive one. The longest tusk recorded for the African forest elephant is a rather thick tusk measuring 241 cm in length and 60 kg in weight (see Table 7). Another two individuals with even larger tusks were shot in the Central African Republic; the larger tusk measured 296 cm in length (the minor tusk of the same individual was 299 cm long, but sensibly lighter) and weighed 70 kg. However, this region of Africa is known to host hybrid individuals between forest and savanna elephants, although the shape of the head and tusks of this Central African individual were very much like those of typical African forest elephants. Interestingly, the largest tusks do not always belong to the biggest elephants. In the case of African savanna elephants, the longest and thickest ones are found in east African populations, where the mean shoulder height is barely over 3 m, compared to the typical 3.2 m or more of elephants from Angola and Namibia.

Extinct proboscideans also developed impressive upper tusks, but this did not occur until the Late Miocene, when the first proboscideans attaining tusks as large as those of living big tuskers appeared. The most impressive tusked proboscideans were the advanced mammutids, stegodontids, and elephants, especially mammoths (*Mammuthus*). Woolly mammoths (*M. primigenius*) are well-known for their incredibly long and curved tusks. In fact, very impressive tusks exceeding 400 cm in length and a mass above 115 kg have been reported from eastern Siberia. However, a really fine big tusker giant mammoth species, such as *M. rumanus*, *M. meridionalis*, *M. trogontherii*, or *M. columbi*, would have had typically very massive tusks over 400 cm in length and around 200 kg in mass each! Actually, several tusks in the area of 500 cm have been reported (see Table 7). World record–sized tusks, however, would have approached a length of 600 cm or more (probably more than 750 cm in the case of the Borson's mastodon "*Mammut*" *borsoni*), while the heaviest must have surpassed 350 kg! Most extinct proboscidean species also had lower tusks, and in some cases these reached massive proportions too. In giant deinothere species for instance, lower tusks approached 150 cm in length and around 25 kg in mass. The most massive lower incisors are probably those of amebelodontids, particularly *Konobelodon atticus*, whose lower massive tusks are up to 161 cm in length with a probable weight of nearly 30 kg each. But the basal elephantid species *Stegotetrabelodon syrticus* had even longer lower tusks, measuring up to 220 cm, although these were very thin (10 x 7 cm) and probably weighed only around 12 kg.

MOLARS

Eritherium, the most primitive proboscideans known so far, possess molars displaying a morphology still close enough to the generalized mammalian condition to be described using the common mammalian dental terminology (see pp. 45–47). The tooth crown is formed by four main cusps arranged into two transverse rows. The crown is relatively low (brachydont) and shows at its base an incomplete cingulum. The cusps pattern can be described as bunodont with just an incipient tendency to bilophodonty. Also noteworthy is that the M2 is the largest of the three molars.

Plesielephantiformes developed a truly bilophodont pattern, in which the two cusps of each row are united by a transverse crest, forming a so-called loph (lophid in the case of lower molars). Moreover, the third molar is now the largest of the three and starts to develop additional cusps behind the posterior loph. The change from a bunodont to a lophodont dental pattern in early proboscideans is linked to a shift in feeding preferences. Apart from plesielephantiformes, also deinotheriids developed fully bilophodont molars. Moeritheres, on the other hand, reversed to a more bunodont dentition. Another major rearrangement of the molar morphology

PROBOSCIDEAN TUSK SIZES

DEINOTHERIIDS AND ELEPHANTIFORMES

Species	Specimen	Length (mm)	Diameter (mm)	Circumference (mm)	Estimated mass (kg)
Phiomia major	CH17–1	450	45 x 75	–	1.2
Prodeinotherium bavaricum	Unterzolling[1]	~630	97 x 81	–	4
Deinotherium giganteum	Kettlasbrunn[1]	~1,300	125 x 170	–	22
Deinotherium proavum	Gela[1]	1,470	117 x 175	–	24

MAMMUTIDS

Species	Specimen	Length (mm)	Diameter (mm)	Circumference (mm)	Estimated mass (kg)
Miomastodon gobiensis	GPM ZR001141	~1,300	103 x 127	–	15
Mammut matthewi	UO Or-7024	2,100	~200	–	68
"*Mammut*" *borsoni*	MIL 560	5,020	190 x 173	575	137
Mammut americanum	UNSM 2-26-34	3,048	210	–	109
Mammut pacificum	WSC 18743	1,996	186	–	56

CHOEROLOPHODONTIDS AND AMEBELODONTIDS

Species	Specimen	Length (mm)	Diameter (mm)	Circumference (mm)	Estimated mass (kg)
Choerolophodon guangheensis	IVPP V17685	~1,300	120 x 96	–	13
Choerolophodon pentelici	LGPUT-NIK-1776	> 2,500	190	560	>65
Gnathabelodon thorpei	FHSM VP-18	2,007	160	471	37
Protanancus tobieni	QA1256-46	1,150	108 x 88	–	9
Konobelodon atticus	Pestszentlőrincz	2,300	144 x 128	419	33
Konobelodon atticus	Pestszentlőrincz[1]	1,610	195 x 110	–	28

GOMPHOTHERIIDS

Species	Specimen	Length (mm)	Diameter (mm)	Circumference (mm)	Estimated mass (kg)
Megabelodon lulli	Neb. Mus. 10 8-14	1,720	126	–	22
Cuvieronius hyodon	Tarija	2,200	–	540	53
Notiomastodon platensis	Pergamino	2,400	–	530	56

STEGODONTIDS AND TETRALOPHODONTIDS

Species	Specimen	Length (mm)	Diameter (mm)	Circumference (mm)	Estimated mass (kg)
Stegodon namadicus	Ghansi	3,226	–	650	137[2]
Stegodon ganesa	NHM 3008	3,890	229 x 201	660	139
Stegodon sp.	Kalpi	3,540	–	540	85
Stegodon trigonocephalus	NNM RGM.DUB 4980	3,150	160 x 165	–	68
Stegodon protoaurorae	KYF-KA007–008	1,770	140 x 144	–	29
Tetralophodon longirostris	Villavieja del Cerro	1,680	127 x 142	–	25
Anancus sivalensis	PUPC 2004/15	2,718	172	541	66
Anancus arvernensis	Stoina	3,710	–	480	70
Paratetralophodon hasnotensis	GSP 15032	1,360	99 x 83	–	9

ELEPHANTIDS

Species	**Specimen**	**Length (mm)**	**Diameter (mm)**	**Circumference (mm)**	**Estimated mass (kg)**
Loxodonta africana	Average (in optimal conditions)	~2,500	~160	~500	~50
Loxodonta africana	World record (longest)	3,490	–	470	~63
Loxodonta africana	World record (heaviest)	3,110	–	616	107[2]
Elephas maximus	Average (in optimal conditions)	~2,000	~135	>400	~30
Elephas maximus	World record (longest)	3,260	–	430	48[2]
Elephas maximus	World record (heaviest)	2,670	–	556	73[2]
Loxodonta cyclotis	Average (in optimal conditions)	~1,800	~130	~400	~25
Loxodonta cyclotis	Word record (longest and heaviest)	2,410	–	584	60[2]
Loxodonta cyclotis	Word record (probable hybrid)	2,960	–	540	70[2]
Stegotetrabelodons orbus	KNM-LT 354	995	61 x 72	–	3.6
Stegotetrabelodons syrticus	Sahabi	~2,800	140 x 135	–	~43
Stegotetrabelodons syrticus	Sahabi[1]	~2,200	100 x 70	–	~12.5
Palaeoloxodon antiquus	Livorno	3,880	–	585	109
Palaeoloxodon antiquus	Aniene	>3,900	270 x 230	770	>190
Palaeoloxodon namadicus	Bilthari	3,660e	–	625	~121
Palaeoloxodon naumanni	Ueno	2,400	–	390	30
Mammuthus subplanifrons	A.2882	~3,684	177 x 160	528	~85
Mammuthus africanavus	Garet et Tir	~2,880	140 x 136	–	~45
Mammuthus rumanus	Laiatico	4,100	260	715	173
Mammuthus meridionalis	Scoppito	3,780	238 x 204	715	159
Mammuthus meridionalis	Georgievsk	3,200	300 x 238	–	185
Mammuthus meridionalis?	Milan museum	3,580	–	890	233
Mammuthus trogontherii	Nosak	4,200	250	–	213
Mammuthus primigenius	Adams mammoth	3,230	155	–	71[2]
Mammuthus primigenius	Nizhnekolymsky	4,050	175	590	115.5[2]
Mammuthus primigenius	Rebrovo	~3,750	190	650	~130[2]
Mammuthus primigenius	Chukoktka	4,300	–	–	84[2]
Mammuthus primigenius	female (longest reported)	2,470	93	–	19.7[2]
Mammuthus columbi	AMNH 22481	4,880	–	650	170
Mammuthus columbi	Zed	3,180	240	–	149
Mammuthus "jeffersoni"	Jackson County	3,277	–	584	81.5[2]
Mammuthus "jeffersoni"	UNSM 1-4-15	3,810	–	737	170
Mammuthus exilis	Channel Islands	1,430	105	–	13

Table 7. Some proboscidean tusks measurements from different clades. The estimated masses of these tusks are derived from Larramendi's (2023) study on proboscidean tusk sizes. [1]Lower tusks; [2]measured weights.

started with the evolution of elephantiformes and was completed with the origin of elephantimorphs.

Early elephantimorphs developed a third loph(id) in their molars, which become also proportionally larger with respect to the jawbone. The tooth main cusps become very large and give origin, by fission, to smaller medial cusps, called mesoconelets (see below). There is also a tendency to develop accessory small cusps (conules) on the posterior or anterior side of the main cusps (cones), producing a rather complex occlusal structure. Moreover, the peculiar mechanism of tooth progression (horizontal succession) and mastication of elephantimorphs causes wear to affect first the most anterior loph(id) and then extend to the second and eventually third loph(id). On each loph of the upper molars is the lingual half that first starts to show signs of wear (the so-called pretrite side) and then the labial one (posttrite side). The reverse occurs in the lower molars. This last particular wear pattern is observed in all elephantimorphs but is reduced to absent in stegodontids and elephants in which the labial and lingual side of the molars come into wear nearly at the same time. In these latter groups, the main cones and mesoconelets tend to become of equal size and are arranged into transverse rows, forming crests.

In elephants, the individual cones lose their identity, become antero-posteriorly compressed and form a unique structure called a plate or lamella (plural lamellae). Each molar is made up of several lamellae (up to 30), which are united at their base. Coronal cementum is deposited between and around the lamellae, consolidating the whole structure. In large teeth, lamellae are still being formed and added to the posterior end of the tooth contained within the alveolus, while the anterior part is already erupting from the gum and coming into wear. During their evolution, elephants increased the height of the lamellae, resulting in the acquisition of hypsodont molars. With wear, the cementum and the enamel capping the lamellae are removed, forming a relatively flat mastication surface characterized by a series of "enamel figures," consisting of an enamel loop enclosing a basin of dentine, with the regions between the lamellae and lateral to them filled with cementum. Because of the different hardness of the three tissues, the enamel ridges project out from the dentine and cementum, forming the functional cutting elements of the elephant molar. The shapes of the worn lamellae (enamel figures) differ among species and are used in the systematics of elephants.

DENTAL TERMINOLOGY

Next, the terminology used to describe the principal molar types in proboscideans, are presented.

Mesial: direction toward the midline of the dental arch. Synonym of "anterior."
Distal: away from the midline of the dental arch. Synonym of "posterior."
Lingual: side of the tooth toward the tongue.
Buccal: side of the tooth toward the cheek or lips.
Occlusal: side of the tooth where mastication takes place.
Cusp: a pointed or rounded (conical) projection of the tooth crown. It is covered by enamel, which is gradually abraded away during mastication, revealing the dentine below, thus forming "wear figures" consisting of dentine basins surrounded by an enamel ridge. The term "cone" ("conid" for lower molars) is usually used as a synonym.
Loph: a ridge of enamel connecting the cusps of an upper molar. The term "lophid" is used for a lower molar.
Crista: a narrow fold of enamel on the flank of the main cusps.
Bunodonty: tooth pattern where cusps are predominant, lophs being much reduced or absent.
Lophodonty: tooth pattern where cusps are no longer distinguishable from the crests or lophs joining them. The lophs join without discontinuity the apexes of the cusps.
Bunolophodonty: tooth pattern where cusps are distinguishable from the lophs joining them. These lophs are discontinuous, with a significant notch in their middle.
Hypsodont: high tooth crown; in hypsodont teeth, crown height (H) is greater than width (W). Two levels of hypsodonty are recognized in this book: subhypsodont ($1.2<H/W<1.5$) and hypsodont ($H/W>1.5$)
Mesodont: moderately high tooth crown ($0.9<H/W<1.2$).
Brachydont (also brachyodont): low tooth crown ($H/W<0.9$).

Plesielephantimorphs

(Bunodont-Bilophodont molar pattern)

Upper molars

Protocone (pr): the main mesiolabial cusp of the tooth.
Paracone (pa): the main mesiolingual cusp of the tooth.
Hypocone (hy): the main distolabial cusp of the tooth.
Metacone (me): the main distolingual cusp of the tooth.
Protoloph (prl): the transverse crest that links protocone and paracone.
Metaloph (mtl): also known as hypoloph, the transverse crest that links hypocone and metacone.
Posterior protocone crista (po-prc): enamel ridge on the distal side of the protocone. It is homologous to the posterior pretrite central conule of elephantiformes.

Lower molars

Protoconid (pd): the main mesiobuccal cusps of the tooth.
Metaconid (md): the main mesiolabial cusps of the tooth.
Hypoconid (hd): the main distobuccal cusps of the tooth.
Entoconid (ed): the main distolingual cusps of the tooth.
Protolophid (pld): transverse crest that links protoconid and metaconid.
Hypolophid (hld): transverse crest that links hypoconid and entoconid.
Talonid (td): structure on the distal part of the tooth. Can be formed by one (hypoconulid) or two cusps (hypocondulid + entoconulid) forming an incipient third lophid (tritolophid).

Upper and lower molars

Cingulum: enamel collar surrounding the tooth base; can be present on the mesial, labial (lc), buccal, and posterior (pc) sides of the tooth.

Posterior cingulum (pc): enamel collar surrounding the posterior (distal) side of the tooth.

Ectoflexus: the indentation on the labial (outer) face of an upper molar between the two principal buccal cusps (paracone and metacone).

Deinotheriids

(deinotheriid lophodont pattern)

Pre-crista: enamel crest descending from the apex of a cusp and running down its anterior side.

Post-crista: enamel crest descending from the apex of a cusp and running down its posterior side.

Ectoloph(id): antero-posterior crest that links the two main labial cones of premolars.

Tritoloph(id): third posterior loph of M1/m1.

Convolute: posterior enamel ornamentation of M2 and M3.

Elephantiformes

(bunolophodont, zygodont patterns)

Median sulcus (mss): antero-posterior sulcus between the pre- and posttrite halves of the tooth.

Pretrite cone (pr): each main cone on the tooth side that comes first into use. In the upper molar the pretrite side is the lingual one; in the lower ones it is the labial side.

Posttrite cone (po): each main cone on the tooth side that comes later into use. In the upper molar the posttrite side is the labial one; in the lower ones it is the lingual side.

Trefoil pattern (clover-leaf): three-lobed enamel loop surrounding a dentine basin that forms on the occlusal plane, when the main cusp and its associated central conules are worn and fused together.

Anterior pretrite central conule (aprcc): conule on the pretrite side of the tooth, anterior to the corresponding main cone.

Posterior pretrite central conule (pprcc): conule on the pretrite side of the tooth, posterior to the corresponding main cone.

Anterior posttrite central conule (apocc): conule on the posttrite side of the tooth, anterior to the corresponding main cone.

Posterior posttrite central conule (ppocc): conule on the posttrite side of the tooth, posterior to the corresponding main cone.

Interloph(id) valley: space between two successive loph(id)s.

Crescentoids: in mammutids, the crest homologous to the posterior pretrite central conule.

Zygodon crest: in mammutids, the crest homologous to the posterior posttrite central conule.

Zygodont pattern: loph(id) structure typical of mammutids, characterized by antero-posteriorly compressed cones, reduced or crest-like central conules, and fine multiplication of mesoconelets.

Choerodonty: multiplication and irregular arrangement of the conelets, typical of, but not limited to, derived choerolophodontids,

Ptychodonty: corrugated enamel outer surface.

Anancoidy: dislocation of the pre– and post–half-loph(id)s belonging to the same loph(id), forming an antero-posterior alternation of lingual and buccal half-loph(id)s.

Stegodonts

(polylophodont pattern)

Crest: the transverse structure formed by the coalescence of the cones and mesoconelets pertaining to the same loph(id). Some authors refer to this structure as a plate, but we confine this term to the special structure present in elephant molars.

Stufen-bildung: step-like enamel wear pattern, forming on the occlusal surface.

Elephants

(lamellar pattern)

Plate/lamella: each elementary unit forming the elephant molar.

Enamel wear figure: the plate cross section that forms on the occlusal surface as it is worn, made of several small or just one large enamel loop (depending on the degree of wear) surrounding a dentine basin.

Loxodont sinus: median expansion of the anterior and/or posterior side of a plate, forming an acute angled loop on the enamel wear figure.

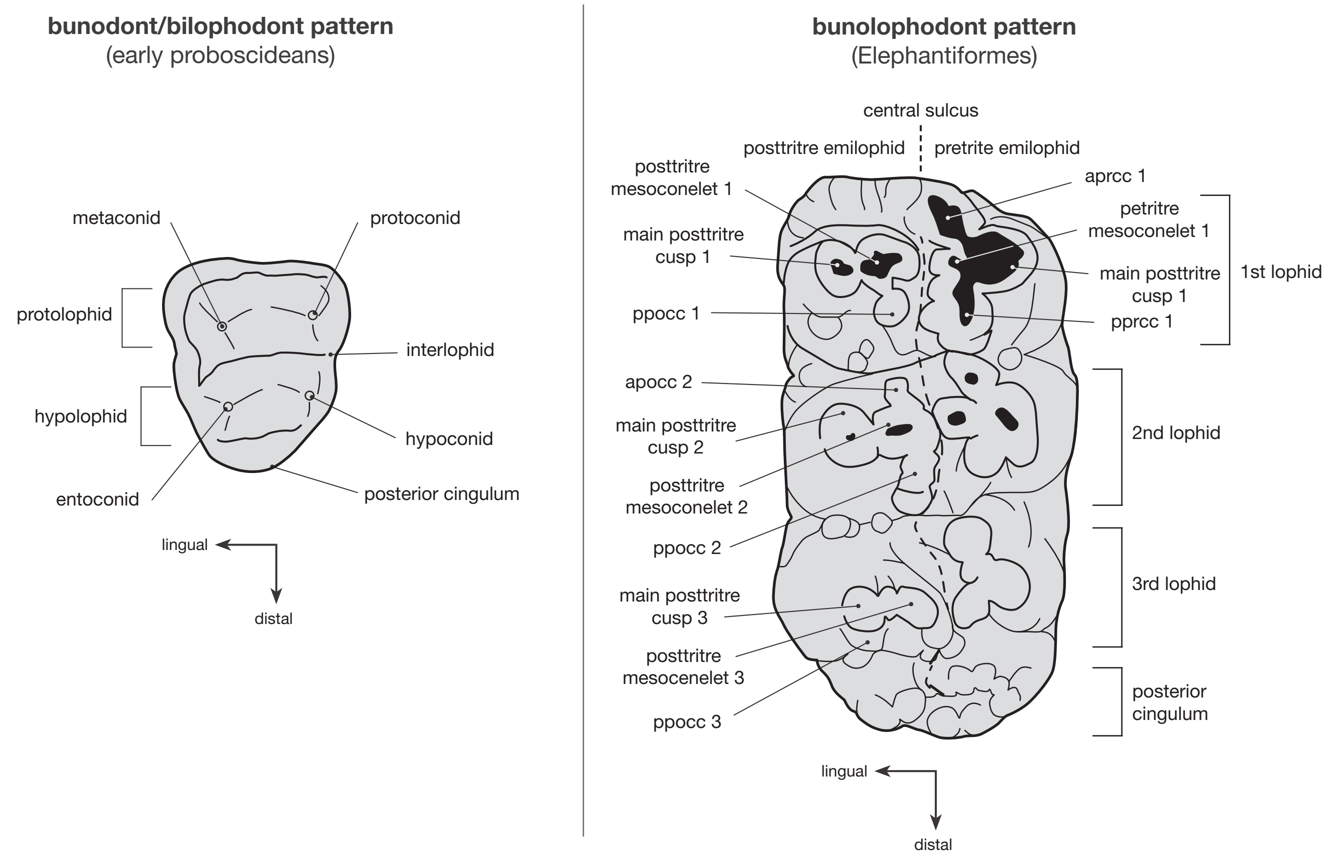
Accessory conule: tubercle occurring on the posterior side of a plate and fusing with it at its base.

Enamel folding: degree of folding of the enamel layer covering each lamella.

Anterior/Posterior platelet (talon): the small plate-like structure occurring on the anterior and posterior ends of a molar. It fuses with the full-plate behind or in front of it and does not possess its own root. Sometimes called, improperly, anterior/posterior talon.

MICROSTRUCTURE OF ENAMEL

Mammalian enamel is characterized by a complex microstructure. The mineralized component is made up of apatite microcrystals arranged into elongated rod-like structures called enamel prisms (prismatic enamel). In proboscideans, prism cross section may be either keyhole shaped (primitive); fan shaped (derived); or Ginkgo leaf–shaped (restricted to the Stegodontidae and Elephantidae among elephantoids). According to the direction of the prisms with respect to each other and to reference planes (enamel-denting junction, or the outer enamel surface) different enamel types have been described. A special type of enamel called 3-D enamel, characterized by enamel bundles directed in the three directions of space, is typical of proboscideans. Other enamel types present in proboscidean enamel is radial enamel and Hunter-Schreger bands. The spatial distribution of the various enamel types within a single tooth is usually referred to as the enamel schmelzmuster, a German term meaning “enamel-pattern.”


bunodont/bilophodont pattern
(early proboscideans)

bunolophodont pattern
(Elephantiformes)

lamellar pattern
(elephants)

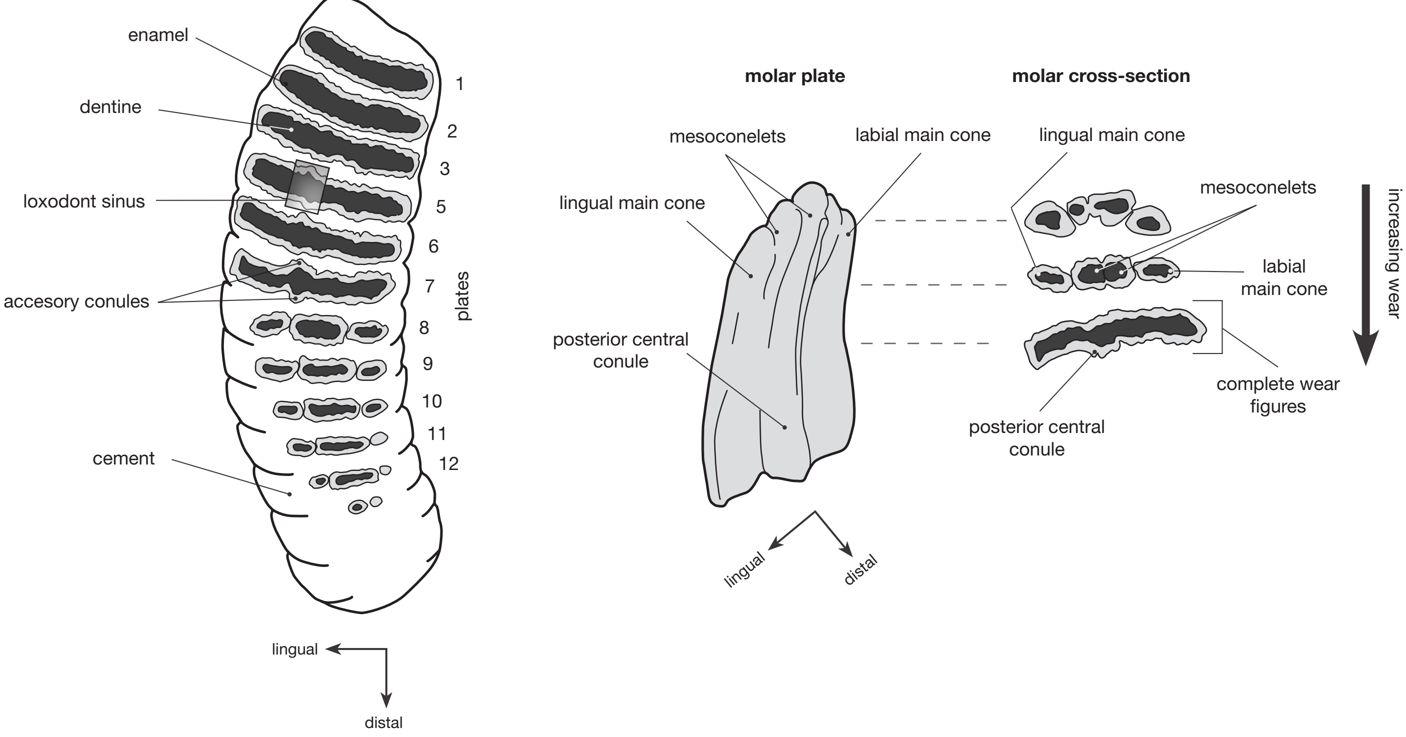


Figure 15. Proboscidean dental structure and nomenclature

Schematic drawings of lower right molars are used to illustrate the three basic proboscidean molar types: the four-cusped bunodont/bilophodont pattern of early proboscideans (e.g., *Eritherium* and *Moeritherium*); the bunolophodont pattern of elephantiforms (e.g., *Gomphotherium*); and the lamellar pattern of modern elephants (parallelized in derived stegodonts). In the bottom right, successive cross sections of an elephant molar plate simulate the development of wear figures on the masticatory surface as tooth wear proceeds. Abbreviations: see pages 45 and 46.

SOFT ANATOMY

THE EARS

The size and shape of the ears of proboscideans, like in many other mammals, have important physiological, ecological and behavioral implications. For their function in body thermoregulation, ear size is especially linked to the animal's body mass and the climatic conditions of its habitat. Ear mobility is also an important "communication" tool, as it can express the animal's mood or warning signals against a perceived threat. The phylogenetic component should also take the following into consideration: The ear morphology of a given species is in fact also dependent on that of its ancestor that might have lived in a different habitat and had a different behavior. Being composed entirely of soft tissue, ears do not fossilize, so we don't have any direct information about their shape and size in fossil proboscideans, with the exception of those of mammoth carcasses preserved in the Arctic permafrost. The shape and relative size of early primitive proboscideans' ears were, in all probability, very different from that of modern elephants because their body size and habitats were markedly distinct. Larger ears probably co-evolved along with body-size increase in more derived species, especially when proboscideans reached very large body sizes, in order to counteract overheating problems associated with having a big body size. Since African elephants (*Loxodonta*) remained confined to the tropics during their evolutionary history, they developed huge but thin ears (about 10 mm thick). *L. africana* ears measure from 150 to 183 cm in length (including the dorsal "turnover" portion) and from 90 to 114 cm in width, and they can reach a weight of 25 kg, while those of the smaller *L. cyclotis* can be up to 137 cm long and 99 cm wide. The enormous ears of African elephants increase the body surface area by 4.2 to 6.5 m^2, corresponding to circa 1/5 of the total body surface, thus greatly enhancing heat exchange. The less warm-adapted *Elephas maximus* has intermediate-sized ears that rarely exceed 85 cm in length and 10 kg in mass. On the other hand, the cold-adapted *Mammuthus primigenius* had thicker (up to 40 mm), but markedly smaller, ears, only about 30–45 cm in length, 10–18 cm wide, with a lateral surface area of less than 0.05 m^2, and a probable weight of circa 1 kg.

THE PROBOSCIS

In living elephants, the proboscis is the most outstanding feature, used to carry out multiple functions, such as: smelling, feeding, watering, dusting, touching, sound production,

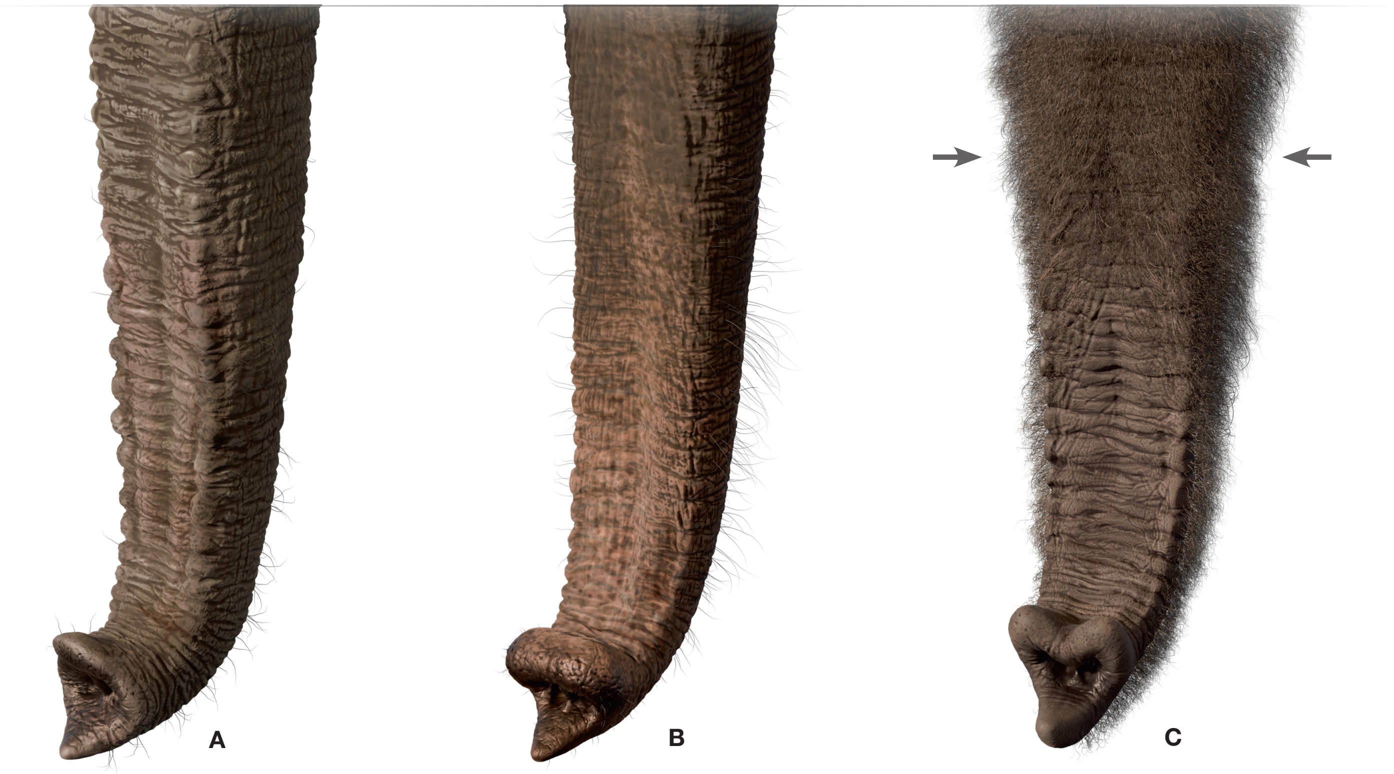


Figure 16. Trunk tip morphology in different elephant species
Structural characteristics of the proboscis: African savanna elephant (A), Asian elephant (B), and woolly mammoth (C). The woolly mammoth trunk morphology is based on the Malolyakhovsky specimen. Some frozen mammoth specimens show a notable lateral expansion in the area marked by arrows. Note the differences on the trunk tips.

lifting objects and holding objects, snorkeling (when swimming), and as a weapon of defense and offense. Its extraordinary strength, flexibility, and maneuverability led early naturalists to consider the proboscis as "the elephant's hand" or as "the snake hand." Indeed, with their trunk, elephants are able to pick up objects as small as a blade of grass using the

Ear size
Height: ~137 cm
Breadth: ~99 cm
Area: ~10,500 cm² (one side)

Ear size
Height: ~183 cm
Breadth: ~114 cm
Area: ~16,250 cm² (one side)

Ear size
Height: ~80 cm
Breadth: ~60 cm
Area: ~3,700 cm² (one side)

Ear size
Height: ~31 cm
Breadth: ~17.5 cm
Area: ~430 cm² (one side)

Figure 17. Ear comparison in living elephants and the woolly mammoth
African savanna elephants have the largest, fan-shaped ears for heat dissipation, while African forest elephants have smaller, oval-shaped ears better suited for dense forests. Asian elephants have smaller, triangular-shaped ears as they need less cooling, and woolly mammoths had the smallest, rounded, human-like ears to conserve heat in cold climates.

trunk tip, or to lift and carry a big tree log. Elephant trunk versatility is on a par with its tactile sensitivity. The most dexterous and sensitive part of the trunk is its tip, possessing finger-like projections (see below), which are controlled by specialized groups of neurons in the portion of the brain responsible for controlling the facial muscles.

The elephant trunk originated from the fusion of nose and upper lip structures and has no bones or cartilage (except at the base of the trunk, where it helps to divide the nostrils). This structure is defined as a muscular hydrostat, which means that it is principally composed of muscles, with a complex muscular arrangement within the organ. Elephants' proboscis has eight major muscles on either side, which can add up to the amazing figure of 150,000 muscle fascicles, which is far more than the total number of muscles in the human body. The proboscis is also composed of connective tissues, blood and lymph vessels, nerves, and a little fat, covered by skin, hair, and bristles. The trunk of adult African elephants can reach a mass of about 150 kg. With one suck, they can pull in around 10 liters of water. Despite these impressive figures, giant extinct elephantids probably doubled or even tripled these values. The number of finger-like structures at the tip of the trunk differs among species. The two extant African elephants have two finger-like lobes, one on the dorsal and the other on the ventral side of the trunk tip. The living Asian elephant has a single finger-like lobe on the dorsal side of the trunk tip, while the ventral margin is thick with a slight concavity at the center. The tip of the trunk of the woolly mammoth possesses a single, well-developed dorsal finger and two shorter finger-like lobes on the ventral side. Jointly, they form a grasping tip that allowed mammoths to collect grass, branches, and leaves probably better than living elephants. Woolly mammoths have, in addition, a unique hooded transverse expansion on the ventral side of the trunk near the tip that might have been used to melt snow before consumption by holding it in the trunk expansion and pressing this against the depression present in the upper lip. This specialized structure would thus represent an adaptation to living in a cold climate.

INTEGUMENT

The integument system of the proboscideans consists of skin, hair, nails, soles of the feet, and glands. These elements have different functions, such as thermoregulation, waste excretion, and protection against environmental threats. Because of their rather thick skin, the term “pachyderm” (“thick skin”) is usually heard when referring to proboscideans.

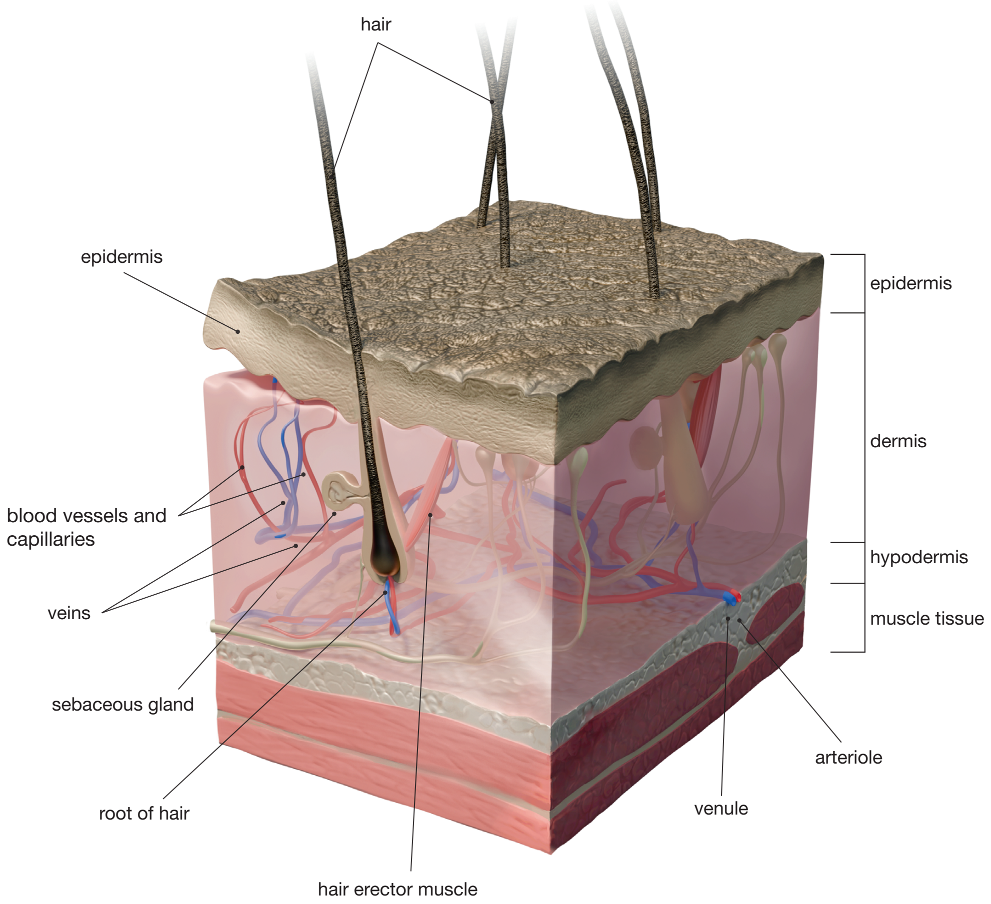


Figure 18. Elephant skin in detail
Simplified cross section of the skin of an extant elephant, showing its layers, main components, and associated structures.

Skin

The skin of proboscideans is very sensitive because it is very rich in nerve endings, and it is by far the largest organ of proboscideans. It accounts for about 8% of the body mass in living elephants, which means that in a fully grown African savanna elephant it can weigh over 500 kg and reach a surface area of 30 m^2, while in the smaller Asian elephant the skin weighs around 300 kg, with a surface area of about 20 m^2. The enormous weight of the skin is largely due to its extreme thickness over most of the animal's body. The thickest skin is found on the head and back, where it can measure from 2.5 to 4 cm. The skin is significantly thinner on the trunk, breast, groin, and legs, measuring approximately 1 cm in thickness. The thinnest skin is that of the ear (1.8 mm on the medial side) and the perianal area (< 1.8 mm). The skin color of both living genera is usually gray, but it may appear brown/reddish or very light to completely dark gray, resulting from wallowing in mudholes. Although extremely rare, true albino elephants have been reported, and depigmented skin in pink patches especially evident in the face, proboscis, ears, abdomen, and temples is common in Asian elephants, especially in Sri Lankan populations.

Hair

Despite people thinking that elephants are hairless animals, they are in fact fully covered with hairs varying in lengths and densities. Predominantly, hairs are present around the eyes, ears, chin, and genitals, and at the end of the tail. Juvenile elephants are hairier than adults, and Asian elephants have considerably more hair than their African counterparts, while a few extinct species such as the woolly mammoth (*Mammuthus primigenius*) possessed a very long and dense coat of fur. In living elephants the body hairs are bristle-like and of a black or grayish-brown color. In woolly mammoths, however, the underhairs were colorless; overhairs and guard hairs ranged from colorless to dingy yellow, bright red/orange, and brown. Hair dimensions in living elephants vary, depending on type and location, but they normally measure about 0.5 mm in diameter and about 20 mm in length, though some can be up to 2 mm thick and 40 cm long in the tail, while those on the proboscis can attain a length of about 25 cm or more. In the extinct woolly mammoth, the hair lengths were approximately from 60 to 105 cm in the case of overhairs; from 12 to 56 cm in guard hairs; and from 5 to 11.5 cm in underhairs. Elephant hair under the microscope shows scales with concentric circles on their cross sections. As other mammals, elephants have vibrissae, that is, whisker type of hairs, located on the trunk tip and used as tactile sensors.

Nails and soles

Both toenails and soles are made of highly keratinized tissue. The thin layer of epidermis (skin) that extends from the base of the nail wall onto the surface of the nail is known as cuticle. The soles and toenails grow approximately 5 to 10 mm per month. The sole surface is cracked, showing a mosaic of fissures that are also visible in the footprints. The forefoot prints of living elephants are relatively circular, whereas those of the hindfoot are oval shaped – narrower and more elongated – but both are about the same length (Fig. 19). Adult male *Loxodonta africana* and *Elephas maximus* footprints usually measure about 55 cm and 45 cm in length, respectively, while the largest footprints produced by individuals of the Petit Loango Reserve *Loxodonta cyclotis* population reach a length of 35 cm at most. Those of female elephants are, on average, about one-quarter smaller than that of males in *Loxodonta africana* and a sixth in *Elephas maximus*. It must be stressed that fossil footprints attributable to *Mammuthus* and *Palaeoloxodon* dwarf the modern elephants' footprints, measuring up to 70 cm. African elephants and woolly mammoths have generally 4 toenails on the front foot and 3 on the hindfoot, while the Asian elephant has typically 5 and 4 toenails, respectively

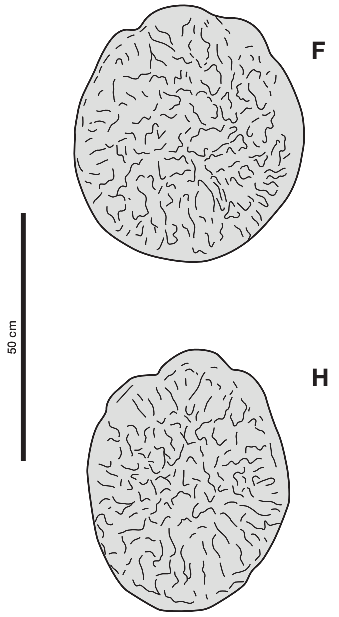


Figure 19. African savanna elephant (*Loxodonta africana*) footprints F: forefoot and H: hindfoot.

Glands

Cutaneous glands of living elephants include the temporal, mammary, and interdigital. However, unlike the vast majority of mammals, elephants do not possess true sweat glands, although the interdigital glands appear to be similar to human eccrine sweat glands. The temporal gland, also known as the musth gland, is the most specialized; it is a modified facial apocrine sweat gland that is unique, among extant mammals, to elephants. It is located subcutaneously on either side of the face under 2 cm thick skin, just halfway between the eye and ear. Frozen mammoth carcasses demonstrated the presence of a musth gland also in this species. Indeed, based on the morphology of temporal fossa, it can be inferred that this gland was probably present in most fossil proboscideans. The gland is composed of numerous lobes and lobules divided by fibrous connective tissue arising from a robust capsule. The temporal gland has a central

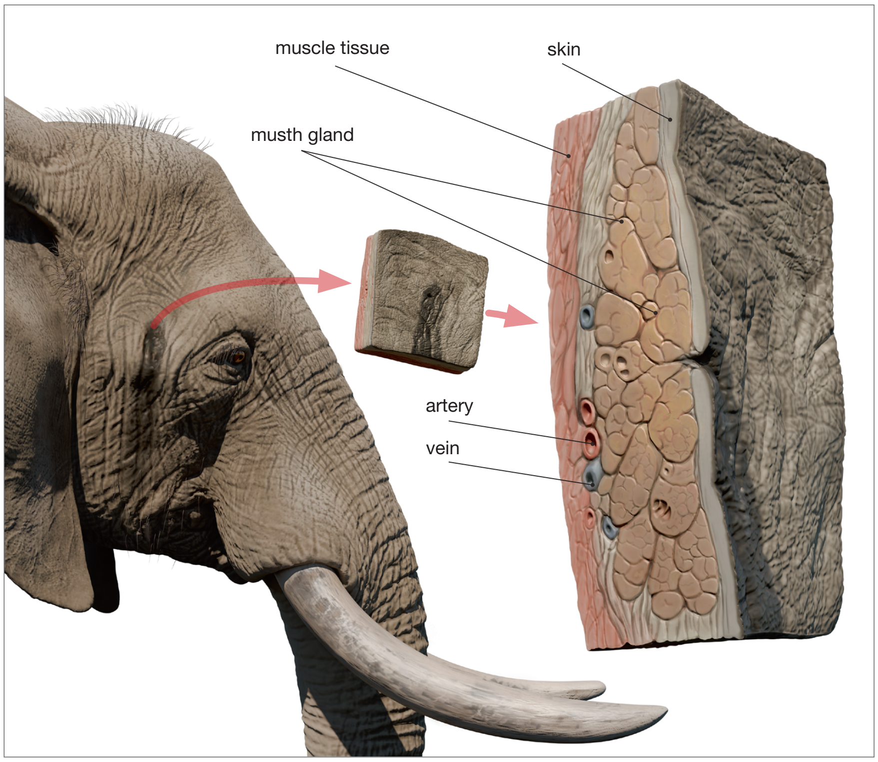


Figure 20. Musth gland anatomy

The illustration shows the location of the musth gland in the temporal region of the elephant's head, accompanied by a cross section of the gland, highlighting its details. From the outside to the inside, we can see the skin, the glandular tissue arranged in lobes, the arteries, veins, and muscle tissue. When it flows through the external opening of the gland, the musth fluid stains the elephant's head. The gland is present in both sexes and does not exist in any other animal. It is a feature that may be unique to advanced proboscideans.

chamber of 1.5 to 2.5 cm in length, leading to an external orifice, secreting oily substances containing cholesterol, phenol, cresol, and farnesol. The musth gland secretion releases into the air chemical messages (detected by males) in the form of very small, scattered particles that are detected and deciphered by the Jacobson organ. The behavioral function of musth gland is discussed on page 66.

Elephant cows have the most human-like mammary glands anywhere in the animal kingdom, located on the chest between the forelegs. The nipples, as in other mammals, are circular. The composition of the milk produced during lactation by both *Elephas* and *Loxodonta* cows is, on average, 80–82.4% water, 5.1–5.2% protein, 9.3–15.1% fat, 0.7–0.9% ash, and about 3.6% lactose, which is similar to that of humans.

MUSCULAR SYSTEM

Muscles are divided into two major types: voluntary and involuntary. The former are associated with the skeletons (skeletal muscles), with which they form an integrated functional system, and are controlled by the animal's will to produce movement. The latter are located in the internal organs, such as the heart and intestine, and are activated independently of the animal's will, often producing rhythmic contractions. Except for its size and proportion, and excluding the highly specialized trunk, the skeletal muscular system of elephants is structurally arranged in a similar way to that of other land mammals. Almost every skeletal muscle is present in two "mirror copies" (left and right) on either half of the body, for a total of 197 pairs, corresponding to 394 individual muscles. This is considerably less than what is found in the human body, which contains about 650 individual skeletal muscles. This is due to the fact that humans possess more numerous muscles in their forearm and hand that are not present in elephants. For example, the pronator quadratus and pronator radii teres, which allow us to rotate our wrists, were lost in the evolution of elephants, so their hands (manus) are fixed in a pronated position, with the soles facing backward. African and Asian extant elephants possess virtually the same muscles, with the exception of an extra muscle overlaying the splenius (a broad muscle in the back of the neck), present only in the Asian elephant, where it gives additional strength and leverage to support the head. The muscle scars found on the bone surface of fossil proboscideans, especially in elephantiformes, indicate that they possessed a skeletal muscle system similar to that of living elephants.

CARDIOVASCULAR SYSTEM

The heart of elephants and sirenians is unique in having a bifid (double-pointed) apex instead of the single-pointed heart of the rest of mammals. The relative size of the elephant heart is comparable to that of other mammals, representing about 0.5% of the body mass. This means that the heart of an adult African elephant could weigh as much as

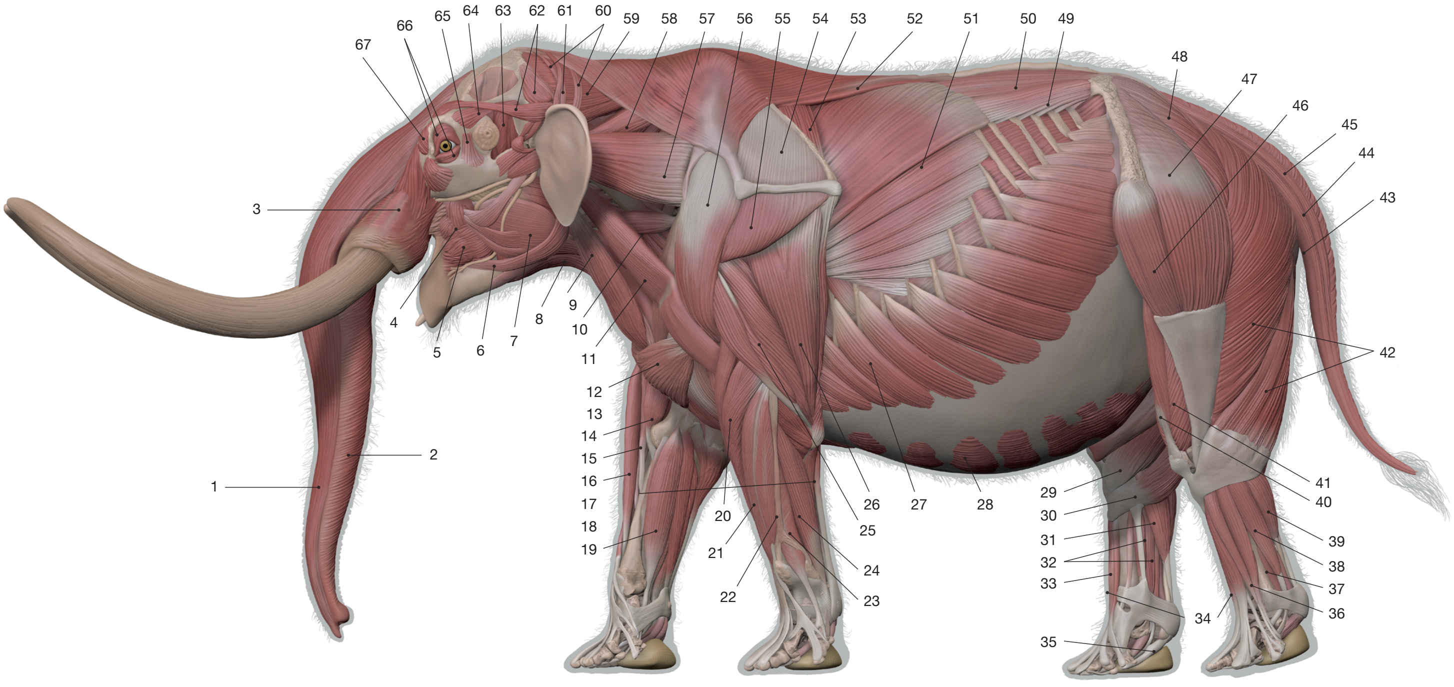


Figure 21. Proboscidean superficial muscles
Muscle restoration of an advanced proboscidean, the American mastodon (*Mammut americanum*), showing superficial and major contour muscles. This reconstruction is based on comparative anatomy of extant elephants, as detailed by Shoshani and Tassy (1996), Marchant and Shoshani (2007), and Goldfinger (2004).

PROBOSCIDEAN MUSCLE NAMES

1	Maxillolabialis	18	Palmaris longus	35	Plantaris	52	Trapezius
2	Pars rimana	19	Flexor carpi radialis	36	Peroneus longus	53	Rhomboid
3	Nasolabialis	20	Brachioradialis	37	Peroneus brevis	54	Infraspinatus
4	Orbicularis oris	21	Extensor communis digitorum	38	Soleus	55	Deltoid scapular portion
5	Depressor labii mandibularis	22	Central tendon	39	Plantaris	56	Deltoid acrominal portion
6	Platysma	23	Extensor digit quinti	40	Rectus femoris	57	Omotransversarius
7	Mentalis	24	Extensor carpi ulnaris	41	Vastus lateralis	58	Levator anguli scapulae
8	Sternomandibularis	25	Triceps brachii, lateral head	42	Biceps femoralis	59	Splenius
9	Sternomastoideus	26	Triceps brachii, long head	43	Sacrococcygeus ventralis	60	Auriculo occipitalis
10	Longus colli	27	External abdominal oblique	44	Sacrococcygeus lateralis	61	Rotator
11	Brachiocephalicus	28	Pectoralis ascendens	45	Sacrococcygeus dorsalis	62	Auricularis
12	Pectoralis descendens	29	Vastus medialis	46	Tensor fasciale latae	63	Temporalis
13	Pectoralis transversus	30	Sartorius	47	Gluteus medius	64	Occipitofrontalis
14	Biceps brachii	31	Gastrocnemius	48	Gluteus superficialis	65	Postorbicularis
15	Pronator teres	32	Flexor digitorum profundus	49	Iliocostalis	66	Omotrachelian
16	Extensor carpi radialis	33	Tibialis cranialis	50	Longissimus	67	Preorbicularis
17	Flexor carpi ulnaris	34	Extensor digitorum longus	51	Longissimus dorsi		

Table 8. Detailed list of muscles located beneath the skin of an advanced proboscidean.

30 kg, but the largest extinct proboscideans may have had hearts approaching 100 kg, the weight of a very large man! The normal heart rate of extant elephants when resting and standing ranges from 24 to 50 beats per minute (bpm), with an average of approximately 35 bpm, which is considerably less than that of humans. The mean systolic arterial blood pressure in elephants is 178.6 ± 2.9 mm Hg, and the diastolic pressure is 118.7 ± 3.1 mm Hg, being both about 50% higher than typical human values. Both the heart rate and blood pressure increase if the animal is lying down. About 113 liters of blood were measured in a 3,200 kg female zoo Asian elephant known as Tulsa, which corresponds to 3.5% of the animal's total weight, about half that of humans. However, it is probable that Tulsa was an overweight animal and that the true blood-volume-to-body-weight ratio in elephants would be greater than 4% in healthy animals.

RESPIRATORY SYSTEM

Nasal passages

Elephants can breathe routinely voluntarily through both the trunk and mouth. Nasal breathing is used most of the time, however. When they are at rest, the respiratory rate is about 5 breaths per minute. The trunk nasal cavity and the nasopharynx are divided into two symmetrical nasal passages, separated by a continuous, fibromuscular nasal septum, which is extremely resistant against collapse. The nasal passages diameter remains constant in the distal ¾ of the proboscis length, while in the remaining proximal ¼, approximately below the level of the eyes, it becomes wider, allowing the elephant to hold water if necessary. As the nasal passages bend backward and enter the cranium, their diameter decreases. On the dorsal portion of the nasopharynx there are multiple ducts that lead to the air-filled sinuses systems in the cranium.

Throat

The throat begins with the pharynx, a cone-shaped tube that is divided into the oropharynx and nasopharynx by the short soft palate, which supplies a passage for the respiratory gastrointestinal tracts. Unique to elephants, and probably many other extinct proboscideans, is the presence of a pharyngeal pouch located on the caudal part of the oropharynx, between the base of the tongue and the front of the epiglottis. The hyoid apparatus supports this pouch, and when empty, it may be used as a resonating chamber. Also, the pharyngeal pouch can store around 4 liters of water for several hours, without hindering breathing or feeding. This water can be either used for drinking or dousing the body in times of stress. The larynx is a short tube formed by the thyroid cartilage, epiglottis, vestibular fold, arytenoid cartilage, vocal fold, and cricoid cartilage. The larynx produces the typical infrasonic vocalizations of elephants (see p. 87), produced by vocal-fold oscillations, driven by air flow. The trachea is about 30 cm long and around 7.5 cm in diameter, which is three times larger than that of humans. It is supported by very large cartilaginous incomplete rings, overlapped and reinforced by a dense fibrous membrane.

Lungs

The lungs of elephants are rather small for their body size, representing only 0.5% of the body mass, which is significantly less than the average ~1.1% found in other land mammals. However, it is not known if the relative lung capacity of elephants is also low compared to that of other land mammals, as no study has been carried out yet to measure lung volumes in these enormous animals. Land mammals' lung volume increases nearly isometrically with size. Maximum lung capacity usually represents around 8% of the body size. If this ratio holds true also for elephants, a 6 tonne fully grown African savanna elephant bull would have a total lung capacity of about 480 liters, a figure that would have been tripled in the largest known fossil proboscidean! Of course, during quiet breathing the lungs would be filled only about half their maximum volume. These estimates, however, are probably somewhat too high, judging from the relatively low weight of elephant lungs. The left lung is slightly smaller than the right one, to make space for the heart. Unlike the rest of mammals, the pleural space is obliterated by connective tissue. This tissue is directly attached to the surfaces of the inner side of the ribs and diaphragm, and therefore elephants rely on direct muscular action to expand their lungs. The peculiar anatomy of elephant lungs and pleura enables them to breath when swimming, using their trunk as a snorkel and keeping their body completely submerged in water, a situation that exerts a large hydrostatic pressure on the lungs.

DIGESTIVE SYSTEM

As in the rest of mammals, the mouth or oral cavity is the place where food begins its journey through the digestive system. It is equipped with several structures that initiate the first processes of digestion, such as salivary glands, teeth, and tongue, the latter weighing up to 14 kg in the African savanna elephant. Elephants' saliva serves as a lubricant for coarse ingesta. The stomach is simple (not chambered) and cylindrical shaped. It is quite different from that of humans and also from that of ruminants (such as cows and deer), because elephants are hind-gut fermenters, so the stomach is mainly a large food-storage area, rather than being the primary site of digestion. The stomach of living elephants can store more than 60 kg of food in adults. The liver of elephants has from 2 to 3 lobes, although two are more commonly found. The liver can weigh more than 80 kg in large bulls and about half that in cows. There is no gall bladder, but bile capillaries are present. The small and larger intestines together can reach a length of about 35 m and can contain over 360 kg of food. The digestion of food is carried out thanks to the symbiotic bacteria that are housed in the part of the large intestine called the cecum. However, only about 44% of the food eaten is digested; the rest is expelled with the feces.

REPRODUCTIVE SYSTEM

The reproductive system of living elephants is unique among mammals in several aspects. The vulva hangs low be-

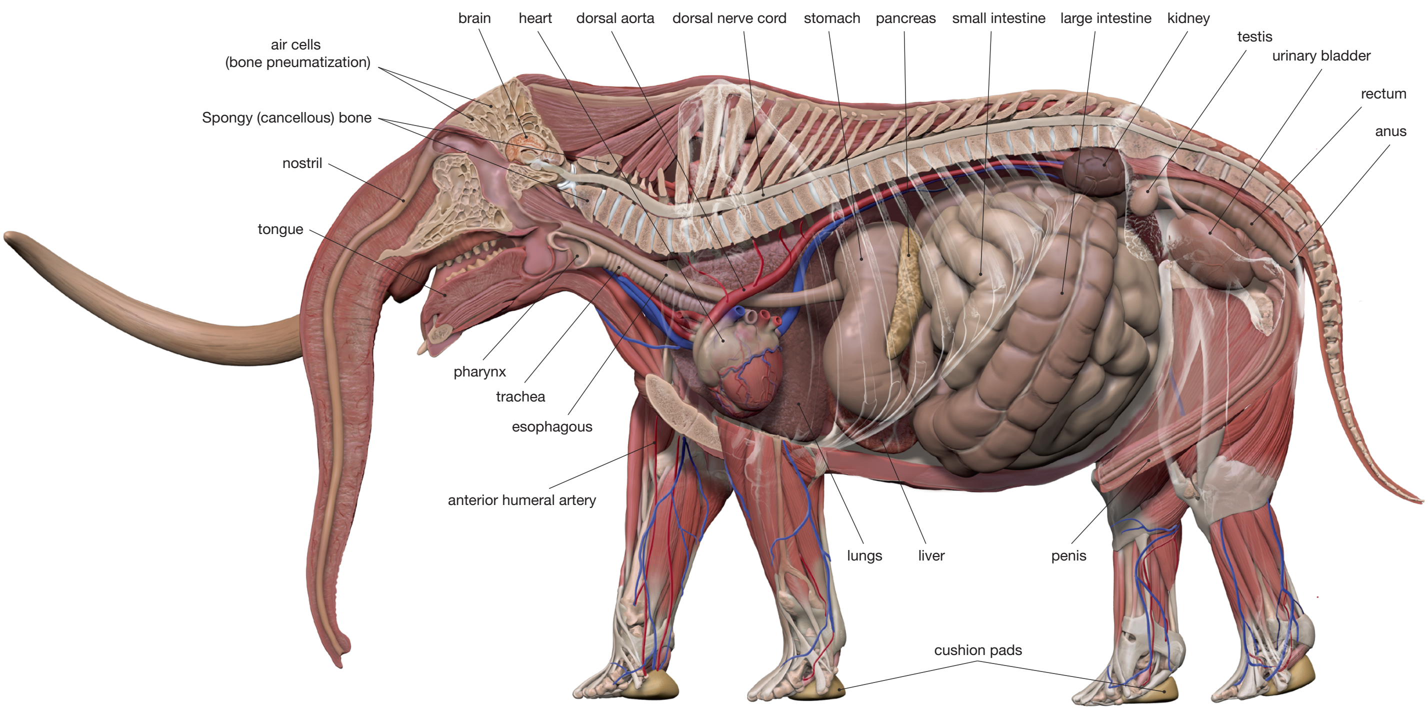


Figure 22. Internal organs of a proboscidean
A simplified reconstruction of the internal organ systems of an advanced proboscidean, the American mastodon (*Mammut americanum*), based in part on the work of Shoshani and Tassy (1996).

tween the hind limbs, reducing the falling distance for the newborn, as the cow gives birth while standing. The clitoris is very pronounced and relatively large, being about 40 cm long, and is controlled by a levator clitoris muscle that helps direct the penis into the urogenital canal during sexual intercourse. This canal represents the distal common passageway for the genital and urinary tracts and is very long, measuring from 1 to 1.4 m in length. The vagina is a folded structure and measures about 30 x 15 x 10 cm. The ovaries are relatively small in adult cows, measuring about 7 x 5 x 2.5 cm.

The male testes are located intraabdominally – a primitive characteristic – and are peculiar in not having a pampiniform plexus for temperature regulation. Given their internal location, the testes maintain, however, a constant temperature of about 36°C. The seminal vesicles are enormous and during breeding periods may contain more than 1.5 liters of fluid each. However, during ejaculation only a small portion is secreted, about 25–150 ml. The penis of adult African savanna elephants is a large organ, capable of measuring over 100 cm in length and 16–20 cm in diameter at its base and weighing up to 27 kg. The end opening is curiously *Y*-shaped. A pair of large levator penis muscles makes the male organ very mobile, a necessary requirement, considering the low position of the female genitalia and the forward opening of the vagina. In full erection, the penis takes on an S shape and can be retroverted during copulation.

URINARY SYSTEM

As in the rest of mammals, the urinary system consists of the kidneys, ureters, bladder, and the urethra. Anatomical differences in these organs between the Asian and African savanna elephant are minor. The elephant kidneys are lobulated and may contain 8–12 renal lobes. Extant adult elephants normally urinate between 5 to 11 liters in one go, and a total of about 50 liters during a day. This last amount corresponds to approximately one-third of the daily water intake.

ENDOCRINE AND IMMUNE SYSTEMS

Along with the nervous system, the endocrine system controls and regulates many of the body's functions. As in all mammalian species, the endocrine system of elephants consists of several glands that produce chemical messengers called hormones, which are released into the bloodstream to act each on a specific organ in another part of the body. In fact, only the cells of the target organ of each gland possess the right receptors to respond to the specific hormone they produce.

Pituitary gland

The pituitary is commonly called the master gland, as it controls the function of most of the other endocrine glands. It is located at the base of the brain next to the hypothalamus. This gland produces, among other secretions, hormones that control growth, blood pressure, and the ovarian cycle in females. In many migratory animals, changes in pituitary activity, possibly triggered by environmental changes, appear to be related to their seasonal behavioral patterns, a possibility that has been suggested also for elephants, which can perform annual migrations between dry and wet seasons.

Pineal gland

The main role of the pineal in vertebrates is in the production of melatonin and in regulation of the circadian rhythm, the so called internal "clock." However, it is still unknown how sleep-wake cycles are controlled in elephants.

Thyroid gland

The thyroids secrete the thyroid hormone, essential for the control of metabolism, and calcitonin. The latter is responsible for calcium regulation and is an antagonist of the parathyroid hormone, in that it tends to decrease the concentration of calcium in the blood.

Adrenal glands

Hormones produced by these glands are corticosteroids or mineralocorticoids. High levels of these hormones are produced when the animal is physically stressed, as during the dry season and lack of rainfall in the wet season.

Endocrine pancreas

The elephant pancreas is found adjacent to the duodenum as in other mammal species. The endocrine function of the pancreas is related to glucose metabolism, and in humans, pancreatic dysfunction is usually related to diabetes. However, no metabolic syndromes associated with endocrine pancreatic dysfunction have been reported so far in elephants.

Like all mammals, proboscideans possess a sophisticated immune system consisting of highly specialized organs and cells with the task of defending the body from external agents (viruses, bacteria, fungi, parasites), which can cause infections and serious diseases. All the components of this defensive system are scattered in different areas of the body and communicate with each other thanks to interconnections called lymphatic vessels. Specifically, the immune system consists of specialized cells, called white blood cells or leukocytes, capable of circulating in both blood and tissues, and lymphatic organs, such as bone, thymus, and lymph nodes. Most notably, the immune system is capable of producing the so-called immunological memory. This allows the immune system to remember the pathogens with which it comes into contact the first time, in order to react more quickly and intensely in case of subsequent contact.

CENTRAL NERVOUS SYSTEM (BRAIN)

The brain is one of the most fascinating organs of living elephants, especially for its large size and complex cortical anatomy, which, in analogy with that of humans, suggest complex cognitive capacities. In elephants, the cerebrum is very wide and flattened (Figs. 23 and 25), with the two hemispheres not covering posteriorly the large cerebellum, which is dorsally exposed. This is a primitive trait among mammals that contrasts markedly with the highly convoluted cerebellar and cerebral cortex, a well-known derived characteristic of the brain of mammals, including humans. The most developed parts of the proboscideans' forebrain are the temporal lobes; they show great complexity and are

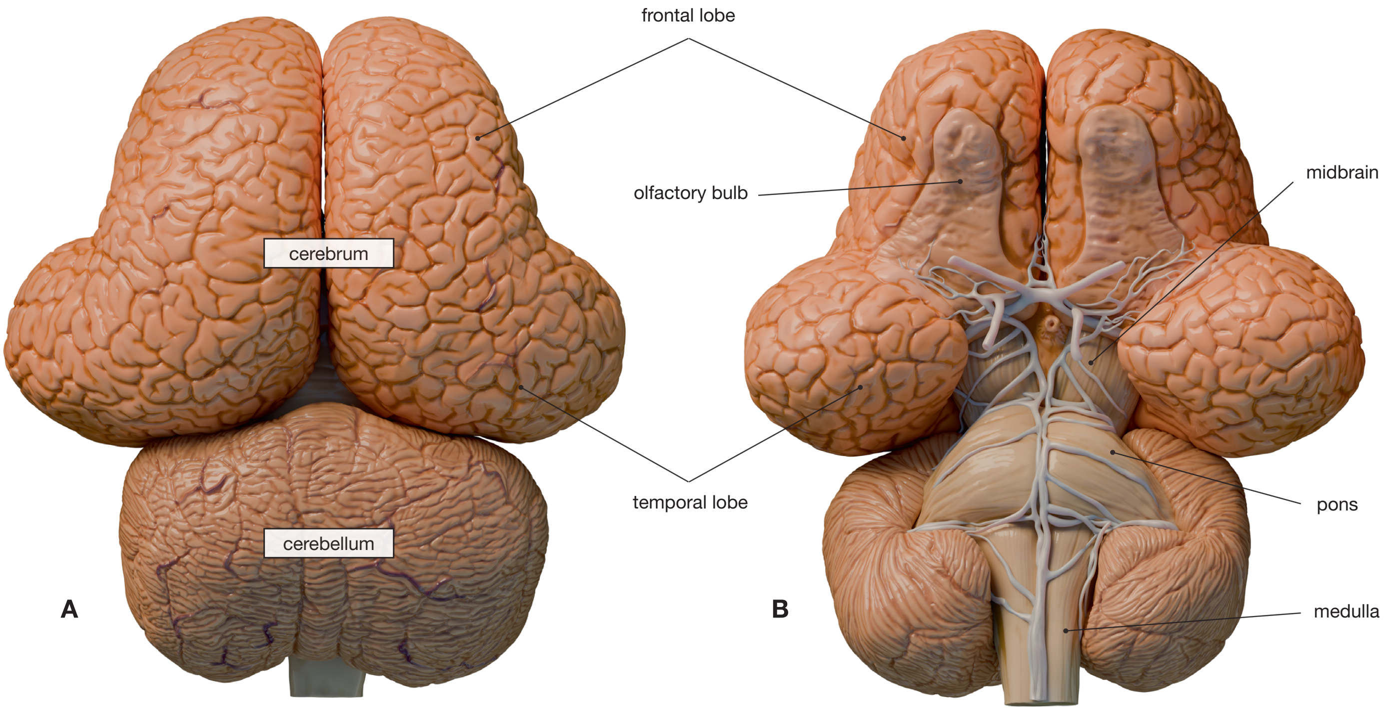


Figure 23. Elephant brain gross morphology

Whole brain shown in dorsal (A) and ventral view (B), highlighting major structures, based on the drawing by Shoshani et al. (2006).

exceptionally large, probably being relatively larger than in any other land mammal known. The olfactory bulbs are also particularly well developed. These brain regions are associated in humans with hearing, learning, memory, and smell, among other functions, and explain why elephants have a great sense of hearing, a sharp sense of smell, and notable memory. On the contrary, elephants have poor vision, especially in bright light, which is in accordance with their ill-defined occipital lobe. In terms of size, the brain of living elephants is huge, ranging in mass from 4 kg to more than 5.5 kg, which is up to four times heavier than that of humans. Some extinct proboscideans had even larger brains (judging from their cerebral cavity), and contrary to what is widely believed, the largest brains of all time, are probably to be found among proboscideans, not whales. Considering just living species, the largest brain is indeed that of sperm whales (*Physeter macrocephalus*), with an average weigh of 7.8 kg; this value is, however, less than the estimated brain mass of the fossil elephant *Palaeoloxodon antiquus* (Table 9). Actually, the largest recorded sperm whale brain had an exceptional mass of 9.2 kg. However, it would not be surprising if future fossil findings of giant elephants of the *Palaeoloxodon* and *Mammuthus* genera revealed an enormous cranial cavity, indicating brains much larger than that.

Intelligence and encephalization quotient

The particularly large brain of modern elephants might justify the common opinion that "elephants are highly intelligent animals." However, rigorous tests to corroborate this assumption are still pending. Nevertheless, recent researches on elephant cognition are providing impressive results. These studies showed that elephants possess indeed great spatial and long-term memory, creativity when solving problems, ability to classify human ethnic groups by odor and clothing color, and the capacity to use and construct elementary tools (such as using sticks in their proboscis to scratch their backs, or placing branches under their feet to avoid sinking in soft ground), and they exhibit unique behaviors (see Behavior section below, p. 83). Brain size, however, is not indicative of high intelligence per se. For example, despite an elephant's brain containing a staggering 257 billion neurons – three times more than in the human brain – 97.5% of them are localized in the cerebellum, while an elephant's cerebral cortex, which is twice as large as that of human, holds only one-third the number of neurons present in the latter. This suggests that the main factor of intelligence is likely the number of neurons in the cerebral cortex rather than sheer brain mass. An easier and quite common method used to measure potential for intelligence is to calculate the so-called encephalization quotient or EQ. The EQ is the ratio between the actual mass of the brain of a given individual and the mass of the brain that is expected for an animal of its size. In this system, an EQ with a value equal to 1.0 is considered "average" or "pro-medium." So, a higher or lower value could be identified as higher or lower than expected brain size and therefore potentially greater or reduced intelligence than the average. It should be noted that a reliable body mass estimation, when this cannot be directly measured (see p. 32 for further details for extinct species), is critical to obtaining accurate EQ values.

When calculating the EQ of a species, several precautions should be taken in order to obtain reliable data, though this is neglected in some studies. For instance, it is quite common to see an EQ calculated by comparing the brain size of an individual with the body mass of other specimens, or averaged values, thus producing inaccurate results. Another aspect that should be taken into consideration is ontogeny, since a negative allometry is observed between brain and body mass during growth. Extant elephants at birth possess a brain of 2.5 kg – which is about half the mass of that of adults – weighing, however, up to 60 times less than fully grown animals. The brain then reaches about 90% of its adult weight between 5 and 15 years, and after that it develops very slowly until ~30–35 years. Thus, the EQ values obtained for very young individuals are relatively much higher than those of adults. For this reason, it is recommended to include only adult individuals when measuring encephalization indexes. Also, sexual dimorphism is an important source of variability when determining EQ in elephants. In general female mammals have/had proportionally larger brains than males, which results in higher EQ values. So, when known, the sex of the individual for which EQ is calculated should be indicated. Despite all the above uncertainties, and keeping in mind that EQ is not straightforwardly related with intelligence, the evolution of the proboscidean brain can be reconstructed by observing how EQ changed through time and in different lineages.

Based on the revised data – especially with regard to body mass estimates among others – presented in this book, EQ shows a threefold increase between primitive Eo-Oligocene proboscideans and living elephants (Table 9). Surprisingly, this is much less than what is generally reported in the literature. It should be noted that among early proboscideans, *Palaeomastodon* shows only a slightly higher EQ than the more archaic *Moeritherium*, a fact probably related to distinct lifestyles. The highest EQ observed among proboscideans is close to 2, which is well below that of modern humans, who surpass 6. On the other hand, there are some extreme cases, including the tiny *Palaeoloxodon* from Spinagallo Cave, Sicily, and *Mammuthus primigenius* from Yuka. Both possess exceptionally high EQs of 4.09 and 3.49, respectively. In the case of the dwarf *Palaeoloxodon*, this can be explained mainly by its paedomorphic condition, which implies an extreme reduction of the pneumaticity of cranial bones, making its skull similar to those modern big-brained juvenile elephants. As for the Yuka female mammoth, its high EQ is due to its ontogenetic age, somewhere between six to nine years. As previously noted, at this age the brain in modern elephants reaches around one-ninth of the adult weight. Assuming a similar pattern for the mammoth, a fully grown Yuka of about 2.8 tonnes would have an EQ of 1.68, which is comparable to modern female elephants. The factors that drove brain size increase during proboscidean evolution are still poorly understood, though there is an apparent correlation with body mass. Ecological factors also seem to have played a significant role.

PROBOSCIDEAN ENCEPHALIZATION QUOTIENTS

Taxon	Specimen	Sex	Endocast volume (ml)	Brain mass (g)	Body mass (g)	EQ
Moeritherium lyonsi	BM 9176	N/A	240	210	150,000	**0.59**
Palaeomastodon beadnelli	NHMUK 8464	F?	771	681	650,000	**0.66**
Mammut borsoni	MCFFM-CLB-1	F	5,133	4,554	8,000,000	**0.73**
Mammut americanum	MCZ 11106	F	4,630	4,107	4,000,000	**1.08**
Stegodon insignis	MNHN-A952	N/A	3,838	3,404	2,000,000	**1.48**
Mammuthus meridionalis	–	N/A	5,828	5,171	7,000,000	**0.91**
Mammuthus columbi	TMM 45609-1	M?	6,232	5,529	9,500,000	**0.78**
Mammuthu primigenius	Yuka (juvenile)	F	5,025	4,458	885,000	**3.47**
Mammuthus primigenius	Expected parameters for adult Yuka	F	5,578	4,948	2,800,000	**1.68**
Palaeoloxodon antiquus	Pian dell'Olmo	M	9,000	7,986	11,500,000	**0.99**
Palaeoloxodon sp. nov. (Spingallo Cave)	MUST N2	F	1,800	1,595	168,000	**4.09**
Palaeoloxodon tiliensis	AMPG T189/96	N/A	3,000	2,660	1,300,000	**1.57**
Palaeoloxodon sp. nov. (Puntali Cave)	MGG skull N9	M?	4,260	3,779	2,000,000	**1.64**
Palaeoloxodon sp. nov. (Puntali Cave)	MGG skull N13	M?	4,300	3,814	2,000,000	**1.65**
Loxodonta africana	Nancy	F	–	4,420	3,505,000	**1.28**
Loxodonta africana	Kenya	F	–	4,050	1,793,300	**1.90**
Loxodonta africana	–	F	–	4,100	2,160,000	**1.68**
Loxodonta africana	–	F	–	4,000	2,537,000	**1.46**
Loxodonta africana	Ngaruka	M	–	5,712	6,654,000	**1.04**
Loxodonta africana	–	M	–	5,300	5,550,000	**1.10**
Elephas maximus	Iki	F	–	4,550	2,267,430	**1.80**
Elephas maximus	Tulsa	F	–	5,220	3,216,000	**1.61**
Elephas maximus	Missy	F	–	5,000	3,450,400	**1.47**

Table 9. Cranial capacity, brain mass, body mass, and EQ (after Manger 2006) in selected adult proboscideans. Data collected and corrected in part from Shoshani et al. (2006) and Benoit et al. (2019). Only specimens with reliable data are included. Extinct species brain masses were obtained using Benoit's (2015) equation, who found that meningeal arteries and veins in proboscideans occupy from ~13–14% of endocranial cavity. Abbreviations: F, female; M, male; N/A, not available.

PERIPHERAL NERVOUS SYSTEM (PNS) AND ORGANS OF SENSE

The peripheral nervous system (PNS) comprises the nerve fibers, both sensory and motor, that connect different organs in the body to the central nervous system. As is typical for amniote vertebrates, modern elephants possess twelve pairs of cranial nerves (12 right and 12 left, they are numbered with Roman numerals from I to XII), so called because they emerge directly from the brain, and 40 pairs of spinal nerves, which instead emerge from the spinal cord. The longest cranial nerve is the vagus (X), which extends to the large intestine, innervating various organs, including the voice box and the heart. The most distinctive cranial nerve of modern elephants, however, is the trigeminal (V), since it is the one that supplies the main sensory and motor fibers of the proboscis. In particular, a branch of the n. trigeminal passes through the infraorbital foramen of the maxillary bone, to give rise to the proboscideal nerve, together with a branch of the facial nerve (VII). The presence of a large infraorbital foramen, such as that observed in elephants, for the passage of the maxillary branch of the n. trigeminus and blood vessels supplying the trunk, can therefore be considered as an indication of the presence of an elephant-like proboscis in fossil forms. This trait is consistently present in all fossil elephants (family Elephantidae). Basal elephantimorphs, such as mammutids and gomphotheres, had two smaller infraorbital foramina, rather than a large one. The dorsal infraorbital foramen probably gave way to a dorsal branch of the maxillary complex of the n. trigeminus, indicating

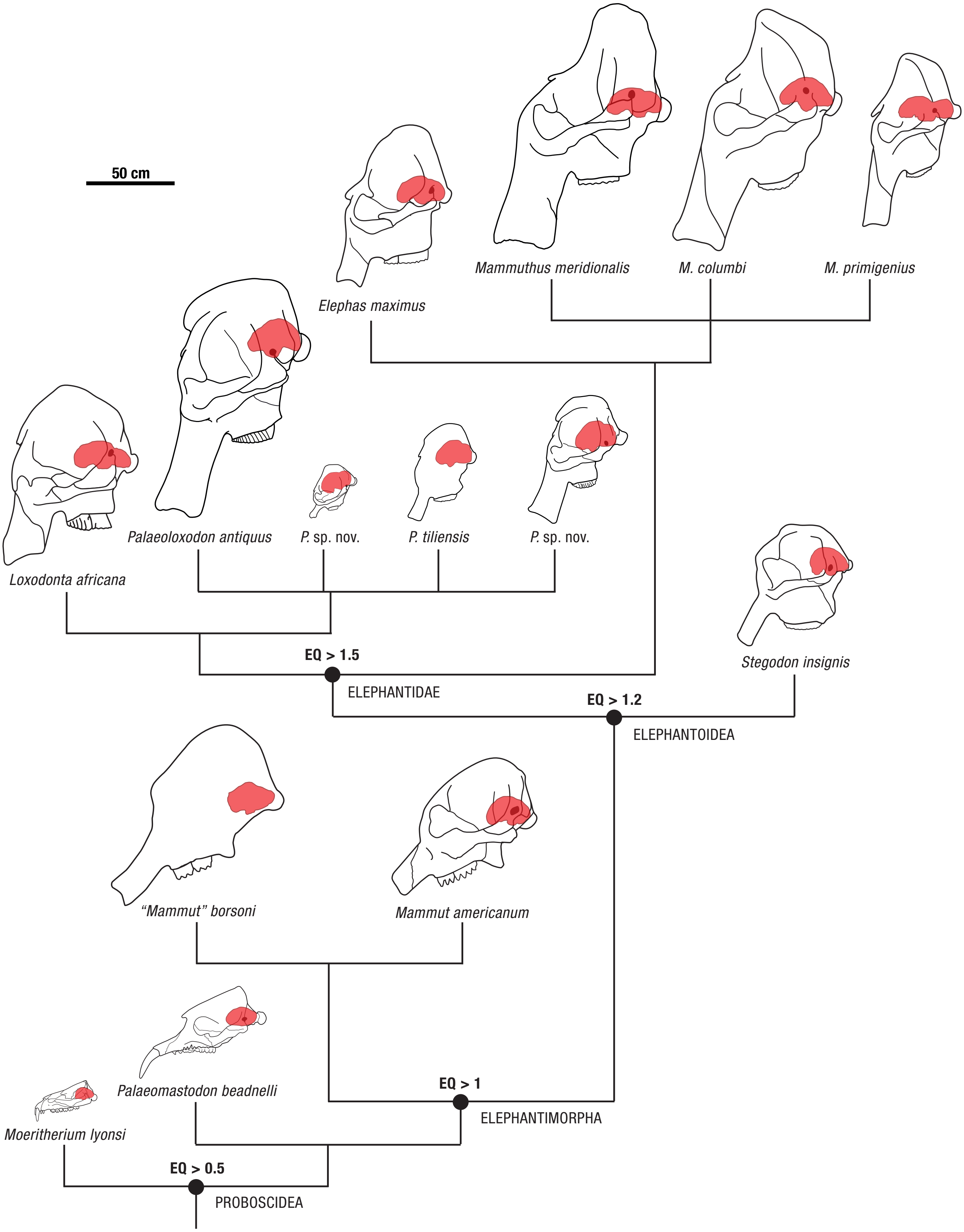


Figure 24. Change in encephalization quotient during proboscidean evolution
Phylogeny of extant and extinct proboscideans for which brain and body mass estimates are available. The endocranial cavities are depicted in orange color. All crania are shown at the same scale. Abbreviations: EQ, encephalization quotient.

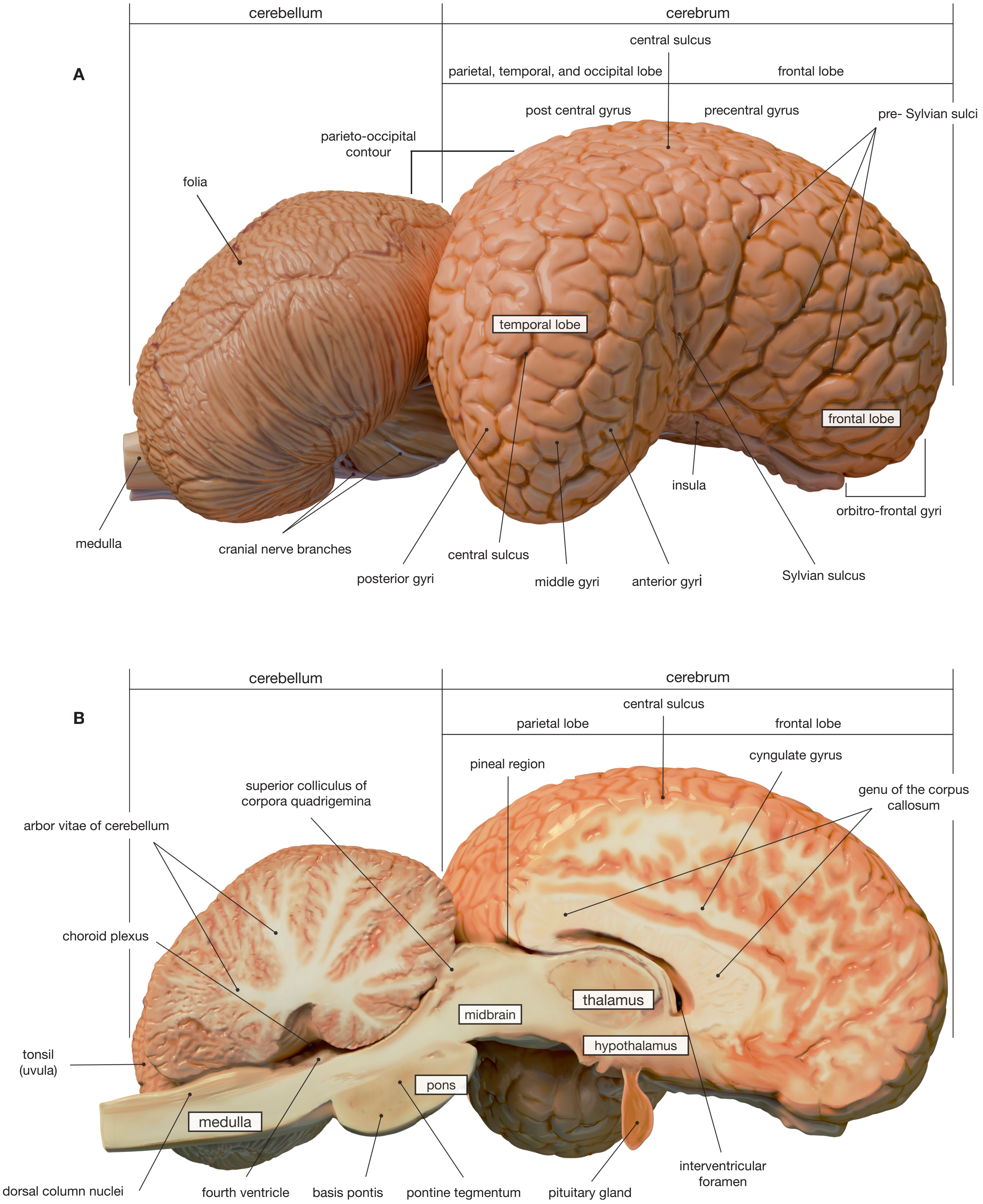


Figure 25. Elephant brain detailed morphology

Lateral (A) and midsagittal (B) views of elephant brain, highlighting small structures, based on the drawing by Shoshani et al. (2006).

that elephantimorphs also had a well-developed proboscis. On the contrary, in the more primitive, non-elephantimorph proboscideans, the infraorbital foramen is markedly smaller, indicating that the maxillary complex was less developed, probably reflecting a much smaller or absent proboscis.

Sight

Sight is probably the least developed sense in elephants, as evidenced by the poor development of the occipital lobe of the brain. Based on the density of light receptors in the retina, modern elephants appear to have visual acuity, i.e. the ability to distinguish minute details of an image, which is about half that of humans and similar to that of a dog. Experiments with elephants in captivity have shown that their vision is good enough to allow them to manipulate objects, even small ones, with the tip of the long proboscis, about 2–3 meters from the eyes, and to recognize visual displays by conspecifics during social interactions. On the contrary, at distances exceeding 20–30 meters their visual capacity seems to perform rather poorly. Elephants are active both during the day and at night, and, like nocturnal animals, they have a particular structure at the back of the eye, called the tapetum lucidum, which reflects the photons entering the eye, improving night vision, and causing the typical eye glare at night. The perception of color vision in elephants is not well understood, although analysis of the visual pigments of the retina suggests that they possess dichromatic vision like most mammals, as opposed to the trichromatic vision in humans. The elephant's large head and side-set eyes limit binocular vision, which can be achieved by bringing the eyes together and raising the head slightly.

Hearing

Hearing in elephants is particularly acute, and it is possible that the strong pneumatization of the skull bones contributes to enhance this sense. Elephants are known to produce infrasonic sounds, like those made by whales, to communicate with conspecifics over great distances. They are in fact capable of hearing very low frequency sounds down to about 17 Hz, which are inaudible to humans. Conversely, elephants are unable to hear sounds with frequencies above 12,000 Hz, while a dog can perceive sounds up to 44,000 Hz. The absence of a secondary lamina within the inner ear suggests that the ability to perceive low-frequency sounds first evolved in elephantimorphs. Elephants are very good at locating where sounds are coming from. It has been suggested that the greater the space between an animal's ears (the interaural distance), the better the ability to localize sound because the difference in time and intensity of a sound reaching each ear can be used as a cue to locate the sound source. The large ears are also very mobile and are directed so as to better locate the origin of the sounds.

Olfaction

Smell is probably the most highly developed sense in elephants. The inhaled air goes up along the proboscis, heating rapidly until it reaches the large nasal cavity, where dozens of turbinates, thin bony or cartilaginous plates, support the olfactory membrane and the nasal mucosa. Numerous olfactory receptors reside in the olfactory membrane, each capable of recognizing a different volatile molecule. The axons of the olfactory neurons then send their stimuli to the large olfactory bulb located in the anterior part of the brain. Elephants have an incredibly high number of olfactory receptors, each coded by a specific gene. At present about 2,000 olfactory receptor genes have been detected in the genome of extant elephants. This is far more than any mammal known.

Like most mammals, elephants have a sort of supplementary olfactory system, represented by the vomeronasal organ (VNO), also called Jacobson's organ, located at the base of the nasal cavity and communicating through a bony canal with the palate. The VNO plays an important role in the perception of nonvolatile chemical stimuli, especially pheromones. These molecules are involved in social and/or reproductive behavior in many mammalian species and are found in body fluids, such as sweat, urine, or temporal gland secretions. To allow this organ to detect the presence of pheromones produced by another individual, the elephant uses the tip of the proboscis as a probe and then places it inside the mouth in contact with the palatine orifices of the VNO. Genetic markers for the presence of a VNO have been detected in the woolly mammoth, and this organ was likely present in other, if not all, proboscideans. As a matter of fact, a VNO is present in most afrotheres. The absence of a VNO in Sirenia, on the other hand, is interpreted as due to their secondary aquatic adaptation. The presence of a well-developed VNO in elephantids would therefore exclude a recent aquatic origin for elephants, or even for proboscideans as a whole, as instead suggested by some authors.

Taste

The ability to discriminate flavors is essential to avoid taking potentially irritating or harmful foods. Elephants possess taste organs located both in the dorsal epithelium of the posterior soft palate and on the tongue. This are represented by the so-called taste buds, also present on the human tongue, which send their taste stimuli to the branches of the lingual and glossopharyngeal nerve. Elephants are able to detect sweet, sour, and bitter substances.

Touch

The sense of touch in elephants is particularly developed in the tip of the proboscis, which is not by chance considered the "hand" of the elephant, also due to its incredible manipulative capacity. The skin covering the tip of the trunk is in fact richly innervated and has a high density of sensory corpuscles, some connected to special vibrissae. The extensive sensorimotor specializations of the proboscis allow for delicate manipulations of objects large and small, and contain a high number of Pacinian corpuscles, specialized cells that can pick up very tiny vibrations. The ability of elephants to detect seismic vibrations suggests that similar cells are also present in the soles of the feet (see p. 87).

DISEASES, PATHOLOGIES, AND PARASITES

Elephants, despite their size and strength, are surprisingly prone to a range of diseases, both infectious and noninfectious. To make matters worse, they often mask signs of illness until it is advanced. The early signs can be subtle: they might eat less, produce different-looking droppings or urine, interact less with the herd, have trouble getting up, stretch oddly, yawn more often, or even twist their trunks in unusual ways. Interestingly, because of how they are built, elephants are not able to cough or vomit, two basic ways other animals clear out infections.

Infectious diseases are caused by pathogens, harmful microorganisms such as bacteria, viruses, fungi, and parasites, that invade the animal's body and disrupt normal functions. Some microorganisms are capable of infecting a wide range of animal species, while others show a high degree of host specificity, infecting only certain species. such as particular pathogens that may affect only proboscideans. Once a pathogen enters the animal's body, it can multiply rapidly. The immune system works to fight off the infection, but its success depends on the type and strength of the pathogen, as well as the animal's overall health. Non-infectious pathologies result from other factors such as genetics, environment, nutrition, aging, or the animal's own immune system.

INFECTIOUS DISEASES

Viruses

One of the most serious threats to elephant health today, both in the wild and in captivity, is a virus called elephant endotheliotropic herpesvirus, or EEHV. With a fatality rate around 85% if untreated, EEHV causes severe internal bleeding in the heart, liver, intestines, and tongue. Young Asian elephants are most affected, but cases have been seen in African elephants too. EEHV belongs to a group of viruses known as Beta-herpesviruses, classified under the genus *Proboscivirus*, and it's not a recent invader of the elephant body. In fact, genetic studies suggest that the first deadly encounter between EEHV and elephants occurred millions of years ago, and that the two have essentially evolved together. Early symptoms like fatigue are vague, and death can occur within 1–3 days. In advanced stages, elephants may show swollen tongues or cyanosis (bluish skin). The virus damages blood vessels, leading to fluid leakage and circulatory shock, the actual cause of death in many cases.

Rabies, one of the oldest recorded diseases in medical history, affects the brain and spinal cord and it is nearly always fatal. In extant elephants, the disease is typically caused by a lyssavirus, a member of the Rhabdoviridae family, which is the same group of viruses responsible for rabies in dogs and other mammals. When an elephant contracts rabies, the symptoms can be dramatic and distressing. The animal drools excessively, stops eating, and vocalizes far more than usual, often in loud, anguished-sounding calls.

Anthrax, another deadly threat, is caused by the bacterium *Bacillus anthracis*. While it tends to make headlines due to its potential use in bioterrorism, anthrax is a naturally occurring disease in wildlife, including elephants. One particularly chilling case was documented in 1947, when an ivory worker became infected while handling a tusk. Only later was it discovered that the tusk had come from an elephant that had died of anthrax. This rare case highlights how, even long after death, an infected elephant can pose a risk to humans.

Bacteria

When it comes to bacterial threats, one of the most significant diseases elephants can face is tuberculosis, or TB. This ancient disease, which also affects humans and many other animals, has been recognized in elephants for over two millennia. In most cases, it is caused by the same culprit behind human TB: *Mycobacterium tuberculosis*. TB in elephants poses unique challenges, not just because it can be hard to detect early, but also because of the potential for transmission between animals and even humans working closely with them. It is a serious issue for both conservationists and zoo veterinarians around the world.

Salmonellosis, a common infectious disease in humans, can also affect elephants, causing gastroenteritis that may progress to septicemia. Often triggered by stress or immune suppression, it leads to symptoms like diarrhea, lethargy, and colic. While frequently reported in captive elephants, its occurrence in wild populations is rare and not well documented.

Noninfectious diseases

Not all health problems elephants face come from germs. Just like people, elephants can suffer from chronic, noninfectious diseases, especially as they get older. Their massive size and long lifespans mean their bodies take a lot of strain over the years. Foot problems are especially common and can be painful and debilitating. Dental disease is another frequent issue, given that elephants go through several sets of teeth in their lifetime, and trouble chewing can have a big impact on overall health. Age-related conditions like osteoarthritis (a degenerative joint disease), atherosclerosis (hardening of the arteries), and even arteriosclerosis can also show up in aging elephants.

Parasites

Elephants, like most four-legged mammals, are hosts to a range of ectoparasites, which are parasites that live on the body's surface. These include various arthropods like biting lice, ear mites, and ticks. One tick, *Amblyomma tholloni*, is not just annoying, it can transmit a disease known as heartwater, caused by the bacterium *Ehrlichia ruminantium*. Flies and mosquitoes also bother them constantly. Horseflies (tabanids), for example, pierce the skin and can spread various diseases. Botflies are especially gruesome. Their larvae burrow into the elephant's skin, or even the gut, nasal passages, or tusk base, causing a severe condition known as myiasis. If the tusk pulp is exposed, it can lead to infections and the formation of "ivory pearls," mineral buildups also seen in fossils.

Not all parasites are harmful. One particularly quirky example involves moths in parts of Asia that hover near an elephant's eye, not to hurt it, but to drink its tears. These moths are after the salt in the tears, and elephants are just one of several herbivores they visit. For reasons still unclear, carnivores don't seem to interest them; perhaps herbivore tears really are tastier!

As for internal parasites, elephants are susceptible to many types of worms, particularly nematodes (roundworms) and trematodes (flukes), which inhabit the digestive system, liver, lungs, muscles, or arteries. Symptoms include diarrhea, weight loss, anemia, and low protein levels.

Among the microscopic parasites, one of the few protozoans known to cause illness in elephants is *Trypanosoma evansi*. This single-celled organism can lead to a disease known as surra, which affects many domestic and wild animals.

Anomalies and injuries

Elephants can suffer life-threatening injuries from predators, fights (see p. 86), or rough terrain. The trunk is especially vulnerable, as severe damage can be fatal. Tusks can also break during combat or heavy use. If the fracture reaches the tusk's pulp, infections can develop, sometimes triggering ivory pearl formation.

Foot injuries from sharp terrain can lead to ulcerative pododermatitis, a potentially fatal secondary infection. Dental anomalies are known, including extra or missing tusks and deformed molars. Since elephant teeth form over long periods, they are vulnerable to deformation from external forces during development when they are not yet fully calcified.

GENES AGAINST CANCER

Tumors are the result of uncontrolled cell duplication caused by a mutation to reproduction control genes. In long-living animals, the opportunities to acquire a cancerous mutation during life are comparatively high, and this is also the case for large organisms, as they are made of a greater number of cells. Proboscideans would thus be expected to show a rather high incidence of tumors, with respect to smaller mammals. Surprisingly, this is not the case in living elephants, despite their large body size and long lifespan. As a matter of fact, elephants have been found to be cancer resistant, with an estimated mortality due to cancer of 5%. This percentage is indeed quite low, if compared for instance with that observed in humans, who show an 11–25% cancer mortality. The explanation for this lower-than-expected rate seems to be related to the possession of multiple copies of tumor suppression genes in the genome of elephants. These genes are involved in DNA repair, resistance to oxidative stress, control of cellular growth, aging, and death. In humans, the majority of tumors are associated with mutations in these control genes. Scientists found that the duplication of tumor-suppressing genes predated the origin of large-bodied proboscideans, as it occurs in several other afrotherian groups, regardless of body size. The possession of genes to suppress cancer in the ancestors of proboscideans was probably one of the key factors that allowed the latter to develop gigantisms during their evolutionary history.

NUTRITION

Although some cartoons may have prompted us to think that elephants may sometimes crunch and swallow smaller animals, they are actually strictly herbivorous. Differently from most large ungulates, however, elephants include an enormous variety of plant food in their diet. This alimentary diversity concerns both the species on which they feed and the part of the plant that is eaten. Of course, to sustain their massive body, adult elephants cannot be too picky, as they need a daily intake of around 100,000 kcal, corresponding to an average of 160–200 kg of wet food per day. Calves start to taste their first plant food at around 5 months of age, while continuing to suckle their mother's milk until 6 years, when they became fully weaned. During this very long period, young elephants learn to recognize the various plants on which their adult diet will be based, and how and when to get them.

We know from direct observation, stomach and drops content analysis, and isotope ratio studies that extant elephants are mixed feeders, which means they include both browsing (leaves, twigs, barks, and roots) and grazing (grass), but also fruits in their diet. The amount of browsing and grazing changes throughout the year, depending on food quality, which is in turn related to the alternation of dry and wet seasons. In the dry season elephants rely mostly on browsing, while in the wet season grazing predominates. Leaves have a greater percentage of proteins and fatty acids than grass, except when the latter is fresh and green, at the beginning of the wet season. The African forest elephant, however, is mostly a browser throughout the year, also including a large percentage of fruit in its diet. During the dry season, food quality drops, especially protein content, and elephants visibly lose condition. Indeed, in case of severe drought mortality can be very high. Elephants feed on more than 100 different plant species, though the bulk of their diet at any time can be represented by only ten to 20 species. The plants eaten change, obviously, according to their seasonal availability. They also carefully avoid poisonous species. The groups of plants making up the diet of the three extant elephant species is surprisingly rather similar, despite their different habitats and tooth morphology, and includes grasses (family Poaceae), sedges (Cyperaceae), palms, (Palmae), and legumes (Fabaceae). Elephants spend nearly half of the day foraging, eating an amount of wet food corresponding to about 4% of an individual body weight. This is nearly half the requirement for smaller herbivores, such as cattle, and is linked to the fact that large mammals are better at keeping their body heat. Elephant herds usually feed during the coolest time of the day, avoiding the warmest hours, during which they rest in the shade. Their size, their long, flexible trunk, and their efficient masticatory apparatus allow elephants to reach and feed on a large variety of plant matter. They can select the part of the plant to eat, so they may strip off leaves from a branch or get to the inner, soft part of the stem, removing the external bark. Elephants also frequently uproot small plants, using the proboscis to get to the succulent roots, but before eating them they remove the dust by beating them against the foreleg. A trunkful of food is about 75 g on average, with 2 to 4 trunkfuls per minute. Even in semidesertic areas, such as in Namibia, elephants are never too far away from water pools. An adult elephant needs, in fact, around 150 liters of water a day, so they are constrained to the steady availability of permanent water sources. When the mineral content of the food is not adequate, elephants will search for a supplementary sodium (Na) intake at specialized licks where they ingest the salt rich soil.

RECONSTRUCTING ANCIENT DIET

Most woody plants today use the C3 photosynthetic pathway, which produces a relatively lower C-13-to-C-12 ratio than that in C4 plants (grass). As we already said, these different ratios are reflected in the carbon isotopic composition of herbivores' teeth and bones. Isotopic analysis of fossil proboscidean enamel suggests that C4 plants formed a significant portion of the diet of many African and Asian proboscideans since the Late Miocene, with the only exception represented by deinotheriids, who appear to have remained predominantly browsers. Similar studies on extant elephants would indicate a diet dominated by C3 browse, though they also have a significant C4 grass component in their feeding habit. The C3-dominated isotopic signal of extant elephants could be explained by the fact that they mostly rely on the higher protein content of woody plant matter to produce tooth and bone collagen, the source of carbon in isotopic analysis.

ENERGETICS

The energy requirement per unit of body weight of a big animal is less than that of a small animal. In other words, bigger animals require proportionally less energy than smaller ones, and thus, large animals possess a lower metabolic rate than smaller animals.

Animals' surface area with similar body proportions scales to a scaling exponent of 0.67. This led early authors in the 19th century to conclude that in warm-blooded animals, such as mammals and birds, metabolic rate is proportional to the surface area because these animals need to produce enough heat through metabolism to balance heat loss over body surfaces. Later, in 1947, a pioneer in the field of animal energetics, Max Kleiber, found that animal respiration rates apparently scale more closely as the 0.75 power of body size and concluded that the basal metabolic rate (BMR) can be calculated as BMR = 70 x Mass0.75 kcal/day. But, since the average daily rate of energy consumption is much higher than the animal's BMR, the field metabolic rate (FMR) is usually twice the BMR. It should be noted, however, that recent studies have shown that the classic three-quarter power law (Kleibers's law) of metabolic rate is not universal and there can be significant variation among species. These differences can be related to taxonomic and/or physiological differences among others. Living elephants consume about 4% of their body mass of wet food (1% of dry food) during 16–18 hours of daily foraging, and lactating females can consume one-half more. Thus, a fully grown, 6,000 kg bull African elephant eats about 240 kg of wet plant material (60 kg dry) and a lactating female weighing 3,000 kg consumes 180 kg of fresh forage (45 kg dry). It has been found that a fully grown, 4,000 kg Asian elephant needs about 100,000 kcal of digestible energy per day. However, because of the less nutritious food of elephants compared to small mammals, regression equations underestimate the energetic caloric intake by about 50%. In any case, for estimating the approximate FMR of extinct small proboscideans, the classical metabolic rate formula might be used. So, the tiny 6 kg *Eritherium* would have had an estimated FMR of 537 kcal per day, and the FMR of a 235 kg *Moeritherium* would have been about 8,402 kcal per day. On the other hand, estimating the FMR of a very large proboscidean is problematic, because if body-size increase is the result of an increased cell number, then the metabolic scaling slope should be 1 (isometric scaling), whereas, if body-size difference is the result of an increased cell size, the expected slope is then around 0.67. Different studies have shown that in closely related species within birds and mammals, the metabolic rate slope scales with an average of ~0.9. Also, despite an elephant weighing about 150,000 times the weight of a mouse, its cells are only twice as large, so the cell size might not differ from living elephants and larger extinct species, and thus, the metabolic rate in giant proboscideans, particularly elephantids, should scale closer to 1 than to 0.67. So, assuming that a very large mammoth weighing 10,000 kg had a similar size-specific metabolic rate scaling similarly to other closely related taxa, and also assuming it had access to nutritious food comparable to that of living elephants, its FMR would have been approximately 230,000 kcal, and it would have needed about 365 kg of wet vegetation (91 kg dry) per day. A colossal proboscidean of 16,000–18,000 kg would have needed around 560–620 kg (140–155 kg dry) of food and would have had an FRM of 350,000–390,000 kcal per day.

REPRODUCTION

GESTATION

Elephants have the longest gestation period of all mammals, surpassing those of the titanic whales. The average elephant pregnancy in both Asian and African elephants lasts approximately 22 months, or about 660 days. Because of several studies that have shown that gestation period scales with body mass in mammals, the incredibly long gestation period of modern elephants might have been surpassed by the largest proboscidean species where females and males were 2 to 3 times heavier than those of living relatives. It should be noted that precocial mammals (those able to move autonomously in their environment after birth), like elephants, have, on average, somewhat longer gestation periods than altricial mammals (those born in a completely helpless condition). However, while the scaling relationships of precocial and altricial mammals are distinct, they retain similar scaling exponents at about 0.19. This suggest that the largest proboscideans' gestation times would last for more than 27 months or 800 days. However, phylogenetic constraint (an evolutionary pattern in which a trait is limited on the future evolutionary pathways that have been set by previous adaptations) appears to play a very restrictive role. So, the gestation period of giant proboscideans would probably not have significantly differed from that of their extant relatives. Recent studies that have used statistical methods that account for the phylogenetic structure of the dataset have shown that the scaling pattern is about 0.08 to body mass in closely related taxa.

The extremely long gestation period observed in the closely related proboscideans and very small (2–5 kg) living hyraxes (their pregnancy can last more than 7.5 months or > 225 days) appear to confirm this and suggest that the scaling exponent of 0.08 may work with reasonable precision for estimating the gestation time of most extinct proboscideans. This would indicate that the largest female proboscideans weighing between 6 and 9 tonnes – 2 to 3 times larger than living relatives – would have a gestation period as long as 23 and 24 months, respectively, while that of the smallest and diminutive basal proboscideans *Eritherium azzazorum*, would last about 12 months. However, since basal proboscideans are separated by tens of millions of years, the scaling exponent of 0.08 might overestimate the actual gestation period of very primitive proboscideans. Using a more generalized scaling exponent of 0.18, about 8 months of gestation period is obtained for *Eritherium*, comparable to similarly sized extant hyraxes. On the other hand, teeth growth and seasonal restrictions suggest that woolly mammoths (*Mammuthus primigenius*) would have a comparable but slightly shorter gestation period, compared with extant elephants, of about 20 months.

PLACENTA AND EMBRYONIC MEMBRANES

Within the uterine cavity of its mother, the baby elephant is surrounded by a set of membranes, which are essential for its development during the 22 months of gestation. The so-called extra-embryonic membranes are tissues produced by the fetus itself, and include the chorion, allantois, and amnion, and a vestigial yolk sac. The chorion is the outermost of these membranes and is in direct contact with the maternal uterus, contributing to the formation of the placenta. The amnion is the innermost and lies closest to the fetus. It grows to enclose the fetus like a balloon. It is filled with a clear fluid, which is generated from many sources, such as the fetal skin, the amnion itself, the fetal kidneys, and possibly the fetal vessels. The fluid-filled allantoic sac, a space formed by two layers of the allantois, lies between the chorion and the amnion. It contributes to the formation of the umbilical cord. The umbilical cord is long (range: 65–170 cm), between 4 and 6 cm in thickness, and usually marginally attached in the term placenta. The development of the elephant fetus requires an efficient means of obtaining nutrients and eliminating waste products. This is achieved by establishing an efficient interface between its vascular system and that of its mother. That interface is the placenta, which forms from the chorion and allantois (chorioallantoic placenta). The elephant placenta is large, heavy, and bulky. Weights of term and immature placentas vary between 8.3 and 22.2 kg. The type of placenta formed by elephants is called "zonary," as the villous tissue that connects the placenta with the maternal blood encircles the equatorial zone of the chorionic sac, though this band might be interrupted at one or more points on the circumferences. In humans, the chorionic villi are instead concentrated in a specific placental disc, and the placenta type is known as "discoidal." The umbilical cord (formerly the body stalk) enters the middle of the placenta. Blood from the fetus reaches the placenta via the umbilical arteries. These arteries branch out into numerous small vessels that terminate into capillary loops in the ends of the placental villi. There, oxygen, nutrients, and wastes are exchanged between fetal and maternal blood, which bathes the villi. A single umbilical vein drains fetal blood back to the body of the fetus. The placental villi are immersed in a place filled with maternal blood that exits from open-ended spiral arteries of the endometrium.

In addition to its primary goal of facilitating transport between mother and fetus, the placenta is also a major endocrine organ that secretes several fetal hormones that have profound effects on both fetal and maternal physiology. The essential features of the fetal membranes and placenta are already established by the first month of intra-uterine development, and they undergo only slight modifications during the subsequent course of gestation. There is great similarity between the placentas of the two African extant elephant species, which is one of the reasons why they can hybridize and deliver a healthy baby. The structure of the elephant placenta shows many similarities to that of sea cows (sirenians), and represents one of the characteristics that has been used to link these two mammalian groups within the clade Tethytheria.

SEXUAL MATURITY

Depending on local climate, resource availability, nutritional conditions, and population densities, the age at first ovulation in the living female elephants varies tremendously, from as young as 7 to as old as 23 years. However, the age of first conception typically occurs in the early teenage years (11–14 years), making the age at first calving, therefore, ~13–16 years. Males are capable of sperm production at a similar age (~14 years), but are not likely to mate until their late twenties, or, more likely, mid-thirties, once they reach full social maturity. Females prefer mating with older males, and older males typically prevent younger males from mating. Although males do not have to be in musth to mate, musth elephants are more successful and sexually active.

MUSTH

Musth is a Hindi term derived from the Farsi (Persian) and Urdu word *mast* and means "intoxicated." When male elephants are in musth, their temporal glands bloat and secret chemical substances, while the elephants constantly dribble urine. This state has a strong impact on their behavior. For instance, they tend to show unpredictable conduct and are very difficult to control, so much so that in captivity they can attack their keepers or trainers and even kill them. In the wild, elephants in musth go through a period of intense aggression toward other males and sexual interest in estrous females, which allow them to perform most of the breeding.

Musth typically does not begin until males reach their late twenties, and the presence of older males can suppress the musth phases in younger males. It is usually only in captive populations or highly demographically disturbed populations that males younger than 25 enter musth.

Males in musth have been shown to investigate preovulatory females and their urine more than non-musth males, which would largely explain why males in musth are reproductively more successful. These are generally the most imponent and strongest males. Therefore, musth seems to be crucial in the social hierarchy among males and results in the transfer of the best and fittest genes to the next generation.

SEXUAL DIMORPHISM

Living elephants are sexually dimorphic in many aspects. The most notable characteristic is probably the body-size difference. Fully grown African savanna elephant (*Loxodonta africana*) males are, on average, about 23% taller and twice as heavy as females, whereas the differences in height at the shoulder and body mass in the Asian elephant (*Elephas maximus*) are, typically, about 15% and 50%, respectively. These great differences can be mainly explained by the later fusion of long bone epiphyses in males, which delay about 15 years more than in females. A marked difference in body size between males and females is not only restricted to living elephants but to the whole order of Proboscidea. A significant size variation within the same species has been reported in basal proboscideans, including *Moeritherium* and *Phiomia*, and in more derived proboscideans, the examples are uncountable. The current data indicates that the sexual size variation in deinotheriids, mastodonts, gomphotheres, amebelodontids, tetralophodontids, mammoths, and other extinct elephants, is comparable with what is observed in extant elephants. Some cases worth noting are found, particularly, in giant palaeoloxodonts, where sexual dimorphism in body size is extreme. In the case of European *Palaeoloxodon antiquus*, the males' long bones are about a third greater than females' in linear dimensions, indicating that males were about 2.5 times heavier than females. Even more notable differences appear to have been in its Indian cousin, *P. namadicus*, where males were 40% – or considerably more – taller than females. This may have had implications in several aspects of their behavior, particularly in sexual behavior (see p. 84). Another sexual dimorphic characteristic is found in the proboscidean skeletons. Males' skeletal elements are larger and more robust than those of females, and, in the case of upper incisors or tusks, these are much more massive and longer (and generally more curved) in bulls. For example, the combined tusks weight at the age of 40 in African savanna elephants is four times heavier in males, and in female mammoth tusks, their diameters and lengths are usually about the half of those of males. This implies that the premaxillaries of male proboscideans are/were generally wider in response to thicker alveolus. However, since the upper incisors of shovel-tusked proboscideans (Amebelodontidae) are mainly functional – used for procuring food – a strong sexual dimorphism in the upper tusks is not present (except for *Platybelodon*). It should be noted, however, that not all female proboscideans possess(ed) upper incisors. For example, in living female Asian elephants, the tusks are absent, and the same has been observed on the Sycilian dwarf *Palaeoloxodon*. But these cases are not unique to the elephant family because this has also been observed in more primitive groups, such as in gomphotheriids like *Gomphotherium angustidens*.

The morphology of the skull is also usually different between females and males. In African savanna elephant males, the head is rounded, whereas that of females is more pointed and has the orbits relatively closer to each other. In the case of extinct proboscideans, the braincase of several species within gomphotheriids and amebelodontids is more domed in males than in females, and the nasal aperture is slightly more anteriorly positioned in females, indicating that males possessed relatively longer proboscises. In living elephants, sexual differences in the mandible are not very evident, apart from their overall size and robustness. However, there appear to be some differences in extinct proboscideans with very long lower jaws, with males having somewhat longer mandibular symphyses, particularly evident in shovel-tusked proboscideans. The most distinguished osteological characteristic differentiating proboscidean sexes, as in other mammals, are the pelvic proportions. It is well known that the pelvic aperture in female elephants is proportionally larger than in males, and that the ratio of the minimum width of the ilium shaft to the maximum horizontal width of the pelvic girdle appears to be the best indicator of the sex of extinct elephants. Similar sexual dimorphism in pelves appears to also be present in mammutids, and probably in most extinct proboscidean clades. On the other hand, the external reproductive organs are different between the two sexes, as in other mammals. The genitals are not easily visible, and in normal circumstances it is very difficult to differentiate between the sexes using mere external appearance. The male testicles are located inside the animal near the kidneys, and the penis is enclosed in a sheath, whereas the female vulva, contrary to most ungulates, hangs low between the hind legs with the opening toward the ground. When an elephant urinates, the sex can be easily determined, but sometimes the clitoris of very young females can be mistaken for a penis. Females can also be distinguished by their breasts. Males' and females' breasts are identical; however, once a female becomes pregnant for the first time, the breasts became larger and more prominent permanently.

ONTOGENY

GROWTH

As noted previously, living elephants have the longest-known pregnancy of all mammals, with an incredible average gestation of around 660 days or 22 months. This enormous period of time makes their embryonic and fetal development exceptionally slow. The first steps of growth are so slow that the pregnancy can only be identified by ultrasound scans after 50 days of fecundation; even after 2 months, the embryo is as small as a human flea (0.04 g in weight). The first heartbeat is only detectable after 80 days, and the proboscis begins to be perceived after 90 days. The fore and hind limb joints are formed by day 103 and a few days later the brain is clearly depicted. After 150 days of gestation, the fetus grows rapidly, and from barely over 100 g at this point, it increases to over 500 g in weight in the next 30 days. By this stage the ears are already large, the temporal glands can be identified, and the full shape of the elephant becomes clear. During the next 16 months, the fetus continues growing to nearly 120 kg until birth. The size at birth, on average, is very similar between *Loxodonta africana* and *Elephas maximus*, measuring about close to 95 cm in height and 120 kg in weight (females might be barely smaller). On the other hand, African forest elephant (*Loxodonta cyclotis*) calves can be below 70 cm high and about 50 kg in mass. Shoulder heights of newborn calves of the Late Pleistocene woolly mammoth (*Mammuthus primigenius*) are estimated to be between 70 and 80 cm and probably weighed about 50–70 kg. On the other hand, the newborns of tiny dwarf *Palaeoloxodon* from Spinagallo Cave, Sicily, were only about 6–7 kg. Both genera of extant *Loxodonta* and *Elephas* rapidly increase their stature during the first ten years of life, and there is not too significant a difference in the growth rate between sexes – particularly in *Loxodont africana*. At this age, both cows and bulls approach and surpass 2 m in shoulder height and weight from 1,500 kg to over 2,000 kg.

AGE GROUPS IN AFRICAN SAVANNA ELEPHANT

Age category	Age interval	Tooth in wear	Skeletal fusion	Status
Calf	0–10	DP2/dp2–DP3/dp3	ilium, ischium, pubis fused at acetabulum in females	From birth until the animal has been weaned off its mother's milk completely
Juvenile / teenager	11–16	DP4/dp4–M1/m1	ilium, ischium, pubis fused at acetabulum in males	Males are capable of sperm production; first calving in females; animals with some social independece
Young adult / subadult	17–30	M1/m1–M2/m2	proximo-distal fusion of limbones in females; humerus distal, ulna proximal, tibia proximo-distal fusion in males	Sexually mature and growing
Adult / prime adults	31–45	M2/m2–M3/m3	Femur proximo-distal, humerus proximal fusion in males	Sexually mature; males still not fully grown but eligible for leadership; fully grown females
Senior / fully grown	46–60	M3/m3 in full use	Radius-ulna distal, metapodial, tarsal-carpal, pelvic edges, rib ends fusion in males	Fully grown males
Senile	> 61	Very worn M3/m3	Sacrum-innominate, vertebral plates fusion in males	Last and declining years; no longer sexually functional

Table 10. A correlation between the various age groups of African savanna elephants (*Loxodonta africana*) and key developmental indicators, including their stages of epiphyseal fusion, dental progression, ontogenetic ages, and associated social roles. Similar patterns are observed in other living elephants, and this was likely true for some extinct proboscideans, especially elephantids. These parameters provide a comprehensive framework for understanding the physical and social maturation of elephants, as well as their life history strategies. The table was developed based on the works of Sikes (1971) and Haynes (2017).

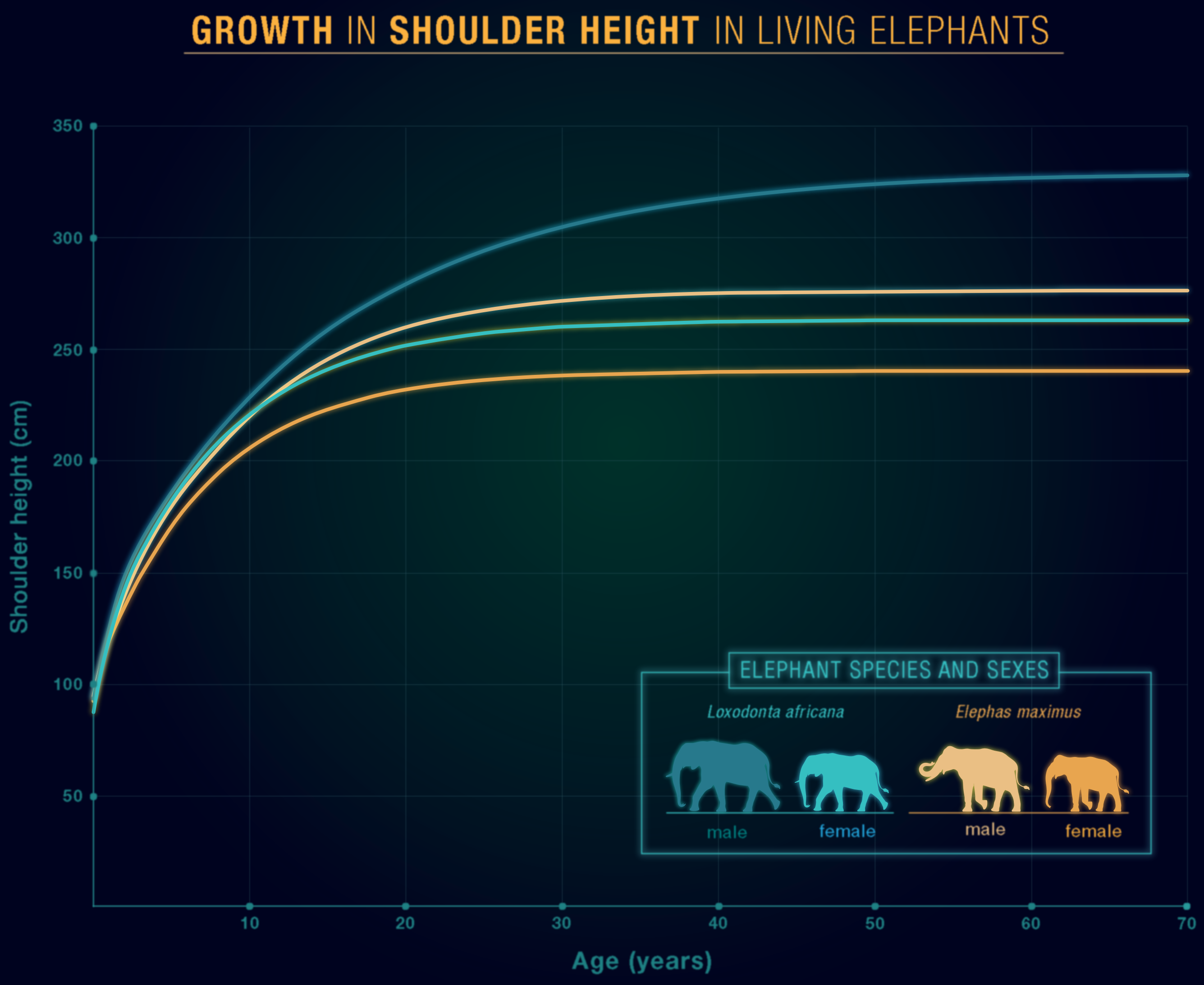


Figure 26. Theoretical von Bertalanffy growth curves for shoulder-height in post-natal male and female living elephants. Birth heights were based on Dale (2010). *Loxodonta africana* growth curves were based on Lindeque and van Jaarsveld (1993) equations, that, in the case of males, was suitably modified to match the optimal condition expected height of 320 cm at limb bone fusion (~45 years). *Elephas maximus* curves were calculated after Sukumar (2003) adjusted von Bertalanffy equations that have been corrected for wild elephants, assuming asymptotic heights (terminal heights) of 240 cm for females and 275 cm for males.

During the following five years, elephant growth rate is still quite fast and then dramatically slows down, especially in females (the slackening is more marked in *Loxodonta* than in *Elephas*), leading to a marked difference in stature between the sexes at around 15 years, where African savanna elephant bulls measure 234–263 cm at the shoulders and cows 220–240 cm, while Asian elephant males are around 235–245 cm high and females 213–220 cm. Then, females of both extant genera moderately and slowly increase their size until their middle twenties or early thirties once the limb-bone fusion is complete, although they might continue growing a little more till 35–40 years of age. On the other hand, males of African savanna and Asian elephants continue growing at a highly constant rate until about 30 years; after that the height increase rate drops greatly – especially in *Elephas maximus* – until the limb bones complete ossification at age 40–45 years (several years earlier in the Asian species). However, after this, males may continue to grow – exceptionally slowly – throughout their lifespan (particularly evident in *Loxodonta africana*). In good conditions the average fully grown shoulder height of a female African elephant is around 260 cm and the body mass is 3,000 kg, whereas those parameters in males are about 320 cm and 6,000 kg, respectively. On the other hand, fully grown Asian elephants shoulder height is typically 275 cm in bulls and 240 cm in cows, whereas body mass is 4,000 kg in males and 2,700 kg in females. Also, it has been found that in African elephants the back length is also closely correlated with age, particularly up to young adult individuals. The back-length growth pattern is comparable to that of shoulder height, and both measures reach to a similar asymptote, although in the case of females, the back length appears to increase slightly faster than shoulder height. The results of several studies focusing on the postnatal growth of living elephants have shown that von Bertalanffy function – a growth model that is widely used to study growth in vertebrates – can be

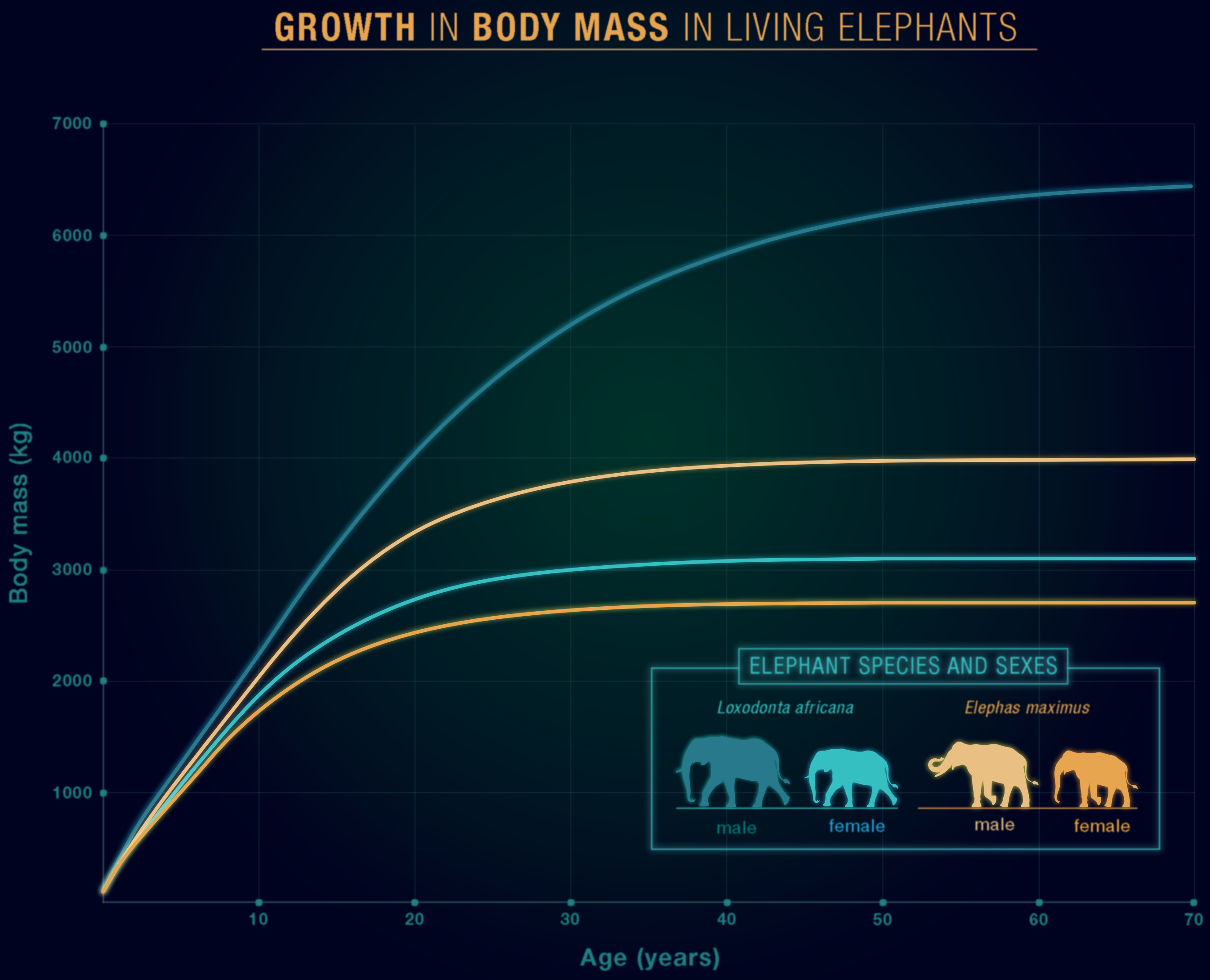


Figure 27. Shoulder-height growth curves in post-natal male and nonpregnant female living elephants. Birth weights were based on Dale (2010). Body masses were calculated from linear regression of cube root of body mass on shoulder based on Larramendi (2016) equations that produce very low average prediction errors and fit with von Bertalanffy curvilinear function.

fitted for elephants and provides very good results in determining rates of growth, especially for the post-weaning ages (three years onward). So, the entire growth curve – year by year – can be plotted on a graph (Fig. 26). The general equation for growth in shoulder height based on von Bertalanffy function is:

$$S_t = S_\infty \left[1 - e^{-K(t-t0)}\right]^{M}$$

where St is the size at time (t); S∞ is the asymptotic size (terminal or maximum size an animal can attain); K is the coefficient of catabolism, a rate constant; t is the age of the animal (in years); t0 is the theoretical age at which the elephant would have zero height (this constant is always artificial); M is the power of the function. On the other hand, among elephants there is a close relationship between body mass and shoulder height, and therefore, several formulas have been proposed in literature to estimate the body mass from shoulder height (Table 11). Apart from size increase, there are some physical modifications accompanying age. Most notable changes can be observed in the ears, where the upper edge begins forming folds, usually after 20 years of age. Also, as a consequence of intraspecific combats and by the contact of thorny plants, the ears tear at the edges, so an individual with very torn ears is probably old. Also, in the case of Asian elephants – most notably in Sri Lankan populations – the ear and trunk depigmentation also increases with age. As in other mammals, the skin becomes more wrinkled with age, and very old specimens have deep and plentiful wrinkles on the face, especially evident in African elephants.

MATHEMATICAL GROWTH EQUATIONS FOR LIVING ELEPHANTS

GROWTH IN SHOULDER HEIGHT

Aplicable to	Equation	Population	Reference
Males *Loxodonta africana* (1–30 years)	$SH_t = 451\ [1 - e^{-0.025\ (t - 11.84)}]$	Luangwa Valley	Hanks (1972)
Females *Loxodonta africana* (1–55 years)	$SH_t = 249\ [1 - e^{-0.097(t - 6.36)}]$	Luangwa Valley	Hanks (1972)
Males *Loxodonta africana*	$SH_t = 336.89\ [1 - e^{-0.07\ (t + 6.67)}]$	Etosha	Lindeque and van Jaarsveld (1993)
Females *Loxodonta africana*	$SH_t = 262.84\ [1 - e^{-0.13(t + 4.05)}]$	Etosha	Lindeque and van Jaarsveld (1993)
Males *Loxodonta africana*	$SH_i = 105.4 + (316.6 - 105.4)\ [1 - e^{(-0.0066t)}]$	Addo and Amboseli	Shrader et al. 2006
Females *Loxodonta africana*	$SH_i = 96.9 + (230.3 - 96.9)\ [1 - e^{(-0.0150t)}]$	Addo and Amboseli	Shrader et al. 2006
Males *Elephas maximus* (0–2 years)	$SH_t = 92.35 + 27.68t$	Southern India	Sukumar et al. (1988)
Females *Elephas maximus* (0–2 years)	$SH_t = 92.06 + 27.16t$	Southern India	Sukumar et al. (1988)
Males *Elephas maximus* (> 3 years)	$SH_t = 232\ [1 - e^{-0.266\ (t - 6.13)}]$	Southern India	Sukumar et al. (1988)
Females *Elephas maximus* (> 3 years)	$SH_t = 256\ [1 - e^{-0.133\ (t + 3.58)}]$	Southern India	Sukumar et al. (1988)

GROWTH IN BACK LENGTH

Aplicable to	Equation	Population	Reference
Males *Loxodonta africana*	$BL_i = 106.2 + (307 - 106.2)\ [1 - e^{(-0.078t)}]$	Addo and Amboseli	Trimble et al. (2011)
Females *Loxodonta africana*	$BL_i = 95.34 + (245.5 - 95.34)\ [1 - e^{(-0.1408t)}]$	Addo and Amboseli	Trimble et al. (2011)

GROWTH IN BODY MASS

Aplicable to	Equation	Population	Reference
Males *Loxodonta africana* (1–30 years)	$BM_t = 5970\ [1 - e^{-0.045\ (t + 9.77)}]^3$	Luangwa Valley	Hanks (1972)
Females *Loxodonta africana* (1–55 years)	$BM_t = 2740\ [1 - e^{-0.066\ (t - 10.48)}]^3$	Luangwa Valley	Hanks (1972)
Males *Elephas maximus* (> 2 years)	$BM_t = 3255\ [1 - e^{-0.149\ (t + 3.16)}]^3$	Southern India	Sukumar et al. (1988)
Females *Elephas maximus* (> 2 years)	$BM_t = 3055\ [1 - e^{-0.092\ (t + 6.15)}]^3$	Southern India	Sukumar et al. (1988)

SHOULDER HEIGHT-BODY MASS RELATIONSHIP

Aplicable to	Equation	Population	Reference
Males *Elephas maximus*	$BM = [(0.057 \times SH) + 0.114]^3$	Southern India	Sukumar et al. (1988)
Females *Elephas maximus*	$BM = [(0.060 \times SH) + 0.335]^3$	Southern India	Sukumar et al. (1988)
Males *Loxodonta africana*	$BM = 3.28 \times 10^{-4} \times SH^{2.899}$	Optimal condition	Larramendi (2016)
Females *Loxodonta africana*	$BM = 3.22 \times 10^{-4} \times SH^{2.886}$	Optimal condition	Larramendi (2016)
Mixed *Elephas maximus*	$BM = 3.32 \times 10^{-4} \times SH^{2.903}$	Optimal condition	Larramendi (2016)

Table 11. Selected growth equations in living elephants, based on von Bertalanffy growth curves. Shoulder height to body mass functions are linear regression equations, which give the best results, especially from juveniles (>2 years) onwards. SHt and SHi is shoulder height in cm; BLi is back length in cm; BMt and BM is body mass in kg; and t is the age in years.

AGEING OF FOSSIL PROBOSCIDEANS: TOOTH REPLACEMENT AND WEAR PATTERN

As is the case for other mammals, in proboscideans tooth eruption pattern and the effect of wear on teeth due to mastication allow us to subdivide the life story of an individual into a number of "dental" stages/ages. In large ungulates, dental maturation (the complete eruption of the permanent dentition) follows sexual maturation, being bracketed between the eruption of the first (M1) and third (M3) molar. In primitive proboscidean species, which still retain the typical mammalian vertical tooth replacement (e.g., plesielephantiformes, moeritheres, deinotheriids, and palaeomastodonts), dental age can be assessed only for dentally immature individuals that have not completed the replacement of the deciduous dentition. When this happens, it could still be possible to broadly discriminate between young-adult, middle-age, and old individuals, based on tooth wear, though it must be taken into consideration that occlusal wear is greatly affected by the abrasiveness of the food. At present, no attempt has been

(continued...)

INDEX

This index covers major proboscidean clades.

PROBOSCIDEAN TAXA

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