Mammoths, mastodonts, and elephants

Biology, behavior, and the fossil record

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Taxonomy: classification of fossil and living forms

1.1. Distribution

Today there are only two genera in the order Proboscidea: *Loxodonta* (the African elephant) and *Elephas* (the Asian elephant). Two other genera, *Mammuthus* and *Mammut*, disappeared from North America about 10,000 years ago, and in South America at that time three genera of gomphotheres (*Cuvieronius*, *Haplomastodon*, and *Stegomastodon*, also considered mastodonts) died out. Those five extinct genera and the two surviving genera were the only proboscideans present in the late Pleistocene (50,000–10,000 years ago) anywhere in the world. Mammoths (*Mammuthus* spp.) were widespread in Europe, northern Asia, North America, and central Mexico, but they never penetrated into South America. Mastodonts (*Mammut*) were found in North America, but members of the separate taxonomic family of animals popularly called gomphotheres were the only South American proboscideans. The genus *Elephas* was present in Africa and Asia, but never in the New World. *Loxodonta* was always restricted to Africa. No proboscideans were ever native to Australia.

1.2. Origins and evolution

Proboscideans are a relatively diverse order, as evidenced by the numerous extinct genera and species in the fossil record. Figure 1.1 shows a possible set of phyletic relationships among the elephant families of the order Proboscidea (after Maglio 1973; following Lister 1989; J. Saunders 1989 personal communication). The earliest members of the order appeared in northern Africa over 50 million years ago, during the early part of the Eocene epoch. The first forms were rather small by modern standards, but were elephantlike in some ways (Mahboubi et al. 1984). Over the next several million years, evolutionary divergence resulted in the development of mastodonts and gomphotheres, distinguished primarily by the shapes of their check teeth. By early Miocene times (about 20 million years ago), gomphotheres and mastodontlike forms had expanded their ranges out of Africa and into Eurasia and eventually North America. By the middle

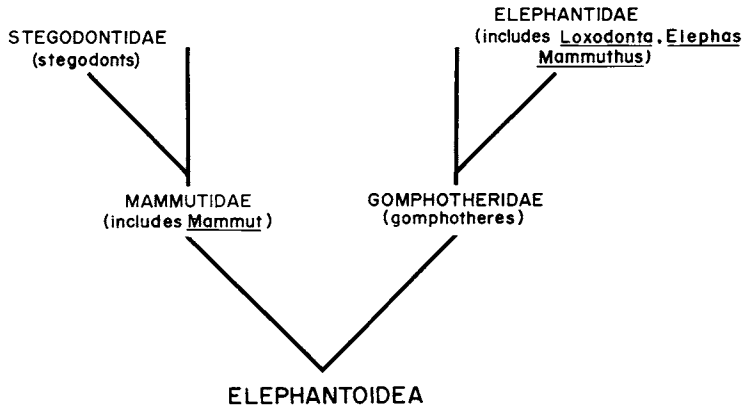

Figure 1.1. Phyletic diagram suggesting the relationships among different taxonomic families of the order Proboscidea.

Miocene (about 15 million years ago), the bones of numerous different subfamilies and genera had appeared in Africa, Eurasia, and North America, figuring prominently in local fossil records.

Throughout the Pliocene-Pleistocene fossil record the most common genus in southern and eastern Africa was *Elephas*, until about 400,000 years ago, when only *Loxodonta* continued to survive in Africa. The use of the generic term *Elephas* to refer to prehistoric European elephants is common in some literature, but it is probably an unjustified case of taxonomic lumping (A. Lister 1990 personal communication). Today *Elephas* is restricted to southern Asia, from India east to Sumatra and Borneo.

1.3. *Mammut*

Mastodonts are primitive proboscideans, insofar as types such as mammutids first appeared so early (by the early Miocene, 20 million years ago) and persisted in the fossil record until the end of the Pleistocene, 10,000 years ago, when they ceased to exist. However, there was considerable diversification within the mastodonts. Note that the term "mastodont," with the letter *t* at the end, refers to *Mammut* and also several other genera such as the gomphotheres. The term "mastodon" has been proposed at various times and by different authorities as a vernacular word referring specifically to *Mammut*, whereas "mastodont" would refer collectively to mastodons and gomphotheres. I use the more inclusive term (with the *t* at the end) even when discussing *Mammut* only, because proper English word formation from the Greek roots of the term requires the final *t* (J. Saunders 1989 personal communication). In this book, the word "mammutid" refers only to *Mammut*.

Figure 1.2. View of the left cheek teeth in the lower jaw of *Mammut americanum*, with the anterior side to the left.

The teeth of *Mammut* were characterized by rounded and pointed enamel-covered cones (Figure 1.2) that wore down with use and flattened out considerably. The teeth would have functioned effectively in clipping or crushing twigs, leaves, and stems, but would not have been suitably adapted for grinding hard or abrasive foods. The *Mammut* diet may have consisted of plants that grew around swamps and ponds in woodlands. Pollen and macrofossils of spruce and other conifers are associated with American mastodonts, but how prominently those trees were featured in the diet is difficult to judge (see Chapter 3).

1.4. *Mammuthus*

Animals classified in this genus appeared in sub-Saharan Africa during the middle Pliocene epoch (about 3–4 million years ago). By the end of the Pliocene and the beginning of the Pleistocene they were extinct in Africa, but widespread in Eurasia, where Soviet scholars classify the earliest members of the group as *Archidiskidon gromovi*. *A. gromovi* is regarded by some systematists as an early form of *A.* (or *Mammuthus*) *meridionalis* (A. Lister 1989 personal communication). Some species lived in relatively warm southern ranges, whereas others were associated with northern

Table 1.1. *Enamel thickness in Mammuthus spp.*

Taxon[a]	Faunal age	Enamel thickness (last molar) (mm)
M. meridionalis	Irvingtonian	2.4–4.0
M. imperator	Middle Irvingtonian to middle Rancholabrean	2.5–3.2
M. columbi	Wisconsin glacial stage	2.0–2.3 (early) 1.5–2.0 (later)
M. primigenius	Rancholabrean	1.0–2.0

[a]These taxonomic classes are those that seem to be most widely applied by other workers, in spite of Kurtén and Anderson's correct insistence on using the earliest established designations. *M. imperator* in this table is called *M. columbi* by Kurtén and Anderson; *M. columbi* in this table refers to the species called *M. jeffersonii* by Kurtén and Anderson.
Source: Data from Kurtén and Anderson (1980).

latitudes. It has been suggested that the largest mammoths were the southern races, but clear evidence for this is elusive. Mammoths seem to have become progressively cold-adapted in Eurasia, successfully colonizing extreme northern Asia and Beringia, and eventually crossing eastward and southward into North America by at least 1.7 million years ago (Webb et al. 1989). Once into interior North America, a lineage of large mammoths, similar to *Mammuthus* (*Archidiskidon*) *meridionalis* of Eurasia, evolved into a species adapted to open habitats–the columbian mammoth, *M. columbi.* A second wave of migration from Asia into North America may have brought the relatively smaller woolly mammoth (*M. primigenius*). The distribution of this late Pleistocene species seems to have been limited to the northern regions of the continent, or near the glacial borders. However, there may be a gradient based on body size and tooth morphology that could indicate that *M. columbi* and *M. primigenius* were not descendants of two entirely separate dispersals, but were geoclinal or chronoclinal variants. No clear differences in postcranial morphology distinguish the two species; enamel thickness is considered partially diagnostic, but individual teeth and even parts of a given tooth have variable enamel thickness (Corner and Diffendal 1983; Kurtén and Anderson 1980) (Table 1.1).

Most researchers agree that mammoths were predominantly grazers. Increasing dental and cranial adaptations for the processing of grass set the mammoths apart from many other proboscideans, with the exception of *Elephas.* Their teeth are large, blocky masses made up of multiple enamel-covered and dentine-cored laminae (Figure 1.3); the laminae are held

Figure 1.3. View of the cheek teeth of *Mammuthus columbi*. Both left and right sides are shown in a broken lower jaw lacking an ascending ramus on the left. Anterior sides are to the left. The smooth-surfaced, peglike teeth on the left are both very worn and are being replaced from behind by the larger teeth.

together with cementum (see the Appendix for further descriptions of elephant teeth).

1.5. Pygmy or dwarf elephantids

Insular proboscidean populations in several widely different parts of the world during the Pleistocene evolved extremely small body sizes, as predicted by the "island rule" of theoretical biology (Lomolino 1985; Sondaar 1977). On the islands of Sicily and Malta, *Palaeoloxodon falconeri* (= *Elephas falconeri* in some literature) was about one-quarter the height

and length of its probable mainland ancestor *P. namadicus* (= *E. namadicus*), whereas another dwarfed form (*P.* or *E. mnaidriensis*) was not quite so small (Caloi et al. 1989). In the northern Channel Islands of California, *Mammuthus exilis* was about half as big as its likely ancestor *M. imperator*. The dwarfed *P.* (or *E.*) *cypriotes* is known from over a dozen sites on the island of Cyprus (Bate 1903; Reese n.d.). There are other possible dwarfed forms, all of which show similar trends in character, such as relatively shortened distal limb elements, cheek teeth that are not as much reduced (compared with those of full-sized ancestors), and skeletal elements such as limb bones that are not as much reduced (Maglio 1973; Roth 1984, in press; Sondaar 1977). Dwarf stegodonts (which are not true elephants in the taxonomic sense), found on several islands in southeast Asia, may have been hunted by colonizing humans during the Pleistocene (Sondaar et al. 1989).

1.6. *Elephas*

This genus originated in sub-Saharan Africa during the Pliocene epoch, ranging throughout Africa and into southern Asia. A form that reached into Europe by the middle Pleistocene has been called *Elephas* in published literature, but the term *Palaeoloxodon* is perhaps more appropriate. As the teeth and skull of *Elephas* evolved throughout the long span of its existence, the overall trend was toward specialized features for processing an abrasive diet, specifically grass. As in mammoths, the skull of *Elephas* is high, with domed forehead, a development associated with a shift in the skull's center of gravity to facilitate grinding food in the mouth (Maglio 1973; Osborn 1942). Only one species survives today, with perhaps three subspecies (*E. maximus maximus* of Sri Lanka, *E. m. indicus* of India, Indochina, and Borneo, and *E. m. sumatranus* of Sumatra).

1.7. *Loxodonta*

Loxodonta is a genus that never left Africa. It first appeared about 4 million years ago, but over its evolutionary life the features of its teeth and skeleton changed very little. Members of this taxon are associated (perhaps only inferentially) with wooded habitats, where browse could have formed a major part of the diet, either seasonally or year-round. *Loxodonta* does not seem to have been a competitor with *Elephas* in Africa, where both genera originally appeared and coexisted through the Pliocene and most of the Pleistocene. *Loxodonta* has never been found in fossil assemblages that also contain *Elephas* in southern Africa, and only rarely has it been found with *Elephas* in sites elsewhere on the continent (Klein 1984). In fact, *Loxodonta* is believed to have been relatively rare in east Africa until after the late Pleistocene disappearance of *Elephas*.

There is only one surviving species, *L. africana*, and possibly two subspecies (*L. a. africana*, the typical savanna and woodland elephant, and *L. a. cyclotis*, the forest elephant of central and western Africa, a smaller animal with different tusk and body morphology). Soviet zoologists consider the two races to be separate species (V. Garutt 1987 personal communication).