Order Proboscidea

*Ursula B. Göhlich**

During their evolution since the Paleogene proboscideans expanded nearly all over the world. Especially in Neogen and Pleistocene times they distributed with numerous species on all continents except Antarctica and Australia and showed a wide range of habitats and climates. Today there are only two living and locally restricted representatives of the order Proboscidea: the Asian elephant (*Elephas maximus*) and the African elephant (*Loxodonta africana*) – the largest landmammals in present time.

So nearly all of the numerous proboscidean taxa are only known fossil, one of the reasons classification and phylogeny of proboscideans are topics of never-ending discussions.

The name "Proboscidea" was first used by ILLIGER in 1811 for recent elephants because of one of their more outstanding characters – the trunk (Lat. proboscis), a boneless fusion of nose and upper lip.

Classification and evolutionary history

Proboscideans are classified into the Tethytheria, together with their extant sister-group Sirenia and with the extinct order Desmostylia. Some authors (e.g. FISCHER 1996: 35) include the extinct Embrithopoda. For classification of the proboscideans see fig. 13.1 (or MCKENNA & BELL 1997: 497-504, SHOSHANI & TASSY 1996, TASSY 1990).

The origin of proboscideans is supposed to have been in Africa in Paleocene times (*Phosphatherium*, see GHEERBRANT et al. 1998), although there are some presumable proboscidean taxa (anthracobunids) of Eocene age documented in southern Asia. But most of these primary, Paleogene forms did not look very "elephant-like". They were pig-sized and nearly trunk- and tuskless (only one pair of their upper and lower incisors were a little bit enlarged – the beginning of the later tusks). In the course of their evolution the proboscideans became larger, the trunk became longer and the tusks and also the cheek teeth became larger. So the cheek teeth of elephantids became the largest of any vertebrate known.

During the earliest Miocene (c. 22 Ma or more) the first proboscideans – primitive elephantoids like "trilophodont gomphotheres" and amebelodons – emigrated from Africa to Asia Minor and southern Asia (KALB et al. 1996: 121, TASSY 1989: 241, 249). A subsequent expansion of early elephantoids during the middle Burdigalian (c. 19-17 Ma) and their first occurrence in western Europe (see RÖGL this volume, chapter 3) where they dispersed rapidly, is called the "Proboscidean Datum Event" (see also TASSY 1989).

The earliest proboscideans in Europe were elephantoids, *Gomphotherium* and *Zygolophodon*, in the early Miocene (MN 3b). They were followed by *Prodeinotherium* and *Archaeobelodon* (MN 4a). Throughout the whole Miocene proboscideans were represented in Europe only by deinotheres and "mastodonts" (more specifically: mammutids, gomphotheres, amebelodons and choerolophodons).

"Mastodon(t)s" is a very current term integrating most Neogene and some Pleistocene proboscideans, but it is a notion without systematic validity. The term "mastodonts" will be used in this paper in the sense of the Elephantoidea except the Elephantidae; it derives from the genusname *Mastodon* (a junior synonym of *Mammut*), the American mastodon (*Mammut americanum*), a member of the family Mammutidae, also called the "true mastodons".

General characters

Skeleton: During their evolution the proboscideans became larger (except dwarf-elephants adapted to isolated island life). As a consequence of their size and great weight some special skeletal-adaptations are present: The legs are in an almost vertical position under the body like columns or pillars. The extremities are graviportal with long proximal and short distal segments. The ulna is stronger than the radius; they are not fused but fixed in pronation-constellation. Manus and carpus are digitigrade and constructed of five fingers and five toes respectively. Fingers and toes half-surround a cushion pad, that makes elephants walk gently. The number of vertebrae in the special regions of the vertebral column may vary according to the species. The vertebrate corpora are short in comparison. Much of the volume of

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* Dr. Ursula B. Göhlich, Institut für Paläontologie und historische Geologie, Richard-Wagner-Str. 10, D-80333 München, Germany

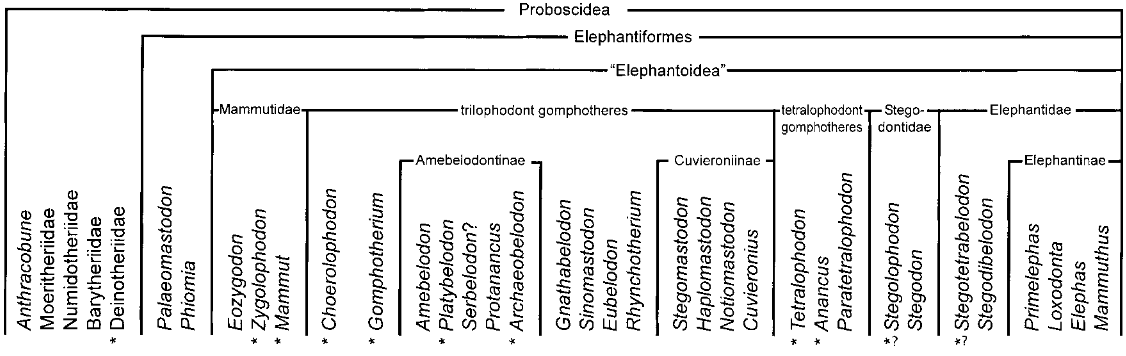

Fig. 13.1. Classification of the Proboscidea (modified after SHOSHANI 1997b, p. 153, fig.16.5, based on a cladogramm), Taxa represented in the European Miocene are indicated by *.

the cranium shows a pneumatisation, that makes the skull lighter. The mandible of earlier elephantoids generally has an elongated symphysis (longirostrin) which is more or less inclined downward. It first shortened (brevirostrin) in progressive "mastodont" taxa and the elephants. Teeth and some skeletal elements show a sexual dimorphism. For more special anatomical characters that make an animal a proboscidean see e.g. SHOSHANI (1996b), SHOSHANI & TASSY (1996: 339f.) and TASSY (1996b).

Dentition: Early in the evolution of the proboscideans the dentition became reduced. The canines were lost, incisors and premolars in advanced forms were reduced in number. Only the developement of three molars and three deciduous molars is constant in all proboscideans. The dental formula varies from I 3/3, C 1/1, P 4/4, M 3/3 in anthracobunes (Eocene, Southern Asia), over I 3/2, C 1/0, P 3/3, M 3/3 in *Moeritherium* (late Eocene through early Oligocene, Africa) and *Numidotherium* (middle Eocene, Africa) to I 1/0, C 0/0, (DP 3/3,) P 0/0, M 3/3 in living elephants. Basically the cheek teeth of proboscideans are brachyodont, only the elephants change to hypsodonty. Studies of the enamel microstructure shows a 3-D-enamel, characterized by three dimensionally interwoven prism-bundles, which only occurs in proboscideans (see PFRETSCHNER 1992). Only *Moeritherium* differs by a more primitive enamel microstructure with horizontal Hunter-Schreger bands.

Tusks are not canines, as often suspected. They are enlarged incisors, to be precise, the pair of second incisors (I2). Ivory is nothing but dentine, only its internal structure (see e.g. SHOSHANI 1996a: 14ff) is outstanding. The transverse cross-section of tusks shows a pattern of bent criss-cross lines, called "engine turning" or "guillochage". This pattern is unique among proboscideans. Most of the Neogene elephantoids possess a pair of upper and lower tusks, called tetrabelodont (four-tusked). The lower tusks become reduced in progressive taxa and are lacking within the elephants. Tusks are root-less and grow for life. Little deciduous tusks are replaced by permanent second incisors in the early lifetime. The upper tusks of many Neogene elephantoid-taxa possess a longitudinal enamel band along the lateral side.

In early proboscideans all teeth of the persistent dentition were in function synchronous, as is typical for most mammals. During the evolution of the proboscideans the cheek teeth became larger in relation to the jaw. So the jaws couldn't accomodate all of the cheek teeth at one time. As a result, proboscideans developed a certain kind of tooth replacement, called "horizontal displacement". Whereas premolars (if existing) replace the milk teeth in a vertical manner, the molars are replaced one after another in horizontal progression. During their usage the teeth move forward. When they are totally worn down, they are forced out. Meanwhile new and bigger teeth are developing from behind and move slowly forward. This kind of tooth replacement is the reason why there are no jaws with complete tooth rows.

Although the molars and premolars of proboscideans are basically bunolophodont different cheek teeth patterns can be differentiated within the proboscideans. The molars and most premolars of deinotheres show a bi- or tri-lophodont structure (fig. 13.2a). Within the "mastodonts" two kinds of cheek teeth patterns can be distinguished: bunodont (fig. 13.2b) and zygodont (fig. 13.2c).

Bunodont teeth consist of a certain number of cone-like elements arranged in several transverse ridges (loph(id)s). Also typical of bunodont teeth are cones (so-called conules) in the transverse valleys, blocking them in the middle part. Based on the number of loph(id)s in the intermediate molars (D4, M1, M2), a primitive trilophodont grade (with three loph(id)s) can be distinguished from an evolved tetralophodont grade. The bun-

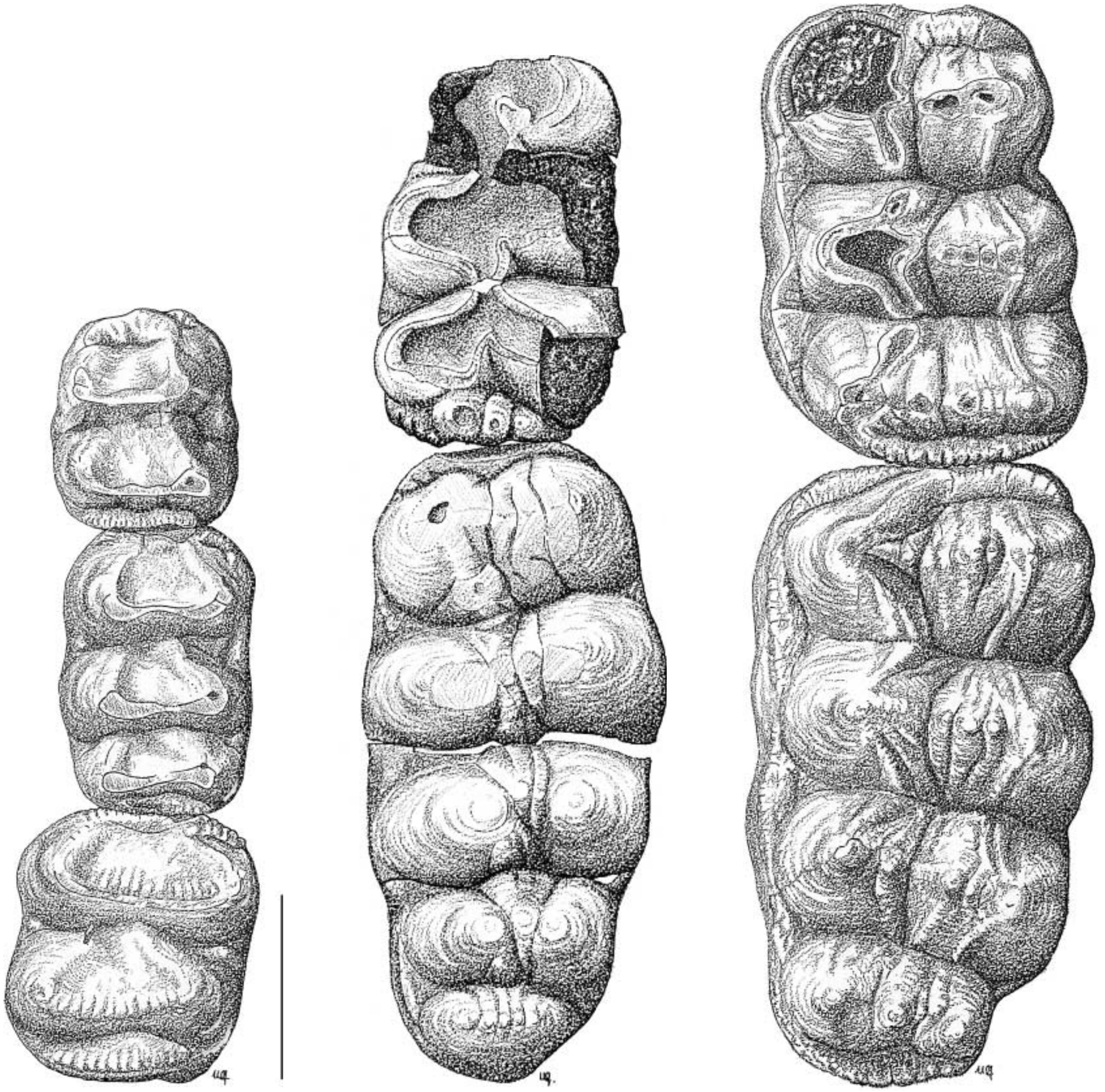

Fig. 13.2. Cheek teeth patterns of proboscideans, 1:2, scale 5 cm;
a, Lophodont pattern of deinotheres. Exemplarely *Deinotherium giganteum* (P_4-M_2 dext.) from Landshut (southern Germany, Upper Freshwatermolasse, middle Miocene), BSP 1963 I 162;
b, Bunodont pattern of gomphotheres. Exemplarely *Gomphotherium angustidens* (M_2-M_3 sin.) from Feldmoching (southern Germany, Upper Freshwatermolasse, middle Miocene), BSP 1993 I 27;
c, Zygodont pattern of mammutids. Exemplarely *Zygolophodon turicensis* (M^2 (inv.)-M^3 dext.) from Ottmaring near Friedberg, (southern Germany, Upper Freshwatermolasse, middle Miocene), BSP 1962 XII 1.

odont pattern is characteristic for gomphotheres, amebelodons and choerolophodons.

In zygodont cheek teeth the transverse ridges are transformed to sharp crests or ridges. The valley-blocking conules are reduced or lacking. Within the "zygodont-lineage" all taxa remain trilophodont. The zygodont teeth-type is typical for all mammutids. In contrast to the mentioned "mastodonts'" cheek teeth, the ones of elephants (elephantids) are of lamellar pattern, but are supposed to be originated from the bunodont type. For more information about the dentition of "mastodonts" see e.g. TASSY (1996a) and TOBIEN (1973b, 1975).

Complementary characters: The diet of proboscideans is strictly herbivorous. Elephants grow continuously throughout life. The lengthening of the limbs in the proboscideans led to a symmetrical locomotion, a racklike gait. They do not "run" in the usual sense of the word; there is no free-flight phase in which all feet are off the ground at the same time. Their high-speed gait is a fast walk. The added length of the trunk, that functions not only as a nose but also as a prehensile organ, makes up for the short neck and therewith for the difficulty of getting the mouth down to the ground for feeding or drinking. Besides sounds like trumpets, growls and rumbles elephants have the ability to communicate by infrasonic noises

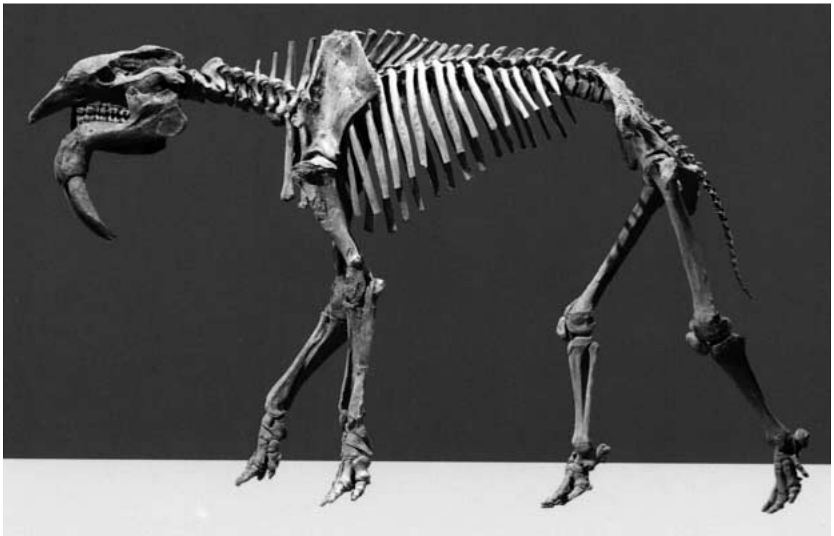

Fig. 13.3. Skeleton of *Prodeinotherium* cf. *bavaricum* from Langenau near Ulm (southern Germany, early Miocene, MN 4b), shoulder height 2,65 m, SMNS (Nr. 41562).

(low-frequency-sounds below the range of human hearing) over long distances.

Proboscideans in the European Miocene

Family Deinotheriidae Bonaparte, 1845: Deinotheres are a conservative group within the proboscideans, not belonging to the elephantoids (see fig. 13.1). They differ from the elephantoids by their skeletal morphology and especially dental characters (fig. 13.2a and 13.3). The most outstanding features are the position and form of the tusks. In contrast to all other proboscideans, deinotheres possess only lower incisors, the upper ones are always lacking. The form and kind of implantation of the lower tusks is extraordinary. They are down-recurved and very strong. The mandibular symphysis is down-curved, too. Also remarkable is the absence of "guillochage" in the lower tusks of deinotheres.

The cranial adaptation indicates a fully functional, but short and tapir-like trunk. Contrary to most advanced proboscideans, deinotheres have a dorsally flat cranium. The molars have only two to three transverse ridges (fig. 13.2a), with very simple cusps and look tapir-like. They are supposed to be ideally suited for processing soft foliage. In contrast to the elephantoids all teeth of the persistant dentition are in function synchronous. The cheek teeth are replaced in a vertical fashion, not in horizontal as most elephantoids do. The large simple lophodont teeth misled early authors to classify them within rhinos, tapirs or ground sloth. Others postulated deinotheres to be related to sirenians, hippopotami or marsupials. Today, most scientists accept deinotheres as members of the proboscideans, but the discussions about the closeness of the relationship of these "less elephant-like" proboscideans are still going on.

Deinotheres originated in Africa where they persisted until Pleistocene times (c. 1 Ma). They reached Europe in the early Miocene (MN 4a), a little bit later than the elephantoids with *Gomphotherium* and *Zygolophodon*.

Two genera lived in Europe: *Prodeinotherium* Ehik, 1930 and *Deinotherium* Kaup, 1829.

Prodeinotherium bavaricum (v. Meyer, 1831) was the first representative in the early Miocene (MN 4) and persisted until the late Miocene. *P. bavaricum*, primitive and small, gave rise to the advanced and larger *Deinotherium giganteum* Kaup, 1928. The latter existed from the early middle Miocene to early Pliocene in all of Europe. It was followed by the biggest deinothere, *Deinotherium gigantissimum* Stefãnescu, 1892, which thrived from late Miocene to Pliocene times in eastern Europe.

Besides the "mastodonts", deinotheres were the largest land-mammals of their time. Within the *Prodeinotherium*-*Deinotherium*-lineage the body-height increased from c. 2,5 m to c. 4 m.

The last Eurasian representatives of the family were of Pliocene age. Deinotheres did not occur in Northern Asia and did not reach the New World. Perhaps this was due to ecological constraints, deinotheres being inhabitants of rather forested environments. For more information on European deinotheres in general see e.g. Bergounioux & Crouzel (1962) and Tobien (1986: 158-183, 1988).

Family Mammutidae Hay, 1922: The members of the mammutids, or "true mastodons", are characterized especially by their zygodont cheek teeth (fig. 13.2c), which mark them as squeezers. The zygodont pattern is caused in yoke-like transverse crests, which are antero-posterior compressed. The "central conules", blocking the valleys, are developed more weakly than in Bunodonts, or are transformed into almost vertical crests called crescentoids, or they are completely lacking. Their intermediate molars (D4, M1, M2) always consist of three transverse ridges. Mammutids never reached an advanced tetralophodont level (with four ridges) in the intermediate molars as Bunodonts did.

Mammutids are supposed to have originated on the African continent. Their first occurrence in Europe in the early Miocene (MN 3b) coincides with that of gomphotheres. But the mammutids

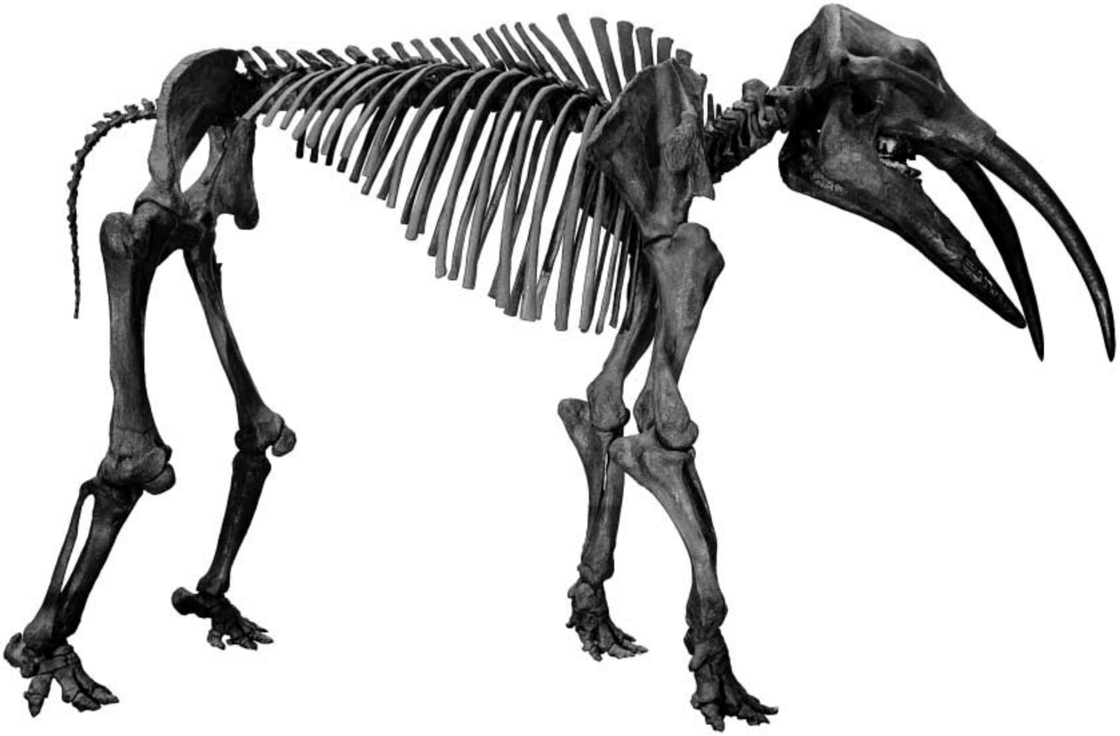

Fig. 13.4. Skeleton of *Gomphotherium* aff. *steinheimense* from Gweng near Mühldorf (southern Germany, Upper Freshwatermolasse, middle/late Miocene), shoulder height 3,05 m, BSP 1971 I 275, (photo: F. Höck).

were less common in European Miocene than the bunodont forms. Moreover, they were less diversified. In the middle Miocene the mammutids reached the New World, and became very successful there (e.g. *Mammut americanum*), but they never populated South America.

In Europe two genera represent the zygodont lineage: *Zygolophodon* VACEK, 1877 and its descendent *Mammut* BLUMENBACH, 1799 (*Zygolophodon* is the senior synonym of *Turicius* OSBORN, 1926, as *Mammut* is of *Mastodon* RAFINESQUE, 1814).

The typical species of Miocene mammutids in Europe is *Zygolophodon turicensis* (SCHINZ, 1824) (fig. 13.2c). It is the first representative of the proboscideans in the early Miocene (beginning with MN 3b) in Europe, besides *Gomphotherium.* Although less common, *Zygolophodon turicensis* shows a wide horizontal extension all over Europe. Its biostratigraphic occurrence is recorded from early to late Miocene (MN 3b to MN 10).

The younger genus *Mammut* (not to be confused with the mammoth (*Mammuthus*), which is an elephantid) is rare in the European Miocene. *Mammut borsoni* (HAYS, 1834) is supposed to have evolved from *Zygolophodon*, perhaps via the intermediate form *Mammut praetypicum* (SCHLESINGER, 1919) – a hypothesis which could not be confirmed yet. Typically, *M. borsoni* is a representative in the Pliocene and existed until the early Pleistocene in some places in Europe. There is only a record of *M.* cf. *borsoni* in the European late Miocene (Pikermi, Greece; MN 12; TASSY 1985: 514). *M. praetypicum* also is a very rarely recorded species known only from eastern Europe. The knowledge about the exact position of the localities and their age is often insufficient. Its record is supposed to have been from late Miocene to Pliocene times.

Some of the evolutionary tendencies within the *Zygolophodon-Mammut* lineage are: the broadening of the molar crowns; the sharpening of the transverse crests; the weakening of the crescentoids; the reinforcement of the oblique position of the lophids in the lower molars; vestigial cement remnants in the transverse valleys; the loss of the enamel band on the upper tusks; the reduction of the number of the premolars until its loss and the reduction of the mandibular symphysis (from a longirostrine to a brevirostrine stage) and of the lower tusks. Whereas the upper tusks in *Zygolophodon* are downcurved, they are straight or upcurved in *Mammut*. For more information on mammutids in general see e.g. TOBIEN (1975, 1996).

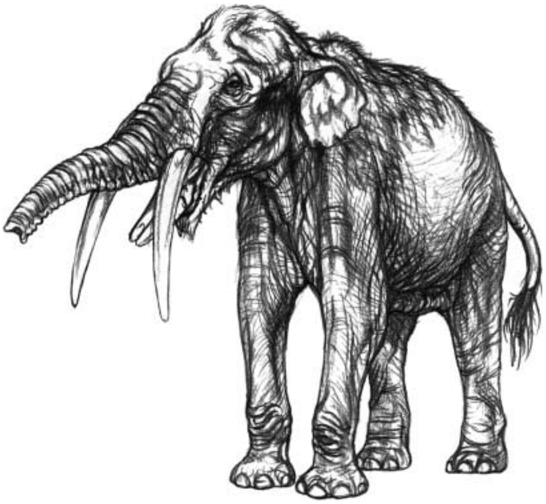

Fig. 13.5. Reconstruction of *Gomphotherium,* made by P. MAJOR under the supervision of O. FEJFAR (from ENGESSER, FEJFAR & MAJOR 1996).

Family Gomphotheriidae HAY, 1922:

"trilophodont gomphotheres": Gomphotheres are the more diversified elephantoids and include most species of bunodont "mastodonts". The gomphotheres s. l. can be divided into the primary "trilophodont gomphotheres" and their direct descendants, the "tetralophodont gomphotheres" (see below). Within the gomphotheres, an evolutionary and biochronological enlargement has been suggested. "Tri-" and "tetralophodont gomphotheres" dispersed widely across Eurasia and Africa, but it seems that only the "Trilophodonts" reached the New World.

The first gomphotheres in Europe were "trilophodont gomphotheres". In the Old World they belong only to one genus: *Gomphotherium* BURMEISTER, 1837 (junior synonyms are *Trilophodon* FALCONER, 1857 and *Serridentinus* OSBORN, 1923) (fig. 13.4 and 13.5).

Gomphotherium is characterized by a longirostrine mandible (with an elongated symphysis) and by both a pair of upper and lower tusks, called tetrabelodont. The upper tusks feature an enamel band on the outside. The lower ones show a pyriform to rounded cross section. Certain characters of the bunodont cheek teeth, the course of the enamel band and the kind of cross section in the lower incisors allow the differentiation of some species.

The first representatives of the genus appeared in the early Miocene (MN 3/4) in western Europe. *G. sylvaticum* TASSY, 1985, formerly often confused with *G. angustidens*, is supposed to be documented until the early/middle Miocene (MN 5) whereas *G. hannibali* WELCOMME, 1994 (whose validity is as yet not certain (pers. comm. P. TASSY, Paris)) is only known from one early Miocene deposit in Southern France. Both species are characterized by simple bunodont molars. They are supposed to have been the most primitive gomphotheres in Europe.

A more evolved trilophodont species is the common type species *Gomphotherium angustidens* (CUVIER, 1817) (fig. 13.2b). In Europe, it is restricted to early middle until early late Miocene (MN 5 - MN 9). Although it is the most popular and abundant representative of "trilophodont gomphotheres" during the European Miocene, its derivation and descendants are unclear.

The contemporary species *G. subtapiroideum* (SCHLESINGER, 1917) is object of never-ending taxonomic discussions. Its cheek teeth seem to be structurally intermediate between bunodont *G. angustidens* and zygodont *Z. turicensis*. Neither the validity of the taxon, nor the relationship of the specimens to the bunodont and the zygodont species is as yet clear.

G. steinheimense (KLÄHN, 1922) is a further advanced "trilophodont gomphothere" only known from the late middle to early late Miocene (MN 7 – MN 9) of southern Germany. In comparison with contemporary *G. angustidens*, the cheek teeth of *G. steinheimense* are larger, especially wider, and show differences in the development of the conules. Also different is the course of the enamel band of the upper incisors and the form of the cross section of the lower tusks. *G. sylvaticum* has been proposed to be the ascendent of *G. steinheimense* (TASSY 1985: 715f).

Similar to or perhaps identical (pers. comm. P. TASSY, Paris) with *G. steinheimense* is the rarely documented species *G.? pyrenaicum* (LARTET, 1859) from a middle Miocene deposit (St. Frajou) in Southern France.

"tetralophodont gomphotheres": During the late middle Miocene "tetralophodont gomphotheres" arose from their trilophodont ascendants. Following recent studies (SHOSHANI & TASSY 1996, appendix B), the "tetralophodont gomphotheres" don't belong to the Gomphotheriidae, but their family status is still uncertain. European representatives are *Tetralophodon* FALCONER, 1857 and its descendant *Anancus* AYMARD, 1855.

The transition from "tri-" to "tetralophodont gomphotheres" is characterized by some evolutionary tendencies. The primary taxon *Tetralophodon longirostris* (KAUP, 1832) (fig. 13.6) differs from *Gomphotherium* by the increase of the number of loph(id)s of the molars such as the last milkmolar (D4), the increased size of the cheek teeth, the subhypsodonty of the grinders and the loss of the enamel band of the upper tusks. Tendencies of shortening the symphysis and reduction of the lower incisors are also recognizable.

T. longirostris occurred during the late middle Miocene (MN8) and is recorded until the late Miocene (MN11) (see GAZIRY 1997). The long accepted hypothesis that it is a direct descendant of trilophodont *G. angustidens,* has recently been disputed.

Similar to, if not identical with *T. longirostris* is KLÄHN's taxon *"Mastodon" gigantorostris* from the Vallesian Dinotheriensands (Germany, MN9). The validity of the Turolian species *T. atticus* (WAGNER, 1857) from Pikermi (Greece, MN11/12) is also obscure.

The terminal stage of the European tetralophodont-lineage is represented by *Anancus arvernensis* (CROIZET & JOBERT, 1828). The advanced characters of this species are: a shortened, brevirostrin mandibular symphysis combined with reduced or without lower incisors; the straightening and lengthening of the upper, enamel-band-less tusks and the loss of the premolars. Also typical is the so-called anancoid pattern of the molars, which means an alternation of the outer and inner half-loph(id)s and an accumulation of cement on the molars. *Anancus* originated first in the late Miocene, so it is not very common in the European Miocene. But it is one of the most widespread gomphotheres during the Pliocene. It is known from Europe, Asia and Africa and persisted until the early Pleistocene.

In spite of a few tetralophodont specimens from North America, it seems that *Tetralophodon* and *Anancus* never immigrated into the New World via the Bering Land Bridge. That may be reasonable because of climatic aspects or the fact that adequate ecological niches already were occupied by descendants of North American "trilophodont gomphotheres".

"Tetralophodont gomphotheres" gave rise to both stegodontids and elephantids, but they originated outside of Europe.

The validity and generic affiliation of the new taxon *Stegotetrabelodon lehmanni* GAZIRY, 1997 and the occurrence of *Stegolophodon* in European Miocene (see GAZIRY 1997) remain to be verified.

For more information on European "tri-" and "tetralophodont gomphotheres" in general see e.g. TASSY (1985, 1996c) and TOBIEN (1973a, 1976,1978, 1986).

Fig. 13.6. *Tetralophodon longirostris* (type mandibule with M_2-M_3 dext.) from Eppelsheim (Germany (Rheinhessen), Dinotheriensande, late Miocene), HLMD Din 111 (photo: HLMD).

Subfamily Amebelodontinae BARBOUR, 1927: Amebelodons are bunodont, predominant trilophodont gomphotheres, and are loosely referred to as the "shovel-tusked gomphotheres" or "shovel-tuskers" because of their most distinctive feature – the flattened, sometimes shovel-like lower tusks. They represent a special evolutionary group within the Gomphotheriidae. Amebelodons originated in Africa. During the early Miocene they invaded Eurasia where they persisted until the late Miocene. In Miocene times they migrated to North-America over the Bering Land Bridge.

There are three representatives in European Miocene: *Archaeobelodon* TASSY, 1984, the more evolved *Platybelodon* BORISSIAK, 1928 and a so-called "grandincisivoid" taxon, whose generic status is not as yet clear.

Archaeobelodon filholi (FRICK, 1933) is the earliest amebelodontid species. It is recorded during the early and middle Miocene (MN 4a–MN 6) of western and central Europe (and Africa). Because the bunodont, trilophodont cheek teeth of *A. filholi* are very similar to that of the contemporary *G. angustidens*, they are often not distinguishable. But *A. filholi* differs from *Gomphotherium* in the lower flattened tusks and in the upper tusks with a lateral enamel band without torsion.

Platybelodon – very common in Asia – is only and rarely known from eastern Europe and is only represented by the middle to late Miocene species *P. danovi* BORISSIAK, 1928 (fig. 13.7). Its most outstanding characteristic are the extremly transversely enlarged, flattened and dorsally excavated lower incisors in the long and ladle-shaped mandibular symphysis – the reason for the notion "shovel-tuskers". In comparison to *Gomphotherium*, the upper incisors are without an enamel band, and are slightly downcurved and reduced in size, being shorter than the symphysis with the oversized and elongated lower incisors.

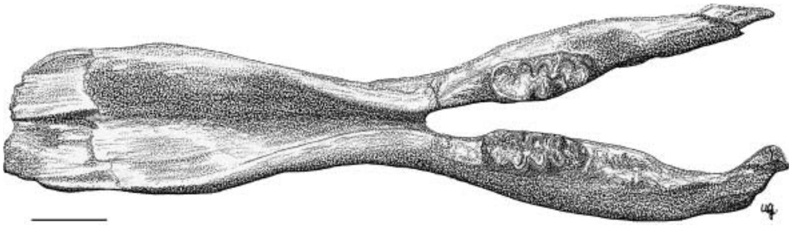

Fig. 13.7. Mandibule of *Platybelodon danovi* from Belomechetskaja (Georgia (Ciscaucasia), late Miocene), c. 1:10, PIN, (redrawn after TOBIEN 1976, fig. 18).

SCHLESINGERS's (1917) taxon *"Mastodon" grandincisivus* – allocated by TOBIEN (1978) to the elephantoid-genus *Stegotetrabelodon* – is classified as an amebelodontid indet. by TASSY (1985: 560ff). This bunodont species is tetralophodont and recorded only in eastern Europe from the middle to the late Miocene.

P. danovi and the "grandincisivoid" specimens of the Old World share the trait of dentinal tubules in the lower tusks, the abundance of cement, especially in the third molars, and also the develepoment of secondary trefoiling (valley blocking conules on both half-sides of the molars) (see TASSY 1985: 785f).

"Choerolophodons": *Choerolophodon* SCHLESINGER, 1917 belongs to the "trilophodont gomphotheres", but its classification within the Gomphotheriidae has recently been disputed (e.g. SHOSHANI 1996b: 153). Its family status is as yet uncertain (see e.g. SHOSHANI & TASSY 1996, appendix B). Although well recorded in southern Asia and Africa, it is not a common representative in the European Miocene. The genus had a perimediterranean distribution in eastern and southeastern Europe. There, it is represented e.g. from Greece, Bulgaria, Ukraine and former Yugoslavia. *Choerolophodon* (including the Asian genus *Synconolophus,* a junior synonym) is characterized by its cheek teeth pattern. Typical for the grinders is choerodonty, a remarkable multiplication and irregular arrangement of the cones (conules and conelets) provided with vertical furrows and rugosities (ptychodonty). Moreover the genus is characterized by plentiful cement on the grinders, the loss of the premolars (P2/, P3/3, P4/4) and D/2, the loss of the lower incisors (at least in the advanced forms) and the loss of the enamel band on the upcurved upper tusks. The cranium is relatively low, compared with *Gomphotherium,* and with different facial proportions (e.g. narrow nasal aperture).

Choerolophodon chioticus is the earliest choerolophodont in eastern and southern Europe (see TOBIEN 1980). It is of Astaracian age. In the late Miocene *C. chioticus* was followed in the eastern Mediterranean region by *Choerolophodon pentelici* (GAUDRY & LARTET, 1856), a more evolved species.

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Tab. 13.1. List of Miocene European species and most published material.

species (*type)	locality (*type)	age	collection	references
**Prodeinotherium bavaricum* (Ehik, 1930)	Dinotheriensande (D) [Eppelsheim, Esselborn, Kettenheim, Wißberg]	MN 9	HLMD, NHMM-LS	Gräf 1957
	Franzensbad (CZ)	MN 5	NHMW	Bergounioux & Crouzel 1962
	Frontenhausen (D)	late Miocene	BSP	Gräf 1957
	*Georgensgmünd? (D)	MN 6	BSP	v. Meyer 1832
	Pontlevoy (F)	MN 5	MNHN	Tassy 1985
**Deinotherium giganteum* Kaup, 1829	Breitenfeld (A)	Pannon C	LMJ	Mottl 1970
	Castrillo de Villavega (E)	Miocene	MNCN	Bergounioux & Crouzel 1962
	Cerecinos de Campos (E)	Miocene	MNCN	Bergounioux & Crouzel 1962
	Dinotheriensande (D) [*Eppelsheim, Esselborn, Wißberg]	MN 9	HLMD, BMNH, HLMD, NHMM-LS	Tobien 1986, Gräf 1957
	Eserovo (BUL)	late Miocene?	BAS	Tobien 1986
	Hinterauerbach (D)	middle/late Miocene	BSP	Gräf 1957
	Husiatyn (UA)	Miocene?	IZAS	Svistun 1974
	Frohnstetten (D)	late Miocene	GPIT	Gräf 1957
	Massenhausen (D)	MN 8/9	BSP	Gräf 1957
	Montredon (F)	MN 10	UCBL, NMB, MHNL, LPVM	Bergounioux & Crouzel 1962, Tobien 1988
Deinotherium gigantissimum Stefănescu, 1892	*Gaiceana (RO)	Mio-?/Pliocene	MNGA	Stefanescu 1892
	Mânazati-Valley (RO)	Mio-?/Pliocene	LPUB	Bergounioux & Crouzel 1962
**Zygolophodon turicensis* (Schinz, 1824)	Benavente (E)	MN 7+8	IGME	Mazo 1996
	Concud (E)	MN 12	MNCN, IPMC	Mazo 1996
	Dinotheriensande (D) [Bermersheim, Esselborn, Gau-Weinheim]	MN 9	HLMD	Tobien 1980, 1986
	*Elgg (CH)	MN 6 or 7	PIMUZ	Tobien 1975
	Malartic (F)	MN 7	MNHN	Tassy 1974, 1985
	Mistelbach (A)	Miocene	NHMW	Schlesinger 1917
	Neudorf a. d. March (SK)	MN 6	NMB	Tobien 1975
	Pontlevoy (F)	MN 5	MNHN, NMB	Tobien 1975
	Rajégats (F)	Astarac	MNHN	Tassy 1985
	Simorre (F)	MN 7	UCBL	Tassy 1985
Mammut praetypicum (Schlesinger, 1919)	*Batta-Érd (H)	late Miocene?	MNMB	Kubiak 1972
Mammut cf. *borsoni* (Hays, 1834)	Pikermi (GR)	MN 11/12	BMNH	Tassy 1985
Gomphotherium sylvaticum Tassy, 1985 (unpublished)	*Artenay (F)	MN 3b	MNHN, NMB	Tassy 1985
	Quinta das Pedreiras (P)	MN 4a	NMB	Tassy 1985
	Pontlevoy-Thenay (F)	MN 5	MNHN	Tassy 1985
Gomphotherium hannibali Welcomme, 1994	*Le Mazet (F)	MN 3/4	LPVM	Welcomme 1994
**Gomphotherium angustidens* (Cuvier, 1817)	Buñol (E)	MN 4	MNCN	Mazo 1996
	Castelneau-Barbarens (F)	middle Miocene	ColVd	**Tassy** 1974, 1985
	Córcoles (E)	MN 4	IGME	Mazo 1996
	Dinotheriensande (D) [Bermersheim, Eppelsheim, Gau-Weinheim, Kettenheim, Wißberg, Wolfsheim]	MN 9	HLMD	Tobien 1980
	En Péjouan (F)	MN 7	MNHN	Tassy 1985, 1996
	La Hidroeléctrica (E)	early/middle Miocene	ColVi	Mazo 1977
	Paracuellos V (E)	MN 6	MNCN	Mazo 1977, 1996

Tab. 13.1. (continued).

species (*type)	locality (*type)	age	collection	references
	Pontlevoy-Thenay (E)	MN 5	MNHN	Tassy 1974
	Quinta das Pedreiras (P)	MN 4b	CSGP	Bergounioux, Zbyszewski & Crouzel 1953, Mazo 1996
	Quinta da Farinheira (P)	MN 4b	CSGP	Bergounioux, Zbyszewski & Crouzel 1953
	Quinta Grande (P)	MN 4b	CSGP	Bergounioux, Zbyszewski & Crouzel 1953
	Conrelas do Cavão (P)	MN 4b	CSGP	Bergounioux, Zbyszewski & Crouzel 1953
	Sansan (F)	MN 6	MNHN	Tassy 1974
	*Simorre (F)	MN 7	MNHN, MHNT, MHNL	Tassy 1985, Bergounioux & Crouzel 1960
	Tetuán de las Victorias (E)	middle Miocene	IAM	Mazo 1977
	Villefranche d'Astarac (F)	MN 7	MHNL	Bergounioux & Crouzel 1960
	Yuncos (E)	MN 5	IGME	Mazo 1977, 1996
Gomphotherium subtapiroideum (Schlesinger, 1917)	*Vordersdorf b.Eibiswald (A)	MN 5	NHMW, LMJ	Mottl 1970, Schlesinger 1917
	Sandelzhausen (D)	MN 5	BSP	Schmidt-Kittler 1972
Gomphotherium steinheimense (Klähn, 1922)	*Steinheim a. A. (D)	MN 7	SMNS, BSP	Klähn 1931
	Massenhausen (D)	MN 8/9	BSP	Göhlich 1998
Gomphotherium aff. *steinheimense*	Gweng bei Mühldorf (D)	MN 8/9	BSP	Göhlich 1998
Gomphotherium? *pyrenaicum* (Lartet, 1877)	*St. Frajou (F)	MN 7	MNHN, MHNT, BSP	Tassy 1985
**Tetralophodon longirostris* (Kaup, 1832)	Belvedere (A)	Pannon D/E	NHMW	Schlesinger 1917
	Breitenfeld (A)	MN 9	LMJ	Mottl 1969, Tobien 1978
	Dinotheriensande (D) [Bermersheim, *Eppelsheim, Esselborn, Westhofen, Wißberg, Wolfsheim]	MN 9	HLMD	Klähn 1922, Gaziry 1994, Tobien 1978, 1980, 1986
	Dorn-Dürkheim 1 (D)	MN 11	SMF	Gaziry 1997
	Kornberg (A)	Pannon	LMJ	Mottl 1969
	Laaerberg (A)	Pannon E	NHMW	Schlesinger 1917
	Mannersdorf (A)	Pannon H/F	NHMW	Schlesinger 1917
	Meidling (A)	Pannon D/E	NHMW	Schlesinger 1917
	Nombrevilla (E)	late Miocene	MNCN, IPMC	Mazo 1977
	Polinyá (E)	MN 9	MGB	Mazo 1977
	Stettenhof (A)	Pannon	NHMW	Tobien 1978
Tetralophodon atticus (Wagner, 1857)	*Pikermi (GR)	MN 11/12	BSP	Tassy 1985
gen. indet. *gigantorostris* (Klähn, 1922)	*Bermersheim (D)	MN 9	NHMM-LS	Tobien 1980, 1986
**Anancus arvernensis* (Croizet & Jobert, 1828)	Concud (E)	MN 12	ColA	Mazo 1977, 1996
	Dorn-Dürkheim 1 (D)	MN 11	SMF	Gaziry 1997
**Archaeobelodon filholi* (Frick, 1933)	Bézian (F)	MN 4	ColBu	Tassy 1989
	*Sansan (F)	MN 6	MNHN	Tassy 1989
Platybelodon danovi (Borissiak, 1928)	*Belomechetskaja (GO)	MN 6	PIN	Tobien 1976
gen. indet. *grandincisivus* (Schlesinger, 1917)	Kertch (UA)	late Miocene	UTE?	Tassy 1985
	Mannersdorf (A)	Pannon H/F	NHMW	Schlesinger 1917
	Orjachovo (BUL)	Sarmat	BAS	Tassy 1985
	Pestszentlörincz (H)	late Miocene	MAFI	Schlesinger 1922
Choerolophodon chioticus Tobien, 1980	*Thymiana 1 (GR)	MN 5	UA	Tobien 1980, Tassy 1985
**Choerolophodon pentelici* (Gaudry & Lartet, 1856)	*Pikermi (GR)	MN 11/12	MNHN	Osborn 1936, Tassy 1985
	Samos (GR)	MN 11-13	NHMW, AMNH	Schlesinger 1917, Osborn 1936
	Veles (MAC)	MN 13	?	Pavlovic & Eremija 1991

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