

# Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior

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## Abstract

With the addition of 13 new taxa, we recognized 175 species and subspecies of proboscideans, classified in 42 genera and 10 families. The three extant species are: forest African elephant (*Loxodonta cyclotis*), bush African elephant (*L. africana*), and Asian elephant (*Elephas maximus*, with three subspecies). Rigorous analysis of characters published or awaiting publication is imperative for better understanding of the cladistic relationships among currently recognized proboscideans. Here we focus on “aquatic ancestry” of Proboscidea, interordinal relationships within Placentalia, proboscidean taxonomy in general and South American in particular, anatomy and physiology and some ecological considerations. New taxa above the family level include sister taxa Mammutida and Elephantida, and Plesielephantiformes as a sister taxon to Elephantiformes. Neontological research is currently under way on the hyoid apparatus, lungs, brain, hearing, ecology and behavior. Topics for future research include: phylogenetic positions of anthracobunids, *Moeritherium*, tetralophodont gomphotheres, *Stegolophodon* and *Stegodon*, and intra-familial relationships among *Loxodonta*, *Elephas* and *Mammuthus*, and continuing studies on encephalization quotient. Certain anatomical features and functions (e.g., the hyoid apparatus that helps in food procurement, in production of infrasonic sounds, and in storing water to be used in time of stress) evolved about 25 million years ago, in time for diversification into new niches when grasses appeared in the landscape.

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## 1. Introduction

A landmark of evolution and natural history of the Proboscidea was established with the publications of the two-part monograph by Osborn (1936, 1942). Regardless if we agree or disagree with Osborn's philosophy, he was the modern stimulus and driving force for research on proboscideans. Such an august authority with the proper connections is unique in his time and probably in perpetuity. For this reason, the 1996 volume on the Proboscidea (Shoshani and Tassy, 1996) was dedicated to Henry Fairfield Osborn, as well as to Heinz Tobien, another great figure in the history of proboscidean research.

Some of the recent advances in proboscidean research were published in Shoshani and Tassy (1996) and in Shoshani (2000). Almost every year there are new

discoveries of fossils, new studies, or new interpretations of previously published material, or of elephants' anatomy and physiology, ecology and behavior, exploration and conservation. In this paper, we will attempt to introduce briefly and summarize the recently published material.

## 2. Taxonomy & classification

### 2.1. Interordinal relationships

#### 2.1.1. Aquatic ancestry

Janis (1988, p. 293, Fig. 1) presented “new views” and depicted that “sirenians”, “desmostylians”, “*Moeritherium*”, and “proboscideans” share aquatic adaptations. Eleven years later, based on studies of a series of African elephant embryos and fetuses estimated gestational ages 58–166 days, Gaeth et al. (1999) found nephrostomes, a feature of aquatic vertebrates, in the mesonephric kidneys at all stages of development. This feature was

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not recorded in the mesonephric kidneys of other viviparous mammals, and thus the inference is that elephants had aquatic ancestors. An alternative possible explanation surmised briefly by Gaeth et al. (1999) is that nephrostomes are normally present during early stages of development (therian plesiomorphy). Due to the long period of pregnancy and development in elephants, nephrostomes are seen during a period longer than that of other placentals. This simple explanation of a paedomorphic feature does not imply any aquatic adaptation.

The idea that *Moeritherium* was adapted to an aquatic or semi-aquatic habitat goes back to Andrews (1906), Matsumoto (1923) and Osborn (1936). These authors relied on morphological and geological settings. It is one thing to infer that some early members of the Proboscidea were adapted to aquatic or semi aquatic habitat, and it is a much bigger step to infer that the living proboscideans (specifically *Loxodonta*) had aquatic ancestry. Almost everything is possible in the evolutionary biology of a lineage, and in this case, it is possible that *Loxodonta* developed nephrostomes independently of aquatic vertebrates. Alternatively, *Loxodonta* retained this plesiomorphic feature that dates further before (earlier than) the root of proboscidean origin. Many more data need to be evaluated before a firmer conclusion can be drawn.

### 2.1.2. Placental interordinal relationships

A review of the literature of placental mammalian interordinal relationships is given in Shoshani (1986), beginning with Gill (1872). All recent publications (e.g., Eizirik et al., 2001; Fischer, 1996; Murphy et al., 2001; Novacek, 1992; Shoshani and McKenna, 1998; Springer and de Jong, 2001; Waddell et al., 1999), regardless whether the data analyzed are morphological, molecular or combined, support the close relationships of Proboscidea and Sirenia (classified in Tethytheria; McKenna, 1975). Except for Fischer (see below) that opposed the following statement, Tethytheria, in turn is joined by Hyracoidea, that is, Paenungulata (Simpson, 1945) a taxon classified in Uranotheria by McKenna et al. (1997).

An exception to the above summary is that of Fischer (1989) and Fischer and Tassy (1993) who asserted that Hyracoidea is the sister-group of Perissodactyla. Seven years later Fischer (1996) depicted an uncertain phylogenetic position of Hyracoidea that might be related to Perissodactyla or to Paenungulata (= Uranotheria).

## 2.2. Intraordinal relationships within Proboscidea

### 2.2.1. Above the family level

2.2.1.1. Taxonomic revisions within South American taxa. Recent publications on South American proboscideans have increased our knowledge on the gom-

phothera fauna of this continent and their origins. Examples of these publications include Alberdi et al. (2002), Campbell et al. (2000), Coltorti et al. (1998), Ficarelli et al. (1997) and Prado et al. (2001, 2002). These are important additions since the summary chapter of Casamiquela et al. (1996).

Prado et al. (2002) recognized only two South American genera with a total of three species: *Cuvieronius*, with one species, *C. hyodon*, and *Stegomastodon*, with two species, *S. waringi* and *S. platensis*. Prado et al. (2002) concluded that *Haplomastodon* Hoffstetter, 1950 is a junior synonym of *Stegomastodon* Pohlig, 1912, and that *Notiomastodon ornatus* Cabrera, 1929 is a junior synonym of *Stegomastodon platensis* (Ameghino, 1888).

Comparing the five South American taxa listed by Casamiquela et al. (1996, p. 316) to the taxa employed by Prado et al. (2002, pp. 276, 280, 282), we note these changes: (1) *Stegomastodon platensis* includes *Stegomastodon superbus* and *Notiomastodon ornatus*, and (2) *Stegomastodon waringi* is now employed instead of *Haplomastodon waringi*. *Cuvieronius hyodon* remains a valid taxon.

2.2.1.2. Taxonomic revisions: general summary. New proboscidean taxa discovered or redefined after the summary of Shoshani and Tassy (1996) are given in Table 1, along with their geological ages and type localities. Osborn (1936, 1942) recognized 352 species and subspecies of proboscideans; they were classified in 40 genera, and eight families. Shoshani and Tassy's (1996) corresponding numbers were 162, 38 (37+ *Anthracobune*), and 8; not the same genera and families (concerning *Anthracobune*'s taxonomy, see footnotes c and e in Table 2). In this report we recognized at least 175 species and subspecies of proboscideans, classified in 42 genera and 10 families (we know of at least two new taxa that are awaiting publication). The difference of five additional genera (42 vs. 37) results from those given in Table 1, whereas the difference of two additional families (8 vs. 10) arises because, in this report, following McKenna et al. (1997), we classify *Palaeomastodon* and *Phiomia* in their respective monotypic families Palaeomastodontidae and Phiomiidae. Of the 13 new taxa listed in Table 1, five were redefined or given new diagnosis (*Deinotherium gigantissimum*, *Gomphotherium angustidens libyicum*, *Morrillia barbouri*, *Loxodonta cyclotis*, and *Palaeoloxodon*). Thus, within the period of seven years at least eight new proboscidean taxa were discovered.

An updated classification of the Proboscidea, incorporating the changes given in Table 1, is provided in Table 2. This classification is not based on a cladistic analysis including new recently described taxa and characters from Gheerbrant et al. (2002); Saegusa and Matsubara (2001); Sanders and Kappelman (2001), and Shoshani et al. (2001a, c). An alternative to this

Table 1

New proboscidean taxa discovered or redefined after the summary of Shoshani and Tassy (1996)<sup>a</sup>

Taxon, Authorship and Year of Publication <sup>b</sup>	Geological Age	Type Locality
Numidotheriidae Shoshani and Tassy, 1992 <sup>†</sup>		
<i>Phosphatherium</i> Gheerbrant et al., 1996		
<i>P. escuilliei</i> Gheerbrant et al., 1996	early Eocene <sup>c</sup>	Ouled Abdoun, Morocco
<i>Daouitherium</i> Gheerbrant and Sudre, 2002		
<i>D. rebouli</i> Gheerbrant and Sudre, 2002 <sup>d</sup>	early Eocene <sup>c</sup>	Ouled Abdoun, Morocco
Deinotheriidae Bonaparte, 1841 <sup>†</sup>		
<i>Deinotherium</i> Kaup, 1829 <sup>†</sup>		
<i>D. gigantissimum</i> Stefanescu, 1892 <sup>e</sup>	late Miocene	Gaiceana, Romania
Mammutidae Hay, 1922 <sup>†</sup>		
<i>Zygodolophodon</i> Vacek, 1877		
<i>Z. aegyptensis</i> Sanders and Miller, 2002	early Miocene	Wadi Moghara, Egypt
Gomphotheriidae Hay, 1922 <sup>†</sup>		
Choerolophodontinae Gaziry, 1976		
<i>Afrochoerodon</i> Pickford, 2001 <sup>f</sup>		
<i>A. kisumuensis</i> (MacInnes, 1942) <sup>f</sup>	middle Miocene	Maboko, Kenya
Gomphotheriinae Hay, 1922		
<i>Gomphotherium</i> Burmeister, 1837		
<i>G. angustidens libycum</i> (Fourtau, 1918) <sup>g</sup>	early Miocene	Wadi Moghara, Egypt
Amebelodontinae Barbour, 1927		
<i>Platybelodon</i> Borissiak, 1928		
<i>P. dangheensis</i> Wang and Qiu (2002) <sup>h</sup>	early Miocene	Danghe area, Gansu, China
Family <i>incertae sedis</i> (tetralophodont gomphothere)		
<i>Morrillia</i> Osborn, 1924		
<i>M. barbourni</i> (Osborn, 1921) <sup>i</sup>	Pliocene, early Pleistocene	Cambridge, Furnas County Nebraska, USA
Stegodontidae Osborn, 1918 <sup>†</sup>		
<i>Stegodon</i> Falconer, 1857		
<i>S. sondaari</i> van den Bergh, 1997	early Pleistocene	Ola Bula Fm., Flores, Indonesia
<i>S. trigonocephalus ngandongensis</i> (van den Bergh, 1997) <sup>j</sup>	late Pleistocene	Ngandong, Java, Indonesia
Elephantidae Gray, 1821		
Elephantinae Gray, 1821		
Loxodontini Osborn 1918		
<i>Loxodonta</i> Anonymous, 1827		
<i>L. cyclotis</i> (Matschie 1900) <sup>k</sup>	Recent (Holocene)	Yaunde, Cameroon
Elephantini Gray, 1821		
<i>Palaeoloxodon</i> Matsumoto, 1924 <sup>†,l</sup>	late Pleistocene	Hamamatsu Fm., Shizuoka Prefecture, Japan
<i>Elephas</i> Linnaeus, 1758		
<i>E. nawataensis</i> Tassy, 2003 <sup>†,m</sup>	late Miocene	Lothagam, Kenya

<sup>†</sup> = extinct taxon.

<sup>a</sup> With the addition of these 13 taxa, we recognized 175 species and subspecies of proboscideans (see text for details). In addition to these changes, there is another possible new species of *Stegotetabelodon*, family Elephantidae, from the late Miocene of Chorora, Awash Basin, Ethiopia (Geraads et al., 2002). Romero-Pitman (1996) and Campbell et al. (2000) reported on a new genus and species—*Amahuacatherium peruvium*. *Amahuacatherium* and *Haplomastodon* are undistinguishable on morphological grounds, and *Amahuacatherium peruvium* matches the characters of *Haplomastodon waringi* (PT, JS, and Marco P. Ferretti, personal communication). For these reasons this taxon is excluded from this table and from the classification, Table 2. Other taxonomic related questions were encountered in the work of Poulakakis et al. (2002) who employed the name *Mammuthus creticus* instead of *Elephas creticus* or *E. (Palaeoloxodon) creticus*, based on the work of Mol et al. (1996). They (Poulakakis et al., 2002) also used the taxon name *Elephas antiquus creutzburgi* instead of *Elephas creutzburgi* or *E. (Palaeoloxodon) creutzburgi*. These are slight modifications to the works of Caloi et al. (1996) and Shoshani and Tassy (1996). Gasparik (2001) allocated four proboscidean species to their respective genera as follows: *Prodeinotherium hungaricum*, *Deinotherium proavum*, *Stegotetabelodon gigantorostri*, and *S. grandincisivus*. Shoshani and Tassy (1996, pages 356, 363, 375) listed *P. hungaricum* and *D. proavum* as junior synonyms of *D. giganteum*, *S. gigantorostri* as *Tetralophodon longirostris gigantorostri*, and *S. grandincisivus* in Proboscidea *incertae sedis*. The taxonomy and systematics of these taxa need to be studied in further detail.

<sup>b</sup> To save space, except for references for authorships of new taxa, all other references to authorships that appear in Osborn (1936, 1942) and in Shoshani and Tassy (1996) are not repeated here.

Table 1 (footnote continued)

<sup>c</sup>In the original description, Gheerbrant et al. (1996) assigned the age of late Paleocene. In Gheerbrant et al. (2002), the age was corrected to earliest Ypresian (early Eocene) not Thanetian (late Paleocene).

<sup>d</sup>In Gheerbrant et al. (2002).

<sup>e</sup>After Markov et al. (2002) and e-mail (May 28, 2003) from Georgi Markov.

<sup>f</sup>After Pickford (2001, 2003), a paraphyletic taxon that includes *C. chiotius* and *C. ngorora*. *Afrochoerodon kisumuensis* is synonymous with *Choerolophodon* “*kisumuensis* group” a stem paraphyletic group of all other species of *Choerolophodon*.

<sup>g</sup>After Sanders and Miller (2002).

<sup>h</sup>Full name of the type locality as given by Wang and Qiu (2002, page 297) is: DH 199910 of Xishuigou, Subei Mongol Autonomous County, Gansu, China.

<sup>i</sup>*Morrillia* Osborn, 1924 was added per McKenna and Bell et al. (1997, page 503), and note Mo1 in Shoshani and Tassy (1996, page 361). Osborn (1921, page 10) described *Tetralophodon barbouri* a new species based on the type specimen, a molar, catalogue no. Nebraska State Museum 4.22.6.16. Osborn (1924, page 1, also in 1936, pages 349–352, 377–379) considered *Morrillia* a subgenus of *Tetralophodon*. Yet, in Osborn (1936, pages 690, 739) *Morrillia* was described as a genus. Type locality for catalogue no. Neb. State Mus. 4-22-6-16 was given in Osborn, 1936 (pages 377, 379).

<sup>j</sup>After van den Bergh (1997) and e-mail (May 28, 2003) from John de Vos.

<sup>k</sup>Grubb et al. (2000) provided morphological evidence to justify the elevation of *cyclotis* from a subspecies of *Loxodonta africana* to a species category. Roca et al. (2001) provided molecular data that corroborated Grubb et al.’s (2000) finding. Yet, Eggert et al. (2002), based also on molecular data, noted that there is no differentiation between *L. cyclotis* and *L. africana* but a difference between geographical groups that do not fit with a clear-cut *cyclotis-africana* separation.

<sup>l</sup>Shoshani and Tassy (1996) considered *Palaeoloxodon* a subgenus of *Elephas*. Shoshani et al. (2001a), based on the work of Inuzuka (1977a, b) and Shoshani and Takahashi’s morphological observations as well as studies of skeletons of *P. naumanni* (J. Shoshani, personal observation, unpublished), suggested that *Palaeoloxodon* is a *bona fide* genus. There are, however, unresolved taxonomic questions concerning the relationships and the separation of all species allocated to *Palaeoloxodon* and all species allocated to *Elephas*. There is also the question of geological age—if *Palaeoloxodon* and *Elephas* are sister groups, what are their earliest known species and how to identify them?

<sup>m</sup>*E. nawataensis* is the earliest known species assigned to *Elephas* (Tassy, 2003).

classification (given in McKenna et al., 1997, and presented in part by Shoshani et al., 2001a), here modified to state that taxa with two lophs, and without inflated postcingulum on M2 (that is, members of the family Numidotheriidae, Barytheriidae, and Deinotheriidae) could be monophyletic, and that this group is the basal unit of Proboscidea, rather than taxa with expanded M2 and M3 that have inflated postcingulum on M2, and M3 with nearly three lophs (e.g., Moeritheriidae) or with three-lophed cheek teeth (e.g., Phiomiidae). Shoshani (1996, p. 171) conducted such a test and found that the score of the tree was raised by 13 steps from the most parsimonious tree. Shoshani et al. (2001a) proposed the name Plesiephantiformes as a sister taxon to Elephantiformes. In that scheme, Plesiephantiformes includes: Moeritheriidae, Numidotheriidae, Barytheriidae, and Deinotheriidae. Elephantiformes includes: Palaeomastodontidae, Phiomiidae, Mammutidae, Gomphotheriidae, tetralophodont gomphotheres, Stegodontidae, and Elephantidae. Here, we exclude Moeritheriidae from Plesiephantiformes, and suggest the synapomorphy of true bilophodonty (character 135 of Tassy, 1996; character 53 of Shoshani, 1996) for Plesiephantiformes. The Elephantiformes clade is supported by 13 synapomorphies, 9 dental and 4 non-dental (Tassy, 1996), or by 11 synapomorphies, 8 dental and 3 non-dental (Shoshani, 1996).

The modified classification (Table 2, incorporating taxa from Table 1) includes changes to facilitate easier relationships in higher and lower categories or ranks, yet this classification is non-ranked above the superfamily

ranking; see footnote a in Table 2. Thus, new higher taxa include Plesiephantiformes, Mammutida and Elephantida (Shoshani et al., 1998). Subfamilies and tribes were added to elucidate cladistic findings. In addition, we now include *Choerolophodon* (subfamily Choerolophodontinae) in the family Gomphotheriidae for the sake of simplification, not on the basis of new cladistic data.

2.2.1.3. *Number of species and subspecies within the Proboscidea.* The revision of the total of 175 species and subspecies of proboscideans includes living and extinct forms. Today we recognize three living species. Two are monotypic and one has three subspecies; they are: the forest African elephant (*L. cyclotis*), the bush African elephant (*L. africana*), and the Asian elephant (*E. maximus*). Grubb et al. (2000) provided morphological evidence for elevating the African elephants subspecies categories to species level, and Roca et al. (2001) provided molecular evidence corroborating these morphological findings. Debruyne et al. (2003) demonstrate on molecular grounds that so-called pigmy elephants of Central Africa belong to *L. cyclotys*. Shoshani and Eisenberg (1982) recognized three subspecies of *E. maximus*: the Sumatran Asian elephant (*E. m. sumatranus*), the mainland Asian elephant (*E. m. indicus*), and the Sri Lankan Asian elephant (*E. m. maximus*). The sequence of listing represents an evolutionary trend (Shoshani, 2000). Thus, *E. m. sumatranus* is suggested to be the most primitive of the three subspecies, *E. m. maximus* the most derived, whereas *E. m. indicus* is an intermediate form. Evidence for this trend includes 20

Table 2

A simplified non-ranked, classification of the Proboscidea at the genus level (modified after Shoshani et al., 1998, and McKenna, Bell et al., 1997), incorporating genera given in Table 1.<sup>a,b</sup>

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Mammalia Linnaeus, 1758  
 Theria Parker and Haswell, 1897  
 Placentalia Owen, 1837 (= Eutheria Huxley, 1880)  
 Epitheria McKenna, 1975  
 Ungulata Linnaeus, 1766  
 Uranotheria McKenna, Bell et al., 1997 (= Paenungulata Simpson, 1945, in part)  
 Tethytheria McKenna, 1975  
 Tethytheria *incertae sedis* Genus *Anthracobune* Pilgrim, 1906<sup>†,c</sup>  
 Proboscidea Illiger, 1811<sup>d,e</sup>  
 Proboscidea *incertae sedis* Family Moeritheriidae Andrews, 1906<sup>†</sup>  
 Genus *Moeritherium* Andrews, 1901<sup>†</sup>  
 Plesielephantiformes Shoshani et al., 2001a  
 Family Numidotheriidae Shoshani and Tassy, 1992<sup>†,f</sup>  
 Genus *Phosphatherium* Gheerbrant et al., 1996<sup>†</sup>  
 Genus *Daouitherium* Gheerbrant and Sudre, 2002 in Gheerbrant et al., 2002  
 Genus *Numidotherium* Mahboubi et al., 1986<sup>†</sup>  
 Family Barytheriidae Andrews, 1906<sup>†</sup>  
 Genus *Barytherium* Andrews, 1901<sup>†</sup>  
 Family Deinotheriidae Bonaparte, 1841<sup>†,g</sup>  
 Genus *Prodeinotherium* Ehik, 1930<sup>†</sup>  
 Genus *Deinotherium* Kaup, 1829<sup>†</sup>  
 Elephantiformes Tassy, 1988  
 Elephantiformes *incertae sedis* Genus *Hemimastodon* Pilgrim, 1912<sup>†,c</sup>  
 Family Palaeomastodontidae Andrews, 1906<sup>†</sup>  
 Genus *Palaeomastodon* Andrews, 1901<sup>†</sup>  
 Family Phiomiidae Kalandadze and Rautian, 1992<sup>†</sup>  
 Genus *Phiomia* Andrews and Beadnell, 1902<sup>†</sup>  
 Elephantimorpha Tassy and Shoshani, 1997 in Shoshani et al., 1998  
 Mammutida Tassy and Shoshani, 1997 in Shoshani et al., 1998<sup>†</sup>  
 Superfamily Mammutoidea Hay, 1922<sup>†</sup>  
 Family Mammutidae Hay, 1922<sup>†</sup>  
 Subfamily Eozygodontinae, McKenna, Bell and Shoshani, 1997 in McKenna, Bell et al., 1997<sup>†</sup>  
 Genus *Eozygodon* Tassy and Pickford, 1983<sup>†</sup>  
 Subfamily Mammutinae Hay, 1922<sup>†</sup>  
 Genus *Zygodolophodon* Vacek, 1877<sup>†</sup>  
 Genus *Mammut* Blumenbach, 1799<sup>†</sup>  
 Elephantida Tassy and Shoshani, 1997 in Shoshani et al., 1998  
 Superfamily Gomphotherioidea Hay, 1922<sup>†</sup>  
 Family Gomphotheriidae Hay, 1922 (trilophodont gomphotheres)<sup>†</sup>  
 Gomphotheriidae *incertae sedis* Genus *Gnathabelodon* Barbour and Sternberg, 1935<sup>†,c</sup>  
 Subfamily Choerolophodontinae Gaziry, 1976<sup>†</sup>  
 Genus *Afrochoerodon* Pickford, 2001<sup>†,h</sup>  
 Genus *Choerolophodon* Schlesinger, 1917<sup>†</sup>  
 Subfamily Gomphotheriinae Hay, 1922<sup>†</sup>  
 Genus *Gomphotherium* Burmeister, 1837<sup>†</sup>  
 Subfamily Amebelodontinae Barbour, 1927<sup>†</sup>  
 Genus *Archaeobelodon* Tassy, 1984<sup>†</sup>  
 Genus *Serbelodon* Frick, 1933<sup>†,c</sup>  
 Genus *Protanancus* Arambourg, 1945<sup>†,c</sup>  
 Genus *Amebelodon* Barbour, 1927<sup>†</sup>  
 Genus *Platybelodon* Borissiak, 1928<sup>†</sup>  
 Subfamily *incertae sedis* Genus *Sinomastodon* Tobien, Chen, and Li, 1986<sup>†,c</sup>  
 Subfamily *incertae sedis* Genus *Eubelodon* Barbour 1914<sup>†,c</sup>  
 Subfamily Rhynchotheriinae Hay, 1922<sup>†</sup>  
 Genus *Rhynchotherium* Falconer, 1868<sup>†</sup>  
 Subfamily Cuvieroninae Cabrera, 1929<sup>†,i</sup>  
 Genus *Cuvieronius* Osborn, 1923<sup>†</sup>  
 Genus *Stegomastodon* Pohlig, 1912<sup>†,j</sup>  
 Genus *Haplomastodon* Hoffstetter, 1950<sup>†,c,j</sup>  
 Genus *Notiomastodon* Cabrera, 1929<sup>†,c,j</sup>  
 Superfamily Elephantoida Gray, 1821  
 Family *incertae sedis* Genus *Tetralophodon* Falconer, 1857 (tetralophodont gomphotheres)<sup>†</sup>

Table 2 (continued)

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Family <i>incertae sedis</i> Genus <i>Morrillia</i> Osborn, 1924 (tetralophodont gomphothere) <sup>†</sup>
Family <i>incertae sedis</i> Genus <i>Anancus</i> Aymard, 1855 (tetralophodont gomphothere) <sup>†</sup>
Family <i>incertae sedis</i> Genus <i>Paratetralophodon</i> Tassy, 1983 (tetralophodont gomphothere) <sup>†,c</sup>
Family Stegodontidae Osborn, 1918 <sup>†,k</sup>
Genus <i>Stegolophodon</i> Schlesinger, 1917 <sup>†</sup>
Genus <i>Stegodon</i> Falconer, 1857 <sup>†</sup>
Family Elephantidae Gray, 1821
Subfamily Stegotetralobelodontinae Aguirre, 1969 <sup>†</sup>
Genus <i>Stegotetralobodon</i> Petrocchi, 1941 <sup>†</sup>
Genus <i>Stegodibelodon</i> Coppens, 1972 <sup>†</sup>
Subfamily Elephantinae Gray, 1821
Genus <i>Primelephas</i> Maglio, 1970 <sup>†</sup>
Tribe Loxodontini Osborn 1918
Genus <i>Loxodonta</i> Anonymous, 1827
Tribe Elephantini Gray, 1821
Genus <i>Palaeoloxodon</i> Matsumoto, 1924 <sup>†</sup>
Genus <i>Elephas</i> Linnaeus, 1758
Genus <i>Mammuthus</i> Brookes, 1828 <sup>†</sup>

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<sup>†</sup> = extinct taxon.

<sup>a</sup>No categories were given for taxa above the Superfamily ranking because of inconsistencies in the literature (see example in note d). According to the International Code of Zoological Nomenclature (The Code; cf. Recommendation 29a and Article 36a), taxonomists have to abide by the rules for the Family Group, but they are not required to follow any rules for ranks above the Family Group. A Family Group includes categories of Superfamily, Family, Subfamily, and Tribe. The Genus category is governed by the Code, and is included for completion. For simplification, some families and genera are listed without indentation but in the sequence as they would appear on a cladogram from the most primitive (listed first) to the most derived (listed last), more or less true due to many cladistic uncertainties. We also followed The Code when it comes to deciding on the name of a taxon and the year of publication. For example, the subfamily “Dinotherina” appears in Bonaparte, 1841, Dinotheridae appears in Bonaparte, 1845, and “Dinotheriidae” in Bonaparte, 1850. The correct citation is “Dinotheriidae Bonaparte, 1841” following The Code, Article 11.7.1.3, which reads “A family-group name of which the family-group name suffix is incorrect is available with its original authorship and date, but with a corrected suffix.” The correct spelling of “Dinotheriidae” is also attributed to Bonaparte, 1841, following The Code, Article 50d “A justified emendation is attributed to the author of the name in its original incorrect spelling and not to the person making the emendation.”

<sup>b</sup>To save space, references for authorships that appear in Osborn (1936, 1942) and in Shoshani and Tassy (1996) are not repeated here.

<sup>c</sup>Shoshani and Tassy (1996, pages 155–156, 352–368) provide additional notes on the taxonomic position and synonymy of this taxon; *Anthracobune* for example has been considered a *bona fide* proboscidean.

<sup>d</sup>Traditionally, Proboscidea was considered an Order, but recently it was given a rank of Parvorder (McKenna, Bell et al., 1997). Naming of the Parvorder category is believed to better reflect the phylogenetic relationships among Sirenia, Desmostylia (extinct), and Proboscidea, all classified within Uranotheria. Ranks are arbitrary choices, but the sequence of their listing and the nesting (indentations) is intended to convey certain cladistic/phylogenetic relationships.

<sup>e</sup>This classification includes 37 of the 38 proboscidean genera (*Anthracobune* is excluded until additional evidence becomes available) listed in Appendices B and C of Shoshani and Tassy (1996), plus 5 genera from Table 1. This classification is based on the available literature; we emphasize, however, that it is a non-cladistic classification, since a rigorous analysis of all the known proboscidean characters (some are not published) has not been conducted. The estimated total number of species and subspecies of proboscideans (extinct and extant) is at least 175, of these only 3 are living, all are classified in 42 genera and 10 families.

<sup>f</sup>Listing of genera within Numidotheriidae is after Gheerbrant et al., 2002.

<sup>g</sup>As noted in the text, and in note e above, certain relationships in this non-cladistic classification require confirmation. For example, deinotheres are believed to be independently derived, and may be placed close to moeritheres and palaeomastodonts, as was suggested by Tassy’s (1982) cladistic analysis, and much as Harris (1978) and later Court (1995) believed. This hypothesis appears to gain support based on the new evidence from Chilga, Ethiopia (Sanders and Kappelman, 2001), who suggest that deinotheres are derived from bunolophodont forms.

<sup>h</sup>The inclusion of *Afrochoerodon* in this table is an error, because it is a paraphyletic taxon and belongs within *Choerolophodon* (cf. footnote f in Table 1); see also “Note Added in Proof”.

<sup>i</sup>The subfamily name of Cuvieroninae is employed as in Shoshani and Tassy (1996) and in Campbell et al. (2000).

<sup>j</sup>According to Prado et al. (2002) *Stegomastodon* Pohlig, 1912 includes *Haplomastodon* Hoffstetter, 1950 and *Notiomastodon* Cabrera, 1929. In this study, until independent research is conducted, we retain *Haplomastodon* and *Notiomastodon* as valid taxa.

<sup>k</sup>Kalb et al. (1996) proposed that *Stegolophodon* and *Stegodon* should be classified within the family Elephantidae.

pairs of ribs in *E. m. sumatranus*, 19 pairs in *E. m. maximus* and *E. m. indicus* (Temminck, 1847). Other characters include forested vs. less forested dwelling, small vs. large body size, ear size, possibly high vs. low incidence of tusks, tusk size and shape (e.g., straight vs. curved), and least vs. most skin depigmentation. Deraniyagala (1955) provided additional characters and discussion on Asian elephant subspecies; cf. Shoshani (2000). Based on DNA isolated from dung,

Fernando et al. (2003) concluded that the elephants from Borneo island (specifically the Malaysian states of Sabah and Sarawak) are “...genetically distinct, with molecular divergence indicative of a Pleistocene colonisation of Borneo and subsequent isolation”. These authors suggest, however “...that a formal reinstatement of the *E. m. borneensis* taxa await a detailed morphological analysis of Borneo elephants and their comparison with other populations”. We concur with

Fernando et al. (2003) that there should also be morphological differences among the recognized Asian elephant subspecies. Further, it would also be a stronger argument for the proposed subspecies if the recent findings of Fernando et al. (2003) would be repeated and corroborated.

In addition to the two species of African elephants currently recognized above, Eggert et al. (2002) reported on what could be interpreted as a possible third species of African elephant for the populations of the forest and savannah elephants of West Africa. Their findings are based on DNA extracted from dung of elephants in Ghana, the Ivory Coast, Mali, and Cameroon. These elephants live in both forest and savannah habitats. Their study suggests that, based on genetic data, the West African populations have been isolated from other elephant populations for as long as 2.4 million years.

There appear to be some confusion as to the concept of species in the classical sense of Mayr (1969) that biological species do not interbreed under natural conditions, but if they do, the offspring are infertile. More recently species definitions have been modified to allow hybridization (cf. Strickberger, 1996, pp. 228–232; 557–560), through introgressive hybridization, as observed in Darwin's finches (Grant and Grant, 1994). The classical biological species concept has been slightly modified to accommodate species that hybridize in nature as long as the hybrid zone is narrow, that is, only a small percentage of the population hybridizes, the rest is ecologically distinct and remains away from the hybrid zones and thus are unable to meet members of the other species, discussed in Grubb et al. (2000).

*2.2.1.4. Recently held meetings on Proboscidea and resulting publications.* By chance in 2001 two proboscidean-related meetings were held (the 8th International Theriological Congress, Sun City, South Africa, August 12–17, and the 1st International Congress of “La Terra degli Elefanti”, The World of Elephants, Rome, Italy, October 16–20). Significant findings were reported in these meetings and in the proceedings and abstracts volumes. The Rome proceedings volume (Cavarretta et al., 2001) is indeed packed with useful information and new data, even though the papers included are expanded abstracts. For example, the first *Stegotetrabelodon* reported from southern Europe (Ferretti et al., 2001), new elephant fauna from the Republic of Djibouti (Chavaillon and Berthelet, 2001), elephants in Rome (Manni, 2001), endemism in the Mediterranean Islands (Palombo, 2001), reconstruction of the facial morphology of deinotheres (Markov et al., 2001), and reports on the finding of the Jarkov mammoth (e.g., Mol et al., 2001). The abstract volume for the 8th International Theriological Congress also contains new data and information, but it is limited in scope.

Abstracts include seasonal dietary changes in elephants (Cerling et al., 2001), new proboscidean fauna from Ethiopia (Sanders and Kappelman, 2001), Eritrea (Shoshani et al., 2001c), and Thailand (Saegusa et al., 2001), and GPS-monitoring of elephants in Meru, Kenya (King et al., 2001).

## 2.2.2. Relationships within the family level

*2.2.2.1. Relationships among Loxodonta, Elephas and Mammuthus.* The fossil record of the two modern genera has been augmented during the recent years. The differentiation of *Loxodonta* and *Elephas* is contemporaneous with extinct genera *Stegotetrabelodon* and *Primelephas*, this second genus once thought to be ancestral to both lineages (Maglio, 1973). Earliest loxodont remains were isolated molars labeled “*Loxodonta* sp. ‘Lukeino stage’” by Tassy (1995). This taxon is found in the late Miocene Lukeino Formation, Baringo Basin (Kenya), and at Lothagam, Kenya, that is, between 7.3 and 5.4 Ma, and is in pene-contemporaneous levels at Nkondo, Nkondo-Kaiso area (Uganda). W.J. Sanders (personal communication, 2003) noted, however, that there is no good faunal evidence to support Nkondo being as old as 7 Ma. It has been described recently at Toros-Menalla (Chad) the locality which yielded the hominid *Sahelanthropus tchadensis*, the fauna of which is estimated between 6 and 7 Ma (Vignaud et al., 2002). The earliest known member of *Elephas* came from the Upper Member of the Nawata Formation, Lothagam area, Kenya (*Elephas nawataensis*, Tassy, 2003). Upper Nawata is dated 6.7–5.2 Ma (Leakey et al., 1996; McDougall and Feibel, 1999). The new species of *Elephas* antedates *Elephas ekorensis*, the species from the Kubi Algi Formation, Turkana, Kenya, of early Pliocene age (Maglio, 1973). Earliest members of the genus *Mammuthus* are not known in the late Miocene. The controversial species *Mammuthus subplanifrons* from the early Pliocene of southern Africa and East Africa is still the oldest known thus far. In any of the two competing hypotheses (a *Mammuthus–Elephas* clade or a *Mammuthus–Loxodonta* clade, see further), phylogeny and known stratigraphic record imply a ghost lineage for *Mammuthus* of circa 2 million years.

Ever since Maglio (1973) published his monograph on the Elephantidae, with morphological data depicting *Mammuthus* and *Elephas* closer to each other than to *Loxodonta*, many people had no reason to doubt his finding. With the advent of molecular techniques, however, it became possible to test this hypothesis using nuclear DNA or mitochondrial DNA. Focusing on most recent publications, some studies, e.g., Debruyne (2001), Debruyne et al. (2003), Thomas et al. (2000) emphasized that *Mammuthus* and *Loxodonta* share close relationships, whereas others (e.g., Yang et al., 1996; Ozawa et al., 1997) reported that *Mammuthus* and

*Elephas* are closer to each other. Thomas and Lister (2001, p. 688) concluded “A *Loxodonta*–*Mammuthus* clade has the strongest support, but *Elephas*–*Mammuthus* cannot be ruled out”. Until additional data are available and more rigorous tests are applied, we leave this issue open, because of the discrepancies of results from molecular studies, and also because investigators who use molecular data do not always employ an outgroup that is the closest living relative from which sequencing is available. In addition, problems related to denatured material have been encountered, and thus incomplete sequencing had also been encountered in trying to resolve the trifurcation of the Elephantinae taxa by molecular methods.

2.2.2.2. *Evolutionary rates among Loxodonta, Elephas and Mammuthus.* In his monograph Maglio (1973) provided evidence for evolutionary rates among *Loxodonta*, *Elephas* and *Mammuthus*, and concluded that *Mammuthus* is the fastest evolving taxon (evolving about twice the rate of *Loxodonta*). Yang et al. (1996) and Shoshani et al. (1998) provided molecular data that *Elephas* and *Mammuthus* evolved faster than *Loxodonta*, corroborating results from morphological data of Shoshani (1986).

2.2.2.3. *Possible mammoth ancestry and radiation in Africa, Eurasia and the Americas.* A simplified mammoth ancestry and inter-relationships was depicted by Shoshani et al. (1998, Fig. 3, p. 104), drawing data from the available literature (e.g., Maglio, 1973; Coppens et al., 1978; Agenbroad, 1994; Lister and Bahn, 1994; Webb and Dudley, 1995; Lambert, 1995; Lister, 1996). These ancestor-descendant relationships that span during the Pliocene and Pleistocene are summarized here for easy reference; an arrow indicates possible direction of evolution. In Africa *Mammuthus subplanifrons* → *M. africanavus*. Either one of these taxa gave rise to *M. meridionalis*, a Eurasian taxon. In Eurasia *M. meridionalis* → *M. trogontherii* → *M. primigenius*. Still in Eurasia, basal *M. meridionalis* → later form of *M. meridionalis* → *M. meridionalis* in Africa. Close to the *M. trogontherii* stock in Eurasia, “*M*” *armeniacus* appeared in the fossil record. In North and Central America: *M. hayi* (a descendant of a basal Eurasian *M. meridionalis*) → *M. columbi*, with three subspecies: *M. c. columbi*, *M. c. jeffersonii* and *M. c. exilis*. In North America, *M. primigenius* (a descendant of a basal Eurasian *M. primigenius*) is an immigrant to the New World. Lister and Sher (2001) proposed an evolutionary scenario at the local population levels for Eurasia. Northeastern Siberia is identified as an area of successive allopatric innovations that spread to Europe. For example, in Siberia, circa 800,000–700,000 years ago, mammoths approached *M. primigenius* morphology in all dental characters, anticipating the European

sequence where typical *M. primigenius* is not older than 190,000 years.

### 3. Anatomy & physiology

#### 3.1. Brain: form, function, encephalization quotient

Our knowledge on elephant brain anatomy and physiology has increased tremendously in the past few years. Cozzi et al. (2001) summarized the available literature they could find and stated that many writers cited papers on brains of elephants from second hand data of old papers dating to the XIX century. Based on dissections and histological examinations of African and Asian elephant brains, Kupsky et al. (2001) provided illustrations to show the location of the hippocampus within the limbic system and close association with the temporal lobe in elephants. Detailed structures are also depicted and described. Function of the hippocampus, based on human’s anatomy and physiology, was inferred by Kupsky et al. (2001) to include learning, memory, and control of behavior. Shoshani et al. (2001b) noted that the temporal lobe is disproportionately large compared to that of humans; they added that the temporal lobe, limbic lobe, and the hippocampus are associated with hearing, learning, memory, and emotion.

The elephant brain possesses a highly convoluted cerebrum and cerebellum that control cognitive and motor coordination, respectively. Further, its lateral portions of the cerebri, or its temporal lobes are relatively very large compared to other brain areas, they are larger and more convoluted than the temporal lobes of human brain. Temporal lobes (part of the brain’s limbic system) in humans are known to function as memory centers. Inferring function from structure, it is believed that elephants have good memories.

Elephants are known to use and make tools (Gordon, 1966, summarized by Shoshani, 2000) and show complex behaviors (Douglas-Hamilton and Douglas-Hamilton, 1975; Moss, 1988; Payne, 1998). The large amount of cerebral cortex, especially in the temporal lobe, and the well developed olfactory and limbic systems, provide anatomical corroboration for these observations.

A measure of an animal to cope with daily living problems is said to be its intelligence. Intelligence is difficult to evaluate; the next best parameter is encephalization quotient, or EQ. According to Jerison (1973, p. 61) EQ is the ratio of actual brain size to expected brain size. The novelty of this approach (adopted by many investigators, e.g., Eisenberg, 1981) is that it is an objective method of estimating the relative size of the brain to the body size. In this system, based on numerous data points on living and extinct

mammals, an EQ value of 1 is considered an “average”, below 1 is considered “below average” and above 1, is considered “above average” EQ value. A domestic horse, for example, has EQ value of 1.07, a Norway rat has 0.79, and a domestic pig has an EQ value of 0.27 (data from Eisenberg, 1981). No one has claimed that there is any direct connection between intelligence and EQ, but there appears to be at least a rough correlation. Members of the order Primates can help make this point. An early member of this order, a lemur (*Lemur*) has an EQ of 1.5, this value has become progressively larger during phylogeny, with a monkey (e.g., *Presbytis*) having 1.7, gorilla has 1.4–1.7, a chimpanzee has 2.0–2.5, *Australopithecus afarensis* has 2.2, *Homo habilis*, 3.1, late *Homo erectus*, 4.0, and *Homo sapiens* 5.8, or can have an EQ as high as 7.7 (data after Eisenberg, 1981; McHenry, 1994).

It is noted, however, that the EQ itself has been a subject of natural selection during a phylogeny of a lineage, as noted, within Primates. Similarly, one of the early proboscideans, the *Moeritherium* had an EQ close to 0.2 (Jerison, 1973), a value that increased during the million of years and reached the value of up to 2.66 in modern elephantids (Shoshani’s data; cf. Fig. 1). Of the 12 elephant brains investigated, 6 were Africans (3 males, 2 females, 1 sex unknown), and 6 were Asians (1 male, 3 females, 2 sex unknown). The average EQ for the African elephants is 1.58, and the corresponding average for the Asians is 2.03. Data available are meager to compare between the sexes.

Based on the data presented in Eisenberg (1981) on mammals in general, and data presented in Shoshani (1998), as well as new data on EQ for elephants since that article, it appears that one can make these general observations. Mammals that have been observed to use tools, have EQ values above 1, and mammals that have been observed to make tools, have EQ values close to or above 2, e.g., elephants, chimpanzees and hominids. Generally, high EQ values are correlated with long period of learning situation, information retrieval based on experience (not preprogrammed), rich but dispersed food source, late sexual maturation, increased active antipredator strategies, and increased potential longevity of life-span (Eisenberg, 1981).

### 3.2. Hyoid apparatus: form and function

Little known, the hyoid apparatus is an important component of the skeletal system, yet, its function is associated with the digestive system—as the tongue attached onto it helps to procure and swallow food, and the respiratory system—as the larynx attached on the hyoid helps control the volume of air inhaled or exhaled, and produces sounds. As will be discussed below, the hyoid apparatus of elephants is unique among mammals, and it together with extrinsic and intrinsic muscles help produce the infrasonic calls discovered only recently (Payne, 1998).

Situated in the gular region, the hyoid apparatus in mammals in general is composed of nine bones (four

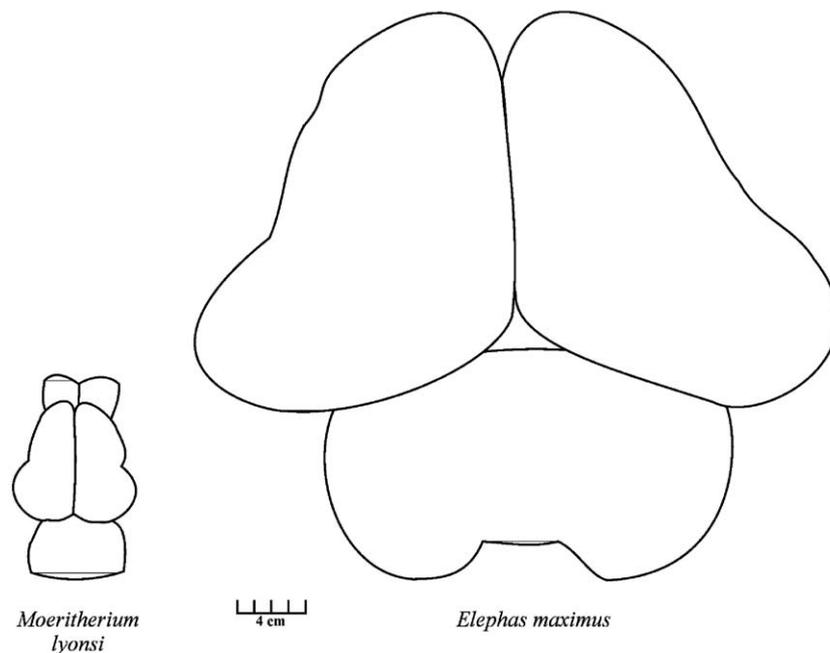


Fig. 1. Simplified drawings of proboscidean brains drawn to scale: *Moeritherium lyonsi* on left and *Elephas maximus* on right. Encephalization quotient (EQ) value of *Moeritherium* as calculated by Jerison (1973) is 0.2 and a high value for *Elephas* (calculated by Shoshani) is 2.7. EQ can be viewed as a character subjected to natural selection during a phylogeny of a lineage, e.g., within Primates and Proboscidea (brain of *Moeritherium* after Jerison, 1973; drawings by Gary H. Marchant).

pairs and one odd) connected to the cranium as a box-like via the cartilaginous tympanohyal. Sometimes the tympanohyal ossifies and the number of bones increases to 11. In all proboscideans examined, from the Miocene to the Holocene, the hyoid apparatus is composed of five bones: a pair stylohyoidea, a pair of thyrohyoidea, and a single basihyoideum. Shoshani and Marchant (2001) provide the most recent findings on the hyoid apparatus of proboscideans. This study is based on examination of 248 bones (194 stylohyoidea, 33 thyrohyoidea, and 21 basihyoidea), some of which are based on dissection of carcasses to understand the muscular associations and functions. In brief, unlike many mammals where the hyoid is a box-like structure, in elephants it is composed of two parts, the upper stylohyoidea and the lower, usually fused, thyrohyoidea and basihyoideum. This loose connection between the upper and lower hyoid elements, together with associated musculature, enables the lowering of the larynx (attached to the lower part) and be more flexible in the variation of sound production. Infrasonic calls production, it is suggested, is possible because of this unique development, as well as the size and laryngeal mechanism, discussed in brief by Meng et al. (1997).

Another function of the hyoid apparatus and the associated musculature is the ability to store water to be used in time of stress. In the gular region, at the base of

the hyoid apparatus there is a pocket-like structure called the pharyngeal pouch (described by Watson, 1875). Observations on elephants in captive and field conditions, show that elephants draw water from this pouch and douse themselves when the ambient temperature is high (e.g., Douglas-Hamilton and Douglas-Hamilton, 1975; Payne, 1998; other details in Shoshani, 1998).

Comparing processes and muscle scars on bones of extinct and living proboscideans, it is suggested that the morphology of the hyoid apparatus probably evolved sometime close to the Oligocene and Miocene boundary, some 25 million years ago. Cladistic analysis of morphological characters resulted in the cladogram shown in Fig. 2. Aside from the function of food procurement, the ability to communicate infrasonically appears to be an important element of herd cohesion over long distances. This plus the ability to store water to be used in time of stress, appear to be paramount development for the diversification into new niches in times when grasses appeared in the landscape (see discussion Shoshani, 1998).

### 3.3. Respiratory: form and function

Early in the 20th century (Todd, 1913) and subsequent investigators (e.g., Short, 1962) observed that

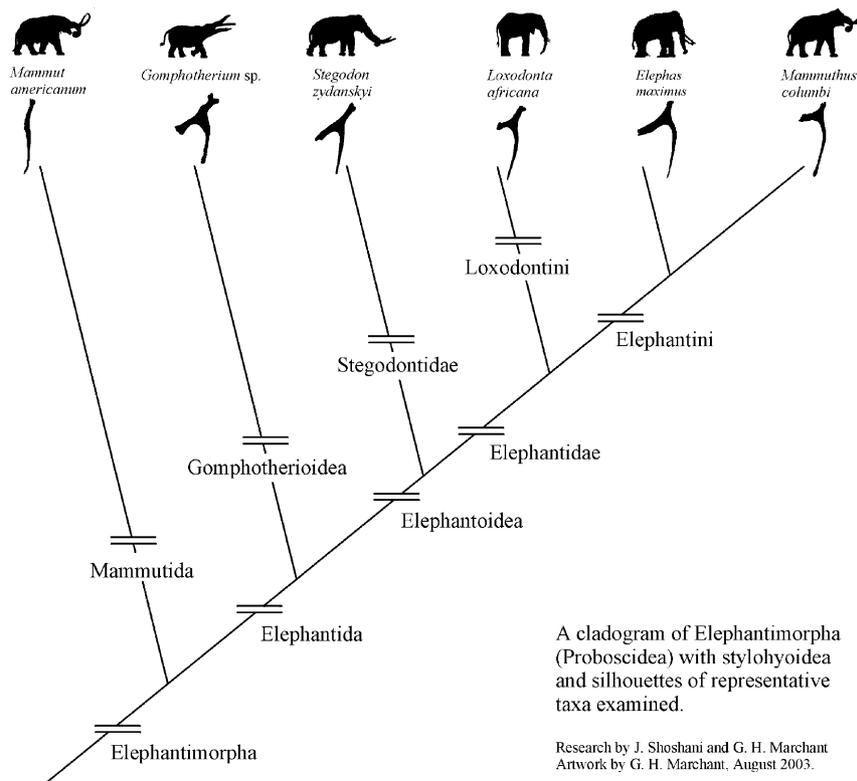


Fig. 2. A cladogram of proboscidean taxa based on hyoid characters presented in Shoshani and Marchant, 2001 (artwork by Gary H. Marchant).

elephants have little or no pleural cavity in adult living elephants. The function of this peculiarity has not been addressed properly, however, West (2001) speculated on the possible functions of the lack of pleural cavity, unfortunately, his arguments lack substance. For example, West (2001) states that absence of a pleural cavity and the associated pressure or lack of it co-evolved with the trunk, which “may have evolved to allow it to snorkel while living in the water”. This is too simplistic an explanation, and could be easily be reversed. In other words, swimming, displaying, drinking and eating (in response to growing taller over many generations) may have provided the stimulus for the development of the trunk. It is probable that the trunk evolved for use on land and secondarily proved useful for snorkelling, and possibly the pleural features are an autapomorphic adaptation for this behavior (but how often do elephants really snorkel?). Earliest proboscideans did not have a proboscis, thus this feature cannot be used in support of the hypothesis that the trunk is associated with the aquatic ancestry of elephants, as proposed by Gaeth et al. (1999). Further, sirenians, purely aquatic mammals, the closest living relatives of proboscideans, have normal lungs with pleural cavities (Rommel and Reynolds, 2000). Additionally, West (2001) erroneously claimed the intra-abdominal testes in elephants as evidence for proboscidean aquatic ancestry (intra-abdominal testes is a primitive mammalian character). As noted above, the hypothesis that proboscideans have aquatic ancestors (Gaeth et al., 1999) requires further evidence, also does the lung peculiar anatomy of adult living elephants.

#### 4. Recent thoughts on extinction of proboscideans

Various ideas have been proposed on the causes of extinctions of proboscideans. Many are related to climatic changes, ecological parameters, and overkill hypothesis (Martin and Klein, 1984; Owen-Smith, 1989; Putshkov, 1997; Graham, 2001). Shoshani and Fisher (1992) summarized the major possible causes for extinction of proboscideans as habitat changes, interspecific competition, specialization, generation time, and over hunting by Paleoindians.

A different idea was proposed by MacPhee (1999) and MacPhee and Marx (1999) who believe that the disappearance of mammoths and other species during the Pleistocene was caused by an apocalyptic disease. Possibly, a disease-causing organism (e.g., virulent viruses) may have been carried by humans or the animals that traveled with them, as they entered North America. Animals of the New World had no immunity to the microbe and were helpless against this ‘Hyperdisease’.

#### 5. Future research

To conduct rigorous cladistic analysis incorporating all the new taxa reported here and soon to be published, is paramount. This includes recently described or mentioned taxa and characters from Gheerbrant et al. (2002), Saegusa and Matsubara (2001), Sanders and Kappelman (2001), and Shoshani et al. (2001a, c). Some of these publications are in abstract form, and thus it is not yet possible to access full description of the characters. Topics to be investigated in the future might include whether anthracobunids should be included in the Proboscidea or as a sister group in the Tethytheria, whether *Moeritherium* should be placed in Plesielephantiformes (cf. Table 1), or as an earlier offshoot of Proboscidea, what is the taxonomic position of Deinotheriidae, and of tetralophodont gomphotheres (i.e., those with four ridges on 4th premolars, the 1st and 2nd molars), should *Stegolophodon* and *Stegodon* be placed in the family Stegodontidae or in the family Elephantidae, and what are the intra-familial relationships among *Loxodonta*, *Elephas* and *Mammuthus*—is it (*Loxodonta* (*Mammuthus* + *Elephas*)) as suggested by the classical morphological data, or (*Elephas* (*Mammuthus* + *Loxodonta*)) based on some molecular data (see discussion above)? In addition, it is suggested that future studies should be continued on the form and function of the brain, infrasonic production and perception, and collect additional data on EQ. The phenomenon of the lack of pleural space in adult elephants is intriguing and requires further research, so is the question of aquatic ancestry. Some of these topics were discussed in Shoshani and Tassy (1996), other were noted above.

#### 6. Concluding remarks

It is the nature of scientific investigation that when certain questions are answered, new ones surface. So is the case in this investigation. A glance at the section Future Research gives this perspective. Nonetheless, much progress has been made since the days when little or no criticism were offered to manuscripts before publication. Modern molecular techniques are employed, but often even these do not produce any better results than the morphological approaches—the *Loxodonta*, *Elephas*, *Mammuthus* is a case in point.

From an evolutionary perspective and the survivability of an individual, or a population (that is, of a species), the most fascinating is the EQ value. Can we correlate EQ value with degree of intelligence, and if so to what extent? The answer is probably yes. It is suggested that EQ values of close to 1+ may be associated with tool using, and that EQ values of close to 2+ may be associated with tool making. Concomitant with the enlargement of the brain (and associated

high EQ value) the co-evolution of infrasonic communication and the ability to store water for many hours and use it only in time of stress, are examples of characters that helped elephants to adapt to diverse habitats.

### 6.1. Note added in proof

Kappelman et al. (2003) reported on five new proboscidean taxa (no names given) from the late Oligocene site of Chilga, Ethiopia. Pickford (2003) named two new genera and species: *Progomphotherium maraisi* and *Afromastodon coppensi*, both placed in the family Gomphotheriidae, and both are from the early Miocene of Namibia. With the deletion of *Afrochoerodon* from Table 2, and with the addition of these taxa, we recognized 177 species and subspecies of proboscideans, classified in 43 genera. These changes will affect entries to Tables 1 and 2. Pickford (2003:217) also used the name *Afromastodon libycus* instead of *Mastodon spenceri* whereas Sanders and Miller (2002:389–391) assigned the name *Gomphotherium angustidens libycum* to *Mastodon spenceri*. In addition Pickford (2003:231–232) used the name *Afrochoerodon ngorora* instead of *Choerolophodon ngorora* of Tassy (1986), and *Afrochoerodon zaltaniensis* instead of *Choerolophodon zaltaniensis* of Gaziry (1987). Pickford (2001:99) also employed the name *Afrochoerodon chioticus* instead of *Choerolophodon chioticus* of Tobien (1980), but see note f in Table 1.

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