

Hyoid apparatus: a little known complex of bones and its “contribution” to proboscidean evolution

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SUMMARY: The hyoid apparatus of extant and extinct proboscidean taxa is composed of five bones found deep in the throat – a pair of stylohyoidea, a pair of thyrohyoidea, and unpaired basihyoideum. These are little known and seldom collected. Functions associated with this apparatus include feeding, sound production (including infrasonic calls), and water storage in the pharyngeal pouch used to spray themselves when excessive heat prevails and there is no water source nearby. These functions are believed to have co-evolved in late Oligocene to early Miocene periods, about 25 million years ago. Results from cladistic analyses of hyoidean characters comprise these relationships: (*Mammot* (*Gomphotherium* (*Stegodon* (*Loxodonta* (*Elephas*, *Palaeoloxodon*, *Mammuthus*)).

1. INTRODUCTION

When the senior author began his study on hyoids of elephants (about 25 years ago) there was little information concerning the hyoid apparatus of proboscideans. A few museums possess these delicate small bones. In paleontological excavations, one often finds portions of a stylohyoid, thyrohyoid or basihyoid. Even hyoid bones of living elephants are often not recognized or are damaged during dissection (cf. Fig. 1). Broken hyoid elements are confused with rib fragments, and one frequently finds them among scraps in neontological or paleontological museum collections. It soon became evident that hyoid bones of proboscideans are rare finds. Shoshani's interest in the hyoid apparatus grew when he learned that in one paper (Green 1956) a stylohyoid which appeared to have been associated with remains of *Amebelodon* (a gomphothere, order Proboscidea; M. Skinner, pers. comm. by way of M. C. McKenna) was described as an antler of an extinct deer, *Meryceros major*, family Antilocapridae, order Artiodactyla. This is an

example of unfamiliarity with these bones and it inspired the launching of a long-term study of the hyoids of proboscideans. In addition, knowledge of the hyoid apparatus of living elephants may help us to better understand fossil taxa and vice versa.

Thus, the objectives of this study have been to systematically study any hyoid bones of proboscideans, photograph and/or draw them, note their positions in the gular region, describe them, their functions, and record any phylogenetic changes among taxa. During the years, we also have provided an overall assessment of the importance of these bones in term of their physiology and evolution.

2. MATERIALS AND METHODS

Details on the osteological material studied are given below. Bones were photographed and drawn in lateral and medial views and cross sections were made. Measurements and other morphological characters were entered into data sheets. A total of 38 characters has been evaluated, of which 20 may be useful in phylo-

genetic and functional analyses (e.g. Shoshani 1986; Shoshani, 1996; Tassy & Shoshani 1988).

2.1 Stylohyoidea

Material of hyoid apparatus of living and extinct proboscideans studied, amount to 194 stylohyoid elements representing 151 individuals: 81 elephantids, 7 stegodontids, 40 gomphotheriids, 22 American mastodons, and 1 deinothere. The breakdown is: 81 elephantids, with at least eleven taxa, e.g. *Loxodonta cyclotis*, *L. africana*, *Elephas maximus*, *E. recki*, *Palaeoloxodon antiquus*, and *Mammuthus primigenius* [112 bones, 31 pairs, 37 odd bones (19 left, 18 right), 13 unknown; 8 males, 20 females, 53 of unknown sex], 7 stegodontids, with at least four taxa, e.g. *Stegodon auro-rae* [7 bones, 0 pairs, 7 odd bones (4 left, 3 right); no sex was assigned], 40 gomphotheriids, with at least four taxa, e.g. *Gomphotherium productum* and *Amebelodon floridanus* [43 bones, 3 pairs, 34 odd bones (20 left, 14 right), 3 unknown; no sex was assigned], 22 American mastodons, *Mammut americanum* [31 bones, 6 pairs, 16 odd bones (10 left, 6 right), 3 unknown; 4 males, 2 females, 16 of unknown sex], and 1 deinothere (*Deinotherium giganteum*).

2.2 Thyrohyoidea

A total of 33 thyrohyoidea was examined, representing 22 individuals. These include: 9 elephantids, 1 stegodontid, 1 gomphotheriid, and 11 American mastodons. The breakdown is: 9 elephantids, that is, *Loxodonta africana*, *Elephas maximus*, and *Mammuthus primigenius* [17 bones; 8 pairs, 1 odd bone, laterality unknown; unknown sexes], 1 stegodontid, that is, *Stegodon zydanskyi* [2 bones; 1 pair, unknown sex], 1 gomphotheriid, that is, *Amebelodon floridanus* [1 bone, laterality and sex unknown], 11 American mastodons, *Mammut americanum* [13 bones; 2 pairs, 6 odd bones (5 left, 1 right), 3 odd laterality unknown; sexes unknown for all].

2.3 Basihyoidea

A total of 21 basihyoidea of proboscideans was examined (12 elephantids, 1 stegodon, 2 gomphotheriids, and 6 mammutid). No breakdown is given since the basihyoid is an odd bone in adult animals. Of these 21 bones, the sex of only 3 proboscideans is known; all are females Asian elephants, *Elephas maximus*.

2.4 Soft tissue

Dissections of gular musculature have been essential for learning about origin and insertion of muscles and to evaluate function in extinct species. We dissected and obtained data from nine specimens of *Loxodonta africana* (n=3) and *Elephas maximus* (n=6). Detailed notes, photographs and drawings of muscles were made with reference to published records (e.g. Eales, 1926).

3. RESULTS AND DISCUSSION

Mammals in general have a hyoid apparatus comprised of nine bones (single basihyal, and paired thyrohyals, ceratohyals, epihyals, and stylohyals). These articulate in a box-like fashion and attach via the tympanohyal cartilages to the basicranium deep in the throat (Fig. 1). Occasionally, the tympanohyals ossify, and the hyoid complex thus comprises of 11 bones (Gasc 1967; Walker and Homberger 1992, personal observations). In extinct and living proboscideans, the ceratohyals and epihyals were lost, creating a gap between the stylohyals and the basihyal-thyrohyal complex (these three bones are often fused and appear as an upside down English letter "U"). Having lost the connection with the epihyals and ceratohyals, the basihyal and the thyrohyals unit descended downwards away from the cranium similar to the situation found in humans (Gray 1901). In a typical mammal, the stylohyals, or stylohyoidea, are straight rod-like bones. In human, the stylohyals are fused to the basicranium; they are longer in males than in females (Gray 1901). In early proboscideans (e.g. *Mammut americanum*), this bone is also simple, but

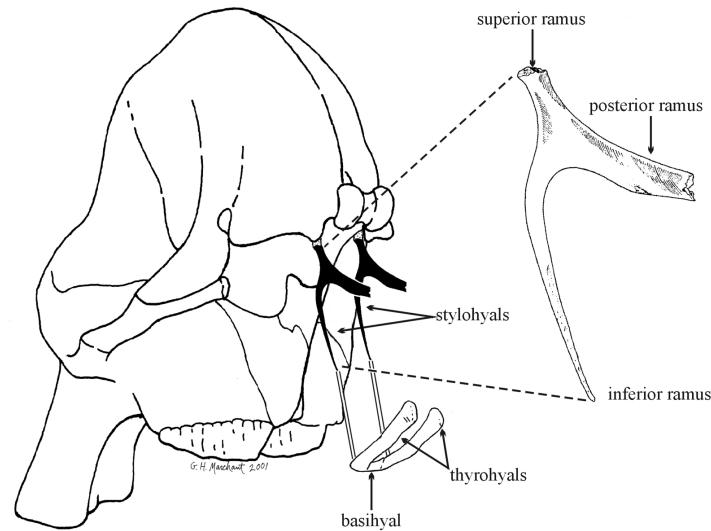


Fig.1 - Cranium of an Asian elephant (*Elephas maximus*) with hyoid bones in place, and labeled stylohyoideum (modified after Inuzuka *et al.* 1975).

often with development of an incipient additional projection. In advanced proboscideans, e.g. gomphotheres and elephantids, an additional process (“arm”) has developed, rendering the bone to look like the English letter “Y”. One “arm” of the “Y” is the superior ramus, the other “arm” is posterior ramus, and the third “arm” is the inferior ramus (Fig. 1; terminology after Inuzuka *et al.* 1975). Superior and inferior rami are the original (primitive) structures; the posterior ramus is a new development within Proboscidea. In elephantid taxa, the posterior ramus serves for attachment of the digastricus muscle that (together with the lateral pterygoid muscle) helps to open the jaw (Garrod 1875; Gasc 1967). In living elephants these paired muscles attach on the hyoid apparatus to make up the muscular tongue: styloglossus (from stylohyoidea), hyoglossus lateralis (from thyrohyoidea), hyoglossus anterior (from basihyoideum), and geniohyoglossus (from mandibular symphysis and basihyoideum). Functions of these muscles are (after Watson 1874; Eales, 1926; Tortora & Anagnostakos 1975): styloglossus – elevates tongue and draws it backwards (retraction); hyoglossus lateralis and hyoglossus anterior – draw tongue

sideways, and help in depression and retraction; geniohyoglossus – depresses and thrusts tongue forward (protraction). These muscles and their relationships to other gular muscles are depicted in figures 2 and 3.

4. EVOLUTIONARY TRENDS OBSERVED

4.1 Basihyoidea

Through time, these bones have become thinner and straighter, and have lost the geniohyoideus ridge. American mastodons and gomphotheres have basihyoidea that are round in cross section; those of stegodontids and elephantids are flattened. Early proboscideans have arched basihyoidea on anterior and posterior sides; those of advanced taxa are straight at front and arched at back. *M. americanum* and gomphotheres possess the geniohyoideus ridge (for attachment of geniohyoideus muscle) on the ventral side of the basihyoideum; all elephantids examined lack this ridge.

4.2 Thyrohyoidea

Through time, these bones have become less

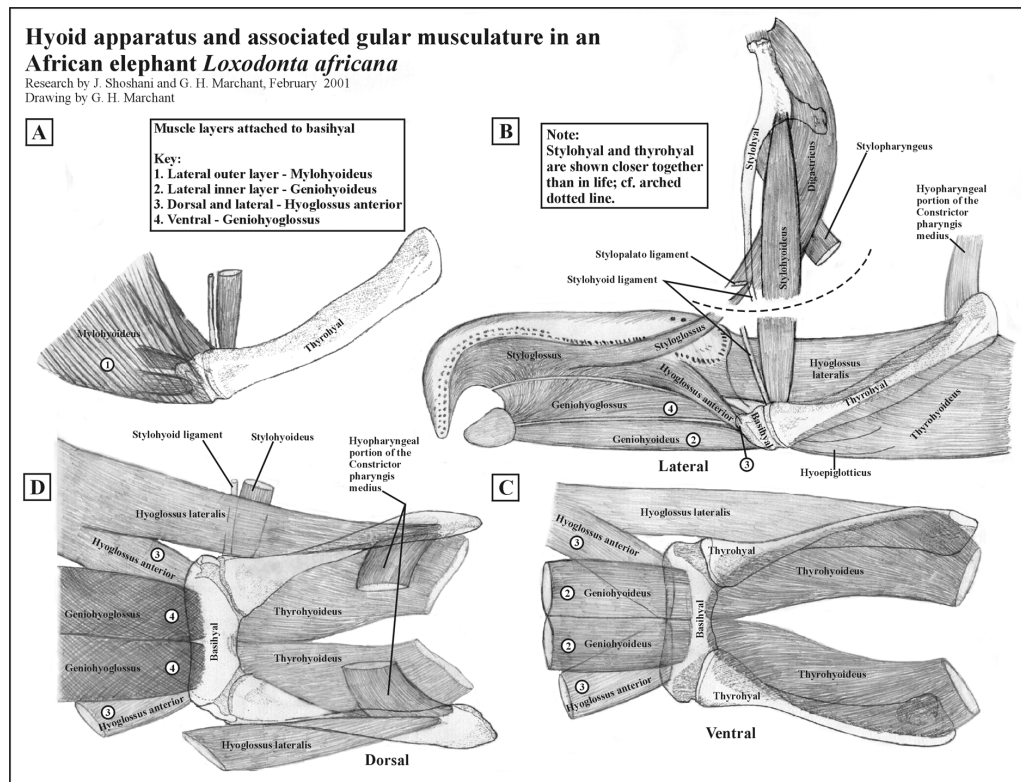


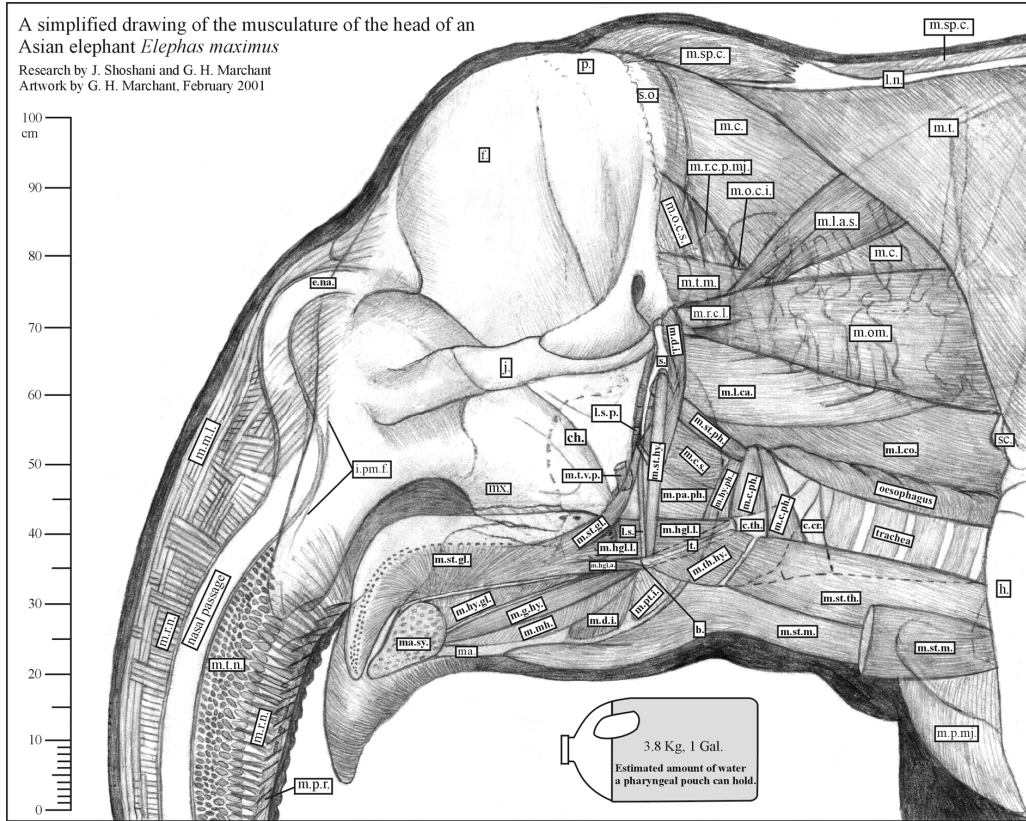
Fig. 2 - Simplified drawings of the hyoid apparatus and associated gular musculature in an African elephant, *Loxodonta africana* (artwork by G.H. Marchant).

robust, more twisted. Examples: American mastodons and gomphotheres have thyrohyoidea that are robust and slightly twisted; in advanced taxa the thyrohyoidea are more delicate and more twisted. In dorsal view, the posterior part of the left thyrohyoideum twists clockwise, and the right thyrohyoideum twists in counterclockwise direction.

4.3 Stylohyoidea

Through time, a new (inferior) ramus have been added, the bones have become thinner, and the inferior ramus has become more twisted and deflected laterally. In addition, there is a change in the ratio of the superior to posterior rami. In American mastodons (*M. americanum*) only the superior and inferior rami are present. Often, a "bud" is present in the place where the posterior ramus develops in advanced pro-

boscideans (gomphotheriids, stegodontids, and elephantids). Early proboscideans have stylohyoidea that are round in cross section; those of elephantids are flattened and more delicate. Primitive proboscideans have inferior rami that have little of no twisting; those of elephantids are twisted. In posterior view, the left stylohyoideum twists clockwise, and the right thyrohyoideum twists in counterclockwise direction. Viewed anteriorly, in the American mastodon, the inferior ramus is about in the line of the combined superior-posterior rami; in gomphotheres and elephantids the inferior ramus becomes deflected laterally. On average, in *M. americanum* the absolute length of the stylohyoideum (combined length of superior-inferior rami) is the largest among the proboscideans examined thus far. In gomphotheres, stegodontids and loxodontines, the ratio of the superior to posterior rami is about 1:1. In many ele-



Bones, muscles, and cartilages key:

Bones:

Basihyal - b.
 Choana - ch.
 External naris - e.na.
 Frontal - f.
 Humerus - h.
 Jugal - j.
 Inter-premaxillary fossa - i.pm.f.
 Mandible - ma.
 Mandibular symphysis - ma.sy.
 Maxilla - mx.
 Parietal - p.
 Scapula - sc.
 Stylohyal - s.
 Supra-occipital - s.o.
 Thyrohyal - t.

Cartilages:

Cricoid cartilage - c.cr.
 Thyroid cartilage - c.th.

Muscles:

Head and Neck

Complexus (Semispinalis capitis) - m.c.
 Levator anguli scapulae - m.l.a.s.
 Ligamentum nuchae - l.n.
 Longus capitis - m.l.ca.
 Longus colli - m.l.co.
 Obliquus capitis superioris - m.o.c.s.
 Obliquus capitis inferioris - m.o.c.i.
 Omotrachealis - m.om.
 Pectoralis major - m.p.mj.
 Pterygoideus internus - m.pt.i.

Rectus capitis lateralis - m.r.c.l.
 Rectus capitis posterior major - m.r.c.p.mj.
 Splenius capitis - m.sp.c.
 Sterno-mandibularis - m.st.m.
 Tensor veli palatini - m.t.v.p.
 Trachelo-mastoideus - m.t.m.
 Trapezius - m.t.

Hyoid and gular

Constrictor pharyngis - m.c.ph.
 Constrictor superioris - m.c.s.
 Digastricus - m.d.i.
 Genio-hyoglossus - m.hy.gl.
 Genio-hyoideus - m.g.hy.
 Hyoglossus anterior - m.hgl.a.
 Hyoglossus lateralis - m.hgl.l.
 Hyopharyngeus - m.hy.ph.
 Mylohyoideus - m.mh.
 Palato-pharyngeus - m.pa.ph.
 Sterno-thyroideus - m.st.th.
 Styloglossus - m.st.gl.
 Stylohyal ligament - l.s.
 Stylohyoideus - m.st.hy.
 Stylopalato ligament - l.sp.
 Stylopharyngis - m.st.ph.
 Thyrohyoideus - m.th.hy.

Trunk

Maxillo labialis (Levator proboscidis) - m.m.l.
 Pars rimana (Depressor proboscidis) - m.p.r.
 Rectus nasi - m.r.n.
 Transverse nasi - m.t.n.

Fig.3 - A simplified drawing of the musculature of the head of an Asian elephant, *Elephas maximus*, with key for bones, cartilages, and muscles (artwork by G.H. Marchant).

phantine specimens (genera *Elephas* and *Mammuthus*), data indicate a shift towards a 1:3 ratio – that is, the superior ramus decreases in length, while the posterior increases.

5. PHYLOGENETIC RESULTS

Inuzuka (1977a, b) considered *Palaeoloxodon* to be distinct from *Elephas*. Inuzuka's (1977a, b) work, our morphological observations, as well as studies of skeletons of *P. naumanni*, have convinced us that the genus *Palaeoloxodon* be considered a *bona fide* taxon and not a subgenus of *Elephas*. Based on results from cladistic analysis (except for results of *Deinotherium*, to be presented elsewhere), of the taxa examined, genera that appear successively on the cladogram, from the most primitive (bottom of cladogram, Fig. 4) to most advanced are: *Mammut*, *Gomphotherium*, *Stegodon*, *Loxodonta*, *Palaeoloxodon/Elephas* and *Mammuthus*. These findings corroborate other morphological results (Maglio 1973; Coppens *et al.* 1978; Shoshani & Tassy 1996). Hyoidean synapomorphies in support of these relationships were provided by Shoshani (1986); Tassy and Shoshani (1988), and results obtained in this study. All taxa studied except *Mammut*, that is, members of the clade Elephantida of Shoshani *et al.*, 1998 [comprising of “(*Gomphotherium* (*Stegodon* (*Loxodonta* (*Elephas*, *Palaeoloxodon*, *Mammuthus*))”)] possess the posterior ramus. In addition, the inferior ramus of the stylohyoid of non-mammutid taxa is deflected laterally. Members in the clade “(*Stegodon* (*Loxodonta* (*Elephas*, *Palaeoloxodon*, *Mammuthus*))” have oval or flattened (non-round) stylohyoid and basihyoid bones in cross sections, have more delicate and more twisted thyrohyoidea, and also have lost the ‘shelf’ observed in gomphotheres. The four elephantids, “(*Loxodonta* (*Elephas*, *Palaeoloxodon*, *Mammuthus*))”, have much twisted thyrohyoid bones (not known in *Palaeoloxodon*), and possess at least one ‘bend’ on the inferior ramus. Finally “(*Elephas* and *Mammuthus*)” have thin stylohyoidea bone in cross section and short superior ramus.

6. FUNCTION AND ADAPTATION

Based on gular musculature of living elephants (e.g. Eales 1926) and morphology of hyoid apparatus, it is hypothesized that extinct American mastodons had similar functional anatomy of the hyoid to those of extant elephants. Thus, it is suggested that *M. americanum* had a 70-90 cm long tongue that could be protruded a short distance from the mouth to grasp leaves and grasses. Together with a flexible trunk, these mastodons could browse on Pleistocene foliage about 7-9 meters above ground [trunk flexibility is deduced from size and position of external naris and from size and numbers of infraorbital canals (many *M. americanum* specimens have two instead of one canal as observed in living elephants; Shoshani, 1986); height above ground is estimated from data on living elephants when standing on hind legs; Shoshani *et al.* 1987]. It is also suggested that *M. americanum* lived in small herds, about 10-15 individuals, and that herd members could have communicated with infrasonic calls with other herds, perhaps a few kilometers away (communication hypothesis is based on hyoid and cochlear anatomy; Meng *et al.* 1997). Further, it is suggested that the hyoid apparatus supported a pouch, and when empty, was used as a resonating chamber (similar to what was observed in howler monkey; Vaughan *et al.* 2000); at other times it was used to store water for drinking or dousing in time of stress (Shoshani 1998). All in all, detailed study of processes and grooves for muscle attachment and twisting of bones on the hyoid apparatus (mostly stylohyoidea) enables us to infer functionality for little known bones. Despite its small size, the hyoid apparatus appears to have been a pivotal structure for adaptation to newly available niches for survival of proboscideans.

7. CONCLUDING REMARKS

The objectives of this study as outlined above were accomplished. We learned that knowledge of the hyoid apparatus from living elephants has helped us better understand fossil taxa and

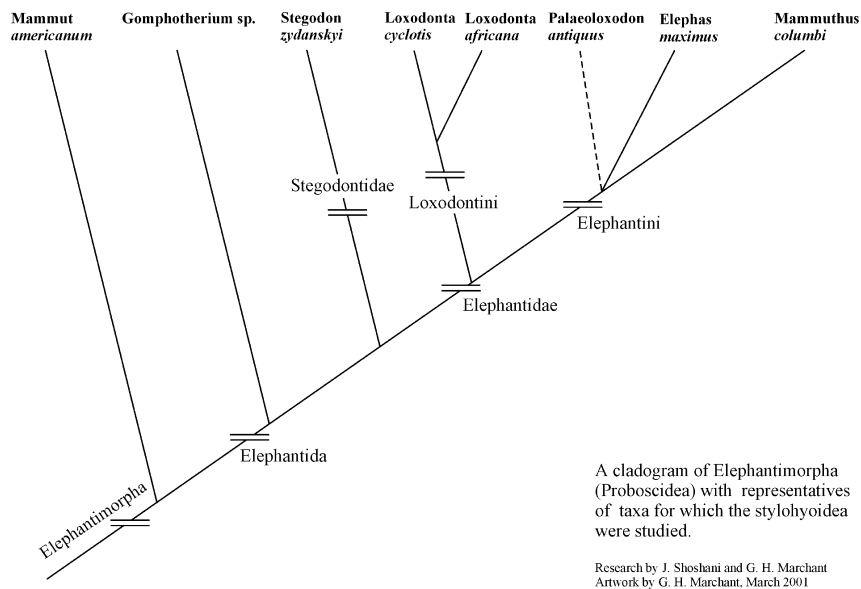


Fig.4 - A cladogram of proboscidean taxa (classified in Elephantimorpha) depicting representatives for which the stylohyoidea were studied (artwork by G.H. Marchant).

vice versa. Characters (and by inference functions), we also learned, appeared to have co-evolved in late Oligocene to early Miocene periods, about 25 million years ago. The small subset of characters on the stylohyoidea of Proboscidea can be used as an example of independent evidence for the relationships among Elephantidae genera. When morphological characters were analyzed cladistically they resulted in the relationships depicted in figure 4. These results are congruent with dental-based (e.g. Coppens *et al.* 1978) and non-dental hypotheses (this study). It appears that the stylohyoideum co-evolved in parallel with dental features.

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