The timing of early Elephantinae differentiation: the palaeontological record, with a short comment on molecular data

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SUMMARY: The differentiation of the extant genera *Elephas* and *Loxodonta* among the Elephantinae (including the extinct genera *Primelephas* and *Mammuthus*) occurred during the late Miocene. Earliest known *Loxodonta* is found in Baringo (Kenya) and Nkondo-Kaiso (Uganda) between 7.3-5.4 Ma. Earliest known *Elephas* is found at Lothagam (Kenya), circa 6-7 Ma. This paleontological record is in accordance with molecular data: mitochondrial DNA provide support for the estimation of an original split for (*Mammuthus, Loxodonta*) and (*Elephas*) dated between 5,6-7,0 Ma.

The clade Elephantidae Gray 1821 include four extinct genera, *Stegotetrabelodon, Stegodibelodon, Primelephas*, and *Mammuthus*, and the two extant genera *Elephas* and *Loxodonta*, the last four genera form the Elephantinae. Several discoveries during the last twenty years in Africa and Arabian Peninsula document aspects of the pattern of differentiation of Elephantinae, that is, the origin of modern genera, and alter previous schemes (the terms "origin" and "differentiation" are used in the hennigian sense, i.e. : the date of origin of a group is that of its sister-group, the date of differentation of a group is that of its first intragroup dichotomy).

The earliest members of the genera *Loxodonta* and *Elephas* are known in the late Miocene and, consequently are contemporaneous of their once supposed "ancestral" taxa, *Stegotetrabelodon* and *Primelephas*. This chronology alters the old picture of a late Miocene origin of Elephantinae followed by their early Pliocene differentiation, according to schemes inherited from Maglio's work in the 1970's.

Earliest loxodonts are isolated molars labelled "*Loxodonta sp.* "Lukeino stage" " by Tassy (1995). This taxon is found in the late Miocene Formations of Lukeino, Baringo Basin (Kenya) and Nkondo, Nkondo-Kaiso area (Uganda), that is, between 7.3 - 5.4 Ma (Lukeino). Known molars (M2, M3, m3) display loxodont derived features typical loxodont wear facets, loops in contact in the middle of the transverse valleys, whatever the stage of wear, narrower lateral margins of enamel loops) allied to primitive features (low laminar frequency, thick enamel) unknown in Pliocene loxodont species, *L. adaurora* and *L. exoptata*.

Earliest member of *Elephas* is *Elephas* sp. nov. from the upper member of the Nawata Formation, Lothagam area (Kenya) (Tassy in press). Upper Nawata is dated 6.7-5.2 Ma (Leakey *et al.* 1996; McDougall & Feibel, 1999). This new species is based on a juvenile mandible with rt.and lt. dp4 and m1, and a portion of lt.m1or2. The oldest known specimen of the early Pliocene species *Elephas ekorensis*, from the Kubi Algi Fm, Turkana (Kenya) are not older than 4.55 Ma (Maglio 1973). Compared to *Elephas ekorensis*, *Elephas* sp. nov. has a more primitive m1 (less plates, pos-

terior plates with four main cusps only, lower laminar frequency, thicker enamel, lower crown, height index low).

Earliest members of the genus *Mammuthus* lineage 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 so far. In any of the two competing hypotheses (a *Mammuthus-Elephas* clade or a *Mammuthus-Loxodonta* clade), phylogeny and known stratigraphical record imply a ghost lineage for *Mammuthus* of circa 2 million years.

Although the palaeontological material is scarce, these discoveries show that earliest modern elephant lineages are contemporaneous with more primitive late Miocene species, that is, *Primelephas gomphotheroides* from East-Africa (Kalb & Mebrate 1993; Kalb *et al.* 1996; Maglio 1973; Maglio & Ricca 1977; Sanders 1997; Tassy 1986, 1994, in press) and *Stegotetrabelodon syrticus* and *S. orbus* from Northern Africa, Abu Dhabi and East-Africa (Kalb & Mebrate 1993; Kalb *et al.* 1996; Maglio 1973, Maglio & Ricca 1977; Petrocchi 1954; Sanders 1997; Tassy 1986, 1994, 1999, in press). These latter taxa may be better treated as "living fossils" than as "ancestors".

Molecular data also contribute to tilt back dates of differentiation of recent Elephantinae: *Elephas maximus*, *Loxodonta africana* and *Mammuthus primigenius*. Recent studies on mitochondrial DNA provide support for the estimation of an original split for (*Mammuthus, Loxodonta*) and (*Elephas*) dated between 5.6-7.0 (Debruyne, in prep.) The differentiation between *Mammuthus* and *Loxodonta* is thought to have taken place before 4.6 Ma, although reliable fossils of the *Mammuthus* lineage are still lacking in the late Miocene. The separation between extant African elephants (bush and forest forms) can be dated 3.5-5.4 Ma. Thus these two lineages look highly differentiated on molecular data although it might be the result of dramatic demographical variations.

These estimations were performed using a separation date between Proboscidea and Sirenia fixed at 60.0 Ma. Only unbiased and weakly saturated markers (12S rDNA, transversions of the cytochrome b) were examined.

In conclusion, it is very likely that elephantine differentiation already occurred seven million years ago.

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