African *Elephas recki*: time, space and taxonomy

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SUMMARY: The African *Elephas* lineage has traditionally been very important for faunal correlation of African paleontology localities, due to the division of the intermediate member, *Elephas recki*, into five time-successive subspecies. This lineage has been proposed as an example of anagenetic change, with each species and/or subspecies evolving directly into the next with no overlap in time. Results from comparison of dental variability in *Elephas recki* to both extant elephant species as well as other African and Eurasian fossil elephants indicate that the variation in the sample of specimens currently attributed to *Elephas recki* exceeds that of many other species, with great variation at the subspecies level as well. Consolidation of the published records of *Elephas recki* subspecies indicate that the ranges for all five subspecies overlap, and are not separated in time as previously proposed. The significant degree of temporal overlap, combined with the wide range in morphological variation suggests that this is not a single species, and a preliminary proposal for taxonomic revision is discussed.

1. INTRODUCTION

The African *Elephas* lineage, consisting of *Elephas ekorensis*, *Elephas recki*, and *Elephas iolensis*, has been very important for faunal correlation in East Africa, and to some extent in South Africa (Beden 1983, 1987; Bromage *et al.* 1995; Cooke & Coryndon 1970; Cooke 1993; Brooks *et al.* 1995; Brunet *et al.* 1995; Coryndon 1972; Harris *et al.* 1988; Harrison & Baker 1997; Hill *et al.* 1992; Kalb & Mebrate 1993; Maglio 1970, 1973; Sanders 1990; White & Suwa 1984). This is due largely to the division of the intermediate member, *Elephas recki*, into five time-successive subspecies, *Elephas recki brumpti, Elephas recki shungurensis, Elephas recki atavus, Elephas recki ileretensis*, and *Elephas recki recki* (Beden 1979). This lineage has been proposed as an example of anagenetic change, with each species and/or subspecies directly evolving into the next with no overlap in time. In addition, the first and terminal species in the lineage, *Elephas ekorensis* and *Elephas iolensis* respectively, have been proposed as extensions of *Elephas recki*, and all three of these species

representing successive stages in one lineage (Cooke & Maglio 1972).

There has been very little quantitative analysis of the variation within *Elephas* species and subspecies, with most researchers relying heavily on descriptions of species and subspecies from previous studies (Maglio 1973; Beden 1979, 1983, 1987a, b). As a result, specimens of *Elephas* are often identified based on the inferred age of the locality, and then used as evidence to support an estimated age. Identification of specimens using this circular reasoning has only confounded the definition and description of each species and subspecies, and increased the heterogenous nature of the specimens assigned to each.

There are two problems with the current accepted anagenetic scheme for the African *Elephas* lineage. First, the variability in each sample of specimens attributed to species and subspecies needs to be reexamined. Second, more crucial to the utility of the members of this lineage as biochronological markers for African localities, a comprehensive survey of faunal assemblages including *Elephas* needs to be done in order to redefine the time ranges for

693

the species and subspecies within the lineage. If the species and subspecies overlap in time and the variation within each taxonomic unit is high, then the evolution of the lineage can no longer be considered as anagenesis, and the usefulness of the African *Elephas* lineage as a biostratigraphic marker will be in question.

2. METHODS

Crania, mandibles and dentition for 25 fossil species and 2 extant elephants have been examined by the author, and this dataset includes 1050 molars (572 fossil molars, 478 extant molars), 142 crania (16 fossil, 126 extant), and 109 mandibles (26 fossil, 83 extant). Species included in this analysis: *Loxodonta africana*, *Elephas maximus* (extant elephants), and *Elephas recki, Elephas antiquus, Loxodonta adaurora*, and *Mammuthus colombi* (fossil elephants). The extant elephants were used as a model for studying variability in fossil taxa because there are abundant specimens of all age groups, and also because the two living species have been divided into subspecies, providing a comparison for the subspecies in the African *Elephas* lineage. A fossil species from each genus was also included for comparison.

The set of dental measurements used in this study follow the methodology outlined in Todd (1997) after Maglio (1973), Beden (1979), Roth and Shoshani (1988) and Roth (1992). These measurements include those made on overall tooth dimensions, as well as those made on each individual tooth plate (Todd, 1997). The degree of morphological variation in *Elephas recki* was compared to the extant species and other fossil elephants in comparison of coefficient of variation and analysis of variance with Tukey-Kramer pairwise mean comparisons. All six molars were examined. Although crania and mandibles are included in the general dataset, sample sizes for the fossil species are too currently too small for reliable statistical testing, and the main focus thus far has been on dentition.

A comprehensive survey of the literature as well as provenience of the specimens included in this study was completed to establish first

and last appearances of species and subspecies throughout Africa. This list relies heavily on published accounts of accurately dated fossil localities, but is the most current for the African Elephantidae. As this is a test of the currently accepted fossil taxa, the original taxonomic identification of specimens (as previously published) was retained unless there was an obvious error (such as a tooth identified as Elephas, which should be allocated to Loxodonta).

3. RESULTS

The first and last appearances of each *Elephas recki* subspecies have been greatly expanded from previous papers. When time ranges are consolidated, it is apparent that all ranges for *Elephas recki* subspecies overlap, and are not separated in time as previously proposed (Fig. 1). In many cases, different subspecies have been identified from the same stratigraphic members at certain localities.
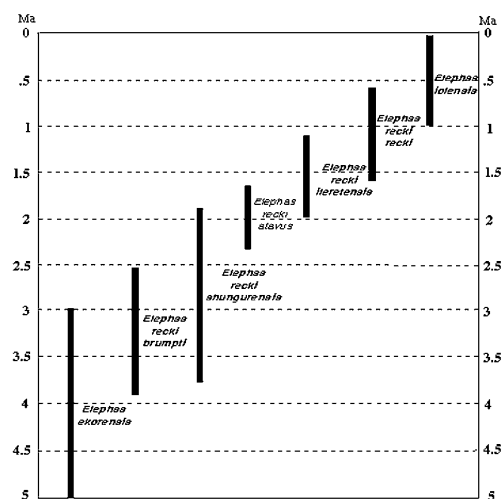

Fig.1 - Revised biochronology of the African *Elephas* lineage. The maximum age for each first appearance is the maximum age estimate for the locality that marks the first appearance of each taxon. The minimum age for each last appearance is the minimum age estimate for the locality that marks the last appearance of each taxon.

Results from comparison of cranial and dental variability in *Elephas recki* to both extant elephant species as well as many other African and European fossil elephants (Todd, 1997), indicate that the overall variation in the sample of specimens currently attributed to *Elephas recki* is consistently high for all measurements on all six molars.

At the subspecies level, the variance in *Elephas recki* exceeds the variance in the extant Asian elephant as well as the African elephant and *Loxodonta adaurora*. This high degree of variation cannot be attributed to geographic differences, as much of the variability occurs in samples of specimens collected from the same sites. *Elephas recki* consistently had higher coefficients of variation and higher variance than the other species in the sample. This high degree of variability was present in all six teeth (dp2, dp3, dp4, M1, M2, M3).

Although the variance is high in individual subspecies of *Elephas recki*, there is considerable morphological overlap in lamellar frequency, enamel thickness, enamel folding and amplitude of folding, height, length and width, all measurements which have been established as reliable for species identification purposes. As a result, it is difficult to separate some of the subspecies on metric data alone. *Elephas recki shungurensis, Elephas recki atavus* and often *Elephas recki ileretensis* are indistinguishable from each other in many instances. *Elephas recki brumpti* groups by itself and *Elephas recki recki* usually groups alone, although sometimes it overlaps with *Elephas recki ileretensis*. An example of this overlap is included in figure 2.

4. CONCLUSIONS

The time ranges for recorded occurrences of each subspecies of *Elephas recki* are not consecutive, but overlap significantly (Fig. 1). This overlap cannot support an anagenetic mode of evolution as previously proposed, and cladogenesis must be inferred (MacFadden 1992). Whether the African *Elephas* lineage represents a branching tree with multiple species (as suggested by the "true" definition of cladogenesis), remains to be determined. The results of this analysis indicate that the traditional view of an anagenetic model cannot be supported.

Based on the morphometric analysis, there are several conclusions that can be made about the African *Elephas* lineage. First, when compared with the extant elephants, the variation present in *Elephas recki* dentition exceeds what is expected for a single species. This variation suggests different taxonomic scenarios: 1) *Elephas recki* is not a single species, 2) the sample of specimens currently attributed to *Elephas recki* includes specimens which may belong in other taxa. Both of these are currently under review by the author and will be presented in the future.
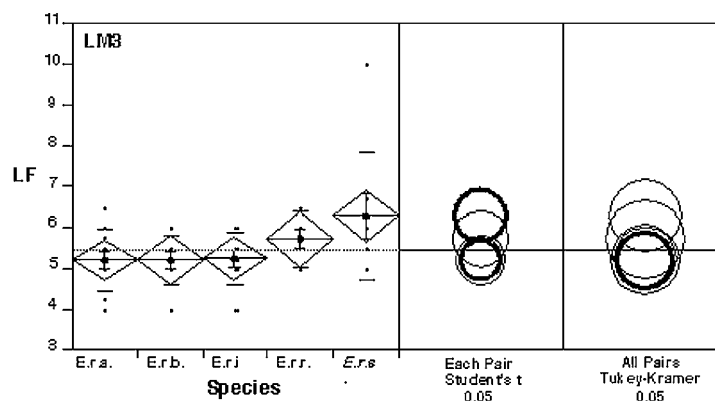

Fig.2 - Range of variation and overlap of means for subspecies of *Elephas recki* lower third molars indicate no significant difference between *Elephas recki atavus, Elephas recki brumpti*, and *Elephas recki ileretensis* for lamellar frequency (*Elephas recki atavus* is in bold text).

The second conclusion is that the subspecies of *Elephas recki* are not distinct from each other in morphology or time range. *Elephas recki brumpti* and *Elephas recki recki* group separately from the rest of the subspecies, while *Elephas recki shungurensis, Elephas recki atavus* and part of *Elephas recki ileretensis* group together. Part of *Elephas recki ileretensis* groups with *Elephas recki recki* in some measurements. The implications of this second conclusion are significant in that it is no longer possible to identify discreet characteristics on individual specimens for species and subspecies identification. As this is not in discordance with the chronological revision, tentative identifications based on relative time period are also problematic.

Any revision of the African *Elephas* lineage will have consequences for biostratigraphic correlation. If *Elephas recki* is a single species with a long time range but few if any subdivisions (subspecies), then its use as a faunal biochron will be limited. Conversely, if there is more than one species in the *Elephas recki* sample, then elephantid diversity during the Plio-Pleistocene of Africa is much greater than previously thought.

Careful analysis of the current state of the African *Elephas* lineage has broad implications for evolutionary scenarios and identification of Plio-Pleistocene elephantids. This is not limited to *Elephas*, as work in progress on *Loxodonta* and *Mammuthus* also indicates wide ranges of variation in measurements and non-metric characters. There are general morphological similarities between subsets of African *Elephas* specimens and Eurasian species, leading to further questions concerning radiations out of Africa, overall elephantid diversity and evolutionary change in the Plio-Pleistocene. There are also temporal and geographical discrepancies which need to be examined in greater detail. Even though adequate numbers of measurements on cranial, mandibular and post-cranial specimens are difficult to obtain because of small samples, non-metric characters will definitely supplement the dental data and need to be included for taxonomic revision.

Is *Elephas recki* a chronospecies or paleospecies? Comparisons with other paleo- and living taxa suggest that current assumptions about *Elephas recki* subspecies as morphologically and temporally discreet units are no longer valid. Revision and reorganization of samples currently attributed to each taxon is currently in progress by the author. *Elephas recki* may still be a valid species, but may be part of a more diverse lineage of African *Elephas* than previously proposed. This revision must encompass analysis of the other African lineages, *Loxodonta* and *Mammuthus*, and a comparative, holistic approach to a revision of the African Elephantidae is necessary.

5. ACKNOWLEDGEMENTS

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