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Peter Grubb

Colin P. Groves
*Department of Archaeology & Anthropology, Australian National University*

Joseph P. Dudley
*Department of Biology and Wildlife, University of Alaska*

Jeheskel Shoshani
*Department of Biology, University of Asmara; Elephant Research Foundation*



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**Cover Page Footnote**
The help received from staff of many museums and national parks where data have been collected is greatly appreciated. Special thanks to Samantha Bricknell, Kes Hillman-Smith, Eleanor Marsac, and Susan K. Bell. This and the following three papers were reviewed by John F. Eisenberg and by Ian M. Redmond.

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EDITORS' NOTES: This and the accompanying three articles that follow may be read in tandem, for they are a cohesive four-part report on taxonomy, habitats, and possible implication of the conservation status of African elephants.

# LIVING AFRICAN ELEPHANTS BELONG TO TWO SPECIES: *LOXODONTA AFRICANA* (BLUMENBACH, 1797) AND *LOXODONTA CYCLOTIS* (MATSCHIE, 1900)

by Peter Grubb [1], Colin P. Groves [2], Joseph P. Dudley [3], and Jeheskel Shoshani # [4]

[1] 35 Downhills Park Road, London N17 6PE, England;
[2] Department of Archaeology & Anthropology, Australian National University, Canberra, ACT 0200, Australia;
[3] Department of Biology and Wildlife, University of Alaska, Fairbanks, Alaska 99775-0180, USA;
[4] Department of Biology, University of Asmara, P. O. Box 1220, Asmara, Eritrea; and Elephant Research Foundation, 106 East Hickory Grove Road, Bloomfield Hills, Michigan 48304, USA.
# To whom correspondence should be addressed.

**Abstract.** Living bush and forest African elephants, hitherto regarded as a single species, are evolutionarily and ecologically distinct forms. They deserve to be ranked as full species: the bush African elephant, *Loxodonta africana* (Blumenbach, 1797), and the forest African elephant *Loxodonta cyclotis* (Matschie, 1900). *L. cyclotis* is phylogenetically more primitive than *L. africana*. The implications of this designation may help in conserving these keystone species.

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## INTRODUCTION

The African elephant, the world's largest living land animal, is generally considered to belong to a single species, *Loxodonta africana*, with two subspecies: the larger Bush African Elephant *L. a. africana* (Blumenbach, 1797) in savannah, bush and lightly forested regions of Africa, and the smaller Forest African Elephant *L. a. cyclotis* (Matschie, 1900), in rain forest (Dudley *et al.*, 1992; Laursen and Bekoff, 1978; Matschie, 1900; Western, 1986). Frade (1955), one of the few authors to propose previously that Bush African elephant (BAE) and Forest African elephant (FAE) are distinct species, pointed out numerous differences in body build, ear shape and tusk form, and in the skull and postcranial skeleton. Allen (1936) tended to accept that they are different species. But Backhaus (1958), on the basis of a visit to the African elephant training station at Gangala na Bodio, in Garamba National Park, Democratic Republic of the Congo (DRC, formerly Zaire), on the boundary of the forest and savannah zones, claimed to find numerous intermediates between Bush and Forest types. This and similar but less substantiated claims (that the two forms are not sharply different) have commonly been used to dismiss any idea that separation of them is taxonomically feasible or desirable.

## MATERIALS AND METHODS

Two of us (PG, CPG) measured 295 African elephant skulls of all ages, from all regions of Africa south of the Sahara. Kes Hillman Smith kindly sent us the measurements for a few others. Data have been entered into a SPSS file (Statistical Package for the Social Sciences) which lays out measurements and identifying information in convenient form for data retrieval. These files are available on request from CPG (other details are given in Groves and Grubb, 2000).

## RESULTS AND DISCUSSION

Combined results of our own and others' data on living elephants, indicate the enormous differences between BAEs and FAEs and the way they are instantly recognizable over vast areas. These observations entirely vindicate Frade's opinion, we are now resurrecting his view that they form two distinct species, *L. africana* (the Bush African Elephant) and *L. cyclotis* (the Forest African Elephant).

The BAEs have larger, broader and more pneumatized crania, especially the forehead, is enormously honeycombed with air cells; FAEs are wider across the skull roof (the temporal lines), are relatively broader across the tusk bases and, especially, have a long "spout", the chin region of the lower jaw. In both species, males grow throughout life, but BAE bulls grow faster and end up much larger (Fig. 1, Table 1).

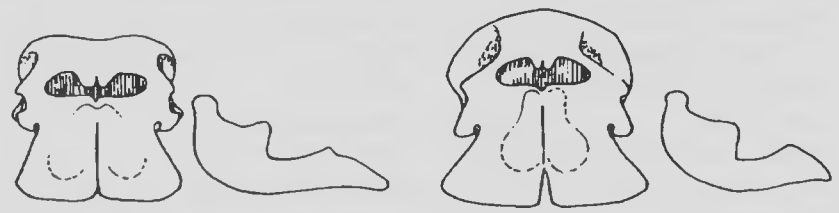


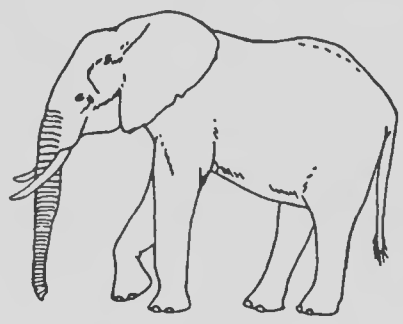
Figure 1. Crania and mandibles of adult males of (left) *Loxodonta cyclotis* and (right) *L. africana* [modified after Kingdon, 1997, p. 308]; cf. Table 1 for comparison.

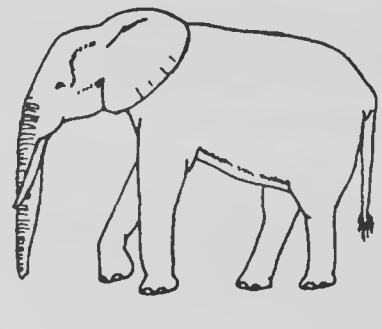
In the field, the two species can be most readily distinguished by the following features (cf. Table 1 for summary). First is the shape and size of the ears: in the BAE they are huge and triangular and tend to overlap across the top of the neck, in the Forest species they are smaller and rounded. Next is the shape of the tusks, which in BAEs are sturdy and curve outward and forward as well as down while in FAEs they are thinner and directed mainly down; FAEs' tusks also tend to be much longer for the size of the animal. The forequarters of FAEs are lower than the hindquarters, and the whole body build is more compact. Strongly pneumatized cranium in the BAEs causes the cranium behind the eyes (the temporal fossae) to flare out below the temporal ridges, whereas in the FAE there is less pneumatization, so the cranium walls drop vertically behind the eyes, and the forehead slopes back more sharply.

When compared to earlier, ancestral African elephants (Shoshani and Tassy, 1996), most of the features in *L. cyclotis* are more primitive with respect to those in *L. africana*, and, as perceptively noted by Kingdon (1979), the *L. cyclotis* skull is similar in many respects to that of *L. adaurora,* which lived in East Africa in the late Pliocene (about 4 to 2 million years ago).

Groves and Grubb (2000) provide evidence that the two species sometimes hybridize where their ranges meet. In summary, we have no evidence of any hybrids in northern DRC, in the Uele River region where forest meets savannah and FAE meets BAE, but hybrids do occur in the Uganda-Congo border region. Many people are under the impression that different species do not hybridize, but this is not so. Hybrid zones between distinct species in the wild have been plentifully reported for warm-blooded vertebrates, both birds (Moore, 1977) and mammals

Table 1. Differences between the two living species of *Loxodonta* [ * ]





| Character | *Loxodonta africana*<br>Bush African Elephant | *Loxodonta cyclotis*<br>Forest African Elephant |
|---|---|---|
| **Shoulder height** [a] | males 3.2 to 4.0 | 2.4 to 3.0 # |
| (in meters) | females 2.2 to 2.6 | 1.8 to 2.4 # |
| **Weight** (in kilograms) | 4,000 to 7,000 | 2,000 to 4,000 # |
| **General build** | more slender | more compact |
| **Body build** | back markedly concave | nearly straight |
| **Withers cf. loins** | about equal | lower |
| **Carriage of head** | high | low |
| **Ears:** general shape | triangular | rounded |
| Ears: lappet | long, pointed | short, round |
| **Tusks**: diameter at base [b] | male: 155 to 196 | male: 70 to 155 # |
| | female: 80 to 119 | female: 57 to 83 # |
| **Tusks**: shape | curved out and forward | straight, downpointing # |
| **Growth**: males | lifelong | lifelong |
| Growth: females | lifelong | ceases at maturity |
| Growth spurt, male only | at Molar IV eruption | none |
| **Skull — cranium**: | | |
| rostrum | more flared | less flared # |
| diploe (pneumatization) | much more marked | little marked # |
| distance between temporal lines | less than length of narial openings | equal to length of narial openings |
| nasal aperture | narrower # | wider |
| anterior end of rostrum | slight dorsal concavity | deep dorsal concavity |
| occipital plane | slopes forward | more upright # |
| posterior palatine foramen | smaller | larger |
| **Skull — mandible**: | | |
| mandible | shorter, taller | longer, lower # |
| mandibular condyles | more rounded | transverse-oval # |
| mandibular symphysis | shorter (mean in adult males 169 mm) | absolutely and relatively longer (mean in adult males, 185 mm) # |
| **Cheek teeth** | high-crowned | lower-crowned # |
| **Stylohyoid bone** | postero-dorsal edge flatter, tip of inferior ramus sharper | postero-dorsal edge sharper, inferior ramus with flattened tip # |
| **Behavior and Ecology:** | | |
| vocalization frequency | lower range of 14-24 hertz # | lower range of 5 hertz |
| habitat | mesic to arid woodland and savannah | moist semi-deciduous and rainforest # |
| fundamental niche | grazer-browser | browser-frugivore |
| social organization | extended family | nuclear family |
| modal group size | 4 to 14 | 2 to 4 |
| bulls | transient associations | solitary |
| **Conservation**: | | |
| total estimated population | 200,000 to 430,000 | 80,000 to 210,000 |
| threat of extirpation | moderate | high |

[ * ]. Illustration by Gary H. Marchant mostly after Sikes' (1971, pp. 12-16) descriptions.

[a]. after Christy (1924), Malbrant and Maclatchy (1949), Morrison-Scott (1947), Roeder (1970), and records at the Powell-Cotton Museum in Birchington, Kent, England.

[b] maximum diameter of incisor alveolus; our own data.

In addition, according to Sikes (1971, p. 15, plate 7) number of nail-like structures varies in both species. At birth, both have five "toes", some wear down and are lost during life; thus, one may observe in adult *L. africana* 4 or 5 on the forefeet, and 3 to 5 on the hind feet; corresponding numbers for *L. cyclotis* are 5 and 4 to 5.

# = a primitive character within Proboscidea (mostly after Shoshani and Tassy, 1996).

(Gray, 1972; Jolly *et al.*, 1997), but in the present case it seems we can speak of just occasional hybrids rather than a hybrid zone, let alone panmixia (interbreeding without any barriers), so the two cannot be said to share a common gene-pool. [It is interesting to note that in captivity there has even been a hybrid between the two different genera of living elephants, *Loxodonta* (African) and *Elephas* (Asian) (Lowenstein and Shoshani, 1996)!]

Ecologically, the two elephant species occupy distinctly different environments, with little habitat overlap (Fig. 2). Most of our knowledge on the ecology and behavior of African elephants comes from studies of *L. africana* (Douglas-Hamilton and Douglas-Hamilton, 1975; Moss, 1988; Poole and Moss, 1981; Sikes, 1971). Only recently has some information become available on *L. cyclotis* (Barnes and Barnes, 1992; Fay and Agnagna, 1991; Turkalo, 1996), and this has recently been highlighted by Tangley (1997). The FAE is much more of a browser and frugivore than the BAE; it lives in much smaller social groups, and it communicates with very low frequency calls, as low as 5 hertz (Tangley, 1997), well below the 14-24 hertz reported for Asian elephants (Payne *et al.*, 1986) and for BAEs (Langbauer *et al.*, 1991). The differences in diet and social behavior are related to habitat but not constrained by it; they are species-specific traits as are those in morphology.

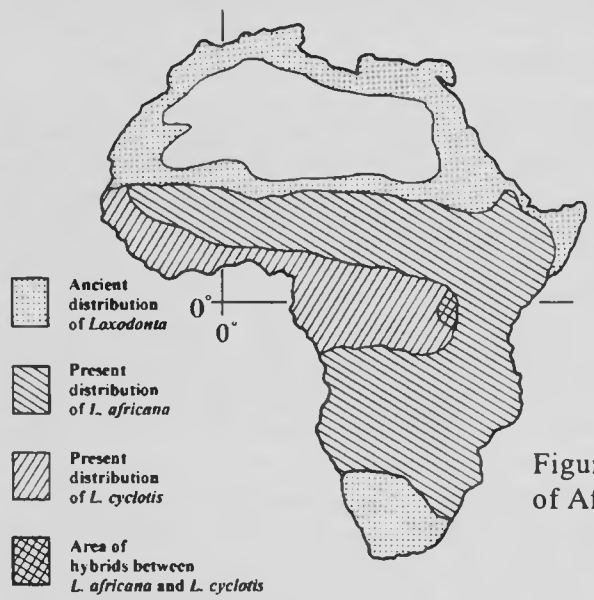



Figure 2. Distribution of African elephants.

Given the degree of these differences, together with emerging data on DNA (work by N. Georgiadis and A. Templeton, reported by Tangley, 1997, plus the findings of Barriel *et al.*, 1999), and the low level of hybridization with inferred genetic independence, it appears that the world's largest living land mammal consists of two species: the massive BAE, *L. africana*, and the much smaller (but still spectacularly large) FAE, *L. cyclotis*.

The ranking of *L. cyclotis* as a distinct species has important implications for conservation strategies, in particular, the need to manage BAEs and FAEs separately. In the 1970s populations of African elephants numbered about 1.5 million; presently, there are about 500,000, of which a quarter to a third are reported to be FAEs (Allen, 1936; Said *et al.*, 1995; Tangley, 1997, p.1417). The Asian elephant, *Elephas maximus*, is likewise threatened; the populations held as quasi-domesticated are not self-sustaining, they are declining at rates equal to or exceeding those in the wild (Sukumar, 1989). The FAE has been recognized as a keystone species (Dudley *et al.*, 1992; Western, 1989) and a super keystone species (Shoshani, 1992, 1993) because of its huge size and the effect it has on its habitat. Protecting elephants implies allocating a large area for their survival, an area which can house numerous other species, large and small, in the same ecosystem.

Biodiversity of large mammals is severely underestimated. The existence of a narrow hybrid zones among large mammals can be detected in casual field surveys, which it is not the case for small mammals and other animals that have to be trapped for close investigation. This simple fact has led to the downgrading of perfectly distinct, diagnosable species to a level where they become taxonomically "invisible" and thus lost to biodiversity studies. There are many examples of large mammal genera in which single species are currently supposed to extend through forest and savannah zones (as in the elephant case treated here), and this series of case studies might be a place to start testing the proposition that their biodiversity has been underestimated.

## Conclusions

Data presented here and by Groves and Grubb (2000) provide evidence for species distinctiveness between the BAE and the FAE, properly designated as *Loxodonta africana* (Blumenbach, 1797) and *Loxodonta cyclotis* (Matschie, 1900). These finding concur with Barriel *et al.*, (1999) observations — "The analyses of extant taxa only and of both extant and extinct taxa show that *L. a. cyclotis* is highly divergent from *L. a. africana*. It is as divergent from *L. a. africana* as *Loxodonta* is divergent from *Elephas*." Elevation of the FAE from a subspecies to a species category, may provide a basis for separate management and conservation strategies leading to better protection for the two African elephants species.

## Acknowledgments

The help received from staff of many museums and national parks where data have been collected is greatly appreciated. Special thanks to Samantha Bricknell, Kes Hillman-Smith, Eleanor Marsac, and Susan K. Bell. This and the following three papers were reviewed by John F. Eisenberg and by Ian M. Redmond.

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