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Do *Loxodonta cyclotis* and *L. africana* interbreed?

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Introduction

The taxonomic status of Forest and Bush African Elephants, *Loxodonta cyclotis* and *L. africana*, should be seen in relation to the pervading assumptions of the middle of this century. The standard works on mammalian taxonomy of this period were by Ellerman and Morrison-Scott (1951) and Ellerman, Morrison-Scott and Hayman (1953). It is impossible to overestimate the influence of these two volumes on taxonomic thinking in mammalogy, even up to the present day; their guiding philosophy, sometimes made quite explicit, was that if two taxa within a genus were allopatric, as a general rule they ought to be treated as conspecific. Ellerman *et al.* (1953), in particular, noted with satisfaction that they had "made some reduction in the currently accepted species" (p. 2), and under *Loxodonta africana africana* they wrote:

> This form and *cyclotis* are sometimes regarded as separate species, on the ground that in areas where the Congo forest abuts on savannah country herds of each form have been seen in the same locality, but not intermingling. But this fact is not necessarily significant since it is conceivable that herds (or large family parties) of elephants of the same form, if normally living some distance from one another, might avoid each other when their wanderings brought them to the same district (Ellerman *et al.*, 1953:156).

It is hardly surprising that the detailed arguments of Frade (1955) for the recognition of Forest and Bush Elephants as separate species have been overlooked for over forty years.

At that time, there was near-universal acquiescence that the nature of a species was that it does not interbreed with other different species, so that when Backhaus (1958) claimed that where their ranges meet, the two putative species of African elephant interbreed freely, it seemed to prove decisively that they were not in fact distinct species. During his visit to the Elephant Training Station at Gangala na Bodio in the Garamba National Park, in what was at that time the Belgian Congo, now Democratic Republic of the Congo (DRC, formerly Zaire), Backhaus observed variations in ear shape and tusk form which, in his estimation, completely bridge the gap between the two taxa. The evidence he presented shows only that both *cyclotis* and *africana* are present near the station; his claim that one could see elephants with *cyclotis*-type ears and *africana*-type tusks was not substantiated. Today, when the interbreeding criterion appears more complicated and the criterion for species status is more usually framed theoretically in terms of genetic integration and operationally by seeking fixed character differences (Christoffersen, 1995), one would look not for the presence or absence of interbreeding *per se* but rather for evidence that gene-flow has been sufficient to fuse the two taxa into a homogeneous mass.

Materials and Methods

The protocol for skull measurements was given by Groves and Grubb (1986; cf. Petter, 1958). Between us we have measured most or all of the African elephant skulls available in European, American, and West African collections and, in response to our 1986 article, Kes Hillman-Smith kindly sent us measurements of further skulls from Garamba National Park. In all, we now have the measurements of 295 African elephant skulls. Because of the enormous age changes, especially in males, not all the skulls can be used in each analysis. We divided them into 9 tooth-eruption stages, as follows: Stage 1 — molar II in position (i.e., in wear); Stage 2 — molar II in process of being shed, molar III coming into position; Stage 3 — molar III in position; Stage 4 — molar III being shed, IV moving into position; Stage 5 — molar IV in position; Stage 6 — molar IV being shed, V moving in; Stage 7 — molar V in position; Stage 8 — molar V being shed, VI moving in; Stage 9 — molar VI in position.

We analyzed these measurements by univariate, bivariate, and multivariate means, trying out different combinations of ages stages until we could achieve good discrimination with the largest possible samples. For the purpose of these analyses, we called all specimens from the forest belt of Central Africa *cyclotis* and all those from the East and South African savannah belt *africana*, and tested specimens from other areas to see where they appeared on the charts, and repeated the analysis until we had the largest possible samples. This process added all West African specimens to the *cyclotis* sample, and all specimens from Ethiopia, Sudan and Chad to *africana*.

Results and Discussion

Figure 1 shows that males of both species continue increasing in size (in prosthion to vertex length, total skull length) throughout life, whereas females slow down after stage 6, though they do continue to increase until stage 9. This is not new information, but the figure simply shows that the skull keeps pace with the overall body size. Fig. 2 shows that it is, on the contrary, only the bull *L. africana* whose tusks continue to enlarge throughout life. Fig. 3 shows that, when stage 9 individuals are considered, there is almost no overlap in skull length between bulls, and none at all between cows (although the samples are rather small, that for female *L. africana* being only 5).

In a few variables, however, *L. cyclotis* is actually larger than *L. africana*. One of these is what we call Spout Length, the antero-posterior diameter of the mandibular symphysis. This is a primitive feature; in the fossil record first the mandibular incisors disappeared, then the spout itself, which contained their alveoli, shortened. From Fig. 4 it can be seen that the disparity increases with age, so that at the largest sizes there is no overlap: skulls of Bush Elephants are absolutely larger, but Forest Elephants have absolutely longer spouts. These analyses confirm what Frade (1955) found on non-metrical features: that the two rank as perfectly distinct species, with absolute differentiation between them.

Figures 5, 6 and 7 show the results of Discriminant Analysis (using SPSS; cf. Grubb *et al.*, 2000). The four samples are males and females of the two species. We used only crania: including mandible measurements would have reduced sample sizes too much. We found that the typical species differences were shown by all skulls from stage 6 upwards. The resulting sample sizes were satisfactorily large: *L. cyclotis* males 26, females 24; *L. africana* males 43, females 24, making 117 skulls in all. In Discriminant Analysis one employs techniques of matrix algebra, weights combinations of measurements to give the maximum differentiation between samples and the minimum variation within samples. In this case, measurements of Bizygomatic Breadth, Occipital Breadth, Postorbital Process Width, Rostrum Length and Rostrum Least Breadth were removed (by the program), as adding no extra information, so that the differentiation between the four samples depends entirely on just four variables: Occipital Height, Postorbital Constriction Width, Prosthion to Vertex length, and Rostrum Greatest Breadth.

Discriminant Function 1, which separates the two species absolutely, accounts for 80.42 percent of the total variation. *L. africana* has, according to the weightings applied to the variables, a long skull with high occiput; *L. cyclotis* has a wider postorbital constriction and relatively broader rostrum. Discriminant Function 2, which separates the two sexes but not absolutely, accounts for 19.04 percent of the variance (the remaining 0.54 percent is "noise"). Males have long skulls but females have a relatively higher occiput.

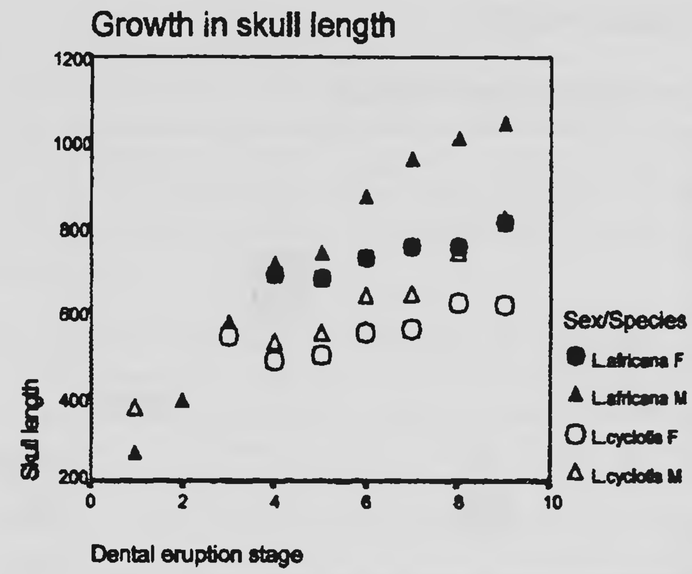


Figure 1. Growth in skull length. Dental eruption stage on Abscissa; Prosthion to Vertex length on Ordinate.

Figures 2 through 7 next page.

Figure 2. Skull length for the two species at full size (eruption stage 9). 1 - Forest Elephant males, 2 - females; 3 - Bush Elephant males, 4 - females. Number of skulls for each sample is given along Abscissa.

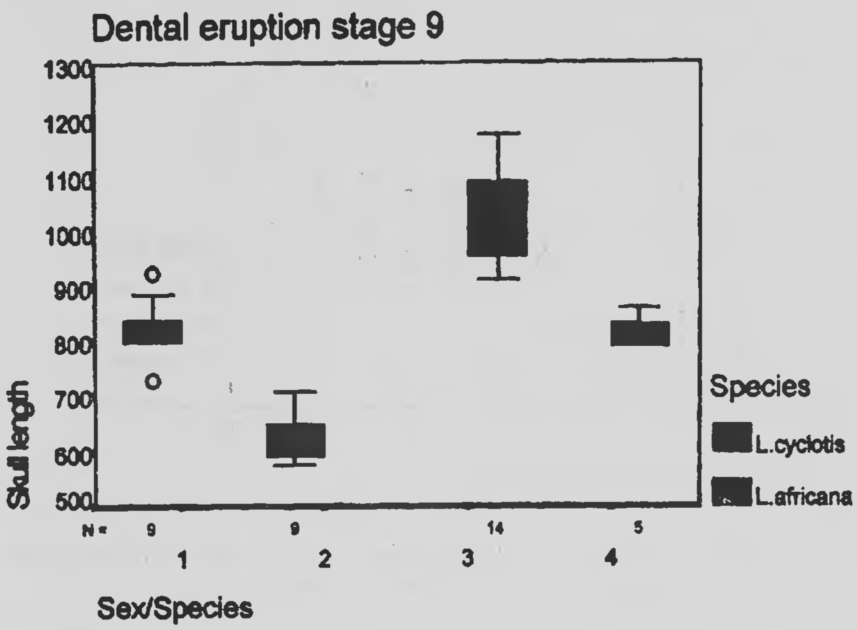
Figure 3. Increase of diameter of tusk alveolus with age.

Figure 4. Relative spout length. Skull length on Abscissa, Spout length on Ordinate.

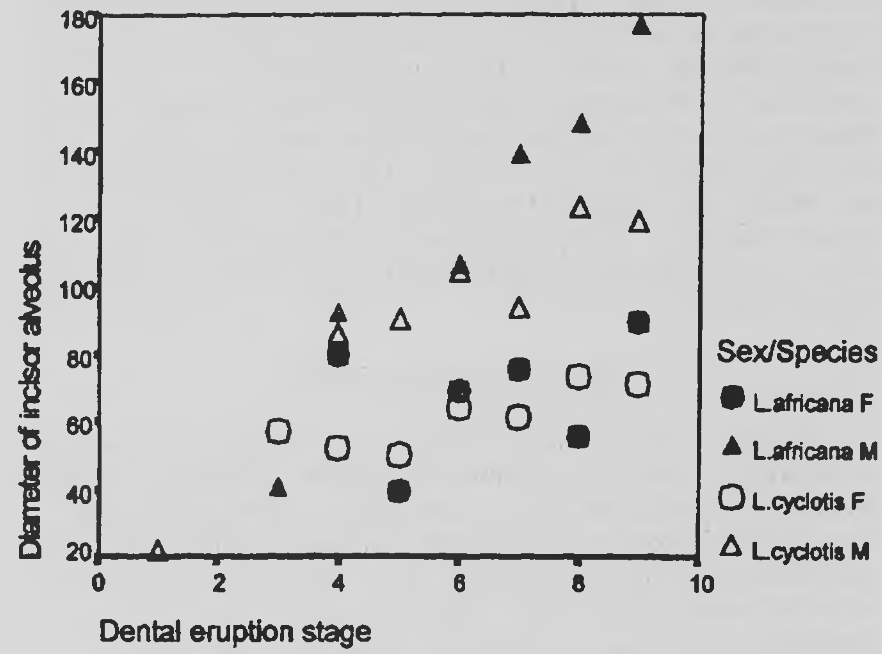
Figures 5-7. Discriminant Analysis of Forest from Bush Elephants, males and females treated separately. Plus signs mark positions of skulls from border areas (entered into the analysis a posteriori). Fig. 5, Virunga National Park, DRC; Fig. 6, Western Uganda; Fig. 7, Uele River district, northern DRC.

It is the skulls from the border areas that are of special interest here. They are of both sexes, and it is noteworthy that all of them assorted with their correct sex, so increasing confidence that their taxonomic status is accurately depicted by the analysis. Fig. 5 shows the position of skulls from the Parc National des Virunga (formerly Parc National Albert), which runs along the border between DRC and Rwanda and Uganda, from the Virunga Volcanoes to just north of Lake Albert. The region is one of forested mountains and lower-lying savannahs, notably the Rutshuru Plains. Most of the skulls fall within the range of either *L. cyclotis* (6 cases) or *L. africana* (3 cases) but at least 3 are definite hybrids, as is one other (which could be a female *cyclotis*). Fig. 6 shows the position of skulls from Western Uganda (Budongo Forest and West Nile District). All could be hybrids. It is noticeable that whereas the Parc National des Virunga hybrids emerge as being more towards *cyclotis*, the Uganda ones are more towards *africana*. Fig. 7 is strikingly different; these are skulls from the Uele River region [most of them in fact are from Parc National de la Garamba, including Gangala na Bodio where Backhaus (1958) reported that he found intermediates]. There is no clear case of a hybrid. The skulls are all within the range of either *cyclotis* or *africana*, and in each case they are scattered within the dispersions of the two species, with no indication of gene-flow. This does not mean that there is no hybridization along the Uele; merely that a presumably random sample of 13 skulls does not include any definite hybrids.

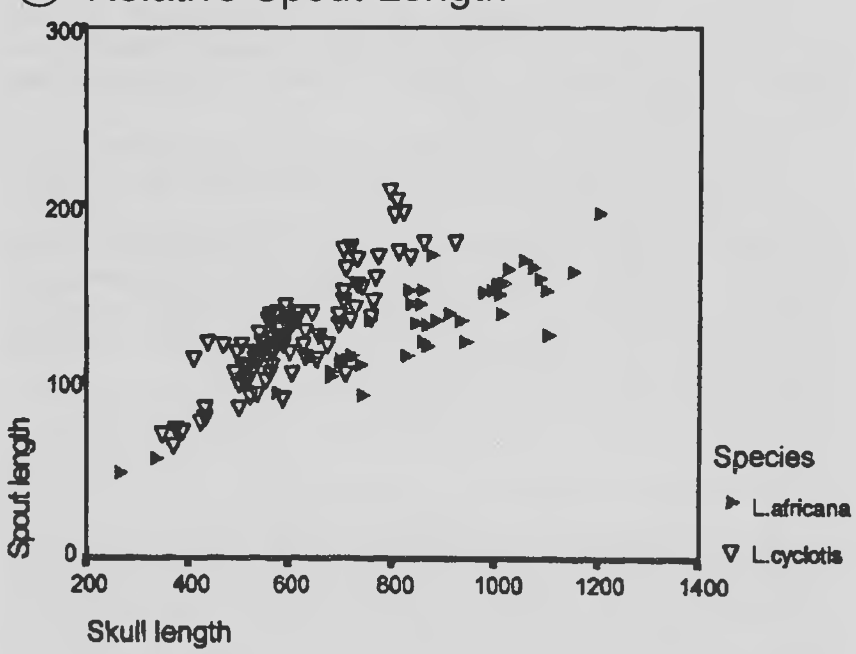
② Skull length



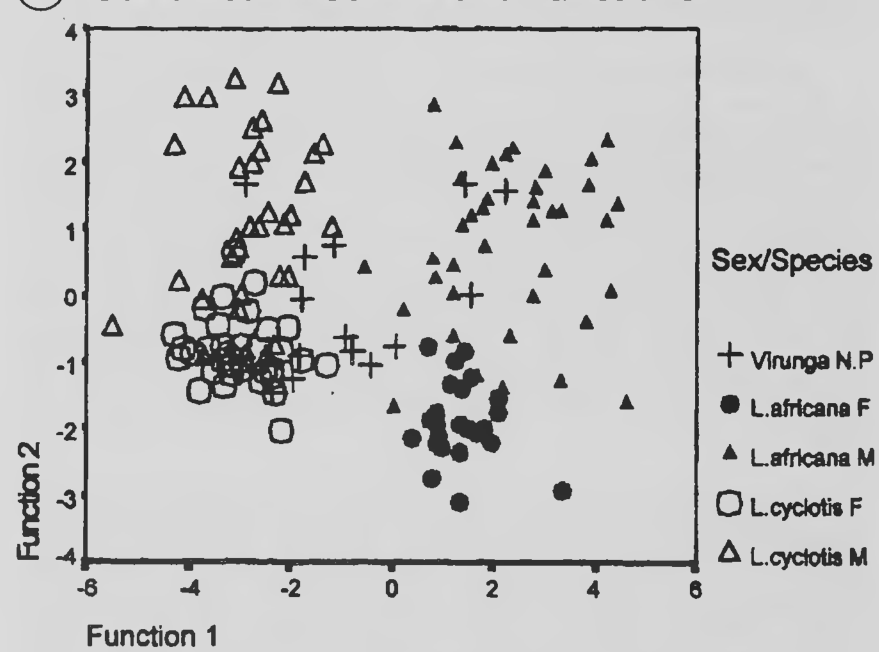
③ Enlargement of tusk sockets



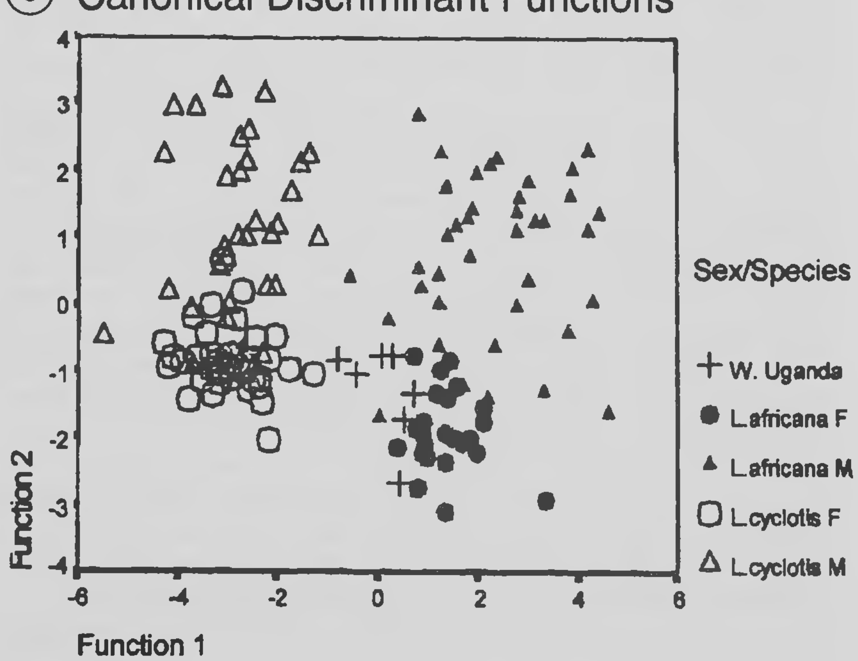
④ Relative Spout Length



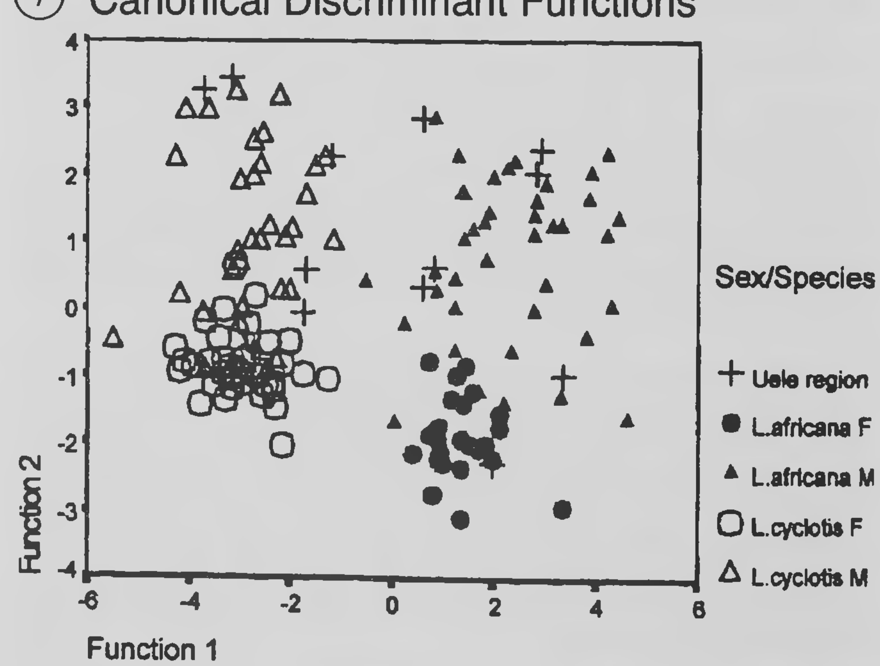
⑤ Canonical Discriminant Functions



⑥ Canonical Discriminant Functions



⑦ Canonical Discriminant Functions



Conclusions

The Forest Elephant and Bush Elephant of Africa constitute two separate, diagnosably distinct species. Where their ranges meet, there may or may not be hybridization. Hybrids occur across the Congo-Rwanda-Uganda border, but apparently "pure" members of both species occur there as well; there is no good evidence for interbreeding in the Uele River region which includes Gangala na Bodio.

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