Elephant, Volume 2, Number 4, pages 1-4

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)

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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.

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).

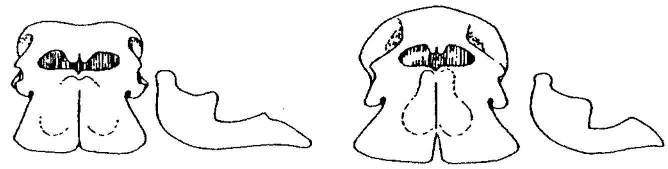


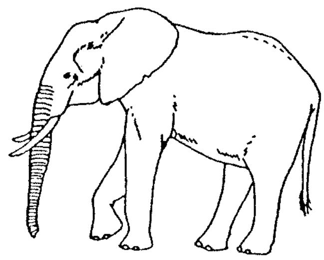
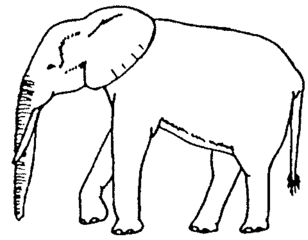
Figure 1. Crania and mandibles of adult males of (left) *Loxodonta cyclotis* and (right) *L. africana* [modified after Kingdon, 1997, p. 308]; cf. Table 1 for comparison.

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* Bush African Elephant	 *Loxodonta cyclotis* Forest African Elephant
Shoulder height [a] (in meters)	males 3.2 to 4.0	2.4 to 3.0 #
	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.

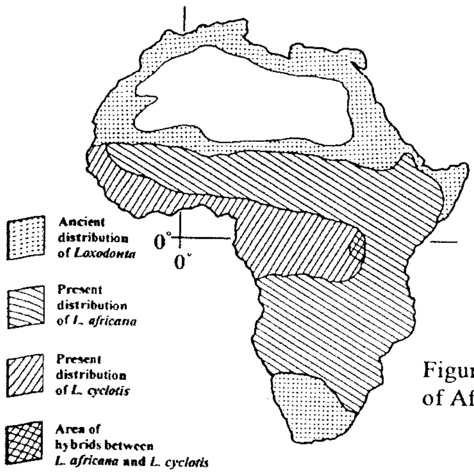


Figure 2. Distribution of African elephants.

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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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. 3 shows that it is, on the contrary, only the bull *L. africana* whose tusks continue to enlarge throughout life. Fig. 2 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.

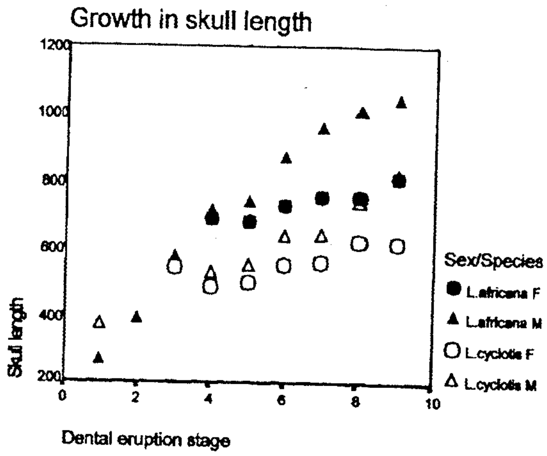


Figure 1. Growth in skull length. Dental eruption stage on Abscissa; Prosthion to Vertex length on Ordinate.

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.

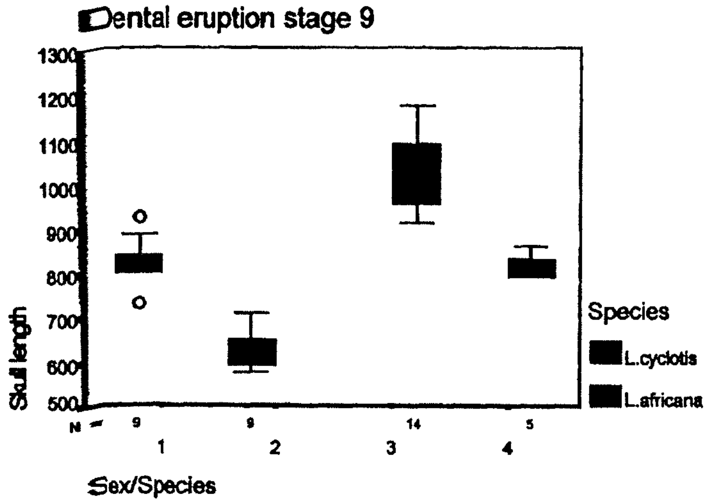
Figure 3. Increase of diameter of tusk alveolus with age.

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

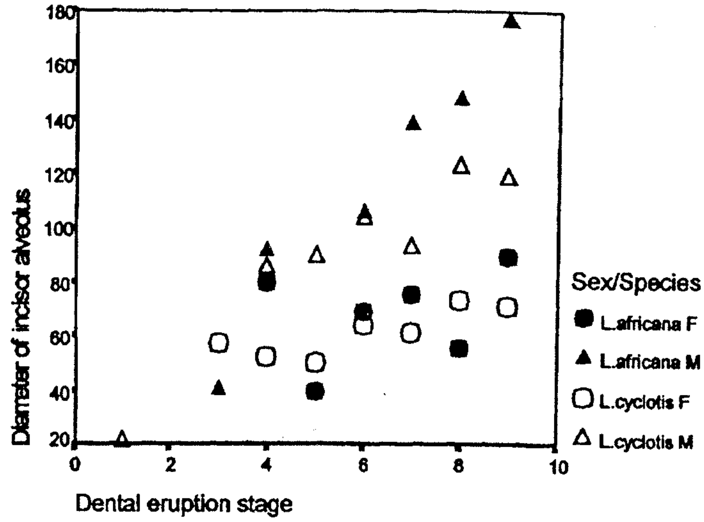
Figures 5-7. Discriminant Analysis of Forest from Bush Elephants, males and females treated separately. Plus signs mark positions of skulls from border areas (entered into the analysis a posteriori). Fig. 5, Virunga National Park, DRC; Fig. 6, Western Uganda; Fig. 7, Uele River district, northern DRC.

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.

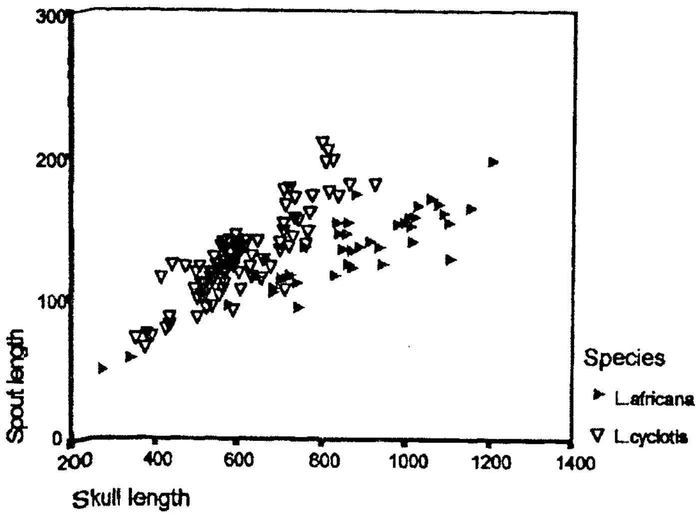
② Skull length



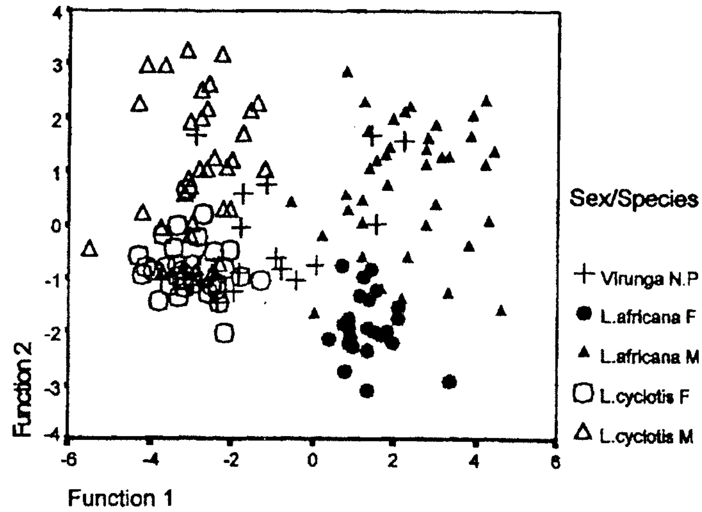
③ Enlargement of tusk sockets



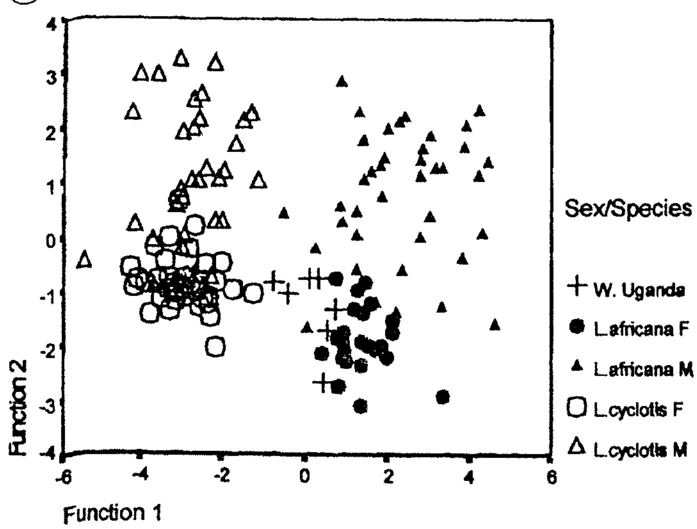
④ Relative Spout Length



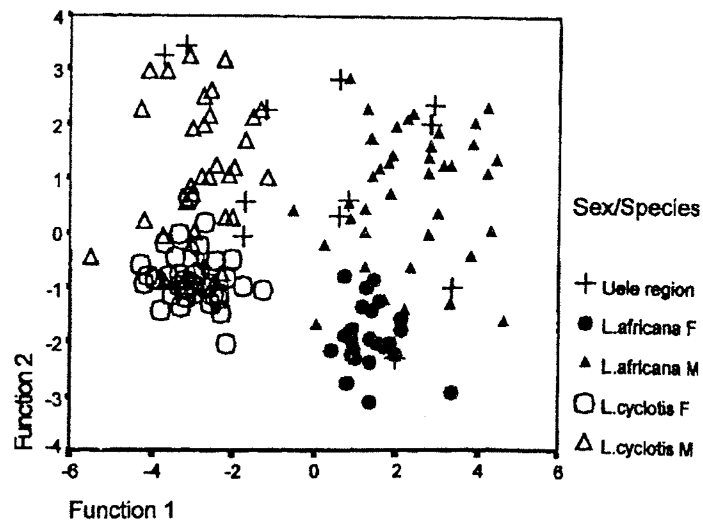
⑤ Canonical Discriminant Functions



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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Elephant, Volume 2, Number 4, pages 7-8

What are the Elephants of West Africa?

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As well as the elephant (*Loxodonta*), three other large mammal species or species-groups have distributions covering both the rainforest bloc and the savannah bloc in Africa: buffalo (*Syncerus*), bushpig (*Potamochoerus*), and bushbuck (*Tragelaphus scriptus* group). The studies of Peter Grubb (1993) have thrown light on how these three species respond taxonomically to this diversity of habitats.

The simplest case is *Potamochoerus* (Grubb, 1993). The Bushpig (*P. larvatus*) is widespread in savannah (or, more strictly, bush) areas from Ethiopia through East Africa into Angola and the Cape; it thrives in Madagascar, where it was introduced in pre-colonial times. The Red River Hog (*P. porcus*) is found in the rainforest zone, from the Democratic Republic of the Congo (DRC, formerly Zaire) through West-Central Africa on through West Africa. The ranges of the two species are mapped by Vercammen *et al.* (1993). Grubb could find no indication of interbreeding between them, though their ranges came close around the Sudan-Congo border and in the Central Rift Highlands where the forest ends and the savannah begins; in fact, *P. larvatus* is found in forested areas in the latter region. In West Africa, he studied specimens or found records of the genus from Senegal, Guinea, Guinea-Bissau, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Benin and Nigeria. All are clearly *P. porcus*, despite the fact that some of the records are apparently from north of the forest zone proper, perhaps (as Grubb suggests) in gallery forest. There is no sign that *P. larvatus* extends into West Africa; in fact, there are no indications that it extends west of about the Garamba region of north east DRC.

The African buffaloes are traditionally all placed in a single species, *Syncerus caffer*, because there is no doubt that the large black savannah buffaloes and the small red forest ones commonly interbreed where their ranges meet, despite being dramatically different (Grubb, 1972). The horns of the East and South African black race (*S. c. caffer*, the Cape Buffalo) sweep out in a wide curve and meet to form a bony "casque" on the forehead, whereas those of the Red Buffalo (*S. c. nanus*) turn simply upward and have only the slightest indication of a "casque". There are two supposedly intermediate races: one from the West African savannah (*S. c. brachyceros*), larger than *S. c. nanus*, often partly or completely black when mature (as, in fact, are a few specimens of *nanus* too), and with more spreading horns; and one from Chad, Sudan and Ethiopia (*S. c. aequinoctialis*) which is essentially a smaller version of the Cape Buffalo. In fact, as Grubb shows, the two are not fully intermediate; *S. c. brachyceros* is essentially a larger Red Buffalo and overlaps with it in its characters, while *S. c. aequinoctialis* is barely if at all distinct from the Cape Buffalo. There is actually a sharp break between them in the Shari River district, southeast of Lake Chad, 15-27°E, 3-12°N, with very little overlap of characters; while in northeastern DRC (in the Garamba region), and in the Central Rift Highlands, typical forest Red Buffaloes come into close contact with big Black Buffaloes with little sign of interbreeding (in the Rift region) or none at all (in Garamba). These sharp breaks are why Grubb refers to "incipient speciation", and it seems clear that today it would be more reasonable to recognize two species, *S. caffer* and *S. nanus*. As in the Bushpig case, the East and South African savannah species does not extend into West Africa; instead, the Red Buffalo (more decisively than the Red River Hog, it would seem) extends out from the forest onto the savannahs West of Lake Chad.

The case of the Bushbuck (*Tragelaphus scriptus*) is yet more complex (Grubb, 1985). Small red bushbuck with white stripes and spots (*scriptus* group) extend throughout the forest bloc and north into the savannah/bush country of West Africa, Chad and Sudan north as far as the Bahr-el-Ghazal. Large sexually-dichromatic bushbuck (males chestnut to dark brown, females redder), with few white markings (*sylvaticus* group), inhabit the savannah/bush country of East and South Africa. The ranges of the two appear to interdigitate in southeastern Sudan, Uganda, and northeastern DRC, with little or no sign of interbreeding. The situation is complicated because there are bushbuck in Ethiopia and in the eastern coastal forests (from Somalia into Tanzania) which are different yet again. Probably the species *T. scriptus* ought to be divided into several species. Be that as it may: the important point is that in all three species, we have a rainforest and a savannah/bush species, which may or may not interbreed, but in any case sparingly and not panmictically. But in West Africa, it is the forest species, not the expected savannah species, which occupies the savannah/bush zone. In the bushpig and bushbuck, the interloper extends into the Sudan; in the buffalo, only to the longitude of Lake Chad.

The fourth savannah/forest group is, of course, the African Elephant. Papers in this volume demonstrate that the Forest

Elephant is a different species, *Loxodonta cyclotis*, from the Bush Elephant, *L. africana*, and that there is some interbreeding between them in the Central Rift region but not, or not detectably, in the Garamba region of northeastern DRC. It is worth asking: what is the case in West Africa?

In the Grubb/Groves craniometry dataset, material from West Africa comes from the following localities: Sierra Leone - Liberia border: Gola (7-8°N, 11-12°W); Liberia: Cavally River (6°N, 8°W); Ivory Coast: Guiglo (6°40'N, 7°28'W), Daloa (6°56'N, 6°28'W), Bouaflé (7°01'N, 5°47'W); Ghana: Nandom (10°57'N, 2°43'W); Togo: Sokodé (8°59'N, 1°11'E); Nigeria: Abeocuta (7°10'N, 3°26'E).

From some of these localities we have fairly respectable samples. In Discriminant Analyses, they were always entered as Unknowns, but every one of the specimens was firmly confirmed as *L. cyclotis*. At least two of the localities (Nandom and Sokodé) are well to the north of the forest bloc. It is worth asking, is the African Elephant analogous to the other three species? Is the Bush Elephant restricted to savannahs east of Lake Chad? And does the Forest Elephant take its place in the savannahs of West Africa?

The answer is no. The elephants are different. We simply have to accept that the Grubb/Groves dataset is in this instance, unrepresentative. Books on East, South and Southwest African wildlife abound, each of them full of pictures of elephants; but it is unexpectedly difficult to find information on West African elephants. The exception is the book in French by Pierre Pfeffer (1989).

Pfeffer is well aware of the differences between the two elephants, although he regards them, in accordance with tradition, as subspecies of just the one species. He notes (Pfeffer, 1989, p. 26) that the relationship between them is by no means simple and gives the following information. In Ivory Coast, between Gagnoa and Sinfra, he found Bush Elephants "mélanges" (intermingled) with elephants showing Forest characters. In northern Togo, in full savannah, he saw clear Forest Elephants. Most recently, in southern Burkino Faso near the Ghana border, he saw groups of plump, short-legged elephants with round ears, coexisting but not interbreeding with much larger, more slender elephants with big triangular ears. He goes on to describe the two and give a few more details on their distribution and, above all, give photos of elephants with the places where they were photographed. He illustrates Forest Elephants in the north of the Central African Republic (Pfeffer, 1989, p. 12) and in Niokolo Koba National Park, Senegal (p. 169), and Bush Elephants at Nazinga and elsewhere in Burkina Faso (pp. 8, 17, 60, 124), in the north of the Central African Republic (pp. 32, 56-57, 62, 77, 88), and in Waza Reserve, northern Cameroon (pp. 110, 136-137), as well as in Chad and East Africa. But he also illustrates an intermediate elephant photographed at Fosse aux Lions, northern Togo (p. 27).

In contrast to the situation with buffalo, bushpig, and bushbuck, savannah elephants (*L. africana*) do extend into the savannahs of West Africa where, it seems, they generally coexist with *L. cyclotis* and occasionally interbreed with them. Sikes (1964) comparison of Nigerian forest and bush elephants led her to conclude that they were sub-species. In fact, Haltenorth and Diller (1977) refer to them as 'eco-types'.

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Are There Pygmy Elephants?

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Introduction

In this volume three papers have argued that there are two species of African elephant: the Bush Elephant (*Loxodonta africana*) and the Forest Elephant (*Loxodonta cyclotis*). Nonetheless, it is probably true to say that there is a significant minority of authors who believe that there is a third species in Africa, a pygmy species that lives only in the depths of the rainforests of Central Africa. The evidence for pygmy elephants was recounted by Heuvelmans (1959) and updated by Roeder (1970, 1975). Significant contributions in more recent times have been by Western (1986), Redmond (1987), Eisentraut and Böhme (1989) and Böhme and Eisentraut (1990). Yet the matter remains controversial.

The Grubb/Groves craniometric dataset includes measurements of all the meaningful specimens that have contributed to the debate. This series of papers on Bush and Forest Elephants seems a good opportunity to comment on the pygmy elephant question from the perspective of actual hard data.

A Brief History of Pygmy Elephants

It is as well to remind ourselves that the Forest African Elephant did not become known to science until the beginning of the 20th century, in a paper by Matschie (1900). In this paper, Matschie actually described three supposedly new elephant species: *Elephas cyclotis*; *Elephas* (*Loxodonta*) *oxyotis* from the upper Atbara River in Sudan, and *Elephas (Loxodonta) knochenhaueri* from Barikiwa in southern Tanzania. The type specimen of *cyclotis* was a male from Yaunde, in southern

Cameroon, living at that time in the Berlin Zoo. From their localities, as well as from our examination of their skulls, the other two presumed species are Bush African Elephants.

Uncertain of whether African elephants should be separated from Asian elephants in a separate subgenus, and apparently even under what name the typical [South African] form of the African elephant should be known, Matschie added that one might prefer to call the first of these *Elephas capensis cyclotis* or *Elephas (Loxodonta) cyclotis*, and the other two *Elephas africanus oxyotis* and *Elephas africanus knochenhaueri*. The rules of nomenclature specify that, if we want to cite the author and date of a scientific name, we place the author and date in parentheses after the name if we place the species or subspecies in a genus different from the one which the original author did [cf. Article 51(c) in International Commission on Zoological Nomenclature, 1985]. In this case, as Matschie ascribed *cyclotis* to the genus *Elephas*, but we today place it in a different genus, *Loxodonta*, the full citation of the scientific name of the Forest African Elephant is *Loxodonta cyclotis* (Matschie, 1900).

The first presumed pygmy elephant was a young female in Hamburg Zoo, caught at Njole in Gabon, described as *Elephas africanus pumilio* by Noack (1906). At an age estimated (by the zoo's director, Carl Hagenbeck) to be about 6 years, this female was the same size as the types of Matschie's *cyclotis* and *oxyotis* (both living in Berlin Zoo), which, from photos published in a popular book some years before, Noack judged to be a mere one and a half years old; as further guarantee of her age, he noted that her tusks were already 12 cm long, whereas in the type of *cyclotis* they were only just beginning to emerge (and in the type of *oxyotis* none were visible). He recognized, however, that the Hamburg female was similar in some respects to *cyclotis*, though her ears were smaller.

This female, the living type specimen of *pumilio*, was, even as Noack was describing her, transferred from Hamburg to New York, where she (under the name "Congo", Fig. 1) was at first identified as an example of *cyclotis*, and later, when her important status was realized, exhibited as *Elephas pumilio* (no longer a subspecies of *E. africanus* but a full species!). Schouteden (1911a) reported on her continued growth, as communicated to him by the New York Zoo's director, Hornaday. In July 1905 she had been 111.7 cm high and weighed 272 kg; by July 1911 she had grown to 152.4 cm in height and 770 kg in weight. Morrison-Scott (1947) says that at her death, in 1915, she was 203 cm in height.

Schouteden (1911b) described a second pygmy elephant, *Elephas africanus fransseni*, from Mpaa, on Lake Mai-Ndombe (at that time called Lake Leopold II) in Democratic Republic of the Congo (DRC), the former Zaire. The type specimen, said to have been one of the largest in the herd, was 166 cm at the shoulder.

Other elephants identified as pygmies, including some zoo animals and some reports from the wild, were mentioned by Morrison-Scott (1947) and Pfeffer (1960), who did not believe in the existence of a pygmy species, and by Heuvelmans (1959), who did. Roeder (1970) gave comparative tables of measurements for what he identified as ordinary Forest Elephants and as the Pygmy species, and later (Roeder, 1975), he described some presumed pygmies from Cameroon. Especially interesting is his table 4 (Roeder, 1970, p. 207) in his 1970 paper, giving the shoulder heights of Forest Elephants captured at Api, in Garamba National Park, DRC, and all of known age. Nine females, 27 years old or more, stood 215-240 cm high; one aged 24-25 was 205 cm; and one aged 19 was 201 cm. Four males, all 27 to 29 years old, were 228-238 cm, and his table 2 (Roeder, 1970, p. 206) records that a

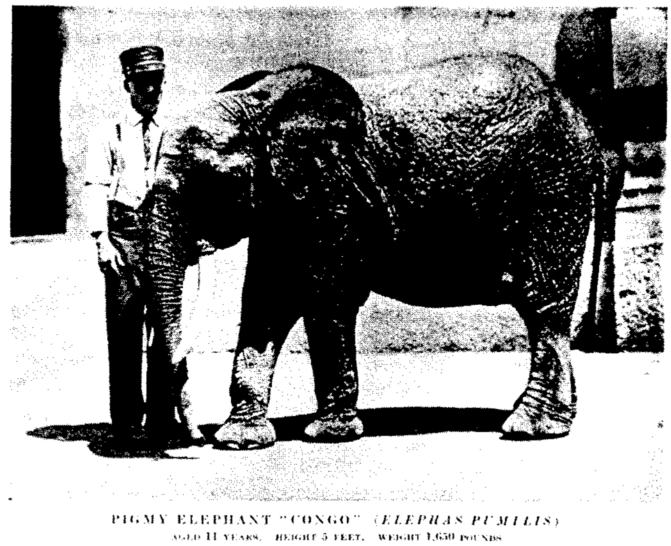

Figure 1. A photograph of "Congo", a female Forest African Elephant, the type of "*Elephas pumilio*", now classified as *Loxodonta cyclotis*.. Note round shape of ear, hence the name ("cycle"=round, "otis"=ear) [after Kunz, 1916, between pages 384 and 385; reprinted with permission from the New York Zoological Society].

17 year old male from Gangala na Bodio was 220 cm high and a 14 year old was 205 cm, while four 9-10 year old females from Gangala and Api were 174-208 cm.

Most recently Eisentraut and Böhme (1989) discussed the question, giving photos of apparently mature bulls of Forest and Pygmy Elephants, and of skulls of the two in the Central African Museum, Tervuren, and frames from a film of a wild pygmy elephant, apparently one of a herd. The following year (Böhme and Eisentraut, 1990) followed this up with photos of presumed pygmies in a private zoo in Liberia (but apparently caught in Congo) and of a wild herd (females and young) in forest photographed by Ambassador Harald Nestroy in the northern Likouala region on the border between Congo/Brazzaville and the Central African Republic. The size of the wild ones could be deduced from the presence in the same photos of a Great White Egret. If this egret is 1 meter high, then the adult elephants, which are shown walking in front of it, would be about 150 cm high. Later, he photographed four much larger elephants in the same clearing, with a Red Buffalo conveniently present as scale. Greenwell (1992, 1993) considered this evidence conclusive of the real existence of a Pygmy species.

Skulls of Pygmy Elephants

It should be noted that the skull of the type of Matschie's *cyclotis* is in the Berlin Museum. It is a male with both third and fourth molars in the jaw (our dental eruption stage 4), interpreted as about 10 years old. Unfortunately, it is not known when he died, thus his age in the photograph seen by Noack (1906) is not clear. The skull length is 590 mm. There is no overall difference in size between stages 4 and 5; the lengths of nine other skulls of these two stages vary from 470 to 630 mm, thus it is on the large side for its age.

A skull in the American Museum of Natural History (New York, New York USA), AMNH 90102, a young female from the zoo and ultimately from the Fernan Vaz district, Gabon, may be that of "Congo", hence the type of Noack's *pumilio*, or it may be that of "Josephine", a second supposed pygmy who was in the same zoo in the 1920s. AMNH 90102 shows all the features that distinguish *L. cyclotis* from *L. africana*. It is not possible to detect its dental eruption stage, but it is certainly quite immature. If it is Congo's, and if Congo really was 6 years old in 1905, and 16 years old when she died in 1916, then we would expect her to have the fourth molar in wear, as in dental eruption stage 5 (Groves and Grubb, 2000). The skull is 535 mm long. Ten female *L. cyclotis* skulls of stages 4 and 5 (which are similar in size, as are those of the males) range from 489 to 568 mm. Thus, if the skull is the type of *pumilio* then it is towards the upper end of the range of *L. cyclotis* of presumed equivalent age.

The type skull of Schouteden's *fransseni* is still in the Tervuren Museum. Its catalogue number is MRAC 3396, a female with the fifth molar in wear (our dental eruption stage 7), and so aged somewhere between 20 and over 30 years of age. It, too, is, in all diagnostic features, a typical skull of *L. cyclotis*. It is 544 mm long. The lengths of 23 *L. cyclotis* skulls of stages 6 and 7 (which do not differ in size) are from 510 to 619 mm (all but three being below 600 mm). Thus, the type of *fransseni* is of typical size for its age, perhaps somewhat on the small side.

The skull figured by Eisentraut and Böhme (1989) as that of a pygmy elephant is likewise in the Tervuren collection. It is MRAC 9524, from Moma, 1°25'S, 23°57'E, in southern DRC; a very aged female, with 6th molars nearly worn out or, in one case, actually lost (i.e., dental eruption stage 9), probably over 60 years old. It, too, is, in its essential features, a skull of *L. cyclotis*. It is 574 mm long; the skulls of eight acknowledged *L. cyclotis* of stage 9 vary from 588 to 706 mm; this skull is the smallest of the adult females we have seen. Consequently, we cannot find that the skulls assessed as those of Pygmy Elephants are anything but specimens of *L. cyclotis*, the Forest African Elephant.

OTHER EVIDENCE

The evidence of measured body sizes does not support the Pygmy Elephant concept. The female Congo, the type of *pumilio*, was 203 cm high at death which is about the same size as a 14 year old female from Garamba, as tabulated by Roeder (1970); if she was indeed 15 years old when she died, this would be exactly right for a female *L. cyclotis* of the same age.

The height of the type of *fransseni* was given as 166 cm. This is way below the figures for females of *L. cyclotis*, and seems not to match with the evidence of the skull (above). We take leave to question whether the measurement, taken under avowedly difficult conditions, is accurate. Certainly in the photos reproduced by Schouteden (1911b, plate 11), the elephant looks as if it was taller than Lieutenant Franssen.

The evidence of Ambassador Nestroy's photos (taken in May 1982) is less clear-cut than it at first appears. In the photo of the group with the egret (Abb. 7), in which young elephants are present, the position of the egret, though obviously behind the lead female, is not at all clear; how much of the body and neck are to be seen in the photo, hence how big (relative to the elephants) the egret actually is, is not as obvious as it might seem. The age of the larger elephants is likewise not known. The photo with the buffalo (Abb. 5) evidently shows only mature males. We are, therefore, comparing herd females, of uncertain size and in any case not necessarily full-grown, with non-herd (breeding) males.

Part of the problem seems to be that many commentators are unfamiliar with the (perhaps rather bizarre and idiosyncratic) growth patterns and social structure of elephants. Elephants grow throughout life, even females, though males much more. Elephant herds are matriarchies. The consequences of these two facts are as follows: (1) females of different ages will be of substantially different sizes, and if the matriarch has died there may well be no extremely large females in the herd; (2) a herd which contains calves will almost certainly contain no mature (breeding-age) males; (3) a group of bulls will be fairly young but mature, so of relatively large size [perhaps related to precocity]; and (4) a bull seen on its own will probably be old, hence of very large size.

CONCLUSIONS

All the evidence so far presented in the literature agrees with these precepts. Based on data we collected, we cannot find evidence for the existence of a pygmy species of elephant. The skulls we examined, purportedly those of Pygmy Elephants, are specimens of the Forest African Elephant, *Loxodonta cyclotis*.

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