Geographic variation within Eastern Chimpanzees (*Pan troglodytes* cf.*schweinfurthii* Giglioli, 1872)

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Introduction

The basic outlines of the present-day taxonomy of chimpanzees was laid by Schwarz (1934), who recognised a single species, *Pan satyrus*, with four subspecies: *P.s.troglodytes* (Central Africa), *P.s.verus* (West Africa), *P.s.schweinfurthii* (East Africa and D.R.Congo north and east of the Congo River) and *P.s.paniscus* (south of the Congo River). The specific name used by Schwarz has been changed: the previous year, Stiles & Orleman (1927) had already shown that the correct name is *Pan troglodytes*; they dated this name from Blumenbach (1799), but the first usage of the name *troglodytes* actually dates from the same author in 1775 (Corbet et al., 1974). The generic name *Pan* Oken, 1816, in wide usage since the early 20th century but strictly speaking unavailable because it comes from a non-binomial work, was finally made available after a long delay in 1985 (Opinion 1368, 1985).

The pygmy chimpanzee or bonobo was elevated to species rank as *Pan paniscus* by Coolidge (1933), although the significance of this act was somewhat marred by the fact that he also listed *Pan schweinfurthii* as a full species; today, the bonobo is invariably placed in a distinct species (Coolidge & Shea, 1982).

As a matter of fact, the basis of Schwarz's revision was never very clear. It is evident from the context that he studied both museum specimens and living animals, but he did not state how many there were of each. He gave quite detailed descriptions of age changes, but again the evidence for these details is not given. Subsequent authors have tended to follow Schwarz, but mostly have seemed uneasy about how they really differ. Groves (1986, Table 9) listed all the characters which had been supposed to differentiate the four Schwarzian taxa, but the result was not entirely satisfactory because more authors had been concerned to compare *Pan paniscus* with an all-purpose *Pan troglodytes* than to compare geographic populations of *Pan troglodytes* with each other. Inspection of photos of chimpanzees of known origin does seem to confirm that *P.t.verus* has a dark midfacial mask when young, of which traces remain in the adult, and has a midline hair parting on the scalp; the brow ridges may be more arched and laterally flared. Of the other two subspecies, *P.t.troglodytes* evidently has earlier and deeper facial darkening, becomes earlier and more totally bald, and may attain enormous body size, all peramorphic conditions relative to *P.t.schweinfurthii*.

Vandebroek (1969) found differences in suture patterns in the orbit between *P.t.verus* and other subspecies. Groves (2001) confirmed this: an ethmo-lacrimal suture occurs in only 21% of *P.t.verus*, but in over 80% of other subspecies. In addition, over 50% of *verus* skulls have an ossicle at lambda, compared to under 30%

of other subspecies. According to Braga (1998), closure of both anterior (facial) and palatal components of the incisive (maxillary-premaxillary) suture occurs earlier in *P.t.verus* than in the other two subspecies (in *Pan paniscus* it occurs still earlier).

Mitochondrial DNA sequencing has added a new dimension to the understanding of chimpanzee interrelationships. Morin et al. (1994) found that *P.t.verus* has uniquely different sequences from *P.t.troglodytes* and *P.t.schweinfurthii*, implying a long time since the two lineages separated; Goldberg & Ruvolo (1997) found that genetic similarity among populations of *P.t.troglodytes* decreases clinally with distance; while Gonder et al. (1997) found that the mtDNA sequences of chimpanzees from Nigeria and northwestern Cameroon are strongly distinct from other chimpanzees, and recommend recognising a fourth subspecies, *P.t.vellerosus*, which is closer to *P.t.verus*. By contrast to the mtDNA sequences, in the nonmetrical cranial characters that separate *P.t.verus* from other subspecies, *P.t.vellerosus* falls with the non-*verus* chimpanzees (Groves, 2001).

Groves et al. (1992) found that craniometric analyses did not separate chimpanzee populations along traditional subspecies lines; in particular, geographic variation among eastern chimpanzees (populations usually combined as *Pan troglodytes schweinfurthii*) seemed to approach or equal that among commonly recognised subspecies. It seems appropriate to begin to investigate the real nature of geographic variation among chimpanzees, beginning with the eastern subspecies.

Material and Methods

The material studied for this exercise is the craniometric dataset reported in Groves et al. (1992). Karl Ammann kindly supplied measurements for two further skulls, from the Bondo district, Uele River.

The list of variables used is given in Appendix 1.

I ran a series of multivariate analyses using SPSS Discriminant. Discriminant (or Canonical) Analysis uses correlation matrices to find the weighted combinations og variables which best discriminate between groups of specimens, maximising between-group variance while minimising within-group variance. Discriminant Function 1 accounts for the largest chunk of the total variance, DF2 for the next largest, and so on until noise begins to overwhelm signal.

Analyses used different combinations of age/sex classes, local population samples, and variables. "Young adults" are skulls in which the third molars have erupted but the spheno-occipital synchondrosis ("basilar suture") remains unfused; "Y/A to Adult" means that the synchondrosis is in process of fusing; "Adult" means that it has completed fusion, so the skull is deemed to have achieved its full growth.

Analyses also used different combinations of variables. In any statistical analysis, the number of variables should not be greater than the number of specimens per group, as this greatly increases the risk of a Type I error (a true null hypothesis incorrectly rejected); so if sample sizes are small the number of variables must be reduced accordingly. I determined which variables seem to be the most efficient discriminators by running analyses using the full variable set, choosing those with the highest weightings on DF1 and 2, and re-running the analysis using only those, and using only those groups with sample size larger than the remaining number of variables. Groups with smaller sample sizes can be included in such an analysis by leaving the specimens ungrouped; the parameters of dispersion will be determined by the groups, and the ungrouped specimens do not have a chance to contribute to this but fall where they may.

The available material of *P.t.schweinfurthii* was grouped geographically into six groups as follows:

Oubangui (including Banzyville, Bumba and Lisala),
Uele (Faradje, Buta and vicinity),
Ituri (Kisangani, Yambuya, Bafwaboli, Ubundu, and east through the Ituri Forest (Mawambi, Epulu) to Lake Albert),
Uganda (Rutshuru district to western Uganda and south to Rwanda and Burundi),
Maniema (including Kivu, Kabambare, Shabunda, Warega, Bukavu, Fizi and Boko),
Marungu.

A single skull was available from Tanzania (Kibwesa), but was too incomplete to be entered into any of the analyses.

Ideally, the sample should be broken down still further, but available material does not permit. Karl Ammann (personal communication) suggests that it might be useful to separate samples from north and south of the Uele River; and that pick-up samples might become available in future.

Results: within *P.t.schweinfurthii*

1. DFA: Both sexes. As a pointer to possible relationships, I simply divided the sample into its geographic groups and included both sexes and young adults as well as adults, using 13 cranial variables. Although failing to separate sexes and ages in this way will risk reducing discrimination power, it equally reduces the probability that simple size effects will predominate. I entered Oubangui, Uele, Ituri, Uganda and Maniema as groups, but the Marungu specimens (of which there were only 5) as unknowns. Fig.1 shows the plot of the first and second functions.

On the first Function, Uganda tends to be distinguished from the other samples; on the second, Uele is fairly well distinguished. The third Function tends to distinguish Ituri, but more poorly. Table 1a shows that, while DF1, as would be expected, accounts for more than half of the total variance, DF2 and 3 both account for over 10%.

Table 1b shows that DF1 is strongly positive on interorbital breadth and orbit breadth, and on face length (nasion-prosthion), but strongly negative on biorbital breadth; DF2 contrasts orbit breadth, nasion-basion distance and braincase breadth (bieuryonic) with biorbital breadth and basion-bregma height; and DF3 contrasts biorbital and bizygomatic breadth and basion-bregma height with nasion-basion distance. It is not easy to give a strict biological meaning to these functions.

Table 1c shows that, perhaps unexpectedly, over half the specimens in each group are differentiated by this analysis.

Of the Marungu specimens, one fell into the Uganda cluster, two into the Uganda-Uele overlap zone, one into Ituri, and one outside any other cluster.

2. DFA: Adult/Young adult females. I next ran an analysis using only females, again from young adult to fully adult (in females, there is no significant change in cranial size or shape after the eruption of the third molars). Sample sizes are now, of course, considerably reduced from those in analysis 1; the variable list was therefore reduced to 7, after an initial run to determine their relative importance, and only the three samples with *n* of at least 7 were entered as groups, the others being left as "unknowns" to fall where they will in the predetermined dispersion.

Table 2a shows that both functions are significant. Fig.2 shows the results: the three samples are well distinguished, Uganda more than the other two. Function 1, along which Uganda is differentiated (by negative values) from the other two samples, contrasts orbital breadth, interorbital breadth and face length (positive) with biorbital breadth and nasion-basion (negative); Function 2, on which Uele is positive and Ituri negative, contrasts nasion-basion, bizygomatic and orbit breadth with biorbital breadth. These contrasts are very much as in the previous analysis.

Over 70% of Ituri and Uele, and over 80% of Uganda, are correctly classified.

Of the unknowns, two Oubangui skulls are inside the Uganda dispersion, two are outside any other sample's range; three Maniema skulls are classified with Uganda, one outside any other; of the two Marungu skulls, one is classed with Ituri, the other outside any group.

3. DFA: Adult/Young adult females, reduced variables list. In order to be able to include more samples, a further DFA was run on females, with the variables reduced to 6, selected so as to allow the maximum number of skulls to be included; even so, some groups still had fewer specimens than the number of variables, so the analysis should be regarded as experimental only. Some specimens from Yambuya (Kisangani district) were added in as unknowns.

Although the first three functions each accounted for over 10% of the total variance, plots of DF3 and against DF1 or 2 did not add anything to the picture, so only the DF1 vs. 2 plot is figured (Fig.3). The groups were poorly separated, and inspection of the summary table (Table 3b) shows that no group was correctly classified at a very high level, although Uganda plus Maniema together were >80% correctly allocated. Yambuya tended to scatter throughout the diagram; the skulls had been acquired by the Tervuren Museum from a biomedical laboratory in Kisangani, and had probably been brought into captivity from a wide area (there are even bonobos in the Yambuya/Kisangani sample).

4. DFA: Adult males. Because male skulls continue until the spheno-occipital synostosis has fused, only full adults could be included in the analysis for males only. Again, both eigenvalues are significant (Table 4a). In Fig.4, Uele is this time much better distinguished from Uganda and Ituri than these are from each other. Function 1, on which Uele is negative and the other two are positive, contrasts orbital breadth, muzzle breadth and braincase breadth (positive) with postorbital, bicanine and bizygomatic breadth and prosthion-staphylion (negative); function 2 essentially contrasts bizygomatic breadth with prostion-staphylion distance.

Over 90% of Uele, over 80% of Uganda, and over 75% of Ituri are correctly classified.

Of the ungrouped specimens, a skull from Ekwangat (not found: possibly Ekwangatana, 2°51'N, 24°05'E) identifies itself as Ituri. All 5 Oubangui skulls are placed within the Ituri dispersion. The type skull of *Simia (Anthropopithecus) adolfi-friederici*, from "Chuma, between Bugoye and Njavaranga" (Bugoye is 2°49'S, 28°42'E, southwest of Lake Kivu), unexpectedly classifies itself as Uele; but, at DF 1 = -1.37 and DF2 = .51, it is (just) on edge of the Ituri dispersion, but it could not be classed among Uganda. Of three Maniema skulls, one is nearest Uele but not within the Uele dispersion, one is near both Uganda and Uele but not within either dispersion, and the third is within the Uganda dispersion. Finally, a skull from Marungu is within either Ituri or Uganda.

4. Univariate: skull length. A few individual measurements are examined separately, especially Prosthion-inion (=greatest skull length, a representation of absolute skull size). The adult males are depicted in Fig.5, young adult to adult females in Fig.6.

The males show a striking division between the three large-sized northwestern samples (Oubangui, Uele, Ituri) and the three small-sized southeastern samples (Uganda, Maniema, Marungu). The three southeastern samples, moreover, progressively reduce in size to the south (Uganda-Maniema-Marungu). A skull from Ubundu, in the Kisangani district, is small like the southeastern samples. The type of *adolfi-friederici*, mentioned above as being on within the Uele/Ituri dispersion while on the borders of the northwestern and southeastern ranges, is at 197mm well within the northwestern range and unlikely to be in the southeastern. One of the Uele males is simply monstrous in size, 224mm, second only to a skull from Yaounde, in Cameroon, which is 235mm (the next largest are are 217, 216, 214, and so on).

The females divide similarly, but not quite so sharply; Ituri females (but n=5 only) average larger than Uele and Oubangui ones, and Maniema females average slightly larger than Uganda ones, leaving Marungu very considerably smaller than the other two southeastern ones. In this case the Kisangani specimen (here, from Yambuya) is large like the northwestern ones.

Results: between *P.t.troglodytes* and *P.t.schweinfurthii*

1. DFA: Adult/Young adult females, border populations examined. The DNA studies (see Introduction) tend to associate *P.t.troglodytes* and *P.t.schweinfurthii* in a clade opposed to *P.t.verus*. The questions must be asked: are these two supposed subspecies morphologically distinct at all? If they are, what is the affiliation of bordering populations? And finally, are they more different from each other than their component samples?

Fig.7 shows the results of comparing the two putative subspecies, but keeping their geographical border samples (Sangha and Oubangui respectively) separate. As an experiment, all ages from young adult to adult, and both sexes, are combined. The Sangha sample fits well into *P.t.troglodytes*, the Oubangui one into *P.t.schweinfurthii*. In as far as the two subspecies are real – and there does seem to be some support for this, although there is wide overlap – the boundary between them seems likely to be the Oubangui River.

Table 5 gives the weights for the raw variables. *P.t.troglodytes* would have large biorbital and bicanine, and to a lesser degree palate, breadths, and a relatively short braincase; *P.t.schweinfurthii* would have a long nasion-basion distance, long face and palate, wide orbits and wide braincase.

2. DFA: Adult/Young adult females, all *P.t.schweinfurthii* samples examined. This analysis and the next examine the question of whether the two putative subspecies are more different from each other than are samples within *P.t.schweinfurthii*. Fig.8 shows that the females of the two subspecies separate on DF1, while the northwestern and southeastern groups of *P.t.schweinfurthii* separate on DF2 (no other functions are significant: Table 6a). Table 6b indicates that

P.t.troglodytes has broad interorbital and bicanine breadth, while *P.t.schweinfurthii* has relative long skull and high palate and nasion-basion lengths. The northwestern *schweinfurthii* samples have long skulls and long faces, the southeastern have high bicanine width and fairly long palates.

Whereas only 66% of *P.t.troglodytes* skulls are correctly classified (Table 6c), fully 81% of Uganda specimens are correctly allocated, as are 16 of the 22 (73%) northwestern *schweinfurthii*, when the three samples are taken together.

3. DFA: Adult males, all *P.t.schweinfurthii* samples examined. The picture for male skulls is very similar (Fig.9): the two subspecies separate on DF1, the regional populations of *P.t.schweinfurthii* on DF2. Table 7b shows that *P.t.troglodytes* have long skulls (contrary to the female analysis), and high biorbital and palate breadths (more congruent with the female analysis); *P.t.schweinfurthii* have long face and palate, and wide orbits and braincase. The northwestern samples have long skulls, long faces and wide braincases, the southeastern have long palates and wide biorbital breadths, and this is fairly consistent with the picture for females.

Only 64% of *P.t.troglodytes* skulls are correctly classified (Table 7c), and 71% of Ugandan, but, taken together, 21 of the 26 (81%) of northwestern *schweinfurthii*.

4. Univariate: Young adult to adult females. Table 8a shows that northwestern females are largest in most cranial measurements; *P.t.troglodytes* and southeastern are smaller, about equivalent in size, indicating that *P.t.troglodytes* is more sexually dimorphic. This is especially noticeable for greatest skull length, face length, and palate length. Among the southeastern groups, Marungu is exceptionally small in greatest skull length, Uganda in face length; Maniema has unusually broad zygomata. Among the northwestern groups, Ituri is largest in most respects.

5. Univariate: Adult males. Table 8b shows that among males, as among females, northwestern are larger than southeastern; in this case, *P.t.troglodytes* are as large as northwestern. Greatest skull length, bizygomatic breadth and biorbital breadth show the most marked differences in this case; in many variables, the (single specimen from) Marungu is as large as a typical northwestern specimen, but retains the short skull, narrow biorbital breadth and short palate of the other southeasterns.

Results: all *Pan troglodytes*

The purpose of the present paper is not to revise the entirety of *Pan troglodytes*, but it may be of interest to see how skull size varies across all population samples. Fig.10 shows the males, Fig.11 the females. Among males, Uele and Cameroon plateau clearly average the largest, while *P.t.vellerosus* and “southeastern” are the smallest; note that populations within *P.t.*cf.*schweinfurthii* include the equal-largest and the equal-smallest skulls. Among females, the relationships are much the same, except that Sangha (but only two specimens!) are the smallest. Occasional giants occur, in both sexes, in several populations.

There are many fewer postcranial specimens than skulls, but it is of interest to see how well skull size reflects body size. Using humerus length as an indication of body size, males in *P.t.troglodytes* are much larger than in *P.t.*cf.*schweinfurthii*: as far as the tiny samples go, the two do not even overlap, despite the fact that one of the “*schweinfurthii*” specimens is from Ituri, a northwestern population (Fig.12). In the females, however, there is no such difference (Fig.13); this is consistent with the greater sexual dimorphism in skull size in *P.t.troglodytes*.

Fig.14 graphs skull length against humerus length, to test whether there are proportional differences between populations. Irrespective of subspecies, the different samples follow the same trend, with the striking exception of the Gabon coast sample of *P.t.troglodytes*, in which, on the face of it, the humerus would appear to continue growing after the skull has ceased. This is a problem to be investigated in a future study.

Discussion and Conclusion

The crania of chimpanzees from the range usually ascribed to *Pan troglodytes schweinfurthii* can be divided into two groups: a northwestern group (from Oubangui, Uele and Ituri districts) and a southeastern group (from Uganda, Maniema and Marungu). The former are large-skulled, with long face, broad braincase and zygomata; the latter are smaller, relatively wide across the orbits and muzzle, and with relatively long palate. The combination of these measurements enables one to discriminate some 70-80% of specimens, and the phenetic distance between them is comparable to that between either of them and *Pan troglodtyes troglodytes*.

There is a creeping tendency in some quarters to give mtDNA-sequencing precedence over morphology as a taxonomic criterion. It is not clear why this should be; morphological differences too are genetically based, even in cases of phenotypic plasticity, and are coded for by one or more nDNA sequences, nDNA being biparentally inherited and subject to recombination, whereas mtDNA is matrilineally inherited and clonal. Morphological differences between populations, being nDNA differences at one remove, therefore offer a more complete picture of genetic differentiation than does mtDNA. The fact that the mtDNA lineages of the putative subspecies *P.t.schweinfurthii* form a subset of the *P.t.troglodytes* clade (Morin et al., 1994) is of great interest in reconstructing the history of female dispersal, but offers an incomplete picture of population interrelationships as a whole, and is silent on the history of drift and natural selection.

The present study deals with craniometry. Other sources of morphological evidence may tell a different story; some chimpanzee specialists, for example, claim to be able to differentiate *Pan troglodytes troglodytes* with some confidence on external appearance. On cranial morphology the differentiation is fair; I have argued that it is around the conventional level of subspecific difference (75%), and that so is the difference between northwestern and southeastern "*schweinfurthii*".

Craniometry therefore indicates that there are two subspecies within what is presently called *Pan troglodytes schweinfurthii*. The type locality of the name *schweinfurthii* is Niam-Niam country, on the upper Uele, so the name is available for the large, northwestern subspecies. The first available name for the small, southeastern subspecies is *marungensis* Noack, 1887. The synonymy is as follows:

1. ***Pan troglodytes schweinfurthii* (Giglioli, 1872)**

1872 *Troglodytes schweinfurthii* Giglioli. Niam-Niam country, upper Uele.
1905 *Fsihego ituriensis* de Pauw. Ituri.
1912 *Simia (Anthropopithecus*) *nahani* Matschie. Banalia, Aruwimi River.

1912 *Simia (Anthropopithecus) ituricus* Matschie. Makala-Avakubi Road, Ituri.
1912 *Simia (Anthropopithecus) adolfi-friederici* Matschie. Bugoye, W.of L.Kivu.
1912 *Simia (Anthropopithecus) kooloo-kamba yambuyae* Matschie. Yambuya, lower Aruwimi.
1914 *Anthropopithecus schubotzi* Matschie. Between Kilo and Irumu, upper Ituri.
1914 *Anthropopithecus steindachneri* Matschie. Moera, north of Beni.

Distribution: North of Congo River, from its junction with the Oubangui, northeast via the Uele into southernmost Sudan, to the Ituri region and Lakes Edward and Albert, and Kisangani district, east to Lake Kivu.
Characters: Large size; relatively long and wide upper face (great orbit and bizygomatic breadths), wide interorbital breadth; wide braincase.
Notes: I have indicated above that one should expect lineage overlap of mtDNA between subspecies, just as there is morphological (=nDNA) overlap. In this regard, it is of some interest that some *P.t.troglodytes* sequences cluster with the main eastern sequences, while sequences from Bondo and from the Bangui Zoo (i.e. from the Uele and Oubangui regions of this paper) are also largely different (Gagneux et al., 2001, Figs. 2, 3). That is to say that differences between *P.t.troglodytes*, *schweinfurthii* and *marungensis* are triangular in mtDNA as they are in craniometrics.

2. *Pan troglodytes marungensis* (Noack, 1887)

1887 *Troglodytes niger* var. *marungensis* Noack. Marungu, west of L.Tanganyika.
1899 *Troglodytes livingstonii* Selenka. Nomen nudum.
1912 *Simia (Anthropopithecus) cottoni* Matschie. Ishasha River, Uganda.
1914 *Anthropopithecus purschei* Matschie. Between L.Kivu and L.Luhondo, Tanzania.
1914 *Anthropopithecus pfeifferi* Matschie. East of Ruzizi R.
1914 *Anthropopithecus graueri* Matschie. Wabembe country.
1914 *Anthropopithecus calvescens* Matschie. Luama R., between Niembo and Kabambare.

Distribution: Rutshuru district to western Uganda south to Rwanda, Burundi and northwestern Tanzania; Kivu district south through Maniema and the Itombwe Mountains, south to Fizi and Marungu.
Characters: Small size, relatively broad muzzle (high biorbital and bicanine widths) and fairly long palate.
Notes: Thompson (2001), and Kingdon (1997), citing unpublished work by Thompson, suggested that the chimpanzee of the Marungu Mountains is *Pan paniscus*, and that, if this is so, the name *marungensis* Noack, 1887 would be a senior synonym of *paniscus* Schwarz, 1929. Certainly it is true that Noack's (1887) contorted description is quite unsatisfactory, and its unadequacies allowed the occasional bonobo that reached Europe prior to 1929 to be designated "*marungensis*", as documented by Thompson (2001). Jo Thompson (personal communication) is no longer of this opinion, and it is now clear that Marungu chimpanzees are small-sized *Pan troglodytes*, and the name *marungensis* is the earliest available name for the southeasternmost subspecies.

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Appendix: list of measurements

PR - prosthion-opisthocranion – from prosthion (anterior point between [but not including] upper central incisors) to opisthion (most remote point on back of braincase)

GL - glabella-opisthocranion – from glabella (convexity between supraorbital tori [brow ridges], above root of nose), to opisthocranion (most remote point on back of braincase)

BZ - bizygomatic width – greatest width across zygomatic arches

EU - bieuryonic breadth – greatest width across braincase (on vault, **not** across supramastoid crests)

PO - postorbital breadth – narrowest width across of constriction between orbits and braincase

BI - inside biorbital breadth – greatest width across orbits (**excluding** the bony ridges lateral to orbits, i.e. the two sockets plus the interorbital pillar)

ORB - breadth of one orbit (typically the left) – just across the socket itself

IO - interorbital breadth – greatest width of interorbital pillar

BC - bicanine breadth (outside alveoli) – greatest width across roots of canines (on the bone not on the teeth themselves)

NP - nasion-prosthion – from nasion (point where nasal and frontal bones meet) to prosthion (lowest point between upper central incisors)

NB - nasion-basion – from nasion (point where nasal and frontal bones meet) to basion (anterior edge of foramen magnum)

BA - basion-bregma – from basion (anterior edge of foramen magnum) to bregma (point where frontal and parietal bones meet)

PS - prosthion-staphylion – from prosthion (anterior point between [but not including] upper central incisors) to staphylion (midline point on back of palate, excluding projection at back of palate)

IN - I2-I2 – breadth outside lateral incisor alveoli (on bone, not on teeth themselves)

MO - M2-M2 – breadth of palate (outside second molar alveoli, on bone not on teeth themselves)
bigonial breadth – breadth of lower jaw, across jaw angles at their widest
bicondylar [mandibular] breadth – breadth of lower jaw, across both mandibular condyles
condylion-gonion – height of ascending ramus of jaw on one side (from lowest point on jaw angle to highest point on condyle)
toothrow length maxillary – length of the five cheekteeth (P3-M3, alveolar)
femur length – greatest length of shaft of femur (so excluding head)
humerus length – greatest length of humerus
radius length – greatest length of radius
tibia length – greatest length of tibia, including malleolus (=projection at bottom)

Captions to Figures

1. Samples of *Pan troglodytes schweinfurthii*, both sexes, all skulls with third molars erupted; (a) DF1 vs 2, (b) DF1 vs 3.

2. Samples of *Pan troglodytes schweinfurthii*, females only, all skulls with third molars erupted, DF1 vs 2.

3. Samples of *Pan troglodytes schweinfurthii*, females only, reduced variables list, all skulls with third molars erupted, DF1 vs 2.

4. Samples of *Pan troglodytes schweinfurthii*, adult males only, DF1 vs 2.

5. Greatest skull length for samples of *Pan troglodytes schweinfurthii*, adult males only. In each case, the central bar is the median, the limits of the box are quartiles, and the ends of the whiskers are maximum and minimum, except for o (=outlier).

6. Greatest skull length for samples of *Pan troglodytes schweinfurthii*, young adult to adult females. In each case, the central bar is the median, the limits of the box are quartiles, and the ends of the whiskers are maximum and minimum, except for o (=outlier) and * (=extreme).

7. Samples of *Pan troglodytes troglodytes* and *schweinfurthii*, both sexes, all skulls with third molars erupted, DF1 vs 2, with geographically marginal samples (Sangha and Oubangui) kept separate.

8. *Pan troglodytes troglodytes* and samples of *P.t.schweinfurthii*, females, all skulls with third molars erupted, DF1 vs 2.

9. *Pan troglodytes troglodytes* and samples of *P.t.schweinfurthii*, adult males, DF1 vs 2.

10. Skull length in populations of *Pan troglodytes*: adult males.

11. Skull length in populations of *Pan troglodytes*: young adult and adult females.

12. Humerus length, as indicator of body size, in samples of *P.t.troglodytes* and *P.t.*cf.*schweinfurthii*: adult males.

13. Humerus length, as indicator of body size, in samples of *P.t.troglodytes* and *P.t.*cf.*schweinfurthii*: young adult and adult females.

14. Relation between skull size (prosthion-inion length) and body size (humerus length) in *P.t.troglodytes* and *P.t.*cf.*schweinfurthii*.

Captions to Tables

1. Statistics for Fig.1. a. Eigenvalues. b. Weights for Functions. c. Summary table.

2. Statistics for Fig.2. a. Eigenvalues. b. Weights for Functions. c. Summary table.

3. Statistics for Fig.2. a. Eigenvalues. b. Summary table.

4. Statistics for Fig.3. a. Eigenvalues. b. Weights for Functions. c. Summary table.

5. Statistics for Fig.7: Weights for Functions.

6. Statistics for Fig.8. a. Eigenvalues. b. Weights for Functions. c. Summary table.

7. Statistics for Fig.9. a. Eigenvalues. b. Weights for Functions. c. Summary table.

8. Statistics for selected cranial variables of *Pan troglodytes troglodytes* and geographic groups of *P.t.*cf.*schweinfurthii*. a. Females (Young adult to adult). B. Males (Adult).

Canonical Discriminant Functions

Y/A to Adult, males and females

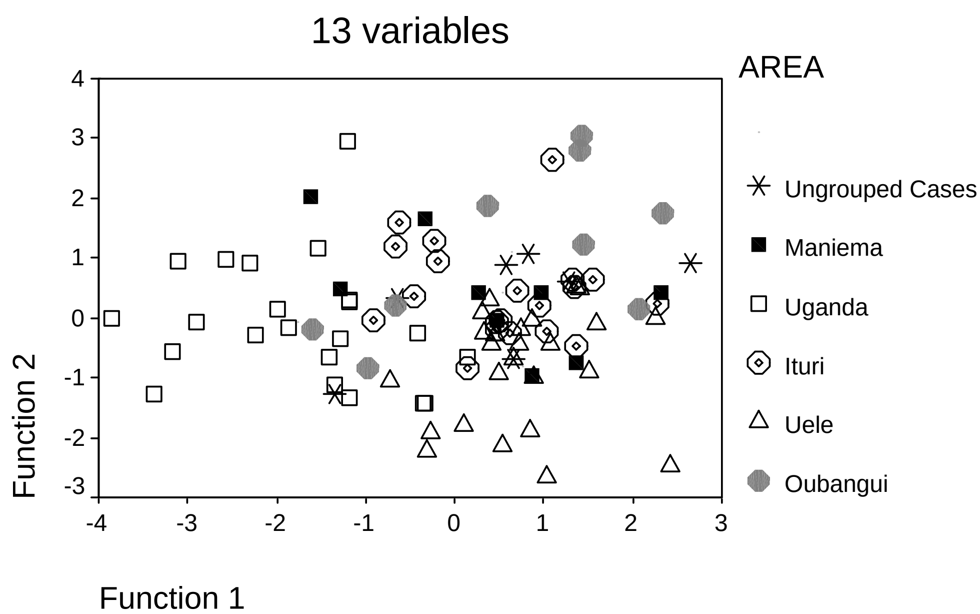


Fig.1a

Canonical Discriminant Functions

Y/A to Adult, males and females

13 cranial variables

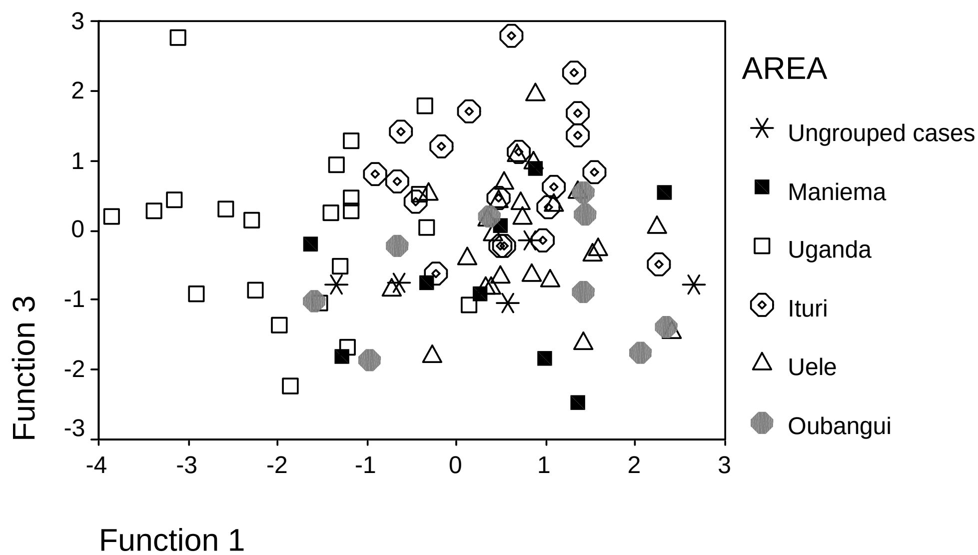


Fig.1b

Table 1a

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.164	60.3	60.3	.733
2	.417	21.6	81.9	.542
3	.277	14.3	96.2	.465
4	.072	3.8	100.0	.260

a First 4 canonical discriminant functions were used in the analysis.

Table 1b

Standardized Canonical Discriminant Function Coefficients

	Function			
	1	2	3	4
PR	.236	.147	.166	.907
GL	-.366	.053	.234	-.396
BZ	.572	.263	.583	-.488
EU	-.241	.565	-.113	.328
PO	.315	-.215	-.453	-.113
BI	-1.305	-1.092	.603	-.010
ORB	.813	.805	.303	.132
IO	1.038	.011	-.497	.255
BC	.113	-.330	-.044	-.069
NP	.723	-.070	-.296	-.588
NB	-.135	.611	-.808	.002
BA	.307	-.568	.502	-.357
PS	-.376	-.218	-.238	.619
IN	-.310	.488	.246	.287

Table 1c

Classification Results

		Predicted Group Membership					Total
	AREA	Oubangui	Uele	Ituri	Uganda	Maniema2	
Count	Oubangui	5	0	1	2	1	9
	Uele	2	15	5	1	2	25
	Ituri	1	1	12	1	5	20
	Uganda	1	1	2	17	1	22
	Maniema	1	1	1	1	5	9
	Ungrouped cases	0	1	1	1	4	7
%	Oubangui	**55.6**	.0	11.1	22.2	11.1	100.0
	Uele	8.0	**60.0**	20.0	4.0	8.0	100.0
	Ituri	5.0	5.0	**60.0**	5.0	25.0	100.0
	Uganda	4.5	4.5	9.1	**77.3**	4.5	100.0
	Maniema	11.1	11.1	11.1	11.1	**55.6**	100.0
	Ungrouped cases	.0	14.3	14.3	14.3	57.1	100.0

a 63.5% of original grouped cases correctly classified.

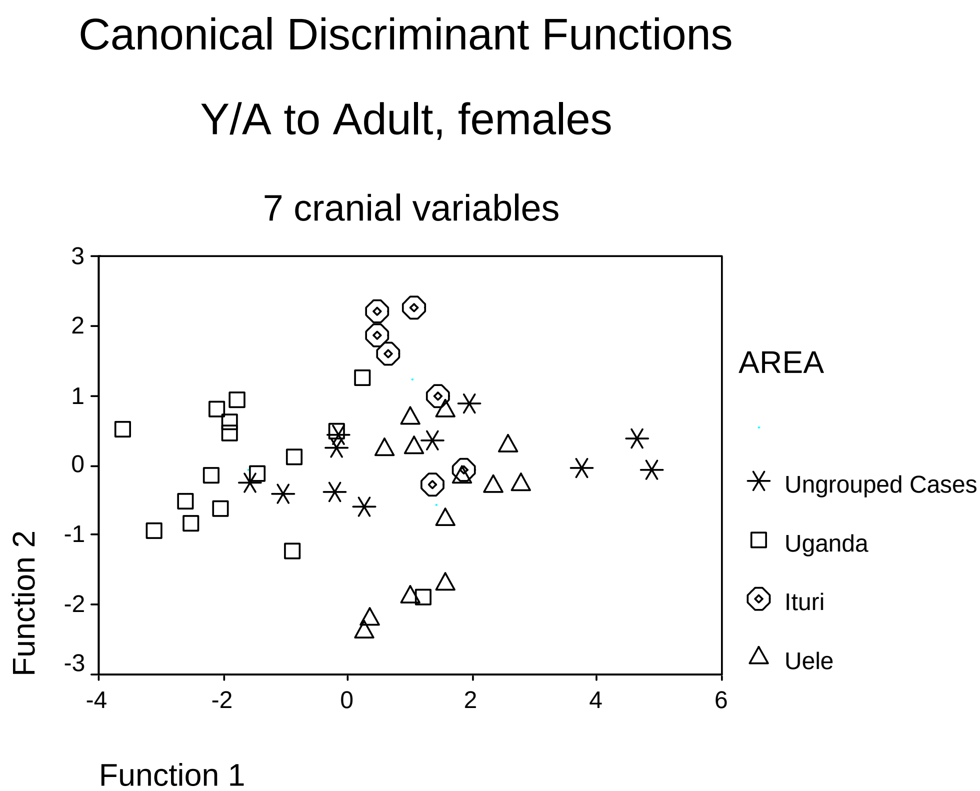


Fig.2.

Table 2a. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2.282	83.5	83.5	.834
2	.451	16.5	100.0	.558

Table 2b. Standardized Canonical Discriminant Function Coefficients

	Function	
	1	2
BZ	.388	.580
BI	-1.787	-.288
ORB	1.505	.591
IO	1.528	-.592
NP	.766	-.114
NB	-.848	.841
BA	.688	-.433

Table 2c. Classification Results

		Predicted Group Membership			Total
	AREA	Uele	Ituri	Uganda	
Count	Uele	10	3	0	13
	Ituri	2	5	0	7
	Uganda	1	2	13	16
	Ungrouped cases	4	3	4	11

%	Uele	**76.9**	23.1	.0	100.0
	Ituri	28.6	**71.4**	.0	100.0
	Uganda	6.3	12.5	**81.3**	100.0
	Ungrouped cases	36.4	27.3	36.4	100.0

a 77.8% of original grouped cases correctly classified.

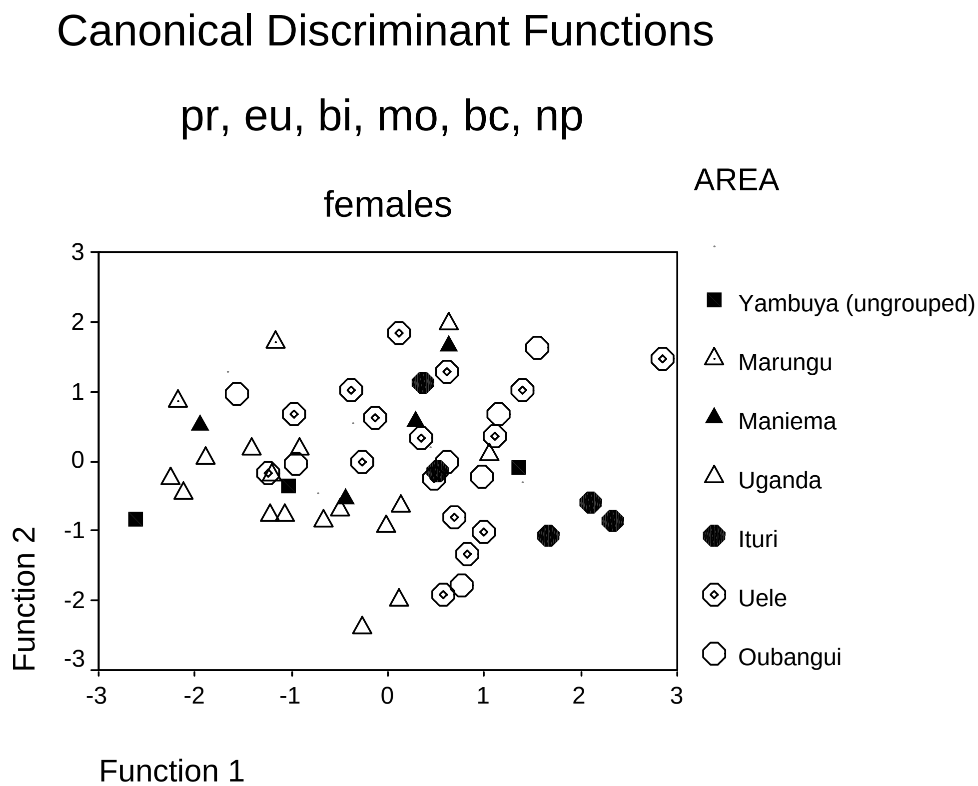


Fig.3.

Table 3a. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	.640	62.4	62.4	.625
2	.214	20.8	83.2	.419
3	.145	14.1	97.3	.356
4	.021	2.0	99.3	.143
5	.007	.7	100.0	.083

a First 5 canonical discriminant functions were used in the analysis.

Table 3b. Classification Results

		Predicted Group Membership						
	AREA	Oubangui	Uele	Ituri	Uganda	Maniema	Marungu	
Count	Oubangui	2	2	0	1	1	1	7
	Uele	3	4	3	2	4	0	16
	Ituri	1	0	3	0	1	0	5
	Uganda	1	1	1	11	2	0	16
	Maniema	1	0	0	0	3	0	4
	Marungu	0	0	0	0	0	2	2
	Ungrouped	1	0	0	2	0	0	3
%	Oubangui	**28.6**	28.6	.0	14.3	14.3	14.3	100.0
	Uele	18.8	**25.0**	18.8	12.5	25.0	.0	100.0

Ituri	20.0	.0	**60.0**	.0	20.0	.0	100.0
Uganda	6.3	6.3	6.3	**68.8**	12.5	.0	100.0
Maniema	25.0	.0	.0	.0	**75.0**	.0	100.0
Marungu	.0	.0	.0	.0	.0	**100.0**	100.0
Ungrouped	33.3	.0	.0	66.7	.0	.0	100.0

a 50.0% of original grouped cases correctly classified.

Canonical Discriminant Functions

Adult males

8 cranial variables

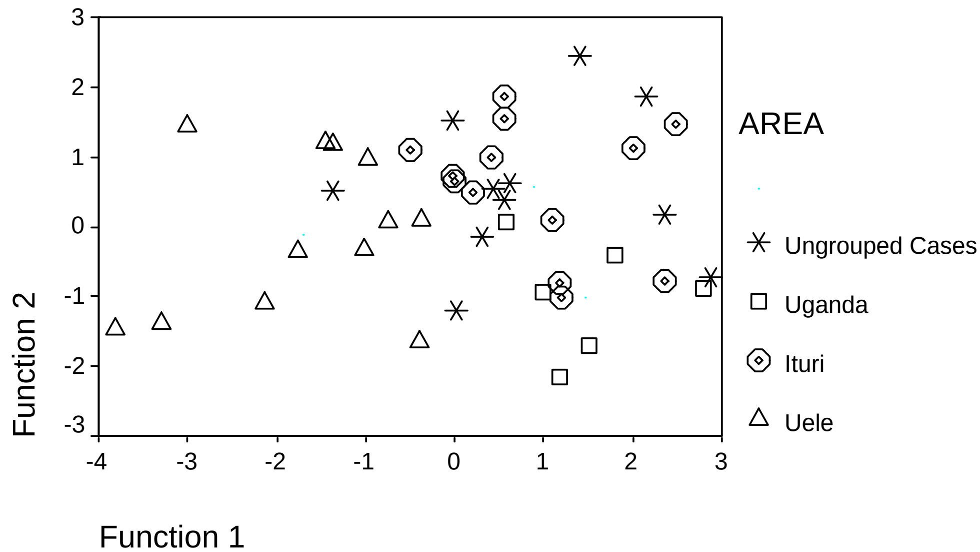


Fig.4.

Table 4a. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2.067	84.7	84.7	.821
2	.374	15.3	100.0	.522

Table 4b. Standardized Canonical Discriminant Function Coefficients

	Function	
	1	2
BZ	-.684	1.038
PO	-.960	-.180
GL	.641	-.265
ORB	1.027	.073
BC	-.723	.133
IN	1.181	.349
EU	.706	.231
PS	-.851	-.694

Table 4c. Classification Results

		Predicted Group Membership			Total
	AREA	Uele	Ituri	Uganda	
Count		11	0	1	12
		0	10	3	13

	Uganda	0	1	5	6
	Ungrouped cases	1	7	3	11
%	Uele	**91.7**	.0	8.3	100.0
	Ituri	.0	**76.9**	23.1	100.0
	Uele	.0	16.7	**83.3**	100.0
	Ungrouped cases	9.1	63.6	27.3	100.0

a 83.9% of original grouped cases correctly classified.

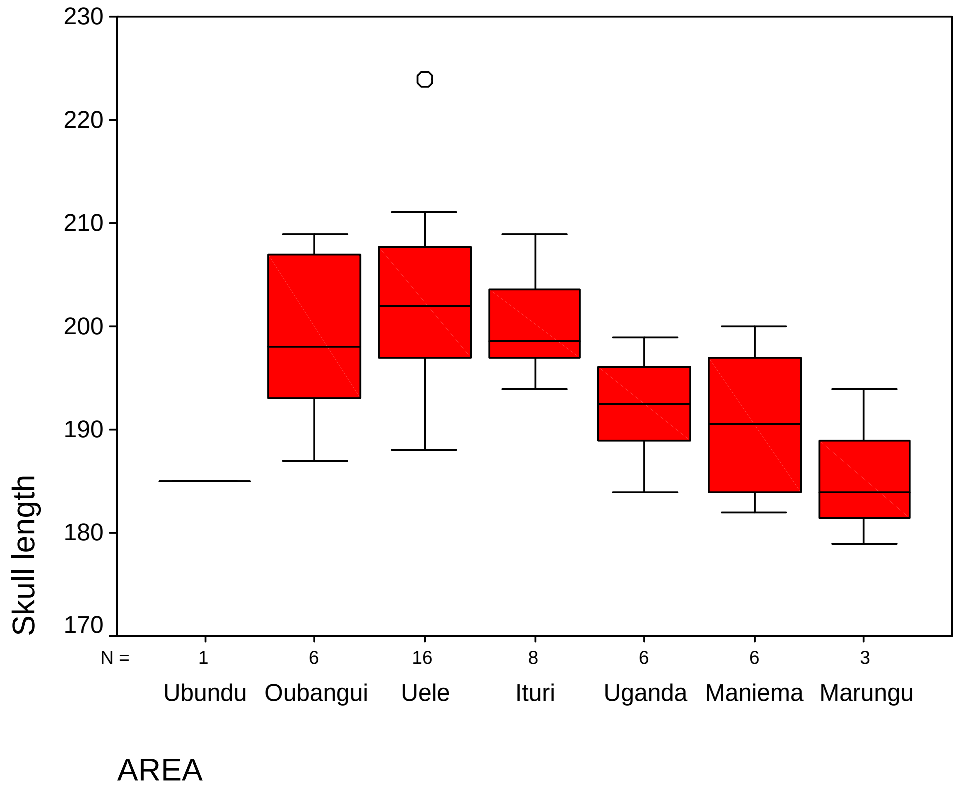

230
220
210
200
190
180
170
Skull length
N =
1
6
16
8
6
6
3
Ubundu
Oubangui
Uele
Ituri
Uganda
Maniema
Marungu
AREA

Fig.5.

Skull length, adult female

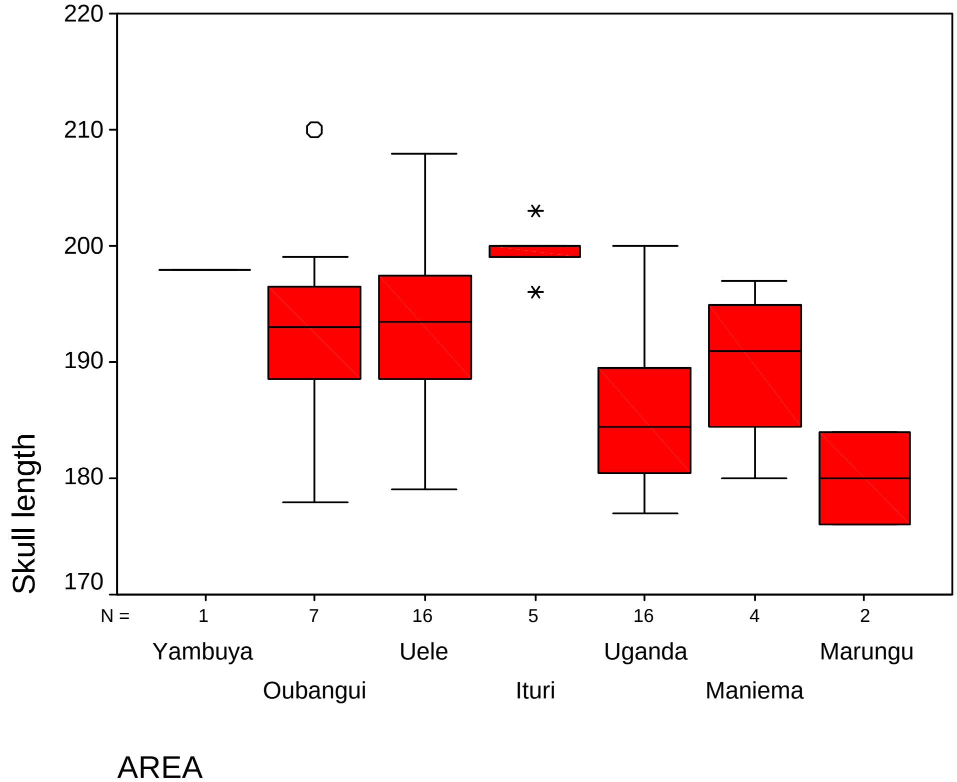


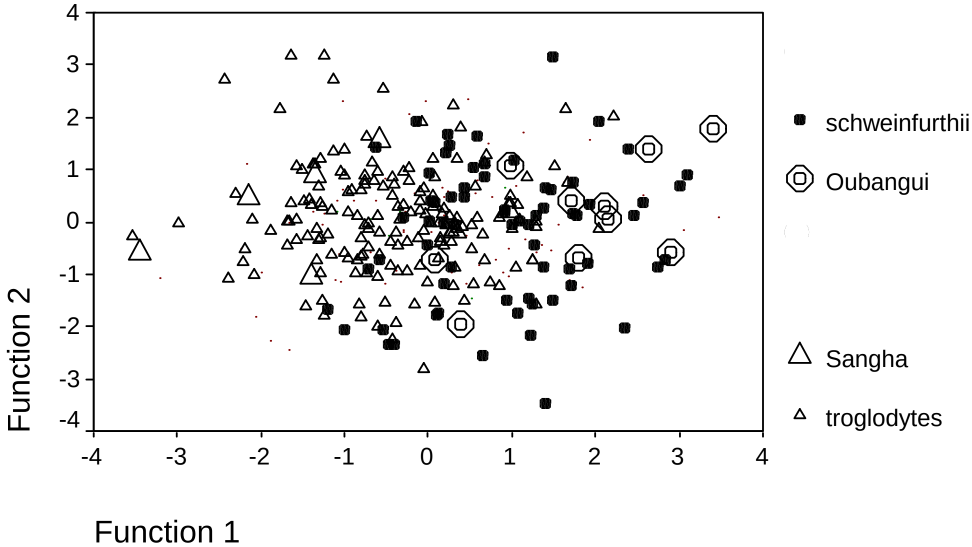
Fig.6

Fig.7

Canonical Discriminant Functions

Y/A to Adult, males and females

13 cranial variables



Standardized Canonical Discriminant Function Coefficients

	Function	
	1	2
PR	-.077	.478
GL	-.350	-.442
EU	.434	.125
BI	-.710	-.186
ORB	.499	.239
IO	-.218	.879
BC	-.457	-.016
NP	.582	.637
NB	.596	-.377
BA	-.019	.296
PS	.545	-.325
IN	-.088	-.189
MO	-.280	-.128

Table 5.

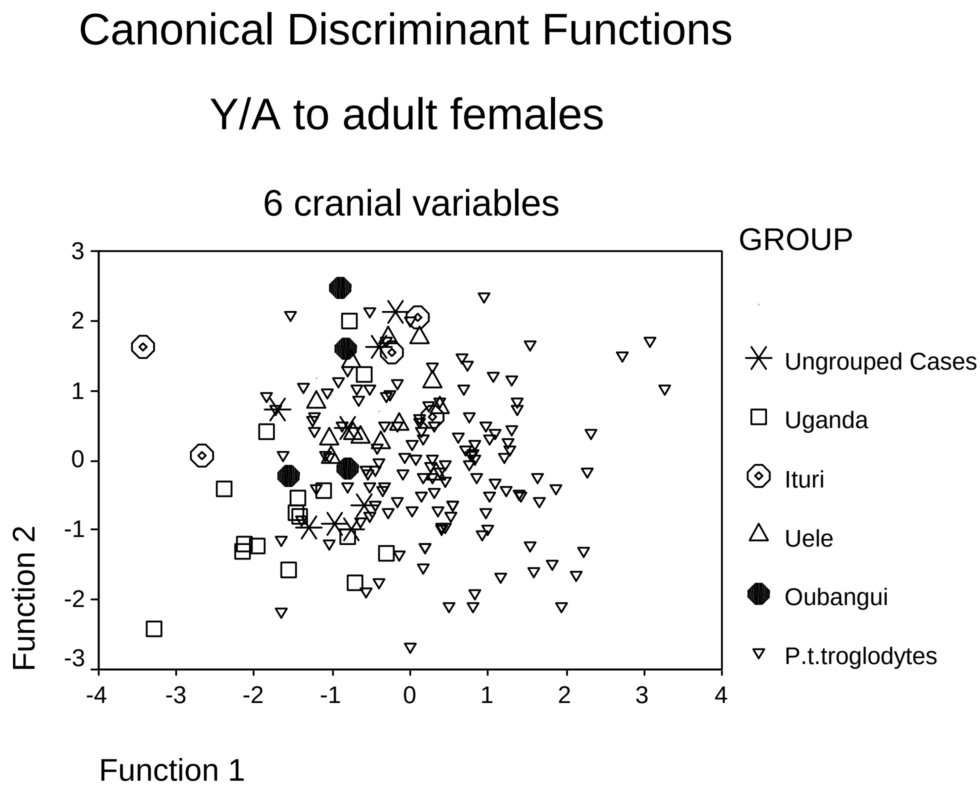


Fig.8.

Table 6a. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	.371	65.3	65.3	.520
2	.154	27.1	92.4	.365
3	.036	6.3	98.7	.187
4	.007	1.3	100.0	.085

a First 4 canonical discriminant functions were used in the analysis.

Table 6b. Standardized Canonical Discriminant Function Coefficients

	Function			
	1	2	3	4
PR	-.451	.573	-1.139	-.517
IO	.957	.273	.281	-.390
BC	.516	-.631	-.499	1.004
NB	-.350	.084	-.162	.378
PS	-.581	-.265	.984	.468
NP	.250	.823	.690	-.109

Table 6c. Classification Results

		Predicted Group Membership					Total
	GROUP	*troglodytes*	Oubangui	Uele	Ituri	Uganda	
Count	*troglodytes*	87	8	16	8	12	131
	Oubangui	0	1	0	1	2	4

	Uele	1	2	9	0	1	13
	Ituri	1	0	1	2	1	5
	Uganda	0	1	2	0	13	16
	Ungrouped cases	0	1	2	1	4	8
%	*troglodytes*	**66.4**	6.1	12.2	6.1	9.2	100.0
	Oubangui	.0	**25.0**	.0	25.0	50.0	100.0
	Uele	7.7	15.4	**69.2**	.0	7.7	100.0
	Ituri	20.0	.0	20.0	**40.0**	20.0	100.0
	Uganda	.0	6.3	12.5	.0	**81.3**	100.0
	Ungrouped cases	.0	12.5	25.0	12.5	50.0	100.0

a 66.3% of original grouped cases correctly classified.

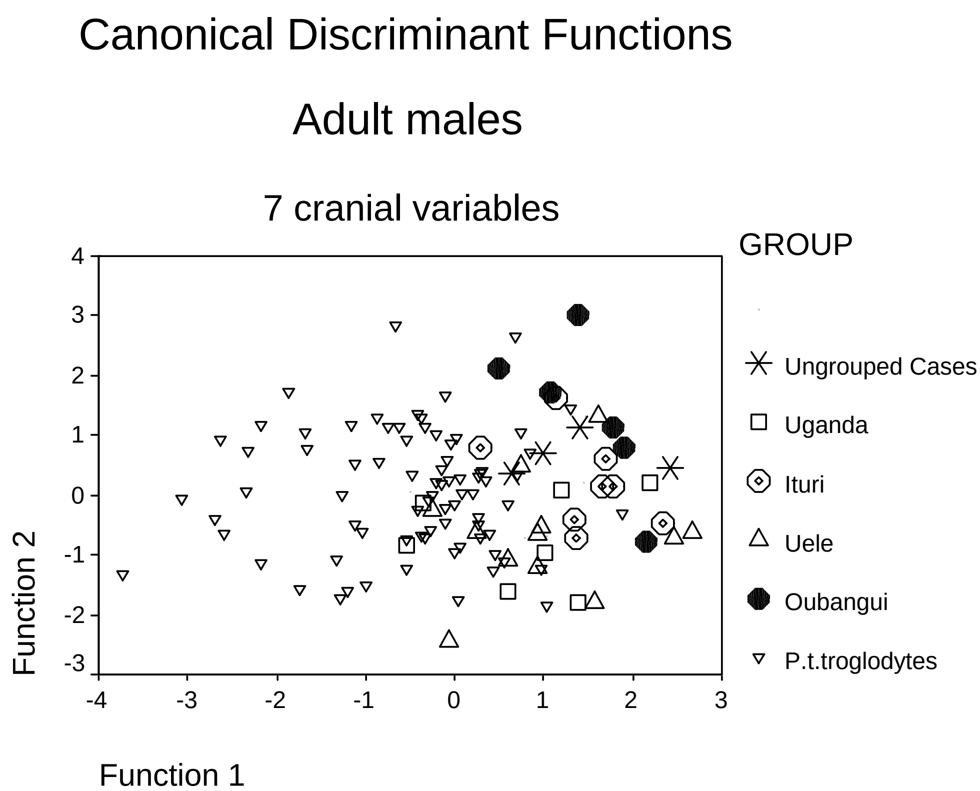


Fig.9

Table 7a. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	.619	66.8	66.8	.618
2	.193	20.8	87.6	.402
3	.077	8.3	95.9	.267
4	.038	4.1	100.0	.192

a First 4 canonical discriminant functions were used in the analysis.

Table 7b. Standardized Canonical Discriminant Function Coefficients

	Function			
	1	2	3	4
PR	-.592	.294	.249	.625
EU	.451	.706	.096	-.205
BI	-.877	-.342	.454	.479
ORB	.930	.189	-.216	.656
NP	.511	.385	.214	.409
PS	.861	-1.048	.210	-.980
MO	-.497	.377	.245	-.568

Table 7 c. Classification Results

		Predicted Group Membership					Total
	ANALYSIS	*troglodytes*	Oubangui	Uele	Ituri	Uganda	
Count	*troglodytes*	50	5	11	3	9	78
	Oubangui	0	5	0	1	0	6
	Uele	1	1	7	0	3	12

	Ituri	0	1	0	6	1	8
	Uganda	1	0	0	1	5	7
	Ungrouped cases	1	4	2	2	1	10
%	*troglodytes*	**64.1**	6.4	14.1	3.8	11.5	100.0
	Oubangui	.0	**83.3**	.0	16.7	.0	100.0
	Uele	8.3	8.3	**58.3**	.0	25.0	100.0
	Ituri	.0	12.5	.0	**75.0**	12.5	100.0
	Uganda	14.3	.0	.0	14.3	**71.4**	100.0
	Ungrouped cases	10.0	40.0	20.0	20.0	10.0	100.0

a 65.8% of original grouped cases correctly classified.

Fig.10

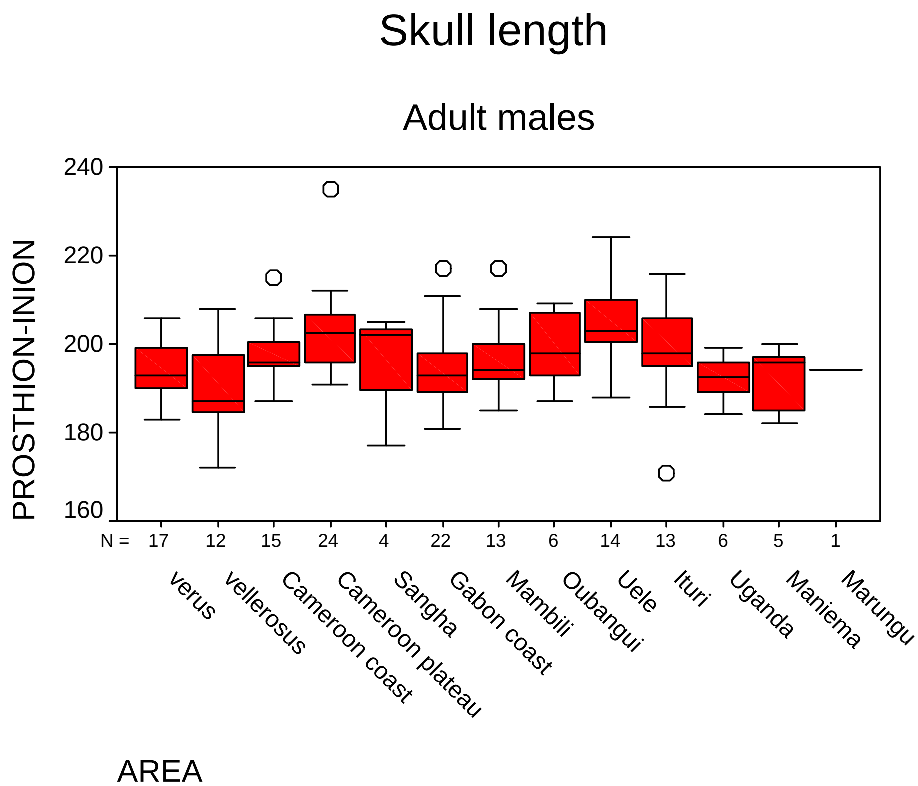

Skull length
Adult males
240
220
200
180
160
PROSTHION-INION
N = 17 12 15 24 4 22 13 6 14 13 6 5 1
verus
vellerosus
Cameroon coast
Cameroon plateau
Sangha
Gabon coast
Mambili
Oubangui
Uele
Ituri
Uganda
Maniema
Marungu
AREA

Fig.11

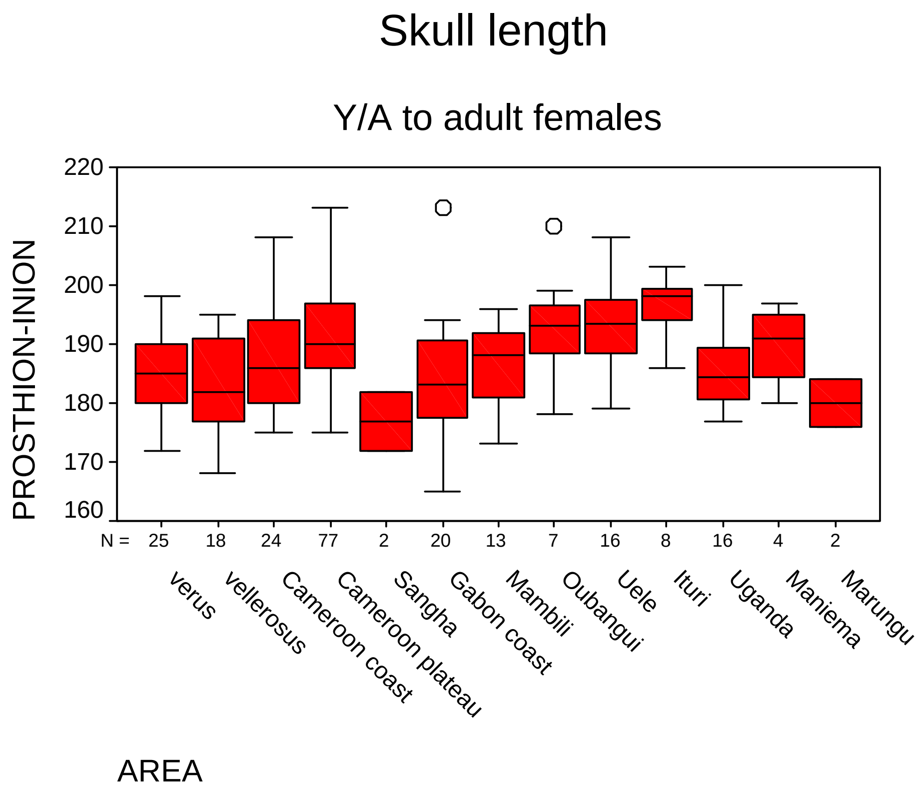

Skull length
Y/A to adult females
PROSTHION-INION
220
210
200
190
180
170
160
N = 25 18 24 77 2 20 13 7 16 8 16 4 2
verus
vellerosus
Cameroon coast
Cameroon plateau
Sangha
Gabon coast
Mambili
Oubangui
Uele
Ituri
Uganda
Maniema
Marungu
AREA

Table 8a.

Group		PR	GL	BZ	BI	IO	BC	NP	PS
P.t.troglodytes	Mean	188.86	133.08	121.38	87.43	21.15	56.40	86.16	72.71
	N	136	136	136	136	137	137	137	136
	SD	8.715	4.823	5.699	5.473	2.838	3.592	7.938	5.629
	Min.	165	120	109	62	15	45	65	61
	Max.	213	148	144	104	31	67	109	100
Oubangui	Mean	193.00	133.57	120.14	86.43	20.71	55.71	91.14	75.86
	N	7	7	7	7	7	7	7	7
	SD	10.263	4.504	5.146	4.237	2.752	3.498	9.564	5.080
	Min	178	127	114	80	16	51	81	70
	Max	210	139	129	93	24	62	108	84
Uele	Mean	192.94	133.19	124.56	87.00	20.88	55.25	90.75	75.56
	N	16	16	16	16	16	16	16	16
	SD	7.141	3.563	5.853	4.590	2.217	3.022	8.481	4.788
	Min	179	125	115	81	17	50	80	69
	Max	208	141	134	95	25	60	110	87
Ituri	Mean	199.17	136.50	126.50	89.83	19.83	56.50	92.50	75.17
	N	6	6	6	6	6	6	6	6
	SD	2.317	4.722	4.231	2.041	3.764	3.209	3.271	5.231
	Min	196	130	121	87	14	53	87	66
	Max	203	143	132	93	24	60	96	80
Uganda	Mean	185.69	132.25	119.31	83.06	16.94	53.53	81.16	72.94
	N	16	16	16	16	16	16	16	16
	SD	6.819	6.202	4.686	4.851	3.060	3.284	7.247	3.605
	Min	177	122	110	76	12	47	73	68
	Max	200	145	127	94	22	61	100	79
Maniema	Mean	189.75	131.75	125.75	84.25	19.50	54.75	88.75	72.75
	N	4	4	4	4	4	4	4	4
	SD	7.274	3.304	3.862	3.202	1.291	4.349	10.112	7.676
	Min	180	128	120	81	18	51	78	64
	Max	197	136	128	87	21	61	102	81
Marungu	Mean	180.00	131.50	118.00	81.50	16.50	52.50	87.00	68.00
	N	2	2	2	2	2	2	2	2
	Min	176	130	115	80	16	51	81	67
	Max	184	133	121	83	17	54	93	69

Table 8b.

Group		PR	GL	BZ	BI	IO	BC	NP	PS
P.t.troglodytes	Mean	198.25	137.59	132.94	90.07	22.57	61.91	91.51	76.68
	N	79	80	80	81	80	79	79	79
	SD	9.280	5.809	6.400	3.924	2.887	3.889	9.366	5.215
	Min	177	125	115	81	16	52	68	61
	Max	235	154	146	103	31	72	121	93
Oubangui	Mean	198.67	138.33	135.60	86.83	20.17	60.67	96.83	77.67
	N	6	6	5	6	6	6	6	6
	SD	8.892	4.885	5.683	4.021	2.483	2.160	4.167	4.761
	Min	187	131	128	82	16	58	91	72

	Max	209	145	141	91	23	64	101	85
Uele	Mean	203.58	137.75	134.67	90.25	21.75	62.50	97.33	82.92
	N	12	12	12	12	12	12	12	12
	SD	9.977	5.190	6.095	3.545	2.633	3.826	7.655	5.807
	Min	188	129	124	87	19	57	87	74
	Max	224	147	143	98	28	68	113	93
Ituri	Mean	200.13	138.25	134.50	89.88	20.50	61.50	96.38	79.25
	N	8	8	8	8	8	8	8	8
	SD	5.194	2.605	5.237	4.016	2.726	2.928	5.370	4.062
	Min	194	135	126	83	17	57	88	75
	Max	209	142	140	95	25	66	103	87
Uganda	Mean	192.86	135.57	126.86	87.00	18.79	58.43	88.29	76.79
	N	7	7	7	7	7	7	7	7
	SD	5.210	5.884	5.273	6.137	2.157	2.992	4.608	3.160
	Min	184	128	121	77	15	54	81	72
	Max	199	146	135	94	22	62	93	81
Maniema	Mean	190.75	135.25	127.00	83.75	17.75	58.00	97.00	75.67
	N	4	4	4	4	4	3	3	3
	SD	8.617	4.573	2.160	2.986	1.500	4.000	2.000	2.082
	Min	182	130	124	80	16	54	95	74
	Max	200	141	129	87	19	62	99	78
Marungu	Mean	194.00	138.00	133.00	85.00	22.00	61.00	100.00	75.00
	N	1	1	1	1	1	1	1	1
Tanzania	Mean					23.00	71.00	90.00	83.00
	N					1	1	1	1

Fig.12

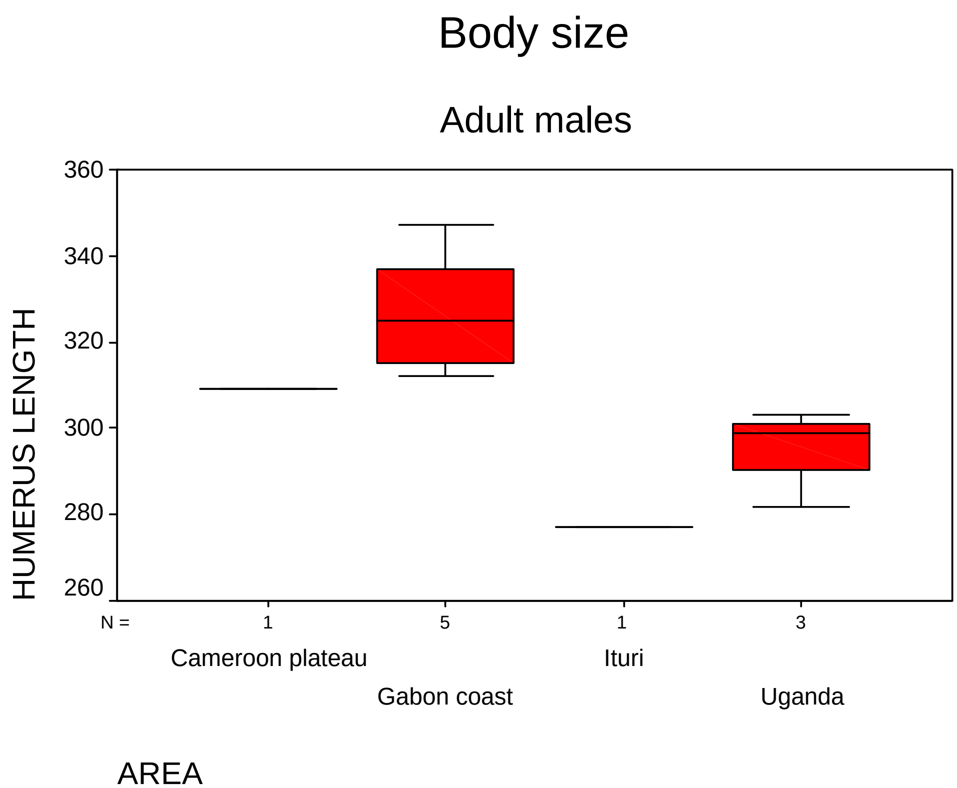
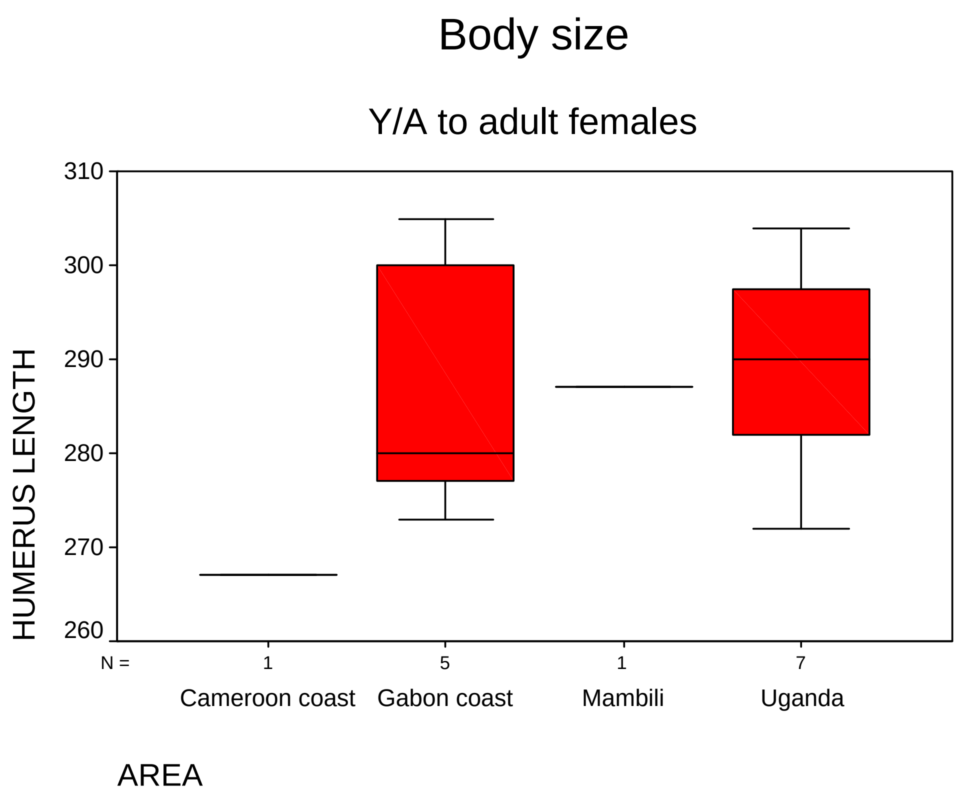
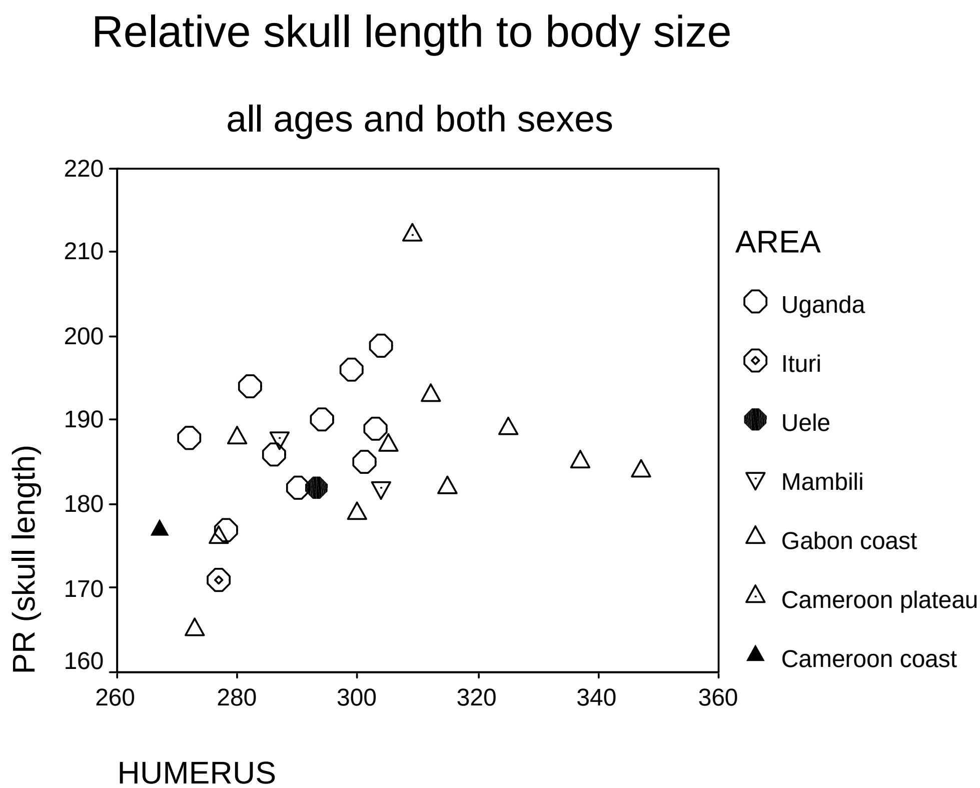

Body size
Adult males
360
340
320
300
280
260
HUMERUS LENGTH
N =
1
5
1
3
Cameroon plateau
Gabon coast
Ituri
Uganda
AREA

Fig.13



Body size
Y/A to adult females
HUMERUS LENGTH
310
300
290
280
270
260
N =
1
5
1
7
Cameroon coast
Gabon coast
Mambili
Uganda
AREA

Fig.14



Relative skull length to body size
all ages and both sexes
220
210
200
190
180
170
160
260
280
300
320
340
360
PR (skull length)
HUMERUS
AREA
Uganda
Ituri
Uele
Mambili
Gabon coast
Cameroon plateau
Cameroon coast