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The Variance of Variation: Geographic Patterns of Coat Colouration in *Anomalurops* and *Anomalurus* (Mammalia, Rodentia, Anomaluridae)[1]

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Abstract. Variation of coat colouration in *Anomalurops beecrofti*, *Anomalurus derbianus*, *A. pelii*, and *A. pusillus* was studied. Character states of the dorsal and ventral colouration were defined for each species and specimens assigned to classes accordingly. Geographic patterns were analysed after excluding sex, age, and collection month as possible causes for different colouration. Considerable differences were found among the first three species, while no differences in colouration were found in *A. pusillus*. *Anomalurops beecrofti* varies in the distribution area mainly in the frequencies of different colour morphs, while in *Anomalurus derbianus* several character states are clearly restricted to defined areas. In *A. pelii* the correlation between colouration and locality is very strong, although its distribution area is much smaller than in the other species. Geographic barriers, especially rivers, are discussed as possible causes for the observed variation.

Key words. Scaly-tailed flying squirrels, morphology, colouration, Africa, biogeography.

1. INTRODUCTION[1]

The history of the African rain forest has attracted the interest of numerous researchers for a long time (e.g. BR→STRUP 1935; FJELDSÅ & LOVETT 1997; GRUBB 1978, 1990; HAMILTON & TAYLOR 1991; LÖNNBERG 1929). Besides more or less direct methods like the analysis of fossil pollen records (e.g. BRENAC 1988; FREDOUX & TASTET 1988; LIVINGSTONE 1966; MALEY 1983, 1991), the recent distribution of species and subspecies of animals was used to reconstruct this history. The anomalurid species investigated here are all able to perform a gliding flight and depend on the occurrence of large trees as starting and landing points. They are strictly arboreal and behave clumsily on the ground, and therefore their current distribution patterns may reveal information on the history of their habitat, the African rain forest.

Considerable differences are found in the variation of coat colouration in the species of Anomaluridae. *Anomalurus pusillus* Thomas, 1887, *Idiurus macrotis* Miller, 1898, *I. zenkeri* Matschie, 1894 and *Zenkerella insignis* Matschie, 1898 show a more or less uniform colouration throughout their distribution range. *Anomalurops beecrofti* (Fraser, 1853) varies in the amount of golden brown colour on the back and reddish colour on the ventral side. The most pronounced colour variation is found in *Anomalurus derbianus* (Gray, 1842), with a range from more or less uniformly brownish individuals to colourful individuals with several defined markings. *Anomalurus pelii* (Schlegel & Müller, 1845) shows only black and white in a specific pattern, but the relative portions of these colours vary.

This study describes the variation of the coat colouration in one species of *Anomalurops* and in three species of *Anomalurus* on the basis of 966 museum specimens. This sample represents the majority of skins of these species kept in research collections worldwide and is regarded as a reliable basis for a study of geographic variation.

2. MATERIAL AND METHODS

2.1. Data basis

Specimens used for this analysis were studied in 15 collections of the following institutes: American Museum of Natural History (AMNH, New York), The Natural History Museum (BMNH, London), Field Museum of Natural History (FMNH, Chicago), Liverpool Museum (LIVCM, Liverpool), Museum National d'Histoire Naturelle (MNHN, Paris), Musée Royal d'Afrique Centrale (MRAC, Tervuren), Naturhistorisches Museum Basel (NHMB, Basel), Naturhistorisches Museum Wien (NMW), Naturhistoriska Riksmuseet (NRM, Stockholm), Naturalis/Nationaal Natuurhistorisch Museum (RMNH, Leiden), Naturmuseum Senckenberg (SMF, Frankfurt/Main), National Museum of Natural History (USNM, Washington), Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK, Bonn), Zoölogisch Museum Amsterdam (ZMA), and Museum für Naturkunde (ZMB, Berlin). The colour and colour patterns were analysed from colour slides taken together with a colour reference. Photographs were taken of the dorsal side of all specimens and as many as possible (depending on the preparation) of the ventral side of *A.*

1 In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

beecrofti and of several specimens of *A. derbianus* and *A. pelii*. Sex was either determined from the skins or labels, from which also the date of collection was recorded. The relative age was estimated from tooth wear if the skull was available (details to be published elsewhere). In addition, slides were taken of 128 specimens of *A. pusillus* and compared but not used in the final analysis because it was not possible to define any differences in colouration. The data basis for the analyses is given in Table 1. The maps given in Figures 3 to 5 are based exclusively on skins with coordinates of the collection locality.

2.2. Statistics

Relationships between the various colouration characters and sex, age, and month of collection were checked with chi-square tests performed in SPSS 10.0. In the reported results the number of specimens used for the and *P* values are given (n.s. = not significant). Additionally, the percentage of cells with an expected frequency less than five (CEF<5) is given when it is higher than 0 analysis (n), the statistic (χ^2), degrees of freedom (d.f.) and the minimum expected frequency (MEF) if it is less than 1. The same test was performed to check for statistically significant differences between geographically neighbouring populations.

3. COLOURATION CODING AND RESULTS

3.1. *Anomalurops beecrofti*

The most frequent colouration of *A. beecrofti* is a silvery-grey on the back with a central stripe of golden brown from the neck over the larger part of the back. The ventral side is basically greyish or yellowish with an orange throat and chest.

Colour variation in *A. beecrofti* can be defined by the extent of the golden brown stripe on the back and the amount of orange colour on the ventral side (Plate I).

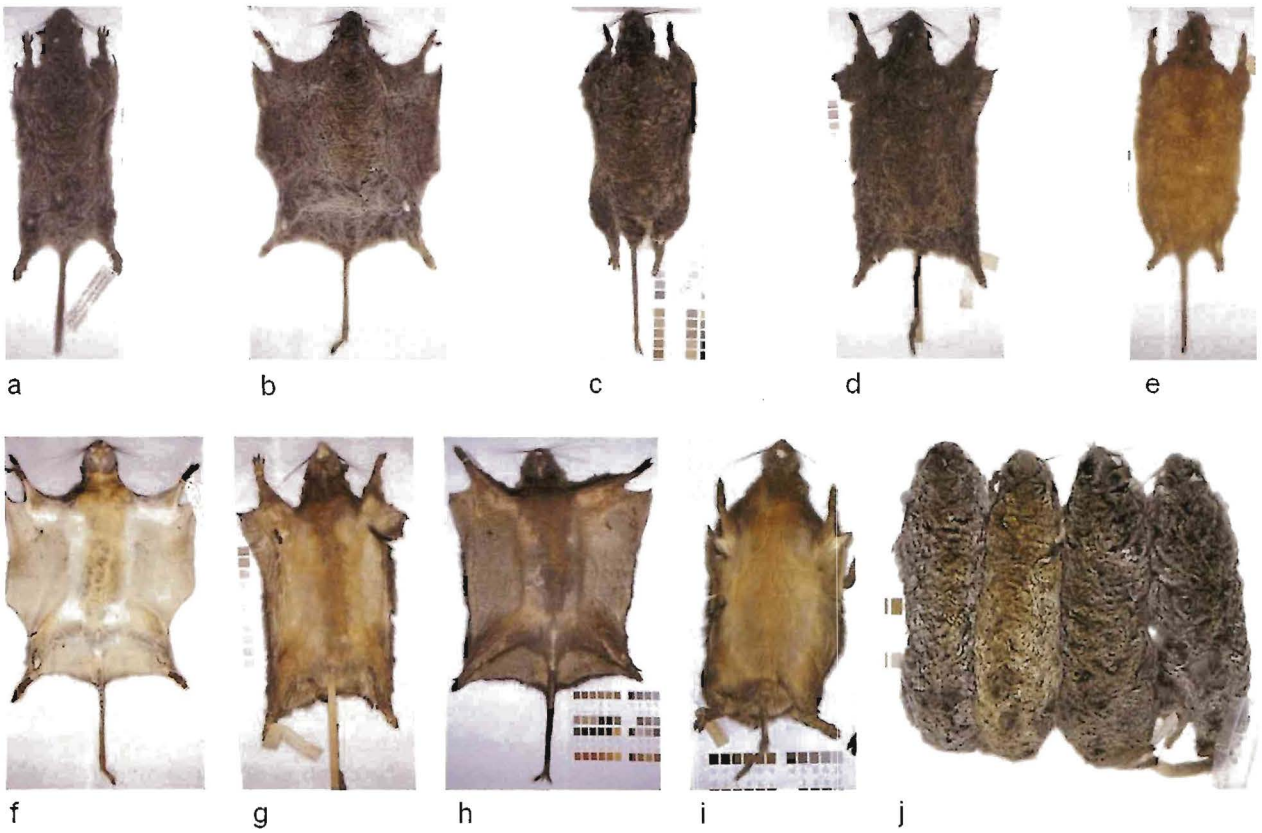

Plate I: Typical representatives of the dorsal and ventral colouration classes in *Anomalurops beecrofti* (see text for details). a: dorsal colouration DC 1 (AMNH 86845), b: DC 2 (BMNH 67.1461), c: DC 3 (USNM 84547), d: DC 4 (BMNH 96.10.9.10), e: DC 5 (BMNH 0.2.5.14), f: ventral colouration VC 1 (BMNH 67.1461), g: VC 2 (BMNH 96.10.9.10), h: VC 3 (ZFMK 64.501), i: VC 4 (MRAC 3234), j: four specimens from the same collection with (from left) DC 2 (NMW B1319), DC 4 (NMW B1325), DC 3 (NMW B1326), DC 2 (NMW B1336).

Colouration codes and frequencies

Dorsal colouration (DC):

1. back completely silvery grey without golden brown parts (4%, n=9).
2. back silvery grey, golden brown central stripe not wider than head (43%, n=98).
3. central stripe wider than head, but at least patagia silvery grey (28%, n=63).
4. back completely golden brown, central part can be slightly darker than patagia (23%, n=52).
5. back and patagia uniformly reddish orange (2%, n=5).

Ventral colouration (VC):

1. light grey or yellowish with or without light yellow central stripe (22%, n=38).
2. light grey or yellowish with orange central stripe (42%, n=71).
3. light orange and/or dark grey with orange central stripe (21%, n=36).
4. uniformly orange (14%, n=24).

Five specimens with the very peculiar dorsal colouration 5 (uniformly reddish orange) were omitted from the analysis because they strongly increased the percentage of cells with expected frequencies less than five and decreased the minimum expected frequency for the chi-square tests.

Dorsal and ventral colouration

When the four specimens with colouration 5 are omitted from the analysis, the percentage of CEF<5 is 25% and the MEF is 1.07. The result shows a strong association between dorsal and ventral colouration (χ^2 22.419, d.f. 9, $p<0.01$).

The interpretation of the uniformly reddish specimens is difficult for two reasons; first because of the very peculiar colour which does not fit into the other definitions of the dorsal colouration and secondly because of the very small number of specimens (5). Thus results from this group have to be treated with caution.

For the other colouration classes the correlation between dorsal and ventral colouration can be best described by differences in the frequencies. Although almost all possible combinations of dorsal and ventral colourations occur, it is obvious that individuals with larger golden brown parts on the back are likely to have also darker and more orange underparts (Fig. 1). The percentage of the two lighter ventral colouration forms decreases regularly from 88% in dorsal colouration (DC) 1 to 79% and 58% in DC 2 and 3 to 41% in DC 4.

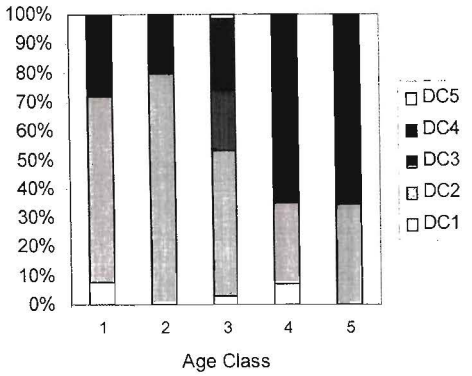

Fig. 1: Correlation between dorsal colouration (DC class 1-5) and associated ventral colourations (VC 1-4) in *Anomalurops beecrofti*.

Colouration and sex

A subsample of 70 males (45%) and 85 females (55%) was available. No significant correlation between dorsal colouration (χ^2 7.585, d.f. 3, P = n.s.) or ventral colouration (χ^2 0.342, d.f. 3, P = n.s.) and sex could be found.

Colouration and age

A total of 160 skins were grouped into age class 1 (16%, n=25), 2 (6%, n=10), 3 (39%, n=62), 4 (25%, n=40), and 5 (14%, n=23). The most reliable results for this relationship were obtained by omitting specimens with dorsal colouration 5 and age class 2. Then the percentage of CEF<5 was 25% and the MEF 1.08. Still the relationship between dorsal colouration and age was not significant (n=149, χ^2 14.226, d.f. 9, P = n.s.).

For the analysis of ventral colouration, the age classes were combined as in the analysis for dorsal colouration. No relationship between ventral colouration and age was found at a percentage of CEF<5 of 38% and a MEF of 2.48.

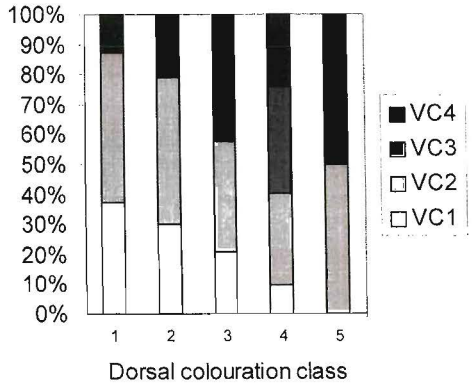

Fig. 2: Correlation between age class and dorsal colouration in *Anomalurops beecrofti*.

However, although no significant relationship for the detailed data set could be found, the dorsal colouration

still shows a tendency towards more golden brown with increasing age (Fig. 2). The percentage of the two more silvery colour classes (DC 1, 2) decreases from 72% and 73% in the young individuals, over 54% in the medium, to 37% and 36% in the older specimens. Thus combined, the correlation is also statistically significant (n=159, χ^2 11.380, d.f. 3, $P < 0.05$). For the ventral colouration no tendencies could be observed.

Colouration and collection month

For this analysis two months each were combined (January and February, March and April, etc.) in order to increase the number of specimens per cell. Still 29% of the cells had an expected frequency of less than five and the MEF was 0.72. However, the data did not show a relationship between dorsal colouration and month of collection (χ^2 10.593, d.f. 15, P = n.s.). The same result (χ^2 19.885, d.f. 15, P = n.s.) was obtained for ventral colouration with 54% of the cells having an expected frequency of less than five and a MEF of 1.92.

Colouration and collection area

Localities of collection and summarising diagrams of colouration class frequencies in respective areas are shown in Figure 3 (border lines between these areas are shown in Fig. 6). Uniformly silvery-grey (DC 1) individuals were only found west of the Congo River, from Sierra Leone to Congo Brazzaville. A single specimen (AMNH 86845) labelled as from the Democratic Republic of Congo was caught very close to the Congo River and may as well have been collected on the western bank. The silvery-grey colouration with a narrow golden brown stripe (DC 2) is shown by 43% of the specimens and thus the most frequent. This colouration is distributed across the whole range of the species. The second most frequent colouration (DC 3, silvery grey with a broad golden brown stripe) is found in 28% of the specimens. This colouration is only missing in Angola and adjacent Democratic Republic of Congo. The distribution of the uniformly golden brown individuals (DC 4), which comprise 23% of the investigated specimens, is completely different. They are not found in West Africa but occur frequently in Cameroon, on Bioko, mainland Equatorial Guinea, and Gabon. Further east, isolated records are from Angola and the Democratic Republic of Congo, particularly from the Kivu area. Specimens from Ukaika and Moera in the Kivu region, shown in Plate I (Fig. j), demonstrate the colour variation in one place, ranging from a narrow golden stripe to completely golden brown (DC 2-4). The least frequent colouration (DC 5, uniformly reddish orange) is limited to Equatorial Guinea and the coastal plains of NW Gabon.

The geographic pattern of the ventral colouration differs from that of the dorsal colouration, although a strong correlation between both exists (Fig. 1). Specimens with light underparts lacking orange (VC 1) are found west of the Dahomey Gap and southeast of the Congo and Ubangi rivers but not in between, with the exception of one specimen from Nigeria. In West Africa and south of the Congo River this is the most frequent colouration. Specimens of VC 2 (light underparts with a little orange) occur mainly east of the Dahomey Gap to the Congo River, and replace the lighter specimens of VC 1 in this area. In West Africa and south of the Congo River only a few scattered specimens of VC 2 can be found but more between the Congo and Ubangi rivers. The distribution of individuals of VC 3 (darker ventral colouration) resembles that of VC 2 with slight differences. It is found in Liberia in the West, and then frequently from Cameroon to River Congo and Bioko. South of the Congo River there is a single locality where colourations 1, 2 and 3 are found together. Between the Congo and Ubangi rivers, the relative frequency of VC 3 increases in a NW/SE transect, while that of VC 2 decreases in the same direction. The majority of individuals of VC 4 (uniformly orange underparts) are found from SE-Nigeria to Gabon, and a few between the Congo and Ubangi rivers. Single specimens of this colouration are also found at the periphery of the range, e.g. in Senegal, Togo, and SE-Democratic Republic of Congo.

Statistically significant differences in the frequencies of the respective colourations were found in several neighbouring populations. In West Africa there are three clear-cut barriers where significant differences are found in the DC and VC frequencies. The westernmost border runs along the Volta Rivers in Ghana and separates specimens from Senegal to W-Ghana from those found in E-Ghana and Togo. The second barrier is represented by the Dahomey Gap separating Togo and Nigeria. A third corresponds to the Nigeria-Cameroon border, with the Cross Rivers or the Cameroon mountains being possible geographical barriers. In Central Africa borders are less clear-cut. Along the Sanaga River only the dorsal colouration frequencies show significant differences. The lower Congo and Ubangi rivers separate different frequencies in the ventral colouration, but only the Ubangi is significant for the dorsal colouration frequencies. For specimens from the area between the Congo and Uëlle rivers, a highly significant border in dorsal colouration frequencies exists along the Aruwimi and Ituri Rivers, but this is not true for the ventral colouration. Individuals from the Kivu area are also significantly different in dorsal and ventral colouration frequencies from those found south of the Congo River. No differences in the dorsal colouration were found between specimens from the northwestern parts of this area and individuals from south of the Congo River, and only slight differences (depending on the data combinations) in the ventral colouration. Finally, a significant borderline in dorsal

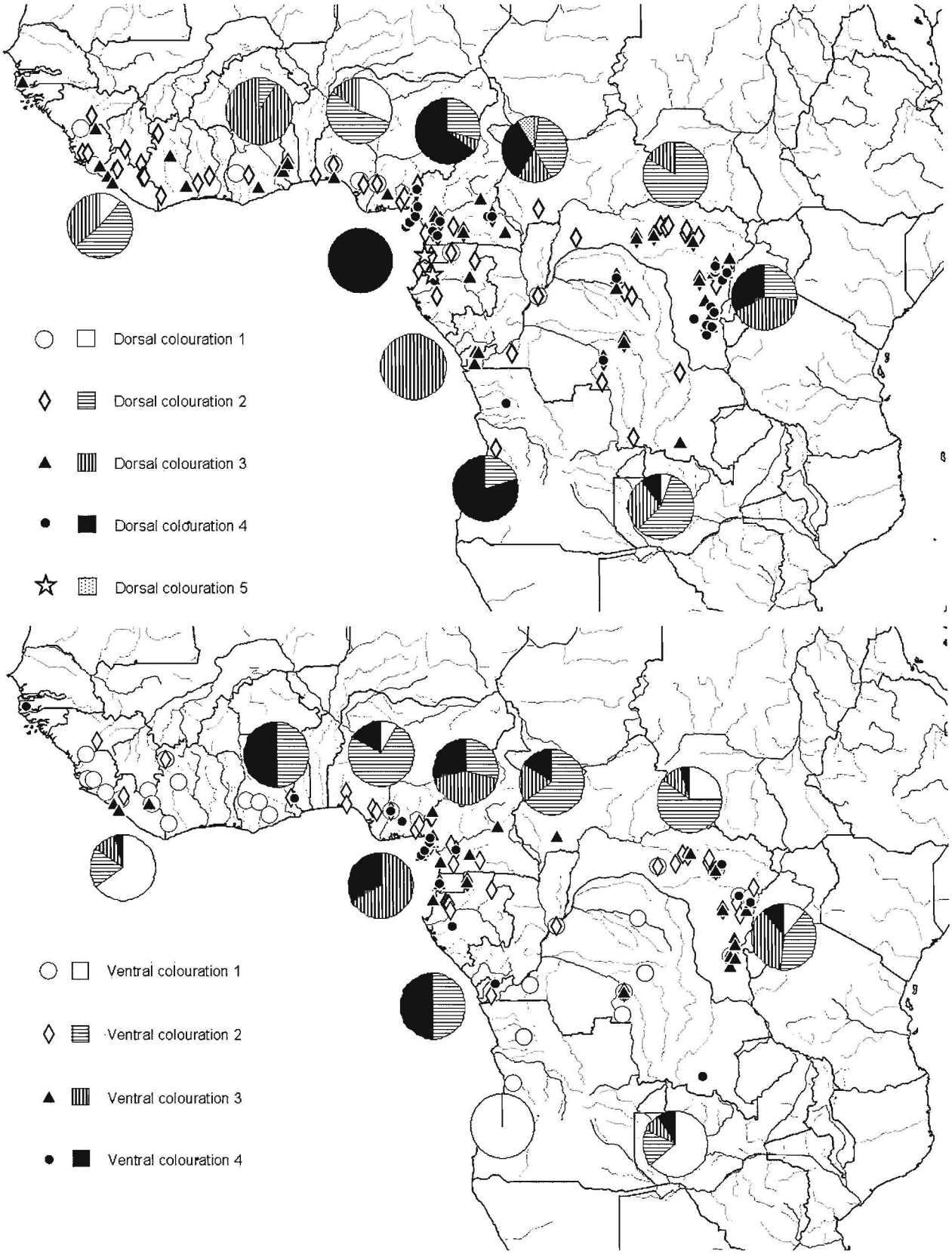

Fig. 3: Geographical distribution of coat colouration in *Anomalurops beecrofti* (see Fig. 6 for border lines).

colouration exists between S-Democratic Republic of Congo and E-Angola. As there is only one ventral colouration type (VC 1) in Angola, no statistical calculation for ventral colour frequencies was possible (the same technical problem applies to the dorsal colouration frequencies on Bioko and in a small area north of the Congo River; see Fig. 3).

3.2. *Anomalurus derbianus*

This species shows the highest variability in colouration (Plate II), ranging from more or less uniformly brownish individuals to specimens with a reddish back, dark grey patagia, black ears and a silvery stripe on the nose. The ventral colouration is much less variable.

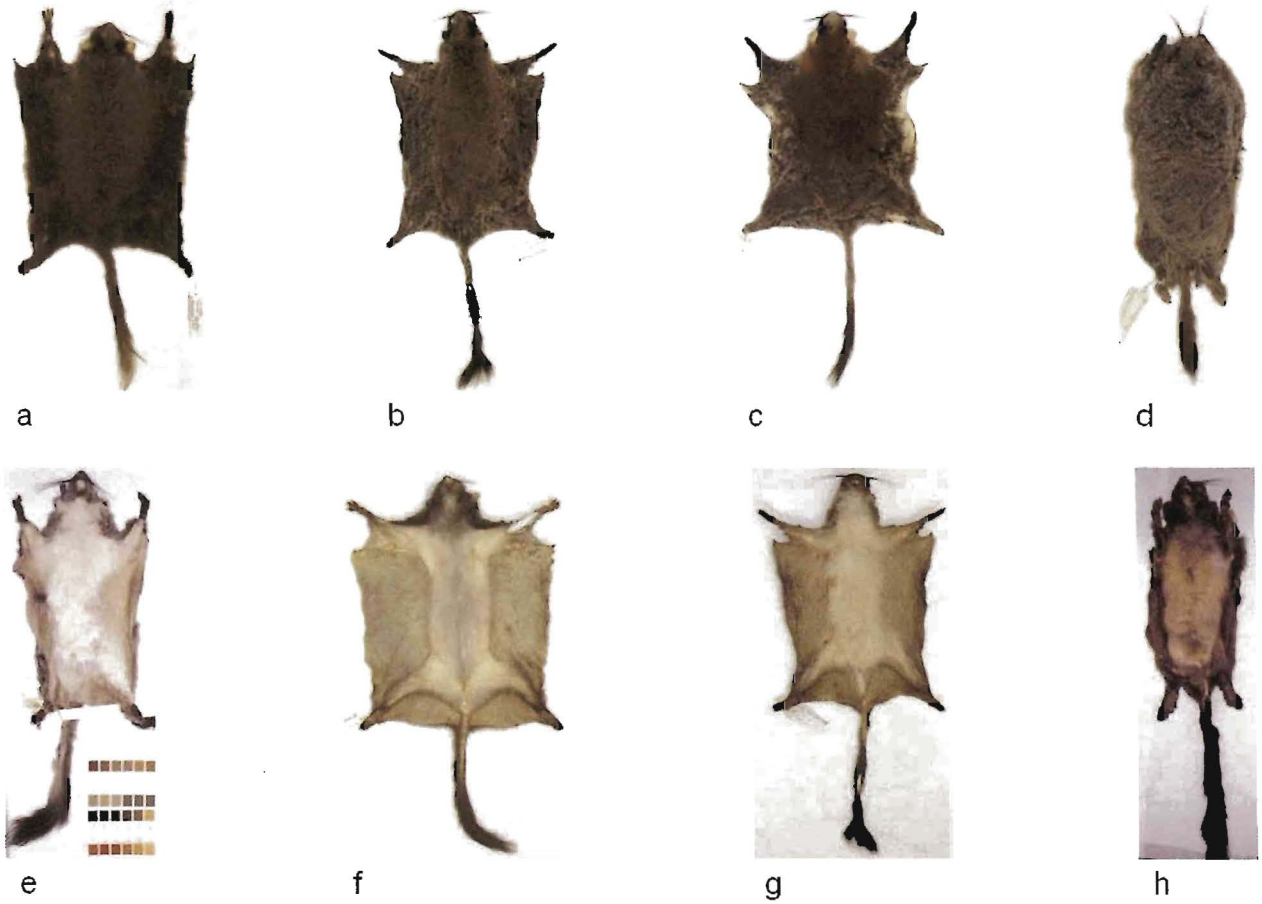

Plate II: Typical representatives of the dorsal and ventral colouration classes in *Anomalurus derbianus* (see text for details). a: dorsal colouration DC 1 (ZFMK 64.491), b: DC 2 (ZFMK 69.148), c: DC 3 (ZFMK 73.363), d: DC 4 (ZFMK 64.817), e: ventral colouration VC 1 (FMNH 88207), f: VC 2 (ZFMK 64.493), g: VC 3 (ZFMK 69.148), h: VC 4 (BMNH 90.6.8.18).

Colouration codes and frequencies

Dorsal colouration (DC):

1. more or less uniformly brown (70%, n=329).
2. back more reddish brown than the rather greyish patagia, no sharp border (19%, n=90).
3. back reddish and patagia dark grey, with sharp border (10%, n=45).
4. silvery grey (1%, n=5).

Ears (E):

1. considerably darker than rest of the head (66%, n=295).
2. more or less the same colouration as the rest of the head (34%, n=154).

Shoulders (S):

1. considerably lighter than neck (42%, n=192).
2. more or less the same colouration as the neck (48%, n=267).

Throat (T):

1. dark ring around neck, mainly closed ventrally (63%, n=85).
2. throat partially light, dark ring ventrally open (37%, n=50).

Ventral colouration (VC):

1. whitish (52%, n=71).
2. greyish without yellow (31%, n=42).
3. yellowish mixed with grey (11%, n=15).
4. light yellow (7%, n=9).

Dorsal and ear colouration

Dorsal and ear colouration show a highly significant correlation. When all character states are used in the analysis, 25% of the cells have an expected frequency of less than five and the MEF is 1.71 (n = 449, χ^2 86.637, d.f. 3, $P < 0.001$). After omitting DC 4, all cells have an expected frequency of more than five and the MEF is 15.20 (n = 444, χ^2 82.553, d.f. 2, $P < 0.001$). The correlation depends on the dorsal colouration class. About half (53%) of the more or less uniformly brown specimens (DC 1) have ears considerably darker than the rest of the head, the others (47%) have ears of the same colour as the head. Individuals with a back slightly (DC 2) or clearly more reddish than the patagia (DC 3) have almost exclusively dark ears (97% and 100% respectively), while most silvery (DC 4) specimens have ears of the same colouration as the head.

Dorsal and shoulder colouration

The correlation for dorsal and shoulder colouration shows results equal to those for dorsal and ear colouration. When all character states are used in the analysis, 25% of the cells have an expected frequency of less than five and the MEF is 2.09 (n = 459, χ^2 194.976, d.f. 3, $P < 0.001$). After omitting DC 4, all cells have an expected frequency of more than five and the MEF is 15.20 (n = 454, χ^2 190.767, d.f. 2, $P < 0.001$). The correlation of dorsal and shoulder colouration also depends on the colouration class. Only 22% of the uniformly brown individuals (DC 1) have light shoulders, but 88% of the specimens with a slightly reddish back (DC 2), and 100% of those with a strongly reddish back (DC 3). None of the silvery individuals (DC 4) have light shoulders.

Ear and shoulder colouration

Ear and shoulder colouration are also significantly correlated (n = 444, χ^2 68.593, d.f. 1, $P < 0.001$). Some 88% of the specimens with light shoulders have dark ears. In the specimens with shoulders of the same colouration as the neck, both types of ear colouration occur equally.

Dorsal and ventral colouration

Correlation between dorsal and ventral colouration appears to be weak. When all four character states for both are used in the analysis, the result is not significant (n = 136, χ^2 14.845, d.f. 9, P = n.s.), but 56% of the cells have an expected frequency less than five and the MEF is 0.13. When DC 4 is omitted from the analysis, 42% of the cells have an expected frequency less than five, the MEF is 0.74 and the result shows a slightly significant correlation between dorsal and ventral colouration (n = 134, χ^2 14.286, d.f. 6, $P < 0.05$). The most reliable results were obtained after ventral colouration 4 was omitted as well. Then the percentage of CEF<5 is 33%, the MEF is 1.20 and the result is significant (n = 125, χ^2 14.367, d.f. 4, $P < 0.01$). Whitish (VC 1) or greyish without yellow (VC 2) underparts are considerably more frequent than the yellowish colouration (VC 3, 4). Ventral parts yellowish mixed with grey (VC 3) are restricted to uniformly brown specimens (DC 1) and to specimens with slightly reddish backs (DC 2). In individuals with strongly reddish backs (DC 3) the greyish ventral parts without yellow (VC 2) prevail with 73%. The sample of silvery-grey specimens is too small (n=2) for any conclusion.

Ventral and throat colouration

Colouration of ventral surface and throat is significantly correlated (n = 133, χ^2 15.352, d.f. 3, $P < 0.005$). Correlation between general ventral colour and throat colour falls in two groups. Ventral whitish and greyish mixed with yellow specimens have about equally open or closed dark rings around the throat, while more than 80% of ventral greyish without yellow and yellowish without grey specimens have a closed dark ring around the throat.

Colouration and sex

A subsample of 177 males (52%) and 165 females (48%) was studied. No correlation between dorsal or ventral colouration and sex could be shown. When all character states for dorsal colouration are used, the percentage of CEF<5 is 25% (n = 342, χ^2 1.704, d.f. 3, P = n.s.), after omitting DC 4 the CEF<5 is 0% (n = 339, χ^2 1.293, d.f. 2, P = n.s.). The same results are obtained for the ventral colouration; with all character states included the percentage of CEF<5 is also 25% (n = 110, χ^2 0.139, d.f. 3, P = n.s.), and without character state 4, the percentage of CEF<5 is 0% (n = 104, χ^2 0.137, d.f. 2, P = n.s.).

Colouration and age

A total of 365 animals were grouped into age classes 1 (12%, n=42), 2 (21%, n=77), 3 (34%, n=125), 4 (27%, n=99), and 5 (6%, n=22). The correlation between dorsal colouration and age gave best results after colouration 4 was omitted from the analysis. This decreased the percentage of CEF<5 to 20% and increased the MEF to 1.80 with no significant correlation (n = 361, χ^2 12.147, d.f. 8, P = n.s.). Due to the much smaller number of recorded ventral colourations, it was difficult to obtain reliable results. Even when colouration 4 and age 1 were omitted from the analysis, the percentage of

CEF<5 was still 41.7% although the MEF increased to 1.48 (n = 104, χ^2 8.771, d.f. 6, P = n.s.). However, the results were not significant in any step of the analysis.

Colouration and collection month

Dorsal colouration and the month of collection showed a significant correlation when two months were combined (January and February, March and April, etc.), and DC 4 was omitted from the analysis (n = 354, χ^2 23.134, d.f. 10, $P < 0.05$). The calculation of an association between ventral colouration and collection month is difficult because of the small number of data for ventral colouration. Most reliable results were obtained by combining three months and by omitting VC 4, thus decreasing the percentage of CEF<5 to 42% and increasing the MEF to 1.90. In this calculation a significant correlation was shown (n = 104, χ^2 14.073, d.f. 6, $P <$ 0.05), although not in all steps of the calculation. This somewhat strange result can be explained by the fact that there also is a highly significant correlation between the collection month and the collection area (n = 359, χ^2 100.606, d.f. 20, $P < 0.001$), with a CEF<5 of 13% after combining two months and omitting specimens from Nigeria, the Cameroon mountains, Bioko and the Democratic Republic of Congo south of the Congo River as well as in all previous steps of the analysis.

Colouration and collection area

Localities and summarising diagrams of colouration class frequencies in the respective areas are shown in Figure 4, border lines between the areas in Figure 6. The uniformly brown dorsal colouration is most frequent and occurs across the entire range of *A. derbianus*. From S-Cameroon to the lower Congo and Ubangi rivers, just a few scattered specimens of this colouration are found, while colouration classes 2 and 3 (more or less pronounced reddish back) are well represented. Class 2 (slightly reddish back) is also rare west of the Dahomey Gap but common in the Mamfe area, Cameroon, and on Bioko, where it occurs together with uniformly brown individuals. Specimens with a bright reddish back strongly contrasting with the greyish patagia are restricted to an area from S-Cameroon to the lower Congo and Ubangi rivers. The very rare uniformly silvery colouration is only found in a few localities close to the borders between Democratic Republic of Congo and Zambia, and between Tanzania and Moçambique.

Borders between morphotypes of ear colouration are not clear-cut, but differences in relative frequencies are found. Individuals with dark ears occur frequently from Cameroon to the Democratic Republic of Congo, except for the very south. High numbers of specimens with ears of the same colouration as the head are found in Angola, Zambia, S-Democratic Republic of Congo and Tanzania. This type is rare in Cameroon and Bioko and absent towards the Congo River and in the western half of the Democratic Republic of Congo. Both colouration forms occur together in West Africa from Liberia to Nigeria, in northeastern Democratic Republic of Congo, and in Uganda.

Individuals with light shoulders occur frequently from Liberia to the rivers Congo and Ubangi, and a few are from Bioko, Democratic Republic of Congo and Uganda. Southeast of the rivers Congo and Ubangi, almost exclusively individuals without light epaulettes were collected, but such individuals also occur in a restricted area from S-Nigeria to SW-Cameroon, and on Bioko. There appears to be a cline from light shoulders in West Africa to dark shoulders in the southern and eastern parts of the range.

Distribution of ventral colouration is less clearly related to locality. Specimens with whitish or greyish ventral parts without yellow are found in the whole area inhabited by *A. derbianus*, with higher numbers of whitish individuals west of the Dahomey Gap and from Congo Brazzaville eastward, and more greyish ones from Nigeria to Gabon and on Bioko. Yellowish specimens are much rarer but widespread. Individuals with a ventral colouration mixture of yellow and grey are found in the Ivory Coast, Cameroon, south of the Congo River, and in Tanzania. A few specimens with yellowish underparts without grey were found in Ghana, Cameroon, on Bioko, and in Tanzania. Both yellowish colouration classes are lacking northeast of the Congo River.

Both open and closed dark rings around the throat are distributed over the whole area, with closed markings being more frequent west of the Dahomey Gap, in Bioko, Angola and northeastern Tanzania, and open markings predominating in Zambia and southern Tanzania. From Cameroon to the Democratic Republic of Congo, open and closed dark rings occur in more or less equal numbers. In the area between the Congo and Ubangi rivers, closed dark rings are more frequent in the east and open markings in the southwest.

Clear-cut borderlines between neighbouring populations exist also in *A. derbianus*. Dorsal and ear colouration frequencies in specimens from West Africa do not differ from frequencies in individuals from Nigeria, but both populations differ significantly in shoulder colouration. Specimens from Nigeria and W-Cameroon are significantly different in dorsal colouration frequency but not in shoulder colouration frequency (ear colouration not calculated). Specimens from Bioko are not different from those from Nigeria, but are significantly different from those from W-Cameroon in dorsal and shoulder colouration. W-Cameroon individuals differ significantly from those from S-Cameroon to Congo and Ubangi rivers in dorsal and shoulder colouration. These rivers form a border for dorsal and shoulder but not for ear colouration.

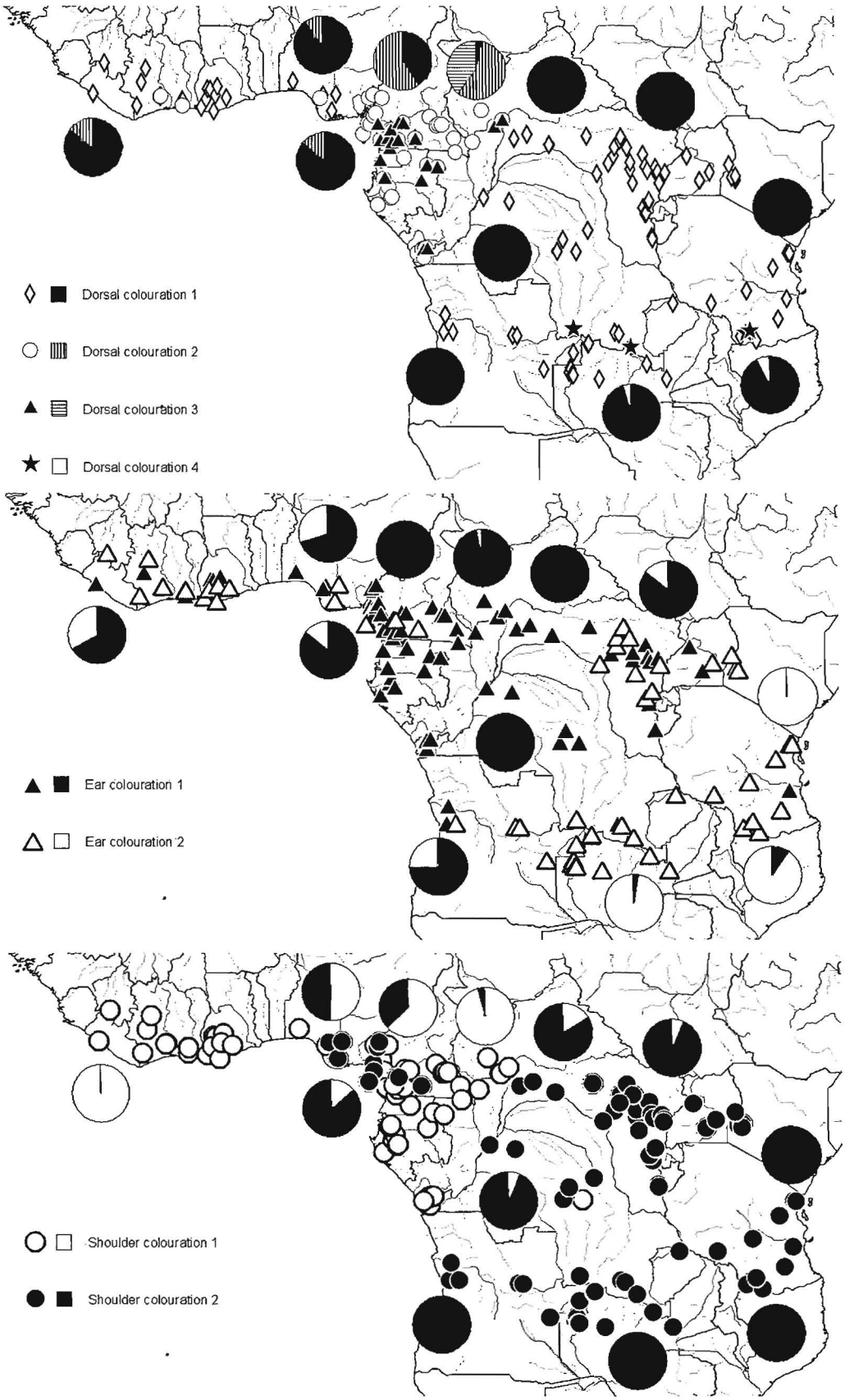

Fig. 4: Geographical distribution of coat colouration in *Anomalurus derbianus* (see Fig. 6 for border lines).

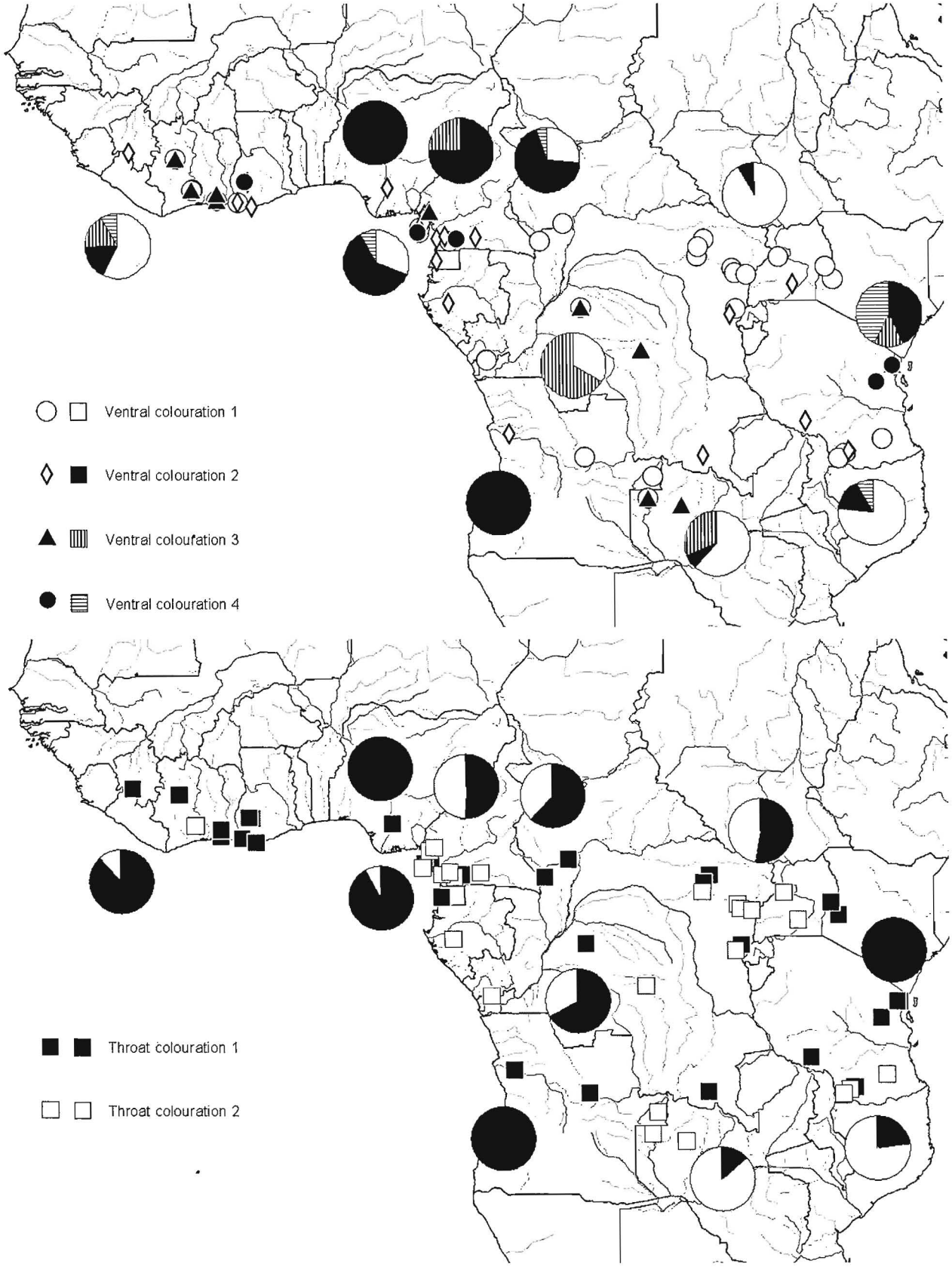

Fig. 4 (continued): Geographical distribution of coat colouration in *Anomalurus derbianus* (see Fig. 6 for border lines).

In N- and C-Democratic Republic of Congo, W-Angola, Uganda and Kenya specimens of *A. derbianus* are remarkably uniform except for a tendency towards ears of the same colour as the rest of the head from NE-Democratic Republic of Congo to Kenya. Finally, one borderline separates specimens from E-Angola, S-Democratic Republic of Congo, Zambia, and Tanzania from the rest of the distribution area. This is best shown by the frequencies of the ear colouration, but it is also parallelled by the occurrence of silvery specimens which are restricted to this southern area.

Differences are less pronounced for the ventral and throat colouration, which is partly due to the smaller data set. This caused problems for a reliable calculation of statistically significant differences. However, in Tanzania specimens from the Usambara Mountains show mainly yellow and yellow mixed with grey underparts, while those from further south are whitish or greyish without yellow.

3.3. *Anomalurus pelii*

This species is generally black with white margins of the patagia, a white tail and a ventral colouration ranging from white to blackish grey. White markings can also be completely absent. The variation in *A. pelii* is mainly defined by the relative portions of black and white (Plate III).

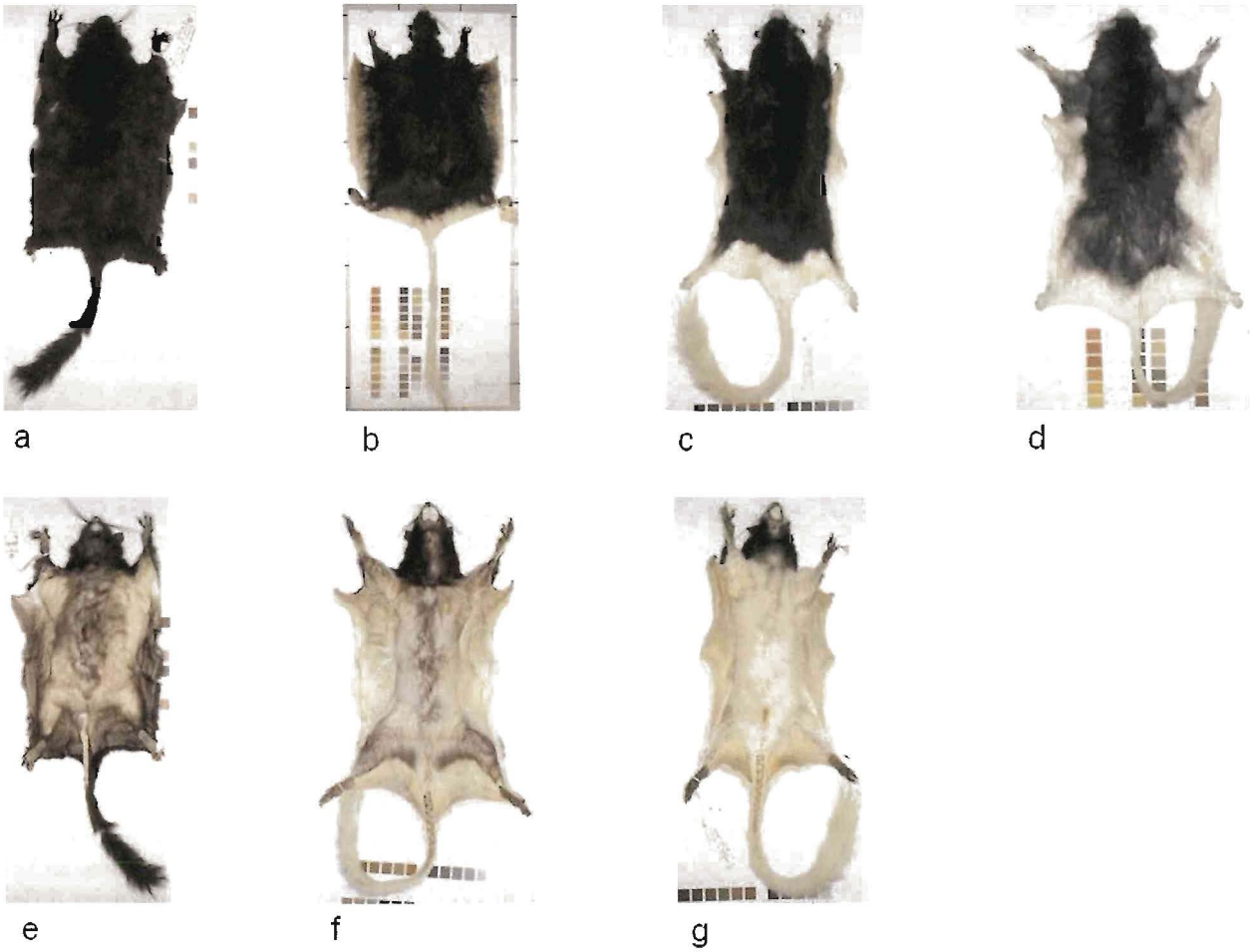

Plate III: Typical representatives of the dorsal and ventral colouration classes in *Anomalurus pelii* (see text for details). a: dorsal colouration DC 1 (ZMA 21.400), b: DC 2 (ZMA 21.262), c: DC 3 (ZMA 21.277), d: DC 4 (ZMA 21.282), e: ventral colouration VC 1 (ZMA 21.400), f: VC 2 (ZMA 21.266), g: VC 3 (ZMA 21.277).

Colouration codes and frequencies

Dorsal colouration (DC):

1. completely black (7%, n=9).
2. white margins less than one-third of pleuropatagia and separated from uropatagia margins (40%, n=55).
3. white margins less than one-half of pleuropatagia, connected with uropatagia margins (23%, n=31).
4. white margins more than one-half of pleuropatagia, shoulder frequently also white (31%, n=43).

Ventral colouration (VC):

1. greyish with blackish central stripe (45%, n=26).
2. white with blackish central stripe (45%, n=26).
3. completely white (10%, n=6).

Dorsal and ventral colouration

A highly significant correlation between dorsal and ventral colouration in *A. pelii* was shown after omitting DC 1 and VC 1 (n = 49, χ^2 13.177, d.f. 2, $P < 0.001$) as well as in all previous steps of the analysis.

In *A. pelii* a correlation between dorsal and ventral colouration is evident, as individuals with a dark dorsal surface tend to be dark on the ventral side, too. The two darker dorsal colouration classes are linked to the darkest ventral colouration in 90% of all specimens, while the relatively rare completely white ventral colouration is restricted to the two dorsal colouration classes with extensive white markings. However, the latter can be combined with every possible ventral colouration, although the darkest colouration is found in less than 12% of the specimens only.

Colouration and sex

A total of 35 males (56%) and 27 females (44%) were available. The data showed no significant correlation between dorsal or ventral colouration and sex.

Colouration and age

Some 117 animals were grouped into age class 1 (5%, n=6), 2 (19%, n=22), 3 (41%, n=48), and 4 (35%, n=41). The data showed no significant association between colouration and age.

Colouration and collection area

Localities and diagrams of colouration class frequencies in the respective areas are shown in Figure 5, border lines between the areas in Figure 6. In spite of the extremely small area inhabited by *A. pelii*, a strong geographic variation exists in the extension of the white markings. West of the Sassandra River only entirely black individuals are found. Specimens with large white markings of the colour classes 3 and 4 are mainly restricted to a relatively small area between the Sassandra and Bandama rivers. In the triangle between the Bandama and Nzi rivers three specimens of the colour classes 2 and 3 were found, thus forming a transition to the area east of the Bandama and Nzi rivers to the Volta River, where exclusively individuals with small white markings of the colour class 2 occur.

3.4. Combined analysis of geographic boundaries

Based on the results shown in Figures 3-5, an attempt was made to identify general borders in the distribution patterns of the characters analysed. Seventeen border lines of different significance for the respective species and colouration characters were recognized (Fig. 6). The Sassandra (Fig. 6, line 1) and Bandama and Nzi (Fig. 6, line 2) rivers obviously are effective barriers for *A. pelii*, but not for *A. beecrofti* and *A. derbianus*. The Volta (Fig. 6, line 3) marks the eastern boundary of the distribution of *A. pelii* and also seems to play a role for *A. beecrofti*. Unfortunately, only very few skins of *A. beecrofti* and none of *A. derbianus* were available from the small area between the Volta and the Dahomey Gap, thus statements concerning this region have to be treated with caution. The Dahomey Gap (Fig. 6, line 4) is a significant barrier for colouration frequencies in *A. beecrofti*, but only the shoulder colouration of *A. derbianus* displays a change there, while dorsal and ear colouration are not affected. An important border line (Fig. 6, line 5) that significantly separates frequencies for almost all investigated characters, except for the shoulder colouration in *A. derbianus*, exists between Nigeria and the highlands of western Cameroon. This highland area differs also from the adjacent plains (Fig. 6, line 6) in the frequencies of dorsal and shoulder colouration of *A. derbianus* and dorsal colouration of *A. beecrofti*. From S-Cameroon to Gabon and SW-Central African Republic, the colouration frequencies are homogenous for *A. derbianus* and quite so for *A. beecrofti*, with the exception of uniformly reddish specimens from a restricted area in the coastal plains of Equatorial Guinea and N-Gabon. Unfortunately very few individuals were collected in Congo Brazzaville, therefore it is not possible to give statements concerning this country. Specimens of *A. derbianus* from the southern tip of South Ogooue (NW of the Congo River, Fig. 6, line 7; see GAUTIER-HION et al., 1999 for definition of the area) show no differences in colouration frequencies to those from S-Cameroon to Gabon. The small sample of *A. beecrofti* from the same area uniformly shows the relatively rare dorsal colouration 3.

Bioko is a special case (Fig. 6, line 8). Specimens of *A. beecrofti* have a uniform dorsal colouration which otherwise is found mainly in W-Cameroon highlands and in Angola. Specimens from Nigeria have completely different colourations. Individuals of *A. derbianus* have identical dorsal colouration frequencies on Bioko and in West Africa (Liberia to Nigeria), but frequencies differ significantly from those of the region between Cameroon and Congo. The frequencies of the ear colouration on Bioko are intermediate to the frequencies in Nigeria and the Cameroon to Congo area. Light shoulders as typical for West Africa occur on Bioko in a frequency intermediate to that of West Africa and Central and East Africa.

The border effect of the lower Congo (Fig. 6, line 9) and Ubangi (Fig. 6, line 10) is also difficult to define. They form clear boundaries for dorsal and shoulder colouration in *A. derbianus*, but not for ear colouration. In

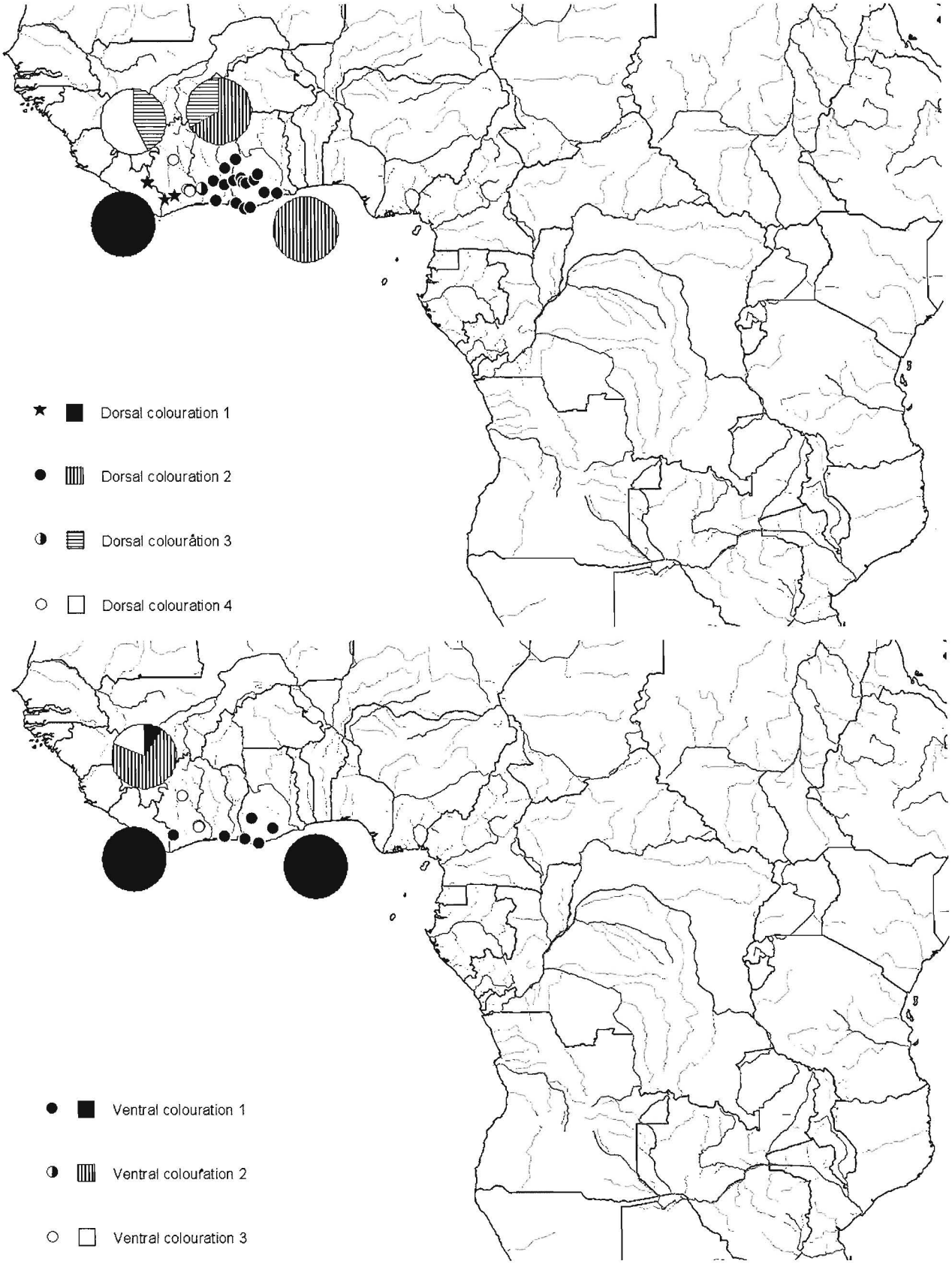

Fig. 5: Geographical distribution of coat colouration in *Anomalurus pelii* (see Fig. 6 for border lines).

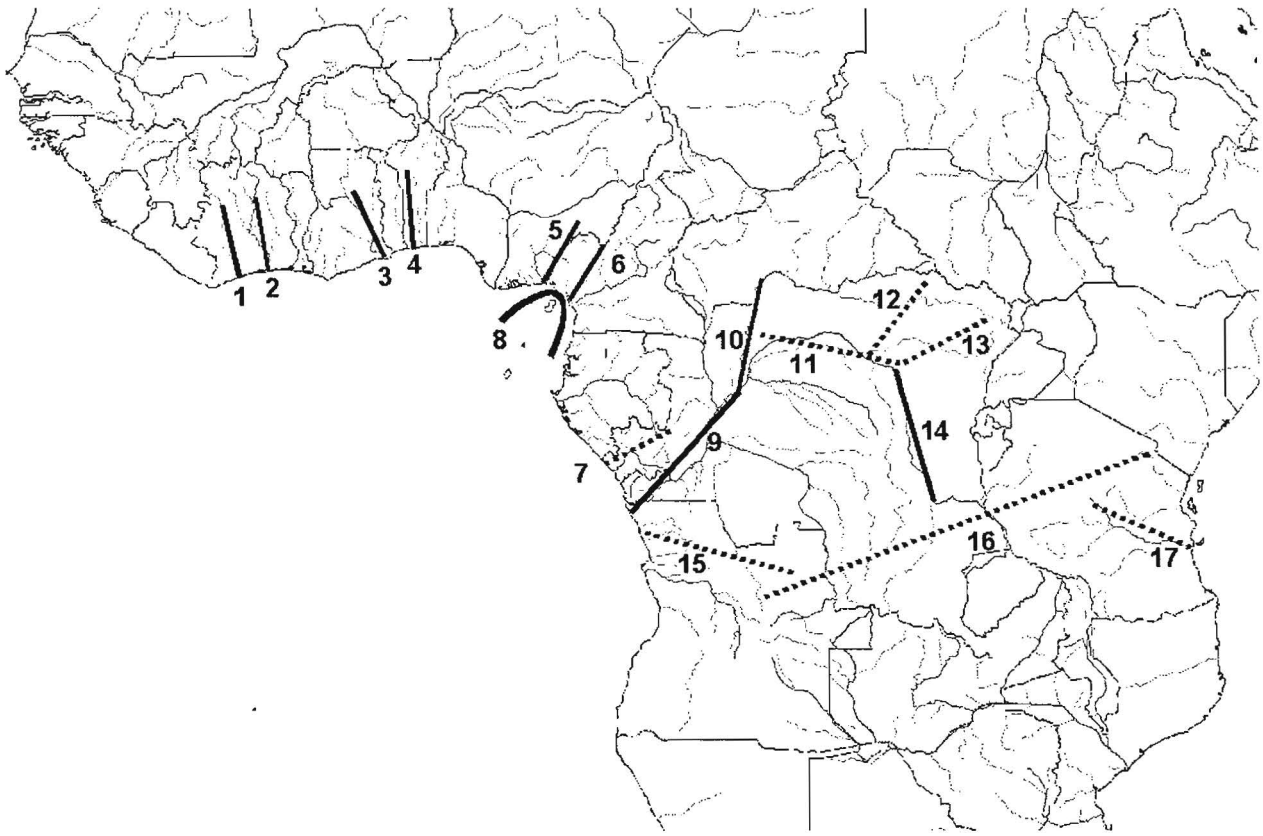

Fig. 6: Border lines of greater (bold) and lesser (dotted) importance for colouration changes in *Anomalurops beecrofti*, *Anomalurus derbianus* and *A. pelii* (see text for details).

A. beecrofti this river system forms a significant barrier for ventral colouration, but only the Ubangi part significantly separates neighbouring populations in dorsal colouration.

Results for the area between the Congo River and the Ubangi, Uëlle, and Kibali river system are also contradictory. For *A. beecrofti*, a significant boundary in dorsal colouration frequencies between the northwestern and southeastern part of the range (Fig. 6, line 13) corresponds to the Aruwimi and Ituri river system, but is not matched by the ventral colouration. Dorsal and shoulder colouration of *A. derbianus* are uniform in this area, but there are differences in ear colouration between specimens from the northwest and souteast (Fig. 6, line 12). However, this boundary lies further west than in *A. beecrofti*. The north bow of the Congo River (Fig. 6, line 11) seems to have no effect on the dorsal, ear and shoulder colouration frequencies in *A. derbianus*. The same applies to the northwestern population of *A. beecrofti*, while southeastern specimens are significantly different from those south of the Congo (Fig. 6, line 14). Specimens of *A. beecrofti* from W-Angola seem to be different from individuals caught in the Congo Basin (Fig. 6, line 15), but the sample size is small. For *A. derbianus* the situation is more complex, because this species occurs also in E-Angola, Zambia, and Tanzania (Fig. 6, line 16). There are only slight differences between specimens from the Congo basin and W-Angola. Light epaulettes are missing in all specimens from Angola, S-Democratic Republic of Congo, Zambia and Tanzania. In the same area (except Angola) the rare uniformly silvery specimens occur, and the highest amount of ears displaying the same colouration as the rest of the head is found here too. In the Usambara Mountains the ventral colouration of *A. derbianus* differs from that of more southern individuals (Fig. 6, line 17).

4. DISCUSSION

Our study has revealed a remarkable mosaic of differences as well as similarities between the respective species. *Anomalurus pusillus*, a species studied but results not shown in detail here, shows a homogeneous brownish colouration throughout its range from Cameroon to E-Democratic Republic of Congo. *Anomalurops beecrofti* varies significantly in the frequencies of the colouration forms but the majority (ca. 70%) of specimens belong to only one of the two colouration forms that occur throughout the distribution area of the spe-

cies. In *Anomalurus derbianus* the correlation between locality and colouration is more pronounced, although dorsal, ear and shoulder colouration follow slightly different geographic patterns. In *Anomalurus pelii* the dorsal colouration follows clear-cut lines, a pattern not found in any other species.

Despite the particular differences between the species, some general geographic patterns can be extracted. Some boundaries seem to have a major impact on the distribution and frequency of the various colour morphs in the studied species (Fig. 6): The Sassandra, the Bandama-Nzi river system, the Volta River and the Dahomey Gap in West Africa, the highlands of W-Cameroon, the lower Congo and Ubangi river system, and a border line running from Katanga to NE-Tanzania, which separates the southwestern parts of the distribution area of *A. derbianus* from the rest. The Congo River seems to have a low impact on the geographic colouration pattern in *A. beecrofti* and *A. derbianus*, especially in its middle part.

Some of these boundaries are found in other mammalian species as well, but others not. Primates are a well-studied group suited for comparison. Subspecific changes occur frequently in the Ivory Coast, often in the vicinity of the Sassandra River (BOOTH 1958; DANDELOT 1965; GRUBB 1990; LERNOULD 1988; OATES 1988). The Bandama River forms a border between subspecies of *Procolobus badius* (BOOTH 1958; OATES 1988). However, both rivers do not seem to represent barriers for guenons as clear as for *A. pelii*. The Dahomey Gap is a well known border for primates species (BOOTH 1958; GRUBB 1990; LERNOULD 1988; OATES 1988). The highlands of W-Cameroon are a centre of endemism for mammals, and also a border for some guenon subspecies (LERNOULD 1988). Further south, the Sanaga River forms a barrier for many primates (LERNOULD 1988). A further subdivision of the area between the Sanaga and Congo and Ubangi rivers, as found in mitochondrial haplotypes of gorillas (CLIFFORD et al. 2004), could not be observed in anomalurids. The lower Congo and Ubangi rivers are common barriers for numerous primates (DANDELOT 1965; GAUTIER-HION et al. 1999; GRUBB 1990; LERNOULD 1988). In the area between the Congo and Ubangi rivers, no river forms an obvious barrier. However, hybridisation zones or changes of subspecies of primates are frequently found north of the Congo River between the lower Ubangi in the west and the Ituri River and the Kivu region in the east (COLYN 1987, 1988; COLYN et al. 1991; DANDELOT 1965; GAUTIER-HION et al. 1999). The Uëlle River, which marks the northern border of the distribution area of the anomalurids, has the same significance for some primates but not for others (COLYN 1987; GAUTIER-HION et al. 1999; LERNOULD 1988). The Congo River, which delimits the inner Congo Basin to the north and forms a significant barrier for primates (COLYN 1987, 1988; COLYN & DELEPORTE 2002; DANDELOT 1965; GRUBB 1990; LERNOULD 1988) and other mammals, seems to have little importance for the distribution of colour patterns in *A. beecrofti* and *A. derbianus*. The Rift Valley is also a significant barrier for guenons (LERNOULD 1988), and although it seems to have no influence on *A. derbianus*, it is the western border for three other species of anomalurids (*A. pusillus*, *Idiurus macrotis*, and *I. zenkeri*). *Anomalurus derbianus* apparently has a high potential of dispersal as the species not only crosses the Rift Valley but also extends far south into Zambia and Tanzania.

Generally the distribution of coat colouration patterns in anomalurids is strongly correlated with the occurrence of larger rivers. This seems remarkable for animals with an ability for gliding flight. *Anomalurus pelii* has been observed to glide for 50 m (DEKEYSER 1954). Distances of 15 to 20 m (DELANY 1975) and even up to 100 m (KINGDON 1974) were reported for *A. derbianus*, and flights over a distance of 250 m are assumed as possible (KINGDON 1974; MACKAY & CUNNIGHAM VAN SOMEREN 1980). However, larger rivers seem to form barriers that are not regularly crossed. Unfortunately not much is known about the behaviour of anomalurids, but their common way of locomotion is gliding flight from one tree to another, starting from and landing on trunks or branches, and then climbing up the trunk for the next start (ADAMS 1894; KINGDON 1974; RAHM 1969).

What do the observed patterns tell us about the evolutionary history of these anomalurids? First, the patterns are more complex than expected. *Anomalurus pelii* is confined to a small area in West Africa where it established three distinct populations separated by the Sassandra and Bandama rivers (Fig. 5). Although genetic data are not yet available, we assume that reduced gene flow exists between the three populations (SCHUNKE & HUTTERER in press).

The situation in *A. derbianus* and *Anomalurops beecrofti* is more complex (Figs. 3, 4). Some of the patterns agree with biogeographic units identified by COLYN & DELEPORTE (2002) in their analysis of forest guenons. Particularly the West Central faunal area (NW of Congo River to Cameroon Mts) is reflected by the distribution of the anomalurids. COLYN & DELEPORTE (2002) found several subunits in the area, apparently a result of fluctuating savanna and forest vegetation in this area in the Quaternary. The distribution of the shoulder colouration in *A. derbianus* (Fig. 4, bottom) fits this picture. During deteriorating conditions, animals with dark shoulders may have retreated into the Congo Basin and the Cameroon Mts refuge, and animals with pale shoulders into a West African refuge. In times of ameliorating conditions, the West African population dispersed into the

former savanna corridor and filled this gap with pale-shouldered animals.

The true picture was certainly more complex, the details, however, must still be filled in. Cladogenesis and secondary hybridization at contact zones have probably obscured the original patterns. The periodic model of cladogenesis in African mammals (GRUBB 1999) seems to be well-suited to explain the current patterns. Genetic data are needed to know to which extent cladogenesis has occurred, and to solve the phylogeography of the group.

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REFERENCES

ADAMS, W. H. (1894): On the habits of the flying-squirrels of the genus *Anomalurus*. Proceedings of the Zoological Society of London: 243-246.

BOOTH, A. H. (1958): The zoogeography of West African primates: A review. Bulletin de l'Institut Français d'Afrique Noire (A) **20**: 587-622.

BRAESTRUP, F. W. (1935): Remarks on climatic change and faunal evolution in Africa. Zoogeographica **2**: 484-494.

BRENAC, P. (1988): Evolution de la végétation et du climat dans l'Ouest Cameroun entre 25 000 et 11 000 ans BP. Actes Xème Symposium Ass. Palynologues Langue Française, Trav. Sect. Sci. Tech. Inst. Français Pondichéry **25**: 91-103.

CLIFFORD, S. L., ANTHONY, N. M., BAWE-JOHNSON, M., ABERNETHY, K. A., TUTIN, C. E. G., WHITE, L. J. T., BERMEJO, M., GOLDSMITH, M. L., MCFARLAND, K., JEFFREY, K. J., BRUFORD, M. W. & WICKINGS, E. J. (2004): Mitochondrial DNA phylogeography of western lowland gorillas (*Gorilla gorilla gorilla*). Molecular Ecology **13**: 1551-1565.

COLYN, M. (1987): Les primates des forêts ombrophiles de la cuvette du Zaire: interprétations zoogéographiques de modèles de distribution. Revue de Zoologie africaines **101**: 181-196.

COLYN, M. (1988): Distribution of guenons in the Zaire-Lualaba-Lomami river system. Pp. 104-124 in: GAUTIER-HION, A., BOURLIÈRE, F., GAUTIER, J.-P. & KINGDON, J. (eds.) A primate radiation: evolutionary biology of the African guenons. Cambridge University Press, Cambridge.

COLYN, M. & DELEPORTE, P. (2002): Biogeographic analysis of Central African forest guenons. Pp. 61-78 in: GLENN, M. E. & CORDS, M. (eds.) The guenons: Diversity and adaptation in African monkeys. Kluwer Academic/Plenum Publishers, New York.

COLYN, M., GAUTIER-HION, A. & VERHEYEN, W. (1991): A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaire Basin. Journal of Biogeography **18**: 403-407.

DANDELOT, P. (1965): Distribution de quelques espèces de Cercopithecidae en relation avec les zones de végétation de l'Afrique. Zoologica africana **1**:167-176.

DEKEYSER, P. L. (1954): A propos des ecureuils volants. Notes africaines **64**:121-124.

DELANY, M. J. (1975): The Rodents of Uganda. Trustees of the British Museum (Natural History), London.

FJELDSÅ, J. & LOVETT, J. C. (1997): Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. Biodiversity and Conservation **6**: 325-346.

FRÉDOUX, A. & TASTET, J. P. (1988): Stratigraphie pollinique et paléoclimatologie de la marge septentrionale du Golfe de Guinée depuis 200.000 ans. Institut Français Pondichery, Travaux Section Science et Technique **25**:175-183.

GAUTIER-HION, A., COLYN , M. & GAUTIER, J.-P. (1999): Histoire naturelle des primates d'Afrique Centrale. ECOFAC, Libreville.

GRUBB, P. (1978): Patterns of speciation in African mammals. Bulletin of Carnegie Museum of Natural History **6**:152-167.

GRUBB, P. (1990): Primate geography in the Afro-tropical forest biome. Pp. 187-214 in: PETERS, G., & HUTTERER, R. (eds.) Vertebrates in the tropics. Proceedings of the International Symposium on Vertebrate Biogeography and Systematics in the Tropics, Bonn, June 5-8, 1989. Museum Alexander Koenig, Bonn.

GRUBB, P. (1999): Evolutionary processes implicit in distribution patterns of modern African mammals. Pp. 150-164 in: BROMAGE, T. G., & SCHRENK, F. (eds.) African biogeography, climate change, & human evolution. Oxford University Press, New York & Oxford.

HAMILTON, A. C. & TAYLOR, D. (1991): History of climate and forests in tropical Africa during the last 8 Million years. Climatic Change **19**: 65-78.

JAHNS, S., HÜLS, M. & SARNTHEIM, M. (1998): Vegetation and climate history of West Equatorial Africa based on a marine pollen record off Liberia (site GIK 16775) covering the last 400,000 years. Revue Palaeobotanie et Palynologie **102**: 277-288.

KINGDON, J. (1974): East African Mammals. An Atlas of Evolution in Africa. Volume II, Part B (Hares and Rodents). Academic Press, London, New York.

LERNOULD, J.-M.(1988): Classification and geographical distribution of guenons: a review. Pp. 54-78 in: GAUTIER-HION, A., BOURLIÈRE, F., GAUTIER, J.-P. & KINGDON, J. (eds.) A primate radiation: evolutionary biology of the African guenons. Cambridge University Press, Cambridge.

LIVINGSTONE, D. A. (1967): Postglacial vegetation of the Ruwenzori Mountains in Equatorial Africa. Ecological Monographs **37**: 25-52.

LÖNNBERG, E. (1929): The Development and distribution of the African Fauna in connection with and depending upon Climatic Changes. Arkiv foer Zoologi **21A (4)**: 1-33.

MACKAY, A. & CUNNINGHAM VAN SOMEREN, G. R. (1980): Some observations on anomalures near Chemisia, north Nandi, Kenya. East African Natural History Society Bulletin (May-June): 42-43.

MALEY, J. (1983): Histoire de la végétation et du climat de l'Afrique nord-tropicale au Quaternaire récent. Bothalia **14 (3-4)**: 377-389.

MALEY, J. (1991): The African rain forest vegetation and paleoenvironments during Late Quaternary. Climatic Change **19**: 79-98.

OATES, J. F. (1988): The distribution of *Cercopithecus* monkeys in West African forests. Pp. 79-103 in: GAUTIER-HION, A., BOURLIÈRE, F., GAUTIER, J.-P. & KINGDON, J. (eds.) A primate radiation: evolutionary biology of the African guenons. Cambridge University Press, Cambridge.

RAHM, U. (1969): Dokumente über *Anomalurus* und *Idiurus* des östlichen Kongo. Zeitschrift für Säugetierkunde **34**: 75-84.

SCHUNKE, A. C. & HUTTERER, R. (in press): Geographic variation in the West African scaly-tailed squirrel *Anomalurus pelii* (Schlegel and Müller, 1845) and description of a new subspecies (Rodentia: Anomaluridae). Pp 321-328 in: HUBER, B. A., SINCLAIR, B. J. & LAMPE, K.-H. (eds.) African Biodiversity: Molecules, Organisms, Ecosystems. Proceedings of the 5th International Symposium on Tropical Biology, Museum Koenig, Bonn. Springer Verlag, Berlin.

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Table 1: Characters and respective numbers of specimens analysed in this study. *A. pusillus* was not analysed in detail because no appreciable variation exists

Character/Species	A. beecrofti	A. derbianus	A. pelii	A. pusillus
Dorsal colouration	227	469	142	128
Ventral colouration	169	137	58	48
Ear colouration	not used	449	not used	not used
Shoulder colouration	not used	459	not used	not used
Throat colouration	not used	135	not used	not used
Sex	156	342	64	not used
Age class	160	365	117	not used
Month of collection	177	359	109	not used
Locality coordinates	208	421	118	113

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