Systematics and Biogeography of the African Scaly-tailed Squirrels (Mammalia: Rodentia: Anomaluridae)

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Contents

1. Introduction

The Anomaluridae are an African rodent group that occurs widespread in rain, mountain and gallery forests from Senegal to Tanzania. With a single exception all anomalurid species are capable to perform gliding flight and thus depend on trees large enough and relatively close together to enable this movement. This combination of a large distribution area and the dependence on trees makes the anomalurids an interesting example for investigations of the historical biogeography of the African rain forests.

Systematics and taxonomy of this group have been under discussion for more then 150 years, since the first description of anomalurids in 1842 (see Chap. 2 for details). After a considerable increase of accepted species in taxonomic reviews this number dropped in the more recent publications to a minimum of the following species that will also be used as a basis in this investigation:

Anomalurops beecrofti Fraser, 1852
Anomalurus derbianus Gray, 1842
Anomalurus pelii Schlegel & Müller, 1845
Anomalurus pusillus Thomas, 1887
Idiurus macrotis Miller, 1898
Idiurus zenkeri Matschie, 1894
Zenkerella insignis Matschie, 1898

However, most reviews on systematics and taxonomy as well as on distribution were restricted to specimens from one country and/or one or a few collections. So far a synopsis of all data available for anomalurids was missing. An exhaustive analysis of as much data as possible was necessary for species with such a widespread distribution to get a closer insight into the structure of this enigmatic group.

The hypothesis that should be tested in this investigation was that there should be distinguishable units within taxa occurring in a range which measures up to 6000 km in diameter. These units should then be used for the reconstruction of the history of anomalurid distribution and allow a review of the taxonomy of the Anomaluridae as well as additional conclusions concerning the history of the African Rain Forest.

In spite of the numerous specimens in several collections the number of publications concerning this group is remarkably small. An overview of the literature on anomalurids including first descriptions etc. is given in Chapter 2. Most information is found on the distribution of the group, mainly in checklists. A few publications deal with the taxonomy of anomalurids, but they are generally restricted to certain geographical areas. Unfortunately there is only very little known on the biology of this fascinating group.

The present investigation used the majority of anomalurid specimens in European and North American collections (Chap. 3) and all available data from these specimens. First a detailed analysis of the colouration was performed for the species with definable differences in colouration and colour patterns (Chap. 4). This led to a number of geographical borderlines along which significant changes for at least one colouration character was observed. By adding a few more lines based on well known geographical obstacles or previously for other species described borderlines four main areas and 23 subareas were defined (Chap. 5) and used for the following analyses. Chapters 6 to 9 give the results of those analyses which yielded the most informative findings. Investigations which revealed no differences between species or geographic populations, namely analyses of the hair surface structure with the scanning electron microscope and the morphology of the postcranial skeleton were omitted.

A number of linear and multivariate statistic methods were used to describe the variation in body size (Chap. 6) and skull size and shape (Chap. 7). The most informative results are presented in the respective chapters.

Besides the morphological and morphometric characters also molecular data were investigated (Chap. 8). Unfortunately it was not possible to get the data set expected from tests made earlier in the project. However, the data set used for the analysis is the best available at present and can be used for an analysis of the phylogenetic relationships within this group. Additionally the data set was used as a model for testing the use of different traditional methods and modern SuperTree approaches for an Ancient DNA problem.

A combined analysis of the morphological, morphometric and molecular data is presented in Chapter 9 along with remarks concerning the taxonomy of the Anomaluridae and a discussion of geographical areas as can be found for anomalurids.

Finally a summary is provided in Chapter 10 and a gazetteer of finding localities for anomalurids.

2. The Anomaluridae: A review of the literature

2.1. Morphology, distribution, and biology of anomalurids

The anomalurids have a specialised area with enlarged, pointed scales on the ventral part of the tail base. The backwards pointing tips of the scales are considered to serve as "climbing-irons", which prevent slipping on tree trunks (Alston, 1875; Bates, 1905; Sanderson, 1940; Durrell, 1952; Dekeyser, 1954; Rahm, 1960, 1969, 1988; Luckett, 1971; Nowak, 1991). This function was observed in the few anomalurids kept in captivity so far (Rahm, 1960; Chalmers, 1963; Crandall, 1964; Blaskiewitz, 1992). It is the name-giving structure for the common name in English ("scaly-tailed squirrels") and German ("Dornschwanzhörnchen"). Other common names ("African flying squirrels" and the French "écureuils volants d'Afrique") refer to the patagium, which all species except for *Z. insignis* have. It extends from the sides of the neck over the wrists and ankles to the upper third of the tail, usually including the area of enlarged scales. The patagium is supported by a cartilaginous rod, which originates from the elbow (Johnson-Murray, 1987). A comparable, but convergently built structure can be found in the fossil †*Eomys quercyi* (Storch et al., 1996) as well as in gliding squirrels (Sciuridae), where a specialised bone originates from the wrist.

Habitus pictures of anomalurids are relatively rare. Colour photographs of *A. derbianus* and *I. macrotis* (Julliot et al., 1998), black-and-white photographs of *A. jacksoni* (Rahm, 1960), *A. pelii* (Rahm, 1961; Walker, 1968) and of freshly killed individuals of *Anomalurus jacksoni* (Allen & Lawrence, 1937), *A. pelii* (Dekeyser, 1954; Kuhn, 1966; Killick-Kendrick, 1973), and *I. macrotis* (Rahm, 1966, 1969) were published. Colour plates can be found for *Anomalurus fulgens* (Alston, 1875), *A. beecrofti* and *A. erythronotus* (Huet, 1884), *Idiurus langi* (Allen, 1922), *Anomalurus fraseri jacksoni* (Bere, 1962), and several species in St. Leger (1931), Booth (1960), Rosevear (1969), Dorst & Dandelot (1970), and Kingdon (1997). A rather sketchy drawing of *I. kivuensis* was made by Durrell (1952); line drawings were published by du Chaillu (1861a), Grassé & Dekeyser (1955), Rosevear (1969), and Happold (1987) and several anatomical and life studies by Kingdon (1974).

Most publications deal with the distribution of anomalurids (Rosevear, 1953; Booth, 1954, 1958; Aellen & Perret, 1958; Eisentraut, 1963; Rahm, 1966; Verheyen, 1968b; Cabral, 1971; Kingdon,

1974, 1997; Robbins, 1978; Grubb, 1983; McLaughlin, 1984; Happold, 1987; Schunke & Hutterer, 2000) or mention them in checklists or collection catalogues (Sjöstedt, 1897a; St. Leger, 1931; Allen & Loveridge, 1933; Allen & Lawrence, 1937; Krumbiegel, 1942; Good, 1947; Schouteden, 1947; Malbrandt & Maclatchy, 1949; Rosevear, 1950, 1953; Hayman, 1951; Ellerman et al., 1953; Ansell, 1960; Booth, 1960; Bere, 1962; Misonne, 1963; Coe, 1975; Happold, 1987; Feiler, 1990). Finding localities are published for Cameroon (Sjöstedt, 1897b; Sanderson, 1940 [collection area today partly belonging to Nigeria]; Perret & Aellen, 1956; Eisentraut, 1963, 1973), Bioko (Thomas, 1904b; Morales Agacino, 1943; Eisentraut, 1973; Pérez del Val *et al.*, 1995), the Democratic Republic of Congo (Allen, 1922; Wettstein-Westersheim, 1925; Gyldenstolpe, 1928; Schouteden, 1947; Fain, 1953; Rahm, 1959, 1960, 1966, 1969; Rahm & Christiaensen, 1963, 1966), Tanganyika (Allen & Loveridge, 1933), Guinea-Bissau (Frade, 1949), Angola (Cabral, 1971), Nigeria (Rosevear, 1953; Happold, 1987), Zambia (Ansell, 1960, 1965, 1978), Côte d'Ivoire (Rahm, 1961; Adam *et al.*, 1970), Liberia (Kuhn, 1965, 1966), Equatorial Guinea (Jones, 1971), Central African Republic (Roche, 1972), Uganda (Delany, 1975), Malawi (Ansell & Dowsett, 1988) and Togo and Benin (Robbins & Van der Straeten, 1996).

The general knowledge on anomalurids is rather scarce (Schlitter, 1989). Although the group seems to be quite abundant at least in West Africa (Adams, 1894; Aellen *et al.*, 1970; but see Allen & Loveridge, 1933 for East Africa), information concerning the biology, ecology and behaviour of its members remains mainly anecdotal. Several short observations on the behaviour have been published by Kingdon (1974). So far the study by Julliot et al. (1998) is the only one explicitly performed on anomalurid behaviour in the field. The authors radio-tracked *A. derbianus* and *I. macrotis* and gave information about home ranges. Additionally estimates for population densities and several observations on the behaviour were provided.
Anomalurids are generally considered to be crepuscular or nocturnal. Activity starts some hours after sunset and terminates long before daybreak in *A. pelii* (Adams, 1894). During daytime anomalurids usually rest in hollow trees (Adams, 1894; Bates, 1905; Good, 1947; Schouteden, 1947; Verheyen, 1951; Dekeyser, 1954; Rahm, 1960; Rahm & Christiaensen, 1963; Jones, 1971; Kingdon, 1974; Julliot et al., 1998). The bottom of the tree holes can be covered nest-like with sticks and branches (Adams, 1894). Occasionally anomalurids can be observed on the outside of tree trunks (Eisentraut, 1973), where they are easily overlooked due to their cryptic coloration and the shadow reduced by the patagium. However, Sanderson (1940) described a different behaviour in *A. beecrofti*. According to this author this species is mainly diurnal and lives in tree parts with dense foliage, but see Rahm (1960). The contradicting information might be due to a generally nocturnal activity, but Kingdon (1974) described occasional sun-bathing. Additionally

the animals may react to disturbance by the observer. Least is known about *Zenkerella insignis*, the only species without patagium. From this species only 11 specimens are recorded in the museums world wide (Pérez del Val et al., 1995). Life observations lack completely. Eisenberg (1981) assumed that *Z. insignis*, because of the different morphology, has also a different behaviour and might be diurnal, but according to Bates (1905) and Good (1947) the species is nocturnal.

Hollow trees used for daytime rest are occasionally shared with other members of the anomalurids (*I. macrotis* and *I. zenkeri*, Rahm, 1966, *A. fraseri*, *A. pelii* and *I. macrotis*, Adam *et al.*, 1970; *A. derbianus* and *I. zenkeri*, Jones, 1971; *A. derbianus* and *I. macrotis*, Julliot *et al.*, 1998) and with bats (*Hipposideros cyclops*, Bates, 1905; Adam et al., 1970; Jones, 1971; Kingdon, 1974; *Tadarida leonis*, Rahm, 1966, 1969; Kingdon, 1974; *Scotophilus nigrita* Kingdon, 1974; *Tadarida* sp., Julliot et al., 1998), *Graphiurus* (Kingdon, 1974), or "certain species of Muridae" (Bates, 1905). *I. macrotis* was frequently observed in colonies of 5 to 6 (Adam et al., 1970; Kingdon, 1974) but Durrell (1952) reported about seventy individuals and Sanderson (1940) and Kingdon (1974) more than 100 in one colony. Of *A. pelii* three were seen in the same tree hole and up to six were reported by natives (Adams, 1894). Jones (1971) found one to three individuals of *A. derbianus* in hollow trees.

The common way of moving in their territory is gliding flight from one tree to the next, starting from and landing on branches or trunks, and then climbing up the trunk for the next start (Adams, 1894; Rahm, 1969; Kingdon, 1974). Gliding flights of 15 to 20 m for *A. derbianus* (Delany, 1975), 50 m for *A. pelii* (Dekeyser, 1954) and *I. kivuensis* (Durrell, 1952) and up to 100 m for *Idiurus* (Grassé & Dekeyser, 1955) and *A. derbianus* (Kingdon, 1974) were reported, but under good conditions flights of up to 250m might be possible (Kingdon, 1974; MacKay & van Someren, 1980). The gliding flight, particularly of *Idiurus*, was described as extremely graceful and with only very slow loss of height (Sanderson, 1940; Durrell, 1954). According to Bates (1905) anomalurids are "among the most strictly arboreal animals that exist", and their way of moving on the floor is described as a rather clumsy hopping (Verheyen, 1951; Rahm, 1960, 1969, 1988; Rosevear, 1969; Kingdon, 1974). For *Anomalurus* the way of climbing up tree trunks was described as "a humping mode of progress like that of a Geometer caterpillar" (Bates, 1905; also observed by Sanderson, 1940; Kingdon, 1974), but *Idiurus* seems to run rather like a mouse (Sanderson, 1940; Durrell, 1952; Kingdon, 1974). *A. derbianus* was watched climbing head down on vertical trunks (Rosevear, 1969; Kingdon, 1974) and also on thin branches (Rahm, 1960; Kingdon, 1974).

Anomalurids are considered strictly herbivorous with a diet consisting of phloem sap, bark, berries, fruits, leaves, and flowers (Adams, 1894; Bates, 1905; Sanderson, 1940; Verheyen, 1951; Rahm, 1969; Kingdon, 1974, 1997; Delany, 1975; Emmons et al., 1983; Julliot et al.,

1998), but Julliot et al. (1998) reported also high numbers of ant and termite remains in the stomach of one individual. At least *A. pelii* (Adams, 1894; Dekeyser, 1954), *I. macrotis* (Durrell, 1952; Adam et al., 1970), and *A. derbianus* (Happold, 1987) seem to have a special preference for oil palm fruits.

Mating seems to occur at different times of the year, in spring (January to March; Kingdon, 1974; Happold, 1987) and September to November (Adams, 1894; Sanderson, 1940; Asdell, 1964; Happold, 1987), but there may be no defined mating seasons at all (Ansell, 1963; Kingdon, 1974). Natives reported common litter sizes of two to three, never more than four in West Africa (Adams, 1894), but generally one or two young or embryos are more often observed (Sanderson, 1940; Durrell, 1952; Dekeyser, 1954; Rahm, 1969; Killick-Kendrick, 1973; Kingdon, 1974; Happold, 1987). The young seem to be precocial (Kingdon, 1974) and are brought food by the parents in mouth and cheeks (Sanderson, 1940). No information concerning the lifespan of anomalurids is published yet. In captivity one *A. derbianus* was kept for one and a half year (Blaskiewitz, 1992), one for 14 months (Rahm, 1960, 1988) and another one for six months (Kingdon, 1974), one *A. jacksoni* was kept for an undetermined time in Kenya (Chalmers, 1963), and several specimens of *Idiurus* survived no more than a few months (Durrell, 1952, 1954). The common method of capturing is smoking of hollow trees (Bates, 1905; Durrell, 1952; Rahm, 1969; Adam et al., 1970). Short comments on their calls are given by Eisentraut (1963) and Kingdon (1974). Anomalurids seem to be quite aggressive when caught and bite and scratch severely (Adams, 1894; Rahm, 1988). At least in West Africa they are eaten and even considered to be the greatest delicacy (Adams, 1894). Nothing is known about the natural enemies of anomalurids. A report of remains from an *Anomalurus* sp. in wild chimpanzee's faeces (Alp & Kitchener, 1993) and another of a blue monkey's predation of *A. derbianus* (Fairgrieve, 1997) might be due to opportunistic capture.

Morphological characters related to the gliding flight were discussed by Jackson (1999), Stafford (1999), and Scheibe & Essner (2000). Contributions to the skeletal anatomy were provided by Alston (1875), Gervais (1853), and Stafford (1999), drawings of a skeleton from *A. pelii* by de Blainville (1839-1864), and a description and drawing of the baculum of *A. f. fraseri* by Didier (1952). Cheek teeth were compared shortly by Frechkop (1936) and Thenius (1989) and in detail by Friant (1945, 1970), Stehlin & Schaub (1951), Wood (1962), and von Koenigswald (2004), incisors by Korvenkontio (1934) and Luckett et al. (1989). Comparative work on the middle ear was performed by Lavocat & Parent (1985). Bugge (1974, 1985) described the carotid arteries. Huet (1884), Tullberg (1899), Rosevear (1969), Luckett & Hartenberger (1985), Wood (1985), and Margry (not dated) commented on several anatomical characters, mainly of the skull and fur. Visceral anatomy was discussed in Alston (1875), the placenta of *Anomalurus* was described in Branca & Cretin (1925) and Luckett (1971, 1985). The musculature was described in detail by

Parsons (1899). De Seabra (1909) published some notes on an *A. fraseri* embryo. The skull of juvenile anomalurids was commented by Frahnert (1998). Histological investigations on the embryology of the scales on the tail were performed by Redlichs (1937), sections of the eye of *I. zenkeri* by Cei (1946). Colour variation was discussed for *A. derbianus* (Thomas, 1904b; Dollman, 1932; Sanderson, 1940; Krumbiegel, 1942; Eisentraut, 1968, 1973; Verheyen, 1968b), *A. beecrofti* (Sanderson, 1940; Krumbiegel, 1942; Eisentraut, 1963, 1973; Verheyen, 1968b), *I. kivuensis* (Durrell, 1952), and *A. pelii* (Dekeyser, 1954; Kuhn, 1966). Malaria parasites have been found in *A. pelii* (Killick-Kendrick, 1973), from which two new *Plasmodium* species have been described. Quentin (1974) found four new species of nematod parasites in *Anomalurus* and *Zenkerella*, Hugot (1982, 1985) three in *I. macrotis*, *A. derbianus* and *A. beecrofti*. A new parasitic mite was described from *I. zenkeri* (Till, 1982).

2.2. Names and their history

2.2.1. Recent taxa

2.2.1.1. Family group names

Anomaluri Waterhouse, 1842b, *Proc. Zool. Soc. London*: 127

This name was used first by Waterhouse without assigning it a rank. Brandt (1855) was the first to use it as a tribus name in a classification.

Anomalurina Gervais, 1853, *Ann. Scien. Nat.* (3) **20**: 246

The Anomalurina with the single genus *Anomalurus* were named as a subgroup of the Hystricidae.

Anomalurini Brandt, 1856, *Compt. Rend. Ac. Scien.* **43**: 142

Besides Anomaluri the name Anomalurini was used by Brandt in his publication 1856.

Anomaluroidea Gill, 1872, *Smithson. Misc. Coll.* **230**: 21

Anomaluridae Gill, 1872, *Smithson. Misc. Coll.* **230**: 21

Both names were given in the "Arrangement of the Families of Mammals", the Anomaluroidea being one of nine superfamilies.

Anomalurinae Alston, 1875, *Proc. Zool. Soc. London*: 95

The name was used in one suggestion for the position of the group within the rodents, as subfamily of the Sciuridae.

Zenkerellinae Matschie, 1898, *Sitzb. Ges. naturf. Freunde, Berlin*: 26
The Zenkerellinae were proposed as one of two subfamilies within the Anomaluridae, Anomalurinae and Zenkerellinae, the latter covering *Zenkerella* and *Idiurus*.

Anomaluroidei Tullberg, 1899, *Über das System der Nagethiere. Eine phylogenetische Studie.* Uppsala: 159
The name was introduced by the author for a section of the Myomorphi which comprised the Anomaluridae and Pedetidae.

Idiuridae Miller & Gidley, 1918, *J. Washington Acad. Sc.* **8**: 442
Idiurinae Miller & Gidley, 1918, *J. Washington Acad. Sc.* **8**: 442
The authors suggested family rank for Idiurinae plus Zenkerellinae, but this idea was not accepted by other authors.

Anomaluroidae Ellerman, 1940, *The families and genera of living rodents. Volume I: Rodents other than Muridae.* London: 535
This name was created for a superfamily which contains only the family Anomaluridae with the subfamilies Anomalurinae and Idiurinae.

Anomaluromorpha Bugge, 1974, *Acta Anatomica* **87**, Suppl. **62**: 48
The Anomaluromorpha are at present widely accepted as monophyletic taxon, comprising the Anomaluridae and Pedetidae. Originally formed on the basis of the cephalic arterial system, it received recently further support from molecular data.

2.2.1.2. Genus group names
Anomalurus Waterhouse, 1842b, *Proc. Zool. Soc. London*: 124
The first name above the species-level provided for the group with the genus type form *Anomalurus fraseri* Waterhouse, 1842. The name was combined of anomalos (‘out of law’) and urá (‘tail’).

Aethurus de Winton, 1898a, *Proc. Zool. Soc. London*: 450
Type species is *Aethurus glirinus* de Winton, 1898, which was considered very early as a synonym of *Zenkerella insignis*. The name may be derived from aethereus (‘living in the air’) and urá (‘tail’).

Idiurus Matschie, 1894, *Sitzber. Ges. Naturf. Freunde, Berlin*: 194
The second genus of the Anomaluridae, of which *Idiurus zenkeri* Matschie, 1894 is the genus type. The meaning of the name is ‘with peculiar tail’.

Anomalurodon Matschie, 1914, *Sitzb. Ges. Naturf. Freunde, Berlin*: 350
According to the author *A. pelii* and *A. auzembergeri* could be placed in the subgenus *Anomalurodon*, *A. auzembergeri* Matschie, 1914 being the genus type.

Anomalurops Matschie, 1914, *Sitzb. Ges. Naturf. Freunde, Berlin*: 351
The genus type for this group is *A. beecrofti* Fraser, 1852. At the time of its creation it contained *A. laniger, A. argenteus, A. beecrofti* and *A. fulgens*. This name is the most controversially discussed one.

Anomalurella Matschie, 1914, *Sitzb. Ges. Naturf. Freunde, Berlin*: 351
The third of the three new subgenera proposed in the paper was supposed to cover *A. pusillus* and *A. batesi*, type specimen being *A. pusillus* Thomas, 1887.

Zenkerella Matschie, 1898, *Sitzb. Ges. Nat. Freunde, Berlin*: 23
The third genus name with *Zenkerella insignis* Matschie, 1898 as type specimen. The genus was named for G. Zenker, Head of the Yaounde Station in Cameroon.

2.2.1.3. Species group names

A. beecrofti

beecrofti Fraser, 1852, *Proc. Zool. Soc. London*: 17
Holotype: ♀, skin and skull, BMNH 52.2.22.12
Anomalurus beecrofti from Bioko was named after J. Beecroft, who was the Governor of the island. It was the third described species of the Anomaluridae still considered valid today and could necessarily only be compared to *A. fraseri* and *A. pelii*.

laniger Temminck, 1853, *Esquisses Zool. sur la Côte de Guiné* **1**: 149
Holotype: ♀, skin and skull, RMNH 26757
The origin of the type specimen of *Anomalurus laniger* is not very precisely known, but seems to be in West Africa. It was explicitly only compared with *A. fraseri* and *A. pelii*.

fulgens Gray, 1869, *Ann. Mag. Nat. Hist.* (4) **3**: 467
Holotype: ♂, skin, BMNH 69.531.1
The type specimen of *Anomalurus fulgens* was collected in Gabon. The description is rather short and deals mainly with the uniform reddish colouration.

argenteus Schwann, 1904, *Ann. Mag. Nat. Hist.* (7) **8**: 70
Holotype: skin and skull, BMNH 2.11.10.7
This form from Abutschi, Nigeria was described as *Anomalurus beecrofti argenteus*. It differs from *A. beecrofti* by the more silvery colouration.

citrinus Thomas, 1916, *Ann. Mag. Nat. Hist.* (8) **18**: 236
Holotype: ♀, skin and skull, BMNH 0.2.5.15
Anomalurus beecrofti citrinus from Equatorial-Guinea was described on the basis of a more yellowish colouration, "varying very much in tone, but averaging very much stronger and darker than in the Gold Coast and Nigerian forms".

chapini Allen, 1922, *Bull. Am. Mus. Nat. Hist.* **47**: 65
Holotype: ♂, skin and skull, AMNH 50480
This name is based on material of The American Museum of Natural History Congo Expedition in 1909 to 1915. *Anomalurops beecrofti chapini* was described from Medje (now Democratic Republic of Congo) in the same paper as *I. langi* and *I. panga*. The name was given for James P. Chapin, one of the members of the expedition. It was compared only with the geographically closest *A. b. citrinus*, from which it differed according to the author by its larger skull, head and body length and its colouration.

hervoi Dekeyser & Villiers, 1951, *2a Conferência Internacional dos Africanistas Ocidentais, Bissau, 1947* **3** (2): 57
Holotype: ♂, skin and skull, MNHN 1952-3
Anomalurops beecrofti hervoi was described from Bignona (Casamance), Senegal and the holotype and the four paratypes came from a locality most to the North and West. They were originally deposited in the Institut Francais d'Afrique Noire in Dakar, but the holotype is now in the Museum National d'Histoire Naturelle in Paris. It was named in the honour of Capitaine Hervo, commandant of the Subdivision of Bignona. The differences from the nominate form are in size ("sa taille est nettement inférieure") and in slight differences in colouration.

schoutedeni Verheyen, 1968a, *Rev. Zool. Bot. Afr.* **78**: 157
Holotype: ♀, skin and skull, MRAC 6428
So far *Anomalurops beecrofti schoutedeni* was the last extant species of Anomaluridae described. It was named for H. Schouteden, who collected the type specimens in the central Democratic Republic of Congo. This form differs from the others by its small size.

A. derbianus

derbianus Gray, 1842, *Ann. Mag. Nat. Hist.* (1) **10**: 262

Holotype: skin, LIVCM D-302

This form was the first species of the Anomaluridae described with the name *Pteromys Derbianus* within the Jerboidae. No explicit dedication is given in the rather short description, but the type specimen from Sierra Leone was deposited in the Museum of the Earl of Derby. It is now in the collection of the Liverpool Museum.

fraseri Waterhouse, 1842b, *Proc. Zool. Soc. London*: 124

Holotype: ♂, skin, BMNH 55.12.24.103

Anomalurus fraseri was described only shortly after *A. derbianus*. The type specimen was collected on Bioko island by Fraser and named in his honour. Waterhouse suggested the name *Anomalurus* and also provided *Aroœthrus* as substitution, in case *Anomalurus* had been used previously.

squamicaudus Schinz, 1845, *Syst. Verzeichn. Säugeth.* **2**: 58

Holotype: see *fraseri*

Pteromys squamicaudus was created as a renaming of *A. fraseri*.

beldeni du Chaillu, 1861b, *Proc. Boston Soc. Nat. Hist.* **7**: 303

Holotype: not seen

Anomalurus Beldeni from Gabon was named in the honour of G. M. Belden “as a token of friendship”. No explicit comparison with other forms was performed, the only reason given for describing a new species reads as follows: “The chief peculiarity of this species is the two distinct colours of the tail which ends in a tuft.”

erythronotus Milne-Edwards, 1879, *Compt. Rend. Acad. Sci., Paris* **89**: 771

Holotype: skin and skull, MNHN 1879-2111

Anomalurus erythronotus is the second form described from Gabon, based on the striking colouration. Unfortunately it is not clear, with which forms it was compared, because the author says that this new form raises the number of species to six, but he explicitly compares it only with *A. beecrofti*, *A. fraseri* and *A. laniger*.

orientalis Peters, 1880, *Monatsb. K. Preuss. Akad. Wiss., Berlin*: 164

Holotype: ♂, juvenile, skin, ZMB 5629

The type specimen of *Anomalurus orientalis* was collected in Zanzibar according to the label, but Pakenham (1984) argued that it was more likely to have come from the mainland of

Tanzania. It was the first record from Eastern Africa. The comparison with *A. fraseri* and *A. beecrofti* is very short.

chrysophaenus Dubois, 1888, *Bull. Soc. Zool. de France, Paris* **13**: 23
Holotype: not seen
The type specimen of *Anomalurus chrysophaenus* from Landana, Cabinda (Angola) was rather shortly compared with the other forms described so far. According to the author no resemblance to any of them was obvious, although the size was closest to that of *A. pelii*.

cinereus Thomas, 1895, *Ann. Mag. Nat. Hist*. (6) **15**: 188
Holotype: skin and skull, BMNH 95.1.17.1
Anomalurus cinereus from Moçambique was compared shortly with *A. orientalis*, probably because of the relatively small distance of the type localities. It differs from this form mainly by its colouration.

jacksoni de Winton, 1898b, *Ann. Mag. Nat. Hist.* (7) **1**: 251
Holotype: ♂, skin and skull, BMNH 99.8.4.44
Anomalurus jacksoni was named in the honour of F. J. Jackson, who collected the type specimen in Uganda. It was compared with *A. cinereus* and *A. erythronotus*, from which two forms it was distinguished by slight differences in skull form and colouration.

nigrensis Thomas, 1904a, *Abstr. Proc. Zool. Soc. London* **10**: 12
Holotype: skin and skull, BMNH 2.11.10.5
Like all first descriptions of anomalurids from this author the one of *Anomalurus fraseri nigrensis* from Nigeria is extremely short. The differential diagnosis consists of the sentence "Similar to true *A. fraseri*, but size smaller and colour paler.", followed by two measurements.

neavei Dollman, 1909, *Ann. Mag. Nat. Hist.* (8) **3**: 351
Holotype: ♀, skin and skull, BMNH 7.12.13.37
Collected in Kambove, Katanga in the South of the Democratic Republic of Congo by S. A. Neave, for whom it was named *Anomalurus neavei*. The author compared it only with *A. cinereus*, the latter having larger tail-scales and a different colouration as well as lacking "black hairs on the claws of the hind feet".

imperator Dollman, 1911, *Ann. Mag. Nat. Hist.* (8) **8**: 257
Holotype: ♀, skin and skull, BMNH 11.6.2.8
The type specimen of *Anomalurus imperator* was collected in Bibianaha, Ghana. It was compared with *A. fraseri nigrensis* and distinguished by "the entire absence of the black ocular and occipital markings" and "the bright buff-coloured tint on the back and shoulders".

griselda Dollman, 1914, *Ann. Mag. Nat. Hist.* (8) **14**: 490
Holotype: ♂, skin and skull, BMNH 14.7.23.14
The third name created by this author was used as the subspecies *Anomalurus fraseri griselda* from Bitye in the Southern part of Cameroon. The short comparison with *A. f. nigrensis* found differences in colouration and larger skull size.

perustus Thomas, 1916, *Ann. Mag. Nat. Hist.* **8** (18): 235
Holotype: ♀, skin and skull, BMNH 16.5.15.9
Anomalurus jacksoni perustus from the central Democratic Republic of Congo was described as new subspecies based on differences in the colouration.

fortior Lönnberg, 1917, *Kungl. Svenska Vet.-Akad. Handl., Stockholm,* (2) **58**: no. 2: 66
Holotype: ♂, skin and skull, NRM A622136
Anomalurus jacksoni fortior was described as new subspecies mainly because of the size. The specimens were collected in Masisi in what is now western Democratic Republic of Congo.

laticeps d'Aguilar-Amat, 1922, *Butlletí Inst. Catalana d'Hist. Nat.* **2**: 53
Holotype: ♂, skin, MZB 522 / 82-0320
Was described as *Anomalurus fraseri laticeps* from the Pico de Santa Isabel, a mountain on the Bioko island with a height of up to 3000 metres. The form was considered to have a wider skull than the nominate form ("Ab *Anomaluro Fraseri* differt praecipue majore latitudine craniale."). So far no author accepted it as a valid (sub)species (for detailed arguments see Cabrera, 1923).

jordani St. Leger, 1935, *Nov. Zool.* **39**: 251
Holotype: ♀, skin and skull, BMNH 35.1.6.80
The type specimen of *Anomalurus jacksoni jordani* was collected in Angola and named after the collector K. Jordan. It differs from *A. j. jacksoni* and the geographically nearest *A. j. perustus* by its larger size and some slight differences in colour.

A. pelii

pelii Schlegel and Müller, 1843-1845, *Verhandeel. over Natuurl. Geschiedn. Nederland. Bezittingen, Zool., publ. by Natuurkundige Commissie in Ostindie*, C. J. Temminck, ed., **1**: pt.2: 109

Syntypes: ♂, skin and skull, RMNH 26761; ♀, skin, RMNH 26762; skull, LIVCM 1981-270

The type specimens (for comments on the syntype series see Largen, 1985) were collected in Daboeram, Ghana and described as *Pteromys (Anomalurus) pelii*. The description is short and the specimens were not explicitly compared with *A. derbianus* or *A. fraseri*, the only other member(s) of the Anomaluridae described at that time.

auzembergeri Matschie, 1914, *Sitzb. Ges. Naturf. Freunde, Berlin*: 350

Holotype: ♂, skin and skull, ZMB 18271

This form was described as *A. auzembergeri* and named after J. Auzemberger, who collected the type specimen in the Côte d'Ivoire. It was distinguished from *A. pelii* by the complete lack of white markings on the upper side.

A. pusillus

pusillus Thomas, 1887, *Ann. Mag. Nat. Hist.* (5) **10**: 440

Holotype: ♀, skin and skull, BMNH 87.12.1.28

Anomalurus pusillus from north-western Republic of Congo was only compared to *A. beecrofti* in a description of four and a half lines. The differential diagnosis was based on the size and the colouration of the underside.

batesi de Winton, 1897, *Ann. Mag. Nat. Hist.* (6) **20**: 524

Holotype: ♂, skin and skull, BMNH 97.12.1.15

Anomalurus batesi was named for G. L. Bates, who collected it in Gabon. No differential diagnosis is given in the description.

I. macrotis

macrotis Miller, 1898, *Proc. Biol. Soc. Washington* **12**: 73

Holotype: ♂, skin and skull, USNM 83625

Idiurus macrotis from Efulen, Cameroon was described four years after *I. zenkeri* and distinguished from this species by its size and several other morphological characters.

kivuensis Lönnberg, 1917, *Kungl. Svenska Vet.-Akad. Handl., Stockholm* (2) **58**: no. 2: 67
Holotype: skin, NRM N.N.
This slightly problematic form was originally described as *Idiurus zenkeri kivuensis*, but obviously belongs to the *macrotis* form (Hayman, 1946; Verheyen, 1963; Schunke & Hutterer, subm.). It was collected in Masisi in the Democratic Republic of Congo.

langi Allen, 1922, *Bull. Amer. Mus. Nat. Hist.* **47**: 69
Holotype: ♂, skin and skull, AMNH 50542
Idiurus langi and *I. panga* were described in the same paper. The name was given to honour Herbert Lang, one of the members of the American Museum of Natural History Congo Expedition. Its differentiation from *I. macrotis* was given as "*Idiurus langi* is smaller than *I. macrotis* in external measurements, but the cranial measurements are practically the same. It differs, however, strikingly in coloration, [...] the general color being much lighter [...]".

panga Allen, 1922, *Bull. Amer. Mus. Nat. Hist.* **47**: 70
Holotype: ♀, skin and skull, AMNH 50605
Like *I. langi* the type specimen of *Idiurus panga* was collected on The American Museum of Natural History Congo Expedition. The type locality is Panga in the Democratic Republic of Congo, 120 kilometres from Medje, where *I. langi* was collected. According to the author it is "[s]imilar to *Idiurus macrotis* Miller, but much smaller and considerably paler throughout" and smaller and different in colouration from *I. panga*.

cansdalei Hayman, 1946, *Ann. Mag. Nat. Hist.* (11) **13**: 211
Holotype: ♂, skin and skull, BMNH 46.579
Described as *Idiurus kivuensis cansdalei* and named for G. S. Cansdale, who collected the type specimen in Ghana. The differential diagnosis is based on colour differences.

I. zenkeri
zenkeri Matschie, 1894, *Sitzb. Ges. Naturf. Freunde*: 197
Holotype: ♀, skin and skull, ZMB 7993
The first species described in the genus was *Idiurus zenkeri* from Yaounde, Cameroon. It was named after G. Zenker, Head of the Yaounde Station.

haymani Verheyen, 1963, *Rev. Zool. Bot. Afr.* **68**: 181
Holotype: ♀, skin and skull, BMNH 48.885
Idiurus zenkeri haymani was one of the few descriptions where the differential diagnosis was based exclusively on morphometric characters. The type specimen was collected in the Mamfe District which is nowadays part of Cameroon. It was named for R. W. Hayman to honour his work on African mammals.

Z. insignis
insignis Matschie, 1898, *Sitzb. Ges. Nat. Freunde, Berlin*: 24
Holotype: ♂, skin and skull, ZMB 10085
The first description of *Zenkerella insignis* was published some months earlier in the same year like that of *Aethurus glirinus*. The type specimen came from Yaounde, Cameroon.

glirinus de Winton, 1898a, *Proc. Zool. Soc. London*: 451
Holotype: ♂, skin and skull, BMNH 98.5.4.6
Was described as *Aëthurus glirinus* in the same year as *Z. insignis*, but the author already mentioned in a note that *Z. insignis* is the valid name, because it was published earlier. This specimen was collected in Gabon.

2.2.2. Fossil taxa
2.2.2.1. Genus group names
†*Paranomalurus* Lavocat, 1973, *Mém. Trav. Inst. Montpellier* **1**: 173
This name was assigned to the first anomalurid fossils from the Early Miocene in Kenya. The type species is †*Paranomalurus bishopi* Lavocat, 1973.

†*Nementchamys* Jaeger, Denys & Coiffat, 1985, *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York: 580
Described on the basis of a lower M1 as †*Nementchamys lavocati* Jaeger, Denys & Coiffat, 1985. The teeth assigned to the species were described by the authors as “very unlike those of any other described extant or fossil rodent”.

†*Pondaungimys* Dawson, Tsubamoto, Takai, Egi, Tun & Sein, 2003, *Annals of Carnegie Museum* **72(3)**: 205
This genus was created for a specimen from Myanmar and thus the first description of an anomalurid from outside Africa.

2.2.2.2. Species group names

bishopi Lavocat, 1973, *Mém. Trav. Inst. Montpellier* **1**: 173

The species was described as †*Paranomalurus bishopi* on the basis of a broken skull from Napak, Uganda. The specimen is large, comparable to *A. pelii* in size.

soniae Lavocat, 1973, *Mém. Trav. Inst. Montpellier* **1**: 187

Like *bishopi* described in †*Paranomalurus* as †*Paranomalurus soniae* from Songhor, Kenya. Holotype is a bone fragment with P4-M2, close to †*P. bishopi* in size.

walkeri Lavocat, 1973, *Mém. Trav. Inst. Montpellier* **1**: 191

Described as †*Paranomalurus walkeri* from Songhor, Kenya. The teeth of the holotype resemble those of †*P. bishopi*, but are smaller.

lavocati Jaeger, Denys & Coiffat, 1985, *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York: 580

This species was described as †*Nementchamys lavocati* from Eastern Algeria and assigned to the Anomaluridae. However, Landry (1999) stated that for this and another (phiomyid) species he did "not find either of these identifications convincing. It is better to leave both of them as Rodentia, incertae sedis, pending the discovery of more revealing details."

wintoni Lavocat, 1973, *Mém. Trav. Inst. Montpellier* **1**: 193

The holotype of †*Zenkerella wintoni* consists of lower jaw with teeth from Songhor, Kenya. The fossil species is smaller than *Z. insignis*.

parvus Winkler, 1992, *J. Vert. Pal.* **12**: 240

After a break of almost 20 years the fossil †*Anomalurus parvus* from Kenya was described, one M3 closely in size to the recent *A. pusillus*.

anomaluropsis Dawson, Tsubamoto, Takai, Egi, Tun & Sein, 2003, *Annals of Carnegie Museum* **72(3)**: 205

The most recently described species is the fossil †*Pondaungimys anomaluropsis* from Myanmar based on a mandibular fragment with M1-3.

2.3. History of anomalurid systematics

In his description of *Anomalurus laniger* Temminck (1853) also published the first taxonomic review of the group, eleven years after the first description (for names and their history see Chap. 2.4). He took all forms described at that time into consideration except for *A. beecrofti*, which was published the year before and would have been the most interesting for comparison. His opinion on the taxonomy of the group was:

Anomalurus pelii
Anomalurus fraseri (syn. *derbianus*, *squamicaudus*)
Anomalurus laniger.

Alston (1875), 33 years after the first description of an anomalurid, published a morphological description and taxonomic review on *Anomalurus*, the only genus at that time. He used all taxa described so far except for *squamicaudus*, a renaming of *A. derbianus*. The forms accepted by Alston were:

Anomalurus fraseri (syn. *derbianus*, *beldeni*)
Anomalurus pelii
Anomalurus beecrofti
?*Anomalurus laniger*
Anomalurus fulgens.

Nine years later the group, still with the single genus *Anomalurus*, was revised by Huet (1884). His results differed not much from the work of Alston (1875), except for *A. erythronotus* and *A. orientalis*, two forms described in the meantime, and the name *squamicaudus* (see above). He also had no doubt about *laniger* being a synonym of *beecrofti*.

Genus *Anomalurus*
A. fraseri (syn. *A. derbianus*, *A. squamicaudus*, *A. beldeni*)
A. pelii
A. beecrofti (syn. *A. laniger*)
A. fulgens
A. erythronotus
A. orientalis

Trouessart (1897) explicitly followed Huet's (1884) classification, completed by the forms described in the meantime, including the new genus *Idiurus*, which in his opinion belonged to the subfamily Anomalurinae. The last form in the list is an *A.* sp. Matschie, 1895 from Uganda, but he left unclear what specimen he meant, because Matschie had not described any anomalurid from this country and never mentioned one in his later papers.

Family Anomaluridae
Subfamily Anomalurinae
Genus *Anomalurus*
A. fraseri (syn. *derbianus, squamicaudus, beldeni*)
A. fulgens
A. erythronotus
A. chrysophaenus
A. pelii
A. orientalis
A. cinereus
A. beecrofti (syn. *laniger*)
A. pusillus
A. sp.
Genus *Idiurus*
I. zenkeri

In his description of *A. auzembergeri* Matschie (1914) also published a review of the taxonomy of the group, excluding *Idiurus* and *Zenkerella*. Matschie, who was considered to be "an outstanding splitter" (Simpson, 1945), suggested subgenus names for every taxon commonly accepted as valid species in recent literature. Although there are some good reasons to keep *Anomalurops* as genus, *Anomalurodon* and *Anomalurella* were in most later publications considered to be synonyms of *Anomalurus* (but see Allen, 1922 for an exception). His taxonomy, which did not mention synonyms or subspecies, reads as follows:
Anomalurodon auzembergeri
Anomalurodon pelii
Anomalurus derbianus
Anomalurus imperator
Anomalurus nigrensis
Anomalurus fraseri
Anomalurus erythronotus
Anomalurus beldeni
Anomalurus chrysophaenus
Anomalurus neavei
Anomalurus cinereus
Anomalurus orientalis
Anomalurus jacksoni

Anomalurops laniger
Anomalurops argenteus
Anomalurops beecrofti
Anomalurops fulgens
Anomalurella pusillus
Anomalurella batesi.

Miller and Gidley (1918) separated the group into two families, the Anomaluridae with the single genus *Anomalurus* and the Idiuridae with the subfamilies Idiurinae and Zenkerellinae, containing *Idiurus* and *Zenkerella*, respectively.
The problem of the rank of *Anomalurops* was addressed in detail by Rümmler (1933). He considered *Anomalurops* and *Anomalurus* to represent two genera, the latter containing *A. fraseri*, *A. pelii* and *A. pusillus*. Unfortunately the author just listed the other names published so far, but did not comment on their status.

When Allen published his checklist in 1939, the majority of taxa from this group was already described, only four forms were subsequently named. Allen was one of the very few authors who accepted the (sub)genera suggested by Matschie (1914), with *Anomalurella* and *Anomalurops* as genus names and *Anomalurodon* as subgenus, unfortunately without giving reasons for this decision. His classification was also the first one that mirrored the general tendency towards "lumping" by making subspecies from part of the numerous names published so far, instead of accepting the majority of taxa as species with a few synonyms.
Family Anomaluridae
Subfamily Anomalurinae
Genus *Anomalurella*
A. pusillus
subspecies *A. p. pusillus*, *A. p. batesi*
Genus *Anomalurops*
A. beecrofti (syn. *Anomalurus laniger*)
subspecies *A. b. beecrofti*, *A. b. argenteus*, *A. b. chapini*, *A. b. citrinus*
Genus *Anomalurus* (syn. *Aethurus*)
A. cinereus
A. erythronotus
A. fraseri (syn. *Pteromys squamicaudus, Anomalurus fraseri laticeps*)
subspecies *A. f. fraseri*, *A. f. beldeni*, *A. f. chrysophaenus*, *A. f. derbianus*, *A. f. griselda*, *A. f. nigrensis*

A. fulgens
A. imperator
A. jacksoni jacksoni
subspecies *A. j. jacksoni*, *A. j. fortior*, *A. j. jordani*, *A. j. perustus*
A. neavei
A. orientalis
Subgenus *Anomalurodon*
A. auzembergeri
A. pelii
Subfamily Idiurinae
Genus *Idiurus*
I. langi
I. macrotis
I. panga
I. zenkeri
subspecies *I. z. zenkeri*, *I. z. kivuensis*
Genus *Zenkerella* (syn. *Aëthurus*)
Z. insignis (syn. *Aëthurus glirinus*)

Ellerman (1940) used the superfamily "Anomaluroidae" with the single family Anomaluridae, as he did for the Pedetidae with a superfamily "Pedetoidae". His detailed taxonomy is given here:
Superfamily Anomaluroidae
Family Anomaluridae
Subfamily Anomalurinae
Genus *Anomalurus* (syn. *Anomalurodon*, *Anomalurella*)
A. fraseri (syn. *derbianus*, *squamicaudus*, *chrysophaenus*, *beldeni*)
subspecies *A. fraseri fraseri*, *A. f. laticeps*, *A. f. griselda*, *A. f. erythronotus*, *A. f. nigrensis*, *A. f. imperator*, *A. f. fortior*, *A. f. perustus*, *A. f. neavei*, *A. f. jordani*, *A. f. jacksoni*, *A. f. orientalis*, *A. f. cinereus*
A. pelii
A. pusillus
subspecies *A. p. pusillus*, *A. p. batesi*
Genus *Anomalurops*
A. beecrofti (syn. *fulgens*, *laniger*)
subspecies *A. b. beecrofti*, *A. b. chapini*, *A. b. citrinus*, *A. b. argenteus*

Subfamily Idiurinae
Genus *Idiurus*
I. zenkeri
subspecies *I. z. zenkeri, I. z. kivuensis*
I. macrotis
I. langi
I. panga
Genus *Zenkerella* (syn. *Aethurus*)
Z. insignis (syn. *glirinus*)

Simpson (1945) postulated a superfamily Anomaluroidea with the extant families Anomaluridae and Pedetidae, the Anomaluridae with the subfamilies Anomalurinae with the single genus *Anomalurus* and the Zenkerellinae with *Idiurus* and *Zenkerella*.

An extensive review of *Idiurus* was given by Hayman (1946). His revised list of named forms reads as follows:
I. zenkeri
I. macrotis
subspecies *I. m.* [*macrotis*], *I. macrotis langi*
I. kivuensis
subspecies *I. k. kivuensis, I. k. panga, I. k. cansdalei*

The next publication on the systematics of *Idiurus* was published seven years later by Verheyen (1963) and like the former combined with the description of a new form.
I. zenkeri
subspecies *I. z. zenkeri* (syn. *kivuensis*), *I. z. haymani*
I. macrotis
subspecies *I. m. macrotis* (syn. *langi*, *panga*), *I. m. cansdalei*

In his key to African mammals Misonne (1971) shrunk the group to the at present generally accepted seven species in the following classification:
Family Anomaluridae
Subfamily Idiurinae
Genus *Idiurus*
I. zenkeri
subspecies *I. z. zenkeri, I. z. haymani*

I. macrotis
subspecies *I. m. macrotis, I. m. cansdalei*
Genus *Zenkerella*
Zenkerella insignis
Subfamily Anomalurinae
Genus *Anomalurus*
A. beecrofti (syn. *argenteus, hervoi, chapini, citrinus, fulgens*)
A. pelii (syn. *auzembergeri*)
A. derbianus (syn. *beldeni, cinereus, chrysophaenus, erythronotus, fortior, fraseri, griselda, imperator, jacksoni, jordani, neavei, nigrensis, orientalis, perustus*)
A. pusillus (syn. *batesi*)

Nowak (1991) published basically the same taxonomy as Misonne (1971), but without mentioning subfamilies or subspecies. He expressed doubts about the status of the *Idiurus* forms *langi* and *panga*.

In one of the latest reviews of the group Dieterlen (1993) also followed the generally accepted taxonomy with a maximum of "lumping":
Family Anomaluridae
Subfamily Anomalurinae
Genus *Anomalurus*
A. beecrofti (syn. *argenteus, chapini, citrinus, fulgens, hervoi, laniger, schoutedeni*)
A. derbianus (syn. *beldeni, chrysophaenus, cinereus, erythronotus, fortior, fraseri, griselda, imperator, jacksoni, jordani, laticeps, neavei, nigrensis, orientalis, perustus, squamicaudus*)
A. pelii (syn. *auzembergeri*)
A. pusillus (syn. *batesi*)
Subfamily Zenkerellinae
Genus *Idiurus*
I. macrotis (syn. *cansdalei, kivuensis, langi, panga*)
I. zenkeri (syn. *haymani*)
Genus *Zenkerella*
Z. insignis (syn. *glirinus*)

Figure 2.1 shows the development of available names and accepted species, subspecies and synonyms from the first description to the present.

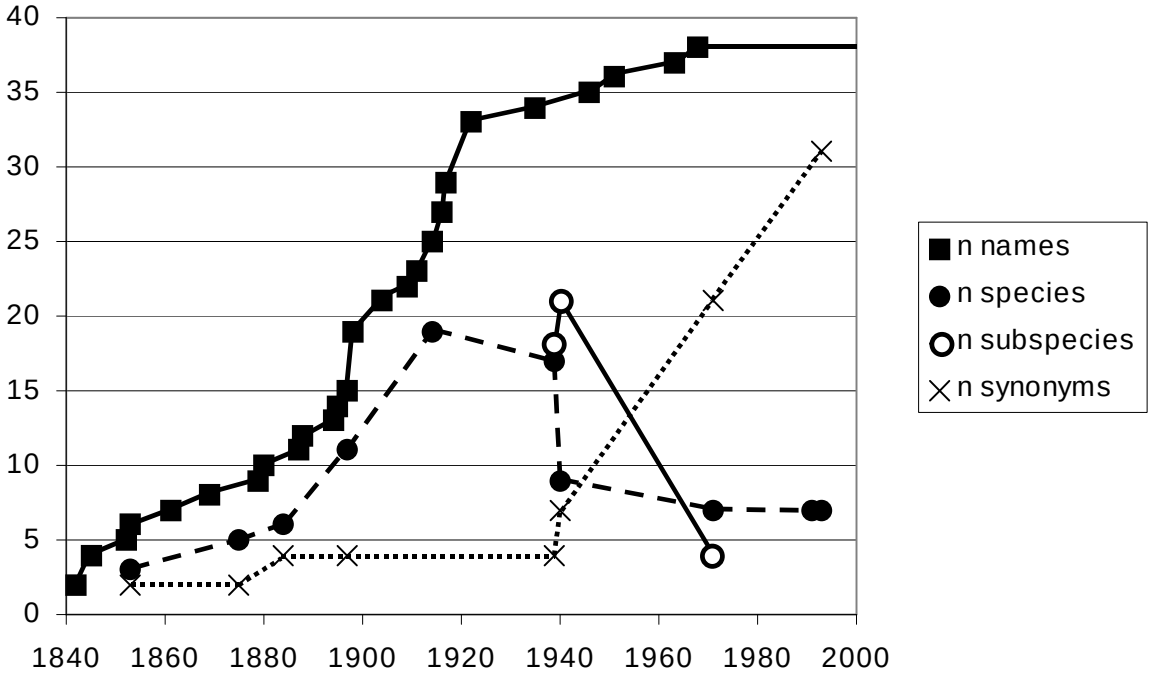


Figure 2.1. Number of available names and accepted species, subspecies and synonyms for the Anomaluridae through time. See text for details.

2.4. Systematic position of the Anomaluridae within the Rodentia

"Thus there is good authority for placing the anomalurids anywhere or nowhere with respect to the classic subdivisions of rodents." (Simpson, 1945)

The first description of *A. fraseri* by Waterhouse (1842a) contained some short comments on the position of it within the rodents. For obvious reasons the species was mainly compared to the true flying squirrels, particularly *Pteromys*, but the author also remarked that some skull characters suggest a closer relationship to the Myoxidae. In a second publication in the same year Waterhouse (1842b) placed *Anomalurus*, *Aplodontia*, *Ascomys*, and *Castor* as aberrant forms within the Sciuridae.

In the first review of the group, Temminck (1853) considered *Anomalurus* to be a subgenus of *Pteromys* and thus made a compromise between the two first descriptions by Gray (1842) and Waterhouse (1842a), with one form described as new species of *Pteromys* and the other in the new genus *Anomalurus*.

In the same year Gervais (1853) placed the "Anomalurina" within the Hystricidae, together with the Capromyna, Echimyna, Hystricina, Synetherina, Chloromyna, and Cœlogenyna. The Pedetina were a subgroup of the Dipodidae.

According to Brandt (1855) the “Anomaluri seu Pteromyoxisciuri” formed a tribe within the subfamily Rhizodontes, which again belonged to the Sciuromorpha. The other tribes within the subfamily were the Campsiuri, Pteromyes and Arctomyes. He commented the position of the group as being an intermediate state between flying squirrels and myoxids, but somehow also making an indirect link (“indirekte Verknüpfung”) with the hystricomorphs. In a subsequent publication one year later (Brandt, 1856) he offered two alternatives: in the first Anomaluri and Pteromyes formed two sections within a tribe Volitantes, which belonged to the subfamily Rhizodontes, again within the family Sciuroides. The second suggested two subfamilies, Anomalurini seu Sciuri Lemuriformes and Sciurini in the family Sciurides, the Anomalurini with the single genus *Anomalurus*.

In Fitzinger’s (1867a, b) opinion *Anomalurus* belonged to the family Myoxi, together with *Myoxus*, *Muscardinus*, *Graphiurus* and *Eliomys*.

According to Gill (1872) the Anomaluroidea with the single family Anomaluridae had the same rank as the Lophiomyoidea, Myoidea (which contained among other families the Pedetidae), Myoxoidea, Saccomyoidea, Castoroidea, Sciuroidea, and Haplodoontoidea. This idea of giving the anomalurids a high rank and thus not being urged to place them within another rodent group was frequently followed later (see below).

Alston (1875) stated on the basis of several morphological characters that “...it appears to be clear that the Anomalure is an aberrant squirrel, with no special affinities to any other family...”. In his opinion the group had to be either a subfamily Anomalurinae within the Sciuridae or a family Anomaluridae within the Sciuromorpha. One year later (Alston, 1876) he made up his mind and placed the Anomaluridae as the first family within the Sciuromorpha. The Pedetinae were considered to be a subfamily of the Dipodidae.

Huet (1884) again considered the group to be aberrant squirrels (“une forme anormale des Sciuridés”), close to *Pteromys*.

Thomas (1896) followed Gill (1872) in placing the anomalurids in an own taxon well separated from every other rodent group. In his classification the Simplicidentati can be subdivided into the Anomaluri with the single family Anomaluridae, Sciuromorpha, Aplodontiae, Myomorpha, and Hystricomorpha.

A relatively large family Anomaluridae was postulated by Trouessart (1897). In his classification the family Anomaluridae comprised the subfamily Anomalurinae with the genera *Anomalurus* and *Idiurus* as well as the extinct subfamilies †Pseudosciurinae, †Trechomyinae, and †Theridomyinae. The Anomaluridae had the same rank as the Pedetidae and for example the Sciuridae.

On the basis of rodent myology Parsons (1899) attempted to clarify the position of the Anomaluridae. But as he considered it “extremely difficult to give an idea of the relationships of

animals in a linear manner", the resulting digram (Fig. 2.2) placed the Anomaluridae between the Sciuromorpha and Myomorpha without providing very much new information. Additionally the author checked explicitly for similarities between *Anomalurus* and *Pedetes*, but was not able to support a closer relationship on the basis of the myology.

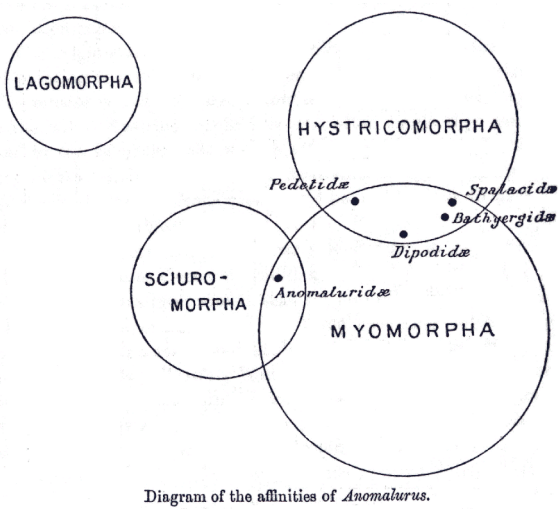


Diagram of the affinities of *Anomalurus*.

Figure 2.2. Systematic position of the Anomaluridae within rodents according to Parsons (1899).

Tullberg (1899) followed Winge (1887) in combining the Anomaluridae and Pedetidae in a section which he named Anomaluroidei, although he was not absolutely sure if they are really closely related. The Anomaluroidei are part of the tribe Sciurognathi and here of the subtribe Myomorphi, which also contains the Ctenodactyloidei and Myoidei. The author also provided the first cladogram of rodents including the anomalurids (Fig. 2.3, p. 27).

In the opinion of Miller and Gidley (1918) the Anomaluridae and Idiuridae, the latter with *Idiurus* and *Zenkerella*, are placed as separate families within the superfamily Dipodoidae. This group also contains the †Paramyidae, Graphiuridae, †Allomyidae, Aplodontidae, †Cylindrodontidae, †Pseudosciuridae, †Mylagaulidae, †Sciuravidae, Zapodidae, Dipodidae, Ctenodactylidae, and Pedetidae.

In 1924 Winge published a new classification of rodents (mainly based on his work from 1887), where the Anomaluridae have the same rank within the Rodentia as the Leporidae, Haplodontidae, Dipodidae, Myoxidae, Muridae, Hystricidae, Sciuridae, and Saccomyidae. The Anomaluridae consist of the †Pseudosciurini, †Trechomyini, Anomalurini with *Anomalurus*, *Aëthurus* and *Idiurus*, †Theridomyini, and Pedetini. The author also provided some kind of cladogram showing the Anomaluridae in a rather central position (Fig. 2.4).

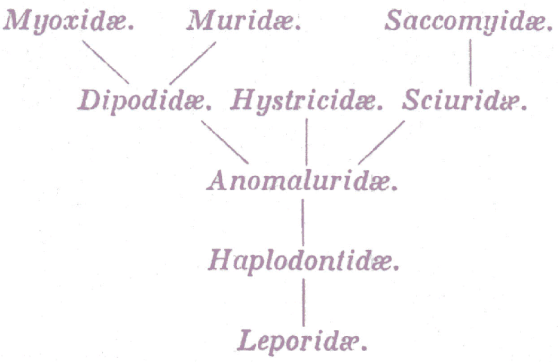


Figure 2.4. Systematic position of the Anomaluridae within the rodents according to Winge (1924).

Simpson (1945) postulated a superfamily Anomaluroidea within the Sciuromorpha *incertae sedis*. The Anomaluroidea comprised the extant families Anomaluridae and Pedetidae and as Anomaluroidea *incertae sedis* the extinct †Pseudosciuridae and †Theridomyidae. However, his

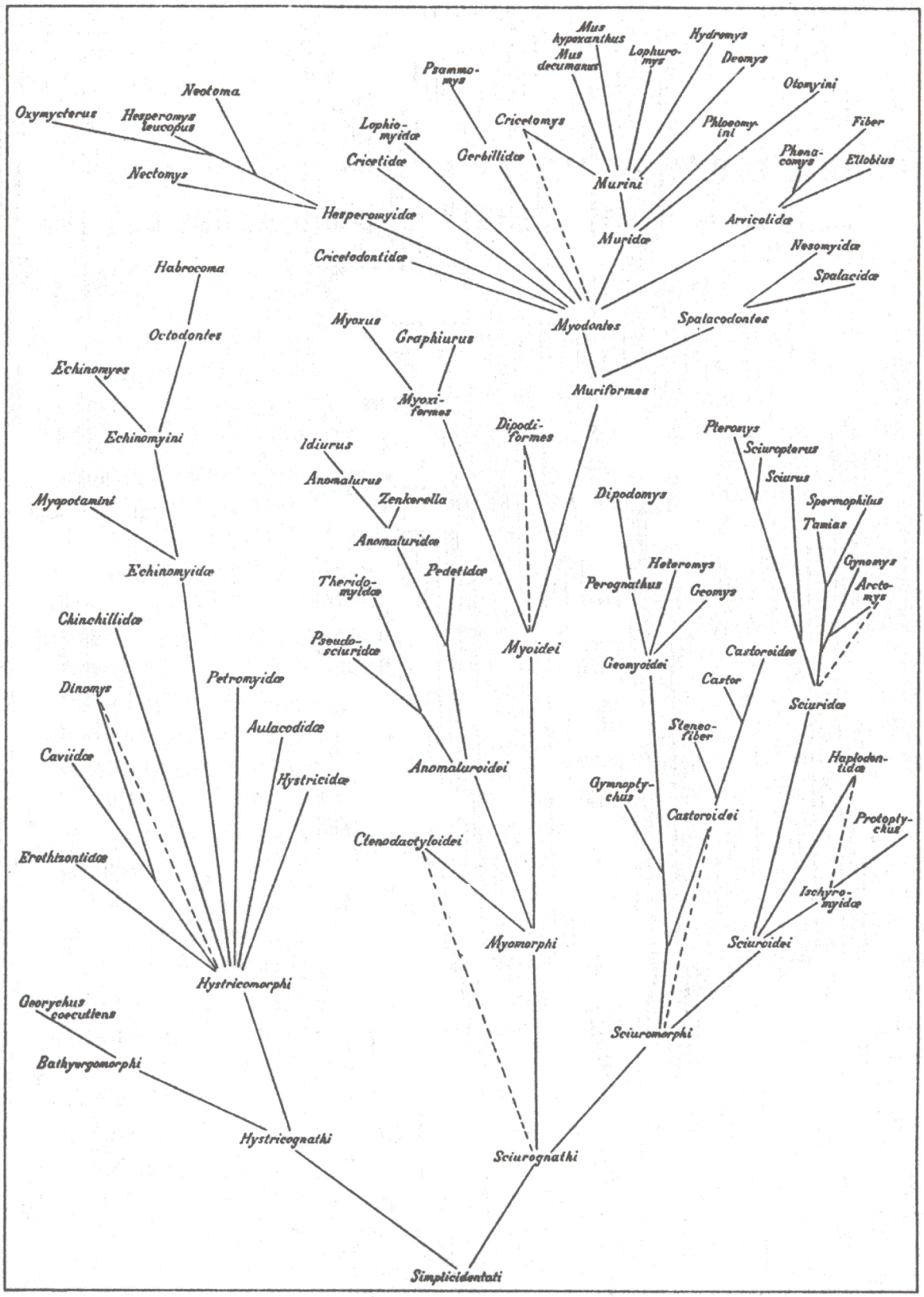


Figure 2.3. Systematic position of the Anomaluridae within the rodents according to Tullberg (1899).

own comment on this group was: “The various groups here questionably united form probably the most dubious considerable section of this dubious order.”

Stehlin and Schaub (1951) suggested as a vague possibility that †Eomyidae and Anomaluridae could be united as Eomyoidea (but see e. g. Lavocat, 1962).

This idea was followed by Grassé and Dekeyser (1955) and Viret (1955), who placed the Anomaluridae with the subfamilies Anomalurinae and Zenkerellinae in the superfamily Eomyoidea. As Grassé and Dekeyser only dealt with living forms, this superfamily comprised only the Anomaluridae; Viret also included the family †Eomyidae. The Eomyoidea had the same rank as the Sciuroidea, Aplodontoidea, Gliroidea, Geomyoidea, and Ctenodactyloidea within the suborder Non-Pentalophodonta.

Wood proposed in 1955 a revised classification of the rodents which divided the Rodentia in the suborders Sciuromorpha, Theridomyomorpha, Castorimorpha, Myomorpha, Caviomorpha, Hystricomorpha, and Bathyergomorpha. The Theridomyomorpha comprised the superfamilies Theridomyoidea and Anomaluroidea, the latter with the single family Anomaluridae and the genera *Anomalurus*, *Idiurus* and *Zenkerella*. As Sciuromorpha or Theridomyomorpha *incertae sedis* he considered the Pedetidae. In 1958 Wood published his doubts about the sense and useful size of suborders for rodent classification and made two new suggestions. One basically followed his proposal from 1955 with the additional suborders Protrogomorpha and a new one for the Ctenodactylidae. Moreover, the Theridomyomorpha were separated (but see Wood & Patterson, 1970), the †Theridomyidae and †Pseudosciuridae were combined in the suborder †Theridomorpha and the Anomaluridae and Pedetidae were united in another new suborder not named in this paper. The other suggestion (see also Wood, 1965, 1974) would only assign taxa of more or less clear affinities to suborders and leave the others not allocated to suborders. In this case there would be the suborders Protrogomorpha, Caviomorpha, and Myomorpha and besides the superfamilies or families Sciuridae, Castoroidea, Theridomyoidea, Ctenodactylidae, Anomaluridae, Pedetidae, Hystricidae, Thryonomyoidea, and Bathyergidae.

Lavocat (1956) answered to Wood’s (1955) publication, which partly used his work as basis, that although he favoured a suborder Theridomyomorpha or Theridomorpha, he did not consider the anomalurids or pedetids to be likely members of that group.

Rosevear (1969) seemed to follow Simpson (1945) in placing the superfamily Anomaluroidea with the single family Anomaluridae within the Sciuromorpha *incertae sedis*.

In 1974 Bugge suggested the name Anomaluromorpha for a new rodent suborder comprising the Anomaluridae and Pedetidae, which achieveded broad acceptance.

Chaline and Mein (1979) followed Tullberg (1899) in dividing the rodents in the sciurognaths and the hystricognaths. The sciurognaths comprised the protrogomorphs, theridomorphs, sciuromorphs, ctenodactylomorphs, and myomorphs. According to the authors the

theridomyoids and anomalurids were united in the theridomorphs, while the pedetoids were found within the ctenodactylomorphs.

A closer relationship between anomalurids and the extinct theridomyids was contradicted by Thenius (1979, 1980).

Eisenberg (1981) followed mainly Wood (1955) and Simpson (1959) with his cladogram in uniting the Anomaluridae and Pedetidae in a taxon Theridomyomorpha. The cladogram showed basically an unresolved polytomy for Sciuromorpha, Theridomyomorpha, Castorimorpha, several branches of the Myomorpha, and the Hystricomorpha.

In 1985 Bugge confirmed the results from his analysis of carotid arterial patterns in rodents, which supported a sister group relationship between Anomaluridae and Pedetidae, that these two taxa should be united in a superfamily Anomaluroidea. The results also stressed the isolated position of the two families within the rodents.

Hartenberger (1985) proposed a sister group relationship between Anomaluroidea with the Anomaluridae and possibly †Theridomyidae and Hystricognathii. In his cladogram the Pedetidae are regarded as *incertae sedis*.

On the basis of several morphological features George (1985) analysed the relationships of the ctenodactylids. The comparison covered the majority of rodent taxa and placed the Anomaluridae and Pedetidae in a dubious position between the hystricognaths on one hand and a myomorph-sciuromorph block on the other hand.

In 1986 Chami-Khazaji provided several possible cladograms for the position of the anomalurids within the rodents, with special regard to fossil forms. The analysis was based on skull characters. Lynn et al. (1986) showed a cladogram based on teeth characters where the Anomaluridae were united with Myomorpha, Gliridae, and †Theridomyidae.

Rahm (1988) followed Bugge (1974) in uniting the Anomaluridae and Pedetidae in the suborder Anomaluromorpha, thus stressing with the use of this name the equal rank of this group with the Sciuromorpha, Castorimorpha, Myomorpha, Glirimorpha, Ctenodactylomorpha, and Hystricognathi.

The new fossil family †Zegdoumyidae was described from North Africa by Vianey-Liaud et al. (1994). They were supposed to be the ancestors of the Anomaluridae and closely related to the extinct †Sciuravidae and to the Gliridae. Two years later (Vianey-Liaud & Jaeger, 1996) the Graphiurinae were excluded from the Gliridae and raised to family rank as Graphiuridae. In this publication both the Anomaluridae and Graphiuridae were considered to be descendants of the †Zegdoumyidae and thus sister taxa.

This theory on the close relationship between Anomaluridae and *Graphiurus* was tested by Bentz (1997) with molecular and morphological characters. The results strongly supported the 'classical' positions with *Graphiurus* originating within the Gliridae and *Anomalurus* and *Pedetes* being sister taxa of doubtful position within the rodents.

One of the latest classifications based on morphological characters by Landry (1999) suggested several new names. Unfortunately the publication lacks a comprehensive summary of the classification, but it seems to be as follows: the rodents are basically divided into three groups, the Entodacrya with the Ctenodactyla and Hystricognathii, the Pedetomorpha which might be closer related to the former, and the Sciurognathii. The latter are divided into the Stegaulata (Sciuridae, Anomaluridae, Aplodontidae, Castoridae, Paramyidae and Ischyromyidae) and the Phaneraulata (Myomorpha, Theridomyidae and Geomyidae).
Recent analyses of molecular data gave further support for the monophyly of the Anomaluridae and Pedetidae (Montgelard et al., 2001, 2002; Huchon et al., 2002), but also demonstrated once more the still unclear position of the taxon within the Rodentia.

References

Adam, F., Bellier, L. & Robbins, L. W. 1970. Deux nouvelles captures d'*Idiurus macrotis* Miller (Rodentia, Anomaluridae) en Côte d'Ivoire. *Mammalia* **34**: 716-718.

Adams, W. H. 1894. On the Habits of the Flying-Squirrels of the Genus *Anomalurus*. *Proc. Zool. Soc. Lond.*: 243-246.

Aellen, V. & Perret, J. 1958. Sur une nouvelle trouvaille de *Zenkerella insignis* Matschie, 1898 (Rodentia, Anomaluridae). *Säugetierkundliche Mitteilungen* **6**: 21-23.

Aellen, V., Heim de Balsac, H. & Vuattoux, R. 1970. A propos des Anomaluridae de Côte-d'Ivoire. *Mammalia* **34**: 159-160.

d'Aguilar-Amat, J. Bta. 1922. Una nova forma de *Anomalurus* de Fernando Póo. *Butlletí de la Institució Catalana d'Historia Natural* **2**: 52-53.

Allen, G. M. 1939. A checklist of African Mammals. *Bull. Mus. Comp. Zool. Harvard Coll.* **83**: 1-763.

Allen, G. M. & Lawrence, B. 1937. Reports on the Scientific Results of an Expedition to the Rain Forest Regions in Eastern Africa. III: Mammals. With field notes by Arthur Loveridge. *Bull. Mus. Comp. Zool. Harvard* **79**: 31-126, 5 pls.

Allen, G. M. & Loveridge, A. 1933. Reports on the Scientific Results of an Expedition to the Southwestern Highlands of Tanganyika Territory. *Bull. Mus. Comp. Zool.* **75**: 47-140.

Allen, J. A. 1922. Sciuridae, Anomaluridae and Idiuridae collected by the American Museum Congo Expedition. *Bull. Am. Mus. Nat. Hist.* **47**: 39-71.

Alp, R. & Kitchener, A. C. 1993. Carnivory in wild chimpanzees, *Pan troglodytes verus*, in Sierra Leone. *Mammalia* **57**: 273-274.

Alston, E. R. 1875. On *Anomalurus*, its Structure and Position. *Proc. Zool. Soc. Lond.*: 88-97.

Alston, E. R. 1876. On the Classification of the Order Glires. *Proc. Zool. Soc. Lond.*: 61-98.

Ansell, W. F. H. 1960. *Mammals of Northern Rhodesia. A revised check list with keys, notes on distribution, range maps, and summaries of breeding and ecological data.* The Government Printer, Lusaka.

Ansell, W. F. H. 1963. Additional breeding data on Northern Rhodesian Mammals. *The Puku, The Occasional Papers of the Department of Game and Fisheries, Northern Rhodesia* **1**: 9-28.

Ansell, W. F. H. 1965. Addenda and Corrigenda to "Mammals of Northern Rhodesia" No. 2. *The Puku, The Occasional Papers of the Department of Game and Fisheries, Northern Rhodesia* **3**: 1-14.

Ansell, W. F. H. 1978. *The Mammals of Zambia.* The National Parks & Wildlife Service, Chilanga, Zambia.

Ansell, W. F. H. & Dowsett, R. J. 1988. *Mammals of Malawi. An annotated check list and atlas.* The Tendrine Press, Zennor, St. Ives, Cornwall.

Asdell, S. A. 1964. *Patterns of Mammalian reproduction. Second edition.* Comstock Publishing Associates, Ithaca, N.Y.

Bates, G. L. 1905. Notes on the Mammals of Southern Cameroons and the Benito. *Proc. Zool. Soc. Lond*: 65-85.

Bentz, S. 1997. *Graphiurus, un genre particulier au sein des Gliridae (Mammalia, Rodentia): Données moleculaires et morphologiques.* Unpublished thesis, Université Montpellier II, Sciences et Techniques du Languedoc, Paleontologie.

Bere, R. M. 1962. *The wild mammals of Uganda and neighbouring regions of East Africa.* East African Natural History Series, Longmans, Green & Co Ltd., London.

Blainville, H. M. D. de 1839-1864. *Ostéographie ou description iconographique comparée du squelette et du système dentaire des Mammifères recents et fossiles pour servir de base à la zoologie et à la géologie. Atlas.* Tome Quatrième. J. B. Baillière et Fils, Paris.

Blaszkiewitz, B. 1992. Einiges zur Haltung und Zucht Hörnchenartiger (Sciuromorpha) im Zoologischen Garten. *Bongo* **20**: 33-38.

Booth, A. H. 1954. The Dahomey Gap and the Mammalian Fauna of the West African forests. *Rev. Zool. Bot. Afr.* **50**: 305-314.

Booth, A. H. 1958. The Niger, the Volta and the Dahomey Gap as geographic barriers. *Evolution* **12**: 48-62.

Booth, A. H. 1960. *Small mammals of West Africa.* West African Nature Handbooks, H. J. Savory (ed.), Longmans, London.

Branca, A. & Cretin, A. 1925. Sur un placenta d'*Anomalurus perei*. *C. R. Assoc. Anat.* **20**: 139.

Brandt 1855. *Mém. de l'Ac. St. Pétersb.* **6**: 298, 299.

Brandt, J. F. 1856. Quelques remarques sur la place que doit occuper le genre *Anomalurus* dans l'ordre des Rongeurs. *Compt. Rend. Ac. Scien.* **43xliii.**: 139-143.

Bugge, J. 1974. The Cephalic Arterial System in Insectivores, Primates, Rodents and Lagomorphs, with Special Reference to the Systematic Classification. *Acta Anatomica* **87**, Suppl. **62**: 1-159.

Bugge, J. 1985. Systematic value of the carotid arterial pattern in rodents, pp. 355-379. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Cabral, J. C. 1971. Existencia em Angola de *Anomalurops beecrofti* (Fraser). *Boletim do Instituto de Investigacao Cientifica de Angola* **8**: 55-63.

Cabrera, A. 1923. Las formas locales de *Anomalurus fraseri*. *Boletín de la Real Sociedad Espa ola de Historia Natural* **23**: 68-69.

Cei, G. 1946. Prime notizie e considerazioni sull'occhio di *Idiurus zenkeri* (Anomaluridae-Rodentia) e su i suoi organi accessori. *Mem. Soc. Tosc. Sci. nat.* **53**: 90-96.

Chaillu, P. B. du 1861a. *Explorations & Adventures in Equatorial Africa; with accounts of the manners and customs of the people, and of the chace of the Gorilla, crocodile, leopard, elephant, hippopotamus, and other animals.* John Murray, London.

Chaillu, P. B. du 1861b. Descriptions of five new species of mammals discovered in western equatorial Africa. *Proc. Boston Soc. Nat. Hist.* **7**: 296-367.

Chaline, J. & Mein, P. 1979. *Les Rongeurs et l'Évolution.* Doin, Paris.

Chalmers, G. 1963. Jackson's scaly-tail (*Anomalurus jacksoni*) in captivity. *International Zoo Yearbook* **4**: 123-124.

Chami-Khazaji, S. 1986. *Relations phylogénétique des Anomaluridae (Mammalia, Rodentia): Apport de l'ostéologie crânienne.* Thesis, Université Pierre et Marie Curie, Paris. 159 pp.

Coe, M. 1975. Mammalian ecological studies on Mount Nimba, Liberia. *Mammalia* **39 (4)**: 523-587.

Crandall, L. S. 1964. *Management of Wild Mammals in Captivity.* Chicago.

Dawson, M. R., Tsubamoto, T., Takai, M., Egi, N., Tun, S. T. & Sein, C. 2003. *Annals of Carnegie Museum* **72(3)**: 203-213.

Dekeyser, P. L. 1954. A propos des écureuils volants. *Notes africaines* **64**: 121-124.

Dekeyser, P. L. & Villiers, A. 1947. Description d'un "*Anomalurops*" de la région de Bignona. *International West African Conference: Compte rendu, (S.l.)* **2, 3**: 57-62.

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

Didier, R. 1952. Etude systématique de l'os pénien des Mammifères. *Mammalia* **16**: 7-23.

Dieterlen, F. 1993. Family Anomaluridae. *In* D. E. Wilson & D.A. M. Reeder (eds.), *Mammal Species of the World. A taxonomic and geographic reference.* 2nd edition, Smithsonian Institution Press, Washington, London.

Dollman, G. 1909. On Mammals collected by Mr. S. A. Naeve, M. A., B. Sc. (Oxon.), in Katanga, Congo Free State. *Ann. Mag. Nat. Hist.* **8, 3**: 348-354.

Dollman, G. 1911. New West-African Rodents. *Ann. Mag. Nat. Hist.* **8, 8**: 257-259.

Dollman, G. 1914. On a new *Anomalurus* from the Cameroons. *Ann. Mag. Nat. Hist.* **8, 14**: 490.

Dollman, G. 1932. Seasonal changes in colour of *Anomalurus jacksoni*. *Proc. Linn. Soc. London*: 68-72.

Dorst, J. & Dandelot, P. 1970. *A field guide to the larger mammals of Africa.* Collins, London.

Dubois, A. 1888. Description d'un rongeur nouveau du genre *Anomalurus*. *Bull. Soc. Zool. France* **8**: 23-24.

Durrell, G. 1952. Pigmy scaly-tail studied in captivity. *Zoo Life* **7**: 12-15.

Durrell, G. 1954. *The Bafut Beagles.* Ballantine Books, New York.

Eisenberg, J. F. 1981. *The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation, and Behaviour.* The University of Chicago Press. Chicago.

Eisentraut, M. 1963. *Die Wirbeltiere des Kamerungebirges unter besonderer Berücksichtigung des Faunenwechsels in den verschiedenen Höhenstufen.* Verlag Paul Parey, Hamburg und Berlin.

Eisentraut, M. 1968. Beitrag zur Säugetierfauna von Kamerun. *Bonn. Zool. Beitr.* **19**.

Eisentraut, M. 1973. Die Wirbeltierfauna von Fernando Poo und Westkamerun unter besonderer Berücksichtigung der Bedeutung der pleistozänen Klimaschwankungen für die heutige Faunenverteilung. *Bonner zool. Monogr.* **3**: 428 pp.

Ellerman, J. R. 1940. *The families and genera of living rodents. Volume I: Rodents other than Muridae.* British Museum (Natural History).

Ellerman, J. R., Morrison-Scott, T. C. S. & Hayman, R. W. 1953. *Southern African Mammals 1758 to 1951: A Reclassification.* British Museum (Natural History), London.

Emmons, L. H., Gautier-Hion, A. & Dubost, G. 1983. Community structure of the frugivorous-folivorous forest mammals of Gabon. *J. Zool., Lond.* **199**: 209-222.

Fain, A. 1953. Notes sur une collection de Rongeurs, Insectivores et Chauves-souris, capturés dans la région d'endémie pesteuse de Blukwa (Ituri, Congo Belge). *Rev. Zool. Bot. Afr.* **48**: 89-101.

Fairgrieve, C. 1996. Meat Eating by Blue Monkeys (*Cercopithecus mitis stuhlmanni*): Predation of a Flying Squirrel (*Anomalurus derbianus jacksonii*). *Folia Primatol.* **68**: 354-356.

Feiler, A. 1990. Distribution of mammals in Angola and notes on biogeography. *In* Peters, G, & Hutterer, R. (Eds), *Vertebrates in the tropics.* Museum Alexander Koenig, Bonn: 221-236.

Fitzinger, L. J. 1867a. Versuch einer natürlichen Anordnung der Nagethiere (Rodentia). *Sitzungsber. math.-naturwiss. Classe kaiserl. Akad. Wiss., Wien* **55**: 453-515.

Fitzinger, L. J. 1867b. Versuch einer natürlichen Anordnung der Nagethiere (Rodentia). *Sitzungsber. math.-naturwiss. Classe kaiserl. Akad. Wiss., Wien* **56**: 57-168.

Flynn, L. J., Jacobs, L. L. & Cheema, I. U. 1986. Baluchimyinae, A New Ctenodactyloid Rodent Subfamlily from the Miocene of Baluchistan. *American Museum Novitates* **2841**: 1-58.

Frade, F. 1949. Algumas novidades para a fauna da Guiné Portuguesa (aves e mammiferos). *Anai, Junta dos Missões Geográficas e de Investigaçoes Colonais* **4(4)**: 165-186.

Frahnert, S. 1998. *Zur Stellung des Bibers (Castoridae: Castor) im System der Nagetiere (Rodentia). Eine craniogenetische Studie zur Ethmoidalregion sciurognather Rodentia.* Wissenschaft und Technik Verlag. Berlin.

Fraser, L. 1852. Description of a new species of *Anomalurus*, from Fernando Po. *Proc. Zool. Soc. Lond.*: 16-17.

Frechkop, S. 1936. Notes sur les Mammifères. XIX. Le hamster montrant la différence fondamentale entre les molaires des Rongeurs et celles des Ongulés. *Bull. Mus. roy. Hist. nat. Belge* **12 (18)**: 1-8.

Friant, M. 1945. La dentition jugale de l'*Anomalurus*, Ecureuil volant d'Afrique. *Rev. Zool. Bot. Afr.* **38**: 206-211.

Friant, M. 1970. La Dentition Jugale de L'*Anomalurus* et de Ses Allies, Rongeurs Arboricoles d'Afrique. *Folia morph., Prague* **18**: 71-77.

George, W. 1985. Reproductive and chromosomal characters of ctenodactylids as a key to their evolutionary relationships, pp. 453-474. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Gervais, P. 1853. Description ostéologique de l'*Anomalurus* et remarques sur la classification naturelle des rongeurs. *Annales de Sciences Naturelles, Zoologie, Paris (3e sér.)* **20**: 238-246.

Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collections, Washington* **230**: 1-98.

Good, A. I. 1947. Les Rongeurs du Cameroun. *Bulletin de la Societé d'Etudes Camerounaises* **17-18**: 5-20.

Grassé, P. P. & Dekeyser, P. L. 1955. Ordre des Rongeurs, pp. 1321-1525. *In* Traité de Zoologie. Anatomie, Systematique, Biologie, P. P. Grassé (Ed.), 17, 2, Paris.

Gray, J. E. 1842. Descriptions of some new Genera and fifty unrecorded Species of Mammalia. *Ann. Mag. Nat. Hist.* **10**: 255-267.

Gray, J. E. 1869. *Anomalurus fulgens*, a new Species from the Gaboon. *Ann. Mag. Nat. Hist.* **(4) 3**: 467.

Grubb, P. 1983. The biogeographic significance of forest mammals in Eastern Africa. *Ann. Mus. Roy. Afr. Centr., Sc. Zool.* **237**: 75-85.

Gyldenstolpe, N. 1928. Zoological Results of the Swedish Expedition to Central Africa 1921. Vertebrata 5. Mammals from the Birunga Volcanoes, North of Lake Kivu. *Arkiv för Zoologi* **20 A (4)**: 1-76.

Happold, D. C. D. 1987. *The mammals of Nigeria.* Clarendon Press, Oxford.

Hartenberger, J. L. 1985. The order Rodentia: Major questions on their evolutionary origin, relationships and suprafamilial systematics, pp. 1-33. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Hayman, R. W. 1946. Systematic Notes on the Genus *Idiurus* (Anomaluridae). *Ann. Mag. Nat. Hist.* **2, 8**: 208-212.

Hayman, R. W. 1951. Notes on some Angolan Mammals. *Publ. Cult. Comp. Diamantes Angola* **11**: 31-35.

Huchon, D., Madsen, O., Sibbald, M. J. J. B., Ament, K., Stanhope, M. J., Catzeflis, F., de Jong, W. W. & Douzery, E. J. P. 2002. Rodent Phylogeny and a Timescale for the Evolution of Glires: Evidence from an Extensive Taxon Sampling Using Three Nuclear Genes. *Mol. Biol. Evol.* **19(7)**: 1053-1065.

Huet, M. 1884. Observations sur le Genre *Anomalurus* et sur les espèces de la Collection du Muséum d'Histoire Naturelle. *Nouvelles Archives du Muséum d'Histoire Naturelle* **6(2)**: 277-290, pls 19-25.

Hugot, J. P. 1982. *Zenkoxyuris quentini* (Nematoda): un nouvel oxyure d'Anomalure. *Bulletin du Museum Nationale d'Histoire Naturelle, Paris, 4e sér., section A (Zool. Biol. Ecol. anim.)* **4 (1-2)**: 49-59.

Hugot, J. P. 1985. Sur le genre *Acanthoxyurus* (Oxyuridae, Nematoda). Etude morphologique. *Bulletin du Museum Nationale d'Histoire Naturelle, Paris, 4e sér., section A (Zool. Biol. Ecol. anim.)* **7 (1)**: 157-179.

Jackson, S. M. 1999. Glide angle in the genus *Petaurus* and a review of gliding in mammals. *Mammal Rev.* **30(1)**: 9-30.

Jaeger, J.-J., Denys, C. & Coiffait, B. 1985. New Phiomorpha and Anomaluridae from the Late Eocene of north-west Africa: phylogenetic implications, pp. 567-588. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Johnson-Murray, J. L. 1987. The Comparative Myology of the Gliding Membranes of *Acrobates, Petauroides* and *Petaurus* Contrasted with the Cutaneous Myology of *Hemibelideus* and *Pseudocheirus* (Marsupialia: Phalangeridae) and with Selected Gliding Rodentia (Sciuridae and Anomaluridae). *Austr. J. Zool.* **35 (2)**: 101-113.

Jones, C. 1971. Notes on the anomalurids of Rio Muni and adjacent areas. *J. Mammal.* **52**: 568-572.

Julliot, C., Cajani, S. & Gautier-Hion, A. 1998. Anomalures (Rodentia, Anomaluridae) in Central Gabon: species composition, population desities and ecology. *Mammalia* **62 (1)**: 9-21.

Killick-Kendrick, R. 1973. Parasitic protozoa of the blood of rodents. 3. Two new malaria parasites of anomalurine flying squirrels of the Ivory coast. *Annales Parasit. hum. comp.* **48 (5)**: 639-651.

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

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals.* Natural World Academic Press, Harcourt Brace & Company, San Diego, London, Boston, New York, Sidney, Tokyo, Toronto.

Koenigswald, W. v. 2004. Enamel Microstructure of Rodent Molars, Classification, and Parallelisms, with a Note on the Systematic Affiliation of the Enigmatic Eocene Rodent *Protoptychus*. *Journal of Mammalian Evolution* **11(2)**: 127-142.

Korvenkontio, V. A. 1934. Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne. Histologisch-phyletische Studie. *Annales Zoologici Societatis Zoologicae-Botanicae Fennicae Vanamo* **2**: 1-274.

Krumbiegel, I. 1942. Zur Kenntnis der Säugetierfauna von Fernando Poo. 8. Beitrag zu den wissenschaftlichen Ergebnissen der Forschungsreise H. Eidmann nach Spanisch-Guinea 1939/40. *Archiv für Naturgeschichte* **11**: 305-349.

Kuhn, H.-J. 1965. A provisional check-list of the mammals of Liberia. *Senck. biol.* **46 (5)**: 321-340.

Kuhn, H.-J. 1966. *Anomalurus pelii auzembergeri* in Liberia. *J. Mamm.* **47**: 334-338.

Landry Jr., S. O. 1999. A Proposal for a New Classification and Nomenclature for the Glires (Lagomorpha and Rodentia). *Mitt. Mus. Nat.kd. Berl., Zool. Reihe* **75 (2)**: 283-316.

Largen, M. J. 1985. Taxonomically and historically significant specimens of mammals in the Merseyside County Museums, Liverpool. *J. Mamm.* **66(2)**: 412-418.

Lavocat, R. 1956. Réflexions sur la classification des rongeurs. *Mammalia* **20**: 49-56.

Lavocat, R. 1962. Réflexions sur l'origine et la structure du groupe des rongeurs. *Problèmes Actuels de Paléontologie evolution des Vertebres, Colloques Internationaux, Centre National de la Recherche Scientifique* **104**: 287-299.

Lavocat, R. 1973. Les Rongeurs du Miocene d'Afrique Orientale. 1. Miocene inferieur. *Mémoires et Travaux de l'Institut de Montpellier* **1**: 1-284.

Lavocat, R. & Parent, J.-P. 1985. Phylogenetic analysis of the middle ear features in fossil and living rodents, pp. 333-354. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Lönnberg, E. 1917. Mammals collected in Central Africa by Captain E. Arrhenius. *Kungl. Svenska Vetenskapsakademiens Handligar* **58, 2**: 1-110.

Luckett, W. P. 1971. The Development of the Chorio-allantoic Placenta of the African Scaly-tailed squirrels (Family Anomaluridae). *Am. J. Anat.* **130**: 159-177.

Luckett, W. P. 1985. Superordinal and intraordinal affinities of rodents: Developmental evidence from the dentition and placentation, pp. 227-276. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Luckett, W. P. & Hartenberger, J.-L. 1985. Evolutionary relationships among rodents: Comments and conclusions, pp. 685-712. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Luckett, W. P., Schrenk, F. & Maier, W. 1989. On the occurrence of abnormal deciduous incisors during prenatal life in African "hystricomorphous" rodents. *Zeitschr. Säugetierk.* **54**.

MacKay, A. & van Someren, G. R. C. 1980. Some observations on anomalures near Chemisia, north Nandi, Kenya. *EANHS Bull. (May-June)*: 42-43.

Margry, C. J. P. J. Not dated. *The Anomalurinae of West Africa, Mammalia, Rodentia.* Thesis, University of Amsterdam: 59 pp.

Malbrandt, R. & Maclatchy, A. 1949. Faune de l'Équateur Africain Francais. tome 2. Mammifères. *Encyclopédie biologique* **36**. Lechevalier, Paris.

Matschie, P. 1894. Neue Säugethiere aus den Sammlungen der Herren Zenker, Neumann, Stuhlmann und Emin. *Sitzungsberichte der Gesellschaft naturforschender Freunde, Berlin*: 194-206.

Matschie, P. 1898. Eine neue mit *Idiurus* Mtsch. verwandte Gattung der Nagethiere. *Sitzungsberichte der Gesellschaft Naturforschender Freunde Berlin*: 23-30.

Matschie, P. 1914. Ein neuer *Anomalurus* von der Elfenbeinküste. *Sitzungsberichte der Gesellschaft Naturforschender Freunde Berlin*: 349-351.

McLaughlin, C. A. 1984. Protogomorph, Sciuromorph, Castorimorph, Myomorph (Geomyid, Anomalurid, Pedetoid, and Ctenodactyloid) Rodents, pp. 267-288. *In* S. Anderson and J. K. Jones Jr. (Eds), *Orders and families of recent mammals of the world.* John Wiley & Sons, New York.

Miller, G. S. 1898. Description of a new Rodent of the genus *Idiurus*. *Proc. Biol. Soc. Washington* **12**: 73-76.

Miller, G. S. & Gidley, J. W. 1918. Synopsis of the supergeneric groups of Rodents. *J. Washington Acad. Sc.* **8**: 431-448.

Milne-Edwards, A. 1879. Note sur une nouvelle espèce du genre *Anomalurus*. *Comptes rendus de l'Académie des Sciences naturelles de Paris* **89**: 771-772.

Misonne, X. 1963. *Les Rongeurs du Ruwenzori et des régions voisines.* Institut des Parcs Nationaux du Congo et du Rwanda, Exploration du Parc National Albert, 2e série, fascicule 14, Bruxelles.

Misonne, X. 1971. Rodentia, pp. 1-39. *In* J. Meester & H. W. Setzer (Eds), *The Mammals of Africa. An identification Manual.* Smithsonian Institution Press, City of Washington.

Montgelard, C., Bentz, S., Douady, C., Lauquin, J. & Catzeflis, F. M. 2001. Molecular phylogeny of the sciurognath rodent families Gliridae, Anomaluridae and Pedetidae, pp. 293-307. *In* Denys, C., Granjon, L. & Poulet, A. (Eds), *Proceedings of the 8th International Symposium on African Small Mammals, Paris, July 1999.*

Montgelard, C., Bentz, S., Tirard, C., Verneau, O. & Catzeflis, F. M. 2002. Molecular Systematics of Sciurognathi (Rodentia): The Mitochondrial Cytochrome b and 12S rRNA Genes Support the Anomaluroidea (Pedetidae and Anomaluridae). *Mol. Phyl. Evol.* **22(2)**: 220-233.

Morales Agacino, E. 1943. Mamiferos de las posesiones espanolas del Golfo de Guinea colectados en la Expedicion de 1933. *Boletín de la Real Sociedad Espanola de Historia Natural* **61**: 511-522.

Nowak, R. M. 1991. *Walker's Mammals of the World. Fifth Edition.* The John Hopkins University Press, Baltimore and London.

Pakenham, R. H. W. 1984. *The mammals of Zanzibar and Pemba Islands.* R. H. W. Pakenham, C. B. E., 9 Kirkwick Avenue, Harpenden, Herts. Al5 2QU. England.

Parsons, F. G. 1899. Position of *Anomalurus* as indicated by its Myology. *J. Linn. Soc. London* **27**: 317-334.

Pérez del Val, J., Juste, J. & Castroviejo, J. 1995. A review of *Zenkerella insignis* Matschie, 1898 (Rodentia, Anomaluridae). First records in Bioko island (Equatorial Guinea). *Mammalia* **59 (2)**: 441-443.

Perret, J.-L. & Aellen, V. 1956. Mammifères du Cameroun de la collection J. l. Perret. *Revue Suisse de Zoologie* **63 (26)**: 395-450.

Peters, W. 1880. Über eine neue Art der Nagergattung *Anomalurus* von Zanzibar. *Monatsberichte der königlich preussischen Akademie der Wissenschaften zu Berlin*: 164-166.

Quentin, J.-C. 1974. Sur les Oxyures d'Anomalures. *Bull. Mus. Natl. Hist. Nat., Paris, 3e sér., no. 256, Zoologie* **178**: 1507-1523.

Rahm, U. 1959. Présence de deux espèces d'*Anomalurus* dans la région du Kahuzi (Kivu, Congo Belge). *Folia scientifica Africae centralis, I.R.S.A.C., Bukavu* **5**: 18-19.

Rahm, U. 1960. L'*Anomalurus jacksoni* de Winton: Répartition, biologie et observations en captivité. *Bull. Societé Royale de Zoologie d'Anvers* **18**: 3-13.

Rahm, U. 1961. Esquisses mammalogiques de basse Côte d'Ivoire. *Bulletin de l'Institut Francais d'Afrique Noire* **23**, sér. A, no. 4: 1229-1265.

Rahm, U. 1966. Les mammifères de la forêt équatoriale de l'Est du Congo. *Annales de Musée Royal Afrique Centrale, Tervuren, sér in-8* **149**: 39-121.

Rahm, U. 1969. Dokumente über *Anomalurus* und *Idiurus* des östlichen Kongo. *Zeitschr. Säugetierk.* **34**: 75-84.

Rahm, U. 1988. Dornschwanzhörnchenverwandte, pp. 116-125. *In Grzimeks Enzyklopädie Säugetiere,* Kindler Verlag, München, Band 3.

Rahm, U. & Christiaensen, A. 1963. Les mammifères de la région occidentale du lac Kivu. *Annales de Musée Royal Afrique Centrale, Tervuren, sér in-8* **118**: 1-83.

Rahm, U. & Christiaensen, A. 1966. Les mammifères de l'île Idjwi (Lac Kivu, Congo). *Annales de Musée Royal Afrique Centrale, Tervuren, sér in-8* **149**: 1-35.

Redlichs, A. 1937. Zur Embryologie der Schwanzschuppen des afrikanischen Dornschwanzhörnchens *Anomalurus* (*erythronotus*?). *Acta societatis biologiae lativae* **7**: 177-199.

Robbins, C. B. 1978. The Dahomey Gap - a reevaluation of ist significance as a faunal barrier to West African high forest mammals. *Bull. Carnegie Mus. Nat. Hist.* **6**: 168-174.

Robbins, C. B. & Van der Straeten, E. 1996. Small mammals of Togo and Benin. II. Rodentia. *Mammalia* **60 (2)**: 231-242.

Roche, J. 1972. Capture de *Zenkerella insignis* (Rongeurs, Anomaluridés) en République Centrafricaine. *Mammalia* **36**: 305-306.

Rosevear, D. R. 1950. Rodents of Nigeria. Part II Squirrels. *The Nigerian Field* **15**: 4-18.

Rosevear, D. R. 1953. *Checklist and Atlas of Nigerian Mammals with a foreword on Vegetation.* F. Howard Doulton & Co., London.

Rosevear, D. R. 1969. *The rodents of West Africa.* British Museum (Natural History), London.

Rümmler, H. 1933. Über die systematische Einteilung der afrikanischen Dornschwanzhörnchen (Anomaluridae). *Sitzungsberichte der Gesellschaft Naturforschender Freunde Berlin*: 389-391.

Sanderson, I. T. 1940. The mammals of the north Cameroons forest area. *Trans. Zool. Soc. London* **24**: 623-725.

Scheibe, J. S. & Essner, R. L., Jr. 2000. Pelvic Shape in Gliding Rodents: Implications for the Launch, pp. 167-184. *In* Goldingay, R. L. & Scheibe, J. S. (Eds), *The Biology of Gliding Mammals.* Filander Press. Fürth.

Schinz, H. 1845. *Systematisches Verzeichniß aller bis jetzt bekannten Säugethiere oder Synopsis Mammalium nach dem Cuvier'schen System. Band 2.* Verlag von Jent und Gaßmann, Solothurn.

Schlegel, H. & Müller, S. 1843-5. Bijdragen tot de natuurlijke geschiedenis der Vliegende eekhorens (Pteromys) door Herm. Schlegel en Sal. Müller. *In* C. J. Temminck (Ed.), *Verhandeelingen over de natuurlijke geschiedenis der Nederlandsche Bezittinge*.

Schlitter, D. A. 1989. African Rodents of Special Concern: A Preliminary Assessment. *In* William Z. Lidicker (Ed.), *Rodents. A World Survey of Species of Conservation Concern*, Occasional Papers of the IUCN Species Survival Commission (SSC) **4**: 33-39.

Schouteden, H. 1947. *De Zoogdieren van Belgisch Congo en van Ruanda-Urundi.* Annalen van het Museum van Belgisch Congo, C, Dierkunde, Reeks 2, Deel 3, Aflevering 1-3, Tervuren.

Schunke, A. C. & Hutterer, R. Subm. Analysis of the geographical populations of *Idiurus* (Anomaluridae; Rodentia; Mammalia) with morphometric skull characters.

Schunke, A. C. & Hutterer, R. 2000. Patchy versus continuous distribution patterns in the African rain forest: the problem of the Anomaluridae (Mammalia: Rodentia). *In* Rheinwald, G. (Ed.), *Isolated Vertebrate Communities in the Tropics. Proc. 4th Int. Symp., Bonn. Bonn. zool. Monogr.* **46**: 145-152.

Schwann, H. 1904. On new Forms of *Anomalurus* and *Sciurus* from Tropical Africa. *Ann. Mag. Nat. Hist.* **7, 8**: 70-73.

Seabra, A. F. de 1909. Note sur un foetus d'*Anomalurus fraserie*. *Lisbonne Bull. Soc. Port. Sci. Nat.* **3**: 79-83.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**: 1-350.

Sjöstedt, Y. 1897a. Die Säugethiere des nordwestlichen Kamerungebietes. *Mitt. a. d. deutschen Schutzgebieten* **10**: 25-50.

Sjöstedt, Y. 1897b. Säugetiere aus Kamerun, Westafrika. *Bihang Till K. Sv. Vet.-Akad. Handl.* **23 (1)**: 1-50.

St. Leger, J. 1931. A Key to the Families and Genera of African Rodentia. *Proc. Zool. Soc. London*: 957-997.

St. Leger, J. 1935. Two new subspecies of mammals from Angola. *Novitates Zoologicae* **39**: 251-252.

Stafford, B. J. 1999. Taxonomy and ecological morphology of the Flying Lemurs (Dermoptera, Cynocephalidae). *UMI Dissertation Services. Ann Arbor, Michigan*.

Stehlin, H. G. & Schaub, S. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweizerische Palaeontologische Abhandlungen* **67**: 1-385.

Storch, G., Engesser, B. & Wuttke, M. 1996. Oldest fossil record of gliding in rodents. *Nature* **379**: 439-441.

Temminck, C. J. 1853. *Esquisses Zoologiques sur la Côte de Guiné. 1e Partie, les Mammiféres.* Esquisses de Zoologie, Leiden.

Thenius, E. 1979. *Die Evolution der Säugetiere. Eine Übersicht über Ergebnisse und Probleme.* Gustav Fischer Verlag. Stuttgart.

Thenius, E. 1980. *Grundzüge der Faunen- und Verbreitungsgeschichte der Säugetiere. Eine historische Tiergeographie.* Gustav Fischer Verlag. Stuttgart.

Thenius, E. 1989. Zähne und Gebiss der Säugetiere. *Handbuch der Zoologie*, **7**(56), Walter de Gruyter, Berlin, New York.

Thomas, O. 1887. Diagnoses of two new Central-African Mammalia. *Ann. Mag. Nat. Hist.* **10 (5)**: 440.

Thomas, O. 1895. Diagnoses of Two new East-African Mammals. *Ann. Mag. Nat. Hist.* **6, 15**: 187-188.

Thomas, O. 1896. On the Genera of Rodents: an Attempt to bring up to Date the current Arrangement of the Order. *Proc. Zool. Soc. London*: 1012-1028.

Thomas, O. 1904a. Abstract of the Proceedings of the Zoological Society of London **10**: 12.

Thomas, O. 1904b. On Mammals from the Island of Fernando Po, collected by Mr. E. Seimund. *Proc. Zool. Soc. London*: 183-184.

Thomas, O. 1916. On Small Mammals obtained in Sankuru, South Congo, by Mr. H. Wilson. *Ann. Mag. Nat. Hist.* **8, 18**: 234-239.

Till, W. M. 1982. Two new parasitic mites from mammals in Central Africa (Acarina: Mesostigmata: Laelapidae and Macronyssidae). *Revue Zool. afr.* **96 (3)**: 522-528.

Trouessart, E.-L. 1897. *Catalogus Mammalium tam viventium quam fossilium. Fasciculus I.* Berolini, R. Friedländer & Sohn.

Tullberg, T. 1899. *Über das System der Nagethiere. Eine phylogenetische Studie.* Akademische Buchdruckerei, Uppsala.

Verheyen, R. 1951. *Contribution à l'étude éthologique des mammifères du Parc National de l'Upemba.* Institut des Parcs Nationaux du Congo Belge, Bruxelles.

Verheyen, W. N. 1963. Contribution à la systématique du genre *Idiurus* (Rodentia-Anomaluridae). *Rev. Zool. Bot. Afr.* **68**: 157-197.

Verheyen, W. N. 1968a. Description d'une nouvelle sous-espèce *d'Anomalurops beecrofti* de la région congolaise (Mamm.). *Rev. Zool. Bot. Afr.* **77**: 157-161.

Verheyen, W. N. 1968b. The Anomalurinae of the Congo (Rodentia: Anomaluridae). *Revue de Zoologie et de Botanique Africaines* **77**: 392-411.

Vianey-Liaud, M. & Jaeger, J.-J. 1996. A new hypothesis for the origin of african Anomaluridae and Graphiuridae (Rodentia). *Palaeovertebrata* **25 (2-4)**: 349-358.

Vianey-Liaud, M., Jaeger, J.-J., Hartenberger, J.-L. & Mahboubi, M. 1994. Les rongeurs de l'eocene d'Afrique nordoccidentale [Glib Zegdou (Algerie) et Chambi (Tunesie)] et l'origine des Anomaluridae. *Palaeovertebrata* **23**: 93-118.

Viret, J. 1955. La denture des rongeurs actuels et fossiles, pp. 1526-1573. *In* P. P.Grassé (Ed.), *Traité de Zoologie. Anatomie, Sytematique, Biologie,* **17**, 2, Paris.

Walker, E. P. 1968. *Mammals of the World.* 2nd ed. Volume 2.

Waterhouse, G. R. 1842a. Observations on the Rodentia. *Ann. Mag. Nat. Hist.* **10**: 197-203.

Waterhouse, G. R. 1842b. *Proc. Zool. Soc. London*: 124-127.

Wettstein-Westersheim, O. 1925. Wissenschaftliche Ergebnisse der Expedition R. Grauer nach Zentralafrika, Dezember 1909 bis Februar 1911. Bearbeitung der Nagetierausbeute. *Annalen des Naturhistorischen Museums in Wien* **36**: 15-24.

Winge, H. 1887. *Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Gnavernes indbyrdes Slægtskab*. Kopenhagen. (Zit. in Tullberg, 1899)

Winge, H. 1924. *Pattedyr-Slaegter. 2. Rodentia, Carnivora, Primates.* H. Hagerups Forlag, Kjobenhavn.

Winkler, A. J. 1992. Systematics and biogeography of Middle Miocene Rodents from the Muruyur Beds, Baringo District, Kenya. *J. Vertebrate Palaeont.* **12 (2)**: 236-249.

Winton, W. E. de 1897. Descriptions of Two new Mammals from West Africa. *Ann. Mag. Nat. Hist.* **6, 20**: 524.

Winton, W. E. de 1898a. On a new Genus and Species of Rodents of the Family Anomaluridae, from West Africa. *Proc. Zool. Soc. Lond.*: 450-454.

Winton, W. E. de 1898b. Descriptions of Three new Rodents from Africa. *Ann. Mag. Nat. Hist.* **7, 1**: 251-254.

Wood, A. E. 1955. A revised classification of the rodents. *J. Mammal.* **36**: 165-187.

Wood, A. E. 1958. Are There Rodent Suborders? *Syst. Zool.* **7**: 169-173.

Wood, A. E. 1962. The juvenile tooth patterns of certain african rodents. *J. Mammal.* **43 (3)**: 310-322.

Wood, A. E. 1965. Grades and clades among rodents. *Evolution* **19**: 115-130.

Wood, A. E. 1974. The evolution of the Old World and New World hystricomorphs. *Symp. zool. Soc. Lond.* **34**: 21-60.

Wood, A. E. 1985. The relationships, origin and dispersal of the hystricognathus rodents, pp. 475-513. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Wood, A. E. & Patterson, B. 1970. Relationships among hystricognathous and hystricomorphous rodents. *Mammalia* **34**: 628-639.

3. Data basis

The present study is based on material from 22 collections (Tab. 3.1). Altogether data from 1581 specimens were collected (Tab. 3.1, 3.2), which represents the major amount of material from anomalurids world wide.

Table 3.1. Number of specimens investigated from the different collections.

AC (Galeries de Paléontologie et d'Anatomie comparée, Paris)	2
AMNH (American Museum of Natural History, New York)	245
BMNH (The Natural History Museum, London)	279
FMNH (Field Museum of Natural History, Chicago)	40
LIVCM (Merseyside County Museum, Liverpool)	2
MNCN (Museum Nacional de Ciencias Naturales, Madrid)	7
MNHN (Museum National d'Histoire Naturelle, Paris)	105
MRAC (Museum Royale d'Afrique Centrale, Tervuren)	323
NHMB (Naturhistorisches Museum Basel)	35
NMK (National Museum of Kenya, Nairobi)	9
NMW (Naturhistorisches Museum Wien)	31
NRM (Naturhistoriska Riksmuseet, Stockholm)	25
RMNH (Naturalis/Nationaal Natuurhistorisch Museum, Leiden)	19
RSM (Royal Scottish Museum, Edinburgh)	1
SMF (Naturmuseum Senckenberg, Frankfurt)	14
SMNK (Staatliches Museum für Naturkunde, Karlsruhe)	4
SMNS (Staatliches Museum für Naturkunde, Stuttgart)	10
USNM (United States National Museum, Washington)	92
ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn)	33
ZMA (Zoölogisch Museum Amsterdam)	137
ZMB (Museum für Naturkunde, Berlin)	167
ZTNHC (Zadock Thomas Natural History Collections, Burlington)	1

In addition to the data collected directly from the investigated material locality data from literature were used for biogeographical analyses, if they were not redundant.

Table 3.2. Material and number of specimens for the different species.

	investigated	**skulls**	**skins**	**tissue**	**additional data from literature**
A. beecrofti	304	215	252	14	25
A. derbianus	738	575	648	18	76
A. pelii	179	146	163	12	6
A. pusillus	152	127	113	6	5
I. macrotis	116	71	60	8	14
I. zenkeri	84	51	48	8	11
Z. insignis	8	3	7	2	4
total	**1581**	**1188**	**1291**	**68**	**141**

All complete skulls as well as skulls of type specimens or of special interest otherwise were photographed on black-and-white film in dorsal and ventral view. Additionally colour slides from all skins together with a colour reference were taken. The complete information given on the labels was also documented, especially for biogeographical data. Information on the sex was either obtained from the skins, or copied from labels, along with body measurements. When skulls were available relative age was estimated from tooth wear. Measurements of skulls were taken with a digital caliper to the nearest 0.01 mm.

Tissue samples for the molecular analysis were usually taken either from muscles of alcohol preserved specimens or from the uropatagium of dried skins.

As far as possible the exact geographical coordinates for the finding localities were recorded. The data came either directly from the specimen label or were searched with computer programs (Microsoft Encarta Weltatlas 2000), online gazetteers (http://www.fallingrain.com/world/, http://testbed.alexandria.ucsb.edu/gazclient/index.jsp), Times Atlas (1956, 1975), and several publications (Sanderson, 1940; Eisentraut, 1963, 1973; Davis & Misonne, 1964; Ansell, 1965, 1978, 1989; Kuhn, 1965; Rahm, 1966; Verheyen, 1968; Aellen et al., 1970; Jones, 1971; Delany, 1975; Happold, 1987; Ansell & Dowsett, 1988; Pérez del Val et al., 1995; Robbins & van der Straeten, 1996; Grubb et al., 1998; Juillot et al., 1998).

For 1427 specimens (90%) it was possible to get precise coordinates (see Appendix 2) which comprises of 497 localities with exact coordinates and 61 localities where the locality could be reconstructed within a very small range. For 69 finding localities is was not possible to get coordinates because of names which occurred several times in the country or could not be found at all.

References

Aellen, V., Heim de Balsac, H. & Vuattoux, R. 1970. A propos des Anomaluridae de Côte-d'Ivoire. *Mammalia* **34**: 159-160.

Ansell, W. F. H. 1965. Addenda and Corrigenda to "Mammals of Northern Rodesia" No. 2. *The Puku, The Occasional Papers of the Department of Game and Fisheries, Northern Rodesia* **3**: 1-14.

Ansell, W. F. H. 1978. *The Mammals of Zambia.* The National Parks & Wildlife Service, Chilanga, Zambia.

Ansell, W. F. H. 1989. *African Mammals 1938-1988.* The Tendrine Press. Zennor, St. Ives, Cornwall.

Ansell, W. F. H. & Dowsett, R. J. 1988. *Mammals of Malawi. An annotated check list and atlas.* The Tendrine Press, Zennor, St. Ives, Cornwall.

Davis, D. H. S. & Misonne, X. 1964. Gazetteer of collecting localities of African rodents. *Museum Royal de l'Afrique Centrale, Tervuren, Belgium, Documentation Zoologique* **7**: 1-100.

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

Eisentraut, M. 1963. *Die Wirbeltiere des Kamerungebirges unter besonderer Berücksichtigung des Faunenwechsels in den verschiedenen Höhenstufen.* Verlag Paul Parey, Hamburg und Berlin.

Eisentraut, M. 1973. Die Wirbeltierfauna von Fernando Poo und Westkamerun unter besonderer Berücksichtigung der Bedeutung der pleistozänen Klimaschwankungen für die heutige Faunenverteilung. *Bonner zool. Monogr.* **3**: 428 pp.

Grubb, P., Jones, T. S., Davies, A. G., Edberg, E., Starin, E. D. & Hill, J. E. 1998. *Mammals of Ghana, Sierra Leone and the Gambia.* The Tendrine Press, Zennor, St. Ives, Cornwall.

Happold, D. C. D. 1987. *The mammals of Nigeria.* Clarendon Press, Oxford.

Jones, C. 1971. Notes on the anomalurids of Rio Muni and adjacent areas. *J. Mammal.* **52**: 568-572.

Julliot, C., Cajani, S. & Gautier-Hion, A. 1998. Anomalures (Rodentia, Anomaluridae) in Central Gabon: species composition, population desities and ecology. *Mammalia* **62 (1)**: 9-21.

Kuhn, H.-J. 1965. A provisional check-list of the mammals of Liberia. *Senck. biol.* **46 (5)**: 321-340.

Pérez del Val, J., Juste, J. & Castroviejo, J. 1995. A review of *Zenkerella insignis* Matschie, 1898 (Rodentia, Anomaluridae). First records in Bioko island (Equatorial Guinea). *Mammalia* **59 (2)**: 441-443.

Rahm, U. 1966. Les mammifères de la forêt équatoriale de l'Est du Congo. *Annales de Musée Royal Afrique Centrale, Tervuren,* sér in-8 **149**: 39-121.

Robbins, C. B. & Van der Straeten, E. 1996. Small mammals of Togo and Benin. II. Rodentia. *Mammalia* **60 (2)**:231-242.

Sanderson, Ivan T. 1940. The mammals of the north Cameroons forest area. *Trans. Zool. Soc. London* **24**: 623-725.

Verheyen, W. N. 1968. The Anomalurinae of the Congo (Rodentia: Anomaluridae). *Revue de Zoologie et de Botanique Africaines* **77**: 392-411.

4. The variance of variation: Geographic patterns of coat colouration in *Anomalurops* and *Anomalurus*

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 colourations. 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.

4.1. Introduction

The history of the African rain forest has attracted the interest of numerous researchers for a long time (e. g. Lönnberg, 1929; Bræstrup, 1935; Grubb, 1978, 1990; Hamilton & Taylor, 1991; Fjeldså & Lovett, 1997). Besides more or less direct methods like the analysis of fossil pollen records (e. g. Livingstone, 1966; Maley, 1983, 1991; Brenac, 1988; Fredoux & Tastet, 1988) 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 contain 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 (Pl. I-VII). *Anomalurus pusillus* Thomas, 1887 (Pl. IV), *Idiurus macrotis* Miller, 1898 (Pl. V), *I. zenkeri* Matschie, 1894 (Pl. VI), and *Zenkerella insignis* Matschie, 1898 (Pl. VII) show a more or less uniform colouration throughout their area of distribution. *Anomalurops beecrofti* (Fraser, 1853) varies in the amount of golden brown colour on the back and reddish colour on the ventral side (Pl. I). 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 (Pl. II). *Anomalurus pelii* (Schlegel & Müller, 1845) shows only black and white in a specific pattern, but the relative portions of these colours vary (Pl. III).

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.

4.2. Material and methods

4.2.1. 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, Wien), Naturhistoriska Riksmuseet (NRM, Stockholm), Naturalis/Nationaal Natuurhistorisch Museum (RMNH, Leiden), Naturmuseum Senckenberg (SMF, Frankfurt), National Museum of Natural History (USNM, Washington), Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK, Bonn), Zoölogisch Museum Amsterdam (ZMA, Amsterdam), 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. 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 (see Chap. 7 for details). Additionally slides taken of 128 specimens of *A. pusillus* were compared but not used in the analysis, because it was not possible to define any differences in colouration. The data basis for the analyses is given in Table 1.

4.2.2. 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 analysis (n), the statistic (χ^2), the degrees of freedom (d.f.) and the *P* value 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 and the minimum expected

Table 1. Characters and respective numbers of specimens analysed in this study. *A. pusillus* was not treated 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

frequency (MEF) if it is less than 1. The same test was performed to check for statistically significant differences between geographically neighbouring populations.

4.3. Colouration coding and results

4.3.1. *Anomalurops beecrofti*

The most abundant colouration of *A. beecrofti* is a silverish 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).

Colouration codes and frequencies

Dorsal colouration (DC):

1. back completely silverish grey without golden brown parts (4%, n=9)
2. back silverish grey, golden brown central stripe not wider than head (43%, n=98)
3. central stripe wider than head, but at least patagia silverish grey (28%, n=63)
4. back completely golden brown, central part can be slightly darker than patagia (23%, n=52)
5. 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 the 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 5 specimens. Thus results from this group have to be treated with caution.

For the other colouration classes the correlation between dorsal and ventral colouration can best be 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.

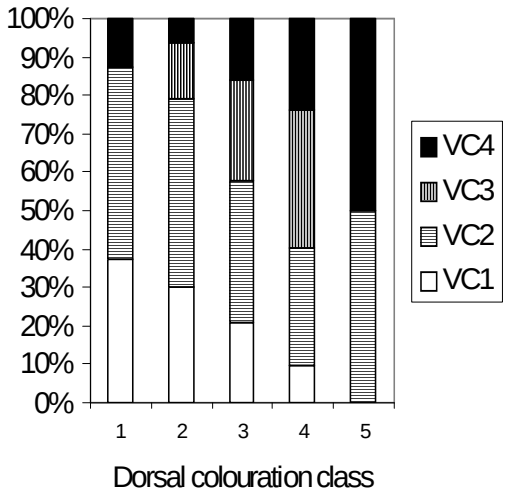


Figure 4.1. Correlation between dorsal colouration classes (DC 1-5) and associated ventral colouration (VC 1-4) in *A. beecrofti*.

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

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 the ventral colouration the age classes were combined like 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.

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 silverish 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.

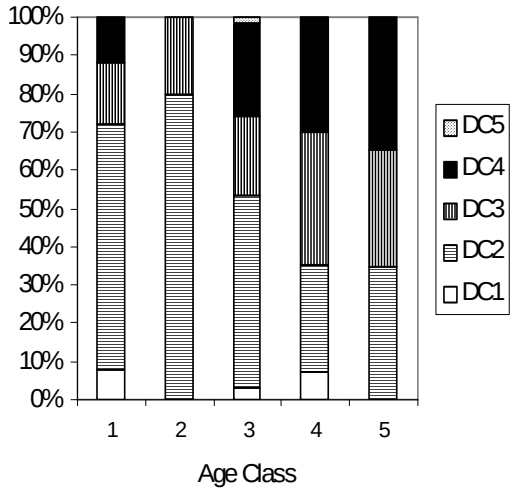


Figure 4.2. Correlation between age class and dorsal colouration (DC) in *A. beecrofti*.

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, no relationship between dorsal colouration and month of collection could be shown (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 summarizing diagrams of colouration class frequencies in respective areas are shown in Figure 3 (border lines between these areas are shown in Figure 6). Uniformly silverish grey (DC 1) individuals were found W of the Congo River only, from Sierra Leone to Congo Brazzaville. A single specimen (AMNH 86845) labelled as from Democratic Republic of Congo was caught very close to the Congo River and may as well have been collected on the western bank. The silverish 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 secondmost frequent colouration (DC 3, silver 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

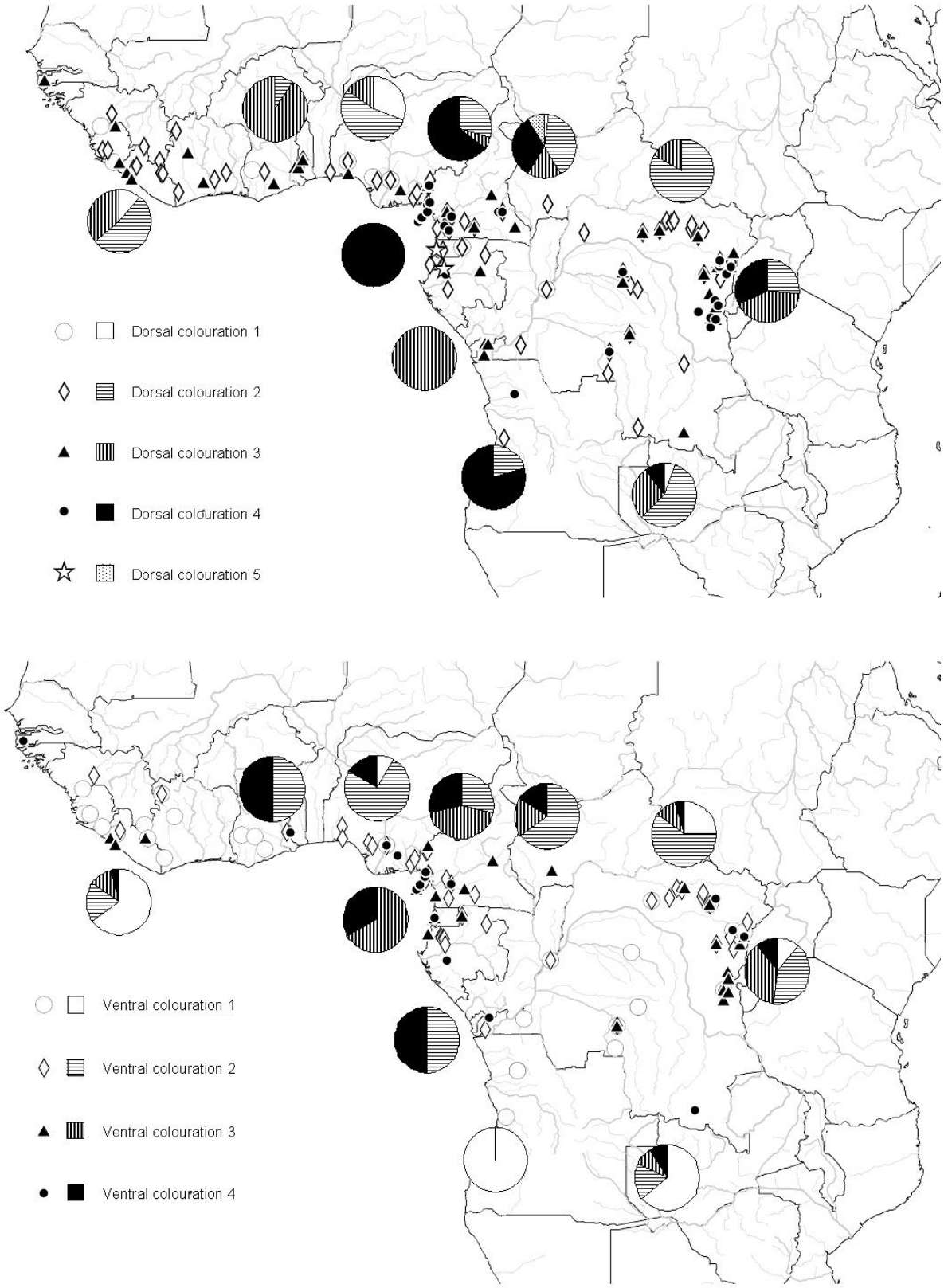


Figure 4.3. Geographical distribution of coat colouration in *A. beecrofti*.

golden brown individuals (DC 4), which comprise 23% of the investigated specimens, is completely different. They are not found W of Cameroon but occur frequently there and on Bioko, mainland Equatorial Guinea, and Gabon. Further east, isolated records are from Angola and Democratic Republic of Congo, particularly from the Kivu area. Specimens from Ukaika and Moera in the Kivu region shown in Plate Ij 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 N 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 W 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 they occur more frequently 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 W, 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 NW/SE direction, 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 clearcut barriers where significant differences are found in the DC and VC frequencies. The westernmost border runs along the Volta River 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 clearcut. Along the Sanaga Rivers 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 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).

4.3.2. *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 silverish stripe on the nose. The ventral colouration is much less variable.

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. silverish 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 silverish (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 silverish individuals (DC 4) has light shoulders.

Ear and shoulder colouration

Ear and shoulder colouration are also significantly correlated (n = 444, χ^2 68.593, d.f. 1, $P < 0.001$). 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 silverish 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

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. However, the results were not significant in any step of the analysis (last analysis: n = 104, χ^2 8.771, d.f. 6, *P* = n.s.).

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 Rivers as well as in all previous steps of the analysis.

Colouration and collection area

Localities and summarizing 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 southern 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 W 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 southern Cameroon to the lower Congo and Ubangi Rivers. The very rare uniformly silverish 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 clearcut, but differences in relative frequencies are found. Individuals with dark ears occur frequently from Cameroon to Democratic

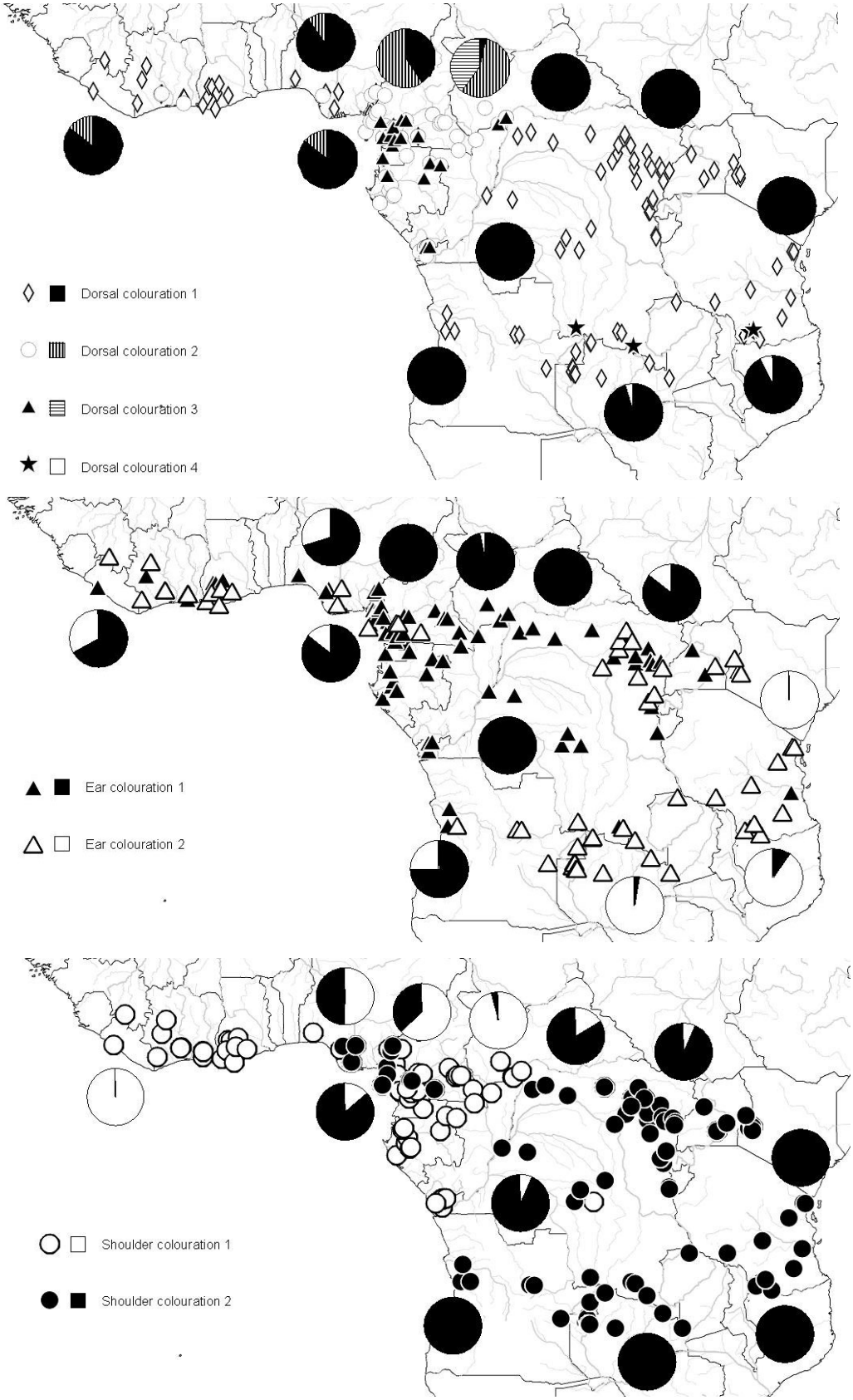


Figure 4.4. Geographical distribution of coat colouration in *A. derbianus*.

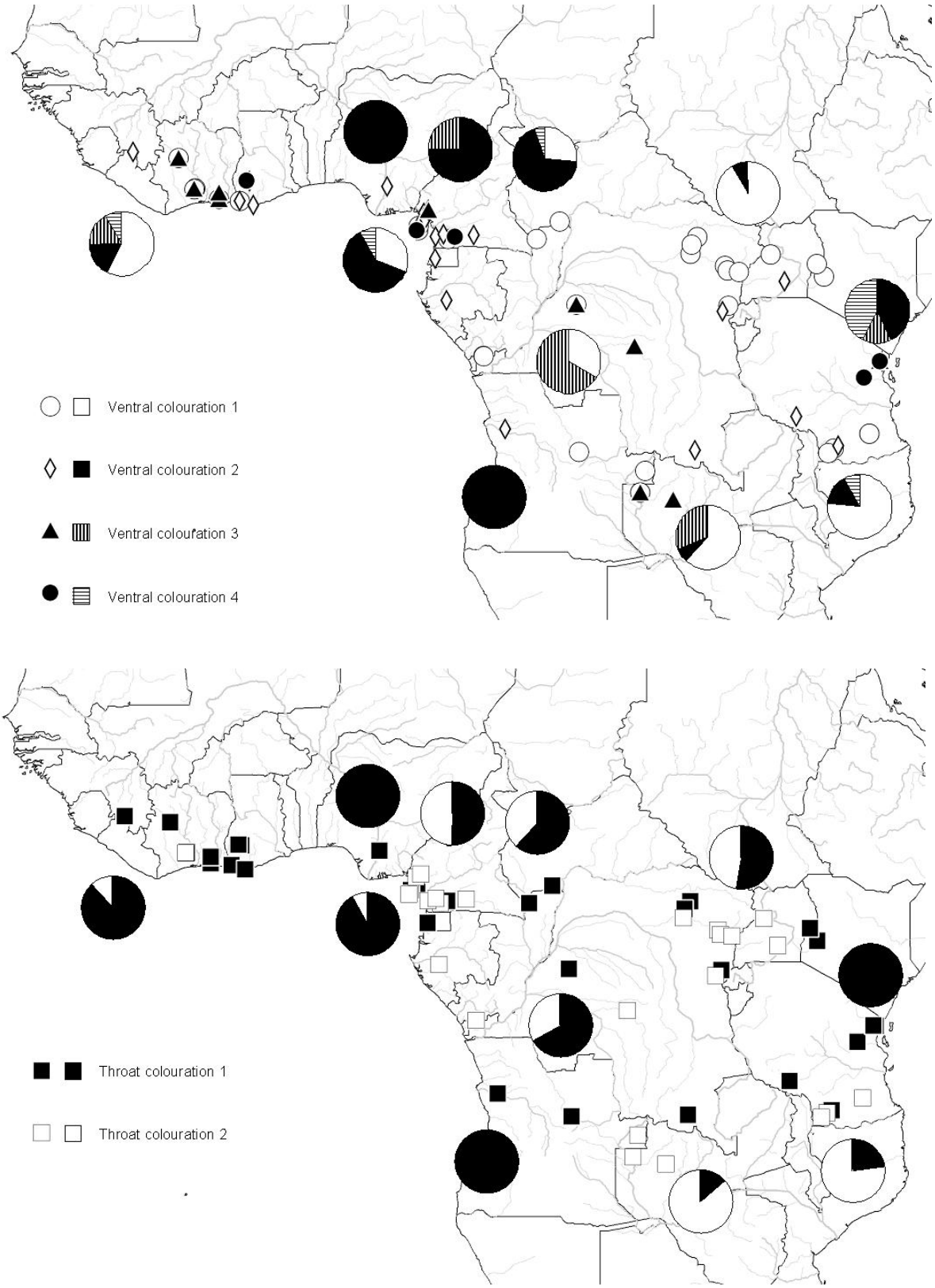


Figure 4.4. (continued) Geographical distribution of coat colouration in *A. derbianus*.

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, southern 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 Democratic Republic of Congo. Both colouration forms occur together in West Africa from Liberia to Nigeria, in the NE Democratic Republic of Congo, and in Uganda. Individuals with light shoulders occur frequently from Liberia to Rivers Congo and Ubangi, and a few in Bioko, Democratic Republic of Congo and Uganda. SE of 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 W 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 mixed of yellow and grey are found in Ivory Coast, Cameroon, S of 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 NE 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 W of the Dahomey Gap, in Bioko, Angola and NE Tanzania, and open markings predominating in Zambia and S Tanzania. From Cameroon to 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 E and open markings in the SW.

Also in *A. derbianus* clearcut borderlines between neighbouring populations exist. 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 line for dorsal and shoulder but not for ear colouration. 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. The last 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 paralleled by the occurrence of silverish 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.

4.3. 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).

Colouration codes and frequencies

Dorsal colouration (DC):

1. completely black (14%, 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* could be 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 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

35 males (56%) and 27 females (44%) with known sex were available. No significant correlation could be shown between dorsal or ventral colouration and sex.

Colouration and age

117 animals were grouped into age class 1 (5%, n=6), 2 (19%, n=22), 3 (41%, n=48), and 4 (35%, n=41). No significant association between colouration and age could be shown.

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. W 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.

4.3.4. Combined analysis of geographic boundaries

Based on the results shown in Figures 3-5, an attempt was made to identify borders in the distribution patterns of the characters analyzed. Seventeen barrier 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 strong 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 seems to play also 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, so statements concerning this region have to be treated with caution. The Dahomey Gap (Fig. 6, line 4) is a significant barrier for

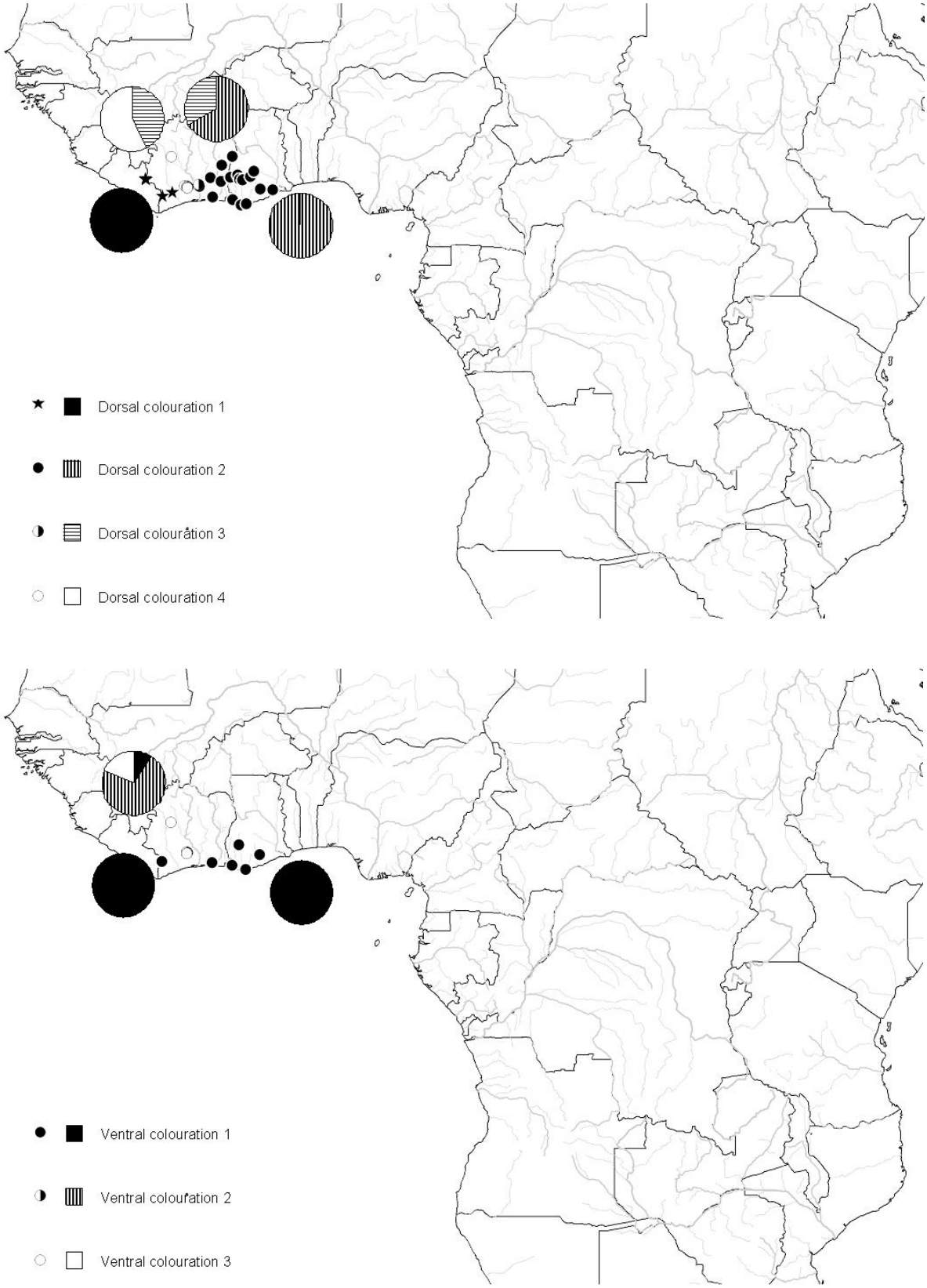


Figure 4.5. Geographical distribution of coat colouration in *A. pelii*.

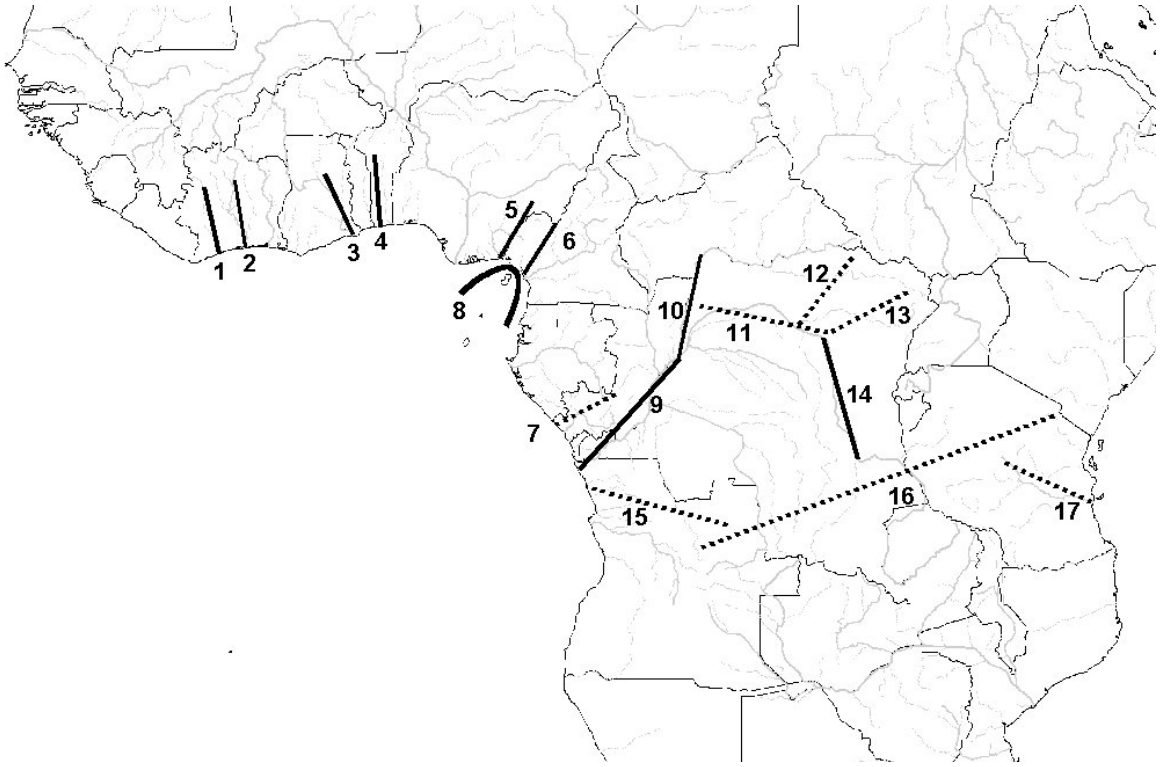


Fig. 4.6. Border lines of higher (bold lines) and lower (dotted lines) importance for colouration changes in *A. beecrofti*, *A. derbianus* and *A. pelii* (see text for details).

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 shows uniformly 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 W Africa (Liberia to Nigeria), but frequencies differ significantly in the region between Cameroon and Congo. The frequency of the ear colouration on Bioko is intermediate to the frequencies in Nigeria and the Cameroon to Congo area. Light shoulders as typical for W Africa occur on Bioko in a frequency intermediate to that of W Africa and C and E Africa.

The border effect of the lower Congo (Fig. 6, line 9) and Ubangi (Fig. 6, line 10) Rivers is also difficult to define. They form clear boundaries for dorsal and shoulder colouration in *A. derbianus*, but not for ear colouration. In *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 NW and SE 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 NW and SE (Fig. 6, line 12). However, this boundary lies further west than in *A. beecrofti*. The northern 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 NW population of *A. beecrofti*, while SE specimens are significantly different from those S 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 western Angola. Light epaulettes are missing in all specimens from Angola, S Democratic Republic of Congo, Zambia and Tanzania. In the same area (except Angola) occur the rare uniformly silverish specimens, 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).

4.4. Discussion

Our study has revealed a remarkable mosaic of differences and similarities between the respective species. *Anomalurus pusillus*, a species studied but not shown in detail here, shows a homogenous 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 species. 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 clearcut lines, a pattern not found in any other species.

Despite of the 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 SW 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 Ivory Coast, often in the vicinity of the Sassandra River (Booth, 1958; Dandelot, 1965; Lernould, 1988; Oates, 1988; Grubb, 1990). 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 species of primates (Booth, 1958; Lernould, 1988; Oates, 1988; Grubb, 1990). The highlands of W Cameroon are a center 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). The lower Congo and Ubangi Rivers are common barriers for numerous primates (Dandelot, 1965; Lernould, 1988; Grubb, 1990; Gautier-Hion et al., 1999). In the area between the Congo and Ubangi Rivers no river forms an obvious barrier. However, hybridisation zones or changes of subspecies of guenons are frequently found N of the Congo River between the lower Ubangi in the west and the Ituri River and the Kivu region in the east (Dandelot, 1965; Colyn, 1987, 1988; Gautier-Hion et al., 1999). The Uele 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; Lernould, 1988; Gautier-Hion et al., 1999). The Congo River which delimits the inner Congo Basin to the north and forms a striking barrier for primates (Dandelot, 1965; Colyn, 1987, 1988; Colyn & Deleporte, 2002; Lernould, 1988; Grubb, 1990) 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. 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. *A. 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 & 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 moving 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; Rahm, 1969; Kingdon, 1974).

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 genetical data are not yet available, we assume that reduced gene flow exists between the three populations (Schunke & Hutterer, in press). The origin of *A. pelii*, however, remains obscure.

The situation of *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 anomalures. 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.

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.

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..

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.

Fredoux, A. & Tastet, J. P. 1988. Stratigraphie pollinique et paléoclimatologie de la marge septentrionale du Golfe de Gunée depuis 200.000 ans. *Inst. Français Pondichery, Trav. Sec. Sci et Techn.* **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. & van Someren, G. R. C. 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* B. A. Huber, B. J. Sinclair & K.-H. Lampe (Eds), *African Biodiversity: Molecules, Organisms, Ecosystems. Proceedings of the 5th International Symposium on Tropical Biology, Museum Koenig, Bonn*. Springer Verlag.

Plates I - VII

Plate I. Typical representatives of the dorsal and ventral colouration classes in *A. beecrofti* (see text for details). a: dorsal colouration (DC) 1 (AMNH 86845), b: DC 2 (BMNH 67.1461), c: DC 3 (NHMN 84547), d: DC 4 (BMNH 96.10.9.10), e: DC 5 (BMNH 0.2.5.14), f: 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).

Plate II. Typical representatives of the dorsal and ventral colouration classes in *A. 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: VC 1 (FMNH 88207), f: VC 2 (ZFMK 64.493), g: VC 3 (ZFMK 69.148), h: VC 4 (BMNH 90.6.8.18).

Plate III. Typical representatives of the dorsal and ventral colouration classes in *A. 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: VC 1 (ZMA 21.400), f: VC 2 (ZMA 21.266), g: VC 3 (ZMA 21.277).

Plate IV. Typical representatives of *A. pusillus* from different geographical areas. a, c: Gabon, area 26 (BMNH 87.12.1.28), b, d: Democratic Republic of Congo, area 32 (AMNH 50512, 50514, 50517, 50518).

Plate V. Typical representatives of *I. macrotis* from different geographical areas. a, d: Côte d‘ Ivoire, area 13 (AMNH 239578, 239579, 241151, 241152), b, e: Cameroon, area 24 (BMNH 48871, 48872, 48873), c, f: Democratic Republic of Congo, area 33 (MRAC 28375, 28376, 28377, 28378,).

Plate VI. Typical representatives of *I. zenkeri* from different geographical areas. a, c: Cameroon, area 24 (BMNH 48.885), b, d: Democratic Republic of Congo, area 32 (AMNH 50545, 50546, 50548, 50550, 50601).

Plate VII. Typical representative of *Z. insignis* from Cameroon, area 27 (BMNH 32.11.26.1).

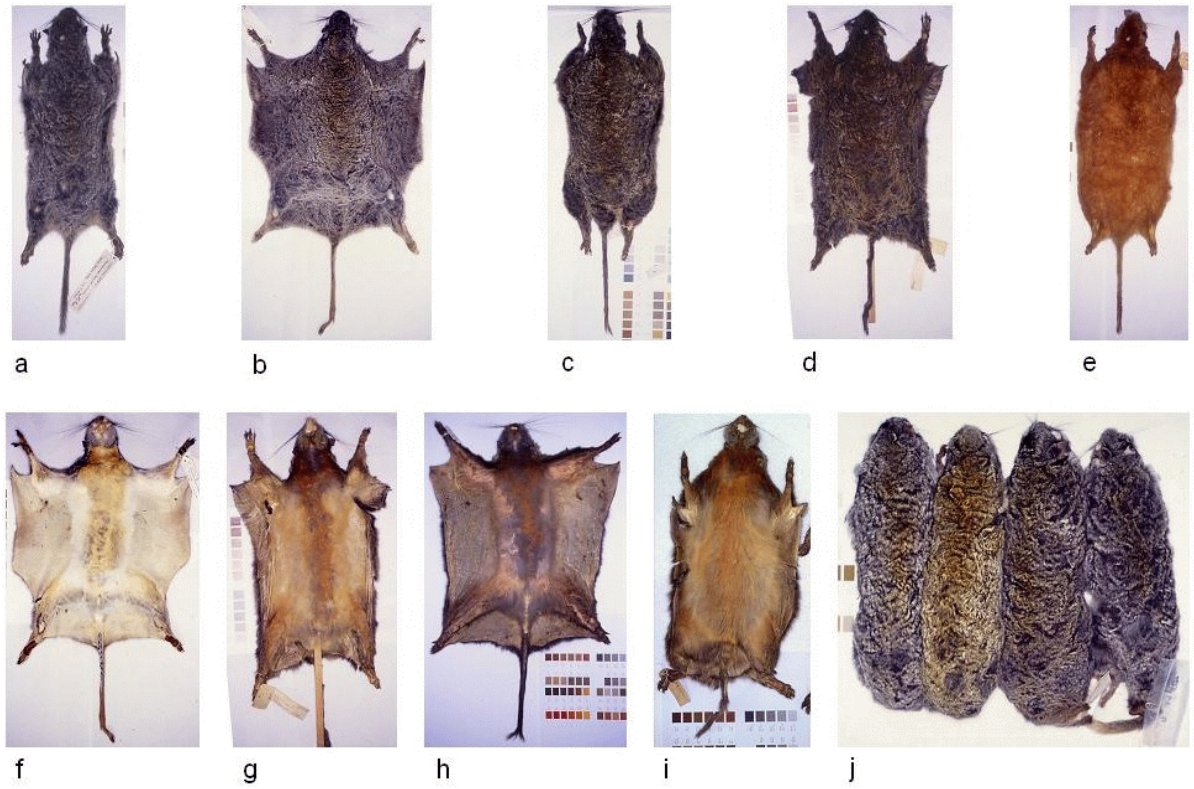
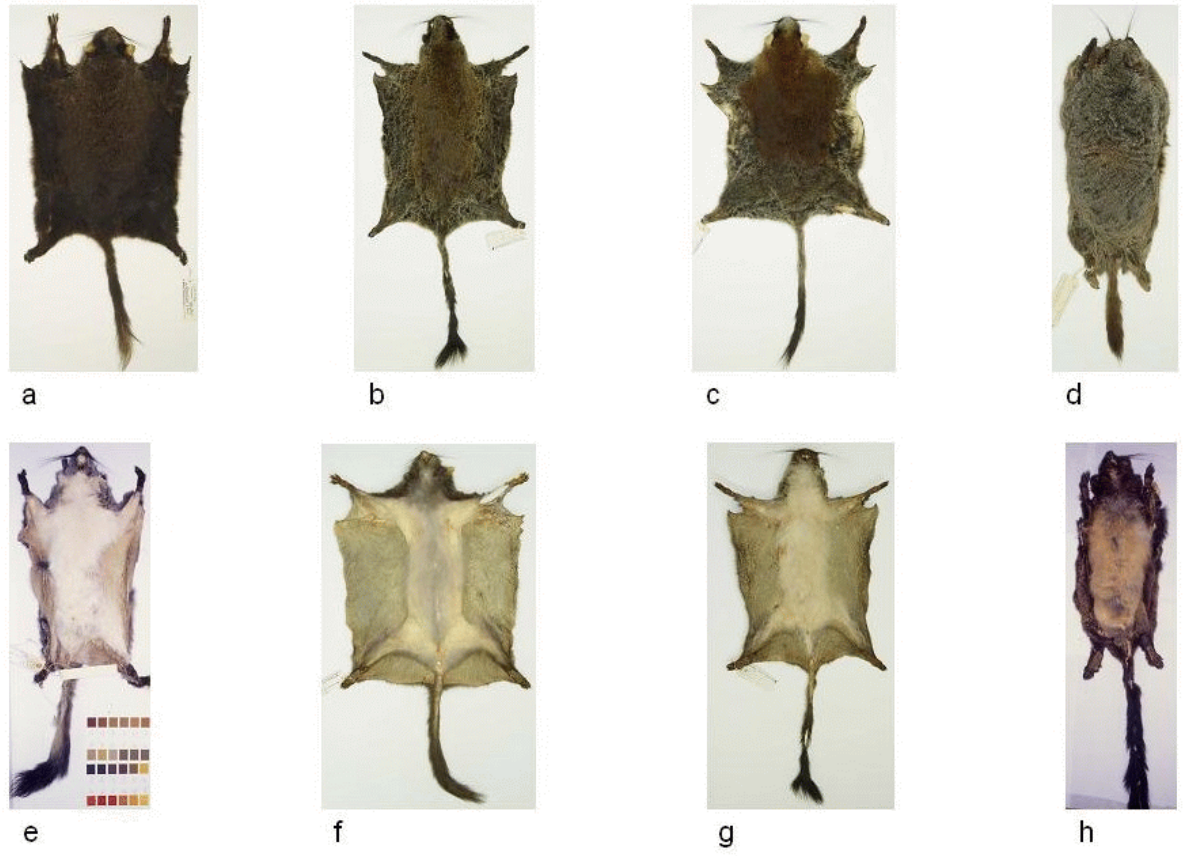


Plate I



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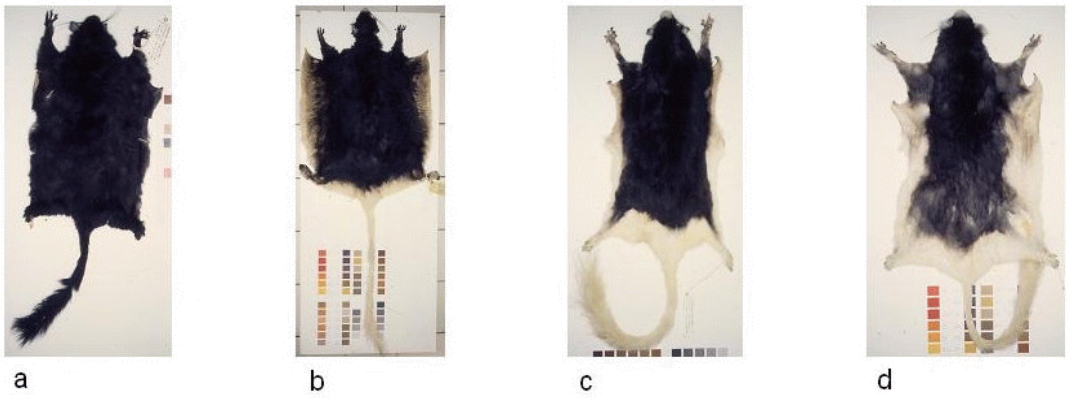

Plate III

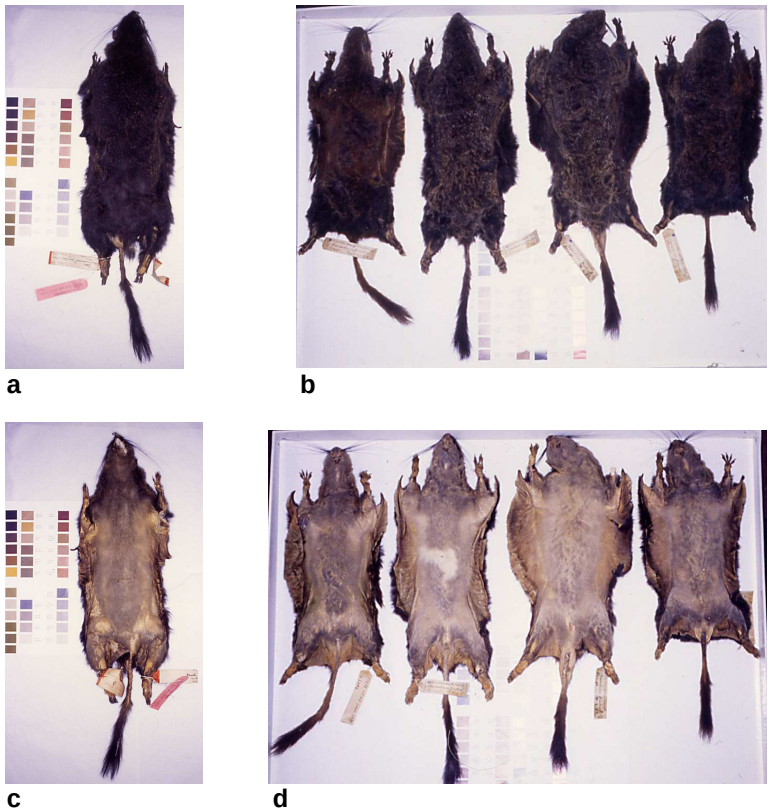

Plate IV

a

b

c

d

e

f

Plate V

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b

d

e

Plate VI

a

b

Plate VII

5. Geographical areas: Definition and species composition

5.1. Definition of areas and subareas

The definition of areas and subareas used in the following chapters is mainly based on the borderlines found for fur colouration (Chap. 4). A few further subdivisions were added, particularly when they represent boundaries of distribution areas for species or previously recognized geographical obstacles.

Generally the distribution area of anomalurids was divided into four main areas with one-digit numbers with four to nine subareas respectively with two-digit numbers (Fig. 5.1).

Area 1: West Africa

Comprises the area from Senegal to the Dahomey Gap in Benin.

Area 11: The westernmost area inhabited by anomalurids from Senegal to Central Liberia. The borderline represents the western border of the distribution area of *A. pelii*.

Area 12: From Central Liberia to the Sassandra River in the Ivory Coast, represents the distribution area of completely black specimens of *A. pelii*.

Area 13: This subarea lies in between the rivers Sassandra and Bandama in the Ivory Coast and is marked by the occurrence of *A. pelii* specimens with extremly high amount of white markings.

Area 14: A relatively large subarea reaching from the Bandama to the Volta River, which represents a likely boundary for *A. pelii* and the West African populations of *I. macrotis*.

Area 15: The subarea between the Volta and the Dahomey Gap, where with the exception of a single *A. derbianus* mainly *A. beecrofti* was collected.

Area 2: Western Central Africa

This area stretches from the Dahomey Gap to the lower Congo and Ubangi rivers and also includes a small area southwest of the Congo River close to the coast.

Area 21: The island of Bioko.

Area 22: The subarea from the Dahomey gap to the River Niger.

Area 23: From the Niger to the Highlands of western Cameroon, represented by the borderline between Nigeria and Cameroon.

Area 24: This area comprises the highlands of western Cameroon and the Cameroon mountains.

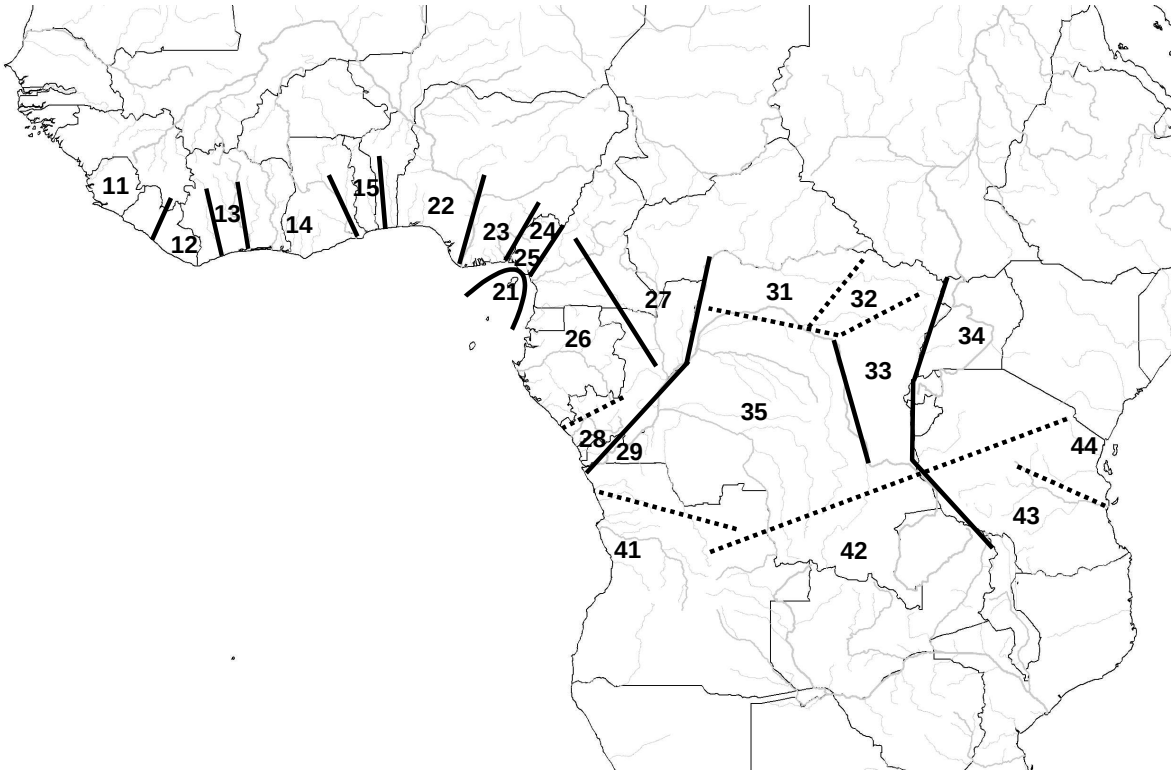

Figure 5.1. Geographical areas as derived from fur colouration (Chapter 4) and previously known borderlines (see text for details).

Area 25: Mount Cameroon.

Area 26: A large subarea from southern Cameroon to Gaboon with the highest number of collected specimens.

Area 27: The area between the rivers Dja and Sangha in the West and Ubangi in the East in southeastern Cameroon and Congo Brazzaville.

Area 28: Southern Congo Brazzaville, Cabinda and a small part of the Democratic Republic of Congo north of the Congo River and south of the River Oguoue.

Area 29: A small area south of the Congo River and west of the 16th degree of longitude.

Area 3: Central Africa

This area consists mainly of the central and northern parts of the Democratic Republic of Congo as well as northern parts east of the Rift Valley.

Area 31: The area north of the Congo from the Ubangi to ca. the 25th degree of longitude. The western borderline is difficult to define and partly represented by a lack of collected anomalurids from this area.

Area 32: The northeastern corner of the Democratic Republic of Congo west of area 31 and southeast to the Aruwimi and Ituri River system.
Area 33: The Kivu area from the Aruwimi and Ituri to the Lukuga River in the South and the Rift Valley in the East.
Area 34: This area lies East of the Rift Valley and comprises Uganda, Ruanda, Burundi as well as parts of Kenya and northern Tanzania.
Area 35: The largest subarea in the Central Democratic Republic of Congo.

Area 4: Southern parts of the distribution area of anomalurids
This area reaches from the western to the eastern coast of Africa, including parts of several countires from Angola to Tanzania.
Area 41: A small area in the West of Angola from the coast to the 15th degree of longitude.
Area 42: This subarea comprises parts of eastern Angola from east of the 19th degree of longitude, southeastern Democartic Republic of Congo, Zambia, and northern Malawi.
Area 43: Southern Tanzania from the Rift Valley to the Rufiji River.
Area 44: Northeastern Tanzania, particularly the Usambara mountains.

5.2. Species composition

The numbers of specimens and the proportion of the species varies considerably between areas and subareas, as far as reflected by the collected individuals. Figure 5.2 gives diagrams for the proportions of specimens from the respective species in the four main areas and for the complete data set. Some general tendencies can be seen like the increasing percentage of *A. derbianus* and *A. pusillus* in northwestern to southeastern direction while *A. beecrofti* and *I. macrotis* have their highest proportions in western Central Africa. However, this can not be caused completely by the different collection methods or interests of the collectors, because there are high numbers of collectors in every area most of which collected only small numbers of specimens (Tab. 5.1).

Table 5.1. Statistics on collections of anomalurids.

	Area 1	**Area 2**	**Area 3**	**Area 4**
number of collectors	71	122	91	38
mean number of collected specimens	4.7	4.0	6.6	3.4
median of collected specimens	1	1	1	1
number of collections with 10 or more collected specimens	6	8	15	2

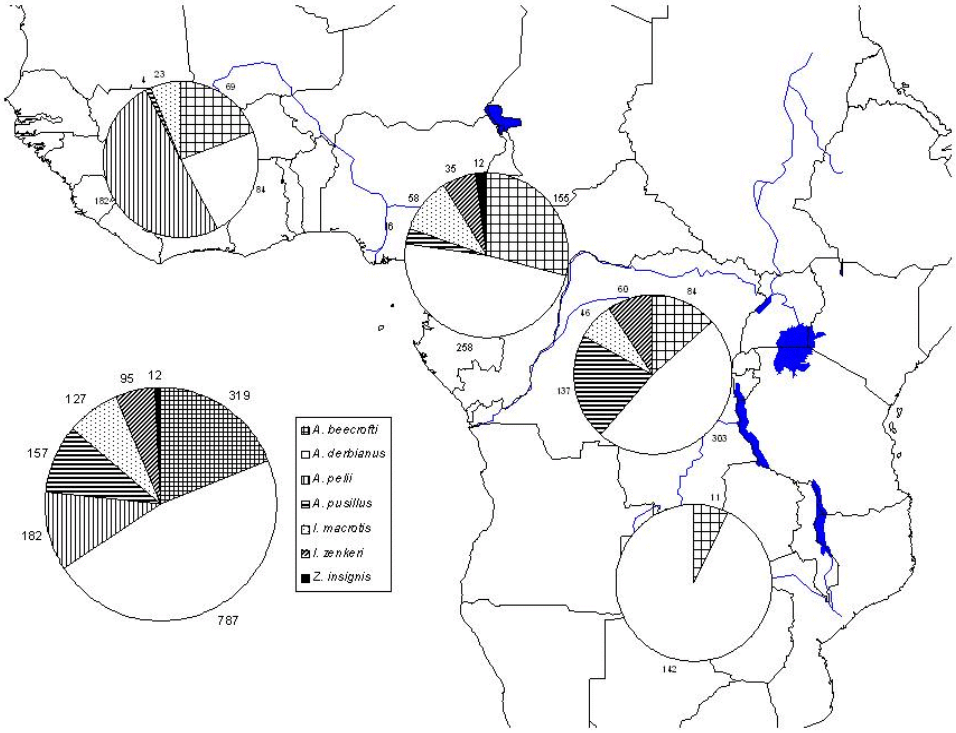

Figure 5.2. Anomalurid species composition in different geographical areas (see text for details).

A more detailed analysis showes also remarkable differences between some neighbouring subareas, while they are in other cases similar (Tab. 5.2, Fig. 5.3).

Table 5.2. Collected specimens of the anomalurid species in different subareas.

Area	*A. beecrofti*	*A. derbianus*	*A. pelii*	*A. pusillus*	*I. macrotis*	*I. zenkeri*	*Z. insignis*	total
11	20	7	0	1	1	0	0	29
12	13	4	15	0	4	0	0	36
13	2	30	71	0	5	0	0	108
14	7	30	70	0	13	0	0	120
15	20	1	0	0	0	0	0	21
21	8	28	0	0	0	0	2	38
22	8	9	0	0	0	0	0	17
23	14	8	0	0	4	0	0	26
24	14	24	0	0	10	3	0	51
25	11	12	0	0	0	0	0	23
26	71	120	0	15	42	29	7	284
27	14	31	0	1	0	3	3	52
28	10	17	0	0	0	0	0	27
29	2	0	0	0	0	0	0	2

Table 5.2. (continued) Collected specimens of the anomalurid species in different subareas.

Area	*A. beecrofti*	*A. derbianus*	*A. pelii*	*A. pusillus*	*I. macrotis*	*I. zenkeri*	*Z. insignis*	total
31	10	33	0	5	1	2	0	51
32	17	111	0	79	10	22	0	239
33	36	72	0	50	34	34	0	226
34	1	16	0	1	1	1	0	20
35	18	46	0	0	0	0	0	64
41	6	4	0	0	0	0	0	10
42	4	98	0	0	0	0	0	102
43	1	31	0	0	0	0	0	32
44	0	7	0	0	0	0	0	7

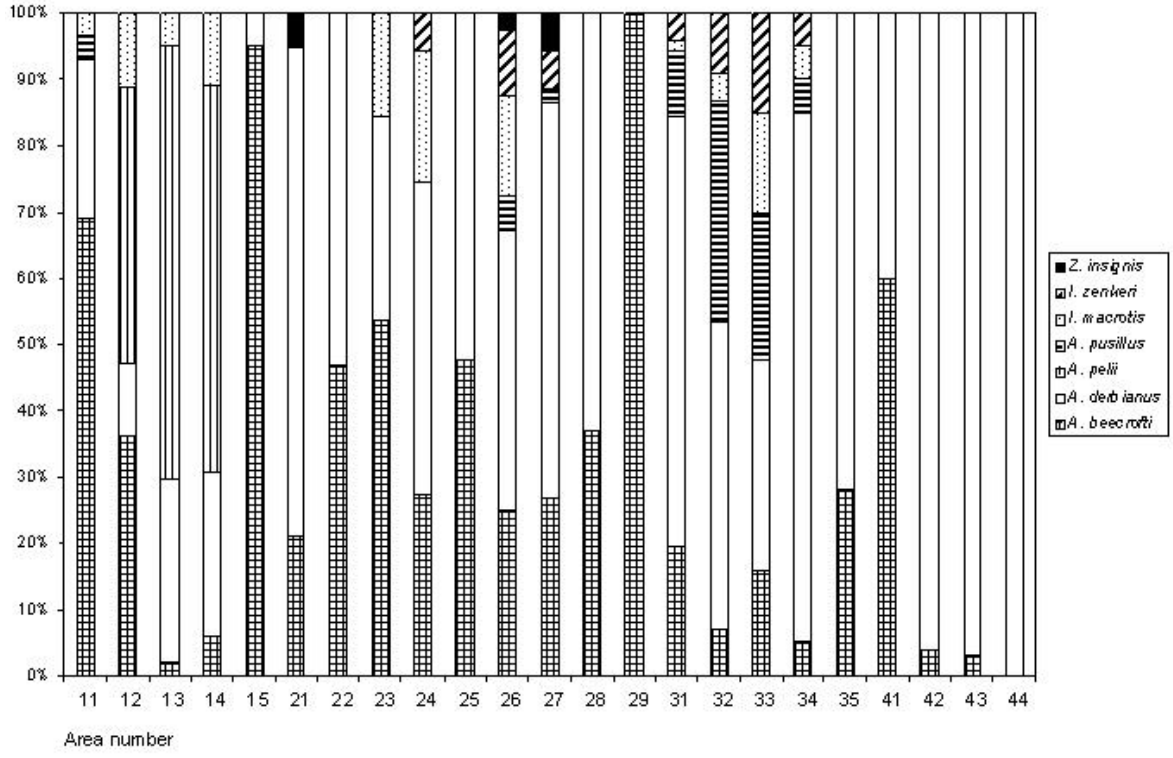

Figure 5.2. Anomalurid species compostion in the different subareas.

6. Body size

Abstract. The standard body size characters total length, tail length, length of hindfoot, and ear length were analysed for 396 specimens of all anomalurid species. The data were taken from labels or from literature. All variables were distributed normally and showed no general age dependence. The three *Anomalurus* species showed sexual dimorphism with females being slightly larger than males. *Anomalurops* females tended also to be slightly larger, but not statistically significant. In *Idiurus* this difference between sexes was not observed, for *Zenkerella* only males were available. Geographical populations can be partially distinguished with body size characters. In *A. beecrofti* populations from distant areas tend to overlap, while neighbouring specimens were frequently separated. In *A. derbianus*, *A. pelii*, and *I. macrotis* geographical populations formed more or less homogenous cluster, with few exceptions of single populations. Specimens from different areas are very well separated in *A. pusillus*, *I. zenkeri*, and *Z. insignis*. Problems of data acquisition and sample size are discussed.

6.1 Introduction

Standard body size characters like total length, head and body length, tail length, length of hindfoot, ear length and weight are as a routine taken when rodents are collected. In several cases species or subspecies can be best distinguished based on their size. Therefore an analysis of body size measurements was interesting in order to see whether these characters support or contradict the colouration patterns (see Chap. 4).

6.2. Material and methods

6.2.1. Data basis

The data for the body size analyses were based on measurements taken in the field by the collector. Later measurements on the dried skins were not reliable because of very different shrinkage depending on preparation technique. The number of adult specimens for the different species used in the analysis is given in Table 6.1.

Table 6.1. Number of adult specimens with recorded body measurements.

A. beecrofti	75
A. derbianus	165
A. pelii	45 (+1 from literature)
A. pusillus	45
I. macrotis	34
I. zenkeri	26
Z. insignis	5 from literature

The data set used consisted of the following standard characters: total length (partially calculated from head and body plus tail length), tail length, length of hindfoot, ear length and weight. Measurements of head and body length (partially calculated from total length minus tail length) are given but not used in the calculations in order to avoid redundant information.

6.2.2. Statistics

Data were tested for normal distribution with the Kolmogorov-Smirnov test. Relationships between body measurements and sex, age, and finding locality were checked with a one-way ANOVA and/or with a Kruskal-Wallis test if variances of the respective characters were not homogeneous. These tests were restricted for each species to specimens of one or two areas (see Chap. 5 for area definition) with the highest number of individuals in order to avoid biases caused by geographic variation.

Multivariate analyses (principal component analysis (PCA) and discriminant analysis (DA)) were calculated with the ln-transformed values for total length (partially calculated from head and body plus tail length), tail length, length of hindfoot, and ear length. Weight was omitted because this character was missing for the majority of specimens. All statistical and multivariate analyses were performed in SPSS 10. 0. For tests of geographical variation specimens were grouped in areas according to Chapter 5.

6.3. Results

6.3.1. *A. beecrofti*

Tests for normal distribution and relationships between characters were restricted to specimens from southern Cameroon to Gabon (area 26, n=22).

The body size measurements were normally distributed in all performed tests. The normal distribution of weight was not tested because of the too small sample sizes within geographical areas. No significant correlation between body size characters and sex or age could be found with the one-way ANOVA or with the Kruskal-Wallis test in case of inhomogenous variances

with the exception of hindfoot length, which showed significant differences between sexes. Figure 6.1 gives boxplots of the tested variables separately for males and females of the geographical areas, showing median and quartiles.

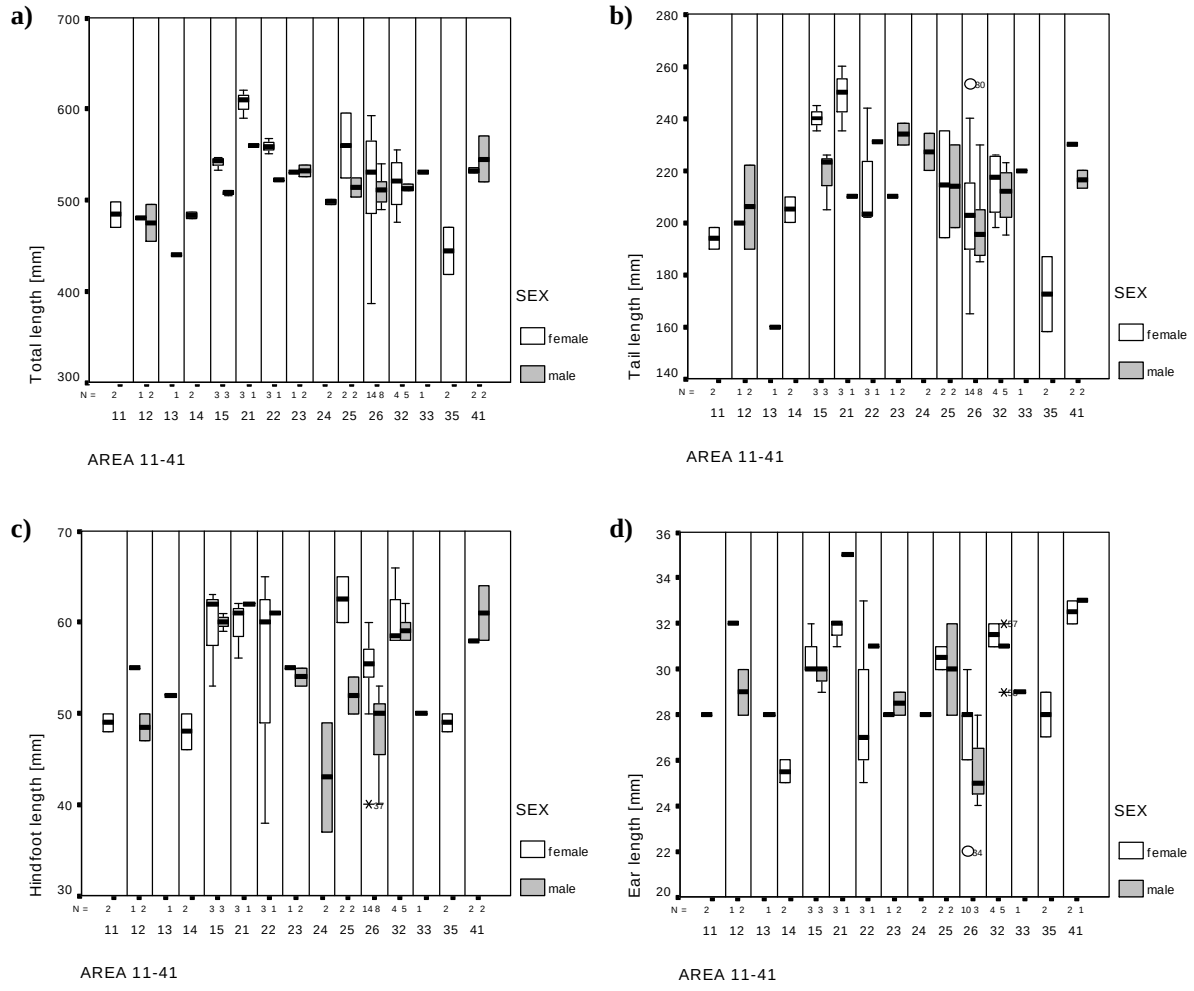

Figure 6.1. Median and quartiles of body size measurements in *A. beecrofti* males and females.

When tested against finding locality all body measurements showed significant differences in the one-way ANOVA and with the Kruskal-Wallis test (total length $P < 0.001$, tail length $P = 0.01$, hindfoot length $P < 0.001$, ear length $P < 0.001$, weight $P < 0.05$). Arithmetic means, ranges and number of specimens are given in Table 6.2.

The principal component analysis (PCA) and the discriminant analysis (DA) showed remarkably similar results for the body size of *A. beecrofti*. The specimens from the areas 1 to 4 (area number see Chap. 5) overlapped more or less completely (Figs 6.2, 6.3), but within these areas the resolution was much better. The populations from West Africa (area 1) could be very well separated with the PCA (Fig. 6.2) and slightly less clearly with the DA (Fig. 6.3). Specimens

Table 6.2. Body size measurements for different geographical populations (area number see Chap. 5, number of specimens in brackets) of *A. beecrofti* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram).

Area	total length	head / body	tail length	hindfoot	ear length	weight
11 (3)	484 (470-498)	290 (280-300)	194 (190-198)	49 (48-50)	28 (28-28)	–
12 (3)	477 (455-495)	273 (265-281)	204 (190-222)	51 (47-55)	30 (28-32)	415 (312-528)
13 (1)	440 (-)	280 (-)	160 (-)	52 (-)	28 (-)	–
14 (2)	484 (480-487)	279 (277-280)	205 (200-210)	48 (46-50)	26 (25-26)	–
15 (6)	524 (505-547)	295 (284-303)	229 (205-245)	60 (53-63)	30 (29-32)	457 (420-477)
21 (4)	595 (560-620)	356 (340-375)	239 (235-260)	60 (56-62)	33 (31-35	890 (760-1040)
22 (4)	550 (522-567)	330 (291-356)	220 (202-244)	56 (38-65)	29 (25-33)	455 (-)
23 (3)	533 (526-539)	299 (296-320)	234 (210-238)	54 (53-55)	29 (28-29)	–
24 (3)	498 (495-501)	271 (267-275)	210 (177-234)	47 (37-54)	28 (28-28)	–
25 (4)	537 (503-595)	323 (295-360)	214 (194-235)	57 (54-65)	30 (28-32)	840 (550-1000)
26 (22)	520 (387-593)	318 (217-380)	202 (165-253)	52 (40-60)	27 (22-30)	–
32 (9)	515 (475-555)	303 (277-330)	212 (195-226)	60 (58-66)	31 (29-32)	–
33 (1)	530 (-)	310 (-)	220 (-)	50 (-)	29 (-)	–
35 (2)	444 (418-470)	272 (260-283)	173 (158-187)	49 (48-50)	28 (27-29)	–
41 (4)	539 (520-570)	316 (300-357)	223 (213-230)	60 (58-64)	33 (32-33)	–

from western central Africa (area 2) overlapped to a large extent, only those from Bioko (area 21) and Mamfe area (area 24) could be separated with the DA (Fig. 6.3), but not with the PCA (Fig. 6.2). The central (area 3) and southern (area 4) populations showed a resolution comparable to the West African specimens, with a complete separation in the DA (Fig. 6.3) and a slightly less clear separation in the PCA (Fig. 6.2). 59.3% of the specimens were assigned correctly in the DA (n=62). This value increased when calculated for females (69.4%, n=36) or males (78.3%, n=26) separately.

6.3.2. *A. derbianus*

Tests for normal distribution, sexual dimorphism and age dependence were performed for the populations from north-eastern Democratic Republic of Congo (area 32, n= 43) and from Zambia (area 42, n= 31), the two largest samples of body measurements from *A. derbianus*.

All characters showed normal distribution for both populations. In the sample from the Democratic Republic of Congo was a strong sexual dimorphism for most measurements detected in the one-way ANOVA (total length $P < 0.05$, tail length $P = 0.005$, hindfoot length $P < 0.05$, ear length P = n.s., weight not calculated). Specimens from Zambia showed statistically significant differences only in hindfoot length ($P < 0.005$). In Figure 6.4 are boxplots of the

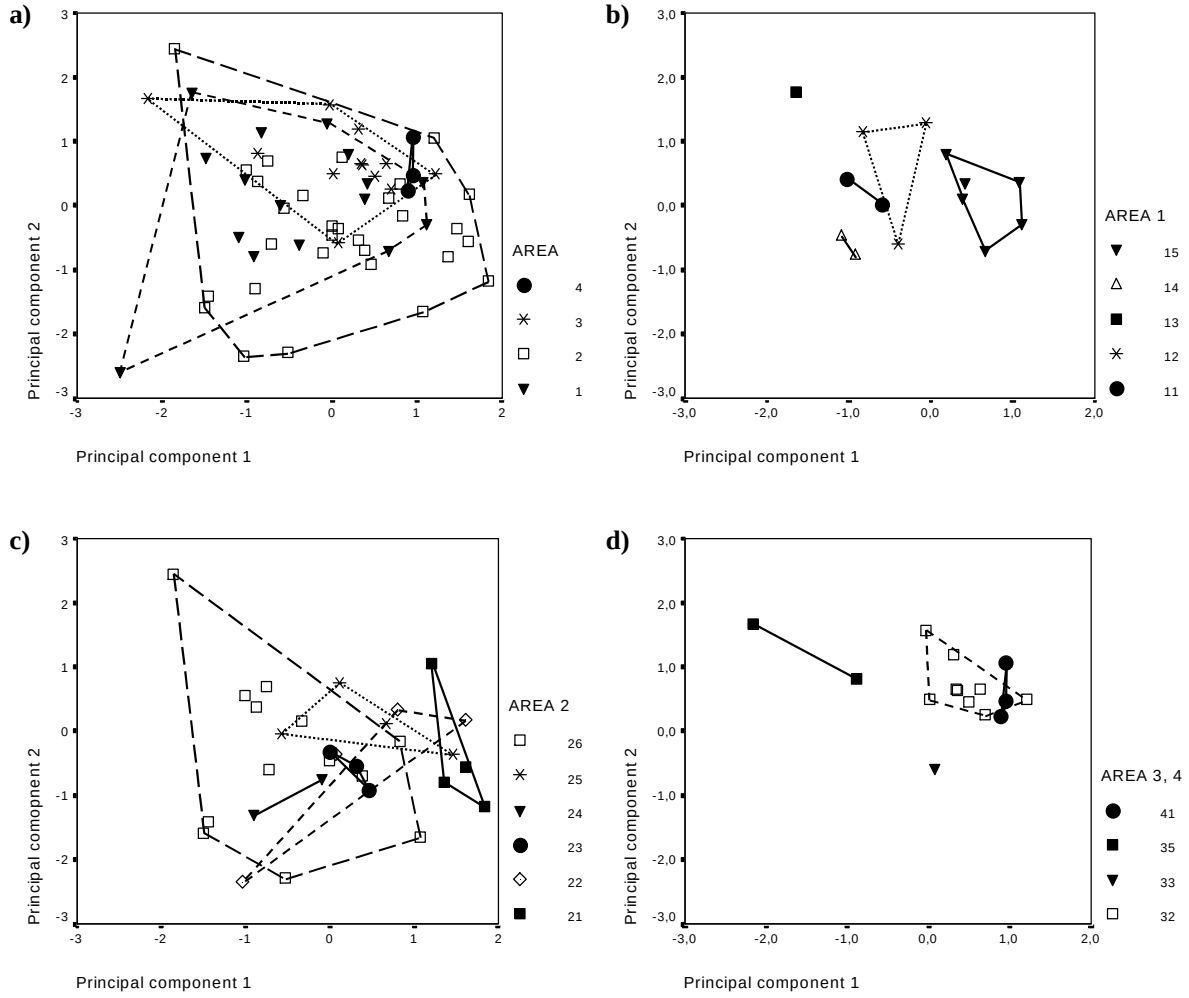

Figure 6.2. Results of the principal component analysis of ln-transformed body size measurements in *A. beecrofti* for main areas (a) and subareas (b-d).

characters shown for females and males respectively. Age dependence was found for tail length in the complete sample from the Democratic Republic of Congo ($P < 0.05$), for ear length in females only ($P < 0.05$, n=18) and for total length in males ($P < 0.05$, n=25). In the sample from Zambia ear length showed a significant correlation with age for the whole population ($P < 0.05$), total length in males ($P < 0.05$, n=16) and none in females (n=15). All body measurements showed highly significant differences between populations from different areas in the one-way ANOVA and with the Kruskal-Wallis test (total length $P < 0.001$, tail length $P < 0.001$, hindfoot length $P < 0.001$, ear length $P < 0.001$, weight $P < 0.01$). Arithmetic means, ranges and number of specimens are given in Table 6.3.

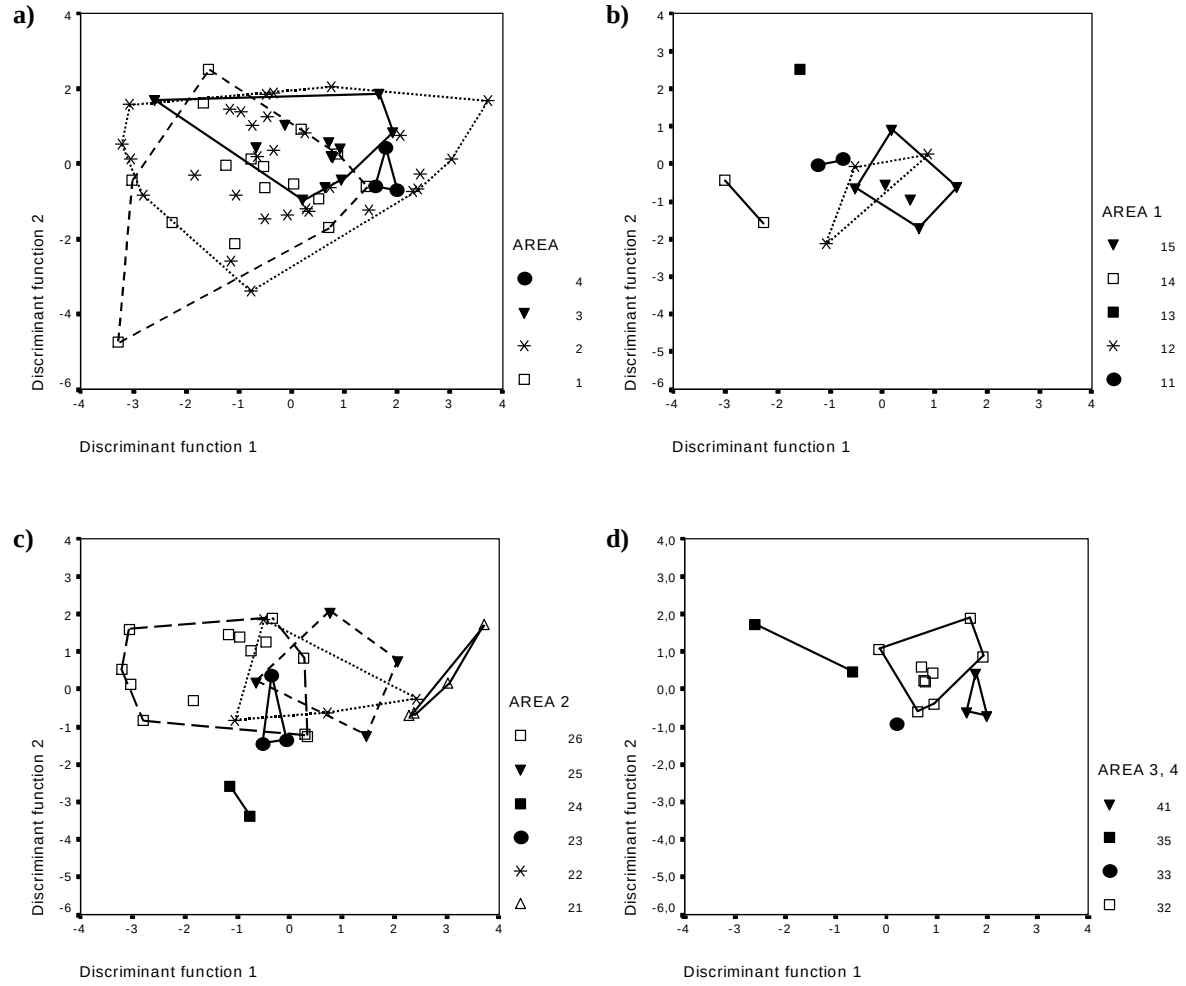

Figure 6.3. Results of the discriminant analysis of ln- transformed body size measurements in *A. beecrofti* for main areas (a) and subareas (b-d).

Table 6.3. Body size measurements for different geographical populations (area number see Chap. 5, number of specimens in brackets) of *A. derbianus* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram).

Area	total length	head / body	tail length	hindfoot	ear length	weight
12 (1)	533 (-)	290 (-)	243 (-)	60 (-)	37 (-)	454 (-)
13 (13)	565 (529-590)	327 (282-350)	235 (190-260)	60 (55-69)	37 (33-40)	710 (480-830)
14 (9)	574 (518-609)	336 (317-385)	239 (195-270)	62 (59-66)	38 (35-40)	685 (454-900)
21 (11)	626 (590-659)	346 (325-360)	280 (260-317)	59 (54-65)	40 (26-45)	890 (855-920)
22 (3)	609 (600-618)	311 (300-320)	293 (280-306)	62 (60-65)	41 (37-47)	–
23 (1)	536 (-)	285 (-)	251 (-)	52 (-)	31 (-)	–
24 (2)	527 (450-603)	259 (224-294)	268 (226-309)	51 (40-61)	28 (23-32)	–
25 (1)	635 (-)	325 (-)	310 (-)	45 (-)	37 (-)	610 (-)

Table 6.3. (continued)

Area	total length	head / body	tail length	hindfoot	ear length	weight
26 (18)	637 (595-742)	331 (315-400)	306 (275-360)	62 (55-69)	37 (34-42)	785 (760-809)
27 (6)	592 (550-636)	324 (305-351)	267 (243-285)	65 (62-68)	37 (34-43)	629 (479-880)
31 (1)	535 (-)	300 (-)	235 (-)	60 (-)	38 (-)	500 (-)
32 (43)	565 (511-621)	314 (239-344)	251 (222-280)	62 (51-69)	38 (35-42)	–
33 (3)	596 (585-607)	344 (332-355)	253 (230-275)	58 (53-63)	35 (34-37)	–
34 (5)	557 (545-565)	307 (295-315)	250 (240-260)	61 (60-62)	40 (-)	354 (-)
35 (7)	562 (529-569)	308 (284-326)	254 (232-276)	59 (57-61)	35 (31-39)	–
41 (1)	602 (-)	334 (-)	268 (-)	66 (-)	43 (-)	–
42 (31)	501(465-535)	280 (260-300)	221 (175-248)	55 (51-58)	36 (33-38)	–
43 (6)	552 (490-675)	317 (309-326)	235 (175-269)	56 (55-58)	39 (39-40)	–
44 (1)	675 (-)	368 (-)	307 (-)	60 (-)	41 (-)	–

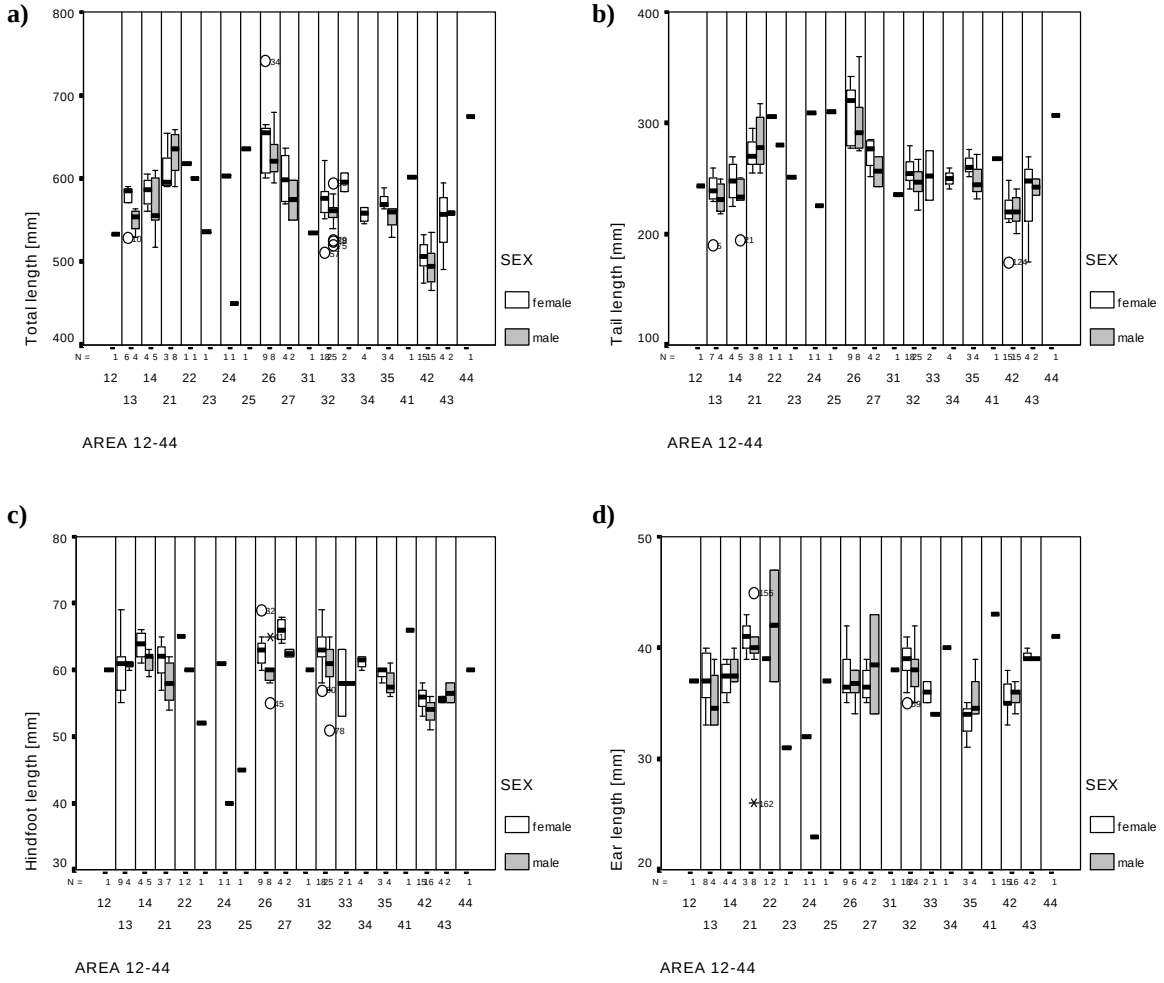

Figure 6.4. Median and quartiles of body size measurements in *A. derbianus* males and females.

The principal component and discriminant analyses showed less clearly defined clusters of (sub)populations in *A. derbianus* than in *A. beecrofti*. Specimens of the areas 1 to 4 overlap in large parts (Figs 6.5, 6.6) and the resolution within the areas is also very bad, except for the southern populations, which did not overlap in both analyses (Figs 6.5, 6.6). In spite of the large overlap between (sub)populations the percentage of correctly assigned specimens (68.0%, n=149) is higher than in *A. beecrofti*. The value increases to 76.4% in males (n=74) and to 70.3% in females only (n=74).

6.3.3. *A. pelii*

For *A. pelii* normal distribution, sexual dimorphism and age dependence were tested for the population between the Bandama and Volta rivers (area 14, n=38).

All characters are normally distributed. The one-way ANOVA showed statistically significant differences between sexes for total length ($P < 0.01$), tail length ($P < 0.005$), and weight ($P < 0.01$). Boxplots of the characters are given separately for females and males in Figure 6.7. No correlation between one of the measured characters and age could be found with the one-way ANOVA and the Kruskal-Wallis test for females (n=15), males (n= 22) or with the sexes combined. *A. pelii* shows no significant differences between specimens from different areas, neither for all specimens in one analysis nor for males only. Arithmetic means, ranges and number of specimens are given in Table 6.4.

Table 6.4. Body size measurements for different geographical populations (area number see Chap. 5, number of specimens in brackets) of *A. pelii* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram); *data from Kuhn (1966).

Area	total length	head / body	tail length	hindfoot	ear length	weight
12 (1)*	850 (-)	405 (-)	445 (-)	75 (-)	43 (-)	1770 (-)
13 (7)	909 (850-990)	438 (412-484)	471 (366-550)	87 (85-91)	45 (40-50)	1780 (1600-2000)
14 (38)	856 (780-973)	427 (368-546)	430 (325-495)	82 (70-92)	45 (39-50)	1591 (1300-2000)

The multivariate analyses of body size yielded no resolution of the subpopulations. The single specimen of the western population lies within the range of the eastern population and the central

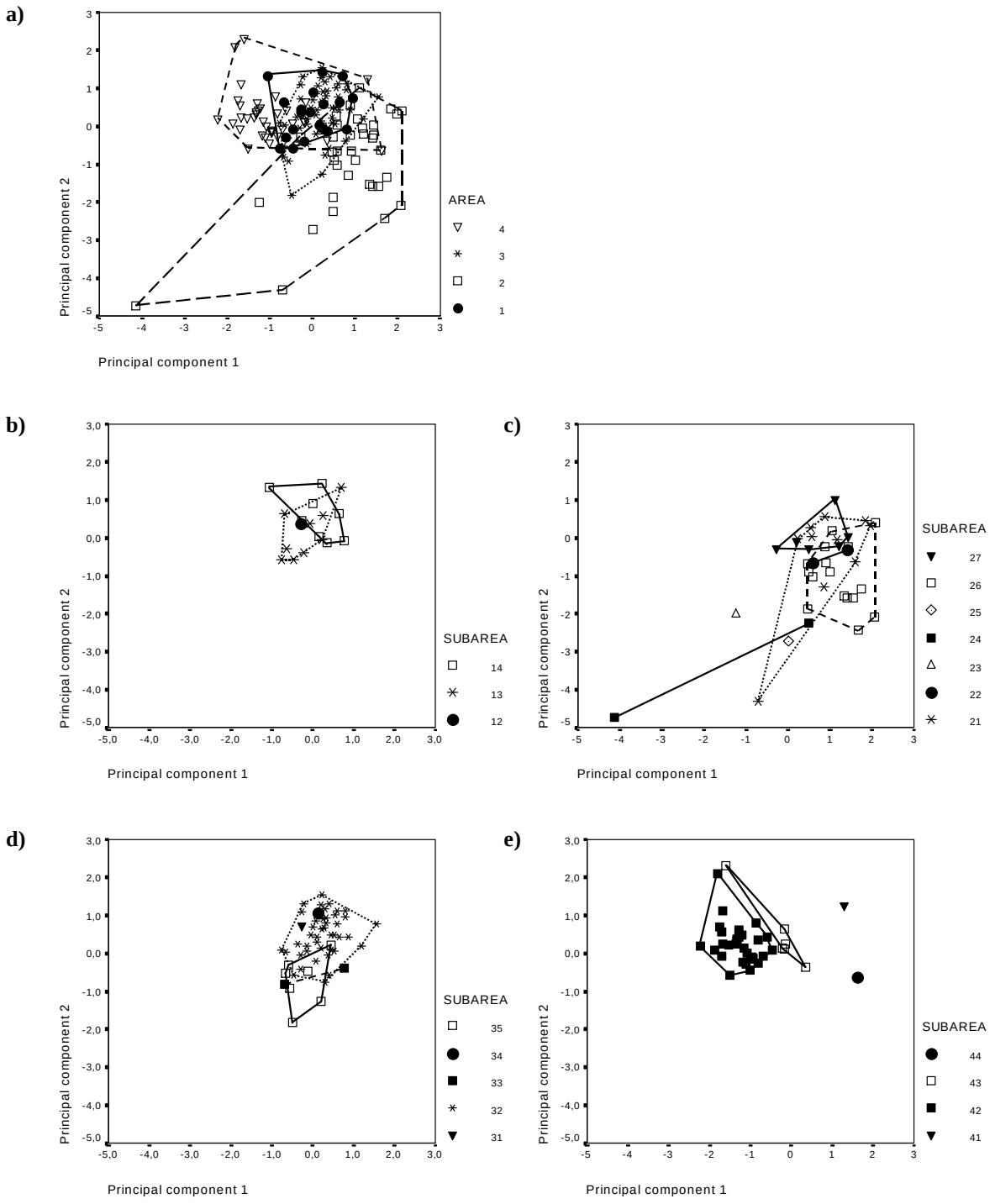

Fig. 6.5. Results of the principal component analysis of ln- transformed body size measurements in *A. derbianus* for main areas (a) and subareas (b-e).

population overlaps with the western (Fig. 6.8). Still 86.0% of the specimens were assigned correctly (n=43) in the discriminant analysis. If calculated for males only in order to include the single specimen from the western part (area 12) the percentage increases to 91.7% (n=24).

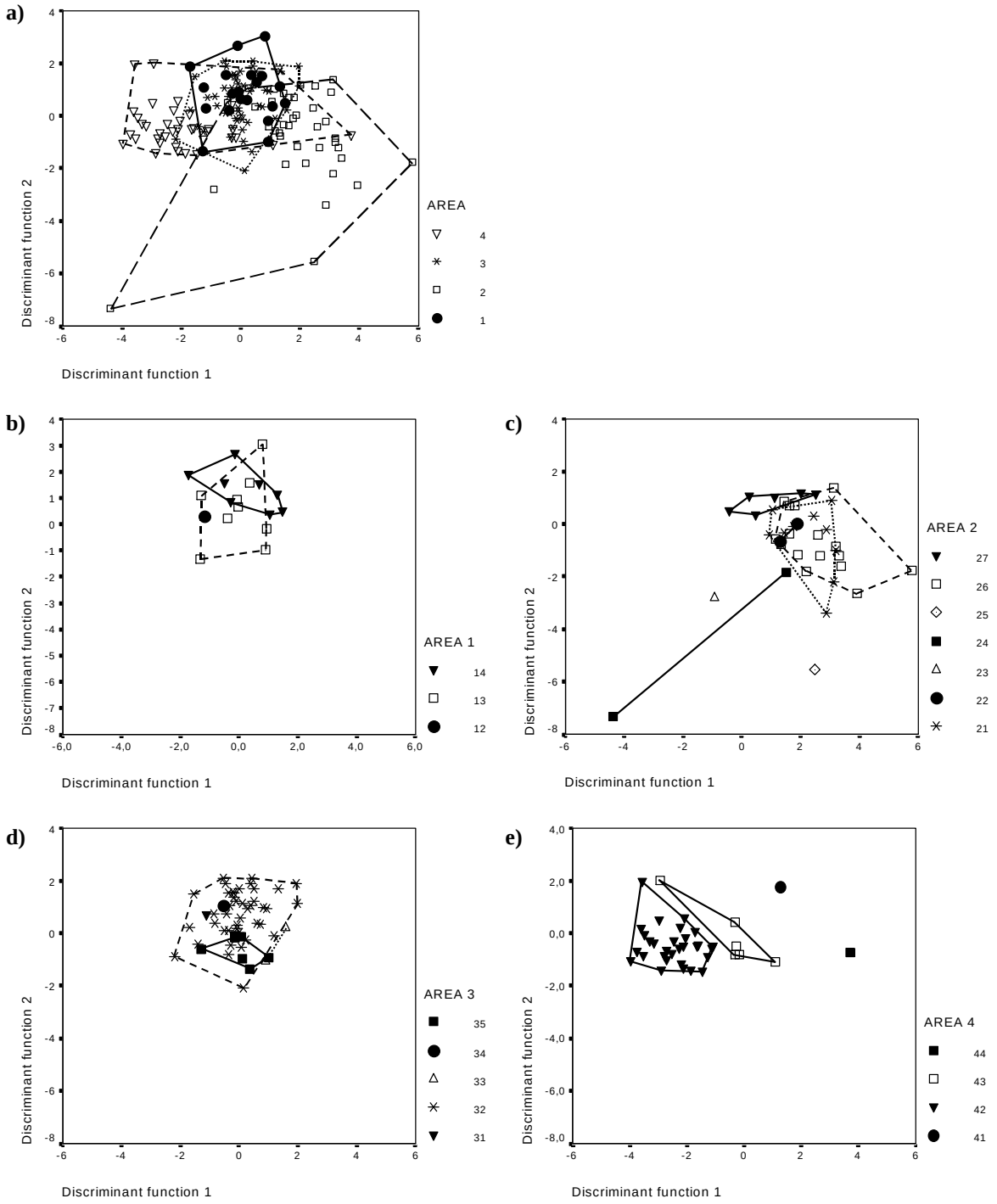

Fig. 6.6. Results of the discriminant analysis of ln- transformed body size measurements in *A. derbianus* for main areas (a) and subareas (b-e).

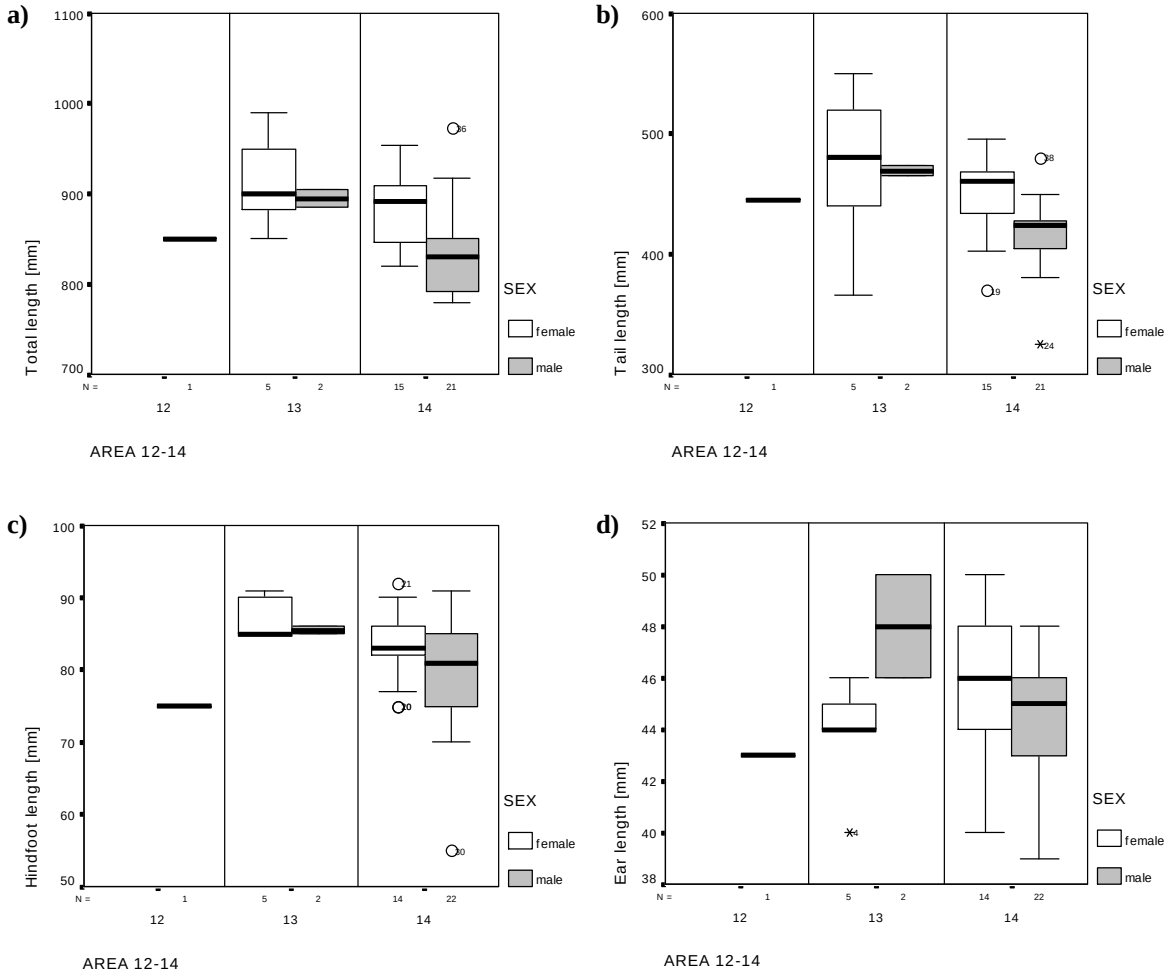

Figure 6.7. Median and quartiles of body size measurements in *A. pelii* males and females.

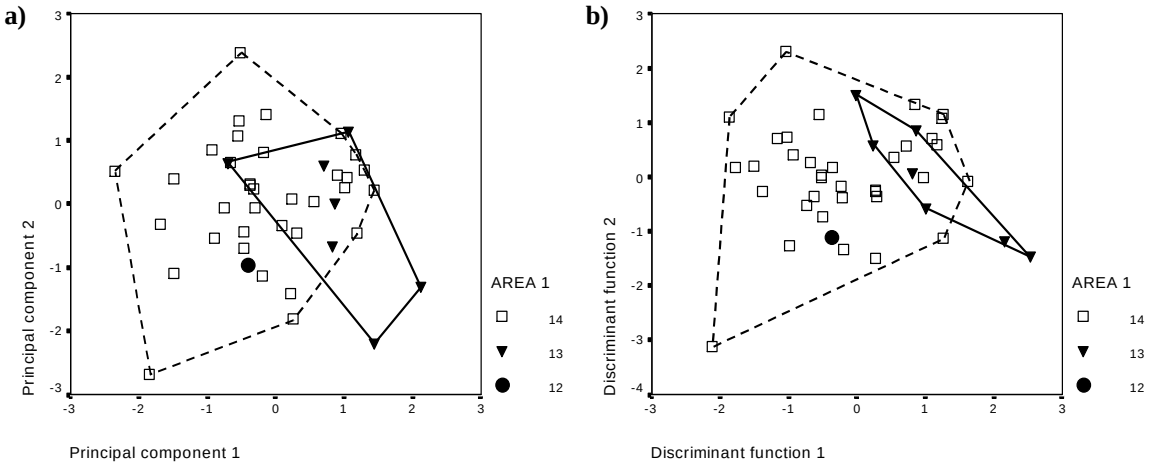

Figure 6.8. Results of the principal component analysis (a) and disciminant analysis (b) of ln-transformed body size measurements in *A. pelii* for subareas.

6.3.4. *A. pusillus*

Normal distribution, sexual dimorphism and age dependence were checked for the *A. pusillus* population from the north-eastern Democratic Republic of Congo (area 32, n = 39).

All characters showed normal distribution (weight not tested), but considerable sexual dimorphism (total length $P < 0.001$, tail length $P < 0.001$, length of hindfoot $P = 0.001$, weight not tested). Figure 6.9 shows boxplots of the characters for females and males. Age dependence was found in the complete population for ear length ($P < 0.05$), but none when checked independently for females (n = 24) and males (n = 15). The one-way ANOVA showed significant differences for hindfoot length ($P < 0.001$) and ear length ($P < 0.01$) between populations from different areas. Arithmetic means, ranges and number of specimens are given in Table 6.5. The two specimens from area 1 could not be assigned to a specific subarea, but they were both collected in Liberia.

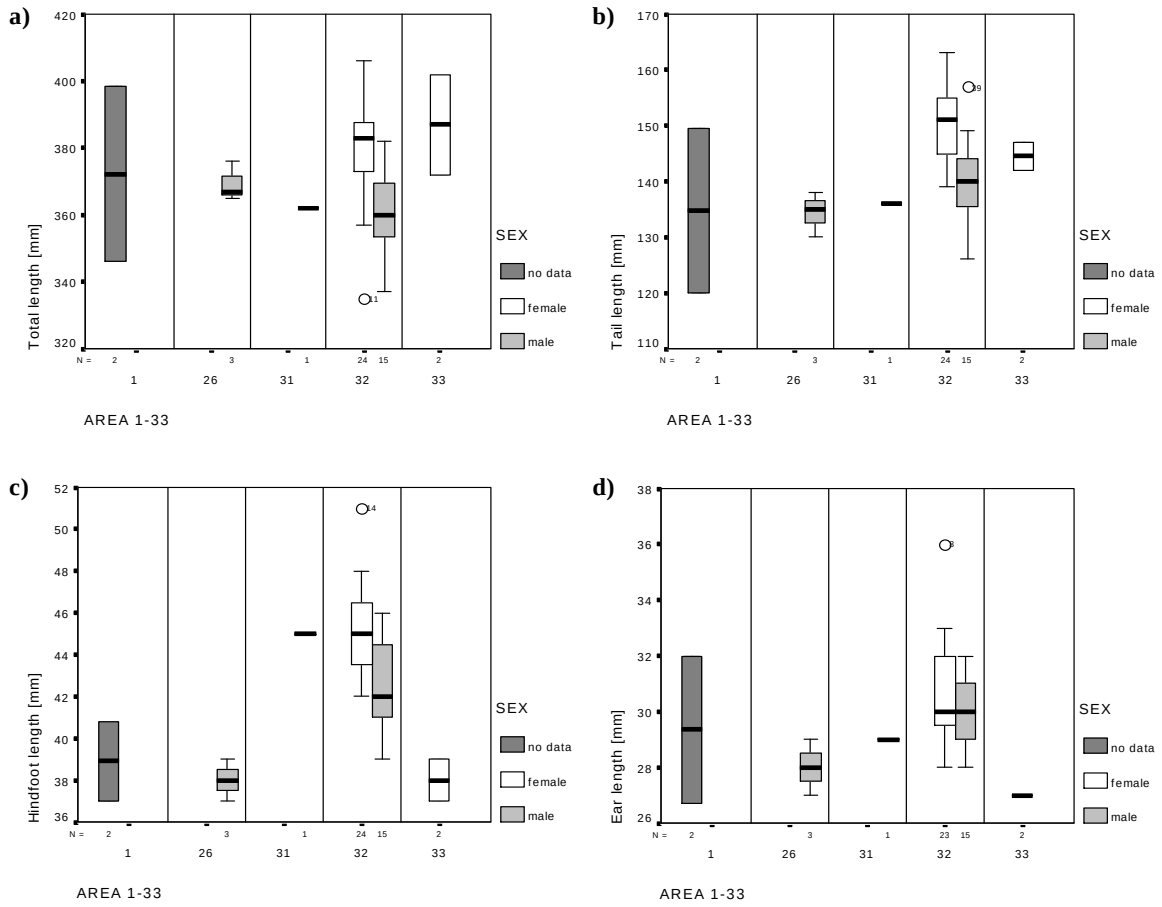

Fig. 6.9. Median and quartiles of body size measurements in *A. pusillus* males and females.

Table 6.5. Body size measurements for different geographical populations (area number see Chap. 5, number of specimens in brackets) of *A. pusillus* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram).

Area	total length	head / body	tail length	hindfoot	ear length	weight
1 (2)	372 (346-399)	238 (226-249)	135 (120-150)	39 (37-41)	29 (27-32)	255 (211-298)
26 (3)	369 (365-376)	235 (230-238)	134 (130-138)	38 (37-39)	28 (27-29)	–
31 (1)	362 (-)	226 (-)	136 (-)	45 (-)	29 (-)	215 (-)
32 (39)	373 (335-406)	227 (194-250)	146 (126-163)	44 (39-51)	30 (28-36)	–
33 (2)	387 (372-402)	243 (230-255)	145 (142-147)	38 (37-39)	27 (27-27)	–

In *A. pusillus* it was possible to separate several geographical populations with the principal component analysis as well as with the discriminant analysis (Fig. 6.10). Exceptions were the single specimen from the north-western Democratic Republic of Congo (area 31), which clustered within the neighbouring population in the north-west of this country (area 32), and one specimen from Liberia, which lies also within the range of the specimens from area 32 in the PCA, but not in the DA. 93.5% of the specimens were assigned correctly by the discriminant analysis (n=46). When calculated for males only, which included at least 3 of the (sub)areas (areas 26, 31, and 32), the percentage increased to 100% (n=19).

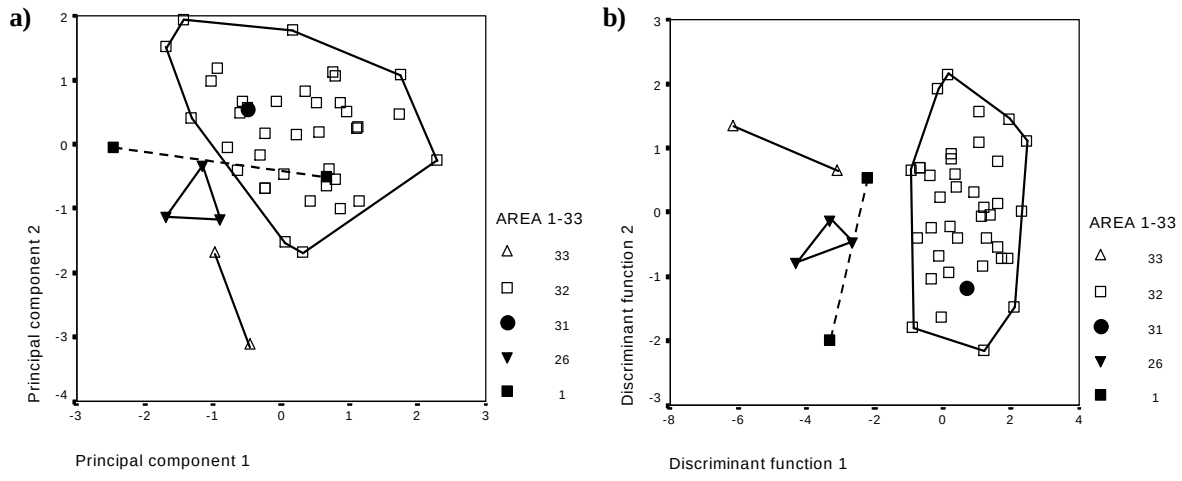

Fig. 6.10. Results of the principal component analysis (a) and disciminant analysis (b) of ln- transformed body size measurements in *A. pusillus* for subareas.

6.3.5. *I. macrotis*

For *I. macrotis* only normal distribution and sexual dimorphism were analysed, because it was not possible to define tooth wear classes for *Idiurus* and *Zenkerella*. The calculations were made for specimens from southern Cameroon to Gabon (area 26, n = 7) and from the north-eastern Democratic Republic of Congo (area 32, n = 9). All measurements were normally distributed and none showed sexual dimorphism in both populations. Boxplots of the variables are shown in Figure 6.11. separately for females and males. Geographical populations differed significantly in the one-way ANOVA in total length ($P < 0.05$) and hindfoot length ($P < 0.005$). Arithmetic means, ranges and number of specimens are given in Table 6.6.

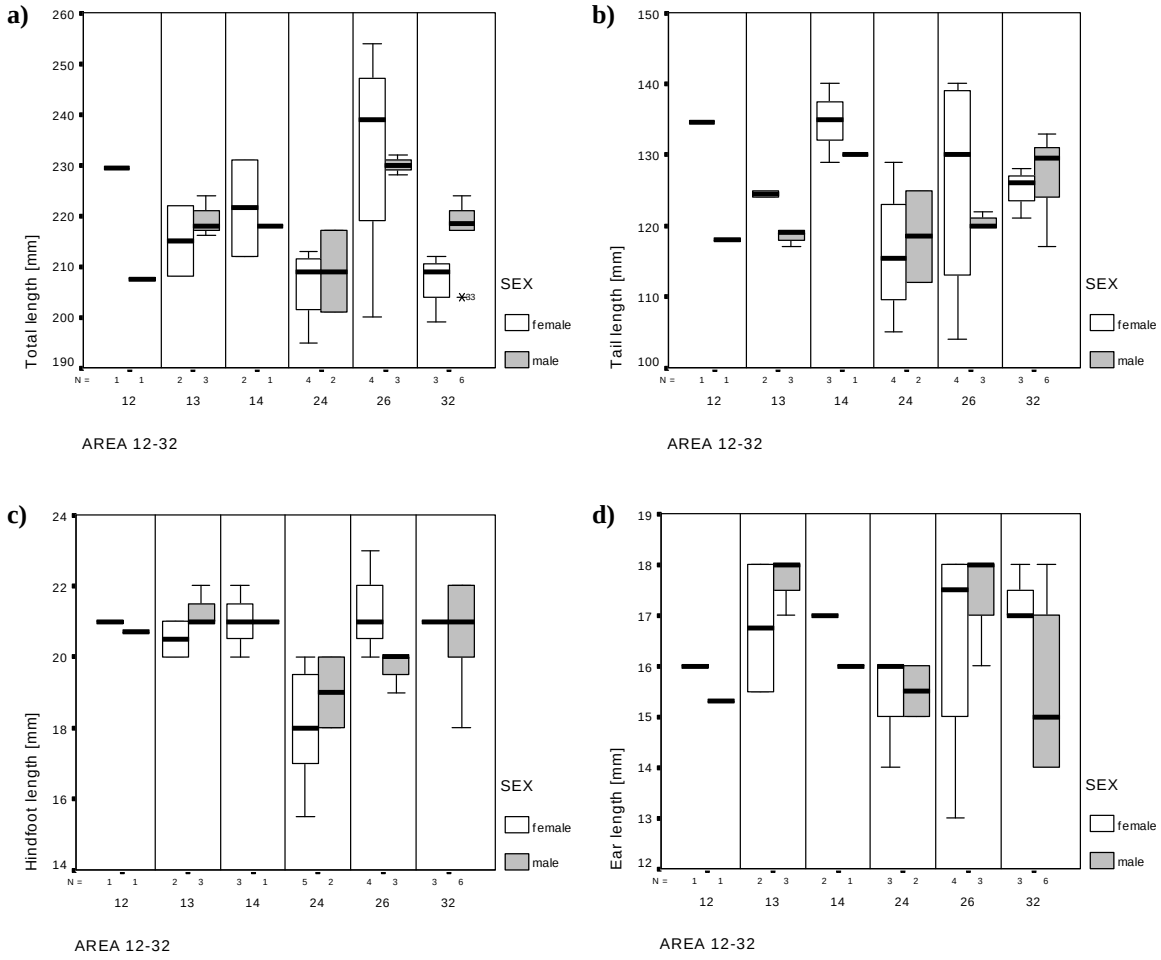

Figure 6.11. Median and quartiles of body size measurements in *I. macrotis* males and females.

Table 6.6. Body size measurements for different geographical populations (area number see Chap. 5, number of specimens in brackets) of *I. macrotis* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram).

Area	total length	head / body	tail length	hindfoot	ear length	weight
12 (2)	218 (208-229)	92 (90-95)	126 (118-135)	21 (21-21)	16 (15-16)	29 (24-35)
13 (5)	218 (208-224)	97 (83-105)	121 (117-125)	21 (20-22)	17 (16-18)	29 (23-40)
14 (4)	220 (212-231)	89 (83-96)	134 (129-140)	21 (20-22)	17 (16-17)	26 (-)
24 (7)	207 (201-217)	91 (84-96)	117 (105-129)	18 (16-20)	18 (14-16)	–
26 (7)	232 (200-254)	108 (96-116)	124 (104-138)	21 (19-23)	17 (13-18)	38 (37-39)
32 (9)	214 (199-224)	87 (78-94)	127 (117-133)	21 (18-22)	16 (14-18)	–

It was not possible to completely separate geographical populations of *I. macrotis* with the principal component analysis (Fig. 6.12) or with the discriminant analysis (Fig. 6.13), although there was less overlap between populations than for example in *A. derbianus* (Figs 6.5, 6.6). The discriminant analysis assigned 67.7% of the specimens correctly (n=31). When analysed separately for the sexes the percentage increased to 73.3% in females (n=15) and to 87.5% in males (n=16).

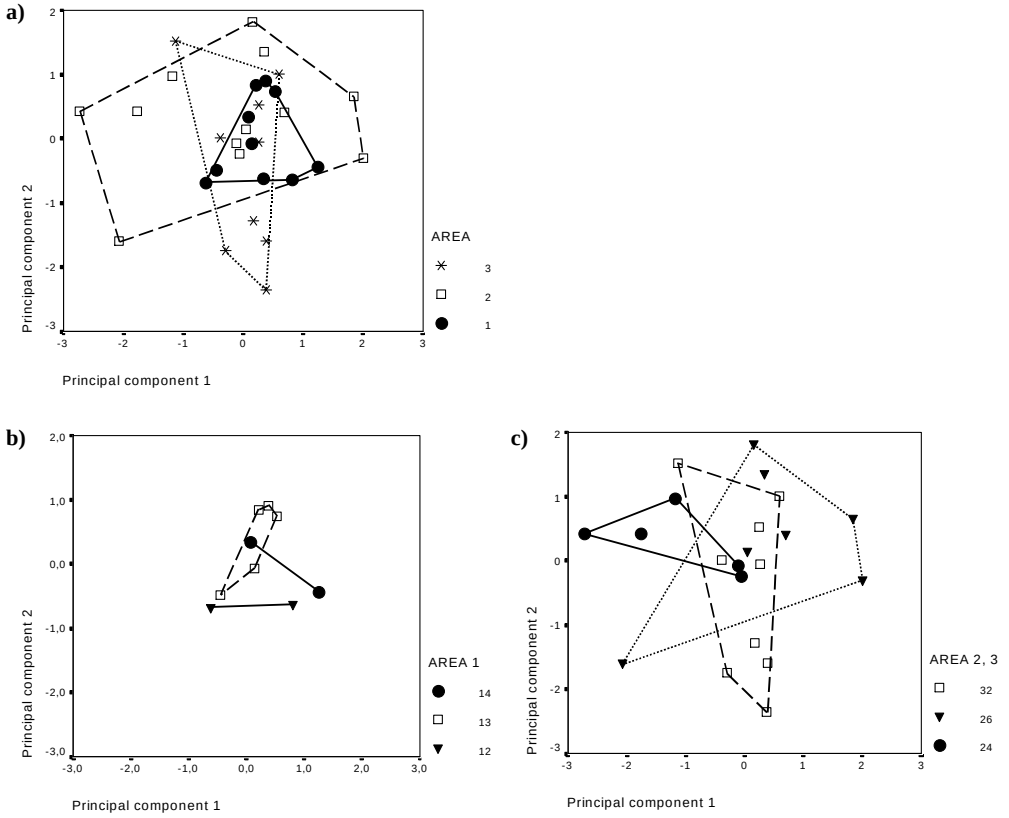

Fig. 6.12. Results of the principal component analysis of ln- transformed body size measurements in *I. macrotis* for main areas (a) and subareas (b-c).

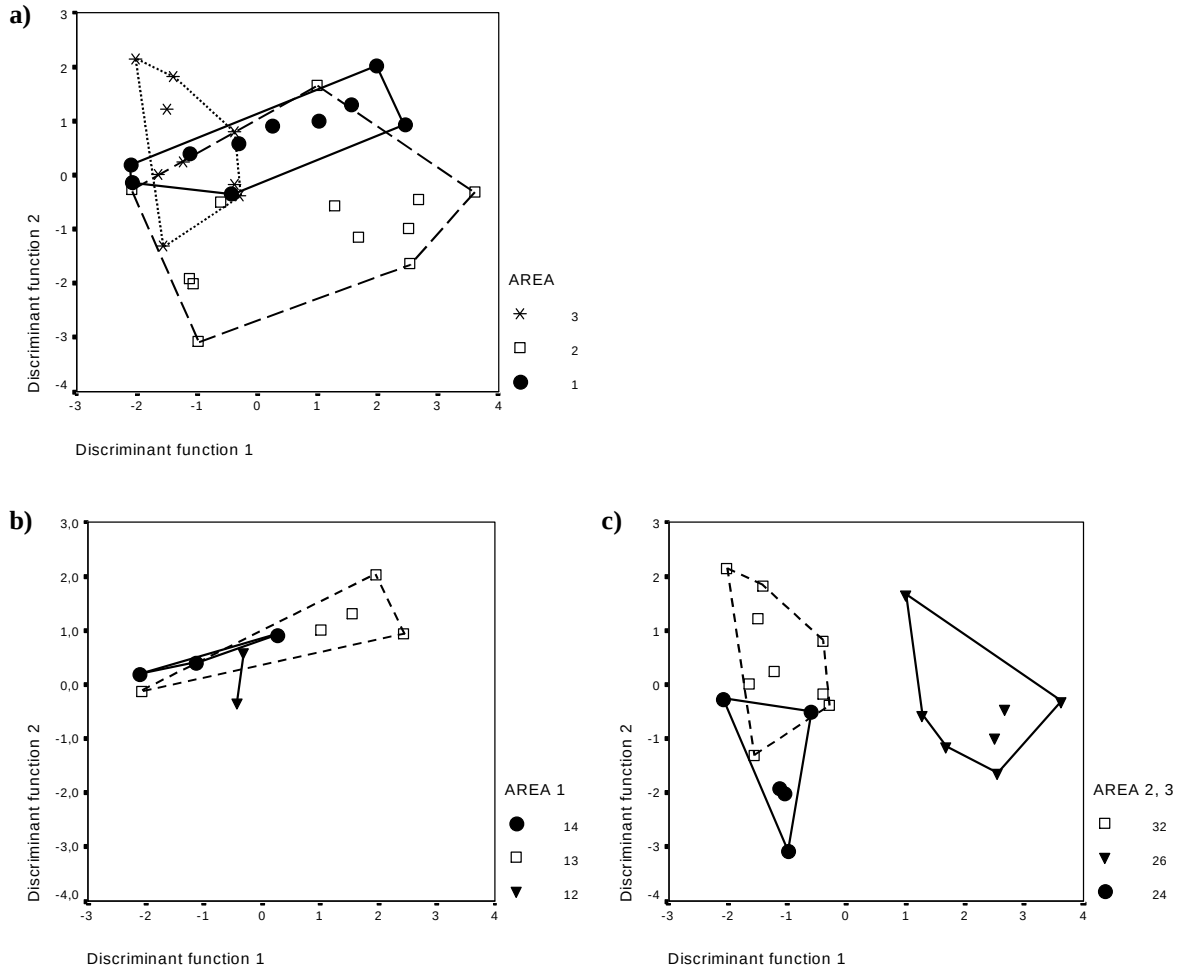

Figure 6.13. Results of the discriminant analysis of ln- transformed body size measurements in *I. macrotis* for main areas (a) and subareas (b-c).

6.3.6. *I. zenkeri*

Tests for normal distribution and sexual dependence were performed for the population from the northeastern Democratic Republic of Congo (area 32, n = 19). All measurements were normally distributed except for ear length ($P < 0.01$) and none showed statistically significant sexual dimorphism (Fig. 6.14). Differences between geographical populations were found for tail length ($P < 0.001$), hindfoot length ($P = 0.001$), and ear length ($P < 0.001$). Arithmetic means, ranges and number of specimens are given in Table 6.7.

In *I. zenkeri* the principal component analysis as well as the discriminant analysis produced a complete separation of the geographical populations (Fig. 6.15). The discriminant analysis assigned 100.0% of the specimens correctly (n=25).

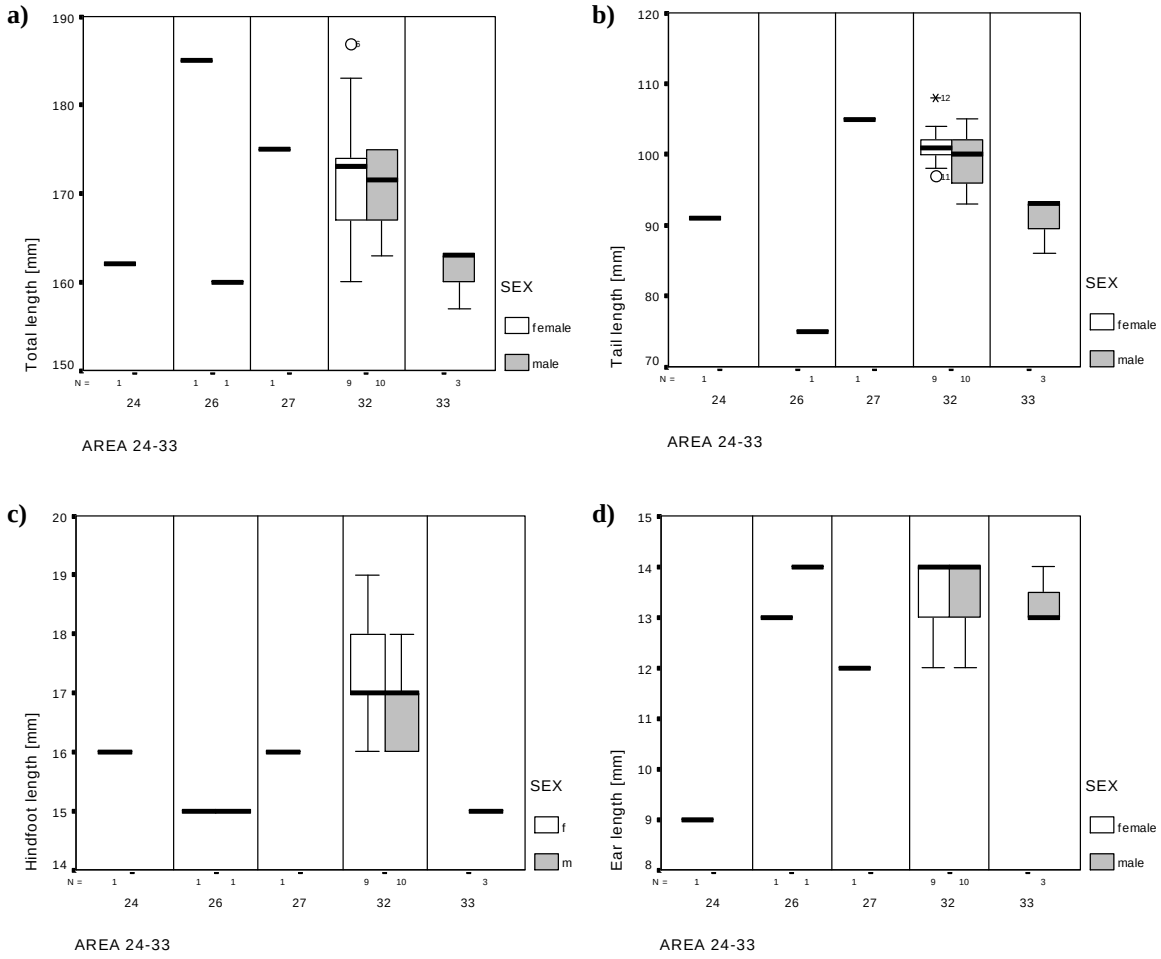

Figure 6.14. Median and quartiles of body size measurements in *I. zenkeri* males and females.

Table 6.7. Body size measurements for different geographical populations (area number see Chapter 5, number of specimens in brackets) of *I. zenkeri* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram).

Area	total length	head / body	tail length	hindfoot	ear length	weight
24 (1)	162 (-)	71 (-)	91 (-)	16 (-)	9 (-)	–
26 (2)	173 (160-185)	85 (-)	75 (-)	15 (15-15)	14 (13-14)	–
27 (1)	175 (-)	70 (-)	105 (-)	16 (-)	12 (-)	–
32 (19)	172 (160-187)	71 (62-86)	100 (93-108)	17 (16-19)	14 (12-14)	–
33 (3)	161 (157-163)	70 (70-71)	91 (86-93)	15 (15-15)	13 (13-14)	–

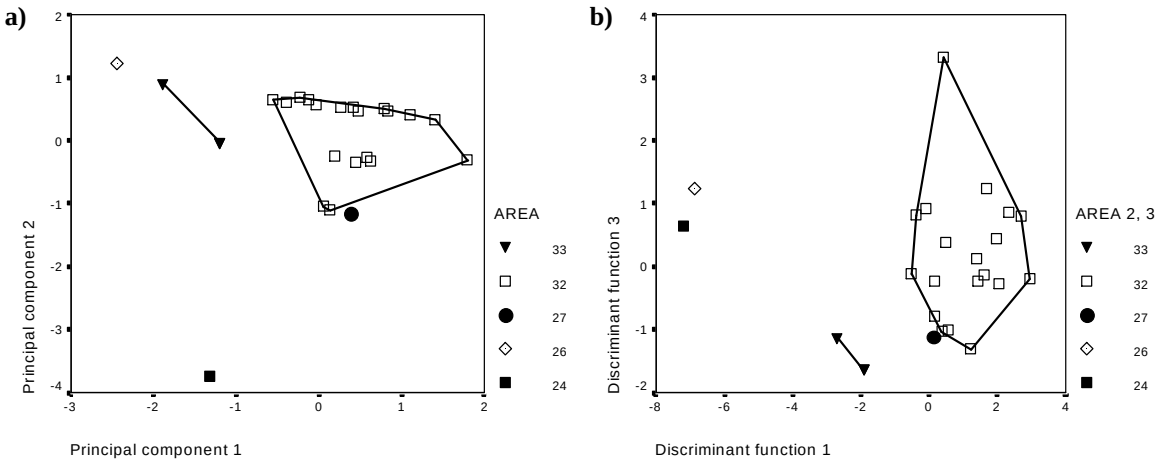

Figure 6.15. Results of the principal component analysis (a) and disciminant analysis (b) of ln-transformed body size measurements in *I. zenkeri* for subareas.

6.3.7. *Z. insignis*

For *Z. insignis* only body measurements from literature were available (Matschie, 1898; de Winton, 1898; Malbrant & Maclatchy, 1949; Aellen & Perret, 1958; Pérez del Val et al., 1995), which were in several cases taken from formalin preserved material. The data from the specimens from southern Cameroon to Gabon (area 26, n = 4) showed normal distribution. It was not possible to test for sexual dimorphism, because four specimens were males and the fifth not determined. The Kruskal-Wallis test showed no statistically significant differences between specimens from Bioko and the mainland. Boxplots of the characters are given in Figure 6.16, arithmetic means, ranges and number of specimens in Table 6.8.

Table 6.8. Body size measurements for different geographical populations (area number see Chap. 5, number of specimens in brackets; data from Matschie, 1898; de Winton, 1898; Malbrant & Maclatchy, 1949; Aellen & Perret, 1958; Pérez del Val et al., 1995 of *Z. insignis* (arithmetic mean, range in brackets; length measurements in millimetres, weight in gram).

Area	total length	head / body	tail length	hindfoot	ear length	weight
21 (1)	365 (-)	187 (-)	178 (-)	40 (-)	23 (-)	460
26 (4)	358 (305-390)	201 (180-225)	157 (125-170)	42 (40-44)	19 (14-22)	–

For the body measurements of *Z. insignis* it was possible to separate the specimen from Bioko (area 21) from the mainland population with the principal component analysis and with the discriminant analysis, although the latter produced only one discriminant function (Fig. 6.17), but 100.0% of the specimens were assigned correctly (n=5).

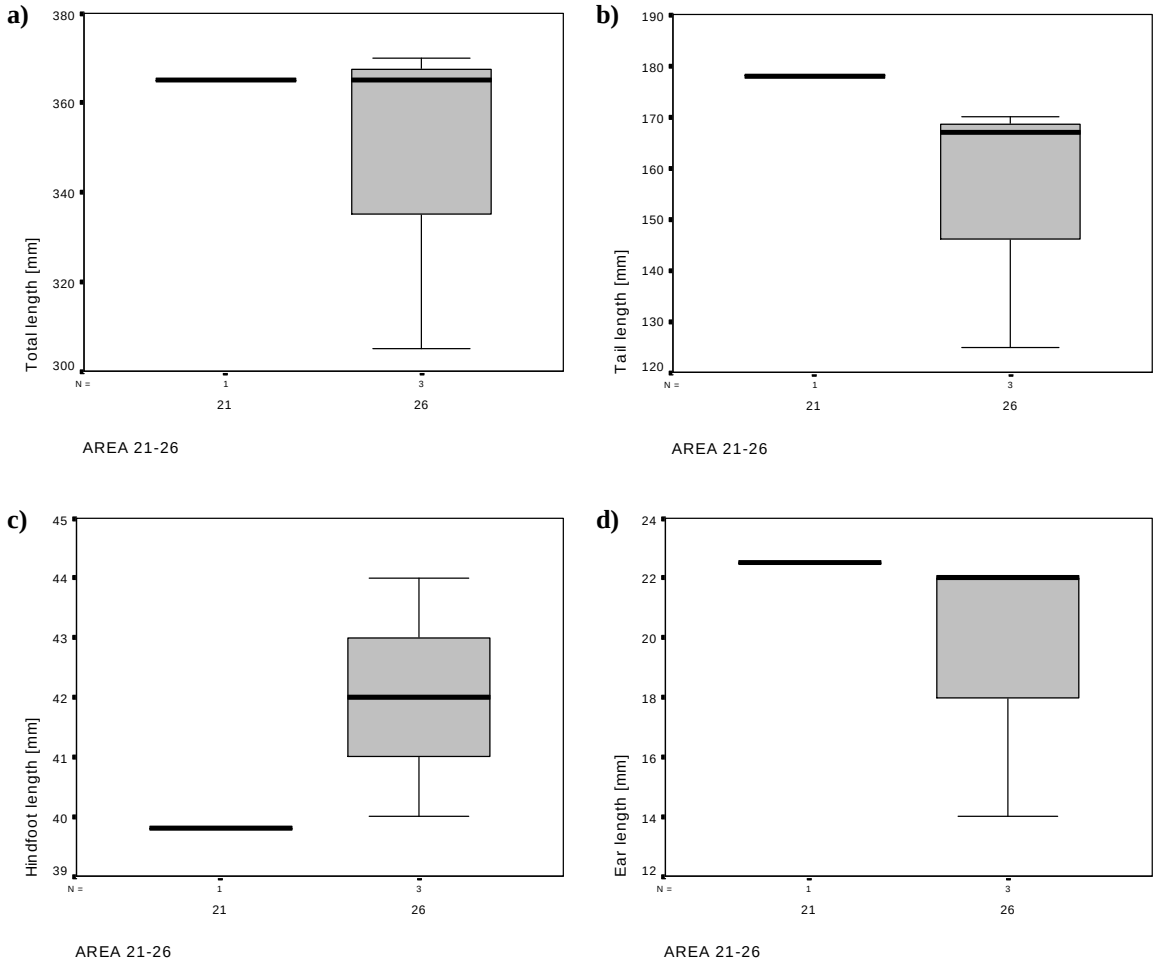

Figure 6.16. Median and quartiles of body size measurements in *Z. insignis*.

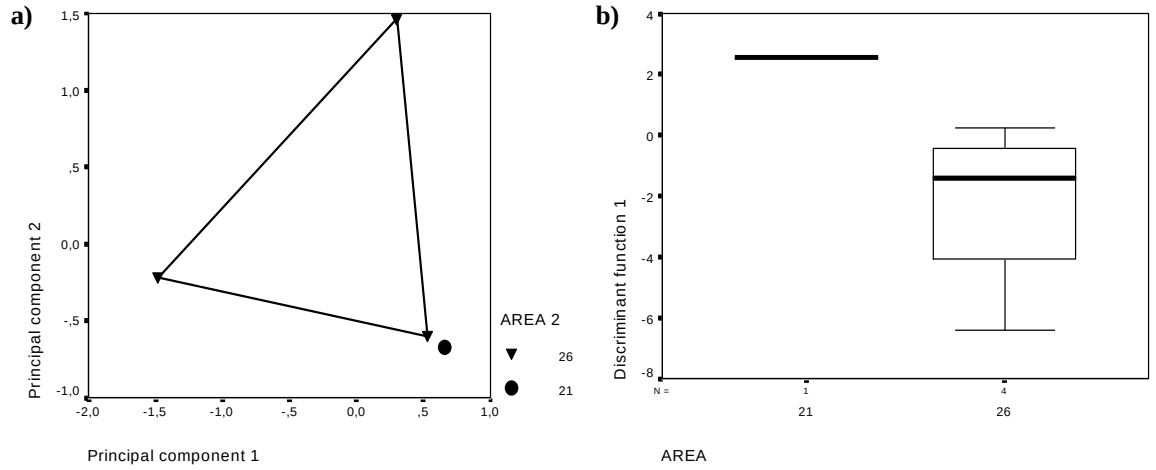

Figure 6.17. Results of the principal component analysis (a) and discriminant analysis (b) of ln-transformed body size measurements in *Z. insignis* for subareas.

6.3.8. Combined analysis of all species

Combined analyses including all seven species yielded a clear separation except for a considerable overlap between *A. beecrofti* and *A. derbianus* (Fig. 6.18). As expected species were mainly separated based on size, as represented by the first axis, only the distinction between *A. pusillus* and *Z. insignis*, which are relatively close in size (Tab. 6.9), is based rather on form differences, as represented by the second axis. 96.9% of the specimens were assigned correctly with the DA (n=360).

Table 6.9. Body size measurements for different species of Anomaluridae (arithmetic mean, range in brackets; in millimetres).

Species	**total length**	**head / body**	**tail length**	**hindfoot**	**ear length**
A. beecrofti	519 (418-620)	308 (217-380)	210 (158-260)	54 (37-66)	29 (22-33)
A. derbianus	567 (450-742)	314 (224-400)	253 (175-360)	60 (40-69)	37 (23-47)
A. pelii	865 (780-990)	429 (368-546)	437 (325-550)	82 (70-92)	45 (39-50)
A. pusillus	373 (335-406)	228 (194-255)	145 (120-136)	44 (37-51)	30 (27-36)
I. macrotis	218 (199-254)	94 (78-116)	124 (104-140)	20 (16-23)	16 (13-18)
I. zenkeri	170 (157-185)	72 (62 - 86)	98 (75-108)	17 (15-19)	13 (9-14)
Z. insignis	359 (305-390)	198 (180-225)	161 (125-178)	41 (40-44)	20 (14-23)

6.4. Discussion

The results for the body size analyses are not unequivocal and show several differences between the species. This could be at least partially caused by the fact that although all measurements are standard characters, they were not taken by the same person, which might in some cases also stress differences between geographical areas if there was just one collector. Additionally sample sizes for several areas were small, in the majority of cases less than 10, which makes reliable statements concerning statistical significance difficult.

However, there are some general and species specific results. First of all, with one exception all characters were normally distributed, which seems to exclude too strong influences by the collector, because most of the specimens used in the analyses were collected by more than one person. Age seems to play a minor role for the measured characters, because the significance was generally low and only for subsamples of populations, e.g. in males only.

The first general statement concerns sexual dimorphism. In the three *Anomalurus* species were statistically significant differences between sexes frequently found. The boxplots of *A. beecrofti*, *A. derbianus*, *A. pelii* and *A. pusillus* show a tendency towards higher values in females than in males, although it was not statistically significant in *A. beecrofti*. In *Idiurus* no sexual dimorphism for body size was found, and it was not possible to check it for *Zenkerella*.

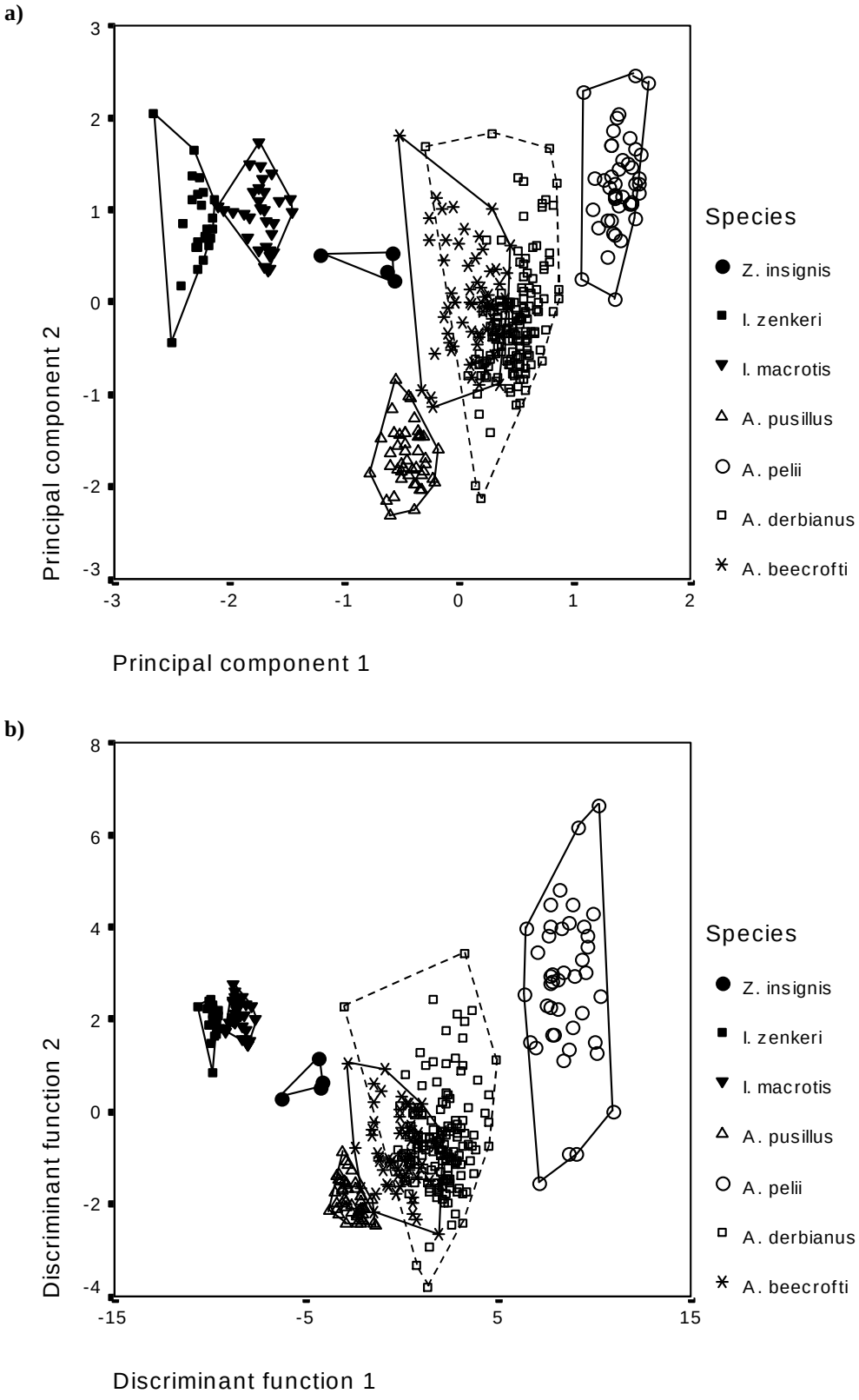

Figure 6.18. Results of the principal component analysis (a) and discriminant analysis (b) of ln-transformed body size measurements in anomalurids for the different species.

In spite of the sexual dimorphism the results of the multivariate analyses did not change basically when performed for the complete sample or for females and males separately, but there are pronounced differences between species. In *A. beecrofti* it was not possible to separate specimens from main areas (area 1-4, see Chap. 5), but the West African (area 1) subpopulations, those from Bioko (area 21), from the Mamfe area (area 24), and the central African (area 3) and the southern populations (area 4) could be distinguished from their neighbouring populations. For *A. derbianus* and *A. pelii* the resolution of geographical populations was rather bad. Besides single specimens of *A. derbianus* from one area only the neighbouring populations from Zambia (area 42) and south-western Tanzania (area 43) could be separated by their body size characters, and all populations of *A. pelii* overlapped to a large extent. Much better was the distinction between populations of *A. pusillus*, where only one Liberian specimen and the single specimen from the north-western Democratic Republic of Congo (area 31) clustered within the population from area 32, while there was no overlap between specimens from the other populations. All populations and subpopulations of *I. macrotis* overlapped more or less, only the specimens from southern Cameroon to Gabon (area 26) could be separated from their neighbours with the discriminant analysis. Finally in *I. zenkeri* and *Z. insignis* there was a clear distinction between all (sub)populations with body size characters possible.

A distinction on the species level was possible for most species except for a considerable overlap in *A. beecrofti* and *A. derbianus*.

However, a larger data set would be desirable in order to draw final conclusions from these findings. Although the absolute sample size seems not to account for the possibility to separate geographical populations, when for example *A. pelii* and *A. pusillus* are compared, it would rise the significance of the results very much, when more populations were represented by more than one to three specimens.

References

Aellen, V. & Perret, J. 1958. Sur une nouvelle trouvaille de *Zenkerella insignis* Matschie, 1898 (Rodentia, Anomaluridae). *Säugetierkundliche Mitteilungen* **6**: 21-23.

Malbrandt, R. & Maclatchy, A. 1949. Faune de l'Équateur Africain Francais. tome 2. Mammifères. *Encyclopédie biologique* **36**. Lechevalier, Paris.

Matschie, P. 1898. Eine neue mit *Idiurus* Mtsch. verwandte Gattung der Nagethiere. *Sitzungsberichte der Gesellschaft Naturforschender Freunde Berlin*: 23-30.

Pérez del Val, J., Juste, J. & Castroviejo, J. 1995. A review of *Zenkerella insignis* Matschie, 1898 (Rodentia, Anomaluridae). First records in Bioko island (Equatorial Guinea). *Mammalia* **59 (2)**: 441-443.

Winton, W. E. de 1898a. On a new Genus and Species of Rodents of the Family Anomaluridae, from West Africa. *Proc. Zool. Soc. Lond.*: 450-454.

7. Skull size and shape

Abstract. For the present analysis up to 64 craniometric characters had been measured for 1085 skulls of all seven species of Anomaluridae. Normal distribution, sexual dimorphism and age dependence of the characters were checked for one to three geographical populations of each species and multivariate analyses (principal component analysis and discriminant analysis) were performed for each of the species (except for *Z. insignis*, where only four skulls were available) and for all species together. The principal component analyses were calculated with ln-transformed values as well as with standardized residuals for gum length. A considerable amount of sexual dimorphism and age dependence was observed, which showed a clear correlation with the number of specimens used in the analyses. However, these factors seemed to be of very little significance for the results of the multivariate analyses. The geographic variation in craniometric characters displayed strong differences between species. In *A. beecrofti*, *A. derbianus*, and *A. pelii* only a small number of geographic populations could be distinguished from the homogenous rest. *A. pusillus*, *I. macrotis*, and *I. zenkeri* showed well defined clusters with little overlap between geographical populations. Species could be relatively well separated with the principal component analyis for ln-transformed values, but unexpectedly no differences could be found with standardized residuals. The factors influencing the results for sexual dimirphism, age dependence and the discriminant analyses are discussed.

7.1. Introduction

A previous analysis of fur colouration (Chap. 4) revealed some strong differences between geographical populations in *A. beecrofti*, *A. derbianus*, and *A. pelii*. For the other species it was not possible to define different colouration classes, but some geographical variation was found in body size characters in these species (Chap. 6). However, differences between geographical populations in colouration is not necessarily matched by body size characters. Therefore the results of the largest data set in the investigation with 1085 skulls with up to 64 measured characters was of special interest.

7.2. Material and methods

Data for the analysis of skull size and shape were based on measurements taken with a digital caliper to the nearest 0.01 mm. For definition of measured characters see Figure 7.1 and Table 7.1.

Table 7.1. Cranial and dental measurements taken from anomalurid skulls (* not measured in *Idiurus* and *Zenkerella*).

TL	total length
CIL	condylo-incisive length
BL	basal length
ZB	zygomatic breadth
RB	breadth of rostrum
NL*	length of nasal bones
NB	breadth of nasal bones
IOB	interorbital breadth
PPOB*	width of postorbital processes
BCB	breadth of braincase
CSB1*	smallest width of sagittal cristae behind postorbital processes
CSB2*	largest width of sagittal cristae
CSB3*	smallest width of sagittal cristae posterior to CSB2
GL	gum length
PPBL	postpalatine basal length
DL	length of diastema
FIL	length of incisive foramen
FIB	width of incisive foramen
BP4	gum width at P4
BM1	gum width at M1
BM3	gum width at M3
CHB	with of choana
BUL	length of bulla
BUB	width of bulla
RH	height of rostrum
ZH	heigth of zygomatic arc
PFZH	height of Pr. frontalis zygomatici
SKH	height of skull at molar teeth
ZP	position of zygomatic arc
BCH	height of braincase
CZB	width between posterior ends of zygomatic arcs
FIOH	heigth of infraorbital foramen
FIOB	width of infraorbital foramen
URL	upper length of rostrum
LRL	lower length of rostrum
ML	length of mandible
MHA	height of mandible at articular process
MHD	height of mandible at diastema
PAAD	distance between articular and angular process
PCH	height of coronoid process
UCL	upper crown length of molar teeth
UAL*	upper alveolar length
UIL	length of upper incisor
UIB	width of upper incisor
UP4L	length of upper P4
UP4B	width of upper P4
UM1L	length of upper M1
UM1B	width of upper M1
UM2L	length of upper M2
UM2B	width of upper M2
UM3L	length of upper M3
UM3B	width of upper M3
LCL	lower crown length of molar teeth
LAL*	lower alveolar length
LIL	length of lower incisor
LIB	width of lower incisor
LP4L	length of lower P4
LP4B	width of lower P4
LM1L	length of lower M1
LM1B	width of lower M1
LM2L	length of lower M2
LM2B	width of lower M2
LM3L	length of lower M3
LM3B	width of lower M3

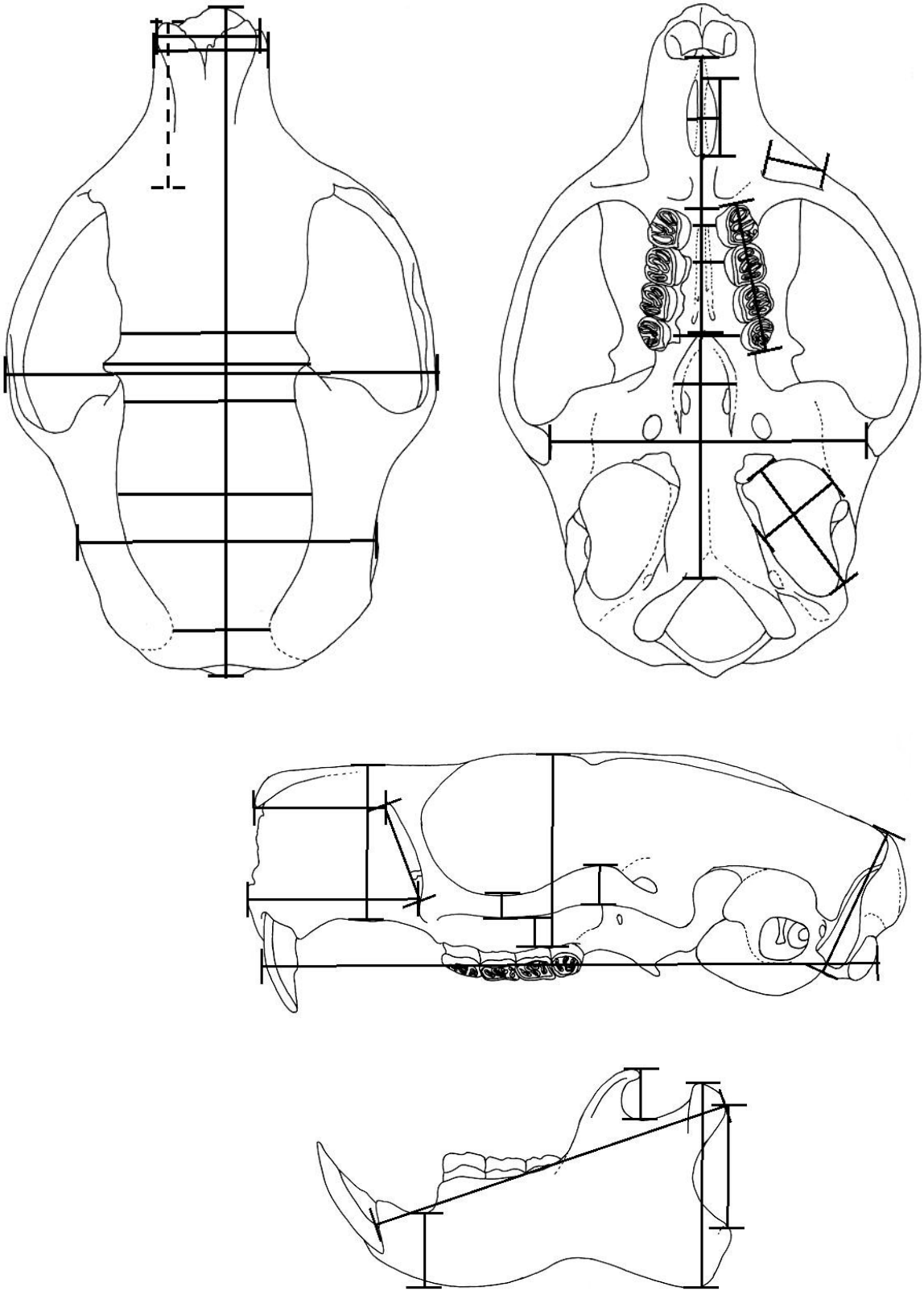

Figure 7.1. Measured characters of skull and mandible, single tooth measurements not shown.

The analysis was restricted to adult specimens, defined by all molar teeth having reached the occlusal level. Table 7.2 gives the number of specimens used in the analysis.

Table 7.2. Number of specimens used for the skull size and shape analysis.

	Age class				
Species	**2**	**3**	**4**	**5**	**all**
A. beecrofti	21	83	56	31	191
A. derbianus	112	226	143	37	521
A. pelii	22	60	56	-	139
A. pusillus	12	68	24	7	112
I. macrotis		age classes not defined			68
I. zenkeri		age classes not defined			51
Z. insignis		age classes not defined			3

7.2.1. Age classes

Specimens of *Anomalurops* and *Anomalurus* were assigned to relative age classes according to wear of molar teeth (Fig. 7.2). For *Idiurus* and *Zenkerella* it was not possible to define age classes because of the completely different dentition (Fig. 7.2).

Age class 1: Juveniles; at least the last molar has not completely reached the occlusal level. Teeth show usually no wear. Members of this age class were not used in the analysis.
Age class 2: Young adults; teeth with only slight traces of wear, especially in the 4th premolar and 1st molar teeth, surrounding enamel ring with partly blunt edges, inner enamel islands at least partly still fused with outer enamel ring.
Age class 3: The most frequent age class; all enamel parts with defined edges, enamel islands separated from surrounding ring, but still in contact with or close to it. The surface of the teeth appears flat.
Age class 4: The secondmost frequent age class; enamel islands separated from each other and the surrounding ring by dentine, inner enamel islands have still at least 50% of their original diameter.
Age class 5: Old animals; inner enamel islands have less than 50% of the original diameter. In very worn teeth these islands can disappear completely.

7.2.2. Statistics

Data were tested for normal distribution with the Kolmogorov-Smirnov test. Relationships between skull measurements and sex, age, and finding locality were checked with a one-way ANOVA and/or with a Kruskal-Wallis test if variances of the respective characters were not homogeneous. These tests were for each species restricted to specimens of one or more areas

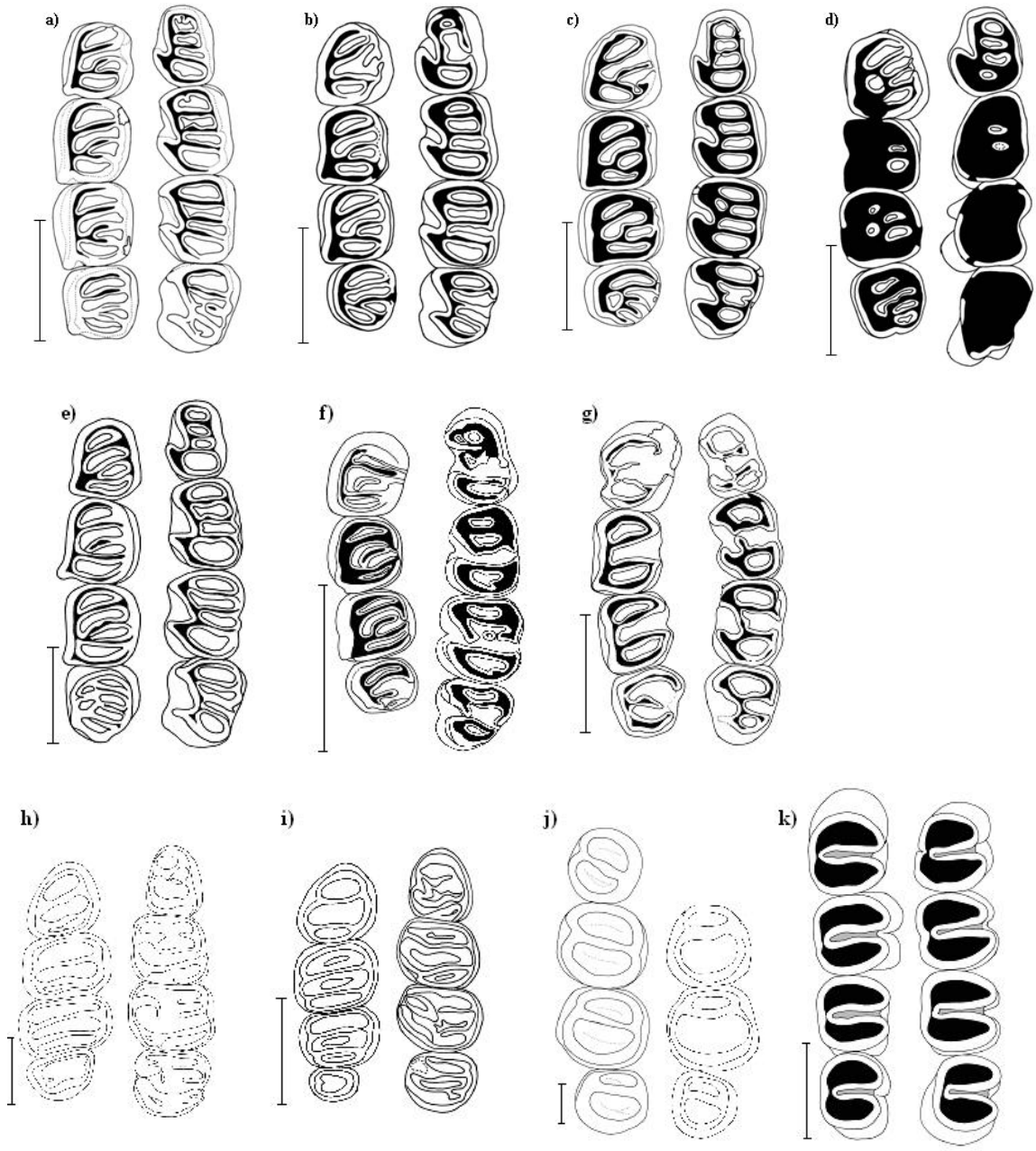

Figure 7.2. Left upper and lower molar teeth of Anomaluromorpha. a-d: Age classes in *A. derbianus*, a: age class 2 (ZFMK 61.957), b: age class 3 (ZFMK 64.492), c: age class 4 (73.363), age class 5 (ZFMK 64.491); e: *A. pelii* (SMNK N.N.), f: *A. pusillus* (ZMB 36326), g: *A. beecrofti* (ZFMK 64.503), h: *I. macrotis* (ZMB 22885), i: *I. zenkeri* (ZMB 22757), j: *Z. insignis* (ZMB 10085, lower P4 missing), k: *P. capensis* (ZFMK 56.946).

(see Chap. 5 for area definition) with the highest number of individuals in order to avoid biases caused by geographic variation.

Multivariate analyses (principal component analysis (PCA) and discriminant analysis (DA)) were calculated with ln-transformed values. All statistical and multivariate analyses were performed in SPSS 10. 0. For tests of geographical variation specimens were grouped in areas according to Chapter 5.

7.3. Results

7.3.1. *A. beecrofti*

Normal distribution, sexual dimorphism, and age dependence were tested for specimens from West Africa (area 1) and the subareas southern Cameroon to Gabon (area 26, n=48) and western Democratic Republic of Congo (area 33, n=18). All characters were normally distributed in all three populations, but several characters showed either sexual dimorphism or age dependence (see Tables 7.3, p. 124 and 7.4, p. 126 for details). Because of this result the multivariate analyses were performed for various combinations of subsamples.

First it was checked how far the number of characters used in the analysis influences the results, because when all characters are used the number of specimens is relatively low, while all excluded characters necessarily also exclude information (Fig. 7.3). For this test all specimens regardless of their sex and age were used in a principal component analysis (PCA), starting with an analysis using all characters, thus reducing the number of specimens to 20 out of 192. In the next analyses the characters were stepwise excluded by the number of specimens for which they were available, with all characters measured for at least 120 specimens (characters n=62, specimens n=38), 130 specimens (characters n=58, specimens n=46), 140 specimens (characters n=56, specimens n=53), 150 specimens (characters n=52, specimens n=65), 160 specimens (characters n=44, specimens n=84), 170 specimens (characters n=31, specimens n=106), and 180 specimens (characters n=14, specimens n=139). In *A. beecrofti* the loss of information and the addition of specimens show a very regular progress with no great changes between neighbouring diagrams (Fig. 7.3). General patterns like the gap between specimens from West Africa (area 1) and Angola (area 4) and the only slight overlap between West African (area 1) and Central African (area 3) individuals remain until more than 50% of the characters are excluded (Fig. 7.3 g) and collapse when the set of characters is reduced to less than 25% (Fig. 7.3 h). In the latter case the data set consists almost exclusively of single tooth measurements. For the following analyses the data set with all characters available for at least 160 specimens was used (Fig. 7.3 f), because it showed the best combination of relatively high numbers of characters (69%) and specimens (44%) respectively.

Figure 7.4 shows again the principal component analysis for the 44 characters available for more than 160 specimens, first for the main areas and than separately for the subareas. The resolution within West Africa (area 1) is relatively good with only very little overlap between subpopulations, while specimens from western Central Africa (area 2) overlap to a large extent, and individuals from Central Africa (area 3) and southern areas (area 4) show a separation of specimens from south of the Congo River (area 35).

In the next step specimens of the age classes 2 and 5 were excluded from the analysis in order to minimise the influence of age dependence of the characters. However, in spite of the at least partially very high amount of age dependent characters the results do not change much (Fig. 7.5).

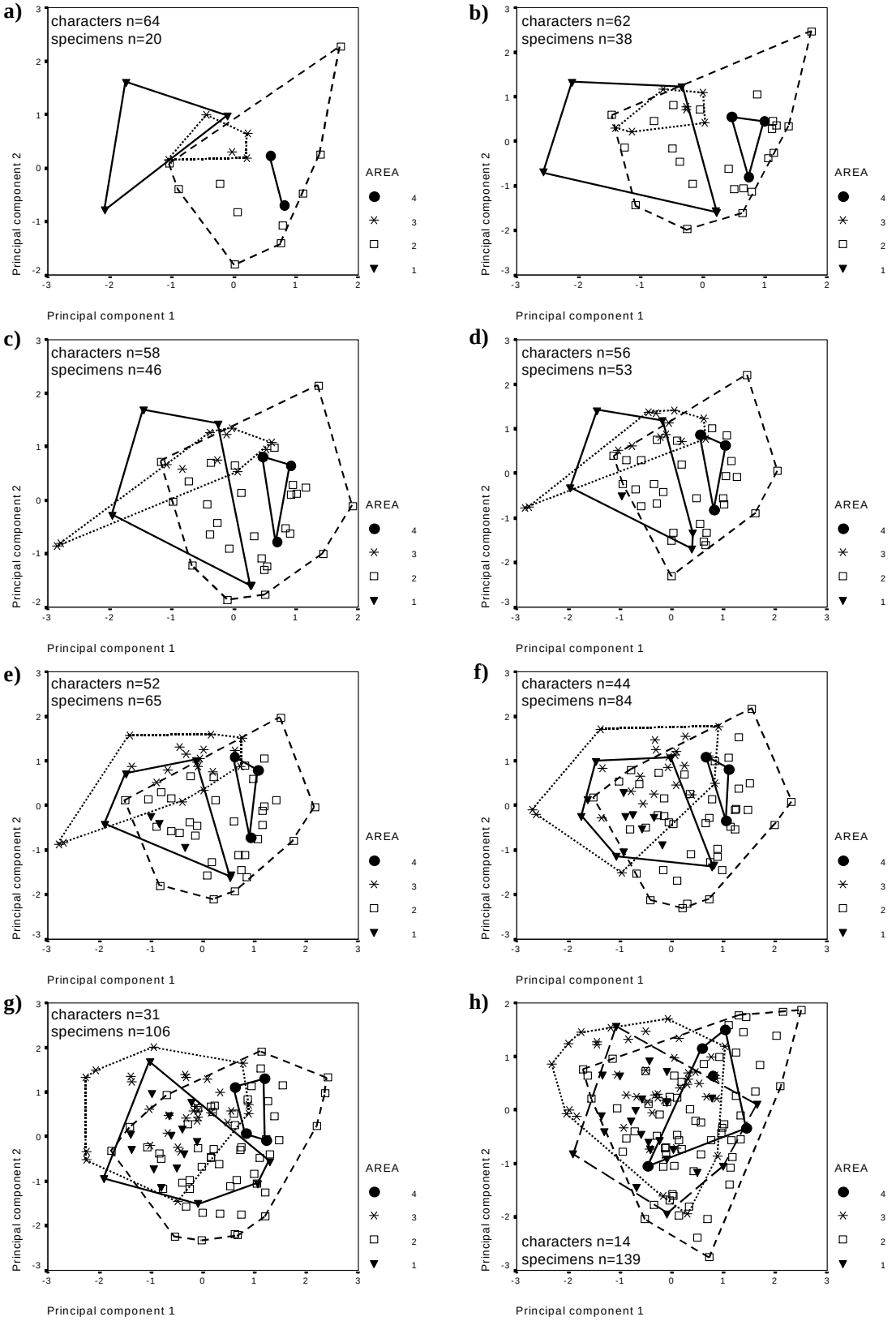

Figure 7.3. Results of the principal component analysis with different numbers of characters for *A. beecrofti*.

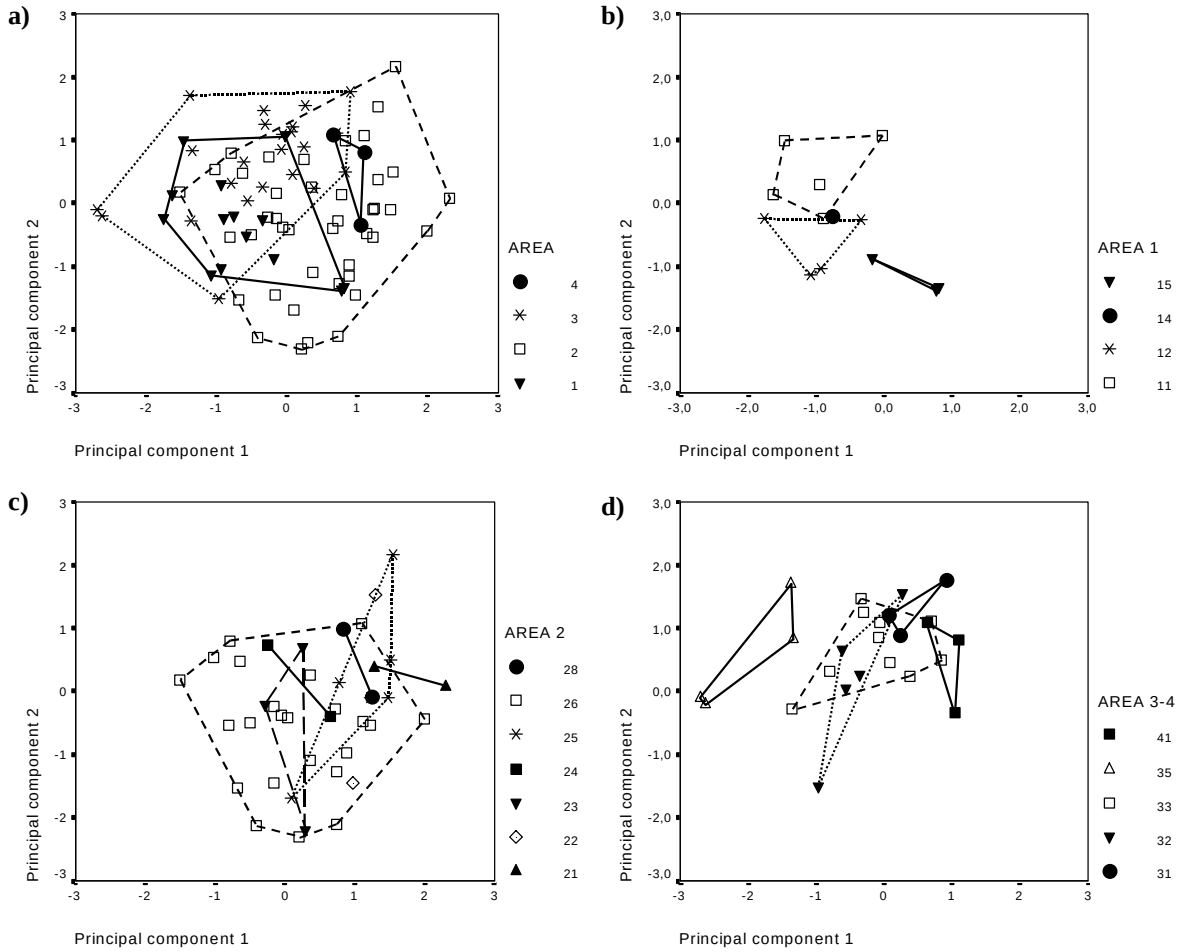

Figure 7.4. Results of the principal component analysis with 44 characters for *A. beecrofti* marked according to the main area (a) and subareas (b-d).

The two following analyses were performed for females (Fig. 7.6) and males (Fig. 7.7) separately and restricted to specimens of the age classes 3 and 4 (see above). In these cases the numbers of specimens decreases considerably (24 females, 17 males) and results are difficult to compare because several subpopulations lack completely in at least one data set and the remaining ones are frequently represented by single specimens only. Additionally, results for females and males are in several cases contradicting, e.g. the main area 2 overlaps with the others in females but not in males, and areas 3 and 4 are well separated in females but only weakly in males.

Finally the calculations were repeated for the complete data set (all ages and sexes) with all characters available for at least 160 specimens, but with the residuals for gum length, in order to analyse particularly differences of shape and exclude size (Fig. 7.8). In this analysis the separation between specimens from Angola (area 4) and West and Central Africa (areas 1 and 3) becomes more pronounced, while the overlap between the latter two and western Central Africa (area 2) increases. The results for the subareas show also slight differences with specimens from

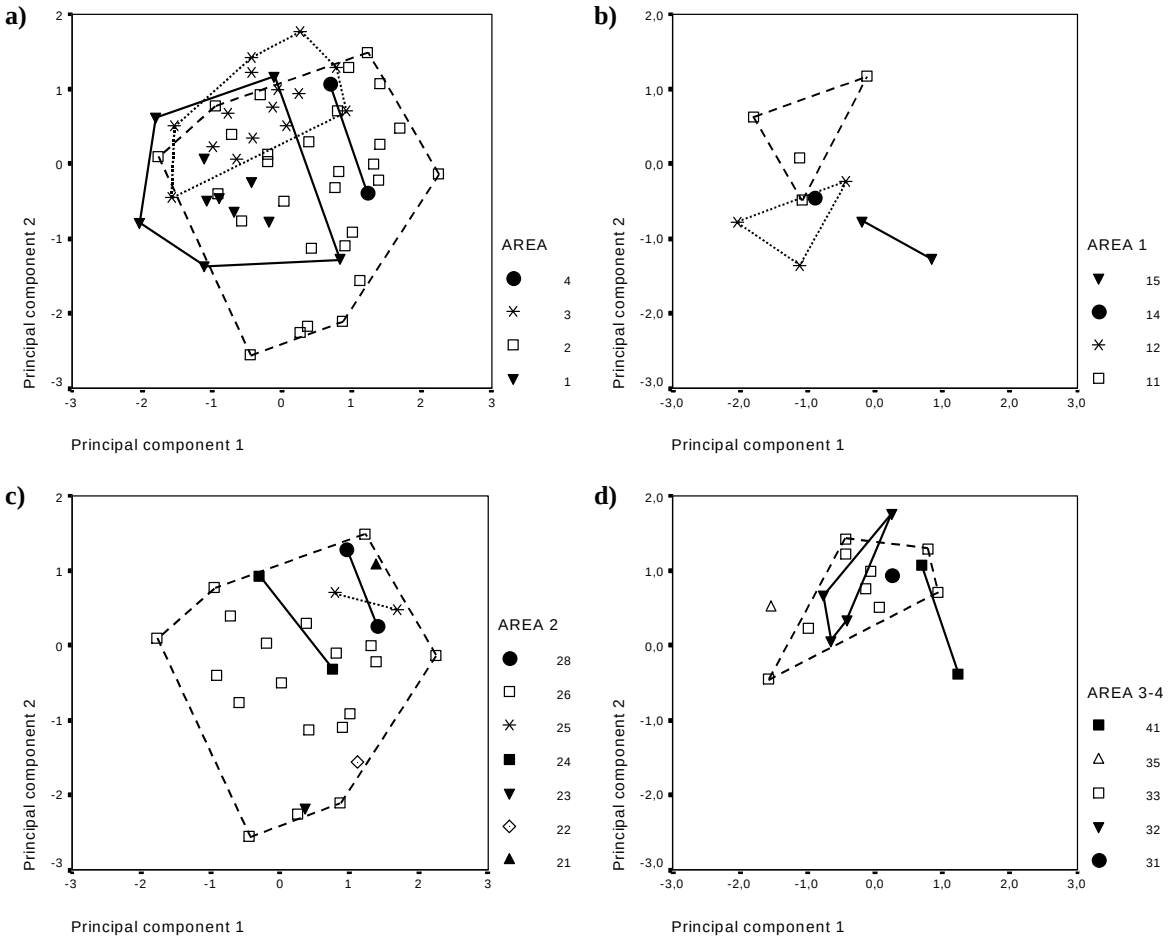

Figure 7.5. Results of the principal component analysis with 44 characters for *A. beecrofti* marked according to the main areas (a) and subareas (b-d) and restricted to specimens of the age classes 3 and 4.

Togo (area 15) now overlapping partly with specimens from eastern Liberia to western Ivory Coast (area 12) and the specimens collected south of the Congo River (area 35) with the other Central African specimens (area 31-33), while the Angolan individuals are now clearly separated. The discriminant analysis for the four main areas (Tab. 7.6, p. 129) yielded correct groupings of 86.8% (n=53) with all characters except for length of nasals included (but with 29 characters, mainly teeth measurements, excluded by SPSS because of failed test of tolerance). When using all characters available for at least 120 specimens the value increases to 89.8% (n=49, 28 characters failed tolerance test), for characters measured for more than 130 specimens it rises to 98.0% (n=49, 16 characters failed tolerance test) and to 100.0% with characters available for at least 140 (n=53, 8 characters failed tolerance test), 150 (n=65), and 160 (n=84) specimens, but drops again to 91.3% when only characters measured for at least 170 specimens were used (n=106) and to 74.8% for characters available for more than 180 specimens (n=151).
For the subareas the discriminant analysis grouped 81.1% of the specimens correctly (n=54, 13 subareas, 39 characters failed tolerance test) when all characters except nasal length were used.

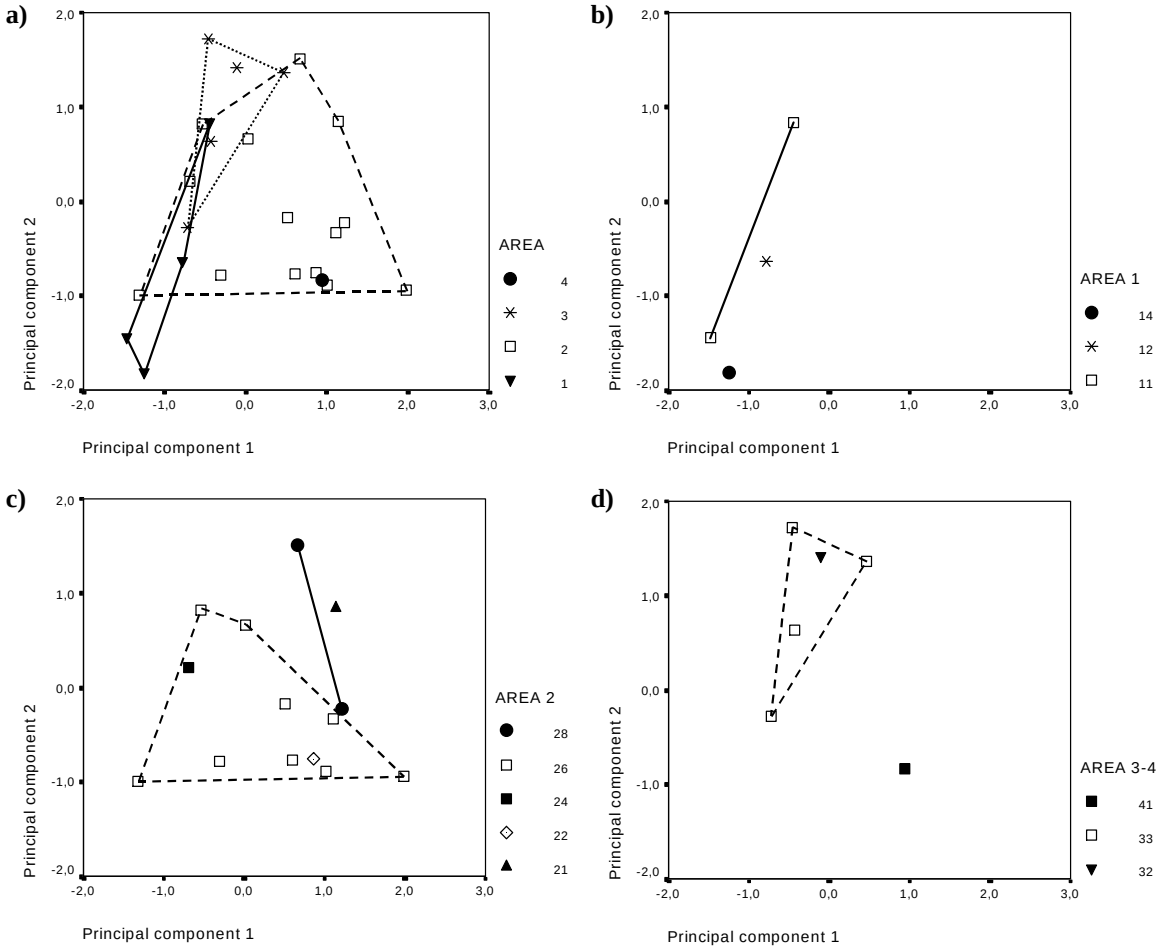

Figure 7.6. Results of the principal component analysis with 44 characters for *A. beecrofti* marked according to the main areas (a) and subareas (b-d) and restricted to females of the age classes 3 and 4.

After restricting the analysis to characters measured for at least 120 specimens the percentage decreased to 79.2 % (n=54, 13 subareas, 38 characters failed tolerance test) and increased again to 86.0% with all characters available for more than 130 specimens (n=60, 15 subareas, 28 characters failed tolerance test), to 89.7 with all characters measured for more than 140 (n=61, 16 subareas, 21 characters failed tolerance test), and to 100.0% for all measurements available for more than 150 (n=65, 16 subareas, 5 characters failed tolerance test) and 160 specimens (n=84, 16 subareas). When only characters measured for at least 170 specimens were used the percentage decreased to 96.0% (n=106, 16 subareas) and to 66.4% for all characters available for more than 180 specimens (n=151, 18 subareas). A summarizing table for the discriminant analysis is given in Table 7.7 (p. 130).

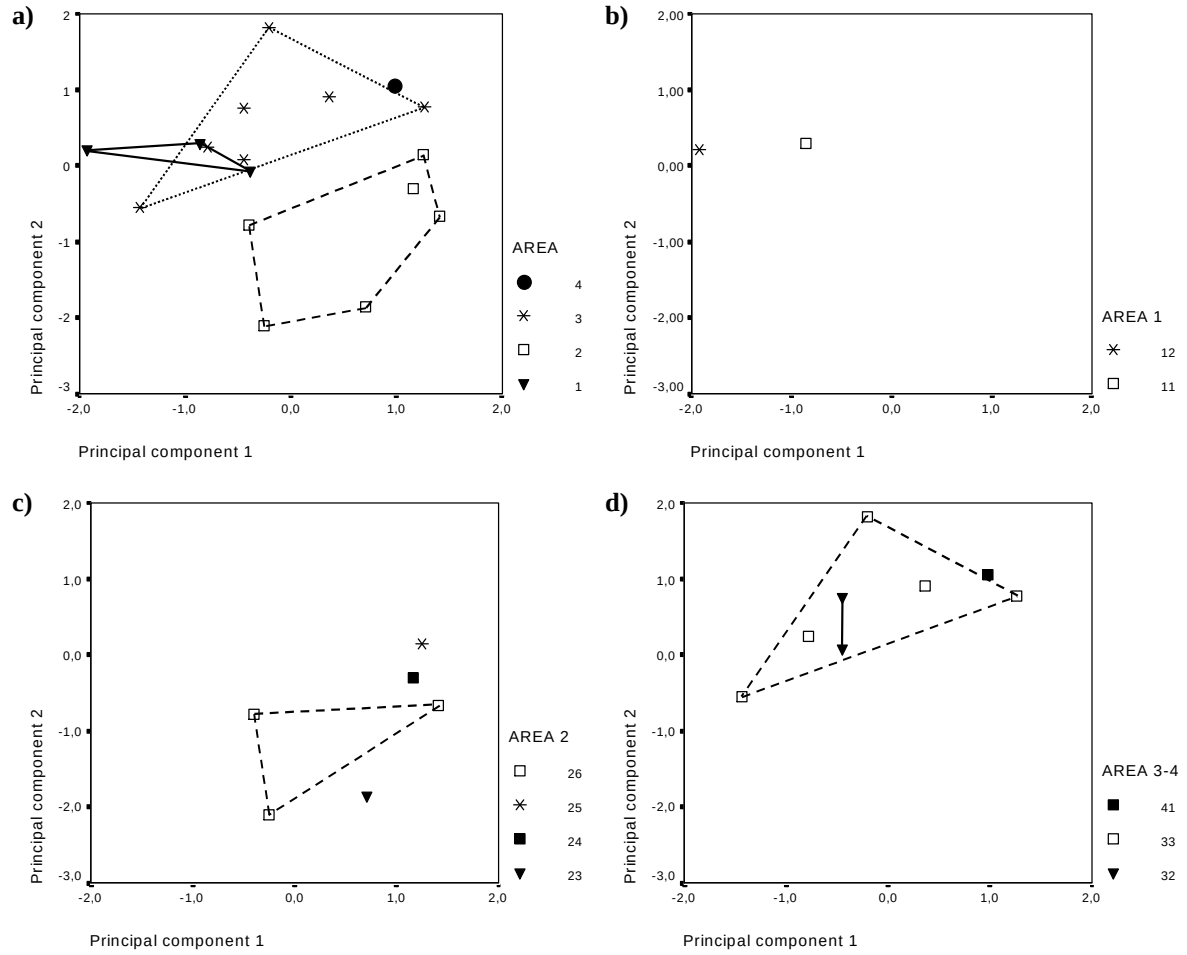

Figure 7.7. Results of the principal component analysis with 44 characters for *A. beecrofti* marked according to the main areas (a) and subareas (b-d) and restricted to males of the age classes 3 and 4.

7.3.2. *A. derbianus*

Tests for normal distribution, sexual dimorphism and age dependence were performed for West Africa (area 1, n=63), and the subareas southern Cameroon to Gabon (area 26, n=65) and north-western Democratic Republic of Congo (area 32, n=98). All characters were normally distributed in all three populations but like in *A. beecrofti* showed for several characters sexual dimorphism and/or age dependence in one ore more of the tested populations (see Tables 7.3, p. 124 and 7.4, p. 126 for details).

First the influence of the number of characters used in the analysis was checked by using all specimens and stepwise excluding characters.

The principal component analysis separated the southern populations (area 4) from the other three main areas when the majority of characters is used (Fig. 7.9 a). Individuals from the main areas 1 to 3 cannot be distinguished with the PCA. With less than 60 characters the specimens

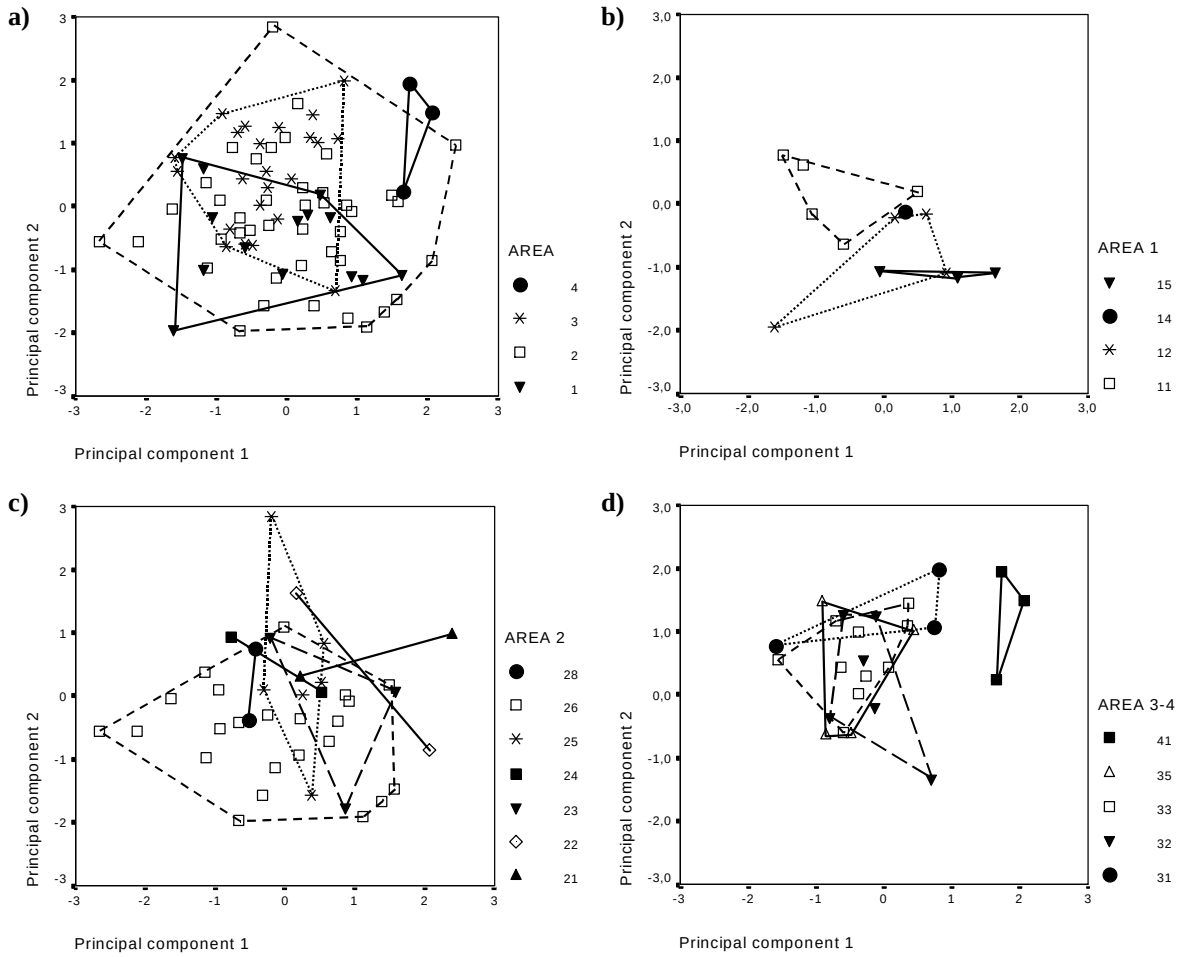

Figure 7.8. Results of the principal component analysis with standardised residuals for gum length for 44 characters for *A. beecrofti* marked according to the main area (a) and subareas (b-d).

from area 4 start to overlap with the others (Fig. 7.9 c) and with less than 40 there is a complete overlap (Fig. 7.9 e-f). The resolution within the main areas calculated with 45 characters is also generally bad with few exceptions (Fig. 7.10). Subpopulations from West Africa (area 1, Fig. 7.10 a) and western Central Africa (area 2, Fig. 7.10 b) show an almost complete overlap. In Central Africa (area 3, Fig. 7.10 c) and the southern area 4 (Fig. 7.10 d) the geographically more distant subpopulations are separated but overlap with the central ones. In Central Africa the specimens from Uganda and adjacent areas (area 34) are separated from individuals from the western Democratic Republic of Congo (areas 31 and 35), but both groups overlap with the specimens from eastern Democratic Republic of Congo (areas 32 and 33). Specimens from the southern Democratic Republic of Congo and Zambia (area 42) are well separated from those from the Usambara mountains (area 44) but both overlap with the individuals collected in southern Tanzania (area 43). These results remain generally the same when calculated only for specimens of age classes 2 and 4 and/or for females and males separately (Figs 7.11 to 7.13).

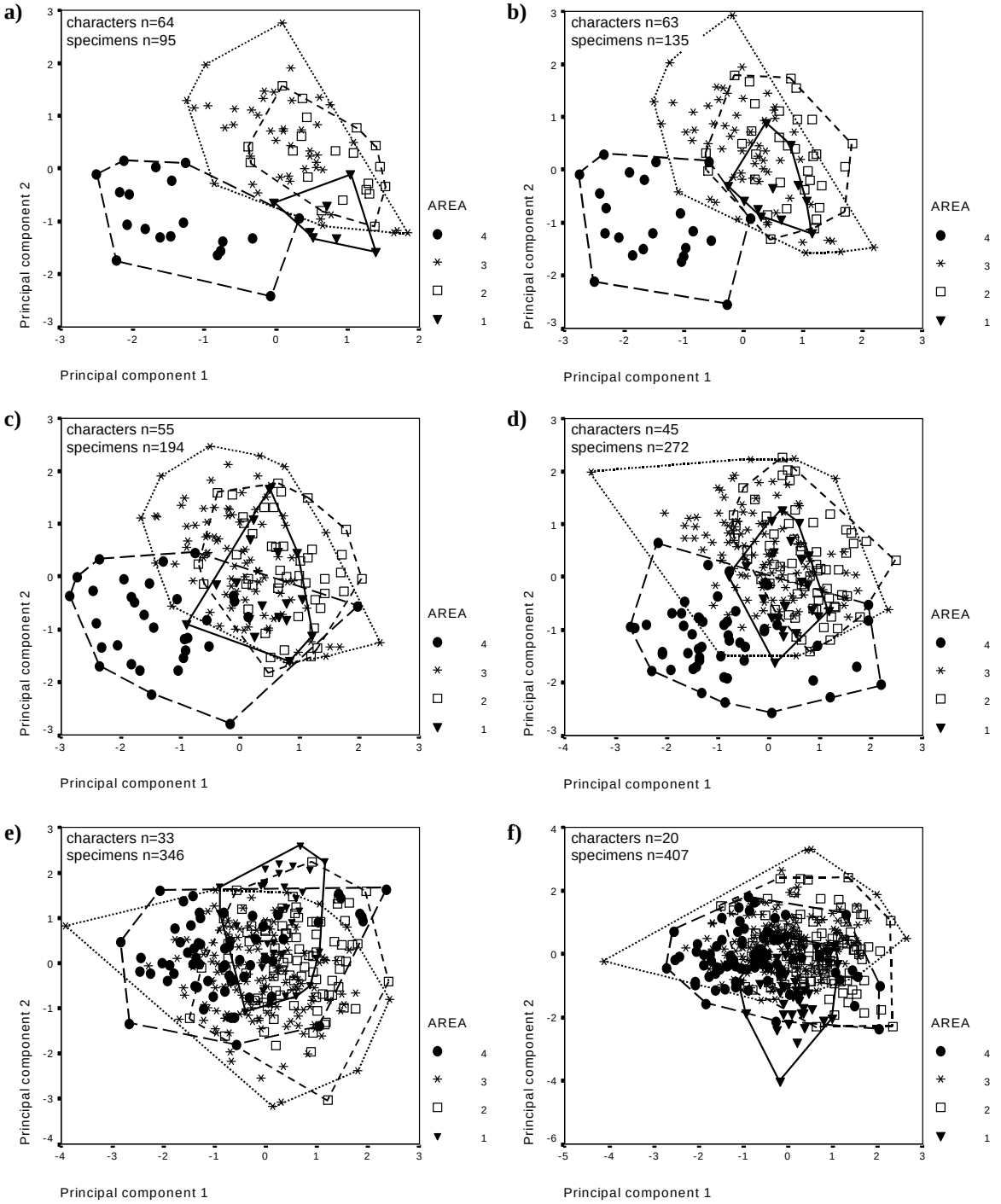

Figure 7.9. Results of the principal component analysis with different numbers of characters for *A. derbianus*.

When calculated with the residuals for gum length including all characters measured for at least 450 specimens the results also did not change much (Fig. 7.14). Generally the resolution becomes worse, especially of the four main areas. For the subareas the patterns are the same as for the ln-transformed values, but less clearly defined.

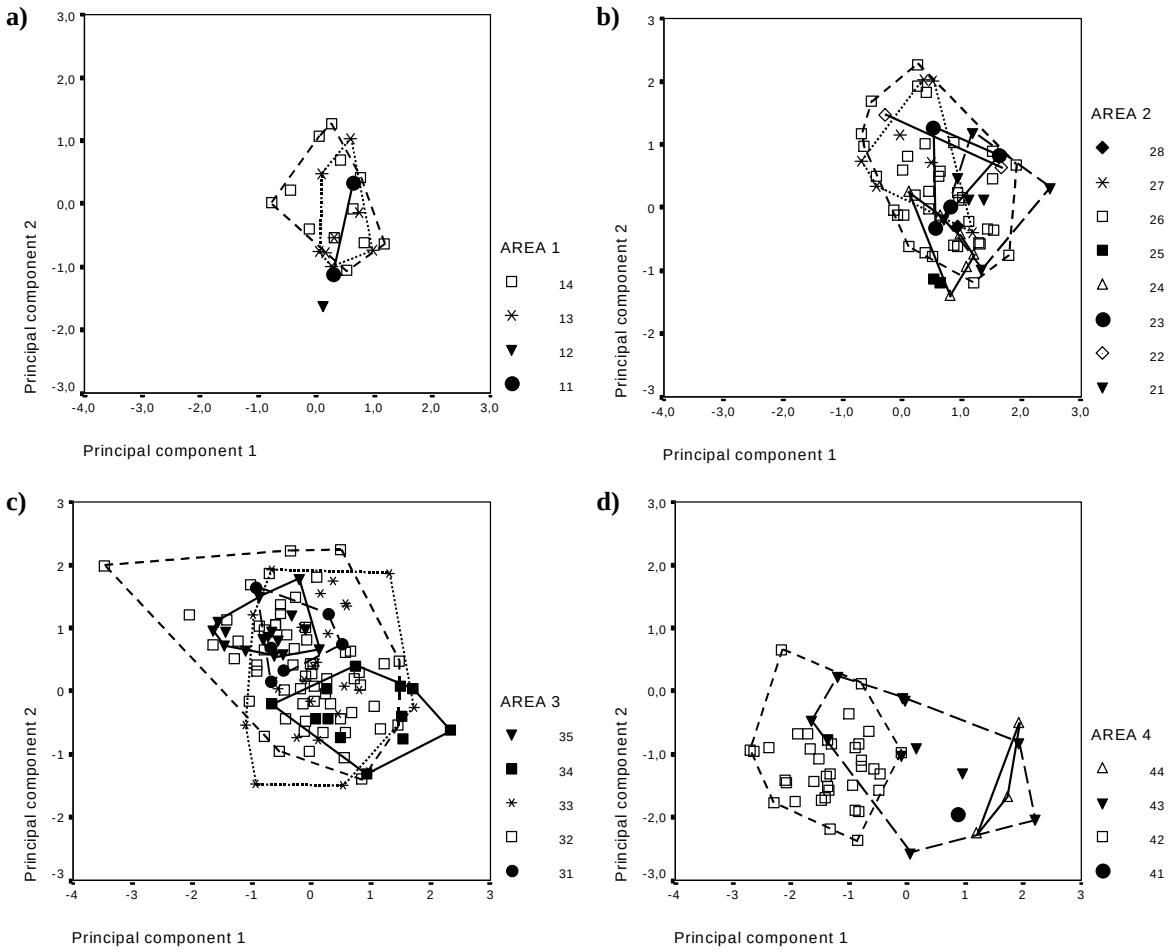

Figure 7.10. Results of the principal component analysis with 45 characters for *A. derbianus* marked according to subareas.

In spite of the bad resolution of geographical populations in the principal component analysis the discriminant analysis (see Tab. 7.6, p. 129) yielded 100.0% of correct groupings for the main areas 1 to 4 with all characters except length of nasals (n=135) which decreased regularly to 97.3% after exclusion of characters measured for less than 400 specimens (n=194), to 93.1% when using only characters available for at least 450 specimens (n=272), to 88.2% with characters measured for more than 475 specimens (n=346), and to 78.2% with characters available for at least 490 specimens (n=407).

Similar results were obtained for the subareas (Tab. 7.7, p. 130) with a correct grouping of 100.0% with all characters except length of nasals (n=135, 17 subareas), 98.9% for characters measured for at least 400 specimens (n=194, 17 subareas), 91.2% with characters available for at least 450 specimens (n=272, 21 subareas), 74.3% with characters measured for more than 475 specimens (n=346, 22 subareas), and 60.8% when using only characters available for more than 490 specimens (n=407, 22 subareas).

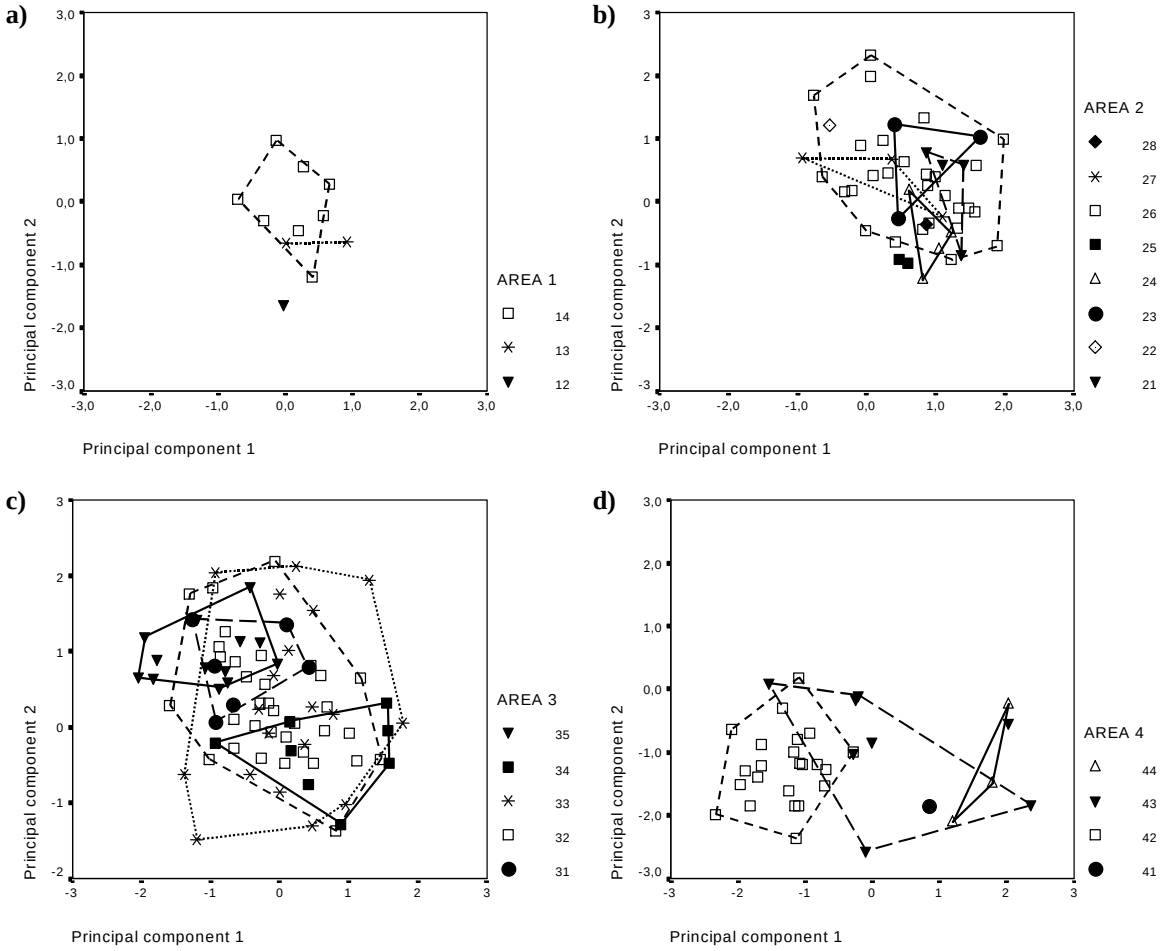

Figure 7.11. Results of the principal component analysis with 45 characters for *A. derbianus* marked according to subareas and restricted to specimens of the age classes 3 and 4.

7.3.3. *A. pelii*

For *A. pelii* tests for normal distribution, sexual dimorphism and age dependence were calculated for specimens from in between the rivers Sassandra and Bandama (area 13, n=64) and Bandama and Volta (area 14, n=49). Like in *A. beecrofti* and *A. derbianus* all characters were normally distributed but showed in several cases sexual dimorphism and/or age dependence (see Tables 7.3, p. 124 and 7.4, p. 126 for details).

The occurrence of *A. pelii* is restricted to West Africa (area 1), so the multivariate analyses were calculated for the subareas 12 to 14. The principal component analysis showed a complete overlap between all three subpopulations, regardless of the number of characters and subsequent number of specimens in the analysis (Fig. 7.15). Results for ln-transformed measurements and residuals for gum length are more or less identical, with specimens from west of the Sassandra River (area 12) being more widespread in the analysis of residuals (Fig. 7.16). An analysis for specimens of the age classes 3 and 4 did also not change the results (results not shown), separate

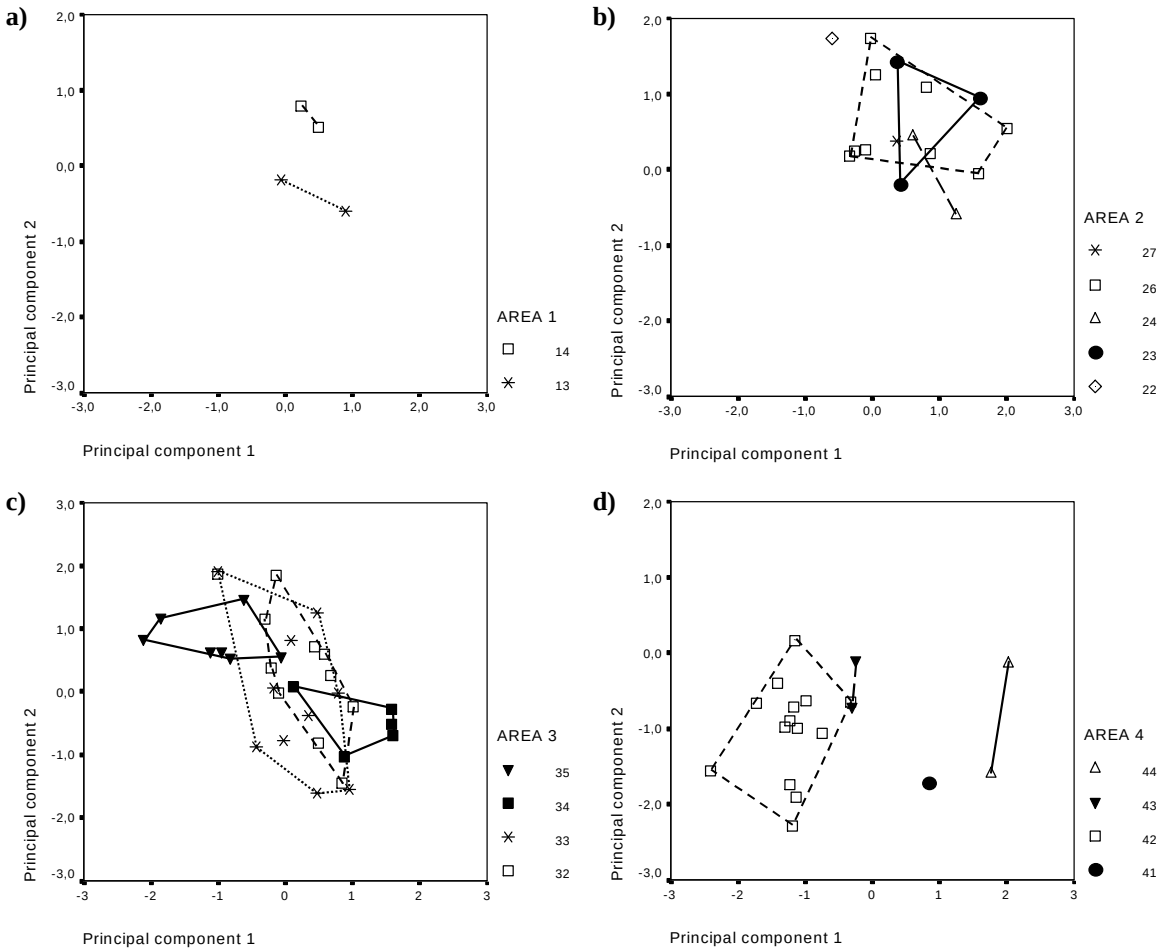

Figure 7.12. Results of the principal component analysis with 45 characters for *A. derbianus* marked according to subareas and restricted to females of the age classes 3 and 4.

analysis for the sexes were not calculated because only one specimen from area 12 was determined.

The discriminant analysis (see Tables 7.6, p. 129 and 7.7, p. 130 for details) yielded 96.3% of correct groupings for all characters except nasal length (n=57, 16 characters failed tolerance test) which increased to 100.0% for characters measured for at least 110 specimens (n=60, 6 characters failed tolerance test), 120 specimens (n=69), and 125 specimens (n=79) and decreased again to 91.3% with characters available for at least 130 specimens (n=93).

7.3.4. *A. pusillus*

Test for normal distribution, sexual dimorphism and, age dependence were performed for populations from southern Cameroon to Gabon (area 26, n=12) and north-western (area 32, n=64) and western (area 33, n=28) Democratic Republic of Congo. All characters were normally distributed, *P*-values for statistically significant sexual dimorphism and/or age dependence are given in Tables 7.3 (p. 124) and 7.4 (p. 126).

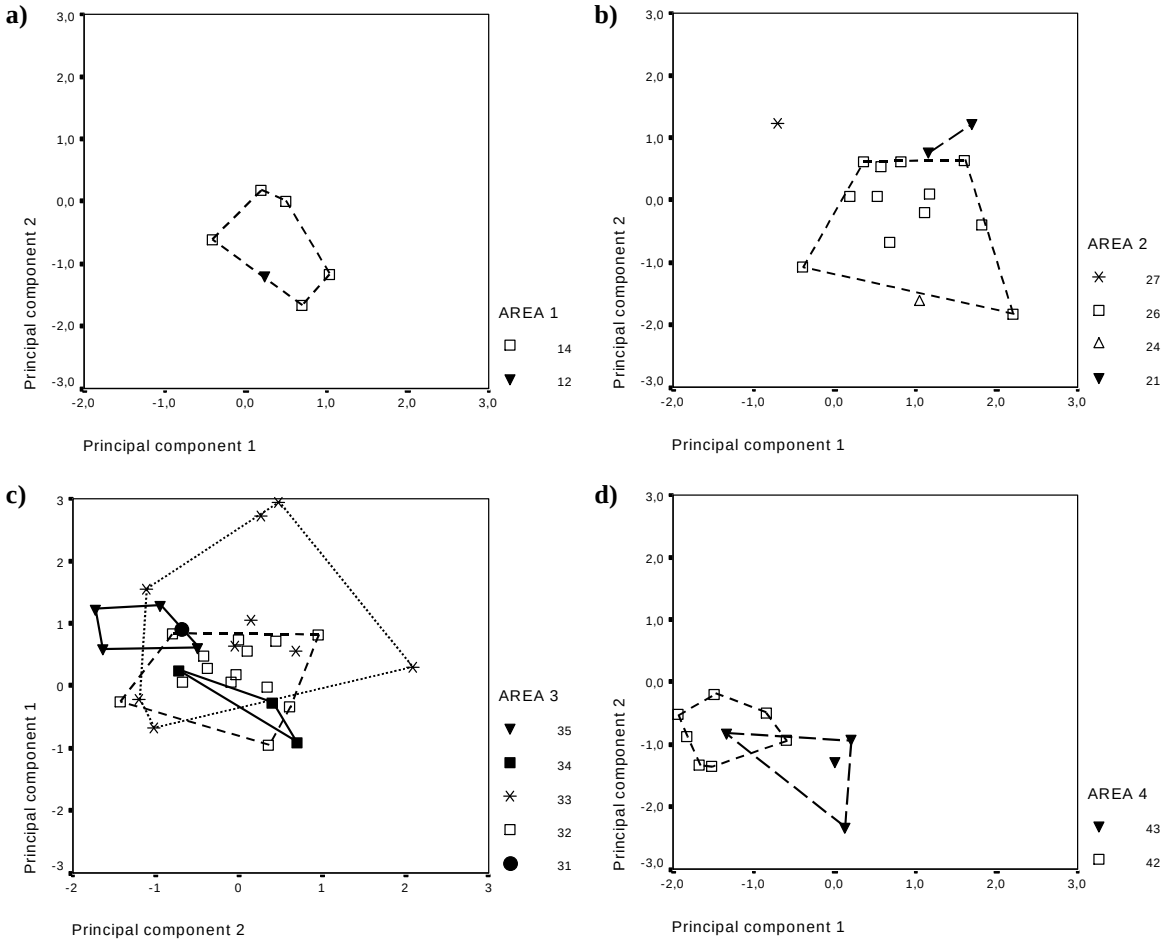

Figure 7.13. Results of the principal component analysis with 45 characters for *A. derbianus* marked according to subareas and restricted to males of the age classes 3 and 4.

The principal component analysis shows a separation between specimens from north-western (area 31) and western (area 33) Democratic Republic of Congo, with individuals from in between (area 32) overlapping with both groups (Fig. 7.17). Specimens from southern Cameroon to Gabon (area 26) are slightly separated from those from the Democratic Republic of Congo until all characters available for at least 100 specimens were used in the analysis. The three specimens from West Africa (area 1, subareas not available) overlap partly with those from southern Cameroon to Gabon (area 26) and one specimen clusters rather with those from north-western Democratic Republic of Congo (area 32). Like in the previous analyses the results for residuals for gum length match those from the ln-transformed values, but the resolution is less clear (Fig. 7.18).

91.8% of specimens were grouped correctly according to the main areas (Tab. 7.6, p. 129) in the discriminant analysis when all characters except nasal length were used. (n=49, 30 characters failed tolerance test, only areas 2 and 3). With all characters measured for at least 90 specimens

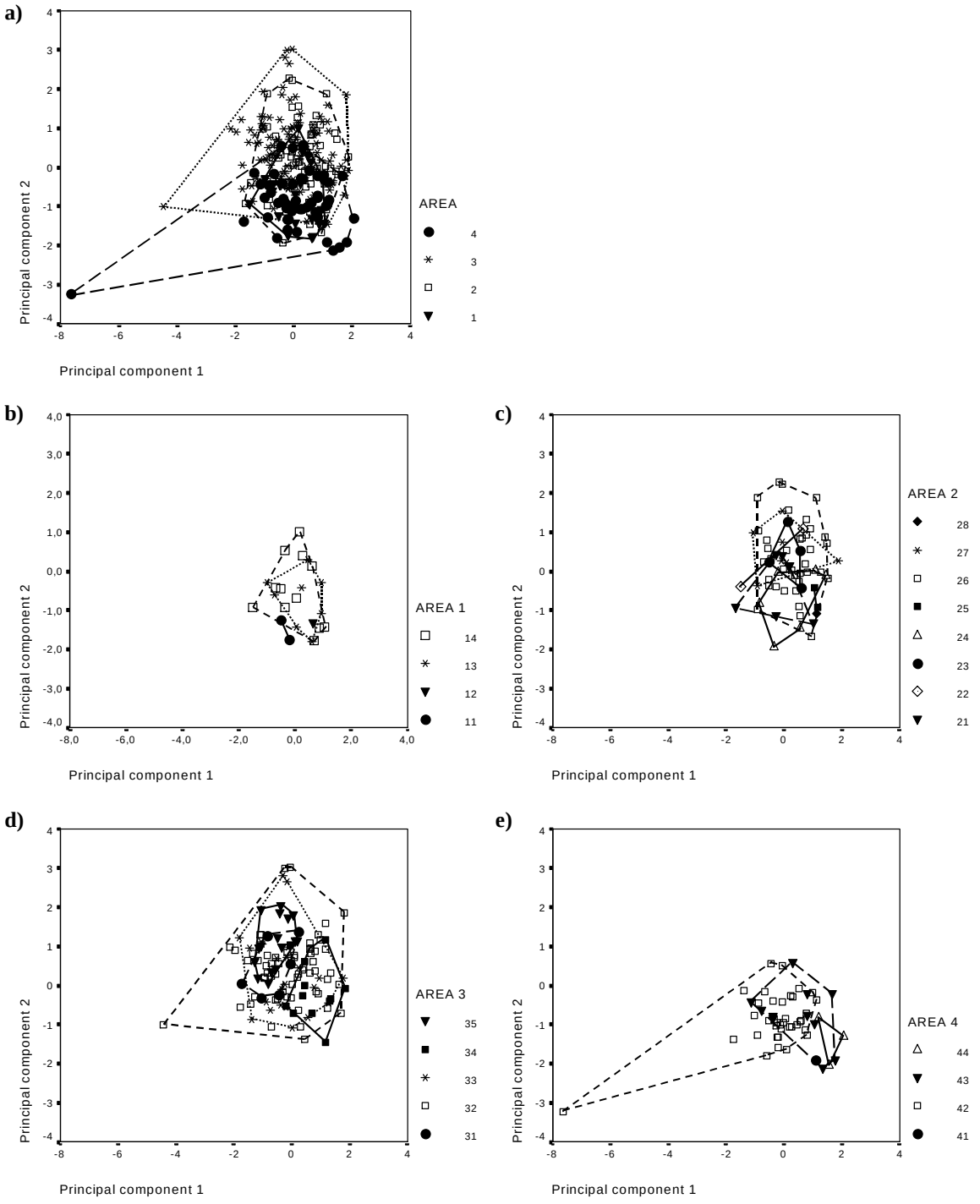

Figure 7.14. Results of the principal component analysis with standardised residuals for gum length for 45 characters for *A. derbianus* marked according to the main areas (a) and subareas (b-e).

only 88.9% were grouped correctly (n=54, 23 characters failed tolerance test, only areas 2 and 3) and 98.1% with all measurement available for at least 95 specimens (n=54, 10 characters failed tolerance test, only areas 2 and 3). The percentage of correct groupings increased to 100.0% with characters available for at least 100 specimens (n=57, areas 1 to 3), 105 specimens

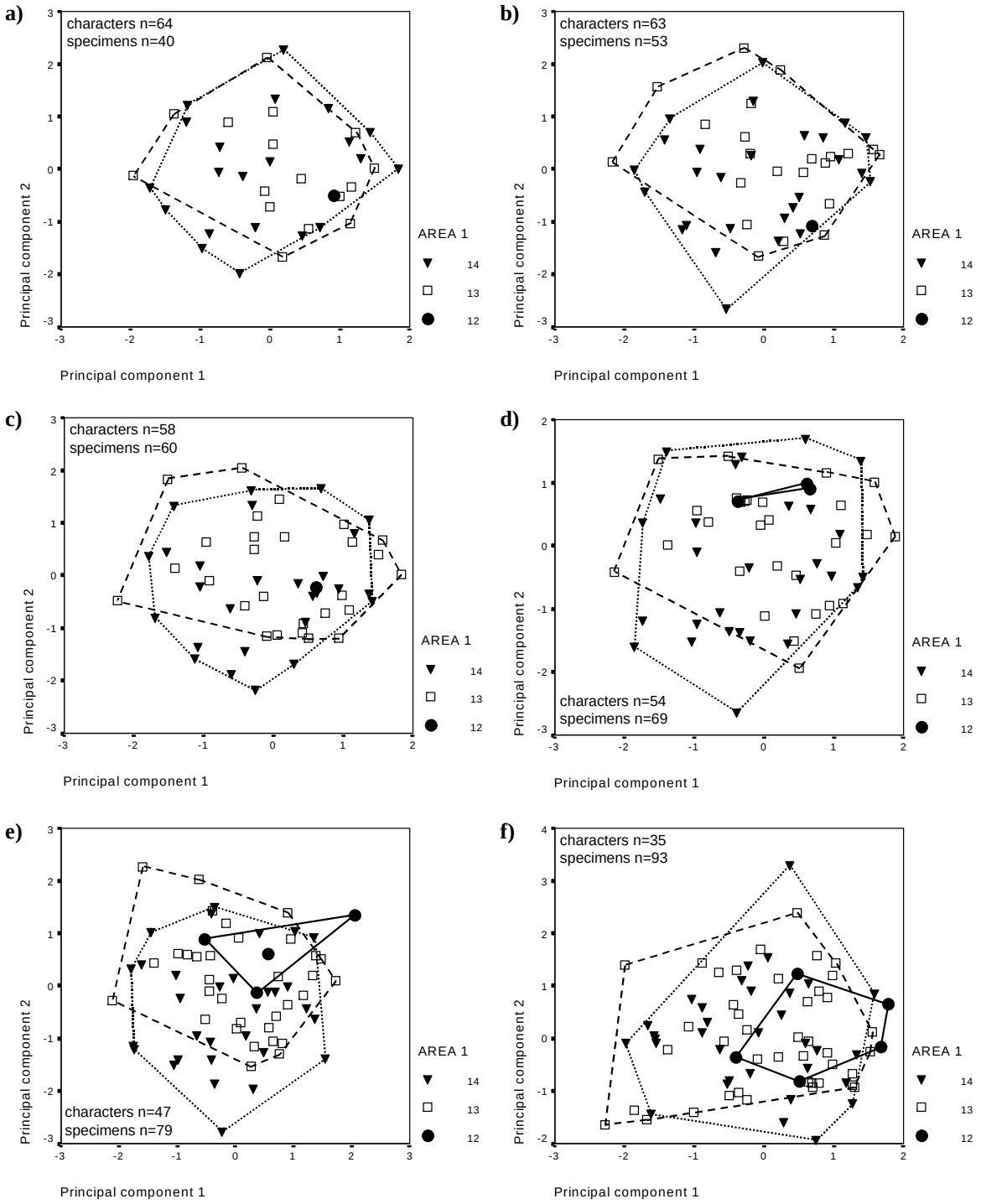

Figure 7.15. Results of the principal component analysis with different numbers of characters for *A. pelii*.

(n=68), and 107 specimens (n=79) and 96.7% with measurements available for at least 110 specimens (n=91).

Groupings according to subareas (except for area 1) were correct in 81.8% of the cases (n=44, 33 characters failed tolerance test, 4 (sub)areas) with all characters except nasal length, in 92.2%

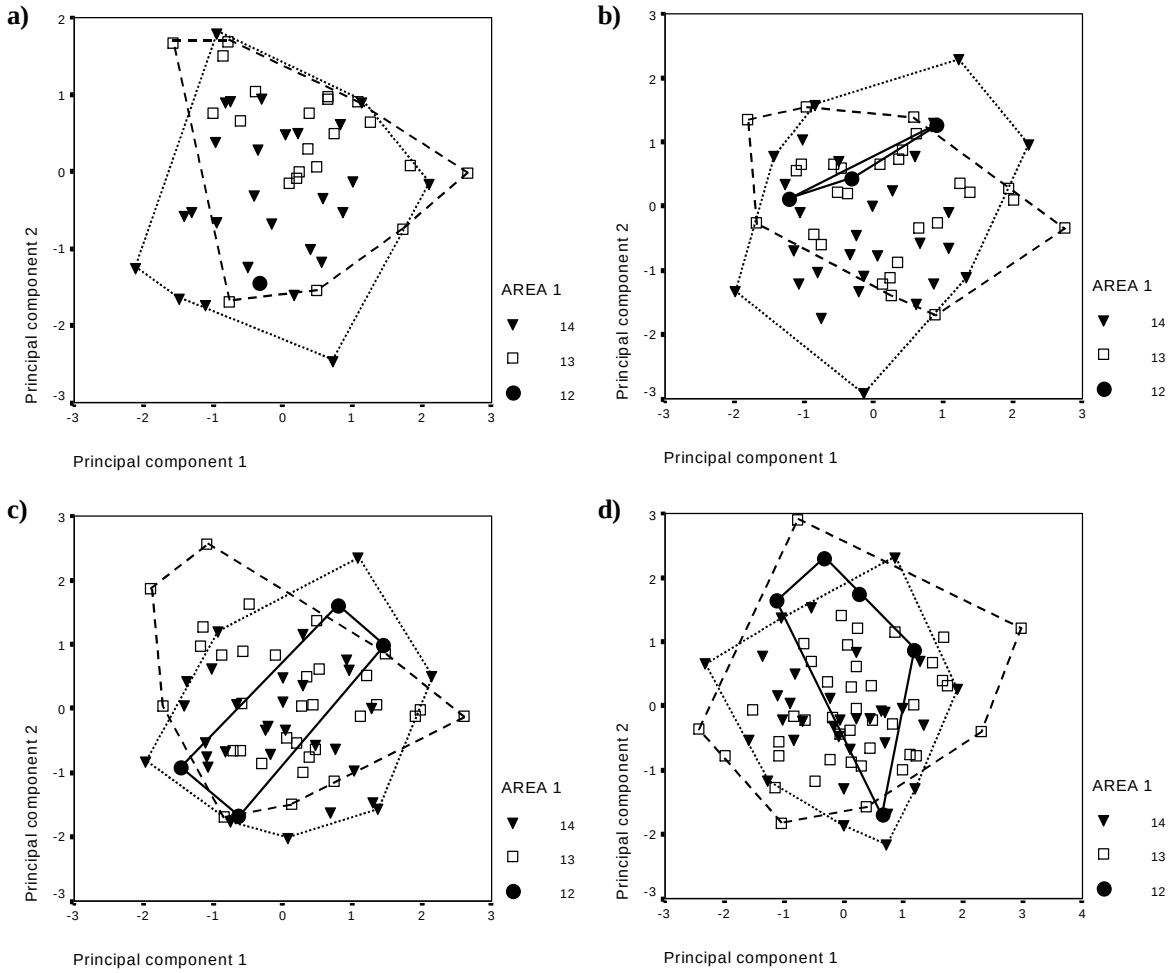

Figure 7.16. Results of the principal component analysis with standardised residuals for gum length for *A. pelii*.

with all characters measured for at least 90 specimens (n=53, 25 characters failed tolerance test, 4 (sub)areas), and 98.0% with characters available for at least 95 individuals (n=51, 14 characters failed tolerance test, 5 (sub)areas). 100.0% of the groupings were correct for characters measured for at least 100 specimens (n=57, 5 (sub)areas) and 105 specimens (n=68). For measurements available for at least 107 and 110 specimens the percentage decreased to 92.2% (n=79) and 83.1% (n=91) respectively (see Tab. 7.7, p. 130).

7.3.5. *I. macrotis*

Normal distribution and sexual dimorphism were tested for three *I. macrotis* populations from West Africa (area 1, n=13), southern Cameroon to Gabon (area 26, n=16), and western Democratic Republic of Congo (are 33, n=18). All characters were normally distributed in every population, for significant sexual dimorphism see Tables 7.3 (p. 124) and 7.4 (p. 126).

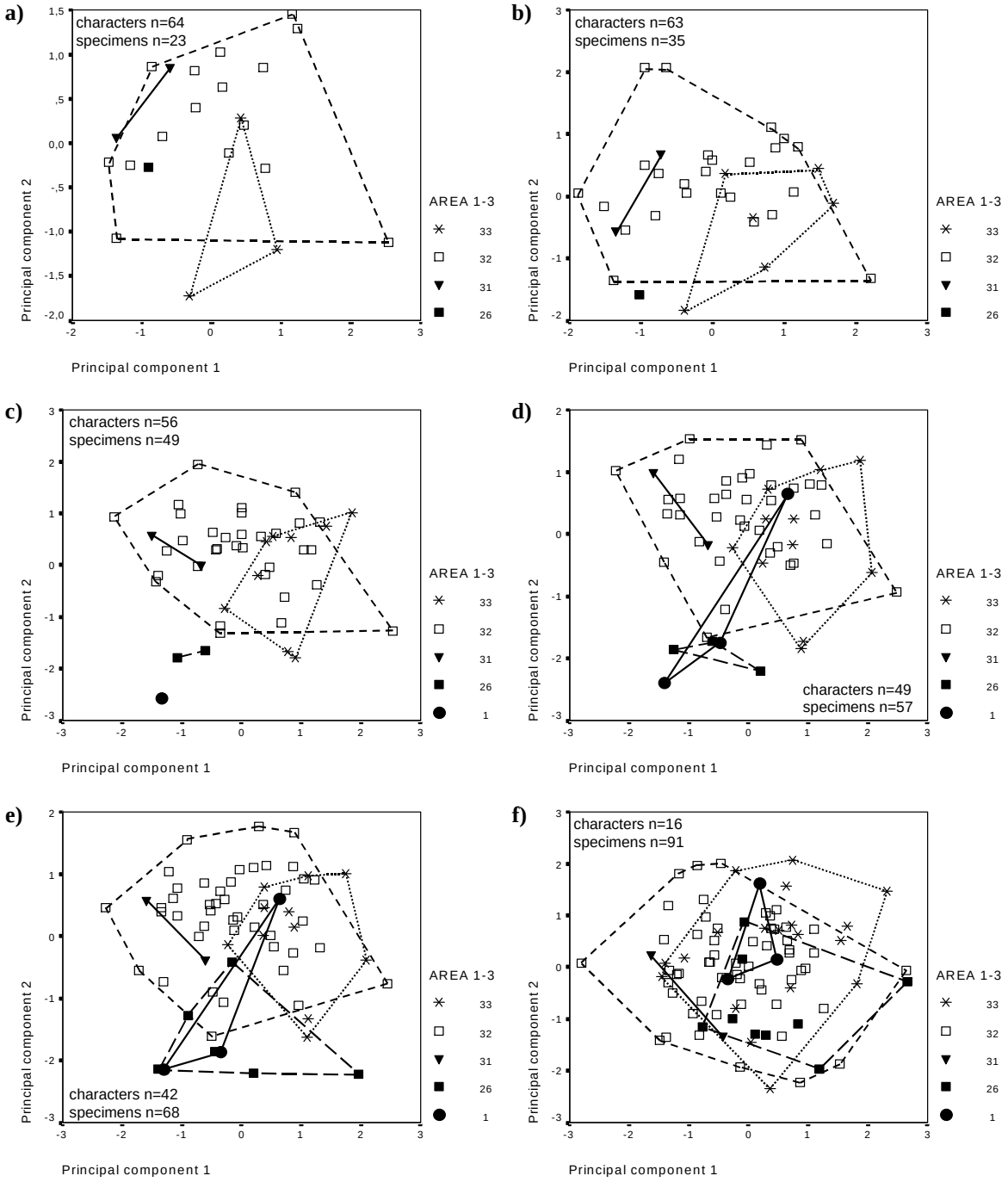

Figure 7.17. Results of the principal component analysis with different numbers of characters for *A. pusillus*.

The principal component analysis achieved a very good resolution of geographical populations (Fig. 7.19). Specimens from West Africa (areas 11 to 14) clustered close together, and also individuals from north-western and western Democratic Republic of Congo (areas 32 and 33). Different results are found for southern Cameroon to Gabon (area 26), specimens from this area are separated from all other individuals until the number of characters is extremely reduced.

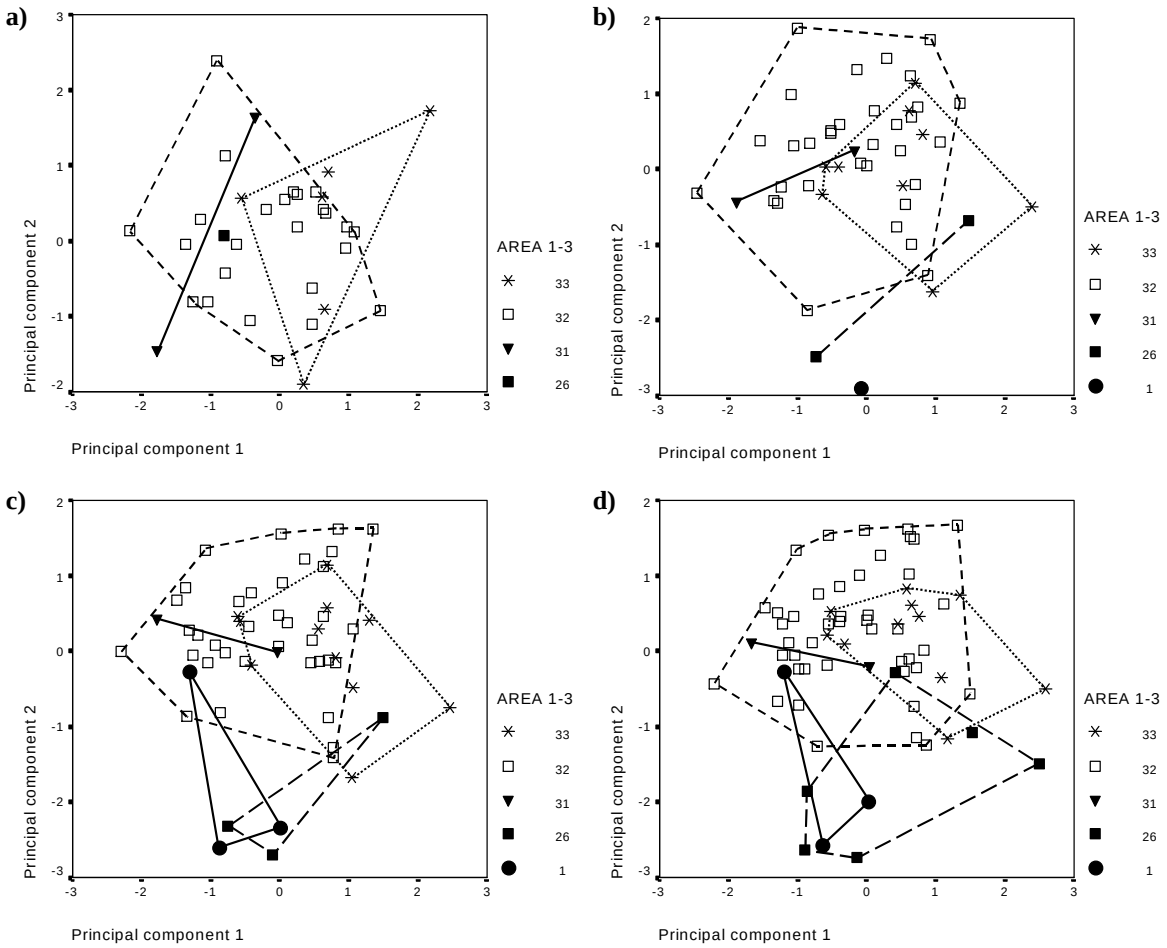

Figure 7.18. Results of the principal component analysis with standardised residuals for gum length for *A. pusillus*.

Specimens from the Mamfe area in north-eastern Cameroon (area 24) and the single specimen from northern Tanzania (area 34) remain isolated in the analysis. The results for the residuals for gum length generally match those for the ln-transformed values, but show a less clear resolution (Fig. 7.20).

The discriminant analysis for all characters measured for at least 25 specimens grouped 70.4% of the specimens correctly to their main area (n=27, 47 characters failed tolerance test). The percentage increased to 87.9 % with all characters available for more than 45 specimens (n=33, 23 characters failed tolerance test) and to 90.9% for characters measured for more than 50 (n=33, 17 characters failed tolerance test) and 55 individuals (n=33, 12 characters failed tolerance test). 100.0% were grouped correctly with measurements available for at least 60 specimens (n=38) and 96.6% when only characters measured for at least 65 specimens were used (n=61; Tab. 7.6, p. 129).

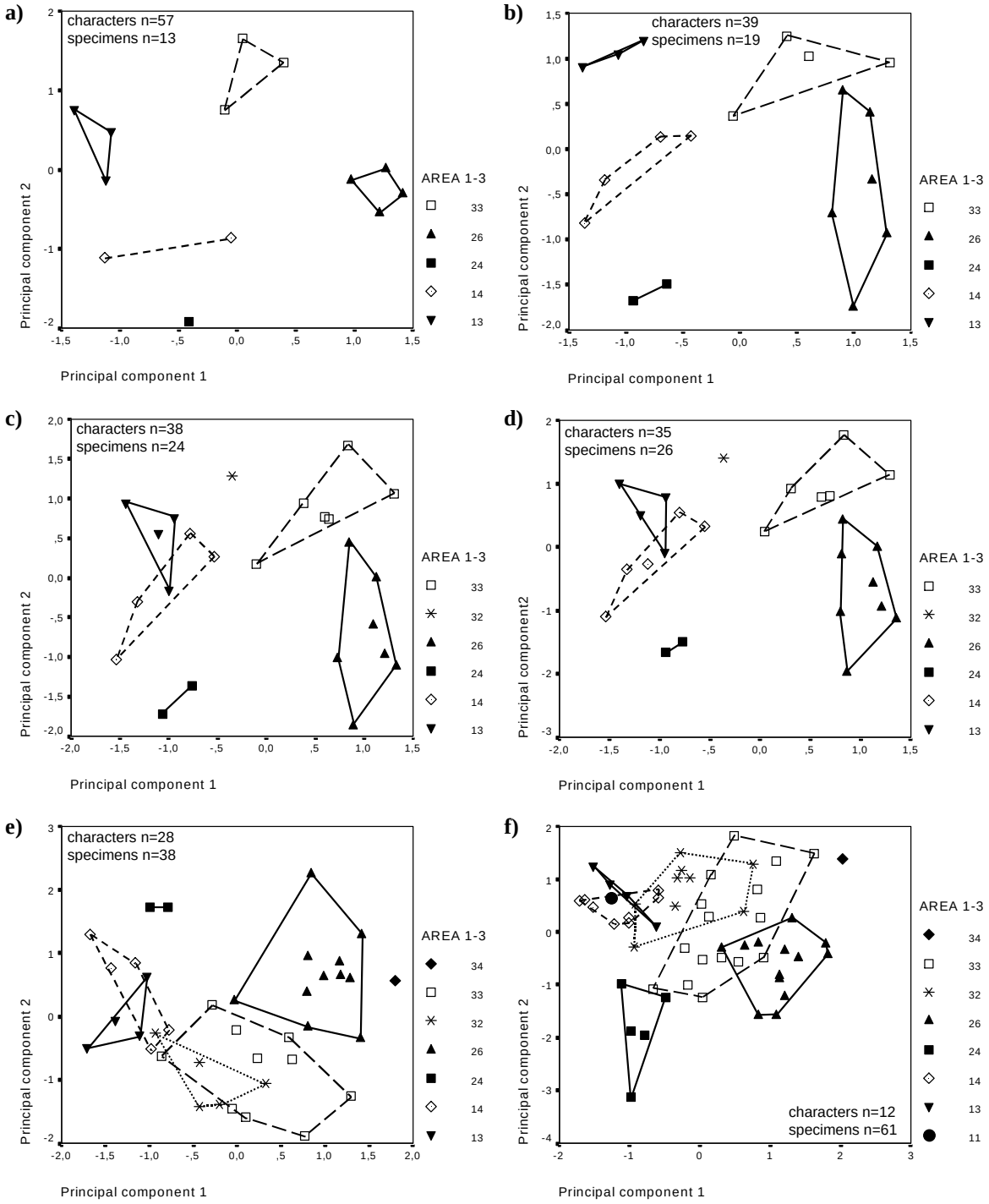

Figure 7.19. Results of the principal component analysis with different numbers of characters for *I. macrotis.*

58.3% of the specimens were grouped correctly according to the subareas when characters measured for at least 25 specimens were used (n=64, 5 subareas, 49 characters failed tolarance test), 56.4% with characters available for at least 45 specimens (n=59, 5 subareas, 25 characters

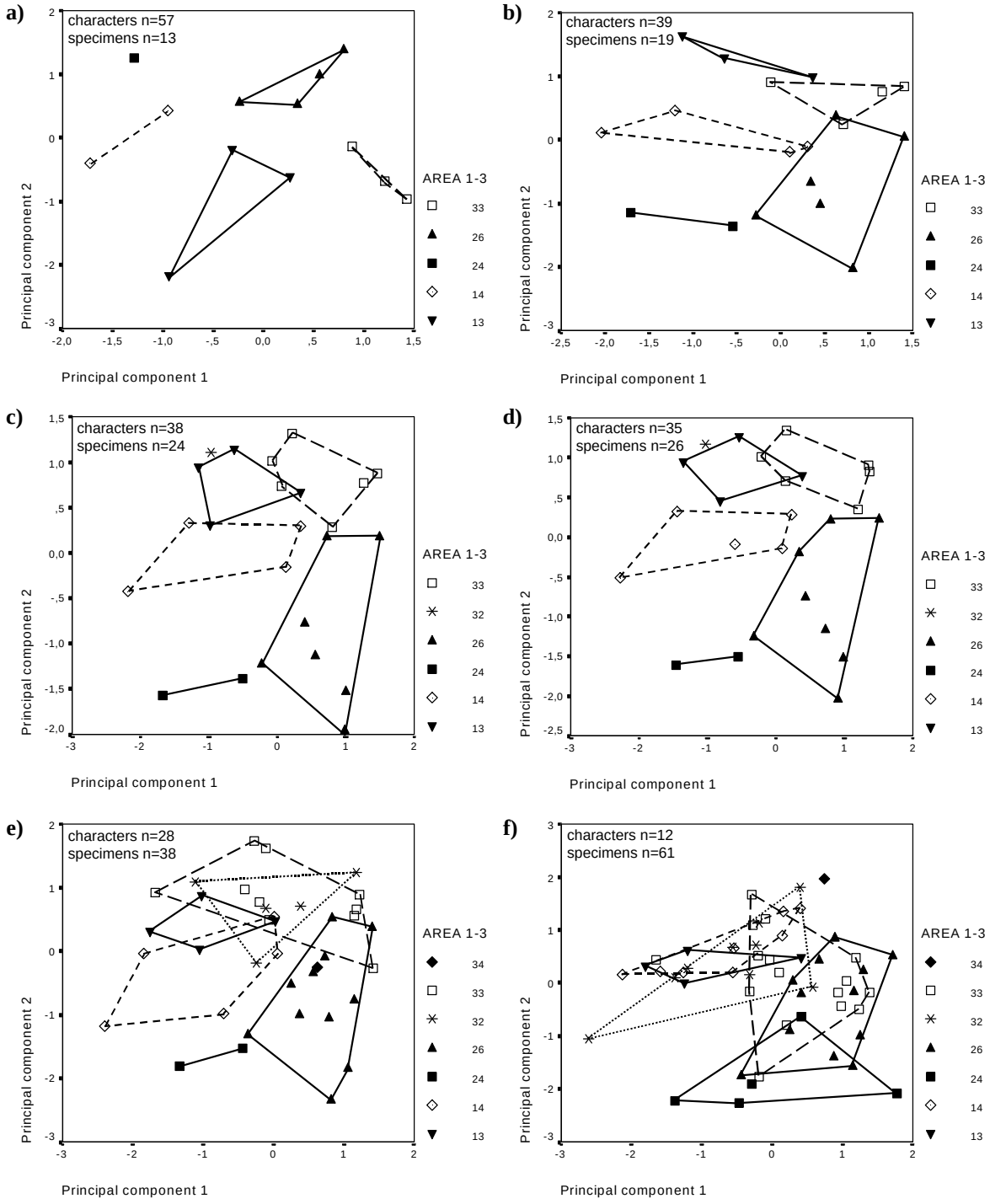

Figure 7.20. Results of the principal component analysis with different numbers of standardised residuals for gum length for *I. macrotis*.

failed tolerance test), 72.5% with measurements available for more than 50 individuals (n=55, 6 subareas, 20 characters failed tolerance test), and 64.6% with characters measured for at least 55 specimens (n=51, 6 subareas, 15 characters failed tolerance test). With characters available for at least 60 individuals 100.0% of the grouping were correct (n=38, 7 subareas) and 91.2% with

characters measured for at least 65 specimens (n=61, 8 subareas). In the latter case the wrong groupings occurred only between the neighbouring subareas 13 and 14 and subareas 32 and 33 (see Tab. 7.7, p. 130).

7.3.6. *I. zenkeri*

For *I. zenkeri* normal distribution and sexual dimorphism were tested for populations from southern Cameroon to Gabon (area 26, n=10) and north-western Democratic Republic of Congo (area 33, n=20). All characters are normally distributed, for statistically significant sexual dimorphism see Tables 7.3 (p. 124) and 7.4 (p. 126).

The principal component analysis separated like in *I. macrotis* the geographical populations very well (Fig. 7.21). The neighbouring populations from north-western and western Democratic Republic of Congo clustered closely together. Specimens from the Mamfe area (area 24) and southern Cameroon to Gabon (area 26) were clearly separated, while for the specimens from

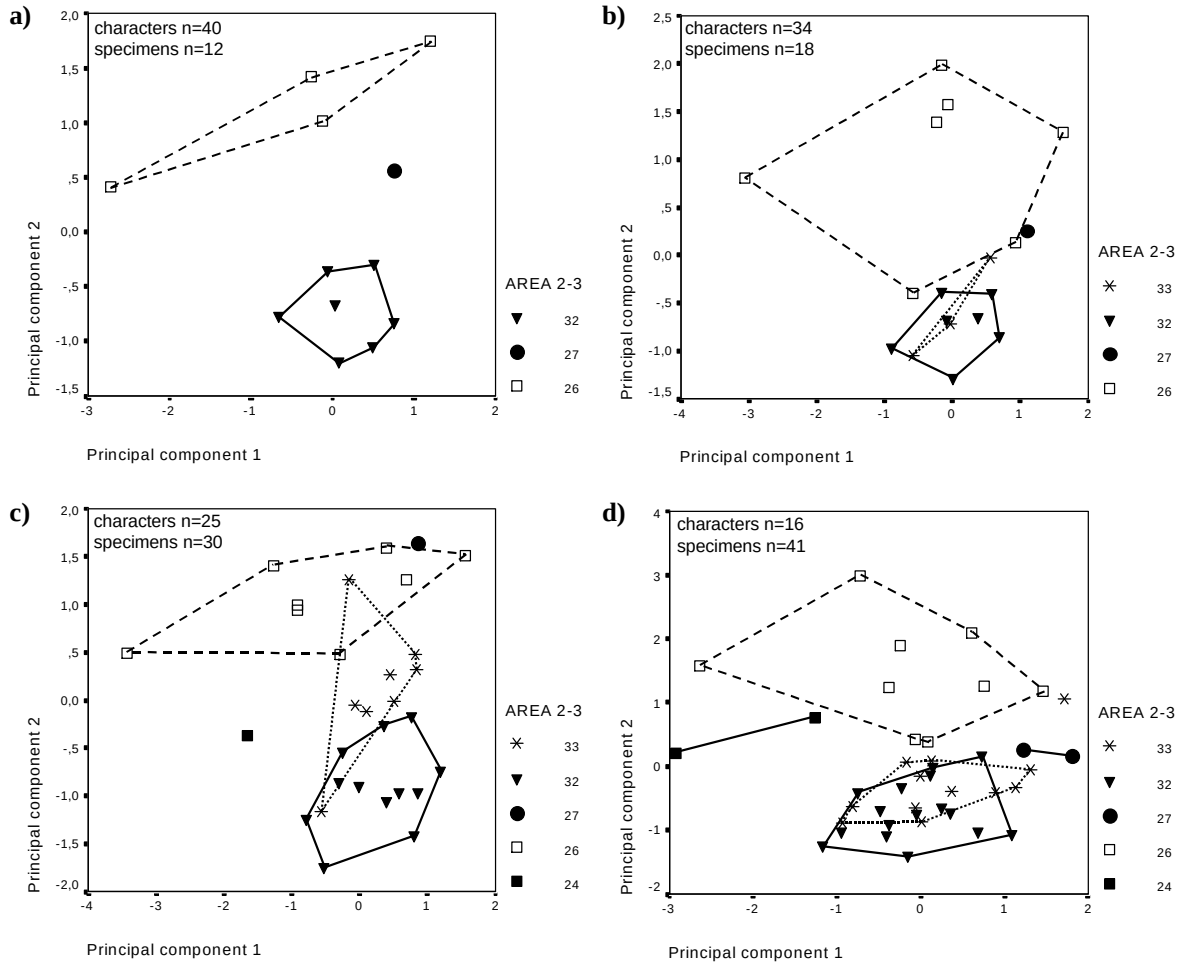

Figure 7.21. Results of the principal component analysis with different numbers of characters for *I. zenkeri*.

south-western Central African Republic (area 27) the separation from area 26 depends on the combination of characters. Particularly for the two small samples the resolution becomes considerably worse when residuals for gum length were used instead of ln-transformed values (Fig. 7.22).

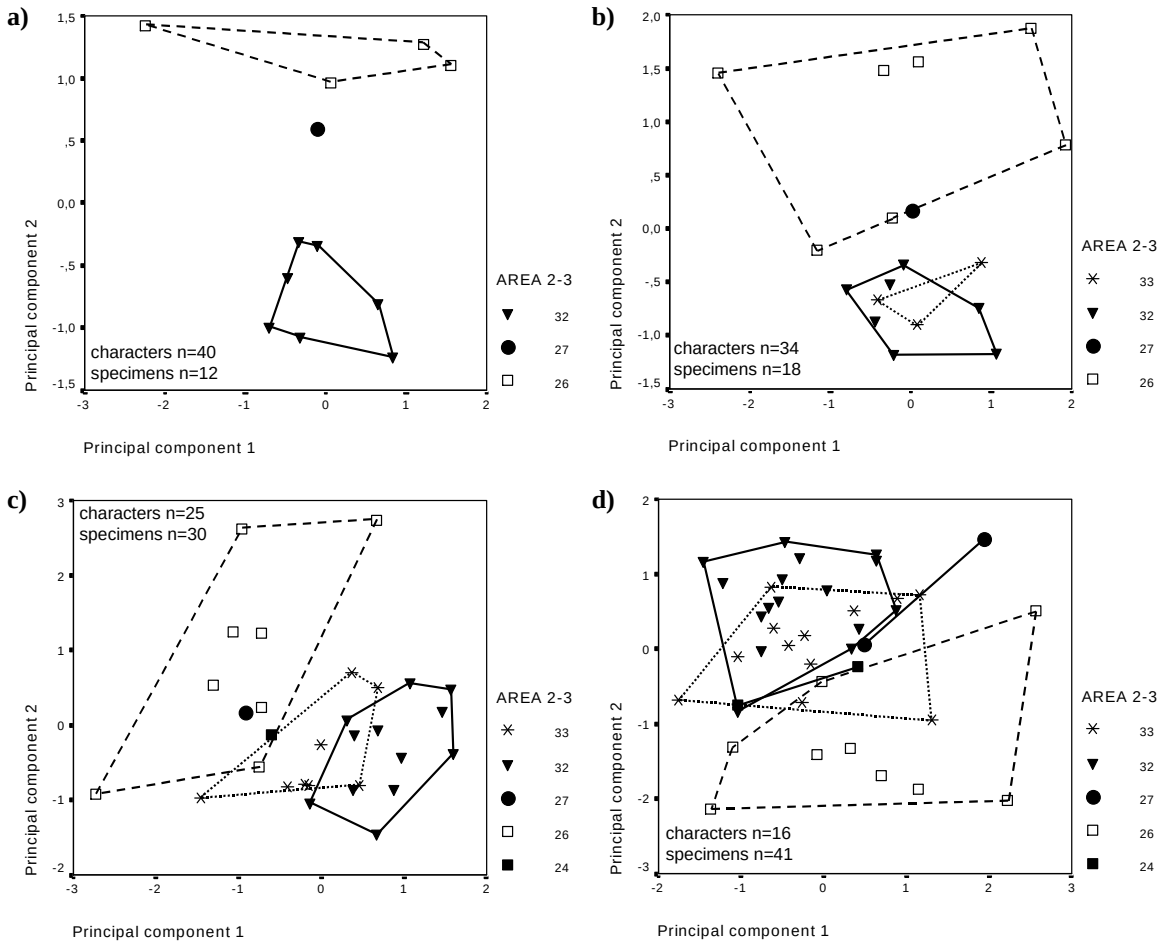

Figure 7.22. Results of the principal component analysis with standardised residuals for gum length for *I. zenkeri*.

The discriminant analysis (Tab. 7.6, p. 129, Tab. 7.7, p. 130) grouped 89.7% of specimens in the correct main area 1 or 2 with characters available for at least 35 specimens (n=29, 30 characters failed tolerance test), 80.6% with characters measured for at least 40 specimens (n=31, 18 characters failed tolerance test), and 100.0% for measurements available for at least 45 specimens (n=30), and 49 specimens (n=41). 48.8% of the specimens were grouped correctly in their subarea when characters measured for at least 35 specimens were used, (n=43, 3 subareas, 31 characters failed tolerance test), for characters available for at least 40 individuals 64.3% were grouped correctly (n=42, 4 subareas, 20 characters failed tolerance test), and 100.0% for measurements available for at least 45 specimens (n=30, 5 subareas) and 49 specimens (n=41, 5 subareas).

7.3.7. *Z. insignis*

For *Z. insignis* only three skulls were available, two males from southern Cameroon and Equatorial Guinea (area 26) and one specimen of unknown sex from the Central African Republic (area 27). Because of this too small data basis no analyses of the skull measurements within this species were calculated.

7.3.8. Combined analysis for all species

In order to complete the analyses the calculations were repeated for specimens of all species together. For the beginning 48 characters were used, 16 were excluded because they were not available for all four *Z. insignis* specimens (Fig. 7.23). In this case the results for ln-transformed values and standardised residuals for gum length displayed striking differences. While it was no problem to separate at least the majority of species with the exception of *A. beecrofti* and *A. derbianus* with ln-transformed characters, the residuals produced a homogenous cloud without the slightest hint of any clustering. Because of this unexpected result the analyses were repeated with 13 characters that displayed obvious differences between species (RB, IOB, BM1, BM2, SKH, ZP, URL, LRL, PAAD, UCL, and LIL; Fig. 7.24). These characters stressed the differences for ln-transformed values and separated all species well except for very few outliers, while still no traces of species or genus clusters can be seen for residuals. The discriminant analysis for the ln-transformed characters yielded 100% of correctly assigned specimens with respect to the species for 48 characters (n=241) and 99.3% of correct groupings with 13 characters (n=602), with only four misidentifications between *A. beecrofti* and *A. derbianus*.

7.3.9. Sexual dimorphism and age dependence

The majority of characters in the analysis show sexual dimorphism and/or age dependence for at least some of the species and geographical populations. Only ten characters show no sexual dimorphism, six no age dependence and none is completely free of both (Tab. 7.3, 7.4).

A closer analysis reveals that sexual dimorphism and age dependence are not equally distributed over the characters. Because sexual dimorphism was checked for 17 populations and age dependence for 11 (not for *Idiurus*), the following correlation factor (CF) is used in order to compare the influences: CF = mean of number of populations with statistically significant differences / number of populations.

The measured characters can be divided into characters of the skull (n=35), the lower jaw (n=5) and the teeth (n=24). For the skull characters the CF is 0.13 for sexual dimorphism and 0.24 for age dependence, for the lower jaw the values are 0.37 and 0.22 respectively and for the teeth 0.14 and 0.30, showing stronger age dependence in skull and teeth, but stronger effect of sexual dimorphism for the lower jaw. When characters are further subdivided into characters of length,

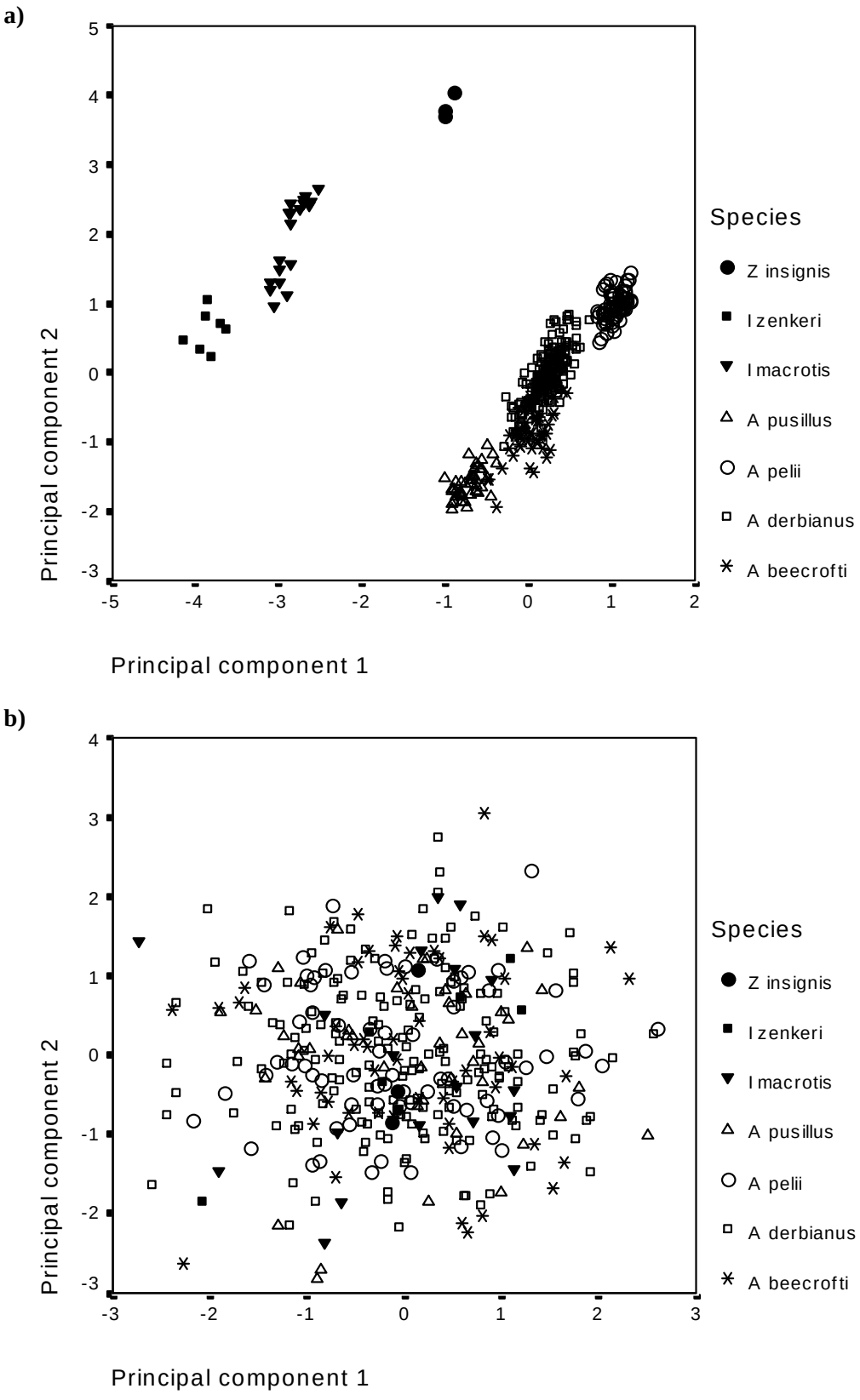

Fig. 7.23. Results of the principal component analysis with ln-transformed values (a) and standardised residuals for gum length (b) with 48 characters for all anomalurid species.

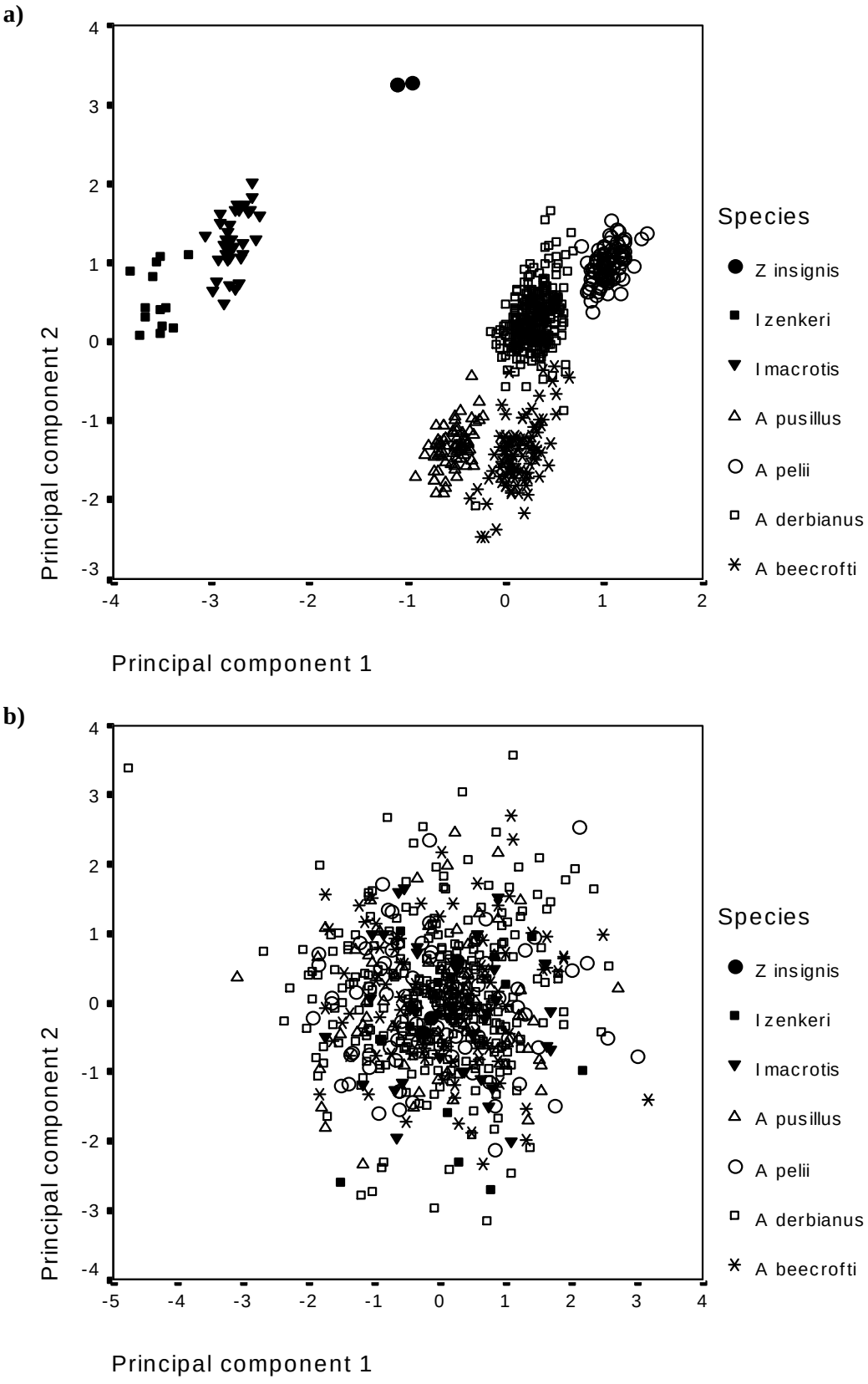

Figure 7.24. Results of the principal component analysis with ln-transformed values (a) and standardised residuals for gum length with 13 characters for all anomalurid species.

Table 7.3. Sexual dimorphism in the characters used for the analyses in different species.

Species	***A. beecrofti***			***A. derbianus***			***A. pelii***		***A. pusillus***			***I. macrotis***			***I. zenkeri***			**total**
Area	**1**	**26**	**33**	**1**	**26**	**32**	**13**	**14**	**26**	**32**	**33**	**1**	**26**	**33**	**26**	**32**	**33**	
n	**36**	**48**	**18**	**63**	**65**	**98**	**64**	**49**	**12**	**64**	**28**	**13**	**16**	**18**	**10**	**21**	**16**	
TL	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.001	n.s.	n.s.	n.s.	*P*<0.05	n.s.*	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	3
CIL	*P*<0.01	n.s.	n.s.	*P*<0.005	n.s.*	*P*<0.001	n.s.	*P*<0.05	n.s.*	*P*<0.005	*P*<0.05	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	6
BL	*P*=0.005	n.s.	n.s.	*P*<0.005	n.s.*	*P*<0.001	n.s.	*P*<0.05	*P*<0.01	*P*<0.01	*P*<0.05	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	7
ZB	*P*<0.05	n.s.	n.s.*	n.s.	n.s.	*P*<0.001	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	3
RB	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.01	*P*<0.01	n.s.	n.s.	n.s.	*P*<0.01*	n.s.	n.s.*	n.s.	n.s.*	n.s.	n.s.	4
NL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.*	n.s.*			n.s.	n.s.	n.s.	0
NB	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	*P*=0.001	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	2
IOB	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	3
PPOB	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.							0
BCB	n.s.	n.s.	n.s.	n.s.	n.s.*	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	*P*<0.005	n.s.	n.s.*	*P*<0.05	n.s.	n.s.	n.s.	3
CSB1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.							1
CSB2	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.							0
CSB3	*P*<0.05	n.s.	n.s.	*P*<0.05*	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.							3
GL	*P*<0.05	n.s.	n.s.	*P*<0.05	n.s.*	*P*<0.01	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	4
PPBL	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.001	n.s.	n.s.	n.s.*	*P*<0.01	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.	3
DL	*P*<0.05	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	4
FIL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	1
FIB	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	1
BP4	n.s.	n.s.	n.s.	n.s.	*P*=0.005	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.005	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2
BM1	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	1
BM3	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	1
CHB	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0
BUL	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.01	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	3
BUB	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.005	*P*=0.005	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	2
RH	*P*<0.05	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05*	n.s.	n.s.	n.s.	3
ZH	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	3
PFZH	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	*P*=0.005*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	1
SKH	*P*<0.05	n.s.	n.s.	*P*<0.01	n.s.	*P*<0.05	*P*=0.005	n.s.	n.s.	n.s.	*P*=0.005	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	6
ZL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*=0.005	2
BCH	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	1
CZB	n.s.	n.s.	n.s.	*P*<0.005	n.s.	*P*<0.01	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.*	*P*<0.05	n.s.	n.s.	n.s.	n.s.	5
FIOH	n.s.*	n.s.*	n.s.	n.s.	n.s.	n.s.	*P*<0.005	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.*	n.s.	n.s.*	1
FIOB	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	0
URL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	*P*<0.05	n.s.	n.s.	n.s.	1
LRL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	0

Table 7.3 (continued). Sexual dimorphism in the characters used for the analyses in different species.

Species	***A. beecrofti***			***A. derbianus***			***A. pelii***		***A. pusillus***			***I. macrotis***			***I. zenkeri***			**total**
Area	**1**	**26**	**33**	**1**	**26**	**32**	**13**	**14**	**26**	**32**	**33**	**1**	**26**	**33**	**26**	**32**	**33**	
n	**36**	**48**	**18**	**63**	**65**	**98**	**64**	**49**	**12**	**64**	**28**	**13**	**16**	**18**	**10**	**21**	**16**	
ML	*P*=0.001	*P*<0.05	*P*=0.001	*P*=0.001	n.s.*	*P*<0.001	n.s.	*P*<0.05	*P*<0.05*	*P*<0.001	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	8
MHD	*P*<0.005	*P*<0.05*	n.s.	*P*<0.001	n.s.	*P*<0.005	n.s.	*P*<0.05	n.s.	*P*=0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	6
MHA	*P*<0.05	*P*<0.01	n.s.	n.s.	*P*<0.05	*P*<0.001	*P*<0.001	*P*<0.05	n.s.	*P*=0.001	*P*=0.005	n.s.	n.s.	*P*<0.01	n.s.	n.s.	n.s.	9
PAAD	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.01	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2
PCH	*P*<0.05	n.s.*	n.s.	*P*<0.05	n.s.	n.s.	*P*<0.005	n.s.		*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	6
UCL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*=0.01	3
UAL	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.01	n.s.	*P*<0.05*	*P*<0.05							4
UIL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05*	*P*<0.05*	*P*<0.05	*P*<0.05*	*P*=0.005	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	5
UIB	n.s.	n.s.	n.s.	*P*<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	*P*=0.005	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2
UP4L	*P*<0.05	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	*P*<0.01	n.s.	n.s.*	n.s.	n.s.*	n.s.	n.s.	2
UP4B	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.*	n.s.	n.s.*	n.s.	n.s.	2
UM1L	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.*	n.s.*	n.s.	n.s.*	n.s.	n.s.	1
UM1B	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.*	n.s.	n.s.	0
UM2L	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.*	n.s.	n.s.*	n.s.	*P*<0.05	2
UM2B	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.*	n.s.	n.s.	0
UM3L	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.*	n.s.	*P*<0.05	1
UM3B	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05*	*P*<0.01	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.*	n.s.	n.s.*	n.s.	*P*=0.005	3
LCL	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	n.s.	*P*<0.05	n.s.	*P*=0.001	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	4
LAL	n.s.	*P*<0.05	*P*<0.005	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.05	*P*<0.05							6
LIL	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	*P*=0.005	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	4
LIB	*P*<0.05*	n.s.	n.s.*	*P*<0.001	n.s.	n.s.	n.s.*	n.s.	n.s.*	*P*<0.05	n.s.*	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.*	3
LP4L	n.s.	*P*<0.05	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.01	n.s.	n.s.*	n.s.*	n.s.*	n.s.	3
LP4B	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.*	n.s.	n.s.*	3
LM1L	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.*	n.s.*	n.s.	n.s.	3
LM1B	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.005	n.s.	n.s.	n.s.	n.s.*	n.s.*	n.s.	n.s.	1
LM2L	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.*	n.s.	*P*<0.01	3
LM2B	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.*	n.s.	n.s.	0
LM3L	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.*	n.s.*	n.s.*	n.s.*	n.s.	0
LM3B	n.s.	n.s.	n.s.	n.s.*	n.s.	*P*<0.05*	n.s.	*P*<0.01	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	*P*<0.05*	n.s.*	n.s.	n.s.	4

width, and height, the CF values of sexual dimorphism and age dependence are 0.17 and 0.17 for length characters, 0.11 and 0.26 for width characters and 0.14 and 0.30 for height characters of the skull and 0.17 and 0.21 for length characters and 0.11 and 0.43 for width characters of the teeth (for the lower jaw four characters were height measurements and only one length character, so they were not further subdivided). These results show medium and more or less similar values for sexual dimorphism and age dependence in length characters, while width and characters have relatively low CF values for sexual dimorphism but high values for age dependence (Tab. 7.5).

Table 7.4. Age dependence in characters used for the analyses for the different species.

Species	***A. beecrofti***			***A. derbianus***			***A. pelii***		***A. pusillus***			**total**
Area	**1**	**26**	**33**	**1**	**26**	**32**	**13**	**14**	**26**	**32**	**33**	
n	**36**	**48**	**18**	**63**	**65**	**98**	**64**	**49**	**12**	**64**	**28**	
TL	n.s.	*P*<0.05*	n.s.	n.s.	n.s.	*P*<0.005	*P*<0.05	n.s.*	n.s.	n.s.*	n.s.	3
CIL	n.s.	n.s.*	n.s.	n.s.	n.s.	*P*<0.005	*P*=0.005	n.s.*	n.s.*	n.s.*	n.s.	2
BL	n.s.	*P*<0.05*	n.s.	n.s.	n.s.	*P*<0.01	n.s.	n.s.*	n.s.	n.s.*	n.s.	2
ZB	n.s.	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.	*P*<0.005*	n.s.	4
RB	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.05	n.s.	2
NL	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	1
NB	n.s.	*P*<0.05*	n.s.	*P*<0.005	*P*<0.05	n.s.	*P*<0.001	n.s.	n.s.	*P*<0.05	n.s.	5
IOB	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*=0.001	*P*=0.001	n.s.	n.s.	n.s.	n.s.	3
PPOB	n.s.	n.s.	n.s.	*P*<0.005	n.s.	*P*<0.005	*P*=0.005	n.s.	n.s.	n.s.*	n.s.	3
BCB	n.s.	*P*<0.005	n.s.	n.s.	*P*<0.05	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	2
CSB1	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	1
CSB2	n.s.	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	n.s.	*P*<0.05	3
CSB3	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.005	n.s.	n.s.*	*P*=0.01	n.s.	*P*<0.01	3
GL	n.s.	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.*	*P*<0.05	4
PPBL	n.s.	*P*<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	1
DL	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.05	n.s.	3
FIL	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	1
FIB	n.s.	*P*<0.05*	n.s.	n.s.	*P*<0.05	*P*<0.001	n.s.	n.s.	n.s.	*P*<0.05	n.s.	4
BP4	*P*<0.05	n.s.*	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	3
BM1	n.s.	n.s.*	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	1
BM3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	1
CHB	n.s.	*P*<0.001	n.s.	*P*<0.05	*P*<0.005	*P*<0.05	*P*<0.05	n.s.	n.s.*	n.s.	*P*<0.05	6
BUL	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	0
BUB	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0
RH	n.s.	*P*=0.001	n.s.	n.s.	n.s.*	*P*<0.05	*P*<0.01	n.s.	n.s.	n.s.	n.s.	3
ZH	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	*P*<0.01	2
PFZH	n.s.	n.s.	n.s.	n.s.	n.s.*	*P*<0.001	*P*<0.05	n.s.*	n.s.	n.s.	*P*<0.05	3
SKH	n.s.	*P*<0.005	n.s.	n.s.*	*P*<0.05*	*P*<0.001	*P*<0.001	n.s.*	n.s.	n.s.	n.s.	4
ZL	n.s.	*P*<0.005	n.s.	*P*<0.05	n.s.*	n.s.	*P*<0.05*	n.s.	n.s.	n.s.*	n.s.	3
BCH	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	2
CZB	n.s.	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	2
FIOH	n.s.	*P*<0.01	n.s.	*P*<0.05	n.s.	*P*<0.001	*P*<0.005	P<0.005*	n.s.	*P*<0.05	n.s.	6
FIOB	n.s.	*P*<0.05	n.s.	*P*<0.05	n.s.	*P*<0.005	*P*<0.01	P<0.005	n.s.	n.s.	n.s.	5
URL	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	1
LRL	n.s.	*P*<0.01	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	n.s.	*P*=0.01	3
ML	n.s.	*P*<0.05	n.s.*	n.s.	n.s.	P<0.005	*P*<0.05	*P*<0.01	n.s.	n.s.	n.s.	4
MHD	n.s.	*P*<0.05	n.s.	n.s.	n.s.*	*P*<0.01	n.s.	n.s.	n.s.	n.s.	n.s.	2
MHA	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	n.s.	*P*<0.05	n.s.	n.s.	n.s.	2
PAAD	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.*	*P*<0.05	n.s.	n.s.	n.s.	n.s.	2
PCH	n.s.	*P*<0.05	n.s.	n.s.	n.s.	P<0.005	n.s.	n.s.	n.s.	n.s.	n.s.	2

Table 7.4 (continued). Age dependence in characters used for the analyses for the different species.

Species	*A. beecrofti*			*A. derbianus*			*A. pelii*		*A. pusillus*			total
Area	1	26	33	1	26	32	13	14	26	32	33	
n	36	48	18	63	65	98	64	49	12	64	28	
UCL	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	0
UAL	n.s.	*P*=0.01	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	1
UIL	n.s.	*P*<0.005	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.01	n.s.	n.s.	n.s.*	n.s.	3
UIB	n.s.	*P*=0.005	n.s.	n.s.	n.s.	*P*=0.001	n.s.	n.s.	*P*<0.05	n.s.*	n.s.	3
UP4L	*P*<0.01	*P*=0.001	*P*<0.05*	n.s.	*P*=0.01	*P*<0.001	*P*<0.001	*P*=0.005	n.s.	*P*<0.001	n.s.	8
UP4B	n.s.	*P*<0.05	n.s.	*P*<0.001	*P*<0.001	*P*<0.001	*P*<0.001	*P*<0.001	n.s.	*P*=0.001	n.s.	7
UM1L	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0
UM1B	n.s.	n.s.	n.s.	*P*<0.001	*P*<0.001*	*P*<0.001	*P*<0.001	*P*<0.001	n.s.	n.s.*	n.s.	5
UM2L	n.s.	*P*<0.05*	n.s.	*P*<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	2
UM2B	n.s.	n.s.	n.s.	*P*<0.001	*P*<0.001	*P*<0.001	*P*<0.001	*P*<0.001	*P*<0.05	*P*<0.05	*P*<0.05	8
UM3L	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0
UM3B	n.s.	n.s.	n.s.	*P*=0.001	*P*<0.001	*P*<0.001	*P*<0.001	*P*<0.001	n.s.	n.s.	n.s.	5
LCL	n.s.	n.s.	n.s.	n.s.	n.s.*	*P*<0.05	n.s.	n.s.	n.s.*	n.s.*	n.s.	1
LAL	n.s.	n.s.*	n.s.*	n.s.	n.s.	P<0.005	*P*<0.05	*P*<0.01	n.s.*	n.s.*	n.s.	3
LIL	n.s.	*P*<0.05	n.s.	n.s.	n.s.	P<0.005	*P*<0.01	*P*<0.05	n.s.	n.s.	*P*<0.01	5
LIB	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	n.s.	n.s.	P<0.005	n.s.	3
LP4L	*P*<0.05	*P*<0.05	n.s.	*P*<0.05	*P*<0.05	*P*<0.001*	*P*<0.001	*P*<0.01*	n.s.	n.s.*	n.s.*	7
LP4B	n.s.	*P*=0.005	n.s.	*P*<0.001	*P*<0.01	*P*<0.001	*P*<0.001	*P*=0.001	n.s.	P<0.005	n.s.	7
LM1L	n.s.	n.s.	n.s.	*P*=0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	1
LM1B	n.s.	n.s.	n.s.	n.s.	n.s.	*P*<0.05	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	3
LM2L	n.s.	n.s.	n.s.	n.s.	n.s.*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0
LM2B	n.s.	n.s.	n.s.	n.s.	n.s.	*P*=0.001	*P*<0.05	*P*<0.05	n.s.	n.s.	n.s.	3
LM3L	n.s.	n.s.	n.s.	*P*<0.05	n.s.	n.s.	n.s.	*P*<0.001	n.s.	n.s.	n.s.	2
LM3B	n.s.	n.s.	n.s.*	n.s.	n.s.	*P*<0.001	*P*=0.001	*P*=0.001	n.s.	n.s.*	n.s.	3

Table 7.5. Distribution of sexual dimorphism and age dependence across different craniometric characters using the correlation factor CF (see text for details).

	sexual dimorphism (17 populations tested)		**age dependence (11 populations tested)**	
characters	**mean**	**CF**	**mean**	**CF**
skull length	2.91	0.17	1.91	0.17
skull width	1.82	0.11	2.82	0.26
skull height	2.43	0.14	3.29	0.30
skull total	2.29	0.13	2.63	0.24
lower jaw	6.20	0.37	2.40	0.22
teeth length	2.93	0.17	2.36	0.21
teeth width	1.80	0.11	4.70	0.43
teeth	2.46	0.14	3.33	0.30

Besides the effects of the measured characters themselves the Spearman's rank-order correlation test shows a strong correlation (Fig. 7.25) between the number of specimens in a population and the number of characters with statistically significant sexual dimorphism (r_s=0.668, P<0.005) and age dependence (r_s=0.758, P<0.01).

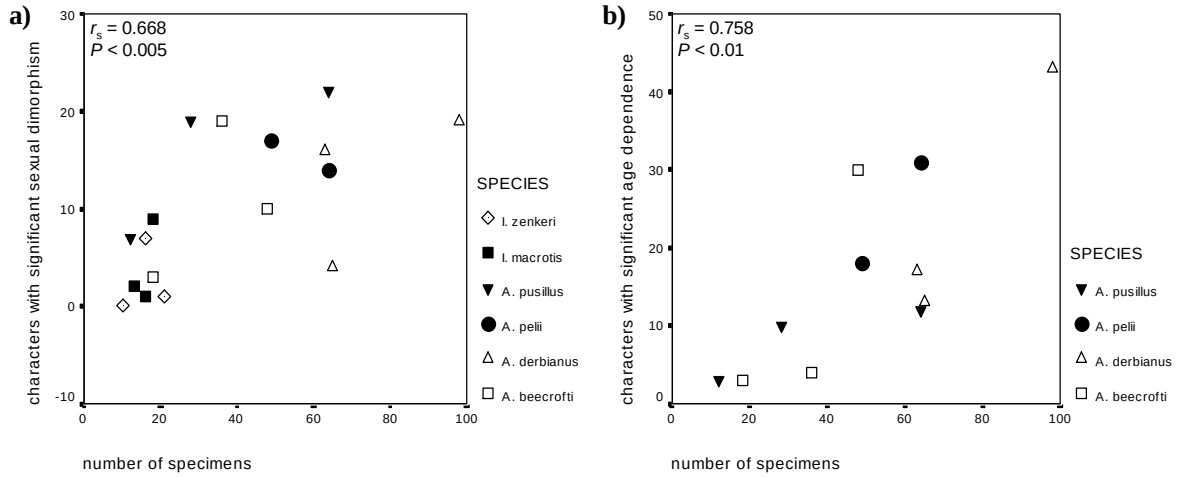

Figure 7.25. Correlation between the number of specimens in a population and the number of characters with statistically significant sexual dimorphism (a) and age dependence (b).

7.3.10. Discriminant analyses

The Tables 7.6.and 7.7 (p. 130) show the correlation between number of characters and specimens used in a discriminant analysis and the percentage of correctly to their (sub)area assigned specimens.

The Spearman's rank-order correlation test reveals also for the discriminant analysis a factor which influences the results, because the percentage of correctly assigned specimens in the discriminant analysis is significantly correlated with the number of characters used in the analysis (r_s=0.641, P<0.001). However, the number of characters needed for 100% of correct groupings is species specific and significantly correlated with the number of specimens (r_s=0.943, P=0.005; Tab. 7.8), but independent from the number of groups (2 to 4 main areas or 3 to 22 subareas; Fig. 7.27).

Table 7.6. Percentages of correctly to main areas assigned specimens depending on number of characters and specimens.

Species	n groups	n characters used	n characters excluded	n characters total	n specimens	% correct groupings
A. beecrofti	4	63	29	34	53	86,8
A. beecrofti	4	62	28	34	49	89,8
A. beecrofti	4	58	16	42	49	98,0
A. beecrofti	4	56	8	48	53	100,0
A. beecrofti	4	52	0	52	65	100,0
A. beecrofti	4	44	0	44	84	100,0
A. beecrofti	4	31	0	31	106	91,3
A. beecrofti	4	13	0	13	151	74,8
A. derbianus	4	63	0	63	135	100,0
A. derbianus	4	55	0	55	194	97,3
A. derbianus	4	45	0	45	272	93,1
A. derbianus	4	33	0	33	346	88,2
A. derbianus	4	20	0	20	407	78,2
A. pusillus	2	63	30	33	49	91,8
A. pusillus	2	61	23	38	54	88,9
A. pusillus	2	56	10	46	54	98,1
A. pusillus	3	49	0	49	57	100,0
A. pusillus	3	42	0	42	68	100,0
A. pusillus	3	26	0	26	79	100,0
A. pusillus	3	16	0	16	91	96,7
I. macrotis	3	57	47	10	27	70,4
I. macrotis	3	39	23	16	33	87,9
I. macrotis	3	38	17	21	33	90,9
I. macrotis	3	35	12	23	33	90,9
I. macrotis	3	28	0	28	38	100,0
I. macrotis	3	12	0	12	61	96,6
I. zenkeri	2	40	30	10	29	89,7
I. zenkeri	2	34	18	16	31	80,6
I. zenkeri	2	25	0	25	30	100,0
I. zenkeri	2	16	0	16	41	100,0

Tab. 7.8. Correlation between number of specimens in the discriminant analyses and number of characters needed for 100% correct groupings (percentage of original data set in brackets).

	n specimens	n characters	n characters/n specimens
A. beecrofti	84 (44.0%)	44 (68.8%)	0,52
A. derbianus	135 (25.9%)	63 (98.4%)	0,47
A. pelii	79 (56.8%)	47 (73.4%)	0,59
A. pusillus	68 (60.7%)	42 (65.6%)	0,62
I. macrotis	38 (55.9%)	28 (48.3%)	0,74
I. zenkeri	41 (80.4%)	16 (27.6%)	0,39

Table 7.7. Percentages of correctly to subareas assigned specimens depending on number of characters and specimens.

Species	n groups	n characters used	n characters excluded	n characters total	n specimens	% correct groupings
A. beecrofti	13	63	39	24	54	81,1
A. beecrofti	13	62	38	24	54	79,2
A. beecrofti	15	58	28	30	60	86,0
A. beecrofti	16	56	21	35	61	89,7
A. beecrofti	16	52	5	47	65	100,0
A. beecrofti	16	44	0	44	84	100,0
A. beecrofti	16	31	0	31	106	96,0
A. beecrofti	18	13	0	13	151	66,4
A. derbianus	17	63	0	63	135	100,0
A. derbianus	17	55	0	55	194	98,9
A. derbianus	21	45	0	45	272	91,2
A. derbianus	22	33	0	33	346	74,3
A. derbianus	22	20	0	20	407	60,8
A. pelii	3	63	16	47	57	96,3
A. pelii	3	58	6	52	60	100,0
A. pelii	3	54	0	54	69	100,0
A. pelii	3	47	0	47	79	100,0
A. pelii	3	35	0	35	93	91,3
A. pusillus	4	63	33	30	44	81,8
A. pusillus	4	61	25	36	53	92,2
A. pusillus	5	56	14	42	51	98,0
A. pusillus	5	49	0	49	57	100,0
A. pusillus	5	42	0	42	68	100,0
A. pusillus	5	26	0	26	79	92,2
A. pusillus	5	16	0	16	91	83,1
I. macrotis	5	57	49	8	64	58,3
I. macrotis	5	39	25	14	59	56,4
I. macrotis	6	38	20	18	55	72,5
I. macrotis	6	35	15	20	51	64,6
I. macrotis	7	28	0	28	38	100,0
I. macrotis	8	12	0	12	61	91,2
I. zenkeri	3	40	31	9	43	48,8
I. zenkeri	4	34	20	14	42	64,3
I. zenkeri	5	25	0	25	30	100,0
I. zenkeri	5	16	0	16	41	100,0

7.3. Discussion

In spite of the numerous statistically significant influences of sexual dimorphism, age dependence, and number of characters used in the analysis and the resulting number of specimens the results of the principal component analyses are remarkably consistent. The stepwise exclusion of characters ordered by the number of specimens they were measured for produced only small changes, although, as expected, the resolution becomes less clear with decreasing number of

characters. No basic changes resulted from the exclusion of the youngest and oldest specimens of the age classes 2 and 5. There are also no large differences in the analyses run with or without nasal length, a character that can only be measured in relatively young animals, because the caudal border fuses more or less completely with the frontal bone in older individuals. A restriction of the specimens used in the analysis to females or males only reduces the number of specimens considerably, because the sex is not known for all skulls. Still the general pattern remains visible, and seemingly clearer distances between clusters might as well be caused by the exclusion of extreme values by chance.

The results of the analyses are different for the respective species. The most abundant species, *A. beecrofti* and *A. derbianus*, show a remarkable overlap between specimens from the four main areas, despite the large geographical distances. In *A. beecrofti* the most distant populations from West Africa (area 1) and Angola (area 4) are separated, while in *A. derbianus* only the populations from Angola to southern Tanzania (area 4) are separated from the others. Within the main areas the resolution of the subareas is partly better, with clear differences between subareas in West Africa for *A. beecrofti* and a separation of specimens from south of the Congo river (area 35) from the other Central African populations (area 31 to 33). West African populations of *A. derbianus* can not be distinguished with the principal component analysis. The results for Central Africa (area 3) and the south-eastern area (area 4) suggest a weak clinal variation. *A. pelii*, the species with the smallest distribution area, shows no differences between specimens from the different subareas. Geographical populations of *A. pusillus* display tendencies towards a clinal variation in the area north of the Congo river (areas 31 to 33) and a separation between the main areas. However, the interpretation is difficult because of the small samples from West Africa (area 1) and western Central Africa (area 2). Different from the larger species *I. macrotis* and *I. zenkeri* show a very clear separation between specimens from different main areas as well as from subareas, with the only exception of the neighbouring subareas 32 and 33 in both species and subareas 11 to 14 in *I. macrotis*.

In spite of the differing results of the principal component analysis it is possible to achieve a 100% separation with the discriminant analysis between main areas and subareas in all species, but this result depends mainly on the sample size and the number of characters used in the analysis.

For all species the resolution of geographical populations is better with the ln-transformed values than with the standardised residuals for gum length. Further analyses of the information content of different characters or character sets, like skull and teeth or length and width characters, particularly in comparison with other rodent groups, would be very interesting.

8. Scaly-tailed squirrels and SuperTrees: The use of different analysis methods for an Ancient DNA problem

8.1. Introduction

As mentioned before the phylogentic relationships within anomalurids have been under discussion for a long time (see Chap. 2 for overview). The often peculiar characters make an outgroup comparison difficult, because frequently none of the different characters or character states is represented in any other rodent group or it seems to be distributed arbitrarily within rodents. Therefore the use of molecular data was a promising approach to gain additional insight into anomalurid systematics. The analyses were performed with fragments of the cytochrome b gene for two reasons. First, being a mitochondrial gene, it was originally available in a high number of copies in every cell, so the probability of recovering at least a few templates from museum material is much higher than for nuclear genes, and second, this gene has proven useful for analyses of phylogenetic relationships within rodent families in numerous previous investigations. Unfortunately, a direct collection of material was not possible due to the extremely large area inhabited by the group, including regions of civil war, occurrence of diseases like Ebola, and areas where anomalurids are protected. Hence, the analysis had to be based on collection material. Anomalurids are very well represented in museums world wide, so it was not difficult to get tissue samples. The problem was the fact that the majority of specimens were not prepared for DNA analyses which resulted in typical problems like very little DNA content in the samples, the remaining DNA being more or less degraded, a high amount of diverse and frequently not documented chemicals from preparation and conservation, and high risk of (cross)contamination (for review see Pääbo et al., 2004). This made the investigation an 'Ancient DNA' project resulting in a fragmentary data set with a high amount of missing data. Three approaches have been described for the combined analysis of data sets with missing data. In the 'total evidence' or SuperMatrix approach the data sets are concatenated directly producing one overall alignment, the so-called SuperMatrix, which is used to reconstruct a phylogenetic tree. The second (SuperTree) approach reconstructs one phylogenetic tree for each data set. All these trees serve as input in a subsequent SuperTree analysis which combines all these overlapping trees into one overall tree, the so-called SuperTree. These two approaches can be classified into 'low level methods' (SuperMatrix approaches) and 'high level methods'

(SuperTree aproaches), according to the distance of the combination from the underlying data (Schmidt, 2003, chap. 7.; note, that 'high' and 'low' do not imply quality.)
Recently, a third 'medium level method' has been suggested (Schmidt, 2003, chap. 7 and pers. comm.). The so-called 'SuperQuartet Puzzling' method (SQP) first reconstructs all possible quartet trees, i.e. unrooted trees with four taxa, using the maximum likelihood framework (ML, cf. e.g. Felsenstein, 1981) for each of the data sets separately. The different sets of quartets are combined according to their likelihoods into a set of so-called 'SuperQuartets' which is then used to reconstruct an overall tree applying a method related to 'Quartet Puzzling' (Strimmer & von Haeseler, 1996; for details concerning SQP see Schmidt, 2003, chap. 7; Fig. 8.1).

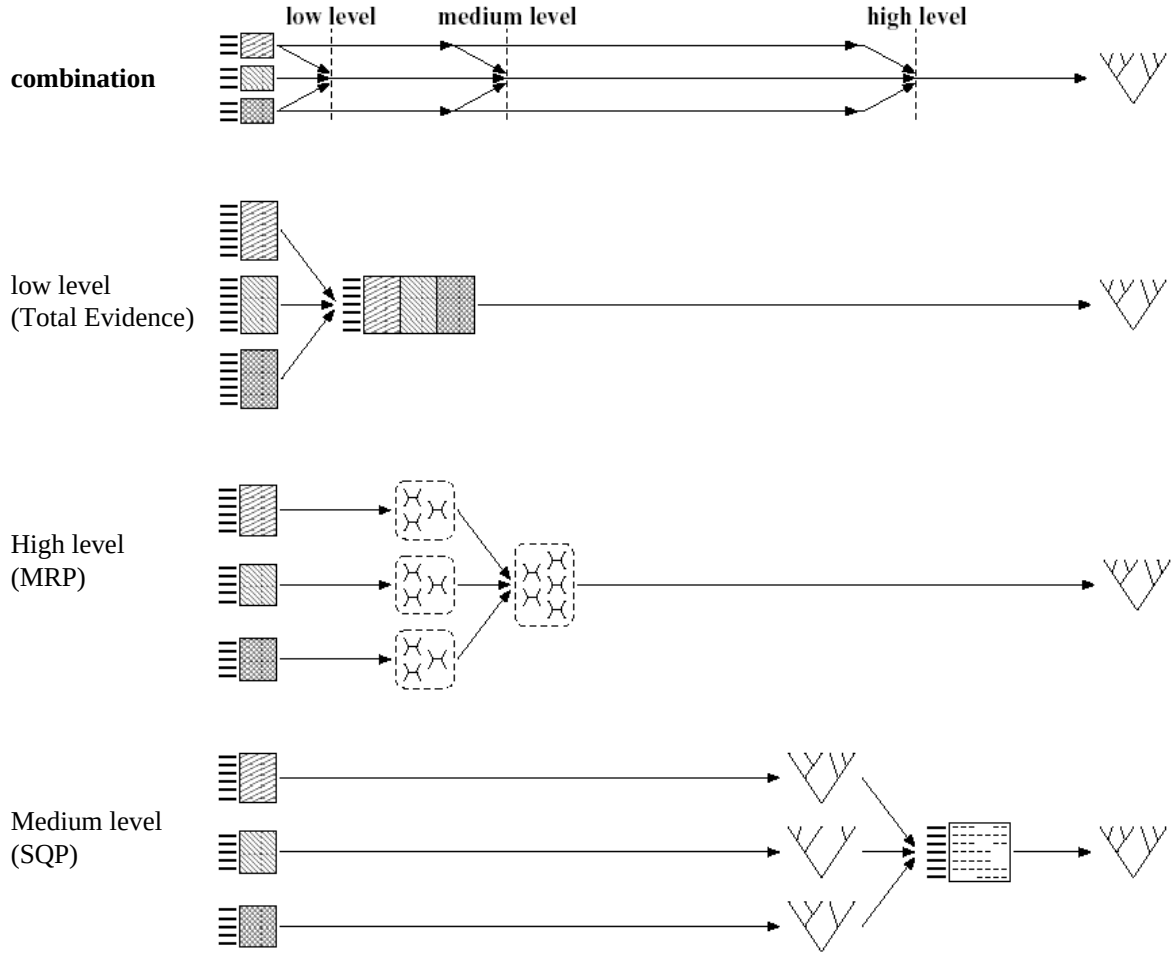

Figure 8.1. Distance between data sets and level of combination (modified from fig 7.1., Schmidt, 2003).

Although there has been a long debate about whether SuperTree or SuperMatrix methods have to be preferred (see de Queiroz et al., 1995, and Bininda-Emonds, 2003, for review), it has been concluded recently that these methods should not be seen as competitive methods but should be

used complementary (Bininda-Emonds, 2004). Accodingly, several analysis methods were tested to extract the maximum possible amount of information from the sequence data set.
The SuperMatrix of all fragments was analysed with two different ML methods as 'total evidence' approach. Furthermore, the most popular SuperTree approach MRP (Matrix Representation with Parsimony; Baum, 1992; Ragan, 1992) has been used as well as the novel SQP method.

8.2. Material and methods

8.2.1. Data basis

The material for this study are samples from dried skins or material stored in ethanol from 10 collections of the following institutes: Museum National d'Histoire Naturelle (MNHN, Paris), Musée Royal d'Afrique Centrale (MRAC, Tervuren), Naturhistorisches Museum Basel (NHMB, Basel), Naturalis/Nationaal Natuurhistorisch Museum (RMNH, Leiden), Naturmuseum Senckenberg (SMF, Frankfurt), Staatliches Museum für Naturkunde (SMNS, Stuttgart), Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK, Bonn), Zoölogisch Museum Amsterdam (ZMA, Amsterdam), Museum für Naturkunde (ZMB, Berlin), and Zadock Thompson Natural History Collections, Vermont. The number of tissue samples for the species is given in Table 8.1. The African springhare *Pedetes capensis* was used as outgroup, because this species is considered to be the closest relative of the anomalurids based on morphological and molecular data (e.g. Tullberg, 1899; Winge, 1924; Simpson, 1945; Bugge, 1974, 1985; Montgelard et al., 2001, 2002; Huchon et al., 2002). Additionally, the following sequences from GenBank were used: *Anomalurus* spec. AJ389526.1, *Idiurus macrotis* AJ389525.1, *Pedetes capensis* U59176.1, U59177.1, and U59178.1 and *P. surdaster* AJ389527.1.

Table 8.1. Number of tissue samples from the different species used for DNA analysis.

Anomalurops beecrofti	14
Anomalurus derbianus	18
Anomalurus pelii	12
Anomalurus pusillus	6
Idiurus macrotis	8
Idiurus zenkeri	8
Zenkerella insignis	2
total	**68**

8.2.2. Procedures

This paragraph explains the general procedure used to obtain the sequences. The detailed protocols are given in the Appendix.

DNA extraction

Initially several DNA-extraction methods were tested. The protocols given in the Appendix have generally achieved the best results.

PCR and cycle sequencing reaction

The study was started with a set of primers developed by Da Silva & Patton (1993). With combinations of these it was possible to obtain sequences of the first ca 800bp of the cytochrome b gene. On this basis it was possible to design several primer pairs for fragments of *ca* 200-300bp. The three primer pairs that worked best and were used for the study are given in Table 8.2.

Table 8.2. Primer pairs used in the analysis (MVZ 23 and MVZ 16-H modified after Da Silva & Patton, 1993).

Primer	Sequence	Fragment
AnoL1	CTAATGACCAATATACGAAAAAC	
AnoH1	AATGAATAGGCAGATGAAGAA	**a**
AnoL2	AACTCACAAYTGCCGAGACG	
AnoH2	RATAGCCGATAGGAGGTTT	**b**
MVZ 23	TACTCTTCCTCCACGAAACAGGITC	
MVZ 16-H	AAATAGGAAYTATCAVTCTGGTTTYAT	**c**

The PCR was conducted either in a Biometra T-Gradient or Applied BioSystems Gene Amp PCR System 2700 thermocycler. The results were checked by agarose gel electrophoresis. If the PCR products were weak, the PCR was repeated up to five times and the products pooled before continuing. PCR products were then cleaned using the Qiagen Gel Extraction Kit according to the manual. The cycle sequencing reaction was performed in the same thermocyclers and with the same primers. The products were cleaned and used for direct sequencing in an ABI Prism 377-96 Seuqencer. All samples were used at least two times with every pair of primers, generally more often, especially when already one fragment had been amplified.

8.2.3. Data analysis

The obtained sequence fragments were aligned using the CLUSTAL W program (Thompson et al., 1994) and corrected manually using BioEdit 5.0.9 (Hall, 1999).

Network analyses have been performed applying the NeighborNet method (Bryant & Moulton, 2004) implemented in the SplitsTree program (version 4beta, Huson, 1998) with default parameters.

For all different data sets as well as for the SuperMatrix, ML trees have been reconstructed using two ML methods, Quartet Puzzling as implemented in the TREE-PUZZLE package (Schmidt et al., 2002) and IQPNNI (Vinh & von Haeseler, 2004). The following options were used in the TREE-PUZZLE analysis: HKY model (Hasegawa et al, 1985) as model of evolution, 5000 puzzling steps, exact maximum likelihood estimation. For the IQPNNI reconstructions HKY model (Hasegawa et al., 1985) was used to model the evolutionary process. At least 100 iterations were run before the 'stopping rule' was applied to estimate the stopping time (Vinh and von Haeseler, 2004).

Missing parameters were estimated from sequence data.The ML trees constructed with IQPNNI were used as input trees for the MRP SuperTree analyses (Baum, 1992; Ragan, 1992). Tree topologies have been encoded to the so-called 'matrix representation' using the program SuperTree version 0.85b by Salamin et al. (2002) and applying the coding scheme by Ragan (1992) and Baum (1992) as well as the scheme by Purvis (1995). The first encodes each branch of a rooted input tree by assigning a '1' to all taxa of the respective branch. All other taxa in that tree get a '0' and all missing taxa a '?'. Purvis (1995) encodes only sister groups, assigning '1' to the taxa of one sister group '0' to the other. Taxa in the rest of the tree and missing taxa are assigned '?'.

From the resulting binary matrix representations, trees were constructed as described by Ragan and Baum (both 1992) using PAUP* Version 4.0b10 (Swofford, 2002).

The 'medium level analyses' have been performed using the implementation of the SQP method as implemented in an upcoming version of TREE-PUZZLE (Schmidt, pers. comm.)

8.3. Results

The quality of the molecular data was strongly influenced by the bad condition of most tissue samples. Consequently it was only possible to amplify very small fragments of the cytochrome b gene. For samples with good DNA the entire 822 bp sequence could be obtained, for the others fragments of 187 to 247 bp could be amplified (Fig. 8.2). In spite of the very small size,

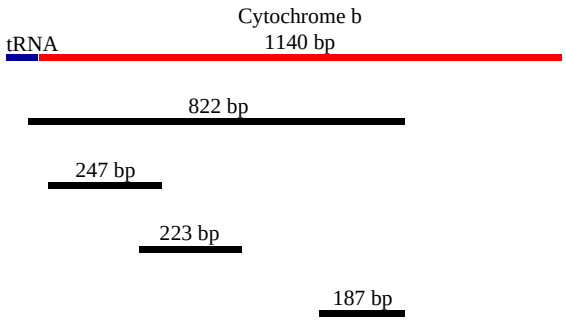

Figure 8.2. Cytochrome b fragments used in the analyses.

fragments of most samples could not be amplified. For the others the PCR product was as a rule weak (Fig. 8.3) and frequently had to be repeated up to five times and the products were pooled before cleaning. In several cases only one or two of the fragments could be amplified (Fig. 8.4).

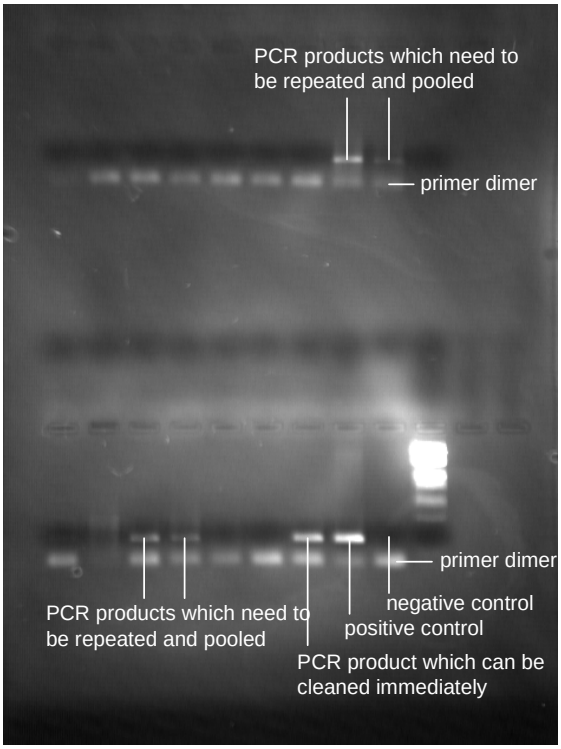

Figure 8.3. Typical PCR products from museum specimens.

8.3.1. Low level combination or total evidence

In a first analysis the complete data set was tested with a NeighborNet analysis (Fig. 8.5). The results show that specimens clustered according to the available fragments rather than to the species. An analysis of the complete data set with PAUP produced a badly resolved cladogram (Fig. 8.6), where only the specimens of *A. pusillus* are considered monophyletic. However, when the cladogram is forced into complete resolution with IQPNNI the results correspond to the currently accepted taxonomy of the anomalurids (Fig. 8.7).

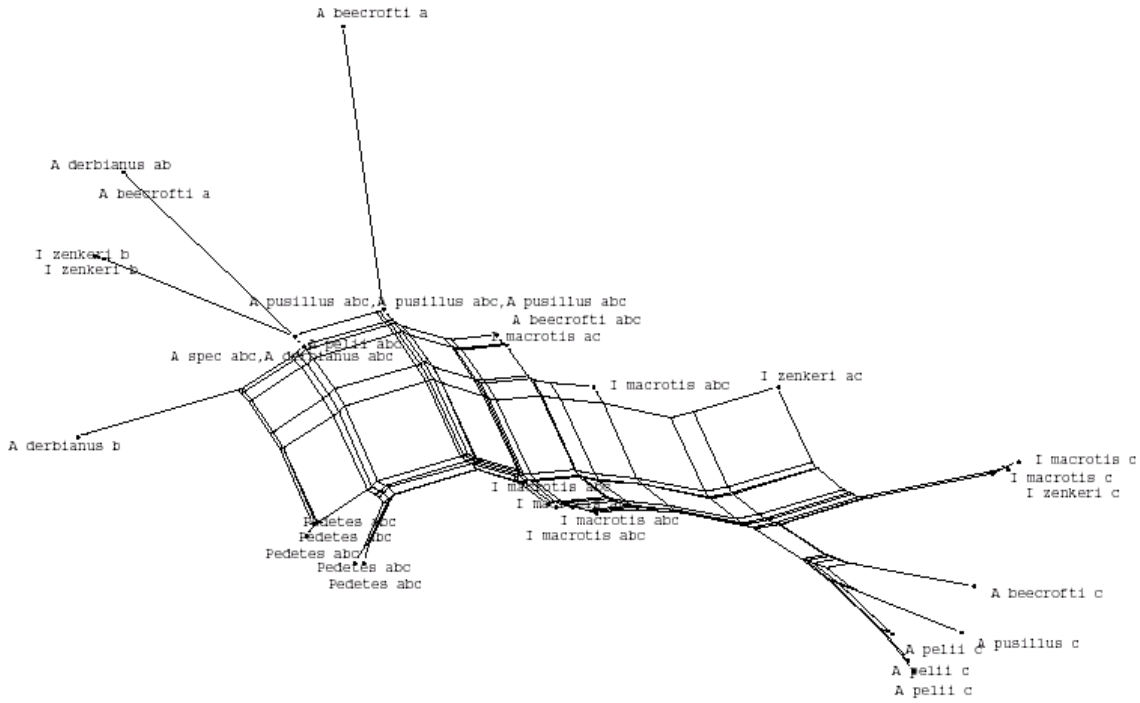

Figure 8.5. Network for all samples obtained with NeighbourNet method (Bryant and Moulton, 2004) as implemented in SplitsTree using default parameters (a, b, c: sequenced fragments for the specimens).

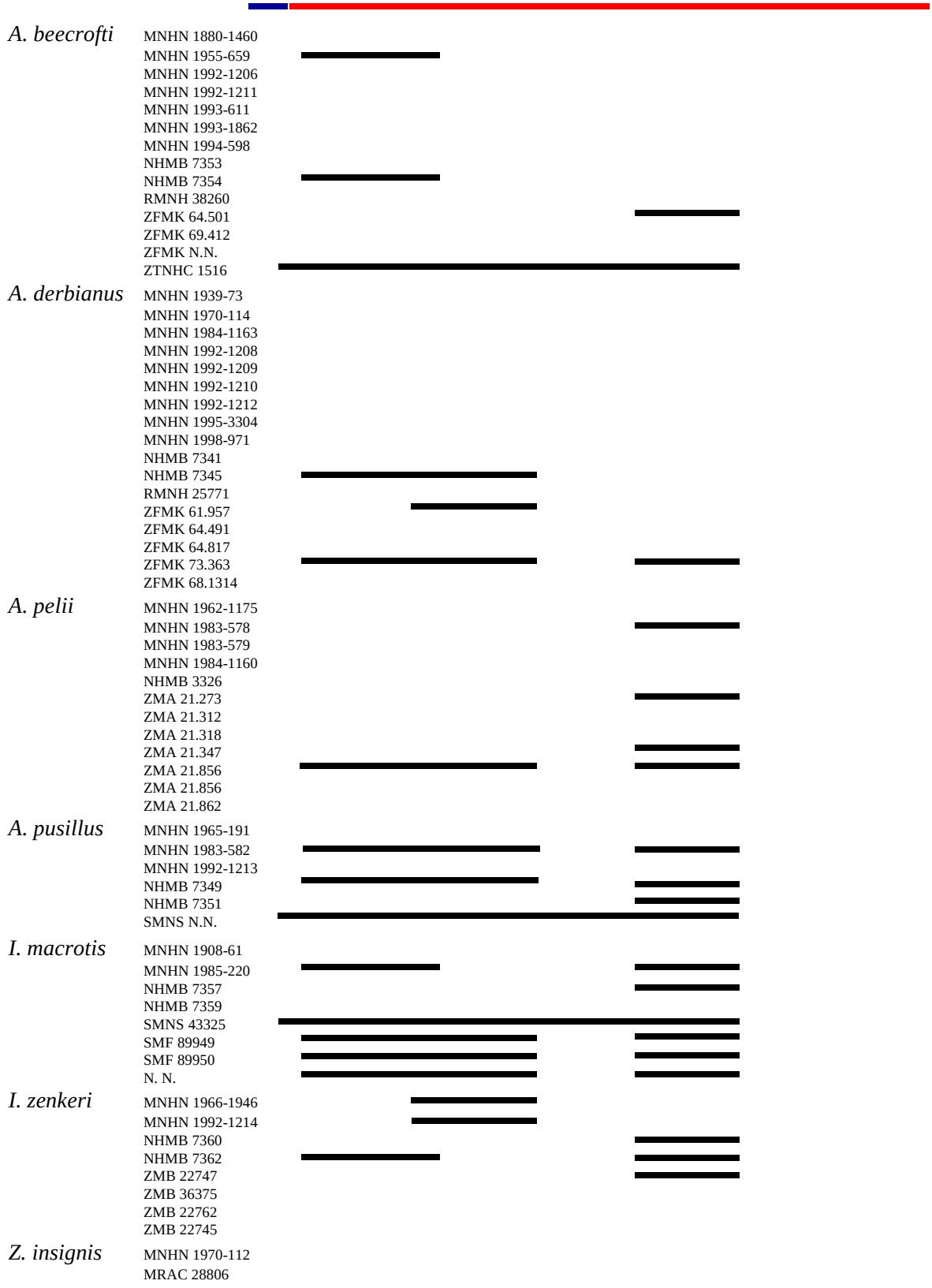

Figure 8.4. Cytochrome b fragments that could be amplified from the available tissue samples.

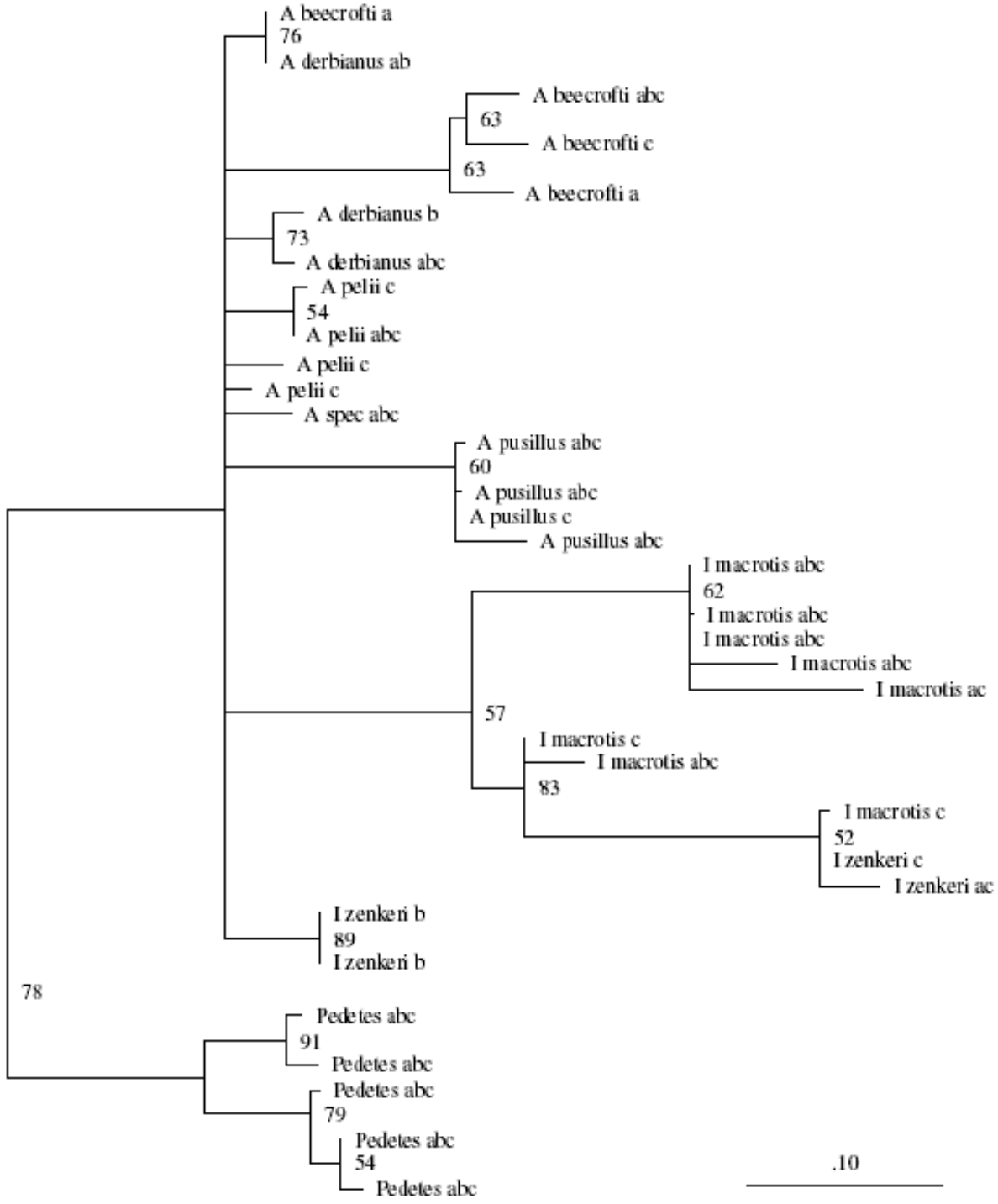

Figure 8.6. Total evidence cladogram calculated with TREE-PUZZLE (a, b, c: sequenced fragments for the specimens; numbers: puzzle support values; see text for details).

For the next step three separate analyses were made for each of the fragments (Fig. 8.8). The resulting cladograms were better resolved due to the completeness of data within the subsamples, but those for the first two fragments showed several outliers. A single specimen of *A. pelii* was

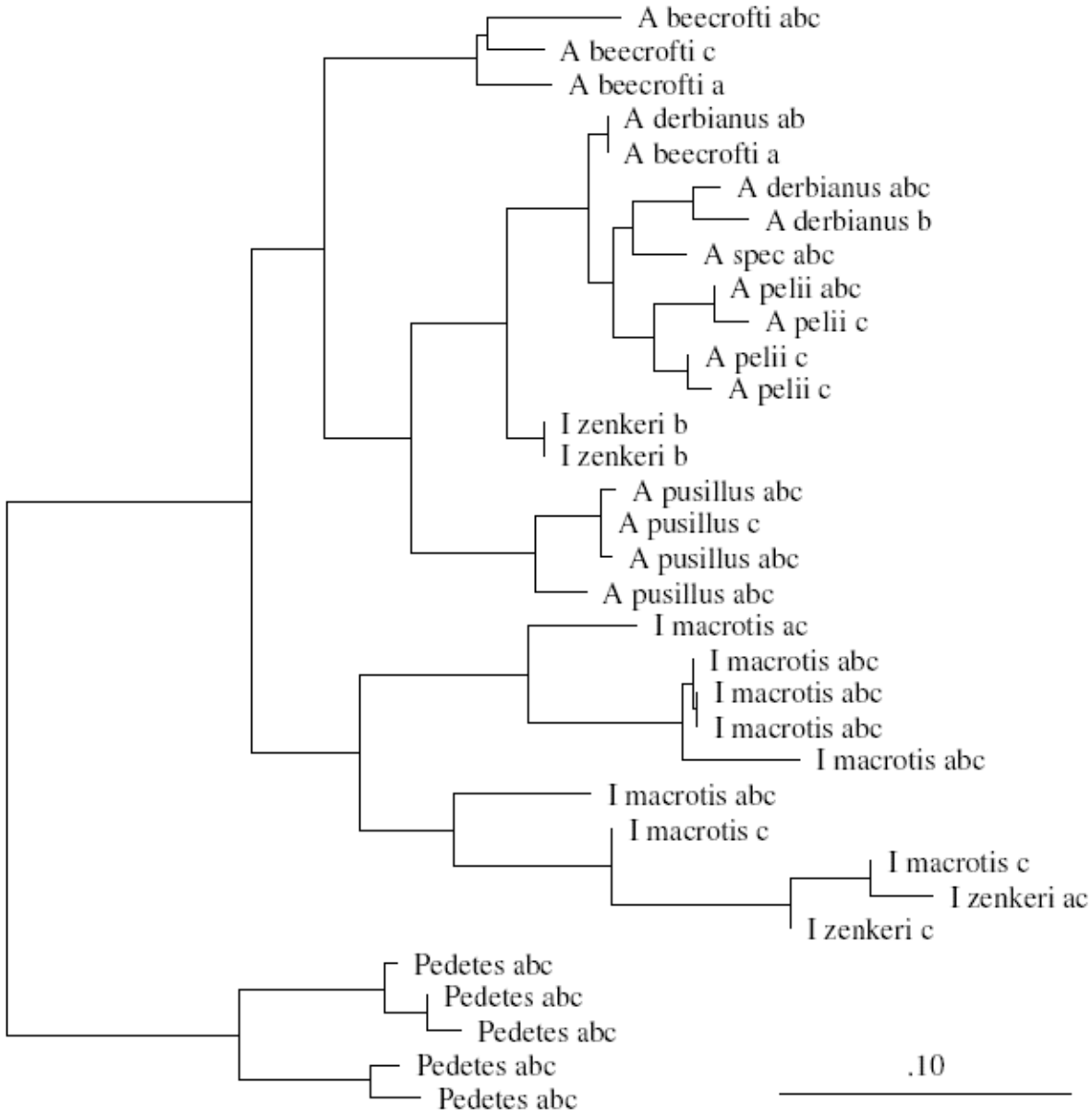

Figure 8.7. Total evidence cladogram calculated with IQPNNI (a, b, c: sequenced fragments for the specimens; see text for details).

found within *A. derbianus*, and single specimens of *A. beecrofti* and *Idiurus* clustered within other (but different) species. Apart from these outliers the species were generally found monophyletic. The best resolution was found with the shortest fragment c, where the cladogram also matched the generally accepted taxonomy of the group. *Idiurus* is monophyletic, although the two species could not be resolved. The Anomalurinae are also monophyletic with *Anomalurops* being the sister group of the three *Anomalurus* species and *A. pusillus* the sister group of the unresolved *A. derbianus* and *A. pelii*.

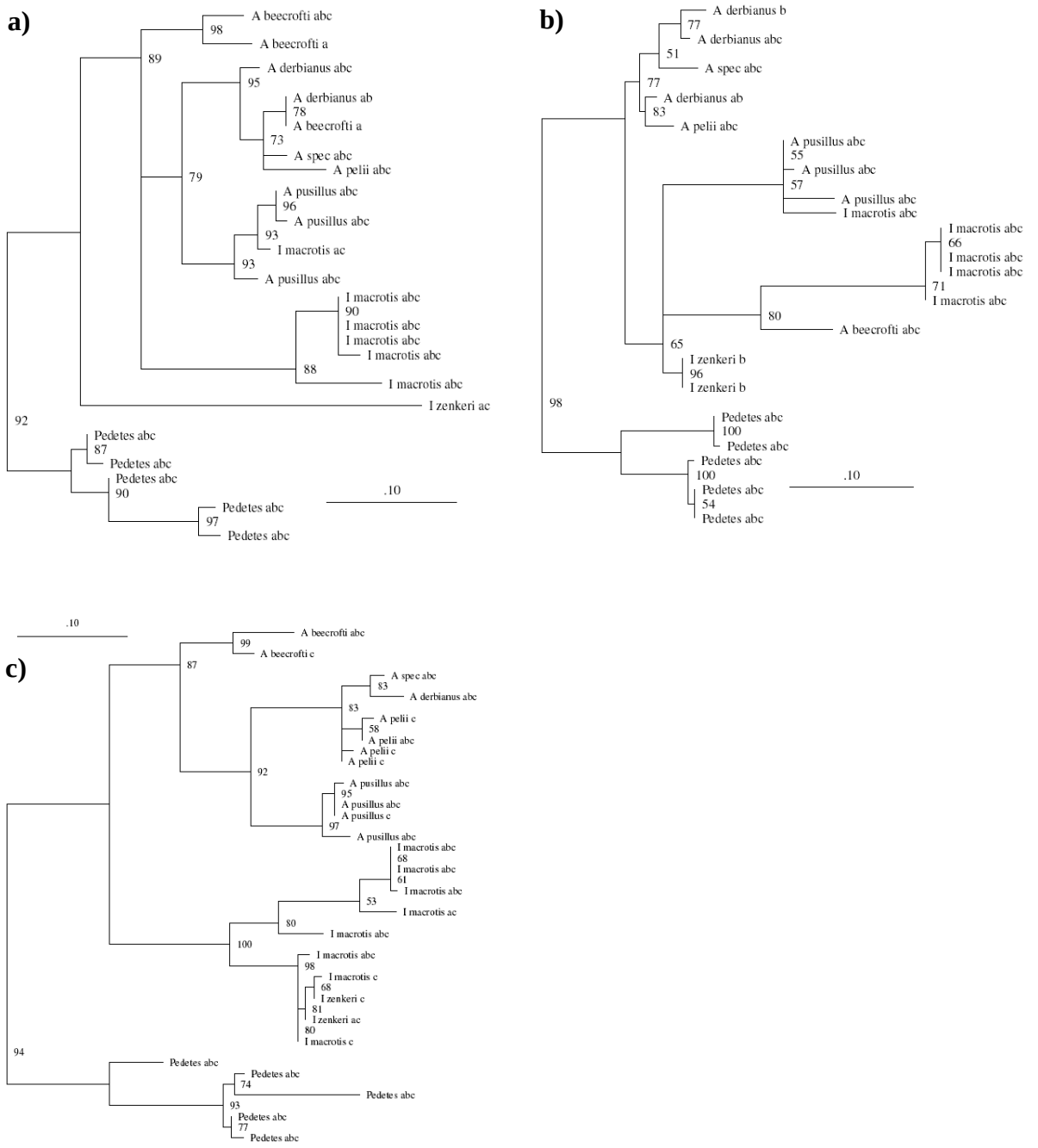

Figure 8.8. TREE-PUZZLE trees for each of the the fragments a, b, and c separately (a, b, c: sequenced fragments for the specimens; numbers: puzzle support values; see text for details).

8.3.2. High level combination or SuperTree

The following analyses were run with two different combinations of the available data with regard to the treatment of the overlapping region o of the first two fragments (Fig. 8.9). In the first case all three complete fragments a, b, and c were used, thus using the overlapping part twice, if both fragments were sequenced for one specimen (‘3 fragments’). For the other case the overlapping part was used as an individual fragment and the two flanking fragments were shortened

appropriately, so the overlapping region was only used once (‘4 fragments’). The analyses were run with Baum/Ragan coding as well as with Purvis coding leading to the four trees presented in Fig. 8.10. For the analysis with 3 fragments the resolution was bad, with one *I. macrotis* and two *I. zenkeri* being the sister group of the unresolved rest. Within this unresolved branch most of the species were found either monophyletic or unresolved, except for single outliers, and a mixed branch for *A. derbianus* and *A. pelii*. When 4 fragments were used the results were better resolved, but contradict each other. With the Baum/Ragan coding *A. beecrofti* appeared as the sister group of a clade mixed of *A. derbianus* and *A. pelii*, while *A. pusillus* is found as sister group of *Idiurus*. With the Purvis coding *A. beecrofti* shows up within *Idiurus* while *A. derbianus*, *A. pelii* and *A. pusillus* build the other branch.

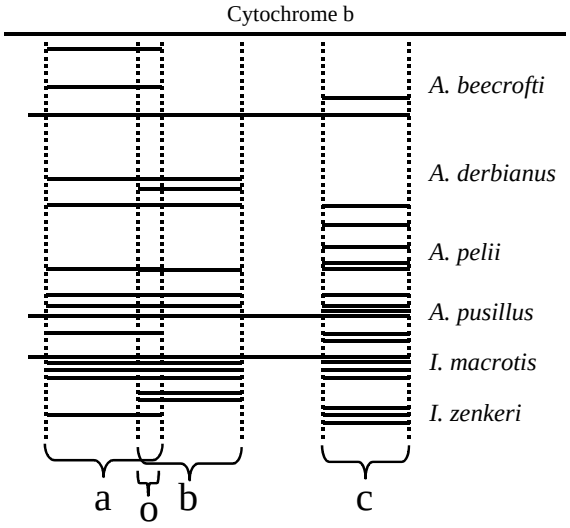

Figure 8.9. This figure shows the three cytochrome b fragments a, b, and c which were used in the analyses as well as the overlap o between fragments a and b (see text for details).

8.3.3. Medium level combination

The medium level combination produced with 3 fragments a well resolved tree with monophyletic *A. beecrofti*, *A. pusillus*, *Idiurus* and a group mixed of *A. derbianus* and *A. pelii* (Fig. 8.11). The cladogram from 4 fragments had a very bad resolution, but it shows no contradictions to the first one.

8.4. Discussion

8.4.1. Comparison of the results

The results obtained with the different methods differ in several aspects. As expected the total evidence analyses yielded very bad resolution due to the high amount of missing data (more than 50%) in the data set. The network showed that in the SuperMatrix the availability of fragments for a specimen had a similar influence like the species they belong to. Consequently, the TREE-PUZZLE cladogram from the SuperMatrix is also badly resolved, although the resolution with IQPNNI brought results that matched the morphological classification.

In separate analyses of the three sequenced fragments the resolution is much better, but the results contradict each other. Additionally, the cladograms from the first two fragments contradict

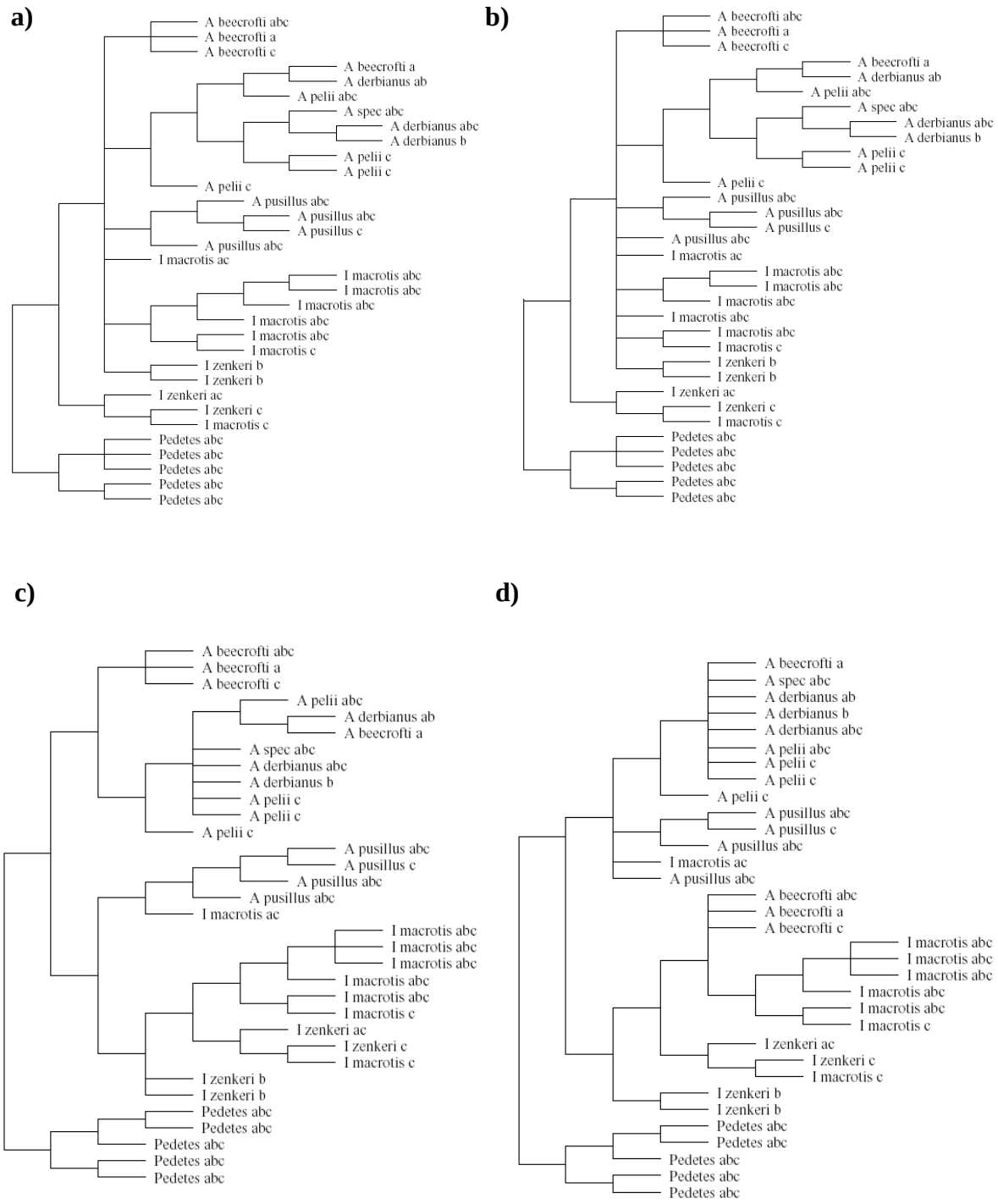

Figure 8.10. Results of the MRP SuperTree analyses with Baum/Ragan (a, c) and Purvis (b, d) coding and 3 (a, b) and 4 (c, d) fragments respectively (a, b, c: sequenced fragments for the specimens; text for details).

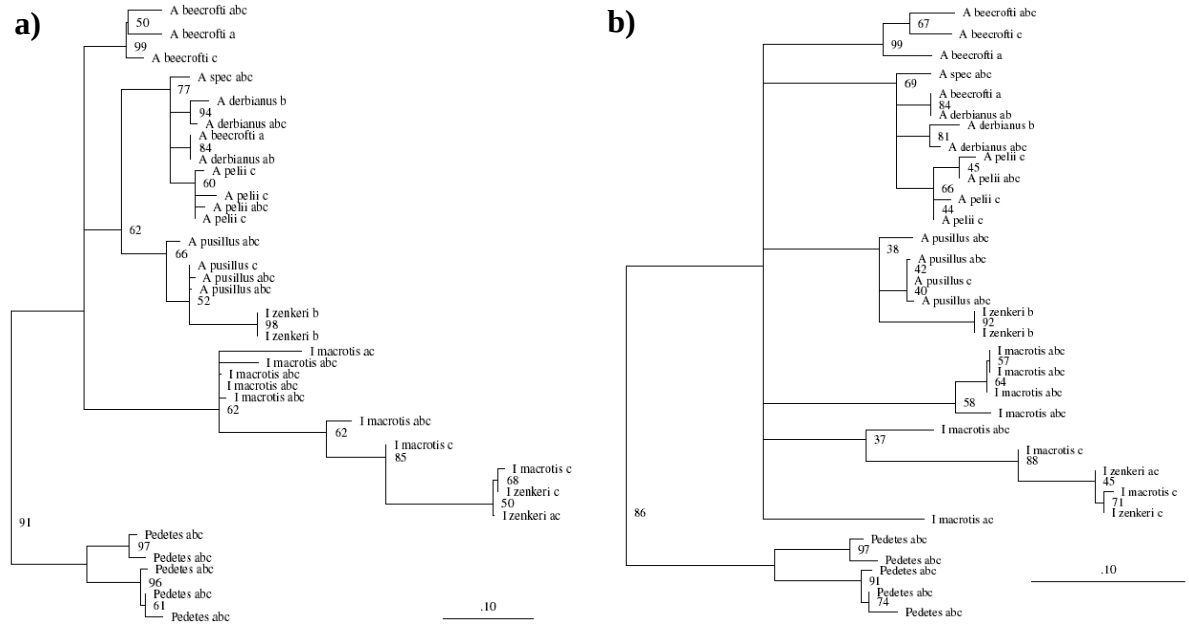

Figure 8.11. Medium level trees obtained with SuperQuartet Puzzling for 3 (a) and 4 (b) fragments (a, b, c: sequenced fragments for the specimens; numbers: puzzle support values; see text for details).

previous morphological and taxonomic results, while the tree found with the shortest fragment matches at least the currently accepted classification at the subfamilies and genera level. When the trees for each fragment were combined the resulting cladograms were badly resolved when 3 fragments were used and appearingly better resolved but contradicting with 4 fragments. Finally the medium level combination resulted in a relatively well resolved cladogram matching the morphological classification.

Summarizing, judging from the comparison with the more reliable morphological systematization, the SuperTree analysis seems to be least suitable for a fragmented DNA data set. Cladograms matching this classification were obtained with IQPNNI for the SuperMatrix, TREE-PUZZLE for the shortest fragment c, and SQP for 3 fragments. The latter is not completely resolved, while in the cladogram from the shortest fragment some individuals are missing because the fragment could not be amplified.

8.4.2. Methodological remarks

In the anomalurid data set on the one hand basal splits are frequently not resolved (see for example Fig. 8.6, 8.10b, or 8.11b) on the other hand there are some cases of obviously closely related species which appeared mixed on one branch (e.g. *A. derbianus* and *A. pelii* in Fig. 8.10). The following points seem to have a great impact of the analysis of this kind of data: For every species there should be at least one complete set with all fragments, otherwise specimens tend to be grouped according to the fragments available rather than to their systematic position (cf. *I.*

zenkeri in the majority of trees). Additionally, the smaller the given data set, the more problems are caused by sequences with numerous alignment ambiguities. Finally, fragments used for analyses should not be too short because of lack of phylogenetic information (e.g. fragment o). The short fragment c with less than 200 bp seems to have a remarkably high amount of phylogenetic information in this group. Since it is also relatively easy to amplify it should be tested for other taxa too, because it might proof useful for analyses with old collection material, from which it is not possible to obtain longer sequences.

8.4.3. Relationships of anomalurid species

Some of the taxa are clearly better supported than others. Though well documented with morphological data the separation of *A. derbianus* and *A. pelii* is obviously difficult with the single sequenced fragments, but they appear as monophyletic in the majority of cladograms. Also very stable is the species *A. pusillus*, which is one of the most reliably recognized taxa. *A. pusillus* is generally found as the sister group of the clade *A. derbianus* and *A. pelii*, and *A. beecrofti* as the sister group of the three *Anomalurus* species. The sister group of the four larger sized species, which are also considered as subfamily Anomalurinae, is *Idiurus*, member of the subfamily Zenkerellinae. Like *A. derbianus* and *A. pelii*, the species *I. macrotis* and *I. zenkeri* are mixed in all cladograms. However, there is a clear congruence between the cladograms resulting in the phylogram given in Figure 8.12. Unfortunately, it had not been possible to get a sequence from *Z. insignis*, the only species not able to perform gliding flight, which is generally placed together with *Idiurus* in the subfamily Zenkerellinae.
The tree topology is supported by several morphological characters (Tab. 8.3).

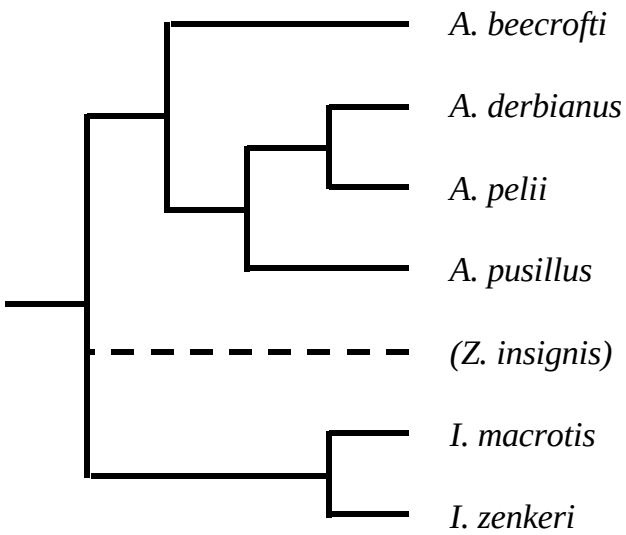

Figure 8. 12. Most likely relationships between anomalurid species as derived from molecular and morphological characters (see text for details).

Tab. 8.3. Some morphological characters supporting branches in the tree topology for Anomaluridae given in Fig. 8.11 (* characters not shown by all specimens).

A. beecrofti
1. white spot/hairs on top of head
2. tail hair not much longer than body hair*
3. underparts yellowish to bright orange
4. four enamel crests on molar teeth
5. cheek teeth row strongly concave

A. derbianus + A. pelii
1. ear colouration different from head colouration*
2. nose lighter than rest of head*

A. derbianus + A. pelii + A. pusillus
1. underparts whitish to light grayish, never orange
2. five enamel crests on molar teeth*
3. cheek teeth row only slightly concave

A. becrofti + A. derbianus + A. pelii + A. pusillus
1. cheek teeth with enamel crests and visible dentine
2. cheek teeth relatively large
3. incisors more or less equally wide and deep in cross-section
4. supporting cartilage rod extends from flat ulnar process
5. zygomatic arc relatively low

I. macrotis + I. zenkeri
1. no enlarged, pointed scales on tail
2. two rows of short, stiff hair on the tail
3. sparse, very long and thin hairs on the tail
4. supporting cartilage rod extends from ulnar crest
4. cheek teeth with three to four crests, no dentine visible
6. total length less than 30 cm

Z. insignis + I. macrotis + I. zenkeri
1. cheek teeth very small
2. incisors extremely elongated and narrow in cross-section
3. zygomatic arc placed relatively high
4. underparts uniformly grey

Z. insignis + A. becrofti + A. derbianus + A. pelii + A. pusillus
1. tail with hair tuft*
2. enlarged, pointed scales on the tail
3. total lenght more than 30 cm

The selection of morphological characters given in Table 8.3. demonstrates the strong congruence between results from DNA sequences and morphology in this group. However, a considerable number of populations from several species do not fit into this general pattern and need further investigation. Unfortunately it had not been possible to obtain sequnces from the enigmatic *Z. insignis*, the only species with contradicting morphological affinities and thus the most interesting for molecular studies.

References

Baum, B.R. 1992. Combining trees as a way of combining data sets for phylogenetic inference, and desirability of combining gene trees. *Taxon* **41**: 3-10.

Bininda-Emonds, O. R. P. 2003. MRP supertree construction in the consensus setting, pp. 231-242. *In* Janowitz, M.F., F.-J. Lapointe, F.R. McMorris, B. Mirkin & F.S. Roberts (Eds), *Bioconsensus. DIMACS: Series in Discrete Mathematics and Theoretical Computer Science, volume 61*. American Mathematical Society-DIMACS, Providence, Rhode Island.

Bininda-Emonds, O. R. P. 2004. The evolution of supertrees. *Trends Ecol. Evol.* **19**:315-322.

Bryant, D. & Moulton, V. 2004. Neighbor-Net: An Agglomerative Method for the Construction of Phylogenetic Networks. *Mol. Biol. Evol.* **21**: 255-265.

Bugge, J. 1974. The Cephalic Arterial System in Insectivores, Primates, Rodents and Lagomorphs, with Special Reference to the Systematic Classification. *Acta Anatomica* **87**, Suppl. **62**: 1-159.

Bugge, J. 1985. Systematic value of the carotid arterial pattern in rodents, pp. 355-379. *In* Luckett, W. P. & Hartenberger, J.-L. (Eds), *Evolutionary relationships among rodents: A Multidisciplinary analysis.* New York.

Da Silva, M. N. F. & Patton, J. L. 1993. Amazonian Phylogeography: mtDNA Sequence Variation in Arboreal Echimyid Rodents (Caviomorpha). *Mol. Phylogenet. Evol.* **2(3)**: 243-255.

Felsenstein, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *J. Mol. Evol.* **17**: 368-376.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser*. **41**: 95-98.

Hasegawa, M., Kishino, H. & Yano, T.-A. 1985. Dating of the human ape splitting by a molecular clock of mitochondrial DNA. *J. Mol. Evol.* **22**: 160-174.

Huchon, D., Madsen, O., Sibbald, M. J. J. B., Ament, K., Stanhope, M. J., Catzeflis, F., de Jong, W. W. & Douzery, E. J. P. 2002. Rodent Phylogeny and a Timescale for the Evolution of Glires: Evidence from an Extensive Taxon Sampling Using Three Nuclear Genes. *Mol. Biol. Evol.* **19(7)**: 1053-1065.

Huson, D. H. 1998. SplitsTree: a program for analyzing and visualizing evolutionary data. *Bioinformatics* **14**: 68-73.

Montgelard, C., Bentz, S., Douady, C., Lauquin, J. & Catzeflis, F. M. 2001. Molecular phylogeny of the sciurognath rodent families Gliridae, Anomaluridae and Pedetidae, pp. 293-307. *In* Denys, C.,

Granjon, L. & Poulet, A. (Eds), *Proceedings of the 8th International Symposium on African Small Mammals, Paris, July 1999*.

Montgelard, C., Bentz, S., Tirard, C., Verneau, O. & Catzeflis, F. M. 2002. Molecular Systematics of Sciurognathi (Rodentia): The Mitochondrial Cytochrome b and 12S rRNA Genes Support the Anomaluroidea (Pedetidae and Anomaluridae). *Mol. Phylogenet. Evol.* **22(2)**: 220-233.

Pääbo, S., Poinar, H., Serre, D., Jaenicke-Després, V., Hebler, J., Rohland, N., Kuch, M., Krause, J., Vigilant, L. & Hofreiter, M. 2004. Genetic Analyses from Ancient DNA. *Annu. Rev. Genet.* **38**: 645-679.

Purvis, A. 1995. A composite estimate of primate phylogeny. *Philos. Trans. R. Soc. Lond. Ser. B* **348**: 405-421.

Queiroz, A. de, Donoghue, M. J. & Kim, J. 1995. Separate versus combined analysis of phylogenetic evidence. *Annu. Rev. Ecol. Syst.* **26**: 657-681.

Ragan, M. A. 1992. Phylogenetic inference based on matrix representation of trees. *Mol. Phylogenet. Evol.* **1**: 53-58.

Salamin, N., Hodkinson, T. R. & Savolainen, V. 2002. Building supertrees: an empirical assessment using the grass family (Poaceae). *Syst. Biol.* **51**: 134-150.

Schmidt, H. A., Strimmer, K., Vingron, M. & von Haeseler, A. 2002. TREE-PUZZLE: Maximum Likelihood Phylogenetic Analysis Using Quartets and Parallel Computing. *Bioinformatics* **18**: 502-504.

Schmidt, H. A. 2003. *Phylogenetic Trees from Large Datasets.* PhD thesis, Düsseldorf.

Shedlock, A. M., Haygood, M. G., Pietsch, T. W. & Bentzen, P. 1997. Enhanced DNA Extraction and PCR Amplification of Mitochondrial Genes from Formalin-Fixed Museum Specimens. *BioTechniques* **22 (3)**: 394-400.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**: 1-350.

Strimmer, K. & von Haeseler, A. 1996. Quartet puzzling: A quartet maximum-likelihood method for reconstructing tree topologies. *Mol. Biol. Evol.* **13**: 964-969.

Swofford, D. L. 2002. *PAUP* - Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.* Sinauer Associates, Sunderland, Massachusetts.

Thompson, J. D., Higgins, D. G. & Gibson, T. J. 1994. CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. *Nucleic Acids Res.* **22**: 4673-4680.

Tullberg, T. 1899. *Über das System der Nagethiere. Eine phylogenetische Studie.* Akademische Buchdruckerei, Uppsala.

Vinh, L. S. & von Haeseler, A. 2004. IQPNNI: Moving Fast Through Tree Space and Stopping in Time. *Mol. Biol. Evol.* **21**:1565-1571.

Winge, H. 1924. *Pattedyr-Slaegter. 2. Rodentia, Carnivora, Primates.* H. Hagerups Forlag, Kjobenhavn.

Appendix: **Protocols for the DNA analysis**

A. DNA-Extraction

1. DNA-Isolation

1.1. Wilson-Buffer

protocol modified after C. Klütsch (pers. comm.)

- cut tissue (up to 1 cm^2) in small pieces
- add 200 µl Wilson-Buffer
- incubate at room temperature for 1 to 4 h
- homogenate with micropestle
- add another 200 µl Wilson-Buffer
- add 2 µl RNAse (10 mg/ml)
- incubate at room temperature for 5 min
- add 20 µl Proteinase K (25 mg/ml)
- 40 µl SDS solution 10%
- incubate at 55°C for 2 to 48 h, where required, add 2-5 µl Proteinase K every 6 - 12 h

Wilson-Buffer

3.025 g Tris
0.9 g EDTA
1.4 g NaCl
250 ml ddH_2O
pH 8.0
store at room temperature

1. 2. DNA Extraction from formalin preserved tissue

Protocol modified after Shedlock et al. (1997)

- dry tissue to avoid traces of Ethanol
- cut tissue into small pieces
- 24h in 1 to 10 ml GTE
- repeat two times
- dry tissue
- QIAamp DNA Mini Kit according to the manual
- add Proteinase K
- 10 µl DTT (154.24 g/mol) 1M
- incubate for 1 to 3 days

GTE

100 mM Glycin (1.502 g / 200 ml)

10 mM Tris-HCl (242.2 g / 200 ml)

1 mM EDTA (74.44 g / 200 ml)

2. DNA-Extraction

- add 600 µl Phenol/Dichlormethane/3-Methyl-1-butanol 25:24:1 or Dichlormethane/3-Methyl-1-butanol 24:1
- vortex
- centrifugate 10 min at 13000 rpm
- transfer upper phase to new tube
- add 600 µl Dichlormethane/3-Methyl-1-butanol 24:1
- vortex
- centrifugate 10 min at 13000 rpm
- transfer upper phase carefully to new tube (avoid any traces of Dichlormethane/3-Methyl-1-butanol)

3. DNA precipitation

- add 40 µl Sodium acetate solution 3M
- add 1 ml Ethanol 96%
- mix carefully
- if no DNA precipitation is visible, keep at -20°C for 15 min
- centrifugate for 10 min at 13000 rpm
- discard supernatant
- add 400 µl Ethanol 70%
- centrifugate for 5 min at 13000 rpm
- discard supernatant
- let DNA pellet dry at room temperature
- dissolve DNA in 20 to 50 µl ddH_20

B. PCR

PCR reaction mix

PCR-Kit from Sigma, for 25 µl reaction:

H_2O	17.2 / 15.2 µl*
10x Buffer	2.5 µl
$MgCl_2$ (25mM)	3.0 / 5.0 µl*
dNTPs (2 mM)	0.5 µl
L-primer (20 pM)	0.3 µl
H-primer (20 pM)	0.3 µl
Taq-polymerase (5U/µl)	0.2 µl
DNA	1.0 µl

*depending on primer combination

Settings of the thermocycler for the PCR

1. 95°C for 5 min (initial denaturation of template DNA)
2. 94°C for 20 s (denaturation)
3. 49°C for 20 s (annealing of the primers to the template DNA)
4. 72°C for 45 s (elongation of PCR product)
5. 35 cycles (repeat steps 2 to 4)
6. 71°C for 8 min (final elongation of PCR product)

Cleaning of the PCR products

Qiagene Gel Extraction Kit according to the manual

C. Sequencing reaction

Cycle sequencing reaction with ABI Prism® BigDye™ Terminater Cycle Sequencing Kit

dry up to 12 µl cleaned PCR product in reaction tubes for cycle sequencing reaction

add:

2.0 µl ReadyMix

0.5 µl $MgCl_2$ (25 mM)

1.0 µl Primer 20 pM

6.5 µl ddH_20

Settings of the thermocycler for the cycle sequencing reaction

1. 94°C for 2 min
2. 92°C for 15 s
3. 50°C for 15 s
4. 60°C for 2 min 30 s
5. 25 cycles of steps 2 to 4
6. 93°C for 20 s
7. 60°C for 15 s
8. 8 cycles of steps 6 to 7

Cleaning of the cycle sequencing products

- transfer cycle sequencing product to a new sample tube
- add 40 µl ddH_20
  5 µl Sodium acetate 3M
  125 µl Ethanol 100%
- centrifuge 20 min at 13000 rpm
- discard supernatant
- wash with 300 µl Ethanol 70% freshly diluted
- centrifuge 5 min at 13000 rpm
- discard supernatant
- dry pellet
- dissolve in 4 µl stop buffer

Sequencing acrylamid gel

12 g Urea
5 ml 29:1 Bisacrylamid
4 ml TBE 10x
15,3 ml ddH_2O
10 µl TEMED
233 µl APS

10x TBE-Buffer for gelelctrophoresis

110.1 g Boric acid
81.9 g EDTA
215.6 g Tris
ad 2 l H_2O

Stop-Buffer

5 ml Formamid

1 ml Blue Dextran-EDTA

morphological characters (see text for details).

9. Conclusions

9.1. Geographical units of anomalurid species

This section gives a combined analysis of geographical units within anomalurid species that can be distinguished by colouration and/or morphometric characters of the body and/or skull.

9.1.1. *Anomalurops beecrofti*

A. beecrofti is the species for which it is most difficult to define geographical units that can be reliably distinguished. The first problem is how to valuate the distribution of colouration forms between specimens from neighbouring areas (see Chap. 4). In spite of the statistically significant differences found in the composition of colouration forms in several cases most of the dorsal colouration and all ventral colouration forms occur in the whole area inhabited by the species. This makes it impossible to assign any one specimen to a certain area, except for the small number of specimens with a completely silverish back which occur only west of the Congo and Ubangi Rivers, and the very few specimens with uniformly reddish back which are restricted to Equatorial Guinea and adjacent Gabon. However, these colouration forms are always mixed with specimens of other colourations. There are also a few small areas where one dorsal or ventral colouration occurs exclusively, but this form can also be found in neighbouring and distant areas and is never matched by the distribution of ventral or dorsal colouration respectively.

Geographical borderlines for *A. beecrofti* supported by several and/or strong differences in single characters are shown on the distribution map in Fig. 9.1. The population from in between the Volta River and the Dahomay Gap can be relatively well distinguished from the neighbouring populations by the composition of dorsal and ventral colourations, body size, and morphometric skull characters, although for some characters the data basis is small. Weaker support is found for the borderline between the population from Nigeria from that from Western Cameroon (areas 24 and 25, see Chap. 5), because the clear differences in dorsal and ventral colouration frequencies are not matched by morphometric characters. Another borderline is represented by the Congo River which separates populations differing considerably in ventral colouration, body size and skull measurements, with differences being strongest along the upper Congo and less pronounced along the lower part of the river. The influence of the lower Ubangi River is difficult to assess because of the very small number of specimens collected in its vicinity. Finally

specimens from Western Angola (area 41) can be distinguished from those from the Southern Democratic Republic of Congo (area 35) by frequencies in dorsal and ventral colouration as well as morphometric body and skull characters.

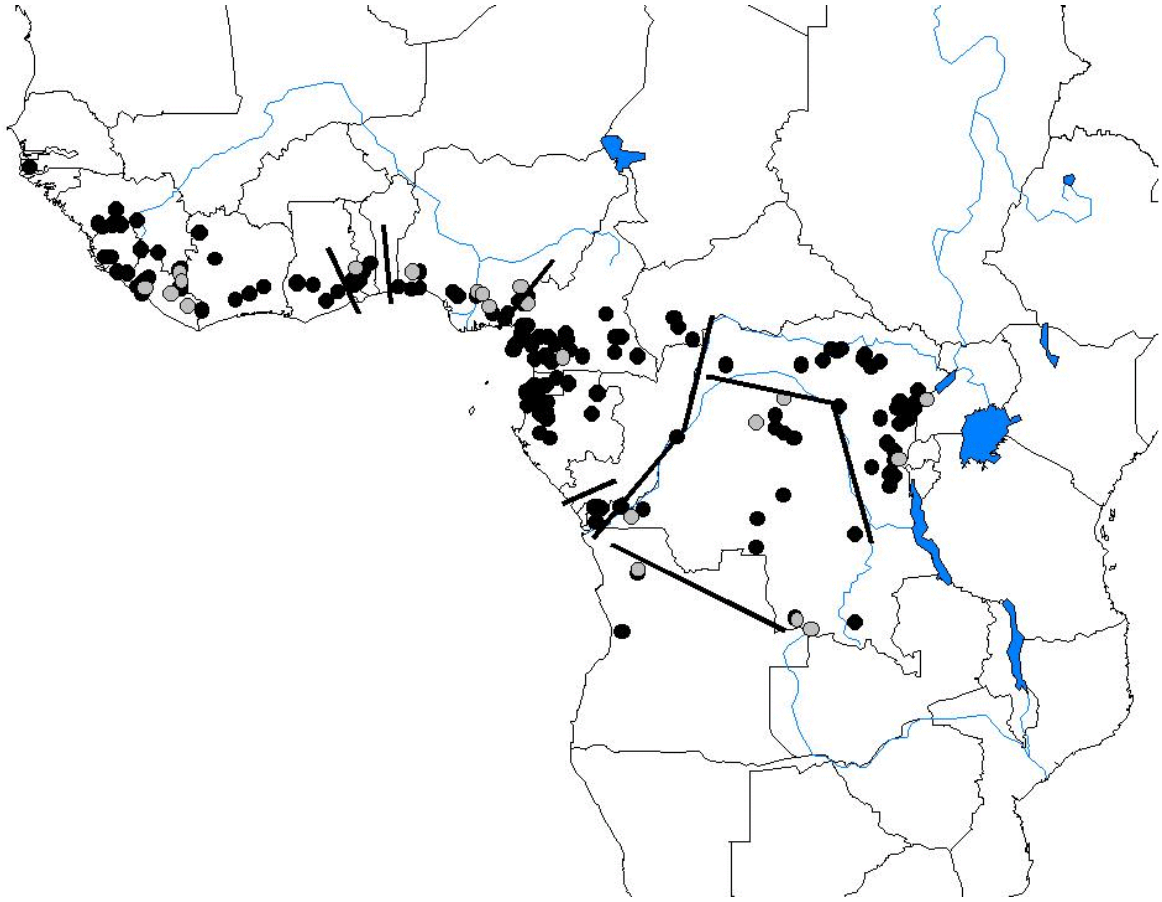

Figure 9.1. Distribution and important borderlines between geographical populations of *A. beecrofti*. From Malawi only a few records of *A. beecrofti* without precise coordinates are published and therefore not shown on this map (black: specimens studied during the present investigation, grey: additional finding localities from literature).

9.1.2. *Anomalurus derbianus*

The geographic distribution of morphological and morphometric characters in *A. derbianus* differs considerably from that in *A. beecrofti*, in spite of the corresponding distribution area. Geographic populations of *A. beecrofti* can generally be defined by different frequencies of colouration forms and separate clusters in principal component analyses of morphometric characters. In *A. derbianus* there are clearcut borderlines for colouration (Fig. 9.2), but always for only one or two characters, while others are not affected. The morphometric characters provide in most cases either a bad resolution or suggest clinal variation.

The West African specimens differ from those of other populations mainly by their consistently light shoulders. They also have a relatively dark and warm brown colouration with slightly

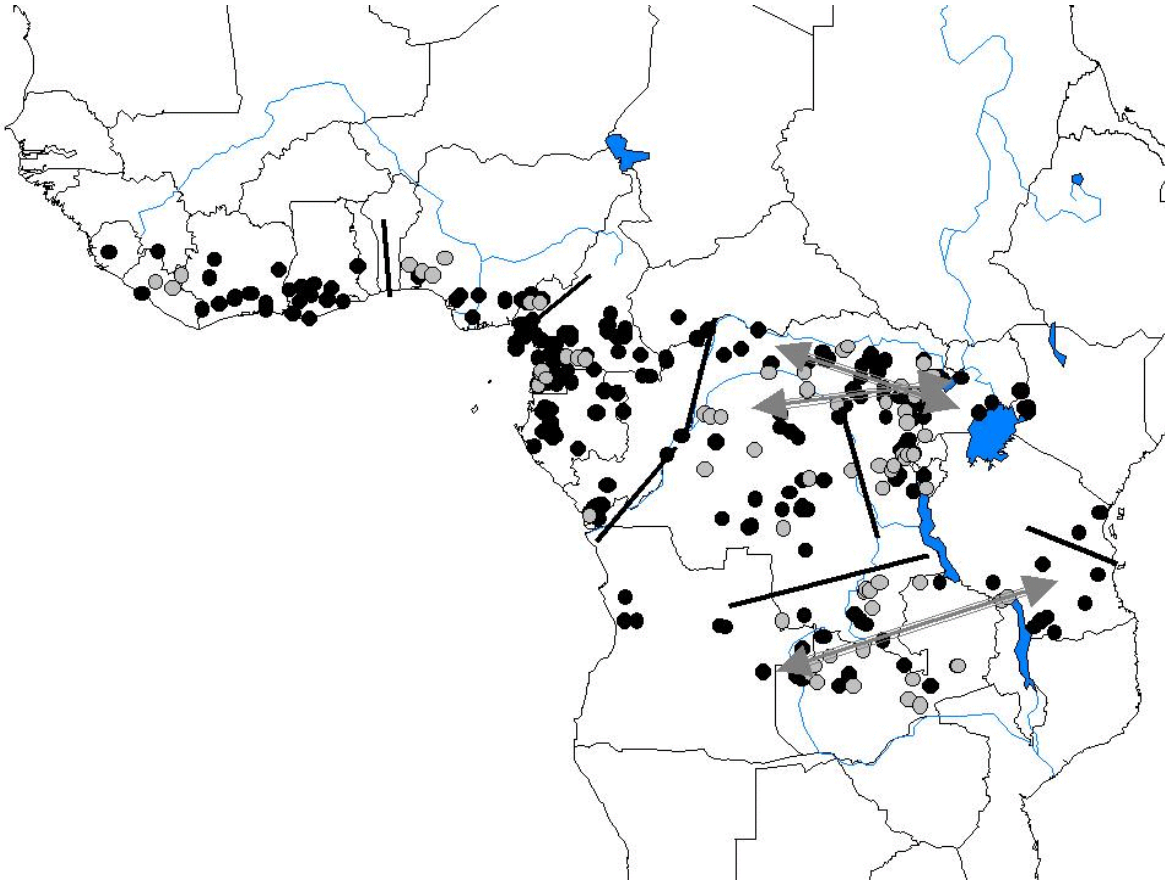

Figure 9.2. Distribution and important borderlines between geographical populations of *A. derbianus* (black: specimens studied during the present investigation, grey: additional finding localities from literature; grey arrows: possible clinal variation).

yellowish epaulettes, but as this tinge could not be precisely defined and reproduced on photographs it was not used in the analysis. However, with some experience it is not difficult to recognize the majority of West African *A. derbianus* by their colouration. Unfortunately it is not possible to show whether the eastern border of this population is formed by the Volta River or the Dahomey Gap, because there was only one specimen available from this area. A second, less clearly defined borderline lies close to the highlands of western Cameroon (areas 24 and 25), but different from *A. beecrofti* specimens of *A. derbianus* from this area are closer to Nigerian individuals than to those from southern Cameroon. The lower Congo and Ubangi Rivers represent strong borderlines for dorsal and shoulder colouration, although they do not affect ear colouration and morphometric characters show a considerable overlap. The middle and upper Congo seems to have a remarkable small influence on the character distribution in *A. derbianus*, although the ear colouration frequencies change from the Kivu area eastwards along the upper Congo and a borderline difficult to define in the northern Democratic Republic of Congo between areas 31 and 32. Finally the southeastern populations are separated from the others by

the ear colouration frequencies and the morphometric skull characters, at least when the majority of characters is used (Chap. 7). Specimens from Western Angola (area 41) are difficult to classify because of their small number, but they might be more similar to those from the central Democratic Republic of Congo, and the specimens from the Usambara Mountains in Tanzania are strongly separated from all other populations by their unique ventral colouration frequencies. Besides these clearcut borderlines there are several examples that rather suggest clinal variation, namely increasing reddish dorsal colouration from West Africa towards the lower Congo and Ubangi Rivers, decreasing dark ear colouration from Central Africa in western and southeastern direction, shoulder colouration from West Africa towards Tanzania (although with some distortion in Nigeria and Cameroon), skull characters from the Western Democratic Republic of Congo (area 31 and 35) to Uganda and Kenya and body and skull characters from Zambia to the Usambara Mountains.

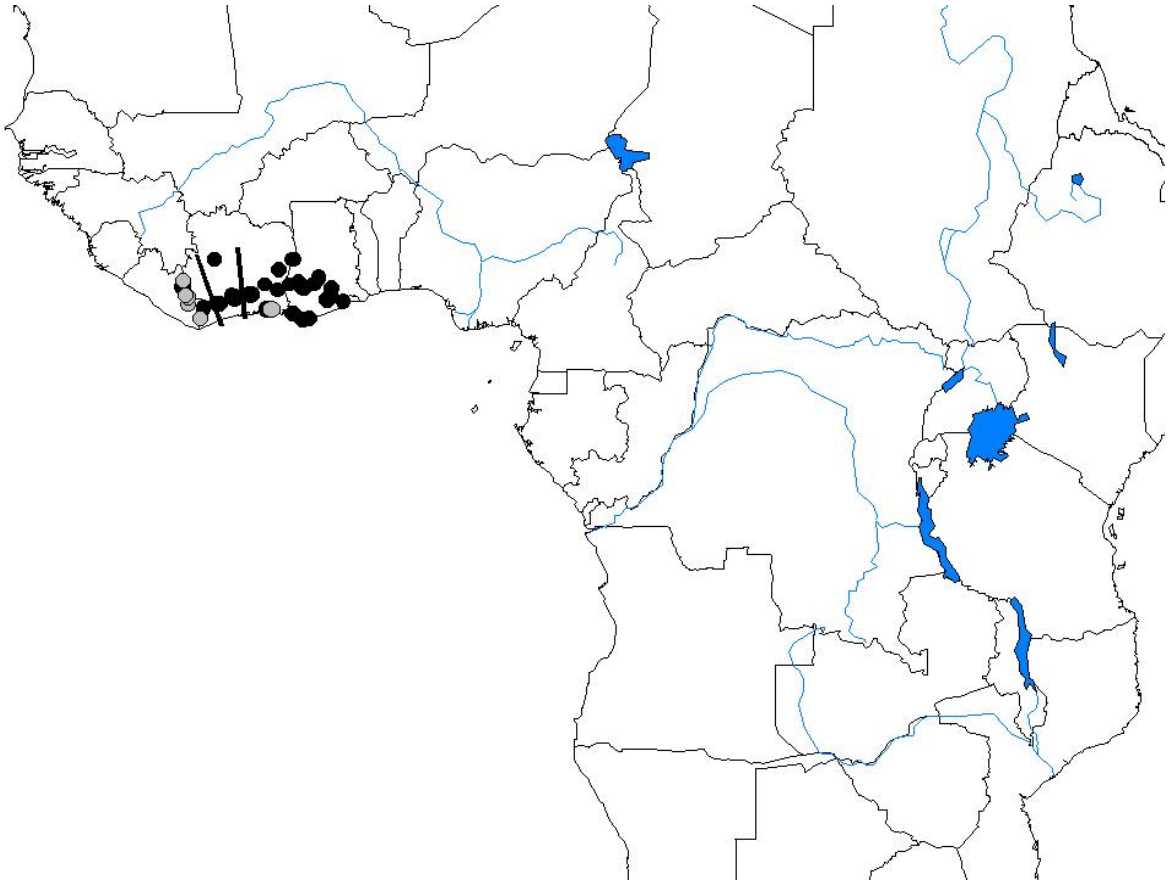

Figure 9.3. Distribution and important borderlines between geographical populations of *A. pelii* (black: specimens studied during the present investigation, grey: additional finding localities from literature).

9.1.3. *A. pelii*

Different from the complex geographic variation in *A. beecrofti* and *A. derbinaus* it is pretty straightforward in *A. pelii*. The dorsal colouration forms are strictly separated by borderlines which correspond to the rivers Sassandra and Bandama in the Ivory Coast (Fig. 9.3), but this separation is not matched by morphometric characters.

9.1.4. *A. pusillus*

In *A. pusillus* yet another pattern of geographic variation is found (Fig. 9.4). This species has a uniform colouration throughout it's distribution area. The body size characters clearly distinguish three populations. One occurs from southern Cameroon to Gabon, the second in the northwestern (areas 31 and 32) and the last in the western Democratic Republic of Congo (area 33). The skull characters suggest a slight clinal variation in the northern Democratic Republic of Congo with specimens from the West (area 31) and the East (area 33) being well separated but both overlap.

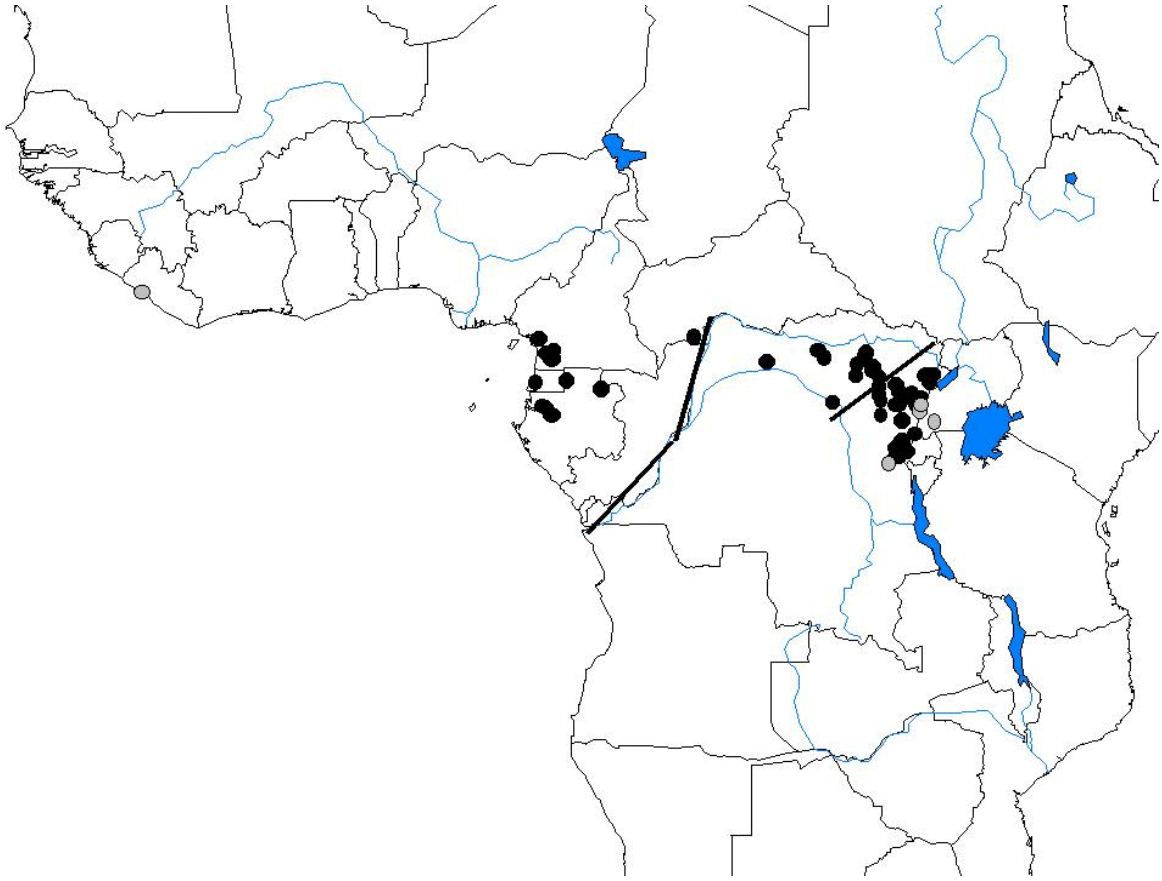

Figure 9.4. Distribution and important borderlines between geographical populations of *A. pusillus*. From the Côte d'Ivoire only a few records of *A. pusillus* without precise coordinates are known and therefore not shown on this map (black: specimens studied during the present investigation, grey: additional finding localities from literature).

with specimens from the area in between (area 32). A relatively large number of skull characters is needed to separate specimens from West and East of the Congo River. Problematical are the specimens from West Africa, because two of them overlap with those from Cameroon to Gabon and are separated from those from Central Africa, while there is one outlier which clusters within the populations from the north-western Democratic Republic of Congo.

9.1.5. *I. macrotis*

Like in *A. pusillus* no colouration classes could be defined for *I. macrotis* and the body measurements of this species overlap to a large extent. However, there is a very clear distinction between geographical populations with skull characters. With a relatively large number of characters populations from all main and subareas can be separated; when the number of characters is reduced five populations can be distinguished. The first is located in West Africa (area 1), the second in the highlands of western Cameroon (area 24), the third in western Central Africa (area 26), the fourth in Central Africa (areas 32 and 33) and the last is represented by a single specimen from northern Tanzania (Fig. 9.5).

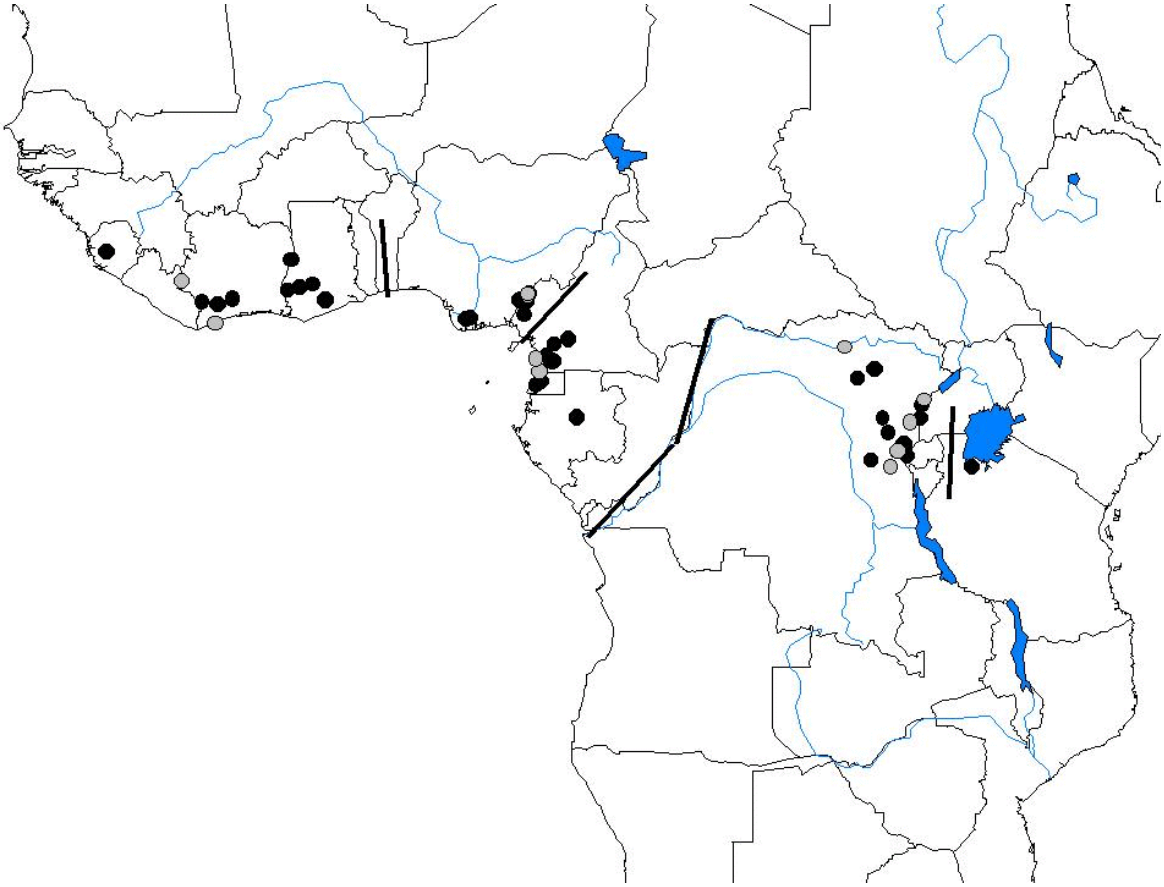

Figure 9.5. Distribution and important borderlines between geographical populations of *I. macrotis* (black: specimens studied during the present investigation, grey: additional finding localities from literature).

9.1.6. *I. zenkeri*

The geographic variation patterns of *I. zenkeri* resemble those of *I. macrotis*, but with some differences. *I. zenkeri* also shows no differences in fur colouration but clearly separate clusters in morphometric characters. Like in *I. macrotis* the population from the highlands of Cameroon are separated from those from southern Cameroon and Equatorial Guinea, but in *I. zenkeri* the clusters for skull characters are matched by those for body size. Specimens from western Central Africa can also be distinguished from those from Central Africa. Difficult to judge is the position of the single specimen from the Central African Republic, because it lies closer to the eastern cluster in body measurements and closer to the western populations in skull measurements.

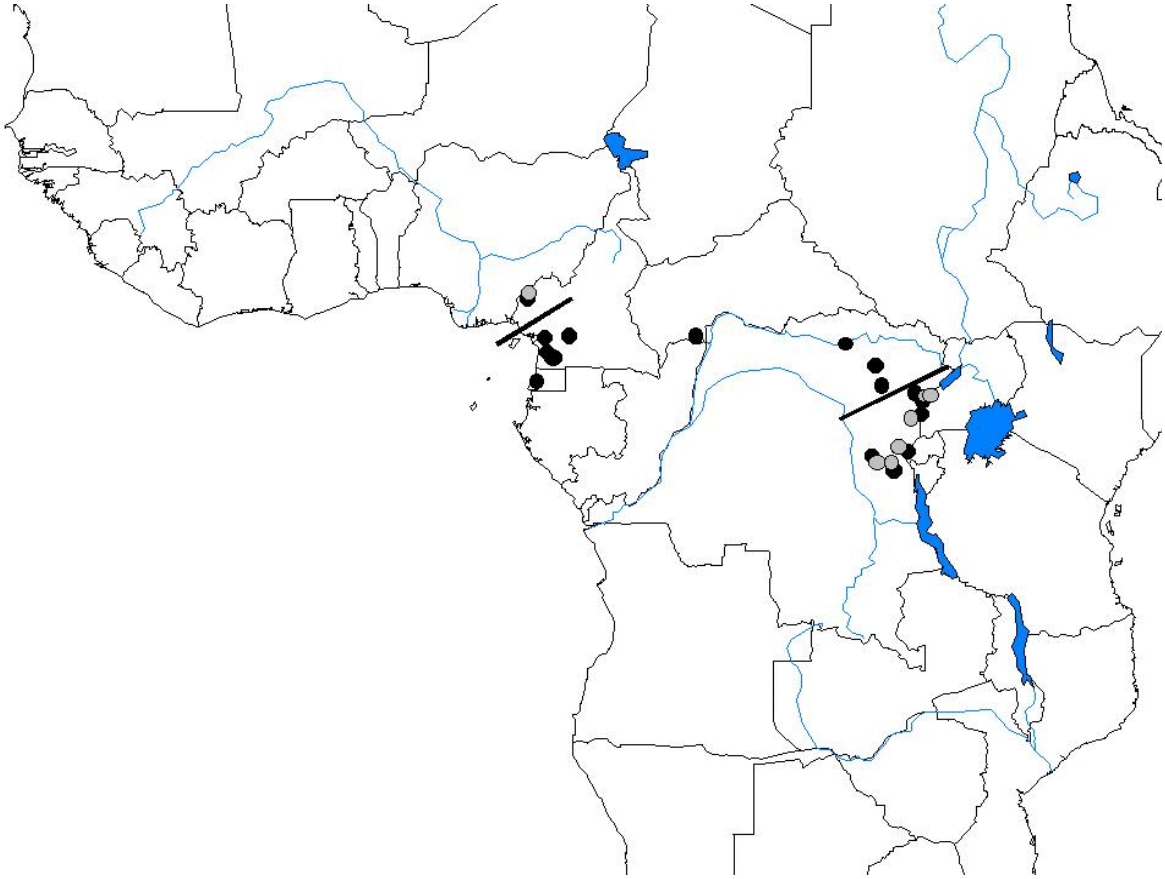

Figure 9.6. Distribution and important borderlines between geographical populations of *I. zenkeri* (black: specimens studied during the present investigation, grey: additional finding localities from literature).

9.1.7. *Z. insignis*

This species occurs only in a relatively small area and the number of specimens is extremely small. With the present data base it is not possible to distinguish separate populations.

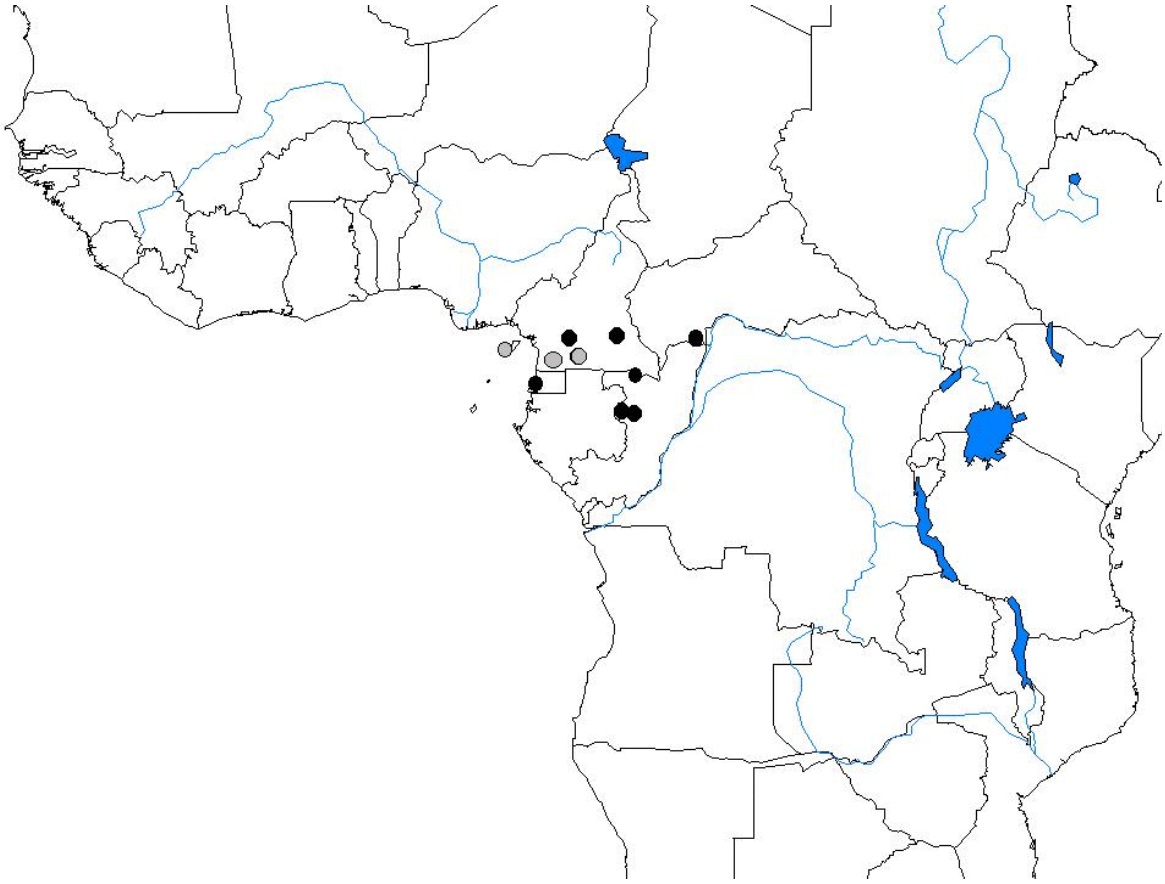

Figure 9.7. Distribution and important borderlines between geographical populations of *Z. insignis* (black: specimens studied during the present investigation, grey: additional finding localities from literature).

9.2. Distinguishable geographic areas for the Anomaluridae

The borderlines that separate geographical units of anomalurid species are shown in Fig. 9.8. Eight to thirteen areas can be clearly distinguished by the species composition (Fig. 9.9) or by differences between populations within one or more species.

The populations from West Africa are relatively homogenous except for *A. pelii*. Unfortunately it is not clear if the eastern borderline of the populations is represented by the Volta River or the Dahomey Gap, because from the small area in between with a single exception exclusively *A. beecrofti* has been collected. Nigeria is relatively poor of species with only *A. beecrofti*, *A. derbianus* and *I. macrotis* having been collected in this country. The highlands of Cameroon are inhabited by very peculiar representatives of the species which occur there. Bioko was colonized only by *A. beecrofti*, *A. derbianus* and *Z. insignis*, and the specimens from this island tend to resemble those from the highlands of Cameroon, except for *Z. insignis*, which was not collected there. In the area between the highlands of Cameroon and the Rivers Congo and Ubangi the

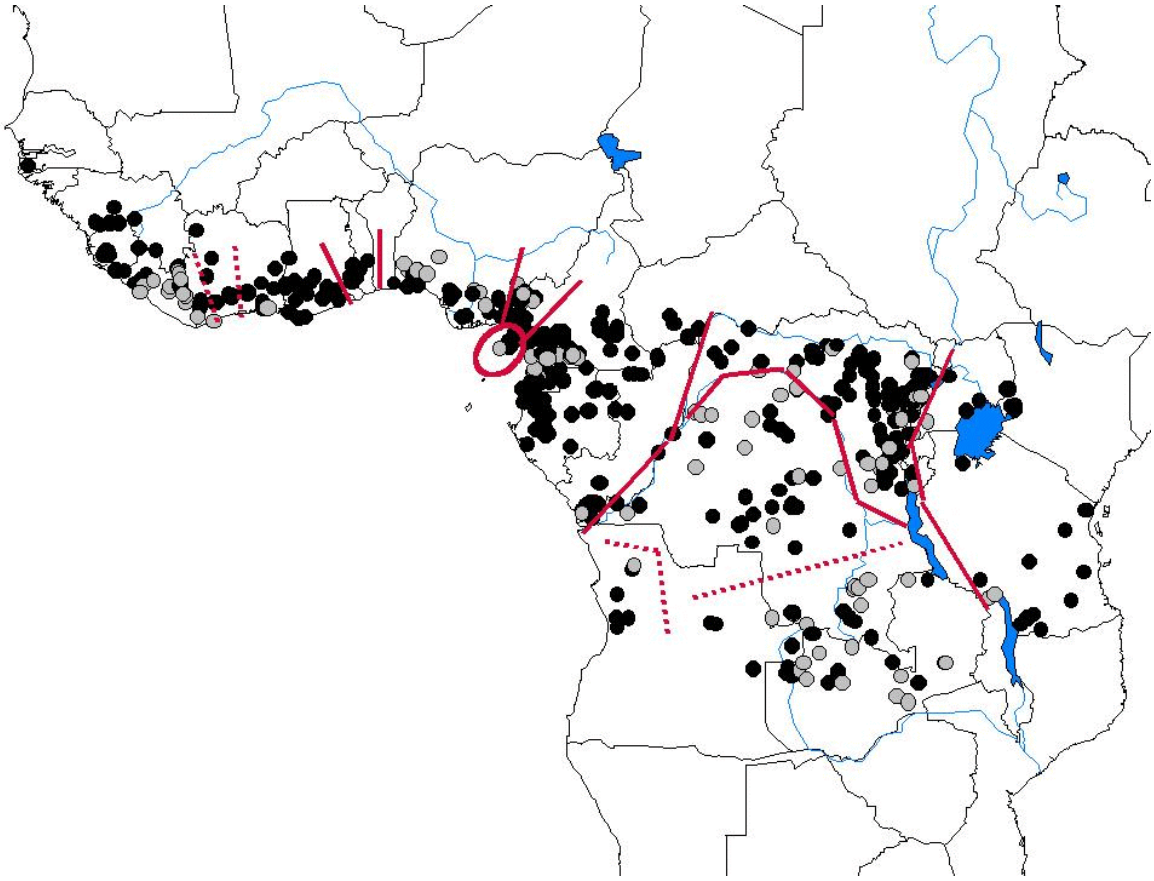

Figure 9.8. Distribution of Anomaluridae in Africa. Lines show important borderlines between areas marked by several changes of characters or species composition.

highest number of species can be found and *A. beecrofti* and *A. derbianus* show a high amount of variation. The area between the rivers Congo, Ubangi, and Uelle is also inhabited by a relatively high number of species, of which several display some geographic variation, but with different borderlines for the respective species. Only *A. beecrofti* and *A. derbianus*, whose populations show only small differences north and south of the river, managed to cross the Congo River. South of the Congo there are only borderlines of lesser importance which separate the populations of the central and southwestern Democratic Republic of Congo from those from western Angola and both from those from central and eastern Angola, southeastern Democratic Republic of Congo and Zambia. The last important borderline is represented by the Rift Valley which was mainly crossed by *A. derbianus*.

9.3. Discussion of biogeographic patterns

The geographical distribution of the Anomaluridae follows generally patterns already well known for other mammals, particularly primates. Common barriers like the Dahomey Gap and the

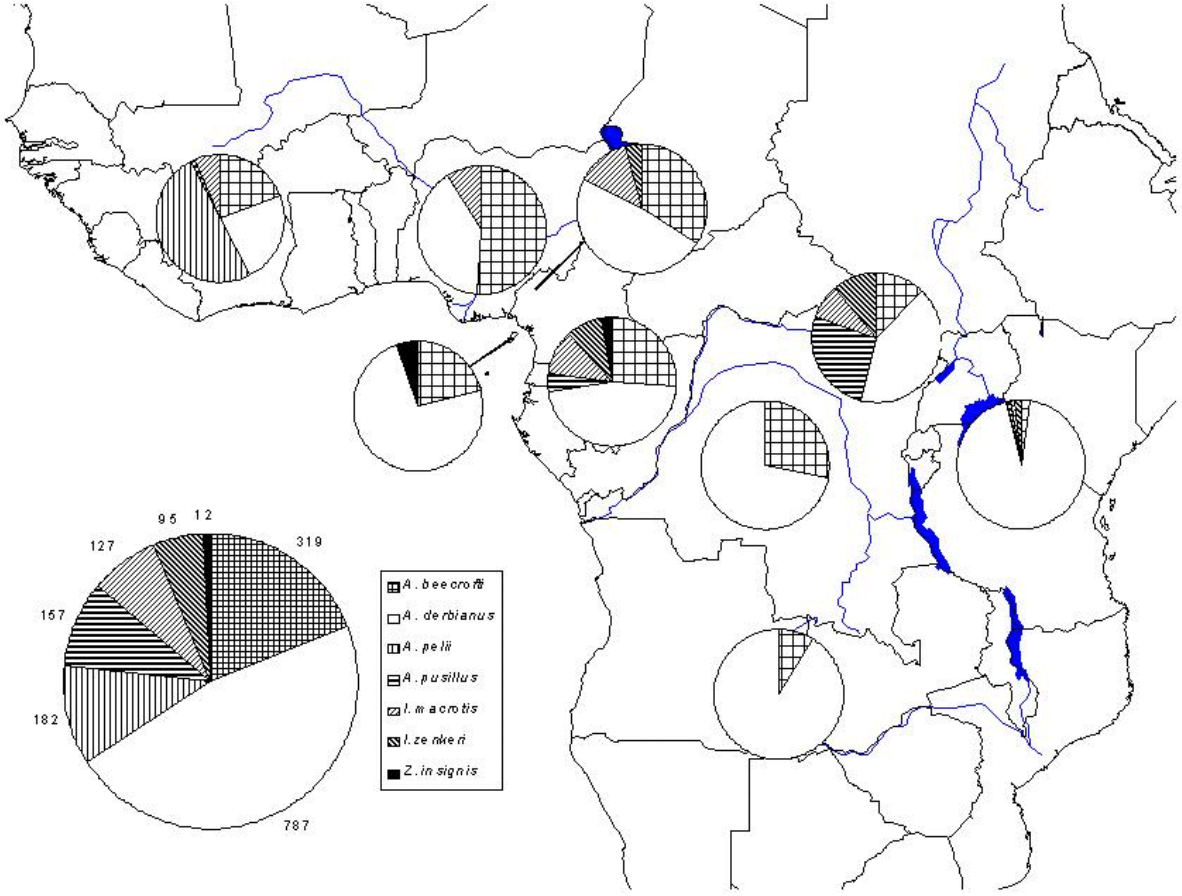

Figure 9.9. Species composition in nine subareas within the distribution area of Anomaluridae.

Congo River seem also to be obstacles for anomalurids in some cases, while in others no impact on certain species or characters is visible. The main center of diversity with six out of seven species corresponds with a well known forest refuge from southern Cameroon to Gabon. Five species respectively occur in West Africa and northwestern Democratic Republic of Congo, also known forest refuges in Africa.

The capability of spreading differs considerably between species. Not surprisingly *Z. insignis*, the only species unable to perform gliding flight, has a very small distribution area. However, it is also one out of three species collected on Bioko, and fossils have been reported from Kenya. Of the two *Idiurus* species one is found regularly in the whole area inhabited by anomalurids except for the parts south of the Congo River while the other lives only in a relativly restricted area from Cameroon to northwestern Democratic Republic of Congo. Within *Anomalurus* the differences are most pronounced, with a very small distribution area in the largest species *A. pelii*, a medium sized in the smallest species *A. pusillus* and the largest distribution area, comprising those of all other species, in the medium sized *A. derbianus*. *A. beecrofti* is found almost as widely distributed as *A. derbianus*, except for the extreme southern and eastern parts. With the

restricted knowledge on the biology of all anomalurid species it remains impossible to draw any conclusion concerning the reasons for the different spreading behaviour, as it seems to be independent from size, and also closely related species can differ considerably.
The same lack of information concerning anomalurid biology makes an interpretation of the species composition in the different areas difficult. While the *Idiurus* species occur with relatively constant percentages there is a general tendency of decreasing percentages in *A. beecrofti* from west to southeast, and the percentages of *A. derbianus* and *A. pusillus* increase in western to eastern or southeastern direction. However, more data are needed to draw conclusions whether these clines are caused by different ecological factors in the respective areas or if they still reflect the traces of spreading, e.g. for *A. pusillus* from a forest refuge in the Kivu area westwards.

9.4. Taxonomic conclusions

As expected the present investigation supports the seven species as the absolute minimum of at least partly sympatric species or species groups. In contrast, a reflection of the very complex variation of the anomalurid species in a more "splitted" taxonomy is almost impossible, although there is good evidence for the existence of at present separated geographic populations. However, a reliable assignment of any one specimen to a certain geographic area is, although with some exceptions, impossible. Most colouration forms occur in more than one area and forms restricted to one area live sympatrically with specimens of more widespread coluration forms, which makes a separation even on the supspecies level very difficult to define. In cases where differences lie rather in size than in colouration there is always an overlap in the measurements, so a definition with morphometric characters is also not reliable. The only exception is found in *A. pelii*, where the size of the white markings is strictly correlated with the finding locality and changes stepwise along the rivers Sassandra and Bandama. In this case it seemed useful to subdivide the species into three subspecies (Schunke & Hutterer, in press a). The taxonomic position of *A. beecrofti* in a separate genus *Anomalurops* is supported by numerous differences in morphology, including fur colouration, molar teeth, skull shape etc.

9.5. Future research

Despite the difficulties to assign geographic populations to clearly defined subspecies the pattern of anomalurid variation makes them interesting species for the investigation of the historical biogeography of the African rain forests. The molecular analysis showed clearly that short fragments of cytochrome b might be sufficient for phylogeographic analyses that can not be performed with morphological characters. However, a very large number of tissue samples from

collections is necessary for molecular analyses because of the relatively small amount of succesful amplifications. Alternatively it would be very desirable to get fresh or ethanol conserved material. The present investigation showed that samples from no more than 13 localities would likely be sufficient for a phylogeographic analysis of a group that covers the vast majority of the African rain forest parallel with several species and promises interesting insights into the history of this fascinating ecosystem.

10. Summary / Zusammenfassung / Resumé

The aim of the present investigation was a better understanding of the systematics and biogeography of the African scaly-tailed squirrels. Therefore 1581 anomalurid specimens from 22 collections were examined and data from skulls, skins, and labels recorded, completed with data from literature. The current knowledge concerning anomalurids was compiled and the information on biology, morphology, biogeography, and the history of taxonomy and systematics within anomalurids and the systematic position of the group within the Rodentia presented. Additionally a gazetteer of finding localities was provided.

Thorough analyses of fur colouration, body size measurements, craniometric characters, and molecular data demonstrated the extremely complex geographic variation of this group. The structure of anomalurid populations and borderlines and/or clines between populations is not straightforward and not easy to translate in an unequivocal taxonomy. However, it was possible to divide the distribution area of the Anomaluridae into eight to thirteen smaller areas, where at least the majority of species is relatively homogenous and generally differs in one or more characters from neighbouring populations. Differences can lie in fur colouration, body size, skull size and shape or in any combination of these.

Due to the use of museum material and the related "Ancient DNA" problems it was not possible so far to reliably analyse differences between geographical populations of one or more species. Still 49 cytochrome b fragments from 28 specimens could be sequenced and allowed the suggestion of a cladogram for six of the seven anomalurid species. Additionally, the data proved the usefulness of the chosen gene region for possible further investigations.

Besides the application of the statistical and data combination methods for the analysis of anomalurid systematics and biogeography it was possible to examine and discuss the usefulness and problems of several of the applied methods more generally.

The present investigation supported the widely accepted (though still discussed) taxonomy with the seven species *Anomalurops beecrofti*, *Anomalurus derbianus*, *A. pelii* (with three subspecies), *A. pusillus*, *Idiurus macrotis*, *I. zenkeri*, and *Zenkerella insignis*. Further analysis particularly with molecular data would be desirable to clarify the history of the distribution of anomalurid species.

Zusammenfassung

Das Ziel der vorliegenden Untersuchung war ein besseres Verständnis der Systematik und Biogeographie der afrikanischen Dornschwanzhörnchen. Dafür wurden 1581 Exemplare aus 22 Sammlungen untersucht und Daten der Schädel, Bälge und Etiketten aufgenommen, vervollständigt durch Literaturangaben. Das gegenwärtige Wissen über Anomaluriden wurde zusammengetragen und die Informationen über Biologie, Morphologie, Biogeographie und die Geschichte der Taxonomie und Sytematik innerhalb der Anomaluriden sowie die systematische Position der Gruppe innerhalb der Rodentia dargestellt. Zusätzlich wurde ein Verzeichnis der Fundorte erstellt.

Gründliche Untersuchungen von Fellfärbung, Körpergröße, craniometrischen Merkmalen und molekularen Daten zeigten die extrem komplexe geographische Variation dieser Gruppe. Die Struktur der Anomaluriden-Populationen und die Grenzen und/oder Klinen zwischen Populationen ist nicht offensichtlich und nicht einfach in eine eindeutige Taxonomie zu übersetzen. Trotzdem war es möglich, das Verbreitungsgebiet der Anomaluridae in acht bis dreizehn Areale zu unterteilen, innerhalb derer zumindest die Mehrheit der Arten relativ einheitlich ist und sich im allgemeinen in einem oder mehreren Merkmalen von benachbarten Populationen unterscheidet. Die Unterschiede können in der Fellfärbung, Körpergröße und Schädelgröße und -form oder in jeder Kombination davon liegen.

Aufgrund der Verwendung von Museumsmaterial und den damit verbundenen ‘Ancient DNA’-Problemen war es bisher nicht möglich, Unterschiede zwischen Populationen einer oder mehrerer Arten verläßlich zu analysieren. Dennoch konnten 49 Cytochrom b-Fragmente von 28 Exemplaren sequenziert werden, die die Erstellung eines Kladogramms für sechs der sieben Anomaluriden-Arten erlaubten. Zusätzlich zeigten die Daten die Brauchbarkeit des ausgewählten Genabschnittes für mögliche weitere Untersuchungen.

Neben der Anwendung der statistischen und Daten-Kombinationsmethoden für die Analyse der Anomaluriden-Systematik und Biogeographie war es möglich, die Verwendbarkeit und Probleme mehrerer der angewandten Methoden allgemeiner zu untersuchen und zu diskutieren.

Die vorliegende Untersuchung unterstützte die von vielen Autoren anerkannte (obwohl immer noch diskutierte) Taxonomie mit den sieben Arten *Anomalurops beecrofti*, *Anomalurus derbianus, A. pelii* (mit drei Unterarten), *A. pusillus*, *Idiurus macrotis, I. zenkeri* und *Zenkerella insignis*. Weiter Untersuchungen, vor allem mit molekularen Daten, wären wünschenswert, um die Geschichte der Verbreitung der Anomaluriden-Arten aufzuklären.

Résumé

L'objectif du présent travail a été de mieux comprendre la systématique et la biogéographie des écureuils volants d'Afrique (Anomaluridae). Ainsi, 1581 spécimens provenant de 22 collections ont pu être examinés. Des informations concernant le crâne, la peau et l'étiquetage sont enregistrées et sont complétées par des données issues de la littérature. Un catalogue des localités est également produit.

Les connaissances actuelles concernant les Anomalurides sont répertoriées, et les informations sur la biologie, la morphologie, la biogéographie, l'histoire de la taxonomie et de la systématique du groupe sont présentées ainsi que la position systématique de la famille au sein des Rodentia. Des recherches approfondies sur la coloration du pelage, sur certaines mesures corporelles et crâniennes et sur des données moléculaires montrent l'extrême complexité de la variation géographique du groupe. La structure des populations d'Anomalurides et les frontières et/ou les clines entre populations ne sont pas aisées à définir. Malgré tout il est possible de sub-diviser l'aire de répartition des Anomalurides en huit et jusqu'à dix parties où la majorité des espèces sont relativement homogènes et diffèrent généralement des populations voisines par un ou plusieurs caractère(s). Ces différences peuvent se trouver dans la couleur du pelage, dans des mesures du corps, dans des mesures ou dans la forme du crâne, ou dans toute combinaison de ces caractères.

L'utilisation de matériel de musée c'est heurté au problème « d'ADN ancien », et il n'a pas été possible dans le présent travail d'analyser de façon fiable les différences entre les populations d'une ou de plusieurs espèces. Néanmoins, 49 fragments du cytochrome b issus de 28 spécimens ont pu être séquencés. Leur analyse a permis de rechercher les relations de parentés pour six des sept espèces connues, et le cladogramme obtenu montre la pertinence de la portion de gène choisie pour de futures investigations phylogénétiques.

En parallèle de l'utilisation de méthodes statistiques et de combinaisons de données pour l'analyse de la systématique et de la biogéographie des Anomalurides, la pertinence des méthodes utilisées ci-dessus ainsi que les problèmes qu'elles posent sont également aborder de façon plus générale.

Les résultats obtenus sont en accord avec le consensus actuel (cependant toujours débattu) qui admet sept espèces valides, *Anomalurops beecrofti*, *Anomalurus derbianus*, *A. pelii* (comprenant trois sous-espèces), *A. pusillus*, *Idiurus macrotis*, *I. zenkeri*, and *Zenkerella insignis*. Pour clarifier l'histoire de la distribution des espèces d'Anomalurides, des recherches complémentaires portant notamment sur des données moléculaires, seraient nécessaires.

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12. Gazetteer of finding localities for Anomaluridae

Locality	Synonyms	Country	Latitude		Longitude		Elevation
Abanga R.		GAB	ca. -0°18'	S	ca. 10°29'	E	
Abatupi/Semliki		DRC	00°45'	N	29°49'	E	
Abolo		CON	00°10'	N	14°14'	E	
Aburi		GHA	05°51'	N	-00°11'	W	
Abutschi	Onitsha	NIG	06°09'	N	06°46'	E	140 m
Abwei		GHA					
Adamso		GHA	06°05'	N	-01°46'	W	
Adiapo-Doumé		IVC	05°20'	N	-04°07'	W	
Afara	Afera	NIG	05°30'	N	07°28'	E	500 ft
Ago Sasa		NIG	06°35'	N	02°45'	E	
Ago Sasa		NIG	06°40'	N	02°46'	E	
Agruma		GAB	not found				
Aguleri		NIG	06°20'	N	06°53'	E	
Ahiérémou		IVC	06°14'	N	-04°56'	W	
Ahiriso		GHA	06°32'	N	-02°20'	W	
Ahoué-Houé		TOG	07°34'	N	00°36'	E	
Akem	Akim	GHA	ca. 06°28'	N	ca. -00°45'	W	
Akengi	Akenge	DRC	02°56'	N	26°49'	E	
Akoafim		CAM	02°19'	N	12°43'	E	
Akoolui	Akoaloui	CAM	02°54'	N	11°55'	E	
Alassa		DRC	between Stanleyville and Avakubi				
Alen		EQU	01°55'	N	10°58'	E	
Alen		CAM	02°23'	N	10°34'	E	
Alto Chicapa		ANG	-10°56'	S	19°09'	E	1300 m
Amadjabe		DRC	-00°4'	S	25°17'	E	
Amani		TAN	-05°05'	S	38°37'	E	3600'
Aguleri		NIG	06°20'	N	06°53'	E	
Angumu		DRC	-00°8'	S	27°43'	E	800 m
Ankole Distr.		UGA	ca -00°30'	S	ca 30°30'	E	
Apéyémé		TOG	07°12'	N	00°42'	E	
Aramboury		?KEN					
Arebi		DRC	02°47'	N	29°35'	E	
Asankrangwa		GHA	05°48'	N	-02°25'	W	400'
Ashanti		GHA	05°51'-07°38'N		-02°15W-0°02'	E	
Assumbo		CAM					
Atene		DRC	-05°25'	S	19°18'	E	
Atolo		CAM	06°11'	N	09°27'	E	1450'
Avakubi		DRC	01°20'	N	27°33'	E	900 m
Axim		GHA	04°52'	N	-02°14'	W	
Ayamiken		EQU	02°07'	N	10°01'	E	

Badou		TOG	07°35'	N	00°35'	E	
Bai Sombe	Bay	CAM	04°27'	N	09°07'	E	
Bali		CAM	05°54'	N	10°01'	E	
Balovale	Zambezi	ZAM	-13°32'	S	23°06'	E	
Bamanya		DRC	00°1'	N	18°24'	E	
Bamba		DRC	10x in the Democratic Republic of Congo				
Bamba Dizi		DRC	-04°45'	S	12°59'	E	
Bamba Kilenda		DRC	-04°54'	S	15°29'	E	
Bamba Mangobia		DRC	-04°45'	S	12°57'	E	
Bambesa		DRC	03°27'	N	25°42'	E	
Banco		IVC	05°22'-05°25'N		-04°01'--04°05'W		
Bange		CAM	03°01'	N	15°07'	E	
Bangu op Busira		DRC	-00°8'	S	19°13'	E	
Bangui		ZAR	04°21'	N	18°33'	E	
Banko (4x)		GUI	10°43'	N	-10°43'	W	
Banso	Kumbo	CAM	06°12'	N	10°41'	E	2100 m
Bantabaré	Bantabiri	Bioko	03°27'	N	08°46'	E	10 m
Banzyville	Mobayi-Mbongo	DRC	04°18'	N	21°11'	E	
Baó Basuala	Basoala East?	Bioko	03°38'	N	08°53'	E	
Baraka		DRC	-04°05'	S	29°05'	E	800 m
Barombi-See		CAM	04°27'-28'	N	09°15'-16'	E	
Basacato del Este		Bioko	03°37'	N	08°54'	E	
Basacato del Oeste		Bioko	03°35'	N	08°37'	E	
Bashauo	Basho	CAM	06°08'	N	09°25'	E	750'/700'
Basile		Bioko	03°42'	N	08°47'	E	
Basoko		DRC	01°14'	N	23°36'	E	
Bassa		LIB	not found				
Basupu		Bioko	03°43'	N	08°40'	E	
Bata		EQU	01°52'	N	09°46'	E	
Batempa		DRC	-04°59'	S	23°41'	E	
Batouri District		CAM	04°15'	N	14°15'	E	
Begoro		GHA	06°22'	N	-00°23'	W	
Belinga		GAB	01°08'	N	13°06'	E	
Bellima, Monbuttu		GAB	00°15'	N	10°11'	E	
Beni		DRC	00°29'	N	29°27'	E	
Benin City		NIG	06°20'	N	05°37'	E	
Benito		EQU	01°34'	N	10°24'	E	
Benito R		GAB	01°35'-01°33'N		11°55'-09°37'	E	
Benito R., 15 mi from coast		EQU	01°34'	N	09°48'	E	
Benito R., 20 mi. fr. coast		EQU	01°32'	N	09°50'	E	
Benito R., 25 mi from coast		EQU	01°30'	N	09°53'	E	
Bertoua		CAM	04°34'	N	13°41'	E	
Bertoua, 30 km W		CAM	04°34'	N	13°24'	E	
Besongabang		CAM	05°44'	N	09°16'	E	450 ft
Bianou	Bianouan	IVC	06°00'	N	-03°11'	W	
Bibianaha		GHA	06°30'	N	-02°08'	W	700'
Bignona		SEN	12°49'	N	-16°14'	W	
Bikiango		CAM	not found				

Bilelipi		Bioko	03°28'	N	08°47'	E	
Bilolo		DRC	00°37'	N	28°45'	E	
Bima		DRC	03°25'	N	25°11'	E	
Bingerville		IVC	05°21'	N	-03°54'	W	
Bionga		DRC	-03°22'	S	28°11'	E	
Bipindi		CAM	03°04'	N	10°24'	E	
Biripange		DRC	riv. close to Kisanga [Kankisi]				
Bisun		EQU	01°25'	N	09°52'	E	
Bitye		CAM	03°01'	N	12°22'	E	2000 ft
Blekoum		IVC	06°23'	N	-03°31'	W	
Blukwa		DRC	01°45'	N	30°35'	E	1750 m
Boangi		DRC	-01°51'	S	20°56'	E	
Bogufluss		TOG	not found				
Bokoro		DRC	-02°50'	S	18°23'	E	
Bokuma		DRC	-00°6'	S	18°42'	E	
Bokungu		DRC	-00°40'	S	22°18'	E	
Bolo		IVC	07°59'	N	-06°43'	W	
Bondo Mabe		DRC	02°36'	N	29°34'	E	
Bondoukou	Boudoukou	IVC	08°01'	N	-02°47'	W	
Bonge		CAM					
Bongouanou		IVC	06°39'	N	-04°12'	W	
Booué		GAB	-00°5'	S	11°56'	E	
Bose		ZAR	05°01'	N	17°04'	E	
Boukoko		CAR	03°54'	N	17°55'	E	
Bouroukrou		IVC	05°51'	N	-04°11'	W	
Budjala		DRC	02°38'	N	19°42'	E	
Budongo Forest		UGA	01°46'	N	31°33'	E	1600 m
Buea		CAM	04°09'	N	09°13'	E	1000 m
Bumba		DRC	2°11'	N	23°30'	E	
Bunia		DRC	1°33'	N	30°14'	E	
Busekera		BUR	not found				2000 m
Bushenyi		DRC	-02°06'	S	29°04'	E	
Buta		DRC	02°48'	N	24°44'	E	
Bwamba		UGA	00°48'	N	30°06'	E	
Bweya		UGA	00°15'	N	32°16'	E	3900'
Cabo San Juan		EQU	ca 01°10'	N	ca 09°20'	E	
Calabar		NIG	04°57'	N	08°18'	E	
Calunda		ANG	-12°07'	S	23°27'	E	
Camabatela		ANG	-08°11'	S	15°22'	E	
Camabatela, 30 km W		ANG	-08°11'	S	15°05'	E	
Cameroun Mt.		CAM	04°13'	N	09°10'	E	
Carmona		ANG	-07°56'	S	15°09'	E	
Canzele		ANG					
Cazombo		ANG	-11°53'	S	22°54'	E	
Cazombo		ANG	-12°09'	S	23°26'	E	
Chemisia		KEN	not found				1980 m
Chinan		ZAM	-13°09'	S	23°21'	E	
Chitokoloki		ZAM	-13°50'	S	23°12'	E	
Chitokoloki, 12 mi NE		ZAM	-13°43'	S	23°19'	E	

Chitokoloki, 15 mi ENE		ZAM	-13°45'	S	23°24'	E	
Como R.		GAB	00°15'	N	10°11'	E	
Como R., 60 mi from Gaboon		GAB	00°17'	N	10°14'	E	
Como R., 70 mi from Gaboon		GAB	00°15'	N	10°21'	E	
Como R., 75 mi from Gaboon		GAB	00°12'	N	10°24'	E	
Conakry		GUI	09°33'	N	-13°40'	W	
Concepcion	Ri-Aba	Bioko	03°20'	N	08°46'	E	
Condéfluß		CAM	not found				
Congolo		ANG	-08°26'	S	20°49'	E	700-800 m
Dabocrom		GHA	04°57'	N	-01°53'	W	
Deaple	Diaple	LIB	06°51'	N	-08°24'	W	
Degie	Digei	LIB	07°06'	N	-10°10'	W	
Dekese		DRC	-00°25'	S	21°20'	E	
Deng	Dengdeng	CAM	05°11'	N	13°31'	E	
Dibamba R./Sanaga R.		CAM	ca. 04°00	N	ca 10°00'	E	
Digei	Degie?	LIB	07°06'	N	-10°10'	W	
Dilolo		DRC	-10°41'	S	22°21'	E	
Dinga		CAM	ca 04°	N	ca 14°	E	
Dipalata		ZAM	-13°19'	S	23°14'	E	
Dipalata, 6 mi N		ZAM	-13°13'	S	23°14'	E	
Dipikar Island		CAM	02°12'	N	10°30'	O	
Djaposten		CAM	03°25'	N	13°32'	E	
Djelube moyenne		DRC	00°34'	N	29°43'	E	
Djugu		DRC	01°55'	N	30°29'	E	
Douala	Duala	CAM	04°02'	N	09°42'	E	
Doumé	Dume	CAM	04°14'	N	13°26'	E	
Du R.	Du Queah-River	LIB	ca 06°12'	N	ca -10°28'	W	
Duside	Du Side Village	LIB	06°21'	N	-10°28'	W	
Ebolowo Elat	Ebolowa	CAM	02°55'	N	11°08'	O	
Edéa		CAM	03°47'	N	10°07'	E	
Edifou		TOG	07°29'	N	00°57'	E	
Efulen		CAM	02°46'	N	10°42'	E	
Ehania		IVC	05°13'	N	-02°46'	W	
Ekododo	Ekodo?	GAB	00°57'	N	09°53'	E	
Elefanten-See		CAM	04°39'-40'	N	09°23'-24'	E	
Elisabetha		DRC	01°09'	N	23°36'	E	
Elisabethville	Elisabethstad	DRC	-11°41'	S	27°29'	E	
Entebbe	Ntebbi	UGA	00°3'	N	32°27'	E	3720'
Epé Lagos		NIG	06°35'	N	03°58'	E	150 ft
Epulu		DRC	01°23'	N	28°30'	E	
Eséka	Esaka	CAM	03°39'	N	10°46'	E	
Eseka, 15 km W		CAM	03°39'	N	10°38'	E	
Eshobi		CAM	05°47'	N	09°22'	E	450'
Essangmvout		CAM	02°49'	N	12°16'	E	
Estrade							
Etaeto	Etaitu	DRC	00°21'	N	28°28'	E	

Etembo		DRC	00°55'	N	28°23'	E	1000'
Etoumbi		CON	00°10'	N	14°53'	E	
Evinayong	Evinatong	EQU	01°29'	N	10°16'	E	
Eyenméyong		CAM	04°11'	N	11°12'	E	
Ezime		TOG	07°29'	N	00°55'	E	
Faranah		GUI	10°02'	N	-10°44'	W	
Farmington River		LIB	06°49'	N	-09°48'	W	
Fazenda Gongolo		ANG	-09°28'	S	14°23'	E	
Fernan Vaz		GAB	-00°26'	S	10°27'	E	
Finca St. Elena		Bioko	not found				
Folepi		CAM	05°45'	N	09°56'	E	2000 ft
Fougamou		GAB	-01°13'	S	10°35'	E	
Foulassi		CAM	02°59'	N	11°57'	E	
Freemantown		LIB	06°15'	N	-09°00'	W	
Fundi		DRC	00°52'	N	27°34'	E	
Fungulemese		DRC	00°10'	N	28°44'	E	
Gabela		ANG	-10°51'	S	14°22'	E	
Gabela, 30 km S		ANG	-11°07'	S	14°22'	E	
Gabon	Ndendi						
	Gabon	GAB	-00°47'	S	10°20'	E	
Gagnoa		IVC	06°08'	N	-05°52'	W	
Gamangui		DRC	02°10'	N	27°15'	E	
Gambi		DRC	-03°28'	S	24°31'	E	
Ganza-Bukena		DRC	-09°13'	S	26°37'	E	
Gaple		LIB	07°08'	N	-08°28'	W	
Gashishima Commune		BUR	not found				2000 m
Goaso	Guaso	GHA	06°49'	N	-02°27'	W	
Godjé		CAM	07°43'	N	13°05'	E	
Gougou		TOG	07°59'	N	01°24'	E	
Grabazouo	Grabagoua	IVC	05°41'	N	-06°13'	W	
Grabo		IVC	04°55'	N	-07°30'	W	
Guaso	Goaso	GHA	06°49'	N	-02°27'	W	
Guéboua I		IVC	05°59'	N	-05°41'	W	
Guéckédou		GUI	08°33'	N	-10°09'	W	
Gugu riv.	Ogou	TOG	07°50'	N	01°19'	E	
Hill Town		LIB	06°37'	N	-10°47'	W	
Hydro		LIB	several times in Liberia				
Ibadan		NIG	07°22'	N	03°53'	E	
Ibembo		DRC	02°38'	N	23°36'	E	
Idjwi		DRC	-02°00'	S	29°10'	E	1620
IET-Station		IVC	05°50'	N	-07°20'	W	
Igangan		NIG	07°40'	N	03°11'	E	
Igovia		NIG	04°58'	N	06°29'	O	
Ikela		DRC	-1°11'	S	23°16'	E	
Ikot-Ekpene		NIG	05°11'	N	07°42'	E	
Ilashe	Iloshi	NIG	07°30'	N	06°30'	E	

Inadana		ZAM	not found				
Inangongo		DRC	probably close to Otsha-Lusilube				
Indole	Ndola	ZAM	-12°57'	S	28°37'	E	
Ingasi, Monbuttu	Ingasse	GAB	01°37'	N	11°26'	E	
Inkongo		DRC	-04°09'	S	22°45'	E	
Iomi		DRC					
Irangi	Kololo	DRC	-01°54'	S	28°27'	E	
Iringa		TAN	-07°46'	S	35°41'	E	5400'
Irumu		DRC	01°27'	N	29°52'	E	
Irumu, 50 m SW		DRC	00°58'	N	29°19'	E	
Isopo		DRC	-02°56'	S	28°17'	E	1050 m
Ituri		DRC	01°51'	N	29°58'	E	
Ituri Forest, 25 km SW Irumu		DRC	01°23'	N	28°38'	E	
Ituri Forest, 40 mi SW Irumu		DRC	01°00'	N	26°16'	E	
Ituri River, 50 m. S. W. Irumu		DRC	00°59'	N	29°19'	O	2500'/3500'
Izongo	Isongo	CAM	04°05'	N	09°01'	E	30 m
Jimbe Stream		ZAM	not found				
Kabambaie		DRC	-05°45'	S	20°49'	E	
Kabenga		DRC	close to Irangi				
Kabingu		DRC	-00°24'	S	29°03'	E	
Kade		GHA	06°06'	N	-00°51'	W	
Kaghasa		DRC	not found				
Kagnol	Kangol	CAM	04°02'	N	14°01'	E	
Kahnple		LIB	07°17'	N	-08°30'	W	
Kahuzi		DRC	-02°15'	S	28°40'	E	2300 m
Kai Mabiala		DRC	-04°50'	S	12°48'	E	
KaCAMega Forest		KEN	00°16'	N	34°44'	E	
Kakanda		DRC	-10°43'	S	26°22'	E	1250m
Kakata	Kaka Town	LIB	06°32'	N	-10°21'	W	
Kalehe	Kalahe Terr. (Kashewe)	DRC	-02°06'	S	28°55'	E	
Kalimbi		DRC	close to Niakalonge (2°20' S, 28°30' E)				
Kalumendo		DRC	00°46'	N	29°37'	E	900 m
Kama River		DRC	-04°08–03°38'S		27°45' - 27°14'	E	
Kambove		DRC	-10°51'	S	26°35'	E	500 m/4400'
Kamituga		DRC	-03°04'	S	28°10'	E	
Kango		GAB	00°10'	N	10°05'	E	
Kankisingi	Kisanga	DRC	-02°41'	S	28°08'	O	
Kansenia		DRC	-10°18'	S	26°04'	E	
Kapsabet		KEN	00°12'	N	35°05'	E	1980 m
Kapsabet		KEN	00°22'	N	35°00'	E	1980 m
Karawa		DRC	03°19'	N	20°17'	E	
Kartoushi		DRC	00°36'	N	29°37'	E	
Kasai R.	Cassai R.	ANG	-11°25'	S	19°10'	E	
Kassai / Sankurru		DRC	ca -04°20'	S	ca 21°00'	E	
Kasaji		DRC	-10°23'	S	23°27'	E	
Kasaji-Malonga		DRC	-10°23'	S	23°18'	E	
Kasempa		ZAM	-13°27'	S	25°49'	E	

Kasempa District		ZAM	-14°00'	S	25°15'	E	
Kasewe		SL	08°19'	N	-12°11'	W	
Kashewe		DRC	close to Irangi				
Kasindi		DRC	00°3'	N	29°41'	E	1000 m
Kassa-Singrobe		IVC	not found				
Kassewe Forest Reserve		SL	08°20'	N	-12°15'	W	
Katanga		DRC	-06°31'	S	25°49'	E	
Katanga		DRC	-05°01'	S	22°08'	E	3800? L
Kateke River		DRC	-09°04'	S	26°43'	E	
Katompe		DRC	-06°08'	S	26°21'	E	
Kavirando		not found					
Kavumu Walikale		DRC	-01°28'	S	28°05'	E	
Kayala Kungu		DRC	-04°43'	S	13°05'	E	
Kaziba		DRC	-09°08'	S	26°52'	E	
Keba		DRC	close to Kisanga [Kankisingi]				
Kellé		CON	-00°3'	S	14°29'	E	
Keri	Kiri	DRC	-01°27'	S	18°59'	E	320 m
Kidima	Makaia N'tete	DRC	-05°33'	S	13°02'	E	
Kifuba		DRC	-04°45'	S	13°10'	E	
Kigezi Distr.		UGA	ca. -01°10'	S	ca 29°40	E	
Kiliza		DRC	-03°42'	S	28°10'	E	1430 m
Kilo		DRC	01°50'	N	30°07'	E	
Kimbidi		DRC	-04°49'	S	13°18'	E	
Kindia		GUI	10°03'	N	-12°51'	W	
Kindu		DRC	-02°57'	S	25°55'	E	
Kiobo-Ngoi	Kiobongoyi	DRC	-04°46'	S	13°05'	E	
Kisala		DRC	-04°46'	S	13°00'	E	
Kisandji		DRC	-08°42'	S	27°22'	E	
Kisangani	Stanleyville, Stanleystad	DRC	00°31'	N	25°12'	E	
Kisanga	Kankisingi	DRC	-02°41'	S	28°08'	E	
Klouto Monts		TOG	06°58'	N	00°39'	E	500-800 m
Koloka		DRC	03°12'	N	24°28'	E	
Kolomba	Kolumba	GUI	08°31'	N	-10°34'	W	
Komadéké		GAB	-00°51'	S	10°32'	E	
Kombone		CAM	04°37'	N	09°18'	E	800 ft
Komi (Sankuru)		DRC	-03°20'	S	23°48'	E	
Kondéyébayé		CAM	02°58'	N	12°05'	E	
Kondué		DRC	-04°58'	S	23°20'	E	
Kongana Camp		CAR	02°47'	N	16°25'	E	
Kotili	Koteli	DRC	02°52'	N	24°32'	E	
Koudou R		CAM	02°01'	N	14°55'	E	
Kpalimé	Palimé	TOG	06°54'	N	00°37'	E	
Kpaudu	Kpandu	GHA	07°00'	N	00°25'	E	
Kpeaple	Quiapiple	LIB	06°37'	N	08°33'	E	
Kribi		CAM	02°56'	N	09°54'	E	
Kumasi		GHA	06°42'	N	-01°37'	W	
Kumba		CAM	04°38'	N	09°26'	E	270 m
Kundelungu		DRC	ca -10°	S	ca 27°	E	
Kunungu		DRC	-02°06'	S	16°26'	E	

La Makandé		GAB	-00°40'	S	11°54'	O	
Ladana		DRC	not found				
Lager IV		CAM	04°27'	N	09°15'	E	
Lagos		NIG	06°29'	N	03°22'	E	
Lakota 15km N.		IVC	06°00'		-05°43'	W	
Lamaboke	La Maboké, Mbaiki	CAR	03°52'	N	17°59'	E	
Lamto		IVC	06°12'	N	-04°58'	W	
Lemba		DRC	-05°15'	S	12°30'	E	
Lesse Gamalendu		DRC	00°43'	N	29°46'	E	
Libreville		GAB	00°23'	N	09°27'	E	
Limbe	Victoria	CAM	04°01'	N	09°11'	E	
Lindi River		DRC	0°35'- -0°30'	N/S	25°07'-28°42'	E	
Lindi River (haute)		DRC	ca -01°40'	S	ca 27°50'	E	
Lipanza		DRC	not found				
Lisala		DRC	02°08'	N	21°31'	E	
Liwale		TAN	-09°45'	S	37°55'	E	
Lobe		CAM	04°37'	N	09°00'	E	
Lobomündung		CAM	02°53'	N	09°54'	E	
Lodja		DRC	-03°29'	S	23°25'	E	
Lolodorf		CAM	03°14'	N	10°43'	E	498 m
Lomié		CAM	03°09'	N	13°37'	E	655 m
Luakela R	Luakara R.	ZAM	-11°32'	S	24°27'	E	
Luali		DRC	-05°05'	S	12°28'	E	
Lubena		DRC	00°28'	N	29°06'	E	
Lubereri		DRC	-00°17'	S	29°03'	E	1700 m
Lubero		DRC	-00°9'	S	29°13'	E	
Lubwaboury		DRC?	not found				
Luebo		DRC	-05°20'	S	21°24'		
Luengba		DRC	00°58'	N	29°11'	E	
Lufu River	Lufubu	ZAM	ca. -08°40'	S	ca. 30°30'	E	
Luholo River	Luhoho	DRC	-01°16'-33'	S	27°53'-28°04'	E	
Lukula		DRC	-05°23'	S	12°56'	E	
Lukolela		DRC	-01°10'	S	17°11'	E	
Lukundu		DRC	-03°11'	S	28°30'	E	
Luluabourg		DRC	-05°53'	S	22°26'	E	
Luna R.		DRC	01°17'	N	29°41'	E	3700'
Lundjulu		DRC	-00°20'	S	28°36'	E	1300m
LuZAMbo		DRC	-04°50'	S	23°26'	E	
Lusewa	Lushewa	TAN	-11°18'	S	36°21'	E	
Lutunguru		DRC	-00°27'	S	28°48'	E	
Luvumbu	Lubumba, Luvamba	DRC	-03°57'	S	29°03'	E	6400'
Lwake, Kabingu		DRC	close to Irangi				
Mabetta	Mabeta	CAM	04°00'	N	09°15'	E	200'
Mabira Forest		UGA	00°37'	N	33°09'	E	
Mabondo		DRC	-02°21'	S	27°10'	E	
Mafia		GHA	06°26'	N	-02°56'	W	
Magrotto		TAN	-05°07'	S	38°45'	E	

Makaia N'tete	Kidima	DRC	-05°33'	S	13°02'	E	
Makanka	Kanka	SL	09°44'	N	12°32'	W	
Makokou		GAB	00°33'	N	12°51'	E	
Makumbi		DRC	-05°50'	S	20°40'	E	
Makwe		DRC	-01°56'	S	28°28'	E	
Malawi, Lake, north end		TAN	ca. 09°25'	S	ca. 33°55'	E	
Malonga		DRC	-10°31'	S	23°27'	E	
Mambaka		DRC	00°51'	N	27°33'	E	
Mamfe		CAM	05°46'	N	09°17'	E	400'
Mampong		GHA	07°03'	N	-01°24'	W	
Mamu		NIG	07°04'	N	03°54'	E	
Mamu River FR		NIG	06°10'	N	07°10'	E	
Manguredjipa		DRC	00°21'	N	28°44'	E	
Mashere		DRC	close to Irangi				
Masisi		DRC	-01°32'	S	28°48'	E	
Matonguine		IVC	not found				
Mawambi		DRC	01°04'	N	28°34'	E	
Mayombe	Mayumbe	DRC	-04°45'	S	14°17'	E	
Mayombo, Liwale		TAN	not found				
Mayumbe		DRC	02°30'	N	27°37'	E	
Mbaiki	Lamaboke	CAR	03°52'	N	17°59'	E	
Mbini	Rio Benito, Rio Muni	EQU	01°29'	N	10°16'	E	
Mbuma		DRC	-04°50'	S	12°54'	E	
Medje		DRC	02°23'	N	27°18'	E	800 m
Mefini (Memfini?)		GAB	ca. -00°53'	S	ca. 10°05'	E	
Mekambo		GAB	01°00'	N	13°57'	E	
Metet		CAM	03°23'	N	11°43'	E	2500Ft.
Mey Joss village	Mayos	CAM	03°55'	N	13°53'	E	
Meyo-Nkoulou		CAM	02°16'	N	11°21'	E	
Mfoa-Arebe	Mfôa	GAB	00°22'	N	10°12'	E	
M'fume		CAM	not found				
Missahohé	Misahöhe	TOG	06°57'	N	00°34'	E	
Mitala		DRC	-02°40'	S	28°07'	E	
Mitowa	Mitawa?	TAN	-08°20'	S	38°32'	E	
Mkpani	M'Kpani, Nkpani	NIG	05°49'	N	08°09'	E	120 m
Mkundi, Liwale		TAN	not found				
Moca		Bioko	03°20'	N	08°39'	E	1200 m
Moera		DRC	00°39'	N	29°30'	E	1100 m
Moloundou	Molundu	CAM	02°02'	N	15°12'	E	
Monda, Nguru Mts.		TAN	-06°08'	S	37°35'	E	
Mondombe	Mondembe	DRC	-00°54'	S	22°48'	E	
Mongbwalu		DRC	01°57'	N	30°01'	E	
Monrovia		LIB	06°18'	N	-10°47'	W	
Monrovia, 50 mls inland		LIB	06°53'	N	-10°22'	W	
Monte Alen	Nkolentangan	EQU	01°40'	N	10°17'	E	
Mosumo		EQU	01°44'	N	10°04'	E	
Moyamba		SL	08°10'	N	-12°26'	W	

Mpéré	Mperi, Fernan Vaz?	GAB	-01°40'	S	09°40'	E	
Mt. Cameroun		CAM	04°13'	N	09°10'	E	
Mt. Elgon		UGA	01°10'	N	34°32'	E	
Mt. Okoro Biko		EQU	01°28'	N	09°52'	E	
Muchinga escarpment		ZAM	-13°03'	S	31°24'	E	
Mugaba		DRC	-02°18'	S	28°36'	E	
Mugesse Forest		MAL	ca -09°40'	S	ca. 33°40'	E	
Muhutaba		DRC	close to Irangi				
Mulungu		DRC	-02°54'	S	27°56'	E	
Mungombe		DRC	-03°08'	S	28°14'	E	
Muramvya		BUR	-03°15'	S	29°36'	E	2000 m
Musaia		SL	09°45'	N	-11°34'	W	1200'
Musake-Hütte, Lager VII		CAM	04°10'	N	09°12'	E	1850 m
Musisi Kauzi		DRC	not found				
Musohopla "Ikela, Musohopla"		DRC	not found				
Mussaka		not found					7000 ft
Mutemute		not found					1000 m
Mutobo		DRC	-01°22'	S	28°52'	E	
Mutwanga		DRC	00°20'	N	29°45'	E	1200 m
Mweias		DRC	not found				3500'
Namalungo		TAN	-10°42'		35°38'		3500 ft
Ndjolé	Ndjoli	GAB	-00°10'	S	10°45'	E	
Ndola	Indole	ZAM	-12°57'	S	28°37'	E	9120'
Ndongo, Lete Country	not found						
Ndungyungo, Liwale		TAN	not found				
N'gahr (Obudu)		not found					
Ngam		CAM	03°00'	N	11°17'	E	
Ngayu		DRC	01°45'	N	27°33'	E	
Ngolole		DRC	-03°08'	S	28°18'	E	1210 m
Ngouma	Ngoko	CAM	01°58'	N	15°31'	E	
Nguilo	Nguelo	TAN	-08°39'	S	33°12'	E	
Niaji		NIG	not found				
Niakoussoué		IVC	06°01'	N	-05°39'	W	
Niambasha	Nyambasha	DRC	-02°08'	S	28°52'	E	
Niamiringi		DRC	probably close to Irangi				
Niapu		DRC	02°25'	N	26°26'	E	800 m
Niébé		IVC	05°22'	N	-07°17'	W	
Niefang, 3 km S		EQU	01°49'	N	10°16'	E	
Nimba Mt		GUI	07°38'	N	-08°22'	W	
Nimba Mts		LIB	ca 07°27'	N	ca -08°37'	W	
Njala		SL	08°07'	N	12°05'	W	
Njuga	Nyuga	TAN	-10°32'	S	35°54'	E	
Nkami		not found					
N'Ko		NIG	05°52'	N	08°10'	E	500 ft
Nkolentangan	Monte Alen	EQU	01°40'	N	10°17'	E	
Ntyonga, Fernan Vaz		GAB	not found				
Nyasa L	Malawi L		-09°29'-14°26'S		33°52'-35°18'	E	

Obala		CAM	04°09'	N	11°31'	E	
Oban (Distr.)		NIG	05°19'	N	08°33'	E	
Obubra		NIG	06°05'	N	08°18'	E	
Obudu		NIG	06°40'	N	09°09'	E	
Oda		GHA	05°54'	N	-00°59'	W	400'
Odiemé	Siènso	IVC	09°25'	N	-07°31'	W	
Ogooue River		GAB	00°10'-0°18'	N	10°20'-10°34'	E	
Ogowe		GAB	not found				
Okaka		NIG	not found				
Okarara		NIG	05°22'	N	08°42'	E	269 m
Okoiyong		CAM	05°45'	N	09°23'	E	450 ft
Okowe		GAB	05°45'	N			
Oku-See	Lager IV	CAM	04°27'	N	09°15'	E	
Oliredou		IVC	06°04'	N	-05°42'	W	
Olokomeji		NIG	07°25'	N	03°32'	E	
Omo Kenya		not found					
Onamele		CAM	not found				
Onate		not found					
Onitsha	Abutschi	NIG	06°09'	N	06°46'	E	140 m
Ora		NIG	08°02'	N	05°03'	E	
Osamang R		EQU	not found				
Ossidinge		CAM	05°55'	N	09°05'	E	
Otsha-Lusilube		DRC	00°30'	N	29°39'	O	1360 m
Ouonga Camp		CAR	02°55'	N	16°21'	E	
Oyem		GAB	01°35'	N	11°34'	E	
Palimé	Kpalimé	TOG	06°54'	N	00°37'	E	
Pamaquelle		CAR	04°32'	N	17°16'	E	
Pampramase		GHA	06°40'	N	02°55'	W	
Panga		DRC	01°50'	N	26°22'	E	
Papekou. Cercle de Gagnoa		IVC	not found				
Parc du Banco		IVC	05°22'-26'	N	04°02-05'	E	
Patokla		IVC	05°28'	N	-07°19'	W	
Paulis		DRC	02°45'	N	27°41'	E	
Pays de Eschiras, Congo Francais		not found					
Peloken	Pelokehn	LIB	05°36'	N	-08°09'	W	
Pilipili		DRC	00°33'	N	27°44'	E	
Poko		DRC	03°09'	N	26°53'	E	
Pujehun		SL	07°21'	N	-11°42'	W	
Quillou		not found					
Quirimbo		ANG	-10°41'	S	14°16'	E	
Quirimbo, 75 km east		ANG	-10°41'	S	14°56'	E	
Rebbo, Bassa		LIB	not found				
Refugium		Bioko	03°37'	N	08°48'	E	2000 m
Rio Benito	Mbini	EQU	01°34'	N	09°36'	E	
Rio Iladyi		Bioko	03°15'-20'	N	08°39'-42'	E	1100 m
Rio Mbia		EQU	02°05'	N	09°57'	E	
Rio Muni	Mbini	EQU	01°29'	N	10°16'	E	

River Cess		LIB	05°27'	N	-09°34'	W	
Rovuma R.		TAN	-11°00'	S	35°15'	E	
Rutovu, Mt.		DRC	-03°49'	S	29°45'	E	
Rutshuru		DRC	-01°10'	S	29°26'	E	
Saibly	Seibli	IVC	06°30'	N	-08°26'	W	
Sakbayémé		CAM	04°02'	N	10°33'	E	
Salujinga		ZAM	-10°58'	S	24°07'	E	
Sanaga R./Ossa L.		CAM	ca. 3°46'	N	ca. 10°02'	E	
Sanghaie	Sangay	DRC	-04°58'	S	23°31'	E	
Sangmélima		CAM	02°55'	N	11°58'	E	782
Sankitta							
Sapele		NIG	05°53'	N	05°40'	E	
Sapoba		NIG	06°06'	N	05°52'	E	
Sarvi		CAM					
Sassandra River		IVC	07°00'	N	-07°03'	W	
Seibli	Saibly	IVC	06°30'	N	-08°26'	W	
Semliki		DRC	-00°8'	S	29°36'	O	525-912m
Seredou		GUI	08°23'	N	-09°39'	W	
Shabunda		DRC	-02°41'	S	27°20'	O	
Shasha		NIG	07°08'	N	04°23'	E	
Siamonrovia		LIB	06°05'	N	-08°14'	W	
Sibiti		KON	-03°41'	S	13°21'	E	
Sièn so	Odienné-Sièn so	IVC	09°25'	N	-07°31'	W	
Sifuri-Mafia		GHA	06°26'	N	-02°56'	W	
Sigi		TAN	-05°00'	S	38°47'	E	
Sinba		CAM	probably close to Tinta				2350 ft
Sindara		GAB	-01°01'	S	10°39'	E	
Singrobe		IVC	06°05'	N	-04°55'	W	
Songndeng	Soñ Kindenge	CAM	03°41'	N	10°53'	E	
Songea		TAN	-10°40'	S	35°38'	E	
Soubré		IVC	05°47'	N	-06°35'	W	
Soubré, 11 km SW		IVC	05°42'	N	-06°40'	W	
Stanley-Falls	Boyoma Falls	DRC	00°30'	N	25°12'	E	
Stanleyville	Kisangani, Stanleystad	DRC	00°31'	N	25°12'	E	
Suam		UGA	01°13'	N	34°42'	E	2400 m
Suku Tadi		DRC	-04°47'	S	12°55'	E	
Tahiré		GUI	09°50'	N	-12°46'	W	
Tandala		DRC	02°57'	N	19°20'	E	
Tappita	Tapeta, Tappi-Town	LIB	06°30'	N	-08°52'	W	
Tchibati		DRC	-02°10'	S	28°46'	E	
Tchimbangu	Tshimbangu	DRC	-06°47'	S	21°17'	E	
Tchimbete, 5km NEE		GAB	00°38'	N	10°27'	E	
Tchimbuende	Chimbuende	ANG	-10°58'	S	19°28'	E	
Temma		IVC	not found				
Tenkere		SL	09°47'	N	-12°00'	W	

Thielen St. Jacques		DRC	-07°02'	S	23°32'	E	
Thysville		DRC	-05°16'	S	14°51'	E	
Timbo		GUI	10°37'	N	-11°49'	W	
Tinta		CAM	06°15'	N	09°30'	E	2350 ft
Titule		DRC	03°17'	N	25°30'	E	
Tokokoe	Tokokwe	GHA	06°43'	N	00°32'	E	
Tombel		CAM	04°45'	N	09°39'	E	380 m
Toulépleu		IVC	06°35'	N	-08°25'	W	
Tshabondo		DRC	-20°06'	S	28°34'	E	
Tshimbangu	Tchimbangu	DRC	-06°47'	S	21°17'	E	
Tshoko		DRC	close to Irangi				
Tshuapa Ikela		DRC	not found				
Tsinga Mbumba	Singa Mbuma	DRC	-04°45'	S	13°05'	E	
Uelleburg		EQU	not found				
Ukaika		DRC	00°45'	N	28°45'	E	900 m
Umuahia		NIG	05°32'	N	07°29'	E	
Unyora, nr. Lke Albert		?DRC/UGA	not found				
Ureka		Bioko	03°15'	N	08°15'	E	
Victoria	Limbe	CAM	04°01'	N	09°11'	E	
Victoria-See/D.O.A.		TAN	Northwest area of Lake Victoria				
Yabrasso		IVC	07°26'	N	-03°26'	W	
Ya R.		CAM	not found				
Yala		KEN	00°6'	N	34°31'	E	
Yalosemba		DRC	02°34'	N	21°47'	E	
Yapo		IVC	05°46'	N	-04°07'	W	
Yapo, Petit		IVC	05°47'	N	04°08'	E	
Yapo-sud		IVC	05°42'	N	-04°05'	W	
Yaunde		CAM	03°52'	N	11°31'	E	1025 m
Yaunde, 30 km N		CAM	04°08'	N	11°31'	E	
Yéalé		IVC	07°31'	N	-8°25'	W	
Yeke-Irangi, Onate		DRC	not found				
Yenagoa		NIG	04°56'	N	06°16'	E	
Yokamba		DRC	-00°1'	S	22°17'	E	
Yombi		GAB	-01°26' or -02°14'	S	11°54'	E	
Zambezi	Balovale	ZAM	-13°32'	S	23°06'	E	
Zambia West 1		ZAM	ca -13°25'	S	ca. 23°50'	E	
Zambia West 2		ZAM	ca. -13°50'	S	ca. 24°10'	E	
Zambia West 3		ZAM	ca. -13°00'	S	ca. 24°00'	E	
Zambia West 4		ZAM	ca. -12°30'	S	ca. 24°50'	E	
Zambia West 5		ZAM	ca. -14°00'	S	ca. 26°00'	E	
Zambia West 6		ZAM	ca. -12°10'	S	ca. 26°30'	E	
Zambia Central 1		ZAM	ca. -13°45'	S	ca. 29°00'	E	
Zambia Central 2		ZAM	ca. -14°45'	S	ca. 28°50'	E	
Zambia Central 3		ZAM	ca. -15°00'	S	ca. 29°25'	E	
Zambia East 1		ZAM	ca. -8°40'	S	ca. 29°25'	E	
Zambia East 2		ZAM	ca. -13°00'	S	ca. 31°20'	E	

Zambo	Beni Zambo	DRC	00°20'	N	29°30'	E	1100 m
Zimmi		SL	07°19'	N	-11°18'	E	
Ziombli		IVC	06°33'	N	-08°23'	W	
Zoatoupsi		CAM	04°09'	N	11°28'	E	
Zwedru		LIB	06°04'	N	-08°08'	W	