TAXONOMY AND HISTORICAL ZOOGEOGRAPHY OF THE RED SQUIRREL, *PARAXERUS PALLIATUS* (PETERS, 1852), IN THE SOUTHERN AFRICAN SUBREGION (RODENTIA: SCIURIDAE)

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The inter- and intraspecific classification of the red squirrel, *Paraxerus palliatus* (Peters, 1852) is reviewed. *Paraxerus* Forsyth Major, 1893, is considered a valid genus with two species, *P. cepapi* (A. Smith, 1836) and *P. palliatus*, within the Southern African subregion. *P. palliatus* is represented by four subspecies, 1) *P. p. ornatus* (Gray, 1864), 2) *P. p. bridgemani* Dollman, 1914, with *tongensis* Roberts, 1931, and *auriventris* Roberts, 1926, as synonyms; 3) *P. p. swynnertoni* (Wroughton, 1908), and 4) *P. p. sponsus* (Thomas & Wroughton, 1908), which may, however, prove to be indistinguishable from the nominate subspecies. Habitat is a determining factor in colour and size variation in the genus. Skull and body measurements from museum specimens and from two field studies in southern Africa indicate that the light-coloured, smaller squirrels (*P. p. bridgemani*) inhabit dry forest, while the largest and darkest forms (*P. p. ornatus*, *P. p. swynnertoni*, and also the extralimital *P. vincenti* Hayman, 1950, *P. vexillarius* (Kershaw, 1923) and *P. lucifer* (Thomas, 1897)) occur in moist evergreen forests. *P. p. sponsus*, which is intermediate in colour and size, occurs in dry to moist forests.

The historical zoogeography of the red squirrel group on the eastern seaboard is discussed. Changes in the sea-level and in the distribution of rain forests, the presence of large stretches of water, as well as the mean annual range of temperature and the length of the warm season or breeding period, have affected the historical distribution patterns of these squirrels.

Keywords: Africa, taxonomy, zoogeography, Rodentia, Sciuridae, *Paraxerus*.

INTRODUCTION

The tree squirrels of southern Africa are represented in the genera *Heliosciurus* Trouessart, 1880, *Paraxerus* Forsyth Major, 1893, and *Funisciurus* Trouessart, 1880. *Paraxerus* is represented by the bush squirrel, *P. cepapi* (A. Smith, 1836), which is widely distributed in southern African woodland, and the red squirrel, *P. palliatus* (Peters, 1852), which inhabits dense vegetation on the Mozambique plain.

Eleven subspecies of *P. palliatus* are listed by Amtmann (1975), namely *auriventris* Roberts, 1926, *barawensis* (Neumann, 1902), *bridgemani* Dollman, 1914, *frerei* (Gray, 1873), *ornatus* (Gray, 1864), *palliatus* (Peters, 1852), *sponsus* (Thomas & Wroughton, 1907), *suahelicus* (Neumann, 1902), *swynnertoni* (Wroughton, 1908), *tanae* (Neumann, 1902) and *tongensis* Roberts, 1931. Of these, the southern African taxa and their distribution are as follows (Fig. 1.): *auriventris* (lower Limpopo River, Mozambique), *bridgemani* (Mozambique, inland from Inhambane, as well as southeastern Tanzania), *ornatus* (Ngoye Forest, Zululand), *palliatus* (northeastern Mozambique), *sponsus* (Inhambane to Beira district, Mozambique), *swynnertoni* (Chirinda Forest, Mt Selinda, Zimbabwe) and *tongensis* (coastal Zululand). In

addition, three extralimital species, *P. lucifer* (Thomas, 1897) on the Nyika Plateau and Misuku Mountain, Malawi, and southwestern Tanzania, *P. vexillarius* (Kershaw, 1923) (with subspecies *vexillarius* and *byatti* Kershaw, 1923) from the mountains of central and eastern Tanzania, and *P. vincenti* Hayman, 1950, from Namuli Mountain, northern Mozambique, have close affinities with, and have on occasion been included in, the *P. palliatus* group, for example by Kingdon (1974). These extralimital taxa are closely related to the southern African taxa and are therefore also discussed, although little information could be obtained on them. *Paraxerus cepapi*, *P. palliatus ornatus* and *tongensis* are the only taxa of southern African tree squirrels that have been studied in any detail (Viljoen, 1975, 1980).

The present study attempts to clarify some aspects of the nomenclature and distribution of *P. palliatus* in the Southern African subregion with reference to some of the extralimital taxa. It is evident that the identification of red squirrel species and subspecies has presented difficulties to a number of authors (Roberts, 1931; Kingdon, 1974; Smithers and Tello, 1976). The following short review of the nomenclature clearly indicates the de-
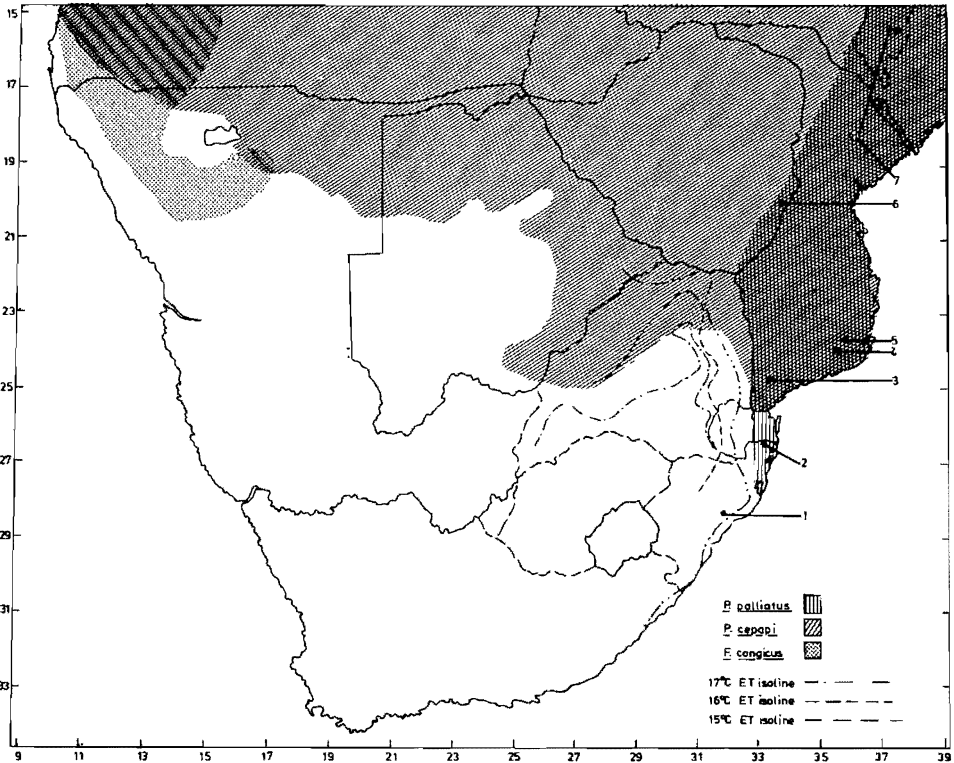
Fig. 1

Distribution of southern African tree squirrels, *Paraxerus cepapi*, *P. palliatus*, *P. vincenti* and *Funisciurus congicus*. Type localities of taxa in the *palliatus* group *(sensu lato)* of red squirrels are: **1** *ornatus* (Ngoye Forest, Eshowe district, Zululand); **2** *tongensis* (Mangusi Forest, northeastern Zululand); **3** *auriventris* (Magude, lower Limpopo River, southern Mozambique); **4** *sponsus* (Coguno, Inhambane district, Mozambique); **5** *bridgemani* (Panda, inland from Inhambane, Mozambique); **6** *swynnertoni* (Chirinda Forest, eastern Zimbabwe); **7** *vincenti* (Namuli Mt, northern Mozambique). Present-day ET isolines (15° C, 16° C and 17° C) are indicated.

gree of confusion that exists at present.

SOUTHERN AFRICAN TAXA. *P. p. sponsus* was described from Coguno, Inhambane district (a moist forest), but is said to occur northwards as far as Beira. Thomas and Wroughton (1907) described *sponsus* as a *Funisciurus* intermediate in size between *P. cepapi* and *P. palliatus*, with the colour pattern of the former and the bright colouring of the latter. (However, this is also the colour pattern of *P. palliatus*.) Its size, particularly that of the skull, is rather smaller than other *P. palliatus* (Tables 1, 3). They incorrectly included *tongensis* in the subspecies *P. p. sponsus*, and separated *ornatus* from both *P. p. sponsus* and *P. p. palliatus*.

Paraxerus cepapi auriventris (Roberts, 1931) was listed as a subspecies of *P. palliatus* by Roberts (1951) and Amtmann (1975).

P. p. bridgemani was recorded inland from In-

hambane by Swynnerton and Hayman (1950) and from southeastern Tanzania by Amtmann (1975). Its occurrence in southern Tanzania is disputed by Smithers and Tello (1976), who pointed out that the type locality of *P. p. palliatus* is just south of the Rovuma River (the northern Mozambique-Tanzania border). They therefore restricted all the light-coloured subspecies (including *P. p. bridgemani*) to the south of the Save River.

I disagree with Kingdon's map of the coastal east and southern African species on which he indicates 'pure *palliatus*', 'pure *cepapi*' and three classes of hybrids: 'predominantly *palliatus* hybrids', 'intermediate hybrids' and 'predominantly *cepapi* hybrids'. He considered three taxa that are clearly *P. palliatus*, i.e., *ornatus*, *swynnertoni* and *sponsus*, as examples of hybridization between *P palliatus* and *P cepapi*. But *P. p. ornatus* is geographically isolated from the other two (Fig. 1), and it is more probable that *P. p. swynnertoni* and *P. p.*

ornatus both evolved in allopatry, as explained below. The only *P. palliatus* taxon that could possibly be confused with *P. cepapi* is *auriventris*, which was described from Maputo. Therefore, Kingdon's notion of a zone of *palliatus/cepapi* hybrids to the east of Lake Malawi cannot be accepted. *Paraxerus p. sponsus*, which represents *P. palliatus* in this 'hybrid' region, very closely resembles *P. p. ornatus* of the south, and the colour difference between them could be caused merely by climate. Also, as will be discussed below, *P. palliatus* and *P. cepapi* are very distinct ethologically and morphologically.

EXTRALIMITAL TAXA. *Heliosciurus lucifer* of Ellerman (1940) is currently considered a species of *Paraxerus* (Amtmann, 1975; Kingdon, 1974).

Smithers and Tello (1976) suggested that *Paraxerus vincenti* should be considered a subspecies of *P. palliatus*, whereas Ellerman *et al.* (1953) mentioned that *P. vincenti*, *P vexillarius* and *P. byatti* may represent a single species (the last two taxa are from the montane forests in central and eastern Tanzania). Conversely, Amtmann (1975) stated that *vexillarius* and *byatti* could possibly be separate species. Kingdon (1974) regarded *laetus* (from east of Lake Malawi) and *byatti* (*P. vexillarius byatti* of Amtmann (1975) from the Uluguru, Usambara and Uzungwa Mountains) as subspecies of *P. lucifer* (which occurs to the north of Lake Malawi). He also suggested (1974) that hybridization may occur between *byatti* and *P p. palliatus* to yield *vexillarius* (all in the Usambaras). Grubb (1978) regarded *vexillarius* and *byatti* as either allospecies or semispecies that are potentially in contact, but with no hybrids, intermediates or localized sympatry known.

Kingdon (1974) also mentioned that *carruthersi* could be grouped with *byatti*. He based his classification of *Paraxerus* as a subgenus of *Funisciurus* on evidence that the mountain squirrel, *Funisciurus carruthersi*, has closer phyletic relationships with *Paraxerus*, especially with *P byatti*, than with squirrels of the genus *Funisciurus*. His descriptions of the septa in the auditory bullae, teeth, voice, nipple count, colour (not striped), tail and

shyness of *carruthersi* indicates that it is a *Paraxerus* and not a *Funisciurus*. But why did Kingdon not consider that *carruthersi* might have been incorrectly classified as a *Funisciurus*? Why include all *Paraxerus* under *Funisciurus*? Another example of an apparent incorrect classification is *Paraxerus boehmi*, which in my judgement should be referred to *Funisciurus*, but this falls outside the scope of the present work.

Kingdon (1974) recognized only four subspecies of *P. palliatus*, namely *tanae* (including *barawensis*), *frerei*, *palliatus* (the nominate subspecies, possibly including *suahelicus*), and tentatively also *bridgemani* (which he considered a *palliatus/cepapi* hybrid).

It is clear that many of the taxa have had a varied treatment in the literature and this raises the question of whether they should all be regarded as subspecies of *P. palliatus*, or whether some of them have attained specific status.

Although Kingdon (1974) classified *Paraxerus* as a subgenus of *Funisciurus*, I have retained it as a valid genus on the grounds of extreme morphological and ethological differences within the subregion (Viljoen, 1980). Smithers (1983) also considered them to be separate genera. If a hybrid between *P. p. palliatus* and *P. cepapi* were to be visualized, it would certainly resemble *bridgemani*, *auriventris* or *tongensis*, and consequently Kingdon (1974) regards *bridgemani* as a hybrid between *P. palliatus* and *P. cepapi*. But when the ethology of *P. palliatus* and *P. cepapi* is studied (Viljoen, 1977, 1980) it is clear that they differ widely in many respects, e.g., oestrus communication is mainly vocal in the territorial *P. cepapi* living in clumped vegetation, whereas it is olfactory in the continuously forested habitat of *P. palliatus*, where home ranges overlap to varying degrees

Grubb (1978) regarded the relationship between *P. cepapi* and *P. palliatus* as an example of secondary intergradation, with intermediates being known. However, interspecific breeding, and even hybridization, between certain subspecies of *P. palliatus* remains doubtful (Viljoen, 1980).

MATERIAL AND METHODS

COLOUR COMPARISONS AND BODY MEASUREMENTS. Colour comparisons were based on, and body measurements taken from labels of, specimens in the following museums: South African Museum, Cape Town 4, Queen Victoria Museum, Zimbabwe 22, National Museum, Bulawayo, Zimbabwe 4, Natal Museum, Pietermaritzburg 8, Transvaal Museum, Pretoria 23, Blantyre Museum, Malawi 2, Maputo Museum, Mozambique 14, and from various published works (Roberts, 1951; Sclater, 1900; Ellerman,

Morrison-Scott and Hayman, 1953; Amtmann, 1975; Smithers and Tello, 1976; Kingdon, 1974). Specimens examined are listed in Appendix I. Mass and standard body measurements (ear, hindfoot *(c.u.)*, total length and tail length (as defined by Cockrum, 1955)) from a study of *P. p. ornatus* and *tongensis* were also included (Viljoen, 1980).

In comparing mass and body measurements (Table 1), data from Roberts (1951) were not included because, as is apparent

Table 1
Body measurements of *Paraxerus vincenti* and various taxa of *P. palliatus* (mean ± 1 *SD* in millimetres).

Taxon and Distribution	Sample size	Head & body	Tail	Hindfoot (c.u.)	Ear	Mass
P. vincenti						
Namuli Mountain, central Mozambique	5	212,0 ± 5,87	209,0 ± 8,94	46,6 ± 1.95	21,1 ± 0,55	—
P. p. sponsus						
Zimbabwe, southern Malawi						
(a) Moist localities	11	202,45 ± 13,31	210,29 ± 13,35	50,73 ± 2,15	21,00 ± 1,12	280,83 ± 38,33 (n = 10)
(b) Dry localities	12	202,42 ± 14,49	198,60 ± 10,93	49,45 ± 2,30	20,04 ± 1.29	269,05 ± 46.65 (n = 4)
P. p. ornatus						
Ngoye Forest	4	216,25 ± 6,5	221,50 ± 11,96	50,75 ± 2,22	20,75 ± 0,96	—
P. p. swynnertoni						
Mount Selinda	9	201,11 ± 14,61	204,88 ± 20,1	51,50 ± 2,88	19,80 ± 1,30	291,5 (n = 1)
auriventris ·						
Magude, lower Limpopo	4	192,50 ± 9,57	172,50 ± 21,02	42,83 ± 1,89	—	—
tongensis						
Manguzi Forest at Maputa	6	181,67 ± 4,08	175,00 ± 7,07	44,72 ± 1,34	15,38 ± 2,67	—

from the fur, he in error considered some juveniles to be adults. Roberts's cranial measurements also differed from those used in the present study.

CRANIAL MEASUREMENTS. Cranial measurements (as defined by Cockrum, 1955) taken on museum specimens and skulls collected during the present study were as follows: 1 Maximum length of cranium: overall length from anterior tip of basals to posterior bulge of braincase, mastoid bullae, or other structure making up the posteriormost part of skull. 2 Minimum interorbital constriction: least distance across top of skull between orbits. 3 Zygomatic breadth: greatest distance across zygomatic arches of cranium at right angle to longitudinal axis of skull, or greatest distance between outer surfaces of zygomata. 4 Cranial breadth: greatest distance across braincase immediately behind zygomatic arches. 5 Nasal length: from a line connecting anteriormost parts to a line connecting the posteriormost extensions of the nasal bones. 6 Nasal breadth: distance from lateralmost point of one nasal to corresponding point of the other. 7 Depth of cranium: vertical distance from a line connecting the tips of upper incisors with the ventralmost portion of posterior part of cranium to the highest part of cranium (taken with a glass slide beneath the skull). 8 Length of the maxillary molar toothrow: distance from anterior alveolus of first premolar to posterior alveolus of posterior molar. 9 Length of mandibular toothrow: same as for the maxillary toothrow.

RESULTS AND DISCUSSION

SUBSPECIES OF THE *PALLIATUS* GROUP. On the Mozambique plain, suitable *P. palliatus* habitat (i.e., dense thickets or forests) occur in isolated geographic islands of vegetation completely separated from neighbouring islands. Here *P. palliatus* exhibits a remarkable spectrum of colour variation on the ventral surface, face and hands, from yellow and pale orange, through varying shades to red. Near Inhambane, the forms *bridgemani* and *sponsus* have been described within 40 km of each other. If habitat is brought into consideration, this colour variation can be better understood. It seems a clear-cut case of dry and moist habitats influencing colour and size, the light-coloured and smaller squirrels (*tongensis* and *auriventris*) being found in dry forest. The two distinguishable populations of *sponsus* (see below), which are intermediate in both colour and size, occur in dry and moist forest, while the largest and darkest forms, i.e., *ornatus*, *swynnertoni*, *vincenti*, *lucifer* and *vexillarius*, occur in the evergreen forest.

Tinley (personal communication) separated the localities of the museum specimens from the Mozambique plain into moist and dry habitats as follows:

Moist: Chipata lighthouse, Chitengo, Inhamitanga, Bunga (an Inselberg in the Gorongoza National Park), Coguno.

Dry: Mabenje and Maringa on the north bank of the Save River, Zinave, Chiniziwa, Panda.

The specimens from the 'moist' forests listed above consistently included darker and slightly larger individuals. In Tables 1 and 3 the squirrels are arranged according to moistness of habitat and show a steady decrease in size from the dark *ornatus* of Ngoye Forest to the light-coloured *tongensis*, the smallest. Marked colour variation is

Table 2

Body measurements of *Paraxerus palliatus ornatus* and the taxon *tongensis* from Zululand (sample size in parentheses, mean ± 1 *SD* in millimetres, mass in grams).

Taxon	Head & body	Tail	Hindfoot (c.u.)	Ear	Mass	Eviscerated mass
P. p. ornatus						
Adult males	219,17(18) ± 6,98	203,48(53) ± 7,08	51,83(61) ± 1,61	20,22(43) ± 1,07	360,91(62) ± 18,30	—
Adult females	225,08(12)± 11,08	204,24(33) ± 10,64	51,79(42) ± 1,89	21,15(32) ± 2,48	378,93(42) ± 23,68	—
Adult total	221,53(30) ± 9,16	203,77(86) ± 8,57	51,81(103) ± 1,72	20,62(75) ± 1,42	368,19(104) ± 22,37	306,1(6) ± 20,29
Subadults	211,88(8) ± 7,40	204,59(24) ± 8,08	51,54(26) ± 2,18	19,98(22) ± 0,72	313,6(24) ± 32,25	271,75(2) ± 0.35
Juveniles	196,0(2) ± 22,63	197,67(3) ± 6,81	44,75(5) ± 14,69	19,36(4) ± 0,78	222,62(5) ± 44,29	—
tongensis						
Adult males	184,0(5) ± 12,63	176,02(13) ± 7,87	43,49(18) ± 1,58	19,63(16) ± 1,50	207,45(29) ± 16,48	187,72(5) ± 17,45
Adult females	190,83(6) ± 6,46	175,53(15) ± 10,23	44,26(18) ± 2,00	19,26(16) ± 1,47	210,60(31) ± 21,62	177,72(4) ± 6.60
Adult total	187.73(11) ± 9,87	176,83(28) ± 9,08	43,88(36) ± 1,80	19,44(32) ± 1,47	209,06(60) ± 19,24	183,28(9) ± 14.01
Subadults	185,33(6) ± 9,85	172,20(10) ± 8,47	43,23(19) ± 0,91	20,18(8) ± 1,12	178,63(24) ± 12,24	164,27(6) ± 6,87
Juveniles	152(1)	161,0(6) ± 6,96	42,47(14) ± 1,66	18,40(11) ± 1,60	139,69(13) ± 22,12	—

also evident in Zululand, where *tongensis* from dry sand forest, such as at Sihangwane and the shores of Lake St Lucia, and from the Mseleni Mission station on the western shores of Lake Sibaya, are paler in colour and smaller in mass than the specimens from moist coastal forests, such as at Manguzi, Kosi Bay and Lake Sibaya's eastern shores.

In the past the recognition and description of subspecies were often based on very few specimens, and it is doubtful whether very small size differences are reliable indicators of subspecies status when they were based on such small samples. Furthermore, individuals were allocated to subspecies on colour differences often less obvious than the moult changes described for *P. p. ornatus* in Viljoen (1980). The number of black bands on the tail hairs was also used as a diagnostic character, but it is not clear whether this included the terminal black band, which would, for example, give both *ornatus* and *tongensis* four instead of the three black bands recorded by Roberts (1951). Moreover, the black bands differ between juvenile and adult fur and can be counted incorrectly in a moulting adult (Viljoen, 1980).

When mean body measurements and mass of adults of the two *P. palliatus* forms from Zululand (Table 2) are compared, it is found that *ornatus* from the Ngoye Forest is significantly (*P* < 0,001) larger than *tongensis* from Lake St Lucia. Ethologically these two forms have much closer affinities with each other than have *P. cepapi* or any of the other *P. palliatus* taxa. However, there are differen-

ces in vocal communication (Viljoen, 1984), use of space and other aspects of behaviour (Viljoen, 1980), which would make interbreeding improbable. Furthermore, they are geographically isolated, Ngoye Forest being an area of 3000 ha separated by approximately 100 km from the nearest *tongensis* habitat.

Roberts (1931: 229) described the colour of *tongensis* as follows, and this can be used as a standard with which the variation in colour of the described taxa of *P. palliatus* can be compared: 'The dorsal general coloration from the forehead to root of tail is freckled brown and yellowish, owing to the annulations of dark brown and pale yellow, on all the hairs; the orange-yellow of the face embraces the snout and the area around and behind the eyes to the base of the ears; the hands and feet are yellowish above and below, the forearms and hind limbs with an external brighter patch, the edges of the tail are decidedly redder than the underparts of the body.' According to Roberts (1951: 366) '*P. p. tongensis* has more black-tipped hairs above and the red of the tail is a darker shade than in *P. p. auriventris*, and in size it is rather larger but the tail is equally short'. However, external and cranial measurements indicate that *auriventris* and *tongensis* are comparable in size (Tables 1, 4). Colour variation between *tongensis* and *auriventris* is similar to that between *tongensis* from different localities. The only distinctive characteristic of *auriventris* is that it has unpigmented foot-soles similar to those of *P. cepapi*, whereas *P. palliatus* has pigmented foot-soles. It is also improbable that *bridgemani* is

Table 3

Cranial measurements of *P.vincenti*, *P.lucifer* and various taxa of *Paraxerus palliatus* (mean ± 1*SD in millimetres*).
1 = maximum length of cranium; 2 = minimum interorbital constriction. 3 = zygomatic breadth. 4 = cranial breadth. 5 = nasal breadth.
6 = nasal length. 7 = depth of cranium. 8 = maxillary toothrow length. 9 = mandibular toothrow length.

Sample size	1	2	3	4	5	6	7	8	9
					P. p. ornatus				
11	50,94 ± 1,63	15,06 ± 0,76	29,35 ± 1,34	21,74 ± 0,43	7,39 ± 0,40	14,95 ± 0,6	620,72 ± 0,67	9,89 ± 0,68	9,82 ± 0,25
					P. vincenti (from Hayman, 1950)				
5	50,44 ± 0,38	15,64 ± 0,23	29,82 ± 0,33	—	—	14,33 ± 0,67	—	9,12 ± 0,13	8,92 ± 0,13
					P. p. swynnertoni				
9	48,44 ± 0,90	14,35 ± 0,91	28,38 ± 0,48	21,06 ± 0,45	7,04 ± 0,39	14,00 ± 0,61	20,31 ± 0,3	79.02 ± 0,1	49,30 ± 0.34
					P. p. frerei				
1	51,20	15,40	29,50	22,75	7,25	16,45	21,85	—	—
					P. lucifer				
1	55,03	14,85	31,60	22,95	8,15	16,25	22,95	10,35	11,10
					P. p. sponsus				
7*	47,91 ± 1,46	13,65 ± 0,59	27,95 ± 1,26	20,72 ± 0,34	7,11 ± 0,4	314,23 ± 0,84	19,98 ± 0,67	—	—
5**	49,52 ± 1,15	14,17 ± 0,45	28,73 ± 0.55	20,87 ± 0,64	7,64 ± 0,52	14,82 ± 0.4	120,84 ± 0.59	—	—
					tongensis				
13	45,3 ± 0,83	13,23 ± 0,35	26,27 ± 0,61	20,45 ± 0,27	6,62 ± 0,32	13,04 ± 0,21	19,08 ± 0,53	8,55 ± 0.5	38,15 ± 0,25
					TM6084				
1	44,95	13,55	26.00	20,25	6,90	12,70	19.45	8,20	—
					TM2367				
1	—	12,70	25,75	19,90	—	—	18,95	7,80	—

*from dry forest at Chiniziwa, Zinave, Beira, Maringa and Mabenje on north bank of Sabi River.
**from moist forest at Gorongoza, Inhamitanga, Chitanga, and Chipate Light House.
***two type specimens in the Transvaal Museum: TM6084 = *tongensis*; TM2367 = *auriventris*.

subspecifically different from either *tongensis* or *auriventris*. The form *tongensis* was described as having the colour of *bridgemani* (based on two specimens from Panda, near Inhambane) but being slightly smaller and with a much shorter tail. Both *tongensis* and *auriventris* can confidently be synonymized with *bridgemani*, the senior synonym.

According to Roberts (1951), *bridgemani* is distinguished from *sponsus* by its paler colour and orange-bordered tail, but the general body dimensions are as in *sponsus*. However, from Table 1 it can be seen that *sponsus* is consistently larger than both *auriventris* and *tongensis*. Smithers and Tello (1976) group *auriventris*, *bridgemani* and *sponsus* together 'in the mean time', but from museum skins it is apparent that *bridgemani*, *auriventris* and *tongensis* bear a closer resemblance to one another and that *sponsus* is much darker, being similar to skins of *ornatus* and *palliatus*. The colouring of *sponsus* from the Bunga Inselberg in the Gorongoza National Park closely resembles the colouring of *ornatus*, which Gray (1864) described as follows: 'back dark, blackish grizzled,

.... head, legs, thighs, underside, and tail very bright red-bay'. Roberts (1951) found a close resemblance between *swynnertoni* (darker) and *sponsus* (lighter) and *ornatus* (intermediate colour): but the external and skull measurements of the last taxon are larger (Tables 1, 3).

Ingoldby (1927) illustrated a colour range related to habitat in *Heliosciurus* similar to that observed in the present study. From inspection of a specimen he could in many cases infer not the geographical locality, but the type of country, in terms of rainfall, vegetation, temperature and altitude, from which it came. The same form had been assigned several different names in various parts of its geographic range, merely because the patches inhabited were not continuous. The deeply coloured, large forms occurred in patches corresponding well with distribution of heavy rainfall and rain forest, and wherever the bush was thinner and the ground-cover lower, forms were slightly smaller and paler, and on the savanna small pale squirrels were found to occur.

The opinion of Smithers and Tello (1976) that light-coloured *P palliatus* occur only south of Save

River is thus an oversimplification. The two subspecies recognized in Tanzania (i.e., *P. p. palliatus* and *P. p. bridgemani*) could have come from two completely different habitats, and one museum specimen collected on the Pinda Peninsula on the Mozambique coast (14° 10' S) by J. L. B. Smith is extremely light-coloured albeit bright. Unfortunately, most museum labels give no indication of habitat. In addition, one of the darkest forms, *ornatus*, is the most southerly and isolated in the Ngoye Forest. Specimens of *P. p. palliatus* were not available for this study, but are listed from northeastern Mozambique (Amtmann, 1975) and central and southern Malawi (Sweeney, 1959). Lawrence and Loveridge (1953) conclude that *P. p. palliatus* from Malawi is probably the same as the form previously recorded from northeastern Mozambique at 11° S and 15° S, but state that the Malawi specimens are markedly more ochraceous, or less red. Furthermore, Neumann (1902) describes *P. p. palliatus* as having a chestnut-red ventrum and tail. Evidence therefore seems to suggest that *P. p. palliatus* is a dark form, and it is more likely that it should be grouped with *P. p. sponsus*.

With regard to the other extralimital taxa, *vexillarius* and *byatti*, the former is known only from two specimens and the colour difference between them as described by Kingdon could have been merely moult changes. Kingdon (1974) states that *vexillarius* is slightly larger than *byatti*, but the measurements show only a 2 mm greater head & body length for the two *vexillarius* specimens and furthermore, a tail length which includes the range of that of *byatti*. We are therefore most probably dealing with a single subspecies.

Ngoye Forest, Chirinda Forest and Gorongoza, where the Bunga Inselberg occurs, are all on old Jurassic/Cretaceous soil, whereas the coastal plain is on early Pleistocene sands. It seems likely that the lighter forms from the coastal plain evolved from the darker forms. As a result of being completely isolated for long periods, the darker squirrels are easily distinguishable, with little colour or size variation within a locality, and have occasionally been accorded specific status.

TAXONOMIC CONCLUSIONS. Four subspecies of *P. palliatus* may be recognized in the Southern African subregion: *P. p. ornatus*, *P. p. bridgemani*, *P. p. sponsus* and *P. p. swynnertoni*. It also seems logical to consider *tongensis* and *auriventris* synonyms of *P. p. bridgemani*.

Within the Southern African subregion the taxa *ornatus* and *swynnertoni*, and outside this region the taxa *vincenti*, *vexillarius* and *lucifer*, have been

isolated for long periods and have evolved diagnostic differences in size, colour, and possibly behaviour. They can at least be regarded as semispecies, which Grubb (1978) defines as either highly distinctive subspecies (in this case *P. p. ornatus* and *P. p. swynnertoni*), or full species whose status is debatable (*P. vincenti*, *P. vexillarius* and *P. lucifer* following Amtmann (1975) in recognizing them as valid species). However, this problem will be solved only by on-the-spot investigations to determine the ethological and ecological separation that has taken place. *Paraxerus p. sponsus* fits descriptions of the nominate *P. p. palliatus*, but too little information is available on the latter subspecies, as well as on the more northerly subspecies *tanae*, *suahelicus*, *barawensis* and *frerei* to state anything new about their relationships.

HISTORICAL ZOOGEOGRAPHY

The present distribution of *P. palliatus* is markedly discontinuous. The following discussion concerns the establishment of the subspecies of *P. palliatus* on the eastern seaboard in relation to prehistoric geology and climate.

CHANGES IN THE DISTRIBUTION OF RAIN FORESTS. Forest connections between Africa and Eurasia existed in the late Oligocene and early Miocene, thus presenting a migration route for squirrels to Africa, but Africa then became relatively dry (Kingdon, 1974). A drier climate became more widespread in the early Miocene (Moreau, 1952; Stuckenberg, 1962; Carcasson, 1964; Axelrod and Raven, 1978), and consequently there were also changes in habitat in both central and in southern Africa. Van Couvering (1980) summarized these changes as follows from the fossil record: the early Miocene equatorial rain-forest community of East Africa remained virtually unchanged for six million years (23–17 m.y. B.P.) and then underwent a major taxonomic overturn, i.e., there was a slow shift in the general environment in East Africa from a non-seasonal climate in which equatorial rain forest was the dominant community type (early Miocene) to a seasonal climate in which savanna-mosaic was the dominant community type (Plio-Pleistocene). The first woodland-dominated habitat appears in the East African fossil record of the Middle Miocene. The Sciuridae are known from the early Miocene where they are represented by *Vulcanosciurus*, and *Paraxerus* and *Xerus* are known from the Plio-Pleistocene

(3–1 m.y. B.P.) and from recent periods (Van Couvering, 1980).

The last hypothermal ended 10 000 to 20 000 years B.P. (Morton, 1967; Coe, 1967; Livingstone, 1975; Axelrod and Raven, 1978). There is some dispute over whether this hypothermal coincided with the pluvial (Carcasson, 1964; Cooke, 1964; Livingstone, 1975), and it seems probable that there were regional differences in climate and hence vegetation after the early Miocene. Axelrod and Raven's (1978) map of the Oligo-Miocene African vegetation shows subtropical laurel forest from the Cape to northern Mozambique, whereas their map of the late Miocene and early Pliocene shows forest cut off at the bight of Maputo. To the north in Mozambique there had then been savanna-woodland as at present. If this vegetation persisted into the Pleistocene, it could possibly be the reason why P. cepapi is distributed up to the bight of Maputo and no further south along the coast. There are also several species of tropical plants, e.g., Salvadora spp., which show similar distribution limits (Tinley, personal communication). Tinley (1967) regards it as probable that a high-rainfall route was available on the Zululand coastal plain from the Mio-Pliocene or early Pliocene, but that after this period the climate became drier or more variable, disrupting the evergreen-forest cover. Stuckenberg (1969) concluded that the South African fauna must have been established in the 14 000 years since the recession of the last glacial, when tropical fauna could extend back into country from which it had previously retreated.

Axelrod and Raven (1978) stated that temperate rain-forest expanded greatly during Pleistocene pluvials in southern Africa, as shown from records near Cape Town. Moreau (1952) also found indications from avifaunal relationships between the Usambara Mountains (where P. vexillarius occurs) in Tanzania and Namuli Mountain in northern Mozambique (where P. vincenti occurs), that there was free interchange of montane forms at some stage of the early Pleistocene, which later ceased, giving a period of half a million years and upwards for the specific differentiation of the avifauna. This is in accord with estimates for differentiation times of mammals and insects. Rodents and other small mammals speciate rapidly, and a single sequence of isolation and dispersal can lead to speciation (Grubb, 1978). Although Bigalke (1968) stated that no mammals are endemic to any of the relic lowland-forest islands on the east coast, the taxa of P. palliatus isolated in forest islands differ widely, e.g., those on the Usambaras (P. v. vexillarius and P. v. byatti), Namuli Mountain (P. vincenti), Chimanimani Mountains (P. p. swynnertoni) and in

Ngoye Forest (P. p. ornatus). Furthermore, Carcasson (1964), with regard to butterfly distribution, found most of the species in the eastern forests to be either endemic species or very distinct subspecies. Carcasson concluded that no broad forest connections have existed since the uplifting of the eastern plateau some time in the Miocene, and that subsequent connections, particularly the more recent ones of the Pleistocene, must have been short-lived and on a narrow front, probably between Lake Tanganyika and Lake Nyassa. This would also be a salient connection as seen from present squirrel distribution patterns.

EFFECTIVE TEMPERATURE. When the present fauna of the Zululand region is studied, there is found to be a dramatic reduction of the tropical fauna in the Lake St Lucia area, for which nothing in the way of habitat, rainfall, temperature, predators or prey can account for per se; it can only be interpreted in the light of the faunal pattern shifting with oscillations in the general thermal pattern (Poynton, 1964). However, sea-level changes in the Pleistocene, and rivers, swamps and lagoons, could also have influenced distribution. As regards temperature, Stuckenberg (1969) considered the drop in mean temperature during the last hypothermal to have been 5° C, and he calculated Effective Temperature throughout South Africa from the formula:

$$ET = 8T + 14AR/AR + 8$$

where T = mean annual temperature and AR = mean annual range of temperature (i.e., difference between means of warmest and coldest months).

He considered ET to be a more important measure of limiting factors than mean temperatures, as did Poynton (1964). The probable 15° C ET isoline of the previous hypothermal and the present-day 17° C isoline, which limit the distribution of the forest cobra Naja melanoleuca and a tree frog Hyperolius pusillus (Stuckenberg, 1969), also limit the distribution of P. palliatus. (See Fig. 1 for present 15° C, 16° C and 17° C isolines as mapped by Stuckenberg (1969).) Stuckenberg (1969) considered four species of tropical snakes and two species of tropical frogs in relation to the present-day 15° C ET isoline and found a considerable measure of correlation, for the greater part excluding these species to the north of the isoline. This is especially interesting in southern Transvaal, the Swaziland middle veld and the Natal midlands, where there are no pronounced topographic features to control dispersal. He

found two non-tropical species of snakes to be included to the south by the 15° C and 16° C ET isolines. The distribution of *P. cepapi* in the Transvaal accords closely with the 16° C ET isoline, although other factors must have been operative in other areas, such as topography (to the east of the Transvaal escarpment) and prehistoric plant dispersal (in coastal Mozambique).

SEA-LEVEL CHANGES. Hobday (1979) recorded the shoreline of both the very early Tertiary (Palaeocene) and the end-Miocene and early Pleistocene as lapping against the Lebombo Mountain Range. King (1951) stated that there has been little physiographic change in Africa since the mid-Miocene (25 m.y. B.P.). Late-Miocene and early Pliocene uplifting accompanied by marginal downwarping caused the sea to cover the entire area of the coastal plain, bevelling it to a low relief (Hobday, 1979). The Cretaceous and Pleistocene marine formations of the Zululand coast extend inland as far as Mtubatuba and the foot of the Lebombo Mountains (King and Belderson, 1961). The oldest dune ridges close to the Lebombo Mountains are of early Pleistocene age, and the youngest ridges date from the late Pleistocene, representing the last interglacial high sea-level (Hobday, 1979).

During the last glacial a marine regression occurred to over 100 m below the present level, bringing the shoreline close to the continental shelf. The plain was therefore 'dry' since the Wurm glacial, but only since the climatic amelioration (17 000 years B.P.) could forest and forest fauna have been redistributed in this region. After 17 000 years B.P. the sea-level also advanced, but data from stable parts of the world indicate that no substantial changes have occurred since the sea attained its present Holocene level on the Zululand coast some 5000 to 6000 years B.P.

Hobday's map of the geology of Lake Sibaya shows Holocene infill in the areas where forest and *P. p. bridgemani* now occur. These squirrels also occur on the high coastal dunes adjacent to the sea, and the conclusion must be that the colonization of *P. p. bridgemani* close to the shoreline has taken place during the last few thousand years.

LARGE STRETCHES OF WATER. The presence of large stretches of water could have had a bearing on the restriction of *P. p. bridgemani* to the north of the St Lucia Estuary (32° 24' S). End-Pleistocene and Holocene advance of the shoreline depressed the river gradients and reduced their capacity for maintaining an outlet to the sea. At Lake St Lucia the closure of Leven Point occurred early during the transgression (Hobday, 1979). The impounded waters rose well above sea-level and flooded low-lying swamps and interdune depressions to both the north and the south. Lake St Lucia once extended 112 km parallel to the coastal dunes (now 40 km), and Lake Sibaya had an initial area of 150 km². Eventually the southward-spreading waters of Lake St Lucia met up with the Umfolozi system. Before the development of flood controls in the lower Umfolozi Valley, the Umfolozi Flats were commonly inundated to elevations of 5 m and more, and 4800 years ago there was a bay 9,6 km wide (Hobday, 1979).

Some tropical species of plants and animals occur only to the northern side of what was, until the agricultural era, a vast marshy area around the lower length of the Umfolozi River on the coastal plain just south of Lake St Lucia (Stuckenberg, 1969). Apart from ET, the presence of large stretches of water could thus have played a role in the decrease in the number of tropical species. The fact that certain taxa, such as *P. p. bridgemani*, occur on the Maphelane dune just south of the Umfolozi River mouth could be an indication that the river originally opened into the sea slightly to the south of Maphelane, thus prohibiting further southward spread of species. The rivers to the north (Mkuze, Mzenene, Hluhluwe and Nyalazi) did not always cross the dune barrier, but the Umfolozi River flowed strongly enough to do so (Hobday, 1965).

Ngoye Forest lies on pre-Cretaceous rocks (Orme, 1973), and Van Wyk (1963) mentioned that the oldest rocks of Natal in the south lie in the Nkandhla region (just west of Ngoye). Frankel (1960) also stated that the major fault to the north of Empangeni (which is just north of Ngoye), the Eteza fault, between the Basement rocks and the Stormberg basalts, which runs northeast from near Empangeni into the Umfolozi area, is post-basalt and probably pre-Cretaceous in age. In this region (Port Dunford) the coastline has not undergone major shifts since the Cretaceous period.

The Port Dunford formation of the last interglacial (128 000 to 73 000 years B.P.), which lies 10 km east of Ngoye Forest on the southern Zululand coastline, shows fossil evidence of elephant, buffalo, other mammalian fauna, and fossil wood, fish and various invertebrates from fresh and brackish water (Hobday, 1979). This sequence records a major back-barrier lagoon which filled, developed into a swamp, and was covered by the sands of the retreating barrier to seaward (Hobday, 1979).

The great differences in colour, size and behaviour between *P. p. bridgemani* and *P. p. ornatus*,

as well as the large gap between their present geographic ranges, suggest that *P. p. ornatus* had been isolated in Ngoye Forest before *bridgemani* became established on the coastal plains, i.e., in the early Pleistocene before the sea-level rose to the Lebombo Mountains. Ngoye Forest (28° 50' S, 31° 42' E) would have been a refuge, and further to the north the Gwaliweni Forest on the Lebombo Mountain Range could have played a similar role. However, there is no evidence of squirrel occupation of the latter forest (Viljoen, 1980), although plant species in Ngoye indicate relationships with Gwaliweni and the forests of Zimbabwe (Chirinda Forest) (Garland, personal communication).

No tree squirrels occur in the inland forests, e.g., those in eastern Transvaal, thus showing that there was probably no squirrel migration to the west of the Lebombo Mountain range. The botanical similarity between Ngoye Forest and Gwaliweni Forest indicates Ngoye's tropical connections to the east of the Lebombo Range rather than to the west. Grubb (1978) stated that no single refugium could have existed in the eastern forest region (in which he includes the whole distribution range of *P. palliatus*), but if *P. p. ornatus* had been established in Ngoye Forest during the early Pleistocene, then there must have been several other similar refugia,

such as Mt Chirinda, Namuli Mt, and the montane forests of Malawi and Tanzania (Usambaras, Uluguru, Uzungwa Mts).

Qudeni Forest (42 km west of Ngoye) is considered to be the northernmost temperate mistbelt forest (Afromontane forest) by Moll (1972), and Ngoye Forest is considered to be the southwestern limit of lowland subtropical forest (Werger, 1978). Ngoye, which has many endemics or valid subspecies, and the forests to the west (Nkandhla and Qudeni) were probably not connected after the early Pleistocene, as a later connection would have introduced *P. p. ornatus* and other endemics into these forests. In the light of the above discussion on coastal forest establishment and sea-level variations, any connection during the Pleistocene to the coastal plain must have been of short duration, and the evergreen forest is not, as Sherry (1977) suggested, a habitat on the edge of the range of the *P. palliatus*, but rather the original habitat of the species. The low-altitude woodland-thicket subspecies probably evolved from the forest stock. Forest origins for the Sciuridae have been proposed by Lönnberg (see Lönnberg (1929) in Grubb (1978)), and Grubb (1978) also concluded that faunal exchange between biomes has been predominantly from forest to savanna.

REFERENCES

AMTMANN, E., 1975. Family Sciuridae. Part 6.1. *In:* MEESTER, J. and SETZER, H. W., eds, *The mammals of Africa: an identification manual*, pp. 1–12. Smithsonian Institution Press, Washington D.C.

AXELROD, D. T. and RAVEN, P. H., 1978. Late Cretaceous and Tertiary vegetation history of Africa. *In:* WERGER, M. J. A., ed., *Biogeography and ecology of southern Africa*, pp. 77–130. Monographiae biologicae 31. W. Junk, The Hague.

BIGALKE, R. C., 1968. Evolution of mammals on southern continents. III. The contemporary mammal fauna of Africa. *Quarterly Review of Biology* **43**: 265–300.

CARCASSON, R. H., 1964. A preliminary survey of the zoogeography of African butterflies. *East African Wildlife Journal* **2**: 122–157.

COCKRUM, E. L., 1955. *Laboratory manual of mammalogy.* Burgess Publ. Co., Minneapolis.

COOKE, H. B. S., 1964. The Pleistocene environment in southern Africa. *In:* DAVIS, D. H. S., ed., *Ecological studies in southern Africa*, pp. 1–23. W. Junk, The Hague.

COE, M. J., 1967. Biogeography and the equatorial mountains. *In:* VAN ZINDEREN BAKKER, E. M., ed., *Paleoecology of Africa and of the surrounding islands and Antarctica*, Vol. II. Balkema, Cape Town.

ELLERMAN, J. R., 1940. *The families and genera of living rodents* (1758–1936), Vol. 1. G. W. C. Holt, London.

ELLERMAN, J. R., MORRISON-SCOTT, T. C. S. and HAYMAN, R. L. W., 1953. *Southern African mammals, 1758–1951: a reclassification.* Trustees of the British Museum (Natural History), London.

FRANKEL, J. J., 1960. The geology along the Umfolozi River,

south of Mtubatuba, Zululand. *Transactions of the Geological Society of South Africa* **63**: 231–263.

GRAY, J. E., 1864. Notice of a new squirrel (*Sciurus ornatus*) from Natal. *Proceedings of the Zoological Society of London* **1864**: 13.

GRUBB, P., 1978. Patterns of speciation in African Mammals. *Bulletin of the Carnegie Museum of Natural History* **6**: 152–167.

HOBDAY, D. K., 1979. Geological evolution and geomorphology of the Zululand coastal plain. *In:* ALLISON, B. R, ed.,. *Lake Sibaya*, pp. 1–20. Monographiae biologicae 36. W. Junk, The Hague.

INGOLDBY, C. M., 1927. Some notes on the African squirrels of the genus *Heliosciurus. Proceedings of the Zoological Society of London* **32**: 471–487.

KING, L. C., 1951. *South African scenery*, 2nd edn. Oliver and Boyd, Edinburgh and London.

KING, L. C. and BELDERSON, R. H., 1961. Origin and development of the Natal Coast. *In: Marine studies off the Natal coast*, pp. 1–34. S2. CSIR Symposium.

KINGDON, J., 1974. *East African mammals (an atlas of evolution)*, Vol. II. Academic Press, London.

LAWRENCE, B. and LOVERIDGE, A., 1953. Zoological results of a fifth expedition to East Africa: mammals from Nyasaland and Tete. *Bulletin of the Museum of Comparative Zoology Harvard* **110**: 1–80.

LIVINGSTONE, D. A., 1975. Late Quaternary climatic change in Africa. *Annual Review of Ecology and Systematics* **6**: 249–280.

MOLL, E. J., 1972. The current status of mistbelt mixed Podocarpus forest in Natal. *Bothalia* **10**: 595–598.

MORTON, J. K., 1967. The flora of the Loma Mountains and Tingi Hills (Sierra Leone). *In:* VAN ZINDEREN BAKKER, E. M., ed., *Palaeoecology of Africa and of the surrounding islands and Antarctica,* Vol. II, pp. 67–69. Balkema. Cape Town.

MOREAU, R. E., 1952. Africa since the Mesozoic, with particular reference to certain biological problems. *Proceedings of the Zoological Society of London* 121: 869–913.

NEUMANN, O., 1902. Einige afrikanische Eichhornchen. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1–8: 175–181.

ORME, A. R., 1973. Barrier and lagoon systems along the Zululand coast, South Africa. Technical report No. 1. Office of Naval Research. *In:* COATES, D. R., ed., *Coastal geomorphology,* pp. 181–217. State University of New York, New York.

POYNTON, J. C., 1964. The biotic division of southern Africa, as shown by the Amphibia. *In.* DAVIS, D. H. S., ed., *Ecological studies in southern Africa.* W. Junk, The Hague.

ROBERTS, A., 1931. New forms of South African mammals. *Annals of the Transvaal Museum* 14: 229.

ROBERTS, A., 1951. *The mammals of South Africa.* Trustees of 'The mammals of South Africa Book Fund', Johannesburg.

SCLATER, W. L., 1900. *The mammals of South Africa,* Vol. 2. R. H. Porter, London.

SHERRY, B. Y., 1977. The red squirrel (*Paraxerus palliatus*) Peters in south-eastern Rhodesia. *Arnoldia* 8: 1–7.

SMITHERS, R. H. N. and TELLO, J. L. P. L., 1976. *Check list and atlas of the mammals of Mocambique.* Museum Memoir No. 8. Trustees of the National Museums and Monuments of Rhodesia, Salisbury.

SMITHERS, R. H. N., 1983. *The Mammals of the Southern African subregion.* University of Pretoria, Pretoria.

STUCKENBERG, B. R., 1962. The distribution of the montane palaeogenic element in the South African invertebrate fauna. *Annals of the Cape Provincial Museum* 2: 190–205.

STUCKENBERG, B. R., 1969. Effective temperature as an ecological factor in southern Africa. *Zoologica africana* 4: 145–197.

SWEENEY, R. C. H., 1959. *A preliminary annotated check-list of the mammals of Nyasaland.* The Nyasaland Wildlife Society,
Blantyre.

SWYNNERTON, G. H. and HAYMAN, R. W., 1950. A check-list of the land mammals of the Tanganyika Territory and the Zanzibar Protectorate. *Journal of the East African Natural History Society* 20: 274–392.

THOMAS, O. and WROUGHTON. R. C., 1907. The Rudd exploration of South Africa: VII. Lists of mammals obtained by Mr. Grant at Coguno, Inhambane. *Proceedings of the Zoological Society of London* 12: 292–294.

TINLEY, K. L., 1967. The moist evergreen forest – tropical dry semi-deciduous forest tension zone in north-eastern Zululand and hypotheses on past temperate/montane rain forest connections. *In:* VAN ZINDEREN BAKKER, E. M., ed., *Paleoecology of Africa and of the surrounding islands and Antarctica,* Vol. II, pp. 82–85. Balkema, Cape Town.

VAN COUVERING, J. A. H., 1980. Community evolution in East Africa during the late Cenozoic. *In:* BEHRENSMEYER, A. K. and HILL, A. P., eds, *Fossils in the making – vertebrate taphonomy and paleoecology,* pp. 272–298. University of Chicago Press. Chicago.

VAN WYK, W. L., 1963. *Groundwater studies in northern Natal, Zululand and surrounding areas.* Memoir No. 52. Geological Survey, Pretoria.

VILJOEN, S., 1975. Aspects of the ecology, reproductive physiology and ethology of the bush squirrel, *Paraxerus cepapi cepapi.* M.Sc. thesis. University of Pretoria.

VILJOEN, S., 1977. Behaviour of the bush squirrel, *Paraxerus cepapi cepapi. Mammalia* 41: 119–166.

VILJOEN, S., 1980. A comparative study of the biology of two subspecies of tree squirrels *Paraxerus palliatus tongensis,* Roberts, 1931, and *Paraxerus palliatus ornatus* (Gray, 1864) in Zululand. D.Sc. thesis. University of Pretoria.

VILJOEN. S., 1984. Communicatory behaviour of southern African tree squirrels *Paraxerus palliatus ornatus, P. p. tongensis, P. c. cepapi* and *Funisciurus congicus. Mammalia* 47(4): 441–461.

WERGER, M. J. A., 1978. Biogeographical division of southern Africa. *In:* WERGER, M. J. A., ed., *Biogeography and ecology of southern Africa,* pp. 145–170. Monographiae biologicae 31. W. Junk, The Hague.

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APPENDIX I

MUSEUM SPECIMENS EXAMINED

Queen Victoria Museum
MOZAMBIQUE: R26 Chiniziwa; R30 Chiniziwa, 1835; R48 Inhamitanga, 1835; R54 Inhamitanga, 1835; S176 Mahange, Lower Sabi, 2132A2; T540 Nyemunza, GonaRheZhoe, 2132Aa; T2061 Mt Selinda, Chirinda Forest; T2062 Mabenje, Sabi River; T2063 Mt Selinda, Chirinda Forest; T2064 Mt Selinda, Chirinda Forest; JT726 Zinave, 2133; JT1784 Zinave, 2133; JT2791 Englande, Coutada 5 – Save; SJL990 Gorongoza, Chitenga, 1834C$_2$; SJL1001 Bunga Inselberg, Gorongoza; SJL1023 Chitenga, Gorongoza, 1834D$_3$; SJL1072 Chipata Lighthouse, 1935; SJL1161 Chitenga, 1834; MSF/MP/1 Chirinda Forest, Mt Selinda; MS/MP/15 Chirinda Forest, Mt Selinda; MSM6 Chirinda Forest, Mt Selinda. MALAWI: NM3437 Nyika Plateau (*Heliosciurus lucifer*).

National Museum, Bulawayo
MOZAMBIQUE: TG1196(50312) Chirinda Forest, Mt Selinda; 1546 Coguno (Inhambane district) (*sponsus*); NM4784 Tambarra. MALAWI: NM12970 Malawi Hill.

Maputo Museum
MOZAMBIQUE: 1 Lourenco Marques (*auriventris*); 16 Maputo; SJL989 Bunga Inselberg, Gorongoza, 1834C$_2$; SJL1071 Chipata Lighthouse 1935B$_3$; SJL1155 Chitengo, 1834C$_4$; SJL1156 Chitengo, Gorongoza, 1834C$_4$; SJL1160 Chitengo, Gorongoza, 1834C$_4$; JT245 Zinave, 2133B$_4$; JT1269 Zinave, 2133B$_4$; JT2078 Zinave, 2133B$_4$; JT2819 Zinave, 2133B$_4$; JT2820 Zinave, 2133B$_4$. MALAWI: 74Rom1266 Malawi Hill; 74Rom1288 Nchisi Mountain.

Natal Museum
NATAL: *Zululand*: N484 Ngoye Forest; N485 Ngoye Forest; 526 Ngoye Forest; 150 Mseleni, Lake Sibaya; 151 Mseleni, Lake Sibaya; 152 Mseleni, Lake Sibaya; 153 Mseleni, Lake Sibaya; 154 Mseleni, Lake Sibaya; 155 Mseleni, Lake Sibaya; 156 Mseleni, Lake Sibaya.

South African Museum
NATAL: *Zululand*: ZM2868, ZM10239–ZM10241 Ngoye Forest.

Transvaal Museum
TANZANIA: 8729 Jozani Forest, Zanzibar (*lasti*); ZIMBABWE: 7737 Mt Selinda (*swynnertoni*); 7738 Mt Selinda (*swynnertoni*); 7739 Mt Selinda (*swynnertoni*); 7740 Mt Selinda (*swynnertoni*); 8607 Mt Selinda (*P. p. swynnertoni*); 6278 Mt Selinda (*swynnertoni*). NATAL: 8764 Ngoye Forest (*ornatus*); 8765 Ngoye Forest (*ornatus*); 6084 (holotype) Manguzi Forest, Maputa (*tongensis*); 6085 Manguzi Forest, Maputa (*P. p. tongensis*); 6086 Manguzi Forest, Maputa (*tongensis*); 6087 Manguzi Forest, Maputa (*tongensis*); 6088 Manguzi Forest (*tongensis*); 7179 Road to Maputa (*tongensis*); 7432 Maputa (*tongensis*); 25994 Kosi Bay (*P. p. tongensis*); 2367 (holotype) Magude (*auriventris*). MOZAMBIQUE: 12591 Pinda Peninsula 14° 10′ S Mozambique (*bridgemani*); 505 Beira (*palliatus*); 6214 Manga, Beira (*palliatus*); 10818 Maringa, Sabi North Bank (*P. sponsus*); 10819 Maringa, Sabi North Bank.