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THE BURROWING GECKOS OF SOUTHERN AFRICA, 1 (REPTILIA: GEKKONIDAE)

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(With two Plates and four Text-figures)

ABSTRACT

This study deals with the entirely terrestrial genera of southern African geckos. Of this group one new genus and two new species were described since the last complete account of the African geckos was published by Loveridge in 1947. Two new subspecies are described in this paper. Morphological descriptions, more detailed than before, are given. The population variation of *Ptenopus* is analysed. Basic aspects of the ecology and the zoogeography of all the species and subspecies are discussed. An attempt is made to establish the phylogenetic and taxonomic affinities of these genera. The results of this investigation are to be published in five parts in this journal.

INTRODUCTION

In 1943 FitzSimons published "The Lizards of South Africa". At that stage it was a complete record of all known Lacertilia occurring in this region. It naturally included an account of the geckos. In 1947 Loveridge revised the African Gekkonidae, disagreeing with FitzSimons on some points. Neither of these two authors proposed a division into subfamilies. Underwood (1954a), working on a world-wide basis, proposed a classification of the Gekkonidae based mainly on the shape of the pupil. According to this classification the six southern African genera *Chondrodactylus, Colopus, Palmatogecko, Ptenopus, Rhoptropella* and *Rhoptropus* belonged to the Diplodactylinae.

Kaokogecko, a genus obviously related to this group, has been described since then (Steyn & Haacke, 1966). This study deals with the taxonomy and ecology of the terrestrial forms of the above-mentioned genera and is in part a re-evaluation of Underwood's classification.

All these genera except the rupicolous genera *Rhoptropus* and *Rhoptropella* are terrestrial forms which show specialized anatomical and ecological adaptations to this way of life. Both FitzSimons (1943) and Loveridge (1947) had very few specimens at their disposal and both authors quoted practically the same sources and records. Little additional information has been published on these genera. Mertens' 1955 and to a lesser degree in his 1971 account on the herpetofauna of South West Africa contributed the greatest number of new locality records. Brain (1962a) published the the only recent taxonomic and zoogeographic work on any member of this group when revising the genus *Ptenopus.* Haacke (1964) described an additional species of the same genus and mentioned ecological and ethological observations of all known species made at the Namib Desert Research Station. Steyn and Haacke (1966), when describing *Kaokogecko,* discussed the relationship of this new genus to *Chondrodactylus, Colopus* and *Palmatogecko* rather superficially. These four genera appear to be closely related.

According to Underwood (1954a) *Ptenopus* is also closely related to these geckos and belongs to the same subfamily. When checking this assumption it became apparent that the four genera listed above are actually more closely related to other African geckos of the subfamily Gekkoninae than to *Ptenopus.* The original purpose of this study was thus to disprove Underwood's subfamilial classification according to the pupil shape, at least as far as the southern African members of the Gekkoninae (sensu Underwood, 1954) was concerned. The fallibility of Underwood's criterion has already been pointed out by Pasteur (1960) in the north African genus *Saurodactylus.* Kluge's paper (1967) proved that the pupil shape of geckos does not demarcate any natural groups. Based on a long series of different anatomical characters he regrouped the geckos into the single family Gekkonidae, consisting of four subfamilies. According to this grouping the southern African geckos which are referred to as "burrowing" geckos in this study, are all true gekkonids while the Diplodactylinae are restricted to the Australian region.

A great wealth of additional material, including two undescribed subspecies and ecological, biological and distributional information has been accumulated since Loveridge's revision (1947). It was therefore considered important to continue with this study of the "burrowing" geckos as a group and to compile all the information available at present. Hecht (1952: 112) states that there are no burrowers amongst the Gekkonidae. It is assumed that he means serpentiform species with degenerate limbs which are common amongst the skinks and which, in fact, do not occur amongst geckos. However, all the true terrestrial geckos burrow to a greater or lesser extent. This behaviour is particularly well developed in the genera discussed in this paper and the extremities have special adaptations to facilitate burrowing. The large genus *Pachydactylus* has a few species, such as *austeni* Hewitt, *kochi* FitzSimons and *mariquensis* Smith which are truly terrestrial. They burrow and even occupy similar ecological

niches to the "burrowing" genera. However, as most species of this genus are rupicolous or arboreal and no clearly developed adaptations for burrowing occur, even in the above-mentioned species, this genus is only mentioned in the discussions regarding the phylogeny and relationships of the different genera. The "burrowing" geckos as discussed in this paper are therefore, according to the latest views (Kluge, 1967), not a taxonomic unit but have a related ecology.

When discussing the distribution of the geckos Underwood (1954a: 484) made special mention of the six South African genera which he considered to belong to the Diplodactylinae and said, "The forms all occur in desert or veld and appear to be adapted to the special conditions of South Africa. Such a number of genera with several peculiar forms of feet in such a restricted area, is somewhat surprising". Arid areas seem to favour speciation in this family (Loveridge, 1947: 15). Although the presence of a great number of endemic species in the south-west arid area of the Ethiopian region might indicate an evolutionary centre it must rather be viewed as a localized response to ecological contitions (Poynton, 1961: 79) which prevailed apparently undisturbed by pluvial periods since the Benguella current drew close to the coast during the Cretaceous period (Koch, 1962: 69).

The distribution of the burrowing geckos is apparently to a large extent determined by the average annual rainfall on a suitable substratum as in some cases it coincides remarkably well with rainfall isohyetes.

The subspecies concept poses a rather awkward problem in gekkonid taxonomy, probably to the same extent as in any other vertebrate group. Step-clines were observed in the distribution of *Chondrodactylus, Ptenopus* and *Colopus*. These rather sudden changes coincide with geographical changes such as differences in rainfall, altitude, substratum or combinations of these factors. As the different populations differ considerably, it was considered useful to restore again the subspecies *maculatus* of *Ptenopus garrulus* and to describe subspecies of *Chondrodactylus angulifer* Peters and *Colopus wahlbergii* Peters.

As the distribution and the phenotype of these geckos show a remarkable correlation with their environment, this study had to be of a combined taxonomic and ecological nature. To illustrate the phylogenetic relationship of these taxa a superficial study of the anatomy of the feet, which show remarkable adapatations for burrowing, was also made.

This study was completed in 1968, but since that year a large number of additional specimens has been obtained and it was felt to be important to check the material, add all the additional distribution records and in general to up-date the original text.

In order to facilitate publication this revised study has been split into the following five sections:

Part 1. Introduction; Material and Methods; Acknowledgements; Gazetteer; Annotated Taxonomic Account; A. *Ptenopus*.
Part 2. B. *Palmatogecko;* C. *Kaokogecko*.
Part 3. D. *Colopus*.
Part 4. E. *Chondrodactylus*.
Part 5. Phylogenetic and Taxonomic Affinities.

To avoid repetition the acknowledgements, gazetteer and the most commonly used references appear only in the first part.

MATERIAL AND METHODS

The bulk of the material which this study is based on is housed in the Transvaal Museum, Pretoria. Since the publication of FitzSimons' monograph on the lizards of South Africa in 1943 large numbers of additional specimens have been collected, in many cases from areas which had not been sampled previously. Of other collections that were utilized in the course of this study the most important is that of the State Museum, Windhoek, South West Africa, the Umtali Museum, Rhodesia and the remarkable collection of the Los Angeles County Museum which has been accumulated by Dr Eric Pianka's team of the University of Texas of which the large sample of *Colopus* specimens was put at my disposal. Although specimens of *Chondrodactylus* and *Ptenopus* were borrowed from the McGregor Museum, Kimberley, the South African Museum, Cape Town and the Port Elizabeth and Durban Museums, none or only a few specimens have been added to those collections since FitzSimons inspected them in connection with his book (1943). The specimens actually studied are listed either as types or at the end of the taxonomic chapters.

Biological, ecological and ethological observations were made by the author on various collecting trips which covered most of the area where the burrowing geckos occur. Most of the specimens were collected while walking at night and carrying a 300–500 candle-power paraffin pressure lamp, while others were collected with the aid of a spotlight or the headlight beam of a truck. Some specimens were also collected by digging up their burrows. Specimens of all the species mentioned have been kept in terraria for varying lengths of time, during which periods further observations were made.

The main reference works used in this study were FitzSimons' "The Lizards of South Africa" (1943) and Loveridge's revision (1947) of the African Gekkonidae. As both publications give very comprehensive synonymy and literature lists, only the original description and the references published since 1947 are listed.

Scale counts on *Ptenopus* were made as follows: With the aid of a ballpoint pen, a straight line was drawn across the top of the head directly above the pupils. The interorbital scales were then counted along this line using the supraorbital folds as endpoints. Similarly the gulars were counted along a straight line across the throat, directly below the pupils. In this case the labials were excluded. The scales around the middle were counted along a line drawn around the body just anterior to the umbilical slit, which then served as marker for the starting and finishing points. These counts were analysed statistically and the range of variation, the arithmetical mean, the standard deviation and the standard error were established for each sample. Furthermore the sex of adults was determined, head/body, eye diameter and tail were measured and the percra ratios calculated (Werner, 1969, 1971), autotomy frequencies within certain populations were established, the position of the fracture plain in tails noted and the number of enlarged tubercles on the base of the tail was counted. For

statistical comparison five specimens were accepted as a minimum series to represent a locality or an area. In some cases, where gaps had to be filled in and where the available material showed a satisfactory degree of homogenity, specimens from a number of neighbouring localities were lumped together to represent an area. Where a number of large samples were found in close proximity, as in the central Namib and the Gemsbok Park, one sample was selected, to facilitate work.

To establish the degree of interpopulation differences or relationship, samples from adjacent populations were compared. The coefficient of difference (= C.D.; Mayr *et al.,* 1953: 146) existing between any two neighbouring samples was calculated for the interorbitals, gulars and the scales around the middle. Mayr *et al.* (1953: 147) demonstrate this method as used to evaluate the differences between two populations of the lizard *Uta ornata* Baird & Girard and warn that it gives only rough approximations, as it is based on a number of assumptions which are not necessarily correct. Keeping this in mind, and also the fact that many of the samples are extremely small, special precautions were taken to reduce the possibility of erroneous conclusions. For each pair of samples the C.D. was established for three different features of scutellation and although indications were found of further definable populations, no new subspecies were described.

The distribution maps show all known and acceptable locality records. These are also listed under the heading "Recorded localites". The source of each record is indicated in brackets following the name. The abbreviations used are as follows:

A = Albany Museum, Grahamstown.
B = National Museum, Bloemfontein.
D = Durban Museum.
F = FitzSimons' Literature List (1943).
K = McGregor Museum, Kimberley.
L = Listed by Loveridge (1947).
M = Listed by Mertens (1955).
M1 = Listed by Mertens (1971).
MCZ = Mus. Comp. Zool., Harvard, Mass., U.S.A.
P = Pianka Collection and/or Pianka (1972).
PE = Port Elizabeth Museum.
S = South African Museum, Cape Town.
SW = State Museum, Windhoek.
TN = Tvl Mus. new; i.e. acquired since 1943.
TO = Tvl Mus. old; i.e. acquired before 1943 and referred to by FitzSimons.
UM = Umtali Museum, Rhodesia.

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As the material and the observations contributing to these papers were accumulated over a period of several years and on various field trips, I benefitted from the kind assistance of many persons, too numerous to be mentioned individually. However, I would like to mention some in particular.

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GAZETTEER

Aarpan, C. 2720 Bc
Abbabis, S.W.A. 2316 Cc
Abrahamskraal, C. (Exact locality unknown)
Adendorp, C. 3224 Bc
Aggenys, C. 2918 Bc
Aha Mtns, B. 1921 Ca
Alfa, S.W.A. 2014 Dc
Alt Wasserfall, S.W.A. 2718 Bc
Amichab (= Anigab) Mtn, S.W.A. 2315 Ba
Angola – S.W.A. Border 18°E 1718 Ac
Angra Pequena = Lüderitzbucht, S.W.A.
Annisfontein, C. 2816 Bd
Aranos, S.W.A. 2419 Aa
Ariamsvlei, S.W.A. 2819 Bb
Arib, S.W.A. 2315 Dd
Asab Station, S.W.A. 2517 Bd
Askham, C. 2620 Dd
Aughrabies Falls, C. 2820 Cb
Auob River, S.W.A., C.
Auros, S.W.A. 2716 Ca
Aus, S.W.A. 2616 Ca
Awasib, S.W.A. 2515 Ad
Beaufort West, C. 3222 Bc
Bergland, S.W.A. 2217 Cc
Berseba, S.W.A. 2517 Dd
Bethanis Waterhole, S.W.A. 2014 Ad
Bethany, S.W.A. 2617 Ac
Blaauwbosch, C. 2820 Bb
Bloeddrif, C. 2816 Bd
Bloukranz = Inkboschpan, C.
Bluesky, S.W.A. 2619 Db
Bokspits, B. 2620 Dc
Boomrivier, S.W.A. 2816 Bb
Boshu Boholu Pan, B. 2522 Aa
Brandberg, S.W.A. 2114 Ba
Brandkaross, C. 2816 Bc
Bruckaros Mtn, S.W.A. 2417 Dd
Büllsport, S.W.A. 2416 Ab
Bundfeldschuh, S.W.A. 2715 Da
Buschpfanne, S.W.A. 2619 Dd
Cape Cross, S.W.A. 2113 Dd
Cape Fria, S.W.A. 1812 Ac
Carnarvon, C. 3022 Cc
Charlottental, S.W.A. 2615 Ca
Chuos Mtns, S.W.A. 2215 Cb
Coen Brits, Tvl. 2229 Dd
Colorado Oos, S.W.A. 2017 Cc
Conception Bay, S.W.A. 2314 Dc
Daberas, C. 2816 Bd
Daberas in Holgat River, C. 2816 Dd
Damara Pan, B. 2222 Ba
Dassiefontein, S.W.A. 2718 Ba
Davignab, S.W.A. 2719 Db
Deelkraal, Tvl. 2327 Bc
Dekar, B. 2121 Da
De Hoop, C. 2817 Aa
De Waal, S.W.A. 2318 Bd
Douglas, C. 2923 Bb
Drotzky's Cave, B. 2021 Ba
Espenheira, A. 1612 Cd
Farquarson, C. 2917 Ad
Fish River Mouth, S.W.A. 2817 Aa
Fonteine, S.W.A. 2014 Ac
Foz de Cunene, A. 1711 Bc
Franken, S.W.A. 1914 Db
Gaias, S.W.A. 2014 Cc
Gakhibane, B. 2621 Da
Ganab, S.W.A. 2315 Ba
Gangwe Pan, B. 2421 Da
Garies, C. 3017 Db
Gemsbokberg, S.W.A. 2817 Bc
Gemsbokbron, S.W.A. 2013 Ba
Gezelskap, C. 2822 Ab
Ghanzi, B. 2121 Da
Goanikontes, S.W.A. 2214 Db
Gobabeb, S.W.A. 2315 Ca
Gomodimo Pan, B. 2223 Db
Goodhouse, C. 2818 Cd
Gorob Mine, S.W.A. 2315 Cb
Grasdrif, C. 2817 Ad
Great Karas Mtns, S.W.A. 2718 Bc
Great Salt Pan, Tvl. 2229 Cd
Groot Aarpan, C. 2720 Bc
Groot Brak, C. 2520 Ab
Groot Kolk, C. 2420 Cc
Gross Tinkas, S.W.A. 2215 Cd
Greylingshof, S.W.A. 2315 Db
Haalenberg, S.W.A. 2615 Cb
Hanaus, S.W.A. 2517 Ad
Hantam, C. 3119 Bc
Henkries, C. 2818 Cc
Hentiesbaai, S.W.A. 2214 Ab
Hoarusib River Mouth, S.W.A. 1912 Ba
Hoasas, S.W.A. 2016 Bc
Holte, C. 2918 Ad
Hotsas, S.W.A. 2215 Cd
Huisis, Gobabis dist., S.W.A. (Exact locality unknown)
Husab, S.W.A. 2215 Ca
Inkboschpan, C. 2720 Ab
Jakhalswater, C. 2817 Dc
Jakkalswater, S.W.A. 2215 Cb
Juliana, Tvl. 2229 Dd
Kakamas, C. 2820 Dc
Kakolo Windmill, A. 1612 Dd
Kalkfontein South, S.W.A. 2818 Bb
Kalkfontein, B. 2220 Bb
Kalksloot Station, C. 2821 Ac
Kamaggas, C. 2917 Cd
Kameelsleep, C. 2520 Dc
Kang, B. 2322 Dd
Kangyane Pan, B. 2322 Cd
Kanus, S.W.A. 2718 Dc
Kanyu, B. 2024 Ba
Kaotwe Pan, B. 2223 Ca
Karibib, S.W.A. 2115 Dd

Karoedap C. 2917 Aa
Keetmanshoop, S.W.A. 2618 Ca
Kenhardt, C. 2921 Ac
Khuis, B. 2621 Db
Khutse Pan, B. 2324 Bc
Kimberley, C. 2824 Db
Klein Spitzkoppe, S.W.A. 2115 Cc
Klinghardt Mtns, S.W.A. 2715 Bd
Klipfontein, C. 2917 Ba
Koanakha Hills, B. 2021 Aa
Koichab Pan, S.W.A. 2615 Bc
Kokong, B. 2423 Ac
Kolmanskop, S.W.A. 2615 Ca
Konkiep, S.W.A. 2617 Ca
Kraaiwater, C. 2918 Ab
Kraikluft, S.W.A. 2718 Ba
Krantzkop, N Bank Orange River (Exact locality unknown)
Kubub, S.W.A. 2616 Ca
Kuboos, C. 2816 Bd
Kuke Pan = Khutse Pan, B.
Kuibis, S.W.A. 2616 Db
Kulsberg, C. 2920 Db
Kwang Pan, C. 2520 Bc
Kwiha, B. 2021 Ab
Ky Ky, C. 2620 Bb
Lacrau, A. 1711 Bc
Lake Dow = L. Xau, B. 2124 Bd
Langer Heinrich, S.W.A. 2215 Cd
Leeudril, C. 2620 Bc
Lekkersing, C. 2817 Cc
Lekuru Pan, B. 2422 Ca
Lephepe, B. 2325 Bd
Letlhakeng, B. 2425 Aa
Louisvale, C. 2821 Ac
Lucas Vley, C. 2919 Dc
Lüderitz, S.W.A. 2615 Ca
Mabuasehubi Pan, B. 2422 Cc
Machuma, B. 2125 Ba
Madube, S.W.A. 2317 Dd
Mahlzeit, S.W.A. 2619 Bd
Makambu, S.W.A. 1718 Ad
Malmesbury, C. 3318 Bc
Maltahöhe, S.W.A. 2416 Dd
Mamono, B. 2220 Ac
Mariental, S.W.A. 2417 Db
Marydale, C. 2922 Ac
Mata Mata, C. 2620 Aa
Matapha Pan, B. 2121 Cd
Middelpits, B. 2621 Db
Miershoopholte, C. 2822 Ac
Mile 66, S.W.A. 2114 Cc
Mile 110, S.W.A. 2113 Bc
Mobutsane, B. 2423 Bc
Modder River, C. 2924 Ba
Molopo River, C. 2615 Ca
Mossamedes, A. 1512 Aa
Mothate Pan, B. 2324 Dd
Munutum River, S.W.A. 1812 Aa
Nabas, C. 2817 Ad
Namutoni, S.W.A. 1816 Dd
Naramoep, C. 2917 Da
Naroep, C. 2918 Ba
Narudas Süd, S.W.A. 2718 Bd
Nasukkel, S.W.A. 2317 Db
Nata, B. 2026 Aa
Naukluft Mtns, S.W.A. 2416 Aa
Nauzerus, S.W.A. 2316 Cd
Niekerkshoop, C. 2922 Bd
Noachabeb, S.W.A. 2718 Bc
Nochaben, S.W.A. 2718 Bc
Nog Verder, S.W.A. 2017 Ac
N.W. Dunefields, S.W.A. 1711 Db
Nossob Camp, C. 2520 Bc
Nuwerus, C. 3118 Ab
Obib, S.W.A. 2816 Ba
Obib Dunes, S.W.A. 2816 Ba
Odila Dam, S.W.A. 1717 Ac
Okahandja, S.W.A. 2216 Bb
Okiep, C. 2917 Db
Okotusu, S.W.A. 1711 Bd
Omaruru River Mouth, S.W.A. 2214 Aa
Onder Swartmodder, C. 2819 Dc
Onguati, S.W.A. 2115 Dc
Oograbies, C. 2917 Aa
O'okiep = Okiep, C.
Orange River Station, C. 2924 Ca
Oranjemund, S.W.A. 2816 Cb
Orupembe, S.W.A. 1812 Ab
Otjimbingwe, S.W.A. 2216 Ac
Otjitambi, S.W.A. 1915 Cc
Ouhandjo, S.W.A. 1712 Cb
Oup = Auob River
Palmenhorst, S.W.A. 2214 Db
Perdepan, S.W.A. 2318 Db
Pforte, S.W.A. 2215 Ca
Plateau, S.W.A. 2616 Da
Pofadder, C. 2919 Ab
Pomona, S.W.A. 2715 Ad
Port Nolloth, C. 2916 Bd
Porto Alexandre, A. 1511 Dd
Prieska, C. 2922 Da
Prince of Wales Bay, S.W.A. 2715 Ab
Quickborn, S.W.A. 2117 Aa
Ramansdrif, S.W.A. 2818 Cd
Rand Riffles, S.W.A. 2214 Dc
Rehoboth, S.W.A. 2317 Ac
Reuning's Prospect, C. 2816 Bb
Riet, S.W.A. 2215 Cb
Rietfontein, C. 2620 Ca
Rietfontein, S.W.A. 2120 Dd
Rietkuil, S.W.A. 2017 Bc
Rio Coroca Mouth, A. 1511 Dd
Rocky Point, S.W.A. 1812 Cd
Rooibank, S.W.A. 2314 Ba
Rosh Pinah, S.W.A. 2716 Dd
Rössing, S.W.A. 2214 Db
Saddle Hill, S.W.A. 1812 Dc
Samangeigei, S.W.A. 1920 Aa
Sandhochte, S.W.A. (Exact locality unknown)
Sandwich Harbour, S.W.A. 2314 Ad

San Remo, S.W.A. 2318 Da
Sarusas, S.W.A. 1812 Cd
Sarusas West, S.W.A. 1812 Cd
Schanzkolk, S.W.A. 2619 Dd
Schirielatz, S.W.A. 2214 Da
Sechomib River E. of dunes, S.W.A. 1812 Ad
Sendelingsdrif, S.W.A. 2816 Bb
Serowe, B. 2226 Bc
Sesriem, S.W.A. 2415 Db
Shimanye, S.W.A. 1718 Da
Sinclair Mine, S.W.A. 2516 Cb
Soebatsfontein, C. 3017 Ba
Sossusvlei, S.W.A. 2415 Cb
Springbok, C. 2917 Db
Springbokvlakte, C. 2817 Ad
Steinkopf, C. 2917 Bc
Stinkfontein, C. 2817 Cd
Stoepjes, C. 3223 Dc
Swakopmund, S.W.A. 2214 Da
Swartmodder, C. 2820 Ba
Swartpoort, C. 2816 Bb
Swemkuil, C. 2923 Ac
S.W.A. - Botswana Border 24°S 2420
Sylvia Hill, S.W.A. 2514 Bb
Tierputs, B. 2221 Aa
Topan Vley, B. 2424 Cb
Torra Bay, S.W.A. 2013 Ac
Touwsrivier, C. 3320 Ac
Tshabong, B. 2622 Ab
Tshane, B. 2421 Bb
Tshipise, Tvl. 2230 Ca
Tsondabvlei, S.W.A. 2315 Cd
Tsondab Plain, S.W.A. 2315 Cc
Tsumkwe, S.W.A. 1920 Da
Tumas Mtns, S.W.A. 2315 Ab
Tuwhe Pan, B. 2420 Ba
Twee Rivieren, C. 2620 Bc
Twilight, S.W.A. 2417 Bb
Twyfelfontein, S.W.A. 2014 Cb
Ubib, S.W.A. 2315 Aa
Ugab River Bridge, S.W.A. 2014 Dd
Uhlenhorst, S.W.A. 2317 Db
Uis, S.W.A. 2114 Bb
Ukwi Pan, B. 2320 Da
Unarus = Ururas?
Union's End, C. 2420 Cc
Unjab River Mouth, S.W.A. 2013 Aa
Upington, C. 2821 Ac
Ururas, S.W.A. 2314 Bd
Vaalpoort, C. 2823 Ac
Vanzylsrus, C. 2622 Cc
Vegkop, S.W.A. 2014 Da
Vergenoeg, S.W.A. 2215 Ac
Verloor = Velloor, S.W.A. 2819 Cb
Victoria West, C. 3123 Ac
Vineta, S.W.A. 2214 Da
Vloorskop, B. 2520 Dd
Voegelfontein, C. 3221 Db
Voigtsgrund, S.W.A. 2417 Cb
Voorloper = Gemsbok, C. 2721 Bd
Vredefontein, C. 2917 Aa
Vrederus, C. 2721 Ad
Vryburg, C. 2624 Dc
Waaihoek, S.W.A. 2616 Ad
Walvisbaai = Walvis Bay, S.W.A. 2314 Ba
Warmbad, S.W.A. 2818 Bc
Wasserfall, S.W.A. 2718 Ba
Waterberg, S.W.A. 2017 Ac
Wegdraai-Middelputs, C. 2620 Cd
Weissenborn, S.W.A. 2616 Ab
Welwitschia Flats, S.W.A. 2214 Db
Westfalenhof, S.W.A. 2216 Ab
Windhoek, S.W.A. 2217 Ca
Wintershoek, S.W.A. 2117 Ab
Witputs Suid, S.W.A. 2716 Da
Wlotzkas Baken, S.W.A. 2214 Ad
Wolferton, C. 2918 Aa
Wolwedans, S.W.A. 2515 Bb
Wortel, S.W.A. 2314 Ab
Xangwa, B. 2022 Ad
Zwart Modder River, C. 2924 Ba

A: Angola
B: Botswana
C: Cape Province
S.W.A.: South West Africa
T: Transvaal

ANNOTATED TAXONOMIC ACCOUNT

The members of the family Gekkonidae are usually small to medium sized lizards and most of the species are nocturnal.

Kluge (1967) recognizes three subfamilies: 1. Eublepharinae, 2. Diplodactylinae, 3. Gekkoninae (two groups).

All the southern African geckos belong to the Gekkoninae and 14 genera are known to occur in this area.

KEY TO THE GEKKONID GENERA OF SOUTHERN AFRICA, AS WELL AS THE SPECIES AND SUBSPECIES OF THE BURROWING GECKOS.

1 Toes webbed. 2
— Toes without web. 3
2 Fingers webbed, digits without adhesive lamellae . . . *Palmatogecko rangei*
— Fingers not webbed, digits with adhesive lamellae . . . *Kaokogecko vanzyli*
3 Digits not dilated, without adhesive lamellae 4
— Digits more or less dilated, with adhesive lamellae 10
4 Digits short, cylindrical, covered above and below with minute scales, clawless in males but toes of females with minute claws (*Chondrodactylus angulifer*) 5
— Digits elongate and strongly clawed 6
5 Ventral scales increase in size laterally; dorsal pattern consisting of more or less angular dark transverse bars; males with a series of prominent, white, dorsolateral spots; angular crossbar on shoulders of females darkest; limbs stout . . . . . *C.a.angulifer*
— Ventral scales decrease in size laterally; back with faint, straight, darkish crossbars; each enlarged tubercle white tipped; no sexual dichromatism; limbs slender . . . . . *C.a.namibensis*
6 Head and body depressed; edge of toes feebly denticulate but not fringed . . . *Narudasia*
— Head short and thick; body cylindrical; toes with a lateral fringe of elongate pointed scales (*Ptenopus*). 7
7 Toes weakly fringed; nasals not swollen; nostril open; peritoneal lining unpigmented . . . . . *P. carpi*
— Toes strongly fringed laterally; nasals more or less swollen; nostril partly closed by internal projection of upper nasal; peritoneal lining usually pigmented 8
8 Fingers depressed, fringed with elongated pointed scales; body scales minute (187–222 around middle) . . . . . *P. kochi*
— Fingers not depressed, edged with pointed triangular scales; body scales usually larger (110–194 around middle) (*P. garrulus*) 9
9 Body scales small (usually more than 160 around middle); dorsally finely mottled to speckled . . . . . *P.g.garrulus*
— Body scales large (usually less than 160 around middle); colour pattern very variable but in its most characteristic form dorsally marked with pairs of large, pale spots alternating with dark blotches; these marks may be partially confluent giving a barred pattern; especially in the southern parts of their distribution usually heavily mottled or spotted . . . . . *P.g.maculatus*
10 Digits each with a strongly developed claw 11
— Digits either clawless or with a minute, inconspicuous, usually retractile claw 15
11 Digits entirely dilated with a single, long, undivided series of transverse, adhesive lamellae; body covered with more or less uniform, small, imbricate scales . . . . . *Homopholis*
— Digits with paired adhesive lamellae 12
12 Digits dilated apically, with paired adhesive plates, which are separated by a longitudinal groove. 13
— Digits cylindrical or compressed apically, more or less dilated a little short of the apex, bearing a series of slightly oblique paired, adhesive lamellae . . . 14

13 Digits with a single pair of distal, adhesive plates . . . . . *Phyllodactylus*
— Digits with two or three pairs of adhesive plates of which the distal pair is separated from the others by a small gap. . . . . *Afroedura*
14 First digit well developed; pupil vertical . . . . . *Hemidactylus*
— First digit rudimentary; pupil rounded . . . . . *Lygodactylus*
15 Digits regularly developed, i.e. more or less of equal size **16**
— Digits very unequal **18**
16 Three or more transverse adhesive lamellae (most distal lamella usually divided) . . . . . *Pachydactylus*
— Two transverse, undivided, adhesive lamellae under each digit (*Colopus wahlbergii*) **17**
17 Dorsal pattern consisting of a vertebral row of large, pale, dark-edged, often more or less confluent spots . . . . . *C.w. wahlbergii*
— Dorsal pattern consisting of a dark-edged, pale, vertebral line which becomes bifurcate on the nape . . . . . *C.w. furcifer*
18 First digit reduced but not rudimentary; most distal adhesive lamella divided; nostril tubular, pierced between three nasals; no femoral pores, preanal pores present or absent . . . . . *Rhoptropus*
— First digit rudimentary; most distal adhesive lamella undivided; nostril not tubular, pierced between first upper labial and postnasal; a long row of femoral pores extends across preanal region . . . . . *Rhoptropella*

A detailed description as well as taxonomic and ecological discussions of the burrowing geckos of southern Africa follows.

A. Genus *PTENOPUS* Gray

Ptenopus Gray, 1865, *Proc. zool. Soc. Lond.* **1865**: 640.
Type species: *Ptenopus maculatus* Gray, 1865.

Stout, small to medium sized, terrestrial, nocturnal geckos, with loud characteristic calls.

Digits free and strongly clawed, with a row of narrow transverse scales ventrally. Fingers compressed or slightly depressed with a lateral fringe of short to elongated spinose scales. Toes depressed and fringed with elongated, pointed scales. Phalangeal formula: manus 2,3,4,5,3, pes 2,3,4,5,4. Head swollen with short, blunt snout; body cylindrical; tail cylindrical, tapering to a fine point. Body covered with small, subequal, smooth, juxtaposed granules or scales. Pupil vertical with straight margins (*Rhoptropus* – type; Underwood, 1954). Extrabrillar fringes very well developed and slightly movable. Preanal sacs present, preanal and femoral pores absent.

Endemic to southern Africa and represented by three species.

DISTRIBUTION: The areas of southern Africa with an average annual rainfall of approx. 250mm or less (Wellington, 1955). Recorded from the southern Kaokoveld, Damaraland, Great Namaqualand, Little Namaqualand, the northern Cape Province and eastwards through all, except the most northern, parts of Botswana into northern Transvaal.

1. *Ptenopus garrulus* (Smith), figs. 1–3.

DIAGNOSIS: A small to medium sized barking gecko which shows considerable geographical variation in size, colour pattern and lepidosis. The fingers have serrated edges, the toes are edged with well developed comb-like fringes and the peritoneum is usually pigmented. The call consists of fewer clicks than that of other species.

POPULATION VARIATION: *Stenodactylus garrulus* was described by Sir Andrew Smith in 1849 from "the sandy parts of the interior of Southern Africa". In 1865 Gray described *Ptenopus maculatus* from Damaraland, but placed it in the family Agamidae. Gunther (1865: 149) was the first to synonymize these two "species" under the older name. Cope (1868) found that for osteological reasons *Ptenopus* is a gekkonid. In 1935 FitzSimons revived *maculatus* as a subspecies of *garrulus* and his view was shared by Loveridge (1947), Mertens (1955, 1971) and Wermuth (1965). The two subspecies were supposed to differ in their colour pattern (vide *maculatus*) as well as in size of the dorsal and ventral scales. Brain (1962a), in his review of the genus, found insufficient evidence to support this and synonymized these two forms again. This was accepted by the author (Haacke, 1964) when comparing the local populations of *Ptenopus* at Gobabeb.

When describing *P. kochi* in 1964, scale counts made under the chin and around the body were used to emphasize the differences between the three species. This proved to be more conclusive than the grouping of the scales according to their small, medium or large size, as used by Brain (1962a). When comparing specimens from south of the Kuiseb River with some from the central Namib gravel plains, a remarkable interpopulation difference was noticed in the size of the interorbital scales.

To study the intraspecific, interpopulation variation, with the purpose of clarifying the status of the previously recognized subspecies, practically all available material from the museums in southern Africa was borrowed. In this way twenty-four samples were obtained. Of each specimen utilized, the number of interorbitals, gulars and scales around the middle were counted. These counts were analysed statistically (Table 1 and fig. 1). To establish the degree of interpopulation difference or relationship, samples from adjacent populations were compared. For each pair of samples the coefficient of difference was established for each of the three different features of the scutellation that were tested (Table 2). Figure 1 clearly shows that the size of the gulars and the scales around the middle vary in direct relation to one another while the interorbitals of several samples vary independently. Therefore when attempting to present these results graphically it was decided to utilize only the data on the gulars and the scales round the middle to provide a clearer picture (Fig. 2). This is different to the original presentation in the thesis where all three aspects were utilized. Samples showing no subspecific differences are joined by a bold black line, which indicates that they could have been drawn from the same population. On the other hand if one of the two utilized characteristics shows a C.D. of 1,28 or higher the other characteristic is indicated by a single thin line, while in the case where both parameters show a C.D. of 1,28 or higher a dotted line joins the two samples to indicate that they have been compared and appear to represent two different populations.

The twenty-four samples of five or more specimens represent the following areas or localities and show the following particulars. The numbers in front of each locality correspond to the numbers in figures 1 and 2 and table 2.

1. Farm Vegkop. According to the late Dr W. J. Steyn (pers. comm.), collector of this series, the substratum consists of red Kalahari-type span.

The scalation, especially around the belly, is finer than is normal for western populations and indicates a strong inclination towards the eastern populations on Kalahari sand. The belly scales are juxtaposed and granular to subimbricate. Although geographically the Gaias (No. 2) sample is closest to that from Vegkop, statistically it shows subspecific differences in all three tested features. Nevertheless these two samples belong to related populations, as they link up through samples 3 and 4, thereby proving a clinal relationship (cf. figs 1 and 2).

In most specimens the dorsal pattern is of clear *maculatus* type, while in a few this is only faintly developed. Surprisingly, the peritoneum of the specimens of this sample, as well as that from the Brandberg (No. 3), is not pigmented. This is unusual for *P. garrulus*.

2. Near Gaias waterhole. These specimens have very large scales, which are imbricate on the belly, and the *maculatus* pattern is well developed. According to the late Dr W. J. Steyn (pers. comm.) they were collected on fairly hard, gravelly soil. The marked differences between this and the Vegkop (No. 1) sample are particularly interesting when viewed in relation to their respective substrata.

3. Brandberg area, mainly from the northern and nort-eastern side of this mountain. Dorsal pattern of normal *maculatus* type. Peritoneum unpigmented, as discussed for the Vegkop (No. 1) sample.

4. Karibib. Mostly dug up from very shallow burrows in hard limey soil, about 5km W. of the village. Typical *maculatus* pattern, with slightly smaller scales, the range of variation of which overlaps that of the fine-scaled Vegkop (No. 1) sample, as well as the large-scaled surrounding western populations.

5. Palmenhorst. This locality lies at the bottom of the Swakop River Canyon, and the specimens were dug up in the coarse, granitic sand of the ravines joining the river. The specimens are large-scaled and have the typical *maculatus* pattern.

6. Central Namib desert. Long series of specimens exist from Ubib, Hotsas and the Tumas mountain, while smaller samples are available from a number of other localities in this area. As these are all very uniform with large scales, which are imbricate on the belly, and the typical *maculatus* markings, the sample from Ubib was used to represent this area in the statistical analysis.

7. Gobabeb S. of the Kuiseb River. Twenty-two specimens from south of the Kuiseb were used in this sample. Although this is one of the longest series of specimens in any of the samples used, they show comparatively little variation, but differ to a surprising extent from the populations north of the river.

No specimens have a HB length longer than 50mm, while this is a common occurrence in adults from the gravel plains north of the river. The interorbital scales are large and flattened and the C.D. for samples 6 and 7 is 1,99, which indicates a 99% symmetrical joint non-overlap. The colour pattern is of basic *maculatus* type, but with a reddish-brown background instead of the darker pattern from the gravel flats, with its prominent black infusions, speckles and dorso-lateral blotches (cf. Haacke, 1964 pl. Va and b). This population apparently has only one type of call, which normally consists of 5 monotonous clicks, while near

Gorob mine two types of call were noticed, of which the monotonous one usually consisted of 6 clicks which followed at a much faster rate (cf. Haacke, 1969).

A group of five juveniles, the scale counts of which fall well within the range of the sample from south of the river, have been kept apart, as their origin is doubtful and they may have been collected on the north bank. Their dorsal markings show slightly more black than specimens of similar size from south of the river and two specimens are marked as having been caught "at the camp site" (Brain, 1959, unpublished field-notes) of the 1959 expedition to that area. This camp was on the northern bank of the Kuiseb River.

Another sample of only four specimens has scale counts and colour patterns corresponding to those from the localities from the central Namib gravel plains. Of these, TM 28619 was collected north of the river by the author and two were again marked as having been collected near the camp (Brain, op. cit.), while the fourth, TM 25980 is only marked "Gobabeb" but, according to the pattern and lepidosis, belongs to the group from north of the river. It is the largest of this group and was quoted as the largest *garrulus* from Gobabeb (Haacke, 1964: 3). However, it is quite distinct from the southern sample, of which all the known specimens are shorter than 50mm.

As no specimens of *garrulus* have been heard or collected by the author yet in the actual bed of the Kuiseb River, the position at Gobabeb appears to be that the Kuiseb River is a distinct barrier between the populations to the north and south of it which is not normally inhabited. However, specimens from southern populations seem to have reached the northern bank where, for example, at the site of the 1959 expedition camp, both forms could be found together and intergrades may be present.

8. Walvisbaai. The sample consists of six specimens which clearly represent two different populations. CR 2080A has large scales and the counts coincide with those of sample No. 7 from south of the Kuiseb River at Gobabeb (Single specimen in No. 8, fig. 1). The colour pattern is also similar. CR 2080B to F, however, have minute scales and the scale counts coincide completely with those from the Kalahari. The colour pattern consists of a mixture of fine reddish, white and black speckles, which is similar to the Kalahari or typical *garrulus* pattern. In the statistical analysis these five specimens were treated as a sample and were compared with the surrounding populations while CR 2080A in fig. 1 is shown as a single specimen on the same level as the other five. This sample poses a particular problem because of its strong affinities with the Kalahari populations. A specimen (CR 3939) with similar characteristics (middle 178, gulars 80) was collected by the author at Sossusvlei.

The following explanations for their presence are possible: (a) An unrecognized sibling species, intermediate between *garrulus* and *kochi,* exists in the interdune spaces of the south-central Namib. (b) Hybrids between the two abovementioned species occur. (c) The Walvis Bay sample is wrongly labelled and was in fact collected in the eastern parts of South West Africa, thus belonging to the typical form, while the specimen from Sossusvlei is an aberrant specimen. This statement appears to be supported by two specimens of *Chondrodactylus a. angulifer* (CR 1030

and 1031), from Rooibank and between Ururas (?) and Walvis Bay, which, according to the label, were collected on the same trip as the controversial *garrulus*. These two specimens are also of the typical or Kalahari form, although in that area the new subspecies described in Part 4 is expected to occur and has actually been collected (cf. Population variation *C.a. angulifer*). (d) The abovementioned specimens are correctly labelled and indicate extraordinary taxonomic conditions existing along the lower course of the Kuiseb River. No definite solution to this problem is possible without further detailed collecting.

9. Lüderitz–Haalenberg area. To obtain a larger sample the specimens from these two localities, which are about 30 km apart, were lumped. Later it was found that the Haalenberg specimens showed a tendency towards larger scales, thus giving lower counts than those from Lüderitz. The colour pattern is reminiscent of the *maculatus* pattern, consisting of alternating black and light blotches as the pale, dorso-lateral ocellate spots are not well developed.

10. Oranjemund area. The specimens of this sample are exceptionally dark and TM 20949 from Oranjemund is probably the darkest of all specimens examined. It is also one of the few specimens examined with a bifurcate tail. The throat of this specimen, as well as that of TM 27716 from 13km E. of Oranjemund, is darkly mottled. The adult from Brandkaross has particularly prominent dark semi-regular blotches (cf. Brain, 1962a, pl. 1a). The scalation is comparatively fine.

11. Goodhouse area. These specimens, which are from Goodhouse, Henkries and Naroep, are all in poor condition. On most specimens the pattern, which consists of dark dorso-lateral blotches, is hardly discernible. The scalation of these specimens is in general very coarse.

12. Little Namaqualand. These specimens, which are from Soebatsfontein, Springbok and Kamaggas, are fairly small (HB length less than 46mm) with a coarse lepidosis. However, they have a mottled, reddish colour pattern similar to the *garrulus* type. In the Port Nolloth area, which is further to the north-west, specimens of similar size occur but have a colour pattern which is so finely speckled that it has a nearly uniform appearance.

13. Keetmanshoop area. Large specimens with average-sized lepidosis and with large irregularly-shaped, but distinctly outlined, dark brown dorsal spots. No light dorso-lateral ocellar spots are present.

14. Karasberg area. Lepidosis comparatively fine. Colour pattern, although reddish, is of *maculatus* type in some specimens, with pale, dorso-lateral spots alternating with dark blotches. Others have dark blotches only or are irregularly speckled with a leaning towards the *garrulus* pattern. This sample is rather heterogeneous, at least as far as colour pattern is concerned.

15. Upington area. Although this sample consists of only five specimens, no two are from the same locality and consequently are rather heterogeneous. Nevertheless they all have the dark-blotched pattern similar to that occurring in the Karasberg-Keetmanshoop area as well as a fairly coarse lepidosis.

16. Douglas area. This sample also consists of specimens from a number of localities. All specimens have a fine lepidosis. Their colour pattern

consists of a finely reticulated network of reddish-brown on a lighter background, with scattered light specks, or of irregular, brown, dorso-lateral blotches on a mottled background. These patterns are considered to be of typical *garrulus* type. No specimen has a HB length of more than 45,5mm.

17. Askham in Kuruman river. In general with very fine lepidosis but, due to larger scales on two specimens (TM 15602, 15615), the range of variation is rather wide. The colour is of *garrulus* type.

18. Twee Rivieren. Fine lepidosis with *garrulus* colour pattern.

19. Kangyane Pan. Lepidosis very fine, especially on the throat which causes an apparent difference between this and other samples of the southern and western Kalahari. The colour pattern is of *garrulus* type.

20. Central Kalahari. This sample includes material collected by Fitz-Simons on the Vernay Lang Kalahari Expedition as well as a few specimens from the Ghanzi area. The lepidosis is very fine and the colour is of typical *garrulus* pattern.

21. Farm De Waal. Although these specimens are all from a relatively small area they show a considerable amount of variation, which is equal to that of samples consisting of specimens from a number of neighbouring localities. This shows that such geographically wide-ranging samples can be acceptable. Ten of these specimens were collected on red Kalahari sand while TM 31617 was found in the bed of the Nossob River which, at that point, is separated from the Kalahari sand by a belt of eroded hills of limey conglomerate, which is between two and five kilometres wide. The presence of this specimen in the river bed is remarkable as the author, who grew up on this farm, had never previously noticed the call or found any specimens in the wide erosion valley. The lepidosis of these speicmens is of medium size and the colour pattern is vaguely reminiscent of *maculatus* type but is reddish-brown with only small indications of the dorso-lateral light blotches. Nevertheless they appear to be of the typical form.

22. Otjiwarongo area. Lepidosis in general very fine. Colour pattern reddish-brown, finely reticulated to speckled, of *garrulus* type.

23. Northern Kalahari, Ngamiland. Lepidosis very fine. Colour pattern finely speckled and reticulated, reddish-brown to brown, of *garrulus* type. The eight specimens are particularly small (max. HB length = 43,5mm). They appear to be mature males as most of them were collected after being located while calling.

24. Northern Transvaal. The colour patterns of all the specimens from Transvaal localities are basically of *garrulus* type consisting of fine reticulations and brownish to white speckles with occasional spot-like concentrations of brown speckles.

Discussion: The results of the counts and calculations are listed in tables 1 and 2 and are graphically presented in figures 1 and 2. The interpretation of the lines in fig. 2 is discussed in the previous chapter. From this figure the following deductions can be made:–

(a) A very uniform group of populations exists in the north-western parts of South West Africa.

(b) A second group of related populations exists in southern South West Africa and the north-western Cape Province.

(c) A third group occurs in eastern South West Africa, northern Cape Province, Botswana and northern Transvaal. Although the samples are

spread over a wide area, which coincides with the distribution of Kalahari sand with less than 500mm mean annual rainfall, they show a surprising degree of homogeneity. A transitional area between groups (b) and (c) exists in the Karasberg–Gemsbok Park area.

When comparing the general distribution of the colour patterns a similar picture presents itself. The typical *garrulus* pattern is restricted to the Kalahari sandveld in the central and eastern parts of the distribution area of this species. Typical *maculatus* is found in north-western South West Africa, while in the southern parts a number of patterns are found which, although not quite typical, are closest to *maculatus* because of their usually bold dark brown to black markings. An exception is the population in the Soebatsfontein–Port Nolloth area, as discussed under sample No. 12, and specimens from farm Gemsbokberg of which the colour is finely speckled to nearly uniform.

The observation that eastern and western populations differ and are distinguishable not only by their colour pattern is further confirmed by studying figure 1, which shows clearly that in general the western populations have larger scales, resulting in low scale counts, while those from the Kalahari sand have finer scales, resulting in higher scale counts. Because of the wide range of variation in most samples a considerable amount of overlap exists, which obliterates any clear-cut borderlines between the eastern and western populations. Nevertheless it can be said that for eastern populations the average number of gulars per sample is higher the 75 and the average number of scales around the middle per sample is above 160. The corresponding averages for western populations lie below these numbers. No such number can be quoted for the interorbitals, as their range of variation is more limited and their size is not always in direct relation to the size of the scales on other parts of the body.

Although there is a remarkable break in the continuity of the western populations, caused by the Kuiseb River, as discussed under sample No. 7, and it can be argued that the populations from north and south of the river at Gobabeb show taxinomically significant differences, a new form has not been described because it can be reasonably assumed that these populations link up across the upper reaches or above the origin of the Kuiseb River. A condition similar to a "Formenkreis" appears to exist in this area, but instead of a ring-shaped distribution these populations occur parallel to each other, separated by the river-bed. The further down-stream the greater the differences become, which ultimately might result in reproductive isolation and speciation. Indications of such possibilities have been mentioned when discussing samples 7 and 8. This problem must be followed up by more extensive collecting in the critical areas.

CONCLUSION: *Ptenopus garrulus* has a blanket distribution. This implies that it occurs practically uninterruptedly over its whole area of distribution, wherever ground suitable for burrowing is available. Although the distribution is relatively continuous, the samples from adjacent areas can show considerable morphological differences which, however, are usually of clinal nature, unless geographical barriers cause a discontinuity, as in the case of the lower Kuiseb River. The variation of the phenotype is usually closely correlated with the variation in the substratum. This is illustrated in the high degree of homogeneity of the population on Kala-

hari sand, in contrast to the more variable western populations, which inhabit a greater variety of substrata. This situation can occur on a smaller scale between two samples, as was discussed for samples No. 1 and 2. As there is a considerable amount of overlap the differences are considered to be clinal. However, as there are two large areas with relatively homogeneous populations, with an apparently narrow belt along which the change from the eastern to the western form occurs, this situation can be described as a step-cline. This transition area roughly coincides with the western border of the Kalahari sand as indicated by du Toit (1954) (figs. 2 and 3). The differences between the western and eastern populations, as discussed above, are considered important enough to make taxonomic distinction between them. The formerly recognized subspecies *P.g. garrulus* in the Kalahari sand and *P.g. maculatus* in the western parts are thus restored. There are indications of more definable populations along the lower Kuiseb and to the south thereof, but due to insufficient and unreliable records no definite conclusions can be reached in this respect.

1a. *Ptenopus garrulus garrulus* (Smith), plates 10 and 11.

Stenodactylus garrulus A. Smith, 1849. Ill. Zool. S. Afr. Rept., Append.: 6.
Ptenopus garrulus part., Boulenger, 1885: 15; Underwood, 1954: 477; Brain, 1962: 3; Kluge, 1967: 30; Pianka, 1971: 1025.
Ptenopus garrulus garrulus, FitzSimons, 1935: 524 and 1943: 12; Loveridge, 1947: 31; Wermuth, 1965: 153.
Ptenopus garrulus maculatus part., Mertens, 1955: 51, pl 5: 16 (San Remo); Mertens, 1971: 44 (Sandfeld).

Type locality: 'Sandy districts of the Interior of South Africa'.

DIAGNOSIS: This subspecies is distinguished from *P.g. maculatus* by its finer lepidosis and by a finely speckled, reddish colour pattern which is comparatively uniform throughout its distribution area. The peritoneal lining is pigmented.

DESCRIPTION: Body elongate, stout, slightly depressed with relatively thick limbs and long toes, hind limbs reach to or beyond elbow when adpressed. Tail cylindrical, thick near the base, tapering to a fine point, not or faintly segmented, varying in length from 61,2 to 76,1 ($\bar{x}$ = 68,9) percra (= percent of rostrum-anus length; Werner, 1971).

Head short and swollen, eye large and bulging, diameter 5,75 percra in ten adults from Kangyane, surrounded by an extrabrillar fringe which is particularly well developed above the eye and can be moved to such an extent that the eye is nearly closed, giving the impression of true eyelids (Bellairs, 1948; Brain, 1962a; Mertens, 1955, pl. 5: 15). Pupil a vertical slit with straight margins (*Rhoptropus*-type, Underwood, 1954). Posterior nasal has an internal, semilunar projection which, depending on its size, obstructs the nostril to a greater or lesser extent. Rostral larger than labials, six-sided, about as broad as high; upper labials six to ten (usually eight to nine); lower labials six to ten (usually eight to nine). Mental about as long as broad with a rounded posterior edge, longer but narrower than adjacent lower labials. Head covered with subuniform, juxtaposed, granular scales of which there are from 36 (rarely fewer) to 49 between the supraorbital ridges; no enlarged chinshields present; chin covered with small, juxtaposed, flat, rounded granules of which from 70

(rarely fewer) to 98 occur in a straight line below eyes. Average number of gulars per sample higher than 75. Number of scales around middle varies from 146 (rarely fewer) to 194, with average per sample higher than 160. Dorsal side of original tail covered with regular, transverse rows of equal-sized, subquadrangular, imbricate scales, larger than those on belly. On the underside they are more pointed and less regular in shape and arrangement. Regenerated tails covered with irregularly arranged and shaped scales.

Tail autotomy can take place anywhere between the tip of the tail and the base. Of 292 preserved specimens 64,7% (189) still had their original tail, 2,4% (7) had tails regenerated from the base while 17,5% (51) had regenerated parts of the tail distally to the base. The rest of the sample was made up of specimens which lost their tails shortly before or during capture or after preservation. Of these, those which lost their tail at the base and those of which the tail broke distally to that position made up 3,4% (10) and 12,3% (51) of the sample respectively. This shows that only 5,8% had lost their tail at the base while 29,8% lost parts further back thereby proving that autotomy in *Ptenopus garrulus* is not confined to the base of the tail. This result differs from Werner's (1964) statement which was based on Brain's (1958) article on desert geckos. In three cases regenerated tails have bifurcate tips.

Brain (1962a: 4) discussed the presence of minute circular pits which appear to enclose minute hairs. The latter are assumed to have a tactile function. The peritonea of all the specimens checked were pigmented.

Sexual dimorphism: In adult males the underside of the base of the tail shows a prominent swelling into which the hemipenes are retracted. A longitudinal row of one to five (usually two) scallop-shaped tubercles, with up-curved tips, occurs on either side of the base of the tail. In females these scales are usually flat and much less conspicuous.

Marked sexual dichromatism exists, as males have a bright sulphur-yellow, roughly heart-shaped area under the throat. In females the throat is white and unmarked as is the rest of the ventrum.

Colour: The basic dorsal colour is a pale reddish- to orange-brown, with brown to dark brown infusions, speckles and reticulations and scattered pale speckles. Although the extrabrillar fringes are very pale to white the head and snout are usually the darkest part of the specimen. The density of the dark dorsal markings varies individually but a certain degree of uniformity is maintained in populations. Dark spots formed by concentrations of the reticulations may occur on the back. Occasionally they are arranged in dorso-lateral rows and are then reminiscent of the *maculatus* pattern, especially if small white spots occur between the large, dark ones. The limbs are irregularly mottled with dark and light speckles and reticulations while the tail is indistinctly banded. Regenerated tails are uniformly light brown. The dorsal colour descends over the lips onto the sides of the lower jaw. The iris is pale buff with reddish-brown dendritic reticulations, which are particularly concentrated in front of and behind the vertical pupil.

A large, vaguely heart-shaped, orange-yellow spot, with the apex pointing forward, occurs on the throat of subadult and adult males. Apart from this mark, the ventra of males and females are immaculately white.

Size: Largest complete specimen and largest male TM 26933 85 (52 + 33)mm, Xangwa. Largest female TM 15601 84,5 (51,0 + 33,5)mm, Askham.

ECOLOGICAL AND FIELD NOTES: A terrestrial, mainly nocturnal inhabitant of areas with Kalahari sand which have an average annual rainfall of about 500mm (20 inches) or less (Wellington, 1955). Only in the Etosha Pan area have specimens been collected in a higher rainfall area. The transitional area between *garrulus* and *maculatus* coincides closely with the western border of the distribution of Kalahari sand as indicated by du Toit (1954). In the southern and eastern parts of its distribution area this subspecies occurs outside du Toit's outlines for Kalahari sand (cf. fig. 3). This can be explained by the fact that the sand has a wider distribution than indicated, and the specimens from Waterpoort and the Tshipise area were definitely collected in typical red Kalahari sand. The area around Kimberley is also typical Kalahari veld, but because of the presence of known rock formations these are indicated on the geological map instead of the soil type.

The preferred habitat is a flat area with fairly compact sand, which is suitable for burrow construction. Actual dunes, such as those occurring in the south-western Kalahari, are avoided and only the interdune spaces are inhabited. A single specimen occurs in each of the self-constructed burrows. The day is usually spent in this burrow, but towards dusk or just after sunset the gecko will appear and take up position at the entrance with about half of its body exposed. During the summer months the males will usually call at dusk, but, especially on overcast days, isolated calls may be heard right through the day. During the winter no vocal activity takes place and it is expected, but has not been confirmed, that *Petenopus* hibernates, at least in the southern parts of its range. The special chapter of the thesis discussing vocal activity has already been published (Haacke, 1969).

The factors influencing the activity of *garrulus* are still completely unknown. For instance, it has been observed that even in summer the openings to their burrows will at times remain blocked with sand for several days and nights. They may also be opened for a short time during the evening and closed again later during the night, while at other times the opening will remain unobstructed continuously for long periods. Vocal activity may cease completely for several weeks during the summer (pers. comm. from Mr E. le Riche, Nossob Camp). For several successive nights one may find no specimens on the surface but suddenly one night they may be encountered in fair numbers. After calling at dusk they may either retire to their burrows as soon as darkness falls or may walk about, apparently in search of food. Specimens have also been noticed abroad without any previous vocal activity that night. Although unusual, occasional specimens may be found walking about on the surface in the late afternoon or during overcast days, when the surface temperature is not very severe.

The structure of the burrows, although varying in detail, follows a certain pattern (Pls 1 and 2). Each burrow has a single opening with a main tunnel, which may reach a depth of as much as 15 inches (approx. 38 cm) (Bradfield in Hewitt, 1935), with from one to six side tunnels, of which usually at least one leads upwards again to just below the surface. The spiral shape and the position of the end directly below the opening.

as described by Bradfield (op. cit.) and repeated by Brain (1962a: 8) for the *maculatus-kochi* complex at Gobabeb, was hardly ever encountered by the author. Instead, it was found that the main tunnel could terminate as much as 60cm from the opening. The entrance is round to oval and from about one and a half to nearly two and a half centimetres in diameter. The first part of the tunnel, from where the gecko surveys the area with part of its body exposed, is horizontally widened. As the males call from here, it has been suggested (Haacke, 1969: 87) that this funnel-shaped part of the burrow acts as an amplifier and contributes to the surprising volume of the call of these rather small geckos. The side tunnels may branch off the main tunnel at any point and may vary in length. Some of these usually lead upwards and have been measured to end from about 2 to 8 cm below the surface. The function of these secondary passages is not quite clear, but they are used as escape hatches when in danger. When digging up these geckos one will usually find them in the end of one of the side tunnels, and often they will suddenly break through the surface from there and try to escape by running away. Another function of these side tunnels may be temperature control. A temperature-gradient is formed, enabling the occupant of the burrow to select the most agreeable spot available. The end of the main tunnel does not necessarily form the deepest point in a burrow, but is found at a lower level than the ends of the side tunnels.

The entrance to the burrow is usually situated in an open, unshaded area, away from tufts of grass and bushes. The amount of shade on the surface above the burrow apparently has a direct influence on the depth of the burrow. Of four burrows which were investigated during October–November 1961 in western Botswana three, which were situated in open, unshaded ground, reached depths of 27, 30 and 35,5cm respectively, while the fourth, which led under a tuft of grass, reached a maximum depth of only 13cm. As the sand surface in that area may reach temperatures which are much higher than the known critical maximum for reptiles it is essential that the burrows reach depths which maintain tolerable conditions. The critical maximum temperature for a single specimen of *garrulus* was was established as being 43,4°C (Stebbins, 1961: 63). The following temperatures were taken at localities in western Botswana:

(a) Xangwa, 18.X.1961, 12h30. No wind.

Air temp. in shade 1m above ground	38,5°C.
Sand surface in unshaded area	56°C.
Sub-surface temperatures at 12cm	35,8°C.
Sub-surface temperatures at 20cm	34°C.
Sub-surface temperatures at 30cm	32,5°C.
Sub-surface temperatures at 35,5cm	31°C.

(b) Tierputs, 10.XI.1961, 12h00. Light breeze.

Air temp. in shade 1m above ground	32,5°C.
Sand surface in unshaded area	55°C.
Sub-surface temperatures at 20cm	30°C.
Sub-surface temperatures at 30cm	29,5°C.

Another excavation made during the same period, but in the morning instead of at midday, indicated that the burrows reach depths

where the temperature remains fairly constant with little fluctuation between day and night.

(c) Tierputs, 5.XI.1961, 08h30. No wind. Hole was closed.

Air temp. in shade 1m above ground	25°C.
Sand surface in unshaded area	31,8°C.
Sub-surface temperatures at 17cm	25°C.
Sub-surface temperatures at 27cm	29°C.

This shows that although the surface is already becoming warmer in the morning sun the underlying layers of sand are still cool from the night, while the lowest part of the burrow has retained a higher temperature from the previous day. The habit of closing the entrance of the burrow with a plug of loose sand probably contributes further to the stabilization of the microclimate in the burrow by reducing circulation and the resulting loss of humidity. The oxygen requirements of this gecko while at rest appear to be very low as it is able to breathe capillary air. This was observed when specimens which had their heads well covered with sand remained in the same position for more than 20 minutes, breathing without obvious difficulty. The burrow could thus remain closed for long periods without any discomfort to the gecko.

These geckos are fairly slow when walking on the surface and can be captured with relative ease when abroad at night. They are not good walkers and will pause frequently, lying flat on their bellies with heads raised. When approached with a lamp at night they may either "freeze" while staring at the lamp or lower their heads with a sideways shaking movement to lie flat on the ground before lying motionless. As they usually match their background colour very well they are effectively camouflaged and are easily overlooked. Occasionally they will try to run away at surprising speed, but are unable to run more than a couple of metres in a spurt. Brain (1962a: 12) describes a threat attitude for this species. The body is raised high off the ground by straightening the legs and the throat is expanded. With further agitation the gecko will open its mouth, hiss and snap its jaws.

While digging, the sand is loosened with the forefoot of one side and is then kicked back with the hindfoot of the same side. After working in this way for some time the gecko switches sides and digs with the legs of other side. The lateral comb-like fringes on the edges of the toes enlarge the surface of the feet considerably. This is advantageous for scooping back the loose sand and may also reduce sinking while walking over a soft surface.

Practically nothing is known about the reproduction of this gecko. Up to now all observations indicate that only males call. This suggests that the call has something to do with reproduction, either by attracting a female or discouraging other males, or both. The marked colour dichromatism in this species, which has been described elsewhere in this study, poses some interesting problems which were discussed by Brain (1962a: 6). The yellow throat of the male apparently acts as a social releaser, which is particularly emphasized during threat. This, however, is only possible if *Ptenopus* is capable of at least some degree of colour vision. As bright colours fade to a shade of grey with reduced light intensity,

colour vision fails soon after sunset. For this reason Brain assumes correctly that if the yellow throat is of importance in courtship this would have to take place during the short period from just before to just after sunset, while it is still light enough to recognize colours. This roughly coincides with the normal period of vocal activity.

A single egg was found at Tshipise on September 2nd, 1962, and when unearthing a burrow at Khutse on January 13th, 1972 three eggs were found. However, some uncertainty surrounds this case since a female *Colopus* has been sharing this burrow for several days. One egg, when accidentally damaged, contained a *Ptenopus* embryo, while the other two failed to hatch which made it impossible to positively identify them. Since burrows were usually located by listening for the call of the males, burrows of females were seldom opened, which accounts for the scarcity of egg records. The smallest neonatus available for this study had a HB length of 23,7mm; it is assumed that this is roughly the minimum size for this gecko and that these specimens had hatched shortly before capture. The ten smallest specimens available from the central and south-western Kalahari with HB lengths of less than 32mm were collected during the months January to April. As some of the specimens collected at the beginning of January had already grown a few millimetres longer than the known minimum size and some of those collected in April were still very close to the minimum, it appears that the young hatch from early summer right into autumn.

The stomach contents of several specimens consisted mainly of termites but the remains of ants, small beetles, Hymenoptera and other small insects were also found. In captivity termites, moths and mealworms are taken (Brain, 1962a). A considerable amount of sand can usually be found in the intestines.

Ptenopus is preyed upon by a variety of predators and *garrulus* has been recorded from the stomach of *Bitis caudalis* (Broadley, 1967, 1972) and two species of *Psammophis* (Brain, 1962a: 9). As the snakes of the last-mentioned genus are diurnal it must be assumed that the geckos were already abroad before dusk. In the south-western parts of its range *garrulus* is preyed upon by the large ground-gecko *Chondrodactylus* and Brain (1962a: 9) suggested that it may be one of the main predators. However, a check of the stomach contents of 25 specimens of *Chondrodactylus* did not show the remains of either *garrulus* or *maculatus*, for which reason it must be considered of less importance than assumed. Remains of *garrulus* are known from owl pellets (Nel & Nolte, 1964: 80) and a specimen was found pinned on an acacia thorn by a shrike at Leeudril. All small carnivores occurring in the same area as this gecko must be considered possible predators as Smithers (1971) found its remains in the stomach contents of the following species in Botswana: African Wild Cat (*Felis lybica*) (p. 125), Bateared Fox (*Otocyon megalotis*) (p. 136) and Genet (*Genetta genetta*) (p. 165) while Broadley (pers. comm.) found it in a Honey Badger (*Mellivora capensis*). Occasionally natural hazards, such as the flooding of normally dry pans or river-beds, can cause havoc, as was observed by Broadley (1967) who collected a long series of drowned specimens at Kangyane Pan.

RANGE: Those parts of southern Africa with an average annual rainfall

of less than 500mm (approx. 20 inches) lying within, and to the east of, those areas which, according to du Toit (1954), are covered with Kalahari sand (Fig. 3).

RECORDED LOCALITIES: Aranos (SW); Askham (F, L, TO); 8 km N.E. of Bokspits, Boshu Boholu Pan (UM); Coen Brits, Colorado Oos (TN); Damara Pan (TO); Deelkraal, De Waal (TN); Douglas (A); 16 km E. of Lake Dow, Drotzky's Cave (UM); Gezelskap (P); 50 km S. of Ghanzi (UM); Gomodimo Pan (F, L, TO); Great Salt Pan (L, TO); Groot Aarpan (P, TN); Groot Kolk (TN); Hoasas (TN, SW); Huisis (SW); Inkboschpan (TN, P); Juliana (TN); Kameelsleep (P, TN); Kangyane Pan, Kanyu (UM); Kaotwe Pan (F, L, TO); Khuis (UM); Khutse Pan (= Kuke Pan) (F, L, TO, TN, UM); Kimberley (L); Koanakha Hills, Kwang Pan, Kwiha (TN); Ky Ky (F, L, K, TO); Leeudril (P, TN); Lower Molopo (K); Mabuasehubi Pan, 17 km S. of Machuma (UM); Madube (SW); Mahlzeit (TN); 75 km S. of Mamono, 250 km S. of Mamono, (UM); Miershoopholte (P); Modder River (F, TO); Namutoni (SW); Niekerkshoop (K); Nog Verder (SW); Nossob Camp (TN); Omatako River (A); Orange River Station (F, L); Oup (= Auob) River (F, L, TO); Quickborn (L); Rietfontein S.W.A. (TN); Rietkuil (SW); San Remo (M); Swartmodder (F, S); Swemkuil (TN) S.W.A. – Botswana border 24°S (UM); Tierputs, 110 km W.S.W. of Tshabong (TN); 11 km S. of Tshabong (P); Tshane (UM); Tshipise, Twee Rivieren, Twilight (TN); 57 km E.S.E. of Ukwi Pan, 33 km N. of Union's End (UM); Vaalpoort (K); Vrederus (P); Vloorskop (UM); Voorloper (P); Vryburg District, Waterberg district S.W.A. (TO); between Wegdraai and Middelputs (A); Wintershoek (SW); Xangwa (TN); Zwart Modder River (L). Unconfirmed auditory reports: Aha Mountains (author); Nata (Mr T. N. Liversidge); Tsumkwe Pan (Mr Hattingh).

MATERIAL EXAMINED: Two hundred and fifty eight specimens.

TRANSVAAL MUSEUM: TM 2804–5 Ky Ky; TM 9517–8 Waterberg dist., S.W.A.; TM 14559–61 Kuke Pan; TM 14562 Gomodimo Pan; TM 14563 Kaotwe Pan; TM 14564 Damara Pan; TM 14952–3, 14955–7 Salt Pan; TM 15600–2, 15604–5, 15607, 15609–11, 15615–6, 15618–9, 15622–3 Askham; TM 20768 Vryburg dist.; TM 24663, 32673–83 Twee Rivieren; TM 26851, 31214–5, 31612–7, 41392–4 Farm De Waal; TM 26914–5 Kwiha; TM 26933–4 Xangwa; TM 27034–5 Tierputs; TM 27431–8, 28502, 30425 Tshipise; TM 28060–2 Farm Swemkuil; TM 28788 Farm Deelkraal; TM 30407–8 Farm Coen Brits; TM 30781–5, 30789–91 Koanakha Hills; TM 32669–72, 37740–3 Leeudril; TM 33285–7, 37630 Schanzkolk; TM 33338 Groot Kolk; TM 33347–57 Nossob Camp; TM 33358 Kwang Pan; TM 37768–77, 37827–8 Kameelsleep; TM 37830–1 Inkboschpan; TM 37967 Mahlzeit; TM 38014–23 Groot Aarpan; TM 38230 Tshipise; TM 39399 Juliana; TM 39489 Colorado Oos; TM 39986–7, 41471–6, 41478, 41488 Khutse Pan; TM 41424–7 Rietfontein, S.W.A.; TM 41724 110 km W.S.W. of Tshabong; TM 42439 Twilight.

UMTALI MUSEUM: UN 823–4 Askham; UM 5478–80 S.W.A. – Botswana Border 24°S; UM 7431–5 16 km S. of Machuma; UM 7436 16 km E. of Lake Dow; UM 7437–40 Kanyu; UM 11278 Khutse Pan; UM 11317–8 Tshane; UM 13193–5 50 km S. of Ghanzi; UM 13817–8 70 km S. of Mamono; UM 14833, 14859–89 Kangyane Pan; UM 14991 240 km S. of

Mamono; UM 15000 57 km E.S.E. of Ukwi Pan; UM 15136, 15186–9 Mabuasehubi Pan; UM 15224–5, 15342 Vloorskop; UM 15362–3, 15401–5, 15424–6 8 km N.E. of Bokspits; UM 15887 Khuis; UM 16302 Drodsky's Cave; UM 22740 Boshu Bohulu Pan.

STATE MUSEUM: CR 1393 a + b Namutoni; CR 2206 Aranos; CR 3175, 3195, 3201, 3886 Farm Hoasas; CR 3343, 3791 Farm Nog Verder; CR 3643 Farm Huisis; CR 3679 Farm Rietkuil; CR 3910 Farm De Waal; CR 4030 Farm Wintershoek; CR 4159 Farm Madube.

KIMBERLEY MUSEUM: Ky Ky (7); Lower Molopo; Niekerkshoop; Vaalpoort.

ALBANY MUSEUM: AM 1967 N.W. Gordonia dist.; AM 2454 between Wegdraai and Middelputs; AM 3992 Douglas; AM 6128 (8) Omatako River.

SOUTH AFRICAN MUSEUM: SAM 3934 Swartmodder.

1b. *Ptenopus garrulus maculatus* Gray

Ptenopus maculatus Gray, 1865. *Proc. zool. Soc. Lond.* **1865:** 640, pl. 38: 1.
Ptenopus garrulus part., Boulenger, 1885: 15; Underwood, 1954: 477; Brain, 1962a: 3; Haacke, 1964: 3; Kluge, 1967: 30.
Ptenopus garrulus maculatus, FitzSimons, 1935: 525 and 1943: 33; Mertens, 1955: 51; Wermuth, 1965: 153; Mertens, 1971: 44.

Type locality: 'Damaraland'.

DIAGNOSIS: In general this subspecies has a coarser lepidosis than the typical form. The colour pattern, which matches the background well and usually consists of large spots or blotches, shows considerable geographic variation. In some localities the peritoneal lining is not pigmented.

DESCRIPTION: Similar to typical *garrulus* but differing in the usually coarser lepidosis and the colour pattern. Scales around middle of the body 116 to 168, gulars 50 to 78 and interorbitals usually from 26 to 42 but in samples 7 to 10, i.e. from the southern Namib (cf. fig. 1) there may be as many as 48. Although a considerable amount of overlap exists, the larger scales produce scale counts which, on an average, are lower than those of typical *garrulus*. Average number of scales per sample around the middle below 160, while that for the gulars is below 75. Except for samples 7 to 9, which were mentioned above and have finer scales, average number of interorbital scales per sample in this subspecies lies below 39 (Fig. 1). Ventral scales, which are larger than in the typical form, are flat, subhexagonal, subimbricate to imbricate and often have a finely serrated posterior edge. Peritoneal lining pigmented, except in specimens from north-east of the Brandberg and from Farm Vegkop.

Sexual dimorphism: As described for *garrulus,* but males from certain localities in Little Namaqualand and the Richtersveld have also a yellow area on the anterior surface of the thigh.

Colour: The colour and pattern are very variable but blend well with the natural background. The *maculatus* pattern in its typical form as described by Gray (1865), occurs only in the area to the north of the Kuiseb River, in particular the central Namib gravel plains. Several variations of this pattern occur, depending on the substratum and the distance from type locality. The typical pattern is as follows: The basic dorsal colour is a pale greyish-yellow, mottled to variegated with brown to black marks.

Five pairs of large subcircular pale dorsolateral spots are usually separated by more or less well-developed black crossbars, which are often disrupted along the vertebral line to form pairs of dorsolateral blotches. Original tails have from six to ten alternating black and white dorsal crossbands, while regenerated tails have irregular dark dorsal markings. Head, limbs and sides of body are marked with irregular white, brown and black speckles. The ventrum is creamy-white.

A large, vaguely heart-shaped, orange-yellow spot, with the apex pointing forward, occurs on the throat of subadult to adult males. Apart from these marks, the ventra of males and females are immaculate.

South of the Kuiseb River a great variety of patterns occur. These usually resemble the colour of the natural background very closely. In most cases some degree of similarity to the typical *maculatus* pattern is maintained. This is mentioned in the discussion of the population variation of the species. The large, ocellar, dorsolateral white spots are either reduced in size or absent, but dark brown to black blotches and speckles usually occur. In the transitional area of this and the typical subspecies, as in the Karasberg area as well as in sandy areas in the southern Namib and Little Namaqualand, the pattern resembles that of the typical form. In such cases the coarse scalation decides the taxonomic affinities. The specimens with the darkest overall appearance occur along the lower course of the Orange River. There the dark mottled markings of the head descend beyond the lower labials onto the sides of the lower jaw and even the throat. Practically uniform light brown specimens occur in the extreme south-west of the range. Males collected in the Richtersveld near Port Nolloth and Annisfontein had yellow areas on the anterior surface of the femur. Specimens from Keetmanshoop area and south thereof into the northern Cape Province usually lack the pale dorsal spots altogether, but have large, irregular-shaped, dark brown, black-edged spots scattered over their backs, while at Farm Gemsbokberg and some sites in the NW Cape Province they are pale beige with a uniformly distributed peppering of fine brown speckles.

Size: On an average, adult specimens of this subspecies attain a larger size than those of the typical form. However, as pointed out above, a large amount of interpopulation variation exists and specimens from Little Namaqualand, the southern Richtersveld and just south of the Kuiseb River are particularly small and adults are as much as 10 mm shorter than adults from most other populations.

Largest specimen and largest female TM 42125 107,1 (62,6 + 44,5)mm, N.W. foot of Brandberg. Largest male CR 4432/9 HB 62,0mm, tail regenerated, Vegkop. Largest complete male, TM 31743 97,0 (58 + 39)mm, Palmenhorst.

Ecological and field notes: This subspecies is an inhabitant of those parts of South West Africa and the northern Cape Province which are within the below 500mm (approx. 20 inch) rainfall zone (Wellington, 1955) but to the west of those parts which are indicated by du Toit (1954) as being covered by Kalahari sand (Fig. 3). In fact, most of the range of this subspecies lies in the below 250mm and even below 125mm mean annual rainfall zone. In the area occupied the substratum varies considerably and is usually of a more compact and harder type than that occupied by the typical subspecies. It varies from clayey and limey soil to coarse or

gritty sand and even fine gravel. However, sandy areas are also inhabited, such as the plains south of the Kuiseb River and other parts of the southern and transitional Namib. It appears that very fine sand and silt are usually avoided as no specimens have been recorded yet in the dry bed of the Kuiseb River and no calls have been noticed, although *P. kochi* is common there. The barrier effect of this substratum has been discussed in the chapter on population variation In contrast to this, in the vicinity of Port Nolloth specimens have been dug from burrows which were actually on low dunes of fine windblown sand. Burrows are usually situated in level open spaces but at Garies they were found on hillsides with remarkably steep slopes.

From rather casual observation it appears that burrows of *maculatus* do not usually reach the same depth and often do not have as many side tunnels as described for *garrulus*. At various localities in the Richtersveld, Little Namaqualand, at Gobabeb south of the river and near Karibib the burrows were rarely deeper than about 130mm. This is not caused by the hardness of the soil as burrows in fine sand, for instance those found near Port Nolloth and at Gobabeb south of the river, were of similar depth to those in hard soil near Karibib, Garies and Nuwerus. To what extent soil temperatures may influence the burrow depth is not clear. A comparison of Weather Bureau records for Ghanzi, Gobabeb and Okiep showed that the highest temperature during a year (1964/65) measured at 10cm below the surface reached just above 40°C in all three cases. However, the average maximum temperature per month at Ghanzi proved to be from one and a half to five degrees higher than those from Okiep and Gobabeb. As the burrows of *g. garrulus* in the Ghanzi area are deeper than those of *maculatus* around Gobabeb and in Little Namaqualand, it appears that the average maximum temperature may have some effect on the depth of the burrow.

Although the depth is apparently not affected, the overall length and the number of side tunnels are certainly greater in an easily workable substratum, such as compact sand. A burrow at Nuwerus in hard soil, which contained an adult male, consisted of a single short tunnel which descended at a steep angle to a depth of about 130mm, while a burrow at Sendelingsdrif, in fine, but compact sand, had six blind side tunnels and a much greater total length.

The dorsal colour pattern usually matches the natural background very well (cf. Haacke, 1964, pl. Va + b). The cryptic effect of these matching colours can be of importance only before darkness settles. The reasons were mentioned in the discussion on the functional significance of the yellow throat of the male of *garrulus*. However, the camouflage effect of a disruptive, but background-matching, pattern on a motionless gecko must be considered to have survival value, even at very low light intensities.

An egg measuring 12,5 x 9,5mm was found on 28 January 1974 in the Namib Park, while juvenile specimens with HB length of less than 32mm have been collected from October to May. This indicates that a similar condition to the one discussed for *garrulus* exists in this subspecies; i.e. that reproductive activity takes place from early summer into autumn. The smallest specimen measured, TM 22659 from Brandkaross, was collected by Dr C. Koch in February 1953 and is 39,2 (23,7 + 15,5)mm long.

The discussion concerning activity rhythm, behaviour and other biological features as described for *garrulus,* also applies to this sub-species in general, but may differ in detail. The observations made by Brain (1962b) at Gobabeb regarding the critical maximum temperatures, burrow structure, behaviour etc. cannot be referred to as it is now known that specimens of the then still unrecognized *P. kochi* were grouped with *P.g. maculatus.*

In general *maculatus* is preyed upon by the same predators as the typical form. It has been recovered from the stomach of *Psammophis leightoni trinasalis* Werner (= *furcatus* Werner, 1910) and *Boaedon fuliginosus mentalis* Günther (Brain, 1962a: 9). A specimen of the snake *Ramphiophis multimaculatus* (A. Smith), apparently containing the original occupant, was dug up from a *Ptenopus* burrow at Annisfontein in the Richtersveld. In captivity both *Bitis peringueyi* (Boulenger) and *B. caudalis* (A. Smith) have taken this gecko quite readily (Brain, 1962a: 9)). *B. cornuta* (Daudin) and *B. schneideri* (Boettger), two further dwarf-adders which occur in part of the range, can also be considered potential predators. *Chondrodactylus* occurs throughout the greater part of the range and occasionally preys on *maculatus* (Brain, 1962a: 9). Owls and small carnivores are rare in the true desert and are only of importance as predators outside this area. The desert golden mole *Eremitalpa granti* (Broom), which feeds on small geckos in capitivity, may also prey on barking geckos in nature.

VOCALITY: Since publishing the report on vocal activity of *Ptenopus* (Haacke, 1969) several additional observations have been made. Counts of the number of clicks per call were made and the number of calls analysed are listed below together with those from the 1969 publication. The order of the localities roughly indicates their relative geographical position from north to south and for comparative purposes the two samples of *g. garrulus* have been included at the end of the list.

NUMBER OF CLICKS PER CALL

Localities	N	1	2	3	4	5	6	7	8	9	10	11	12	13	Range	$\bar{x}$
Fonteine	35					15	19	1							5– 7	5,4
Brandberg . . .	78					4	2	2	6	16	25	13	7	3	5–13	9,7
Kl. Spitzkoppe .	73				4	26	40	3							4– 7	5,6
nr Gorob Mine .	10				1	2	7								4– 6	5,6
Gobabeb	13				2	10	1								4– 6	4,9
Tsondab Plains .	46			2	9	33	2								3– 6	4,8
Tsondabvlei . . .	141				9	61	43	24	4						4– 8	5,7
Springbokvlakte .	55					4	2	31	15	2	1				5–10	7,2
Tsauchab River .	56					3	28	24	1						5– 8	6,4
Rosh Pinah . . .	94	3	59	30	2										1– 4	2,3
Boomrivier . . .	94				16	27	39	12							4– 7	5,5
Grasdrif.	5					3	2								5– 6	5,4
Reuning's Pr. . .	27			5	19	3									3– 5	3,9
Swartpoort . . .	107				4	29	45	21	8						4– 8	6,0
Sendelingsdrif .	111		4	84	21	2									2– 5	3,2
Annisfontein . .	104				34	49	19	2							4– 7	4,9
Daberas	109		2	61	40	5	1								2– 6	3,5
Vredefontein. . .	171			7	48	80	30	4	2						3– 8	4,9
Nuwerus	145				1	4	39	41	45	14	1				4–10	7,0
Nossob Camp . .	241				5	47	110	59	13	6	1				4–10	6,2
De Waal	60			6	42	12									3– 5	4,1

$\bar{x}$ = 5,3

This indicates that the range of variation is greater than previously assumed. The peculiar short call with a strongly emphasized first click from Rosh Pinah and the long monotonous calls from the north-western foot of the Brandberg are particularly outstanding. The average call for *Ptenopus garrulus* and in particular *maculatus* appears to consist of about five clicks

RANGE: South West Africa and the north-western Cape Province, west of those areas covered by Kalahari sand. Possibly extending into the Great Karoo (Fig. 3).

RECORDED LOCALITIES: Abbabis – Nauzerus (K); Aggenys, Alfa (TN); Alt Wasserfall (F, L, TO); Amichab Mountain, Annisfontein (TN); Ariamsvlei, Asab Station, btwn Auros and Klinghardt's Mountains (TN); Aus (L, K, S); btwn Aus and Bethany (F); Awasib (TN); Bergland (SW); Bloeddrif, Brandberg N.E. corner (TN); N.W. of Brandberg, W. of Brandberg 83 km from Uis Mine (SW); S.W. of Brandberg (M); Brandkaross (TN); Chuos Mountains (M); Daberas (TN); btwn Dassiefontein and Noachabeb (F, L. TO); De Hoop, Farquarson, N.W. of Fish River mouth, Fonteine (TN); Gaias (SW); Garies, Gemsbokberg (TN); Goanikontes (M); Gobabeb (TN, SW); Goodhouse (S); nr Gorob Mine (TN); Great Fish River 23 km from Berseba (F, L, TO); Great Karas Mountains (S, TO); Gross Tinkas (TN); Haalenberg (F, L, TO, TN); Henkries (S); Holte, Hotsas (TN); btwn Jakhalswater and Vioolsdrif (S); Jakkalswater (TN); Kakamas (F, L, S); Kalkfontein South (S); Kalksloot Station (TN); Kamaggas (F, L, PE, TO); Karibib (TN); Keetmanshoop (L, A, S, TO); Kenhardt (F, L); Klein Spitzkoppe (TN); Kraaiwater (S); Kuboos (K); Kuibis (F, L); Langer Heinrich, Lekkersing (TN); Louisvale (A); Lüderitz (F, M, L, A, TO); Lucas Vley (TN); Mariental (K); Btwn Mariental and Rehoboth, Marydale (F, L); Nabas (TN); Naroep (S); Narudas Süd (F, L, S, TO); Btwn Nochaben and Kanus (TO); Nuwerus (L, TN); Okahandja (F, A, TO, SW); Onder Swartmodder (TN); Onguati (SW); Oranjemund (TO); 13 km E. of Oranjemund (TN); Otjimbingwe (L); Otjitambi (S); Palmenhorst, nr Pforte (TN); 8 km E. of Port Nolloth (F, L, TO, TN); 8 km N.E. of Port Nolloth, 17 km N. of Port Nolloth (TN); Btwn Port Nolloth and Klipfontein (F, TO); Prieska, Prince of Wales Bay (F, L); Rehoboth (F, L); Riet (TN); Rietfontein, Cape P. (F, L, A); Rooibank (SW); Rosh Pinah, 33 km S.E. of Rosh Pinah (TN); Rössing Mountains (F, L, A, TN); Sandhochte (S); Sarusas (SW); Schanzkolk, Sendelingsdrif, Sesriem (TN); Sossusvlei (M, SW); Soebatsfontein (F, L, TO); Springbok, Springbokvlakte (TN); Btwn Steinkopf and Ramansdrif (S); 25 km N.E. of Stinkfontein, Swartpoort, Tsauchab River 40 km W. of Sesreim, Tsondabvlei, Tsondab Plains, Tumas Mountain, Twyfelfontein, Ubib (TN); Ugab River Bridge, Uis (SW); Upington (S); Vegkop, Vergenoeg (SW); Walvisbaai (M, SW); Warmbad, Welwitschia flats, Westfalenhof (TN); Windhoek vicinity (M); Witputs Suid (TN); Wolferton (S).

Doubtful record: The record from Adendorp near Graaf Reinet is so far removed from all other known records that it is viewed with suspicion. Unfortunately the original specimen, which was deposited in the Port Elizabeth Museum, is no longer available. However, a report of *Ptenopus* calls which were heard in the Middelburg (C.P.) area some years ago

suggests that the range of *P. garrulus* could actually extend into the southern parts of the Great Karoo.

MATERIAL EXAMINED: Four hundred and eight specimens.

TRANSVAAL MUSEUM: TM 3024–5 Alt Wasserfall; TM 3028 btwn Dassiefontein and Noachabeb; TM 3029 Narudas Süd; TM 3458–9 Keetmanshoop; TM 10887 Okahandja; TM 12603 Gt. Karas Mts; TM 15354, 15356–7, 15376, 15634 Nochaben-Kanus; TM 15375, 28340–1 Haalenberg; TM 15379–80, 15382–3, 15637, 15639 Lüderitzbucht; TM 15737, 15952 Soebatsfontein; TM 17804, 17823, 17825 Gt Fish River valley 23 km from Berseba; TM 17983–4 8 km E. of Pt Nolloth; TM 18014–5 btwn Klipfontein and Pt Nolloth; TM 18136 nr Kamaggas; TM 20736–7, 24939, 28977–82 Karibib; TM 20949 Oranjemund; TM 22287 Aggenys; TM 22659, 26456 Brandkaross; TM 23928, 28983–4 Rössing; TM 22982, 34198, 34305–8, 35304 Sendelingsdrif; TM 24992, 25980, 25987, 28619 Gobabeb N. of river; TM 24995, 25041, 25882, 25886, 25891, 28456–63, 28620–4, 31368–70 Gobabeb S. of river; TM 24996, 25042–3, 25989, 25994 Gobabeb possibly N. of river; TM 25024 Sesriem; TM 27214 N.E. of Brandberg; TM 27577 Springbok; TM 27658 Farm Holte; TM 27716 13 km E. of Oranjemund; TM 27766 btwn Auros and Klinghardt's Mtns; TM 27942 25 km N.E. of Stinkfontein; TM 28023–5 Farm Lucas Vley; TM 28043 Kalksloot Station; TM 31342–4 5 km N.N.W. of Gorob Mine; TM 31743–8 Palmenhorst; TM 32062–3 nr Pforte; TM 32122 Amichab Mtn; TM 32161–74 Ubib; TM 32188–97 Hotsas; TM 32242–4 Gross Tinkas; TM 32274–6 Langer Heinrich; TM 32307–10 Riet; TM 32325 Jakkalswater; TM 32687–8 Farm Vergenoeg; TM 32704–13 Tumas Mtn; TM 33287 Warmbad; TM 33779–81 Swartpoort; TM 33990 Nuwerus; TM 33991–7 Garies; TM 34097–9 Farquarson; TM 34108–9 De Hoop; TM 34196–7, 34199 Daberas; TM 34287, TM 34288–91 8 km N.E. of Port Nolloth; TM 35270–5, 35278 Annisfontein; TM 34542 Gobabeb N. of river; TM 35251 17 km N. of Port Nolloth; TM 35265–7 11 km N. of Bloeddrif; TM 35312–4 Nabas; TM 35317 Springbokvlakte; TM 35367–73, 35418–20, 35422–4 Rosh Pinah; TM 35386 Witputs Suid; TM 35417–25 33 km S.E. of Rosh Pinah; TM 35454 16 km N.W. of Fish River mouth; TM 35472 Lekkersing; TM 35485–6 18 km S. of Lekkersing; TM 35673 Westfalenhof; TM 35759 Awasib; TM 36774 Onder Swartmodder; TM 36877–9, 41479–80 Gobabeb S. of river; TM 36895–906, 36909–14, 37177–9 Tsondab Plains; TM 36941–61, 37142–52 Tsondabvlei; TM 36992–5 Tsauchab River 40 km W. of Sesriem; TM 37585 Ariamsvlei; TM 39474–6 Gobabeb; TM 41723 Welwitschia Flats; TM 41801 Asab Station; TM 41894–7 Gemsbokberg; TM 42124–30 Brandberg N.E. corner; TM 42183 Twyfelfontein; TM 42229 Fonteine; TM 42275–80 Klein Spitzkoppe.

SOUTH AFRICAN MUSEUM: SAM 2369 btwn Steinkopf and Ramansdrif; SAM 2552–6 Henkries; SAM 2557 Wolferton or Wolftoon; SAM 2558–9 Sandhochte; SAM 2561–3 Naroep; SAM 1139–40 South Africa; SAM 3498 Kraaiwater; SAM 15952 Upington; SAM 16663 Kalkfontein South; SAM 17298 a + b Otjitambi; SAM 17304 Keetmanshoop; SAM 17730, 17744, 17748 a + b Aus; SAM 18373 Kakamas; SAM 18696–700 Goodhouse; SAM 18702–3 Gt Karas Mountains; SAM 19064, 19068 Jakhalswater – Vioolsdrif.

STATE MUSEUM: CR 1711a+b Okahandja; CR 1965 Gobabeb S. of river; CR 2008 a – c Rooibank; CR 2080 a – f 5 km E. of Walvisbaai; CR 2146 Farm Bergland; CR 2235 Kahn River nr Onguati; CR 2770 Sarusas; CR 3884 a – d N.E. of Brandberg; CR 3928 Ugab River Bridge; CR 3939 Sossusvlei; CR 4010 80 km from Uis W. of Brandberg; CR 4027 N.W. of Brandberg; CR 4421/1–2 Uis; CR 4425 Farm Alfa; CR 4432/1–15 Farm Vegkop; CR 4444/1–3, 4455/1–10 nr Gaias.

KIMBERLEY MUSEUM: Specimens unnumbered. Aus; Ababis-Nauzerus (2); Kuboos; Mariental.

ALBANY MUSEUM: AM 1118 (2) Rietfontein, C; AM 2392 German South West Africa; AM 5332 Keetmanshoop; AM 5381 Lüderitzbucht; AM 6091 Okahandja; AM 6354 Rössing; AM 5279 Louisvale.

PORT ELIZABETH MUSEUM: PEM 1490/8–11 Kamaggas.

SENCKENBERG MUSEUM: SMF 46706–7, 46743, 46842, 49448, 49744, 49843 Sossusvlei.

2. *Ptenopus kochi* Haacke, fig. 4.

Ptenopus kochi Haacke, 1964. *Sci. Pap. Namib Des. Res. Stat.* **25**: 1, pls. I – V.
P. kochi, Mertens, 1971: 45.
Ptenopus garrulus maculatus part., FitzSimons, 1943: 13 (Rooibank only); Mertens 1955: 51 (SMF 45601 5 km E of Walvisbaai on eastern slope of dune).
Ptenopus garrulus part., Brain, 1962a (Various specimens from Gobabeb).

Type locality: Gobabeb on Kuiseb River, central Namib Desert, South West Africa.

DIAGNOSIS: General appearance similar to that of *P. garrulus* but differing therefrom in its slightly larger and stouter shape, much finer lepidosis, depressed toes and fingers fringed by combs of elangated, pointed scales and different colour pattern. The preferred habitat and the call are also characteristic.

DESCRIPTION: In general lepidosis and shape are similar to those of *P. garrulus*, but differ in much finer scalation, swollen nostrils which always have an internal valvular projection, flattened fingers with comb-like fringe of elongated scales along edges and more robust and larger form.

Body covered with minute, flattened scales, numbering 187 to 226 ($\bar{x}$ = 206,9) around middle of body, 78 to 99 ($\bar{x}$ = 85,7) gulars and 42 to 58 ($\bar{x}$ = 49,1) interorbitals. Upper labials 8 to 11, lower labials 8 to 12, no enlarged chinshields present. Nostrils pierced between two swollen nasal scales, which form a prominent, though flattened, protrusion, and are separated from their fellows behind the rostral by a single internasal granule; internal nasal projection always present. Toes and fingers flattened and fringed laterally, with combs of greatly elongated, pointed scales, usually best developed along posterior edge of terminal half of digits. Peritoneal lining pigmented. Tail covered with transverse rows of fine scales and a double row of slightly enlarged ventral scales; length varying from 79,4 to 103,3 percra (N = 35, $\bar{x}$ = 85,8); tapering to a fine tip and autotomizing at any point of its length. Very often only the very tip is lost and has regenerated. Of 61 examined specimens 57,4% still had their original tail, while those of 3,5% were regenerated from the base, 29,6% distally to the base, 8,0% had tails broken and lost at the base while 1,6% had its tail lost distally to the base.

Sexual dimorphism: The postanal region of males is swollen and protrudes slightly on both sides of the tail. On either side of this swelling one to three enlarged, pointed, tubercular scales occur. The postanal region of females is not markedly swollen, but one to three slightly enlarged tubercular scales, which are smaller than in males, occur on either side of the base of the tail.

Marked sexual dichromatism is present. The gular area of adult females is uniformly white, while in males it is bright sulphur-yellow. This colour is less restricted in this species than in either *garrulus* or *carpi* and may spread over the labials onto the side of the snout. The row of lateral spots on the body may also be yellow in males.

Colour: Basic dorsal colour is reddish-brown, with dark brown infusions, speckles or fine reticulations, which are darker laterally. An irregular row of light spots, which may be yellow in adult males, occurs laterally to dorso-laterally on the body. Young specimens are often covered with fine white, as well as dark brown, specks. The dorsal colouring usually extends down over the labials onto the sides of the lower jaw. The tail is usually marked with a dorsal row of light blotches on a darker, mottled background, or may be nearly uniformly light brown, similar to the rest of the body. Regenerated tails are uniformly light brown dorsally. The underside of the body, limbs and tail is white. In adult females all and juveniles the chin and throat are white, while in subadult to adult males they are sulphur-yellow. This colour spreads over the labials onto the sides of the head. The circumorbital ring of scales is white. The iris is brown and marked with dark brown dendritic lines anterior and posterior to the pupil, leaving a lighter area above and below the pupil.

Size: Largest complete specimen and largest male TM 28809 (Holotype) 121,6 (64,8 + 56,8)mm. Largest complete female TM 25947 115,8 (60,8 + 55,0)mm. Largest female TM 28447 HB = 62,8mm, tip of tail lost. All specimens from Gobabeb.

Ecological and Field notes: *Ptenopus kochi* is a terrestrial, nocturnal inhabitant of the fine sand of the interdune spaces and low dunes of the northern half of the southern Namib and its dry river-courses. The preferred habitat is fine sand and specimens have been collected in the silt of the bed and the banks of the Kuiseb River, on the interdune spaces to the south of it at Gobabeb and on low dunes near Walvisbaai and on farms Greylingshof and Weissenborn.

The day is spent in self-constructed burrows, from which they emerge at sunset to take up position at the entrances. From here these geckos keep a look-out for food and the males will call (Figs. 8 and 9). As in the case of *garrulus,* practically nothing is yet known regarding the activity rhythm of this species as no long-term observations have been made. The call and vocal activity have been discussed (Haacke, 1969). In search of food, which consists of small invertebrates such as termites, ants, small beetles, arachnids and others, they will venture away from their burrows. They have not been personally observed on the surface during the day, but Mertens (1955: 51) reports that Dr Scherz noticed a *Ptenopus* specimen at Sossusvlei during the day, after a shower of rain had fallen during the previous night. As *kochi* is the most common barking gecko in that area, it is possible that it was this species which was observed. Their walk is

rather slow and, because of their structure, appears ungainly. They pause frequently, lying flat on their bellies with heads raised. Nevertheless, when in danger, they can run at surprising speed, but also for short distances only. When caught, specimens will usually emit a squeak and bite. Defensive behaviour as described by Brain (1962a) for *garrulus* and *carpi* has not yet been observed in this species.

The burrow structure is similar to that of *garrulus,* but is more elaborate and extensive. At Gobabeb, where most of the specimens were collected by digging up the burrow, these burrows reached a depth of as much as 40cm and the end of the main tunnel was often from 75 to 90cm from the entrance. Owing to the relatively soft substratum the area around the entrance usually caves in to some extent and forms a slight funnel-like depression (Haacke, 1969: 85). Several blind side-tunnels branch off from the main tunnel and lead up to just below the surface and in many cases when the burrow was disturbed the occupant has tried to escape by breaking the surface and running away. Burrowing is performed in the usual gecko fashion, as described for *garrulus.* The large surface area of the fringe-lined fingers of *P. kochi* enables this species to burrow in fine sand. This habitat, in its extreme form such as the silt deposits in the bed of the Kuiseb River and the lower slopes of actual dunes, is avoided by both other known species of barking gecko. Another anatomical feature which makes this species more suited to life in fine sand is the internal valvular projection of the nostril which, by closing the nostril, prevents the entry of sand. Although it appears that the nostril cannot be closed voluntarily it has been noticed that external pressures on the nasal swellings will close the nostril completely. This mechanism would come into action when the gecko closes its hole with sand by pushing forward with its snout or when it tries to harden the tunnel walls by tapping them with its head, as has been observed in a terrarium.

Practically nothing is known about the reproduction of this species. It is assumed that the calls of the males attract the females, as discussed for *garrulus.* This would indicate that mating could take place during most of the summer months. A single egg, measuring 14,5 x 10,5 mm, was found in a burrow at Gobabeb on 20 September 1965. This egg was at a depth of only 10cm below the surface. The smallest juvenile available (CR 4095) was collected during November at Farm Weissenborn and measures 46,5 (25,0 + 21,5)mm. The next in size is TM 20717, which is 51,5 (29,2 + 22,3)mm long. It was collected in October 1941 by Dr Austin Roberts and, in South African collections, is the first specimen of this species ever to be collected, but was not recognized as such until this investigation. From these very scanty observations it appears that eggs may be laid early in spring and that the young hatch during early summer.

P. kochi has not yet been recorded from the stomach of any snake. However, as it has been taken in terraria, it can be assumed that it is preyed upon by the various adders occurring in its range, such as *Bitis caudalis, B. peringueyi* and to a lesser extent *B. cornuta* and *B. arietans.* Other snakes, such as *Ramphiophis multimaculatus* (A. Smith) and the diurnal *Psammophis* species are also possible predators. In certain areas *Chondrodactylus angulifer* occurs sympatrically with *kochi,* and may occasionally prey on it. Remains of *Ptenopus,* which can be assumed to be *kochi,* were found in owl pellets

at Sossusvlei. The various small carnivores occurring mainly along the dry river beds can also be counted as possible predators.
Natural hazards, such as floods of the rivers, as observed by Koch (1963) at Gobabeb, can cause the death of many specimens by drowning.

VOCALITY: Since the publication of the paper on the vocality of barking geckos (Haacke, 1969) no further information on this species was obtained.

RANGE: The dunefields of the south-central Namib desert (Fig. 4).

RECORDED LOCALITIES: Gobabeb (TN, SW); Greylingshof, Koichab Pan, Rooibank, Sandwich Harbour (TN); Sossusvlei (M, TN, SW); Tsauchab River 40km W. of Sesriem, Tsondabvlei, Ururas (TN); Walvisbaai (M, SW); Weissenborn, 15km W. of Wolwedans (SW); 8km S. of Wortel (TN).

MATERIAL EXAMINED: Seventy-nine specimens.

TRANSVAAL MUSEUM: TM 20717, 25885, 25888 Rooibank; TM 24993–4, 25880–1, 25883–5, 25887, 25889–90, 25947, 28625–7, 28442–55, 28809, 30198–200, 31367, 32334, 39471–73, 41481 Gobabeb; TM 28388 Farm Greylingshof; TM 29666 Sandwich Harbour; TM 31651–6 Sossusvlei; TM 32040–2 8 km S. of Wortel; TM 36863–5 Ururas; TM 36918–21, 36940 Tsondabvlei; TM 36988–91 Tsauchab River 40km W. of Sesriem; TM 37136–7 Koichab Pan.

STATE MUSEUM: CR 2081, 2944 a + b Walvisbaai; CR 2676, 2759, 2768, 2816 Gobabeb; CR 3913, 3994 A – D Sossusvlei; CR 4095 Farm Weissenborn; SM 5189 15km W. of Wolwedans.

SENCKENBERG MUSEUM: SMF 45601 5km E. of Walvisbaai.

3. *Ptenopus carpi* Brain, fig. 4.

Ptenopus carpi Brain, 1962. *Cimbebasia* **1**: 14, pls 1b, c & e, fig. 1b.
P. carpi, Haacke, 1964: 3, pls IIb, IIIc, IVc, Vd; Wermuth, 1965: 153; Mertens, 1971: 44.

Type locality: Gobabeb on Kuiseb River, South West Africa.

DIAGNOSIS: General appearance similar to *P. garrulus* and *P. kochi,* but differing from them in its slightly slimmer body, longer and more slender legs and coarser lepidosis. Compressed fingers without a fringe of elongated scales while fringe along edge of toes is only poorly developed. Nasals not swollen and nostrils open without internal projection. Peritoneal lining unpigmented and colour pattern and call, as well as preferred habitat, are characteristic.

DESCRIPTION: Superficially of similar appearance and scalation to *garrulus* and *kochi,* but differing from both on points mentioned under diagnosis. In relation to short and swollen head, body and limbs appear more slender than in other species. Eyes large and bulging, varying from 7,2 to 8,4 ($N = 27$, $\bar{x} = 7{,}9$) percra in adults. Limbs longer in relation to body length (Brain, 1962: 17). Lepidosis rather coarse, especially on the body, where it consists of rounded, flat to granular scales. Ventral scales very variable in shape and size, may be oval, pointed to subhexagonal, juxtaposed and subimbricate to imbricate. Number of scales around middle varies from 105 to 131 ($\bar{x} = 117{,}4$), while the variation in the gulars is 58 to 74 ($\bar{x} = 65{,}1$) and in the interorbitals is 36 to 50 ($\bar{x} = 43{,}1$).

Upper labials 8 to 11, usually 10; lower labials 9 to 14, usually 12; no enlarged chinshields present; mental and rostral without notches and larger than adjacent labials. Nostril pierced between two (three in one case) nasal scales, which are usually not swollen. Nasals separated from their fellows by enlarged internasal (occasionally two or more smaller scales) in contact with rostral. Nostril usually completely open, but in a few specimens posterior nasal has a poorly developed internal projection. Fingers compressed, slender with a serrated edge formed by a row of short, pointed, triangular scales. Toes slender with a poorly developed fringe of elongated, pointed scales, best developed along posterior edge of distal half of digits. Tail slender, tapering gradually, ending in a rather blunt tip and covered with fairly regular, transverse rows of flattened to elongate, subimbricate scales. Regenerated tails covered with irregular, rounded, subimbriate scales. Tail length varying from 63,3 to 76,6 ($N = 30$, $\bar{x} = 71{,}3$) percra. Tail or part thereof can be shed at any point. Of 46 specimens 73,9% still had their original tails, 17,4% had the tail regenerated while the tails of another 6,5% were lost from a point distally to the base and only a single specimen (2,2%) had its tail broken at the base and lost. Peritoneal lining unpigmented.

Sexual dimorphism: Postanal region of males swollen and protruding slightly on both sides of tail. On either side of this swelling is a row or cluster of three to seven large, and often some smaller, pointed, tubercular scales. Postanal region in females not markedly swollen and enlarged scales, if present, very reduced in size.

Marked sexual dichromatism was described for this species by Brain (1962: 15), who collected the type series during May 1959. Males had a yellow throat, but in females it was white. However, females collected during October 1963 had a similar heart-shaped mark on the throat to that of the males, only smaller. In a female collected at Rocky Point in October 1965 the heart-shaped mark was mesially bisected and consisted of two oblong elliptical spots. These differing observations suggest that females may undergo seasonal colour changes. No subsequent observations were possible to solve this problem.

Colour: The basic dorsal colour is creamy white with fine orange-brown speckles and reticulations. The back is marked with three to five dark brown crossbars which range from the neck to the base of the tail. The tail is marked with five to nine similar transverse bands, but unmarked when regenerated. The limbs are usually creamy white with orange-brown speckles, but may also be marked with dark grey blotches. The supra-orbital area is blue-grey, due to the dark eyeballs showing through the skin. The ventrum is white, with a heart-shaped yellow mark on the throat. This mark is absent in juveniles and appears to be seasonal in adult females. The iris is pale buff marked with reddish-brown dendritic lines anterior and posterior to the pupil, leaving a lighter area above and below the pupil.

Specimens from the northern Namib are much darker with an overall dusky appearance. The dark crossbands have no clear edges and are much wider and tend to fuse on the side of the body, thereby giving the effect of light crossbands on a dark background. The dorsal side of the head is also dark.

Size: Largest specimen and largest female TM 25971 104,4 (60,4 + 44,0)mm. Largest male TM 25966 102,5 (59,0 + 43.5)mm. Both are paratypes from Gobabeb.

ECOLOGICAL AND FIELD NOTES: A terrestrial, nocturnal inhabitant of the gravel plains of the northern Namib desert, an area with an average annual rainfall of less than 125mm (approx. five inches) (Wellington, 1955). In the south the range terminates abruptly on the northern bank of the Kuiseb River, while the other borders, except along the coast, are not yet clearly defined. All localities from whence this species has been recorded have an altitude of 571 metres (less than 2 000 feet) above sea level (Wellington, 1955) and lie within the fog belt of the Atlantic coast.

The preferred habitat is flat to gently undulating gravel plains, such as those found to the north of the Kuiseb River. Apart from occasional rocky outcrops, granite boulders or hills, these flats are very exposed and usually devoid of vegetation. After the rare thunderstorms in the Namib a sparse cover of short grass will appear for a few weeks in those areas which are more than about 30km from the coast. No grass grows near the coast but xerophytic shrubs such as Arthraerura leubnitzae and others occur. The coastal fogs are a common occurrence and contribute to the surprisingly high relative humidity of the desert nights.

This gecko has not been found in similar concentrations as *garrulus* and *kochi*, which accounts for the scarcity of field observations and the lack of biological and ethological data. As calls, attributed to this species, have been heard at sunset, at the same time as the other species were calling, it is assumed that its general behaviour is similar to that of those species.

A burrow containing a single subadult male reached a depth of 25cm and terminated approximately 28cm from the entrance. It had two blind side passages and was made in extremely hard soil (Brain, 1962a: 16). The author has not yet succeeded in locating an occupied burrow, but a few burrows attributed to this species were found on the gravel plains north of Gobabeb. These were comparatively shallow, short and had fewer side tunnels than the burrows of *kochi* found south of the Kuiseb River.

Practically nothing is known about the activity rhythm of this species. Although Brain (1962a) collected a good series during May 1959, subsequent collectors have found only odd specimens or none at all at various times of the year. As no *Ptenopus* calls are heard at Gobabeb during the winter months it appears that the seasonal activity of *carpi* is similar to that of the other species.

P. carpi has been collected only at night. Their normal gait is fairly slow. When approached with a lamp they will sometimes "freeze" in a standing position, but more often will sink to the ground with a sideways shaking of the body and then lie motionless. Because of their cryptic colouring they are then well camouflaged and difficult to detect. When disturbed they will sometimes try to escape by running at a surprising speed, but for a short distance only. At times this gecko will assume a characteristic threat attitude, which was described by Brain (loc. cit.). When disturbed the gecko raises its body high off the ground by straightening its legs, at the same time the throat is expanded, thereby displaying the yellow markings, if present. In extreme threat the mouth is opened

(cf. Brain, 1962a, pl. 1c), the gecko hisses, snaps its jaws and may bite at the cause of agitation.

The activity range of the type series extended between 10,2° and 19,0°C, of which the minimum is a surprisingly low temperature for reptiles. The mean critical maximum for six specimens was established as 42,7°C, while panting started at a mean of 34,8°C (Brain, loc. cit.).

Digging is performed in the same manner as that described for *garrulus*. The short fringes of the toes appear to be quite adequate for digging in the harder substratum of the gravel plains and appear to be an adapation to this habitat. Similarly, the longer legs of this species appear more suitable for life on the rougher, more uneven surface of the gravel plains than the thick, short ones of *garrulus* and *kochi*.

Apart from the fact that the females collected during October 1963 at Gobabeb each contained two well developed eggs and that all four specimens collected near Gemsbokbron in April 1965 were juveniles nothing is known about the reproduction.

The stomach contents of a number of specimens consisted of ants, termites, small beetles, fish-moths and the remains of other small unidentifiable insects. A surprising amount of sand was found in the digestive tract. Some specimens contained parasitic threadworms.

The natural enemies have not yet been established but are probably very similar to those preying on *P.g. maculatus*. *Bitis caudalis, B. arietans* and *Rhamphiophis multimaculatus* are the most likely snake predators. *Chondrodactylus* may occasionally take a specimen. The effect of predation by owls and small carnivores must be negligible because of the very inhospitable biotope occupied by this species, which is avoided by these predators, except near large rock outcrops and dry river beds, which offer shelter to them.

VOCALITY: Since the paper on the vocality of barking geckos appeared (Haacke, 1969) vocal activity of a barking gecko was noted at Ururas on the gravel flats north of the Kuiseb River. The calls consisted of, as previously described, a monotonous series of clicks uttered at a very slow but constant repetition rate and with a rather low pitch. These calls were heard after dark so that no specimens were actually observed while calling *Ptenopus kochi* was heard calling at the same time and specimens were found walking on the surface when visiting the dry river bed later in the evening. However, on the gravel plain where these peculiar calls were heard, no *P. garrulus maculatus* were either seen or heard although several specimens of *P. carpi* were collected while active on the surface. It is thus considered safe to assume that these calls were uttered by the species under discussion. Since no tape recorder was available only the number of clicks per call were counted. From the results listed below it appears that the call is more variable than that of other *Ptenopus* species. It consists of as many as 20 clicks and because of the slow repetition rate also lasts longer. Although the number of clicks of 57 calls were counted the number per call varied fairly evenly over the whole observed range from three to 20 clicks without any noticeable preference. This indicates that *P. carpi* has a much less specific call than the other species and that a considerably larger sample has to be analysed before a clear picture can emerge.

Calls of *P. carpi* at Ururas. Clicks per call in brackets: 4(3) 2(4) 2(5) 2(6) 2(7) 3(8) 2(9) 4(10) 3(11) 4(12) 6(13) 1(14) 4(15) 5(16) 3(17) 6(18) 3(19) 2(20). Range = 3 to 20, $\bar{x}$ = 12,2.

RANGE: The gravel plains of the central and northern Namib Desert from the Kuiseb River in the south to at least as far north as Rocky Point (Fig. 4).

RECORDED LOCALITIES: Cape Cross, nr Gemsbokbron in Unjab River (SW); Gobabeb, Hentiesbaai, Omaruru River Mouth, Rocky Point, 33km N.W. of Rooibank on road to Walvisbaai (TN); 17km E. of Sarusas West (SW); Swakopmund, Ururas (TN); Vineta (SW).

MATERIAL EXAMINED: Fifty-seven specimens.

TRANSVAAL MUSEUM: TM 25966–79, 25981–6, 25990–3, 25997–8, 26207, 28614–8, 32332–3 Gobabeb; TM 31463 Rocky Point; TM 32327–8 33km N.W. of Rooibank on road to Walvisbaai; TM 36375 Omaruru River Mouth; TM 36838–9 Swakopmund; TM 36854–61 Ururas; TM 39917 Hentiesbaai.

STATE MUSEUM: CR 2166 Vineta; CR 2581 Cape Cross; CR 3956 17km E. of Sarusas West; CR 4470/1–4 nr Gemsbokbron.

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TABLE 1. Statistical data of samples checked: (a = gulars, b = interorbitals, c = scales round middle).

Locality		N	Range	Mean	S.D.	S.E.
Kamaggas area	(a)	8	60– 75	65,8	4,87	1,72
	(b)	8	31– 37	34,0	1,85	0,65
	(c)	8	125–140	134,6	5,04	1,78
Pt. Nolloth area	(a)	4	69– 73	71,5	—	—
	(b)	4	36– 42	40,0	—	—
	(c)	4	139–147	144,0	—	—
Goodhouse area	(a)	12	55– 68	61,8	3,45	1,00
	(b)	12	33– 40	36,1	2,23	0,64
	(c)	10	116–141	129,7	9,36	2,96
Pofadder–Kakamas	(a)	3	58– 65	61,3	—	—
	(b)	3	34– 37	35,7	—	—
	(c)	3	133–139	136,7	—	—
Oranjemund area	(a)	5	67– 75	70,2	3,63	1,63
	(b)	5	34– 47	38,4	5,86	2,62
	(c)	5	140–163	150,8	9,94	4,43
Lüderitz–Haalenberg	(a)	9	59– 76	68,0	6,48	2,16
	(b)	9	38– 47	42,4	3,17	1,06
	(c)	9	131–152	143,4	6,60	2,20
Gobabeb, S. of river	(a)	22	50– 63	56,9	3,67	0,78
	(b)	22	40– 47	43,1	2,13	0,45
	(c)	22	120–144	131,2	6,27	1,34
Gobabeb, possibly N. of river	(a)	5	54– 57	55,4	1,34	0,60
	(b)	5	40– 45	42,2	1,92	0,86
	(c)	5	127–135	131,5	3,61	1,61
Gobabeb, N. of river	(a)	4	52– 66	56,5	—	—
	(b)	4	31– 34	32,5	—	—
	(c)	4	122–140	131,0	—	—
Rooibank	(a)	3	59– 63	61,0	—	—
	(b)	3	34– 42	38,0	—	—
	(c)	3	125–152	136,0	—	—
Walvis Bay	(a)	1	65	—	—	—
	(b)	1	47	—	—	—
	(c)	1	136	—	—	—
Walvis Bay (?)	(a)	5	81– 93	87,0	4,42	2,21
	(b)	5	40– 45	42,8	1,93	0,96
	(c)	5	170–177	173,4	2,70	1,35
nr Gorob mine	(a)	3	51– 55	53,0	—	—
	(b)	3	31– 37	33,3	—	—
	(c)	3	110–121	117,3	—	—
nr Tumas Mtn	(a)	10	51– 59	54,7	2,76	0,87
	(b)	10	27– 34	30,5	2,68	0,85
	(c)	10	112–131	123,9	5,78	1,83
Hotsas	(a)	10	50– 58	54,9	3,00	0,95
	(b)	10	29– 35	31,4	2,01	0,64
	(c)	9	116–127	121,9	3,95	1,32
Ubib	(a)	14	50– 59	55,0	2,69	0,72
	(b)	14	28– 38	31,9	3,51	0,94
	(c)	14	120–144	129,3	6,34	1,69
Palmenhorst	(a)	6	58– 63	60,7	2,25	0,92
	(b)	6	28– 34	31,7	2,28	0,93
	(c)	6	120–135	128,5	5,65	2,31
Vergenoeg	(a)	2	53– 56	54,5	—	—
	(b)	2	28– 29	28,5	—	—
	(c)	2	124–134	129,0	—	—

Locality		N	Range	Mean	S.D.	S.E.
Karibib	(a)	9	58– 68	63,8	4,55	1,52
	(b)	9	28– 38	30,1	3,44	1,15
	(c)	9	128–152	141,1	7,99	2,66
Brandberg area	(a)	7	55– 65	58,7	3,64	1,37
	(b)	7	31– 37	34,3	2,14	0,81
	(c)	6	132–148	140,8	6,01	2,46
nr Gaias	(a)	12	52– 62	58,1	2,78	0,80
	(b)	5	26– 32	30,2	2,49	1,11
	(c)	12	116–138	128,9	7,69	2,22
Vegkop	(a)	15	64– 77	69,6	4,15	1,07
	(b)	8	34– 41	37,1	2,80	0,99
	(c)	15	137–168	156,4	7,75	2,00
Sarusas (most northern record)	(a)	1	60	—	—	—
	(b)	1	32	—	—	—
	(c)	1	137	—	—	—
Otjitambi	(a)	2	57– 63	60,0	—	—
	(b)	2	30– 30	30,0	—	—
	(c)	2	142–150	146,0	—	—
Namutoni	(a)	2	80– 82	81,0	—	—
	(b)	2	37– 39	38,0	—	—
	(c)	2	172–183	177,5	—	—
Keetmanshoop	(a)	5	60– 72	67,2	4,60	2,06
	(b)	5	31– 41	36,0	4,00	1,79
	(c)	5	142–147	144,5	1,82	0,81
Karasberg area	(a)	9	65– 78	71,9	4,01	1,34
	(b)	9	32– 42	37,2	3,15	1,05
	(c)	8	135–159	149,0	8,23	2,91
Upington area	(a)	5	56– 76	67,2	7,60	3,40
	(b)	5	34– 40	36,0	2,41	1,08
	(c)	5	141–158	152,0	2,18	0,97
Askham	(a)	15	72– 89	79,7	4,60	1,19
	(b)	14	37– 49	44,4	3,34	0,89
	(c)	15	147–180	165,2	8,99	2,22
Twee Rivieren	(a)	12	75– 85	78,5	2,61	0,76
	(b)	12	37– 49	43,1	3,09	0,89
	(c)	12	157–174	166,4	6,23	1,80
De Waal	(a)	14	72– 81	77,4	2,72	0,76
	(b)	14	34– 45	40,0	2,86	0,79
	(c)	14	153–175	165,2	7,56	2,10
Otjiwarongo area	(a)	10	75– 96	82,6	6,22	1,97
	(b)	10	39– 46	43,6	2,01	0,64
	(c)	10	168–193	176,6	7,84	2,61
Northern Kalahari	(a)	12	77– 91	82,7	4,14	1,20
	(b)	12	36– 45	41,6	2,64	0,76
	(c)	12	169–190	177,1	6,49	1,87
Central Kalahari	(a)	8	80– 91	86,0	3,21	1,13
	(b)	8	38– 48	42,8	3,41	1,21
	(c)	8	166–186	178,3	7,25	2,56
Douglas area	(a)	7	70– 81	76,1	4,22	1,59
	(b)	7	40– 48	44,2	2,87	1,08
	(c)	7	159–180	166,4	6,90	2,61
Kangyane Pan	(a)	32	82– 98	89,4	4,32	0,76
	(b)	32	38– 46	43,3	2,54	0,45
	(c)	32	160–194	179,9	7,42	1,31
Northern Transvaal	(a)	15	73– 93	82,2	4,98	1,29
	(b)	15	34– 47	40,5	2,77	0,72
	(c)	15	164–184	174,8	6,28	1,62

TABLE 2. Coefficient of difference between various populations of *Ptenopus garrulus* (cf. Fig. 2).

The conventional level of subspecific difference is 1,28 which indicates a 90% joint non overlap.
O = below the level of conventional subspecific distinctness.
X = at or above the level of conventional subspecific distinctness.

Localites		Gulars	Interorbs	Scales round middle
1. Vegkop	– 2. nr Gaias	1,66 X	1,30 X	1,77 X
„	– 3. Brandberg	1,40 X	0,57 O	1,13 O
„	– 4. Karibib	0,67 O	1,12 O	0,97 O
„	– 22. Otjiwarongo	1,25 O	1,35 X	1,30 X
„	– 23. N. Kalahari	1,57 X	0,83 O	1,45 X
2. nr Gaias	– 3. Brandberg	0,02 O	0,88 O	0,87 O
„	– 5. Palmenhorst	0,52 O	0,31 O	0,03 O
3. Brandberg	– 4. Karibib	0,62 O	0,75 O	0,02 O
„	– 5. Palmenhorst	0,40 O	0,45 O	1,06 O
„	– 22. Otjiwarongo	2,50 X	2,39 X	2,54 X
4. Karibib	– 5. Palmenhorst	0,46 O	0,28 O	0,92 O
„	– 6. C. Namib	1,24 O	0,07 O	1,25 O
„	– 21. De Waal	1,87 X	1,57 X	1,55 X
„	– 22. Otjiwarongo	1,75 X	2,47 X	2,24 X
5. Palmenhorst	– 6. C. Namib	1,15 O	0,03 O	0,07 O
„	– 7. Gobabeb S. of river	0,64 O	2,59 X	0,30 O
„	– 8. Walvis Bay?	3,94 X	2,64 X	5,38 X
6. C. Namib:	– 7. Gobabeb S. of river	0,30 O	1,99 X	0,15 O
„	– 8. Walvis Bay?	4,44 X	2,00 X	4,83 X
„	– 9. Lüderitz–Haalenberg.	1,44 X	2,04 X	1,20 O
„	– 13. Keetmanshoop	2,65 X	0,82 O	2,72 X
„	– 21. De Waal	4,14 X	1,27 O	3,02 X
„	– 22. Otjiwarongo	2,44 X	2,79 X	3,87 X
7. Gobabeb S. of river	– 8. Walvis Bay?	3,72 X	0,07 O	5,27 X
„	– 9. Lüderitz–Haalenberg.	1,09 O	0,13 O	0,95 O
„	– 13. Keetmanshoop	1,23 O	1,16 O	1,65 X
„	– 21. De Waal	3,21 X	0,62 O	2,29 X
„	– . Gobabeb N. of river?	0,30 O	0,22 O	0,03 O
8. Walvis Bay?	– 9. Lüderitz–Haalenberg.	1,74 X	0,08 O	6,45 X
9. Lüderitz–Haalenberg	– 10. Oranjemund	0,12 O	0,52 O	0,30 O
„	– 11. Goodhouse	1,17 O	1,27 O	1,15 O
„	– 12. Kamaggas	0,20 O	1,67 X	0,76 O
„	– 13. Keetmanshoop	0,07 O	0,89 O	0,14 O
„	– 14. Karasberg	0,28 O	0,82 O	0,38 O
10. Oranjemund	– 11. Goodhouse	1,21 O	0,19 O	1,09 O
„	– 12. Kamaggas	0,52 O	0,59 O	1,01 O
„	– 13. Keetmanshoop	0,36 O	0,24 O	0,58 O
„	– 14. Karasberg	0,22 O	0,13 O	0,90 O
„	– 15. Upington	0,28 O	0,29 O	0,10 O

Localities		Gulars	Interorbs	Scales round middle
11. Goodhouse	– 12. Kamaggas	0,49 O	0,51 O	0,34 O
„	– 13. Keetmanshoop . .	0,68 O	0,01 O	1,33 X
„	– 14. Karasberg	1,37 X	0,21 O	1,10 O
„	– 15. Upington.	0,59 O	0,02 O	1,93 X
12. Kamaggas	– 15. Upington.	0,12 O	0,47 O	2,41 X
13. Keetmanshoop	– 14. Karasberg	0,55 O	0,17 O	0,44 O
„	– 15. Upington.	0,00 O	0,00 O	1,90 X
„	– 17. Askham	1,36 X	1,14 O	1,74 X
„	– 18. Twee Rivieren . .	2,42 X	1,00 O	2,69 X
„	– 21. De Waal	1,39 X	0,58 O	2,79 X
14. Karasberg	– 15. Upington	0,40 O	0,23 O	0,29 O
„	– 17. Askham	0,79 O	1,12 O	0,94 O
„	– 18. Twee Rivieren . .	1,00 O	0,95 O	1,20 O
15. Upington	– 16. Douglas	0,64 O	1,57 X	1,59 X
„	– 17. Askham	1,03 O	1,46 X	1,12 O
„	– 19. Kangyane	1,84 X	1,47 X	2,73 X
„	– 20. C. Kalahari . . .	0,81 O	0,89 O	2,79 O
„	– 24. N. Transvaal . . .	1,19 O	0,87 O	2,69 X
16. Douglas	– 17. Askham	0,53 O	0,02 O	0,08 O
„	– 18. Twee Rivieren . .	0,35 O	0,20 O	0,00 O
„	– 19. Kangyane	1,56 X	0,18 O	0,94 O
„	– 20. C. Kalahari . . .	1,33 X	0,24 O	0,84 O
„	– 24. N. Transvaal . . .	0,66 O	0,67 O	0,64 O
17. Askham	– 18. Twee Rivieren . .	0,17 O	0,20 O	0,06 O
„	– 19. Kangyane	1,09 O	0,19 O	0,89 O
„	– 24. N. Transvaal . . .	0,26 O	0,64 O	0,63 O
18. Twee Rivieren	– 19. Kangyane	1,57 X	0,03 O	0,99 O
„	– 20. C. Kalahari . . .	1,29 X	0,46 O	0,88 O
„	– 21. De Waal	0,21 O	0,34 O	0,09 O
„	– 24. N. Transvaal . . .	1,15 O	0,44 O	0,67 O
19. Kangyane	– 20. C. Kalahari . . .	0,45 O	0,08 O	0,11 O
„	– 21. De Waal	1,68 X	0,62 O	0,98 O
„	– 22. Otjiwarongo . . .	0,65 O	0,07 O	0,22 O
„	– 23. N. Kalahari. . . .	0,79 O	0,52 O	0,19 O
„	– 24. N. Transvaal . . .	0,77 O	0,52 O	0,48 O
20. C. Kalahari	– 21. De Waal	1,45 X	0,45 O	0,88 O
„	– 22. Otjiwarongo . . .	0,36 O	0,15 O	0,11 O
„	– 23. N. Kalahari. . . .	0,45 O	0,20 O	0,87 O
„	– 24. N. Transvaal . . .	0,46 O	0,37 O	0,25 O
21. De Waal	– 22. Otjiwarongo . . .	0,58 O	0,74 O	0,74 O
„	– 23. N. Kalahari. . . .	0,77 O	0,29 O	0,85 O
„	– 24. N. Transvaal . . .	0,75 O	0,09 O	0,69 O
22. Otjiwarongo	– 23. N. Kalahari. . . .	0,00 O	0,43 O	0,04 O
„	– 24. N. Transvaal . . .	0,04 O	0,64 O	0,13 O
23. N. Kalahari	– 24. N. Transvaal . . .	0,05 O	0,20 O	0,18 O

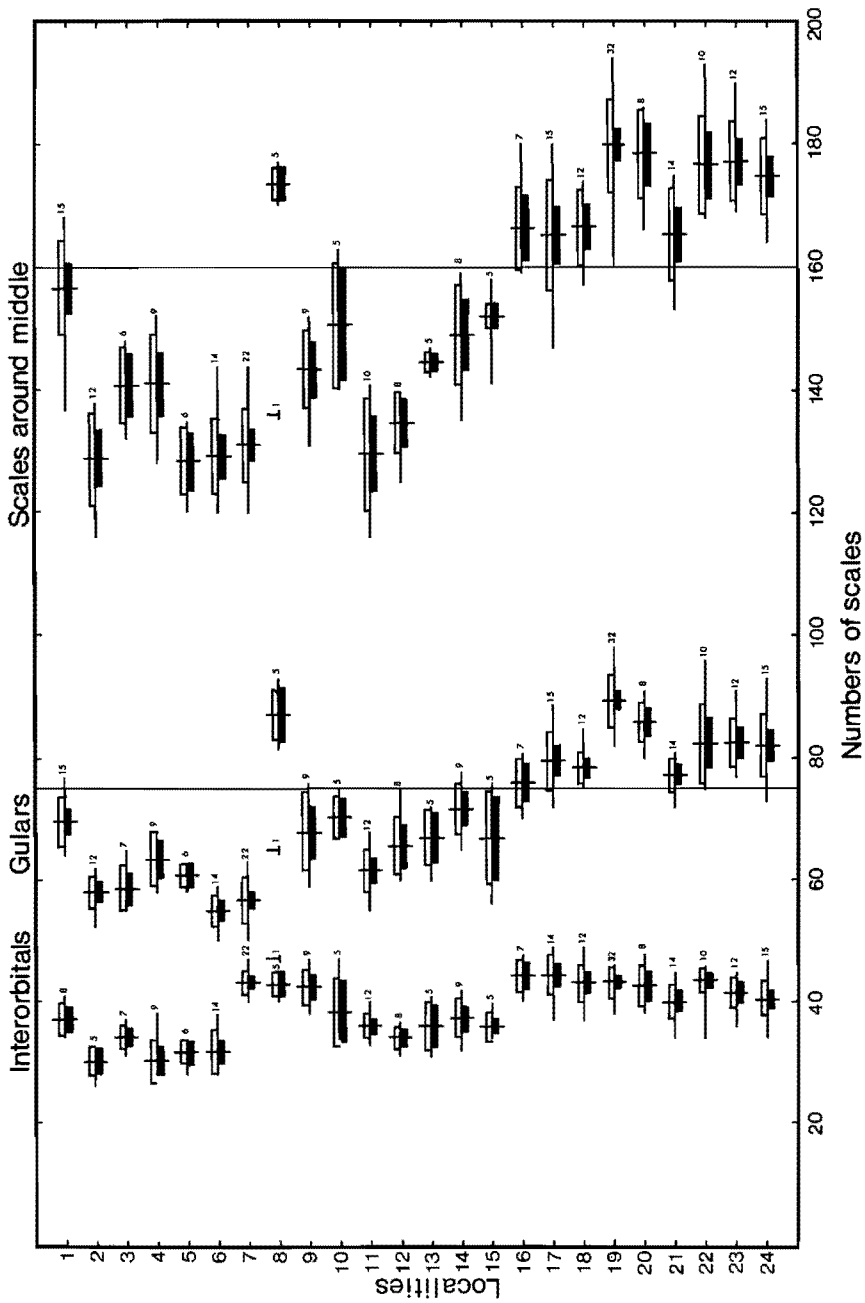

FIG. 1. Interpopulation variation in the scalation of *Ptenopus garrulus*. Vertical line = arithmetic mean; horizontal line = observed range; open horizontal bar = standard deviation; solid horizontal bar = 2 × standard error.
1. Vegkop, 2. nr. Gaias, 3. Brandberg, 4. Karibib, 5. Palmenhorst, 6. C. Namib, 7. Gobabeb S. of river, 8. Walvis Bay (?), 9. Lüderitz–Haalenberg, 10. Oranjemund, 11. Goodhouse, 12. Kamaggas, 13. Keetmanshoop, 14. Karasberg, 15. Upington, 16. Douglas, 17. Askham, 18. Twee Rivieren, 19. Kangyane, 20. C. Kalahari, 21. De Waal, 22. Otjiwarongo, 23. N. Kalahari, 24. N. Transvaal.

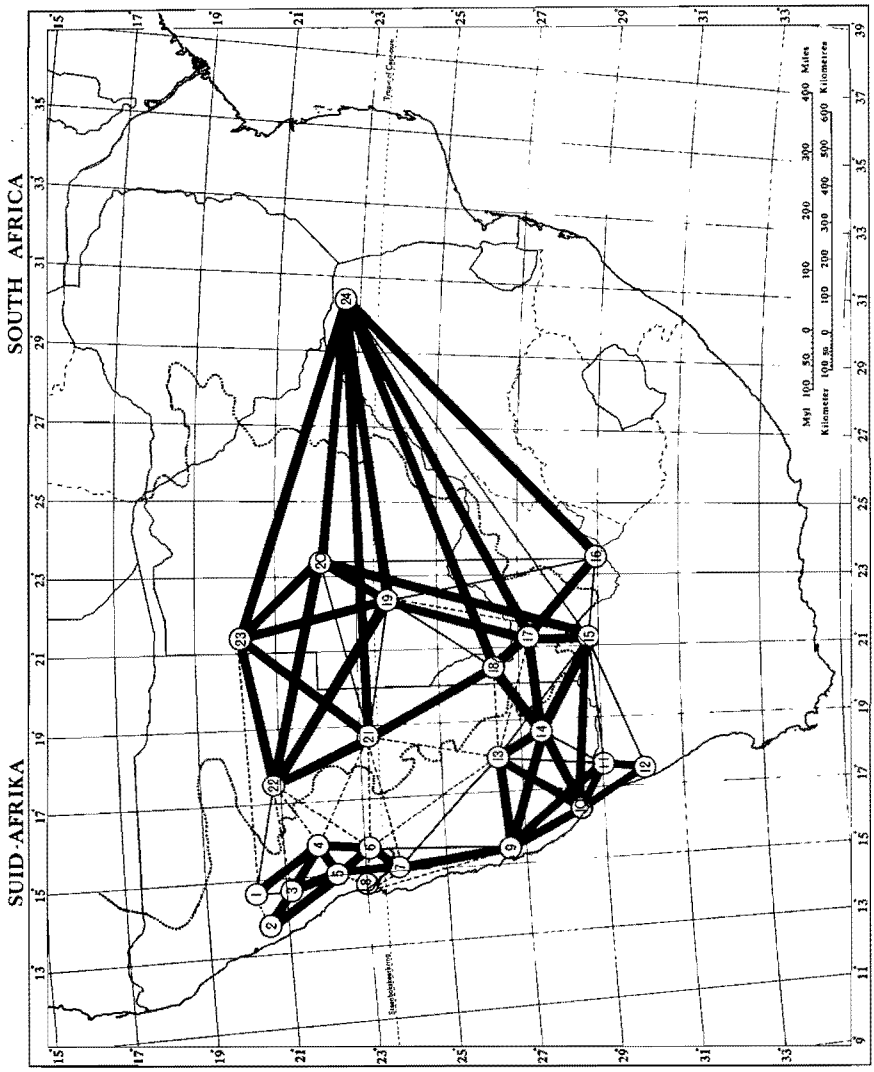

FIG. 2. Interpopulation relationship of *Ptenopus garrulus* according to the numbers of gulars and scales around the middle. Thick lines = no subspecific differences observed. Thin line = difference at subspecific level in one of characters compared. Broken lines = difference between two samples with regard to two compared characters of subspecific level. Thick dotted line = outline of the Kalahari (du Toit, 1954).

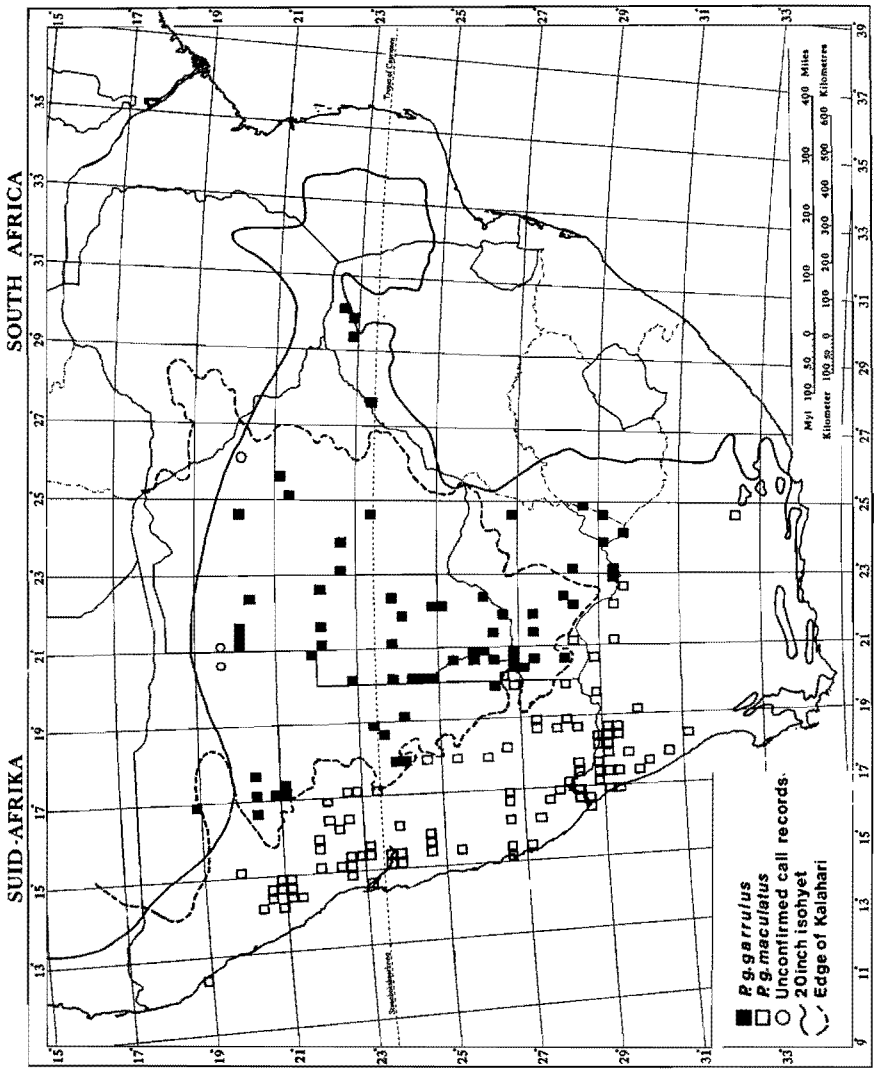

FIGURE 3. Distribution of *Ptenopus garrulus*.

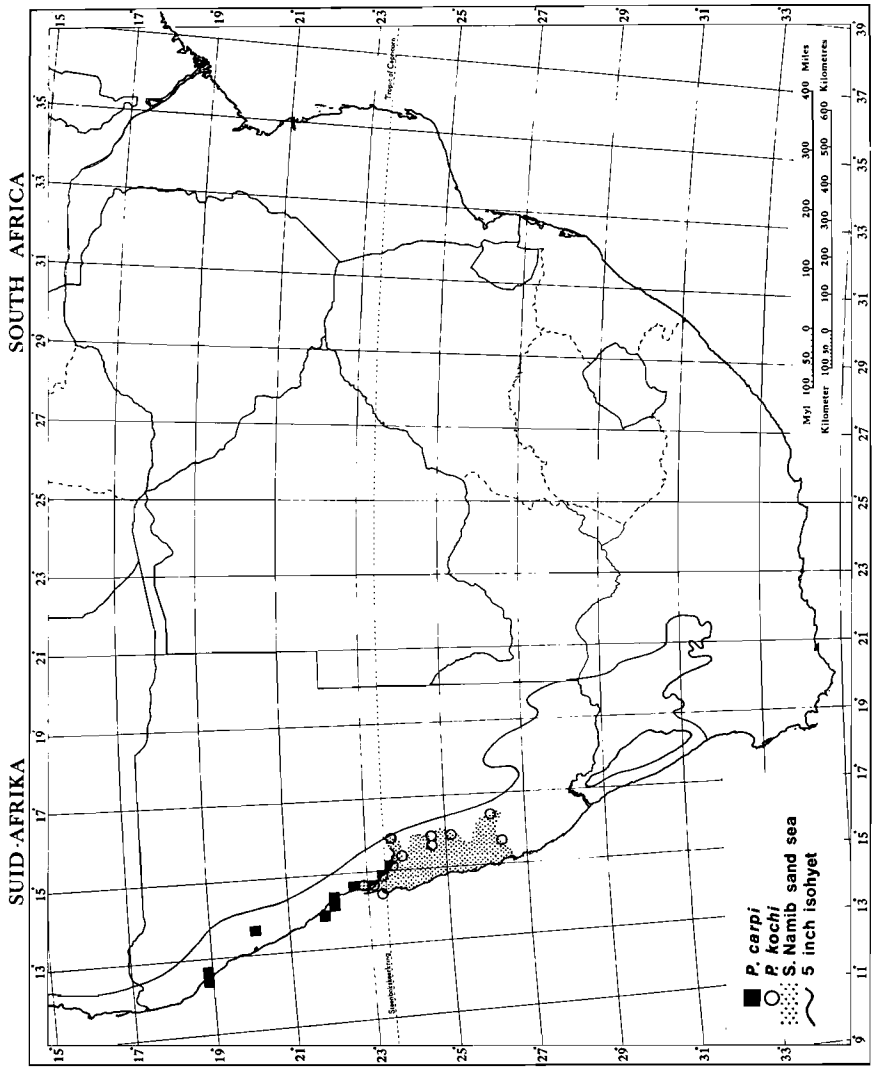

FIGURE 4. Distribution of *Ptenopus carpi* and *Ptenopus kochi*

PLATE 10

Plaster cast of a burrow of *Ptenopus g. garrulus* from near Khutse Pan, Botswana. Adult female.

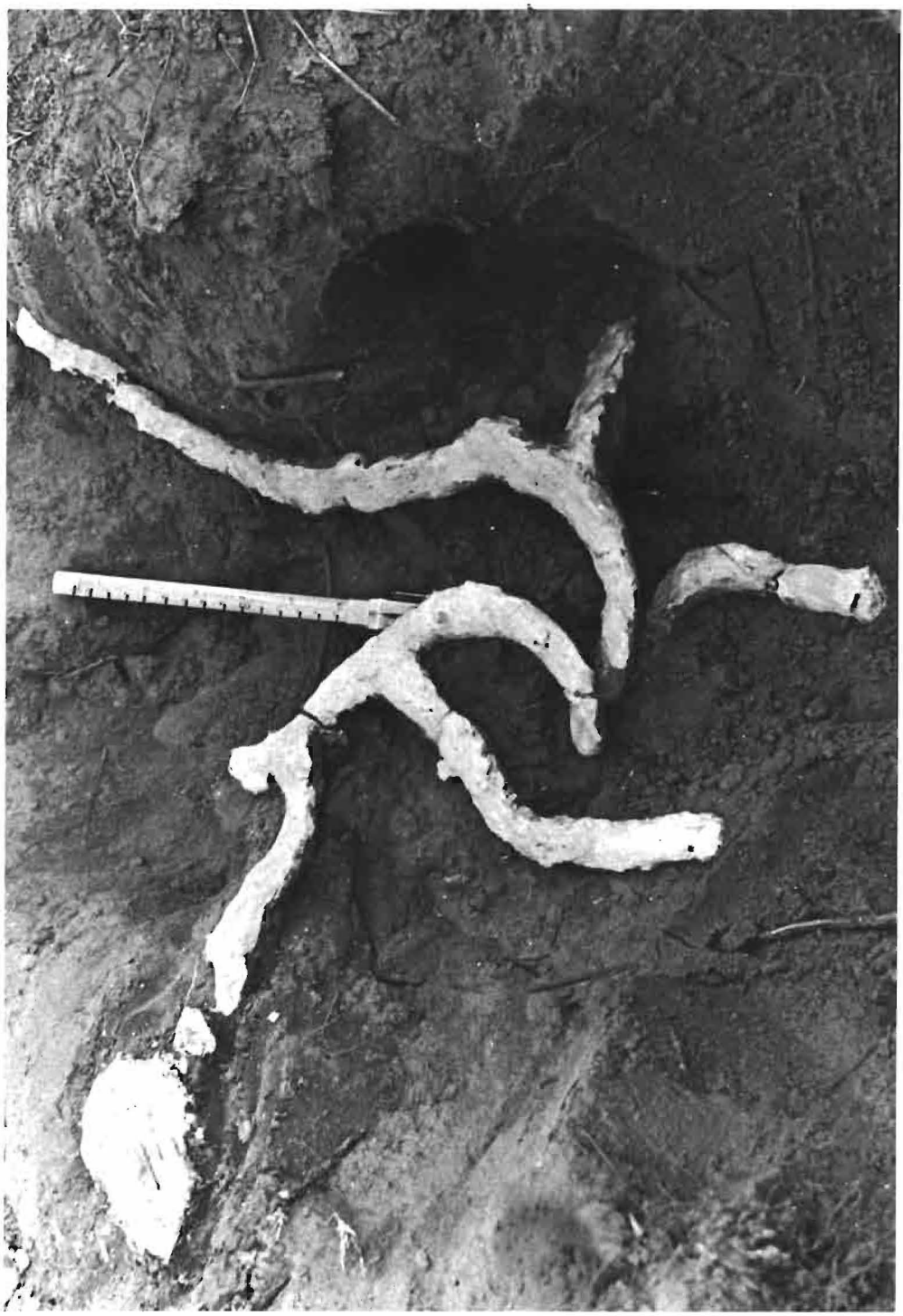

PLATE 11

Plaster casts of burrows of *Ptenopus g. garrulus* from near Khutse Pan, Botswana. Fig. 1. Subadult male. Fig. 2. Juvenile.