A Review of Taxonomy and Ecology of Gerbilline Rodents of the Central Namib Desert, with Keys to the Species (Rodentia: Muridae)

M. Griffin
Ministry of Wildlife Conservation and Tourism, Private Bag 13306, Windhoek, Namibia

The taxonomy, distribution, and ecology of six species of gerbilline rodents occurring in the central Namib Desert, four in the genus *Gerbillurus*, are reviewed. The high species richness is unique in southern Africa; moreover, four species have terminal range limits within the area. Higher and more predictable rainfall areas support higher gerbil densities. Population densities and, for at least two species, distributions vary with changing environmental conditions. Over a 13-year period, central Namib Desert gerbils were found to feed and breed opportunistically.

INTRODUCTION

Nearly all recent biogeographical reviews of central Namib gerbils have presented limited or incorrect information on the presence and distribution of some species (Davis, 1975; De Graaff, 1981; Meester, Rautenbach, Dippenaar and Baker, 1986; Schlitter, 1973; Smithers, 1983; Stuart, 1975*b*). This has led to incorrect assumptions in ecological papers (Holm and Scholz, 1980; Laycock, 1975; Nott and Savage, 1985; Seely, 1977). Central Namib gerbils are well differentiated, however, particularly when complete specimens are available. A review of present knowledge concerning the taxonomy and ecology of central Namib gerbils, intended to serve as a basis for future studies on their biology and ecology, is presented here.

The subfamily Gerbillinae awaits a thorough assessment of relationships among its various taxa, in particular the relationships between the genera *Tatera* and *Gerbillurus,* and among species comprising the genus *Gerbillurus.* There is little agreement as to which family Gerbillinae should be aligned, and it may merit separate family status (Chaline, Mein and Petter, 1977; Viegas-Pequignot, Petit, Benazzou, Prod'Homme, Lombard, Hoffschir, Descailleaux, and Dutrillaux, 1986). Other opinions relevant to higher taxonomic relationships have recently been published by Schlitter, Rautenbach and Coetzee (1984), Pavlinov (1982), Petter (1973, 1983), Chaline and Main (1979), Meester *et al.* (1986), Qumsiyeh, 1986.

STUDY AREA AND METHODS

The central Namib Desert (Fig. 1) occupies an area of gravel plains and sand dunes transversed from east to west by ephemeral watercourses. A comprehensive geographical description of the region has been provided by Logan (1960), substrates by Scholz (1972), and vegetation by Robinson (1976). Cyclic and unpredictable rainfall is characteristic of the area (Lancaster, Lancaster and Seely, 1984; Pietruszka and Seely, 1985), with the east-west gradient being an important feature. Fieldwork summarized in this review started in 1976 after several high rainfall years when rodent populations were high, and continued intermittently until 1989 when most of the area had experienced several years of drought. During the course of approximately 16 000 trapnights, all habitats (Fig. 1) were snap- and live-trapped to determine species composition and relative abundance. Relatively few sites were examined in the virtually inaccessible sand sea south of the Kuiseb River. In addition, owl pellets from numerous localities were analysed. Specimens have been deposited in the mammal collection of the State Museum, Windhoek. The following review thus constitutes a synthesis of thirteen years of study in the central Namib, supplemented by information from available literature.

RESULTS

Six species of gerbilline rodents were found to occur in the central Namib: *Desmodillus auricularis, Gerbillurus paeba, G. tytonis, G. setzeri, G. vallinus,* and *Tatera leucogaster.* They constituted approximately 95 % of over 800 small mammals captured during the study. Figure 1 shows localities for which specimens/records are available, and Fig. 2 illustrates the size range, general appearance and pelage of central Namib gerbils. The gazetteer lists localities of biogeographical importance. Quantitative results are summarized within the text, but detailed data are not presented here. Results for each species appear in phylogenetic order below.

Desmodillus auricularis (A. Smith, 1834)

The short-tailed gerbil belongs to a monotypic genus with a wide southern African distribution. No subspecies are recognized because of local variability (Petter, 1975). It is not easily

Griffin, M., 1990. A review of taxonomy and ecology of gerbilline rodents of the Central Namib Desert, with keys to the species (Rodentia: Muridae). *In:* Seely, M. K., ed., *Namib ecology: 25 years of Namib research,* pp. 83–98. Transvaal Museum Monograph No. 7, Transvaal Museum, Pretoria.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

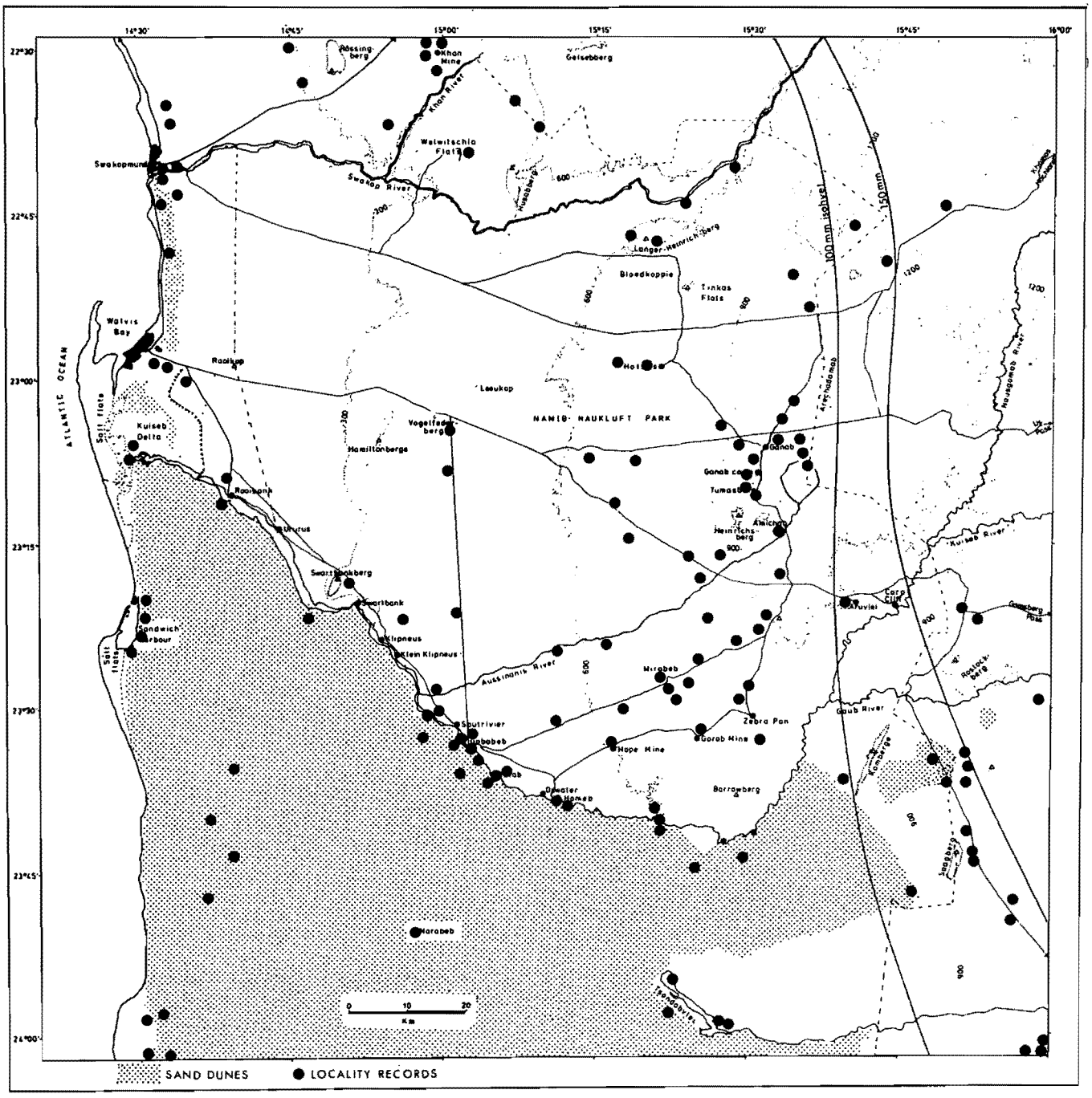

Fig. 1

Sampling sites, literature records, owl pellet collection sites, and other records of gerbils in the central Namib Desert.

confused with any other gerbil species (Figs 2 & 3) but could be confused superficially with the pouched mouse *(Saccostomus campestris)* which occurs in many central Namib areas, especially after good rain years (Griffin, in preparation).

Short-tailed gerbils occurred throughout the study area (Fig. 4) but rarely in shifting dune sand. They occasionally penetrated the dunes up to 3 km along interdune valleys. Populations at Conception Bay (24° 01′ S, 14° 33′ E) and Sandwich Harbour seemed to be completely isolated by shifting sand dunes. *Desmodillus auricularis* occured all along the northern and eastern fringe of the sand sea and in the Kuiseb River bed where the river directly borders the gravel plains.

Little is known of the ecology of the central Namib form other than that numbers vary depending on veld condition. Trapping

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

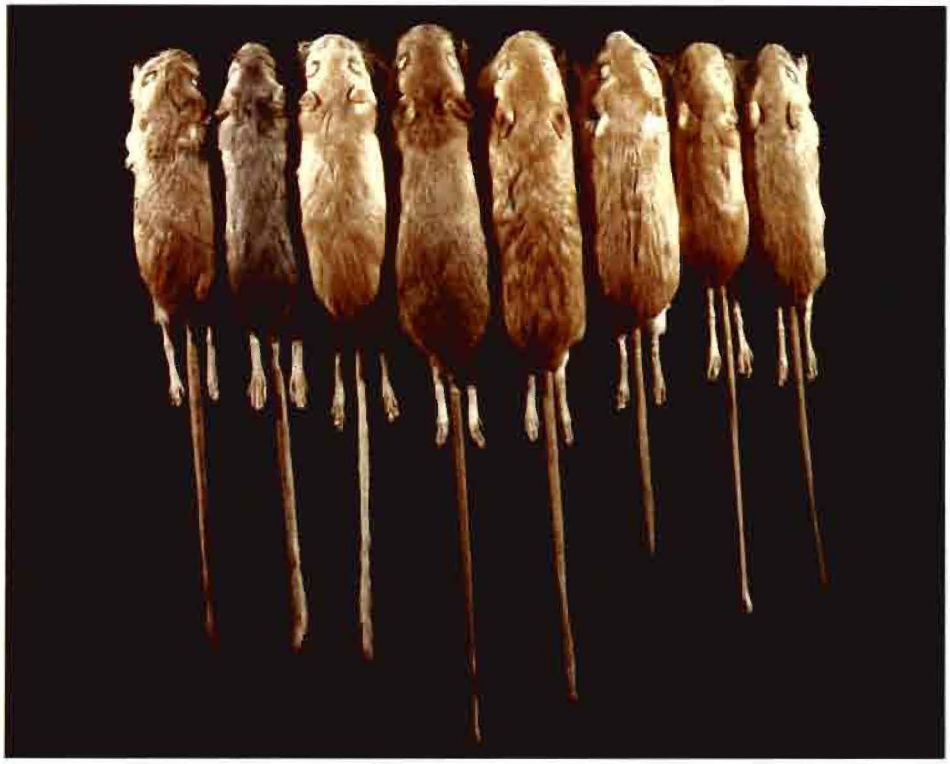

Fig. 2

Relative sizes, appearances, and pelages of central Namib Desert gerbils. Left to right: *Gerbillurus vallinus; Gerbillurus* cf. *setzeri,* typical grey form; *Gerbillurus setzeri; Tatera leucogaster,* atypical dark individual from the Kuiseb River; *Tatera leucogaster,* typical central Namib form; *Desmodillus auricularis; Gerbillurus tytonis; Gerbillurus paeba.*

results showed that *D. auricularis* prefers semi-hard substrates of the gravel plains and localized drainage courses with some grass cover. Individuals were more frequently found in the pro-Namib (the area between the escarpment in the east, and the arid Namib in the west), where populations appear to be more stable. *Desmodillus auricularis* was the rarest of the five widespread gerbil species studied, i.e., the mean trap success rate was less than 0,1 % with a maximum of 5 % on rare occasions in the pro-Namib. Owl pellets from this area occasionally contained a majority of this species.

A small sample of stomachs showed short-tailed gerbils to be omnivorous, feeding on seeds and leafy matter, as well as arthropods. Shortridge (in Thomas and Hinton, 1925) stated that they were primarily insectivorous in the Rooibank area. This conclusion was based on the presence of locust remains in a number of burrow systems.

Gerbillurus paeba (A. Smith, 1836)

Pygmy gerbils are widely distributed in southern Africa. They show the least degree of development of the auditory bullae and occipital-mastoid region (Fig. 5) within the genus. They are generally recognized as distinct from the so-called '*vallinus*' group *(Gerbillurus vallinus, G. tytonis,* and *G. setzeri)* and may eventually be placed in a separate genus or realigned with the northern African *Gerbillus* group (Davis, 1975). Based on relative underdevelopment of the mastoid region, Pavlinov (1982) created the new subgenus, *Progerbillurus,* to distinguish *G. paeba* from all other members of the genus.

Two subspecies have been described from the study area, *G. p. oralis* Thomas and Hinton, 1925 (Rooibank) and *G. p. swakopensis* Roberts, 1951 (Swakopmund), and a third, *G. p. swalius* Thomas and Hinton, 1925, from 30 km to the northeast of the study area (Karibib). Because these populations are continuous, no subspecies are now recognized (Petter, 1975; Meester *et al.,* 1986). On the basis of the broad range of variation of morphological characters in animals from this region, I would concur.

Of the six species of gerbils studied, pygmy gerbils had the widest habitat tolerance; they were essentially ubiquitous, being absent only from rocky areas and possibly the deep sand dunes (Fig. 6). They were found co-existing with each of the other species, though rarely in equal numbers, i.e., high densities of pygmy gerbils were usually associated with low densities of other gerbils and vice versa. Pygmy gerbils were predictably caught on sandy river-fringing substrates and along local drainage courses with some grass cover, i.e., in places apparently not highly favoured by other gerbils except *Tatera leucogaster.* During periods of drought, pygmy gerbils were rarely found in syntopy with either *G. setzeri* or *G. tytonis* – two habitat specialists.

Stomach contents revealed that pygmy gerbils are omnivo-

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

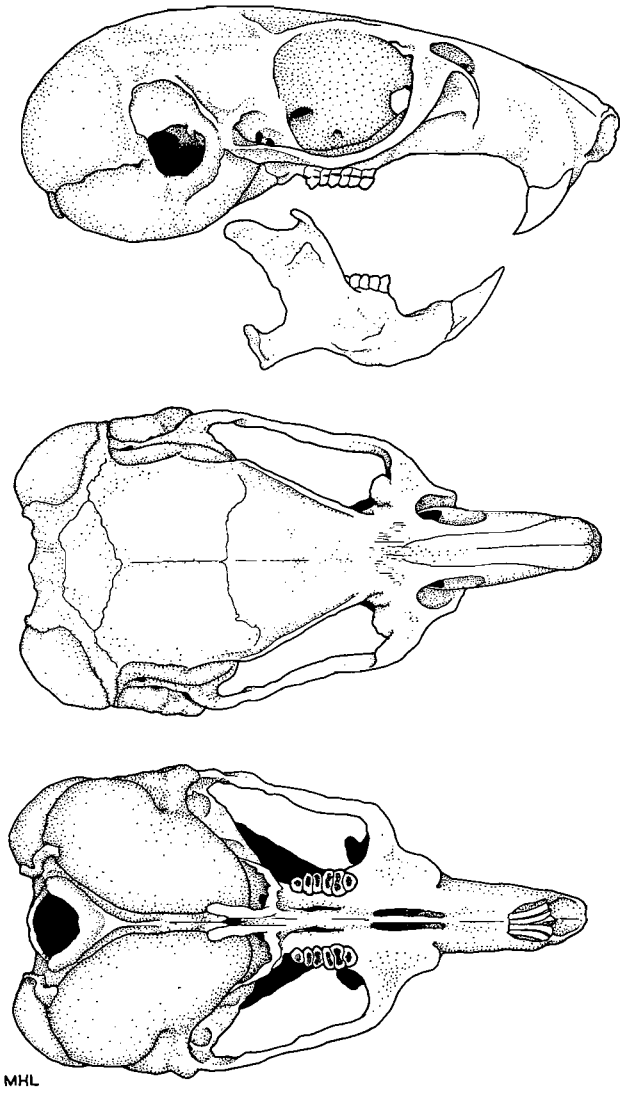

Fig. 3
Desmodillus auricularis skull. Greatest length of skull = 36,8 mm.

rous. On several occasions arthropods made up the bulk of gut contents. Overall, pygmy gerbils did not exhibit a specific breeding season in the central Namib, appearing to be opportunistic. Boyer and Dednam (personal communication), however, describe seasonal breeding during a 15-month sampling period.

Gerbillurus tytonis (Bauer and Niethammer, 1960)

The dune gerbil was described from skulls found in owl pellets from Sossus Vlei (24° 44′ S, 14° 20′ E), 80 km S of the study area (Bauer and Niethammer, 1960). The dune gerbil is the smallest of the old '*vallinus*' group and shows the least development of the bullae and occipital-mastoid region within this group (Fig. 7). No races are described. More recently Petter (1983), using the short posterior palatal foramen of *G. tytonis* (a *Tatera* character), proposed the subgenus *Paratatera* to separate it from the rest of the '*vallinus*' group. Schlitter *et al.* (1984) did not concur.

The hind foot of the dune gerbil is considerably longer and broader (Fig. 8) than in *G. paeba.* The hairs between the toes are also longer and tend to give a snowshoe effect when the foot is spread. Presumably this is an adaptation for moving on loose, wind-blown sand.

This species was restricted to the sand dune sea between Swakopmund and Lüderitz (Fig. 9), and marginally entered the farming areas in the southeast of its range where there is suitable habitat. Within the study area it was found in all dune areas, coastal as well as inland. Consistently higher densities were found on vegetated dunes and hummocks on the eastern edge of the sand and sea. It was occasionally found in the Kuiseb and Swakop River beds, and on immediately adjacent gravel plains.

Trapping surveys, conducted in vegetated dunes and adjacent Kuiseb River bed in 1976 and in the Swakop River bed and adjacent vegetated dunes at Swakopmund in 1978, showed *G. tytonis/G. paeba* ratios in the dunes of 1 : 1 and in the river bed about 1 : 4. Those years were characterized by high rainfall and high overall rodent populations. No habitat niche partitioning in the dune fields was observed during these two surveys (but see Boyer, 1988, for data from dryer years). During periods of high gerbil densities in the southern Namib, *G. paeba* is more often trapped in the open spaces between vegetation clumps and *G. tytonis* is more often trapped in close proximity to vegetation clumps (J. U. M. Jarvis, personal communication). *Gerbillurus tytonis* may be the only species of gerbil predictably inhabiting the vegetationless, main sand sea.

The dune gerbil is omnivorous. Arthropods occasionally made up the bulk of stomach contents. Sexually active animals were found during all seasons. Boyer and Dednam (personal observation) found seasonal breeding during a 15-month study.

Gerbillurus setzeri (Schlitter, 1973)

The Namib brush-tailed gerbil was relatively recently described (Schlitter, 1973), and the type series is from the vicinity of Gobabeb. Namib brush-tailed gerbils occur from southern Angola to the central Namib; its southern limit, as now understood, is in the narrow gravel and sand plains corridor between the Gaub and Tsondab Rivers. It shows the greatest overall size (Fig. 2) and greatest auditory bullae-mastoid region development for the genus (Fig. 10). No subspecies have been described.

Namib brush-tailed gerbils were found on gravel and compacted sand plains throughout the study area (Fig. 11). They were found occasionally in closely adjoining sand dunes (at Natab in 1969 (Schlitter, 1973) and in 1976) during periods of high overall gerbil densities. Namib brush-tailed gerbils were regularly collected on compacted sandy substrates north of the Kuiseb River but they seemed to prefer semi-compacted vegetationless gravel plains, described as 'shallow calcareous soils with a slight gypsum crust and with a grit blanket' (Scholz, 1972). They live singly or in small family groups and their

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

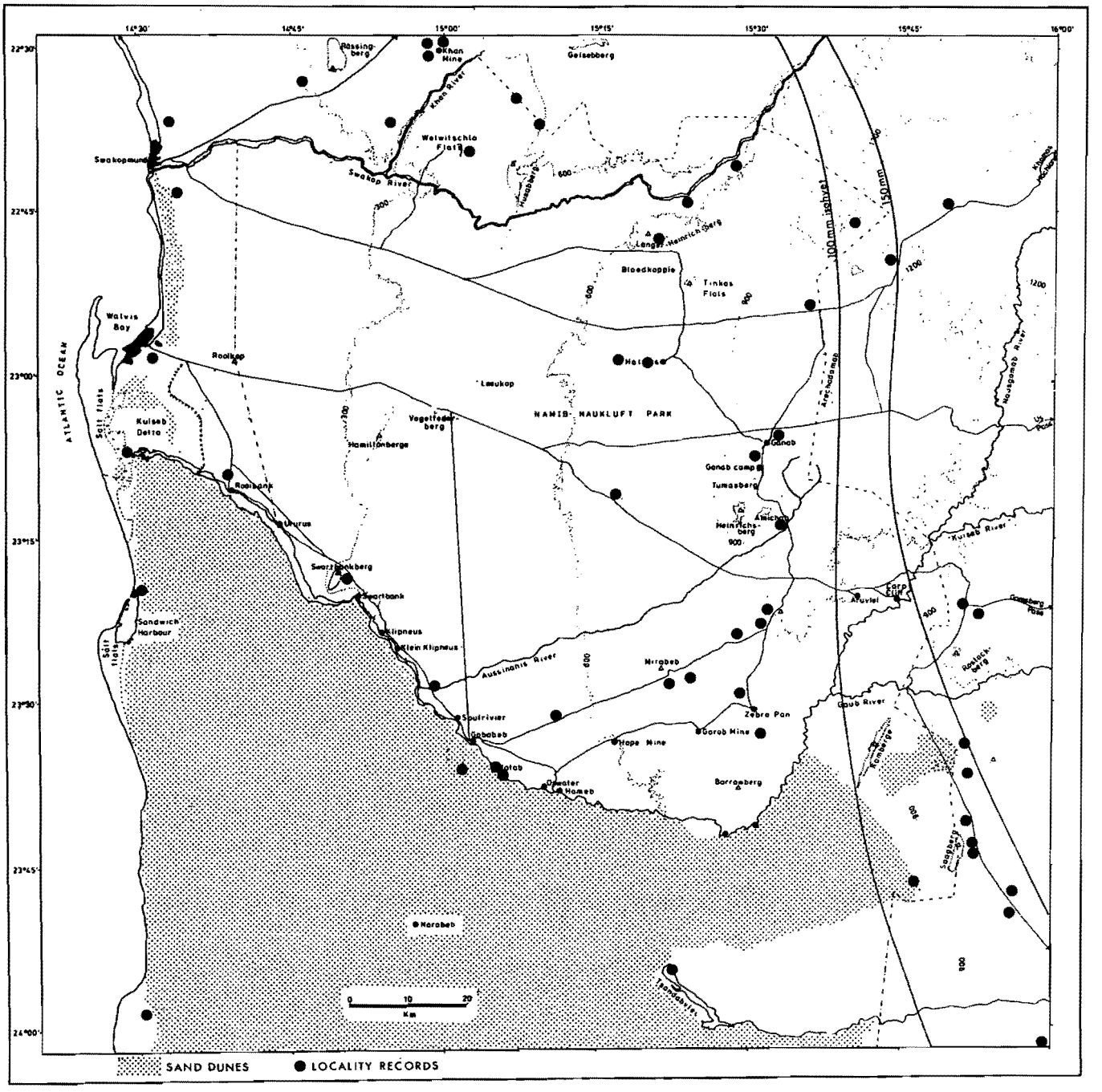

Fig. 4

Distribution of the short-tailed gerbil, *Desmodillus auricularis,* in the central Namib Desert.

burrows are isolated and often conspicuous in calcareous soils owing to excavated soil being a lighter shade than the surrounding, semi-compacted substrate. This situation was also favoured by the short-eared elephant shrew *(Macroscelides proboscideus).* Trap lines successful for *G. setzeri* also included that species. Vegetation seemed to play a negative role in habitat selection, the more barren the situation, the greater the trapping success. Trapping success ranged from 4 % to 0,1 % (with one exception). Namib brush-tailed gerbils gave the impression of being evenly distributed over the region (providing the substrate was correct). A single relatively dense population was located on the farm Donkerhoek on the eastern edge of the study area (which is also the eastern edge of their distribution). On a vegetationless sandy plain, trap success

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

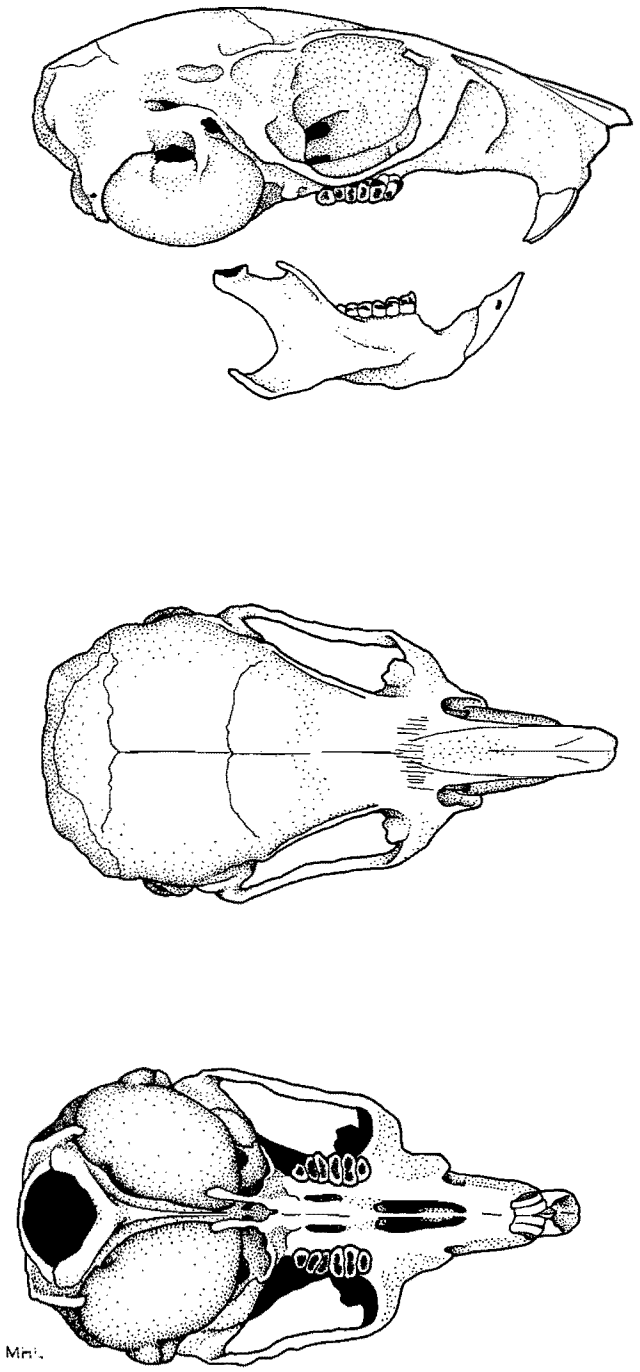

Fig. 5

Gerbillurus paeba skull. Greatest length of skull = 27,8 mm.

rates of 9 % were recorded continuously over a 3-month period.

Namib brush-tailed gerbils were found to be omnivorous. Stomachs from the Donkerhoek population contained only arthropod material. Overall, they did not exhibit a specific breeding season, reproductive animals being found during all seasons.

Gerbillurus* cf. *setzeri

An undescribed form of brush-tailed gerbil occured from the northern edge of the study area, immediately north of the Swakop River (Fig. 11), north to at least the Kunene River. Within the study area it is known from only three specimens, where it coexists with the locally common *G. setzeri.* Further north it became more common, and in some areas it was the dominant small mammal. It has a distinctive grey dorsal pelage (Fig. 2). Its taxonomic status is uncertain and is now under investigation (Griffin and Gordon, in preparation); it is probable that this is the form mentioned by Coetzee (in Davis, 1975). No intermediate forms between this and the normal blond *G. setzeri* have been found in the study area.

Nothing is known about the ecology of this form from the study area; however, observations on a long series from Damaraland and Kaokoland suggest that it is ecologically and taxonomically very closely related to, if not the same as, *G. setzeri.*

Gerbillurus vallinus (Thomas, 1918)

Namaqua brush-tailed gerbils have a relatively restricted distribution: the northwestern Cape Province northwards to around Solitaire (23° 53′ S, 16° 01′ E) on the southeastern edge of the central Namib Desert. The species exhibits an intermediate development of the bullae and mastoid-occipital region of the skull, i.e., intermediate between the dune gerbil and the Namib brush-tailed gerbil (Fig. 12).

This species was only recently (1985) found to occur within the study area (Fig. 11). All previous fieldwork in the north failed to yield specimens, as did an intensive survey on the Naukluft pro-Namib plains immediately to the south of the study area. While attempting to determine the southernmost distribution limit of *G. setzeri,* however, several specimens of *G. vallinus* were collected on the Tsondab River floodplain, an area with low ground cover and no shrubs or trees. This population was isolated, neither entering the central Namib via the Tsondab River, nor in contact with populations to the southeast of the escarpment. There is, however, no geographic feature to prevent periodic invasion from this population in the southeast. The pelage of Tsondab specimens agrees with Lundholm's (1955) description of *G. v. seeheimi.*

A long series of *G. vallinus* is available from the Brukkaros Mountain area, 300 km south of the central Namib site. Data used in the keys are from this population, whereas Fig. 12 is drawn from a Tsondab River specimen. These latter specimens resemble the Brukkaros sample in most respects, as well as a small series from Zwartmodder, 110 km to the south of the study area.

Tatera leucogaster (Peters, 1852)

The bushveld gerbil has a wide southern African distribution but previous to this study it had not been recorded from the central Namib Desert. It is the largest of local gerbilline rodents, approaching 80 g in mass, and has the least developed occipital-mastoid region in the subfamily (Fig. 13).

The distribution of bushveld gerbils was limited to sandy (not dune) and semi-sandy substrates north and east of the sand sea (Fig. 14) and particularly sandy plains along localized river courses. They were rarely found within the sand sea or on smooth barren substrates similar to those favoured by

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

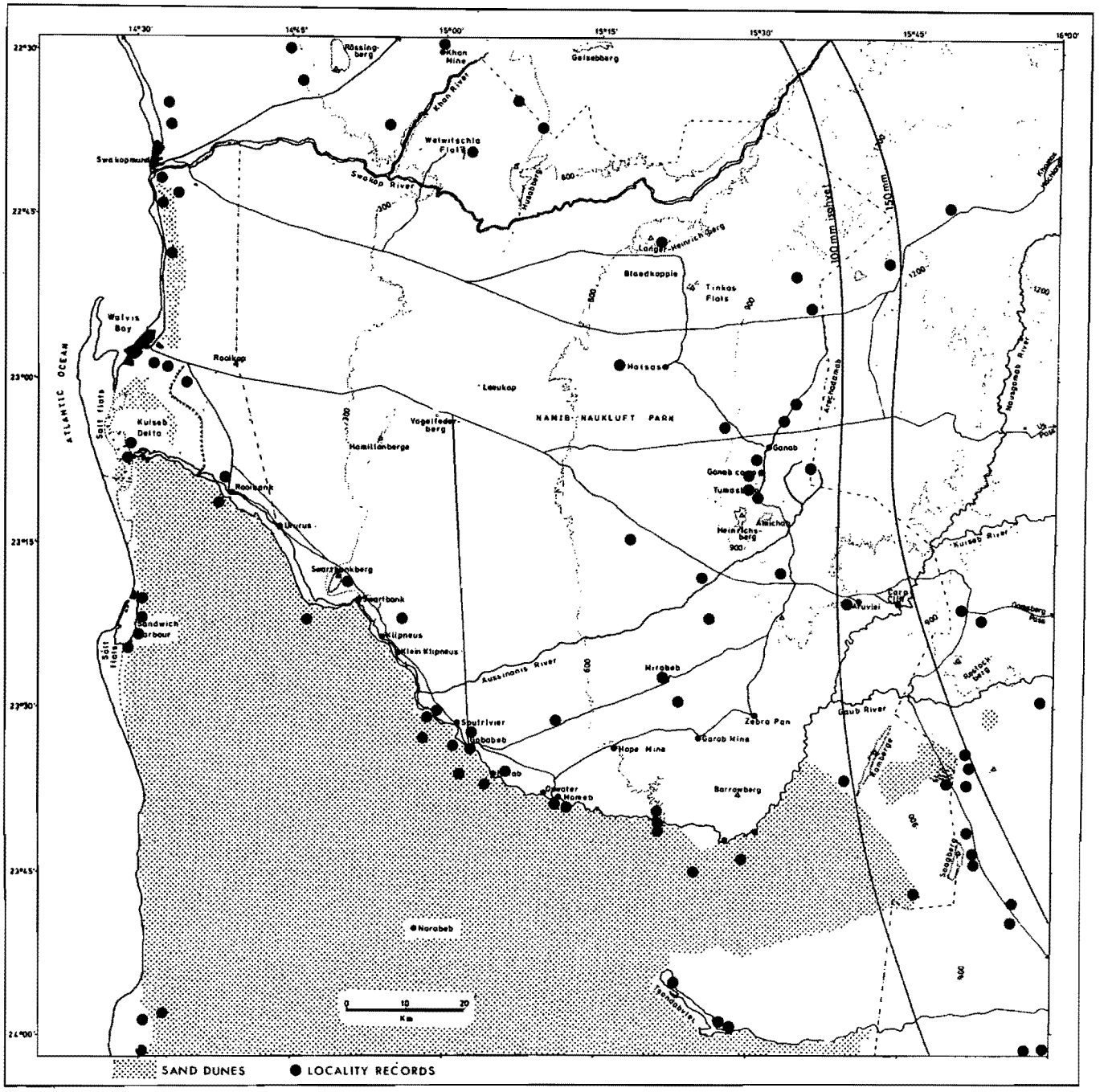

Fig. 6

Distribution of the pygmy gerbil, *Gerbillurus paeba,* in the central Namib Desert.

G. setzeri.

The distribution of the species within the study area (Fig. 14) expanded after a number of good rainfall years. During the period 1978–1980 densities were highest in the Tumasberg-Ganab area (where it normally does not occur), with trapping successes in excess of 50 % having been recorded. Population density diminished rapidly to the west. As conditions became more arid during the study, numbers dropped and whole colonies disappeared. By 1983 no *T. leucogaster* could be found west of 15° 45′ E. Colonies still flourished in the eastern pro-Namib, particularly in the river valleys. Bushveld gerbils were usually found in large localized colonies.

In 1976 an isolated colony of *T. leucogaster* was found in dense riverine forest, 16 km east of Homeb in the Kuiseb River. The colony covered an estimated area of 100 m^2, consisted of 6–8 excavations, and a single adult was trapped.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

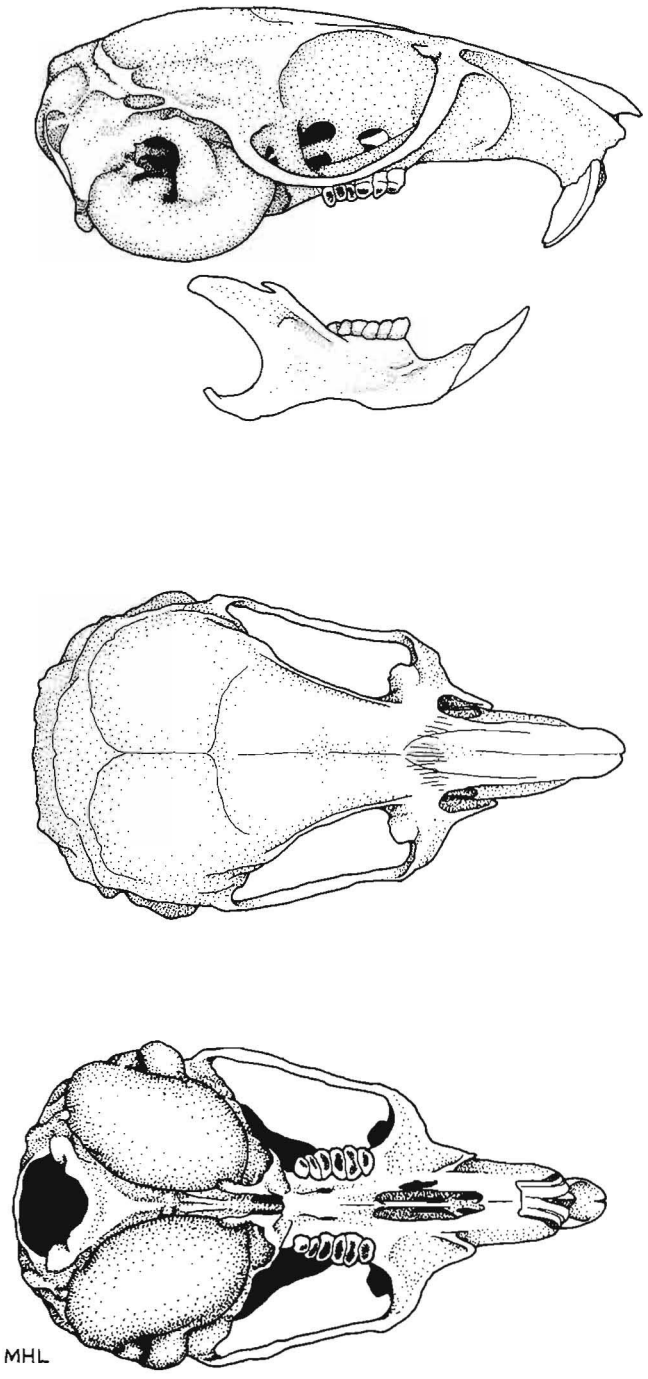

Fig. 7

Gerbillurus tytonis skull. Greatest length of skull = 28,7 mm.

Fig. 8

Relative broadness of hind feet: *Gerbillurus tytonis* on left, and *G. paeba* on right. Both animals of same mass.

A year later, the colony had disappeared. The animal collected at this colony is darker than any other Bushveld gerbil collected in the study area (Fig. 2).

Reproductively active individuals were found in all seasons. Bushveld gerbils examined had been feeding on seeds and leafy matter and some stomachs contained remnants of arthropods.

DISCUSSION

With six species of gerbilline rodents occurring in the central Namib, four alone in the genus *Gerbillurus,* this region harbours one of the most species-rich gerbil faunas in southern Africa. Gerbils are also the most abundant small mammals in the central Namib Desert. Early taxonomic work, however, was hampered by inadequate study material and therefore an incomplete understanding of the range of morphological variation in the various species. The species now known as *Gerbillurus tytonis,* for example, was originally described from skulls (only) as *Gerbillus (Gerbillurus) vallinus tytonis* (Bauer and Niethammer, 1960). Herold and Niethammer (1963), and Coetzee (1969), also recognized two distinguishable forms of '*G. vallinus*' in the central Namib, one living on gravel plains and one in adjacent sand dunes. Based on skull characters only, Davis (1968) considered both taxa to merit species status. Schlitter (1973) concurred and described the pelage and other external morphological characters of *G. tytonis* for the first time. After Schlitter's clarification, most later ecologists still erroneously assumed that any small gerbil in the dunes was *G. paeba* (Holm and Scholz, 1980; Seely, 1976; Laycock, 1975; Nott and Savage, 1985).

Although *Gerbillurus setzeri* was described only in 1973 (Schlitter, 1973), in all previous literature it was referred to as *Gerbillus* (or *Gerbillurus) vallinus* and was well documented from the area (Roberts, 1951; Lundholm, 1955; Meester, 1963; and Coetzee, 1969). Failure to state that the proposed name covered gerbils previously identified as *G. vallinus* from this area led to the conclusion that *G. vallinus* and *G. setzeri* occur sympatrically in the Gobabeb area at least. This misunder-

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

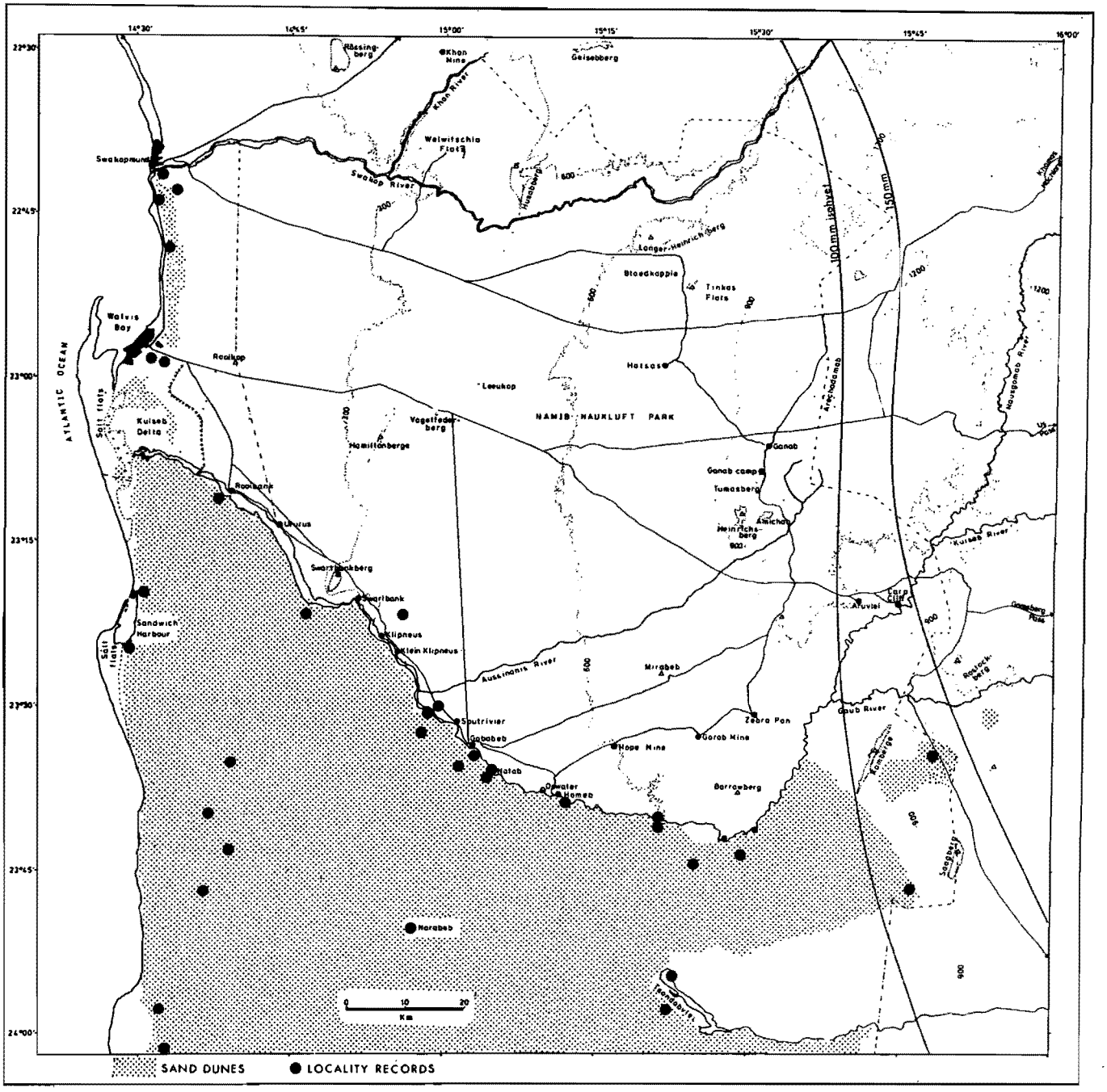

Fig. 9

Distribution of the dune gerbil, *Gerbillurus tytonis,* in the central Namib Desert.

standing has been perpetuated in subsequent literature. The fact that this obvious species had gone undetected until the Smithsonian Institution field teams collected it in the late 1960s is remarkable, especially in view of the large number of gerbilline forms (e.g., *G. paeba* subspecies) which were described earlier from the area we now know as the range of *G. setzeri.* Thomas's original description (1918) of the pelage of *G. vallinus* (based on a single damaged specimen) from the northern Cape very closely matches the pelage of *G. setzeri.* Thus if one critically compares this original description of *G. vallinus* with specimens of *G. setzeri* from the central Namib, they would be assumed to be referable. Lundholm (1955), in the original description of his new subspecies from Namibia, stated that 'specimens [of *G. vallinus*] in the collection of the

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

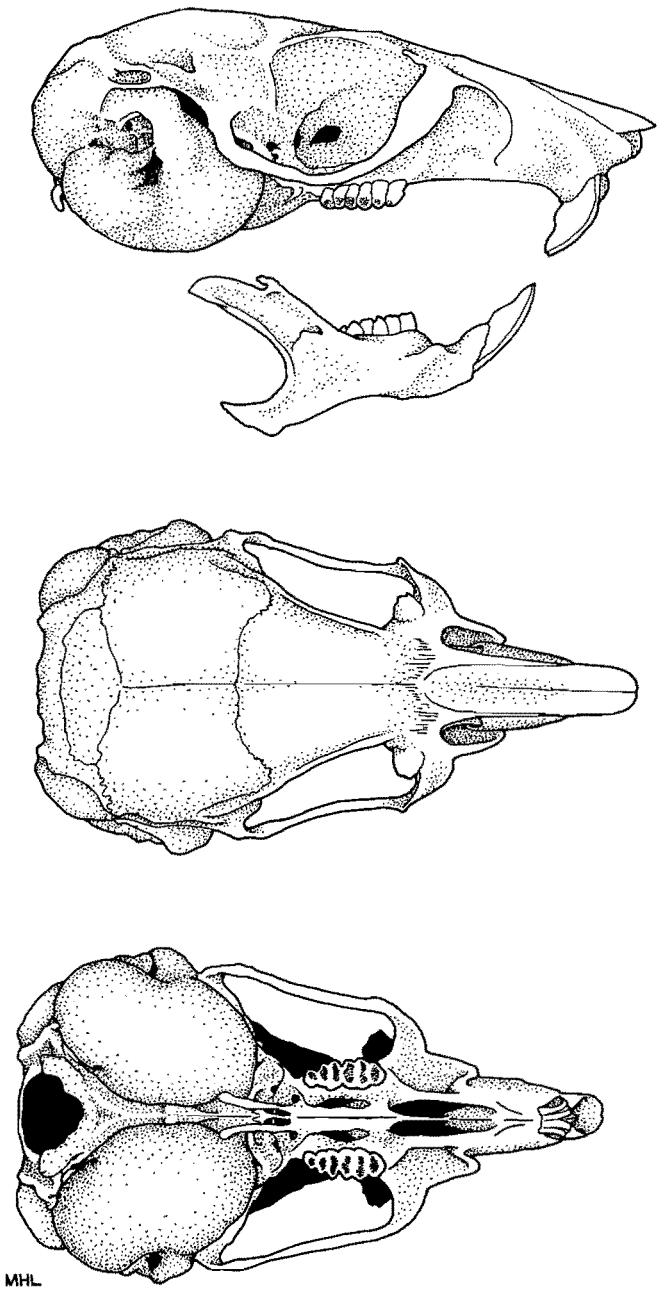

Fig. 10

Gerbillurus setzeri skull. Greatest length of skull = 31,4 mm.

Transvaal Museum collected at Swakopmund agree with his [Thomas's] description'. However, *G. vallinus* specimens from Namibia do not match this description, and this gave rise to *G. vallinus seeheimi* (Lundholm, 1955). The pelage of *G. v. seeheimi* and *G. setzeri* cannot be confused. Thus, the possibility that the type specimen of *G. vallinus* is aberrant cannot be discounted.

The extent of variation within *G. vallinus*, and thus the validity of the two subspecies, is still unresolved (C. G. Coetzee, personal communication). Both races are reported from Berseba; however, I have only encountered animals referable to *G. v. seeheimi* there.

The numerous terminal range limits that fall within the study area are unique despite the species richness (Griffin, in preparation). In most instances substrate or degree of aridity are thought to be the limiting factors (Seely and Griffin, 1986). For example, *G. tytonis* is restricted to sand dunes and these do not extend north of the Swakop River. Less understandable is the southern range limit of *G. setzeri* between the Gaub and Tsondab Rivers, as similar habitat continues to the south between the dune sea and the escarpment.

Since previous records of *G. vallinus* from the central and northern Namib, Damaraland, Kaokoland, and Angola (Crawford-Cabral, 1986) most certainly refer to *G. setzeri,* this disjunction at the Tsondab River is also apparently the northern range limit for *G. vallinus.* From habitat preference descriptions (Smithers, 1983, De Graaff, 1981) one would expect *G. vallinus* to be restricted to less arid river valleys in the pro-Namib. *G. vallinus* may invade the western region during less arid periods, which may account for early records of *G. vallinus* from this area. The few early records from the study area and north that I have been able to trace have been referable to *G. setzeri.* As now understood, there is a 21 km gap between the northern range limit of *G. vallinus* and the southern range limit of *G. setzeri,* and apparently no '*vallinus*' type gerbil inhabits the Namib plains to the south, below the escarpment.

Both *D. auricularis* and *G. paeba* were found throughout the study area, except in the deep sand sea. After good rain years when the sand sea is temporarily covered in grass, these species probably disperse throughout the area, thus accounting for the isolated populations at Sandwich Harbour and Conception Bay.

During extended periods when the central Namib is very arid, *T. leucogaster* is only marginally present in eastern river valleys. It moves westward into temporarily hospitable areas. In 1978, for instance, it was collected in the Mirabib area but during succeeding years was found only 50 km east. In 1978 it invaded the dune sea area near Kamberg, where high populations survived in interdune valleys until around 1982. This may be a common dispersal strategy as similar observations were made in the study area for *Saccostomus campestris, Mus indutus, Hystrix africaeaustralis, Ictonyx striatus, Phacochoeris aethiopicus* and *Tragelaphus strepsiceros* (Griffin, in preparation). The sandy river courses which cross the central Namib facilitate east-west movement (Logan, 1960; Coetzee, 1969).

Improved environmental conditions did not affect distribution of all gerbil species, but in most instances resulted in denser populations of 'local' gerbils, presumably because of increased food supply. *Gerbillurus paeba, D. auricularis* and *G. tytonis* showed large population increases after rain-induced vegetation appeared. In contrast, after rains, areas that were previously occupied by *G. setzeri* only were invaded by other species, sometimes in great numbers. The one dense population of *G. setzeri* was found on a vegetationless gravel/sand plain which suggests that it was responding to something else besides vegetation. Stomach contents confirm that this population was feeding on arthropods. All species were found to

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

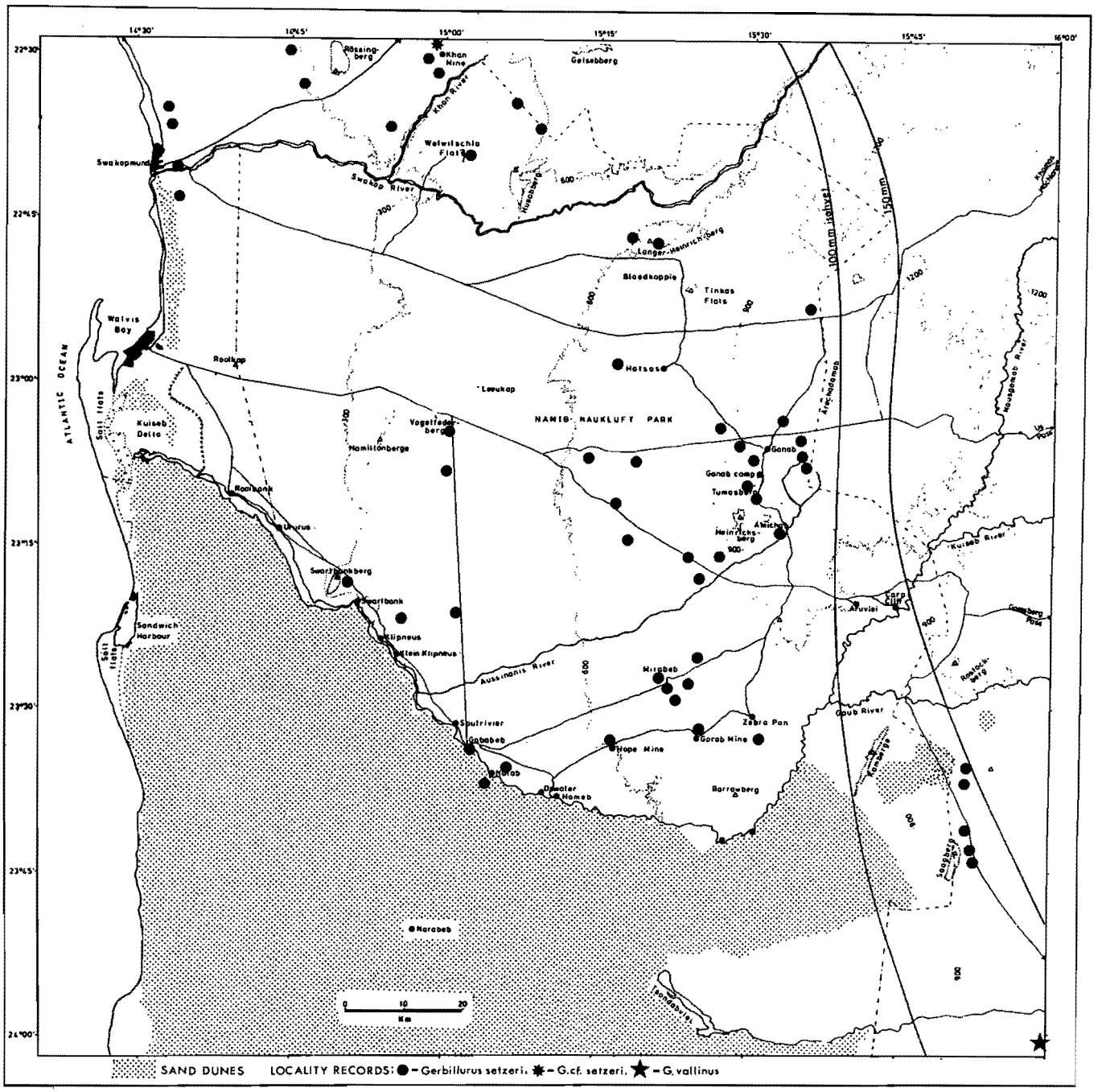

Fig. 11

Distribution of the Namib brush-tailed gerbil, *Gerbillurus setzeri,* and the Namaqua brush-tailed gerbil, *G. vallinus* in the central Namib Desert.

ingest arthropods at times and in some individuals arthropods made up the bulk of stomach contents. It was not possible, however, to relate these instances to local conditions, or to assess the role of individual preference and/or availability of arthropods.

All species exhibited periods when a large section of the population were reproductively active, but these periods were not consistent over the 13-year study period, i.e., they were temporally dynamic. For *G. paeba* and *G. tytonis,* Boyer (1988) found summer reproduction during a 15-month study period, and Withers (1979, 1983) found the same in three non-gerbilline species. My accumulated observations on feeding and breeding, however, suggest that these animals are highly opportunistic.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

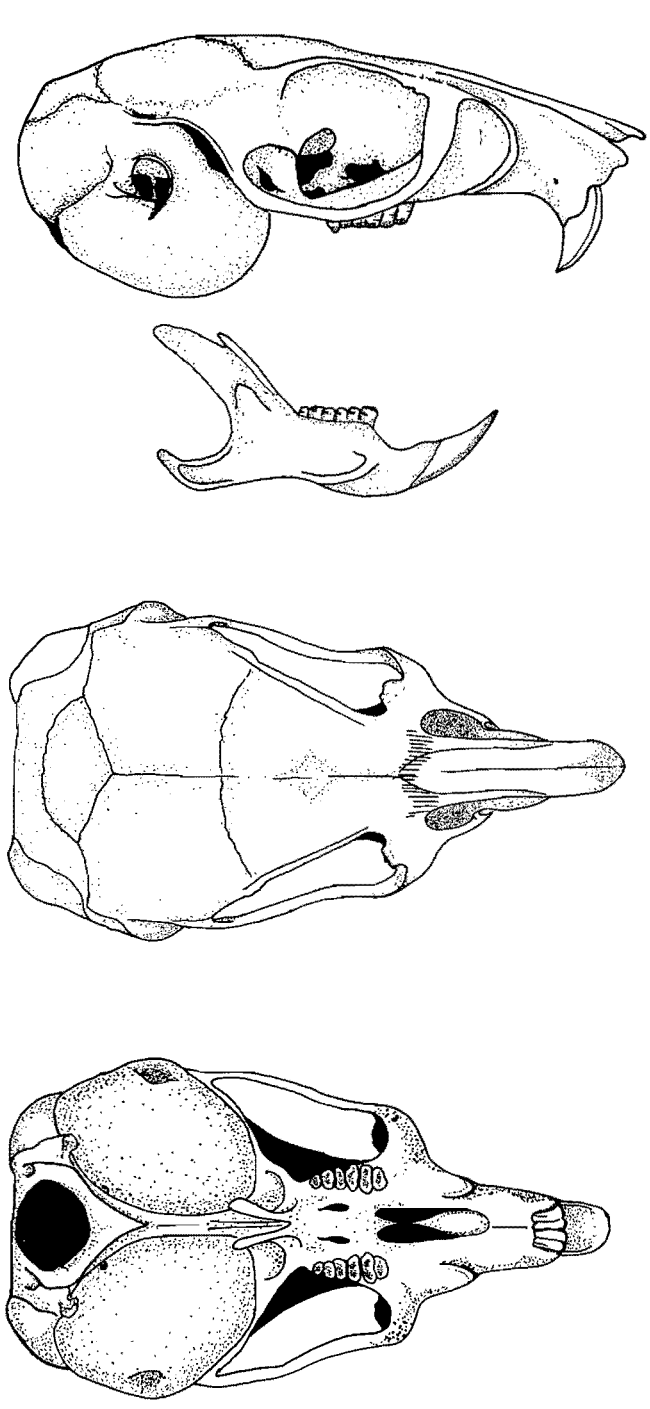

Fig. 12

Gerbillurus vallinus skull. Greatest length of skull = 29,5 mm.

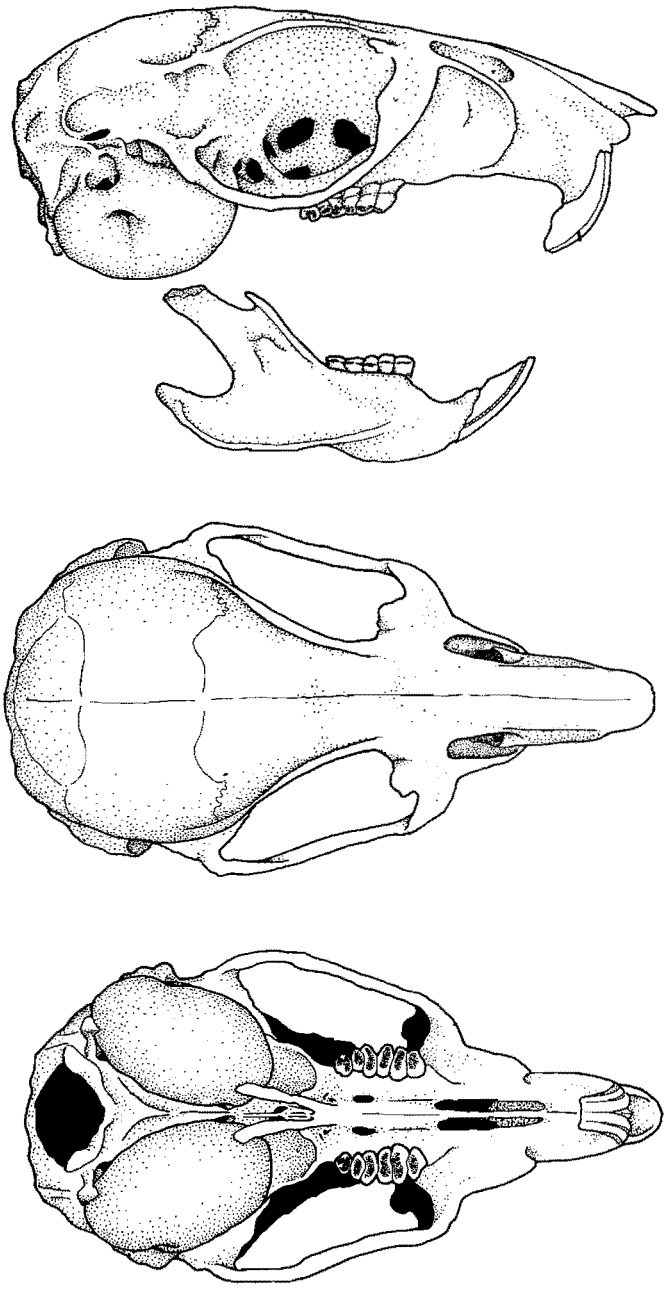

Fig. 13

Tatera leucogaster skull. Greatest length of skull = 34,7 mm.

The long-term relationship and interactions between *G. paeba* and *G. tytonis* populations in the dunes are still not clear. Strategies may differ depending on environmental conditions. Standing diversity may be low (one gerbil species) in the deep sand sea and outside recruitment may be a rare phenomenon. In contrast, in the ecotone along the Kuiseb River the standing diversity may be higher (up to 5 species of gerbils) and constant, but with relative densities varying from season to season.

Ecological partitioning between *G. paeba* and *G. setzeri* is also not clear. At low densities both species occur sympatrically, but as either population approaches relatively dense levels, the other species disappears from the area. This may be more habitat-related than displacement. Dense populations of *G. setzeri* may be very short-lived as the overall basic carrying capacity of the preferred habitat may be low.

Gerbillurus vallinus collected in the Tsondab valley were in a clear numerical minority. This contrasts with my observations

luced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

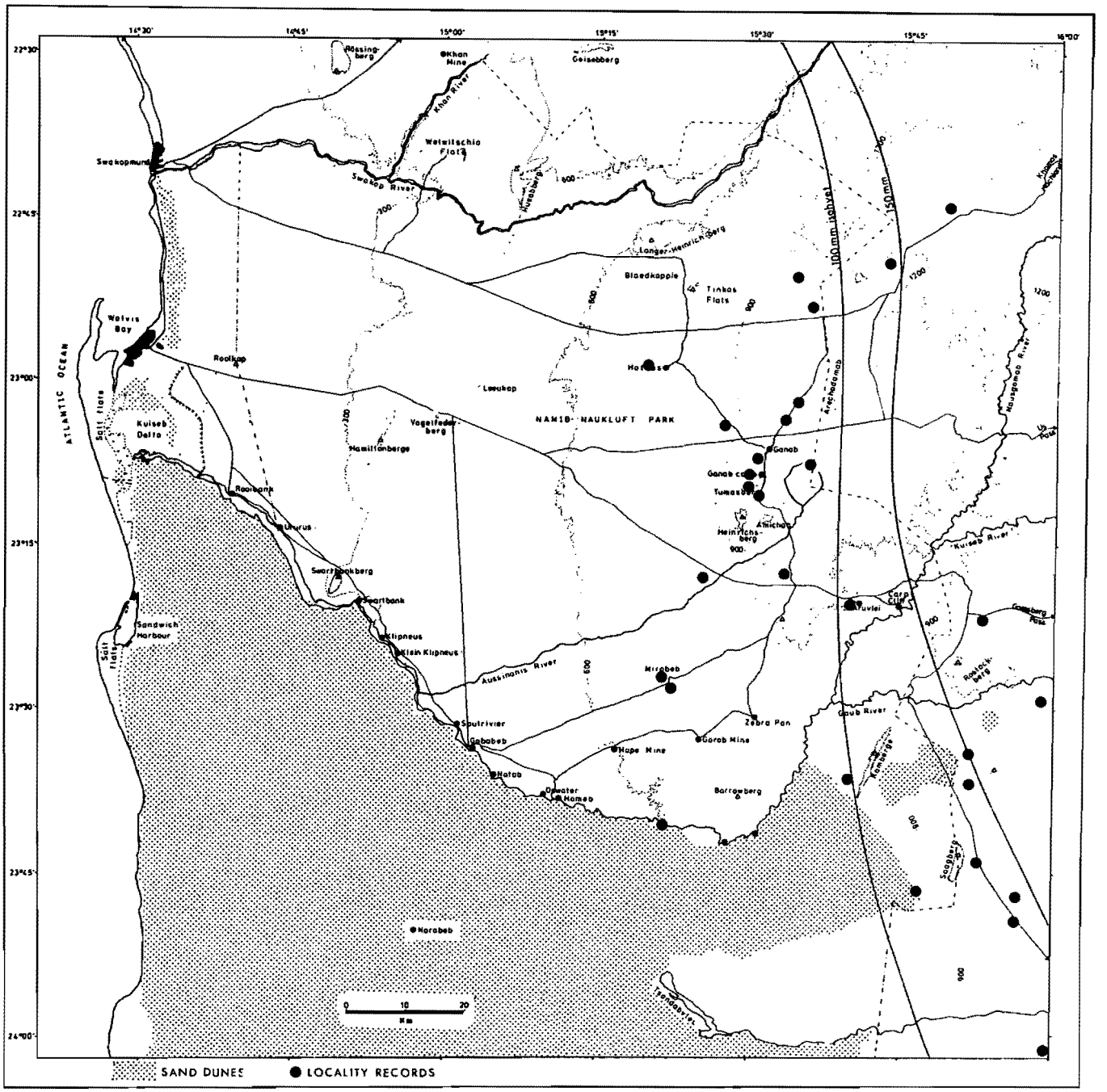

Fig. 14

Distribution of the bushveld gerbil, *Tatera leucogaster,* in the central Namib Desert.

in the Brukkaros-Berseba area where, in suitable habitat, it is the dominant rodent. This has also been observed in the Northern Cape (B. H. Erasmus, personal communication).

Owl pellet analyses also suggest predominance of gerbils in the central Namib small mammal fauna. Gerbils were the dominant mammal in most owl pellet analyses published for the area (Bauer and Niethammer, 1960; Brain, 1974; Brain and Brain, 1977; Nel, 1969; Niethammer, 1968; Stuart, 1975*a;* Tilson and Le Roux, 1983; Vernon, 1971). Spot checks of owl pellets at established sites suggested that owls were responding to changing local gerbil populations. For example, at present *G. setzeri* is the primary gerbil eaten by owls in the Mirabib area, but in the late 1970s *Tatera leucogaster* was, for a short period, the dominant food item there.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

CONCLUSIONS

Six species of gerbilline rodents, four of which are in the genus *Gerbillurus*, occur in the central Namib Desert. This high diversity is unique in southern Africa. The ranges of three species of *Gerbillurus* are characterized by a linear north-south aspect, and all three species have terminal range limits within the area. *Gerbillurus tytonis* and *G. setzeri* are Namib Desert endemics. Another species, *Tatera leucogaster*, is bounded by the east-west aridity factor, and *Desmodillus auricularis* and *Gerbillurus paeba* exhibit no distributional limits in the area.

Past records of *Gerbillurus vallinus* from the area may also refer to *G. setzeri* or *G. tytonis* but, without voucher specimens, these records cannot be verified. Environmental conditions, in particular rainfall, have a great influence on population densities and distribution of some species. It is therefore possible that *G. vallinus* could, at times, extend its present island population in the southeastern corner of the study area further into the central Namib Desert.

The eastern areas of the central Namib Desert have consistently higher gerbil densities, presumably because of higher and more predictable rainfall. Only *G. setzeri* selects arid rather than mesic conditions.

During periods of low population density, core populations of most species probably survive *in situ*, and spread out when conditions improve. Only *T. leucogaster* and probably *G. vallinus* disappear, and later re-invade from the eastern margin.

Populations of gerbils respond to local and current environmental conditions. My overall conclusion, that central Namib Desert gerbils are opportunistic feeders and breeders, was based on samples taken over a 13-year period. In an area characterized by environmental extremes, only by conducting long-term studies can the population dynamic strategies of highly opportunistic organisms be elucidated.

Keys to the species of *Gerbillurus, Tatera* and *Desmodillus* in the central Namib Desert

Owing to greater geographic variation in some key characters, the use of the keys on specimens from outside the central Namib could result in erroneous identifications. These key should be used to indentify only *adult* specimens.

Live animals and skins:

1 Tail < 85 % of head & body length, no brush at distal end. Post-auricular spot larger than ear. Body sturdy and robust. ..... *Desmodillus auricularis*

— Tail length ≥ than head & body, often with conspicuous terminal brush. Post-auricular spot small or absent. Body less robust. 2

2 Soles of hind feet devoid of fur. Distal end of tail often with numerous long hairs, but not a conspicuous brush. Adult mass ≤ 75 g. ..... *Tatera leucogaster*

— Soles of hind feet partially or completely covered with fur. Tail with or without distal brush. Adult mass < 50 g. 3

3 Hind foot (with claw) < 32 mm, mass ≤ 30 g. Margin of ear darker than rest of ear. Tail tip often slightly tufted but never a conspicuous brush. At least median ¾ of dorsal saddle with grey-rooted hairs. ..... *Gerbillurus paeba*

— Margin of ear darker, or not darker, than rest of ear. Most of dorsal saddle with grey-rooted hairs, or only median ⅔. Tail with a terminal brush, but not always well developed. 4

4 Hind foot < 34 mm. Entire dorsal saddle (red-brown and often with conspicuous infusions of grey or black) with grey-rooted hairs, no white-rooted hairs under flanking sides of saddle. Tail brush well developed, deep red to black, and dorsal tail stripe extending at least half-way up tail. This brush often conspicuously darker than rest of dorsal surface. Mass < 42 g. ..... *Gerbillurus vallinus*

— Hind foot ≤ 36 mm. Flanking sides of dorsal saddle with or without white-rooted hairs. No conspicuous infusions of dark hairs in dorsal saddle (not to be confused with grey underfur showing through). Tail stripe same colour as overall dorsal colour, never darker. Tail brush may be silver-grey but not darker. Mass up to 50 g. 5

5 Adult size larger, mass up to 50 g. Dorsal colour a light cream/beige, never brown or red and less sharply demarcated from ventral white. At least the median ¾ of dorsal saddle with grey-rooted hairs. Margin of ear never darker than rest of ear. Tail brush, silver-grey in colour, very well developed. ..... *Gerbillurus setzeri*

— Adult size smaller, mass up to 35 g. Dorsal colour a dull uniform red-brown and sharply demarcated from ventral white. Only middle ⅔ of dorsal saddle with grey-rooted hairs; flanking sections of dorsal saddle have white roots. In live animals, the red-brown dorsal colour is not so obvious, but the dorsal 'stripe' of grey-rooted hair, as opposed to white-rooted hairs on flanking sides, is often clearly visible. Tail brush developed to a lesser degree. Margin of ear darker than rest of ear. ..... *Gerbillurus tytonis*

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

Skulls:
The presence of grooved upper incisors and semi-laminated cheekteeth distinguishes the gerbils from all other local rodents.

The skulls of *G. vallinus* and *G. setzeri* are very similar and are presently distinguishable only in relative terms. In addition, *'vallinus* type' skulls that are damaged, as in some owl pellets, may be impossible to identify to species.

1 Auditory bullae extremely well developed (Fig. 3), usually projecting well beyond occipital plane. In lateral view, posterior section of bullae twice as large as anterior section. First molar with three alveoli. .... *Desmodillus auricularis*
— Auditory bullae developed to a lesser degree, rarely projecting far beyond occipital plane. In lateral view, anterior section of bullae larger than posterior section. First molar with four alvioli. 2
2 Occipital region not well developed (Fig. 13), in lateral view size of posterior section of bullae ≤ 25 % that of anterior section. Crown length of molar tooth row > 5,0 mm. ..... *Tatera leucogaster*
— Occipital region developed to a greater degree, in lateral view, size of posterior section of bullae 30 % – 40 % that of anterior section. Crown length of molar tooth row < 5,0 mm. 3
3 Occipital region developed to a lesser degree, bullae do not extend past occipital plane, oblique length of bullae < 10,5 mm. 4
— Occipital region developed to a greater degree, bullae projecting to occipital plane, or extending beyond. Oblique length of bullae > 9,6 mm. 5
4 Occipital region less developed (Fig. 5). Oblique length of bullae < 9,0 mm. Greatest width of skull (at zygomatic arch or auditory bullae) < 14,8 mm. Posterior palatal foramen rarely < 1,6 mm ..... *Gerbillurus paeba*
— Occipital region more developed (Fig. 7). Oblique length of bullae ≥ 9,3 mm. Greatest width of skull (usually at auditory bullae) > 15,5 mm. Posterior palatal foramen < 1,7 mm. ..... *Gerbillurus tytonis*
5 Occipital region less developed (Fig. 12). Oblique length of bullae < 10,8 mm. Greatest width of skull (usually at auditory bullae) < 17,2 mm. Posterior palatal foramen < 2,0 mm. ..... *Gerbillurus vallinus*
— Occipital region more developed (Fig. 10). Oblique length of bullae > 10,3 mm. Greatest width of skull (always at auditory bullae) > 16,9 mm. Posterior palatal foramen > 1,7 mm. ..... *Gerbillurus setzeri*

ACKNOWLEDGEMENTS

I am most grateful to the following persons for contributing in various ways: B. Colahan, P. Coulson, C. G. Coetzee, B. H. Erasmus, C. Krüger Förtsch, D. H. Gordon, B. Horbert, J. U. M. Jarvis, J. A. J. Meester, J. Pallet, M. R. Perrin, I. L. Rautenbach, M. K. Seely and V. J. Wallis. Surveys on the farm Cha're were conducted with the kind permission of Mr and Mrs Probst. My cohorts in gerbil research, D. Boyer and R. E. Griffin, were always very helpful. I would especially like to thank E. Joubert, who was most encouraging throughout the study, and M. Leisner, AKA Nielsen, for finding the time between sign-writing to draw gerbil skulls.

REFERENCES

BAUER, K. and NIETHAMMER, J., 1960. Über eine kleine Säugetierausbeute aus Südwest-Afrika. *Bonner Zoologische Beiträge* **10**: 236–262.
BOYER, D. C., 1988. Effect of rodents on plant recruitment and production in the dune area of the Namib desert. M.Sc. thesis, University of Natal.
BRAIN, C. K., 1974. The use of microfaunal remains as habitat indicators in the Namib. *South African Achaeological Society Goodwin Series* No. 2: 55–60.
BRAIN, C. K. and BRAIN, V., 1977. Microfaunal remains from Mirabib: some evidence of paleo-ecological changes in the Namib. *Madoqua* **10**(4): 285–294.
CHALINE, J., MEIN, P. and PETTER, F., 1977. Les grandes lignes d'une classification evolutive des muroidea. *Mammalia* **41**(3): 245–252.
CHALINE, J. and MEIN, P., 1979. *Les Rongeurs et l'evolution.* Doin, Paris
COETZEE, C. G., 1969. The distribution of mammals in the Namib Desert and adjoining inland escarpment. *Scientific Papers of the Namib Desert Research Station* **40**: 23–36.
CRAWFORD-CABRAL, J., 1986. A discussion of the taxa to be used in a zoogeographical analysis as illustrated in Angolan Muroidea. *Cimbebasia* (A)**8**(19): 161–166.
DAVIS, D. H. S., 1968. Rodentia, Gerbillinae: Genera *Tatera* and *Gerbillurus*. *In:* MEESTER, J., ed., *Smithsonian Institution preliminary identification manual for African mammals* **18**(2):1–5.
DAVIS, D. H. S., 1975. Genera *Tatera* and *Gerbillurus*. *In:* MEESTER, J. and SETZER, H. W., eds, *The mammals of Africa: an identification manual*, part 6.4, pp. 1–7. Smithsonian Institution Press, Washington D.C.
DE GRAAFF, G., 1981. *The rodents of southern Africa.* Butterworths, Pretoria.
HEROLD, W. and NIETHAMMER, J., 1963. Zur systematischen Stellung des südafrikanischen *Gerbillus paeba* Smith, 1834 (Rodentia: Gerbillinae) auf Grund seines alveolenmusters. *Säugetierkundliche Mitteilungen* **11**: 49–58.
HOLM, E. and SCHOLZ, C. H., 1980. Structure and pattern of the Namib desert dune ecosystem at Gobabeb. *Madoqua* **12**(1): 5–39.
LANCASTER, J., LANCASTER, N. and SEELY, M. K., 1984. Climate of the central Namib Desert. *Madoqua* **14**: 5–61.
LAYCOCK, P. A., 1975. A brief trapping survey in an inter-dune valley in the Namib Desert. *Madoqua* **2**(4): 95–97.
LOGAN, R. F., 1960. The Central Namib Desert, South West Africa. *National Academy of Sciences National Research Council,* Publication 758, Washington D.C.
LUNDHOLM, B., 1955. Description of new mammals. *Annals of the Transvaal Museum* **22**(3): 279–303.
MEESTER, J., 1963. Some mammals from the Namib Desert. *Scien-*

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).

tific Papers of the Namib Desert Research Station **14**: 241–248
MEESTER, J. A. J., RAUTENBACH, I. L., DIPPENAAR, N. J. and BAKER, C. M., 1986. *Classification of southern African mammals.* Transvaal Museum Monograph No. 5, Transvaal Museum, Pretoria.
NEL, J. A. J., 1969. The prey of owls in the Namib Desert. 1. The Spotted Eagle owl, *Bufo africanus,* at Sossus vlei. *Scientific Papers of the Namib Desert Research Station* **43**: 55–58.
NIETHAMMER, J., 1968. Gewölluntersuchungen aus Südwestafrika. *Journal S.W.A. Wissenschaftliche Gesellschaft* **22**: 5–39.
NIETHAMMER, J., 1974. Neue Gewölle aus Südwestafrika. *Journal S.W.A. Wissenschaftliche Gesellschaft* **29**: 133–170.
NOTT, K. and SAVAGE, M. J., 1985. Observations on the utilization of a dune succulent by Namib faunae. *South African Journal of Zoology* **20**(4): 269–271.
PAVLINOV, I. Y., 1982. Phylogeny and classification of the subfamily Gerbillinae. *Byulletin' Moskovskogo Obschestva Ispytatelei Prirody, Otdel Biologicheskii* **87**(2): 19–31.
PETTER, F., 1973. Tendances evolutives dans le genre *Gerbillus* (Rongeurs, Gerbillides). *Mammalia* **37**(4): 631–636.
PETTER, F., 1975. Subfamily Gerbillinae. *In:* MEESTER, J. and SETZER, H. W., eds, *The mammals of Africa: an identification manual,* part 6. Smithsonian Institution Press, Washington D.C.
PETTER, F., 1983. *Paratatera,* sous-genre nouveau de *Gerbillurus* Shortridge, 1942 (Rongeurs, Gerbillides). *Mammalia* **47**: 265–266.
PIETRUSZKA, R. D. and SEELY, M. K., 1985. Predictability of two moisture sources in the Namib Desert. *South African Journal of Science* **81**: 682–685.
QUMSIYEH, M. B., 1986. Phylogenetic studies of the rodent family Gerbillidae: 1. Chromosomal evolution in the southern African complex. *Journal of Mammalogy* **67**(4): 680–692.
ROBERTS, A., 1951. *The mammals of South Africa.* Trustees 'The Mammals of South Africa Book Fund', Johannesburg.
ROBINSON, E. R., 1976. Phytosociology of the Namib Desert Park. Unpublished M.Sc. thesis, University of Natal.
SCHLITTER, D. A., 1973. A new species of gerbil from South West Africa with remarks on *Gerbillus tytonis* Bauer and Niethammer, 1959 (Rodentia: Gerbillinae). *Bulletin of the Southern California Academy of Sciences.* **72**: 13–18.
SCHLITTER, D. A., RAUTENBACH, I. L. and COETZEE, C. G., 1984. Karyotypes of southern African gerbils, genus *Gerbillurus* Shortridge, 1942 (Rodentia: Cricetidae). *Annals of Carnegie Museum* **53**(18): 549–557.
SCHOLZ, H., 1972. The soils of the Central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua* **2**(1): 33–51.
SEELY, M. K., 1977. Sand solidified by gemsbok urine as selected burrow sites by gerbils. *Zoologica africana* **12**: 247–249.
SEELY, M. K. and GRIFFIN, M., 1986. Animals of the Namib Desert: Interactions with their physical environment. *Revue de Zoologie africaine* **100**: 47–61.
SMITHERS, R. H. N., 1983. *The mammals of the Southern African subregion.* University of Pretoria, Pretoria.
STUART, C. T., 1975*a*. A short note on the diet of *Tyto alba* at Sandwich Harbour, Namib Desert Park, South West Africa. *Madoqua* **2/4**: 103.
STUART, C. T., 1975*b*. Preliminary notes on the mammals of the Namib Desert Park. *Madoqua* **2/4**: 5–68.
THOMAS, O., 1918. New species of *Gerbillus* and *Taterillus*. *Annals and Magazine of Natural History* (9)**2**: 148.
THOMAS, O. and HINTON, M. A. C., 1925. On mammals collected in 1923 by Captain G. C. Shortridge during the Percy Sladen and Kaffrarian Museum expedition to South-West Africa. *Proceedings of the Zoological Society of London* **1**: 221–246.
TILSON, R. L. and LE ROUX, P., 1983. Resource partitioning in coexisting Namib Desert owls, *Bubo africanus* and *Tyto alba, Madoqua* **13**(3): 221–226.
VERNON, C. T., 1971. An analysis of owl pellets collected in southern Africa. *Ostrich* **43**: 109–124.
VIEGAS-PEQUIGNOT, E., PETIT, D., BENAZZOU, T., PROD'HOMME, M., LOMBARD, M., HOFFSCHIR, F., DESCAILLEAUX, J. and DUTRILLAUX, B., 1986. Evolution chromosomique chez les rongeurs. *Mammalia* **50**: 164–202.
WITHERS, P. C., 1979. Ecology of a small mammal community on a rocky outcrop in the Namib Desert. *Madoqua* **11**(3): 229–246.
WITHERS, P. C., 1983. Seasonal reproductionn by small mammals of the Namib Desert. *Mammalia* **47**(2): 195–204.

GAZETTEER OF SELECTED MARGINAL LOCALITIES

Desmodillus auricularis
Anichab at 23° 20′ S & 14° 31′ E
Conception Bay at 23° 55′ S & 14° 30′ E
Tsondab Vlei at 23° 54′ S & 15° 23′ E

Gerbillurus paeba
Anichab at 23° 20′ S & 14° 31′ E
Conception Bay at 24 01′ S & 14° 34′ E
Conception Bay at 23° 55′ S & 14° 30′ E
Sandwich Harbour at 23° 24′ S & 14° 29′ E

Gerbillurus tytonis
Anichab at 23° 20′ S & 14° 31 E
Conception Bay at 24° 01′ S & 14° 35 E
Kamberg area at 23° 34′ S & 15° 49′ E
Namibvlakte at 23° 46′ S & 15° 48′ E
Sandwich Harbour at 23° 24′ S & 14° 29 E
Swakopmund at 22° 40′ S & 14° 32 E
Swakopmund, 10 km SE at 22° 43′ S & 14° 34 E

Gerbillurus setzeri
Farm Donkerhoek 416 at 23° 35′ S & 15° 52′ E
Farm Samara 400 at 23° 48′ S & 15° 56′ E

Gerbillurus vallinus
Farm Abbabis 3 at 23° 59′ S & 16° 00′ E

Tatera leucogaster
Hotsas at 22° 57′ S & 15° 20′ E
Kuiseb river at 23° 39′ S & 15° 21′ E
Mirabib at 23° 27′ S & 15° 21′ E

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2009).