Structure and pattern of the Namib Desert dune ecosystem at Gobabeb

by

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ABSTRACT

Composition and patterns of the main biotic and abiotic components of the system are outlined. Notes on biology and ecology of 137 recorded animal species are given, with special attention to the apterous arthropods which dominate the system. The results of a one-year trapping survey are used to illustrate habitat preferences, diel activity cycles and seasonal occurrences of the majority of the species. Endemism and geographical distribution of the beetle fauna are discussed. Illustrations include a site map; histograms of trapping results against yearly and daily climate and against habitat; photographs of a selection of the arthropods; and distribution maps of most of the recorded beetle species.

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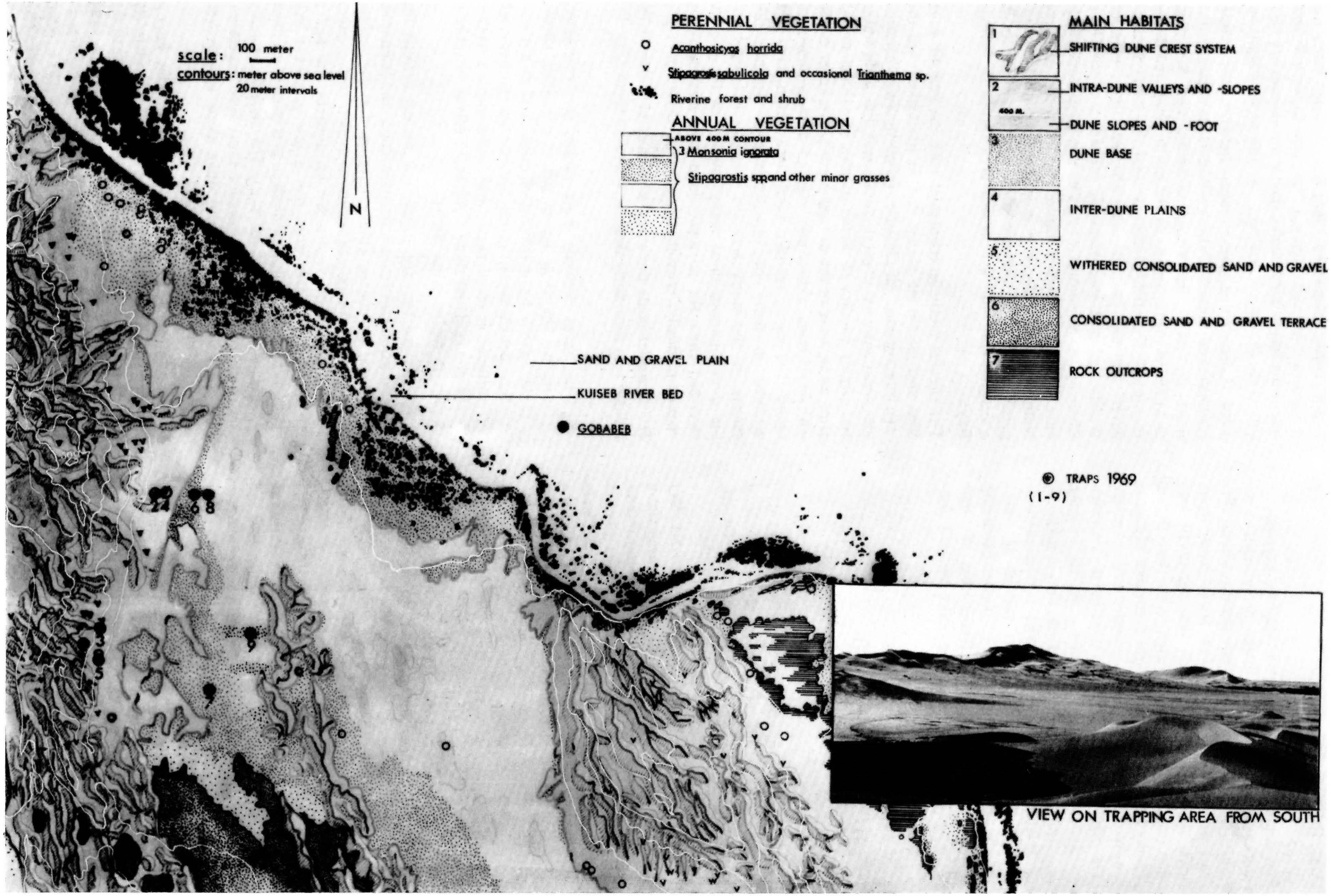

FIGURE 1: Map of the study area and surroundings indicating elevations, geomorphology and the distribution of vegetation.

is gradually replaced by more hardy desert forms on the gradient of desertification from east to west. Where river-beds have rocky banks, their communities are very similar to those of inselbergs at the same longitude.

3.1.4 Large dune areas occur between the Aus—Lüderitz and Kuiseb Canyon—Walvis Bay lines in the south, and on the north coast of South West Africa up to Moçamedes in Angola in the north. Scattered dunes and small dune fields occur around the lower Orange River, between Lüderitz and Elizabeth Bay, between Walvis Bay and Swakopmund, and north of the Ugab River on the Skeleton Coast. The two large dune fields have led to a distinction between northern and southern Namib. Faunistically it is more appropriate to distinguish between a southern area (south of Lüderitz), a central area and a northern area (north of Walvis Bay).

The present study is concerned with the central dune area and inter-dune plains, and in particular with the area directly south of Gobabeb (about halfway between the vegetationless coastal dunes and the semi-stable and largely overgrown inland dunes). The dunes in this area, as in most of the central Namib, are linear dunes with barchanoid ridges and with an average height of about 100 m above the inter-dune plains, and are oriented in more or less continuous north—south ranges. In the study area the fauna is not purely of the dune biotope, since many species of the Kuiseb river-bed enter the adjacent dune area marginally or opportunistically, creating an ecotonal diversity.

On a smaller scale the study area may be further subdivided into four fairly discrete substrate types (Fig. 1):

(i) The plains between dune ranges (or interdunes) are like the large desert plains described above, but have a hight content of dune sand in the surface pebble layer. In the study area the bed-rock surfaces in small areas, and in the south a terrace of consolidated dune sand and pebbles of alluvial origin replaces the plains.

(ii) The dune foot (or base) is a distinct area at the transition from plains to dune slope, and is characterised by coarse white quartz sand at the surface and the formation of regular ripples of micro-dunes which vary between a few centimetres and half a metre high. This area has a few species which specialise in using the detritus precipitated in these micro-dunes (e.g. No. 110). The relative stability of the coarse sand allows for short-lived vegetation to grow after rains, and dune slope species and plains species overlap here.

(iii) The dune slopes (or plinths) cover the largest surface area of the dunes and consist of moderately fine and compacted sand. This area has most of the perennial vegetation, and the hummocks of sand precipitated around these plants are the centres of animal activity on the dune slopes. The plant hummocks provide shelter from heat, protection from predators and food and moisture (see perennial vegetation below). Very few animals feed on the plants themselves.

An important feature of the dune slopes is the retention of moisture in the sand (see Holm & Edney 1973) and the cohesion of sand grains at night, which make this area most suitable for tunnelling. The cohesion of the sand particles is an involved phenomenon, dependent on i.a. temperature and moisture, and even at relative humidities of 50 % or lower the surface becomes firm enough for tunnelling in the sand at night. At sunrise the dune slopes are studded with tunnels of all sizes but with rising temperature the entrances collapse, soon leaving no trace of fossorial activity on the surface.

The valleys between dune crests above the slopes are similar to the slopes in vegetation and faunal composition. The sand is softer and finer in these troughs, perennial plants more abundant and detritus precipitation probably higher due to wind breaks on all sides. Most dune slope species are more abundant in these valleys than on the exposed slopes.

(iv) The dune crest system consists of the actual crest, the slip-face of loose sand which is formed by precipitation of sand on the leeward side of the crest and the base of this slip-face (or avalanche base) where it meets the firm dune slope. On the windward side the crest may be soft to firm depending on how long the winds have blown in the same direction, and with a change in wind direction the whole system gradually changes over to the other side. As the wind pattern is strongly seasonal (Fig. 2), slip-faces face predominantly east in summer and sporadically change to west in winter. The fauna of the slip-face are all sand-divers, and with change in wind direction change over to the leeward side where the sand is loose, wind force is low and detritus precipitation is highest of all areas in the dunes.

Wind-blown detritus and airborne sand are precipitated on the leeward slip faces by the leeward vacuum created by the barchan-type crests. This detritus then swirls on the slip-face and accumulates in cushions in the wind-still spots, and the small detritivores use the same eddies to transport them to the food. Unconsumed detritus becomes submerged by sand, and is eventually utilised by tenebrionid larvae, Thysanura and probably some of the adult tenebrionids. Heavier particles of detritus collect at the slip-face base, where species or both the dune slope and slip-face may be found browsing amongst them.

The sand of the slip-face is of very homogeneous grain size, and the grains are smoothly polished. On a set of imperial measure soil sieves a 1 kg sample from a dune crest gave the following breakdown:

retained on 30 meshes/inch:	–
retained on 50 meshes/inch:	14%
retained on 100 meshes/inch:	81%
retained on 200 meshes/inch:	5%
passed through 200 meshes/inch:	0,01%

The smoothness of grains and absence of dust are essential for the sand-diving insects, as is demonstrated by the effect of placing them in ordinary building sand. The beetles soon wear their appendages down to stumps. More information on the properties of dune sand in relation to the psammophilous animals is given by Robinson & Seely (in prep.).

The dune crest never supports any vegetation. The only protection from heat is the steep 32° angle which affords shade for a few hours every day and the loose sand which permits sand-diving. The dune crest community and food chain are dependent on wind-blown detritus as basic energy source.

Several authors have given general descriptions of the geomorphology of the area (e.g. Koch 1961, Kühnelt 1969, Coetzee 1969, Seely 1978c) and many more detailed and specialised analyses of aspects of geomorphology and geology of the central Namib have been published recently (Barnard 1973; Besler 1970, 1972, 1975a, 1975b, 1976; Goudie 1970, 1972; Logan 1972; Nagtegaal 1973; Rust 1975; Scholz 1973; Selby 1976; Wieneke & Rust 1973, 1976). A fuller description of the dune environment will be given by Robinson & Seely (in prep.).

3.2 Climate

The climate data given in this paper are all from the First Order weather station of the South African Weather Bureau at Gobabeb, about 1,5 km NW of the study site.

3.2.1 Wind is ecologically the most important factor in the system. Not only is the structure and texture of the substrate largely determined by wind action (see 'substrate' above), but the wind regime also controls the temperatures and humidities, distributes the basic energy source (detritus) and determines modes of locomotion of the arthropods. The general annual regime is fairly pedictable and more or less conforms with the pattern recorded for 1969 (Fig. 2). In summer the winds are mainly westerly and stable, rarely reaching gale strength but also with few calms. Cool and moist sea air is brought in by these westerly winds, but occasional north winds may be hot and dry. In winter regular spells of east winds alternate with periods of calm or moderate westerly winds. These easterly 'berg' winds reach high velocities at about two-weekly intervals, and spells of east wind are marked by high temperature maxima and humidities as low as 0 – 5 % RH due to an air drop of about a thousand metres from the Khomas Hochland escarpment. Easterly storms usually set in before dawn, reach a peak at

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which are commercially harvested in the lower Kuiseb, are round and spiny, with a diameter of about 100 – 150 mm. They are favoured by the oryx, and once broken the succulent flesh and seeds attract a variety of arthropods. The seeds constitute a high percentage of the diet of the gerbils (No. 3) when available, and are also sought out by those tenebrionids which can break the shells with their mandibles, and also by the narra "cricket" (No. 52).

The narra seems to require dune sand and subterranean water, and may be a useful indicator of water. It only grows near river-beds or former river-beds, e.g. the lower Kuiseb delta and the underground course of the Koichab. In the latter case whole valleys full of narra plants were observed in 1977 to have died, presumably due to pumping operations in Koichab pan and a subsequent drop in the water table. At the Uri Hauchab mountain in the dunes, the only narra plants grow above the subterranean lower course of a fountain. Large stands of narra also occur SW of Gobabeb in the dunes, probably on subterranean branches of the Kuiseb-Tsondab system. In the study area the plants grow on lower dune slopes near the Kuiseb River, and become progressively smaller and scarcer towards the south.

Trianthema hereroensis Schinz is a non-spiny succulent cushion plant which grows on the higher dune slopes and in valleys on the dunes. Although the plant is evergreen and very succulent, it is not usually eaten, except after rains when two weevils (Nos. 99 and 103) and several lepidopterous larvae (Wharton, pers. comm.) feed on it (see Fig. 4). Flowers are small, and attract a variety of flies and wasps. Salticid spiders are commonly found in flowering plants. Of the three perennials in the area, *T. hereroensis* is the only species which extends into the mobile coastal dunes where not even short-lived annuals can grow.

The rain dependent annuals only appear after rains of above 20 mm within a short period, as was e.g. recorded at Gobabeb in 1967 and 1969*. In 1968, when only 10 mm was recorded, they were completely absent. Small grasses, mainly *Stipagrostis* spp. (e.g. *S. gonatostachys*), predominate in this group, which otherwise consists of a few lilies (e.g. *Hexacyrtis dickiana*) and one small dichotomous plant with a deep root bulb, *Monsonia ignorata* Merxm. & Schreiber. The annuals can only take root on the relatively stable sands of the lower dune slopes and plains (Fig. 1). The growth of a dense cover of grasses is followed by a well synchronised emergence of a great variety of arthropod primary feeders, which reach extremely high population densities followed by equally dramatic population 'crashes' after a few weeks when the plants have died. Densities of *Eustolopus octoseriatus* (No. 130) reached such high levels in 1967 that it was impossible to walk in the plains without continually stepping on these beetles.

* Seely (1978a) independently arrived at a figure of 20,6 mm.

The annuals also attract permeants from the sub-desert and savanna, such as large herbivores and associated dung beetles, mammalian and avian predators and alate insects. The rain-flora thus supports a whole short-lived ecosystem within the permanent detritus-based system, and the frequency of its occurrence for any given spot is about once in three years at the longitude of Gobabeb, probably becoming more frequent towards the east and less frequent towards the coast. This would necessitate prolonged quiescences for the arthropod consumers which specialise on the rain-flora. The grasses last for about one month after rains (depending on weather conditions), and the lilies and *Monsonia* sp. outlast grasses by a few weeks. The food supply is so short-lived that it is not overtaken by primary feeders and the bulk is uprooted by wind and changing sand-surface levels, and is eventually distributed through the dune area as probably the major part of the detritus deposits (Robinson & Seely, in prep.).

Apart from intensive studies on *Welwitschia mirabilis* (which does not occur in the study area), few of the plants of the central Namib have been intensively studied. Giess (1962, 1968), Walter (1962) and Robinson (1976) recorded the floristics of the area, and Herre (1974/1975), Walter (1976) and Seely, de Vos & Louw (1977) published ecological observations on some of the plants. Seely (1978a, b) analysed the productivity of the annuals in relation to rainfall and included useful check-lists of species compositions.

5 CONSUMERS: VERTEBRATES

Since this study was mainly concerned with the endemic arthropods, our less detailed notes on the vertebrates are given in this separate chapter. Information from the extensive literature on vertebrates of the Namib is not repeated or quoted as this would be beyond the scope of the study, and selected references are provided instead.

5.1 Primary feeders

Species recorded in the study area are the oryx, *Oryx gazella* (No. 1) and hare, *Lepus capensis* (No. 2) (see Dixon, 1975), both of which are migrants from the overgrown inland dunes and sub-desert. Both species were rare in the study area and the wingless scarabs (Nos. 87 and 88) which usually occur with them, were also rarely trapped. Some omnivorous species contribute to primary consumption, and these are discussed elsewhere. Even normally carnivorous species e.g. the spotted hyaena (Stuart 1976) and certain geckos and lizards (see below) eat vegetable matter on occasions. Ostriches were sighted in the area on one occasion, but do not usually enter the dunes. Granivorous birds invade the area when seed is plentiful, but are not resident in the dunes.

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Prey sp.	1 ♂	1 ♀	Total
No. 58	13	8	21
No. 68	3	5	8
No. 69	4	4	8

The second species of barking gecko, *P. kochi* (No. 11) has a more restricted distribution and is probably restricted to the central dune area. It is, as is the case with the previous species, never found on higher dune slopes or the dune crest. The contents of four stomachs taken on two different dates clearly show the opportunistic feeding pattern which is characteristic of desert animals. It is interesting to note that vegetable matter occurs in the diet, as in the case of *Aporosaura* (No. 13):

Prey sp.	♀ 26.II	♂ 26.II	♀ 22.III	♀ 22.III	Total
No. 59	–	–	15	31	46
No. 59	59	67	–	–	126
No. 62	10	27	–	–	37
No. 69	23	7	–	–	30
No. 30	1	1	–	–	2
No. 84	–	–	3	–	3
grass seeds	–	7	–	–	7
grass leaves	–	–	*	–	*

Palmatogecko rangei (No. 12) is strictly nocturnal, and tunnels in the dune slopes but also hunts in the dune crest and plains areas (Fig. 4). The species occurs in all dune areas of the Namib, as is the case with *Aporosaura* (No. 13) and *Bitis peringueyi* (No. 7). The extraordinary webbed toes of this gecko enable it to walk rapidly on soft sand, and to dig tunnels in the soft sand of the dune slopes very effectively. The animal is very weakly pigmented and appears translucent. It uses its tongue to wipe dust off the large and exposed eyes. *Palmatogecko* is the most abundant nocturnal reptile in the dunes, and seems to be more active in summer (Fig. 2). It is heavily preyed upon by various vertebrates and possibly even sparassid-spiders (Lawrence 1959), and in turn seems to feed on all nocturnal dune arthropods of manageable size, as reflected in stomach contents:

Prey sp.	(unsexed) 19.IV. 1967	(unsexed) 3.IV. 1968	♂ 26.II. 1969	♀ 26.II. 1969	Total
No. 116	1	1	–	–	2
No. 117	1	1	–	–	2
No. 127	1	1	–	–	2
No. 43	–	–	–	2	2
No. 84	–	–	–	1	1
No. 59	–	–	1	–	1

Meroles cuneirostris (No. 14) is a fast-moving diurnal lizard, and the ecological counterpart of *Aporosaura* (No. 13) on the dune slopes and foot. It shelters and dives into the soft sand under the hummocks of perennial plants (Fig. 4). Specimens were trapped throughout 1969 (Fig. 2). Individuals and age classes vary much in colour, and the identification of juveniles of especially this species and two other *Meroles* spp. which occur on the banks of the Kuiseb river-beds is not easy. Behaviour is similar to that of *Aporosaura*, but the slip-face habitat is exchanged for that of the plant hummocks. Both lizards have hard blade-like scales on the front of the upper jaw, which enable them to dive into soft sand while running at full speed. The diet consists of any of the small arthropods in its habitat, as the stomach contents show:

Prey sp.	1 (unsexed) winter 1968	1 (unsexed) winter 1968	1 (unsexed) winter 1968	1 with yoked eggs 22.III. 1969	Total
No. 121	2	2	–	11	15
No. 123	–	4	–	–	4
No. 116	–	–	1	–	1
No. 129	–	1	–	–	1
No. 68	–	–	–	1	1
Unidentified solpugid	1	–	–	–	1
Unidentified spider	2	–	–	–	2

An extensive analysis of the diet of this species was given by Robinson & Cunningham (1978).

Aporosaura anchietae (No. 13) is a fast moving diurnal lizard of the dune crest system (Fig. 4), with territories and harems on the dune slip-faces where they mainly hunt for small arthropods and grass seeds in the detritus. The biology, physiology and behaviour of this animal have been the subject of a number of studies (Louw 1972; Louw & Holm 1972; Holm 1973; Robinson 1977; Robinson & Cunningham 1978). Juveniles have bright yellow tails, adults are cryptically coloured. Specimens were trapped regularly throughout 1969 except in a two month spell between April and May (Fig. 2). The diel activity is distinctly bimodal in summer and unimodal in winter (Fig. 3), and the underlying circadian rhythms for these patterns were investigated by Holm (1973). Stomach content analyses are given in Louw & Holm (1972) and much more extensively by Robinson & Cunningham (1978), and are not repeated here.

Chamaeleo namaquensis (No. 15) was only seen once in the study area, but is relatively common in the overgrown inland dune area. It can manage even the largest and hardest dune tenebrionids. The biology and ecology were discussed by Burrage (1973).

Typhlosaurus braini (No. 9) is the most elongated legless lizard known. It is active throughout the year (Fig. 2), mostly among *S. sabulicola* hummocks in the dunes (Fig. 4). It presumably lives on the dune termite (No. 59) and the thysanurans which are particularly abundant in its habitat. Like the mole (No. 4) it has a

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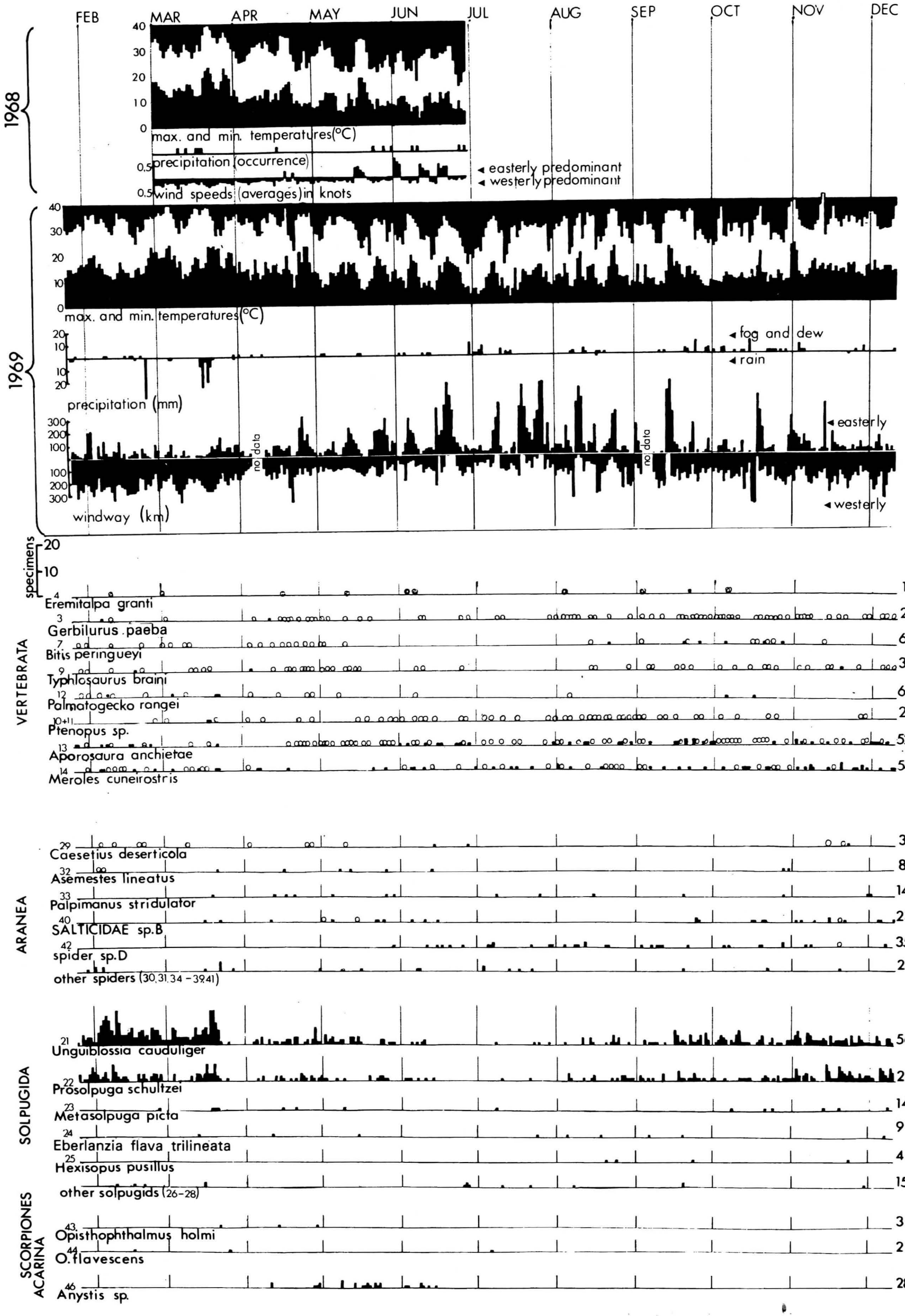

FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1968
max. and min. temperatures(°C)
precipitation (occurrence)
wind speeds (averages) in knots
◄ easterly predominant
◄ westerly predominant
1969
max. and min. temperatures(°C)
◄ fog and dew
◄ rain
precipitation (mm)
no data
◄ easterly
◄ westerly
windway (km)
specimens
VERTEBRATA
Eremitalpa granti
Gerbilurus paeba
Bitis peringueyi
Typhlosaurus braini
Palmatogecko rangei
Ptenopus sp.
Aporosaura anchietae
Meroles cuneirostris
ARANEA
Caesetius deserticola
Asemestes lineatus
Palpimanus stridulator
SALTICIDAE sp.B
spider sp.D
other spiders (30,31,34 – 39,41)
SOLPUGIDA
Unguiblossia cauduliger
Prosolpuga schultzei
Metasolpuga picta
Eberlanzia flava trilineata
Hexisopus pusillus
other solpugids (26–28)
SCORPIONES
ACARINA
Opisthophthalmus holmi
O. flavescens
Anystis sp.

FIG. 2

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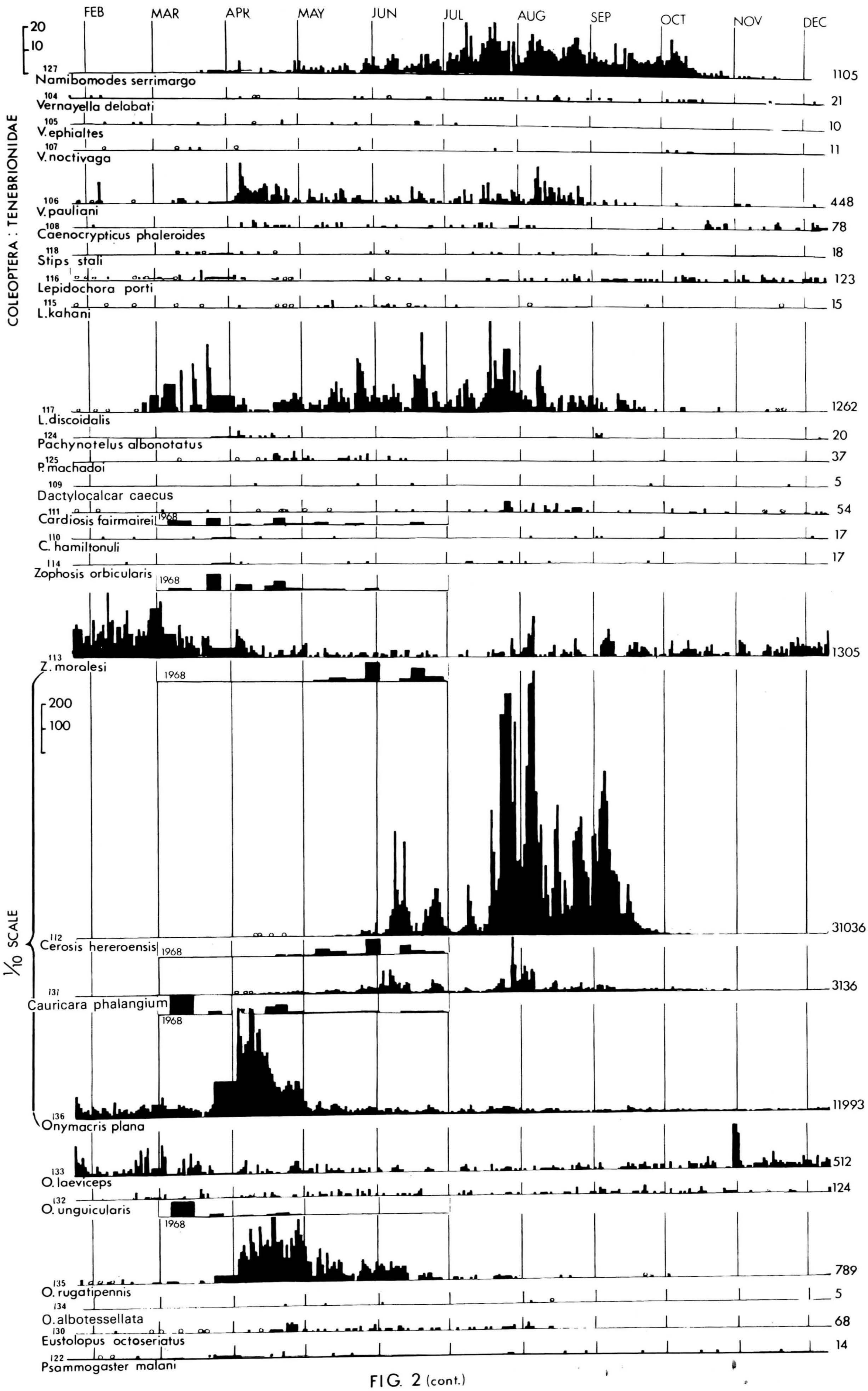
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COLEOPTERA : TENEBRIONIDAE
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104 Vernayella delobati 21
105 V. ephialtes 10
107 V. noctivaga 11
106 V. pauliani 448
108 Caenocrypticus phaleroides 78
118 Stips stali 18
116 Lepidochora porti 123
115 L. kahani 15
117 L. discoidalis 1262
124 Pachynotelus albonotatus 20
125 P. machadoi 37
109 Dactylocalcar caecus 5
111 Cardiosis fairmairei 1968 54
110 C. hamiltonuli 17
114 Zophosis orbicularis 1968 17
113 Z. moralesi 1968 1305
200
100
1/10 SCALE
112 Cerosis hereroensis 1968 31036
131 Cauricara phalangium 1968 3136
136 Onymacris plana 11993
133 O. laeviceps 512
132 O. unguicularis 1968 124
135 O. rugatipennis 789
134 O. albotessellata 5
130 Eustolopus octoseriatus 68
122 Psammogaster malani 14

FIG. 2 (cont.)

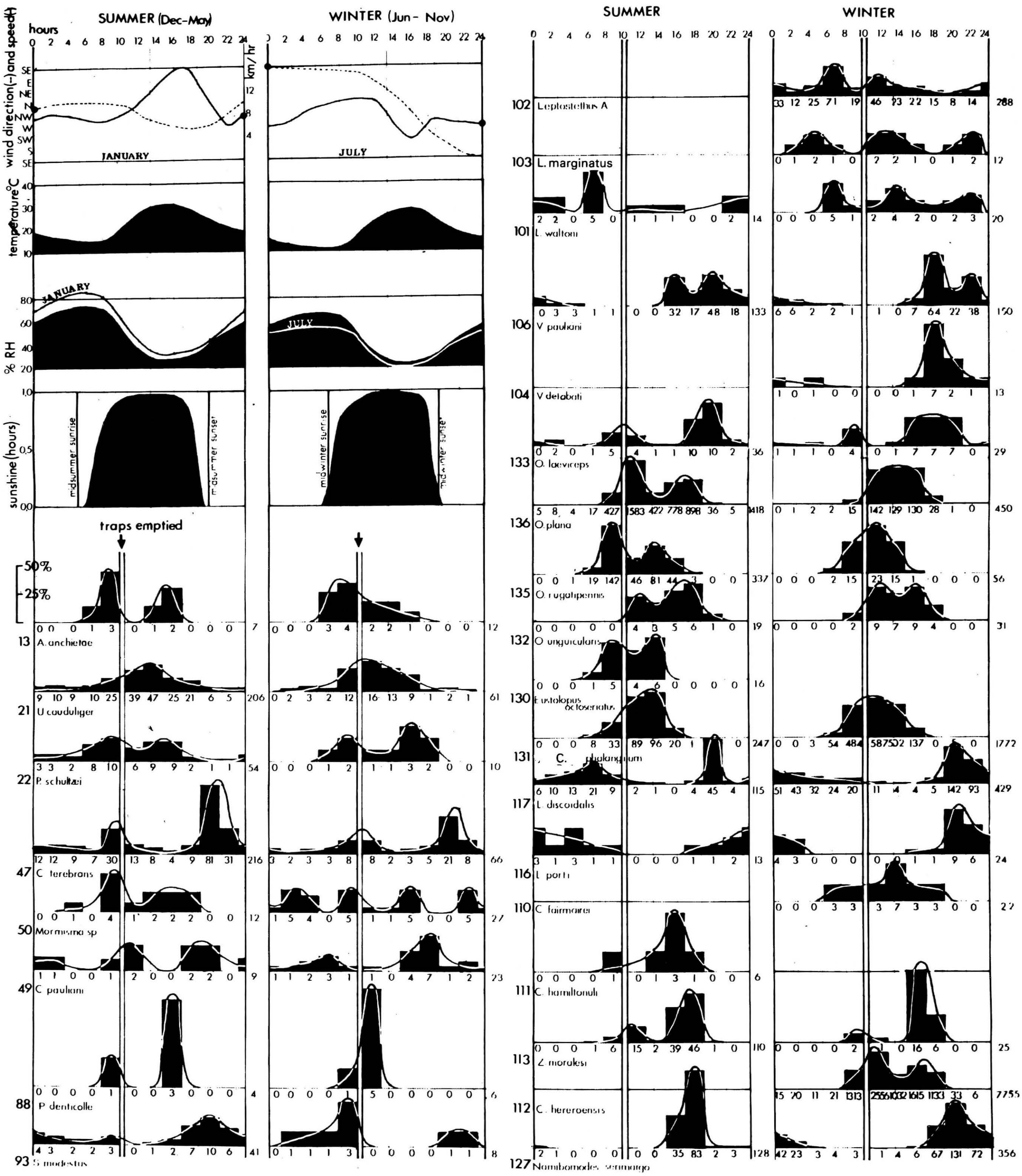


FIGURE 3: Average daily cycles of macroclimate for summer and winter months, with totalled trappings of four timed pit traps. Curves on histograms are hand-fitted for easier reading. Missed or partially missed trapping days on individual traps are omitted from the data.

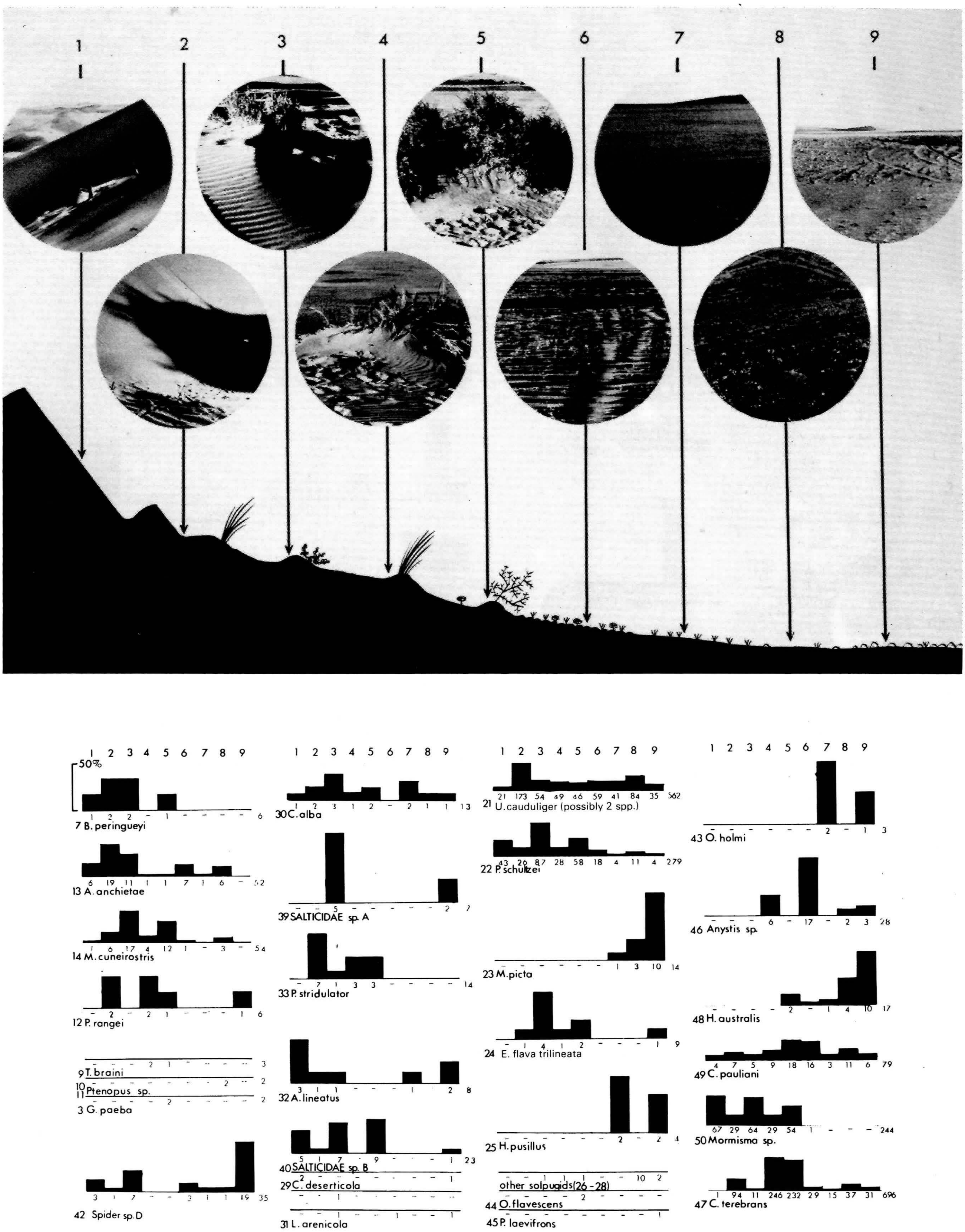
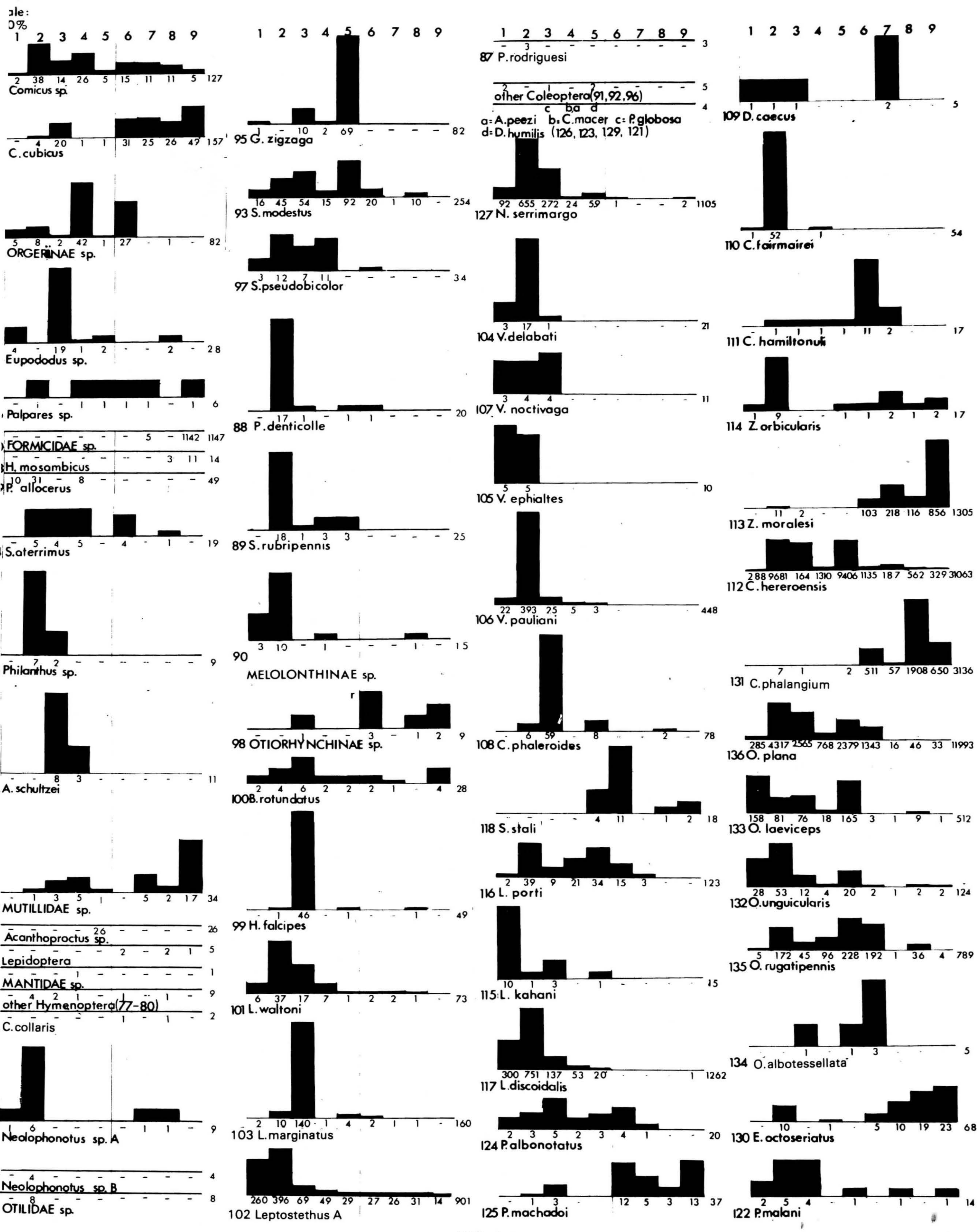


FIG. 4

FIGURE 4: Diagrammatic cross-section through the study area with positions and photographs of the nine trapping stations (plan in Fig. 1), and percentages of the various species trapped in each. Code numbers precede species names, specimens are recorded for every column and are followed by totals. Columns 1 to 9 correspond with trapping stations 1 to 9.
Histograms are crudely corrected for missed trapping days, and are not evaluated statistically (see text).



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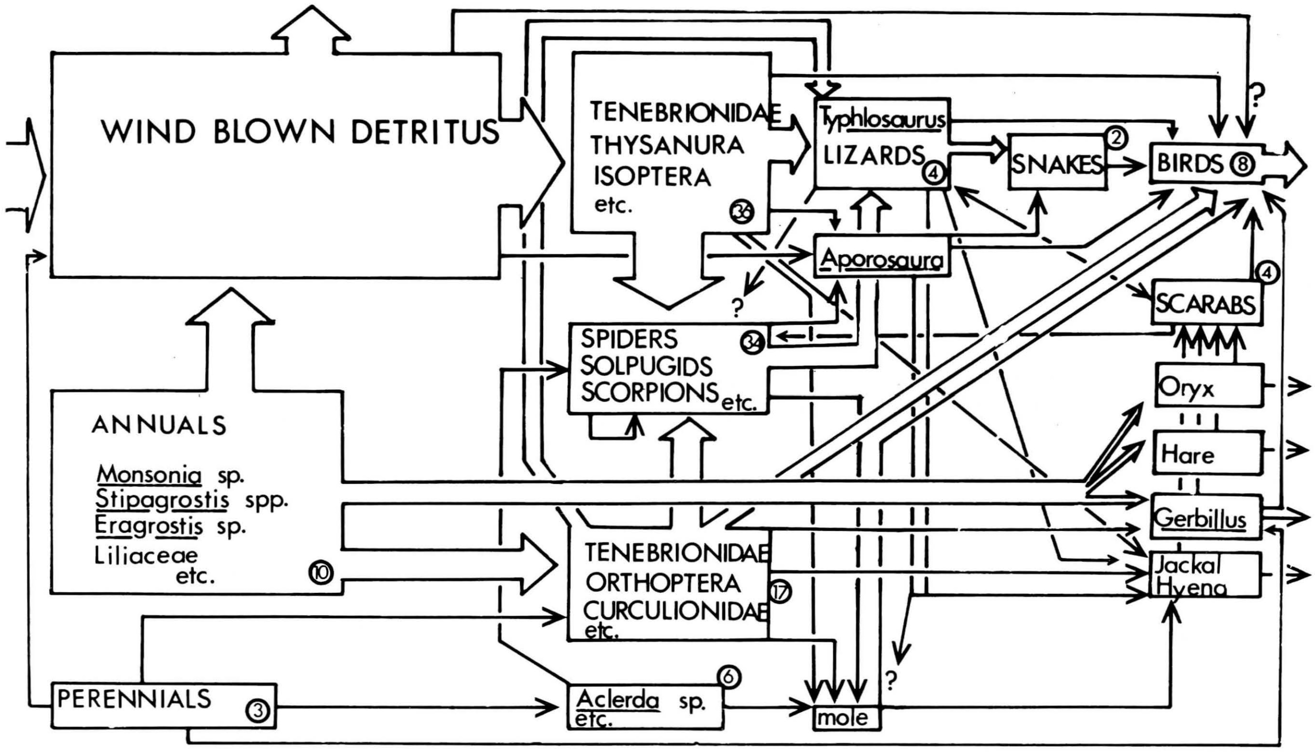

FIG. 5

FIGURE 5: Trophic web of the dune ecosystem south of Gobabeb. Circled numbers are numbers of species in the various trophic categories. Widths of arrows reflect crude estimates of energy flow.

combine well with alateness (none of the sand-diving species is alate). The spatial distribution of detritus deposits, and their persistent nature, probably reduces the need to fly in detritivores, which might add to the high incidence of apterousness in this trophic category, very markedly expressed in the family Tenebrionidae, which is also predominantly apterous in other ecosystems such as e.g. the Kalahari and the savanna systems in Africa.

It is difficult to assign food niches to the various taxa, since virtually all desert animals are more or less euriphagous opportunists. The trophic web given in Fig. 5 must therefore be seen as a rather crude generalisation. For convenience, we shall discuss the arthropods under their predominant functions as primary feeders, detritivores, coprophages and predators.

6.1 Primary feeders

Virtually all primary feeders among the arthropods in the system are dependent on rain and only emerge after rain. Emergence is timed to coincide with the growth stage of the host plant which is then attacked (see Fig. 2). Primary feeders on the perennials include most of the species with wide distribution elsewhere, and with a few exceptions these too were only recorded in the study area after rains. A number of detritivores and omnivores also utilise the green growth after rain, with spectacular increases in their populations, mostly due to influx from surrounding areas and increased activity, sometimes combined with real population build-up (see Nos. 47, 106, 135, 136 in Fig. 2).

A few primary feeders are little or only indirectly affected by rain. These include the floricolous flies and wasps (Nos. 85 – 86, 77 – 80), the narra-cricket (No. 52) and the pseudococcid (No. 62). Most of these, including the unidentified and presumably sap-sucking Heteroptera (Nos. 63 – 65) and the buprestid and meloid species (Nos. 94 – 96) were rare in the study area.

Nos. 53 – 57: Grasshoppers and locusts. Apart from No. 53 which is endemic and apterous, all these orthopterans are widespread alate species which occur after rain and feed on the annual grasses. *Crypsicerus cubicus* (No. 53) is the dominant species and well adapted to the desert conditions. It is cryptically coloured with short antennae which fit into grooves on the head (Brown 1962), and has hindlegs which are bright red on the inside. The species is found on the lower dune slopes and plains where the annual grasses grow after rain (Fig. 4). The first peak in population activity (Fig. 2) was early in April and only first instar nymphs were recorded. Later all stages occurred, and at the end of June much predation by birds and arthropod predators was evident, whereafter the population rapidly declined and disappeared.

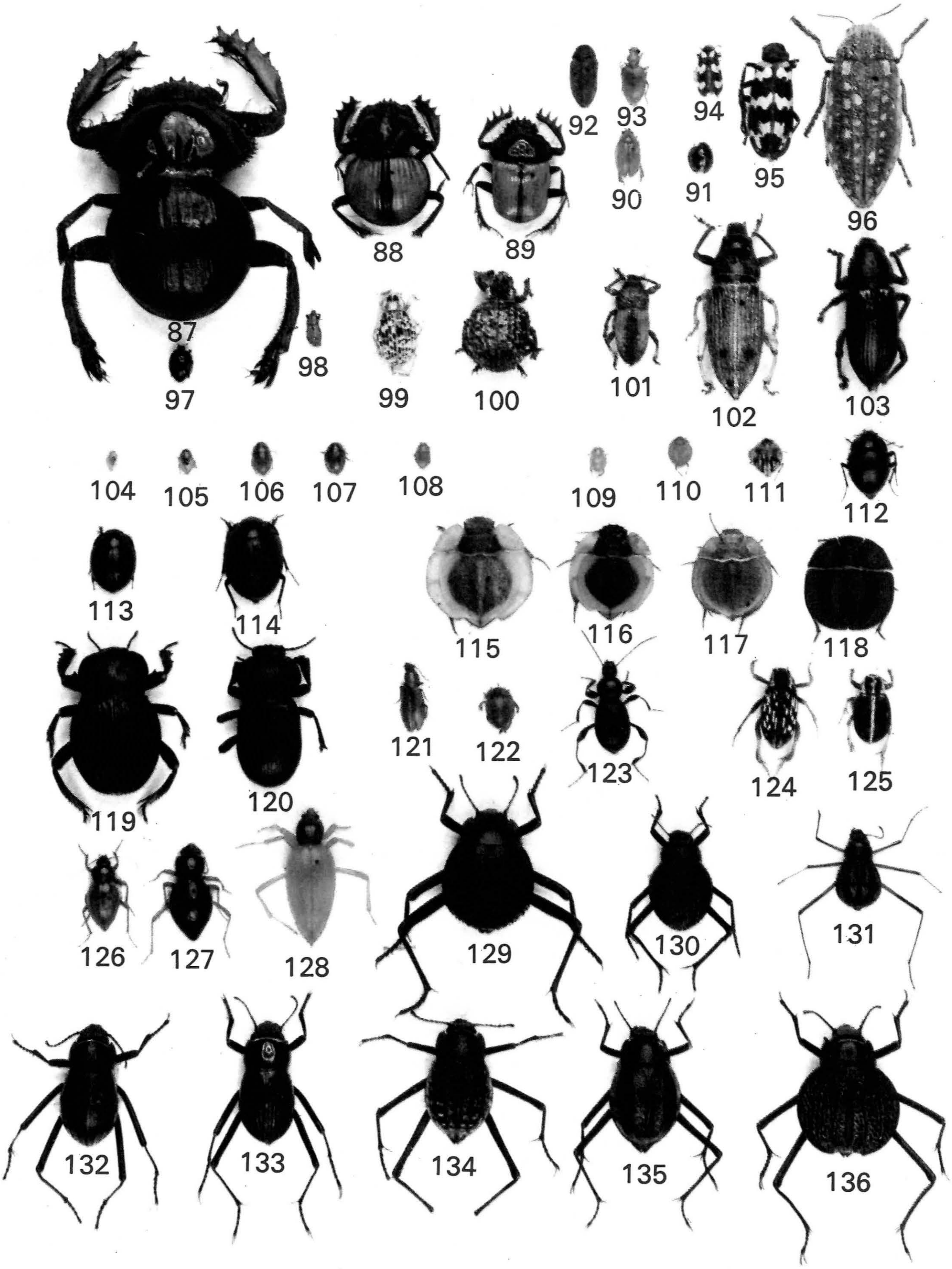

FIG. 6

FIGURE 6: Beetles recorded during the 1969 trapping survey in the dunes south of Gobabeb. Numbers relate to the check-list on p. 34—36.

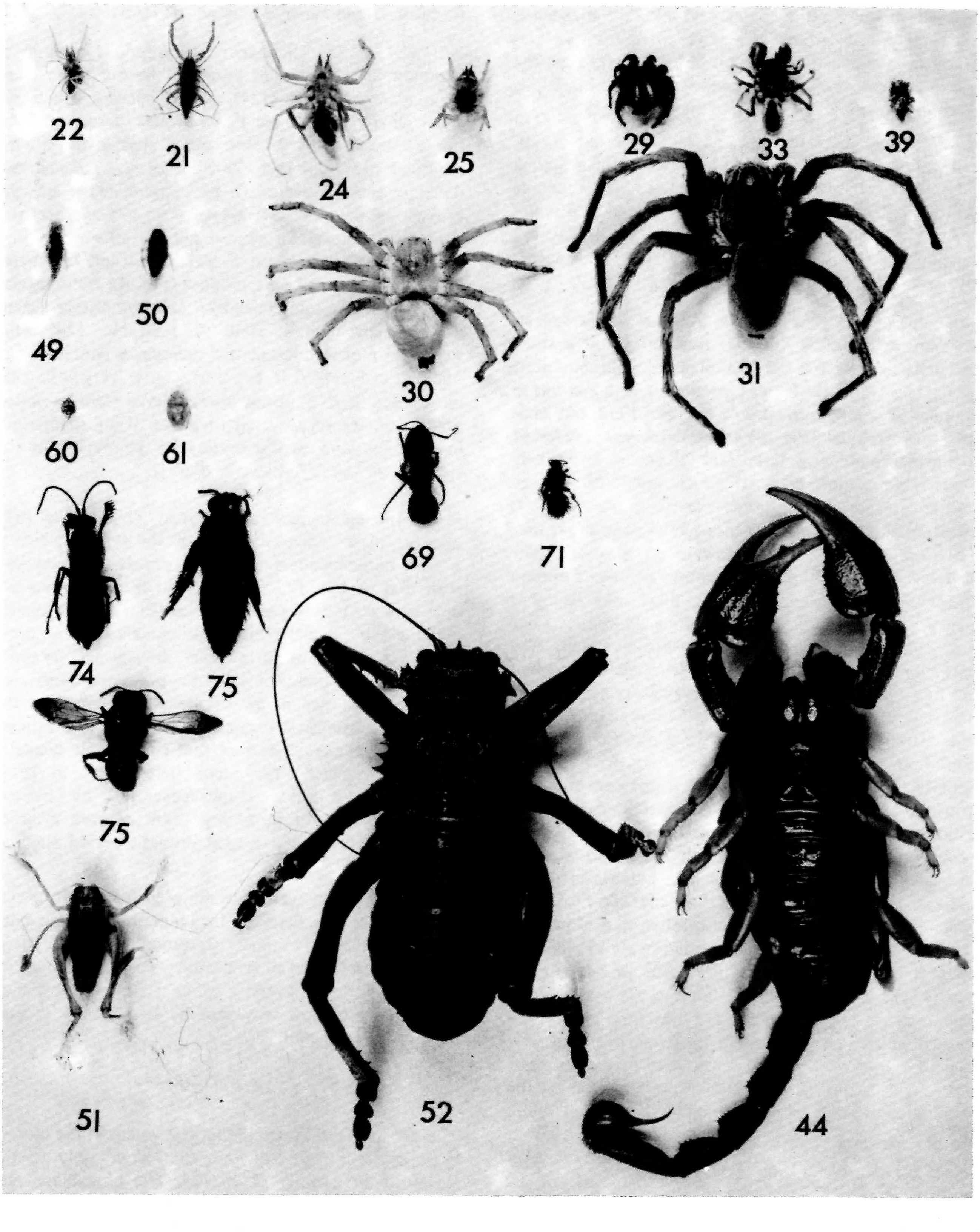

FIGURE 7: Some of the more common non-coleopterous arthropods recorded during the 1969 trapping survey in the dunes south of Gobabeb. Numbers relate to the check-list on p. 34–36.

/ soft-shelled and slow-moving animals by birds
ıropods, the population was not overtaken by
lators, and dead but intact specimens littered
es at the end of July. No. 103 is similar to
habits, but is not as abundant (Fig. 2). It
Trianthema exclusively (Fig. 4).

4 — 125: The *Pachynotelus* spp. The two most ı species of this genus in the study area are *notatus* (No. 124) and a species which we nally hold to be *P. machadoi* (described from thern Namib). Two other species have been l near Gobabeb. No. 125 is the smaller and ommon species (Fig. 2), and feeds on the in the plains (Fig. 4). No. 124 is rare and als survive for shorter periods after rains (Fig. / feed mainly on *S. sabulicola* and are there-stly trapped on the dunes (Fig. 4). Both species clearly rain-dependent, and completely absent years such as 1968. At least No. 124 seems a moisture-terminated quiescence, since a small on emerged in September after very little rain ıst (Fig. 2). Both species have well-developed on the legs, which they use to dig themselves ight, and to dig craters for egg-laying at the f grasses. Activity is diurnal.

0: *Eustolopus octoseriatus*. This is the only of the tribe Adesmiini in the system which is rain-dependent form. Its occurrence coincides at of No. 125 (Fig. 2), and feeding habits are nilar. It is a plains species (Fig. 4) and tunnels sand at night. Single individuals may be found season, but after rains the species becomes ely abundant. In 1967 an estimated density of ecimen per metre square was reached in the and over 3 000 specimens were trapped in a pit three days. The fact that comparable densities ot reached after much better rains in 1969, s that a prolonged quiescence may be possible, could result in a large synchronised crop of ıals after an extended drought period such as d 1967.

te primary feeders were not well covered by this Several species of Lepidoptera occur on both ennial and annual vegetation (Wharton, pers. and at least one aphid species is present. esence and diversity of other alate groups, such Heteroptera, may also be significantly greater flected in our list.

tritivores and omnivores

ritus feeders are the largest group in the system ıs of individuals and are second only to the rs in number of species. The abundance and cal importance of the detritivores in the Namib dune ecosystem has been pointed out by Koch and others (e.g. Lawrence 1959, Seely 1978c). stribution of the abundant detritus to various was described under 'wind' above, and the variety of habitats combined with the heterogeneity of the detritus itself, offers a wide variety of niches to detritivores. The detritus consists of grass seeds, grass blades and stalks, dead arthropods and other animal and vegetable matter. Particle size varies from whole grass clumps to organic dust. Little is known about the feeding preferences of the various detritivore species, but it may be assumed that the energy- and protein-rich parts will be preferred by most species (within their capability of physically ingesting them), and that the quality of a given sample of detritus would decline with feeding much more rapidly than the quantity. Thus the large accumulations of detritus on dune slip-faces may often not signify an abundance of food for all detritivores, and the advantages of exploiting new supplies first may be great. This may explain why the most successful species on the dune crest (e.g. Nos. 110 and 117) are those which are able to withstand the desiccation of eastern storms (which carry the highest load of fresh detritus).

The most important groups in this feeding category are the tenebrionids, with about thirty species and the thysanurans with four. The detritus ant (No. 69) probably contributes substantially to detritus removal, since it is one of the numerically dominant species, but is also predatory on small arthropods. A number of species alternate opportunistically between primary feeding and detritus feeding (see 'primary feeders' above) and few detritivores are not attracted to arthropod or other animal carcasses in their habitat (rotten meat is an excellent bait for virtually all detritivores of the dune crest). Some of the detritivores in our discussion are classified as such by inference rather than observation and in a few cases (e.g. 121, 126, 128) this designation of trophic niche is no more than a guess.

Once detritus becomes submerged in sand, it is even more difficult to establish its fate. In shallowly submerged deposits there are usually some tenebrionid larvae and many thysanurans, and also some of the smaller tenebrionids. It is, however, not known whether all tenebrionid larvae feed on detritus only, since the roots of the perennial plants and even the annuals offer an alternative source of underground food.

Nos. 47 – 50: The thysanurans. These animals, like the tenebrionids and arachnids, are well pre-adapted to desert life by way of their diet, their ability to crawl into small hideouts and their drought resistance. It is likely that myrmecophilous and termitophilous species of thysanurans occur in the area apart from the four free-living species we recorded. No. 49 is the largest, and has black and ochre bands. Its activity is mainly nocturnal-crepuscular (Fig. 3), and it occurs all over the area (Fig. 4) throughout the year (Fig. 2), but was not recorded in February and March, suggesting that the population only became established after the rains. This species either tunnels or sand-dives, and otherwise has the habit of lying in a shallow depression in the sand with the exceptionally long antennae and cerci stretched out on the surface. No. 47 is the most common species and occurs mainly in the sand hummocks under perennials (Fig. 4). Activity is distinctly bimodal in summer and winter, with peaks after sunrise and around sunset (Fig. 3). Activity increased significantly after rain and during spells of east wind (Fig. 2). No. 48 is strictly a plains dweller (Fig. 4) and is a very smooth light silvery grey species. It is present but not common throughout the year (Fig. 2) and is nocturnal. No. 50 is the most specialised species of the group and occurs in the dune crest area (Fig. 4). A distinct diel activity pattern was not recorded (Fig. 3), because the species becomes active during strong winds at any time of the cycle. The yearly trapping data show a near perfect correlation between east wind occurrences and activity of the species (Fig. 2). This as yet undescribed species is cryptically coloured, very robust, virtually naked and has short transformed cerci. It is a very competent sand-diver and was never found far from the slip-faces. Edney (1971a) and Holm & Edney (1973) have reported on behaviour and physiology of some of these thysanuran species.

Nos. 104 – 109: Small nocturnal tenebrionids. It is noteworthy that all these closely related species of below 3 – 4 mm in length are nocturnal. Diurnal activity for this size range of apterous ground-dwellers is probably restricted by the poor volume to surface area ratio and consequent vulnerability to overheating and dessication. The six species all occur on dune sand exclusively, and are sand-diving. They all seem to occur throughout the year, but the activity of No. 106 increased following the rains, and was markedly higher in winter. Habitat niches overlap, with all the *Vernayella* species occurring on the dune crest, with only slight differences in activity on the crest slip-face or slip-face base between the species (Fig. 4). No. 108 is clearly a dune slope species concentrating around *Trianthema*, while No. 109 also seems to occur in the sandier parts of the plains (Fig. 4). We only had the opportunity to observe Nos. 106 and 107 feeding on small detritus particles, but it is not unreasonable to assume that this is what all these species feed on. No. 104, which is the palest and smallest of the species, is more often found in detritus pockets than on the sand surface.

No. 109, which belongs to the tribe Zophosini, is a globose species with extreme morphological adaptations to a submerged way of life, and it probably rarely surfaces. It was previously believed to be blind, but has well hidden and protected eyes (Penrith 1974 and pers. comm.). This group of small tenebrionids showed the greatest degree of niche overlap between species in this study, and would probably need a more refined and intensive approach to be understood.

No. 122: *Psammogaster malani*. This small species is quite unrelated to the above. It is a sluggish crepuscular animal, often found in submerged detritus. It occurs throughout the year (Fig. 2), mostly near the dune crest but also on sandy spots throughout the area (Fig. 4).

ly widespread, but as it is restricted to the dunes se to river-beds and mountains it may be regarded a marginal species in the study area.

. 131: *Cauricara phalangium.* Ecologically this cies belongs to the previous group, since it is a fast l small diurnal tenebrionid. It belongs to a different e, however, and has a very different morphology l behaviour from the species above. The extremely g legs of the species enable it to achieve high ed on the plains, and also serve to lift the body ay from the hot sand surface (Henwood 1975a) d thus to enable it to be active throughout the on period (Fig. 3). It is strictly a plains dweller ig. 4) and is winter active (Fig. 2). The slender ild of these beetles is a disadvantage under windy nditions, and unlike the other detritivores, it is most tive between spells of east wind (Fig. 2). Sand- ving is also impossible for this species, and at night ey attach themselves to grass clumps and pebbles, iere they are preyed upon by spiders, solpugids d scorpions, which usually leave the thorax, head and gs of the beetles still firmly attached to the grass ems. The trophic, habitat and diel activity niches of is species overlap widely with those of No. 113, d the population of the latter decline when *C. alangium* becomes active. Food is, however, much ore plentiful in winter, which makes it possible for . *moralesi* to maintain a population in spite of much che overlap with *C. phalangium.*

os. 115 — 118: The Eurychorini. These are all octurnal species of medium size and with more or less rcular and flat bodies, probably originally evolved for ving under bark and rock, and further adapted to and-diving by the loss of sculpture and the addition f scales in the genus *Lepidochora.* The *Lepidochora* pecies are heavily preyed upon by *Palmatogecko* and piders, and instances of predation by both were often een. No. 115 is the largest of the species occurring Gobabeb. It occurs throughout the year (Fig. 2), strictly nocturnal, and it is restricted to the dune rest area (Fig. 4). No. 116 is smaller than the revious species, and not as flat. It occurs on the une slopes (Fig. 4) and is more active in summer Fig. 2). The activity is strictly nocturnal and decreases ith decrease in temperature, with a resultant marked hift to the early night hours in winter (Fig. 3). oth No. 115 and 116 are able to withstand low emperatures, and were found on the surface at ambient emperatures of below 5°C. No. 117 is much more bundant and active than the previous two species, nd clearly more so in winter and after rain (Fig. 2). ctivity is very closely correlated with wind, as in the ase of other dune crest detritivores. This species only aves the slip-face when it migrates to another (Fig. 4). ince we had no timed trap on the slip-face, the diel ctivity in Fig. 3 is based on traps outside the normal icrohabitat of the species. It consequently reflects iese odd migrations and is therefore rather misleading. n the slip-faces activity is crepuscular-nocturnal, but ie animals come out and forage *en masse* during the day whenever wind is strong enough to import detritus. One morphological feature of the species which distinguishes it from the other *Lepidochora* species and is probably an adaptation to the facultatively diurnal way of life, is the pigmentation of the body. Apart from the *Onymacris* spp., this species has attracted most attention from physiologists and ethologists (Kühnelt 1969; Louw & Hamilton 1972; Seely & Hamilton 1976; Hamilton & Seely 1976 and references under general tenebrionid work below). No. 118 is a dune foot species at Gobabeb (Fig. 4), and clearly a plant satellite throughout its distribution. It was found to be strictly nocturnal, it occurred throughout the year and was more active after rains (Fig. 2). Its niche overlaps with that of No. 116, but we suspect that factors other than time/space niche differences separate these two species.

Nos. 132 – 136 and 129: The large Adesmiini. Most of the studies on physiology, behaviour, morphology and biology on Namib insects were done on the members of this group (Edney 1971a, b; Hamilton 1973, 1975; Hamilton, Buskirk & Buskirk 1976; Hamilton & Seely 1976a, b; Henwood 1975a, b; Holm & Edney 1973; Marcuzzi & Lafisca 1977; Roer 1971, 1975; Seely in press), and their taxonomy and habitat preferences have also recently been thoroughly revised (Penrith 1975, 1979). Little therefore remains to be added, and we only give some brief notes of our own.

Nos. 129 and 135 are immigrants into the study area from the Kuiseb River after rain. The latter species managed to maintain a population on the dune slopes (Fig. 4) for several months after the rain in 1969 (Fig. 2). Both species are strictly diurnal and are clearly plant satellites. The distribution is closely associated with river-beds and the relict population at Meob is therefore very interesting (Fig. 8). No. 134, which is held to be a subspecies of No. 135 by Penrith (1975, 1979), has a waxy covering, is diurnal and occurs on the overgrown inland dunes independently from river-beds (Fig. 8). It only reaches as far west as Gobabeb occasionally. The habitat preference is slightly different from No. 134 (Fig. 4), and the larval and ecological differences suggest that No. 134 and 135 are sibling species rather than subspecies of each other. The three species are not very efficient sand-divers, and shelter just submerged under soft sand beneath plants at night.

Nos. 132, 133 and 136 are highly adapted dune species. No. 136 is a fast diurnal runner (Fig. 3) on the dune slopes (Fig. 4), which shelters under dune grass or narra-hummocks between spells of running, and at night. Individuals may apparently spend months submerged in the sand under narra-bushes (Roer 1971). Like the other large tenebrionids they may have an adult lifespan of several years (one specimen marked at an unknown age was retrieved alive after two years). The species is widespread in all parts of the central Namib dunes except on the coast (Fig. 8), and a subspecies occurs in the southern Namib dunes. Apart from detritus, this species was seen to feed on narra-seeds and a variety of dead vertebrates and arthropods. The rains late in 1968 and early in 1969 had a spectacular effect on the dune population (Fig. 2). Nos. 132 and 133 are very similar in size and appearance, and occupy very much the same niche. Both are crepuscular but not strictly so, and No. 133 is sometimes active throughout cool days and warm nights (Fig. 3), while No. 132 is crepuscular on the inland edge of its distribution while it is diurnal at the coast. These and other morphological and behavioural differences in these two ecological equivalents clearly illustrate the differences in the inland and coastal dune environments to which they are respectively adapted. Thus No. 133 in the dry and hot inland has a white wax secretion on the integument, which is lacking in No. 132, but lacks the grooves on the elytra which seem to assist with "fog basking" (Hamilton & Seely 1976a, b) – perhaps more appropriately "fog bathing" – by which No. 132 collects the frequent fog precipitations in its habitat for drinking. No. 133 climbs up *S. sabulicola* stems when these plants are in seed and feed on the seeds, while No. 132 in its relatively vegetationless habitat has not acquired this habit. Both species sand-dive in the slip-face for shelter, and forage mainly near the slip-face base and to a lesser extent on the dune slopes and slip-face. No. 133 is decidedly more active in summer, when fewer of No. 132 were recorded at Gobabeb (Fig. 2). No. 132 was not recorded at Gobabeb between 1960 and 1968, but was present from then on and seems to be disappearing from the area now (Seely, pers. comm.). Neither species seems to have benefited directly from the rain-flora, as would be expected of dune crest dwellers (Fig. 2).

The tribe Molurini is relatively poorly represented in the dunes (No. 127 and 128). No. 127 is a common species which is found in association with *S. sabulicola* hummocks near the dune crest system (Fig. 4), and population activity is significantly higher in winter and is closely correlated with east wind spells (Fig. 2). Activity is nocturnal, and drops with temperature (Fig. 3). A second species, *N. zarcoi*, is more confined to the dunes on the Kuiseb river-bank. No. 128 was not recorded in the study area in 1969, but has since been collected there. It is a strictly nocturnal species which seems to be active only after rain, and which probably has short-lived adults.

No. 126 is nearly as rare as No. 128. Only one specimen was trapped at Gobabeb in 1969, and very few have ever been collected. We suspect adults of this species have a very short period of above-ground activity. At Tsondabvlei a number of adults was dug out from deep under a *S. sabulicola* tuft. The species seems to be limited to the marginal dunes near river-beds (Fig. 8).

No. 123 is a very common species at the coast, where it occurs in a niche similar to that of No. 127. At Gobabeb we recorded it on three occasions (Fig. 2), but it is clear that it occurs there marginally and may be completely absent at times. At the coast it is present abundant in summer.

ne-edge species which
d washes in the insel-
near vegetation. They
may occasionally be
ult to decide to what
he dune system form
y. Other tenebrionids
hysa spp. may also
e areas and may even
limited scale. Apart
groups and species of
studies have dealt with
eb in general, or with
oups. Apart from the
1962a, b) studies by
1975), Holm & Edney
eely (1973) were also

ust mention the ants
os. 58, 59). Of these
tive in the system at
r after rain, and gra-
ee No. 70 on Fig. 2).
d elsewhere, and their
contribution to detritus
ed by our methods.
ot only detritivorous,
No. 62 for honeydew,
rthropods. Nests seem
e "war" between two
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tors in the dunes is
at of primary feeders
dering their position
The fourteen spider
scorpions which were
plete list for the area;
or twice, and the
not recorded at all

prey on small geckos
and solpugids were
rionids (*Lepidochora*,
ra species). Smaller
sanurans and ants.
between the arachnid

ecies were low, and a
fore precluded. The
has been commented
es below), and an
presently underway
mm.). We therefore
own which do not on

their own do justice to this group (which is evolutionally, behaviourally and ecologically at least as interesting as the tenebrionids in the Namib dunes).

Nos. 29 – 42: The spiders. While trapping results of all spiders were low (Fig. 2), some of the species' habitat preferences can be read from Fig. 4. The salticids (Nos. 39 – 41), palpimanids (Nos. 33, 38) and thomicid (No. 35) are invariably found in or near plants, while the large nocturnal sparassids (Nos. 30, 31, 34) hunt over the whole area. No. 30 is often found on the dune crest, and has the unique behaviour of "cartwheeling" down the slip-face to evade enemies. All sparassids dig tunnels in the firm dune slopes in which they shelter in daytime. One of the most extremely adapted spiders is No. 29, which lives in the loose sand of the slip-face near the crest. It is a small, very robust species with short hairy legs, and can bury itself very rapidly in the soft slip-face by lying on its back and working the sand around it upwards with the legs.

Nos. 21 – 28: The solpugids. The three diurnal species (Nos. 21 – 23) were trapped in much larger numbers than the remaining five nocturnal species and are all more abundant in summer (Fig. 2). No. 21 occurs all over the area (Fig. 4) and is highly thermophilic, being most active at noon, both in summer and winter (Fig. 3). No. 22 is similar in size, prefers the dune slopes (Fig. 4) and has a bimodal-diurnal activity cycle in summer and winter (Fig. 3). The latter species is reddish like the dune sand, and hunts on the ground as well as up the stems of *S. sabulicola* plants. Nos. 23 and 25 are clearly restricted to the plains, with the former diurnal and the latter nocturnal. No. 25 is very robust and buries itself in the sand as does spider No. 29.

Nos. 43 – 45: The scorpions. Very few of these were trapped, but habitat preferences could be determined from burrows. No. 43 tunnels in sandy spots in the interdune plain, No. 44 under plants near the dune foot and No. 45 is petrophilous.

No. 46: The velvet mite. These bright red predatory mites occurred after rains in the dunes and the population persisted for about three months (Fig. 2) on the lower dune slopes and interdune plains (Fig. 4).

The arachnid fauna of the Namib Desert has been studied extensively by R. F. Lawrence (1959, 1962a, b, 1965a, b, 1967, 1969, 1972) and subsequently by Lamoral (1972) and Newlands (1972).

Predators amongst the insects are, with a few exceptions, alate and wide-spread species. The two tettigoniids (No. 51 and 52) are at least partially predatory. No. 51 is strictly nocturnal and occurs throughout the year (Fig. 2) mainly on the dune slopes (Fig. 4). This species, like some of the thysanurans, is often found in a shallow depression on the slopes, with the extremely long antennae stretched out on the sand surface. Whether or not this is an ambush posture could not be established. No. 52 was only found near narra bushes (Fig. 4) or traversing dune slopes from one of these to the other. Of the predacious hemipterans, only No. 61 was trapped in significant numbers. This species occurs throughout the year (Fig. 2) mainly under *Trianthema* (Fig. 4). The neuropterans of the Namib have not been studied systematically, and it is possible that more than two species (No. 66, 67) occur in the dunes at Gobabeb. Both species were rarely seen (Fig. 4). The only mantid species (No. 68) was found in a *Trianthema* plant.

Of the large number of hymenopterans, only the dominant ones were recorded, and only the two apterous species were trapped in significant numbers (No. 71 and 72). Both occurred throughout the year (Fig. 2), with No. 71 on the dune slopes and the much smaller No. 72 mainly in the interdune plains (Fig. 4). The most common wasp in the dunes is No. 74 (Fig. 2), which tunnels in the dune slopes but hunts spiders, mainly sparassids, in all habitats (Fig. 4). The parasitic No. 76 is as yet the only recorded encyrtid species from the area, and was bred from No. 62 (Prinsloo & Annecke 1976).

A revision of the Miscophini (Sphecidae) with very interesting data on the Namib fauna, is at present in preparation (Ole Lomholdt, in prep.). Through courtesy of the author we have had parts of the manuscript which deal extensively with matters of zoogeography and adaptation in this group, and contains many interesting notes, but we prefer not to forego the publication of these results here.

Amongst the flies, two asilid species (Nos. 82, 83) were regularly seen. Both occurred throughout the year (Fig. 2) and hunted mainly on the dune slopes (Fig. 4). No. 82 was seen to take *Cerosis* (No. 112) on several occasions. The flies of South West Africa were revised recently by Lindner (1972, 1973, 1975), but no systematic survey of the dune-living forms has been done.

Three predacious beetles were recorded (Nos. 91, 93 and 97), and the larvae of the meloids (Nos. 94 and 95) are known to be predators, mostly on eggs of locusts and grasshoppers. No. 91 is a predator of aphids, which occur mainly on *S. sabulicola* grass. No. 97 is present throughout the year (Fig. 2) on dune sand (Fig. 4), and the histerids are known to feed mainly on maggots. No. 93 belongs to a tribe which is myrmecophilous, and this carabid is probably associated with the detritus ant (No. 69). Although it occurs throughout the year, a significant increase in activity was noted after the rains early in 1969 (Fig. 2). The beetles roam around hummocks of perennials on the dune slope (Fig. 4) at night. They are common throughout the central Namib dunes.

6.4 Coprophages and scavengers

While most detritivores will be attracted to carcasses to feed on them, a number of species are specialists in this food niche. Coprophages are few, and detritivores were never seen to feed on droppings.

The biology of the two wingless scarabs (*Pachysoma* spp. Nos. 87, 88) was recently described (Holm & Scholtz 1979, Holm & Kirsten 1979), and will be only briefly mentioned. No. 87 is a large species which occurs where oryx graze after rain, and forages exclusively on their dung. No. 88 is a small species which feeds on any droppings it can find, and also forages vegetable matter. This species is therefore intermediate between a coprophage and a detritivore. A small *Onthophagus* sp. was recorded on two occasions in the dunes, but is not included in the list since the records are most probably of stray specimens from the nearby Kuiseb river-bed. Both *Pachysoma* species are more abundant after rain (Fig. 2), and are strictly diurnal (Fig. 3). Their tunnels are excavated in the firmer parts of dune slopes (Fig. 4).

No. 84 is a small fly which may be found on the *Pachysoma* species as well as on No. 89, and these flies obviously use the scarabaeids to transport them to food. On several occasions the scarabaeids were seen entering their burrows with forage, and with flies on their back, to emerge without either. The advantages of apterousness in the Namib dunes are strikingly illustrated by this alate species being a transport-commensal of an apterous species.

No. 89 is a scavenger, and was only found to feed on carcasses. It has the same time and space niche as the *Pachysoma* species, and a similar distribution (see Holm & Kirsten, 1979). No. 92 is a well-known and cosmopolitan scavenger, but was rarely recorded in the study area since, unlike No. 89 which is attracted to dead lizards, snakes and gerbils, it only breeds in carcasses of large animals.

7 SPACE-TIME NICHES

In a previous paper (Holm & Edney 1973) the diel activity patterns of some of the arthropods as illustrated by timed trappings were discussed. Experiments with *Aporosaura* (Holm 1973) support the theory that unimodal diurnal winter activity and bimodal diurnal summer activity are temperature induced strategies, at least in this species, and also clearly showed these patterns to be innate in this species. One possible reason for the differences between the rhythms of different species which Holm & Edney (1973) mentioned was the niche-exclusion principle, and when annual and spatial distributions are compared with diel activities, there seems to be more evidence for this, as examination of groups of closely related species may show:

Five *Onymacris* species occur at Gobabeb, of which one (No. 135) is an opportunistic intruder in the area after rain, and not part of the normal niche pattern. The remaining four species occur throughout the year (Fig. 2). No. 132 is a coastal species which overlaps

ıread of prey species over time
prey scarcity, and therefore
rt for predators, (ii) synchro-
in each species for intra-
mating, territoriality, etc.),
ıllopatric activity of different
ative interspecies interactions
on for shelter and food) and
in morphological and physio-
different habitat and climate
ition might strengthen habitat
ne food source is fed on at
lifferent species (Robinson &

D DISTRIBUTION OF

f the 50 beetle species recorded
b is given in Fig. 8, and that
arabs is given in Holm &
e remaining 13 species, No.
entral Namib, whilst numbers
nown to be widespread. The
ining 9 species is insufficiently
cies are rare in the study area,
e marginally.

Gobabeb dune species with
s that 25 (or 60 %) are endemic
ıne area. A further 5 (or 12 %)
and southern Namib, and the
central and northern Namib.
occur throughout the Namib,
demism of the dune bettles at
to 76 % in the unlikely case
h unknown distribution prove
w of the beetles have been
allow an analysis of sub-
it may safely be predicted that
Generic endemism for the dune
out 50 % for the whole Namib,
0 %) are endemic to the central

mainly apterous, and may be
ers, plains runners and satellites
rops. The non-endemic species
ic immigrants.

species may further be divided
central group, an inland group
read species. At Gobabeb the
ominate (Nos. 87 – 89, 93, 99,
07, 108, 109, 110, 112, 115,
astal species which occur up to
123 and 132, while Nos. 104,
3 and 136 are typical central
esting and at present inexplic-
ccur in the dunes from south to
g being one between Koichab

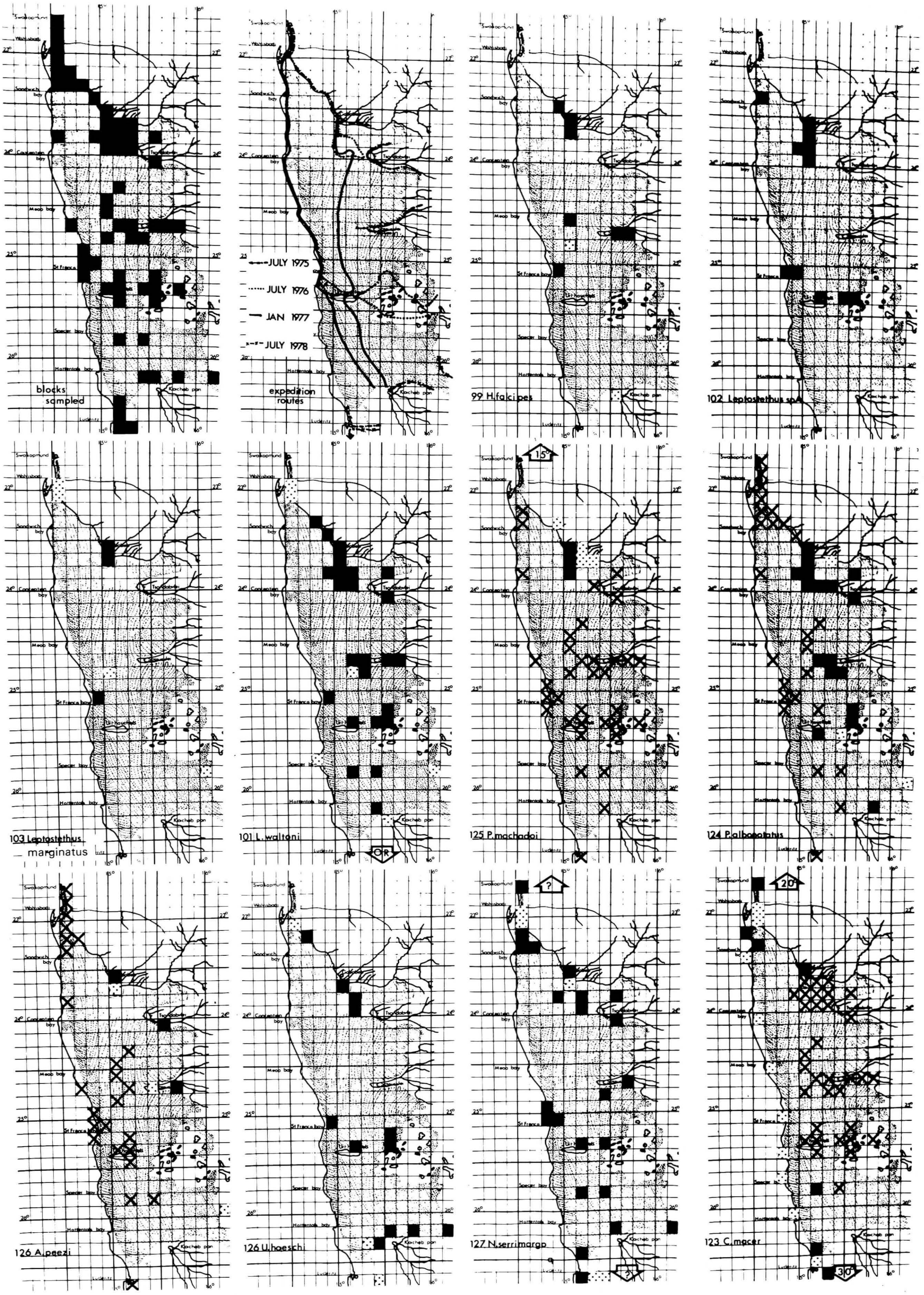
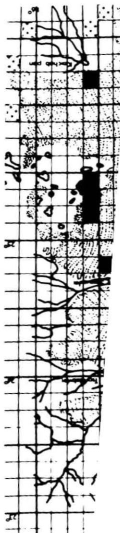


FIGURE 8: Maps of the central Namib with total blocks censussed from 1975 to 1978, routes of the four expeditions and recorded distribution for 34 of the beetle species of the Gobabeb dunes. Stippling indicates dune ranges, black blocks are records from our survey and dotted blocks records from other collections (see acknowledgements). The latter blocks vary in accuracy, up to an error of ¼°. Crosses are blocks in which we have reason to believe species do not normally occur.



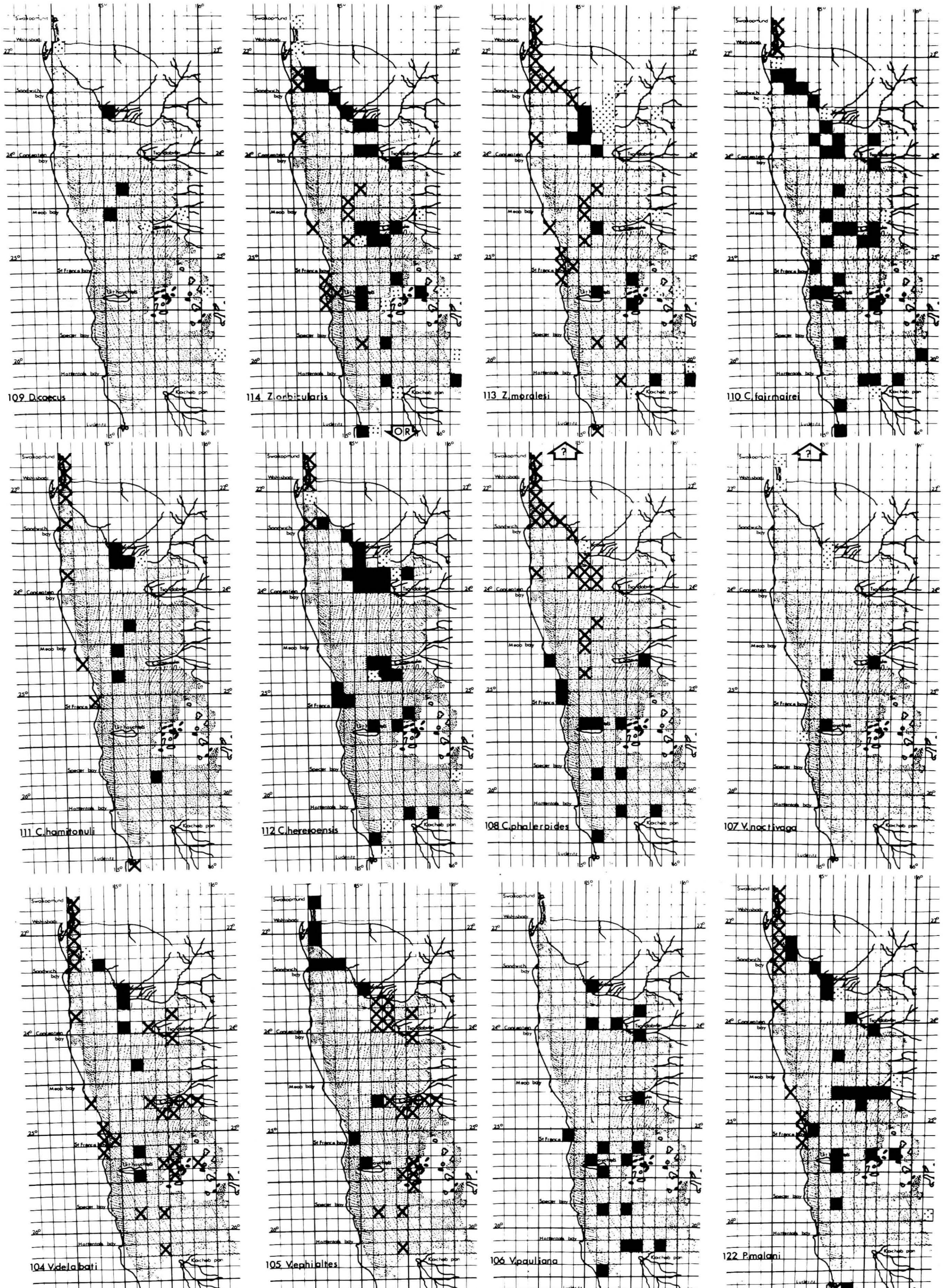

109 D.coecus
114 Z.orbicularis
113 Z.moralesi
110 C.fairmairei
111 C.hamiltonuli
112 C.hereroensis
108 C.phaleroides
107 V.noctivaga
104 V.delabati
105 V.ephialtes
106 V.pauliana
122 P.malani

Fig 8 (cont)

ena would overstep the aims
ch occur in this category
121, 126, 129, 130, 134
pected, this group contains
extend beyond the central

r that distribution limits of
nt, but extend and contract
the periphery of the species'
32 was not recorded at
has been constantly present
seems to be disappearing
rs. comm.). Similarly, No.
ars and not in others, and
nly found at Gobabeb after
collecting. Most boundaries
s are unlikely to be main-
(with the exception of some
en coastal species) the areas
related species are generally
likely determined by niche

G. vallinus (Thomas))
nsis Bauer & Niethammer

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bensis Broadley
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31	–	–	*Leucorchestris arenicola* Lawrence
32	–	Drassidae	*Asemesthes lineatus* Purcell
33	–	Palpimanidae	*Palpimanus stridulator* Lawrence
34	–	Sparassidae	*Orchestrella browni* (Lawrence)
35	–	Thomicidae	*Hirrius bidentatus* Lawrence
36	–	Drassidae	*Camillina corrugata* Lawrence
37	–	Eresidae	*Seothyra* sp.
38	–	Palpimanidae	*Palpimanus namaquensis* Simon
39	–	Salticidae	a. (yellow species)
40	–	–	b. (yellow species with black stripe)
41	–	–	c. (species with red carapace)
42	–	?	d. (cryptically mottled species)
43	Scorpiones	Scorpionidae	*Opistophthalmus holmi* (Lawrence)
44	–	–	*Opistophthalmus flavescens* Purcell
45	Scorpiones	Buthidae	*Parabuthus laevifrons* Simon
46	Acari	Anystidae	*Anystis* sp.
47	Thysanura	Lepismatidae	*Ctenolepisma terebrans* Silvestri
48	–	–	*Hyperlepisma australis* Wygodzinsky
49	–	–	*Ctenolepisma pauliani* Wygodzinsky
50	–	–	*Mormisma* sp.
51	Orthoptera	Tettigoniidae	*Comicus* sp.
52	–	–	*Acanthoproctus* sp.
53	–	Acrididae (s. lat.)	*Crypcicerus cubicus* Saussure
54	–	–	*Trachypetrella andersoni* (Stål)
55	–	–	*Acrotylus patruelus* (Herrich-Schaeffer)
56	–	–	*Scintharista magnifica* Uvarov
57	–	–	*Sphyngonotus scabriculus* (Stål)
58	Isoptera	Hodotermitidae	*Hodotermes mosambicus* (Hagen)
59	–	Rhinotermitidae	*Psammotermes allocerus* Silvestri
60	Hemiptera	Dictiopharidae	Orgeriinae sp.
61	–	Cydnidae	*Eupododus* sp.
62	–	Coccidae	*Aclerda* sp.
63-65	–	(Unidentified Heteroptera spp.)	
66	Neuroptera	Myrmeleonidae	*Palpares* sp.
67	–	–	(Unidentified sp.)
68	Dictyoptera	Mantidae	(Unidentified yellow sp.)
69	Hymenoptera	Formicidae	*Camponotus detritus* Emery
70	–	–	(Unidentified small black sp.)
71	–	Bradynobaenidae	*Apterogyna schultzei* Andre
72	–	Mutillidae	(Unidentified small yellow sp.)
73	–	Scoliidae	*Campsomerus collaris* Sichel
74	–	Pompilidae	*Schistonyx aterrimus* Arnold
75	–	Philanthidae	*Philanthus* sp.
76		Encyrtidae	*Mayridia arida* Prinsloo
77-80	–	(Unidentified Apocrita spp.)	
81	Diptera	Otilidae	(Unidentified sp.)
82	–	Asilidae	*Neolophonotus* sp. a. (large)
83	–	–	*Neolophonotus* sp. b. (small)
84	–	Sphaeroceridae	*Leptocera* sp.
85-86	–	(Unidentified Cyclorrhapha spp.)	
87	Coleoptera	Scarabaeidae	*Pachysoma rodriguesi* (Ferreira)
88	–	–	*Pachysoma denticolle* Péringuey
89	–	–	*Scarabaeus rubripennis* (Boheman)
90	–	–	(Melolonthinae sp.)
91	–	Coccinellidae	*Exochomus* sp.
92	–	Dermestidae	*Dermestes maculatus* de Geer
93	–	Carabidae	*Singiliomimus modestus* Péringuey
94	–	Meloidae	(Unidentified small sp.)

95	–	–	*Gorrisia zigzaga* Marseul
96	–	Buprestidae	*Julodis mitifica* Boheman
97	–	Histeridae	*Saprinus pseudobicolor* Marseul
98	–	Curculionidae	(Otiorhynchinae, small green sp.)
99	–	–	*Hyomora falcipes* Marshall
100	–	–	*Brachycerus rotundatus* Péringuey
101	–	–	*Leptostethus waltoni* Waterhouse
102	–	–	*Leptostethus* sp. a (large, blue)
103	–	–	*Leptostethus marginatus* Waterhouse
104	–	Tenebrionidae	*Vernayella delabati* Koch
105	–	–	*Vernayella ephialtes* Koch
106	–	–	*Vernayella pauliani* Koch
107	–	–	*Vernayella noctivaga* Koch
108	–	–	*Caenocrypticus phaleroides* Koch
109	–	–	*Dactylocalcar caecus* Gebien
110	–	–	*Cardiosis fairmairei* Péringuey
111	–	–	*Cardiosis hamiltonuli* Koch
112	–	–	*Cerosis hereroensis* Gebien
113	–	–	*Zophosis (Gyrosis) moralesi* (Koch)
114	–	–	*Zophosis (Gyrosis) orbicularis* Deyrolle
115	–	–	*Lepidochora kahani* Koch
116	–	–	*Lepidochora porti* Koch
117	–	–	*Lepidochora discoidalis* (Gebien)
118	–	–	*Stips stali* (Haag)
119	–	–	*Gonopina tibialis* (F.)
120	–	–	*Parastizopus armaticeps* (Péringuey)
121	–	–	*Derosphaerius humilis* Péringuey
122	–	–	*Psammogaster malani* Koch
123	–	–	*Carchares macer* Pascoe
124	–	–	*Pachynotelus albonotatus* Haag
125	–	–	*Pachynotelus machadoi* Koch
126	–	–	*Archinamibia peezi* Koch
127	–	–	*Namibomodes serrimargo* (Gebien)
128	–	–	*Uniungulum hoeschi* Koch
129	–	–	*Physadesmia globosa* (Haag)
130	–	–	*Eustolopus octoseriatus* Gebien
131	–	–	*Cauricara phalangium rufofemorata* (Gebien)
132	–	–	*Onymacris unguicularis* (Haag)
133	–	–	*Onymacris laeviceps* Gebien
134	–	–	*Onymacris albotessellata* Schulze
135	–	–	*Onymacris rugatipennis* (Haag)
136	–	–	*Onymacris plana plana* (Péringuey)

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