

# Structure and pattern of the Namib Desert dune ecosystem at Gobabeb

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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.

## 1 INTRODUCTION

This paper is primarily intended as a field guide to the Namib Desert dune ecosystem in the area south of Gobabeb. The unique ecology of the Namib dunes has attracted researchers from across the world to the research station at Gobabeb. A field guide for scientists to the general ecological pattern of the system is long overdue.

We have condensed data which one of us (E. H.) collected during a three-year stay at Gobabeb (1967 – 1970), and which was previously only available as an unpublished MSc thesis of the University of Pretoria. We also added records and notes of four subsequent expeditions into the central Namib which we did under the auspices of the University of Pretoria. The results presented here cover a wide field, and are not intended to compare with those of the many excellent specialised studies done at Gobabeb since the early 1960's. Our references were selected to serve as background and introduction to specialised fields of research, and not as a comprehensive bibliography on Namib research.

## 2 METHODS

### 2.1 Trapping

The trapping survey on which most of the present paper is based was done during 1969, with a preliminary trial run in 1968. The traps were fully described by Holm & Edney (1973) and the problems encountered with statistical analyses of the results are discussed in the same paper.

The results in Figs 2, 3 and 4 are based on catches of nine of these unbaited pit traps, four of which were fitted with mechanisms to separate 2,2-hourly catches, given in Fig. 3. Trap No. 1 was placed on an east-facing dune slip face, and was fed by a flat funnel with the same circumference as the other traps. This trap filled up with sand with every strong wind, and could not follow the leeward slip-face with change in wind direction as the fauna does. As the whole insect activity on the dune crest is concentrated on the slip-face, and activity increases with wind velocity, this trap undersampled the dune crest fauna to an extent that made only qualitative sampling possible. Trap No. 8 was installed three months after the others, while trap No. 3 was also prone to fill up with sand. The remaining six traps were non-functional for between 15 and 20 days during 1969, but not necessarily on the same days.

We have multiplied the catches of traps 1, 3 and 8 with factors to bring them on a par with the average 18 missed trapping days of the other traps for Fig. 4. It is appreciated that this crude procedure could not compensate for the probably very heterogeneous missed catches on different days in the yearly cycle, and this circumstance made further statistical analyses of the data meaningless. Similarly, daily trappings in Fig. 2

were corrected for the number of non-functional traps for any given day, but because of the spatial heterogeneity of trapping sites, these corrections did little to improve the statistical reliability of the data. The average error in the data is 258 missed trap-days, or about 10 % of the possible trap-days. Data on strictly seasonal species will be affected most.

The timed catches given in Fig. 3 are affected in some cases by the relative abilities of the different species to jump from one tin to the other (which, again, depended on the sand level within the tins). Thus Nos. 21 and 22 are known to be strictly diurnal, and the night catches are due to this error in these very active species. In other cases, a few odd catches may be attributed to disturbed specimens or specimens with disorientated cycles (e.g. No. 136).

Most trapped animals were marked with paint and released near the traps. Only in exceptional cases were animals removed for identification.

The animals of the dune fauna have a poorly developed sense of vertigo as would be expected in a natural surrounding which lacks sharp precipices. Pit trapping is therefore very successful in the dunes, and observations have shown that at least the diurnal species run straight into the traps without hesitating. There is a possibility that animals were attracted to the traps by the smell of others already in the traps, but the funnel-lids and the fact that traps were emptied daily (between 10h00 – 10h30) would have limited this to a minimum. On a few occasions when the flooded Kuiseb River prevented access to the traps, they were not serviced for several days. On these occasions animals died in the traps and olfactory attraction could have considered enhanced catches. For other days, as in Fig. 2, as well as in Figs 3 and 4, attraction would be rather similar for the various traps or time segments.

The trapping results obviously do not reflect densities, but rather densities  $\times$  activity of the various species. Since activity is closely correlated with energy turnover, the results may be used as a crude indication of ecological dominance. The nine traps were placed in such a way that their own surface areas were roughly proportionate to the surface area of the various habitats of the study site (i.e. more traps were placed in the larger habitats) and apart from the dune crest fauna which was undersampled, due to the failure of trap No. 1, the trapping results are probably a fair reflection of the relative ecological dominance of the various species.

### 2.2 Observations

A few intensive surveys of animal activity (see Holm & Edney 1973) and many hours of observation during the servicing of traps, field work on other projects and collecting expeditions, were used in our discussions and interpretations.

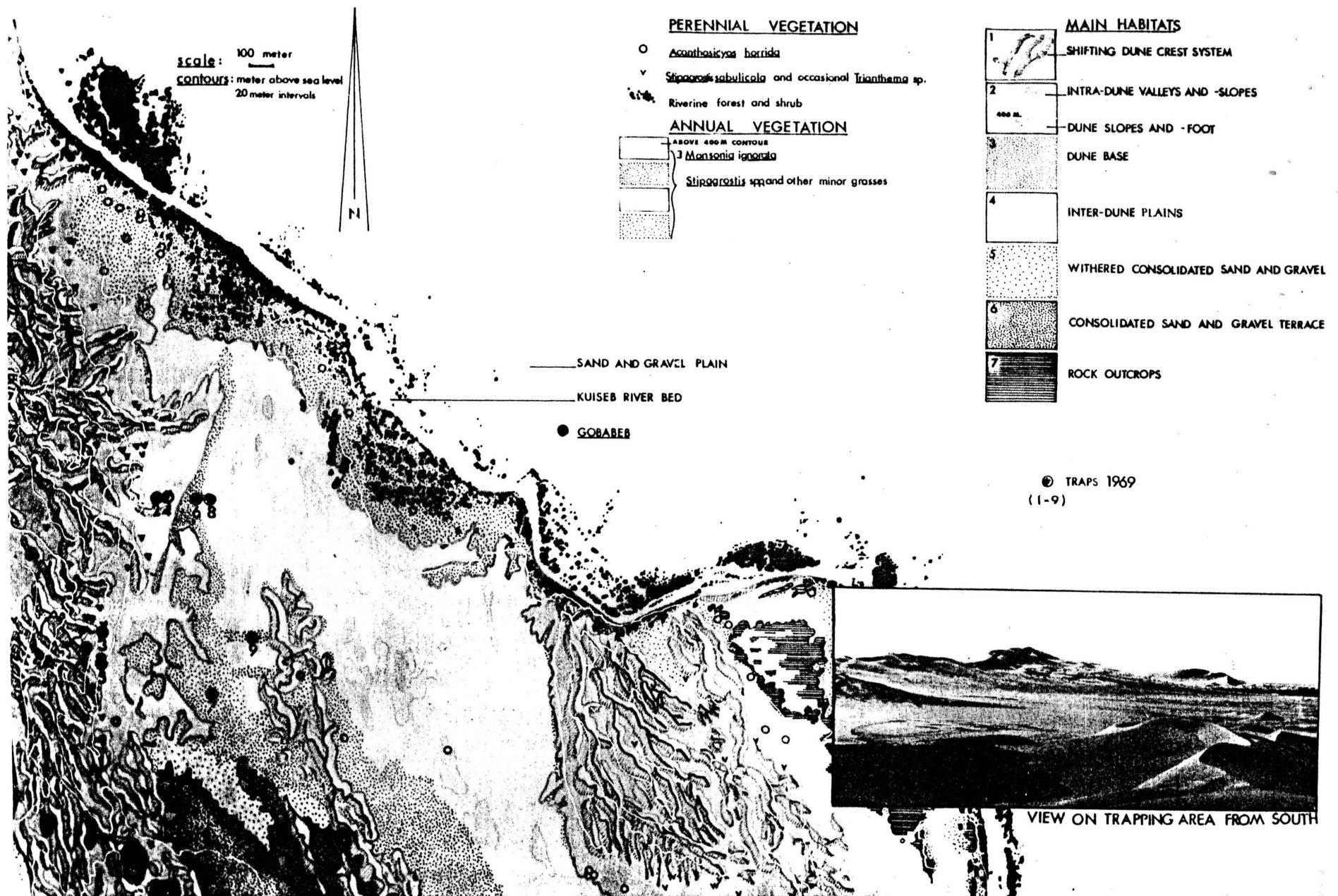


FIGURE 1: Map of the study area and surroundings indicating elevations, geomorphology and the distribution of vegetation.

### 2.3 Distribution survey

Data on distribution were gathered on four expeditions from 1975 to 1978 (Fig. 8). These expeditions were done with post graduate and senior undergraduate students, and sampling was mostly done for 24 hours in an  $\frac{1}{8}^\circ$  block. The collected material was preserved and identified, and other records housed in the two major collections of Namib beetles, i.e. the Transvaal Museum and the Windhoek State Museum, were added to our own. Distribution limits of species which extend outside the central Namib are mainly based on material in these two collections. Only the beetle distribution is mapped, since material of other groups was not intensively collected and was disseminated to various specialist taxonomists. Only the distribution of beetles occurring in the study area is given, the distribution of other species of the Namib will be given and discussed elsewhere.

## 3 PHYSICAL ENVIRONMENT

### 3.1 Substrate

The study site is situated at S 23°37' E 15°01', and at a basal altitude of 400 m above sea level (Fig. 1). It is situated centrally in the Namib Desert, which may be divided into four major biotopes:

3.1.1 The sub-desert (often called the 'pro-Namib') forms a transition between the semi-arid Namaqualand mountains in the south and Khomas Hochland mountains in the west, and the coastal strip of the Namib proper. In the southern coastal area this biome extends with little change up to the Cape Peninsula, and the coastal Namaqualand should probably be included in the Namib rather than the Karoo. In the far south, and north of the Khomas Hochland, the sub-desert becomes ill-defined and grades into the desert plains and coastal dunes.

3.1.2 Extensive desert plains occur north and south of the central Namib dune-sea, and isolated smaller plains occur within all dune areas and between individual dunes. These plains are characterised by the lack of vegetation except in the short periods following the isolated and sporadic rain showers in the desert. Where the sub-desert plains mostly have vegetation and consist of stabilised dune sands mixed and interspersed with gravel and rock outcrops, the desert plains are barren gravel and coarse sand, underlain by gypsum dust with a high salinity, often with salt crusts at or near the surface.

3.1.3 Savanna and Namaqualand enclaves occur on rock outcrops and along river-beds in the desert. Rock outcrops occur throughout the sub-desert, desert plains and dune areas. Their height and position from east to west determine the degree of aridity but all are characterised by succulent vegetation and inland and sub-desert faunal elements. The dry river-beds or 'wadis' support a more definite savanna fauna and flora, which

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 high 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 peren-



nial 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 predictable 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

noon and subside before sunset, at the same time rotating from SE through E to NE.

3.2.2 Temperatures are highly dependent on wind direction and the short east wind spells in winter cause the average maximum temperatures for summer (32°C) and winter (27°C), and the average minimum temperatures for summer (15°C) and winter (10°C) to differ by only 5°C. Highest maximum temperatures are above 40°C in summer and about 35°C in winter, with an absolute high of 42.3°C between 1960 and 1970. Although the macroclimatic temperature conditions are therefore hardly extreme in the Namib compared to inland deserts such as the Kalahari, temperatures may change very rapidly with change in wind direction. Changes of up to 15°C in maximum or minimum temperature within a matter of days are common, and temperature changes of the same magnitude may occur within hours on a given day. It must further be borne in mind that the dune environment offers little shade, and surface temperatures of above 70°C are recorded for screen temperatures below 40°C. On the red north-facing dune slopes, surface temperatures would undoubtedly be even higher. Frost was never noted at Gobabeb, although surface minimum temperatures below 0°C were recorded.

3.2.3 Humidities at Gobabeb vary widely, are usually negatively correlated with temperature and also wind-controlled. The lowest humidities (0 – 5 % RH) occur with easterly storms, and noon humidities are rarely above 50 % RH. Daily averages are about 60 % RH for summer and 35 % RH for winter. In summer saturation is often reached when advective sea fog covers the area in the early mornings. Fog precipitation is highest in spring but may occur throughout the year, mostly between midnight and 08h00 (Fig. 2). The average fog precipitation is 30 mm p.a., which is more than the average rainfall of about 25 mm p.a.

Rainfall was exceptionally high in 1969, with 66 mm recorded in a two-month period. These rains produced an exceptionally good cover of annual vegetation, which was completely absent in 1968 when less than 20 mm rain was recorded (Fig. 2). Rainfall is apparently bimodal, with the highest probability for occurrence in late summer. Showers are extremely localised, resulting in sharp-edged patches of grasslands.

For those arthropods which are directly dependent on water, the amount of precipitation is less crucial than the frequency. When occurrences of rain, fog and dew are added, the maximum spell between precipitation of some kind was about 2 weeks in 1969. Fog occurrences and utilisation by the arthropods are discussed by Seely (1979).

Evaporation is about 3 500 mm p.a., which is not much higher than in the inland savanna, e.g. at Windhoek. In the central Namib most of the evaporation takes place in winter during east wind spells, while evaporation is highest in summer in the inland.

The macroclimate at Gobabeb was first analysed by Schulze (1969), and a further summary was provided by Seely & Stuart (1976). Further discussions of the climate were given by Goudie (1972), Besler (1972), Seely (1978c) and Robinson & Seely (in prep.), while many of the papers dealing with geohistory and geomorphology contain information on the present and past climate (see references under 'substrate' above). Microclimatic data were given in many of the papers on behaviour and physiology of the invertebrate and small vertebrate fauna (e.g. Edney 1971; Hamilton 1971, 1973, 1975; Hamilton & Seely 1976a, 1976b; Henwood 1975a, 1975b; Holm & Edney 1973; Kühnelt 1969; Louw 1972, Louw & Hamilton 1972; Seely & Hamilton 1976; Seely (in press), and a summary of microclimate may be found in Robinson & Seely (in prep.).

#### 4 THE VEGETATION AND ITS ECOLOGICAL ROLE

Ecologically, plants in the study area fall into two distinct groups, the first comprising the larger perennial plants and the second the small and short-lived annuals which only appear after sufficient rain.

The perennials consist of three species. *Stipagrostis sabulicola* (Pitger) de Winter, a hard and spiny dune grass which grows to over one metre in height, is the dominant species of this group on the dune slopes. Normally there is little green growth on the tussocks, and most growth takes place after rain. As discussed above, the most important ecological role of these plants is providing shelter and a modified substrate, and for the precipitation of wind-blown detritus and fog. In periods of slow growth, only the root pseudococcid (No. 62), an undescribed agriline stem-boring buprestid (which was not recorded in the study area) and a lepidopteran (Wharton, pers. comm.) are known to feed on the grass. After rains the green grass is eaten by the oryx, several curculionids (Nos. 101–103), locusts and grasshoppers, tenebrionids and aphids (the latter was also not recorded during the survey). The inflorescences are frequented by the buprestid (No. 96), and two *Onymacris* spp. (Nos. 133 and 134) have acquired the technique of climbing up the stems to feed on the ripe seed of the grasses. Dead growth and the remainder of the seed eventually enter into the detritus pool.

*Acanthosicyos horrida* Welw., the narra plant, is a spiny semi-succulent, evergreen cucurbit shrub. Large plants may grow to about one metre tall and may sprawl over hummocks of up to ten metres in diameter. The ecological role is similar to that of *S. sabulicola*, and here too very little vegetative tissue is used by consumers. The yellow flowers are eaten by the meloid (No. 94) and the buprestid (No. 96) and are visited by a variety of wasps and flies. When the flowers drop off, *O. plana* and probably other scavengers feed on them (Seely, pers. comm.). The fruits,

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.



## 5.2 Larger predators

These include the jackal, *Canis mesomelas* (No. 5), the brown hyaena, *Hyena brunnea* (No. 6) and several snakes and birds of prey. All feed mainly on arthropods, but also take smaller mammals, reptiles and birds.

The jackal is quite abundant in the dune area, and reaches particularly high densities along the coast. Tracks following those of gerbils and moles were often seen in the mornings, and droppings contained many arthropods shells (see also Stuart 1976).

The brown hyaena (No. 6) is rare in the area, and apart from two sightings, the only tracks of this animal were seen during 1969. Only recently the spotted hyaena has been seen near Gobabeb, and it is possible that the brown hyaena is disappearing in this area.

Two species of grass snakes were observed in the area. The most common species, *Psammophis leightoni namibensis* (No. 8) was often found in hummocks of perennials at the dune foot, and two instances of predation on *Meroles* sp. (No. 14) were witnessed in the study area. The other species, *P. notostictus* was seen in the study area once. A review of the two species was given by Broadley (1975).

The sidewinding adder, *Bitis peringueyi* (No. 7) is one of the best adapted desert vertebrates of the Namib. It has a mode of locomotion similar to that of the unrelated American sidewinders (Gans & Mendelssohn 1971) and several other behavioural and morphological adaptations to the dune environment. The eyes are situated on top of the head, which is cryptically coloured like the rest of the body. The snake submerges itself in dune sand by moving the ribs sideways until only the top of the head is exposed. It is in this position that it lies waiting for prey. The snake's tail is thin, and is black in some specimens. A specimen which one of us (E. H.) held in captivity at Gobabeb, used this black tail tip successfully as a lure to attract *Aporosaura* (No. 13) specimens in the cage by wriggling it above the sand surface. The behaviour was observed repeatedly on this specimen, but this lure is apparently not always employed. At night the snakes roam over the dunes in the characteristic sidewinding fashion, and probably hunt *Palmatogecko* (No. 12). A further interesting observation was made on a captive snake which had been exposed to desiccation and was subsequently sprinkled with water. The snake immediately coiled with the head in a central position and flattened the fore-body, thus forming a funnel with its body to channelise the water to the mouth (see also Louw 1972 and Robinson & Hughes 1978). In the dunes, a specimen was once found at noon in a tussock of *Eragrostis spinosa* grass. On this particularly hot day the snake apparently took refuge from the intolerable surface temperature by climbing into the plant. The sidewinder is very common in the study area and throughout the central Namib dunes. Six specimens were trapped in pit traps, all between mid-August

and November, while there was a period of three months in winter in which activity declined sharply and no snakes were seen (Fig. 2). All specimens were trapped on the dune slopes and crest (Fig. 4). The biology of the species was recently described by Robinson & Hughes (1978).

Important larger avian predators in the dunes are the pied crow (No. 20), the owls (Nos. 18 and 19) and the goshawk (No. 17). These species all take small vertebrates as well as arthropods. The crows and goshawks are often seen on dune crests, watching the slip-face for movement and then striking at beetles or lizards. The diet of the owls has been extensively studied by examination of pellets (Bauer & Niethammer 1959; Nel 1969; Stuart 1975), and while it consists mainly of small mammals, it also includes reptiles, birds and arthropods. On several occasions occupied and unoccupied roosts of the barn owl were found deep in the dune area on dune slopes under *S. sabulicola* plants. Owls can therefore be expected to be active throughout the dune area, and not only within reach of river-beds and mountains.

## 5.3 Small predators

These include the golden mole *Eremitalpa granti namibensis* (No. 4), three geckos (Nos. 10 – 12), three lizards (Nos. 9, 13, 14), the chameleon (No. 15), the desert chat (No. 16) and a number of insectivorous birds which may occasionally enter the area. Few of the species are strictly predatory, and the two omnivorous gerbil species (No. 3) are also discussed under this heading.

The Namib golden mole (No. 4) is a voracious insectivore which mainly inhabits the overgrown inland dunes, but whose distribution extends as far west as does the distribution of the dune grasses. It mainly feeds on root pseudococcids (No. 62) off the roots of dune grasses, but even took medium sized *Palmatogecko* (No. 12) in captivity. The biology of the species was recorded in some detail by Holm (1969). One specimen was trapped in 1969, and the nocturnal activity of the species is limited to the dunes and was recorded throughout the year (Fig. 2).

Two species of barking geckos were found in the study area. Both are nocturnal, but also emerge on cold overcast days. *Ptenopus garrulus* (No. 10) is a widespread species, but is restricted to the plains in the study area (Fig. 3). Members of the genus are all fossorial, and make characteristic territorial barking noises at their tunnel entrances (see Brain 1962; Haacke 1969, 1974, 1975, 1976a – c). Stomach contents of two specimens taken on 26.11.1969 (both with inactive gonads) corroborated earlier observations that these geckos mainly feed on social insects:



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 peren-

nial 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

habit of moving either on the surface or just submerged, and leaves very characteristic tracks. The species seems to be abundant wherever dune grasses grow. The nose is sharply pointed, and the lizard can swim into (even relatively compacted) sand at an amazing speed.

*Gerbillurus paebe* (No. 3), the pygmy gerbil, is commonly found in the area south of Gobabeb, where it mostly constructs its burrow under narra plants (Fig. 4). This species roams over all habitats at night, feeding on arthropods and seeds, chiefly on those of the narra. It is apparently heavily preyed upon by owls and jackals (see above). Activity is seemingly constant throughout the year (Fig. 2). Another species, *G. vallinus*, was recorded in the study area on occasion, but seems to prefer the Kuiseb river-banks (see also Laycock, 1975).

The only insectivorous bird which resides more or less permanently in the area is the desert chat (No. 16), and a nest was found on a small rock in the study area. This species was mostly seen hunting on the plains, often feeding on ants at the ants' nest entrances. After rains a variety of insectivorous birds (and even birds which are normally not insectivorous like geese and herons) converge on the area and feed on the abundant arthropods.

The general fauna and ecology of the area have been discussed in many of the specialised papers on the Namib Desert, and in some papers devoted entirely to this purpose (Lawrence 1959; Koch 1961; Robinson & Seely, in prep.), while a number of papers have appeared which deal with groups of the vertebrate fauna (e.g. mammals: Coetzee 1969; reptiles: Mertens 1972; Haacke 1975, 1977; birds: Willoughby 1969, 1971; Prozesky 1969; Dixon 1973).

## 6 CONSUMERS: INVERTEBRATES

A study on micro-organisms (le Roux 1970) revealed low levels of microbes in the sand, and even in the detritus of the dunes at Gobabeb, with the highest counts (in most groups) in the interdune plains and lowest counts in dune slope sands. Few nitrifying bacteria were present in dune sand and none in the interdune, while levels of cellulose degrading fungi were low even in sand with detritus.

Nothing is known of non-arthropod invertebrate animals in the dunes.

The arthropods, on the other hand, are the most important consumers in the system in terms of diversity, energy turnover and key functions, and the community in the dunes at Gobabeb is taxonomically, physiologically and behaviourally one of the best studied in southern Africa.

At order level the composition of the arthropod groups seems normal (although the relatively small community of only about 120 species makes such a statement rather meaningless). Coleoptera account for roughly one-third of the species, and Hymenoptera and Diptera occur in about the normal proportion of approximately 5–10% each. Lepidoptera (not recorded in this study) are apparently scarce with only a few known highly adapted species, while spiders, solpugids and thysanurans are exceptionally well represented. Within the orders and families the distribution of groups becomes progressively more uneven. Thus 70% of all beetle species are tenebrionids, of which 70% in turn are represented by the tribes Adesmiini, Zophosini and Eurychorini. Similar one-sided representations are found within the scarabalids, weevils, spiders and solpugids. At genus level the species distribution becomes extremely uneven (see e.g. *Onymacris*, *Lepidochora*, *Vernayella* and *Leptostethus* against the many genera with only one representative). This progressive unevenness down the taxonomical hierarchy combined with the high endemism within the well-represented groups (see below) lends itself to interesting speculation on the evolution of the fauna which, however, goes beyond the scope of this study.

When numerical dominance is considered (as roughly reflected in Fig. 2) the beetles, and more specifically the tenebrionids, are responsible for the major proportion of the fauna and are probably responsible for most of the energy turnover as they are low in the trophic chains, small and extremely active.

Two-thirds of the recorded arthropod species are apterous, and few of the alate species are endemic or specially adapted to the system. This high incidence of aptery is partly due to the success of apterous groups (e.g. the tenebrionids, spiders, solpugids and thysanurans) and partly due to endemic aptery (e.g. among the scarabaeids). The most obvious reason for aptery is the coastal position of the desert and the high incidence of seaward storms, but a number of other factors may contribute. Fossorial life (and in some habitats sand-diving) is essential in most niches, and does not

FIGURE 2: Daily macroclimate and total daily trappings of nine pit traps for four months of 1968 and eleven months of 1969. Numbers above species names are code numbers (see p. 34–36), numbers behind histograms are totals of specimens trapped.

For 1968 only weekly averages of the dominant Tenebrionidae are given, and traps were only operated every second week.

For 1969 all daily trappings are recorded, with the dominant Tenebrionidae on  $\frac{1}{10}$  scale. Circles are sightings or records of fresh tracks. For the periods 25.II – 1.III; 3.III – 8.III; 22.III – 2.IV; 22.VII – 24.VII and 24.VII – 27.VII averages are given, but where these are below one, totals are recorded on the first days of the period.

For No. 69 only the occurrence of alates (vertical arrows, also on No. 70) is recorded, since these ants could climb out of the traps. Histograms are not corrected for missed trapping days on individual traps (see text).

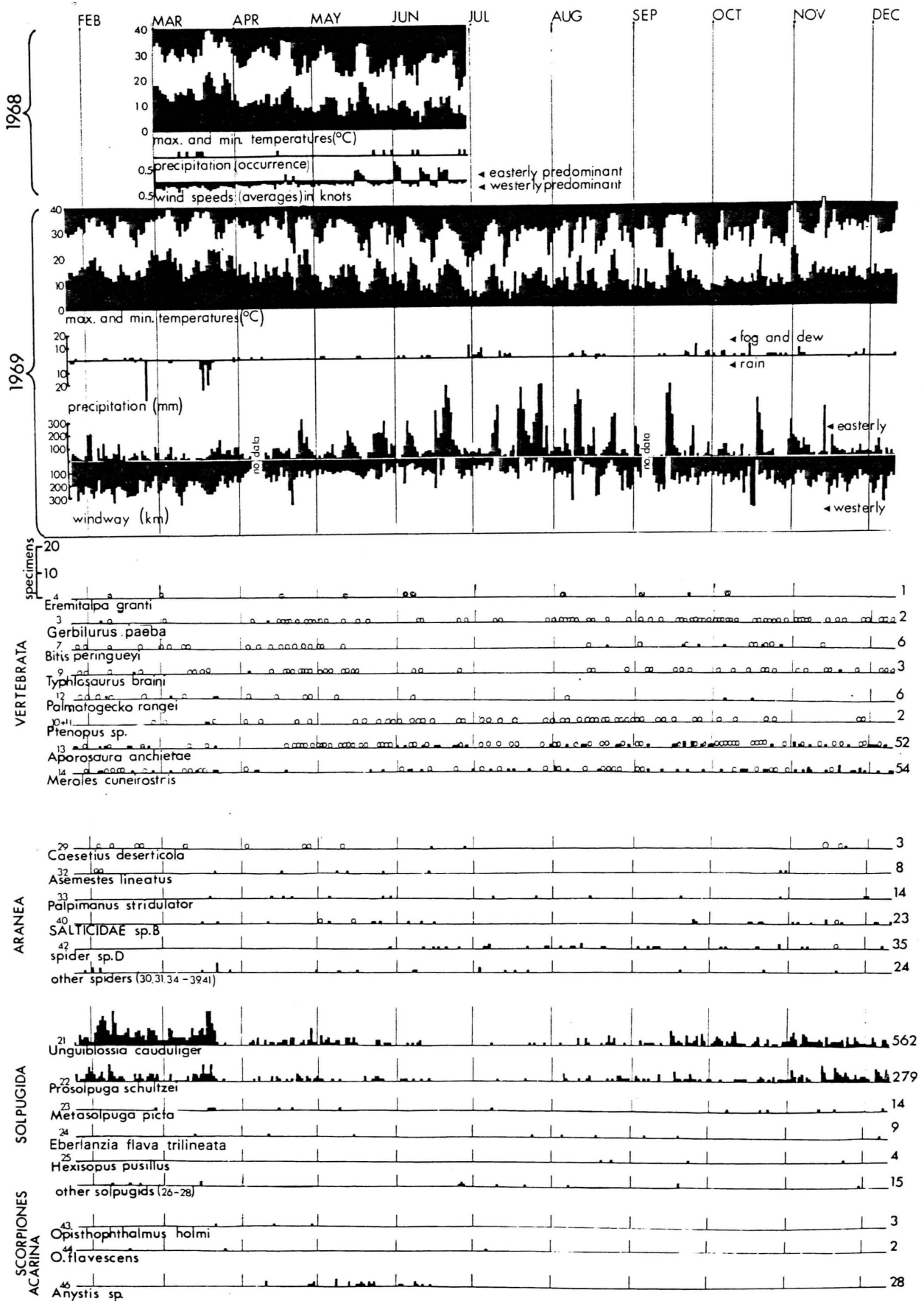


FIG. 2

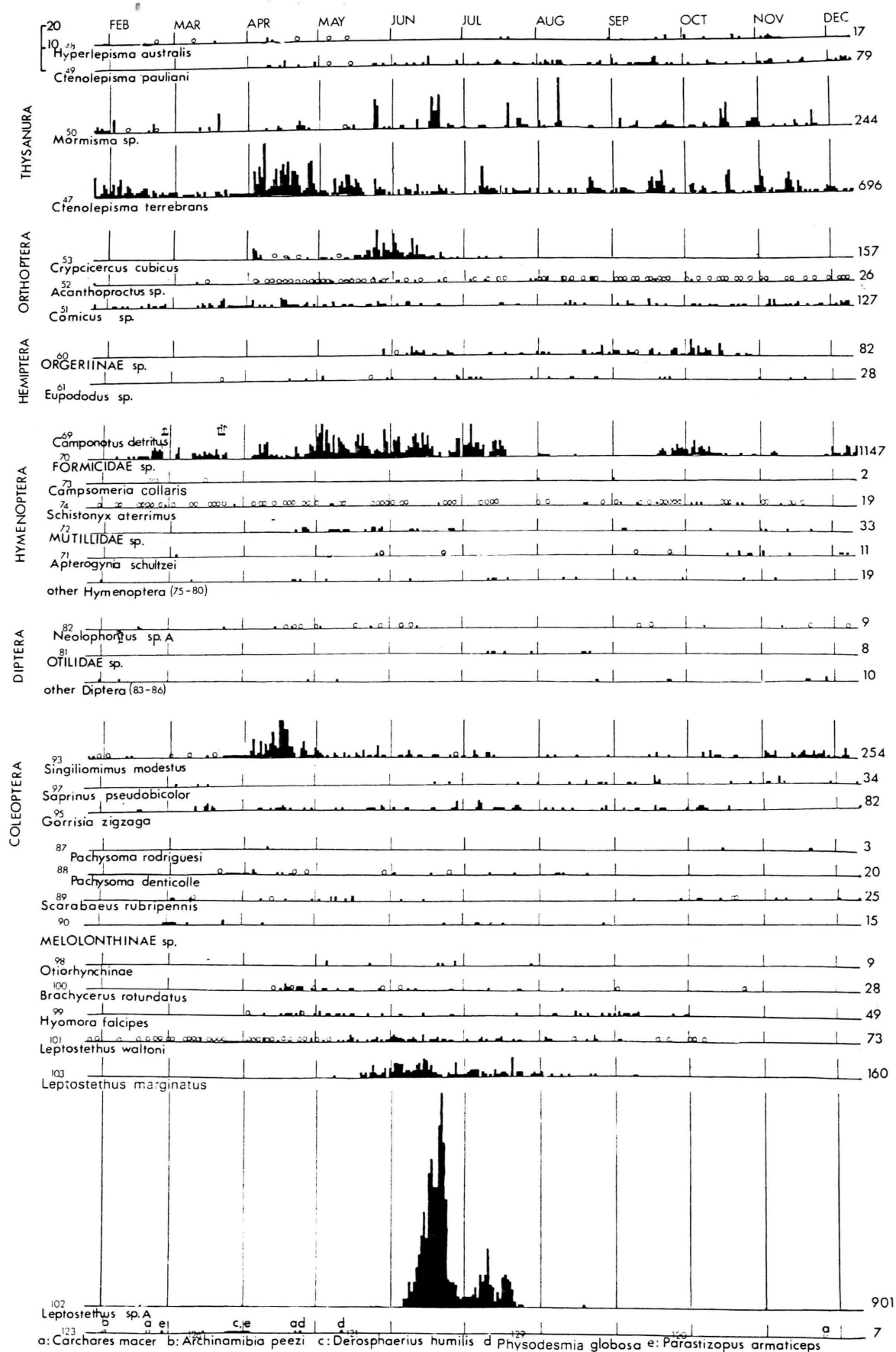


FIG. 2 (cont.)



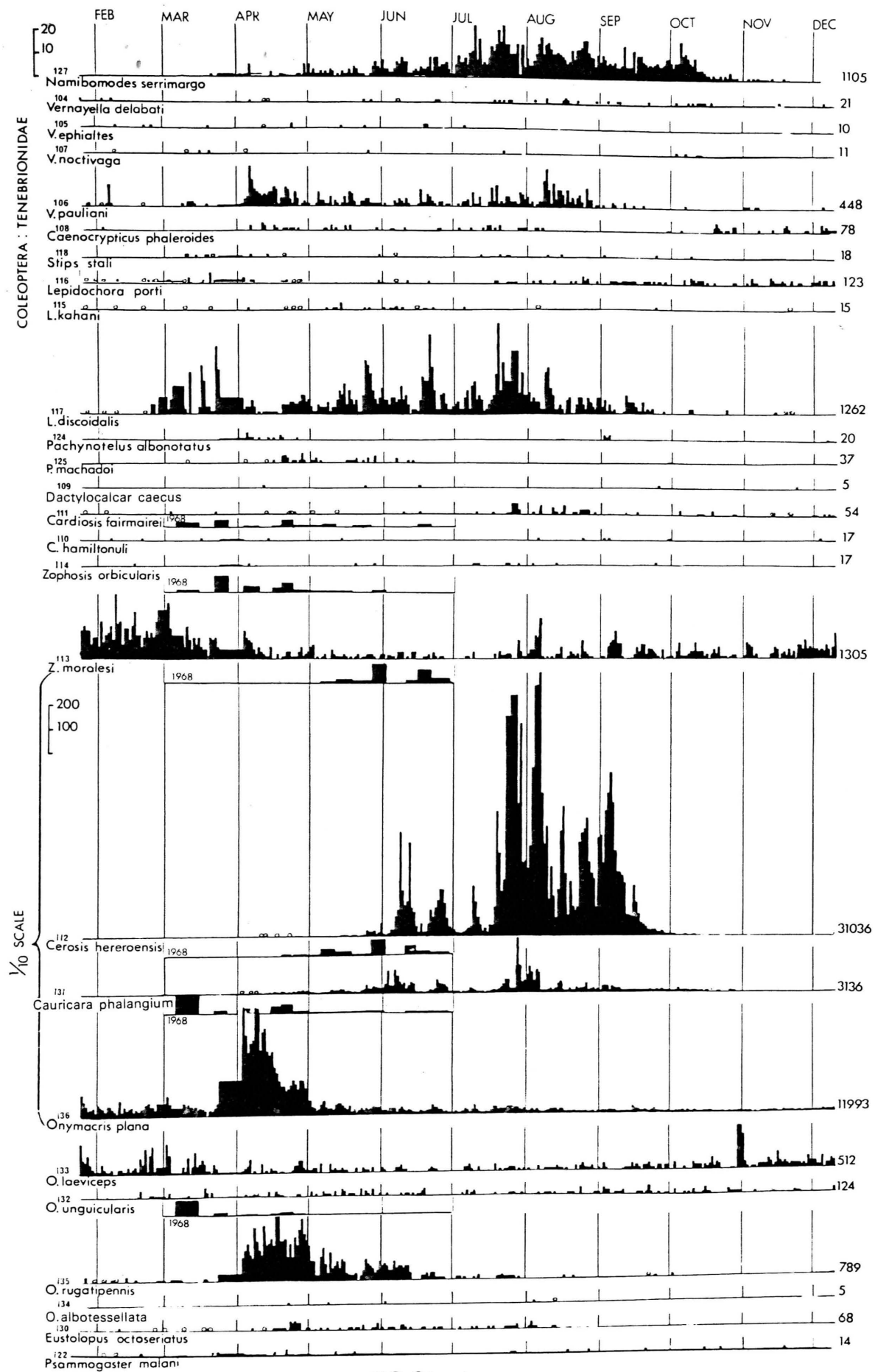


FIG. 2 (cont.)

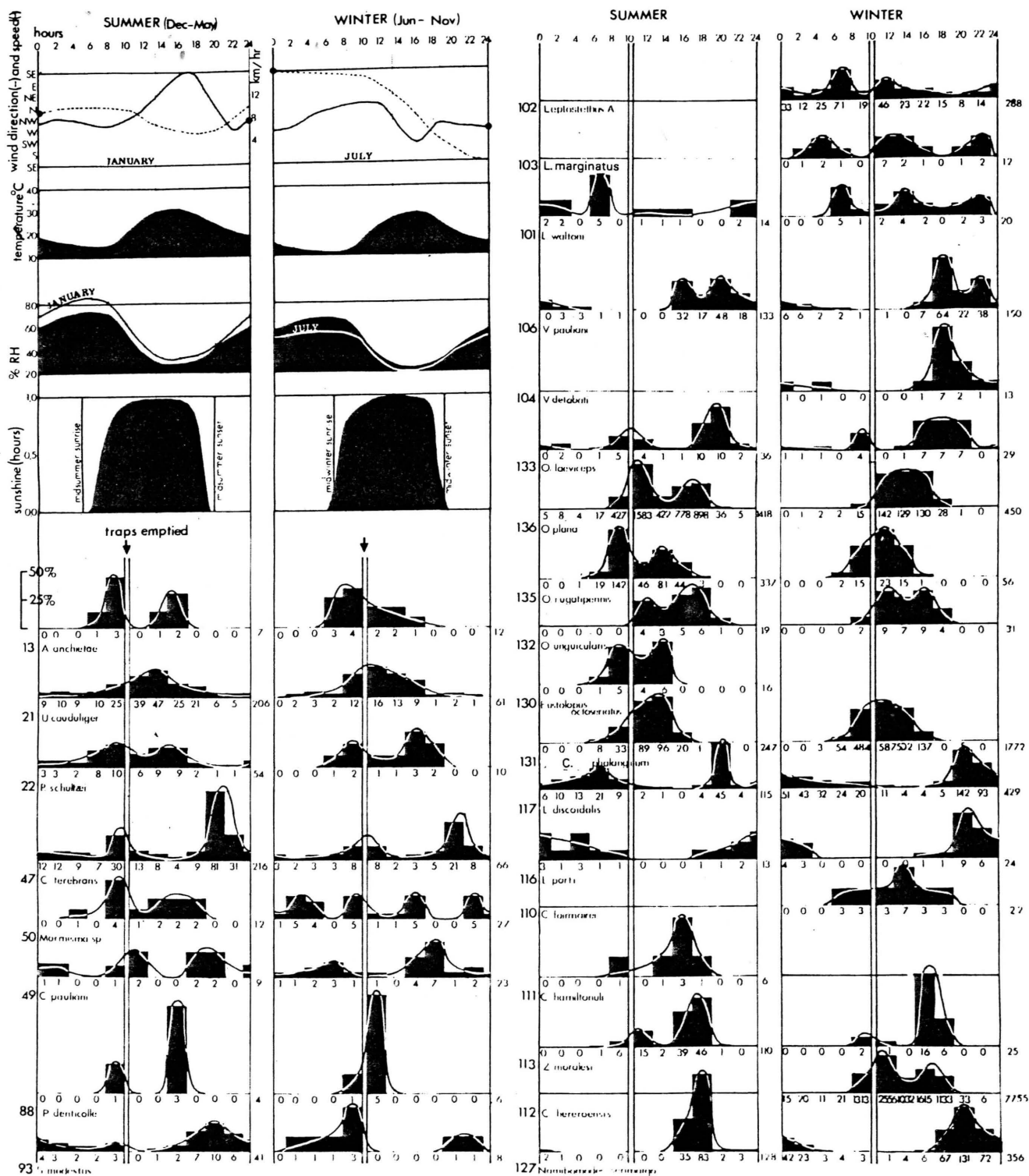


FIG. 3

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.

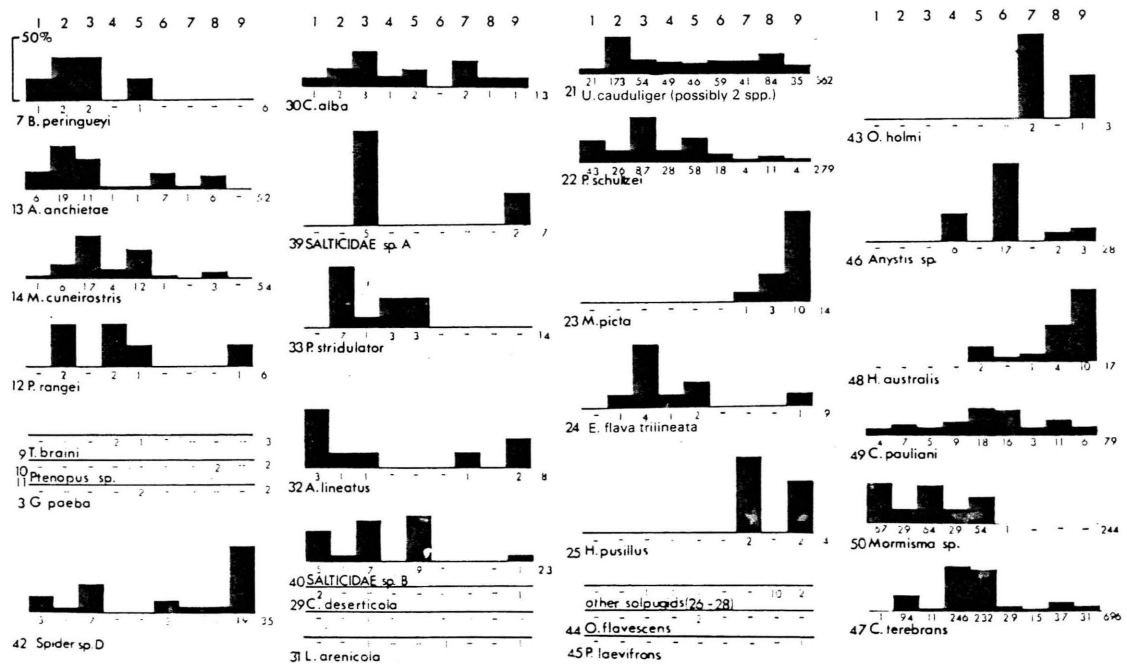
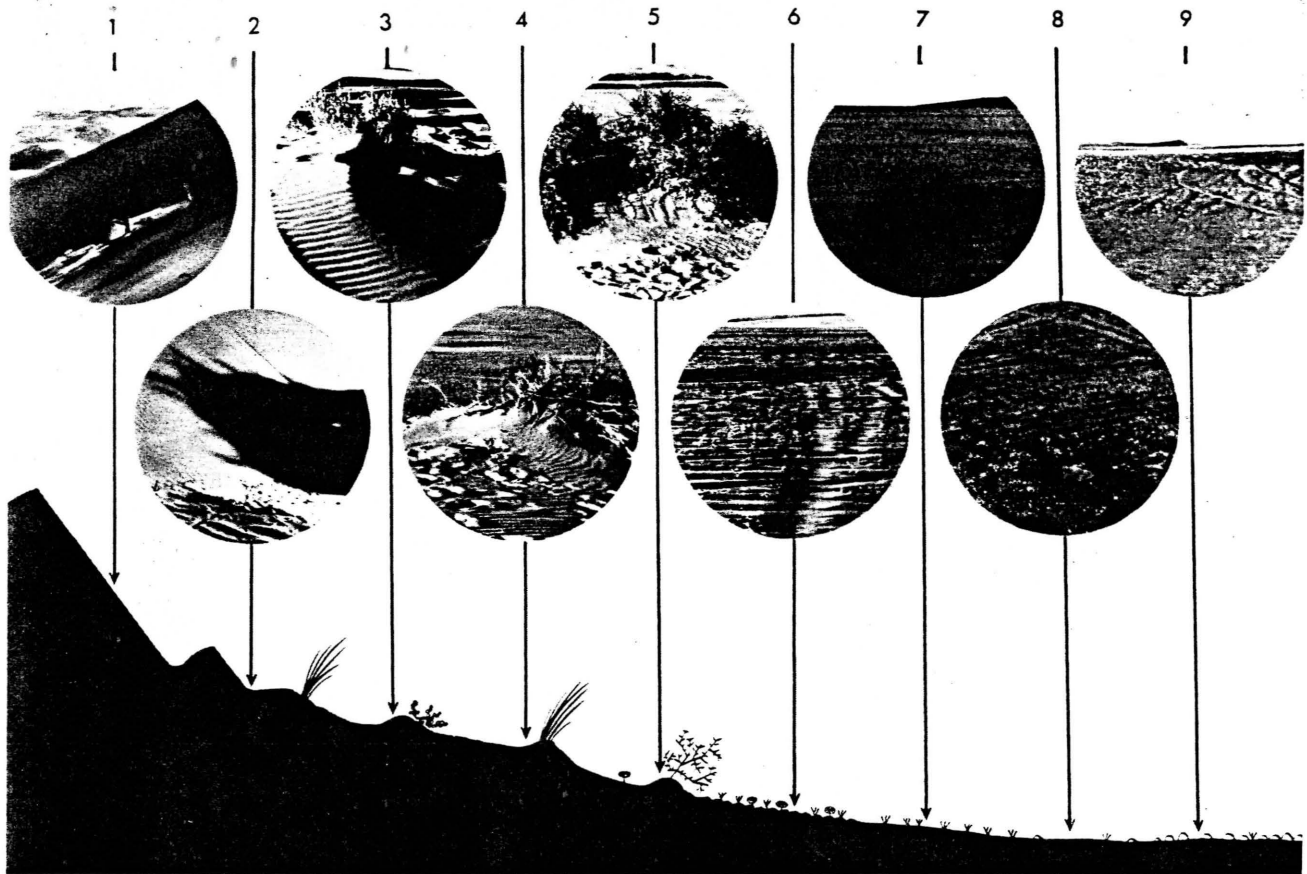


FIG. 4

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).

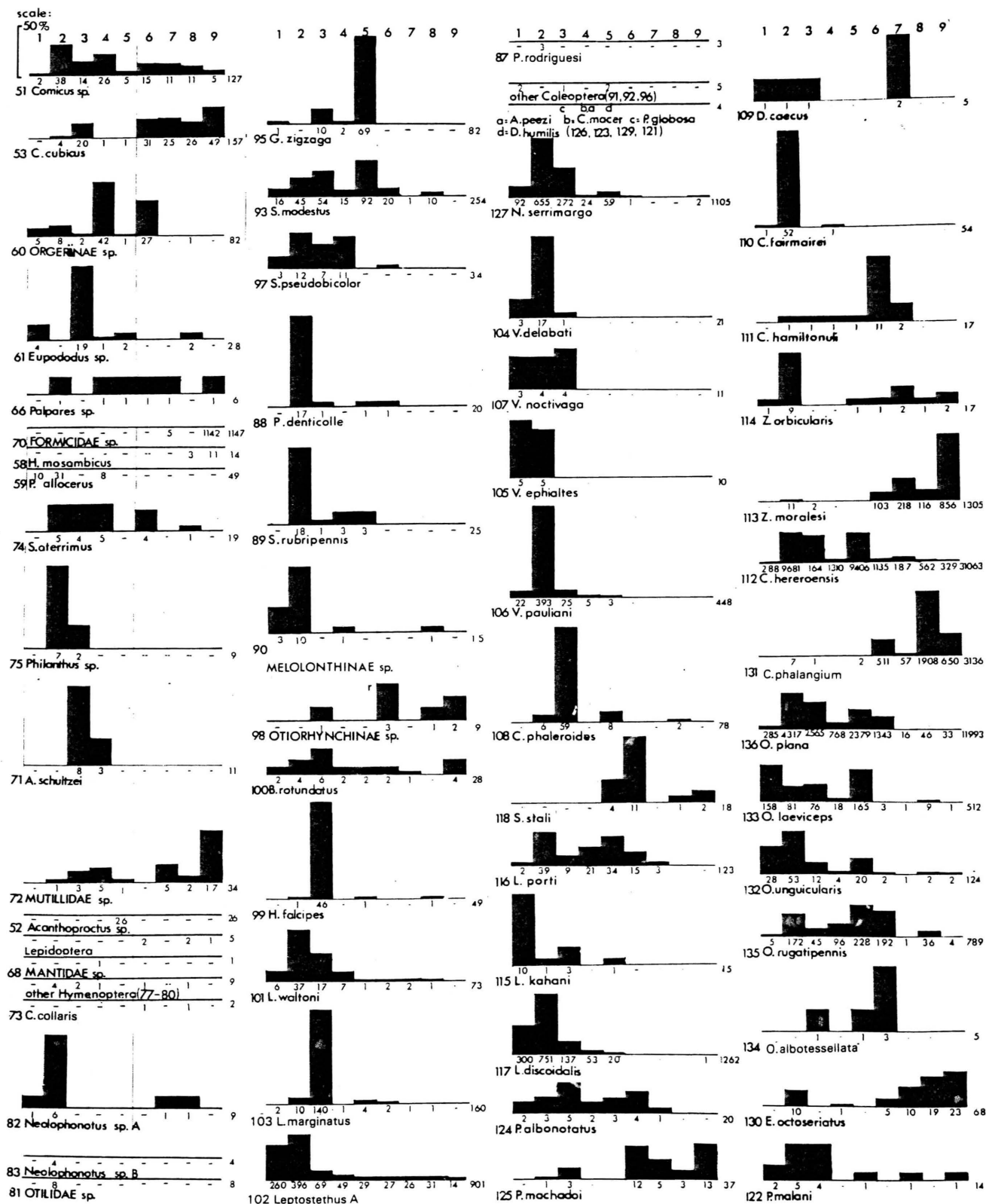


FIG. 4 (cont)



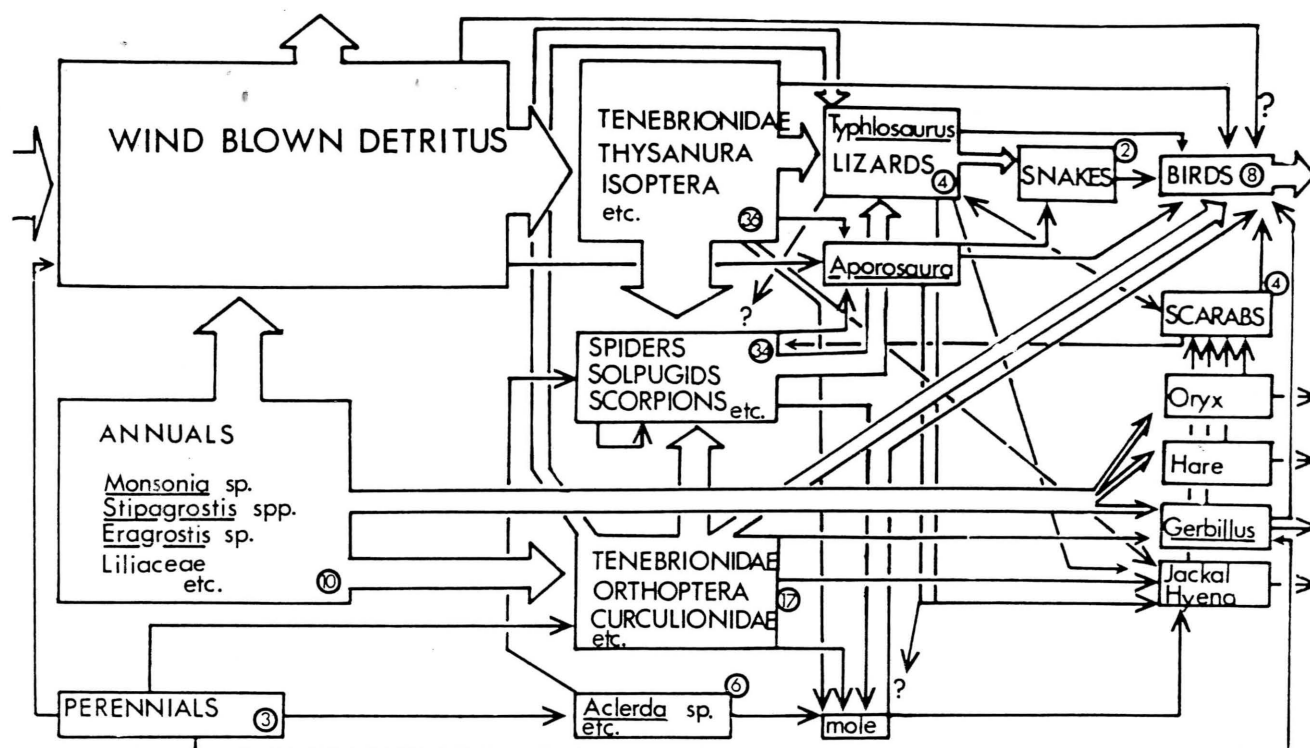


FIG. 5

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.

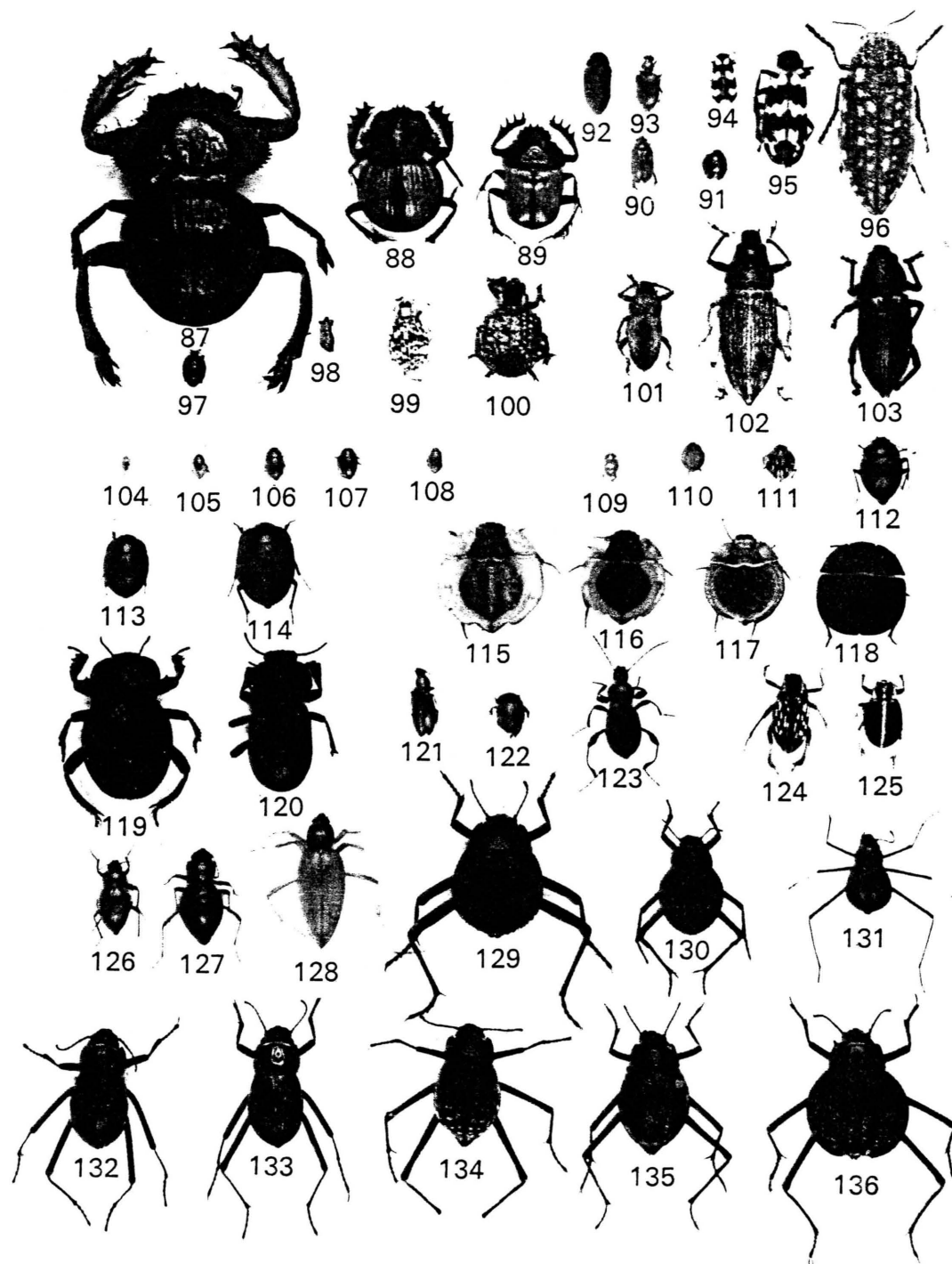


FIG. 6

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.

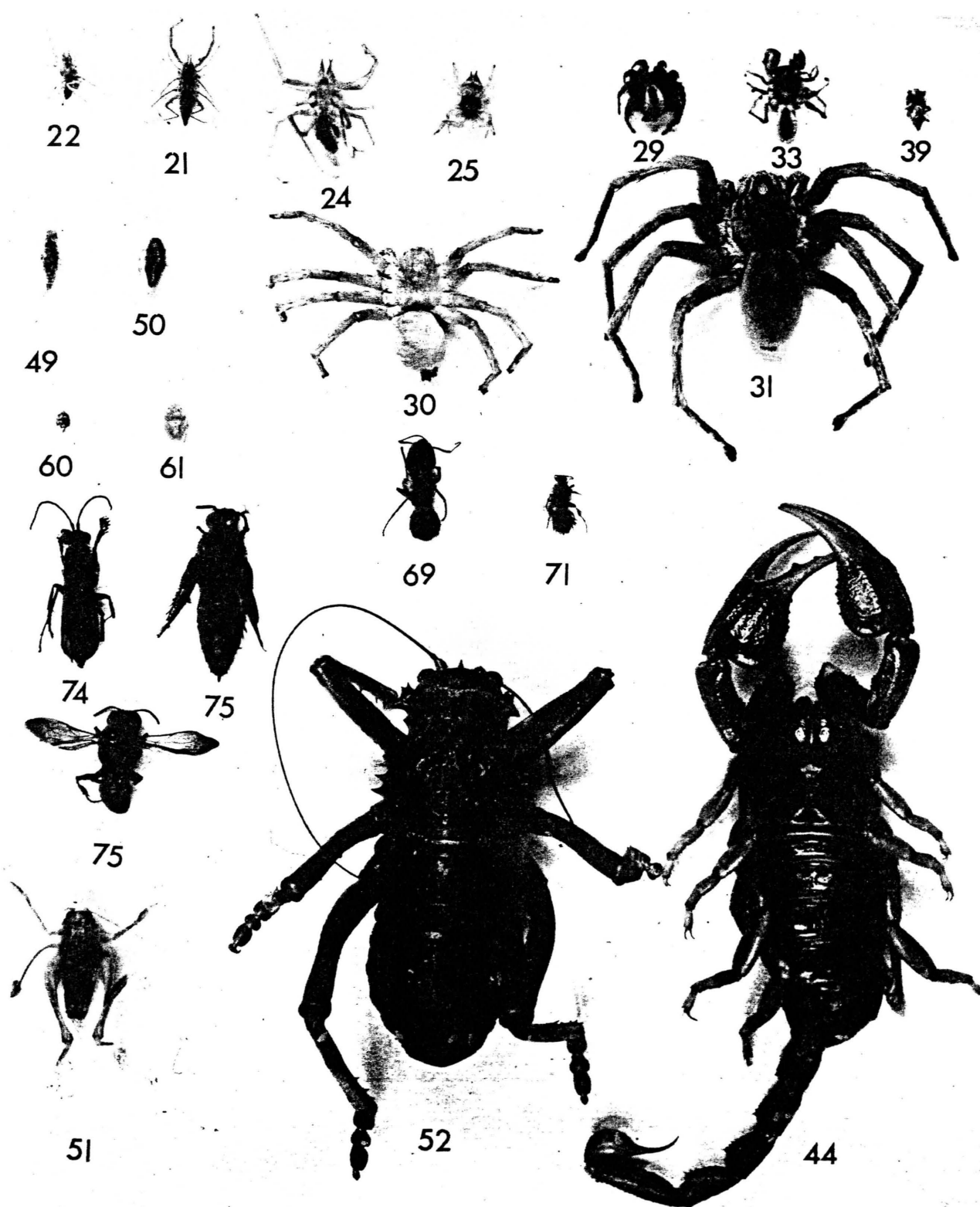


FIGURE 7: Some of the more common non-coleopterous arthropods recorded during the 1969 trapping survey in the dunes south of Gobabeb. Numbers relate to the check-list on p. 34-36.

Nos. 58 – 59: Termites. Whilst No. 59 may be found in the dunes long after rains, No. 58 only seems to maintain colonies permanently in areas with fairly regular rains (see Coaton & Sheasby 1973). Both species were recorded in the dune area in 1969, with No. 58 mainly in the plains and No. 59 higher on the slopes and in dune valleys (Fig. 4). Both species produced alates in February and March 1969 after the rains. Both species may equally well be classed as detritivores, since they also collect dry grass.

No. 60: The dictyopharid species. This small cryptically coloured species was first recorded in this trapping survey, and has as yet not been named. It occurs on the dune slopes and dune foot in winter, and might be rain dependent as the members of the family are sap-suckers. It is a diurnal species, a very good jumper and is brachypterous.

Nos. 98 – 103: The weevils. All the weevil species are only active as adults after rain. No. 98 is a small green species which is only found in the plains and dune foot area (Fig. 4). It was predominant in stomach contents of *Aporosaura* (Louw & Holm 1973) but since few were trapped (Fig. 2) the species was presumed to move around very little. No. 99 occurs exclusively under *Trianthema* shrubs (Fig. 4), and is rarely seen on the surface, except after rain (Fig. 2). No. 100 occurs mainly on the dune slopes but also in the plains, wherever the lily, which it feeds on, grows. While it is certain that *B. rotundatus* is the common *Brachycerus* species in the area, there may be other species associated with less abundant lily species since most lilies are attacked by *Brachycerus* spp. The curculionid fauna on the short-lived annual vegetation in the Namib has not been surveyed systematically, and may prove a most rewarding field for taxonomists. Nos. 101 – 103 all belong to the genus *Leptostethus*, and these three species show a curious trimodal diel activity (Fig. 3) which may not be significant for Nos. 101 and 103, but for No. 102 is well demonstrated. This modality is not understood. All three species occur on the dune slopes and No. 103 also wanders over the crest area resulting in high catches in trap 4 due to the channelling effect of the slip-face base (Fig. 4). The delay in emergence after rain is proportional to size differences, whilst the population lifespan is inversely proportional to body size and population size (Fig. 2). All the *Leptostethus* spp. show thanatosis as a reaction to disturbance. They lay their eggs at the base of plants after digging a crater in the sand with their hind legs. No. 101 is a hardy species, and individuals found early in 1969 were survivors of the population which emerged after the rain late in 1968. It is euryphagous, feeding on the annuals but also on *Trianthema*, *S. sabulicola* and even *A. horrida*. No. 102 is a beautiful large blue weevil, and not yet described. It only feeds on green *S. sabulicola* leaves after rains, and populations are then very large but short-lived (Fig. 2). In the period 1964 to 1969, the species only occurred in the exceptionally rainy years of 1967 and 1969. In spite of heavy predation on these

relatively soft-shelled and slow-moving animals by birds and arthropods, the population was not overtaken by the predators, and dead but intact specimens littered the dunes at the end of July. No. 103 is similar to 102 in habits, but is not as abundant (Fig. 2). It feeds on *Trianthema* exclusively (Fig. 4).

Nos. 124 – 125: The *Pachynotelus* spp. The two most common species of this genus in the study area are *P. albonotatus* (No. 124) and a species which we provisionally hold to be *P. machadoi* (described from the northern Namib). Two other species have been recorded near Gobabeb. No. 125 is the smaller and more common species (Fig. 2), and feeds on the grasses in the plains (Fig. 4). No. 124 is rare and individuals survive for shorter periods after rains (Fig. 2). They feed mainly on *S. sabulicola* and are therefore mostly trapped on the dunes (Fig. 4). Both species are very clearly rain-dependent, and completely absent in dry years such as 1968. At least No. 124 seems to have a moisture-terminated quiescence, since a small population emerged in September after very little rain in August (Fig. 2). Both species have well-developed bristles on the legs, which they use to dig themselves in at night, and to dig craters for egg-laying at the stems of grasses. Activity is diurnal.

No. 130: *Eustolopus octoseriatus*. This is the only member of the tribe Adesmiini in the system which is a true rain-dependent form. Its occurrence coincides with that of No. 125 (Fig. 2), and feeding habits are also similar. It is a plains species (Fig. 4) and tunnels into the sand at night. Single individuals may be found out of season, but after rains the species becomes extremely abundant. In 1967 an estimated density of one specimen per metre square was reached in the plains, and over 3 000 specimens were trapped in a pit trap in three days. The fact that comparable densities were not reached after much better rains in 1969, suggests that a prolonged quiescence may be possible, which could result in a large synchronised crop of individuals after an extended drought period such as preceded 1967.

The alate primary feeders were not well covered by this survey. Several species of Lepidoptera occur on both the perennial and annual vegetation (Wharton, pers. comm.) and at least one aphid species is present. The presence and diversity of other alate groups, such as the Heteroptera, may also be significantly greater than reflected in our list.

## 6.2 Detritivores and omnivores

The detritus feeders are the largest group in the system in terms of individuals and are second only to the predators in number of species. The abundance and ecological importance of the detritivores in the Namib Desert dune ecosystem has been pointed out by Koch (1961) and others (e.g. Lawrence 1959, Seely 1978c). The distribution of the abundant detritus to various habitats 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 desiccation. 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).

It is a very widely adapted species with wide distribution in the dune areas.

Nos. 110 — 114: Small diurnal tenebrionids. All members of this group belong to the Zophosini, which is a very widespread and successful diurnal group in Africa and which is also extremely successful in the Namib Desert (Koch 1962, 1969; Schulze 1974; Penrith 1977). No. 110 is a small species with yellow markings and which normally occurs on the dune crest (Fig. 4) but is sometimes found to traverse dune slopes from one slip-face to the other. Activity is strictly diurnal (Fig. 3) throughout the year but more prominent in winter (Fig. 2). They are very efficient sand-divers and are active during storms, when they are carried by wind eddies on the slip-face to land with the detritus. The fast and erratic movements combined with the yellow colour make these insects hard to see in whirling sand and detritus. They are attracted in great numbers to carcasses of reptiles or gerbils near the slip-face. Hamilton (1971) reported on the biology of the species. No. 111 is a smaller congener of No. 110 which was only recently discovered due to its small size and cryptic colouration (Koch 1969). It occurs throughout the year (Fig. 2) but from visual observations in 1968 and 1969, is more abundant in March and April. The species is restricted to the dune foot (Fig. 4) where it uses the detritus catchment of the micro-dune (see 'substrate' above). Activity is diurnal (Fig. 3). No. 112 is a very fast runner, with a bluish wax secretion on the black integument. It is the most numerous species in the system and is strictly a winter form with population activity peaks coinciding with spells of east wind (Fig. 2). It occurs on the dune slopes and dune foot, between the areas of activity of No. 110 on the one side and Nos. 131 and 113 on the other (Fig. 4). Activity is clearly bimodal (Fig. 3). No. 113 is a bit slower and more compactly built than the previous species. It is one of few species in the system with a pronounced summer activity, although it occurs throughout the year (Fig. 2). It occurs on the plains and dune foot (Fig. 4), and the diurnal activity is clearly bimodal with emphasis on afternoon activity (Fig. 3). Stomach contents of this species revealed small seeds and fragments of grasses, but specimens were seen to feed on thysanurans on two occasions where it is not certain whether they killed them or found them dead. After the rains, feeding on green grass was repeatedly observed. At night the beetles sleep under tufts of grass or pebbles, often half exposed, and they do not dive into the sand. Of 400 specimens which were marked on three different occasions, trap retrieval of marked individuals in each instance decreased sharply after about ten days, and we suspect the adults to be short-lived in contrast to the larger tenebrionids in the area. No. 114 is very similar in appearance and habits to No. 113, and is more common in the river-bed. In the study area it occurred throughout the year (Fig. 2) and in all habitats, but most specimens were trapped at the slip-face base (Fig. 4). It is also a diurnal species and

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

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

Nos. 115 — 118: The Eurychorini. These are all nocturnal species of medium size and with more or less circular and flat bodies, probably originally evolved for living under bark and rock, and further adapted to sand-diving by the loss of sculpture and the addition of scales in the genus *Lepidochora*. The *Lepidochora* species are heavily preyed upon by *Palmatogecko* and spiders, and instances of predation by both were often seen. No. 115 is the largest of the species occurring at Gobabeb. It occurs throughout the year (Fig. 2), is strictly nocturnal, and it is restricted to the dune crest area (Fig. 4). No. 116 is smaller than the previous species, and not as flat. It occurs on the dune slopes (Fig. 4) and is more active in summer (Fig. 2). The activity is strictly nocturnal and decreases with decrease in temperature, with a resultant marked shift to the early night hours in winter (Fig. 3). Both No. 115 and 116 are able to withstand low temperatures, and were found on the surface at ambient temperatures of below 5°C. No. 117 is much more abundant and active than the previous two species, and clearly more so in winter and after rain (Fig. 2). Activity is very closely correlated with wind, as in the case of other dune crest detritivores. This species only leaves the slip-face when it migrates to another (Fig. 4). Since we had no timed trap on the slip-face, the diel activity in Fig. 3 is based on traps outside the normal microhabitat of the species. It consequently reflects these odd migrations and is therefore rather misleading. On the slip-faces activity is crepuscular-nocturnal, but the 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



throughout the year, but is more abundant in summer. Nos. 119, 120 and 121 are dune-edge species which occur along all the river-beds and washes in the inselbergs, in relatively loose sand near vegetation. They are all nocturnal and individuals may occasionally be found in the dunes. It is difficult to decide to what extent these odd intruders into the dune system form part of the ecological community. Other tenebrionids like *Eurychora* spp. and *Epiphysa* spp. may also enter the marginal dunes in some areas and may even maintain populations there on a limited scale. Apart from the references cited under groups and species of tenebrionids above, a number of studies have dealt with the tenebrionid fauna at Gobabeb in general, or with aspects pertaining to several groups. Apart from the pioneering work by Koch (1961, 1962a, b) studies by Edney (1971b), Hamilton (1973, 1975), Holm & Edney (1973), Lawrence (1959) and Seely (1973) were also undertaken.

Finally under detritivores we must mention the ants (Nos. 69, 70) and termites (Nos. 58, 59). Of these only No. 69 is permanently active in the system at Gobabeb; the other species enter after rain, and gradually disappear in dry years (see No. 70 on Fig. 2). These species have been discussed elsewhere, and their relative population activities and contribution to detritus removal could not be established by our methods. The detritus ant (No. 69) is not only detritivorous, but also tends the aphids and No. 62 for honeydew, and furthermore preys on small arthropods. Nests seem to be territorial, since a full scale "war" between two colonies was witnessed on a bare dune slope by W. J. Hamilton (pers. comm.).

### 6.3 Predators and parasitoids

The diversity of arachnid predators in the dunes is extremely high compared with that of primary feeders and detritivores, especially considering their position above the second trophic level. The fourteen spider species, eight solpugids and two scorpions which were recorded are probably not a complete list for the area; many were only collected once or twice, and the chances that other species were not recorded at all are good.

The largest spiders may be able to prey on small geckos (Lawrence 1959), and spiders and solpugids were repeatedly seen to feed on tenebrionids (*Lepidochora*, *Zophosis*, *Cerosis* and *Cauricara* species). Smaller species probably feed on thysanurans and ants. Predation also occurs within and between the arachnid groups.

Trapping results of all but two species were low, and a full ecological analysis is therefore precluded. The biology of most of the species has been commented on by Lawrence (see references below), and an ecological survey of the group is presently underway at Gobabeb (Wharton, pers. comm.). We therefore only provide a few notes of our 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 *Cerosia* (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 histrids 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



widely with the two central dune species Nos. 133 and 136, which in turn overlap with the inland species No. 134 (Fig. 8). No. 132 and 133 are dune crest species, while 134 and 136 are dune slope and dune foot species respectively. Lastly, No. 133 is crepuscular to nocturnal, while the other species are bimodal diurnal in summer and mostly unimodally diurnal in winter (Fig. 3). In combination, all these species, which are of approximately equal size and have similar (detritus) diets therefore have space/time niches which in some way or another separate them from their congeners.

Another clear example of niche exclusion is found in the small diurnal and fast-running tenebrionids, Nos. 131, 113, 112, 110 and 114. One species (No. 114) is rare in the area, and the few recorded specimens were taken in winter. Species 131 and 112 are winter active forms whilst 113 is much more abundant in summer and 110 occurs throughout the year (Fig. 2). Numbers 131 and 113 are plains runners, 112 occurs on the dune slopes and 110 on the dune crest (Fig. 4). The species are all diurnal, but of the two species in the plains which are partly seasonally separated, 113 has a bimodal and 131 a unimodal activity pattern (Fig. 3). All these species have similar distributions in the dune area (Fig. 8). (All but No. 131 belong to the Zophosini, and this example can be expanded to include other zophosine species of the Namib which do not occur at Gobabeb.)

A similar example is that of the eurychorine species Nos. 115 – 118. Unfortunately activity reflected by trap results of two of the species was low, but it is clear that the adults of No. 116 are predominantly summer active and 117 predominantly winter active. Diel activity of 116 and 117 only differs by the latter having a marked activity peak on winter mornings (not recorded by trappings in Fig. 3: see above), which is absent in the other two species which are nocturnal. No. 118 occurs on the plains, No. 116 on the dune slope and Nos. 115 and 117 on the dune crest (Fig. 4). All four species are geographically more or less sympatric (Fig. 8). In this group, only Nos. 117 and 115 do not show a clear time or space separation, and these two species are respectively the largest and smallest of the four, and therefore probably have niche differences other than time or space.

Lastly, it is interesting to note that time-space niche separation between members of the short-lived (and therefore much less homeostatic) rain system is relatively poor. The tenebrionids 130, 124 and 125 and the weevils Nos. 99 – 103 all have to be active in the same part of the yearly cycle after rain. All these species are chiefly diurnal. Nos. 125 and 130 are plains species, the other tenebrionids and all the weevils occur mainly on the dune slopes. Between the weevils at least specialisation in food plant seems to result in some niche separation, but between 103 and 102, and 99 and 102, this separation seems absent (Fig. 4).

The reasons for niche separation in this system have not been investigated, and we can only speculatively

list them as (i) an even spread of prey species over time and space to enhance prey scarcity, and therefore increase the search effort for predators, (ii) synchronised sympatric activity in each species for intra-specific interactions (mating, territoriality, etc.), (iii) desynchronised or allopatric activity of different species to prevent negative interspecies interactions (hybridisation, competition for shelter and food) and (iv) *a priori* differences in morphological and physiological adaptiveness to different habitat and climate conditions. Food competition might strengthen habitat divisions, since the same food source is fed on at different times by the different species (Robinson & Seely, in prep.).

## 8 ENDEMISM AND DISTRIBUTION OF THE BEETLES

The distribution of 34 of the 50 beetle species recorded in the dunes at Gobabeb is given in Fig. 8, and that of the three true scarabs is given in Holm & Scholtz (1979). Of the remaining 13 species, No. 93 is endemic to the central Namib, whilst numbers 91, 92 and 95 are known to be widespread. The distribution of the remaining 9 species is insufficiently known and all these species are rare in the study area, probably occurring there marginally.

An analysis of the 41 Gobabeb dune species with known distribution shows that 25 (or 60 %) are endemic to the central Namib dune area. A further 5 (or 12 %) occur in both central and southern Namib, and the same number share the central and northern Namib. A further 3 (or 7 %) occur throughout the Namib, bringing the Namib endemism of the dune beetles at Gobabeb to 92 % (or to 76 % in the unlikely case that all the species with unknown distribution prove to be widespread). Few of the beetles have been sufficiently studied to allow an analysis of sub-specific endemism, but it may safely be predicted that this will be even higher. Generic endemism for the dune beetles at Gobabeb is about 50 % for the whole Namib, but only 3 genera (or 10 %) are endemic to the central dune area.

The endemic beetles are mainly apterous, and may be grouped into dune dwellers, plains runners and satellites of rivers and rock outcrops. The non-endemic species are mostly alate sporadic immigrants.

The central Namib dune species may further be divided into a coastal group, a central group, an inland group and a group of widespread species. At Gobabeb the widespread species predominate (Nos. 87 – 89, 93, 99, 101 – 103, 106 – 107, 108, 109, 110, 112, 115, 117, 122, 127, 128). Coastal species which occur up to Gobabeb are Nos. 105, 123 and 132, while Nos. 104, 111, 116, 118, 122, 133 and 136 are typical central dune stock. Many interesting and at present inexplicable distribution limits occur in the dunes from south to north, the most striking being one between Koichab

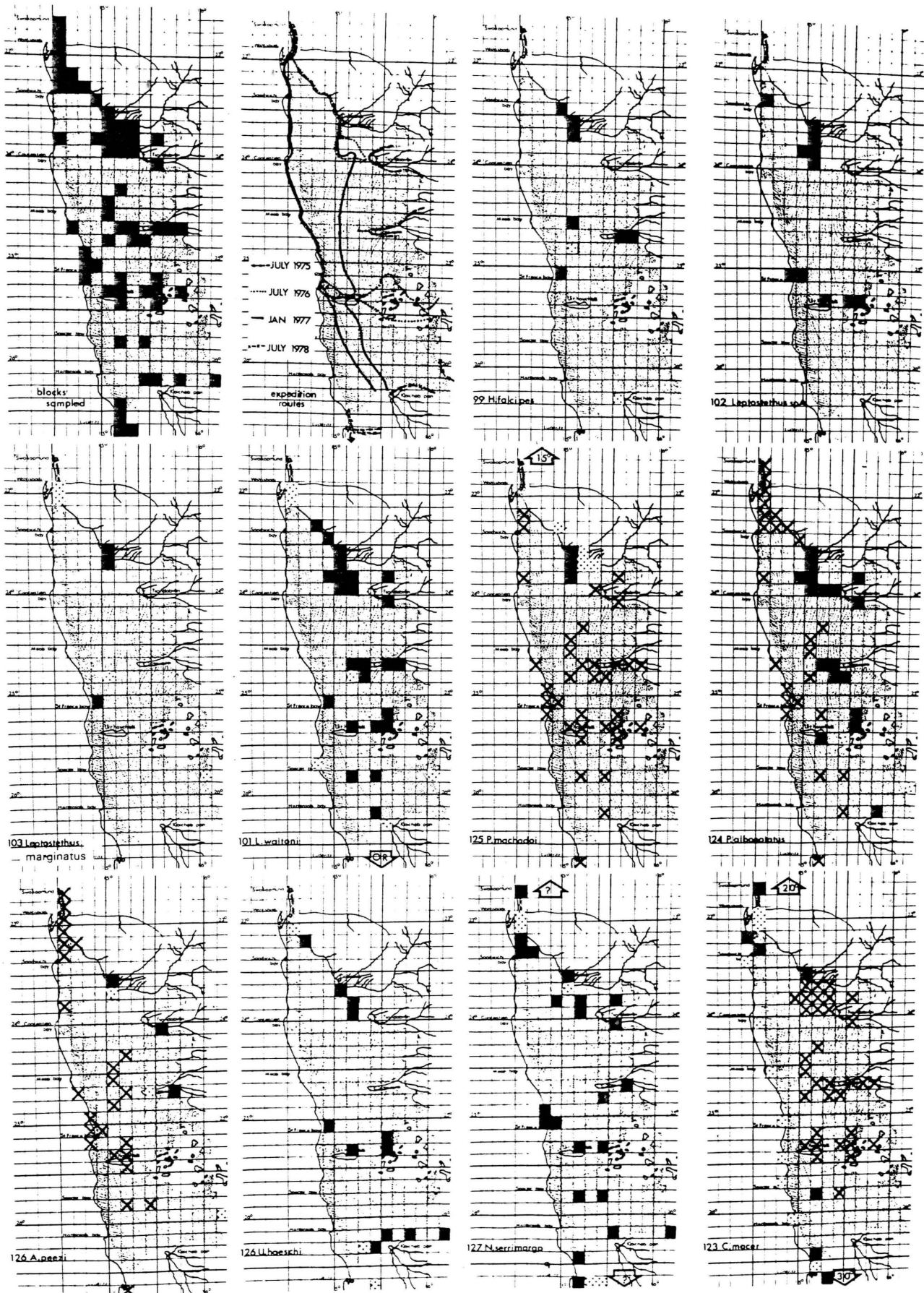
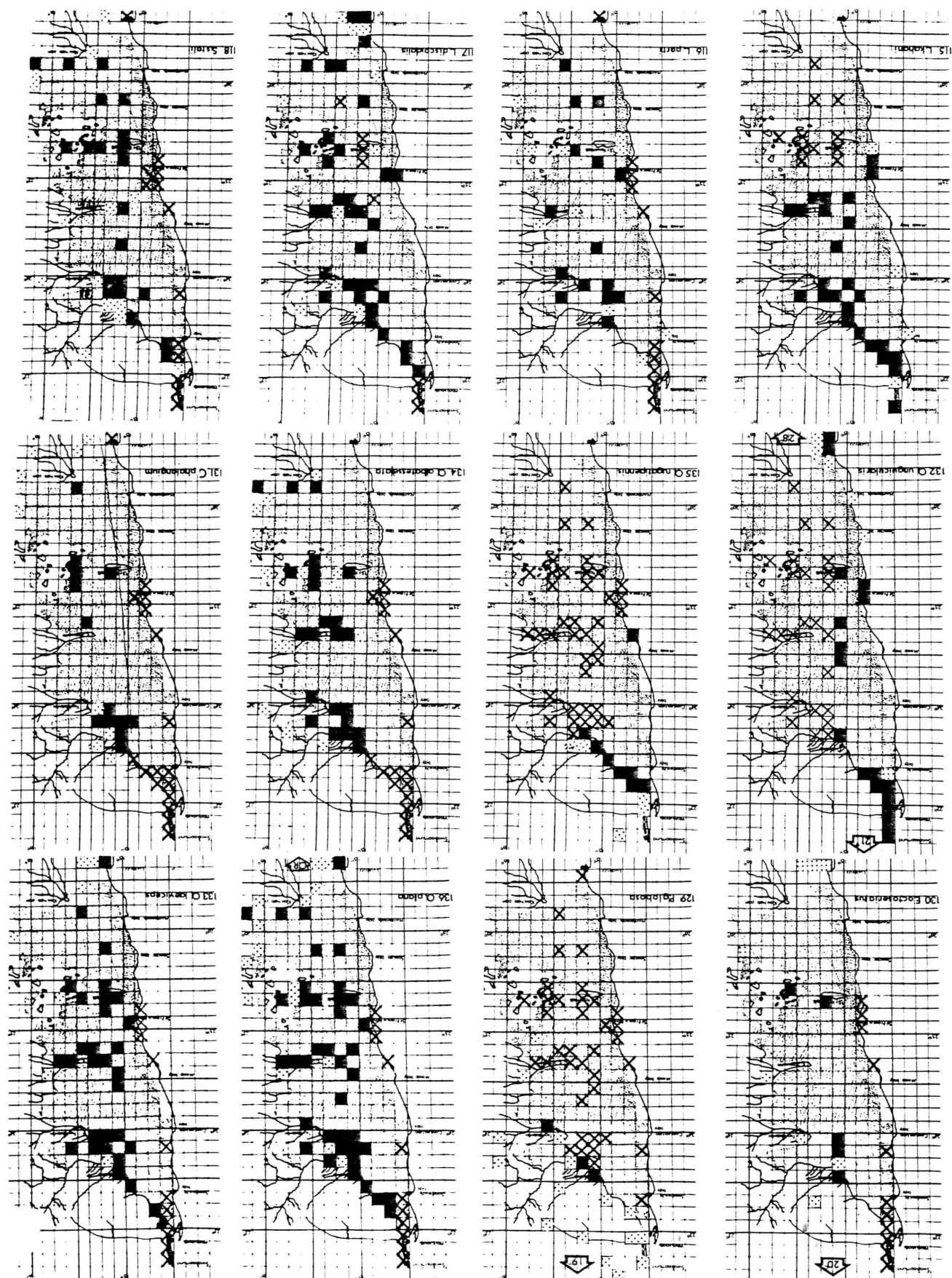


FIGURE 8: Maps of the central Namib with total blocks censused from 1975 to 1978, routes of the four expeditions and recorded distribution for 34 of the beetle species of the Gobabeb dunes. Stippling indicates dune ranges, black blocks are records from our survey and dotted blocks records from other collections (see acknowledgements). The latter blocks vary in accuracy, up to an error of  $\frac{1}{4}$ . Crosses are blocks in which we have reason to believe species do not normally occur.

Fig 8 (cont)





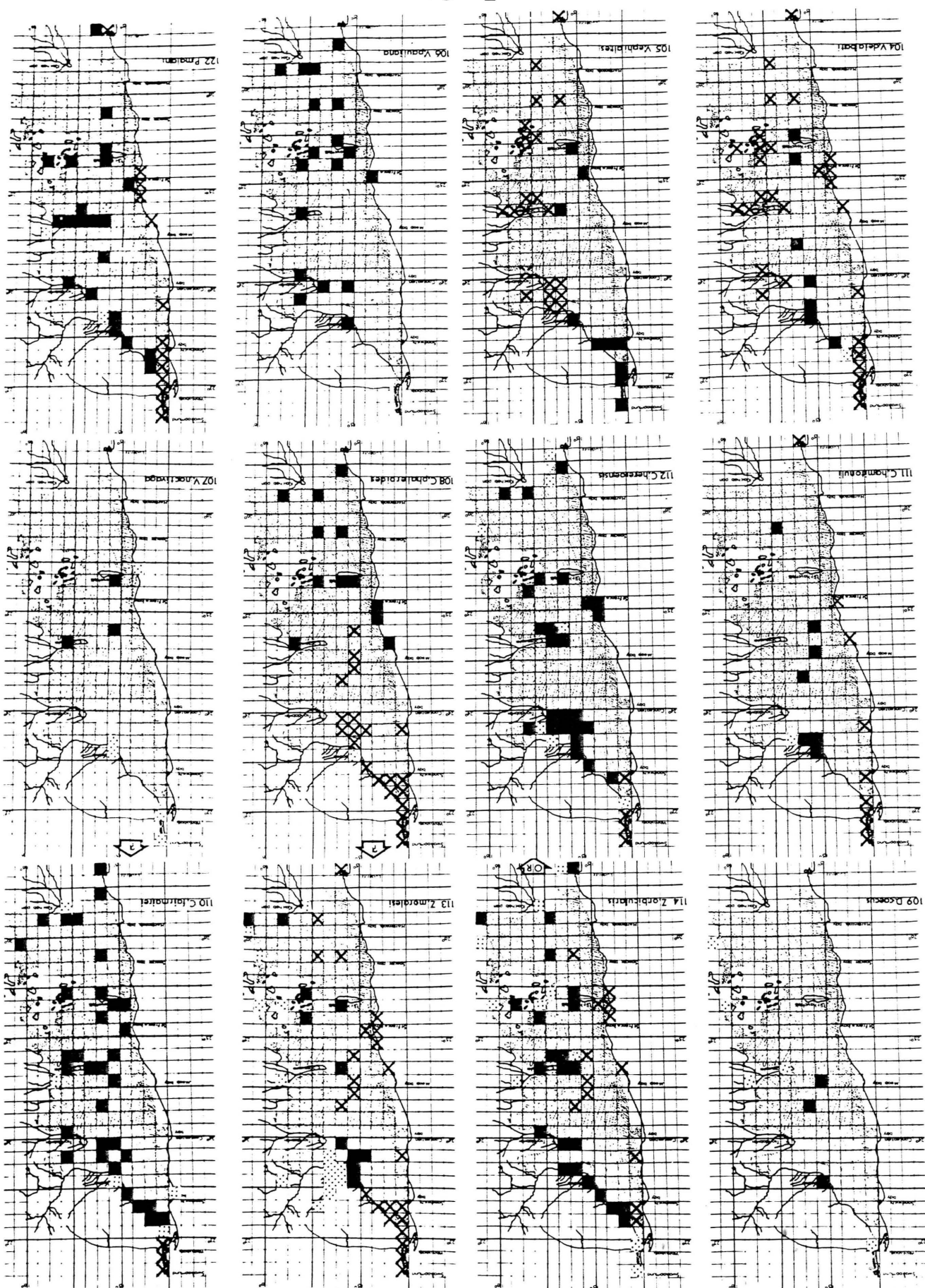


Fig 8 (cont)

Pan and Spencer Bay (northern limit of many species such as *Pachysoma bennigseni*, *Lepidochora pilosulae*, etc.) and one south of Walvis Bay (southern limit of e.g. *Cardiosis triangulifera*, *Lepidochora eberlanzi parva* etc.). These (probably historic) boundaries between species and communities cannot be interpreted only by the composition of the fauna that occurs at Gobabeb, and will be dealt with elsewhere.

Species Nos. 124, 125 and 131 are plains runners. They occur on plains near river-beds and rock outcrops, but also on interdune plains far removed from these. Their habitat preferences are not apparent at the resolution of the distribution maps, but can be seen in Fig. 4.

The species associated with river-beds and rocky terrain all enter the study area from the nearby Kuiseb river-bed (Fig. 1). Their distribution is chiefly sub-desertic, with extensions along river-beds and around inselberg formations. The present distribution and the differences in isolated populations of this fauna may shed more light on the history of migrations of dune barriers and climatic changes of the area (see e.g. No. 135), but

an analysis of these phenomena would overstep the aims of this paper. Species which occur in this category are Nos. 113, 114, 119 — 121, 126, 129, 130, 134 and 135. As could be expected, this group contains most of the species which extend beyond the central Namib.

It is important to remember that distribution limits of the species are not constant, but extend and contract with temporary changes at the periphery of the species' distribution. Thus No. 132 was not recorded at Gobabeb before 1968, and has been constantly present since then. At present it seems to be disappearing from the area (Seely, pers. comm.). Similarly, No. 134 is present in some years and not in others, and Nos. 111 and 128 were only found at Gobabeb after several years of intensive collecting. Most boundaries of distribution in the dunes are unlikely to be maintained by competition, since (with the exception of some north-south barriers between coastal species) the areas of overlap between closely related species are generally wide (Fig. 8), and are more likely determined by niche preferences.

## 9 LIST OF ANIMALS RECORDED

Code No.	Order	Family	Species
1	Artiodactyla	Bovidae	<i>Oryx gazella</i> (L.)
2	Lagomorpha	Leporidae	<i>Lepus capensis</i> L.
3	Rodentia	Cricetidae	<i>Gerbilurus paeba</i> Smith (+ <i>G. vallinus</i> (Thomas))
4	Insectivora	Chrysochloridae	<i>Eremitalpa granti namibensis</i> Bauer & Niethammer
5	Carnivora	Canidae	<i>Canis mesomelas</i> Schreber
6	—	Hyenidae	<i>Hyena brunnea</i> Thunberg
7	Squamata	Viperidae	<i>Bitis peringueyi</i> (Boulenger)
8	—	Colubridae	<i>Psammophis leightoni namibensis</i> Broadley
9	—	Scincidae	<i>Typhlosaurus braini</i> Haacke
10	—	Gekkonidae	<i>Ptenopus garrulus</i> (Smith)
11	—	—	<i>Ptenopus kochi</i> Haacke
12	—	—	<i>Palmatogecko rangei</i> Anderson
13	—	Lacertidae	<i>Aporosaura anchietae</i> (Bocage)
14	—	—	<i>Meroles cuneirostris</i> (Strauch)
15	—	Chamaeleonidae	<i>Chamaeleo namaquensis</i> Smith
16	Passeriformes	Turdidae	<i>Cercomela tracterac</i> (Wilkes)
17	Falconiformes	Falconidae	<i>Falco rupicoloides</i> Smith
18	Strigiformes	Strigidae	<i>Bubo africanus</i> (Temminck)
19	—	Tytonidae	<i>Tyto alba</i> (Blyth)
20	Passeriformes	Corvidae	<i>Corvus albus</i> Statius-Müller
21	Solpugida	Melanoblossiidae	<i>Unguiblossia cauduliger</i> Lawrence
22	—	Solpugidae	<i>Prosolpuga schultzei</i> (Kraepelin)
23	—	—	<i>Metasolpuga picta</i> (Kraepelin)
24	—	Daesiidae	<i>Eberlanzia</i> sp.
25	—	Hexisopidae	<i>Hexisopus pusillus</i> Lawrence
26	—	Daesiidae	<i>Eberlanzia</i> sp. ( <i>notata</i> Lawrence in litt.)
27	—	—	<i>Eberlanzia flava trilineata</i> Lawrence
28	—	—	<i>Blossiola sabulosa</i> Lawrence
29	Aranea	Zodariidae	<i>Caesetius deserticolus</i> Simon
30	—	Sparassidae	<i>Carparachne alba</i> Lawrence



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

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

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