Species composition of and biological notes on Tenebrionidae of the lower Kuiseb River and adjacent gravel plain

by

Robert A. Wharton*

and

Mary Seely

Desert Ecological Research Unit
P.O. Box 1592, Swakopmund
South West Africa/Namibia

Received: 15 September 1981

*Present address:
Department of Entomology
Texas A & M University
College Station
Texas 77843

ABSTRACT

Sixty-two species of Tenebrionidae in fourteen tribes were captured during one year in pitfall traps on the gravel plain and in the Kuiseb river-bed of the central Namib Desert, South West Africa/Namibia. These data, augmented by extensive observations in the field, were used to outline the local distribution, habitat, phenology and behaviour of these beetles.

CONTENTS

1 INTRODUCTION

The Namib Desert of SWA/Namibia supports a rich tenebrionid fauna (Gebien, 1939; Koch, 1961, 1962; Holm and Edney, 1973; Holm and Scholtz, 1980). Endrödy-Younga (1978) discusses the distribution patterns of southern African groups, including those of the Namib Desert. Penrith (1977, 1979) tabulates habitat preferences for Zophosini and Adesmiini.

The central portion of this coastal desert is sharply divided into three major habitat types: dune field, river-bed, and gravel plain (Koch, 1961; Holm and Edney, 1973) (Fig. 1, Plate I). Much emphasis has been placed on the biology of dune tenebrionids, with special regard to their adaptations (e.g. Hamilton, 1971; Louw, 1972; Louw and Hamilton, 1972; Hamilton, 1973, 1975; Henwood, 1975a, 1975b; Hamilton and Seely, 1976; Seely and Hamilton, 1976; Seely, 1979; and references listed above). However, comparatively little has been published on the tenebrionids of the river-bed habitat (e.g. Hamilton *et al.*, 1976; Hamilton and Penrith, 1977; Roer, 1977); and almost nothing on those of the gravel plain. The present work is intended to fill this gap by complementing the work of Holm and Scholtz (1980) on the dune fauna, and by providing base line information for detailed autecological studies. In addition, our data were collected in the vicinity of Gobabeb (24°34′S, 15°03′E) following the unusually heavy rains of 1976 and 1978 (Fig. 2). During 1976 and 1978 over 100 mm of rain fell, while during the ten-year period 1962–1972 the mean annual rainfall was less than 20 mm (Seely and Stuart, 1976). It is hoped, therefore, that our results might be used for comparison with data collected during drier periods.

The river-bed habitat represents a mesic refuge more or less continuous with inland regions of higher rainfall and greater ground cover. A variety of microhabitats not found in the adjacent dunes and gravel plains (e.g. in litter and beneath logs) is associated with the *Acacia*-dominated woodland. In the central Namib Desert, both the Kuiseb and Swakop river-beds provide such sites. Both rivers arise in the central highlands, carve canyons through the escarpment and eastern portion of the gravel plain, and form a broad, shallow flood-plain as they near the coast (Stengel, 1964). Flooding is seasonal, usually reaching the lower portions of the rivers during the late summer months, but rarely flowing into the Atlantic (Stengel, 1964). Holm and Edney (1973), Hamilton and Penrith (1977), and Theron, van Rooyen and van Rooyen (1980) give a detailed picture of the microhabitats in the Kuiseb River near Gobabeb, while Giess (1962) provides an earlier description of the vegetational component.

TABLE 1: Mean annual rainfall across the central Namib Desert. These values include the unusually high rainfall years of 1976 and 1978, therefore probably over-estimating the long-term mean.

	Location	*Rainfall (mm)*	*No. of years*
Walvis Bay	coastal	15	19
Gobabeb	56 km inland	32	13
Ganab	100 km inland	94	11

The gravel plain extends more or less continuously from the Kuiseb River to the Kaokoveld, and from the coast inland to the escarpment (see also Koch, 1961 for a more detailed description). Vegetation patterns are closely correlated with the substrate (Robinson, 1976) and the patchy and sporadic nature of the rainfall (Seely, 1978). In general, however, there is a gradual increase in both vegetation cover (particularly grasses) (Willoughby, 1971; Robinson, 1976) and rainfall (Table 1) from the coast inland. To some degree, the gravel plain resembles the broad interdune valleys of the eastern portion of the dune field. On the gravel plain, however, there are more boulder-strewn areas for petrophilous species, as well as a greater variety of vegetation. Of special interest are the small (3–5 m^2) granite and quartz outcrops and the larger inselbergs. Besler (1972) gives a detailed picture of the geomorphology of

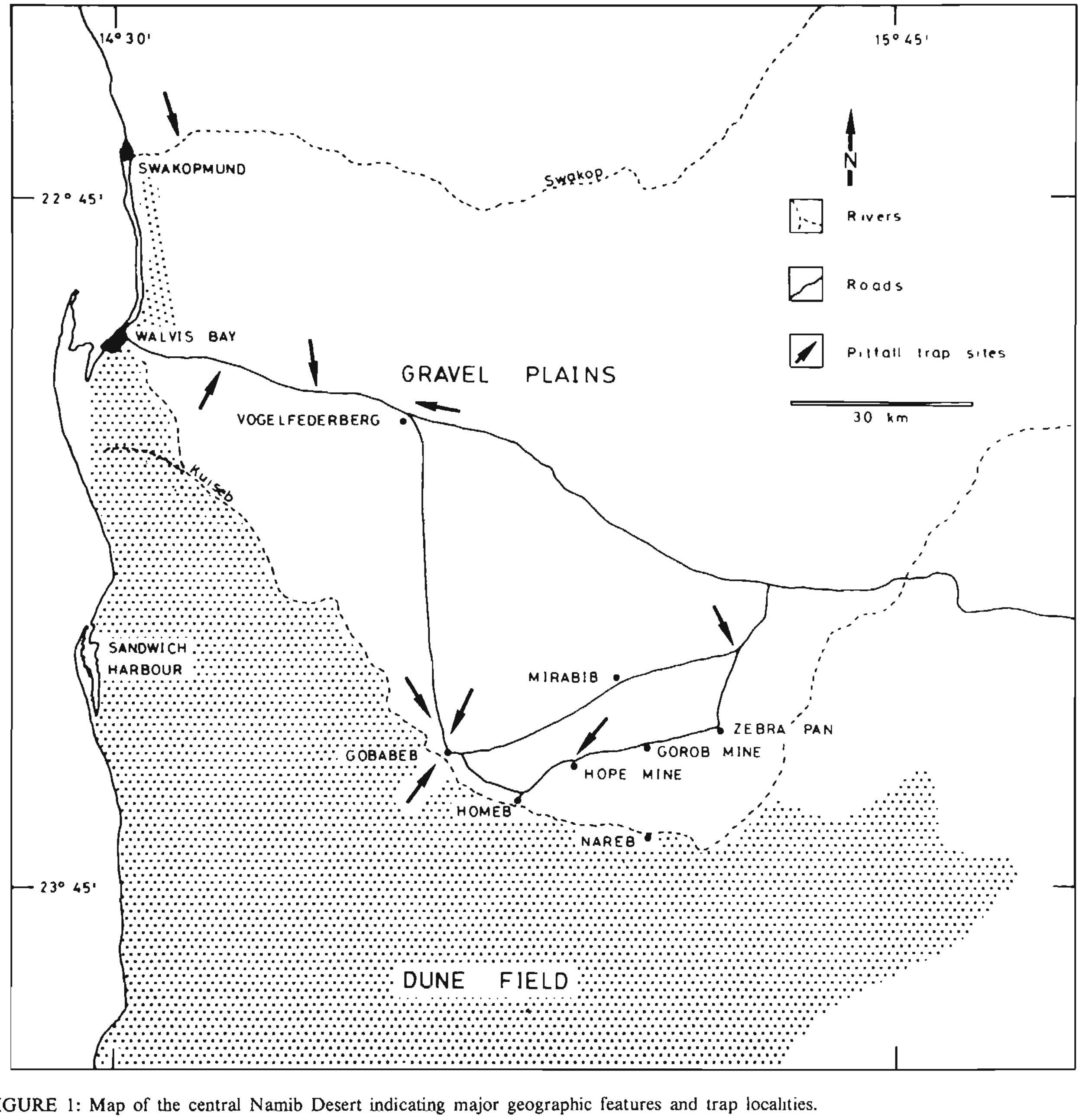

FIGURE 1: Map of the central Namib Desert indicating major geographic features and trap localities.

PLATE 1: The plains (foreground), Kuiseb River and linear dunes of the central Namib Desert at Gobabeb. (Photo: J. D. Ward)

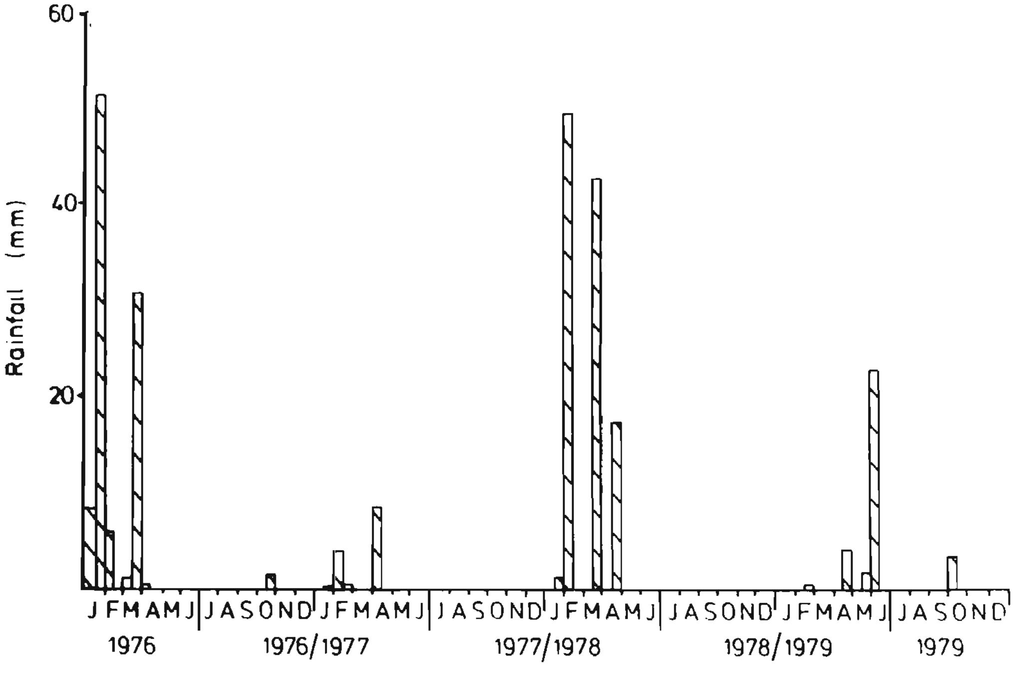

FIGURE 2: Half-monthly rainfall data for Gobabeb, presented in annual periods from July–June (118 mm total from 1976 is the greatest ever recorded for Gobabeb).

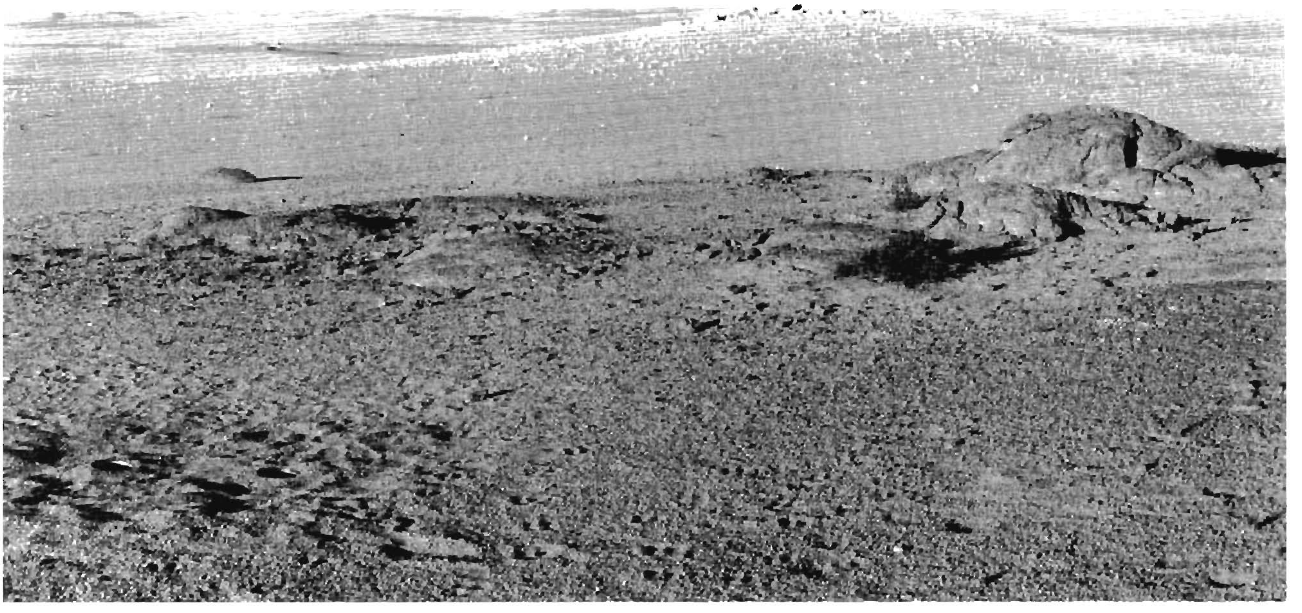

PLATE 2: A detail of pitfall trap set I with trap group C in the lower left of the photograph and the quartz koppie where trap group D is located in the middle distance. Group E is situated behind the koppie out of view. (Photo: V. Gray)

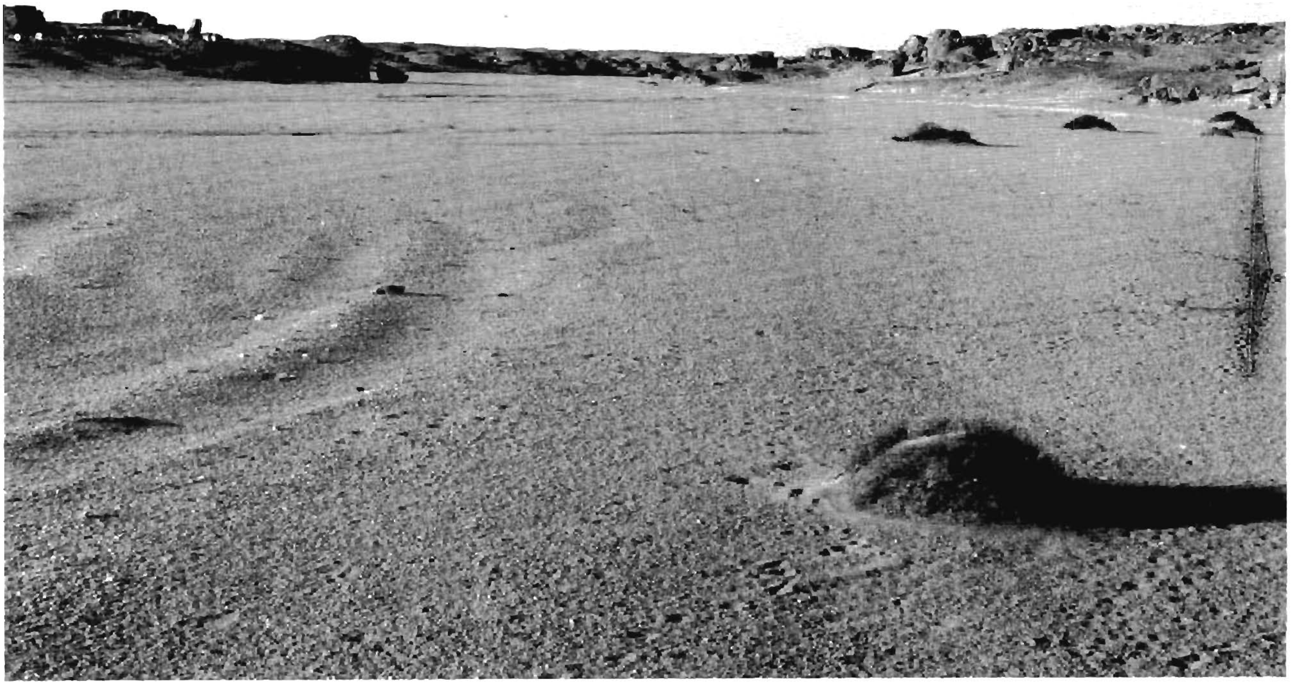

PLATE 3: The dry wash passing through the gravel plain where pitfall trap set II was located for one year. (Photo: V. Gray)

the central Namib gravel plain; and Robinson (1977) lists the vegetation for the inselberg Mirabib.

2 MATERIALS AND METHODS

Three sets of unbaited pitfall traps were used as the primary survey method. All beetles were live-trapped and released two to three metres from the trap after each census. Traps were examined every two to seven days. Meteorological data for the trapping period were obtained from the First Order Weather Station at Gobabeb.

Pitfall traps, Set I. Traps were set out in February, 1976 to record seasonal and yearly changes in populations of four species: *Zophosis (Calosis) amabilis* Deyrolle, *Metriopus (Metriopus) depressus* (Haag), *Physosterna cribripes* (Haag), and *Zophosis (Gyrosis) moralesi* (Koch). This set consisted of five groups of three traps each, located on the gravel plain 5 km north of the Namib Research Institute, Gobabeb (Fig. 1). The three traps in each group were set about 1 m from each other, with the distance between groups ranging from 66 to 400 m (Plate II). Traps were set in the following habitats: broken granite boulders (groups A and C), grassy, gypsum-gravel flats (group E), the interface of these two areas (group B), and a small quartz outcrop (group D). Plant density near each group of traps was measured using a point-centered quarter method (Mueller-Dombis and Ellenberg, 1974) to provide an additional factor for comparing possible habitat preferences of the four species. Traps were made from tin cans 24,0 cm high and 15,5 cm in diameter buried with their upper rims flush with the soil surface. Records from Feb. 1976 – Dec. 1979 were used for this study; and beetles from the three traps of each group were pooled for total counts.

Pitfall traps, Sets II and III, were set out in November, 1978 to record differences in arthropod species composition between the gravel plain and the Kuiseb river-bed. Traps were made from a variety of plastic and tin containers buried with their upper rims flush with the soil surface. Traps were maintained for one year (Nov. 1978 – Nov. 1979).

Pitfall traps, Set II. This set consisted of four groups, each approximately 1 km apart, located on the gravel plain north of Gobabeb (Fig. 1). The first two groups were established in washes which connected to the Kuiseb river-bed 4–5 km to the south. The first wash (10 traps) was distinguished by the presence of a large nara bush (*Acanthosicyos horrida* Welw. ex Bentham & Hooker fil.) and several smaller shrubs (primarily *Zygophyllum stapffii* Schinz and *Blepharis obmitrata* C. B. Clarke). The first wash was more or less continuous with the adjacent plain, lacking well-defined banks or channels in the trap area. The second wash (10 traps) was larger (50–100 m wide), with granite ledges forming a well-defined channel (Plate III). The vegetation was dominated by *Zygophyllum simplex* L. during the first half of the trap period, but all plants died, and most were blown apart during the first east wind period in May, 1979. Thereafter, the trap area contained only a few low bushes of *Psilocaulon salicornioides* (Pax) Schwantes. The third and fourth trap areas were on the open gravel plain with considerably less vegetation. The third group (10 traps) was located near small granite and quartz outcrops. The fourth group (7 traps) was initially set away from outcrops and vegetation, although a sparse covering of *Stipagrostis ciliata* (Desf.) De Winter appeared in this area in July, 1979 following 25 mm of rain in the first week of June.

Pitfall traps, Set III. This set was placed in the Kuiseb river-bed at Gobabeb (Fig. 1). Three tin cans 16–22 cm in diameter were maintained in place throughout the year. These were placed beneath a large *Acacia erioloba* E. Meyer, a large *Ficus sycomorus* L. (both trees with crown diameter > 10 m), and on the open sand near a rock outcrop at the dune river-bed interface. Seven to ten additional traps were used in this area, but were frequently moved to sample a variety of microhabitats and to avoid flooding when the river flowed.

Ethylene glycol pitfall traps. Eight tin cans containing ethylene glycol as a preservative were maintained between Nov. 1978 and Nov. 1979 for comparison with live-trapping methods. Two traps were located in the Kuiseb river-bed at Gobabeb, and the remainder were on the gravel plain at distances up to 70 km north and east of Gobabeb. Two of the traps (Set IV) were maintained throughout the year on the gravel plain 23 and 60 km east of Gobabeb (Fig. 1) to provide an indication of east-west distribution patterns. The remaining traps were operated for periods of 2–6 months.

Other survey methods. Pitfall trap sets II and III were operated in conjunction with detailed observations and foot surveys at least once a week to corroborate trap data on seasonality, relative abundance, and species composition in relation to various microhabitats. Behavioural data and diel activity were also recorded at these times. Less intensive surveys on foot were made in the Kuiseb River Canyon and on the gravel plain around Hope and Gorob Mines, Ganab, Mirabib, Zebra Pan and Vogelfederberg.

The species below and in Table 2 are listed alphabetically by tribe. Tribal names are those listed by Koch (1961) and Gebien (1937–41). Where usage differs, Gebien's terminology is included parenthetically behind Koch's. The only exception to Koch's terminology is the inclusion of *Vansonium* Koch in the Calognathini rather than as a separate tribe.

For trap sets II, III and IV, species recorded less than 5 times during the year are defined as rare, those recorded 5–100 times are defined as uncommon, and those recorded more than 100 times are defined as abundant. Species trapped only once during the year are not included. Seasons are used to conveniently divide the year, but are not necessarily correlated with particular climatic conditions (summer: Jan.—March, autumn: April—June, winter: July—Sept., spring: Oct.—Dec.).

Voucher specimens have been deposited in the Transvaal Museum (Pretoria), State Museum (Windhoek), and the Namib Research Institute reference collection (Gobabeb).

3 RESULTS

The Tenebrionidae far exceeded all other arthropod families both in numbers of individuals and numbers of species trapped during the study period. Ninety-eight per cent of the tenebrionids in the central Namib are apterous (Koch, 1961); and in most cases, pitfall trap catches accurately reflected either relative abundance or vagility as verified by other survey methods. Exceptions (e.g. *Zophosis (Gyrosis) moralesi* (Koch)) are noted in the list below. Winged forms (*Cheirodes* sp., *Clitobius* sp., *Derosphaerius* sp., *Gonocephalum* sp., *Himatismus* sp., and *Neocaedius* sp.), while at least seasonally abundant in the trap areas, were not adequately sampled using pitfall traps. Koch (1961) records both *Microderopsis benguelensis* Haag and *Caenocrypticus phaleroides* Koch from the Kuiseb river-bed at Gobabeb, but neither was found during our survey. It is possible that the lower Kuiseb is a marginal habitat for both these species, and that neither has yet built up large populations following the 1976 flooding.

For convenience of classification several definitions are used here; however, as Koch (1961) notes, some species may be classified into several categories either in different parts of their range or during different seasons. Many Namib species are dependent on vegetation while foraging or during quiescent periods. Koch (1952) terms these species plant followers. Later, Koch (1961) divides this category into stationary (species permanently associated with a single plant) and errant (those which move from plant to plant) plant followers. In addition to plant followers, some Namib Desert tenebrionids forage on the open, level plain away from vegetation, others are petrophilous (seeking shelter or foraging in rocky areas) and a few are subcavernicolous (preferring crevices and small caves in rocky areas). Nearly all species dig beneath the surface. Medvedev (1968) distinguishes between psammophytic diggers and true burrowers. The former (called sand swimmers or sand divers by some authors) dig into the soil without forming a burrow — allowing the sandy substrate to close in behind them as they dig. The latter dig well-defined tunnels beneath the surface.

These and other characteristics of the distribution and behaviour of the species observed are summarised in Table 2. Further information has been included in the following species list.

ADESMIINI (see also Penrith, 1979)

Cauricara (Cauricara) eburnea (Pascoe); Gobabeb forms the eastern limit of its range (Penrith, 1979). Greatest activity at Gobabeb is in late autumn and winter, beginning with the first east wind period. Trap catches do not accurately reflect abundance, since this species was often observed to avoid broken ground in the vicinity of traps.

Cauricara (Cauricara) velox albovillosa (Péringuey) was most active during the winter. Pitfall traps do not accurately reflect abundance, except possibly at the end of the season. Like *C. (C.) eburnea, C. (C.) velox albovillosa* was active at midday, and actively avoided pitfall traps early in the season. An increase in trap catches for September (Fig. 3) was apparently the result of a

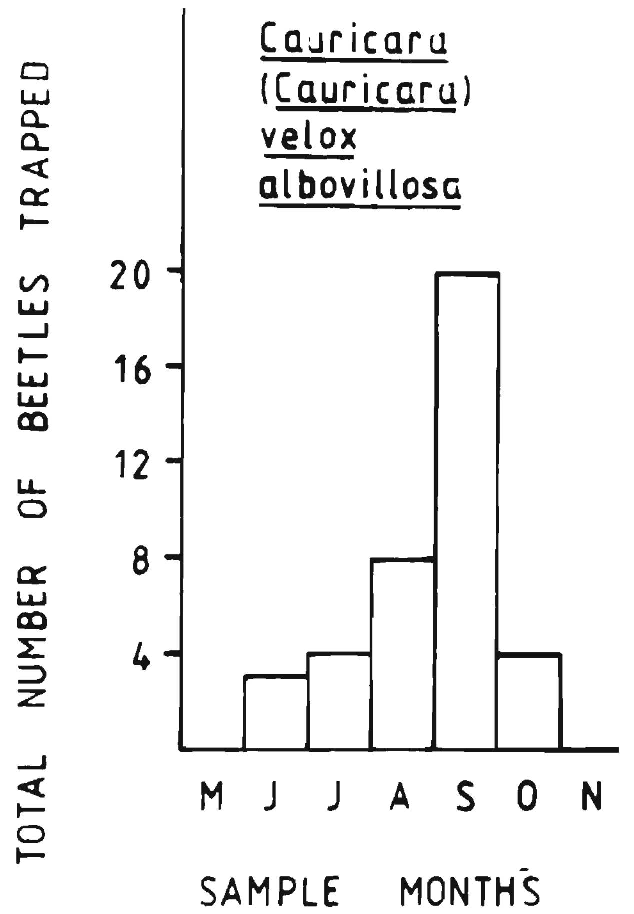

FIGURE 3: Collections of *Cauricara (C.) velox albovillosa* from pitfall trap set II, showing dramatic increase in September 1979.

behavioural change since other survey methods failed to indicate an increase in abundance over other months. Observations suggest that aging individuals may be less capable of avoiding the traps. *C. (C.) velox albovillosa* is an ecological homologue of the closely-related, interdune valley inhabiting *C. (C.) phalangium* (Gebien).

Epiphysa arenicola Penrith, although often associated with vegetation, also forages in open areas. Specific microhabitat preferences could not be discerned for this

TABLE 2: Habitats, foraging associations, diel periodicity, retreats, occurrence and phenology of the tenebrionid species encountered in this study. — (Notations used for occurrence: A = abundant; R = rare; U = uncommon; X = present)

	HABITATS						FORAGING ASSOCIATION			DIEL PERIODICITY			RETREATS			OCCURRENCE					PHENOLOGY											
	PLAIN				DUNE		Plant follower		Open																							
	Open plain	Rocky outcrops	Sandy washes	RIVER-BED	Interdune valley	Dune base	Stationary	Errant		Diurnal	Nocturnal	Crepuscular	Psammophytic diggers	True burrower	Under rocks, logs, etc.	Trap sets II	Trap sets III	23 km east of Gobabeb	60 km east of Gobabeb	Kuiseb Canyon	J	F	M	A	M	J	J	A	S	O	N	D
ADESMIINI																																
Cauricara (Cauricara) eburnea (Pascoe)	X	X							X	X			X			U	–															
Cauricara (Cauricara) velox albovillosa (Péringuey)	X								X	X			X			U	–															
Epiphysa arenicola Penrith	X	X	X	X				X	X		X					U	U															
Epiphysa punctatissima Penrith				X							X					–	–			X												
Metriopus (Metriopus) depressus (Haag)	X	X						X		X		X			X	A	–	X														
Onymacris rugatipennis albotessellata Schulze				X		X		X	X	X			X			–	–			X												
Onymacris rugatipennis rugatipennis (Haag)				X				X		X			X			–	A															
Physadesmia globosa (Haag)			X	X				X		X			X			A	A															
Physosterna cribripes (Haag)		X	X					X		X			X		X	A	–	X	X													
Stenocara aenescens Haag	X							X	X	X						–	–		A													
Stenocara gracilipes Solier				X				X		X						–	A			X												
CAENOCRYPTICINI (=CRYPTICINI)																																
Caenocrypticus peezi Koch				X			X				X		X			–	U															
Caenocrypticus uncinatus Gebien		X									X				X	–	–	X														
CALOGNATHINI																																
Vansonium bushmanicum Koch	X				X				X		X			X		U																
CRYPTOCHILINI																																
Pachynotelus lineatus Haag				X				X		X				X		–	R															
DROSOCHRINI (HELOPININI)																																
Diestecopus histrio Koch	X	X							X		X				X	U	–															
Nicandra sp.				X							X				X	–	U		U	X												
EPITRAGINI																																
Himatismus sp.				X							X					–	R															

(Table 2 cont.)

	HABITATS						FORAGING ASSOCIATION			DIEL PERIODICITY			RETREATS			OCCURRENCE					PHENOLOGY											
	PLAIN				DUNE		Plant follower		Open							Trap sets																
	Open plain	Rocky outcrops	Sandy washes	RIVER-BED	Interdune valley	Dune base	Stationary	Errant		Diurnal	Nocturnal	Crepuscular	Psammophytic diggers	True burrower	Under rocks, logs, etc.	II	III	23 km east of Gobabeb	60 km east of Gobabeb	Kuiseb Canyon	J	F	M	A	M	J	J	A	S	O	N	D
EURYCHORINI																																
Acestophanus sp.	X								X		X				X	—	—	U	U													
Eurychora sp. A	X								X		X					A	—															
Eurychora sp. B				X				X			X	X				—	A															
Eutichus wahlbergi Haag	X								X		X				X	—	—	U	U													
Geophanus sp.				X							X				X	—	A															
Stips dohrni (Haag)			X								X		X			U	—	X	X													
Stips stali Haag				X		X		X			X		X			—	A															
MELANIMINI (=OPATRINI)																																
Cheirodes spp.			X	X							X					U	A															
MOLURINI																																
Namibomodes zarcoi Koch				X		X		X			X		X			—	A															
Psammodes sp.	X								X				X			R	—	U	U													
Pterostichula sp.	X															—	—		U													
Somaticus aeneus (Solier)	X									X						—	—		R													
Somaticus bohemani (Haag)				X					X	X						—	—			X												
Synhimba melancholicum Koch	X								X		X		X			R	—	U														
Synhimba sp.	X								X		X		X			A	—															
Trachynotidus cf. *rufozonatus*	X															R	—	R	R													
OPATRINI (including PEDININI and STIZOPINI)																																
Clitobius sp.				X							X					—	A															
Ennychiatus fitzsimmonsi Koch	X										X					—	—		U													
Gonocephalum sp.				X							X					—	U			X												
Leubbertia plana Koch				X							X				X	—	R			X												
Neocaedius sp.				X							X					—	A															
Parastizopus armaticeps (Péringuey)	X		X						X		X			X		A	—															
Planostibes dentipes Koch	X			X							X				X	—	U	X	U													
Stizopina spp. near *Planostibes*	X	X									X					U	—	U	U													
Psammogaster malani Koch				X		X	X				X		X			—	U															
Stenolamus sp.		X									X				X	—	—	U														
PLATYNOTINI (=GONOPINI)																																
Gonopus tibialis Fabricius			X	X				X			X			X		U	A															

(Table 2 con.)

	HABITATS						FORAGING ASSOCIATION			DIEL PERIODICITY			RETREATS			OCCURRENCE					PHENOLOGY											
	PLAIN				DUNE		Plant follower		Open							Trap sets																
	Open plain	Rocky outcrops	Sandy washes	RIVER-BED	Interdune valley	Dune base	Stationary	Errant		Diurnal	Nocturnal	Crepuscular	Psammophytic diggers	True burrower	Under rocks, logs, etc.	II	III	23 km east of Gobabeb	60 km east of Gobabeb	Kuiseb Canyon	J	F	M	A	M	J	J	A	S	O	N	D
SCAURINI																																
Carchares macer Pascoe				X		X					X				X	–	U															
Herpiscius sp.				X							X				X	–	R															
TENTYRIINI																																
Asphaltesthes impressipennis Fairmaire	X			X							X					–	A	X	A	X												
Derosphaerius sp.				X							X				X	–	U															
Rhammatodes aequalipennis Péringuey			X				X?	X			X					A	–	X	X													
Rhammatodes longicornis Haag		X		X					X			X			X	A	U	X	X	X												
Rhammatodes subcostatus Koch				X					X		X	X	X?		X	–	U															
Rhammatodes tagenesthoides Koch		X							X		X	X			X	U	–															
ZOPHOSINI																																
Zophosis (Calosis) amabilis Deyrolle	X								X	X			X			A	–															
Zophosis (Carpiella) latisterna Koch	X						X		X	X	X?		X			U	–															
Zophosis (Gyrosis) devexa Péringuey	X							X		X			X			A	–	X	X													
Zophosis (Gyrosis) moralesi (Koch)	X				X				X	X			X			A	–	X														
Zophosis (Gyrosis) orbicularis Deyrolle				X		X		X		X			X			–	A															
Zophosis (Occidentophosis) cerea Penrith		X	X					X	X	X			X		X	A	–	X	X													
Zophosis (Occidentophosis) parentalis (Péringuey)		X							X	X					X	–	–	R														
Zophosis (Protodactylus) giessi Koch				X			X			X	X?		X			–	R															
Zophosis (Zophosis) dorsata Péringuey	X								X	X			X			U	–	X	X													
Zophosis (Zophosis) mniszechi Deyrolle	X		X		X			X	X	X			X			–	–	A	A													

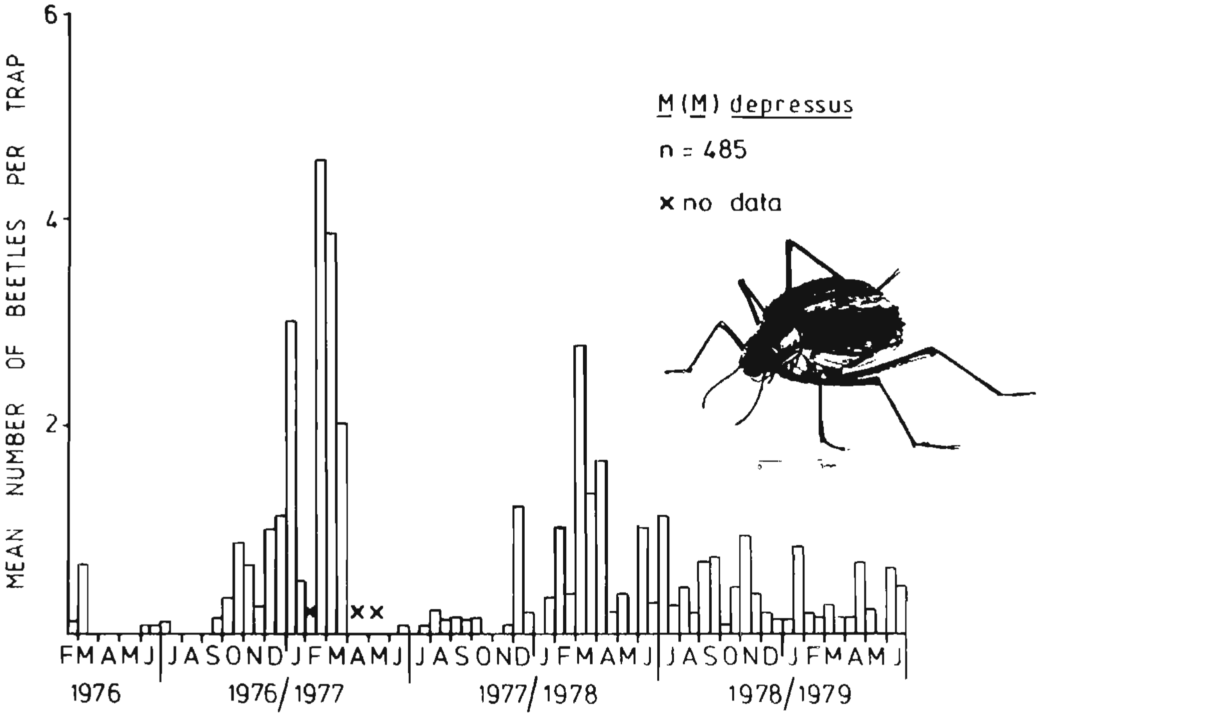

FIGURE 4: Mean number of *Metriopus (M.) depressus* collected per day from 15 traps of set I. Data averaged for half-monthly intervals from mid-February 1976 to December 1979 inclusive.

species. Digging habits are unknown but it will occupy old, abandoned burrows. Laboratory feeding experiments using solifuges and geckos from Gobabeb showed that the rounded shape and extremely hard integument form an important defence against these powerfully jawed nocturnal predators.

Epiphysa punctatissima Penrith was not found at Gobabeb during the study period, but in the Kuiseb River Canyon area to the east.

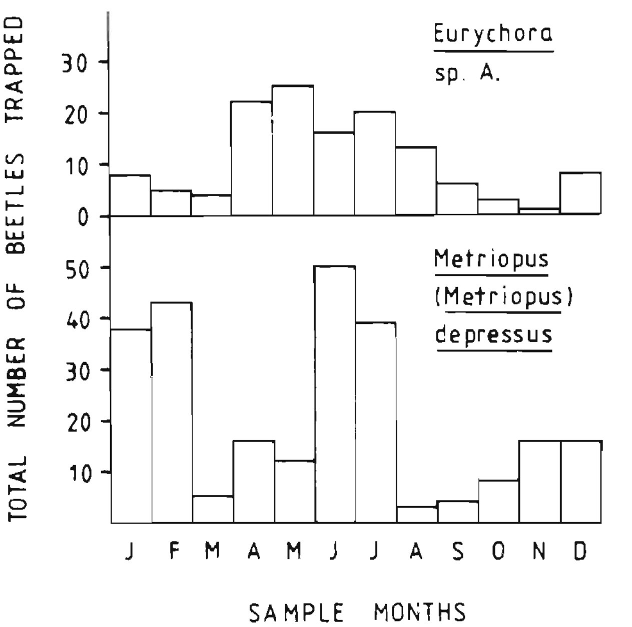

FIGURE 5: Collections of *Eurychora* sp. A and *Metriopus (M.) depressus* from pitfall trap set II from November 1978 to October 1979 inclusive.

Metriopus (Metriopus) depressus (Haag): interpretation of seasonal activity was difficult because of the great increase in activity during and following rains and precipitating fogs. Monthly catches for trap sets I and II

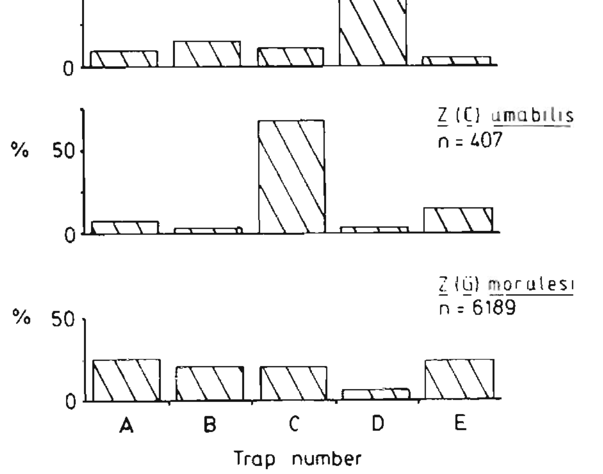

FIGURE 6: Habitat preferences indicated by distribution of captures. See text for substrate and plant density characteristics of each trap group.

are shown in Figs. 4 and 5. Beetles were often found gregariously under rocks or as psammophytic diggers under rocks when not foraging. Habitat preferences are indicated in Fig. 6. *M. (M.) depressus* feeds on newly sprouted plants when these are available.

Onymacris rugatipennis albotessellata Schulze is replaced in the river-bed by *O. r. rugatipennis* (Haag) in the vicinity of Homeb (with *O. r. albotessellata* moving out into the dunes further westward). It is more active in slightly more exposed microhabitats than the nominate subspecies. Populations of *O. r. rugatipennis* and *O. r. albotessellata* are not separated by geographical barriers.

Onymacris rugatipennis rugatipennis (Haag) forages in the river-bed wherever food is available, but avoids dense vegetation and compact substrates. Hamilton *et al.* (1976) state that *Eragrostis spinosa* (L. fil.) Thunb. was the favoured foraging plant of this species; but Hamilton and Penrith (1977) found it most commonly associated with *Nicotiana glauca* R. Graham. Between Nov. 1978 and Nov. 1979, *O. r. rugatipennis* foraged most frequently around *E. spinosa*, the most productive bush in the study site, but moved to *Ficus sycomorus* in large numbers (Fig. 7) following fig drop at the end of December. Hamilton *et al.* (1976) describe the social organisation; Roer (1977) describes the behaviour; and Holm and Edney (1973) and Hamilton *et al.* (1976) discuss temperature-related activity rhythms. One female was observed ovipositing on an open sandy surface in a sparsely vegetated portion of the river-bed. Eggs were placed singly 80±5 mm deep (N=3, t/ovip = 40–60 sec).

Physadesmia globosa (Haag) was most commonly encountered in the river-bed on litter beneath trees. It extends out into plains via those sandy washes with vegetation or shaded banks, avoiding extensive activity in the open. Of 1 183 individuals recovered from trap set II, 98,5% were from the wash habitats. The slight depression in trap catches for Feb. – March (7% of total catch, Fig. 8) was correlated with high summer temperatures and a consequent restriction of activity around more sheltered environments away from pitfall traps. It thus did not necessarily represent a decrease in population density for this period. Decrease in activity during midday was also most noticeable during this period. There were no noticeable food preferences. One individual ate 5 live termites (*Psammotermes allocerus* Silvestri) as they were tossed out of a burrow in the river-bed by an excavating solifuge. Response to fig fall was similar to that found in *O. r. rugatipennis* (Fig. 7). *Physadesmia globosa* is broadly sympatric with *Physosterna cribripes* (Haag), and both are abundant in washes. However, *P. cribripes* moves onto harder substrates from washes, whereas *P. globosa* moves into washes from sandy substrates. The two species are

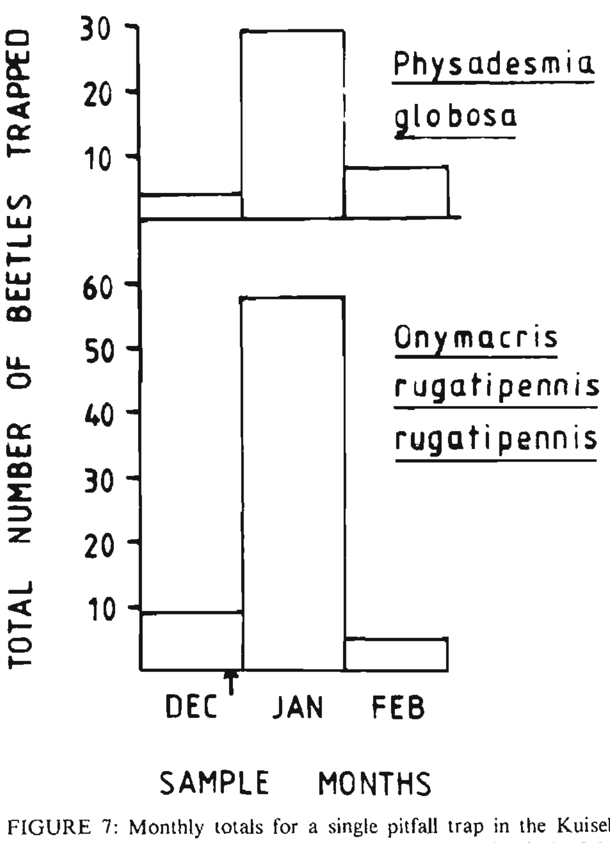

FIGURE 7: Monthly totals for a single pitfall trap in the Kuiseb River beneath *Ficus sycomorus*. The response to fig fall (↑) of the two species most commonly trapped at this site (*Physadesmia globosa* and *Onymacris r. rugatipennis*) was significantly different from uniform (chi-square, $p<0{,}005$).

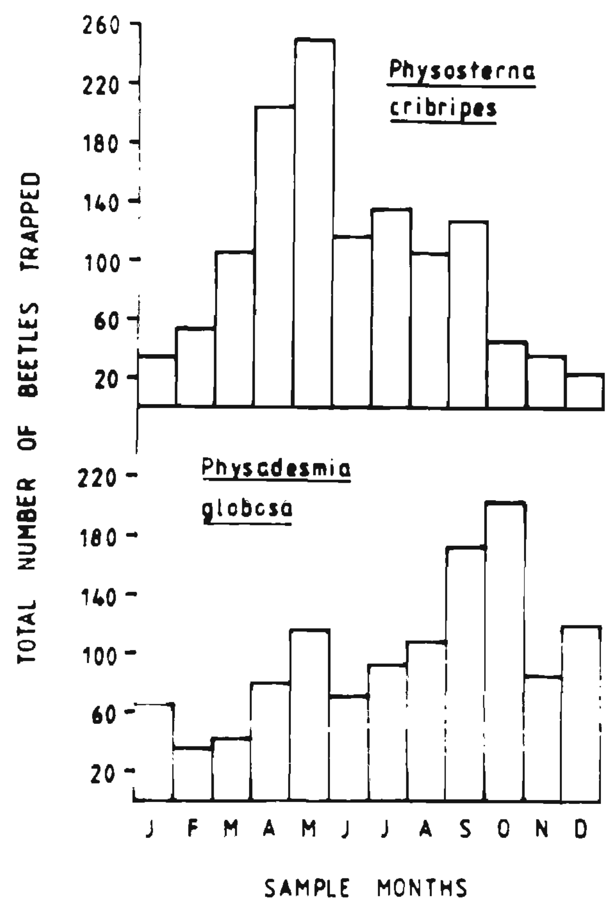

FIGURE 8: Collections of *Physosterna cribripes* and *Physadesmia globosa* from pitfall trap set II, November 1978 to October 1979 inclusive.

closely related. Hamilton and Penrith (1977) give further details on the habitat preferences of *P. globosa.*

Physosterna cribripes (Haag) was the most frequently trapped species on the gravel plain; and was only rarely encountered at the edge of the river-bed. Of 1 234 individuals recovered from trap set II, 76,5% were from the wash habitat. There was a noticeable depression in activity during the spring and summer months (Fig. 8). Increase in trap catches during April and May was partially due to increase in vagility, especially during east wind periods. Trap catches from set I are shown in Fig. 9. More petrophilic than *P. globosa,* this species often seeks shelter in rock crevices or under rocks at midday or during the night. Preference for coarser substrates (Fig. 6) is reflected in a harder integument and more depressed habitus compared with *P. globosa. P. cribripes* is omnivorous, but was frequently encountered

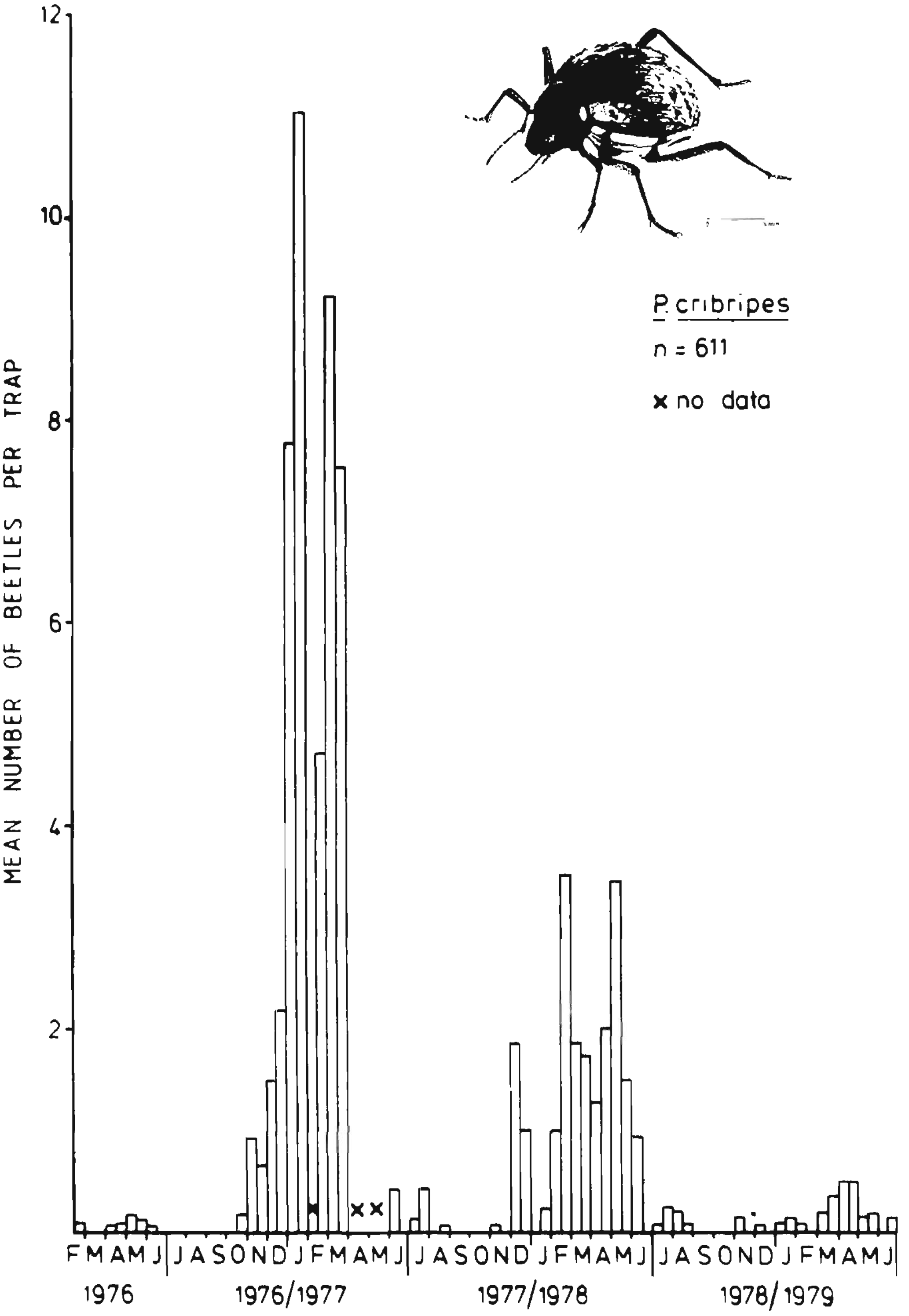

FIGURE 9: Mean number of *Physosterna cribripes* collected per day from 15 pitfall traps of set I. Data averaged for half-monthly intervals from mid-February 1976 to December 1979 inclusive.

foraging on green vegetation and developing seeds up in low *Zygophyllum simplex* bushes.

Stenocara aenescens Haag was found on open plains with moderate vegetation cover, but not in the immediate vicinity of the research station.

Stenocara gracilipes Solier is a widespread species (Penrith, 1979) confined to mesic riverine habitats in more arid climates. *S. gracilipes* usually retreats to more heavily shaded areas and decreases activity at midday (especially during hotter periods), whereas *O. r. rugatipennis* and *P. globosa* dig beneath the surface to escape midday heat. Of the three large diurnal adesmiines found in the Kuiseb river-bed, *P. globosa* and *S. gracilipes* forage more commonly beneath trees or in more shaded habitats, but *O. r. rugatipennis* prefers more exposed habitats (see also Hamilton and Penrith, 1977).

CAENOCRYPTICINI (=CRYPTICINI)

Caenocrypticus peezi Koch was found in leaf and pod-littered substrates, especially beneath acacias. Low numbers trapped were more indicative of low vagility, small size of the species, and trap placement rather than abundance.

Caenocrypticus uncinatus Gebien, although not found in pitfall traps, was frequently encountered under small rocks in boulder-strewn areas of the gravel plain 20–30 km east of Gobabeb.

CALOGNATHINI

Vansonium bushmanicum Koch was most active in November. It was not found in washes nor around vegetation. This species was previously recorded only from the dune field in the vicinity of Gobabeb (Koch, 1961). Unlike *Calognathus* Guerin, the only other member of this tribe, *Vansonium* did not occur in dense, social aggregations in the study area. A strong, rapid digger, *Vansonium* burrows in a manner identical to *Calognathus:* sand is thrown out behind the abdomen with the combined action of three legs on one side alternating with the three legs of the opposite side. Sand is thrown up to 30 mm behind the tip of the abdomen. During burrow construction, the beetle repeatedly backs out of the hole, then digs in again.

CRYPTOCHILINI

Pachynotelus lineatus Haag was collected in low numbers throughout the year, but rarely in pitfall traps. It was most frequently encountered on sandy, well-shaded, leaf-littered substrates.

Four other *Pachynotelus* spp. were observed during the study period both in the dune field and on the gravel plain 50–60 km east of Gobabeb. Like members of the closely-related Calognathini, rapid sand-kicking with legs on alternate sides of the body is typical, with the species forming discrete burrows in more compact sands (e.g. *P. machadoi* Koch). Greatest activity was correlated with appearance of reproductive structures in grasses (especially *Stipagrostis* spp.), which in turn is strongly correlated with rainfall events of 20 mm or more (Seely, 1978). *Pachynotelus* spp. regularly climb vegetation to forage on developing reproductive structures. In *P. machadoi,* and probably other species as well, the fore tarsal claws are used to pry open leaf sheaths to expose developing seeds or anthers. The burrowing and feeding behaviour described above are quite possibly applicable to most members of this genus.

DROSOCHRINI (=HELOPININI)

Diestecopus histrio Koch was found to be a strictly seasonal species seeking shelter under small rocks during the day.

Nicandra sp., although uncommon in pitfall traps, was frequently found beneath logs in all portions of the river-bed. This species, or a closely related one, was also collected on the gravel plain 50–80 km east of Gobabeb in vegetated washes.

EPITRAGINI

Himatismus sp. is a fully winged species not adequately surveyed during this study. Koch (1961) states that it is arboricolous.

EURYCHORINI

Acestophanus sp. and *Eutichus wahlbergi* Haag were most commonly found under rocks. While usually associated with ants, the exact nature of this association is uncertain.

Eurychora sp. A: pitfall trap catches were greatest during autumn and early winter months (Fig. 5). This species seeks refuge in old burrows during the day. The dorsal surface is covered with a thick layer of waxy filaments, which functions at least in part as a predator deterrent (R. W., pers. obs.). The wax layer accumulates dirt, plant debris, etc., and thereby also functions in camouflage for this slow-moving species.

Eurychora sp. B was particularly abundant in areas with good litter cover; and was most frequently trapped during the early autumn. It is similar in appearance to sp. A, but lacks a waxy secretion on the dorsal surface.

Geophanus sp. forages on sandy soils with a thin layer of decomposing leaf litter. It was most frequently collected under logs during the day.

Stips dohrni (Haag) was most frequently trapped during the autumn and winter months.

Stips stali (Haag), like *S. dohrni,* was occasionally found in old, abandoned burrows. Wharton (ms.) studied the biology of *S. stali* at Gobabeb.

MELANIMINI (=OPATRINI)

Cheirodes spp. were commonly encountered in the spring months, but were rarely taken in pitfall traps. The largest of three species was found both in the river-bed and in washes on the gravel plain; the other two were collected only in the river-bed.

MOLURINI

Namibomodes zarcoi Koch occurred in areas with a moderate cover of *Acacia* leaf litter. It was the only one of three central Namib *Namibomodes* species regularly found in the river area. However, it is best classified as an ecotonal species since it was never found away from dune sand.

Psammodes sp. is a large, sexually dimorphic species having a densely haired male sternum.

Pterostichula sp. was found only in one trap area 60 km east of Gobabeb, and only during the winter months.

Somaticus aeneus (Solier) was uncommon at Ganab, rare at Mirabib, and not found in the vicinity of Gobabeb. Other all-black *Somaticus* species may have a similar distribution pattern, but were not collected during this study.

Somaticus bohemani (Haag) was found only in the Kuiseb Canyon area during the present study; and was collected no closer than 30 km east of Gobabeb.

Synhimba melancholicum Koch was an eastern species ranging westward only about as far as Gobabeb in 1979.

Synhimba sp. was collected most commonly around small quartz outcrops. It is covered with a white pulverulent layer in life. Trap records suggested that the distribution of the two *Synhimba* species overlaps only slightly.

Trachynotidus cf. *rufozonatus*, collected only once at Gobabeb, was uncommon in the Mirabib vicinity.

OPATRINI (including PEDININI and STIZOPINI)

Clitobius sp. and *Neocaedius* sp. were particularly noticeable in the spring months. Although similar in overall appearance, differences in the shape of the fore tibia of these winged species suggest different digging methods (see also Medvedev, 1968).

Ennychiatus fitzsimmonsi Koch was not found in the Gobabeb vicinity, but did occur further to the east.

Gonocephalum sp. is a fully winged species which was not adequately sampled.

Luebbertia plana Koch was found only very rarely in the vicinity of Gobabeb. However, it was commonly collected from beneath logs and stones 40 km east of Gobabeb in the Kuiseb River Canyon.

Parastizopus armaticeps (Péringuey) was particularly active in washes. It was trapped most frequently in the spring (44% of catch in set II) and infrequently in the autumn (11% of catch in set II). This species is capable of excavating deep burrows (mean length = 465 mm, N = 2) in compact, sandy soils. Those examined (N = 4) were occupied by one male and one female each. Schulze and Brown (1975) also discuss burrowing activities and brood-care in this species.

Planostibes dentipes Koch was found in the Kuiseb River Canyon, the Kuiseb river-bed at Gobabeb and out on the gravel plain 60—80 km east of Gobabeb. Collection records suggest that it prefers sandy substrates with moderately heavy cover of *Acacia* and *Euclea* leaf litter. This species often shelters under logs during the day.

Stizopina spp. near *Planostibes:* at least two species were found uncommonly on the gravel plain in the Gobabeb vicinity and in rockier habitats to the north (Vogelfederberg) and east (Hope and Gorob Mines). Individuals from Gobabeb were all trapped at the base of bushes; and were not found during the summer months.

Psammogaster malani Koch occurred on the south bank of the Kuiseb River in sandy areas. This species was found to shelter during the day in buried detritus pads at the base of rocky outcrops. It was rare in pitfall traps during every month except June, when more than fifty were collected.

Stenolamus sp. occurred in the same microhabitat as *Caenocrypticus uncinatus* in the rocky areas to the east of Gobabeb (e.g. Hope and Gorob Mines).

PLATYNOTINI (=GONOPINI)

Gonopus tibialis Fabricius was the most frequently trapped tenebrionid in the river-bed, where it occurred most commonly in wooded areas with moderate litter cover. It was confined mostly to washes on the gravel plain. Individuals often sheltered gregariously under logs during the day. The activity peak in autumn months (Fig. 10) was due to an increase in vagility. Tschinkel (1979) reports on ovoviviparity in some South African Gonopini. In June, 1979, several individuals of *G. tibialis* were confined in a glass terrarium and the sand sieved at 2-day intervals. Eggs were first produced after twenty-two days. They were elongate-oval, and 1,5 × 2,4 mm.

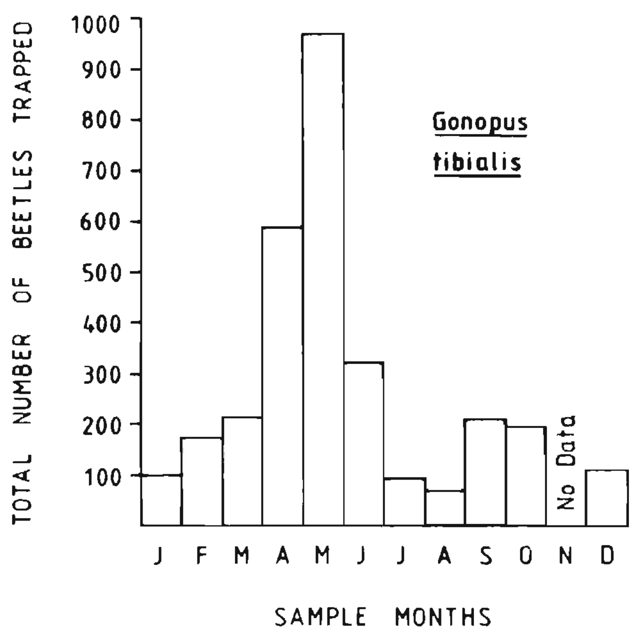

FIGURE 10: Collections of *Gonopus tibialis* from pitfall trap set III (2 traps) from December 1978 to October 1979 inclusive.

Brinck (1956) discusses burrowing in a *Gonopus* species; and Schulze (1978) discusses burrowing in three *Gonopus* species.

SCAURINI

Carchares macer Pascoe shelters gregariously under logs in the river-bed during the day.

Herpiscius sp., though rarely trapped, was uncommon under logs at Gobabeb. Both scaurine species were observed feeding on a variety of animal and vegetable matter.

TENTYRIINI

Asphaltesthes impressipennis Fairmaire occurred in vegetated habitats with moderate litter cover; and was absent from the plain in the vicinity of Gobabeb.

Derosphaerius sp. is similar to, but larger than the dune-dwelling *D. humilis* Péringuey. Both are fully winged species.

Rhammatodes aequalipennis Péringuey was collected almost exclusively in washes. Forty-nine per cent of the individuals from trap set II were trapped during the winter months.

Rhammatodes longicornis Haag was a facultatively nocturnal species commencing activity around rocky cliffs as portions of the cliffs become well-shaded. It was active at midday in larger caves. Forty-eight per cent of the individuals in trap set II were taken during the summer months. This beetle was associated with large rocky outcrops on all soil types. It was observed feeding on seeds, owl pellets, and dead mosquito larvae on mud of a dried pool.

Rhammatodes subcostatus Koch was associated with rocky cliffs, foraging around their bases on sandy substrates on the south side of the Kuiseb river-bed. It was uncommon in traps all of which were placed outside their preferred habitat. Response to shade was similar to that of *R. longicornis*, but *R. subcostatus* was not found in caves or deep crevasses during the day.

Rhammatodes tagenesthoides Koch was only found around small rocky outcrops in the Gobabeb area.

TABLE 3: Absolute density of all plants and absolute frequency of *Stipagrostis ciliata*, *S. subacaulis* and *Zygophyllum simplex* near the five groups of pitfall traps in set I.

Trap	*Plants* m^{-2}	*S. ciliata*	*S. subacaulis*	*Z. simplex*	*Others*
A	43	100%	0	10%	10%
B	87	100%	0	10%	0
C	2	80%	20%	70%	10%
D	76	90%	20%	70%	10%
E	16	100%	30%	50%	30%

ZOPHOSINI (see Penrith, 1980)

Zophosis (Calosis) amabilis Deyrolle, although found throughout the year, exhibited a marked decrease in trap catches for June–August (5% of total catch for trap set II). Other survey methods showed that the decrease during winter was due to an actual change in abundance rather than vagility. *Z. (C.) amabilis* is primarily a coastal species, ranging inland to the Gobabeb area in the central Namib. Individuals forage on the open gravel plain away from vegetated patches (Fig. 6, Table 3; Wharton, 1980); exhibit a weak fog response (Wharton, 1980); and have an exceptional tolerance to heat and low humidity (Edney, 1971; Wharton, 1980). Trap

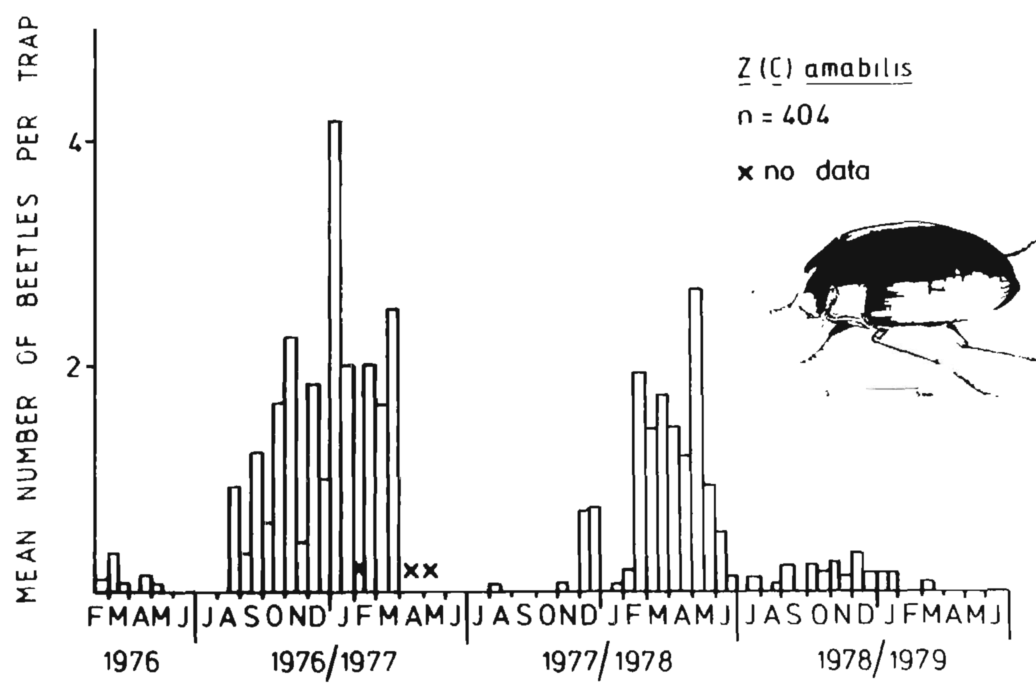

FIGURE 11: Mean number of *Zophosis (Calosis) amabilis* collected per day from 15 traps of set I. Data averaged for half-monthly intervals from mid-February 1976 to October 1979 inclusive.

catches for set I are illustrated in Fig. 11. All *Zophosis (Calosis), Zophosis (Occidentophosis)* and *Zophosis (Zophosis)* species collected during this study were observed to be omnivorous.

Zophosis (Carpiella) latisterna Koch showed an increase in vagility during the east wind season which was similar to that observed for *Zophosis (Dactylocalcar) caecus* Gebien and *Zophosis (Protodactylus) giessi* Koch. Otherwise, *Z. (C.) latisterna* is restricted to detritus pads (Koch, 1962). This species was collected on the open gravel plain, but not in washes. Collection in the Gobabeb vicinity represented a not unexpected range extension for this species.

Zophosis (Gyrosis) devexa Péringuey was the most commonly-encountered gravel plain zophosine. The largest numbers were trapped in September (Fig. 12). This species will forage in the open, but observations suggest it prefers detritus pads and small grass clumps (Wharton, 1980).

Zophosis (Gyrosis) moralesi (Koch) was particularly active during and immediately following light rains of 1–5 mm in Jan., Feb. and April; and during precipitating fogs which remained throughout the morning (see also Seely, 1979; Wharton, 1980). The immediate response to heavier rainfall was less pronounced. Observations suggested that the beetles forage gregariously, leading to difficulty in interpretation of trap data unless corroborated by other survey methods. The activity of the gravel plain population is bimodal (Wharton, 1980). Holm and Edney (1973) and Holm and Scholtz (1980) discuss interdune valley populations. Trap catches for set I are illustrated in Fig. 15.

Zophosis (Gyrosis) orbicularis Deyrolle was found to be an ecotonal species which often climbs into small grass clumps to feed on developing seeds. It is very similar morphologically to *Z. (G.) moralesi,* but does not enter the gravel plain. *Z. (G.) orbicularis* occurred primarily around the base of dunes, and is thus spatially separated from the adjacent interdune valley inhabiting *Z. (G.) moralesi* population (see also Holm and Scholtz, 1980).

Zophosis (Occidentophosis) cerea Penrith frequently seeks shelter under rocks during quiescent periods. Foraging activity is bimodal during hot days, unimodal on cooler days (Wharton, 1980). This species forages preferentially in slightly more vegetated portions of the gravel plain than does *Z. (C.) amabilis*. It lives in more exposed habitats than either the coastal *Z. (O.) damarina* (Péringuey) or the more easterly-distributed *Z. (O.) parentalis* Penrith, thus retaining fewer of the petrophilic habits of the genus. *Z. (O.) cerea* is also the only one of the three central Namib species covered with a waxy dorsal covering. This covering may be an important factor in water balance for this species, as was found by Hadley (1979) for *Cryptoglossa verrucosa* (Le Conte).

Zophosis (Occidentophosis) parentalis Penrith occurred among and under rocks in the Gorob Mine area. It overlapped the distribution of *Z. (O.) cerea* in this region, although *Z. (O.) cerea* was always more abundant where the two were collected together.

Zophosis (Protodactylus) giessi Koch was observed only during the day, though Koch (1962) records it as being nocturnal. A very small species, it was found in leaf litter or crawling rapidly over open areas during the east wind season.

Zophosis (Zophosis) dorsata Péringuey has a white, powdery, dorsal covering. It was trapped most frequently on the open plain in non-vegetated to sparsely vegetated areas, and around small quartz outcrops.

Zophosis (Zophosis) mniszechi Deyrolle was not found in the immediate vicinity of Gobabeb. At Mirabib, it has habits similar to *Z. (O.) cerea,* preferring small, grassy washes to open, non-vegetated plains. Activity was bimodal on hot days, unimodal on cooler days (Fig. 13, Fig. 14).

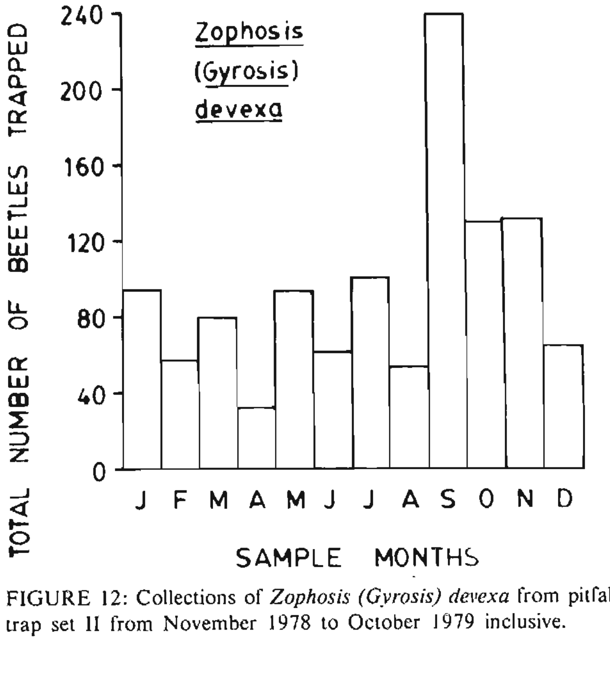

FIGURE 12: Collections of *Zophosis (Gyrosis) devexa* from pitfall trap set II from November 1978 to October 1979 inclusive.

4 DISCUSSION

Although pitfall traps have frequently been used for studies of ground-dwelling arthropods, Southwood (1966) states that such traps are of little value for directly estimating populations or comparing communities. Ahearn (1971) presents a summary of similar statements by other workers, but indicates that pitfall traps could be useful for measuring changes in behaviour, distribution, abundance, dispersal, and density. More recently, Baars (1979) has shown that mean densities cannot be determined without additional information on trap efficiency, mean locomotory activity, length of individual activity period, and mortality during the activity season – factors which all vary from species to species. In the central Namib, for example, the highly vagile *Cauricara (C.) eburnea* and *C. (C.) velox albo-*

villosa avoided pitfall traps whereas *Zophosis (G.) moralesi* and *Physadesmia globosa* did not. *Onymacris plana* (Péringuey) was actually attracted to pitfall traps. Species of relatively high mean density, but low vagility (e.g. *Caenocrypticus peezi*) were under-represented in pitfall trap catches. In several cases (e.g. *Z. (C.) latisterna, P. globosa*) increases or decreases in trap catches clearly represented changes in vagility rather than population density. Despite these reservations we have used pitfall trapping as our primary method of data collection. However, the results have been extensively supplemented with information gained from field observations and foot surveys. Thus it is felt that these data present a fairly accurate description of the species involved.

Temperature, wind, and precipitation are important factors regulating activity in the central Namib. Hamilton (1971, 1973, 1975) and Holm and Edney (1973) show that periods of activity (at least for diurnal species) are largely dependent on surface temperatures. Many species exhibited a bimodal activity curve (Fig. 13) on hot days and a unimodal peak (Fig. 14) on cooler days. This was not an obligatory seasonal phenomenon since changes from bimodal to unimodal patterns took place during the rarely-occurring cool days in mid-summer and *vice versa* in mid-winter. Temperature-activity curves were somewhat species-specific, with relatively high tolerance shown by species such as *Z. (C.) amabilis* and much lower tolerance by *Z. (G.) moralesi* and *P. globosa*. Some of the less tolerant species (e.g. *P. globosa, Physosterna cribripes*) tended to be more restricted in activity to well-shaded microhabitats during hot periods, both daily and seasonally. Temperature was less important for nocturnal species since fluctuations in the central Namib are less extreme.

Strong east winds, occurring predominantly from May through July, provoked unusual activity in many Namib species. *Z. (C.) latisterna* and *Z. (P.) giessi* were noticeably more active during east wind periods. *P. cribripes* and *Gonopus tibialis* also tended to be more active during this period. Louw and Hamilton (1972) suggest that strong winds enhance foraging success for some species and activity is therefore more pronounced at this time. Strong east winds were also important in dispersal, as evidenced by the trapping of several gravel plain species in the dunes and several dune species on the plain during east wind periods.

Species such as *Metriopus (M.) depressus* and *Z. (G.) moralesi* greatly increased their activity during or immediately following light rains and precipitating fogs. In

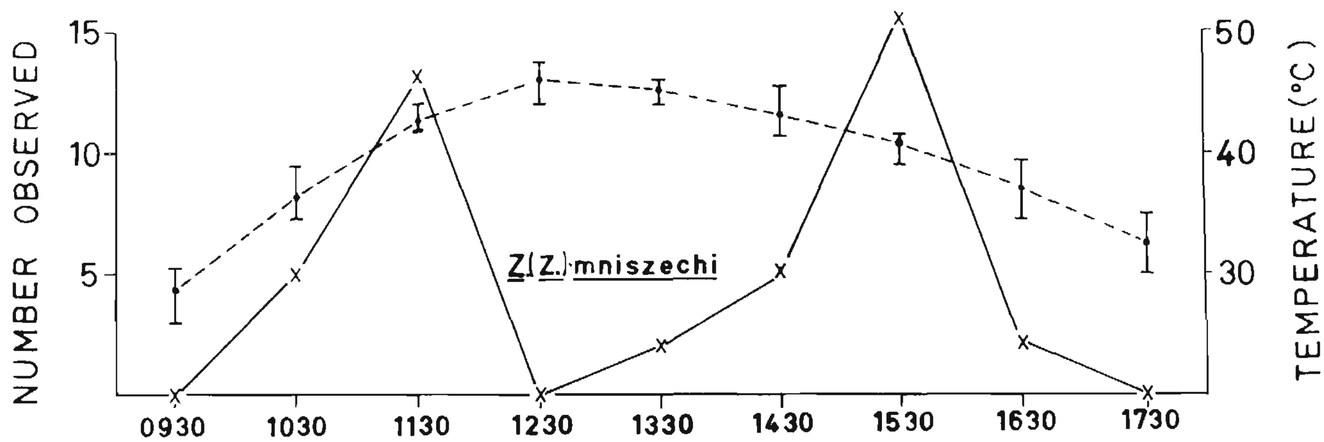

FIGURE 13: Bimodal activity pattern for *Zophosis (Z.) mniszechi* active on hot days on the gravel plain east of Gobabeb. Ground surface temperatures represented by dashed line.

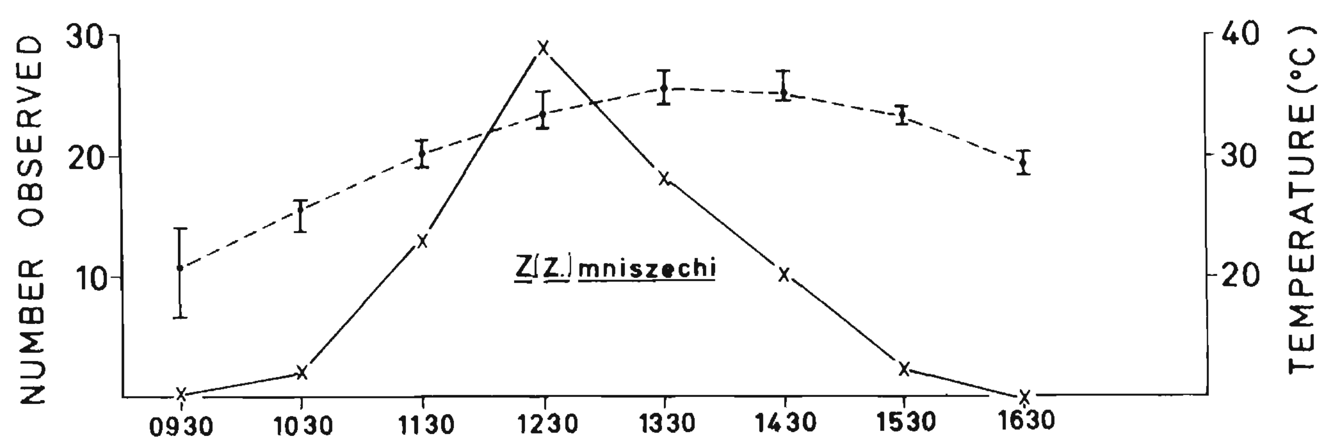

FIGURE 14: Unimodal activity pattern for *Zophosis (Z.) mniszechi* active on cooler days on the gravel plain east of Gobabeb. Ground surface temperatures represented by dashed line.

contrast, heavy rains depressed activity of most species. Psammophytic diggers may be unable to penetrate the wet sand layer formed during these heavy rains.
The three-year trapping records for set I (Figs. 4, 9, 11, 15) showed an important correlation between unusually heavy rainfall (Fig. 2) and long-term population changes. Fig. 15 shows that the build-up in population size for *Z. (G.) moralesi* was more rapid than that for *P. cribripes* (Fig. 9) and *M. (M.) depressus* (Fig. 4). This suggests a shorter life cycle for *Z. (G.) moralesi*, resulting in the production of more generations per year than for the larger adesmiines. If the gap between heavy rainfall in early 1976 (Fig. 2) and increase in trap catch later that year was due to larval and pupal developmental time, then the immature stages develop more rapidly in the smaller zophosines.

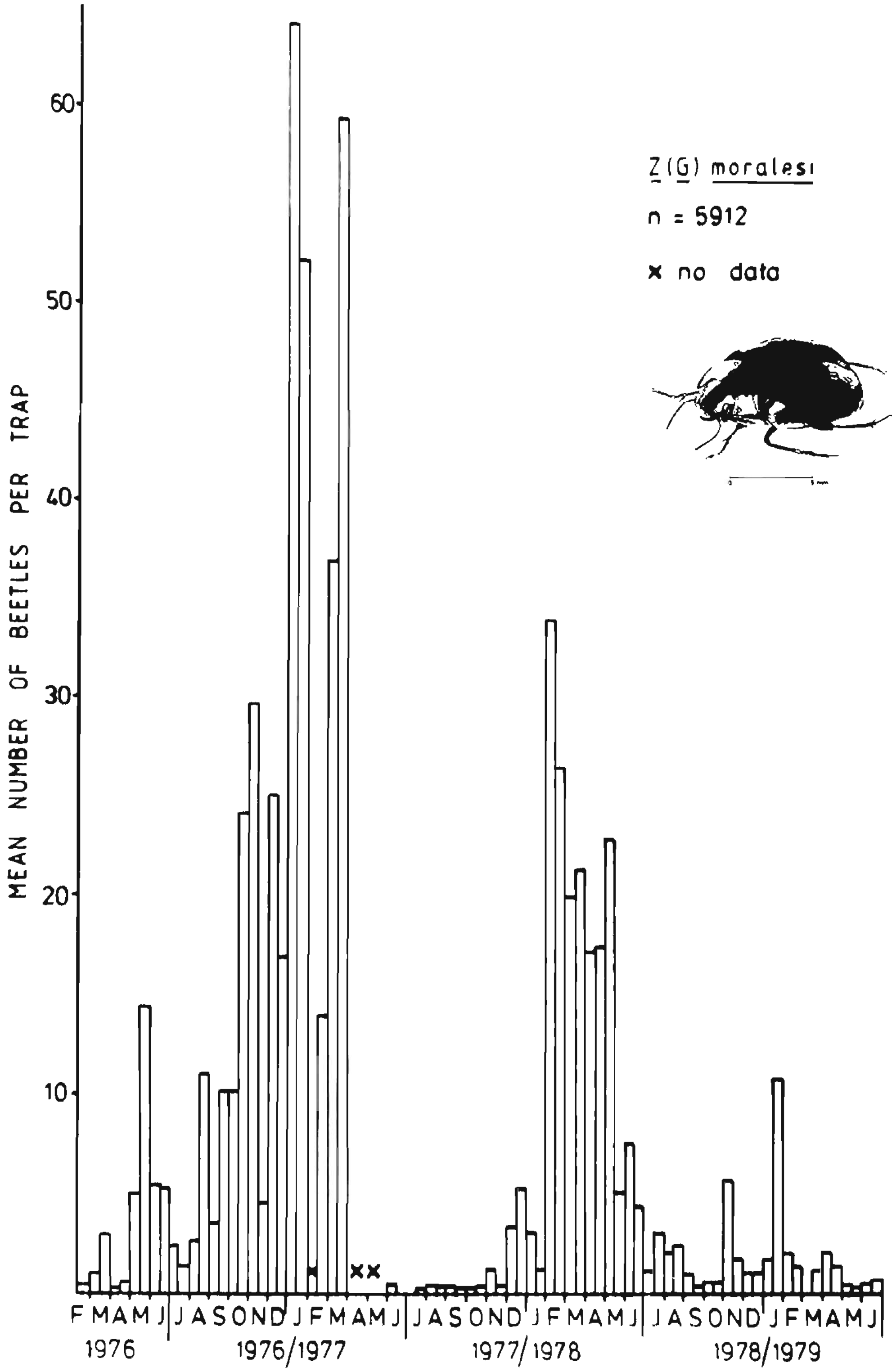

FIGURE 15: Mean number of *Zophosis (Gyrosis) moralesi* collected per day from 15 traps of set I. Data averaged for half-monthly intervals from mid-February 1976 to December 1979 inclusive.

Strict seasonal activity was particularly evident in *C. (C.) velox albovillosa, Diestecopus histrio* and many of the Molurini. Although monthly trap catches for other species showed a pattern which was significantly different from uniform (chi-square, $p<0{,}005$; Figs. 8, 10, 12), behavioural changes in response to climatic factors make seasonal interpretation of trap catch data difficult. The possibility of behavioural changes associated with reproductive cycles also cannot be excluded from consideration.

What appeared to be seasonal activity at Gobabeb (based on a one-year trapping programme) may have been due to climatically induced range expansion of species usually confined to other areas. The penetration of species from the east on the gravel plain was strongly correlated with vegetation cover and the food it provides. Rainfall, which determines the amount of cover, is thus an important governing factor. Several species not found in the river-bed (e.g. *Z. (Z.) mniszechi, Psammodes* sp., *Trachynotidus* cf. *rufozonatus*) moved closer to the coast (approaching Gobabeb) during periods of higher rainfall and more extensive grass cover, but retreated out past Ganab during dry periods with little vegetation cover. During droughts, they may disappear from the plains entirely as adults. The range of riverine species may also expand. For example, *O. r. rugatipennis* moved out from the river-bed onto the adjacent grass-covered dunes and plain for several months following the heavy rainfall of 1976. The highly variable nature of rainfall events in the Namib, and the ability of some species to rapidly occupy temporarily suitable habitats, make this an important factor to consider when discussing distribution patterns.

Many of the central Namib tenebrionids are wide-ranging (Koch, 1961; Penrith, 1977, 1979), and no attempt will be made here to discuss overall distribution patterns. However, collection records revealed several local patterns. The river-beds form mesic corridors through the otherwise harsh environment of the Namib Desert. A few species living along the cooler, foggy coastal strip move up the Kuiseb river-bed as far as Gobabeb, but do not penetrate much further (e.g. *Carchares macer*). Several species extend their ranges from the higher rainfall areas of the central highlands down into the Namib via larger river-beds (e.g. *Stenocara gracilipes, G. tibialis, P. dentipes*). Species such as *Planostibes dentipes* and *Asphaltesthes impressipennis* also penetrated the eastern border of the gravel plain during the study period, but never reached the longitude of Gobabeb on the plain (see also Table 2).

A few species (e.g. *P. globosa, G. tibialis*) have extended their range out into the gravel plain from the river-bed by means of the larger washes. Some of these species (most notably *P. globosa* and *S. gracilipes*) have moved out of the river-bed onto the grounds of the Namib Research Institute because of the shelter provided by the buildings and gardens. Three species *(Z. (G.) moralesi, Z. (Z.) mniszechi, Vansonium bushmanicum)* occurred both in the interdune valleys and on the gravel plain, but were absent from the river-bed. In *Z. (G.) moralesi*, there is apparently little gene flow across the river-bed between gravel plain and interdune valley populations, perhaps due to the presence of *Z. (G.) orbicularis* along the dune river-bed ecotone.

Habitat preferences for the four species collected from the pitfall traps of set I are shown in Fig. 6. For each species, the distribution pattern among trap groups was significantly different from uniform (chi-square, $p<0{,}005$). Traps in group D were located on a small quartz outcrop. *M. (M.) depressus* and *P. cribripes* were captured most frequently in this group of traps. Since plant density around traps of group D was not significantly different from that around groups A and B (Table 3), rocky substrate rather than vegetation may be an important habitat requirement for these two species. *Z. (C.) amabilis* was captured most frequently in traps of group C. Plant density was lowest for this set of traps (Table 3); and observations confirmed that foraging occurred primarily on the open plain away from vegetation.

Some of the more easterly-distributed species may be absent or very rare in the Gobabeb vicinity because of the lack of specialised microhabitats. Thus more petrophilic species such as *Caenocrypticus uncinatus* and *Z. (O.) parentalis* might be found more readily around Gobabeb if there were an abundance of large, rocky outcrops providing angular rock fragments such as are found at Hope and Gorob Mines. The large inselbergs of the gravel plain harbour a separate fauna not readily sampled with pitfall traps. Of special note are the adesmiines *Renatiella fettingi* (Haag) and *Alogenius favosus* (Erichson).

Holm and Scholtz (1980) state that "virtually all desert animals are euriphagous opportunists". While this may be an oversimplification, the tenebrionid species for which we have adequate observations are all opportunistic omnivores. The pronounced attraction of *O. r. rugatipennis* and *P. globosa* to figs (Fig. 7) is a typical response to temporarily available resources. Most of the adesmiines and zophosines treated here were observed to feed on animal remains and faeces while foraging for plant material. Most species foraged on the surface and climbing behaviour was observed for only a few species. *Pachynotelus* spp. regularly climbed vegetation to feed; and *M. (M.) depressus, P. cribripes* and *Z. (G.) orbicularis* often did so.

5 CONCLUSION

The relatively dense populations of many Namib Desert tenebrionids, together with their non-cryptic foraging habits, provide excellent opportunities for study. Initial observations on the presence and distribution of tenebrionids in the dune environment have been rapidly followed by studies on their ecology, physiology and behaviour. While the dune fauna has been most intensively examined, the faunas of the river-bed and gravel plain are equally diverse. Their study could also yield valuable comparative information on many aspects of this desert ecosystem.

6 ACKNOWLEDGEMENTS

This study would not have been possible without the kind assistance of Drs S. Endrödy-Younga and M.-L. Penrith in the identification of the Tenebrionidae. We accept full responsibility, however, for all identifications of field-collected material. Many people assisted in the collection of material from the pitfall traps. For this we are especially indebted to Misses K. O'Brien and V. Gray. Mr S. Louw confirmed the identification of some of the Molurini; and Drs Endrödy-Younga and Penrith contributed many useful suggestions. The University Research Division of the CSIR and the Transvaal Museum are thanked for financial assistance and the Department of Agriculture and Nature Conservation for facilities and permission to work in the Namib-Naukluft Park.

7 REFERENCES

AHEARN, G. A.
1971: Ecological factors affecting population sampling of desert tenebrionid beetles. *Am. Midl. Nat.* 86:385–406.

BAARS, M. A.
1979: Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41:25–46.

BESLER, H.
1972: Klimaverhältnisse und klimageomorphologische Zonierung der Zentralen Namib (Südwestafrika). *Stutt. Geogr. Stud.* 83:1–209.

BRINCK, P.
1956: The food factor in animal desert life. In: Wingstrand, K. G. (Ed.). *Bertil Hanstroem: Zoological Papers in Honour of His 65th Birthday, November 20th, 1956*, pp. 120–137. Lund: Zoological Institute.

EDNEY, E. B.
1971: Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiol. Zool.* 44:61–76.

ENDRÖDY-YOUNGA, S.
1978: Coleoptera. In: Werger, M. J. A. (Ed.). *Biogeography and Ecology of Southern Africa.* Dr W. Junk, The Hague, pp. 797–821.

GEBIEN, H.
1939: Körperbau und Lebensweise der Wüstentenebrioniden. *VII Int. Kongr. Entomol. Berlin* 1:118–132.
1937–1941: Katalog der Tenebrioniden. Teil I. *Publ. Mus. Entomol. Pietro Rossi Duino*: 1–381; Teil II & III. *Mitt. Münchn. Entomol. Ges.* 28–32:373 pp., 32–34:122 pp.

GIESS, W.
1962: Some notes on the vegetation of the Namib Desert with a list of plants collected in the area visited by the Carp-Transvaal Museum Expedition during May 1959. *Cimbebasia* 2:1–35.

HADLEY, N. F.
1979: Wax secretion and color phases of the desert tenebrionid beetle *Cryptoglossa verrucosa* (Le Conte). *Science* 203:367–9.

HAMILTON, W. J. III.
1971: Competition and thermoregulatory behavior of the Namib Desert tenebrionid beetle genus *Cardiosis. Ecology* 52:810–822.
1973: *Life's Color Code.* New York, McGraw-Hill. 238 pp.
1975: Colouration and its thermal consequences for diurnal insects. In: Hadley, N. (Ed.). *Environmental Physiology of Desert Organisms.* Stroudsburg, Pa., Dowden, Hutchinson, and Ross. 283 pp.

HAMILTON, W. J. III, BUSKIRK, R. E., and BUSKIRK, W. H.
1976: Social organization of the Namib Desert tenebrionid beetle *Onymacris rugatipennis. Can. Entomol.* 108:305–316.

HAMILTON, W. J. III and PENRITH, M.-L.
1977: Description of an individual possible hybrid tenebrionid and the habitat preference of the parental species. *Can. Entomol.* 109:701–710.

HAMILTON, W. J. III and SEELY, M. K.
1976: Fog basking by the Namib Desert beetle, *Onymacris unguicularis. Nature* 262:284–285.

HENWOOD, K.
1975a: Infrared transmittance as an alternative thermal strategy in the desert beetle *Onymacris plana. Science* 189:993–994.
1975b: A field-tested thermoregulation model for two diurnal Namib Desert tenebrionid beetles. *Ecology* 56:1329–1342.

HOLM, E. and EDNEY, E. B.
1973: Daily activity of Namib Desert arthropods in relation to climate. *Ecology* 54:45–56.

HOLM, E. and SCHOLTZ, C. H.
1980: Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. *Madoqua* 12:3–39.

KOCH, C.
1952: S.A. Tenebrionidae. XII. Supplementary notes to preliminary articles nos. I, III, V and VIII. *Ann. Transv. Mus.* 22:79–196.
1961: Some aspects of the abundant life in the vegetationless sand of the Namib Desert dunes. *J. S. W. Afr. sci. Soc.* 15:8–34.
1962: The Tenebrionidae of Southern Africa, XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Ann. Transv. Mus.* 24:61–106.

LOUW, G. N.
1972: The role of advective fog in the water economy of certain Namib Desert animals. *Symp. zool. Soc. Lond.* 31:297–314.

LOUW, G. N. and HAMILTON, W. J. III.
1972: Physiological and behavioural ecology of the ultrapsammophilous Namib Desert tenebrionid, *Lepidochora argentogrisea. Madoqua (II)* 1:87–95.

MEDVEDEV, G. S.
1968: *Fauna of the USSR: Darkling Beetles.* Leningrad, Akademiya Nauk, USSR. Translated from Russian by Indian National Scientific Documentation Centre, New Delhi, 1977.

MUELLER-DOMBIS, D. and ELLENBERG, H.
1974: *Aims and Methods of Vegetation Ecology.* New York, Wiley. 547 pp.

PENRITH, M.-L.
1977: The Zophosini (Coleoptera: Tenebrionidae) of western southern Africa. *Cimbebasia Mem.* 3:1–291.
1979: Revision of the western southern African Adesmiini (Coleoptera: Tenebrionidae). *Cimbebasia* (A) 5:1–94.
1980: Revision of the Zophosini (Coleoptera: Tenebrionidae). Part 1, Introduction. *Cimbebasia* (A) 6:1–16.

ROBINSON, E. R.
1976: *Phytosociology of the Namib Desert Park, South West Africa.* MSc Thesis, University of Natal, Pietermaritzburg, S. Africa. pp. 220.
1977: List of plant species from the Mirabib Hill Area. Madoqua **10** (4):295–297.

ROER, H.
1977: Areas and adaptation of the Namib Desert beetle (*Onymacris r. rugatipennis*) (Haag, 1875) (Col.: Tenebrionidae, Adesmiini) to the Kuiseb River bed in South West Africa. *Zool. Jb. Syst.* **104**:560–576.

SCHULZE, L.
1978: The Tenebrionidae of southern Africa, XLV. Description of some larvae of the subgenera *Gonopus* and *Agonopus* of the genus *Gonopus* (Coleoptera). *Ann. Transv. Mus.* 31:1–16.

SCHULZE, L. and BROWN, J. M. M.
1975: A review of silk production in Arthropoda with special reference to spinning in tenebrionid larvae (Coleoptera). *Transv. Mus. Mem.* **19**:1–51.

SEELY, M. K.
1978: Grassland productivity: The desert end of the curve. *S. Afr. J. Sci.* 74:295–297.
1979: Irregular fog as a water source for desert dune beetles. *Oecologia* 42:213–227.

SEELY, M. K. and HAMILTON, W. J. III.
1976: Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora,* from the Namib Desert. *Science* 193:484–486.

SEELY, M. K. and STUART, P.
1976: Namib climate: 2. The climate of Gobabeb, ten-year summary 1962/72. *Namib Bulletin Suppl.* No. 1: *Transv. Mus. Bull.,* 7–9.

SOUTHWOOD, T. R. E.
1966: *Ecological Methods, with Particular Reference to the Study of Insect Populations.* London, Methuen & Co. 391 pp.

STENGEL, H. W.
1964: Die Riviere der Namib und ihr Zulauf zum Atlantik. I. Teil: Kuiseb und Swakop. *Scient. Pap. Namib Des. Res. Sta.* 22:1–50.

THERON, G. K., VAN ROOYEN, N. and VAN ROOYEN, M. W.
1980: Vegetation of the lower Kuiseb River. *Madoqua* 11:327–345.

TSCHINKEL, W.
1979: Ovoviviparity in some tenebrionid beetles. *Coleopt. Bull.* 32:315–317.

WHARTON, R. A.
1980: Colouration and diurnal activity patterns in some Namib Desert Zophosini (Coleoptera: Tenebrionidae). *J. Arid Environ.* 3:309–317.
Diel periodicity, dispersal, and longevity in *Stips stali* (Haag) (Coleoptera: Tenebrionidae: Eurychorini). (Unpublished manuscript)

WILLOUGHBY, E. J.
1971: Biology of larks (Aves: Alaudidae) in the central Namib Desert. *Zool. Afr.* 6:133–176.