
Notes on Faunas Bordering On the Namib Desert

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Distribution maps of Buprestidae and Cetoniinae from the areas surrounding the Namib Desert are used to investigate the limits of the Namib by excluded taxa. It emerges that the Namib north of 24° S is bordered by a recent savanna fauna as well as savanna relicts, apparently of various ages. In the south the Namib is bordered by a coastal Cape-Namaqualand fauna near 29° S latitude. This Namaqualand fauna has recently isolated relatives along the inselbergs of the eastern Namib edge. It is suggested that the Namaqualand fauna extended along the coast north of 29° S, and was recently displaced from the Namib proper by dunefield expansions.

INTRODUCTION

In recent years a number of taxonomic revisions of taxa in the Namib entomofauna have appeared, most of which include notes on relationships and distribution patterns within the Namib Desert (e.g., Endrödy-Younga, 1986; Penrith, 1975, 1977, 1979, 1981*a, b*; Irish 1986; Thomson 1988). Analyses of the historical implications of these relationships and distributions were done by Endrödy-Younga (1982, 1986) and Penrith (1980). Ecological subdivisions of the Namib were commented on by Koch (1962), Holm and Scholtz (1980) and Robinson and Seely (1980), among others.

Although the Namib is generally agreed to have sufficient endemics (albeit on subgeneric and lower levels) to regard it as a distinct zoogeographical province, few workers have attempted to relate the Namib province zoogeographically to other African provinces. One noteworthy exception is the paper on mammal distribution by Coetzee (1983). Otherwise the descriptive zoogeography of southern Africa by Endrödy-Younga (1978) and papers on relationships between the Namib and Kalahari by Louw (1983, 1986) and Penrith (1984) shed some light on this subject.

A difficulty with any zoogeographical discussions of the Namib lies in the ecological and faunistic heterogeneity within the region. Dunes, gravel plains, inselbergs and river courses carry their own exclusive and yet endemic faunas. These are each differently related to faunas of other southern African subregions or zoogeographical 'provinces'. For this reason, as well as the several other reasons mentioned in a previous paper (Holm and Scholtz, 1983), I attempted to define the Namib by some excluded taxa rather than by endemics. For this purpose it was not necessary to hypothesize a Namib region, but only to trace the distribution limits of known savanna and Cape-Namaqualand taxa. The areas not entered by these taxa were then considered the limits of the Namib by exclusion rather than by endemics. In the process it emerged that both groups selected for this study (Buprestidae and Cetoniinae – Coleoptera) segregated into three distinct groupings, namely isolated relicts, a Cape-Namaqualand grouping

in the south, and a savanna grouping in the north. These groupings were subsequently investigated separately.

METHODS

The groups selected for this study (Buprestidae: subfamilies Acmaeoderinae, Julodinae, Polycestinae; Cetoniinae: tribes Cetoniini, Gymnetini, Diplognathini) were chosen because I have first-hand knowledge of their distribution and systematics, and both are well represented in Namibia and the Cape, and are absent from the dunes and gravel plains of the Namib.

For distribution limits all those species of the genus *Acmaeodera* in the Buprestidae, and all those species in the three cetoniine tribes with either a presence in Namibia or north of the Western Cape (i.e., in Namaqualand) were selected. Distribution limits were then hand-fitted around known collecting localities for each species. These distribution limits were subsequently superimposed in four groups: *Acmaeodera* species conforming to a savanna distribution (Fig. 1); *Acmaeodera* species with a Cape-Namaqualand distribution (Fig. 2); Cetoniinae with a savanna distribution (Fig. 3) and Cetoniinae with a Cape-Namaqualand distribution (Fig. 4). In each case iso-species density lines at five species intervals were heavily outlined to emphasize the species density gradient. The part of the Namib completely uninhabited on each map was shaded. Finally, all the iso-species density lines and the uninhabited parts of the Namib of all four maps were superimposed (Fig. 5).

For maps of relicts (Figs 6–17), both 'true' relicts and phylogenetic relicts (see below) were selected from all of the Buprestidae subfamilies and Cetoniinae tribes mentioned above. The known distribution of these is respectively given in Figs 6–12 and 14–16, while Fig. 13 summarizes the distribution limits of the true relicts, and Fig. 17 those of the phylogenetic relicts.

THE SAVANNA ELEMENTS ON THE NAMIB BORDER

Figures 1 and 3 show a strong similarity, and the following

patterns can be observed:

1. The northern Namib (17° S to 24° S) has a direct interface with savanna elements.
2. The savanna fauna intrudes to the coast near 23° S (Kuiseb and Swakop Rivers), but there is already a marked decrease in the number of savanna species much further inland (between 16° E and 17° E).
3. The species density of savanna forms tapers off sharply to virtual total absence, both towards the Namib and the southern Kalahari. In contrast, distributions extend with a very gradual decrease in species densities northeastwards, and also southeastwards around the Kalahari-Karoo regions.

The fact that the savanna fauna of northern Namibia is connected to the South African and East African savanna by a trans-Botswana corridor is well documented (e.g., Endrödy-Younga, 1978). The Kalahari forms a southern specialized extension of this corridor, at least in some groups of insects (Holm and Scholtz, 1983). From this study it emerges that the savanna of northern Namibia is hardly wider than the trans-Botswana corridor, and has a southern limit between 23° S and 24° S. This is borne out by several other studies. Roer (1978) recorded 23 species of Micropteriginae bats from Namibia. Six of these are only present in the extreme north and probably represent tropical intrusions. Of the remaining seventeen species, eleven do not reach further south than 24° S. Nine of these extend into Botswana, and may be considered typical savanna elements. Koch (1955) finds the same southern limit for his 'trans-Botswana' group of Tenebrionidae. Wharton (1981) mapped distributions of Namibian solpugids, and more than half of those recorded outside the Namib proper have northern or southern distribution limits near 24° S. The map of Coetzee (1983) is less conclusive, but does show a marked increase of distribution limits north of 24° S, forming three discernible clusters. Undoubtedly these represent southern limits of savanna forms. Liversidge (1962) draws the southern border for two thirds of all Namibian savanna birds between 22° S and 24° S, and shows the southern half of Namibia to be conspicuously lacking in both savanna and Cape elements. Poynton (1962) indicates that of the seven frog species crossing the Botswana corridor into Namibia, the most widespread extend to 24° S.

It is therefore clear that in several groups other than those investigated here, the northern Namib is bordered by a savanna fauna on the eastern side, and this savanna fauna stops rather abruptly at 24° S in the south.

The intrusions of savanna elements into the Namib along river courses is even more marked in mammals (Coetzee, 1983) than in the insect groups discussed here. Undoubtedly these intrusions were also much more pronounced during pluvial spells in history, and the present isolation between northern and southern Namib may indeed be one of these repeated temporary events (Endrödy-Younga, 1986).

The eastern border of the northern Namib is also richly endowed with savanna and arid savanna relicts of various ages (see 'relicts' below). This area has probably seen several expansions of alternating moist and arid savanna faunas during pluvials and interpluvials in the past, as it harbours

faunas of both the present and older historical interfaces between the northern Namib and savanna, and no faunal elements of other zoogeographical provinces (either relictual or contemporary) were recorded exclusively in this region in the groups investigated.

One ultrasammophilous buprestid genus, *Lepidoclema* Bellamy and Holm (1985), has its closest relatives in the trans-Botswana savanna belt, and the members of the weevil genus *Leptostethus*, which radiated dramatically in the Namib, seem to have a similar origin (Thomson, 1988). Many of the other 'Namib' beetles may turn out to derive from savanna forms through the interface with the trans-Botswana savanna fauna.

THE CAPE-NAMAQUA ELEMENTS ON THE NAMIB BORDER

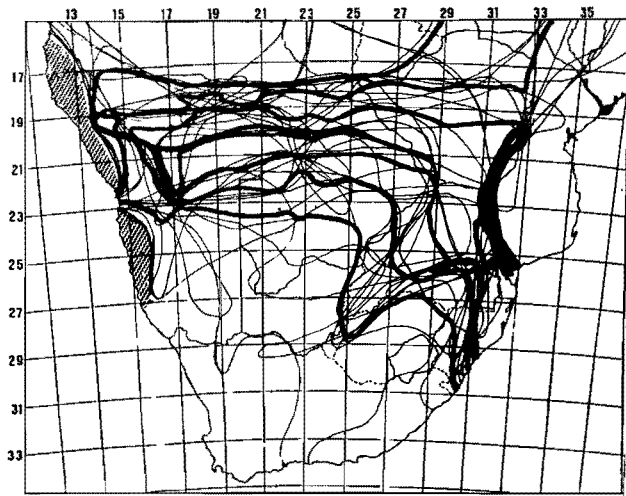
Figures 2 and 4 again show a marked similarity, with the bulk of species in the western Cape and a rather sharp termination of their northward extensions along the coast at about 29° S. From here, single species extend northwards along the eastern edge of the Namib. These species are closely related to the Cape fauna, and not to the savanna fauna. Liversidge (1962) indicates that more than half of the birds of the western Cape reach up to 29° S in the north, but no further.

At present most of these extensions of Cape fauna are found on inselbergs in the so-called 'pro-Namib'. Poynton (1962) also illustrates such a case in the frog *Rana grayi*, which has an easterly and a westerly extended Cape distribution in the terminology of Endrödy-Younga (1978). The species occurs conjunctly with the Cape populations up to 29° S in the north, and then in two isolated montane relict populations further north along the eastern edge of the Namib. A recent survey by the State Museum, Windhoek, produced a host of Cape buprestids from Rössing mountain, which has not yet been fully evaluated. Undoubtedly, our knowledge of the montane fauna of the pro-Namib is far from complete. At present one can only speculate on the historical zoogeography of this faunal element:

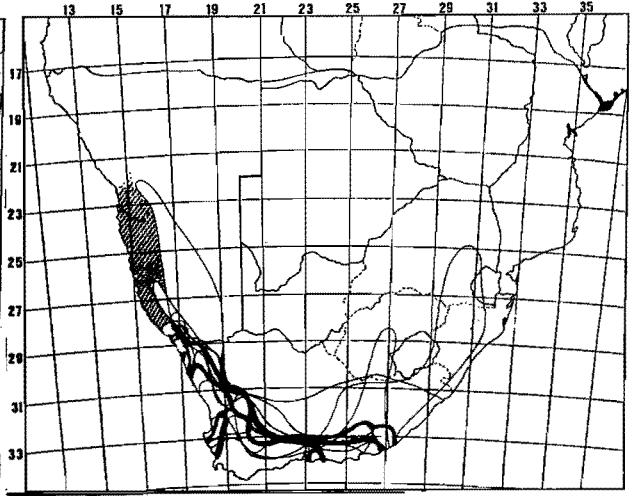
The fact that such an otherwise exclusively Cape genus as *Nothomorpha*, and several other Buprestidae species only subspecifically different from their coastal Namaqualand counterparts, occur on Rössing mountain (and some Cape-related Cetoniinae even on the Hartmansberge in the Kaokoveld) and, furthermore, that the Namaqualand fauna they derive from is restricted to coastal flatlands, suggests that the present

Figs 1-5

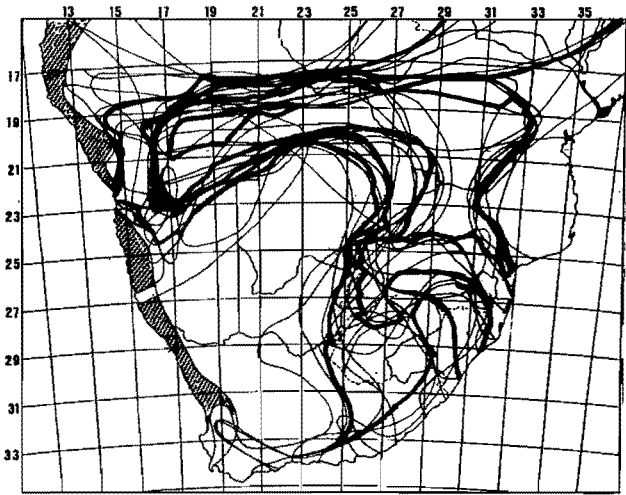
Distribution limits and iso-species density lines of Namibian *Acmaeodera* species (Coleoptera: Buprestidae) and Cetoniinae species (Coleoptera: Scarabaeidae). Stippled areas represent the Namib as variously defined by absence of any of the species. Heavy lines are iso-species densities at 5 species intervals, thin lines are individual species distribution limits. 1: distribution of the 21 species of *Acmaeodera* with mainly savanna distribution (Relict species of Figs 6-10 excluded); 2: distribution of the 15 species of *Acmaeodera* with mainly Cape-Namaqualand distribution; 3: distribution of the 21 species of Cetoniinae with mainly savanna distribution; 4: distribution of the 14 species of Cetoniinae with mainly Cape-Namaqualand distribution; 5: iso-species density lines and uninhabited Namib of Figs 1-4 superimposed.



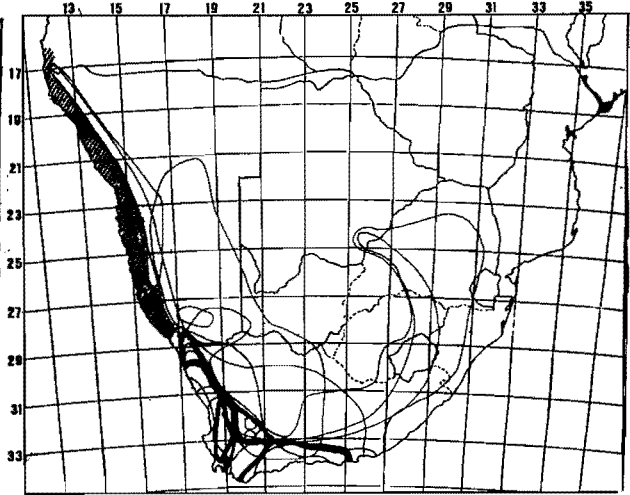
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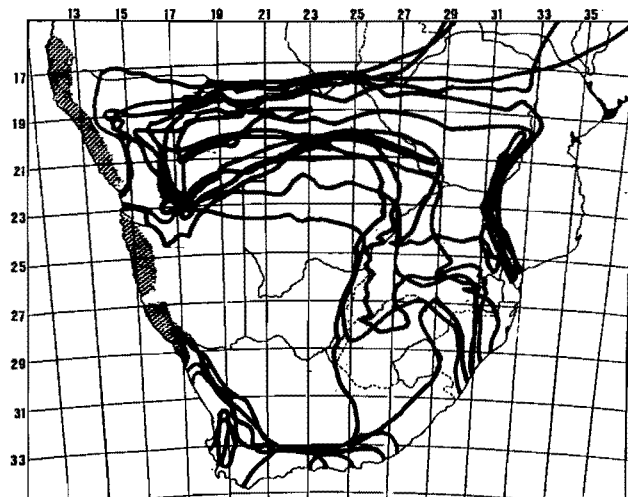
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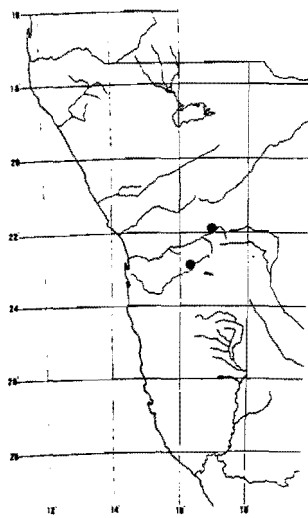
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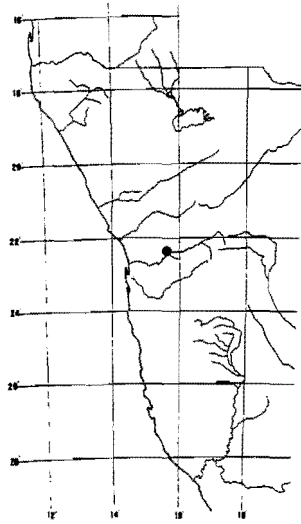
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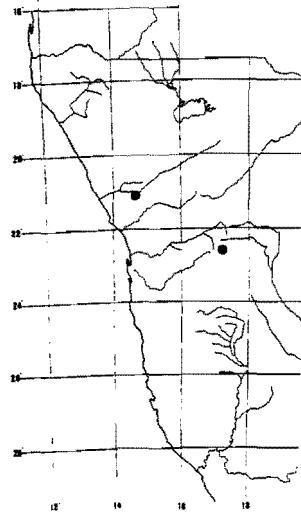
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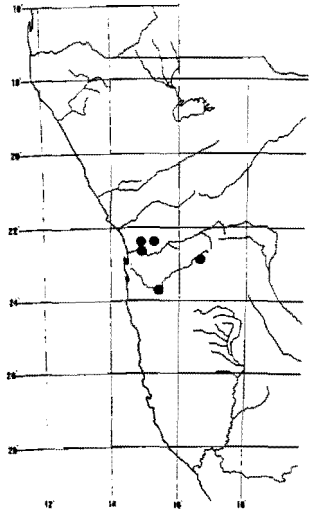
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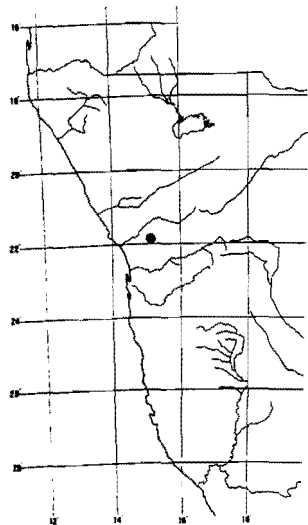
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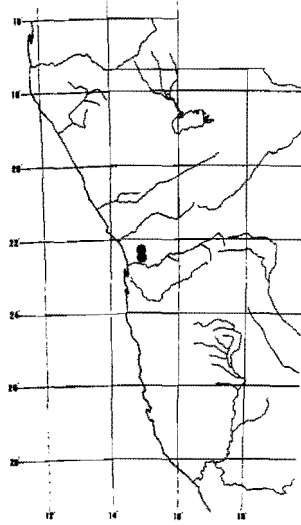
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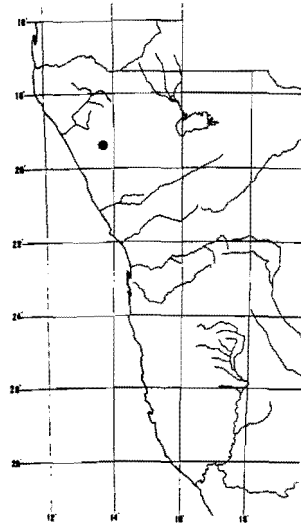
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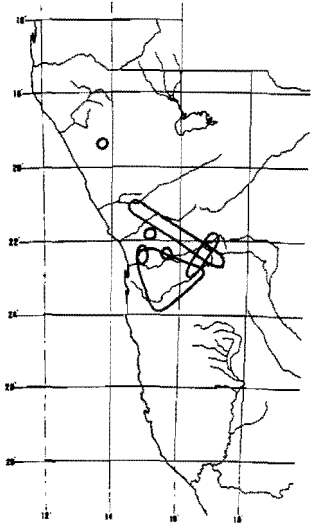
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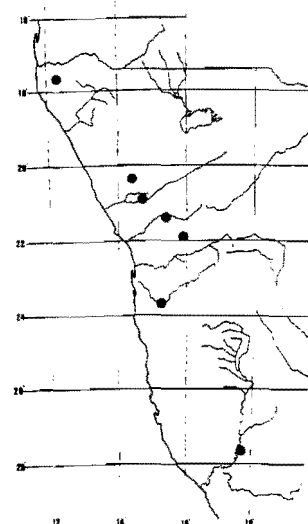
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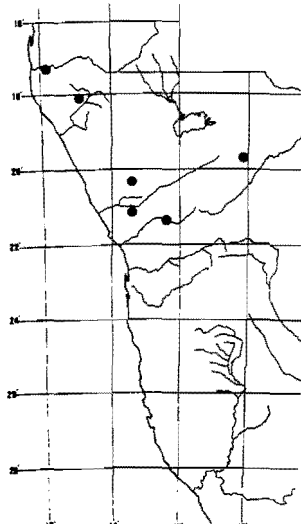
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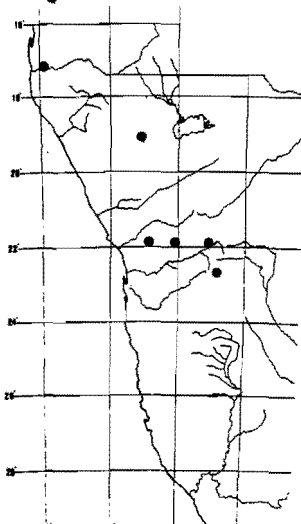
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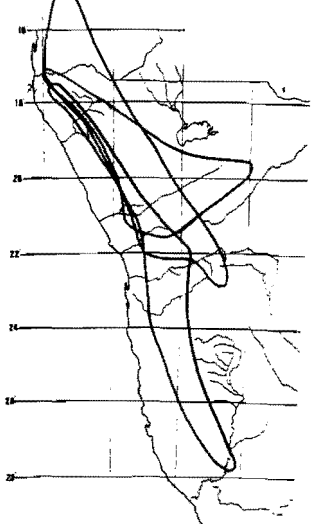
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pro-Namib Cape relicts and extensions are left over from a period in the rather recent past when the whole west coast (probably up to the north-central Namib and perhaps up to north of the Cunene River) was inhabited by a Cape Namaqualand fauna. Aridification and, perhaps more importantly, sand dune extension may have isolated remnants of this fauna on inselbergs on the eastern edge of the Namib (rather unusual habitats for the same groups in Namaqualand, where they occur in coastal flatlands).

At least two non-tenebionid beetle groups with psammophilous representatives in the Namib have their closest relatives in Namaqualand. These are the wingless *Scarabaeus* species (of the species-group formerly known as *Neopachysoma*), and the desert-adapted *Julodis* species, e.g., *J. kochi* Ferreira.

RELICT TAXA ON THE NAMIB BORDER

In both the Cetoniinae and Buprestidae there is a high incidence of relict taxa on the eastern border of the Namib. The affinities of these relicts with other zoogeographical regions and provinces can possibly shed light on historical circum-Namib faunas.

The term 'relict' is unfortunately not used very consistently in the literature. Darlington (1957) defines a relict as either a phylogenetic survivor with most of its relatives extinct (phylogenetic relict), or a localized survivor with its relatives in adjacent geographical regions extinct (geographical relict). Similar definitions are provided by Brown and Gibson (1983) and Cox and Moore (1980) – the latter replacing 'geographical relict' with 'climatic relict'. Crowson (1981) singles out the geographical aspect.

It is evident that a phylogenetic 'relict' may be widespread and a geographical 'relict' may be phylogenetically uniquely evolved rather than an isolated survivor. Both these cases therefore deviate from the classical usage of the term relict, and the qualifications 'geographical' or 'phylogenetic' relict should be applied to these qualified cases. The unqualified term 'relict' should be reserved for the classical situation where a species is both geographically restricted and a more or less isolated phylogenetic survivor. It should also be borne in mind that all three terms are relative, and only serve a purpose in comparison to relationships and distribution ranges in the closest relatives.

For the purpose of the present analysis I have identified seven relict species and three phylogenetic relict species in three tribes of Namibian Buprestidae (Acmaeoderinae, Julodinae and Polycestinae). The distribution maps of these ten

species are given in Figs 6–17. The distribution data and phylogenetic relationships are from Holm (1978; 1982; 1985; 1986a, b).

Affinities of the relict taxa

Three of the relict *Acmaeodera* species (*A. (Rugacmaeodera) kosterae* Holm, Fig. 10; *A. (Ptychomus) cobosi* Holm, Fig. 7; *A. (Paracmaeodera) longa* Holm, Fig. 6) belong to conservative species groups and have their closest relatives in East Africa and Somalia. One *Acmaeodera* species (*A. (A.) liessnerae* Holm Fig. 9) and one polycestine species (*Thurmtaxisia schoemani* Holm, Fig. 12) have their closest relatives in the mediterranean region. The latter is the only representative of its genus in Africa. *Nothomorhoides irishi* Holm (Fig. 11) is monotypic and intermediate between the Cape genus *Nothomorpha* and the Nearctic genus *Acmaeoderoides*. Lastly, *Acmaeodera hedwigae* Obenberger (Fig. 8) is closest to the Cape *Acmaeodera* species.

The majority of these relicts probably originated from a trans-African savanna stock with a preference for arid savanna, and were isolated through one or another of the pluvial events that separated the arid savannas in the southwest and northeast of the continent. In some cases the relicts are more probably leftovers from northern extensions of the Cape fauna. It is noteworthy that the distributions form a close cluster (Fig. 13) on the main present-day interface between Namib and savanna (Figs 1 & 3) and on the northernmost inland extension of the Cape fauna (Figs 2 & 4).

Affinities of the phylogenetic relicts

The more widespread buprestine phylogenetic relicts in Namibia are *Acmaeodera (A.) louwi* Holm (Fig. 14) with closest relatives in Madagascar; *Julodella bicolor* (Obst) (Fig. 15) with closest relatives in East Africa and the Near East (although one other but not particularly closely related species of this genus occurs in the Cape); and *Julodis vylderi* Kerremans (Fig. 16), which belongs to a species group within *Julodis* with a Northeast African and Mediterranean distribution.

Acmaeodera louwi must be a very old phylogenetic relict of Gondwana origin. The affinities of the other two species agree with the arid African savanna origin of the majority of true relicts discussed above. The distribution of all three species overlaps in the middle of the length of the Namib and hugs the eastern edge of the desert (Fig. 17).

CONCLUSIONS

The two beetle groups investigated in this study and studies on several other animal groups show that the northern Namib is bordered by savanna elements in the east, down to 24° S in the south. The southern limit of the Namib, near 29° S, is formed exclusively by Cape-Namaqualand elements. In between there is an area poorly inhabited by both faunas, defined by Coetzee (1983) as 'Dwarf shrub mosaic area'.

From present distributions of both the widespread and the relict savanna species in Namibia, and the various levels of their taxonomical affinities to taxa in other zoogeographical provinces, it is inferred that the northern Namib has repeatedly interfaced with savanna faunas at different times in history. These faunas must at least occasionally have been continuous

Figs 6–17

6–13: Distribution of relict Buprestidae species in Namibia. 6: *Acmaeodera (Paracmaeodera) longa* Holm; 7: *Acmaeodera (Ptychomus) cobosi* Holm; 8: *A. (A.) hedwigae* Obenberger; 9: *A. (A.) liessnerae* Holm; 10: *A. (Rugacmaeodera) kosterae* Holm; 11: *Nothomorhoides irishi* Holm; 12: *Thurmtaxisia schoemani* Holm; 13: superimposed distribution limits of Figs 6–12.

14–17: Distribution of phylogenetic relict Buprestidae in Namibia. 14: *Acmaeodera (A.) louwi* Holm; 15: *Julodella bicolor* (Obst); 16: *Julodis vylderi* Kerremans; 17: superimposed distribution limits of Figs 14–16.

with Somalian and even Mediterranean faunas. The present fauna of this area is still partially continuous with the east African savanna fauna. This savanna interface with the Namib contributed significantly to the present highly sand-adapted Namib fauna, as witnessed by beetle genera such as *Zophosis*, *Leptostethus* and *Lepidoclema*.

The abrupt termination of the coastal Cape-Namaqualand fauna at about 29° S, and its sparse perpetuation on the

inselbergs of the eastern Namib boundary, combined with the species level relationship between these and the coastal Namaqualand relatives, suggests an extension of Namaqualand fauna on the Namib coast in the recent past, which was subsequently restricted to relicts on the inland mountains by sand dune extensions, while a few species adapted to the psammophilous lifestyle.

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Namib Biogeography, as Exemplified Mainly by the Lepismatidae (Thysanura: Insecta)

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A resumé of current progress in Namib Desert biogeography is given, based primarily on data available for the Lepismatidae and Tenebrionidae. The Namib is treated as an integral part of the African South West Arid Region. The origin of the South West Arid fauna is considered to have been in a desert pre-dating the Gondwana split. The present ultrapsammophilous Namib fauna originated from the Gondwana Desert fauna, to the south of the present Namib. They dispersed northwards following both sand movement and the development of the Namib climate. Their relationship with the psammophilous Kalahari Desert fauna is discussed. Much significance is attached to the evolutionary consequences of the difference between coastal and inland dune faunas. New data on the origin of certain inland northern Namib dune faunas are presented. Gaps in present knowledge are pointed out.

Biogeographical analysis of any specific taxon is only possible once systematic studies have advanced far enough to allow phylogenetic analysis. The main obstacle to progress in Namib biogeography remains the paucity of advanced systematic studies. What follows is therefore based primarily on those taxa for which such studies are available, namely some groups of Tenebrionidae (Penrith and Endrödy-Younga, various papers), the Lepismatidae (Irish, much still unpublished), and the Schizodactylidae (Irish, 1986a). While it is realized that different taxa will react differently to similar circumstances, the existence of general faunal trends cannot be denied. Biogeography attempts to find these underlying patterns in the apparent chaos of taxon-specific historical environmental responses. The scenario presented below is heavily biased towards the observed situation in the Lepismatidae. Different and conflicting interpretations, based on evidence for other taxa, do exist. Given the present incomplete evidence it is not yet possible to decide which reflect gross faunal and which taxon-specific histories.

Historically, physically and biologically the Namib Desert is an integral part of the African South West Arid Region, and it should not be studied in isolation. The South West Arid Region has a long history of aridity, which can be traced back to the existence of a desert in central Gondwana pre-dating its breakup in the late Jurassic, about 130 million years (Ma) ago (continental configurations and dates based on Smith, Hurley and Briden, 1981). Under present climatological conditions, arid areas are found in the western central parts of all sufficiently large land masses in temperate latitudes, suggesting that the supercontinent Gondwana inevitably had to include an arid area or areas. Supportive evidence comes from Gondwana geology indicative of aridity (Martin, 1961). This 'Gondwana Desert' and its surrounding semiarid areas existed for a sufficiently protracted time to allow an endemic xerophilous fauna to evolve. Such long-term aridity does not imply a

stagnant situation, however, as that would hardly account for the observed diversity in the present South West Arid Region (Penrith, 1986b). This aridity also pre-dates the existence of the Namib Desert, and should not be confused with the oft-repeated statement by Koch (1961) that the Namib is the 'oldest desert in the world'. The latter misconception was adequately discounted by Endrödy-Younga (1982a).

Following breakup, elements of the Gondwanan desert fauna remained present in arid areas on the southern African subcontinent, becoming the ancestors of the present South West Arid fauna. Such elements of the fauna as became isolated on other continental plates either survived in whatever patches of relative aridity remained when their plates moved into more tropical latitudes, or became extinct. One survivor, which demonstrates the South West Arid Region's ancient links with South America, is the lepismatid *Stylifera galapagoensis* (Irish, 1988a). There are also links with the deserts of Central Asia via the Indian subcontinent, for example the cricket family Schizodactylidae (Irish, 1986a) and the tenebrionid subgenus *Zophosis (Septentriophosis)* (Penrith, 1986a). Clear links with the xerophilous fauna of Australia are unknown, probably because Australia's far southern latitudinal location for much of the time following breakup was unsuitable for the survival of a desert fauna.

Climatological conditions on the present African continent probably differ considerably from those reigning when it was a part of Gondwana, and the time during and following breakup was probably characterized by gradual but ever-present climatological fluxes. One result of these was the repeated establishment of an interpluvial 'arid corridor' from South through East to North East and North Africa (Balinsky, 1962). Although the corridor was probably only arid savanna and not true desert (Cooke, 1962; Irish, 1986b), it did allow two-way movement of xerophilous taxa between arid southern and northern Africa. Such taxa, being pre-adapted to arid conditions, often under-

went speciation explosions when presented with the new environment on the opposite side of the continent. Thus, the lepismatid genus *Ctenolepisma*, originating in the northern hemisphere, spread to southern Africa and gave rise to the prolific southern African species groups of the subgenus *Sceletolepisma* (Irish, 1987). Similarly, *Zophosis* (*Hologenosis*) (Penrith, 1986a) and the tenebrionid genera *Adesmia* and *Renatiella* (Penrith, 1986b) spread northwards from their southern origins, but in many cases it is difficult to decide whether African/eastern Palaearctic distributions are the result of Gondwanan or post-Gondwanan dispersal, or a combination of both. The north-south movements enriched the already extensive autochthonous South West Arid fauna. At a later stage the South West Arid Region also made a one-way contribution to the fauna of St Helena Island, by rafting, for example *Ctenolepisma sanctaehelenae* (Irish, 1987).

In many examined South West Arid endemic groups, the most plesiomorphic (primitive, ancestral) species inhabit the Karoo (= interior Cape Province of South Africa), the southern parts of Namibia and/or the Kaokoveld (= northwestern Namibia). These are areas of generally rocky or at least not excessively sandy substrates, indicating that these conditions probably prevailed in much of the Gondwana Desert. It does not imply that the Gondwana Desert occupied the same spatial area, or that this area has remained unchanged since. Whenever and wherever sandy substrates occurred, it must be assumed that psammophilous taxa evolved from the more plesiomorphic non-psammophilous taxa, in both Gondwana and post-Gondwana times. Accepting that psammophily is a difficult attribute to delimit, it does seem as though the most plesiomorphic surviving psammophiles inhabit the Kalahari Desert and its outliers (dune patches) in the northern Karoo, indicating that the Kalahari, too, had an endemic fauna at an early stage. This non-psammophilous/Karoo to psammophilous/Kalahari evolutionary sequence is well illustrated in the schizodactylid genus *Comicus* (Irish, 1986a). Endrödy-Younga (1978, 1982a) previously suggested that the South West Arid fauna had an initially non-psammophilous origin in an area with karroid type vegetation, while Penrith (1979) deduced that the tenebrionid tribe Adesmiini evolved in an area resembling the present Karoo/Kalahari.

Concurrently with breakup, the South Atlantic Ocean opened up, and on the west coast of the southern African subcontinent those factors which are today causative for the Namib climate gradually came into play. Before its climate existed, the Namib, from a biological viewpoint, was no different from the rest of the Gondwana Desert, and hence did not exist as a separate entity. The use of climate in defining the Namib is justified by numerous studies that have shown the Namib fauna's relation to the very specific Namib climate, as summarized by, for example, Seely (1978) and Holm and Scholtz (1980). The area where the Namib climate started evolving was probably previously a part of the Gondwana Desert, and inhabited by its fauna. As today, the coastal climate was much milder (lower temperatures, more regular precipitation, aseasonality) than that of the harsh interior, but it was still a desert. Its aridity discouraged more mesic faunas from invading it, but at the same time the relatively less harsh conditions provided a considerable adaptive evolutionary impetus for the Gondwanan Desert fauna, the members of which

were pre-adapted and in the right place at the right time, and consequently had a virtual monopoly on the many unfilled niches which gradually became available as the proto-Namib climate continued evolving. In this way the first Namib endemics came to be.

While the clear south to north evolutionary gradients in the majority of ultrapsammophilous taxa can be adequately explained in terms of sand movement (see below), similar phenomena in marginally or non-psammophilous taxa (e.g., in the Lepismatidae, the subspecies of both *Monachina stilifera* – Irish, 1988b – and *Thermobia nebulosa* – Irish, 1988d), cannot. These taxa indicate that not only the sand (or at least that portion of it bearing the present ultrapsammophilous fauna), but the Namib climate as a whole had a southern spatial origin. The South Atlantic opened from south to north over a period of millions of years, and the associated climatic changes on its shores probably also came about gradually, spreading northwards. Just as the psammophilous taxa followed the sand northwards, so some non-psammophilous taxa evidently followed the climate northwards.

The bulk of the non-psammophilous Gondwanan fauna which invaded the Namib probably did so in a straightforward manner, from east to west at various places, or became Namib taxa simply by staying put and adapting as the climate changed. This component of the Namib fauna today includes those taxa inhabiting the plains and hillsides, which are all more apomorphic (advanced, derived) than their relations in the interior, but usually not nearly as apomorphic as their relations on the Namib dunes (*cf.* also Endrödy-Younga, 1982a).

Sand and dunes are features of deserts, and the young Namib must have included other sand or dunes apart from those carrying the bulk of the present fauna. We have to assume that such early dunes were also inhabited by psammophilous taxa. The Tsondab Sandstone formation (TSF) in the central Namib, with an estimated age of 15–50 Ma, shows fossil traces of such a psammophilous fauna (Ward, 1988). However, these psammophiles cannot be considered directly ancestral to the present psammophilous Namib fauna, as that would be incompatible with the latter's clearly more recent temporal and more southern spatial origin. The TSF fauna may represent either a psammophilous invasion of the Namib similar to but pre-dating the present one, or remnants of a pre-Namib Gondwana Desert fauna in the area. Why they have apparently left no direct descendants is difficult to explain, but the climatic implications of the layer of calcrete which overlies the TSF may hold the key to their eventual fate. On the other hand, as Endrödy-Younga (1982a) pointed out, dunes and psammophiles do not necessarily imply aridity.

The present psammophilous Namib fauna is also descended from the Gondwanan fauna, and many taxa probably evolved on the shores of the proto-Atlantic in an environment similar to the present coastal Namib. Sandy pockets at river mouths in the Namaqualand area (Endrödy-Younga, 1982a), sand accumulations in the lower Orange River area (Endrödy-Younga, 1982b; Penrith, 1984a) and coastal/littoral dunes (Endrödy-Younga, 1978), specifically in the western Cape (Penrith, 1986b), have been mentioned as possible areas of origin for various psammophilous Namib taxa. Being confined to sand, their invasion of the Namib largely followed sand

movements. The principle of dune dispersal was established by Endrödy-Younga (1982*b*), though many details of past dune movements still require additional study. As a result of dune dispersal in a unidirectional wind regime, there are clear south to north evolutionary trends in many of the Namib's psammophilous, and all of its ultrapsammophilous taxa. The relatively more plesiomorphic taxa (whether genera, species, subspecies or clinal morphs) are usually found in the far southern Namib or on the Namaqualand coast, while the more apomorphic taxa occur in the northern Namib or on the south-western Angolan coast, with intermediate forms in between. Examples are the clinal morphs of the lepismatid *Sabulepisma multiformis* (Irish and Mendes, 1988), and in the Tenebrionidae the species of *Onymacris* in general, and the subspecies of *O. unguicularis* in particular (Penrith, 1984*a*), the species of *Brinckia* (Penrith, 1986*c*), and the species of *Zophosis (Cardiosis)* (Endrödy-Younga, 1986). This places the origin of the present psammophilous fauna clearly to the south of their present distribution. Indirect dating, by reference to present rates of dune movement, dates this origin at less than 100 000 years B.P. (Endrödy-Younga, 1982*a*). (The geological age of the present main Namib dune sea is estimated to be Late Pliocene – Korn and Martin, 1957, in Ward, 1988).

The geological extent of the Kalahari sand system, as well as the present distribution of typical Kalahari genera such as the tenebrionid genus *Tarsoconodes* (Penrith, 1987), show that the Kalahari Desert in the past extended into what is now southern Central Africa. The 15°–20° northward latitudinal shift of the African continent, as well as climatological changes following the breakup of Gondwana, eventually caused true desertic conditions to be presently restricted to the southwestern Kalahari only. This is where today the most apomorphic Kalahari psammophilous taxa occur, though earlier evolved and less apomorph psammophiles occur throughout the Kalahari. Examples are the *terebrans*-lineage of *Ctenolepisma* (Irish, 1987), and *Zophosis (Heliophosis)* (Penrith, 1986*a*).

The southwestern Kalahari fauna is also found on what are today largely isolated dune patches in far southeastern Namibia and especially Bushmanland (= interior of northwestern Cape Province). Some representatives of this fauna evidently dispersed from sand to sand on both sides of the present Orange River into the Namib, possibly at the same time as the main stream of proto-Namib taxa from Namaqualand reached the Orange River area. This is clear from the distribution of the common Kalahari species *Ctenolepisma terebrans*, which eventually invaded the southern Namib, and in which the Namib populations have started to evolve away from the typical Kalahari form (Irish, 1987). During this movement, *C. terebrans* populations were isolated on sandy patches here and there and gave rise to separate species such as *C. psammophila*, *C. placida*, *C. luederitzi* and an undescribed species from the Noachabeb dunes (90 km SSE Keetmanshoop). The Kalahari endemic *Zophosis (Heliophosis)* is thought to have given rise to the Namib *Zophosis (Onychosis)* in similar manner (Penrith, 1986*a*). Dispersal also took place in the opposite direction, with the Namaqualand fauna contributing to that of the southwestern Kalahari, as is evident from the coastal ancestry of the Kalahari *Onymacris multistriata* (Penrith, 1984*a*). A situation broadly comparable to the scenario presented above can also be observed in the

psammophilous tenebrionid subtribe Stizopina (Penrith, 1982, 1984*b*).

Probably only at a much later stage, the northern Namib received a small number of colonists from the northern Kalahari, for example *Ctenolepisma subterebrans* (Irish, 1987), but there seems to have been very little other simple east-west colonization of the Namib by earlier evolved Kalahari psammophiles. In the southern Namib the line between Namib and Kalahari faunas is absolute, following the escarpment. A case in point is the Daweb dunes just south of Maltahöhe, which have a pure Kalahari fauna, despite the fact that they are 120 km removed from the nearest extensive Kalahari dunes, and only 60 km from the escarpment, below which the Namib fauna predominates.

The Orange River seems to have been of lesser or sporadic importance as a gene barrier, since many psammophilous southern Namib species, for example *Ctenolepisma pauliani* or *Onymacris hottentota* occur on both sides of the river. The boundary between related Namib and Namaqualand species often lies further south, at the Holgat or Buffels Rivers. That the latter two were important barriers in the past is implied by, for example, the subspecies of both *Zophosis (Z.) prona* (Penrith, 1981*a*) and *Onymacris paiva* (Penrith, 1984*a*). The bulk of the true ultrapsammophiles of the main Namib dune sea do not occur south of the Orange; their southern distributional limit is usually the Lüderitz area, though a number of taxa range south along the coast at least to Bogenfels and inland as far south as the Obib dunes, or just north of them. The discovery of ultrapsammophilous taxa in some of the latter areas took place relatively recently, and the full extent of the fauna is not yet known.

At the time that the psammophilous Namaqualand fauna, supplemented by the Kalahari fauna via Bushmanland, was establishing itself in the far southern Namib, a splitting of the fauna into a coastal and an inland component seems to have taken place. A major causative factor for this was the physical and climatological differences between the predominantly vegetationless, cool and moist coastal dunes and the more vegetated, hotter and drier inland dunes. Analogous to the present situation in the northern Namib, such conditions arose whenever the cumulative effect of the less dominant westerly component of the predominantly southerly to southwesterly winds, combined with the northwesterly trend of the coastline, caused coastal dunes to move inland. The very different conditions under which the Namaqualand and Kalahari faunas evolved may also have predisposed some taxa towards one or the other region within the Namib, cf. the subspecies of *Onymacris boschimana*. The possibility of different spatial or temporal origins for the coastal and inland dune sand respectively, seems unlikely on the basis of evidence gathered since being mentioned by Irish (1986*a*). The distinction between coastal and inland faunas is not absolute, however, since the slipface/dune-crest habitat in the inland dunes shares many similarities with the coastal dunes, and coastal species penetrate far inland on dune crests. The reverse is not true, and inland species are usually absent from the coast. The historical separation, and not present environmental conditions, is probably the primary cause of all east-west distributional gradients presently observed in the main Namib dune sea. Examples of such coastal/inland taxon pairs are *Comicus arenarius* and

C. calcaris (Irish, 1986a), *Sabulepisma multiformis* and *Swalepisma mirabilis* (Irish and Mendes, 1988), and the subspecies of *Onymacris rugatipennis* (Penrith, 1984a).

Various factors point to the fact that the main Namib dune sea was, until relatively recently, either less extensive or consisting of several unconsolidated dune fields. The presently isolated petrophilous faunas of the Hauchab and Uri-Hauchab inselbergs have not yet speciated (Endrödy-Younga, 1982a). The plains-living Namib genus *Crypsicerus* of the orthopteran family Lathiceridae includes only two species, one found north and one south of the main dune sea (Irish, 1988c). The non-ultrapsammophilous fauna of the Meob/Conception area is virtually the same as that found north of the Kuiseb River, though isolated from the latter by at least 60 km of dunes, as witness the distributions of for example *Ctenolepisma detritus* (Irish, 1987), *Onymacris marginipennis* (Penrith, 1984a), and the lizard *Meroles knoxii* (Haacke, 1982). While there is at present no real barrier to the dispersal of ultrapsammophiles between the dune sea south of the Kuiseb River and the Kuiseb-Swakop coastal dune strip, the fact that *Zophosis (Cardiosis) triangulifer* only occurs in the latter dunes (Endrödy-Younga, 1982b, 1986) suggests that this, too, is a recent connection.

Within the (inland) main Namib dune sea one often finds closely related ultrapsammophilous taxa with sympatric macro- and microdistributions (effectively occupying what appear to be the same niches), for example the lepismatids *Namibmormisma muricaudata* and *N. setosa* (Irish, 1986b), or species of the tenebrionid genera *Lepidochora*, *Zophosis (Cardiosis)* and *Vemayella* (Endrödy-Younga, 1982b). The latter author suggested repeated invasions by related but distinct dune dispersed taxa originating from the same or different ancestral dune areas to explain this phenomenon. Alternatively (Endrödy-Younga, 1986), it may also be the result of the recent merging of previously separated dune fields. Whatever the historical reason, the situation is today perpetuated by the fact that food is probably not a limiting factor for detritivores in this particular ecosystem. What we are fortunate enough to be witnessing in the Namib today is what in many other ecosystems could be compared to the height of the speciation explosion following on the first availability of a new environment, and preceding later extinctions or improved niche separation. Given the implied extremely young age of the system, this may yet happen in the Namib too.

On the whole the (inland) main Namib dune sea is faunistically relatively homogenous (cf. maps in Holm and Scholtz, 1980). East-west distributional gradients were discussed above. There are no appreciable south-north distributional gradients, even in taxa such as *Sabulepisma mirabilis*, which shows south-north clinal variation in the Namib as a whole (Irish and Mendes, 1988). Because Gobabeb lies adjacent to this fauna, it is the best studied in the Namib, while other faunas, including the plains immediately north of the Kuiseb, remain poorly known.

North of the Kuiseb and Swakop Rivers, major dunes are absent as far north as the Torraabai area, 290 km north of Swakopmund. The plains do, however, harbour a highly specialized psammophilous fauna which lives in the windblown sand and detritus mixture which accumulates around the base of vegetation on even the hardest substrates (= shrub coppice

dune, dune hummock or dune knoll habitat). Examples are *Ctenolepisma namibensis* and *C. ossilitoralis*. In the Skeleton Coast area (= far northern Namib) the distinction between plains hummocks and dune hummocks breaks down in the excessively sandy habitat, and an admixture of the faunas occurs. The origin of these animals is not yet certain, and awaits complete study of certain undescribed Namib lepismatid genera. Some components clearly originated in this habitat in Namaqualand and spread northwards, but others seem to have had a northern origin. Irish (1987) discussed a possible local reversal of the usual south-north evolutionary trend to explain the *Ctenolepisma* species, and mentioned the alternative possibility of a northern Kalahari origin for these taxa. Penrith (1986a) also found the hummock-dwelling *Zophosis (Protodactylus)*, *Z. (Dactylocalcar)* and *Z. (Latipleurosia)* to have northern origins.

Returning to the formal dune fauna; the northern Namib dunes, at least in the south, are mostly coastal only, and a large part of their fauna is identical to that of the coastal main Namib dune sea. Where the fauna differs, as for example in *Zophosis (Cardiosis)*, the present coastal rather than inland southern Namib taxa can be shown to have been ancestral to the northern Namib taxa (Endrödy-Younga, 1986). Very few of the main Namib dune sea's inland species are found in the northern Namib. Where inland southern Namib species do occur in the northern Namib, they are usually slipface/dune-crest dwellers, such as *Ctenolepisma pauliani* or *Sabulepisma multiformis*. Common taxa primarily associated with dune hummocks or marginal dune areas in the inland main Namib dune sea, for example both *Namibmormisma* spp., *Ctenolepisma terebrans*, *C. spinipes*, *Onymacris rugatipennis* and *O. plana*, are absent from the northern Namib. This indicates that past connections between the southern and northern Namib consisted mostly of coastal, vegetationless dunes with many slipfaces. A continuous coastal dune strip, such as presently found in the Kuiseb-Swakop or Torraabai-Hoarusib areas, would satisfy these requirements, but the evidence that follows rather points to disconnected moving barchan trains (Endrödy-Younga, 1982b), such as presently found in the Khumib-Engo region. Irish (1986a) roughly calculated the average *minimum* age for cessation of barchan movement in the latter case at 5000–6000 years B.P.

Between Swakopmund and Torraabai, the northward sand movement had some interesting spin-offs, all associated with major river-beds. It seems as though coastal sand was canalized into the interior up some river valleys. The differing interior vs. coastal conditions then had an evolutionary effect on the sand-associated fauna. No such effect has yet been observed for the first major rivers northwards, the Swakop and Omaruru, but this may be due to lack of study. In the next river, the Ugab, near Brandberg Wes, at a point about 65 km from the coast, a patch of windblown sand along the canyon walls, less than a hectare in extent, harbours a most interesting fauna which includes the dune gecko *Palmatogecko rangei*. The lepismatid found here is *Ctenolepisma ugabensis*, which is of subcoastal ancestry. It also occurs some 40 km further upstream on the Vegkop-Duineveld dunes, and nowhere else (Irish, 1987). The latter are an extensive vegetated dune field lying directly north of Brandberg, and the fauna of the Brandberg Wes sand patch indicates that the Vegkop dunes were colonized at least par-

tially by Namib psammophiles moving up the Ugab Valley on windblown sand.

The same phenomenon, but on a much more impressive scale, can be observed in the Huab River valley. Being a larger river in a much more deeply incised valley, it probably captured much more sand than the Ugab, and hence afforded the associated psammophiles a better chance of survival and subsequent speciation, besides capturing a larger variety to begin with. Windblown sand and small dunes along the edges of the Huab Valley, starting (present knowledge) just west of the original farm Krone, across De Riet and Vrede to Bethanis, harbour a unique fauna. In spite of being a relatively minor sand concentration, Bethanis, by virtue of lying adjacent to a major road, is the type locality of most of the endemics found on these dunes. All show clear affinities with and descent from the Namib coastal dune fauna. In effect, this sand represents a piece of the Namib which has been blown inland, complete with 'white' *Onymacris* beetles. In the area between the Vegkop and Huab dunes, accumulations of windblown sand are common, and bidirectional dispersal probably occurred. The distribution of the psammophilous *Zophosis* (*Dactylocalcar inflatus*), found in both areas but nowhere else (Penrith, 1981b), may be as a result of this.

At the Huab River mouth is a small barchan field, and for some distance north of it isolated barchans can be found. All harbour an impoverished version (this impression may be due to inadequate sampling) of the normal northern Namib dune fauna (= *p.p.* southern Namib coastal dune fauna). From Torrabaai northwards to the Khumib River, the northern Namib dune fauna is well represented. The coastal dune strip in the Torrabaai-Hoarusib area is on average only 10 km wide, but there are indications that even here different species with different ancestries are more common on the coastal or inland sides of the dunes respectively (Irish and Mendes, 1988). Between the Khumib and Engo Rivers there is no continuous dune field, but numerous moving barchan trains. Their fauna is inadequately known. Between the Engo and Kunene Rivers, there is again a major dune field. Its coastal fauna is largely similar to that of the rest of the northern Namib, but because it stretches quite some distance inland, a new inland dune fauna has again started to evolve from the coastal fauna. This can be seen in the inland populations of the normally coastal *Comicus arenarius* (Irish, 1986a). *Onymacris brainei* (Penrith, 1984a) may have evolved in a similar manner from the coastal *O. marginipennis*, and at least some of the several other

endemic psammophiles known from the Hartmann Valley and Marienfluss may have had a similar origin.

Lack of personal collecting experience north of the Kunene River, and a total lack of information on the psammophilous Lepismatidae of southwestern Angola do not allow me to comment in detail on the Angolan Namib. A general impression from other groups is that the Kunene River was not always effective as a gene barrier in the past (and possibly still is not). In ultrapsammophilous groups, the most apomorphic taxa usually occur in the Angolan Namib.

One aspect of Namib biogeography that has emerged quite clearly so far, is the role of the coastal dunes as a species reservoir and a dispersal vessel, and the fact that wherever this sand and its associated fauna has been blown inland, new taxa have evolved. This is seen especially well in the northern Namib, where time has not yet obliterated the trails, and the striking subspeciation of *Onymacris langi* (Penrith, 1984a) may possibly be explained in this manner. Another aspect, which can be seen in both *Zophosis* (Penrith, 1986a) and the *Adesmiini* (Penrith, 1986b), is the evolutionary bipolarity of South West Arid endemic taxa. Within a given lineage, South West Arid endemics are represented by both the most plesiomorphic taxa (relicts of the Gondwanan Desert fauna) and the most apomorphic taxa (ultrapsammophilous Namib dune-dwellers). It follows that while the Namib fauna, particularly the Namib dune fauna, is decidedly not the 'oldest desert fauna in the world', their ancestors did inhabit a very ancient desert.

Gaps in our knowledge which presently hamper progress in the biogeographical understanding of the Namib include the lack of completed revisions in many psammophilous groups under study, the lack of local taxonomic expertise in many important groups which include psammophiles, the lack of study material in many of the less popular psammophilous taxa, and insufficient collecting for all groups (except possibly Tenebrionidae) in especially southwestern Angola and to an only slightly lesser extent in Namaqualand, the interior far northern and far southern Namib, the southwestern Kalahari, and the very many isolated sandy/dune patches throughout the South West Arid Region. An uncertain aspect which also requires further study relates to events which took place during the very long time span between the breakup of Gondwana (130 Ma) and the onset of the present ultrapsammophilous dispersal (100 000 years B.P.), specifically whether or not the present dispersal is the first and only one of its kind.

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POSTSCRIPT

Since the above was written in 1987, the evolution of the subgenera of *Ctenolepisma* was found to be more complicated (Irish, 1990: Ph.D. thesis, University of Pretoria, 'Phylogeny of the Lepismatidae (Thysanura), with a revision of the southern African genera') than was suggested on p. 62. A revision of *Gopsilepisma* (Irish, 1989, *Cimbebasia* **11**: 135–144) has clarified the position with regard to dispersal against the dominant wind direction in northern Namib hummock dwellers (p. 64) somewhat. Taxa described in both the latter work and in Irish (1988, *Cimbebasia* **10**: 31–46) have reaffirmed the distinctiveness of both the southwestern Kalahari/Bushmanland dune fauna (p. 63) and the Huab dunes (p. 65).

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Commentary on the Insect Fauna of the Lower Kuiseb River, Namib Desert

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Surveys revealed the presence of a diverse insect community living within the confines of the lower Kuiseb River course in the central Namib Desert. More than 700 species, in 15 orders, were recorded. The fauna is largely non-endemic and mostly widely distributed, which can be attributed to the mainly non-desertic and widely distributed floral composition of the Kuiseb River biotope. The faunal composition of the area, and the species associated with the dominant perennial vegetation, are discussed.

INTRODUCTION

The seasonally dry Kuiseb River, which has its origin in the central highlands of Namibia, stretches for some 440 km in a generally southwesterly to northwesterly direction to reach the Atlantic Ocean near Walvis Bay (Stengel, 1964). Below the escarpment, the river cuts across the central Namib Desert, separating a vast sand dune sea to the south and quartz-gravel plains to the north.

The insect fauna of the dune biotope (summarized by Holm and Scholtz, 1980) has been the subject of extensive research which has formed a major facet of the scientific endeavour in the central Namib during the past 25 years. This has resulted in a sound taxonomic, biogeographic, ecological and physiological knowledge of the largely endemic fauna of psammophilous tenebrionid beetles, thysanurans and ants, which constitute the major invertebrate fauna of the dunes. More recently, emphasis has also been placed on the insects of the gravel plains (e.g., Wharton, 1980; Wharton and Seely, 1982; Marsh, 1986b).

In contrast to the sparsely vegetated dune and plain biotopes, the Kuiseb River bed supports a comparatively diverse flora comprising a variety of mostly non-desertic perennial and annual plants, most of which are listed by Seely, Buskirk, Hamilton and Dixon (1981). This plant community supports a rich invertebrate fauna dominated by insects in several different orders. Unlike those of the dunes and plains, the insects of the Kuiseb River have received very little scientific attention. In an attempt to gain a preliminary knowledge of the species composition and major habitat preferences in this biotope, surveys of the insects of the lower Kuiseb River in the vicinity of Gobabeb (Fig. 1) were conducted. The results of these surveys are presented here.

METHODS

The surveys were conducted along a 70 km stretch of the lower Kuiseb River, from the Namib Research Institute at

Gobabeb (24° 34' S, 15° 03' E) upstream in an easterly direction (Fig. 1). The upper reaches of this part of the river are characterized by the narrow, sparsely vegetated Kuiseb Canyon, while the lower part, downstream from the vicinity of Homeb, forms a broad, well-vegetated alluvial flood plain. The flood plain downstream from Gobabeb was also sampled for a distance of about 15 km. A detailed description of the vegetation and topography of the area where the study took place is provided by Theron, Van Rooyen and Van Rooyen (1980) and Seely *et al.* (1981).

The surveys were conducted over a total of 44 days, with more or less continuous collecting throughout each day, and in the evening, on four occasions during February, March and July, 1983, and July 1984. In all, 14 entomologists participated in the surveys at various times.

Emphasis was placed on sampling from the following perennial plants, which form the main floral component of the study area: *Acacia albida* Del., *A. erioloba* E. Mey., *Tamarix usneoides* E. Mey. ex Bunge, *Euclea pseudebenus* E. Mey. ex A. DC, *Salvadora persica* L., *Pechuel-Loeschea leubnitziae* (Kuntze) O. Hoffm., *Ficus sycamoros* L., *F. cordata* Thunb. and *Cladoraphis spinosa* (L. F.) S. M. Phillips. In addition, 12 species of mostly annual herbaceous plants were also sampled.

Sampling of the vegetation was done by repetitive and systematic sweeping and beating of plants at short intervals along the river-bed. Methods for collecting flying insects in general included the use of light traps, Malaise traps and yellow pan traps, whereas unbaited pit-fall traps and extraction funnels were used to sample the ground-living and leaf litter fauna. Hand collecting and host plant rearing from pods, fruit and galls supplemented these sampling techniques.

RESULTS AND DISCUSSION

The surveys revealed the presence of a diverse insect community living within the confines of the lower Kuiseb River

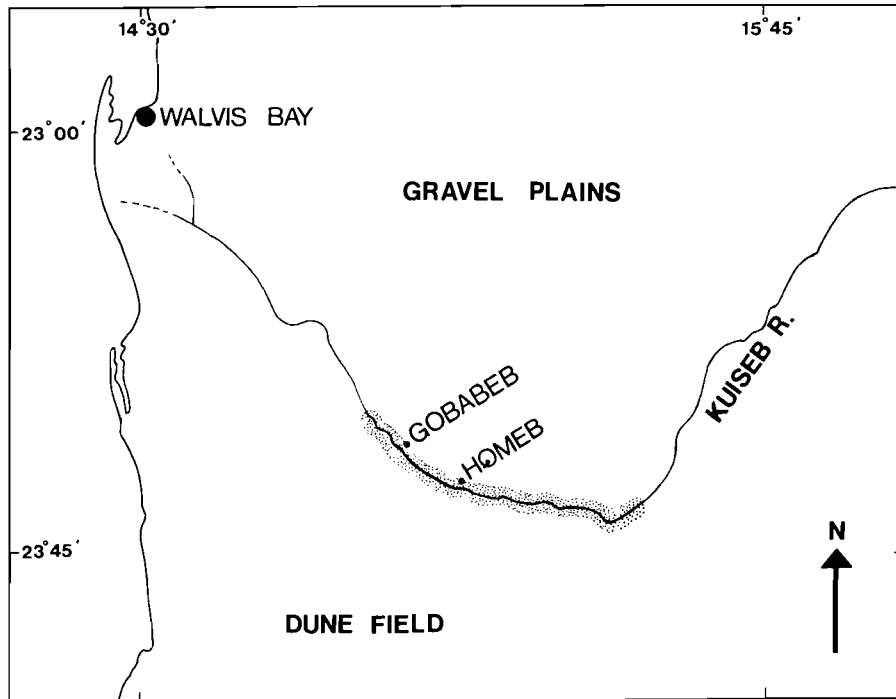


Fig. 1

Map of the central Namib Desert, indicating the part of the lower Kuseb River (stippled) where the surveys were conducted.

course. More than 6500 specimens were collected and studied, which represent 161 families of insects in 15 orders, and a total of at least 719 different species. The number of families and species in each order is summarized in Table 1. Our poor knowledge of the insects of southern Africa and the Afrotropical Region as a whole was reflected in the survey material, much of which remains unidentified at or below the generic level. Taxa identified to species level are listed in Appendix 1.

Those taxa for which taxonomic and distributional information is available reveal that, in contrast to the fauna of the dunes, high endemism is not a feature of the Kuseb River insect fauna (Fig. 2). Only a few species, most of which belong to the Hymenoptera and Coleoptera, are at present known to be 'endemic' to the Kuseb River. In all probability, further collecting will show them to be more widely distributed. The distribution of the fauna as a whole is otherwise varied, and composed of several major components, as shown in Fig. 2. All of these components are evidently well represented in the fauna of the Kuseb River biotope, as reflected by the geographical occurrence of 231 sufficiently known species in various orders (Fig. 2). Included in the fauna are species that are also found in the other Namib biotopes, species that are limited to the more arid western parts of southern Africa, and others which are widely distributed throughout sub-Saharan Africa. Some species range as far as the Nearctic, Palearctic and Indo-Pacific Regions. Certain species, especially amongst the heteropterous bugs, parasitic wasps, Lepidoptera and non-phytophagous Coleoptera, are cosmopolitan.

The occurrence of these distributional elements can be attributed to the composition of the Kuseb River flora, which contains, as far as woody perennials are concerned, a mainly non-desertic and widely distributed component, with some species such as *Ficus sycomorus*, *Salvadora persica* and *Acacia albida* ranging far beyond the limits of the southern African subregion. The more ephemeral components of the flora that were sampled, as well as the other annuals listed by Seely *et al.* (1981), provide a similar picture and include, amongst others, well-known exotics such as *Nicotiana glauca* R. C. Grah., *Datura stramonium* L. and *Solanum nigrum* L. It is this dominantly non-endemic floral component that attracts an equally non-endemic and widely distributed insect fauna into the central Namib Desert along a corridor formed by the Kuseb River. A discussion on the composition and certain host associations of this fauna follows.

FAUNAL COMPOSITION

Hemiptera

The well-wooded acacia woodland and the dense stands of several other woody and herbaceous plants provide ideal habitats for Hemiptera, which form the larger part of the phytophagous guild of the Kuseb insect fauna. Species of bugs were present, often in great numbers, on 14 of the 21

Table 1
Number of families and species in each of the orders of insects recorded during the surveys.

Order	Number of families	Number of species
Blattodea	1	2
Coleoptera	36	133
Diptera	24	50
Grylloidea	2	2
Hemiptera	26	110
Hymenoptera	40	300
Isoptera	2	2
Lepidoptera	13	70
Mantodea	1	4
Neuroptera	6	28
Odonata	2	4
Orthoptera	4	5
Psocoptera	1	1
Thysanoptera	2	4
Thysanura	1	4
TOTAL:	161	719

plant species that were sampled. They belong to 26 families, all of which have cosmopolitan distributions. In all, some 110 species of Hemiptera were recorded. Those species that could be determined to at least the generic level indicate a dominance of widely distributed taxa, many of which seem to be polyphagous on a wide range of plants within the Kuiseb biotope. Amongst the suborder Homoptera, for instance, cicadellids such as *Exitianus nanus* (Distant) and *Circulifer tenellus* (Baker) are known to occur far beyond the geographical limits of the Afrotropical Region, where they are found in a variety of habitats: the former species in India and Iraq, the latter in North and South America, Europe and Australia. Similarly, the aphid *Hyalopterus pruni* (Geoffroy), which feeds on a variety of plants, is almost cosmopolitan in its distribution. Other identified homopterans include mostly cicadellids and psyllids, and these are generally more restricted in their distribution, occurring throughout southern Africa, with only a few species, such as *Colposcena australis* Hollis and *C. namibensis* Hollis (Psyllidae) preferring the arid western areas of the subregion.

The same generalities apply to the suborder Heteroptera, especially amongst the species of Lygaeidae, Tingidae and Nabidae. Three commonly encountered phytophagous species, namely *Paromius gracilis* (Rambur) (Lygaeidae), *Bagrada hilaris* (Burmeister) (Pentatomidae) and the tingid *Galeatus scrophicus* Saunders, occur throughout Africa as well as in parts of Europe and Asia. Amongst the predaceous fauna, *Nabis capsiformis* Germar (Nabidae) is cosmopolitan, whereas *Geocoris scutellaris* Puton extends its range through Africa to the Middle East (Slater, 1964). These two predators, and particularly *N. capsiformis*, are common in the study area where they probably prey upon the rich fauna of small insects associated with the many plants on which these bugs were found.

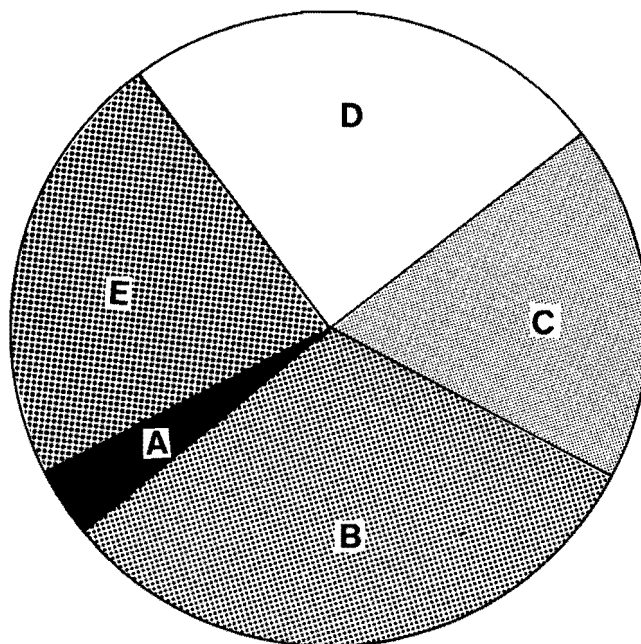


Fig. 2

Diagram depicting the major distributional components of the insect fauna of the lower Kuiseb River biotope; species whose distribution include: **A** the Kuiseb River only; **B** the arid western parts of Southern Africa, including other Namib biotopes; **C** Southern Africa; **D** the Afrotropical Region; **E** Africa and other zoogeographical regions. The proportional size of each component is based on the distribution of 231 species in various orders.

Neuroptera

Southern Africa has a rich fauna of ant-lions, lacewings and their allies. Twelve families, which include many taxa found in arid habitats, occur in the region. Six of these families, comprising 28 species in 23 genera, are known from the Kuiseb River biotope. The biology of most of these species is poorly understood, but the sandy river-bed substrate, acacia woodland with its abundance of detritus, and the rocky slopes of the canyon wall, form ideal habitats for the predaceous immature stages of these insects.

The Psychopsidae (moth lacewings) are represented by a single species of the endemic African genus *Silveira*, namely *S. jordani* Kimmins, which was originally described from the central Namib and is now known to be widespread in Namibia and the Cape Province of South Africa. The green lacewings (Chrysopidae) are represented by a more widely distributed fauna which includes five genera, all of which extend their range beyond Africa. The species represented by these genera are common and have all been recorded previously from Namibia and other southern African localities. Four genera of Coniopterygidae, each known from a single undetermined species, are known to occur in the Kuiseb River. These genera are all widespread, even cosmopolitan, and two of them, namely *Aleurothrix* and *Coniopteryx*, have previously been recorded from Namibia through described species taken in the Kaokoveld (Meinander, 1972).

Certain species of the families Ascalaphidae, Nemopteridae

and Myrmeleontidae appear to be endemic to the Namib Desert. A single undescribed species of *Semirhynchia* (Nemopteridae), which occurs in the dunes and along the Kuiseb, has not been found elsewhere in southern Africa. This is also the case with an undescribed species of Ascalaphidae. One undescribed species of Palparinae (Myrmeleontidae) appears to be unique to the Kuiseb River, whilst the remaining fauna of this family, which is by far the most numerous and important neuropterous component, includes species that are widespread in southern Africa.

Coleoptera

In contrast to a mainly endemic psammophilous tenebrionid element of the dune biotope (Holm and Scholtz, 1980), the fauna of the Kuiseb River course is a rich assemblage of non-endemic coleopterous taxa. In all, 133 species in 102 genera and 36 families were recorded, with additional species of mostly ground-living Tenebrionidae recorded in the literature (Wharton and Seely, 1982). Except for the well-known tenebrionid *Onymacris rugatipennis rugatipennis* (Haag), endemism seems to be absent in this fauna. The few new species of Coccinellidae, Buprestidae, Curculionidae, Malachiidae and Melyridae that have been described from material collected during these surveys, probably have a wider distribution.

Available information on the distribution patterns of the beetles shows that almost half of the taxa identified to species are widespread in southern Africa or sub-Saharan Africa. This element of the fauna includes mainly the xylophagous groups such as cerambycids, anobiids, bostrychids, Brentids and buprestids, the fungivores (Lathridiidae) and predators such as coccinellids and staphylinids. About 25 % of the remaining species are restricted in their distribution to the arid southwestern parts of the southern African subcontinent, and include mostly phytophages of the families Curculionidae, Apionidae and Chrysomelidae. A further 25 % of the identified species are known only from the Namib, and this element includes the majority of the detritivorous tenebrionids, some of which occur in two or more of the major biotopes of the central Namib, others being widely distributed from south to north along the entire desert. A very small component of the fauna seems to be cosmopolitan, and includes species such as the cigarette beetle *Lasioderma serricornis* (Fabricius) (Anobiidae), the saw-toothed grain beetle, *Oryzaephilus surinamensis* (L.) (Silvanidae), *Carpophilus hemipterus* (L.) (Nitidulidae) and two species of predaceous coccinellids, namely *Cheilomenes lunata* (Fabricius) and *Hippodamia variegata* (Goeze).

Diptera

Flies constitute one of the larger orders of insects, and this group of ubiquitous organisms is probably well represented in the various habitats of the Kuiseb River biotope. However, only about 50 species in 24 families were recorded, which is undoubtedly an underestimate of the actual dipteran fauna of the area. Apart from the phytophagous family Tephritidae, most of the other material remains unidentified, and little is known about the Diptera of the Kuiseb River. Wharton (1982) recently dealt with some mydas flies from the central Namib and recorded three species of this family from the river-bed.

The Tephritidae, whose larvae attack the fruit, flowers, seeds and stems of a wide range of plants, are represented

by seven species with varied distribution patterns. Two species, namely *Didacus ciliatus* (Loew) and *Dioxya sororcula* (Wiedemann), are extremely widespread, their range including the African continent, some east and west coast islands such as Mauritius, Madagascar and Madeira, as well as the Arabian peninsula and India. The other five species, *Terellia xanthochaeta* Munro, *T. australis* (Bezzi), *Leucothrix barbata* Munro, *Hyaloctoides semiater* (Loew) and *Pardalaspis quina-ria* Bezzi are known only from the arid parts of Namibia and from few other southern African localities (Cogan and Munro, 1980).

Lepidoptera

The 70 species of Lepidoptera that were collected revealed the presence of an extremely wide-ranging fauna of common moths and butterflies. Of the 36 species of moths for which specific names are available, almost half are cosmopolitan, or known to extend their range throughout Africa to parts of Europe, Asia and the Orient. Included amongst these species are well-known hawk moths (Sphingidae) such as *Agrius convolvuli* (L.), *Hippotion celerio* (L.) and *Hyles lineata livornica* (Esper), in addition to a number of noctuids such as *Sphingomorpha chlorea* (Cramer), *Prodotis stolidus* (Fabricius) and *Spodoptera exigua* (Hübner). A similar distribution pattern is found amongst the butterflies, and 50 % of the species that were recorded occur throughout the Afrotropical Region and in parts of the Palaearctic and Oriental realms. Such widespread species include some common butterflies such as *Hypolimnas missipus* (L.) (Nymphalidae), *Lampides boeticus* (L.) (Lycaenidae), and the pierid, *Belenois aurota* (Fabricius).

Most of the remaining lepidopterous species that were recorded occur widely throughout sub-Saharan Africa. None was found to be restricted to the Namib, and only four species seem to be confined to the southern African subcontinent.

Although no host plant information is available, there is evidence that many species in the Kuiseb River are dependent on the acacia woodland, which dominates the vegetation. Eleven species of moths and butterflies, of which the larvae are known to be phytophagous on acacias, were recorded. These include some widespread Afrotropical species such as *Cyligramma latona* (Cramer), *S. chlorea* and *Achaea lienardi* (Boisduval) (all Noctuidae), as well as two lycaenid butterflies, *Azonus jesous* (Guérin-Ménéville) and *A. ubaldus* (Stoll). The lasiocampid moth *Gonometa postica* Walker, which is commonly found in association with acacias in the dry western parts of southern Africa, was also recorded.

Hymenoptera

The Hymenoptera constitute an extensive group of highly specialized insects with diverse habitat requirements. Forty of the 60 families of Hymenoptera known from the Afrotropical Region were recorded, and more than 300 species of both parasitic and aculeate groups were represented.

The rich insect fauna of the Kuiseb biotope forms the basis of the wide range of parasitic Hymenoptera found in the area. More than two-thirds of all Afrotropical families of Parasitica are represented by some 150 species, a few of which have been dealt with by Prinsloo (1985). Although many of these species have not yet been described, only a few belong to new supraspecific taxa, and at least 50 of the 65 named genera are

cosmopolitan, the remainder being widely distributed in Africa. The available material shows a dominance of genera that are parasitic in the immature stages of Hemiptera, Lepidoptera and xylophagous Coleoptera, of which a rich fauna is associated with the dense riparian vegetation and abundance of dead wood in the river-bed. Scelionid egg parasitoids of the genera *Gryon* and *Trissolcus* are particularly abundant and are probably parasitic in the eggs of the many lygaeid, mirid, pentatomid and other heteropterous bugs found on these plants. Evaniid wasps, which are exclusively parasitic in the oothecae of cockroaches, were commonly encountered amongst the dead wood.

The area is equally rich in aculeate Hymenoptera, and 20 of the 28 families that occur in the Afrotropical Region are now known from the area. Most genera, of which 55 have been identified, are widespread in Africa, whereas a few are known to be cosmopolitan. Only a small element of the aculeate fauna appears to have a more restricted distribution. This includes a few genera and species which are known only from the arid western parts of the southern African subregion, such as an unidentified species of the genus *Myrmecopteryna* (Plumariidae), *Apterogyna schultzei* André (Bradyobaenidae), which is also found in the dunes and gravel plains, and a few species of sphecid and pompilid wasps and bees. One of these, *Braunsapis albipes* (Friese) (Anthophoridae), is perhaps the most common aculeate in the Kuiseb, where the adults visit a large variety of plants. This species, which is also found in the dunes and on the plains, nests in dead wood or in the hollow and pithy stems of annual plants. Few species of ants are known from the area (Marsh, 1986a). A recent revision of the Miscophini (Sphecidae) of southern Africa (Lomholdt, 1985) mentions several species from the Namib Desert, some of which are from the Kuiseb River.

Other orders

Apart from the dominant insect orders of the Kuiseb River bed, several smaller, less abundant and well-known groups were present (Table 1), each represented by species reflecting a trend in distribution similar to that found amongst the dominant orders.

Species with extremely wide distributions were found amongst the Thysanoptera and Odonata, each of which is represented by a few species. The dragonflies mainly frequent the man-made wells in the Kuiseb River bed and include *Pantala flavescens* (Fabricius) and *Tholymis tillarga* (Fabricius), two libellulids that extend their range throughout Africa, Asia and Australia and, in the case of the former, also North and South America (Pinhey, 1985). A less widely distributed element is present amongst the Isoptera, Thysanura, Orthoptera and Mantodea, with a few species, such as the thysanurans *Ctenolepisma terebrans* Silvestri and *C. grandipalpis* Escherich (Lepismatidae), and the termite *Psammodermes allocerus* Silvestri (Rhinotermitidae), being restricted to the arid western region of southern Africa.

PLANT ASSOCIATIONS

The nine species of perennial woody and herbaceous plants that dominate the lower Kuiseb River course in the area where the study was conducted, are listed in the 'Methods' section. It is this floral element which, to a large extent, supports the

insect fauna of the area. The following discussion briefly considers the insects that were found to be associated with each of these plants.

Acacia albida

Although *Acacia albida* is the dominant plant species in the area, insects are only found in great abundance and diversity on this tree when it is in bloom. Despite extensive sampling, only 21 species of insects were recorded on this plant out of the flowering season during February and March. Of these, only 7 were phytophagous, five belonging to the Hemiptera, the other two being weevils.

Diversity of phytophages increased more than five-fold during July when *A. albida* was in full bloom. Phytophagous Hemiptera and Coleoptera included some 40 species in several families. Diptera and aculeate Hymenoptera, which were virtually absent during late summer, were abundant on the flowers and accounted for 18 species in 15 families, whereas the southern subspecies of the desert locust, *Schistocerca gregaria flaviventris* (Burmeister), was also recorded.

Both adults and nymphs of an unidentified alydid bug were commonly found feeding on fallen pods, and an apparently new species of bruchid weevil develops in the seeds.

In all, 103 species of insects in 54 families and five orders were recorded from *A. albida*.

Acacia erioloba

This acacia was represented in the area mainly by large old trees, which made sampling difficult. Only 19 species of insects were recorded, the majority of which were Hemiptera and Coleoptera, seven species of the former order and two of the latter being phytophagous. In general, the fauna associated with this plant was found to be much the same as that on *A. albida* during summer, and almost all the beetle species taken on *A. erioloba* were also recorded on *A. albida*. *Acacia erioloba* was not in bloom when sampled during July, and insect diversity had hardly changed.

Three species of seed-infesting bruchids are known to develop on *A. erioloba* in southern Africa, of which *Bruchidius senegalensis* (Pic) and *Caryedon multinotatus* (Pic) are now known from the Kuiseb River biotope.

Salvadora persica

Few insects seem to be associated with this widely distributed plant when it is not in bloom. Extensive sampling yielded low numbers of only 15 species during summer, many of these being parasitic Hymenoptera and predaceous beetles that are not dependent on the plant. Diversity increased sharply during July, when 70 species were recorded on flowering plants. Few insects seem to feed on the great abundance of fleshy green foliage produced by this plant throughout the year. Virtually no insect damage was observed and, in addition to predaceous Hemiptera and Coleoptera and parasitic Hymenoptera, about 70% of the insects recorded from this plant were wasps, bees and beetles which are associated with the flowers. *Salvadora persica* extends its range far beyond the Afrotropical Region, and a number of insects with equally wide distributions are to be found on this plant in the Kuiseb. These include the phytophagous bugs *Bagrada hilaris* (Pentatomidae) and the tingid *Galeatus scrophicus*, the predaceous bug *Nabis capsiformis*

(Nabidae), the predaceous coccinellid beetle *Hippodamia variegata*, and *Homalotylus flaminus* (Dalman), an encyrtid parasitoid.

Euclea pseudebenus

This hardy tree is more or less restricted in its distribution to the arid areas of Namibia (Coates Palgrave, 1984). Although 49 species of insects were found on *E. pseudebenus*, most of these do not seem to be primarily associated with this plant and include a large number of visitors which were also commonly encountered on various other plants in the study area. Few phytophagous species were present, and these included two undetermined cicadellids, one lygaeid bug and an apparently host-specific weevil of the genus *Apion* (Apionidae). The last species, which is undescribed, was collected during both summer and winter, and is also known from *E. pseudebenus* in the Naukluft area on the eastern edge of the Namib.

The fruit of this tree, which is abundant during February and March, yielded no insects. Adults of the fruitfly *Leucothrix barbata* Munro were present on the foliage, but the fruit showed no traces of larval infestation.

Ficus sycomorus* and *F. cordata

Not much is known about the insect fauna of these two fig-trees which are mainly found along the upper reaches of the river course. Wharton, Tilson and Tilson (1980) mention a complex of five chalcidoid fig wasps associated with *F. sycomorus*. These were also encountered during the surveys, and include *Ceratosolen arabicus* Mayr (Agaonidae), a widely distributed African pollinator of *F. sycomorus*, in addition to five agaonid inquiline. Wharton *et al.* (1980) also mention a lymantriid which defoliates the leaves of *F. sycomorus*. This moth, *Naroma varipes* (Walker), is widespread, and has been recorded from wild figs in other parts of southern Africa, as well as Zaïre, and east and west equatorial Africa (Pinhey, 1975). *Ficus sycomorus* yielded few other phytophagous insects, all of which belong to the Hemiptera. One of these, namely *Pauropsylla longipes* Hollis (Psyllidae), was recently described from East and West Africa and in association with *Ficus* sp. in Tanzania (Hollis, 1984).

The only insect collected on *F. cordata* is a widespread African thrips, *Dolicholepta karneyi* (Faure).

Tamarix usneoides

This xerophytic plant appears to harbour a rich fauna of phytophagous Hemiptera, yielding more than 30 species, many of which unfortunately remain undetermined. These include 10 species of cicadellids in addition to a variety of lygaeids, mirids and tingids. The polyphagous *Nysius natalensis* Evans (Lygaeidae), and *Galeatus scrophicus* (Tingidae), which is also known from Europe and Asia, were found to be particularly abundant. A complex of psyllids is known to feed on species of the genus *Tamarix* throughout its global distribution (Hollis, 1974). Two of these species, *Colposcena namibiensis* Hollis and *C. australis* Hollis, which were originally described from *T. usneoides* in the study area, were also encountered.

The coleopterous fauna found on *T. usneoides* comprised mainly predators, and only one phytophagous species appears to feed on tamarisk. This weevil, *Corimalia damarensis*

Marshall, is the only sub-Saharan species of a widely distributed and mainly extra-African genus of some 30 species, many of which are known to feed on species of *Tamarix* in various parts of the world (Pajni and Bhateja, 1982).

In all, about 65 species of insects were found on this plant.

Pechuel-Loeschea leubnitziae

This indigenous herbaceous shrub was found to support some 75 species of insects which often occurred in abundance during summer, as well as in winter when the plant is in bloom. Phytophagous species for which specific identities and host information are available, are mostly widely distributed polyphages. Such species include the common southern African lygaeid bug *Nysius natalensis*, which attacks several agricultural crops, and *Paromius gracilis* (Rambur), a species of the same family which occurs throughout Africa, Europe and Asia (Slater, 1964). Similarly, two species of thrips of the family Phlaeothripidae, namely *Haplothrips nigricornis* (Bagnall) and *H. tardus* Priesner, are found in the flowers of *P. leubnitziae*. They also occur on various other plants, and are widely distributed, the latter species ranging as far as Egypt and Israel.

Apart from those species mentioned, 20 other hemipteran species were found, and these form the largest part of the phytophagous insect component on *P. leubnitziae*. Few other plant-feeding insects were present, the most common being an undescribed species of *Rhynchaenus* (Curculionidae) and the chrysomelid *Trichaspis pilosula* (Boheman), which was originally described from the Kuiseb River in 1862.

Cladoraphis spinosa

This perennial grass, which is found in the arid western parts of South Africa and Namibia, often occurs in dense stands in the river-bed where the survey was conducted, and was found to support large numbers of insects during summer as well as winter. About 91 species in 52 families and 6 orders abound on this grass. Many of these are, however, not primarily associated with *A. spinosa*, but seem to use this dense and low-growing spiny plant as a protective shelter. These insects include a large number of non-phytophagous Diptera, Coleoptera and Hymenoptera, many of which were also found on other plant species in the area. A few others, such as the encyrtid parasitoids *Cheiloneurus kuisebi* Prinsloo, *Mayridia maryae* Prinsloo and *Anagyrus amnicus* Prinsloo, are found only on this grass, where they are probably parasitic on certain host-specific scale insects.

The phytophagous guild associated with *C. spinosa* is typical of grasses, comprising a large variety of hemipterous bugs and leafhoppers, representing ten different families. Little is known about the biology and specific identity of these insects, although a few, such as *Paradorydium quadrangulum* (Naudé) and *Exitianus nanus* (Distant), are common southern African grass-feeding leafhoppers, whereas *Paromius gracilis* has previously been reported as feeding on grasses in Egypt (Slater, 1964).

CONCLUDING REMARKS

The present overview of the diverse insect community of the lower Kuiseb River, although based on preliminary surveys,

for the first time provides clues as to its composition and the habitat preferences of its constituent taxa. A more complete view of the insect fauna of this biotope will require further collecting, in the present study area and farther afield, combined with much greater taxonomic input, in the form of both

basic descriptive and revisionary studies. However, I believe that a large proportion of the fauna, including especially those species that dominate the major habitats of the river-bed, has been sampled, thus providing important baseline information on the insects of this poorly known ecosystem.

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Appendix 1

Kuiseb River insect surveys: alphabetical list of taxa identified to species level, including species (marked with an asterisk) recorded from the literature.

ORDER COLEOPTERA

Family Anobiidae

Lasioderma serricornis (Fabricius)

Family Anthicidae

Anthicus crinitus Laferté
Anthicus techowi Pic

Family Apionidae

Corimalia damarensis Marshall

Family Bostrychidae

Enneadesmus forficula Fairmaire
Lyctus brunneus Stephens
Xylion plurispinius Lesne
Xylionulus transvena Lesne

Family Brentidae

Orfilaia vulsellata (Gyllenhal)

Family Bruchidae

Bruchidius senegalensis (Pic)
Caryedon multinotatus (Pic)

Family Buprestidae

Acmaeodera liessnerae Holm
Acmaeodera louwi Holm
Acmaeodera signifera varicolor Boheman
Chalcogenia sculptilis Gory
Chrysobothris dorsata (Fabricius)
Lepidoclema parva Bellamy & Holm

Family Cerambycidae

Acanthophorus capensis White
Crossotus plumicornis Serville
Ossibia prob. *fuscata* (Chevrolat)
Zoodes prob. *liturifer* Walker

Family Chrysomelidae

Trichaspis pilosula (Boheman)

Family Cleridae

Eunatalis parva (Schenkling)

Family Coccinellidae

Brumus nigrifrons Gerstäcker
Chelomenes lunata (Fabricius)
Hippodamia variegata (Goeze)
Nephus whiteheadi Fürsch
Rodolia argodi Sicard
Scymnus levaillantii Mulsant

Family Curculionidae

Leptostethus marginatus Waterhouse
Leptostethus waltoni Waterhouse
Microlarinus lypriformis (Wollaston)
Rhynchaenus nr. *minusculus* Marshall
Sibinia luteoviridis Gyllenhal
Sibinia nr. *micros* Caldara

Family Dermestidae

Attagenus jecundus Péringuey

Family Elateridae

Anchastus granulipennis Lesne

Family Hybosoridae

Hybosorus prob. *illigeri* Reiche

Family Lathridiidae

Melanophthalma capicola Belon
Melanophthalma ophthalmica Dajoz

Family Melyridae

Attalus oberprieleri Wittmer
Attalusinus dentipes Wittmer

Colotes pallidulus Wittmer

Family Nitidulidae

Carpophilus hemipterus (Linnaeus)

Family Passandridae

Hectarthrum prob. *simplex* Murray

Family Ptinidae

Stethomezium nr. *squamosum* Hinton

Family Scarabaeidae

Namibiotalpa fossilis Scholtz & Evans

Family Silvanidae

Oryzaephilus surinamensis (Linnaeus)

Family Staphylinidae

Paederus prob. *sabaesus* Erichson

Family Tenebrionidae

Caenocrypticus peezi Koch
Cauricara prob. *velox* (Péringuey)
Epiphysa arenicola Penrith
Epiphysa punctatissima Penrith*
Leubbertia plana Koch*
Namibomodes zarcoi Koch*
Onymacris rugatipennis albotessellata Schulze
Onymacris rugatipennis rugatipennis (Haag)
Pachynotelus albostrigatus Haag
Pachynotelus lineatus Haag*
Physadesmia globosa (Haag)
Planostibes dentipes Koch*
Psammogaster malani Koch
Rhammatodes aequalipennis Péringuey
Rhammatodes longicornis Haag*
Rhammatodes subcostatus Koch*
Somaticus bohemani (Haag)
Stenocara gracilipes Solier
Stips stali (Haag)
Zophosis devexa Péringuey
Zophosis giessi Koch
Zophosis orbicularis Deyrolle

Family Thorictidae

Thorictus namibensis John

ORDER DIPTERA

Family Mydidae

Namadytes prozeskyi Hesse*

Family Tephritidae

Didacus ciliatus (Loew)
Dioxya sororcula (Wiedemann)
Hyaloctoides semiater (Loew)
Leucothrix barbata Munro
Pardalaspis quinaria Bezzi
Terellia australis (Bezzi)
Terellia xanthochaeta Munro

ORDER GRYLLOIDEA

Family Gryllidae

Brachytrupes membranaceus Drury

ORDER HEMIPTERA

SUBORDER HETEROPTERA

Family Lygaeidae

Dieuches herero Breddin
Engistus hottentotti Slater
Geocoris scutellaris Puton
Hyalochilus scudderii Slater
Leptodemus irroratus Slater
Microspilus kafferensis Slater

Nysius natalensis Evans

Paromius gracilis (Rambur)
Remundiareana horvathi (Reuter)
Spilostethus pandurus elegans (Wolff)

Family Nabidae

Nabis capsiformis Germar

Family Pentatomidae

Bagrada hilaris (Burmeister)
Nezara viridula (Linnaeus)

Family Tingidae

Galeatus scrophicus Saunders

SUBORDER HOMOPTERA

Family Aphididae

Hyalopterus pruni Geoffroy

Family Cicadellidae

Aconurella compta (Naudé)
Aconurella minutissima (Matsumura)
Austroagallia cuneata (Cogan)
Baicalutha hebe (Kirkaldy)
Circulifer tenellus (Baker)
Coloborrhis corticina Germar
Empoascaanara ethiopia Dworakowska
Exitianus nanus (Distant)
Paradorydium quadrigranum (Naudé)
Penthimia vinula Stal

Family Psyllidae

Colposcena australis Hollis
Colposcena namibiensis Hollis
Pauropsylla longipes Hollis

Family Trioziidae

Trioza capensis Hollis

ORDER HYMENOPTERA

Family Agaonidae

Apocrypta longitarsus (Mayr)
Ceratostenes arabicus Mayr
Eukoebelea sycomorae Wiebes
Koebelea gigas (Mayr)
Sycophaga sycomorae (Linnaeus)

Family Anthophoridae

Amegilla niveata (Friese)
Amegilla niveosens (Cockerell)
Braunsapis albipennis (Friese)

Family Aphelinidae

Marietta leopardina Motschulsky
Azotus capensis Howard

Family Apidae

Apis mellifera Linnaeus

Family Bradynobaenidae

Apterogyna schultzei André

Family Chrysididae

Chrysis delicatula Dahlbom
Chrysis stilboides Spinola

Family Dryinidae

Bocchus bini Olmi
Gonatopus johnsi Olmi
Tridryinus ampuliciformis (Turner)

Family Encyrtidae

Adelencyrtus inglisiae Compere & Annecke
Anagyrus amnicus Prinsloo
Cheiloneurus kuisebi Prinsloo

Homalotylus africanus Timberlake
Homalotylus flaminus (Dalman)
Mayridia arida Prinsloo & Annecke
Mayridia maryae Prinsloo
Prochiloneurus aegyptiacus (Mercet)
Psyllaephagus io Prinsloo

Family Eupelmidae
Metapelma rparia Prinsloo

Family Formicidae
Camponotus detritus Emery
Monomorium damarense Forel
Ocymyrmex robustior Emery
Ocymyrmex velox Santschi
Pheidole tenuinodis Mayr

Family Gasteruptiidae
Gasteruption ornaticipes Kieffer

Family Platygasteridae
Synopeas bicolor Sundholm
Synopeas nigerrimus Sundholm

Family Pompilidae
Agenioideus brevis Arnold
Agenioideus decipiens (Bischoff)
Agenioideus gibber (Arnold)
Agenioideus tripartitus Arnold
Agenioideus varians Arnold
Aporinellus trifasciatus Arnold
Arachnotheutes botswanus Wolf
Aplopops ferrugineus Magretti
Ceropales africana Moczar
Ceropales cribrata Costa
Ceropales karoensis Arnold
Ceropales kriebbaumeri Magretti
Ceropales punctulata Arnold
Ceropales waltoni Moczar
Dicyrtomellus rufomemoratus Bischoff
Elaphrosyrus insidiosus Smith
Eoferreola melanostoma Cameron
Evagetes argenteodecoratus Cameron
Hemiceropales ? punctulatus Arnold
Homonotus ? aegyptiacus Radoszkowski
Homonotus dispersus Arnold
Schistonyx atterimus Arnold
Schistonyx ? sinuatus (Bischoff)
Teinotrachellus damarensis Arnold

Family Pteromalidae
Catolaccus crassiceps (Masi)

Family Scelionidae
Breviscelio crenatus Sundholm
Gryon gnidus (Nixon)
Gryon saxatilis (Kieffer)

Family Sphecidae
Miscophus deserticolus Turner
Miscophus fluviatilis Lomholdt
Miscophus oraniensis Brauns
Namiscophus namaquensis Lomholdt
Saliostethus unguilatus Lomholdt
Solierella rhodesiana Arnold
Solierella scrobiculata Arnold

ORDER ISOPTERA

Family Rhinotermitidae
Psammotermes allocerus Silvestri

ORDER LEPIDOPTERA

Family Arctiidae
Utetheisa pulchella (Linnaeus)

Family Ethmiidae
Ethmia ? oculigera (Moschler)

Family Gelechiidae
Grandipalpa robusta Janse
Ornativaiva kalahariensis (Janse)*

Family Geometridae
Rhodometra saccharia (Linnaeus)

Family Lasiocampidae
Concaedes carinata (Wallengren)
Gonometta postica Walker
Sena parva (Aurivillius)

Family Lycaenidae
Azanus jesous jesous (Guérin-Ménéville)
Azanus baldus (Stoll)
Lampides boeticus (Linnaeus)

Family Lymantriidae
Naroma varipes (Walker)

Family Noctuidae
Achaea catella Guenée
Achaea lienardi (Boisduval)
Agrotis ipsilon (Hufnagel)
Agrotis ? segetum (Denis & Schifferrmüller)
Ctenusa varians (Wallengren)
Cyligramma latona (Cramer)
Heliolithis armigera (Hübner)
Heteropalpia cortyoides Berio
Ophiura umbriiinea Hampson
Platysenta conducta (Walker)
Platysenta pauperata (Walker)
Polydesma umbricola Boisduval
Prodotis stolidia (Fabricius)
Raghuva stigmatia Hampson
Sphingomorpha chlorea (Cramer)
Spodoptera exigua (Hübner)
Spodoptera ciliium Guenée
Thria robusta Walker
Ulotrichopus tinctipennis (Hampson)

Family Nymphalidae
Acraea natalica natalica Boisduval
Acraea nohara nohara Boisduval
Danaus chrysippus aegyptius (Schreber)
Hypolimnas misippus (Linnaeus)

Family Pieridae
Belenois aurota aurota (Fabricius)
Catopsilia florella (Fabricius)
Colotis amata calais (Cramer)
Nepheronia buquetii (Boisduval)

Family Pyralidae
Etiella zinckenella (Treitscke)
Euchromius ocellus (Haworth)
Hellula undalis (Fabricius)
Tegostoma comparalis (Hübner)

Family Sphingidae
Agrius convolvuli (Linnaeus)
Hippotion celerio (Linnaeus)
Hyles lineata livornica (Esper)

Family Tortricidae
Cryptophlebia peltastica (Meyrick)

ORDER NEUROPTERA

Family Chrysopidae
Brinckochrysa michaelsoni (Esben-Petersen)
Brinckochrysa turkanensis (Navas)
Chrysoperla zastrawi (Esben-Petersen)
Italochrysa turneri (Kimmins)
Italochrysa vansoni Tjeder
Mallada tacta (Navas)
Suaris jeaneli (Navas)

Family Myrmeleontidae
Centroclisis brachygaster (Rambur)
Creoleon africanus (Rambur)
Creoleon mortifer (Walker)
Golafrus oneili (Péringuey)
Myrmeleon alcestris Banks
Myrmeleon obscurus Rambur
Myrmeleon pallescens (Navas)

Family Nemopteridae
Laurhervasia namibica Mansell

Family Psychopsidae
Silveira jordani Kimmins

ORDER ODONATA

Family Gomphidae
Paragomphus genei (Selys)

Family Libellulidae
Pantala flavescens (Fabricius)
Sympetrum fonscolombei (Selys)
Tholymus tillarga (Fabricius)

ORDER ORTHOPTERA

Family Acrididae
Acrotylus patruelis (Herrich-Schaeffer)
Anacridium moestum (Serville)
Schistocerca gregaria flavescens (Burmeister)

Family Schizodactylidae
Comicus campestris Irish
Comicus capensis Brunner v. Wattenwyl

ORDER THYSANOPTERA

Family Phlaeothripidae
Dolicholepta karneyi (Faure)
Haplothrips nigricornis (Bagnall)
Haplothrips tardus Priesner

ORDER THYSANURA

Family Lepismatidae
Ctenolepisma grandipalpis Escherich
Ctenolepisma terebrans Silvestri
Monomachina schultzei Silvestri