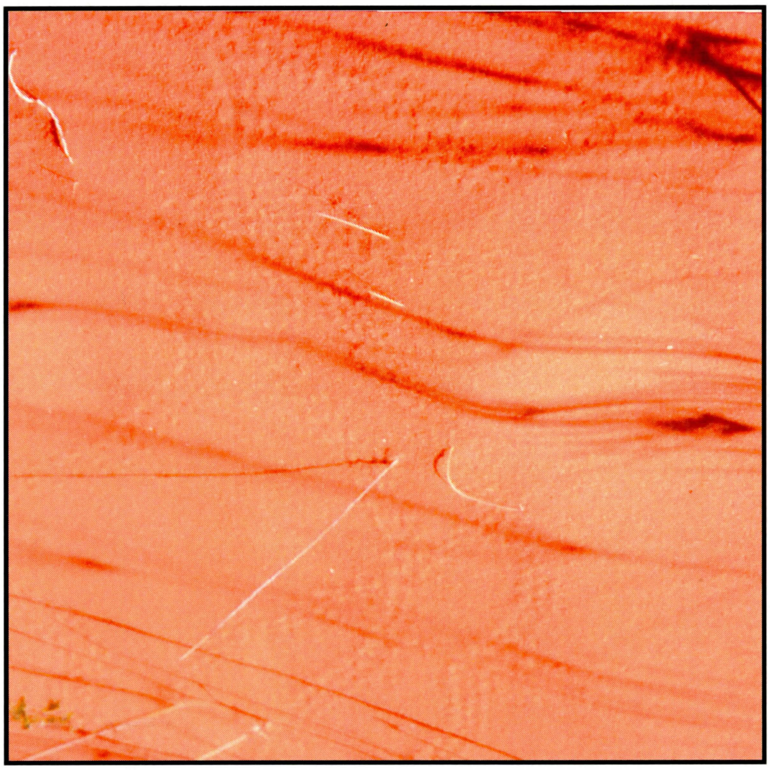
Using insects to evaluate the biogeographic status of isolated dune patches in southern Namibia



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USING INSECTS TO EVALUATE THE BIOGEOGRAPHIC STATUS OF ISOLATED DUNE PATCHES IN SOUTHERN NAMIBIA

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ABSTRACT

Ad hoc sampling by the staff of the National Museum of Namibia indicated that isolated dunes above the escarpment in southern Namibia tend to carry Kalahari-related insect fauna. A comparative study of the psammophilous insects in southern Namibia was conducted with the objective of developing a biogeographical interpretation of the origin, dispersal and survival of the psammophilous fauna of isolated inter-Kalahari-Namib dune patches. By determining whether incidence is related to primary dune fauna presence (*i.e.* survival) on the dune patches or secondary colonization (*i.e.* immigration), reconstruction of the 'pattern and process' of dune fauna vagility scenarios can take place. Since psammophilous insects can be ~~implemented~~ used as sand dispersal indicators, the hypothesis under investigation was whether these isolated dune patches are barchan dunes that ~~got~~ became detached from the modern-day Kalahari Dune Sea, or relicts of a larger palaeo-Kalahari sand mass.

After studying topographical maps, 21 study sites were chosen to be representative of a number of observed lines formed by isolated dunes, or isolated dune clusters, where no line was formed. These study sites ranged from central Namibia, just south of Rehoboth, to the far southern parts of the country, just north of Noordoewer. The five control sites in the main Kalahari were chosen to roughly correspond with the latitudinal setting of the study sites, from central to southern Namibia.

During the fieldwork component of the study, three collecting methods were ~~employed~~ used, *viz.* pitfall trapping, yellow pan trapping and UV light trapping. Traps were not baited, and Monoethylene glycol served as trap preservative. A sand sample was taken at each of the study and control sites (save for the southernmost control site, *viz.* Eenzaamheid). After a 72 hour trapping period, traps were retrieved and the arthropod material was preserved in 70% ethanol. Sorting and identification of the collected material commenced in the laboratory.

Although an array of methods ~~were~~ was used to attain the greatest scope of data, during identification of the material the emphasis was mainly on the extrication of apterous invertebrates, and specifically psammophilous insects.

time
seasons

A total of 27 644 individuals were recorded over the 26 sampled sites, of which 18 277 were of the family Tenebrionidae (66.12%). Eight orders of Arthropoda were recorded, representing 52 families and 184 species. Itaga, the northern-most control site, had the highest species richness (43 arthropod species), while Middelpos (one of the southern-most study sites) had the highest Shannon's diversity index (3.41) and evenness (0.99).

Of the 15 psammophilous species identified and utilized in the analyses, 10 were Tenebrionidae species, three were species of the family Lepismatidae and two were species of the dune cricket family, Schizodactylidae. Employing tenets of Historical and Ecological Biogeography, augmented by some principles of Island Biogeography, psammophile species richness and diversity indices were analyzed for correlation between control sites and study sites. Analyses were performed firstly by comparing sites down specific dune lines or clusters, and secondly according to increasing distance from the main Kalahari Dune Sea. Strong negative correlations were observed down the Konkiep Dune Line, as well as the Maltahöhe and Karas Dune Clusters. Using Sorenson's qualitative index of similarity to sites with regard to psammophilous species richness, it was found that a high similarity exists between the Mukorob and Tses Dune Lines, as well as between some control sites and some sites in the Karas Dune Cluster.

Although a strong correlation exists between psammophilous species diversity of the Kalahari and the isolated dunes, it was concluded that the isolated dunes are, most probably, remnants of a larger semi-arid to arid palaeo-Kalahari dune sea that existed during or just after the breakup of the Gondwana supercontinent. Substratum interconnectivity during glacial maxima probably facilitated later immigrations of Kalahari psammophiles to nearby, flatter areas. The Orange River played a major role by serving as refuge for species survival, as well as being the center from which the Namib ultra-psammophiles and the Kalahari psammophiles speciated.

O.R. + ultra-psammophiles
relationship?

UITTREKSEL

Ad hoc monsterneming deur die personeel van die Nasionale Museum van Namibië het aangedui dat geisoleerde duine bokant die eskarpement in suidelike Namibië geneig is om Kalahari-verwante insek fauna te dra. ‘n Vergelykende studie van psamofiele insekte in suidelike Namibië is uitgevoer met die doelstelling om ‘n biogeografiese interpretasie te ontwikkel aangaande die oorsprong, verspreiding en oorlewing van die psamofiele fauna van geisoleerde inter-Kalahari-Namib duinkolle. Deur te bepaal of voorkoms verwant is aan primêre duin fauna teenwoordigheid (bv. oorlewing) op duinkolle of sekondêre kolonisering (bv. immigrasie), kan die rekonstruksie van “patroon en proses” van duin fauna lewensvatbaarheid scenarios herskep word. Aangesien psamofiele insekte gebruik kan word as sandverspreidings indikatore, is die hipotese ondersoek of hierdie geisoleerde duinkolle barkaan duine is wat afgesny is van die moderne Kalahari Duin See, of slegs relikte is van ‘n groter palaeo-Kalahari sandmassa.

Na deeglike bestudering van topografiese kaarte is 21 studie lokaliteite gekies om verteenwoordigend te wees van ‘n aantal waargenome lyne gevorm deur geisoleerde duine, of geisoleerde duingroepe waar geen lyn gevorm is nie. Hierdie studie lokaliteite strek vanaf sentrale Namibië, net suid van Rehoboth, tot die ver suidelike dele van die land, noord van Noordoewer. Die vyf kontrole lokaliteite in die hoof Kalahari is gekies om rofweg te korreleer met die breedtegraads-verspreidig van die studie lokaliteite vanaf sentrale tot suidelike Namibië.

Gedurende die veldwerk komponent van die studie was drie versamelings metodes gebruik nl. putvalle en geelpanvalle sowel as UV ligvalle. Aas was nie gebruik in die valle nie, en Mono-etileen glukol het gedien as preserveermiddel. ´n Sandmonster is geneem by elk van die studie en kontrole lokaliteite (behalwe vir die mees suidelike kontrole area, *viz.* Eenzaamheid). Na ´n 72 uur valperiode was valle ingesamel waarna materiaal bewaar is in 70% etanol.

Sortering en identifikasie van die versamelde materiaal het in aanvang getree in die laboratorium. Alhoewel ‘n verskeidenheid van metodes gebruik is om die

grootste hoeveelheid data te verkry, was die beklemtoning gedurende identifikasie van materiaal hoofsaaklik op die isolasie van vlerklose invertebrata, en hoofsaaklik psamofiele insekte.

´n Totaal van 27 644 individue is aangeteken in die 26 monsternemingslokaliteite, waarvan 18 277 van die familie Tenebrionidae was (66.12%). Agt ordes van Artropoda is aangeteken, verteenwoordigend van 53 families en 184 spesies. Itaga, die mees noordelike studie gebied het die meeste spesie gehad (43 artropoda spesies), terwyl Middelpos (een van die mees suidelike studie areas) die hoogste Shannon diversiteits indeks (3.41) asook hoogste gelykheid (0.99) gehad het. Van die 15 psamofiele spesies wat geidentifiseer en gebruik is, was 10 Tenebrionidae spesies, drie was spesies van die Lepismatidae familie en twee spesies van die duinkriek familie, Schizodactylidae.

Deur gebruik te maak van die doktrine van Historiese en Ekologiese Biogeografie, aangevul deur sommige beginsels van Eiland Biogeografie, psamofiele insek oorvloed en diversiteits indekse, is daar geanaliseer vir ´n korrelasie tussen kontrole en studie areas. Analises is eerstens uitgevoer deur gebiede met mekaar te vergelyk op spesifieke duinlyne of -groepe, en tweedens na gelang van ´n toenemende afstand vanaf die hoof Kalahari Duinsee. Sterk negatiewe korrelasies is waargeneem op die Konkiep Duinlyn, sowel as die Maltahöhe en Karas Duingroepe. Deur gebruik te maak van Sorenson se kwalitatiewe indeks van ooreenstemming met betrekking tot psamofiele spesie oorvloed, is dit gevind dat ´n hoë ooreenstemming voorkom gekom het tussen die Mukorob en Tses Duinlyne, sowel as tussen sommige van die kontrole gebiede in die Karas Duingroep.

Alhoewel ´n sterk korrelasie gevind is tussen psamofiele spesies diversiteit van die Kalahari en geisoleerde duine, was die gevolgtrekking dat geisoleerde duine heelwaarskynlik remnante is van ´n semi-ariede tot ariede palaeo-Kalahari duin see wat voorgekom het gedurende of net na die opbreek van die Gondwana superkontinent. Substraat verbinding gedurende glasiale maksima het heelwaarskynlik latere immigrasies van Kalahari psamofiele to nabygleë afgeplatte areas vergemaklik. Die Oranjerivier het ´n sterk rol gespeel as ´n

toevlugsoord vir spesies oorlewing, sowel as ´n sentrale gebied vanwaar die Namib ultra-psamofiele en Kalahari psamofiele versprei het.

KEY WORDS

Kalahari, isolated dunes, psammophiles, psammophilous, Tenebrionidae, palaeoenvironment, Namibia, dunes, Namib, palaeo climate

CHAPTER 1

Introduction

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1.1. INTRODUCTION

Many intricacies and controversies exist on the age and the origin of the sands of the Namib and the Kalahari. Intermittently dispersed between these two large sand bodies are a number of isolated dune patches, each one seemingly different in physical character and harboring a distinct assemblage of fauna and flora. The current investigation deals with the analysis of insect distribution patterns to ultimately understand the movement and origin of the isolated dune patches.

This introductory chapter outlines the motivation for the project, which forms part of a greater biogeographical palaeoenvironmental study on the origin of above mentioned dune patches in southern Namibia. Key events that led to the origin of the African continent and modern weather patterns are described, with the aim to establish the significance of the objective, rationale and hypotheses of this dissertation, all of which are discussed in Chapter 2.

The geological origin of the study area is discussed in detail in Chapter 1, while the geomorphological aspects of the individual sites are properly dealt with in Chapter 3.

in more detail

1.2. EARLY STAGES OF THE AFRICAN CONTINENT

During the Early Paleozoic (Table 1.1), southern Africa lay at the center of the Gondwana supercontinent and bordered South America in the west, Antarctica in the east and the Falkland Plateau in the south (Tankard, Jackson, Eriksson, Hobday, Hunter & Minter, 1982).

Table 1.1. Geological Time Scale, adapted from SA Committee for Stratigraphy 2001. (Ma: Millions of annums before the present) * First phase of Gondwana breakup; ** Second phase of Gondwana breakup; *** Origin of modern climate in southern Africa.

Phanerozoic Eon (543 Ma to present)	**Cenozoic Era** (65 Ma to today)	Quaternary (1.8 Ma to today) Holocene 10,000 years to today) Pleistocene (1.8 Ma to 10,000 yrs) Tertiary (65 to 1.8 Ma) Pliocene (5.3 to 1.8 Ma) Miocene (23.8 to 5.3 Ma) Oligocene (33.7 to 23.8 Ma) *** Eocene (54.8 to 33.7 Ma) Paleocene (65 to 54.8 Ma)
	Mesozoic Era (248 to 65 Ma)	Cretaceous (144 to 65 Ma) ** Jurassic (206 to 144 Ma) * Triassic (248 to 206 Ma)
	Paleozoic Era (543 to 248 Ma)	Permian (290 to 248 Ma) Carboniferous (354 to 290 Ma) Pennsylvanian (323 to 290 Ma) Mississippian (354 to 323 Ma) Devonian (417 to 354 Ma) Silurian (443 to 417 Ma) Ordovician (490 to 443 Ma) Cambrian (543 to 490 Ma) Tommotian (530 to 527 Ma)
Precambrian Time (4,500 to 543 Ma)	**Proterozoic Era** (2500 to 543 Ma)	Neoproterozoic (900 to 543 Ma) Vendian (650 to 543 Ma) Mesoproterozoic (1600 to 900 Ma) Paleoproterozoic (2500 to 1600 Ma)
	Archaean (3800 to 2500 Ma)	
	Hadean (4500 to 3800 Ma)	

1.2.1. Gondwana

Topographically, the southern African part of Gondwanaland had an elevated northern interior containing a few fault-controlled basins (e.g. Kalahari and Waterberg), bounded to the south by a broad platform on which the main Karoo Basin was located. The tectonic evolution of this part of southwestern Gondwana affected the palaeogeography and regional climates under which the Karoo Supergroup accumulated. During the Late Carboniferous the southern part of Gondwana drifted over the South Pole resulting in an ice sheet over the highlands (Smith, Eriksson & Botha, 1993). As Gondwana drifted out of polar latitudes, the receding ice sheets left a broad, shallow epicontinental sea on the floor of which offshore muds of the Ecca Group accumulated out of suspension settling. Deltas prograded into the margins of the Ecca sea and eventually combined to form broad alluvial plains on which floodplain deposits of the Beaufort Group were laid down (Smith *et al.*, 1993). During the Triassic, progressive aridification prevailed and the broad alluvial flats of the Beaufort gave way to playa lakes, ephemeral streams and eolian dune fields of the Stormberg Group (Tankard *et al.*, 1982). During this time, the Orange-Vaal drainage system and the Kalahari basin were the control centers of epeirogenic sedimentation (Tankard *et al.,* 1982). Basin-wide volcanic outpourings during the Early Jurassic marked the breakup of Gondwana and the end of Karoo sedimentation.

1.2.2. Breakup of Gondwana

The first phase of the breakup of Gondwana involved separation on the eastern flank of the Mozambique Ridge, 190-160 Ma (Tankard *et al.*, 1982). During the second phase (135-130 Ma) South America and Africa separated and the South Atlantic was initiated (Tankard *et al.*, 1982). Before divergence, the Falkland plateau lay between the African and Antarctic plates, in close proximity to the southern and southeastern margin of South Africa (Figure 1.1). The initial separation between the African and Antarctic plates is believed to have taken place during the Late Jurassic (Tankard *et al.,* 1982). The Falkland Plateau remained with the South American plate and separated from the African plate during the Early Cretaceous (Table 1.1). The movement of the South American, African and Antarctic plates took place at a triple junction, which existed since the Early Paleozoic (Tankard *et al.,* 1982) (Figure 1.1).

1.3. ORIGIN OF MODERN CLIMATE IN SOUTHERN AFRICA

Although Africa and Antarctica finally separated during the Late Jurassic, modern climate and oceanic circulation can only be traced back to the establishment of the Circum-Antarctic Current in the Late Oligocene, after the separation of Antarctica from Australia and the south Tasman Rise (Van Zinderen Bakker, 1975). The latter statement is confirmed, in a sense, by deep sea drilling, which found that Early Oligocene temperatures of deep water were very similar to sea temperatures today (Van Zinderen Bakker, 1975). Although the East Antarctic Ice Sheet only accumulated during the Middle to Late Miocene (Tankard *et al.,* 1982), the environment suitable for desiccation was well underway during the Miocene.

Climate in Namibia is strongly influenced by the existence of two high-pressure cells, namely the South Atlantic and South African anticyclones. The aridity of the Namib Desert is caused mainly by two factors: Firstly, the Cold Benguela current has an aridifying effect on the adjacent coast by condensing moist sea air and forming coastal fog banks (Tankard & Rogers, 1978). Secondly, the South Atlantic anticyclone situated just off of the southwestern Namibian coast, together with the Cold Benguela, causes a southwesterly influx of dry air year round (Lancaster, 1980; Tankard *et al.*, 1978). This effect is weakened in winter when the anticyclone moves in a southwesterly direction, but intensifies in the months between October and April (summer), when a thermal low-pressure cell develops over the northwestern Kalahari (Lancaster, 1980).

It seems that the South African anticyclone has a greater effect on the general climate of Namibia than the South Atlantic high-pressure cell. According to Lancaster (1981), the South African anticyclone moves northward during winter months, strengthens in size and becomes elongated in a NE-SW direction as it centers itself over Mpumalanga (Lancaster, 1980). The anticyclonic fashion of the wind patterns during this time are somewhat reflected in the sand patterns of the fixed dunes of the Kalahari (Figure 1.2), which form a semicircle with a radius of about a 1000 km (Lancaster, 1980).

In winter, winds in Zimbabwe are southeast or easterly, becoming northeast over the central Kalahari and northwesterly over the southern parts. With the southward movement and weakening of the South African anticyclone during summer, warm moist air from the Indian Ocean moves in over the subcontinent, bringing orographic rain to the Kalahari and some parts of Namibia (Lancaster, 1980).

1.3.1. Implication of glacial maxima on arid areas

Although climatic conditions over the South African subcontinent have been relatively stable for thousands of years, the development of such conditions took place gradually and was marked by different phases.

Fluctuations in Antarctic ice sheet deposits and the northern hemisphere glaciations have an influence on a number of factors controlling overall climatic systems. During glacial times, the circum-Antarctic current (which supplies the cold surface water for the Cold Benguela) lowers ocean temperatures and leads to a subsequent northward shift in the Cold Benguela. Although the eastern side of the African continent receives warm, tropical waters, the overall cooling effect of the glaciation affects oceans worldwide (Van Zinderen Bakker, 1975).

Another implication of this global cooling is that the cyclonic winter rains, which currently occur~~s~~ only in the southern Cape, ~~is~~ are extended further inland, which leads to Van Zinderen Bakker's (1975) notion that the southern Namib and the Transitional Namib (between the Olifants and the Orange Rivers) received more rain during these colder periods. Although this is true for the southern part of the Namib, the northern Namib and the Kalahari receives less rain due to a general decrease in evaporation (Tyson, 1986), which could be the cause for the northward extension of the Namib sands. Van Zinderen Bakker (1975) also speculates that these glaciations provided opportunity for contact between eastern arid areas and consequent diversification of arid biota.

It seems that the Late Glacial Maximum (18 000 - 21 000 BP) had a significant northward shifting effect on the Southern Polar Front (Van Zinderen Bakker, 1975). The southern Atlantic Ocean expanded northward as much as 10° in latitude, which in turn shifted the South Atlantic anticyclone in a northward direction and accelerated the aridifying effect of oceanic circulation patterns on the west coast (Tankard *et al.,* 1982).

1.4. SEDIMENTATION

Prevailing wind patterns directly control~~s~~ the movement of sand and dune formation. In the presence of suitable sand-moving winds, formation and mobility of sand dunes depend on the erodibility and erosivity of the sand. (Lancaster, 1980; Thomas & Leason, 2005). Vegetation cover of less than 14%, the position of the vegetation relative to the dune orientation and net soil moisture are all factors that influence the mobility of the dunes (Thomas, Knight & Wiggs, 2005). External sources of sand may include fluvial or deltaic systems, playas or beaches, whilst internal sources may comprise the deflation of interdunes or reactivation of older dunes (Lancaster, 1990).

Irish (1990) and Van Zinderen Bakker (1975) noted that the Namib and the Kalahari should not be considered as two separate entities, but rather as components of the Southwestern Arid Environment. Although rainfall in the Kalahari is highly seasonal and surface water virtually absent during the dry season, the area receives between 550 and 660 mm mean annual precipitation and can thus not be considered true desert country (Thomas and Shaw, 1991).

1.4.1. The Kalahari Semi-arid Biome

The mere existence of fixed dunes in the Kalahari is an indicator of drier spells and their extent (Lancaster, 1980). By comparing fixed and active dunes in the present, shifts in climatic belts and changes in wind regimes can be identified and measured (Tankard *et al.,* 1982). Lancaster (1981) describes the southeastern dunes (the dunes between Mariental and the Orange River) as parallel linear ridges, 5 – 10 m high, with a NW or NNW to SE or SSE alignment (Tyson, 1986) (Figure 1.3). Tankard *et al.* (1982) noted that the dune ridges join in Y-junctions open to the northwest. According to Lancaster (1980), one should not be misguided by the simplified explanations of above described and illustrated general correspondence of dune orientation to modern-day wind regimes.

The occurrence of a number of fixed dunes at an almost perpendicular orientation to mentioned anticyclonic wind regimes can not be considered a mere coincidence. Lancaster (1980) explains that different groups of dunes, although geographically separate, but having similar orientations, may represent similar periods of dune formation under a particular wind regime. Initial Kalahari sand deposition may have taken place in northwestern Botswana dating back to the Tertiary.

Lancaster (1980) identifies three main periods of Quaternary dune formation, *i.e.* arid periods, which ~~is~~ are reflected in three distinct groups of fixed dunes (Figure 1.3). The first of the three groups, *i.e.* the oldest dunes, were formed in northwestern Botswana *ca* 30 000 Ma (Lancaster, 1980). Van Zinderen Bakker (1975) corroborates this proposed age by linking the primary eolian Kalahari sands to the lowering of eastern oceanic sea temperatures during the Oligocene. The second group of dunes, those in northeastern Botswana, was mobile approximately during the Late Glacial Maximum, 18 000 Ma, while the southern Kalahari dunes appear to be the younger of the three groups, with dune activity commencing approximately 12 000 years ago and well into the Holocene (Lancaster, 1980). These southernmost dunes lie south of 23° South and between 18° and 22° East (Stokes, Haynes, Thomas, Horrocks, Higginson & Malifa, 1998).

1.4.2. The Namib Desert Biome

Namib dunes are formed under a coastal wind regime. The barchan dunes between Lüderitz and the Kuiseb River are of a NW-SE orientation in the south, changing to a N-S orientation further north (Lancaster, 1980). Two eminent entomologists, Gebien and Koch (Endrödy-Younga, 1981) argued that the initiation of the Namib took place when the Cold Benguela became closely associated with the west coast of Namibia during the Cretaceous Era. They supported their hypothesis referring to the high level of endemism, specialization and speciation that took place in the Tenebrionidae (Coleoptera) (*cf.* Chapter 2). According to Tankard *et al.* (1978), desiccation in southern Africa took place progressively, commencing in the Late Tertiary and was fully established only in the Quaternary, with the result that the Namib Desert is much more youthful than was originally suspected. Lancaster (1984) confirmed the latter after studies at the Tsondab River where deposits vary from lower gravels and cobbles (evidence of high-energy fluvial systems) to upper sands, silts and clays (low energy fluvial systems) deposited towards the Late Cenozoic.

The Tsondab Sandstone Formation (TSF) represents the first record of terrestrial sedimentation in the central Namib Desert. Ward (1988), although confirming the origin of the Namib to be of Early to Middle Tertiary, suggests that the TSF, which attains a maximum thickness of 220m, entails a Cenozoic arid period preceding the Cold Benguela current (Late Miocene). The latter suggestion implies that the South Atlantic anticyclonic circulation, not the upwelling of the Benguela, would mainly control aridity in this area.

These arguments have been the basis for the dedication of a number of scientists from an array of disciplines attempting to disprove the interpretation of certain evolutionary concepts and subsequent proposal for the extreme age of the Namib.

Two hypotheses on the origin of Namib sands were proposed (Lancaster & Ollier, 1983; Lancaster 1990). The first was by Lancaster (1981), who, following Rogers (1977 in Lancaster 1990), postulated that the sands of the Namib were alluvially transported by and originated from the Orange River. Preliminary estimates of the age of the Namib suggests 50 000 to 100 000 years, based on the amount of sand entering the Namib near Lüderitz. The Auchas and Arrisdrift terrace deposits in the Orange Megavalley raise questions regarding the sand deposition off of the African west coast. Deposition of fossils at these two sites took place as a result of backfilling in the lower reaches of the proto-Orange River Valley during a transgression (Pickford & Senut, 2003). These sea level rises occur during interglacial periods, whilst regressions (sea level falls) occur during polar glaciations (Tankard *et al.,* 1982). During glacial maxima sufficient flow for the proto-Orange River was therefore established to carry vast amounts of sediment towards the ocean. A paradox is created in the sense that, during glacial maxima, the interior of the continent was much drier due to a decrease in oceanic condensation, although the western part of the subcontinent received more cyclonic winter rains, as has been noted in previous paragraphs.

Besler and Marker (1979, in Lancaster, 1990), argued that the Tsondab Sandstone Formation served as source and long-term sand storage unit from where the modern Namib sands had their origin. This hypothesis, however, was proven highly unlikely through various analyses of particle size distribution and grain mineralogy of sands present in the Namib (Lancaster *et al.,* 1983). The sands probably have a much more complicated history than what is currently suspected when considering that during glacial transgressions, wide strips of littoral beach was exposed. These areas, in combination with conditions supporting the increase of weathering and erosion, were favorably located for inland eolian transport of material.

With the evidence presented on climatic conditions, it seems apt to deduce that a palaeoecoline (a gradual transition from one palaeohabitat to another), if not an abrupt palaeoecotone (an explicit boundary between two palaeohabitats) existed between the Namib Desert and the Kalahari Dune Sea during glacial maxima, but probably only after the onset of modern climate in southern Africa.

The possibility exists that, during large glacial maxima, a continuous arid sand-mass or at least interconnected sand bodies, occupied the whole of the interior of the southwestern part of the African continent, whilst the climate of a large part of the southern Namib was temperate and most likely covered by Cape-type flora (Du Pont & Wyputta, 2003; Endrödy-Younga, 1978).

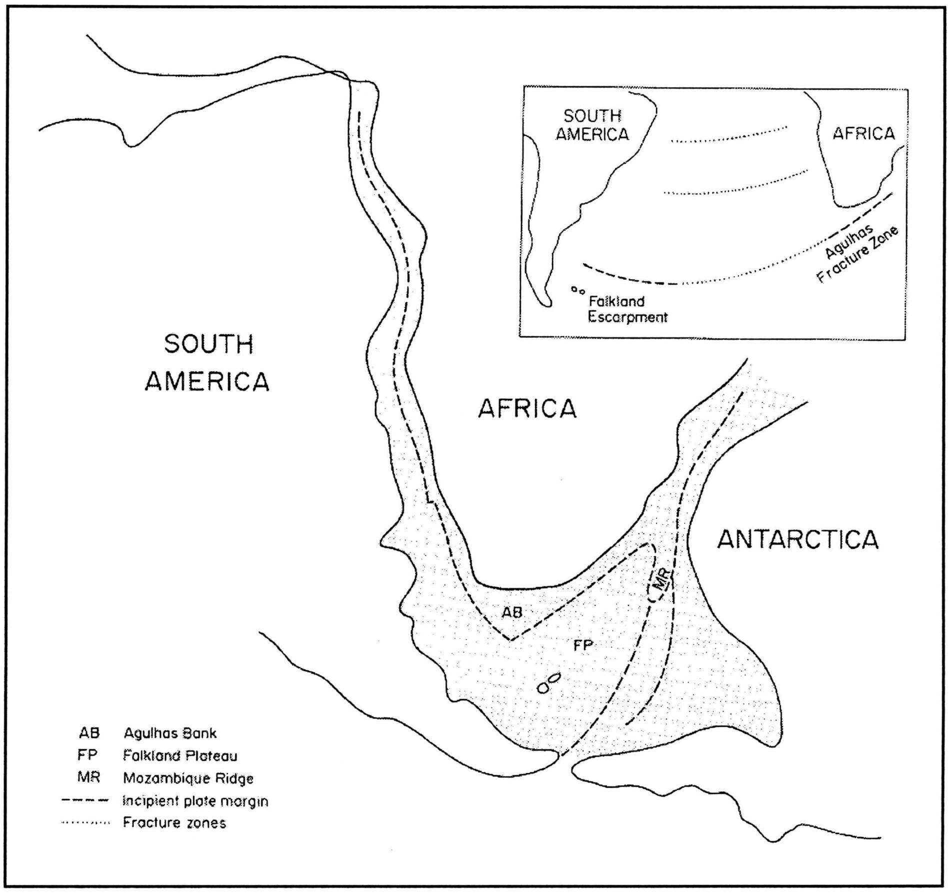

Figure 1.1. Pre-Cretaceous reconstruction of southern Africa within Gondwanaland, and the consequent movement of the plates from a triple junction (Tankard *et al.*, 1982).

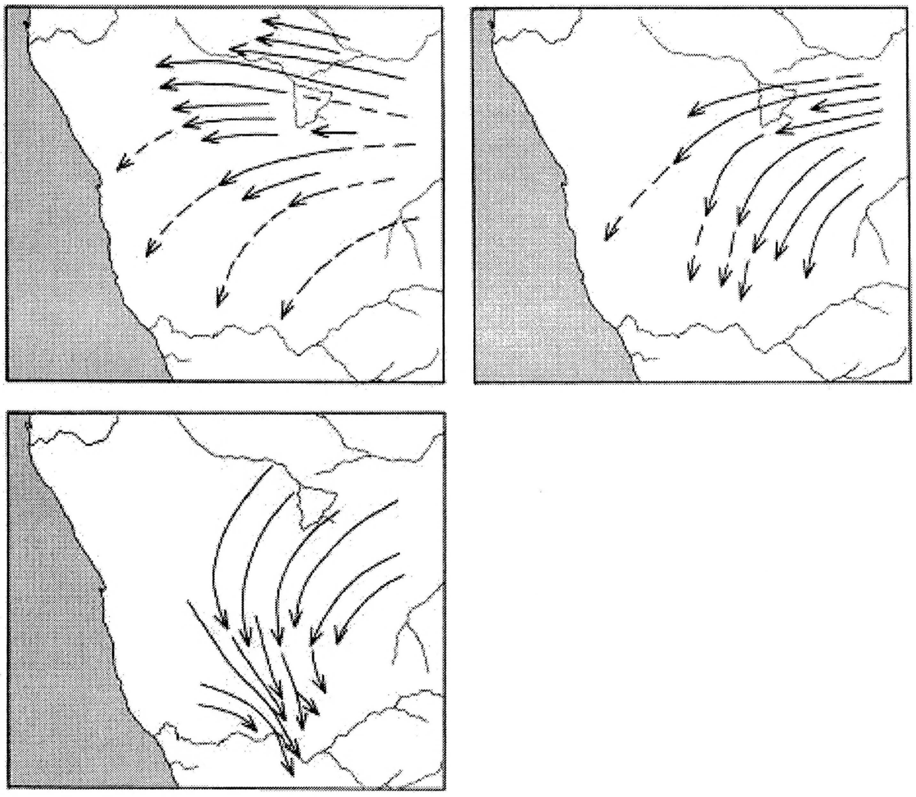

Figure 1.2. Potential sand flow in interior southern Africa as a result of anticyclonic wind circulation (Lancaster, 1980).

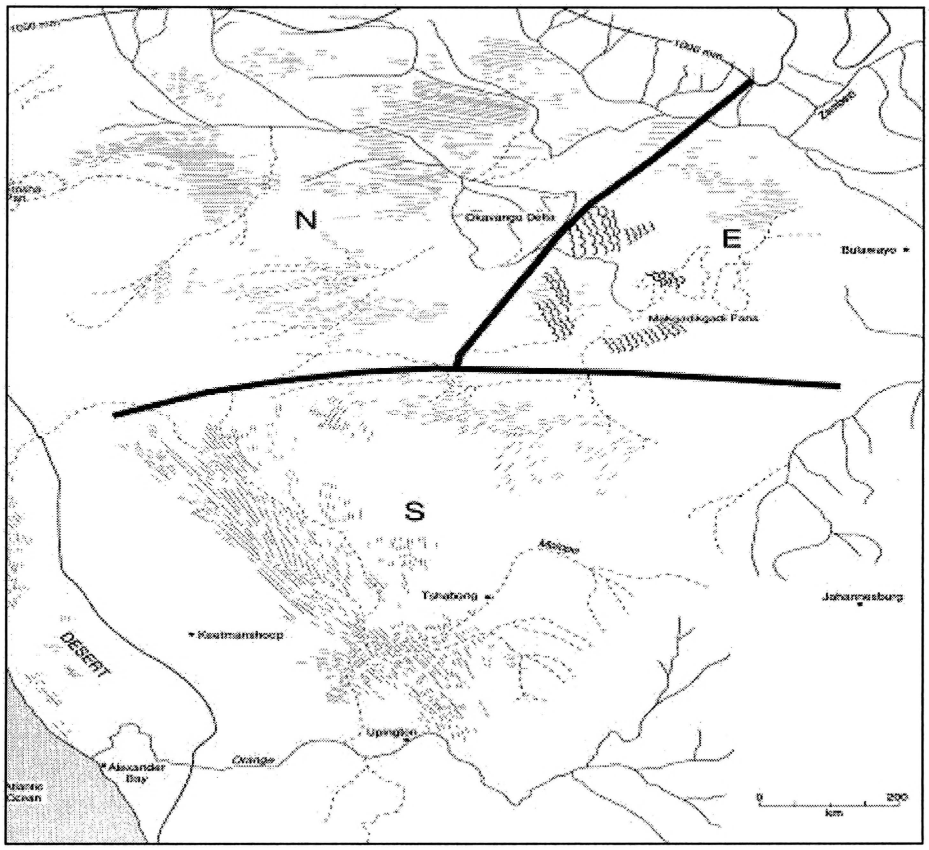

Figure 1.3. Dune alignment in the three major dune fields of the Kalahari, southern Africa. N: Northern dunefield, E: Eastern dunefield, S: Southern dunefield (Thomas & Shaw, 1991).

1.5. REFERENCES

DUPONT M.L. & WYPUTTA U. 2003. Reconstructing pathways of Aeolian pollen transport to the marine sediments along the coastline of SW Africa. Quaternary Science Reviews. **22**: 157-174.

ENDRÖDY-YOUNGA, S. 1978. Coleoptera. Pp 797-823. *In:* Werger M.J.A. (Ed). *Biogeography and ecology of Southern Africa*. Den Haag: Junk.

ENDRÖDY-YOUNGA, S. 1981. The evidence of Coleoptera in dating the Namib Desert re-examined. *Palaeoecology of Africa* **15**: 217-223.

IRISH, J. 1990. Namib biogeography, as exemplified mainly by the Lepismatidae (Thysanura: Insecta). Pp 61-66. *In:* Seely, M.K. (Ed.). *Namib Ecology: 25 years of Namib research. Transvaal Museum Monograph* **7**. Transvaal Museum, Pretoria.

LANCASTER, N. & OLLIER, C.D. 1983. Sources of sand for the Namib sand Sea. *Zeitschrift für Geomorphologie N.F.* **45**: 71-83.

LANCASTER, N. 1980. Palaeoenvironmental implications of fixed dune systems in southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **33**: 327-346.

LANCASTER, N. 1981. Spatial variations in linear dune morphology and sediments in the Namib sand sea. *Palaeoecology of Africa* **15**:173-182.

LANCASTER, N. 1984. Palaeoenvironments in the Tsondab Valley, central Namib Desert. *Palaeoecology of Africa* **16**: 411-419.

LANCASTER, N. 1990. Regional aeolian dynamics in the Namib. Pp. 17-26. *In:* Seely, M.K. (Ed.). *Namib Ecology: 25 years of Namib research. Transvaal Museum Monograph* **7**. Transvaal Museum, Pretoria.

PICKFORD, M. & SENUT, B. 2003. Miocene palaeobiology of the Orange River Valley, Namibia. *Geological Survey of Namibia Memoir* **19**:1-22.

SA COMMITTEE FOR STRATIGRAPHY 2001. *Stratigraphy of Southern Africa*. Council for Geoscience, Pretoria.

SMITH, R.M., ERIKSSON, P.G. & BOTHA, W.J. 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of southern Africa. *Journal of African Earth Sciences* **16**(1/2): 143-169.

STOKES, S., HAYNES, G., THOMAS, D.S.G., HORROCKS, J.L., HIGGINSON, M. & MALIFA, M. 1998. Punctuated aridity in southern Africa during the Last Glacial Cycle: The chronology of linear dune construction in the northeastern Kalahari. *Palaeogeography, Palaeoclimatology, Palaeoecology* **137**: 305-322.

TANKARD, A.J. & ROGERS, J. 1978. Late Cenozoic palaeoenvironments on the west coast of southern Africa. *Journal of Biogeography* **5**: 319-337.

TANKARD, A.J., JACKSON, M.P.A., ERIKSSON, K.A., HOBDAY, D.K., HUNTER, D.R. & MINTER, W.E.L. 1982. *Crustal evolution of southern Africa. 3.8 billion years of earth history*. Springer-Verlag, New York.

THOMAS, D.S.G. & LEASON, H.C. 2005. Dunefield activity response to climate variability in the southwest Kalahari. *Geomorphology* **64**: 117-132

THOMAS, D.S.G. & SHAW, P.A. 1991. *The Kalahari environment*. Cambridge University Press, Cambridge.

THOMAS, D.S.G., KNIGHT, M. & WIGGS, G.F.S. 2005. Remobilization of southern African desert dune systems by twenty-first century global warming. *Nature* **435**: 1218-1221.

TYSON, P.D. 1986. *Climatic change and variability in southern Africa*. Oxford University Press, Oxford.

VAN ZINDEREN BAKKER, E.M. 1975. The origin and palaeoenvironment of the Namib Desert Biome. *Journal of Biogeography* **2**: 65-73.

WARD, J.D. 1988. Eolian, fluvial and pan (playa) facies of the Tertiary Tsondab Sandstone Formation in the central Namib Desert, Namibia. *Sedimentary Geology* **55**: 143-162.

CHAPTER 2

Rationale & Hypotheses

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2.1. INTRODUCTION

Charles Koch (1961, 1962) first introduced the term 'ultra-psammophilous' to refer to ‘organisms loving vegetationless (ultra-desertic) sand' or as 'strictly dune-loving fauna', with the suggestion that these organisms cannot live on the extra-dune sands. The 'philous' termination of the term has the implication that 'ultra-psammophiles’ prefer the loose sandy substrate they live in. Koch further described the feeding ecology of certain ultra-psammophilous tenebrionid beetles. He proposed that these apterous, omnivorous organisms 'depend' on the inclined slopes of the dunes and the action of wind thereupon, which results in the deposition of debris, the main source of food and only source of moisture, specifically metabolic water, for these insects. Koch (1961, 1962) determined that the ultra-psammophiles of the Namib are most likely descendants of a palaeo-stock of xerophilous Tenebrionidae beetles. The latter are very sensitive to change in climate, substrate and vegetation, and also susceptible to geographic and ecological isolation on account of their apterism.

fog?

Endrödy-Younga (1982) later summarized the adaptations of ultra-psammophiles to their sandy habitat, as noted by Koch (1961), and used the term 'hyper-psammophilous'. This referred to both the morphological and behavioral character of the tenebrionid beetles (*e.g.* the manner in which they use their hypertrophic claws to dive into the loose sand to avoid predators), as well as the ecological character of their hyper-arid environment.

Koch (1955, 1962), described the psammophilous character of several lineages of the Tenebrionidae family endemic to the Namib Desert, and noted that there are no ultra-psammophilous tenebrionids in the Kalahari, only plant-followers (Koch, 1961). Hence the term 'psammophilous' only refers to organisms commonly found on and associated with sandy substrates (Penrith, 1984) and has no *bona fide* reference to feeding ecology, life history strategies or means of dispersal.

In later studies, these two terms have been used loosely and without definition, sometimes causing contradiction. Holm (1990) refers to an ultra-psammophilous buprestid genus, *Lepidoclema*. By Koch's definition this would entail a morphological and ecological restriction to sand dunes, but the fact that buprestids can fly confuses the issue. It is therefore assumed that Holm refers to the fact that *Lepidoclema* has never been sampled in environments other than open desert sands and that the life cycle of these insects is dependant on these conditions.

Present knowledge on psammophiles and ultra-psammophiles is largely based on Namib entomofauna, specifically Tenebrionidae lineages, but some reference in the literature is also made to psammophilous members of other orders. In this project the primary focus was on the distribution, ecology and phylogenetic adaptational trends of apterous psammophiles.

The larvae of some families of Neuroptera, such as Myrmeleontidae and Nemopteridae, are commonly found associated with sandy habitats (Mansell, pers. comm). Even though ~~the~~ these groups are winged in the adult phase, the pit-building habit of the larvae of certain genera of Myrmeleontidae, the relatively long lifespan of larvae compared to adults (Mansell, 1985) and their association with sand allows for some justification into investigating the degree of strict psammophily of some species. Irish (1990) discusses the transformation of the more plesiomorphic, xerophilous fish moth and cricket taxa which probably existed during the Gondwana era, into more apomorphic psammophilous genera such as *Ctenolepisma* (Lepismatidae: Thysanura) and *Comicus* (Schizodactylidae: Orthoptera). He furthermore uses plesiomorphic and apomorphic characteristics of psammophilous Namib taxa within these orders to illustrate the progression of hyper aridity in the Namib Desert. Where cited literature on the species employed in this dissertation does not clearly refer to such species as being restricted to Kalahari or Namib related sands, such species will be referred to as secondary psammophiles.

Although the Tenebrionidae fauna of the Kalahari has not been studied as extensively as that of the Namib, Penrith (1984) suggested that an endemic psammophilous element of Kalahari tenebrionids is well developed. She based her opinion on a number of preliminary studies (Penrith, 1984; Louw, 1983; 1986). Endemic lineages of psammophilous Kalahari Tenebrionidae includes genera, subgenera and large species groups of various tribes (Penrith, 1984), while endemicity in the Namib only occurs on subgeneric and lower levels (Louw, 1983).

Irish (1990) supports the suggestion that a Gondwana desert occupied an extended part of the southwestern interior of Africa (*cf.* Chapter 1), but that the climatic conditions were that of arid savanna and not of a true desert. Even though the degree of the aridity of the Gondwana desert is unresolved, climatic conditions allowed for the establishment of a xerophilous insect fauna (Irish, 1990). During times of increased aridity speciation of psammophiles took place (Penrith, 1984) in such a manner that the insects hence forth, even during times when climates were more temperate, preferred the more arid parts of their local environment.

Endrödy-Younga (1978) introduced the concept of pocket-speciation to rationalize how hyperpsammophiles came to inhabit the Namib Desert. He maintained that, during times of increased precipitation, species from a xerophilous ancestral stock (Koch, 1961; 1962) became isolated on sandy 'islands'. With increased aridity and subsequent expansion of the Namib, these species had the pre-acquired advantage of adaptation (Irish, 1990), enabling occupation and domination of their now extended habitat, as the sands of the Namib spread from south to north. It was thus assumed that the sandy islands served as vessels of translocation for psammophilous insects.

Koch based his theory of the Namib being the oldest desert (Koch, 1961) on the relatively high endemicity of psammophilous Coleoptera found in the Namib. In contrast, Penrith (1984) and Irish (1990) suggested that, due to their extreme (pre-acquired) adaptability, the evolution of psammophiles were rapid during aridification and subsequent dune formation. Endrödy-Younga (1978) confirms the latter and adds that no Coleoptera tribe in its entirety is endemic to the barren dunes of the Namib, and that the extreme aridification and consequent expansion of dune systems rather induced the elimination of species than promote speciation.

2.2. RATIONALE & HYPOTHESES

years
seasons

Ad hoc sampling by entomologists (past and present) of the National Museum of Namibia indicated that isolated dunes above the escarpment in southern Namibia tend to carry Kalahari-related insect fauna. With the background of Chapter 1, the implication is that these isolated dunes may either be barchan dunes that were detached from the main Kalahari Dune Sea, or that they represent the relictual remains of a larger palaeo-Kalahari dune sea.

In this study the term 'psammophiles' is used to refer to insects that are sand loving, or as noted otherwise. The adjective 'psammophilous' is used to refer to the morphological adaptations of such insects to be confined to dune sand.

Literature (noted under 2.1) supports the use of psammophiles as indicators of the movement of sand dunes. Analytic examination of the fauna associated with isolated dunes in southern Namibia may provide information to help resolve questions regarding the origin of such isolated dune patches.

Following the basic tenets of logical empiricism (Wiley, 1981), the following two hypotheses are tested for:

H_1: There is a significant statistical difference between the psammophilous species composition of the main Kalahari (serving as the control) and the isolated dunes, which indicates the main Kalahari to have been the source from which the psammophilous insects on the isolated dunes originated.

H_0: No significant difference between the psammophilous species composition of the main Kalahari and the isolated dunes exists.

Covering law: Evolution occurs such that species become adapted to dune sand in such a way that they cannot survive on a substrate with any other character than that of dune sand.

Ancillary principle: The origin and pattern of movement of the isolated dunes can be reconstructed using data generated by the psammophilous insects associated with the isolated dunes.

why elaborate on Namib + then exclude it from consideration?

2.3. BIOGEOGRAPHICAL CONDUITS

Historical Biogeography focuses mainly on extinct taxa, aiming to reconstruct the sequence of origin, dispersion and extinction of species subject to the influence of major abiotic events (such as continental drifting and climatic fluctuations). In Ecological Biogeography, use is made of extant species and their ecological interactions in the present and the recent past to explain distribution patterns (Meyers & Giller, 1988).

Within Historical Biogeography, two approaches exist, *viz.* Dispersal Biogeography and Vicariance Biogeography. Dispersal Biogeography is concerned with the distribution of organisms themselves from a centre of origin over a pre-existing barrier by a process called 'jump dispersal'. Vicariance Biogeography investigates the distribution of unrelated taxa, disregarding their own movement, which became vicariant through common processes (such as continental drift) that brought about barriers. Vicariance Biogeography aims at making deductions about the processes that caused fractionality, by determining and implementing sequences of disjunction of a once continuous biota.

Vicariance Biogeography again has two approaches, *viz.* Panbiogeography and Phylogenetic Biogeography. Croizat (1967, in Meyers *et al.*, 1988) formulated a method using 'dispersal tracks' in Panbiogeography. These tracks combine the origin and distribution history of unrelated taxa, which, plotted together, predicts centers of dispersal of a greater pool of species where such tracks overlap. The Phylogenetic Biogeography approach of Vicariant Biogeography strictly implements the phylogenetic relationship between taxa, in contrast with Panbiogeography where phylogeny plays a secondary role (Wiley, 1981; Meyers *et al.*, 1988).

In the biogeographical analyses to test for the hypothesis of this undertaking, partially combined avenues of Historical and Ecological focuses will be followed. A firm background of historical processes of the larger environment was established in Chapter 1 (Introduction), while a thorough ecological description of the immediate area is discussed in Chapter 3 (Study sites). In Chapter 6 (Analyses), historical detail is provided on the origin and phylogeny of different families, tribes or species, as well as maps of current distribution and reference to the ecological influences.

The following hypothetical scenarios are considered under which the first hypothesis could either be accepted or rejected:

2.2.1. First scenario

A statistical gradient exists between the control sites and the study sites, indicating the main Kalahari to be the origin of the psammophiles, and the first hypothesis is accepted. This can be evident with a reduction in species diversity with increasing distance from the control sites (*i.e.* some psammophilous Kalahari species are absent, no new species are added).

Feasible explanations:

a. Range expansion:

A process by which a taxon expands its distribution across the boundaries of its initial range into an area of favorable ecological conditions over an extended period of time (Meyers *et al.*, 1988).

b. Jump dispersal:

A very rare process whereby one or a few members of a species reach another area with favorable ecological conditions beyond a geographical barrier (Meyers *et al.*, 1988). Jump dispersal will be an option in cases when general patterns indicate range expansion with non-compliance of some sampling sites. In this case, the founder population would be the main Kalahari (*i.e.* control sites), and geographical barriers could include non-perennial rivers, small mountain ranges etc., that subsisted while other isolated dunes were interconnected with each other and the main Kalahari.

2.2.2. Second scenario

Species composition is similar between all the study sites and the control sites, thus the zero-hypothesis is accepted.

Feasible explanations:

Such a scenario would support the null hypothesis (H_0). However, it could also imply that there are certain differences between the species inhabiting the different dune systems, but that insufficient temporal isolation had elapsed for proper speciation to take place. Such populations could then be referred to as biotypes (*i.e.* strains of existing species) (*sensu* Bernays & Chapman, 1994).

2.2.3. Third scenario

No pattern is detectable, with all the study sites statistically differing from each other, as well as from the control sites. The zero-hypothesis is accepted.

Feasible explanation:

a. Mosaic speciation over an extended period of time caused unrecognizable patterns in terms of the original dispersal trends of the insect communities.

b. Species distribution took place in a manner that deviates from the straightforward 'carry' during the movement of sand.

2.2.4. Fourth scenario

Some pattern is detectable, with only some of the study sites statistically resembling each other, and/or the control sites. The zero-hypothesis is accepted.

Feasible explanation:

Vicariance Biogeography: Some pattern might exist which indicates that the origin of the psammophiles were from a source other than the main Kalahari Dune Sea. The psammophilous species originated from (a) greater pool(s) of insects and, following a number of disjunctions in their distribution, became vicariant as a result of the establishment of a number of ecological barriers. Phylogenetic information can either corroborate the observed patterns or contradict them.

2.3. REFERENCES

BERNAYS, E.A. & CHAPMAN, R.F. 1994. *Host-plant selection by phytophagus insects*. Chapman & Hall, New York.

ENDRÖDY-YOUNGA, S. 1978. Coleoptera. Pp 797-823. *In:* Werger M.J.A. (Ed). *Biogeography and ecology of Southern Africa*. Den Haag: Junk.

ENDRÖDY-YOUNGA, S. 1982. Dispersion and translocation of dune specialist tenebrionids in the Namib area. *Cimbebasia* (A) **5**: 257-271.

HOLM, E. 1990. Notes on faunas bordering on the Namib Desert. Pp 55-60. *In:* Seely, M.K. (Ed.) *Namib Ecology: 15 years of Namib research. Transvaal Museum Monograph* **7**. Transvaal Museum, Pretoria.

IRISH, J. 1990. Namib biogeography, as exemplified mainly by the Lepismatidae (Thysanura: Insecta). Pp 61-66. *In:* Seely, M.K. (Ed.) *Namib ecology: 25 years of Namib research. Transvaal Museum Monograph* **7**. Transvaal Museum, Pretoria.

KOCH, C. 1955. Monograph of the Tenebrionidae of Southern Africa. Vol. 1. (Tentyriinae, Molurini – Trachynotina: *Somaticus* Hope). *Transvaal Museum Monograph*. Transvaal Museum, Pretoria.

KOCH, C. 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert. Positive psammotropism in tenebrionid-beetles. *Journal of the South West African Scientific Society* **15**: 8-34 and 77-92 (plates).

KOCH, C. 1962. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* **24**: 61-106 and plates 9-15.

LOUW, S.vdM. 1983. The Diversity and daily and seasonal activity of ground-living Tenebionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. *Cimbebasia* (A) **7**: 35-56.

LOUW, S.vdM. 1986. Periodicity in and ecological equivalence between the ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems with notes on phylogentic relationships. *Navorsinge van die Nasionale Museum, Bloemfontein* **5**: 301-324.

MANSELL, M.W. 1985. Order Neuroptera (Lacewings). Pp 181-187. *In:* Scholtz, C.H. & Holm, E. (Eds.) *Insects of Southern Africa*. Butterworth Publishers, South Africa.

MEYERS, A.A & GILLER, P.S. 1988. *Analytical Biogeography. An integrated approach to the study of animal and plant distributions.* Chapman and Hall, New York.

PENRITH, M-L. 1984. Origin of sand-adapted tenebrionid beetles of the Kalahari. Pp 153-166. *In:* De Graaf, G. & Janse van Rensburg, D. (Eds.) *Proceedings of a Symposium on the Kalahari Ecosystem*, October 1983, Pretoria. Supplement to *Koedoe*.

WILEY, E.O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley & Sons, New York.

CHAPTER 3

Study Sites

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3.1. INTRODUCTION

The Republic of Namibia, formerly know as South West Africa, lies between the 17th and 29th degree latitude and 11th and 21st degree longitude, with the Caprivi Strip occupying a narrow area between the 21st and 26th degree longitude. It is a relatively large country encompassing 824 292 km^2, with a total population amounting to only two people per km^2. The highest point in Namibia is in the Brandberg (2573 m), and the highest peak in the southern part of the country is in the Great Karas Mountains (2202 m). The country has perennial rivers where it borders South Africa in the south (*i.e.* Orange River), and Angola (Cunene in the northwest, Kavango in the northeast), Botswana (Kwando in the southeast Caprivi) and Zimbabwe (Zambezi in the northeast Caprivi) in the north (Schneider, 2004). The rest of the inland rivers only flow after good showers of rain, but often can stay dry for years on end. Namibia has a punctuated rainy season: a shorter season in October and November, and the main season from January to March. As a result of the high temperatures, the evaporation rate for the inland plateau is very high (Schneider, 2004).

The fieldwork component of this study entailed the sampling of 26 distinct sites in a broad east – west band across southern Namibia. Of these, four were situated in the main Kalahari Dune Sea in southeastern Namibia and served as control sites. The remaining 22 sites were chosen after meticulous analyses of aerial photographs that identified the positions of the different isolated dunes. Figure 3.1 depicts some relevant isolated dune patches amid the sand seas of the Namib and Kalahari. The specific sites were chosen where isolated dunes suggested possible linear dispersal tracks. Where no line was obvious, sites were chosen to get the greater coverage of an area in which a number of isolated dunes occur (Figure 3.2.).

season?

Table 3.1 lists all the sites that were studied, along with their Global Positioning System (GPS) references. Sampling of 25 sites took place in 2003. After sorting and quantifying the data the need developed for the re-sampling of the sites Bruinheuwel, Norachas, Middelpos and Haribes in 2004, as well as the sampling of an additional control site (Eenzaamheid) in the far southern part of the Namibian Kalahari Dune Sea.

Map preferred

Table 3.1. Sampled dune lines in southern Namibia, the respective study sites and GPS coordinates.

Dune line/cluster	GPS coordinates
Main Kalahari Line (control sites)	
Wildheim Ost	S26°24’43.1”; E19°35’18.2”
Itaga	S23°46’51.5”; E17°43’17.0”
Middelplaas	S24°16’45.1”; E18°34’03.3”
Vredeshoop	S27°03’17.8”; E19°31’41.8”
Eenzaamheid	S27°41’30.6”; E19°38’15.9”
Mukorob Line	
Habis	S25°52’32.1”; E18°37’02.9”
Dorn-Daberas	S25°34’50.5”; E18°18’47.5”
Goamus	S25°10’10.0”; E18°11’00.0”
Haribes	S24°37’13.4”; E17°32’42.3”
Tses Line	
Averas	S26°27’25.8”; E19°14’48.4”
Tses	S25°55’12.5”; E18°10’54.5”
Kaitzub	S25°12’55.4”; E17°35’57.1”
Lichtenfels	S25°38’36.9”; E17°43’17.7”

Table 3.1. (*continued.*)

Dune line/cluster	GPS coordinates
Maltahöhe Cluster	
Burgsdorf Noord	S25°00’28.8”; E16°53’20.1”
Amhub	S25°20’13.0”; E16°49’27.7”
Kronenhof	S25°29’00.1”; E16°27’24.0”
Karas Cluster	
Donkermodder	S26°53’45.8”; E18°39’23.6”
Verschluss	S26°51’41.1”; E18°23’11.1”
Aikanes	S26°53’10.8”; E18°09’50.9”
Gründorn	S27°26’14.8”; E18°13’39.3”
Oase	S27°13’57.2”; E17°54’28.4”
Konkiep Line	
Sandverhaar	S26°50’55.1”; E17°23’40.4”
Untersee	S26°09’04.2”; E17°14’55.1”
Grünau Cluster	
Middelpos	S28°14’12.7”; E17°51’11.3”
Norachas	S28°03’31.0”; E18°08’21.2”
Bruinheuwel	S28°30’26.8”; E18°09’42.1”

3.2. ENVIRONMENTAL FACTORS

In arid regions insect population dynamics and diversity are affected by numerous environmental factors, some of lesser importance than others. In such regions the majority of species are psammophiles and ultra-psammophiles, the majority of which, in turn, are apterous phytophages and detritivores, thus depending on the dune substratum and vegetation for all their biological processes.

3.2.1. Substratum

Psammophiles are morphologically adapted to occupy a certain habitat with very narrow specifications with regard to substratum, *i.e.* the geological and morphological makeup of the sand they live in. In some cases, the local geology underlying the study dune provides an indication of what can be expected of the mineral makeup of the dune sands. In other cases, where the sand was transported over long distances, the geology surrounding the dune serves as no indicator of dune mineralogy and sand-transport is, in fact, reflected in grain-size analyses and the physical morphology of the dune (J. Irish, pers. comm.).

3.2.1. (a) Geology

In the far southern parts of Namibia, the geology (in small parts of the Orange River Group and Vioolsdrif Suite) dates back to 2000-1800 Ma (Figure 3.3) (*cf.* Chapter 1 for origin of geological strata). Parts of the Namaqualand Complex (1800-1000 Ma) also occur in southern Namibia (Schneider, 2004). A large part of southeastern Namibia lies within the Nama Group (dating back 600 - 540 Ma (Figure 3.3), which can be subdivided into the Fish River Subgroup and the Schwarzrand and Kuibis Subgroups. The Nama Group has a geological makeup of basal quartzites overlain by shale, sandstone and minor limestone. The relatively young Karoo Supergroup (300 – 180 Ma) underlies the largest number of the isolated dunes that were sampled during this study. This Supergroup mainly consists of sedimentary rocks (i.e. sandstones, shales, mudstones and siltstones) with some igneous material in the form of dolerite dykes and sills. The Kalkrand Basalts is the uppermost exposed part of the Karoo Supergroup in southern Namibia, the equal of the South-African Drakensberg Basalts (≈180 Ma), and can be found to the northwest of Mariental (Schneider, 2004).

3.2.1. (b) Sand grain size

Sand grain size provides information regarding the quality of the substrate, *i.e.* the degree of coarseness and fineness of particular bodies or layers of sand. Apterous Coleoptera (especially detritivorous Tenebrionidae) show a definite substratum preference (Louw, 1979). Hypothetically therefore, predictions on species compositions can be made and tested between dunes with similar substrata, by determining sand grain size composition of the sampled dunes and comparing these data with the particular substratum-specific faunal groups sampled.

One sand sample was taken at each study site (*cf.* Chapter 4) and sieved through geological sieves of various mesh-sizes. The results are listed in Table 3.2, represented on bar graphs (Appendix B) and referred to in the text.

Table 3.2. Grain sizes (expressed in percentage) of sands sampled at the isolated dune sites in southern Namibia (2003).

Sieve size (mm)	**2**	**1.4**	**1**	**0.71**	**0.5**	**0.25**	**0.125**	**0.088**	**0.053**	**<0.053**
Itaga	0.02	0.01	0.08	0.68	1.96	64.06	25.47	4.41	3.18	0.21
Middelplaas	0.00	0.00	0.02	0.16	5.95	67.52	22.34	3.00	1.02	0.03
Goamus	0.00	0.05	0.02	0.08	0.99	54.28	31.59	7.70	5.01	0.36
Haribes	0.00	0.01	0.05	0.10	0.27	19.41	63.36	8.11	8.08	0.54
Burgsdorf Noord	0.13	0.02	0.06	0.09	1.08	64.25	25.27	5.30	3.54	0.29
Amhub	0.02	0.01	0.01	0.03	0.57	65.52	26.98	4.83	2.02	0.07
Tses	0.00	0.00	0.03	0.01	0.74	66.51	29.47	2.66	0.57	0.03
Dorn-Daberas	0.01	0.00	0.07	0.06	1.76	66.52	23.15	4.19	3.44	0.79
Habis	0.00	0.01	0.18	3.25	24.03	45.07	16.72	5.05	5.15	0.46
Kaitzub	0.02	0.02	0.07	0.06	0.29	25.42	60.80	8.06	4.93	0.38
Lichtenfels	0.01	0.02	0.05	0.07	0.11	48.35	44.81	5.33	1.22	0.00
Untersee	0.00	0.02	0.03	0.84	10.55	47.64	27.75	6.97	5.62	0.62
Sandverhaar	0.00	0.00	0.00	0.03	0.25	58.52	35.54	4.29	1.24	0.11
Averas	0.00	0.01	0.03	0.04	0.20	50.63	41.26	5.08	2.56	0.27
Wildheim Ost	0.04	0.02	0.05	0.20	4.41	51.43	34.49	4.97	3.71	0.60
Vredeshoop	0.00	0.00	0.02	0.03	0.14	44.72	49.33	4.66	1.16	0.03
Donkermodder	0.03	0.09	0.32	2.45	11.16	42.46	29.43	6.80	6.43	0.64
Verschluss	0.00	0.00	0.01	0.07	0.51	64.94	31.09	2.70	0.54	0.04
Aikanes	0.00	0.00	0.03	0.02	0.21	47.53	46.88	3.62	1.49	0.23
Oase	0.00	0.00	0.02	0.06	1.36	57.02	33.95	4.75	2.55	0.31
Gründorn	0.00	0.04	0.03	0.41	4.30	57.78	28.42	4.87	3.54	0.63
Norachas	0.00	0.00	0.25	3.77	18.79	35.87	21.29	7.63	9.78	2.45
Middelpos	0.00	0.08	1.45	14.55	22.50	27.64	19.46	6.21	7.00	0.96
Bruinheuwel	0.00	0.02	0.08	1.45	17.23	52.30	21.98	4.29	2.45	0.26
Kronenhof	0.00	0.00	0.03	0.12	0.37	64.82	23.94	6.88	3.80	0.10

3.2.1.1. Kalahari Dune Line (control sites)

The control sites are all situated in the Kalahari Dune Sea, and were chosen in such a way as to be representative of the Kalahari dunes furthest west, with a large north to south coverage. All the study sites are named after the farms on which they are situated. A total of five sites were sampled in the main Kalahari namely Itaga (the northernmost control site), Middelplaas, Wildheim Ost, Vredeshoop and Eenzaamheid (the southernmost control site). These dunes all form part of a 'dune tongue system' with an orientation ranging from NNW (Itaga) to WNW (Eenzaamheid) (Appendix A, Figures 1-5).

On the additional site that was sampled only in 2004, a dune on the farm Eenzaamheid, no sand analyses was done. Appendix B, Figures 1-4 depicts the sand grain size distribution of the other four sites, and from the graphs it is clear that all four sites had a very similarly sized sand particle constitution with the largest fraction in the range of 0.25 mm and 0.125 mm. The Vredeshoop site had a slight finer constitution, with the largest part of the sand sample being 0.125 mm in size.

3.2.1.2. Mukorob Dune Line

The northernmost dune line that was sampled is one that lies in a northwesterly direction, almost parallel with the tongues of sand formed by the western flank of the Kalahari Dune Sea. The farm Haribes lies within the top exposed layer of the Karoo Supergroup, *i.e.* the Kalkrand Basalts. The study sites of Goamus and Dorn-Daberas are also situated within the Karoo Supergroup, while the Habis site lies within a large area of Kalahari related sands.

Sampled dunes of Goamus, Habis and Dorn-Daberas also form part of long, continuous dune lines orientated in a northwesterly direction (Appendix A, Figures 6, 7 & 8), while the dunes sampled on the farm Haribes are only small patches of sand located in a local depression (Appendix A, Figure 9).

Dorn-Daberas and Goamus both had a sand grain size distribution with maximum grain fractions in the range of 0.25 mm (Appendix B, Figures 6 & 7), followed by a smaller fraction in the range of 0.125 mm. Habis and Haribes had their maximum grain fractions in the range of 0.125 mm, followed by a smaller fraction in the range of 0.5 mm (Appendix B, Figures 5 & 8).

3.2.1.3. Tses Dune Line

The line formed by the isolated dunes on the Tses line are situated, very similar to the Mukorob line, in a northwesterly direction, but less obviously parallel to the Kalahari tongues (Figure 3.2). Although covered by Kalahari related sands, the sampled site of Tses lies on top of dolerite dykes and sills of the Karoo Supergroup, while Lichtenfels and Kaitzub lie within the Fish River Subgroup. The Averas site is situated within the true Kalahari, bordering on the Fish River Subgroup.

Consistent with many of the sampled dunes, the dunes on the farm Averas are orientated in a northwesterly direction (Appendix A, Figure 10), while the sampling site of Tses formed part of a long dune line, orientated WNW (Appendix A, Figure 11). Both the dunes sampled at the sites of Kaitzub and Lichtenfels are situated in, what appears to be, fossil riverbeds. (Appendix A, Figures 12 & 13).

The sites of Averas and Lichtenfels both had a sand grain size distribution with maxima in the range 0.25 mm and 0.125 mm (Appendix B, Figures 9 & 12), while Tses had a maximum sand fraction in the 0.25 mm range and a smaller fraction in the 0.125 mm range (Appendix B, Figure 10), and Kaitzub a maximum in the 0.125 mm range and a smaller fraction in the 0.25 mm range (Appendix B, Figure 11).

3.2.1.4. Maltahöhe Dune Cluster

Burgsdorf, Amhub and Kronenhof are three distinct dune patches situated closer to the Namib Desert. The Kronenhof dunes are situated beneath the escarpment and the Burgsdorf and Amhub dunes just above it. Geologically, the Amhub site lies within the Fish River Subgroup. While the eastern part of the farm Burgsdorf Noord lies within the Fish River Subgroup, the western part of the farm is situated within the Kuibus and Swarzrand Subgroup (both part of the Nama Group).

The dunes sampled on the farms Burgsdorf Noord and Amhub both lie in what seems like wide fossil riverbeds with a northerly orientated mountainous area directly to the east of the dunes (Appendix A, Figures 14 & 15). The dunes on the farm Kronenhof also lie due west of a mountainous area (escarpment), and in relatively close proximity of a river and its catchment (Appendix A, Figure 16).

The sand grain size distribution of these three sites (Appendix B, Figures 13, 14 & 15), are sorted almost identically, with the largest fraction of the sand being of size 0.25 mm, a smaller fraction being in the range of 0.125 mm and so forth.

3.2.1.5. Karas Dune Cluster

The dune cluster formed by these five sampled sites is comprised of smaller patches of sand that do not form a clear line (Figure 3.2). The farm Donkermodder lies within the Fish River Subgroup, and in the Klein Karas

Mountains. The sampled dune is part of a longer dune line that is divided by a deep river cutting. Furthermore, this dune line lies due west of the Klein Karas Mountains (Appendix A, Figure 17).

The Verschluss study site is also situated in the Fish River Subgroup, and also borders the Klein Karas Mountains to the east (Appendix A, Figure 18). Another site that borders the Klein Karas Mountains to the east is that on the farm Aikanes (Appendix A, Figure 19). The underlying geology of these dunes is sedimentary shale and sandstone of the Beaufort Group, belonging to Karoo Supergroup.

The farm Gründorn lies completely within Kalahari related sands, within a system of dunes that are orientated at right angles from each other, *i.e.* either a northwesterly or a northeasterly direction (Appendix A, Figure 20).

The area around the Oase site is relatively flat (Appendix A, Figure 21), adjacent to a dry fossil riverbed that forms part of the Löwen River catchment system, which passes through the area in close proximity of the sampled site. The area is almost completely situated within the Karoo Supergroup.

According to Appendix B, Figures 17, 19 & 20, Verschluss, Gründorn and Oase all had sand fraction distribution maxima in the 0.25 mm range, with slightly smaller fractions in the 0.125 mm ranges, not dissimilar of many of the other sites sampled. The grain size distribution of the dunes on the farm Aikanes had two peaks of almost similar value in the ranges 0.25 mm and 0.125 mm (Appendix B, Figure 18).

photos?

3.2.1.6. Konkiep Dune Line

Two sites were sampled in the Konkiep sands (Figure 3.1), namely Sandverhaar and Untersee. Both these farms are geologically situated within the Fish River Subgroup of the Nama Group.

The study dune on the farm Sandverhaar again lies directly due west of a mountainous area (Appendix A, Figure 22), while the Untersee dunes lie within a wide riverbed cutting in a mountainous environment (Appendix A, Figure 23).

Almost similar to the sand grain size distribution of Donkermodder, Untersee had a wide distribution between the ranges of 0.71 mm to 0.53 mm, also with a peak at 0.25 mm and a somewhat smaller peak in the range of 0.125 mm (Appendix B, Figure 22). The largest sand fraction of the Sandverhaar dunes is in the size range of 0.25 mm and 0.125 mm (Appendix B, Figure 21).

3.2.1.7. Grünau Dune Cluster

No apparent dune line could be observed from the isolated dunes in this far southern part of Namibia (Figure 3.1), resulting in the random sampling of the three selected sites. These included isolated dunes situated on the farms Middelpos Norachas and Bruinheuwel.

The farm Middelpos lies within the Karoo Supergroup, with intrusive dolerite dykes and sills on the northern and southeastern parts of the farm. Appendix A, Figure 24 shows that, again, the isolated dune that was sampled is situated on the western side of a mountainous area. The sampled dune forms part of a number of dunes in this area, all having a northerly orientation, parallel to one another.

The southeastern part of the farm Bruinheuwel is situated in the Namaqua Metamorphic Province, with the northern and southwestern most parts of the farm overlying the Karoo Supergroup. Like many other sampled dunes, the sampled dune and the other surrounding dunes are orientated due northwest (Appendix A, Figure 26).

The farm Norachas overlies Karoo Supergroup dolerite dykes and sills, with a patch of Kalahari related sands in the northwestern corner of the farm. The dune that was sampled is one in a strip of dunes that lies on the leeward side of a mountain, forming a 'sand band', more or less orientated in a northwesterly direction (Appendix A, Figure 25).

Sand grain sizes on both the farms Bruinheuwel and Norachas had an even distribution between the sizes 0.71 mm and 0.53 mm, with the largest fraction in the size range of 0.25 mm (Appendix B, Figures 24 & 25). Observed dune sand on the farm Middelpos appeared much coarser, compared to other sites, and this is reflected in Appendix B, Figure 23, which shows that the Middelpos site is the only one that had a fraction of the total sand sample grain size composition in the 1 mm range.

3.2.2. Vegetation

Dune vegetation cover serves as shelter for diurnal insects due to temperature extremes in these sandy environments. Rainfall and general climate are two primary environmental factors that determine the composition of dune vegetation, other than the geology and geomorphology of the area.

Irish (1994) identifies four different biomes (excluding the Etosha basin) in Namibia, based on dominance or co-dominance of different plant life forms (Figure 3.4).

The relevant Namibian biomes are categorized as follows:

Desert biome: Therophytic dominance
Succulent Karoo Biome: Chamaephytic dominance
Nama-Karoo Biome: Chamaephytic-hemicryptophytic co-dominance
Savanna Biome: Phanerophytic-hemicryptophytic co-dominance

Figure 3.4 depicts the two biomes relevant to this study namely the Nama-Karoo and Savanna Biomes, wherein the totality of the study sites are located.

3.2.2. (a) Savanna Biome

The Kalahari ecosystem has been ascribed many a nametag, with the criteria for each being grossly diverse. Louw & Seely (1982) refer~~s~~ to the Kalahari as an edaphic desert, where a deep layer of sand prevents the accumulation of surface water, even though precipitation would permit a more lavish plant community. Lovegrove (1993) confirms this and in addition ascribes the lack of accumulation of surface water to the regular, localized, rapid but violent thunderstorms that the Kalahari experience.

Irish (1994) includes the Kalahari in his classification of the Savanna Biome. Furthermore, Giess (1971, in Brown, Macdonald & Brown, 1985) subdivides the Savanna Biome according to isohyets, with Mixed Tree and Shrub Savanna between 200 mm and 300 mm, Camel thorn Savanna between 300 mm and 400 mm and Woodlands and Forest Savanna between 400 mm and 500 mm in the far north of the country. This dissertation abides by the methodology of objective biome categorization used by Irish (1994).

Source of rainfall data?

3.2.2. (b) Edaphic Savanna

Irish (1994) discussed two factors that would cause vegetation to differ from what would be expected in a certain area, based on the local climate. These two factors are edaphic factors, namely (a) shallow impervious layers, and (b) sandy substrates. The latter is applicable to the remainder of the 22 study sites not situated in the true Kalahari.

The effect of the sandy substrates on dominant vegetation types can again be related back to the amount of rainfall received in that specific area (Irish, 1994), as illustrated by Table 3.3. The water holding capacity of the sand of a specific area is influenced by the size of the grains. Because there is less runoff, coarse sand (of more arid parts) generally retains water better than finer soils. More water can filter into coarse sand, which leads to weaker capillary forces and consequently less evaporation. Although these sands are less fertile, plants that grow in it have more water at their disposal (Van der Walt & Le Rich, 1999).

Table 3.3. The edaphic effect of deep sand on life form dominance in different biomes. Phanerophytes usually refer to trees, chamaepytes to shrubs and hemicryptophytes to perennial grass (Irish, 1994).

	Dominant plant life forms	
Biome	**Normal**	**Deep sand / dunes**
Savanna	Phanerophytes & hemicryptophytes	Phanerophytes & hemicryptophytes
Nama-Karoo, higher rainfall	Chamaephytes & hemicryptophytes	Phanerophytes & hemicryptophytes
Nama-Karoo, lower rainfall	Chamaephytes & hemicryptophytes	Hemicryptophytes

Dunes in the southern Kalahari extend the Savanna Biome well into an area with Nama-Karoo climate, as is the case for the sampled sites of Wildheim Ost and Eenzaamheid. In the drier far southern part of the Nama-Karoo Biome, savanna vegetation is restricted to dunes, with the wide inter-dune valleys still supporting normal dominant groups of chamaephytes and hemicryptophytes. As rainfall increases eastward, savanna vegetation encroaches on the inter-dune valleys.

The rainfall of the complete study area in southern Namibia is summarized in Figure 3.5, whilst the rainfall and vegetation types occurring across each dune line is discussed separately below.

3.2.2.1. Kalahari Dune Line (control sampling sites)

Of the five control sites, the farm Eenzaamheid receives the least average annual rainfall (100 mm – 150 mm), while Vredeshoop and Wildheim Ost receive about 150 mm – 200 mm rain a year (Figure 3.5). Itaga annually receives about 200 mm rain, and Middelpos 200 mm+ (Figure 3.5).

Rainfall during the sampling period was restricted to a thunderstorm in the Eenzaamheid area in 2004, preceding the placement of traps, as well as 3 mm rain in the Itaga area on the 3rd day of the three-day sampling period during 2003.

Itaga, Middelplaas and Vredeshoop are the only control sites that that truly lie within the Savanna Biome. The sites of Wildheim Ost and Eenzaamheid were included as control sites, since these closely border and totally resemble the characters of the described area. These two sampling sites are situated on the long northwest/southeasterly orientated dunes of the southern Kalahari that extend into the Nama-Karoo Biome (*sensu* Lovegrove, 1993).

The dune vegetation of these five sites was observed to be homogenous, save for minor differences aberrations at some sites caused by recent rain. Consistent with the Savanna Biome classification, dune vegetation at these sites included *Acacia erioloba* (camel thorn), *A. haematoxylon* (gray camel thorn), *A. mellifera* (black thorn), *Boschia albitrunca* (shepherd's tree) and *Rhigozum trichotomum* (driedoring shrub). Hemicryptophytes were mainly species of *Stipagrostis* and *Eragrostis.* Kalahari Dune grass (*Stipagrostis amabilis*), a successful colonizer of unstable dune tops and endemic to the Kalahari (Van der Walt & Le Rich, 1999), was a very prominent feature of the dunes sampled as control sites (Figure 3.6). The Wildheim Ost study dune had a canopy dominated by grass with ~~less~~ fewer trees and shrubs, with the opposite in the case for Itaga. Middelplaas had grass debris covering the study dune, accompanied by a number of *Acacia* species, with vegetation at the Vredeshoop site being dominated by *S. amabilis,* with sparse *Acacia* trees.

3.2.2.2. Mukorob Dune Line

The study sites Habis, Dorn-Daberas and Goamus occur in the vicinity of the 150 mm isohyet (Figure 3.5), while the northwestern most site on this dune line, Haribes, annually receives an average of approximately 200 mm rainfall (Figure 3.5).

The Dorn-Daberas site was densely vegetated with *S. amabilis* and plenty of grass debris covering the entirety of the dune (Figure 3.7). A number of *Acacia* shrubs such as *A. mellifera* were also noted. *Acacia* shrubs dominated the study site of Habis, with sparse grass cover occurring on the dune (Figure 3.8). The Haribes dunes were also densely vegetated by shrubs such as *R. trichotomum*, with only a little grass cover. This dune was frequented by cattle, which grazed in the area.

Although the inter-dune valleys on the Goamus farm had thick foliage of perennial grass and trees, the study dune was sparsely covered with grass and an occasional shrub.

3.2.2.3. Tses Dune Line

All four of the study sites on the Tses Dune Line receive an annual average rainfall of about 150 mm a year, save for Averas that lies between the isohyets of 150 mm – 200 mm (Figure 3.5).

Many *Acacia* (*A. erioloba* and *A. haematotoxylon*) and *Boschia albitrunca* trees, *R. trichotomum* shrubs (Figure 3.9), and a fairly dense grass cover (*S. amabilis*) were present at the Averas sampling site. The dune on which sampling was done is in close proximity of a rural gravel road, and sheep grazed on the dune and in the area. Vegetational cover of the dunes at Lichtenfels and Kaitzub was peculiar and didn't resemble that of any other of the studied dunes. These dunes are situated in continuous flat areas that become flooded during the occasional thunderstorms in the area, which suggested that the dunes are more likely to be source-bordering dunes receiving input from alluvial sands. The dunes were sparsely covered with shrubs, and lacked the characteristic *Eragrostis* and *Stipagrostis* grasses of the Kalahari dunes. The Tses study site boasted a diversity of *Acacia* trees, *R. trichotomum* shrubs and a dense cover of *Eragrostis* grass.

3.2.2.4. Maltahöhe Dune Cluster

Both the Amhub and Kronenhof sampling sites receive on average 150 mm rain per annum, whilst the Burgsdorf Noord sampling site receives and annual average rainfall between 150 mm and 200 mm (Figure 3.5).

photos

The dune sampled on the farm Amhub had vegetation consisting of a fair amount of Acacia shrubs such as *A. hebaclada* in particular, and a number of *R. trichotomum* shrubs. Cattle on the farm had extensively grazed upon the once-dense grass cover, and plenty of grass debris was noted.

Save for a few *Boschia albitrunca* trees, the Kronenhof sampling dunes were completely covered with perennial grass and grass debris (Figure 3.11). Although the dune is situated in a camp used for sheep grazing, the animals never fed on the grass on the dunes, evident from the short stubs of grass in the inter-dune valleys and the undamaged grass on the dune crests.

The dune that was sampled on the farm Burgsdorf Noord was also used for sheep grazing, but the dune vegetation consisted of only sparse clumps of grass, no trees or shrubs, and very little debris.

3.2.2.5. Karas Dune Cluster

The entirety of the 5 dunes sampled on the Karas Dune Line falls in an area receiving 100 mm – 150 mm of rain on average a year (Figure 3.5).

The study dune on the farm Gründorn demonstrates strong hemicryptophytic dominance with plenty of *Stipagrostis* and other grass covering the dune crest, and a few *Boschia albitrunca* trees and *Acacias* along the lower part of the dune slope.

Euphorbia shrubs were prominent on the study dune and the surrounding area on the farm Oase, with small patches of *Stipagrostis* and a few scattered *R. trichotomum* shrubs. Vegetation on the Aikanes dunes was almost absent, save for a few clumps of *S. amabilis* and a few *Euphorbia* shrubs, while the study site of Verschluss displayed a wealthy grass cover supplemented with few *Acacia* trees and *Euphorbia* shrubs. The sampled dune is situated within a camp occasionally used for sheep grazing, resulting in grass debris scattered over the dune and a more sparsely vegetated inter-dune valley (Figure 3. 12). Similar to the Aikanes dunes, the dune sampled on the Donkermodder farm is a patch of sand where the modest vegetation was limited to a few clumps of dune grass.

3.2.2.6. Konkiep Dune Line

The farm Sandverhaar lies in an area annually receiving 100 mm – 150 mm rain, while Untersee, north of the town Bethanie annually receives about 100 mm (Figure 3.5). Vegetation on the Sandverhaar sampling dune was dominated by *Stipagrostis amabilis*, and *Acacia erioloba* dominated the inter-dune valleys (Figure 3.13). The Untersee study site received substantial amounts of rain in the weeks prior to sampling, and a dense dune cover of a *Tribulus* sp. (Zygophyllaceae) as well as perennial grasses distinguished these dunes from all the other study sites (Figure 3.14). Only a few *Acacia* trees and shrubs were noticed in the immediate vicinity of the site.

3.2.2.7. Grünau Dune Cluster

The southernmost sampling sites, namely Norachas, Bruinheuwel and Middelpos all lie in an area receiving very little rain (50 mm – 100 mm average per year) (Figure 3.5), and none received any rain preceding sampling in both 2002 or 2003.

The three sites were all completely dominated by grass spp., complying with the expected vegetation dominance of lower rainfall areas of the Nama-Karoo (Table 3.3). Grass debris was ample on the Norachas (Figure 3.15) and Bruinheuwel dunes, and although overall vegetation and debris was not sparse at the Middelpos site (Figure 3.16), the veld was in poor condition. Veld fires in 1991 damaged a large part of the Middelpos farm, including the study dune, and recovery is still sluggish due to the lack of rain (Mr. Aggenbach, pers. comm.). Louw (1979) is of the opinion that fire is as an important factor for insect community structure as rainfall, soil and temperature. In the hope of obtaining samples of greater diversity, re-sampling was conducted on the same dune in 2004, but conditions were the same, if not worse.

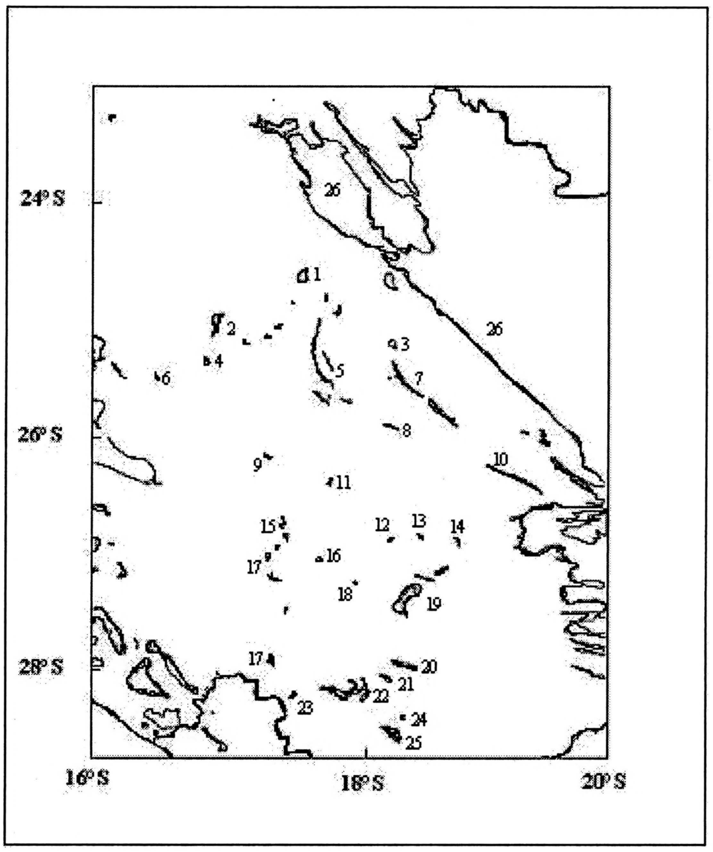

Figure 3.1. Isolated sand dunes in southern Namibia. (1: Haribes Basin; 2: Daweb-Burgsdorf; 3: Goamus; 4: Amhub; 5: Lewer/Fish dunes; 6: Kronenhof-Ginas dunes; 7: Daberas-Mukurob dunes; 8: Tses dune; 9: Untersee; 10: Kuubmaams dune 11: Gavaams dunes; 12: Aikanes dunes; 13: Verschluss dunes; 14: Donkermodder dunes; 15: Sandverhaar dunes; 16: Koubisberg; 17: Konkiep dunes; 18: Holoog; 19: Klein Karas dunes; 20: Grünau South-west dunes; 21: Norachas dunes; 22: Bloukrans-Ysterputs dunes; 23: Onder-Gamkab + Aussenkehr dunes; 24: Pollux; 25: Soekwater; 26: Contiguous SE-NW orientated sand dunes of the Kalahari)

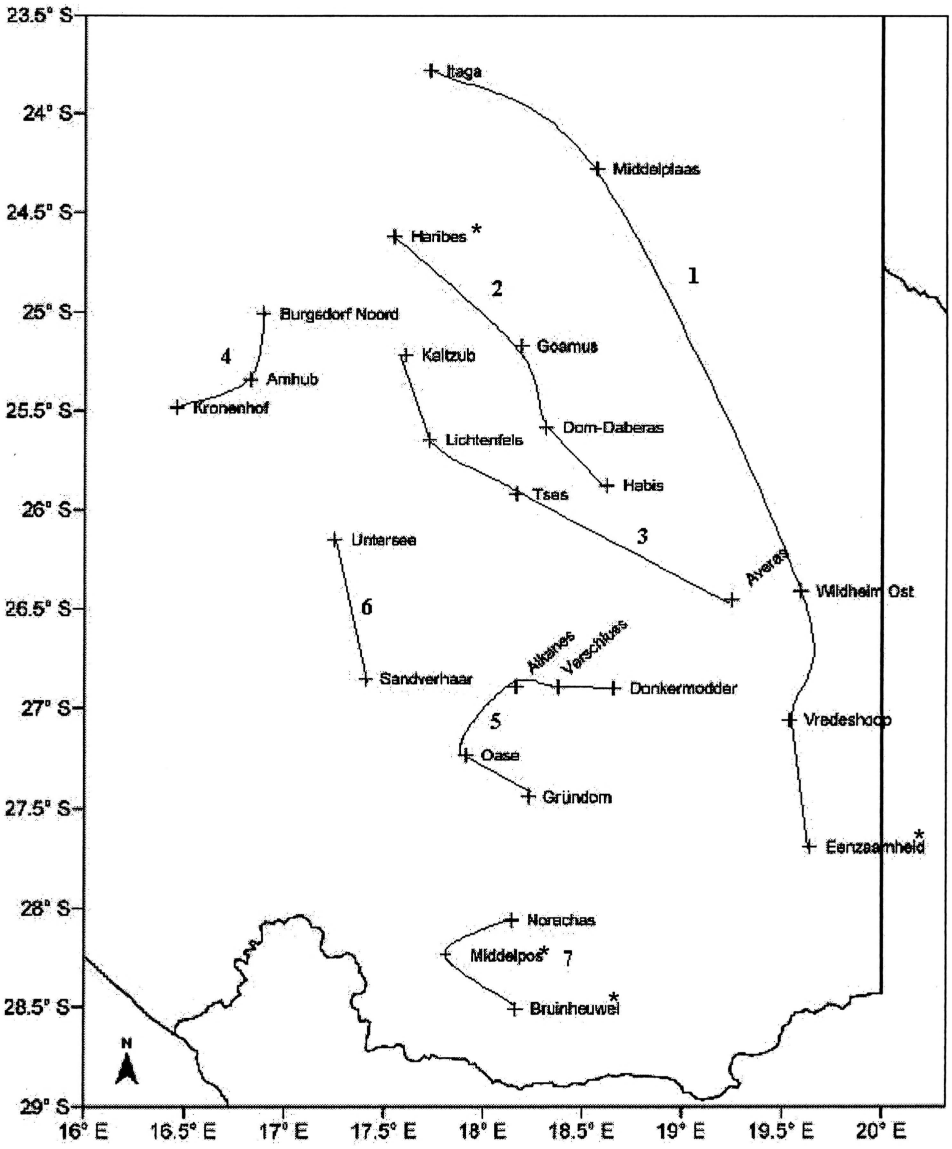

Figure 3.2. Study sites in southern Namibia. 1. Main Kalahari Dunes; 2. Mukorob dunes; 3. Tses dunes; 4. Maltahöhe dunes; 5. Karas dunes; 6. Konkiep dunes; 7. Grünau dunes.* Sites sampled or resampled in 2004.

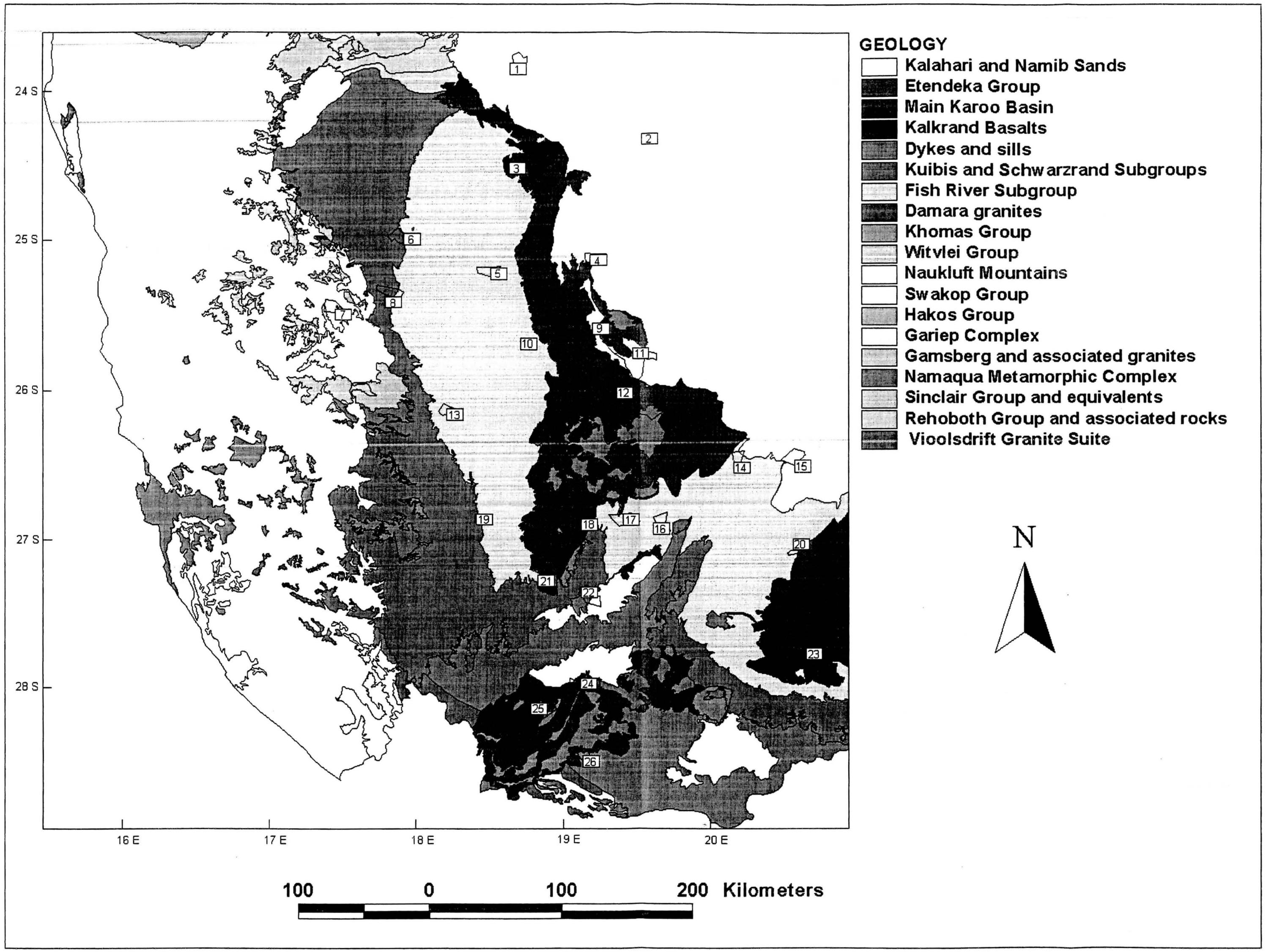

Figure 3.3. Geological map of southern Namibia. 1: Itaga, 2: Middelplaas, 3: Haribes, 4: Goamus, 5: Kaitzub, 6: Burgsdorf Noord, 7: Kronenhof, 8: Amhub, 9: Dorn Daberas, 10: Lichtenfels, 11: Habis, 12: Tses, 13: Untersee, 14: Averas, 15: Wildheim Ost, 16: Donkermodder, 17: Verschluss, 18: Aikanes, 19: Sandverhaar, 20: Vredeshoop, 21: Oase, 22: Gründorn B, 23: Eenzaamheid, 24: Norachas, 25: Middelpos and 26: Bruinheuwel.

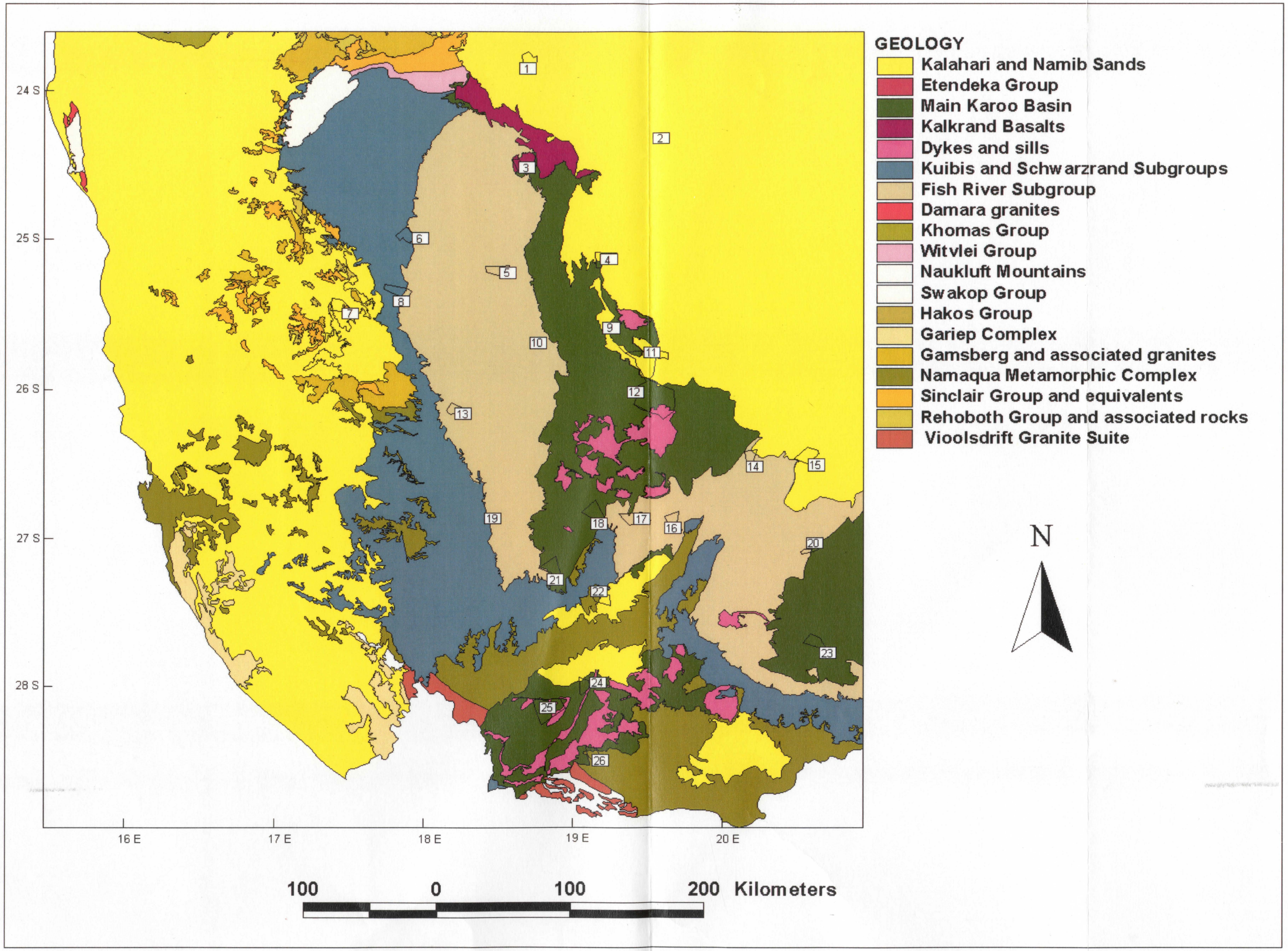

Figure 3.3. Geological map of southern Namibia. 1: Itaga, 2: Middelplaas, 3: Haribes, 4: Goamus, 5: Kaitzub, 6: Burgsdorf Noord, 7: Kronenhof, 8: Amhub, 9: Dorn Daberas, 10: Lichtenfels, 11: Habis, 12: Tses, 13: Untersee, 14: Averas, 15: Wildheim Ost, 16: Donkermodder, 17: Verschluss, 18: Aikanes, 19: Sandverhaar, 20: Vredeshoop, 21: Oase, 22: Gründorn B, 23: Eenzaamheid, 24: Norachas, 25: Middelpos and 26: Bruinheuwel.

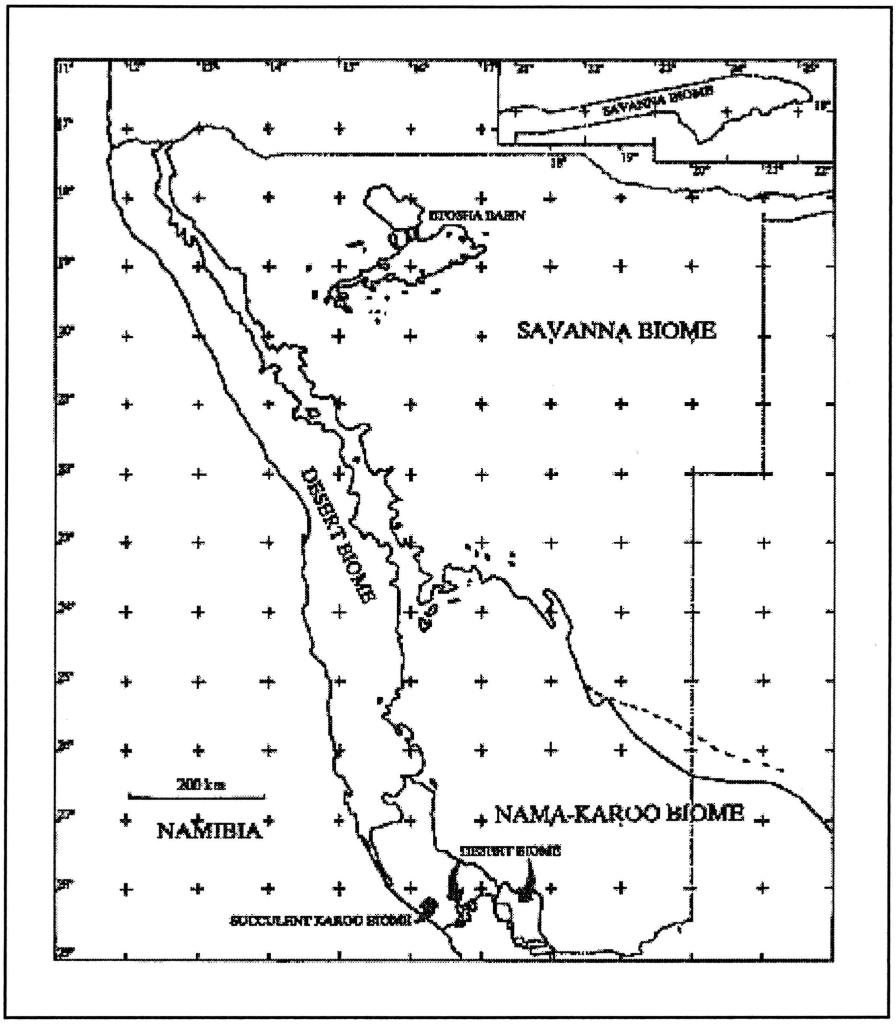

Figure 3.4. Biomes of Namibia (Irish, 1994).

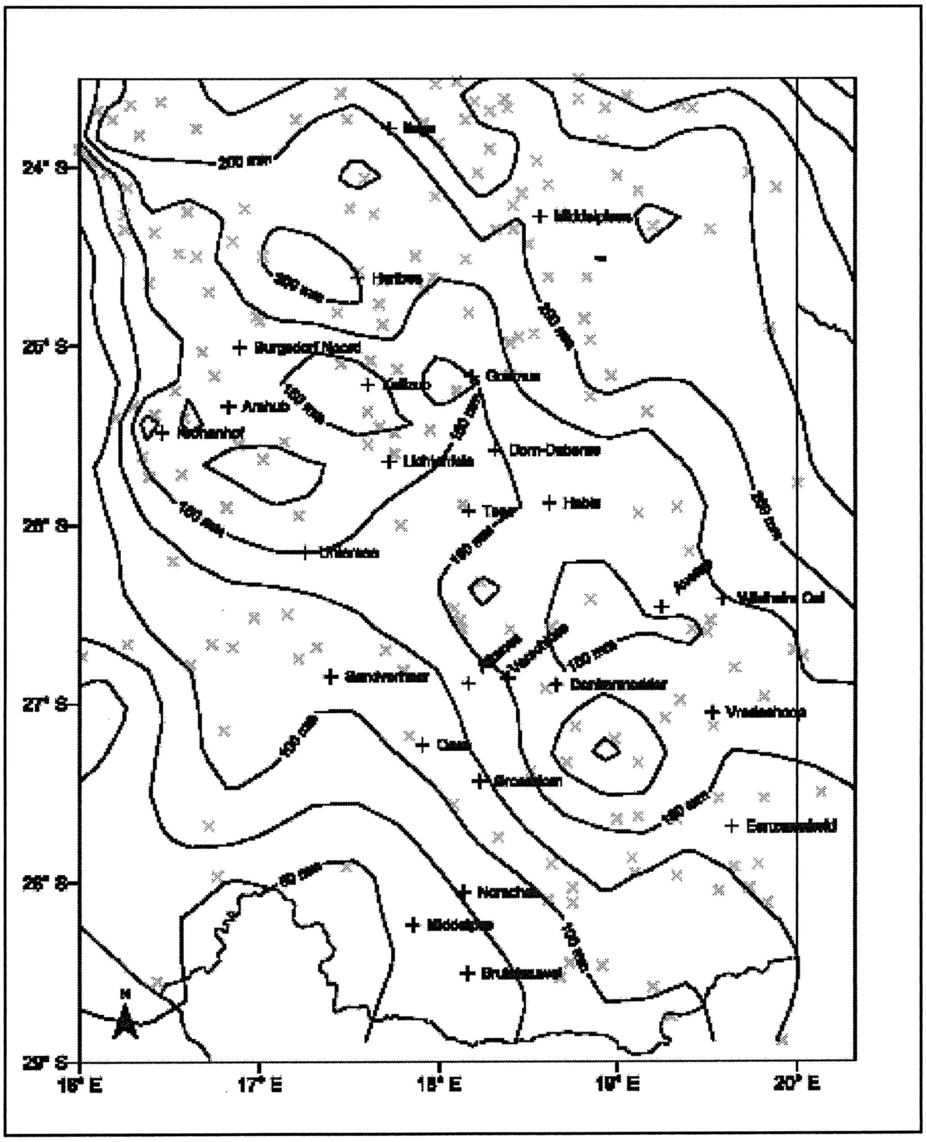

Figure 3.5. Precipitation (isohyets) at various study sites in southern Namibia. (Prepared by J. Irish from data supplied by the Namibian Meteorological Services.)

Figure 3.6. Wildheim Ost study site, featuring *Stipagrostis amabilis* and *Acacia haematoxylon* (April, 2003).

Figure 3.7. Typical Kalahari vegetation, including *Acacia mellifera*, at the Dorn-Daberas study site (April, 2003).

Figure 3.8. Habis study site vegetated by shrubs and some *Acacia* trees (April, 2003).

Figure 3.9. *Rhigozum trichotomum* shrubs and *Acacia erioloba* trees at Averas study site (April, 2003).

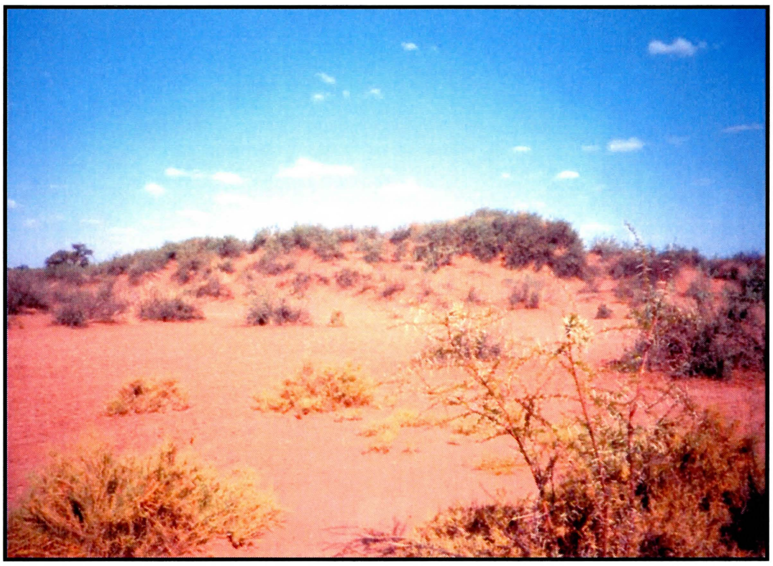

Figure 3.10. Kaitzub study site with vegetation uncommon to Kalahari dunes (April, 2003).

Figure 3.11. Dense grass cover and *Boschia albitrunca* trees at the Kronenhof study site (April, 2003).

Figure 3.12. Sparsely vegetated inter-dune valley at the Verschluss study site (April, 2003).

Figure 3.13. Sandverhaar study site where dunes are primarily covered with *Stipagrostis amabilis* grass.

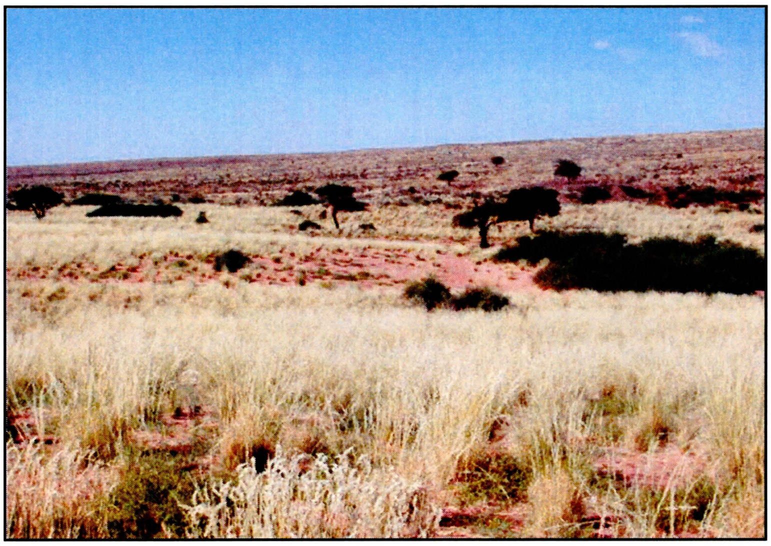

Figure 3.14. Dense perennial grass cover at Verschluss study site (April, 2003).

Figure 3.15. Grass and small shrubs covered dunes on Norachas farm (April, 2003).

Figure 3.16. Middelpos study site (April, 2003), visibly affected by drought after fire damage in 2002.

3.3. REFERENCES

BROWN, C.J., MACDONALD, I.A.W., & BROWN, S.E. 1985. Invasive alien organisms in South West Africa/Namibia. *South African National Scientific Programmes Report.* **119**: 1-74.

IRISH, J. 1994. The biomes of Namibia, as determined by objective categorization. *Navorsinge van die Nasionale Museum, Bloemfontein.* **10**(13): 550-592.

LOUW, S.vdM. 1979. *Ecological equivalence and phylogeny of Tenebrionidae (Coleoptera) as indicators of the connection between Namib and Kalahari dunes.* Unpublished M.Sc Thesis, University of Pretoria, Pretoria.

LOUW, G.N. & SEELY, M.K. 1982. *Ecology of desert organisms.* Longman Group Limited, London.

LOVEGROVE, B. 1993. *The living deserts of southern Africa.* Fernwood Press, South Africa.

SCHNEIDER, G. 2004. *The Roadside Geology of Namibia.* Gebrüder Borntraeger, Berlin-Stuttgart.

VAN DER WALT, P. & LE RICH, E. 1999. *The Kalahari and its plants.* Published by the authors, Pretoria.

CHAPTER 4

Materials & Methods

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4.1. INTRODUCTION

The 2003 fieldwork component was carried out at the end of March extending into the middle of April. Additional sampling of four sites commenced at the beginning of April 2004. It was determined that, in this particular area in Namibia, the optimum time for arthropod sampling is the end of March since this time roughly marks the end of the rainy season and usually results in an abundance of arthropods (and less trap losses due to rain).

Namib populations differ

Material for the study was collected during fieldwork using various collecting methods, after which the data was processed in the laboratory.

4.2. FIELDWORK

dates times

With the aim of this study being to compare psammophilous arthropods inhabiting an array of sandy habitats, various collecting methods were applied. Since the logistics of the study called for travelling long distances between sites in a relatively time period, the choice of methods was based primarily on the simplicity of each method. A general sampling protocol was assembled by the project coordinators in 2001, which was adapted according to the practicality of the methods (4.2.1 - 4.2.5). Literature (Schmera *et al.*, 2004; Sutherland, 1996) on related studies corroborated the recommendations of the project coordinators to make use of pitfall traps, water bowl traps and light traps in order to optimise sampling efficiency.

Standard sampling protocol called for the installation of one trapline at each of the respective 26 sites. Each trapline included 10 pitfall traps, 10 yellow pan traps and a ultraviolet (UV) light trap. Pitfall traps and yellow pan traps were put out in pairs, 15 m between pairs forming a straight trapline with a total length of 150 m along the crest of the sampling dune. One sand-sample was taken at each sampling site on the crest of the dune at a depth of roughly 30 cm. Traps were not monitored and the material was collected after 72 hours.

4.2.1. Pitfall trapping

For the purpose of studying psammophilous tericolous insects, pitfall traps have been used with success in numerous cases (Louw, 1982; Greenslade, 1964). Sutherland (1996) advised the use of a larger number of traps instead of using traps with larger circumferences that would trap more insects, in order to attain a balance between quantitative and qualitative sampling, i.e. number of arthropods collected *vs.* size of sampling area. For this reason, 10 cylindrical plastic bowls of 100 mm diameter and 90 mm height (500 cm^3) were used as pitfall traps on each trapline.

Greenslade (1964) established that sinking the pitfall trap into the ground with the lip of the container level with the surrounding ground surface, proves to be very successful. The traps were thus dug into the sand with the rim of each flush on the edge of the surrounding substrate surface (Figure 4.1).

Various factors influence the quality and quantity of arthropods collected in pitfall traps. In studies where fauna of a large number of different study sites are compared, it is impossible to accommodate all the variables that influence both the study sites and the activity patterns of the fauna. To maximize trap efficiency, the daily activity patterns and feeding habits of the arthropods were considered, where possible.

Many diurnal insects are attracted to shade (Louw, 1979), which was why the pitfall traps were installed in the natural shade of the dune vegetation. Many of the sampled dunes are sparsely vegetated (*cf.* Chapter 3), with the result that some traplines slightly crisscrossed the crest of the dune although the sampling protocol called for a straight trapline. Another motivation for placing pitfall traps close to dune vegetation was to counteract the risk of traps filling with sand and to avoid losses due to animals trampling on or drinking the preservative agent in the traps.

Crisscrossing traplines complicate the retrieval of traps. Hence, the beginning and end of each trapline was marked with a yellow bowl and a GPS (Global Positioning System) reading was taken at the onset and end of each trapline to simplify trap retrieval. Since many of the study sites were located close to secondary roads, the use of more conspicuous markers such as coloured flags or tags was prevented.

With the advantage that it does not evaporate easily, 100 ml of colourless Monoethylene glycol (MEG) was used as preservative agent. The lack of colour prevents a bias toward certain species of insects visually stimulated by certain colours. For the same reason of impartiality, traps were not baited. In a study on Carabidae populations, Greenslade (1964) found that no variation existed in catches when he tested for the efficiency of baited versus un-baited pitfall traps. Also, when using baited traps it is advised not to use it in combination with a preservative agent, which would mask the essence of the bait (Sutherland, 1996). Not using a preservative agent would, however, lead to predation in traps, with the implication that traps would need to be monitored as regularly as once a day. Daily monitoring was not possible during this study.

4.2.2. Yellow pan trapping

In arid environment studies, sparse vegetation usually raises some skepticism about the practicality of the use of yellow pan traps. Although the greater amount of psammophiles and ultra-psammophiles are apterous ground-dwelling coleopterans, note has been made of ultra-psammophilous species of Buprestidae (Holm, 1990) and other psammophilous floricolous insects. Bearing this in mind, the use of yellow pan traps (water bowl traps) to attract flying, floricolous insects was legitimized in some way, since it was opted rather for overkill than subjective sampling that could possibly result in an inadequacy of data. In addition, an opportunity was created to compare the effectiveness of pitfall trapping and yellow-pan trapping in studying arthropod fauna on dunes.

Literature (Sutherland, 1996; Dent & Walton, 1997) suggests that yellow is the colour most suitable for water bowl traps, although Schmera *et al.* (2004) found that using white and light blue traps presented no significant difference in results.

The yellow pans used in this study each had a 25 mm rim, a 170 mm diameter, a depth of 15 mm and a total capacity of 350 cm^3 (ml) (Figure 1). On each trapline, 10 yellow pans (Figure 1) were placed alongside each pitfall, in close proximity of dune vegetation, but in such a way that the vegetation did not obscure the visibility of the pan. Each pan was placed level with the dunes' surface, with the rim of the pan covered with sand in order to prevent wind from sweeping it away. Covering the rim of the pan with sand also aided in the traps' accessibility by ground dwelling insects. Traps were not baited and 100 ml of MEG in each yellow pan served as preservative agent.

4.2.3. UV Light trapping

Many flying insects, such as certain Scarabaeidae species, are attracted to light in the UV spectrum (Sutherland, 1996). This also proved to be true for dune crickets of the genus *Comicus* (Schizodactylidae).

Each light trap comprised a plastic lid, 2 rectangular Perspex® plates that slide into one another at a right angle, and a 5ℓ bucket connected to the bottom of the plate-configuration in which the arthropods collected (Figure 4.2). The Perspex® plates promoted 360 degree visibility of the UV light tube that was attached to it, and served as a guide for flying insects to be trapped in the bucket with 500 ml MEG.

For each site, one battery powered UV light trap was installed. The 12V battery, equipped with a day-night sensor, had a lifetime of roughly 8 hours, so light trapping was effective for only the first night of the 72 hour sampling period.

4.2.4. Sand sampling

Other components of the larger Palaeoenvironment Project (*cf.* Chapter 1), included the analysis of the physical, chemical and mineralogical characteristics of sand-samples taken at each of the sampled sites (excluding Eenzaamheid). Physical characteristics analyzed and tabled include dune grain sizes (Appendix B), and discussed in Chapter 6 in correlation with the results derived from the indicative insect groups.

The upper layers of sands on the crests of dunes are subjected to continuous deflation or deposition by wind, while the upper 50 cm of dunes are furthermore subjected to considerable bioturbation induced by burrowing organisms and the movement of larger animals (E. Marais, pers. comm.).

Vegetation acts as sedimentary traps (Bullard *et al.*, 1997). The grain size composition of substratum in the immediate vicinity of vegetation can thus be expected to represent sand that has been mobilized by current wind regimes, rather than the dune habitat *sensu lato*. In addition, the larvae, as well as nocturnal and/or crepuscular adults of most psammophilous species, either occur underneath vegetation where shade regulates extreme fluctuations in microclimate, or they burrow well below the dune surface in open areas to depths where soil temperatures and humidity are more stable. For these reasons, samples for grain analyses were taken in open areas, away from vegetation, at a depth of 30 cm in order to ensure reasonable representation of grain size fractions that signifies the character of the habitat substratum. At a depth of 30 cm, sand composition is not affected by weather conditions immediately before or during sample taking. Despite the fact that mixing (homogenization) through bioturbation would have taken place, a sample taken at such a depth will provide sufficient information regarding the primary microhabitat that allows reproduction and/or survival of the psammophilous fauna (E. Marais pers. comm.).

Sand samples of 500-800 g were taken and stored separately in 500 cm^3 Twirlpak® bags, marked with the date, name of the site and the GPS reference.

4.2.5. Collecting and preservation

After 72 hours, all traps were collected. Material from pitfall traps, yellow pan traps and UV light traps were marked and preserved separately. Excess preservative agent was drained using a simple funnel, constructed by removing the bottom of a 2ℓ soft drink bottle and using narrow-mesh gauze sleeve inside the funnel, in which the material was collected. The content of the sleeve was then transferred to 500 cm^3 Twirlpak® bags (Figure 4.3 & 4.4) by rinsing it with 70% ethanol (C_2H_5OH). The bags were labeled with the date, name of the site and GPS reference. Where traps were filled with sand, the entire content of the trap was stored in large capacity plastic (grocery) bags.

Some minor trap losses occurred at the Donkermodder study site (one yellow pan trap and one pitfall trap), the Aikanes study site (two yellow pan traps and two pitfall traps) and the Middelplaas control site (two yellow pan traps and one pitfall trap). These losses came about due to strong wind in the area that either swept the traps off the dune, or completely covered it with sand.

4.3. LABORATORY

The extraction, sorting and some identification of the arthropod-material were done in the laboratory in Bloemfontein. Additional identification not performed by specialists was done at the National Museum of Namibia. The Department of Soil, Crop and Climate Sciences of the University of the Free State performed all the sand analyses.

4.3.1. Extraction methodology

About 15% of the total ~~amount~~ number of yellow pan traps and pitfall traps were completely covered with sand. The problem with traps being filled by sand on the first day of trapping is that those traps are rendered futile for the remainder of the trap days. Nevertheless, the contents of such traps were also preserved and scrutinized for insects during the extraction and sorting process.

Many of the retrieved traps contained sand of varying amounts. In order to separate the insects from the sand, the material was washed through a fine-meshed sieve with hot water (in order to restore flexibility of the insect limbs as not to damage it). The sieve retained the arthropod-material and some plant material, while the sand fraction was collected in a bucket beneath the sieve and disposed of. The material in the sieve was then transferred to 350 cm^3 plastic jars and preserved in 70% ethanol. Material collected from different trap types and on different sites were marked and preserved separately.

4.3.2. Sorting methodology

The sorting of the material commenced by emptying the contents of the jar into a sorting pan with 370 mm x 270 mm x 50 mm dimensions, and removing all the larger particles of plant debris with pincers. A dissecting microscope was used to examine the said debris for smaller insects that tend to get lodged between twigs or leaves.

The arthropod-material was sorted into morphospecies, with all the individuals of a particular morphospecies preserved together in a separate Polytop^{TM} bottle. A reference collection was assembled in the course of the sorting process, where RTU (recognizable taxonomic unit) numbers were assigned (1 through 184) to each morphospecies. The Polytop^{TM} bottles containing the arthropods were marked with the RTU numbers of the relevant morphospecies, the name of the site where the sample was collected, as well as the type of trap that was used.

The contents of each Polytop^{TM} bottle was subsequently counted and logged in an unelaborated universal dataset using the Microsoft® Windows Excel program.

4.3.3. Identification methodology

Levels of identification varied between levels 1 through level 3 (Appendix C). Level 1 identification was performed by experts, which included the identification of Nemopteridae and Myrmeleontidae (Neuroptera) by Dr. M. Mansel[1], some Tenebrionidae (Coleoptera) by Professor S. Louw[2], the Lepismatidae (Thysanura) and Schizodactylidae (Orthoptera) by Dr. J. Irish[3], while Mr. C. Haddad[2] and Mr. L. Lotz[4] identified the Arachnida.

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[4] Mr. L. Lotz, National Museum, P.O. Box 266, Bloemfontein, 9301, South Africa

Level 2 identification was done either by using keys of identification cited in literature, or by careful comparison with specialist-identified material in the National Museum of Namibia. Literature was used identifying Tenebrionidae tribes such as Caenocrypticini, (Endrödy-Younga, 1996), Cryptochilina (Penrith & Endrödy-Younga, 1994), Adesmiini (Penrith, 1979), Zophosini (Penrith, 1984) and Molurini (Koch, 1955).

For Level 3 identification, either no literature was available or no identified material was available in the National Museum of Namibia. These arthropods was regarded of lesser relevance in the study, and no expert identification was called for. For these specimens, morphospecies names sufficed.

4.4. ANALYSES

Computer programs used during the analysis of the data and the drawing of maps and figures in this dissertation included the following:

- Microsoft ® Excel 2002
- Data Analyses Plus® 3.0, statistical add-ins for Microsoft® Excel
- STATISTICA® 5.1 for Windows
- ArcView® GIS 3.2 for Windows

Figure 4.1. Pitfall trap and yellow plate trap utilized to collect arthropod-material on dunes in southern Namibia (2003, 2004).

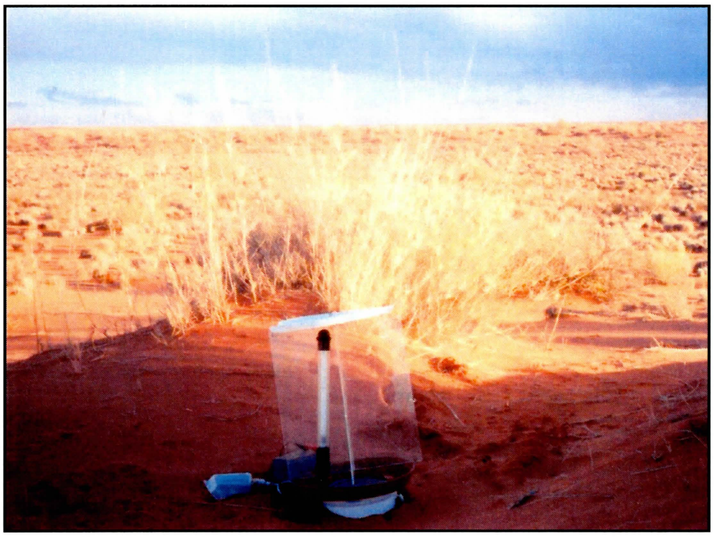

Figure 4.2. Ultraviolet light trap, connected to a 12V battery and an automatic day-night sensor, used to collect arthropod-material on dunes in southern Namibia (2003, 2004).

Figure. 4.3. Transferring arthropods to 500ml Twirlpak® bag at the end of a three-say sampling period on dunes in southern Namibia (2003, 2004).

Figure 4.4. Field preservation of arthropod-material in 70% ethanol while collecting arthropods on dunes in south-central Namibia (2003, 2004).

4.5. REFERENCES

BULLARD, J.E., THOMAS, D.S.G., LIVINGSTONE, I. & WIGGS, G.F.S. 1997. Dunefield activity and interactions with climatic variability in the southwest Kalahari Desert. *Earth surface processes and landforms* **22**: 165-174.

DENT, D.R. & WALTON, M.P. 1997. *Methods in Ecological and Agricultural Entomology*. CAB International, Wallingford.

ENDRÖDY-YOUNGA, S. 1996. Revision of the tribe Caenocrypticini (Coleoptera: Tenebrionidae: Tentyriinae).*Transvaal Museum Monograph* **11**. Transvaal Museum, Pretoria.

GREENSLADE, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *The Journal of Animal Ecology* **33**: 301-310.

HOLM, E., 1990. Notes on faunas bordering on the Namib desert. In: Seely, M.K. (Ed.) *Namib ecology: 25 years of Namib research.* 55-60. Transvaal Museum Monograph **7**. Transvaal Museum, Pretoria.

KOCH, C. 1955. Monograph of the Tenebrionidae of southern Africa. (1) Tentyriinae, Molurini, Trachynotina, *Somaticus*. *Transvaal Museum Memoir* **7**: 1-242.

LANCASTER, N. 1978. The pans of the southern Kalahari, Botswana. *Geographical Journal* **144**: 81-98.

LOUW, S.vdM. 1979. *Ecological equivalence and phylogeny of Tenebrionidae (Coleoptera) as indicators of the connection between Namib and Kalahari dunes*. Unpublished M.Sc Thesis, University of Pretoria, Pretoria.

LOUW, S.vdM. 1982. The diversity and daily and seasonal activity of ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. *Cimbebasia* (A) **7**(3): 35-56.

PENRITH, M.-L, 1979. Revision of the Western Southern African Adesmiini (Coleoptera: Tenebrionidae). *Cimbebasia* (A) **5**(1): 3-94.

PENRITH, M.-L. & ENDRÖDY-YOUNGA, S., 1994. Revision of the subtribe Cryptochilina (Coleoptera: Tenebrionidae: Cryptochilini). *Transvaal Museum Monograph* **9**. CTP Book Printers, Cape Town.

PENRITH, M.-L. 1984. Revision of the Zophosini (Coleoptera: Tenebrionidae) Part 10. Key to the subgenera, supplement, evolution and biogeography of the tribe, and catalogue. *Cimbebasia* (A) **6**(10): 418-502.

SCHMERA, D., TOTH, M., SUBCHEV, M., SREDKOV, I., SZARUKAN, I., JERMY, T., & SZENTESI, A.A. 2004. Importance of visual and chemical cues in the development of an attractant trap for *Epicometis (Tropinota) hirta* Poda (Coleoptera: Scarabaeidae). *Crop Protection* **23**(10): 939-944.

SUTHERLAND, W.J. 1996. *Ecological Census Techniques. A handbook.* Cambridge University Press. Cambridge.

CHAPTER 5

Results

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5.1. INTRODUCTION

This investigation focussed on collecting and identifying apterous, ground dwelling arthropods, isolating psammophilous species from the more generalist terricolous specimens (*cf.* Chapter 2).

For sampling said arthropods, pitfall traps, yellow plate traps and ultra violet (UV) light traps were used as an opportunistic means to attain the greatest scope of data, but during identification of the material the emphasis was mainly on the extrication of apterous invertebrates. Mention is made of all the arachnids collected at the various sites, mainly for interest sake, but also for use in possible future publications. The same applies for the order Neuroptera, since the use of Neuroptera as sand indicators was deemed ineffective. Dr M. Mansell (*cf.* Chapter 4) identified four new species of Myrmeleontidae (Neuroptera), which are noted at all the relevant study sites.

The largest amount of UV light trap material and specific groups of insects collected in the pitfall traps and yellow plate traps were eliminated and not identified during the sorting and identification process due to their predetermined irrelevance in this study. These include groups in the order of Coleoptera and the gross amount of other winged orders such as Lepidoptera, Diptera, Hemiptera, Homoptera and Hymenoptera. Where a winged specimen is listed it is for interest sake only, unless otherwise noted. From here on ‘specimens recorded’, percentages and statistics refer only to listed identified material, and exclude all said groups.

At the sites where data recording took place in 2003 and 2004, only data from 2004 is listed and used. The reason for this is that the sites resampled presented greater species abundance in 2004, and statistical complexity is avoided. Where traps went missing or were covered with sand, no statistical compensation was incorporated in the final numbers, percentages or statistics.

A total number of 184 species were recorded from eight orders and 52 families (Appendix C). Identification of the material took place on three levels and is listed as such next to the specific species (*cf.* Chapter 4 and Appendix C). A total number of 27 644 individuals were recorded, of which 18 277 were of the family Tenebrionidae (66.12%). Figure 5.1 depicts total numbers of arthropods *versus* the numbers of tenebrionids recorded on the various dune lines and clusters, while Figure 5.2 graphs the numbers of arthropods *versus* numbers of tenebrionids recorded at the individual sites. Figure 5.3 compares the number of individuals to the number of species recorded. These figures were statistically assembled into Shannon's index of diversity (H') (Figure 5.4) with an additional index of evenness (E). Shannon's index of diversity integrates a measure of evenness of abundances, but an additional measure of evenness (E) was calculated in aid of statistical analyses. Figure 5.5 depicts the number of Tenebrionidae as a percentage of the total number of arthropods sampled on each dune line or cluster, accompanied by the average Shannon's index of diversity for each line or cluster.

H' and E are calculated as follows:

$H' = -\Sigma p_i \ln p_i$ where p_i is the proportion of individuals found in the ith species

$E = H' / \ln S$ where E varies between 0 (heterogenous sample) and 1 (uniform sample).

While Chapter 5 is basically a regurgitation of data, figures and statistics, a detailed analyses of the data and anomalies ensues in Chapter 6.

5.2. KALAHARI DUNE LINE (CONTROL SITES)

A total number of 2 235 arthropods (Figure 5.1) were recorded of which 1 593 were members of the family Tenebrionidae (71.27%). The average diversity index for the Kalahari Dune Line amounted to 2.31 (Figure 5.5). At four of the five sites *Gonopus tibialis* dominated Tenebrionidae numbers. Only at one site (Wildheim Ost) does *G. tibialis* occur together with *G. agrestis*, with the latter only in very small numbers. At the other sites where *G. tibialis* did occur, it dominates and no *G. agrestis* specimens were recorded. Other tenebrionids that occurred in high numbers at the various sites were *Onymacris multistriata* and *Herpiscius spinolai*.

5.2.1. Wildheim Ost

At this first control site, 978 individuals from 32 invertebrate species were collected (Figure 5.3), representing nine families and three orders (Table 5.1). The diversity index for the site amounts to $H' = 2.40$ ($E = 0.69$) (Figure 5.4). Of the nine families, five were insect families and four of the five were from the order Coleoptera. Two new Myrmeleontidae (Neuroptera) species from the genera *Centroclisis and Syngenes* were recorded.

Of the total of 32 species collected, 15 were species of 7 different tribes of Tenebrionidae. Members of the family Tenebrionidae constituted 70.14% of the total of 978 arthropods collected at Wildheim Ost (Fig. 5.2). The most abundant Tenebrionidae species were *Onymacris multistriata* (28.22%), followed by *Herpiscius spinolai* (27.30%) and *Gonopus agrestis* (5.93%).

→ Annex
Data analysis here

Table 5.1. Arthropods collected at the Wildheim Ost study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Physosterna cribripes* Haag
		Onymacris multistriata Haag-Rutenberg
	Drosochrini	*Drosochrus* sp.
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips dohrni (Haag)
		S. gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
		Tarsocnodes ephialtes Koch
	Scaurini	*Herpiscius spinolai* Solier
	Zophosini	*Zophosis amita* Penrith
		Zophosis sp.
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus tibialis Fabricius
		G. agrestis Fahraéus
Chrysomelidae	*Pseudocolaspis* sp.	
Histeridae	*Dahlgrenius* sp.	
Scarabaeidae	*Schizonycha* sp.	
	Metacatharsius sp.	
	Onthophagus sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Palparellus dubiosus Péringuey	
	Furgella damarinus Péringuey	

Combine all sites

Table 5.1. (*continued.*)

NEUROPTERA	
	Centroclisis spec. nov. 2
	Myrmeleon doralice Banks
	Syngenes spec. nov. 3
	Golafrus oneili Péringuey
ARACHNIDA	
Eresidae	*Seothyra fasciata* Purcell
Gnaphosidae	*Asemesthes lineatus* Purcell
Salticidae	*Menemerus* sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
	Parabuthus ?granulatus (Hemprich & Ehrenberg)

5.2.2. Itaga

Table 5.2 lists the 43 species (Figure 5.3), 16 families and seven orders of Arthropoda that were collected at this site. A total of 387 individuals were recorded, and the diversity index for Itaga amounts to *H'* = 2.64 (*E* = 0.70) (Figure 5.4). Twelve of the 16 arthropod families noted were insect families and six of the 12 were from the order Coleoptera. A new myrmeleontid (Neuroptera) species of *Centroclisis* was recorded.

Of the total of 43 species, 19 were species of 8 different tribes of Tenebrionidae. The Tenebrionidae comprised 79.33% of the total of 387 arthropods collected (Figure 5.2), of which the most abundant species were *Renatiella scrobipennis* (37.73%) followed by *Gonopus tibialis* (10.85%) and *Herpiscius spinolai* (9.82%).

Table 5.2. Arthropods collected at the Itaga study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Caenocrypticini	*Caenocrypticus phaleroides* Koch
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips dohrni (Haag)
		S. gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
		Psammodes vialis Burchell
		Tarsocnodes ephialtes Koch
	Opatrini	*Caedius* sp.
		Calaharena dutoiti Koch
		Parastizopus armaticeps Péringuey
		Gonopus tibialis Fabricius
	Scaurini	*Herpiscius spinolai* Solier
	Tentyriini	*Rhammatodes striatulus* Koch
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
		Z. amita Penrith
		Z. jacoti Penrith
Bruchidae	*Spermophagus* sp.	
Carabidae	*Boeomimetus ephippium* Boheman	
	Passalidius fortipes (Boheman)	
	Cypholoba alstoni (Péringuey)	
Curculionidae	sp.	
Histeridae	*Dahlgrenius* sp.	

Table 5.2. (*continued.*)

COLEOPTERA	
Histeridae	*Pholioxenus* sp.
Scarabaeidae	*Caccobius* sp.
	Metacatharsius sp.
	Scarabaeus proboscideus (Guerin)
	Scarabaeus sp.
	Gymnopleurus humanus MacLeay
HEMIPTERA	
Lygaeidae	*Geocoris* sp.
Pentatomidae	sp.
HYMENOPTERA	
Bradynobaenidae	*Micatagla schultzei* (André)
NEUROPTERA	
Myrmeleontidae	*Centroclisis* spec. nov. 2
ORTHOPTERA	
Schizodactylidae	*Comicus calaharicus* Irish
THYSANURA	
Lepismatidae	*Ctenolepisma terebrans* Silvestri
ARACHNIDA	
Hexisopodidae	*Chelypus weulischi* Roewer
Ammoxenidae	*Ammoxenus coccineus* Simon
Prodidomidae	*Theuma maculata* Purcell
Buthidae	sp.

Table 5.2. *(continued.)*

ARACHNIDA	
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
	Parabuthus ?granulatus (Hemprich & Ehrenberg)

5.2.3. Middelplaas

A total of 424 individuals representing 36 species (Figure 5.3), 15 families and four arthropod orders were collected at Middelplaas and listed in Table 5.3. The Shannon diversity index (*H'* = 3.0) and evenness (*E* = 0.84) is shown on Figure 5.4. Nine of the 15 families were insect families and six of the nine were Coleoptera.

Of the total of 36 species, 13 were tenebrionid species of 7 different tribes. The Tenebrionidae constituted 67.69% of the total of 424 arthropods sampled (Fig. 5.2). The most abundant Tenebrionidae species were *Onymacris multistriata* (15.57%), followed by *Renatiella scrobipennis* (14.15%) and *Gonopus tibialis* (11.08%).

Only eight of the ten yellow plate traps and nine of the pitfall traps could be retrieved, possibly due to sheep grazing in the camp in which traplines were put out.

Table 5.3. Arthropods collected at the Middelplaas study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips dohrni (Haag)
		S. gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
		Tarsocnodes ephialtes Koch
	Scaurini	*Herpiscius spinolai* Solier
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
COLEOPTERA		
Tenebrionidae	Zophosini	*Z. amita* Penrith
	Caenocrypticini	*Caenocrypticus phaleroides* Koch
	Opatrini	*Gonopus tibialis* Fabricius
Bruchidae	*Spermophagus prevetti* Borowiec	
Carabidae	*Cypholoba alstoni* (Péringuey)	
Chrysomelidae	*Macrocoma* sp.	
	Pseudocolaspis sp.	
Histeridae	*Dahlgrenius* sp.	
Scarabaeidae	*Caccobius* sp	
	Metacatharsius sp.	
	Scarabaeus sp.	
	Scarabaeus flavicornis (Boheman)	
	Aphodius sp.	

Table 5.3. (*continued.*)

NEUROPTERA	
Myrmeleontidae	*Myrmeleon doralice* Banks
Nemopteridae	*Derhynchia vansoni* Tjeder
ORTHOPTERA	
Schizodactylidae	*Comicus calaharicus* Irish
ARACHNIDA	
Daesiidae	*Biton pearsoni* (Hewitt)
Gnaphosidae	*Setaphis bilinearis* Tucker
	Asemesthes lineatus Purcell
	Xerophaeus sp.
	Asemesthes sp.
Philodromidae	*Hirriusa* sp.
Salticidae	*Menemerus* sp.
	Phlegra sp.
Buthidae	sp.
Pseudoscorpiones	*Opistophthalmus ?holmi* (Lawrence)

5.2.4. Vredeshoop

At this southernmost control site 180 individuals from 33 species (Figure 5.3) from 14 families and six orders of Arthropoda were collected (Table 5.4). The diversity index for the site amounts to *H'* = 3.34 (*E* = 0.96) (Figure 5.3). Of the 14 families, nine were insect families and four of the nine were from the order Coleoptera. Three new species of Myrmeleontidae (Neuroptera) from the genera *Centroclisis, Syngenes* and *Cueta* were noted.

Of the total of 33 species, 11 were species of 7 different tribes of Tenebrionidae. The Tenebrionidae constituted 54.44% of the total of 180 arthropods sampled

(Figure 5.2). The most abundant Tenebrionidae species were *Herpiscius spinolai* (14.44%), *Eurychora nitida* (11.11%) and *Onymacris multistriata* (9.44%).

Table 5.4. Arthropods collected at the Vredeshoop study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
		Psammodes vialis Burchell
	Opatrini	*Calaharena dutoiti* Koch
	Scaurini	*Herpiscius spinolai* Solier
	Zophosini	*Zophosis amita* Penrith
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus tibialis Fabricius
Carabidae	*Cypholoba alstoni* (Péringuey)	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Peritrichia bella* Moser	
HEMIPTERA		
Pentatomidae	sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Palparellus dubiosus Péringuey	

Table 5.4. (*continued.*)

NEUROPTERA	
Myrmeleontidae	*Centroclisis* spec. nov. 2
	Palpares immensus McLachlan
	Myrmeleon doralice Banks
	Syngenes spec. nov. 3
	Cueta spec. nov. 4
ORTHOPTERA	
Gryllidae	*Gryllus* sp.
Schizodactylidae	*Comicus calaharicus* Irish
THYSANURA	
Lepismatidae	*Ctenolepisma latera* Irish
ARACHNIDA	
Daesiidae	*Namibesia* sp.
Gnaphosidae	*Zelotes oneili* (Purcell)
	Asemesthes lineatus Purcell
Salticidae	*Menemerus* sp.
	Pseudicius sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
	Parabuthus schlechteri Purcell
Solpugidae	*Zeria* sp.

5.2.5. Eenzaamheid

A total of 266 individuals from 31 species (Figure 5.3), 12 families and four orders of Arthropoda were collected at this site and listed in Table 5.5. The diversity index for the site amounts to $H' = 0.16$ ($E = 0.05$) (Figure 5.4). Of the 12 families, seven were insect families and six of the seven were from the order Coleoptera. A new species of Myrmeleontidae (Neuroptera) from the genus *Syngenes* was collected.

Of the total of 31 species collected, 15 were species of six different tribes of Tenebrionidae, where the tenebrionids constituted 80.83% of the total 266 arthropods (Figure. 5.2). The most abundant Tenebrionidae species were *Eurychora nitida* (24.81%), followed by *Phanerotomea monacha* (19.92%) and *Gonopus tibialis* (9.02%).

Table 5.5. Arthropods collected at the Eenzaamheid study site (2004).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips gebieni (Hesse)
		Stipsosoma sp.
		Geophanus plicicollis Fairmaire
	Molurini	*Phanerotomea monacha* Koch
		Psammodes vialis Burchell
	Scaurini	*Herpiscius spinolai* Solier
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey

Table 5.5. (*continued.*)

COLEOPTERA		
Tenebrionidae	Zophosini	*Zophosis* sp.
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus agrestis Fahraéus
		G. tibialis Fabricius
Bruchidae	sp.	
Carabidae	*Cypholoba alstoni* (Péringuey)	
	Passalidius fortipes (Boheman)	
Curculionidae	sp.	
Histeridae	*Dahlgrenius* sp.	
	Dahlgrenius sp. 2	
Scarabaeidae	*Metacatharsius* sp.	
	Scarabaeus sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Syngenes spec. nov. 3	
	Golafrus oneili Péringuey	
ARACHNIDA		
Ammoxenidae	*Ammoxenus coccineus* Simon	
Gnaphosidae	*Asemesthes lineatus* Purcell	
Gnaphosidae	*Setaphis* sp.	
Salticidae	*Pseudicius* sp.	
Buthidae	*Parabuthus kalaharicus* Lamoral	

5.3. MUKOROB DUNE LINE

Very similar to the Kalahari Dune Line, the Tenebrionidae constituted 71.26% of the total number of arthropods recorded (2 388 Tenebrionidae out of 3 351 arthropods) (Figure 5.1), with an average diversity across the four sites of 2.63 (Figure 5.5). *Eurychora nitida* was recorded in dominating numbers across all four sites. Other Tenebrionidae species that occurred frequently were *Stips gebieni* and *Gonopus tibialis*.

5.3.1. Habis

A total of 181 individuals from 27 species (Figure 5.3), nine families and four orders of Arthropoda were collected at the Habis study site (Table 5.6). A diversity index *H'* = 2.9 (*E* = 0.86) (Fig. 5.4) was calculated for the site. Of the nine represented families, all were insect families and five of the nine were from the order Coleoptera. One new species of Myrmeleontidae (Neuroptera) from the genus *Creoleon* was sampled.

Of the total of 27 species, 12 were species of five different tribes of Tenebrionidae. This family constituted 60.77% of the total of 181 arthropods collected (Figure 5.2), with the most abundant species being *Stips gebieni* (30.94%) followed by *Eurychora nitida* (12.71%) and *Gonopus agrestis* (5.52%).

Table 5.6. Arthropods collected at the Habis study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Physosterna cribripes* Haag
		Onymacris multistriata Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
		Stips gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
		Somaticus incostatus (Gebien)
		Psammodes vialis Burchell
		Psammodes sp.
	Scaurini	*Herpiscius spinolai* Solier
	Opatrini	*Gonopus agrestis* Fahraéus
Carabidae	*Cypholoba alstoni* (Péringuey)	
Chrysomelidae	*Monolepta* sp.	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Caccobius* sp.	
	Metacatharsius	
	Scarabaeus proboscideus (Guerin)	
	Gymnopleurus humanus MacLeay	
THYSANOPTERA		
Thripidae	sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	

Table 5.6. (*continued.*)

NEUROPTERA	
Myrmeleontidae	*Palparellus dubiosus* Péringuey
	Creoleon spec. nov.
	Furgella damarinus Péringuey
ORTHOPTERA	
Gryllidae	*Gryllus* sp.
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
	Comicus calaharicus Irish
THYSANURA	
Lepismatidae	*Ctenolepisma pluriseta* Silvestri

5.3.2. Dorn-Daberas

A total of 317 individuals from 32 species (Figure 5.3), 16 families and six orders of Arthropoda were collected at this site and listed in Table 5.7. The diversity index for the site amounts to $H' = 2.56$ ($E = 0.74$) (Figure 5.4). Of the 16 families, 10 were insect families and five of the 10 were from the order Coleoptera.

Of the total of 32 species, 11 were species of seven different tribes of Tenebrionidae. The Tenebrionidae comprised 70.98% of the total of 317 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Eurychora nitida* (35.65%), followed by *Herpiscius spinolai* (12.30%) and *Gonopus tibialis* (10.73%).

Table 5.7. Arthropods collected at the Dorn-Daberas study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
	Eurychorini	*Eurychora nitida* Haag
		Stips gebieni (Hesse)
		Stipsosoma sp.
	Molurini	*Psammodes vialis* Burchell
	Scaurini	*Herpiscius spinolai* Solier
	Zophosini	*Zophosis amita* Penrith
	Opatrini	*Parastizopus armaticeps* Péringuey
		Stizopus sp.
		Gonopus tibialis Fabricius
	Tentyriini	*Rhammatodes striatulus* Koch
Bruchidae	*Spermophagus prevetti* Borowiec	
Carabidae	*Cypholoba alstoni* (Péringuey)	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Metacatharsius* sp.	
	Scarabaeus proboscideus (Guerin)	
HEMIPTERA		
Pentatomidae	*Mecidea* sp.	
	sp.	
Reduviidae	sp.	
BLATTODEA		
Polyphagidae	*Tivia* sp.	

Table 5.7. (*continued.*)

ORTHOPTERA	
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
THYSANURA	
Lepismatidae	*Ctenolepisma terebrans* Silvestri
ARACHNIDA	
Gnaphosidae	*Zelotes oneili* (Purcell)
	Setaphis bilinearis Tucker
	Asemesthes lineatus Purcell
Prodidomidae	*Prodidomus*
Salticidae	*Menemerus*
	Pseudicius
Sparassidae	*Orchestrella* sp.
Thomisidae	*Misumenops rubrodecoratus* Millot
Buthidae	sp.
	Parabuthus kalaharicus Lamoral

5.3.3. Goamus

A total of 484 individuals from 25 species (Figure 5.3), 11 families and four orders of Arthropoda were collected at this site and listed in Table 5.8. The diversity index for the site amounts to H' = 1.70 (E = 0.53) (Figure 5.4). Of the 11 families, 6 were insect families, of which four were from the order Coleoptera.

Of the total of 25 species, 12 were species of six different tribes of Tenebrionidae. The Tenebrionidae constituted 87.60% of the total of 484 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Stips gebieni* (57.85%), followed by *Gonopus tibialis* (17.77%) and *Eurychora nitida* (4.75%).

Table 5.8. Arthropods collected at the Goamus study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Physosterna cribripes* Haag
		Onymacris multistriata Haag-Rutenberg
		Stenocara gracilipes Solier
		Renatiella scrobipennis (Haag)
	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
		Stips gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
	Zophosini	*Zophosis amita* Penrith
	Opatrini	*Gonopus agrestis* Fahraéus
		G. tibialis Fabricius
	Caenocrypticini	*Caenocrypticus phaleroides* Koch
Carabidae	*Crepidogastrinus kochi* Basilewsky	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Metacatharsius*	
	Scarabaeus proboscideus (Guerin)	
	Schizonycha sp.	
	Sparrmannia flava Arrow	

Table 5.8. (*continued.*)

NEUROPTERA	
Nemopteridae	*Derhynchia vansoni* Tjeder
THYSANURA	
Lepismatidae	*Ctenolepisma latera* Irish
ARACHNIDA	
Gnaphosidae	*Asemesthes lineatus* Purcell
Philodromidae	*Thanatus pagenstecheri* Strand
Salticidae	*Menemerus* sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
Scorpionidae	*Opistophthalmus holmi* (Lawrence)

5.3.4. Haribes

A total of 134 individuals from 30 species (Figure 5.3), 15 families and seven orders of Arthropoda were collected at this site and listed in Table 5.9. The diversity index for the site amounts to $H' = 3.40$ ($E = 0.99$) (Figure 5.4). Of the 15 families, eight were insect families and four of the eight were from the order Coleoptera. One new species of Myrmeleontidae (Neuroptera) from the genus *Centroclisis* was collected.

Of the total of 30 species, eight were species of four different tribes of Tenebrionidae. The Tenebrionidae represented 26.87% of the total of 134 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Gonopus agrestis* (11.19%), followed by *Eurychora nitida* (5.22%) and *Phanerotomea monacha* (2.99%).

Table 5.9. Arthropods collected at the Haribes study site in southern Namibia (2004).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Physosterna cribripes* Haag
		Onymacris multistriata Haag-Rutenberg
	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
		Stipsosoma sp.
	Molurini	*Phanerotomea monacha* Koch
		Psammodes vialis Burchell
	Opatrini	*Gonopus agrestis* Fahraéus
Chrysomelidae	*Pseudocolaspis* sp.	
Histeridae	*Dahlgrenius* sp.	
	Dahlgrenius sp. 2	
Scarabaeidae	*Lepisia virescens* Péringuey	
	Caccobius sp.	
	Metacatharsius sp.	
	Sparrmannia flava Arrow	
NEUROPTERA		
Myrmeleontidae	*Centroclisis* spec. nov. 2	
	Myrmeleon doralice Banks	
ORTHOPTERA		
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl	
BLATTODEA		
Blattellidae	*Namablatta bitaeniata* Stål	

Table 5.9. (*continued.*)

THYSANOPTERA	
Thripidae	sp.
THYSANURA	
Lepismatidae	*Ctenolepisma pluriseta* Silvestri
ARACHNIDA	
Daesiidae	*Namibesia* sp.
Gnaphosidae	*Zelotes oneili* (Purcell)
	Asemesthes lineatus Purcell
Idiopidae	*Gorgyrella* sp.
Lycosidae	*Evippa* sp.
Salticidae	*Menemerus* sp.
	Pellenes sp.
Zodariidae	*Heradida griffinae* Jocqué
Buthidae	sp.

5.4. TSES DUNE LINE

The total number of Tenebrionidae sampled over the four sites of the Tses Dune Line was 2 888, which constituted 92.09% of the 3 136 arthropods recorded (Figure 5.1) on this dune line. The average diversity index across the four sites on this dune line was calculated to be 1.75 (Figure 5.5), which is relatively low and caused by a high abundance of only one or two species. The most frequently recorded species of Tenebrionidae were *Stips gebieni*, which occurred in dominating numbers across all of the four sites. Species that occurred in notable numbers across at least two of the four sites were *Onymacris multistriata*, *Somaticus incostatus* and *Parastizopus armaticeps*.

5.4.1. Averas

A total of 632 individuals from 41 species (Figure 5.3), 16 families and four orders of Arthropoda were collected at this site and listed in Table 5.10. The diversity index for the site amounts to $H' = 2.69$ ($E = 0.72$) (Figure 5.4). Of the 16 families, nine were insect families, of which six were from the order Coleoptera. Two new species of Myrmeleontidae (Neuroptera) from the genera *Syngenes* and *Cueta* were collected.

Of the total of 41 species, 13 were of seven different tribes of Tenebrionidae. The Tenebrionidae made up 75.47% of the total of 632 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Herpiscius spinolai* (24.37%), followed by *Onymacris multistriata* (19.94%) and *Stips gebieni* (18.04%).

Table 5.10. Arthropods collected at the Averas study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips dohrni (Haag)
		Stips gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
	Scaurini	*Herpiscius spinolai* Solier
	Zophosini	*Zophosis amita* Penrith
	Tentyriini	*Rozonia strigicollis* Fairmaire
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus agrestis Fahraéus
		G. tibialis Fabricius
Carabidae	*Cypholoba alstoni* (Péringuey)	
	Crepidogastrinus kochi Basilewsky	
Chrysomelidae	*Monolepta* sp.	
Dermestidae	*Attagenus* sp.	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Caccobius* sp.	
	Metacatharsius sp.	
	Onthophagus sp.	
	Gymnopleurus humanus MacLeay	
	Gymnopleurus aenescens Wiedemann	

Table 5.10. (*continued.*)

NEUROPTERA	
Myrmeleontidae	*Palparidius capicola* Péringuey
	Palparellus dubiosus Péringuey
	Furgella damarinus Péringuey
	Palpares immensus McLachlan
	Myrmeleon doralice Banks
	Syngenes spec. nov. 3
	Golafrus oneili Péringuey
	Cueta spec. nov. 4
Nemopteridae	*Derhynchia vansoni* Tjeder
ORTHOPTERA	
Gryllidae	*Gryllus* sp.
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
ARACHNIDA	
Hexisopodidae	*Chelypus hirsti* Hewitt
Ammoxenidae	*Ammoxenus coccineus* Simon
Nemesiidae	*Hermacha lanata* (Purcell)
Salticidae	*Menemerus* sp.
Zodariidae	*Capheris* sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
	Parabuthus ?granulatus (Hemprich & Ehrenberg)

5.4.2. Tses

A total of 2018 individuals from 26 species (Figure 5.3), 12 families and five orders of Arthropoda were sampled at this site and listed in Table 5.11. The diversity index for the site amounts to *H'* = 0.67 (*E* = 0.21) (Figure 5.4). Of the 12 families, five were insect families, all of which were from the order Coleoptera.

Of the total of 26 species, 12 were species of five different tribes of Tenebrionidae. The Tenebrionidae constituted 98.56% of the total of 2018 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Stips gebieni* (86.97%), followed by *Onymacris multistriata* (5.05%) and *Somaticus incostatus* (2.68%).

Table 5.11. Arthropods collected at the Tses study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Stenocara gracilipes Solier
		Renatiella scrobipennis (Haag)
	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
		Stips gebieni (Hesse)
	Molurini	*Phanerotomea monacha* Koch
		Somaticus incostatus (Gebien)
		Psammodes vialis Burchell
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
		Zophosis giessi Koch
	Opatrini	*Gonopus agrestis* Fahraéus
Histeridae	*Dahlgrenius* sp. 2	

Table 5.11. (*continued.*)

COLEOPTERA	
Scarabaeidae	*Scarabaeus proboscideus* (Guerin)
	Aphodius sp. 3
HEMIPTERA	
Pentatomidae	sp.
Reduviidae	sp.
HYMENOPTERA	
Colletidae	sp.
ORTHOPTERA	
Gryllidae	*Gryllus* sp.
ARACHNIDA	
Hexisopodidae	*Chelypus lennoxae* Hewitt
Daesiidae	*Namibesia* sp.
	Biton pearsoni (Hewitt)
Gnaphosidae	*Asemesthes lineatus* Purcell
Salticidae	*Menemerus* sp.
	Phlegra sp.
Zodariidae	*Capheris* sp.

5.4.3. Kaitzub

A total of 334 individuals from 32 species (Figure 5.3), 16 families and seven orders of Arthropoda were sampled at this site and listed in Table 5.12. The diversity index for the site amounts to $H' = 1.42$ ($E = 0.41$) (Figure 5.4). Of the 16 families, 11 were insect families, of which six were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus *Syngenes* was recorded.

Of the total of 32 species, 13 were species of five different tribes of Tenebrionidae. The Tenebrionidae constituted 90.12% of the total of 334 arthropods collected (Figure 5.2). The most abundant Tenebrionidae species were *Stips gebieni* (75.15%), followed by *Physosterna cribripes* (3.29%), *Rhammatodes striatulus* and *Parastizopus armaticeps* (both 2.10%).

Table 5.12. Arthropods collected at the Kaitzub study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Physosterna cribripes* Haag
		Onymacris multistriata Haag-Rutenberg
		Epiphysa flavicollis (Fabricius)
	Eurychorini	*Stips dohrni* (Haag)
		*Stips gebieni (*Hesse)
		Stipsosoma sp.
	Molurini	*Somaticus incostatus* (Gebien)
	Opatrini	*Stenolamus* sp.
		Parastizopus armaticeps Péringuey
		Gonopus agrestis Fahraéus
		Stizopus sp.

Table 5.12. (*continued.*)

COLEOPTERA		
Tenebrionidae	Tentyriini	*Rozonia strigicollis* Fairmaire
		Rhammatodes striatulus Koch
Bruchidae	*Spermophagus* sp.	
Carabidae	sp.	
Chrysomelidae	*Monolepta* sp.	
	Macrocoma sp.	
Hydrophilidae	*Helochares* sp.	
Scarabaeidae	*Macrophylla* sp.	
	Schizonycha sp.	
	Sparrmannia flava Arrow	
HEMIPTERA		
Lygaeidae	*Nysius* sp.	
HOMOPTERA		
Cicadellidae	sp.	
NEUROPTERA		
Myrmeleontidae	*Golafrus oneili* (Péringuey)	
	Syngenes spec. nov. 3	
ORTHOPTERA		
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl	
THYSANURA		
Lepismatidae	*Ctenolepisma latera* Irish	

Table 5.12. (*continued.*)

ARACHNIDA	
Daesiidae	*Biton pearsoni* (Hewitt)
Gnaphosidae	*Zelotes oneili* (Purcell)
Salticidae	*Phlegra* sp.
Sparassidae	*Orchestrella* sp.
Buthidae	*Parabuthus ?granulatus* (Hemprich & Ehrenberg)

5.4.4. Lichtenfels

A total of 152 individuals from 25 species (Figure 5.3), eight families and four orders of Arthropoda were sampled at this site and listed in Table 5.13. The diversity index for the site amounts to *H'* = 2.25 (*E* = 0.70) (Figure 5.4). Of the eight families, four were insect families, of which two were from the order Coleoptera. Two new Myrmeleontidae (Neuroptera) species of the genera *Creoleon* and *Syngenes* were recorded.

Of the total of 25 species, 12 were species of seven different tribes of Tenebrionidae. The Tenebrionidae comprised 79.61% of the total of 152 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Stips gebieni* (47.37%), followed by *Somaticus incostatus* (14.47%) and *Parastizopus armaticeps* (5.26%).

Table 5.13. Arthropods collected at the Lichtenfels study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Physosterna cribripes* Haag
	Caenocrypticini	*Caenocrypticus wittmeri* Endrödy-Younga
	Eurychorini	*Geophanus plicicollis* Fairmaire
		Stips gebieni (Hesse)
		Stipsosoma sp.
	Molurini	*Phanerotomea monacha* Koch
		Somaticus incostatus (Gebien)
	Zophosini	*Zophosis amita* Penrith
	Opatrini	*Parastizopus armaticeps* Péringuey
		Stizopus sp.
		Stizopus sp. 2
	Tentyriini	*Rhammatodes striatulus* Koch
Tenebrionidae	sp.	
Carabidae	*Passalidius fortipes* (Boheman)	
THYSANOPTERA		
Thripidae	sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Creoleon spec. nov.	
	Syngenes spec. nov. 3	
ORTHOPTERA		
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl	

Table 5.13. (*continued.*)

ARACHNIDA	
Gnaphosidae	*Zelotes oneili* (Purcell)
	Asemesthes lineatus Purcell
Pisauridae	*Rothus auratus* Pocock
Salticidae	*Yogetor* sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
	Parabuthus brevimanus (Thorell)

5.5. MALTAHÖHE DUNE CLUSTER

The majority of the arthropod material sampled on the Maltahöhe Dune Cluster was of the family Tenebrionidae (51.20%). A total number of 623 arthropods were sampled, of which 319 were of the family Tenebrionidae (Figure 5.1), and the average diversity index for the dune cluster amounted to 2.69 (Figure 5.5). Tenebrionidae species that dominated in numbers at specific sites varied between *Onymacris multistriata*, *Eurychora nitida* and *Gonopus agrestis*, which all occurred in numbers worth mentioning, on at least two of the three sites.

5.5.1. Burgsdorf Noord

A total of 288 individuals from 27 species (Figure 5.3), nine families and six orders of Arthropoda were collected at this site and listed in Table 5.14. The diversity index for the site amounts to H' = 2.93 (E = 0.89) (Figure 5.4). Of the nine families, six were insect families and three of these six were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus C*entroclisis* was recorded.

Of the total of 27 species, 12 were species of five different tribes of Tenebrionidae. The Tenebrionidae made up 55.26% of the total of 288 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Parastizopus armaticeps* (17.98%), *Onymacris multistriata* (10.53%) and *Psammodes vialis* (9.65%).

Table 5.14. Arthropods collected at the Burgsdorf Noord study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Epiphysa flavicollis (Fabricius)
		Renatiella scrobipennis (Haag)
	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
	Molurini	*Phanerotomea monacha* Koch
		Psammodes vialis Burchell
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
		Zophosis amita Penrith
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus agrestis Fahraéus
		Neocaedius sp.
Tenebrionidae	sp.	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Xeloma maura* (Boheman)	
	Caccobius sp.	
	Metacatharsius sp.	
	Onthophagus sp.	

Table 5.14. (*continued.*)

COLEOPTERA	
Scarabaeidae	*Sparrmannia flava* Arrow
	Heteronychus sp.
NEUROPTERA	
Myrmeleontidae	*Centroclisis* spec. nov. 2
ORTHOPTERA	
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
THYSANURA	
Lepismatidae	*Ctenolepisma pluriseta* Silvestri
BLATTODEA	
Blattelidae	*Namablatta bitaeniata* Stål
ARACHNIDA	
Gnaphosidae	*Asemesthes lineatus* Purcell
Salticidae	*Menemerus* sp.
Buthidae	sp.

5.5.2. Amhub

A total of 124 individuals from 17 species (Figure 5.3), 10 families and four orders of Arthropoda were sampled at this site and listed in Table 5.15. The diversity index for the site amounts to $H' = 2.68$ ($E = 0.94$) (Figure 5.4). Of the 10 families, seven were insect families, of which five were from the order Coleoptera.

Of the total of 17 species, five were species of four different tribes of Tenebrionidae. The Tenebrionidae constituted 45.16% of the total of 124 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Eurychora nitida* (23.39%), *Zophosis deyrollei rufipennis* (13.71%) and *Gonopus agrestis* (4.03%).

Table 5.15. Arthropods collected at the Amhub study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
	Eurychorini	*Eurychora nitida* Haag
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
		Zophosis amita Penrith
	Opatrini	*Gonopus agrestis* Fahraéus
Carabidae	*Anthia circumscripta* Klug	
Dermestidae	*Attagenus* sp.	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Xeloma maura* (Boheman)	
	Metacatharsius	
	Schizonycha sp.	
	Sparrmannia flava Arrow	
ORTHOPTERA		
Gryllidae	*Gryllus* sp.	

Table 5.15. (*continued.*)

THYSANURA	
Lepismatidae	*Ctenolepisma pluriseta* Silvestri
ARACHNIDA	
Daesiidae	*Namibesia* sp.
Gnaphosidae	*Asemesthes lineatus* Purcell
	Xerophaeus sp.

5.5.3. Kronenhof

A total of 271 individuals from 27 species (Figure 5.3), 11 families and five orders of Arthropoda were sampled at this site and listed in Table 5.16. The diversity index for the site amounts to $H' = 2.45$ ($E = 0.74$) (Figure 5.4). Of the 11 families, eight were insect families of which five were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus *Centroclisis* was recorded.

Of the total of 27 species, eight were species of six different tribes of Tenebrionidae. The Tenebrionidae constituted 55.72% of the total of 271 arthropods sampled (Figure 5.2). The most abundant Tenebrionidae species were *Onymacris multistriata* (41.33%), followed by *Eurychora nitida* (6.64%) and *Gonopus agrestis* (5.54%).

Table 5.16. Arthropods collected at the Kronenhof study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmini	*Renatiella scrobipennis* (Haag)
		Onymacris multistriata Haag-Rutenberg
	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
	Molurini	*Hypomelus* sp.
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
	Opatrini	*Gonopus agrestis* Fahraéus
	Caenocrypticini	*Caenocrypticus phaleroides* Koch
Carabidae	*Anthia circumscripta* Klug	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Caccobius* sp.	
	Metacatharsius sp.	
	Scarabaeus proboscideus (Guerin)	
	Scarabaeus sp.	
	Sparrmannia flava Arrow	
Trogidae	*Omorgus squalidus* Olivier	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Palparellus dubiosus Péringuey	
	Furgella damarinus Péringuey	
	Centroclisis spec. nov. 2	
	Myrmeleon doralice Banks	

Table 5.16. (*continued.*)

ORTHOPTERA	
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
THYSANURA	
Lepismatidae	*Ctenolepisma pauliani* Wygodzinsky
ARACHNIDA	
Ammoxenidae	*Ammoxenus coccineus* Simon
Gnaphosidae	*Zelotes oneili* (Purcell)
	Asemesthes lineatus Purcell
Buthidae	sp.

5.6. KARAS DUNE CLUSTER

Of the total of 2108 arthropods collected on the Karas dune cluster, only 33.87% were of the family Tenebrionidae. The average diversity index over the 5 study sites was calculated to be 1.74 (Figure 5.5). Although Tenebrionidae material constituted more than 50% of the total species composition recorded at the sites Aikanes, Gründorn and Oase, only 8.57% of species sampled at Donkermodder were Tenebrionidae, and only 7.28% at Verschluss. Three species of Tenebrionidae dominated recordings, mainly at the three former mentioned sites. These were *Cimicia spinipes*, *Stips gebieni* and *Onymacris multistriata*.

Material from other orders that were recorded in high numbers was from the families Nemopteridae (Neuroptera) and Scarabaeidae (Coleoptera).

5.6.1. Donkermodder

A total of 140 individuals from 25 species (Figure 5.3), 13 families and five orders of Arthropoda were collected at this site and listed in Table 5.17. The diversity index for the site amounts to *H'* = 2.44 (*E* = 0.76) (Figure 5.4). Of the 13 families, seven were insect families and five of these seven were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus *Creoleon* was recorded.

Of the total of 25 species, four were species of four different tribes of Tenebrionidae. The Tenebrionidae constituted 8.57% of the total of 140 arthropods sampled (Figure 5.2). The Tenebrionidae species were *Cimicia spinipes* (6.43%), *Onymacris multistriata* (0.71%), *Stips gebieni* (0.71%) and *Zophosis gordoniae* (0.71%).

Due to strong winds that covered all the pitfall and yellow plate traps with sand during the three sampling days, only nine of the ten pitfall traps could be retreived. It is not known when exactly the traps were covered with sand and how this influenced the total number of specimens collected.

Table 5.17. Arthropods collected at the Donkermodder study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
	Eurychorini	*Cimicia spinipes* Fairmaire
		Stips gebieni (Hesse)
	Zophosini	*Zophosis gordoniae* Penrith
Curculionidae	*Leptostethus argentatus* Thompson	
Dytiscidae	*Eretes stricticus* Linnaeus	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Metacatharsius* sp.	
	Gymnopleurus humanus MacLeay	
	Schizonycha sp.	
	Rhyssemus sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Palparellus dubiosus Péringuey	
	Creoleon spec. nov.	
	Furgella damarinus Péringuey	
Nemopteridae	*Derhynchia vansoni* Tjeder	
ORTHOPTERA		
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl	
THYSANURA		
Lepismatidae	*Ctenolepisma terebrans* Silvestri	

Table 5.17. *(continued.)*

ARACHNIDA	
Hexisopodidae	*Chelypus hirsti* Hewitt
Gnaphosidae	*Asemesthes lineatus* Purcell
Philodromidae	*Hirriusa* sp.
Salticidae	*Menemerus* sp.
Zodariidae	*Capheris* sp.
Buthidae	sp.
	Parabuthus granulatus (Hemprich & Ehrenberg)

5.6.2. Verschluss

A total of 1250 individuals from 28 species (Figure 5.3), 15 families and five orders of Arthropoda were sampled at this site and listed in Table 5.18. The diversity index for the site amounts to H' = 0.79 (E = 0.24) (Figure 5.4). Of the 15 families, eight were insect families and four of these eight were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus *Creoleon* was recorded.

Of the total of 28 species, nine were species of six different tribes of Tenebrionidae. The Tenebrionidae constituted 7.28% of the total of 1250 arthropods sampled (Figure 5.4). The most notable Tenebrionidae species were *Stips gebieni* (5.60%), followed by *Onymacris multistriata* (0.40%) and *Horotoma pronamibensis* (0.32%).

Table 5.18. Arthropods collected at the Verschluss study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
	Cryptochilini	*Horotoma pronamibensis* Penrith & Endrödy-Younga
		Pachynotelus leucinus Koch
	Eurychorini	*Cimicia spinipes* Fairmaire
		Stips dohrni (Haag)
		Stips gebieni (Hesse)
	Molurini	*Psammodes vialis* Burchell
	Caenocrypticini	*Caenocrypticus phaleroides* Koch
	Opatrini	*Stizopus* sp.
Curculionidae	*Leptostethus argentatus* Thompson	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Metacatharsius* sp.	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Creoleon spec. nov.	
	Palpares immensus McLachlan	
	Myrmeleon doralice Banks	
Nemopteridae	*Derhynchia vansoni* Tjeder	
ORTHOPTERA		
Schizodactylidae	*Comicus calaharicus* Irish	
THYSANURA		
Lepismatidae	*Ctenolepisma latera* Irish	

Table 5.18. (*continued.*)

ARACHNIDA	
Hexisopodidae	*Chelypus hirsti* Hewitt
Eresidae	*Seothyra fasciata* Purcell
Gnaphosidae	*Zelotes oneili* (Purcell)
	Asemesthes lineatus Purcell
	Zelotes pulchripes (Purcell)
Philodromidae	*Thanatus pagenstecheri* Strand
Salticidae	*Menemerus* sp.
Buthidae	*Hottentotta arenaceus* Birula
Scorpionidae	*Opistophthalmus ?holmi* (Lawrence)

5.6.3. Aikanes

A total of 282 individuals from 14 species (Figure 5.3), five families and three orders of Arthropoda were sampled at this site and listed in Table 5.19. The diversity index for the site amounts to $H' = 1.27$ ($E = 0.48$) (Figure 5.4). Of the five families, two were insect families of which one is from the order Coleoptera.

Of the total of 14 species, 10 were species of six different tribes of Tenebrionidae. The Tenebrionidae constituted 98.58% of the total of 282 arthropods sampled (Fig. 5.2). The dominant Tenebrionidae species were *Stips gebieni* (54.61%), *Onymacris multistriata* (31.21%) and *Horotoma pronamibensis* (4.96%).

Sparse vegetation cover and strong winds during the three sampling days led to some of the traps being covered with sand, hence only eight pitfall traps and eight yellow plate traps could be recovered. Resampling during 2004 was not possible due to flooding of ephemeral rivers and streams that prevented access to the study site.

Table 5.19. Arthropods collected at the Aikanes site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Cryptochilini	*Horotoma pronamibensis* Penrith & Endrödy-Younga
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips gebieni (Hesse)
		Stipsosoma sp.
	Opatrini	*Stizopus* sp.
	Tentyriini	*Rhammatodes striatulus* Koch
Tenebrionidae	sp.	
THYSANURA		
Lepismatidae	*Ctenolepisma terebrans* Silvestri	
ARACHNIDA		
Hexisopodidae	*Chelypus hirsti* Hewitt	
Zodariidae	*Capheris* sp.	
Buthidae	*Hottentotta arenaceus* Birula	

5.6.4. Gründorn

A total of 225 individuals from 17 species (Figure 5.3), eight families and four orders of Arthropoda were sampled at this site and listed in Table 5.20. The diversity index for the site amounts to *H'* = 1.92 (*E* = 0.68) (Figure 5.4). Of the eight families, six were insect families and four of these six were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus *Cueta* was recorded.

Of the total of 17 species, eight were species of five different tribes of Tenebrionidae. The Tenebrionidae constituted 84.00% of the total of 225 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were *Phanerotomea* sp. (38.22%), *Phanerotomea monacha* (21.78%) and *Zophosis deyrollei rufipennis* (18.22%).

Table 5.20. Arthropods collected at the Gründorn study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
	Molurini	*Phanerotomea monacha* Koch
		Phanerotomea sp.
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus tibialis Fabricius
Carabidae	*Cypholoba alstoni* (Péringuey)	
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Metacatharsius* sp.	
	Gymnopleurus humanus MacLeay	

Table 5.20. (*continued.*)

NEUROPTERA	
Myrmeleontidae	*Palparellus dubiosus* Péringuey
	Cueta spec. nov. 4
ORTHOPTERA	
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
ARACHNIDA	
Gnaphosidae	*Xerophaeus* sp.
Salticidae	*Menemerus* sp.

5.6.5. Oase

A total of 211 individuals from 24 species (Figure 5.3), 15 families and five orders of Arthropoda were sampled at this site and listed in Table 5.21. The diversity index for the site amounts to $H' = 2.28$ ($E = 0.72$) (Figure 5.4). Of the 15 families, six were insect families of which three were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species of the genus *Creoleon* was recorded.

Of the total of 24 species, six were species of four different tribes of Tenebrionidae. The Tenebrionidae constituted 68.25% of the total of 211 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were *Eurychora nitida* (47.87%), followed by *Stips dohrni* (9.95%) and *Parastizopus armaticeps* (9.00%).

Table 5.21. Arthropods collected at the Oase study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Eurychorini	*Eurychora nitida* Haag
		Stips dohrni (Haag)
	Molurini	*Somaticus incostatus* (Gebien)
		Tarsocnodes ephialtes Koch
	Zophosini	*Zophosis amita* Penrith
	Opatrini	*Parastizopus armaticeps* Péringuey
Carabidae	*Crepidogastrinus kochi* Basilewsky	
Dytiscidae	*Eretes stricticus* Linnaeus	
NEUROPTERA		
Myrmeleontidae	*Palparidius capicola* Péringuey	
	Palparellus dubiosus Péringuey	
	Creoleon spec. nov.	
ORTHOPTERA		
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl	
THYSANURA		
Lepismatidae	*Ctenolepisma terebrans* Silvestri	
ARACHNIDA		
Solpugidae	*Zeria* sp.	
Daesiidae	*Hemiblossia termitophila* Lawrence	
Hexisopodidae	*Hexisopus lanatus* (Koch)	
Ammoxenidae	*Ammoxenus coccineus* Simon	

Table 5.21. (*continued.*)

ARACHNIDA	
Caponiidae	*Caponia capensis* Purcell
Gnaphosidae	*Setaphis bilinearis* Tucker
	Asemesthes lineatus Purcell
Philodromidae	*Hirriusa* sp.
Salticidae	*Phlegra* sp.
Buthidae	*Parabuthus leavifrons* (Simon)
	Parabuthus ?granulatus (Hemprich & Ehrenberg)

5.7. KONKIEP DUNE LINE

Of the 366 arthropods sampled at the two sites of the Konkiep Dune Lline, 48.09% (176) were Tenebrionidae specimens (Figure 5.1), with an average diversity of 2.89 (Figure 5.5). Of the Tenebrionidae, only *Onymacris multistriata* occurred in large numbers at both the Sandverhaar and Untersee sites, while species of Nemopteridae (Neuroptera) and Scarabaeidae (Coleoptera) dominated the sampled material.

5.7.1. Sandverhaar

A total of 277 individuals from 28 species (Figure 5.3), 12 families and five orders of Arthropoda were collected at this site and listed in Table 5.22. The diversity index for the site amounts to *H'* = 2.99 (*E* = 0.90) (Figure 5.4). Of the 12 families, nine were families of Coleoptera.

Of the total of 28 species, nine were species of five different tribes of Tenebrionidae. The Tenebrionidae constituted 47.29% of the total of 277 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were *Cimicia spinipes* (16.97%), followed by *Onymacris multistriata* (11.55%) and *Parastizopus armaticeps* (9.39%). One species of Nemopteridae (Neuroptera), *i.e. Derhynchia vansoni*, constituted 19.49% of the total number of arthropods collected.

Table 5.22. Arthropods collected at the Sandverhaar study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Cryptochilini	*Pachynotelus leucinus* Koch
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips dohrni (Haag)
	Zophosini	*Zophosis deyrollei rufipennis* Péringuey
	Opatrini	*Parastizopus armaticeps* Péringuey
		Gonopus agrestis Fahraéus
Bruchidae	*Caryedon* sp.	
Curculionidae	*Leptostethus argentatus* Thompson	
Histeridae	Dahlgrenius sp. 2	
Scarabaeidae	*Lepisia virescens* Péringuey	
	Peritrichia bella Moser	

Table 5.22. (*continued.*)

COLEOPTERA	
Scarabaeidae	*Caccobius* sp.
	Metacatharsius sp.
	Schizonycha sp.
HEMIPTERA	
Cydnidae	sp.
NEUROPTERA	
Myrmeleontidae	*Palparellus dubiosus* Péringuey
	Furgella damarinus Péringuey
	Myrmeleon doralice Banks
Nemopteridae	*Derhynchia vansoni* Tjeder
ORTHOPTERA	
Schizodactylidae	*Comicus capensis* Brunner v. Wattenwyl
ARACHNIDA	
Gnaphosidae	*Zelotes oneili* (Purcell)
	Setaphis bilinearis Tucker
	Asemesthes lineatus Purcell
Lycosidae	*Evippa* sp.
Salticidae	*Phlegra* sp.

5.7.2. Untersee

A total of 89 individuals from 20 species (Figure 5.3), nine families and five orders of Arthropoda were sampled at this site and listed in Table 5.23. The diversity index for the site amounts to $H' = 2.78$ ($E = 0.93$) (Figure 5.4). Of the nine families, seven were insect families, of which four were from the order Coleoptera.

Of the total of 20 species, seven were species of six different tribes of Tenebrionidae. The Tenebrionidae constituted 50.56% of the total of 89 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were *Eurychora nitida* (24.72%), followed by *Onymacris multistriata* and *Psammodes vialis* (both 7.87%).

Thirty-nine other Coleoptera specimens were sampled, including a species of *Metacatharsius* (Scarabaeidae) that constituted 19.10% of the total sample of specimens.

Table 5.23. Arthropods collected at the Untersee study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Drosochrini	*Drosochrini* sp. 2
	Eurychorini	*Eurychora nitida* Haag
	Molurini	*Psammodes vialis* Burchell
	Zophosini	*Zophosis amita* Penrith
	Opatrini	*Gonopus agrestis* Fahraéus
Carabidae	*Boeomimetus ephippium* Boheman	

Table 5.23. (*continued.*)

COLEOPTERA	
Histeridae	*Dahlgrenius* sp. 2
Scarabaeidae	*Lepisia virescens* Péringuey
	Peritrichia bella Moser
	Chasme kochi Schein
	Metacatharsius sp.
	Scarabaeus sp.
	Schizonycha sp.
HEMIPTERA	
Pentatomidae	sp.
ORTHOPTERA	
Gryllidae	*Gryllus* sp.
THYSANURA	
Lepismatidae	*Ctenolepisma pluriseta* Silvestri
ARACHNIDA	
Gnaphosidae	*Asemesthes lineatus* Purcell
Salticidae	*Pseudicius* sp.

5.8. GRÜNAU DUNE CLUSTER

A total of 292 arthropods were sampled across the three sites, of which 99 (33.9%) were of the family Tenebrionidae (Figure 5.1). The average Shannon's diversity index amounted to 3.11 (Figure 5.5) for the dune cluster. Of the Tenebrionidae, *Cimicia spinipes* was recorded in dominating numbers at both the Middelpos and Bruinheuwel sites. About 30% of the material collected at the Middelpos and Bruinheuwel sampling sites were spiders, while species of Scarabaeidae (Coleoptera) and Myrmeleontidae (Neuroptera) dominated sample numbers at Norachas.

5.8.1. <u>Middelpos</u>

A total of 77 individuals from 31 species (Figure 5.3), 20 families and six orders of Arthropoda were sampled at this site and listed in Table 5.24. The diversity index for the site amounts to $H' = 3.41$ ($E = 0.99$) (Figure 5.4). Of the 20 families, 10 were insect families, all of which were from the order Coleoptera. One new Myrmeleontidae (Neuroptera) species within the *Cueta* genus was recorded.

Of the total of 31 species, six were species of three different tribes of Tenebrionidae. The Tenebrionidae constituted 29.87% of the total of 77 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were *Cimicia spinipes* (12.99%), followed by *Renatiella scrobipennis* (11.69%). The rest of the specimens just constituted 1.3% each.

Table 5.24. Arthropods collected at the Middelpos site in southern Namibia (2004).

COLEOPTERA		
Tenebrionidae	Adesmini	*Renatiella scrobipennis* (Haag)
	Cryptochilini	*Pachynotelus granaticollis* Gebien
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
		Stips dohrni (Haag)
		Stipsosoma sp.
Bruchidae	sp.	
Histeridae	*Dahlgrenius* sp. 1	
	Dahlgrenius sp. 2	
HEMIPTERA		
Berytidae	*Gampsocoris*	
Cydnidae	sp. 2	
Pentatomidae	sp.	
NEUROPTERA		
Myrmeleontidae	*Cueta* spec. nov. 4	
	Pamares damarus Mansell	
ORTHOPTERA		
Gryllidae	*Gryllus* sp.	
Schizodactylidae	*Comicus calaharicus* Irish	
THYSANURA		
Lepismatidae	*Ctenolepisma terebrans* Silvestri	

Table 5.24. (*continued.*)

ARACHNIDA	
Daesiidae	*Namibesia* sp.
Caponiidae	*Diploglena capensis* Purcell
Gnaphosidae	*Setaphis bilinearis* Tucker
	Asemesthes lineatus Purcell
Palpimanidae	*Palpimanus* sp.
Philodromidae	*Hirriusa* sp.
	Thanatus pagenstecheri Strand, 1906
Salticidae	*Phlegra* sp.
Salticidae	*Pseudicius* sp.
Salticidae	*Phlegra* sp. 2
Scorpionidae	sp.
Sparassidae	*Orchestrella* sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
Pseudoscorpiones	sp.

5.8.2. Norachas

A total of 79 individuals from 23 species (Figure 5.3), 15 families and six orders of Arthropoda were sampled at this site and listed in Table 5.25. The diversity index for the site amounts to H' = 3.02 (E = 0.96) (Figure 5.4). Of the 15 families, eight were insect families, three of which were from the order Coleoptera. A new Myrmeleontidae (Neuroptera) species within the genus *Creoleon* was recorded.

Of the total of 23 species, four were species of three different tribes of Tenebrionidae. The Tenebrionidae constituted 8.86% of the total of 79 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were

Stenocara gracilipes (3.80%), followed by *Rozonia strigicollis* (2.53%). The other two Tenebrionidae species were each represented by one specimen only (1.27%).

Table 5.25. Arthropods collected at the Norachas study site in southern Namibia (2003).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Stenocara gracilipes* Solier
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
	Tentyriini	*Rozonia strigicollis* Fairmaire
Histeridae	*Dahlgrenius* sp. 2	
Scarabaeidae	*Caccobius* sp.	
	Aphodius sp.	
	Metacatharsius sp.	
HYMENOPTERA		
Anthophoridae	*Xylocopa hottentotta* Smith	
NEUROPTERA		
Myrmeleontidae	*Palparellus dubiosus* Péringuey	
	Creoleon spec. nov.	
ORTHOPTERA		
Gryllidae	*Gryllus* sp.	
Schizodactylidae	*Comicus calaharicus* Irish	

Table 5.25. (*contibued.*)

THYSANURA	
Lepismatidae	*Ctenolepisma terebrans* Silvestri
ARACHNIDA	
Ammoxenidae	*Ammoxenus coccineus* Simon
Gnaphosidae	*Setaphis bilinearis* Tucker
	Asemesthes lineatus Purcell
Philodromidae	*Thanatus pagenstecheri* Strand
Salticidae	*Pellenes* sp.
Zodariidae	*Capheris* sp.
Buthidae	*Parabuthus brevimanus* (Thorell)
	Parabuthus leavifrons (Simon)
Solpugidae	*Solpugiba* sp.

5.8.3. Bruinheuwel

A total of 136 individuals from 25 species (Figure 5.3), 11 families and four orders of Arthropoda were sampled at this site and listed in Table 5.26. The diversity index for the site amounts to $H' = 2.91$ ($E = 0.90$) (Figure 5.4). Of the 11 families, three were insect families, one of which is from the order Coleoptera. A new Myrmeleontidae (Neuroptera) species within the *Centroclisis* genus was recorded.

Of the total of 25 species, eight were species of four different tribes of Tenebrionidae. The Tenebrionidae constituted 50.74% of the total of 136 arthropods sampled (Figure 5.2). The dominant Tenebrionidae species were

Phanerotomea monacha (22.79%), *Cimicia spinipes* (16.91%), *Gonopus agrestis* and *Eurychora nitida* (both 3.68% of the total number of Tenebrionidae sampled).

Table 5.26. Arthropods collected at the Bruinheuwel study site in southern Namibia (2004).

COLEOPTERA		
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg
		Renatiella scrobipennis (Haag)
	Eurychorini	*Cimicia spinipes* Fairmaire
		Eurychora nitida Haag
	Molurini	*Phanerotomea monacha* Koch
		Psammodes vialis Burchell
		Tarsocnodes ephialtes Koch
	Opatrini	*Gonopus agrestis* Fahraéus
NEUROPTERA		
Myrmeleontidae	*Palparellus dubiosus* Péringuey	
	Centroclisis spec. nov. 2	
	Cymothales illustris Navás	
THYSANURA		
Lepismatidae	*Ctenolepisma terebrans* Silvestri	
ARACHNIDA		
Agelenidae	*Agelena suboculata* Simon	
Gnaphosidae	*Setaphis bilinearis* Tucker	
	Asemesthes lineatus Purcell	

Table 5.26. (*continued.*)

ARACHNIDA	
Philodromidae	*Hirriusa* sp.
Sparassidae	*Orchestrella* sp.
Theridiidae	*Euryopis* sp.
	Dipoena sp.
Zodariidae	*Capheris* sp.
Buthidae	*Parabuthus granulatus* (Hemprich & Ehrenberg)
	Parabuthus brevimanus (Thorell)
	Hottentotta arenaceus Birula
	Parabuthus leavifrons (Simon)
Solpugidae	*Zeria schlechteri* (Purcell)

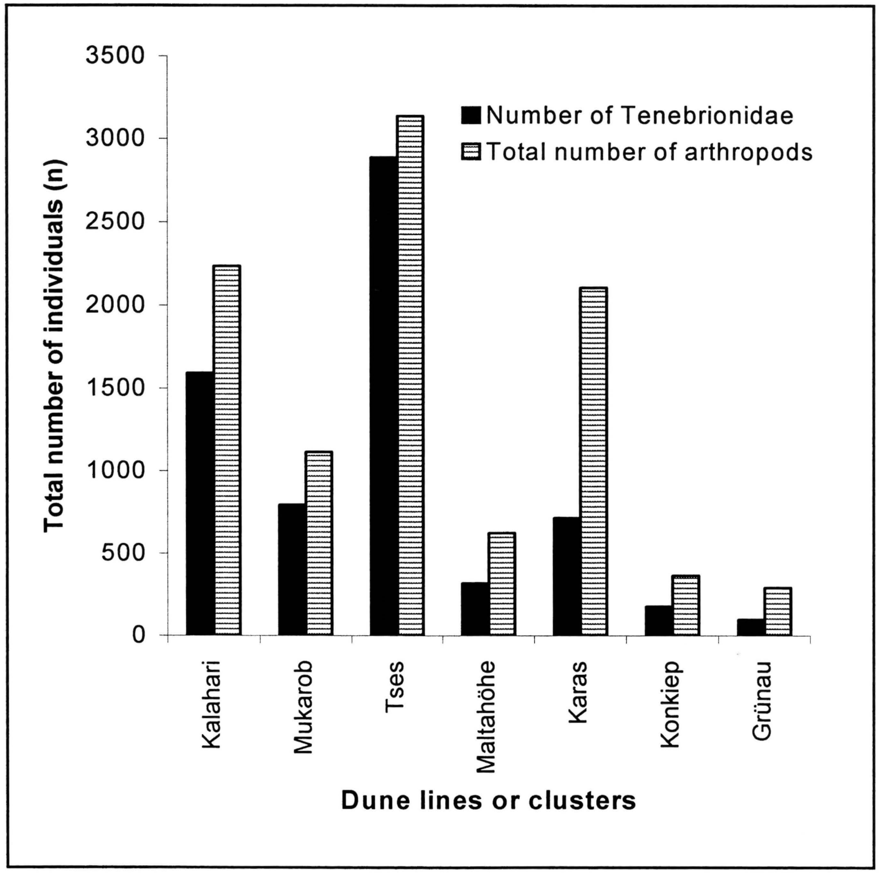

Figure 5.1. Total numbers of Arthropods *versus* total numbers of Tenebrionidae recorded on seven different dune lines/clusters in southern Namibia (2003, 2004).

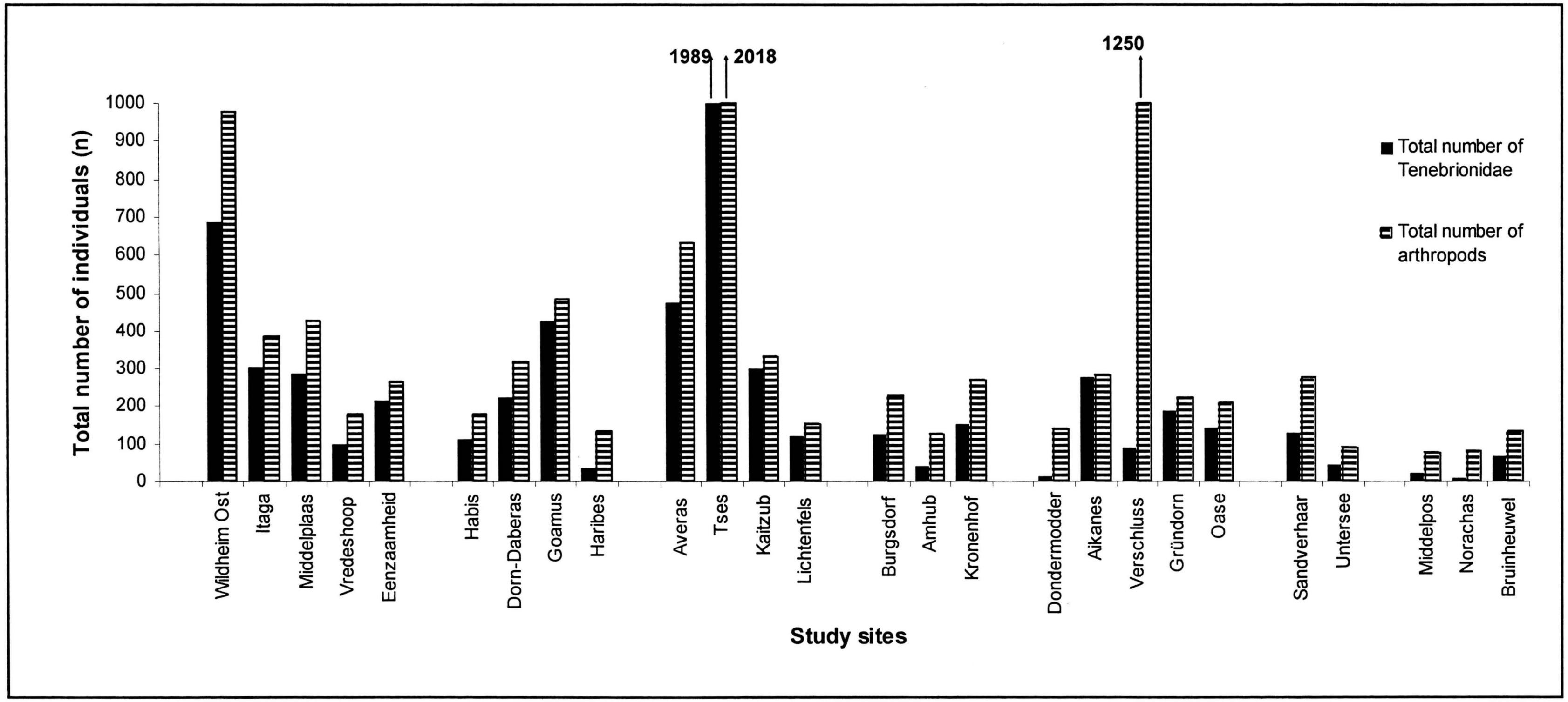

Figure 5.2. Total numbers of arthropods *versus* total numbers of Tenebrionidae recorded at the 26 sampling sites in southern Namibia (2003, 2004).

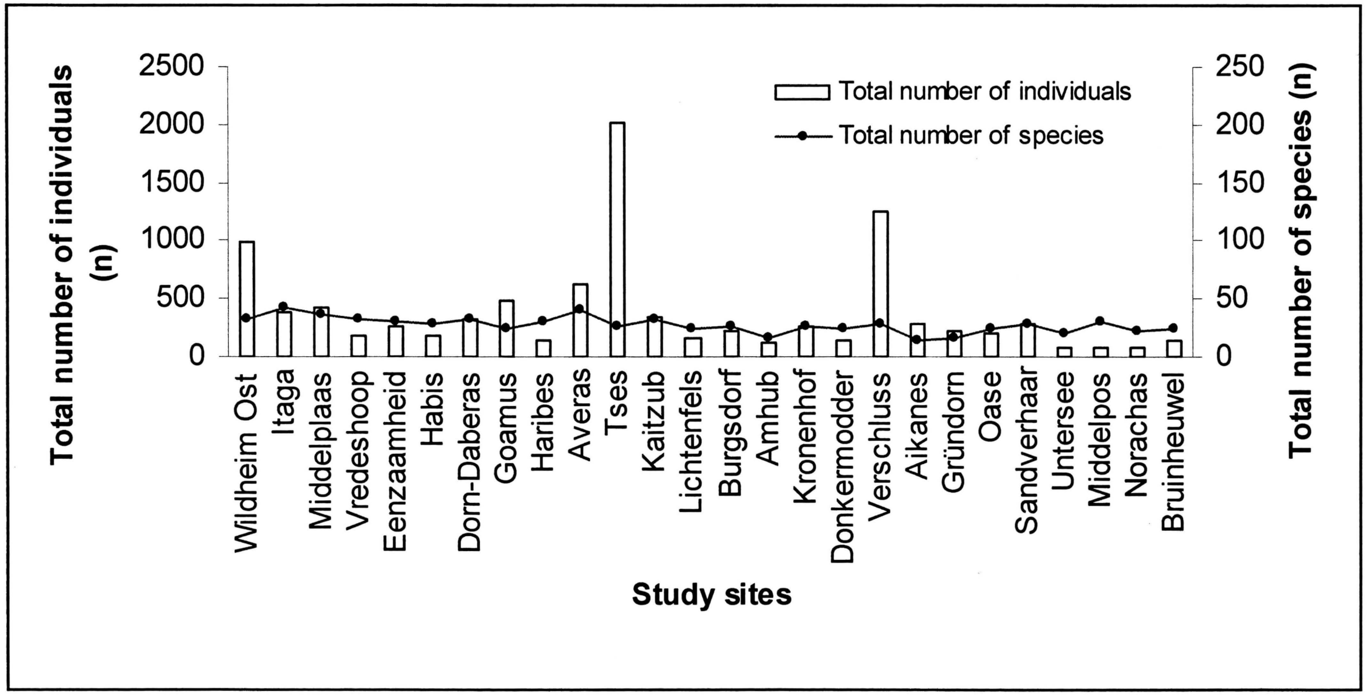

Figure 5.3. A comparison between the total number of species and the total number of arthropods recorded on 26 study sites in southern Namibia (2003, 2004).

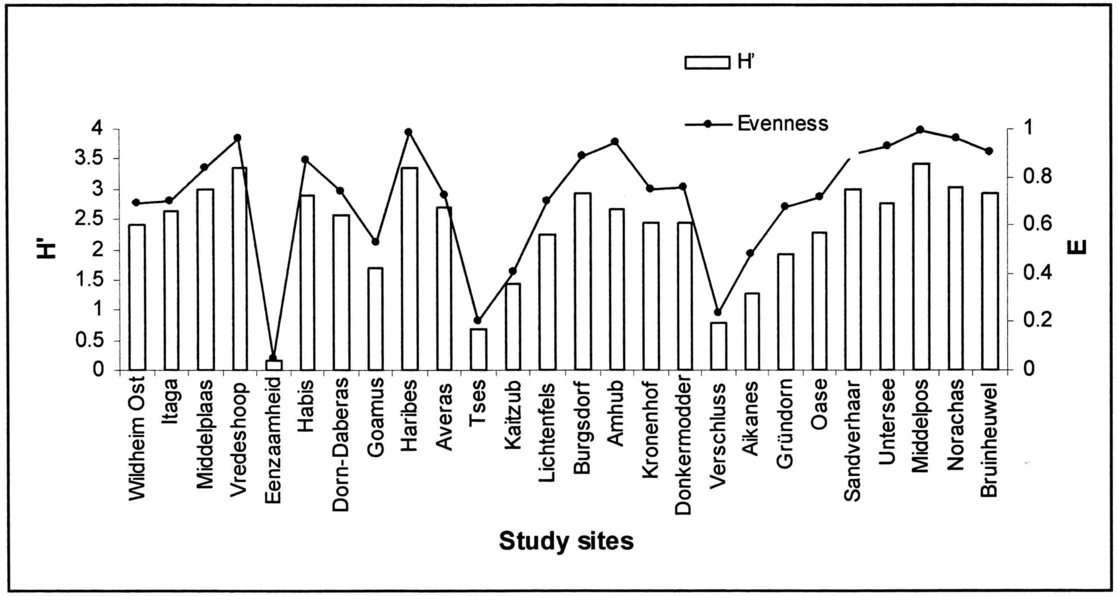

Figure 5.4. Diversity (*H'*) and evenness (*E*) of arthropods collected at 26 study sites in southern Namibia (2003, 2004).

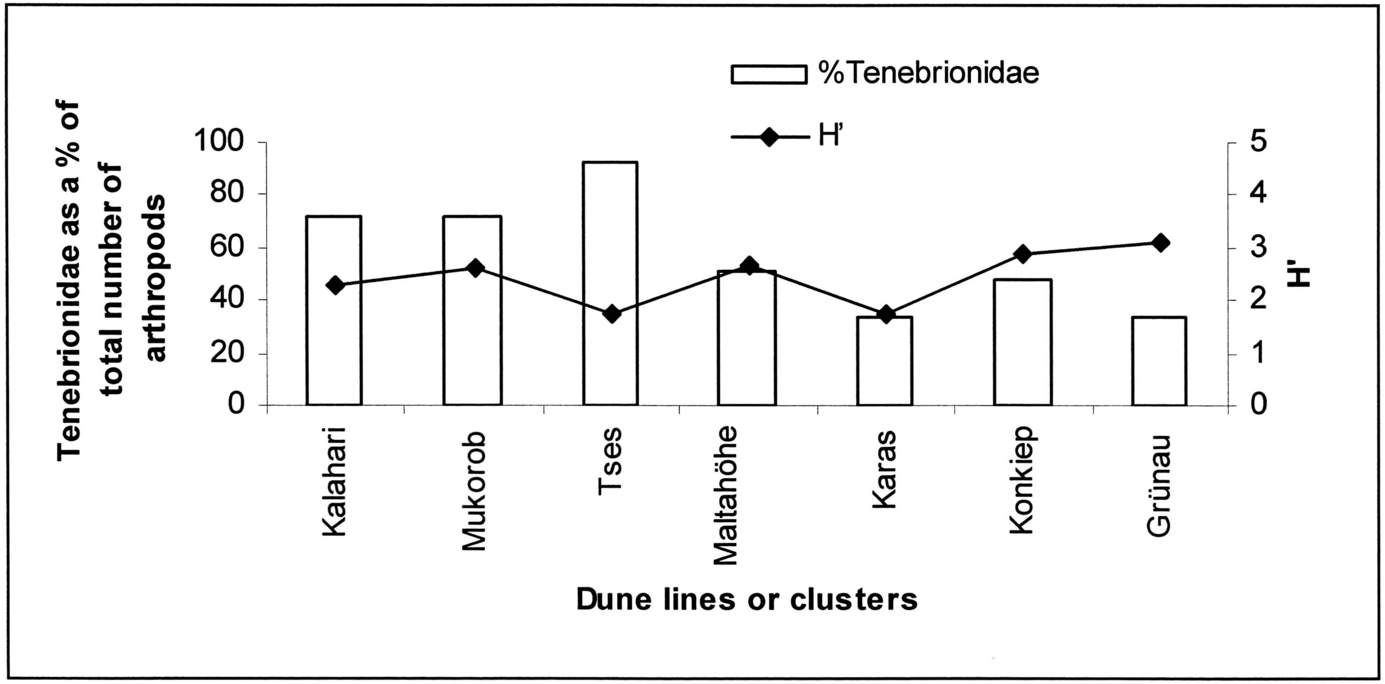

Figure 5.5. Total numbers of Tenebrionidae, depicted as percentages of total numbers of arthropods, as well as average Shannon diversity indices for 7 dune lines/clusters in southern Namibia (2003, 2004).

CHAPTER 6

Analyses & Discussion

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6.1. INTRODUCTION

The climatic zonation that existed before, during and after the breakup of the Gondwana supercontinent can still be observed to some extent in the presence of specific endemic groups of plesiomorphic insect taxa in certain regions. From the high number of endemic plesiomorphic species still present in the Western Cape, it can be deduced that this area underwent little climatic fluctuation during and after the establishment of modern climatic condition in southwestern Africa (Endrödy-Younga, 1978). In addition, the presence of derived Cape-type species throughout the Karoo, Namib and Kalahari establishes the Western Cape, along with central Africa as two significant centers of origin (Endrödy-Younga, 1978; Irish, 1990). A south to north and north to south radiation of apterous species is comprehended by the presence of apomorphic derivatives of Cape-type and central Africa-type entomofauna on dune systems in Namibia. An interpluvial arid corridor between these two main centers of origin was proposed, which facilitated the movement of xerophilous insects between north and south, as well as east to west (*cf.* Chapters 1 & 2).

how?

ok

After careful examination of the arthropod material sampled during this study and review of appropriate literature, 10 species of darkling beetles (Tenebrionidae: Coleoptera), three species of fish moths (Lepismatidae: Thysanura) and two dune cricket (Schizodactylidae: Orthoptera) species were identified as definite psammophiles. Table 6.1 lists all psammophiles collected during this study.

criteria?

Table 6.1. Psammophilous species ~~employed~~ used in the biogeographical analyses of insects occurring on isolated dunes in southern Namibia (2003 – 2004). (ID: Specialist that provided identification. Where no reference is made to an expert identification, level 2 identification was performed either by using taxonomic keys, or by careful comparison with specialist-identified material in the National Museum of Namibia).

COLEOPTERA			**ID**
Tenebrionidae	Adesmiini	*Onymacris multistriata* Haag-Rutenberg	S. Louw
Tenebrionidae	Caenocrypticini	*Caenocrypticus phaleroides* Koch	S. Louw
Tenebrionidae	Cryptochilini	*Pachynotelus granaticollis* Gebien	S. Louw
Tenebrionidae	Cryptochilini	*Pachynotelus leucinus* Koch	S. Louw
Tenebrionidae	Eurychorini	*Cimicia spinipes* Fairmaire	S. Louw
Tenebrionidae	Eurychorini	*Stips gebieni* (Hesse)	S. Louw
Tenebrionidae	Opatrini	*Calaharena dutoiti* Koch	
Tenebrionidae	Zophosini	*Zophosis rufipennis* Péringuey	S. Louw
Tenebrionidae	Zophosini	*Zophosis gordoniae* Penrith	
Tenebrionidae	Zophosini	*Zophosis deyrollei jacoti* Penrith	
ORTHOPTERA			
Schizodactylidae		*Comicus calaharicus* Irish	J. Irish
Schizodactylidae		*Comicus capensis* Brunner v. Wattenwyl	J. Irish
THYSANURA			
Lepismatidae		*Ctenolepisma terebrans* Silvestri	J. Irish
Lepismatidae		*Ctenolepisma pluriseta* Silvestri	J. Irish
Lepismatidae		*Ctenolepisma latera* Irish	J. Irish
Lepismatidae		*Ctenolepisma pauliani* Wygodzinsky	J. Irish

which are not definite? see 155

6.2. TENEBRIONIDAE (COLEOPTERA) PSAMMOPHILES

Different groups of organisms react differently to short-term environmental fluctuations (Endrödy-Younga, 1978). The wingless tenebrionids are, in comparison, less responsive in terms of dispersal than, for example, certain groups of vertebrates or plants, mainly as a result to their means of dispersal. More adaptive Tenebrionidae lineages adopted psammophilous characters allowing them to inhabit arid to hyper-arid environments as climatic conditions in southwestern Africa gradually dried out, while others became isolated in whatever patches of relatively intact habitat remained (*sensu* Endrödy-Younga, 1978; Irish, 1990; Penrith, 1984c, 1984d; Koch, 1962a;). With respect to tribal and subtribal distribution of Tenebrionidae, no real discrepancy exists between southern African dune systems (Penrith, 1984d).

6.2.1. Adesmiini (Tentyriinae)

A total of 915 individuals of *Onymacris multistriata* was sampled at all of the five control sites, as well 17 of the study sites (Figure 6.1). According to Penrith (1984c), the species is widely distributed on Kalahari related sands between 23°S and 29°S, and 17°E and 23°E, and probably originated in the southwestern part of this area (Penrith, 1984d). This apomorphic genus is suggested to be of post-Gondwana origin (no similar species are found on other southern continents), and the divergence of the genus took place as a result of increased aridity and the deposition of sand pockets in the lower Orange River (Penrith, 1986). The whole *Onymacris* genus has a strong preference for sand (*sensu* Penrith, 1984d), and *O. multistriata* is endemic to the Kalahari sands (Louw, 1984).

6.2.2. Cryptochilini (Tentyriinae)

Two species of *Pachynotelus* were recorded. One individual of *P. granaticollis* was collected at the Middelpos study site (Figure 6.2), and one individual per site of *P. leucinus* was collected at Sandverhaar and Verschluss (Figure 6.3).

Pachynotelus belongs to the most plesiomorphic lineage of Cryptochilina, although it possesses of all the apomorphies related to the strict psammophily of the genus (Penrith & Endrödy-Younga, 1994). An explanation for the low recording frequency of *Pachynotelus* could be that Cryptochilina is a temperate group and that their emergence strongly correlates with vegetation and the first spring rains (Penrith *et al.*, 1994). This is somewhat contradictory to the fact that, during and just prior to the study period, the site of Middelpos received no rain in almost three years. The distribution and origin of *Pachynotelus* might be another explanation for their low abundance. According to Penrith *et al.* (1994), the subtribe Cryptochilina had its center of origin in the Namaqua area north and south of the Orange River, and only one species of *Pachynotelus* presently has a range extending eastward into the southwestern Kalahari dunes, whilst others are restricted to the Namib Desert and the pro-Namib. Phylogenetically, Cryptochilini is also related to the two tribes endemic to the Namib Dessert, *viz.* Calognathini and Vansoniini (Koch, 1962a).

6.2.3. Eurychorini (Tentyriinae)

Not much published information on the origin and biogeography of Eurychorini exists and the tribe has not recently been revised. The *Stips* group of Eurychorini has its distribution in the central parts of the Southwestern Zone, extending south of the Orange River, and as far north as the southern parts of Angola and east into the Kalahari dunes of Botswana (Endrödy-Younga, 1978). Koch (1955) delimits the distribution of Eurychorini to the temperate, entire southern half, of the African continent, and adds that this tribe, along with the tribe of Molurini, is autochthonous, though not endemic, to Africa. It can be assumed that the tribe of Eurychorini had a southwestern origin, due to the concentration of genera in that area.

The psammophilous *Cimicia spinipes* is listed as one of the species limited to the southern Namib Desert between the Orange and the Koichab Rivers (Koch, 1955). Although *Stips* is described as a usually extra-dune genus, save for two psammophilous species in the Namib, *viz.* *S. stali* and *S. dorsocostata* (Koch, 1962b), it is deduced that *Stips gebieni* is psammophilous, since it was determined that the species habitat of strict preference is the vegetational plinth of the Kalahari dunes (Louw, 1982).

but in crest

A total of 162 specimens of *Cimicia spinipes* were recorded at all of the five control sites and nine of the study sites (Figure 6.4), while *Stips gebieni* was sampled in large numbers (2835 individuals in total) at 15 sites (all of the five control sites and 10 study sites) (Figure 6.5).

6.2.4. Zophosini (Tentyriinae)

Penrith (1984b) postulated that Zophosini originated after the breakup of Gondwana, since the tribe does not occur on other southern continents such as South America or Australia. Seeing as northern Namibia and the southwestern part of Angola is the only area where all three of the relict lineages and the highest number of species and subgenera occur, this area is proposed as the centre of origin of the tribe (Penrith, 1984b). The fairly derived tribe of Zophosini probably diverged due to climatic fluctuations during the Quaternary and Late Tertiary (after modern-day climatic conditions in southwestern Africa were initiated, *cf.* Chapter 1).

The larger part of the 56 psammophilous *Zophosis* species that occur in the Kalahari are endemic (Penrith, 1984d). The subgenus *Heliophosis,* as well as the *Zophosis deyrollei* species group, constitutes two of the four dominant psammophilous *Zophosini* lineages in the Kalahari dune sea. *Zophosis (Heliophosis) gordoniae* was recorded at one study site only, *i.e.* Donkermodder (Figure 6.6), while *Z. deyrollei jacoti* was only sampled at Middelplaas, one of the control sites (Figure 6.7). Although supposedly widely distributed in the Kalahari, zophosines are cryptic insects (Penrith, 1984b) and not easily sampled by employing unbiased sampling methods such as the ones used in this study. *Hologenosis*, the least derived of the subgenera (Penrith, 1984a & b) is widely distributed across Africa, with a clear concentration of species in the southwestern part of the continent (Penrith, 1984a). The most abundant *Zophosis* species, *Zophosis (Hologenosis) rufipennis*, was recorded at three control sites and five study sites (Figure 6.8).

6.2.5. Caenocrypticini (Tentyriinae)

Seven specimens of *Caenocrypticus (Psammotopulus) phaleroides* were collected at two of the control sites (Middelplaas and Itaga) and three study sites (Goamus, Kronenhof and Verschluss) (Figure 6.9).

The tribe Caenocrypticini is postulated to have a central Gondwana origin (specifically the western part of the present Namibia) (Endrödy-Younga, 1996) when, presumably, more temperate climatic conditions prevailed. Evidence for this is provided in the distribution of the extant, most plesiomorphic South African species of the tribe. The latter do not occur in the ultrapsammophilous conditions of the central Namib Desert, while the primitive subgenera of the tribe are distributed in an arch to the north and south of the center of the observed emanations, *i.e.* the central Namib. According to Endrödy-Younga (1996), the common ancestors of these primitive species had disappeared during the rapid desiccation of the west coast of southern Africa. Although the entire tribe favours sandy substrates and arid to semi-arid climatological conditions, only some species of two subgenera, *i.e. Vernayella* and *Psammotopulus*, managed to adapt to ultra-psammophilous conditions. The lineage comprising *Vernayella* retains the most derived characters of the two most apomorphic subgenera of Caenocrypticini, although *Caenocrypticus (Psammotopulus) phaleroides* was the first of the psammophiles to penetrate the Namib area. This is evident by the fact that *C. (P.) phaleroides* is the only psammophilous species that occurs in all of the three biogeographically separated sections of the Namib, while the other psammophiles are morphologically restricted to the isolated northern, central and southern sections of the desert (Endrödy-Younga, 1996). The latter statement relates back to the suggestion in Chapter 1 of an ancient, well-interconnected or continuous sand-mass occupying the southwestern African interior.

6.2.6. Opatrini (Tenebrioninae)

Calaharena dutoiti was recorded only at two of the control sites, namely Vredeshoop (one individual) and Itaga (four individuals) (Figure 6.10). No specimens were collected at any of the study sites.

so why continue?

Calaharena is one of the most derived of the psammophilous genera of Stizopina (Penrith, 1982). Although the present distribution range of *Calaharena* extends between 18°S and 30°S, 18°E and 23°E (Penrith, 1982) (Figure 6.10), the remaining four genera in the group occurs only in a narrow strip along the Namibian west coast (from the Orange River northwards to 23°S). The most plesiomorphic genus in the group (*i.e. Sphaerostibes*) has only been recorded from one locality in northern Namaqualand (south of the Orange River) (Penrith, 1982).

6.3. LEPISMATIDAE (THYSANURA) PSAMMOPHILES

Irish (1990) makes use of the dispersal of the psammophilous fish moth species, *Ctenolepisma terebrans*, to illustrate the movement of the African continent in a northerly direction after the breakup of Gondwana. Using evidence of typical Kalahari taxa that presently occur well into southern parts of central Africa, he argues that, geologically, the true Kalahari sand system reached much further north than its present-day restriction to the southwestern part of Africa. This argument is supported by apomorphic species occurring in the southwestern corner of the Kalahari sand seas (from where they dispersed further *via* sand pockets), while other, more plesiomorphic species in the same lineages occur throughout the entire Kalahari system (Irish, 1990).

sand distribution as evidence?

Four species of Lepismatidae were sampled, all of which are psammophilous and belong to the genus *Ctenolepisma,* and specifically the subgenus *Sceletolepisma* (Irish, 1987). *Ctenolepisma (S.) terebrans* is typically associated with sparsely vegetated dunes, such as the southwestern-most dunes of the Kalahari (well into western Botswana), the drier parts of the former Cape Province and the vegetated interdune valleys of the Namib Desert up to the Kuiseb River (Irish, 1987). During the present study, *C. (S.) terebrans* was recorded at six of the southwestern-most study sites (Figure 6.11) and one, more central site, *viz*. Dorn-Daberas. *C. (S.) pluriseta* was previously reported to be sparsely distributed between the Cape Peninsula and Tanzania, with a preference of and concentration in the red sands of the Kalahari sand sea and its fringes (Irish, 1987). Recent observations, however, delimits the distribution of the species to the southern parts of the Kalahari (Irish, pers. comm.). The species was recorded at five of the northern study sites (central Namibia) (Figure 6.12) and none of the control sites.

Irish (1987) described the phylogeny of C. *(S.) latera* and restricted the species' distribution to the red sandy substrates of southwestern Kalahari. A total of 16 individuals were recorded across four study sites during sampling in 2003 (Figure 6.13).

Eng

C. *(S.) pauliani*, the most apomorphic species in the genus, known to be restricted to the Namib Desert between the Cunene River in northern Namibia and Port Nolloth (Irish, 1987). The species is ultra-psammophilous (dives into loose sand) and the only species in the genus that occurs on barren, vegetationless dunes. The five individuals were collected at one study site only, *viz.* Kronenhof (Figure 6.14) (the study site in closest proximity to the Namib).

say earlier

6.4. SCHIZODACTYLIDAE (ORTHOPTERA) PSAMMOPHILES

Of the only two genera in the Schizodactylidae family, *Comicus* is the more apomorphic by virtue of morphological characters, as well as its secondary apterism (Irish, 1986). The origin of the family is suspected to date back to the late Jurassic when India was still in contact with Africa. Four species of the more plesiomorphic, winged genus, *Schizodactylus*, persists in India in the subtropical climatological conditions subject to which the family possibly had its origin. All but two plesiomorphic *Comicus* species, which still inhabit hard substrates, are psammophilous, with the psammophile pre-adaptations possibly acquired due to the climatic fluctuations during and after the breakup of Gondwana (Irish, 1986).

According to Irish (1986), *Comicus capensis* occur only in riverbeds, interdune valleys and at dune bases, while only *C. calaharicus*, the more apomorphic and likely descendant of *C. capensis*-like ancestors, occurs on proper dunes. Contrary to what is expected from its distribution in the literature, *C. capensis* was recorded on 12 study dunes (and none of the control sites) (Figure 6.15), whilst *C. calaharicus* was sampled at four of the five control sites and at three additional study sites (Figure 6.16).

6.5. BIOGEOGRAPHICAL ANALYSES

With the palaeoclimatological background and ecological principals set, a simple hypothesis was formulated in Chapter 2. Utilizing the distribution patterns of psammophilous insects, the central aim of this study was to test for a significant statistical difference between the psammophilous species composition of the main Kalahari (serving as control) and pre-identified isolated dunes by means of various analysis techniques based on different biogeographical hypotheses. The specific methodologies that were selected for use from the range of existing possibilities, were chosen on the basis of their simplicity and follows Endrödy-Younga (1982) who states that 'Events take a much more simple course in nature than we often postulate to them'.

When considering the theory of Island Biogeography, proposed by MacArthur & Wilson (1963, in Rosenzweig, 1995), an island is defined as a self-contained region whose species originated entirely by immigration from outside the region. Immigration implies the arrival of a species propagule sufficient to establish a population. It is not considered as immigration if the species already exists on the island by the time that the propagule arrives.

Since the first hypothesis aims at determining whether the isolated dunes are fragmented islands originating from the Kalahari 'mainland', or rather relictual remains of a larger palaeo-sand sea, some principles of island biogeography can be applied. For the Kalahari Dune Sea to be considered the 'mainland' , it has to be assumed that the modern-day interrelated dunes of the Kalahari offer no ecological restriction for the dispersal of the dune-substrate confined psammophiles.

Only then is it accepted that the larger sand mass of the Kalahari will include a wider variety of habitats than the smaller sand 'islands' and will therefore harbor more species. In addition, if the Kalahari Dune Sea was the 'mainland' from which the psammophiles on the isolated dunes emigrated, the immigrant species should all be represented at the control sites, while not all species present at the control sites necessarily have to appear at the study sites due to different mechanisms and routes of dispersal. Island species diversity will decrease with an increase in distance from the mainland. Also, natural barriers will influence the number of species successfully colonizing an island (Rosenzweig, 1995). Such natural barriers include physical barriers, such as mountain ranges and rivers, but very importantly also barriers such as unfavorable habitat with respect to substrate, vegetation and climate.

Techniques employed to analyze alpha diversity of each site entailed tabling presence and absence of psammophilous species sampled, and species richness (n). Beta diversity was analyzed by correlating species richness of consecutive sites, firstly down a pre-identified dune line or dune cluster, and secondly according to increasing distance from the main Kalahari using Pearson's correlation coefficient (R^2). Sorenson's qualitative index of similarity and a cluster analysis of grain size distribution was applied as an additional measure of beta diversity.

6.5.1. Presence and absence

The method of using presence and absence of species was used in a similar study by Endrödy-Younga (1982), when he employed insect psammophiles to investigate the possibility of an earlier sand continuity in the now-segregated dune fields of the Namib Desert.

For this method of analysis, two approaches were taken. The first was to investigate whether the presence of psammophilous species increase or decrease along the six pre-identified dune lines/clusters in comparison with the main Kalahari dune line (Tables 6.2 (a) and (b)). The second approach in analyzing presence and absence was to test whether the presence of psammophilous species increase or decrease with increasing distance from the main Kalahari. The distances were determined by taking cross sections on a 1:250 000 topographical map in a straightforward fashion, from east (where the first dense concentration of Kalahari dunes are observed) to west (the study site in question) (Tables 6.3 (a) and (b)). When comparing species presence/absence between study sites and main Kalahari sites, the five control sites are considered a unit after the abovementioned assumption that the Kalahari Dune Sea does not restrict the distribution of psammophiles.

Table 6.2. (a) Presence and absence of psammophilous Tenebrionidae on various pre-identified dune lines and clusters in southern Namibia (2003, 2004). (x: present study records; o: presence cited in the literature (cf. Figures 6.1 through 6.16)).

		Tenebrionidae (Coleoptera)	*Onymacris multistriata* Haag-Rutenberg	*Caenocrypticus phaleroides* Koch	*Pachynotelus granaticollis* Gebien	Pachynotelus leucinus Koch	*Cimicia spinipes* Fairmaire	*Stips gebieni* (Hesse)	*Zophosis rufipennis* Péringuey	*Zophosis gordoniae* Penrith	*Zophosis deyrollei jacoti* Penrith	*Calaharena dutoiti* Koch
Kalahari Dune Line	Eenzaamheid		x				x	x	x	o	x	
	Vredeshoop		x				x	x				x
	Wildheim Ost		x				x	x				
	Middelplaas		x	x			x	x	x		o	o
	Itaga		x	x			x	x	x			x
Mukorob Dune Line	Habis		x					x				
	Dorn-Daberas		x					x				
	Goamus		x	x				x				
	Haribes		x									
Tses Dune Line	Averas		x				x	x				
	Tses		x					x				
	Lichtenfels		x					x				
	Kaitzub		x					x				
Karas Dune Cluster	Donkermodder		x				x	x		x		
	Verschluss		x	x		x	x	x				
	Aikanes		x				x	x				
	Oase		o									
	Gründorn		x				x		x			
Grünau Dune Cluster	Norachas		o				x					
	Middelpos		o		x		x					
	Bruinheuwel		x				x					
Konkiep Dune Cluster	Sandverhaar		x			x	x		x			
	Untersee		x									
Maltahöhe Dune Cluster	Kronenhof		x	x	o				x			
	Amhub		x						x			
	Burgsdorf Noord								x			

Table 6.2. (b) Presence and absence of psammophilous Lepismatidae and Schizodactylidae on various pre-identified dune lines and clusters in southern Namibia (2003, 2004). (x: present study records; o: presence cited in the literature (*cf.* Figures 6.1 through 6.16)).

		Lepismatidae (Thysanura)	*Ctenolepisma terebrans* Silvestri	*Ctenolepisma pluriseta* Silvestri	*Ctenolepisma latera* Irish	*Ctenolepisma pauliani* Wygodzinsky	**Schizodactylidae (Orthoptera)**	*Comicus calaharicus* Irish	*Comicus capensis* Brunner v. Wattenwyl
Kalahari Dune Line	Eenzaamheid				o			o	
	Vredeshoop				x			x	
	Wildheim Ost		o		o			x	o
	Middelplaas		o	o	o			x	
	Itaga			o				x	
Mukorob Dune Line	Habis		o	x	o			x	x
	Dorn-Daberas		x	o	o				x
	Goamus		o	o	x				o
	Haribes			x	o				x
Tses Dune Line	Averas		o		o			o	x
	Tses			o	o				o
	Lichtenfels			o	o				x
	Kaitzub			o	x				x
Karas Dune Cluster	Donkermodder		x		o				x
	Verschluss				x			x	o
	Aikanes		x		o				o
	Oase		x						x
	Gründorn								x
Grünau Dune Cluster	Norachas		x					x	o
	Middelpos		x					x	o
	Bruinheuwel		x						o
Konkiep Dune Cluster	Sandverhaar								x
	Untersee			x					o
Maltahöhe Dune Cluster	Kronenhof		o			x			x
	Amhub			x					o
	Burgsdorf Noord			x					x

Table 6.3. (a) Presence and absence of psammophilous Tenebrionidae at various study and control sites in southern Namibia (2003, 2004). Sites are pre-arranged according to increasing distance from the main Kalahari Dune Sea. (x: present study records; o: presence cited in the literature (*cf.* Figures 6.1 through 6.16)).

		Distance from Main Kalahari (km)	**Tenebrionidae (Coleoptera)**	*Onymacris multistriata* Haag-Rutenberg	*Caenocrypticus phaleroides* Koch	*Pachynotelus granaticollis* Gebien	*Pachynotelus leucinus* Koch	*Cimicia spinipes* Fairmaire	*Stips gebieni* (Hesse)	*Calaharena dutoiti* Koch	*Zophosis rufipennis* Péringuey	*Zophosis gordoniae* Penrith	*Zophosis deyrollei jacoti* Penrith
Main Kalahari Dune line	Itaga	0		x	x			x	x	x	x		x
	Middelplaas	0		x	x			x	x	o	x		o
	Vredeshoop	0		x				x	x	x			
	Eenzaamheid	0		x				x	x		x	o	
	Wildheim Ost	20		x				x	x				
	Donkermodder	50		x				x	x			x	
	Averas	53		x				x	x				
	Goamus	70		x	x				x				
	Habis	75		x					x				
	Haribes	78		x									
	Verschluss	78		x	x		x	x	x				
	Dorn-Daberas	80		x					x				
	Aikanes	100		x				x	x				
	Gründorn	120		x				x			x		
	Tses	125		x					x				
	Kaitzub	128		x					x				
	Lichtenfels	145		x					x				
	Norachas	154		o				x					
	Oase	160		o									
	Bruinheuwel	170		x				x					
	Sandverhaar	178		x			x	x			x		

Table 6.3. (a) (*continued*).

	Distance from Main Kalahari (km)	**Tenebrionidae (Coleoptera)**	*Onymacris multistriata* Haag-Rutenberg	*Caenocrypticus phaleroides* Koch	*Pachynotelus granaticollis* Gebien	*Pachynotelus leucinus* Koch	*Cimicia spinipes* Fairmaire	*Stips gebieni* (Hesse)	*Calaharena dutoiti* Koch	*Zophosis rufipennis* Péringuey	*Zophosis gordoniae* Penrith	*Zophosis deyrollei jacoti* Penrith
Burgsdorf Noord	180									x		
Middelpos	188		o		x		x					
Amhub	215		x							x		
Untersee	233		x									
Kronenhof	260		x	x	o					x		

Table 6.3. (b) Presence and absence of psammophilous Lepismatidae and Schizodactylidae at various study and control sites in southern Namibia (2003, 2004). Sites are pre-arranged according to increasing distance from the main Kalahari Dune Sea. (x: present study records; o: presence cited in the literature (*cf.* Figures 6.1 through 6.16)).

		Distance from Main Kalahari (km)	**Lepismatidae (Thysanura)**	*Ctenolepisma terebrans* Silvestri	*Ctenolepisma pluriseta* Silvestri	*Ctenolepisma latera* Irish	*Ctenolepisma pauliani* Wygodzinsky	**Schizodactylidae (Orthoptera)**	*Comicus calaharicus* Irish	*Comicus capensis* Brunner v. Wattenwyl
Main Kalahari Dune line	Itaga	0			o				x	
	Middelplaas	0		o	o	o			x	
	Vredeshoop	0				x			x	
	Eenzaamheid	0				o			o	
	Wildheim Ost	20		o		o			x	o
	Donkermodder	50		x		o				x
	Averas	53		o		o			o	x
	Goamus	70		o	o	x				
	Habis	75		o	x	o			x	x
	Haribes	78			x	o				x
	Verschluss	78				x			x	o
	Dorn-Daberas	80		x	o	o				x
	Aikanes	100		x						o
	Gründorn	120								x
	Tses	125			o	o				o
	Kaitzub	128			o	x				x
	Lichtenfels	145			o	o				x
	Norachas	154		x					x	o
	Oase	160		x						x
	Bruinheuwel	170		x						o
	Sandverhaar	178								x

Table 6.3. (b) (*continued.*)

	Distance from Main Kalahari (km)	**Lepismatidae (Thysanura)**	*Ctenolepisma terebrans* Silvestri	*Ctenolepisma pluriseta* Silvestri	*Ctenolepisma latera* Irish	*Ctenolepisma pauliani* Wygodzinsky	**Schizodactylidae (Orthoptera)**	*Comicus calaharicus* Irish	*Comicus capensis* Brunner v. Wattenwyl
Burgsdorf Noord	180			x					x
Middelpos	188		x					x	o
Amhub	215			x					o
Untersee	233			x					o
Kronenhof	260		o			x			x

Table 6.4. Psammophile species richness over seven dune lines and clusters in southern Namibia (2003, 2004). (L: Dune line; S: Study site; n: Total number of psammophiles).

L	S	n
Kalahari Dune Line	Eenzaamheid	8
	Vredeshoop	6
	Wildheim Ost	7
	Middelplaas	11
	Itaga	8
Mukorob Dune Line	Habis	7
	Dorn-Daberas	6
	Goamus	7
	Haribes	4
Tses Dune Line	Averas	7
	Tses	5
	Lichtenfels	5
	Kaitzub	5
Karas Dunes	Donkermodder	7
	Gründorn	8
	Verschluss	6
	Aikanes	3
	Oase	4
Grünau Dunes	Norachas	5
	Middelpos	6
	Bruinheuwel	4
Konkiep Dunes	Sandverhaar	5
	Untersee	3
Maltahöhe Dunes	Kronenhof	7
	Amhub	4
	Burgsdorf-Noord	3

6.5.1.1. Discussion

When regarding the five control sites of the Kalahari as one entity, it is clear from Table 6.4 that, in comparison to the study sites, the Kalahari has the highest species richness of psammophiles. Save for two species of Tenebrionidae (*Pachynotelus granaticollis* and *P. leucinus*) and one species of Lepismatidae (*Ctenolepisma pauliani*), the entire compliment of 16 psammophilous species are represented within the Kalahari. As mentioned earlier, the genus era *Pachynotelus* and *C. pauliani* is are largely restricted to the Namib Desert.

While the species composition of Habis (the site in closest proximity to the main Kalahari, Table 6.3) exactly matches that of the main Kalahari with regard to Lepismatidae and Schizodactylidae (five of the six species are represented), only two of the eight tenebrionids recorded on the Kalahari Dune Line occurred at this site. Other sites where tenebrionid psammophile species were present in mentionable numbers were low in lepismatid and schizodactylid species, and *vice versa*. Save for Lepismatidae and Schizodactylidae species richness that appears to decrease along the Mukorob Dune Line, no apparent decrease along the specific dune lines or clusters is observed.

Presence and absence data plotted according to increasing distance from the main Kalahari reveals a slightly different picture. When examining data on Table 6.3 (a), it seems that there is a slight decrease in species from sites closest to the main Kalahari (Donkermodder) to Haribes (78 km from the main Kalahari), and again from Verschluss (78 km from the main Kalahari) to Lichtenfels (145 km from the main Kalahari). Sandverhaar and Middelpos, two very southwesterly sites, as well as Kronenhof, the westernmost study site, have high tenebrionid psammophile diversities in comparison to the other study sites in closer proximity to the main Kalahari.

6.5.2. Correlation between main Kalahari Dune Sea and isolated dunes

Figure 6.17 depicts the results when the seven different pre-identified dune lines or clusters were analyzed for linear correlation with Pearson's R^2, using psammophile species richness, expressed by n (total number of psammophilous species for a specific site).

Although only a slight correlation, there is a decrease in species richness from north to south on the main Kalahari Dune Line. A strong correlation exists down the Mukorob and Tses Dune Lines, as well as the Karas Dune Cluster, where species richness decreases from sites closer to the main Kalahari in a northwesterly or southwesterly direction. There is a hundred percent correlation between the two sites on the Konkiep Dune Line, with species richness increasing from south to north-northwest, and a very strong correlation on the Maltahöhe Dune Cluster where species richness decreases in a northeasterly direction.

The other approach in this analysis was to correlate psammophile species richness with the relative distance of each site from the main Kalahari dunes. The results show a poor negative correlation coefficient (Pearson's R^2 = -0.59) (Figure 6.18), mainly due to erratic 'highs' in numbers of psammophiles with increasing distance from the main Kalahari dune sea.

6.5.2.1. Discussion

The observed negative correlation on the main Kalahari Dune Line was expected, since species diversity tends to decrease from the northwestern Kalahari sands toward the far southwestern corner as climate and vegetation changes from Savanna to Nama-Karoo (*cf.* Chapter 3).

The decreasing trend is strongly influenced by the high number of psammophilous species recorded at Middelplaas, and much fewer at Vredeshoop and Eenzaamheid. The high diversity of psammophiles encountered on the dune sampled at Middelplaas can most likely be attributed to the dense cover of grass debris, which would have served as a food source to a number of psammophilous tenebrionids (*cf.* Chapter 3). Eenzaamheid had a comparatively low species abundance and diversity (Figures 5.3 & 5.4), with the bulk of the material sampled representing two species only. Sampling at the Vredeshoop site delivered a small, but very diverse, assemblage of arthropods (Figures 5.2-5.4), but included only three psammophilous species.

Although Figure 6.17 demonstrates a good correlation for the Mukorob Dune Line, Figure 5.2 shows a general increase in the number of invertebrate individuals and the number of Tenebrionidae sampled along this Line, with a sudden drop in numbers at the northwestern most study site on the Line, *viz.* Haribes. The low psammophile species richness observed at this site is a direct result of the low species abundance (*cf.* Chapter 5) which might have been caused by the geographical setting of the study site, or due to disturbance in dune cover by the animals grazing in the camp (*cf.* Chapter 3). When omitting psammophile data for Haribes, R^2 for the Mukorob Dune Line amounts to 0, indicating a homogenous distribution of species richness.

Figures 5.2 and 5.3 indicate extremely high numbers of tenebrionids and individuals sampled at the Tses study site, which also have a dominating effect on the total numbers of individuals and tenebrionids collected on the dune line (Figure 5.1). When referring to results in Chapter 5, it is clear that one species only (*Stips gebieni*) constituted 87% of the 2018 invertebrates sampled at the site. This extreme is, however, diminished in Figures 5.4 and 5.5, with Shannon's diversity and evenness for the site and the dune line being exceptionally low in comparison to the other sites and lines.

Although the Donkermodder and Verschluss study sites on the Karas Dune Cluster delivered a small abundance of tenebrionids (Figure 5.2), the species composition consisted of high numbers of psammophilous invertebrates (Table 6.4). A mediocre number of arthropods and Tenebrionidae were sampled at Oase (Figure 5.2), with high diversity and evenness in species composition (Figure 5.4). The strong negative correlation in species richness decrease down the Karas Dune Cluster (Figure 6.17) is partially due to the fact that no psammophilous tenebrionids were sampled at this site (in the literature, *Onymacris multistriata* has been noted to occur there), and only one species each of Lepismatidae and Schizodactylidae psammophiles. The same situation applies to Gründorn (Figures 5.2 and 5.4), where only four psammophiles were sampled (Table 6.4). The unusual vegetational cover (dominated by *Euphorbia* species) of the Oase sampled dune raised some questions about the source of the sands, since it was located in close proximity of a fossil riverbed (*cf.* Chapter 3). No such irregularities could, however, be pinpointed at the Gründorn site.

The Grünau Dune Cluster had the overall lowest species abundance (Figure 5.1), but still a high Shannon's diversity coefficient that is distributed very evenly (Figure 5.4) and included a comparative psammophile species component (Table 6.4.). After comparing the sand grain size distribution of the Middelpos study site (Appendix 1, Figure 23) to others, it was originally suspected that the site would not accommodate many psammophile invertebrates. Since psammophiles are known to morphologically be explicitly adapted to specific substratum characteristics, recording the highest psammophilous compliment (Table 6.4) on this Dune Cluster at a site with the coarsest substratum and the lowest precipitation (Chapter 3) was peculiar.

6.5.3. Similarity between different control and study sites

Sorenson's qualitative index of similarity was used to examine the relationships between sites in terms of psammophile species richness and diversity. This coefficient does not take into account species abundance (Magurran, 1988), which is an advantage in this case since species abundance is subject to unpredictable variables (such as climatic conditions and vegetation), which differs widely between sites. Using an equation that includes abundance would obscure the results strived for in this investigation.

This analysis entailed comparing the study and control sites with each other, two at a time, by means of Sorenson's qualitative index of similarity (C_S). Figure 6.19 presents the relationships. Since only a few psammophilous species were sampled and employed in the analyses, similarity indices lower than 0.7 became insignificant, and were consequently not considered.

C_S is calculated as follows:

$C_S = 2j / (a + b)$ where j is the number of species found in both sites, a is the total number of species found a site a, and b the total number of species found at site b. C_S varies between 0 (no similarity) and 1 (total similarity).

In augmentation to the results obtained by Sorenson's index, the sand grain size distribution of each of the study and control sites are depicted on a cluster analyses graph (Figure 6.20). No analyses and discussion on sorting parameters and heavy mineral content of the sand bodies are included in this dissertation, but it was deemed necessary to include some reference to the physical quality of the substrate within and upon which the organisms occur.

6.5.3.1. Discussion

Similarity measured between the 26 sites was quite high. Two centers of very high similarity in psammophile species richness were identified. The first was between the sites Tses, Lichtenfels, Habis, Dorn-Daberas and Goamus, and the second was between Wildheim Ost, Averas, Donkermodder, Verschluss and Aikanes. Another minor center of similarity existed between Bruinheuwel, Norachas, Middelpos, Gründorn and Oase. When comparing Figure 6.19 to relationships between sand grain size distributions depicted in Figure 6.20, the same patterns are not found. Sites closely relating to each other with regard to psammophiles, such as Tses, Lichtenfels and Kaitzub have no similarity in sand grain size distribution. This also applies to the sites of Wildheim Ost and Averas. Sites that are situated closely to one another, such as Aikanes and Verschluss, and Verschluss and Donkermodder, are unrelated with regard to psammophile species composition, while other sites such as Norachas and Wildheim Ost, and Norachas and Averas are more than 80% similar. The same outcome is observed from the sand fraction composition. Thus, when probing for a distribution pattern, it seems that the observed similarities between sites are quite random and not indicative of true patterns.

Study sites that were non-compliant and raised questions under 6.5.2.1. (Haribes, Vredeshoop, Gründorn, Oase and Middelpos) were all found to be at least 70% similar to all the other study and control sites, although not necessarily similar to sites in the close vicinity.

Three sites that are the least related to the other sites according to C_S (Figure 6.19) are Sandverhaar, Kronenhof and Burgsdorf Noord. Sampling at Kronenhof, the study site situated beneath the western escarpment and closest to the Namib Desert, did however, yield the Kalahari endemic *Onymacris multistriata* and four other psammophilous tenebrionids. This site was also the only one where the Namib endemic fish moth, *Ctenolepisma pauliani*, occurred.

O. multistriata, together with four other psammophiles, were recorded at Sandverhaar, while *C. pluriseta*, another species believed to prefer the red sands of the Kalahari, occurred at Burgsdorf Noord.

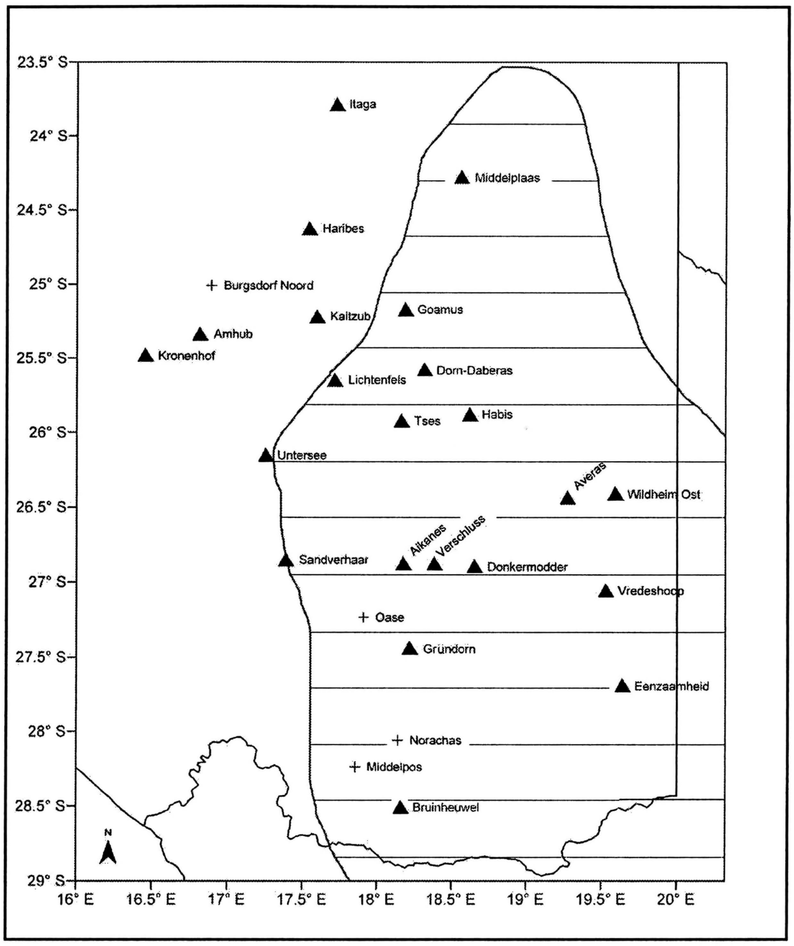

Figure 6.1. Distribution of psammophilous insects in southern Namibia (2003 – 2004). Closed triangles: Present study records of *Onymacris multistriata* (Haag-Rutenberg); Shaded area: Distribution of *O. multistriata* cited in the literature (Penrith, 1984c).

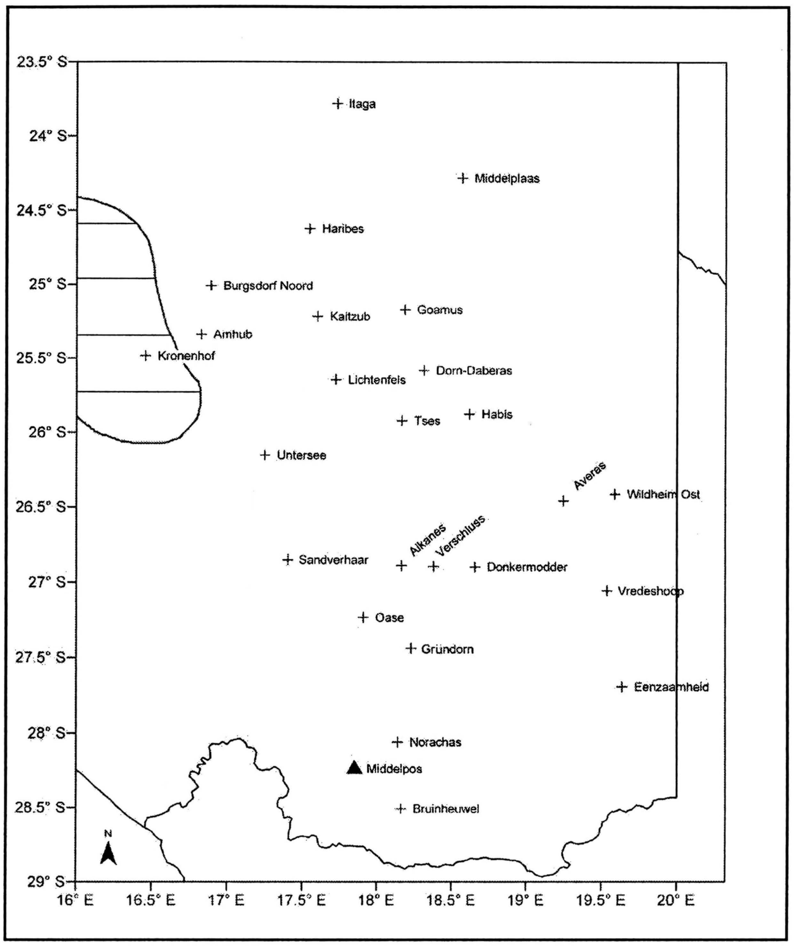

Figure 6.2. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Pachynotelus granaticollis* Gebien; Shaded area: Distribution of *P. granaticollis* cited in the literature (Penrith *et al.*, 1994).

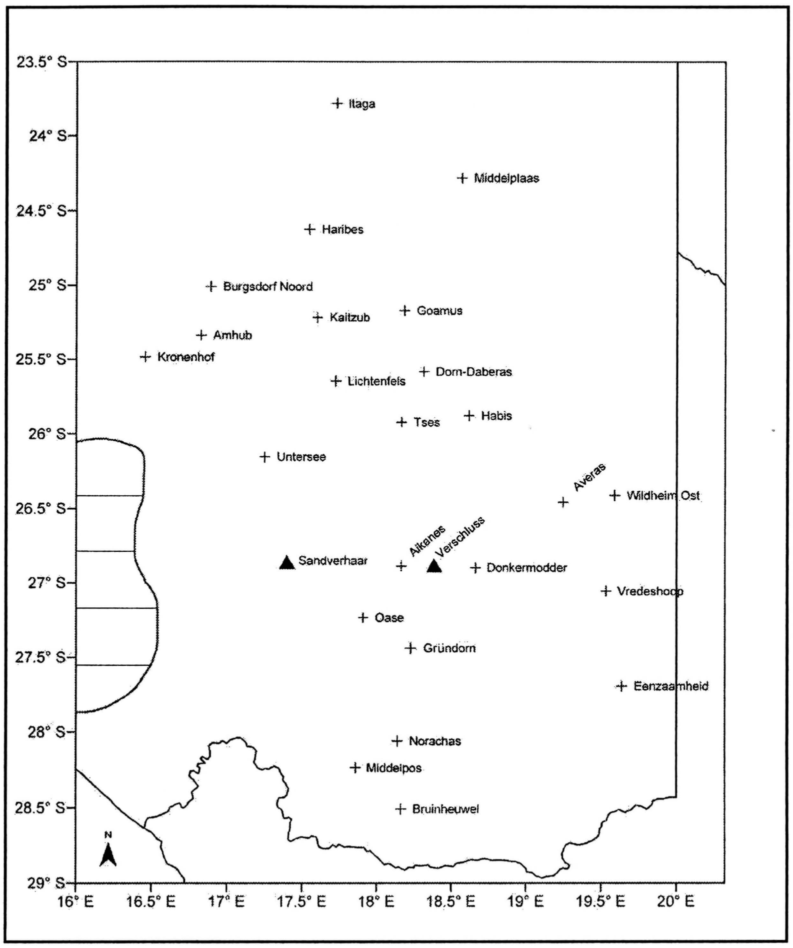

Figure 6.3. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Pachynotelus leucinus* Koch; Shaded area: Distribution of *P. leucinus* cited in the literature (Penrith *et al.*, 1994).

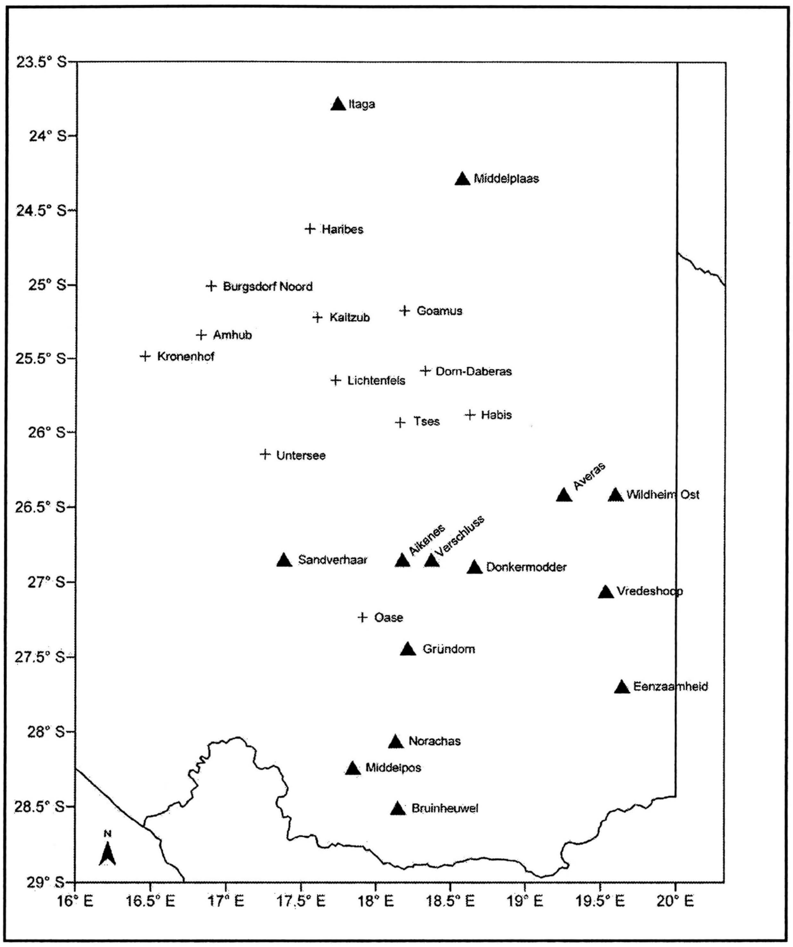

Figure 6.4. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Cimicia spinipes* Fairmaire.

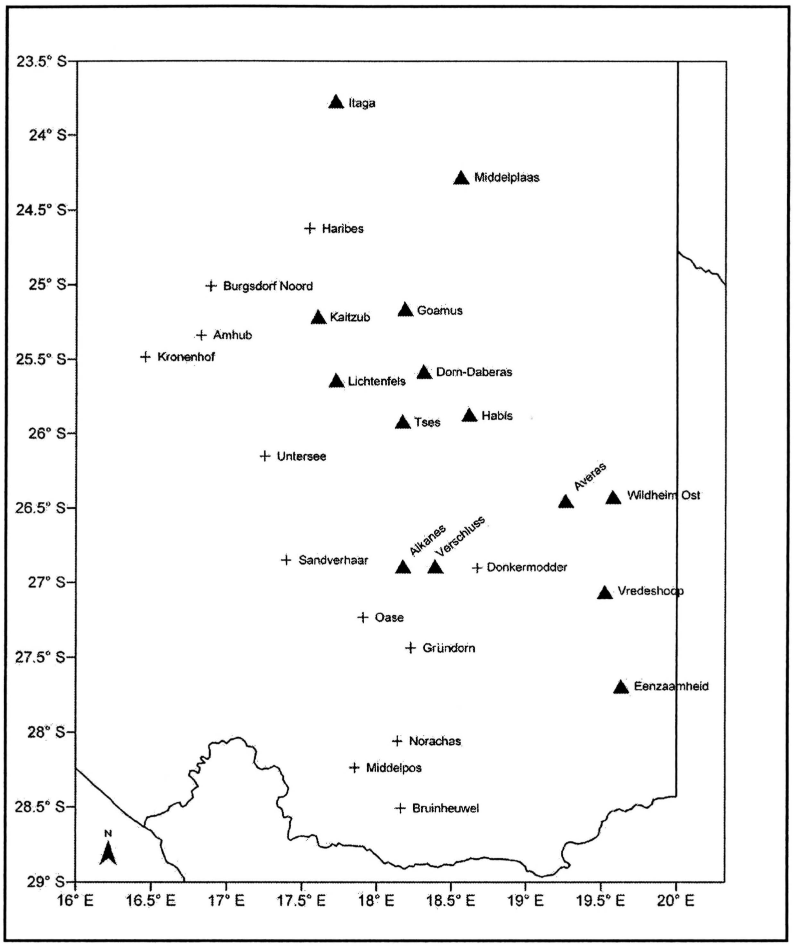

Figure 6.5. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Stips gebieni* (Hesse).

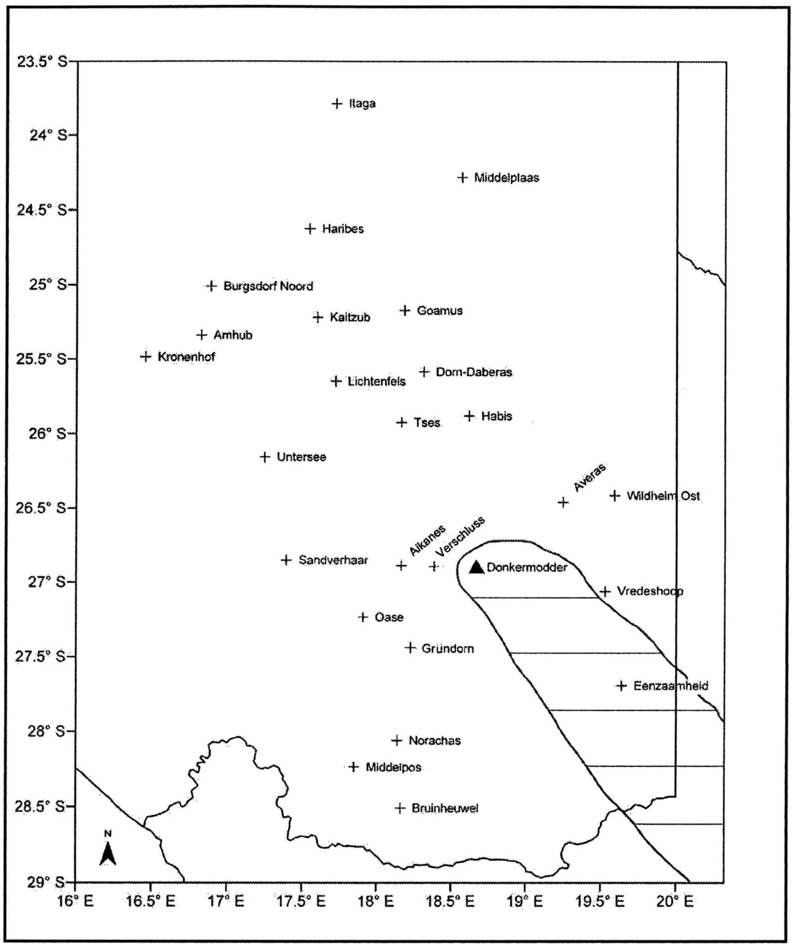

Figure 6.6. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Zophosis (Heliophosis) gordoniae* Penrith; Shaded area: Distribution of *Z. (H.) gordoniae* cited in the literature (Penrith, 1981).

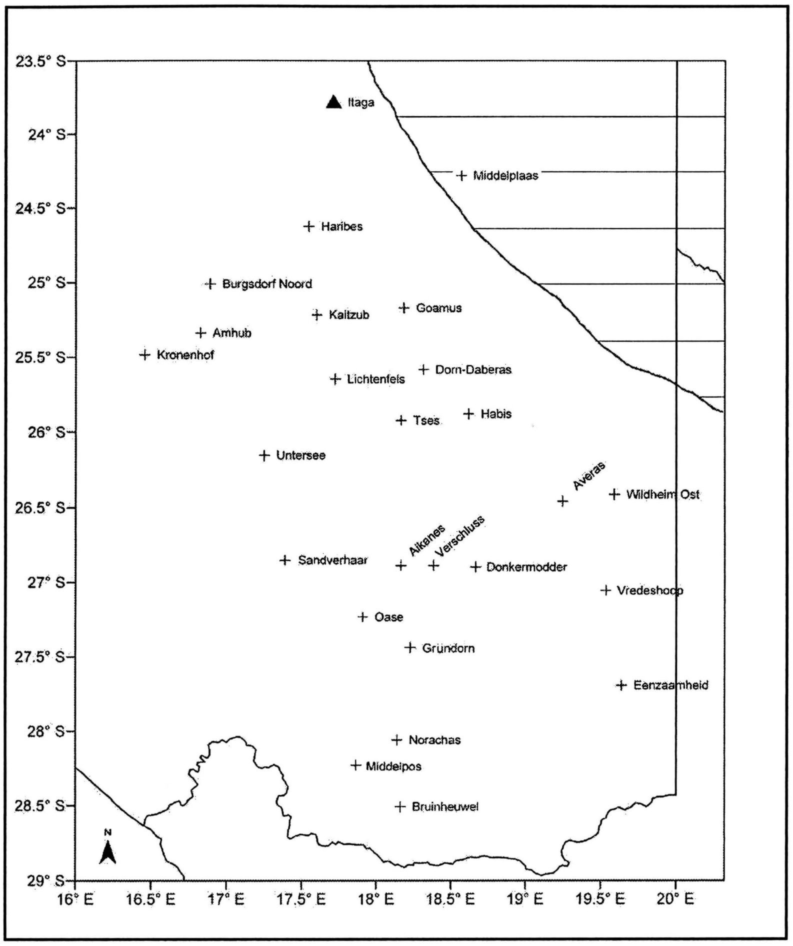

Figure 6.7. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Zophosis (Zophosis) deyrollei jacoti* Penrith; Shaded area: Distribution of *Z. (Z.) deyrollei jacoti* cited in the literature (Penrith, 1981).

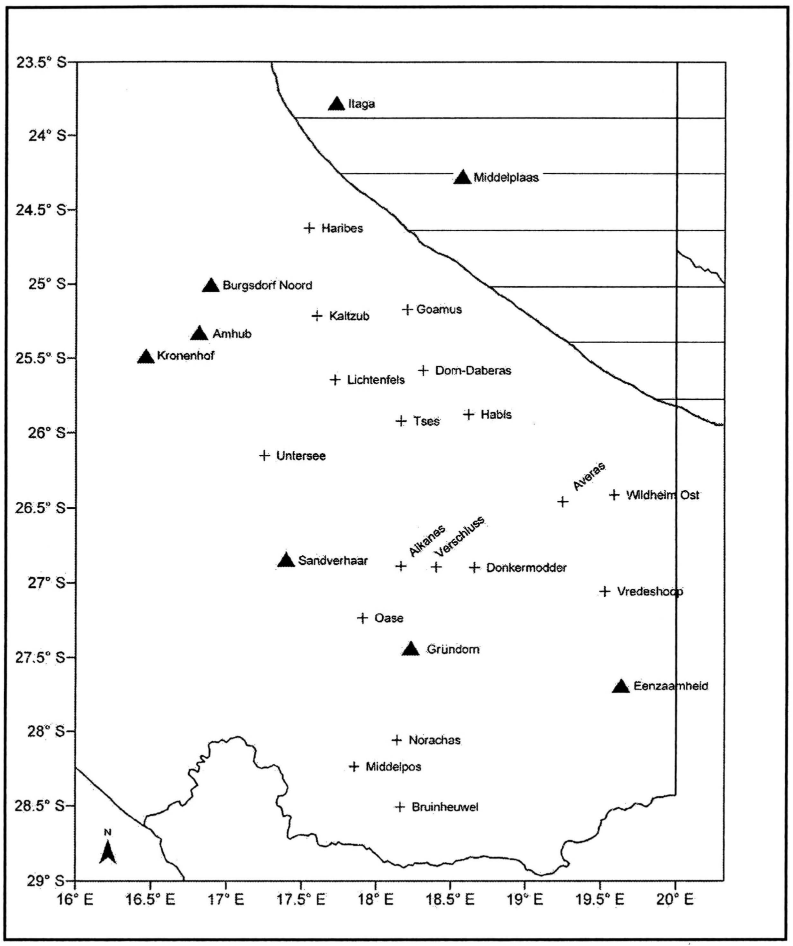

Figure 6.8. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Zophosis (Hologenisis) rufipennis* Péringuey; Shaded area: Distribution of *Z. (H.) rufipennis* cited in the literature (Penrith, 1984a).

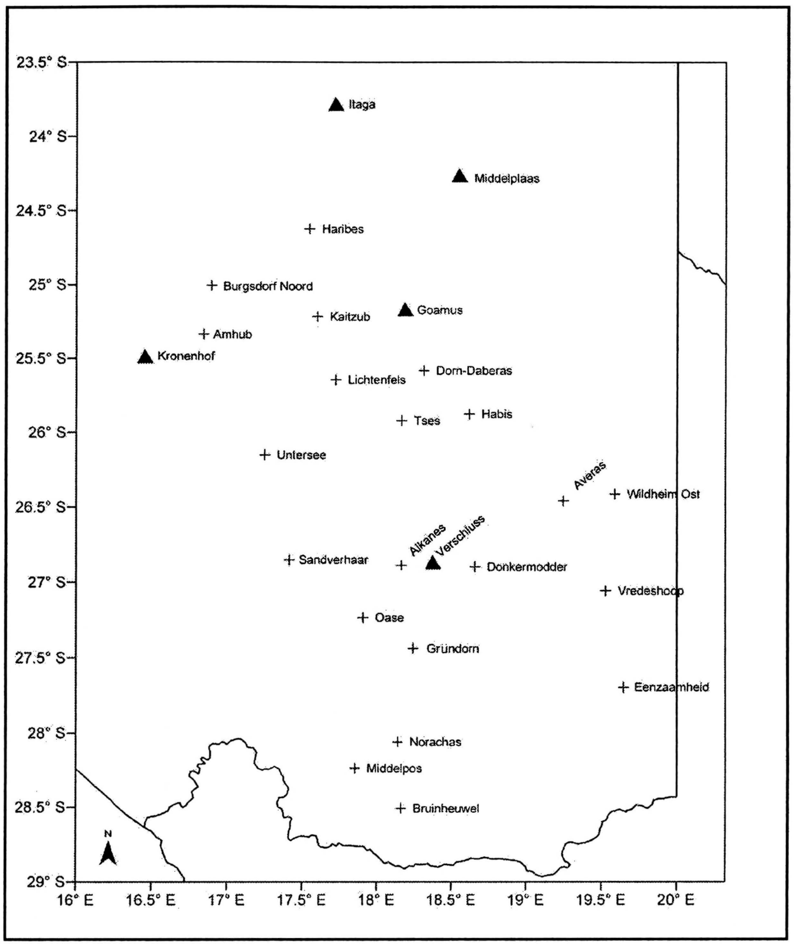

Figure 6.9. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Caenocrypticus (Psammotopulus) phaleroides* Koch.

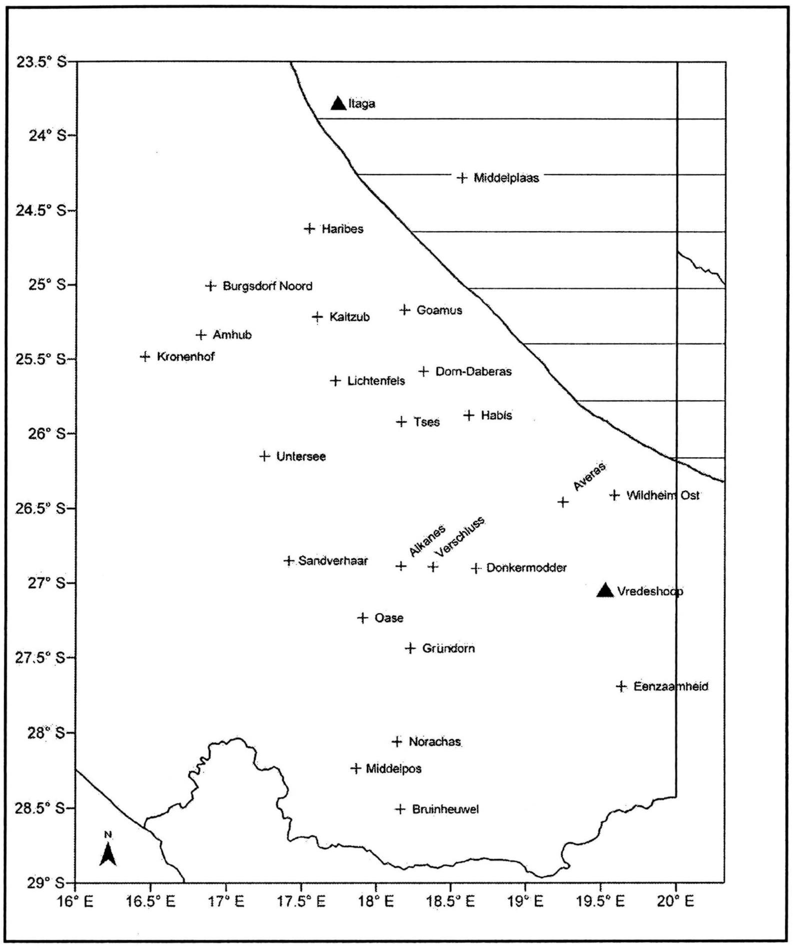

Figure 6.10. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Calaharena dutoiti* Koch; Shaded area: Distribution of *C. dutoiti* cited in the literature (Penrith, 1982).

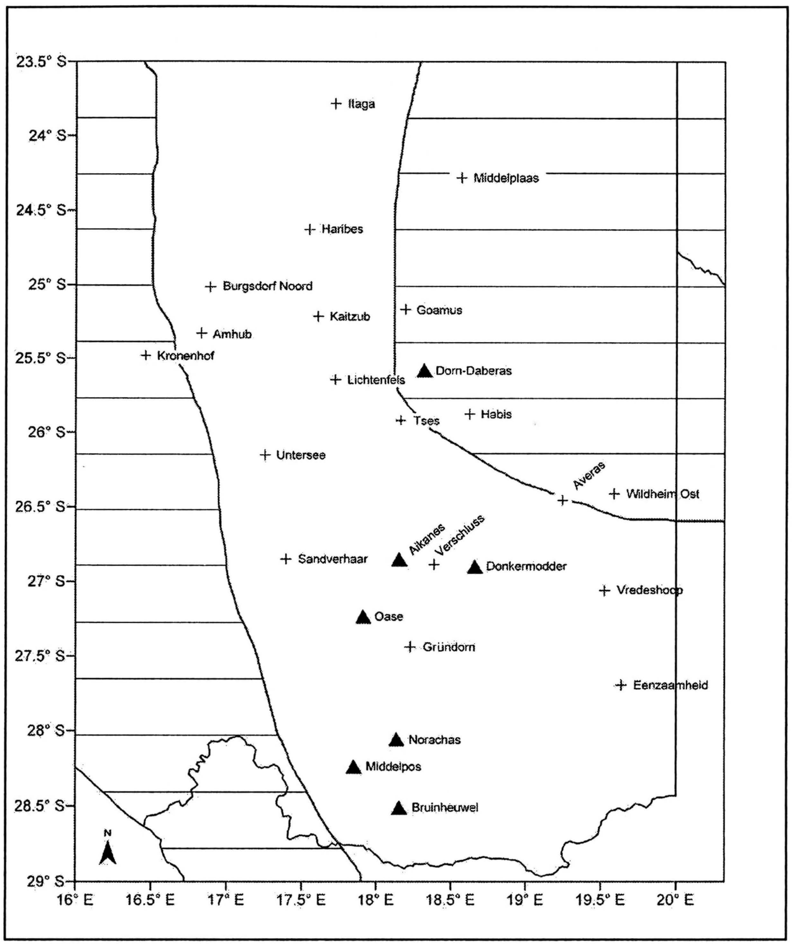

Figure 6.11. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Ctenolepisma (Sceletolepisma) terebrans* Silvestri; Shaded areas: Distribution of *C. terebrans* cited in the literature (Irish, 1987).

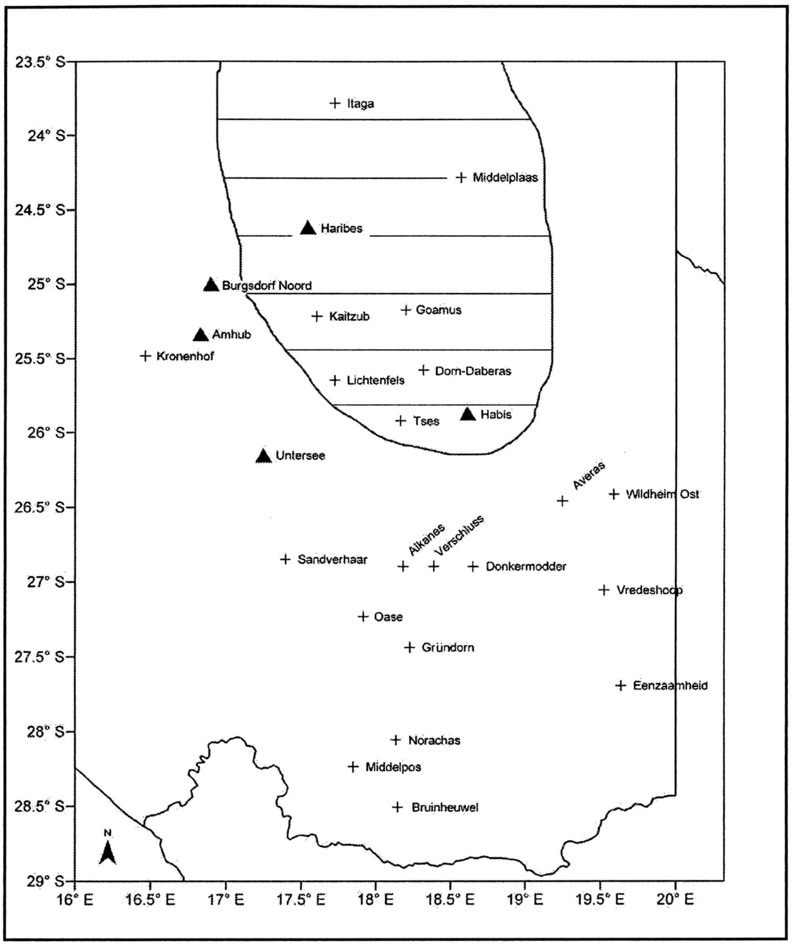

Figure 6.12. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Ctenolepisma (Sceletolepisma) pluriseta* Silvestri; Shaded area: Distribution of *C. (S.) pluriseta* cited in the literature (Irish, 1987).

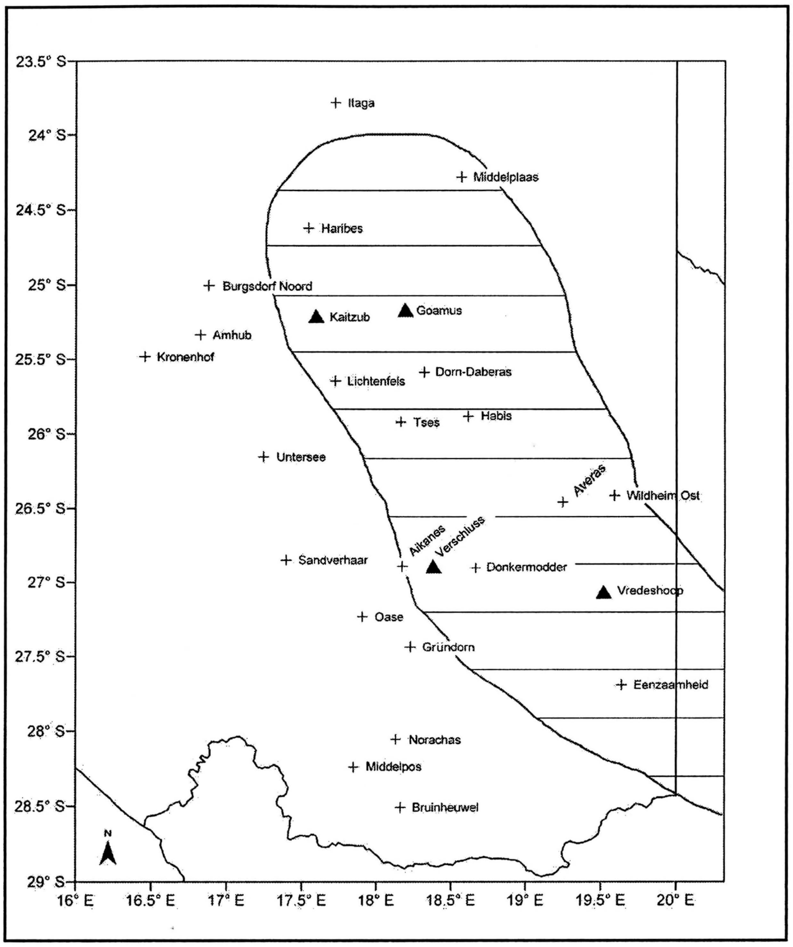

Figure 6.13. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Ctenolepisma (Sceletolepisma) latera* Irish; Shaded area: Distribution of *C. (S.) latera* cited in the literature (Irish, 1987).

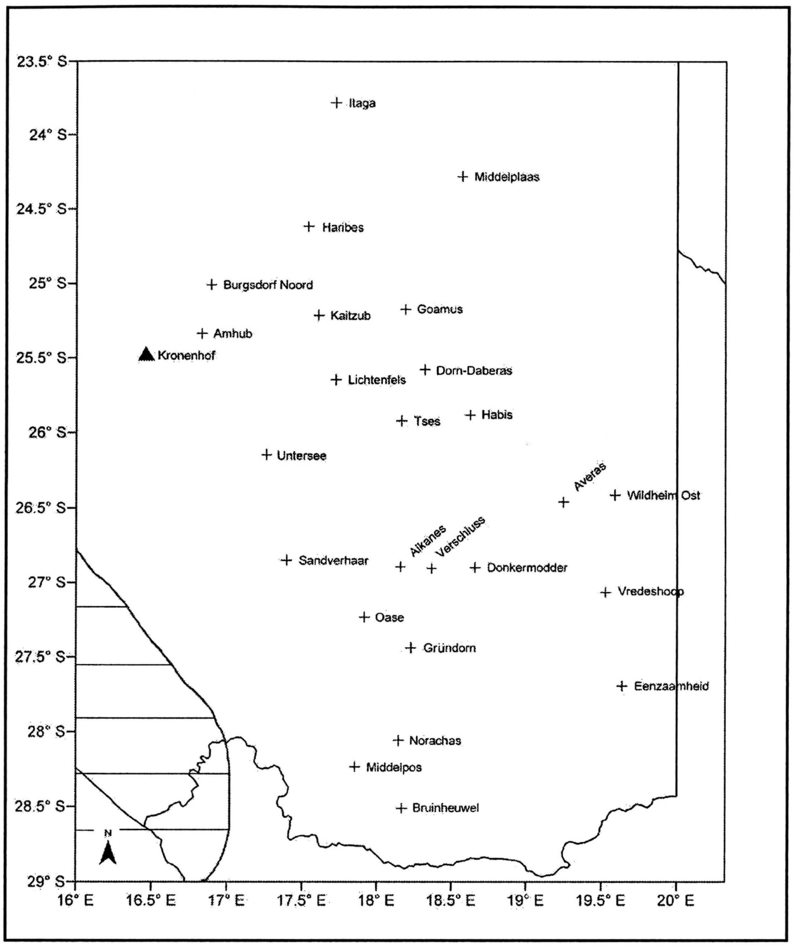

Figure 6.14. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Ctenolepisma (Sceletolepisma) pauliani* Wygodzinsky; Shaded area: Distribution of *C. (S.) pauliani* cited in the literature (Irish, 1987).

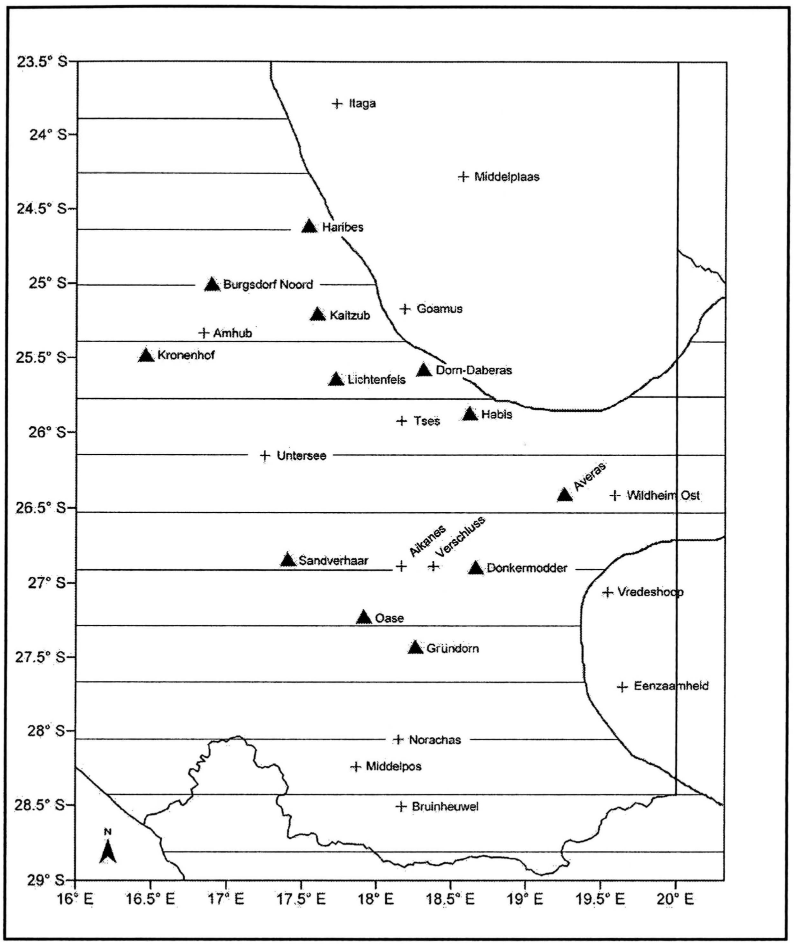

Figure 6.15. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Comicus capensis* Brunner v. Wattenwyl; Shaded area: Distribution of *C. capensis* cited in the literature (Irish, 1986).

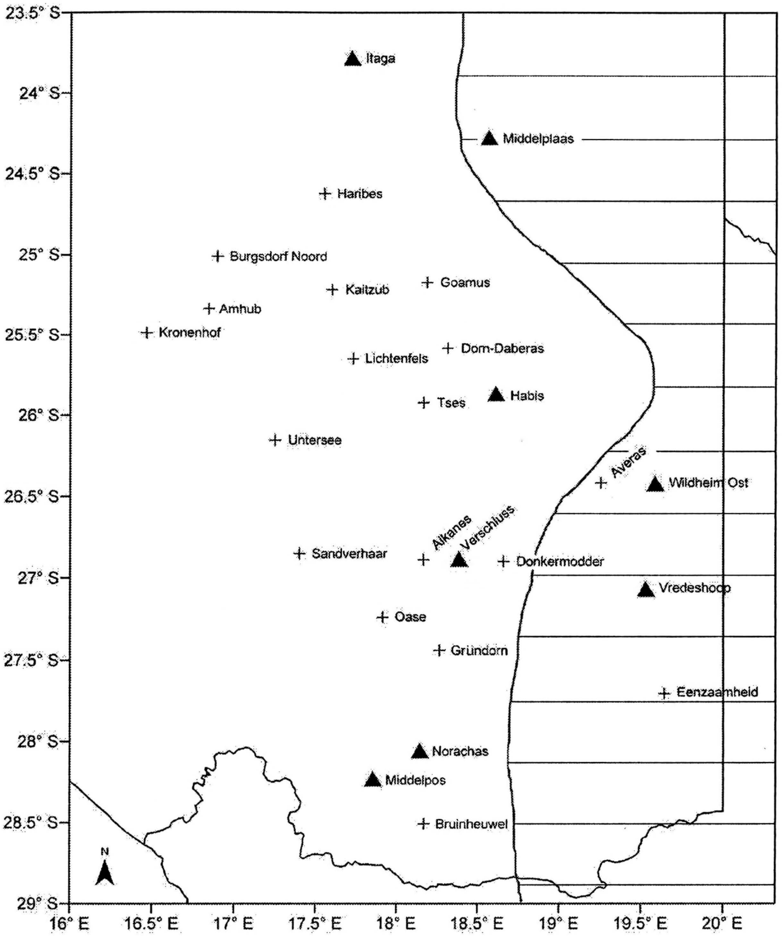

Figure 6.16. Distribution of psammophilous insects in southern Namibia (2003, 2004). Closed triangles: Present study records of *Comicus calaharicus* Irish; Shaded area: Distribution of *C. calaharicus* cited in the literature (Irish, 1986).

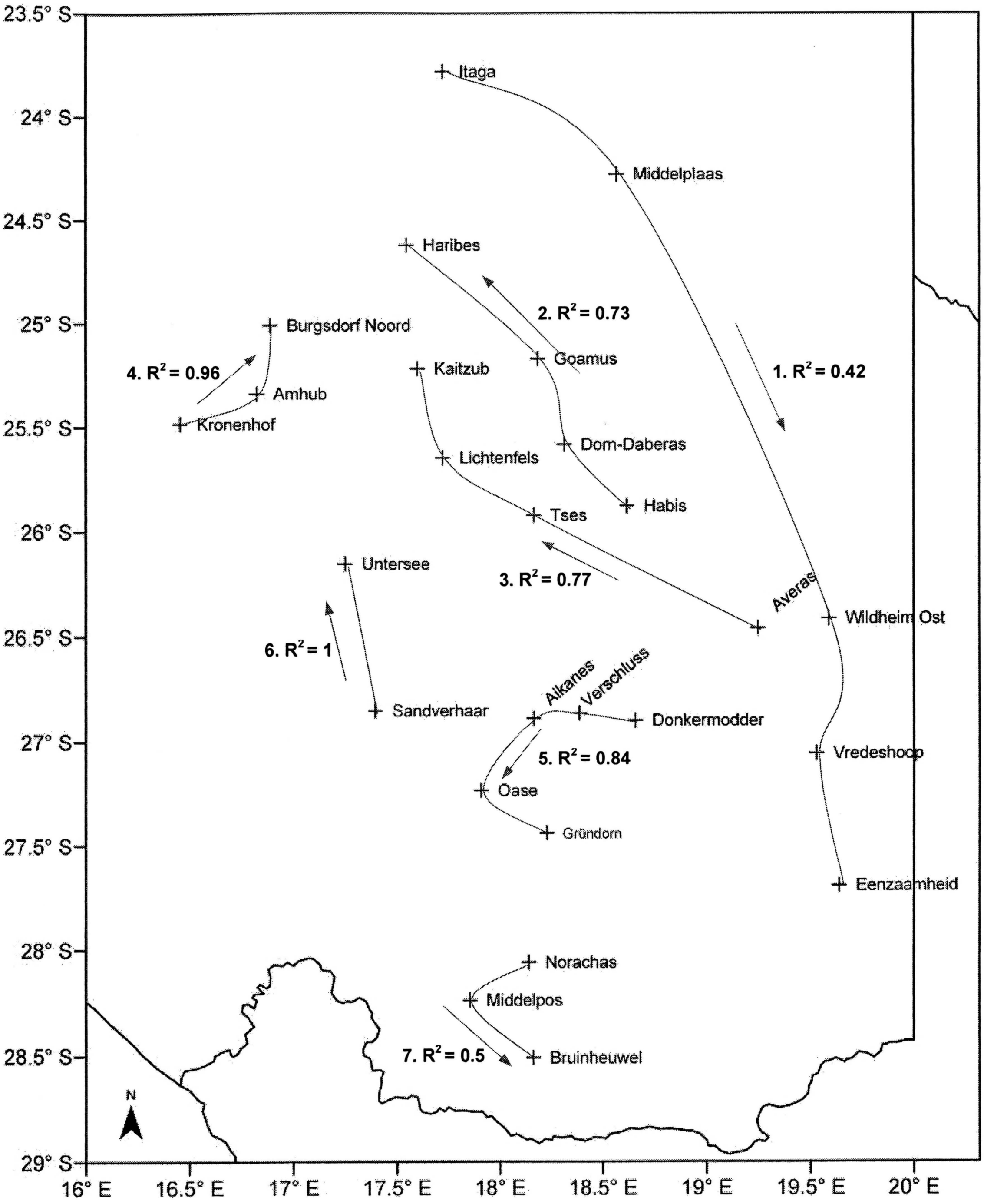

Figure 6.17. Psammophile species richness and Pearson's R^2 over 7 dune lines in southern Namibia (2003, 2004). 1. Main Kalahari dunes; 2. Mukorob dunes; 3. Tses dunes; 4. Maltahöhe dunes; 5. Karas dunes; 6. Konkiep dunes; 7. Grünau dunes. Arrows indicate the direction of decrease in diversity.

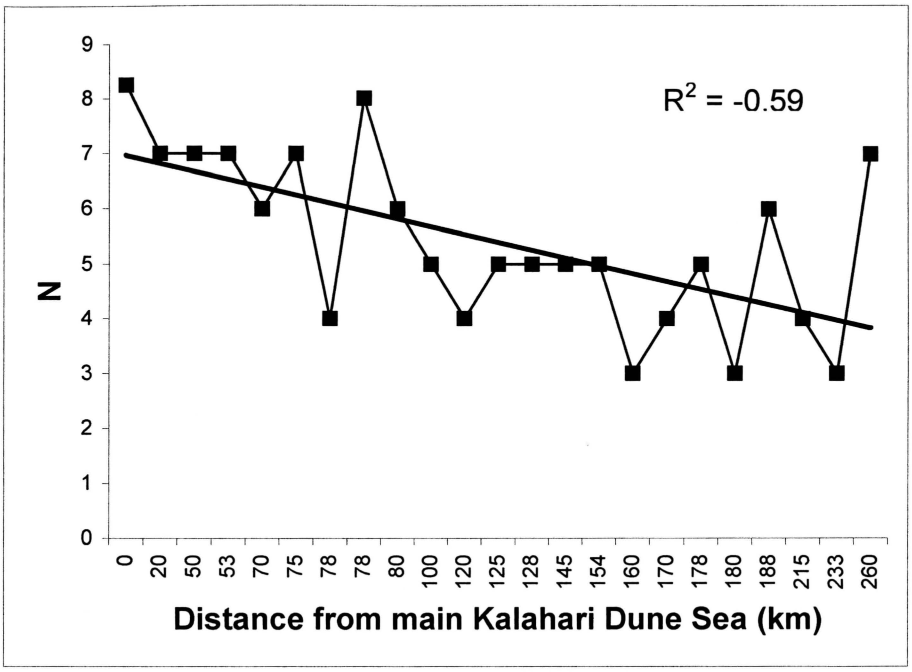

Figure 6.18. Psammophile species richness in southern Namibia (2003, 2004) plotted according to increasing distance from the main Kalahari dunes. (R^2): Pearson's correlation coefficient.

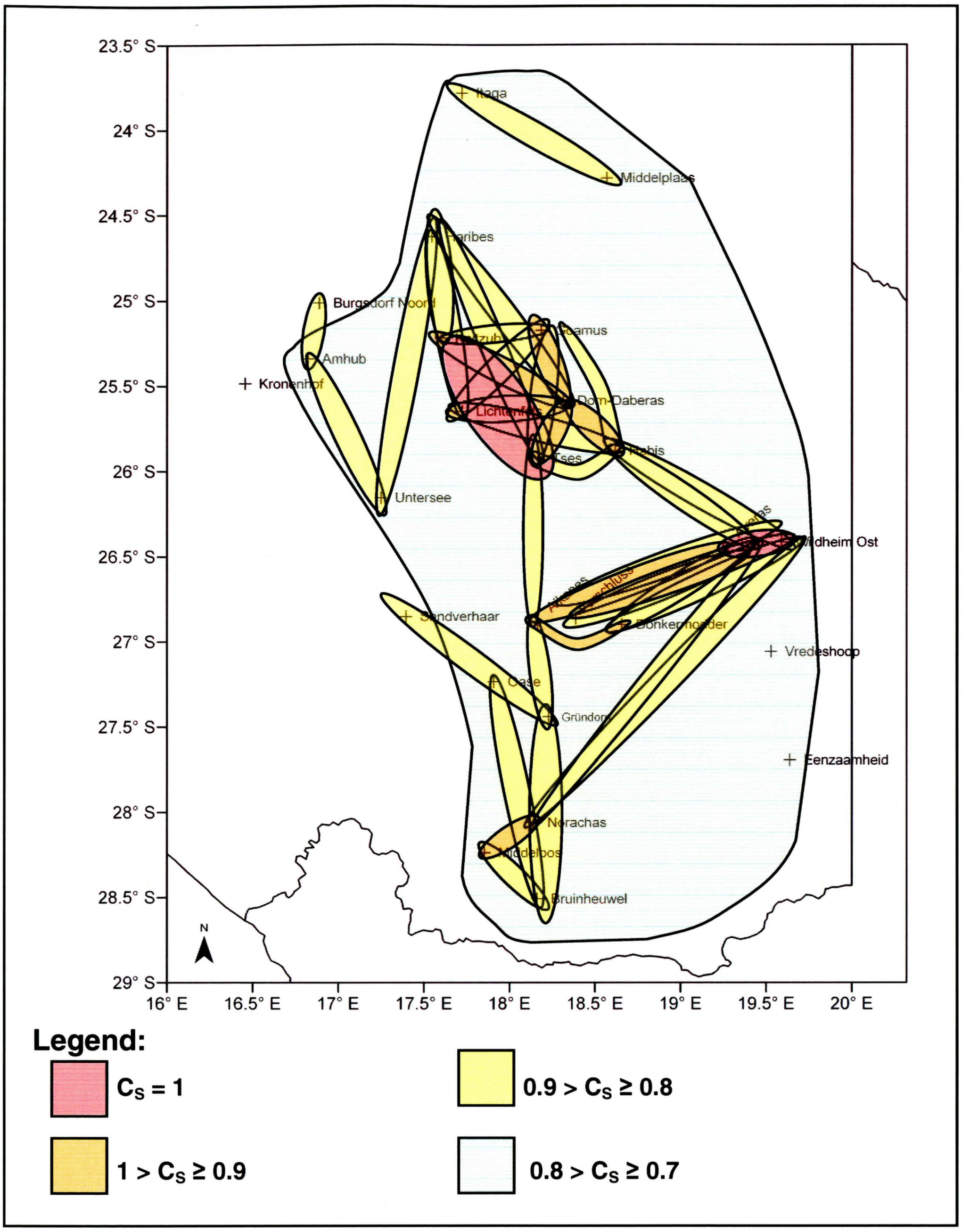

Figure 6.19. Similarity between study sites with regard to psammophile diversity and species richness in southern Namibia (2003, 2004), as indicated by Sorenson's qualitative index of similarity (C_S).

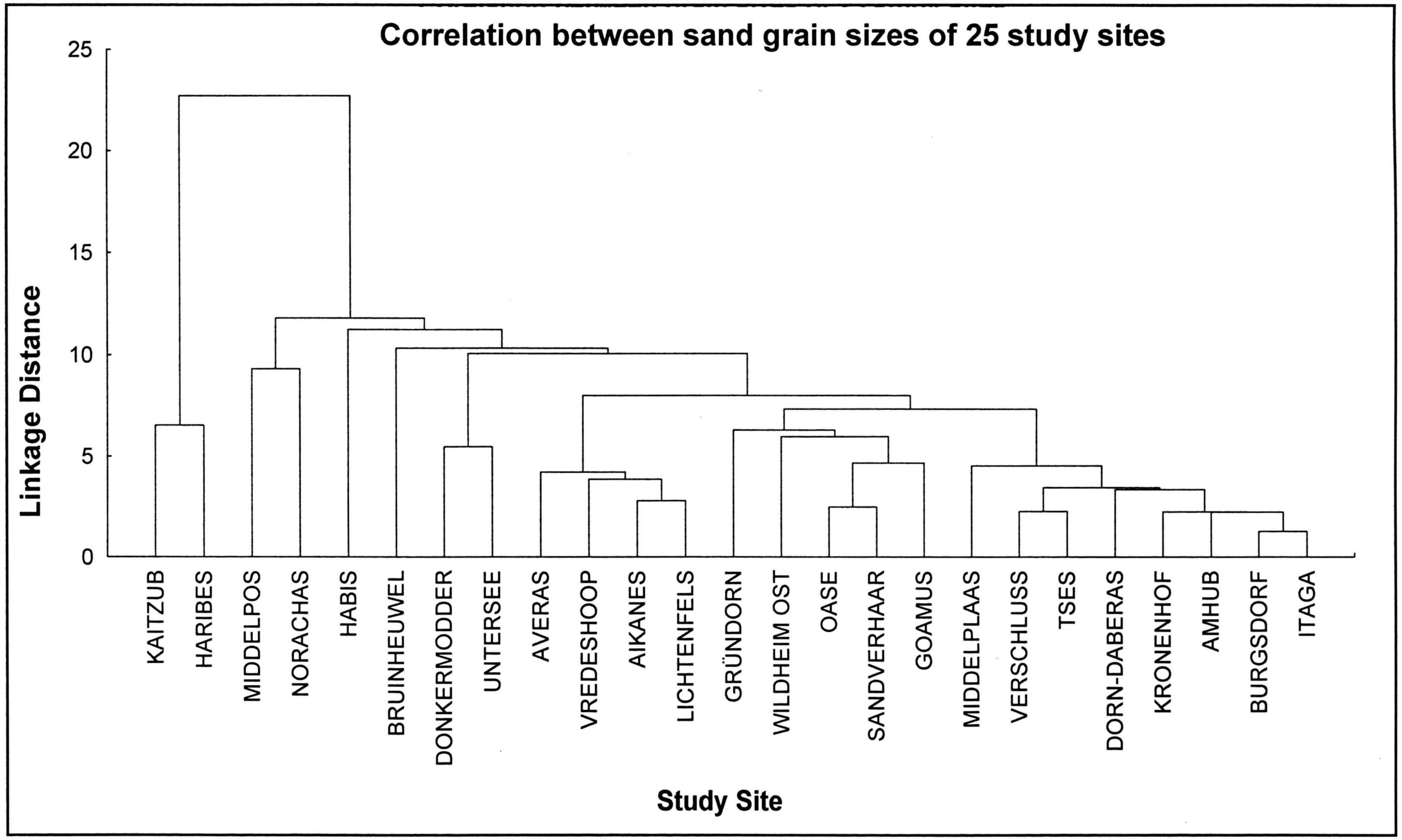

Figure 6.20. Cluster analysis graph of the sand grain size distribution of 25 study sites in southern Namibia (2003, 2004). The linkage distance is inversely proportional to the extent of similarity.

6.6. REFERENCES

ENDRÖDY-YOUNGA, S. 1978. Coleoptera. Pp 797-823. *In:* Werger M.J.A. (Ed). *Biogeography and ecology of Southern Africa*. Den Haag: Junk.

ENDRÖDY-YOUNGA, S. 1982. Dispersion and translocation of dune specialist tenebrionids in the Namib area. *Cimbebasia* (A) **5**(9): 257-271.

ENDRÖDY-YOUNGA, S. 1996. Revision of the tribe Caenocrypticini (Coleoptera: Tenebrionidae: Tentyriinae).*Transvaal Museum Monograph* **11**: 1-74.

IRISH, J. 1986. The species of *Comicus* Brunner V. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navorsinge van die Nasionale Museum, Bloemfontein* **5**(10): 253-276.

IRISH, J. 1987. Revision of the genus *Ctenolepisma* Escherich (Thysanura: Lepismatidae) in southern Africa. *Cimbebasia* (A) **7**(11): 147-207.

IRISH, J. 1990. Namib Biogeography, as exemplified mainly by the Lepismatidae (Thysanura: Insecta). Pp. 61-66. *In*: Seely, M.K. (Ed.), *Namib Ecology: 25 years of Namib research*. *Transvaal Museum Monograph* No. **7**. Transvaal Museum, Pretoria.

KOCH, C. 1955. Monograph of the Tenebrionidae of southern Africa. (1) Tentyriinae, Molurini, Trachynotina, *Somaticus*. *Transvaal Museum Memoir* **7**: 1-242.

KOCH, C. 1962a. The Tenebrionidae of Southern Africa. XXXI. Comprehensive notes on the Tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* **XXIV**(2,3): 61-106.

KOCH, C. 1962b. Tenebrionidae of southern Africa XXXII. New psammophilous species from the Namib Desert. *Annals of the Transvaal Museum* **XXIV**(2,3): 107-159.

LOUW, S. vdM. 1982. The diversity and daily and seasonal activity of ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. *Cimbebasia* (A) **7**(3): 35-56.

LOUW, S. vdM. 1984. Comparison of the faunistics and ecological patterns of the ground-living beetle faunas of the Kalahari and Namib Desert. Pp 153-166. *In:* De Graaf, G. & Janse van Rensburg, D. (Eds.) *Proceedings of a Symposium on the Kalahari Ecosystem*, October 1983, Pretoria. Supplement to *Koedoe*.

MAGURRAN, A. E. 1988. *Ecological diversity and its measurement.* University Press, Cambridge.

PENRITH, M.-L. & ENDRÖDY-YOUNGA, S., 1994. Revision of the subtribe Cryptochilina (Coleoptera: Tenebrionidae: Cryptochilini). *Transvaal Museum Monograph* **9**: 1-144.

PENRITH, M.-L. 1981. Revision of the Zophosini (Coleoptera: Tenebrionidae) Part 2. The subgenus *Zophosis* Latreille, and seven related south-western African subgenera. *Cimbebasia* (A) **6**(2): 17-109.

PENRITH, M-L. 1982. The genus *Calaharena* Koch (Coleoptera: Tenebrionidae: Opatrini: Stizopina). *Cimbebasia* (A) 5(**8**): 252-255.

PENRITH, M.-L. 1984a. Revision of the Zophosini (Coleoptera: Tenebrionidae) Part 10. The subgenus *Hologenosis* Deyrolle. *Cimbebasia* (A) **6**(6): 228-289.

PENRITH, M.-L. 1984b. Revision of the Zophosini (Coleoptera: Tenebrionidae) Part 10. Key to the subgenera, supplement, evolution and biogeography of the tribe, and catalogue. *Cimbebasia* (A) **6**(10): 418-502.

PENRITH, M-L. 1984c. New taxa of *Onymacris* Allard, and relationships within the genus (Coleoptera: Tenebrionidae). *Annals of the Transvaal Museum* **33**(31): 511-533.

PENRITH, M-L. 1984d. Origin of sand-adapted tenebrionid beetles of the Kalahari. Pp 153-166. *In:* De Graaf, G. & Janse van Rensburg, D. (Eds.) *Proceedings of a Symposium on the Kalahari Ecosystem*, October 1983, Pretoria. Supplement to *Koedoe*.

PENRITH, M-L. 1986. Relationships in the tribe Adesmiini (Coleoptera: Tenebrionidae) and a revision of the genus *Stenodesia* Reitter. *Annals of the Transvaal Museum* **34**(13): 275-302.

ROSENZWEIG, M.L. 1995. Species diversity in space and time. University Press, Cambridge.

CHAPTER 7

Conclusion

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7.1. TENEBRIONIDAE DIVERSITY AND SPECIES RICHNESS

Louw (1979) noticed that, when comparing species diversity of apterous Coleoptera, Tenebrionidae in the Namib Desert comprised 80% of the total, whilst in the Kalahari Dune Sea, only 60% of apterous Coleoptera species were tenebrionids. In corroboration with the latter, the tenebrionid-component of the apterous invertebrates collected during this study also dominated species diversity and richness indices at the majority of sites sampled (Chapter 5).

Not only do the tenebrionids belong to the largest insect order, but members belonging to this family are exceptionally adaptive to extreme climatic fluctuations, compared to other insect orders, hence the aptness of their use as biogeographic indicators in this study.

7.2. PSAMMOPHILE DISTRIBUTION

A total of 15 16? invertebrates from the families Tenebrionidae (Coleoptera), Lepismatidae (Thysanura) and Schizodactylidae (Orthoptera) were identified as strict dune-sand followers. Sand grain size, however, was determined not to be a common demeanor when it came to species distribution. When sand grain size fraction maxima of the study and control sites were cluster analyzed (Figure 6.20), no correlation was found with similarities between sites as indicated by psammophile species richness. There was were not, however, great differences in grain size maxima distributions in any case. In Appendix 2, Figures 1 through 25 it is clear that the most frequently observed fraction sizes, and consequently the greatest proportion of sand ranged between 0.5 mm and 0.125 mm in size. Lancaster (1986) determined the mean sand grain size of Kalahari dunes to range between 0.17 mm and 0.34 mm, with a distinct change in mean grain size from dune crests to interdune valleys. He also noted a regional change, with sand grain size becoming finer from the northwest and west towards the southeast, which he suggested paralleled the direction of sand movement. The latter observation, however, deals with detailed analytical calculations, subsequent to the execution of a more sand-focused collecting methodology, and requires a sound knowledge of dune geomorphology. Since this study focused on the distribution of insects, observations made on the sand particles solely serve as approximate indicators of the preferred physical environment of the said organisms, and do not directly relate to the movement of sands.

Possibly the most determinant analysis in this venture was that of testing for presence and absence of psammophiles at the control sites, and comparing the results with that of the study sites. It can be argued that, due to possible inadequate sampling, many psammophilous species were falsely absent from sites, but if we refer to distribution maps cited in the literature (Chapter 6, Figures 6.1 through to 6.16), we see that expansions were much more frequently added to known distribution areas than *vice versa*.

When referring to the analyses of presence and absence (Tables 6.2 (a) and (b)), the first conclusion is that none of the studied sites were sourced from recent odd events, such as local outcrop weathering or a river that dried up. This is evident from the fact that psammophiles were present on all the sites sampled, and probably imply that at least some of these sites were once interconnected.

7.3. BIOGEOGRAPHICAL PATTERNS

A deduction that can be made from the presence and absence data (Tables 6.2 (a) and (b)), as well as the correlation and similarity figures (Figures 6.17 through 6.19), is that the first hypothesis is supported, *i.e.* that the main Kalahari Dune Sea was the origin of the insects in question and subsequently the source of sand. This, however, would still be highly speculative.

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For the Kalahari to have served said purposes, many assumptions have to be made. Firstly, one had to assume that no isolation of species presently persists in the main Kalahari Dune Sea, that psammophiles are free to roam the entirety of the dune system, but only remain on the specific sampled control sites due to ecological preference. This assumption was made in Chapter 6 (6.5.1) when the data was analyzed for presence and absence of psammophiles. Only if this can be confirmed can it be claimed that all the psammophilous species recorded on the isolated dunes, save for three species, occur in the Kalahari. Two of the three species not sampled in the Kalahari are Namib endemics, whilst the remaining species is generally scarce.

When considering the scenario that there is a poor correlation between species richness and increasing distance from the main Kalahari (Figure 6.18), due to study sites in closer proximity to the control sites (see Tables 6.2 (a) and (b)), more questions arise. Another imprudent assumption has to be made. This assumption would entail that, true to the Island Biogeography Theory (MacArthur and Wilson, 1963, in Rosenzweig, 1995), immigration and extinction rates on an island reaches equilibrium 'faster' on smaller islands than on larger ones. Factors that control these rates include island size, which result in smaller islands having a lower species packing capacity as a result of ~~less~~ fewer available niches. It could then be assumed that the 'gaps' in the presence of certain species down a particular dune line is as a result of smaller dune patches having higher species turnover rates. Since the psammophiles were phylogenetically all treated evenly, the aforementioned assumptions and ensuing explanations are highly unlikely.

Figure 7.1 depicts the postulated source of the bulk of psammophilous species that were studied (Chapter 6.2 through 6.4). When considering the source and distribution of the tenebrionids in question, the general center of speciation is indicated to be the Southwestern Zone. This is the area covering the southwestern coastline from north of the true Cape into southern Angola. The area occupied by the Namib is included in its entirety, and the zone extends into the Kalahari *via* the Orange River (Endrödy-Younga, 1978). The Schizodactylidae and Lepismatidae, on the other hand, are derived from ancestry in central Africa, while the genera in question all originated in the Kalahari (Irish, 1986, 1987, 1990).

The hypothesis formulated in Chapter 2 was that the isolated dunes became inhabited by psammophilous species that had their center of distribution in the Kalahari Dune Sea. The proposed process supporting such a distribution of species was palaeoclimatic fluctuations which caused recurring dry spells in the interior of southwestern Africa, to such an extent that bodies of sand became mobile and interconnected the, now patchy, isolated dunes (Chapter 1).

The most likely conclusion is that of Vicariance Biogeography, explained in Chapter 2, where species become isolated due to the establishment of natural barriers. The first hypothesis is therefore rejected. Some pattern does exist, but only indicates that the origin of the psammophiles were from different sources, including the area which is occupied by present day Namib, as well as the main Kalahari Dune Sea. The implication of this conclusion is that the isolated dunes are most likely relicts of a Gondwana or post-Gondwana desert (*sensu* Irish, 1990; Endrödy-Younga, 1978), which occupied a large part of the southwestern interior of Africa. Contact between the, now, isolated dunes and the Kalahari occurred during glacial maxima (Van Zinderen Bakker, 1975; Irish, 1990; Endrödy-Younga, 1978), when prevailing arid climatic conditions facilitated the movement of sand-adapted invertebrates.

According to Irish (1990), the most plesiomorphic psammophiles inhabit the Kalahari, and in the Namib Desert apomorphies increase from south to north. Referring to the phylogenetic position of the relevant taxa in their tribes (Chapter 6.2 through 6.4), the studied psammophiles are generally fairly apomorphic descendants within their lineages, with their predecessors all originating in the area now occupied by the Namib Desert (hence forth referred to as the 'pre-Namib'). The final conclusion, which seems to at least hold true for the area investigated during this study, is that the psammophiles now inhabiting the Kalahari Dune Sea and the isolated dunes in-between the two large Kalahari and Namib sand bodies, dispersed from the 'pre-Namib' area across the entire southwestern interior. This would have been supported by a homogenous arid climate and sandy substrate, after the first stage of Gondwana breakup in the Jurassic (206 to 144 Ma, Chapter 1), but before the desiccation of the Namib in the Oligocene (33.7 to 23.8 Ma, Chapter 1) that gave rise to the hyper-arid environment it is now. At the onset of the desiccation events, the psammophiles inhabiting the 'pre-Namib' either went extinct, or remained in refugia where vegetation and other environmental factors were favorable. Such refugia would be rocky islands (Irish, 1990) or sandy pockets (Endrödy-Younga 1978) along the Orange River where these plesiomorphic species persist to this day. Because the remaining individuals were from a stock of xerophilous insects (Koch 1961, 1962), when hyper-aridity in the Namib started spreading from south to north, the psammophiles would have been able to invade an entire niche, basically without competition, and rapid speciation ensued. As was mentioned in Chapter 2, the high endemism of the Namib Desert has nothing to do with age, but rather reflects the adaptiveness of the invertebrates. This conclusion supports the notion of the Namib and Kalahari being two entities which were extensively isolated in space and time, but then only since the Miocene (23.8 to 5.3 Ma). Before that, the interior of Namibia was probably quite homogenously semi-arid to arid.

Although many autochthonous processes contributed to the sand accumulation of the Namib, the main input was from the Orange River (Lancaster,1990) in a straight forward manner from south to north, and via sea level regressions (*cf.* Chapter 1). Considering that the Namib and Kalahari psammophile insect fauna were ultimately sourced from south of the Orange River, and that insect psammophily developed due to isolation on sand-pockets, such as the ones derived at the mouth of the Orange River (Endrödy-Younga, 1978), the riparian dunes flanking the River probably served as one of the major psammophile sinks during above mentioned events. Penrith (1986) proposed that the divergence of the genus *Onymacris* into the Kalahari Dune Sea was facilitated by the Orange River, and this probably holds true for other psammophilous species as well. Present data, however, does not seem to reconcile with the latter statement. Table 6.4 depicts an average to low psammophile species richness for sites in closest proximity of the sandy banks of the Orange River, *viz*. the Grünau Dune Cluster. This could, however, be false negatives in recordings. Another cause might be the prevailing wind direction in that vicinity. According to Lancaster (1980), fixed dune systems just north of the Orange River indicate northwesterly palaeowind regimes, which would prohibit the riparian sands in question to spread in the opposite direction.

A motivation for the fact that more psammophile species occur in the Kalahari than on the studied isolated dunes is related to habitat structure, simply because a larger area supports more available niches and subsequently, more species. Also, the core of the Kalahari Dune Sea has climatically remained unchanged for an extended period of time. Due to more available niches, psammophiles in this part of the main Kalahari could remain unaffected during wetter and drier spells, while a sudden change in climate could be catastrophic for the inhabitants of a small sand island with little habitat diversity. The possibility of further immigration of species from the main Kalahari in a westerly direction is also considered. The high diversity of psammophilous species on the Mukorob and Tses Dune Lines (Chapter 6) can be explained by later glaciations (after the Miocene), where flatter areas in close proximity of the main Kalahari (Chapter 3), such as these are, could readily receive sand and invertebrate input from the main Kalahari Dune Sea.

7.4. FUTURE PROSPECTS

One of the intricacies when seeking to understand biogeographical processes in trying to determine the consequential patterns is that, ultimately, all conclusions are speculative. The best is to accept those deductions established by thorough analyses, both supportive and non-supportive of a particular hypothesis. Another difficulty when pursuing biogeographical patterns is that the investigator often develops a preconception of patterns during the course of data assemblage and analysis, and results may be interpreted (even sampled) accordingly. If all these obstacles were overcome and the most likely conclusions are reached, then there is still a question of whether the observed patterns are the real end products of certain processes, or just a statistical solution to a given equation.

For an extended area with such a dense distribution of possible sites to investigate, a suggestion is that more sites be sampled, over longer study periods that are seasonally representative. Psammophilous arthropods are, as previously mentioned, highly seasonal and have a variation in diel cycles within groups. These are all factors that influence sample size and variation. Also, many local and regional physical and climatic influences on the origin and availability of substratum and its vegetational cover can cause one dune patch to vary greatly from the next, even if they are just 10 km apart, which in turn are determinants for species composition of such dune patches.

The size of the dune patch is one of the most important determining factors in diversity analyses. Since interdune substrata often resembles that of the bordering dunes, it is not always possible to delimit the boundaries of a specific dune. Methods such as studying dune patches from Landsat imagery proved to be of only slight assistance when trying to compare dune patch sizes.

Proper geomorphological studies on the isolated dunes, as well as determining the relevant ages of such dunes, will help elucidate some inconsistencies created by gaps in invertebrate data sets, and may be the ultimate key to confirming or rejecting any proposed patterns suggested by the insects.

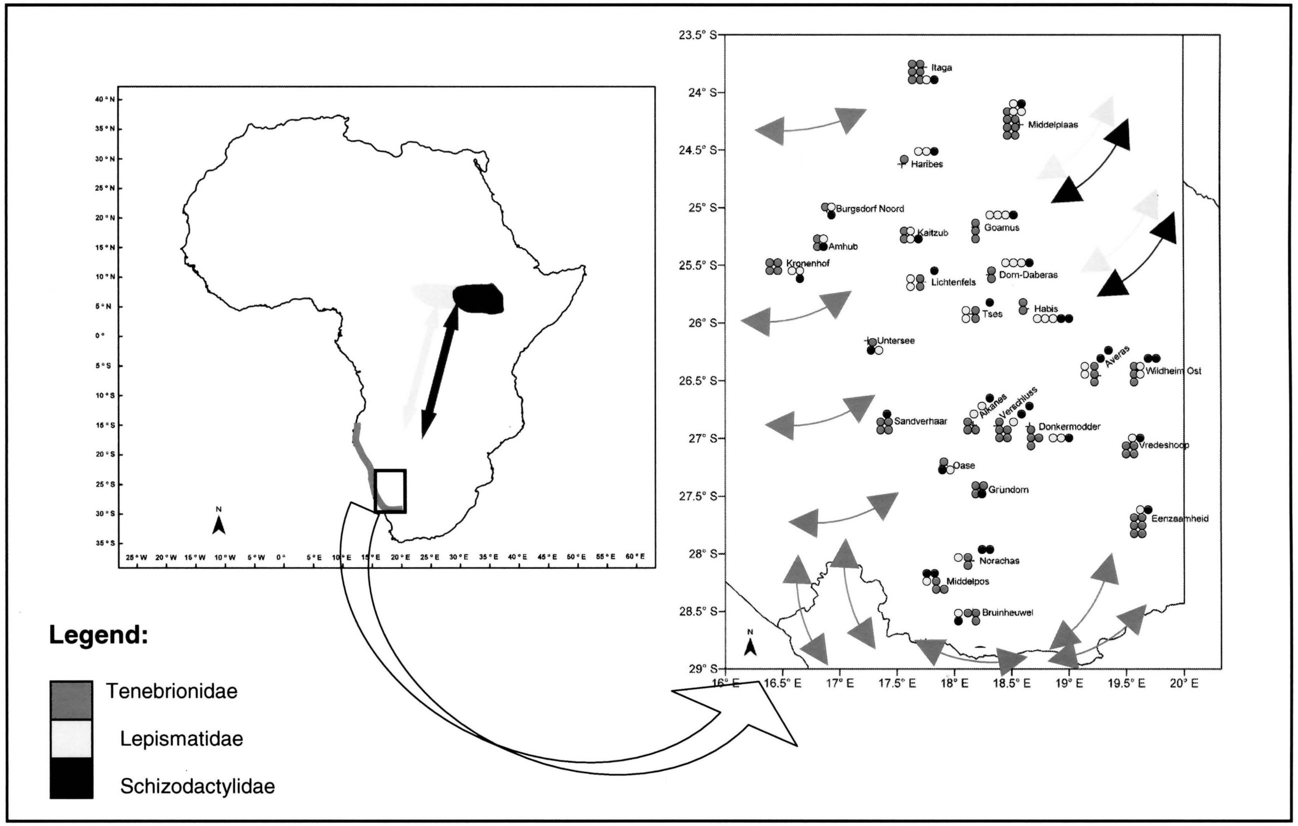


Figure 7.1. A rough graphic presentation of the origin of the three psammophilous insects groups studied in southern Namibia (2003, 2004) (left), and their consequent inter-distribution (right) between the Namib, intermittent isolated dune patches and the Kalahari Dune Sea. Distribution data also includes literature records.

7.5. REFERENCES

ENDRÖDY-YOUNGA, S. 1978. Coleoptera. Pp 797-823. *In:* Werger M.J.A. (Ed). *Biogeography and ecology of Southern Africa*. Den Haag: Junk.

IRISH, J. 1986. The species of *Comicus* Brunner V. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navorsinge van die Nasionale Museum, Bloemfontein* **5**(10): 253-276.

IRISH, J. 1987. Revision of the genus *Ctenolepisma* Escherich (Thysanura: Lepismatidae) in southern Africa. *Cimbebasia* (A) **7**(11): 147-207.

IRISH, J. 1990. Namib biogeography, as exemplified mainly by the Lepismatidae (Thysanura: Insecta). Pp 61-66. *In:* Seely, M.K. (Ed.) *Namib ecology: 25 years of Namib research. Transvaal Museum Monograph* **7**. Transvaal Museum, Pretoria.

KOCH, C. 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert. Positive psammotropism in tenebrionid-beetles. *Journal of the South West African Scientific Society* **15**: 8-34 and 77-92 (plates).

KOCH, C. 1962. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum* **24**: 61-106 and plates 9-15.

LANCASTER, N. 1980. Palaeoenvironmental implications of fixed dune systems in southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **33**: 327-346.

LANCASTER, N. 1986. Grain-size characteristics of linear dunes in the southwestern Kalahari. *Journal of Sedimentary Petrology* **56**: 395-400.

LANCASTER 1990. Regional Aeolian dynamics in the Namib. Pp 39-45. *In:* Seely, M.K. (Ed.) *Namib ecology: 25 years of Namib research. Transvaal Museum Monograph* **7**. Transvaal Museum, Pretoria.

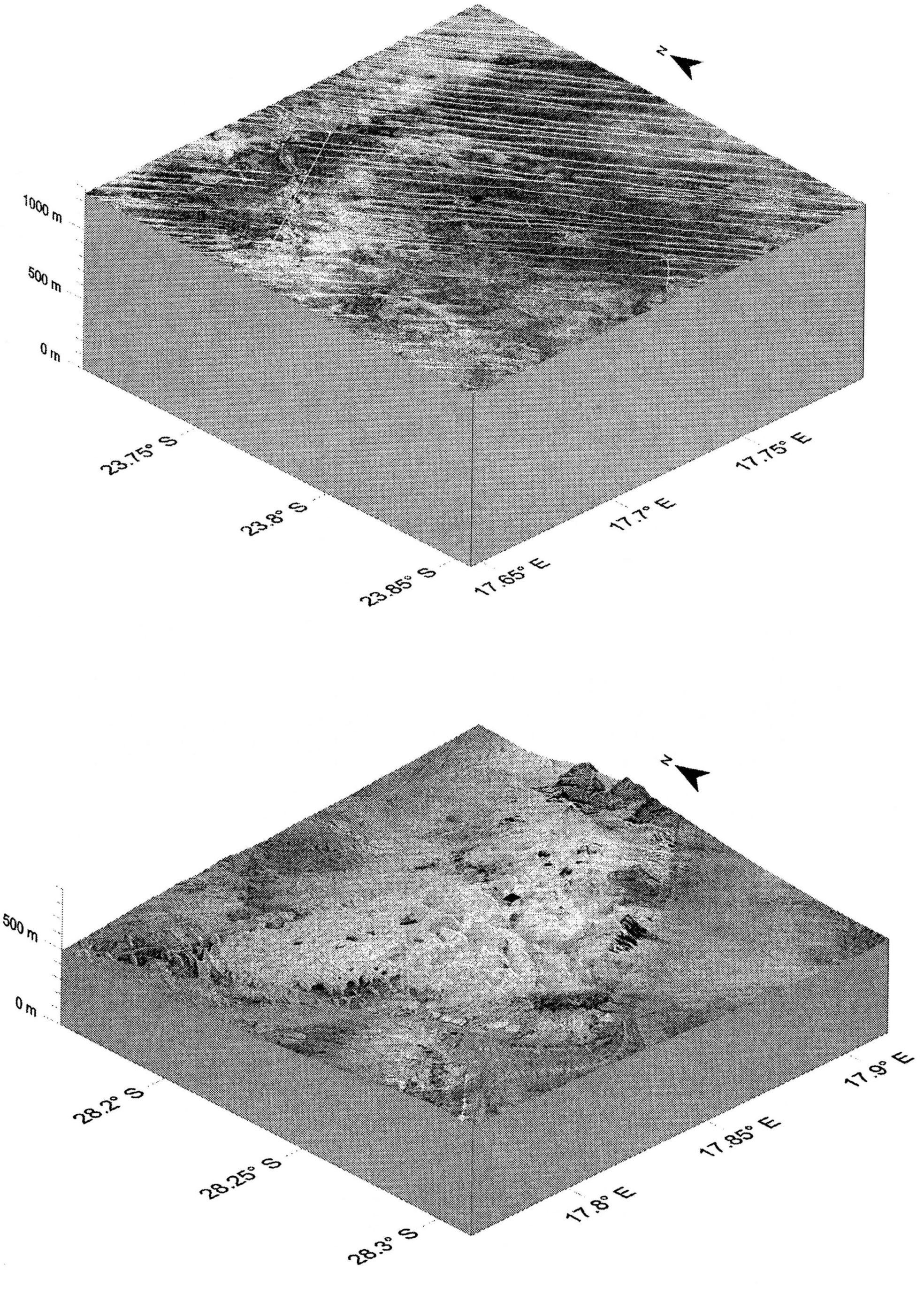
LOUW, S. vdM. 1979. *Ecological equivalence and phylogeny of Tenebrionidae (Coleoptera) as indicators of the connection between Namib and Kalahari dunes*. Unpublished M.Sc Thesis, University of Pretoria, Pretoria.

PENRITH, M-L. 1986. Relationships in the tribe Adesmiini (Coleoptera: Tenebrionidae) and a revision of the Genus *Stenodesia* Reitter. Annals of the Transvaal Museum **34**(13): 275-302

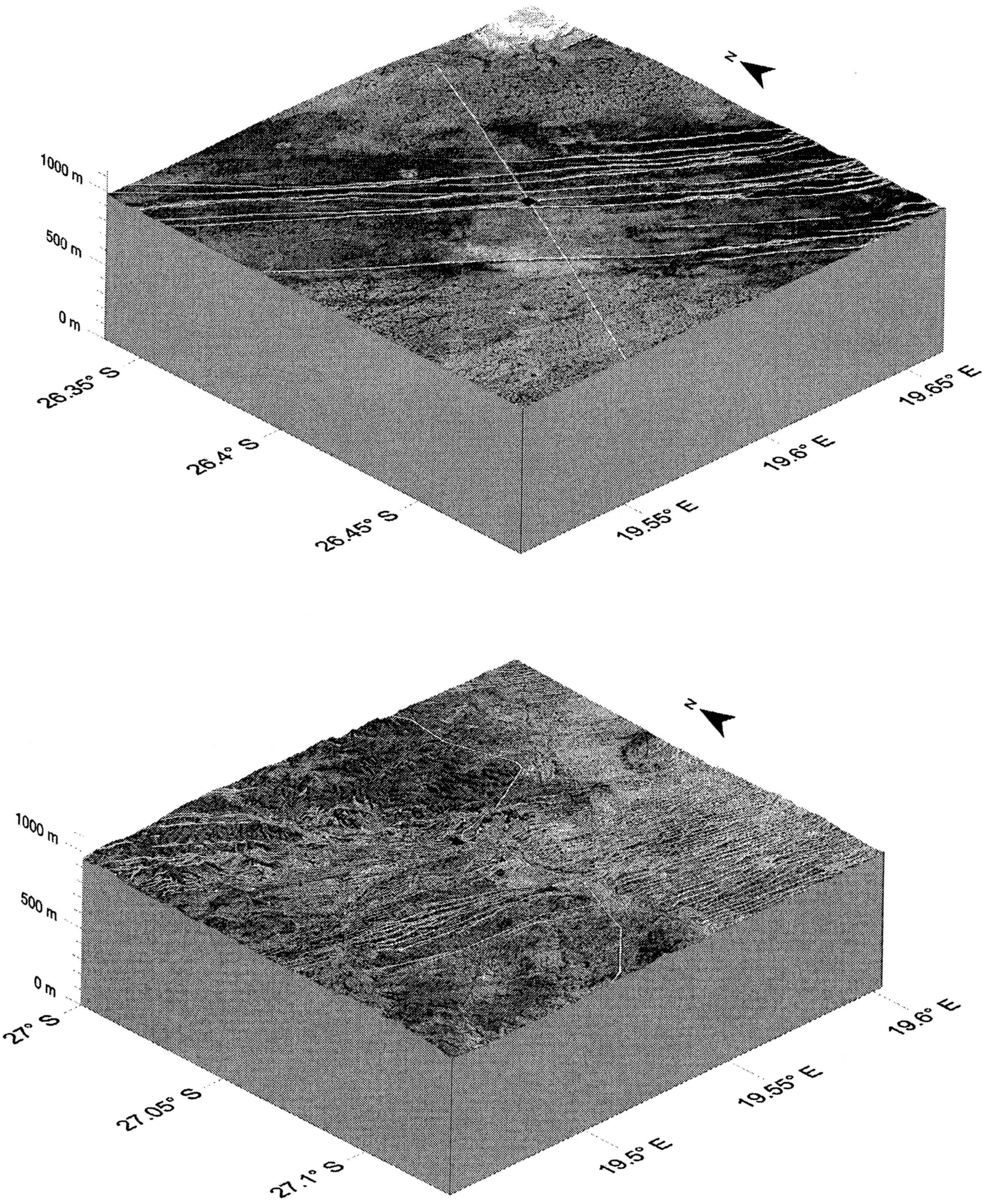
ROSENZWEIG, M.L. 1995. *Species diversity in space and time*. University Press, Cambridge.

VAN ZINDEREN BAKKER, E.M. 1975. The origin and palaeoenvironment of the Namib Desert Biome. *Journal of Biogeography* **2**: 65-73.

APPENDIX A



Arial aspects adapted from Landsat images. Figures 1 & 2 (from top to bottom): Itaga & Middelplaas.



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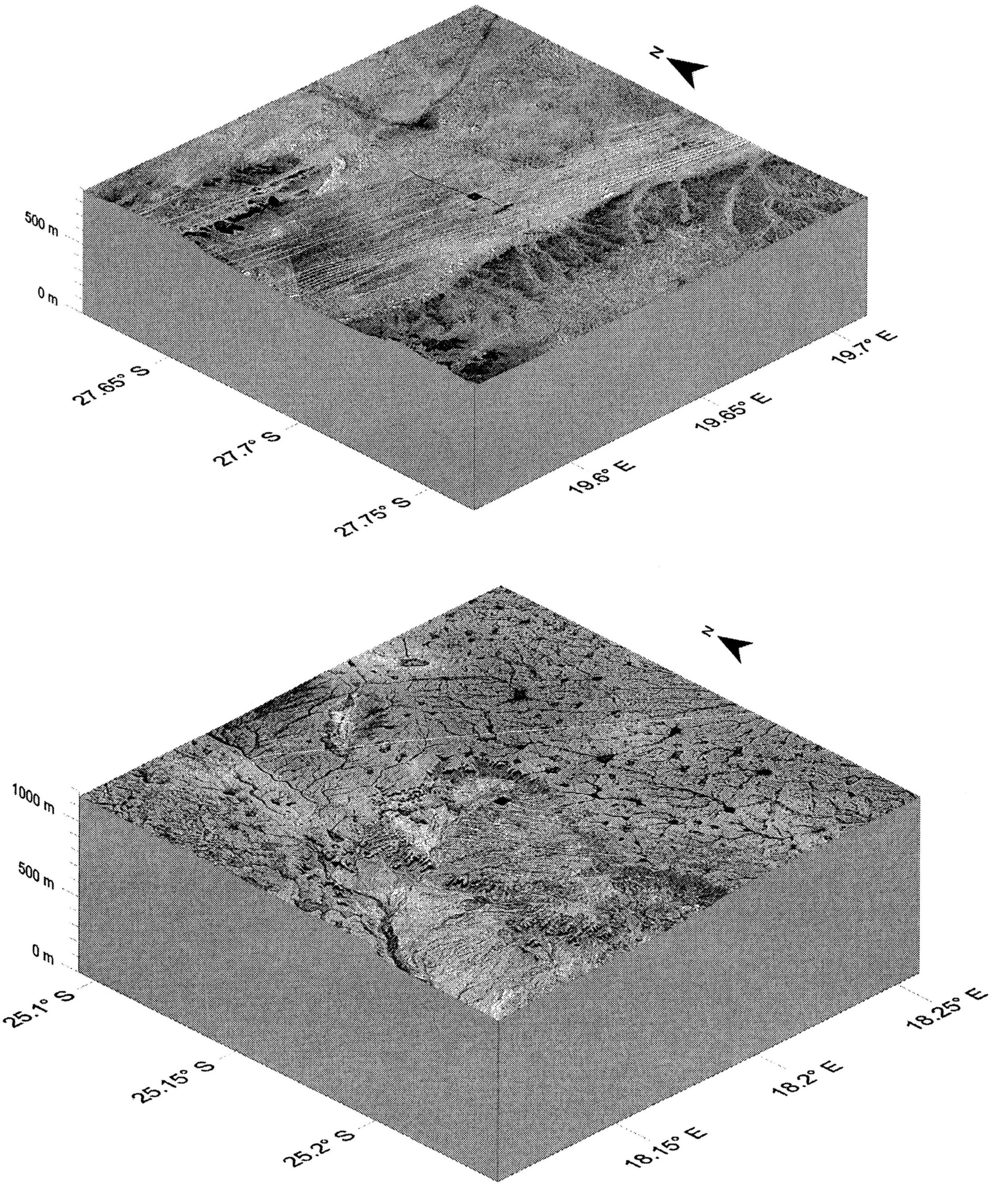

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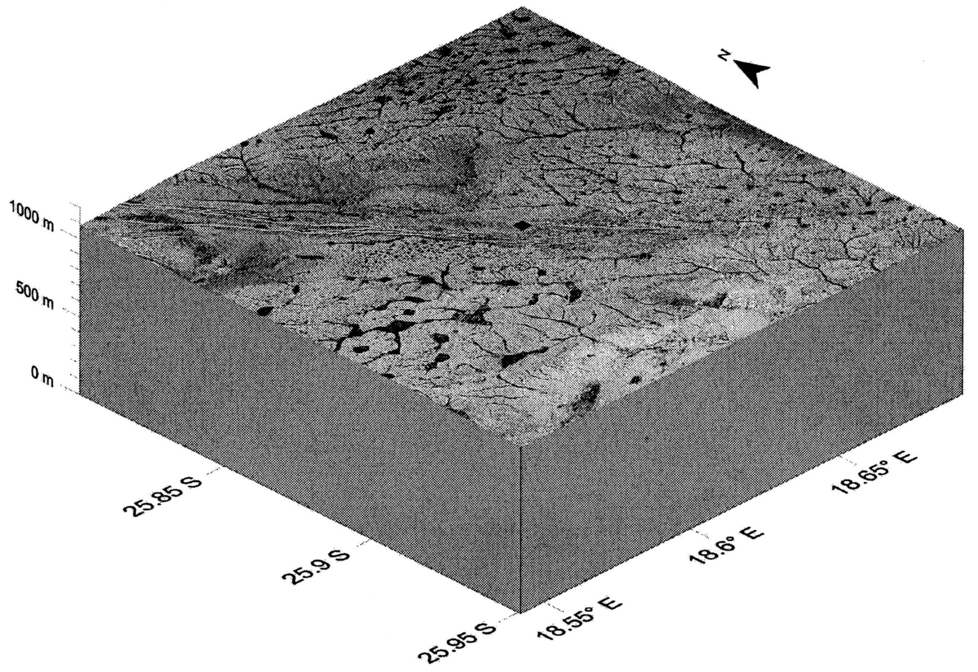

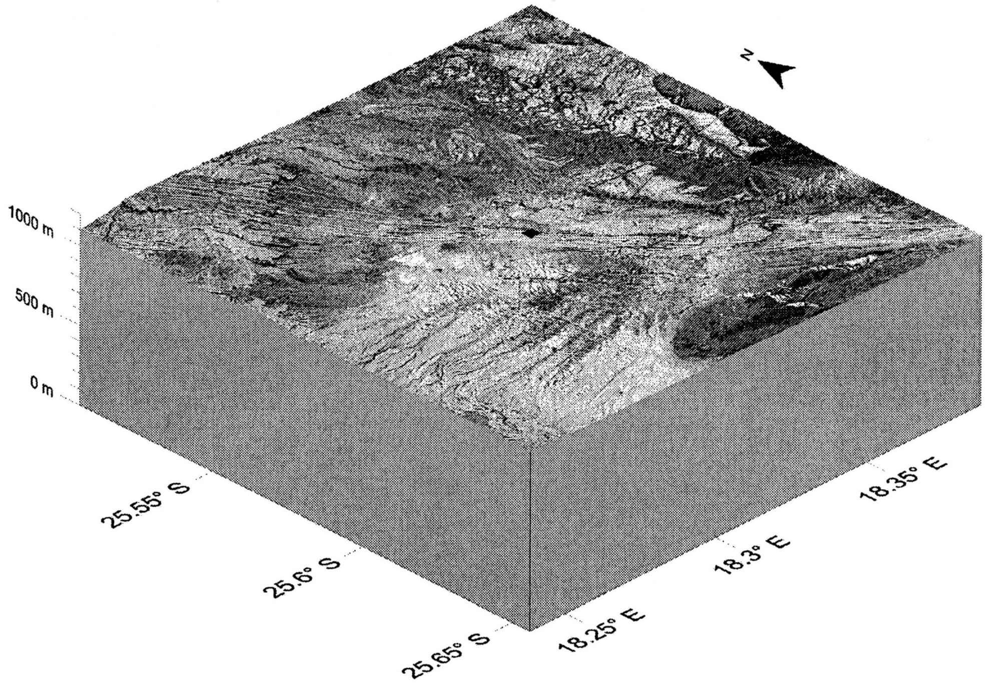

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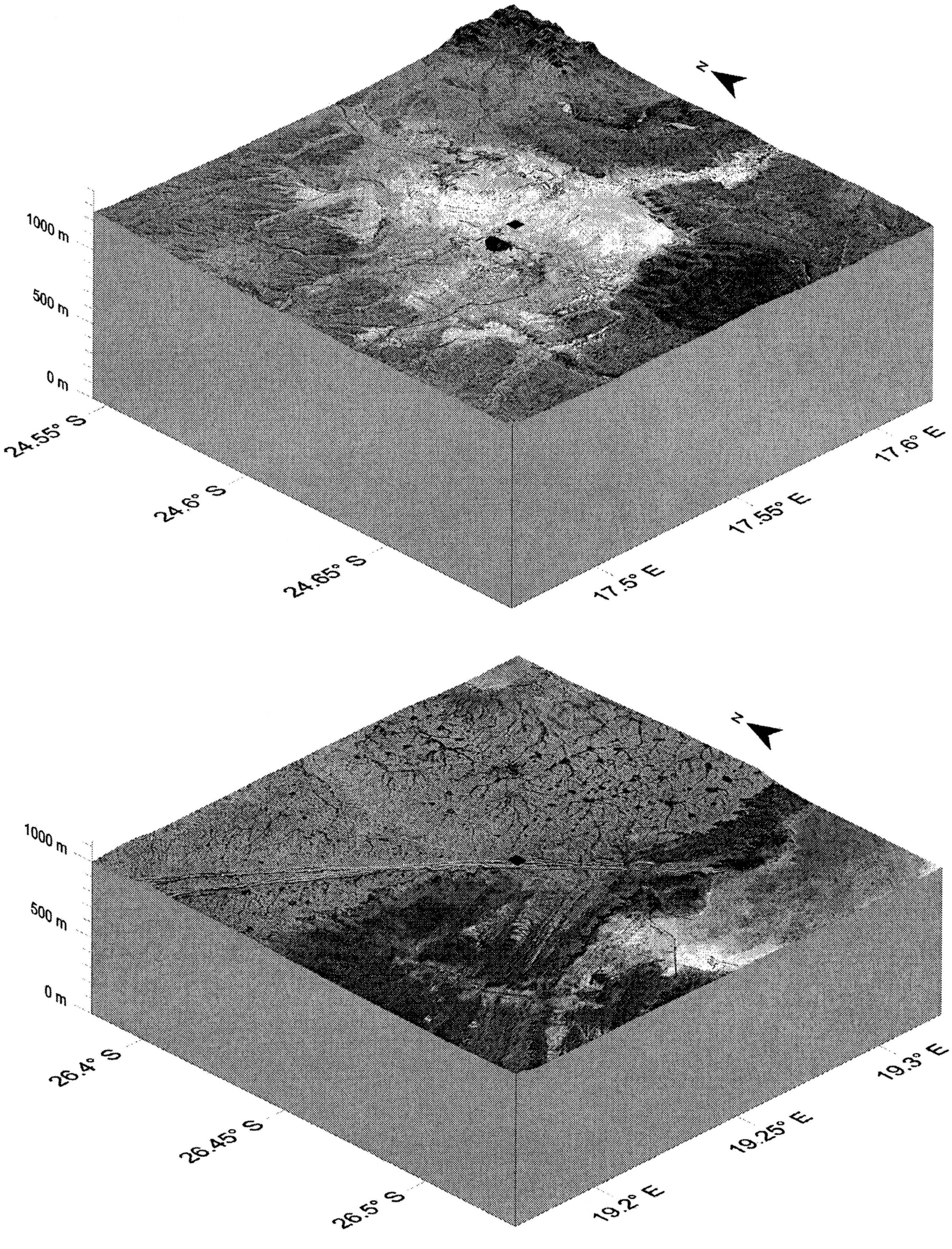
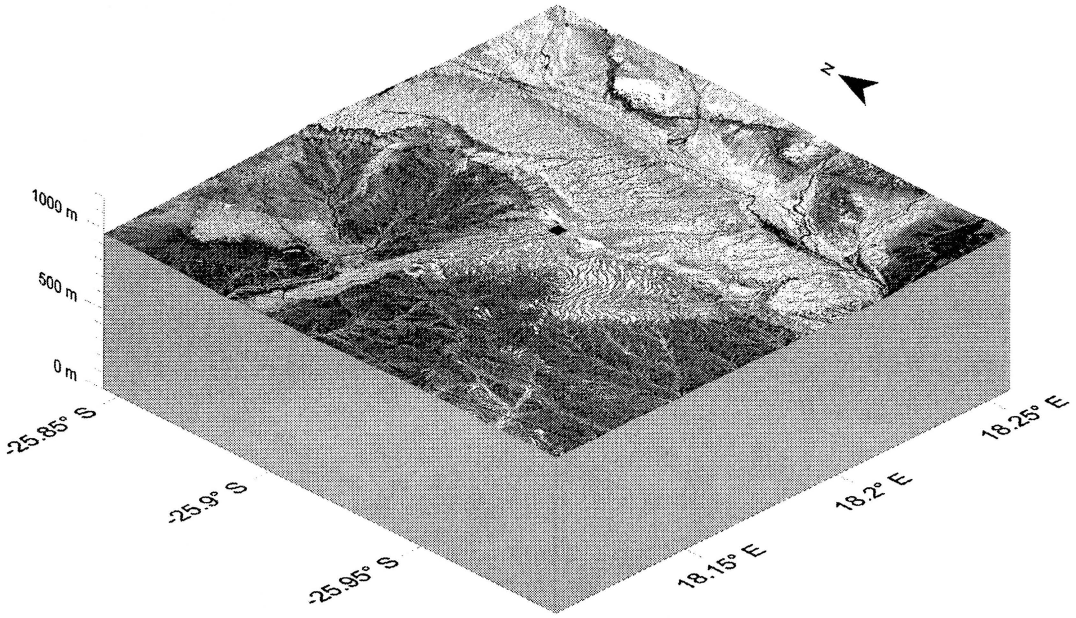
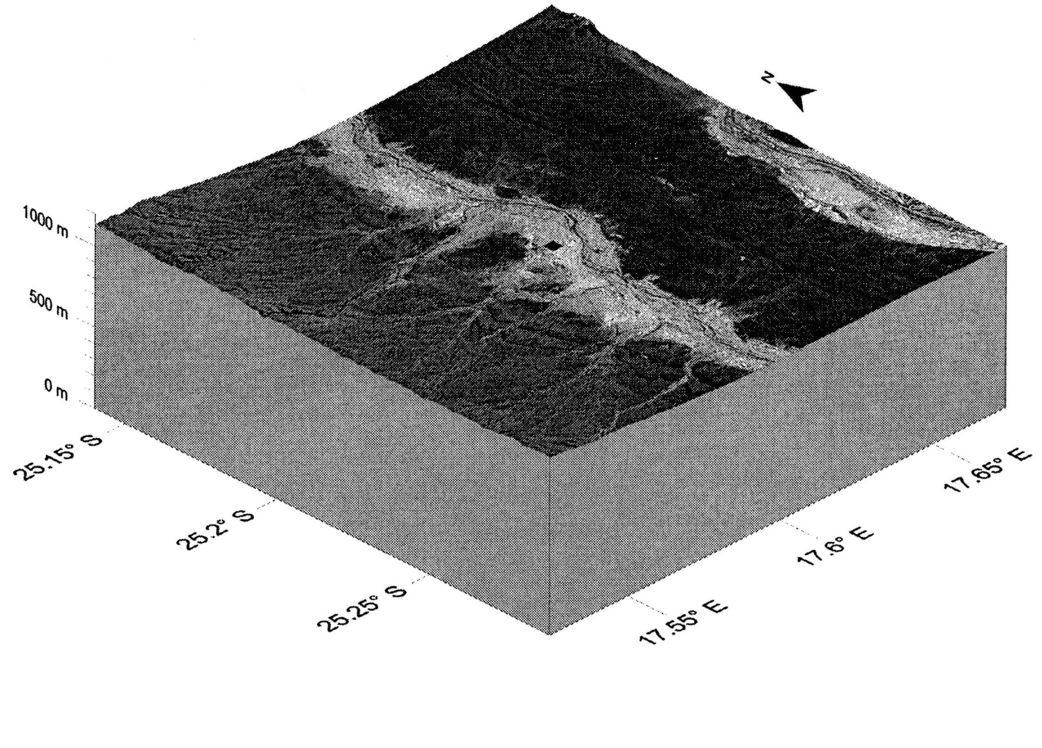
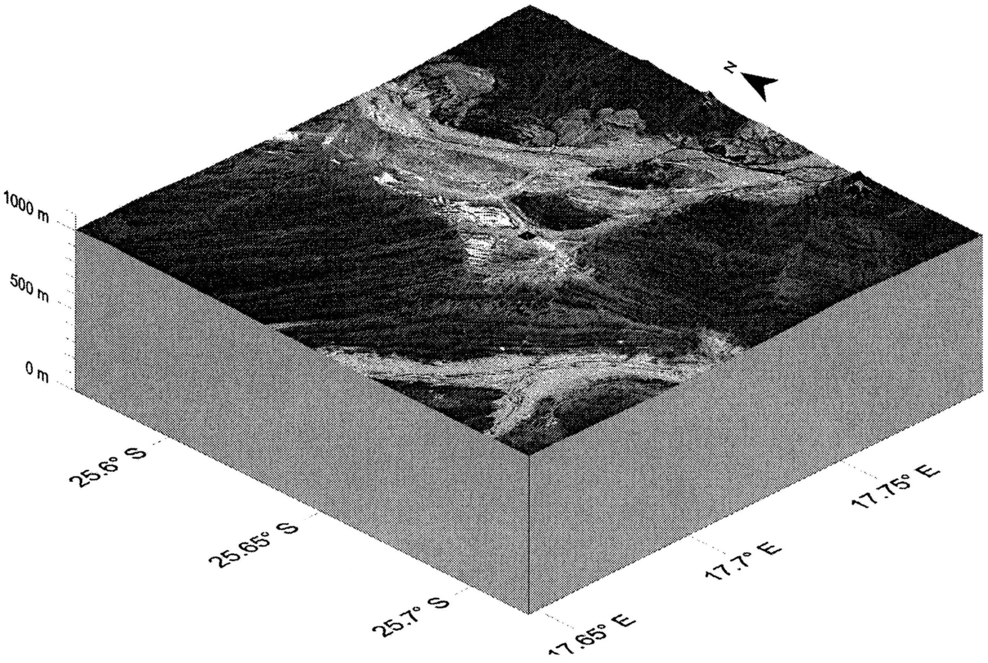


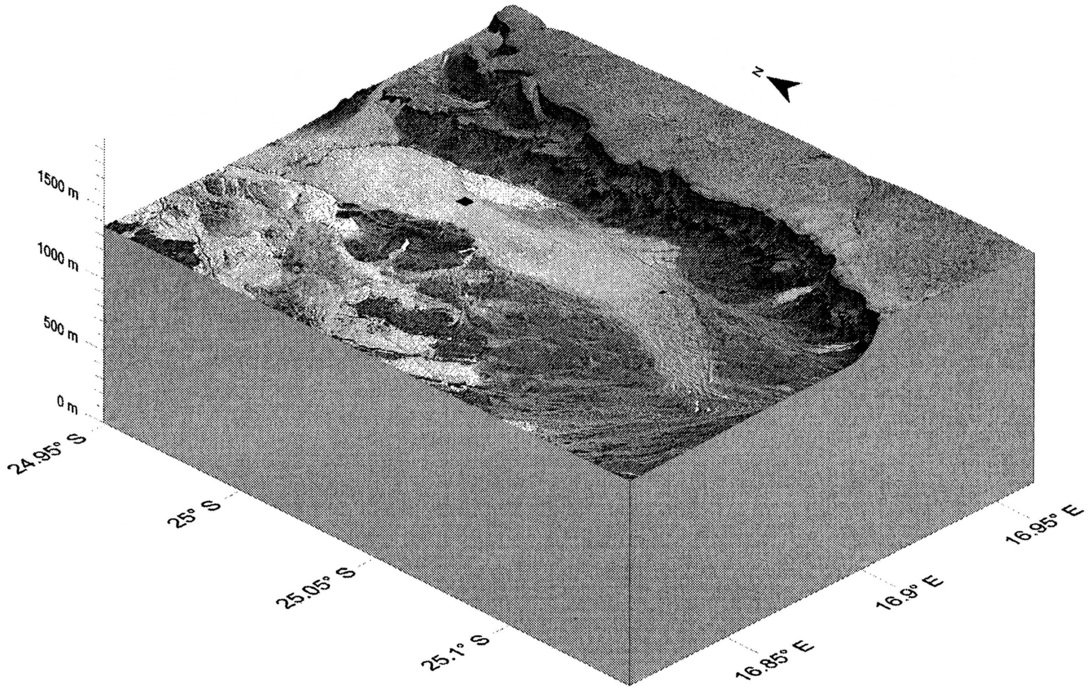
Arial aspects adapted from Landsat images. Figures 9 & 10 (from top to bottom): Haribes & Averas.



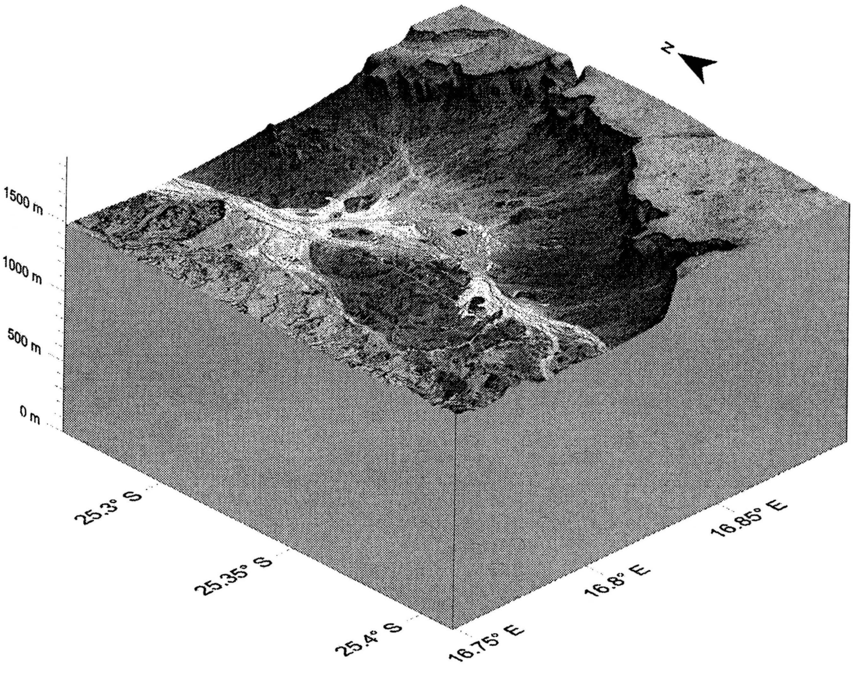


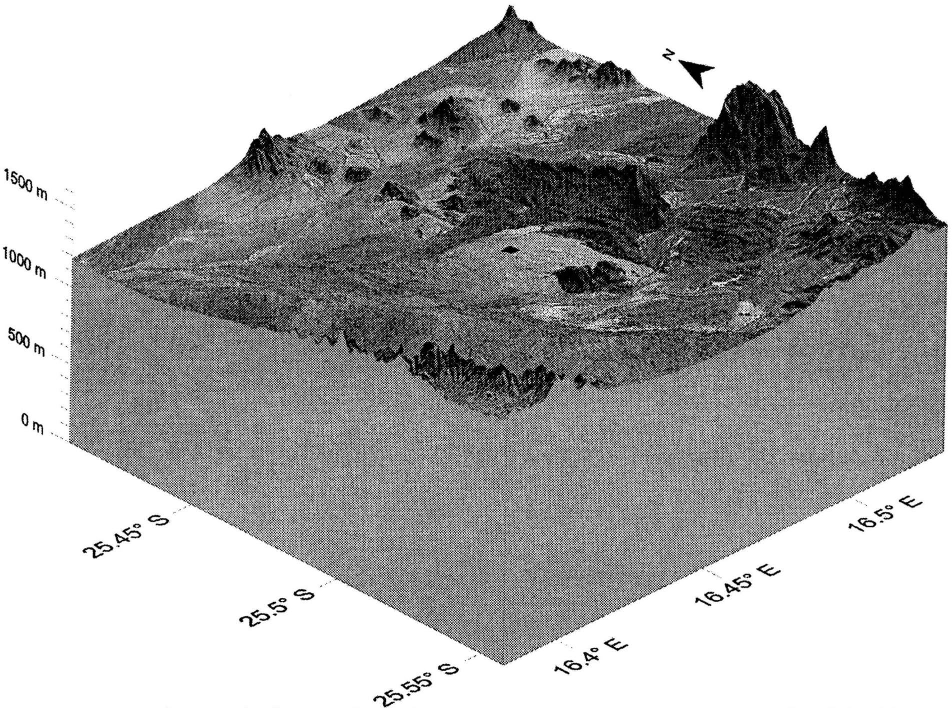
Arial aspects adapted from Landsat images. Figures 11 & 12 (from top to bottom): Tses & Kaitzub.



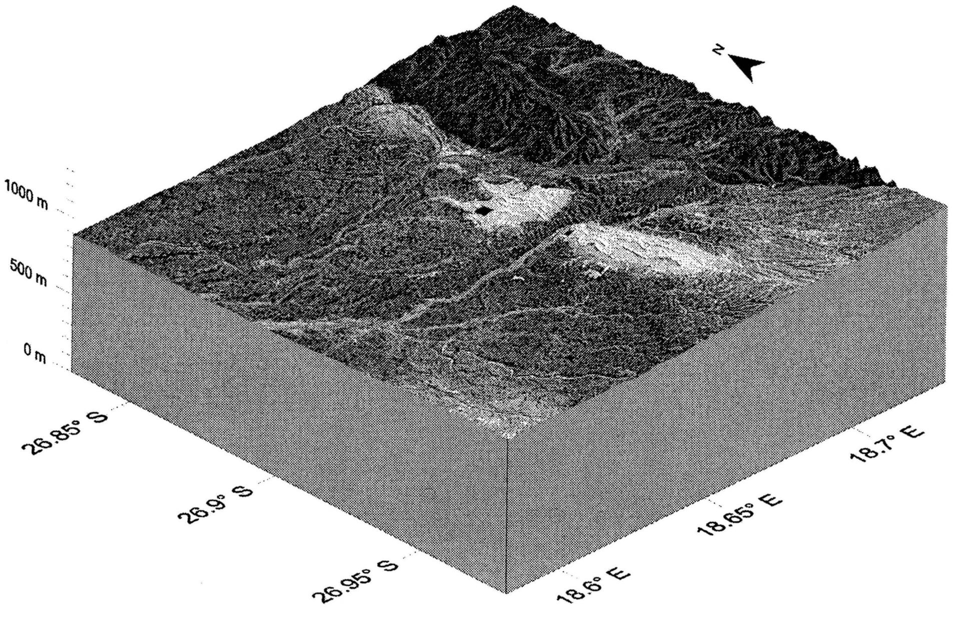


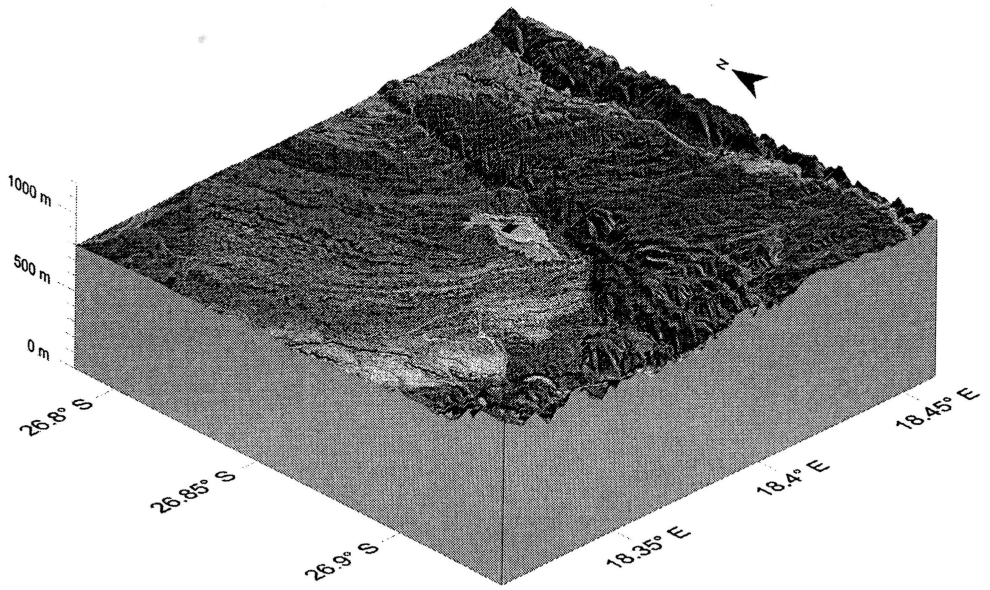
Arial aspects adapted from Landsat images. Figures 13 & 14 (from top to bottom): Lichtenfels & Burgsdorf Noord.



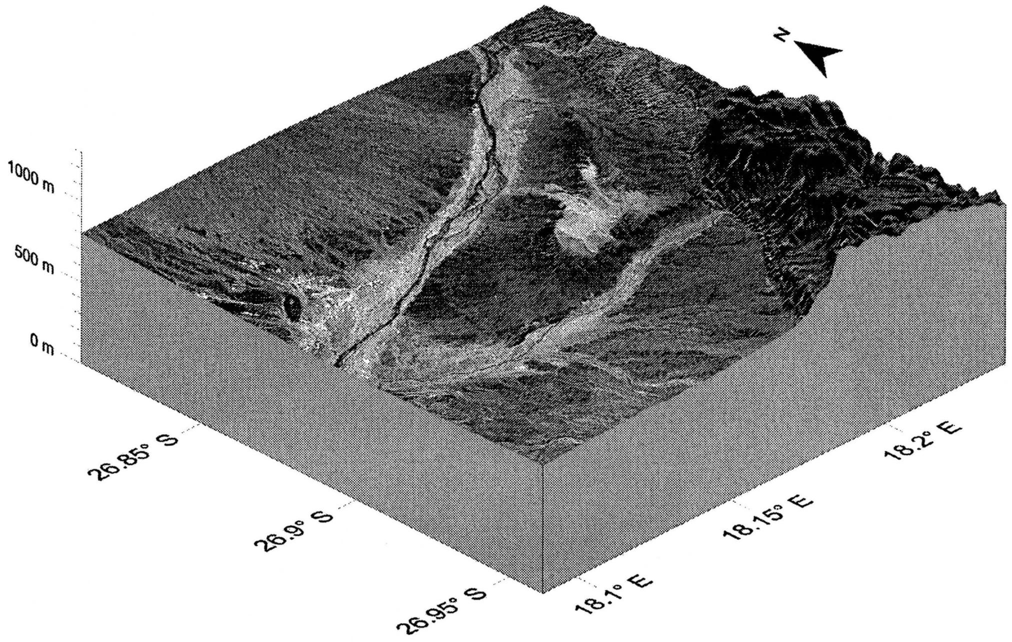


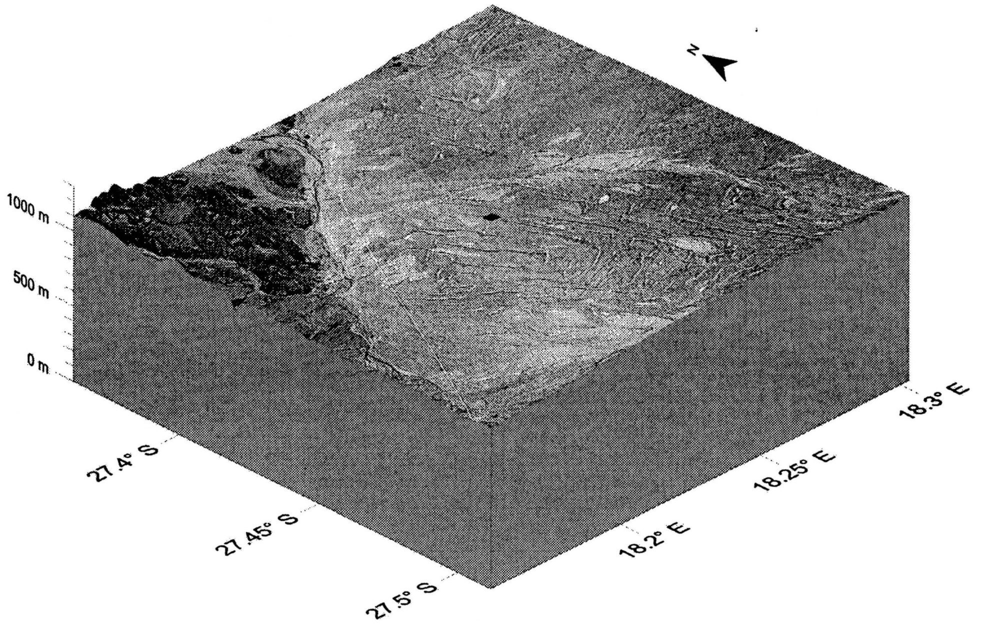
Arial aspects adapted from Landsat images. Figures 15 & 16 (from top to bottom): Amhub & Kronenhof.



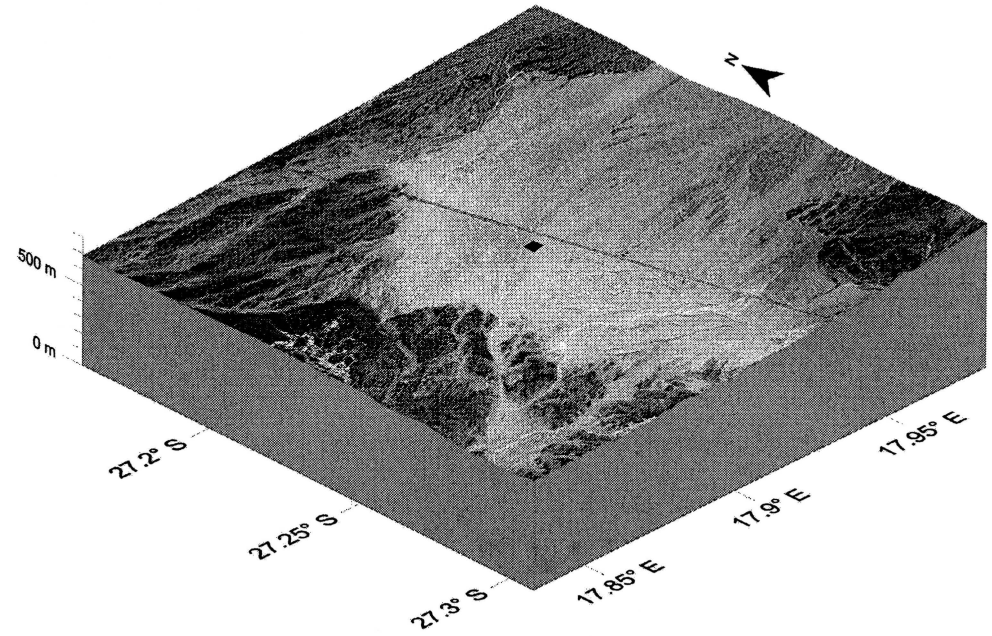


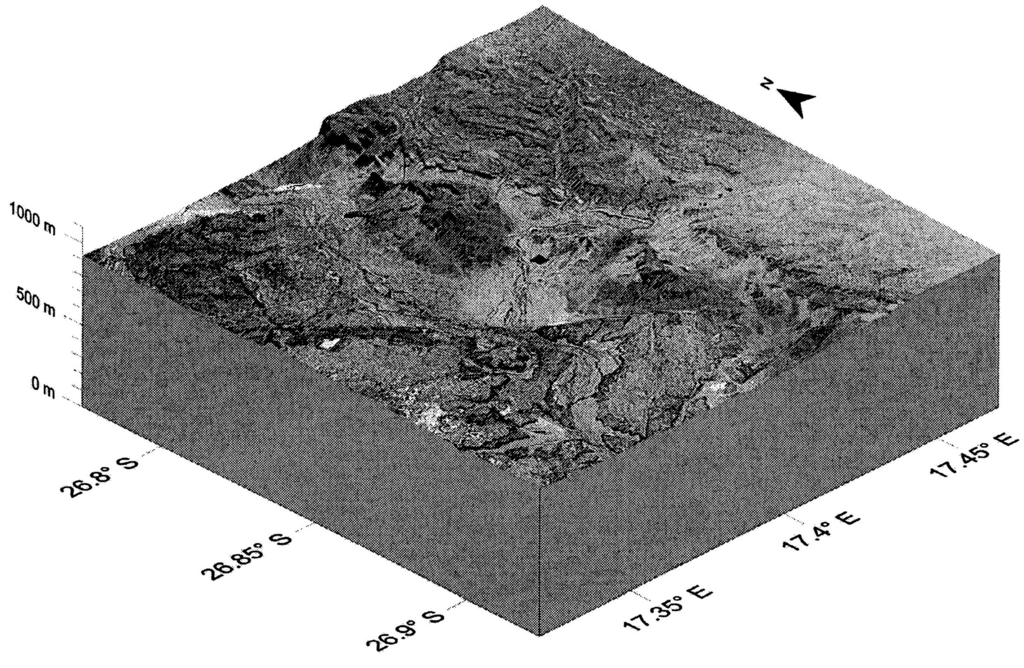
Arial aspects adapted from Landsat images. Figures 17 & 18 (from top to bottom): Donkermodder & Verschluss.



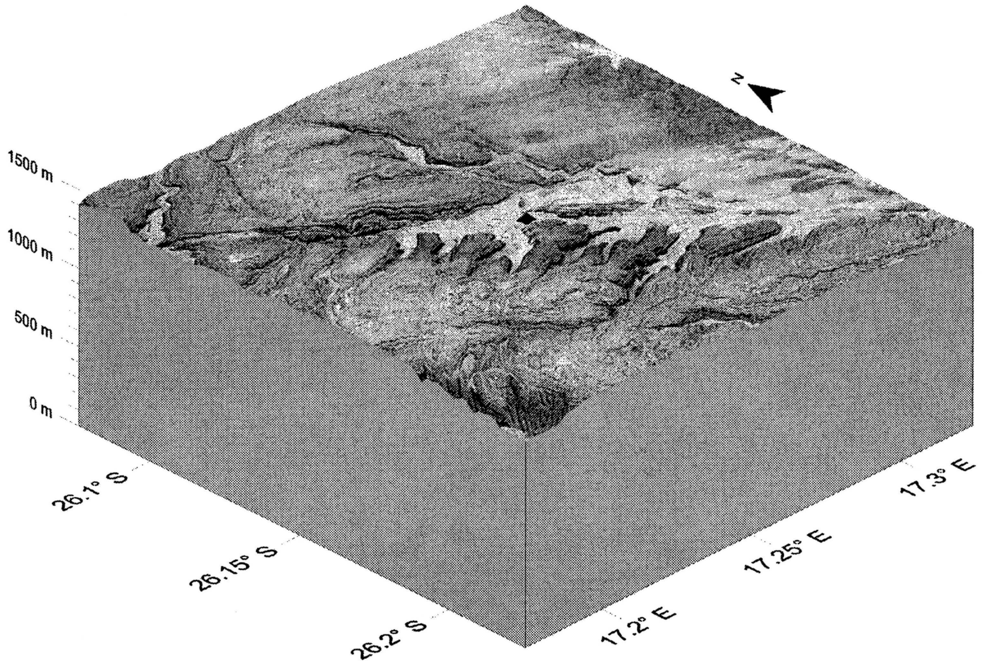


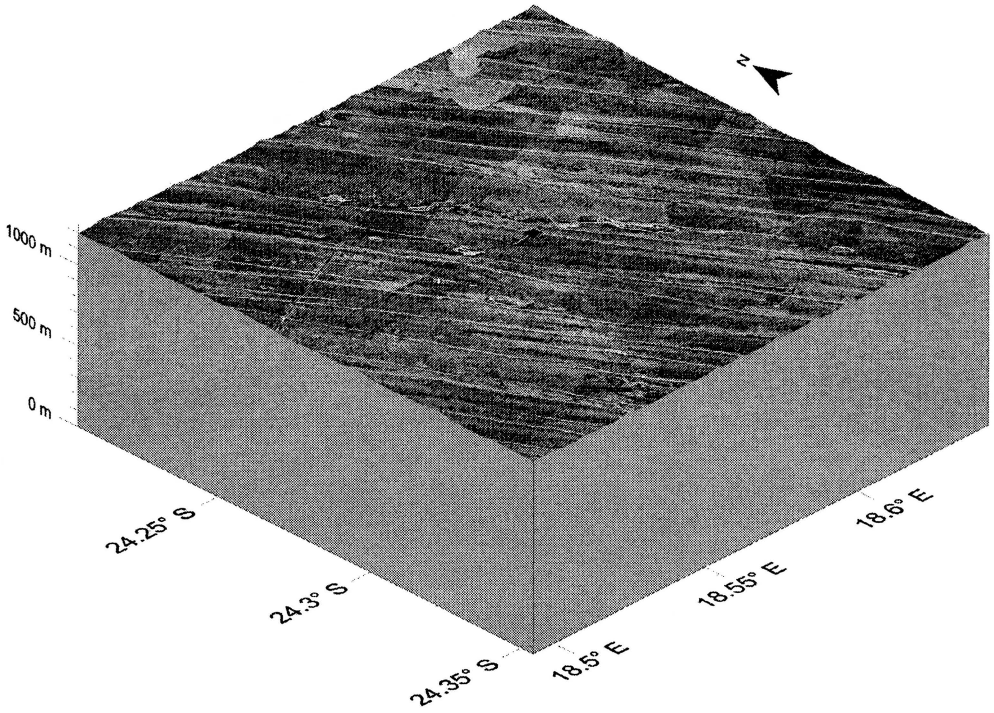
Arial aspects adapted from Landsat images. Figures 19 & 20 (from top to bottom): Aikanes & Gründorn.



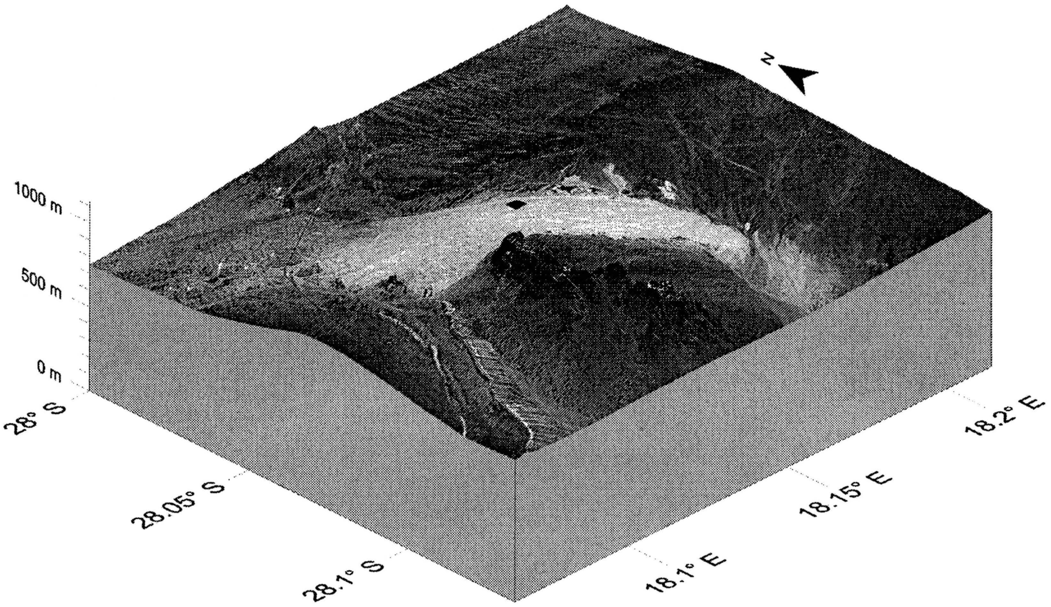


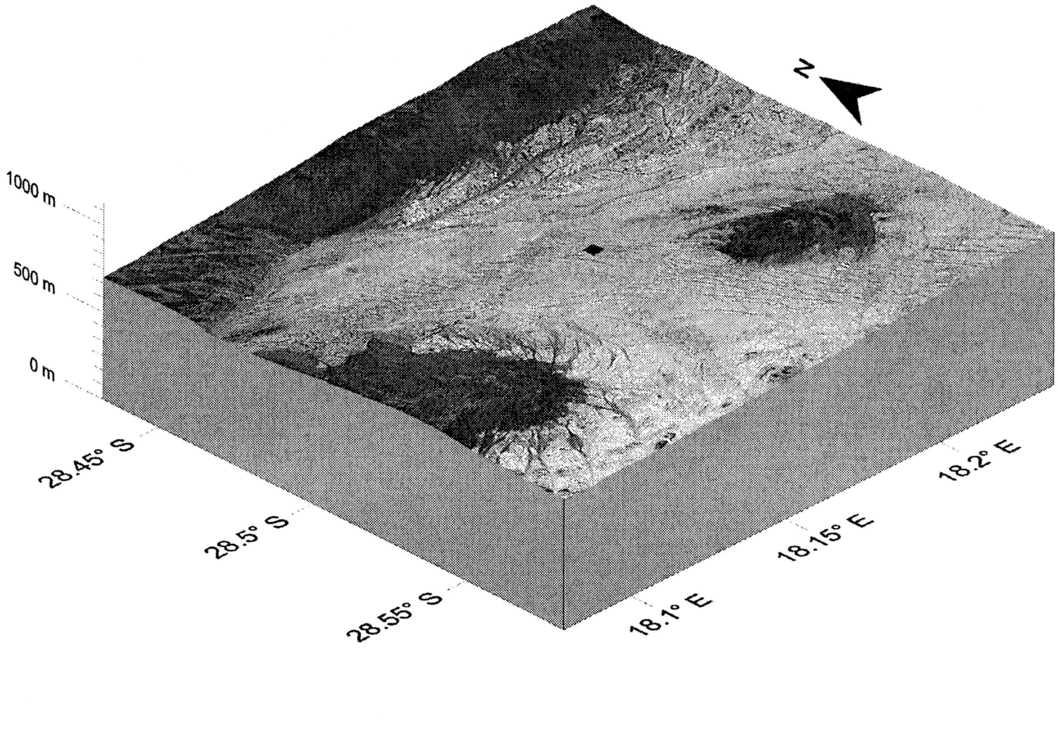
Arial aspects adapted from Landsat images. Figures 21 & 22 (from top to bottom): Oase & Sandverhaar.





Arial aspects adapted from Landsat images. Figures 23 &24 (from top to bottom): Untersee & Middelplaas.





Arial aspects adapted from Landsat images. Figures 25 & 26 (from top to bottom): Norachas & Bruinheuwel.

APPENDIX B

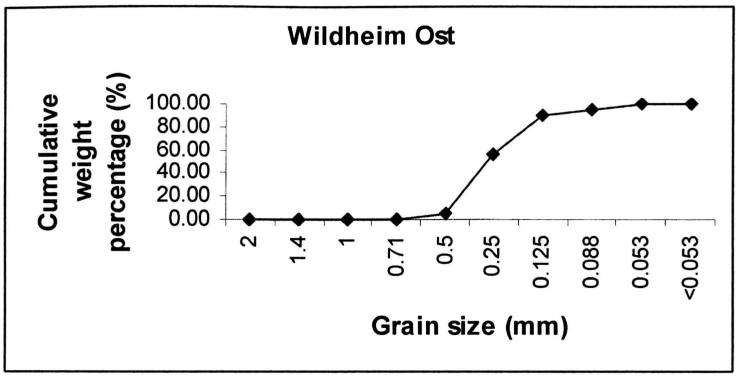


Figure 1. Wildheim Ost sand grain size distribution.

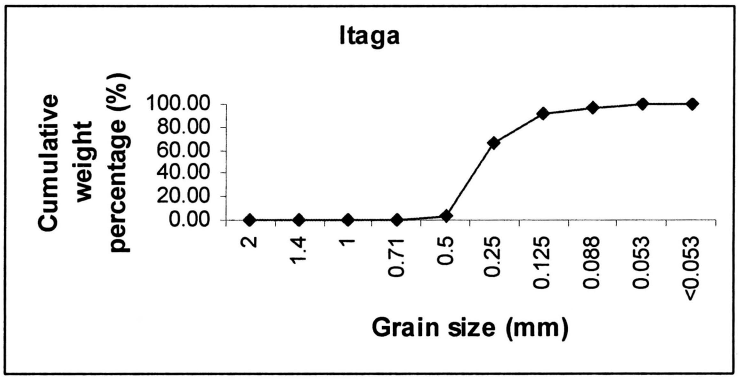


Figure 2. Itaga sand grain size distribution.

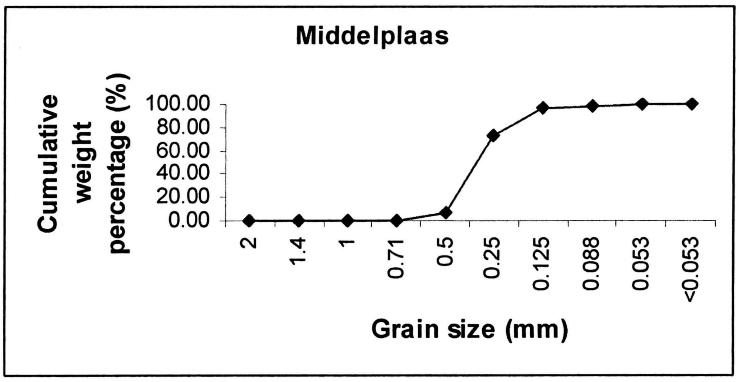


Figure 3. Middelplaas sand grain size distribution.

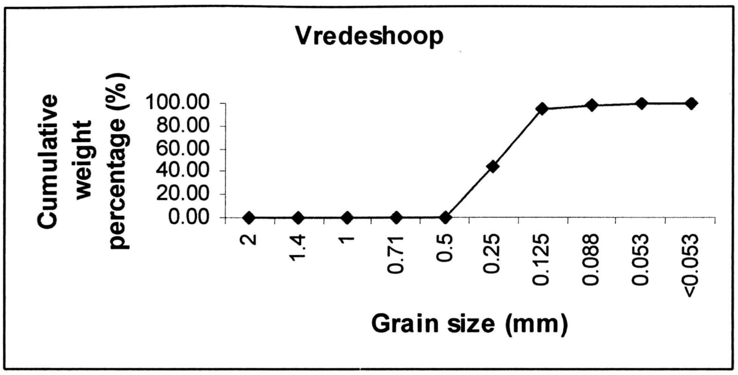


Figure 4. Vredeshoop sand grain size distribution.

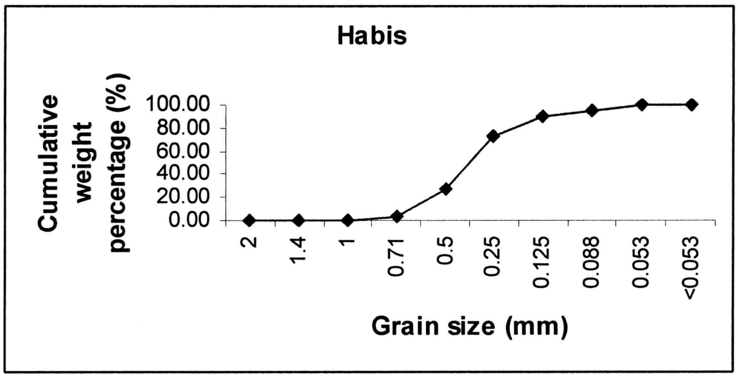


Figure 5. Habis sand grain size distribution.

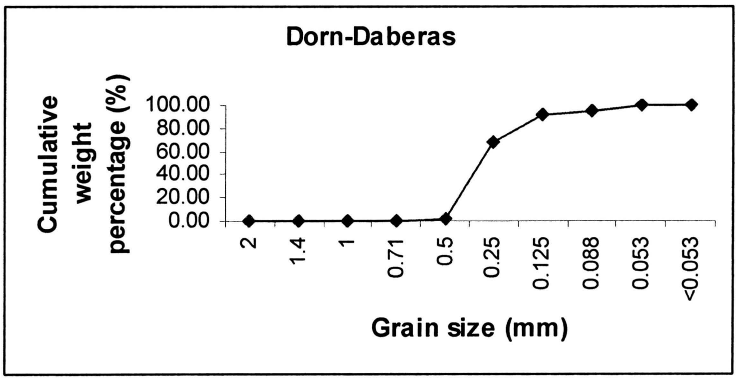


Figure 6. Dorn-Daberas sand grain size distribution.

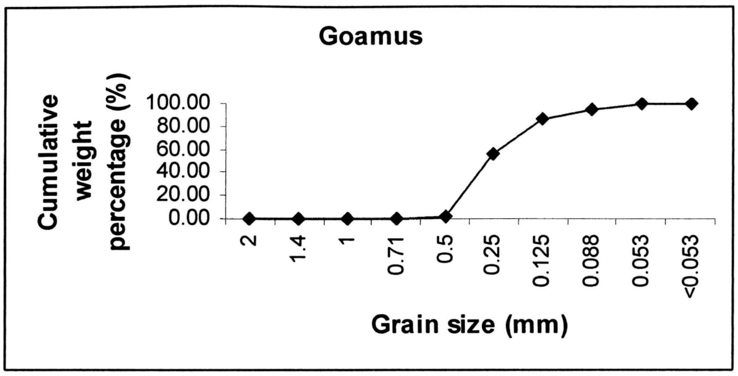


Figure 7. Goamus sand grain size distribution.

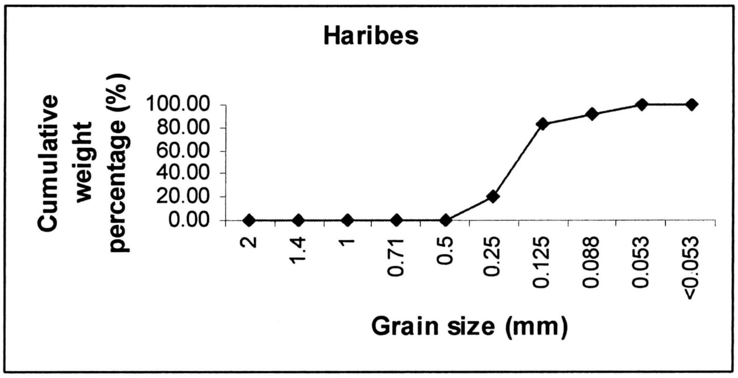


Figure 8. Haribes sand grain size distribution.

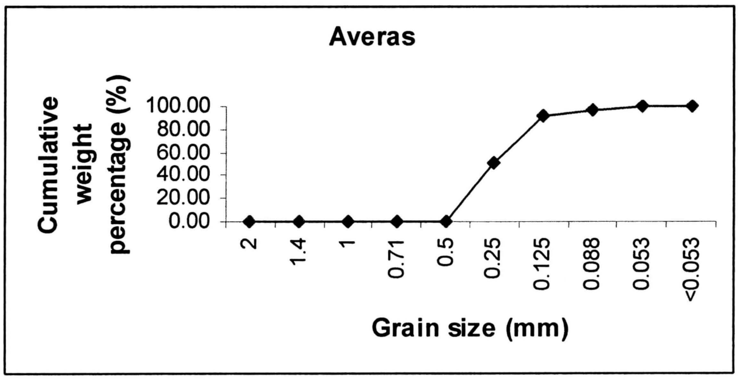


Figure 9. Averas sand grain size distribution.

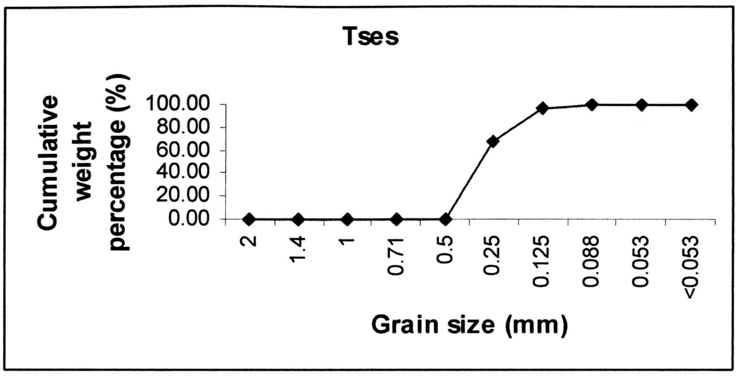


Figure 10. Tses sand grain size distribution.

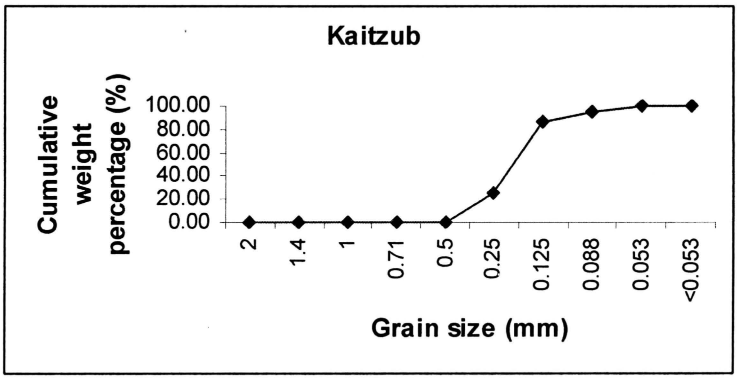


Figure 11. Kaitzub sand grain size distribution.

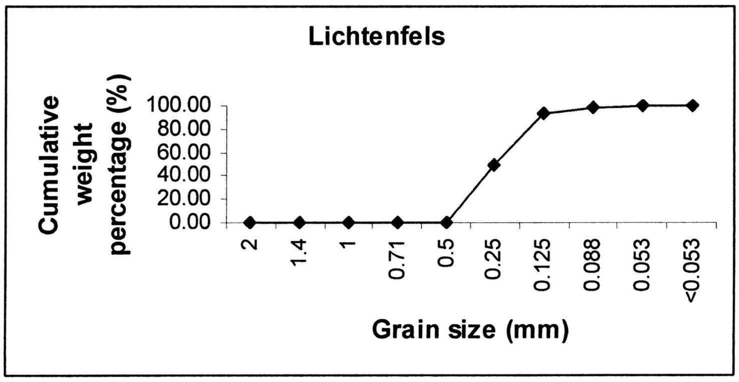


Figure 12. Lichtenfels sand grain size distribution.

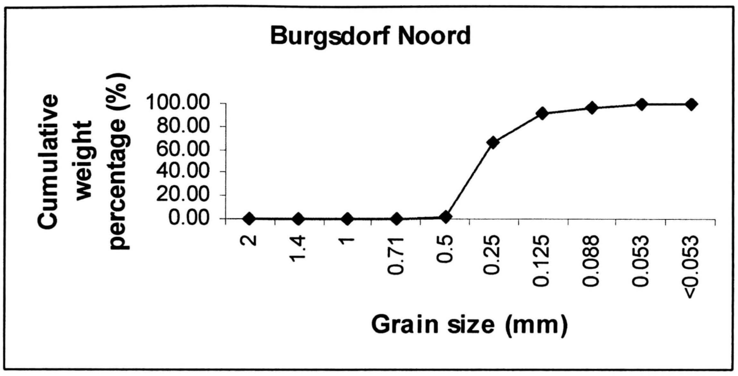


Figure 13. Burgsdorf Noord sand grain size distribution.

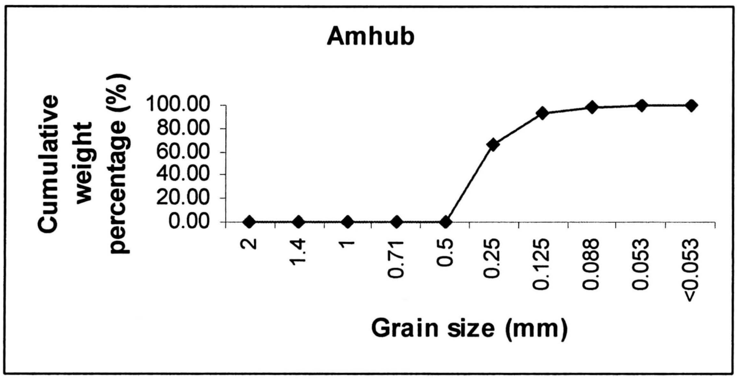


Figure 14. Amhub sand grain size distribution.

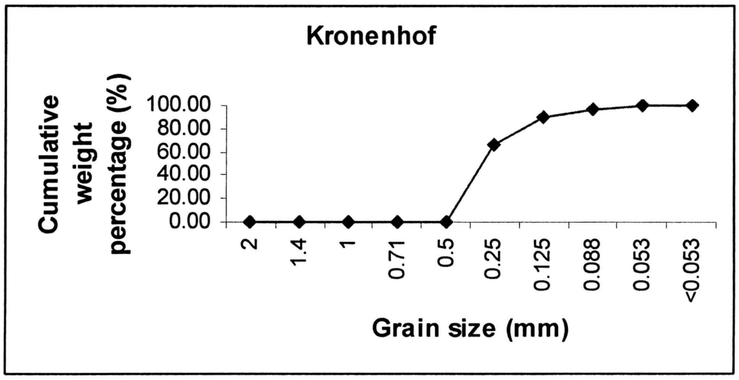


Figure 15. Kronenhof sand grain size distribution.

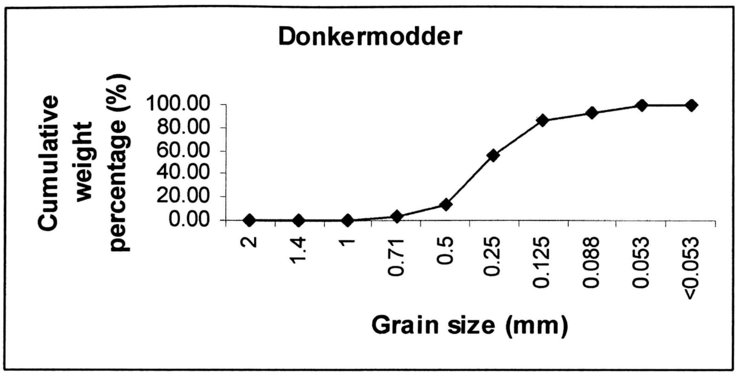


Figure 16. Donkermodder sand grain size distribution.

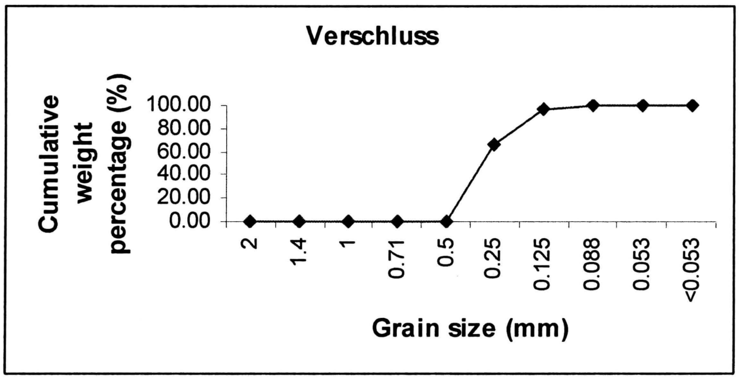


Figure 17. Verschluss sand grain size distribution.

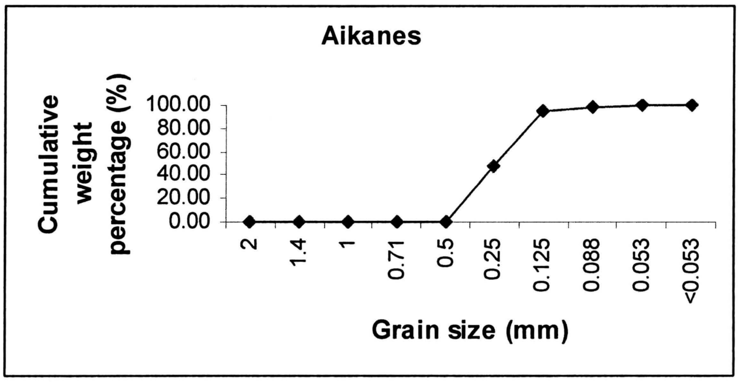


Figure 18. Aikanes sand grain size distribution.

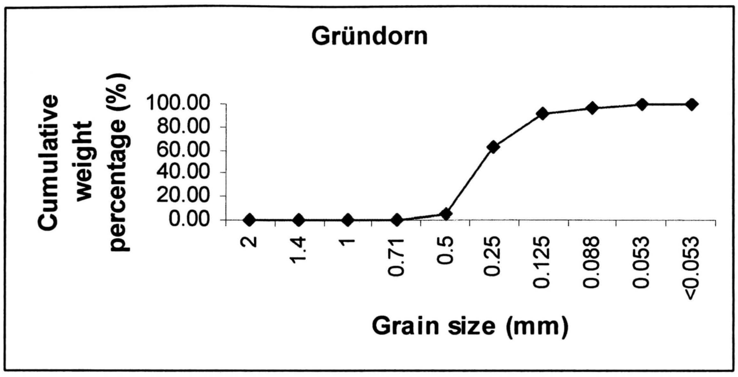


Figure 19. Gründorn sand grain size distribution.

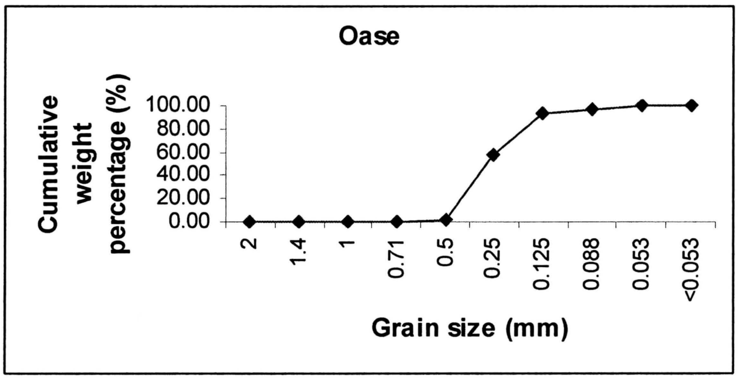


Figure 20. Oase sand grain size distribution.

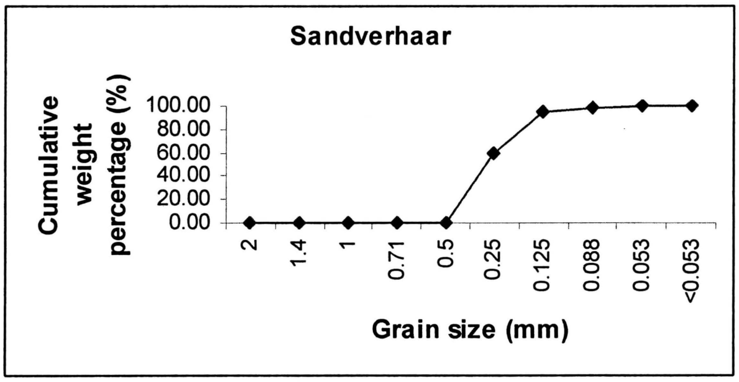


Figure 21. Sandverhaar sand grain size distribution.

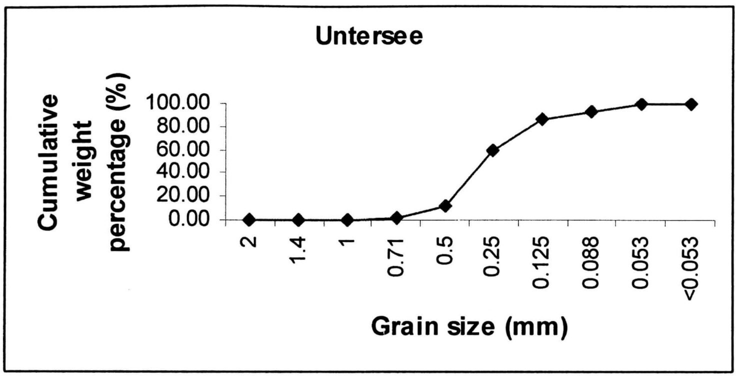


Figure 22. Untersee sand grain size distribution.

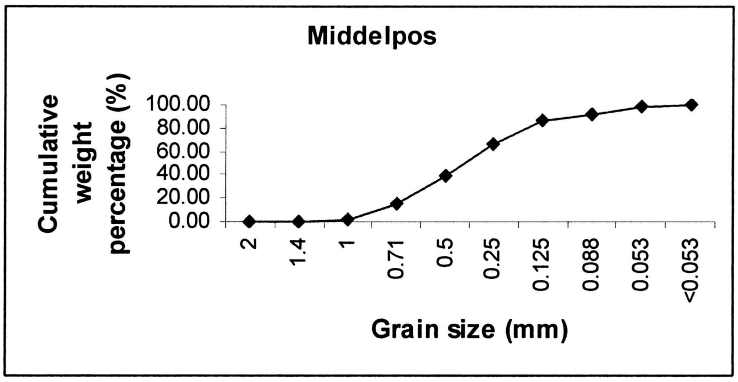


Figure 23. Middelpos sand grain size distribution.

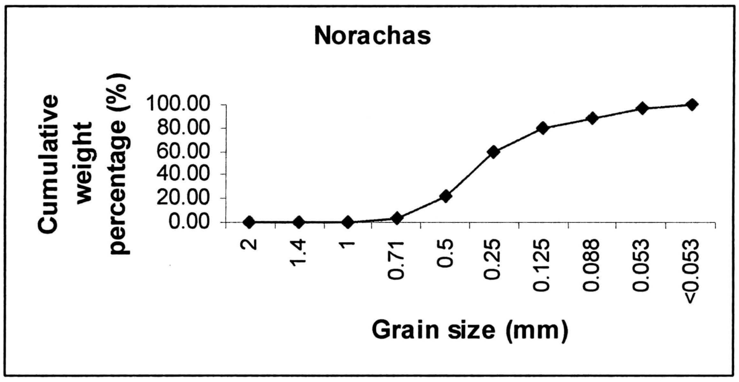


Figure 24. Norachas sand grain size distribution.

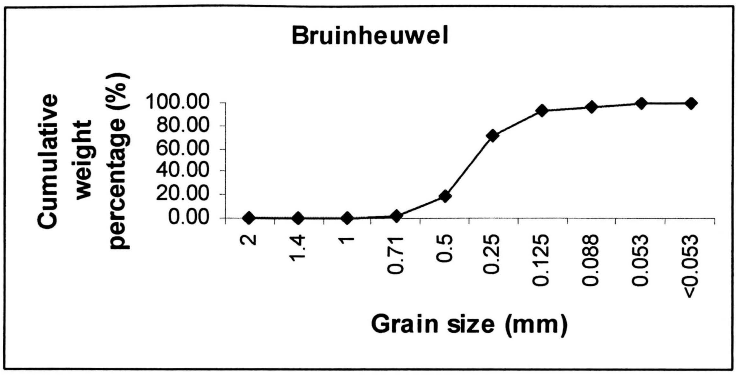


Figure 25. Bruinheuwel sand grain size distribution.

APPENDIX C

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Arachnida	Agelenidae			*Agelena suboculata* Simon	1	C. Haddad
	Ammoxenidae			*Ammoxenus coccineus* Simon	1	C. Haddad
	Caponiidae			*Diploglena capensis* Purcell	1	C. Haddad
	Caponiidae			*Caponia capensis* Purcell	1	C. Haddad
	Daesiidae			*Namibesia* sp.	1	C. Haddad
	Daesiidae			*Biton pearsoni* (Hewitt)	1	C. Haddad
	Daesiidae			*Hemiblossia termitophila* Lawrence	1	C. Haddad
	Eresidae			*Seothyra fasciata* Purcell	1	C. Haddad
	Gnaphosidae			*Zelotes o'neili* (Purcell)	1	C. Haddad
	Gnaphosidae			*Setaphis bilinearis* Tucker	1	C. Haddad
	Gnaphosidae			*Asemesthes ineatus* Purcell	1	C. Haddad
	Gnaphosidae			*Xerophaeus* sp.	1	C. Haddad
	Gnaphosidae			*Zelotes pulchripes* (Purcell)	1	C. Haddad
	Gnaphosidae			*Asemesthes* sp.	1	C. Haddad
	Gnaphosidae			*Setaphis* sp.	1	C. Haddad
	Hexisopodidae			*Chelypus weulischi* Roewer	1	C. Haddad
	Hexisopodidae			*Chelypus hirsti* Hewitt	1	C. Haddad
	Hexisopodidae			*Hexisopus lanatus* Koch	1	C. Haddad
	Hexisopodidae			*Chelypus lennoxae* Hewitt	1	C. Haddad
	Idiopidae			*Gorgyrella* sp.	1	C. Haddad
	Lycosidae			*Evippa* sp.	1	C. Haddad
	Nemesiidae			*Hermacha lanata* (Purcell)	1	C. Haddad
	Palpimanidae			*Palpimanus* sp.	1	C. Haddad
	Philodromidae			*Hirriusa* sp.	1	C. Haddad
	Philodromidae			*Thanatus pagenstecheri* Strand	1	C. Haddad
	Pisauridae			*Rothus auratus* Pocock	1	C. Haddad

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Arachnida	Prodidomidae			*Prodidomus* sp.	1	C. Haddad
	Prodidomidae			*Theuma maculata* Purcell	1	C. Haddad
	Salticidae			*Menemerus* sp.	1	C. Haddad
	Salticidae			*Pellenes* sp.	1	C. Haddad
	Salticidae			*Phlegra* sp.	1	C. Haddad
	Salticidae			*Pseudicius* sp.	1	C. Haddad
	Salticidae			*Yogetor* sp.	1	C. Haddad
	Salticidae			*Phlegra* sp.	1	C. Haddad
	Sparassidae			*Orchestrella* sp.	1	C. Haddad
	Theridiidae			*Euryopis* sp.	1	C. Haddad
	Theridiidae			*Dipoena* sp.	1	C. Haddad
	Thomisidae			*Misumenops rubrodecoratus* Millot	1	C. Haddad
	Zodariidae			*Capheris* sp.	1	C. Haddad
	Zodariidae			*Heradida griffinae* Jocqué	1	C. Haddad
	Buthidae			*Buthidae* sp. 1	1	L. Lotz
	Buthidae			*Parabuthus granulatus* (Hemprich & Ehrenberg)	1	L. Lotz
	Buthidae			*Parabuthus brevimanus* (Thorell)	1	L. Lotz
	Buthidae			*Hottentotta arenaceus* Birula	1	L. Lotz
	Buthidae			*Parabuthus kalaharicus* Lamoral	1	L. Lotz
	Buthidae			*Parabuthus leavifrons* (Simon)	1	L. Lotz
	Buthidae			*Parabuthus ?granulatus* (Hemprich & Ehrenberg)	1	L. Lotz
	Buthidae			*Parabuthus schlechteri* Purcell	1	L. Lotz
	Buthidae			*Parabuthus ?kalaharicus* Lamoral	1	L. Lotz
	Pseudoscorpiones			sp. 1	2	C. Haddad
	Scorpionidae			*Opistophthalmus ?holmi* (Lawrence)	1	L. Lotz

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Arachnida	Scorpionidae			*Opistophthalmus holmi* (Lawrence)	1	L. Lotz
	Solpugidae			*Zeria* sp.	1	C. Haddad
	Solpugidae			*Zeria schleteri* (Purcell)	1	C. Haddad
	Solpugidae			*Solpugiba* sp.	1	C. Haddad
	Solpugidae			*Zeria* sp. 2	1	C. Haddad
Blattodea	Blattellidae			*Namablatta bitaeniata* Stål	2	
	Polyphagidae			*Tivia* sp.	2	
Coleoptera	Bruchidae			*Spermophagus* sp.	1	S. Louw
	Bruchidae			*Caryedon* sp.	3	
	Bruchidae			*Spermophagus prevetti* Borowiec	1	S. Louw
	Bruchidae			*Spermophagus* sp. 2	3	
	Bruchidae			sp.	3	
	Carabidae			*Cypholoba alstoni* (Péringuey)	2	
	Carabidae			*Anthia circumscripta* Klug	2	
	Carabidae	Brachininae		*Crepidogastrinus kochi* Basilewsky	2	
	Carabidae	Harpalinae		*Boeomimetus ephippium* Boheman	1	S. Louw
	Carabidae	Lebiinae		sp.	3	
	Carabidae	Scaritinae		*Passalidius fortipes* (Boheman)	2	
	Chrysomelidae	Eumolpinae		*Macrocoma* sp.	1	S. Louw
	Chrysomelidae	Eumolpinae		sp.	3	
	Chrysomelidae	Galerucinae		*Monolepta* sp.	2	
	Crysomelidae	Eumolpinae		*Macrocoma* sp.	1	S. Louw
	Curculionidae			*Leptostethus argentatus* Thompson	1	S. Louw
	Curculionidae			sp.	3	

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Coleoptera	Curculionidae	Brachderinae		sp.	3	
	Dermestidae			*Attagenus* sp.	3	
	Dytiscidae			*Eretes stricticus* Linnaeus	2	
	Histeridae			*Dahlgrenius* sp.	1	S. Louw
	Histeridae			*Dahlgrenius* sp. 2	1	S. Louw
	Histeridae			*Pholioxenus* sp.	3	
	Hydrophilidae			*Helochares* sp.	3	
	Scarabaeidae	Aphodiinae		*Aphodius* sp.	1	S. Louw
	Scarabaeidae	Aphodinae		*Aphodius* sp. 2	3	
	Scarabaeidae	Aphodinae		*Aphodius* sp. 3	3	
	Scarabaeidae	Cetoniinae		*Xeloma maura* (Boheman)	1	S. Louw
	Scarabaeidae	Dynastinae		*Heteronychus* sp.	3	
	Scarabaeidae	Melolonthinae		*Macrophylla* sp.	3	
	Scarabaeidae	Melolonthinae		*Schizonycha* sp.	3	
	Scarabaeidae	Melolonthinae		*Sparrmannia flava* Arrow	2	
	Scarabaeidae	Rutelinae	Hopliini	*Lepisia virescens* Péringuey	2	
	Scarabaeidae	Rutelinae	Hopliini	*Peritrichia bella* Moser	2	
	Scarabaeidae	Rutelinae	Hopliini	*Chasme kochi* Schein	2	
	Scarabaeidae	Scarabaeinae		*Caccobius* sp.	1	S. Louw
	Scarabaeidae	Scarabaeinae		*Metacatharsius* sp.	1	S. Louw
	Scarabaeidae	Scarabaeinae		*Onthophagus* sp.	3	
	Scarabaeidae	Scarabaeinae		*Scarabaeus proboscideus* (Guerin)	2	
	Scarabaeidae	Scarabaeinae		*Scarabaeus* sp.	3	
	Scarabaeidae	Scarabaeinae		*Gymnopleurus humanus* MacLeay	2	
	Scarabaeidae	Scarabaeinae		*Rhyssemus* sp.	3	
	Scarabaeidae	Scarabaeinae		*Gymnopleurus aenescens* Wiedemann	2	

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Coleoptera	Scarabaeidae	Scarabaeinae		*Scarabaeus flavicornis* (Boheman)	2	
	Tenebrionidae			sp.	3	
	Tenebrionidae			sp. 2	3	
	Tenebrionidae		Adesmiini	*Physosterna cribripes* Haag	1	S. Louw
	Tenebrionidae		Adesmiini	*Onymacris multistriata* Haag-Rutenberg	1	S. Louw
	Tenebrionidae		Adesmiini	*Stenocara gracilipes* Solier	1	S. Louw
	Tenebrionidae		Adesmiini	*Epiphysa flavicollis* (Fabricius)	1	S. Louw
	Tenebrionidae		Adesmini	*Renatiella scrobipennis* (Haag)	1	S. Louw
	Tenebrionidae		Caenocrypticini	*Caenocrypticus wittmeri* Endrödy-Younga	2	
	Tenebrionidae		Caenocrypticini	*Caenocrypticus phaleroides* Koch	1	S. Louw
	Tenebrionidae		Cryptochilini	*Horotoma pronamibensis* Penrith & Endrödy-Younga	1	S. Louw
	Tenebrionidae		Cryptochilini	*Pachynotelus granaticollis* Gebien	1	S. Louw
	Tenebrionidae		Cryptochilini	*Pachynotelus leucinus* Koch	1	S. Louw
	Tenebrionidae		Drosochrini	*Drosochrini* sp.	2	
	Tenebrionidae		Drosochrini	*Drosochrus* sp. 2	3	
	Tenebrionidae		Epitragini	*Derosphaerius kraatzi* Westwood	2	
	Tenebrionidae		Eurychorini	*Cimicia spinipes* Fairmaire	1	S. Louw
	Tenebrionidae		Eurychorini	*Geophanus plicicollis* Fairmaire	1	S. Louw
	Tenebrionidae		Eurychorini	*Eurychora nitida* Haag	1	S. Louw
	Tenebrionidae		Eurychorini	*Stips dohrni* (Haag)	1	S. Louw
	Tenebrionidae		Eurychorini	*Stips gebieni* (Hesse)	1	S. Louw
	Tenebrionidae		Eurychorini	*Stipsosoma* sp.	2	
	Tenebrionidae		Molurini	*Phanerotomea monacha* Koch	1	S. Louw
	Tenebrionidae		Molurini	*Somaticus incostatus* (Gebien)	1	S. Louw
	Tenebrionidae		Molurini	*Psammodes vialis* Burchell	1	S. Louw

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Coleoptera	Tenebrionidae		Molurini	*Tarsocnodes ephialtes* Koch	2	
	Tenebrionidae		Molurini	*Phanerotomea* sp.	1	S. Louw
	Tenebrionidae		Molurini	*Hypomelus* sp.	2	
	Tenebrionidae		Molurini	*Psammodes* sp.	2	
	Tenebrionidae		Opatrini	*Parastizopus armaticeps* Péringuey	1	S. Louw
	Tenebrionidae		Opatrini	*Gonopus agrestis* Fahraéus	1	S. Louw
	Tenebrionidae		Opatrini	*Stenolamus* sp.	3	
	Tenebrionidae		Opatrini	*Stizopus* sp.	2	
	Tenebrionidae		Opatrini	*Neocaedius* sp.	2	
	Tenebrionidae		Opatrini	*Caedius* sp.	2	
	Tenebrionidae		Opatrini	*Stizopus* sp.	2	
	Tenebrionidae		Opatrini	*Calaharena dutoiti* Koch	2	
	Tenebrionidae		Opatrini	*Gonopus tibialis* Fabricius	2	
	Tenebrionidae		Praeugini	*?Dysgena* sp.	2	
	Tenebrionidae		Scaurini	*Herpiscius spinolai* Solier	1	S. Louw
	Tenebrionidae		Tentyriini	*Rozonia strigicollis* Fairmaire	1	S. Louw
	Tenebrionidae		Tentyriini	*Rhammatodes striatulus* Haag-Rutenberg	1	S. Louw
	Tenebrionidae		Zophosini	*Zophosis rufipennis* Péringuey	1	S. Louw
	Tenebrionidae		Zophosini	*Zophosis amita* Penrith	1	S. Louw
	Tenebrionidae		Zophosini	*Zophosis giessi* Koch	1	S. Louw
	Tenebrionidae		Zophosini	*Zophosis gordoniae* Penrith	2	
	Tenebrionidae		Zophosini	*Zophosis deyrollei jacoti* Penrith	2	
	Tenebrionidae		Zophosini	*Zophosis* sp.	3	
	Trogidae			*Omorgus squalidus* Olivier	2	
Hemiptera	Berytidae			*Gampsocoris* sp.	3	

Order	Family	Subfamily	Tribe	Species	Identification	Expert
Hemiptera	Cydnidae			sp. 1	3	
	Cydnidae			sp. 2	3	
	Lygaeidae			*Nysius* sp.	3	
	Lygaeidae	Geocorinae		*Geocoris* sp.	3	
	Pentatomidae			*Mecidea* sp.	3	
	Pentatomidae			sp.	3	
	Reduviidae	Piratinae		sp.	3	
Homoptera	Cicadellidae			sp.	3	
Hymenoptera	Anthophoridae			*Xylocopa hottentotta* Smith	3	
Hymenoptera	Bradynobaenidae			*Micatagla schultzei* (André)	1	S. Louw
	Colletidae			sp.	3	
Neuroptera	Myrmeleontidae			*Golafrus oneili* (Péringuey)	1	M. Mansell
	Myrmeleontidae			*Palparidius capicola* Péringuey	1	M. Mansell
	Myrmeleontidae			*Palparellus dubiosus* Péringuey	1	M. Mansell
	Myrmeleontidae			*Creoleon* spec. nov.	1	M. Mansell
	Myrmeleontidae			*Furgella damarinus* Péringuey	1	M. Mansell
	Myrmeleontidae			*Centroclisis* spec. nov. 2	1	M. Mansell
	Myrmeleontidae			*Palpares immensus* McLachlan	1	M. Mansell
	Myrmeleontidae			*Myrmeleon doralice* Banks	1	M. Mansell
	Myrmeleontidae			*Syngenes* spec. nov. 3	1	M. Mansell
	Myrmeleontidae			*Golafrus oneili* Péringuey	1	M. Mansell
	Myrmeleontidae			*Cueta* spec. nov. 4	1	M. Mansell
	Myrmeleontidae			*Pamares damarus* Mansell	1	M. Mansell