The soil microarthropods of the Namib Desert: A patchy mosaic
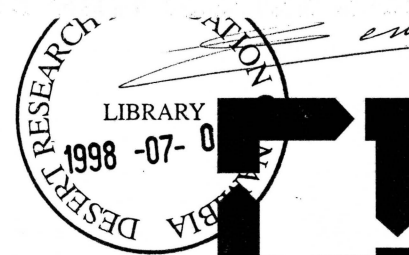
Henri M. ANDRÉ, Mundon-Izay
NOTI & Kathryn M. JACOBSON

H. M. André
U. R. Faune du sol
Musée royal de l'Afrique centrale
B-3080 Tervuren, Belgium
& Université Catholique de Louvain
Écologie & biogéographie
Place Croix du Sud, 5
B-1348 Louvain-la-Neuve, Belgium
E-mail: henri.andre@euronet.be

M.-I. Noti
Dépt d'Entomologie
Institut royal des Sciences naturelles de Belgique
29 rue Vautier
B-1000 Bruxelles, Belgium

K. M. Jacobson
Dept of Biology
Grinnell College
Grinnell IA 50112, USA
E-mail: jacobsok@ac.grin.edu

The soil microarthropods were sampled in the three major habitats of the Namib Desert, namely the gravel plain, an ephemeral river and sand dunes. In spite of severe climatic conditions and low soil organic matter content, microarthropods extracted through CCl_4 flotation were found to be surprisingly diversified and abundant. A total of 47 microarthropod species were collected, including 30 mite and one collembolan species. Actinedida were the richest mite order sampled. Micro-arthropod densities varied from zero under the annual form of *Stipagrostis ciliata* to 687 individu-als/dm^2 under *Welwitschia* and were poorly correlated with soil properties measured. Contrary to mites, collembolan density was affected by artificial watering. Microarthropod and mite richness was correlated with soil properties and together cation K^+ and Na^+ concentrations ex-plained 69% of the mite richness. Comparisons made with the soil mesofauna from other deserts (Chihuahuan, Mojave, Negev, southern Australia) highlight the abundance and richness of the Namib microarthropods.

Les microarthropodes du sol du désert du Namib: une mosaïque en patchwork — Les micro-arthropodes du sol ont été étudiés dans les trois principaux habitats du désert du Namib, à savoir la plaine à gravier, une rivière intermittente et les dunes de sable. En dépit de conditions climatiques sévères et de faibles teneurs en matières organiques du sol, les microarthropodes récoltés par flottaison au CCl_4 se sont révélés étonnamment diversifiés et abondants. Au total, 47 espèces de microarthro-podes ont été récoltées, parmi lesquelles 30 espèces d'acariens et une seule de collemboles. Les Actinedida sont les Acariens les plus riches. La densité des microarthropodes varie de zéro sous la forme annuelle de *Stipagrostis ciliata* à 687 individus/dm^2 sous *Welwitschia* et semble peu corrélée aux propriétés du sol mesurées. Contraire-ment aux acariens, la densité des collemboles est affectée par un arrosage artificiel. La richesse spécifique des microarthropodes et des acariens est corrélée avec les propriétés du sol et, ensemble, les concentrations en cations K^+ et Na^+ expliquent 69% de la richesse des acariens. Les comparaisons avec la mésofaune du sol d'autres déserts (Chihuahua, Mojave, Negev, Australie méridionale) mettent en évidence l'abondance et la richesse des microarthropodes du Namib.

Key words: mesofauna, Acari, Collembola, density, distribution, biodiversity, Namibia.

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INTRODUCTION

The peculiarity of the interstitial mesofauna living in fine sand was stressed as early as 1977 by Coineau & Massoud. Although the originality of this fauna in the Namib Desert was again outlined by Coineau & Seely (1983), it remains poorly known and most studies have been largely of a taxonomic nature. New soil mites were described from the Namib by Piffl (1965), Fain et al. (1993), Judson (1994) and André (1996). Lepismatidae were studied by Watson (1987), Watson & Irish (1988), Irish (1988, 1989, 1990), and Irish & Mendes (1988) while Thibaud & Massoud (1988) listed and described four collembolan species.

Since Coineau & Seely's (1983) publication, the single study dealing with the ecology of Namib soil micro-arthropods was published by Marsh (1987) who investigated the mesofauna found in litter collected around *Welwitschia* and in the soil beneath the plants. She gave a first list of micro-arthropods, especially mites, identified to the family level and first estimates of densities. Mite densities were found to vary from 0.004 to 0.009 individuals/m^2 between *Welwitschia* plants and from 0.2 to 15 individuals/m^2 below them.

In comparison, North American Desert microarthropods are much better known. From the 970 publications of the Jornada bibliography issued from 1900 to 1995[1], several of them are devoted to the mesofauna. The species abundance distribution patterns of mites and collembolans were studied in relation with soil decomposition as well as their contribution to nutrient cycles and their role in the foodweb (see reviews by Whitford et al. [1983] and Whitford & Parker [1989]).

[1] The list of publications is available at URL http://jornada.nmsu.edu/JRNBIB.htm.

This survey was conducted to get a first overview of the soil microarthropods by sampling special microhabitats scattered in the three major habitats of the Namib Desert, namely the gravel plain, an ephemeral river and sand dunes. Special attention was given to mites and collembolans. Sampling was designed to examine the relationships between soil properties and the abundance patterns and biodiversity of microarthropods.

MATERIAL AND METHODS

Study sites

The survey was conducted in the surroundings of the Desert Research Institute at Gobabeb (24°34'S, 15°03'E). The station is located adjacent to the ephemeral Kuiseb River, which forms a linear oasis of riparian vegetation, cutting the desert in two, the dune sea to the south and the gravel plain northward (Fig. 1).

The three habitats, the river banks and bed, the dunes and the gravel plain were visited from 8 to 19 June 1993 and different microhabitats were sampled (Table 3). Special attention was given to microhabitats unique to Namib. In the gravel plain, samples were taken under the endemic plant, *Welwitschia mirabilis* (Fig. 2), as well as among the annual and perennial form of *Stipagrostis ciliata*. Samples from *S. ciliata* were respectively taken at plot #30 and 31 (23°29'S 15°17'E, Fig. 3). In plot #30, rain fell three months before sampling but there had not been any rainfall for at least the four previous years. A rocky area close to the Mirabeb Inselberg was also explored. In the sand dunes, sampling was made under the nara, *Acanthosicyos horridus*, also endemic and one of the Namib's most characteristic plant, or near the perennial dune grass, *Stipagrostis sabulicola* (Fig. 4). Last, some samples were also taken along the Kuiseb

Fig. 1. — The ephemeral Kuiseb River forms a linear oasis of riparian vegetation, cutting the desert in two, the dune sea to the south (right) and the gravel plain northward (left).
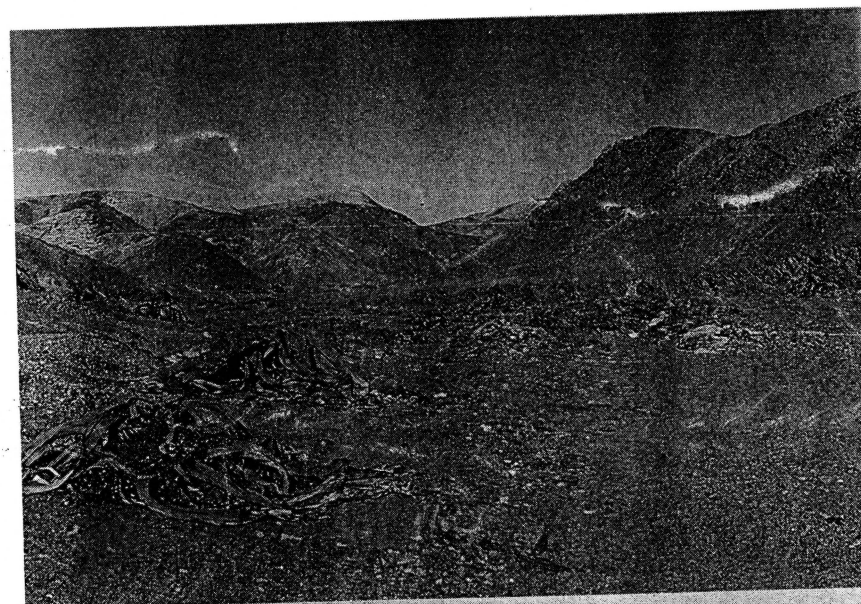

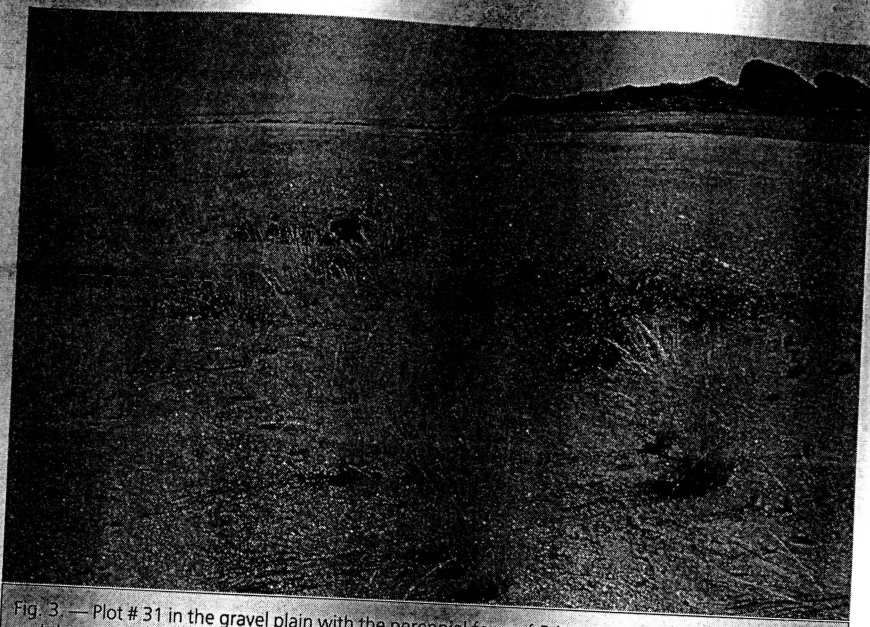Fig. 2. — *Welwitschia mirabilis* at Welwitschia Wash in the gravel plain.

Fig. 3. — Plot # 31 in the gravel plain with the perennial form of *Stipagrostis ciliata* in the foreground and the Mirabeb Inselberg in the background.

Fig. 4. — *Stipagrostis sabulicola* in the foreground and, further, naras in the Nara Valley.

River, one of the 12 highly characteristic ephemeral rivers which transect the Namib Desert in Namibia (Jacobson *et al.*, 1995).

Sampling and sample extraction

In the sand, 55 cm³ samples were taken with a glass cylinder at different depths. Elsewhere, the soil was dug and the core device of 35 mm diameter briefly described by André *et al.* (1994) was again used to yield 48 cm³ samples at different depths. Mostly, paired samples were taken, one for fauna extraction and another for soil analyses.

In different places, a 1-m² sampling parcel was isolated from adjacent area with metallic plates driven in the soil down to 20-30 cm. These plates were intended to prevent movement of organisms into the parcel from the adjacent soil. Samples were taken within the parcel before and 48 h after wetting the soil (10 l water/m², i.e. the minimal amount of rain required in the Namib Desert for germination of plant seeds [Jacobson, 1996a] and macrofungi [Jacobson, 1996b]) (Table 3).

Samples were kept in sealed plastic bags and processed within 48 h by the carbon tetrachloride flotation method (André & Noti, 1993). Individuals collected from the tetrachloride were transferred into alcohol for storage and later identification. All mites and collembolans were mounted for identification. The material is deposited in the *Musée royal de l'Afrique centrale*.

Soil analyses

Soil moisture content and pH were measured directly after sampling at the Gobabeb station. Soil moisture was determined gravimetrically by drying a pre-weighed soil sample in an oven at 70°C for a minimum of two days.

Other analyses (52 samples) were carried out at the *Laboratoire de pédologie* of the *Université Catholique de Louvain* at Louvain-la-Neuve and included granulometry by sedimentation method as well as parameters listed in table 1. Total nitrogen was extracted following Kjedahl's method while carbon extraction was carried out using Walkey & Black's method (Duchaufour, 1965). Na$^+$, K$^+$ and Mg$^+$ cation concentrations were extracted using lactate acetate while CaCO$_3$ was dosed following Marcour's method.

RESULTS

Soil analyses

As expected, there is a clear-cut difference between granulometry of the gravel plain soil and that of sand dune (Fig. 5A). In the former, ultrafine sand particles (50-100 μm) are a major component (14 to 30 %) together with 100-200 μm particles (27-42 %) while in the latter, 100-200 μm particles largely dominate (75 to 79 %). The Kuiseb River soil presents various profiles (Fig. 5B), reflecting the variable soil horizons laid down by seasonal floods (Abrams *et al,*. 1997; Jacobson *et al.*, 1995). In the river bed, the profile varies with depth and silt (55%) and clay (24 %) dominate at the soil surface. In contrast at -30 cm, the profile is that of dune sand. On the north bank under the *Ficus*, however, the profile correspond to that of the gravel plain soil.

Mean values of measured soil parameters are listed in table 1. All untreated samples contained less than 1% water except those from the Kuiseb River (Fig. 6). Due to watering treatment, the soil moisture rose as high as 3% depending on the substrate and depth (Fig. 6). Under *Welwitschia* however, watering had little effect (mean moisture before watering: 0.70 % ± 0.18 vs. 0.84 % ± 0.23
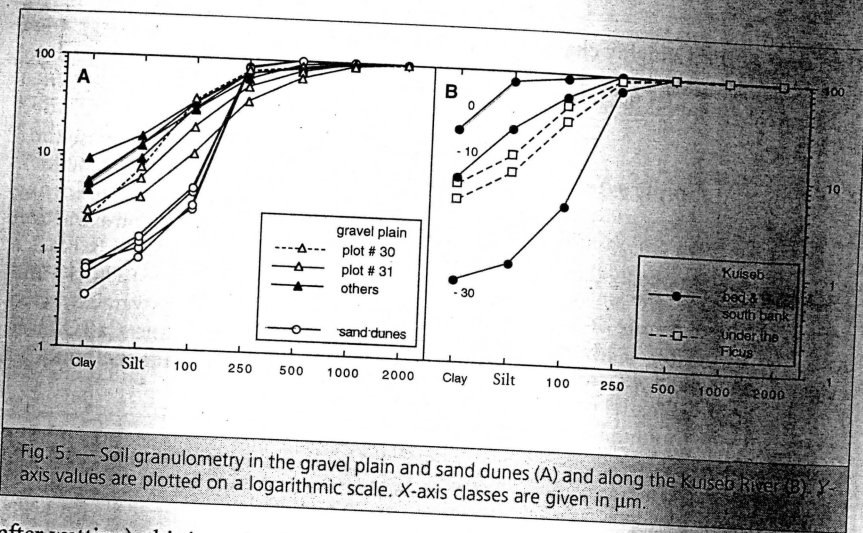
Fig. 5. — Soil granulometry in the gravel plain and sand dunes (A) and along the Kuiseb River (B). Y-axis values are plotted on a logarithmic scale. X-axis classes are given in µm.

Fig. 6. — Soil moisture and C/N ratio distribution among the microhabitats sampled.

after wetting), this is probably related to the "mild" microclimate recorded under this plant (Marsh, 1990). The importance of the vegetation on the distribution of nutrients is also outlined in Fig. 3. The C/N ratio is much higher in vegetated areas, namely the Kuiseb River sites and gravel plain sites noted for their vegetation in the study sites section.

Only the pH exhibited significant differences between the three zones (Table 1). The Kuiseb River is distinctive in having high concentrations in organic matter, organic carbon, total nitrogen and a high C/N ratio. High concentrations of carbonates and calcium carbonates are characteristic of the gravel plain where the soil surface consists largely of gypsum.

We found no significant differences in cation concentrations between the three zones, except for Mg^+ which is less abundant in the sand dunes than in the Kuiseb area.

List of species

A total of 391 microarthropods were collected, including 183 mites and 171 collembolans, and 47 microarthropod species were recognized (Table 2), including 30 mites and one Collembola species. Mites comprised 4 gamasid species, 2 Acaridida, 7 Oribatida, and 17 Actinedida (Endeostigmata and Tarsonemida included).

Oribatida comprised many primitive genera. Most of them were collected from the Welwitschia litter. However, the euoribatid nymphs were found under the nara in the sand dunes and an adult Oribatulidae, unfortunately lost during the sample processing, was noticed in a sample from the Ficus litter near the Kuiseb River.

Actinedida were the richest mite order sampled and also contained the richest

family, the Tydeidae. This family was represented by six species consisting of at least a new genus and two new species.

The most abundant mites were Dolychocybidae found in the litter under Welwitschia with a density of about 270 to 400 individual/dm². The most frequent was the endeostigmatid Speleorchestes collected from the Euphorbia litter on rocks, in the gravel between and under Stipagrostis ciliata (perennial form) and under Welwitschia, and also in the sand under a Stipagrostis species in the Kuiseb River floodplain (Nara trail).

All four gamasid species were found in three samples taken in the Kuiseb River floodplain. Remarkably, these samples, not artificially wetted, were among the moistest (moisture content: 2.34 ± 0.41%).

Only one collembolan species, Folsomides cf angularis was found. The true identity of this species, already cited from the Namib Desert by Thibaud & Massoud (1988), remains enigmatic as it is highly variable. Either the species is

Table. 1. — Mean values ± SD of soil parameters estimated in the three major habitats of the Namib Desert and relationships between microarthropod species richness and soil parameters considered singly and estimated through the coefficient of determination, r².

	Gravel plain	Kuiseb River	Sand dunes	
Soil moisture (%)°	0.29 ± 0.24 a	2.82 ± 2.74 a	0.19 ± 0.04	0.001
pH	8.88 ± 0.45 ab	7.95 ± 0.19 ac	8.25 ± 0.27 b	
organic C (%)	0.35 ± 0.38 a	1.41 ± 1.30 ac	0.07 ± 0.07 c	0.265
organic matter (%)	0.60 ± 1.00 a	2.43 ± 2.24 ac	0.11 ± 0.12 c	0.265
total N (%)	0.07 ± 0.05 a	0.14 ± 0.11 ac	0.04 ± 0.01	
C/N ratio	3.46 ± 3.46 a	7.81 ± 5.51 ac	1.60 ± 1.61 c	0.733
CO_2^+ (%)	1.84 ± 0.96 ab	0.64 ± 0.48 a	0.29 ± 0.08 b	0.001
$CaCO_3$ (%)	3.07 ± 1.61 ab	1.06 ± 0.80 a	0.48 ± 0.13 b	0.001
Na^+ (meq./100 g soil)	0.65 ± 1.20	0.31 ± 0.30	0.56 ± 0.26	
K^+ (meq./100 g soil)	0.91 ± 1.64	0.82 ± 0.72	0.64 ± 0.13	
Mg^+ (meq./100 g soil)	0.75 ± 0.73	1.02 ± 0.71 c	0.27 ± 0.06 c	

Same subscripts designate values significantly different at level p < 0.001 (bold) or p < 0.01 (not bold).
* Differences not significant due to the low number of samples (some sand samples were upset during the moisture measurement).
° watered samples not included.
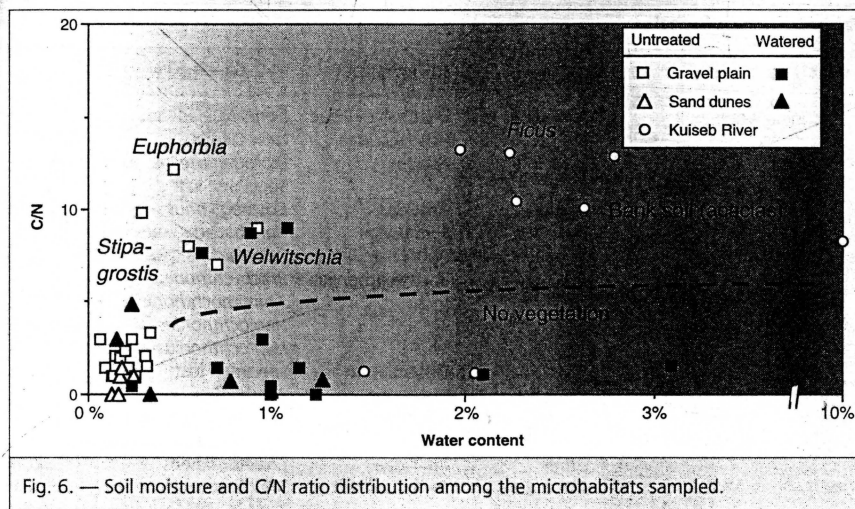Coefficient of determination r², significant at level p < 0.001 (**) or p < 0.01 (*).

Table 2. — List of species.

Class	Order	Family	Species	L
Arachnida Acari	Gamasida	Digamasasellidae	Dendrolaelaps sp.	
		Rhodacaridae	New Genus ?	743
		Ascidae	Protogamasellus sp.	288
			Specimen lost	
	Acaridida	Acaridae	Cosmoglyphus n. sp.	
		Suidasiidae	Namibacarus sabulosus	
	Oribatida	Aphelacaridae	Aphelacarus sp.	
		Brachychthoniidae	Brachychthonius sp.	
			Amnemochthonius sp.	190
			Haplochthonius sp. 1	243
			Haplochthonius sp. 2	260
		Oribatulidae	specimen lost	
		Euoribatida	wrinkled nymph	
	Endeostigmata	Nanorchestidae	Speleorchestes sp.	330
		Terpnacaridae	Alycosmesis sp.	130
	Other	Bdellidae	undetermined	320
	Actinedida	Tydeidae	Triophtydeinae (n. gen.)	180
			Tydeus sp.	370
			Orthotydeus sp.	
			Metalorryia sp.	223
			Tydaeolus n. sp.	135
			Metatydaeolus n. sp	190
		Caeculidae	Allocaeculus sp.	
		Stigmaeidae	Stigmaeus sp.	450
		Barbutiidae	Namibarbutia seelyae	396
		Cheyletidae	undetermined	253
		Linotetranidae	Linotetranus mirabebensis	390
		Tenuipalpidae	undetermined	265
		Tarsonemidae	undetermined	155
		Dolichocybidae	undetermined	245
	Araneae		Immature	
	Pseudoscorpionida	Cheiridiidae		
Insecta	Protura			
	Thysanura	Lepismatidae	Nebkhalepisma australis	
	Collembola	Isotomidae	Folsomides cf angularis	425
	Dyctioptera	Blattaria		
	Psocoptera		Hyperetes sp.	
			Liposcelis sp.	
	Thysanoptera		larva	
			apterous specimen	
	Homoptera	Cicadellidae	Exitianus sp.	
			?Neolimnus sp.	
	Heteroptera		Larva	
	Coleoptera	Tenebrionidae	Larva	
		Scarabeoidea	Larva	
	Diptera		Larva	
			Larva	

L : Mean length of adults in µm.

The Pseudoscorpion is
Apocheiridium cf. chamberlini
Godfrey, 1927 (det. V. Mahnert)

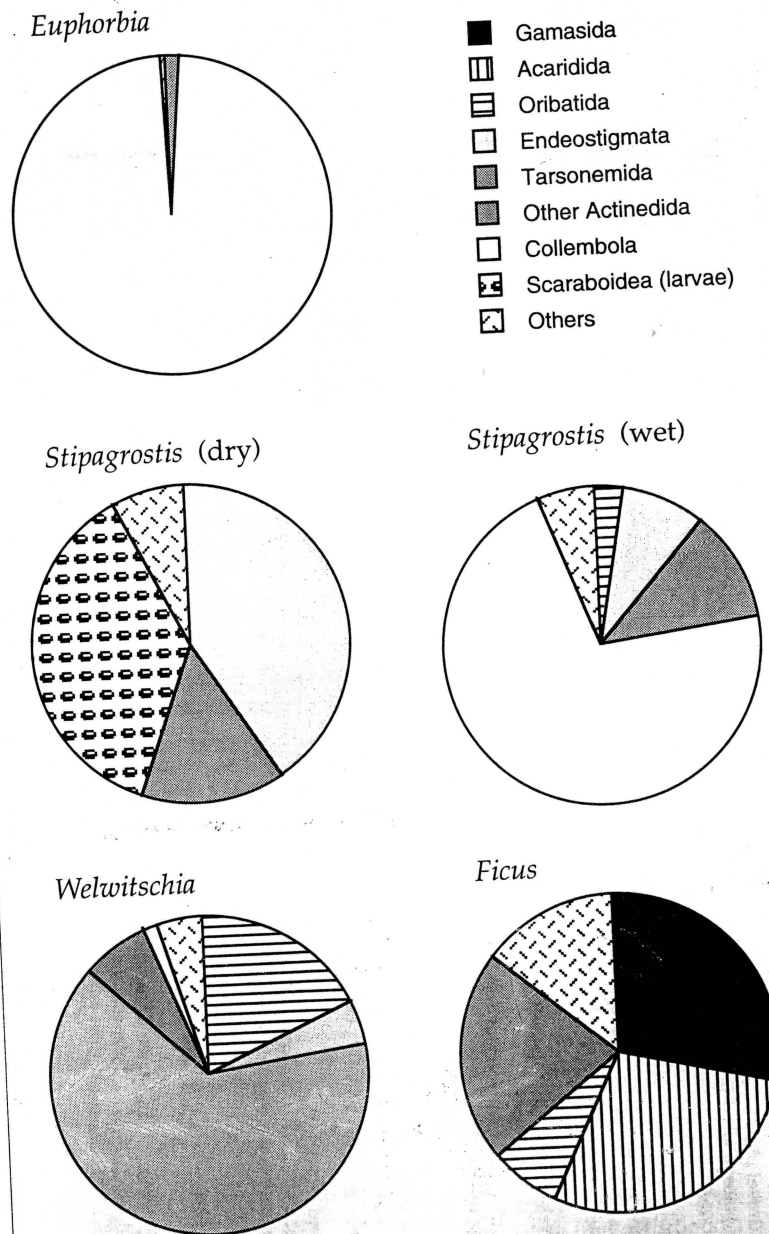Fig. 7. — Major group abundance in some microhabitats.

Legend: Gamasida, Acaridida, Oribatida, Endeostigmata, Tarsonemida, Other Actinedida, Collembola, Scaraboidea (larvae), Others

Pie charts: Euphorbia, Stipagrostis (dry), Stipagrostis (wet), Welwitschia, Ficus

Table 3. — List of microhabitats sampled together with the richness (s) and density (d) of microarthropods, mites and collembolans they shelter.

Code	Location	Microhabitat	Watering	Depth (in cm)	microarthropods d	microarthropods s	mites d	mites s	collembolans d	collembolans s
Gravel plain										
CA	Mirabeb (right)	*Euphorbia* litter on rocks	—	0 (3x)	354	3	5	1	347	1
SA+	Plot # 30	under *Stipagrostis ciliata* (annual form)	W	0, 5, 10	0	0	0	0	0	0
SA-	Plot # 30	between *St. ciliata* (annual f.)	W	0, 5, 10	0	0	0	0	0	0
SP+	Plot # 31 (Mirabeb)	under *St. ciliata* (perennial f.)	—	0, 5 (3x), 10, 10, 20	150	7	24	4	0	0
			W	0, 5, 5, 5, 10, 10	61	8	15	5	38	1
SP-	Plot # 31 (Mirabeb)	between *St. ciliata* (perennial f.)	—	0, 5, 15	90	1	90	1	0	0
			W	0, 5, 15	74	2	12	1	62	1
WM-	Welwitschia Wash	between *Weltwischia mirabilis* ♂	—	5, 15, 25	7	1	7	1	0	0
WF-	Welwitschia Wash	close to the root of a *W. mirabilis* ♀	—	20, 30	0	0	0	0	0	0
WM+	Welwitschia Wash	litter under a *W. mirabilis* ♂	—	0, 10, 25	347	7	337	6	0	0
			W	0, 5, 10	687	13	651	10	17	1
Kuiseb River										
KB	Gobabeb	bank soil	—	0, 5, 10	14	2	7	1	0	0
KF	Gobabeb	litter under the *Ficus*	—	0, 5, 10	106	10	92	8	0	0
Sand dunes										
	Gobabeb	under naras	—	15, 15, 25	0	0	0	0	0	0
	Gobabeb (nara trail)	litter under Acacias	—	0 (3x)	10	9	7	3	0	0
	Gobabeb (nara trail)	under *Stipagrostis* (tuft)	W	0, 5, 10	2	1	2	1	0	0
		under naras	W	0, 5, 10	45	5	36	3	0	0
			W	0, 5, 10	11	2	35	1	0	0
		under *Stipagrostis sabulicola*	—	5, 10 (5x), 15	5	1	5	1	0	0
		under *Trianthema hereroensis*	—	10 (3x)	0	0	0	0	0	0
		detritus under naras	—	0, 10, 20	18	3	14	2	0	0

Shaded lines and "W" in the column "watering" indicates watered samples. Depths are given for each sample in a microhabitat. There may be several samples taken at the same depth. Densities are expressed in number of individuals/dm².

Table 4. — Total and partial R^2 of linear multiple regression analysis of animal density and richness on soil properties listed in table 1.

		Total R^2	R^2 of soil property combinations	
Arthropod	density	0.381		
	richness	0.676	$(K^+ \sim C/N)$: 0.640	$(K^+ \sim C/N \sim Na)$: 0.655
Acari	density	0.617	$(K^+ \sim Na^+)$: 0.545	$(K^+ \sim Na^+ \sim C/N)$: 0.587
	richness	0.728	$(K^+ \sim Na^+)$: 0.691	

remarkably adaptable since it has been recorded from Belgium, France, Morocco, Kenya, and Namibia, or it constitutes a complex of cryptic species.

Among the other microarthropods, all species were not necessarily soil-dwellers. This is the case of the Chaeri-diidae, a false scorpion family known to be corticolous, and the cicadellid genus, *Neolimnus*, a common grass feeder.

Microarthropod density and distribution

Densities of microarthropods estimated in different microhabitats varied from zero under the annual form of *Stipagrostis ciliata* to 687 individuals/dm² under *Welwitschia* after watering (Table 3). Mite density reached up to 651 individuals/dm² in the same microhabitat while collembolans were the most abundant in the *Euphorbia* litter (347 individuals/dm²) (Table 3). Densities are particularly low in the sand dunes unless some detritus or a thin layer of litter are present.

Mite and collembolan abundance varied greatly depending on the micro-habitat. Collembola represented 98% of microarthropods in the *Euphorbia* litter and were also dominant under the perennial form of *Stipagrostis ciliata* after wetting (Fig. 7). Mites, especially Endeostigmata, were dominant in the same habitat without water treatment and under *Welwitschia* where many Oribatida were collected. Oribatida were also present under the *Ficus* along the Kuiseb together with gamasid and acarid mites.

Effect of watering

It is difficult to assess the effect of watering on mites as no spectacular changes in density appeared after wetting the soil (Table 3). In contrast, watering did seem to affect collembolan densities. Except at the *Euphorbia* sites, these insects were only observed on the gravel plain after wetting the soil (Table 3).

Microarthropod diversity

The richest microhabitats were soils covered with litter, especially that of *Welwitschia* (19 microarthropod species, all samples combined, among which 15 mites) and *Ficus* (10 microarthropod species, 8 mites, see table 3). In contrast, the thin litter of *Euphorbia* on rocks was nearly monospecific as the fauna was dominated by *Folsomides* cf. *angularis* (98 % of arthropods).

Another microhabitat of interest is provided by the gravel colonized by the perennial form of *Stipagrostis ciliata* which sheltered, all samples combined, 12 arthropod species among which were 8 mite species.

Stepwise multiple regressions were applied to the arthropod richness and density to test which soil parameters affect them (Table 4). The soil properties explained less than 40% of the variations
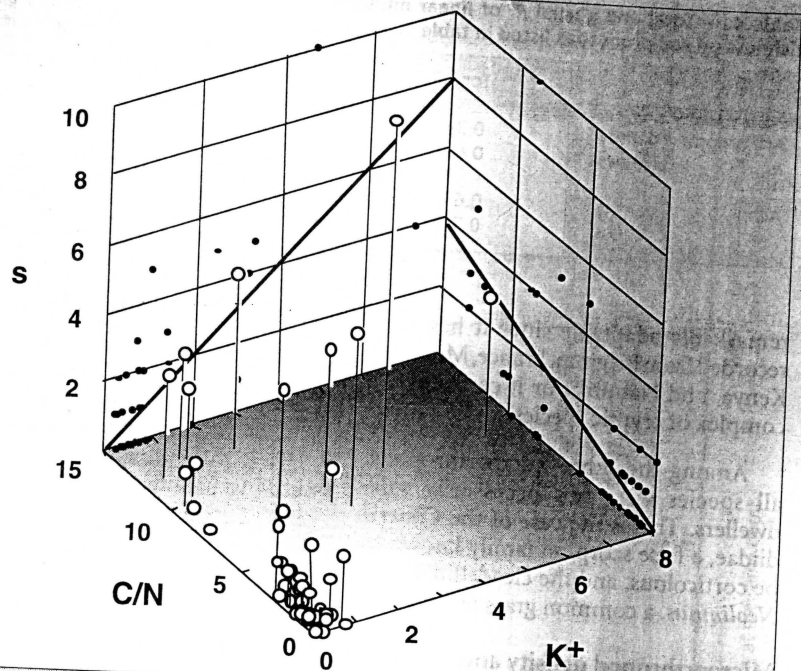
Fig. 8. — Variation of the microarthropod richness in relation to the C/N ratio and potassium concentration (meq/100 g soil).

in density. Three factors were most critical for explaining arthropod richness, the C/N ratio and K^+ and Na^+ concentrations. Together they accounted for two thirds of the variance in richness ($R^2 = 0.655$, $n = 52$, $p < 0.001$), the first two accounting for 64% (Fig. 8). The coefficients of determination estimated for each variable considered singly are given in Table 3. Some of them, CO_3, $CaCO_3$ and the soil moisture, are not correlated at all with species richness.

Mite density and richness were most effectively explained by soil properties (Table 4). Together, K^+ and Na^+ concentrations, explain 69% of the mite richness.

DISCUSSION

It is important to outline the severity of climatic conditions in the Namib Desert. Rainfall is spatially erratic and highly unpredictable from year to year. The mean annual rainfall over most of the Namib is considerably less than 100 mm/yr (Lancaster et al., 1984) and at Gobabeb is 19 mm (Jacobson & Jacobson, in press). The aridity of this region is reflected in our sampling of soil moisture content (Table 1). It is 10-15 times lower than that of coastal dune sand near Montpellier (André et al., 1994) and slightly lower than that of the Negev during the dry season (Steinberger, 1990). However, soil moisture may be locally influenced by the presence of plants such as Welwitschia which contribute to maintain a special microclimate beneath them (Marsh, 1990). Riparian soils remain moist for long periods after flooding and the high soil moisture content of the Kuiseb River sites reflects the flooding regime in 1993 (Jacobson, 1996b).

The soil organic matter content (Table 1) is also especially low, much lower than that observed in the Negev by Steinberger (1984) under perennial shrubs ($\approx$ 5%) and lower or comparable to those recorded in North American deserts by Crawford (1988) (from 0.69 to 2.61% depending on the vegetation).

The mesofauna

This study provides a first survey of the microarthropod fauna in the three major habitats of the Namib Desert. Its composition is similar to that observed in North American Deserts or in the Negev. Clearly, the nanorchestid Speleorchestes and a tarsonemid species are major components as in the northern Chichuahuan desert while Tydeidae and Bdellidae are also important taxa (Steinberger & Whitford, 1984, 1985; Cepeda-Pizarro & Whitford, 1989; Steinberger, 1990). The genus Speleorchestes was the only one collected at all stations in a study carried out at White Sands National Monument (Santos & Whitford, 1983), it was recovered in appreciable numbers in nearly all stations visited by Wallwork et al. (1985) in the Chihuahuan Desert and occurred in the southern and northern part of the Mojave (Wallwork, 1972; Franco et al., 1979), in the Negev (Steinberger, 1990) and in semi-arid eastern Australia (Noble et al., 1996). As in North American Deserts and in semi-arid eastern Australia, several tydeid species seem to coexist (Cepeda-Pizarro & Whitford, 1989; Noble et al., 1996) and Actinedida appear to have established themselves in the predatory niches restraining Gamasida to moistest microhabitats. Oribatida comprise many primitive genera recognized for their ability to colonize dry habitats and the same or closely related genera have been identified in North American Deserts, in the Negev and in semi-arid eastern Australia (Wallwork, 1972; Wallwork et al., 1985; Steinberger & Whitford, 1984, 1985; Cepeda-Pizarro & Whitford, 1989; Steinberger & Wallwork, 1985; Steinberger, 1990; Noble et al., 1996).

The Namib fauna sampled is however original and many species are probably new. Two actinedid mites, a Linotetranidae, a rare family also recorded from North American Deserts and from the Negev, and a Barbutiidae, another rare family, have been described from the material collected (André, 1996). Among tydeid mites, one genus and two other species are undescribed and the Cosmoglyphus hypopods also represent an new species.

Arthropod species may be specific to one of the three major habitats, sand dune, river bank and gravel plain as reviewed by Seely & Griffin (1986). Among the soil fauna, Caeculidae are usually restricted to rocky habitats and are to be found in the gravel plain. In contrast, Nematalycidae are adapted to living in dune sand (Coineau et al., 1978). Surprisingly, we have not collected any nematalycid specimens and this raises the question of their density or their specificity to a peculiar microhabitat[2]. According to Coineau & Seely (1983), these mites are abundant under different plants such as Stipagrostis sabulicola, Trianthema hereroensis or Astenatherum. Unfortunately, the collecting method they used does not allow the estimation of density. Lastly, other species such as the endeostigmatid Speleorchestes or the collembolan Folsomides cf. angularis seem to be present everywhere in the Namib Desert.

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[2] This might be related to our difficulties in sampling at specific depths due to the sand fluidity, sampling with Gut's (1987) auger might offer an alternative.

Table 5. — Comparison of microarthropod densities (number of individuals/m²) in different deserts or sandy habitats.

Habitat & location	Microhabitat	Density*	Soil moisture (%)	Mean annual rainfall (mm)	Organic matter (%)	Source ***
Namib Desert	under *Stipagrostis ciliata* (perennial grass)	8 700[F]	0.15 ± 0.07	< 50**	0.16 ± 0.24	(1)
Montpellier seashore	no vegetation	175 000[F]	3.78 ± 0.42	760	0.16 ± 0.05	(2)
Negev Desert	under *Hommada scoparia* (perennial shrub)	200 - 400[B] **26 500[B]**	≈ 0.1 - 0.2 **≈ 6 - 14**	89	5.84 ± 2.24	(3)
Mojave Desert	litter beneath *Juniperus* bush	1 630[B]	?	104	?	(4)
Chihuahuan Desert	under mesquite plants, *Prosopis glandula*	≤ 10 000[B] **40-90 000[B]**	≈ 1 - 2 **≈ 5**	211	2.8 - 7.4	(5)
Chihuahuan Desert	under a tabosa grass swale *Hilaria mutica*	1 260[B] **48 400[B]**	≈ 3 **≈ 5 - 13**	225	8.21 ± 0.42	(6)

*   The superscript after densities designates the extraction method, [F]: CCl₄ flotation method, [B] : Berlese-Tullgren funnel. Bold figures refer to values observed after rainfalls.

**   from Jacobson *et al.* (1995).

***   References : (1) This study; (2) André *et al.* (1994); (3) Steinberger (1990); (4) Wallwork (1972); (5) Steinberger & Whitford (1984); (6) Steinberger & Whitford (1985).

Many species are tiny and six of them, less than 200 μm long, belong to the microfauna. The size of animals is of importance in the debate on biodiversity and we refer the reader to a previous discussion (André *et al.* 1994).

Microarthropod density and distribution

Microarthropod densities seem to attest the high efficiency of the sampling procedure, especially if they are compared to estimates already published. The microarthropod densities at Welwitschia Wash varied, according to Marsh (1987), from 0.0009 individuals/m² between the *Welwitschia* to 15 individuals/m² beneath the plants. For the same site, our estimates are, respectively 700 and 35 000 individuals/m², i.e. densities several thousand times higher. Such a difference is probably explained by the CCl₄ flotation method much more efficient than the Berlese-Tullgren funnel extraction used by Marsh (1987). The low efficiency of the latter method [3] is illustrated by the experiment of Crawford & Seely (1994) who submitted grass-containing bags buried in the Namib dunes to the funnel extraction and did not collect any microarthropods after 48 hours.

Comparisons with data from other deserts are more tentative due to differences in microhabitat and microclimate (Table 5). For instance in the Negev, highest densities, 26 500 individuals/m², were recorded under a perennial shrub, *Hammada scoparia*, and after rainfalls when the soil moisture varied

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[3]   The efficiency of funnel method for extracting corticolous Actinedida proved to be at most 5% (André & Lebrun, 1979)

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between 6 and 14% (Steinberger, 1990). Over the dry season, the population densities declined markedly to a range of 200 to 400 individuals/m². These densities are 22 to 75 times lower than those recorded for instance under the perennial form of *Stipagrostis ciliata*, where the soil moisture content was only 0.15 ± 0.07% ($n = 7$) and the litter negligible. Similar comparisons may be made with North American Deserts (Table 5). In spite of the low soil moisture combined to its low organic matter content, the microarthropod density of the Namib Desert is far from being negligible and sustains the comparison with other less severe deserts. Again, this might be explained by the efficiency of the flotation method. For comparison, table 5 mentions also the density observed on a seashore in southern France where the same extraction method was used. This comparison suggests the importance of soil moisture as a limiting factor.

Fig. 7 and estimates of ß diversity suggest a high degree of spatial heterogeneity of the soil fauna. For comparison, soil mite ß' values estimated from Stanton (1979) were much lower and varied between 0.13 and 0.49, Costa Rican litter samples being more heterogeneous than their North American equivalents. The desert appears to be a mosaic of microhabitats more or less favorable and regulating the distribution of microcoenoses.

While the densities of table 3 may seem high, there are a number of reasons why they may be underestimated. Firstly, soil microarthropods exhibit diel periodicity that allow them to avoid extremes in temperature or desiccation, with the highest populations occurring near the surface in the early morning (Whitford *et al.* 1981). Whitford *et al.* (1981) attributed these fluctuations to vertical migrations. MacKay *et al.* (1987) confirmed previous observations but

suggested that these fluctuations might also be explained by the capacity of microarthropods to enter anhydrobiosis. As we sampled at different times of the day but never in the early morning, it is likely that microarthropod densities are still underestimated. Secondly, for practical reasons, sampling was limited to the upper layers of the soil and further sampling should be made deeper in the soil. Indeed below about 30 cm, temperature and humidity in the sand are relatively constant at values agreeable to life (Seely, 1983). Thirdly, comparative study of samples revealed the high heterogeneity of the soil fauna and its aggregative distribution. This again makes it difficult to get a precise estimation of densities. Finally, the survey was undertaken in areas deprived of water for several years and we have no estimates of the densities reached after a rainfall.

Vertical migrations and anhydrobiosis

We found only one collembolan species, *Folsomides* cf. *angularis*, and only in the gravel plain. The species was already cited from the Namib by Thibaud & Massoud (1988) and was collected from fine sand by Y. Coineau as well as three other species. The highest density of *F.* cf. *angularis* (347 individuals/dm²) was observed in the litter of an *Euphorbia* gathered in a rocky area of Mirabeb. It must be emphasized that this area had not been watered and the soil moisture content was rather low (0.45%). Elsewhere in the gravel plain, collembolans were less abundant and collected only after watering. The immediate numerical response to artificial rainfall by the collembolans was already observed by Steinberger *et al.* (1984) in North American deserts. *Folsomides angularis* is known to enter anhydrobiosis (Poinsot-Balaguer & Barra, 1982). Anhydrobiontic collembolans are thus present in dry soils and anhydrobiosis is quickly reversed

when the soils are wetted. As these anhydrobiontic individuals were never sampled during our study and lateral immigration was prevented in the wetted areas, collembolans probably migrate from the lower layers of the soil once anhydrobiosis is reversed. Both the "migration" and "cryptobiosis" hypotheses advanced and discussed by MacKay *et al.* (1984) seem to apply to collembolans.

In contrast, watering did not have an effect on mite populations as already observed by Steinberger *et al.* (1984), none of the mite species collected has been proved to be anhydrobiontic and no anhydrobiontic specimen was collected during this study even though the flotation method allows pupating or freshly dead animals to be collected (André & Noti, 1993). This observation would be in favor of the diurnal migration of mites, especially actinedid mites, an hypothesis also supported by Steinberger & Wallwork (1985) from their data from the Negev. However, Whitford (1989) offered indirect evidence that some species of fungiphagous mites would remain inactive in dry soils in a state of "cryptobiosis".

Soil properties, density and biodiversity

Contrary to our results, a correlation between soil moisture and microarthropod density was found by Steinberger & Whitford (1984, 1985). However, their conclusions are not directly applicable to our survey. Indeed, Steinberger & Whitford's conclusions are based on a study conducted over several months and take into account the impact of rainfalls. In this study, the fauna was observed in the absence of any rainfall and in extreme conditions of drought. Apparently, microarthropods are adapted to such conditions and soil moisture is no longer

In the absence of rainfalls, soil moisture is probably a rough parameter, little likely to explain the arthropod densities in deserts. Measures of pF at a very fine scale might provide an alternative and give an estimate of the water locally available to the fauna. Vannier (1967, 1970, 1971) demonstrated that the limit of water availability for certain isotomid Collembola was found at pF 4.2 while in some oribatid mites it was found at around pF 5.

An adequate energy and nutrient supply in the form of plant litter is more important than water as a factor affecting numerical responses of soil fauna (Steinberger *et al.*, 1984). Tydeid, nanorchestid, stigmaeid and tarsonemid population densities are significantly correlated with the amount of organic matter in the Chihuahuan Desert (Steinberger & Whitford, 1984). In semi-arid Eastern Australia, mite density is correlated with organic carbon (Noble *et al.*, 1996). In this study, mite population densities are significantly correlated with cations K^+ and Na^+ as well as with the C/N ratio. The biological meaning of the correlation between mite density and cations K^+ and Na^+ remains unclear even in the light of previous experimental works (Anderson *et al.* 1985) and field observations (Usher, 1976; Booth & Usher, 1984) dealing with these cations. According to Usher (1976), the potassium content might be a reflexion of the active roots or mycorrhiza in the soil and interpreted in relation to the rhizosphere. In this context, Blackith's (1974) conjecture that, in nutrient poor environments, there will be a close correspondence between plants and arthropods cannot be rejected as previously suggested by Booth & Usher (1984) after studying the soil fauna of a cold desert (Antarctica).

Better than density, the species richness is explained in terms of soil

properties. Both arthropod and mite richness are highly correlated with cations K^+ and Na^+ as well as with the C/N ratio. This accords with Santos & Whitford's (1983) finding that the greatest microarthropod diversity was under shrubs at the base of dunes and the lowest in unvegetated areas in the center of dunes.

CONCLUSIONS

In spite of severe climatic condition and low soil organic matter content, the Namib Desert soil microarthropods were found to be surprisingly diversified and abundant. So far, previous works considered, they comprise 4 gamasid species, 7 Oribatida, 2 Acaridida, 28 Actinedida and 4 Collembola. These figures are already higher than the 18 mite and 3 collembolan species recognized by Wallwork (1972) after a study which extended over a period of 9 months in the Mojave Desert. They are also higher than figures published by Steinberger (1990) with 21 mite species from the Negev and by Wood (1971) who distinguished 23 mite and 6 collembolans species from desert soils in southern Australia but definitely lower than those recorded in the Chihuahuan Desert with a large variety of litter types. No doubt, many more species are still awaiting to be discovered through future investigations.

Nevertheless, this survey offers only a limited view of the Namib Desert fauna as it results from a 2-week sampling campaign following a long dry period. In particular, the question of faunal activity after rainfall has not been examined and warrants attention given the importance of rain-induced decomposition in the Namib Desert (Jacobson & Jacobson, in press). From this perspective, the desert soil microarthropod community, composed essentially of opportunistic species, might best be viewed as a patchy

end on the volume and duration of the most recent rains, the presence of plants and organic matter, and some soil properties.

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