

# Survey of mites in caves and deep soil and evolution of mites in these habitats

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**Abstract:** We studied adaptations to subterranean environments in Acari. Mite populations of two caves and of the mineral horizon of soil from three forest sites were analysed. In the soil, body length was limited by the pore size. The proportions of (i) predators, (ii) phoretic mites, and (iii) primitive oribatids were higher in caves. This was potentially explained by (i) polyphagy or predation on other groups and reduced interspecific competition, (ii) the fragmented structure and liability to flooding of the cave habitat, and (iii) the higher humidity in caves. Adaptations to dry habitats probably greatly influenced the evolution in Oribatida. It is proposed that numerous mites colonized caves directly from deep soil without a surface stage.

**Résumé :** Nous avons étudié les adaptations des acariens aux habitats souterrains en analysant les populations d'acariens de l'horizon minéral de trois sols forestiers et de deux cavernes. Dans le sol, la taille du corps est limitée par la taille des pores. Les proportions (i) de prédateurs, (ii) phorétiques et (iii) d'oribates primitifs sont plus grandes dans les cavernes. Cela peut s'expliquer par (i) la polyphagie ou la prédation sur d'autres groupes et la compétition interspécifique réduite, (ii) la structure fragmentée de l'habitat et la survenance d'inondations dans les grottes et (iii) la plus grande humidité des cavernes. Les adaptations à un habitat sec semblent avoir grandement influencé l'évolution des oribates. Nous émettons l'hypothèse selon laquelle nombre d'acariens ont colonisé les cavernes directement depuis le sol profond, sans passage par un stade de surface.

## Introduction

Colonization of soil pores represents an important step in the evolutionary history of arthropods. Actually, high relative humidity has turned soil into the obligate stepping stone from aquatic towards terrestrial life (Ghilarov 1959; Vannier 1973, 1987; Villani et al. 1999). A number of surface arthropods invaded caves (Holsinger 2000) either to escape dryness and warmth after the Quaternary Ice Age (climatic-relict model) or to actively exploit an available niche (local habitat-shift model). After colonizing soil or caves, some species evolved adaptations (e.g., extra-optic sensory traits) or lost useless structures (e.g., eyes and pigments).

Adaptation remains one of the most controversial areas of study. As mites are very abundant and diverse in most ecosystems (Walter and Proctor 1999), they represent an ideal group for studying such questions, and caves should furnish

a unique opportunity for effective analysis (Christiansen 1992).

Although caves and deep soil share a number of environmental features (darkness, narrow temperature range, relative humidity close to saturation, etc.), they nonetheless differ in at least two ways. First, caves provide a wide inhabitable space in comparison to the small pores of the soil. Second, caves are more liable to catastrophic flooding than most soils. By bringing in mites living in surface habitats, flooding contributes to the diversity and unpredictability of populations in the cave environment. These differences should have induced targeted adaptations in the organisms living in these habitats.

Troglomorphisms (i.e., adaptations to cave life; e.g., longer claws) and euedaphomorphisms (i.e., adaptations to life in deep soil; e.g., short antennae) are well known in the Collembola (e.g., Christiansen 1960, 1965, 1985; Thibaud 1967, 1970; Vannier and Thibaud 1978). In contrast, Palacios-Vargas (1996) deplored the lack of detailed studies on adaptations of mites to subterranean habitat. A small body (Zacharda 1979; Karg 1993; Striganova 1996) or, conversely, a strikingly elongated body (Nematolycidae, Coineau et al. 1978) has often been cited as characteristic of deep soil mites. Karg (1993) mentioned dechitization and shorter legs in deep soil gamasids. Zacharda (1979) proposed that both troglomorphisms (elongation and attenuation of chelicerae, pedipalps, legs, and chaetotaxy, including slender trichobothria, and integument depigmentation and dechitization) and euedaphomorphisms (integument dechitization and depigmentation, reduction or suppression of eyes, shortening of appendages and chaetotaxy, trichobotria clavate, and parallel solenidia on tarsus I) occur in the Rhagidiidae.

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Finally, the protero-hysterosomatic articulation of some deep soil oribatids could help them move in pores (Grandjean 1969; Lebrun and Wauthy 1981).

Although numerous lists of mite species collected from caves have been published (e.g., Palacios-Vargas et al. 1998; Lundqvist et al. 1999; Culver et al. 2000), abundance and species richness appear systematically underestimated because of inadequate sampling techniques. Five supposed troglobites (i.e., species that live and breed only in caves) were found in Belgium (Leruth 1939; Lebrun 1967). Endogeic (i.e., living in the mineral horizons of the soil) mites were seldom sampled, as most authors argued that soil microarthropods were confined to the topsoil (e.g., Murphy 1953; Wallwork 1970; Petersen and Luxton 1982; Larink 1997). However, many mites were collected when sampling extended deeper into the soil (see review by André et al. 2002). For instance, Moskacheva (1967) collected numerous oribatids down to a depth of 64 cm in a mixed forest. Sampling to depths of 10–50 cm in a forest soil, Lebrun and Wauthy (1981) collected seven endogeic oribatid species. Ducarme et al. (2004) registered 24 mite species occurring below a depth of 15 cm.

The present study addressed the question of adaptations of mites to caves and deep soil. We hypothesized that adaptations to caves would differ from adaptations to deep soil, given the different environmental features of these two habitats. Habitat selection and trophic level of geographically close endogeic and cave populations were investigated.

## Materials and methods

### Sampling

The study was conducted in Rochefort, South Belgium (50°10'N, 5°13'E). The climate is temperate oceanic. Mean annual rainfall is 846 mm and mean annual temperature is 8.7 °C. Five locations were sampled (see Tables 1 and 2): two caves (Han and Nou-Maulin), two calcareous forest soils situated above the caves, and one non-calcareous forest soil equidistant from both caves (Epraves).

Population data were obtained from 65 samples (48 cm<sup>3</sup>) collected in May and November 2000 at each study location. A corer (diameter 3.5 cm) was used to take samples vertically from a sediment pile in caves, thus allowing animals running on the surface to be collected, and horizontally from the side of a trench, 15–20 cm deep in the mineral horizon of forest soils. In January 2001, 16 additional samples were taken at each location after cave flooding. In total, the samples collected during this study constituted 15 distinct sets (five locations × three sampling periods).

### Mite extraction

Animals were extracted by two methods: the Berlese–Tullgren funnel method and the DBE flotation method (Ducarme et al. 1998). Fifty samples from each May and November sampling set and all the samples (16) from each January sampling set were treated with the Berlese–Tullgren funnels. Light bulbs (15 W), 10 cm above the intact samples,

**Table 1.** Characteristics of cave sampling locations.

Characteristic	Han	Nou-Maulin
Length (km)	12	1.6
Status	Touristic	Cavers only
Distance to nearest entrance (m)	350	65
Alluvium	Silty	Sandy
Flooded in winter	Yes	Yes

were lit 1 week after the beginning of the extraction process. Extraction lasted 3 weeks. The mean temperature in the extraction room was 20 °C.

The 15 samples remaining in each May and November sampling set were stored in Norvanol before extraction with the DBE flotation method (Ducarme et al. 1998). This method was used to overcome the possible inefficiency of the Berlese–Tullgren method for extracting some taxa (André et al. 2002).

### Mite identification

Mites were mounted in lactic acid or in Hoyer medium for identification purposes. Contrary to common practice, all stases (developmental stages) were identified, in most cases to the species level, with few exceptions (early stases of Parasitidae, Rhodacaridae, Veigaiidae, and Oppiidae, representing 1.6% of the total number of collected mites). Some species could not be identified accurately because only immatures were found or because relevant taxonomic data were lacking.

### Taxonomy

Species collected in this study can be related to four of seven orders constituting the Acari (Evans 1992, p. 382), namely Mesostigmata, Prostigmata, Astigmata, and Oribatida. However, mite taxonomy is undergoing drastic changes owing to the recent use of cladistic methods. Norton (1998) has demonstrated that Astigmata originates from a group of Oribatida, i.e., the Desmonomata. Yet, in this study, data on Oribatida and Astigmata were analyzed separately to facilitate the comparison between our results and those of previous studies.

Likewise, Endeostigmata, traditionally classified within Prostigmata, was considered to be paraphyletic by O'Connor (1984) and therefore split into two distinct groups: Sphaerolichida, close to Prostigmata, and Endeostigmata s. str., close to Oribatida. Sphaerolichida scarcely appeared in our study (only 6 specimens were collected) and so we decided to cluster it with Prostigmata, while Endeostigmata s. str. was treated as a separate order.

### Statistical analyses

In our samples, a total of 20 *Haplochthonius simplex* individuals were collected, scattered in samples from nearly all locations.<sup>3</sup> This species is known to occur mainly in houses or other xeric habitats. It probably contaminated the Berlese–Tullgren funnels during extraction, as previously indicated by Grandjean (1946). These contaminant data were

<sup>3</sup>A list of collected species is available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3589. For more information on obtaining material refer to [http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub\\_e.shtml](http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml).

**Table 2.** Characteristics of deep soil sampling locations.

Characteristic	Epraves (Bestin wood)	Han	Nou-Maulin
Subsoil	Schist	Limestone	Limestone
Soil type			
Belgian typology	fGbb	AbB	Gbbk
FAO typology	Umbric Leptosol	Eutric Cambisol	Rendzic Leptosol
Litter type	Moder	Moder	Mull
Litter thickness (cm)	2–5	2–5	1–10
Vegetation	<i>Quercus petraea</i> , <i>Carpinus betulus</i>	<i>Quercus petraea</i> , <i>Fagus sylvatica</i>	<i>Tilia cordata</i> , <i>Quercus robur</i> , <i>Carpinus betulus</i> , <i>Acer campestre</i> , <i>Acer pseudoplatanus</i> , <i>Fraxinus excelsior</i> , <i>Corylus avelana</i> , <i>Hedera helix</i> , <i>Rubus</i> sp.

accordingly discarded from the subsequent statistical analyses.

Indicator species of cave and deep soil habitats were defined using the IndVal index (Dufrene and Legendre 1997), which has the advantage over other methods (e.g., TWINSpan) of being independent of species relative abundance and flexible with regard to site categorization: one is not constrained in the choice of site clusters by the classification procedure used (McGeoch and Chown 1998). This index is the product of species specificity (the mean abundance of individuals in a given set of samples divided by the sum of the mean abundances over all sets) and fidelity (the proportion of samples within the set that contain the species) multiplied by 100. Each species is supposed to be an indicator of the set where its indicator value is maximal compared with that in other sets from each level of the chosen classification of samples. A random reallocation of samples among sets is used to test this with Student's *t* test, assuming a normal distribution of the permuted statistics. Indicator values of species from the first level (trivial partition where all sites belong to a single set) cannot be tested. We defined instead a minimum indicator value of 50 for a species to be considered ubiquitous. This limit was the minimum fidelity found in the indicator species of our data set.

To investigate the general association between morphology and distribution patterns, 22 morphological traits were studied (Table 3) for every indicator species of cave or deep soil habitat (to eliminate accidental species that could obscure an existing pattern) using digital photographs of Hoyer-mounted individuals and Scion Image software (Scion Corporation 2000) for measurements. A canonical discriminant analysis was carried out on morphological data and on all combined ratios, using habitat (cave or soil) as a discriminant variable. Analysis was applied to the entire data set and within each mite order.

## Results

### Collected mites

A total of 3181 mites (113 species) were collected in soils and 371 mites (72 species) were collected in caves.<sup>4</sup> Predators accounted for 17% and 27% of the collected mites in deep soil and caves, respectively, and similar proportions were found with both of the extraction methods.

**Table 3.** List of studied morphological traits and taxa in which they were measured.

Observed trait	Taxa
Body length <sup>a</sup>	All mites
Body maximal width	All mites
Leg I length	All mites
Leg II length	All mites
Leg III length	All mites
Leg IV length	All mites
Shape of trichobothria	E, O, P <sup>b</sup>
Length of trichobothria	E, O, P
Shape of solenidia ω and φ (leg I)	E, O, P
Length of solenidia ω and φ (leg I)	E, O, P
Number of solenidia on tarsus I	Rhagidiidae
Position of solenidia on tarsus I	Rhagidiidae
Length of chelicerae	All mites
Chelicerae maximal width	All mites
Length of movable digit	All mites
Width of movable digit	All mites
Width of fixed digit	All mites
Claw I length	All mites
Curve ratio of claw I	All mites
Number of claws I	All mites
Number of claws III	All mites
Number of eggs	All gravid females

<sup>a</sup>Body length was measured on elongated specimens from the rostrum tip to the rear of the hysterosoma. The curve ratio of claws was defined as the distance between the vertex and the line joining the ends of the curve divided by the distance between the base and the tip of the claw.

<sup>b</sup>E, Endeostigmata; O, Oribatida; P, Prostigmata.

Regarding oribatid mites, the family Brachychthoniidae was represented by *Liochthonius* and *Paraliochthonius* species in caves and by *Sellnickochthonius* species in deep soil. The ratio of primitive oribatids to total oribatids was higher in caves (0.65 for the number of species and 0.79 for raw abundance) than in soils (0.41 for the number of species and 0.33 for raw abundance). Primitive oribatids were defined as all oribatid species except the Brachypylina. The proportion of mites belonging to Dichosomata (oribatids with a proterohysterosomatic articulation, Grandjean 1969) was also higher in caves than in soils: 57% vs. 35% for the number of species and 75% vs. 30% for raw abundance.

<sup>4</sup>The occurrence of species in the sampling locations is available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3589. For more information on obtaining material refer to [http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub\\_e.shtml](http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml).

Prostigmata were represented by two major groups: Eupodina (45% of all prostigmatid mites) and Tarsonemina (38%). The ratio Eupodoidea : (Eupodoidea + Tydeoidea) was used to assess the primitive character of prostigmatid populations. Indeed, the superfamily Eupodoidea presents many plesiomorphic characters compared with Tydeoidea, its sister superfamily: the latter has more specialized mouthparts (palp, chelicera) and a poorer organotaxy (chaeto-, solenidio-, and poroidotaxy) than the former. The ratio was found to be similar in caves (0.75 for the number of species and 0.85 for raw abundance) and in soils (0.79 for the number of species and 0.88 for raw abundance). Such a ratio could not be applied to Tarsonemina because phylogenetic relationships are masked within this taxon (Lindquist 1986).

### Indicator species

The IndVal method revealed that 21 and 20 mite species were indicators of the deep soil and cave habitats, respectively (Table 4). Among these species, five have already been considered as endogeic and four as cave dwellers. The genus *Alicorhagia* was selected as ubiquitous.

The proportion of indicator species that were predators was higher in caves than in deep soil (40% vs. 24%, Table 4), as already noted for the entire data set. Eight indicator species from the cave community were potentially phoretic, i.e., belonging to families in which phoresy is known to occur frequently, whereas only one such species was found in soils (Table 4). If Mesostigmata, a group that includes many phoretics, is discarded, the number of phoretic indicator species in caves and soils becomes 5 and 0, respectively.

A canonical discriminant analysis of morphological traits of indicator species showed a clear distinction between habitats: cave mites can be larger than soil mites (Fig. 1). Other traits did not show any specific trend. This was further confirmed by a comparison of indicator species belonging to the same family group. Within each group, the mean body length of cave species was always greater than that of soil species (Table 5), as were the mean lengths of leg II, trichobothria, and solenidia  $\omega$  and  $\phi$  on leg I. However, if the last three measures were relativized to body length, the difference vanished. Species of the family Rhagidiidae that were indicators of the soil environment had parallel rhagidial organs (*Hammenia macrostella* and *Shibaia longisensilla*) and (or) clavate trichobothria (*H. macrostella*), whereas the indicators of the cave environment (*Poecilophysis spelaea*) exhibited oblique rhagidial organs and filiform trichobothria. Chelicerae were larger in the cave species, both in absolute terms and relative to body length (298  $\mu\text{m}$  for *P. spelaea* vs. 55 and 119  $\mu\text{m}$  for *H. macrostella* and *S. longisensilla*, respectively).

## Discussion

### Habitat

In this study, deep soil and cave mites showed similar trends in their organisation: a number of indicator species were stenocious, i.e., endogeic or troglobitic (at least 20% of mites in each habitat if only indicator species confirmed by literature are considered). This is interesting because the cave environment is fragmented, whereas the deep soil is more continuous. Mechanisms leading to such conservative

evolution of habitat occupancy are not yet understood (see Storch and Frynta 1999, pp. 591–592 for possible factors).

Some species appear to inhabit deep soil rather than litter. This is illustrated by *Medioppia obsoleta*: its abundance in deep soil (19% of collected mites) contrasts with its wide repartition but generally low abundance in forest litter (Lebrun et al. 1989; Römbke et al. 1996). Conversely, some other species prefer the litter habitat, as demonstrated by *Oppiella nova*, for instance. Finally, in some species, the optimal habitat depends on the stage, as exemplified by the oribatid *Hypochthonius rufulus*: immatures are found in deep soil, whereas adults inhabit only the litter (e.g., Wauthy 1982).

Cave populations also appear to be of a mixed nature. They include surface species, probably provided each year by flooding, and potential or known cave dwellers.

Only one species was an indicator of both habitats. The genus *Alicorhagia* is known worldwide from relatively undisturbed forest habitats (Walter 2001) but has been abundantly collected from deep soil (Ducarme et al. 2004) and caves (Palacios-Vargas 1996). Its feeding type, mainly nematophagous but polyphagous in the absence of nematodes (Walter 1988), could account for its large ecological distribution.

### Life history tactics

In accordance with Palacios-Vargas et al. (1998), we observed the coexistence of numerous predators and phoretic mite species in caves. Four predator species, four phoretic species, and four phoretic predator species were detected among the cave indicator species (Table 4). Gers (1998) proposed five potential explanations for the observed abundance of predator mite species in caves: (1) differential efficiency of extraction methods; (2) locally patchy distribution of preys; (3) preys belonging to non-sampled groups; (4) life cycle of preys being shorter than that of the predator; and (5) predators being polyphagous and opportunist, in connection with their state of hunger. In this study, the use of two different extraction methods invalidates hypothesis 1: the proportion of predators extracted by Berlese–Tullgren funnels (active method) and by DBE flotation (passive method) was identical. Hypotheses 2 and 4 probably did not prevail in our study: possible heterogeneity in distribution of preys in both space and time should have been smoothed because numerous samples were taken in different seasons. Both hypotheses 3 and 5 could explain the abundance of predators in our samples, even if it is difficult to estimate their relative importance. Polyphagy in troglobitic mites has been considered as an adaptation to lack of food (Barr 1968; Hüppop 2000).

The coexistence of numerous predators in caves is perhaps an indication that interspecific competition both between predators and between preys is low (Sih et al. 1985). This low interspecific competition could facilitate colonization and influence the appearance of cave dwellers. Furthermore, predators can actually be responsible for differences in habitat occupancy (e.g., Richman and Price 1992; Holt and Lawton 1994). The fact that a number of species in caves are stenocious could result from noncompetitive coexistence limiting the need to colonize new habitats (e.g., Wolff and Dueser 1986; Conner and Bowers 1987).

**Table 4.** Indicator species of deep soil and cave habitats according to the IndVal index; potentially phoretic and predatory species are indicated.

Species	Order <sup>a</sup>	Indicator value	Pref. hab. <sup>b</sup>	Phoretic	Predatory
<b>Deep soil</b>					
<i>Medioppia obsoleta</i> (Paoli, 1908)	O	100	DS ?		
<i>Hypochthonius rufulus</i> Koch, 1836 (immature)	O	98	DS ?		
<i>Nanorchestes</i> sp.	E	89	?		
<i>Claveupodes</i> sp.	P	89	?		
<i>Eulohmannia ribagai</i> Berlese, 1910	O	89	DS <sup>c</sup>		
<i>Micropopia minus</i> (Paoli, 1908)	O	89	DS <sup>d</sup>		
<i>Oppiella nova</i> (Oudemans, 1902)	O	87	Surface		
<i>Leptogamasus suecicus</i> (Trägårdh, 1936)	M	84	Surface	×	×
<i>Cocceupodes</i> sp.	P	82	?		
<i>Sellnickochthonius jacoti</i> (Evans, 1952)	O	78	?		
<i>Neotrichoppia confinis</i> (Paoli, 1908)	O	78	?		
<i>Nothrus silvestris</i> Nicolet, 1855	O	72	Surface		
<i>Hammenia macrostella</i> Zacharda, 1980	P	67	DS <sup>e</sup>		×
<i>Oehserchestes</i> sp.	E	67	?		
<i>Rhodacarellus apophyseus</i> Karg, 1971	M	56	DS <sup>f</sup>		×
<i>Veigaia exigua</i> (Berlese, 1917)	M	56	Surface		×
<i>Coccotydaeolus</i> sp.	P	56	?		
<i>Tydaeolus</i> sp.	P	56	?		
<i>Gehypochthonius rhadamantus</i> Jacot, 1936	O	56	DS <sup>c</sup>		
<i>Suctobelbella sarekensis</i> (Forsslund, 1941)	O	56	Surface		
<i>Shibaia longisensilla</i> (Shiba, 1969)	P	44	Surface		×
<b>Cave</b>					
<i>Rhodacarus aequalis</i> Karg, 1971	M	50	Surface		×
<i>Bakerdania</i> sp. 1	P	50	?	×	
<i>Bakerdania</i> sp. 2	P	50	?	×	
<i>Arctoseius venustulus</i> (Berlese, 1917)	M	33	Surface	×	×
<i>Pachyseius angustus</i> Hyatt, 1956	M	33	Surface	×	×
<i>Pachyseius angustiventris</i> Willman, 1935	M	33	Cave <sup>f</sup>	×	×
<i>Rhodacarus agrestis</i> Karg, 1971	M	33	Surface		×
<i>Veigaia ?paradoxa</i> Willman, 1951	M	33	Cave <sup>f</sup>		×
<i>Vulgarogamasus</i> sp.	M	33	?	×	×
<i>Riccardoellinae</i> sp.	P	33	Cave <sup>g</sup>		
<i>Benoinyssus ?ereynetoides</i> (Strandtmann and Prasse, 1977)	P	33	DS <sup>h</sup>		
<i>Pygmephorus</i> sp.	P	33	?	×	
<i>Tarsonemus</i> sp.	P	33	?	×	
<i>Poecilophysis (Procerocheles) spelaea</i> (Wankel, 1861)	P	33	Cave <sup>e</sup>		×
<i>Liochthonius leptaleus</i> Moritz, 1976	O	33	?		
<i>Liochthonius propinquus</i> Niedbala, 1972	O	33	?		
<i>Liochthonius strenzkei</i> Forsslund, 1963	O	33	?		
<i>Nanhermannia</i> sp. (immature)	O	33	Surface		
<i>Lauropopia neerlandica</i> (Oudemans, 1900) (immature)	O	33	Surface		
<i>Phthiracarus</i> sp.	O	33	?		
<b>Both habitats</b>					
<i>Alicorhagia</i> sp.	E	80	Ubiquitous <sup>i</sup>		

<sup>a</sup>M, Mesostigmata; P, Prostigmata; E, Endeostigmata; O, Oribatida.

<sup>b</sup>Pref. hab., preferential habitat according to the literature (DS, deep soil).

<sup>c</sup>Lebrun and Wauthy 1981.

<sup>d</sup>Ducarme et al. 2004.

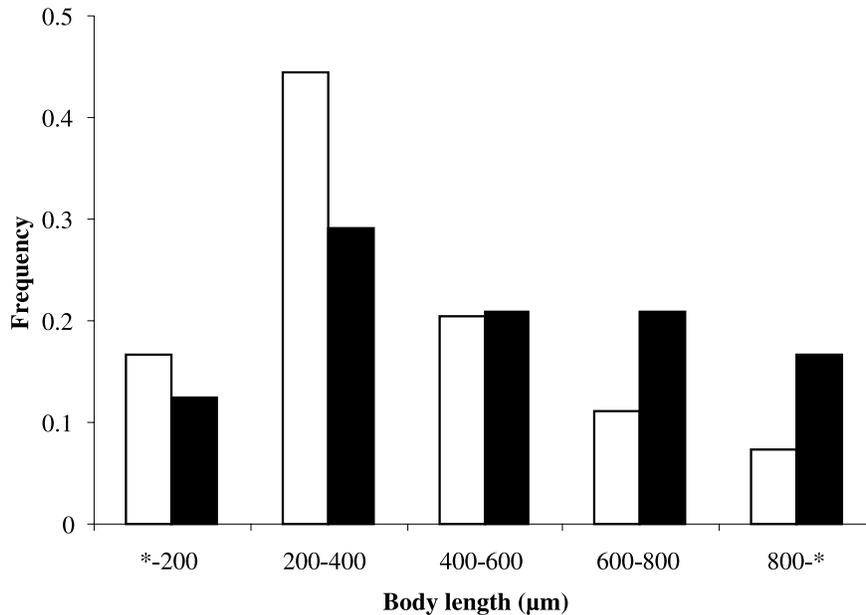
<sup>e</sup>Zacharda 1980.

<sup>f</sup>Karg 1993.

<sup>g</sup>Unpublished data.

<sup>h</sup>Strandtmann and Prasse 1976.

<sup>i</sup>Walter 2001.

**Fig. 1.** Frequency distribution of body length ( $\mu\text{m}$ ) of indicator species of caves (black bars) and deep soil (white bars).**Table 5.** Average body length ( $\mu\text{m}$ ) of indicator species of deep soil and cave habitats.

Deep soil		Cave	
Species	Body length	Species	Body length
<b>Rhodacaridae</b>			
<i>Rhodacarellus apophyseus</i>	366	<i>Rhodacarus aequalis</i>	588
		<i>Rhodacarus agrestis</i>	645
Mean	<b>366</b>	Mean	<b>617</b>
<b>Parasitidae</b>			
<i>Leptogamasus suecicus</i>	<b>610</b>	<i>Vulgarogamasus</i> sp.	<b>1053</b>
<b>Veigaiidae</b>			
<i>Veigaia exigua</i>	<b>491</b>	<i>Veigaia ?paradoxa</i>	<b>1065</b>
<b>Eupodidae</b>			
<i>Claveupodes</i> sp.	227	<i>Benoinyssus ?ereynetoides</i>	285
<i>Cocceupodes</i> sp.	281		
Mean	<b>254</b>	Mean	<b>285</b>
<b>Rhagidiidae</b>			
<i>Shibaia longisensilla</i>	583	<i>Poecilophysis (Procerocheles) spelaea</i>	1033
<i>Hammenia macrostella</i>	309		
Mean	<b>446</b>	Mean	<b>1033</b>
<b>Tydeoidea</b>			
<i>Tydaeus</i> sp.	154	<i>Riccardoellinae</i> sp.	465
<i>Coccytydaeus</i> sp.	154		
Mean	<b>154</b>	Mean	<b>465</b>
<b>Brachychthoniidae</b>			
<i>Sellnickochthonius jacoti</i>	148	<i>Liochthonius leptaleus</i>	197
		<i>Liochthonius propinquus</i>	180
		<i>Liochthonius strenzkei</i>	220
Mean	<b>148</b>	Mean	<b>199</b>

Note: mean within each group is bold-faced.

Given the high proportion of phoretic mites among the cave indicator species, phoresy appears to be largely used for dispersal in fragmented cave environments, mainly between caves belonging to unconnected networks. Moreover, if the cave itself can be viewed as a set of habitable patches (clay surfaces) separated by inhospitable areas (Tercafs and Henry 1999), phoresy could even be useful for dispersal inside the cave. In addition, phoresy is considered an efficient strategy for overcoming perturbations such as seasonal flooding (Athias-Binche 1994). Recall that by bringing in mites living in surface habitats, flooding contributes to the diversity and unpredictability of populations in the cave environment. Therefore, environmental (flooding) and dispersal (fragmented habitat) constraints, which, with internal dynamics, determine the actual species pool (Belyea and Lancaster 1999), substantially complicate the cave ecosystem, which was once considered simple (Poulson and White 1969). Of the life-history tactic categories described by Siepel (1994), most cave mites are expected to belong to group II, which is characterized by the following features: facultative or carrier-specific phoresy, low egg production, and slow development. Phoresy is also usually seen as a preliminary stage towards parasitism (Houck and Cohen 1995; Kaliszewski et al. 1995). This evolution towards parasitism could have already happened (e.g., in bat parasites) or could be currently happening in caves, but considerable further research would be needed to confirm this.

In the scavenger and fungivore guilds, patterns of habitat segregation among Brachychthoniidae species have been reported: only *Liochthonius*-like species have been observed in other Belgian caves (unpublished data) and in Polish mines (Skubala and Klys 2002). This switch could be explained on the basis of tegumentary adaptations, i.e., as a result of stronger chitinization in the *Sellnickochthonius* species than in the *Liochthonius* species (Grandjean 1963, and personal observations). If there is a connection between resistance to drought (i.e., the capability to retard water loss) and integument chitinization (Lebrun 1971), one would predict that lower resistance to drought would account for the occupation of caves by the *Liochthonius* species. Yet this hypothesis is weakened by evidence of the commonness of this genus in grassland and forest litter in varied climatic conditions (e.g., Wauthy 1982; Subias and Gil-Martin 1997; Behan-Pelletier 1999). Without information on resistance to drought in the two genera, it is not possible to draw any conclusions.

### Evolutionary considerations

The Brachypylina is the most diverse cohort within the Oribatida, accounting for 35 of 50 families in Belgian deciduous forests (Lebrun et al. 1989; see other examples in Weigmann and Kratz 1981 and Subias and Gil-Martin 1997). The ability of brachypylinid species to colonize numerous habitats could result from great resistance to drought. This could explain why the proportion of brachypylinid species increases substantially from humid to xeric habitats (Table 6). The ability to resist drought could be due to tegumentary adaptations (see above), tracheal system development, or physiological adaptations (e.g., Madge 1964a, 1964b; Lebrun 1971; Vannier 1973; Alberti and Coons 1999). In-

**Table 6.** Changes in the ratio of number of primitive oribatid species to total number of oribatid species in mite assemblages from a series of habitats of increasing relative humidity (R.H.).

Microecosystem	Ratio (%)	R.H. (%)
Bark (south exposure)	10 <sup>a</sup>	68–77 <sup>b</sup>
Bark (west exposure)	17 <sup>a</sup>	87–89 <sup>b</sup>
Litter	31 <sup>a</sup>	88–90 <sup>c</sup>
A <sub>n</sub> soil horizon	38 <sup>d</sup>	~100 <sup>e</sup>
B soil horizon	41 <sup>f</sup>	~100 <sup>e</sup>
Cave	65 <sup>f</sup>	100 <sup>f</sup>

<sup>a</sup>Lebrun 1971.

<sup>b</sup>Prinzing 2003.

<sup>c</sup>Westbrook et al. 2003.

<sup>d</sup>Ducarme et al. 2004.

<sup>e</sup>Vannier 1987.

<sup>f</sup>This study.

deed, the cuticle of adult brachypylinid species usually appears more strongly chitinized than that of other oribatids, except those in the Euphthiracaroida, Phthiracaroida, and many in the Desmonomata. Cerotegument (Madge 1964a; Vannier 1976) and cuticular porosity (Alberti and Norton 1997) probably also affect water loss.

The occurrence of water-balance adaptations in the most speciose and evolved group in the Oribatida agrees with Ghilarov's hypothesis that arthropods invaded soils as an intermediate environment between aquatic and terrestrial environments. Accordingly, two main cave colonization paths can be proposed. The first is acknowledged in all biospeleological studies (e.g., Holsinger 2000). It states that arthropods, originating from the soil according to Ghilarov's hypothesis, invaded the surface habitat and only subsequently invaded caves. Cave brachypylinid species must have followed this path, as their drought resistance adaptations could have resulted only from a surface life. But another path could have been followed by other arthropods, which could have colonized caves directly from deep soil, without a surface stage. This could be the evolutionary path followed by cave mites exhibiting primitive features, such as the Endeostigmata, the Eupodoidea, or some "primitive" oribatids such as *Liochthonius* species. A third evolutionary path could exist: arthropods living originally in caves could have invaded the surface habitat. To our knowledge, only one study has considered this possibility (Desutter-Grandcolas 1993), demonstrating its occurrence in one genus of cave cricket. To date, no data supporting this hypothesis are available in mites.

The high proportion of primitive oribatids could also be interpreted as an indication of the usefulness of a supple protero-hysterosomatic articulation, which provides great agility and high flexibility (Grandjean 1969) and is found in all primitive oribatids except the Desmonomata (poorly represented in this study). Yet this was scarcely supported by our data: the proportion of mites belonging to Dichosomata was higher in caves, where mites could walk freely on the surfaces of sediment piles (see hereafter), than in deep soil, in which an articulation could be used to move in tortuous pores. As for the prostigmatid mites, there is no evidence that primitive taxa would be dominant in either habitat.

### Body size

The presence of larger species in caves than in deep soils showed that at least some mite species live at the surface of cave sediment. Indeed, the pores of the cave sediment were as small as the pores of the soil, thus preventing large species from moving in them. Christiansen et al. (1961) reached a similar conclusion for cave springtails: most of them walk on the surface of the sediment. In contrast, soil dwellers have to cope with a selective pressure on body size: they obviously cannot be larger than the largest pores. The ability to explore smaller pores also allows soil dwellers to avoid predation and take advantage of the microflora (Vreeken-Buijs et al. 1998). Environment productivity (Shvarts and Demin 1994), humidity (Remmert 1981), and biotic interactions (Barbault 1988) may also influence body size.

The morphology of the collected Rhagidiidae species was similar to Zacharda's (1979) description: parallel rhagidial organs and clavate trichobothria were detected in some soil species, whereas large chelicerae were found in the cave species. Based on the literature, we expected that longer legs and sensory organs would be the general rule in cave mites. This hypothesis was verified insofar as that, within families, trichobothria and tarsus I solenidia were longer in cave species than in soil species. Yet, because the bodies of mites in caves were longer than those of mites in soils, the sizes of these organs relative to that of the body did not differ between habitats. Bernini (1980) and Bruckner (1995) proposed an explanation for the lack of troglomorphisms in Oribatida at the supraspecific level: for these tiny animals, the subterranean environment may spatially resemble soils, so that further morphological adaptations did not evolve. However, body length appears to be a major difference between cave and deep soil mites, the latter being characterized by a smaller body apparently adapted to the porosity of the deep soil habitat. Other adaptations are to be found at the species level and remain to be described.

### Conclusions

Adaptations specific to cave and deep soil environments have been shown to occur. These were linked to environmental differences such as available space, humidity, spatial structure, and flooding liability. Mechanisms of morphological, physiological, and biochemical changes supporting these adaptations remain to be elucidated. Study of mites could help in understanding the genetic basis of these adaptive features.

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