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Habitat stratification stratifies a local population: ecomorphological evidence from a bisexual, mobile invertebrate (*Carabodes labyrinthicus*; Acari)

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We present preliminary evidence that local populations may be differentiated among habitat strata also in mobile, sexually reproducing invertebrates. We considered *Carabodes labyrinthicus*, an oribatid mite species, sampled from the endogeic (below litter layer) and the epigeic stratum in a forest. We found that the endogeion was used by only a few females. Most interestingly, endogeic and epigeic males differed with respect to physiologically relevant traits such as body volume and sensillus shape. Supplementary genetic investigations corroborated this differentiation between strata. Non-parametric tests, jackknife and bootstrap resampling consistently confirmed our findings; indicating that highly robust patterns can be detected even from small samples such as ours. Finally, we found that epigeic males showed a distinctly bimodal distribution of morphology, where one of the two peaks matched the unimodal distribution of endogeic males. We conclude that the population investigated may be gradually differentiated between stratum specialists that are restricted to the epigeion, and stratum generalists.

Introduction

Most habitats are structurally stratified and the strata are inhabited by distinct sets of animal species (e.g. Basset *et al*. 2001). Only a few species are generalists and occur in several strata. However, even in such generalistic species habitat stratification may be important. Different groups of animals may use different strata, and hence the 'stratum-niche breadth' of an individual animal may be much smaller than that of the whole population. Such an intrapopulation differentiation of the stratum niche can be recognized from stratum-specific differences between animals in terms of morphology, gender, or genetics, and has been repeatedly demonstrated for vertebrates (review in Smith & Skúlason 1996). Vertebrates, however, may be special.

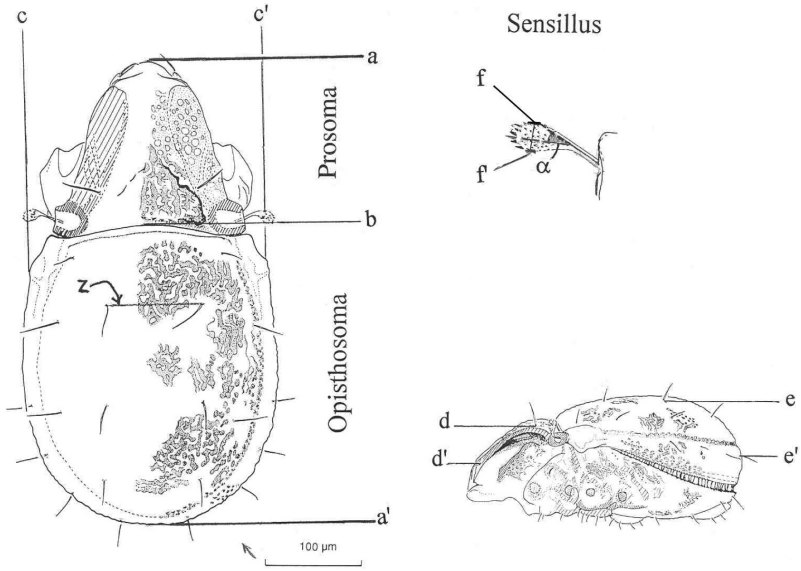

Fig. 1. Dorsal and lateral views of *Carabodes labyrinthicus*. The following measures were recorded: Prosoma length [a–b]; prosoma height [d–d´]; opisthosoma length [b–a´]; opisthosoma width [c–c´]; opisthosoma height [e–e´]; width of sensillus head [f–f´]; inclination of sensillus head [α]; shape of structures that touch line [z] = (number of "ridges")/(total number of "ridges", "tuberculous ridges" and "tubercles"); angle of structures that touch [z] = (number of "ridges" or "tuberculous ridges" rectangular to [z])/(total number of "ridges" and "tuberculous ridges" touching [z]). We approximated the total volume of an animal as the sum of two spheres. The radii of the two spheres were ((([a–b] × 0.5) + [d–d´]) × 0.5), and ((([b–a´] × 0.5) + ([c–c´] × 0.5) + [e–e´]) × 0.33). Figure from Beck and Woas 1991.

Many vertebrates, but only some invertebrate taxa, are territorial, which increases the chance of intrapopulation differentiation in vertebrates (Mayr 1963). The few investigations on small-scale spatial differentiation of invertebrate populations considered extreme cases: species that disperse only rarely or very slowly, reproduce asexually or parthenogenetically, are distributed across biogeographically different slopes of a canyon or across host species that rarely co-occur (Janson 1983, Johannesson *et al.* 1993, Emelianov *et al.* 1995, Pavliček & Nevo 1996, Tessier & Leibold 1997, Mopper & Strauss 1998, Sato *et al.* 2000). Only Parsonage and Hughes (2002) considered a sexually reproducing, highly mobile invertebrate species (a snail) distributed across adjacent habitat strata, but found only little evidence for intra-population differentiation of the stratum niche. Thus, it remains unclear whether in a sexually reproducing, highly mobile invertebrate species a local, syntopic population may consist of distinct phenotypes specialized on distinct habitat strata (Pianka 1988).

Intraspecific differentiation in general has only rarely been investigated in terrestrial microarthropod taxa like Collembola and oribatid mites. Mostly, it has been investigated between populations, rather than within populations. For instance, Woas (1981), Bernini *et al.* (1988), Frati *et al.* (1992), Nübel-Reidelbach (1994), and Fujikawa (1995) investigated populations at geographically distinct sites. Posthuma (1990) investigated populations at sites of different toxic contamination. Finally, Weigmann (1999), and Zieglar *et al.* (1990) investigated populations in different landscapes or landscape compartments. The few investigations on the within-population level focused on either seasonal polymorphism, stratum-specific distribution of ontogenetic stages, or the spread of an invading species across strata (Leinaas 1981, von Allmen & Zettel 1982, Sabelis 1985, Bedos & Cassagnau 1988), i.e., on indicators of temporary rather than permanent patterns.

Carabodes labyrinthicus Michael is an obligatory bisexual oribatid mite species (Wunderle 1992; Fig. 1) that displays a remarkably wide

distribution both at the global scale (Travé 1963, Solhøy 1975, Reeves 1998) and at the scale of local habitats (Travé 1963, Weigmann & Kratz 1981). Even syntopically within a small area of a forest the stratum-niche of *C. labyrinthicus* includes both major strata recognized by oribatologists and soil zoologists: the endogeion, i.e. the humus and the fermentation layer, and the epigeion, i.e. the litter layer, the stumps, the trunk bases, the trunks, and the tree crowns (e.g., Eisenbeis & Wichard 1987, Wunderle 1992, Hansen 2000). Although living conditions within the endogeion and the epigeion are not homogeneous, the living conditions in the epigeion differ fundamentally from those in the endogeion. In the epigeion, desiccation and air velocity are higher, and cavities are larger, than in the endogeion (Haarløv 1960, Vannier 1970). Also, most places in the epigeion are separated from most places in the endogeion by distances equivalent to several thousand body lengths of *C. labyrinthicus*. Overall, *C. labyrinthicus* colonizes two distinct and extensive habitat strata. Despite the wide extension of the endogeion and the epigeion, *C. labyrinthicus* is sufficiently mobile to move between any place in the endogeion and any place in the epigeion within at most a few days. The evidence is, first, that *C. labyrinthicus* can move at a speed of several cm per minute (Wunderle 1992). Second, the abundances of *C. labyrinthicus* at intermediate levels of tree trunks fluctuate during the course of a day, which indicates diurnal vertical movements of many animals across a meter or more (Wallwork 1976, Prinzing 1996), even though it is not known whether these movements extend downward into the endogeion, or whether only certain phenotypes of *C. labyrinthicus* move while others stay.

Here we present a pilot study in which we assessed whether a local population of *C. labyrinthicus* is differentiated into animals with different stratum niches. For this purpose we compared adult animals sampled from the endogeion and the epigeion of a small area (80 m^2) within a forest with respect to their morphology, gender and a small set of genetic traits. Moreover, we explored whether the limited sample size of our pilot study already permits unbiased morphological and genetic patterns to be described. For this purpose we applied and compared non-parametric analyses, jackknife resampling and bootstrap resampling.

Materials and methods

Sampling

We sampled *C. labyrinthicus* over two years (1992, 1993) in an area of 80 m^2 within a colline deciduous forest dominated by *Quercus robur* L. and *Fagus sylvatica* L., located in the Hohenlohe region in southwestern Germany (site description in Landesanstalt für Umweltschutz 1986). Each year we sampled twice, in spring and autumn (31 Mar. 1992 and 1 Oct. 1992, 22 Mar. 1993 and 13 Oct. 1993). These periods do not coincide with fundamental differences in *C. labyrinthicus*' two-year life cycle. Both periods show similar adults:immatures ratios, males:females ratios, numbers of gravid females and numbers of adults emerging from the bark (Luxton 1981, Büchs 1988, Wunderle 1992). All samples were taken between 11.30 a.m. and 3.00 p.m., thus they represented approximately the same stage within a possible diurnal vertical migration cycle of *C. labyrinthicus*. Within both strata, endogeion and epigeion, we sampled a variety of microhabitats to fully encompass the respective structural variability. In the endogeion we sampled the humus and the fermentation layer; in the epigeion we sampled the litter layer, the moss cover on trunk bases, the stumps and the bark of tree trunks at breast height. We took two samples from each of these six microhabitats at each of the four dates. Sampling and extraction methodology has been described in detail by Wunderle (1992). In short, the samples of the endogeion and of the epigeic litter consisted of soil cores of 32 cm^2 and were heat-extracted by a Berlese funnel (Dunger & Fiedler 1989). Bark and moss cover were sampled by brushing the bark surface (André 1979), stumps were sampled by manually extracting material. Oribatida were then sorted out focally under a stereomicroscope. Twenty-six of the samples contained adult *C. labyrinthicus* (juveniles were not considered because they could not be determined to species level), and the total sample size was 53 animals (Appendix).

Sexing

We determined the gender from the presence of an ovipositor. To compare the frequency distribution of genders between the endogeion and the epigeion we used a V^2 test, which is, in principle, a Chi^2 test adjusted for small sample sizes (Statsoft Inc. 1999). To test whether, despite the small sample size, the results are robust and not biased by outliers we used bootstrap (n = 4000) and jackknife resampling. For each resampled sample we then re-analyzed the frequency distribution of genders across strata. These procedures estimate what can be expected from further sampling the population by resampling the sample (Manly 1997, SPSS Inc. 1998, Simon 1990–1999).

Morphological investigations

For our measurements we used a drawing apparatus attached to a Leitz Dialux 20 microscope. Prior to the measurements animals were preserved in warm lactic acid to lighten the cuticula. We considered traits for which (i) measurement of a large number of animals was practicable; and (ii) some intraspecific variation had already been observed in other oribatid mite species (e.g., Beck 1965, Woas 1981, Nübel-Reidelbach 1994, Fujikawa 1995, Weigmann 1999).

The traits fall within two broad groups. The first group comprises of three traits related to the physiological performance of animals in the endogeion *vs*. the epigeion. The second group comprises seven traits without clear relationship to the physiological performance of the animals in different strata. We expected that a between-phenotype differentiation of the stratum niche would result in a stratum-specific differentiation of the first group of traits, while a differentiation of the second group would be much less likely.

Group 1: (a) The approximate body volume (Fig. 1), which in turn was closely correlated to body length (r_p = 0.95). Large volume corresponds to a small relative body surface and thus to a lower sensitivity to the desiccation stress in the epigeion (Eisenbeis 1989). In addition, large body volume hinders the penetration into the small cavities in the endogeion (Haarløv 1960). Overall, small animals should perform best in the endogeion, large animals in the epigeion. (b) The width of the sensillus head (average of left and right sensillus; Fig. 1); (c) The inclination of the sensillus head (average of left and right sensillus; Fig. 1). The sensillus head is the sensory organ of oribatid mites that perceives air velocity (Pauly 1956). The shape ranges from large, bifurcating "antlers" in species inhabiting sheltered habitats, to small "clubs" in species inhabiting exposed habitats and in aquatic species. This interspecific variation is interpreted as an aero(hydro)dynamic adaptation to movements of the ambient medium: subtle in sheltered habitats, vigorous in exposed or aquatic habitats (Pauly 1956, Aoki 1971, Walter & Behan-Pelletier 1999). At the intraspecific level, within *C. labyrinthicus*, the variation is much smaller, basically all sensillus heads are club-shaped, but with a large variation in the width and inclination. Also this variation can have aerodynamic consequences. An aerodynamic, streamlined sensillus head would be one that is slender and posteriorly inclined (principles described in Nachtigall 1985). So animals with such a sensillus head should perform best in the epigeion while those with a thick, upright sensillus head should perform best in the endogeion. At a regional scale Fujikawa (1995) has already found similar relationships between body size and sensillus shape and habitat conditions: animals were smaller and had thicker sensilli in moist forests than on dry acres.

Group 2: (a–b) prosoma length and height; (c–e) opisthosoma length, width and height; (f–g) shape and orientation of the structures on the opisthosoma surface (Fig. 1).

We present the measurements of all traits in the Appendix. Several of the traits were correlated with body volume. We standardized each of these traits by taking the residuals from a linear regression against body volume (Ricklefs & Miles 1994). This procedure completely eliminated the interactions of traits with body volume (n = 50, $r < 0.028$, $p > 0.85$), which means that there were no allometric relationships. Absence of allometries seems to be a common phenomenon in many traits of oribatid mites (e.g., Woas 1981, Nübel-Reidelbach 1994).

We analyzed the difference between animals from the endogeion and the epigeion, separately

for both groups of traits, using discriminant function analysis (DFA). We chose DFA because it is considered to be statistically superior to logistic regression for our type of data since none of the independent variables was categorical (Efron 1975, Press & Wilson 1978, Hosmer & Lemeshow 1989). We also applied a multivariate ANOVA with stratum as factor and the morphological traits as dependent variables, which led to very similar results as the DFA. We therefore only present the DFA results. DFA was preferable because based on the discriminant function it was possible to score each animal along a morphological gradient from endogeion to epigeion. In the DFA we additionally calculated (i) the standardized coefficients of the independent variable in the discriminant function; (ii) the test statistics for the individual independent variables as well as the for the full discriminant function model; and (iii) the concordance, i.e. the proportion of animals that was assigned correctly to endogeion, or epigeion, by the discriminant function (SPSS Inc. 1998, Statsoft Inc. 1999). We calculated concordances with and without weighting by group size and present the results of the unweighted analysis, which were more conservative.

Results of DFA may be biased by outliers (which violate the normality assumption) in particular when the sample size is small as in our case (Manly 1997). We, therefore, assessed the bias of our results in three ways. First, we assessed the bias of the parameter estimates. We used bootstrap resampling (n = 5000; SPSS Inc. 1998) to estimate what can be expected from further sampling the population by resampling the sample (Manly 1997, Simon 1990–1999). Second, we assessed the bias of the parametric test statistics of the discriminant function model. We used a non-parametric Mann-Whitney U-test (Lamprecht 1992) comparing the rank-transformed scores of epigeic animals and endogeic animals along the discriminant axis. Third, we assessed the bias of the concordances. We used jackknife resampling, i.e. we omitted one animal in turn when calculating the discriminant function and then used this function to assign the omitted animal to a stratum (SPSS Inc. 1998). This jackknife approach yields distinctly lower concordances than the standard approach when the calculation of the discriminant function is biased by a few extreme animals (Manly 1997).

We also assessed bias due to confounding variables. We tested how *gender*, *season* and *year* interact with the morphological traits using multivariate ANOVA (MANOVA) with Type VI sums of squares (Statsoft Inc. 1999). We selected all factors which showed even an extremely weak interaction ($p < 0.4$), then we included *stratum* as an additional factor into the model and tested whether its effect on morphology is still significant.

Genetic investigations

We conducted the polymerase chain reaction (PCR) by random amplified polymorphic DNA (RAPD) which is highly appropriate for intra-population studies on small organisms (Rafalski 1998, Wolff & Morgan-Richards 1999). We first washed the animals two times in 0.85% NaCl solution, and then grounded them in a micromortar in 10 μl NaCl solution under liquid nitrogen. We found that efficient washing removed viable microorganisms from the mites. We extracted the mite DNA by InVISorb Genomic DNA kit (InViTek GmbH company) with time for lysis of cell hybris set to two hours. The RAPD IV primer (= sequence 5´-CGGCCCCTGT-3´; Invitek GmbH) gave a fingerprint with 5 to 8 main bands and up to 9 weak bands.

Using a single primer restricted our genetic investigation to a very small set of genetic traits. Hence, our genetic investigation could only supplement the results from our morphological investigations. For a stand-alone genetic investigation a larger set of primers is needed (Rafalski 1998, Wolff & Morgan-Richards 1999). But this would require a much larger sample size because only a single primer could be applied per animal. A larger sample, however, was not available in our pilot study.

We performed the PCR in 50 μl cups, containing 1 μl Taq-Polymerase (GibcoBRL), 5 μl 10× buffer, 1.5 μl mM $MgCl_2$, 5 μl 2.5 mM dNTP, 50 pmol RAPD IV primer and 40 μl DNA extract. We conducted the PCR in 0.2-ml tubes without oil overlaying. After a hot start (120 sec at 94 °C) we performed 40 cycles as follows:

40 sec at 94 °C, 40 sec at 36 °C, 80 sec at 72 °C (GeneAmp PCR System 2400, Perkin Elmer). We loaded PCR products in slots of special agarose gel (1.5%, Agarose MS, Boehringer Mannheim), and after gel running and staining with Ethidiumbromid we photographed the gel with a digital camera to register densiometric curves using GelCompar 4.0 software (Applied Maths 1996, Labes *et al*. 1996).

This photographic registration method permitted the use of not only the presence or absence of bands, but also the width of the bands (with a minimum width of zero for absent bands). This is an important advantage because main bands may contain multiple DNA sequences (Gu *et al*. 1999). In fact, we found that the width of a band could vary strongly among individuals. Moreover, based on this registration method, the genetic similarity between two individuals could be characterized by the Pearson correlation coefficient across band widths, rather than band-matching coefficients across presences and absences of bands (Labes *et al*. 1996). The Pearson coefficient is preferable because it is less sensitive to differences between the DNA-amounts of the PCR-samples, and to peak/shoulder mismatches (Applied Maths 1996).

To test the reproducibility of the results, a second PCR was performed on the DNA extract of most animals, sometimes with a double number of cycles. Every PCR included reaction controls and was placed in a separated lab with filtered air condition. We found that both PCRs gave consistent patterns.

In the statistical analysis, we calculated a matrix of Pearson correlation coefficients across all pairs of animals, and used principle component analysis (PCA) to describe the major components of variation in this matrix (Applied Maths 1996, Statsoft Inc. 1999). To analyze the genetic differences between animals from endogeion and epigeion we used two methods: (i) A discriminant function analysis (DFA *see* above). The DFA was based on the scores of animals along the first and second component of the PCA. These two components represented 68% of the total genetic variance among the animals. (ii) A sign test (Zar 1984) testing the expectation that for most animals within-stratum similarity was larger than between-stratum similarity. The within-stratum similarity of a given animal was the mean of the Pearson correlation coefficients between this animal and the other animals from the same stratum (endogeion or epigeion). Between-stratum similarity was the mean correlation with animals from the other stratum.

We assessed possible biases of the DFA due to outliers using bootstrap resampling, Mann-

Table 1. Discriminant function analyses of the relationship between stratum (endogeion *vs.* epigeion) and three morphological traits that affect the physiological performance of animals in endogeic and epigeic environments (Material and methods). *See* also Fig. 2.

Trait	Standardized coefficient	Percentage of bootstrap analyses that yield the same sign	F_1	p
Males and females (n = 50)				
Body size	0.873	100	7.74	0.013
Width of sensillus head	–0.285	73.3	0.61	0.151
Inclination of sensillus head	0.471	87.2	1.37	0.152
Full model:				
Parametric test: Wilk's λ = 0.81, $F_{3,46}$ = 3.63, p = 0.020, non-param. test: Z = 2.34, p = 0.004				
Concordance = 72%, jackknife concordance = 70%				
Males (n = 28)				
Body size	0.796	100	6.36	0.019
Width of sensillus head	0.116	60.9	0.08	0.779
Inclination of sensillus head	0.870	98.6	5.41	0.029
Full model:				
Parametric test: Wilk's λ = 0.63, $F_{3,24}$ = 4.70, p = 0.010, non-param. test: Z = 3.20, p = 0.001				
Concordance = 75%, jackknife concordance = 71%				

Whitney *U*-test and jackknife resampling as described in the morphological analysis. We also assessed bias due to confounding variables using the MANOVA procedure described in the morphological analysis.

Results

Sex ratio

In the endogeion, males were more common than females (9:2), while in the epigeion the sex ratio was approximately equal (22:19). This difference was only marginally significant ($n = 52$, $V^2 = 2.8$, $p = 0.094$; original data in Appendix), which also reflects the limited sample size. However, the scarcity of females was clearly confirmed in 96.6% and 100%, respectively, of our bootstrap and jackknife resampling analyses.

Morphology

Traits that are related to the animals' performance under endogeic and epigeic living conditions indeed differed between endogeic and epigeic animals. As expected, epigeic animals displayed a large body size combined with a thin, posteriorly inclined sensillus head (Table 1: males and females, Fig. 2a). The full discriminant function model was statistically significant but when we inspected the unique contribution of the individual variables to the discriminatory power of the model we found that only body size was significant (Table 1: males and females). This situation, however, changed when we restricted the analysis to males (*see* below and Table 1: males).

We found no biases that could have lead to a morphological difference between animals from the two strata. First, the difference was not biased by the fact that often several animals had been taken from the same sample. Fig. 2 shows that these animals were in general no more similar to one another than to other animals from the same stratum. Second, despite the small sample size the morphological difference between endogeic and epigeic animals was not biased by outliers: the bootstrap analyses clearly

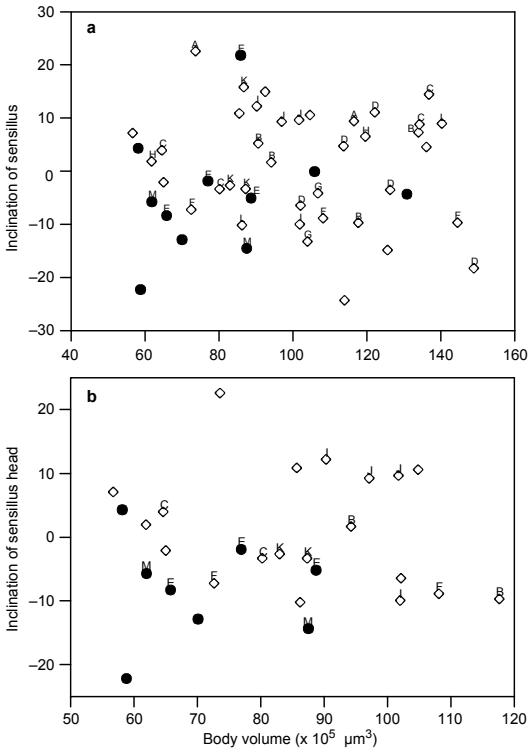

Fig. 2. Body volume and inclination of the sensillus of animals from the endogeion (dots) and the epigeion (squares). — **a**: male and female animals. — **b**: only male animals. Sensillus inclination is given as residuals against body volume. The three traits are related to the animals' physiological performance in endogeion and epigeion and permit the discrimination of endogeic from epigeic animals (Table 1). Each symbol represents one animal. Letters indicate animals taken from the same sample.

confirmed the sign of the parameter estimate for *body size* found in the original analysis; the non-parametric Mann-Whitney *U*-test confirmed the parametric significance tests of the discriminant-function model; and the jackknife concordance was almost as large as the standard concordance (Table 1: males and females). Third, the morphological difference between endogeic and epigeic animals was not biased by the year of investigation, because year did not interact with morphology (MANOVA with morphological traits as dependent variables: $n = 50$, $F_{3,46} = 0.57$, $p = 0.639$). Fourth, we tested whether the difference was biased by the two factors which did interact with morphology: season (spring *vs*. autumn; MANOVA: $n = 50$, $F_{3,46} = 3.05$, $p = 0.038$),

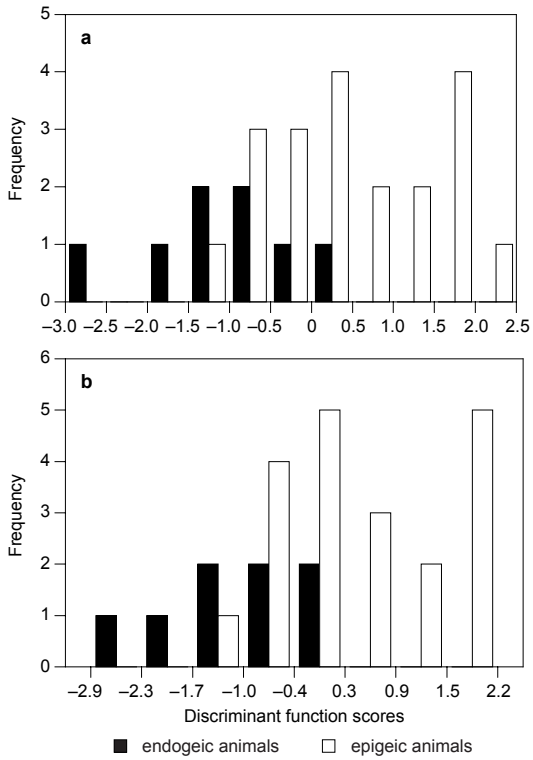

Fig. 3. Frequency distribution of scores of males along the discriminant-function axis calculated from body size and sensillus shape (Table 1). **a** and **b** differ in the number of intervals selected; **a**: automatic integer-mode default setting in Statistica (Statsoft Inc. 1999), **b**: arbitrary reduction of intervals. In both graphs epigeic animals show a bimodal distribution. Note that due to the small sample size we could not reliably assess the frequency distribution of animals along the discriminant axis calculated from the genetic traits.

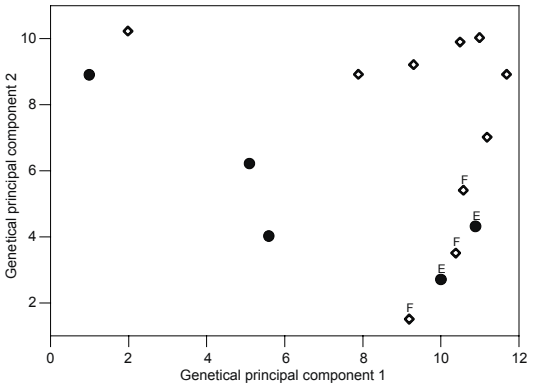

Fig. 4. Genetic patterns of male animals from the endogeion (dots) and the epigeion (squares). The axes are the first and second components of a principle component analysis, explaining 37% and 31% of the genetic variation, respectively. Each symbol represents one animal. Letters indicate animals taken from the same sample.

and, in particular, gender (MANOVA: $n = 49$, $F_{3,45} = 17.22$, $p < 0.005$). We included *season* and *gender* together with *stratum* as factors into a MANOVA of the morphological traits, and found that the interaction between stratum and morphology became even more significant than in the above DFA ($n = 49$, $F_{3,43} = 4.15$, $p = 0.011$). Also, when we restricted the above DFA to males we found that the morphological difference between endogeic and epigeic animals was very clear ($p = 0.010$; Table 1: males, Fig. 2b; a restriction to females was not practicable as only two females were found in the endogeion). When we inspected the unique contribution of the individual traits to the discriminatory power of this male-specific model we found that not only was the body size significant but also the inclination of the sensillus (Table 1: males). The effects of both variables were also clearly corroborated by the bootstrap analysis (Table 1: males).

In the latter, male-specific DFA we found a conspicuous pattern. The frequency distribution of epigeic males along the discriminant axis was bimodal, where one of the two peaks matched the unimodal distribution of endogeic animals (Fig. 3).

As expected, traits that are not related to the animals' performance under endogeic and epigeion living conditions did not differ between endo- and epigeic animals (DFA: $n = 51$, $F_{7,43} = 0.91$, $p = 0.511$; concordance = 69, jackknife concordance = 59%). Even when body volume was included as an additional variable, the differentiation was only weak (DFA: $n = 51$, $F_{8,42} = 1.65$, $p = 0.16$).

Genetics

In our supplementary genetic analysis we again omitted females because they were almost absent from the endogeion (*see* above) and because gender may interact with genetics (MANOVA: $n = 29$, $F_{2,26} = 2.15$, $p = 0.14$). Although only preliminary in nature (*see* Material and methods), the results confirmed the differences between epi-

and endogeic males observed in the morphological investigations. First, the DFA across the first and second genetic principle components gave a nearly significant difference between endo- and epigeic animals (n = 15, $F_{2,12}$ = 3.76, p = 0.054, concordance = 73%; Fig. 4). Both principle components showed a (nearly) significant unique contribution to the discriminatory power of the DFA model ($F_{1,12}$ = 4.88 and 4.28, p = 0.047 and 0.061, respectively). Interestingly, the scores of animals along the genetic discriminant function correlated to the scores along the morphological discriminant function (n = 14, $r_{Pearson}$ = 0.55, p = 0.04, $r_{Spearman}$ = 0.65, p = 0.012). For instance, an epigeic animal that was most similar to the endogeic animals genetically was also most similar morphologically. Second, the sign test across pairwise genetic correlations showed that for 11 animals within-stratum correlations were higher than between-stratum correlations, whereas for only 3 animals it was vice versa (Z = 1.84, p_1 = 0.030). In other words, the genetic similarity was significantly larger between animals of the same stratum then than between animals of different strata.

We found no biases that could have led to a genetic difference between animals from the two strata. First, the difference was not biased by the fact that in a few cases several animals had been taken from the same sample. These animals contributed particularly little to the difference between endogeic and epigeic animals (Fig. 4). Second, despite the small sample size the genetic difference between endogeic and epigeic animals in the DFA was not biased by outliers: 100% and 97%, respectively, of the bootstrap analyses confirmed the signs of the parameter estimates found in the original analysis; the non-parametric Mann-Whitney U-test confirmed the parametric significance tests of the discriminant-function model (n = 15, Z = –2.45, p = 0.014); and the jackknife concordance was as large as the standard concordance (i.e. 73%). Third, the difference was not biased by season, because season did not interact with the two genetic principle components (MANOVA: n = 15, $F_{2,12}$ = 0.015, $p > 0.9$). Fourth, the difference was not biased by year, because also year hardly interacted with the genetic principle components (MANOVA; n = 15, $F_{2,12}$ = 1.11, p = 0.36). Moreover, when we included *year* together with *stratum* as factors into a MANOVA we still found a significant interaction between genetics and stratum (n = 15, $F_{1,11}$ = 4.74, p = 0.033).

Discussion

We found that the stratification of the forest investigated may indeed stratify the population of *C. labyrinthicus*. Females were largely restricted to the epigeic stratum. And epigeic males differed from endogeic males in terms of morphology and a small set of genetic traits. Despite the small sample size of this pilot study the morphological and genetic results showed no discernable bias. Re-analyses based on non-parametric tests, jackknife resampling and bootstrap resampling consistently confirmed the results.

We found that females were somewhat underrepresented (*see* Luxton 1981 for other examples) and largely restricted to the epigeion. This restriction matches observations indicating that also juveniles are restricted to the epigeion. As habitats of juveniles, only corticolous lichens have been described (Wunderle 1992, Seniczak & Dąbrowski 1993, Prinzing 1996). Such lichens, and the underlying bark, often fall off the trees and form a part of the litter layer, but they do not occur in the endogeion. In accordance with this, Büchs (1988) and Wunderle (1992) found that populations of *C. labyrinthicus* at tree bark are autochtonous.

On the other hand, we found that males occurred in both, epigeion and endogeion. The males apparently grew up in the epigeion (*see* above), and they had to visit the epigeion to find the females. Hence, we suppose that many males migrate from epi- to endogeion and back. A possible advantage of such a migrant-male strategy would be that the males do not use the resources required by the immatures. On the other hand, temporal emigration of males from the epigeion need not constrain the sperm supply of the epigeic females as they might be able to store sperms (Walter & Proctor 1999). Migration of males has already been suggested for other (oribatid) Acari (Nagelkerke *et al.* 1996, Søvik *et al.* 2003). And in a number of Oribatida species male migration might be expected as it would maximize the males' reproductive output (Walter

& Proctor 1999), namely in the numerous species in which males are rare or live short (Solhoy 1975 for *C. labyrinthicus*, Luxton 1981, Convey 1994a, Søvik & Leinaas 2003). Nevertheless, to our knowledge no definite observations of sex-specific migrations in Oribatida are available, and for non-oribatid mites most observations indicate a migration of females rather than males (Walter & Proctor 1999).

The clearest and most interesting result of our study is the morphological difference between epigeic and endogeic males. We see four possible causes.

First, phenotypic modification by endo- and epigeion. Such a modification, however, is unlikely. It is unlikely during the juvenile stage because juveniles seem to be largely absent from the endogeion (*see* above). It is also unlikely during the adult stage, because all the traits we investigated are very rigid (Sellnick & Forsslund 1952) and there does not seem to be any discernable growth during the adult stage (Convey 1994b for another Oribatida).

Second, genetic isolation between endo- and epigeion. Such isolation, however, is also unlikely. There seems to be an extensive migration of adult males between endo- and epigeion given that females and juveniles are largely restricted to the epigeion (*see* above). This is also evidence against a scenario of secondary contact between two separate, cryptic species, an endogeion specialist and an epigeion specialist.

Third, correlation between stratum use and life expectancy. Most animals seem to grow up in the epigeion (*see* above) and, with increasing age, male adults seem to migrate from the epigeion towards the endogeion. Hence, animals from the endogeion might be those that survived for a long time, whereas epigeic animals include such which will die before they reach the endogeion. If life expectancy correlates to morphology or genetics, morphological or genetic differences between endo- and epigeic animals will occur. We cannot rule out this mechanism, but it seems insufficient as an explanation for the observed bimodal distribution of traits among epigeic animals.

Fourth, within-epigeion-differentiation of phenotypes or genotypes. A differentiation between animals that migrate between epi- and endogeion and others that tend to stay within the epigeion might take place already within the epigeion (*see* Zaslavskaya & Takeda 1998, Sato *et al*. 2000, Pakkasmaa & Piironen 2001 for other taxa in other habitats). Indeed, within the epigeion *C. labyrinthicus*' uses fundamentally different microenvironments such as bark crevices and cryptogam crusts (Lewis 1962, Prinzing 1996, Prinzing & Wirtz 1997). These microenvironments may modify the phenotype of animals (Flatt *et al*. 2001 for lizards) and induce reproductive and genetic isolation (Nevo *et al*. 2000). Reproductive isolation might occur if the microenvironment influences the interaction between males and females during transfer of spermatophores (*see* evidence in Witte 1991) or the efficiency of alarm and aggregation pheromones (Norton 1998, Walter & Proctor 1999, Alberti & Coons 1999, Shimano *et al*. 2002, Raspotnig *et al*. 2003). Such a modification of, or isolation between, inhabitants of crevice and cryptogams would also explain the observed bimodality of morphological traits among epigeic animals. Hence, within-epigeion differentiation may explain our observations. However, at the moment it is still fully speculative.

In conclusion, there might be a gradual differentiation between residents in the epigeic stratum (most females and a part of the male population) and migrants. Future investigations will have to test whether this differentiation occurs consistently across sites and daytimes. Moreover, the mechanisms of this differentiation need to be studied, including the diet and movement of different stages and genders, the number of hatching males and females and their respective longevities, the mate selection and sperm storage, and the phenotypic and genotypic differentiation between different epigeic microenvironments.

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Appendix. Basic measurements of the animals investigated. The morphological traits are explained in Fig. 1; lengths, widths and heights are given in µm; date: 1, 2, 3, 4 = spring 1995, autumn 1995, spring 1996, autumn 1996. Blank = missing value (animals with damaged body parts).

	Prosoma		Opisthosoma			Sensillus head		Structures at line 'z': proportion of			
Stratum	Length	Height	Length	Width	Height	Width	Inclination	ridges	structures rectangular to 'z'	Gender	Date
Epigeion	147.9	65.1	308.3	256.2	88.2	10.8	39.0	0.3	0.4	Female	1
Epigeion	137.5	54.6	395.8	308.3	81.9	12.0	35.0	0.2	0.2	Female	1
Epigeion	150.0	52.5	370.8	295.8	75.6	12.0	37.0	0.1	0.2	Female	3
Epigeion	135.4	35.7	287.5	254.1	81.9	12.0	44.0	0.4	0.0	Male	3
Epigeion	125.0	67.2	343.7	260.4	90.3	12.0	36.5	0.2	0.5	Male	1
Epigeion	150.0	35.7	308.3	256.2	88.2	11.0	34.0	0.0	0.0	Male	2
Epigeion	145.8	63.0	354.1	291.6	79.8	12.0	3.0	0.2	0.6	Female	3
Epigeion	156.2	52.5	322.9	266.6	81.9	12.0	26.0	0.0	0.2	Male	3
Epigeion	145.8	54.6	316.6	281.2	73.5	11.3	29.0	0.3	0.2	Female	3
Epigeion	150.0	50.4	349.9	318.7	96.6	14.0	37.5	0.3	0.4	Female	3
Epigeion	129.1	56.7	354.1	268.7	100.8	14.0	18.0	0.0	0.0	Male	3
Epigeion	114.6	56.7	331.2	229.1	52.5	12.0	24.0	0.3	0.0	Male	1
Epigeion	164.6	50.4	345.8	333.3	92.4	13.3	45.0	0.2	0.4	Female	1
Epigeion	156.2	67.2	354.1	339.5	77.7	14.0	39.0	0.1	0.3	Female	1
Epigeion										Male	1
Epigeion	143.7	52.5	306.2	256.2	75.6	12.0	19.0	0.0	0.1	Male	1
Epigeion	125.0	50.4	314.5	239.5	56.7	12.6	18.0	0.3	0.4	Male	2
Epigeion	160.4	42.0	318.7	291.6	86.1	12.6	19.0	0.2	0.2	Male	1
Epigeion	170.8	54.6	329.1	312.5	79.8	13.0	32.0	0.0	0.2	Female	1
Epigeion	139.6	63.0	360.4	316.6	75.6	13.3	39.5	0.0	0.4	Female	1
Epigeion	150.0	46.2	397.9	318.7	90.3	14.6	14.0	0.0	0.2	Female	1
Epigeion	162.5	54.6	356.2	324.9	77.7	13.3	25.5	0.0	0.5	Female	1
Epigeion	137.5	46.2	289.5	229.1	56.7	10.6	26.0	0.0	0.0	Male	2
Epigeion	158.3	63.0	364.5	302.0	81.9	14.0	14.0	0.4	0.1	Female	3
Epigeion	129.1	52.5	329.1	258.3	75.6	14.0	13.0	0.1	0.0	Male	4
Epigeion	143.7	67.2	385.4	322.9	79.8	12.0	40.0	0.0	0.0	Female	4
Epigeion	156.2	58.8	385.4	312.5	90.3	13.3	22.0	0.4	0.1	Female	3
Epigeion	131.2	48.3	306.2	237.5	75.6	11.0	14.0	0.0	0.0	Male	3
Epigeion	147.9	65.1	345.8	293.7	73.5	13.3	17.5	0.5	0.4	Male	3

continues

Appendix. Continued.

	Prosoma		Opisthosoma			Sensillus head		Structures at line 'z': proportion of			
Stratum	Length	Height	Length	Width	Height	Width	Inclination	ridges	structures rectangular to 'z'	Gender	Date
Epigeion			466.6	250.0	79.8	10.0	50.0			Male	3
Epigeion	141.6	48.3	354.1	287.5	77.7	12.6	22.0	0.3	0.2	Female	4
Epigeion	143.7	54.6	345.8	283.3	77.7	12.6	12.5	0.0	0.1	Female	4
Epigeion	129.1	48.3	308.3	225.0	60.9	12.0	21.5	0.0	0.2	Male	2
Epigeion	152.1	50.4	368.7	302.0	77.7	12.0	34.5	0.2	0.2	Female	2
Epigeion	145.8	54.6	343.7	279.1	77.7	13.3	15.5	0.2	0.1	Male	4
Epigeion	135.4	60.9	329.1	266.6	73.5	12.0	36.0	0.0	0.0	Male	4
Epigeion	145.8	52.5	339.5	275.0	75.6	11.3	34.0	0.2	0.3	Male	2
Epigeion	139.6	50.4	343.7	279.1	79.8	11.3	35.0	0.1	0.4	Male	2
Epigeion	131.2	50.4	347.9	260.4	67.2	12.0	20.0	0.3	0.3	Male	4
Epigeion	141.6	56.7	316.6	256.2	73.5	13.3	20.0	0.0	0.1	Male	4
Epigeion	145.8	46.2	339.5	272.9	63.0	11.3	39.0	0.3	0.3	Female	4
Endogeion	158.3	42.0	279.1	218.7	67.2	11.3	23.5	0.0	0.0	Male	3
Endogeion	131.2	21.0	370.8	316.6	60.9	12.0	26.0	0.0	0.3	Female	1
Endogeion	137.5	37.8	295.8	239.5	77.7	11.6	8.0	0.3	0.1	Male	1
Endogeion	129.1	58.8	360.4	300.0	75.6			0.1	0.3	Male	1
Endogeion	129.1	48.3	297.9	235.4	54.6	13.3	–3.0	0.0	0.0	Male	2
Endogeion	131.2	60.9	389.5	304.1	79.8	12.6	25.5	0.0	0.0		2
Endogeion	131.2	52.5	295.8	237.5	58.8	12.0	14.0	0.0	0.4	Male	2
Endogeion	145.8	54.6	312.5	270.8	75.6	12.6	9.0	0.3	0.7	Male	2
Endogeion	137.5	58.8	331.2	260.4	73.5	12.6	18.5	0.0	0.1	Male	2
Endogeion	145.8	48.3	312.5	270.8	75.6	13.3	45.0	0.1	0.2	Female	2
Endogeion	137.5	56.7	306.2	260.4	67.2	13.3	20.0	0.0	0.2	Male	2
Endogeion	137.5	54.6	295.8	239.5	63.0	11.6	12.0	0.2	0.0	Male	2