ECOLOGICAL TRAITS INDICATE NICHE DIFFERENTIATION IN BORNEAN DACETINE SPECIES (MYRMICINAE: FORMICIDAE)

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INTRODUCTION

In the leaf litter layer of tropical rain forests the dacetines are one of the most species-rich group of ants (Ward 2000). More than 870 species have been recorded worldwide; 90 % of these small Myrmicine ants species belong to the genera *Strumigenys* and *Pyramica* (Bolton 2000). Dacetines have specialized trap-jaw mandibles for the capture of small invertebrate prey (Gronenberg 1996). The Malesian region harbors over 260 species; 20 *Pyramica* and 68 *Strumigenys* species are reported from Borneo alone (Bolton 2000). In Gunung Mulu National Park (Sarawak, Malaysia) we found 29 species of *Stumigenys* and *Pyramica* in leaf litter and soil, with many of them co-occurring in the same habitat: in a single forest type, the alluvial forest, we recorded 18 sympatric species in a sample area of 20 m² (Mezger & Pfeiffer, unpublished). Even in temperate regions these genera are very species-rich, with (e.g.) 22 species found in North America (Wilson 1953). Some dacetine species live in parabiotic associations with other ant species: a *Strumigenys* species from Java shares its nest with *Diacamma* and *Pachycondyla* (Kaufmann *et al.* 2003), while *Pyramica maynei* from West Africa is reported to live together with *Platythyrea conradti* (Yeo *et al.* 2006). *Strumigenys rotogenys* from Borneo shares its nest with *Pyramica mitis* (Mezger & Pfeiffer 2008). These patterns of dense species co-occurrence are strong indicators of tight niche assemblage among dacetine ants because, according to niche theory, completely similar species cannot exist together

(Chase & Leibold 2003). It is postulated that Dacetini are adapted to hunt different types of prey since their characteristic mandibles differ in shape and size (Traniello 1989, Hölldobler & Wilson 1990). However, not only morphometric properties are important for prey capture in an ant but also its ability to approach a prey organism (Masuko 1984). Therefore walking speed is an important ecological trait in ants, influencing foraging area size and speed during approach to a prey item. The food preferences of ants can be assessed by "cafeteria" experiments (e.g. Wilson 2005), while analyses of stable isotopes in ant specimens can indicate species' positions in the food chain (Fiedler *et al.* 2007).

In this study we tested the hypothesis that walking speed, morphometric characteristics, and/or stable isotope values differ among three species of *Strumigenys* and one *Pyramica* species that co-occurred in alluvial forest, including two species sharing a nest with each other.

STUDY AREA AND METHODS

Our study was conducted in Gunung Mulu National Park (4°57'N, 114°47'E) (Mulu NP) in Sarawak (Malaysia) on Borneo. The climate in this area is tropical wet, with mean temperatures of about 26°C and 4000 to 5000 mm rain per year (Sarawak Weather Service, pers. comm.). While Mulu NP is covered with several types of forest (Hazebroek & Morshidi 2001), we focused our study on the alluvial forest around the park headquarters at the foot of the mountain. A detailed description of the study area is given elsewhere.
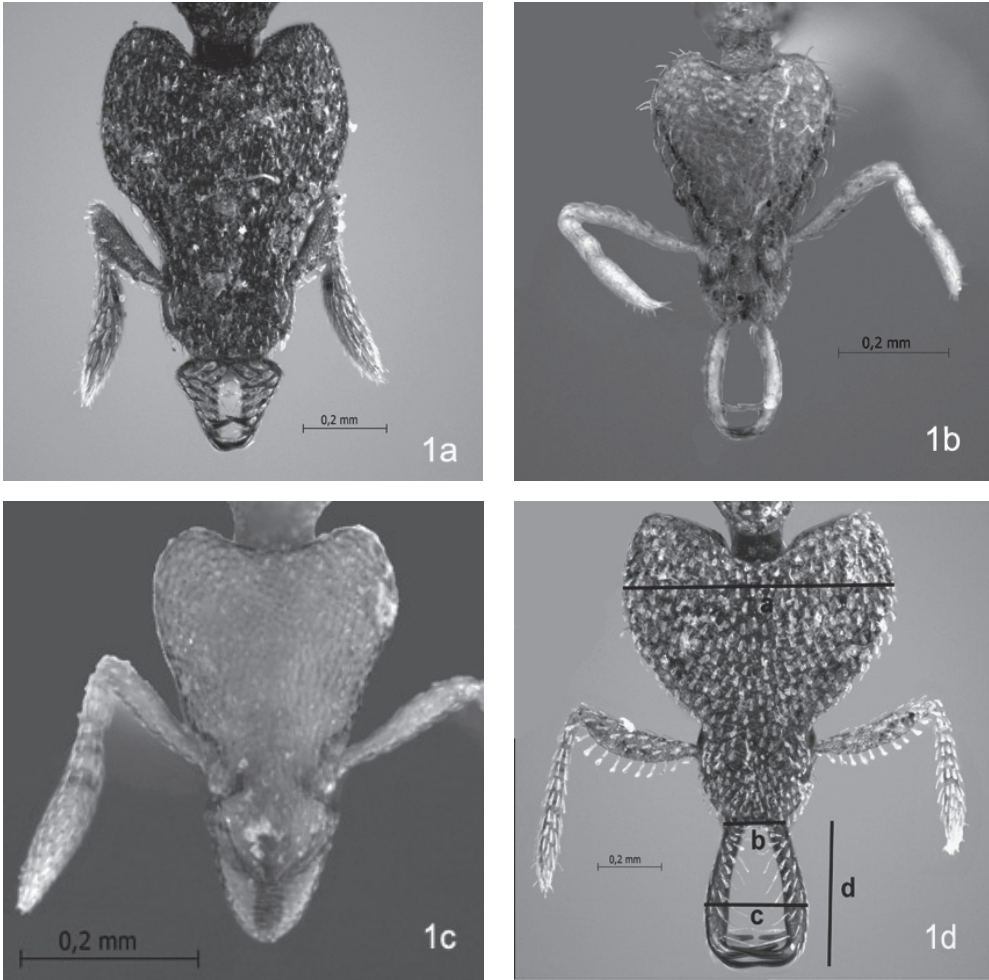
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FIG. 1a-d. Heads of four dacetine species showing the different form of the mandibles. a) *S. aechme,* b) *S. rofocala*, c) *P. mitis*, d) *S. rotogenys*. Fig. 1d includes the measurements of four morphometric properties: head width = a, mandible base width = b, maximum mandible width = c, mandible length = d.

This study was performed from 30 March to 8 April 2007 and from 7 August to 6 September 2007. We collected opportunistically nine nests of four dacetine species (Fig. 1a-d): one colony of *Strumigenys aechme* (9 worker ants), two nests of *S. rofocala* (11 and 13 worker ants), five colonies of *S. rotogenys* (10 worker ants in each colony), and one nest of *Pyramica mitis* (27 worker ants). The *P. mitis* colony shared their nest with *S. rotogenys* (Mezger & Pfeiffer 2008). All ant nests were transferred to small terrariums with a floor of plaster of Paris to keep a constant moisture level. Since the ant colonies refused all kinds of offered food, we conducted all experiments soon after nest collection. Experiments were carried out outside the lab under a shady roof to keep the ants in their natural climate regime. To measure their walking speed, we put the ants individually on a piece of white paper. Without disturbing the ant we marked its position with a pencil every five seconds. When the ant stopped or reached the edge of the paper, the run was stopped. Every ant individual was tested for ten to fifteen runs. Each run took 45 to 90 seconds. For statistical analyses we used the mean of all runs of a particular individual.

We used data on occurrences in leaf litter or topsoil of the studied dacetine species from a species diversity study conducted with the Winkler method in the alluvial forest of Mulu NP, where we established two transects with 10- and 20-m² samples, respectively (Mezger & Pfeiffer, in prep.). From all captured species we collected samples for analysis of stable N isotopes in order to assess their trophic position. These specimens were killed in ethanol and dried in an electric drying apparatus at 30°C before they were preserved in pure NaCl. The analyses were done at the Centre for Stable Isotope Research and Analysis at the University of Göttingen with an isotope mass spectrometrometer (Delta Plus with Conflo III interface, Finnigan MAT) and an NA1110 element analyzer (CE -Instruments). As unit we give the relative value (delta-value) between the 15N content of the reference (atmospheric nitrogen) and the $_{15}$N content of the respective sample (Fiedler *et al.* 2007). A detailed description of this method will be published elsewhere (Mezger, Dyckmans and Pfeiffer, in prep.).

Voucher specimens of all colonies are kept at the "Antbase.net Collection" at the University of Ulm (ABNC), with Automontage© photographs of the four species being available via http://www.antbase.net. Species were identified using Bolton (2000). For identification and measurement we used a Leica MZ16 stereo microscope with magnification up to 115x with a calibrated micrometer. We measured five morphometric properties of each studied ant

species to compare their morphology. For each species ten individuals were measured. All measurements of the head were recorded in full face view (Fig. 1d). We measured mandible length from the base to the outer top of mandibles. Mandible width was recorded in two ways, in both cases from the outer edges: 1) we measured the width at the base of the mandibles, and 2) we measured the widest distance of both mandibles. In the case of *P. mitis* with triangular mandibles the base was taken as the widest point and both measurements were identical. Head width was measured at the broadest point behind the eyes. For tibia length, we measured the tibia of one of the middle legs. All statistical analyses were calculated with STATISTICA 6.

RESULTS

All nests of the three species *S. rofocala*, *S. rotogenys*, and *P. mitis* were found in soil attached to small saplings about 10 cm above the ground, while we collected *S. aechme* from a nest inside a small piece of dead wood lying on the ground. In the Winkler samples, specimens of *S. rofocala* (n = 805) were found significantly more often in the leaf litter (n = 537) than in the topsoil (n = 268) (Chi² = 89.89, p < 0.0001). Sixty-four individuals of *P. mitis* were collected; this species was significantly more common in the topsoil (41 individuals) than in the leaf litter (23 individuals) (Chi² = 5.06, p < 0.03). *S. rotogenys* (n = 3) and *S. aechme* (n = 1) were found in small

TABLE 1. Morphometric and ecological properties of four dacetine species (n = 4 x 10 individuals). Measurements are given in μm (SD in parentheses), stable nitrogen content is given as delta-value, the difference between the content of $_{15}$N in atmospheric nitrogen and the $_{15}$N of the respective sample. For the five morphometric properties we calculated ANOVAs (Kruskal-Wallis ANOVA, *Chi² = 23.3, **Chi² = 40.0, p < 0.0001, H post hoc test). Different letters behind the values indicate significant differences between the respective characters. $_1$) = isotope value of these species differs significantly (U-test: U = 5.0, p < 0.03).

Dacetine-Species	*S. rofocala*	*S. aechme*	*S. rotogenys*	*P. mitis*
Mandible length*	22.9 (± 1.10) [abc]	22.8 (± 2.28) [abd]	50.7 (± 3.56) [ac]	16.6 (±0.84) [bcd]
Mandible base width**	10.0 (± 1.05) [a]	19.8 (± 2.04) [b]	24.6 (± 3.89) [b]	13.8 (± 0.79) [a]
Mandible width (maximum)**	14.7 (± 0.95) [ad]	25.0 (± 2.11) [abc]	31.3 (± 2.21) [bc]	13.8 (±0.79) [ad]
Head width**	35.8 (± 1.32) [abd]	57.3 (± 2.16) [abc]	94.9 (± 2.56) [bc]	26.9 (± 1.66) [ad]
Tibia length**	28.8 (± 0.42) [abd]	26.1 (± 1.29) [abc]	37.3 (± 0.78) [bc]	16.4 (± 0.84) [ad]
Foraging strata	litter / soil	litter	litter	soil
Isotope value	7,13 [1]	4,26	5,59 [1]	5,21
Mandible shape	small and long	diamond shaped	large and long	triangular
Nest habitat	soil at saplings	dead wood	soil at saplings	soil at saplings

TABLE 2. Factor loadings of five morphometric properties including the explained variance and fraction of total variance. This give the correlation of the respective variable with the factor. Almost all of the variance is explained by the first factor.

Morphometric property	Factor 1	Factor 2
Mandible length	-0,934	0,301
Mandible base width	-0,897	-0,410
Mandible width (maximum)	-0,965	-0,140
Head width	-0,992	0,086
Tibia length	-0,980	0,140
Explained variance	4,553	0,306
Fraction of total variance	0,911	0,061

individual numbers and restricted to leaf litter samples.

The three *Strunigenys* species differed in respect of their stable isotope values: *Strumigenys aechme* had a mean delta-value of 4.26 ‰ $_{15}$N (n = 3, SD ± 0.59), *S. rotogenys* had a mean delta-value of 5.59 ‰ $_{15}$N (n = 7, SD ± 0.34), and for *S. rofocala* we found a mean delta-value of 7.13 ‰ $_{15}$N (n = 7, SD ± 1.51), though due to the small sample size only the difference between *S. rotogenys* and *S. rofocala* was significant (U-test: U = 5.0, p < 0.03). For *P. mitis* we only tested a single colony and recorded a delta-value of 5.21 ‰ $_{15}$N, similar to that recorded for its parabiotic partner *S. rotogenys*.

The five morphometric measurements mandible length, mandible base width, maximum mandible width, head width, and tibia length (see Table 1 for an overview of all data) differed significantly between the four species (Kruskal-Wallis ANOVA, p < 0.0001). We calculated a PCA with two axes derived from these measurements (Table 2). Factor values for each of the two axes differed significantly between the four species (Kruskal-Wallis ANOVA first axis: $H_{3,40}$ = 36.16, p < 0.0001; second axis $H_{3,40}$ = 28,23, p < 0.0001; all species differed among each other, according to the H post hoc test) (Fig. 2).

Walking speed of the ant species differed significantly (ANOVA $F_{3,106}$ = 47.6, p < 0.0001, HSD-test, Fig. 3), with *S. rufocala* running more quickly
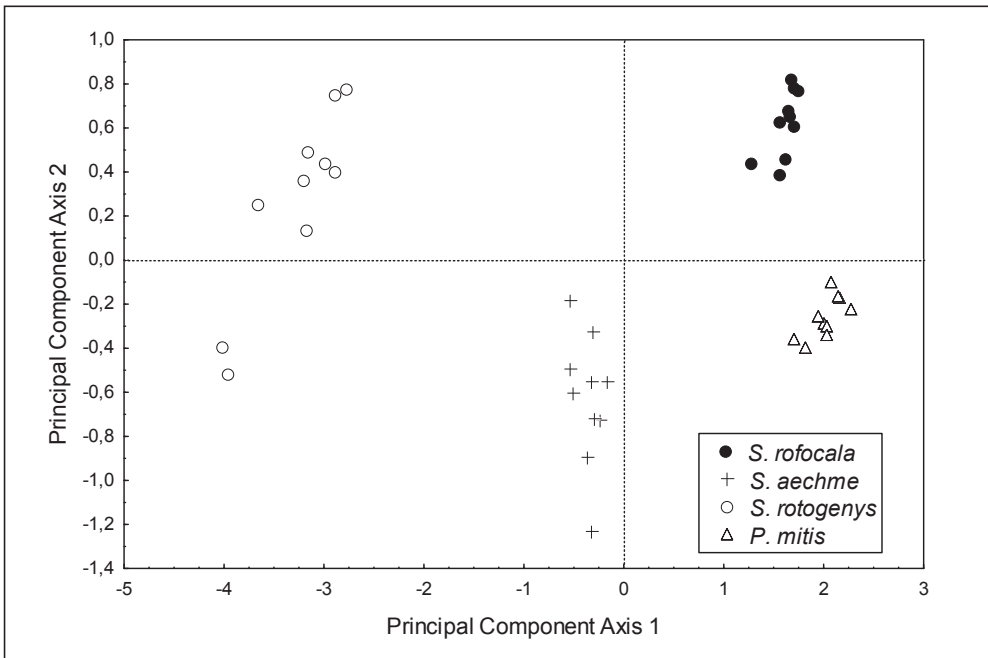

FIG. 2. Principal component analysis (PCA) of the five morphometric properties of four dacetine species (three *Strumigenys* species: *S. aechme*, *S. rofocala*, and *S. rotogenys* and one *Pyramica* species: *P. mitis*). For each species we plotted ten individuals in the reduced space of the first two principal components.
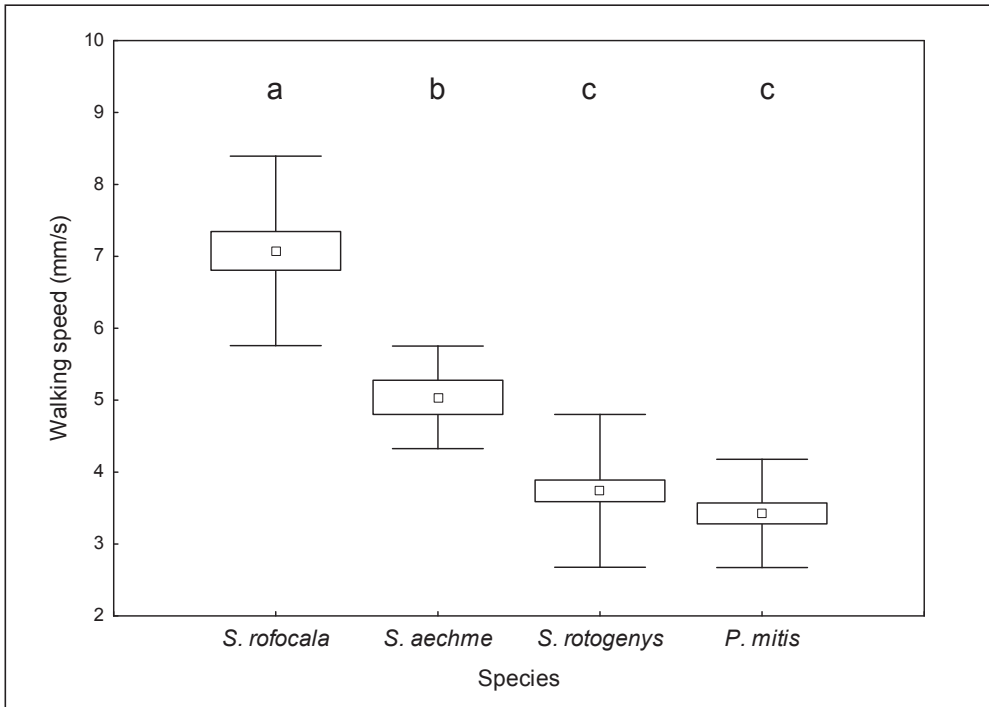
FIG. 3. Walking speed of four dacetine species (three *Strumigenys* species: *S. aechme*, *S. rofocala*, and *S. rotogenys* and one *Pyramica* species: *P. mitis*). Significant differences are marked with letters (ANOVA $F_{3,36}$ = 482.9, p < 0.0001, HSD post hoc test).

than *S. aechme*, while the parabiotic species *S. rotogenys* and *P. mictis* had a lower walking speed. There was no correlation between walking speed and tibia length (Spearman R = 0.19, p = 0.22).

DISCUSSION

Our results show that the three tested *Strumigenys* species differed in walking speed and/or morphometric properties, both pointing to a niche differentiation among the species of this genus. These findings were corroborated by differences in the stable isotope signatures of these sympatric species, which indicated their distinct trophic positions (Fiedler *et al*. 2007).

In contrast, the parabiotic species *P. mitis* and *S. rotogenys* had similar isotope values, which may be an indication of a cleptobiotic or parasitic relationship between these nest-sharing species. On the other hand, these species differed in their morphological values, as well as in shape and dentition of the mandibles. These differing morphological traits could be

an adaptation to the preferred foraging strata of both species, since dense subterranean habitats require different abilities of moving and prey capture than fairly open leaf litter layers: *S. rotogenys* with its trap-jaw mandibles and long legs preferred leaf litter, while *P. mitis* with triangular mandibles and the shortest measured tibia length was more common in the soil.

There might be some tendency of the *Strumigenys* species to prefer the leaf litter layer as a foraging area, as large trap-jaw mandibles might be more useful for hunting inside the litter layer than in the soil. *Pyramica* species, on the other hand, seem to be subterranean hunters, e.g. Masuko (1984) showed in his experiments that *Pyramica hexamera*, a soil-living species, is an unsuccessful hunter on the surface, but is effective in hunting diplurans and centipedes in endogeic foraging areas. However, not only foraging habitat but also hunting strategies vary among certain dacetine species: contrary to many *Strumigenys* species like *S. solifrontis*, which slowly approach their prey (Masuko 1984), *Pyramica* species like *P. bentens*

are ambush predators that hide in soil particles and arthropod excrements and wait for their collembolan prey (Masuko 2009).

Wilson (1953) put forward the hypothesis that although many dacetines in North America are ecologically similar, species sympatry is maintained due to their low population densities. In the alluvial forest of Borneo we extracted soil and leaf litter with the Winkler method and found on one square meter of ground a mean of 34 individuals of two or three dacetine species, and a maximum 210 individuals of five species (Mezger & Pfeiffer, unpubl. results). These numbers demonstrate the high diversity and abundance of dacetine ants compared with other common ant genera like *Pheidole* or *Tetramorium*, which respectively reached mean densities of 23 specimens and 13 specimens per m² (Mezger & Pfeiffer, unpubl. results). Therefore dacetine ants have a high density in tropical forests, and even if many individuals of a colony stay in their nest it can be assumed that there are regular (direct and indirect) interactions among the foragers of different species, so they might influence each other, even at high prey densities. So Wilson's (1953) hypothesis might be a less useful one when applied to species-rich tropical communities.

Quantitative direct observations of the hunting behavior of all species would provide the best data for an assessment of trophic niche differentiation. But when we tested the four dacetine species for their food preferences in cafeteria experiments by offering different species of soil arthropods, including collembolans and mites (see Wilson [2005] for details), all species refused every type of food in captivity and collected not a single potential prey organism. These tests, which were conducted over a period of two days, checking for hunting activity night and day (Mezger, own observations), were therefore not included in our paper. Likewise, Masuko (1984) reported that some dacetine species did not show their natural feeding behavior in artificial foraging arenas.

Additional to these feeding experiments we dissected all nests for prey or prey remains, but only in one colony of *S. rotogenys* did we find a single worker ant carrying a medium-sized collembolan. Wilson (1953) reported that many of the species that he observed preferred a similar kind of prey: entomobryoid and symphypleonan Collembola. These groups of bristletails seem to be an important type of prey for Asian dacetine species too. Masuko (2009) reports that *Pyramica benten* prefers Entomobryidae as prey

and that this species is more effective in hunting bristletails of this family than other collembolan families. Three *Strumigenys* species from Japan, with long and slender mandibles, are reported to accept a larger prey spectrum than *Pyramica* species, e.g. *P. canina*, which has short, triangular mandibles (Masuko 1984).

Although an analyses of many more dacetine species with more traits would be necessary for a complete confirmation of the hypothesis that the coexistence of tropical dacetine ants in their habitat is due to their differing niche requirements rather than to low species competition, our results showed that the three *Strumigenys* species tested differed in the traits speed, morphological characteristics, and isotope value. The *Pyramica* species differed from these species in morphology and preferred foraging stratum, though it shared some traits with its parabiotica partner. Although we present results for only four species of these species-rich genera, our results are very valuable given the difficulty of gathering information about these cryptic ants. More research will be necessary to uncover the niche differentiation of these species, so hopefully our results may stimulate further research on more dacetine species.

ACKNOWLEDGMENTS

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