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ECOLOGY AND NATURAL HISTORY OF MELANESIAN ANTS

Ph.D. Thesis

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Annotation.
The ecology of ant assemblages in New Guinea rainforest was studied with main focus on ground foraging and canopy fauna. Assemblage structure as well as interspecific interactions were investigated. Available data on species distribution of Melanesian ants were assembled and biogeogrpahical affinities of New Guinea fauna were assessed.

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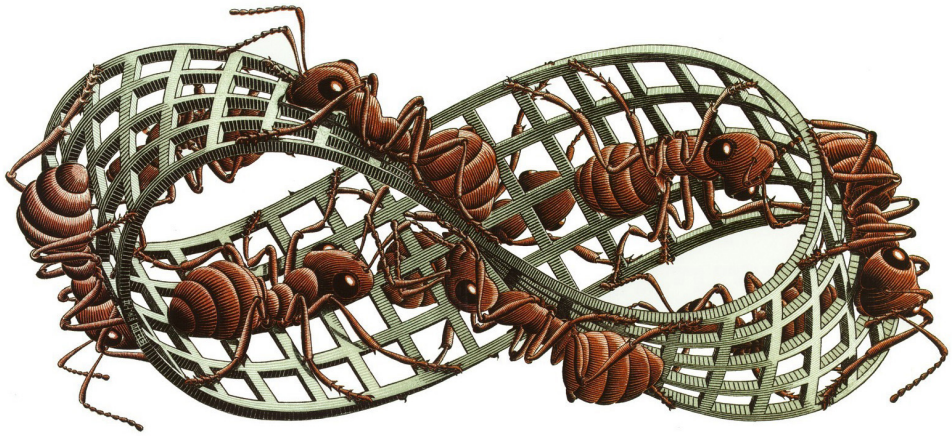

I hereby declare that I worked out this thesis on my own using the cited literature only.

29 September 2007 Milan Janda

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PODĚKOVÁNÍ / ACKNOWLEDGEMENTS

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'Get up at half-past five, bath, and coffee. Sit down to arrange and put away my insects of the day before, and set them in a safe place to dry. Breakfast at eight; out to the jungle at nine. Then we wander about in the delightful shade, along paths made by the Chinese wood cutters till two or three in the afternoon, generally returning with fifty or sixty beetles, some very rare or beautiful, and perhaps a few butterflies. Change clothes to sit down to kill and pin insects, Charles doing the flies, wasps and bugs; I do not trust him yet with beetles. Dinner at four, then at work again till six; coffee. Then read or talk, or if insects very numerous, work again till eight or nine. Then to bed.'

Alfred Russel Wallace - The Malay Archipelago (quotation from a letter written on May 28th, 1854).

INTRODUCTION / ÚVOD

Existuje řada důvodů, proč se zabývat biologií mravenců (Hymenoptera: Formicidae). Tento hmyz je přítomen ve většině terestrických ekosystémů, jedná se o nápadnou, druhově poměrně bohatou skupinu s rychlou reakcí na změny prostředí, většinou jde o predátory a oportunisty s velkým vlivem např. na tvorbu půdy, disperzi a predaci semen rostlin i na strukturu společenstev ostatních bezobratlých. Jsou vhodnými kandidáty pro monitorování změn způsobených změnou klimatu, fragmentací biotopu atd. (Agosti 2000). Je také známo, že mravenci dominují tropickým pralesům (Erwin 1982; Floren et al. 2002) a někde představují až 94% členovců v insekticidních vzorcích z korun tropických stromů, přičemž mohou tvořit až 86% biomasy těchto vzorků (Davidson et al. 2003).

Tato práce se zabývá různými aspekty ekologie a evoluce mravenců, se zaměřením na pralesní faunu Melanésie. Hlavními podklady jsou data a materiál shromážděný v průběhu dvou let terénního výzkumu na Nové Guineji. Předkládané rukopisy představují prvotní zpracování přibližně 20% z celkového objemu získaných dat. Hlavním cílem bylo vytvořit základní přehled o ekologii a biogeografii novoguinejské fauny, který bude sloužit jako východisko pro další studie.

Úvodní kapitola shrnuje současné znalosti o distribuci mravenců Austronéské oblasti a sleduje hlavní biogeografické trendy ve složení fauny Nové Guineje a okolí. Druhá kapitola se zabývá popisem společenstev mravenců v nížinném pralese Nové Guineje a je základním přehledem o druhovém složení a habitatových preferencích fauny v nižších patrech lesa. Hlavním cílem bylo zhodnotit základní charakteristiky místních společenstev a porovnat je se staršími studiemi melanéské fauny i s daty dostupnými z jiných tropických oblastí. Třetí kapitola popisuje krátkodobý výzkum fauny obývající koruny stromů v nížinném pralese, stratifikaci druhů a jejich pohybovou aktivitu. Čtvrtá kapitola se detailněji zabývá daty pocházejícími z vnadících pastí, které byly součástí pracovního protokolu popsaného kapitole II. V tomto případě bylo hlavním cílem zjistit pohybovou aktivitu mravenců v jednotlivých vrstvách lesa a zjistit mezidruhové interakce na potravních zdrojích. Na jejich základě pak zhodnotit roli „dominantních“ druhů ve společenstvu, zejména jejich eventuální vliv na aktivitu ostatních druhů. Detailněji jsou také diskutovány podobnosti s životními strategiemi mravenců JV Asie, Austrálie i Neotropické oblasti.

Naše práce se dotýká několika aktuálních témat výzkumu mravenců. Jedná se především a teorie komplementární distribuce dominantních druhů (teorie mozaiky, (Leston 1973) a efektu těchto dominant na druhovou bohatost okolní fauny (kapitola IV). Další tématem je také vyhodnocení predačního vlivu mravenců na ostatní hmyz obývající zejména tropické lesy, které úzce navazuje na dosavadní výzkum herbivorního hmyzu (Novotny et al. 1999; Novotny et al. 2002a; Novotny et al. 2002b). Většina studií zabývajících se experimentálně predací hmyzu (Dyer 2002; Olson 1991; Floren et al. 2002) považuje mravence za klíčové predátory, zásadně ovlivňující složení hmyzích společenstev v tropech. Nedávné studie však naznačují (Davidson et al. 2003), že potravu mnohých arboreálních druhů tvoří především cukerné složky pocházející z pěstovaných trofobiontů (např. Coccoidea). Znalost složení arboreální fauny, jejich prostorové aktivity, abundance a trofické pozice jsou tak důležitými faktory pro odhad aktuální míry

predace ostatního hmyzu. Prvotním krokem takového postupu je i zjištění lokálních dominant (behaviorálních i numerických) a jejich aktivity, např. za použití vnadících pastí jak je ukázáno v kapitolách III a IV. Budoucí rozšíření těchto informací o izotopická data ze studovaných lokalit pak následně umožní poměrně přesný dohad aktuální predační zátěže.

Kapitoly II.-IV. představují několik různých metodologických přístupů ke studiu ekologie společenstev mravenců, zatímco kapitola I. je historicko-geografickým náhledem na melanéskou faunu, za použití základních fylogenetických metod. Tyto tématicky jednotné práce doplňuje příloha ve formě publikovaného článku zabývajícím se evolucí sociálního parazitizmu u mravenců. I když jde o výsledek především z předcházející magisterské práce, tato studie představuje aplikaci fylogenetických metod při interpretaci ekologie a životních strategií mravenců, a je doplněním metodologických přístupů představených v předchozích kapitolách. Další studie zabývající se ekologií tropického hmyzu a volně navazující na předkládanou práci jsou uvedeny v seznamu publikací.

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Part I.

Biogeography of New Guinea ants: a first overview

(Milan Janda & Marek L. Borowiec; mns.)

BIOGEOGRAPHY OF NEW GUINEA ANTS: A FIRST OVERVIEW.

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INTRODUCTION

Ant diversity in New Guinea has been estimated to be among the highest in the world (Snelling 1998; Wilson 1959). At the same time, the local ant fauna is still poorly known. Over 500 ant species have been reported from the whole island, representing an interesting combination of Australian and Southeast Asian taxa (Bolton 1995). The first accounts on Melanesian ants were published as early as the 1860's (Smith1860, 1865), when the first species were described from A. R. Wallace's collections. Among the first people to devote their efforts to describing Melanesian ant taxa were C. Emery in the late 19th century and H. Donisthorpe in the 1930's. Further important contributions were made by W.L. Brown (in the 1950's) and R.W. Taylor (1960-1980's), both of whom published numerous revisions and new descriptions of Melanesian ant taxa. Among the most significant contributors to our knowledge of New Guinean ant fauna is E.O. Wilson. On the basis of his field work in the 1950s, he managed to outline the basic characteristics of Melanesian ant communities, as well as to collect new species and revise the classification of several known taxa. However, despite these efforts, a large proportion of New Guinean ants is still in desperate need of further taxonomic and ecological studies. For most of the species, there is barely any information, except for the original description, not to mention any information about the ecology of species or whole assemblages. Limited surveys carried out within the past few years (e.g. Snelling 1998) confirmed that the New Guinean ant fauna is extraordinarily rich; it has been estimated that about 15 to 20% of local ant species may remain unknown by science (Snelling 1998).

The Melanesian ant fauna has been usually described as an intersection of Oriental and Australian elements with an exceptionally high proportion of endemic species (Wilson 1959; 1961). However, any detailed assessment of the contribution of both biogeographical regions to

the composition of New Guinea fauna is still missing. Here, we provide a brief overview of the biogeographic patterns for Melanesia and surrounding regions, based on available data. We further provide an updated species list for New Guinea and adjacent islands and discuss the generic affinities of the ant fauna to the Oriental and Austronesian regions.

METHODS

Geological History

The west Malay Archipelago and most of Southeast Asia formed from fragments which broke off from Australia and drifted northwards, colliding with the Eurasian plate. This process started in the early Paleozoic (c. 400Ma), which means that most of Southeast Asia, although of Australian origin, had already been in its present position before many recent plant and animal taxa evolved (Turner et al 2001). Consequently, most plants and animals occurring in West Malaysia are considered to be predominantly of Southeast Asian origin. However, their history may still reflect part of the geological history of this region, as many microplates remained separate for a long time, or other barriers persisted. Moreover, large parts of Southeast Asia and West Malaysia were submerged several times, e. g. in the late Eocene (c. 40Ma) as well as during recent interglacial periods.

New Guinea island has quite a complicated geological history. The southern part (up to the central cordillera) has always been attached to Australia (at least until 15Ma ago), while the northern part is an amalgamation of more than 30 terrenes of various origin, including island arcs, pieces broken off from Australian or the New Guinean continents and also parts of trapped sea floor (Turner et al. 2001). Comprehensive reviews of the geological history of the region can be found in de Boer (1995) and reference therein). A pictorial summary for the last 50 Ma was developed by Hall (1995) and can be found at: http://www.gl.rhul.ac.uk/searg/index.html. These two sources were used for relating the area-cladograms resulting from our analyses with the geological history of Southeast Asia and Austronesia.

Biogeographic analyses

We assembled distribution data for all ant genera available to date for the Oriental and Austronesian regions from literature, public databases and museum collections (http://stri.discoverlife.org/mp/20q?search=Formicidae;www.antweb.net; http://anic.ento.csiro.au /entomid-png/; www.entu.cas.cz/png/ants; Ant collections in Museum of Comparative Zoology, Harvard Univ., and in Bolton et al. 2006). Because of the general lack of information about the distribution of individual species from many of the target regions, we focused mainly on the generic level, for which approximate distributions are better known. Detailed knowledge about the ant fauna of Southeast Asia is mostly missing, as many areas are yet unexplored and only morphospecies lists are produced by most ecological studies (including this one), which cannot be cross-referenced between sites and regions. Research effort is highly unequal across Southeast Asia and most of the regions are undersampled. Therefore, any conclusions based on the comparison of species lists in this study should be taken with caution.

We established unit areas on the basis of geological information (Hall 2002), previous biogeographic studies of the region (Boer and Duffels 1996; Heads 2001; Turner et al. 2001; Welzen et al. 2001) and the distributions of taxa included in our analyses. The unit areas (referred to also as 'areas of endemism') may be characterized by the occurrence of one or more endemic taxa (although not necessarily at the generic level). Although many areas could be divided more finely according to their geological history, this would lead to a large amount of missing information, because many taxa are known from only a limited number of collections. Therefore, we grouped several small areas together, despite their different geological origin (e.g. Sulawesi). The majority of areas are identical with those established by Turner et al (2001), defined on the basis of the distribution of a wide range of animal and plant taxa throughout Southeast Asia. In this study, we use the terms 'unit areas' or 'areas of endemism' rather for the biotas of particular areas than for the geological areas themselves. Twenty five such unit areas were established throughout Southeast Asia and Austronesia. Additional data from three neighboring biogeographical regions (Afrotropical, Palearctic, India) were included, creating a matrix of 28 geographical units by 136 genera. The list of unit areas used in this study and their geographic delimitations are summarized in Appendix 1 and Figure 2.

Distributions of individual genera were assessed and divided into 22 categories to describe the actual faunal composition of the unit areas and for assessing the contribution of different biogeographical areas to local fauna (Appendix 1, second column). These categories combined previously established unit areas into traditionally recognized biogeographical regions. On the basis of this assessment, some genera were also qualified as 'widespread' (occurring in at least four large biogeographical regions), or 'endemic' for a particular area.

Genera with the centre of distribution in a particular area, but marginally extending to another area, were assigned to their main area of distribution only. For example, the genera *Leptomyrmex* and *Rhytidoponera* are represented in the Philippines by few species, although they occur predominantly within Austronesia, with the centre of their diversity in Australia and New Guinea. These two genera were therefore considered as 'Austronesian+New Guinean' taxa in our analyses (Appendix 1) and their occurrence in the Phillipines and Sulawesi is considered as an Austronesian element extending into the Oriental region. Species extending further within the Malay archipelago, and up to Malay peninsula, would be classified as "Oriental+Austronesian" (e.g. genus *Echinopla*, Appendix 1).

The distribution matrix of 136 ant genera and 28 unit areas was used as input data for parsimony analysis of endemicity (PAE), a method of cladistic biogeography which classifies areas by their shared taxa (Rosen 1978). After the addition of 38 characters describing the relationship among the study genera, primary Brooks Parsimony Analysis (BPA) was performed. BPA uses standard parsimony analysis to construct a cladogram of the areas on the basis of the occurrences of species and their reconstructed ancestors (Brooks 1990). The data were coded using assumption A0 (general patterns have vicariant events as their common cause; Zandee & Ross 1987). A taxon was coded by '1' when present in a particular area, its absence by '0' and '?' if data on its distribution were unknown. Relationships among ant genera were derived from recent studies of ant phylogeny based on molecular data (Brady et al. 2006). Few biogeogroaphical units were excluded form analyses because of incomplete data (e.g. Vanuatu).

Data matrices were analyzed in the program NONA (Goloboff 1997), through the environment of the program Winclada (Nixon 2000). For a search algorithm, we used parameters: 'hold/100000; mult*100; max*; (with TBR branch swapping). Bootstrap support values were calculated on the basis of 1000 replications.

Both methods have received some criticism in the past and especially the applicability of PAE is known to be questionable (for review of objections see e.g. VanVeller et al. 2002). However, despite their limitations, both methods are useful for a primary assessment of biogeographic processes within a target area. We did not aim to produce a detailed analysis in this study, but rather to describe basic biogeographical patterns of ant taxa and compare them with results from other animal and plant groups from the Oriental and Austronesian regions, using comparable methods. Although the use of higher taxonomic units in cladistic biogeography analyses may be questionable, only generic distribution data represents a relatively complete, available dataset for Asian ants.

RESULTS AND DISCUSSION

Biogeographical affinities

On the basis of published literature, database records, museum collections and our own field data, we assembled a species list of the ants of New Guinea (including the Bismarck Archipelago) with 741 species from 86 genera and nine subfamilies, whereas at least 559 species are known from New Guinea island itself. The check list is published and regularly updated at: http://stri.discoverlife.org/mp/ 20q? guide=Ants_New_Guinea; and (including source literature) at: www.entu.cas.cz/png/ants).

The species list assembled during this study contributed an additional 100+ species to the fauna of New Guinea, compared to previously published records in the Bolton catalogue (1995), and represents the most comprehensive list of New Guinean ant fauna to date. Comparison of species lists (however incomplete they are) suggests that New Guinea shares the highest proportion of its fauna with Australia, being 72 species. It also has at least 63 species in common with the Philippines, but much smaller species overlap with Sulawesi and Sumatra (Tab. 1).

Accurate species lists were not available for all areas. At least 545 species (74 %), but only one genus (*Ancyridris*) appear to be endemic to New Guinea and the Bismarck Archipelago. Approximate numbers of endemic species in other areas are summarized in Tab 3. The highest number of endemic genera (21) is found in Australia. Ten endemic genera are distributed across the whole Austronesian region (Tab. 2), while only six genera are endemic to the rest of the Oriental region (SE Asia mainland + SE Asia islands).

Tab. 1. Numbers of species shared among selected regions of Southeast Asia; total numbers of species in bold.

	N. Guinea	Philippines	Sulawesi	Sumatra
N. Guinea	**741**			
Philippines	63	**395**		
Sulawesi	7	21	**111**	
Sumatra	15	34	7	**260**
Australia	72	?	?	?

Tab 2. Numbers of endemic genera in different parts of the Oriental and Austronesian regions.

Region	**No. Gen.**
New Guinea	1
SE Asia islands	4
SE Asia mainland	2
Austronesia	10
Australia	21
SE Asia + India	2

Tab 3. Number of species reported for selected areas and the proportion of endemic species in the local fauna.

	New Guinea	Philippines	Sulawesi	Sumatra	Java	Thailand	Vietnam	N. Caledon.	India
Sp. recorded	741	395	111	260	298	248	142	92	546
% endemism	73.5	55.9	73.9	69.2	49.0	29.4	40.1	82.6	72.9

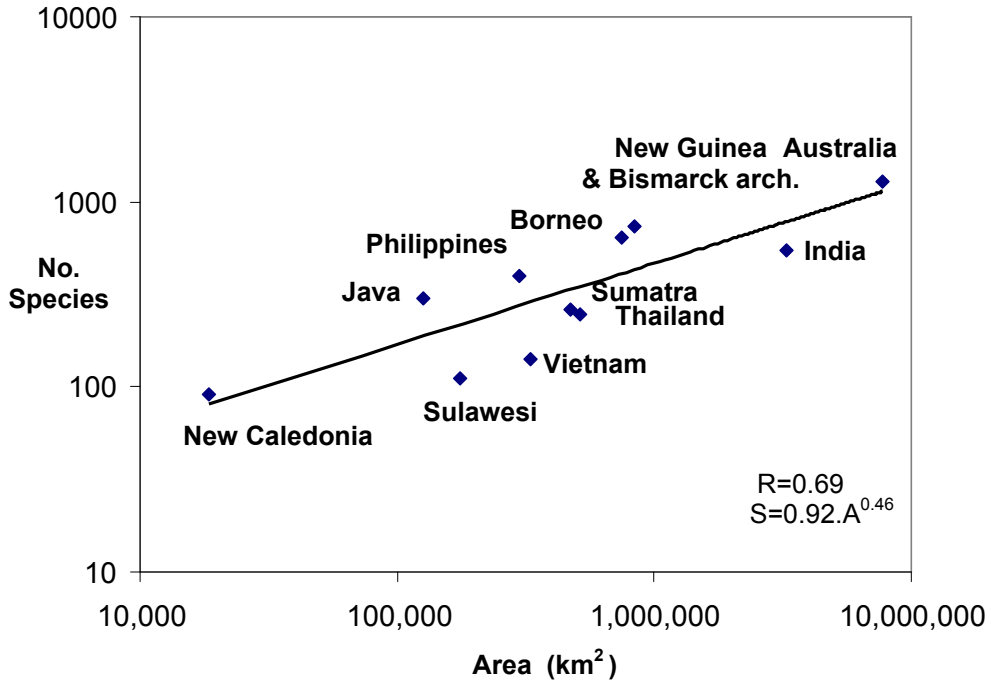


Fig. 1. Species-area relationship (logarithmic scale) for available species lists from the Oriental and Austronesian regions. Species lists are based on data published at: http://stri.discoverlife.org /mp/20q?search=Formicidae; www.antweb.net; http://anic.ento.csiro.au/entomid-png/; and in Bolton et al. 2006)

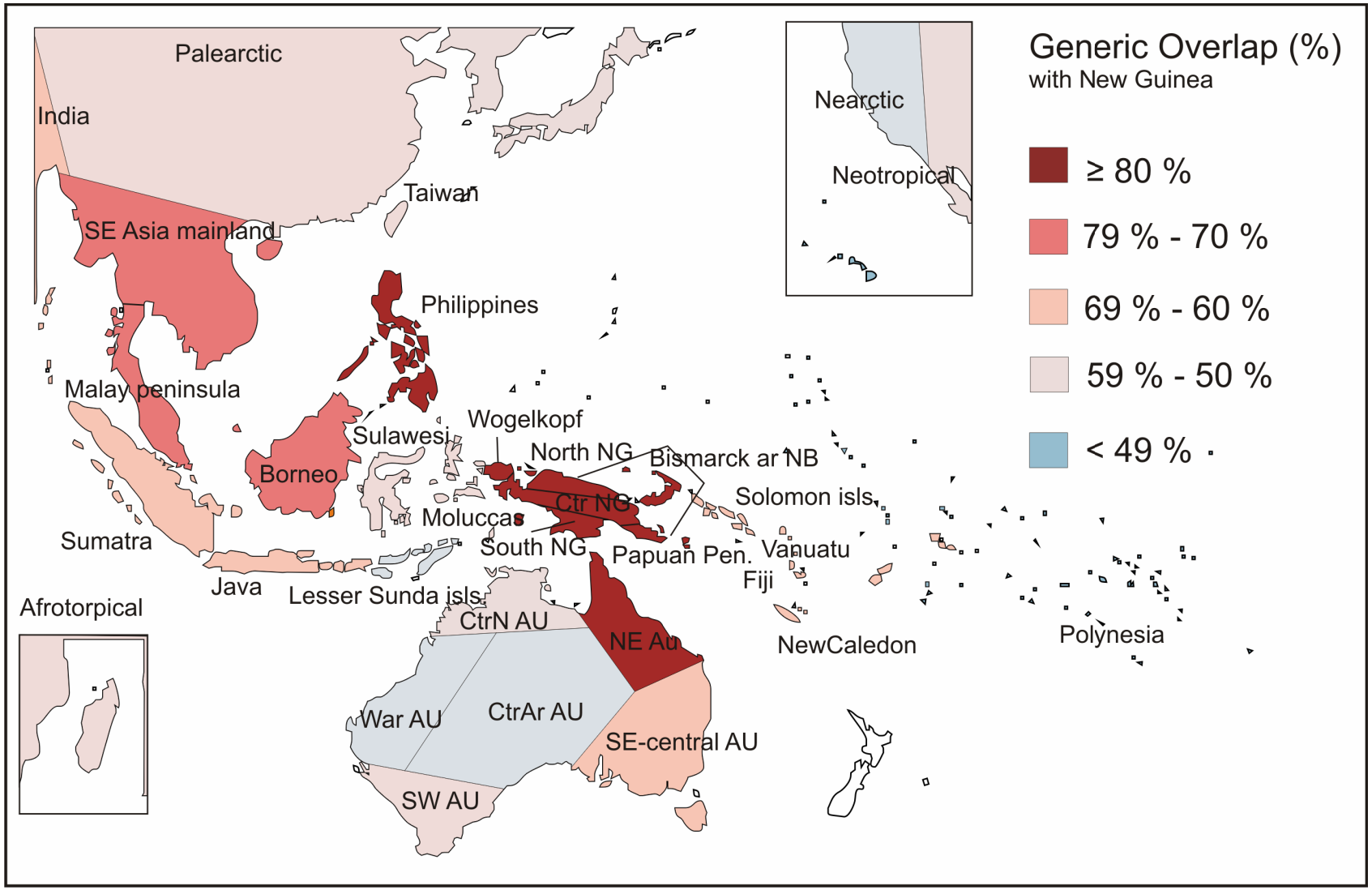
The species – area curve for the main areas of the Oriental and Austronesian regions is presented in Fig 1. The regression line has a slope of approximately $S= 0.9135.A^{0.4557}$ (R=0.69). The position of the New Guinea territory, above the curve of the species-area relationship (Fig. 1), suggests that it has a slightly more diverse fauna than comparable regions (100 spp more then Borneo). However, such a difference might well be a consequence of different sampling efforts and different 'habitat diversity' of individual regions (e.g. different size of islands and archipelagos allocated to the compared geographical units). If we would consider only the New Guinea mainland, without adjacent archipelagos including New Britain, then there are just 559 known species. Therefore, we can only declare that New Guinea has indeed a very rich ant fauna, although not exceptionally richer than comparable landmasses within Southeast Asia. The same can be said about the number of endemic species.

A basic comparison of species lists available for several areas suggest that the Philippines have a similar proportion of endemic species as New Guinea (73%). On the other hand, less than

50% of the local species pool may be endemic in Java. Comparison of absolute numbers of shared genera (Tab 4, Fig. 2) is of only limited applicability, as it reflects several patterns together, and is heavily influenced by the different size and character of the areas. Vanuatu and Polynesia overlap with New Guinea by only 21 or 33 genera respectively, while the Philippines by 69 genera. Consequently, the two oceanic areas may be considered as less similar (Fig 3). However, their genera completely overlap with New Guinea and may in this sense be considered more similar than the Philippines, which share 84% of its total genera.

New Guinea shares the highest number of its genera (77, 89%) with Australia, of which the majority (76) occur within tropical Northeast Australia. Many genera (73, 85%) are shared between New Guinea and the Southeast Asian islands (Borneo, Sumatra etc.), when their fauna are pooled together (Tab. 4 - SE Asia islands). When considering individual 'units' (areas of endemism), then the highest proportion of genera shared with New Guinea is found in the Philippines (69 species, 80%), the Southeast Asian mainland and Borneo (Tab 3, Fig 2). The genera occurring in New Guinea represent from 98 to 100% of the entire fauna in Polynesia, Fiji, Vanuatu and the Solomon Islands (Tab. 4).

Fig. 2. (following page) Delimitation of biogeographical areas of SE Asia and Austronesia and their generic overlap with New Guinea. Similarity is expressed by the percentage of genera which a particular area share with New Guinea. (Column 'C/NG' in Tab. 4.). Percentage similarity roughly corresponds with similarity based on Sorensen index (column 'S' in Tab. 4) which also considers actual size of fauna of compared area. Area delimitations and distribution data for the 136 genera used in this study are summarized in Appendix 1. Positions and delimitations of Afrotropical, Nearctic and Neotropical areas does not reflect their actual geographic positions and division used in analyses, but are included just for displaying the faunal similarity


Palearctic
India
Taiwan
SE Asia mainland
Philippines
Malay peninsula
Wogelkopf
Sulawesi
North NG
Bismarck ar
NB
Borneo
Ctr NG
Solomon isls
Moluccas
Sumatra
South NG
Papuan Pen.
Vanuatu
Fiji
Java
Lesser Sunda isls
CtrN AU
NE Au
NewCaledon
Polynesia
War AU
CtrAr AU
SE-central AU
SW AU
Afrotorpical
Nearctic
Neotropical
Generic Overlap (%)
with New Guinea
≥ 80 %
79 % - 70 %
69 % - 60 %
59 % - 50 %
< 49 %

Tab. 4 Generic overlap between New Guinea (including Bismarck Archipelago) and biogeographical areas of SE Asia and Austronesia. Similarity is based on species lists and expressed by the percentage of shared genera and Sorensen's index. Column 'C': numbers of genera which a particular area shares with New Guinea. Column 'C/NG': percentage which genera of a particular area are represented in the fauna of New Guinea (86 genera is 100%). Column 'B" represents number of genera known in a particular area and column 'C/B' shows the percentage of genera which share with New Guinea represents in local fauna of an area. 'S' shows similarity between both faunas based on the Sorensen index.

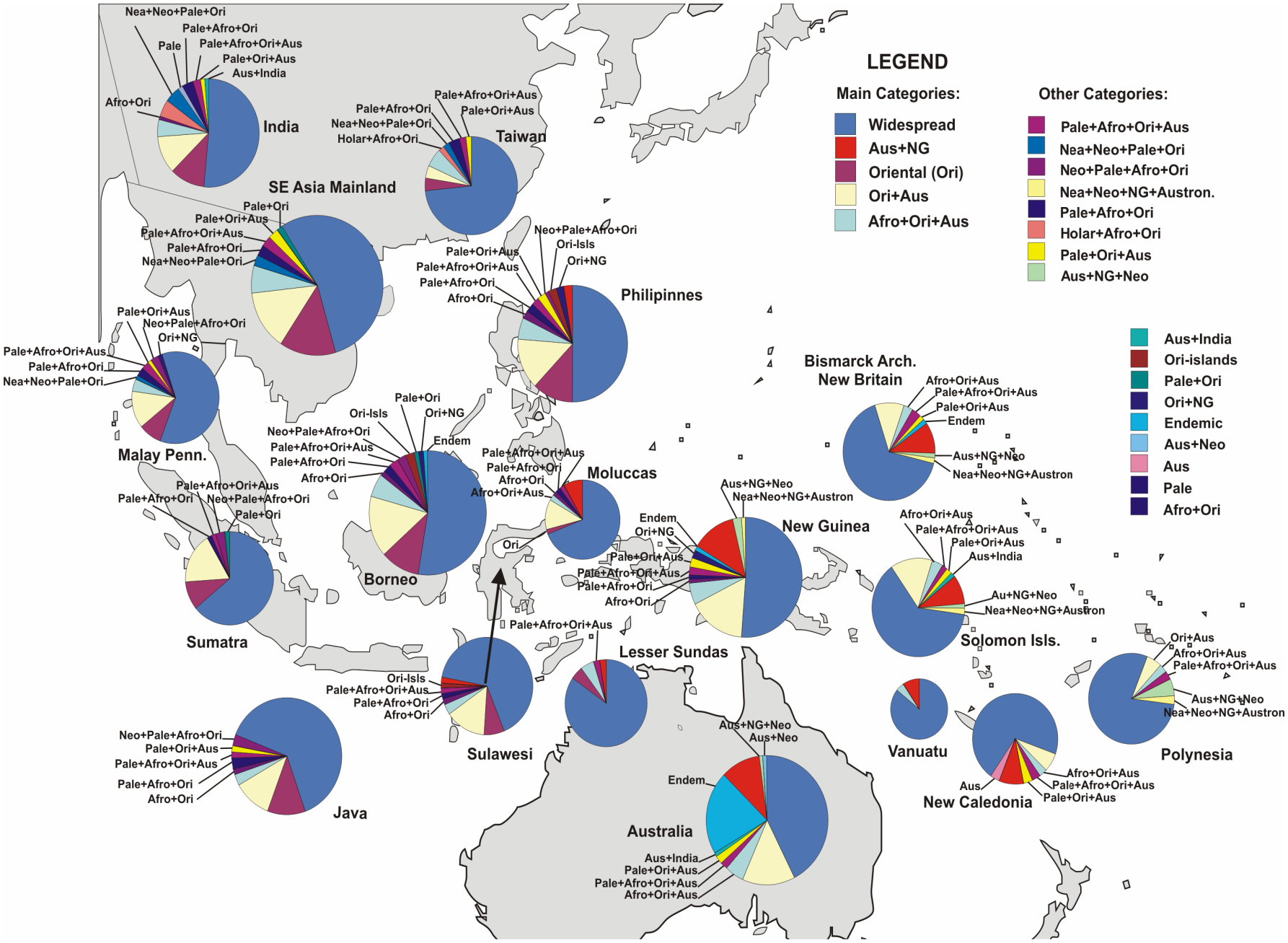
Area	C Genera shared with NG	C/NG % overlap with NG (86=100%)	B Genera occurring	C/B % shared genera	S Sorensen similarity
Austronesia	86	100	111	77	0.873
Australia complete	77	90	101	76	0.842
NE Australia	76	88	91	84	0.859
SE Asia islands	73	85	95	77	0.807
SE Asia islands + mainland	73	85	98	74	0.793
Philippines	69	80	84	82	0.812
SE Asia mainland	66	77	85	78	0.772
Borneo	64	74	82	78	0.762
Malay Peninsula	61	71	72	85	0.772
East Austronesia	60	70	62	97	0.811
SE-Central Australia	58	67	76	76	0.716
India	57	66	80	71	0.687
Sumatra	56	65	66	85	0.737
Solomon Islands	53	62	54	98	0.757
Java	52	60	63	83	0.698
Central North Australia	50	58	57	88	0.699
Sulawesi	49	57	55	89	0.695
Moluccas	46	53	48	96	0.687
SW Australia	45	52	57	79	0.629
Taiwan	44	51	49	90	0.652
Central-Arid Australia	40	47	48	83	0.597
Neotropical	38	44	46	83	0.561
Western Arid AU	37	43	46	80	0.561
Lesser Sunda Islands	37	43	39	95	0.592
Polynesia	33	38	33	100	0.555
Fiji	32	37	32	100	0.542
New Caledonia	30	35	31	97	0.513
Vanuatu	21	24	21	100	0.393

Generic composition of individual areas, illustrated in Fig. 3, shows that the highest proportion of genera (44) can be considered 'widespread', that is occurring in at least four (mostly five or six) main biogeographic regions. These genera represent a major component of the fauna in all areas, ranging from 50% (Philippines) to 86% (Vanuatu) of the local genera. Not surprisingly, these widespread genera are major contributors to the fauna of small oceanic islands (Taiwan, Fiji, Lesser Sunda & etc.).

Widespread genera are also an important element (51%) in the New Guinea fauna (Fig 3). Oriental + Austronesian and Australian + New Guinean genera represent 16% and 13% of the total fauna, respectively. The rest (15%) is mostly formed by genera with various combinations of Austronesian + Oriental and Afrotropical/Neotropical/Palearctic distribution. There are only two genera shared between the Oriental region and New Guinea which do not occur in Australia at the same time.

The group of Oriental + Austronesian genera is equally represented in all areas of the oriental region, contributing from 11% (India) to 18% (Sumatra) to the local fauna, but is completely missing from Vanuatu and Lesser Sunda Islands. Australia + New Guinea-based genera occur in the fauna of only three areas west of Weber's line, that is: the Philippines (2 genera) Sulawesi (1) and Lesser Sunda Islands (1). On the other hand, these genera represent a significant contribution to the fauna of the Solomon Islands, Vanuatu and New Caledonia. Alternatively, there is only one Oriental-based genus in the Moluccas, two in the Sunda Islands, and four at Sulawesi. A second major component of these areas (after the widespread genera) is Oriental-Austronesian genera, which reach their highest diversity in Australia, New Guinea and Borneo.

Fig. 3. (following page) Generic composition of major unit areas (and their combinations) displayed as contribution of different biogeographical regions to local fauna. Biogeographical affinities of genera are based on the centre of their distribution. Area delimitations and distribution data for the 136 genera used in this study are presented in Appendix 1. Five major biogeographic categories (widespread; AU+NG; Ori; Ori+Aus; Afro+Ori+Aus) are displayed without labels.


LEGEND
Main Categories:
Widespread
Aus+NG
Oriental (Ori)
Ori+Aus
Afro+Ori+Aus
Other Categories:
Pale+Afro+Ori+Aus
Nea+Neo+Pale+Ori
Neo+Pale+Afro+Ori
Nea+Neo+NG+Austron.
Pale+Afro+Ori
Holar+Afro+Ori
Pale+Ori+Aus
Aus+NG+Neo
Aus+India
Ori-islands
Pale+Ori
Ori+NG
Endemic
Aus+Neo
Aus
Pale
Afro+Ori
India
Taiwan
SE Asia Mainland
Philipinnes
Malay Penn.
Borneo
Sumatra
Moluccas
New Guinea
Bismarck Arch.
New Britain
Solomon Isls.
Lesser Sundas
Sulawesi
Java
Australia
Vanuatu
New Caledonia
Polynesia

There is an evident change in the faunal composition between the Austronesian and Oriental regions, which is detectable along both sides of the traditionally recognized borders (either in the form of Weber's or Wallace's line). The proportions of Australia + New Guinea-based and Oriental fauna switch between the Philippines and Sulawesi on one side and the Sunda Islands and the Moluccas on the other. Both groups contribute a maximum of 10% to the total pool of genera, while the major proportion of faunas are composed of widespread and Oriental + Austronesia taxa, whose change is not apparent along Weber's line. Subsequently, the generic similarity of the Moluccas and Sunda islands expressed by Sorensen's index (Tab. 4) is in overall more similar to Sulawesi and the Phillipines than to New Guinea.

The fact that island faunas are mostly recruiting from easily propagating taxa has been well described for many taxa (MacArthur and Wilson 1967), as well as for South Pacific ants. Wilson (1961) suggested that patterns observed in the distribution of Melanesian ants might be best explained in terms of a taxon cycle, with initial dispersal by marginal or ephemeral habitat species, followed by adaptation to more stable forest habitats with a loss of vagility (Holloway 1998). Consequently, many oceanic islands will be inhabited by lineages with high proportions of mobile, r-selected species, the pattern observed in this study (Fig. 3).

It should be stressed that biogeographical comparisons based mainly on presence/absence of genera may have limited applicability and can lead to biased conclusions. One of the main problems is that different levels of species diversity between study regions are not considered. Consequently, several areas sharing just a few expansive species of particular genera may be considered closely related, although these genera attain most of their species richness just within one or a few neighbouring regions (e.g. genera *Gnamptogenys* or *Opisthopsis* in this study). In addition, genus can be considered as a rather artificial taxonomic unit which does not disperse or speciate as whole. Therefore, implications arising from biogeographical analyses at the generic level should be interpreted with precaution.

Parsimony analyses

Parsimony Analysis of Endemicity resulted in 12 equally parsimonious trees (length=272, CI=0.47, RI=0.72), of which strict consensus is shown in Fig 4. Primary BPA resulted in 36 equally parsimonious trees (length=315, CI=0.47, RI=0.72), of which the unrooted strict consensus is plotted in the map of the region (Fig. 5). Addition of a zero outgroup to both matrices always changed the polarization of the resulting trees (with Polynesia being most basal), as well as doubling the number of cladograms. It also caused a less resolved topology of consensus in PAE analysis. Therefore, unrooted cladograms were used for displaying relationships among areas. A further advantage of unrooted area networks is that they can combine several biogeographically incompatible patterns and still provide a single or few area cladograms (van Welzen et al 2003).

Strict consensus of PAE trees contained three basic clades: i) Afrotropical; ii) New Guinea + Australia + Solomon islands + group of east pacific islands; iii) Palearctic and a clade containing all units of the Oriental region, but containing also monophyletic clade of Philippines, Lesser Sundas and the Moluccas (Fig. 4). All parts of New Guinea formed a monophyletic group with Northeast Australia as a sister clade and representing thus one area of endemism.

Topology of the consensus tree resulting from BPA differed primarily from PAE by lack of monophyly of the Oriental region. A majority of geographical units were arranged in a concatenated pattern and successively splitting from common ancestors (Fig 5). The Austronesian region consisted of three monophyletic clades, with the Solomon Islands splitting first. The second clade was formed by the monophyletic New Guinea subregions, while the third consisted of paraphyletic Australia with New Caledonia, Fiji and Polynesia as the terminal group.

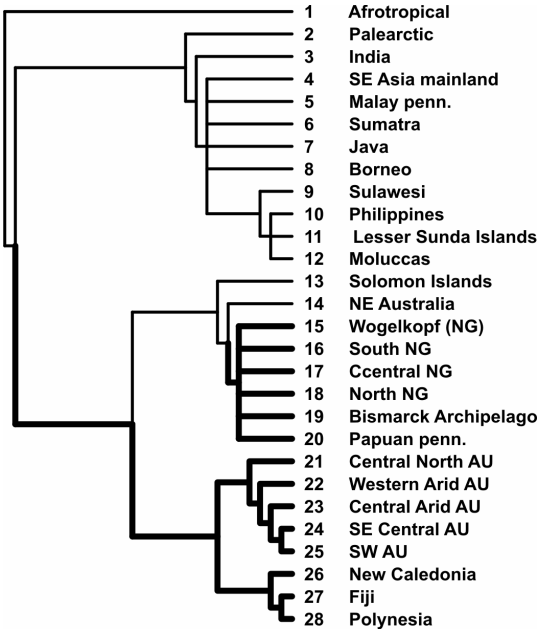


Fig. 4. Strict consensus of 12 equally parsimonious trees resulting from PAE analysis of distribution data of 136 genera. 28 biogeographical unit areas correspond with delimitations at Figs.2 & 5. Data matrix used for analysis is in Appendix 2.

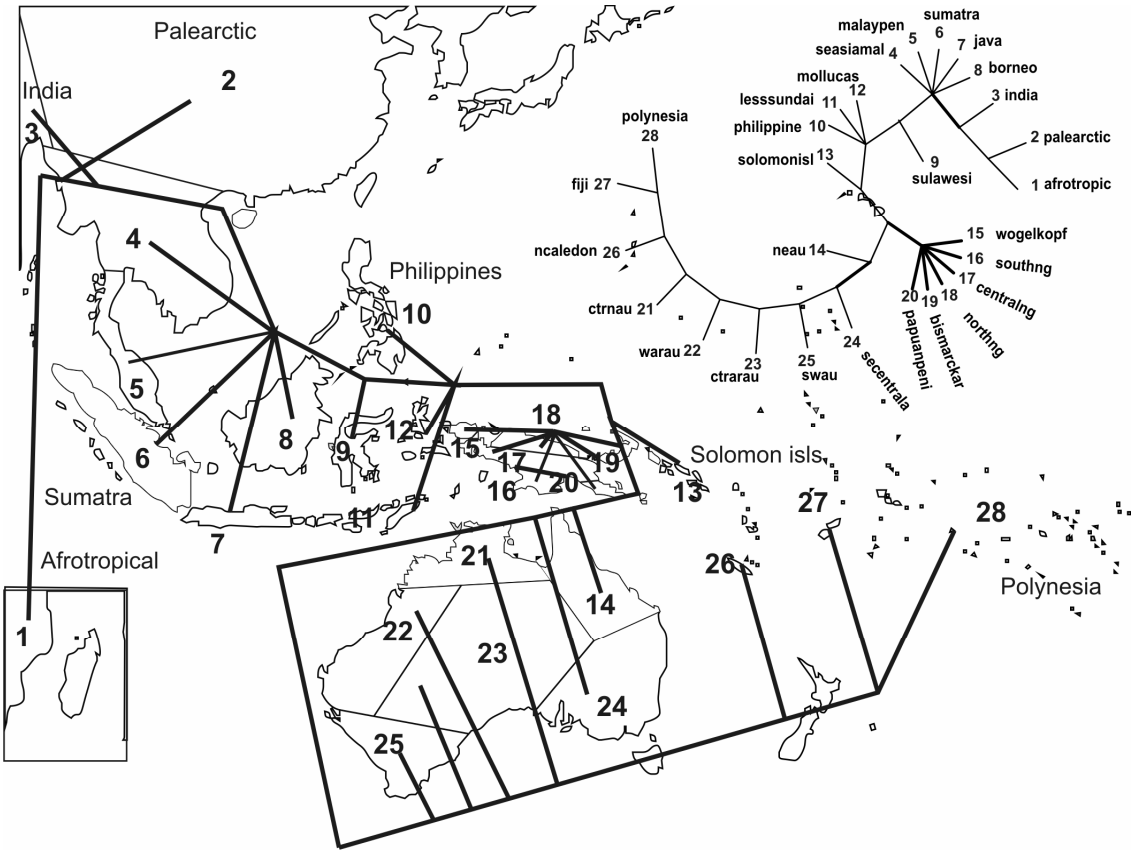


Fig. 5. Plot of unrooted area network resulting from BPA analysis onto a map of the region. Unrooted consensus tree of biogeographical units in upper right corner, branches in bold indicate bootstrap support over 50%.

Although the PAE resulted in a branching pattern seemingly reflecting the major historical division of the Oriental and Austronesian regions, the position of several terminals suggest that it reflects rather the overall faunal similarity of the unit areas (e.g. position of Northeast Australia as a sister clade of New Guinea, supported by 10 homoplasious characters). The positions of the Moluccas and Sunda Islands, which are nested deeply within the Oriental region, correspond with their higher faunal similarity to Sulawesi and the Philippines (Tab. 4), although they share many genera with New Guinea as well.

With several exceptions, the area network resulting from the BPA (Fig. 5) has close correspondence to the geographical distances and dispersal routes among the unit areas. However, there are some patterns congruent with geological history e.g. successive splitting of Sulawesi, the Moluccas, New Guinea and the Southeast Asian mainland is in good agreement with the geological area cladogram for the Outer Melanesian Arc presented by de Boer (1995; Fig. 50, p. 223).

The west-east division of Austronesia + Polynesia and Southeast Asia + Palaearctic in our tree can cross either along Weber's or Huxley's lines, but not across Wallace's line. Our BPA tree shows several patterns congruent with results presented by Turner et al (2001), which were based on the distributions of 29 monophyletic groups of animals and plants across Southeast Asia and Austronesia. The major differences are in the position of the Moluccas, which are integrated within the Southeast Asian islands in our study, and the positions of Fiji, Polynesia and New Caledonia, which are incorporated within successively splitting Australian regions. The overall pattern suggests (on the basis of character optimisation in the cladogram) that reconstructed relationships among areas are heavily influenced by taxa dispersing between the Austronesian and Oriental areas.

The close relationship between New Guinea and the Philippines (Fig 5), with high generic and species overlap, suggests either their common geological origin or the existence of a dispersal route. According to geological reconstructions, between 30 and 20My ago, central New Guinea and the Sepik arc were partly joined by a system of island arcs with fragments of the East Philippines and Sulawesi, which thus created a zone suitable for dispersal (de Boer 1995).

Distributional patterns of the ant genera occurring in New Guinea show that these are quite evenly distributed over the island, with no evidence of any limit in distribution within a particular geologically defined area. Such a pattern is indeed different from the distribution exhibited by some other Melanesian insects, such as Cicadas (de Boer 1995) or water striders

(Polhemus 1996). This may be a consequence of good dispersal qualities of many ant taxa. This means that it may be questionable to use ants for reconstructing the geographic history of regions.

Two major patterns are expected for the Malay archipelago and the West Pacific: clades that dispersed from east to west (e.g. from New Guinea to Southeast Asian mainland) and clades that dispersed in the opposite direction (Van Welzen at al. 2003). The peculiarity of the Southeast Asian region is that it consists of a more-or-less linear sequence of areas, rather than a reticulate pattern. Thus, in order to disperse e.g. from Thailand to Fiji, it is almost unavoidable to pass through the Malay Peninsula, Sumatra (or Java or Borneo), Sulawesi, the Moluccas, New Guinea and the Solomon islands (Turner et al 2001). Because the areas of endemism lie in a concatenated pattern, clades starting in different areas will display the same pattern, if the area cladogram is unrooted.

Whether our results can by interpreted as a representation of historical relationships, in the sense of geological origin, is questionable. The usual interpretation of vicariant patterns in BPA analysis is that they indicate a former union of areas, and when an area cladogram is supported by non-homoplasious synapomorphies, a common geological origin is assumed (Van Welzen et al 2003). Several studies suggest that such a pattern may not hold for Southeast Asia (e.g. Holloway and Ross 1998). In light of geological history, it is very unlikely that all areas of Southeast Asia and the West Pacific were united and formed a single ancestral area. Therefore, most of the vicariance relationships shown in Fig. 5 (BPA) should be explained rather by dispersal in combination with pseudo-vicariance (speciation) (Van Welzen et al 2003). A single ancestral area is, however, likely to be a consequence of sister group relationships between New Guinea and Australia. According to geological reconstructions, both lands were originally connected. At the same time, the southern parts of New Guinea were submerged from 28 to 10 million years ago and only the central cordillera was above sea level (deBoers 1995). It can be expected that most of the extant genera were already in place or invaded again from north Australia soon after the marshy lowland of New Guinea re-emerged (10My).

Tectonic history shows that the collision of major plates (Pacific, Australian, Eurasian, Indian, Indian Ocean and Philippine) resulted in two waves of Australian microplates moving towards the Eurasian plate. The oldest microplates formed most of Southeast Asia and the western portion of the Malay Archipelago (c. 90Ma). These areas were already Asian for most extant taxa. The second wave started c 15 Ma and has recently formed the stepping stones between the Australian and Eurasian plates. It is hypothesized (Van Welzen at al. 2003) that

many of the microplates were submerged and only emerged after collision with other microplates. Thus, taxa on both sides of Weber's line, and on many of Malaysian islands, could only have extended their range through dispersal. However, relationships among some species, or rather populations, in Malaysia may support the idea of a single ancestral area (Pulvers and Colgan 2007). There is firm evidence of fluctuating sea levels during glacial and interglacial periods in Southeast Asia. During the last glacial era (18 thousand years ago), a global sea level drop of 100-150 m occurred during which many areas of Southeast Asia were connected and formed a single 'ancestral area'; such a connection likely enabled extensive migrations of species and, consequently, vicariance relations among areas. This was, however, too recent an event to influence relationships among areas in our genera cladogram, as most of the ant lineages evolved between 90 to 60 M years ago (Brady et al 2006).

CONCLUSIONS

The list of ant species compiled in this study represents the most complete overview of ants occurring in New Guinea and adjacent areas to date. Comparison of ant faunas among areas of Southeast Asia suggests that the New Guinea fauna is indeed very rich, with many endemic species; however, it is probably not exceptionally richer than comparative areas such as Borneo. At the same time, many areas of the Oriental and Austronesian regions are yet unexplored and undersampled. Therefore, comparisons based on such incomplete species lists are only preliminary. New Guinea ant fauna has its strongest affinities to Australia, with which it shares the highest proportion of species and genera, as well as part of its geological history. A high proportion of species and genera is also shared with Melanesia and the Philippines; this is somewhat surprising and suggests either some common ancestral area or rather utilization of a dispersal route created by island arcs which existed between both areas between 30 and 20 Million years ago. A high proportion of the ant fauna of Southeast Asia and Austronesia is composed of widespread genera, which often represent a major component of island faunas. Areas east of New Guinea and Australia are inhabited mainly by widespread genera with smaller proportions of Oriental and Austronesia - based taxa. The island fauna along the border between the Oriental and Austronesian regions is a mixture of elements from both areas; however, Oriental affinities slightly prevail. At the same time, a considerable proportion of the Southeast Asian and Austronesian fauna consist of genera distributed uniformly across the whole region,

with the centre of their diversity in the Oriental and Melanesian islands. Preliminary biogeographic analyses revealed that relationships among local faunas correspond with both dispersal and vicariance patterns. The relationships revealed among some areas are in concordance with geological history, while others correspond with dispersal routes found for other insect groups. Clearly a more sophisticated approach is necessary to reconstruct the historical relationship among ant faunas in Melanesia and surrounding regions, where a focus on members of some better known genera will be necessary.

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							Oriental						SEAsia islands						Austronesia				New Guinea				East Austronesia				
	Biogeographicall units	**Neartctic**	**Neotropical**	**Palearctic**	**Afrotorpical**	**Oriental**	**India**	**SE Asia mnl.+Isls**	**SE Asia mainland**	**Taiwan**	**Malay penn.**	**SEAsia islands**	**Sumatra**	**Java**	**Borneo**	**Philipinnes**	**Sulawesi**	**Austronesia**	**Lesser Sunda isls.**	**Moluccas**	**Austro-Papuan**	**New Guinea mnl.**	**Bismarck arch.+New Britain**	**Australia**	**East Austronesia**	**Solomon isls**	**Vanuatu**	**New Caledonia**	**Fiji**	**Polynesia**
	Abbreviations:	Nea	Neo	Pal	Afro	Ori	India				Mal. penn							Austron				NG		Au						Poly
	Subregions:																					Centr.NG		CtrAr AU						
																						N NG		CtrN AU						
																						PapuanPen.		NE Au						
																						S NG		SW AU						
Genus	**Biogeo. distrib**																					Wogelkopf		WAr AU						
Myrmicaria	afro+ori	0	0	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	1	0	0	0	0	0	0	0	0	0	0
Simopone	afro+ori	0	0	0	1	1	0	1	1	?	1	1	?	?	?	1	?	1	?	?	1	1	?	0	0	0	0	0	0	0	0
Calyptomyrmex	afro+ori+au	0	0	0	1	1	1	1	1	?	1	1	?	?	1	1	?	1	?	?	1	1	1	1	0	0	0	0	0	0
Metapone	afro+ori+au	0	0	0	1	1	1	1	1	1	1	1	1	?	1	1	?	1	?	?	1	1	?	1	1	1	?	0	0	0
Mystrium	afro+ori+au	0	0	0	1	1	0	1	1	?	?	1	1	?	1	1	?	1	?	?	1	1	?	1	0	0	0	0	0	0
Polyrhachis	afro+ori+au	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Rhoptromyrmex	afro+ori+au	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1	0	?	0	0	0	0
Adlerzia	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Anisopheidole	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Doleromyrma	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Epopostruma	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Froggattela	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Machomyrma	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Melophorus	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Mesostruma	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Myrmecia	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Myrmecorhynchu	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Nothomyrmecia	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Notostigma	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Onychomyrmex	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Peronomyrmex	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Pseudonotoncus	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Stigmacros	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Teratomyrmex	au	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Stereomyrmex	au+india	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0
Calomyrmex	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	0	0	0	0	0	0
Colobostruma	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	1	1	1	0	0	0	0
Leptomyrmex	au+ng	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	1	?	?	1	1	?	1	1	?	1	1	0	0
Notoncus	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	1	0	0	0	0	0	0
Opisthopsis	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	1	1	0	0	0	0
Orectognathus	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	1	1	0	0	1	0	0
Papyrius	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0
Podomyrma	au+ng	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	1	1	?	0	0	0
Prolasius	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	1	0	0	0	0	0	0
Rhytidoponera	au+ng	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	?	1	0	0
Turneria	au+ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0
Adelomyrmex	au+ng+neo	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	?	?	0	1	1
Rhopalothrix	au+ng+neo	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	?	1	1	1	0	0	0	1
Loweriella	borneo	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rogeria	nea+neo+ng+austr	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	?	0	1	1
Stenama	nea+neo+pale+ori	1	1	1	0	1	1	1	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liometopum	nea+pal+ori	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Messor	nea+pal+afr+ori	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Temnothorax	nea+pal+afr+ori	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptothorax	nea+pal+afr+ori	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heteroponera	neo+au	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Centromyrmex	neo+pal+afr+ori	0	1	1	1	1	0	1	1	?	1	1	1	1	1	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0
Dorylus	neo+pal+afr+ori	0	1	1	1	1	1	1	1	?	1	1	1	1	1	0	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Ancyridris	ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0
Myrmoteras	ori	0	0	0	0	1	1	1	1	?	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0	0	0	0
Odontoponera	ori	0	0	0	0	1	1	1	1	?	1	1	?	1	1	1	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Overbeckia	ori	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paratopula	ori	0	0	0	0	1	1	1	1	0	?	1	1	?	1	1	1	0	?	?	0	0	0	0	0	0	0	0	0	0
Recuvidris	ori	0	0	0	0	1	1	1	1	0	?	1	?	1	1	1	1	1	1	?	0	0	0	0	0	0	0	0	0	0
Gauromyrmex	ori	0	0	0	0	1	0	1	1	0	?	1	1	?	?	1	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Gesomyrmex	ori	0	0	0	0	1	1	1	1	?	1	1	?	1	1	1	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Lophomyrmex	ori	0	0	0	0	1	1	1	1	1	1	1	1	?	1	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Gesomyrmex	ori	0	0	0	0	1	1	1	1	?	?	1	?	1	1	1	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Herpegnatos	ori	0	0	0	0	1	1	1	1	?	?	1	?	1	1	1	?	0	?	?	0	0	0	0	0	0	0	0	0	0
Acanthomyrmex	ori	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	0	0	0	0	0	0	0	0	0	0

Appendix 1 **Distribution data for ant genera areas used in this study; biogeogrpahicall delimitation of unit areas and their repsective membership in wider biogeographical regions**

Unit areas and their abbreviations corresponds with Figs. 2 & 3.

							Oriental																									
													SEAsia islands						Austronesia												
																							New Guinea				East Austronesia				
Genus	**Biogeo. distrib**	**Neartctic**	**Neotropical**	**Palearctic**	**Afrotorpical**	**Oriental**	**India**	**SE Asia mnl.+Isls**	**SE Asia mainland**	**Taiwan**	**Malay penn.**	**SEAsia islands**	**Sumatra**	**Java**	**Borneo**	**Philipinnes**	**Sulawesi**	**Austronesia**	**Lesser Sunda isls.**	**Moluccas**	**Austro-Papuan**	**New Guinea mnl.**	**Bismarck arch.+New Britain**	**Australia**	**East Austronesia**	**Solomon isls**	**Vanuatu**	**New Caledonia**	**Fiji**	**Polynesia**
Vombisidris	ori+au	0	0	0	0	1	1	1	1	?	?	1	1	?	1	?	1	1	?	?	1	1	?	1	0	0	0	0	0	0
Mayriella	ori+au	0	0	0	0	1	1	1	1	?	1	1	1	1	1	1	?	1	?	?	1	1	?	1	0	?	0	0	0	0
Myopias	ori+au	0	0	0	0	1	0	1	1	1	?	1	1	1	1	1	1	1	?	?	1	1	?	1	1	1	?	0	0	0
Myopopone	ori+au	0	0	0	0	1	1	1	1	?	1	1	1	1	1	1	1	1	?	1	1	1	?	1	1	1	?	0	0	0
Philidris	ori+au	0	0	0	0	1	1	1	1	?	1	1	1	?	1	1	?	1	?	1	1	1	1	1	1	1	?	0	1	0
Rhopalomastix	ori+au	0	0	0	0	1	1	1	1	?	1	1	?	1	1	1	?	1	?	?	1	1	1	1	0	0	0	0	0	0
Romblonella	ori+au	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	1	1	?	?	1	1	1	1	1	1	?	0	1	1
Iridomyrmex	ori+au	0	0	0	0	1	1	1	1	1	1	1	1	?	?	1	?	1	?	1	1	1	1	1	1	1	?	1	1	1
Diacamma	ori+au	0	0	0	0	1	1	1	1	?	1	1	1	1	1	1	1	1	?	1	1	1	?	1	0	0	0	0	0	0
Dilobocondyla	ori+au	0	0	0	0	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	?	1	0	0	0	0	0	0
Echinopla	ori+au	0	0	0	0	0	0	1	1	?	1	1	1	1	1	1	1	1	?	1	1	1	?	1	0	0	0	0	0	0
Lordomyrma	ori+au	0	0	0	0	1	0	1	1	?	?	1	?	?	1	1	?	1	?	?	1	1	1	1	1	1	?	1	1	0
Euprenolepis	ori+au	0	0	0	0	1	0	1	1	?	?	1	1	?	1	1	?	1	?	?	1	1	?	0	1	1	?	0	0	0
Anillomyrma	ori+au	0	0	0	0	1	1	1	1	?	?	1	?	?	1	?	?	1	?	?	1	0	0	1	0	0	0	0	0	0
Anonychomyrma	ori+au	0	0	0	0	1	0	1	1	0	1	1	1	?	?	?	1	1	?	1	1	1	1	1	1	1	?	0	0	0
Liomyrmex	ori+ng	0	0	0	0	1	0	1	1	?	1	1	?	?	?	1	?	1	?	?	1	1	?	0	0	0	0	0	0	0
Dacetinops	ori+ng	0	0	0	0	1	0	1	1	0	?	1	?	?	1	1	?	1	?	?	1	1	?	0	0	?	0	0	0	0
Chimaeridris	ori-isls	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	?	?	0	0	0	0	0	0	0	0	0	0
Proatta	ori-isls	0	0	0	0	1	0	1	1	0	0	1	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudaphonomy	ori-isls	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannomyrmex	ori-isls	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Formica	pal	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cataglyphis	pal+afro	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasius	pal+nea+ori	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Emeryopone	pal+ori	0	0	1	0	1	0	1	1	?	?	1	1	?	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
Lepisiota	pale+afro+ori	0	0	1	1	1	1	1	1	1	1	1	?	1	1	1	?	1	?	?	0	0	0	0	0	0	0	0	0	0
Cataulacus	pale+afro+ori	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	?	0	0	0	0	0	0	0
Pheidologeton	pale+afro+ori+au	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0
Plagiolepis	pale+afro+ori+au	0	0	1	1	1	1	1	1	?	1	1	?	?	1	1	?	1	?	?	1	1	1	1	1	1	?	1	0	1
Bothriomyrmex	pale+ori+au	0	0	1	0	1	1	1	1	1	1	1	?	1	?	1	?	1	?	?	1	1	?	1	1	1	?	0	0	0
Ochetellus	pale+ori+au	0	0	1	0	1	0	1	1	?	?	1	?	?	?	1	?	1	?	?	1	1	1	1	1	0	?	?	1	0
Myrmica	pale+ori+nea+neo	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aenictus	widespread	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	?	0	0	0
Acropyga	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Amblyopone	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	0	1
Anochetus	widespread	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1
Anoplolepis	widespread	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	0	0	0	0	0	1
Aphaenogaster	widespread	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	0	0	0
Camponotus	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cardiocondyla	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1
Carebara	widespread	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1
Cerapachys	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Crematogaster	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Cryptopone	widespread	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1	?	?	1	1	1	1	1	1	?	1	?	1
Discothyrea	widespread	1	1	0	1	1	1	1	1	1	1	1	?	1	1	1	?	1	?	?	1	1	?	1	1	1	?	1	0	0
Dolichoderus	widespread	1	1	1	0	1	1	1	1	?	1	1	1	1	1	1	1	1	?	?	1	1	1	1	0	?	?	1	0	0
Eurhopalothrix	widespread	1	1	0	0	1	0	1	1	?	1	1	?	?	1	1	?	1	?	?	1	1	1	1	1	1	1	1	1	1
Gnamptogenys	widespread	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0
Hypoponera	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1
Leptanilla	widespread	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	?	1	1	1	1	1	1	?	0	0	0
Leptogenys	widespread	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Meranoplus	widespread	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	0	0
Monomorium	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Myrmecina	widespread	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	?	0	1	0
Odontomachus	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1
Oecophylla	widespread	0	0	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0
Pachycondyla	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0
Paratrechina	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pheidole	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Platythyrea	widespread	0	1	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	0	1
Ponera	widespread	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	?	1	1	1
Prionopelta	widespread	1	1	0	1	1	0	1	1	?	?	1	?	1	1	1	?	1	?	?	1	1	1	1	1	?	?	1	0	1
Pristomyrmex	widespread	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
Probolomyrmex	widespread	0	1	1	1	1	1	1	1	?	1	1	?	1	1	1	?	1	?	?	1	1	?	1	1	1	?	0	0	0
Proceratium	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?
Prenolepis	widespread	1	1	1	0	1	1	1	1	?	1	1	1	?	1	?	?	1	?	?	1	1	?	0	0	0	0	0	0	0
Pseudolasius	widespread	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Pyramica	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1
Solenopsis	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
Sphinctomyrmex	widespread	0	1	0	1	1	1	1	1	0	?	1	?	?	?	?	?	1	?	?	1	1	?	1	1	0	0	1	0	0
Strumigenys	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tapinoma	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
Technomyrmex	widespread	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1
Tetramorium	widespread	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tetraponera	widespread	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	?	0	0	0
Vollenhovia	widespread	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

```
Character No.:          1         2         3         4         5         6         7         8         9         0
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palearctic    11111110011100011110100111111111101111111111111111011110111111110100111100011111101101010001101010000 1
india         11111110001101011111101111111111111111111111111111011110111111111000011101111111110110100000110101111011
seasiamal     11111110011101011111101101111111111?0?11111111110111111111101111001111111111111110101111010110101111011
malaypen      111111100?110?011111101101111111111100011111111101111111111101111001111?111111110?0?11?0?0?10101?1011
sumatra       111111100111 0?01111??0?101111111111100011?111111101111?111100111100111?11???1110101?11010?10101?1011
java          111111100?110?011111107101111111?11000111111111101111?111100111100111??111111110?0?11?0?0?1101011?0??
borneo        11111110011101011111?0110111111111110001111111111011111111100111110111111111111110?0?111010110101110 1?
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lesssundaisls 111?1?100?110?01111????10?111111??11000111?111111011117111100111?0?11????????11?0?0????0?0?11101?????
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centralng     11101110 1?111001111 0?1110?111111111?11000111?111111111111111110011110?01111111?111100000100100111010111 1
northng       11101110111110011110111011111111?11000111?111111111111111110011110101111111?111100000100100111010111 1
bismarckarnb  11101110 1?111001111 0?1110?111111??11000111111?111?111111111001111 0?0111??????111000 0?00?001110101?11
papuanpenin   11101110111110011110?1110?1111111111000111?111111111111111110011110101111111111111000001001001110101111
neau          11101111011101011110111001111111111000111111111111111111111100111101011101111111100000101010111110 1111
secentralau   11101011001101111110110100111011111110001010111111110111111110011110101110001111111000000101001111011 1
ctrnau        11101111011100011110110100111111000100010111111111011110111100111100011001010111010000000010011010101 1
swau          01101011001101111110110100110111000100010101101111101101111001111010111000101011100000001010011110101 1
ctrarau       11101011001100 1?111011010011011100010001010110111010110111100111100011000010101110000001010011010101 1
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ncaledon      01100000001100010100000100110101000000011100101111101111100001110000010001011110000000000000110100111
fiji          01100000100000011110000100000000000100011?011101101111111100001110001 1?000001100000000000001010101011
polynesia     01100110101100011110000100000000000100011101100110111111110000111000111000000??0000000000000000000000 1

                        1         2         3         4         5         6         7
100           12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
afrotorpical  11101111000000001101000011000110000011011000000011001100000001001111100000
palearctic    11111111011000001011100011000110100011111000000010010100001010010000000 0
india         11111111010001001111000011010110000011111101010011010000001010010111000 1
seasiamal     11101111111001001111?000110101101000111111010101?1101?101001010011110000?
malaypen      11101111111?001001101?000110101102001111111?0101011101?10000?010011?10000?
sumatra       ?1101111?1?001001101100011010110?000111111010101?101?10100?01001???00001
java          11101111???001001101100011010110?00011?11?0?0?0??101110?00101001???0000?
borneo        11101111?111010011011000110101102000111111010102?110111010010101 1???00001
philippines   11101111?100100110110001101011010011?111010102?110111000110101111?10001?
sulawesi      ??101111???001001101100011010110?00011?1110?0?01?101?100001010 1???00001
lesssundaisls ??101111???00?001?01?000110101102?0?011?11?0?0?0??1???100001010?1???0000?
mollucas      ??101111???001001101?000110?0110?01011?11?0101012 11??10000?0?0?1???0000?
wogelkopf     01101111?0100100100110001100?110101011?1100111?1?111?100?00?1??1???0000?
Southng       01101111101001001001100011001110101011?1100111111111111001001111?1?1100001
centralng     01101111?0100100100110001100?110101011111100111 1?1111100?00?11?1???00001
northng       01101111101001001001100011 00?110101011?1100111 1?1111100?00?11?1???00001
bismarckarnb  01101111?0100?001001?000110 0?110101011?1100111111111111100?00??111???0000?
papuanpenin   01101111101001001001100011001110101011?1100111111111111001001111?1?1100001
neau          01101111001011111001110111101111111101101101111111111111101000101101101001
secentralau   01101111001010111001111111101011101011010010001111111110100100010110 1100
ctrnau        01101111000010101001010111000110101101101000000011111000001000000101101000
swau          01101111000000111001110111101010101011010000001111100000100000010110 1000
ctrarau       01101111000000101001010111001010101011010000001011100000000000001011 01000
warau         01101101000000101001010111 0000?0101011010000001001110000000000001011111000
solomonisls   01101111001001001001100011 000??000110?01011010001110111111?1000001?11100010000
ncaledon      00100000001000001001010101000000100001010000000011011000000000000011000000
fiji          00101111001000001001000000000000001000?101000101000001010000000111000000000
polynesia     00101111000000001001000000000000000001010000000001101110000010111000000000
```

Appendix 2A: Data matrix for PAE and BPA analyses. Genera distribution (136 characters) and their phylogenetic relationship (38 char) for 28 areas included in analyses. Individual areas correspond with regions in Fig.1 and Appendix 1; or represents their eventual subdivisions.

0 _Aenictus_
1 Cerapachys
2 **30_Aenictus_+Cerapachys**
3 Acanthomyrmex
4 Acropyga
5 Anoplolepis
6 **19_Acropyga+Anoplolepis**
7 Adlerzia
8 Adelomyrmex
9 Mystrium
10 Amblyopone_
11 **35_Mystrium+Amblyopone_**
12 Ancyridris
13 Anillomyrma
14 Anisopheidole
15 **34_Odontomachus+Odontoponera+Anochetus**
16 **33_Odontomachus+Odontoponera**
17 Anochetus
18 Odontomachus
19 Odontoponera
20 Bothriomyrmex
21 Calomyrmex
22 Calyptomyrmex
23 Carebara
24 Cataglyphis
25 Cataulacus
26 Meranoplus
27 **1_cataulacus+meranoplus**
28 Pheidologeton
29 **2_cataulacus+meranoplus+pheidologeton**
30 Crematogaster
31 **3_meranopl+cataula+pheidologeton+cermatogaster**
32 Mayriella
33 Metapone
34 **4_mayriella+metapone**
35 Cardiocondyla
36 Temntothorax
37 Leptothorax
38 **8_Temnothorax+Leptothorax**
39 Tetramorium
40 Vollenhovia
41 **6_Vollenhovia+Tetramorium**
42 Rhopalomastix
43 **9Cardiocondyla+Temnothorax+Leptothorax**
44 **7_Vollenhovia+Tetramorium+Rhopalomastix**
45 Myrmecina
46 **5_meranopl+cataula+pheidolog.+cermatog.+mayriella+metapone**
47 **10=9Cardioc.+Temnot.+Leptothorax+7_Vollenh.+ Tetramor+ Rhopalomastix+Myrmecina**
48 **5+10_myrmicinae**
49 Orectognathus
50 Pheidole
51 Pyramica
52 Strumigenys
53 **12_Pyramica+Strumigenys**
54 Eurhopalothrix
55 **11_Orectognathus+Pheidole**
56 **13_Pyramica+Strumigenys+Eurhopalothrix**
57 **14=11+13**
58 Aphaenogaster
59 Stenama
60 Messor
61 **15_Aphenogaster+Stenama+Messor**
62 Camponotus
63 Polyrhachis
64 **17_Camponotus+Polyrhachis**
65 Chimaeridris
66 Colobostruma
67 Centromyrmex
68 Hypoponera
69 **32_Centromyrmex+Hypoponera**
70 Cryptopone
71 Dacetinops
72 Diacamma
73 Dilobocondyla
74 Discothyrea
75 Probolomyrmex
76 **36_Discothyrea+Probolomyrmex**
77 Proceratium
78 **36_Discothyrea+Probolomyrmex+Proceratium**
79 Dolichoderus
80 Doleromyrma
81 Dorylus
82 Formica
83 Gauromyrmex
84 Gesomyrmex
85 Echinopla
86 Emeryopone
87 Epopostruma
88 Euprenolepis
89 Froggattela
90 Gesomyrmex
91 Gnamptogenys
92 Rhytidoponera
93 **21_Gnamptogenys+Rhytidoponera**
94 Heteroponera
95 **22_Gnamptog.+Rhytidoponera+Heteroponera**
96 Herpegnatos
97 **24_Philidris+Turneria+Papyrius+Anonychomyrma**
98 Leptomyrmex
99 **25_Philidris+Turneria+Papyrius+Anonych.+Leptomyr.**
100 Iridomyrmex
101 Lasius
102 Lepisiota
103 Leptanilla
104 Leptogenys
105 Liometopum
106 Tapinoma
107 **26_Liometopum+Tapinoma**
108 Technomyrmex
109 **27_Liometopum+Tapinoma+Technomyrmex**
110 Liomyrmex
111 Lophomyrmex
112 Lordomyrma
113 Loweriella
114 Machomyrma
115 Myopopone
116 Melophorus
117 Mesostruma
118 Monomorium
119 Myrmicaria
120 Myrmica
121 **16_Monomorium+Myrmicaria**
122 Myopias
123 Myrmecia
124 Nothomyrmecia
125 **28_Myrmecia+Nothomyrmecia**
126 Tetraponera
127 **29_Myrmecia+Nothomyrmecia+Tetraponera**
128 Myrmecorhynchus
129 Myrmoteras
130 Notoncus
131 Oecophylla
132 **18_Oecophylla+Notoncus**
133 Notostigma
134 Ochetellus
135 Onychomyrmex
136 Opisthopsis
137 Overbeckia
138 Pachycondyla
139 Paratrechina
140 Prenolepis
141 **20_Paratrechina+Prenolepis**
142 Pseudolasius
143 Paratopula
144 Peronomyrmex
145 Philidris
146 Turneria
147 **23_Philidris+Turneria**
148 Papyrius_
149 Anonychomyrma
150 Plagiolepis_
151 Platythyrea
152 Podomyrma
153 Ponera
154 Prionopelta
155 Pristomyrmex
156 Pseudonotoncus
157 Proatta
158 Prolasius
159 Pseudaphonomyrmex
160 Recuvidris
161 Rhopalothrix
162 Rhoptromyrmex
163 Rogeria
164 Romblonella
165 Solenopsis
166 Simopone
167 Sphinctomyrmex
168 **31_Simopone+Sphinctomyrmex**
169 Stereomyrmex
170 Stigmacros
171 Teratomyrmex
172 Tyrannomyrmex
173 Vombisidris

Appendix 2b: List of characters for data matrix of PAE and BPA analyses. Characters combining several genera and indicating their phylogenetic relationship (bold) were used only for BPA analysis.

Part II.

Diversity and community ecology of New Guinea ants: an overview

(Milan Janda & Marek L. Borowiec; mns.)

DIVERSITY AND COMMUNITY ECOLOGY OF NEW GUINEA ANTS: AN OVERVIEW.

Milan Janda[1] & Marek L. Borowiec[2]

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INTRODUCTION

Current scientific knowledge of Melanesian ant fauna suffers from a combination of a highly diverse fauna in an inaccessible area. However, this situation is still typical for many tropical countries, namely in Southeast Asia. Despite research efforts conducted by several scientists from the 1950's to 1970's (Brown 1954; Brown 1957; Room 1975b; Taylor 1968; Taylor 1977; Wilson 1958; Wilson 1959b; Wilson 1967), and who contributed important taxonomic revisions and descriptions of Melanesian ants, virtually no study focusing on the ecology of the New Guinea ant fauna exist to date. The only exceptions are two pioneering works of Wilson (Wilson 1959a; Wilson 1959), who described briefly local ant assemblages. A similar situation applies to any quantitative investigation of ant fauna, which is lacking as well. Although a few recent surveys of Melanesian ants occurred (e.g. Snelling 1998a,b), most of them produced little more than species lists (which still represent very valuable information), and are not very suitable for wider comparisons with other tropical areas.

Here, we present the first analyses of data based on an investigation of ant assemblages surveyed in the primary lowland forest of east New Guinea, using quantitative collecting methods. Our aim was to provide a basic overview of species richness and the structure of ant assemblages inhabiting the rainforest understory. We further compared the local fauna with data available from different parts of Southeast Asia and other tropical regions. In addition to an assessment of the assemblage's richness and composition, we focused in more detail on microhabitat and nesting preferences, as well as assessing the contribution of the three collecting methods applied.

METHODS

Study site and sampling methods

The study area was situated 20 km north of Madang, Papua New Guinea. Research sites were located in a primary lowland perhumid forest around Baitabag village (GPS, 50-100 m a.s.l.). This area is classified as a mixed evergreen hill forest (Paijmans 1976); 152 species of woody plants with DBH ≥5 cm per hectare; (Novotny et al. 2002) interspersed with patches of secondary regrowth due to the locally practiced slash-and-burn agriculture. Average annual rainfall in the Madang area is 3,558 mm, with a moderate dry season from July to September; the mean air temperature is 26.5 ^{0}C.

We surveyed the ant fauna by establishing six 20 x 20 m square plots in which bait traps were laid in a square grid. The study plots were randomly selected within approximately nine square km of primary forest, and were at least 500 m apart from one another. The survey was conducted between January to November 2004.

In each plot, 25 bait traps (BT) were placed on the ground, separated by 5 m intervals. One meter from each ground plot, another twenty five baits were placed on vegetation in an identical grid fashion between 1 and 2 m above the forest floor. Vegetation baits were placed on randomly selected living plants, including herbs, trees and lianas. Commercial canned tuna baits were used as baits, as is standard in studies of foraging ant communities. Baits were visited and sampled one and three hours following their exposure. All present ants were counted and several individuals of each species were collected without disturbing the remaining ants. In addition to bait traps, nine m^2 of leaf litter samples were collected and processed in Winkler extractors (WE). At ten metre intervals along a transect, one square meter of leaf litter (including pieces of rotten wood) was thoroughly examined and sifted through a mesh with 1cm^2 openings. Nine samples were taken inside each plot and processed according to the protocol of Bestelmayer et al. (2000), with an extraction period of three days.

In addition to these methods, each plot was exhaustively searched (hand collected - HC) for ants, where any available type of nesting microhabitat was surveyed up to a height of two metres from the forest floor. When an ant colony (or single workers of uncommon species) was discovered, at least ten specimens were collected and placed into a vial with alcohol. Microhabitat preferences and nest types were recorded for most of the hand collected samples. Highly abundant

species were usually not collected repeatedly and their abundance might therefore be underestimated. Four person-hours of collecting were approximately spent within each plot. Usually two persons participated in the collecting, thus two hours were spent at each plot. Only one plot was investigated per day and sampling was never performed during or soon after a rain. The air temperature in the understory during the activities ranged between 26 to 32.8 ^{o}C (mean 29.5, SD=1.03). Ant specimens were mounted and sorted into morphospecies. Voucher specimens were databased and determined to the most available taxonomic level by the use of literature or comparison with museum collections (Museum of Comparative Zoology, Harvard University), or with higher classifications following Bolton (1995, 2006). All voucher specimens are deposited in the Ant Reference Collection at the Biology Centre, Czech Academy of Sciences in Ceske Budejovice, Czech Republic. Photographs of the voucher specimens are accessible at the open-access database 'Ants of New Guinea' on www.entu.cas.cz/png/ants.html.

Species richness and the adequacy of our sampling was assessed using rarefaction curves generated by random re-orderings (50 times) of samples using EstimateS, version 7.5.1 (Colwell 2005). Species-accumulation curves relate the sampling effort (e.g., number of samples) to the cumulative number of species to evaluate sampling effectiveness (e.g., Longino and Colwell 1997; Wagner 1997). Curves were generated from pooled data, which included all methods used at the plot as well as for each method separately. Species occurrences (rather than numbers of individuals) were used to examine species richness, because ants are social and therefore spatially clumped (King 2007). The Chao 2 index (Chao 1988), as calculated together with the number of singletons and doubletons (i.e. species occurring only once or twice) was used to estimate asymptotic species richness of the study site. Rank-occurrence diagrams were constructed for all types of collecting methods. Differences in species rank occurrence distributions were tested by the Kruskal-Wallis test using STATISTICA 7.0 for Windows (StatSoft, Inc.; Tulsa, OK, USA). Comparison of sample-based rarefaction curves with the observed number of species plotted against species occurrences was used to assess differences in species richness between our study and other comparative surveys.

Nesting and foraging preferences based on hand collected samples were analysed by direct gradient analysis (redundancy analysis - RDA) in CANOCO (TerBraak and Šmilauer 1998). Up to thirty nest types and foraging environments originally recorded in the field were divided into 15 and 11 major categories respectively (Figs. 6, 7). Occurrence data for all species were pooled according

to their generic identity and only genera with more than five occurrences were included in the analyses. Although hand collecting data are not usually quantitative, and may be biased by personal preferences for particular microhabitats, equal sampling effort and the broad investigation of all plots assured representative examination of all potential nesting sites in our study. Representation of individual nesting categories thus represent all events in which a particular microhabitat was occupied by an ant species, independent of their actual frequency within the plot.

RESULTS

A total of 194 species from 52 genera were recorded in the six study plots when data from all three collecting methods were combined. This represents about 26% of the species and 60% of the genera currently described from New Guinea. There were 49 to 117 ant species within plots, with mean species richness per plot of 75.4 species (SD=22.8, n=6). The observed species accumulation curve for all methods combined shows a decreasing rate of species accrual, but does not reach an asymptote and continues to rise with increasing sample size (Fig. 1). This indicates that sampling at the site is still incomplete. On the other hand, the incidence-based estimator Chao-2 reached an asymptote, suggesting that at least 237 species may occur at the study site. The number of unique species remained relatively constant with increased sample size, representing approximately 28% of the total fauna (mean singletons=55).

Incomplete sampling is more evident when comparing accumulation curves from each method separately (Fig 1b). Only the species accumulation curve for the bait trap samples seems to approach an asymptote, which suggests that baiting recorded the majority of the local fauna detectable by this method. Individual methods yielded different species richness, with Winklers capturing as much as 123 species, while hand collecting and bait traps recorded 88 and 63 ant species, respectively. There were two times more species per one bait on the ground (mean=2.06 SD=0.94, n=150) than on the vegetation (mean=0.85 SD=0.73, n=150). On average, we recorded 11.7 (SD=4.9, n=54) ant species in one square meter of leaf litter using the Winklers.

Tab. 1. Number of species and genera recorded in all six study plots by all methods.

subfamily	genera	species	Prop. of NG genera (%)
Aenictinae	1	1	100
Amblyoponinae	2	2	50
Cerapachyinae	1	4	33
Dolichoderinae	5	6	45
Ectatomminae	1	3	50
Formicinae	6	15	46
Myrmicinae	22	117	62
Ponerinae	12	38	100
Proceratiinae	2	8	100
Total	**52**	**194**	**62**

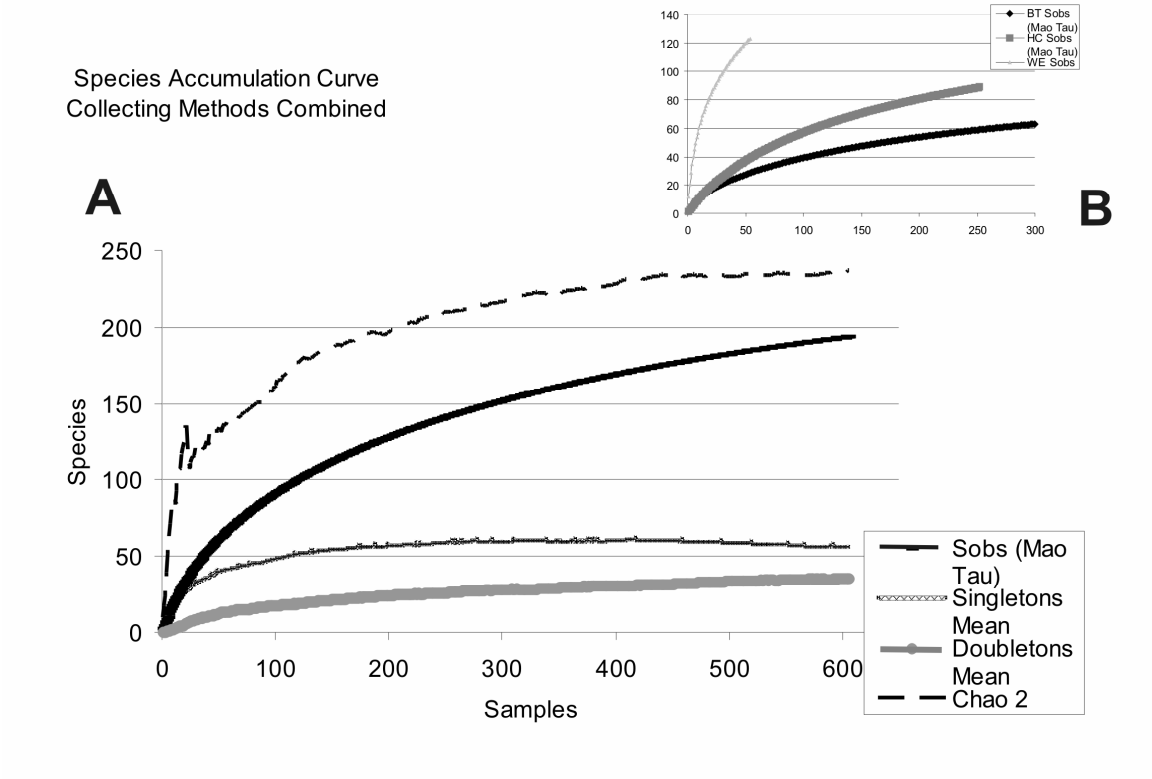

Fig. 1. Species accumulation curve (Mao Tau function in EstimateS) and the Chao 2 total species richness estimator for all sampling methods combined. Fig 1B Species accumulation curves (Mao Tau) for different collecting methods.

Twenty one species were sampled in all three methods. The highest overlap of species shared between methods was between hand collecting and bait traps (39 spp., Fig. 2); both tended to record mainly ground-foraging ants. On the other hand, the least number of species (29 spp., Fig. 2) was shared between bait trapping and leaf litter samples. Hand collecting and leaf litter samples had 11 species in common, which were not recorded by other method. The number of species and overlaps among all methods are summarized in Fig 2.

As shown in Fig. 3, species occurrence rank differed among methods as well (Kruskal-Wallis, Chi-Square = 9.8 df = 2 p = .0073). The twenty most frequent leaf litter species together made up 50 % of total species occurrences. For the hand collection and bait trap samples, twenty of the most common species represented 60% and 81% of all species occurrences, respectively. Hand collecting samples did have the highest proportion of singletons, represented by 36 species (40%), while leaf litter and bait traps had slightly lower proportions of unique species, representing 36% (23 spp.) for bait traps and 37% (46 spp.) in the case of leaf litter samples.

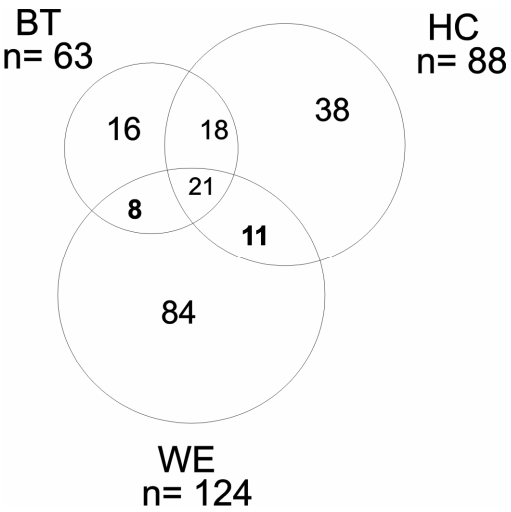

Fig. 2. Overlap among collecting methods expressed in recorded species. Total of 194 species were recorded by all three methods.

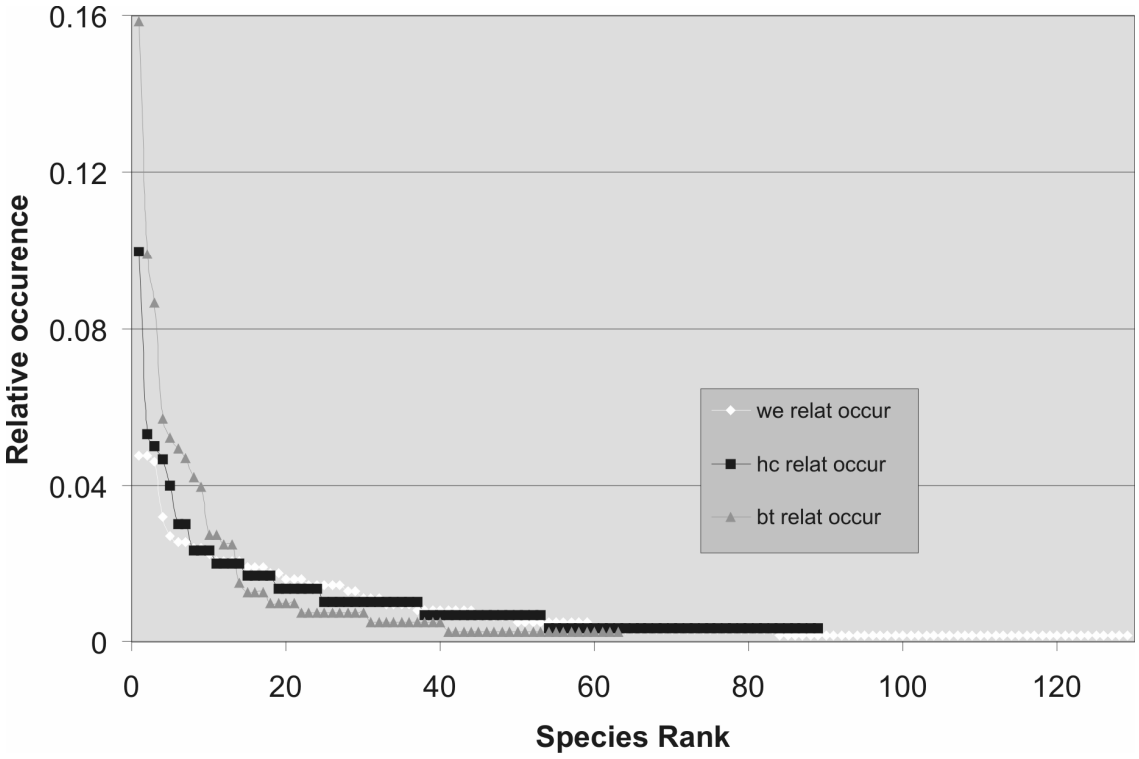

Fig 3. Species–occurrence rank for the three collecting methods. WE – Winkler leaf litter samples; HC – Hand collecting; BT – Bait traps.

Assemblage composition

Members of nine ant subfamilies, out of the eleven present in Melanesia, were recorded within the six sampling plots in primary lowland forest. The fifty two genera recorded represent 60% of the genera currently known from New Guinea. The vast majority of species (117 spp.) belonged to the subfamily Myrmicinae, while the remaining subfamilies were represented by much fewer species (Tab. 1). Relative incidence of the most frequent genera and species obtained by the different collecting methods are summarized in Fig. 5 and Tab. 2.

The most species rich genera were *Pheidole* (32 spp.), *Strumigenys* (19 spp.) and *Tetramorium* (12 spp.), all of which occurred predominantly in the leaf litter. Biogeographic affinities of the assemblages, based on generic composition, are illustrated in Fig 4. The majority of genera (61%) belong to 'widespread' taxa, while Australia + New Guinea, as well as Oriental + Austronesian genera, each represent 10% of the assemblage. Members of *Pheidole* occurred with the highest frequency, followed by *Crematogaster* and *Rhytidoponera* for samples from all collecting methods pooled together (Fig. 5). If leaf litter samples are considered separately, then the

most frequent genera were typical representatives of the cryptic Myrmicinae and Ponerinae genera, namely *Strumigenys, Pheidole, Monomorium Oligomyrmex* and *Hypoponera*, which all accounted for 51% of total species occurrences. The genus *Hypoponera* occurred in 90% of the leaf litter samples, with an average of 1.5 species per sample. *Strumigenys* occurred in 85 % of the Winklers, reaching an average frequency of 1.6 species per each sample (further details Tab. 2).

In terms of species, the leaf litter was dominated by *Hypoponera sp. 1* and *Strumigenys sp. 2*, which both occurred in 55% of the samples. The most common species in the hand collected samples was *Camponotus vitreus* (11.9%), while *Crematogaster cf. polita* was the most frequent at bait traps (16%).

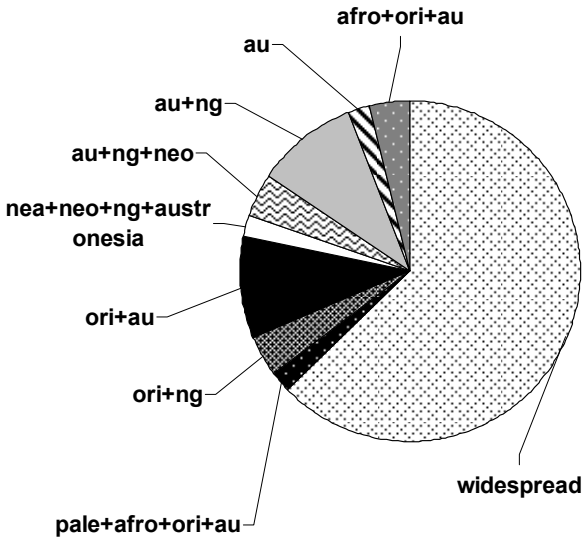

Fig. 4. Biogeographic affinities of genera recorded within six study plots of primary forest.
widespread – genera occurring in more than 5 major world biogeographic regions;
(pale – Palearctic; afro – Afrotropical; ori – Oriental; au – Australia; ng – New Guinea (including Bismarck Archipelago); nea – Nearctic; neo – Neotropical;)

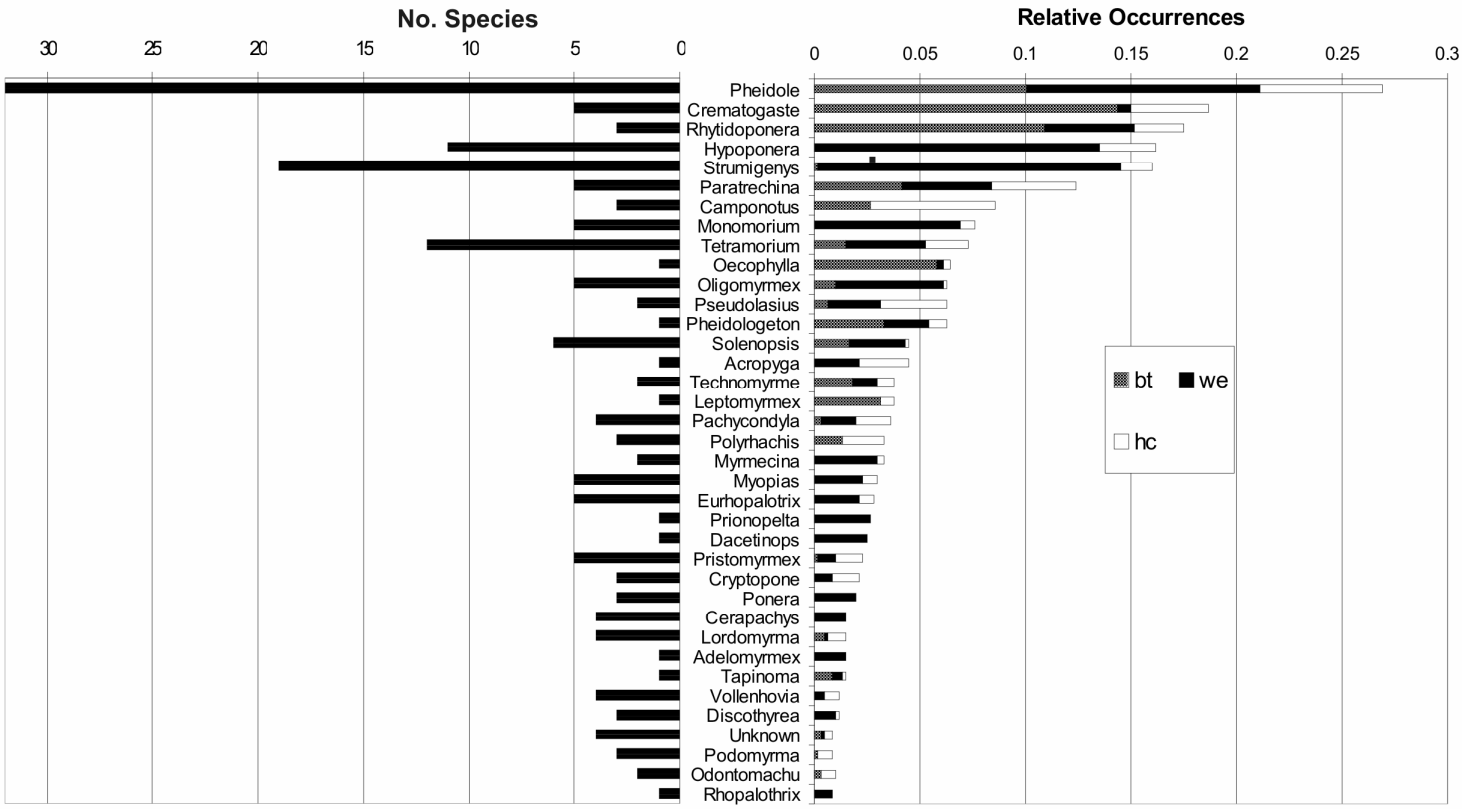

Fig. 5. Relative occurrences of genera in samples, according to collecting method (A), and number of species recorded (B). Data from all plots combined

Tab. 2. The ten most common species recorded during the study, according to collecting methods.

WE	WE occur	% occur	HC	Hc occur	% occur	BT	BT occu	% occur
Hypoponera sp. 1	30	55.6	*Camponotus vitreus*	30	11.9	*Crematogaster cf. polita*	64	21.3
Strumigenys mayri	30	55.6	*Paratrechina sp. 3*	16	6.3	*Rhytidoponera aenescens*	40	13.3
Monomorium sp. 1	29	53.7	*Pseudolasius sp. 2*	15	6.0	*Oecophylla smaragdina*	35	11.7
Hypoponera sp. w1	20	37.0	*Acropyga sp. 1*	14	5.6	*Paratrechina sp. 3*	23	7.7
Pheidole sp. 6	17	31.5	*Crematogaster cf. polita*	12	4.8	*Crematogaster sp. 3*	21	7.0
Paratrechina sp. 3	16	29.6	*Pheidole sp. 10*	9	3.6	*Pheidologton affinis*	20	6.7
Prionopelta sp. w1	16	29.6	*Polyrhachis sp. 2*	9	3.6	*Leptomrymex puberulus*	19	6.3
Carebara sp. 4	15	27.8	*Cryptopone cf. motschulskyi*	7	2.8	*Pheidole sp. 10*	17	5.7
Pseudolasius sp. 2	15	27.8	*Hypoponera sp. 1*	7	2.8	*Rhytidoponera strigosa*	16	5.3
Pheidole sp w6	14	25.9	*Pachycondyla stigma*	7	2.8	*Camponotus vitreus*	11	3.7

Tab. 3. Most common genera in the leaf litter samples and their comparison with data from other regions. Data from other regions are based on Agosti (2000).

New Guinea		Most frequent genera in Biogeographic region					
No. sp / Sample	**No.sp total (n=54)**	**New Guinea (n=54)**	**%**	**Australian (n=170)**	**%**	**Oriental (n=130)**	**%**
1.5	10	Hypoponera	90.74	Hypoponera	100	Strumigenys	100
1.6	15	Strumigenys	85.19	Pheidole	94.1	Tetramorium	100
1.2	17	Pheidole	64.81	Strumigenys	94.1	Monomorium	92.3
0.8	4	Monomorium	59.26	Solenopsis	76.5	Oligomyrmex	92.3
0.6	3	Oligomyrmex	44.44	Oligomyrmex	70.6	Odontoponera	84.6
0.5	3	Paratrechina	42.59	Paratrechina	70.6	Pheidole	84.6
0.5	3	Rhytidoponera	40.74	Ponera	58.8	Myrmecina	76.9
0.4	8	Tetramorium	33.33	Monomorium	52.9	Odontomachus	69.2
0.3	2	Myrmecina	33.33	Rhytidoponera	52.9	Hypoponera	61.5
0.3	1	Prionopelta	29.63	Tetramorium	47.1	Lophomyrmex	53.8

Nesting preferences

Nesting and microhabitat preferences recorded for the 87 hand-collected species were divided into 15 categories, as shown in Fig 6. The majority of species with two and more occurrences were found in two (17 spp.) or three (14 spp.) different microhabitats. The highest proportion of species (31 spp.) was found nesting in dead rotting logs on the forest floor. The second most favorite habitat was dead twigs and branches on the ground (27 spp.). The number of nesting sites inhabited by a particular genera was positively correlated with their species richness (Spearman $R = 0.68$, $p < 0.00$, $n=38$).

Figure 6 shows genera with 5 or more records and the proportion of individual microhabitats in which they were collected. Myrmicinae species were distributed equally across all investigated microhabitats, while Ponerinae were found mainly in different types of rotting wood. The lowest number of species (3) was found nesting on vegetation leaves. Among the most conservative genera were *Cryptopone* (3 spp., 3 microhabitats), *Hypoponera*, and *Acropyga* (1 spp., 4 microhabitats), occurring predominantly in different types of rotting wood and in the leaf litter; as well as the arboreal genus *Polyrhachis* (4 habitats, 3 spp.). On the other hand, the species-rich genera *Pheidole*, *Paratrechina* and *Crematogaster* inhabited up to 8 different microhabitats.

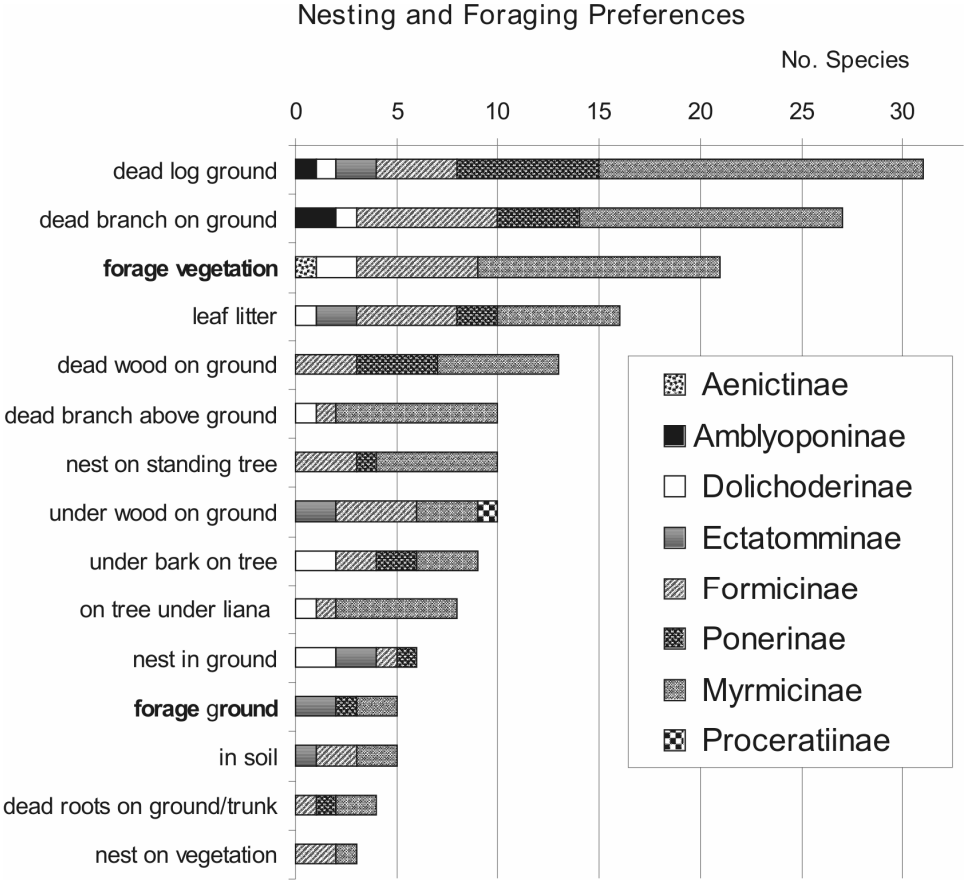

Fig. 6: Nesting and foraging preferences (bold) for ants from different subfamilies recorded by hand collecting.

Redundancy analysis of microhabitat preferences based on occurrence data revealed a significant effect of nesting site on assemblage composition ($p=0.002$, $F=2.1$, $df=1$), but explained only 2.3% of the variability in the data. Three major groups of genera with different nesting tendencies emerged in the data. As shown in Figure 7 (left upper quadrate), vegetation and understory are dominated by arboreally nesting members of the Myrmicinae and Formicinae subfamilies (*Crematogaster, Camponotus, Podomyrma* etc.). A second distinctive group (upper right quadrate) consisted of mainly large-sized species nesting in the soil, foraging on the ground or in the leaf litter (genera *Leptomyrmex*, *Odontomachus* etc.). The third and most diverse group consisted of genera occupying different stages of decaying wood and occurring under the bark of living trees (lower left & right quadrates). These microhabitats were inhabited by many species of the genera *Pheidole, Paratrechina* or *Pachycondyla*.

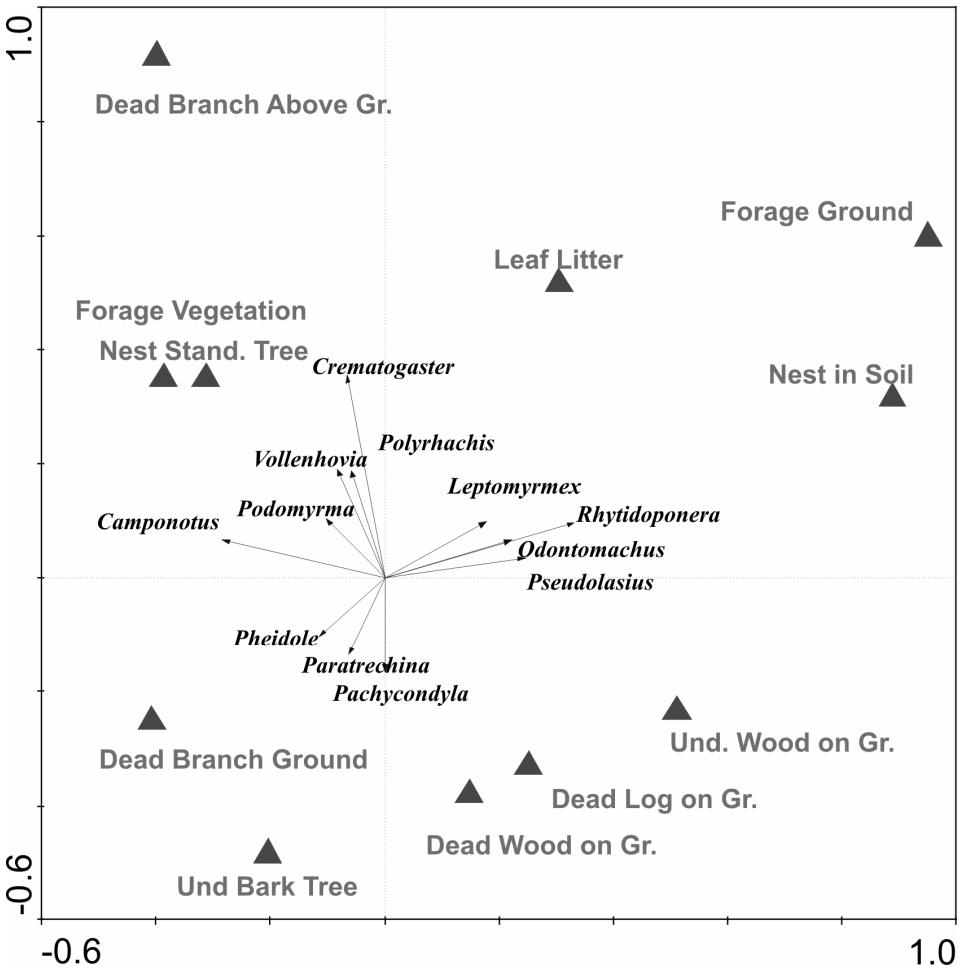

Fig. 7. RDA analysis of nesting and foraging preferences. Only genera with a fit range above two percent are shown. Several categories from Fig. 6 with lower number of occurrences were combined together: '*nest standing tree', 'nest vegetation'* and *'under liana on tree'* were combined into **'nest standing tree'**; Categories '*nest in ground'* and *'nest in soil'* were combined into **'nest in soil'**. Category '*dead roots on ground'* is contained in '**dead wood on ground'**.

DISCUSSION

Our study revealed ant assemblages of high species richness in the lowland rainforest of New Guinea, which ranks among the most species-rich fauna known to date for tropical ants. Only two comparable data sets exist from New Guinea. The first is based on the large-scale collections of Wilson (1959a) from the Busu River in Morobe province, where he collected 172 species from 51 genera over an area of approximately 5 km^2. He did not use any quantitative methods. His data are based on general hand-collection, focused on a thorough investigation of any available microhabitat in the understory, including leaf litter.

A second and even more exhaustive sampling was performed during two surveys by Snelling at Lakekamu (South New Guinea; Snelling 1998a) and in the northeast part of the New Guinea Indonesian province of West Papua (Snelling 1998b). Snelling reported 119 and 85 species from two neighboring sites in the lowland rainforest of West Papua, while he found 250 ant species in Lakekamu. in the latter survey was conducted using 266 mainly hand collected samples, of which just 12 samples came from sifted leaf litter. The aggregate area surveyed in Lakekamu was about 1 km^2 , which suggests an exceptional diversity of the local ant fauna.

Our record of 194 species is very comparable with the results of both studies and suggests that ant assemblages at Baitabag are typical for New Guinea. Although scattered across an area of approximately 4 km^2, our data are based on detailed investigation of 2400 m^2 (6*plots 20x20m) of forest understory, which represents an area smaller than those investigated by Wilson (1959b), but not dramatically larger than those explored by Snelling (1998b).

An investigation of New Guinea ant fauna by Room (1975a) is only partly comparable with our study, due to the inadequate sampling of the rainforest habitat. Room found 156 ant species collected in 270 $1m^2$quadrates, scattered across an area of about 20 km^2. However, his study examined 9 different types of habitats, ranging from primary forest through several types of plantations (cocoa, oil palm etc.) to savanna. Only forty samples containing 49 ant species were taken from primary forest, whereas he reports the same richness for rubber plantations as well.

Further comparisons with other studies suggest that our site ranks among the most species-rich assemblages described from tropical areas. Although many tropical data sets are not fully comparable among each other due to differences in sampling methodology, or size of study areas, we can compare our results with the partial data originating from the three most exhaustive surveys of rainforest ants, which partially overlapped in sampling methodology. Bruhl (1998) reports exceptionally rich assemblages from Sabah in Borneo, where he found 524 species from 73 genera in plots encompassing area of 6 ha. Such species richness is still very comparable with our data set, which represents collections from an area four times smaller and, unlike Bruhls' study, does not include samples from the canopy. When individual methods were considered separately, Bruhl (1998) found 139 species in 60 square meters of leaf litter, while in our study it was 123 species in 54 m^2 of litter. His investigation of the forest floor and lower vegetation strata yielded 113 species, while we found 133 species in the same layer, although over a smaller area (2400 m^2). Similarly to Borneo, (Verhaagh 1990) reported 520 species in a 1000-ha area in the Panguana Reserve, Peru.

Although both of these studies do not provide relative abundances or other measures of inventory completeness, they employed a major collecting effort, using diverse sampling methods.

Probably the most complete inventory of rainforest ant fauna was conducted by Longino et al. (2002) from the neotropical seasonal rainforest of Costa Rica. A long term exhaustive inventory of an area about 1500 ha in size revealed 437 ant species using eight sampling techniques, including canopy fogging, Berlese soil samples, hand collecting and other methods. According to sample-based rarefaction curves for all eight methods combined, the Costa Rica inventory yielded approximately 330 species from 2400 species occurrences, compared to our 196 species from 2467 species occurrences. When considering just leaf litter samples, Longino et al. (2002) found 197 species from 1416 occurrences, while our study yielded 123 species at only half of the species-occurrences (630). Furthermore, they reported 65 species from 200 bait traps in ten transects, while there were 63 species at 300 baits in our study. If measured by species occurrences, this represents 30 species from 100 occurrences in our study versus 40 from Costa Rica. Considering the much higher sampling effort and especially size of area explored, these partial comparisons suggest that the rainforest at our New Guinea locality may indeed harbor at least a comparable ant species richness.

The majority of other comparable tropical studies revealed lower ant species richness, either in the leaf litter or forest understory (e.g. 10-27 species per 10 leaf litter samples in Tanzanian rainforest (Robertson 2002); 197 species, 47 genera in 200 m2 of leaf litter from 10 localities across >400km^2 of lowland forest in Ghana (Belshaw and Bolton 1994). Although very similar in taxonomic composition, ant assemblages from the Australian tropics are also less species rich than those in New Guinea (e.g. Andersen 1995). Andersen (1992) found 173 species from 46 genera across a wide range of rainforest localities in the Northern Territory; a similar situation is known from Queensland. This is not surprising, because Australian tropical forests are of a limited area, relatively young and were repeatedly reduced during the past glacial periods.

Overlap between methods

Each collecting method implemented in our study was aimed to focus on particular properties or an ecological group of ant assemblages in the rainforest understory. Therefore, data from each method will be analyzed separately in further detail in upcoming studies. Of the three

methods used, leaf litter samples recorded a markedly higher number of species (123, 67% of them unique) than hand collecting (88 spp, 43 % unique) or bait traps (63 spp, 25%unique) (Fig 2). This is due to the generally high levels of species richness for leaf litter fauna in the tropics (Agosti 2000), as well as due to the great effectiveness of Winkler samples to record this fauna (Bestelmeyer et al. 2000). All three methods did overlap in recording 10% of the total fauna (21 spp). Bait trapping was the most general method as it yielded only 16 species not detectable by the other methods.

The lowest overlap in recorded species (Fig. 2) was among WE and BT (8 species considering overlap just between these two methods), while the highest was between bait traps and hand collecting (18 species, Sorensen = 0.517). This is not surprising, as both methods are used to record a similar fauna, although they are usually used to study different properties of assemblages (e.g. behavioral interactions vs. nesting preferences). Although hand collecting can be highly affected by personal experiences and collecting approach, and its results may have only limited comparability among different studies, it represents a highly effective and exhaustive method in recording ant species, which may be difficult to detect by other quantitative methods.

Bait traps were dominated by several highly frequent species (C*rematogaster cf. polita*, *Rhytidoponera aenescens* and *Oecophylla smaragdina* Fig. 3) which often monopolized food sources. Only *Camponotus vitreus* occurred with a higher frequency in the hand collected samples (Tab. 2. 12%), while the slope of the rest of the species rank curve was more even. The same was true for leaf litter samples, which were dominated by just three species with occurrences of over 50% (Fig. 3, Tab. 2), again, the rest of the rank curve was quite even.

Assemblage composition

The highest proportion of the ant fauna recorded in our study was comprised of globally distributed genera (25). Austronesian and Oriental elements were represented by five and eleven genera respectively. Furthermore, five genera were worldwide tropical specialists, while six occurred only within the old-word tropics.

The ground foraging fauna (BT+HC) was dominated mainly by *Pheidole*, *Crematogaster Camponotus* and *Rhytidoponera* (frequency occurrences Fig. 5), while the leaf litter fauna consisted mainly of the cryptic genera *Hypoponera*, *Strumigenys*, *Oligomyrmex* and *Pheidole*. Leaf litter ants

were also among the most species rich in our samples (Fig 5). The 32 species of the diverse genus *Pheidole* clearly outnumbered all other genera. *Strumigenys* and *Tetramorium* were represented by 19 and 12 species respectively, and the rest of the genera were mostly represented by less than 10 species. The generic composition at our locality is similar to those described from north Australia (Shattuck 1999), as well as from Borneo (Brühl 2001); however, the relative species proportions of some genera vary. The most remarkable difference is the conspicuous under-representation of *Polyrhachis* and *Camponotus* species in our samples. Although both of them are mainly arboreal genera, several investigations using comparable methods with our study reported higher species richness of both genera in the understory.

For example *Polyrhachis* represented from 13% to 18% of the species in the north Australian seasonal tropics (Woinarski et al. 1998; Reichel and Andersen 1996), or 9% of the species in a Borneo rainforest (Brühl 1998). *Camponotus* represented up to 5 % of the understory ant species in Australia and 14 % of total fauna in Borneo, (Brühl 1998) while these amounted to only 2% in our samples.

When leaf litter fauna was considered separately, the proportion of major subfamilies fell to within the usual values reported from the world's tropics: 52 to 65% for Myrmicinae and 20-30% for Ponerinae. In our study, both families represented 61% and 23% of species respectively. Table 3 compares the relative frequency and species richness of the dominant leaf litter genera with data from other regions (Agosti 2000). The assemblage structure at our locality is more similar to the Australian region than to peninsular Malaysia and Borneo, where *Tetramorium* and *Monomorium* are more frequent (Tab. 3), together with a high proportion of genera typical for the Oriental region (i.e. *Odontoponera* and *Cerapachys*). On the contrary, *Hypoponera* seems much more abundant in New Guinea and the Australian region (Agosti 2000). *Pheidole* is clearly prominent in all three regions (as well as throughout the rest of world's tropics (Agosti, 2000)). *Strumigenys* and *Hypoponera* alternate between the second and third most species-rich genera in Australia and New Guinea, while *Tetramorium*, *Carebara* or *Pyramica* predominate in the rest of the Oriental region (Agosti 2000; Brühl 2001).

Microhabitat preferences

Most recorded microhabitats (Fig. 6) are identical with nesting sites; nevertheless, foraging preferences are included as well. Clearly the most favourite microhabitat occupied by the highest number of species, and with high frequency (103 occurrences), were various types of dead rotting wood on the forest floor, as represented by the categories 'dead log on ground' and 'dead branch on ground' (Fig 6). This was previously noted by Wilson (1959a), who further divided rotting wood into five categories according to their degree of decay and described the ant species typical for those stages. Although we did not specifically test those categories in our study, we found several species or genera during our observations which were less specific in their nest preferences than mentioned by Wilson (1959a), e.g. *Acropyga* and *Pseudolasius*. Dead twigs or logs are among the most abundant available nesting sites, at least in Melanesian rainforests. Several hypotheses exist as to why they are favoured by so many species. This may be especially due to the presence of a uniform environment (temperature, humidity), stable cavities and providing a dual purpose for nesting and foraging in the surrounding soil and litter (Wilson 1959a).

Although the majority of recognized microhabitats did not share many ant species, several nesting/foraging sites appeared closely related in terms of species overlap, according to the RDA analysis. For example, ants foraging on vegetation were very similar to those nesting in trees (Fig 7), while the fauna inhabiting dead logs on the ground was similar to those found in dead pieces of wood, but apparently quite different from ants inhabiting dead twigs (Fig 7).

Three main tendencies in microhabitat preferences were recognised in this study (i.e. arboreal, soil + leaf litter, decaying wood) and the taxa occupying them are in agreement with data from other tropical areas and, thus, not very unexpected (Agosti 2000). What seems surprising, however, is the relatively narrow range of habitat types for most taxa. For example, despite that *Pheidole* and *Crematogaster* species were found in up to 8 different microhabitats, most of them belonged to one of the main categories (i.e. decaying wood and arboreal strata). Although both genera are known to nest within a wide range of habitats in other geographical areas, species in lowland rainforests seemed relatively fixed to just several related types of microhabitats. In general, conservative preferences for nest types were remarkable for the majority of ant taxa, as 60% (n=50) of species had just two or three nesting sites while only 24% occurred within four and more different microhabitats.

CONCLUSIONS

Our inventory represents the first quantitative assessment of the rainforest ant fauna of New Guinea. We found local ant assemblages of high richness, being at least comparable with other hyperdiverse tropical sites. Furthermore, we report the highest species richness (117 spp.) occurring within a single rainforest patch so far surveyed for ants. Although the sampling effort shown here does not represent a complete inventory of the site, statistical estimators suggest that the addition of just several more plots would likely yield a majority of the local species pool. Our study further confirms the necessity of applying several alternative collecting methods for inventorying such a complex environment as a tropical rainforest. Locally found ant genera represented a high proportion of the regional generic pool; local assemblages had close affinities to North Australian ants, however, faunal similarity to Oriental region was evident as well.

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Part III

Canopy assemblages of ants in a New Guinea rainforest

(Milan Janda[1,2], Martina Konečná[1]; mns.)

CANOPY ASSEMBLAGES OF ANTS IN A NEW GUINEA RAINFOREST

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ABSTRACT

We explored ant assemblages in two common tree species in primary lowland forest of New Guinea using direct canopy access and tuna bait traps. The nineteen trees investigated were occupied by 21 ant species of which 18 were canopy inhabitants. On average we found only 3.6 ant species on each tree and 3 species per bait. Height of bait position was positively related to ant species richness, with the upper parts of the canopy being occupied by the highest number of species. On the other hand, tree identity and study site did not have any effect on ant species richness nor on structure of the ant assemblages. Ant species appeared to be distributed randomly and we did not detect an ant mosaic at the study sites, although its existence cannot be excluded at different spatial scales. Although one of the two dominant species (*Crematogaster cf. polita*) did have a negative effect on the abundance of some species co-occurring at food sources, it was able to tolerate most of the ants sharing the same food sources. The majority of species found in the canopy were generalised omnivores, which depended mainly on trophobionts or plant exduates.

INTRODUCTION

Ants play key ecological roles as predators, herbivores or mutualists and may influence the abundance and composition of numerous insect taxa in an ecosystem (Hölldobler and Wilson 1990). Many studies have demonstrated that ants dominate the canopy of lowland rainforests (e.g. Floren and Linsenmair 1997; Stork 1991; Wagner 1997) and are often considered as the most important predators, strongly influencing the composition of arthropod fauna by exerting high predation pressure (Floren et al. 2002). On the other hand, several recent studies showed that a significant proportion of ecologically dominant ant species are partly herbivorous, deriving nutrients from plant exudates or insects feeding on plants (Blüthgen et al. 2003; Davidson et al. 2003).

Traditionally, it is believed that spatial distribution of some arboreal ant species is arranged in a mosaic (Room 1971). This hypothesis predicts that a limited number of dominant ants (i.e. species with traits such as large colonies, high recruitment or aggressive behaviour) is distributed in a three-dimensional mosaic fashion with mutually exclusive territories maintained by interspecific competition (Room 1971; Leston 1978). Moreover, several studies suggest that dominant ants can influence the structure of the rest of the arboreal community (Room 1971; Majer 1976; Blüthgen and Fiedler 2004). Ant mosaics were described from a variety of tropical habitats, especially from agricultural systems and secondary forests (e.g., Room 1971; Room 1975b; Taylor 1977a; Majer 1993; Majer et al. 1994; Dejean et al. 1994); however, several studies did not find any evidence of ant mosaics in other ecosystems, for example, primary rainforests of SE Asia (Floren and Linsenmair 2000; Ribas and Schoereder 2002). There is good evidence that non-random co-occurrence patterns are common in ant assemblages, regardless of dominance status (Gotelli and Ellison 2002; Sanders et al. 2003 and etc.). However, recent re-analyses of mosaic data revealed many cases where dominant species exhibit rather random co-occurrence patterns, suggesting that interspecific competition may not shape their distribution, or that its effect is weak (Sanders et al. 2007). Evidently, ant assemblages may differ markedly in their organizational patterns; the processes which may lead to a mosaic-like distribution are not yet sufficiently understood.

Insecticidal fogging and direct canopy access are the most common approaches for investigating of inaccessible canopy fauna. Both methods have their advantages as well as limitations for reliable estimations of ant assemblages' composition, and ideally both should be used simultaneously (Floren 2005). However, direct canopy access, in contrast to fogging, enables examination of canopy fauna by the use of bait traps or direct hand collecting. In this way, one can obtain more detailed information about species nesting preferences, stratification or behavioural interactions. Although baiting methods usually record only a proportion of ant species occurring in a tree, they represent a sufficient method for determining ecologically and behaviourally dominant ants. Furthermore, they can provide information on habitat use and activity patterns at a very fine scale (Bestelmeyer 1997). Problems related to bait selectivity may be overcome by using baits which are particularly palatable to many ants and are known to attract predatory, generalist as well as 'herbivorous' ant species (Hölldobler and Wilson 1990). In such cases, a low predation rate on the baits is a good indicator of an overall low predation risk. When data from baiting and canopy fogging were compared directly, neither fogging nor bait traps differed significantly with respect to

the number of species classified as dominants or those that occurred in higher numbers in the trees (Floren 2005).

We investigated the composition of ant assemblages living in the canopy of two locally widespread tree species in lowland rainforest on Papua New Guinea. Although there are several significant studies of Melanesian ants (Wilson 1958; Wilson 1959a; Wilson 1959b, Taylor 1977b; Taylor 1978; Room 1975a; Room 1975b; Snelling 1998), this region remains largely unexplored, including the ant fauna of New Guinea. Some authors (Wilson 1958; Wilson 1959a; Room 1975; Majer 1993 and Missa 1998) described a mosaic-like pattern of ant distribution for this area, although the reported ant mosaics were not tested for non-random co-occurrence patterns of species on the basis of null models (Albrecht and Gotelli 2001), and were, thus, based either on association indices between pairs of species or just on mere observations.

The aim of our study was to survey the canopy ant assemblages in lowland primary forest of New Guinea and focus on the determinants of ant community composition, including the effect of inter-specific interactions, tree species and tree height. Our goal was to determine the ecologically dominant ants, assess their activity and distributional patterns, and their impact on other ant species within the community.

Though both study sites have been extensively explored for some insect groups (Novotny et al. 2002a), only a few limited investigations of ant assemblages occurred there (Novotny et al. 1999). Thus, our intention was to obtain general information about ant assemblages within the study area before focusing on more specific questions about the relationships of the canopy ants and insects interacting with them.

Protein based bait traps (tuna mixed with oil) were used as a collecting method assuming that they would attract a large proportion of the ants occurring in the canopy. This presumption was based on the fact that arboreal ants are known to be nitrogen-limited, in contrast to terrestrial ants which are more carbohydrate-limited (Davidson 1997; Tobin 1994; Yanoviak and Kaspari 2000). Therefore, we expected that canopy ants would prefer protein baits over carbohydrate baits, as has been observed, for example, by Yanoviak & Kaspari (2000) and Hahn and Wheeler (2002) in the Panama rainforest. Moreover, tuna baits usually capture a wider spectrum of ant species than sugar (CHO) baits, such as many general-scavengers or opportunists, and not only predatory species (Agosti 2000).

METHODS

Study site and sampling methods

The study area was located in the vicinity of Madang, Madang province, Papua New Guinea. Two study sites were located in primary lowland perhumid forests around Baitabag (145°47`E 5° 08`S, 50-100 m a.s.l.) and Ohu (145°41`E 5° 16`S, ca. 200 m a.s.l.). The two localities are about 30 km apart, but are connected by a continuous mosaic of primary and secondary forests. The area is covered with species-rich evergreen rainforest (152 species of woody plants with DBH ≥5 cm per hectare (Novotny et al. 2002b). The terrain is hilly, so the canopy is relatively open. The primary forest at both sites is fragmented by 10-30 year old patches of secondary vegetation on abandoned food gardens created as a part of the traditional swidden agriculture. Average annual rainfall in the Madang area is 3,558 mm, with a moderate dry season from July to September; mean air temperature is 26.5 ^{0}C.

Nineteen mature individuals of two locally widespread tree species, *Ficus subtrinervia* Lauterb. & K.Schum (Moraceae) and *Pouteria maclayana* (F. Muell.) Baehni, (Sapotaceae), were selected for our study. Ten individual trees, five from each species, were surveyed at Ohu and five individuals of *F. subtrineriva* and four of *P. maclayana* in Baitabag. These tree species were selected for their relatively high abundance at both localities and their architecture, which is more-or-less typical of a grown canopy tree of the lowland New Guinea forest. The surveyed trees ranged from 22 to 32 meters high (mean = 26, SD= 2.39) with trunk diameters at breast height (DBH) of 50 to 200 cm. All trees were located within primary forest and separated by at least 300 meters from each other. The overall area across which the trees were distributed was approximately 9 km^2 at each site. All trees were surveyed from June to October 2004.

Ants were sampled at tuna baits, set on small square pieces of gauze (5 x 5 cm) and tacked down to bark or leaves on every tree. Two tea spoons of crushed tuna meat with vegetable oil were used to attract ants. Baits were, as far as possible, set at 2, 5, 10 and 15 meters height from the tree base. Above 15 m, baits were placed at 2-metre intervals until the highest accessible section of the crown was reached, which was typically 3-4 m below the top of the tree canopy. In order to cover a larger area of a tree, bait traps were also placed on lateral branches at every suitable occasion. The intention was to distribute all baits across the accessible parts of a tree crown as evenly as possible. In cases when more traps were set at the same height, they were always spaced at least two metres from each other in any direction. From 5 to 15 (mean=10.5, SD=2.39) baits were set on individual

trees, depending on tree height, size, and branching pattern of the crown. All baits were checked after one and three hours of exposure. Number of ant species and number of individuals for each species present at the baits were recorded (or estimated for numbers above 100 approximately) during each control. Ants were always counted only within a 10 x 10 cm square, measured from the centre of the bait. Several ant individuals were removed by forceps and stored in 95% ethanol for identification. In addition to the bait traps, trees were manually searched for other foraging and nesting ants. Single-rope climbing technique (Perry 1978) was used to move along the trees. Two trees a day were explored at most; usually one in the morning and one during early afternoon. The survey was never performed during or soon after a rain. Ant specimens were mounted and sorted into species; voucher specimens were databased and determined to the most available taxonomic level by the use of literature or comparison with museum collections (Museum of Comparative Zoology, Harvard University). All voucher specimens are deposited in the Ant Reference Collection at the Biology Center, Czech Academy of Sciences in Ceske Budejovice, Czech Republic, under Accession Numbers: MJ0236-MJ4288. Photographs of the voucher specimens are accessible at the open-access database 'Ants of New Guinea' on www.entu.cas.cz/png/ants.html.

Data analysis

The effect of environmental factors (site, tree species and height) on ant species richness was tested using Generalized Linear Models (GLM) in STATISTICA 7.0 for Windows (StatSoft, Inc.; Tulsa, OK, USA). Our data set was unbalanced due to different numbers of baits exposed at various heights on every tree, as determined by tree architecture. To ensure a balanced design for statistical analyses, tree height was divided into three intervals (0-10, 10-20, and >20m) and the average number of ant species per bait in a particular height interval was calculated. Data were square-root transformed to achieve normal and homoscedastic distribution.

The composition of ant assemblages was analyzed by methods of gradient analysis using CANOCO, (TerBraak and Šmilauer 1998). The effect of the environmental variables on the species composition of ant assemblages was tested using redundancy analysis (RDA). RDA is a method of direct gradient analysis that identifies multidimensional axes explaining most of the variation in the response variables by the explanatory environmental and spatial variables (Ter Braak 1988). The contribution of each environmental variable was tested by Monte Carlo permutation test (MCP). The

effect of tree species and locality on the composition of ant species was tested using the average abundance of each ant species per tree, regardless of height. RDA with split-plot design was used to assess the effect of height and collecting time on the composition of ant assemblages recorded at baits (15). Tree identity (1-19) and collecting times (T1, T3) were used as covariables when testing the effect of height, while only tree identity was used as a covariable to test the effect of time. The number (log transformed) of canopy species on all baits was used as input data. Non-canopy species (*Leptomyrmex puberulus* Wheeler, 1934; *Pachycondyla sp. 1 Diacamma rugosum* Le Guillou, 1842), as well as foraging species (*Camponotus sp. 3, Camponotus sp.6* and *Camponotus sp. 7*), were omitted from both the RDA as well as the GLM analyses. Similarity of species composition among individual trees was assessed by the Sorensen index and the effect of tree distance on assemblage similarity was assessed by regression.

Repeated measure ANOVA was used to assess the effect of interspecific interactions on the abundance of ants, which co-occurred at the same bait. Co-occurrence was considered in cases where more than one species were recorded on a particular bait during both time intervals. Only species with more than five co-occurrences were included in the analyses (i.e.: *Crematogaster cf. polita* Smith, 1865*, Camponotus vitreus* (Smith)*, Tapinoma melanocephalum* (Fabricius) *and Paratrechina longicornis* (Latreille)). All of the other species were combined into one category ('*other species*'). If more than two such species occurred simultaneously at a bait, the abundances of these non-target species were pooled and tested against the abundance of the target species.

We defined dominant species as those that increased their abundance over the course of observations at the baits and eventually had some direct effect on the abundance of one or more submissive species. The Monopolization Index (MI), sometimes also called 'Ecological Dominance Index' (Andersen 1992b; LeBrun 2005), was used as a measure of dominance. MI is the proportion of baits monopolised by a particular species from the total number of baits occupied by this species. Any species captured bait if it was in sole possession of the bait (by at least 3 workers) during the second sampling period.

Null model analyses (Gotelli 1996) were used to test the statistical significance of the patterns of species co-occurrence at surveyed trees. We tested whether ant communities are randomly assembled, following the approach of Gotelli and Ellison (2002). A presence-absence matrix was constructed (21 rows x 19 columns), with ant species as rows and individual trees as columns. We constructed one matrix for all recorded species and another for the most abundant

species only i.e. those occurring at more than ten baits (*Cr. cf. polita*, *Ca. vitreus, O. smaragdina*). C-scores (Stone and Roberts 1990) were calculated as a metric for co-occurrence within the matrices.

C-Score measures the average number of checkerboard units (CU) between all possible pairs of species. CUs are sites where one of the species in the pair occurs and the other does not. The C-score for a whole assemblage is the mean of all C-scores for species pairs within it. Observed C-scores were than compared with 5000 C-scores generated from randomly constructed null assemblages using a fixed-equiprobable null model (SIM2 in (Gotelli 2000). In this null model, only the row sums are fixed, and the columns (=trees) are treated as equiprobable. Thus, each species occurrence is randomly re-shuffled within each row of the matrix. This null model treats all of the sites as equally suitable for all species (Haukisalmi and Henttonen 1998). The modelled distribution of C-scores was used to determine the exact tail probability for the observed value (Gotelli and Ellison 2002). A mean C-score (averaged across all pairs of species) significantly greater than that expected by chance indicates assemblages structured by competition. (Sanders et al 2007). C-scores not significantly larger indicate random species distribution, and C-scores smaller than expected by chance indicate species aggregation. All analyses were performed using EcoSim 7.0 (Gotelli and Entsminger 2005).

Trophic position of each ant species was assigned on the basis of literature (Blüthgen et al. 2003; Davidson et al. 2003; Shattuck 1999). Unidentified species were classified into trophic groups on the basis of their generic identity.

RESULTS

There were 17 ant species recorded on baits, and an additional 4 species were found foraging or nesting in dead branches and epiphytes (Fig. 1). Of these 21 species, 18 can be considered as canopy inhabitants including 15 visiting baits (according to information in literature and our observations at the site). Abundance and presence-absence data of these fifteen species were therefore included into the analyses. Two hundred baits were exposed on 19 trees, of which 169 (84.5 %) were visited by ants. On average, there were 3.6 (SD=1.46) ant species present on each tree and 3 (SD=1.2) species per bait. The number of ant species present at each bait increased with

height above the ground, while the effect of individual trees, tree species, and study site were not significant (Table1, Fig. 2).

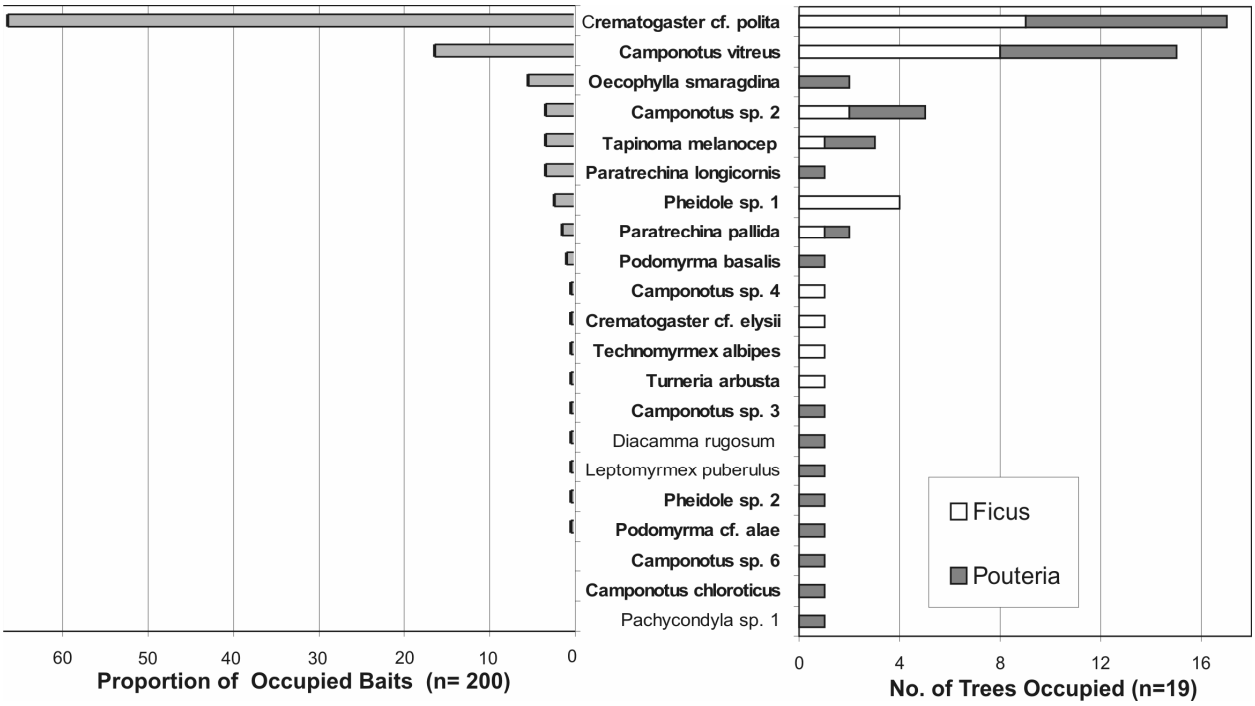

Fig. 1. Proportion of baits occupied by all species recorded at the study trees (left) and number of trees at which particular species were present (right). White columns represent *Ficus subtrinervia*, gray represent *Pouteria maclayana*. Arboreal species are in bold.

Tab.1. Results of GLM analysis of the effect of environmental factors (site, tree species and height) on ant species richness. Only height of bait position had a significant effect on species richness.

Variable	Effect	df	F	Explained variability (%)	p
Height R	**Fixed**	**2**	**10.73**	**1.07**	**0.0002**
Locality	Fixed	1	0.02	0.00	0.8912
Tree species	Fixed	1	1.39	0.07	0.2563
Tree ind.(Locality*Tree)	Random	16	1.02	0.81	0.4631
Tree sp.*Height R	Fixed	2	2.68	0.27	0.0830

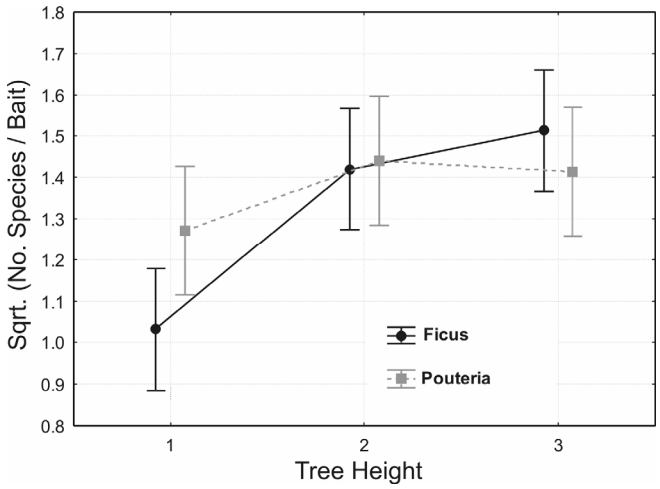

Fig. 2. Relationship between bait height (divided into three categories) and ant species richness per bait (square root transformed). *Ficus* is represented by the black line and *Pouteria* by the gray line. Vertical bars denote 0.95 confidence intervals.

The two tree species differed in bait occupancy (ANOVA, $p<0.00$, df=4). 22 % of baits on *Ficus* were empty, while these comprised only 7% on *Pouteria*. More than 77% of the baits on *Pouteria* were visited by only one ant species, compared to 55% of baits on *Ficus*. Furthermore, baits placed at a lower position on the trunk (up to 14 m) were less occupied than baits placed higher in the tree crown (both tree species analysed together, Fisher's exact test $p<0.00$).

According to the RDA of average species abundances per tree locality and tree species did not have any significant effect on ant assemblage structure (Monte Carlo permutation test, 499 permutations; Locality: F=1.45, p=0.22, df=1; tree species F=1.36, p=0.21, df=1). On the contrary, height did have a significant effect and explained 12.1 % of the variability in ant assemblage composition (Fig. 3, RDA, Monte Carlo permutation test, 499 permutations, F=94.15, p=0.002, df=1). There was no significant relationship between similarity of ant assemblage composition (expressed by the Sorensen index) and distance among individual trees (R= 0.007, $p<0.00$, n=171).

Faunal similarity among trees separated from 0.3 to 3 km was not distinguishable from those separated by 30 km of rainforest.

Some ant species increased, while others decreased, in abundance with height above the ground (Fig. 3). The abundance of *Crematogaster cf. polita* in particular, and to a lesser extent also of *Camponotus spp.*, increased with height while the abundance of *Pheidole sp. 1* and *Oecophylla smaragdina* decreased. The abundance-height response of the remaining species, although appearing positive or negative, is difficult to assess as they were mostly found on only a few baits.

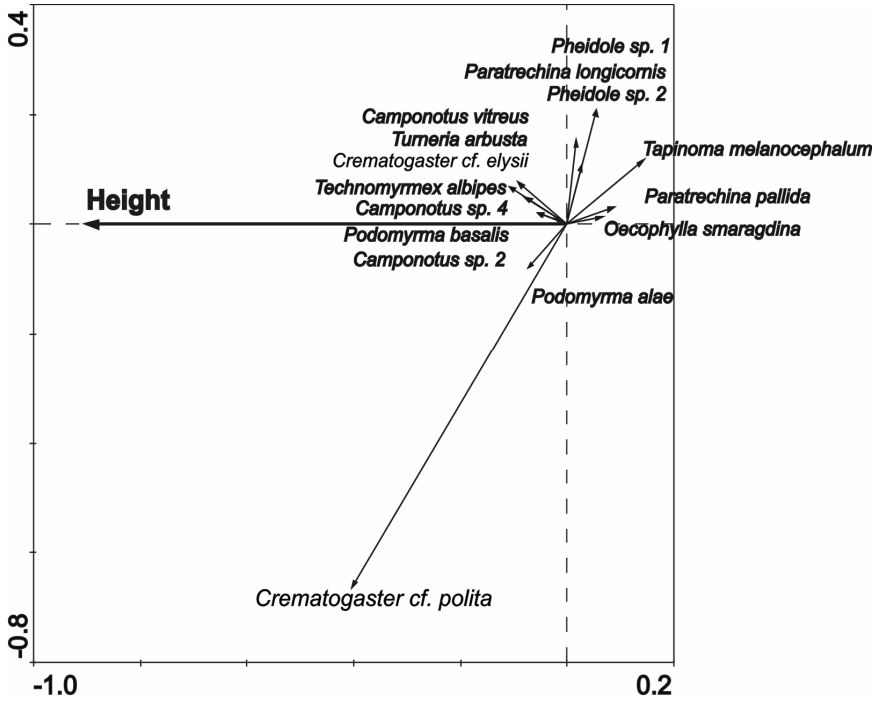

Fig. 3. RDA ordination diagram of the effect of bait height position on composition of canopy ant assemblages. The abundance of *Crematogaster cf. polita* and several *Camponotus* species increased with height. Bait height explained 19.7 % of the variability in ant assemblage composition.

The composition of ant assemblages changed significantly between one and three hours after bait exposure (RDA, Monte Carlo permutation test, 499 permutations, F=12.361, p=0.002, df=2), although this change over time explained only a small portion of the overall variability among the samples (2 %). This was primarily due to the abundance of *Crematogaster cf. polita*, which increased over time, while there was no significant effect on other species.

Crematogaster cf. polita was the most widespread species in terms of occupied trees (17) as well as baits (66.5%), followed by *Camponotus vitreus* Smith, 1860 (15 trees, 16.5% of baits). These two species clearly outnumbered all other species. *Camponotus sp. 1* and *Pheidole sp. 1* were markedly less abundant on baits, but still present on five and four trees respectively.

Crematogaster cf. polita was also found on the highest number of solely occupied baits (n=101, out of 133 at which it was present, monopolisation index MI = 0.73). Although it occurred on fewer baits (11), *Oecophylla smaragdina* was the second most successful species in dominating baits (n=9, MI=0.82). *Camponotus vitreus* was recorded alone on 7 baits, while it co-occurred with other species on 26 baits (MI=0.27).

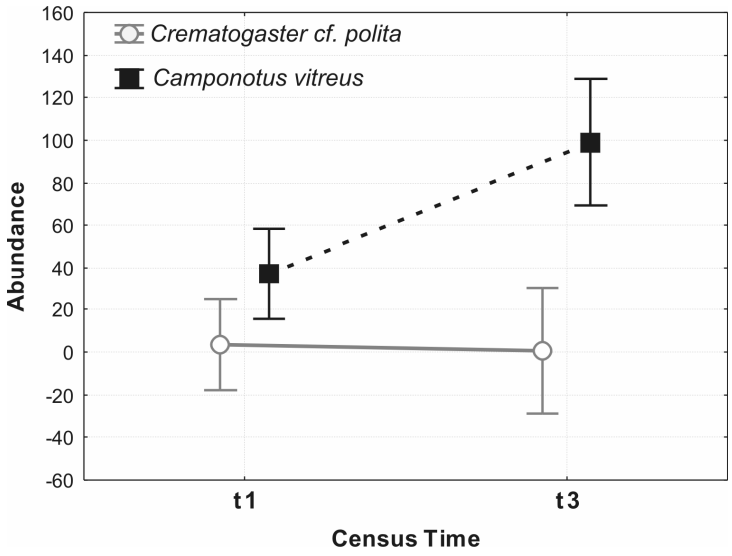

Fig. 4. Relationship between census time (1 and 3 hours) and abundance of *Camponotus vitreus* and *Crematogaster cf. polita* co-occurring at the same baits. The number of *Camponotus vitreus* decreased with increasing number of *Crematogaster cf. polita* workers at a bait. *C. cf. polita* is however able to tolerate *C. vitreus* at the food source to some extent.

The two most common species, *Crematogaster cf. polita* and *Camponotus vitreus*, differed in their abundances on baits in which they co-occurred (Repeated measure ANOVA, N=20, F=14.91, p=0.0005); the number of their workers also changed with collecting time (F=28.32, P<0.0001). As abundance of *Crematogaster sp.1* increased, the number of *Camponotus vitreus* decreased (Fig. 4, F= 34.95, p<0.0001). On the other hand, *Crematogaster cf. polita* did not have any effect on other co-occurring species (n=9, F=3.5, p=0.089,). *Camponotus vitreus* (n=6, F=0.33, p=0.5), *Paratrechina sp.1* (n=4, F=3.77, p=0.09) and *Tapinoma melanocephalum* (n=6, F=2.17, p=0.17) did not significantly change their abundance when co-occurring with other species (not including *Crematogaster cf. polita*), although the number of interactions used in the analyses was rather low.

Co-occurrence analysis based on a null model did not detect any non random patterns in species composition of canopy fauna. Ant assemblages from all trees appeared to be random subsets of the overall species pool, while the same was true for the three most abundant species analysed separately. The observed C-score in our data for the fixed-equiprobable model did not significantly differ from the mean C-score of simulated matrices (observed (all spp.): 2.81, simulated: 2.65,

SD=0.04; $p_{(obs.<= exp.)}$ = 0.78; observed (dominants)= 6.33, simulated: 3.41, SD=9.8; $p_{(obs.<= exp.)}$ = 0.94).

DISCUSSION

We found lower ant species richness per tree in comparison with the majority of other canopy studies in lowland tropical forests (e.g. 7 - 20 spp. per tree in Borneo, fogging, (Floren 2002); 10 spp. per tree (Schonberg et al. 2004); 14-20 spp. per tree (Armbrecht et al. 2001)). On the other hand, several authors described canopy assemblages with similar species richness as in our study (Majer et al. 1993, 32 spp at 20 trees). Although we recorded rather low ant species richness, we believe that our consistent results and minimum of species yielded by exhaustive additional searching reflects the general pattern of ant richness in the canopy at both localities. Furthermore, past investigations at one of the localities (Novotny et al. 1999) using termite baits yielded a similar diversity i.e. 17 ant species foraging on 43 trees in the understory.

Alternatively, the low diversity of ants detected in our study could be a consequence of the short collecting period and eventual selectivity of tuna baits (Agosti 2000). A low epiphyte load on the trees, a relatively open canopy as well as partial fragmentation of the primary forest at both localities may be other contributing factors. While precipitation and temperature are known to affect ant activity at some rainforest areas (Hahn and Wheeler 2002), it is unlikely that these factors played an important role in our case. North-East New Guinea has generally very low seasonality and previous studies (Novotny 1998; Novotny et al. 2002b) found just small seasonal changes in activity and occurrence of insect herbivores living in the canopy at both study sites.

In addition, the relatively low species richness could be caused by moderate fragmentation of the forests surrounding our study sites. Fragmentation is known to decrease species richness (Barbosa 2002; Ross et al. 2002) in comparison with completely undisturbed areas. However, this is also unlikely as both sites are known to have rich ground-foraging and leaf litter fauna (up to 120 ant species per single plot of 20 x 20m) comparable to completely undisturbed sites throughout the rest of the country (Janda and Borowiec *in prep.*). Therefore, it is likely that the ant diversity we detected is typical for average sized trees of the lowland forest in New Guinea. Preliminary investigations from 1 ha plots of primary forest indicate comparable numbers (Janda et al. in prep). Our limited surveys done at freshly cut large canopy tress at undisturbed sites of primary forest

found between 12 to 25 ant species per tree (n=6), but in this case all inspected trees were large, conspicuous, emergent trees with a high epiphyte load (Janda 2006).

Our study showed that tree identity cannot be used as an indicator of the composition and species richness of ant communities. This is not surprising, because ants are known to be unspecialized to particular plants, with the exception of several myrmecophytic species. However, what seems surprising is the high similarity of the ant fauna between the two sampling sites, which are located 30km apart. Although both localities shared only six (29%) ant species, the same two most abundant species occupied the majority of trees at both sites. Our findings suggest that trees at our study sites can be dominated by just several ant species, which might be distributed over large distances. Although the study localities are connected by a mosaic of primary and secondary forest, the investigated trees were between 300 m to 30 km apart.

The effect of height on ant species richness and abundance emerged as the most important factor in our study. Although such a relationship is not necessarily surprising, it has been reported in just a few studies for canopy ants (Schonberg et al. 2004). Height had a strong positive effect on the abundance of *Crematogaster spp*., (mainly *C. cf. polita*) as well as several other species including all *Camponotus spp*., both *Podomyrma spp*., *Technomyrmex albipes* and *Turneria arbusta*. All of them represent ants typically nesting in the upper part of the canopy. On the contrary, it had a negative effect on the abundance of *Pheidole spp*., *Paratrechina* spp. and *Oecophylla.* Except for *Oecophylla*, which is typically arboreal, all of the other species are known to nest mainly in tree bark or under lianas in the understory at the study sites (Janda and Borowiec *in prep.*). Although *O. smaragdina* is an arboreally nesting species, it occurred at higher abundances in the lower parts of trees. This is in concordance with our findings from the understory strata (Janda et al in prep), as well as with the observations of Andersen and Room from Australia (Andersen 1992a; Room 1975b), where this species was found to forage mainly in the understory and on the ground. This situation can be a consequence of N limitation of *Oecophylla* in the canopy. This highly predatory species might therefore migrate to the ground strata to acquire animal prey, which is more abundant in the leaf litter and less N limited in comparison with the canopy (Davidson 2003).

Several explanations are possible for the higher richness (or abundance of some) of ants in the upper canopy. Most likely, the upper parts of trees offer numerous nesting and feeding opportunities and, therefore, nests of arboreal species are located mostly in the upper or middle

portions of the crown. Alternatively, the central and upper portions of the tree crown may have more favourable microclimatic conditions than the lower parts of a tree (Basset et al. 2001). On the other hand, bait occupancy and ant abundance may be higher in the lower parts of trees (up to 14m), where baits were usually placed on the central trunk, so that foraging workers had a higher probability of discovering and monopolising the food source. This, however, does not seem to be the case, as low occupancy of baits placed at the main trunk suggests a higher activity of most of the arboreal species in the upper crown.

We predicted that communities are structured by competition and thus species co-occurrence patterns will be segregated. However, we did not find any evidence of an ant mosaic in our data, as the observed species co-occurrence was within the 95% limits of the frequency distribution for randomized matrices. Similar results arose even if only the 3 most dominant (frequent) species were analysed. This may be a consequence of the highly homogenous distribution of the two most abundant species, which occupied the majority of trees investigated (17 out 19), whereas the remaining species were quite rare and with patchy distribution. We could not detect whether the distribution of the two behavioural dominants (*C. cf. polita* and *O. smaragdina*) was complementary and, thereby, affected by negative interactions at the study sites, due to the low number of trees (2) occupied by the second dominant. Our results, however, might well be in accordance with previous findings that biological processes (such as competition) may not always be the determinant of ant spatial distribution, which might also arise from stochastic processes (Ribas and Schroeder, 2002). At the same time, we can not completely exclude that our findings are a consequence of an insufficient sample size, or a large spatial scale at which the trees were investigated. Without broadening our sample size in future research, we can not exclude the possibility of an ant mosaic at our study site.

Comparison to earlier investigations of the canopy fauna from New Guinea shows a certain overlap between species, albeit their dominance status may differ (due to variability in their distribution and the method used for determining dominance). In addition to *O. smaragdina* and *Technomyrmex albipes* as recorded in our study, Room (1975b) found *Anoplolepis longipes* and *Crematogaster sp. R114* as the dominant ants in tree crop plantations in south New Guinea. An ant mosaic – like distribution was also reported from a locality 30 km north from one of our study sites. One *Crematogaster* species was found to dominate the canopy of 12 out of 21 trees, which were fogged within a $1km^2$ of primary forest (Missa 1998). The author reported two dominant ant species,

Crematogaster major and *Oecophylla smaragdina*, as being distributed in a complementary mosaic, with the latter species tolerating several subordinate species. However, these data, as well as those of Room (1975b), have not been tested by the null model approach, and thus it is not possible to confirm the non-random co-occurrence pattern of the dominant species.

Although *Cr. cf polita* did have an evident effect on the decreasing abundance of *Ca. vitreus*, it was able to tolerate this species to some extent (Fig. 4). This pair seems to be an example of a dominant –subordinate relationship among ant species. Both ants live in a competitive-coexistence relationship (Tokeshi 1999), in which *Camponotus* may occupy the same trees, as well as food sources, with *Crematogaster*, until the local abundance of the dominant reaches a certain threshold. *Camponotus vitreus* specializes on quickly locating and using food sources, before they are monopolised by the dominant *Crematogaster*, which has slower recruitment. Furthermore, we did not detect any effect of *C. cf polita* on the abundance of other species co-occurring at the baits. This suggests that other species are able to coexist with the dominant not only within its territory, but also to some extent at the food sources. Such coexistence may be facilitated by a sufficient abundance and diversity of alternative food sources in the canopy or due to temporal partitioning in resources, which has been observed in several other ant communities (Bestelmeyer 2000; Briese and Macauley 1980; Campos et al. 2007; Cerda et al. 1997). On the other hand, an observation of agonistic behaviour between two species, which usually ends with the exclusion of one of them from baits or experimentally added resources, does not mean that these species compete and exclude each other under natural conditions (Ribas and Schroeder 1998). Consequently, the importance of behavioural dominance and its implications in competition displacement should be viewed with caution, as Andersen and Patel (1994) have suggested. At the same time, it should be stressed that our results are based on a limited number of observations over a short time period, and, therefore, we could not assess all interactions which eventually occurred at the baits.

The four most abundant species in our study overlapped with those studied by Novotny et al. (1999) at one of our study sites and exhibiting high foraging activity on termite baits. In contrast to our study, *Tapinoma melanocephalum* occurred in the highest proportion of trees investigated (43 out of 46). However, the remaining species exhibited similar abundance patterns in the canopy as found in our study, with several *Camponotus species*, including *C. vitreus*, occupying 54% of the trees, *Oecophylla* (23%) and several *Crematogaster* species, including *C. cf. polita*, which occurred in 37% of the trees. Such a high overlap of abundant ants found at many different tree species

suggest a high spatial and temporal composition stability of the local ant assemblage, at least in terms of dominant species.

Although we did not specifically test food preferences in our study, it is possible to determine the approximate trophic position of the recorded species on the basis of known dietary preferences, as well as d15N isotopic levels analysed in other studies (e.g. Bluethgen et al. 2003, Davidson et al. 2003). Low d15N levels are found in ant species that commonly forage for nectar on understory or canopy plants, while intermediate levels occur in species with large colonies that are highly abundant on nectar and honeydew sources and are predacious. The highest levels are found in predominantly predatory ground foraging species (Bluthgen et al. 2003).

Tapinoma melanocephalum, *Paratrechina spp*. and especially *Oecophylla smaragdina* exhibit a high level of predation in our assemblages, based on the data of Davidson et al. (2003) and Bluetghen et al. (2003) for rainforest ants from Brunei and Australia. The genera *Crematogaster* and *Technomyrmex* occupy an intermediate position and utilize mainly honeydew and nectar sources, combined to some extent with predation. Low trophic positions are occupied by the genus *Camponotus*, which is mainly nectarivorous or trophobiotic (Bluthgen et al. 2003, Davidson 2003). This proportion of different feeding strategies within an assemblage suggests that predatory ants do not represent a majority of the biomass in the tree canopy (predatory species accounted for 13% of baits inhabited), but that a majority of the canopy fauna consists of 'herbivorous' and generalist ant species (87% of baits occupied). The distribution of these species is particularly shaped by productive honeydew sources, which are more predictable than prey (Blüthgen and Fiedler 2002).

CONCLUSIONS

We found canopy ant assemblages in the lowland rainforest of New Guinea with rather low species richness and dominated by only a few abundant species. This might be a consequence of various biotic factors of the local forest, but seems to be a natural condition of local ant assemblages. Tree height had a positive effect on species richness of the assemblage. However height had positive effect on abundance of some while negative effect on abundance of other species. Assemblage structures at closely spaced trees were indistinguishable from those situated thirty kilometres away and appeared to be random subsets of the local species pool. We did not find any evidence of an ant mosaic, in which one dominant species uniformly occupied the majority of the studied trees;

however disproving or confirming its existence will require further investigation of more canopy assemblages at the study sites. The highest proportion of ants, in terms of biomass, as well as species occurring in the canopy of the studied trees, were generalist omnivores and ants dependent mainly on trophobiosis.

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Part IV.

Dominance hierarchy and interspecific interactions in ant assemblages in the New Guinea rainforest.

(Milan Janda, Simona Poláková and Jiří Hulcr; mns.)

DOMINANCE HIERARCHY AND INTERSPECIFIC INTERACTIONS IN ANT ASSEMBLAGES IN THE NEW GUINEA RAINFOREST.

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Abstract

Ant assemblages foraging at ground and understory vegetation of New Guinea rainforest were investigated with use of tuna bait traps. In total, 63 species from 26 ant genera were recorded of which four were determined as behaviourally or numerically dominant. Two forest strata differed markedly in bait occupancy, species richness and abundance, as considerable proportion of ant species occurred either on the ground or vegetation. Although ant species exhibited predominantly random co-occurrence patterns at the local scale; we detect unimodal relationship between species richness and abundance of dominants, which is traditionally considered as a result of competitive interactions. Local assemblages showed strong affinities to the Australian rainforest fauna, with genera *Crematogaster*, *Rhytidoponera* and *Pheidole* being the most frequent taxa occurring at the baits.

INTRODUCTION

Studies of ant assemblage organization have repeatedly revealed several functional patterns, such as a species richness-dominance relationship or a mosaic-like distribution. The pivotal role in the maintenance of these patterns has been often attributed to interspecific competition. Competitively superior ants (i.e. dominant species) have been assumed to influence the composition and relative abundance of local ant faunas through competitive suppression or exclusion of some, but not other species (Andersen and Patel 1994; Hölldobler and Wilson 1990; King 2007; Morrison 1996; Savolainen and Vepsäläinen 1988).

As a result of interspecific competition, dominant species are hypothesized to create spatial co-occurrence patterns, which can lead to a mosaic-like distribution of ant species. Ant mosaic theory, originally proposed by Leston (1973), has been one of the fundamental theories explaining spatial distribution of ants. It proposes that ant assemblages dominated by the same species may resemble each other in terms of species composition (compared to communities dominated by different species). Although ant mosaics were described for a number of tropical agricultural habitats (e.g. Majer and Queiroz 1993; Room 1971), or disturbed secondary rainforests (Dejean et al. 1994), the evidence of ant mosaics in primary tropical forests remains contradictory. Several authors argue that the final structure of rainforest communities is to a great extent produced by stochastic events and that species composition is rather unpredictable in space and time (Floren and Linsenmair 2000).

The relationship between dominance and species richness is considered to be one of the most essential assemblage-level patterns in ants. It has been traditionally regarded as the outcome of an interaction between local environmental conditions and the extent of interspecific interactions (Parr et al. 2005). It was defined in the form of the dominance-impoverishment rule (Holldobler and Wilson 1990): the fewer ant species in a local community, the more likely the community is to be behaviourally dominated by one or two species. However, as Parr at al. (2005) stress, the direction of this causality was reversed in some studies, and emphasis was placed on the effect that dominant ants have on species richness, not vice versa (e.g. Andersen 1992; Morrison 1996). Several studies found that the relationship between species richness and abundance of the dominant ants was convex unimodal or negative monotonic across a wide variety of scales and habitats (Andersen 1992; Morrison 1996; Parr et al. 2005).

The ascending portion of the unimodal curve is thought to correspond with increasing habitat favourability for ants. As conditions begin to improve, the abundance of all ants begins to increase, as does species richness (Andersen 1995b; Andersen 1997b). The descending part of the relationship is attributed to an increase in the abundance of dominant ants to such an extent that they reduce species richness via competitive exclusion (Andersen 1992).

While a unimodal relationship might indicate competition, the question of whether it can arise also by other mechanisms, has not been addressed until recently. Such a relationship is typical also for other assemblages (e.g. Caley and Schluter 1996), and may not be a consequence of local interactions, but of stochastic processes or processes operating at larger scales (e.g. historical and biogeographical constraints, immigration and extinction events) (Parr et al. 2005). Recent studies

suggest that, although interspecific competition can be important in the dominance-richness relationship, regional processes might constrain this relationship to a given form, while local factors (such as variation in abundance) can substantially modify it (Parr et al. 2005).

Behavioural or ecological (numerical) dominance in ants is a consequence of particular biological traits, such as a large colony or body size, aggressive and territorial behaviour, fast recruitment of nestmates to food sources, intensive foraging activity or a combination of these features. Because of these features, dominant ants are likely to influence not only the rest of the local ant assemblage, but also other organisms within the same habitat. For example, many dominant ant species have been considered to affect other insects by intensive predation pressure. According to Davidson (1997; 1998) canopy ants should display higher activity and aggression (and thus behavioural dominance) than species living in forest litter. This may be due to a higher abundance of carbohydrates in the canopy, higher predictability of plant exudates as a resource, and the feasibility of monopolization of the canopy space due to its interconnectivity (Basset et al. 2001; Dejean and Corbara 2003).

In this study, we described ant assemblages, their dominance structure, and the processes maintaining this structure in a lowland rainforest of New Guinea. A well-established baiting method and real-time observations were used to quantitatively sample and describe ant assemblages foraging on the ground and in the understory vegetation. We addressed the following questions:

i) what are the dominant ant species within the assemblage and how does their activity and importance differ in different forest strata,

ii) what is the relationship between dominance and richness of ant assemblages on the local scale, and

iii) what are the co-occurrence patterns of ant species at the local scale, and to what extent are the communities structured by competition?

METHODS

Study site and sampling methods

The study area was situated 20 km north of Madang, Papua New Guinea. Research sites were located in a primary lowland perhumid forests around Baitabag (GPS, 50-100 m a.s.l.). The forests are classified as mixed evergreen hill forest (Paijmans 1976) (152 sp. of woody plants with DBH ≥5 cm per hectare; (Novotny et al. 2002) interspersed with patches of secondary regrowth due to the locally practiced slash-and-burn agriculture. The average annual rainfall in the Madang area is 3,558 mm, with a moderate dry season from July to September; the mean air temperature is 26.5 ^{0}C.

We surveyed ant fauna by establishing six 20 x 20 m square plots in which bait traps were laid in a square grid. Study plots were randomly selected within approximately nine square km of primary forest, and were at least 500 m apart from one another. The survey was conducted between January and October 2004. Commercial canned tuna was used as bait, which is the standard in studies of foraging ant communities. A majority of rainforest ants exhibit at least partial omnivory (Blüthgen et al. 2003; Davidson 2005), and our preliminary experiment showed that tuna baits proved to be attractive to a great proportion of local ant species.

In each plot, 25 baits were placed on the ground, separated by 5 m intervals (baits referred to as BT-G hereafter). One meter from each ground plot, a further 25 baits were placed on vegetation in an identical grid fashion between 1 and 2 m above the forest floor (BT-V; 'G' and 'V' refer to ground and vegetation strata). Vegetation baits were placed on randomly selected living plants, including herbs, trees and lianas. Ground baits consisted of two teaspoons of tuna meat laid on 10 x 10 cm platforms of leaf cutouts; each vegetation bait of the same dimension was wrapped in a small square piece of gauze (5 x 5 cm) and attached to bark or leaves. Baits were visited and sampled one (t1) and three hours (t3) following their exposure; each bait was observed for a period of 10 seconds and interactions among ant species were recorded. All ants present were counted and several individuals of each species were collected without disturbing the remaining ants. Only individuals occurring directly on a platform of a ground bait or present within 10 x 10 cm area around the centre of a vegetation bait were recorded. All baiting sessions started between 9:30 and 11:00 in the morning hours and continued to the early afternoon. Baiting was never performed during or soon after a rain. The air temperature in the understory before the first control ranged between 26 to 28.8 ^{o}C (mean 27.6, SD=1.03). In addition to bait traps, 9 m^2 of Winkler leaf litter samples were taken and four person-hours of hand collecting were spent within each plot to thoroughly survey the local

ant assemblages. These additional data will be published elsewhere (Janda and Borowiec *in prep*.) and are not included in this study.

Collected ant specimens were sorted into morphospecies, databased and determined to the lowest possible taxonomic level with the use of literature, direct comparison to specimens in the Museum of Comparative Zoology, Harvard University, and with the help of collaborating specialists. All voucher specimens are deposited in the Ant Reference Collection at the Institute of Entomology, Biology Center of the Czech Academy of Sciences in Ceske Budejovice, Czech Republic. Photographs of many voucher specimens are accessible through the public database 'Ants of New Guinea' at www.entu.cas.cz/png/ants.html.

Measuring dominance

There are various definitions of dominance in ant assemblages. In the present study, two concepts of dominance were applied: i) behavioural (accompanied with aggression) (Cerda et al. 1997; LeBrun 2005) and ii) ecological (numerical) dominance (e.g. Andersen 1992; Davidson 1998). Three categories of interspecific interactions were recognized i) expulsion ii) withdrawal and iii) co-occurrence. Expulsion / withdrawal occurred when one species caused another to retreat at the end of a sampling period (t3) after previously co-existing (during the t1 census). Co-occurrence was noted when two or more species occurred together during both census times. Only species represented by at least three workers at the bait were considered to co-occur. The dominance status of each species was determined on the basis of observed interactions and abundances on baits by calculating the following indices:

i) Monopolization index (MI) i.e. the percentage of baits at which a particular species was the only species present out of all of the baits at which it occurred (Cerda et al. 1997; Santini et al. 2007). Any species was considered to have monopolized the bait if it was the only species present, with a minimum of 3 individuals at both census times, or if it was in sole possession of the bait during the second census, after prior co-occurrence with another species. This index was calculated to compare our results to dominance measures found in other studies, rather than to define dominant species.

ii) Dominance index (DI) i.e. the ratio of times a particular dominant species caused the expulsion of other species (a win) divided by the number of all interspecific interactions. The main difference from MI is that the dominance index does not consider baits occupied solely by one species. Species with high DIs are mainly those exhibiting strong behavioural dominance.

iii) Abundance score (AC). A widely accepted measure for determining a species' ecological dominance is the ratio of its foraging success to its abundance in the environment (Andersen 1992). It is often calculated as the ratio of worker abundance at baits (expressed as a scale) to worker abundance at pitfall traps (Andersen 1992; Cerdá et al. 1997). In concordance with other studies (Parr et al. 2005), mean abundance at baits was used to determine the numerically dominant species, because pitfall traps were not part of the collecting protocol. A frequency distribution of abundance scores (Fig. 2) can be used as an indicator of the relative dominance of individual species (Andersen 1997b). The abundance of each species was scored using a six-point scale (Andersen 1997b, Parr et al. 2005): 1 = 1 individual, 2 = 2-5 individuals, 3 = 6-10 individuals, 4 = 11-20 individuals, 5 = 21-50 individuals, 6 = > 50 individuals. Only data from the first census were included in order to prevent repeated counting of the same individuals.

An ant species was considered dominant in a sample if its DI > 0.5 (wins more frequent than other outcomes) or if its mean AC ≥ 4.0. This value represents a minimum of 10 workers present at a bait and also a major gap in the distribution of mean AC values of frequent species. Dominance and monopolization indices were calculated separately for each stratum, even if a species occurred in both strata. Only species with more than 10 occurrences in the ground samples or with more than 5 occurrences in the vegetation samples were included in the analysis, because ant foraging activity in vegetation is generally lower in comparison with the forest floor (Feener and Schupp 1998; Room 1975a). Our approach does not always allow for distinguishing species exhibiting behavioural dominance (aggression) from those exhibiting only ecological (numerical) dominance (increasing workers' abundance on a bait). Nevertheless, application of both dominance measures allows for the recording of species expressing either type of dominance strategy. Our sites had very high species richness at the baits, while the interactions among species were not distributed equally nor were there enough repetitions. These factors prevented the construction of dominance matrices (e.g. Fellers 1987; LeBrun 2005; Morrison 1996).

Statistical analyses

Insufficient normality and homogeneity of variances in species richness and abundance data forbid the use of parametric methods. The effect of individual plots on species richness and abundance were tested by Kruskal Wallis test, while to determine whether species richness and mean abundance score on traps differed among strata (Ground and Vegetation), the Mann-Whitney test was used.

Differences in species richness between neighbouring baits from both strata (e.g. bait number A1-ground and A1-vegetation) were assessed by the Wilcoxon pair-matched test, while the independence of species richness of these traps was tested by Spearman correlation. The same tests were also used for assessing the differences in species richness between the two census times (t1, t3) and for correlations between the different dominance measures (MI, DI, AC).

The two-tailed Fisher's exact test was used to test for the effect of the ground and vegetation stratum on the changes in species richness or species exchange (one species being replaced by another while species richness on a bait does not change) between the two census times. All these analyses were performed in software STATISTICA 7.0 for Windows (StatSoft, Inc.; Tulsa, OK, USA).

The effects of stratum and census time on ant species distribution among samples was assessed by direct gradient analysis (redundancy analysis - RDA) using CANOCO (terBraak & Smilauer 1998). Both presence-absence and abundance data were used for assessing the effect of bait position while only abundance data were used for analysing the effect of census session. RDA was selected because our data were heterogeneous and contained many rare species, which may affect a CCA analysis (Leps and Smilauer 2003). Significance of the canonical axes was tested by the Monte-Carlo permutation test (499 permutations). Individual trap positions with two levels (ground/tree) were used as covariables. For these analyses, occurrence of a species on a bait during any or both collecting sessions was considered a presence; the sum of the number of workers present during both census sessions was used as the abundance measure.

The relationship between species richness and the abundance of dominants was analysed by local regression using the LOESS smoother regression model in the R statistical package (R Foundation for Statistical Computing). The best fit generalized linear model was selected on the basis of the lowest AIC statistics. The relative abundance of a dominant species (defined on basis of DI or AC) at every bait was calculated as the proportion of its abundance score value (1-6) to the

sum of scores of all species that occurred simultaneously at the particular bait. Only data from the first census (1 hour following bait deployment) were analysed. Data from the ground and vegetation strata were analysed separately as both strata differed in species richness.

Species co-occurrence

Null model analyses (Gotelli and Graves 1996) were used to test the statistical significance of the patterns of species co-occurrence in our samples. We tested whether ant communities are non-random assemblages (against a null hypothesis that they are randomly assembled) following the approach of Gotelli and Ellison (2002). Species occurrences at each bait were summed for both census times. A presence-absence matrix for each plot was constructed where data were organized as species in rows and samples in columns (individual baits, n=25). We constructed 12 separate matrices (6 ground bait sets and 6 vegetation bait sets) with all occurring species, and another 11 matrices for dominant ants only (one of the plots had 1 dominant only). The C-scores (Stone and Roberts 1992) were calculated as a metric for co-occurrence within the matrices. C-Score measures the average number of checkerboard units (CU) between all possible pairs of species. CUs are sites where one of the species in the pair occurs and the other does not, and are calculated as: $CU = (r_i\text{-}S) * (r_j\text{-}S)$, where S is the number of shared sites (sites containing both species) and r_i and r_j are the row totals for species i and j. The C-score is larger for species pairs that show less co-occurrence (Ribas and Schoereder 2002). The C-score for a whole assemblage is the mean of all C-scores for species pairs within it. Observed C-scores were than compared with 5000 C-scores generated from randomly constructed null assemblages using a fixed-equiprobable null model (SIM2 in Gotelli and Arnett 2000). The modeled distribution of C-scores was used to determine the exact tail probability for the observed value (Gotelli and Ellison 2002). The mean C-score (averaged across all pairs of species) significantly greater than that expected by chance indicate assemblages structured by competition (Sanders et al. 2007). C-scores greater or smaller, but not significantly than expected, indicate random species distribution, while C-scores smaller than expected by chance indicate species aggregation. All analyses were performed using EcoSim 7.0 (Gotelli and Entsminger 2005).

RESULTS

In total, 63 species from 26 ant genera were recorded. There were 55 species recorded on the ground baits and 23 species on the vegetation baits. Forty species occurred solely on the ground, eight were found exclusively on the vegetation, while 15 species were shared between the two strata.

Plots did not differ in species richness *(*Kruskal-Wallis, df = 5*,* Chi-Square = 9.9, p=0.078*)* or in ant abundance (Kruskal-Wallis, df = 5, Chi-Square = 5.5, p=0.3572). Ground baits were occupied more frequently (98%, 148 baits) in comparison to vegetation baits (67%, 101 baits). The species richness on baits did not differ between collecting times (Wilcoxon, BT-G (t1vst3): p=0.32; BT-V (t1vst3): p=1). In total, 49 and 45 species were recorded on the ground during the first (t1) and third census (t3), respectively, while there were 22 (t1) and 20 (t3) species recorded on the vegetation.

The two strata differed significantly in species richness (Mann-Whitney, df=1*,* p<0.00, Z=9.81*)*, with ground baits occupied by about two times more species than those on the vegetation (mean No. $Sp._{BT\text{-}G}$ = 2.06, SD=0.94; mean No. $Sp._{BT\text{-}V}$= 0.85, SD=0.73; Fig. 1).

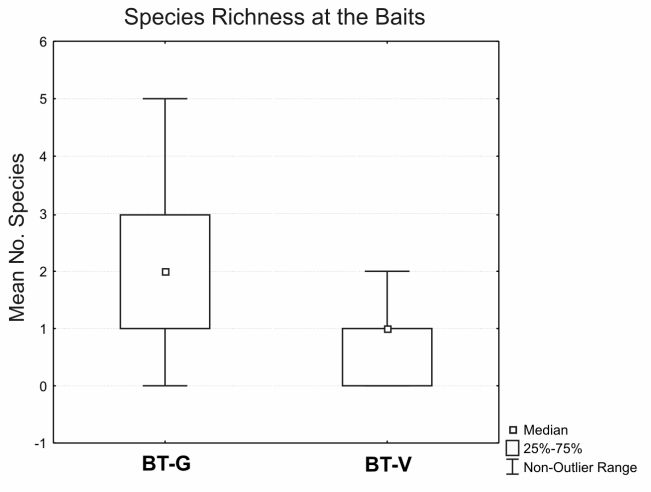

Fig. 1. Mean number of species at tuna baits in two forest strata (BT-G: ground; BT-V: vegetation). Species presence during any of two census times was considered. The two strata differed significantly in species richness (Mann-Whitney, df=1*,* p<0.00, Z=9.81)

In contrast to species richness, mean abundance scores of individual traps (1-6) were higher in the vegetation than on the ground during both collecting intervals (Mann-Whitney, df=1, t1: p<0.05, Z =-2.91; t3: p<0.05, Z=-2.92). Both strata did not differ in the relative proportion of species occurring in each abundance category (1-6) (Fisher's exact test p=0.085); that is, the numbers of species within different abundance categories were comparable. There was, however, a higher frequency of recorded occurrences of single foraging workers (without regard to species identity; category AC=1) on the forest floor in comparison to the vegetation (Fisher's exact test p<0.00). Ant

species richness in adjacent trap sets in the different strata was not autocorrelated. Species richness differed significantly between adjacent ground and vegetation bait sets (Wilcoxon test, $p<0.00$, $Z=8.23$), while there was no correlation of species richness between those traps across all trap sets (Spearman correlation, $R= -0.120$). Community turnover between the two census sessions differed significantly between the strata. Species richness decreased more frequently in the ground baits then in the vegetation baits ($n_{ground} =41$; $n_{vegetation} =20$). Also, a greater number of species was exchanged between the two sessions in the ground baits ($n_{ground} =23$; $n_{vegetation} =6$; decrease: Fisher's exact test, $p=0.0039$; exchange: $p=0.0014$). This suggests that the ant assemblages on the vegetation baits were more stable in terms of species composition than those on the ground.

The RDA using presence/absence data showed that stratum had a significant effect ($df=1$, $F=14.6$, $p=0.002$) on community composition and explained 4.2% of the variability in the species assemblage. All variables, including individual baits as covariables, explained 46% of the variability in the composition of the whole assemblage ($df= 149$, $F=14.7$, $p=0.002$). Use of individual traps' positions as the covariables, and thereby filtering off their effect, allowed for the direct testing of the differences between strata (ground, vegetation). The high percentage of variability explained by trap position is obvious, as it includes many degrees of freedom, corresponding to 25 trap sites in six plots ($df=149$). On the other hand, the absolute contribution of different strata to the explained variability of the assemblage is higher, as it represents 4.2%, but with only two degrees of freedom. This suggests that the effect of forest strata is much higher than the effect of sampling position, and that ground and vegetation traps from one sampling site did not affect each other considerably.

The RDA using abundance data (number of individuals pooled across both census sessions) revealed similar pattern as species occurrences and stratum accounted for 1.8% of the variability ($df=1$, $F=6.6$, $p=0.002$). Census time (t1, t3) did have a significant effect on assemblage composition ($F = 6.3$, $p=0.02$) as well, but explained only 0.7% of the variability in the data.

Species dominance

Four species were identified as dominant within our plots on the basis of the DI and mean AC values (Tab. 1). These were *Oecophylla smaragdina, Crematogaster cf. polita, Pheidologeton affinis* and *Crematogaster* sp. 3. All four dominants, except for *Crematogaster sp. 3*, had high DI (between 0.58 and 1) as well as AC values (Tab. 1). Although *Crematogaster sp. 3* had a lower DI (0.36), indicating that its behavioural dominance was not very strong, it had high abundance scores (4.0 at t1) suggesting that the species was dominant numerically/ecologically. Although the DI and average abundance score values were preferred to MI when assessing dominance in our results, the values of all indices were correlated (Spearman corr., DI versus mean AC: r = 0.70, n = 17; MI versus DI: r=0.85, n = 17; mean AC versus MI: r = 0.78, n=18).

Tab. 1. Overview of the most abundant species and their dominance characteristics. Species considered dominant and values critical for the classification of their dominance status are marked in **bold.** Only species with >10 occurrences at BT-G and >5 occurrences at BT-V were considered.
No. Baits G/V – Number of baits (out of 150) at which species occurred; MI - Monopolization index;
DI – Dominance index; AC – Mean abundance score for collecting time (t1,t3) and strata (G,V).
Mean AC – mean abundance score for both times and strata pooled.

Species	No. Bai G/V	MI G	MI V	DI G	DI V	Mean DI	AC t1 G	AC t1 V	AC t3 G	AC t3 V	Mean AC
Crematog. cf. polita	33/31	0.76	0.97	**0.65**	**0.86**	0.76	**4.73**	**3.72**	**5.44**	**4.68**	4.64
Oecophylla smaragdina	27/8	0.71	1	**0.68**	**1**	0.84	**4.07**	**4**	**4.32**	**4.75**	4.28
Crematogaster sp. 3	1/29	-	0.76	-	0.36	0.36	-	**4**	-	**4.25**	4.13
Pheidologeton affinis	23/0	0.74	-	**0.58**	-	0.58	**4.54**	-	**5.15**	-	4.84
Paratrechina sp. 3	25/0	0.16	-	0.09	-	0.09	2.63	-	2.68	-	2.66
Leptomyrm. puberulus	18/0	0.17	-	0.06	-	0.06	3.00	-	2.58	-	2.79
Rhytidoponera strigosa	17/0	0.12	-	0.08	-	0.08	1.44	-	1.20	-	1.32
Pheidole sp. 10	11/8	0.00	0.63	0.00	0	0.00	2.63	3.33	2.71	4.00	3.17
Rhytidoponera inops	10/0	0.40	-	0.20	-	0.20	1.56	-	2.00	-	1.78
Technomyrmex albipes	8/5	0.50	0.6	0.38	0.5	0.44	3.57	3	5.40	3.67	3.91
Camponotus vitreus	2/15	-	0.4	-	0	0.00	-	2.1	-	1.91	2.01
Pheidole sp. 11	2/5	-	0.6	-	0.33	0.33	-	4.6	-	5.00	4.80
Rhytidopon. aenescens	42/0	0.07	-	0.09	-	0.09	1.60	-	1.68	-	1.64

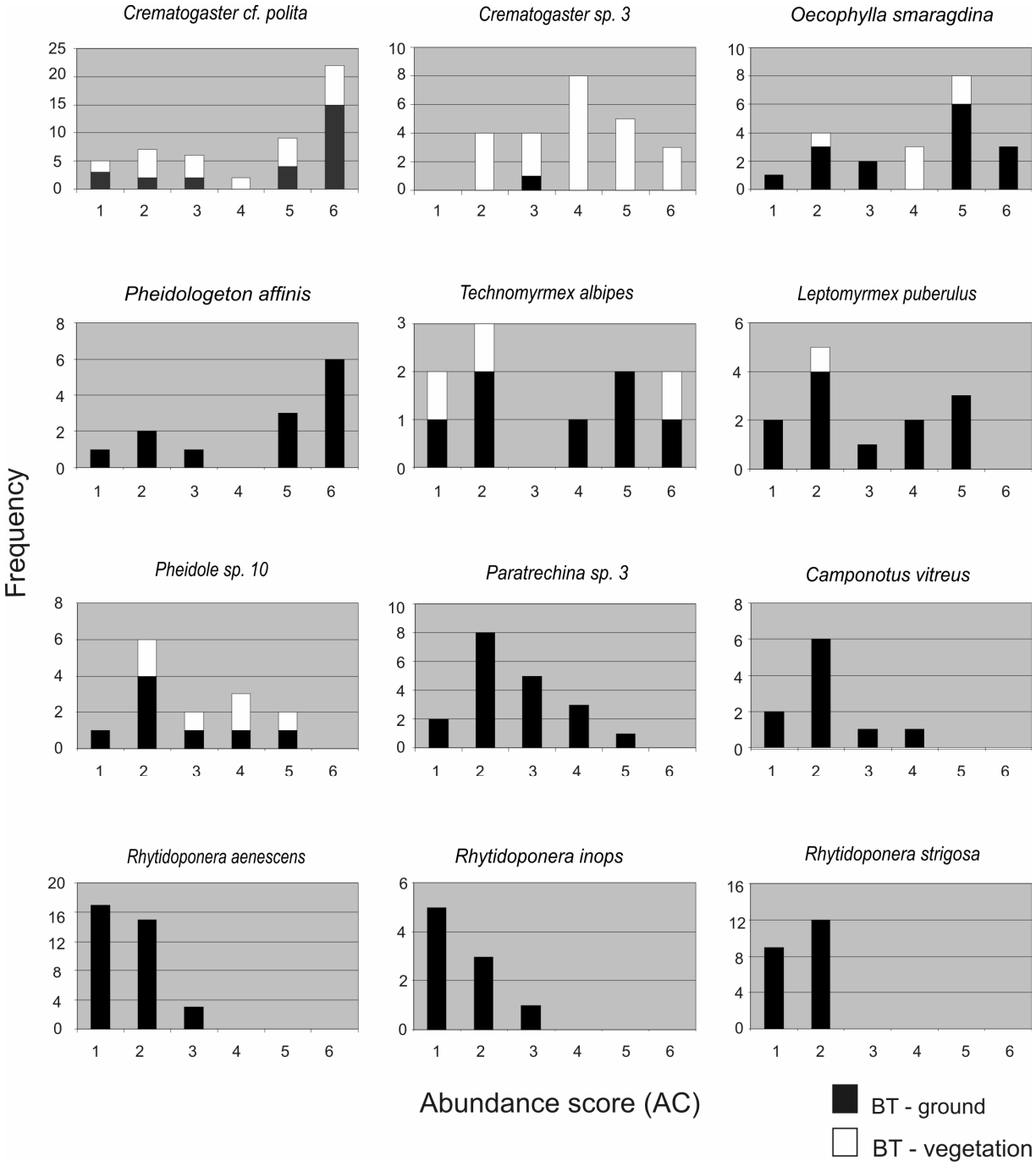

Fig. 2. Frequency distribution of abundance scores at baits (AC 1-6) for the twelve most common species, including dominants (first four graphs). Only data from first census time (t1) are considered. Black and white bars represent ground and vegetation records, respectively.

The frequency distribution of abundance scores (AC) (Fig. 2) confirmed the dominance position of several individual species. Species with distributions skewed far to the right (*Crematogaster cf. polita*, *Oecophylla smaragdina* and *Pheidologeton affinis*, Fig. 2) exhibited high behavioural dominance. Species with distributions skewed to the left (e.g. *Rhytidoponera spp.*, *Camponotus vitreus* and *Paratrechina sp.3*) had low behavioural dominance, while species with relatively even distributions had moderate behavioural dominance (*Crematogaster sp. 3*, *Technomyrmex albipes*, Fig. 2).

Behavioural dominance (frequency of wins) did not differ between strata (vegetation: 32% n=58; ground 21% n=262) (Fisher's exact test, p=0.085). The dominant species (all pooled together) were equally successful in both strata and won 65% of their interspecific interactions on the ground and 64% in the vegetation.

The GLM model with loess smoother revealed a unimodal relationship between the relative abundance of dominants and the number of species at baits. In the ground samples, the correlation is positive where the abundance of dominants is low (10-15%), but strongly negative where the abundance of dominants exceeds a certain threshold level (bandwidth = 0.67, degree = 2; Fig. 3). In the vegetation stratum, the relationship curve is more leptokurtic and even (bandwidth = 0.75, degree = 2; Fig. 3), while species richness reaches its maximum at medium levels of dominance, i.e. between 38 and 60 percent.

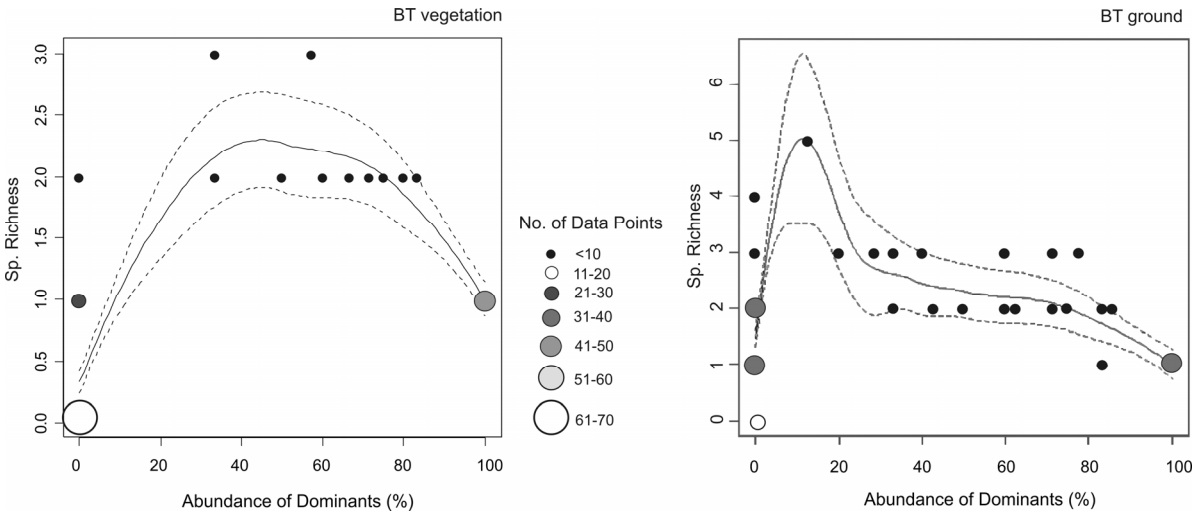

Fig 3: Relationship between relative abundance of dominant ants and sp. richness. (X axis represents % of total AC of all species co-occurring at the bait, Y axis shows number of species present at the bait). Left: BT – vegetation; Right: BT – ground. Size of data points correspond with number of records for the given value.

Species co-occurrence

Within plots, we predicted that communities are structured by competition and thus species co-occurrence patterns will be segregated. However, this was true for ground baits in only two plots and for vegetation baits in one plot (Tab. 2). Furthermore, we detected one case of species aggregation in the ground baits (plot 7). In plots where segregation occurred on the ground, the same pattern did not occur in the vegetation, and vice-versa. When dominant species were analysed separately, competition was detected at two plots where either segregation or aggregation was detected previously (plots 7 and 3). The assemblages from eight out of twelve examined sets (6 plots x 2 strata) appeared to be random subsets of the overall species pool. All exhibited a segregated pattern when data from all plots were pooled together according to strata.

Tab. 2. Results from null model analyses of co-occurence patterns for all species at plots (left) and for dominants only (right). The first column indicate plot and forest strata (G/V), the observed C-score is the C-score calculated from the observed assemblages, and the simulated C-score is the mean C-score for 5000 randomly assembled communities. The observed C-score P is the one-tail probability that the observed index was greater than expected by chance. An SES (standardized effect size) > 2 indicates segregation (**seg.**), and an SES < 2 indicates significant species aggregation (**agr.**).

	All species						Dominants					
Plot/ Strata	**Obs. matrix**	**Rand. matrix**		**P values**			**Obs. matrix**	**Rand. matrix**		**P values**		
BT-G	**C-Score**	**Mean of simul.**	**sd**	**(Obs>Exp)**	**SES**	**Pattern**	**C-Score**	**Mean of simul.**	**sd**	**(Obs>Exp)**	**SES**	**Pattern**
1	5.81	5.51	0.41	0.242	0.74		3.67	2.99	0.93	0.613	0.72	
2	**7.97**	**6.98**	**0.46**	**0.006**	**2.15**	**Seg**	48.00	30.18	11.79	0.165	1.51	
3	5.46	4.45	0.53	0.024	1.90		15.00	14.71	12.68	0.687	0.02	
4	**4.08**	**3.72**	**0.17**	**0.005**	**2.10**	**Seg**	12.00	10.18	3.00	0.415	0.61	
6	4.05	3.55	0.21	0.003	2.37		5.67	3.95	1.75	0.433	0.98	
7	**4.38**	**7.02**	**0.36**	**1.000**	**-7.23**	**Agr**	**40.33**	**20.57**	**5.47**	**0.000**	**3.61**	**Seg**
BT-V												
1	5.20	5.32	1.58	0.520	-0.07		17.00	5.57	7.98	0.328	1.43	
2	6.50	5.52	0.83	0.127	1.19		20.00	13.99	5.16	0.374	1.16	
3	**15.83**	**9.65**	**2.73**	**0.016**	**2.27**	**Seg**	**60.00**	**26.14**	**12.63**	**0.025**	**2.68**	**Seg**
4	2.52	2.53	0.12	0.592	-0.09		2.33	2.08	0.46	0.745	0.54	
6	5.62	4.78	0.80	0.154	1.05		-	-	-	-	-	
7	3.62	3.25	0.25	0.062	1.45		7.00	5.10	3.11	0.73	0.61	

Species composition of assemblages

Although total species richness was high, most of the species were rare (Tab. 3). Only 12 species occurred more than ten times at the baits. *Crematogaster*, *Rhytidoponera* and *Pheidole* were the most common genera and occupied 33%, 23% and 22% of the baits (n=300), respectively (Tab. 3).

Genus	Occurr.	% of baits (n=300)	No. Species
Crematogaster	97	32.33	4
Rhytidoponera	69	23.00	3
Pheidole	65	21.67	17
Oecophylla	35	11.67	1
Paratrechina	27	9.00	2
Camponotus	23	7.67	2
Pheidologeton	23	7.67	1
Leptomyrmex	19	6.33	1
Technomyrmex	13	4.33	1
Solenopsis	10	3.33	4
Polyrhachys	8	2.67	3
Tetramorium	8	2.67	5
Tapinoma	6	2.00	1
Oligomyrmex	5	1.67	3
Pachycondyla	4	1.33	1
Pseudolasius	4	1.33	1
Anonychomyrma	3	1.00	1
Cardiocondyla	3	1.00	1
Lordomyrma	3	1.00	3
Aphenogaster	2	0.67	1
Odonotomachus	2	0.67	1
Diacamma	1	0.33	1
Podomyrma	1	0.33	1
Strumigenys	1	0.33	1
Hypoponera	1	0.33	1
Pristomyrmex	1	0.33	1

Tab 3. List of genera recorded at baits with numbers of their occurrences and species.

Only ten genera were represented by more than one species; the most species rich was *Pheidole* with 17 species, followed by *Tetramorium* (five species), and *Crematogaster* and *Solenopsis* (four species each). The most frequently occurring ants without regard to strata were *Crematogaster cf. polita*, *Rhytidoponera aenescens Oecophylla smaragdina* and *Crematogaster sp. 3*. If the different strata were considered separately, then the five most frequent species on the

ground were *Rhytidoponera aenescens, Crematogaster cf. polita, Oecophylla smaragdina, Paratrechina sp. 3 and Pheidologeton affins*. Baits in the vegetation were most frequently inhabited by *Crematogaster cf. polita*, *Crematogaster sp. 3*, *Camponotus vitreus* and *Pheidole sp. 10*. (Fig. 4). As seen in Fig. 4, several species did overlap between the ground and trees (n=18), but only a few of them reached similar abundances in both strata, namely *Crematogaster polita* and to a lesser extent *Pheidole sp. 10* and *Technomyrmex albipes*. All other species showed a strong preference for a particular stratum or occurred only within one of them.

Contrary to the majority of ground-foraging species, there were no vegetation-foraging ants (considered those with more then 3 occurrences) which were present exclusively on trees. Even species with a strong preference for the vegetation, such as *Crematogaster sp. 3* and *Camponotus vitreus*, were spotted at least once on the ground baits. More interestingly, the tree-nesting *Oecophylla* was even found to be more active on the ground than in the understory.

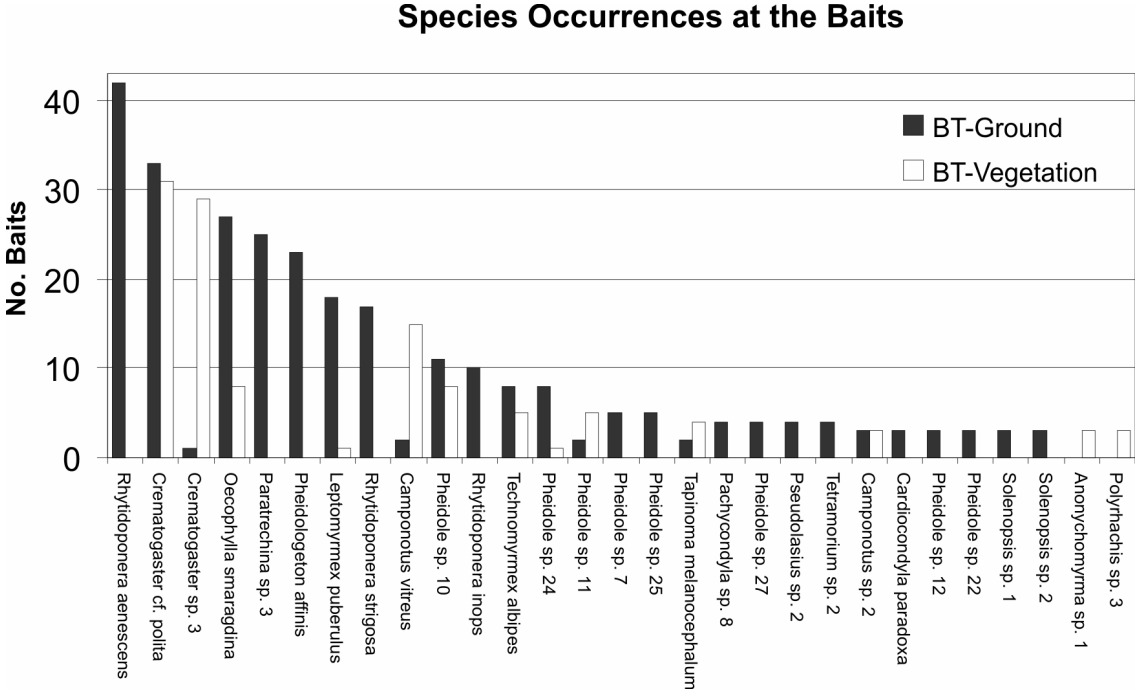

Fig. 4. Species occurrences at baits with regard to forest strata. Number of baits visited at ground (black bars) or vegetation (white bars) without regard to census time. Only species with above three occurrences in total are shown.

DISCUSSION

This study demonstrated high species richness recorded at tuna baits in the lowland primary forest of New Guinea. The sixty three species found at the baits represent approximately 8% of all described ant species from New Guinea (741 spp.) and 29% of the ant species recorded so far at the study area (Janda and Borowiec *in prep*).

We found an evident effect of strata on the composition of rainforest ant assemblages. A considerable proportion of ant species occurred either on the ground or vegetation and both forest layers differed in richness, bait occupancy and species abundance. There was, however, almost no effect of census interval, suggesting that one collecting time would be sufficient for assessing the approximate composition of the assemblage. Nevertheless, such an approach would not allow for the collecting of adequate information about species interactions and dominance levels. Although it can be expected that closely placed traps might be more likely occupied by the same species, our analyses revealed much stronger effect of strata on the composition of fauna than the trap position. Not only did ground and vegetation baits differ in species richness, there was no correlation in species richness between them, excluding the possibility that richer ground traps were close to richer vegetation traps and vice versa.

Dominance structure of assemblage

The three arboreal species *Oecophylla smaragdina, Crematogaster cf. polita, Crematogaster sp. 3* and the ground nesting *Pheidologeton affinis* were determined as the dominant ants in this study. All of them occurred at a high proportion of the baits, dominated and monopolized the majority of baits at which they occurred and achieved high mean abundance scores as well (Tab.1, Fig 2). At least three of these species occur commonly across all of New Guinea and are known to be dominant elsewhere (Hölldobler and Wilson 1990).

There was good congruence between all the dominance measures used in our study (MI, DI, AC). All species with high DI also had high monopolisation index (MI) values. However, several species with relatively high MI (*Rhytidoponera inops*, MI=0.4; *Camponotus vitreus*, MI=0.4) had low values of DI. This suggests that there could be problems in using MI for determining dominance status, because this index considers the presence of a species at all baits regardless of whether interspecific interactions occur or not. It can therefore overestimate the dominance status of

abundant opportunistic species, which may occur solely on baits, as for example *Rhytidoponera inops* and *Camponotus vitreus* in this study.

Comparison between average AC and DI can reveal different strategies for some species. For example, *Pheidole sp. 10* had an average abundance score (AC=3.17) together with a zero DI (Tab.1), suggesting that, although this species can reach higher abundances on baits, it is not a strong competitor and is able to tolerate other species or loses in interspecific confrontations. Further comparisons of the dominance indices for the two dominant *Crematogaster* species shows that *Crematogaster cf. polita*, although attaining a similar occurrence frequency and abundance score in the vegetation as *Crematogaster* sp. 3, is a markedly better competitor and behaviourally superior to its congener (DI=0.86 vs. DI=0.36). This might also be related to its ability to forage extensively in the litter.

Ant dominance is often vaguely defined in many studies (Room 1975a). Also, only one approach is often used to determine dominant species in those studies, but they do not specify which type of dominance they address (behavioural or numerical). On the basis of our results, we suggest that both types of indices (DI, AC) should be used simultaneously to reveal dominant species in an assemblage, unless the study specifically focuses on behavioural interactions (dominance) among individual workers.

In contrast to other studies (Yanoviak and Kaspari 2000) and the predictions of Davidson (1996), we did not detect significantly higher levels of dominance in the vegetation; dominant ants seemed to be equally successful in winning interspecific interactions in both strata. On the other hand, if species would be differentiated on the basis of their nesting strata, and not according their actual foraging activity, then arborally nesting ants would be considered as being highly dominant (44% of wins) in comparison to terrestrial ants (12.8% of wins, Fisher's exact test, $p<0.00$). In general, our findings are in concordance with the hypothesis that arboreally nesting ants are more N-limited, and show higher behavioural dominance, in comparison with litter ants (Davidson 1998). Tree nesting species were among the most frequent and highly dominant species on baits, although they were active in both forest strata.

Room (1975b), on the basis of workers' biomass in chemical knockdown and hand collecting samples from cocoa plantations, reported an additional three dominants from New Guinea. He described *Technomyrmex albipes* as the most dominant ant followed by *Anoplolepis gracilipes* and *Oecophylla smaragdina*. *A. gracilipes* is a locally common species in New Guinea, but it is often

confined to disturbed areas and was not recorded during our survey. Although *T. albipes* is a common species at our study site, it occurred with low frequencies in our research plots (13 occurrences), which did not allow for an assessment of its dominance. It seems that it could reach dominant status, as it exhibited relatively high abundance scores and medium DI.

Oecophylla is a well-known dominant across the world's tropics, including Australia, where, however, it may be locally suppressed by the highly dominant *Iridomyrmex* (Andersen 1992). *Crematogaster*, *Pheidole* and *Monomorium* (i.e. Generalized Myrmicinae after Andersen 1995a) are subdominant and moderately competitive ants in warm open habitats of Australia, but assume behavioural dominance in warm, shady habitats (Vanderwoude 1997). This is also the case for New Guinea lowland forests, where, in contrast to Australia, the dominant *Iridomyrmex* is often missing. On the other hand, other opportunistic genera, such as *Paratrechina, Rhytidoponera, Odontomachus* or *Tetramorium*, seem to be pure competitors in a majority of habitats, often being locally abundant. Although our data confirmed a significant shift between Australia and New Guinea in the dominance position for *Crematogaster* or *Oecophylla*, this was not the case for the above-mentioned opportunistic genera.

Dominance-richness relationship

Our short-term behavioural data produced a unimodal relationship between species richness and the abundance of dominant species at baits. Despite the fact that there was a marked difference in both the total and mean species richness between the vegetation and ground strata, both reached similar values of species richness at medium levels of dominant abundance, i.e. 2.25-2.5 species per bait at 50 % of the dominance level (Fig. 3).

Unimodal relationship has been repeatedly reported for ant assemblages (Adler et al. 2007; Andersen 1992; Bestelmeyer 2000) across many different habitats or continents and is considered to be a general characteristic for ant interactions at baits (Parr et al. 2005). In most studies, data from a single habitat type did not reveal the whole course of the curve (e.g. Andersen 1992). Traditionally, the dominance-richness relationship was regarded as the outcome of an interaction between local environmental stress and the extent of interspecific interactions i.e. behavioural dominance (Parr et al. 2005). As demonstrated by Parr and coworkers (2005) on the basis of the null model approach, several alternative explanations exist for the unimodal shape of this relationship. It might result from

species-abundance frequency distributions, which can produce both the ascending as well as the descending part of the relationship. The ascending portion of the curve can be a function of the way in which community assembly leads to a skewed abundance frequency distribution (see Bell 2001; Hubbell 2001; Tokeshi 1999), while stress is not required to produce low richness and dominance, as is often assumed (Parr et al 2005). Furthermore, null models suggest that the presence of both high richness and high dominance levels are possible under conditions similar to the aggregation model of coexistence proposed by Atkinson & Shorrocks (1981). Here, the higher levels of intraspecific competition relative to interspecific competition enable inferior competitors to coexist, thereby maintaining high species richness (Parr et al. 2005). Therefore, the question arises of why the combination of high species richness and dominance is uncommon in ant assemblages. In natural conditions, usually where there is more than one dominant ant species across a number of baits, the number of species coexisting at a bait is low. One possible explanation is that interspecific competition is much more pronounced than intraspecific competition in ants, which makes coexistence via the aggregation model unlikely (Parr et al. 2005). Field data (Andersen 1992), as well as null models (Parr et al. 2005), suggest that the descending part of the dominance-richness relationship can result from the constraints associated with the shape of the abundance frequency distributions, as well as interspecific competition. It seems that regional processes might constrain the dominance-richness relationship, while local factors, such as competition, may alter it further (Parr et al. 2005).

One major difference between our study and those examining dominance-richness relationships in ants is that most authors present data on much larger scales, across several habitat or continents. Therefore, in contrast to our study, which used single baits, data from one study plot or locality are usually considered as basic data points in assessing this relationship. As a result, important differences in the expression of the humped diversity pattern arise between habitats. For example, Andersen (1992) found only the descending part of the relationship in savanna plots, while the ascending portion was detected just in forest sites. The disclosure of the whole course of the unimodal relationship between local diversity and abundance of dominants at the scale of several plots is therefore surprising. If we assume habitat favourability to be more-less uniform, and species richness is relatively high within our plots, then the unimodal relationship is likely to be produced by local interactions, such as competition. On the other hand, considering the random co-occurrence

patterns detected for dominant ants (see below), our data suggests that other local factors, in addition to competition, are likely to have significant effects on the structuring of ant assemblages.

Species co-occurrence patterns

We found all types of co-occurrence patterns at the local scales of the ground and vegetation strata within our plots. Random co-occurrence patterns were found in 8 out of 12 assemblages, although we expected all assemblages to exhibit segregated patterns. According to theories of competitive asymmetry and ant mosaics, competing species should i) co-occur less often than expected by chance among communities and ii) within communities, species that co-occur should exploit different resources (Brown and Wilson 1956). We thus expected that complementary exclusion of dominant species within plots would be even more pronounced and, hence, lead to strongly segregated distribution patterns. This was, however, the case for only two plots, in which a high C-score (segregation) was detected for the whole assemblage.

Our findings are in partial contrast with many previous studies, which showed that competition affects interspecific spatial patterns among nests (Acosta et al. 1995; Bernstein and Gobbel 1979) and the spatial distribution of foragers (Baroni Urbani 1991; Bernstein 1975). Our findings are surprising, because our data come from observations at baits, where the effects of behavioural interactions should be most pronounced (Sanders et al. 2007).

Only a few studies have reported random co-occurrence patterns at the local scale. However, there is growing evidence based on null model analyses of random co-occurrence within ant communities (Gotelli and Ellison 2002; King 2004; King 2007; Ribas and Schoereder 2002). Recent community-wide tests for competition induced assembly rules have so far revealed a contrasting view that competition, at least in the form of competition hierarchies, is not obviously impacting community-wide assembly patterns (King 2007). Furthermore, experimental studies suggest that some behaviourally dominant species have no obvious impact on the vast majority of co-occurring species (Gibb and Hochuli 2003), if any species at all (King and Tschinkel 2006). However, the patterns of non randomness in species spatial distribution at the local scale might also arise from mechanisms other than competition, such as neutrality (Bell 2005), spatial heterogeneity or different migration ability (Molofsky and Bever 2002).

There are several alternative explanations for the situation at the local scale, in which ants potentially interact, where species co-occurrence patterns were mostly random and there was no obvious effect of behaviourally dominant species on the co-occurrence patterns. First, if ants are good dispersers and forage freely across the whole study plot, then there would be random mixing of all species (Sanders et al. 2007). However, this seems unlikely at least for ground-foraging ants which maintain territories between 2-3m from the nest, but may be the case for arborally nesting species, which seem to forage for longer distances (Dejean and Corbara. 2003; Gove and Majer 2006). Second, because we combined counts of ants from two observations, and baits were exposed just for 3 hours, we may not have been able to detect the temporal partitioning of resources (Albrecht and Gotelli 2001). However although we detected some effect of census time on the composition of the assemblages at the baits, there was not a large turnover of species between collecting times, especially in the case of dominants. Our data thus contribute to the growing evidence that, in some cases, competition between ant species does not appear to form competition hierarchies at the local scale at which species actually interact (King 2007).

Habitat preferences

We did detect significantly higher species diversity on the ground than in the understory vegetation. This is in accordance with the general presumption that the ground layer offers a wide range of favourable nesting habitats and that baits can also be visited by many leaf-litter dwelling species. A number of studies report lower ant richness and activity in the understory (e.g. Feener and Schupp 1998; Reichel and Andersen 1996; Room 1975a) in comparison to the ground; a similar situation was reported from New Guinea cocoa plantations by Room (1975b). In addition, vegetation traps can have a lower probability of occupancy as a consequence of their distribution in three-dimensional space in contrast to the ground baits, which are distributed in two-dimensional space. Not unexpectedly, the less species rich vegetation baits were more stable in terms of species occurrence and exchange. Conversely, high species richness on the ground contributed to a higher fluctuation of species.

The predictions of Davidson and Tobin (Davidson et al. 2003; Tobin 1998 ("1997")), that ant activity and behavioural dominance is higher in forest canopy than on the forest ground, were based on evidence, for example, from Neotropical rainforests (Davidson 1998). In contrast to our study,

which recorded much higher bait occupancy and species richness on the ground, Yanoviak and Kaspari (2000) found no difference in species richness between the canopy and litter of a Panama forest. In addition, they reported higher ant activity and behavioural dominance in the canopy. In comparison to New Guinea, the Panamian ant assemblages were quite discrete with no overlap between litter and canopy species. Unlike our study, Yanoviak and Kaspari (2000) presented data for a whole span of canopy height and thus our results from the understory are not fully comparable. On the other hand, an analogous study comparing ground and understory vegetation assemblages with baits placed on trunks (Hahn and Wheeler 2002) found a similar pattern, with arboreal ants exhibiting higher activity than terrestrial species. In Panama, however, ant activity in the canopy and understory seemed to be affected by seasonality, which is more pronounced there in comparison to our New Guinea site (Kaspari and Weiser 2000; Hahn and Wheeler 2002). Nevertheless, our preliminary investigations further support rather low species richness and activity of canopy ant assemblages in New Guinea in comparison to ground foraging fauna (Janda and Borowiec *in prep*.) Although there appear to be even lower ant activity on trunks than in the upper canopy, overall richness and occupancy at the baits seem to be still markedly lower in the upper canopy than in the ground strata (Janda and Konecna *in prep*.).

In contrast to Yanoviak and Kaspari (2000), our data do not support the findings of higher recruitment rates to protein baits in the canopy as reported by them from the Neotropics. On the other hand, our results agree with their findings of higher average abundances at occupied baits in the canopy. In our study, higher mean abundance on the vegetation baits was caused by a markedly higher frequency of single foraging workers occurring on the ground baits. Single workers in terrestrial assemblages usually represented opportunistic species with small- to medium-sized colonies, which are often behaviourally subordinate (Hahn and Wheeler 2002). Otherwise, the ground and vegetation strata did not differ in the proportion of species from each abundance category. Moreover, the mean abundance of the four species occurring frequently in both strata did not differ, indicating that they maintain similar numbers of workers at the food source independently of microhabitat (although frequency of occurrence may differ).

One of the main factors contributing to the mutual resemblance of both strata was the tendency of arboreal or vegetation-based species to forage on the ground. Every species with more than four occurrences in the vegetation was recorded at least once in the litter. Furthermore some arboreal species (*Oecophylla smaragdina, Technomyrmex albipes*) were even more frequent on the

forest floor than on vegetation (Fig. 4). The reverse is not true for the majority of terrestrial species. A similar situation was earlier reported by Wilson (1959) and Room (1975a), who mentioned the tendency of highly arboreal species to occur in the lower arboreal zone or forage on the ground (although Room (1975a) noted occasional foraging of *Rhytidoponera araneoides* on cocoa trunk*s)*. In contrast to our data, Wilson (1959) also records *Polyrhachis erosispina* and *Anonychomyrma scrutator* as common arboreal inhabitants of the ground stratum. A similar situation was reported from Australian rainforests, where *Oecophylla* and *Camponotus vitreus* forage on the forest floor and many other arboreal species are active on low vegetation (Andersen and Spain 1996). In sum, our results confirm the important affect of forest stratum on species composition of ant assemblages; however the differences in ant fauna seem to be less pronounced in New Guinea than in the Neotropics.

Assemblage composition

The ant species recorded during our survey were typical representatives of the Melanesian fauna and many dominants were identical or closely related to Australian rainforest species. Twenty two out of twenty six genera were in common with the records of Room (1975a), who studied ground foraging ants at various habitats in the southeastern part of New Guinea. However, he reported only 14 of our genera from primary forest and the remaining eight genera from various disturbed habitats, such as rubber, cocoa, coffee and oil palm plantations. Nevertheless, his sampling effort was lower than in our study. Due to problems with identification, only 11 species were found in both Room's (1975a) and the present studies, which is probably an underestimate.

Since New Guinea ants represent an intersection of the Australian and SE Asian fauna, the generic composition of our assemblage was quite similar both to North Australian and Bornean tropical rainforests.

We found the highest generic overlap (21 gen.) with the ground foraging and vegetation fauna of Sabah (Brühl et al. 1998) and the monsoon rainforest around Darwin, in the Australian Northern Territory, (19 gen., Reichel and Andersen 1996). There were fewer shared species (14 and 13 spp.) with studies from the Kimberly region, the English Company Islands in Australia (Woinarski et al. 1998), or from the Philippines (Samson et al. 1997). However, all of the studies differ in their methodology to some extent and it is likely that certain groups were undersampled.

Most of the other studies did record lower frequency of the genera *Technomyrmex*, *Leptomyrmex*, *Anonychomyrma* and *Lordomyrma*, which are common foragers in the New Guinea forest. On the other hand, we found a noticeably lower proportion of *Camponotus, Polyrhachis* and *Iridomyrmex* species than in comparable studies from Australia and Borneo (e.g. Brühl et al. 1998; Reichel and Andersen 1996).

Life strategies in assemblage

Using Andersen's functional groups approach (1995a), which considers habitat requirement and competitive interactions, the majority of species we recorded can be classified as "opportunists" (e.g. *Rhytidoponera, Tetramorium, Paratrechina and Tapinoma*) and "generalized Myrmicinae" (*Crematogaster, Pheidole, Monomorium*). In his system, *Oecophylla* is considered as a 'tropical climate specialist' while *Anonychomyrma* is classified among 'Dominant Dolichoderinae'. Although the 'Functional groups' approach is more useful for large-scale comparisons among communities or habitats (e.g. Andersen 1997a) than for describing an assemblage at one type of homogenous habitat, it is helpful for validating major resemblances between New Guinea and north Australian rainforest fauna, where functional group composition is very similar to the situation reported in this study (Reichel and Andersen 1996).

Another approach in describing the structure of ant assemblages is based on foraging strategies (Wilson 1971), although this system partially overlaps dominance status and food preferences. We recorded all basic foraging strategies established by Wilson (1971). 'Opportunists' are those which find food resources quickly, but are easily affected by the presence of other ants and quickly withdraw when challenged (*Rhytidoponera*, *Paratrechina, Pachycondyla, Camponotus vitreus*). 'Extirpators' take longer to locate a food source, but recruit to the food in large numbers and aggressively attack competing species (*Pheidologeton affinis* and other dominants). 'Insinuators' are usually small species which are able to sneak up to a food source without alarming other species (Morrison 1996) (*Tetramorium, Lordomyrma, Cardiocondyla*).

Based on food preferences, the majority of our species can be roughly classified (after Wilson 1971) as general predators/scavengers (*Rhytidoponera, Oecophylla, Pheidole, Tetramorium, Crematogaster*), pastoralists (*Crematogaster, Anonychomyrma, Pseudolasius*) or a combination of both strategies. Nevertheless, a description of the local assemblage based solely on the baiting

method may be biased, as tuna baits are selective (Agosti 2000) and have a tendency to attract only species from particular trophic positions. Although we did not specifically test food preferences during this survey, it is possible to assess species' trophic position on the basis of analysis of d15N isotopic ratios data for rainforest ants from North Queensland (Blüthgen et al. 2003). Following the data of Bluthgen et al (2003), ants exhibiting a high level of predation in our assemblages were *Tapinoma melanocephalum*, *Paratrechina spp*. and *Rhytidoponera spp.* Intermediate positions were occupied by *Oecophylla*, *Crematogaster, Anonychomyrma* and *Technomyrmex*, while intermediate and lower levels were found for the genus *Camponotus* including *C. vitreus* and *Polyrhachys* spp. This implies that the highest trophic positions were occupied predominantly by subordinate species from the ground-foraging stratum with small or medium sized colonies. On the other hand, highly abundant and behaviourally dominant species utilize honeydew and nectar sources, combined with predation. Subordinate species living primarily in the canopy stratum (e.g. *Polyrhachis spp*. *C. vitreus*) are mainly nectarivorous or trophobiotic herbivores. This suggests that many abundant and behaviourally dominant ants occurring in New Guinea lowland forests are not necessarily strong predators of other insects, as has often been assumed for many canopy species (Floren et al. 2002; Olson et al. 1991). There is growing evidence from tropical areas that many canopy species do not acquire nitrogen primarily from predation. On the other hand, the high activity of those dominant species at protein baits can be viewed as being parallel to the effective discovery and utilization of insect prey occurring in the vegetation or forest litter. A critical evaluation of actual feeding habits of dominant species, and their actual predatory effect, is necessary for assessing their predation effect on other insect fauna. To what extent foraging activity of dominant ants affects other potential prey occurring in the vegetation or forest litter remains to be examined by alternative methods.

CONCLUSIONS

Our study supports earlier findings of markedly different patterns in ant species richness, abundance, and foraging activity between ground and understory strata in a rainforest. However, dominance levels somewhat differed from those reported by other studies. In contrast to other areas, we recorded a certain species overlap between strata, caused by the intensive foraging activity of a few arboreal species on the forest floor. Several species identified as behaviourally or ecologically dominant were related or identical with dominant species and genera described from other sites in

Austronesia and Southeast Asia. The overall generic similarity of our assemblage shows strong affinities to the Australian rainforest fauna. Although we detected mostly random co-occurrence patterns among ants, the relationship between local species richness and behavioural dominance appeared to be unimodal, suggesting that interspecific interactions could play an important role in structuring local assemblages. Finding these two seemingly contradictory patterns within the same assemblage will require further investigation of our data. On the basis of null models, we showed that assemblages traditionally considered to be structured by a dominant species may in fact exhibit random co-occurrence patterns. Our results contribute to the growing evidence of random assembly patterns within ant communities.

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Appendix 1

Phylogeny of Lasius ants based on mitochondrial DNA and morphology, and the evolution of social parasitism in the Lasiini (Hymenoptera: Formicidae)

(Milan Janda, Dagmar Folková, Jan Zrzavý,
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Phylogeny of *Lasius* ants based on mitochondrial DNA and morphology, and the evolution of social parasitism in the Lasiini (Hymenoptera: Formicidae)

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Abstract

Phylogeny of ants of the tribe Lasiini (*Lasius*, *Acanthomyops*, *Prenolepis*, *Euprenolepis*, *Paratrechina*, *Pseudolasius*, and *Myrmecocystus*) was analysed using 81 morphological, ecological, and behavioural characters (for 41 species) and mitochondrial DNA sequences (COI, COII, tRNA-Leu; for 19 species). The free-living subgenus *Lasius* s. str. is paraphyletic with respect to the rest of genus; the traditional ''genus'' *Acanthomyops* should be considered a part of *Lasius* s. lat.; free-living subgenus *Cautolasius* is a member of the clade of socially parasitic *Lasius* ants (=*Chtonolasius* + *Acanthomyops* + *Austrolasius* + *Dendrolasius*). The tree topology is congruent with two alternative scenarios of origin of the temporary social parasitism: (i) a single origin of the parasitic strategy in a derived subclade of *Lasius* and a secondary loss of this trait in *Cautolasius*, (ii) a parallel origin of the social parasitism within the clade of hypogeic *Lasius* ants (in *Chtonolasius*, and in *Acanthomyops* + *Dendrolasius* + *Austrolasius*). Emery's rule in the strict sense does not apply to this group because most parasites exploit any ecologically available, even phylogenetically distant host species. The parasitic strategy in *Lasius* could have originated from the aggressive interactions between cofounding queens during pleometric colony founding and/or from the secondary queen adoption.
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1. Introduction

1.1. Taxonomy and phylogeny of Lasius

Lasius Fabricius, 1818 (Hymenoptera: Formicidae: Lasiini) is one of the most abundant ant genera in the Holarctics (Wilson, 1955). This genus includes 86 extant species, some of which are the overriding dominants of local myrmecofaunas. Although it contains numerous abundant and ecologically important species that are often subjected to ecological and sociobiological studies, little is known about its phylogeny. Despite the detailed studies on the taxonomy of some *Lasius* taxa in the last two decades (e.g. Seifert, 1983, 1988, 1990, 1992, 1997), relationships between species and subgenera have not yet been studied thoroughly.

In his revision, Wilson (1955) recognised four subgenera within *Lasius*, i.e., *Cautolasius* Wilson, 1955; *Chtonolasius* Ruzsky, 1913; *Dendrolasius* Ruzsky, 1913; and *Lasius* (s. str.). Later, an additional subgenus, *Austrolasius* Faber, 1967 was established for a newly described species *L. reginae* and for *L. carniolicus*, the latter species previously classified within *Chtonolasius*. The most important characters that are considered since Wilson (1955) as subgenus-specific include length of the palpal segments, shape of the mandible, eye and head size, size of the metapleural gland opening, and body colouration. With the exception of *Cautolasius,* monophyly of the *Lasius* subgenera has never been doubted by morphologists

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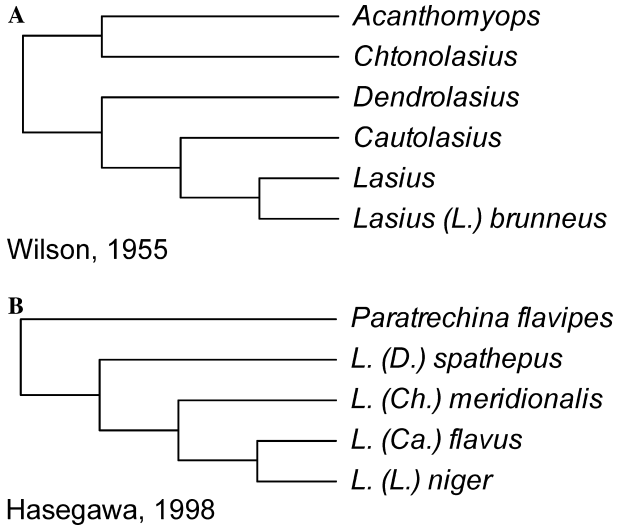

Fig. 1. Relationship among *Lasius* subgenera as proposed by (A) Wilson (1955) and (B) Hasegawa (1998).

and has also been confirmed by numerous ecological and sociobiological characters (Seifert, 1992).

The first attempt to reconstruct relationships between the *Lasius* subgenera was published by Wilson (1955); however, his tree-like diagram (Fig. 1A) was not supported by any explicit phylogenetic analysis. According to him, the ancestor of *Lasius* was similar to recent Nearctic *L. pallitarsis* (=*L. sitkaensis*). Wilson (1955) also hypothesised that the *Chtonolasius* + *Acanthomyops* clade represents the basalmost subclade of *Lasius* (*Lasius* in the traditional sense is hence paraphyletic in the respect of *Acanthomyops*), and that *Dendrolasius* is a sister group of the *Lasius* s. str. + *Cautolasius* clade. The reduction of palps and eyes and the light body colouration, all shared by *Cautolasius* and *Chtonolasius*, were interpreted as a consequence of the independently acquired subterranean mode of life of both subgenera.

Another reconstruction of the *Lasius* phylogeny (Hasegawa, 1998) was derived from mitochondrial cytochrome *c* oxidase subunit I (COI) gene. This phylogeny included only four species, each belonging to a separate subgenus, with the branching pattern as follows: *Dendrolasius* + (*Chtonolasius* + (*Cautolasius* + *Lasius*)) (Fig. 1B). In both hypotheses, the social parasitism seems to represent a plesiomorphic feature of *Lasius* ants, or a character evolved several times in parallel.

1.2. Evolution of social parasitism and Emery's rule

The socially parasitic species that depend upon labour forces of the workers of other, free-living species represent one of the most fascinating phenomena of ant biology. Three distinct forms of social parasitism exist, viz., temporary social parasitism, dulosis (=slavery), and inquilinism (Buschinger, 1990; Hölldobler and Wilson, 1990).

In temporary parasites, a newly fertilised queen finds the host colony and arranges her own adoption by the host ants either by forcibly subduing the workers, or by conciliating them. The original host queen is then assassinated either by the intruder, or by her own workers who come to favour the parasite (Hölldobler and Wilson, 1990). The host workers who become subservient to the parasite queen begin to rear her brood and then slowly die out and are gradually replaced by workers of the parasite species.

Dulotic species depend on their hosts' labour forces during their entire lifetime. Workers of dulotic species raid nests of suitable host species and carry larvae and pupae back to their own nest. Slaves that have emerged from the stolen pupae perform most of the colony work, while the dulotic species' workers are specialised exclusively to execute the raids.

The inquilines are characterised by their permanent coexistence with queens of their host species (Buschinger, 1990). The inquiline worker caste is often completely lost and only the sexual offspring is produced.

Social parasitism in ants is scattered taxonomically as well as geographically. Most of the parasites are found among the northern temperate members of the Formicinae and Myrmicinae, while they seem to be quite rare in the other taxa and parts of the World (see Wilson, 1984; Hölldobler and Wilson, 1990; Ward, 1996). Phylogenetic relationships between parasites and their host(s) are frequently debated. According to the so-called Emery's rule, derived primarily from the observed morphological similarity between the host and its parasite (Le Masne, 1956), social parasites are usually closely related to their hosts. In the strict form of Emery's rule each parasite is the sister species of its host (Buschinger, 1990). In looser versions, the non-parasitic outgroup clade most closely related to the parasite includes all the parasite's host species (Ward, 1996), and the social parasites can radiate also to less related host species (Parker and Rissing, 2002). Two basic evolutionary questions related to Emery's rule have been posed by Carpenter et al. (1993). (i) Do host and parasite have an immediate common ancestor (and if so, which speciation mode, sympatric or allopatric, led to formation of two ecologically interconnected sister species)? (ii) Do the ecological and host-deception requirements restrict social parasites to the related hosts? (Parker and Rissing, 2002).

Recent studies have found a few cases congruent with the strict and /or loose versions of Emery's rule (Bourke and Franks, 1991; Lowe and Crozier, 1997; Schultz et al., 1998; Savolainen and Vepsäläinen, 2003), various ambiguous and complex patterns in both wasps and ants (Carpenter et al., 1993; Baur et al., 1996; Sanetra and Buschinger, 2000), and several cases contradicting the

rule in the ants (Agosti, 1994; Ward, 1989, 1996; Radchenko, 1997; Heinze, 1998). Sympatric speciation hypothesis (see possible mechanisms in Buschinger, 1990; Bourke and Franks, 1991) has been tested against the strict and loose definition of the Emery rule by Wilson (1971), Buschinger (1990), and Ward (1996).

If the host–parasite relationship is not too tight, the social parasites could exploit a wide array of host species (Parker and Rissing, 2002). Not only phylogeny but also ecological features of the parasite and host taxa could play an important role in the establishment of host–parasite relationships, which can be the major reason for the (occasional?) usage of a more distant host by a parasite. If we assume that chemical and behavioural communication cues are similar within a genus or a species complex, we can expect that a suitable host can come from a diverse spectrum of species.

1.3. Temporary parasitism in Lasiini

Compared to well-studied *Formica* where temporary parasitism is widespread and highly diverse, information on *Lasius* and its relatives is much less complete (see Table 1). Numerous species of *Austrolasius*, *Chtonolasius* and *Dendrolasius* are known as obligate temporary parasites of *Lasius* s. str. (Hölldobler and Wilson, 1990; Seifert, 1996). Moreover, *Austrolasius* and *Dendrolasius* use *Cautolasius* species as their hosts, and *Dendrolasius* is also a hyperparasite of parasitic *Chtonolasius*. Some species of *Lasius* s. str. are reported to be parasitised by *Acanthomyops* (Wing, 1968; Cover and Sanwald, 1988). However, there is no information on the colony-founding behaviour of many *Acanthomyops* species, and we therefore cannot decide whether all *Acanthomyops* species are temporary parasites or not.

Few detailed reports on parasitic colony foundation in various *Lasius* species are available, usually from laboratory observations (but see Sciaky and Rigato, 1987). Interestingly, different clades of parasitic *Lasius* ants show different colony founding strategies, which may cast some doubts on a single origin of the social parasitism within the genus.

When trying to enter the nest of a host species, a queen of *Chtonolasius* (*L. umbratus*, *L. mixtus*, *L. distinguendus*) kills a host worker (e.g., *L. niger*, *L. alienus*) in the vicinity of its nest and seizes it with her mandibles. She rubs the captured worker with her antennae and legs, probably in order to transfer the host colony odour onto her body, and after that she tries to enter the nest. The behaviour of the host workers towards an intruding heterospecific queen is rather hostile but usually only a few workers attack her directly. In this case, the queen defends herself only by using the legs, not mandibles (Sciaky and Rigato, 1987). Nothing is known about the fate of the host queen after intrusion of the *Chtonolasius* parasitic queen.

A different strategy has been described for *Austrolasius*. Before a queen of *L. reginae* enters the host nest, she tries to provoke comfort behaviour in the host workers by licking them to avoid aggressive interactions (Faber, 1967). Killing of a host worker has not been reported. When the parasitic queen approaches the host queen, she flips the host queen over on her back, grabs her thorax and kills the host queen by grasping her neck in her mandibles (Faber, 1967).

Despite their abundance, nothing is known about the colony-founding behaviour and queen strategy in *Dendrolasius* ants. The *Acanthomyops* queens are reported to enter *Lasius* s. str. colonies without killing host workers (Cover and Sanwald, 1988).

In the present paper, we attempt

(1) to formulate a well-supported hypothesis on the species-level relationships within *Lasius* s. lat. and related genera, based on a combination of all available non-molecular (morphological, ecological, and behavioural) and molecular (mitochondrial cytochrome *c* oxidase subunits I and II genes, mitochondrial tRNA-Leucine gene) data;
(2) to address questions concerning the evolution of social parasitism and the validity of Emery's rule in the Lasiini (has social parasitism one or multiple origins and how closely related are the parasites to their hosts?);
(3) to find possible morphological and ecological preadaptations to and adaptations linked with the origin of parasitism in the Lasiini.

2. Materials and methods

2.1. Taxa and characters examined

Altogether 86 recent *Lasius* species and 16 species of *Acanthomyops* have been described (Bolton, 1995). We included 31 species from these two genera in our study, together with 10 additional species as representatives of possible formicid outgroups (for phylogenetic position of the Lasiini see Astruc et al., 2004). The non-sequence (morphological, ecological, and behavioural) dataset (''morphology'' and ''MEB'' hereinafter) has primarily been constructed on the basis of published morphological and ecological studies on *Lasius* and *Acanthomyops* (Wing, 1968; Yamauchi and Hayashida, 1970; Yamauchi, 1978; Kupyanskaya, 1987; Seifert, 1988, 1990, 1992; Agosti and Bolton, 1990; Agosti, 1991; Bolton, 1994). All available specimens were re-examined by using Scaning Electron Microscopy. The characters examined are listed in Appendix A and the character states' distribution among studied taxa in Appendix B.

Table 1
Overview of host–parasite relationship within the studied group

Parasite	Host	Distrib.	Record
L. (A.) carniolicus	***L. (Ca.) flavus***	wPAL	Schmid (1975)
	L. (L.) piliferus	wPAL	Buschinger and Seifert (1997)
	L. (L.) alienus	wPAL	Seifert (1996)
L. (A.) reginae	***L. (L.) alienus***	wPAL	Faber (1967), Buschinger and Seifert (1997)
	L. (Ca.) myops	wPAL	Seifert (1996)
L. (D.) fuliginosus	***L. (Ch.) umbratus***	PAL	Donisthorpe (1922), in Wilson (1955) Yamauchi and Hayashida (1968), Seifert (1996)
	L. (Ch.) rabaudi	PAL	Donisthorpe (1922), in Wilson (1955) Yamauchi and Hayashida (1968), Stärcke (1944), in Wilson (1955)
	L. (L.) niger	PAL	Stärcke (1944), in Wilson (1955), Seifert (1996) Furukava (1959), in Yamauchi and Hayashida (1968)
	L. (Ch.) mixtus	PAL	Seifert (1996)
	L. (L.) alienus	PAL	Stärcke (1944), in Wilson (1955)
	L. (L.) brunneus	PAL	Seifert (1996)
L. (D.) spathepus	*L. (L.) sp.*	Japan	Yamauchi and Hayashida (1968)
L. (D.) teranishii	***L. (Ca.) flavus***	Japan	Yamauchi and Hayashida (1968)
L. (Ch.) bicornis	*L. (L.) sp.*	PAL	Collingwood (1979)
L. (Ch.) citrinus	***L. (L) brunneus***	PAL	Seifert (1996)
L. (Ch.) crinitus	***L. (L.) niger ?***	India	Collingwood (1982)
L. (Ch.) distinguendus	***L. (L.) alienus***	wPAL	Seifert (1988)
L. (Ch.) jensi	***L. (L.) alienus***	wPAL	Seifert (1988, 1996)
L. (Ch.) meridionalis	***L. (L.) psammophilus***	wPAL	Seifert (1996)
	L. (L.) alienus	HOL	Seifert (1996)
	L. (L.) niger	HOL	Seifert (1996)
L. (Ch.) mixtus	***L. (L.) niger***	PAL	Donisthorpe (1922), in Wilson (1955), Seifert (1988)
	L. (L.) alienus	PAL	Donisthorpe (1922), in Wilson (1955), Collingwood (1979)
L. (Ch.) umbratus	***L. (L.) niger***	HOL	Göswald (1938), in Wilson (1955), Hölldobler (1953), Seifert (1996), Seifert (1988)
	L. (L.) alienus	HOL	Göswald (1938), in Wilson (1955), Hölldobler (1953), Seifert (1996), Seifert (1988);
	L. (L.) emarginatus	wPAL	Seifert (1988)
	L. (L.) brunneus	PAL	Collingwood (1979)
	L. (L.) psammophilus	wPAL	Seifert (1996)
L. (Ch.) rabaudi	***L. (L.) niger***	PAL	Stärcke (1944), in Wilson (1955)
L. (Ch.) sabularum	***L. (L.) niger***	wPAL	Seifert (1996)
L. (Ch.) subumbratus	***L. (L.) pallitarsis***	NEA	Wheeler (1917), in Wilson (1955)
	L. (L.) neoniger	NEA	Wheeler (1917), in Wilson (1955)
Acanthomyops latipes	***L. (L.) alienus***	NEA	Cover and Sanwald (1988)
	A. interjectus	NEA	Cover and Sanwald (1988)
	L. (L.) neoniger	NEA	Wing (1968)
Acanthomyops murphyi	***L. (L.) neoniger***	NEA	Cover and Sanwald (1988)
Acanthomyops claviger	*L. (L). sp.*	NEA	Wing (1968)

Species included in the present analysis are boldfaced. NEA, Nearctic region; wPAL, western Palearctic region; PAL, whole Palearctic region; HOL, Holarctic region.

2.2. DNA extraction, PCR amplification, sequencing, and alignments

Total genomic DNA was extracted from 20 species (for details see Table 2 on MPE website) using DNeasy Tissue Kit (Qiagen). Fragments of mitochondrial DNA corresponding to the 3′ end of cytochrome *c* oxidase subunit I (COI), intergenic spacer (ITS), tRNA-leucine, and the 5′ end of cytochrome *c* oxidase subunit II (COII) were amplified using the following oligonucleotides: George 5′-ATA CCT CGA CGT TAT TCA GA-3′ and Marylin 5′-TCA TAA GTT CAR GTA TCA TTG-3′ for PCR;

Table 2
List of species included in this study

Name	Data available	Locality	GenBank Accession No.
Acanthomyops californicus (Wheeler 1917)	COI + COII + L + MEB	Sierra Juarez, La Rumorosa, Mexico (R.A. Johnson)	AY452145
Acanthomyops claviger (Roger, 1862)	MEB	Nemaha Co. Goff, Kansas, USA	
Acanthomyops interjectus (Mayr, 1866)	MEB	literature data used only	
Acanthomyops latipes (Walsh, 1863)	MEB	Coconino Co. Flagstaff, Arizona, USA	
Euprenolepis sp.	MEB	Baitabag vill., Madang, Papua New Guinea	
Myrmecocystus semirufus Emery, 1893	COI + COII + L + MEB	Mexico, (P.S. Ward, 14292)	AY452158
Paratrechina arenivaga (Wheeler, 1905)	COI + COII + L + MEB	Highlands Co. Archbold Biol. Sta., Florida, USA	AY452159
Paratrechina bourbonica (Forel, 1886)	COI + COII + L + MEB	Highlands Co. Archbold Biol. Sta., Florida, USA	AY452160
Paratrechina longicornis (Latreille, 1802)	COI + COII + L + MEB	Highlands Co. Archbold Biol. Sta., Florida, USA	AY452161
Paratrechina parvula (Mayr, 1870)	MEB	literature data used only	
Paratrechina vividula (Nylander, 1846)	MEB	Yole Co. Davis, California, USA, (P.S. Ward, 14403)	
Plagiolepis sp.	COI + COII + L + MEB	Mosh Chenar, Iran, (M. Janda, L - 1/001)	AY452162
Prenolepis imparis (Say, 1836)	COI + COII + L + MEB	Napa Co. Mt. George, California, USA, (P.S. Ward, 143356)	AY452163
Pseudolasius sp.	COI + COII + L + MEB	Baitabag vill., Madang, Papua New Guinea	AY452164
Lasius (Austrolasius) carniolicus Mayr, 1861	MEB	Melanos Mt., Levidi, Greece	
Lasius (Austrolasius) reginae Faber, 1967	MEB	Prague, Czech Republic	
Lasius (Cautolasius) flavus (Fabricius, 1782)	COI + COII + L + MEB	Siskiyou Co. Klamath NF, California, USA, (P.S. Ward, 14395)	AY452146
Lasius (Cautolasius) nearcticus Wheeler, 1906	MEB	The Bowl, Guadaloupe N. Park, Texas, USA	
Lasius (Chtonolasius) bicornis (Foerster, 1850)	MEB	H. Dúbrava-Boky, Slovakia	
Lasius (Chtonolasius) distinguendus (Emery, 1916)	COI + COII + L + MEB	Klokočov, Slovakia	AY452149
Lasius (Chtonolasius) jensi Seifert, 1982	COI + COII + L + MEB	Havraníky, Czech Republic, (M. Janda, L - 1/009)	AY452150
Lasius (Chtonolasius) meridionalis (Bondroit, 1920)	COI + COII + L + MEB	Havraníky, Czech Republic, (M. Janda, L - 1/010)	AY452148
Lasius (Chtonolasius) mixtus (Nylander, 1846)	COI + MEB	Rydeč, Czech Republic; see Steiner et al. (2004)	AY225879
Lasius (Chtonolasius) umbratus (Nylander, 1846)	COI + COII + L + MEB	Holašovice,Czech Republic, (M. Janda, L - 1/011)	AY452151
Lasius (Dendrolasius) fuliginosus (Latreille, 1798)	COI + COII + L + MEB	České Budějovice, Czech Republic, (M. Janda, L - 1/003)	AY452147
Lasius (Dendrolasius) spathepus (Wheeler, 1910)	MEB	Japan (no other data available)	
Lasius (Dendrolasius) teranishii Wheeler, 1928	MEB	Shizuoka, Mt. Fuji, Japan	
Lasius (Lasius) alienus (Foerster, 1850)	COI + COII + L + MEB	Havraníky, Czech Republic, (M. Janda, L - 1/004)	AY452152
Lasius (Lasius) brunneus (Latreille, 1798)	COI + COII + L + MEB	České Budějovice,Czech Republic, (M. Janda, L - 1/005)	AY452153
Lasius (Lasius) emarginatus (Olivier, 1792)	COI + COII + L + MEB	České Budějovice, Czech Republic, (M. Janda, L - 1/006)	AY452154
Lasius (Lasius) flavescens Forel, 1904	MEB	Chimgan Mts., Tashkent, Uzbekistan	
Lasius (Lasius) grandis Forel, 1909	MEB	Dj. Toubkal, Asni, Morocco	
Lasius (Lasius) japonicus Santschi, 1941	MEB	Paekdusan Mt., North Korea	
Lasius (Lasius) koreanus Seifert, 1992	MEB	Paekdusan Mt., North Korea	
Lasius (Lasius) neoniger Emery, 1893	MEB	Lexington, Massachusetts, USA	
Lasius (Lasius) niger (Linnaeus, 1758)	COI + COII + MEB	České Budějovice,Czech Republic, (M. Janda, L - 1/007)	AY452155
Lasius (Lasius?) pallitarsis (Provancher, 1881)	COI + COII + L + MEB	Trinity Co. Mt. Eddy, California, USA, (P.S. Ward, 14376)	AY452156
Lasius (Lasius) psammophilus Seifert, 1992	COI + COII + L + MEB	Měčichov, Czech Republic, (M. Janda, L - 1/008)	AY452157
Lasius (Lasius) sakagamii Yamauchi and Hayashida, 1970	COI + MEB	for morphology only literature data used; see Steiner et al. (2004)	AY225864
Lasius (Lasius) sitiens Wilson, 1955	MEB	Cochise Co., Portal, Arizona, USA	
Lasius (Lasius) turcicus Santschi, 1921	COI + MEB	Ihlara Valley, Turkey; see Steiner et al. (2004)	AY225881

Their locality information, collector, collection number, data partition (L = tRNA-Leu, MEB = morphology, ecology, behavior), and GenBank Accession Nos. are given. COI data for *L. mixtus*, *L. turcicus* and *L. sakagamii* were obtained from GenBank (see Steiner et al., 2004). The COI sequences from the study by Hasegawa (1998) could not be used for confrontation with the present dataset since they are not deposited in any public database.

and M13 5′-CAG GAA ACA GCT ATG AC3′ ; F 5′-TGG CAG AAT TTA GTG CAT TGG-3′ ; R 5′-GGA GAA TTT GAA TTT TGG AGA GA-3′ and T7 5′-TAA TAC GAC TCA CTA TAG GG-3′ for sequencing (Wetterer et al., 1998). Polymerase chain reaction (PCR) amplifications were performed in 25 μl volume: 1 U *Taq* polymerase (TopBio), 10× *Taq* buffer, 1.75 mM $MgCl_2$ (Promega), 200 μM of each dNTP, 25 pmol of each primer and 50–100 ng template DNA (Wetterer et al., 1998). The temperature profile for PCR amplification included an initial denaturation step of 95 °C for 5 min followed by 9 cycles of 95 °C for 1 min, 40–49 °C for 2 min and 72 °C for 1 min and 19 cycles of 95 °C for 1 min, 50 °C for 2 min and 72 °C for 1 min with a final extension step of 72 °C for 5 min. Amplified fragments were separated by agarose gel electrophoresis. Bands of expected size were purified in QIAquick Gel Extraction kit (Qiagen), and cloned using the TOPO TA Cloning kit (Invitrogen). The templates isolated using QIAprep Spin Miniprep kit (Qiagen) were sequenced using the CEQ DTCS Kit (Beckman Coulter) in 20 μl volume according to the manufacturer's instructions. Both strands of the DNA fragments were sequenced using four oligonucleotides on the CEQTM 2000 DNA Analysis System sequencer (Beckman Coulter). Complete sequences were analysed using Chromas ver. 1.45 (McCarthy, 1998) and DNASTAR ver. 4.0 (DNASTAR, 1999).

Only sequences of 3′ fragment of COI (211 bp; ∼ bases #1324–1536 of *Drosophila melanogaster*; GenBank Accession No. NC_001709), tRNA-Leu (73 bp), and 5′ fragment of COII (303 bp; ∼ bases #0–306 of *Drosophila melanogaster*) were used for further analysis, as ITS sequences were of highly unconserved lengths (they were included in preliminary analyses only to test their information content). Length of the ITS region varied from 33 bp in *Paratrechina bourbonica* to 123 bp in *Myrmecocystus semirufus*. For *L. niger*, the tRNA-Leu region was not determined and this species was therefore excluded from some molecular and combined analyses. The sequences were aligned using ClustalX (Thompson et al., 1997–2001); since COI and COII sequences were protein-coding genes of highly constrained lengths, the alignments were stable and unequivocal. The tRNA-Leu region was aligned using Malign (Wheeler and Gladstein, 1994), with the gap to substitution cost ratio 4:1 and transversion to transition ration 3:1 (heuristic algorithm "build," branch swapping options "alignswap alignaddswap treeswap treeaddswap," command "contig" applied to prefer alignments with fewer gap locations, i.e., with contiguous gaps made of more positions). All alignments are included in Appendix C.

2.3. Data combination and phylogenetic analysis

The two analysed datasets differ considerably in species samples, one subordinated to the other (19 species for which complete molecular characters were present; 22 more species for morphology, 4 of which have also incomplete molecular data). Four character partitions were analyzed separately as well as simultaneously as follows:

(1) separate analyses for individual data partitions (MEB, COI, COII, tRNA-Leu) of 19 species for which complete data are available;
(2) three different data-partition combinations of 19 species (COI + COII, COI + COII+ tRNA-Leu, MEB + COI + COII + tRNA-Leu);
(3) morphology of all 41 species;
(4) combination of all morphological and molecular characters of these 41 species (missing molecular characters of 22 species were substituted by question marks).

Nucleotide sequences of COI + COII + tRNA-Leu used in analysis contained 177 cladistically informative characters. The COI and COII sequences were also translated into amino acids (29 cladistically informative characters) to inspect alternative levels of the same phylogenetic information (Agosti et al., 1996; Freudenstein et al., 2003). The combined nucleotide-amino acid analyses of COI + COII (and COI + COII + tRNA-Leu + MEB as well) were constructed using non-redundant coding method according to Freudenstein et al. (2003), which yielded 16 informative amino acid characters. In the combined analyses, the morphology:nucleotides:amino acids weight ratio was set to 1:1:1. Gaps were treated as missing data, transversion:transition ratio was 1:1.

To determine congruence between four (MEB, COI, COII, tRNA-Leu) different data partitions of the 19 taxa for which all data sets were available, the incongruence length difference (ILD; Mickevich and Farris, 1981) has been calculated (NONA: 1000 replications) as the amount of the additional homoplasy that results solely from combining the different data sets.

Maximum-parsimony analysis was applied to all data matrices using NONA (Goloboff, 1999: heuristic option "hold100000 mult*100 hold/1000," unconstrained "mult*max*" search strategy). Bremer (decay) values of branch support were calculated (NONA: option "bsupport100000") as the difference in length between the shortest topology that lacks the node of interest and the shortest topology that contains it. Partitioned Bremer support (PBS; see Baker and DeSalle, 1997; Wahlberg and Nylin, 2003) for separate data partitions (morphology, COI, COII, tRNA-Leu) was calculated using PAUP* (Swofford, 2002). Bootstrap analysis was performed to test additionally the robustness of individual clades of the parsimony trees (NONA: "mult*1000 max*100 hold/100"). For the character optimisation, the "unambiguous" option (NONA) was applied.

To test the possibility that simultaneous inclusion of all the 22 "incompletely known" taxa into the combined dataset might distort their relationships because of co-occurrence of too numerous "missing characters," the trees including 19 species represented by all data partitions plus one incompletely known species were constructed and analysed.

For comparison of queen head length/width ratio between parasites and their closely related free-living species we have used *t* test for independent samples (Statistica 6.0, Statsoft, USA; for data on 23 analysed species, see Seifert, 1988, 1992).

3. Results

Results of the incongruence test show that the morphological characters were significantly incongruent with all molecular data in combination as well as with the individual molecular data partitions. Moreover, also the tRNA-Leu sequences are not congruent with the cytochrome *c* oxidase subunits, and only COI and COII data partitions were found to be congruent ($p = 0.1287$). This allows to combine all data partitions and to analyse them simultaneously with caution only as some problematic groupings may be expected (see PBS analysis below).

The maximum parsimony analysis of COI + COII + tRNA-Leu nucleotide data of 19 species represented by all data resulted in two trees (482 steps, CI 0.54, RI 0.63; not shown). In the strict consensus of the trees, *Lasius* s. lat. together with *Acanthomyops* forms a monophyletic but largely unresolved group with only three distinct subclades: (i) *Chtonolasius*; (ii) *Lasius* s. str. part. (*L. emarginatus* + *L. alienus* + *L. psammophilus*), and (iii) *Dendrolasius* + *Acanthomyops*. Separate analysis of the COI + COII amino acid characters yielded eight trees (46 steps, CI 0.71, RI 0.84) with the topology slightly different from nucleotide data (not shown), where *Myrmecocystus* forms a sister group of *Lasius* s. lat., the latter split into five subclades with no hierarchical structure (*Acanthomyops, Chtonolasius, Dendrolasius, Cautolasius*, and *Lasius* s. str. including *L. pallitarsis*). Combination of COI + COII + tRNA-Leu nucleotide data with non-redundantly coded amino acid COI + COII characters resulted in a tree topology more resolved than the purely nucleotide tree (505 steps, CI 0.54, RI 0.63, 2 trees; Fig. 2), with the two subclades: (i) *Lasius* s. str., not including *L. pallitarsis*; (ii) its sister clade formed by *Chtonolasius* and the unresolved polytomy of *L. pallitarsis, Cautolasius* and *Dendrolasius* + *Acanthomyops*.

Separate analyses of individual molecular partitions (not shown here) allow to study their contribution to the combined molecular tree topology. In the COI tree (nucleotides + non-redundantly coded amino acids; gaps = ?; 193 steps, CI 0.58, RI 0.67, 2 trees) *Lasius* s. str. is paraphyletic with *L. brunneus* being the basalmost species, followed by the rest of *Lasius* s. str. (*L. alienus*, *L. psammophilus*, *L. emarginatus*) and an unorthodox clade including *Chtonolasius*, *Cautolasius* + (*Dendrolasius* + *Acanthomyops*), and *L. pallitarsis* + *Myrmecocystus*. The COII tree (nucleotides + non-redundantly coded amino acids; no gaps; 263 steps, CI 0.53, RI 0.62) shows *Myrmecocystus* as a sister group of *Lasius*

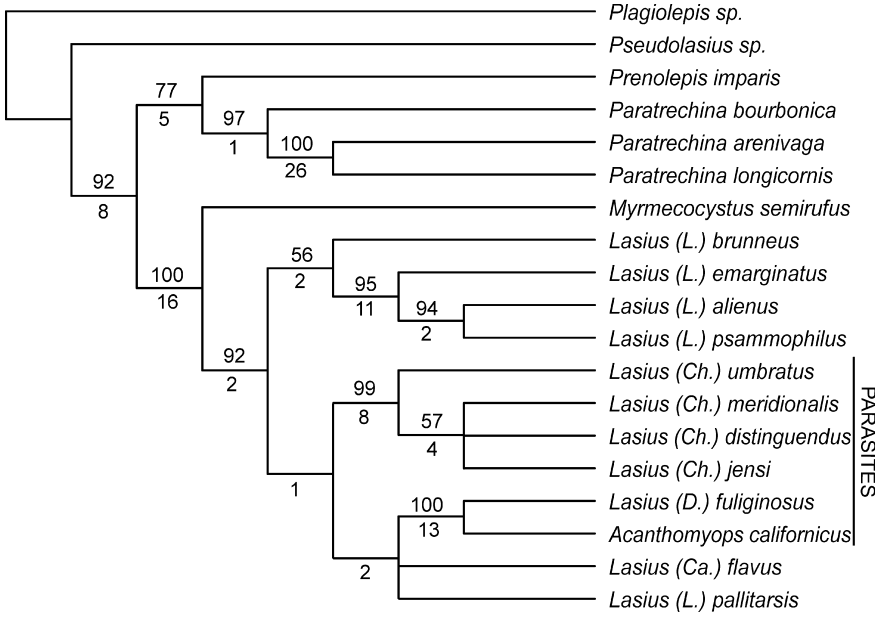

Fig. 2. Strict consensus of two trees of 505 steps (CI 0.54, RI 0.63) based on nucleotide and non-redundantly coded amino acid COI + COII + tRNA-Leu characters, with Bremer support indices shown below and bootstrap values above the branches.

s. lat., the latter further split into three subclades: *Chtonolasius, Lasius* s.str. (excluding *L. pallitarsis*), and ((*L. pallitarsis* + *Cautolasius*) + (*Dendrolasius* + *Acanthomyops*)). The combined tree of COI + COII genes (nucleotides + non-redundantly coded amino acids; gaps = ?; 465 steps, CI 0.54, RI 0.63, 2 trees) differs from the COII tree only in the resolving the basal polytomy: *Lasius* s. str. (excluding *L. pallitarsis*) is a sister group of the rest of *Lasius* s. lat. The tree derived from tRNA-Leu nucleotide sequences (gaps = ?; 34 steps, CI 0.70, RI 0.77, 173 trees) includes only two non-trivial clades, (i) *Cautolasius* + (*Dendrolasius* + *Acanthomyops*), and (ii) *Chtonolasius* + *Pseudolasius*; in other words, neither *Lasius* s. lat., nor *Myrmecocystus* + *Lasius* s. lat. are monophyletic.

Analysis of morphological characters of the 19 "molecular" taxa resulted in a single tree (183 steps, CI 0.47, RI 0.71) with a quite different topology (Fig. 3): *Lasius* s. str. is a paraphyletic stem lineage of all other *Lasius* s. lat. species (including *Acanthomyops*), with *L. pallitarsis* being the most basal species; *Cautolasius* is a sister group of all parasitic species ((*Acanthomyops* + *Dendrolasius*) + *Chtonolasius*); *Myrmecocystus* is a sister group of the *Lasius* s. lat. clade.

The combined analysis of all data partitions of the 19 "molecular" species (MEB + nucleotides + non-redundantly coded amino acids) yielded a single cladogram (710 steps, CI 0.51, RI 0.64; Fig. 4). *Myrmecocystus* is a sister group of *Lasius* + *Acanthomyops, Lasius* s. lat. is split into two subclades: *Lasius* s. str. and *L. pallitarsis* + (*Chtonolasius* + (*Cautolasius* + (*Dendrolasius* + *Acanthomyops*))). This topology is not in conflict with the tree based on molecular data only (Fig. 2), but there are few topological conflicts between combined and morphological trees. Namely, *Lasius* s. str. (except *L. pallitarsis*) is monophyletic in the former and paraphyletic in the latter, *L. pallitarsis* is the basalmost *Lasius* s. lat. species according to morphological characters but it is a sister group of the parasitic clade in the combined tree, and *Cautolasius* forms a sister species of *Dendrolasius* + *Acanthomyops* clade in the combined tree while it is a sister species of the whole parasitic group in the morphological one.

Analysis of the morphological characters of all the 41 species resulted in 84 trees (288 steps, CI 0.36, RI 0.78; Fig. 5), and, finally, the combined analysis of all available characters and all 41 taxa resulted in 2 most parsimonious trees (856 steps, CI 0.45, RI 0.70; Fig. 6). In both cases, the phylogenetic relationships are in general agreement with results of the 19-species morphological and combined analyses, respectively.

In the trees including 19 species represented by all data partitions plus one incompletely known species, the 22 incompletely represented species group at positions identical to (or compatible with) those positions where they are situated in the all-species trees, with a single exception. *L. mixtus* is a sister group of the whole *Chtonolasius* + *Cautolasius* + *Acanthomyops* + *Austrolasius* + *Dendrolasius* clade in the all-species tree, and a sister group of the other *Chtonolasius* species in the (19 + 1)-species tree.

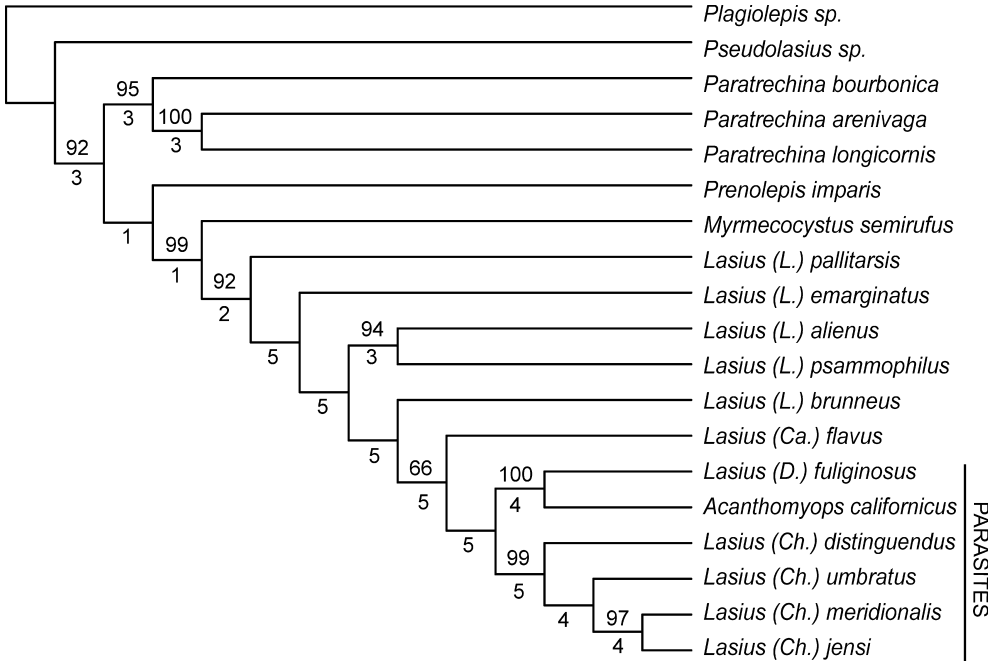

Fig. 3. Tree resulting from analysis of morphological characters (183 steps, CI 0.47, RI 0.71) of the species for which the molecular data were available. Bremer support indices are shown below and bootstrap values above the branches.

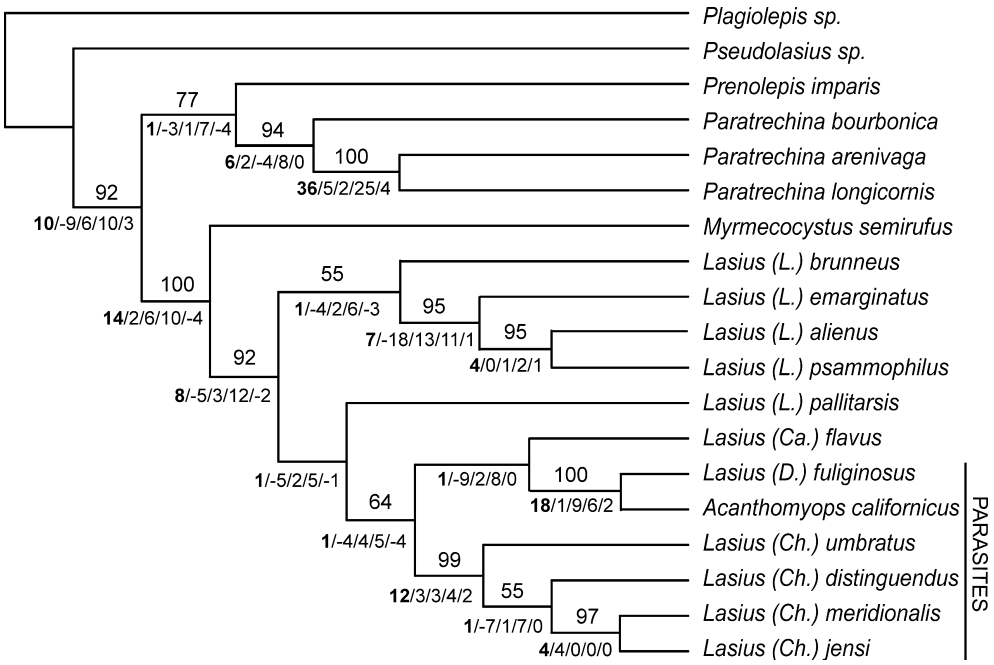

Fig. 4. Tree resulting form analysis of combined data (nucleotide, non-redundantly coded amino acid, and morphological characters) for 20 species for which all datasets were available (710 steps, CI 0.51, RI 0.64). Total and partitioned Bremer support indices are shown below branches in following order: **total**/morphology/COI/COII/tRNA-Leu. Bootstrap values are shown above branches.

4. Discussion

4.1. Relative quality of character partitions and their performance in the combined analysis

The PBS values reveal that morphological, ecological, and behavioural (MEB) data partition contributes positively to the branch support of 6 nodes of the 19-species combined tree, is neutral for one node, and is negative for 9 nodes. Similar ratio of positive/neutral/negative (6:4:6) holds for the tRNA-Leu data. On the contrary, both COI and COII contribute positively to the majority of nodes (14:1:1 and 15:1:0, respectively), and the combined-tree topology is heavily determined by the COI + COII phylogenetic signal (Fig. 4). There are only few nodes for which there is no conflict between the data partitions (i.e, there are no negative Bremer support values): they include *Chtonolasius, Acanthomyops* + *Dendrolasius*, plus three nodes within *Paratrechina, Lasius* s. str., and *Chtonolasius*. The nodes at which the molecular data partitions are in unanimous disagreement with the MEB characters are exceptional. The clades supported exclusively by the COI + COII data partitions, with conflicting MEB and tRNA-Leu, are, e.g., *Lasius* s. lat., *Lasius* s. str., *L. pallitarsis* + parasites clade, *Chtonolasius* + *Cautolasius* + *Dendrolasius* + *Acanthomyops* clade, as well as the *Cautolasius* + *Dendrolasius* + *Acanthomyops* clade (with neutral tRNA-Leu).

By combining all of the datasets, we have identified nodes that may potentially change with the addition of new data, i.e., nodes where different data partitions conflict stronghly with each other (basalmost *Lasius* phylogeny, position of *L. pallitarsis* and *Cautolasius*), and nodes that are unlikely to change with future new data, i.e., where all data partitions are in agreement (monophyly of *Acanthomyops* + *Dendrolasius* + *Austrolasius*?).

4.2. Relationships within the Lasiini

Species relationships revealed by the present analysis differ from those proposed by Wilson (1955) and Hasegawa (1998). All trees support monophyly of the *Lasius* s. lat. (with *Acanthomyops* nested deeply within the former genus).

The position of *L. pallitarsis* in most analysis makes the monophyly of *Lasius* s. str. unlikely. Although his scheme of the *Lasius* phylogeny strongly differs from our results, Wilson (1955, p. 15): regarded "*L. sitkaensis*" (=junior synonym of *L. pallitarsis*) as similar to "prototypic *Lasius*" because of "generalised morphology and because of character of female and male mandible" of this species. This is in agreement with our results based on morphology (Fig. 5); however, combined analyses suggest its position as a sister species of the parasitic clade (including *Cautolasius* and*Acanthomyops*). Monophyly of the remaining species of *Lasius* s. str. is supported by molecular (except *L. brunneus*, Fig. 2) and combined analyses (Figs. 4 and 6), and is corroborated by the absence of teeth on the male mandible. However, this subgenus is paraphyletic in both morphological trees (Figs. 3 and 5), and its monophyly is weakly supported even in the molecular and combined trees.

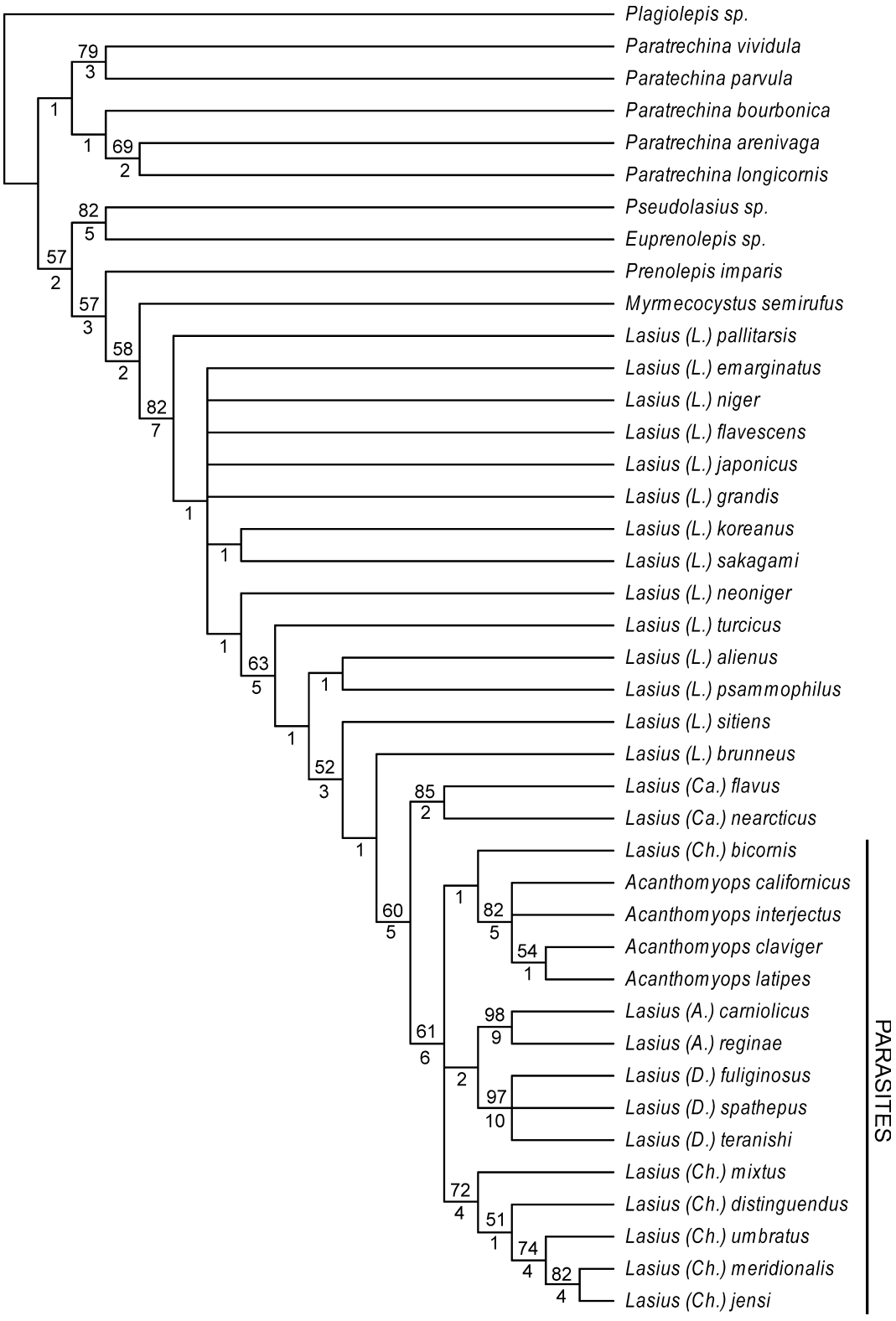

Fig. 5. Strict consensus of 84 trees (288 steps, CI 0.36, RI 0,78) from analysis of morphology of all 41 studied species. Bremer support indices are shown below and bootstrap support above the branches.

Non-parasitic species of *Lasius* thus represent a paraphyletic stem lineage of a clade including the remaining, parasitic subgenera (including *Acanthomyops*), which is supported, e.g., by the shape of mandible, shortened maxillary palps, head wider than thorax, and morphology of the metapleural glands. The free-living *Cautolasius* seems

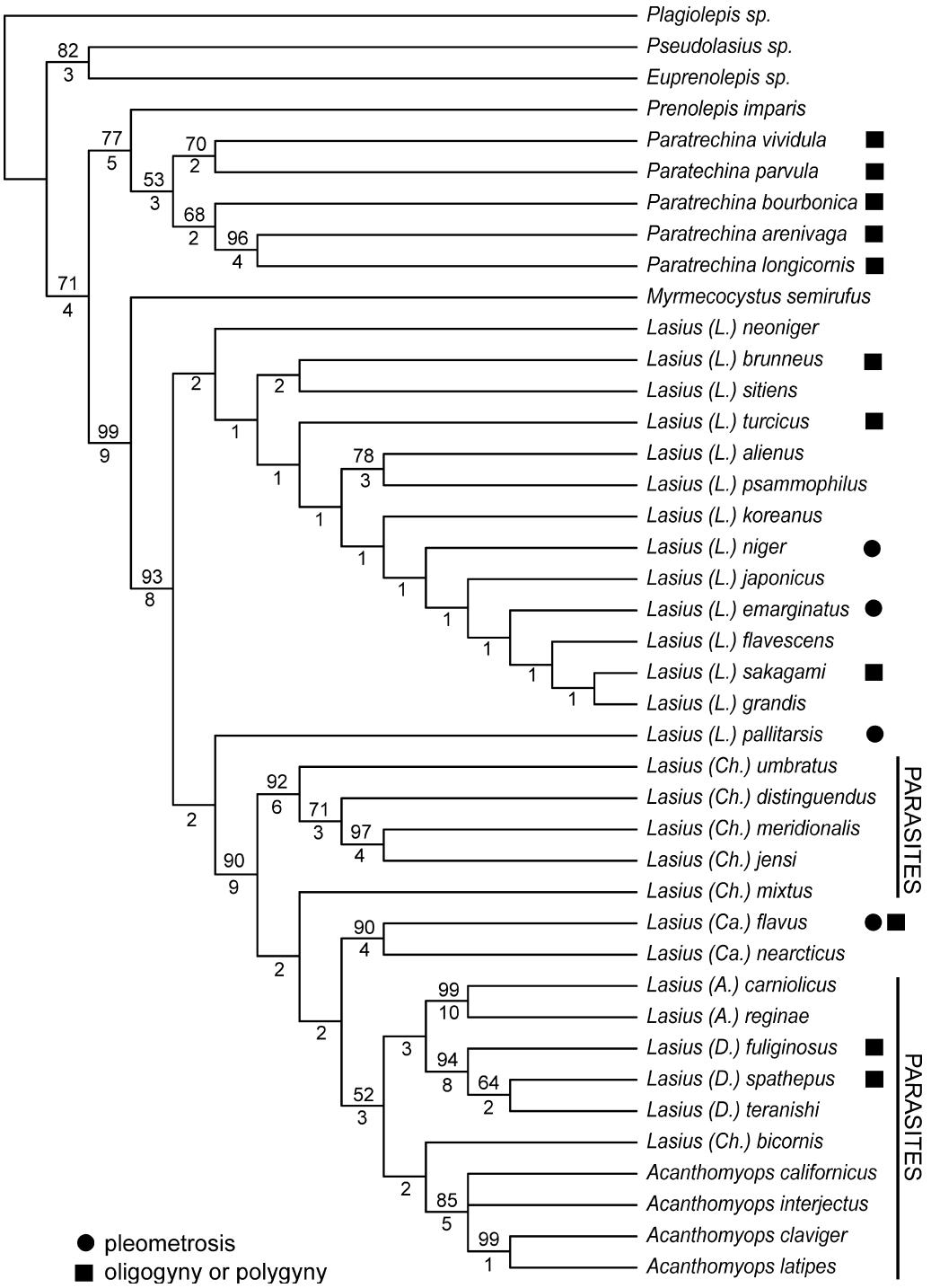

Fig. 6. Strict consensus of 2 trees (856 steps, CI 0.45, RI 0.70) from combined analysis of all nucleotide, non-redundantly coded amino acid, and morphological characters. Remaining species are considered to be haplometric and monogynous. Position of *L. mixtus* and *L. bicornis* is discussed in text. Bremer support indices are shown below and bootstrap support above the branches. Distribution of the pleometric colony foundation and of oligogynal/polygynal colony structures are shown.

to be a sister group of that parasitic clade, based on the morphological data; however, according to the molecular and combined analyses it is a member of the parasitic clade itself. Hence, the uncertain position of *Cautolasius* is the most serious problem resulting from conflict between morphological and molecular data sets.

The parasitic subgenus *Chtonolasius* cannot be considered monophyletic because of the position of *L. bicornis* and *L. mixtus* in the 41-species trees. The aberrant position of *L. bicornis* (as a sister species of *Acanthomyops*) is retained even if it is added as a sole incompletely represented species to the 19-species tree (*L. bicornis*,

Cautolasius a *Acanthomyops* + *Dendrolasius* then form a clade), and may be caused by the peculiar morphology of this species (short head, short scape, character of the clypeal pubescence). In addition, even if *Acanthomyops* is removed from the dataset, *L. bicornis* is still a sister group of *Cautolasius* within the *Cautolasius* + *Dendrolasius* + *Austrolasius* clade, not closely related to other *Chtonolasius* species. On the other hand, *L. mixtus* groups as a basal species of *Chtonolasius* in the (19 + 1)-species tree, which corroborates its traditional subgeneric classification. *Chtonolasius* s. str. (not including *L. bicornis*) is a sister group of the *Cautolasius* + *Dendrolasius* + *Austrolasius* + *Acanthomyops* clade (Fig. 6). Monophyly of *Chtonolasius* s. str. is supported by pubescence on the scape, head surface and hind tibia, and by shape of the scape in the queens.

Monophyly of *Dendrolasius* is well supported by the structure of the metapleural glands, enlargement of eyes in the workers, and special structure of scutum; monophyly of *Austrolasius* is supported by number of morphological synapomorphies, e.g., by the typical shape and dentition of mandible, reduced pubescence of metapleural gland, and reduced body size of the queens. The sister-group relationship of *Dendrolasius* and *Austrolasius* is supported by shared morphology of the queen petiole, queen physogastry, and the shared parasitism on *Cautolasius*. However, only morphological characters of *Austrolasius* have been analysed yet.

The close relationships of *Lasius* and *Acanthomyops* were hypothesised by many authors (e.g., Wing, 1968; Cover and Sanwald, 1988), and Wilson (1955) considered *Acanthomyops* closely related to *Chtonolasius*. In the present analysis, the species of *Acanthomyops* are always deeply nested within the *Lasius* s. lat., as a sister group of the *Dendrolasius* + *Austrolasius* clade (Figs. 5 and 6), with uncertain position of *L. bicornis*. *Acanthomyops* was already classified as a subgenus of *Lasius* (Mayr, 1866), but Creighton (1950) re-elevated it to full generic rank, which was accepted by Wing (1968) in his comprehensive revision.

We therefore propose to include *Acanthomyops* back into *Lasius* and reclassify it as a further *Lasius* subgenus. *Lasius* will then include six subgenera (*Lasius* s. str.,*Cautolasius*, *Dendrolasius*, *Austrolasius*, *Acanthomyops*, *Chtonolasius*). At present, *L. mixtus* should be considered basal *Chtonolasius*; *L. bicornis* has to be classified outside the established subgenera as "*Lasius incertae sedis*"; *L. pallitarsis* seems to be worthy of elevation to a subgeneric rank (M. Janda, in prep.).

4.3. Evolution of the temporary social parasitism and Emery's rule

Our results offer two alternative evolutionary scenarios of origin of the social parasitism within *Lasius* s. lat.:

(i) Social parasitism has originated only once within *Lasius* s. lat. as an autapomorphy of the *Chtonolasius* + *Cautolasius* + *Acanthomyops* + *Dendrolasius* + *Austrolasius* clade, secondarily lost in *Cautolasius*.
(ii) Parasitism arose independently, at minimum, in *Chtonolasius* and in *Acanthomyops* + *Dendrolasius* + *Austrolasius* subclade. The latter conclusion might appear to agree with the hypothesis proposed by Hasegawa (1998) that parasitism evolved independently in *Dendrolasius* and in *Chtonolasius*, but his hypothesis was based on a different topology of relationship between these taxa (Fig. 1B), which is in conflict with our findings. The parallel origins of the social parasitism is supported also by different colony founding strategies in *Chtonolasius* and *Austrolasius* (see Introduction); however, there is no information concerning colony founding behaviour in *Dendrolasius* and *Acanthomyops*.

Our results do not support Emery's rule in the strict sense because no parasitic species is closely related to a single host species. Our data, however, provide some support for the more loose definitions of the rule: for example, both *Dendrolasius* and *Austrolasius* utilise host species of *Cautolasius* (though not exclusively), which is their closest free-living relative. On the contrary, the host spectrum of *Chtonolasius* includes phylogenetically distant *Lasius* s. str. species (*L. brunneus*, *L. alienus*, *L. emarginatus*, *L. niger*, and *L. pallitarsis*). A similar situation applies to the host range of *Acanthomyops*, whose species are reported to use *L. alienus* and *L. neoniger* as their hosts. *Austrolasius* does parasitise its close free-living relative, *Cautolasius*, but *Austrolasius* species are also commonly found to utilise more remote species, e.g., *L. alienus*. *Dendrolasius*, one of the most derived parasites within *Lasius*, has the widest host spectrum, including members of the closely related *Chtonolasius* and *Cautolasius*, as well as the more distant *Lasius* s. str. (for details see Table 1). This can result from fast, radiative speciation: the newly formed species are morphologically and ecologically still so similar that they could enter host–parasite relations regardless their precise sister-group proximity. The close relationship of some free living species (*L. pallitarsis*, *Cautolasius*) to their parasites (*Chtonolasius* and *Dendrolasius* + *Austrolasius*, respectively; see Table 1) fits the hypothesis proposed by Savolainen and Vepsäläinen (2003) for inquilines. They stated that a single sympatric speciation event through intraspecific parasitism would be hypothesized if the parasite clade was the closest relative to one of the host species.

4.4. Origin of the social parasitism

Several possible preadaptations enabling evolution of the temporary social parasitism in ants have been pro-

posed (Hölldobler and Wilson, 1990): (i) adoption of young inseminated queens by conspecific colonies (=secondary polygyny, multiple-queen structure), (ii) occupation of multiple nests (=polydomy), some of which are, at least temporarily, without resident queens, and (iii) high population densities. All these traits could be found in some non-parasitic and parasitic *Lasius* species. Some species of *Dendrolasius* parasites form secondarily polygynous (=multiple-queen) and polydomous colonies as well but this appears to be a derived trait because the other parasitic species are strictly monogynous and the polydomy has not yet been reported for them.

Adoption of newly inseminated queens to the nest, which leads to formation of a polygynous colony, resembles invasions of the host-species colonies by the young queens of social parasites (Buschinger, 1990). Recent study of evolution of inquiline parasitism in *Myrmica* ants, where acceptance of extra queens to colonies is widespread (Savolainen and Vepsäläinen, 2003), also strongly suggests that this behaviour is linked with the origin of parasitic strategy. However, most *Lasius* and *Acanthomyops* adult colonies are strictly monogynous, and polygynous and oligogynous colony structures have been reported only from a few species of *Lasius* s. str. (*L. turcicus*, *L. sakagamii*, *L. brunneus*), *Cautolasius* (*L. flavus*), and *Dendrolasius* (*L. fuliginosus*, *L. spathepus*). Nevertheless, even in some of the monogynous species (e.g., *L. pallitarsis*, *L. niger*, *L. emarginatus*, and also in *L.* (*Cautolasius*) *flavus*) young inseminated queens join together and cooperate to found a new colony (so-called pleometrosis). The cofounders become intolerant to each other after emergence of the first workers, and the dominant queen expels or kills the other females so that the colony becomes secondarily monogynous. Distribution of pleometrosis and multiple-queen colony structure on the combined tree (Fig. 6) suggests that both traits have originated many times independently within the genus studied, and that pleometrosis is not causally nor phylogenetically joined with the polygynous colony organisation (*L. flavus* could be an exception in sharing both characters). As neither pleometrosis nor polygyny are obligatory traits of the species in question (according to Seifert, 1996, about 25% of European colonies of *L. niger* could have been founded pleometrically), their presence in a species could most likely reflect the local environmental and/or social conditions.

On the other hand, the occurrence of pleometrosis in *L. pallitarsis* and secondarily polygynous *L. flavus* (which represent the free-living species most closely related to the parasites) suggests that this trait can yet be somehow connected with the origin of the temporary parasitic strategy. Aggressive competition among the cofounding queens leads to the formation of a queens' hierarchy and to spatial separation of the queens' chambers inside a single nest (Waloff, 1957). Consequently, the nest of *L. flavus* can be constructed by unrelated queens whose workers can sometimes share a common space. The nest mound is then a complex of separate colonies rather than an integral, interconnected unit (Boomsma et al., 1993). This type of aggressive dominance interactions among queens could be an evolutionary basis for parasitic colony foundation, and killing of one of the queens (the "host" queen) could evolve from this openly aggressive behaviour. Furthermore, the secondary adoption of newly inseminated queens is also reported from *L. flavus*, at least in laboratory conditions (Boomsma et al., 1993). Unfortunately nothing is known about the social structure of other *Cautolasius* species.

The fragmentary and scattered reports on behaviour and colony-founding strategies of the parasitic *Lasius* species do not allow us to build a detailed hypothesis about the evolution of social parasitism within the group. Nevertheless, some subgenus-specific differences in parasitic strategies and host spectra seem evident. A primitive parasitic strategy might include killing of a host worker prior to entering the host nest, which is reported from relatively basal *Chtonolasius*. This behaviour has not yet been reported from the more derived parasitic groups. The opposite end of the parasitic behavioural spectrum is represented by the highly derived strategy of *Austrolasius*, where the host-worker killing is probably absent and the parasite kills the host queen (Faber, 1967).

4.5. Ecological and morphological differences between free-living and parasitic ants

The social parasitic strategies influence the parasites' morphology, and some convergent morphological changes are widespread even among unrelated parasitic ants (Douwes, 1990; Hölldobler and Wilson, 1990). Although this applies mostly to more derived types of social parasitism (dulosis, inquilinism), some of these morphological apomorphies are present also in *Lasius*. For example, the head wider than thorax in the sexual castes (char. 30) is characteristic for all parasitic *Lasius* subclades. Similar changes of the head size and shape, compared to their non-parasitic relatives, were also recorded from parasitic genera *Epimyrma*, *Doronomyrmex*, *Harpagoxenus*, and *Teleutomyrmex* (Douwes, 1990). The increase of head width appears to be a direct adaptation for successful entering the host nest; on the other hand, it could be a mere consequence of the inverse change of thorax size. It is known that the mass of nutritional reserves (stored in the thorax) is strongly reduced in the queens that do not found their colonies independently (Hölldobler and Wilson, 1990; Keller, 1993). Comparison of queen head length/width ratio between parasites and their closely related free-living species supports the second option. Head width did not

change synchronously with the conversion to parasitic mode of life and its size in the free-living species does not significantly differ from that of parasites (t test for independent samples: $p = 0.241$, $t = 1.035$, $N = 23$).

Reduction of exocrine glands in the parasites is another frequently described morphological change linked with the origin of social parasitism (Hölldobler and Wilson, 1990). The reduction (to various degrees) of the metapleural gland opening is shared by the reproductive castes of parasitic *Lasius* subgenera, but it is not present in *Cautolasius*. The most derived state (opening very reduced and without guard hairs) is present in the queens and males of *Dendrolasius* (though the gland opening is well-developed in the *Dendrolasius* workers, probably because of their secondarily epigeic activity).

Physogastry, conspicuous enlargement of the ovaries and whole abdomen shortly after fertilisation, is an additional widespread adaptation to the parasitic way of life, enabling relatively small queens to produce numerous eggs during a short period. Within *Lasius*, it is a synapomorphy of *Austrolasius* and at least some *Dendrolasius* species (char. 65). Their queens (namely those of *Austrolasius*) are of the smallest size in comparison with the other parasites and with the free-living species.

In addition to morphological changes linked with the parasitic way of life, we can observe ecomorphological changes that are associated with the derived mode of activity of *Lasius* species. Primitively, the workers are epigeic. On the contrary, free-living *Cautolasius* as well as parasitic *Chtonolasius, Acanthomyops* and *Austrolasius* show without exception hypogeic activity. Not surprisingly, this mode of life is associated with the reduction of palpal segmentation in all castes, with reduction of eye size in workers, and also with the loss of cuticular pigmentation so that the hypogeic species are yellow and shiny. These characters have secondarily been lost in parasitic *Dendrolasius*, which is epigeic and black-pigmented, and whose workers have secondarily prolonged palps.

In conclusion, our results seem to support a single origin of the temporary parasitic strategy in a single derived subclade of *Lasius*, associated with a number of morphological and ecological adaptations, and a secondary loss of this trait in *Cautolasius*. Alternatively, the social parasitism may have originated twice in parallel within the clade of hypogeic *Lasius* ants (in *Chtonolasius* and in *Acanthomyops* + *Dendrolasius* + *Austrolasius*). Emery's rule in the strict sense does not apply to this group because most parasites exploit any ecologically available, even phylogenetically quite distant host species. Our study suggests that the parasitic strategy in *Lasius* could have originated from the aggressive interactions between cofounding queens during pleometric colony founding and/or from the secondary queen adoption.

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Appendix A. List of morphological and ecological characters used in analysis

The metric measurements data were adopted from the literature (Seifert, 1988, 1990, 1992; Trager, 1984; Wing, 1968) but were accepted only if the measuring methods were evidently comparable between different authors. Selected measurements were processed using the cluster analysis in order to define separate states of morphometric characters. Both Ward's and Unweighted pair-group average methods were applied (using program Statistica 6.0, Statsoft, USA) to determine the clusters of species with similar values of metric measurements. The multistate characters were treated as ordered ("additive"), except for character Nos. 18, 48, 49, 64, 79. If more than one character state were present in a single species, the character was treated as polymorphic.

Abbreviations: W – worker, Q – queen, M – male, L – larva.

1. WQ, Mandible: last basal teeth not clearly separated from masticatory border (0), basal border in right angle with masticatory border (1).
2. WQ, Offset basal teeth absent (0), present (1).
3. W, Mandible with 6 (0), 7 (1), 8 (2) teeth.
4. W, Shape of mandible long and narrow with long apical teeth, strongly curved in apical half (0), not strongly curved in apical half (1).
5. M, Mandible lacking preapical cleft (0), cleft present (1).
6. M, Mandible: basal angle always broadly rounded, masticatory border curving gradually into basal margin (0), distinctly marked, clearly separating masticatory border from basal margin (1).
7. M, Teeth (intercalary, basal) on masticatory border absent (0), present (1).

8. M, Number of teeth on masticatory border (if present) under 4 (0), over 6 (1).
9. WQM, Maxillary palp segments number: 6 (0), 2-4 (1).
10. QM, Maxillary palp reach to in front of eye border (0), long, reach at the back of an eye (1).
11. WQ, Maxillary palp length of 5th and 6th segments conspicuously reduced to 4 (0), length of 5 and 6 segments almost the same like of the 4th (1).
12. WQ, Maxillary palp: length of 4th segment less than 0,12 head width (0), more than 0,14 head width (1).
13. W, Maxillary palp 4th segment conspicuously reduced to 3rd segment (0), almost the same length as 3rd (1).
14. W, Maxillary palp terminal segment (6th) conspicuously shorter than subterminal (5th) segment (0), slightly shorter, same or longer as a subterminal segment (1).
15. WQM, Compound eyes situated posterior on the head (0), anterior on the head (1).
16. W, Maximal eye length less than 0.20 head width (0), more then 0.20 head width (1).
17. WQM, Scape not exceeding head (0), long, exceeding by more then half its length the posterior border of head (1).
18. W, Scape pubescence character: appressed, smooth surface (0), decumbed to suberect surface, with hairs (1), erect, rough surface (2).
19. W, Scape: setae absent (0), few (1), many (2).
20. Q, Scape: setae absent (0), few (1), many (2).
21. Q, Scape pubescence character: fully appressed, smooth surface (0) moderately pubescent, decumbed (1), subdecumbed, rough surface (2).
22. Q, Scape not flattened (0), flattened (1).
23. W, Clypeal pubescence dilute in all castes (0), dilute or dense in one caste (1), dense in all (2), dense or very dense in one caste (3).
24. W, Genae setae absent (0), few (1), many (2).
25. Q, Genae setae absent (0), present (1).
26. W, Whole surface of head without setae (0), with setae (1).
27. Q, Whole surface of head without setae (0), covered by setae (1).
28. Q, Head pubescence dilute (0), dense (1).
29. WQM, Head and alitrunk with simple setae (0), setae in distinct pairs (1).
30. QM, Head width narrower than thorax (0), broader than thorax (1).
31. W, Occipital border straight (0), straight to feebly convex (1), strongly convex (2).
32. Q, In side view scutum overhangs pronotum no (0), yes (1).
33. QM, Propodeal spiracle rather elliptical (0), rather circular (1).
34. WQM, Metanotal spiracle not prominent (0), prominent (1).
35. M, Wings without discoidal cell (0), with discoidal cell (1).
36. QM, Wings hyaline uniformly in basal 1/3 (0), brownish in basal part (1).
37. W, Mesothorax not constricted (0), constricted (1).
38. W, Suture between propodeum and metapleural region not very conspicuous (0), conspicuous, clearly visible (1).
39. W, Declitivity of propodeum lower than mesonotum (0), propodeum higher or of the same height as mesonotum (1).
40. W, Thorax: Declivitous face of propodeum long relative to dorsum absent (0), present (1).
41. QM, Metapleural gland and its guard hairs reduced - not visible in lateral view, placed lateroposteriorly (0), at least small opening visible from lateral view (1).
42. QM, Maximum dimension of metapleural gland opening less wide than the maximum diameter of the outer margin of propodeal spiracle (0), more wide (1).
43. W, Maximum dimension of metapleural gland opening less or same wide as maximum diameter of outer margin of propodeal spiracle (0), more wide than propodeal spiracle (1).
44. W, Metapleural gland opening with a little guard hairs (0), opening with many guard hairs (1).
45. WQM, Petiole vertical or not strongly inclined (0), inclined (1).
46. QWM, Petiole in frontal and lateral view thin (0), thick and rounded (1).
47. W, Petiole in lateral view emarginated, with sharp pit (0), blunt tip (1).
48. W, Petiole: in frontal view sides parallel (0), convex (1), diverging dorsad (2).
49. W, Petiole: shape of dorsal crest stright (0), emarginated (1), curved (2).
50. WQM, Base of gaster not concealing petiole, usually without a distinct impression (0), base of gaster with an impression from above base of gaster (1).
51. WQM, Tergite and sternite not fused anteriorly (0), fused anteriorly (1).
52. WQM, Structure of proventriculi *Prenolepis* type (0), *Lasius* type (1).
53. WQM, Helcium simple (0), bipartite (1).
54. WQM, Helicium set ventraly (0), set anteroventraly (1).
55. Q, Hind tibia: setae absent (0), few (1), many (2).
56. W, Hind tibia: setae absent (0), few (1), many (2).
57. W, Hind tibia: length of setae to 30 μm (0), to 60 μm (1), over 60 μm (2).
58. M, Pygostylus absent (0), present (1).
59. M, Cranial apodeme unsclerotised (0), sclerotised (1).
60. M, Subgenital plate: sclerotised line along hind border not developed (0), developed (1).

61. M, Subgenital plate: exserted knobs in insertion of setae absent (0), present (1).
62. M, Subgenital plate having relatively straight posterior border, posteriolateral corners not projecting posteriorly (0), different (1).
63. QM, Overall body colour light to dark brown (0), shining black (1).
64. W, Overall body colour light to dark brown (0), yellow (1), shining black (2).
65. Q, Queen physogastric no (0), yes (1).
66. Q, Overall body size not over 5 mm (0), about 5 mm and more (1).
67. W, Worker caste monomorphic (0), polymorphic in size (1).
68. W, Head length to 700 μm (0), to 1150 μm (1), over 1150 μm (2).
69. W, Head length/head width ratio to 1.01 (0), to 1.16 (1), over 1.16 (2).
70. W, Scape length/head length ratio to 0.75 (0), to 0.85 (1), to 1.05 (2), over 1.05 (3).
71. Q, Head length to 900 μm (0), to 1300 μm (1), over 1300 μm (2).
72. Q, Head width to 800 μm (0), to 1800 μm (1), over 1800 μm (2).
73. Q, Head length/head width ratio to 0.95 (0), over 0.95 (1).
74. Q, Scape length/head length ratio to 0.65 (0), to 0.81 (1), to 0.91 (2), over 0.91 (3).
75. Q, Scape length/head width ratio to 0.64 (0), to 0.73 (1), to 0.80 (2), over 0.80 (3).
76. L, Neck absent (0), present (1).
77. L, Anus position terminal or subterminal (0), ventral or anteroventral or posteroventral (1).
78. L, Nude pupae absent (0), present (1).
79. Colony founding independent (0), parasitic on *Lasius* s. str. (1), parasitic on *Cautolasius* (2), parasitic on *Chtonolasius* (3).
80. Activity of workers epigeic (0), hypogeic (1).
81. Colony monogynous (0), oligogynous or polygynous (1).

Appendix B. Matrix of morphological and ecological characters used to infer phylogeny of the Lasius

	000000000111111111122222222223333333333444444444455555555556666666666777777777788
	123456789012345678901234567890123456789012345678901234567890123456789012345678901
Plagiolepis sp.	1000????01111111012??001?1??0020?1??00001?111112+11?01?1??????00000?????????11?00?
Pseudolasius sp.	0100??1?10-0?-10022+?012?1??0010?1??00001?100111?11?01?2??????01001????????10?010
Euprenolepis sp.	1001????10-01-1?112+?002?1??0?10?0??11101?00011??11?01?2??????01000???????????010
Myrmecocystus semirufus	1010101?01010001102+?002?1??0?00?1??10101?110111&00?10?2??????00111????????11?00?
Prenolepis imparis	1000000-01111101122?0021110000?11010001?111111210010?2?1????00110??3?????00101*
Paratrechina vividula	1000110-01111111121+10021110100?11011001?111111211001+1?0????00000023?????01101*
Paratechina parvula	1000110-01111111120?1002?1101000?11011001?111111211001+???0????00000022?????01101*
Paratrechina bourbonica	1000110-011111111120?002?1??1010?11011001?111110011001+1?0????000?0012?????01100*
Paratrechina longicornis	1000110-01111111000?000?1??1010?11011101?111110011001+1?0????00010012?????01100*
Paratrechina arenivaga	1000110-01111111010?001?1??1010?11011101?111110211001117?0????010?0012?????01100*
Acanthomyops claviger	0110111110---10002001000100001101101000010010001100110?0?10000010101102110010011?
Acanthomyops californicus	0110111110---10001001000100001001101001017100002001107?0?10000010101112111-100?1?
Acanthomyops interjectus	0110111110---10002001000100101101101000017?0100011001107?0?10000010102012171110?1?
Acanthomyops latipes	0110111110---10001101000111001101101000010010012200110?0?10000010101102110010011?
Lasius (*A.*) *carniolicus*	0121111100000000021110201017011000?000110000111200110+10100010110010?001??100+10
Lasius (*A.*) *reginae*	0121111100000000001001020?0010110000?000110000111200110001000-10001011001?001??100+10
Lasius (*D.*) *fuliginosus*	0110000-00001101010010001000012100010011001101112001100001000-10010121102122107?100$0*
Lasius (*D.*) *spathepus*	0110000-00001101002201201010012100010011001101010011022?1001012?102022103?100$0*
Lasius (*D.*) *teranishi*	0110000-00001101010011201000012100010011001101122001100+?1001012?102?321033100$0?
Lasius (*Ca.*) *flavus*	10101?10010001000100102000010010000000111111000200011010-11000010101112101210001*
Lasius (*Ca.*) *nearcticus*	10101?1*01000100010010200001007000000011111100020001101011000010101?210??10001?
Lasius (*Ch.*) *umbratus*	01101111000000000112103211110110000100111001000110011022010000010101122102210011O
Lasius (*Ch.*) *meridionalis*	01101111000000000212113211110110000100111001001000*0011022110000010101122103310011O
Lasius (*Ch.*) *jensi*	011011100000000000212113211110110000100111001000120011022010000010101122103310011O

Appendix B (*continued*)

Lasius (*Ch.*) *distinguendus*	0110111100000000012110321101011000010011100100011001101101000001010112210221001l0
Lasius (*Ch.*?) *bicornis*	0110111100000000000001100001011000010011100100011001l000-10000010101111101110011O
Lasius (Ch.) *mixtus*	0110111000000000010110321101011000010011100100001*00110110100000101011221022100110
Lasius (*L.*) *brunneus*	1010110-01111101000000200001000000000011111100001001l010-11110000101122101110000*
Lasius (*L.*) *alienus*	1020000-01111101010110210001000000000011111100011001l01011110000101122102210000O
Lasius (*L.*) *niger*	1020000-01111101021220321111000000000011111100011001l022111110000101122102210000O
Lasius (*L.*) *emarginatus*	1020000-01111101021220221111000000000011111110000*00110222111100001011221O?3100000
Lasius (*L.*) *psammophilus*	1020000-01111101010110210001000000000011111100011001l0-10111100001011221O--100000
Lasius (*L.*) *flavescens*	1020000-01111101022210221111000000000001111100001*00110221111100101011221O??10000?
Lasius (*L.*) *turcicus*	1010000-01111101010110211001000000000011111000010011011011110000101121102210000*
Lasius (*L.*) *japonicus*	1020000-01111101021220321111000000000011111100011001l022211110000101122102210000?
Lasius (*L.*) *grandis*	1020000-01111101012220221111000000000011111100011001l022211110000101122102?100000
Lasius (*L.*) *koreanus*	1020000-01111101010120321111000000000011111100100001l022011110000101122102200000
Lasius (*L.*) *neoniger*	1010000-01111101011210221111000000000011111100011001l022?111100001O?1?210??100000
Lasius (*L.*) *sakagamii*	1020000-01111101012220321111000000000011111100100001l022211110000lO?122102?100000
Lasius (*L.*) *sitiens*	1010000-01111101010010000001000000000011111100011001l000?111100001O?1?210??100010
Lasius (*L.*?) *pallitarsis*	0120111001111101012210121111001000000011111100011001l022?111100001O212210--100000

Abbreviations: polymorphic characters: char. states 0,1 = *, char. states 0,2 = &, char. states 1,2 = +, char. states 1,2,3 = $; inapplicable character = –; unknown character = ?

Appendix C. COI, COII and tRNA-Leu nucleotide sequences alignment

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Pseudolasius sp.            TATCCTGATTTTTATTTATC ATGAAATATTATTTCATCGA TTGGATCATTAATCTCTATT ATCAGAATAGTATTTCTAAT ATTTTTAACCTGAGAAGCAT
Lasius (Ca.) flavus         TATCCAGATACATACCTTTC ATGAAATATTACTTCTTCTA TTGGATCTTTAGTTTCAATC ATTAGACTTATTTTTTTAAT ATACTTAATTTGAGAATCCT
Lasius (D.) fuliginosus     TATCCAGATACATACCTTTC ATGAAATATTATTTCTTCTA TTGGATCTTTAATCTCAATC ATTAGACTTATCTTTTTAAT ATACTTAATTTGAGAATCTT
Lasius (Ch.) meridionalis   TATCCAGACACATACCTTTC ATGAAATATTATTTCTTCTA TTGGATCTTTAATTTCAATA ATTAGACTTATTTTTTTAAT ATACTTAATTTGAGAATCAT
Lasius (Ch.) distinguendus  TATCCAGACACATACCTTTC ATGAAATATTATTTCCTCTA TTGGATCTTTAATTTCAATA ATTAGACTTATTTTTTTAAT ATACTTAATTTGAGAATCAT
Lasius (Ch.) jensi          TATCCAGACACATACCTTTC ATGAAACATTATTTCTTCTA TTGGATCTTTAATTTCAATA ATTAGACTTATTTTTTTAAT ATACTTAATTTGAGAATCAT
Lasius (Ch.) umbratus       TATCCAGACACATACCTTTC ATGAAATATTATTTCTTCTA TTGGATCTTTAATTTCAATA ATTAGACTTATTTTTTTAAT ATACCTAATTTGAGAATCAT
Lasius_(Ch.)_mixtus         TATCCAGATACATACCTTTC ATGAAATATTATTTCTTCTA TTGGATCTTTAATTTCAATA ATTAGACTTATTTTCTTAGT TTATCTAATTTGAGAATCTT
Lasius (L.) alienus         TATCCAGATACATATCTCTC ATGAAATATTATCTCTTCTA TTGGATCCTTAATTTCAATT ATTAGACTCATTTTTTTAAT GTACCTAATTTGAGAATCCT
Lasius (L.) brunneus        TATCCAGATACATACCTTTC ATGAAATATTATCTCTTCTA TTGGATCCTTAATTTCAATT ATCAGACTCATTTTTTTAAT ATATTTAATTTGAGAATCTT
Lasius (L.) sakagamii       TATCCAGATACATATCTCTC ATGAAATATTATCTCTTCTA TTGGATCTTTAATCTCAATT ATTAGACTCATCTTTTTTAT GTACCTAATTTGAGAATCCT
Lasius (L.) turcicus        TATCCAGATACATATCTTTC ATGAAATATCGTCTCTTCTA TCGGATCATTAATTTCAATT ATTAGACTCATTTTTTTTAT GTATTTAATTTGAGAATCCT
Lasius (L.) emarginatus     TACCCAGATACATACCTCTC ATGAAATATTATCTCTTCTA TTGGATCCTTAATTTCAATT ATTAGACTCATTTTTTTTAT GTACCTAATTTGAGAATCCT
Lasius (L.) niger           TATCCAGATACATATCTTTC ATGAAATATTATCTCTTCTA TTGGATCCTTAATTTCAATT ATTAGACTTATTTTTTTTAAT GTACCTAATTTGAGAATCCT
Lasius (L.) pallitarsis     TACCCGGATACATACCTTTC AATGAACATTATTTCTTCTA TCGGATCTTTAATTTCAATA ATTAGGCTTATTTTTCTAAT ATATTTAATTTGAGAATCTT
Lasius (L.) psammophilus    TATCCAGATACATATCTCTC ATGAAATATTATCTCTTCTA TTGGATCCTTAATTTCAATT ATTAGACTCATTTTTTTTAT GTACCTAATTTGAGAATCCT
Myrmecocystus semirufus     TATCCAGATACTTATCTTTC ATGAAATATTATTTCTTCAA TTGGATCTATAATTTCAATC ATTAGACTTATTTTTTTTAT ATACTTAATCTGAGAATCTT
Paratrechina arenivaga      TATCCTGATACATACTTATC ATGAAACATTATTTCCTCAA TAGGATCATTTATCTCAATT ATTAGCCTAATTTATTTAAT TTATTTAATTTGAGAATCAT
Paratrechina bourbonica     TATCCAGATAATTTTTTATC ATGAAATATTATCTCATCTA TTGGATCATTTATTTCAGTT ATTAGATTAATTTTTTTAAT TTATCTAATTTGAGAGTCTC
Paratrechina longicornis    TATCCTGATACATACCTATC GTGAAACATTATTTCTTCTA TTGGATCATTTATTTCAATT ATTAGCCTAATTTATTTAAT TTATTTAATTTGAGAATCAT
Plagiolepis sp.             TATCCAGATTCTTACTTATC TTGAAACATTATCTCATCCA TTGGCTCATTTATATCTATT ATTAGATTAATTTTCCTAAT ATTTCTAATCTGAGAAGCTC
Prenolepis imparis          TATCCTGATACATATTTATC TTGAAACATTATCTCCTCTA TTGGATCATTAATTTCAATA ATTAGTTTAATTTTATTATA TTATTTAATTTGAGAATCAT
Acanthomyops californicus   TATCCAGATACATACCTTTC ATGAAATATTATTTCTTCTA TTGGATCTTTAATCTCAATC ATTAGACTTATCTTTTTAAT ATACTTAATTTGAGAATCTT

Pseudolasius sp.            TATCGTCAAAACGACTAGTA TTAAATGTATTTTTTTTAAG ATCTTCCTTAGAGTGACTAA GAA---ATTACCCTCCAATT AATCATAGATATAATGAAAT
Lasius (Ca.) flavus         TATCTTCTAAACGAATAATT TTAAATTTATTTTTTTTAAA TTCATCTCTTGAATGATTAA GAA---CTTACCCTCCATTA AATCATAGATATAATGAAAT
Lasius (D.) fuliginosus     TATCCTCAAAACGAATAATT CTAAATTTATTTTTTTTAAA TTCATCTCTCGAATGATTAA GAAGAACTTATCCACCACTA AATCATAGATATAATGAAAT
Lasius (Ch.) meridionalis   TATCTTCTAAACGAATAATT TTAAATTTATTCTTTTTAAA TTCATCTCTCGAATGATTAA GACTTTTTTATCCTCCATTA AATCACAGATATAATGAAAT
Lasius (Ch.) distinguendus  TATCTTCTAAACGAATAATT TTAAATTTATTCTTTTTAAA TTCATCTCTCGAATGATTAA GACTTTTTTATCCTCCATTA AATCACAGATATAATGAAAT
Lasius (Ch.) jensi          TATCTTCTAAACGAATAATT TTAAATTTATTCTTTTTAAA TTCATCTCTCGAATGATTAA GACTTTTTTATCCTCCATTA AATCACAGATATAATGAAAT
Lasius (Ch.) umbratus       TATCCTCTAAACGAATAATT TTAAATTTATTCTTTTTAAA TTCATCTCTTGAATGATTAA GACCTTATTATCCTCCATTA AATCACAGATACAATGAAAT
Lasius_(Ch.)_mixtus         TATCTTCTAAACGAATAATT TTAAATTTATTTTTTTTAAA TTCATCTCTTGAATGATTAA GACTTTATTACCCCCCATTA AATCATAGATATAATGAAAT
Lasius (L.) alienus         TATCTTCAAAACGAATAATT TTAAATTTATTTTTTTTAAA CTCATCTCTTGAATGATTAA GAT---CATATCCTCCATTA AATCATAGATATAATGAAGT
Lasius (L.) brunneus        TATCTTCTAAACGAATAATC TTAAACTTATTTTTTTTAAA TTCATCTCTTGAATGATTAA GAC---CATACCCTCCATTA AATCACAGATATAACGAAAT
Lasius (L.) sakagamii       TATCTTCAAAACGAATAATT TTAAATTTATTTTTTTTAAA CTCATCTCTTGAATGATTAA GAT---CTTATCCCCCATTA AATCACAGATATAATGAAGT
Lasius (L.) turcicus        TATCCTCTAAACGAATAATC TTAAATTTATTTTTCTTAAA TTCATCTCTTGAATGATTAA GAC---CATACCCTCCATTA AATCACAGATATAACGAAGT
Lasius (L.) emarginatus     TATCTTCAAAACGAATAATT TTAAATTTATTTTTTTTAAA CTCATCTCTTGAATGATTAA GAT---CATATCCTCCATTA AATCATAGATATAATGAGGT
Lasius (L.) niger           TATCTTCAAAACGAATAATT TTAAATTTATTTTTTTTAAA CTCATCTCTTGAATGATTAA GAT---CATATCCTCCATTA AATCATAGATATAATGAAGT
Lasius (L.) pallitarsis     TATCTTCTAAACGAATAATT TTAAACTTATTTTTTTTAAA TTCTTCTCTTGAATGATTAA GAA---CATACCCCCCGTTA AATCACAGATATAATGAAAT
Lasius (L.) psammophilus    TATCTTCAAAACGAATAATT TTAAATTTATTTTTTTTAAA CTCATCTCTTGAATGATTAA GAT---CATATCCTCCATTA AATCATAGATATAATGAAGT
Myrmecocystus semirufus     TATCTTCTAAACGTATAATT CTTAATTTATTTTTTTTAAA TTCTTCCCTTGAATGATTAA GAT---CATATCCCCCTCTC AATCACAGTTATAATGAAAT
Paratrechina arenivaga      TATCCTCTAAACGTATTATT CTTAATATATTTTTTTTAAA TTCATCTCTAGAATGATTAA GAC---CGTACCCCCCCAATT AATCACAGTTATAACGAAAT
Paratrechina bourbonica     TATCGTCTAAACGATTAATT TTAAATATATTTTTTTTAAA TTCATCCTTAGAATGATTAA GTC---CCTACCCCCCAATT AATCACAGATACAATGAAAT
Paratrechina longicornis    TATCCTCTAAACGTATAATT CTTAATATATTTTTTTTAAA TTCATCTCTAGAATGATTAA GGC---CATACCCCCCAATT AATCACAGTTATAATGAAAC
Plagiolepis sp.             TATCCTCTAAACGACTAATT TTAAATATATTTTTCTTAAA TTCTTCCCTAGAATGATTAA GTC---CCATACCTCCTATT TCTCATAGATACAACGAAAT
Prenolepis imparis          TATCTTCTAAGCGATTAATT TTAAATATATTTTTTATAAA TTCATCATTAGAATGATTAA GAT---CATTCCCTCCTGTT AACCATAGTTATAACGAAAT
Acanthomyops californicus   TATCCTCAAAACGAATAATT CTAAATTTATTTTTTTTAAA TTCATCTCTCGAATGATTAA GAAGAACTTATCCACCACTA AATCATAGATATAATGAAAT
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(*continued on next page*)

Appendix C (*continued*)

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Pseudolasius sp.            TCCCTCAACTATTAATACCT GATTAATTTCTCTACAAAAC TCAAATTCACCTTCCTATGA TATAATAATCTTTTTTCATG ATTTTACAATAATAATTTTA
Lasius (Ca.) flavus         TCCCTCAATTATAAATACCT GATTATTATCACTTCAAAAT TCAAATTCTCCAACCTATGA TATAATAATTTTTTTTCACG ATTTTACTATAATAATTTTA
Lasius (D.) fuliginosus     TCCTTCAATTATAAATACTT GATTATTATCTCTTCAAAAT TCAAATTCTCCAACTTATGA TATAATAATTTTCTTCCACG ATTTTACCATAATAATTTTA
Lasius (Ch.) meridionalis   TCCTTCAATTATAAATACTT GATTATTATCCTTACAAAAT TCAAATTCTCCAACATATGA TATAATAATTTTTTTTTCATG ATTTCACTATAATAATTTTA
Lasius (Ch.) distinguendus  TCCTTCAATTATAAATACTT GATTATTATCCTTACAAAAT TCAAATTCTCCAACATATGT TATAATAATTTTTTTTTCATG ATTTCACTATAATAATTTTA
Lasius (Ch.) jensi          TCCTTCAATTATAAATACTT GATTATTATCCTTACAAAAT TCAAATTCTCCAACATATGA TATAATAATTTTTTTTTCATG ATTTCACTATAATAATTTTA
Lasius (Ch.) umbratus       TCCTTCAATTATAAATACTT GATTATTATCCCTACAAAAT TCAAATTCTCCAACATATGA TATAATAATTTTTTTTTCATG ATTTTACTATAATAATTTTA
Lasius_(Ch.)_mixtus         TCCTTCAATT---------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) alienus         CCCTTCAATTATAAATACCT GATTATTATCTCTCCAAAAT TCAAATTCTCCAACTTATGA CATAATAATTTTTTTTTCATG ATTTTACTATAATAATTTTA
Lasius (L.) brunneus        TCCTTCAATTATAAATACCT GATTGTTATCCCTCCAAAAT TCAAATTCCCCAACATATGA TATAATAATTTTTTTTCCATG ATTTTACTATAATAATTTTA
Lasius (L.) sakagamii       CCCTTCAATT---------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) turcicus        TCCCTCAATT---------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) emarginatus     CCCTTCAATTATAAATACCT GATTATTATCTCTCCAAAAT TCAAATTCTCCAACCTATGA CATAATAATTTTTTTTTCATG ATTTTACCATAATAATTTTA
Lasius (L.) niger           CCCTTCAATTATAAATACCT GATTATTATCTCTCCAAAAT TCAAATTCTCCAACCTATGA CATAATAATTTTCTTTCATG ATTTTACCATAATAATTTTA
Lasius (L.) pallitarsis     TCCCTCGATTATAAATACTT GATTACTGTCACTTCAAAAT TCAAATTCTCCAACCTATGA TATAATAATTTTTTTTTCATG ATTTCACTATAATAATTTTA
Lasius (L.) psammophilus    CCCTTCAATTATAAATACCT GATTATTATCTCTCCAAAAT TCAAATTCTCCAACTTATGA CATAATAATTTTTTTTTCATG ATTTTACTATAATAATTTTA
Myrmecocystus semirufus     TCCTTCTATCATTAATACTT GATTATTATCTCTCCAAAAC TCAAACTCACCAACCTATGA TATAATAATTTTTTTTCCATG ATTTCACTATAATAATTTTA
Paratrechina arenivaga      CCCTTCAATTATTAACTCTT GAACTCTCTCAATACAAAAC TCCAACTCCCCAATTTATGA TATGATAATCTTCTTTCATG ATTTTACTATAATAATTTTA
Paratrechina bourbonica     TCCTGCAATTATTAATACTT GAACTTATCCCTTCAAAAT TCAAACTCTCCAATTTATGA TATAATAATTTTTTTTCCATG ATTTTACTATAATAATCCTTA
Paratrechina longicornis    TCCTTCAATTATTAACTCTT GAACTCTCTCAATACAAAAC TCTAACTCCCCAATCTATGA TATGATAATCTTCTTTCATG ATTTTACTATAATAATTTTA
Plagiolepis sp.             TCCCTCTATTATTAATACTT GACTAATTTCTCTCCAAAAT TCTAATTCTCCCACTTATGA CATAATAATTTTTTTTTCACG ATTTCACCATAATAATTTTA
Prenolepis imparis          TCCAGCAATTATTAATACTT GGGCATTACCCCTTCAAAAT TCTAATTCTCCCATATATGA TATAATAATTTTCTTTCATG ACTTTACTATAATAATCCTA
Acanthomyops californicus   TCCTTCAATTATAAATACTT GATTATTATCTCTTCAAAAT TCAAATTCTCCAACTTATGA TATAATAATTTTCTTCCACG ATTTTACCATAATAATTTTA

Pseudolasius sp.            ACATTCATTATAATATTAAT TTTTTTCATCATATATTCAA TAATTAATAACAAATTCACT AACCGATTTATACTTCAAGG ACATACTATTGAACTAATTT
Lasius (Ca.) flavus         ATCTTTATTACTCTTCTTAT TCTATTTATTATATTTTCTA TAATCAACAATAAATTAATT AATCGATTTCTACTCCAAGG ACACTTAATTGAATTAATTT
Lasius (D.) fuliginosus     ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTTCTA TAATTAATAATAAGTTAATT AATCGATTTTTACTACAAGG ACATTTAATTGAACTAATTT
Lasius (Ch.) meridionalis   ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTTCTA TAATCAATAATAAATTAATT AATCGATTCTTACTTCAAGG ACATTTAATTGAATTAATTT
Lasius (Ch.) distinguendus  ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTTCTA TAATCAATAATAAATTAATT AATCGATTCTTACTTCAAGG ACATTTAATTGAATTAATTT
Lasius (Ch.) jensi          ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTTCTA TAATCAATAATAAATTAATT AATCGATTCTTACTTCAAGG ACATTTAATTGAATTAATTT
Lasius (Ch.) umbratus       ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTTCTA TAATCAATAACAAATTAATT AATCGATTCTTACTTCAAGG ACATTTAATTGAATTAATTT
Lasius_(Ch.)_mixtus         -------------------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) alienus         ATTTTTATTACCCTTCTTAT TTTATTTATTATATTTACCA TAATTAATAATAAATTAATT AACCGATTCTTACTTCAAGG TCACTTAATTGAATTAATCT
Lasius (L.) brunneus        ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTACCA TAATCAATAATAAATTAATT AATCGATTTTTACTCCAAGG TCATTTAATTGAACTAATCT
Lasius (L.) sakagamii       -------------------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) turcicus        -------------------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) emarginatus     ATTTTTATTACCCTTCTTAT TTTATTTATTATATTTACCA TAATTAATAATAAATTAATT AACCGATTCTTGCTTCAAGG CCACTTAATTGAACTAATTT
Lasius (L.) niger           ATTTTTATTACCCTTCTTAT TTTATTTATTATATTTACCA TAATTAATAATAAATTAATT AACCGATTCTTACTTCAAGG CCACTTAATTGAACTAATTT
Lasius (L.) pallitarsis     ATCTTTATTACCCTTCTTAT TCTATTTATTATATTTACTA TAATTAATAATAATTTAATT AATCGATTTTTACTACAAGG ACATTTAATCGAATTAATTT
Lasius (L.) psammophilus    ATTTTTATTACCCTTCTTAT TTTATTTATTATATTTACCA TAATTAATAATAAATTAATT AACCGATTCTTACTTCAAGG TCACTTAATTGAATTAATCT
Myrmecocystus semirufus     ATTTTTATTACTCTTCTTAT TTTATTCATTATATTTTCTA TAATTAAAAATAAATTAATT AATCGATTTTTACTTCAAGG ACACTTAATTGAATTAATTT
Paratrechina arenivaga      ACATTTATTACTTTAATAAT TTTTTTTATTATATATTCTA TAGTTAATAATAAATTTATT AACCGATTTCTTCTCCAAGG CCATTTAATTGAATTAATCT
Paratrechina bourbonica     ACTTTTATTACTTTAATAAT TTTTTTTATTATATATTTCAA TAATTAACAATAAATTTATT AATCGATTTCTTCTTCAAGG TCATTCAATTGAATTAATCT
Paratrechina longicornis    ACTCTCATTACTTTAATAAT TTTTTTTATTATATACTCTA TAGTTAATAATAAATTTATT AACCGATTTCTTCTCCAAGG TCATTTAATTGAATTAATCT
Plagiolepis sp.             ATTTTCATTACCTTACTCAT CTTTTTTATTATATATATAA TAATCAACAATAAACTTATT AACCGATTTCTTCTGCAAGG CCATCTAATTGAATTAATTT
Prenolepis imparis          ATTTTTATTACTCTTTTAAT TTTTTTTATTATATTTACAA TAATTAATAATAAATTTATT AACCGATTTCTTTTACAAGG TCATCTTATTGAATTAATTT
Acanthomyops californicus   ATTTTTATTACTCTTCTTAT TTTATTTATTATATTTTCTA TAATTAATAATAAATTAATT AATCGATTTTTACTACAAGG ACATTTAATTGAACTAATTT

Pseudolasius sp.            GAACAATTATTCCTATATTA ATTTTAATTTTTATTGCCAT CCCTTCAATTAAAATCCTTT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (Ca.) flavus         GAACAATTACTCCTATAATT ATTTTAATTTTAATTGCAAT TCCCTCAATTAAAATTTTAT ACTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (D.) fuliginosus     GAACAATTACTCCTATAATT ATTTTAATTTTAATTGCAAT TGCTTCAATTAAAATTTTAT ACTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (Ch.) meridionalis   GAACTATTACTCCCATAATT ATTTTAATTTTAATTGCAAT TCCTTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (Ch.) distinguendus  GAACTATTACTCCCATAATT ATTTTAATTTTAATTGCAAT TCCTTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (Ch.) jensi          GAACTATTACTCCCATAATT ATTTTAATTTTAATTGCAAT TCCTTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (Ch.) umbratus       GAACTATTACTCCTATAATT ATTTTAATTTTAATTGCAAT TCCTTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius_(Ch.)_mixtus         -------------------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) alienus         GAACAATTACCCCTATAATT ATTTTAATTTTAATTGCAAT TCCCTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (L.) brunneus        GAACAATTACACCCATGATT ATTTTAATTTTAATCGCAAT TCCTTCAATTAAAATCTTAT ATTTAACAGATGAAATATTT AATAACAAAATTACAATTAA
Lasius (L.) sakagamii       -------------------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) turcicus        -------------------- -------------------- -------------------- -------------------- --------------------
Lasius (L.) emarginatus     GAACAATTACTCCTATAATT ATTTTAATTTTAATTGCAAT TCCCTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Lasius (L.) niger           GAACAATTACTCCTATAATT ATTTTAATTTTAATTGCAAT TCCCTCAATTAAAATTTTAT ATTTGACAGATGAAATATTT AATAATAAAATCACAATTAA
Lasius (L.) pallitarsis     GAACAATTACTCCTATAATT ATTTTGATTTTAATTGCAAT TCCCTCAATTAAAATCTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACTATTAA
Lasius (L.) psammophilus    GAACAATTACCCCTATAATT ATTTTAATTTTAATTGCAAT TCCCTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATTACAATTAA
Myrmecocystus semirufus     GAACAATTACTCCAATAATT ATTTTAATTTTAATTGCAAT TCCTTCTATCAAAATTCTTT ATTTAACAGACGAAATATTT AATAATAAAATTACAATCAA
Paratrechina arenivaga      GAACTATTACTCCTATAATT ATTTTAATTTTTATTGCAAT TCCTTCTATTAAAATTCTTT ATCTTACTGATGAAGTATTT AACAACAAACTAACAATTAA
Paratrechina bourbonica     GAACAATTACTCCCATAATT ATTTTAATCTTTATTGCTAT CCCTTCAATTAAAATTCTCT ACCTCACAGACGAAATATTT AATAATAAATTAACAATTAA
Paratrechina longicornis    GAACTATTACTCCTATAATT ATTCTAATTTTTATTGCAAT TCCTTCTATTAAAATTCTTT ATCTTACCGATGAAATATTT AACAACAAATTAACAATTAA
Plagiolepis sp.             GAACTATTACTCCAATAATT ATTTTAATCTTTATTGCTAT CCCCTCAATTAAAATTTTAT ATTTAACAGATGAAATATTT AATAATAAAATCTCTATTAA
Prenolepis imparis          GAACATTCACCCCTATAATT ATCTTAATTTTTATTGCTAT TCCATCAGTTAAAATCTAT ATATCACTGATGAAATATAT GATAATAAACTTACAATTAA
Acanthomyops californicus   GAACAATTACTCCTATAATT ATTTTAATTTTAATTGCAAT TCCTTCAATTAAAATTTTAT ACTTAACAGATGAAATATTT AATAATAAAATTACAATTAA

Pseudolasius sp.            AACTATTGGACATTTTAATA TGGCAGA--ATA-AGTGCAA TAGATTTAAACTCTATTAAT AAATATTT-TAAAAA-TTAT TTTATTAAAA
Lasius (Ca.) flavus         ATCTATAGGTCATTTTAATA TGGCAGA--ATTTAGTGCAT TGGATTTAAATCCCAATAAA AAAGATTT-TATTTATTTCT TTTATTAAAA
Lasius (D.) fuliginosus     ATCTTTAGGCCATTTTAATA TGGCAGA--CTT-AGTGCAT TGGATTTAAATCCCAATAAT AAAGATTT-TATTTATTTCT TTTATTAAAA
Lasius (Ch.) meridionalis   ATCTATAGGTCACTTTAATA TGGCAGA--ATTTAGTGCAT TAGATTTAAACTCTAATAAT AAAGATTT-TATTTACTTCT TTTATTAAAA
Lasius (Ch.) distinguendus  ATCTATAGGTCACTTTAATA TGGCAGA--ATTTAGTGCAT TAGATTTAAACTCTAATAAT AAAGATTT-TATTTACTTCT TTTATTAAAA
Lasius (Ch.) jensi          ATCTATAGGTCACTTTAATA TGGCAGA--ATTTAGTGCAT TAGATTTAAACTCTAATAAT AAAGATTT-TATTTACTTCT TTT-TTAAAA
Lasius (Ch.) umbratus       ATCTATCGGCCACTTTAATA TGGCAGA--ATTTAGTGCAT TAGATTTAAACTCTAATAAT AAAGATTT-TACTTACTTCT TTTATTAAAA
Lasius_(Ch.)_mixtus         -------------------- -------------------- -------------------- -------------------- ----------
Lasius (L.) alienus         ATCTGTAGGTCATTTTAATA TGGCAGA--ATTTAGTGCAT TGGATTTAAACCCCAATAAT AAAGATTT--A--T---TCT TTTATTAAAA
Lasius (L.) brunneus        ATCTGTAGGTCACTTTAATA TGGCAGA--ATT-AGTGCAT TGGATTTAAACCCCAATTAT AAAGGTTTATTTTTACACCT TTTATTAAAA
Lasius (L.) sakagamii       -------------------- -------------------- -------------------- -------------------- ----------
Lasius (L.) turcicus        -------------------- -------------------- -------------------- -------------------- ----------
Lasius (L.) emarginatus     ATCTGTAGGCCATTTTAATA TGGCAGA--ATTTAGTGCAT TGGATTTAAACCCCAATAAT AAAGATTT--ACTT---TCT TTTATTAAAA
Lasius (L.) niger           ATCTGTAGGTCAT------- -------------------- -------------------- -------------------- ----------
Lasius (L.) pallitarsis     ATCTGTCGGCCACTTTAATA TGGCGGA--ATTTAGTGCAT TGGATTTAAATCCCAATAAT AAAGATCT-TACTTACCTCT TTTATTAAAA
Lasius (L.) psammophilus    ATCTGTAGGTCATTTTAATA TGGCAGA--ATTTAGTGCAT TGGATTTAAACCCCAATAAT AAAGATTT--A--T---TCT TTTATTAAAA
Myrmecocystus semirufus     ATCTATCGGACACTTTAATA TGGCAGA--ATTTAGTGCAT TGGATTTAAACCCCAATTAT AAAGATTT--A--T---TCT TTTATTAAAA
Paratrechina arenivaga      ATCACTAGGCCATTTTAATA TGGCAG---A-TTAGTGCAT TGGATTTAAACCCCAAATAA AAAGTTAT-TG--T--ATCT TTTATTAAAA
Paratrechina bourbonica     ATCATTAGGTCATTTTAATA TGGCAGATAAATTAGTGCAT TGGATTTAAACCCCAAATAA AAAGATAT--AT-T--GTCT TTTATTAAAA
Paratrechina longicornis    ATCATTAGGTCATTTTAATA TGGCAG---ATTTAGTGCAT TGGATTTAAGCCCCAAATAA AAAGTTAT-TG--T--ATCT TTTATTAAAA
Plagiolepis sp.             ATCAATTGGCCATTTTAATA TGGCAGAT-AA--AGTGCAT TGGACTTAAACCCCACTAAT GAAGACAA--ATAT--GCCT TCTATTAAAA
Prenolepis imparis          ATCTTTAGGTCACTTTAATA TGGCAGA-AATTTAGTGCAT-TGGACTTAAATCCCAAATAT AAAG--AT--A--T---TCT TTTATTAAAA
Acanthomyops californicus   ATCTTTAGGCCATTTTAATA TGGCAGA--CTT-AGTGCAT TGGATTTAAATCCCAATAAT AAAGATTT-TATTTATTTCT TTTATTAAAA
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COI: 1-210, COII: 211-513, tRNA-Leu: 514-570.

Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2004.07.012.

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Appendix 2

Publications and Curriculum Vitae

FURTHER PUBLICATIONS:

Dunn, RR, Sanders NJ, Fitzpatrick MC, Laurent E, Lessard JP, (Janda M. and 16 further co-authors) et al. 2007: Global ant (Hymenoptera: Formicidae) biodiversity and biogeography – a new database and its possibilities. – Myrmecological News 10: 77-83.

Janda, M., Klimes, P. & Borovwiec, M.L. 2007: Ecology of New Guinea ants (Hymenoptera: Formicidae) – exploring an unknown fauna. – Myrmecological News 10: 109.

Novotny, V., S. E. Miller, J. Hulcr, R. A. I. Drew, Y. Basset, M. Janda, G. P. Setliff, K. Darrow, A. J. Stewart, J. Auga, B. Isua, K. Molem, M. Manumbor, E. Tamtiai, M. Mogia, and G. D. Weiblen. 2007. Low beta diversity of herbivorous insects in tropical forests. Nature 448:692-695.

Novotny, V., Drozd, P., Miller, S. E., Kulfan, M., Janda, M., Basset, Y., Weiblen, G. D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**:1115-1118

Janda, M. & Alpert, G. (2005-7) Ants of New Guinea. (species list at: http:// pick5.pick.uga.edu /mp /20q?act?x_checklist&guide=Ants_New_Guinea).

Novotny, V., Miller, S. E., Leps, J., Bito, D., Janda, M., Hulcr, J., Basset, Y., Damas & K. Weiblen, G. D. (2004) No tree an island: the plant-caterpillar food web of secondary rainforest in New Guinea. *Ecology Letters* **7**: 1090-1100

Janda, M., Folkova, D., Zrzavy, J. (2004) Phylogeny of *Lasius* ants based on mitochondrial DNA and morphology, and the evolution of social parasitism in the Lasiini (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 33 (3): 595-614

Novotny, V., Miller, S.E., Cizek, L., Leps, J., Janda, M., Basset, Y., Weiblen, G.D., Darrow, K. (2003) Colonising aliens: caterpillars (Lepidoptera) feeding on *Piper aduncum* and *P. umbellatum* in rainforests of Papua New Guinea. *Ecological Entomology*, 28, 704–716

In submission:

Hlavac, P., Janda, M. (2007) New genus of Lomechusini (Coleoptera: Staphylinidae, Aleocharinae) from Papua New Guinea associated with *Leptogenys* Roger. *subm. to Zootaxa*.

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Professional Appointments:
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Lectures and Conferences
(oral presentations only)

2007 – Central European Conference of Myrmecology, Szeged, Hungary; Ecology of New Guinea Ants

2006 – IUSSI Conference, Washington; Ecology of New Guinea Ants – exploring the unknown fauna

2005 - Evolution of social parasitism in ants, insights from phylogeny. Universität Regensburg

Professional Travel and Residence
2001– 2004, New Guinea Binatang Research Center, Madang, Papua New Guinea.
August 2005 – Smithsonian Tropical Research Institute, Panama;
October 2005, September 2006 - Museum of Comparative Zoology, Harvard University, USA,