

Diversity and ecology of arboreal ant communities of *Camponotus* (Hymenoptera: Formicidae) in a New Guinea rainforest with descriptions of four new species

Petr KLIMES & Archie MCARTHUR



Abstract

New Guinea is one of the last remaining regions of extensive tropical forest and is an important biodiversity hotspot, yet most of its canopy ant species are poorly known. Here, we provide the first study of arboreal ant communities of the genus *Camponotus* MAYR, 1861 from a lowland rainforest in New Guinea. We censused *Camponotus* nests in trees from two 0.32 ha forest plots in primary forest (389 trees) and secondary forest (296 trees) and explored their species diversity and nesting preferences. In total, 293 nests of 19 species were found. In 16 of the 19 species, major workers exhibited a set of morphological traits (i.e., flattened anterior part of head, swollen fore femora and maximal distance between frontal carinae greater than a third of head width) associated with phragmosis, an adaptation for arboreal nesting. In primary forest, we detected 15 species in 124 nests versus only eight species in 169 nests in secondary forest. Only four species were shared between the two forest plots. *Camponotus* species differed significantly in their preferences for nesting microhabitats in both forest plots, ranging from species that were opportunistic and relatively abundant to those that specialized and nested only in living tree branches high in the canopy where they tended myrmecophilous scale insects. Of the 19 species collected, 13 are newly reported for New Guinea, including four that are described here as new species: *Camponotus anezkae* sp.n., *Camponotus rotundus* sp.n., *Camponotus triangulatus* sp.n. and *Camponotus wanangus* sp.n. In addition, *Camponotus aruensis* KARAVAEV, 1933 is redescribed. Diagnostic features for species identification, digital photos of all available castes and morphological measurements are provided. The study demonstrates the high diversity of arboreal *Camponotus* ants and their nesting habits within a single tropical forest site.

Key words: Formicinae, arboreal insects, Coccoidea, species richness, taxonomy, tree canopies, tropical ecosystems.

Myrmecol. News 20: 141-158

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 14 March 2013; revision received 24 February 2014; accepted 26 March 2014

Subject Editors: Nicholas J. Gotelli & Herbert Zettel

Petr Klimes (contact author), Institute of Entomology, Biology Centre of ASCR and Faculty of Science, University of South Bohemia, Branisovska 31, CZ-370 05 České Budějovice, Czech Republic; New Guinea Binatang Research Center, P.O. Box 604, Madang, Papua New Guinea. E-mail: peta.klimes@gmail.com

Archie McArthur, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia. E-mail: archie.mcarthur@samuseum.sa.gov.au

Introduction

Tropical forests are the most diverse ecosystems in the world. Their canopies alone support an estimated 40% of extant species of which 10% are thought to be canopy specialists, mainly consisting of insects and other arthropods (BASSET & al. 2003). However, relatively little is known about canopy insect fauna and a large proportion of the species living in trees remains undescribed (BASSET 2001, BASSET & al. 2003). Developing both taxonomical and ecological knowledge of the canopy fauna is hence crucial as primary forests are increasingly under threat from logging and agriculture (PRIMACK & CORLETT 2005, SHEARMAN & BRYAN 2011). Ants are known to be exceptionally abundant in tropical forest canopies, where they can represent 20 - 50% of arthropod biomass (FLOREN & LINSÉNMAIR 1997, DEJEAN & al. 2007). Diversity of arboreal ants can also be high in tropical trees. For instance, a single large tree flogged in a Peruvian forest yielded 43 species (WILSON 1987) and recent estimates suggest that up to half of all ant

species are associated with tropical forest canopies (FLOREN & al. 2014).

The genus *Camponotus* (Formicinae) was first described by Gustav Mayr (MAYR 1861). Today, it is the largest genus of ants in the world with over 1500 species described (BOLTON 2012). *Camponotus* ants are widespread in most terrestrial ecosystems, where they nest in a great variety of habitats from the ground to trees (HÖLLDOBLER & WILSON 1990, MCARTHUR 2007). Most *Camponotus* species are dimorphic, i.e., they have two morphologically distinct castes of minor and major workers, with the major workers usually having an enlarged mesosoma and head when compared to minor workers. Other species are polymorphic, i.e., they have a range of body sizes within a colony, without discrete size castes (SHATTUCK 1999, MCARTHUR 2007). The minor workers are the most frequently observed caste on vegetation, where they search for insect prey, plant exudates and Homopteran honeydew (HÖLLDOBLER & WIL-

SON 1990, SHATTUCK 1999). Some species of *Camponotus* are also known for their mutualistic relationships with particular myrmecophytic trees which are protected against damage by herbivorous insects by ant workers, while in return the plants provide the ants with nesting space (LETOURNEAU & al. 1993, FEDERLE & al. 1998, EDWARDS & al. 2010). *Camponotus* has been reported to be one of the most diverse ant genera present in tropical tree canopies (WILSON 1987, RYDER WILKIE & al. 2010, FLOREN & al. 2014). Yet most studies of arboreal *Camponotus* have focused on single species (e.g., LETOURNEAU & al. 1993, FEDERLE & al. 1998, PFEIFFER & LINSSENMAIR 2000) rather than on whole communities.

In some arboricolous species of *Camponotus*, major workers exhibit phragmosis, a behavioural and morphological adaptation of blocking the nest entrances using their flattened cork-shaped heads (WHEELER 1927). Phragmosis was first noted in *Camponotus truncatus* (SPINOLA, 1808) (FOREL 1874) in the subgenus *Colobopsis* MAYR, 1861. However, morphological traits associated with phragmosis and arboricolous nesting in *Camponotus* can also be found in species of several other subgenera, i.e., *Myrmambly* FOREL, 1912, *Hypercolobopsis* EMERY, 1920, *Pseudocolobopsis* EMERY, 1920 and *Paramyrmambly* SANTSCHI, 1926. As the subgeneric classification of *Camponotus* is in need of revision (see Taxonomy section), we avoid subgeneric affiliations and instead define "*Camponotus* species with phragmosis" hereafter as species having the following distinct morphological traits: I) the largest distance between the frontal carinae in workers is greater than one third of head width, II) enlarged fore femora in workers (at least 1.5 times the thickness of mid and hind femora), and III) flattened or truncated front part of head (usually only in major workers and queens). These traits likely evolved repeatedly within the genus as adaptations to nesting in vegetation, where workers typically use cavities excavated by other insects or create galleries within the branches themselves (EMERY 1925, WILSON 1974).

New Guinea is one of the last three major tropical wilderness areas and supports approximately 5% of global biodiversity (MITTERMEIER & al. 2003). Ant diversity on this large tropical island is among the highest worldwide (SNELLING 1998). Up to 120 ant species have been found in a single patch of 400 m² of lowland forest (JANDA & al. 2007) and approximately 900 species have been recorded from New Guinea to date (JANDA & al. 2011). As a result of this enormous diversity and relatively short taxonomical history, many species are still undescribed and the biology of most New Guinean species is unknown (SNELLING 1998). Current literature is rather scarce for *Camponotus* from New Guinea and nearby islands, with 31 species described or reported from the region so far (JANDA & al. 2011, BOLTON 2012). Information for arboreal nesting species is particularly lacking: For instance, four of the nine New Guinean *Camponotus* species currently listed in arboricolous subgenus *Colobopsis* were described solely from queens (BOLTON 2012). Here we provide the first extensive study on the diversity, nesting ecology and taxonomy of tropical arboricolous *Camponotus* communities from a lowland rainforest in Papua New Guinea.

Material and methods

Study site: We surveyed *Camponotus* communities in a lowland rainforest near Wanang village in the Ramu River

basin, Madang Province, Papua New Guinea (100 - 200 m a.s.l., 05° 14' S 145° 11' E). The climate in the region is humid with a mean annual rainfall of 3600 mm, mean air temperature of 26°C, and a weak dry season from July to September (MCALPINE & al. 1983). Wanang tribe, the customary landowners who traditionally practice slash-and-burn agriculture, provided the unique opportunity for destructive sampling of a young (approx. ten years old) secondary forest plot and an old growth primary forest plot destined for food gardens. The two 1-ha plots, which were one kilometre apart, were censused for plants and then felled and sampled for several canopy insect groups, including ants. For details on vegetation structure and plant diversity see WHITFIELD & al. (2012).

Sample collection and material: Arboreal ants were collected from all felled trees with diameter at breast height (dbh) ≥ 5 cm in primary and secondary forest plots. For this study sampling efforts were focused in a 0.32 ha (40 × 80 m) area of each 1-ha plot, with a total of 685 trees rigorously censused for *Camponotus* nests, including one tree at the border of the secondary forest 0.32 ha plot where *C. anezkae* sp.n. was recorded. Nest height above ground (distance in metres), nesting microhabitat and tree species were recorded for each ant nest. In addition, we noted when symbiotic scale insects (Coccoidea) were present within or outside of nests.

A series of workers, males and queens (if found) was collected from every nest in a tree by dissecting the nest and tree with a bush knife (each nest series coded HP and four digits hereafter). For further details on sampling design and whole community analyses see KLIMES & al. (2012). The material was transferred to vials with 96% ethanol and stored at minus 20°C at the Institute of Entomology of Biology Centre CAS, Czech Republic (IECA). Ants were sorted first to genera and morphospecies using keys (BOLTON 1994, SHATTUCK 1999). All *Camponotus* spp. were then identified to species by comparing them to the type material from museums, photographs of type specimens and available literature (BOLTON 2012, MCARTHUR 2007, 2012, and literature listed there). Vouchers of all species (Tab. 1) are deposited under the species codes in reference collections of PK (IECA) and their photos will be provided at www.newguineants.org. For new species the material is deposited also in several other institutions as specified below.

Acronyms of depositories:

- SAMA South Australian Museum, Adelaide, Australia
- IECA Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic
- NAIC National Agricultural Insect Collection, National Agricultural Research Institute, Port Moresby, Papua New Guinea
- NHMW Naturhistorisches Museum, Vienna, Austria
- SIZK Schmalhausen Institute of Zoology of the Ukrainian National Academy of Sciences, Kiev, Ukraine

Ecological analysis: The unique datasets used here represent a census of nests within a forest plot rather than random sampling of ant species from a larger area. Hence, this method enables us to look for the first time in comprehensive detail at the diversity of the whole community and species ecology within a forest area, which would not be possible when exploring trees using other methods (e.g., tree fogging, baits). However, as the large scope and demands of such sampling did not allow us to replicate the

Tab. 1: List of *Camponotus* species found nesting in trees with dbh ≥ 5 cm in New Guinea lowland rainforest (685 trees in total) and their occurrences in a primary forest 0.32 ha plot (PF) and a secondary forest 0.32 ha plot (SF). Numbers show total number of nests, number of trees with nests, and number of host tree species and families per ant species. Species are ordered by their total nest abundance. The species newly reported for New Guinea are marked by asterisks and the four described in this study as new are marked in bold.

<i>Camponotus</i> species		Phragmosis	N of nests			Occupied trees	
Species name	Sp. code		PF	SF	All	N of trees	N of tree species (families)
<i>C. cf. macrocephalus</i> (ERICHSON, 1842)*	CAMP010	Yes	5	107	112	88	26 (13)
<i>C. vitreus</i> (F. SMITH, 1860)	CAMP001	Yes	63	11	74	64	36 (22)
<i>C. aruensis</i> KARAVAIEV, 1933*	CAMP004	Yes	3	23	26	24	12 (8)
<i>C. chloroticus</i> EMERY, 1897	CAMP012	No	0	20	20	15	11 (4)
<i>C. sanguinifrons</i> VIEHMEYER, 1925	CAMP008	Yes	20	0	20	11	3 (3)
<i>C. cf. conithorax</i> EMERY, 1914*	CAMP006	Yes	7	0	7	7	7 (7)
<i>C. dorycus confusus</i> EMERY, 1887	CAMP016	No	7	0	7	7	5 (4)
<i>C. trajanus</i> FOREL, 1912*	CAMP007	Yes	5	0	5	5	5 (4)
<i>C. aff. pictostriatus</i> KARAVAIEV, 1933*	CAMP011	Yes	0	4	4	4	2 (2)
<i>C. aff. poecilus</i> EMERY, 1893*	CAMP005	Yes	3	0	3	3	3 (3)
<i>C. quadriceps</i> (F. SMITH, 1859)	CAMP013	Yes	1	2	3	3	1 (1)
<i>C. wanangus</i> sp.n.*	CAMP003	Yes	3	0	3	2	2 (2)
<i>C. rotundus</i> sp.n.*	CAMP014	Yes	2	0	2	2	2 (1)
<i>C. cf. variegatus</i> (F. SMITH, 1858)	CAMP018	No	2	0	2	2	2 (2)
<i>C. cf. polynesianus</i> EMERY, 1896*	CAMP017	Yes	1	0	1	1	1 (1)
<i>C. triangulatus</i> sp.n.*	CAMP019	Yes	1	0	1	1	1 (1)
<i>C. sp. 020 aff. janeti</i> FOREL, 1895*	CAMP020	Yes	1	0	1	1	1 (1)
<i>C. anezkae</i> sp.n.*	CAMP022	Yes	0	1	1	1	1 (1)
<i>C. sp. 021 aff. janeti</i> FOREL, 1895*	CAMP021	Yes	0	1	1	1	1 (1)
<i>Camponotus</i> with phragmosis (16 species)		Yes	115	149	264	186	63 (26)
<i>Camponotus</i> without phragmosis (3 species)		No	9	20	29	24	18 (7)y
Whole community (19 species)		Yes	124	169	293	202	67 (26)

forest plots, our tree samples within the plots are pseudo-replicated for comparison among forest types. In such cases, the careful use of inferential statistics is still appropriate (OKSANEN 2001). These recommendations are followed here and direct statistical comparisons of the two plot datasets are avoided.

Tree-based species accumulation curves were generated to explore the relationship between observed *Camponotus* species richness and the cumulative number of trees in each of the two plots (Mao Tau function with 95% Confidence Intervals) (Fig. 1) using the program EstimateS v. 8.2 with 100 randomisations of sample order (COLWELL 2009). Number of nests per nest site (i.e., nesting microhabitat) in forest plots was explored using the categories following KLIMES & al. (2012), but some of them were merged here for simplicity: Nests in twigs and nests in branches were considered together, as were nests on the bark and under the bark (i.e., seven categories listed in Fig. 2). Ant nesting microhabitat and nest height preferen-

ces were independently assessed for the ant communities of each of the two plots using a multivariate redundancy analysis (RDA) of matrices, where the first matrix presented nest records times ant species presence and the second matrix nest records times environmental predictors (nest categories scored as dummy variables and nest height in metres) (LEPS & SMILAUER 2003). Centring without standardisation by species was chosen as optimal for datasets, where distribution of species abundance (here nest records) is uneven with many rare species (LEPS & SMILAUER 2003). The significance of all canonical axes (F-ratio, 999 permutations, $P \leq 0.05$) was calculated and ordination diagrams constructed using Canoco for Windows Version 4.56 (TER BRAAK & SMILAUER 1998).

Measurements and indices: Examination of specimens was carried out using a Mitutoyo 209116 micrometer attached to an Olympus XZ microscope fitted with a cross-hair at magnifications of 20 to 80 \times (following MCARTHUR 2009). Photographs of specimens were taken with a Nikon

D600 camera fitted with a Zeiss 25 mm Luminar lens, extensions and Nikon Control Pro2 computer program in SAMA. Photos of the queens and males not available in SAMA were taken with a Leica DFC450 camera fitted with macroscope Leica Z16 APO and folded in Helicon Focus version 5.3 X64 (in IECA).

We followed SORGER & ZETTEL (2011) in measuring holotype specimen plus two workers from each paratype series and caste (i.e., one minor and one major worker with the smallest head width and one minor and one major worker with the largest head width) to assess the intraspecific variability. Alates were also measured for each species whenever available (one male and one gyne per species).

Parameters used:

- CI cephalic index = $HW / HL \times 100$
 EL maximum eye length
 FCD frontal carinae distance = maximum distance between the carinae, ignoring any abrupt curvature at ends
 FT1 maximum thickness of front femur
 FT2 maximum thickness of middle femur
 FT3 maximum thickness of hind femur
 HL head length = maximum distance between anterior clypeus and vertex with both in one horizontal plane
 HW maximum head width not including the eyes
 ML mesosoma length = diagonal length of mesosoma in side view, from angle at which pronotum meets cervix to posterior basal angle of metapleuron
 PW pronotal width = maximum width in dorsal view
 SI scape index = $SL / HW \times 100$
 SL maximum scape length from its anterior to posterior margin, in horizontal plane

Measurements of all morphological traits presented hereafter are in millimetres.

Results

Species diversity and nesting ecology

In total 19 species of *Camponotus* were found nesting in the 685 trees censused. The accumulation curve for species was considerably lower in the secondary forest plot where only eight species (Mao Tau Sp. observed, 95% CI ± 2.48) were recorded in 296 trees in total. The species richness there was about half that found in the primary forest plot, which yielded 15 species (95% CI ± 2.95) in 389 trees in total (Fig. 1). Overall, 86 trees (22%) hosted at least one nest of *Camponotus* in primary forest. In contrast, occupancy of trees was almost double this value in secondary forest (116 trees, 39%).

Sixteen of the 19 species collected possessed phragmosis (Tab. 1), and occupied 264 nests in total. The three species without phragmosis, i.e., *Camponotus chloroticus* EMERY, 1897, *C. dorycus confusus* EMERY, 1887 and *C. cf. variegatus* (F. SMITH, 1858) were relatively rare and comprised only 10% of nesting records (29 of 293 nests) of the genus in total (Tab. 1). The number of *Camponotus* species nesting per tree varied greatly from zero to four species (primary forest plot: mean = 0.31, SD = 0.7, max = 4; secondary forest plot: mean = 0.57, SD = 0.9, max = 3). The abundance of the species also varied significantly (Tab. 1). The most abundant species, *Camponotus cf. macrocephalus* (ERICHSON, 1842) with 112 nests in total, was also the most widespread species in the secondary forest

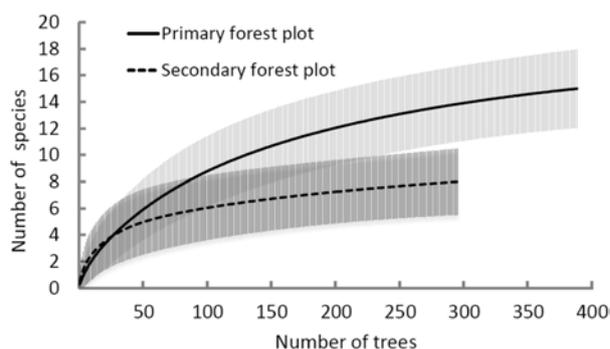


Fig. 1: Species accumulation curves (Mao Tau function \pm 95% CI) of all *Camponotus* ant species nesting in trees with dbh ≥ 5 cm in 0.32 ha plot of primary forest and in 0.32 ha plot of secondary forest.

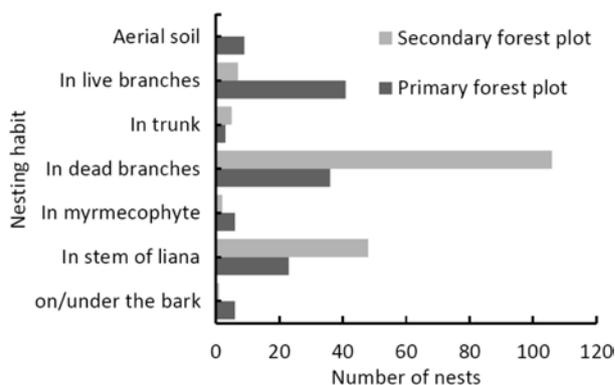


Fig. 2: Nesting habits of the *Camponotus* ant community in two 0.32 ha rainforest plots.

plot (107 nests). The second most abundant species was *Camponotus vitreus* (F. SMITH, 1860) with 74 nests in total, and this was the most widespread species in the primary forest plot (63 nests). In contrast, there were also species found nesting at considerably lower densities; seven species occupied only one to two trees per plot (Tab. 1).

Distribution of nesting microhabitats utilised by *Camponotus* varied greatly between the forest types (Fig. 2). In the secondary forest plot, most nests were recorded inside dead branches (63%) and dry liana stems (28%), while in the primary forest plot the nests were most often found in live branches (33%) and nesting habitats were more evenly distributed (Fig. 2). Nests found in aerial soil (i.e., soil and debris under roots of epiphytes and mosses) were limited to the primary forest plot (7%).

The RDA analysis showed significant effects of environmental variables on the *Camponotus* ant communities in both the primary forest plot (significance of all canonical axes: $F = 2.5$, $p = 0.001$, variability explained by all canonical axes 13.4%) and the secondary forest plot ($F = 4.5$, $p = 0.001$, 14.2% respectively). Species differed in their tendency to nest in particular tree microhabitats in each of the forest plots. There was a strong association of *Camponotus sanguinifrons* VIEHMEYER, 1925, *C. rotundus* sp.n. and *C. wanangus* sp.n. with live branches in the high canopy of primary forest trees (Fig. 3a), while *C. cf. macrocephalus* and *C. aruensis* KARAVAIEV, 1933 were usually collected nesting in dry branches and lianas in secondary forest trees (Fig. 3b). However, some species were oppor-

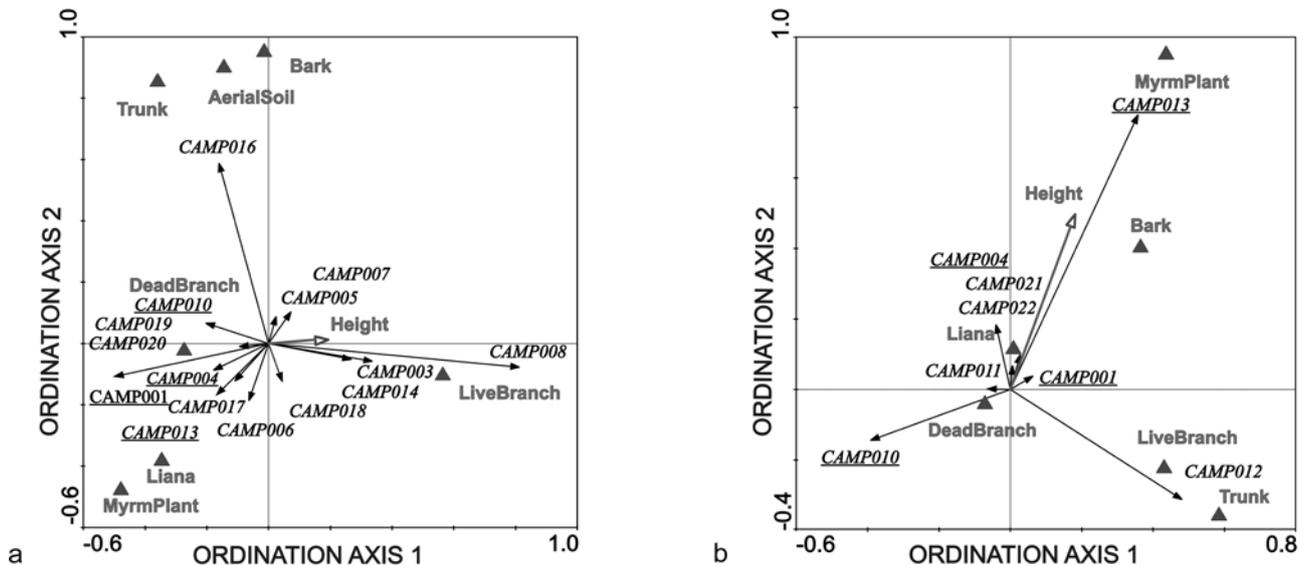


Fig. 3: Species-environment ordination diagram (RDA analysis) of *Camponotus* ant nests in trees a) in the primary forest plot and b) in the secondary forest plot. Variation of ant species composition is related to the explanatory variables height (distance of a nest from the ground) and the microhabitat in which ant species nested. Symbols refer to centroids of explanatory variables (triangles) and to species (arrows). The first two ordination axes explain together 11.7% (primary forest) and 10.9% (secondary forest plot) of variation in the species data. Ant species identities are indicated by species codes, codes in underlined letters refer to the species common for both forest plots (for full species names see Tab. 1).

tunistic in their nesting habits. For example *C. vitreus* nests were collected from a wide range of microhabitats as aerial soil, under bark, in branches, in lianas (in both forest types), and in myrmecophytes in primary forest (in the epiphytic ant-plant *Hydnophytum moseleyanum* BECC.). Interestingly, the other three species shared between the two forest plots preferred the same microhabitat in both plots (Fig 3), with nests of *Camponotus* cf. *macrocephalus* occurring in dead branches, nests of *C. quadriceps* (F. SMITH, 1859) in myrmecophytic plants, and nests of *C. aruensis* in lianas. The three species lacking phragmosis (Tab. 1) were also arboricolous. They were found nesting mostly within tree branches or lianas, with the exception of *C. dorycus confuses*, which was usually found in aerial soil and inside termite nests on trunks (Fig. 3).

In contrast to the relatively high specialisation to particular nesting microhabitats, the host specificity of *Camponotus* species to particular tree species and plant families appeared low, with multiple tree species from various plant families being occupied (Tab. 1). The only exception to this was *C. quadriceps*, which in both plots was found nesting exclusively in its myrmecophytic host tree *Endospermum labios* SCHODDE in agreement with previous studies (LETOURNEAU & al. 1993) (Tab. 1, Fig. 3). However, this species occupied only one sampled tree in primary and two trees in secondary forest plot. When excluding the species with ≤ 3 occupied trees per plot, there were 7.6 (SD = 9.5) and 9.8 (SD = 7.7) tree species per ant species used as hosts on average in primary forest and secondary forest plot respectively.

Regarding the symbiosis with scale insects (Coccoidea), except for a few cases of externally feeding scale insects on twigs tended by *Camponotus* ants (six cases), most Coccoidea were found inside galleries in live twigs and branches of host trees (33 cases), where they were observed to be tended by both major and minor workers. The

overall presence of scale insects in *Camponotus* nests was considerably higher in the primary forest plot than in the secondary forest plot: 29 cases and four ant species partners in primary forest versus four cases and two ant species partners in secondary forest. However, this difference was driven by the presence of *Camponotus sanguinifrons* which was the most common species found with scale insects in primary forest (24 cases).

Systematics

The number of characters used in the following descriptions was chosen from the spreadsheet in MCARTHUR (2007) as the minimum required to conveniently make a positive identification of a species. The genus *Camponotus* is currently in need of molecular and taxonomical revision, since some of the 50 subgenera described may not represent natural groups (SCHLÜNS & CROZIER 2013). The subgeneric classification of *Camponotus* has been queried by BROWN (1972), who described it as "weak and inconsistent". This view was repeated by BOLTON (1995: p. 130) who stressed that many of the subgenera in *Camponotus* were "weak, poorly defined and untrustworthy". For these reasons no attempt is made to assign these new species to a subgenus of *Camponotus*. However, all species described below are *Camponotus* species with phragmosis (i.e., sharing the distinct morphological traits defined in the Introduction).

Camponotus anezkae sp.n. (Figs. 4 - 5)

Etymology: named after the patron saint of Czechs, St. Agnes (Anezka) and dedicated to the beloved daughter of PK.

Type material: Holotype (minor worker, SAMA): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 25.X.2007, HP0616, leg. P. Klimes". Paratypes: from the same nest series, labelled as above: 2 mi-



Fig. 4: *Camponotus anezkae* sp.n., major worker above, minor worker below.



Fig. 5: *Camponotus anezkae* sp.n., gyne above, male below.

Tab. 2: Morphological measurements of *Camponotus* species described in this study (see methods for definition of parameters). Values for holotypes (minor workers) and values for paratype workers with the smallest and the largest head width (separately for major and minor workers) are provided.

	CI	EL	FCD	FT1	FT2	FT3	HL	HW	ML	PW	SI	SL
a) <i>C. anezkae</i> sp.n.												
Holotype	92	0.28	0.43	0.27	0.18	0.20	0.90	0.83	1.25	0.65	122	1.01
Paratype majors	94	0.34	0.71	0.36	0.26	0.26	1.53	1.44	1.50	0.90	72	1.03
	99	0.37	0.75	0.41	0.25	0.24	1.47	1.45	1.56	1.05	69	1.00
Paratype minors	92	0.22	0.41	0.27	0.19	0.22	0.88	0.81	1.30	0.60	121	0.98
	94	0.28	0.42	0.34	0.25	0.25	0.89	0.84	1.35	0.66	125	1.05
b) <i>C. rotundus</i> sp.n.												
Holotype	96	0.19	0.52	0.29	0.20	0.18	0.82	0.79	1.08	0.52	70	0.55
Paratype majors	83	0.24	0.72	0.30	0.20	0.25	1.12	0.93	0.98	0.58	60	0.56
	83	0.20	0.75	0.31	0.18	0.21	1.13	0.94	1.23	0.60	63	0.59
Paratype minors	89	0.18	0.44	0.28	0.18	0.15	0.88	0.78	0.76	0.60	64	0.50
	89	0.24	0.55	0.33	0.22	0.20	0.98	0.87	1.25	0.58	63	0.55
c) <i>C. triangulatus</i> sp.n.												
Holotype	74	0.21	0.41	0.31	0.22	0.23	0.96	0.71	1.36	0.58	142	1.01
Paratype majors	91	0.31	0.65	0.37	0.25	0.26	1.27	1.15	1.60	0.81	63	0.72
	92	0.32	0.67	0.46	0.30	0.33	1.35	1.24	1.63	0.87	61	0.76
Paratype minors	76	0.24	0.34	0.31	0.17	0.16	0.89	0.68	1.33	0.53	129	0.88
	78	0.26	0.36	0.29	0.17	0.18	0.95	0.74	1.38	0.58	128	0.95
d) <i>C. wanangus</i> sp.n.												
Holotype	89	0.24	0.58	0.35	0.21	0.23	1.30	1.16	1.74	0.94	103	1.20
Paratype majors	88	0.34	0.91	0.46	0.30	0.30	1.78	1.58	1.98	1.12	56	0.89
	83	0.37	0.99	0.52	0.30	0.37	2.28	1.89	2.52	1.37	67	1.26
Paratype minors	95	0.26	0.52	0.36	0.20	0.24	1.18	1.12	1.68	0.9	105	1.18
	87	0.29	0.60	0.42	0.31	0.29	1.48	1.29	1.77	1.01	95	1.23
e) <i>C. aruensis</i>												
Majors	89	0.28	0.58	0.31	0.20	0.20	1.10	0.98	1.05	0.68	71	0.70
	89	0.30	0.64	0.35	0.21	0.22	1.18	1.05	1.24	0.76	62	0.65
Minors	82	0.20	0.43	0.31	0.18	0.19	0.78	0.64	0.70	0.50	122	0.78
	95	0.22	0.47	0.30	0.15	0.16	0.75	0.71	0.95	0.51	103	0.73

nor workers, 2 major workers, 1 queen (SAMA); 1 minor worker and 1 major worker (NHMW, NAIC); one individual of each caste (IECA).

Other material examined (in ethanol): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 25.X.2007, HP0617, leg. P. Klimes". 8 minor workers, 8 major workers, 2 queens (SAMA); and other material from the type locality (IECA).

Description: Photos of major worker and minor worker are given in Figure 4, and gyne and male in Figure 5. Morphological measurements of workers are provided in Table 2a, and of alates below. The species is dimorphic.

Major worker: Structures: in side view, front of head convex, only a change in radius separates the clypeus from its posterior. Mesosoma fairly evenly convex, with distinct metanotum resembling a trough. Propodeal angle well rounded and about 120°, declivity nearly concave, ratio dorsum / declivity about 0.8. Node front convex, back mostly straight, summit blunt. Fore femora about 1.5 times thicker than others. Integument glossy, very finely reticulate especially laterally on mesosoma and coxae. Head in front view: sides weakly convex and tapering to the front, vertex weakly convex; most of clypeus, anterior head and closed mandibles form a circular flattish surface, coarsely punctate. Anterior margin of clypeus projecting a little, notched in centre. Mandibles with four teeth. Frontal carinae distance approximately half of head width.

Pilosity: erect setae very sparse, none on gula, a few decumbent on scapes and tibiae, adpressed setae sparse all over.

Colour: mostly black, coxae and sutures of gaster whitish-yellow, head light brown except vertex which is darker.

Minor worker: Structures: in side view, anterior front of head and clypeus convex, separated by a depression. Mesosoma convex with metanotum resembling a trough, propodeal angle rounded, declivity nearly concave, ratio dorsum / declivity about one. Node tall, its front convex, back mostly straight, summit blunt. Fore femora about 1.5 times thicker than others. Integument similar to major workers but without punctures on head. Head in front view: sides straight, tapering to front, vertex convex; anterior margin of clypeus convex and projects strongly, without a carina. Mandibles with four teeth. Frontal carinae distance approximately half of head width.

Pilosity: similar to major worker.

Colour: mostly black, mandibles, clypeus and scapes brown. Coxae and sutures of gaster whitish-yellow.

Gyne: Measurements: CI = 90, EL = 0.47, FCD = 0.70, HL = 1.54, HW = 1.38, ML = 2.67, PW = 1.24, SI = 84, SL = 1.16.

Structures: head form similar to major worker. Pronotum strongly convex, propodeum more rounded than in workers, propodeal declivity nearly straight, node as in major worker. Fore femora only slightly wider than others.

Pilosity: as in major worker.

Colour: as major worker but front of head whitish-yellow.

Male: Measurements: CI = 97, EL = 0.33, FCD = 0.24, HL = 0.67, HW = 0.65, ML = 1.5, PW = 1.02, SI = 112, SL = 0.73.



Fig. 6: *Camponotus rotundus* sp.n., major worker above, minor worker below.

Structures: in side view, pronotum dorsum nearly semicircular, node front and back near parallel, summit convex. In front view, head sides tapering to the front, vertex strongly convex; eyes very large protruding, their length of nearly half head length. Node small, summit blunt. Fore femora only slightly wider than others.

Pilosity: extremely sparse, no setae on tibiae and scapes.

Colour: mostly grey black, with light brown tarsi.

Diagnosis: The combination of evenly convex mesosoma, presence of deep metanotal groove and rounded propodeal angle in major and minor workers distinguishes this species from all other *Camponotus* species with phragmosis. *Camponotus flavocassis* DONISTHORPE, 1941 from New Guinea resembles *C. anezkae* sp.n. in convex shape of pronotum and mesonotum, mesosoma reticulation, pubescence and lighter front of the head. However, *C. flavocassis* differs significantly in slightly humped propodeum meeting propodeal declivity at an abrupt right angle, and much smaller distance among frontal carinae approaching only one third of head width.

Note: Head colouring of *Camponotus anezkae* sp.n. varies greatly within a nest in both major workers and queens from yellow to black, probably depending on the age and sclerotisation of individuals.

Biology: Only one nest of the species was discovered in the studied forest plots. The species occupied twigs of a hollow liana along the main trunk of a canopy tree *Melanolepis multiglandulosa* RCHB.F. & ZOLL. (Euphorbiaceae) at height 10 - 13 m above ground in the secondary forest. Several nest chambers with brood and several hundred workers were noted in the main trunk as well as in branches of the liana, probably forming a single colony.

Camponotus rotundus sp.n. (Figs. 6 - 8)

Etymology: Named for the nearly circular shape of the head in minor workers.

Type material: Holotype (minor worker, SAMA): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 21.IV.2007, HP0084, leg. P. Klimes". Paratypes: From the same nest series, labelled as above: 4 minor workers, 2 major workers, 3 males (SAMA); 1 minor worker and 1 major worker (NHMW, NAIC); 1 male, 2 minor workers and 2 major workers (IECA).

Other material examined (in alcohol): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 23.VIII.2007, HP0618, leg. P. Klimes", 8 minor workers, 2 major workers (SAMA); and other material from the type locality (IECA).

Description: Photos of major worker and minor worker are given in Figure 6, and a male in Figure 7. Morphological measurements of workers, labelled as above: 4 minor workers, 2 major workers, 3 males (SAMA); 1 minor worker and 1 major worker (NHMW, NAIC); 1 male, 2 minor workers and 2 major workers (IECA).

Major worker: Structures: in side view, front of head weakly convex from vertex to frontal triangle with a rounded angle of about 135° separating the flattened part of the clypeus and mandibles; finely reticulate. Mesosoma glossy, finely reticulate, pronotum strongly convex, remainder of the mesosoma weakly convex; propodeal angle rounded and about 135°, declivity mostly straight; ratio dorsum / declivity about one. Node thin, front and back mostly straight, summit narrowly rounded. Fore femora about 1.5 times thicker than others. Integument glossy. Head in front



Fig. 7: *Camponotus rotundus* sp.n., male.

view: coarsely punctate, sides straight, diverging to front, vertex mostly flat. Most of clypeus, anterior head and closed mandibles forming a delimited flattish surface. Clypeus with distinct central carina, anterior margin narrow. Frontal carinae distance wide, about 4/5 of head width.

Pilosity: mesosoma with a few erect setae; head with plentiful short erect setae, most of them clavate. Mandibles with short erect setae, some of them clavate. Scape with erect short setae.

Colour: bicoloured; mesosoma and appendages light brown, head distinctly dark brown.

Minor worker: Structures: in side view, front of head smoothly convex with only a change in radius separating the clypeus; mesosoma evenly convex, metanotum indistinct, propodeal angle well rounded, declivity straight, ratio dorsum / declivity about one. Node thin, front and back mostly straight, summit narrowly rounded, wide in rear view. Fore femora about 1.5 times thicker than others. Integument glossy. Head in front view: finely and widely punctate, sides convex, weakly tapering to the front, vertex convex; most of clypeus and closed mandibles forming a circular flat surface, but truncated to a much less extent than in major workers. Anterior margin of clypeus wide, projecting a little and mostly straight, with weak central carina. Frontal carinae distance smaller than in majors, approaching two thirds of head width.

Pilosity: in side view, plentiful short erect setae widespread on mesosoma, head, scapes, tibiae, less on gaster, plentiful raised short setae on gula. Mandibles with short erect setae.

Colour: similar to major workers.

Male: Measurements: CI = 88, EL = 0.38, FCD = 0.41, HL = 0.96, HW = 0.84, ML = 1.77, PW = 0.88, SI = 75, SL = 0.63.

Structures: in side view, mesosoma elongate with dorsum mostly flat, node triangular. In front view, head sides straight and strongly tapering to the front. Vertex strongly convex, slightly flattened in centre. Eye length of nearly



Fig. 8: Nest of *Camponotus rotundus* sp.n. in a live hollow branch with scale insects of the genus *Myzolecanium* (Coccidae) tended by workers (Photo P. Klimes).

half head length. Frontal carinae separated by more than a third head width, front femora not enlarged.

Pilosity: short erect setae on scape.

Colour: light brown body with yellow legs, except for the head dark brown as in workers.

Queen: unknown.

Diagnosis: Distinguished from other *Camponotus* species with phragmosis by being one of the smallest species and by the nearly circular head in front view in minor workers. *Camponotus hosei* FOREL, 1911 minor worker, described from Borneo (major unknown), is similar in the shape of mesosoma dorsum and node. However, *Camponotus rotundus* sp.n. can be distinguished from minor workers of this related species by its distinct colouration (much lighter mesosoma and gaster compared with the head), indistinct metanotal groove, presence of erect setae on genae and gula and punctate head.



Fig. 9: *Camponotus triangulatus* sp.n. major worker above, minor worker below.

Biology: The species was found nesting in galleries inside living hollow branches and twigs in the canopies of the host trees at a height of 10 to 17 m. It was tending numerous scale insects (*Myzolecanium* spp., Coccidae) for honeydew within these nests (Fig. 8). This species was quite rare at the studied site as it occurred exclusively in the primary forest plot and occupied only two trees. The host trees belonged to two different species, *Dysoxylum brassii* MERR. & L. M. PERRY (Meliaceae) and *Chisocheton ceramicum* (Meliaceae), both of medium size (dbh = 15 cm). A nest was estimated to have at least a thousand workers. However, the workers were not actively foraging in the canopy outside their nests, but moved very slowly within branches. This suggests a cryptic life for the species and a high dependence on honeydew provided by endophytic homopterans.

Camponotus triangulatus sp.n. (Fig. 9)

Etymology: Named after the triangular shape of clypeus in minor workers.

Type material: Holotype (minor worker, SAMA): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 21.VIII.2007, HP0213, leg. P. Klimes". Paratypes: From the same nest series, labelled as above: 2 minor workers, 2 major workers (SAMA); 1 minor worker and 1 major worker (NHMW, NAIC); 2 minor workers and 2 major workers (IECA).

Description: Photos of major worker and minor worker are given in Figure 9. Morphological measurements of workers are provided in Table 2c. Scape length is greater in minor than major workers, the latter having considerably shortened scapes compared with their head width. Species is dimorphic.

Major worker: Structures: in side view, front of head weakly convex with 135° angle separating the forehead from the clypeus which is straight. Pronotum strongly convex, mesonotum weakly convex and propodeum dorsum weakly concave, metanotum shallow, the propodeal angle well rounded, declivity straight, ratio dorsum / declivity about 1.2. Node thick, front convex, back mostly straight, summit blunt. Fore femora about 1.5 thicker than others. Integument: glossy, very finely striate. Head in front view: sides straight and near parallel, vertex straight; most of clypeus, anterior head and closed mandibles forming a circular flat surface. Anterior margin of clypeus projecting a little, concave in the centre, clypeus with four to six distinct parallel ridges posteriorly, similar ridges also on front of head at sides of clypeus. Mandibles with six teeth. Frontal carinae distance approximately half of head width.

Pilosity: erect setae very sparse, none on mesosoma or gula, a few sparse short decumbent setae, no erect setae on scapes.

Colour: mostly black-brown; mesonotal suture, coxae and suture of gaster whitish-yellow.

Minor worker: Structures: in side view, front of head weakly convex overall, clypeus depressed. Pronotum slightly convex, mesonotum convex and propodeum dorsum raised up and weakly concave, metanotum indistinct, propodeal angle narrowly rounded, declivity straight, ratio dorsum / declivity about 1. Node thick, front convex, back mostly straight, summit blunt. Fore femora about 1.5 times thicker than others. Integument: similar to major workers, but less glossy. Head in front view: sides straight, weakly tapering to the front, vertex convex; clypeus anterior margin projecting strongly like two sides of an equilateral triangle,



Fig. 10: *Camponotus wanangus* sp.n., major worker above, minor worker below.

without a carina. Mandibles with four teeth. Frontal carinae separated by half of head width.

Pilosity: erect setae very sparse, none on mesosoma or gula, a few more short decumbent setae than in major workers, no erect setae on scapes.

Colour: mostly black. Mesonotal suture, mandibles and coxae whitish-brown. Tarsi and basal area of scapes light-brown.

Queen and male: unknown.

Diagnosis: In minor worker, the anterior margin of clypeus projects strongly and resembles two sides of an equilateral triangle, whereas in major worker it is concave. These characters separate it from all other *Camponotus* species with phragmosis.

Biology: We discovered only one nest of this species in the primary forest plot. It occupied a dead branch in a *Macaranga punctata* K. SCHUMC tree of small size (dbh = 9 cm, nest 7 m above ground) and it shared the tree with another common arboricolous ant species at the site, *Anonychomyrma* cf. *scrutator* SMITH, 1859. It did not tend scale insects and it was not observed to be nesting in live branches. Workers were also found to be foraging actively on the nearby trees and vegetation. This may suggest opportunistic feeding and nesting behaviour, but more ecological data are needed due to the rarity of this species in our studied forest.

Camponotus wanangus sp.n. (Figs. 10 - 11)

Etymology: Named after its type locality Wanang village in Papua New Guinea and dedicated to the Wanang people and their forests.

Type material: Holotype (minor worker, SAMA): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 3.X.2007, HP0208, leg. P. Klimes". Paratypes: from the same nest series, labelled as above: 4 minor workers, 2 major workers, 1 queen, 2 males (SAMA); 1 minor worker and 1 major worker (NHMW, NAIC); one individual from each caste (IECA).

Other material examined (in alcohol): "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 23.VIII.2007, HP0623, leg. P. Klimes", 10 minor workers, 3 major workers, 2 males (SAMA); and other material from the type locality (IECA).

Description: Photos of the major and minor worker, queen and male are given in Figures 10 - 11. Morphological measurements of workers are provided in Table 2d and of alates below. The species is dimorphic.

Major worker: Structures: in side view, front of head nearly convex with a little flattening at the clypeus and mandibles, only slightly longer than wide. Pronotum, mesonotum and propodeum mostly straight, metanotum a distinct trough, its spiracle well below dorsum, propodeal angle well rounded and about 90°, declivity concave, ratio dorsum / declivity about 0.8. Node thick with front and back mostly straight, summit is convex. Fore femora about 1.5 times thicker than others. Integument finely punctate with a few deeper pits on head. Head in front view: sides straight, nearly parallel; vertex slightly convex. Most of clypeus, anterior head and the closed mandibles forming a circular flat surface. The anterior margin of clypeus projecting a little, notched in the centre. Mandibles with five teeth. Frontal carinae separated by half of head width.

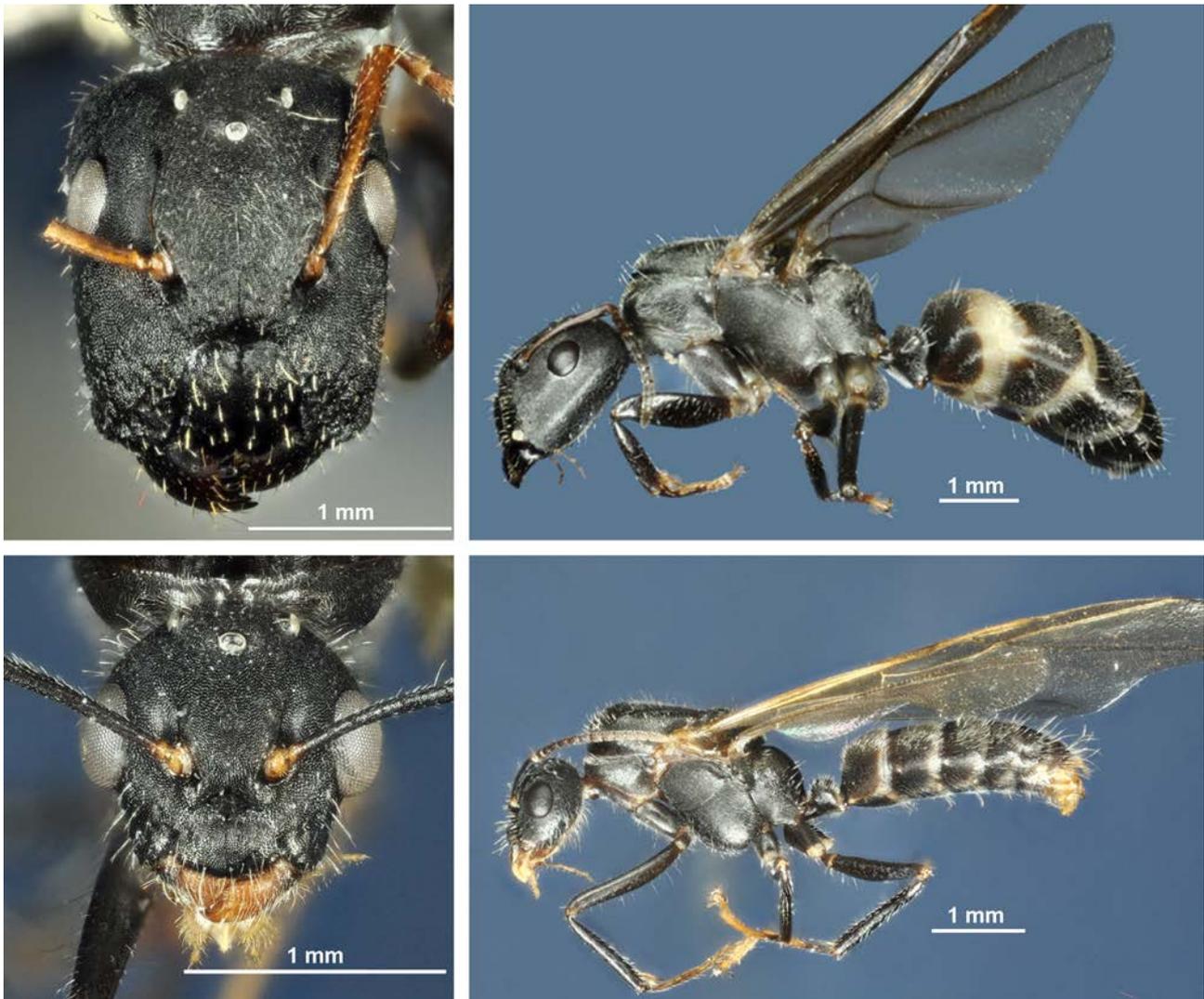


Fig. 11: *Camponotus wanangus* sp.n., gyne above, male below.

Pilosity: plentiful short erect setae all over head, less on mesosoma, short erect setae on scapes (only visible in front view), plentiful fine pubescence on mesosoma, less on head and gaster.

Colour: mostly black with brownish antennae and tarsi, pubescence white.

Minor worker: Structures: in side view, anterior front of head and clypeus evenly convex, back nearly straight; dorsum of mesosoma similar to major worker: pronotum and mesonotum dorsum convex. Metanotum, its spiracle and integument similar to major worker. Head in front view: sides weakly convex, nearly parallel, vertex convex. The anterior margin of clypeus slightly convex. Mandibles with five teeth. Scape with a few short erect setae. Frontal carinae separated by half of head width.

Pilosity and colour: similar to major worker.

Gyne: Measurements: CI = 77, EL = 0.44, FCD = 0.88, HL = 2.07, HW = 1.59, ML = 3.04, PW = 1.60, SI = 75, SL = 1.19.

Structures: in side view, mesosoma mostly straight, propodeal angle rounded, declivity straight, node thick, with convex summit. In front view, head sides straight and

parallel, eyes slightly larger when compared to major worker.

Pilosity: short erect setae plentiful all over, especially on scape and legs.

Colour: similar to workers.

Male: Measurements: CI = 91, EL = 0.41, FCD = 0.54, HL = 1.04, HW = 0.95, ML = 2.46, PW = 1.25, SI = 110, SL = 1.05.

Structures: in side view, form of mesosoma and node similar to queen. In front view, head sides straight and tapering to the front. Vertex strongly convex. Frontal carinae separated by more than a third of head width, front femora not visibly enlarged.

Pilosity: similar to workers, but setae on cheeks and vertex of the head twice as long.

Colour: black, except light brown tarsi.

Diagnosis: The shape of the head, mesosoma and petiolus in major and minor workers resemble that of *Camponotus leonardi* EMERY, 1889. The two species can be well separated by the presence of the erect setae on gula (plentiful in *C. wanangus* sp.n. but absent in *C. leonardi*) and longer propodeal declivity (ratio dorsum / declivity

about 0.8 in *C. wanangus* sp.n. and 1.5 in *C. leonardi*). In major workers, the anterior part of head and clypeus is much more truncated and delimited from posterior part in *C. leonardi* (unlike in *C. wanangus* sp.n.).

Biology: *Camponotus wanangus* sp.n. was found nesting only in primary forest and at a relatively low density of three nests per 0.32 ha. It occupied two trees, a medium-high tree, *Chisocheton ceramicum* (MIQ.) (Meliaceae), and a high-canopy tree, *Teijsmanniodendron bogoriense* KOORD (Lamiaceae). It nested inside of cavities in live branches at a height of 14 to 21 m. Nests consisted of several hundred workers. Interestingly, the species also shared the trees with other *Camponotus* species: *C. sanguinifrons* and *C. cf. macrocephalus* in *T. bogoriense*, and with *C. rotundus* sp.n. in *Chisocheton ceramicum*. The workers of *C. wanangus* sp.n. were observed to tend scale insects (Coccidae) inside nest galleries in twigs and branches of *C. ceramicum*.

Redescription of *Camponotus aruensis* KARAVAIEV, 1933 (Figs. 12 - 13)

Notes: Karavaiev described a "badly damaged ant" from Dobo-Wammar Island in the Aru group of Islands of Indonesia (between Australia and New Guinea) as the type for *Camponotus aruensis* (KARAVAIEV 1933). He wrote that it had been caught on a low plant and described its head, scape, eye, mandibles and in particular its distinguishing character viz. "pointed propodeal angle". The holotype was examined by AM in the Schmalhausen Institute of Zoology of the Ukrainian National Academy of Science, Kiev (Ukraine) and is photo-documented in MCARTHUR (2012). Karavaiev assigned the species to subgenus *Colobopsis* and to the *conicus* species group following the definition of EMERY (1925), because of its cone-shaped propodeum. He described a minor worker and provided clear drawings of head, node and mesosoma (KARAVAIEV 1933). However, he did not specify its small size, its sparse pilosity or its integument. We believe that descriptions of other castes have never been published.

Type material examined: Holotype (minor worker, damaged, pinned, SIZK): Indonesia, "Aru Islands, Dobo Wammar Is."

Other material examined: "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), 6.VI.2007, HP0030, leg. P. Klimes", 1 major worker and 1 minor worker, pinned, in each of SAMA, NAIC, NHMW, and SIZK; one individual of each caste (IECA). "Papua New Guinea: Madang Province, Wanang (05° 14' S, 145° 11' E), HP0625 and HP0626, 9.VI.2007, leg. P. Klimes", 4 minor workers, 4 major workers, 2 queens, 1 male (SAMA); and other material in alcohol (IECA).

Description: Photos of the major and minor worker, queen and male are given in Figures 12 - 13. Morphological measurements of workers are provided in Table 2e, and of alates below. Measurements of head size and pronotal width are enlarged in major workers compared with minor workers, but scape lengths differ little. The species is dimorphic.

Major worker (first description): Structures: in side view, neck attached to head lower down than with most *Camponotus*, and in that respect back of head resembling *Camponotus saundersi* EMERY, 1889. Pronotum strongly convex, mesonotum weakly convex, metanotal groove deep, with protruding spiracles, propodeum flat on top and meet-

ing with concave declivity at a rounded right angle. Node thick and tall, with parallel sides, when viewed from behind summit nearly flat. Front femora almost double the thickness of mid and hind femora. Integument glossy, finely reticulate. Head in front view: sides nearly parallel and very weakly convex, vertex strongly convex. Eyes large, touching lateral cephalic outline in upper third of head. Frontal carinae wide, with distance between them almost two thirds of head width. The anterior part of head including clypeus and mandibles quite flat, separated from the posterior part of head by a distinct angle of about 150°. Head integument glossy, finely punctate on frons. Clypeus and the surrounding frontal parts of head are deeply sculptured, on clypeus two distinct longitudinal carinae, anterior margin of clypeus narrow (one fourth of head width) and mostly straight, mandibles with six or seven teeth.

Pilosity: erect setae extremely sparse, mostly confined to mandibles and funiculus, short indistinct adpressed setae plentiful.

Colour: head and mesosoma mostly black, except for light brown frontal third of head, and coxae. Scapes, tibiae and tarsi lighter yellow.

Minor worker (in support of Karavaiev's description): Structures: in side view, neck attached to head lower down as in major worker, pronotum and mesonotum convex, metanotal groove deep with protruding spiracles, propodeum strongly convex on top, forming a distinct blunt tooth that meets with the concave declivity at protruding 80° angle. Mesosoma with distinct reticulation, glossy. Node tall, sides parallel, wide when viewed from behind, summit nearly flat; gaster with a few short setae on dorsum. Front femora double the thickness of mid and hind femora. Head in front view: sides nearly straight, weakly tapering to the front, vertex weakly convex. Eyes, frontal carinae and integument similar to major. Clypeus rounded, transversely without sculpture and glossy, its anterior margin wide (three fourth of head width), weakly convex, mandibles appear to have six or seven teeth.

Pilosity: sparse, with a few short erect setae at front of head and gaster, a few adpressed on gaster.

Colour: mostly black, with contrastingly light yellow appendages with exception of femora which are brownish.

Gyne (first description): Measurements: CI = 88, EL = 0.42, FCD = 0.60, HL = 1.12, HW = 0.99, ML = 1.93, PW = 1.12, SI = 80, SL = 0.79.

Structures: in side view, mesosoma dorsum mostly flat, pronotum convex, propodeal angle rounded, declivity mostly straight, node small and thick, convex summit. In front view, head similar to major worker, with straight and parallel sides, vertex convex, front of head and clypeus with deep parallel longitudinal grooves. Eyes only slightly larger than in major workers.

Pilosity: sparse.

Colour: dark brown with whitish-yellow femora and suture of gaster; otherwise similar to major worker.

Male (first description): Measurements: CI = 81, EL = 0.32, FCD = 0.22, HL = 0.62, HW = 0.50, ML = 1.3, PW = 0.75, SI = 104, SL = 0.52.

Structures: in side view, mesosoma dorsum mostly weakly convex, propodeal angle rounded, declivity mostly straight, node similar to gyne. In front view, head sides straight and strongly tapering to the front, vertex semi-circular, eye length about half of head length.



Fig. 12: *Camponotus aruensis* major worker above, minor below and rear view of node.

Pilosity: sparse.

Colour: yellowish-brown.

Diagnosis: The colour of workers is black with contrastingly light brown appendages and this colour pattern is consistent within colonies and is the same for the type specimen from Aru island. In side view, the mesosoma dorsum of the minor worker of *C. aruensis* is similar to that of the related species *Camponotus conicus* MAYR, but the latter has a pointed rearward projection on its node whereas in *C. aruensis* node is rounded and taller. In front view, the head in workers of *C. conicus* is nearly circular whereas the head sides are only weakly convex in *C. aruensis*.

Biology: *Camponotus aruensis* was one of the common *Camponotus* species in secondary forest (23 nests per 0.32 ha), but was relatively uncommon in primary forest (three nests per 0.32 ha). It was not specialized to particular host trees as it occupied in total 24 trees of 12 species in eight families (Tab. 1). The stratification of nests varied between five (nests in liana stems) to 21 m above ground (in dry twigs), however, most of the nests were found in the canopy. The nests were of relatively small size usually not exceeding 500 workers. In contrast to most of the *Camponotus* species in this study *C. aruensis* nested exclusively in dead and dry hollow branches, twigs and lianas. This may explain why it was more common in secondary forest, where such nesting habitats were more com-

mon (Fig. 2). *Camponotus aruensis* was not observed to be tending scale insects (Coccidae) directly in their nests. However, workers were occasionally observed foraging with ants *Technomyrmex albipes* (F. SMITH, 1861) to colonies of scale insects that were sucking on twigs and leaf stems high in the canopy.

Discussion

The total diversity of *Camponotus* ants in the forest studied was 19 species. Some studies have found higher numbers of *Camponotus* species in equatorial rainforests, e.g., 29 species by WILSON (1987) and 44 species by RYDER WILKIE & al. (2010). However, these authors focused on specific trees sampled across a larger area using canopy fogging rather than on complete records of nests within small continuous forest patches. Here, for the first time, we report the total diversity of *Camponotus* communities in continuous rainforest plots. We found that canopy-dwelling *Camponotus* with phragmosis made up the majority of the *Camponotus* species in terms of both nest abundance and species diversity. This indicates their high contribution to arboricolous insect fauna in tropical forests and the importance of such morphological adaptations for nesting in trees.

Our results demonstrate that many related ant species are able to coexist within a single forest site in New Guinea.



Fig. 13: *Camponotus aruensis*, gynes above, male below.

Although there was a large proportion of trees without any *Camponotus* nests (70%), the genus made up a significant proportion of the whole ant communities in the studied plots, being the most species-rich arboreal genus and yielding 18% of all ant species and 20% of all ant nests at the site (KLIMES 2011; P. Klimes, unpubl.). The surprisingly low occupancy of trees within forests by these common ants can be explained by the relatively high density of smaller trees without any ant nests reported from the lowland continuous forests and a strong correlation of number of nests and ant diversity with tree size (CAMPOS & al. 2006, KLIMES & al. 2012). Indeed, we also found cases of several *Camponotus* species nesting in a single tree, notably within tall primary forest trees.

How so many ant species can coexist in tropical canopies is still an outstanding question for myrmecologists and is not well resolved (DEJEAN & al. 2007). The unique data on nesting ecology of individual species within the same genus presented here may provide a potential explanation for these coexistence patterns. We found that species which appear similar in their general ecology and morphology can still remarkably differ in their nesting preferences in terms of successional forest stage and nesting microhabitat. However, in contrast to the specific *Camponotus* ant-host interactions described from southeastern Asia (e.g., LETOURNEAU & al. 1993, FEDERLE & al. 1998, EDWARDS & al. 2010), *Camponotus* communities studied here were surprisingly nonspecific to their tree hosts in both primary and secondary forest. These findings are congru-

ent with the analyses of the whole arboreal ant community at the same site (see KLIMES & al. 2012). In particular, it is the affinity of ant species to certain nest sites rather than specific relationships with particular tree host species that appears to be the important factor influencing such communities. However, additional analysis of data from more plots specifically testing for separate effects of these drivers and including also spatial relationships are still needed to explicitly quantify these factors.

Another possible explanation for the coexistence of ant species within the forest is that the ant species vary in their preferences for food resources (DAVIDSON & al. 2003, DEJEAN & al. 2007). Indeed, our results suggest that some *Camponotus* species with phragmosis live cryptically within the branches and are probably dependent on the honeydew of endophytic coccids, whereas others may utilize food resources distributed across the whole canopy, such as extrafloral nectaries, other homopterans and insect prey (HÖLLDOBLER & WILSON 1990, FEDERLE & al. 1998). Most of the scale insects found within the nests belonged to the genus *Myzolecanium* BECARRI (P. Gullan, pers. comm.), which have also been recorded in the nests of other arboreal ant genera in Papua New Guinea (GULLAN & al. 1993; P. Klimes, unpubl.). However, the specificity of the relationships between ants and *Myzolecanium* species is largely unknown as taxonomic revision of this genus of Coccidae is needed due to the presence of undescribed species (P. Gullan, pers. comm.). A recent phylogenetic study suggests that the symbiosis between Camponotini ants and

sap-feeding insects such as Coccidae was crucial for the development of the unique bacterial endosymbiosis with *Blochmannia* in those ants (WERNEGREEN & al. 2009).

The results of this study have important implications for conservation of ant fauna in the tropics. First, primary forests can provide more varied nesting opportunities and larger numbers of high-canopy trees than secondary forests and plantations (FAYLE & al. 2010, KLIMES & al. 2012). Hence, it is not surprising that more species of *Camponotus* were found nesting in the primary forest plot than the secondary forest plot. However, in both forest types there were also many *Camponotus* species found nesting at low densities (e.g., only one or two nests discovered in total in 0.64 ha of forest). This was true also for the new species described here. These may be particularly rare native ant species of New Guinean forests and hence could be more endangered than other more widespread species in our study, such as *Camponotus vitreus* and *Camponotus aruensis*, by the increasing rate of conversion of primary tropical forest to plantations and secondary forests (SHEARMAN & BRYAN 2011). However, it is important to stress that we still know relatively little about the vulnerability of these species to rainforest disturbance. For example, we cannot exclude the possibility that the observed rarity of some species in our study could be driven by factors such as exclusion of the species by dominant ant species in our plots (DEJEAN & al. 2007, RIBEIRO & al. 2013) or possible genuine patchy distribution of the species within the forest.

Although we are confident that our forest plots represent by structure a typical primary and early-successional secondary vegetation in Papua New Guinea lowlands (WHITFIELD & al. 2012), our data are limited to a single locality and two forest plots only. Comparable plot-based data are unfortunately lacking as previous studies were limited to canopy fogging and observations at baits (RIBEIRO & al. 2013, FLOREN & al. 2014). Future studies across more localities that gather further distributional and ecological data for arboreal ant species are needed to answer the above questions. However, the fact that we found similar nesting preferences for species occurring in both forest plots implies that the patterns in species composition and their nesting preferences were driven by distribution of their nesting microhabitats in each of the studied forests rather than being a random result of the particular (non-replicated) plot that was sampled. It should be noted that such records are not easy to obtain without exploring the nests directly, due to the cryptic behaviour and nesting habits of many *Camponotus* species. For instance, a large scale sampling of canopy trees with baits across several different forest sites in the Papua New Guinea lowlands recorded only seven *Camponotus* species, which indicates that even distributional data are difficult to obtain (M. Laponce & P. Klimes, unpubl.). In this respect, the data on diversity and nesting habits of *Camponotus* species presented here are unique.

Although this study summarizes the results from only a single rainforest site, it makes a significant contribution to our knowledge of *Camponotus* ants of New Guinea and demonstrates how little we know about the alpha taxonomy of ants in the region. From 31 *Camponotus* species previously described or reported from the island (JANDA & al. 2011, BOLTON 2012), nine species are reported as new for

New Guinea (see Tab. 1) and four species are described here as new (13 of the 19 species in total, 70%). We regard these taxa as clearly distinct from the species reported for the island before. However, it should be stressed that for some species reported here (Tab. 1, *Camponotus* cf., aff. spp.) more material from other localities and regions including molecular data are needed to assess their species name status, since the variability in some *Camponotus* taxa can be high. This situation is complicated by the fact that many tropical species were described long ago, often from only a single caste (BOLTON 2012, MCARTHUR 2012). Despite these difficulties, we hope this study may promote future work on the taxonomy and ecology of poorly known ant fauna from New Guinea rainforests and other remote tropical regions.

Acknowledgements

PK is grateful to the customary landowners of Wanang (PNG) for allowing him to work in their forests and to V. Novotny and staff of the New Guinea Binatang Research Center for all technical and logistic assistance. AM is thankful for the use of facilities of the South Australian Museum and help from C.H. Watts, P. Hudson and J. Weyland. Tree species identifications were provided by K.Q. Damas, G.B. Weiblen and T.J.S. Whitfield, and M. Janda provided facilities for digital documentation of part of the specimens. T.M. Fayle, N.S. Plowman and three anonymous referees made valuable comments on the manuscript. This work was supported by the Czech Science Foundation (P505/12/P875), the Czech Ministry of Education (LH11008), Darwin Initiative for the Survival of Species (19008), institutional support RVO:60077344 and by the project Biodiversity of forest ecosystems CZ.1.07/2.3.00/20.0064 co-financed by the European Social Fund and the state budget of the Czech Republic.

References

- BASSET, Y. 2001: Invertebrates in the canopy of tropical rain forests: How much do we really know? – *Plant Ecology* 153: 87-107.
- BASSET, Y., KITCHING, R.L., MILLER, S.E. & NOVOTNY, V. 2003: Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy. – University Press, Cambridge, MA, 474 pp.
- BOLTON, B. 1994: Identification guide to the ant genera of the world. 1st edition. – Harvard University Press, Cambridge, MA, 222 pp.
- BOLTON, B. 1995: A new general catalogue of the ants of the world. – Harvard University Press, Cambridge, MA, 504 pp.
- BOLTON, B. 2012: Bolton's catalogue and synopsis of ants of the world. Version 1st January 2012. – <<http://gap.entclub.org/contact.html>>, retrieved on 6 March 2013.
- BROWN, W.L. 1972: A comparison of the Hylean and Congo-West African rain forest ant fauna. In: MEGGERS, B.J., AYENSU E.S. & DUCKWORTH W.D. (Eds.): Tropical forest ecosystems in Africa and South America, a comparative review. – Smithsonian Institution Press, Washington, DC, pp. 161-185.
- CAMPOS, R.I., VASCONCELOS, H.L., RIBEIRO, S.P., NEVES, F.S. & SOARES, J.P. 2006: Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. – *Ecography* 29: 442-450.

- COLWELL, R.K. 2009: EstimatesS: Statistical estimation of species richness and shared species from samples. Version 8.2. – <<http://purl.oclc.org/estimates>>, retrieved on 12 December 2011.
- DAVIDSON, D.W., COOK, S.C., SNELLING, R.R. & CHUA, T.H. 2003: Explaining the abundance of ants in lowland tropical rainforest canopies. – *Science* 300: 969-972.
- DEJEAN, A., CORBARA, B., ORIVEL, J. & LEPONCE, M. 2007: Rainforest canopy ants: the implications of territoriality and predatory behavior. – *Functional Ecosystems and Communities* 1: 105-120.
- EDWARDS, D.P., ANSELL, F.A., WOODCOCK, P., FAYLE, T.M., CHEY, V.K. & HAMER, K.C. 2010: Can the failure to punish promote cheating in mutualism? – *Oikos* 119: 45-52.
- EMERY, C. 1925: Hymenoptera. Fam. Formicidae. Subfam. Formicinae. Genera Insectorum Volume 183. – Louis Desmet-Verteneuil, Brussels, 304 pp.
- FAYLE, T.M., TURNER, E.C., SNADDON, J.L., CHEY, V.K., CHUNG, A.Y.C., EGGLETON, P. & FOSTER, W.A. 2010: Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. – *Basic and Applied Ecology* 11: 337-345.
- FEDERLE, W., FIALA, B. & MASCHWITZ, U. 1998: *Camponotus (Colobopsis)* (MAYR 1861) and *Macaranga* (THOUARS 1806): A specific two-partner ant-plant system from Malaysia. – *Tropical Zoology* 11: 83-94.
- FLOREN, A. & LINSENMAYER, K.E. 1997: Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, with special reference to Formicidae. In: STORK, N.E., ADIS, J. & DIDHAM, R.K. (Eds.): *Canopy arthropods*. – Chapman & Hall, London, UK, pp. 344-381.
- FLOREN, A., WETZEL, W. & STAAB, M. 2014: The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. – *Myrmecological News* 19: 65-74.
- FOREL, A. 1874: Les fourmis de la Suisse. Systématique, notes anatomiques et physiologiques, architecture, distribution géographique, nouvelles expériences et observations de mœurs. – *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften* 26: 1-452.
- GULLAN, P.J., BUCKLEY, R.C. & WARD, P.S. 1993: Ant-tended scale insects (Hemiptera: Coccidae: *Myzolecanium*) within lowland rain forest trees in Papua New Guinea. – *Journal of Tropical Ecology* 9: 81-91.
- HÖLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – Harvard University Press, Cambridge, MA, 732 pp.
- JANDA, M., KLIMES, P. & BOROWIEC, M. 2007: Ecology of New Guinea ants (Hymenoptera: Formicidae) – exploring an unknown fauna. – *Myrmecological News* 10: 109.
- JANDA, M., KOTRLA, J., BOROWIEC, M., RIHA, P., KLIMES, P. & ALPERT, G. 2011: The ants of New Guinea: species checklist and database of melanesian ant fauna. Version 22.02.11. – <<http://www.newguineants.org>>, retrieved on 12 February 2013.
- KARAVAIEV, V. 1933: Ameisen aus dem Indo-Australischen Gebiet, VII. – *Konowia* 11: 305-320.
- KLIMES, P. 2011: Diversity and ecology of arboreal ant communities in a tropical lowland forest. – Ph.D. Thesis, University of South Bohemia, Faculty of Science, České Budějovice, Czech Republic, 91 pp.
- KLIMES, P., IDIGEL, C., RIMANDAI, M., FAYLE, T.M., JANDA, M., WEIBLEN, G.D. & NOVOTNY, V. 2012: Why are there more arboreal ant species in primary than in secondary tropical forests? – *Journal of Animal Ecology* 81: 1103-1112.
- LEPS, J. & SMILAUER, P. 2003: *Multivariate analysis of ecological data using CANOCO*. – University Press, Cambridge, MA, 269 pp.
- LETOURNEAU, D.K., ARIAS, G.F. & JEBB, M. 1993: Coping with enemy-filled space: herbivores on *Endospermum* in Papua New Guinea. – *Biotropica* 25: 95-99.
- MAYR, G. 1861: *Die europäischen Formiciden. Nach der analytischen Methode bearbeitet*. 1st Edition. – C. Gerolds Sohn, Vienna, 80 pp.
- MCALPINE, J.R., KEIG, G. & FALLS, R. 1983: *Climate of Papua New Guinea*. – CSIRO and Australian National University Press, Canberra, 200 pp.
- MCARTHUR, A.J. 2007: A key to *Camponotus* MAYR of Australia: In: SNELLING, R.R., FISHER, B.L. & WARD, P.S. (Eds.): *Advances in ant systematics (Hymenoptera: Formicidae) homage to E.O. Wilson – 50 years of contributions*. – *Memoirs of the American Entomological Institute* 80: 290-351.
- MCARTHUR, A.J. 2009: New species, new status and new synonymy for *Camponotus* from Australia (Hymenoptera: Formicidae). – *Myrmecological News* 12: 273-286.
- MCARTHUR, A.J. 2012: *A guide to Colobopsis ants of the world*. – South Australian Museum, Adelaide, 234 pp.
- MITTERMEIER, R., MITTERMEIER, C.G., BROOKS, T.M., PILGRIM, J.D., KONSTANT, W.R., DA FONSECA, G. & KORMOS, C. 2003: *Wilderness and biodiversity conservation*. – *Proceedings of the National Academy of Sciences of the United States of America* 100: 10309-10313.
- OKSANEN, L. 2001: Logic of experiments in ecology: Is pseudo-replication a pseudoissue? – *Oikos* 94: 27-38.
- PFEIFFER, M. & LINSENMAYER, K.E. 2000: Contribution to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera: Formicidae). – *Insectes Sociaux* 47: 123-132.
- PRIMACK, R.B. & CORLETT, R. 2005: *Tropical rain forests: an ecological and biogeographical comparison*. 2nd edition. – Blackwell Publishing Ltd, Cornwall, UK, 336 pp.
- RIBEIRO, S.P., ESPÍRITO SANTO, N.B., DELABIE, J.H.C. & MAJER, J.D. 2013: Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy. – *Myrmecological News* 18: 113-120.
- RYDER WILKIE, K.T., MERTL, A.L. & TRANIELLO, J.F.A. 2010: Species diversity and distribution patterns of the ants of Amazonian Ecuador. – *Public Library of Science One* 5: e13146.
- SCHLÜNS, E.A. & CROZIER, R.H. 2013: Molecular phylogenetics of the ant genus *Camponotus*. Project 1.1. Taxonomy research & integration network (TRIN). – <http://www.taxonomy.org.au/ants_1.1.html>, retrieved on 20 September 2013.
- SHATTUCK, S.O. 1999: *Australian ants: their biology and identification*. *Monographs on Invertebrate Taxonomy Series*. 3rd edition. – CSIRO Publishing, Collingwood, VIC, Australia, 256 pp.
- SHEARMAN, P. & BRYAN, J. 2011: A bioregional analysis of the distribution of rainforest cover, deforestation and degradation in Papua New Guinea. – *Austral Ecology* 36: 9-24.
- SNELLING, R. 1998: The social Hymenoptera. A biological assessment of the Lakekamu Basin, Papua New Guinea. – *RAP Working Papers* 9: 39-47.
- SORGER, D.M. & ZETTEL, H. 2011: On the ants (Hymenoptera: Formicidae) of the Philippine Islands: V. The genus *Odonto-*

- machus* LATREILLE, 1804. – Myrmecological News 14: 141-163.
- TER BRAAK, C.J.F. & SMILAUER, P. 1998: CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). – Microcomputer Power, Ithaca, NY, 351 pp.
- WERNEGREEN, J.J., KAUPPINEN, S.N., BRADY, S.G. & WARD, P.S. 2009: One nutritional symbiosis begat another: phylogenetic evidence that the ant tribe Camponotini acquired *Blochmannia* by tending sap-feeding insects. – BioMed Central Evolutionary Biology 9 (292): 1-18.
- WHEELER, W.M. 1927: The physiognomy of insects. – Quarterly Review of Biology 2: 1-36.
- WHITFELD, T.J.S., NOVOTNY, V., MILLER, S.E., HRCEK, J., KLIMES, P. & WEIBLEN, G.D. 2012: Predicting tropical insect herbivore abundance from host plant traits and phylogeny. – Ecology 93: S211-S222.
- WILSON, E.O. 1974: The soldier of the ant, *Camponotus (Colobopsis) fraxinicola*, as a trophic caste. – Psyche 81: 182-188.
- WILSON, E.O. 1987: The arboreal ant fauna of Peruvian Amazon forests: a first assessment. – Biotropica 19: 245-251.