

Taxonomic updates for some confusing Micronesian species of *Camponotus* (Hymenoptera: Formicidae: Formicinae)

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Abstract

Indo-Pacific members of the speciose and morphologically confusing group of *Camponotus* ants that resemble *C. maculatus* (FABRICIUS, 1782) have recently been the subject of a molecular phylogeny, and that analysis is used here as guidance to update the taxonomy of the Micronesian species. It is now known that Micronesian and some Melanesian specimens previously identified as *C. chloroticus* EMERY, 1897 are not closely related to Polynesian, Fijian, and Melanesian specimens identified by the same name, and that the form on Palau presently identified as *C. irritans kubaryi* MAYR, 1876 is not closely related to *C. irritans* (SMITH, F., 1857). We therefore examined the morphologies of 185 specimens previously assembled for molecular analysis, plus five *C. chloroticus* and two *C. kubaryi* syntypes. Principal component analyses were conducted to understand shape differences and match modern specimens to types. The syntypes of *C. chloroticus*, which are from Tonga and southeastern New Guinea, matched the species that is today represented by collections from Polynesia, Fiji, and Melanesia. Thus, specimens mostly from Micronesia and formerly identified as *C. chloroticus* are here described as *Camponotus micronesicus* sp.n. In addition, *C. kubaryi* stat. rev. is returned to species status, and *Camponotus tol* sp.n., a new species from the Micronesian island of Chuuk, is described.

Key words: *Camponotus micronesicus* sp.n., *Camponotus tol* sp.n., *Camponotus kubaryi* stat. rev., *Camponotus chloroticus*, new species, Micronesia, Melanesia, Chuuk, Papua New Guinea, Pohnpei, Vanuatu.

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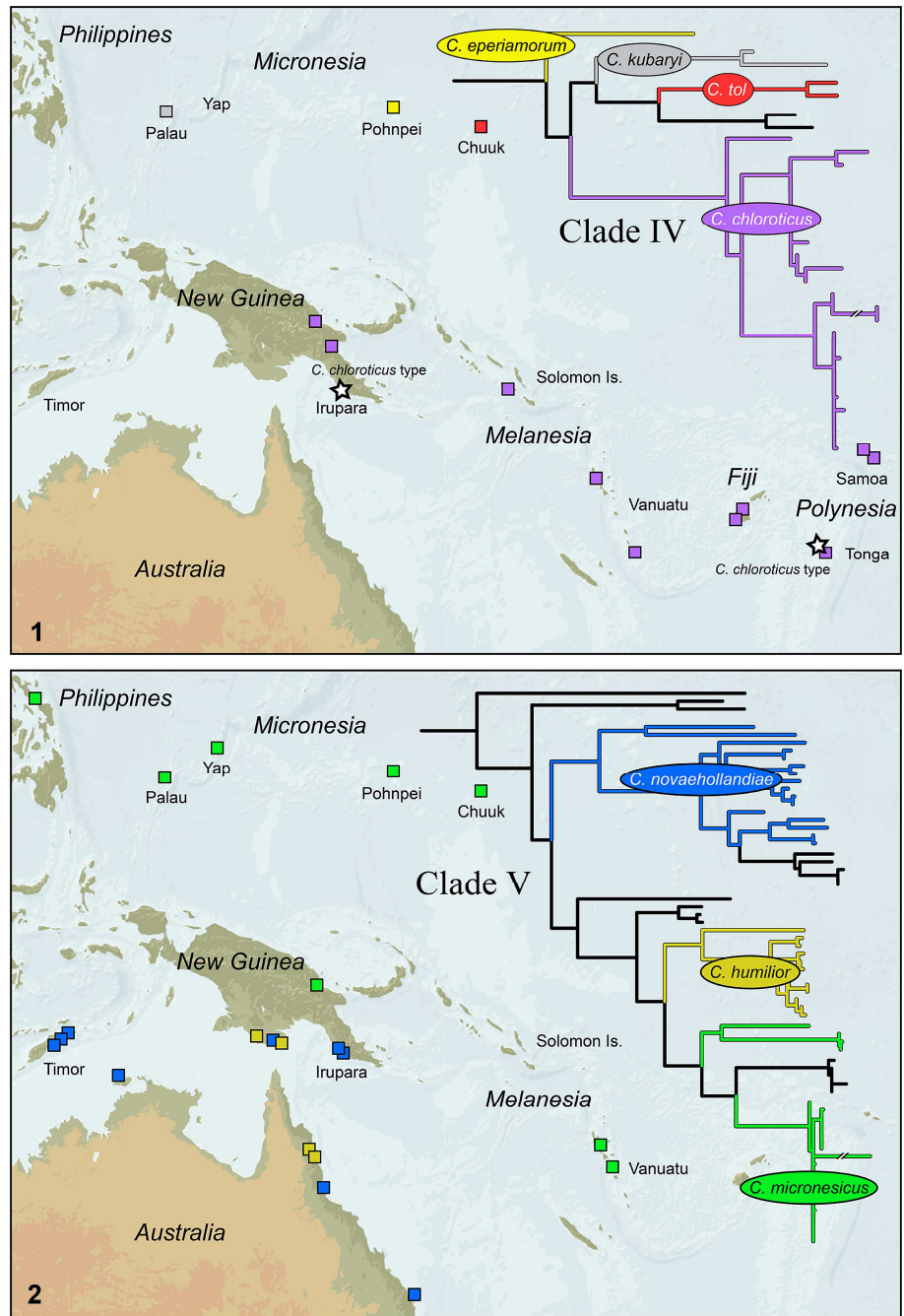
Introduction

A recent molecular analysis of 344 *Camponotus* specimens, focusing on species similar to *Camponotus maculatus* (FABRICIUS, 1782) in the Indo-Pacific, suggested several novel relationships (CLOUSE & al. 2015). After phylogenetic reconstruction, one unexpected result was that the widespread species commonly identified as *Camponotus chloroticus* EMERY, 1897 in Micronesia is not closely related to specimens referred to by the same name in Polynesia and Fiji, and these two unrelated forms are sympatric in Melanesia. (Fiji is often described as part of Melanesia but is more accurately described as an "archipelago located between Melanesia and Polynesia" (SARNAT & ECONOMO 2012).) The molecular analysis also indicated that three other forms in Micronesia are distinct species: *Camponotus eperiamorum* CLOUSE, 2007b from Pohnpei Island, an unidentified species on Tol Island in Chuuk State, and *Camponotus kubaryi* MAYR, 1876 stat.

rev. in Palau (a subspecies of *Camponotus irritans* prior to this study) (Figs. 1, 2).

Given that what has been called "*Camponotus chloroticus*" across the Pacific is actually two species, the first question is which of the two forms is the true *C. chloroticus*, and which needs to be described. Correctly identifying specimens that generally resemble *C. chloroticus* is important not only for the accuracy of faunistic surveys but also for understanding their behavior and ecology, which at present appears to be as similar as the morphology. It has been reported that both *C. micronesicus* sp.n. and *C. chloroticus* prefer coastal habitat (CLOUSE 2007a; SARNAT & ECONOMO 2012), which is commonly disturbed by humans and storms, and a preference for secondary habitat has been demonstrated for at least one of these forms in New Guinea (KLMES & MCARTHUR 2014). However, it is also likely that at least where they are sympat-

Figs. 1 - 2: Clades IV (1) and V (2) from the molecular phylogeny of CLOUSE & al. (2015), highlighting the species examined in this paper. Collection localities on the maps are for specimens in the molecular phylogeny used in the morphological analyses here. Colors match between branches in the phylogeny, species labels, and locality markers, and the localities of *Camponotus chloroticus* type specimens are shown by stars. Collection localities of all terminals in the molecular phylogeny can be seen in CLOUSE & al. (2015).



ric they partition resources in subtle ways rather than directly compete.

The best preserved specimen among the *Camponotus chloroticus* syntypes is from Irupara, New Guinea (10° 4' 36.48" S, 147° 42' 39.96" E), southeast of Port Moresby, on the southeastern end of the island. This locality puts it inside the range of the clade of "*C. chloroticus*" specimens found in Melanesia, Fiji, and Polynesia (Fig. 1). However, the clade of mostly Micronesian "*C. chloroticus*" extends to Vanuatu and Papua New Guinea as well (Fig. 2), so the type from Melanesia could be either species. Only a detailed morphological examination can resolve which of these two species that have been called *C. chloroticus* match with the *C. chloroticus* syntypes, or, in fact, whether the syntypes are actually specimens of *C. novaehollandiae* MAYR, 1870 or *C. humilior* FOREL, 1902, which also extend into New Guinea.

The types of *Camponotus kubaryi* stat. rev. and the modern Palauan specimens in our molecular phylogeny are large- and dark-headed forms that roughly resemble each other and the specimen discussed in CLOUSE (2007a) under the species code "*Camponotus* sp. 1945". In the molecular phylogeny, *C. irritans* was represented by a single COI sequence in the BOLD database (RATNASINGHAM & HERBERT 2007) from a specimen collected in India and identified as such; this sequence was 20% different from the two Palauan specimens of *C. kubaryi* stat. rev. in our phylogeny. Moreover, the Palauan specimens were recovered on a long branch among other Micronesian forms, away from not only the one identified *C. irritans* specimen in the analysis, but also the many unidentified specimens from across Southeast Asia and the Indo-Pacific. Therefore, our goal with this form was to determine whether modern Palauan collections in the molecular phylogeny and types of

Tab. 1: Definitions of measurements.

Name	Abbr.	Description
Eye length	EL	Dorsal-ventral distance in lateral view
Eye width	EW	Anterior-posterior distance in lateral view
Forecoxa length	FCL	Length down middle in lateral view
Head length	HL	Distance from mid-vertex to anterior edge of clypeus in frontal view
Head width	HW	Distance across imaginary line through middle of the eyes, including the eyes, in frontal view
Scape length	SL	Distance from antennal insertion to distal end in frontal view
Mesosoma length	ML	Weber's distance (distance from anterior pronotum to posterior propodeum, in lateral view)
Midtibia length	MTL	Total length measured down middle
Petiole height	PH	Maximum height of petiole, seen in lateral view, orthogonal to PL
Petiole length	PL	Distance from anterior articulation with alitrunk to posterior articulation with gaster
Cephalix index	CI	$(HW \times 100) / HL$
Scape index	SI	$(SL \times 100) / HW$

C. kubaryi stat. rev. are the same species, and subsequently, since this lineage showed no close relationship with specimens identified as *C. irritans* in the molecular phylogeny, to decide if the morphological evidence supported returning it to species status.

Thus, guided by the molecular phylogeny of CLOUSE & al. (2015), and with the aim of clarifying and updating the taxonomy of the *Camponotus maculatus*-like species in Micronesia, we analyzed a morphological data set collected from the same specimens assembled for the molecular phylogeny, as well as type specimens.

Material and methods

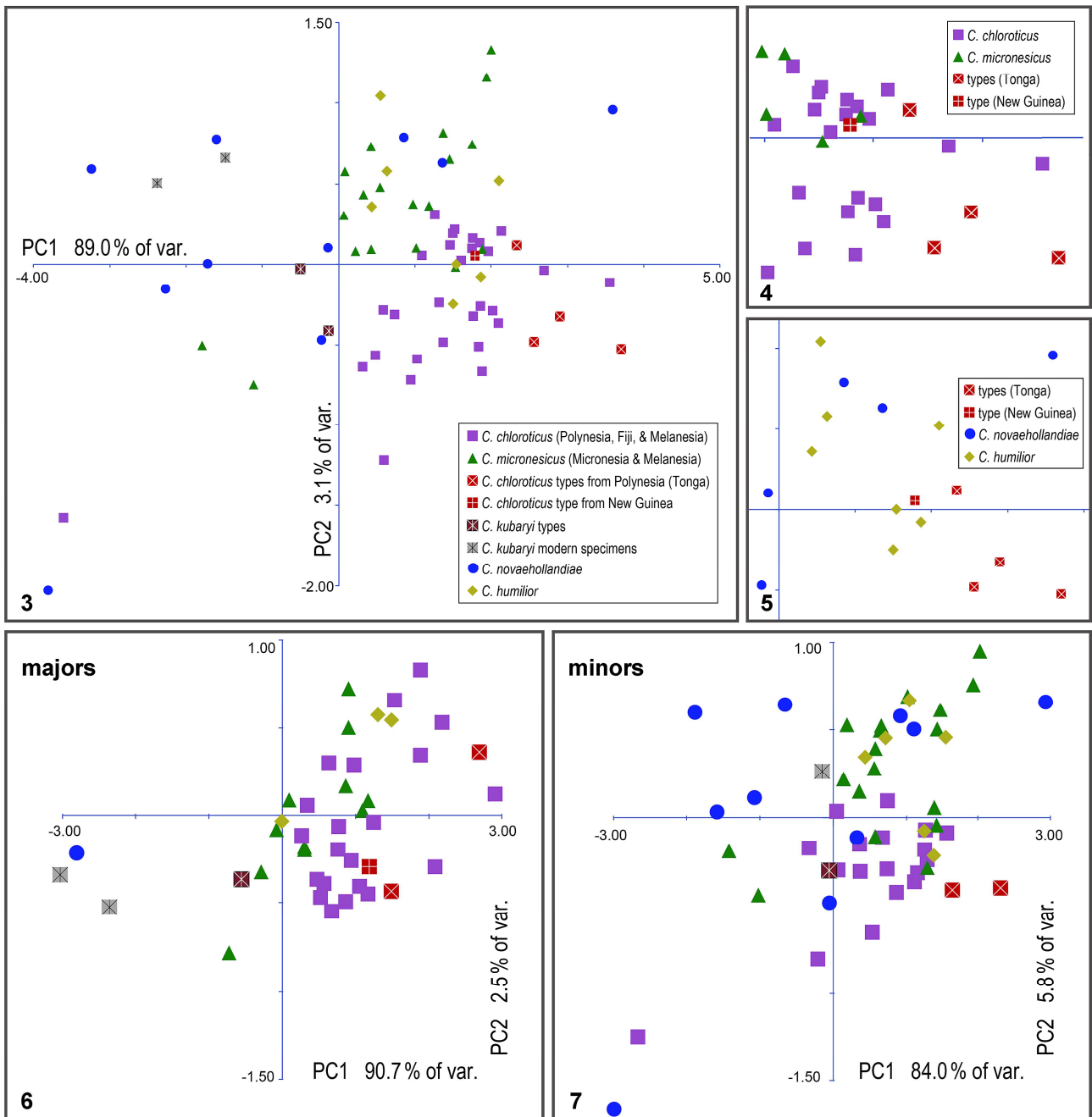
We examined the morphologies of 75 majors and 110 minors assembled for the molecular analysis, five syntypes of *Camponotus chloroticus*, and two syntypes of *C. kubaryi*. There were 54 cases of a major associated with a minor (on the same pin or part of a colony series). Many of these specimens were successfully sequenced, constituting 103 terminals in the molecular phylogeny of CLOUSE & al. (2015) (details available in Table S1, as digital supplementary material to this article, at the journal's web pages). Majors and minors had the same ten measurements recorded, which were chosen based upon their taxonomic promise after preliminary examinations, and which are defined in Table 1. We also used two standard indices made from these data, Cephalic Index (the width to length ratio of the head) and Scape Index (the ratio of the scape length to the head width). The indices are reported but were not used in principal component analysis (PCA) so as to not overweight their constituent measurements in the analysis.

We also noted various discrete characters, including coloration and pilosity. These latter characters are considered labile in ants, but they have been shown to be diagnostic in the genus, which lacks many character options overall. For example, *Camponotus eperiamorum* on Pohnpei Island is distinguished from *C. micronesicus* sp.n. (which is on the same island) almost entirely by the former's bicolorous body and lack of long hairs along the side of the head (CLOUSE 2007b). These small morphological differences disguise the fact that the two species are very dis-

tantly related, as is now known from the molecular phylogeny (CLOUSE & al. 2015).

PCA is often used to explore multivariate data for patterns that may correlate with data categories. Data are transformed into variables ("principal components") that are uncorrelated linearly, account for different percentages of the total variation in the original values, and are composed of different weightings ("loadings") of the original values. With morphological data, PCA can be used to test for subtle shape differences between castes, populations, or putative species (recent examples from ants include GRÜTER & al. 2012, YATES & al. 2014). We thus used PCA to ask whether the type specimens of *Camponotus chloroticus* and *C. kubaryi* stat. rev. were similarly shaped as modern specimens suspected of being the same species. Principal component analysis (PCA) requires all measurements to be available for each vector calculation, so for terminals without one or the other caste, values were extrapolated using simple linear models built by correlating the same measurement (e.g., head width) between all paired majors and minors in the dataset. PCAs were performed in R using the "princomp" command. We show the relationship between the first and second principal components for those specimens that represent the species of special interest here: *C. chloroticus*, *C. micronesicus* sp.n., *C. kubaryi* stat. rev., *C. novaehollandiae*, and *C. humilior*. One PCA analysis used major-minor pairs with missing data replaced by extrapolated values, and the other PCA analyses were done on majors and minors separately, using only observed measurements.

Except where otherwise noted (i.e., images from AntWeb.org), color photographs were taken with a JVC KY-F70B digital camera (www.pro.jvc.com) mounted on a Leica MZ 12.5 stereomicroscope (www.leica-microsystems.com). Images were captured at different focal planes and subsequently combined using the application Auto-Montage Pro Version 5.00.0271 by Syncroscopy (www.syncroscopy.com). Measurements were taken using microscopes at Harvard University and the American Museum of Natural History, using a reticle in one of the eyepieces and a conversion table for each magnification, or were taken from photo-



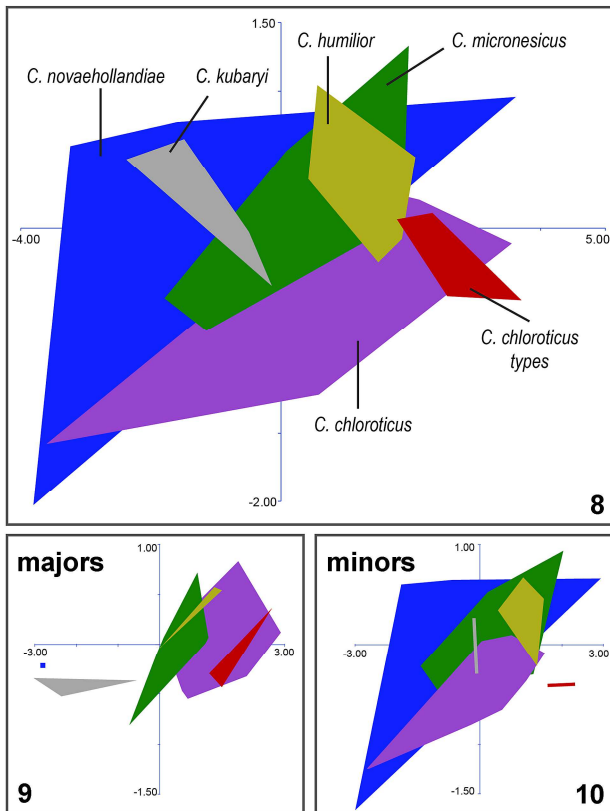
Figs. 3 - 7: Relationships between Principal Components 1 and 2 for the Principal Component Analysis of morphological measurements taken from specimens in the molecular phylogeny of CLOUSE & al. (2015) and types for the species of interest in this study. Figure 3 shows all species together, with missing measurements (including in cases when minor or major specimens are not associated), and figures 4 and 5 show magnified views of the same scatterplot, with some species removed. Figures 6 and 7 show majors and minors separately, without missing data extrapolated.

graphs with scale bars. Figures 1 - 35 were made in Adobe Photoshop v. 12.0 and Illustrator v. 15.0.0 (Adobe Systems, Mountain View, CA).

Results

In all PCAs, the first component was responsible for the bulk of the variance, and our different measurements contributed fairly equally to this component. For the combined analysis of major and minor workers, with missing values replaced by extrapolated ones, the first component of the PCA analysis accounted for 89% of the variance

(Figs. 3 - 5, 8). The loadings for the measurements contributing to this component were nearly equal; 18 out of 20 loadings were between -0.21 and -0.24, and the smallest two were -0.20 (petiole height of the minors) and -0.16 (head width of the minors). These results were similar for the PCAs of the majors and minors independently. For the majors, the first component accounted for 91% of the variance (Figs. 6, 9), and loadings of the measurements for this component ranged between -0.31 and -0.33. For the minors, the first component accounted for 84% of the variance (Figs. 7, 10), and the loadings ranged from



Figs. 8 - 10: Simplified representation of the PCA plots shown in Figs. 3 - 7, with the total area covered by individual points colored as single blocks. Figure 8 shows all species together, with missing measurements (including in cases when minor or major specimens are not associated), and figures 9 and 10 show majors and minors separately, without missing data extrapolated.

-0.30 and -0.34, except for head width (-0.24). The second component added between 3% (majors and minors together and just majors) and 6% (just minors) to the cumulative explanation of the variance.

In scatterplots between the first and second components, Polynesian, Fijian, and Melanesian *Camponotus chloroticus* specimens clustered with the *C. chloroticus* syntypes, and Micronesian and Melanesian *C. micronesicus* sp.n. specimens formed another cluster that overlapped little with the *C. chloroticus* syntypes. This was true for the combined analysis of major and minor workers (Figs. 3 - 5, 8), and majors and minors separately (Figs. 6, 7, 9, 10). Our PCA analyses also recovered *C. kubaryi* stat. rev. as similar in shape to many *C. novaehollandiae* and *C. micronesicus*, but molecular analyses recover it as not closely related to either of these species. The *C. kubaryi* stat. rev. syntype of a major worker matched the specimens resembling this species in the molecular phylogeny (terminal names PAL.2.CAM.Babeldoab and PAL.3.CAM.Mecherchar), but the minor syntype that was mounted well enough for measuring (see AntWeb.org, CASENT-0904014) is large for a minor, clearly falling between the other minor syntype and the majors in size (Tab. 2). Nonetheless, the coloration, pilosity and head shapes of the syntypes and other large, dark-headed *Camponotus* collected from Palau suggest these specimens represent a single, if

variable, species. The head shapes of majors seem most variable in the concavity of the vertex and degree of tapering toward the mandibles (Figs. 11, 12, 14), but for *Camponotus* this amount of variation is not uncommon.

We were able to discern some consistent morphological differences between *Camponotus micronesicus* sp.n. and *C. chloroticus*. Specimens of *C. micronesicus* sp.n. are slightly more concave at the vertex and have longer scapes than *C. chloroticus*, especially among the minors: the Scape Index (ratio of the scape length to the head width) for *C. micronesicus* sp.n. was measured at a minimum of 175 in minors, which is larger than the maximum SI measured for *C. chloroticus* minors (154; Tab. 2). Perhaps the most reliable and easily seen character is that *C. chloroticus* specimens have distinct standing hairs on the lower, proximal hind femur and on the propleuron, and these are absent in *C. micronesicus* sp.n. (Clade V, Fig. 2). These hairs are in fact almost always present on the new species from Chuuk, *C. kubaryi* stat. rev. from Palau, and *C. eperiamorum* on Pohnpei; thus, they appear to be a synapomorphy of Clade IV in the molecular phylogeny (Fig. 1). Interestingly, in Emery's description of *C. chloroticus*, based on types from Polynesia and Melanesia, he notes (EMERY 1897) that the hairs are close to those of *C. kubaryi*. Propleuron and hind femurs hairs are distinct on the Tongan syntypes for *C. chloroticus*, and on most of the *C. kubaryi* stat. rev. types, but the New Guinean syntype for *C. chloroticus* is mounted such that the hind femur hairs cannot be seen, and the propleuron appears smooth (Figs. 17 - 20).

In summary, it was already clear from the molecular phylogeny of CLOUSE & al. (2015) that Polynesian, Fijian, and some Melanesian specimens that looked like *Camponotus chloroticus* are a distinct species that is genetically distant from similar-looking specimens in Micronesia, as well as the morphologically variable species *C. humilior* and *C. novaehollandiae* (which are found mostly in Australia and New Guinea). Therefore, the key question was whether the type specimens of *C. chloroticus* and Polynesian, Fijian, and Melanesian specimens in the molecular phylogeny tentatively identified as *C. chloroticus*, besides sharing their ranges in Polynesia and New Guinea, have morphological characters that also overlap. We found that besides having similar morphometric characters, the Polynesian syntypes of *C. chloroticus* and modern specimens have the same pilosity (standing hairs on the hind femur and propleuron), which in fact distinguishes the whole of Clade IV in the molecular phylogeny (Fig. 1). The *C. chloroticus* syntype from Irupara is difficult to connect to either species, for its shape is intermediate, and its diagnostic pilosity is difficult to see; however, its short scapes and wide head appear to ally it with the Tongan syntypes more than the Micronesian specimens.

The molecular phylogeny also showed that specimens from Palau that have been treated as a subspecies of *Camponotus irritans* are in fact not a color morph of any named species, especially not *C. irritans*, a specimen of which was recovered in the molecular phylogeny far from the Palauan ones. The key morphological question with the Palauan specimens has been whether they were close enough to the type specimens of *C. kubaryi* stat. rev. to be considered the same species. Their overall similar appearance and shared small island home inclines one to favor

Tab. 2: Means and ranges of morphological measurements (in mm) of type specimens and, for *C. chloroticus* and *C. kubaryi* stat. rev., modern specimens used in PCA analyses, for comparison to historical types.

	<i>C. micronesicus</i> sp.n.			<i>C. chloroticus</i>						<i>C. kubaryi</i> stat. rev.				
	type specimens			New Guinean syntype	Tongan syntypes			non-type specimens			syntypes	non-type specimens		
	Avg.	Range	n		Avg.	Range	n	Avg.	Range	n		Avg.	Range	n
Majors														
EL	0.50	0.45 - 0.55	9	0.51	0.49	0.48 - 0.51	2	0.48	0.40 - 0.50	20	0.56	0.60	0.60 - 0.60	2
EW	0.39	0.35 - 0.45	9	0.33	0.30	0.25 - 0.35	2	0.37	0.30 - 0.40	20	0.40	0.45	0.45 - 0.45	2
FCL	1.27	1.20 - 1.40	9	1.22	1.02	1.01 - 1.04	2	1.15	1.00 - 1.31	20	1.46	1.50	1.45 - 1.55	2
HL	2.33	2.15 - 2.50	9	2.36	2.23	2.15 - 2.32	2	2.21	1.85 - 2.40	20	2.56	2.85	2.75 - 2.95	2
HW	2.07	1.85 - 2.30	9	2.20	1.96	1.88 - 2.04	2	2.00	1.45 - 2.25	20	2.40	2.70	2.65 - 2.75	2
ML	2.84	2.65 - 3.00	9	2.61	2.65	2.57 - 2.73	2	2.70	2.38 - 2.85	20	3.16	3.45	3.35 - 3.55	2
MTL	1.69	1.55 - 1.80	9	1.66	1.50	1.44 - 1.55	2	1.70	1.55 - 2.10	13	1.97	2.05	2.00 - 2.10	2
PH	0.78	0.60 - 0.90	8	0.76	0.67	0.59 - 0.75	2	0.75	0.60 - 0.81	16	0.73	1.08	1.05 - 1.10	2
PL	0.63	0.55 - 0.65	9	0.47	0.46	0.43 - 0.49	2	0.60	0.44 - 0.75	18	0.56	0.80	0.75 - 0.85	2
SL	1.85	1.70 - 1.95	9	1.68	1.60	1.55 - 1.64	2	1.65	1.44 - 1.85	20	2.10	2.18	2.15 - 2.20	2
CI	89	86 - 92	9	93	88	–	2	90	78 - 96	20	94	95	93 - 96	2
SI	90	83 - 98	9	76	82	76 - 87	2	84	73 - 124	20	88	81	80 - 81	2
Minors														
EL	0.42	0.40 - 0.45	8		0.39	0.38 - 0.40	2	0.43	0.38 - 0.55	18	0.46		0.45	1
EW	0.32	0.30 - 0.35	8		0.31	0.30 - 0.31	2	0.33	0.30 - 0.40	18	0.36		0.35	1
FCL	1.05	0.95 - 1.15	8		0.92	–	1	1.05	0.90 - 1.40	18	1.24		1.10	1
HL	1.50	1.35 - 1.65	8		1.61	1.57 - 1.64	2	1.66	1.55 - 2.10	17	1.82		1.60	1
HW	1.07	1.00 - 1.15	8		1.20	1.18 - 1.23	2	1.29	1.20 - 1.60	17	1.50		1.20	1
ML	2.36	2.20 - 2.50	8		2.25	–	1	2.40	2.20 - 3.05	18	3.00		2.45	1
MTL	1.61	1.50 - 1.70	8		1.31	–	1	1.59	1.40 - 1.95	15	2.48		1.70	1
PH	0.59	0.55 - 0.65	6		0.55	–	1	0.63	0.50 - 0.75	15	0.84		0.70	1
PL	0.56	0.50 - 0.60	7		–	–	0	0.57	0.50 - 0.70	16	0.36		0.60	1
SL	1.96	1.75 - 2.10	8		1.54	1.45 - 1.63	2	1.83	1.60 - 2.45	18	2.02		2.00	1
CI	71	67 - 74	8		75	–	2	78	74 - 82	17	82		75	1
SI	183	175 - 191	8		128	123 - 133	2	143	129 - 154	17	134		167	1

this hypothesis, and we found no strong evidence against it in our examination of their morphology.

Thus, the totality of molecular and morphological evidence leads us to propose the following taxonomic updates. We describe Micronesian and Melanesian specimens formerly identified as *Camponotus chloroticus* and falling in Clade V of the molecular phylogeny as a new species, *C. micronesicus* sp.n., including New Guinean and Vanuatu specimens that are separated by a clade of morphologically and molecularly distinct Vanuatu specimens. We did not designate as a paratype the Philippine minor specimen recovered in the *C. micronesicus* sp.n. clade (PHIL.6.CAM. Panicuason), since it is distinctly larger and darker than Micronesian specimens, and it was recovered on a long branch in the molecular phylogeny. Hybridization, whether historic or ongoing, remains a plausible explanation for some of the more confounding specimens in *Camponotus*, including the distinct Vanuatu and Philippine specimens. We also return *C. kubaryi* stat. rev. to species status, and we here describe the new form collected from Chuuk as *Camponotus tol* sp.n. Taxonomic

histories below are from BOLTON (1995) and WILSON & TAYLOR (1967).

***Camponotus chloroticus* EMERY, 1897**

(Figs. 15 - 20; Tabs. 2, 3)

Camponotus maculatus ssp. *chloroticus* EMERY, 1897.

Combination in *Camponotus* (*Myrmoturba*), as *Camponotus* (*Myrmoturba*) *maculatus chlorotica* var. *chlorogaster*: EMERY, 1914.

Camponotus (*Myrmoturba*) *maculatus pallidus* var. *samoensis* SANTSCHI, 1919, unavailable name. Homonym of *Camponotus irritans samoensis* (SMITH, 1857).

Camponotus (*Myrmoturba*) *maculatus* ssp. *sanctae crucis* MANN, 1919.

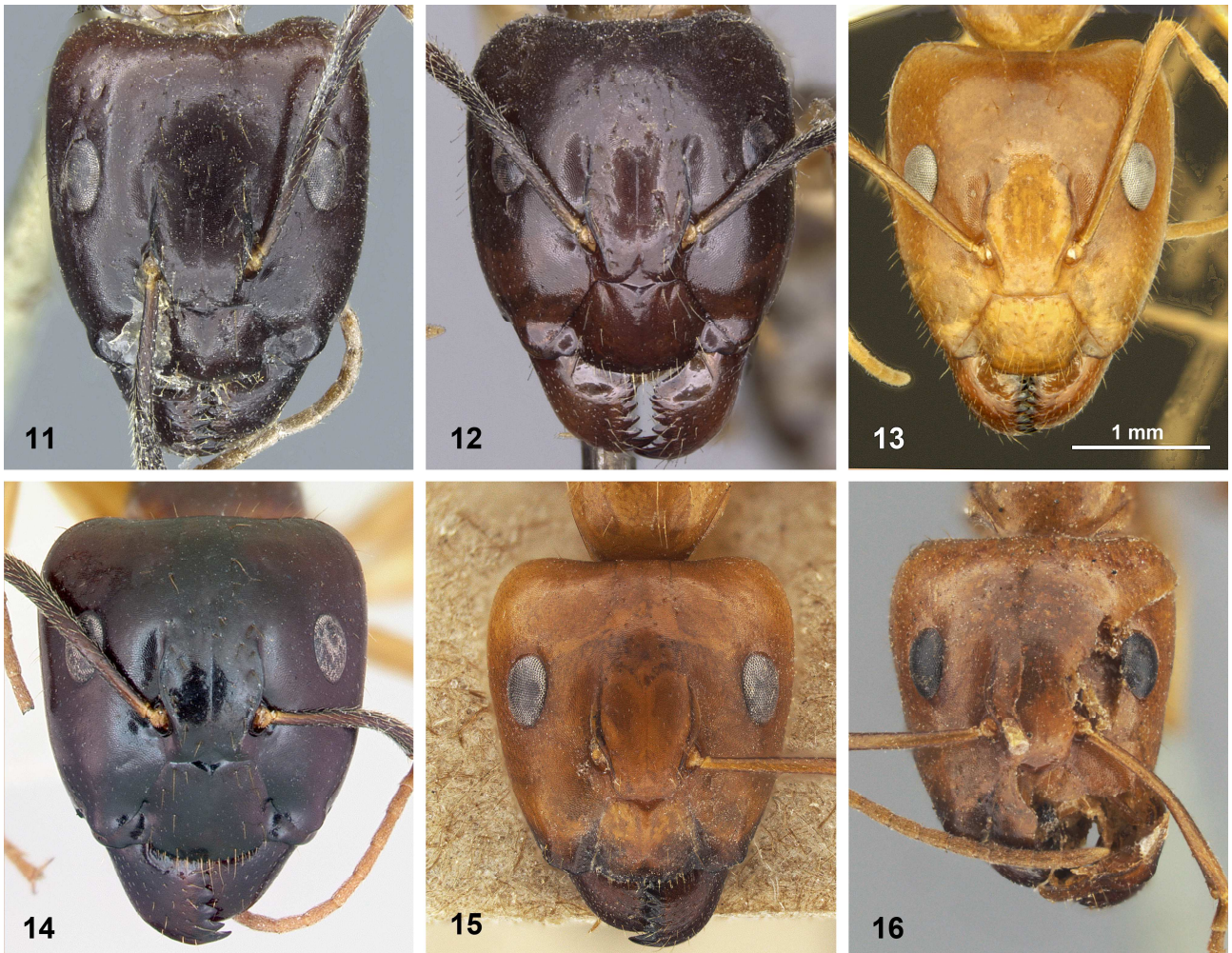
Subspecies of *Camponotus irritans*: EMERY 1920.

Combination in *Camponotus* (*Tanaemyrmex*): EMERY 1925.

Subspecies of *Camponotus irritans*: KARAVAEV 1933.

Raised to species: WILSON & TAYLOR 1967.

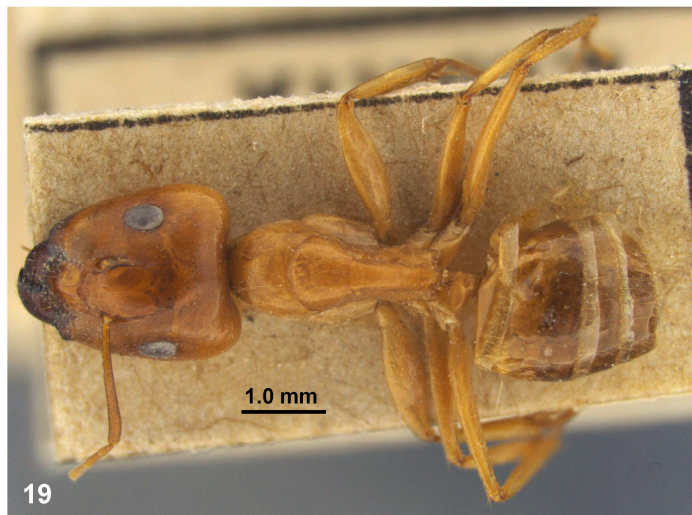
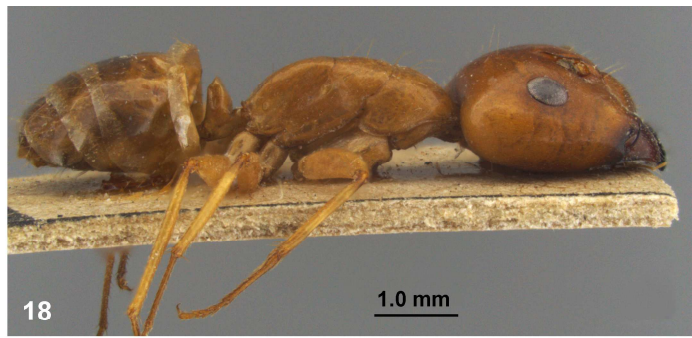
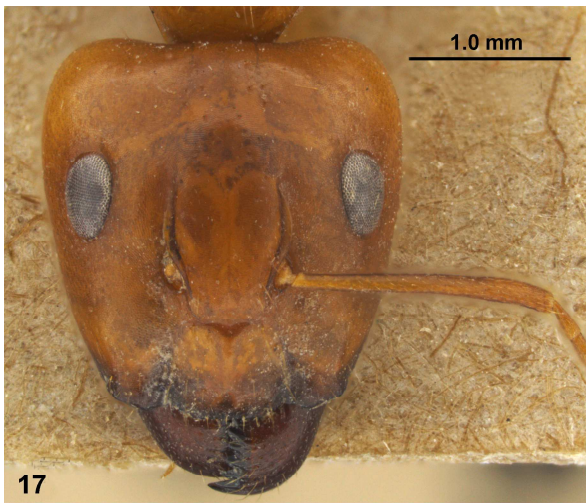
Comments: *Camponotus chloroticus* was originally described by EMERY (1897) as a subspecies of *C. macula-*



Figs. 11 - 16: Syntypes of *Camponotus kubaryi* stat. rev. (11 - 12; CASENT0904012 and CASENT0910153, from www.AntWeb.org, photographs by Zach Lieberman), holotype of *C. micronesicus* sp.n. (13), specimen of *C. kubaryi* stat. rev. collected from Peliliu Is. (14; CASENT0173088, from www.AntWeb.org, photograph by April Nobile), and syntypes of *C. chloroticus* from New Guinea (15) and Tonga (16). Scale bar in Fig. 13 applicable to Figures 11 - 16.

Tab. 3: Caste and label transcriptions for the syntypes of *Camponotus chloroticus* EMERY, 1897.

	Pin 1	Pin 2	Pin 3	Pin 4
Caste	Major	2 Minors	Major	Major
Label 1	N. GUINEA MER. IRUPARA Agosto Otto. 1889 L. LORIA	Tonga Mus. God	Tonga Mus. God	Tonga-Ins.
Label 2	TYPUS	SYNTYPUS <i>Camponotus Chloroticus</i> (Emery, 1897)	SYNTYPUS <i>Camponotus Chloroticus</i> (Emery, 1897)	SYNTYPUS <i>Camponotus Chloroticus</i> (Emery, 1897)
Label 3	Museo Civico di Genova	MUSEO GENOVA coll. C. Emery (dono 1925)	MUSEO GENOVA coll. C. Emery (dono 1925)	MUSEO GENOVA coll. C. Emery (dono 1925)
Label 4	SYNTYPUS <i>Camponotus chloroticus</i> (Emery, 1897)			
Label 5	<i>irritans</i> Sm. subsp. <i>chloroticus</i> Em.			
Label 6	<i>Camponotus irritans</i> F. Sm. subsp. <i>chloroticus</i> Emery n. subsp.			



Figs. 17 - 20: Syntype of *Camponotus chloroticus* from New Guinea in frontal (17), lateral (18), and dorsal (19) views, and the original locality label (20).

tus, as follows: "I bought from Godeffroy Museum [Hamburg, 1861 - 1885] specimens of this form from the Tonga Islands and New Britain, under the name *C. pallidus*. ... For the shape of the various parts of the body, for the pubescence, the very weak sculpture and the hairs, it is very close to the *C. Kubaryi*, MAYR [specific epithet capitalized in original], particularly the oceanic specimens and those from New Guinea. ... Maximum size is 8 mm; reddish-yellow, dirt-like color; head darker and more red, abdomen more or less blackish in its rear."

We do not know which aspects of the pilosity EMERY noticed as being similar to that of *Camponotus kubaryi* stat. rev., but the presence of standing hairs on the proximal hind femur and on the propleuron in both species is one of the few readily discernable synapomorphies of an important clade of *Camponotus* in the Pacific and one of the key characters used to distinguish *C. chloroticus* from *C. micronesicus*. Using this pilosity character, overall similarity in size, shape, and coloration, as well as our finding of only one such yellow *Camponotus* species in the same islands, we confirm here that the Tongan syntypes of *C. chloroticus* (Figs. 15, 16) match the species in Clade IV, which extends from New Guinea to Polynesia (Fig. 2).

The *Camponotus chloroticus* syntype from Irupara, New Guinea (Figs. 17 - 20), is not as clearly aligned with the Tongan syntypes or modern specimens from the Polynesian, Fijian, and Melanesian clade, partially due to its mounting, which limits our view of the important pilosity characters. However, the New Guinean syntype has dis-

tinctly shorter scapes than almost all *C. micronesicus* sp.n. specimens measured, measuring just at the lower limit of the range, and producing a scape index for the New Guinea syntype that is smaller than all *C. micronesicus* specimens measured but within the range for *C. chloroticus*. The petiole length of the New Guinean syntype is also similar to that of *C. chloroticus* specimens, and altogether we have more support for it being *C. chloroticus* than *C. micronesicus* sp.n. Other options for the identity of the New Guinean syntype include an undescribed form, or, if it is truly missing the hind femur and propleuron standing hairs, an oddly concolorous *C. humilior* (which tends to be bicolorous); *C. novaehollandiae* is too large, also usually bicolorous, and, from our PCA analysis, slightly different in shape.

To the original description we add a summary of our morphological observations of this species, combining syntypes and modern specimens, as follows (also see Tabs. 2, 3). **Majors:** EL 0.48 (range 0.40 - 0.51), EW 0.36 (0.25 - 0.40), FCL 1.14 (1.00 - 1.31), HL 2.22 (1.85 - 2.40), HW 2.00 (1.45 - 2.25), ML 2.69 (2.38 - 2.85), MTL 1.68 (1.44 - 2.10), PH 0.74 (0.59 - 0.81), PL 0.58 (0.43 - 0.75), SL 1.65 (1.44 - 1.85); CI 90 (78 - 95), SI 83 (73 - 124). Mesosoma light yellow, gaster same color as mesosoma or slightly darker, head color usually darker than mesosoma; head tapering, vertex usually slightly concave; hind femur and propleuron with standing hairs. **Minors:** EL 0.42 (0.38 - 0.55), EW 0.33 (0.30 - 0.40), FCL 1.04 (0.90 - 1.40), HL 1.66 (1.55 - 2.10), HW 1.28 (1.18 -

1.60), ML 2.39 (2.20 - 3.05), MTL 1.58 (1.31 - 1.95), PH 0.62 (0.50 - 0.75), PL 0.57 (0.50 - 0.70), SL 1.80 (1.45 - 2.45); CI 77 (74 - 82), SI 142 (123 - 154). Mesosoma usually light yellow, gaster and head usually same color as mesosoma or slightly darker; head tapering, vertex convex and occipital carina present; hind femur and propleuron with standing hairs.

***Camponotus kubaryi* stat. rev. MAYR, 1876**

(Figs. 11, 12, 14; Tab. 2)

Combination in *Camponotus* (*Myrmoturba*): FOREL 1914.

Combination in *Camponotus* (*Tanaemyrmex*): EMERY 1925.

Subspecies of *Camponotus maculatus*: EMERY 1896.

Subspecies of *Camponotus irritans*: EMERY 1920, KARAVAIIEV 1929.

Comments: MAYR'S (1876) description of this species consists of a few lines that describe it as 7.5 - 9.5 mm long, reddish-brown, and with a darker head, mandibles, and antennae, plus some description of characters that do little to distinguish it beyond being in the genus *Camponotus*. Although this species is restricted to the islands of the Republic of Palau, which constitute an area of less than 500 km² over 800 km away from any major landmass, it still shows noticeable morphological variation (for example, the head shapes and colors of syntypes shown in Figs. 11, 12). This may be due to the fact that the country is comprised of over 200 small limestone islands, which may divide this species into many somewhat isolated populations. Nonetheless, despite variation in tone and shade, and the degree to which the head is tapered and the vertex concave, it is the only *Camponotus* in Micronesia with a large, dark head, and its restriction to Palau makes identification straightforward. Still, we add to the original description this summary from our morphological examinations, combining syntypes and modern specimens. **Majors:** EL 0.59 (range 0.56 - 0.60), EW 0.43 (0.40 - 0.45), FCL 1.49 (1.45 - 1.55), HL 2.75 (2.56 - 2.95), HW 2.60 (2.40 - 2.75), ML 3.35 (3.16 - 3.55), MTL 2.02 (1.97 - 2.10), PH 0.96 (0.73 - 1.10), PL 0.72 (0.56 - 0.85), SL 2.15 (2.10 - 2.20); CI 94 (93 - 96), SI 83 (80 - 88); mesosoma medium yellow, head and gaster much darker, approaching black; head tapering and vertex distinctly concave; standing hairs present on propleuron and hind femur. **Minors:** EL 0.46 (0.45 - 0.46), EW 0.36 (0.35 - 0.36), FCL 1.17 (1.10 - 1.24), HL 1.71 (1.60 - 1.82), HW 1.35 (1.20 - 1.50), ML 2.73 (2.45 - 3.00), MTL 2.09 (1.70 - 2.48), PH 0.77 (0.70 - 0.84), PL 0.48 (0.36 - 0.60), SL 2.01 (2.00 - 2.02); CI 79 (75 - 82), SI 150 (134 - 167); mesosoma light yellow, head and gaster much darker, approaching black; head tapering and vertex convex.

These characters match those of three other specimens not used in this study but described in CLOUSE (2007a) under the species code "sp. 1945". One of the majors is shown in Figure 14, and the specimens can now be securely identified as *C. kubaryi* stat. rev. The two majors had total lengths of 8.2 and 7.9 mm, matching MAYR'S original description, and the following other measurements are very similar to those of the specimens we examined here: HL 3.00, HW 2.83, SL 2.30, CI 94, and SI 81 for the larger specimen, and HL 2.73, HW 2.63, SL 2.07, CI 96, and SI 87 for the smaller. Likewise, the minor specimen of "sp. 1945" is very similar to the ones here: HL 1.77, HW 1.33, SL 1.77, CI 75, and SI 133.

***Camponotus micronesticus* sp.n. BLANCHARD & CLOUSE**
(Figs. 21 - 29; Tab. 4)

Type material: Holotype major worker, Federated States of Micronesia: Pohnpei Island, Nah Islet, 1 m a.s.l. (6° 51' 11.2" N, 158° 21' 16.3" E), 15.IX.2010, leg. R. Clouse and P. Sharma. Paratypes (8 major workers, 8 minor workers), detailed collection information provided in Table 4. All specimens are deposited in the Museum of Comparative Zoology, Harvard University, Massachusetts, USA.

Description of holotype major worker (Figs. 21 - 23): EL 0.55, EW 0.40, FCL 1.30, HL 2.50, HW 2.25, ML 3.00, MTL 1.80, PH 0.85, PL 0.65, SL 1.95; CI 90, SI 87.

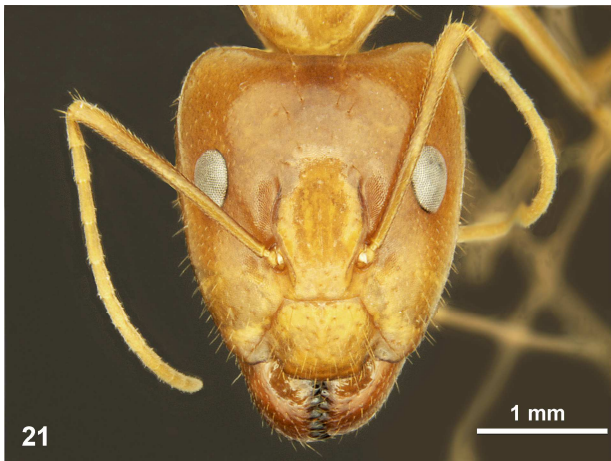
Masticatory margin with six teeth that diminish in size unevenly from the apical tooth; teeth 2 - 5 similar in size, sixth tooth (not visible when mandibles closed) distinctly smaller. Clypeus continuing anteriorly past mandibular insertions one fourth its total height, then slightly convex. Posterior margin of clypeus straight to slightly concave, antennal insertions separated from clypeus by a distance almost equal to the distance from nearest clypeal margin to clypeal midpoint. Posterior head margin weakly concave to nearly flat. In frontal view: eyes located halfway between posterior clypeal margin and vertex; inner eye margins halfway between frontal lobes and sides of head; eyes not extending past lateral margin of head. Antennae 12-segmented. Antennal scape reaching past the posterior margin of head by a distance 1 - 2 times the width of the scape at its apex. Mesosoma in profile gently sloping from anterior pronotum to dorsal propodeum, with slightly steeper propodeal declivity. Petiolar node sloping evenly up to and down from its apex.

Color: Gaster and mesosoma uniformly yellow-orange, the head ranging from slightly to considerably darker orange-brown. Vertex to posterior frons and anterior frontal lobes orange brown, anterior frons and clypeus yellow-orange; central posterior head and frontal carina dark orange brown. Mandibles dark reddish brown, lighter at insertions, mandibular teeth black. Each gastral tergite with hyaline margin along posterior fifth.

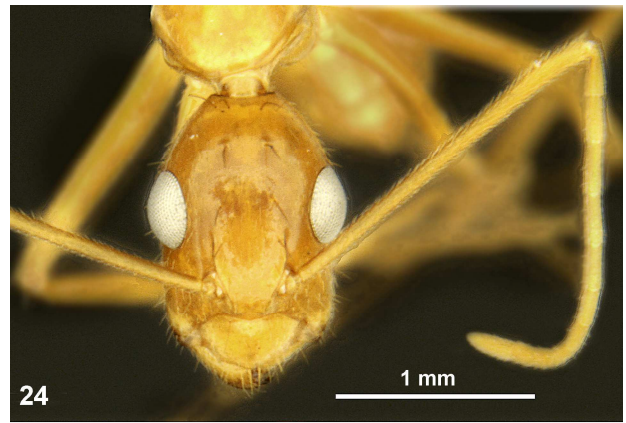
Pilosity: Layer of small, recumbent, light hairs all over head. Longer, standing hairs numerous on front, back, and sides of head, longer at vertex and more dense on clypeus. From frontal view, area between eyes and frontal carina, two rows of long, standing hairs extending from vertex to mid-clypeus. Dorsal pronotum, mesonotum and vertex of propodeal angle with long standing hairs. Propleuron standing hairs lacking. Each gastral tergite with 10 to 20 long standing hairs encircling tergite immediately before hyaline margin along posterior edge; 5 to 10 longer standing hairs encircling tergite halfway between hyaline margin and posterior edge of previous tergite. Hind femur standing hairs lacking.

Sculpturing: Head, mesosoma, and gaster surface glossy; genae, clypeus, and mandibles weakly punctured.

Description of paratypes: Majors resembling holotype in coloration and pilosity, mesosoma ranging from light yellow to orange-yellow, heads sometimes distinctly darker than mesosoma but not brown. Generally same size or smaller than holotype (ML 2.65 - 3.00, HW 1.85 - 2.30), with similar head shapes (CI 86 - 92). Relative scape lengths more variable (SI 83 - 98). Minors approximately 15% -



Figs. 21 - 23: Holotype of *Camponotus micronesicus* sp.n. in frontal (21), dorsal (22), and lateral (23) views.

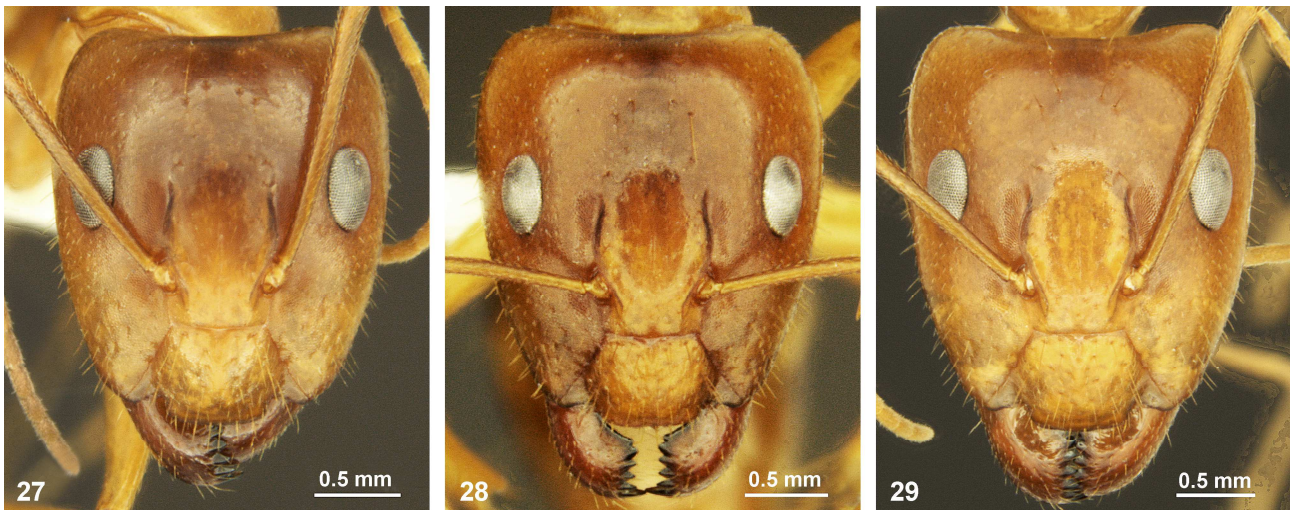


Figs. 24 - 26: Paratype of *Camponotus micronesicus* sp.n. collected with the holotype, in frontal (24), dorsal (25), and lateral (26) views.

20% smaller than majors (ML 2.2 - 2.5) but with much narrower heads (CI 67 - 74) and proportionally longer, more variable scapes (SI 175 - 191). Mesosoma coloration more consistently light yellow with similar or only slightly darker heads. Occipital carina always present. Measurements of minor worker collected with holotype and shown in Figs. 24 - 26: EL 0.40, EW 0.30, FCL 0.95, HL 1.35, HW 1.00, ML 2.30, MTL 1.50, PH 0.51, PL 0.50, SL 1.85; CI 74, SI 185.

Differential diagnosis: In Micronesia there are four closely related *Camponotus* species that resemble *C. maculatus* (characters for which are described and illustrated in MCARTHUR & LEYS 2006): *C. micronesicus* sp.n., *C. eperiamorum*, *C. kubaryi* stat. rev., and *C. tol* sp.n. Of these species, only *C. micronesicus* sp.n. is mostly concolorous yellow-orange, and with the other three species

being island endemics, *C. micronesicus* sp.n. can be collected alongside only one of them at a time (CLOUSE 2007a). In Melanesia collections of *C. micronesicus* sp.n. are near those of three other described *C. maculatus*-like species: *C. choloroticus*, *C. novaehollandiae*, and *C. humilior*. However, only the latter two share the lack of propleuron and hind femur standing hairs with *C. micronesicus* sp.n., and although uniformly yellow-orange specimens of *C. humilior* and *C. novaehollandiae* are occasionally seen, both species tend to be strongly bicolorous. Moreover, the head length and width measurements for both majors and minors of *C. novaehollandiae* are approximately 25% larger than those of *C. micronesicus* sp.n., and we have no evidence that the ranges of these species overlap exactly with *C. micronesicus* sp.n. (*C. humilior* and *C. novaehollandiae* enter New Guinea only along the



Figs. 27 - 29: Frontal views of *Camponotus micronesicus* sp.n. types (collection details in Table 4): paratype FSM.13. CAM.Yap (27), paratype FSM.4. CAM.Chuuk (28), and holotype FSM.10. CAM.Pohnpei (29).

Tab. 4: *Camponotus micronesicus* sp.n. types and closely related specimens from Melanesia. Specimens are identified by their terminal name in CLOUSE & al. (2015), followed by original collection codes.

Specimen(s)	Collection Data
Holotype major, FSM.10.CAM.Pohnpei, 832.CAM.2.1	Federated States of Micronesia: Pohnpei Island: Nah Islet (6° 51' 11.2" N, 158° 21' 16.3" E), 15.IX.2010, leg. R. Clouse and P. Sharma
Paratype minor, FSM.10.CAM.Pohnpei, 832.CAM.2.1	Federated States of Micronesia: Pohnpei Island: Nah Islet (6° 51' 11.2" N, 158° 21' 16.3" E), 15.IX.2010, leg. R. Clouse and P. Sharma
Paratype major and minor, FSM.13.CAM.Yap, 845.CAM.1.1	Federated States of Micronesia: Yap Island, Mt. Madeqdeq at 159 m (9° 31' 32.5" N, 138° 6' 54.1"E), 23.IX.2010, leg. R. Clouse and P. Sharma
Paratype major and minor, FSM.4.CAM.Chuuk, 813.CAM.2.1	Federated States of Micronesia: Chuuk, Tol Island at 120 m (7° 19' 27.3" N, 151° 36' 50.6" E), 8.IX.2010, leg. R. Clouse, P. Sharma, and Techuo family
Paratype major, FSM.5.CAM.Chuuk, 813.CAM.3.1	Federated States of Micronesia: Chuuk, Tol Island at 120 m (7° 19' 27.3" N, 151° 36' 50.6" E), 8.IX.2010, leg. R. Clouse, P. Sharma, and Techuo family
Paratype major and minor, FSM.6.CAM.Chuuk, 813.CAM.4.1	Federated States of Micronesia: Chuuk, Tol Island at 120 m (7° 19' 27.3" N, 151° 36' 50.6" E), 8.IX.2010, leg. R. Clouse, P. Sharma, and Techuo family
Paratype major and minor, FSM.9.CAM.Pohnpei, 832.CAM.1.1	Federated States of Micronesia: Pohnpei Island, Nah Islet (6° 51' 11.2" N, 158° 21' 16.3" E), 15.IX.2010, leg. R. Clouse and P. Sharma
Paratype major and minor, PAL.1.CAM.Ngarchelong, 52761 & JCM0148a	Republic of Palau: Ngarchelong State, Ngarchor Island (7° 44.964' N, 134° 37.418' E), 3.V.2008, leg. J. Czekanski-Moir
Paratype major and minor, PNG.9.CAM.Madang, 9335.1	Papua New Guinea: Lepa Island (5° 10' 48.0" S, 145° 49' 40.8" E), 6.XI.2010, leg. M. Janda
Paratype major and minor, VAN.2.CAM, CR-111103-14	Vanuatu: Efate Is., 3 km west of Epao Village at 200 m (17° 36' 55.8" S, 168° 28' 27.3" E), 2.XI.2007, leg. C. Rabeling and E.O. Wilson

southern coast, where we have no *C. micronesicus* sp.n. collections).

The most difficult cases of identification will be between *Camponotus micronesicus* sp.n. and *C. chloroticus* specimens collected from Vanuatu, where they are sympatric and look nearly identical. Our best advice for identification is to check for hairs on the propleuron and hind femur, which should be absent in *C. micronesicus* sp.n. and present in *C. chloroticus*. In addition, *C. chloroticus* minors usually have a larger cephalic index (74 - 82 vs. 67 - 74) and smaller scape index (123 - 154 vs. 175 - 191), both resulting from having a wider head; majors show the same trend, although those of *C. chloroticus* are highly variable (Tab. 2).

Habitat: This species is found in disturbed forest, both natural (e.g., reef islets, which are washed over during

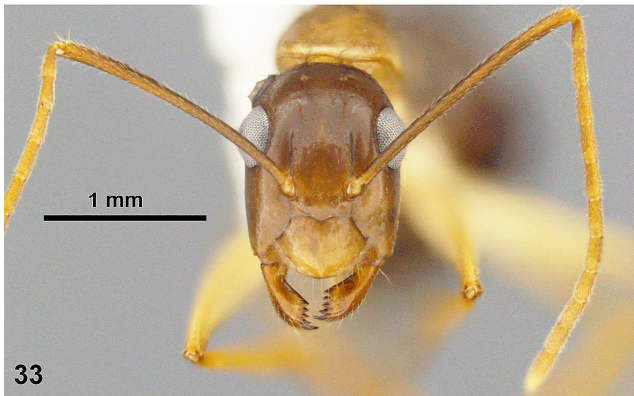
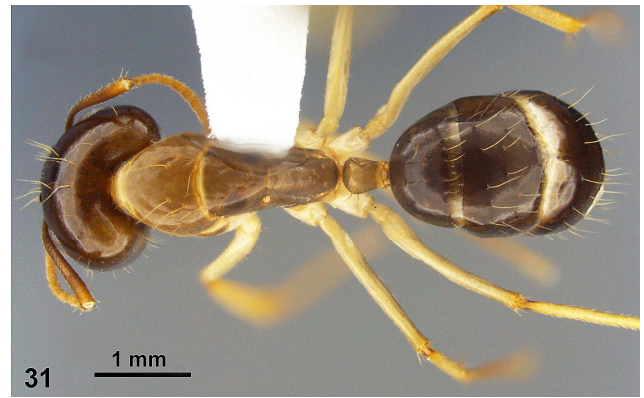
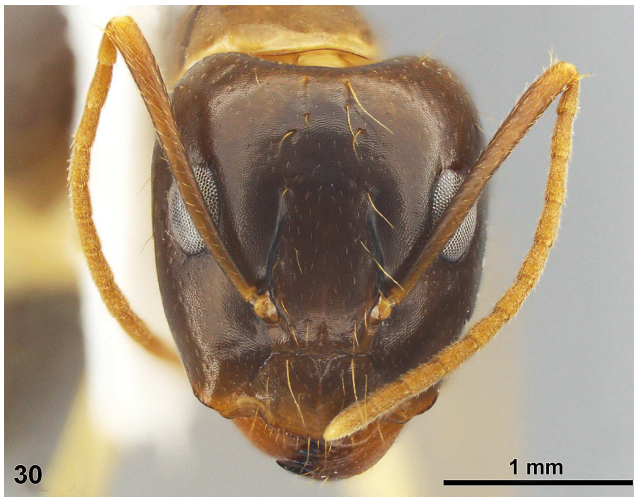
heavy storms) and anthropogenic (e.g., agroforest at low and middle elevations).

Etymology: This species is named for Micronesia, the predominant region where it is found.

Comments: All paratypes are listed in Table 4 by their terminal name in CLOUSE & al. (2015). A sample of some of the variation in head shape of major workers from across Micronesia is shown in Figures 27 - 29.

***Camponotus tol* sp.n. GIBSON & CLOUSE** (Figs. 30 - 35)

Type material: Holotype major worker. Federated States of Micronesia: Chuuk, Tol Island at 120 m (7° 19' 27.3" N, 151° 36' 50.6" E), leg. R. Clouse, P. Sharma, and Techuo family. Paratypes, (3 major workers, 9 minor workers), same collection data as holotype. Twelve additional minors stored in 95% EtOH, as well as two minors each



Figs. 30 - 35: Holotype of *Camponotus tol* sp.n. in frontal (30), dorsal (31), and lateral (32) views, and minor paratype from the same collection in frontal (33), dorsal (34), and lateral (35) views.

with one leg removed and used for DNA extraction, also same collection data as holotype. All specimens are deposited in the Museum of Comparative Zoology, Harvard University, Massachusetts, USA.

Description of holotype major worker (Figs. 30 - 32): EL 0.48, EW 0.30, FCL 1.05, HL 2.05, HW 1.84, ML 2.51, MTL 1.54, PH 0.54, PL 0.60, SL 1.77; CI 90, SI 96.

Mandible outer margin gently curved to an apex of about 75 degrees, the masticatory margin straight in front view. Mandibles tightly closed, masticatory margin with five visible teeth that gradually diminish in size from apex. Clypeus continuing anteriorly past mandibular insertions a distance slightly less than length of apical tooth, then straight across. Posterior clypeus curved anteriorly forming bilobed appearance, antennal insertions separated from

clypeus by a distance almost equal to the distance from nearest clypeal margin to clypeal midpoint. Head slightly longer than wide. Vertex weakly concave. In frontal view eyes located halfway between posterior clypeal margin and vertex; inner margins halfway between frontal lobes and sides of head; eyes not extending past lateral edge. Antennae 12-segmented. Antennal scape length extending past the vertex by a distance of 2 - 3 times the width of the scape at the apex. Mesosoma in profile gently sloping from anterior pronotum to dorsal propodeum, with moderate propodeal declivity.

Color: Distinct bicoloration: head mostly glossy brown, mesosoma uniform light yellow-brown, gaster glossy brown. Gradual lightening from vertex down to mandibles. Vertex to posterior clypeus same glossy brown as gaster. Black

outlining along frontal carina. Anterior clypeus to mandibular insertions light yellow-brown. Mandibles lighter brown than vertex down to posterior clypeus. Teeth of mandibles, scrobes, sutures, and joints on the head darker than surrounding cuticle. Each gastral tergite with hyaline margin along posterior fifth.

Pilosity: Layer of short, recumbent, light hairs all over head. Long, yellow, standing hairs numerous on front, back, and sides of head. In frontal view, area between eyes and frontal carina with two rows of long, standing hairs extending from vertex to mid-clypeus. Row of long hairs extending across anterior clypeal edge. From dorsal view, mesosoma with two side-by-side groups of standing hairs on pronotum, four long hairs with some small hairs per group; one group of standing hairs on mesonotum, with three long hairs and some small hairs; two groups of standing hairs clustered on propodeum, with three long hairs per group; layer of short recumbent hairs all over each appendage, decreasing in length from trochanter to tarsus. Propleuron standing hairs indistinct but present. Each gastral tergite with 20 to 30 long, yellow, standing hairs encircling tergite immediately before hyaline margin along posterior edge; 10 to 20 longer standing hairs encircling tergite halfway between hyaline margin and posterior edge of previous tergite. Standing hairs on hind femur indistinct but present.

Sculpturing: Head and gaster surface glossy; genae weakly punctured. Mesosoma surface smooth and shiny, although not glossy.

Description of paratypes: Majors closely resembling holotype except vertex and mandibles more reddish-brown; overall slightly larger (ML 2.6 - 2.75 and HW 1.88 - 1.95); CI same (90) but SI smaller (87 - 92), indicating consistency in head shape and scape absolute length in larger specimens. Minors closely resembling majors in coloration and pilosity. Slightly smaller than majors (ML 2.00 - 2.25) and with significantly narrower heads and longer, more variable scapes (CI 76 - 80, SI 157 - 172). Scapes extending beyond vertex by a range of 25% - 50% of total scape length. Posterior clypeus lighter brown than holotype. Eyes extending past lateral outline of head. One minor with open mandibles has six visible teeth on masticatory margin that gradually diminish in size from the apex. Measurements of minor collected with holotype and pictured in Figures 33 - 35: EL 0.45, EW 0.33, FCL 0.82, HL 1.34, HW 1.05, ML 2.08, MTL 1.31, PH 0.45, PL 0.45, SL 1.73; CI 78, SI 165.

Differential diagnosis: The only specimens from Chuuk that might be mistaken for *Camponotus tol* sp.n. are very dark, small *C. micronesicus* sp.n., but *C. tol* sp.n. has hairs on the propleuron and hind femur, and *C. micronesicus* sp.n. does not. Among other similar species in Micronesia, *C. tol* sp.n. is not as starkly bicolored as *C. eperiamorum*, and it is approximately 75% the overall size of *C. kubaryi* stat. rev.

Habitat: This species was collected from low-elevation, mixed agroforest (120 m a.s.l.) on Tol Island in Chuuk Lagoon. This island is the largest in the region, and reaches a maximum elevation of 439 m, but it shows evidence of agroforestry and agro-native mixed forest at all elevations. Specimens were collected from one colony and appeared to be less abundant on the island than *Camponotus micronesicus* sp.n.

Etymology: The specific epithet is a noun in apposition to the genus that refers to the type locality, Tol Island (pronounced "tōl," as in the common word "toll"). Tol is the largest island inside the main atoll and island group of Chuuk State in the Federated States of Micronesia. The island is sometimes written as "Ton," as the phonemes "l" and "n" are not distinct in Chuukese.

Comments: *Camponotus tol* is part of a larger clade in the molecular phylogeny (Clade IV; Fig. 2) that includes *C. chloroticus*, *C. kubaryi* stat. rev., an undescribed species collected in Papua New Guinea and Indonesia, and an endemic species found on the nearby Micronesian island of Pohnpei, *C. eperiamorum* (CLOUSE 2007b, CLOUSE & al. 2015). These species are all larger than *C. tol*, and they are also distinguished by their coloration: *C. chloroticus* and the unnamed species are lighter, *C. kubaryi* stat. rev. is darker, and *C. eperiamorum* contrasts more in shade among the mesosoma, head, and gaster. All of these species have the distinctive hairs on the propleuron and hind femur, but only *C. tol* sp.n. has such a distinctive double row of long hairs down the front of the head. Overall, *C. tol* sp.n. is distinct as a dusky, small, member of the *Camponotus maculatus*-like species in the Pacific.

Discussion

We have used the results of a molecular study to guide us in updating the taxonomies of a few members of one of the most confusing groups of ants in the Indo-Pacific. Combining those results with the morphological study here, the *Camponotus* species that resemble *C. maculatus* in Micronesia are now well understood. They consist of three closely related island endemics (*C. eperiamorum*, *C. kubaryi* stat. rev., and *C. tol* sp.n.) and one widespread species, *C. micronesicus* sp.n. Nonetheless, even with a fresh perspective on the relative utility of various morphological characters in *Camponotus*, based on a broad sample of specimens and a detailed examination, questions remain. Most pressing is gaining a better understanding of what forms are in Melanesia and to what degree the ranges of *C. chloroticus*, *C. micronesicus* sp.n., *C. humilior*, and *C. novaehollandiae* overlap. Our hypothesis that the syntype from Irupara in New Guinea is indeed *C. chloroticus* is worth testing with more samples from that area, and it seems likely the large landmasses of Melanesia hold a number of taxonomic surprises in this group.

We advise that future work on *Camponotus* species resembling *C. maculatus* begin with analyses of molecular data, as reliance on morphological characters among these species has led to many decades of taxonomic instability and, in most cases, erroneous groupings. Nevertheless, as *C. micronesicus* sp.n. demonstrates, molecular data do not provide the final answer, for the molecular phylogeny placed some highly variant Vanuatan forms within a clade we would otherwise readily consider this species based on appearance. There is clearly a close relationship there, but the issue of hybridization in this group is ripe for further investigation. We even retain some doubt about specimens from New Guinea and the Philippines tentatively considered here as *C. micronesicus* sp.n., the latter of which we did not designate as a paratype. The New Guinean specimens are nearly indistinguishable from Micronesian ones but are separated in the molecular phylogeny by distinctly different looking Vanuatan specimens

(some of which are all black), and the Philippine specimens places confidently among *C. micronesicus* sp.n. in the molecular phylogeny but has a very different size and coloration.

Camponotus species that resemble *C. maculatus* are common, highly visible members of the ant fauna in the Pacific (unlike in Australia, where they are mostly nocturnal), and they may have utility as models of speciation and convergence. It appears that understanding their diversity and relationships will be an iterative process, but we have shown here that with ample sampling of specimens and characters, advances can be made. We encourage field collections of this group whenever possible, as well as continued rounds of molecular and morphological analyses.

Acknowledgments

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