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Introduced *Pheidole* of the world: taxonomy, biology and distribution

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Abstract

The objective of this study is to provide a detailed taxonomic resource for identifying and studying ants in the genus *Pheidole* that have established beyond their native ranges. There is an increasing need for systematists to study taxa of specific concern to 21st century environmental, food security and public health challenges. Systematics has an important role to play in both the theoretical and applied disciplines of invasion biology. Few invaders impact terrestrial ecosystems more than ants. Among the world's 100 worst invasive species is the cosmopolitan and highly destructive *Pheidole megacephala* (Fabricius). Accurate identification of *P. megacephala* is imperative for the success of screening, management and eradication programs designed to protect native ecosystems from the impacts of this destructive species. However, accurate identification of *Pheidole* species is difficult because of their taxonomic diversity, dimorphic worker caste and lack of taxonomic resources. Illustrated keys are included, along with the taxonomic history, taxonomic diagnoses, biological notes and risk statements for the 14 most invasive members of the genus. Global distribution maps based on over 14,000 specimen and literature records are presented for each species. These results of this work will facilitate identification of pest species, determination of climatic and habitat requirements, discovery of pest origins, horizon scanning and assessment of invasion pathways. The following new synonym is proposed, with the senior synonym listed first and the junior synonyms in parentheses: *Pheidole indica* Mayr (= *P. teneriffana* Forel, and its synonyms *P. taina* Aguayo and *P. voeltzkowii* Forel). *Pheidole navigans* Forel, **stat. rev.**, **stat. n.** is removed from synonymy and

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elevated to species rank. It is proposed that records of *P. moerens* Forel outside of the Mesoamerica and the Caribbean refer instead to *P. navigans* or other heterospecific taxa in the *P. flavens* species complex. We propose that the names *P. anastasii* Emery and *P. floridana* Emery have been widely misapplied to North American outdoor records of *P. bilimeki* Mayr. It is suggested that the synonymy of *P. lauta* Wheeler be transferred from *P. floridana* Emery to *P. bilimeki* Mayr.

Keywords

Applied systematics, big-headed ant, invasive species, invasive ants, identification key, Lucid key, *Pheidole megacephala*, port of entry, species distribution

Introduction

The science of systematics has historically focused on the discovery, description and classification of life on earth with relatively little attention given to the ecological or economic impact of the study taxon. Today, there is an increasing need for systematists to study taxa of particular concern to 21st century environmental, food security and public health challenges. Systematics has an important role to play in both the theoretical and applied disciplines of invasion biology (Gotzek et al. 2012; Le Roux and Wieczorek 2009). Although biological invasion is most closely associated with the recent range expansions of species during the Anthropocene, the dispersal of colonist taxa into novel ecosystems is as old as life itself. Study of contemporary invasion ecology and its evolutionary consequences informs a deeper understanding of prehistoric patterns and processes. Correspondingly, study of ecological and evolutionary impacts of ancient colonization events gives historical context to contemporary invasions. Systematics can help bridge this gap separating invasion biology from biodiversity science by advancing integrative theories such as taxon cycles (Economo and Sarnat 2012; Ricklefs and Bermingham 2002). Systematics is also critical to the success of invasive species management. Pest screening, early detection programs and monitoring efficacy all depend on accurate, species-level identifications. Obtaining high-confidence identifications is particularly difficult for hyper-diverse groups such as insects. The few taxonomic resources that exist for insect identification are too often dated, regional, poorly illustrated, and inaccessible to non-specialists.

Invasive species are among the most significant drivers of global change, and few invaders impact terrestrial ecosystems more than ants (Lach and Hooper-Bùi 2009). Of the approximately 15,000 described ants species, more than 100 have established populations outside of their native ranges (McGlynn 1999). Although invasive ants are economically costly in both urban and agricultural areas, the most serious consequences of their introduction may be ecological. Invasive ants can greatly modify ecosystems by reducing native ant diversity, displacing other arthropods, negatively impacting vertebrate populations, and disrupting ant-plant mutualisms (Suarez et al. 2009).

A small subset of introduced ants have become highly destructive invaders, five of which are currently listed among the world's 100 worst invasive species (Lowe et al. 2000). Unfortunately, detection of non-native ants is hampered by the taxonomic

specialization required for accurate species identification of these tiny and overwhelmingly diverse insects. Most of the scientists responsible for identifying ant specimens for pest screening, early-detection programs and monitoring initiatives are not trained ant taxonomists. Although advances in specimen imaging, interactive keys and online resources are welcome developments, increasing the taxonomic capacity for identifying invasive, introduced and commonly intercepted ant species remains a challenge (Sarnat 2011).

Among the world's 100 worst invasive species (Lowe et al. 2000) is the cosmopolitan and highly destructive *Pheidole megacephala* (Fabricius), known commonly as the big-headed ant. Accurate identification of *P. megacephala* is imperative for the success of screening, management and eradication programs designed to protect native ecosystems from harmful impacts. Many non-specialists – and many myrmecologists – have confused other species of *Pheidole* with *P. megacephala* (Wetterer, 2012). This is not surprising. *Pheidole* (Formicidae: Myrmicinae) is arguably the most speciose monophyletic ant genus in the world, with over 1,000 extant valid species, 138 valid subspecies (Bolton 2014) and hundreds of undescribed species. Accurate identification of *Pheidole* species is especially difficult because of their taxonomic diversity, dimorphic worker caste, and lack of taxonomic resources. The term '*Pheidole* sp.' is ubiquitous across ecological and biodiversity publications, including many that focus on tramp ants (e.g. Passera 1994). Recent revisions of *Pheidole* (Eguchi 2001b; 2004b; 2008; Eguchi et al. 2007; Fischer and Fisher 2013; Fischer et al. 2012; Longino 2009; Longino and Cox 2009; Sarnat 2008; Wilson 2003) have advanced the taxonomy of this difficult group. Even at the pace of these past decades, it will be generations before modern identification resources will be available for the majority of known species.

Identification resources for diagnosing the world's 14 most invasive *Pheidole* species are presented here (Table 1). These resources include a fully illustrated key, specimen photographs and distribution maps, in addition to sections on taxonomic history, taxonomic diagnoses, biology, and risk statements. The results of this work will facilitate identification of pest species, determination of climatic and habitat requirements, discovery of pest origins, horizon scanning, and assessment of invasion pathways.

This analysis of the world's introduced *Pheidole* indicates that two of the most widespread tramp species, *P. indica* Mayr and *P. teneriffana* Forel, each the subject of considerable research and attention, are actually conspecific. This underscores the importance of systematics in understanding biodiversity dynamics in the Anthropocene.

Defining invasiveness

Biological invasion is a process that is most simply described by successive stages of transport, introduction, establishment and spread (Vermeij 1996). Quantifying invasiveness is a difficult task, but one made easier by the unified framework for biological invasion proposed by Blackburn et al. (2011). We incorporate *Pheidole* taxa into this framework in an effort to advance comparative invasion biology, but acknowledge

Table 1. Species of *Pheidole* recorded as established outside of their native bioregion. The clade or species group to which each species belongs is listed and defined by the given authority. Clade names are informal designations and are given to convey broad evolutionary relationships among the species. Asterisks (*) note clade designations that are presumed based on morphological similarity.

Species	Clade/Group	Native bioregion	Source
P. anastasii Emery	*punctatissima* clade	Neotropics	(Economo et al. 2015, unpublished data; Moreau 2008)
P. bilimeki Mayr	*punctatissima* clade	Neotropics	(Economo et al. 2015, unpublished data ; Moreau 2008) (as *P. floridana*)
P. fervens Smith, F.	*fervens* clade	Indoaustralia	(Economo et al. 2015)
P. flavens Roger	*flavens*-complex	Neotropics	(Economo et al. 2015; Moreau 2008)
P. indica Mayr	*fervens* clade	Indoaustralia	(Economo et al. 2015, unpublished data)
P. megacephala (Fabricius)	*megacephala* group	Afrotropics	(Economo et al. 2015)
P. navigans Forel	*flavens*-complex	Neotropics	Unpublished data (see discussion under species account)
P. noda Smith, F.	*noda* clade	Indoaustralian	(Economo et al. 2015)
P. obscurithorax Naves	*fallax* clade	Neotropics	(Economo et al. 2015; Moreau 2008)
P. parva Mayr	*parva* clade	Indoaustralia /Indomalaya	(Economo et al. 2015)
P. proxima Mayr	**ampla* group	Indoaustralia (Australia)	–
P. punctatissima Mayr	*punctatissima* clade	Neotropics	(Economo et al. 2015, unpublished data)
P. rugosula Forel	**variabilis* clade	Indoaustralia (Australia)	(Economo et al. 2015)
P. vigilans (Smith, F.)	undefined	Indoaustralia (Australia)	–

that these categories fail to convey the idiosyncrasies of each lineage's invasion history. Separating native range from introduced range is similarly problematic. It is likely that all the treated species are expanding their range within their native biogeographical region as the result of human activity and global environmental change. We therefore define introduced populations strictly as those occurring beyond the lineage's native biogeographic realm.

Following the Blackburn et al. (2011) framework, we assign four *Pheidole* lineages to category 'C0' (individuals released into the wild in location where introduced, but incapable of surviving for a significant period) (Table 2). *Pheidole noda* fits this category, as it is recorded as being introduced only in European greenhouses and is not known to have established permanent populations outside its native range in Asia. The other three species we assigned to the 'C0' category all belong to the Mesoamerican *P. punctatissima* clade. All three have been reported as occurring indoors beyond their native bioregion. Of these, *P. bilimeki* is the most widespread and maintains established reproducing outdoor populations in the southern United States. While it can be argued that these northern populations resulted from human-mediated dispersal, they remain contiguous with putatively native Mesoamerican populations, thus we refrain from defining them as introduced.

Nine lineages are assigned to category 'D2' (individuals surviving in the wild in locations where introduced, with reproduction occurring, and population self-sustaining).

Table 2. Biological characteristics of introduced *Pheidole* species arranged by species name. Sizes (head width measured in mm) are the same as the observed values reported in the species accounts. Invasiveness codes refer to Blackburn et al. (2011). Asterisks indicate name used in reference is considered here to be either a junior synonym or misapplication. References listed: (1) Birkemoe and Aak 2008, (2) Longino and Cox 2009, (3) Naves 1985, (4) Wilson 2003, (5) Morrison 1996, (6) Passera 1994, (7) Reimer 1994, (8) Martínez 1996, (9) Chen et al. 2011, (10) Wilson and Taylor 1967, (11) Boer and Vierbergen 2008, (12) Sarnat and Economo 2012, (13) Longino 2014, (14) Martínez 1992, (15) Fischer and Fisher 2013, (16) Hölldobler and Wilson 1990, (17) Hoffmann 1998, (18) Delabie et al. 1995, (19) Yamamoto et al. 2009, (20) Yamawo et al. 2012, (21) King and Tschinkel 2007, (22) Storz and Tschinkel 2004, (23) Man and Lee 2012, (24) Green and Gunawardana 2006, (25) Berry et al. 1997, (26) Harris et al. 2005, (27) Wilson 1987, (28) Terayama et al., (29) Yamane et al.

Species	Size of major (HW)	Size of minor (HW)	Gyny	Colony structure	Colony foundation	Colony size	Indoor pest	Forages on or nests in vegetation	Invasiveness
P. anastasii	0.83–1.05	0.38–0.50	monogynous [1]	polydomous [2]	–	–	yes [1, 2]	yes [2]	C0
P. bilimeki	0.75–1.04	0.42–0.52	monogynous [1, 3*, 4*]	polydomous [4*]	dependent [3*]	600–4000 [3*, 4*, 27*]	yes [1, 2]	yes [2]	C0
P. fervens	1.13–1.44	0.52–0.63	polygynous [5-7]	polydomous, unicolonial [7, 8]	–	ca. 1000 [9]	yes [10, 11]	yes [12]	D2
P. flavens	0.68–0.83	0.34–0.45	–	–	–	2000+[4]	no	yes [13]	D2
P. indica	1.32–1.74	0.50–0.65	polygynous [28]	polydomous [14]	dependent [14]	500–1000	no	yes [15]	D2
P. megacephala	1.10–1.54	0.50–0.61	polygynous [16]	unicolonial [17]	dependent [17]	10,000+ (?)	yes	yes [11, 18]	E
P. navigans	0.84–0.88	0.40–0.45	monogynous	monodomous [3*]	dependent [3*]	600+[3*]	no	–	D2
P. noda	1.58–1.82	0.57–0.66	polygynous (?) [19, 28]	–	dependent (?) [19]	3000 [28]	no	yes [20]	D2
P. obscurithorax	1.47–1.70	0.60–0.67	monogynous [21]	monodomous [21, 22]	–	~10,000 [21]	no	–	D2
P. parva	0.85–0.92	0.39–0.50	–	–	–	–	yes [23]	yes [15]	D2
P. proxima	0.95–1.05	0.46	–	monodomous [24]	–	–	yes [25]	–	D2
P. punctatissima	0.86–1.06	0.44–0.50	–	–	–	–	yes [2]	yes [2]	C0
P. rugosula	0.88	0.45	–	–	–	–	yes [25, 26]	yes [25]	D2
P. vigilans	1.30	0.55	–	–	–	–	yes [25]	–	D2

The least invasive of these are likely the three Australian species (*P. proxima*, *P. rugosula*, *P. vigilans*) that have established persistent populations in New Zealand, but have not been reported from elsewhere (although *P. vigilans* is reported as introduced in Western Australia). Only *P. rugosula* has been listed in examined interception records, and that was a single New Zealand record from Australia (Ward et al. 2006). *Pheidole parva*, *P. fervens* and *P. indica* are all from the Indomalayan bioregion and have managed to establish reproducing outdoor populations beyond their native range. Although the propagule pressure of these species is relatively strong, as evidenced by their frequent interception at ports of entry (Table 3), the introduced populations of all three tend to be small and relatively localized. *Pheidole obscurithorax* and the *P. flavens*-complex (including *P. flavens* and *P. navigans*) are both Neotropical lineages that have established persistent and actively spreading populations in the southern United States. The former is documented as causing a greater ecological impact, but the latter is more widespread and appears to have greater propagule pressure, as evidenced by high numbers of interception records and establishment of at least temporary populations in California and several Pacific Islands.

Pheidole megacephala is the only species assigned to category 'E' (fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence). The vast majority of introduced *Pheidole* specimen and occurrence records are attributed to *P. megacephala*. It is the most geographically widespread species in the entire genus and its impact on native ecosystems and agriculture are extensively documented.

Characteristics of introduced *Pheidole*

General characteristics and characters associated with invasion success

All *Pheidole* species treated here have a dimorphic worker caste. Their colonies typically have hundreds to thousands of workers. They are all generalist foragers that feed on some combination of dead arthropods, living arthropods, seeds and human foodstuffs. The aforementioned characteristics are shared by nearly all of their congeners, however, and cannot be considered promoters of invasion success among *Pheidole*. There is a suite of biological characters that are broadly associated with introduced populations of invasive ants, including unicoloniality and omnivory (Holway et al. 2002). Unicoloniality – defined as the ability to form expansive and polygynous (multiple queened) supercolonies – has only been observed in *P. megacephala* (Table 1). Only three other species (*P. fervens*, *P. indica* and *P. noda*) are reported to be at least facultatively polygynous. Four species besides *P. megacephala* are reported to exhibit polydomous populations (*P. anastasii*, *P. bilimeki*, *P. fervens* and *P. indica*).

One interesting pattern deserving further study is the propensity of introduced *Pheidole* to use vegetation for either foraging or nesting (Table 1). *Pheidole* species, in general, are most strongly associated with the ground, and exploitation of the vegetative or arboreal strata is relatively uncommon. One potential reason that foraging

Table 3. Specimen and literature records of *Pheidole* species intercepted at international ports of entry. The original determinations for specimens included here are available on Antweb.org. [1] Antweb.org (Available from http://www.antweb.org. Accessed 20 March 2015); [2] Boer and Vierbergen 2008; [3] Boer 2015; [4] Ward et al. 2006; [5] Wheeler 1934.

Species	Taxonomic notes	Unique collections	Native bioregion	Bioregion of interception	Record source
P. bilimeki Mayr		4	Neotropical	Nearctic	[1]
P. cf. *bilimeki*		3	Neotropical	Nearctic	[1]
P. dossena Wilson		1	Neotropical	Holarctic	[2]
P. fervens Smith, F.		235	Indomalaya	Australasia	[4]
P. fervens Smith, F.		5	Indomalaya	Nearctic	[1]
P. fervens Smith, F.			Indomalaya	Indoaustralia	[5]
P. fervens Smith, F.			Indomalaya	Holarctic	[3]
P. fervida Smith, F.		2	Indomalaya	Nearctic	[1]
P. flavens Roger		2	Neotropical	Nearctic	[1]
P. flavens-complex		6	Neotropical	Nearctic	[1]
P. harrisonfordi Wilson			Neotropical	Holarctic	[3]
P. hyatti Emery			Nearctic	Indoaustralia	[5]
P. indica Mayr		1	Indomalaya	Australasia	[4]
P. indica Mayr		8	Indomalaya	Nearctic	[1]
P. indica Mayr			Indomalaya	Holarctic	[3]
P. laticornis Wilson			Neotropical	Holarctic	[3]
P. megacephala (Fabricius)		890	Afrotropical	Indoaustralia	[5]
P. megacephala (Fabricius)		11	Afrotropical	Nearctic	[1]
P. noda Smith, F.		2	Indomalaya	Australasia	[1]
P. noda Smith, F.		2	Indomalaya	Nearctic	[1]
P. noda Smith, F.			Indomalaya	Indoaustralia	[5]
P. nr. *colpigaleata*		1	Indomalaya	Nearctic	[1]
P. nr. *mantilla*		2	Neotropical	Nearctic	[1]
P. nr. *marcidula*		1	Neotropical	Nearctic	[1]
P. oceanica Mayr		< 5	Australasian	Australasia	[4]
P. pallidula (Nylander)		2	Holarctic	Nearctic	[1]
P. pallidula (Nylander)			Holarctic	Holarctic	[3]
P. parva Mayr		1	Indomalaya	Nearctic	[1]
P. cf. *parva*		1	Indomalaya	Nearctic	[1]
P. perpusilla Emery		2	Neotropical	Nearctic	[1]
P. cf. *pubiventris*		1	Neotropical	Nearctic	[1]
P. punctatissima Mayr			Neotropical	Holarctic	[3]
P. cf. *punctatissima*		12	Neotropical	Nearctic	[1]
P. cf. *punctatissima*			Neotropical	Indoaustralia	[5]
P. punctulata Mayr		1	Afrotropical	Nearctic	[1]
P. radoszkowskii Mayr			Neotropical	Holarctic	[3]
P. rugosula Forel		1	Australasia	Australasia	[4]
P. sexspinosa Mayr		1	Australasian	Australasia	[4]

Species	Taxonomic notes	Unique collections	Native bioregion	Bioregion of interception	Record source
P. sp. mg126	nr. *longispinosa*	1	Afrotropical	Nearctic	[1]
P. sp. POE fallax group-a	*fallax* group	1	Neotropical	Nearctic	[1]
P. sp. POE pilifera group-a	*pilifera* group	1	Neotropical	Nearctic	[1]
P. sp. POE dilligens group-a	*dilligens* group Wilson	1	Neotropical	Nearctic	[1]
P. sp. POE-F	*megacephala* group	1	Afrotropical	Nearctic	[1]
P. sp. POE-G	*megacephala* group	1	Afrotropical	Nearctic	[1]
P. sp. POE-H	*flavens* group Wilson	1	Neotropical	Nearctic	[1]
P. sp. POE-I	*flavens* group Wilson	1	Neotropical	Nearctic	[1]
P. spec. 1				Holarctic	[3]
P. spec. 2				Holarctic	[3]
P. subarmata Mayr			Neotropical	Holarctic	[3]
P. susannae Forel		2-5	Neotropical	Holarctic	[2]
P. susannae Forel		1	Neotropical	Nearctic	[1]
P. umbonata		< 5	Indoaustralia	Australasia	[4]

and nesting in vegetation is overrepresented among the introduced species is that, if quarantine interception records are any indicator, human-mediated dispersal events are predominately associated with commercial trade of plants or plant material (Suarez et al. 2005; Ward et al. 2006). Furthermore, none of the introduced *Pheidole* species are strictly arboreal, and their capacity for occurring on vegetation reflects the type of broad habitat tolerances required for successful establishment.

Taxonomic patterns

Although referring to each of the included lineages as a discrete biological species is convenient, there are at least some instances – including the *P. flavens* species complex and *P. megacephala* complex – that defy such neat classification. A disproportionate number of synonyms and infraspecific names in the genus *Pheidole* belong to the lineages treated here, and this pattern holds true across the Formicidae. We offer several explanations for this pattern. The first is attributed to nomenclatural artifact. Taxonomists unfamiliar with distant faunas and working outside of a global context often described introduced populations as new species. The second explanation for the myriad names associated with invasive species reflects a truly biological pattern: *invasive populations tend to be derived from geographically widespread and morphologically variable lineages*. Geographically widespread species have greater propagule pressure because they are broadly exposed to opportunities for human-mediated dispersal (Theoharides and Dukes 2007). The taxonomic work undertaken during this study suggests the phenotypic diversity of many of these introduced lineages is only a thumbnail of a much broader morphological spectrum observed across their respective native ranges.

Morphological patterns

The 14 *Pheidole* species treated here do not adhere to a particular morphotype, especially when phylogenetic relationship is corrected for. Although none of the species occupy the extreme ends of the genera's size spectrum, they do range from small to large. None of these species exhibit aberrant or specialized morphology, such as spinescence. (Although not treated in this review, the *P. sexspinosa* complex is a spinescent lineage that is considered a tramp ant around the Pacific and has likely increased its range with the help of human-mediated transport.)

Phylogenetic patterns

Invasive *Pheidole* species are not evenly dispersed across the phylogeny (Economo et al. 2015). Rather, a few lineages tend to be responsible for spawning successful invaders. In particular, the *punctatissima* clade, *flavens* clade, *fervens* clade have each given rise to multiple introduced species (Table 1). The most parsimonious explanation for this pattern is that at least some promoters of invasion success are plesiomorphic traits inherited from common ancestors. More generally, all of the known clades to which invasive *Pheidole* belong can broadly be considered tramp groups composed of species that exhibit relatively wide geographic ranges, few habitat constraints, and high infraspecific variability.

Biogeographical patterns

Strong biogeographical patterns among introduced *Pheidole* are difficult to find. One pattern shared by all introduced *Pheidole* is that they invariably occupy low elevation habitat. This is not surprising, as connectivity is much greater between lower elevation sites (e.g. coastlines and shipping ports) than among higher elevation sites (e.g. montane forests). The invasive *Pheidole* invariably come from tropical and subtropical lineages, but this pattern broadly reflects the richness patterns across the entire genus (Economo et al. 2015). The Neotropical, Afrotropical and Indomalayan regions have all produced *Pheidole* lineages that have invaded other bioregions. Australia is nominally home to three invasive *Pheidole* species, but the introduced populations of all three are restricted to the island of New Zealand (in addition to Lord Howe Island in one instance) and are not likely capable of invading another continental system. Although the common recipient of non-native *Pheidole* introductions, and ant introduction in general (McGlynn 1999), Oceania is the only tropical bioregion from which a successful invader has not evolved. *Pheidole sexspinosa* Mayr and possibly *P. oceanica* Mayr are native to Oceania and widely considered tramp species, but thus far there is no evidence that either has ever successfully established outside the Pacific.

Methods

Taxon selection

The taxa treated here represent all *Pheidole* species known to have been introduced outside of their native biogeographic region. These taxa span the spectrum from species that have become naturalized across the globe (such as the highly invasive *P. megacephala*) to species known only to have established temporary indoor populations beyond their native region (such as *P. noda*). We do not include species that are repeatedly intercepted by quarantine but are never recorded as establishing non-native populations. The species included here represent the vast majority of published *Pheidole* quarantine interceptions records (Table 3), and have proven the most capable among their congeners of establishing beyond their native range.

In addition to the quarantine intercepts, there are many synanthropic tramp species of *Pheidole* that are likely expanding across their native bioregion with the inadvertent assistance of human exploration and commerce. This is particularly true in Oceania, where species such as *P. oceanica*, *P. umbonata* Mayr and *P. sexspinosa* are widespread across the entire region. However, we were unable to confirm any records of their introduction outside of Oceania. While excluded from our current study, we advise readers to be aware of these and similarly widespread species. Their expansive ranges increase the propagule pressure for anthropogenic dispersal, and their high tolerance for habitat disturbance pre-adapts them for establishing beach-head populations outside their native ranges.

Occurrence and specimen records

Our biogeographic data are taken from the Global Ant Biodiversity Informatics (GABI) project, a database consolidating literature, museum, and biodiversity database records on ant species distributions (Suppl. material 1). Each literature record for an occurrence outside the putative native range was examined by reviewing the primary reference and evaluating it for veracity and accuracy. Specimen records included in the GABI database were similarly evaluated. Literature records considered to be derivative (e.g. checklists referring to a previously published record) and records from online checklists were excluded unless the primary reference or specimen record was confirmed. A confirmed literature record in the context of this study means only that the valid name or a synonym was verified as appearing in the text, and does not imply that the species identification was accurate. We verified a total of 14,162 occurrence records.

Locality references of literature records were converted to coordinates where possible. First, all variables that described the location of a record were merged into a single string that contained all descriptive information about a location. Unique values were extracted from these strings resulting in a total of 3,803 unique locations. Locations that referred to large areas such countries or states (n=221)

were removed from these 3,803 locations. All of the remaining unique locations were then converted to coordinates using the Bing geocoding API (Microsoft 2015). From these unique locations 1,265 were geocoded with a tolerable precision (+/- 10 km) for a global distribution study. These geocoded locations were manually checked for inconsistencies. Of the remaining 2,538 locations the coordinates given in the database were assigned as the correct coordinates when available (n=1,349). This resulted in a total of 968 locations that lacked coordinates. These records contained problematic locality names and were geocoded manually by correcting the locality name and using the GEOLocate web application (Rios and Bart 2010). Of these 968 records 83 were incorrect and could not be geocoded, and 210 did not refer to a point location (country or state).

Illustrations

Original specimen images taken by the authors were taken using the Auto-Montage software package (Syncroscopy) in combination with a JVC KY-F7U digital camera mounted on a Leica MZ16 dissecting scope, and the software package Helicon Focus in combination with a Leica DFC450 digital camera mounted on a Leica M205C dissecting scope. Vector artwork used to illustrate character states referred to in the taxonomic key and species diagnoses were made in Adobe Illustrator by tracing specimen photographs. All specimen images are available from Antweb.org and can be searched for using the specimen identifier. All vector illustrations are available from the 'Introduced *Pheidole* taxonomic characters' media gallery on Antkey.org (http://antkey.org/en/gallery?f[0]=im_field_smg_galleries%3A33508).

List of abbreviations of museum collections

The abbreviations follow Evenhuis (2009) and are used in the text in place of the full museum collection name. Type material from these collections examined by the authors is noted in the species accounts.

ANIC Australian National Insect Collection (Canberra, Australia)
BMNH The Natural History Museum (London, United Kingdom)
CASC California Academy of Sciences (San Francisco, California, USA)
MCSN Museo Civico di Storia Naturale "Giacomo Doria" (Genoa, Italy)
MCZC Harvard Museum of Comparative Zoology (Cambridge, Massachusetts, USA)
MHNG Natural History Museum of Geneva (Geneva, Switzerland)
MNHN Muséum National d'Histoire Naturelle (Paris, France)
NHMB Naturhistorisches Museum (Basel, Switzerland)
NHMW Naturhistorisches Museum Wien (Vienna, Austria)
USNM United States National Museum of Natural History (Washington D.C., USA)

Measurements

Measurements reported here include those taken and reported by various researchers. Original measurements taken by the authors were made with a stereo microscope at 40× magnification using a dual-axis stage micrometer wired to digital readouts. Morphometric measurements were recorded in thousandths of millimetres, but are reported here to the nearest hundredth as a range from minimum to maximum across all measured specimens. Specimens for measurements were chosen to reflect potential morphological variation across the full geographic range. The number of specimens from which measurements were taken for a given caste is referred to by *n*. Measurements for Neotropical *Pheidole* include data supplied by John Longino. Measurements for Old World *Pheidole* include values reported in previously published studies (Eguchi 2001a; 2004b; 2008; Eguchi et al. 2007; Fischer and Fisher 2013).

EL Eye Length (mm): Maximum diameter of eye measured in profile view.

HL Head Length (mm): Maximum distance from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin of the head, measured in full-face view; in majors, measured from midpoint of tangent between anteriormost position of clypeus to midpoint of tangent between posteriormost projection of the vertex.

HW Head Width (mm): Measured at widest point of the head, in full-face view behind eye level.

SL Scape Length (mm): Maximum scape length, excluding basal condyle and neck.

CI Cephalic Index: HW / HL × 100.

SI Scape Index: SL / HW × 100.

Identification keys to introduced species of *Pheidole*

Readers are warned that there are hundreds of native *Pheidole* species that are not treated in the following keys. The keys are most useful for diagnosing *Pheidole* specimens intercepted at quarantine facilities, collected from regions with depauperate native *Pheidole* diversity (such as small islands), and in highly disturbed habitats such as urban areas. Even in urban areas, however, there remains considerable likelihood that native *Pheidole* species occur that are not treated here, and readers are cautioned to use these keys judiciously.

Lucid3 Key

An interactive and fully illustrated Lucid3 key that includes all *Pheidole* species treated in this study is available from the website Antkey.org (Sarnat and Suarez 2012) at the following URL: http://antkey.org/en/content/key. To use this key for introduced *Phei-*

dole identification, users are advised to first filter by the genus *Pheidole*, then proceed by using the 'best' and 'next best' functions. Users are referred to documentation and video tutorials on the webpage for additional instructions and best practices.

Major workers only

1 Postpetiole swollen relative to petiole; either with a posterodorsal and anteroventral bulge (Fig. 1) or with a single dorsal bulge (Fig. 2) **2**

– Postpetiole not swollen relative to petiole (Fig. 3) **3**

2 Postpetiole with a posterodorsal (Fig. 1a) and anteroventral (Fig. 1b) bulge. Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Head heart-shaped (Fig. 6); dorsal surface smooth, glossy and entirely lacking strong rugoreticulate sculpture ..... ***megacephala***

– Postpetiole forming a high dorsally bulging dome that is tallest at midpoint (Fig. 2a); ventral margin flat to very weakly convex (Fig. 2b). Promesonotum in profile with two convexities (Fig. 5), the large anterior dome in addition to a distinct prominence on the posterior slope. Head subquadrate (Fig. 7); dorsal surface covered in strong longitudinal rugae that form a reticulated network laterally and posteriorly (Fig. 8) ..... ***noda***

3 Promesonotum in profile with two convexities (Fig. 5), the large anterior dome in addition to a distinct mound or prominence on the posterior slope. Relatively large species with long limbs (HW major > 1.10 mm, HW minor > 0.50 mm). Head with strong rugoreticulate sculpture at least on posterolateral lobes (Fig. 8) **4**

– Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope (sometimes with a weak protuberance or inconspicuous mound). Size and relative limb length variable. Posterolateral lobes variably sculptured including glossy (Fig. 9), rugose (Fig. 10) and punctate (Fig. 11); if strongly rugoreticulate on posterolateral lobes then small species (HW < 1.00 mm) **6**

4 Head almost entirely covered by network of intersecting rugae (Fig. 12a), lacking long, well-organized and parallel longitudinal rugae on the frons (Fig. 12b). Frontal carinae indistinct, quickly becoming integrated into dense rugoreticulum that covers the entire face. Antennal scrobes entirely lacking. Antennal insertions surrounded by deeply excavated pits (Fig. 12c). Head sometimes a lighter reddish brown than the mesosoma ..... ***obscurithorax***

– Head rugoreticulate on posterolateral lobes and laterad of frontal carinae (Fig. 13a), but frons dominated by long, well-organized and parallel longitudinal rugae (Fig. 13b). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (Fig. 13c). Antennal insertions not surrounded by deeply excavated pits. Head usually a similar shade as the mesosoma **5**

5 Frontal carinae relatively longer, extend 4/5 distance of head before terminating (Fig. 14). Promesonotal prominence flatter, less pronounced (Fig. 63a). Propodeal spine weaker, narrower at base, weakly downcurved at apex (Fig. 63b).....***fervens***

– Frontal carinae relatively shorter, extend 3/4 distance of head before terminating (Fig. 15). Promesonotal prominence rounder, more pronounced (Fig. 64a). Propodeal spine stouter, broader at base, relatively straight (Fig. 64b) ..... ***indica***

6 Posterolateral lobes lacking sculpture (including foveolate ground sculpture, carinae and rugae) posterior to maximum extent of antennal scapes in repose (Fig. 9). Head glossy, lacking foveolate ground sculpture. Promesonotal dorsum glossy, lacking foveolate ground sculpture or striae (Fig. 23) **7**

– Posterolateral lobes with foveolate ground sculpture (Fig. 11), carinae (Fig. 12) or rugae (Fig. 12) distinctly present posterior to maximum extent of antennal scape (if absent then remainder of face is strongly foveolate). Promesonotal dorsum with foveolate ground sculpture, striae or both **8**

7 Petiolar node strongly punctate (Fig. 16). Metapleuron with moderate rugulae and some weak punctation (Fig. 16). Hypostomal bridge with a small median tooth in addition to a pair of larger inner teeth (Fig. 18) .....***proxima***

– Petiolar node mostly glossy (Fig. 17), not covered by punctate sculpture. Metapleuron almost completely glossy with strongly reduced carinulae and lacking punctation (Fig. 17). Hypostomal bridge with two well-developed inner teeth but lacking a median tooth (Fig. 19)..... ***vigilans***

8 Promesonotal dorsum glossy with thin but distinct subparallel striae running oblique to the longitudinal midline (Fig. 20). Head with distinct parallel rugae extending from frontal lobes posterior to apices of frontal carinae. Shorter lengths of rugae present across entire posterior region of head and extending to posterior margin in full-face view (Fig. 24). ..... ***rugosula***

– Promesonotal dorsum with various sculpture patterns including transversely striate (Fig. 21), longitudinally striate to rugoreticulate (Fig. 22), and lacking striae (Fig. 23); but never with subparallel striae running oblique to the longitudinal midline. Head variously sculptured, but if sculpture reaches posterior head margin in full-face view it is either strongly rugoreticulate (Fig. 26) or foveolate (Fig. 11).....**9**

9 Posterolateral lobes, including posterior head margin, strongly rugoreticulate (Fig. 26). Promesonotum in dorsal view strongly transverse with strongly projecting shoulders (Fig. 28). Promesonotal dorsum rugoreticulate with distinct long longitudinal striae in addition to shorter sections of transverse and intersecting striae (Fig. 22)..... ***parva***

– Posterolateral lobes variously sculptured, but posterior head margin always free of distinct rugae (Fig. 25) or rugoreticulum (Fig. 27). Promesonotum in dorsal view less transverse with weakly projecting shoulders in dorsal view (Fig. 29). Promesonotal dorsum variously sculptured (including transversely striate (Fig. 21), foveolate or both), but never rugoreticulate with distinct long longitudinal striae **10**

10 Gaster with entire first tergite glossy (Fig. 32). Postpetiole relatively narrow (Fig. 30); distinctly less than 2× petiolar width in dorsal view. Promesonotal dorsum usually with distinct transverse striae (Fig. 21), but sometimes lacking distinct striae. Posterolateral lobes variably sculptured. (*P. flavens*-complex) **11**

– Gaster with at least anterior 1/3 of first tergite matte (Fig. 33). Postpetiole relatively broad; distinctly more than 2× petiolar width in dorsal view (Fig. 31). Promesonotal dorsum usually foveolate and never with distinct transverse striae. Head often entirely foveolate (Fig. 11), but portions of posterolateral lobes can be glossy. Posterolateral lobes never with distinct rugae **12**

11 Antennal scrobe distinct, narrow and shallow, but capable of receiving the entire antennal scape in repose (Fig. 71a); bordered by strong, unbroken frontal carina mesially (Fig. 71b); depression marked by a continuous smooth surface entirely (or nearly entirely) uninterrupted by rugulae. The rugulae of the frons extend to approximately an eye's length distance from the posterior head margin. Promesonotal dorsum with distinct transverse striae (Fig. 21) ..... ***navigans***

– Antennal scrobe broad, ill-defined, incapable of receiving the entire antennal scape in repose (Fig. 72a); bordered by relatively weak and interrupted frontal carina mesially (Fig. 72b); depression opaque and strongly punctate. The rugulae of the frons of variable length but never reach posterior head margin. Promesonotal dorsum variable, but if transverse striae are present they rarely reach across entire surface ..... ***flavens***

12 Head bicolored, the yellowish posterior two-thirds contrasting with the darker brown anterior third and rest of body (Fig. 34)..... ***punctatissima***

– Head uniform in color (Fig. 35), from yellow to reddish brown; same color as associated minor workers **13**

13 Color usually yellow. Head width sometimes wider (HW 0.74–1.16 mm). Prefers understory habitat. Typically nests arboreally in live plant cavities, under bark, and in dead sticks and branches on or above forest floor ..... ***anastasii***

– Color usually red brown. Head width sometimes narrower (HW 0.71–1.07 mm). Prefers open, disturbed habitat. Generalist nest microhabitats, including under stones and dead wood. ..... ***bilimeki***

Minor workers only

1 Head predominantly glossy (Fig. 36), lacking punctation and or rugae above eye level **2**

– Head conspicuously punctate (Fig. 37) and/or rugose (Fig. 38) above eye level.. **8**

2 Postpetiole swollen relative to petiole; either with a posterodorsal and anteroventral bulge (Fig. 1) or with a single dorsal bulge (Fig. 2)..... **3**

– Postpetiole not swollen relative to petiole (Fig. 3) **4**

3 Postpetiole with a posterodorsal (Fig. 1a) and anteroventral (Fig. 1b) bulge. Antennal scapes surpass posterior head margin by approximately same length as eye

(Fig. 40). Promesonotum in profile forming a single dome, lacking a distinct mound or prominence on the posterior slope (Fig. 42) ..... ***megacephala***

– Postpetiole forming a high dorsally bulging dome that is tallest at midpoint; ventral margin flat to very weakly convex (Fig. 2). Antennal scapes surpass posterior head margin by approximately twice the eye length (Fig. 39). Promesonotum in profile with two convexities, the large anterior dome (Fig. 44a) in addition to a distinct prominence on the posterior slope (Fig. 44b) ..... ***noda***

4 Promesonotum in profile with two convexities, the large anterior dome (Fig. 43a) in addition to a distinct prominence on the posterior slope (Fig. 43b). Antennal scapes relatively long, surpassing posterior head margin by a distance equal (Fig. 40) to or greater than (Fig. 39) eye length. Posterior head margin strongly convex (Fig. 44) to weakly convex (Fig. 45) in full-face view. Color variable.....**5**

– Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Antennal scapes relatively short (Fig. 41), either failing to surpass posterior head margin, or surpassing it by less than the distance of eye length. Posterior head margin weakly convex (Fig. 45) to weakly concave (Fig. 46) in full-face view. Color yellow to brown.....**7**

5 Posterior margin strongly convex in full-face view such that the head outline forms a single unbroken curve from eye to eye (Fig. 44). Petiole and postpetiole strongly sculptured laterally (Fig. 47). Antennal scapes extremely long, surpassing posterior head margin by more than 2× eye length (Fig. 39) .... ***obscurithorax***

– Posterior head margin weakly convex to flat in full-face view (Fig. 45). Petiole and postpetiole glossy to very weakly sculptured laterally (Fig. 48). Antennal scapes long, but not surpassing the posterior head margin by more than 2× eye length **6**

6 Promesonotal prominence more flat (Fig. 49a). Metanotal depression deeper (Fig. 49b). Eye relatively small, eye length distinctly less than length of antennal segment 10 (Fig. 65) ..... ***fervens***

– Promesonotal prominence more convex (Fig. 50a). Metanotal depression shallower (Fig. 50b). Eye relatively large, eye length subequal to length of antennal segment 10 (Fig. 66) ..... ***indica***

7 Antennal scapes surpass posterior head margin by approximate distance of eye length (Fig. 40). Mesopleuron entirely glossy (Fig. 51a). Propodeal spines weakly produced and dentiform (Fig. 51b). Petiole almost entirely glossy.....***vigilans***

– Antennal scapes reach but do not surpass posterior head margin (Fig. 41). Mesopleuron entirely punctate (Fig. 52a). Propodeal spines moderately produced and spiniform (Fig. 52b). Petiole distinctly sculptured except for apical portion of node..... ***proxima***

8 Head with well-defined, long segments of rugae running longitudinally from below the eyes to the posterior head margin (Fig. 38). Frontal carinae distinct and reaching towards the posterior head margin, although they may occasionally be interrupted (Fig. 38). Punctate ground sculpture present on lateral

surfaces of head and just mesad of the frontal carinae, but median portion of head with a large glossy section (Fig. 38). (Native to Australia).....***rugosula***

– Head, including the area mesad of the frontal carinae, entirely covered by reticulated network of punctures, giving it a dull appearance (Fig. 37); if rugae are present they are generally short segments and mostly restricted to posterior portion of head. Frontal carinae not distinct posterior to eye level.....**9**

9 Gaster with at least anterior 1/3 of first tergite matte (Fig. 33). Hairs on mesosoma stout, stiff, of equal length and arranged in pairs (Fig. 53). Antennal scapes lack standing hairs (Fig. 55); scapes surpass posterior head margin by a distance equal to or greater than eye (Fig. 40).....**10**

– Gaster with entire first tergite glossy (Fig. 32). Hairs on mesosoma fine, flexuous, of unequal length and not arranged in pairs (Fig. 54). Antennal scapes with erect to suberect hairs (Fig. 56); scapes reach posterior head margin but do not surpass it by a distance equal to or greater than eye length (Fig. 41)..... **12**

10 Posterior head margin more broad (Fig. 57). Antennal scapes relatively short (SI 95–108). Color usually brown but occasionally yellow..... ***bilimeki***

– Posterior head margin more narrow (Fig. 58). Antennal scapes relatively longer (SI 103–125). Color variable **11**

11 Color usually clear yellow orange (gray brown in one population on Caribbean coast of Panama). Typically nesting in live plant cavities in wet forest understory ..... ***anastasii***

– Color red brown to nearly black. Typically nesting in open, disturbed habitats..... ***punctatissima***

12 Posterior portion of head with many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (Fig. 59). Antennal scapes do not surpass posterior head margin (Fig. 41) ..... ***parva***

– Posterior portion of head lacking many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (Fig. 60). Antennal scapes often, but not always, surpass posterior head margin; if they do it is usually by a distance less than eye length.....***flavens*** complex

Combined major and minor workers

1 **Major + minor** Postpetiole swollen relative to petiole (Fig. 1, Fig. 2).....**2**

– **Major + minor** Postpetiole not swollen relative to petiole (Fig. 3) **3**

2 **Major + minor** Postpetiole with a posterodorsal (Fig. 1a) and anteroventral (Fig. 1b) bulge. Promesonotum in profile forming a single dome (Fig. 4, major; Fig. 42 minor), lacking a distinct mound or prominence on the posterior slope. **Major** Head heart-shaped (Fig. 6); posterodorsal surface smooth, glossy and entirely lacking strong rugoreticulate sculpture (Fig. 9). **Minor** Antennal scapes surpass posterior head margin by approximately same length as eye (Fig. 40)..... ***megacephala***

– **Major + minor** Postpetiole forming a high dorsally bulging dome that is tallest at midpoint (Fig. 2a); ventral margin flat to very weakly convex (Fig. 2b). Promesonotum in profile with two convexities, the large anterior dome in addition to a distinct mound or prominence on the posterior slope (Fig. 5, major; Fig. 43, minor). **Major** Head subquadrate (Fig. 7); dorsal surface covered in strong longitudinal rugae that form a reticulated network laterally and posteriorly (Fig. 8). **Minor** Antennal scapes surpass posterior head margin by approximately twice eye length (Fig. 39) ..... ***noda***

3 **Major + minor** Promesonotum in profile with two convexities, the large anterior dome in addition to a distinct mound or prominence on the posterior slope (Fig. 5, major; Fig. 43, minor). Relatively large species with long limbs (HW major > 1.10 mm, HW minor > 0.50 mm). **Major** Head with strong rugoreticulate sculpture at least on posterolateral lobes (Fig. 8). **Minor** Head glossy (Fig. 36); sculpture restricted to at most a few arcuate carinae between eye and antennal insertion. Antennal scapes with erect hairs (Fig. 56); scapes surpass posterior head margin by at least a distance equal to or greater than eye length (Fig. 39) **4**

– **Major + minor** Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope (sometimes with a weak protuberance or inconspicuous mound). Size and relative limb length variable. **Major** Head with variable sculpture patterns including glossy (Fig. 36), punctate (Fig. 37) and rugose (Fig. 38); if strongly rugoreticulate on posterolateral lobes then small species (HW < 1.00 mm). **Minor** Head variable in sculpture. Antennal scapes with (Fig. 56) or without (Fig. 55) erect hairs; scapes never surpassing posterior head margin by a distance equal to or greater than eye length **6**

4 **Major** Head almost entirely covered by network of intersecting rugae (Fig. 12a), lacking long, well-organized and parallel longitudinal rugae on the frons (Fig. 12b). Frontal carinae indistinct, quickly becoming integrated into dense rugoreticulum that covers the entire face. Antennal scrobes entirely lacking. Antennal insertions surrounded by deeply excavated pits (Fig. 12c). Head often a lighter reddish brown than the mesosoma. **Minor** Posterior head margin strongly convex in full-face view such that the head outline forms a single unbroken curve from eye to eye (Fig. 44). Petiole and postpetiole strongly sculptured laterally (Fig. 47). Antennal scapes extremely long, surpassing posterior head margin by more than 2× eye length (37) ..... ***obscurithorax***

– **Major** Head rugoreticulate on posterolateral lobes and laterad of frontal carinae (Fig. 13a), but frons dominated by long, well-organized and parallel longitudinal rugae (Fig. 13b). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (Fig. 13c). Antennal insertions not surrounded by deeply excavated pits. Head usually a similar shade as the mesosoma. **Minor** Posterior head margin weakly convex to flat in full-face view (Fig. 45). Petiole

and postpetiole glossy to very weakly sculptured laterally (Fig. 48). Antennal scapes long, but not surpassing the posterior head margin by more than 2× eye length **5**

5 **Major** Frontal carinae relatively longer, extend 4/5 distance of head before terminating (Fig. 14). Promesonotal prominence flatter, less pronounced (Fig. 63a). Propodeal spine weaker, narrower at base, weakly downcurved at apex (Fig. 63b). **Minor** Promesonotal prominence more flat (Fig. 49a). Metanotal depression deeper (Fig. 49b). Eye relatively small, eye length distinctly less than length of antennal segment 10 (Fig. 65)..... ***fervens***

– **Major** Frontal carinae relatively shorter, extend 3/4 distance of head before terminating (Fig. 15). Promesonotal prominence rounder, more pronounced (Fig. 64a). Propodeal spine stouter, broader at base, relatively straight (Fig. 64b). **Minor** Promesonotal prominence more convex (Fig. 50a). Metanotal depression shallower (Fig. 50b). Eye relatively large, eye length subequal to length of antennal segment 10 (Fig. 66)..... ***indica***

6 **Major** Posterolateral lobes lacking sculpture (including foveolate ground sculpture, carinae and rugae) posterior to maximum extent of antennal scapes in repose. Head glossy, lacking foveolate ground sculpture. Promesonotal dorsum glossy, lacking foveolate ground sculpture or striae (Fig. 23). **Minor** Head predominantly glossy, lacking punctation and or rugae above eye level. Promesonotal dorsum also glossy without punctate ground sculpture or striae **7**

– **Major** Posterolateral lobes with foveolate ground sculpture (Fig. 11), carinae or rugae (Fig. 12) distinctly present posterior to maximum extent of antennal scape (if absent then remainder of face is strongly foveolate). Promesonotal dorsum with foveolate ground sculpture, striae or both. **Minor** Head above eye level with punctate ground sculpture (Fig. 37), rugae (Fig. 38) or both. Promesonotal dorsum with foveolate ground sculpture, distinct striae or both but never glossy **8**

7 **Major** Petiolar node strongly punctate (Fig. 16). Metapleuron with moderate rugulae and some weak punctation (Fig. 16). Hypostomal bridge with a small median tooth in addition to a pair of larger inner teeth (Fig. 18). Smaller (HW < 1.0 mm). **Minor** Antennal scapes reach but do not surpass posterior head margin (Fig. 41). Mesopleuron entirely punctate (Fig. 52a). Propodeal spines moderately produced and spiniform (Fig. 52b). Petiole distinctly sculptured except for apical portion of node. Smaller (HW < 0.48 mm) ..... ***proxima***

– **Major** Petiolar node mostly glossy (Fig. 17), not covered by punctate sculpture. Metapleuron almost completely glossy with strongly reduced carinulae and lacking punctation (Fig. 17). Hypostomal bridge with two well-developed inner teeth but lacking a median tooth (Fig. 19). Larger (HW > 1.2 mm). **Minor** Antennal scapes surpass posterior head margin by approximate distance of eye length (Fig. 40). Mesopleuron entirely glossy (Fig. 51a). Pro-

podeal spines weakly produced and dentiform (Fig. 51b). Petiole almost entirely glossy. Larger (HW > 0.52 mm)..... ***vigilans***

8 **Major** Promesonotal dorsum glossy with thin but distinct subparallel striae running oblique to the longitudinal midline (Fig. 20). Head with distinct parallel rugae extending from frontal lobes posterior to apices of frontal carinae. Shorter lengths of rugae present across entire posterior region of head and extending to posterior margin in full-face view (Fig. 24). **Minor** Head with well-defined, long segments of rugae running longitudinally from below the eyes to the posterior head margin (Fig. 38). Frontal carinae distinct and reaching towards the posterior head margin, although they may occasionally be interrupted (Fig. 38). Punctate ground sculpture present on lateral surfaces of head and just mesad of the frontal carinae, but median portion of head with a large glossy section (Fig. 38)..... ***rugosula***

– **Major** Promesonotal dorsum with various sculpture patterns including transversely striate (Fig. 21), longitudinally striate to rugoreticulate (Fig. 22), and lacking striae (Fig. 23); but never with subparallel striae running oblique to the longitudinal midline. Head variously sculptured, but if sculpture reaches posterior head margin in full-face view it is either strongly rugoreticulate (Fig. 26) or foveolate (Fig. 11). **Minor** Head, including the area mesad of the frontal carinae, entirely covered by reticulated network of punctures, giving it a dull appearance (Fig. 37); if rugae are present they are generally short segments and mostly restricted to posterior portion of head. Frontal carinae not distinct posterior to eye level.....**9**

9 **Major** Posterolateral lobes, including posterior head margin, covered in rugoreticulum (Fig. 26). Promesonotum in dorsal view transverse with strongly projecting shoulders (Fig. 28). Promesonotal dorsum rugoreticulate with distinct long longitudinal striae in addition to shorter sections of transverse and intersecting striae (Fig. 22). **Minor** Posterior portion of head with many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (Fig. 59). Antennal scapes with many erect hairs (Fig. 56); scapes do not surpass posterior head margin (Fig. 41)..... ***parva***

– **Major** Posterolateral lobes variously sculptured, but posterior head margin always free of distinct rugae (Fig. 25) or rugoreticulum (Fig. 27). Promesonotum in dorsal less transverse with weakly projecting shoulders in dorsal view (Fig. 29). Promesonotal dorsum variously sculptured (including transversely striate (Fig. 21), foveolate or both), but never rugoreticulate with distinct long longitudinal striae. **Minor** Posterior portion of head lacking many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (Fig. 60). Antennal scapes with (Fig. 56) or without (Fig. 55) many erect hairs. Scapes often, but not always, surpass posterior head margin; if they do it is usually by a distance less than eye length **10**

10 **Major + minor** Gaster with entire first tergite glossy (Fig. 32). **Major** Postpetiole relatively narrow; distinctly less than 2× petiolar width in dorsal view

(Fig. 30). Posterolateral lobes variably sculptured. **Minor** Hairs on mesosoma fine, flexuous, of unequal length and not arranged in pairs (Fig. 54). Antennal scapes with many erect to suberect hairs (Fig. 56), especially on the anterior margin. Postpetiole narrow in dorsal view, only slightly broader than petiole (Fig. 61). (*P. flavens*-complex) **11**

– **Major + minor** Gaster with at least anterior 1/3 of first tergite matte (Fig. 33). **Major** Postpetiole relatively broad; distinctly more than 2× petiolar width in dorsal view (Fig. 31). Promesonotal dorsum usually foveolate and never with distinct transverse striae. Head often entirely foveolate (Fig. 11), but portions of posterolateral lobes can be glossy. Posterolateral lobes never with distinct rugae. **Minor** Hairs on mesosoma stout, stiff, of equal length and arranged in pairs (Fig. 53). Antennal scapes lack many erect to suberect hairs (Fig. 55). Postpetiole broad in dorsal view, distinctly broader than petiole (Fig. 62) **12**

11 Antennal scrobe distinct and narrow, shallow but capable of receiving the entire antennal scape in repose (Fig. 71a); bordered by strong, unbroken frontal carina mesially (Fig. 71b); depression marked by a continuous smooth surface entirely (or nearly entirely) uninterrupted by rugulae. The rugulae of the frons extend to approximately an eye's length distance from the posterior head margin. Promesonotal dorsum with distinct transverse striae (Fig. 21) ..... ***navigans***

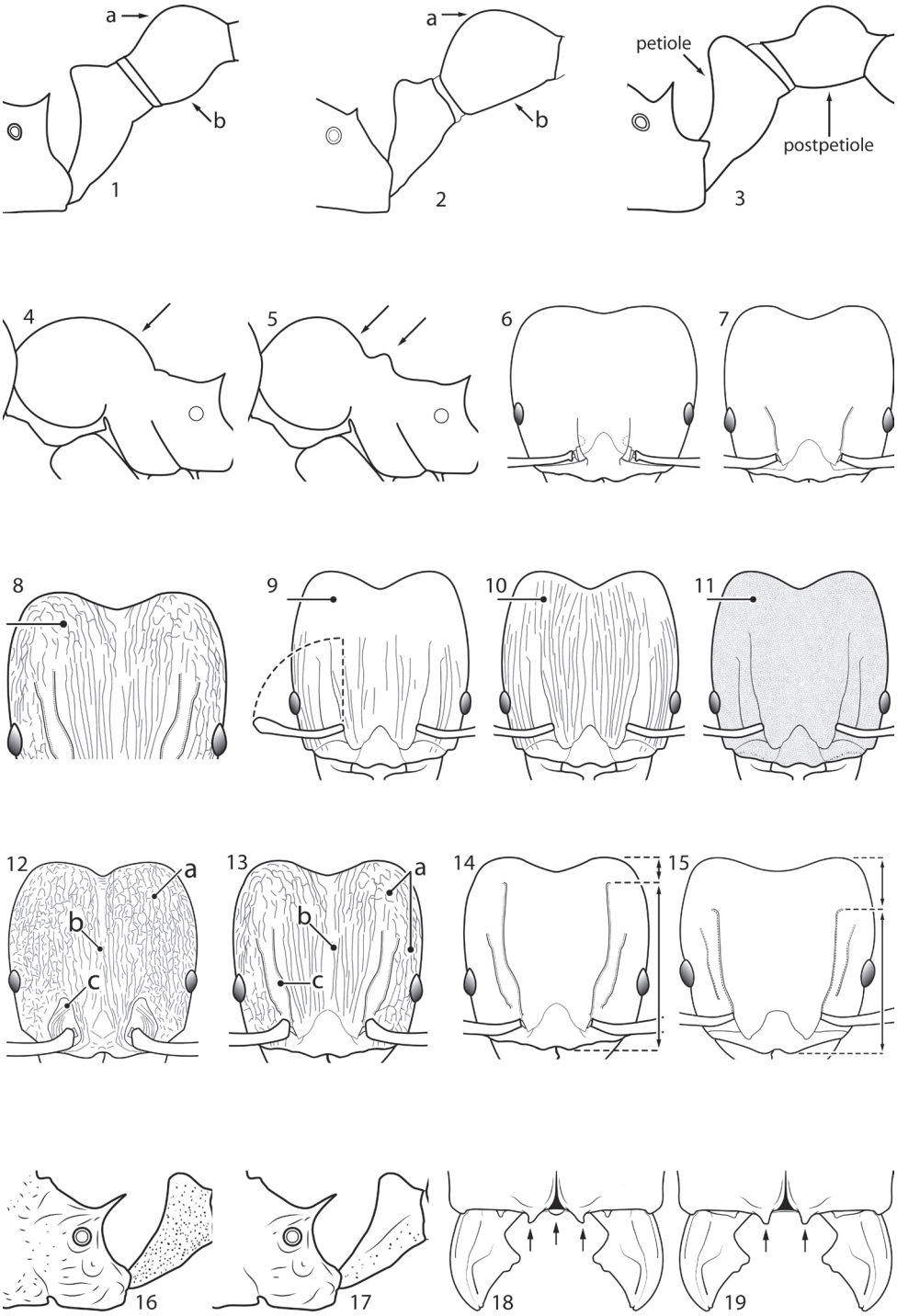
– Antennal scrobe broad, ill-defined, incapable of receiving the entire antennal scape in repose (Fig. 72a); bordered by relatively weak and interrupted frontal carina mesially (Fig. 72b); depression opaque and strongly punctate. The rugulae of the frons of variable length but never reach posterior head margin. Promesonotal dorsum variable, but if transverse striae are present they rarely reach across entire surface ..... ***flavens***

12 **Major** Head bicolored with the yellowish posterior two-thirds contrasting with the darker brown anterior third and rest of body (Fig. 33). **Minor** Posterior head margin relatively narrow (Fig. 58). Antennal scapes relatively long (SI 103–125). Color red brown to nearly black..... ***punctatissima***

– **Major** Head uniform in color, from yellow to reddish brown; same color as associated minor workers (Fig. 35). **Minor** Posterior head margin relatively narrow or broad. Antennal scapes variable length. Color brown or yellow **13**

13 **Major + minor** Prefers understory habitat. Typically nests arboreally in live plant cavities, under bark, and in dead sticks and branches on or above forest floor. **Major** Color usually yellow. Head width sometimes wider (HW 0.74–1.16 mm). **Minor** Posterior head margin more narrow (Fig. 58). Antennal scapes relatively longer (SI 103–125). Color brown or yellow ..... ***anastasii***

– **Major + minor** Prefers open, disturbed habitat. Generalist nest microhabitats, including under stones and dead wood. **Major** Color usually red brown. Head width sometimes narrower (HW 0.71–1.07 mm). **Minor** Posterior head margin more broad (Fig. 57). Antennal scapes relatively short (SI 95–108). Color usually brown but occasionally yellow ..... ***bilimeki***


a
b
1
a
b
2
petiole
postpetiole
3
4
5
6
7
8
9
10
11
12
a
b
c
13
a
b
c
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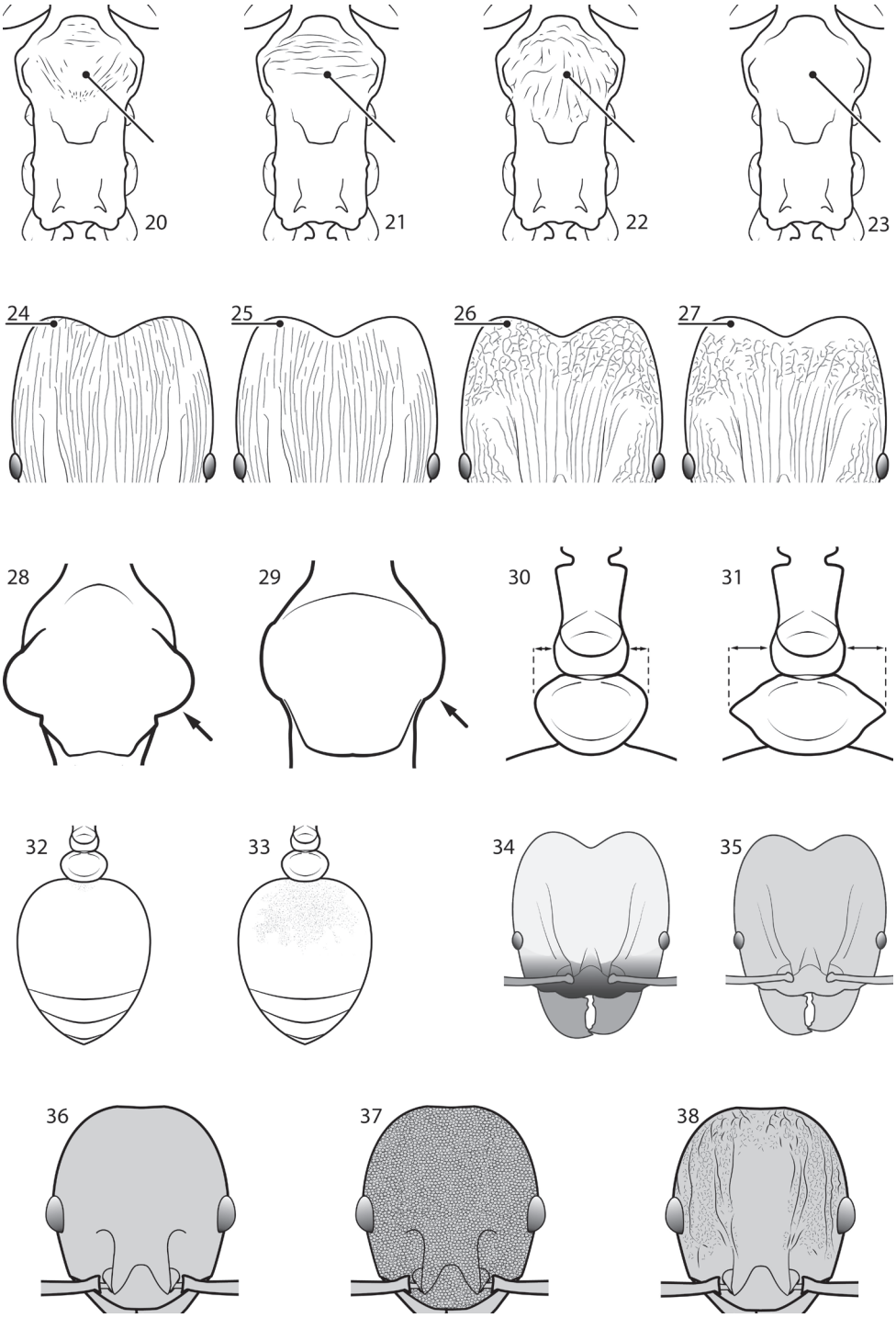
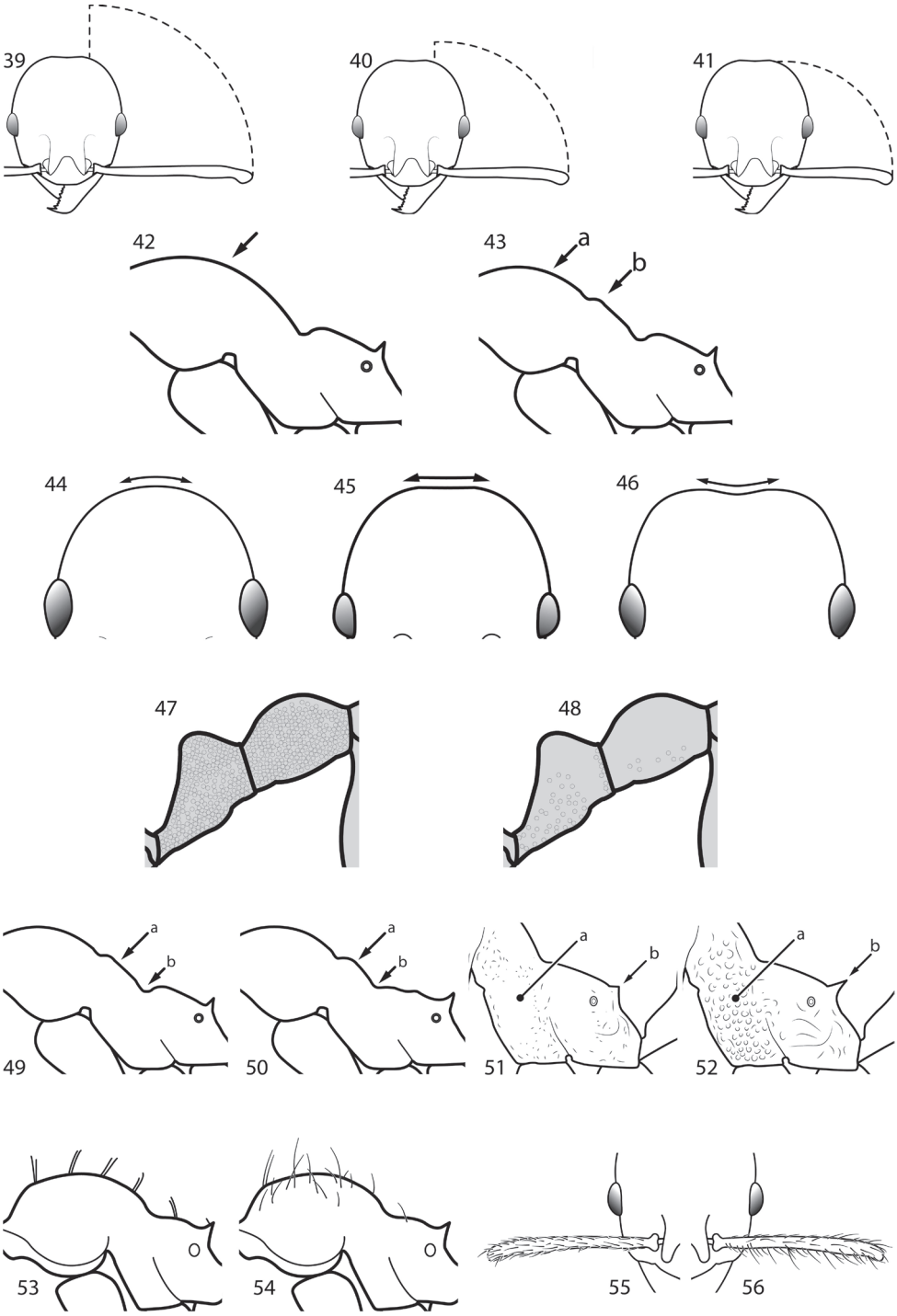
18
19

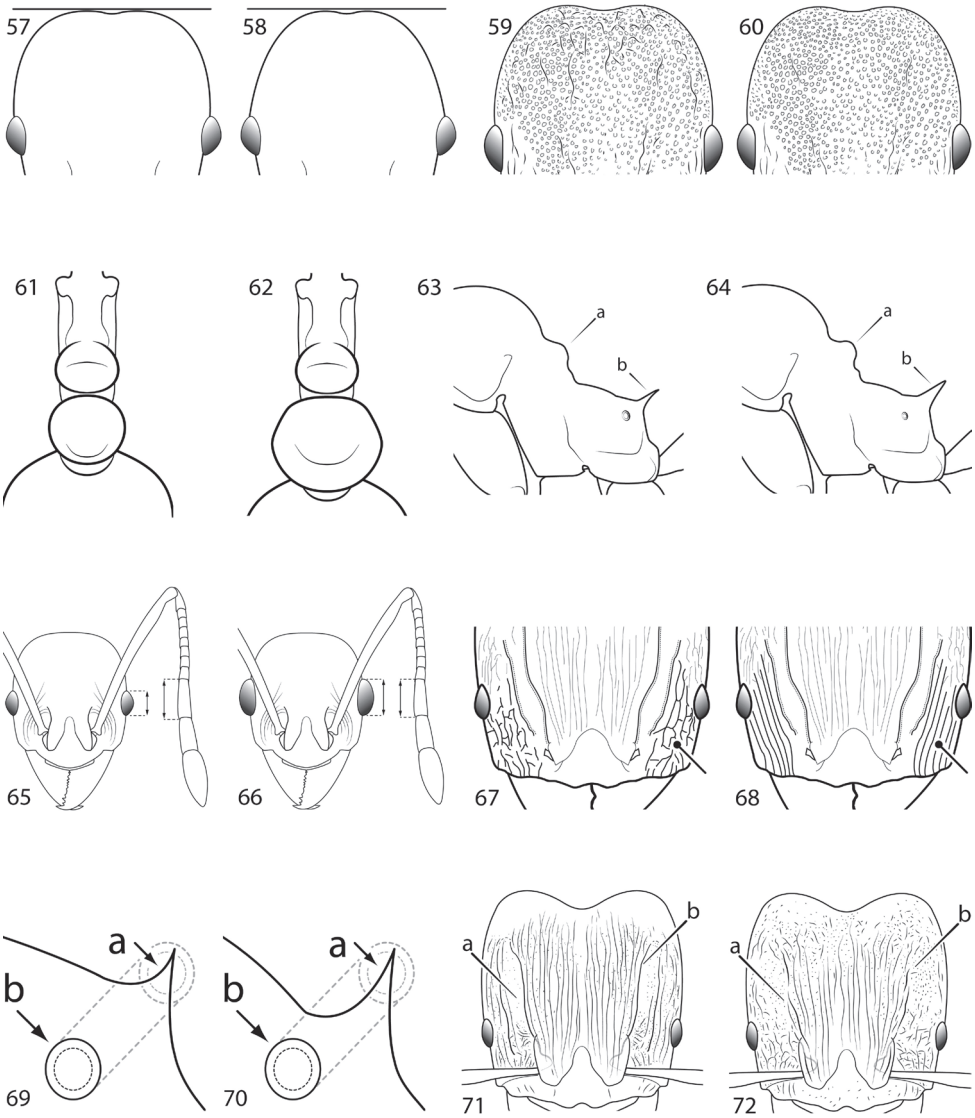
Figures 1–19.



Figures 20–38.

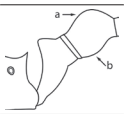
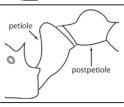
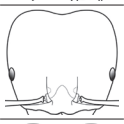
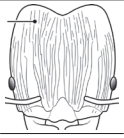
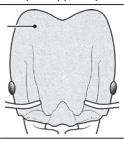


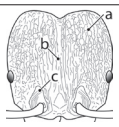
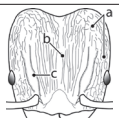
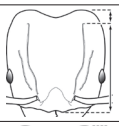
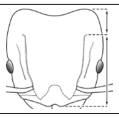
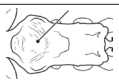
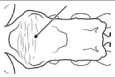
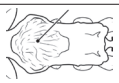
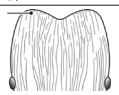
Figures 39–56.

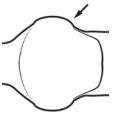
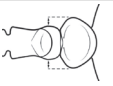
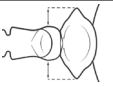
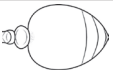
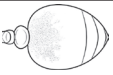
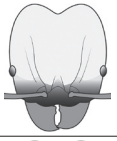
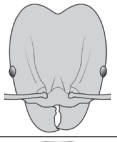
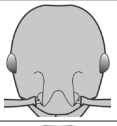
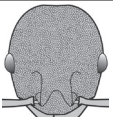


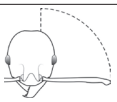
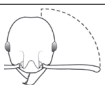
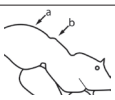
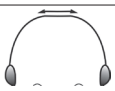
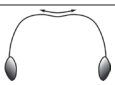
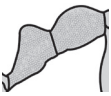
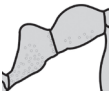
Figures 57–72.

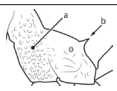
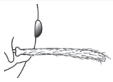
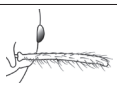
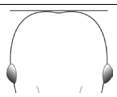
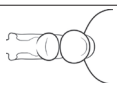
Table 4. Illustrated glossary of morphological characters used to diagnose introduced *Pheidole* species. Numbers refer to Figs 1–72. Larger versions of the illustrations are presented in preceding plates. Figures are referred to in the taxonomic keys and species diagnoses.

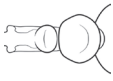
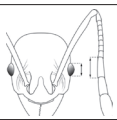
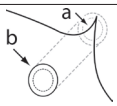
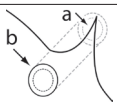
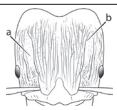
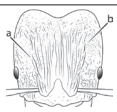
N	Ilustration	Description
1		Postpetiole swollen relative to petiole. Postpetiole with a posterodorsal bulge (**a**) and anteroventral bulge (**b**) (major and minor worker). Diagnostic character of *P. megacephala* among introduced *Pheidole*
2		Postpetiole forming a high dorsally bulging dome that is tallest at midpoint (**a**); ventral margin flat to very weakly convex (**b**) (major and minor worker). Diagnostic character of *P. noda* among introduced *Pheidole*
3		Postpetiole not swollen relative to petiole (major and minor worker). Separates all introduced *Pheidole* species from *P. megacephala* and *P. noda*
4		Promesonotum in profile forming a single dome, lacking a distinct mound or prominence on the posterior slope (major worker)
5		Promesonotum in profile with two convexities, the large anterior dome in addition to a distinct mound or prominence on the posterior slope (major worker)
6		Head heart-shaped (major worker). Diagnostic character of *P. megacephala* among introduced *Pheidole*
7		Head subquadrate (major worker)
8		Cephalic dorsum with strong rugoreticulate sculpture, at least on posterolateral lobes (major worker)
9		Posterolateral lobes lacking sculpture (including foveolate ground sculpture, carinae and rugae) posterior to maximum extent of antennal scapes in repose (major worker)
10		Posterolateral lobes rugose or rugulose (major worker)
11		Posterolateral lobes punctate or foveolate (major worker)

N	Ilustration	Description
12		Head almost entirely covered by network of intersecting rugae (a), lacking long, well-organized and parallel longitudinal rugae on the frons (b). Frontal carinae indistinct, quickly becoming integrated into dense rugoreticulum that covers the entire face. Antennal scrobes entirely lacking. Antennal insertions surrounded by deeply excavated pits (c). Diagnostic characters of *P. obscurithorax* major workers among introduced *Pheidole*
13		Head rugoreticulate on posterolateral lobes and laterad of frontal carinae (a), but frons dominated by long, well-organized and parallel longitudinal rugae (b). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (c). Antennal insertions not surrounded by deeply excavated pits. Illustration applies to *P. indica* and *P. fervens*
14		Frontal carinae relatively longer, extend 4/5 distance of head before terminating (major worker). Diagnostic character separating *P. fervens* from *P. indica*
15		Frontal carinae relatively shorter, extend 3/4 distance of head before terminating (major worker). Diagnostic character separating *P. indica* from *P. fervens*
16		Petiolar node strongly punctate and metapleuron with moderate rugulae and some weak punctation (major worker). Diagnostic character separating *P. proxima* from *P. vigilans*
17		Petiolar node mostly glossy, metapleuron almost completely glossy with strongly reduced carinulae and lacking punctation (major worker). Diagnostic character separating *P. vigilans* from *P. proxima*
18		Hypostomal bridge with a small median tooth in addition to a pair of larger inner teeth (major worker). Diagnostic character separating *P. proxima* from *P. vigilans*
19		Hypostomal bridge with two well-developed inner teeth but lacking a median tooth (major worker) Diagnostic character separating *P. vigilans* from *P. proxima*
20		Promesonotal dorsum glossy with thin but distinct subparallel striae running oblique to the longitudinal midline (major worker). Diagnostic character separating *P. rugosula* from other introduced *Pheidole*
21		Promesonotal dorsum with distinct transverse striae (major worker). Character present among some species of the *P. flavens* complex, including *P. navigans*
22		Promesonotal dorsum rugoreticulate with distinct long longitudinal striae in addition to shorter sections of transverse and intersecting striae (major worker). Illustration refers to *P. parva*
23		Promesonotal dorsum glossy, lacking foveolate ground sculpture or striae (major worker). Character useful for separating *P. vigilans* and *P. proxima* from *P. rugosula*.
24		Head with distinct parallel rugae extend from frontal lobes posterior to apices of frontal carinae. Shorter lengths of rugae present across entire posterior region of head and extending to posterior margin in full-face view (major worker). Diagnostic character useful for separating *P. rugosula* from other introduced *Pheidole*, especially those introduced in New Zealand

N	Ilustration	Description
25		Posterolateral lobes variously sculptured, but posterior head margin always free of distinct rugae or rugoreticulum (major worker). Illustration refers to *P. flavens*, *P. navigans* and other members of the *P. flavens* complex
26		Posterolateral lobes, including posterior head margin, strongly rugoreticulate (major worker). Illustration refers to *P. parva* and character is useful for separating that species from those of the *P. flavens* complex and the *P. punctatissima* clade
27		Posterolateral lobes variously sculptured, but posterior head margin always free of rugoreticulum (major worker)
28		Promesonotum in dorsal view strongly transverse with strongly projecting shoulders (major worker). Illustration refers to *P. parva* and character is useful for separating that species from those of the *P. flavens* complex and the *P. punctatissima* clade
29		Promesonotum in dorsal view less transverse with weakly projecting shoulders in dorsal view (major worker)
30		Postpetiole relatively narrow, distinctly less than 2× petiolar width in dorsal view (major worker). Character useful for separating members of the *P. flavens* complex, including *P. flavens* and *P. navigans*, from those of the *P. punctatissima* clade
31		Postpetiole relatively broad, distinctly more than 2× petiolar width in dorsal view (major worker). Character useful for separating members of the *P. punctatissima* clade from those of the *P. flavens* complex, including *P. flavens* and *P. navigans*
32		Gaster with entire first tergite glossy (major and minor worker). Character useful for separating members of the *P. flavens* complex, including *P. flavens* and *P. navigans*, from those of the *P. punctatissima* clade
33		Gaster with at least anterior 1/3 of first tergite matte (major and minor worker). Character useful for separating members of the *P. punctatissima* clade from those of the *P. flavens* complex, including *P. flavens* and *P. navigans*
34		Head bicolored with the yellowish posterior two-thirds contrasting with the darker brown anterior third and rest of body (major worker). Diagnostic character for separating *P. punctatissima* from all other introduced *Pheidole*
35		Head uniform in color (major worker). Character used to separate *P. anastasii* and *P. bilimeki* from *P. punctatissima*
36		Head predominantly glossy, lacking punctation and or rugae above eye level (minor worker). Character used to separate *P. indica*, *P. fervens*, *P. obscurithorax*, *P. proxima* and *P. vigilans* from all other introduced *Pheidole*.
37		Head, including the area mesad of the frontal carinae, entirely covered by reticulated network of punctures, giving it a dull appearance; if rugae are present they are generally short segments and mostly restricted to posterior portion of head (minor worker). Character used to separate *P. anastasii*, *P. bilimeki*, *P. flavens*, *P. navigans* and *P. parva* from all other introduced *Pheidole*

N	Ilustration	Description
38		Head with well-defined, long segments of rugae running longitudinally from below the eyes to the posterior head margin. Frontal carinae distinct and reaching towards the posterior head margin, although they may occasionally be interrupted. Punctate ground sculpture present on lateral surfaces of head and just mesad of the frontal carinae, but median portion of head with a large glossy section. Diagnostic characters separating *P. rugosula* from all other introduced *Pheidole*
39		Antennal scapes extremely long, surpassing posterior head margin by more than 2× eye length (minor worker). Diagnostic character separating *P. obscurithorax* from *P. fervens* and *P. indica*
40		Antennal scapes surpass posterior head margin by approximately same length as eye (minor worker)
41		Antennal scapes relatively short, either failing to surpass posterior head margin, or surpassing it by less than the distance of eye length (minor worker)
42		Promesonotum in profile forming a single dome, lacking a distinct mound or prominence on the posterior slope (minor worker)
43		Promesonotum in profile with two convexities, the large anterior dome (**a**) in addition to a distinct prominence on the posterior slope (**b**) (minor worker)
44		Posterior margin strongly convex in full-face view such that the head outline forms a single unbroken curve from eye to eye (minor worker). Diagnostic character for separating *P. obscurithorax* from *P. fervens* and *P. indica*
45		Posterior head margin weakly convex to flat in full-face view (minor worker). Diagnostic character for separating *P. fervens* and *P. indica* from *P. obscurithorax*
46		Posterior head margin weakly concave in full-face view (minor worker)
47		Petiole and postpetiole strongly sculptured laterally. Diagnostic character for separating *P. obscurithorax* from *P. fervens* and *P. indica*
48		Petiole and postpetiole glossy to very weakly sculptured laterally (minor worker). Diagnostic character for separating *P. fervens* and *P. indica* from *P. obscurithorax*
49		Promesonotal prominence relatively flat (**a**); metanotal depression relatively deep (**b**) (minor worker). Diagnostic character for separating *P. fervens* from *P. indica*

N	Ilustration	Description
50		Promesonotal prominence relatively convex (**a**); metanotal depression relatively shallow (minor worker). Diagnostic character for separating *P. indica* from *P. fervens*
51		Mesopleuron entirely glossy (**a**); propodeal spines weakly produced and dentiform (**b**) (minor worker). Diagnostic character for separating *P. vigilans* from *P. proxima*
52		Mesopleuron entirely punctate (**a**); propodeal spines moderately produced and spiniform (**b**) (minor worker). Diagnostic character for separating *P. proxima* from *P. vigilans*
53		Hairs on mesosoma stout, stiff, of equal length and arranged in pairs (minor worker). Diagnostic character for separating *P. anastasii*, *P. bilimeki* and *P. punctatissima* from *P. flavens*, *P. navigans* and *P. parva*
54		Hairs on mesosoma fine, flexuous, of unequal length and not arranged in pairs (minor worker). Diagnostic character for separating *P. flavens*, *P. navigans* and *P. parva* from *P. anastasii*, *P. bilimeki* and *P. punctatissima*
55		Antennal scapes lack standing hairs (minor worker). Diagnostic character for separating *P. anastasii*, *P. bilimeki* and *P. punctatissima* from *P. flavens*, *P. navigans* and *P. parva*
56		Antennal scapes with erect to suberect hairs (minor worker). Diagnostic character for separating *P. flavens*, *P. navigans* and *P. parva* from *P. anastasii*, *P. bilimeki* and *P. punctatissima*
57		Posterior head margin relatively broad (minor worker). Diagnostic character for separating *P. bilimeki* from *P. anastasii* and *P. punctatissima*
58		Posterior head margin more narrow (minor worker). Diagnostic character for separating *P. anastasii* and *P. punctatissima* from *P. bilimeki*
59		Posterior portion of head with many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (minor worker). Diagnostic character for separating *P. parva* from *P. flavens* and *P. navigans*
60		Posterior portion of head lacking many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (minor worker). Diagnostic character for separating *P. flavens* and *P. navigans* from *P. parva*
61		Postpetiole narrow in dorsal view, only slightly broader than petiole (minor worker). Diagnostic character for separating *P. flavens* and *P. navigans* and from *P. anastasii*, *P. bilimeki* and *P. punctatissima*

N	Ilustration	Description
62		Postpetiole broad in dorsal view, distinctly broader than petiole (minor worker). Diagnostic character for separating *P. anastasii*, *P. bilimeki* and *P. punctatissima* from *P. flavens* and *P. navigans*
63		Promesonotal prominence relatively flat (**a**); propodeal spine relatively weak, narrow at base, weakly downcurved at apex (**b**) (major worker). Diagnostic character for separating *P. fervens* from *P. indica*
64		Promesonotal prominence convex and pronounced (**a**); propodeal spine relatively stout, broad at base, straight (**b**) (major worker). Diagnostic character for separating *P. indica* from *P. fervens*
65		Eye relatively small, eye length distinctly less than length of antennal segment 10 (minor worker). Diagnostic character for separating *P. fervens* from *P. indica*
66		Eye relatively large, eye length subequal to length of antennal segment 10 (minor worker). Diagnostic character for separating *P. indica* from *P. fervens*
67		The carinae between eye and mandible are branching and reticulated (major worker). Diagnostic character for separating *P. fervens* from *P. oceanica*
68		The carinae between eye and mandible are parallel and not reticulated (major worker). Diagnostic character for separating *P. oceanica* from *P. fervens*
69		The length of propodeal spine equal to or less than the diameter of propodeal spiracle (minor worker). Diagnostic character for separating *P. fervens* from *P. oceanica*
70		The length of propodeal spine greater than the diameter of propodeal spiracle (minor worker). Diagnostic character for separating *P. oceanica* from *P. fervens*
71		Antennal scrobe distinct and narrow, shallow but capable of receiving the entire antennal scape in repose (**a**); bordered by strong, unbroken frontal carina mesially (**b**); depression marked by a continuous smooth surface entirely (or nearly entirely) uninterrupted by rugulae (major worker). Diagnostic character for separating *P. navigans* from *P. flavens*
72		Antennal scrobe broad, ill-defined, incapable of receiving the entire antennal scape in repose (**a**); bordered by relatively weak and interrupted frontal carina mesially (**b**); depression opaque and strongly punctate. Diagnostic character for separating *P. flavens* from *P. navigans*

Species accounts

Pheidole anastasii **Emery**
Figs 74, 88a

anastasii. *Pheidole anastasii* Emery 1896: 76 (s.w.) COSTA RICA, Jiménez, [MCSN]. Queen described Forel 1901: 78. Junior synonym of *bilimeki* Mayr: Wilson 2003: 378. Revived status: Longino and Cox 2009: 40. *Nec* M.R. Smith 1933, Naves 1985, Boer and Vierbergen 2008.

Diagnosis among introduced *Pheidole*. Color usually dull yellow to dull brownish yellow. **Major** HW 0.83–1.05, HL 0.90–1.11, SL 0.49–0.62, CI 88–98, SI 50–61 (n=43, Longino pers. comm.). Head uniform in color (Fig. 35); subquadrate (Fig. 7); often entirely punctate (Fig. 11), but portions of posterolateral lobes can be glossy. Posterolateral lobes never with distinct rugae. Promesonotum in profile forming a single dome (Fig. 4). Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole relatively broad; distinctly more than 2× petiolar width in dorsal view (Fig. 31). First gastral tergite with anterior third to entire surface matte. **Minor** HW 0.38–0.50, HL 0.44–0.59, SL 0.44–0.58, CI 82–90, SI 106–120 (n=49, Longino pers. comm.). Head dull, entirely covered by reticulated network of punctures (Fig. 37). Posterior head margin relatively narrow and rounded (Fig. 58). Antennal scapes lack standing hairs (Fig. 55); scapes surpass posterior head margin by a distance equal to or greater than eye (Fig. 40). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Hairs on mesosoma stout, stiff, of equal length and arranged in pairs (Fig. 53). Postpetiole narrow in dorsal view, only slightly broader than petiole. Gaster with at least anterior 1/3 of first tergite matte (Fig. 33).

Identification, taxonomy and systematics. *Pheidole anastasii*, *P. bilimeki* and *P. punctatissima* all belong to the *P. punctatissima* clade (Economo et al. 2015). These ants are all relatively small species characterized by densely punctate ground sculpture that gives them a dull, matte appearance. Among species treated here, the *P. punctatissima* clade species are most easily confused with those of the closely related *P. flavens* complex. Major and minor workers are most reliably diagnosed from those of the *P. flavens* complex by the relatively broad postpetiole (Fig. 31, major; Fig. 62, minor) and the matte anterior portion of the gaster (Fig. 33) in addition to other characters listed in the key. The minor workers can also be confused with those of Asian native *P. parva*, but can be distinguished by the more uniform and stout mesosomal hairs (Fig. 53), and by the antennal scapes which lack erect hairs (Fig. 55) and tend to surpass the posterior head margin by a distance equal to or greater than eye (Fig. 40). In the Neotropics, there are many native species that closely resemble *P. anastasii* (Wilson 2003), and identification of the minor worker subcaste is especially challenging.

Among introduced members of the clade, the major workers of *P. punctatissima* are immediately distinguished from those of both *P. anastasii* and *P. bilimeki* by the bicolored head (Fig. 33). The minor workers of *P. punctatissima* tend to have narrower posterior head margins and longer antennal scapes than those of *P. anastasii* and *P. bilimeki*. Separating *P. anastasii* from *P. bilimeki* is particularly difficult. They are most reliably distinguished by ecological characteristics, with the former preferring to nest arboreally and the latter preferring to nest under stones or in dead wood. The morphological characters separating these two species are highly variable, but the major workers of *P. anastasii* tend more often towards yellow (*versus* tending towards brown in *P. bilimeki*) and can have relatively wider heads (HW 0.74–1.16 mm *vs*. 0.71–1.07 mm). The minor workers of *P. anastasii* tend to have more narrow heads posteriorly then *P. bilimeki* (Fig. 58 *vs*. Fig. 57) and relatively longer scapes (SI 103–125 *vs*. 95–108). See Longino and Cox (2009) for additional details.

Adding to the already confusing taxonomy separating *P. anastasii* and *P. bilimeki* is the widespread application of the name *P. floridana* Emery to populations across the southern United States. The first record of *P. floridana* from Florida was the type series described by Emery from Coconut Grove (Miami area) in 1895. Smith (1930) recorded *P. floridana* in his original list of Florida ants, and added *P. anastasii* three years later (1933), stating only "This species [*P. anastasii*], which was originally described from Costa Rica, is recorded here for Florida on the basis of information secured from Dr. Wheeler…I have seen the same species in greenhouses in the District of Columbia, New Jersey, and Illinois." The previous year (1932) Wheeler, who had received type material of *P. floridana* from Emery (Wheeler 1908c), included *P. floridana* and *P. anastasii* in his own list of Florida ants.

Naves (1985) in his study of Florida *Pheidole*, also recognized both species and distinguished *P. anastasii* from *P. floridana* by the matte base of the gaster in the former and the glossy gaster in the latter. Indeed, the type specimens of *P. floridana* from Coconut Grove are consistent with this characterization (CASENT0904424, CASENT0904425). Naves wrote that the Miami area was the only place where he was able to locate *P. floridana*. *Pheidole anastasii*, in contrast, was reported by Naves as widely distributed across the state.

Deyrup et al. (1988), lamenting the taxonomic confusion surrounding *P. floridana*, *P. flavens* and *P. anastasii* in Florida, stated, "Traditionally (Creighton 1950; Smith 1979) the name *P. floridana* has been applied to a widespread upland species that has a distinctive matte area on the base of the first gastral tergite and very evenly rugose head…This is the species we report from the Keys [Florida]." Subsequent reviews of Florida ants have thus excluded *P. anastasii* from their lists (Deyrup 2003; Deyrup et al. 2000; Moreau et al. 2014). Wilson (2003) followed Deyrup in treating all outdoor populations from the United States as *P. floridana*, but conceded that his concept of *P. floridana* could represent a northern geographic variant of *P. bilimeki* or an endemic species modified by intergradation with a *P. bilimeki* immigrant population.

With respect to all outdoor North American records, we follow Wheeler (1932), Smith (1933), and Naves (1985) in treating the localized glossy-gaster *P. floridana* as distinct from the widespread matte-gaster species referred to as *P. anastasii* by the aforementioned authors. However, the relatively short scapes and posteriorly broad heads of the minor workers, together with the habitat and nesting preferences of the matte-gaster species suggests the name *P. bilimeki* Mayr more accurately applies to this widespread taxon than does *P. anastasii* Emery. The issue is discussed in further detail under the *P. bilimeki* section.

Biology. *Pheidole anastasii*, named by Emery on behalf of Sig. Anastasio Alfaro, is a Neotropical species that is occasionally found indoors beyond its native range. Although at least some arboreal colonies appear to be polydomous, *P. anastasii* is a low-impact adventive that has thus far shown little capacity for becoming a significant invader. The biology of *P. anastasii*, especially across its native range in Costa Rica and in comparison to *P. bilimeki* was reviewed by Longino and Cox (2009). The species was noted as being among the most abundant ants in the low arboreal forest understory of La Selva Biological Station (Costa Rica). Although tolerant of disturbance, *P. anastasii* requires some vegetation cover and does not occur in open areas. All collections reviewed by Longino and Cox were from wet forest habitats. Most were from below 500 m elevation, but several ranged to a maximum of 1200 m. The propensity for the species to be inadvertently transported to greenhouses across the world is predicted by its arboreal foraging and nesting habits. Longino and Cox (2009) observed the species nests in almost any kind of cavity or sheltered space, including live stems, and that workers often build galleries and tunnels with carton or earthen construction. The species was reported to occur in lowland second growth, evergreen forest, coffee plantation, limestone, ravine, mixed hardwood-pine forest, wet forest, on karst, and cloud forest. It was also reported to nest in dead sticks and branches on or above the forest floor, under bark flaps on tree trunks, beneath epiphytes and under stones.

Distribution. *Pheidole anastasii* is a Neotropical native that ranges from Mexico to southern Central America or northern South America. We consider many of the outdoor records of *P. anastasii* from the southern United States to refer instead to *P. bilimeki* (see discussion above). There are, however confirmed records of the species from heated indoor locations – especially greenhouses. In North America there are records from hothouses in Washington D.C. and New York (Longino and Cox 2009), and also from Massachusetts. In Europe, the Netherlands occurrences reported as *P. anastasii* by Boer and Vierbergen (2008) refer to *P. bilimeki* (Boer, pers. comm.). The records from Denmark and Norway might also refer to *P. bilimeki*, but until specimens can be examined we follow the authors' use of *P. anastasii* (Birkemoe and Aak 2008; Lomholdt 1986).

Risk statement. *Pheidole anastasii* is a synanthropic species with a high tolerance for habitat disturbance. It is occasionally found in human habitations and in greenhouses. There is little indication that is causes significant impact to agricultural systems or native ecosystems. The species is a quarantine risk, and is thought to be transported with fresh plant material.

***Pheidole bilimeki* Mayr**
Figs 75, 88b

bilimeki. *Pheidole bilimeki* Mayr 1870b: 985 (s.) MEXICO (Bilimek) [NHMW]. Lectotype (s.) designated: Wilson 2003: 378. *Nec* Donisthorpe 1946, Wittenborn and Jeschke 2011.

deplanata. *Pheidole floridana* var. *deplanata* Pergande 1896: 883 (s.w.) MEXICO, Tepic (Eisen and Vaslit) [USNM]. Junior synonym of *bilimeki* Wilson 2003: 378.

antoniensis. *Pheidole floridana* var. *antoniensis* Forel 1901b: 364 (s.w.) COLOMBIA, San Antonio, Sierra Nevada de Santa Marta (Forel) [MHNG]. Junior synonym of *bilimeki*: Wilson 2003: 378.

annectens. *Pheidole punctatissima* subsp. *annectens* Wheeler, W.M. 1905: 93 (s.) BAHAMAS, Mangrove Key, Andros Island (Wheeler) [MCZC]. Junior synonym of *bilimeki*: Wilson 2003: 378.

insulana. *Pheidole punctatissima* subsp. *insulana* Wheeler, W.M. 1905: 93 (s.w.) BAHAMAS Southern Bight, Andros Islands; BAHAMAS, Blue Hills, New Providence Island (Wheeler) [MCZC]. Junior synonym of *bilimeki*: Wilson 2003: 378.

venezuelana. *Pheidole anastasii* var. *venezuelana* Forel 1905b: 159 (s.m.) VENEZUELA, Caracas (Meinert) [MHNG]. Junior synonym of *bilimeki*: Wilson 2003: 378.

johnsoni. *Pheidole anastasii* var. *johnsoni* Wheeler, W.M. 1907: 272 (s.w.m.) HONDURAS, Manatee (Johnson) [MCZC]. Junior synonym of *bilimeki*: Wilson 2003: 378.

ares. *Pheidole floridana* subsp. *ares* Forel 1908: 57 (s.w.m.) COSTA RICA, Cote du Tablazo, 1500 m; COSTA RICA, San Juan de Tobozi, 1400 m (Biolley) [MHNG]. Junior synonym of *bilimeki*: Wilson 2003: 378.

lauta. *Pheidole lauta* Wheeler, W.M. 1908c: 470 (s.w.q.m.) U.S.A. Subspecies of *floridana*: Creighton 1950: 179. Junior synonym of *floridana*: Gregg 1959: 21. See also Wilson 2003: 424. **n. syn.**

cellarum. *Pheidole anastasii* var. *cellarum* Forel 1908: 55 (s.w.) greenhouses in Zurich (SWITZERLAND), Kew (GREAT BRITAIN), Dresden (GERMANY) [MHNG]. Description of queen (as *P. anastasii*, based on material from Guatemala intercepted at Hamburg; material labeled incorrectly as *cellarum* types in Forel collection): Forel 1901a: 78. Description of queen in key: Forel 1915: 34. Junior synonym of *bilimeki*: Wilson 2003: 378.

rectiluma. *Pheidole rectiluma* Wilson 2003: 493 (s.w.) NICARAGUA, Hotel Selva Negra, 139 km north of Matagalpa, 1200 m (Kugler & Hahn). Junior synonym of *bilimeki*: Longino 2009: 16.

Diagnosis among introduced *Pheidole*. Color usually red brown, rarely yellow brown. **Major** HW 0.75–1.04, HL 0.79–1.13, SL 0.44–0.57, CI 87–97, SI 50–65 (n=39, Longino pers. comm.). Head uniform in color (Fig. 35); subquadrate (Fig. 7); often entirely punctate (Fig. 11), but portions of posterolateral lobes can be glossy. Posterolateral lobes never with distinct rugulae. Promesonotum in profile forming a single dome (Fig. 4). Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole

relatively broad; distinctly more than 2× petiolar width in dorsal view (Fig. 31). First gastral tergite with anterior third to entire surface matte. **Minor** HW 0.42–0.52, HL 0.47–0.59, SL 0.40–0.54, CI 83–93, SI 88–108 (n=38, Longino pers. comm.). Head, including the area mesad of the frontal carinae, entirely covered by reticulated network of punctures, giving it a dull appearance (Fig. 37). Posterior head margin relatively broad and flat (Fig. 57). Antennal scapes lack standing hairs (Fig. 55); surpass posterior head margin by a distance equal to or greater than eye (Fig. 40). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Hairs on mesosoma stout, stiff, of equal length and arranged in pairs (Fig. 53). Postpetiole narrow in dorsal view, only slightly broader than petiole. Gaster with at least anterior 1/3 of first tergite matte (Fig. 33).

Identification, taxonomy and systematics. *Pheidole bilimeki* is a member of the Neotropical *P. punctatissima* clade, together with *P. anastasii* and *P. punctatissima* (Economo et al. 2015). Among species treated here, it is easily confused with the aforementioned and members of the *P. flavens* complex. Minor workers can also be confused with those of *P. parva*. See section under *P. anastasii* for identification notes. In the southeastern United States, *P. bilimeki* is often confused with *P. floridana* Emery, which is discussed in more detail below. In the Neotropics, there are many native species that closely resemble *P. bilimeki* (Wilson 2003).

We propose the synonymy of *P. lauta* Wheeler to be transferred from *P. floridana* to *P. bilimeki*. In his original description Wheeler (1908c) wrote, "…the worker has the base of the gaster opaque whereas this is shining in the specimen of *floridana* given me by Prof. Emery." The description and the photographs we have examined of the type specimens all agree with the concept of *P. bilimeki* used here and in Longino and Cox (2009).

Should *P. floridana* therefore be synonymized under *P. bilimeki*? Wilson (2003) offered that the former might represent the northernmost population of the latter, and recent phylogenetic analyses (Economo et al. 2015; Moreau 2008) show these two as sibling taxa. Based on the results of her analysis, Moreau (2008) found that her samples of *P. bilimeki* (Costa Rica, RA0162) and putative *P. floridana* (Florida, RA0331) were each other's closest relatives, and that this pair was sister to *P. anastasii* (Costa Rica). The result is also supported by Economo et al. (2015), which found a shallow divergence separating *P. bilimeki* from putative *P. floridana*, especially compared to the deep divergence separating these sister taxa from *P. anastasii*. Moreau (2008) concluded that in order for *P. anastasii* to be a valid member of *P. bilimeki*, as proposed by Wilson (2003), *P. floridana* would also have to be accepted as a synonym of *P. bilimeki*.

We suggest that this conundrum stems from the common misapplication of the name *P. floridana* (a shiny gaster species) to collections of what are in fact the North American population of *P. bilimeki* (a matte gaster species). Naves (1985) came to a similar conclusion in his revision of the *Pheidole* of Florida, "*P. floridana* seems to be confined to southeast Florida in the Miami area. This is the only place where I was able to locate this species. Due to its close relationship to *P. anastasii* the latter has been misidentified as *P. floridana* many times, thus, mistakenly extending the supposed

range of *P. floridana. P. anastasii* is actually the species widely distributed in Florida, while *floridana* is absent or at least must be rare in most of the state."

One explanation for the confusing phylogenetic results is that RA0331 actually refers to *P. bilimeki* Mayr, and that true members of *P. floridana* Emery from the Miami area were not included in the aforementioned phylogenetic analyses. The samples of RA0331 were collected in central Florida from Polk County, well outside the Miami area from which the *P. floridana* Emery is known (Naves 1985). Deyrup, who collected and identified the specimens of RA0331, has previously (2003; 1988; 1989) applied the name *P. floridana* to matte gaster specimens that earlier authors (Naves 1985; Smith 1933; Wheeler 1932) would have considered *P. anastasii* Emery, and that we consider *P. bilimeki* Mayr.

To properly ascertain the taxonomic status of *P. floridana* Mayr we suggest a future phylogenetic analysis that includes specimens matching the type material of *P. floridana*, preferably from the Miami area. If there is evidence supporting the conspecificity of samples matching our concept of *P. bilimeki*, then the validity of *P. floridana* Emery must be revaluated. If, rather, the *P. floridana* samples are heterospecific with respect to *P. bilimeki*, then there are at least two hypotheses that could explain this result. One is that *P. floridana* is endemic to Florida. The second, perhaps more compelling albeit ironic explanation, would propose the Miami population of *P. floridana* is conspecific with a Neotropical species inadvertently introduced to Florida. Miami is a major shipping port and was the gateway for many introduced ants over the past two centuries (Deyrup et al. 2000).

Biology. The taxonomic confusion surrounding whether published accounts refer to our proposed concept of *P. bilimeki*, or instead to either *P. floridana* or *P. anastasii*, makes it difficult to ascertain the natural history of the species. The following account given by Longino and Cox (2009), however, refers definitively to *P. bilimeki*. They report that *P. bilimeki* is a common species in open, recently or frequently disturbed habitats. In Costa Rica it occurs in lowland dry forest, lowland wet forest, and montane habitats to about 1500 m elevation. It is a common ant of roadsides, nesting under stones or in dead fence posts. It is a frequent pest ant in houses and is a common ant at baits in second growth dry forest vegetation in seasonally dry Guanacaste Province. It can also be abundant and dominant in large disturbances deep within primary forest reserves. We tentatively treat the account given by Wilson (2003) for *P. floridana* as referring to the North American population of *P. bilimeki*. That account stated that winged reproductives have been found in nests during September and October, and that the species occurs in a variety of woodland habitats, nests in soil, litter, and rotten wood, and in both xeric and mesic situations. It also noted the observation of Stefan Cover that colonies are monogynous, may contain 1000 or more ants, and are sometimes polydomous. Cover observed that the species is omnivorous, but does not appear to harvest seeds (but see Naves 1985). Naves (1985) discussed the biology of *P. bilimeki* (as *P. anastasii*) in Florida. He found the species most often nesting under the bark at the base of pines or along the roots, but occasionally found it nesting in the soil. The colonies he observed supported over 600 workers with a 5:1 ratio of minors to majors. Mature colonies were monogynous, although in laboratory conditions colonies

that lost their original queen would accept other conspecific queens. Several colonies were discovered with two or three founding females, but laboratory experiments found that one would kill the others before the rearing of the first brood. Naves also recorded that the species feeds on seeds, fruits, and scavenges on small dead arthropods and is predaceous on small live arthropods.

Distribution. *Pheidole bilimeki* is a Neotropical native that ranges from northern South America to southern North America and across the Caribbean. The records included here from the southern United States have previously been treated as *P. anastasii* and *P. floridana* (see discussion). *Pheidole bilimeki* was not reported from Florida until 1932 (Wheeler). While it is possible that the penetration of *P. bilimeki* into the southern United States represents a recent dispersal event, even one that has been anthropogenically facilitated, there are several reasons for considering *P. bilimeki* as native to the region. Firstly, the range of North American populations appear contiguous with those of Mexico and the Caribbean, and gene flow among them is probable. Secondly, populations from Florida are known to host two parasites, a mermithid that parasitizes workers, and a hymenopteran parasite species of the genus *Orasema* (Naves 1985). *Pheidole bilimeki* has been recorded from greenhouses in Illinois and Ohio in North America. The species has also been found indoors and greenhouses across Europe, including the Netherlands (Boer and Vierbergen 2008), Germany (Forel 1908), Great Britain (Forel 1908), Ireland (Stelfox 1927), and Switzerland (Forel 1908). The only occurrence of *P. bilimeki* in Jamaica is reported by Wilson (2003). Although the species might occur there, it is also possible that Wilson was referring to *P. jamaicensis* Wheeler. The single Mauritius occurrence is of a single minor worker examined by Donisthorpe (1946), but this specimen more likely refers to the superficially similar *P. parva* which is widespread across the island and its neighbors in the Indian Ocean.

Risk statement. *Pheidole bilimeki* is a synanthropic species with a high tolerance for habitat disturbance. It is occasionally found indoors, especially in greenhouses. There is little indication that is causes significant impact to agricultural systems or native ecosystems.

Pheidole fervens **F. Smith**

Figs 76, 88c

fervens. *Pheidole fervens* Smith, F. 1858: 176 (s.) SINGAPORE (BMNH). Lectotype (s.) (CASENT0901520) designated: Fischer and Fisher 2013: 322.

pungens. *Solenopsis pungens* Smith 1861: 48. INDONESIA, Menado, Sulawesi (A.R. Wallace). Combination in *Pheidologeton*: Donisthorpe 1932: 469; in *Pheidole*: Bolton 1995: 328. Junior synonym of *Pheidole fervens*; lectotype (s.) designated: Eguchi 2004b: 198.

javana. *Pheidole javana* Mayr, 1867: 66 (s.w.) INDONESIA, Batavia [Jakarta], Java. Junior synonym of *Pheidole fervens*: Wilson and Taylor 1967: 45. Lectotype (s.) designated: Eguchi 2004b.

cavannae. *Pheidole cavannae* Emery 1887: 464 (footnote) (s.) NEW CALEDONIA. Subspecies of *Pheidole oceanica*: Emery 1914: 401. Junior synonym of *Pheidole fervens*: Wilson and Taylor 1967: 45.

dharmsalana. *Pheidole javana* var. *dharmsalana* Forel 1902c: 184, 198 (s.) INDIA, Dharmsala (Sage). [Also described as new by Forel 1902: 546]. Subspecies of *Pheidole fervens*: Bolton 1995: 320. Junior synonym of *Pheidole fervens*; lectotype (s.) designated: Eguchi 2004b: 198.

amia. *Pheidole amia* Forel 1912: 60 (s.w.) TAIWAN, Takao [Kaohsiung]. Junior synonym of *Pheidole fervens*; lectotype designated: Eguchi 2004b: 197.

dolenda. *Pheidole javana* var. *dolenda* Forel 1912: 60 (s.w.) TAIWAN, Akau. Subspecies of *Pheidole fervens*: Bolton 1995: 320. Junior synonym of *Pheidole fervens*; lectotype designated: Eguchi 2004b: 198.

nigriscapa. *Pheidole oceanica* subsp. *nigriscapa* Santschi, 1928: 48 (s.w.) SAMOA, Apia, Upolu (H. Swale). Junior synonym of *Pheidole fervens*: Wilson and Taylor 1967: 45.

tahitiana. *Pheidole oceanica* subsp. *nigriscapa* var. *tahitiana* Santschi [in Cheesman and Crawley 1928]: 516. FRENCH POLYNESIA, Tahiti. Unavailable name; material referred to *Pheidole fervens* by Wilson and Taylor 1967: 45.

desucta. *Pheidole javana* var. *desucta* Wheeler, W.M. 1929: 2 (s.w.q.) CHINA, Back Liang. Subspecies of *Pheidole fervens*: Bolton 1995: 320. Junior synonym of *Pheidole fervens*: Eguchi 2001a: 53. Lectotype designated: Eguchi 2004b.

soror. *Pheidole javana* var. *soror* Santschi 1937: 369 (s.w.) TAIWAN, Hokuto. Subspecies of *Pheidole fervens*: Bolton 1995: 330. Junior synonym of *Pheidole fervens*; lectotype designated: Eguchi 2004b: 198.

azumai. *Pheidole nodus* st. *azumai* Santschi 1941: 274 (s.w.) JAPAN, Tennooji, Osaka. Junior synonym of *Pheidole fervens*; lectotype designated: Eguchi 2004b: 198.

Diagnosis among introduced *Pheidole*. Color yellowish brown to dark brown. **Major** HW 1.13–1.44, HL 1.13–1.56, SL 0.80–0.95, CI 92–100, SI 61–71 (n=15, Eguchi 2001a; 2008; Fischer and Fisher 2013). Head square to subquadrate (Fig. 7); rugoreticulate on posterolateral lobes and laterad of frontal carinae (Fig. 13a), but frons dominated by long, well-organized and parallel longitudinal rugae (Fig. 13b). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (Fig. 13c). Frontal carinae relatively longer, extend 4/5 distance of head before terminating (Fig. 14). Promesonotum in profile with two convexities (Fig. 5), the large anterior dome in addition to a distinct mound or prominence on the posterior slope. Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.52–0.63, HL 0.66–0.73, SL 0.77–0.87, CI 79–88, SI 133–154 (n=16, Eguchi 2001a; 2008; Fischer and Fisher 2013). Head predominantly glossy (Fig. 36), lacking punctation or rugulae above eye level. Posterior head margin weakly convex to flat in full-face view (Fig. 45). Antennal scapes long (e.g. Fig. 39), but not surpassing the posterior head margin by more than 2× eye length. Promesonotum in profile with two convexities, the large anterior dome (Fig. 43a) in addition to a distinct prominence on the posterior slope (Fig. 43b). Promesonotal prominence

relatively flat (Fig. 49a). Metanotal depression relatively deep (Fig. 49b). Petiole and postpetiole glossy to very weakly sculptured laterally (Fig. 48). Postpetiole not swollen relative to petiole (Fig. 3).

Identification, taxonomy and systematics. *Pheidole fervens* is a medium to large sized species with long limbs. It belongs to the *P. fervens* clade along with its Australasian congeners *P. cariniceps*, *P. hospes*, *P. impressiceps*, and *P. oceanica* (Economo et al. 2015). The major workers have strong cephalic rugulae that become reticulated towards the posterior of the head and the minor workers have completely glossy heads with very long antennal scapes. Majors and minors of the species can be separated from those of *P. megacephala* and *P. noda* by the postpetiole which is not swollen compared to the petiole (Fig. 3), and the promesonotum which has the large anterior dome in addition to a distinct prominence on the posterior slope (Fig. 5, major; Fig. 43, minor). The minors of *P. fervens* can also be separated from those of *P. megacephala* by their larger size and longer antennal scapes (Fig. 39). The majors are easily distinguished from *P. megacephala* by the very sculptured head (Fig. 13).

Among species treated here, *P. fervens* is most easily confused with its close relative, *P. indica*, and the characters used to separate these two are subtle. For both subcastes, the promesonotal prominence is flatter in *P. fervens* (Fig. 49a, minor; Fig. 63a, major) compared to that of *P. indica* (Fig. 50a, minor; Fig. 64a, major). The eyes of *P. fervens* minors (Fig. 65) are relatively smaller than those of *P. indica* minors (Fig. 66), especially in comparison to antennal segment 10. The propodeal spines of *P. fervens* are weaker, narrower, and more downcurved in majors of *P. fervens* (Fig. 63b) compared to those of *P. indica* (Fig. 64b). Readers are referred to Eguchi (2004b; 2008) for characters used to separate *P. fervens* and *P. indica* from their Asian congeners.

In the Pacific Island region *P. fervens* is often confused with the nearly identical *P. oceanica*, which is native to that region. The carinae between eye and mandible are branching and reticulated in the majors of *P. fervens* (Fig. 67), versus parallel and not reticulated in those of *P. oceanica* (Fig. 68). This character was erroneously reversed in the key provided in Sarnat and Economo (2012). The minors are more difficult to separate, but in *P. fervens* the length of propodeal spine is equal to or less than the diameter of propodeal spiracle (Fig. 69), whereas in *P. oceanica* it is greater (Fig. 70).

Biology. For such a ubiquitous species across its native and introduced range, very little is known about the biology of *Pheidole fervens*. It is a synanthropic species with a high tolerance for disturbance (Eguchi 2004b; Fischer and Fisher 2013; Martínez 1996), but can also thrive under some degree of canopy cover (Morrison 1996; Sarnat and Economo 2012). In Fiji, where it is likely a recent colonizer, it was collected most frequently in human dominated landscapes between 0–800 m, although several collections were also made from primary forest at low elevations. In Hawaii, where it is definitely an introduced species, it is more abundant locally in wet regions than *P. megacephala* (Gruner et al. 2003) and occurs in the hot lowlands only below 900 m (Reimer 1994). In the Philippines, *P. fervens* is found in irrigated lowlands (rice fields) where it is characterized as dominant species capable of displacing *S. geminata* in the dry season (Way et al. 1998). In Japan it occurs in open land grading to forest

edge (Harada et al. 2009; Ogata 1981). *Pheidole fervens* recruits in large numbers to bait and forages both on the ground and on vegetation (Sarnat and Economo 2012). Baiting experiments on Pacific Islands found that *P. fervens* can act as a numerically and behaviorally dominant species capable of excluding other invasive ant species (including *Anoplolepis gracilipes*, *Nylanderia bourbonica*, and *Tetramorium bicarinatum*) from baits (Morrison 1996). Although foragers can be slow to discover food resources, once found they can recruit in large numbers and displace competing species (Morrison 1996). Experiments in China suggest that *P. fervens* can provide some degree of biotic resistance to the Red Imported Fire Ant (*Solenopsis invicta*) by acting in groups to dismember the limbs of individual fire ants (Chen et al. 2011). Martínez (1996) suggested the California population of *P. fervens* was polydomous, and Passera (1994) suggested the Hawaii population is unicolonial and polygynous, but detailed colony-level studies of the species are required to verify these claims. Wittenborn and Jeschke (2011) attributed their assertion that *P. fervens* practices dependent colony founding to Harris et al. (2005a), but we were unable to find any reference to colony foundation in that report and cannot substantiate their evidence.

Distribution. We consider *Pheidole fervens* as native to a broad expanse of the Indo-Malay region spanning from India east to the Philippines and south to the islands west of New Guinea. This is a broad and admittedly arbitrary boundary, but a more precise circumscription of the native range requires a population-level analysis outside the scope of the present study. In particular, it is difficult to ascertain the extent of its range into the Pacific Island region prior to the Anthropocene. The only known occurrence of *P. fervens* from New Guinea was a single record from the westernmost part of the island (Emery 1887b). East of New Guinea, however, the species is established on nearly all islands of the Pacific, including those which were uninhabited by any ant prior to human arrival. Although it is quite possible that *P. fervens* reached some of these islands without human assistance – especially those between Taiwan and mainland Japan – we treat these as introduced populations. And although established on Mauritius, the species is rarely encountered there and is currently known from only two localities (Fischer and Fisher 2013). The only record of introduction in North America is a California population that established nests in cracks of roads and along the sides of buildings in a two-block area of downtown Los Angeles (Martínez 1996). *Pheidole fervens* has been collected from greenhouses in the Netherlands (Boer and Vierbergen 2008), and is frequently intercepted by quarantine inspections (Ward et al. 2006).

Risk statement. *Pheidole fervens* can be a dominant species where it is locally abundant. Although few studies have measured the effect of *P. fervens* on native ecosystems, we predict that it could negatively impact native arthropods. We were unable to find documentation on the effect of *P. fervens* on agricultural systems, but it can be among the most abundant ant species in irrigated lowland crop systems such as rice fields. *Pheidole fervens* can also be an indoor nuisance species (Wilson and Taylor 1967), but is not a risk for structural damage. According to New Zealand records, the species is among the most commonly intercepted ants in that country (Ward et al. 2006). Sixty-

nine percent of the interceptions were in freight from Fiji (> 92% from the Pacific Islands). Interceptions were mostly in fresh produce (69%) and cut flowers (8%). *Pheidole fervens* was also intercepted multiple times in air passengers' luggage and shipping containers. The species could become more globally widespread in the future.

Pheidole flavens **Roger**

Figs 77, Fig. 88d

flavens. *Pheidole flavens* Roger 1863a: 198 (s.w.q.) CUBA. Wheeler, W.M. 1905: 92 (m.). Neotype designated: Barrajagua, Las Villas, CUBA (E.O. Wilson): Wilson 2003: 419.

tuberculata. *Pheidole exigua* var. *tuberculata* Mayr 1887: 585 (s.) St. Catharina, BRAZIL. Subspecies of *flavens*: Emery 1894: 157. Junior synonym of *flavens*: Wilson 2003: 419.

vincentensis. *Pheidole flavens* var. *vincentensis* Forel 1893a: 411 (s.w.q.m.) SAINT VINCENT. Junior synonym of *flavens*: Wilson 2003: 419.

gracilior. *Pheidole flavens* r. *gracilior* Forel 1901a: 78 (s.w.q.) GERMANY (intercepted in quarantine, from West Indies). Junior synonym of *flavens*: Wilson 2003: 419.

haytiana. *Pheidole flavens* var. *haytiana* Forel 1907: 6 (w.) HAITI, Port-au-Prince (Keitel). Wheeler, W.M. & Mann, 1914: 24 (s.q.m.). Junior synonym of *flavens*: Wilson 2003: 419.

spei. *Pheidole flavens* st. *spei* Santschi 1930: 77 (s.w.) CUBA, Pinar del Rio, Punta Esperanza, 4.i.2030, 7 s., 10 w. (Bierig). Junior synonym of *flavens*: Wilson 2003: 419.

aechmeae. *Pheidole floridana* subsp. *aechmeae* Wheeler, W.M. 1934: 166 (s.w.) MEXICO, Camaron near Mirador, Vera Cruz, in *Aechmea bracteata*, No. 472 (Skwarra). Junior synonym of *flavens*: Wilson 2003: 419.

greggi. *Pheidole greggi* Naves, 1985: 62, figs. 21, 45, 57 (s.w.) U.S.A., Miami, Florida, 19.xii.1945 (W.F. Buren). Junior synonym of *flavens*: Wilson 2003: 419.

Diagnosis among introduced *Pheidole*. See notes under *P. flavens*-complex. Neotype major: HW 0.72, HL 0.74, SL 0.42, CI 103, SI 58. Paraneotype minor: HW 0.34, HL 0.42, SL 0.34, CI 124. SI 100. Non-type measurements, major: HW 0.68–0.83, HL 0.74–0.88, SL 0.39–0.42, CI 87–97, SI 52–59. Non-type measurements, minor: HW 0.34–0.45, HL 0.39–0.49, SL 0.34–0.42, CI 81–93, SI 89–104.

Identification, taxonomy and systematics. *Pheidole flavens* belongs to the *P. flavens*-complex along with a putatively large number of other nominal taxa. However, the *P. flavens* group as conceived by Wilson (2003) is now known to be polyphyletic (Economo et al. 2015; Moreau 2008). Readers are referred to the *P. flavens*-complex for additional discussion of identification, taxonomy and systematics. The taxonomy of *P. flavens* and its close relatives remains in a state of confusion. It is beyond the scope of the present study to resolve this issue, but we contribute the following discussion as a step towards that goal.

Pheidole flavens was originally described by Roger from Cuba, but the type material is considered to be lost. Wilson (2003) designated a neotype from Cuba and synonymized a total of eight nominal taxa with *P. flavens*. Of these, *P. greggi* Naves (Florida) and perhaps *P. flavens* st. *spei* Santschi (Mexico) are most similar to the Cuban neotype. They, together with the types of *P. moerens* subsp. *creola*, are the only specimens examined thus far that have clearly reticulated rugulae posterior to the scrobes of major workers. Naves' (1985: fig. 55) concept of *P. flavens* Roger, at least as evidenced by his figures and descriptions, more closely matches our concept *P. navigans*, a species that is spreading across the southeastern United States. The syntype major of *Pheidole flavens* var. *vincentensis* Forel differs substantially from the neotype in that the head is completely glossy between the rugulae, which are themselves entirely longitudinal and do not extend far beyond the maximum extent of the antennal scapes in repose. These characters make it at least superficially more similar to *P. moerens* and *P. navigans*. *Pheidole flavens* r. *gracilior* and *P. navigans* were both described by Forel from workers intercepted at a Hamburg quarantine facility, which is testament to the dispersive ability of this complex. The syntype major of the latter species and that of *P. floridana* subsp. *aechmeae* Wheeler, also described from Mexico, are quite similar. *Pheidole exigua* var. *tuberculata* Mayr has the strongly convex head and promesonotal dome of *P. exigua* Mayr, and also exhibits tuberculate angles on the mesonotal declivity. Type specimens of *P. flavens* var. *haytiana* Forel were not examined for this study.

The only material from outside Central America and the Caribbean that we were able to confirm as matching the Wilson's neotype was from Florida. The Florida populations referred to here as *P. flavens* and *P. navigans* are almost certainly heterospecific. We suspect that Nearctic records of *P. flavens* outside of Florida such as those reported from Louisiana (Colby and Prowell 2006; Dash and Hooper-Bùi 2008) refer to either *P. bilimeki* or the species we are treating as *P. navigans* in the southeastern USA.

Biology. The biology of *Pheidole flavens*, as currently conceived, was reviewed by Wilson (2003) with contributing observations by Jack Longino. The species prefers rotting wood, but also nest beneath the bark of trees, in dead knots on tree trunks, in sod on rocks, in the soil beneath stones, and in epiphyte masses. In the Caribbean it is recorded from forests and thickets from sea level to 900 m, and in Costa Rica it occurs in both wet and dry forests below 1000 m. The nest galleries are diffuse and irregular. Mature colonies are large containing up to thousands of workers. Workers collect small arthropods and will recruit to sugar baits.

Distribution. *Pheidole flavens* is among the most widespread and abundant species of its genus in the New World, although this range might be representative of multiple cryptic species. As currently conceived, however, we consider *P. flavens* native from southern Mexico east through the Caribbean and south to Uruguay and northern Argentina. It is difficult to know whether the disjunction separating the western and eastern regions of South America is accurate or a sampling artifact. The Florida population is believed to have derived from an accidental introduction by commerce (Deyrup et al. 2000; Wilson 2003).

Risk statement. *Pheidole flavens* (or at least it's very close relatives) are easily transported long distances, and are known to hitchhike with fresh plant material (Wilson 2003). However, the species is not known to cause significant impact to agricultural systems or native ecosystems, and is not considered a house pest (Hedges 1998; Klotz et al. 1995).

Pheidole flavens-complex

Fig. 88e

The *P. flavens*-complex is defined here to include *P. flavens* Roger, *P. moerens* Wheeler, *P. navigans* Forel, and their respective junior synonyms. A clear understanding of the phylogenetic relationship among the aforementioned taxa that are invading regions beyond the Neotropics remains a challenge for future studies (Sarnat et al. 2014).

Diagnosis among introduced *Pheidole*. Color variable. **Major** Head subquadrate (Fig. 7). Longitudinal carinae extend from anterior frons margin a variable distance beyond frontal carinae, but never reach posterior head margin (Fig. 25). Rugae of posterolateral lobes variable from mostly absent, to predominantly longitudinal, to distinctly reticulated. Posterior head margin always free of distinct rugae (Fig. 25) or rugoreticulum (Fig. 27). Microsculpture of posterolateral lobes variable from glossy to moderately punctate. Hypostoma with stout median and submedian teeth (Fig. 19). Promesonotal dorsum usually with distinct transverse striae (Fig. 21), but sometimes lacking distinct striae. Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Promesonotum not strongly transverse with strongly projecting sides in dorsal view (Fig. 29). Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole relatively narrow in dorsal view; distinctly less than 2× petiolar width. Gaster with entire first tergite glossy (Fig. 32). **Minor** Head covered in punctate microsculpture, giving it a dull appearance. Posterior portion of head lacking many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (Fig. 60). Antennal scapes often, but not always, surpass posterior head margin; if they do it is usually by a distance less than eye length. Antennal scapes with standing hairs present (Fig. 56). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Hairs on mesosoma fine and flexuous, not arranged in pairs (Fig. 54). Pronotal humeri not angular. Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole relatively narrow (Fig. 30); distinctly less than 2× petiolar width in dorsal view. Gaster with entire first tergite glossy (Fig. 32).

Identification, taxonomy and systematics. Members of the *P. flavens*-complex are small species ranging from yellowish to dark reddish brown. The head and mesosoma of the minor workers are covered by densely punctate ground sculpture. The head of the major worker tends to be shinier with the posterior margin always free of sculpture. Among the species treated here, those of the *flavens* complex are most easily

confused with those of the closely related and often sympatric *P. punctatissima* clade (*P. anastasii*, *P. bilimeki*, *P. punctatissima*). The postpetiole is narrower in the *P. flavens* complex (Fig. 30, major; Fig. 61, minor) relative to those of the *P. punctatissima* clade (Fig. 31, major; Fig. 62, minor). The gaster is completely glossy in both subcastes of the *P. flavens* complex (Fig. 32), while at least the basal portion of the first gastral tergite is matte in those of the *P. punctatissima* clade. In the *P. flavens* complex the minors have finer hairs of variable lengths on the mesosoma (Fig. 54) and the antennal scapes have many erect to suberect hairs (Fig. 56). In contrast the *P. punctatissima* clade have thicker mesosoma hairs of equal length (Fig. 53) and lack erect antennal scape hairs (Fig. 55). The minors of the *P. flavens* complex are very difficult to distinguish from those of *Pheidole parva*. They can be separated by the lack of interlacing striae on the posterior head margin (Fig. 60, *P. flavens* complex *vs*. Fig. 59, *P. parva*). See key for additional characters.

The *P. flavens* group as defined by Wilson (2003) is now known to be polyphyletic (Moreau 2008), and unpublished data analyzed by the authors suggests that the *P. flavens* complex as defined by Wilson also lacks monophyly. *Pheidole exigua* is morphologically quite similar to the aforementioned taxa, and future attempts to define the *flavens* complex clade should include it in analyses, along with *P. glomericeps* and possibly other species not initially considered by Wilson.

The most recent phylogeny of *Pheidole* includes eight taxa that form a well-supported *P. flavens* clade (Economo et al. 2015). The clade consists of taxa that have been determined by various ant taxonomists as *P. moerens*, *P. flavens*, *P. glomericeps*; several morphospecies including *Pheidole* sp. JTL-177 and a *P. flavens*-complex taxon recently established on Vanuatu (Sarnat et al. 2014); and also the species we refer to as *P. navigans* Forel. Although these taxa represent only a fragment of the diversity attributed to the *P. flavens* complex, the analysis demonstrates the taxonomic confusion of the clade. For example, the *P. moerens* sample from the Dominican Republic is most closely related to the taxa recently discovered on Vanuatu in the South Pacific. There is strong support for these taxa being more closely related to *Pheidole* JTL-177 (Venezuela) and two taxa from Central America determined as *P. flavens* (collection codes PSW16014 and JTL4928) then to *P. navigans* from Alabama (collection code PSW15833) and Venezuela (collection code PSW16167). The Alabama and Venezuela *P. navigans* are actually most closely related to a taxon determined as *P. glomericeps* (collection code Wa-D-01-2-16).

Pheidole indica **Mayr**

Figs 73, 78, 88f

indica. *Pheidole indica* Mayr 1879: 679 (s.w.q.) INDIA, Calcutta [NHMW, paralectotype s.w., examined]. Forel 1902b: 199 (m.); Imai et al. 1984: 6 (k.). Lectotype designated Eguchi 2004b: 199 (s.).

Note. Material of the unavailable name *Pheidole javana* r. *jubilans* var. *formosae* Forel 1912: 60 referred to *Pheidole indica*: Eguchi 2004b: 199.

striativentris. *Pheidole striativentris* Mayr 1879: 678 (s.) INDIA: Calcutta. Forel 1902b: 195 (w.q.). Junior synonym of *indica*: Eguchi 2004b: 199.

teneriffana. *Pheidole teneriffana* Forel 1893b: 465 (s.w.) SPAIN, Canary Is. (s.) Laguna, Tenerife (M. Medina); (q.) Las Palmas, Canarías (Cabrera y Díaz). [Also described as new by Forel 1894a: 160.] Queen described: Santschi 1908: 521. Male described: Gómez and Espadaler 2006: 229. **n. syn.**

voeltzkowii. *Pheidole voeltzkowii* Forel 1894b: 227 (s.w.m.) MADAGASCAR. Queen described: Forel 1897: 207. Junior synonym of *teneriffana*: Fischer and Fisher 2013: 340. **n. syn.**

himalayana. *Pheidole indica* r. *himalayana* Forel 1902b: 185 (s.), 199 (w.) INDIA. [Also described as new by Forel 1902a: 546.] Raised to species: Bingham 1903: 265. Subspecies of *indica*: Emery 1921: 91; Menozzi 1939: 298; Pisarski 1967: 385. Junior synonym of *indica*: Eguchi 2004b: 198.

rotschana. *Pheidole indica* r. *rotschana* Forel 1902b: 185 (s.), 199 (w.m.) INDIA: Poona, Orissa, Trevandrum and Thana. Lectotype designated Eguchi 2004b: 199 (s.) INDIA: Poona. Imai et al. 1984: 6 (k.). [Also described as new by Forel 1902a: 546.] Raised to species: Bingham 1903: 264. Subspecies of *indica*: Forel 1909b: 394; Forel 1911a: 222. Junior synonym of *indica*: Eguchi 2004b: 199.

taina. *Pheidole teneriffana* subsp. *taina* Aguayo 1932: 219 (s.) CUBA, Holguín, viii.1930 (C.G. Aguayo). Junior synonym of *teneriffana*: Wilson 2003: 640. See also: Baroni Urbani 1968: 438; Snelling, R.R. 1992: 121. **n. syn.**

Diagnosis among introduced *Pheidole*. Light to dark reddish brown. **Major** HW 1.32–1.74, HL 1.31–1.76, SL 0.73–0.91, CI 94–117, SI 47–62 (n=22). Head subquadrate (Fig. 7); rugoreticulate on posterolateral lobes and laterad of frontal carinae (Fig. 13a), but frons dominated by long, well-organized and parallel longitudinal rugae (Fig. 13b). Frontal carinae extend 3/4 distance of head before terminating (Fig. 15). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (Fig. 13c). Hypostoma with weakly produced median tooth and submedian teeth. Promesonotum in profile with two convexities (Fig. 5), the large anterior dome in addition to a distinct mound or prominence on the posterior slope. Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.50–0.65, HL 0.60–0.74, SL 0.64–0.81, CI 72–90, SI 120–149 (n=20). Head predominantly glossy (Fig. 36), lacking punctation and or rugae above eye level. Posterior head margin weakly convex to flat in full-face view (Fig. 45). Antennal scapes long (e.g. Fig. 39), but not surpassing the posterior head margin by more than 2× eye length. Promesonotum in profile with two convexities, the large anterior dome (Fig. 43a) in addition to a distinct prominence on the posterior slope (Fig. 43b). Promesonotal prominence relatively convex (Fig. 50a). Metanotal depression relatively shallow (Fig. 50b). Petiole and postpetiole glossy to very weakly sculptured laterally (Fig. 48). Postpetiole not swollen relative to petiole (Fig. 3).

Identification, taxonomy and systematics. *Pheidole indica* is a medium to large reddish brown species with relatively long limbs. It belongs to the *P. fervens* clade along

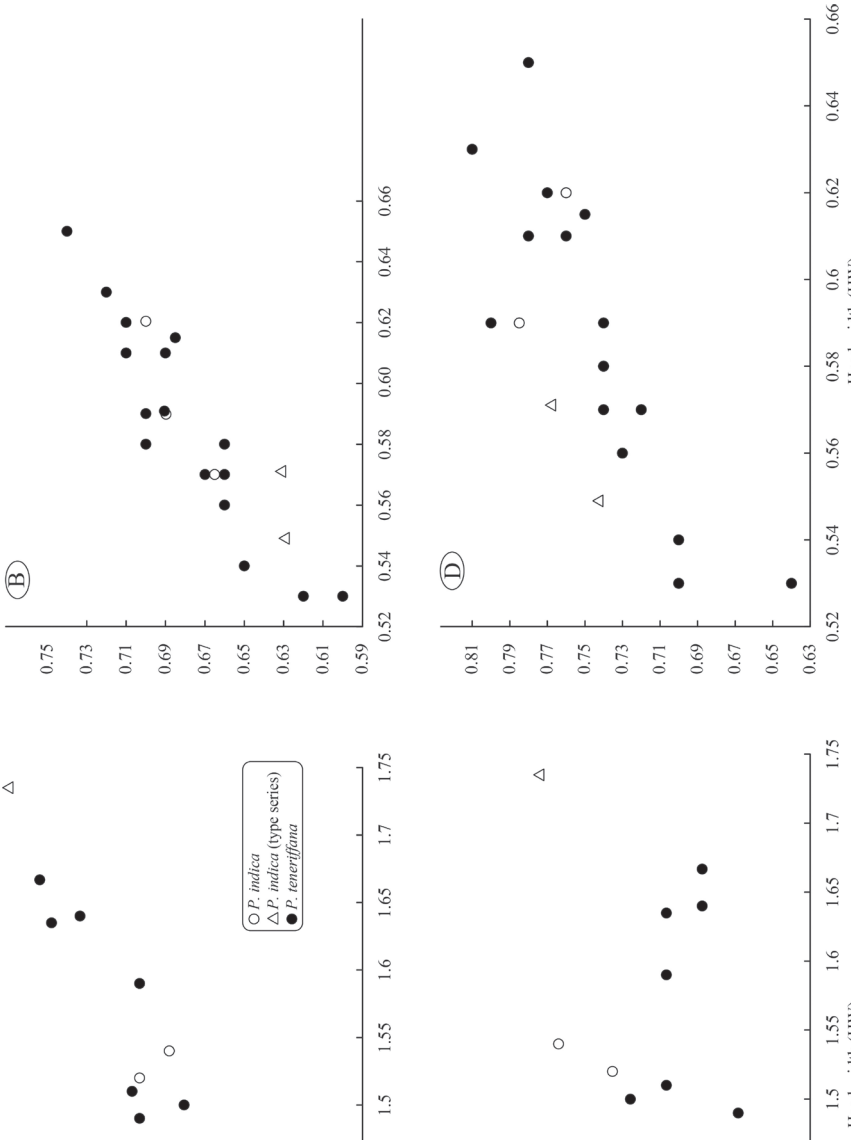


Figure 73. Relative morphometric measurements of *P. indica* paralectotypes, specimens previously determined as *P. indica*, and specimens previously determined as *P. teneriffana*. All values are in mm. **A** Head length *vs.* head width, major workers. **B** Head length *vs.* head width, minor workers. **C** Scape length *vs.* head width, major workers **D** Scape length *vs.* head width, minor workers.

with its Australasian congeners *P. cariniceps*, *P. fervens*, *P. hospes*, *P. impressiceps*, and *P. oceanica* (Economo et al. 2015, unpublished data). The major and minor workers are distinguished from those of *P. megacephala* by the lack of a swollen postpetiole (Fig. 3). The majors are also easily separated from those of *P. megacephala* by the strongly sculptured head (Fig. 13). The minors can be confused with those of *P. megacephala* because both have glossy heads. However, the minors of *P. fervens* can be separated from those of *P. megacephala* by the relatively longer antennal scapes (Fig. 39 *vs*. Fig. 40) and the presence of a promesonotal prominence (Fig. 43 *vs*. Fig. 42). *Pheidole indica* is broadly sympatric with *P. noda* and *P. fervens*. It is easily separated from the former by the lack of a swollen postpetiole (Fig. 3 *vs*. Fig. 2). Separation from *P. fervens* is quite difficult, and readers are referred to corresponding section under that species for distinguishing characters. Readers are referred to Eguchi (2004b; 2008) for characters used to separate *P. indica* and *P. fervens* from their Asian congeners.

Pheidole indica was originally described from India. Eguchi (2004b) synonymized several other Asian congeners under *P. indica* and discussed taxonomic differences used to distinguish it from *P. fervens* and other morphologically similar species. We synonymize *P. teneriffana* under *P. indica* based on morphological analysis of the type specimens and genetic analysis of previously determined specimens (unpublished data). Forel, in his original description of *P. teneriffana*, noted the similarity between it and *P. striativentris* [= *indica*].

The biogeographical origin of *P. teneriffana* has been a minor mystery of the past century, as revealed by the recent review of the species by Wetterer (2011). There appeared to be general consensus that *P. teneriffana* was native to at least some portion of North Africa, Arabia, the Middle East or the Mediterranean. Santschi (1918), suggested the upper Nile area (South Sudan). Wilson (2003) suggested North Africa and potentially the Canary Islands. Collingwood et al. (2004) suggested it was native throughout northern Africa and observed it to be, "spreading over a wide front in the Middle East, Arabia and the Mediterranean countries." Wetterer (2011) found the distribution of *P. teneriffana* enigmatic, "Curiously, most Old World records of *P. teneriffana* are subtropical, but all New World records are tropical, except one from California…If *P. teneriffana* is truly native across North Africa, it is remarkable how few records I found from any North African country other than Egypt."

Biology. In Asia *P. indica* is known to nest in soil or under stones in open and dry habitats (Eguchi 2004b). It is among the most widespread *Pheidole* species in Asia. In the Caribbean Wetterer (2011) found *P. indica* [as *P. teneriffana*] almost exclusively on beaches and at highly disturbed urban sites, particularly in waterfront areas. In northern Africa, Santschi (1908) noted the tramp-like distribution of what he treated as *P. teneriffana*, "This species, described by Forel on samples from the Canary Islands, was sent to me from Cairo. I discovered it most recently in Sousse [Tunisia], in the park, near the port. As it does not exist in the interior, I think it is one species cosmopolitan tendencies. It nests in the ground and under stones." Santschi (1934) later reported the species from Alexandria, Egypt, and noted that *P.*

teneriffana was rarely reported far from seaports. Collingwood et al. (1997) reported that in the United Arab Emirates, *P. indica* [as *P. teneriffana*] was populous in irrigated gardens and along the coast where it appeared to be spreading rapidly, possibly to the detriment of local species. The species has also been reported from urban areas of the Balearic Islands where it is common in the gardens and trees and on sidewalks near the harbor (Gómez and Espadaler 2006). Fischer and Fisher (2013) reported *P. indica* [as *P. teneriffana*] from the Malagasy region. It was collected on the Comoros, Mauritius, the Seychelles, and from coastal towns in Madagascar, usually from under stones, ground nests, or foraging on the ground or lower vegetation in urban or garden habitats at elevations below 300 m. It was also found on Mayotte in native littoral and secondary forest below 10 m.

Perhaps the most detailed study of *P. indica* in the New World comes from the account of Martínez (1992) who reported a vigorous population, represented by a putatively single polydomous colony spanning several hectares, that was discovered in Long Beach, California in 1989. Martínez (1992) reportedly observed 23 inseminated queens from a single colony that was changing nest sites (although no details are given for how he knew the queens were inseminated). He described the colony nests as low mounds on the soil, along curbs or sidewalks, at the edges of lawns, in cracks in pavement, and at the bases of trees. New colonies were started by budding. Workers foraged night and day unless temperature exceeded 26 °C, taking seeds and scavenging dead or dying insects. They were observed feeding on sweet or greasy foods, but were not seen tending aphids. Martínez (1992) observed the species attacking native ants, including *Pogonomyrmex californicus* (Buckley). More remarkably, he reportedly observed *P. indica* destroying colonies and taking over nest sites of *Linepithema humile*. Despite the purported success of these battles, *P. indica* must have lost the larger war against *L. humile*, as the eventual extirpation of the Californian population was attributed to the Argentine ant (Gulmahamad 1999).

Distribution. We treat all occurrence records from the regions of Indomalaya west of the Korean Peninsula as native. The Korean and Japanese populations are considered introduced (Choi and Bang 1993; Choi et al. 1993a; Choi et al. 1993b; Terayama 1992), and additional portions of the range in Asia might also have resulted from anthropogenic transport. *Pheidole indica* has been introduced to scattered localities across the globe, although the vast majority of these records were attributed to its junior synonym, *P. teneriffana*. Introduced populations have been reported from the Mediterranean, northern Africa, the Malagasy region, Western Australia, Peru, the Caribbean, and southern California.

Risk statement. *Pheidole indica* is not considered to be a major pest to either agriculture or native ecosystems. Although the species is tolerant of disturbed and urban areas, we found no reports of it infesting structures. Few studies have measured the effect of *P. indica* on ecosystem health, but we predict that it could negatively impact native arthropods. The species is continuing to spread across the globe and further studies are required to test its ecological and agricultural impact outside its native range.

***Pheidole megacephala* (Fabricius)**
Figs 79, 88g

edax. *Formica edax* Forskål 1775: 84 (w.) EGYPT. Junior synonym of *megacephala*: Emery 1892: 160; Dalla Torre 1892: 90. [If synonymy correct then *edax* is the senior name; however, under Art. 23.9 of ICZN (1999) *edax* is a *nomen oblitum*.]

megacephala. *Formica megacephala* Fabricius, 1793: 361 (s.) MAURITIUS 'Ile de France' [presumed lost]. Neotype (s.) designated: MAURITIUS, Camizard Mt., Bambous, 20.3328 S, 57.723 E, 375 m, rainforest, ex rotten log, collection code BLF12051, 27.v.2005 (*B.L. Fisher et al.*) (CASC: CASENT0104990): (Fischer and Fisher 2013): 332. Latreille 1802: 232 (q.); Mayr 1861: 70 (s.w.q.m.); Wheeler, G.C. & Wheeler, J. 1953: 75 (l.). Combination in *Pheidole*: Roger 1863b: 30. [*P. megalocephala* Schulz 1906: 155; unjustified emendation.] Current subspecies: nominal plus *costauriensis*, *duplex*, *ilgi*, *impressifrons*, *melancholica*, *nkomoana*, *rotundata*, *speculifrons*, *talpa*.
Note: *Pheidole megacephala* Smith, F. 1860: 112 is a junior synonym of *Carebara diversus* (Jerdon): Emery 1893: 206.

trinodis. *Myrmica trinodis* Losana 1834: 327, pl. 36, fig. 6 (w.) ITALY, Piedmont. Junior synonym of *megacephala*: Roger 1863b: 30.

pusilla. *Oecophthora pusilla* Heer 1852: 15, pl. 1, figs. 1-4 (s.w.q.m.) PORTUGAL, Madeira I. Combination in *Pheidole*: Smith, F. 1858: 173. Subspecies of *megacephala*: Emery 1915b: 235. Senior synonym of *janus*: Mayr 1886: 360; of *laevigata* Smith: Roger 1859: 259; Emery 1915b: 235; of *laevigata* Mayr: Mayr 1870b: 981 (footnote). Junior synonym of *megacephala*: Wheeler, W.M. 1922b: 812.

laevigata. *Myrmica* (?) *laevigata* Smith 1855: 130, pl. 9, figs. 7, 8 (w.) GREAT BRITAIN, Battersea. Junior synonym of *Pheidole pusilla*: Roger 1859: 259; of *Pheidole pallidula*: Smith 1858: 282; of *Pheidole megacephala*: Roger 1863: 30; of *Pheidole pusilla*: Emery 1915: 235.

agilis. *Myrmica agilis* Smith, F. 1857: 71 (w.) MALAYSIA, Malacca. Combination in *Pheidole*: Donisthorpe 1932: 449. Junior synonym of *megacephala*: Eguchi 2008: 56.

janus. *Pheidole janus* Smith, F. 1858: 175, pl. 9, figs. 13-17 (s.w.) SRI LANKA. Junior synonym of *pusilla*: Mayr 1886: 360.

testacea. *Atta testacea* Smith, F. 1858: 168 (s.w.) BRAZIL. Combination in *Pheidole*: Mayr 1886: 360. Junior synonym of *megacephala*: Brown 1981: 530.

perniciosa. *Oecophthora perniciosa* Gerstäcker 1859: 263 (w.) MOZAMBIQUE. [Also described as new by Gerstäcker 1862: 516.] Combination in *Pheidole*: Roger 1863b: 31. Junior synonym of *megacephala*: Emery 1915b: 235.

suspiciosa. *Myrmica suspiciosa* Smith, F. 1859: 148 (w.) INDONESIA, Aru I. (A.R. Wallace). Junior synonym of *megacephala*: Donisthorpe 1932: 455.

laevigata. *Pheidole laevigata* Mayr 1862: 747 (s.) BRAZIL. Unresolved junior secondary homonym of *Pheidole laevigata* Smith, F. Junior synonym of *Pheidole pusilla*: Mayr 1870: 981 (footnote).

scabrior. *Pheidole megacephala* var. *scabrior* Forel 1891: 178 (s.w.) MADAGASCAR. Junior synonym of *megacephala*: Fischer and Fisher 2013: 333.

picata. *Pheidole megacephala* var. *picata* Forel 1891: 178 (s.w.) MADAGASCAR. Subspecies of *megacephala*: Forel 1895: 49; of *punctulata*: Forel 1897: 186; Forel 1905: 163; Santschi 1910: 370. Raised to species: Emery 1915b: 245; Wheeler, W.M. 1922a: 1019. Junior synonym of *megacephala*: Fischer and Fisher 2013: 333.

gietleni. *Pheidole punctulata* r. *gietleni* Forel 1905b: 164 (s.w.) MADAGASCAR. Subspecies of *picata*: Emery 1915b: 245. Junior synonym of *megacephala*: Fischer and Fisher 2013: 333.

bernhardae. *Pheidole picata* var. *bernhardae* Emery 1915b: 245 (s.w.) MADAGASCAR. [First available use of *Pheidole punctulata* r. *spinosa* var. *bernhardae* Forel, 1905: 164; unavailable name.] Junior synonym of *megacephala*: Fischer and Fisher 2013: 333.

Diagnosis among introduced *Pheidole*. Light brown to dark brown. **Major** HW 1.10–1.54, HL 1.04–1.59, SL 0.59–0.76, CI 97–106, SI 47–58 (n=19, Fischer and Fisher 2013). Head heart-shaped (Fig. 6); posterior 1/3 of dorsal surface smooth, glossy and entirely lacking rugoreticulate sculpture. Hypostoma lacking distinct median and submedian teeth. Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Postpetiole with a posterodorsal (Fig. 1a) and anteroventral (Fig. 1b) bulge. **Minor** HW 0.50–0.61, HL 0.57–0.68, SL 0.61–0.72, CI 86–92, SI 114–122 (n=20, Fischer and Fisher 2013). Head predominantly glossy (Fig. 36), lacking punctation and or rugae above eye level. Antennal scapes surpass posterior head margin by approximately same length as eye (Fig. 40). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Postpetiole with a posterodorsal (Fig. 1a) and anteroventral (Fig. 1b) bulge.

Identification, taxonomy and systematics. *Pheidole megacephala* is a medium sized species of variable color that is most easily recognized outside of its native range by the heart-shaped head and bulging postpetiole. It belongs to a diverse and taxonomically confusing clade of morphologically similar taxa centered in the Afrotropical and Malagasy regions. Both major and minor workers are distinguished from all other introduced *Pheidole* by the swollen shape of the postpetiole (Fig. 1). *Pheidole noda* also has a swollen postpetiole, but whereas the postpetiole of *P. megacephala* is characterized by a posterodorsal and anteroventral bulge, that of *P. noda* is formed as a high dorsally bulging dome that is tallest at its midpoint.

Pheidole megacephala has often been confused for *P. pallidula* Nylander in Europe, especially in the Mediterranean region. The introduced populations of *P. megacephala* can be distinguished from *P. pallidula* by the following characters. For both major and minor workers the postpetiole of *P. megacephala* has a posterodorsal (Fig. 1a) and anteroventral (Fig. 1b) bulge, while that of *Pallidula* is not swollen relative to petiole (Fig. 3). The propodeal spines of both subcastes are distinct in *P. megacephala* but are strongly reduced in *P. pallidula*. Additionally, the major worker of *P. megacephala* has a heart shaped head that broadens significantly posterior to eye-level (Fig. 6) while the head of *Pallidula* is more rectangular (more approximate to Fig. 7).

Accurate identification within the Afrotropics is more problematic. While for Madagascar previously described subspecies have been synonymized with *P. megacephala* (Fischer and Fisher 2013), the taxonomy of the *megacephala* group in Africa remains rather chaotic with a number of unrevised subspecies, most of which remain insufficiently characterized. In a taxonomic overview of the group, Emery (1915) studied type and non-type material of *P. megacephala*-related species, yet for several subspecies he was not able to define clear species limits from the multitude of different, yet highly similar, phenotypes. We suspect that some of those names are probably due to intraspecific variation within *P. megacephala* and *P. punctulata* Mayr. Other, morphologically unique taxa like *P. megacephala nkomoana* Forel are clearly valid biological species. However, without a comprehensive taxonomic treatment supported by a robust phylogeny, the following species characterizations may be subject to future taxonomic changes.

Within the *megacephala* group, minor workers are difficult to separate morphologically and thus have only limited use for species identification, but the majors tend to be more distinct in their morphologies and can be separated by differences in head and body shape and sculpture, and in size and pilosity, although the limits are often unclear and characters are sometimes distributed along a continuum rather than being separated into distinct, clear-cut states.

Major workers of *P. megacephala melancholica* Santschi are characterized by presence of weak punctures on the majority of the head, including the sides in lateral view, promesonotum with punctures and irregular transverse rugulae, and moderately abundant short and stout standing hairs on head and body, whereas major workers of *P. megacephala* entirely lack punctures on the posterior 1/3 of the head, have a mostly smooth and glossy promesonotum, and often possess longer, more flexuous standing hairs, which often branch at the tips. *Pheidole megacephala nkomoana* majors are characterized by a weakly defined antennal scrobe and relatively long frontal carinae that reach about ¾ towards the posterior head margin, two well-defined submedian hypostomal teeth, a weak prominence on the promesonotal dome, and very long, flexuous standing hairs on the dorsal promesonotum. Also the spines tend to be shorter than in *P. megacephala*, in length almost equal to the diameter of the propodeal spiracle. Both subspecies have been described from and collected in western African forests. Another closely related species to *P. megacephala* is *P. punctulata*. It is very widespread in sub-Saharan Africa and usually found in dry forests and grassland habitats. Morphologically close to *P. megacephala*, its major workers can be distinguished by their often enlarged and strongly heart-shaped heads, the presence of a softly or superficially punctuated sculpture on parts of the head dorsum, promesonotum, postpetiole and gaster, and relatively uniform, short and stout, erect hairs covering the body. Minor workers tend to be slightly larger and more robust than in *megacephala*, often with a few oblique carinae present between the eyes and the mandibles and reaching the posterior eye level, the hairs similar as in major workers and usually more abundant than in *P. megacephala*.

Morphologically very similar to *P. punctulata* are *P. megacephala ilgi* Forel, *megacephala impressifrons* Wasmann, and *megacephala rotundata* Forel. Like *P. punctulata*,

they are usually found in drier forest and grassland habitats and their workers seem to be highly polymorphic, which means that in addition to normal major workers, colonies are capable of producing so-called supermajors. These supermajors possess a very strongly heart-shaped head, which can be disproportionately big compared to the size of the mandibles and the rest of their bodies. As Emery (1915) stated for *P. megacephala rotundata*, on first glace they look quite distinct from *P. punctulata*, but at closer examination of series with different major worker sizes it seems impossible to define species limits. From our own observations it seems likely that these subspecies are a result of sampling bias and phenotypic variation within *P. punctulata*, rather than historic speciation events (Fischer et al., in preparation). Incomplete sampling can also be a problem when only smaller major and minor workers are collected, which are often very similar to those of *P. megacephala*, with very similar head sculpture and general morphology.

In the Malagasy region, *P. megacephala* can be confused with three other species: *Pheidole punctulata spinosa* Forel, which, on average, has longer spines, a slightly higher propodeum and a more extensively smooth and glossy posterior portion of the head in the larger major workers. *Pheidole megatron*, which was described from the Comoros and is possibly present in the Northwest of Madagascar as well, is characterized by major workers with a less heart-shaped, and slightly more rectangular head shape, and sometimes sculpture and rugulae present on the posterior head portion (see Fischer and Fisher 2013). Finally, *P. decepticon*, described from Mayotte and distributed over several of the smaller Southwest Indian ocean islands, is characterized by possessing a denser, more prominent and longer pilosity as well as slightly smaller, less rounded ventral bulges on the postpetiole in both minor and major workers (see Fischer and Fisher 2013). It is however possible that *P. decepticon* is a geographic variation of and conspecific with *P. punctulata spinosa*.

Biology. *Pheidole megacephala* is listed among the top five invasive ants (Lowe et al. 2000). Although this species prefers humid and disturbed habitats where it is usually found in very high abundances (Burwell et al. 2012; Hoffmann et al. 1999; Wilson 2003), it can generally be found in a large variety of landscapes, from coastal habitats to human settlements and plantations in lower elevations, degraded dry forest, to mid-elevation rainforest or even montane forest – in Papua New Guinea up to 2150 meters altitude (Fischer and Fisher 2013). The distribution range and activity of *P. megacephala* appears to be somewhat limited by susceptibility to desiccation and higher temperatures. Thus, colonies are often found in more humid microhabitats, and workers tend to forage inside the leaf-litter and at night, or even build covered trails (Greenslade 1972, personal observations). However, some studies reported that on smaller islands or after successful introduction in a new area, *P. megacephala* expanded its range and invaded into the forest interiors where it attacked and displaced other introduced and natively occurring ant species (Burwell et al. 2012; Hoffmann 1998). In a citrus orchard in Tanzania for example, *P. megacephala* was able to partly displace highly territorial and competitive *Oecophylla* weaver ants (Seguni et al. 2011). *Pheidole megacephala* is an especially common and abundant nuisance and pest on islands, which are generally more strongly impacted by invasions of alien species.

Part of the success of *P. megacephala* as a pantropic pest species is its generalist behavior. Like many other *Pheidole* species its diet is broadly omnivorous with a large proportion of its food probably acquired by scavenging on the ground. *Pheidole megacephala* is also a good predator with an efficient nest mate recruitment that enables the species to dominate baits and to retrieve prey too large for single workers to carry (Dejean et al. 2008; Dejean et al. 2007). Devastating effects on the abundance and diversity of native invertebrates, in northern Australia for example, are well documented (Hoffmann 1998; Hoffmann et al. 1999; Hoffmann and Parr 2008). *Pheidole megacephala* has also been documented to negatively impact agricultural systems. Workers tend plant and crop-damaging scale insects for honeydew (Campbell 1994; Gaigher et al. 2011; González Hernández et al. 1999; Greenslade 1972; Petty and Tustin 1993; Reimer et al. 1993), protect plants with extrafloral nectaries from phytophagous insects and possibly collect seeds (Hoffmann 1998). A recent study experimentally evaluating the performance in interference competition found that *P. megacephala* ranked lowest among seven of the world's worst most destructive invasive ant species (Bertelsmeier et al. 2015). The authors, citing Dejean et al. (2008) suggested that *P. megacephala* does not dominate invaded ant communities through direct physical interactions (interference competition) but by raiding their colonies.

Nesting sites are variable and can occur in any crack and crevice that is large enough for them to enter, including soil, inside rotting logs, under rocks, in houses or in tree bark. As in several other invasive ant species, colonies are polygynous, and dependently founded via budding, with nests in large areas often forming supercolonies (Hoffmann 1998) that aggressively fight other ants or outcompete them by depleting their prey and other resources (Dejean et al. 2008; Fournier et al. 2009; Hoffmann et al. 1999; Vanderwoude et al. 2000).

Distribution. *Pheidole megacephala* is a cosmopolitan species that has established across the globe as a household and agricultural pest throughout the tropics. Wetterer (2012) provided a detailed review of the worldwide spread of *P. megacephala*, and cites Wheeler's statement (Wheeler 1922a) that it is most likely of Afrotropical or Malagasy origin, the only two regions with a diversity of related species ("subspecies and varieties"). Theoretically it is possible that a common ancestor of *P. megacephala* and the Malagasy endemics *P. punctulata spinosa*, *P. megatron* and *P. decepticon* arrived on the islands in prehistoric times, diversified there, and that *P. megacephala* was later transported to all other regions including Africa only after the arrival of humans. But the distribution of *P. megacephala* on Madagascar strongly resembles the distributions of other invasive species on the island – e.g. those of *Monomorium floricola*, *M. pharaonis*, *Tapinoma melanocephalum*, *Technomyrmex albipes*, *Trichomyrmex destructor*. While *P. punctulata spinosa* has established a broad distribution range across the island's variable habitats and elevations, *P. megacephala*, like the other invasives, is found mostly along the coast, in low elevation and disturbed habitats or near human settlements.

Similar to Wheeler's observation, our argument for the "out-of-Africa" hypothesis is an overall much higher complexity in different morphotypes and species-level diversity in African *megacephala* group taxa and the presence of both, very closely, but also

more distantly related taxa (e.g *Pheidole aurivillii* Mayr). For these reasons and for the purposes of this study, we consider all records from Africa to represent the native range of *Pheidole megacephala*. However, a further resolution will require a comprehensive phylogeographic study of the species and its allied taxa, especially from the poorly studied and sampled African region.

Populations of *P. megacephala* recorded from the southwestern extent of the Arabian Peninsula are treated as native as this region is commonly considered as belonging to the Afrotropics. However, recent studies on generic distributions of global ant diversity that find little support for including any portion of the Arabian Peninsula in the Afrotropics (unpublished data). Until robust phylogeographic data is available for *P. megacephala*, this decision must be considered tentative and open to future revision.

We do agree with Wetterer's (2012) conclusions that records of *P. megacephala* from Mediterranean Europe northward are either temporary indoor records or misidentifications of *P. pallidula*. Outside of Africa, the Malagasy region and the range of *P. pallidula* (western Palearctic), *P. megacephala* is easily recognized as it does not co-occur with species of similar morphology. We therefore consider all records reviewed from outside the aforementioned regions as confirmed unless otherwise stated.

Dubious records. The following records are considered dubious mostly because there is reason to believe they represent misidentifications of *P. pallidula*. However, it is possible that some of the following literature records were based on accurate identifications, but that *P. megacephala* was since extirpated from the referenced localities. This latter possibility is plausible especially for the Mediterranean region where *L. humile* has established a stronghold. For example, (Heer 1852) described *Oecophthora pusilla* (=*P. megacephala*) as ubiquitous on the island of Madeira, "In the town of Funchal there is probably not a single house that does not harbor millions of the tiny creatures…" Less than a century later Wheeler (Wheeler 1927b) reported, "Now it is an interesting fact that the Argentine ant, soon after its arrival in Madeira, completely replaced the *Pheidole* as a house ant." Similar instances of well-established populations of introduced ant species becoming locally extirpated have been documented (Moreau et al. 2014; Wetterer 2006).

ALGERIA: The material referred to by André (1883) *P. megacephala* is distinguished by that author from *P. pallidula* only by the difference in size of the propodeal spine, and was otherwise observed to be identical. Considering the other characters separating these two species discussed earlier, we tentatively consider this record to be a misidentification of *P. pallidula*. CROATIA: The material listed from this country (Petrov and Collingwood 1992; Petrov and Legakis 1996) is considered to refer to *P. pallidula* according to Bračko (2006). EGYPT: Egypt is the type locality of the *nomen oblitum Formica edax* Forskål. Emery (1892) wrote that *edax* is undoubtedly a small *Pheidole*, and possibly refers to *P. megacephala*. Dalla Torre (1892) was also uncertain as to which species (or even genus) the name *edax* referred to. Given the uncertainty of these two authors, the occurrence of *P. pallidula* in Egypt and the unconfirmed single literature record of Bakr et al. (2007), it is difficult to know when *P. megacephala* was first reported from Egypt. FRANCE: Bignell (1901) reported the ant species listed in his study of Corsica were

identified by Saunders, who is known to have confused *P. pallidula* for *P. megacephala*. As *P. pallidula* was not listed in the publication, we consider the record to either be a misidentification of that species or from an extirpated population. GREECE: The only primary references to an outdoor occurrence we could confirm are Collingwood (1993) and Borowiec and Salata (2012). The former authors reported *P. megacephala* was found only once during their study of five Greek islands on the threshold of a small hotel in Pigadhia on Karpathos. The second study reported finding the species on a road in Crete. The record from Macedonia in (Karaman 2011) is from material identified by Petrov. We tentatively follow (Bračko 2006) as treating this as a misidentification of *P. pallidula*. ITALY: Piedmont is the type locality for *Myrmica trinodis* Losana which was synonymized with *megacephala* by Roger in 1863. Losana also lists a *M. megacephala* Latrielle in the same publication. Latrielle never described any species by the name *megacephala*, however. Losana might have instead been referring to *Messor megacephala* Leech (= *Messor barbarous* Mayr). Regardless, the original description of *M. trinodis* states that the species was collected from outdoor gardens. There is some reason to suspect this name might refer instead to *P. pallidula*, as the only verifiable occurrences of *megacephala* in Italy since are for specimens collected from plant nurseries, greenhouses and cargo hangars used for holding imported plants, fruits and vegetables (Jucker et al. 2008; Limonta and Colombo 2003). MOROCCO: Saunders (1888) appears to be the only primary reference for *P. megacephala* occurring in Morocco, but it is likely that the author was referring to misidentified material of *P. pallidula* (Wetterer 2012). This view is further evidenced by Cagniant and Espadaler (1993) who were unable to find the species in their survey. SPAIN: We consider the following records from the Balearic Islands and Gibraltar to refer to *P. pallidula* (Saunders 1888; Saunders 1904; Walker 1889). USA: The specimens reported in Fischer and Fisher (2013) from Arizona were from a quarantine collection intercepted from Florida, and there is no reason to believe the species has ever established in Arizona. Wetterer (2012) cited a specimen record of *P. megacephala* from Catalina Island (California). If the identification proves accurate, it is the only known record from that island and the population has since been extirpated (perhaps by *L. humile*). However, a population (CASENT0248690) has been discovered recently in southern California (Orange Co.). Although *P. megacephala* is listed in the Missouri Ants web page (2015), we cannot verify the entry with any specimen or literature record.

Risk statement. *Pheidole megacephala* is known as a major agricultural and ecological pest species (Williams 1994) and its widespread pantropic distribution and often very close association with humans make it a high-risk invasive species with a serious potential for ecological, agricultural and economic damage. In Ward et al. (2006) it has been the most intercepted exotic ant species (890 out of 4355 interception records between 1955 and 2005) arriving with trade products in New Zealand. Many aspects of its biology indicate that it is highly adaptable and thus able to survive outside of its preferred habitat, by finding suitable microhabitats for nesting and by killing or outcompeting native species. Although mutualistic relationships with scale insects and other crop pests are dominant in agricultural systems with introduced *P. megacephala*, positive side-effects on plant fitness have been observed as well (Bach 1991).

***Pheidole navigans* Forel, stat. rev., stat. n.**
Figs 80, 88h

navigans. *Pheidole flavens* r. *navigans* Forel 1901a: 79 (s.w.) GERMANY (intercepted in quarantine from Veracruz, Mexico) [MHNG, examined photographs of CASENT0908269 (s.), CASENT0908270 (w). Junior synonym of *flavens*: Wilson 2003: 419. **stat. rev., stat. n.**

Pheidole moerens (*nec* Forel): M.R. Smith 1967, Wojcik 1975, Glancey 1976, Naves 1985, Deyrup 1988, Deyrup 2000, Dash 2008, MacGown 2010, Guénard 2012. [We propose the preceding authors misapplied the name *P. moerens* Forel to material considered here as referring to *P. navigans* Forel. *Pheidole moerens* remains a valid name].

Diagnosis among introduced *Pheidole*. Color reddish brown. **Major** HW 0.84–0.88, HL 0.88–0.91, SL 0.46–0.48, CI 95–99, SI 53–56 (n=4). Head subquadrate (Fig. 7). Longitudinal carinae of the frons extend to approximately an eye's length distance from the posterior head margin (Fig. 25). Rugae of posterolateral lobes predominantly longitudinal. Posterior head margin always free of distinct rugae (Fig. 25) or rugoreticulum (Fig. 27). Microsculpture of posterolateral lobes glossy to weakly punctate. Antennal scrobe distinct and narrow, shallow but capable of receiving the entire antennal scape in repose (Fig. 71a); bordered by strong, unbroken frontal carina mesially (Fig. 71b); depression marked by a continuous smooth surface entirely (or nearly entirely) uninterrupted by rugulae. Hypostoma with stout median and submedian teeth. Promesonotal dorsum with distinct transverse striae (Fig. 21). Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Promesonotum not strongly transverse with strongly projecting sides in dorsal view (Fig. 29). Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole relatively narrow in dorsal view; distinctly less than 2× petiolar width (Fig. 30). Gaster with entire first tergite glossy (Fig. 32). **Minor** HW 0.40–0.45, HL 0.45–0.50, SL 0.40–0.44, CI 86–92, SI 96–102 (n=8). Head covered in punctate microsculpture, giving it a dull appearance (Fig. 37). Antennal scapes reach or weakly surpass posterior head margin; if they do it is usually by a distance less than eye length. Antennal scapes with standing hairs present (Fig. 56). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Hairs on mesosoma fine and flexuous, not arranged in pairs. Pronotal humeri not angular. Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole relatively narrow (Fig. 30); distinctly less than 2× petiolar width in dorsal view. Gaster with entire first tergite glossy (Fig. 32).

Identification, taxonomy and systematics. *Pheidole navigans* is a small, short-limbed, reddish brown species that belongs to the *P. flavens* complex. See discussion under corresponding section of *P. flavens* complex for how to distinguish this species from introduced *Pheidole* outside the complex. Within the complex, minor workers are impossible to distinguish based on known characters. Major workers can be

separated from those of *P. flavens* by the combination of predominantly longitudinal rugae on the posterolateral lobes, the more distinct and narrow antennal scrobe bordered mesially by strong, unbroken frontal carina, and the more continuously glossy scrobe depression.

Although the type locality of *Pheidole navigans* is Germany, the species was originally described by Forel from specimens intercepted during quarantine inspection of orchids originating from Veracruz, Mexico. We revive this name from synonymy and elevate it to species rank so that it can be applied to a putative species that has recently established in the southeastern United States and Hawaii. This ant has most often been referred to as *P. moerens* since it was first reported from Alabama nearly fifty years ago by M.R. Smith (1967). However, the examination of type specimen photographs (MCZ-ENT00009137) suggests that these introduced populations are heterospecific with *P. moerens* Wheeler.

Whether the introduced populations are actually conspecific with *P. navigans* Forel will require a thorough revision of this taxonomically vexing species complex. Of all the type material we have examined, however, that of *P. navigans* bears the closest resemblance in gross morphology. Thus we propose *P. navigans* Forel be used in place of *P. moerens* for referring to the aforementioned introduced populations. Future systematic study of this species should also examine *P. floridana* subsp. *aechmeae* (currently synonymized under *P. flavens*, but also recorded from Veracruz, Mexico) and *P. flavens* var. *mediorubra* Santschi (described from Loreto, Argentina and currently treated as a synonym of *P. alacris* Santschi).

The major workers of *Pheidole navigans* differ from those of *P. moerens* in the following respects. They exhibit a distinct and narrow antennal scrobe capable of receiving the entire antennal scape in repose. The scrobe is bordered by a strong, unbroken frontal carina mesially, and the depression is marked by a continuous smooth surface entirely (or nearly entirely) uninterrupted by rugulae. The rugulae of the frons extend to approximately an eye's length distance from the posterior head margin. The anterior portion of the promesonotum is crossed by long and distinct transverse striae.

The examined major workers of *P. navigans* from Alabama (CASENT0106664) and Venezuela (CASENT0248831), along with those from Florida and Hawaii, and a specimen imaged from Paraguay (CASENT0178020), share a notably consistent morphology for being spread across such as wide range. The characteristics shared among these majors include the following. Frontal carinae strongly produced, forming the mesad border of a shallow but well-demarcated antennal scrobe capable of accommodating the entire scape in repose. Antennal scrobe weakly foveolate. Cephalic carinulae mostly longitudinal with very little reticulation posterior to the eye. Cephalic carinulae extending up to, but not beyond the medial excision ('V') of the posterior head margin. Promesonotal dome with a relatively low profile, mesonotal declivity short and relatively gradual. In dorsal view, promesonotum weakly punctate, anterior portion with distinct transverse carinulae. Although we tentatively treat the specimen from California (CASENT0005742) as *P. navigans*, it differs morphologically from

the aforementioned specimens and bears closer resemblance to *P. exigua* var. *tuberculata* Mayr (currently synonymized under *P. flavens*).

The similarity of these northern hemisphere specimens to the one from Paraguay raises the possibility that these putatively conspecific populations originated in South America. Indeed, the Paraguay specimen was collected in the Reserva Natural del Bosque Mbaracayú near the Río Paraná – a region infamous for serving as a cradle of ant invasion (Suarez and Tsutsui 2008).

Biology. In Florida, Naves (1985) reported *Pheidole navigans* (as *P. moerens*) nesting under boards, at base of oak trees and fence posts, along roots, under palm leaves, inside wall crevices, and rarely in the ground. The chambers are built with small soil or debris particles and have small openings. Most nuptial flights occur in July. The species was found to practice dependent nest founding, but became monogynous before the first brood was reared. Mature colonies can support over 100 majors and over 500 workers. They feed on seeds and scavenge and prey on small dead or live arthropods, and forage very close to the nesting sites. Deyrup (2000) also provided observations of this species (as *P. moerens*) from Florida, adding that it occurs in both disturbed areas and mesic or moist woods, also nests in hollow twigs, nuts and in leaf litter, and is occasionally arboreal.

Distribution. The precise native range of *P. navigans* is unknown, but it is certainly of Neotropical origin. The record of the species from the Paraná region of South America suggests it could be South America. We tentatively treat both known South American records (Paraguay and Venezuela) as native, and the Mexican record as introduced, but other scenarios are equally possible. *Pheidole navigans* was first reported as introduced in the United States by M.R. Smith (1967) under the name *P. moerens*. The name *P. moerens* has since been applied to North American records from Alabama (Glancey et al. 1976; Smith 1967), California (Garrison 1996; Martínez 1997), Florida (Deyrup et al. 1988; Deyrup et al. 2000; Wojcik et al. 1975), Louisiana (Dash and Hooper-Bùi 2008), Mississippi (MacGown and Hill 2010), North Carolina (Guénard et al. 2012) and Texas (Wilson 2003). We tentatively treat all of these records as *P. navigans*, but the California and Texas records could also belong to another species in the *flavens* complex. In the Pacific, *P. navigans* is established in Hawaii (Gruner et al. 2003). We cannot confirm whether the *P. moerens* records from Cocos Island (Solomon and Mikheyev 2005) or the indoor records from a butterfly house in the northwestern United States (collection code KRW26Feb99) refers to *P. navigans* or another member of the *flavens* complex.

Risk statement. The species most often referred to as *P. moerens* in the southeastern United States, and treated here as *P. navigans*, has been expanding its range since it was first reported in Alabama in 1967. However, this species is not considered a major pest and is only occasionally reported to enter houses (Deyrup et al. 2000). In Louisiana *P. navigans* is considered a pest (Dash and Hooper-Bùi 2008). *Pheidole navigans* could become more regionally and possibly globally widespread in the future.

***Pheidole noda* F. Smith**
Figs 81, 88i

noda. *Pheidole nodus* Smith, F. 1874: 407 (s.) JAPAN, Hyogo. Forel 1900: 268 (w.); Wheeler, W.M. 1906: 309 (q.); Ogata 1982: 196 (m.); Wheeler, G.C. & Wheeler, J. 1953: 75 (l.).

rhombinoda. *Pheidole rhombinoda* Mayr 1879: 678 (s.) INDIA, Calcutta [NHMW]. Bingham 1903: 251 (q.). Subspecies of *noda*: Wheeler, W.M. 1929: 3; Santschi, 1937: 371. Junior synonym of *noda*: Yasumatsu 1962: 96. [Misspelled as *rhomboida* by Santschi 1925: 83.]

micantiventris. *Pheidole rhombinoda* var. *micantiventris* Mayr 1897: 427 (s.) SRI LANKA. Junior synonym of *noda*: Yasumatsu 1962: 96.

taprobanae. *Pheidole rhombinoda* var. *taprobanae* Forel 1902c: 178 (s.), 195 (w.) SRI LANKA (Yerbury) [MHNG]. [Unresolved junior primary homonym of *taprobanae* Smith, F. 1858: 175.] [Also described as new by Forel 1902b: 544.] Subspecies of *rhombinoda*: Forel 1913b: 662; of *noda*: Santschi 1937: 371. Junior synonym of *noda*, lectotype designated: Eguchi 2008: 59.

treubi. *Pheidole treubi* Forel 1905a: 19 (s.q.) INDONESIA, Bogor [Buitenzorg], Java [MHNG]. Junior synonym of *noda*, lectotype (s.) designated: Eguchi 2001b: 18.

stella. *Pheidole rhombinoda* subsp. *stella* Forel 1911c: 380 (s.) INDIA, Sikkim, Himalaya, 1200 m [MHNG]. Subspecies of *noda*: Wheeler, W.M. 1929f: 3. Junior synonym of *noda*, lectotype (s.) designated: Eguchi 2008: 59.

formosensis. *Pheidole rhombinoda* var. *formosensis* Forel 1913a: 193 (s.w.q.m.) TAIWAN, Kankau, [MHNG] (H. Sauter). Subspecies of *noda*: Santschi 1937: 370. Junior synonym of *noda*: Eguchi 2008: 59.

praevexata. *Pheidole nodus* var. *praevexata* Wheeler W.M. 1929: 3 (s.w.q.) JAPAN, Okayama (H. Sauter). Junior synonym of *noda*: Yasumatsu 1962: 96.

Pheidole nodus st. *rhombinoda* var. *gratiosa* Santschi 1937: 371, unavailable name. Material referable to this form: Eguchi 2008: 59.

flebilis. *Pheidole nodus* var. *flebilis* Santschi 1937: 370 (s.w.) TAIWAN, Hori [NHMB]. Junior synonym of *noda*: Eguchi 2008: 59.

Diagnosis among introduced *Pheidole*. Medium to dark reddish brown. **Major** HW 1.58–1.82, HL 1.69–1.91, SL 1.00–1.12, CI 93–98, SI 56–65 (n=5, Eguchi 2008). Head subquadrate (Fig. 7). Head rugoreticulate on posterolateral lobes and laterad of frontal carinae (Fig. 13a), but frons dominated by long, well-organized and parallel longitudinal rugae (Fig. 13b). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (Fig. 13c). Promesonotum in profile with two convexities (Fig. 5), the large anterior dome in addition to a distinct mound or prominence on the posterior slope. Postpetiole forming a high dorsally bulging dome that is tallest at midpoint (Fig. 2a); ventral margin flat to very weakly convex (Fig. 2b). **Minor** HW 0.57–0.66, HL 0.71–0.82, SL 0.91–1.07, CI 80–82, SI 157–162 (n=5, Eguchi 2008). Head predominantly glossy

(Fig. 36), lacking punctation and or rugae above eye level. Posterior head margin strongly convex (Fig. 44). Antennal scapes long (e.g. Fig. 39), but not surpassing the posterior head margin by more than 2× eye length. Promesonotum in profile with two convexities, the large anterior dome (Fig. 43a) in addition to a distinct prominence on the posterior slope (Fig. 43b). Petiole and postpetiole glossy to very weakly sculptured laterally (Fig. 48). Postpetiole forming a high dorsally bulging dome that is tallest at midpoint; ventral margin flat to very weakly convex (Fig. 2).

Identification, taxonomy and systematics. *Pheidole noda* is a large, long-limbed, dark colored species most easily recognized by its distinctly enlarged dome-like postpetiole. The species belongs to a clade of large-bodied species that has diversified across Indomalaya (Economo et al. 2015). Although both *P. noda* and *P. megacephala* are considered to have an enlarged postpetiole, they are very different in shape. That of the former is dome-like (Fig. 2) and that of the latter has an anteroventral bulge in addition to the posterodorsal bulge (Fig. 1). The majors of *P. noda* are easily separated from those of *P. megacephala* by the strongly sculptured face (Fig. 8 *vs*. Fig. 9). The minors both have glossy faces, but those of *P. noda* are larger with relatively longer antennal scapes (Fig. 39 *vs*. Fig. 40). *Pheidole noda* is occasionally confused with other Asian tramp *Pheidole*, including *P. fervens* and *P. indica*, but both major and minor workers are easily separated from these by the enlarged postpetiole. Readers are referred to Eguchi (2008) for characters used to separate *P. noda* from its other Asian congeners.

Biology. Despite being a relatively common species across its native range, little is known about the biology of *P. noda*. The species is apparently easy to keep in laboratory settings, and Yamamoto et al. (2009) reported that they kept a colony with five dealated queens, suggesting dependent colony foundation or polygyny. The authors also noted that in Japan it nests in the ground but also forages in vegetation. *Pheidole noda* was the most frequent visitor to extrafloral nectaries of *Mallotus japonicus* in an experiment conducted in Japan (Yamawo et al. 2012). Eguchi (2008) observed that *P. noda* occurs from open lands to relatively developed forests, and nests in the soil, under shelters on the ground, and in rotting logs. Eguchi (2004a) noted that the species takes seeds of sesame and amaranth put on the ground, and majors serve as repletes. During a recent survey in Yunnan, China, the species was found to occur in rubber tree plantations and rainforest between 550 and 1219 m (Liu et al. 2015).

Distribution. *Pheidole noda* is considered native across mainland Asia, occurring from western India east to Japan. Forel (1903) reported the species from the Andaman Islands but it was not recovered during a more recent survey of the islands (Mohanraj et al. 2010). There is geographic disjunction between the mainland Asia population and the populations from the southern islands of Indonesia. The majors of the Indonesian taxon, originally described as *Pheidole treubi* Forel, were considered a distinct population by (Eguchi 2001b), but conspecific with *P. noda*. Although not included on the map, if verified, the records from the Russian Far East (Kupianskaia 1990) would be the most northern extent of the native range. The dispersive capacity of *P. noda* is demonstrated by its colonization of Volcano Island (Nishino-shima Island), which is 22 ha in size and located 1,000 km south of mainland Japan. The island erupted in

1973, virtually eradicating all life. *Pheidole noda* was the only ant species discovered during the 1983 survey, and was one of only two discovered during the 2004 survey (the other being *Tetramorium bicarinatum*).

The only confirmed record of *P. noda* occurring outside of its putative native range is from a glasshouse in Italy (Limonta and Colombo 2003), where it was found together with *P. megacephala* and *Tetramorium bicarinatum* on nursery plants imported from Asia. The species was also found on plant material imported from Asia and intercepted at quarantine facilities in Washington and Hawaii.

Risk statement. *Pheidole noda* is not considered an agricultural, ecological or structural pest species, although it is often associated with disturbed habitats. The species is also not known to have established outdoors beyond its native range. However, perhaps because it can be easily maintained in artificial nests, colonies with laying queens listed as *Pheidole noda* and *Pheidole* cf. *noda* are available for sale from businesses advertising on the internet. The shipment of this species outside its native range to hobbyists increases its chances of accidental release into non-native habitats.

Pheidole obscurithorax **Naves**

Figs 82, 88j

obscurithorax. *Pheidole fallax* subsp. *obscurithorax* Naves 1985: 61 (s.w.) ARGENTINA, Alta Gracia, Córdoba (Bruch). [First available use of *Pheidole fallax* st. *arenicola* var. *obscurithorax* Santschi 1923: 58; unavailable name.] Raised to species; lectotype (s.) (CASENT0913311, NHMB) designated: Wilson 2003: 331.

Diagnosis among introduced *Pheidole*. Medium reddish brown to dark brown. **Major** HW 1.47–1.70, HL 1.49–1.84, SL 0.98–103, CI 92–99, SI 58–70 (n=3). Head subquadrate (Fig. 7); almost entirely covered by a network of intersecting rugae (Fig. 12a), lacking long, well-organized and parallel longitudinal rugae on the frons (Fig. 12b). Frontal carinae indistinct, quickly becoming integrated into dense rugoreticulum that covers the entire face. Antennal scrobes entirely lacking. Antennal insertions surrounded by deeply excavated pits (Fig. 12c). Head often a lighter reddish brown than the mesosoma. Promesonotum in profile with two convexities (Fig. 5), the large anterior dome in addition to a distinct mound or prominence on the posterior slope. Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.60–0.67, HL 0.78–0.85, SL 0.94–1.08, CI 76-82, SI 152–173 (n=5). Head predominantly glossy (Fig. 36), lacking punctation and or rugae above eye level. Posterior margin strongly convex in full-face view such that the head outline forms a single unbroken curve from eye to eye (Fig. 44). Antennal scapes extremely long, surpassing posterior head margin by more than 2× eye length (Fig. 39). Promesonotum in profile with two convexities, the large anterior dome (Fig. 43a) in addition to a distinct prominence on the posterior slope (Fig. 43b). Mesopleuron mostly sculptured. Postpetiole not swollen relative to petiole (Fig. 3). Petiole and postpetiole strongly sculptured laterally (Fig. 47).

Identification, taxonomy and systematics. *Pheidole obscurithorax* is a member of the New World (and polyphyletic, see Moreau 2008) *P. fallax* species group defined by Wilson (2003). It is a large dark species over 6 mm in body length. The species is easily distinguished from *P. megacephala* by the much larger body size and relatively reduced postpetiole, in addition to the strongly sculptured head of the major worker (Fig. 12), and the much longer antennal scapes of the minor. It is separated from other New World species treated here, including those of the *P. punctatissima* clade and *P. flavens* complex, by the much larger size, prominence on the posterior slope of the promesonotum (Fig. 5, major; Fig. 50, minor), densely rugoreticulate face of the major (Fig. 12), and smooth head and long antennal scapes of the minor. The Old World species *P. fervens*, *P. indica*, and *P. noda* all have majors with strongly sculptured head and minors with smooth heads, and the reader is referred to the key for characters used to separate these from *P. obscurithorax*.

Biology. In its introduced range of the southeastern United States, *P. obscurithorax* is characterized by its large size, large nest mounds, very active foraging and fast recruitment to bait such as cookie crumbs (King and Tschinkel 2007). It nests in soil in open areas, where it produces conspicuous nests, each generally with a single large opening often covered by a leaf or other collected material (Storz and Tschinkel 2004). The species is an omnivorous scavenger of dead arthropods (possibly including dead fire ants), and less frequently of plant material such as flower petals (Storz and Tschinkel 2004). Studies in its introduced range found evidence that *P. obscurithorax* is monogynous and is spreading by natural dispersal of winged females in addition to human-mediated long-distance dispersal (King and Tschinkel 2007). The species was most often found associated with disturbed habitats such as lawns and roadsides, but there are also records of it occurring in natural areas such as hardwood forests (Wilson 2003). However, its steady expansion across the southeastern United States and co-occurrence with *S. invicta* suggest it is an important species to monitor.

Distribution. *Pheidole obscurithorax* is presumed native to the South American region of Argentina, Paraguay and southern Brazil that includes the Paraguay, La Plata and Parana Rivers. This flood-prone area is the cradle of many other well-known invasive ants including fire ants (*Solenopsis invicta* Buren and *S. richteri* Forel), the Argentine ant (*Linepithema humile*), and many lesser-known species that were anthropogenically introduced (King and Tschinkel 2007; Storz and Tschinkel 2004; Suarez and Tsutsui 2008; Wilson 2003). Most of these species, including *P. obscurithorax*, were first introduced to North America via the Mobile, Alabama shipping port pathway. *Pheidole obscurithorax* was introduced to Mobile, Alabama around 1950 (Naves 1985) and subsequently expanded its range to include Florida, Georgia, Mississippi and Texas (Storz and Tschinkel 2004; Wilson 2003). Additional occurence records, including the first record for Bolivia, were published (Wetterer et al. 2015) just as this manuscript was going to press, and were not included in the present study.

Risk statement. *Pheidole obscurithorax* is not currently considered a pest in its introduced range, as it does not sting and is not known to infest dwellings or structures (King and Tschinkel 2007). However, the species is an aggressive predator (Deyrup et

al. 2000) and may have the potential to become a pest or to negatively impact native species if its populations continue to grow and spread. *Pheidole obscurithorax* is thought to spread across the southeastern United States by mated queens (not colony fragments) that are being transported in substrates such as potted plants. It is possible that *P. obscurithorax* could become more widespread regionally and globally in the future.

Pheidole parva **Mayr**

Fig. 83, Fig. 88K

parva. *Pheidole parva* Mayr 1865: 98, pl. 4, fig. 28 (s.w.) SRI LANKA [NHMW]. Bingham 1903: 245 (q.).

decanica. *Pheidole parva* var. *decanica* Forel 1902c: 175 (s.), 192 (w.q.m.) INDIA, Cochin (Rothney) [MHNG]. [Also described as new by Forel 1902b: 542.] Junior synonym of *parva*; lectotype designated: Eguchi, Yamane & Zhou 2007: 261.

sauteri. *Pheidole sauteri* Wheeler, W.M. 1909: 334 (s.w.) TAIWAN, Kaoshung (H. Sauter) [MCZC cotype 20671] Junior synonym of *parva*: Eguchi, Yamane & Zhou 2007: 262.

mala. *Pheidole rinae* var. *mala* Forel 1911b: 205 (s.w.) INDONESIA, Semarang, Java (Jacobson) [MHNG]. Lectotype (s.) designated: Eguchi 2001a: 39. Junior synonym of *parva*: Eguchi, Yamane & Zhou 2007: 262.

tipuna. *Pheidole rinae* r. *tipuna* Forel 1912: 68 (s.w.) TAIWAN, Takao (H. Sauter) [MHNG]. Junior synonym of *parva*; lectotype (s.) designated: Eguchi, Yamane & Zhou 2007: 262.

bugi. *Pheidole bugi* Wheeler, W.M. 1919: 66 (s.w.) MALAYSIA, Sarawak, Borneo (R. Thaxter) [MCZC cotype-8947]. Lectotype (s.) designated: Eguchi 2001a: 37. Junior synonym of *parva*: Eguchi, Yamane & Zhou 2007: 262.

farquharensis. *Pheidole flavens* var. *farquharensis* Forel 1907: 91 (w.) SEYCHELLES, Farquhar Atoll, v–xii.1905 (J.S. Gardiner) [BMNH]. Junior synonym of *parva*: Fischer and Fisher 2013: 340.

tarda. *Pheidole* (*Pheidole*) *tardus* Donisthorpe 1947: 285 (q.) MAURITIUS, Rose Hill, 07.v.1946 (R. Mamet) [BMNH]. Junior synonym of *parva*: Fischer and Fisher 2013: 341.

Diagnosis among introduced *Pheidole*. Yellowish brown to dark brown. **Major** HW 0.85–0.92, HL 0.96–1.07, SL 0.41–0.45, CI 85–92, SI 45–51 (n=11, Eguchi et al. 2007). Head subquadrate (Fig. 7). Posterolateral lobes, including posterior head margin, covered in rugoreticulum (Fig. 26). Antennal scrobes indistinct to moderately impressed, but frontal carinae always forming a border capable of accepting the antennal scape (Fig. 13c). Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Promesonotum in dorsal view transverse with strongly projecting shoulders (Fig. 28). Promesonotal dorsum rugoreticulate with distinct long longitudinal striae in addition to

shorter sections of transverse and intersecting striae (Fig. 22). Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.39–0.50, HL 0.43–0.54, SL 0.38–0.46, CI 88–94, SI 84–102 (n=17, Eguchi et al. 2007). Posterior portion of head with many short to medium length segments of striae distinctly interlaced among punctate ground sculpture (Fig. 59). Antennal scapes with erect to suberect hairs (Fig. 56); scapes do not surpass posterior head margin (Fig. 41). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Pronotal humeri angular (Fig. 28). Hairs on mesosoma fine, flexuous, of unequal length and not arranged in pairs (Fig. 54). Postpetiole not swollen relative to petiole (Fig. 3); postpetiole narrow in dorsal view, only slightly broader than petiole (Fig. 61).

Identification, taxonomy and systematics. *Pheidole parva* is a very small and inconspicuous species that is thus far reported only from Asia, a few localities in Arabia, and the islands of the Indian Ocean and the Pacific Ocean. It belongs to an Old World clade scattered across Indomalaya and into Oceania, and was treated as part of the *P. rinae* complex by Eguchi et al. (2007). The minor workers are completely covered in punctate sculpture and are difficult to differentiate from those of the Neotropical *P. flavens* complex. The similarity is so close that an introduced population of *P. parva* from the Seychelles was described by Forel, on the basis of the minor worker, as *Pheidole flavens* var. *farquharensis*. The similarity is entirely convergent, as these lineages are distantly related. *Pheidole parva* minors can be separated from those of the *P. flavens* complex most reliably by the interrupted striae that are interlaced among the punctate ground sculpture of the posterior head (Fig. 59 *vs*. Fig. 60). This character can also be viewed in the dorsal view. *Pheidole parva* minors can be separated from those of the *P. punctatissima* clade treated here by the glossy gaster (Fig. 32 *vs*. Fig. 33) and finer mesosomal hairs of unequal length (Fig. 54 *vs*. Fig. 53). The major workers are characterized by a defined and moderately depressed antennal scrobe and a thick network of reticulated rugulae on the posterior lobes. This pattern is most similar to that of the broadly sympatric *P. fervens* and *P. indica*, but *P. parva* is much smaller than those species (HW < 0.95 mm *vs* HW > 1.10 mm) and lacks the distinct prominence on the posterior slope of the promesonotal dorsum (Fig. 4 *vs*. Fig. 5). The majors of *P. parva* can be separated from those of the *P. flavens* and *P. punctatissima* group species treated here by the much stronger and more reticulated carinae which reach the posterior margin (Fig. 26 *vs*. Fig. 25 and Fig. 27) in addition to other characters given in the key. Readers are referred to Eguchi (2008; 2007) for characters separating *P. parva* from its Asian congeners.

Biology. Little is known about the biology of *P. parva*, but it does appear to be expanding its range and is worth monitoring in the future as it exhibits a high tolerance for disturbance. Eguchi (2008) observed that the species seems to inhabit open lands and forest edges, and has probably expanded its range in some part as the result of human commerce. *Pheidole parva* was one of the most commonly collected ants in a myrmecological study of agricultural fields in Vietnam and Okinawa (Anh et al. 2010; Suwabe et al. 2009). A recent study of 18 structure invading pest ants of healthcare

facilities in Singapore found *P. parva* the most frequently encountered species (Man and Lee 2012). *Pheidole parva* and *Pheidole megacephala* were the two most common ant species encountered and together accounted for over 50% of the total collection (25.9% and 25.2%, respectively). In Mauritius and the Seychelles *P. parva* can be locally abundant and can be found in soil and leaf litter, under stones or root mats, in rotten logs, foraging on or nesting in the ground, as well as in lower vegetation and even under the bark of live trees (Fischer and Fisher 2013). It was collected there in parks, gardens, mangrove, coastal scrub, degraded dry forest, littoral and mixed forest, and rainforest, in elevations between 1–445 m. It was collected inland on the Arabian Peninsula from date tree orchards, banana plantations and under potted plants between 675–735 m elevation (Fischer and Fisher 2013).

Distribution. *Pheidole parva* is considered here as native to the Indo-Malay region. The species is recorded from the Asian mainland from India east to China. We consider the records from Indonesia, Borneo, the Philippines and Taiwan to be native, but much of this distribution could represent a more recent anthropogenic expansion. We consider the records from the Okinawa and Kagoshima prefectures of Japan to be introduced along with the records from Palau to represent introduced populations, but it is difficult to know whether the species arrived in these islands before, with or after the arrival of humans. The species is introduced in the Seychelles, Mauritius, Saudi Arabia and the United Arab Emirates (Fischer and Fisher 2013). *Pheidole parva* was also collected from hothouses in Austria and Germany.

Risk statement. *Pheidole parva* is not currently considered to be a significant pest species, and no impacts on agricultural systems or native ecosystems have been documented as of yet. The species is known to invade structures, however, and its prevalence in Singapore health care facilities (Man and Lee 2012) suggests it could become a more widespread nuisance pest in the future. Live colonies have been reported from various ships (Fischer and Fisher 2013) and should be screened for during quarantine inspections.

Pheidole proxima **Mayr**

Fig. 84, 88L

proxima. *Pheidole proxima* Mayr 1876: 104 (s.w.) AUSTRALIA, Peak Downs, Queensland [NHMW, examined]. Current subspecies: nominal plus *bombalensis*, *transversa*.

Diagnosis among introduced *Pheidole*. Reddish brown. **Major** HW 0.95–1.05, HL 1.04–1.21, SL 0.44–0.50, CI 87–92, SI 42–52 (n=4). Head subquadrate (Fig. 7). Posterolateral lobes lacking sculpture (including foveolate ground sculpture, carinae and rugae) posterior to maximum extent of antennal scapes in repose (Fig. 9). Head glossy, lacking foveolate ground sculpture. Hypostomal bridge with a small median tooth in addition to a pair of larger inner teeth (Fig. 18). Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope.

Promesonotal dorsum glossy, lacking foveolate ground sculpture or striae. Pronotal striae in dorsal view mostly absent (Fig. 23). Metapleuron with moderate rugulae and some weak punctation (Fig. 16). Petiolar node strongly punctate (Fig. 16). Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.46, HL 0.52, SL 0.40, CI 90, SI 86 (n=1). Head predominantly glossy (Fig. 36), lacking punctation and or rugae above eye level. Posterior head margin weakly convex (Fig. 45) to weakly concave (Fig. 46) in full-face view. Antennal scapes reach but do not surpass posterior head margin (Fig. 41). Mesopleuron entirely punctate (Fig. 52a). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Propodeal spines moderately produced and spiniform (Fig. 52b). Petiole distinctly sculptured except for apical portion of node. Postpetiole not swollen relative to petiole (Fig. 3).

Identification, taxonomy and systematics. *Pheidole proxima* is a relatively small, brownish yellow, short-limbed species with a strongly shining integument. The phylogenetic placement of *P. proxima* is unknown, but it almost certainly clusters within an Old World clade that has radiated across Australia and New Guinea. The species is slightly smaller than *P. megacephala*, but both have workers with almost entirely glossy faces. The postpetiole of *P. proxima* is not swollen relative to the petiole (Fig. 3), as it is in *P. megacephala* (Fig. 1). The head of the major is subquadrate (Fig. 7), while that of *P. megacephala* is more heart-shaped (Fig. 6). The antennal scapes of the minor do not surpass the posterior head margin (Fig. 41), as they do in *P. megacephala* (Fig. 40). The other two *Pheidole* species established in New Zealand are *P. rugosula* and *P. vigilans*. The glossy face of *P. proxima* easily separates both worker castes of from those of *P. rugosula*. In addition to being significantly smaller (major HW < 1.0 mm, minor HW < 0.48 mm) than *P. vigilans* (major HW > 1.2 mm, minor HW > 0.52 mm), the major of *P. proxima* is more sculptured (Fig. 16 *vs*. Fig. 17), and the hypostomal bridge has a distinct median tooth (Fig. 18 *vs*. Fig. 19). The minors of *P. proxima* are separated from those of *P. vigilans* by the shorter scapes (Fig. 41 *vs*. Fig. 40), more sculptured mesopleuron (Fig. 52a *vs*. Fig. 51a), and more robust propodeal spines (Fig. 52b *vs*. Fig. 51b). Additional taxonomy of these species is discussed in (Berry et al. 1997).

Comparison of the *Pheidole proxima* Mayr type series and images of the two subspecies suggests that all three taxa are heterospecific. There is some reason to believe, however, that the name *P. proxima* Mayr does not apply perfectly to the species recently introduced to New Zealand. The specimens examined from New Zealand conflict with Mayr's original description and type specimens on several points. The pronotal dorsum of the type major worker is transversely rugose whereas that of the New Zealand specimens are completely glossy. Although we were unable to examine minors from the type series, Mayr described the head of the minor worker as coriaceous and striate-rugose with scapes that barely exceed the posterior margin. In contrast the minor workers from New Zealand have heads that are completely glossy and scapes that do not exceed the posterior head margin. Forel, in his description of *P. proxima* subsp. *bombalenis*, describes the minor worker as identical to *P. proxima* Mayr with the exception of having longer propodeal spines. The specimen images of the *P. bombalensis* syntype minor show a strongly sculptured face, similar to the pattern described by Mayr. The major workers from the

type series are larger than the New Zealand specimen we measured (HW 1.03–1.05 mm *vs*. HW 0.95 mm), have relatively narrower heads (CI 87–89 *vs*. CI 92), and relatively shorter antennal scapes (SI 42–46 *vs*. SI 52). While a more exhaustive survey of Australia's *Pheidole* may reveal the New Zealand population to be more closely related to another species from that fauna, we follow Berry et al. (1997) in using *P. proxima* Mayr.

Biology. The only natural history published for *P. proxima* was recorded by Green and Gunawardana (2006) from their work with the New Zealand incursion. They reported that *P. proxima* produced large nests recognizable by tiny conical mounds of sandy or grainy material above the ground near the entrance. The size of the mounds varies with soil type, with mounds as small as 5 mm high by 200–300 mm in diameter. They are tolerant to disturbance and capable of invading structures. The minor and major workers are both active foragers and were observed recruiting to both sweet and savory baits in high numbers.

Distribution. *Pheidole proxima* Mayr is native to Queensland, Australia. The sparse records of the species are scattered from Cape York at the northernmost tip of the continent down to the Gold Coast. The species is introduced to New Zealand and was first detected during a 2004 survey of the Port of Napier following an incursion of *Solenopsis invicta* (Green and Gunawardana 2006). The species is now widespread across the North Island from the Napier-Hastings area to Auckland.

Risk statement. *Pheidole proxima* is at most considered a nuisance species in New Zealand on account of its ability to infest structures. However, very little is known about the species, including its impact on agricultural systems and native ecosystems. There is little reason to believe that it will become globally or regionally widespread.

Pheidole punctatissima **Mayr**

Figs 85, 88M

punctatissima. *Pheidole punctatissima* Mayr 1870a: 400 (s.w.) MEXICO (E. Norton) [NHMW]. Description of queen: Forel 1908: 52. Lectotype (major worker, CASENT0601256) designated: Longino and Cox 2009: 41. See also: Wilson 2003: 618.

napaea. *Pheidole punctatissima* subsp. *napaea* Wheeler, W.M. 1934: 165 (s.w.) MEXICO, Mirador, Veracruz (E. Skwarra). Junior synonym of *punctatissima*: Brown 1981: 525.

Diagnosis among introduced *Pheidole*. Body reddish brown to nearly black. **Major** HW 0.86–1.06, HL 0.94–1.13, SL 0.56–0.63, CI 92–97, SI 57–68 (n=9, Longino pers. comm.). Head bicolored with the yellowish posterior two-thirds contrasting with the darker brown anterior third and rest of body (Fig. 34). Head subquadrate (Fig. 7); often entirely foveolate (Fig. 11), but portions of posterolateral lobes can be glossy. Posterolateral lobes never with distinct rugae. Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Promesonotal dorsum usually foveolate and never with distinct transverse striae. Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole relatively broad; distinctly

more than 2× petiolar width in dorsal view (Fig. 31). Gaster with at least anterior 1/3 of first tergite matte (Fig. 33). **Minor** HW 0.44–0.50, HL 0.54–0.59. SL 0.55–0.58, CI 79–85, SI 114–125 (n=14, Longino pers. comm.). Head, including the area mesad of the frontal carinae, entirely covered by reticulated network of punctures (Fig. 37). Posterior head margin relatively narrow (Fig. 58). Antennal scapes lack standing hairs (Fig. 55); scapes surpass posterior head margin by a distance equal to or greater than eye (Fig. 40); scapes relatively long (SI 103–125). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Hairs on mesosoma stout, stiff, of equal length and arranged in pairs (Fig. 53). Postpetiole not swollen relative to petiole (Fig. 3). Postpetiole broad in dorsal view, distinctly broader than petiole (Fig. 62). Gaster with at least anterior 1/3 of first tergite matte (Fig. 33).

Identification, taxonomy and systematics. *Pheidole punctatissima* is a small species with entirely punctate minor workers that are usually dark red brown to nearly black. The major workers are easily recognizable by the distinct bicolored head which is dark anteriorly and yellowish white posteriorly. *Pheidole punctatissima* is a member of the Neotropical *P. punctatissima* clade, together with *P. anastasii* and *P. bilimeki* (Economo et al. 2015). Among species treated here, it is easily confused with the aforementioned and with members of the *P. flavens* complex. Minor workers can also be confused with those of *P. parva*. Within the *P. punctatissima* clade, the major workers of *P. punctatissima* are immediately distinguished from those of both *P. anastasii* and *P. bilimeki* by their bicolored heads (Fig. 33). The minor workers of *P. punctatissima* tend to have relatively narrower posterior head margins and longer antennal scapes than those of *P. anastasii* and *P. bilimeki*, but separation can be difficult. See section under *P. anastasii* for identification notes.

Biology. *Pheidole punctatissima* is a weedy species that tends to be arboreal and prefers open, disturbed habitat (Longino and Cox 2009). It is most commonly found nesting in dead wood on the ground or in dead tree branches. Wilson (2003) reported winged reproductives were found in nests during April and July. Specimen records retrieved from Antweb.org indicate the species was collected from 10–2500 m elevation (570 m average). *Pheidole punctatissima* has also managed to establish indoors in several European countries. Colonies were found in Denmark infesting a hospital and in Norway inhabiting private homes and a nursing home (Birkemoe and Aak 2008). Birkemoe and Aak (2008) speculated that the species was inadvertently imported along with nursery plants.

Distribution. *Pheidole punctatissima* is considered here as broadly native to the Neotropics from southern Mexico to northern South America. We tentatively treat the Caribbean records as native but these might represent more recent human-mediated dispersal events. The records from southern Brazil, reported at least in part from 10 different urban centers (Lutinski et al. 2013), have not been verified with specimen examination. Should the records refer to *P. punctatissima* Mayr and not one of its many morphologically similar congeners we would consider this to be an introduced population. Indoor colonies were found in Denmark and Norway (Birkemoe and Aak 2008).

Risk statement. *Pheidole punctatissima* is considered a nuisance pest that can infest structures both in its native and introduced ranges (Longino and Cox 2009). The presence of this species in hospitals and nursing homes suggest it could be a potential nuisance.

Pheidole rugosula **Forel**
Figs 86, 88N

rugosula. *Pheidole variabilis* var. *rugosula* Forel 1902a: 423 (s.w.) AUSTRALIA, Bong-Bong, N.S.W. (Froggatt). Raised to species Berry et al. 1997: 29.
Note: The elevation to species rank proposed by Berry et al. (1997) had been heretofore overlooked by Bolton (2014).

Diagnosis among introduced *Pheidole*. Yellowish brown. **Major** HW 0.88, HL 0.94, SL 0.45, CI 94, SI 51 (n=1). Head subquadrate (Fig. 7); with distinct parallel rugae extending from frontal lobes posterior to apices of frontal carinae. Shorter lengths of rugae present across entire posterior region of head and extending to posterior margin in full-face view (Fig. 24). Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Promesonotal dorsum glossy with thin but distinct subparallel striae running oblique to the longitudinal midline (Fig. 20). Pronotal striae in dorsal view mostly oblique (Fig. 20). Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.45, HL 0.48, SL 0.41, CI 95, SI 91 (n=1). Head with well-defined, long segments of rugae running longitudinally from below the eyes to the posterior head margin (Fig. 38). Frontal carinae distinct and reaching towards the posterior head margin, although they may occasionally be interrupted (Fig. 38). Punctate ground sculpture present on lateral surfaces of head and just mesad of the frontal carinae, but median portion of head with a large glossy section (Fig. 38). Antennal scapes reach but do not surpass posterior head margin (Fig. 41). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Postpetiole not swollen relative to petiole (Fig. 3).

Identification, taxonomy and systematics. *Pheidole rugosula* is a small, brownish yellow, short-limbed species with moderate head sculpturing that most likely belongs to the Australian-New Guinea clade that includes close relatives of *P. variabilis* Mayr. The head sculpturing of both the major (Fig. 10) and the minor (Fig. 38) is distinct among all other *Pheidole* species treated here. These characters easily separate *P. rugosula* from *P. megacephala* (Fig. 24, Fig. 36). These same characters, together with a more sculptured promesonotal dorsum (Fig. 20, major) and stout propodeal spines, can be used to separate *P. rugosula* from its two other congeners that are established in New Zealand, *P. proxima* and *P. vigilans* (which is also much larger, major HW > 1.20 mm). There is a bewildering diversity of native Australian (and to a lesser extent New Guinea) *Pheidole* that approach the morphology of *P. rugosula*. Additional characters for identifying New Zealand *Pheidole* species are provided in Berry et al. (1997). A significant revision of the *P. variabilis* group is required before *P. rugosula* can be reliably separated from these species.

Biology. In New Zealand, *P. rugosula* is strongly associated with human disturbance and is the most commonly encountered of the four *Pheidole* species established in New Zealand (Berry et al. 1997). It has been recorded frequently from gardens, orchards, structures and urban areas. The species was reported nesting in compost, in the soil of vegetable gardens, in the soil of lawns, and near rubbish baskets (Berry et al.

1997; Harris et al. 2005b). It has also been recorded as scavenging dead arthropods, human food waste, nuts and seeds, and is often found associated with rotting fruit (Berry et al. 1997; Harris et al. 2005b). Other collection records suggest *P. rugosula* will forage arboreally. Berry et al. (1997) also mention that label data suggests the species was collected several times attacking ootheca of mantids, including those of the native mantid *Orthodera novaezealandiae* (Colenso).

Distribution. *Pheidole rugosula* is believed to be native to the New South Wales region of Australia. The only country where the species has established is New Zealand (Berry et al. 1997). Berry et al. (1997) published museum records of *P. rugosula* from New Zealand. The first known occurrence of *P. rugosula* in New Zealand is from Takapuna, where it was collected in 1958 and it had reached Auckland by 1963. Since then it has been found across the Auckland and Waikato regions.

Risk statement. *Pheidole rugosula* is considered to be a nuisance pest around urban areas in New Zealand (Harris et al. 2005b), where foragers are attracted to pet food left out and to windfall fruit. Although it occurs in native habitats in New Zealand, its impacts are unknown. Collection data indicating a *P. rugosula* attack of native mantids suggest it could have some negative impact on native biodiversity, however.

Pheidole vigilans **(F. Smith)**

Figs 87, 88O

vigilans. *Atta vigilans* Smith, F. 1858: 166 (w.) AUSTRALIA, Melbourne [BMNH, MCZC]. Combination in *Aphaenogaster*: Dalla Torre 1893:108; in *Pheidole*: Emery 1915a: 69.

dolichocephala. *Pheidole dolichocephala* André 1896: 262 (s.) AUSTRALIA, Western Australia [MNHN]. Junior synonym of *vigilans*: Brown 1971: 13.

parallela. *Pheidole ampla* var. *parallela* Forel 1902a: 435 (s.w.m.) AUSTRALIA, N.S.W. (Froggatt) [ANIC]. Junior synonym of *vigilans*: Brown 1971: 13.

yarrensis. *Pheidole ampla* var. *yarrensis* Forel 1902a: 434 (s.w.q.) AUSTRALIA, Yarra districts, Victoria (Froggatt) [MHNG]. Junior synonym of *vigilans*: Brown 1971: 13.

norfolkensis. *Pheidole ampla* subsp. *norfolkensis* Wheeler, W.M. 1927: 134, fig. 3 (s.w.) AUSTRALIA, Norfolk Island (A.M. Lea) [MCZC]. Donisthorpe 1941: 91 (q.m.). Junior synonym of *vigilans*: Brown 1971: 13.

Diagnosis among introduced *Pheidole*. Smooth yellowish to reddish brown. **Major** HW 1.30, HL 1.43, SL 0.68, CI 91, SI 52. Head subquadrate (Fig. 7); glossy, lacking foveolate ground sculpture. Posterolateral lobes lacking sculpture (including foveolate ground sculpture, carinae and rugae) posterior to maximum extent of antennal scapes in repose (Fig. 9). Hypostomal bridge with two well-developed inner teeth but lacking a median tooth (Fig. 19). Promesonotal dorsum glossy, lacking foveolate ground sculpture or striae. Promesonotum in profile forming a single dome (Fig. 4), lacking a distinct mound or prominence on the posterior slope. Metapleuron almost completely

glossy with strongly reduced carinulae and lacking punctation (Fig. 17). Petiolar node mostly glossy (Fig. 17), not covered by punctate sculpture. Postpetiole not swollen relative to petiole (Fig. 3). **Minor** HW 0.55, HL 0.58, SI 0.55, CI 95, SI 101. Head predominantly glossy (Fig. 36), lacking punctation and or rugae above eye level. Antennal scapes surpass posterior head margin by approximate distance of eye length (Fig. 40). Mesopleuron entirely glossy (Fig. 51a). Promesonotum in profile forming a single dome (Fig. 42), lacking a distinct mound or prominence on the posterior slope. Propodeal spines weakly produced and dentiform (Fig. 51b). Petiole almost entirely glossy. Postpetiole not swollen relative to petiole (Fig. 3).

Identification, taxonomy and systematics. *Pheidole vigilans* is a large, light colored, glossy species native to Australia and introduced in New Zealand. The species belongs to an Old World clade centered in Australia. The glossy head of the majors and minors give it a superficial appearance to *P. megacephala*, but it is substantially larger than that species. Additionally, the postpetiole of *P. proxima* is not swollen relative to the petiole (Fig. 3) as in *P. megacephala* (Fig. 1), and the head of the major is subquadrate (Fig. 7), while that of *P. megacephala* is more heart-shaped (Fig. 6). Readers are referred to the section under *P. proxima* and *P. rugosula* for a discussion of how to differentiate it from the other *Pheidole* species established in New Zealand. Additional taxonomy of these species is discussed in (Berry et al. 1997). Within Australia, there are many taxa similar to *P. vigilans* and its close relative *P. ampla* Forel. However, a revision of that fauna is required before it can be reliably diagnosed there.

Biology. Records show it has established in urban areas and been found with fruit, in gardens, indoors and nesting in failing pasture (Berry et al. 1997).

Distribution. Pheidole *vigilans* is considered endemic to the south eastern corner of Australia (Brown 1971). Heterick et al. (2013) reported *P. vigilans* as introduced to Perth in Western Australia. The species was first collected outside of Australia in Kerikeri, New Zealand in 1956, and remains the least frequently collected *Pheidole* species in New Zealand (Berry et al. 1997; Cumber 1959). Although *Pheidole ampla* subsp. *norfolkensis* Wheeler was originally described as endemic to the Norfolk Islands, Brown (1971) later proposed that the species was introduced to those islands.

Risk statement. *Pheidole vigilans* is not considered a pest in New Zealand, but it has been collected from urban areas and may be a minor garden nuisance (Harris et al. 2005c).

Dubious and erroneous records of introduced *Pheidole* species

The following species were reported by McGlynn (1999) as introduced in Hawaii based on Nishida (1996a): *Pheidole barbata* W.M. Wheeler, *P. fervida* F. Smith, *P. hyatti* Emery, *P. punctatissima*, and *P. noda*. These records refer to quarantine interceptions (Wheeler 1934b), and it is doubtful that any of the aforementioned species ever established in Hawaii. We propose that *P. barbata*, and *P. hyatti* be removed from future lists of tramp ants. The URL referred to in Nishida (1996a) is obsolete, but the data is available at Nishida (1996b).

Pheidole fervida is also reported by McGlynn (1999) as introduced in Tahiti based on putative specimens at the LACM. These records are unverified, however, and it is possible that the Tahiti specimens actually refer to *P. fervens*. While *P. fervida*, as it is currently recognized (e.g. Eguchi 2008) is reported as occurring widely across Asia (Guenard and Dunn 2012), we do not consider any of these records to represent recent introductions outside of its native range. However, the species does exhibit synanthropic habits and may yet prove itself as an important tramp ant.

Pheidole guineensis Fabricius is a West African species that has likely never established outside of its native range. The species most often misidentified in museum collections and in the literature as *P. guineensis* is *Tetramorium bicarinatum* (Nylander). Between 1862 (Mayr 1862; Roger 1862) and 1977 (Bolton 1977) The latter species was universally and mistakenly referred to as *Tetramorium guineensis* Fabricius. Readers are referred to Bolton (1977) for a thorough explanation of the taxonomic history.

Pheidole micula Wheeler is a species native to the southwestern United States (Moody and Francke 1982; Wheeler and Wheeler 1973; Wilson 2003). Ward (2005) unintentionally reported the species as introduced in California (pers. comm. December 17, 2013).

Pheidole umbonata Mayr is reported by McGlynn (1999) as introduced to Polynesia and possibly New Caledonia. Although this synanthropic species is widely distributed across Oceania, and is very tolerant of disturbed habitats (Sarnat and Economo 2012), we consider *P. umbonata* to be native throughout the Pacific. Morphological (Wilson and Taylor 1967) and molecular (unpublished) variation throughout the Pacific populations suggest that the species is not a recent introduction to any of the Polynesian, Micronesia or Melanesian countries where it is found. The New Caledonia record reported by Emery (1914) was determined by Wilson and Taylor (1967) as referring to a different species. Although we are unaware of any confirmed records from New Caledonia, it is quite possible the species does occur there.

Plates

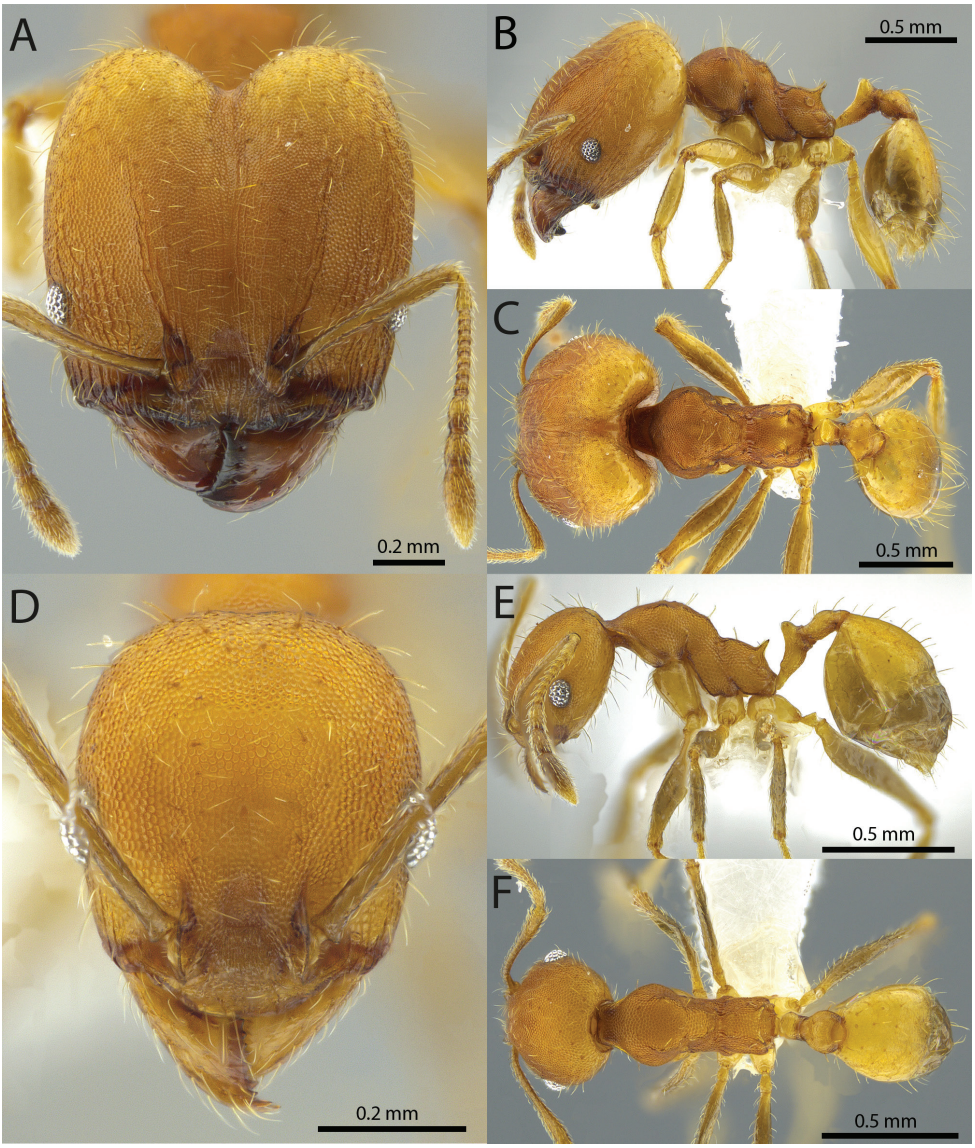


Figure 74. *Pheidole anastasii* Mayr. Major worker, CASENT0613680: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0619900: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photograph by Jeremy Pillow.

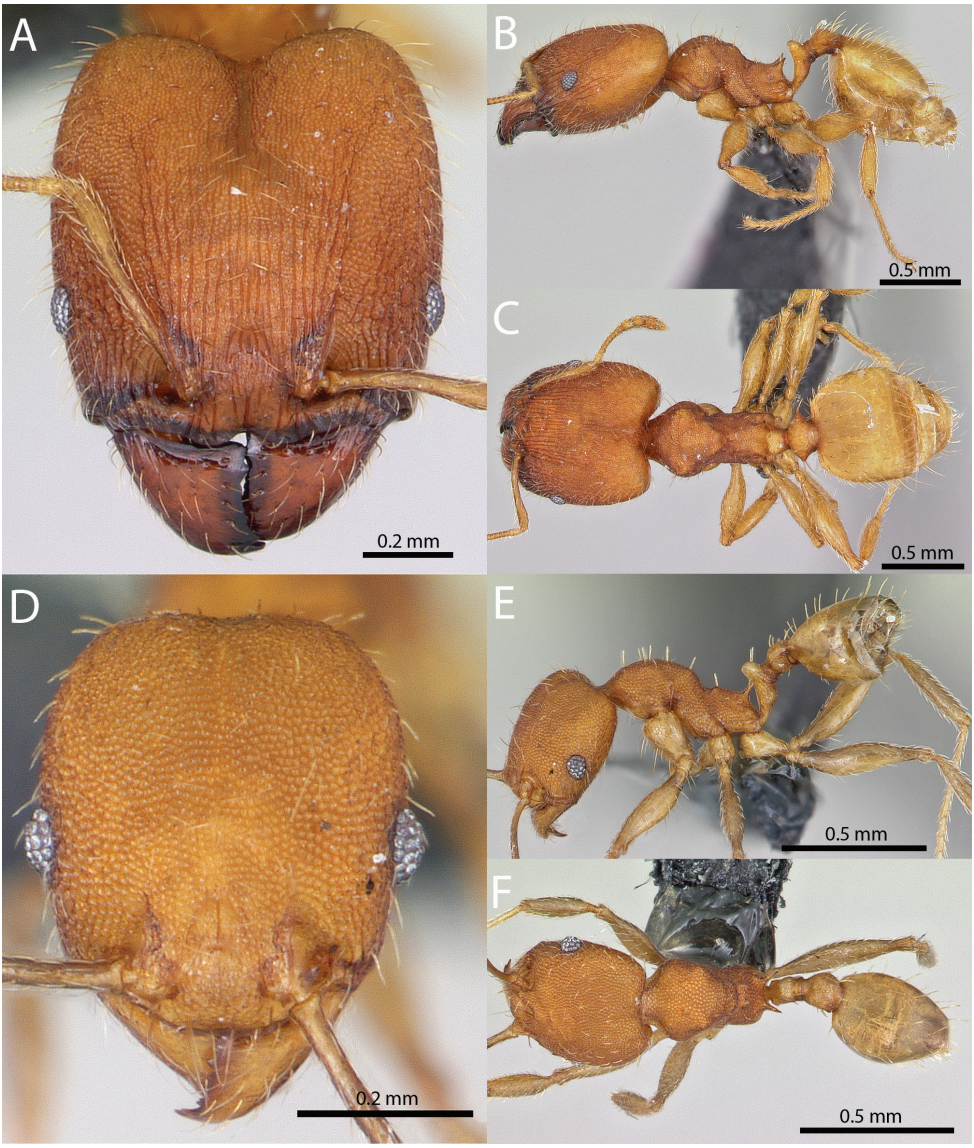


Figure 75. *Pheidole bilimeki* Mayr. Major worker, CASENT0173659: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0173658: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by April Nobile.

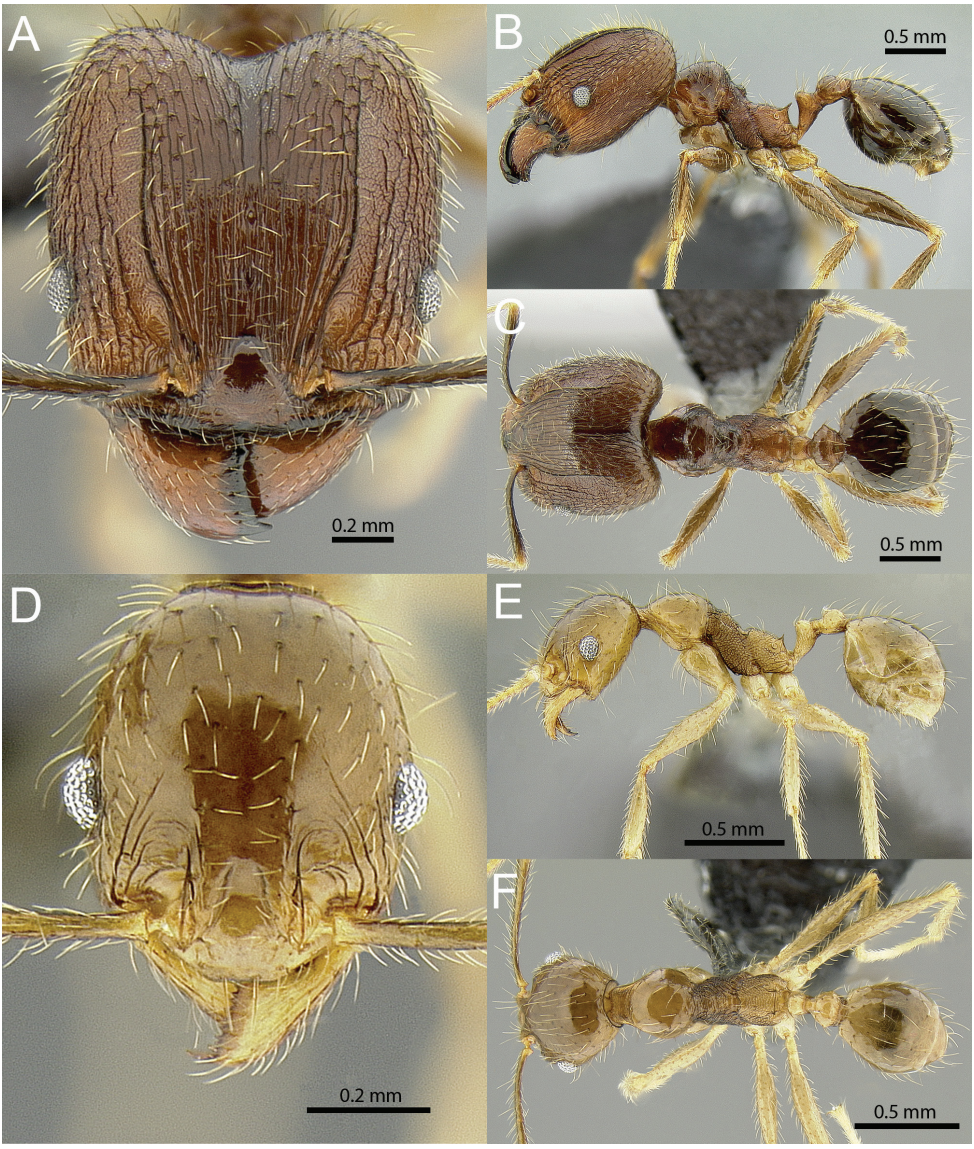


Figure 76. *Pheidole fervens* F. Smith. Major worker, CASENT0171099: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0171076: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Eli Sarnat.

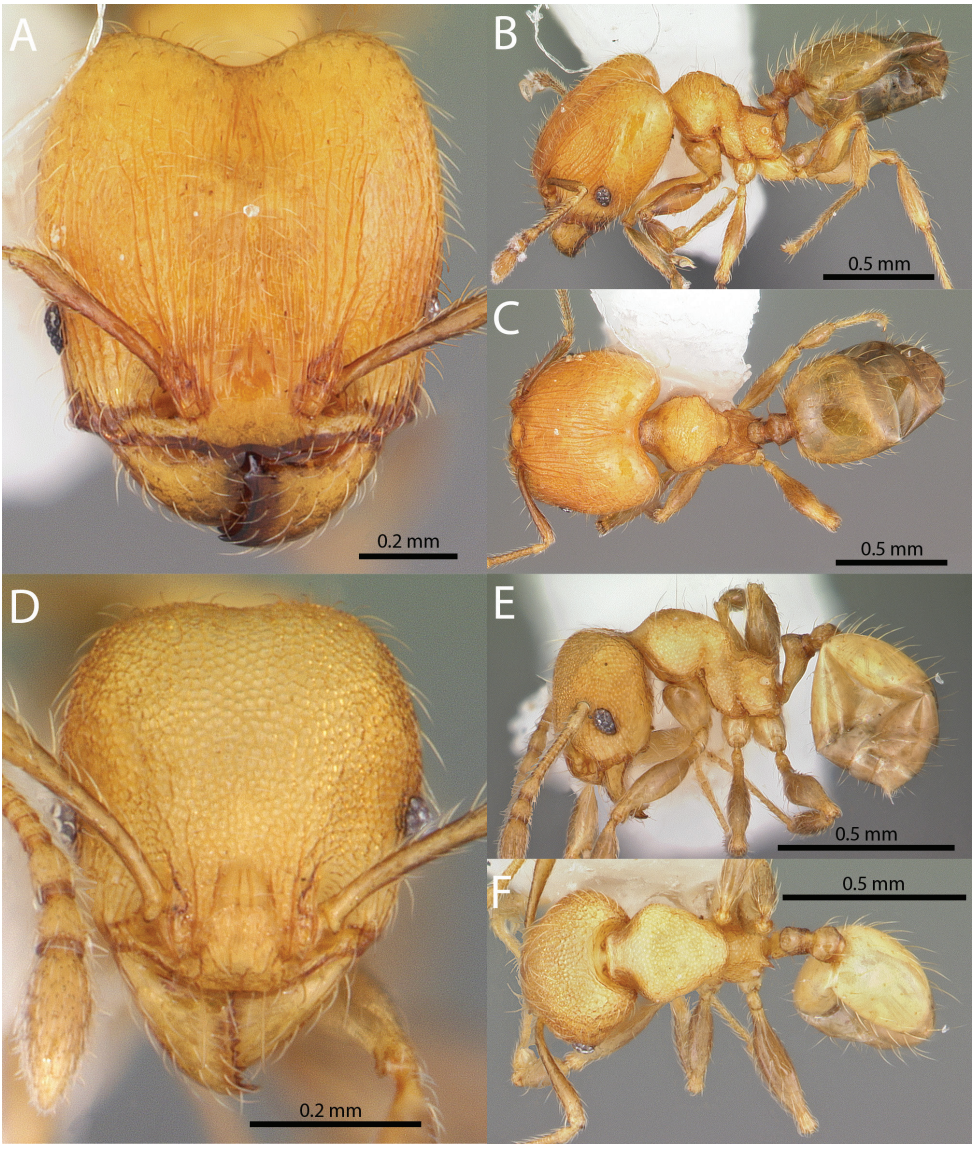


Figure 77. *Pheidole flavens* Roger. Major worker, CASENT0104398: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0104397: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by April Nobile.

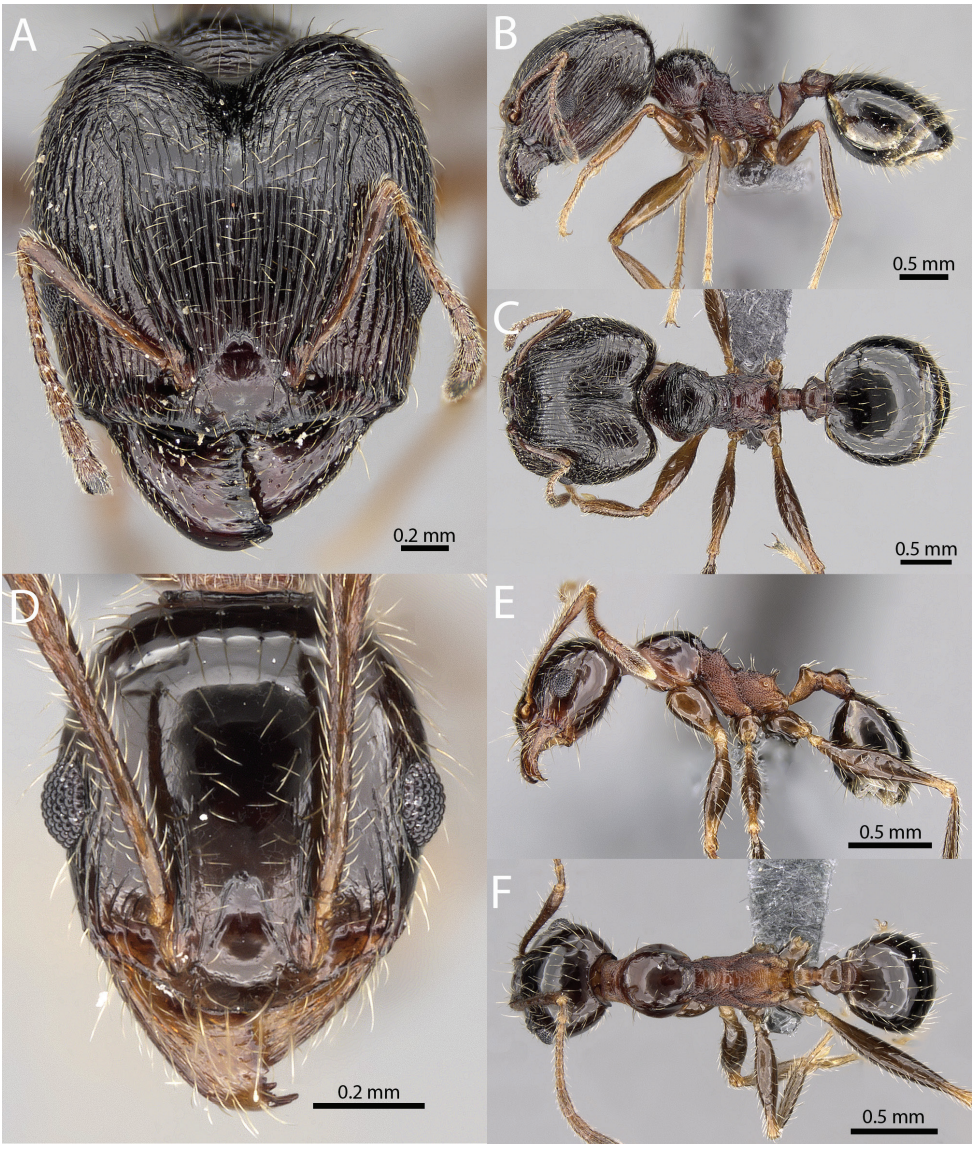


Figure 78. *Pheidole indica* Mayr. Major worker, CASENT0264427: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0263700: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Estella Ortega.

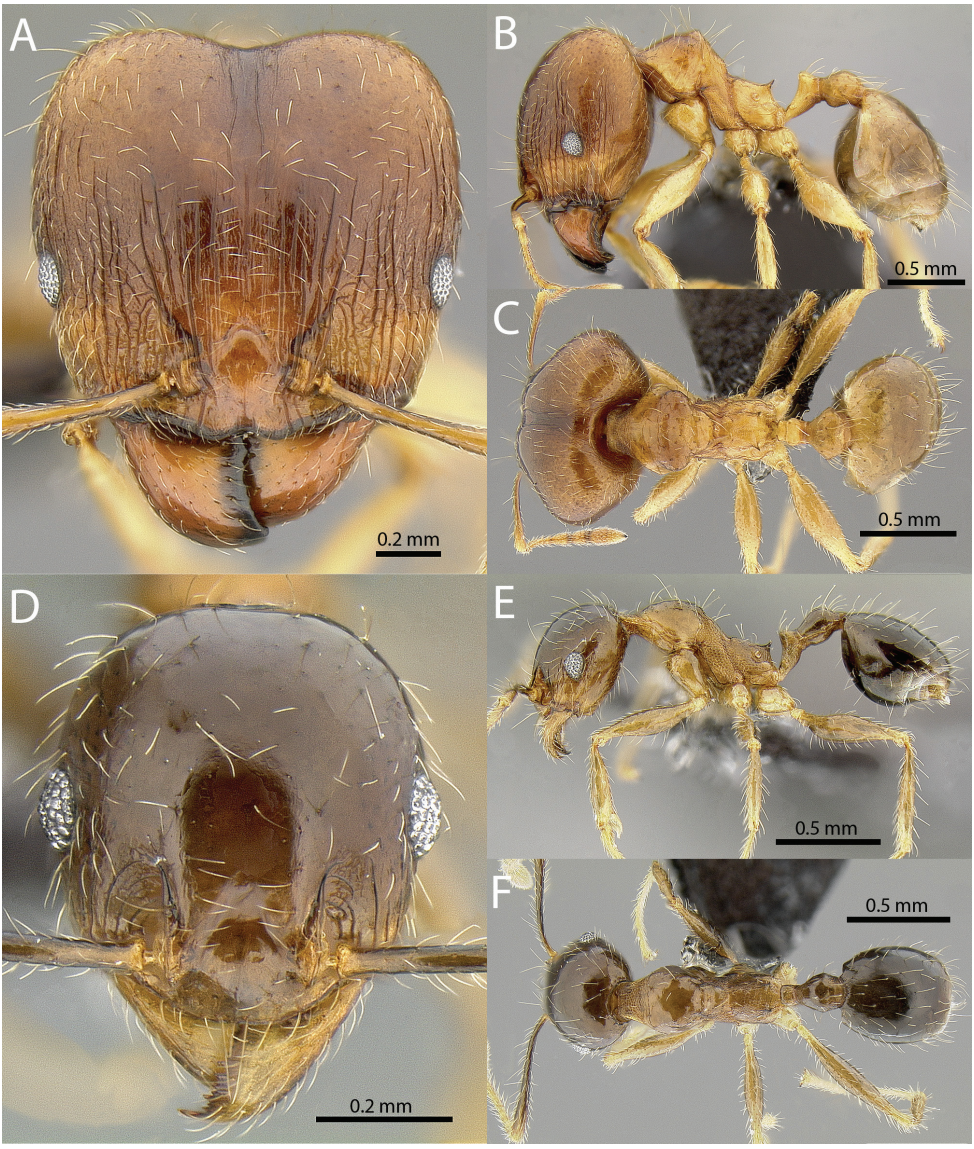


Figure 79. *Pheidole megacephala* (Fabricius). Major worker, CASENT0171036: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0171092: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Eli Sarnat.

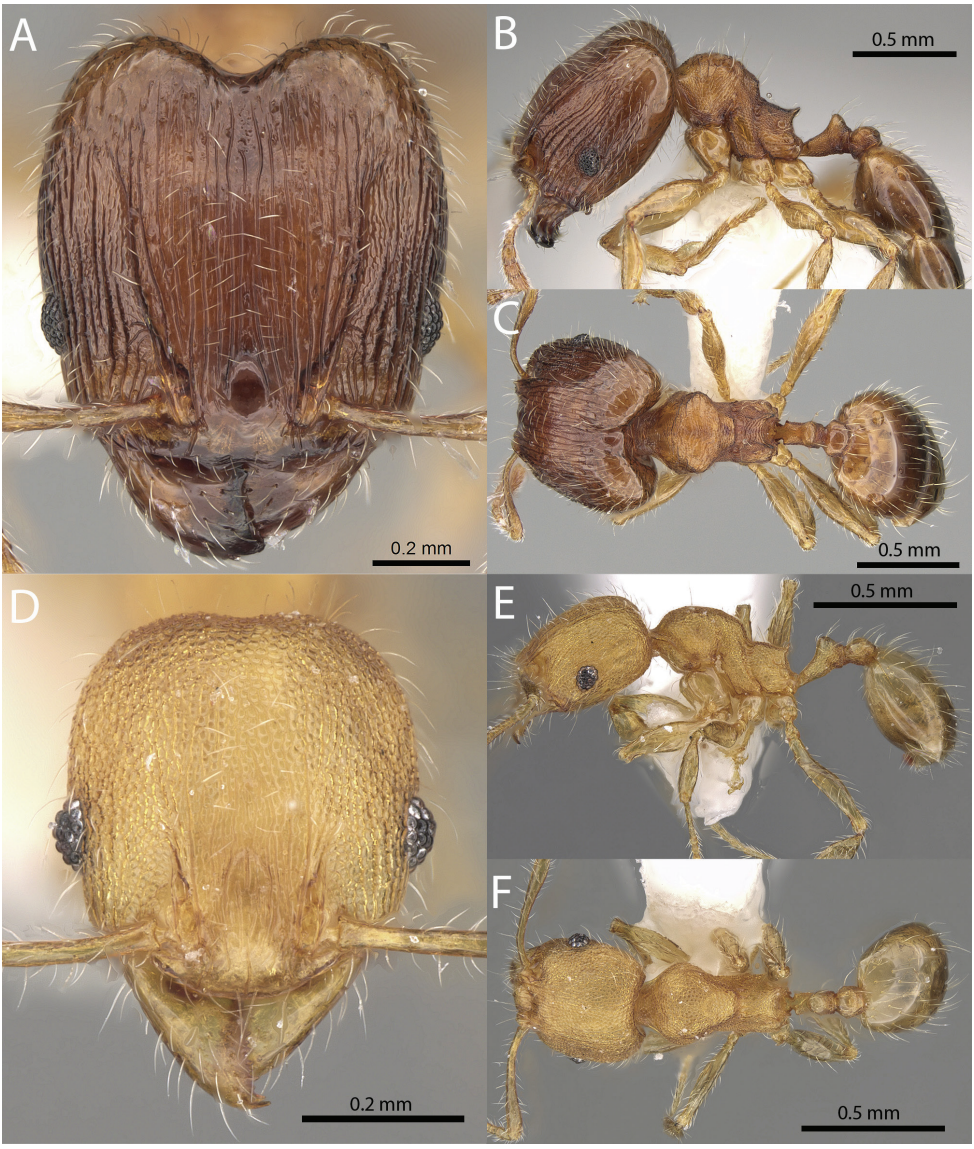


Figure 80. *Pheidole navigans* Forel. Major worker, BPBMENT2006029775: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, BPBMENT2006029771: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Eli Sarnat.

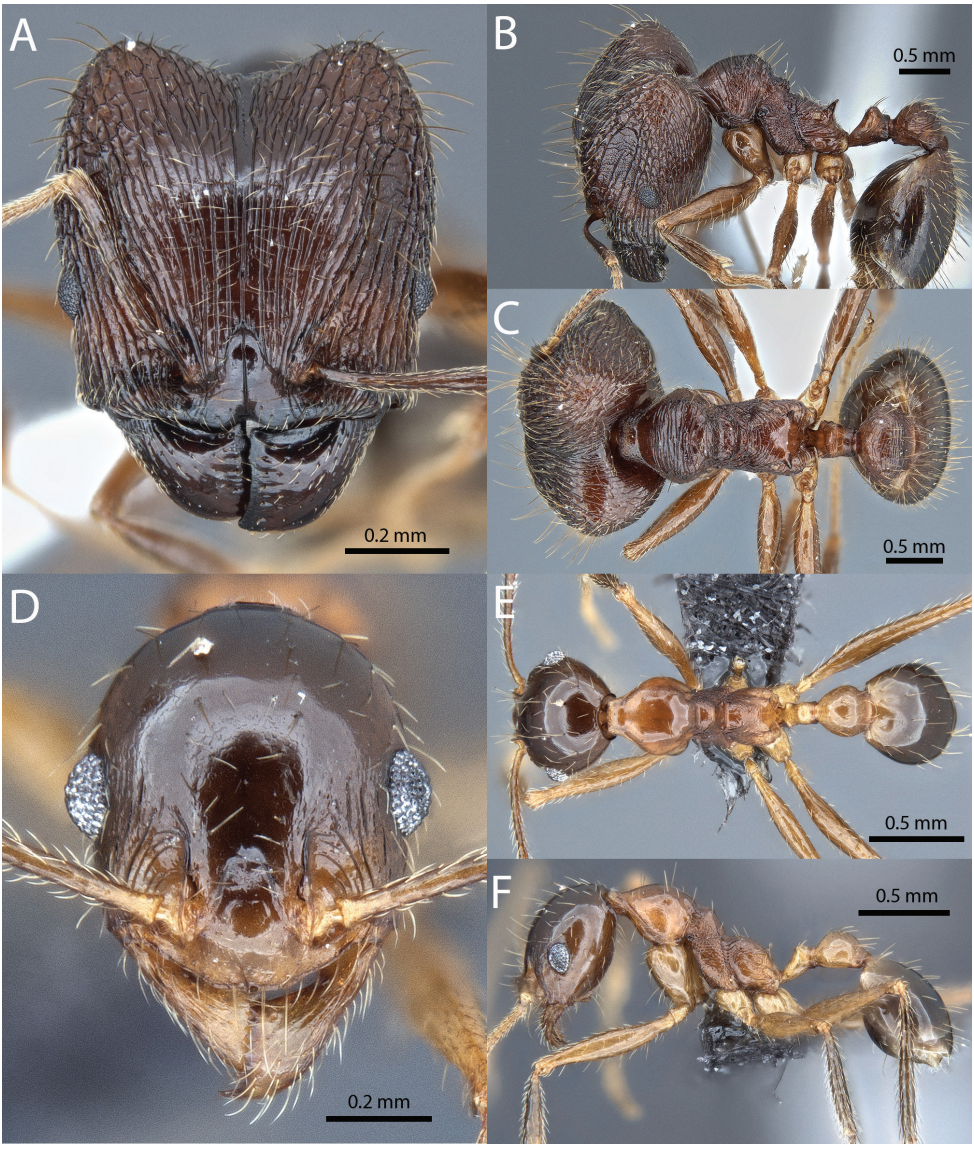


Figure 81. *Pheidole noda* F. Smith. Major worker, CASENT0282545: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0741212: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Masako Ogasawara.

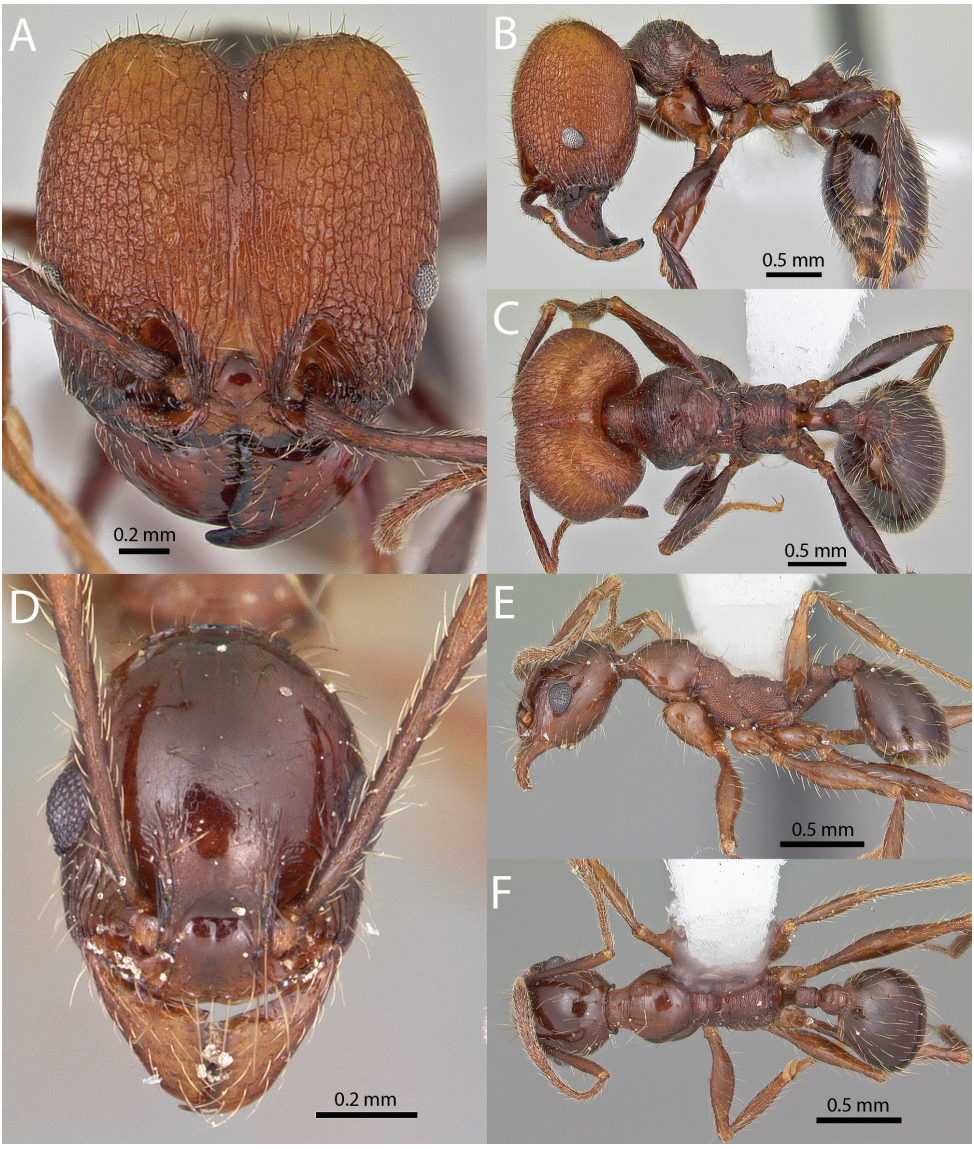


Figure 82. *Pheidole obscurithorax* Naves. Major worker, CASENT0178041: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0104420: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by April Nobile.

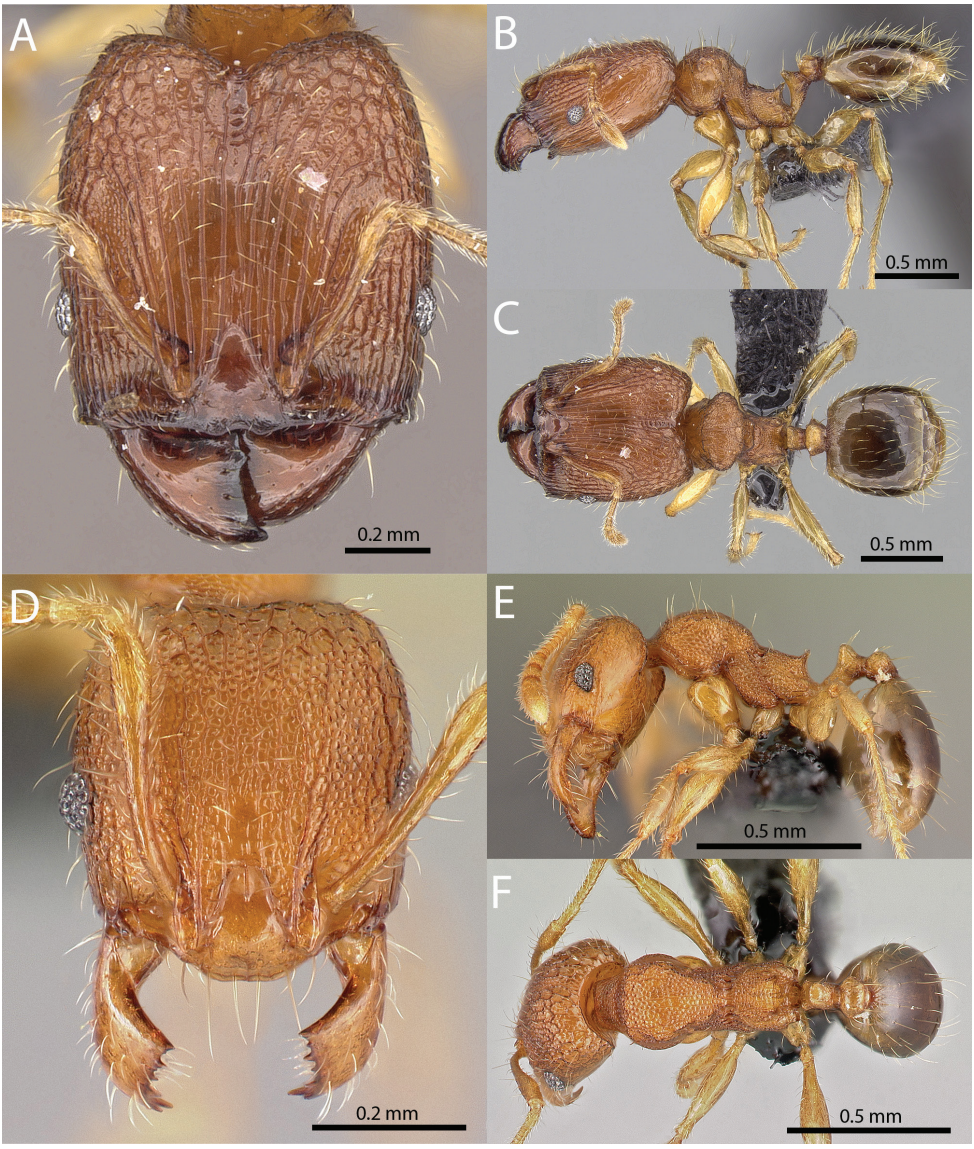


Figure 83. *Pheidole parva* Mayr. Major worker, CASENT0160280: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0160528: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Estella Ortega.

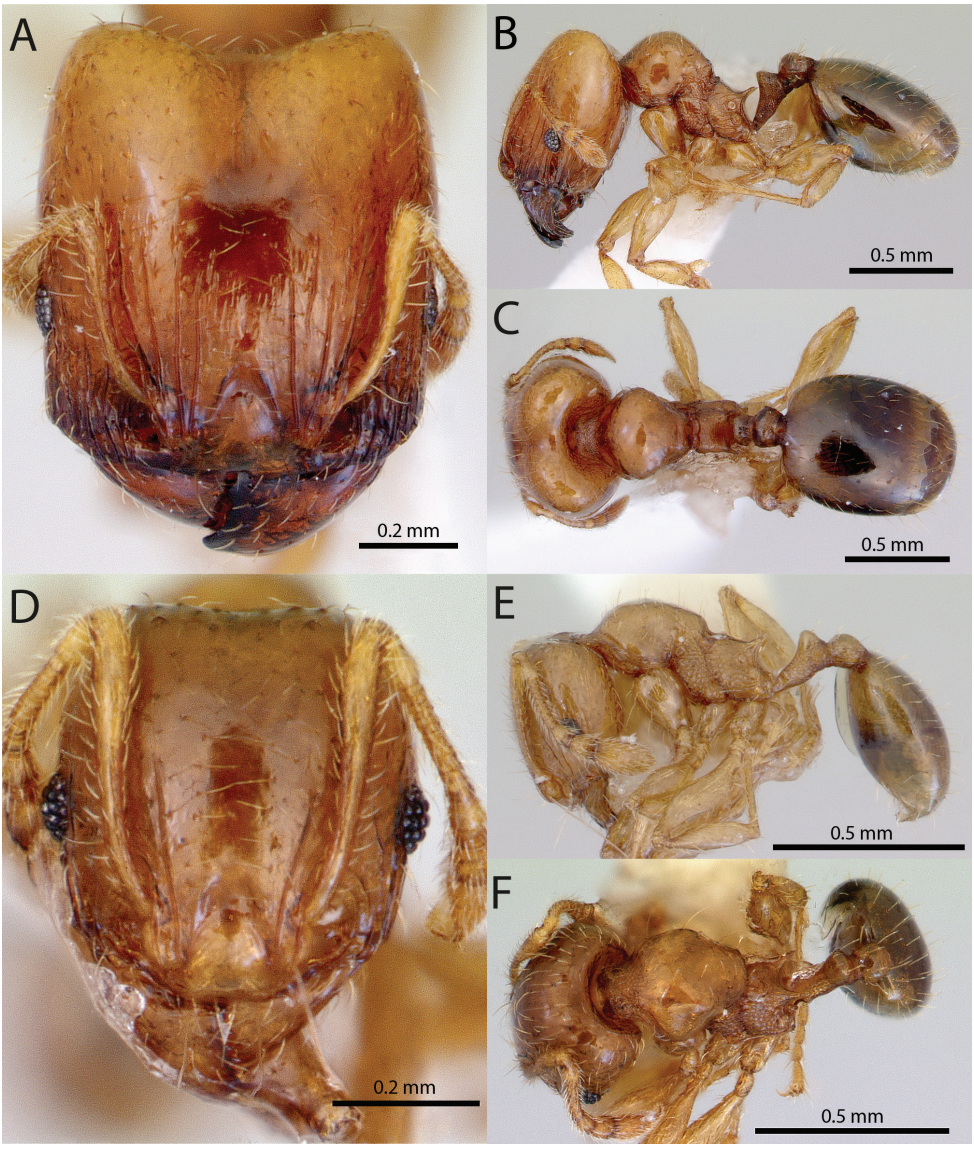


Figure 84. *Pheidole proxima* Mayr. Major worker, CASENT0172362: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0172363: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by April Nobile.

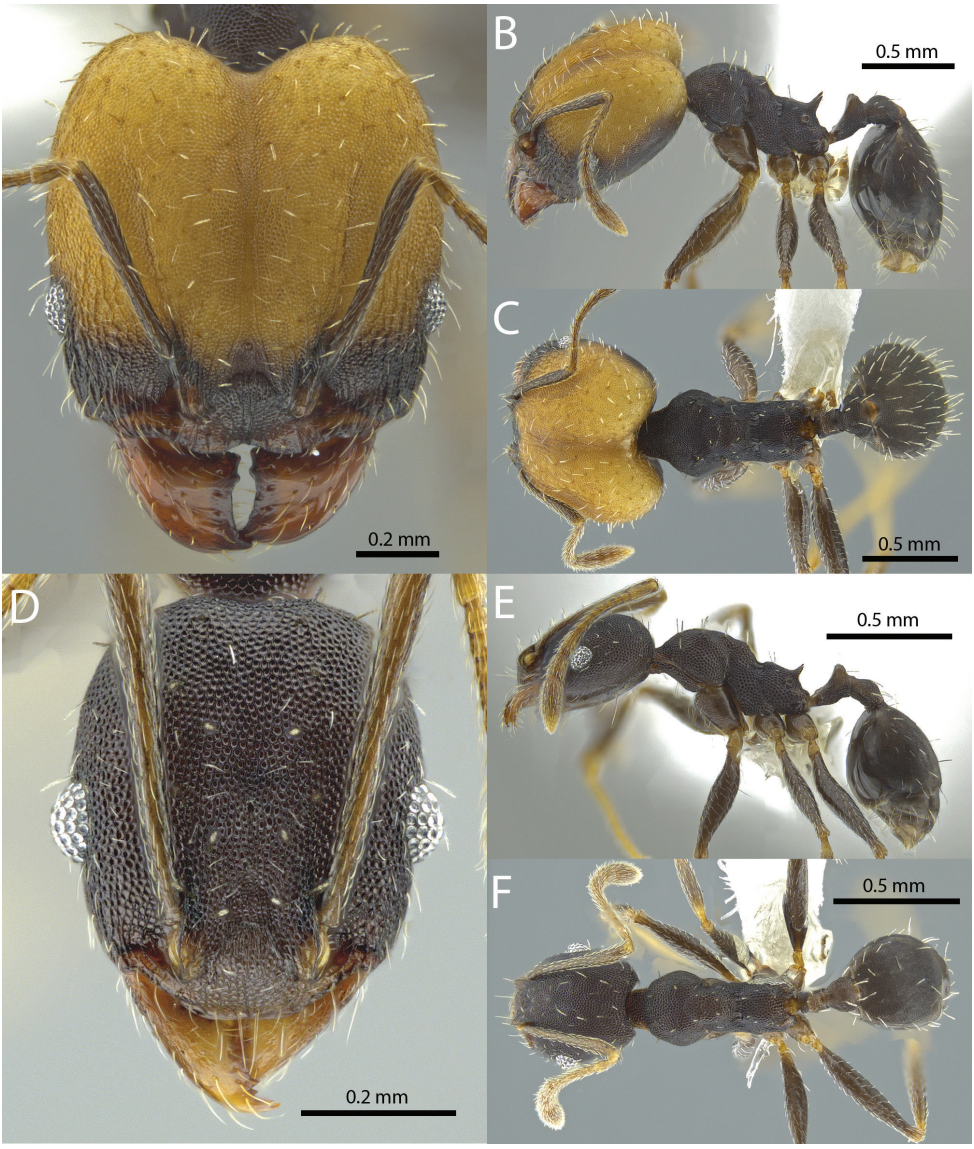


Figure 85. *Pheidole punctatissima* Mayr. Major worker, CASENT0619681: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0619442: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photograph by Jeremy Pillow.

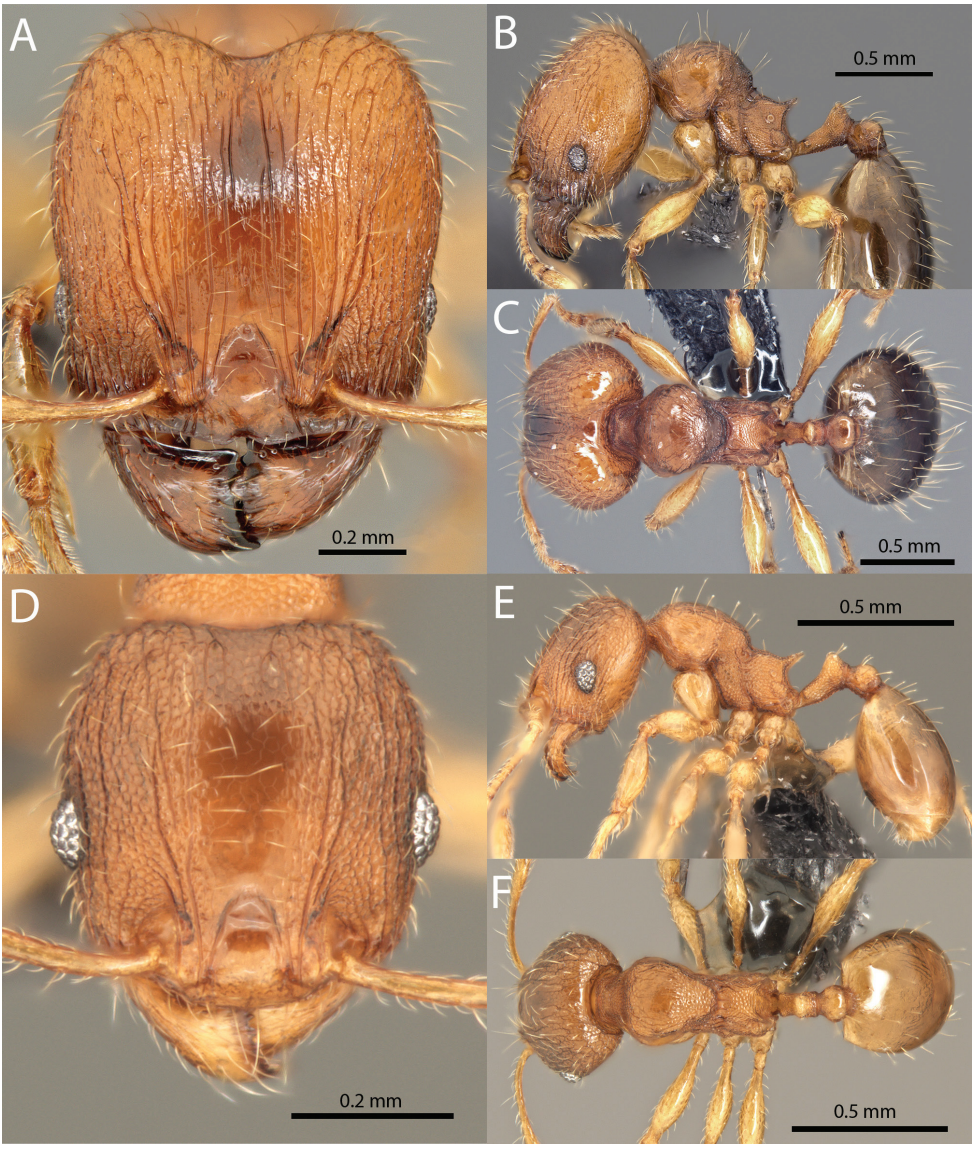


Figure 86. *Pheidole rugosula* Forel. Major worker, CASENT0717051: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0717052: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Masako Ogasawara.

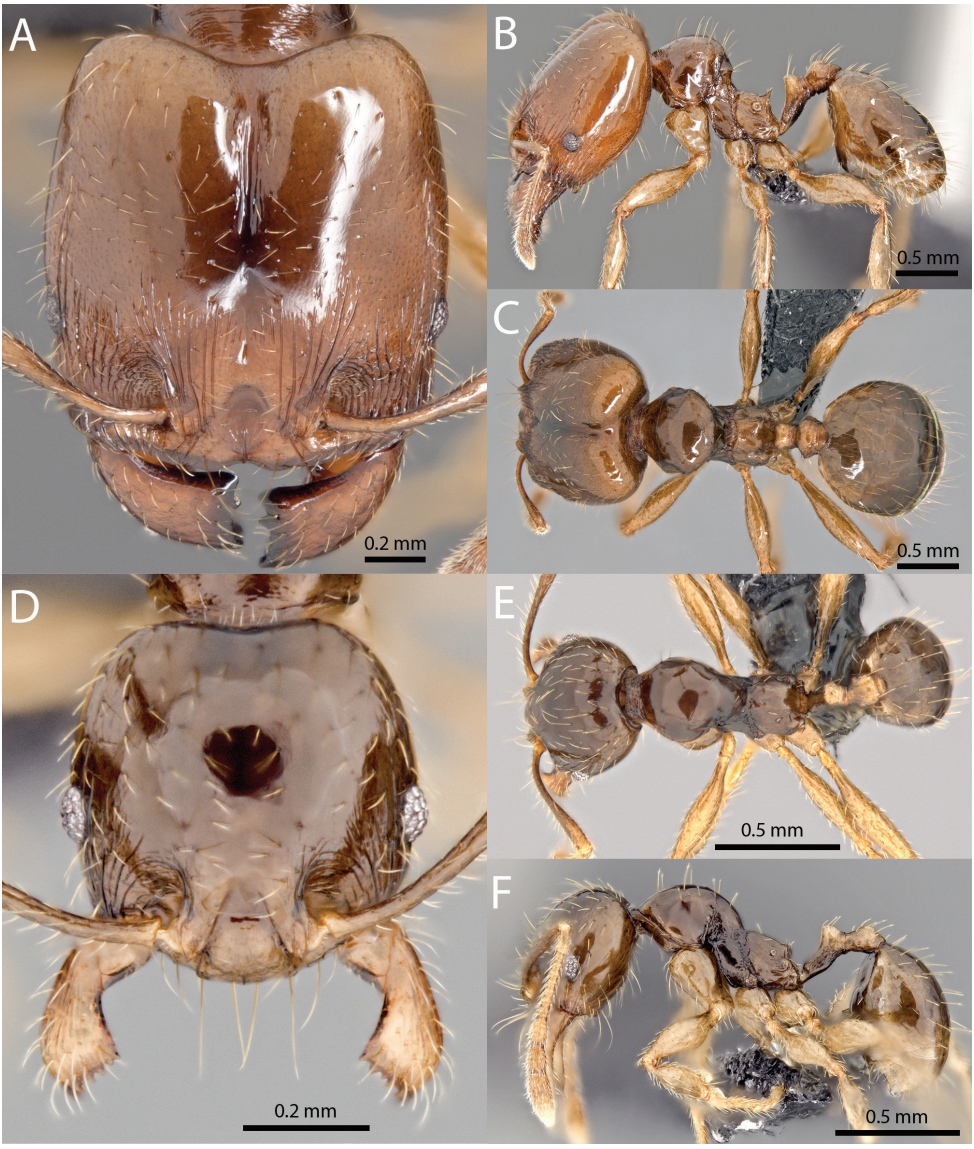


Figure 87. *Pheidole vigilans* F. Smith. Major worker, CASENT0717430: **A** full-face view **B** lateral view **C** dorsal view. Minor worker, CASENT0717429: **D** full-face view **E** profile view **F** dorsal view. From Antweb.org, photographs by Masako Ogasawara.

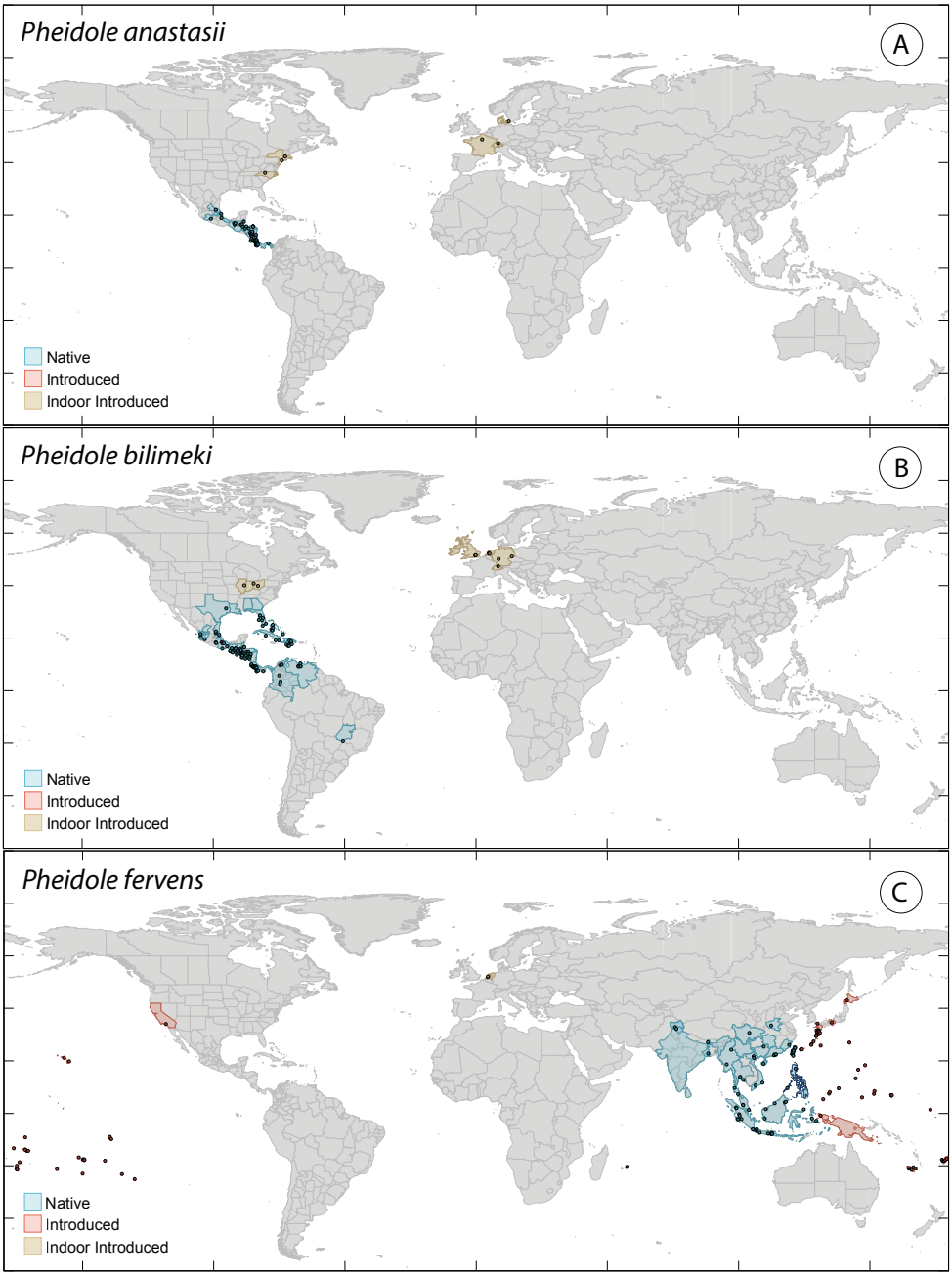


Figure 88. Geographic distribution of introduced *Pheidole* species. **A** *P. anastasii* Emery **B** *P. bilimeki* Mayr **C** *P. fervens* F. Smith .Circle symbols represent georeferenced localities. Shaded polygons represent administrative units from which the respective species have been recorded as occurring. Larger countries are subdivided into states or provinces for increased geographic resolution. Blue = putative native occurrence records. Red = putative introduced occurrence records. Yellow = records for indoor occurrences (heated buildings, greenhouses, etc.) in regions where the species is incapable of year-round outdoor survival.

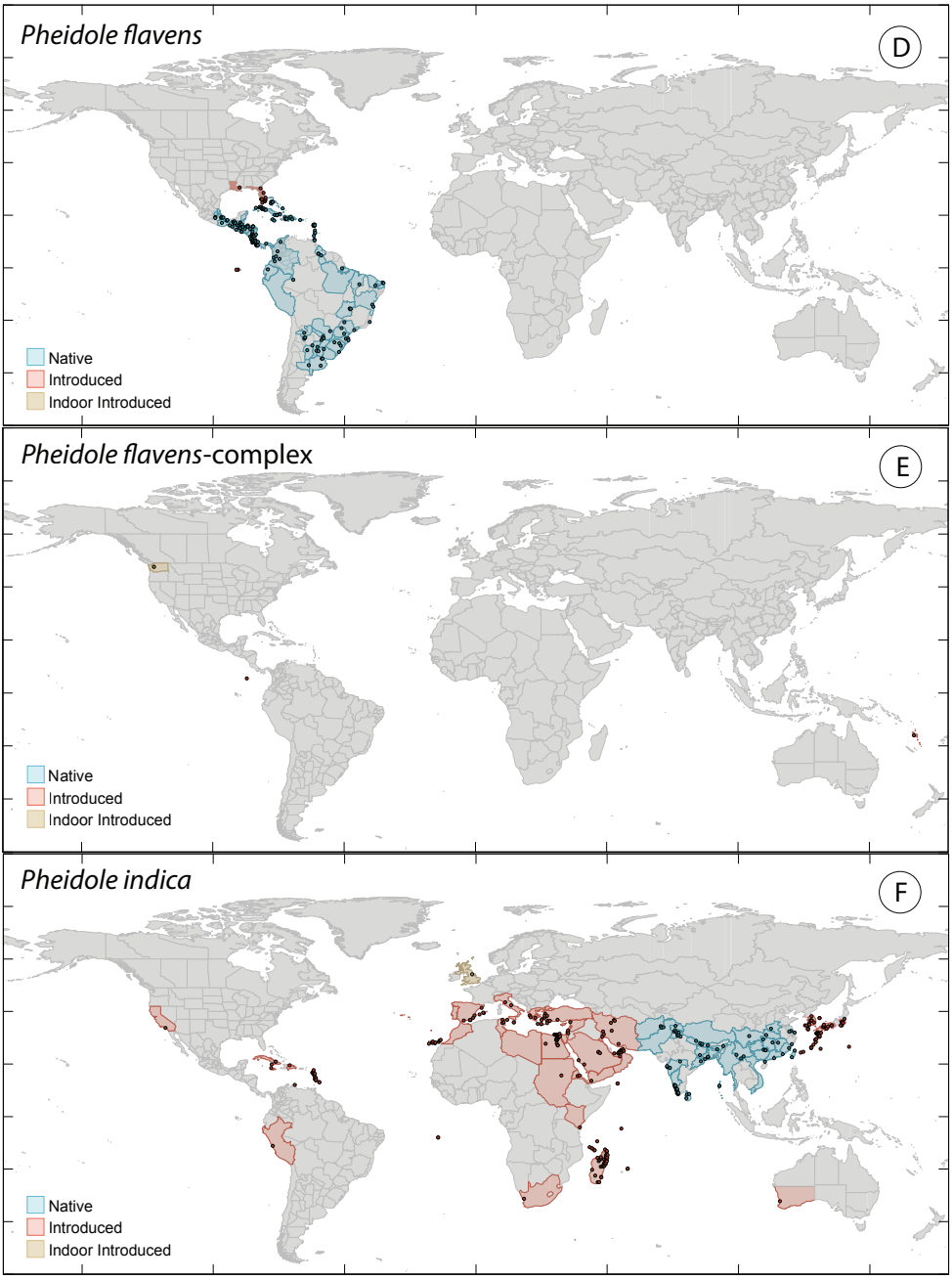


Figure 88. Continued. Geographic distribution of introduced *Pheidole* species. **D** *P. flavens* Roger **E** *P. flavens*-complex (excluding determined records of *P. flavens* Roger and *P. navigans* Forel) **F** *P. indica* Mayr. Circle symbols represent georeferenced localities. Shaded polygons represent administrative units from which the respective species have been recorded as occurring. Larger countries are subdivided into states or provinces for increased geographic resolution. Blue = putative native occurrence records. Red = putative introduced occurrence records. Yellow = records for indoor occurrences (heated buildings, greenhouses, etc.) in regions where the species is incapable of year-round outdoor survival.

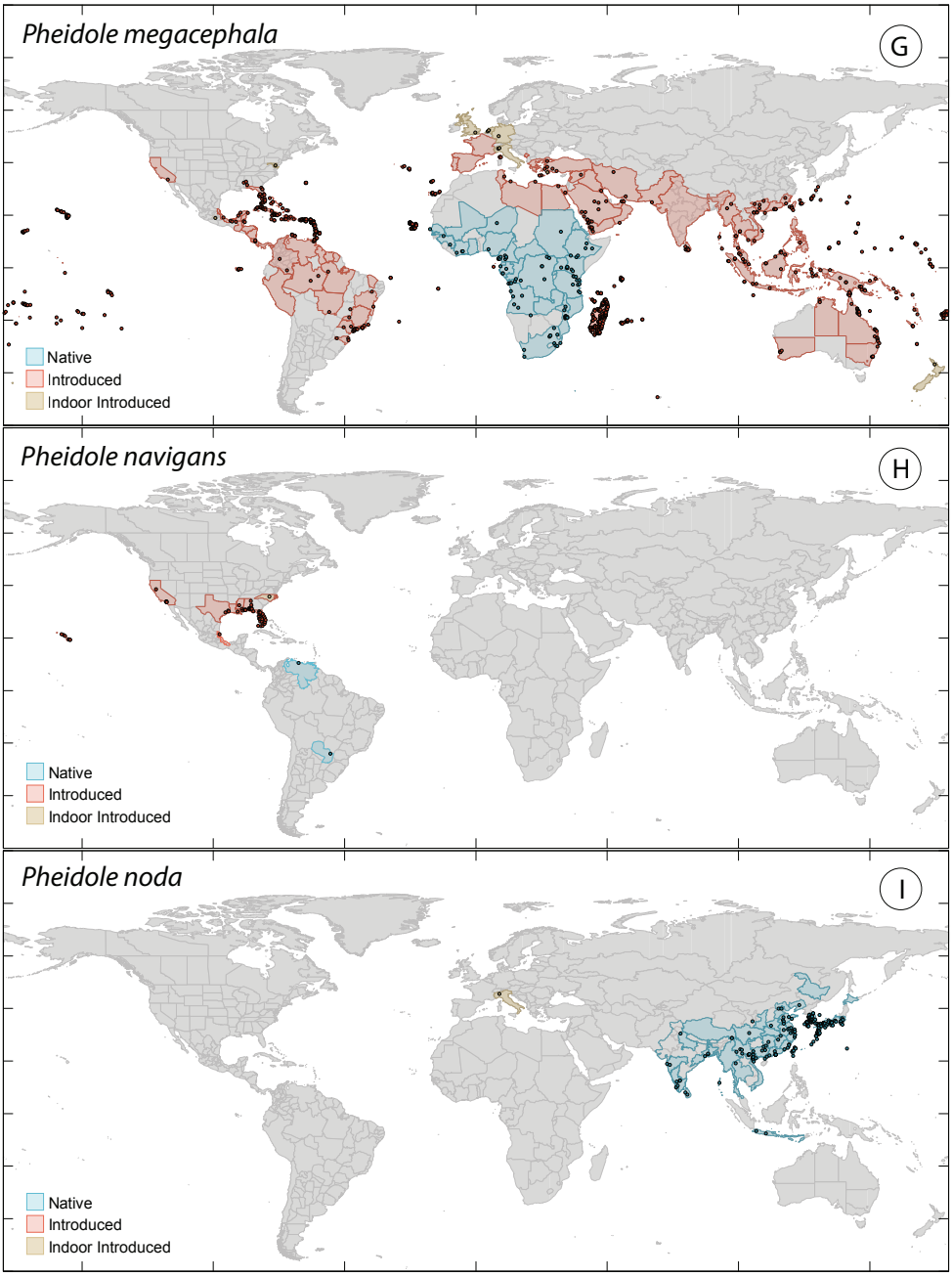


Figure 88. Continued. Geographic distribution of introduced *Pheidole* species. **G** *P. megacephala* (Fabricius) **H** *P. navigans* Forel **I** *P. noda* F. Smith. Circle symbols represent georeferenced localities. Shaded polygons represent administrative units from which the respective species have been recorded as occurring. Larger countries are subdivided into states or provinces for increased geographic resolution. Blue = putative native occurrence records. Red = putative introduced occurrence records. Yellow = records for indoor occurrences (heated buildings, greenhouses, etc.) in regions where the species is incapable of year-round outdoor survival.

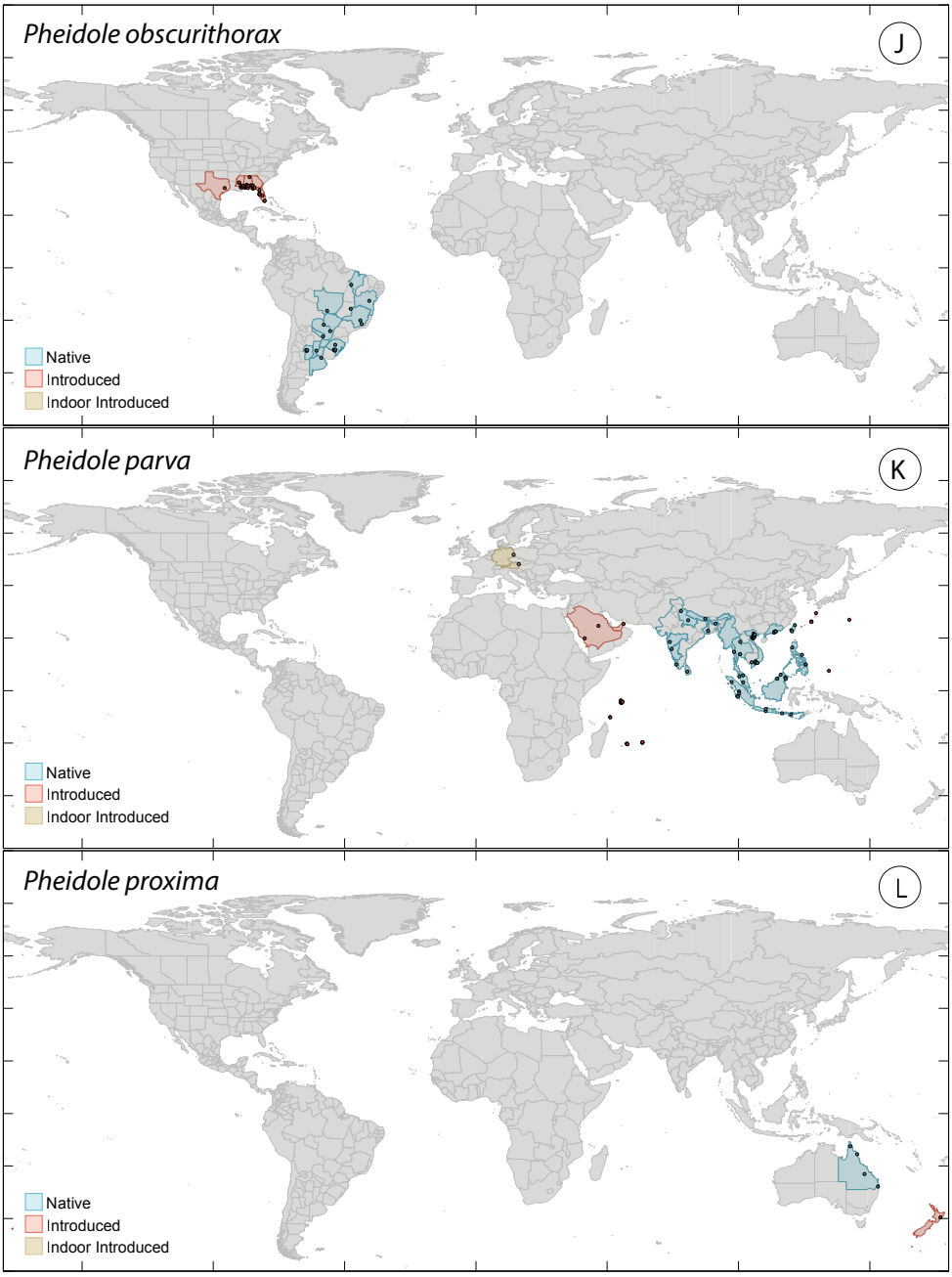


Figure 88. Continued. Geographic distribution of introduced *Pheidole* species. **J** *P. obscurithorax* Naves **K** *P. parva* Mayr **L** *P. proxima* Mayr. Circle symbols represent georeferenced localities. Shaded polygons represent administrative units from which the respective species have been recorded as occurring. Larger countries are subdivided into states or provinces for increased geographic resolution. Blue = putative native occurrence records. Red = putative introduced occurrence records. Yellow = records for indoor occurrences (heated buildings, greenhouses, etc.) in regions where the species is incapable of year-round outdoor survival.

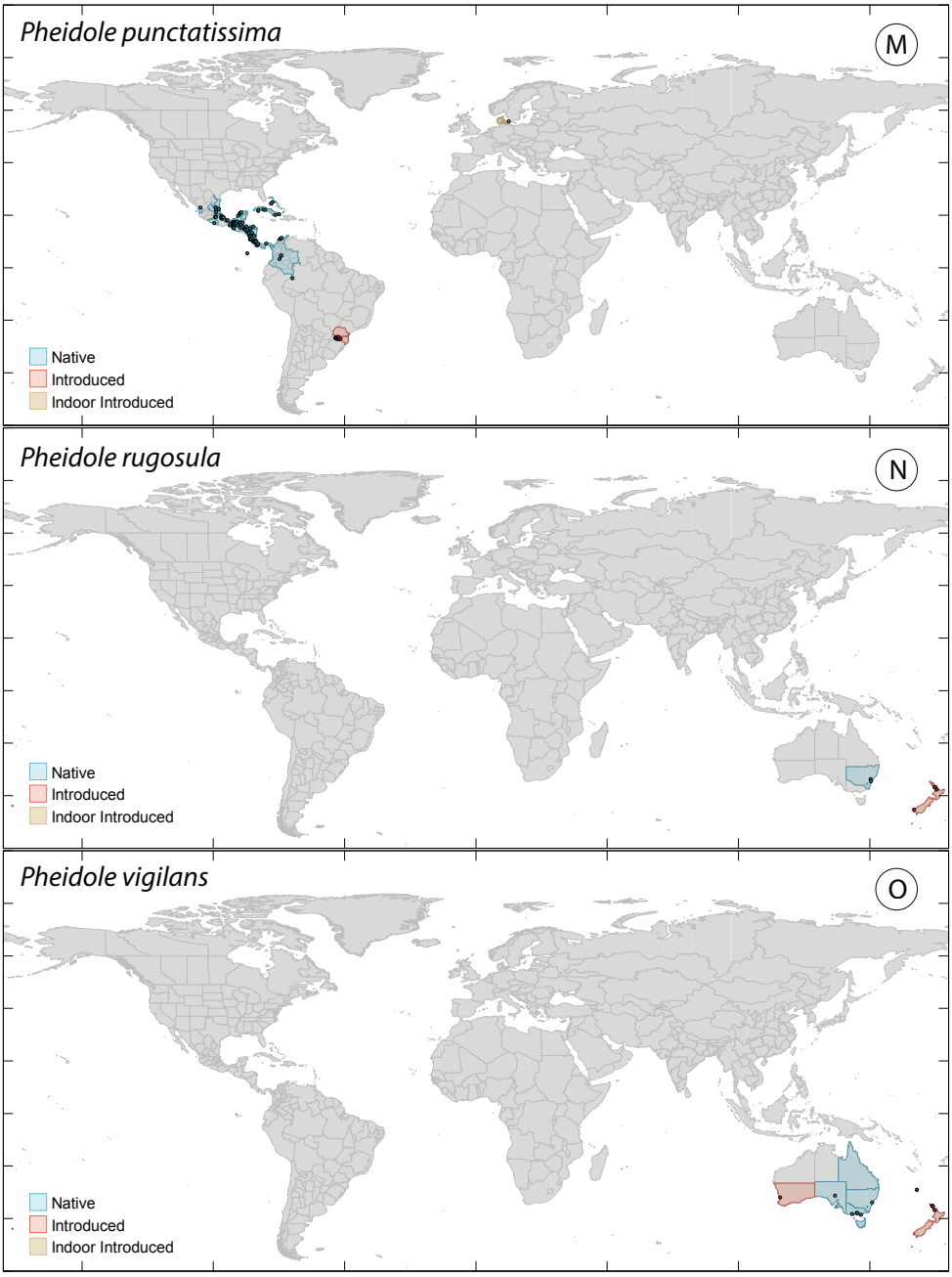


Figure 88. Continued. Geographic distribution of introduced *Pheidole* species. **M** *P. punctatissima* Mayr **N** *P. rugosula* Forel **O** *P. vigilans* (F. Smith).Circle symbols represent georeferenced localities. Shaded polygons represent administrative units from which the respective species have been recorded as occurring. Larger countries are subdivided into states or provinces for increased geographic resolution. Blue = putative native occurrence records. Red = putative introduced occurrence records. Yellow = records for indoor occurrences (heated buildings, greenhouses, etc.) in regions where the species is incapable of year-round outdoor survival.

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Supplementary material 1

Biogeographic data

Authors: Eli M. Sarnat, Georg Fischer, Benoit Guénard, Evan P. Economo

Data type: specimens data

Explanation note: Occurrence data used for analyses and generation of distribution maps (Figure 88) sorted by GABI number. GABI number refers to unique code assigned to each individual record of the Global Ant Biodiversity Informatics. 'Accession number' refers to specific accession codes for each individual record within the database. If the record refers to specimen data, the unique specimen identifier code is included in the Accession number field. 'Bentity2' refers to the geographic unit used to map species distribution (Guénard et al., in prep.). The Precision field provides a rough estimate of the geocoded location accuracy. Manual: location was manually geocoded after correcting the locality (old names, changing borders, wrongly translated). Source: coordinates are taken from the original data (the published coordinates). All other values are derived through geocoding the locations with the Bing geocode API. These values give an estimate of the accuracy which can include anything from an exact address to a small island. The more precise this value describes a location the more likely it is for a location to be accurately geocoded. An 'address' is for example likely to be more accurate than a 'bay'.

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RESEARCH ARTICLE

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Revision of the green lacewing subgenus *Ankylopteryx* (*Sencera*) (Neuroptera, Chrysopidae)

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Abstract

The Australasian and Oriental green lacewing subgenus *Ankylopteryx* (*Sencera*) Navás (Chrysopinae: Ankylopterygini) is examined and its diversity and placement among other members of the tribe Ankylopterygini is discussed. After study of specimens spanning the full distribution and anatomical range of variation for the subgenus, all prior putative species, resulting in the sole valid species are newly synonymized, *Ankylopteryx* (*Sencera*) *anomala* (Brauer). Accordingly, the following new synonymies are established: *Sencera scioneura* Navás, **syn. n.**, *S. feae* Navás, **syn. n.**, and *S. exquisita* Nakahara, **syn. n.** [all under the name *A.* (*S.*) *anomala*]. A lectotype is newly designated for *A.* (*S.*) *anomala* so as to stabilize the application of the name. To support our hypotheses, the wing and general body coloration as well as the male genitalia are reviewed. We elaborate on the possibility of *A.* (*S.*) *anomala* being nothing more than an autapomorphic species of *Ankylopteryx* Brauer, as it was originally described. The species is not sufficiently distinct to warrant recognition as a separate subgenus within the group, and most certainly not as its own genus as has been advocated by past authors. Nonetheless, we do not for now go so far as to synonymize the subgenus until a more extensive phylogenetic analysis is undertaken with multiple representative species from across *Ankylopteryx* and other ankylopterygine genera. Lastly, we comment on the biology of *A.* (*S.*) *anomala* in terms of the attraction of males to methyl eugenol and on the widespread practice of splitting within Chrysopidae.

Keywords

Ankylopterygini, Australasia, Oriental, Chrysopinae, lacewing, semiochemicals, taxonomy

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Introduction

The green lacewings (Chrysopidae) of the Australasian and Oriental regions comprise a diverse, yet poorly studied fauna (e.g., Nakahara 1955; New 1980; Brooks 1983, 1997; Tsukaguchi 1995; Yang et al. 2005; Winterton et al. 2012), with several genera in need of revision. One such genus is *Ankylopteryx* Brauer, including the subgenus *Sencera* Navás (Fig. 1) (Brooks and Barnard 1990; Brooks 1997). This subgenus is rarely encountered but distributed throughout the Orient and Australasia, ranging from Nepal to Vanuatu. *Sencera* was proposed by Navás (1924) to separate the species *Sencera scioneura* Navás from the remainder of the genus *Ankylopteryx* [this species is herein considered a synonym of *Ankylopteryx anomala* (Brauer)]. The description of the genus was based on the lack of the intramedial (*im*) cell in the forewing despite the fact that, apart from this isolated venational difference, all other characters were identical with *Ankylopteryx*. Two further taxa were added later — *A. feae* (Navás) in 1929 and *A. exquisita* (Nakahara) in 1955 (both originally proposed within *Sencera*) (Navás 1929; Nakahara 1955), bringing the diversity to four nominal species and almost exclusively known only from their type series. The late Nathan Banks (1868–1953) mentioned, but never published, his speculation of the possible synonymy of *A. anomala* and *A. scioneura* (Banks' suspicion was specifically mentioned by Nakahara 1955), but otherwise there has been no evaluation of the circumscription of species within *Sencera* beyond Brooks and Barnard (1990), Tsukaguchi (1995), and Yang et al. (2005).

Here we present a brief review of the subgenus based on the most extensive sampling of these rare lacewings, and elaborate and expand upon Nathan Banks' suspicions. Indeed, others have also noted similarities which, when taken into a broader context, suggest that it is not only the species that are suspect but the subgenus as a whole. Brooks (1983) recognized the striking similarity between *Ankylopteryx s.str*. and *Sencera*, emphasizing genitalic characters that united the two. He elaborated on their relationship and later demoted *Sencera* to subgeneric rank within *Ankylopteryx* (Brooks and Barnard 1990). The fact that some Oriental and African *Ankylopteryx* have a dramatically reduced *im* cell (Brooks 1983; Brooks and Barnard 1990; Tsukaguchi 1995) suggests the possibility that such species might form a grade relative to the loss observed in *Sencera*. Indeed, Tsukaguchi (1995) considered *Sencera* as a junior synonym of *Ankylopteryx*, and this synonymy should likely be re-established. Accordingly, it is important to re-evaluate diversity within *Sencera* and to determine whether further putative apomorphies for the group might be discovered. In addition to the few specimens of the four species that are known, we have examined individuals from various geographic localities. We amassed the largest sampling of this rare group, newly documenting the observed variation and providing a revised description and circumscription of the included species. This is done in the hopes that it will enhance our understanding of the patterns of variation across their range as well as ultimately permit revised hypotheses of relationship (Grimaldi and Engel 2007).

Material and methods

The higher classification followed is that of Brooks and Barnard (1990), and the morphological terminology used is that of New (1989), Brooks and Barnard (1990), and Aspöck and Aspöck (2008), the latter for genitalic structures. Measurements were made using an ocular micrometer. Photomicrographs were prepared using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and then arranged in Adobe Photoshop CS5. Dissections of the genitalia were made under an Olympus microscope. The terminalia were cleared in 10% KOH, washed twice in dH_2O, and stained with chlorazol black in 80% ethanol. Line drawings were prepared in Adobe Illustrator CS5.

In total we examined 49 specimens during the course of this study, which are deposited in the following institutions and were provided through the generosity of the named curators:

NHML The Natural History Museum, London, United Kingdom (Ben Price)
CAS California Academy of Sciences, San Francisco, California, USA (Norman Penny)
CSCA California State Collection of Arthropods, California Department of Food & Agriculture, Sacramento, California, USA

High-resolution photographs of historical type material that was otherwise not available for loan were contributed by the following:

NHMW Naturhistorisches Museum, 2. Zoologische Abteilung, Vienna, Austria (Harald Bruckner), for *A. anomala*.
NMNS National Museum of Nature and Science, Department of Zoology, Tsukuba-shi, Ibaraki, Japan (Utsugi Jinbo), for *A. exquisita*.
MCSN Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy (Maria Tavano), for *A. feae.*
ZMB Museum für Naturkunde, Berlin, Germany (Lukas Kirschey, Michael Ohl), for *A. scioneura.*

Systematics

Tribe Ankylopterygini Navás
Genus *Ankylopteryx* Brauer

Subgenus *Sencera* Navás

Sencera Navás 1925: 26. Type species: *Sencera scioneura* Navás 1925, by original designation. Brooks 1983: 6 [keyed as genus]; Brooks and Barnard 1990: 157 [demoted

to subgeneric rank, redescribed]; Tsukaguchi 1995: 10, 122 [synonymy with *Ankylopteryx*]; New 2003: 92 [keyed as subgenus of *Ankylopteryx*]; Yang et al. 2005: 51 [keyed as subgenus of *Ankylopteryx*].

Diagnosis. The subgenus *Sencera* differs from *Ankylopteryx s.str.* only in the absence of the forewing '*im*' cell (Fig. 2). Brooks and Barnard (1990) mentioned further differences in the forewing length, ratio of forewing length and width, and ratio of head and compound eye widths but these are all overlapping with those values for species of *Ankylopteryx s.str*. The same is true for the slight color differences noted between the two.

***Ankylopteryx* (*Sencera*) *anomala* Brauer**
Figs 1–14

Ankylopteryx anomala Brauer 1864: 901. Lectotype ♂, NHMW (*visum*).
Sencera scioneura Navás 1924 [1925]: 27. Holotype ♂, ZMB (*visum*). **Syn. n.**
Sencera feae Navás 1929: 371. Holotype ♂, MCSN (*visum*). **Syn. n.**
Sencera feai Navás 1930: 23 [*lapsus calami pro S. feae* Navás 1929].
Sencera exquisita Nakahara 1955: 143. Holotype ♂, NMNS (*visum*). **Syn. n.**
Ankylopteryx (*Sencera*) *anomala* Brauer: Brooks and Barnard 1990: 157 [combination implied].
Ankylopteryx (*Sencera*) *scioneura* (Navás): Brooks and Barnard 1990: 157 [combination implied].
Ankylopteryx (*Sencera*) *feae* (Navás): Brooks and Barnard 1990: 157 [combination implied].
Ankylopteryx (*Sencera*) *exquisita* (Nakahara): Brooks and Barnard 1990: 157 [combination implied]; Yang et al. 2005: 56.
Ankylopteryx exquisita (Nakahara): Tsukaguchi 1995: 131.

Diagnosis. As for the subgenus (*vide supra*).

Description. ♂. Overall color in live specimens light green with mostly greyish brown and some whitish markings (Fig. 3); in dried specimens green areas appears pale yellow or light brown.

Head: vertex smooth, raised and flat; laterally pale green, medially light green, with brown marking medially above toruli [varying in size and intensity of coloration from faint to dark, heart-shaped marking]. Frons smooth and flat; light green to whitish [in some specimens slightly darker than vertex] with small brown marking medially below toruli [varying in size and intensity of coloration from not visible to clearly visible marking (size about distance between toruli)]. Malar space broad; with brown marking extending from mandibular base to lower compound eye margin and epistomal sulcus. Clypeus smooth, slightly raised, indented medially at apical margin; medially light green to whitish, laterally and apically with brown marking. Labrum smooth, flat, apical margin simple without indentation, with brown markings basolaterally and apically. Mandible smooth, apex pointed; dark brown. Maxillary palp light green, fifth

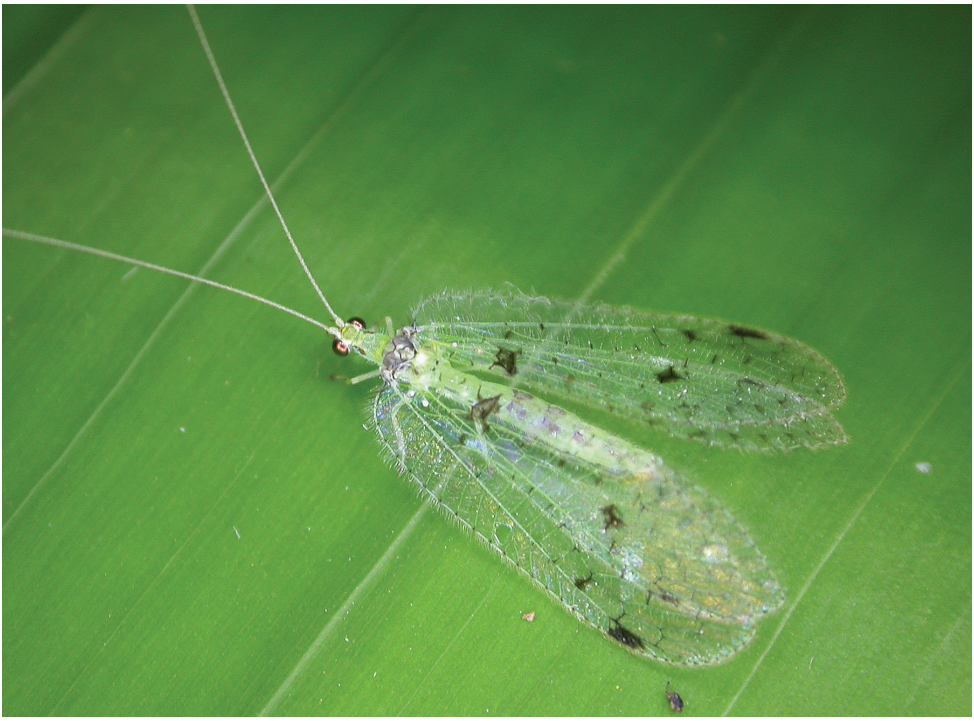


Figure 1. Photograph of live male of *Ankylopteryx* (*Sencera*) *anomala* (Brauer) from Chiang Mai, Thailand (photograph by S.L. Winterton).

palpomere brown. Labial palp light green, third palpomere brown. Gena ventrally flat; light green [in few specimens with brown marking medially]. Scape short and broad (ca. 1.25 times as long as wide); light green to whitish with brown marking laterally [varying in size and intensity of coloration from absent to dark brown longitudinal band]. Pedicel short (ca. 1.1 times as long as wide); light green to whitish. Flagellomeres ca. 2.4 times as long as wide; light green to whitish; setae in 4 rows, long (varying within single flagellomere from as long as flagellum width to twice as long), brown.

Thorax: pronotum ca. 0.9 times as long as wide; light green with brown longitudinal marking anterolaterally [varying in size from spot anteriorly to stretching over 2/3 of pronotum and intensity of coloration from almost not visible to dark brown]; setae whitish, long. Meso- and metathorax light green laterally and ventrally, dorsally mostly brown-greyish with some light green and pale green [intensity of brown greyish markings varying]; setae whitish, microsetae dense, long setae sparse. Prescutum with more light green than brown-greyish in some specimens; setae whitish, microsetae dense, long setae sparse. Metascutum with whitish marking; setae whitish, microsetae dense, long setae sparse medioanteriorly. Postmetascutellum light green with small brown-greyish marking anteriorly; setae whitish, microsetae dense, long setae sparse.

Legs: light green, fifth tarsomere and pretarsal claws dark brown; most specimens with brown marking mediodistally on pro- and mesotibia [varying in size and intensity

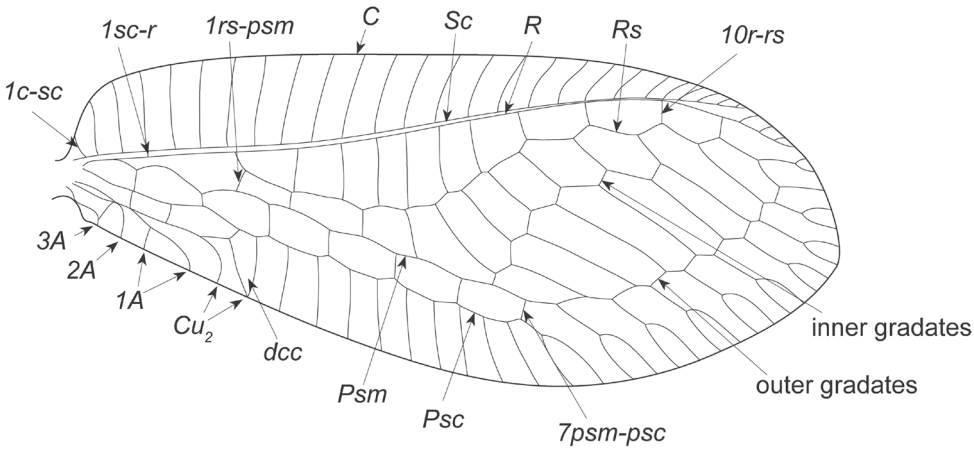
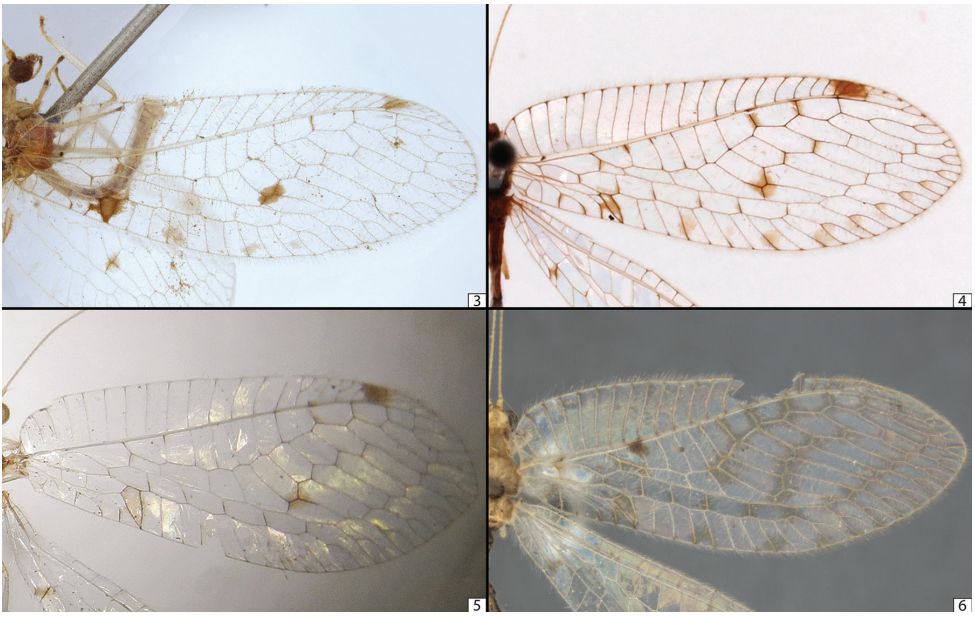


Figure 2. Line drawing of forewing of *Ankylopteryx* (*Sencera*) *anomala* (Brauer).

of coloration of marking from absent on both legs to well-defined dark brown spots on both legs, marking on mesotibia mostly smaller than on protibia]; setae long, mostly whitish, some brown. Pretarsal claws dilated basally.

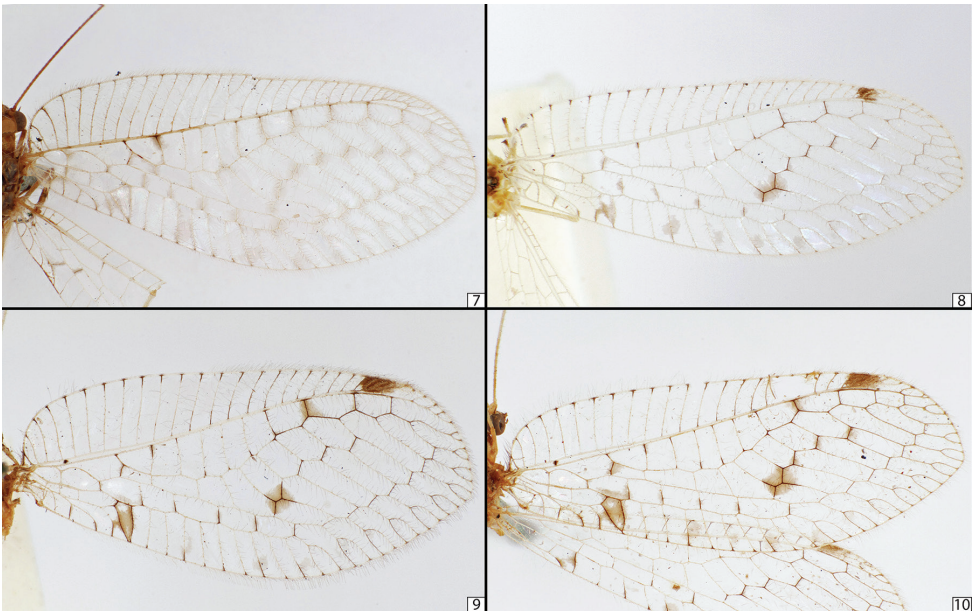
Forewing (Figs 2–10): mean length 10.7 mm; wing ca. 2.6 times as long as wide, slightly pointed apically. Veins mostly pale green [varying from almost all pale green to several veins dark at joints to various veins completely dark]; setae whitish [some setae partially brown, corresponding with wing markings]. Markings on membrane vary from almost absent (with small, faint, light-brown markings) to several dark-brown markings; costal area broad (ca. 0.3 times as wide as total wing width, varying between 0.27–0.33 mm); pterostigma varying from faint light brown (almost absent) to dark brown, extending over 4 crossveins (*2sc-r* – *5sc-r*); *1c-sc* (basal costal crossvein) brown at wing margin; *1sc-r* (bsx) brown; *1rs-m* brown in some specimens; *1r-rs* brown in some specimens. Membrane sometimes with brown marking surrounding *r-rs* (radial crossveins) crossveins (normally *7r-rs* – *10r-rs*), with brown marking in some specimens at *Rs* on a few *r-rs*. Venation as in most Ankylopterygini except *im* cell absent; *Psm* continuous with outer gradates; number of inner gradates varying from 5–7 (number varies also in a single individual, with left and right wings bearing different numbers); veins mostly brown, with brown marking on surrounding membrane of some veins in several specimens; basal inner gradate meeting *Psm*; most specimens with brown marking surrounding base of inner gradates; number of outer gradates varying from 6–8 (varying also between wings in same individual); faint brown coloration on surrounding membrane of outer gradates in a few specimens; *Cu2* and *1A* with brown marking at wing margin in some specimens; *dcc* closed, marked brown [varying in coloration from light to dark brown and in size of marking from not filling the entire cell to extending into the surrounding cells]; 5 *psm-psc* (crossveins between *Psm* and *Psc*) apical of *dcc*, some crossveins with light brown markings surrounding vein in several specimens; light brown markings surrounding



Figures 3–6. Photographs of forewings of *Ankylopteryx* (*Sencera*) *anomala* (Brauer) **3** Lectotype male from Pulo Milu, Nicobar Islands, India (NHMW) (photograph by Harald Bruckner) **4** Holotype male (mirrored) of '*Sencera exquisita* Nakahara' from Taiwan, China (NMNS) (photograph by Utsugi Jinbo) **5** Holotype male (mirrored) of '*Sencera feae* Navás' from Bhamò, Myanmar (MCSN) (photograph by Maria Tavano) **6** Holotype male (mirrored) of '*Sencera scioneura* Navás' from New Britain, Papua New Guinea (ZMB) (photograph by Lukas Kirschey). All photographs used with permission.

some terminal branches of *Psc*; junction of wing margin and veins brown in most specimens, especially in apical half of wing.

Hind wing: narrow (ca. 3.5 times as long as wide), apically more strongly pointed than forewing. Veins mostly pale green [varying from almost all pale green to some veins brown at joints, only few veins completely brown]; setae pale [some setae partially brown, corresponding with wing markings]. Costal area narrow (ca. 0.11 times as wide as total wing width). Several *r-rs* (*Rx*) with brown markings surrounding vein (normally *6r-rs – 9r-rs*) in most specimens, or only brown veins without surrounding marking; number of inner gradates varying from 3–5 (varies also between wings in same specimen); veins mostly brown; basal inner gradate meeting *Psm*; most specimens with brown marking surrounding base of inner gradates; number of outer gradates varying from 4–7 (also varies at times between wings in same specimen); veins mostly brown. Area between Cu_2 and basal-most terminal branch *Psc* with brown marking [varying in size and intensity of coloration]. Light brown markings surrounding some terminal *Psm* branches in some specimens; some *psm-psc* with small light brown markings surrounding vein in some specimens, two apicalmost *psm-psc* brown in most specimens; junction of wing margin and veins brown in most specimens, especially in apical half of wing.



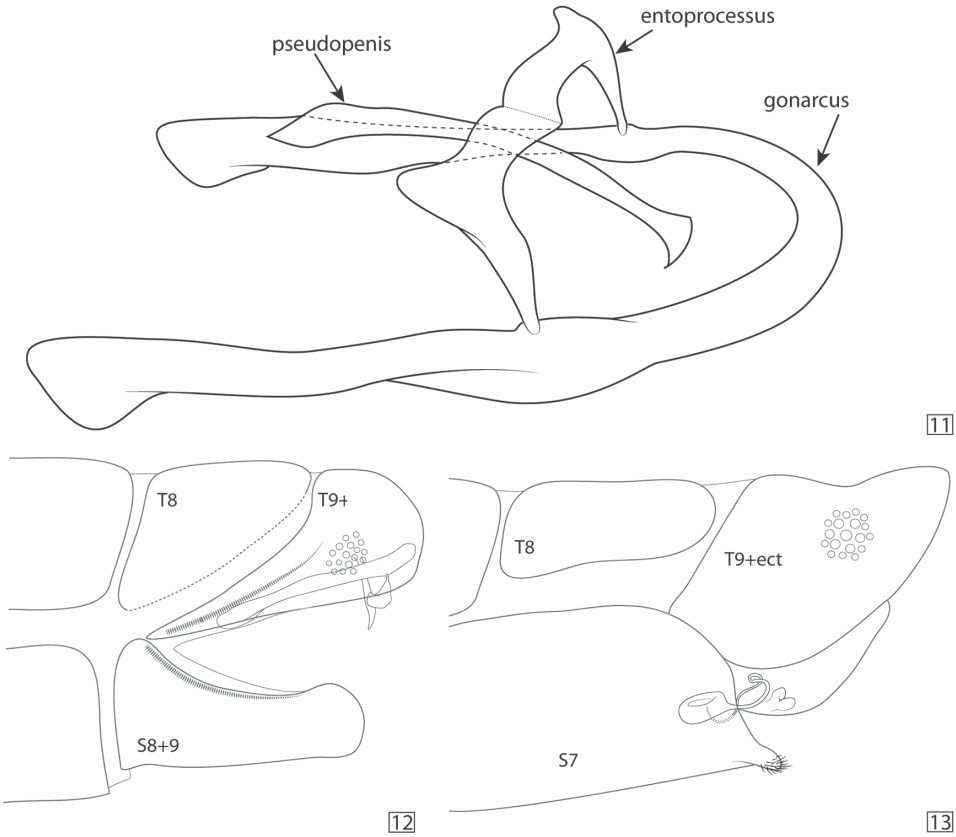
Figures 7–10. Photographs of forewings of *Ankylopteryx* (*Sencera*) *anomala* (Brauer) showing gradations in wing colouration, from almost unmarked (**7**), to slightly marked (**8**), to more strongly marked (**9**), and ultimately to very strongly marked (**10**). Specimens from Vanuatu (**7**), Brunei (**8**), Myanmar (**9**), and Hainan, China (**10**). All photographs by L.C.V.B.

Abdomen: Terga light green with brown-greyish markings dorsally on terga IV–IX, markings broader on anterior terga. Sterna light green; sterna VIII+IX fused. Setae whitish, microsetae dense, long setae more sparse.

Genitalia (Figs 11, 12): Only gonarcus, entoprocessus, and pseudopenis present. Gonarcus broadened at several locations, especially at apex of lateral arms [variation in general width of gonarcus between specimens; medial arch of gonarcus varying from smooth and only slightly broadened to having broader area forming small horn-like structure]. Entoprocessus loosely attached at narrow connection point to gonarcus; broadened medially, arms meeting medially, forming arch from gonarcus over pseudopenis. Pseudopenis long, subapically broadened and pointed apically [pseudopenis does not stain well in some specimens]. Gonosaccus with few gonosetae.

♀. Characters as in male except terminalia: *Terminalia* (Fig. 13) Sterna VII straight, apically slightly pointed ventrally, with setae at apex. Subgenitale and spermatheca with spermaduct present; subgenitale bilobed apically; spermatheca round (as wide as long); spermaduct coiled, ca. 2 times as long as spermatheca.

Measurements. Based on average from 5 specimens: Head 0.74 times as long as wide; upper distance between compound eyes 1.22 times lower distance between compound eyes; clypeus 0.51 times as long as wide; labrum 0.52 times as long as wide; malar space 1.09 times as long as mandibular base is broad; scape 1.09 times as long as wide; pedicel 1.19 times as long as wide; flagellomeres 3.7 times as long as wide (meas-



Figures 11–13. Male and female terminalia of *Ankylopteryx* (*Sencera*) *anomala* (Brauer). **11** Line drawing of male genitalic sclerites **12** Lateral view of male abdominal apex with genitalia **13** Lateral view of female abdominal apex with genitalia.

ured medially on flagellum); thorax 1.43 times as long as wide (measured in dorsal view); pronotum 0.95 times as long as wide (measured in dorsal view); forewing 2.62 times as long as wide; forewing costal width 0.3 times width of forewing; hindwing 3.57 times as long as wide; terga 1.51 times as long as wide (average of third tergum, difficult to measure when dry).

Lectotype (here designated). ♂, [India], M, Novara [Reise], 1857–59, Milu, Nicob. (Fig. 3) [this is the first specimen referred to by Brauer (1864) in "Ins. Nicobaricae Milu et Sambelong", where Milu refers to today's Pulomilo or sometimes as Pulo Milu, a small island off the north coast of Little Nicobar], deposited in NHMW. We have selected this syntype specimen to serve as the lectotype given the fact that it preserves the most characters (the paralectotype is today in exceedingly poor condition), and better ensures the correct application of the epithet. It should be noted that at some point holotype and paratype labels were placed on Brauer's series, likely by a curator of the collection as these are newer labels, but these have no standing as

Brauer himself never selected an individual to act as the name-bearing type and no subsequent designations of lectotype have ever been published. Thus, those labels have no nomenclatural standing and this is fortunate as the 'paratypus' label was placed on the most complete specimen (here selected as the lectotype), and the 'holotypus' label on the least well preserved specimen (thus serving the least value to taxonomic stability had they any validity).

Paralectotype. ♂, [India], O, Novara Reise, 1857–59, Sambelong, Nicob. [this is the second specimen referred to by Brauer (1864), "Ins. Nicobaricae Milu et Sambelong", with Sambelong today being the island of Grand Nicobar], deposited in NHMW.

Additional material examined. In addition to the syntype series, a total of 47 specimens available for study (21 ♂♂, 11 ♀♀, 15 sex undetermined), institutional repository and original identification of material indicated in square brackets: **AUSTRALIA:** 1♂, label imprecise: "Australia?", date unknown; collector unknown [BMNH: originally as *S. scioneura*]. **BRUNEI:** 3♂♂, 1 sex indet., June 16th 1984, collector A. Saman, Triencide trap [BMNH: originally as *S. anomala*]. **CHINA:** 1 sex indet., Hainan, You Boi, 1911, collector unknown [BMNH: originally as *S. exquisita*]. **INDIA:** 1 sex indet., Pirmed, 3400 ft., May 4th–6th 1937, collector Travencore [BMNH: indet. #1]. **INDONESIA:** 1♀, Sulawesi, Utaria, October 1985, collector unknown, Project Wallace of the R. Ent. Soc. Lond. [BMNH: originally as *S. anomala*]. **MALAYSIA:** 1♂, 2 sex indet., Bettotan near Sandakan, individual dates of July 26th, July 30th, and August 3rd 1927, collectors C.B.K & H.M.P [BMNH: originally as *S. anomala*]; 2♂♂, 1 sex indet., Cameron Highlands, May 22nd 1983, Methyl Eugenol lure trap, collector R.A.I. Drew [CSCA: indet]; 1♂, 3 sex indet., Kedah, nr. Jitra, individual dates of April 4th, 10th, and 11th 1928, collector H.M. Pendlebury [BMNH: indet. #2]; 6♂♂, Selangor, Gomback, Ulu Gomback Research Station, March 16th–17th 2006, 03°19'29"N 101°45'11"E, Steiner trap, Methyl Eugenol, collector T. Dikow [5♂♂ CSCA: indet; 1♂ CAS: indet.]; 1♀, Selangor, Ulu Langat, November 2nd 1981, collector K.R. Tuck [BMNH: indet. #2]. **MYANMAR:** 2♂♂, 1♀, Tenasserim, 1938, collector McLachlan [BMNH: indet. #1]; 1♂, Bhamò, Birmania, vii.1886 [MCSN: holotype of *S. feae*]. **NEPAL:** 1♂, 1 sex indet., Chitwan, Sauraha, December 26th 1981 – January 9th 1982, collector L. Jessop [BMNH: originally as *S. feae*]. **PAPUA NEW GUINEA:** 1♀, Finschhafen, April 9th 1944, collector E.S. Ross [CAS: indet]; 1♂, Neu-Britannien, Ralum, F. Dahl S., zum Licht sufl., auz Juli 96., 13.12.96 [ZMB: holotype of *S. scioneura*]. **SRI LANKA** [Ceylon]: 1♀, Galle, February 10th 1907, collectors Bainbrigge & Fletcher [BMNH: originally as *S. feae*]; 1 sex indet., Kottawa, April 24th 1892, collector unknown [BMNH: indet. #1]; 1♀, Nawalapitiya, 1938, collector McLachlan [BMNH: indet. #1]; 1♀, detailed locality unknown, 1938, collector McLachlan [BMNH: indet. #1]. **VANUATU** [New Hebrides]**:** 1♀, Erromanga, July 1930, collector L.E. Cheesman [BMNH: originally as *S. scioneura*]; 2♀♀, Malekula, Ounua, March-April 1929 and May 1930, collector L.E. Cheesman [BMNH: originally as *S. scioneura*]. **TAIWAN** [Central Formosa]: 2 sex indet., Suishako, 1911, collector unknown [BMNH: originally as *S. exquisita*]; 1♂, Hori Formosa, 5.v.1939,

Tomio Kaneko [NMNS: holotype of *S. exquisita*]. **THAILAND:** 1♀, Chiang Mai Province, Samoeng Tai, 600m, July 14th 2013, 18.8598°N 98.6507°E, collector S. Winterton [CSCA: indet]; 1♂, 3 sex indet., Trang Province, Khao Chong, October 20th–27th and December 1st–8th 2008, 7 32' N 99 47' E, collectors P. Kongnoo & T. Tongrod [CSCA: indet].

Comment. Although previous authors have alluded to other, putative species in *Sencera* (e.g., New 2003), we cannot confirm any such diversity and all of those forms result from splitting species based on minor variations in wing pattern and coloration. We have found that such patterns are merely variants of a single widespread species. The patterns only superficially appear to be geographically distinct when looking at very small sample sizes from isolated geographic localities (*vide infra*).

Discussion

Systematics

We compared the four nominal species in *Sencera* (*A. anomala*, *A. exquisita*, *A. feae,* and *A. scioneura*) as well as several undetermined specimens, some of which were considered putatively new species. Even at first glance over previously determined material it was evident that there is and has been a great amount of confusion when it comes to identifying specimens to one of the original four species. The species in *Sencera* were established on differences in wing coloration (Figs 3–6), some of which overlap, and the original descriptions are not unambiguous, often failing to mention any clear distinction from other species. The wing coloration can vary from multiple large dark areas in the fore and hind wings (Fig. 10) to just barely-visible, pale spots (Fig. 7). As the species are all comparatively rare, suitable samples have been difficult for authors to obtain. With a comparatively larger sample size of 49 specimens (large for a group of four, rarely-encountered taxa!) that span the geographic gaps between the previously isolated localities of the extremes in variation, we discovered that these color patterns cannot be sorted into definite groups. The specimens collected in the easternmost regions (mostly '*A. scioneura*' from Vanuatu) are generally less colored than specimens in the west and north ('*A. feae*' and previously undetermined specimens from northern India, or '*A. exquisita*' from near Hong Kong and Taiwan). In the intervening regions, such as Thailand, specimens show somewhat intermediate wing colorations (e.g., *A. anomala*), and often certain color patterns are unique to a single individual. The same applies for slightly varying sizes in body length and wing width. Ultimately, rather than distinct species there is a continuous variation of wing coloration and width as well as darkness of the body, with numerous overlapping combinations which can to some degree be associated by locality. It is understandable that past researchers who had only seen the extremes of these color forms described them as individual species, and failed to detect the actual continuous variation. The wing coloration does not only vary greatly between but also slightly within specimens

— one side having a different degree of coloration than the other. Since wing venation is known to vary between the two sides (Barnard 1984; pers. obs.), it is unclear how reliable small differences in forewing coloration may be for the circumscription of distinct species. Even if, for example, specimens with almost no markings on the forewing would be grouped together, then there remain intermediates that show only scant markings. This is more complicated on the other end of the spectrum, when one individual has strongly marked wings but may lack merely one spot relative to another, virtually identical specimen.

Just as with wing coloration, the intensity of markings on the pronotum and whether a spot is present and the degree of its development on the protibia vary similarly. Some specimens from Brunei lack this protibial spot, in others it is small but present — suggesting that this character is almost as variable as the wing coloration. All other characters are similar to the remaining specimens and this missing spot is not mentioned in any description and does not seem to be indicative of an endemic 'spotted-protibia species'. More importantly, we dissected the male genitalia from specimens representing the full spectrum of coloration and found no significant differences among them. The genitalia of some specimens are slightly thicker but these are exceedingly small variations and seem to be correlated with body size and degree of pigmentation rather than any boundary between taxa. Accordingly, there are no discrete units identifiable across the variation observed, and our larger sample sizes are indicative of a single, widespread, and variably-colored species. This has served as the basis for our aforementioned synonymies.

Not only has the similarity of those previously recognized species within *Sencera* been striking, but also the dramatic sameness of the subgenus and *Ankylopteryx s.str*. As mentioned in the original description of *Sencera*, the only difference between these groups is the absence of the *im* cell (Navás 1924). Given that one of the original species of *Sencera* was originally placed within *Ankylopteryx*, the agreement between the two is obvious, and one can rightly question whether it is worth retaining the former as a distinct group. Both *Ankylopteryx s.str*. and *Sencera* possess only a gonarcus, entoprocessus, and pseudopenis (Fig. 11) (Brooks 1983; Brooks and Barnard 1990), and this condition is likely a synapomorphy supporting *Ankylopteryx s.l*. Brooks (1983) emphasized the genitalic structure as reflecting the close relationship between *Sencera* and *Ankylopteryx*, and further noted the considerable similarity between them and *Parankylopteryx* Tjeder. The arcessus of *Parankylopteryx* is fused with the gonarcus and not detached (as the 'pseudopenis') as in the other two genera. The same author also mentioned several species of *Ankylopteryx* occurring in Africa and the Oriental region that have a small, somewhat reduced *im* cell (e.g., *A. doleschali* Brauer, *A. obliqua* Banks, and *A. decorsei* Navás), and Tsukaguchi (1995) also noted the considerable similarity with some Asian species (e.g., *A. gracilis* Nakahara). These are eminent arguments for the notion that *Sencera* is nothing more than an autapomorphic species of *Ankylopteryx* in which the reduction of the *im* cell has reached its apogee (i.e., complete absence) relative to others in the genus. This position is presently only speculative and so we have avoided formalizing a reinstatement of the synonymy for the generic groups until

after it can be tested in a comprehensive cladistic analysis. Nonetheless, Tsukaguchi's (1995) original synonymy seems to have been prescient.

The synonymy of the four species of *Sencera* discussed here begs mention of an issue common to the taxonomy of lacewings. Within Chrysopidae there are a vast number of species and genera that are characterized by exceptionally small differences in trifling traits by comparison to their closest relatives, and such supraspecific groups are frequently monotypic (Brooks and Barnard 1990; Winterton and Brooks 2002). The trend of often unjustified splitting — describing new species and even genera based on such minimal variations — is not beneficial and complicates research on this interesting family, particularly when many are not correlated with significant differences in the genitalia. The situation is exacerbated when these differences are based on single traits and supporting data are not provided. The history of chrysopid taxonomy is one of consistently reorganizing units into smaller groups, or describing newly discovered variants as new genera without demonstrating the concomitant, reciprocal monophyly of the most similar genus when such a newly described taxon is established. Many taxa should be revisited to address this ongoing issue and ultimately provide a more rigorous classification for evolutionary studies within Chrysopidae (Winterton and Brooks 2002). As it stands, the current taxonomic situation tends to obscure relationships owing to the retention of groups strongly suspected as paraphyletic, and thereby limiting the predictive value of the classification and our understanding of evolutionary phenomena.

Biology

Males of *Sencera* are attracted to methyl eugenol (IUPAC: 1,2-Dimethoxy-4-prop-2-en-1-ylbenzene) (Tsukaguchi 1995; Pai et al. 2004; pers. obs.), a phenylpropanoid found in many plants (Tan and Nishida 2012). This suggests a potential for collecting with special baits as has been done with males of the fruit fly genus *Bactrocera* Macquart (Leblanc et al. 2009). Insects attracted to methyl eugenol have been observed to acquire the chemical from different orchid flowers. Along with dacine fruit flies, males of *Sencera* were found on an orchid of the genus *Bulbophyllum* Thouars (Epidendroideae: Podochileae) in high abundance (Fig. 14).

Hitherto, the known number of chrysopid taxa attracted to methyl eugenol is low. Apart of *Sencera* it has been shown to attract only *Mallada basalis* (Walker) in Hawaii (Suda and Cunnington 1970) and a species of *Cunctochrysa* Hölzel in the Philippines (Umeya and Hirao 1975). During a recent field trip to Ghana in 2014 large numbers of males of an unidentified species of *Parankylopteryx* were observed similarly attracted to methyl eugenol and terpinyl acetate (IUPAC: 2-(4-Methyl-3-cyclohexen-1-yl)-2-propanyl acetate) (Martin Hauser, Stephen Gaimari pers. obs.). Other chemicals that have been found to attract male chrysopids are methyl salicylate for *Chrysopa nigricornis* (Burmeister) (James 2003) and iridol for *C. oculata* Say (Chauhan et al. 2007). This raises the question as to whether these chemicals are analogous in structure and result in similar physiological and behavioral responses for the animals.

Figure 14. Photograph of a live male of *Ankylopteryx* (*Sencera*) *anomala* (Brauer) from Kuala Lumpur, Malaysia at a flower of an unidentified orchid species of the genus *Bulbophyllum* Thouars (Orchidaceae: Epidendroideae) (photograph by P.T. Ong, used with permission).

Such observations raise many questions, including whether or not such a chemical association is pervasive across the clade comprising *Parankylopteryx*, *Ankylopteryx s.str.*, and *Sencera*, and whether such attraction might even represent a synapomorphy for this or a more inclusive group. It is important to investigate whether males of species of *Ankylopteryx* are attracted to this chemical and if this can be found throughout Ankylopterygini. More importantly, it remains to be discovered what the true biological significance of this trait is. Given that the baits only attract males, one immediately wonders whether these are components of semiochemicals produced by the females or if they play some other role in courtship and mating behaviors (Aldrich et al. 2009). On the surface it seems as though these may act to gather males into mating leks, from which either a chemical cue or mere location attracts females. It is possible that methyl eugenol attracts males because they in turn use it to produce female attractants, as seen in fruit flies. As of yet, this remains untested but represents a significant area

of chemical ecology and behavior for investigation. Moreover, as alluded to above, discovery of the specific attractants involved for both males and females offers the possibility of amassing material for once 'rare' or 'uncommon' taxa, as well as hitherto unknown species, much as was the case when similar chemicals were found to lure male orchid bees (e.g., Dodson et al. 1969; Dressler 1982). Future collecting trips should target sampling with varied baits to see how broadly across chrysopids they are attractive and/or whether different taxa are attracted to different chemicals.

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Systematics and biology of *Xylocopa* subgenus *Schonnherria* (Hymenoptera, Apidae) in Argentina

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Abstract

Biological information on the species of the large carpenter bee *Xylocopa* subgenus *Schonnherria* occurring in Argentina is revised. Based on the appraisal of museum specimens, the study of type material, and field surveys conducted across 15 provinces between 2007 and 2011, the following seven species are recognized for the country: *X. bambusae* Schrottky, *X. chrysopoda* Schrottky, *X. macrops* Lepeletier de Saint Fargeau, *X. simillima* Smith *X. splendidula* Lepeletier de Saint Fargeau, *X. pulchra* Smith, and *X. viridis* Smith. Previous literature records of *X. dimidiata* Latreille, *X. subcyanea* Pérez, and *X. varians* Smith for the province of Misiones appear to have been misidentified specimens, although the presence of these species in Argentina cannot be entirely ruled out given the proximity of this province to Brazil and Paraguay where they occur; *X. boops* Maidl was described from a male specimen with unusually enlarged eyes and is newly synonymized under *X. macrops*. Males and females of all species are diagnosed, described, and figured, including details of the male genitalia. Taxonomic comments, data on the geographical distribution and nesting substrates, and identification keys to all Argentinean species of *Schonnherria* are provided. The nesting biologies of *X. splendidula* and *X. viridis* are documented.

Keywords

Anthophila, carpenter bees, host plants, nesting biology, pollinators, Xylocopini

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Introduction

Large carpenter bees of the genus *Xylocopa* Latreille (Apidae: Xylocopini) are conspicuous, commonly encountered, and fascinating elements of the melittofauna in many regions of the world. These usually robust, large, hairy bees nest in solid wood including structural timbers or in dead stalks of plants (hence their common name), althought some species nest in the ground. The more than 470 species are currently grouped in 31 subgenera, and approximately 100 species (in 12 subgenera) are recorded from the Neotropical region (Ospina 2000; Michener 2007; Moure 2007). The social behavior of *Xylocopa* is interesting and still poorly studied. Some species may live solitarily while others in semisocial or primitively eusocial nests, where the oldest female (mother or sister) feeds via trophallaxis both young females and males. Variation among polulations in these social behaviors may occur (Michener 1990). The diversity of mating behaviors is another interesting aspect of the biology of *Xylocopa*. For example, males in some species exhibit a lek-like mating behavior, defending areas that do not contain resources and at which females are attracted via pheromones. In other species, males patrol nesting or foraging sites and intercept females at flight (e.g., Gerling et al. 1989; Vinson and Frankie 1990; Prager and Richardson 2012). The male morphological modifications associated with such a diversity of mating behaviors are also outstanding. They range from the enlargement of the compound eyes, distinctly modified legs with a number of spines and protuberances of diverse shapes and sizes (Lucia et al. 2014), to the development of large pheromonal glands that change the configuration of the mesosoma (Minckley 1994).

Carpenter bees are also economically important. Some species are effective pollinators of diverse crops, including passion fruit, squash, tomato, Brazilian nut tree, and eggplant, and they are already being used for this purpose in different countries (e.g., Keasar 2010; Giannini et al. 2015). Additionally, some species such as *X. virginica* (Linnaeus) in North America or *X. frontalis* (Olivier) in South America may become an annoyance for people when nesting in houses or buildings. First, the large body size, the loud buzzing produced when flying or making their nests, and the approching behavior exhibited by males when patrolling a mating site, make these bees intimidating. Second, the various nest entrances and tunnels built inside the timber deface and may also weaken the nesting timber, thus causing structural damage and requiring control (Barrows 1980).

Despite the interesting biology, ecological importance and potential for development in crop pollination, most species of *Xylocopa* remain both biologically and taxonomically unknown. As for other taxa (Gonzalez et al. 2013), the diversity of *Xylocopa* is largely unexplored in many regions of the world and many species are difficult to nearly impossible to identify. Species from many areas are known only from the type specimen, a small number of specimes or from a single sex, the available descriptions do not allow for reliable identifications, and identification keys, when available, are poorly illustrated or not illustrated at all.

As part of an on-going effort to reduce such a taxonomic impediment and to increase our understanding of the biology of Neotropical carpenter bees, here we revise the species of *Xylocopa* subgenus *Schonnherria* Lepeletier de Saint Fargeau occurring

in Argentina. This subgenus is the second most species-rich group of *Xylocopa* in the Western Hemisphere, containing about 30 species that range from southern United States to southern Argentina (Michener 2007). Here we recognized seven of the 11 species currently listed for the country (Hurd 1978); three of them appear to be records from misidentified specimens and one is placed in synonymy. We provide diagnoses, illustrations, descriptions, taxonomic comments, and information on the distribution to all species known to the country. This work is a continuation of a series of contributions dealing with the systematics and biology of carpenter bees in Argentina (Lucia and Abrahamovich 2010; Lucia et al. 2010; Ávalos-Hernández et al. 2011; Stuke et al. 2011; Lucia et al. 2012; Lucia and Gonzalez 2013; Lucia et al. 2014; Lucia et al. 2015).

Material and methods

Morphological terminology generally follows that of Hurd and Moure (1963) and Michener (2007). The use of ventroapical plate of the male gonocoxite and lateral carina of the penis valve follows Michener (1975) and Minckley (1998); supraorbital line refers to the upper ocular tangent and is used here to indicate the position of the laterall ocelli in frontal view. External morphological features were studied using a Nikon SMZ 745T stereomicroscope. Photographs were taken with a Canon Power Shot® A520 digital camera attached to a steromicroscope and images were assembled using CombineZM open software (Hadley 2011). Species redescriptions emphasize structural characters, such as punctation, and are based on the examined specimens to include possible variations among characters. Ten specimens of each species were measured, except for *X. chrysopoda* Schrottky and *X. pulchra* Smith from which we were only able to measure two specimens of each. Measurements were taken with an ocular micrometer and were rounded to the nearest tenth of a millimeter; mean values and ranges are given in millimeters. Total body length was measured from the head to the apex of metasoma in lateral view; forewing length was measured at the anterior margin, from the apex of the costal esclerite to the wing apex; mesosoma width was measured between the outer borders of the tegulae; metasoma width was measured across the second tergum. The following abbreviations are used in the descriptions: T, S, F, and OD for metasomal terga and sterna, flagellar segments, and maximum diameter of the median ocellus, respectively. Male genitalia were mounted on metal studs and coated with gold-palladium for examination with a scanning microscope (SEM) Jeol-JSM-6360MV.

The primary types of all species treated herein were examined, as well as a total of 1702 specimens from all provinces of Argentina deposited in the following institutions and personal collections. The curators who kindly arranged the loans or allowed access to the collection in their care are indicated parentheses:

BMNH British Museum Natural History, London, UK (D. Notton)
CZ Private Collection of "Caire-Zelich", Entre Ríos, Argentina (L. Caire-M. Zelich)

FAUBA Facultad de Agronomía Universidad de Buenos Aires, Buenos Aires, Argentina (J. P. Torretta)
IADIZA Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (G. Debandi)
IFML Fundación Miguel Lillo, San Miguel de Tucumán, Argentina (M.V. Colomo de Correa)
MACN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (A. Roig Alsina)
MLP Museo de La Plata, La Plata, Argentina (A. Lanteri)
MMP Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina (J. Farina)
MNCN Museo Nacional de Ciencias Naturales, Madrid, España (M. Paris)
MNHN Muséum National d'Histoire Naturelle, Paris, France (C. Villemant, A.Touret-Alby)
MZUSP Museu de Zoologia, Universidade de São Paulo, Brazil (R. Gonçalves)
NMW Naturhistorisches Museum Wein, Wein, Austria (D. Zimmermann-M. Vizek)
SEMC Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (M.S. Engel, J. Thomas, Z. Falin)
USNM National Museum of Natural History, Washington, DC, USA (B. Harris, S. Brady)
ZMB Museum für Naturkunde, Humbold-Universität zu Berlin, Berlin, Germany (F. Koch, V. Ritcher)

Information on the distribution was taken from literature and from specimen labels. The biogeographic provinces referred in the distribution account for each species followed those of Cabrera and Willink (1980). Complete label data for the examined material are available as supplemental material [online only]. Label data were transcribed literally, with bars "//" indicating information recorded on different labels.

Surveys for specimens as well as for nests of *Xylocopa* were conducted by M.L. between 2007 and 2011 across 15 provinces. The following provinces could not be sampled: Formosa, San Juan, La Pampa, Neuquén, Rio Negro, Santa Cruz, and Tierra del Fuego. When nests were found, the following variables were recorded: type of substrate and location (dead wood, structural timber, etc), plant species, and height above ground. Adults found inside nests were collected, killed, and deposited as vouchers in MLP. In the laboratory, the internal nest architecture was studied using three-dimensional molds made of liquid silicone rubber, as described in Lucia et al. (2014). Photographs of the nests were taken with a Panasonic® FZ18 digital camera.

Measurements of internal nest features were taken from the molds using a caliber. Mean values are provided with standard deviations. We used a Pearson correlation analysis to test for association between the following variables: tunnel length and tunnel width, total number of tunnels per nest and maximum diameter of the tree branch

where the nest was found, total number of brood cells and total number of tunnels, and number of cells per number of tunnels and tunnel length.

Results

Systematics

Genus *Xylocopa* Latreille, 1802

Subgenus *Schonnherria* Lepeletier de Saint Fargeau, 1841

Xylocopa (*Schonnherria*) Lepeletier de Saint Fargeau, 1841: 207. Type species: *Xylocopa micans* Lepeletier de Saint Fargeau, 1841, by designation of Sandhouse, 1943: 598.
Xylocopa (*Schönherria*) Dalla Torre, 1896, 202, *lapsus calami pro Schonnherria* Lepeletier de Saint Fargeau, 1841 (not Burmeister, 1855: 417 [Coleoptera: Scarabaeoidea]).
Shornherria Ashmead, 1899: 71, error for *Schonnherria* Lepeletier de Saint Fargeau, 1841.
Xylocopa (*Schoenherria*) Hurd and Moure 1963: 118, *lapsus calami pro Schonnherria* Lepeletier de Saint Fargeau, 1841.
Xylocopa (*Ioxylocopa*) Hurd and Moure 1963: 116. Type species: *Xylocopa chrysopoda* Schrottky, 1902, by original designation; Minckley 1998: 36 [synonymy with *Schonnherria*].
Xylocopa (*Xylocospila*) Hurd and Moure 1963: 109. Type species: *Xylocopa bambusae* Schrottky, 1902, by original designation; Minckley 1998: 36 [synonymy with *Schonnherria*].

Diagnosis. Species in the subgenus *Schonnherria* are small (15 mm) to moderately large bees (~24 mm), often with metallic highlights on all tagmata. *Schonnherria* can be distinguished from all other New World subgenera of *Xylocopa* by the following combination of characters: female mandible bidentate (except tridentate in *X. viridigastra* Lepeletier de Saint Fargeau, 1841), with apical tooth about as broad as or broader than basal tooth; T1 with complete gradulus on both sexes, remaining terga with gradulus absent (except in the male of *X. bambusae* with gradulus also on T2); male genitalia with a large spine of the ventral margin of the gonocoxite and the apex of the gonostylus bifid.

Species accounts

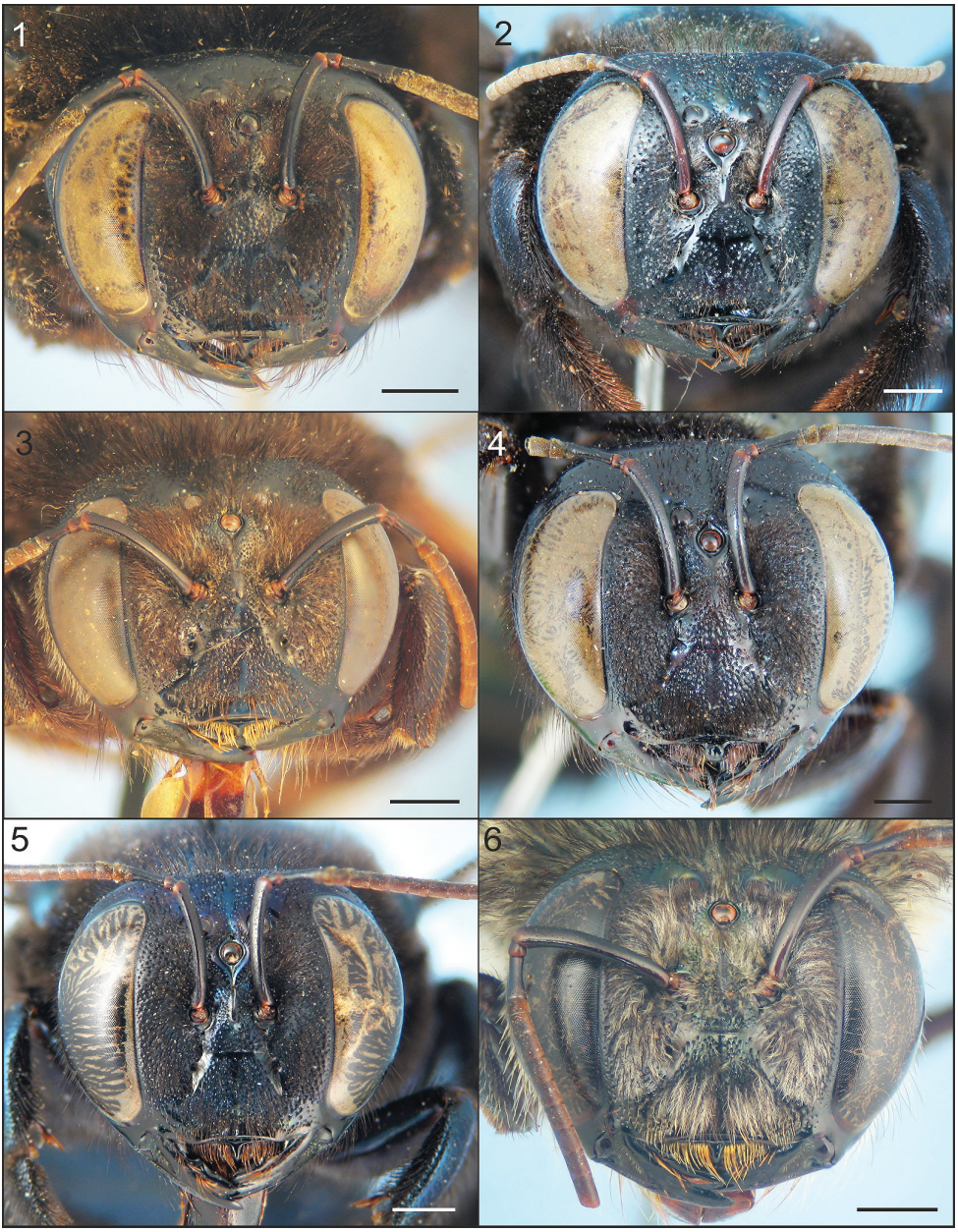
Xylocopa bambusae Schrottky, 1902
Figures 1, 7, 13, 19, 25, 30, 35, 40, 57

Xylocopa bambusae Schrottky, 1902: 475 (holotype: MZUSP; ♂, Rio Grande do Sul, Brazil) (examined)

Xylocopa eburnea Friese, 1903: 202 (lectotype: ZMB; ♂, Rio Grande do Sul, Brazil); Hurd and Moure 1961: 186 (lectotype designation and synonym with *bambusae*)
Xylocopa bellula Brèthes, 1916: 413 (holotype: MACN; ♀, Misiones, Argentina (examined); Hurd and Moure 1961: 187 (synonym with *bambusae* and unneccesary lectotype designation)
Xylocopa (*Xylocospila*) *bambusae*: Hurd and Moure 1963: 109.

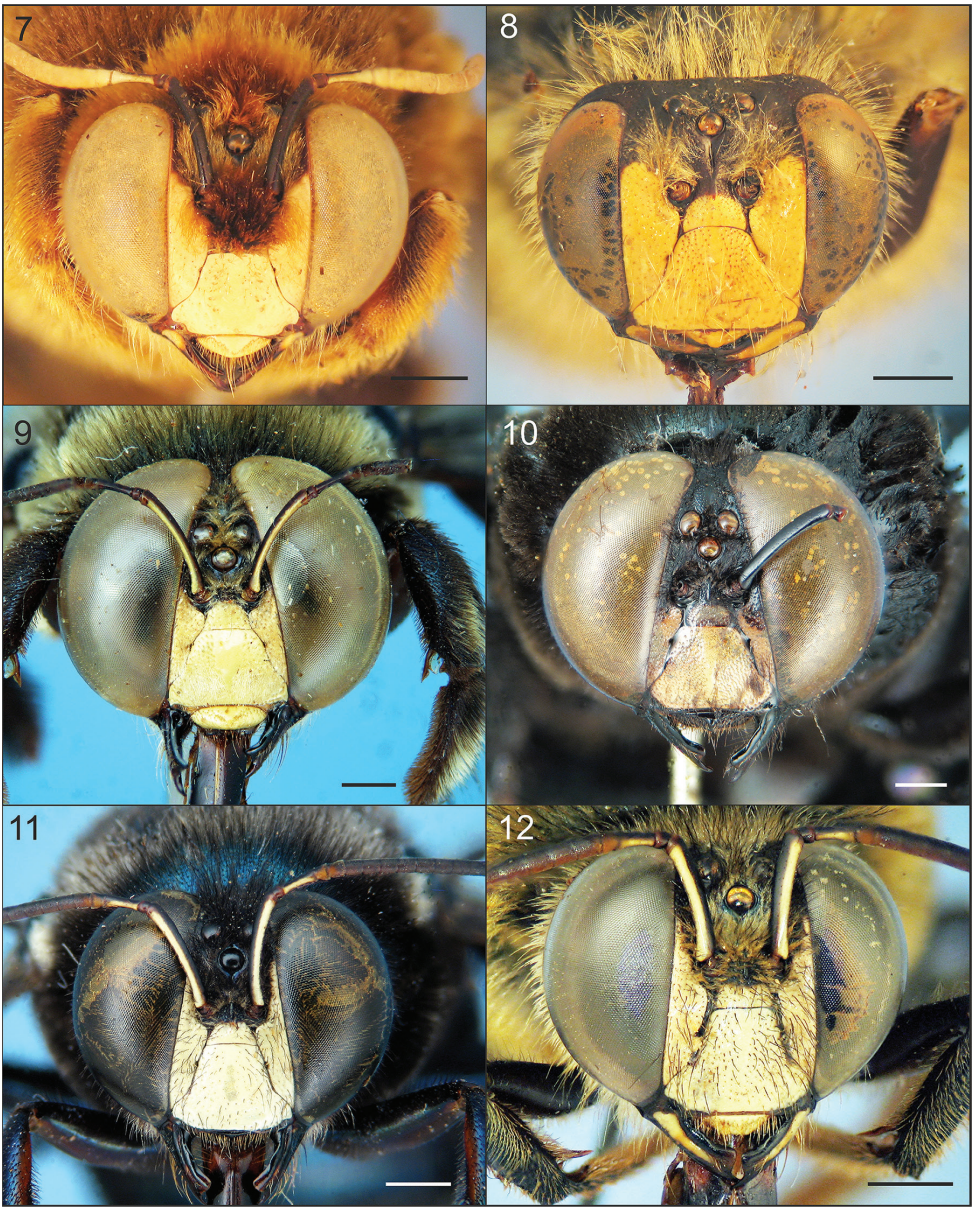
Diagnosis. The female of this species can be easily distinguished from other Argentinean species of *Schonnherria* by the following combination of characters: small body size (body length 14–17 mm); integument dark brown to black throughout, without metallic highlights; clypeus flat in profile, not elevated from adjacent paraocular area; clypeoalveollar distance long, about twice as long as longitudinal diameter of antennal socket; frontal carina projected into a distinct tubercle just above or at the upper tangent of anntenal sockets (Fig. 1); vertex and metasomal terga with large impunctate areas (Fig. 13); wings dark brown with weak coppery highlights basally, violet distally. The male can be easily recognized by the following combination of characters: small body size as in the female; body pubescence long, dense (obscuring integument in most areas), yellowish to reddish brown; supraclypeal area with a distinct tuft of long, erect, dense setae obscuring integument (Fig. 7); T1–T5 dark reddish brown, each with a distinct, broad, median yellow maculation on disc, sides and distal margins (inmaculate areas) densely covered by long, dense dark brown setae (Fig. 19). The female of this species superficially resembles *X. splendidula* and other small species of *Schonnherria* such as *X. lucida* Smith and *X. muscaria* (Fabricius) (not occurring in Argentina); however, those species have distinct metallic blue highlights on the body as well as different patterns in the punctation, pubescence, and wing coloration. The supraclypeal tuft of setae and pale maculations on the metasomal terga of the male of *X. bambusae* are so distinctive and unique among species of *Schonnherria* that these characters have been used to justify its recognition in a different subgenus.

Female. Body length 15.9 (14.0–17.3); head length 4.2 (3.9–4.4); head width 4.9 (4.6–5.0); mesosoma width 5.7 (5.2–6.0); metasoma width 6.5 (5.8–6.8); forewing length 13.2 (12.3–13.7); forewing width 3.8 (3.6–4.0). *Coloration.* Integument dark reddish brown to black throughout, without metallic highlights, light brown on anterior face of F2–F9 and impunctate distal margins of metasomal terga and sterna. Wings dark brown with coppery highlights basally, golden iridescent. *Pubescence.* Dark brown to black. Head with scattered setae on vertex, gena, and clypeus distally (Fig. 1). Mesosoma with abundant, plumose setae except nearly asetose on discs of mesoscutum and mesoscutellum. T1 with scattered plumose setae on basal half, scattered, very short simple setae on distal half; T2–T4 medially with very short, simple setae, each seta barely exiting puncture; T3–T6 with long setae laterally; T5 with short (~1.0× OD), simple setae on disc; T6 with dense, long, both simple and plumose setae (Fig. 13); sterna with longer, denser, semierect setae than on terga. *Sculpturing.* Weakly imbricate to smooth and shiny. Vertex and upper gena largely impunctate, punctures small and scattered. Mesoscutum with scattered, coarse punctures on anterior margin



Figures 1–6. Faces of females of *Xylocopa* subgenus *Schonnherria* from Argentina. **1** *X. bambusae* **2** *X. macrops* **3** *X. pulchra* **4** *X. simillima* **5** *X. splendidula* **6** *X. viridis*. Scale bars: 1 mm.

and lateral to parapsidal lines, impunctate otherwise; mesoscutellum largely impunctate, with large, scattered punctures on disc. Metasomal terga with circular to ovoid punctures as large and coarse as those on mesoscutellum, most punctures separated by at least two times a puncture width, punctures denser laterally and on T5; sterna



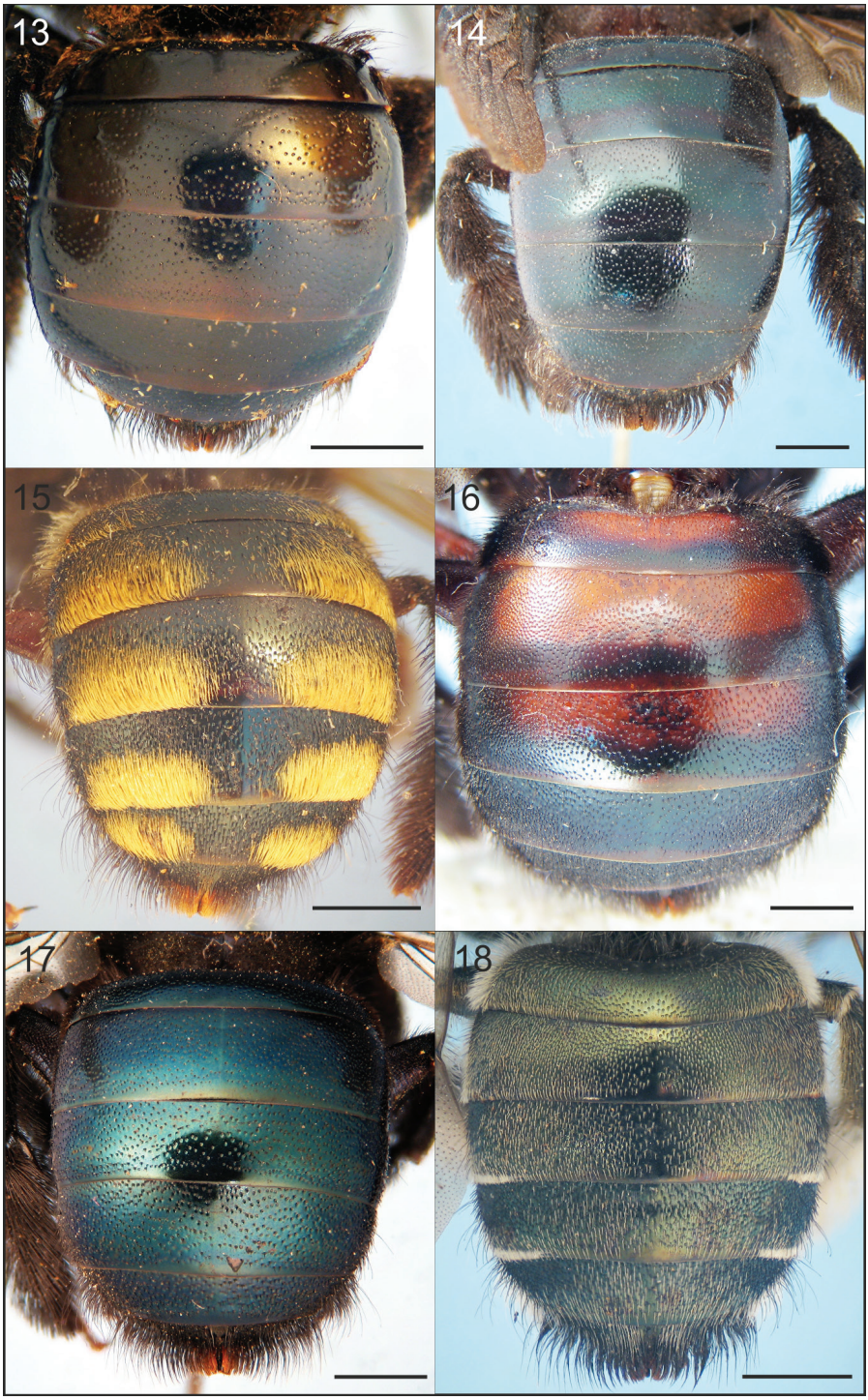
Figures 7–12. Faces of males of *Xylocopa* subgenus *Schonnherria* from Argentina. **7** *X. bambusae* **8** *X. chrysopoda* **9** *X. macrops* **10** *X. simillima* **11** *X. splendidula* **12** *X. viridis*. Scale bars: 1 mm.

with elongate punctures on discs, punctures contiguous laterally, becoming sparser medially. *Structure.* Head broader than long (1.1–1.2:1); compound eyes with inner margins parallel; proportion of upper to lower interocular distance 1:1; middle interocular distance 2.9–3.0; vertex broad, distance between median ocellus and posterior margin of vertex 3.2–4.3 OD; orbitoccipital distance 0.75–0.85; lateral ocelli on

supraorbital line; interocellar distance to ocelocular distance 1.0–1.3:1; interocellar to ocelloccipital 0.7–0.9:1; ocellocular to alveolocellar 0.6–0.7:1; orbitoccipital to ocellocular 1.1–1.3:1; alveolocular to interalveolar 0.9–1.1:1; clypeoalveolar distance long, about twice as long as longitudinal diameter of antennal socket; clypeocellar distance to distance between median ocellus and posterior margin of vertex 1.2–1.3:1; frontal carina projected into a distinct tubercle just above or at the upper tangent of anntenal sockets; clypeus broader than long, 2.0–2.4:1; proportion of length of scape, pedicel and F1–F4: 2.5–2.9:0.3–0.4:1:0.3–0.4:0.3–0.4:0.4, respectively; labrum broader than long, with three basal tubercles, median tubercle distinct, longitudinally enlongate, sublateral tubercles small, obscured by pubescence. Mesoscutellum gently convex; metanotum and propodeum obliquely inclined.

Male. As in the female, except for usual secondary sexual characters and as follows: body length 15.9 (15.0–16.7); head length 3.5 (3.5–3.6); head width 4.4 (4.4–4.6); mesosoma width 6.3 (6.0–6.6); metasoma width 6.6 (6.0–7.0); forewing length 11.6 (11.0–12.7); forewing width 3.6 (3.4–3.8). *Coloration.* Cream to yellowish maculations as follows: labrum, mandible basally, clypeus, supraclypeal area, paraocular area (except on upper one-third), anterior surface of flagellum (Fig. 7), outer surface of profemur basally, outer surfaces of protarsi, and discs of T1–T6 (maculations narrower on apical terga, sometimes absent on T4–T6) (Fig. 19). Wings subhyaline, yellowish with faint coppery highlights. *Pubescence.* Longer, denser than on female, yellowish to reddish brown, darker on face, vertex, sides of mesoscutum, mesoscutellum, metanotum, and inmaculate areas of terga (Fig. 19); supraclypeal area with a distinct tuft of long, erect, dense setae obscuring integument (Fig. 7); discs of mesoscutum and mesoscutellum asetose; maculated areas of terga with scattered erect setae. *Sculpturing.* Vertex and gena more densely punctate than in female, punctures separated by 1–2 times a puncture width; tegula impunctate, smooth and shiny on disc, otherwise dull, punctate (1–2 times a puncture width). Metasomal terga densely punctate (a puncture width or less) on inmaculated areas, including distal margins; punctures scattered on maculated areas. *Structure.* Middle interocular distance 2.0–2.1; distance between median ocellus and posterior margin of vertex 2.2–2.9 OD; orbitoccipital distance 0.4–0.6; interocellar to ocelocular distance 2.3–3:1; interocellar to ocelloccipital 1.2–1.4:1; ocellocular to alveolocellar 0.2–0.4:1; orbitoccipital to ocellocular 1.7–2.2:1; alveolocular to interalveolar 0.8–0.9:1; clypeoalveolar distance 1.5× longitudinal diameter of antennal socket; clypeocellar distance to distance between median ocellus and posterior margin of head 1.3–1.6:1; frontal carina strongly elevated, short 0.7–0.8, not tuberculiform as in female; clypeus broader than long, 1.5–1.6:1; proportion of length of scape, pedicel and F1–F4: 2.5–2.7:0.3–0.4:1:0.4:0.4:0.4. Mesoscutellum nearly flat, exposed, along same inclined plane with metanotum and base of propodeum; protrochanter with distinc spine; ventral surface of metatrochanter and metafemur basally glabrous, distinctly protuberant. Genitalia as in Figs 25, 30, 35, 40.

Distribution. This species is also known from Brazil and Paraguay (Table 1). In Argentina it has only been recorded from the province of Misiones, which is included in the Paranaense biogeographic province (Fig. 57).



Figures 13–18. Dorsal view of metasoma of females of *Xylocopa* subgenus *Schonnherria* from Argentina. **13** *X. bambusae* **14** *X. macrops* **15** *X. pulchra* **16** *X. simillima* **17** *X. splendidula* **18** *X. viridis*. Scale bars: 2 mm.

Table 1. Summary of species of *Xylocopa* subgenus *Schonnherria* occuring in Argentina with information on their distribution. Province: BA = Buenos Aires; CA = Catamarca; CH = Chaco; CO = Córdoba; CT = Corrientes; ER = Entre Rios; FO = Formosa; JU = Juyuy; LP = La Pampa; LR = La Rioja; MZ = Mendoza; MI = Misiones; NQ = Neuquén; RN = Río Negro; SJ = San Juan; SL = San Luis; ST = Salta; SG = Santiago del Estero; SF = Santa Fe; TU = Tucumán. ? = province listed in the literature, but not confirmed in this study. General distributions were extracted from Hurd (1978), Moure (2007), and Montalva et al. (2008).

Species	General distribution	Distribution in Argentina	Altitude (m.a.s.l) in Argentina
X. bambusae Schrottky	Argentina, Brazil, Paraguay	MI	50–200
X. chrysopoda Schrottky	Argentina, Brazil	MI	170
X. macrops Lepeletier de Saint Fargeau	Argentina, Bolivia, Brazil, Colombia, Paraguay, Peru	BA, CH, CT, ER, FO, JU?, MI, SF, SG?, TU	0–1100
X. pulchra Smith	Argentina, Brazil, Colombia, Paraguay	MI, ST	170
X. simillima Smith	Argentina, Bolivia, Brazil, Paraguay, Peru	MI	170
X. splendidula Lepeletier de Saint Fargeau	Argentina, Brazil, Chile, Paraguay, Peru, Uruguay	BA, CA, CH, CH, CO, CT, ER, FO, JU, LP, LR, MZ, MI, NQ, RN, ST, SJ, SL, SF, SG, ST, TU	0–2700
X. viridis Smith	Argentina, Bolivia, Brazil, Colombia, Costa Rica, French Guiana, Guatemala, Guyana, Mexico, Panama, Paraguay, Peru	MI	170

Comments. Hurd and Moure (1961: 186–187) designated a male and a female syntype as the lectotype of *X. eburnea* and *X. bellula*, respectively. In both cases Hurd and Moure (1961) unambiguously selected a specimen, provided information on the label data and repository collection, and clearly designated it as the sole name-bearing specimen, thus complying with the ICZN, Article 74. Such lectotypes designations appear to have been missed by Moure (2007: 673) who indicated syntypes for both species. The lectotype designation is valid for *X. eburnea* because Friese clearly mentions the existence of several males and females in the original description. However, the lectotype designation is unnecessary for *X. bellula* because Bréthes indicated a single female in the original description, which is currently housed at MACN. This specimen has a locality label that reads "Misiones, XII-1911, Abel Muniez", a label in Bréthes' handwriting and a holotype label [probably added recently]. Two other females, each bearing a locality label that reads "Misiones", are also found with that specimen; one of them bears a lectotype label. Perhaps because of the additional two specimens, Moure and Hurd (1961) thought of them as syntypes and designated as lectotype the female collected on 1911. Curiously, the lectotype label is not found in that specimen but in one of the two additional females. To avoid further confusion, we added a red label with the following note to the type: 'This is the true type as indicated in Bréthes' (1913) original description. M. Lucia & V.H. Gonzalez 2015'.

Despite actively searching for nests as well as specimens of this species in insect collections and in the field, the only specimens available to us were those collected by Peter Jörgensen at different times of the year in Misiones during the first decade of

1900 (see supplemental material). The species has not been collected ever since. The nesting biology of this *X. bambusae* is unknown, although it presumably nests in bamboo stalks (Schrottky 1902).

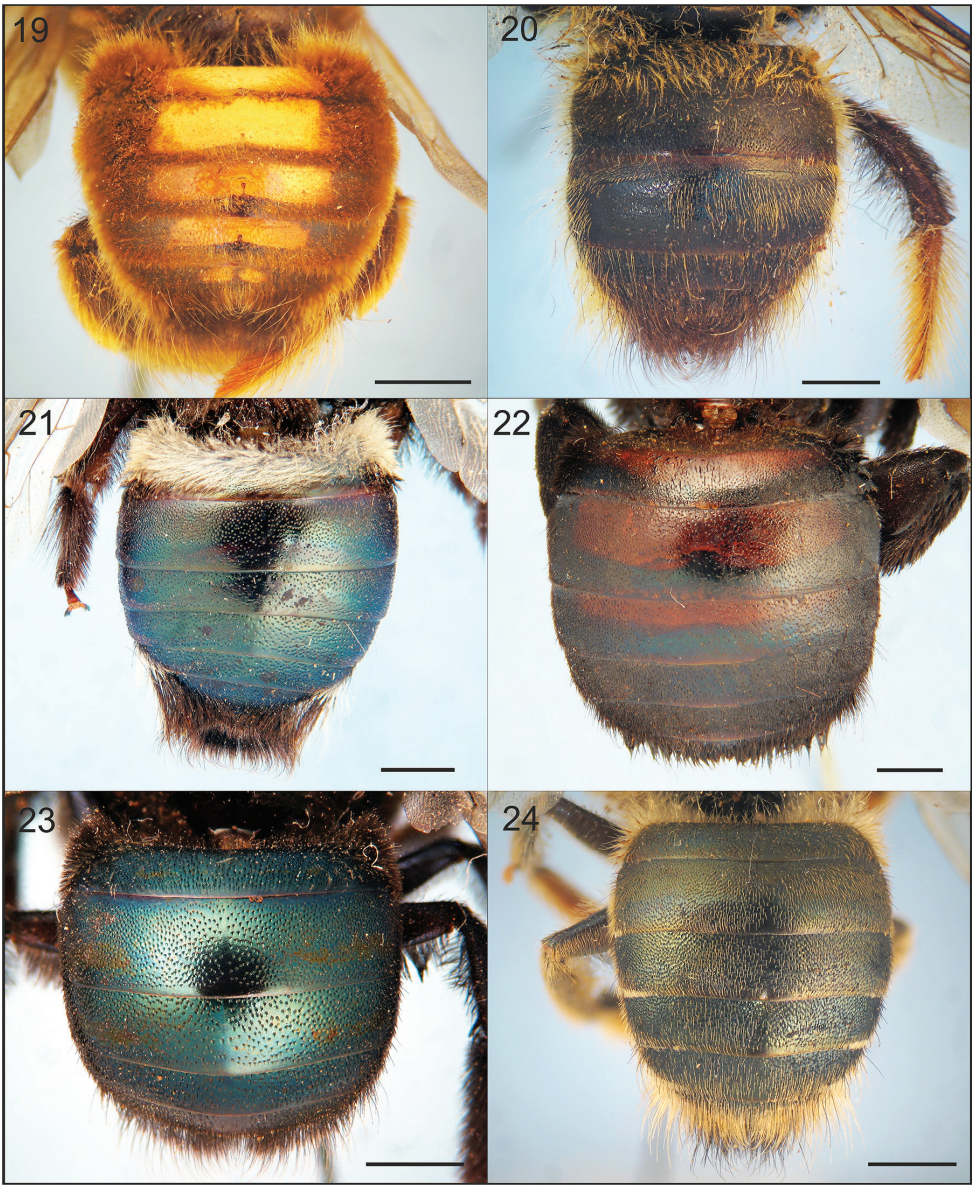
Xylocopa chrysopoda **Schrottky, 1902**

Figures 8, 20, 26, 31, 36, 41, 58

Xylocopa chrysopoda Schrottky, 1901: 214 (*nomen nudum*)
Xylocopa chrysopoda Schrottky, 1902: 475 (holotype: MZUSP; ♂, Jundiaí, São Paulo, Brazil) (examined)
Xylocopa (*Ioxylocopa*) *chrysopoda*: Hurd and Moure 1963: 116.

Diagnosis. This species is known only from the male. It can be distinguished from other Argentinean species of *Schonnherria* by the following combination of characters: small body size (body length 17.0–17.7); integument dark brown to black throughout, at most with faint metallic highliths on metasomal terga; compound eyes not enlarged, parallel or nearly so (Fig. 8); metasomal terga uniformly punctate, punctures separated by 1–2 times a puncture width, with distinctly long (≥ 2.0 OD) setae on discs (Fig. 20).

Male. Body length 17.3 (17.0–17.7); head length 3.5 (3.5–3.6); head width 4.4; mesosoma width 6.0; metasoma width 6.7 (6.6–6.8); forewing length 14; forewing width 3.5 (3.4–3.6). *Coloration.* Integument dark brown to black except tarsi light reddish brown and cream to yellow maculations as follows: outer surface of mandible (except margins), clypeus, supraclypeal area basally, and paraocular area (except on upper one-third) (Fig. 8). Wings sybhyaline, yellowish, with weak coppery highlights. *Pubescence.* Long, dense, predominantly yellowish, setae dark brown to black on vertex, metafemur basally, dorsal surface of metatibia, and discs of T2–T7 (variably mixed with yellowish setae) (Fig. 20). *Sculpturing.* Integument largely imbricate among punctures, nearly smooth and shiny on outer surface of mandible, labrum, maculate areas of face, and discs of mesoscutum and mesocutellum. Upper paraocular area, frons, and interocellar area with coarse, contiguous punctures; vertex and gena with punctures sparser than on upper paraocular area. Discs of mesoscutum and mesoscutellum largely impunctate, otherwise punctures shallower than and about as dense as those on vertex. Discs of metasomal terga uniformly punctate, setiferous punctures circular to ovoid, separated by 1–2 times a puncture width, distal margins impunctate (Fig. 20); sterna more densely punctate than on terga. *Structure.* Head broader than long (1.2–1.3:1); compound eyes not enlarged, parallel or nearly so (Fig. 8); proportion of upper to lower interocular distance 0.9–1:1; upper interocular distance 6.3–6.9× OD; middle interocular distance 2.60; distance between median ocellus and posterior margin of vertex 2.6–2.7 OD; orbitoccipital distance 0.60; lateral ocelli on supraorbital line; interocellar distance to ocelocular distance 1.2–1.3:1; interocellar to ocelloccipital 0.5–1.1:1; ocellocular to alveolocellar 0.5–0.6:1; orbitoccipital to ocellocular



Figures 19–24. Dorsal view of metasoma of males of *Xylocopa* subgenus *Schonnherria* from Argentina. **19** *X. bambusae* **20** *X. chrysopoda* **21** *X. macrops* **22** *X. simillima* **23** *X. splendidula* **24** *X. viridis*. Scale bars: 2 mm.

1.2–1.5:1; alveolocular to interalveolar 1.1–1.2:1; clypeoalveolar distance 1.5 times longitudinal diameter of antennal socket; clypeocellar distance to distance between median ocellus and posterior margin of head 1.4–1.5:1; frontal carina elevated, short 0.8–0.9; clypeus broader than long, 0.6:1; proportion of length of scape, pedicel and F1–F4: 2.3:0.4:1:0.4:0.5:0.6, respectively. Mesoscutellum nearly flat, exposed, along

same inclined plane with metanotum and base of propodeum; metatibia apically swollen on inner surface. Genitalia as in Figs 26, 31, 36, 41.

Female. Unknown.

Distribution. This species is known only from Brazil and the province of Misiones in Argentina, the latter area included in the Paranaense biogeographic province (Fig. 58).

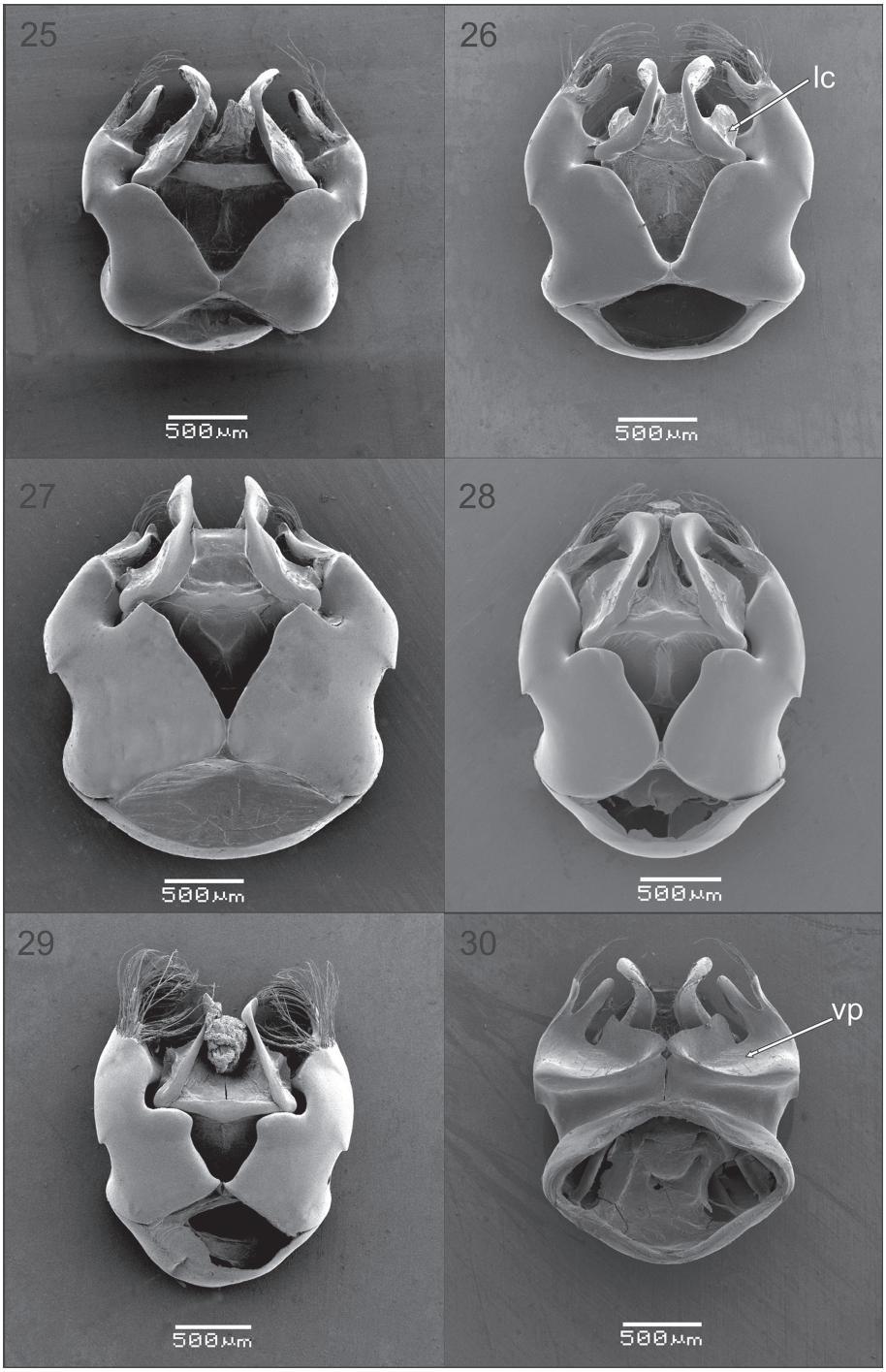
Comments. Schrottky (1912) suggested that *X. chrysopoda* may be the male of *X. pulchra*, a species currently known from the female sex. As for *X. bambusae*, these two species are rarely collected and are currently known from a limited number of specimens. We did not collect nor examine specimens of *X. chrysopoda* from Argentina captured in the last 100 years.

Xylocopa macrops **Lepeletier de Saint Fargeau, 1841**

Figures 2, 9, 14, 21, 27, 32, 37, 42, 55

Xylocopa macrops Lepeletier de Saint Fargeau, 1841: 209 (holotype: ♂, Brazil, whereabouts unknown)
Xylocopa crotalariae Schrottky, 1901: 212, 214 (*nomen nudum*)
Xylocopa crotalariae Schrottky, 1902: 472 (holotype: MZUSP; ♀, Jundiaí, São Paulo, Brazil) (examined); Hurd and Moure 1963: 302 (synonym with *macrops*)
Xylocopa boops Maidl, 1912: 325 (holotype: NMW; ♂, Brazil) (examined, **syn. n.**)
Xylocopa (*Schonnherria*) *macrops*: Hurd and Moure 1963: 302

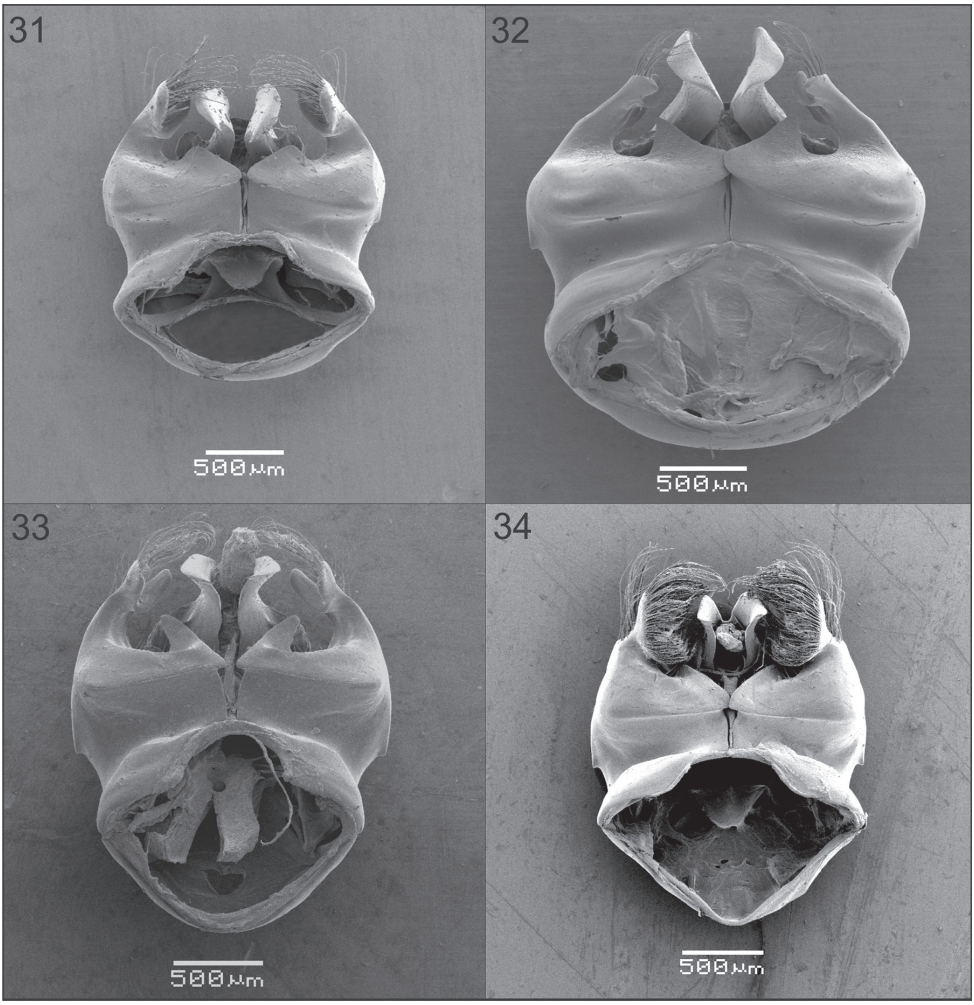
Diagnosis. The female of this species can be distinguished from other Argentinean species of *Schonnherria* by the following combination of characters: medium-sized bees (18–22 mm); body pubescence black; integument black throughout with very weak metallic blue, often most evident on mesoscutum, tegula, outer surfaces of pro- and mesotibiae, and metasomal terga; clypeus depressed basally on disc, dorsolaterally elevated from adjacent paraocular area (Fig. 2); vertex, behind lateral ocelli, with coarse punctures separated by 1–2 times a puncture width; metasomal terga sparsely punctate, punctures coarse and separated by at least two times a puncture width (Fig. 14); wings black with metallic green and violet highlights. The male can be easily recognized by the following combination of characters: compound eyes enlarged, strongly convergent dorsally (Fig. 9); meso- and metasoma with distinct metallic blue highlights; metasoma sparsely punctate with very short setae, each seta barely exiting puncture; discs of S2–S6 each with sublateral yellow maculation. The female of this species superficially resembles that of *X. simillima* and *X. dimidiata* Latreille (not occurring in Argentina, see below) in the body size and black color of the integument, pubescence and wings. However, it can be separated from both species primarily by the midbasal tubercle of the labrum and the shape of clypeus. In those species the labrum has a single, large, capitate tubercle and the disc of the clypeus is flat. In *X. macrops* the labrum has three tubercles, a longitudinally elongated median tubercle and two small sublateral tubercles, and the clypeus is basally depressed, dorsolaterally elevated



Figures 25–30. Genital capsule of males of *Xylocopa* subgenus *Schonnherria* from Argentina. All figures in dorsal view except Fig. **30** in ventral view. **25, 30** *X. bambusae* **26** *X. chrysopoda* **27** *X. macrops* **28** *X. splendidula* **29** *X. viridis*. Abbreviations: lc = lateral carina of penis valve; vp: ventroapical plate of gonocoxite.

from adjacent paraocupar area. The male can be confused with that of *X. splendidula* by the compound eyes strongly convergent dorsally and the blue metallic highlights of the metasoma. However, in *X. macrops* the metafemur is distinctly modified, with the ventral margin strongly protuberant, the metabasitarsus is robust and shorter than the metatibia. In *X. splendidula* both the metafemur and metabasitarsus are unmodified, and the latter is longer than the metatibia; also, yellow maculations are absent from the labrum and discs of the sterna (present in *X. macrops*).

Female. Body length 19.6 (18.3–21.7); head length 5.1 (4.8–5.4); head width 6.1 (5.8–6.4); mesosoma width 6.6 (6.2–7.0); metasoma width 7.6 (7.2–8.0); forewing length 15.9 (15.0–17.3); forewing width 4.8 (4.4–5.4). *Coloration.* Integument dark reddish brown to black with weak metallic blue-green highlights, particularly on mesoscutum and metasomal terga. Wing dark brown to black with metallic violet-green highlights. *Pubescence.* Predominantly black, except by pale setae intermixed with black setae on face and sides of T4–T6 and S4–S6 (sometimes absent). Head with abundant setae, scattered on gena. Mesosoma with abundant, plumose setae, nearly asetose on discs of mesoscutum and mesoscutellum. T1 with plumose setae on basal half, with very short simple setae on distal half, each seta barely exiting puncture; T2–T5 with short setae as on distal half of T1, setae longer and denser on sides of T5 and T6 (Fig. 14); sterna with longer setae than on terga, setae progressively becoming denser and longer towards apical segments. *Sculpturing.* Weakly imbricate to smooth and shiny. Clypeus with dorsolateral elevated area impunctate; vertex sparsely punctate, punctures denser behind lateral ocellus (1–2 times a puncture width), becoming sparser and shallower on upper gena. Mesoscutum with coarse, sparse punctures as on vertex along anterior margin and lateral to pasapsidal lines, impunctate otherwise; mesoscutellum largely impunctate on anterior half. Metasomal terga with circular to ovoid punctures smaller than those on posterior half of mesoscutellum, punctures separated by 2–3 times a puncture width, denser and elongated on T5 (Fig. 14). *Structure.* Head broader than long (1.1–1.3:1); compound eyes with inner margins parallel; proportion of upper to lower interocular distance 0.8–0.9:1; middle interocular distance 3.7–4.0; vertex broad, distance between median ocellus and posterior margin of vertex 3.7–4.1 times OD; orbitoccipital distance 0.7–0.9; lateral ocelli below supraorbital line; interocellar distance to ocelocular distance 0.8–1.0:1; interocellar to ocelloccipital 0.5–0.6:1; ocellocular to alveolocellar 0.6–0.8:1; orbitoccipital to ocellocular 0.8–1:1; alveolocular to interalveolar 1.0–1.2:1; clypeoalveolar distance short, about as long as longitudinal diameter of antennal socket; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.8–1:1; frontal carina elevated and forming a low tubercle near lower tangent of antennal sockets, continuing dorsally into a low carina (Fig. 2); clypeus broader than long, 2.1–2.3:1, depressed basally on disc, dorsolaterally elevated from adjacent paraocular area; supraclypeal area depressed on disc, laterally elevated from adjacent paraocular area; proportion of length of scape, pedicel and F1–F4: 2.9–3.5:0.3–0.4:1:0.3–0.4: 0.4–0.5:0.4–0.5, respectively; labrum broader



Figures 31–34. Ventral view of genital capsules of males of *Xylocopa* subgenus *Schonnherria* from Argentina. **31** *X. chrysopoda* **32** *X. macrops* **33** *X. splendidula* **34** *X. viridis.*

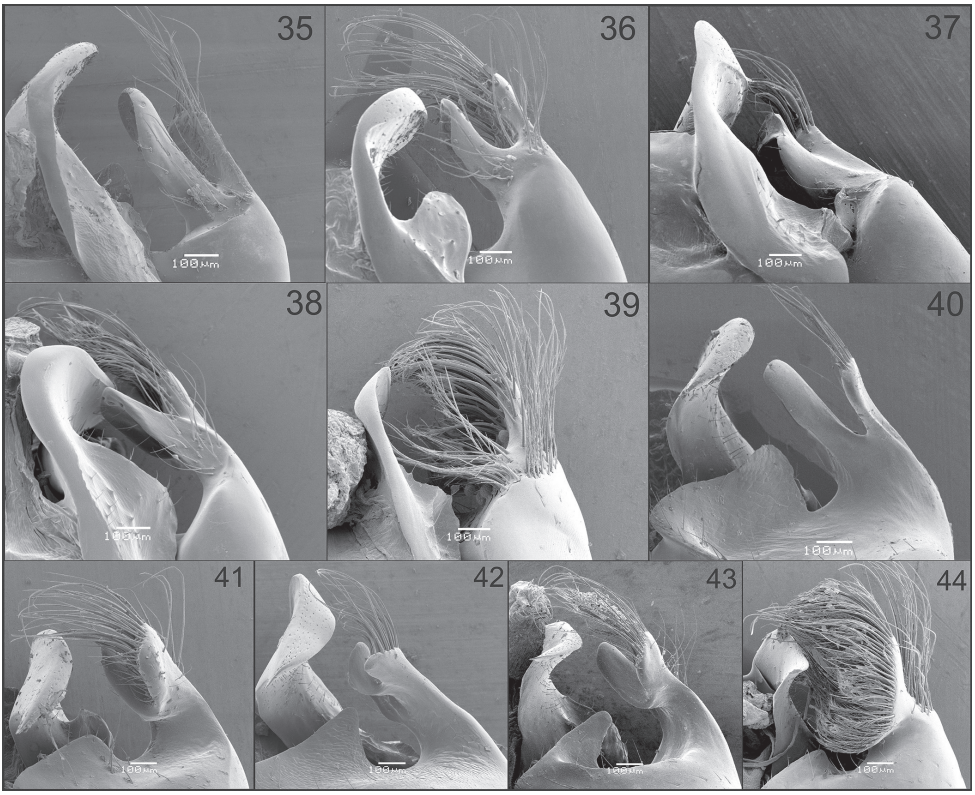
than long, with three basal tubercles, median tubercle distinct, longitudinally elongate, sublateral tubercles small, obscured by pubescence. Mesoscutellum gently convex; metanotum and propodeum vertical.

Male. As in the female, except for usual secondary sexual characters and as follows: body length 21.6 (20.7–22.7); head length 5.1 (4.9–5.4); head width 6.2 (6.0–6.4); mesosoma width 7.3 (7.0–7.6); metasoma width 7.7 (7.2–8.0); forewing length 15.5 (14.3–16.0); forewing width 4.1 (4.0–4.4). *Coloration.* Integument with distinct metallic blue-green highlights. Cream to yellow maculations as follows: labrum, mandible basally (sometimes absent), clypeus, supraclypeal area, inferior paraocular area, anterior surface of scape, and discs of S2–S6 each with sub-

lateral, triangular maculation (sometimes absent on S2, S5 and S6). Wings hyaline to subhyaline with weak golden highlights. *Pubescense.* Longer and denser than on female, predominantly whitish, except dark brown to black on: interocelar area, vertex, pronotal lobe, metepisternum, propodeum, procoxa, inner surfaces of profemur and protarsi, remaining legs excluding posterior margin of metatibia, sides of T1, T5, T6, sides of sterna, and discs of S4–S6. White pubescence on T1 dense, nearly obscuring integument. *Sculpturing.* Coarser and denser than in female, particularly on sides of mesoscutum and mesoscutellum, and terga (Fig. 21). *Structure.* Compound eyes strongly converging dorsally, proportion of upper to lower interocular distance 0.1–0.2:1; upper interocular distance 0.5–0.8 times OD; middle interocular distance 2.0–2.2; distance between median ocellus and posterior margin of vertex 3.6–4.2 OD; orbitoccipital distance absent due to enlargement of eyes; lateral ocelli well below supraorbital line; interocellar distance to ocelocular distance 4.0–9.0:1; interocellar to ocelloccipital 0.2–0.3:1; ocellocular to alveolocellar 0.1:1; orbitoccipital to ocellocular reduced, alveolocular to interalveolar 0.4–0.6:1; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.5–0.6:1; clypeus broader than long, 1.5–1.7:1; proportion of length of scape, pedicel and F1–F4: 3.0–3.2:0.3–0.4:1:0.2–0.3:0.3–0.4:0.4–0.5, respectively. Legs robust; mesobasitarsus shorter than mesotibia; metacoxa and metatrochanter toothed; metafemur protuberant ventrally; metatibia with distinct cavity distally on inner surface bordered by two spinous projections, inner projection triangular, short, outer projection broader than and about as long as tibial spur; metabasitarsus robus, shorter than metatibia. Genitalia as in Figs 27, 32, 37, 42.

Distribution. This species appears to be widely distributed in South America, occuring from Colombia to Brazil (Table 1). We examined or collected specimens from the following nine provinces in Argentina (Fig. 55): Buenos Aires, Chaco, Corrientes, Entre Ríos, Formosa, Misiones, Salta, Santa Fe, and Tucumán. Hurd (1978) also recorded this species from Jujuy and Santiago del Estero. It occurs in the following biogeographic provinces: Chaqueña, Pampeana, Paranaense, and Yungas.

Comments. Maidl (1912) described *X. boops* based on a single male from an unspecified location in Brazil. The species was later listed by Hurd (1978) from Tafi, Province of Tucuman, Argentina. We examined the type specimen currently deposited at NMW (Figs 49–52) as well as the male specimen from Argentina deposited at USNM. Both specimens closely agree with *X. macrops* in all morphologically external characters, including the genitalia, except by the size of their compound eyes. In these specimens the eyes are extremely large and convergent above so that their upper margins are nearly in contact dorsally (Figs 49, 50). Such upper interorbital distance is about 0.23 times OD in the type of *X. boops* whereas it ranges from 0.54–0.72 times OD in specimens of *X. macrops* (n = 10). The shapes of the gonocoxite, apex of gonostylus, and lateral carina of the penis valve, which have proven to be reliable in species recognition in *Schonnherria* (Figs 25–44), are identical between *X. boops* and *X. macrops*. Thus, it seems to us that *X. boops* was described from an individual of



Figures 35–44. Dorsal (**35–39**) and ventral (**40–44**) views of apex of gonostylus and penis valve of males of *Xylocopa* subgenus *Schonnherria* from Argentina. **35, 40** *X. bambusae* **36, 41** *X. chrysopoda* **37, 42** *X. macrops* **38, 43** *X. splendidula* **39, 44** *X. viridis*.

X. macrops with unusually large eyes and we have decided not to recognize this species. Here it is synonymized under *X. macrops*.

Hurd (1978: 25) listed *X. subcyanea* Pérez from Misiones and Torreta et al. (2010) from Paraná, province of Entre Rios. We were not able to capture or find any specimen of this species from Argentina in the field or in the collections we visited. However, a single female of *X. macrops* deposited at MACN and labeled "Paraná, Noviembre, n° 190", was erroneously identified as *X. subcyanea*. Likewise, the two female specimens recorded by Torreta et al. (2010) as *X. subcyanea* (deposited at FAUBA) turned out to be *X. macrops*. Thus, it appears that records of this species for Argentina are misidentified specimens. We examined the type of *X. subcyanea* currently deposited at MNHN and also examined specimens of this species from Brazil. The female of *X. subcyanea* can be distinguished from that of *X. macrops* by the upper gena densely punctate (largely impunctate in *X. macrops*), disc of clypeus flat, uniformly punctate (largely impunctate and depressed basally in *X. macrops*), punctures of terga elongate, dense (punctures circular and sparse in *X. macrops*), and wings subhyaline, brownish (dark brown to black in *X. macrops*).

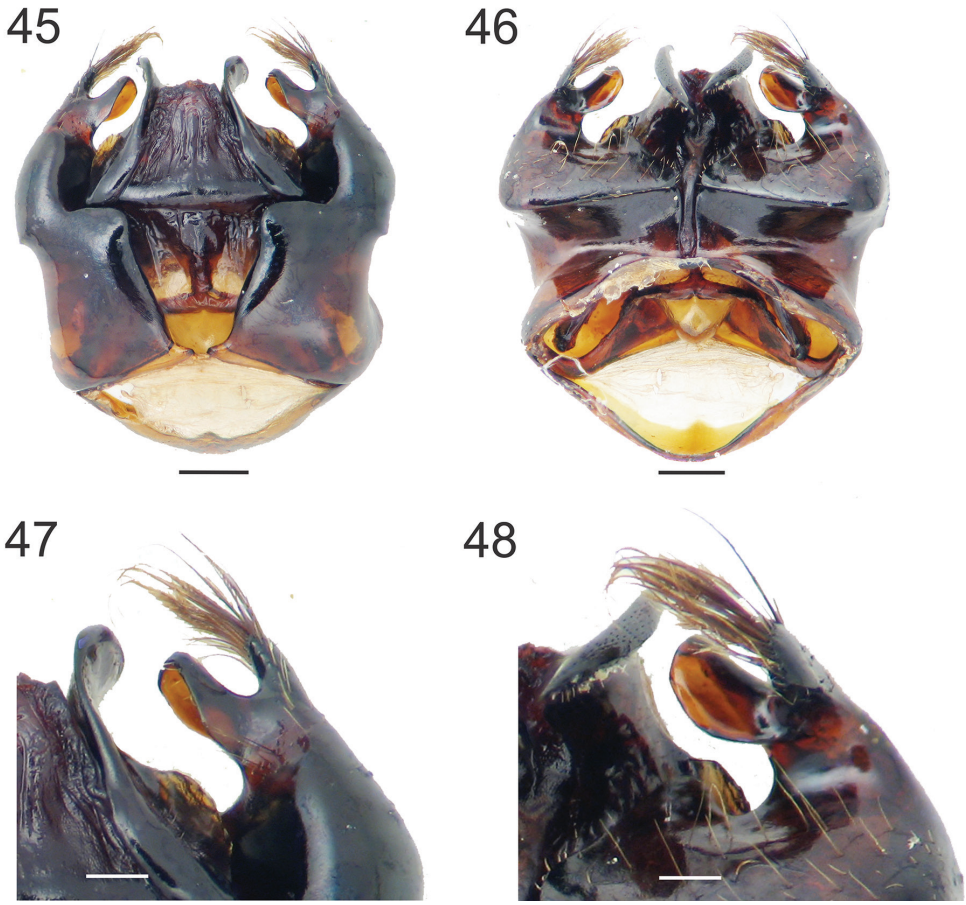
***Xylocopa pulchra* Smith, 1854**
Figures 3, 15, 58

Xylocopa pulchra Smith, 1854: 361 (holotype: BMNH 17B.188; ♀, Rio, Brazil) (examined)
Xylocopa (*Schonnherria*) *pulchra*: Hurd and Moure 1963: 123.

Diagnosis. This species is known only from the female. It can be easily recognized by the following combination of characters: small body size (body length 15–17 mm); upper gena and vertex densely punctate, punctures separated by at most a puncture width; wings subhyaline, yellowish; metasoma dark brown to black with weak blue-green metallic highlights; and discs of T2–T5, each with a broad, medially interrupted apical band of dense yellowish setae (Fig. 15).

Female. Body length 16 (15.3–16.7); head length 4.1 (4.0–4.2); head width 5.1 (5.0–5.2); mesosoma width 5.7 (5.6–5.8); metasoma width 6.1 (6.0–6.2); forewing length 11.3 (10.7–12.0); forewing width 3.2. *Coloration.* Integument dark brown to black including tegula, with weak blue-green higlights on metasoma. Wings subhyaline with weak golden highlights, veins yellowish-brown. *Pubescence.* Dark brown to black, except: anterior surface of metatibia distally, outer surface of metabasitarsus, and sides of S2–S4 with whitish setae; metabasitarsus externally with pale hairs; discs of T2–T5 each with a broad, medially interrupted apical band of dense yellowish setae (Fig. 15). Mesosoma with abundant plumose setae except on discs of mesoscutum and mesoscutellum. *Sculpturing.* Weakly imbricate to smooth and shiny. Vertex and upper gena densely punctate, punctures separated by at most a puncture width. Mesoscutum with punctures separated by 1–2 times a puncture width, smooth and shiny on disc; mesoscutellum with punctures smaller and sparser than those on mesoscutum, except smooth and shiny on disc. Metasomal terga with circular to ovoid punctures separated by 1–2 times a puncture width, punctures denser laterally and on apical terga; sterna impunctate mediolongitudinally with punctures sparser than on terga. *Structure*. Head broader than long (1.2–1.3:1); proportion of upper to lower interocular 1:1; middle interocular distance 3.2–3.6; vertex broad, distance between median ocellus and posterior margin of vertex 4.0–4.5 OD; orbitoccipital distance short, 0.5–0.7; lateral ocelli on supraorbital line; interocellar distance to ocelocular distance 0.9–1:1, interocellar to ocelloccipital 0.8:1; ocellocular to alveolocellar 0.7:1; orbitoccipital to ocellocular 0.7–0.9:1; alveolocular to interalveolar 1.1–1.2:1; clypeocellar distance to distance between median ocellus and posterior margin of vertex 1.2:1; frontal carina low; clypeus broader than long (2.2–2.3:1); proportion of length of scape, pedicel and F1–F3: 3.9:0.4:1: 0.5:0.5:0.6, respectively; labrum broader than long, with three basal protuberances, median tubercle distinct, longitudinally elongate, sublateral tubercles small, obscured by pubescence. Mesoscutellum gently convex; metanotum and propodeum subvertically inclined.

Male. Unknown



Figures 45–48. Male genital capsule of *Xylocopa simillima*. **45, 46** dorsal and ventral views respectively **47, 48** detail of the apex of gonostylus and penis valve in dorsal and ventral views. Scale bars: 0.5 mm

Distribution. Hurd (1978: 23) listed this species from Brazil, Paraguay, possibly Colombia, and the provinces of Misiones and Salta in Argentina (Fig. 58). It occurs in the Paranaense biogeographic province (see comments below).

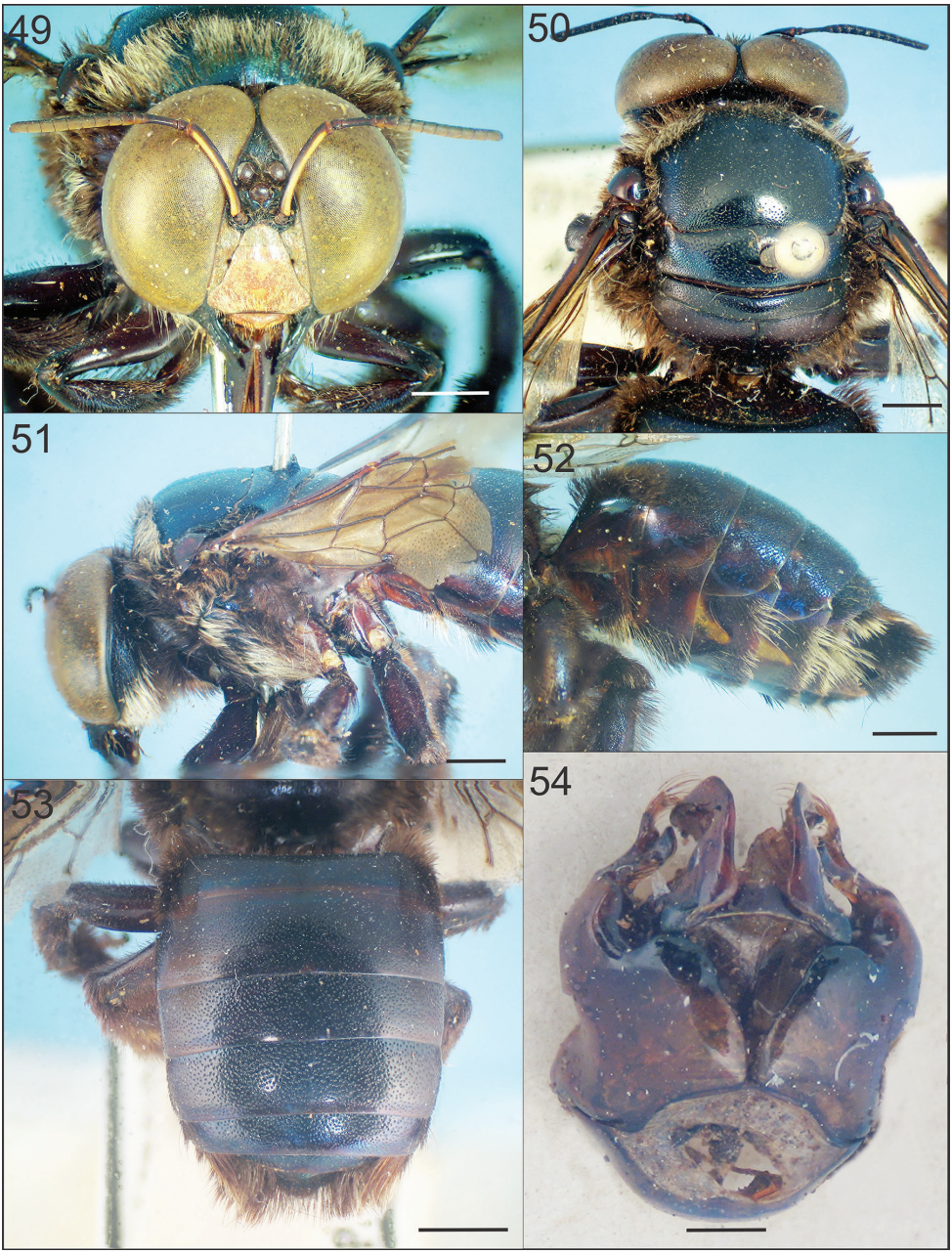
Comments. *Xylocopa pulchra* is known only from the female, and the male of *X. chrysopoda* may be conspecific with this species, as suggested by Schrottky (1902). As for *X. bambusae* and *X. chrysopoda*, this species is rare in collections, and it has not been captured in the last 65 years. In addition to the type, we were only able to examine a historical specimen from Misiones deposited at MLP and specimen from Pocitos, Salta, deposited at USNM. The presence of this species in Colombia needs to be confirmed (Gonzalez et al. 2009).

***Xylocopa simillima* Smith, 1854**
Figures 4, 10, 16, 22, 45–48, 58

Xylocopa simillima Smith, 1854: 357 (holotype: BMNH 17B.196; ♀, Australia) (examined)
Xylocopa mendax Maidl, 1912: 319 (syntype: NMW; ♀, Rio Grande, Brazil); Hurd and Moure 1961: 191 (synonym with *simillima*)
Xylocopa rotundiscuta Brèthes, 1916: 418 (lectotype: MACN; ♀, Misiones, Argentina) (examined); Hurd and Moure 1961: 191 (lectotype designation and synonym with *simillima*)
Xylocopa (*Schonnherria*) *simillima*: Hurd and Moure 1963: 123.

Diagnosis. The female of this species can be distinguished from other Argentinean species of *Schonnherria* by the following combination of characters: large body size (body length 20–23 mm); labrum basally with a distinct, large, single capitate tubercle about as large as median ocellus; integument dark brown to black throughout, with basal three or four terga often with distinct broad, light reddish brown bands on discs (rarely orange) (Fig. 16); metasomal terga with punctures circular to ovoid, sparsely punctate on discs of basal terga (2–4 times a puncture width), punctures denser laterally and on apical terga; discs of basal terga with very short, black, simple setae, each seta barely exiting puncture, setae increasing in length laterally and on apical terga. The male can be easily recognized by the combination of compound eyes strongly convergent dorsally (Fig. 10), metasomal terga dark brown to black with basal terga light reddish brown on discs, and wings dark brown.

Female. Body length 21.8 (20.3–23.0); head length 5.8 (5.5–6.1); head width 6.6 (6.4–7.0); mesosoma width 7.5 (7.2–8.4); metasoma width 9.1 (8.8–9.6); forewing length 19.6 (18.6–19.7); forewing width 5.7 (5.6–6.2). *Coloration.* Integument black with posterior margin of mesoscutellum and basal three or four metasomal terga with broad, light reddish brown bands on discs (terga rarely orange). Wings dark brown with violet highlights. *Pubescence.* Dark brown to black. Head with scattered setae on vertex, gena, paraocular area, and clypeus distally. Mesosoma with abundant, plumose setae except nearly asetose on disc of mesoscutum and posterior half of mesoscutellum. T1 with scattered plumose setae on basal half; distal half of T1, as on discs of T2–T5, with very short (0.2–0.3 times OD), appressed simple setae, each barely exiting puncture, setae becoming longer and denser towards apical terga; disc of T6 and sides of T1–T6 each with long, semierect, simple and plumose setae; sterna with semierect, long setae as long as those on sides of terga. *Sculpturing.* Weakly imbricate to smooth and shiny. Vertex and upper gena largely impunctate, punctures denser behind lateral ocelli. Mesoscutum with punctures slightly smaller and denser than those on vertex on anterior margin and lateral to parapsidal lines, impunctate otherwise; mesoscutellum largely impunctate, punctures separated by at least two times a puncture width. Terga with circular to ovoid punctures as large and coarse as those on mesoscutellum, separated by 1–2 times a puncture width, denser laterally on each tergum and towards apical segments; sterna with punctures smaller, nearly contiguous laterally, larger and sparser medially. *Structure.* Head broader than long (1.1–1.2:1);



Figures 49–52. Male holotype of *Xylocopa boops*. **49** Facial view **50, 51** Head and mesosoma in dorsal and lateral views **52, 53** Metasoma in lateral and dorsal views **54** genital capsule in dorsal view. Scale bars: 2 mm, 0.5 mm (Fig. **54**).

compound eyes with inner margins parallel; proportion of upper to lower interocular distance 0.8–0.9:1; middle interocular distance 4.2–4.5; vertex broad, distance between median ocellus and posterior margin of vertex 4.6–5.3 OD; orbitoccipital distance short 1.1–1.3; lateral ocelli below supraorbital line; interocellar distance to ocelocular distance 0.6:1; interocellar to ocelloccipital 0.3–0.4:1; ocellocular to alveolocellar 0.7–0.9:1; orbitoccipital to ocellocular 1.0–1.3:1; alveolocular to interalveolar 1.2–1.4:1; clypeoalveolar distance about 1.8 times longitudinal diameter of antennal socket; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.7–0.9:1; frontal carina moderately elevated, forming a small tubercle just above lower tangent of anntenal sockets; clypeus broader than long, 2.2–2.5:1; proportion of length of scape, pedicel and F1–F4: 2.9–3.2:0.2–0.4: 1:0.3–0.4:0.4–0.5:0.4–0.5, respectively; labrum basally with a distinct, large, single capitate tubercle about as large as median ocellus. Mesoscutellum gently convex; metanotum and propodeum vertical in profile.

Male. As in the female, except for usual secondary sexual characters and as follows: body length 22.6; head length 5.7; head width 6.8; mesosoma width 8.8; metasoma width 9.8; forewing length 20.6; forewing width 5.6. *Coloration*. Clypeus, supraclypeal area and lower paraocular area yellow. S*tructure.* Head broader than long (proportion 1.2:1); compound eyes enlarged, strongly converging dorsally (Fig. 10); proportion of upper to lower interocular distance 0.3:1; upper interocular distance 1.6 OD; middle interocular distance 2.3; distance between median ocellus and posterior margin of vertex 4.2 OD; orbitoccipital distance absent due to enlargement of eyes; lateral ocelli below supraorbital line; interocellar to ocelocular distance 4:1; interocellar to ocelloccipital 0.2:1; ocellocular to alveolocellar 0.1:1; orbitoccipital to ocellocular reduced; alveolocular to interalveolar 0.4:1; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.7:1; clypeus broader than long, 1.7:1; proportion of length of scape, pedicel and F1–F4 2.8:0.4:1:0.2:0.4:0.4, respectively. Genitalia as in Figs 45–48.

Distribution. This species occurs in Misiones (Fig. 58), an area that is included within the Paranaense biogeographic province.

Comments. Brèthes' original description of *X. rotundiscuta* was based on three females. To stabilize this name, Hurd and Moure (1961: 191) unambiguously designated one of the syntypes as the lectotype. This specimen, deposited at MACN, has a locality label that reads "Misiones", a catalogue number 7597 [misinterpreted by Hurd and Moure as 2597], a handwritten number 765 [interpreted by Hurd and Moure as 753], and a lectotype label. Such a valid designation appear to have been missed by Moure (2007: 668).

Xylocopa splendidula **Lepeletier de Saint Fargeau, 1841**

Figures 5, 11, 17, 23, 28, 33, 38, 43, 56

Xylocopa splendidula Lepeletier de Saint Fargeau, 1841: 190 (holotype: ♀, Brazil, whereabouts unknown, see comments below)

Xylocopa (*Schonnherria*) *splendidula*: Hurd and Moure 1963: 123.

Diagnosis. Both sexes of this species can be distinguished easily from other Argentinean species of *Schonnherria* by the following combination of characters: small to medium body size (body length 13–19 mm); body pubescence entirely black in the female, in the male with dense off-white pubescence on mesepisternum, tegula anteriorly, sides of mesoscutum and mesoscutellum, and dorsum of T1; meso- and metasoma with distinct metallic blue highlights; wing membrane subhyaline with weak violet highlights; male compound eyes enlarged, dorsally convergent, with upper margins separated by at least 2.7 times OD (Fig. 11); and hind leg of male unmodified, except by metatibia with long, slender subapical projection on inner margin, similar in size and thickness to tibial spur. This species can be confused with *X. macrops*, particularly the male, by the compound eyes distinctly convergent dorsally, metasoma with metallic blue highlights, off-white pubescence on mesosoma and T1, and wings subhyaline. However, in *X. macrops* the compound eyes are larger and closer dorsally (0.54–0.72 times OD) than in *X. splendidula* and the hind leg is distinctly modified, with coxa and trochanter each bearing a tooth or spine, femur strongly protuberant ventrally, tibia with two large subapical spines on its inner margin, and basitarsus robust, shorter than the tibia (slender and longer than tibia in *X. splendidula*). In addition, the labrum is yellow and the metasomal sterna are maculated in *X. macrops* (labrum and metasoma inmaculate in *X. splendidula*).

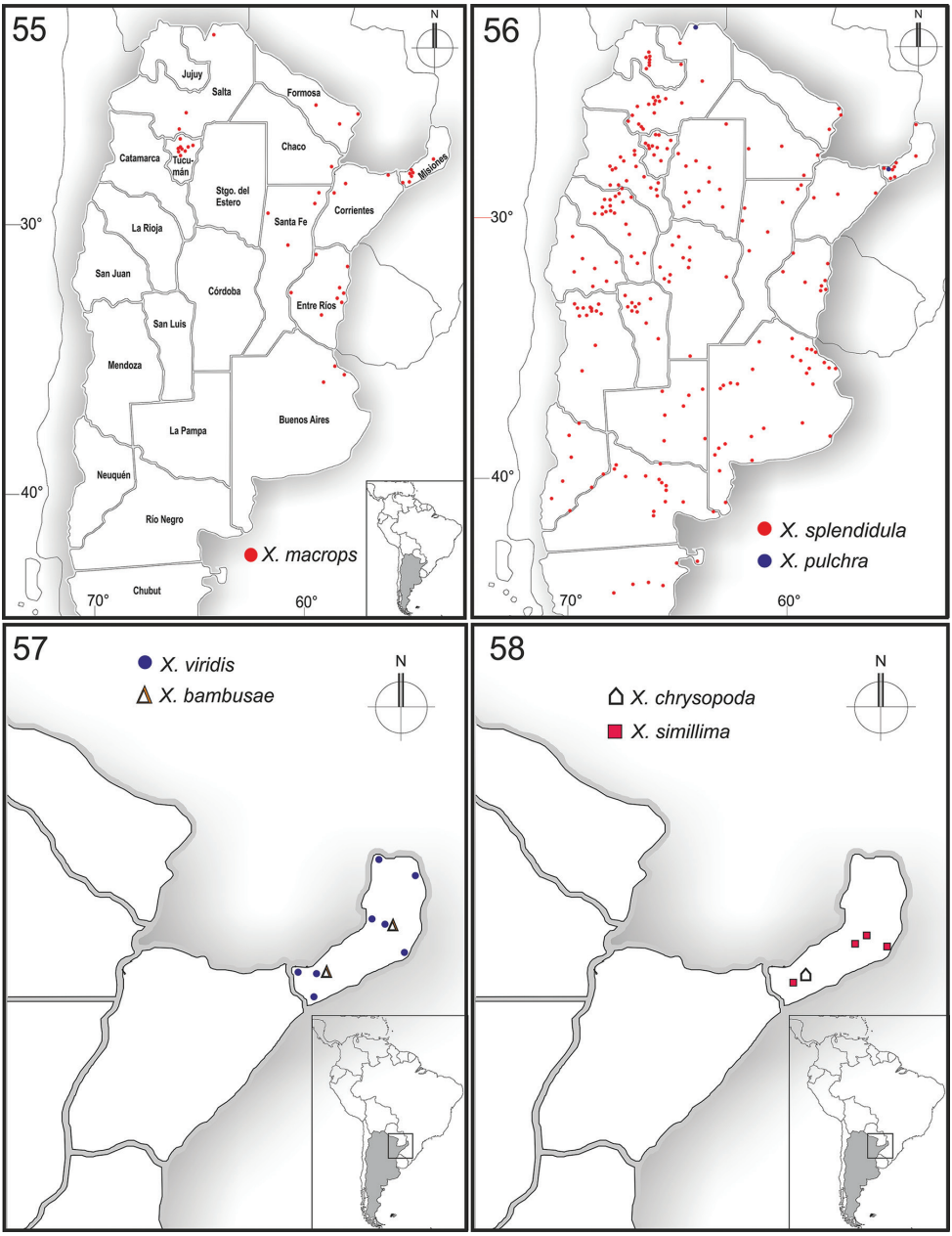
Female. Body length 17.2 (16.6–18.3); head length 4.9 (4.7–5.0); head width 5.5 (5.2–5.8); mesosoma width 6.3 (5.8–6.6); metasoma width 7.1 (6.6–7.5); forewing length 13.3 (12.7–14.0); forewing width 3.7 (3.6–3.8). *Coloration*. Integument dark brown to black with distinct metallic blue highlights, particularly dorsum of meso- and metasoma. Wings subhyaline with weak violet highlights. *Pubescence.* Dark brown to black, except patch of off-white setae on sides of T5. Head with abundant setae, scattered on gena and vertex. Mesosoma with abundant, plumose setae except nearly asetose on disc of mesoscutum and anterior half of mesoscutellum. T1 with scattered plumose setae on basal half; distal half of T1, as on discs of T2–T5, with very short, appressed simple setae, each barely exiting puncture, setae becoming longer and denser towards apical terga; disc of T6 and sides of T1–T6 each with long, semierect, simple and plumose setae; sterna with semierect, long setae as long as those on sides of terga. *Sculpturing.* Weakly imbricate to smooth and shiny. Vertex and upper gena with punctures separated by 1–2 times a puncture width, punctures scattered on upper gena. Mesoscutum with punctures separated by 1–2 times a puncture width, punctures becoming sparser towards center to completely absent on disc; mesoscutellum largely impunctate, with few, scattered punctures. Metasomal terga with circular to ovoid punctures separated by 1.0–1.5 times a puncture width, punctures becoming denser laterally and towards apical terga; sterna with elongate punctures on discs, punctures contiguous laterally, becoming sparser medially. *Structure.* Head broader than long (1.1–1.2:1); compound eyes with inner margins parallel; proportion of upper to lower interocular distance 0.8–0.9:1; middle interocular distance 3.4–4.0; vertex broad, distance between median ocellus and posterior margin of vertex 3.7–4.4 OD; orbitoccipital distance 0.6–0.8; lateral ocelli below supraorbital line; interocellar distance to ocelocular distance 0.9–1:1; interocellar to ocelloccipital 0.5–0.6:1; ocellocular to alveolo-

cellar 0.6–0.8:1; orbitoccipital to ocellocular 0.9–1.1:1; alveolocular to interalveolar 1.0–1.3:1; clypeoalveolar distance 1.3 times longitudinal diameter of anntenal socket; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.8–1:1; frontal carina moderately elevated, forming a small protuberance at level of lower tangent of anntenal sockets; clypeus broader than long, 2.1–2.3:1; proportion of length of scape, pedicel and F1–F4: 3.2–3.5:0.3–0.5:1:0.3–0.4:0.4–0.5:0.4–0.5, respectively; labrum broader than long, with three basal protuberances, median tubercle distinct, longitudinally elongate, sublateral tubercles small. Mesoscutellum gently convex; metanotum and propodeum subvertically inclined.

Male. As in the female, except for usual secondary sexual characters and as follows: body length 16.1 (13.3–18.6); head length 4.7 (3.8–4.4); head width 4.9 (4.6–5.2); mesosoma width 6.2 (5.6–6.8); metasoma width 6.8 (6.6–7.6); forewing length 12.6 (12.0–13.3); forewing width 3.3 (3.2–3.4). *Coloration.* Clypeus, supraclypeal area, paraocular area, and anterior surfaces of scape and F1 yellow (Fig. 11). *Pubescense.* Off-white pubescence on mesepisternum, tergula anteriorly, sides of mesoscutum and mesoscutellum, and dorsum of T1. *Sculpturing.* Punctures denser than in the female, particularly on metasomal terga. *Structure.* Compound eyes enlarged, strongly converging dorsally, upper orbital margins separated by at least 2.7 times OD; proportion of upper to lower interocular distance 0.4–0.6:1; upper interocular distance 2.0–2.9 times OD; middle interocular distance 1.7–2.0; distance between median ocellus and posterior margin of vertex 2.6–3.1 OD; orbitoccipital distance 0.1–0.2; lateral ocelli below supraorbital line; interocellar distance to ocelocular distance 2.0–4.5:1; interocellar to ocelloccipital 0.3–0.5:1; ocellocular to alveolocellar 0.1–0.2:1; orbitoccipital to ocellocular 0.5–1:1; alveolocular to interalveolar 0.5–0.7:1; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.9–1.1:1; clypeus broader than long, 1.4–1.6:1; proportion of length of scape, pedicel and F1–F4 2.8–3.1:0.3–0.4:1:0.3–0.4:0.4–0.5:0.4–0.5, respectively. Legs slender, unmodified, except metatibia with long, slender subapical projection on inner margin, similar in size and thickness to tibial spur; mesobasitarsi longer than tibiae. Genitalia as in Figs 28, 33, 38, 43.

Distribution. This species is presumably widespread in South America (Table 1) as well as in Argentina, where it has been found in all provinces except Tierra del Fuego and Santa Cruz (Fig. 56). It occurs in all biogreophic provinces except subantartica. The southernmost collection locality for this species is Altares, Province of Chubut, near parallel 43°.

Comments. Lepeletier de Saint Fargeau (1841) described this species based on a female specimen from Brazil, which is presumably deposited at MNHN as indicated in the original publication. We received a female specimen from the MNHN identified as the type of *X. splendidula*. The complete label data for this specimen are as follows: "Museum Paris-EY0000001755 // Type ? [red label] // del` emb. del` Uruguay jusquiana missions [handwritten-round label] // splendidula [handwritten]". Because this specimen was collected in Uruguay, not in Brazil, it is not the true type of *X. splendidula*. We also examined from the same museum three specimens of *X. splendidula*



Figures 55–58. Collection localities for species of *Xylocopa* subgenus *Schonnherria* in Argentina.

from Brazil, but the label data do not agree with those indicated in the original description. Therefore, the whereabouts of the type of *X. splendidula* are currently unknown.

In specimens of both sexes the color of legs, propodeum, mandibles and tegulae ranged from black to dark brown, and that of the metasoma from greenish to bluish. The presence of tufts of white setae on the sides of the terminal terga is also a variable character.

***Xylocopa viridis* Smith, 1854**
Figures 6, 12, 18, 24, 29, 34, 39, 44, 57

Xylocopa viridis Smith, 1854: 360 (holotype: BMNH 17B.186; ♂, Rio Tapajós, Pará, Brazil) (examined)
Xylocopa (*Schonnherria*) *viridis*: Hurd and Moure 1963: 123.

Diagnosis. Both sexes of this species are easily recognized by the distinctive metallic green highlights on all tagmata, body pubescence yellowish, and metasomal terga uniformly covered by long, appressed simple setae on discs, and with white, tomentose, plumose setae on apical margins laterally (Figs 18, 24).

Female. Body length 16.7 (14–18); head length 4.5 (4.3–4.7); head width 5.1 (4.6–5.4); mesosoma width 5.9 (5.4–6.2); metasoma width 6.5 (6.0–6.8); forewing length 11.7 (11.0–12.3); forewing width 3.1 (3.0–3.2). *Coloration.* Integument dark brown to black with strong metallic green highlights. Wing subhyaline with weak golden highlights. *Pubescence.* Predominantly whitish to yellowish; black or gray setae on face, vertex, upper gena, mesoscutum, mesoscutellum, sides of T2–T5, and most of T6, S5 and S6; ferrugineous setae on inner surface of tarsi. Head and mesosoma with abundant setae, except asetose on discs of mesoscutum and mesoscutellum. Basal half of T1 with scattered, semierect simple setae; distal half of T1 and T2–T6 with appressed setae on discs, each setae at least twice as long as a puncture width, becoming longer towards apical terga, apical margins laterally with dense, white tomentum of appressed plumose setae (Fig. 18); disc of T6 and sides of T1–T6 each with long, semierect, simple and plumose setae; sterna with semierect, long setae as long as those on sides of terga. *Punctation.* Weakly imbricate to smooth and shiny. Vertex densely punctate, punctures separated by at most a puncture width, becoming enlongate and sparser on upper gena. Mesoscutum with punctures separated by 1–2 times a puncture width, punctures becoming sparser towards center to completely absent on disc; mesoscutellum largely impunctate, with few, scattered punctures. Terga densely and uniformly punctate, setiferous punctures elongate, separated by a puncture width or less; sterna with punctures sparser than on terga. *Structure.* Head broader than long (1.1–1.2:1); compound eyes with inner margins parallel; proportion of upper to lower interocular distance 0.9:1; middle interocular distance 3.2–3.5; vertex broad, distance between median ocellus and posterior margin of vertex 3.7–4.6 OD; orbitoccipital distance 0.6–0.8; lateral ocelli below supraorbital line; interocellar distance to ocelocular distance 0.9–1.1:1; interocellar to ocelloccipital 0.6–0.7:1; ocellocular to alveolocellar 0.6–0.7:1; orbitoccipital to ocellocular 1.0–1.2:1; alveolocular to interalveolar 0.9–1.1:1; clypeoalveolar distance about as long as longitudinal diameter of anntenal socket; clypeocellar distance to distance between median ocellus and posterior margin of vertex 0.9–1:1; frontal carina moderately elevated, slightly protuberant at level of lower tangent of anntenal sockets; clypeus broader than long, 2.1–2.2:1; proportion of length of scape, pedicel and F1–F4: 3.5–3.8:0.4:1:0.4:0.5–0.6:0.5–0.6, respectively. Labrum broader than long, with three basal protuberances, median tubercle distinct,

longitudinally elongate, sublateral tubercles small. Mesoscutellum gently convex; metanotum and propodeum vertical in profile.

Male. As in the female, except for usual secondary sexual characters and as follows: Body length 15.3 (14.3–16.3); head length 3.7 (3.5–3.8); head width 4.3 (4.0–4.4); mesosoma width 5.6 (5.2–6.0); metasoma width 6.1 (5.6–6.6); forewing length 12.1 (11.3–12.7); forewing width 3.2 (3.0–3.4). *Coloration.* Outer surface of mandible, labrum, clypeus, supraclypeal area, and anterior surfaces of scape, F1 and F2 yellow. Tegula reddish brown. *Pubescence.* Longer and denser than in female. *Structure.* Compound eyes with inner margins slightly converging dorsally; proportion of upper to lower interocular distance 0.8:1; upper interocular distance 4.0–4.6 OD; middle interocular distance 1.9–2.0; distance between median ocellus and posterior margin of vertex 2.4–2.7 OD; orbitoccipital distance 0.2–0.3; interocellar distance to ocelocular distance 1.8–2.2:1; interocellar to ocelloccipital 0.7–1:1; ocellocular to alveolocellar 0.2–0.3:1; orbitoccipital to ocellocular 0.8–1:1; alveolocular to interalveolar 0.6–0.7:1; clypeocellar distance to distance between median ocellus and posterior margin of head 1.2–1.3:1; clypeus broader than long, 1.4–1.6:1; proportion of length of scape, pedicel and F1–F4: 2.8–3:0.4–0.6:1:0.4–0.5:0.5–0.6:0.5–0.6, respectively. Legs slender, unmodified, except metatibia with blunt subapical projection on inner margin, shorter and thicker than tibial spur; mesobasitarsi longer than tibiae. Genitalia as in Figs 29, 34, 39, 44.

Distribution. This species has been recorded from Bolivia, Brazil, Colombia, Costa Rica, French Guiana, Guatemala, Guyana, Mexico, Panama, Paraguay and Peru (Moure 2007). In Argentina, it is known only from the province of Misiones (Fig. 57), which is included within the Paranaense biogeographic province.

Comments. *Xylocopa viridis*, ranging from southern Mexico to Argentina, appears to be composed of multiple species. An appraisal of museum specimens under *X. viridis* deposited at SEMC from locations across its distribution range revealed considerable variation in body pubescence, punctation, body size, and shape of the apical projection of the inner surface of the male metatibia. A similar case seems to occur in *X. varians* Smith, a species with metallic green highligths that has also been recorded from Misiones and presumably confused with *X. viridis*. We studied the male holotype of *X. viridis* and the female type of *X. varians*, both from Brazil, as well as specimens of both species from Brazil and other countries in South America. We observed that both sexes of *X. varians* can be distinguished from those of *X. viridis* primarily by the terga with black setae on their discs (yellowish in *X. viridis*) and the upper gena of the female densely punctate, with a narrow impunctate band behind the outer margins of the compound eyes (upper gena sparsely punctate and with broad impunctate band behind outer margins of compound eyes in *X. viridis*). We found a female and male specimen from Misiones, both identified by P.H. Hurd as *X. varians*. These specimens are deposited at MACN and SEMC respectively, and their complete label data are as follows: "7596" // Misiones // 766 // Xylocopa varians Smith, P.H. Hurd 59 (MACN); "Misiones, Pindapoy, II-1956 // SEMC 1232909". Both specimens agree with the characters listed for *X. viridis* and thus the record of *X. varians* for Argentina appear to be based on misidentified specimens.

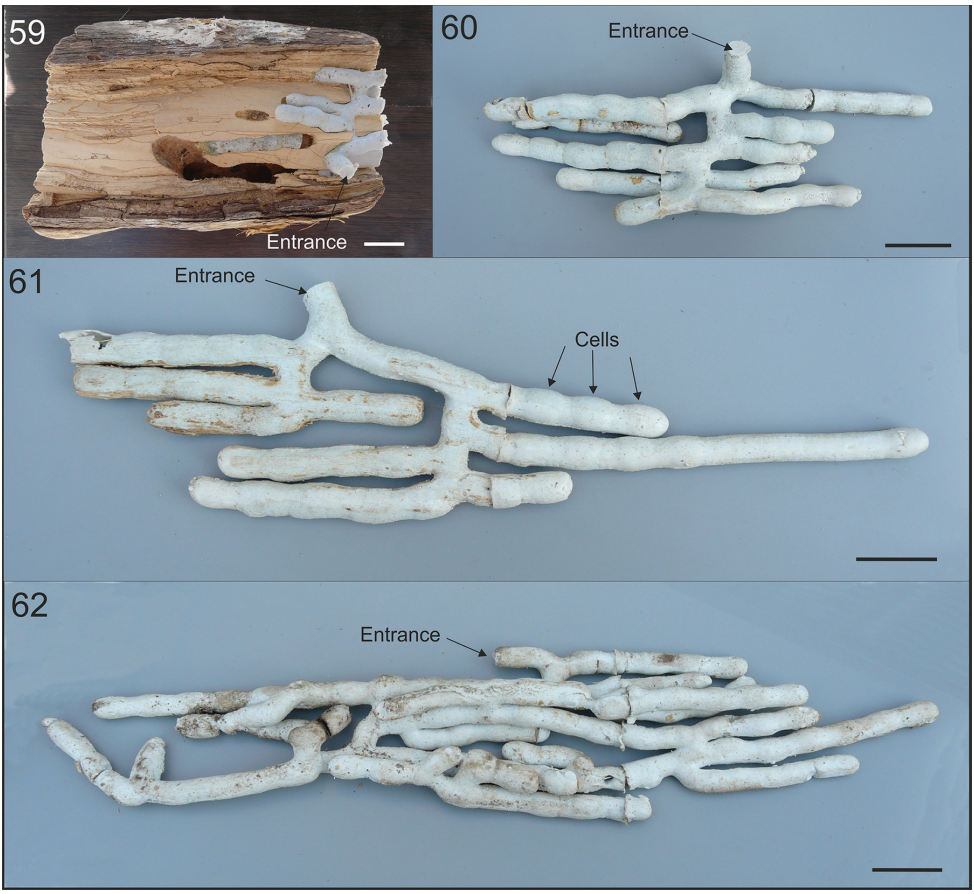
Specimens of *X. viridis* from Argentina and southern Brazil also seem to be different from those of northen Brazil, particularly in the length of the setae on metasomal terga, the color of tegulae, and the shape of the apical projection on the inner surface of male metatibia. Such differences are suggestive of a distinct species and further studies are needed to determine the species limits of *X. viridis*.

Nesting biology of *X. splendidula* and *X. viridis*

Four nests of *X. splendidula* and 10 nests of *X. viridis* were found in total. Nests of *X. splendidula* were found in Villa Atamisqui (28º27' 36"S, 63º 50'53"W, 123 m.a.s.l) in Santiago del Estero and the following three localities in the province of Buenos Aires: Berisso (34°53'12"S, 57°53'41"W, 6 m.a.s.l), Gral. Dorrego (38°52'37"S, 61°27'41"W, 32 m.a.s.l), and Mercedes (34°38'57"S, 59°24'50"W, 39 m.a.s.l). These nests were found inside dead branches of the following plant species: *Syagrus romanzoffiana* (Cham.) Glassman (Arecaceae), *Stetsonia coryne* (Salm-Dyck) Britton & Rose (Cactaceae), *Salix* sp. (Salicaceae), and *Parkinsonia aculeata* L. (Fabaceae). Sometimes nests of *Xylocopa* (*Neoxylocopa*) *augusti* Lepeletier de Saint Fargeau as well as *X. frontalis* were found in the same branch with nests of this species.

Nests of *X. viridis* were collected in two localities in the province of Misiones: Loreto (27°20'16"S, 55°31'55"W, 175 m.a.s.l.) and Iguazú (25°40'41"S, 54°26'58"W, 191 m.a.s.l). All nests were found inside dead branches of *Hovenia dulcis* Thunb. (Rhamnaceae). As in *X. splendidula*, nests of *X. frontalis* were also found in the same branch with nests of *X. viridis.*

As in other species of *Xylocopa* (e.g., Camillo and Garófalo 1982; Gonzalez et al. 2009, Lucia et al. 2014), nests of both species were built inside dead, dry wood, and consisted of a single entrance connected to a system of branched tunnels through a vestibule (Figs 59–62). The tunnels were parallel to the wood grain with the barrel-shaped brood cells built at the end of each tunnel, which were separated from each other by partitions of sawdust. These partitions were thinner in the center, smooth and concave on their outer surfaces, but coarse and flat on their inner surfaces. In both species the length of the tunnel was not significantly correlated with its diameter (Pearson correlation coefficient, *X. viridis*: $r = 0.15$, $p = 0.28$; *X. splendidula*: $r = -0.17$, $p = 0.31$), and the number of tunnels per nest was not significantly correlated with the diameter of the branch where the nest was found (*X. viridis*: $r = 0.57$, $p = 0.08$; *X. splendidula*: $r = 0.064$, $p = 0.94$). The total number of brood cells varied among nests and species (Table 2) and it was significantly correlated with the total number of tunnels per nest (*X. viridis*: $r = 0.96$, $p < 0.05$; *X. splendidula*: $r = 0.99$, $p < 0.05$), but independent of the diameter of the branch (*X. viridis*: $r = 0.60$, $p = 0.09$; *X. splendidula*: $r = 0.07$, $p = 0.93$); the number of cells per tunnel was independent of the length of the tunnel (*X. viridis*: $r = 0.37$, $p = 0.08$; *X. splendidula*: $r = 0.13$, $p = 0.46$). Dimensions of some features of the nest of both species are indicated in Table 2.



Figures 59–62. Nests of *Xylocopa viridis* (**59–61**) and *X. splendidula* (**62**) in Argentina. **59** Section of tree branch showing an opened nest with tunnels filled with silicone rubber **60–62** Extracted molds from tree branch showing arrangement of tunnels and brood cells. Scale bars: 2 cm

Table 2. Measurements (mm) of the nests of *X. splendidula* and *X. viridis* from Argentina. Means are given with standard deviation followed by the range and sample size in parenthesis.

Nest feature	*Xylocopa splendidula*	*Xylocopa viridis*
Branch diameter	83.8 ± 40.8 (53.0–142.0, *n* = 4)	113.0 ± 15.6 (95.0–128.0, *n* = 10)
Nest entrance diameter	7.0 ± 0.76 (6.0–8.0, *n* = 8)	7.5 ± 0.76 (7.0–9.0, *n* = 20)
Vestibule	16.2 ± 6.3 (12.0–20.0, *n* = 5)	22.4 ± 2.8 (13.0–26.0, *n* = 9)
No. Tunnels	8.8 ± 10.2 (3.0–24.0, *n* = 4)	5.3 ± 4.6 (1.0–14.0, *n* = 10)
Tunnel diameter	8.8 ± 1.0 (6.9–11.2, *n* = 35)	9.8 ± 0.9 (7.9–12.0, *n* = 53)
Tunnel length	51.7 ± 26.0 (12.0–113.0, *n* = 35)	56.5 ± 24.8 (18.0–153.0, *n* = 35)
Number of cells per nest	18.5 ± 23.8 (4.0–54.0, *n* = 4)	12.6 ± 13.8 (0.0–36.0, *n* = 10)
Cell partition	3.5 ± 0.8 (3.0–5.0, *n* = 15)	4.6 ± 1.1 (2.5–6.0, *n* = 23)
Cell length	12.1 ± 1.4 (10.0–15.0, *n* = 75)	11.4 ± 1.8.8 (9.0–19.0, *n* = 127)

The number of adult females present at the time of collection ranged from one to six in nests of *X. viridis* ($\bar{x}$= 2.3 ± 1.8) and from one to four in nests of *X. splendidula* ($\bar{x}$ = 2.7 ± 1.2); adult males were found only in three nests of *X. viridis* ($\bar{x}$ = 2.0, 1–3, ± 1.0) and in one nest of *X. splendidula* (7 males). Females were not dissected to examine the ovarian development or the presence of sperm in their spermatheca. Three females and one male of *X. viridis* were found dead inside the nest and were parasitized by the conopid fly *Physocephala* sp.; likewise, *P. wulpi* Camras was found parasitizing adults of *X. splendidula* (Stuke et al. 2011).

Discussion

The presence of seven of the 11 species of *Xylocopa* (*Schonnherria*) recorded for Argentina by Hurd (1978) are confirmed. One of the four remaining species, *X. boops*, is known only from the type and appears to have been described from a male specimen of *X. macrops* with unusually large compound eyes. Thus, here it is interpreted as synonym of that species (see species account). The remaining three species, *X. dimidiata*, *X. subcyanea*, and *X. varians*, occur in Brazil and Paraguay and were recorded from Misiones, a province that shares borders with both countries. We did not find any specimens of these species collected in Argentina nor did we capture any of them during the field surveys in Misiones or in any other province of the country. However, we examined a few female specimens of *X. simillima*, *X. macrops*, and *X. viridis* from Misiones that had been identified under those names (see species account). Thus, such records of *X. dimidiata*, *X. subcyanea*, and *X. varians* for Argentina seem to have been misidentified specimens. Yet, we still do not rule out entirely the possibility that these species existed or still exist in Misiones because of the proximity of this province to Brazil and Paraguay, and because three other species, namely *X. bambusae*, *X. chrysopoda*, and *X. pulchra*, were collected in Misiones during the early 1900's and have not been collected since.

Only two of the seven species of *Xylocopa* (*Schonnherria*) occurring in Argentina are widely distributed in the country. *Xylocopa splendidula* exhibits the widest range, found everywhere except in Tierra del Fuego and Santa Cruz (Fig. 56), while *X. macrops* occurs across the northwest, from Tucumán to Jujuy, and across the east, from northern Buenos Aires to Misiones (Fig. 55). Both species are abundant and frequently found in open fields and urban habitats. The remaining species have been recorded only from Misiones (Figs 57, 58). These species appear to occur across the Paranaense biogeographic province or Interior Atlantic Forest, an ecoregion that consists mostly of rainforests and encompases Misiones, eastern Paraguay, and southeastern Brazil (Cabrera and Willink 1980; Giraudo et al. 2003). Thus, Misiones seems to be at the border of their distribution.

In this study we were able to recognize a number of structural characters in both sexes that seem reliable in species recognition, such as size, shape, density, and distribution of punctures, length, density and type of setae, male sexual secondary

modifications (projections of legs, particularly on inner surface of metatibia), and features of the male genitalia. Althought some of these characters have been mentioned by some authors, to date, an emphasis has been made to use patterns of coloration of wings and pubescence (e.g., Schlindwein et. al. 2003). We have made an effort to document and illustrate these structural characters and to them in the keys as well as in the diagnoses and descriptions. Distinctive characters of the genital capsule of the male include the shape of the medial margin of the gonocoxite in dorsal view (Figs 25–29), shape of the ventroapical plate (Figs 30–34), thickness of the penis valve and shape of the lateral carina of the penis valve, and pubescence of the apex of the gonostylus (Figs 35–44, 47, 48). For example, in *X. splendidula* the ventroapical plate has a well developed, nearly digitiform posteromedial lobe (Figs 33, 43) whereas it barely projects in *X. chrysopoda* (Figs 31, 41); in *X. macrops* the penis valve, in dorsal view, is robust and basally broad (Fig. 37) whereas it is slender across its length in *X. viridis* (Fig. 39); in *X. chrysopoda* the lateral carina of the penis valve is short and projects into a lobe (Fig. 36) whereas in *X. splendidula* it is longer, extending towards the apex of the penis valve (Fig. 38); in *X. viridis* both lobes of the apex of the gonostylus are densely covered by long, plumose setae (Figs 39, 44) whereas in *X. macrops* the inner lobe is asetose and the outer is sparsely covered by simple setae (Figs 37, 42). These characters may also prove to be useful in future phylogenetic analyses.

The nesting biologies documented here for *X. splendidula* and *X. viridis* agree with those of other species of the genus that nest in solid wood, including species of *Schonnherria* (e.g., Jörgensen 1909; Bertoni 1911; Strand 1912; Gonzalez et al. 2009; Lucia et al. 2014). In addition to the nesting substrates recorded in this work, nests of *X. splendidula* have been found in dead wood of the following species: *Populus piramidalis* (Salicaceae), *Arundo donax* (Poaceae), *Salix* sp. (Salicaceae), *Populus* sp., *Melia azedarach* (Meliaceae), and *Broussonetia papyrifera* (Moraceae) (Holmberg 1884; Friese 1908; Jörgensen 1909; Telleria 2000). Such a wide range of plants used as nesting substrates in *X. splendidula* contrast with that of *X. viridis*, in which all 10 nests were found using the same plant species (*Hovenia dulcis,* Rhamnaceae). For both species, the number of cells per nest was significantly correlated with the number of tunnels, and both variables were independent of the diameter of the branch; likewise, the number of cells per tunnel was independent of the length of the tunnel. Thus, the observed variation among nests is probably due to ontogenic differences rather than substrate limitations, as suggested for other species (e.g., Camillo and Garófalo 1982). The same ontogenic differences could also explain the variation in the number of adult females found among nests.

The province of Misiones contains the highest diversity of large carpenter bees in Argentina (Lucia et al. 2014) and future conservation efforts as well as comparative bionomic studies on this group should be focused on this area. We do not know if the same pattern of diversity occurs in other groups of bees, but Misiones is an area well known to contain a high diversity of other organisms, including birds (e.g., Rabinovich and Rapoport 1975; Giraudo et al. 2003).

Key to species of *Xylocopa* subgenus *Schonnherria* in Argentina

Females

Note. The female of *X. chrysopoda* is unknown.

1 Labrum basally with a distinct, large, single capitate tubercle about as large as the median ocellus (Fig. 4); metasomal terga dark brown to black with basal three or four terga often with broad, light reddish brown bands on discs (Fig. 16) [sometimes terga largely orange]; wings dark brown with violet highlights; large bees (body length 20–23 mm) ..... ***X. simillima*** **Smith**

– Labrum basally with a longitudinally elongated median tubercle and two small sublateral tubercles (often obscured by dense setae); color of metasomal terga variable, never orange or with light reddish brown bands; color of wings variable, hyaline to black; small to medium-sized bees (body length 14–22 mm)..... **2**

2(1) Discs of T2–T5, each with a broad, medially interrupted apical band of dense yellowish setae (Fig. 15), integument not visible among setae...***X. pulchra*** **Smith**

– Discs of T2–T5 without broad, medially interrupted apical bands of dense yellowish setae **3**

3(2) Mesoscutellum posteriorly and metasomal terga with distinct metallic green or blue highlights; wings hyaline or subhyline with light reddish brown veins **4**

– Mesoscutellum posteriorly and metasomal terga dark brown to black without metallic highlights, at most with very weak blue reflections; wing membrane and venation dark brown to black..... **5**

4(3) Metasomal terga with metallic green highlights, densely and uniformly punctate except along midline, setiferous punctures elongate, separated by a puncture width or less; T1–T5 with yellowish setae on discs, apical margins laterally with dense, white tomentum of appressed plumose setae (Fig. 18); upper gena densely punctate, punctures elongate, separated by 1–2 times a puncture width ..... ***X. viridis*** **Smith**

– Metasomal terga with metallic blue highlights, sparsely punctate, setiferous punctures circular or slightly ovoid, separated by 1–3 times a puncture width; discs of T1–T5 with dark brown to black setae, apical margins without tomentum (Fig. 17); upper gena sparsely punctate, punctures circular or slightly ovoid, separated by at least two times a puncture width..... ..... ***X. splendidula*** **Lepeletier de Saint Fargeau**

5(3) Clypeus flat in profile, dorsolaterally not elevated from adjacent paraocular area; supraclypeal area flat, frontal carina projected into a distinct tubercle just above or at the upper tangent of anntenal sockets (Fig. 1); vertex, behind lateral ocelli, largely impunctate, punctures small and scattered; small bees (body length 14–17 mm) (Misiones, rarely collected) .....***X. bambusae*** **Schrottky**

– Clypeus depressed basally on disc, dorsolaterally elevated from adjacent paraocular area; supraclypeal area depressed on disc, laterally elevated from adjacent

paraocular area, frontal carina elevated and forming a low tubercle near lower tangent of antennal sockets, continuing dorsally into a low carina (Fig. 2); vertex, behind lateral ocelli, densely punctate, punctures coarse, separated by 1–2 times a puncture width; larger bees (body length 18–22 mm) (widespread in northern Argentina, commonly collected) .....***X. macrops*** **Lepeletier de Saint Fargeau**

Males

Note. The male of *X. pulchra* is unknown.

1 Compound eyes strongly convergent dorsally, upper interocular distance less than three times OD (Fig. 9) **2**

– Compound eyes not distinctly convergent dorsally, inner margins parallel or nearly so, upper interocular distance at least four times OD (Fig. 7) **4**

2(1) Upper interocular distance 0.4 to 0.6 times lower interocular distance; small bees (body length 13–19 mm) .. ***X. splendidula*** **Lepeletier de Saint Fargeau**

– Upper interocular distance 0.1 to 0.3 times lower interocular distance; larger bees (body length 21–23 mm) **3**

3(2) Labrum black (Fig. 10); wings dark brown; metasomal terga dark brown to black with basal three or four terga often with broad, light reddish brown bands; discs of S2–S6 inmaculate ..... ***X. simillima*** **Smith**

– Labrum yellow (Fig. 9); wings hyaline to subhyaline; metasomal terga with metallic blue highlights, without light reddish bands; discs of S2–S6 each with sublateral yellow maculations. ***X. macrops*** **Lepeletier de Saint Fargeau**

4(1) Supraclypeal area with a distinct tuft of long, erect, dense setae obscuring integument (Fig. 7); protrochanter with distinc spine; ventral surface of metatrochanter and metafemur basally glabrous, distinctly protuberant; T1–T5 dark reddish brown, each with a distinct, broad, median yellow maculation on disc, sides and distal margins (inmaculate areas) densely covered by long, dense setae (Fig. 19)..... ***X. bambusae*** **Schrottky**

– Supraclypeal area without a tuft of long, erect, dense setae; protrochanter without spine or tubercle; ventral surface of metatrochanter and metafemur basally pubescent, not distinctly protuberant; T1–T5 inmaculate..... **5**

5(4) Metasomal terga with distinct metallic green highlights, densely and uniformly punctate, setiferous punctures elongate, separated by a puncture width or less; T1–T5 with short (≤ 1.0 OD) setae on discs, apical margins laterally with dense, white tomentum of appressed plumose setae (Fig. 24); sterna with sparse, short setae on discs, not obscuring integument (commonly collected)..... ***X. viridis*** **Smith**

– Metasomal terga dark reddish brown to black, at most with weak metallic highlights, setiferous punctures circular to ovoid, separated by 1–2 times a puncture width; T1–T5 with distinctly long (≥ 2.0 OD) setae on discs, apical margins without tomentum (Fig. 20); sterna with distinctly long, dense setae partially obscuring integument (rarely collected)... ***X. chrysopoda*** **Schrottky**

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