Zootaxa 4599 (1): 001–126
https://www.mapress.com/j/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4599.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:7CDD24FF-5BA3-4D06-898D-A3E220515D4C

ZOOTAXA

4599

Pheidole (Hymenoptera, Formicidae) of Middle American Wet Forest

JOHN T. LONGINO
Department of Biology, University of Utah, Salt Lake City, Utah, 84112, USA. E-mail: john.longino@utah.edu.

Magnolia Press
Auckland, New Zealand

Accepted by K. Williams: 11 Feb. 2019; published: 6 May 2019

JOHN T. LONGINO
***Pheidole* (Hymenoptera, Formicidae) of Middle American Wet Forest**
(*Zootaxa* 4599)

126 pp.; 30 cm.

6 May 2019

ISBN 978-1-77670-662-4 (paperback)

ISBN 978-1-77670-663-1 (Online edition)

FIRST PUBLISHED IN 2019 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/j/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

Abstract

The ant genus *Pheidole* is a highly diverse lineage of ants that are dominant elements of tropical and subtropical ecosystems throughout the world. Biodiversity inventory projects in Middle American wet forests (southern Mexico to Costa Rica, lowland rainforest to high montane forest) allow an improved taxonomy of the genus in this region. An identification guide to 234 species in the region is provided, using a "bird guide" approach. Species are arranged in order of minor worker head width and scape length, and each species has a fixed layout that includes habitat and microhabitat information, standard views (minor lateral, minor face, major face), and a distribution map. The following **new synonyms** are proposed: *biconstricta* Mayr 1870 (= *inermis* Mayr 1870), *carapuna* Mann 1916 (= *tristicula* Wilson 2003), *fimbriata* Roger 1863 (= *soesilae* Makhan 2007), *insipida* Forel 1899 (= *fariasana* Wilson 2003, *mooreorum* Wilson 2003), *longiscapa* Forel 1901 (= *cocciphaga* Borgmeier 1934), *plebecula* Forel 1899 (= *perdiligens* Wilson 2003, *texticeps* Wilson 2003), *nitidicollis* Emery 1896 (= *chalcoides* Wilson 2003), *nubicola* Wilson 2003 (= *cielana* Wilson 2003, *petrensis* Wilson 2003), *simonsi* Wilson 2003 (= *arctos* Wilson 2003, *gangamon* Wilson 2003, *thrasys* Wilson 2003), *striaticeps* Mayr 1870 (= *chloe* Forel 1908), *transversostriata* Mayr 1887 (= *scalaris* Wilson 2003), *vafra* Santschi 1923 (= *laticornis* Wilson 2003). The following 57 **new species** are described: *ajaxigibba, andersoni, angustinigra, atitlana, balatro, belonorte, besalon, bicornisculpta, brownampla, cahui, caliginosa, carinitida, corniclypeus, costaricensis, cusuco, depressinoda, eosimilis, familiaparra, fincanaranjo, hansoni, hectornitida, hitoy, huarache, imbrilis, indagarama, kasparii, kelainos, lagunculiminor, lamancha, laselvoides, lineafrons, luteagossamer, machaquila, marmor, moskitia, muralla, musacolor, musinermis, natalie, nephele, obturaculum, passivaeferox, perissothrix, platyscapa, probolonotum, rima, rogeripolita, savegre, sensipelada, sepultura, tapanti, tikal, tinamu, tsontekonwei, tuculutan, xiloa, zannia.*

Key words: Neotropics, taxonomy, identification, new species, Myrmicinae

Introduction

The ant genus *Pheidole* is a major component of tropical and subtropical ant communities throughout the world. Over 80 species can co-occur in local faunas (Longino and Colwell 2011) and there are more than 1100 species known for the genus as a whole (Wilson 2003, Moreau 2008). In many habitats they are ecologically dominant, being generalist omnivores that rapidly recruit to diverse food sources. These are ants that the general public often encounters (as the ants at the picnic) and that scientists frequently study. Studies of *Pheidole* have informed macroecology (Economo, Klimov *et al.* 2015; Economo, Sarnat *et al.* 2015; Economo *et al.* 2019), community ecology (Mertl *et al.* 2010, Tschá and Pie 2018), sociobiology (Mertl and Traniello 2009), caste differentiation (Lillico-Ouachour and Abouheif 2016), and neurobiology (Waxman *et al.* 2017). However, the basic taxonomy of the genus is in a nascent stage. Knowledge of the existence and spatial extent of genetic and morphological clusters is rudimentary, and identification tools are limited. In this work I provide an improved "biodiversity map" for *Pheidole* in wet forest habitats of Middle America.

Our increasing understanding of the nature of biological diversity makes any rigid definition of species untenable. In most cases, genetic differentiation of local populations long precedes morphological differentiation. DNA barcoding, increasingly augmented with nuclear sequence data, reveals high numbers of distinctive genotypic clusters. Cryptic species abound, in allopatry and sympatry, and morphological differentiation may be

extremely subtle or completely undetectable. That there is a finite set of true species in nature, waiting to all be discovered, is a poor metaphor for biology. O'Hara (1993) recommended a cartographic metaphor, in which our description of biological diversity is a map, and maps can be made at any scale. On maps, a category like "city" or "mountain" is a cartographic generality. No one denies that cities exist, but "city" is not precisely defined. A large scale map may have "Los Angeles" represented as a single black circle, while a finer scale map of the area within that circle may have Los Angeles, Glendale, Pasadena, Burbank, etc. Species can be viewed the same way. As a matter of convention, we may choose to use a species name for a common morphology over a wide geographic range, acknowledging that it is composed of perhaps hundreds of genetically differentiated clusters. In other cases, we may choose to name one of those local clusters when there is sufficient evidence for its distinctness and some reason for giving it a name. Those reasons could include local conservation programs, regional inventory efforts, and natural history or other studies that focus on a particular local population. The work presented here is an identification guide to a list of species known to occur in wet forests of Middle America. Some are existing names and some are described as new, but it should be understood that this is just a map, useful for some applications but not all, and certain to be revised and refined at ever increasing resolution.

Beyond making the map itself is the challenge of identification. The time will come when machines will identify specimens for other machines, communicating in DNA sequences and clustering algorithms. There will then be the need for translation for humans, converting a code number for a genetic cluster (e.g., "BIN"s of the COI barcoding efforts) into words in human language and information on what the organism looks like, where it lives, and what it does. And before machine-based identification is universally available, users will still want to attempt identification by what an organism looks like. In traditional insect taxonomy, the dichotomous key has been the standard means of identification. Dichotomous keys are very effective tools when the number of species is small, or the taxon of interest has large numbers of discrete morphological characters that can be used to unambiguously split the taxon into subgroups. *Pheidole* has neither characteristic. There are hundreds of species, and they somewhat evenly fill morphology space (Pie and Traniello 2007). Most characters are continuous, not discrete. A dichotomous key with hundreds of species that differ by continuous characters is a nightmare. In this work I have taken a "bird guide" approach, providing a tabular identification tool. Species are arranged in order by two measurements (head width and scape length of the minor worker), with standard views, a map, and habitat notes for each species.

This work is focused on a geographic region and habitat, as a result of a series of quantitative inventory projects in Middle America. Projects ALAS and TEAM surveyed La Selva Biological Station and the adjacent elevational gradient (the Barva Transect) on the Atlantic slope of Costa Rica. Project LLAMA surveyed wet forest sites from Chiapas, Mexico, to Nicaragua. Project ADMAC surveyed wet forest sites in Veracruz and Oaxaca states in Mexico and in the Talamanca range of Costa Rica. These projects all focused on moist to wet forest habitats, from sea level to 2600 m elevation. They included extensive Winkler sampling of forest floor leaf litter and rotten wood, collections at ground baits, beating samples, Malaise trap samples, and hand collecting. In addition to these large projects, I have carried out individual collecting extensively in Costa Rica, and in the vicinity of the quantitative sampling sites in the large projects. The result is a large specimen set for the region, allowing for better assessment of character variation, geographic range, and habitat preferences, all of which inform species delimitation.

The geographic scope is the Mexican states of Veracruz, Oaxaca, and Chiapas, south to Costa Rica. The taxon selection is (1) all named species whose type localities fall within this region, and (2) all other species identified by me as occurring in the region. It is not a thorough checklist and does not include unverified literature references to occurrences. I have not extensively surveyed museum collections or the material of other collectors. I hope this identification guide will serve as a tool to allow others to identify such material. The guide will work best for wet to moist habitats, from mature forest to weedy open areas. Middle American habitats that are undersampled are seasonal dry forest, arid or semiarid areas, and the extensive pine forests from Mexico to northern Nicaragua. This work will be of less use in these habitats.

A synoptic list of species in the guide is followed by a taxonomic section. The taxonomic section does not contain every species in the synoptic list, but only those (1) that are new species, described here; (2) for which formal taxonomic changes are needed, primarily synonymies; and (3) species for which additional observations or comments are reported.

Characters. *Pheidole* species have discrete major and minor workers. Each caste has distinctive characters

that can aide in species separation. In some cases multiple species may have indistinguishable minor workers but distinctive major workers, and in other cases the reverse is true.

Antennal segments. *Pheidole* workers typically have 12-segmented antennae. Two of the smallest species in Middle America have reduced numbers, 10 segments in *P. perpusilla* and 11 segments in *P. mendicula*. These differences are noted in Plate 1.

Occipital carina. This character is important in minor workers. The occipital foramen is surrounded posteriorly and laterally by a differentiated cuticular rim: the occipital carina (Gauld and Bolton 1988) [in some Old World species the carina extends anteriorly as the genal carina]. In minor workers of most species the occipital carina is not visible in full-face view. In some cases it is visible as a narrow rim. But in a few species it is highly developed as a flaring collar that encloses (and presumably protects) the articulation of the head and mesosoma. In these cases it is easily visible in face view. It is termed the "nuchal collar" in Wilson (2003).

Sculpture. In minor workers, sculpture of the head, mesosoma, and gaster are all important. Minor worker face sculpture is highly variable, in some cases intraspecifically, but there are two common patterns: completely smooth and shining, and uniformly foveolate (foveolae are small pits). Less often the face is rugose. Often faint rugulae may overlie foveolate sculpture. The side of the mesosoma may be uniformly foveolate, or there may be smooth shiny patches on the side of the pronotum, on the katepisternum, or both. These sculptural features may also be overlain with rugae of varying distribution and strength. A common condition is for the first gastral tergum (fourth abdominal tergum) to be completely smooth and shining. In some species a portion of the tergum is sculptured, usually a shagreening (very fine granular microsculpture) that makes the surface dull instead of shining. The entire tergum may be sculptured, or some portion anteriorly, grading to smooth and shining posteriorly. The sculpture may be faint, requiring that the specimen be tilted at certain angles to see it. Also, one can be fooled by dirty specimens with surface films covering the gaster. For example, when specimens are collected with greasy baits like tuna or cookies they may acquire a grease layer that obscures surface sculpture.

In major workers, face sculpture varies among species, from densely sculptured to smooth and shining, and everything in between. Sculpture of the mesosoma is more intraspecifically variable and I have not used it to differentiate species. Gastral sculpture can be smooth or shagreened, as in minor workers, but is not always the same as the minor workers (e.g., within a species, major workers may have a shagreened gaster and minor workers a smooth and shiny gaster).

Pilosity. Pilosity varies greatly among species and is an excellent character for species-level distinctions. Pilosity may be abundant or sparse, flexuous or stiff. The pilosity of the hind tibia (mid tibia is often the same) often provides species-level characters. The tibia may appear completely bare, with very short, fully appressed pubescence and no erect setae. It may be densely clothed in short, subdecumbent to suberect pubescence that appears very uniform in length, and with no erect setae. It may have one of the above states of underlying pubescence, but in addition several long erect setae. It may be covered entirely with long erect setae, with no differentiation of long setae and underlying pubescence. It may have an underlying pubescence grading into suberect setae of varying length, so that it blurs the distinction among the previously described conditions. Tibial pilosity sometimes very clearly differentiates species that are otherwise difficult to tell apart.

In major workers, when in full-face view, the appearance of pilosity on the sides of the head is often of species-level diagnostic value. Some species show no projecting pilosity at all. Some have dense decumbent short or long pubescence. Some have abundant long or short erect setae. Tibial pilosity of major workers usually but not always parallels that of the minor workers. Pilosity on the gastral dorsum is highly variable. Some species have the first gastral tergum entirely bare and with sparse, short, fully appressed pubescence. Others have dense long subdecumbent pubescence and no erect setae. The majority of species have erect setae of some form, either short and stiff or long and flexuous.

Hypostomal teeth. The ventral surface of the head in ants is formed by the genal bridge. In major workers, the anterior margin of the genal bridge forms a nearly right angle, and a thin, shelf-like hypostomal sclerite extends inward to the buccal cavity. The juncture of the genal bridge and the hypostomal sclerite is the hypostomal margin. There is nearly always a pair of teeth at the inner margin of the hypostomal sclerite, bordering the bases of the mandibles. These are the *Outer Hypostomal Teeth*. Less regularly present are a pair of teeth on the hypostomal margin itself. When present, these teeth are always more closely spaced than the outer teeth, and are the *Inner Hypostomal Teeth*. There may also be a median tooth on the hypostomal margin. The median tooth, when present, often seems intraspecifically variable in size and distinctness. The great majority of wet forest *Pheidole* have

distinct inner hypostomal teeth, which vary in position. The two most common states are (1) relatively stout teeth that are about midway between the midline and the outer hypostomal teeth, and (2) thin, often needle-like ("acicular") teeth that are widely spaced, close to the outer hypostomal teeth.

Scrobes. The antennal scrobes are depressions or grooves beneath the scapes. Some majors have evenly convex faces, with no hint of a scrobe. Many species have shallow scrobes, ranging from a barely discernable flattening beneath the scape to a conspicuous depression. Often the sculpture in a scrobe is weaker than the sculpture around it, to the extent of forming a smooth shiny patch surrounded by foveate or rugose sculpture. In some cases the scrobe is very strongly developed, forming a deep channel with distinct dorsal and ventral margins, such that the scape can be completely recessed and protected within it.

Scape. The scape base may be terete (round in cross section) or strongly flattened, and it may be gently or strongly curved where it attaches to the head.

Postpetiole. The postpetiole in dorsal view assumes a variety of shapes. In some cases the sides are smoothly rounded, in some the shape is trapezoidal, and in others the sides are produced as acute, angular ("conulate") projections.

Measurements. HL: head length; in full-face view, maximum length of head, from line tangent to anteriormost projection of head capsule or clypeus to line tangent to posteriormost projection of vertex margin (including occipital carina, if visible).

HW: head width; in full-face view, maximum width of head capsule **not including eyes** (if eyes protrude beyond margins of head, measured above or below eyes, depending on which is widest).

SL: scape length; length of scape shaft from apex to basal flange, not including basal condyle and neck.

EL: eye length; maximum length of compound eye, with head oriented to maximize length (i.e., not full-face view).

WL: mesosoma length (Weber's length); in lateral view, distance from base of anterior face of pronotum (at inflection point between downward-sloping anterior face and flange-like anteriormost projection of pronotum [the latter extending to foramen and usually partially hidden by head capsule]) to posteriormost extension of metapleural or propodeal lobes (whichever extends further).

PSL: propodeal spine length; viewed laterally such that side of spine is roughly perpendicular to viewing angle, distance from inflection point between dorsal face of propodeum and base of spine to tip of spine.

PTW: petiole width; maximum width of petiole in dorsal view.

PPW: postpetiole width; maximum width of postpetiole in dorsal view.

CI: cephalic index; 100*HW/HL.

SI: scape index; 100*SL/HW.

PSLI: propodeal spine index; 100*PSL/HL.

PPI: Postpetiole index; 100*PPW/PTW.

Identification. The characters and measurements described above are multiple axes that define a multidimensional morphology space, and the hundreds of *Pheidole* species somewhat uniformly fill that space. An approach to identification is to use a species x character matrix that allows one to locate species that are close together in character space. An example of software that provides for the construction of matrix keys is Lucid (www.lucidcentral.com). I have made a character matrix for all New World *Pheidole* species, using the data format of Lucid. The data matrix and instructions for importing it into Lucid are available at https://sites.google.com/site/newworldpheidole. The limited set of characters are not designed to identify every species but instead to narrow the search, after which other resources such as species descriptions, web-based species pages, and image libraries can be consulted.

Six primary measurements - HL, HW, and SL for each of the two worker castes - are highly effective for locating species in morphology space. When many specimens are measured for a "species" in the narrowest sense (a COI cluster of < 3% divergence, with specimens morphologically similar and not showing any signs of bimodality in characters), the coefficient of variation (ratio of standard deviation to the mean) is often ~5%. Thus, most individuals of a species can be expected to be within a range of plus or minus 10% of the mean. The character matrix described above incorporates this bracketing of measurements.

In this work an identification guide is provided in the form of a series of plates that organize species from smallest to largest, based on average minor worker HW. Within HW values, species are sorted by SI (scape index). Each species displays HW, SI, habitat preference, microhabitat summary, images showing three standard views

(minor lateral, minor face, major face), and a distribution map based on material I have examined. Note that the maps only show the region of the study and not the full range of each species. Habitat preference encapsulates elevational, moisture, and disturbance gradients. Species can typically be assigned to one of three major elevational zones: lowland (0-1000 m), montane (1000-2000 m), and high montane (> 2000 m). Moisture gradients go from wet (rainforest, cloud forest) to moist (moderately seasonal but evergreen forest) to dry (strongly seasonal dry forest). To use the guide to identify a collection, one can measure HW and SI of a minor worker and go to that HW in the guide. Working up and down from there, to plus or minus 10% of the value, one can make a list of potential species based on SI, geographic range, and general appearance. Other resources such as AntWeb (additional images and specimen records) and diagnostic notes in original descriptions can then be used to further support a particular identification.

Methods

Observations were made at 63x magnification with a Leica MZ12.5 dissecting microscope. Measurements were made with a dual-axis micrometer stage with output in increments of 0.001 mm. However, variation in specimen orientation, alignment of crosshairs with edges of structures, and interpretation of structure boundaries resulted in measurement accuracy to the nearest 0.02 to 0.005mm, depending on sharpness of the defined boundary. All measurements are presented to the nearest 0.01 mm.

Species were determined as new by using the matrix key to locate all morphologically similar species and then comparing each one, using additional characters, evidence of sympatry, and in some cases COI data (the mitochondrial "DNA Barcode," Ratnasingham and Hebert 2007). COI data were obtained from the Barcode of Life Data System (BOLD) database (http://www.boldsystems.org). In new species descriptions, the diagnosis is a combination of (1) a brief text description of key morphological features, (2) measurements, and (3) differentiating features of similar species. Measurements are means and can be expected to show plus or minus 10% variability. New species are only described when both minor and major workers are available and there is sufficient material from one population to provide an adequate type series to distribute to multiple institutions.

All holotypes and paratypes associated with the new species described here have unique specimen-level identifiers ("specimen codes") affixed to each pin. Specimen codes may have been provided by particular institutions and thus bear their prefix (e.g., "CASENT" for codes provided by the California Academy of Sciences), but specimen codes do not imply ownership and are meant to be permanent identifiers independent of the institution to which they belong. In species descriptions, specimen codes are listed only for holotypes; codes for other specimens can be found on AntWeb. Specimen codes should not be confused with collection codes, which are associated with particular collection events. Many different specimens can have the same collection code. When reported, collection codes follow the collector. Latitude and longitude are reported in decimal degrees followed by an error term. Specimen collection data are derived from a specimen database and are not direct transcriptions of labels. Images of holotypes, distribution maps, and all specimen data on which this paper is based are available on AntWeb (www.antweb.org). Composite images were created using Leica Application Suite V3.7 from source images captured using a Leica Z16 APO stereomicroscope coupled with a Leica DCF450 camera. All images were edited in Adobe Photoshop CS6 (Adobe Systems Inc., California, USA). Distribution maps were plotted with SimpleMappr (Shorthouse 2010). Specimen codes of imaged specimens in identification plates are in Table 1.

Repositories. Collections are referred to by the following acronyms:

BMNH	The Natural History Museum, London, U.K.
CAS	California Academy of Sciences, San Francisco, CA, USA.
DZUP	Museu de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.
JTLC	John T. Longino, personal collection, Olympia, WA, USA.
MCSN	Museo Civico de Storia Naturale "Giacomo Doria," Genoa, Italy.
MCZC	Museum of Comparative Zoology, Cambridge, MA, USA.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland.
NHMW	Naturhistorisches Museum, Vienna, Austria.

MUCR Universidad de Costa Rica, San Pedro, Costa Rica.
UNAM Universidad Nacional Autonoma de Mexico, Mexico D. F., Mexico.
USNM National Museum of Natural History, Washington, DC, USA.
UVGC Colleción de Artrópodos, Universidad del Valle de Guatemala, Guatemala City, Guatemala.

Synoptic List

* Species with comments in Taxonomic Section, but no nomenclatorial change.
** Species poorly known; not in identification guide. *Pheidole confoedusta* is known from one major worker from Xalapa, Veracruz, Mexico. *Pheidole defecta* is known from one major worker from an unspecified site in Guatemala. *Pheidole tillandsiarum* was collected in epiphytes in Veracruz, Mexico and could be *P. flavens* or *P. navigans*.

absurda Forel 1886
= *ridicula* Wheeler 1916
acamata Wilson 2003
agricola Wilson 2003
ajax Forel 1899
ajaxigibba **New Species**
albipes Wilson 2003
alfaroi Emery 1896
amabilis Wilson 2003
anastasii Emery 1896
andersoni **New Species**
angulifera Wilson 2003
angusticeps Wilson 2003
= *gradifer* Wilson 2003
angustinigra **New Species**
anima Wilson 2003
arachnion Wilson 2003
= *iracunda* Wilson 2003
arboricola Wilson 2003
arhuaca Forel 1901
= *bimons* Forel 1912
atitlana **New Species**
balatro **New Species**
beloceps Wilson 2003
belonorte **New Species**
besalon **New Species**
biconstricta Mayr 1870
= *bicolor* Emery 1890
= *burtoni* Mann 1916
= *festata* Wheeler 1925
= *holmgreni* Wheeler 1925
= *hybrida* Emery 1894
= *inermis* Mayr 1870 **New Synonym**
= *lallemandi* Forel 1901
= *rubicunda* Emery 1890
= *surda* Forel 1912
bicornis Forel 1899
bicornisculpta **New Species**
bigote Longino 2009
bilimeki Mayr 1870

= *annectens* Wheeler 1905
= *antoniensis* Forel 1901
= *ares* Forel 1908
= *cellarum* Forel 1908
= *deplanata* Pergande 1896
= *insulana* Wheeler 1905
= *johnsoni* Wheeler 1907
= *lauta* Wheeler 1908
= *rectiluma* Wilson 2003
= *venezuelana* Forel 1905
biolleyi Forel 1908 *
= *tristani* Forel 1908
boliviana Wilson 2003
= *mincana* Wilson 2003
= *scitula* Wilson 2003
boltoni Wilson 2003
= *humida* Wilson 2003
boruca Wilson 2003
brachyops Wilson 2003
brandaoi Wilson 2003
branstetteri Longino 2009
brownampla **New Species**
browni Wilson 2003
bucculenta Forel 1908
cahui **New Species**
caliginosa **New Species**
carapuna Mann 1916
= *chaquimayensis* Wheeler 1925
= *tristicula* Wilson 2003 **New Synonym**
carinata Wilson 2003
carinitida **New Species**
carinote Longino 2009
cataphracta Wilson 2003
caulicola Wilson 2003
ceibana Wilson 2003
celaena Wilson 2003
centeotl Wheeler 1914
cerina Wilson 2003
chalca Wheeler 1914
chocoensis Wilson 2003
christopherseni Forel 1912
citrina Wilson 2003
colobopsis Mann 1916
confoedusta Wheeler 1909 **
corniclypeus **New Species**
costaricensis **New Species**
cramptoni Wheeler 1916
= *petiolicola* Wheeler 1921
cusuco **New Species**
daphne Wilson 2003
dasypyx Wilson 2003
debilis Longino 2009

deceptrix Forel 1899
= *chiapasana* Wilson 2003
= *variceps* Wilson 2003
defecta Santschi 1923 **
depressinoda **New Species**
diabolus Wilson 2003
diana Forel 1908
dossena Wilson 2003
dryas Wilson 2003
ectatommoides Wilson 2003
eosimilis **New Species**
eowilsoni Longino 2009
epiphyta Longino 2009
erratilis Wilson 2003
= *petersoni* Wilson 2003
exarata Emery 1896
= *grantae* Forel 1908
excubitor Wilson 2003
fallax Mayr 1870
= *britoi* Forel 1912
= *colombica* Forel 1886
= *fallacior* Forel 1901
= *ovalis* Forel 1912
= *rubens* Forel 1899
familiaparra **New Species**
fimbriata Roger 1863
= *diversa* Smith 1860
= *soesilae* Makhan 2007 **New Synonym**
= *tucumana* Forel 1913
fincanaranjo **New Species**
fiorii Emery 1890
flavens Roger 1863
= *aechmeae* Wheeler 1934
= *gracilior* Forel 1901
= *greggi* Naves 1985
= *haytiana* Forel 1907
= *spei* Santschi 1930
= *tuberculata* Mayr 1887
= *vincentensis* Forel 1893
floricola Wilson 2003
fossimandibula Longino 2009
gauthieri Forel 1901
= *oxymora* Forel 1912
glomericeps Wilson 2003
gouldi Forel 1886
guerrerana Wilson 2003
gulo Wilson 2003 *
gymnoceras Longino 2009
hansoni **New Species**
harrisonfordi Wilson 2003
= *prolixa* Wilson 2003
= *ruida* Wilson 2003

= *tenebra* Wilson 2003
hasticeps Wilson 2003
hazenae Wilson 2003
hector Wilson 2003
hectornitida **New Species**
hirsuta Emery 1896
hitoy **New Species**
hizemops Wilson 2003
hoelldobleri Wilson 2003
huarache **New Species**
imbrilis **New Species**
indagarama **New Species**
indagatrix Wilson 2003
innupta Menozzi 1931
insipida Forel 1899
= *fariasana* Wilson 2003 **New Synonym**
= *mooreorum* Wilson 2003 **New Synonym**
janzeni Longino 2009
jelskii Mayr 1884
= *emiliae* Forel 1901
= *antillensis* Forel 1901
= *arenicola* Emery 1894
karolmorae Longino 2009
karolsetosa Longino 2009
kasparii **New Species**
kelainos **New Species**
kukrana Wilson 2003
laelaps Wilson 2003
lagunculiminor **New Species**
lagunculinoda Longino 2009
lamancha **New Species**
laselva Wilson 2003
= *ebenina* Wilson 2003
laselvoides **New Species**
leoncortesi Longino 2009
lineafrons **New Species**
longinoi Wilson 2003
longiscapa Forel 1901
= *cocciphaga* Borgmeier 1934 **New Synonym**
= *martensis* Forel 1914
lourothi Wilson 2003
lucaris Wilson 2003
lustrata Wilson 2003
luteagossamer **New Species**
machaquila **New Species**
mackayi Wilson 2003
maja Forel 1886
mallota Wilson 2003
mantilla Wilson 2003
marmor **New Species**
megacephala (Fabricius 1793)
[synonymy not shown]

mendicula Wheeler 1925
mesomontana Longino 2009
monteverdensis Wilson 2003
moskitia **New Species**
multispina Wilson 2003
muralla **New Species**
musacolor **New Species**
musinermis **New Species**
nasutoides Holldobler and Wilson 1992
natalie **New Species**
navigans Forel 1901
nebulosa Wilson 2003
= *scabriventris* Wilson 2003
nephele **New Species**
nigella Emery 1894
= *dimidiata* Emery 1894
nigricula Wilson 2003
nitella Wilson 2003
nitidicollis Emery 1896
= *chalcoides* Wilson 2003 **New Synonym**
= *sagana* Wheeler 1934
nubicola Wilson 2003
= *cielana* Wilson 2003 **New Synonym**
= *petrensis* Wilson 2003 **New Synonym**
oaxacana Wilson 2003
obturaculum **New Species**
olsoni Wilson 2003
onyx Wilson 2003
otisi Wilson 2003
pararugiceps Longino 2009
passivaeferox **New Species**
perissothrix **New Species**
perpusilla Emery 1894
= *breviscapa* Forel 1899
= *decem* Forel 1901
= *emersoni* Wheeler 1922
phanigaster Longino 2009
piceonigra Emery 1922
picobarva Longino 2009
platyscapa **New Species**
plebecula Forel 1899
= *perdiligens* Wilson 2003 **New Synonym**
= *texticeps* Wilson 2003 **New Synonym**
potosiana Wilson 2003
prattorum Wilson 2003
probolonotum **New Species**
prostrata Wilson 2003
protensa Wilson 2003
psilogaster Wilson 2003
pubiventris Mayr 1887
= *indistincta* Forel 1899
= *cearensis* Forel 1901

= *nevadensis* Forel 1901
= *timmii* Forel 1901
= *variegata* Emery 1896
pugnax Dalla Torre 1892
punctatissima Mayr 1870
= *napaea* Wheeler 1934
purpurea Longino 2009
radoszkowskii Mayr 1884
= *acuta* Emery 1894
= *australis* Emery 1890
= *luteola* Forel 1893
= *medialis* Wilson 2003
= *opacissima* Forel 1901
= *paranana* Santschji 1925
= *parvinoda* Forel 1912
rectisentis Wilson 2003
rectispina Wilson 2003
rectitrudis Wilson 2003
renae Wilson 2003
rhinoceros Forel 1899
rhinomontana Longino 2009
rima **New Species**
rogeri Emery 1896
rogeripolita **New Species**
roushae Wilson 2003
rugiceps Wilson 2003
sabina Wilson 2003
sagittaria Wilson 2003
savegre **New Species**
scrobifera Emery 1896
sebofila Longino 2009
sensipelada **New Species**
sensitiva Borgmeier 1959
sepultura **New Species**
sicaria Wilson 2003 *
simonsi Wilson 2003
= *arctos* Wilson 2003 **New Synonym**
= *gangamon* Wilson 2003 **New Synonym**
= *thrasys* Wilson 2003 **New Synonym**
sparsisculpta Longino 2009
spathipilosa Wilson 2003
specularis Wilson 2003
striaticeps Mayr 1870
= *chloe* Forel 1908 **New Synonym**
stulta Forel 1886
= *championi* Forel 1899
= *sima* Forel 1912
subarmata Mayr 1884
= *borinquenensis* Wheeler 1908
= *cornutula* Emery 1890
= *dentimentum* Santschi 1929
= *elongatula* Forel 1893

= *hondurensis* Mann 1922
= *imbecillis* Emery 1906
= *nassavensis* Wheeler 1905
= *nefasta* Santschi 1929
susannae Forel 1886
= *atricolor* Forel 1901
= *evoluta* Borgmeier 1929
= *obscurior* Forel 1886
= *partita* Mayr 1887
synanthropica Longino 2009
synarmata Wilson 2003
tanyscapa Wilson 2003
tapanti **New Species**
tennantae Wilson 2003
tenuicephala Longino 2009
tikal **New Species**
tillandsiarum Wheeler, W.M. 1934 **
tinamu **New Species**
tisiphone Wheeler 1911
traini Wilson 2003
transversostriata Mayr 1887
= *lacerta* Wheeler 1922
= *nigridens* Forel 1901
= *scalaris* Wilson 2003 **New Synonym**
truncula Wilson 2003
tschinkeli Wilson 2003
tsontekonwei **New Species**
tuculutan **New Species**
tuxtlasana Wilson 2003
ulothrix Wilson 2003
umphreyi Wilson 2003
ursus Mayr 1870
= *cressoni* (André 1887)
= *gracilinoda* Forel 1904
vafra Santschi 1923
= *idiota* Santschi 1923
= *laticornis* Wilson 2003 **New Synonym**
vallifica Forel 1901
veletis Wilson 2003
verricula Wilson 2003
vestita Wilson 2003
violacea Wilson 2003
vorax (Fabricius 1804)
= *apterostigmoides* Weber 1943
= *cephalica* Smith 1858
= *incrustata* Forel 1908
= *opaca* Mayr 1862
= *sarrita* Forel 1908
walkeri Mann 1922
= *arietans* Wilson 2003
= *glyphoderma* Wilson 2003
= *triumbonata* Wilson 2003

wardi Wilson 2003
xiloa **New Species**
xyston Wilson 2003
zannia **New Species**

TABLE 1. Specimen codes of images in identification plates. All original images are on AntWeb, except major worker of *P. traini* and major and minor workers of *P. lourothi* and *P. verricula*, which are from the MCZ image database. AntWeb image credits: A. Nobile, B. Bartholomew, B. Boudinot, B. Broyles, D. Flocken, E. Ortega, E. Prado, J. Longino, J. Pillow, J. Russ, M. Esposito, M. Pierce, S. Bylsma, S. Hartman, S. Oswald, S. Ware, and Z. Lieberman.

species	minor face	minor profile	major face
absurda	CASENT0635430	CASENT0635430	CASENT0103139
acamata	JTLC000016314	JTLC000016314	JTLC000016315
agricola	CASENT0641073	CASENT0641073	CASENT0641074
ajax	INBIOCRI001280418	INBIOCRI001280418	INBIOCRI001280413
ajaxigibba	CASENT0638167	CASENT0638167	CASENT0638172
albipes	JTLC000009724	JTLC000009724	JTLC000010035
alfaroi	INB0003659308	INB0003659308	INB0003665062
amabilis	CASENT0610089	CASENT0610089	INBIOCRI002279941
anastasii	CASENT0619900	CASENT0619900	CASENT0613680
andersoni	CASENT0645180	CASENT0645180	CASENT0645179
angulifera	CASENT0610094	CASENT0610094	INBIOCRI001281572
angusticeps	JTLC000003294	JTLC000003294	JTLC000016320
angustinigra	CASENT0612853	CASENT0612853	CASENT0612769
anima	CASENT0610102	CASENT0610102	JTLC000016321
arachnion	INB0003213761	INB0003213761	INB0003622434
arboricola	CASENT0610092	CASENT0610092	INBIOCRI001218031
arhuaca	CASENT0610096	CASENT0610096	CASENT0610097
atitlana	CASENT0612670	CASENT0612670	CASENT0612671
balatro	CASENT0615088	CASENT0615088	CASENT0616276
beloceps	CASENT0625437	CASENT0625437	INBIOCRI001282094
belonorte	CASENT0609314	CASENT0609314	CASENT0609313
besalon	CASENT0631746	CASENT0631746	CASENT0631747
biconstricta	INBIOCRI002279529	INBIOCRI002279529	INBIOCRI002272024
bicornis	CASENT0635437	CASENT0635437	INBIOCRI001281880
bicornisculpta	CASENT0637204	CASENT0637204	CASENT0637206
bigote	JTLC000014969	JTLC000014969	CASENT0603300
bilimeki	JTLC000015322	JTLC000015322	JTLC000003345
biolleyi	CASENT0635438	CASENT0635438	INBIOCRI002272045
boliviana	CASENT0635439	CASENT0635439	CASENT0635440
boltoni	CASENT0624221	CASENT0624221	INBIOCRI002279980
boruca	CASENT0624232	CASENT0624232	INBIOCRI002279551
brachyops	CASENT0624234	CASENT0624234	INBIOCRI002279627
brandaoi	CASENT0611587	CASENT0611587	CASENT0611585
branstetteri	CASENT0609077	CASENT0609077	CASENT0609076
brownampla	CASENT0636683	CASENT0636683	CASENT0636682
browni	CASENT0644961	CASENT0644961	CASENT0644960

.....continued on the next page

TABLE 1. (Continued)

species	minor face	minor profile	major face
bucculenta	CASENT0624235	CASENT0624235	JTLC000016331
cahui	CASENT0611059	CASENT0611059	CASENT0611056
caliginosa	CASENT0632079	CASENT0632079	CASENT0631248
carapuna	CASENT0635448	CASENT0635448	INBIOCRI002279593
carinata	INB0003668047	INB0003668047	CASENT0635170
carinitida	CASENT0631619	CASENT0631619	CASENT0631620
carinote	JTLC000014049	JTLC000014049	JTLC000014045
cataphracta	CASENT0635450	CASENT0635450	INBIOCRI001282224
caulicola	CASENT0624250	CASENT0624250	INBIOCRI001282237
ceibana	CASENT0624251	CASENT0624251	JTLC000016343
celaena	CASENT0635452	CASENT0635452	INBIOCRI001238128
centeotl	CASENT0281761	CASENT0281761	CASENT0281760
cerina	INB0003604676	INB0003604676	INB0003604679
chalca	CASENT0631888	CASENT0631888	CASENT0631889
chocoensis	CASENT0624003	CASENT0624003	CASENT0619326
christopherseni	CASENT0612251	CASENT0612251	CASENT0612252
citrina	CASENT0623856	CASENT0623856	CASENT0624045
colobopsis	CASENT0619698	CASENT0619698	CASENT0619464
corniclypeus	CASENT0623852	CASENT0623852	CASENT0623849
costaricensis	CASENT0637142	CASENT0637142	CASENT0637143
cramptoni	CASENT0635457	CASENT0635457	INBIOCRI001282205
cusuco	CASENT0617764	CASENT0617764	CASENT0617763
daphne	INBIOCRI001231279	INBIOCRI001231279	INBIOCRI001230999
dasypyx	CASENT0627923	CASENT0627923	JTLC000016358
debilis	CASENT0608860	CASENT0608860	INB0003622662
deceptrix	CASENT0611123	CASENT0611123	CASENT0611124
depressinoda	CASENT0611610	CASENT0611610	CASENT0611611
diabolus	CASENT0635458	CASENT0635458	INBIOCRI001282176
diana	CASENT0635459	CASENT0635459	INBIOCRI001283476
dossena	CASENT0635460	CASENT0635460	INBIOCRI002279458
dryas	CASENT0644190	CASENT0644190	CASENT0644189
ectatommoides	CASENT0613731	CASENT0613731	CASENT0619909
eosimilis	CASENT0619639	CASENT0619639	CASENT0619392
eowilsoni	CASENT0608880	CASENT0608880	CASENT0608866
epiphyta	CASENT0608899	CASENT0608899	CASENT0608898
erratilis	CASENT0635462	CASENT0635462	INBIOCRI001282704
exarata	CASENT0635463	CASENT0635463	INBIOCRI001282197
excubitor	INB0003207486	INB0003207486	INB0003207483
fallax	CASENT0635464	CASENT0635464	INBIOCRI002279694
familiaparra	CASENT0631330	CASENT0631330	CASENT0631331
fimbriata	CASENT0178018	CASENT0178018	CASENT0235906
fincanaranjo	CASENT0632180	CASENT0632180	CASENT0632181

.....continued on the next page

TABLE 1. (Continued)

species	minor face	minor profile	major face
fiorii	CASENT0635466	CASENT0635466	INBIOCRI002279397
flavens	CASENT0635467	CASENT0635467	INBIOCRI002279782
floricola	CASENT0619559	CASENT0619559	CASENT0619558
fossimandibula	CASENT0608948	CASENT0608948	JTLC000007165
gauthieri	CASENT0635470	CASENT0635470	INBIOCRI001282212
glomericeps	JTLC000014003	JTLC000014003	JTLC000014002
gouldi	CASENT0635469	CASENT0635469	INBIOCRI002279354
guerrerana	CASENT0629401	CASENT0629401	CASENT0629400
gulo	CASENT0604487	CASENT0604487	CASENT0604488
gymnoceras	CASENT0608958	CASENT0608958	INB0003659251
hansoni	INBIOCRI001282783	INBIOCRI001282783	CASENT0636565
harrisonfordi	INBIOCRI001281896	INBIOCRI001281896	INBIOCRI001281891
hasticeps	CASENT0609377	CASENT0609377	CASENT0609378
hazenae	CASENT0635473	CASENT0635473	CASENT0635472
hector	CASENT0644173	CASENT0644173	CASENT0644172
hectornitida	CASENT0637216	CASENT0637216	CASENT0637217
hirsuta	CASENT0635475	CASENT0635475	CASENT0635474
hitoy	CASENT0636895	CASENT0636895	CASENT0644296
hizemops	INBIOCRI001283057	INBIOCRI001283057	INBIOCRI001283056
hoelldobleri	CASENT0635476	CASENT0635476	INBIOCRI002281892
huarache	CASENT0611594	CASENT0611594	CASENT0611593
imbrilis	CASENT0637138	CASENT0637138	CASENT0637137
indagarama	INBIOCRI002281912	INBIOCRI002281912	CASENT0636566
indagatrix	CASENT0635478	CASENT0635478	INBIOCRI002272029
innupta	CASENT0635479	CASENT0635479	JTLC000001496
insipida	CASENT0609201	CASENT0609201	CASENT0609200
janzeni	CASENT0608993	JTLC000007093	CASENT0608973
jelskii	CASENT0178032	CASENT0178032	CASENT0178031
karolmorae	CASENT0608995	CASENT0608995	INBIOCRI002279843
karolsetosa	CASENT0609024	CASENT0609024	INBIOCRI002279842
kasparii	CASENT0637175	CASENT0637175	CASENT0637174
kelainos	CASENT0646303	CASENT0646303	CASENT0646308
kukrana	CASENT0624444	CASENT0624444	CASENT0624445
laelaps	CASENT0645810	CASENT0645810	JTLC000016423
lagunculiminor	CASENT0610937	CASENT0610937	CASENT0610935
lagunculinoda	CASENT0609878	CASENT0609878	CASENT0609553
lamancha	CASENT0641070	CASENT0641070	CASENT0641071
laselva	CASENT0619411	CASENT0619411	CASENT0619410
laselvoides	CASENT0635481	CASENT0635481	INBIOCRI002279737
leoncortesi	CASENT0609115	CASENT0609115	CASENT0609134
lineafrons	CASENT0644874	CASENT0644874	CASENT0644875
longinoi	CASENT0635483	CASENT0635483	INBIOCRI001281901

.....continued on the next page

TABLE 1. (Continued)

species	minor face	minor profile	major face
longiscapa	CASENT0625349	CASENT0625349	CASENT0625352
lourothi	LACMENT141832	LACMENT141832	LACMENT141832
lucaris	CASENT0635484	CASENT0635484	INBIOCRI001218047
lustrata	CASENT0644963	CASENT0644963	INBIOCRI001281956
luteagossamer	CASENT0628293	CASENT0628293	CASENT0628292
machaquila	CASENT0614275	CASENT0614275	CASENT0614273
mackayi	JTLC000007340	JTLC000007340	JTLC000007339
maja	JTLC000015319	JTLC000015319	JTLC000015318
mallota	CASENT0631379	CASENT0631379	CASENT0631380
mantilla	CASENT0646670	CASENT0646670	INBIOCRI002279466
marmor	JTLC000009812	JTLC000009812	JTLC000009834
megacephala	CASENT0056016	CASENT0056016	CASENT0104990
mendicula	CASENT0635488	CASENT0635488	INBIOCRI002279723
mesomontana	CASENT0609005	CASENT0609005	INB0003214187
monteverdensis	CASENT0635489	CASENT0635489	INBIOCRI002279752
moskitia	CASENT0612083	CASENT0612083	CASENT0612085
multispina	CASENT0635492	CASENT0635492	INBIOCRI002279766
muralla	CASENT0615596	CASENT0615596	CASENT0615595
musacolor	CASENT0636692	CASENT0636692	CASENT0636691
musinermis	CASENT0631279	CASENT0631279	CASENT0631280
nasutoides	CASENT0635495	CASENT0635495	CASENT0635494
natalie	CASENT0628204	CASENT0628204	CASENT0628205
navigans	CASENT0104526	CASENT0104526	CASENT0104525
nebulosa	CASENT0635497	CASENT0635497	INBIOCRI001237483
nephele	CASENT0609969	CASENT0609969	CASENT0609968
nigella	JTLC000014444	JTLC000014444	JTLC000014443
nigricula	CASENT0635498	CASENT0635498	INBIOCRI002279729
nitella	CASENT0635499	CASENT0635499	INBIOCRI001282703
nitidicollis	CASENT0635500	CASENT0635500	INBIOCRI001218677
nubicola	CASENT0640820	CASENT0640820	CASENT0640821
oaxacana	CASENT0612754	CASENT0612754	CASENT0612755
obturaculum	CASENT0640872	CASENT0640872	CASENT0640871
olsoni	INB0003213400	INB0003213400	INB0003211782
onyx	CASENT0635501	CASENT0635501	INBIOCRI002281490
otisi	CASENT0635502	CASENT0635502	INBIOCRI002279779
pararugiceps	INB0003210732	INB0003210732	INB0003213441
passivaeferox	CASENT0625443	CASENT0625443	INBIOCRI002279624
perissothrix	CASENT0611501	CASENT0611501	CASENT0611573
perpusilla	CASENT0635503	CASENT0635503	INBIOCRI001218647
phanigaster	CASENT0609108	CASENT0609108	CASENT0609087
piceonigra	CASENT0601284	CASENT0601283	CASENT0601284
picobarva	CASENT0610055	CASENT0610055	CASENT0610059

.....continued on the next page

TABLE 1. (Continued)

species	minor face	minor profile	major face
platyscapa	CASENT0619607	CASENT0619607	CASENT0619339
plebecula	CASENT0635536	CASENT0635536	INBIOCRI002279634
potosiana	CASENT0609506	CASENT0609506	CASENT0609503
prattorum	CASENT0635505	CASENT0635505	JTLC000003456
probolonotum	CASENT0631750	CASENT0631750	CASENT0631751
prostrata	CASENT0635506	CASENT0635506	INBIOCRI001282579
protensa	CASENT0635507	CASENT0635507	JTLC000006302
psilogaster	CASENT0635508	CASENT0635508	INBIOCRI001243032
pubiventris	JTLC000007354	JTLC000007354	JTLC000007355
pugnax	CASENT0635513	CASENT0635513	CASENT0635512
punctatissima	CASENT0619442	CASENT0619442	CASENT0619681
purpurea	CASENT0609144	CASENT0609144	CASENT0609143
radoszkowskii	CASENT0766183	CASENT0766183	CASENT0318453
rectisentis	CASENT0624140	CASENT0624140	CASENT0624141
rectispina	CASENT0635516	CASENT0635516	INBIOCRI001242943
rectitrudis	CASENT0635517	CASENT0635517	INBIOCRI002272038
renae	CASENT0644959	CASENT0644959	INBIOCRI001282061
rhinoceros	CASENT0635518	CASENT0635518	JTLC000002907
rhinomontana	CASENT0610083	CASENT0610083	CASENT0610082
rima	CASENT0633307	CASENT0633307	CASENT0633308
rogeri	CASENT0635519	CASENT0635519	INBIOCRI001282986
rogeripolita	JTLC000006466	JTLC000006466	CASENT0636564
roushae	CASENT0610899	CASENT0610899	CASENT0610898
rugiceps	CASENT0635520	CASENT0635520	INBIOCRI002279971
sabina	CASENT0645862	CASENT0645862	CASENT0645864
sagittaria	CASENT0635521	CASENT0635521	INBIOCRI002279739
savegre	CASENT0646331	CASENT0646331	CASENT0646332
scrobifera	CASENT0635523	CASENT0635523	INBIOCRI002281993
sebofila	CASENT0610095	CASENT0610095	INBIOCRI001282230
sensipelada	CASENT0631274	CASENT0631274	CASENT0631275
sensitiva	CASENT0635525	CASENT0635525	INBIOCRI001242794
sepultura	JTLC000014192	JTLC000014192	JTLC000014191
sicaria	CASENT0635526	CASENT0635526	INBIOCRI002281990
simonsi	CASENT0635528	CASENT0635528	INBIOCRI001237520
sparsisculpta	INB0003214413	INB0003214413	INB0003214434
spathipilosa	CASENT0635530	CASENT0635530	INBIOCRI001218131
specularis	CASENT0635480	CASENT0635480	INB0003659292
striaticeps	CASENT0635532	CASENT0635532	JTLC000002903
stulta	JTLC000014071	JTLC000014071	JTLC000014070
subarmata	CASENT0635533	CASENT0635533	INBIOCRI001281170
susannae	CASENT0635534	CASENT0635534	INBIOCRI001283041
synanthropica	CASENT0609038	CASENT0609038	CASENT0609037

.....continued on the next page

TABLE 1. (Continued)

species	minor face	minor profile	major face
synarmata	INBIOCRI002728547	INBIOCRI002728547	INBIOCRI002728510
tanyscapa	INB0003696373	INB0003696373	INB0003696376
tapanti	CASENT0637803	CASENT0637803	CASENT0637804
tennantae	CASENT0635535	CASENT0635535	INBIOCRI001242645
tenuicephala	CASENT0609055	CASENT0609055	CASENT0609054
tikal	CASENT0645182	CASENT0645182	CASENT0645181
tinamu	CASENT0646317	CASENT0646317	CASENT0646320
tisiphone	CASENT0611632	CASENT0611632	CASENT0611633
traini	MEKOU221454	MEKOU221454	holotype
transversostriata	CASENT0635522	CASENT0635522	INBIOCRI002279609
truncula	CASENT0635537	CASENT0635537	INBIOCRI001283920
tschinkeli	CASENT0610637	CASENT0610637	CASENT0610639
tsontekonwei	CASENT0624314	CASENT0624314	CASENT0624331
tuculutan	CASENT0612788	CASENT0612788	CASENT0612794
tuxtlasana	CASENT0645885	CASENT0640546	JTLC000016564
ulothrix	CASENT0635538	CASENT0635538	INBIOCRI002279936
umphreyi	CASENT0636802	CASENT0636802	INBIOCRI002279630
ursus	INBIOCRI001280928	INBIOCRI001280928	CASENT0919789
vafra	CASENT0635482	CASENT0635482	INBIOCRI001282718
vallifica	CASENT0635691	CASENT0635691	CASENT0635689
veletis	CASENT0645891	CASENT0645891	JTLC000016570
verricula	paratype	paratype	holotype
vestita	CASENT0635539	CASENT0635539	INBIOCRI002272032
violacea	CASENT0635545	CASENT0635545	JTLC000001485
vorax	CASENT0635540	CASENT0635540	INBIOCRI002279426
walkeri	CASENT0610099	CASENT0610099	CASENT0610100
wardi	CASENT0617188	CASENT0617188	CASENT0617187
xiloa	CASENT0619379	CASENT0619379	CASENT0619635
xyston	CASENT0640900	CASENT0640900	CASENT0640897
zannia	CASENT0615627	CASENT0615627	CASENT0615634

Taxonomic Section

Pheidole ajaxigibba new species

(Plate 51)

Pheidole JTL-223: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Puntarenas: Sirena, Corcovado NP, 8.48067 -83.58885 ±1 km, 25 m, 29-Jun-2013, rainforest, nest in dead wood (J. Longino, JTL8286.1) [MUCR, unique specimen identifier CASENT0638172]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, MCZC, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head tapered posteriorly to narrow neck and strongly developed occipital carina; promesonotal groove deep and broad; mesonotum strongly protruding in lateral view; pronotum smooth and shining; katepisternum with faint foveolation and strong longitudinal rugulae; propodeal spines long,

thin, about as long as posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal and gastral dorsum, tibiae; color yellow orange. ***Major***: inner hypostomal teeth widely spaced, in form of small, inconspicuous denticles; scape base terete; face with foveolation overlain with reticulate rugulae throughout, these becoming more longitudinally oriented posteriorly; propodeal spines about two thirds length of posterior face of propodeum; gastral dorsum sericeous/striolate on anterior two thirds, fading to smooth and shiny posteriorly; face and sides of head covered with dense, decumbent, somewhat silky pubescence; abundant erect setae on mesosomal and gastral dorsum, tibiae.

Measurements, minor worker: HW 0.65, HL 0.89, SL 1.29, EL 0.15, WL 1.22, PSL 0.23, PTW 0.12, PPW 0.20, CI 73, SI 197, PSLI 35, PPI 161 (n=4).

Measurements, major worker: HW 1.38, HL 1.43, SL 1.23, EL 0.21, WL 1.57, PSL 0.24, PTW 0.23, PPW 0.37, CI 96, SI 89, PSLI 18, PPI 161 (n=4).

Biology. This species occurs in lowland rain forest. A nest was collected in dead wood, in a dead horizontal tree trunk about 1 m above the ground. Minor workers have been collected in beating samples from low vegetation and in a Malaise trap.

Comments. This species and *P. ajax* are similar. *Pheidole ajaxigibba* differs in the much more produced mesonotum and the bright yellow color. It is allopatric with *P. ajax*, the two appearing to be complementary forms on the two sides of Costa Rica.

Etymology: Similar to *P. ajax* but with more pronounced mesonotum.

Pheidole andersoni **new species**
(Plate 12)

Pheidole JTL-230: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Chiapas: 19km ENE Tonalá, 16.15630 -93.59920 ±100 m, 1250 m, 15-Jul-2007, second growth wet forest, nest in clay soil (J. Longino, JTL6054) [UNAM, unique specimen identifier CASENT0645179]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, UNAM, USNM].

Geographic range. Mexico (Chiapas), Guatemala.

Diagnosis. ***Minor***: face and mesosoma foveolate, with foveolation faint to absent on lower half of katepisternum; promesonotal groove absent; propodeal spines one fourth to one fifth length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum and gaster; tibiae with 2-3 erect setae; color orange. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; face with distinct scrobes, delimited dorsally by frontal carinae and forming concave trough below them, ventral and posterior margins less delimited, surface of scrobe smooth and shiny; head weakly depressed posteriorly; face surface generally shiny, space between frontal carinae smooth, space between eye and antennal fossa and vertex lobes with widely separated, subparallel, longitudinal carinae; propodeal spines one half length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.45, HL 0.49, SL 0.41, EL 0.10, WL 0.56, PSL 0.03, PTW 0.08, PPW 0.14, CI 91, SI 93, PSLI 6, PPI 168 (n=5).

Measurements, major worker: HW 0.81, HL 0.98, SL 0.44, EL 0.14, WL 0.82, PSL 0.07, PTW 0.19, PPW 0.33, CI 83, SI 54, PSLI 8, PPI 176 (n=5).

Biology. This species occurs in cloud forest habitats. Minor and major workers recruit to baits on the forest floor and occur in Winkler samples. Two nests have been observed. One was in a vertical clay bank at a trail edge. A small cylindrical clay turret extended horizontally from the bank, 5-10 mm long and 3-4 mm wide. A major worker was at the entrance. A partial excavation revealed a chamber a few cm deep with many minor and major workers. A second nest was in bare soil of a road in a coffee farm (no further observation details).

Comments. A set of species occurs from the southern U.S.A. to Costa Rica that share a habitus. The minor workers of most species are similar to the common *P. flavens* and thus easily escape detection in mixed samples and samples without major workers. The major workers have subrectangular heads, HW is in the 0.7-1.0 range, the antennae are short (SI 40-55), the antennal scrobes are well marked, the frontal carinae are expanded to form the

pronounced dorsal margin of the scrobes, the face is generally shiny with widely separated longitudinal carinae distributed in various ways, the vertex lobes are pronounced and with a deep posterior sinus separating them, and in profile the posterior part of the head is often compressed. Most species are orange, but *P. zannia* in Honduras appears to be in a mimicry complex and has divergent harlequin color, with black head and gaster and sharply contrasting orange mesosoma. This species also has the minor worker face smooth and shiny rather than foveolate. All of the species appear to nest in soil.

The species are distributed in a mosaic across Middle America, with various degrees of allopatry, parapatry, and narrow sympatry. *Pheidole mera* is known from south Texas in the U.S.A. *Pheidole andersoni* is a cloud forest species in the Sierra Madre de Chiapas and adjacent parts of Guatemala. *Pheidole tikal* is in the Petén region of Guatemala. *Pheidole zannia* occurs in cloud forests of central Honduras. *Pheidole natalie* has a somewhat disjointed distribution, with morphologically very similar populations in cloud forests of southern Mexico (Oaxaca), northern Honduras (Cusuco), and Nicaragua. *Pheidole corniclypeus* occurs in lowland rainforests in eastern Honduras, Nicaragua, and possibly into northeastern Costa Rica. *Pheidole costaricensis* occurs in lowland to lower montane wet forest in Costa Rica, and there is the potential for another lowland Pacific slope species in Costa Rica. The one well-documented case of sympatry is the co-occurrence of *P. natalie* and *P. corniclypeus* on one mountainside in central Nicaragua.

Etymology: In honor of Bob Anderson, Coleopterist, who has contributed so much to Neotropical myrmecology.

Pheidole angustinigra **new species**
(Plate 15)

Pheidole JTL-200: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Zacapa: 7.5km NE Teculután, 15.04367 -89.67501 ±200 m, 475 m, 28-Jun-2009, grassy slope, at bait (J. Longino, JTL6776-s) [MCZC, unique specimen identifier CASENT0612769]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC, USNM, UVGC]; same data except JTL6787-s [DZUP]; same data except JTL6788-s [JTLC].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face foveolate; promesonotal groove distinct, impressed; entire mesosoma foveolate; propodeal spines about one half length of posterior face of propodeum; gaster shagreened on anterior half, rest smooth and shining; mesosomal dorsum and gaster with abundant, short, stiff setae; tibiae without erect setae; color dark brown to black. ***Major***: inner hypostomal teeth absent; scape base terete; space between eye and antennal fossa foveolate, overlain with rugulae; medial frons between frontal carinae foveolate, overlain with fine, longitudinal carinulae; rest of face smooth and shining; propodeal spines about one half length of posterior face of propodeum; gastral dorsum shagreened on anterior half, fading to smooth and shining posteriorly; sides of head lacking erect setae; other pilosity similar to minor worker; color dark brown.

Measurements, minor worker: HW 0.46, HL 0.55, SL 0.58, EL 0.13, WL 0.69, PSL 0.04, PTW 0.09, PPW 0.14, CI 85, SI 126, PSLI 10, PPI 154 (n=2).

Measurements, major worker: HW 0.91, HL 0.98, SL 0.62, EL 0.15, WL 0.84, PSL 0.07, PTW 0.15, PPW 0.23, CI 92, SI 68, PSLI 9, PPI 152 (n=3).

Biology. This species is known from one site in Guatemala. It was an area of dry scrub habitat. Minor and major workers recruited to multiple ground baits placed on a grassy slope and in a stream gully.

Comments. In Economo *et al.* (2019) this species (as JTL200) is very close to *P. angusticeps*. The measurements and general habitus are similar, but the species differ strongly in color of the minors and majors (black vs. orange) and the sculpture of the major face (mostly smooth and shiny vs. entirely foveolate).

Etymology: Related to *P. angusticeps*, with black color.

Pheidole atitlana **new species**
(Plate 32)

Pheidole JTL-195: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Suchitepéquez: 3km S Vol. Atitlán, 14.55383 -91.1932 ±14 m, 1790 m, 16-Jun-2009, cloud forest, at bait on ground (J. Longino, JTL6720-s) [MCZC, unique specimen identifier CASENT0612671]. PARATYPES: major, minor workers: same data as holotype [JTLC, MCZC]; same data except 4km S Vol. Atitlán, 14.54826 -91.19294 ±56 m, 1575 m (LLAMA, Ba-B-09-2-04-01) [CAS]; Volcán Atitlán, 9.5km SE Santiago Atitlán, 14.55838 -91.19133 ±100 m, 2015 m, 10-Sep-2008, cloud forest, ex sifted leaf litter (M. G. Branstetter, MGB932) [UVGC]; Refugio El Quetzal, 14.55483 -91.19299 ±50 m, 1838 m, 15-Jun-2009, oak forest, ex sifted leaf litter (R. S. Anderson, RSA2009-102) [USNM].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face foveolate, overlain with faint reticulate rugulae; promesonotum box-like, promesonotal groove weakly impressed; entire mesosoma foveolate, dorsal pronotum overlain with reticulate rugulae; propodeal spines about one half length of posterior face of propodeum; gaster smooth and shining; mesosomal dorsum and gaster with abundant, flexuous setae; tibiae with abundant, short, suberect setae (not differentiated into appressed pubescence and standing setae); color dark red brown. ***Major***: inner hypostomal teeth distinct, closely-spaced; scape base terete; face entirely foveolate, overlain throughout with weak reticulate rugulae; propodeal spines about one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae, other pilosity similar to minor worker.

Measurements, minor worker: HW 0.55, HL 0.60, SL 0.55, EL 0.11, WL 0.73, PSL 0.08, PTW 0.10, PPW 0.18, CI 92, SI 99, PSLI 14, PPI 175 (n=5).

Measurements, major worker: HW 1.17, HL 1.24, SL 0.62, EL 0.15, WL 1.00, PSL 0.09, PTW 0.17, PPW 0.42, CI 95, SI 53, PSLI 8, PPI 251 (n=2).

Measurements, queen: HW 1.09, HL 0.93, SL 0.60, EL 0.29, WL 1.54, PSL 0.10, PTW 0.26, PPW 0.61, CI 118, SI 55, PSLI 9, PPI 237 (n=1).

Biology. This species is known from one locality, in mature cloud forest on the slopes of Volcán Atitlán, between 1500-2100 m elevation. Workers occur at ground baits and in Winkler samples of sifted litter and rotten wood. A dealate queen was collected in a Winkler sample.

Comments. *Pheidole atitlana* is part of a clade that contains *P. rectitrudis*, *P. beloceps*, and others (Economo *et al.* 2019, as JTL195).

Etymology: From the type locality.

Pheidole balatro **new species**
(Plate 12)

Pheidole JTL-158: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Olancho: 9km N Catacamas, 14.93492 -85.90708, ±50 m, 1350 m, 11 May 2010, mixed hardwood forest, at bait (Project LLAMA Ba-C-02-2-02-05) [CAS, unique specimen identifier CASENT0635416]. PARATYPES: major, minor workers: same data as holotype [CAS, JTLC]; same data except 14.93627 -85.90477, ±50 m, 1330 m, 10 May 2010, second growth mixed hardwood forest, at bait (Project LLAMA Ba-C-02-3-01-01) [DZUP, JTLC, MCZC, USNM].

Geographic range. Guatemala, Honduras, Costa Rica.

Diagnosis. ***Minor***: face smooth and shiny; posterior margin of head mostly rounded with small medial emargination in face view; promesonotal groove absent; dorsal and lateral pronotum smooth and shiny; mesonotum and dorsal propodeum faintly foveolate; katepisternum mostly smooth and shiny, with strip of foveolation posteriorly; propodeal spines spiniform, about one third length of posterior face of propodeum; gaster smooth and shining; erect setae on mesosomal dorsum and gaster; tibiae without erect setae; bicolored, with sharply contrasting black head and gaster, light orange mesosoma. ***Major***: head somewhat heart-shaped, cordate, with strong posterior emargination; inner hypostomal teeth stout, closely spaced; scape base terete; face mostly foveolate overlain with rugulae, these longitudinal anteriorly, becoming reticulate posteriorly, sculpture fainter on vertex lobes; propodeal spines somewhat posteriorly directed, about one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant short erect setae; abundant short erect setae on mesosomal dorsum and gaster; tibiae without erect setae; color as in minor worker.

Measurements, minor worker: HW 0.44, HL 0.46, SL 0.49, EL 0.11, WL 0.59, PSL 0.06, PTW 0.09, PPW 0.12, CI 95, SI 113, PSLI 13, PPI 122 (n=6).

Measurements, major worker: HW 0.81, HL 0.79, SL 0.52, EL 0.12, WL 0.72, PSL 0.08, PTW 0.13, PPW 0.18, CI 103, SI 64, PSLI 10, PPI 136 (n=5).

Measurements, queen: HW 0.81, HL 0.70, SL 0.57, EL 0.24, WL 1.19, PSL 0.08, PTW 0.23, PPW 0.33, CI 115, SI 71 (n=1).

Biology. *Pheidole balatro* inhabits mature and second growth mesophyll cloud forests, variably mixed with pine, oak, and *Liquidambar*, from 650-1650 m elevation. It has been most commonly collected at baits on the forest floor and in Winkler samples of sifted leaf litter and rotten wood. Major workers commonly occur together with minor workers in baiting and Winkler samples. It can be locally abundant, occurring in a high proportion of samples.

Comments. DNA sequencing and morphology suggest that *P. balatro* and *P. tuxtlasana* are sister species. *Pheidole tuxtlasana* is a lowland rainforest species occurring from Veracruz, Mexico to the Caribbean coast of Honduras. *Pheidole balatro* is a montane species that occurs from northern Honduras to northwestern Costa Rica. The two species occur in close proximity in northern Honduras, but segregate by elevation. *Pheidole balatro* is relatively abundant in Honduras. Beyond Honduras it is known from a single collection by Alex Smith in the Cordillera de Guanacaste, Costa Rica. Conspecificity of Honduran and Costa Rican populations is confirmed by COI barcoding. The species has not been recorded from Nicaragua, in spite of quantitative sampling in several montane sites. The Costa Rica population could be disjunct, or the species could be present in Nicaragua at low density and as yet escaping detection.

Pheidole balatro is part of a striking mimicry complex found in montane forests of Middle America, centered in Honduras. *Pheidole zannia* is another Honduran species that is common in montane sites, is about the same size as *P. balatro*, and shares the striking harlequin color pattern. The two species are often sympatric. They are distantly related, being phylogenetically widely separated. In each case their closest relatives do not have the harlequin pattern. Although not as common, in the same habitats there is an undescribed *Tapinoma* species and an undescribed *Brachymyrmex* species that also share the sharp harlequin pattern. These patterns are otherwise unknown in *Tapinoma* and *Brachymyrmex*.

Etymology: In ancient Rome a balatro was a professional jester, in reference to the harlequin coloration.

***Pheidole belonorte* new species**
(Plate 8)

Pheidole JTL-225: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Olancho: 9km N Catacamas, 14.93833 -85.90315 ±50 m, 1290 m, 10-May-2010, mixed hardwood forest, at bait (LLAMA, Ba-C-02-4-04-12) [MCZC, unique specimen identifier CASENT0613794]. PARATYPES: major, minor workers: same data as holotype [MCZC]; same data except Ba-C-02-4-04-03 [CAS].

Geographic range. Mexico to Nicaragua.

Diagnosis. ***Minor***: face foveolate, overlain with reticulate rugulae; posterior margin of head weakly emarginate in face view; promesonotal groove absent; pronotal dorsum with faint foveolation overlain with weak rugulae; lateral pronotum smooth and shiny; katepisternum foveolate; propodeal spines short, upturned, about one fourth length of posterior face of propodeum; gaster smooth and shining; erect setae on mesosomal dorsum and gaster; tibiae without erect setae; color yellow brown. ***Major***: head elongate, subrectangular; inner hypostomal teeth stout, closely spaced; scape base terete; face with very shallow scrobal impressions, not delimited; anterior half of face with faint foveolation, overlain with subparallel, longitudinal carinae between eye and antennal fossa and between frontal carinae, posterior face and vertex lobes smooth and shiny; propodeal spines short, upturned, about one fifth length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant short erect setae; abundant short erect setae on mesosomal dorsum and gaster; tibiae with 0-3 suberect setae.

Measurements, minor worker: HW 0.43, HL 0.48, SL 0.36, EL 0.07, WL 0.52, PSL 0.05, PTW 0.08, PPW 0.13, CI 89, SI 85, PSLI 12, PPI 157 (n=5).

Measurements, major worker: HW 0.79, HL 0.97, SL 0.40, EL 0.11, WL 0.76, PSL 0.06, PTW 0.15, PPW 0.30, CI 81, SI 51, PSLI 8, PPI 196 (n=5).

Biology. This species inhabits mature lowland wet forest and lower cloud forest. Minor and major workers recruit to ground baits and are collected in Winkler samples of sifted leaf litter and rotten wood from the forest floor.

Comments. *Pheidole belonorte* is a northern version of *P. beloceps*. DNA barcoding puts Costa Rican (La Selva) *P. beloceps* and Nicaraguan *P. belonorte* in different clusters. *Pheidole belonorte* has the major worker with larger, more rectangular head, with vertex lobes smooth and shiny. This species occurs elsewhere in Nicaragua, Honduras, and Chiapas, Mexico, but so far appears rare in Guatemala, with only one tentative record of a minor worker. The minors are indistinguishable from Costa Rican *P. beloceps*. Among the mounted material, the only site where both species are known to occur is Cerro Musún in southern Nicaragua. During quantitative sampling in 2011, *P. beloceps* was in the miniWinkler transects at 700-800m elevation; *P. belonorte* was in higher elevation maxiWinklers, 1000-1400m. Previously, all specimens were identified as a more broadly defined *P. beloceps*. On AntWeb, I reidentified all material north of Musún as *P. belonorte*, including material in ethanol that I did not re-examine. For Musún, I identified all material below 800m as *P. beloceps*; all material above as *P. belonorte*. Ethanol material should be re-examined, although minors cannot be separated at this point.

Etymology: A northern version of *P. beloceps*.

Pheidole besalon **new species**
(Plate 38)

Pheidole JTL-262: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Veracruz: Estación de Biología Los Tuxtlas, 18.58461 -95.07375 ±20 m, 150 m, 31-May-2016, mature wet forest, nest in clay bank (J. Longino, JTL9557) [UNAM, unique specimen identifier CASENT0631747]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC, UNAM].

Geographic range. Mexico (Veracruz).

Diagnosis. ***Minor***: face mostly smooth and shiny, with faint foveolation between eye and frontal carinae; head weakly tapering posteriorly; promesonotal groove impressed; dorsal pronotum weakly foveolate; lateral pronotum smooth and shiny; katepisternum foveolate; propodeal spines about one third length of posterior face of propodeum; gaster smooth and shining; abundant flexuous erect setae on mesosomal dorsum and gaster, tibiae; color red brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base thickened, about as wide as apex; face evenly covered with foveolation overlain with reticulate rugae; propodeal spines one fourth length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with decumbent to fully appressed pilosity; dorsal face and mesosoma nearly devoid of pilosity, with inconspicuous short subdecumbent setae; tibiae with long but fully decumbent setae (in contrast to minor worker); gastral dorsum with abundant flexuous erect setae.

Measurements, minor worker: HW 0.58, HL 0.73, SL 0.99, EL 0.16, WL 0.98, PSL 0.05, PTW 0.12, PPW 0.16, CI 79, SI 172, PSLI 9, PPI 134 (n=1).

Measurements, major worker: HW 1.24, HL 1.29, SL 1.03, EL 0.21, WL 1.31, PSL 0.08, PTW 0.22, PPW 0.32, CI 97, SI 83, PSLI 6, PPI 143 (n=1).

Biology. This species inhabits mature lowland rainforest. Only one collection is known, from Los Tuxtlas Biological Station. A nest was in a vertical clay bank in forest. A large irregular opening led to shallow chambers.

Comments. The minor worker of this species has the general habitus of *P. indagatrix*, *P. purpurea*, and others. The major worker has a uniformly and densely sculptured face, the scapes are flattened, and the pilosity on the side of the head is appressed (similar to *P. susannae*). This combination of minor and major worker characters is unique.

Etymology: Greek for brick, in reference to being found in a vertical clay bank.

Pheidole biconstricta

Pheidole biconstricta Mayr, 1870a: 399. Lectotype major and paralectotype minor worker: Colombia, Santa Fé de Bogotá (Lindig) [NHMW, lectotype major, unique specimen identifier CASENT0916051] (AntWeb image examined).

Pheidole inermis Mayr, 1870b: 984. Lectotype major and paralectotype minor worker: Mexico (Norton) [NHMW, unique specimen identifier CASENT0601290] (AntWeb image examined). **New Synonym**.
For full synonymy see AntCat.org.

Comments. *Pheidole inermis* is a version of *P. biconstricta* that lacks any trace of a propodeal spine. There is continuous variation in the size of the propodeal spine in *P. biconstricta*, and in some cases it is reduced to a minute denticle. DNA barcoding data places three specimens that lack the propodeal spine among *P. biconstricta* specimens. I treat *P. inermis* as an extreme of variation within *P. biconstricta*.

Pheidole bicornisculpta **new species**
(Plate 39)

Pheidole JTL-247: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: 8km S Santa Maria, 9.56866 -83.95125 ±50 m, 1550 m, 29-Jun-2015, cloud forest, in ant *Piper* (J. Longino, JTL9379) [MUCR, unique specimen identifier CASENT0637206]. PARATYPES: major, minor worker, alate queen; same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: head subquadrate, posterior margin weakly emarginate; face fully foveolate, overlain with faint rugulae; promesonotal groove absent; dorsal pronotum foveolate rugulose, fading to smooth on dorsal mesonotum; lateral pronotum and katepisternum smooth and shining medially, foveolate peripherally; propodeal spines triangular, about one third length of posterior face of propodeum; gaster smooth and shining; abundant, flexuous setae on mesosomal and gastral dorsum; tibiae with abundant short suberect setae; color yellow brown. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; frontal carinae produced anteriorly as elevated, triangular teeth, most visible in profile; head elongate rectangular; scrobes shallowly impressed; face heavily sculptured, reticulate rugose throughout; propodeal spines triangular, about one third length of posterior face of propodeum; gastral dorsum smooth and shiny; abundant erect setae on sides of head; mesosomal and gastral pilosity similar to minor worker.

Measurements, minor worker: HW 0.59, HL 0.68, SL 0.37, EL 0.13, WL 0.86, PSL 0.05, PTW 0.16, PPW 0.21, CI 87, SI 63, PSLI 9, PPI 130 (n=1).

Measurements, major worker: HW 0.72, HL 0.92, SL 0.40, EL 0.14, WL 0.99, PSL 0.07, PTW 0.20, PPW 0.25, CI 78, SI 55, PSLI 10, PPI 128 (n=1).

Measurements, queen: HW 0.61, HL 0.70, SL 0.40, EL 0.22, WL 1.16, PSL 0.10, PTW 0.24, PPW 0.35, CI 87, SI 66, PSLI 16, PPI 146 (n=1).

Biology. This species is known from one collection from a cloud forest site. The nest was in a myrmecophytic *Piper*, identified as *P. fimbriulatum*. The ants inhabited the clasping petiolar chambers and the hollow stems. The colony was polygynous or there were multiple colonies in the same plant, because four dealate queens occurred in the collection.

Comments. The minor workers of this species are unusual in exhibiting characteristics of the major worker, with subquadrate heads and foveolate/rugose face sculpture. The close relatives of this species, *P. bicornis* and *P. passivaeferox*, have typical minor workers with rounded heads and mostly smooth faces. Nevertheless, the worker castes of *P. bicornisculpta* are fully dimorphic. The major workers of this species have a single median ocellus on the face. Minor workers also have faint vestiges of a median ocellus.

See further discussion under *P. passivaeferox*.

Etymology: Similar to *P. bicornis* but with more sculptured face.

Pheidole biolleyi

Pheidole Biolleyi Forel, 1908: 48. LECTOTYPE major worker (here designated): Costa Rica, La Palma, 1600 m (P. Biolley) [MHNG, unique specimen identifier JTLC000014077, examined].

Pheidole Biolleyi subsp. *Tristani* Forel, 1908: 50. LECTOTYPE major worker (here designated): Costa Rica, Cartago, 1450 m (Biolley) [MHNG, examined]. Synonymy by Wilson, 2003: 170.

Comments. The syntype series of *P. biolleyi* subsp. *tristani* consists of two species. A major worker, designated here as the lectotype of *tristani*, is the same as *P. biolleyi* and maintains Wilson's synonymy of *tristani* under *biolleyi*. A minor worker from Santa Maria de Dota is identified here as the new species *P. tinamu*. I chose to maintain the synonymy by making the major worker the lectotype, rather than making the minor worker the lectotype and resurrecting *P. tristani*, so that *P. tinamu* could have a major worker as a holotype and be based on a full type series of fresh material.

Pheidole brownampla **new species**
(Plate 16)

Pheidole JTL-242: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Limón: Cerro Plátano, 9.86688 -83.24151 ±50 m, 1120 m, 19-Jun-2015, cloud forest, along steep ridge near peak, at bait (ADMAC, Ba-E-03-1-02-02) [MUCR, unique specimen identifier CASENT0636682]. PARATYPES: major, minor workers: same data as holotype [MUCR]; same data except 9.86621 -83.24203 ±50 m, 1110 m (Ba-E-03-1-04-11) [MCZC]; 9.86552 -83.24254 ±50 m, 1090 m (Ba-E-03-2-01-11) [CAS]; 9.86439 -83.24371 ±50 m, 1050 m (Ba-E-03-2-04-04) [USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face uniformly foveolate; posterior margin of head weakly emarginate in face view; promesonotal groove absent; promesonotal dorsum and dorsal face of propodeum smooth and shiny; lateral pronotum smooth and shiny; katepisternum smooth and shiny anteroventrally, with posterior and dorsal strip of foveolation; propodeal spines about one half length of posterior face of propodeum; gaster smooth and shining; mesosomal and gastral dorsum, tibiae with abundant erect setae; color orange. ***Major***: head subrectangular; inner hypostomal teeth stout, closely spaced; scape base terete; weak scrobal impressions on face, weakly delimited dorsally by frontal carinae; face mostly foveolate, with longitudinal carinulae on anterior third to half, thin posterior strip on vertex lobes smooth and shiny; propodeal spines triangular, about one third length of posterior face of propodeum; gastral dorsum smooth and shining; side of head with erect setae; mesosomal and gastral dorsum, tibiae with abundant suberect setae.

Measurements, minor worker: HW 0.47, HL 0.49, SL 0.44, EL 0.13, WL 0.59, PSL 0.05, PTW 0.09, PPW 0.12, CI 96, SI 94, PSLI 11, PPI 141 (n=2).

Measurements, major worker: HW 0.92, HL 1.04, SL 0.45, EL 0.15, WL 0.75, PSL 0.05, PTW 0.13, PPW 0.21, CI 89, SI 49, PSLI 6, PPI 162 (n=2).

Measurements, queen: HW 0.69, HL 0.69, SL 0.42, EL 0.21, WL 1.05, PSL 0.07, PTW 0.20, PPW 0.28, CI 100, SI 61, PSLI 10, PPI 140 (n=1).

Biology. This species occurs in cloud forest. Minor and major workers recruit to ground baits, and workers occur in Winkler samples of sifted litter and rotten wood.

Comments. This species is very similar to *P. browni*, differing in the larger head of the major worker (HW > 0.89 vs. < 0.76).

Etymology: Similar to *P. browni* but larger.

Pheidole cahui **new species**
(Plate 26)

Pheidole JTL-188: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Petén: Cerro Cahuí, 16.99944 -89.70443 ±24 m, 130 m, 24-May-2009, moist forest, nest in soil (J. Longino, JTL6696) [MCZC, unique specimen identifier CASENT0611056]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM, UVGC].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face smooth and shining; head rounded posteriorly to medially flattened posterior margin; occipital carina thin; promesonotal groove absent, promesonotum evenly convex; lateral pronotum smooth and shiny; katepisternum faintly foveolate with traces of superimposed rugulae; dorsal mesonotum and dorsal face of

propodeum with a few transverse carinulae; propodeal spines absent; gaster smooth and shining; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color orange. ***Major***: inner hypostomal teeth stout, closely spaced; scape base subterete, narrower than apical portion; head subrectangular; antennal scrobe present, short, well-delimited and forming distinct dorsal concavity beneath frontal carina, scrobe surface smooth and shining; entire face (excluding scrobes) with irregular but largely longitudinal carinulae, interspaces smooth to faintly microsculptured; propodeal spines triangular, about one fifth length of posterior face of propodeum; gastral dorsum smooth; abundant, erect, flexuous setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.51, HL 0.57, SL 0.53, EL 0.12, WL 0.70, PSL 0.00, PTW 0.10, PPW 0.12, CI 90, SI 105, PSLI 0, PPI 130 (n=2).

Measurements, major worker: HW 1.30, HL 1.60, SL 0.59, EL 0.20, WL 1.25, PSL 0.07, PTW 0.27, PPW 0.47, CI 81, SI 45, PSLI 5, PPI 176 (n=2).

Measurements, queen: HW 1.23, HL 1.31, SL 0.63, EL 0.31, WL 1.79, PSL 0.08, PTW 0.41, PPW 0.71, CI 94, SI 51, PSLI 6, PPI 174 (n=1).

Biology. This species is known from one site, a reserve with somewhat seasonal moist forest. Minor and major workers recruit to ground baits. A nest was discovered by following workers from a nocturnal ground bait. The entrance was a simple hole in the soil beneath a leaf. An alate queen was collected in a beating sample.

Comments. The minor worker of this species is similar to *P. hasticeps*. The major is very different, with antennal scrobes and heavily sculptured face.

Etymology: From the type locality.

Pheidole caliginosa **new species**
(Plate 55)

Pheidole JTL-252: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Cerro Plano, 9.48141 -83.96276 ±100 m, 1070 m, 6-Jul-2015, ridgetop cloud forest, at bait (ADMAC, Ba-E-06-1-03-11) [MUCR, unique specimen identifier CASENT0631248]. PARATYPES: major, minor workers: same data as holotype [MCZC, MUCR]; same data except Ranchos Tinamu, 9.48686 -83.95215 ±100 m, 720 m, 9-Jul-2015, montane wet forest, near pasture, at bait (ADMAC, Ba-E-07-1-03-03) [CAS]; Ba-E-07-1-03-04 [JTLC, DZUP]; Ba-E-07-1-03-08 [JTLC, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head rounded behind; promesonotal groove present, distinctly impressed; pronotum entirely smooth and shining; katepisternum foveolate; propodeal spines about half length of posterior face of propodeum; gaster smooth and shining; mesosomal and gastral dorsum, tibiae with abundant erect dark amber setae; color dark brown to black. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face mostly smooth and shining, with longitudinal carinulae between eye and antennal fossa, a few longitudinal carinulae medial to frontal carinae; propodeal spines about one third length of posterior face of propodeum; gastral dorsum smooth and shining; side of head with erect setae; mesosomal and gastral dorsum, tibiae with abundant erect dark amber setae.

Measurements, minor worker: HW 0.75, HL 0.88, SL 1.10, EL 0.18, WL 1.16, PSL 0.11, PTW 0.18, PPW 0.26, CI 86, SI 147, PSLI 14, PPI 145 (n=2).

Measurements, major worker: HW 1.46, HL 1.51, SL 1.08, EL 0.23, WL 1.46, PSL 0.13, PTW 0.31, PPW 0.42, CI 96, SI 74, PSLI 9, PPI 137 (n=2).

Biology. This species occurs in lowland to lower montane wet forest. Minor and major workers recruit to ground baits, and workers occur in Winkler samples of sifted litter and rotten wood. A few minor workers have been collected in beating samples.

Comments. This species is similar to *P. hector* and *P. hectornidita*. Compared to both species, the head of the minor worker is more rounded behind, with less developed occipital carina. Both it and *P. hector* have dark amber setae.

Etymology: Latin for dark.

Pheidole carapuna

Pheidole (Pheidole) carapuna Mann, 1916: 432, pl. 3, fig. 22. Lectotype major and paralectotype minor worker: Brazil, Rondonia: Madeira-Mamore rail track, km 284 (W. M. Mann) [MCZC] (examined).

Pheidole carapuna var. *chaquimayensis* Wheeler 1925: 20. Syntype major worker, male: Peru: Chaquimayo, under bark of a mouldering stem, Dec 20th (N. Holmgren) (not examined). Synonymy by Wilson, 2003: 672.

Pheidole tristicula Wilson, 2003: 768, figs. Holotype major worker and associated paratype minor worker: Peru, Madre de Dios: Cuzco Amazonico, 15 km northeast of Puerto Maldonado, Tambopata (Stefan Cover and John E. Tobin) [MCZC] (examined). **New Synonym**.

Comments. *Pheidole carapuna* as interpreted here is a widespread species that occurs from Mexico to northern South America, as far south as Peru. Wilson (2003) commented on the closeness of *P. carapuna* and *P. tristicula*. I consider the slight morphological differences cited to differentiate them to be intraspecific variation. There is no evidence of multiple sympatric forms, and DNA sequence data (unpublished) suggest a single widespread species.

Pheidole carinitida new species

(Plate 23)

Pheidole JTL-257: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Cerro Plano, 9.48141 -83.96276 ±100 m, 1070 m, 6-Jul-2015, ridgetop cloud forest, at bait (ADMAC, Ba-E-06-1-05-11) [MUCR, unique specimen identifier CASENT0631620]. PARATYPES: major, minor workers: same data as holotype [MCZC, MUCR]; same data except 9.48264 -83.96264 ±10 m, 1070 m, 4-Jul-2015, ex sifted leaf litter (ADMAC, Wa-E-06-2-24) [CAS]; 9.48297 -83.96211 ±10 m, 1060 m (Wa-E-06-2-40) [DZUP, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face foveolate, overlain with faint reticulate rugulae to variable extent; vertex margin weakly emarginate in face view; frontal carinae expanded and elevated anterolaterally, forming short teeth that project over clypeus; promesonotal groove absent; dorsal pronotum foveolate, overlain with reticulate rugulae; lateral pronotum and katepisternum foveolate; propodeal spines about two thirds length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum and gaster; tibiae without erect setae; color dark brown. ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; face foveolate overlain with longitudinal carinulae on anterior portion of face, fading to smooth and shiny on vertex lobes; propodeal spines one third to one half length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum and gaster; tibiae without erect setae.

Measurements, minor worker: HW 0.50, HL 0.52, SL 0.46, EL 0.10, WL 0.60, PSL 0.07, PTW 0.08, PPW 0.14, CI 96, SI 92, PSLI 14, PPI 170 (n=2).

Measurements, major worker: HW 1.05, HL 1.11, SL 0.52, EL 0.14, WL 0.83, PSL 0.09, PTW 0.17, PPW 0.34, CI 95, SI 50, PSLI 9, PPI 203 (n=2).

Biology. This species inhabits montane wet forest. Minor and major workers recruit to ground baits and are collected in Winkler samples of sifted leaf litter and rotten wood from the forest floor.

Comments. This species appears to be a montane version of the lowland species *P. carinote*, both species known only from the Pacific slope of Costa Rica. *Pheidole carinitida* differs in the major having a largely smooth and shiny face, and the minor worker tibia lacks erect setae.

Etymology: Similar to *P. carinote*, but with shinier major worker.

Pheidole corniclypeus new species

(Plate 13)

Pheidole JTL-219: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Nicaragua, Matagalpa: RN Cerro Musún, 12.96002 -85.23219 ±60 m, 730 m, 3-

May-2011, tropical wet forest, at bait (LLAMA, Ba-D-01-1-03-04) [MCZC, unique specimen identifier CASENT0623849]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, MCZC, USNM]; same data except 12.95944 -85.22526 ±100 m, 680 m (Ba-D-01-2-04-12) [JTLC].

Geographic range. Honduras, Nicaragua, Costa Rica.

Diagnosis. ***Minor***: face and mesosoma foveolate, with foveolation absent on anteroventral portion of katepisternum; promesonotal groove absent; propodeal spines one fourth to one third length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum and gaster; tibiae with 3-4 erect setae; color orange. ***Major***: lateral clypeus with a prominent blunt tooth, porrect, anterolateral to termination of frontal carina and contiguous with anterior border of antennal fossa, in profile view as long as flared anterolateral margin of frontal carina, and the gap between the two forming a deep V-shaped notch; inner hypostomal teeth distinct, closely spaced; scape base terete; face with distinct scrobes, delimited dorsally by frontal carinae and forming concave trough below them, ventral and posterior margins less delimited, surface of scrobe smooth and shiny; head moderately depressed posteriorly; face surface generally shiny, overlain with subparallel carinae, these longitudinal anteriorly, divergent and oblique on vertex lobes; propodeal spines one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.45, HL 0.48, SL 0.45, EL 0.10, WL 0.58, PSL 0.04, PTW 0.08, PPW 0.13, CI 93, SI 99, PSLI 8, PPI 166 (n=6).

Measurements, major worker: HW 0.98, HL 1.18, SL 0.43, EL 0.14, WL 0.89, PSL 0.07, PTW 0.19, PPW 0.35, CI 83, SI 44, PSLI 7, PPI 187 (n=5).

Biology. This species occurs in lowland rainforest. Minor and occasionally major workers recruit to ground baits, and minor workers occur in Winkler samples of sifted litter and rotten wood.

Comments. This species is primarily known from a few collections from Cerro Musún in central Nicaragua. The major workers are easily identifiable by the unique clypeal teeth. Minor workers are very difficult to separate from other *P. flavens*-like species when in mixed samples, and from other members of the species complex in general. The sympatric *P. natalie* has the katepisternum completely foveolate. *Pheidole corniclypeus* and the parapatric *P. costaricensis* have the anterolateral katepisternum smooth and shiny, and at present they appear indistinguishable. DNA barcodes cluster a specimen from the La Moskitia region of Honduras, several specimens from Musún, and a specimen from the Cordillera de Guanacaste in northwest Costa Rica (Cerro Cacao at 740 m). The BOLD image of the Guanacaste specimen is a minor worker and is consistent with being a member of this species complex. See additional comments under *P. andersoni*.

Etymology: Referring to the spines projecting from the clypeus.

Pheidole costaricensis **new species**
(Plate 19)

Pheidole JTL-279: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Limón: Cerro Platano, 26km WSW Limón, 9.86439 -83.24371 ±50 m, 1050 m, 19-Jun-2015, mature cloud forest, under stone (J. Longino, JTL9332) [MUCR, unique specimen identifier CASENT0637143]. PARATYPES: major, minor workers: same data as holotype [MCZC, MUCR]; same data except 9.86621 -83.24203 ±50 m, 1110 m, at bait (ADMAC, Ba-E-03-1-04-06) [CAS]; 9.86439 -83.24371 ±50 m, 1050 m, at bait (Ba-E-03-2-05-16) [USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face and mesosoma foveolate, anteroventral katepisternum smooth and shining; promesonotum evenly convex, promesonotal groove absent; propodeal spines one fourth length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum and gaster; tibiae with 2-3 erect setae; color orange. ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; face with distinct scrobes, delimited dorsally by frontal carinae and forming concave trough below them, ventral and posterior margins less delimited, surface of scrobe smooth and shiny; head weakly depressed posteriorly; face surface generally smooth and shiny, with sparse, feeble longitudinal carinulae; propodeal spines one fourth length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.48, HL 0.51, SL 0.48, EL 0.11, WL 0.63, PSL 0.04, PTW 0.09, PPW 0.14, CI 93, SI 102, PSLI 7, PPI 161 (n=4).

Measurements, major worker: HW 1.03, HL 1.24, SL 0.48, EL 0.14, WL 0.98, PSL 0.07, PTW 0.18, PPW 0.36, CI 83, SI 47, PSLI 7, PPI 200 (n=3).

Biology. This species occurs in lowland rain forest to lower cloud forest habitats. Minor and occasional major workers recruit to ground baits. Workers occur in Winkler samples. One nest was observed in soil beneath a stone.

Comments. This species remains poorly delimited. The type locality is a cloud forest site southwest of Limón, where minor workers were definitively associated with major workers. At La Selva Biological Station and the lower Barva transect above it, many minor workers that have been collected at baits and in Winkler samples are tentatively identified as *P. costaricensis*. However, no major workers have been collected from this area. Three of the minor workers have DNA barcodes and form a tight cluster, near the cluster of *P. corniclypeus*. Given the inability to morphologically distinguish minor workers of *P. costaricensis* and *P. corniclypeus*, and the proximity of true *P. corniclypeus*, there is the possibility that both species could occur on the Barva transect. A population was sampled on the Pacific slope of Costa Rica, in lower montane forest above the Rio Savegre, and minors were associated with major workers. These major workers are somewhat intermediate between *P. costaricensis* and *P. corniclypeus*, with more pronounced facial carinae, and small bulges on the lateral clypeus where the large teeth are on *P. corniclypeus*. Finally, BOLD has a tight cluster of specimens from the lowland dry forest of Guanacaste, close to the clusters for *P. corniclypeus* and *P. costaricensis*. Images of these specimens include a lateral view of a major worker, and there is no evidence of a clypeal bulge or tooth. See additional comments under *P. andersoni*.

Etymology: From the type locality.

Pheidole cusuco **new species**
(Plate 51)

Pheidole JTL-277: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Cortés: PN Cusuco, 15.48965 -88.23383 ±55 m, 1300 m, 31-May-2010, mesophyll forest, at bait (LLAMA, Ba-C-06-1-02-03) [MCZC, unique specimen identifier CASENT0617747]. PARATYPES: major, minor workers: same data as holotype [MCZC]; same data except Ba-C-06-1-02-08 [CAS]; Ba-C-06-1-02-11 [USNM]; 15.49037 -88.23402 ±70 m, 1330 m (Ba-C-06-1-03-06) [DZUP]; 15.49076 -88.23446 ±40 m, 1360 m, (Ba-C-06-1-04-05) [JTLC].

Geographic range. Guatemala, Honduras.

Diagnosis. ***Minor***: sculpture of variable strength; strongest with face fully foveolate, overlain with faint rugulae, pronotal dorsum foveolate overlain with distinct reticulate rugulae, lateral pronotum fully foveolate; weakest with weak foveolation and medial shiny spaces on face, pronotal dorsum foveolate with shiny patches, lateral pronotum largely smooth and shiny; katepisternum always foveolate; head somewhat elongate but rounded posteriorly; promesonotal groove distinctly impressed; propodeal spines about one fifth length of posterior face of propodeum; first gastral tergite smooth and shining; abundant erect setae on mesosomal and gastral dorsum, tibiae; color brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face with faint foveolation overlain with reticulate rugulae on anterior half, a few longitudinal carinulae on anteromedian frons, rest of face smooth and shiny; propodeal spines about one third length of posterior face of propodeum; first gastral tergite smooth and shiny; sides of head with abundant erect setae; mesosomal and gastral dorsum, tibiae with abundant erect setae.

Measurements, minor worker: HW 0.66, HL 0.78, SL 0.96, EL 0.15, WL 1.02, PSL 0.05, PTW 0.12, PPW 0.18, CI 86, SI 144, PSLI 8, PPI 144 (n=3).

Measurements, major worker: HW 1.13, HL 1.17, SL 0.97, EL 0.19, WL 1.24, PSL 0.07, PTW 0.19, PPW 0.28, CI 97, SI 86, PSLI 6, PPI 148 (n=2).

Biology. This species occurs in cloud forest, where it can be locally abundant. Minor and major workers recruit to ground baits, but are infrequently collected in Winkler samples of sifted litter and rotten wood.

Comments. DNA barcoding places this species very close to *P. luteagossamer*. The two species are parapatric, with *P. cusuco* occurring in southern Guatemala and northern Honduras, and *P. luteagossamer* occurring from

central Honduras to northern Nicaragua. The two species differ in color (*P. cusuco* is brown, *P. gossamer* is yellow) and the distinctive silky pilosity of the major worker of *P. luteagossamer*.

Etymology: From the type locality.

***Pheidole depressinoda* new species**
(Plate 5)

Pheidole JTL-190: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Petén: Cerro Cahuí, 17.00203 -89.70922 ±153 m, 155 m, 24-May-2009, tropical moist forest, at bait (LLAMA, Ba-B-05-3-04-19) [MCZC, unique specimen identifier CASENT0611611]. PARATYPES: major, minor workers, male: same data as holotype [MCZC, USNM]; same data except 16.99876 -89.71038 ±206 m, 150 m (Ba-B-05-3-03-01) [DZUP, JTLC, UVGC]; 17.00222 -89.71709 ±57 m, 150 m, nest in dead stick (J. Longino, JTL6677) [CAS, JTLC].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face largely smooth and shining, with foveolate sculpture between eye and antennal fossa, very faint traces of foveolate sculpture elsewhere; promesonotal groove absent; side of mesosoma and dorsal face of propodeum foveolate (side of pronotum with variable presence of a smooth patch), promesonotal dorsum smooth and shiny; propodeal spines about one third length of posterior face of propodeum; postpetiole longer and broader than petiolar node, but dorsoventrally depressed, lower than petiolar node in profile (typical postpetiolar shape of *P. punctatissima* and relatives); gaster mostly smooth and shining, with very small area of shagreening near postpetiolar insertion; face, mesosoma, and gaster with short, stiff, erect dorsal setae, tibiae lack erect setae; color distinctively bicolored; head, mesosoma, gaster, and forecoxae dark brown, antennal scapes, middle and hind coxae, tibiae and tarsi contrasting light ivory color, femora darker, but lighter than main body. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; face with shallow antennal scrobes, not distinctly delimited, scrobe surface foveolate; face mostly foveolate, stronger anteriorly, fading posteriorly, vertex lobes smooth and shiny, foveolation overlain with longitudinal rugulae on anterior half of head, ventral to scrobe and in medial space between frontal carinae; propodeal spines about one third length of posterior face of propodeum; gastral dorsum with faint shagreening on anterior third, smooth and shining elsewhere; sides of head, mesosomal dorsum, and gastral dorsum with abundant short erect setae, tibiae with no erect setae or with 1-2 inconspicuous setae.

Measurements, minor worker: HW 0.39, HL 0.46, SL 0.43, EL 0.10, WL 0.50, PSL 0.04, PTW 0.07, PPW 0.14, CI 85, SI 110, PSLI 9, PPI 194 (n=2).

Measurements, major worker: HW 0.83, HL 0.96, SL 0.47, EL 0.12, WL 0.76, PSL 0.06, PTW 0.13, PPW 0.28, CI 86, SI 56, PSLI 7, PPI 212 (n=2).

Biology. This species is known from one site, a reserve with somewhat seasonal moist forest. Minor and major workers recruit to ground baits. Workers occur in Winkler samples of sifted litter and rotten wood. A nest was discovered by following workers from a bait to a soft rotten stick in the litter.

Comments. DNA sequence data place this species near *P. bilimeki* and *P. punctatissima* (Economo *et al.* 2019, as JTL190) (note that "*floridana*" in Economo *et al.* is the Florida population of *P. bilimeki*, see Sarnat *et al.* 2015). The broad, depressed postpetiole is typical of this complex, which includes *P. anastasii*, *P. bilimeki*, and *P. punctatissima*. However, the sculpture and color are unusual. Most members of the group are uniformly foveolate on the face and mesosoma, in contrast to the extensive smooth areas on this species. The contrasting brown and white coloration is also distinctive. Both these characters are convergent with the superficially similar but unrelated species *P. albipes*, which is also common at the type locality. This may be some form of local mimicry.

Etymology: Referring to the depressed postpetiole which is characteristic of *P. punctatissima* and relatives.

***Pheidole eosimilis* new species**
(Plate 54)

Pheidole JTL-210: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Nicaragua, Matagalpa: 3km N Rio Blanco, 12.96018 -85.22488 ±50 m, 690 m, 1-May-2011, mature wet forest, nest in rotten wood (J.Longino, JTL7435) [MCZC, unique specimen identifier CASENT0619392]. PARATYPES: major, minor workers, queen: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM].

Geographic range. Nicaragua, Costa Rica.

Diagnosis. ***Minor***: clypeus completely smooth, without medial carina; face smooth and shining; promesonotal groove very weakly impressed; mesosoma almost entirely smooth and shining; propodeal spines long, about as long as posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color dark brown. ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; face foveolate throughout, overlain with reticulate rugulae, rugulae more longitudinally oriented anteriorly; propodeal spines about one half length of posterior face of propodeum; gastral dorsum very faintly foveolate on anterior third, fading to smooth and shiny; abundant erect setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.71, HL 0.78, SL 1.08, EL 0.15, WL 1.16, PSL 0.12, PTW 0.13, PPW 0.17, CI 90, SI 153, PSLI 16, PPI 138 (n=10).

Measurements, major worker: HW 2.46, HL 2.53, SL 1.13, EL 0.27, WL 1.91, PSL 0.19, PTW 0.36, PPW 0.61, CI 97, SI 46, PSLI 8, PPI 169 (n=2).

Measurements, queen: HW 2.27, HL 2.06, SL 1.18, EL 0.37, WL 2.55, PSL 0.17, PTW 0.54, PPW 0.84, CI 110, SI 52, PSLI 8, PPI 156 (n=1).

Biology. This species occurs in lowland to lower montane wet forest. Minor workers and occasional major workers recruit to ground baits. Workers occur in Winkler samples of sifted leaf litter and rotten wood. Two nests have been observed, both in rotten wood. One nest contained a seed cache. Another nest was in a cavity in a 15-20 cm diameter dead buttress, a few cm above ground. The entrance was covered with a thin-walled dome of accreted organic material, with two entrance holes in the dome.

Comments. This species is very similar to *P. eowilsoni*, with which it is sympatric. The minor worker of *P. eowilsoni* has a longitudinal median carina on the clypeus. The major worker has the vertex lobes smoother, the scape base is flatter, and the anterior face of the petiolar node is less differentiated from the peduncle. Although very similar to *P. eowilsoni*, COI barcode data widely separate the two species.

Etymology: Similar to *P. eowilsoni*.

Pheidole familiaparra **new species**
(Plate 53)

Pheidole JTL-254: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Ranchos Tinamu, 9.48544 -83.95394 ±100m, 760m, 9-Jul-2015, montane wet forest, near edge of pasture, at bait (ADMAC, Ba-E-07-1-02-12) [MUCR, unique specimen identifier CASENT0631331]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head tapering posteriorly; occipital carina moderately developed; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum uniformly foveate; propodeal spines long, similar in length to posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color yellow. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base subterete, narrower than apical portion; face with irregular rugulose foveolate sculpture anteriorly, fading to smooth and shining posteriorly; promesonotal groove impressed; propodeal spines about half length of posterior face of propodeum; gastral dorsum smooth and shining; abundant erect setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.69, HL 0.93, SL 1.32, EL 0.17, WL 1.26, PSL 0.21, PTW 0.16, PPW 0.22, CI 74, SI 193, PSLI 31, PPI 143 (n=1).

Measurements, major worker: HW 1.55, HL 1.65, SL 1.24, EL 0.25, WL 1.71, PSL 0.21, PTW 0.28, PPW 0.43, CI 94, SI 80, PSLI 13, PPI 153 (n=2).

Biology. This species occurs in montane wet forest. It is known from ground baits.

Comments. See under *P. tinamu*. A collection of a major worker from a site in northern Costa Rica, in the Cordillera de Guanacaste, is tentatively identified as this species.

Etymology: In honor of the extended Parra family who helped us during expeditions to the Río Savegre area in 2015: Rafael, Marieugenia, and Daniela Parra from Santa María de Dota, and Santiago Parra from Ranchos Tinamu.

Pheidole fimbriata

Pheidole fimbriata Roger, 1863: 196. Holotype major worker: "Rio Paraguay" (not examined). Full synonymy not listed.
Pheidole soesilae Makhan, 2007: 1, figs. 1, 2. Holotype major worker: Suriname (not examined). **New Synonym**.

Comments. *Pheidole fimbriata* is a widespread species, occurring from Mexico to Paraguay and Argentina. The images of the holotype major in Makhan's publication are of this highly distinctive species.

Pheidole fincanaranjo new species

(Plate 32)

Pheidole JTL-250: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: 9km SSE Santa María, 9.56866 -83.95125 ±50 m, 1550 m, 29-Jun-2015, cloud forest, on steep slope, probably old 2nd growth, near pasture, at bait (ADMAC, Ba-E-05-3-04-08) [MUCR, unique specimen identifier CASENT0632181]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face foveolate overlain with faint irregular rugulae; vertex margin shallowly emarginate in full face view; promesonotal groove very weakly impressed; pronotal dorsum foveolate overlain with conspicuous reticulate rugulae; lateral pronotum and katepisternum foveolate; propodeal spines as long as posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal and gastral dorsum, tibiae; color red brown. ***Major***: inner hypostomal teeth large, closely spaced; scape base terete; face mostly foveolate, overlain with longitudinal carinulae between eye and antennal fossa and in medial area between frontal carinae, posterior margin of vertex lobes smooth and shiny; propodeal spines about two thirds length of posterior face of propodeum; gastral dorsum smooth and shiny; abundant erect setae on sides of head, tibiae, mesosomal and gastral dorsum.

Measurements, minor worker: HW 0.55, HL 0.55, SL 0.44, EL 0.11, WL 0.64, PSL 0.12, PTW 0.11, PPW 0.15, CI 99, SI 80, PSLI 22, PPI 143 (n=1).

Measurements, major worker: HW 0.92, HL 0.94, SL 0.45, EL 0.15, WL 0.84, PSL 0.15, PTW 0.20, PPW 0.32, CI 98, SI 49, PSLI 16, PPI 162 (n=1).

Biology. This species occurs in cloud forest. Major and minor workers recruit to ground baits, and workers occur in Winkler samples of sifted litter and rotten wood.

Comments. *Pheidole fincanaranjo* is similar to *P. specularis*, differing in the larger size in general (minor worker mean HW 0.55 vs. 0.47, major worker mean HW 0.92 vs. 0.87), and the longer spines and dorsal reticulate rugose sculpture of the minor worker. *Pheidole specularis* is a widespread lowland species, found near *P. fincanaranjo* at lower elevations.

Etymology: Finca Naranjo was the name of the farm where the type specimens were collected.

Pheidole gulo

Pheidole gulo Wilson, 2003: 295. Holotype major worker: Nicaragua, Rio Kukra (Ivette Perfecto) [MCZC, examined].
Pheidole JTL197: morphospecies code previously used on AntWeb.

In most populations of *P. gulo*, the minor worker has a fully foveolate face and mesosoma. Specimens from Los Tuxtlas Biological Station in Veracruz, Mexico, and from the slopes of Volcán Atitlán in Guatemala have the face

and parts of the pronotum smooth and shining. There is no known site of sympatry of the two forms. The morphospecies code JTL197 was used for the shiny form of *P. gulo*. In Economo *et al.* (2019) a shiny specimen from Volcán Atitlán is genetically close to a foveolate specimen from Nicaragua. Pending further evidence, I treat this as one species with geographic variation.

***Pheidole hansoni* new species**
(Plate 28)

Pheidole JTL-140: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Guanacaste: Cerro Cacao, 10.92682 -85.46823 ±2 km, 1100 m, 13-Feb-1995, moist forest, nest under stone (J. Longino, JTL3659) [MUCR, unique specimen identifier CASENT0636565]. PARATYPES: major, minor workers: same data as holotype [JTLC, MCZC, MUCR].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face foveolate, overlain with irregular rugulae, rugulae becoming more longitudinal medially; promesonotal profile somewhat box-like, promesonotal groove very shallowly impressed, posterior mesonotum dropping steeply to propodeum; entire mesosoma foveolate, overlain with a lattice of rugulae on dorsal pronotum; propodeal spines upturned, about half as long as posterior face of propodeum; gaster smooth and shining; abundant flexuous erect setae on mesosomal and gastral dorsa, lacking on tibiae; color dark red brown. ***Major***: inner hypostomal teeth large, closely spaced; scape base terete; face with longitudinal rugulae and faint foveolation between eye and frontal carinae, very feeble longitudinal carinulae on frontal space between frontal carinae (variably present), rest of face smooth and shining; propodeal spines about a third to half length of posterior face of propodeum; gastral dorsum smooth and shining; abundant, erect, flexuous setae on face, sides of head, mesosomal dorsum, and gastral dorsum; tibiae lacking erect setae or with one or two inconspicuous setae; in one series, setae on head subdecumbent, giving somewhat wooley appearance; color dark red brown.

Measurements, minor worker: HW 0.53, HL 0.56, SL 0.47, EL 0.10, WL 0.64, PSL 0.09, PTW 0.10, PPW 0.15, CI 94, SI 90, PSLI 17, PPI 157 (n=5).

Measurements, major worker: HW 1.02, HL 1.09, SL 0.51, EL 0.13, WL 0.82, PSL 0.10, PTW 0.18, PPW 0.34, CI 94, SI 50, PSLI 10, PPI 181 (n=3).

Biology. This species occurs in montane moist to wet forest. One collection was from a nest under a stone in mature forest. Another collection was major and minor workers at a ground bait.

Comments. The few collections of this species come from widely separated populations in Costa Rica, and the major workers exhibit a relatively broad range of measurements (one each from three populations: HW 0.99-1.10, CI 92-97). *Pheidole carinitida* is superficially similar but has enlarged frontal carinae and a more impressed promesonotal impression, in both minors and majors.

Etymology: In honor of Paul Hanson, who has been a tireless facilitator and promoter of entomological research in Costa Rica.

***Pheidole hectornitida* new species**
(Plate 48)

Pheidole JTL-246: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: 8km S Santa Maria, 9.57653 -83.95188 ±20 m, 1510 m, 29-Jun-2015, cloud forest, nest in dead wood (J. Longino, JTL9387) [MUCR, unique specimen identifier CASENT0637217]. PARATYPES: major and minor worker: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head tapering behind to moderately developed occipital carina; promesonotal groove present, distinctly impressed; pronotum entirely smooth and shining; katepisternum with mixture of faint foveolation and irregular rugulae, shiny; propodeal spines spiniform, about half length of posterior face of propodeum; gaster smooth and shining; mesosomal and gastral dorsum with abundant flexuous erect setae;

tibiae with erect setae; color red brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face mostly smooth and shining, with longitudinal carinulae between eye and frontal carinae; propodeal spines about one third length of posterior face of propodeum; gastral dorsum smooth and shining; side of head with erect setae; mesosomal and gastral dorsum with abundant erect setae; tibiae with erect setae.

Measurements, minor worker: HW 0.68, HL 0.92, SL 1.26, EL 0.17, WL 1.24, PSL 0.07, PTW 0.14, PPW 0.21, CI 74, SI 186, PSLI 11, PPI 154 (n=2).

Measurements, major worker: HW 1.32, HL 1.37, SL 1.20, EL 0.20, WL 1.49, PSL 0.11, PTW 0.24, PPW 0.32, CI 97, SI 91, PSLI 9, PPI 137 (n=2).

Biology. This species occurs in cloud forest. Minor and major workers recruit to ground baits, and workers are occasionally collected in Winkler samples of sifted litter and rotten wood. One nest was observed in a large dead log. The wood was solid but breakable by hand. The nest chambers were deep in the log.

Comments. This species is very similar to *P. hector*, with similar head shape and general habitus. In minor workers the pilosity is not as dark and the propodeal spines are shorter (PSLI ~11 vs. ~30). In major workers the face is more uniformly smooth and shining, without patches of faint foveolation. A collection from a nearby, lower elevation site (850 m) is of a single minor worker and a single major worker at a bait. These specimens are smaller than the other collections, with minor worker HW 0.52 and major worker HW 1.14. In all other respects they are similar to the other collections. They are possibly specimens from an incipient colony, and the measurements are not included in the means reported above.

Etymology: Similar to *P. hector*, but the face of the major worker is smooth and shiny.

Pheidole hitoy **new species**

(Plate 38)

Pheidole JTL-245: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Limón: Res. Biol. Hitoy-Cerere, 9.66824 -83.02232 ±50 m, 170 m, 12-Jun-2015, tropical rainforest, at bait (ADMAC, Ba-E-02-2-02-15) [MUCR, unique specimen identifier CASENT0644296]. PARATYPES: major and minor worker: same data as holotype [JTLC, MCZC, MUCR]; same data except 9.6671 -83.02202 ±50 m, 180 m (Ba-E-02-2-04-06) [CAS, DZUP, JTLC, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head rounded behind, with thin occipital carina; promesonotal groove present, distinctly impressed; anterior face of pronotum foveolate with a few transverse carinulae dorsal face smooth and shining, lateral face mostly smooth with some faint foveolation along ventral margin; katepisternum foveolate; propodeal spines long and thin, about as long as posterior face of propodeum; gaster smooth and shining; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae with erect setae; color red brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face mostly smooth and shining, with longitudinal carinulae between eye and frontal carinae, irregular faint patches of foveolation elsewhere; propodeal spines about as long as posterior face of propodeum; gastral dorsum smooth and shining; side of head with erect setae; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae with erect setae.

Measurements, minor worker: HW 0.58, HL 0.70, SL 0.93, EL 0.14, WL 0.92, PSL 0.15, PTW 0.10, PPW 0.17, CI 82, SI 162, PSLI 27, PPI 162 (n=2).

Measurements, major worker: HW 1.18, HL 1.28, SL 0.96, EL 0.18, WL 1.20, PSL 0.17, PTW 0.19, PPW 0.28, CI 92, SI 81, PSLI 14, PPI 149 (n=2).

Biology. This species occurs in lowland rainforest. Minor and major workers recruit to ground baits.

Comments. This species is very similar to *P. indagatrix*, differing in the longer propodeal spines (minor worker PSLI ~27 vs. < 20).

Etymology: From the type locality.

Pheidole huarache **new species**

(Plate 22)

Pheidole JTL-170: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Petén: Cerro Cahuí, 16.99876 -89.71038 ±206 m, 150 m, 24-May-2009, tropical moist forest, at bait (LLAMA, Ba-B-05-3-01-01) [MCZC, unique specimen identifier CASENT0611593]. PARATYPES: major, minor workers: same data as holotype [DZUP, JTLC, MCZC]; same data except Ba-B-05-3-01-12 [CAS, USNM]; 17.00227 -89.71939 ±60 m, 305 m (Ba-B-05-4-04-06) [UVGC].

Geographic range. Mexico (Veracruz) to Guatemala (Petén).

Diagnosis. ***Minor***: face smooth and shining; head evenly rounded posteriorly; occipital carina thin; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum uniformly foveate; propodeal spines about half length of posterior face of propodeum; gaster smooth and shining; dorsal setae of mesosoma and gaster somewhat stiff and dark, sparse; tibiae with 0-2 erect setae; color dark brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base subterete, narrower than apical portion; face with irregular rugulae between eye and antennal fossa, rest of face mostly smooth and shining, with variably developed faint etching on sides posterior to eye; propodeal spines about half length of posterior face of propodeum; gastral dorsum smooth and shining; side of head lacking erect setae; rest of pilosity pattern similar to minor worker.

Measurements, minor worker: HW 0.49, HL 0.54, SL 0.57, EL 0.13, WL 0.66, PSL 0.05, PTW 0.12, PPW 0.15, CI 91, SI 118, PSLI 10, PPI 131 (n=2).

Measurements, major worker: HW 0.78, HL 0.81, SL 0.56, EL 0.14, WL 0.78, PSL 0.07, PTW 0.15, PPW 0.20, CI 96, SI 73, PSLI 8, PPI 134 (n=2).

Biology. This species occurs in moist to seasonally dry habitats, often in secondgrowth habitats. It is common at ground baits, and majors and minors are recruited. Workers are also found in Winkler samples of sifted litter and rotten wood.

Comments. This species is like a small version of *P. leoncortesi*, with similar dark setae. The measurements are similar to two species from Peru, *P. gagates* and *P. machetula*. Compared to *P. gagates*, the minor worker has more abundant and darker setae and the major worker has erect setae on the sides of the head. Compared to *P. machetula*, the setae are darker and the propodeal spines are longer (mean PSLI 10 vs. 3).

Etymology: From a pre-Columbian word for sandal. These ants were underfoot in the Tikal area, a major site of Mayan civilization.

Pheidole imbrilis **new species**
(Plate 7)

Pheidole JTL-241: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Limón: Cerro Platano, 26km WSW Limón, 9.86713 -83.24141 ±20 m, 1130 m, 18-Jun-2015, mature cloud forest, night foragers (J. Longino, JTL9329-s) [MUCR, unique specimen identifier CASENT0637137]. PARATYPES: major, minor workers: same data as holotype [MUCR, MCZC]; same data except 9.86439 -83.24371 ±50 m, 1050 m, 19-Jun-2015, at bait (ADMAC, Ba-E-03-2-04-05) [CAS, JTLC, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; promesonotal groove absent; entire mesosoma smooth and shiny except for faint foveolation on dorsal face of propodeum; anterior and dorsal faces of pronotum separated by a single transverse carina; propodeal spines short triangular denticles; gaster smooth and shining; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae lack erect setae; color light yellow brown. ***Major***: inner hypostomal teeth very reduced, inconspicuous tubercles about half way between midline and outer hypostomal teeth; scape base terete; face mostly smooth and shining, with longitudinal carinulae on anterior third; propodeal spines short triangular denticles; gastral dorsum smooth and shining; side of head with erect setae; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae with 0-2 erect setae.

Measurements, minor worker: HW 0.42, HL 0.46, SL 0.42, EL 0.10, WL 0.54, PSL 0.01, PTW 0.08, PPW 0.11, CI 92, SI 99, PSLI 4, PPI 136 (n=2).

Measurements, major worker: HW 0.87, HL 0.97, SL 0.48, EL 0.12, WL 0.76, PSL 0.02, PTW 0.15, PPW 0.24, CI 90, SI 55, PSLI 2, PPI 159 (n=2).

Biology. This species occurs in cloud forest. Minor and major workers recruit to ground baits, and workers occur in Winkler samples of sifted litter and rotten wood.

Comments. This species is very similar to *P. laselva* and *P. laselvoides*, differing in the broader head (HW 0.87 vs. < 0.8) and reduced facial carinulae of the major worker, and the overall lighter color of both worker castes.

Etymology: Latin, "of rain," in reference to the incessant and voluminous rain that occurred during field sampling at the type locality.

***Pheidole indagarama* new species**
(Plate 45)

Pheidole JTL-153: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Heredia: La Selva Biological Station, 10.43215 -84.01511 ±20 m, 50 m, 16-May-2000, secondgrowth rainforest, ex *Goethalsia meiantha* (ALAS, FOT/51/03) [MUCR, unique specimen identifier CASENT0636566]. PARATYPES: major, minor worker, queen: same data as holotype [CAS, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shiny; head tapering behind to moderately developed occipital carina; promesonotal groove present, distinctly impressed; promesonotum entirely smooth and shining; katepisternum uniformly foveolate; propodeal spines spiniform, about one third length of posterior face of propodeum; gaster smooth and shining; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae with erect setae; color red brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face uniformly foveolate, with longitudinal carinulae between eye and frontal carinae; propodeal spines about one fourth length of posterior face of propodeum; gastral dorsum very faintly foveolate on anterior half; side of head with abundant erect setae; mesosomal and gastral dorsum with abundant erect setae; tibiae with erect setae; head bright yellow, contrasting with darker red brown mesosoma and gaster.

Measurements, minor worker: HW 0.62, HL 0.79, SL 1.06, EL 0.17, WL 1.00, PSL 0.07, PTW 0.11, PPW 0.16, CI 78, SI 172, PSLI 11, PPI 143 (n=3).

Measurements, major worker: HW 1.23, HL 1.27, SL 1.04, EL 0.20, WL 1.25, PSL 0.09, PTW 0.18, PPW 0.24, CI 97, SI 85, PSLI 7, PPI 136 (n=2).

Measurements, queen: HW 1.48, HL 1.30, SL 0.82, EL 0.37, WL 2.20, PSL 0.19, PTW 0.47, PPW 0.74, CI 114, SI 55, PSLI 13, PPI 157 (n=1).

Biology. This species occurs in lowland rainforest. It is arboreal, known from canopy fogging samples and specimens collected in a fresh treefall. Major workers, minor workers, males, and dealate queens have occurred in these samples.

Comments. This species is known only from La Selva Biological Station, from two canopy fogging samples (taken from different trees on different dates) and in a hand collection in a new treefall. It appears to be a local variant of the widespread *P. indagatrix*, specialized for the high canopy. The only consistent character difference in workers is the color of the major worker. Throughout the range of *P. indagatrix*, from Guatemala to Panama, major workers are dark red brown. *Pheidole indagatrix* is very common at ground baits and nests in leaf litter, in rotten wood, and in dead stems in the low arboreal zone. At La Selva Biological Station, *P. indagatrix* is a common ground ant, while *P. indagarama* is known only from the canopy. There is a tendency for majors of *P. indagatrix* to have heavier sculpture on the gaster. Major workers of *P. indagarama* have the first gastral tergite nearly smooth, with very faint foveolate sculpture on the anterior half.

Two dealate queens and some *Pheidole* males were found in the same 1 m^2 fogging funnel with abundant minor and major workers of *P. indagarama.* These were assumed to be from one colony, and thus the queens conspecific with the workers. The queens have the mesoscutum and scutellum completely smooth and shining, and the first gastral tergite is almost entirely smooth and shining. *Pheidole indagatrix* queens from the Cordillera de Tilarán, 85 km west of La Selva, have the mesoscutum and scutellum coarsely sculptured, and the first gastral tergite is strongly shagreened and opaque. An isolated queen from a different fogging sample from La Selva is tentatively identified as *P. indagatrix*. It is lighter colored but otherwise has the heavier sculpture of the Cordillera de Tilarán specimens.

Etymology: Referring to this species being an arboreal version of *P. indagatrix*.

Pheidole insipida

Pheidole kingi r. *insipida* Forel, 1899: 76. Lectotype major worker (here designated): Mexico, Veracruz: Cordoba (Salle) [BMNH, unique specimen identifier CASENT0901556] (AntWeb image examined). Syntype minor worker from Guerrero not conspecific.

Pheidole insipida: Kempf, 1972: 195 (raised to species).

Pheidole mooreorum Wilson, 2003: 209, figs. Holotype major worker and associated paratype minor worker: Mexico, Veracruz, Los Tuxtlas, 10km NNW Sontecomapan, 18°35'N 95°05'W, 200m, 20 Mar 1985, ground foragers, rainforest (P. S. Ward 7339) [MCZC] (examined). **New Synonym**.

Pheidole fariasana Wilson, 2003: 155, figs. Holotype major worker and associated paratype minor worker: Mexico, Tamaulipas, 1mi E Gomez Farias, 1400', 23 Dec 1972, deciduous tropical forest, nesting in ground under stone (R. J. Hamton, A. B. Hamton, B. S. Ikeda) [MCZC] (examined). **New synonym**. Synonymized under *P. mooreorum* by Longino, 2009: 56.

Comments. *Pheidole insipida* was overlooked in Wilson's 2003 revision. AntWeb images of the major worker match the common, widespread species that heretofore was identified as *P. mooreorum*. I have collected material of this species 50 km north of the type locality, and from the nearby type locality of *P. mooreorum*. This material closely matches the images of the type.

Pheidole kasparii new species

(Plate 5)

Pheidole JTL-248: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: 8km S Santa Maria, 9.57666 -83.94911 ±20 m, 1700 m, 25-Jun-2015, cloud forest, under epiphytes (J. Longino, JTL9356) [MUCR, unique specimen identifier CASENT0637174]. PARATYPES: major, minor worker, dealate queen: same data as holotype [MUCR]; same data except 9.56895 -83.94756 ±20 m, 1770 m, 25-Jun-2015, cloud forest, nest under epiphytes (J. Longino, JTL9358) [CAS, DZUP, JTLC, MCZC, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; vertex margin shallowly emarginate in full face view; promesonotal groove absent; pronotum entirely smooth and shiny; katepisternum shiny, with varying development of faint foveolation; propodeal spines in form of obtuse to right angles, not spiniform; gaster smooth and shining; abundant erect setae on mesosomal and gastral dorsum; tibiae lack erect setae; color red brown to yellow (color variation can be intracolonial). ***Major***: median hypostomal tooth strongly developed; inner hypostomal teeth very weakly developed, hardly visible, closer to outer hypostomal teeth than to medial tooth, recessed, not on ventral margin of hypostomal bridge; ventral margin of head in profile view convex; scape base terete; face mostly smooth and shiny, with longitudinal carinulae between eye and antennal fossa; propodeal spines in form of short, triangular teeth, < one fifth length of posterior face of propodeum; gastral dorsum smooth and shiny; abundant erect setae on sides of head, mesosomal and gastral dorsum; tibiae lack erect setae.

Measurements, minor worker: HW 0.41, HL 0.43, SL 0.34, EL 0.10, WL 0.47, PSL 0.01, PTW 0.07, PPW 0.09, CI 96, SI 85, PSLI 2, PPI 129 (n=2).

Measurements, major worker: HW 0.79, HL 0.87, SL 0.40, EL 0.12, WL 0.68, PSL 0.02, PTW 0.12, PPW 0.16, CI 91, SI 50, PSLI 3, PPI 133 (n=2).

Measurements, queen: HW 0.87, HL 0.81, SL 0.48, EL 0.26, WL 1.39, PSL 0.00, PTW 0.27, PPW 0.38, CI 108, SL 55, PSLI 0, PPI 139.

Biology. This species occurs in cloud forest to high montane oak forest. It is locally abundant around the type locality. Minor and major workers recruit to ground baits, and workers occur in Winkler samples of sifted litter and rotten wood. Nests have been found under epiphytes on recent branchfalls, under epiphytes on clay banks (road cut), in an acorn amongst ground litter, and in a cavity in a low, moss-covered live stem of *Siparuna*.

Comments. A complex of very similar species occurs in wet forests of Costa Rica: *P. kasparii*, *P. nitella*, and *P. sagittaria*. *Pheidole kasparii* as currently understood is a narrow endemic, known only from the vicinity of the type locality, and allopatric to the other two. *Pheidole nitella* and *P. sagittaria* occur on the Atlantic slope of Costa Rica, where they are sympatric.

The minor workers of the complex are not readily distinguishable, sharing the habitus of being very small, almost completely smooth and shining, and with very short propodeal spines that are no more than low angles in profile. The major workers are more distinct. The inner hypostomal teeth of *P. kasparii* are farther apart and smaller than the teeth of *P. nitella* and *P. sagittaria*, and recessed behind the ventral margin of the hypostomal bridge. *Pheidole sagittaria* has the ventral margin of the head in profile very flat, while on *P. kasparii* and *P. nitella* it is more convex. The head of *P. nitella* is relatively more narrow than the heads of *P. kasparii* and *P. sagittaria* (CI ~84 vs. 90-95).

Etymology: In honor of ant ecologist extraordinaire, Mike Kaspari.

***Pheidole kelainos* new species**
(Plate 46)

Pheidole JTL-070: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Limón: Res. Biol. Hitoy Cerere, 9.66773 -83.02953 ±50m, 150m, 13-Jun-2015, rainforest stream edge, nest in soil (J. Longino, JTL9268) [MUCR, unique specimen identifier CASENT0646308]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head somewhat tapering posteriorly; occipital carina moderately developed; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum uniformly foveate; propodeal spines long, similar in length to posterior face of propodeum; gaster smooth and shining; coarse, black, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color black. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base subterete, narrower than apical portion; face irregularly and shallowly rugulose foveolate over entire surface, rugulae fading posteriorly; propodeal spines long and thin, similar to minor; gastral dorsum shallowly foveolate on anterior third; abundant erect setae on sides of head, mesosomal dorsum, tibiae, gastral dorsum.

Measurements, minor worker: HW 0.62, HL 0.79, SL 1.1, EL 0.16, WL 1.06, PSL 0.15, PTW 0.11, PPW 0.19, CI 79, SI 177, PSLI 24, PPI 165 (n=2).

Measurements, major worker: HW 1.34, HL 1.42, SL 1.14, EL 0.21, WL 1.44, PSL 0.19, PTW 0.24, PPW 0.36, CI 95, SI 85, PSLI 14, PPI 151 (n=2).

Biology. This species occurs in lowland rainforest. It is known from two collections. At La Selva Biological Station a single minor worker was collected at a ground bait. At Hitoy Cerere, the type locality, a nest was found at a stream edge in forest. The nest was in rocky, sandy soil of a steep shaded bank, near the water. The entrance was an irregular hole, leading to a nest chamber about 10 cm deep. The chamber contained adult males, major and minor workers, and brood.

Comments. This species is most similar to *P. indagatrix*, with which it is sympatric. It differs in darker, coarser pilosity and longer propodeal spines (mean PSLI 24 vs. 14).

Etymology: Greek for black, in reference to the black setae.

***Pheidole lagunculiminor* new species**
(Plate 49)

Pheidole JTL-187: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Izabal: 17km ESE Morales, 15.40857 -88.69701 ±54 m, 530 m, 19-May-2009, lowland wet forest, nest in clay bank (J. Longino, JTL6631) [MCZC, unique specimen identifier CASENT0610935]. PARATYPES: major, minor worker, queen: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM, UVGC].

Geographic range. Guatemala, Honduras.

Diagnosis. ***Minor***: face shining, with patches of very faint foveolation; head rounded behind; occipital carina thin; promesonotal groove absent; lateral pronotum with sculpture similar to face; katepisternum uniformly

foveate; propodeal spines short, upturned, one quarter to one third length of posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color red brown. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; face foveolate throughout, overlain with reticulate rugulae; propodeal spines about one third length of posterior face of propodeum; gastral dorsum foveolate/shagreened on anterior third, rest smooth and shiny; abundant erect setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.64, HL 0.73, SL 0.95, EL 0.14, WL 0.98, PSL 0.05, PTW 0.11, PPW 0.16, CI 88, SI 147, PSLI 8, PPI 146 (n=2).

Measurements, major worker: HW 2.12, HL 2.34, SL 1.08, EL 0.27, WL 1.65, PSL 0.13, PTW 0.30, PPW 0.59, CI 91, SI 51, PSLI 6, PPI 200 (n=2).

Measurements, queen: HW 1.81, HL 1.69, SL 1.05, EL 0.36, WL 2.22, PSL 0.08, PTW 0.40, PPW 0.71, CI 107, SI 58, PSLI 5, PPI 178 (n=1).

Biology. This species occurs in lowland to lower montane wet forest, in second growth vegetation or mature forest. Minor and major workers recruit to ground baits. Nests are in clay banks. The nest entrance is a clay turret that protrudes a few cm from the bank, with a circular or slit-shaped entrance. One or a few chambers occur at about 10 cm depth, horizontally or obliquely downward into the bank. One fully excavated colony had a single colony queen. In one case a few seeds were found in a chamber.

Comments. This species is a smaller version of *P. lagunculinoda*. The minor worker of *P. lagunculiminor* has fainter sculpture on the face; the postpetiole is not enlarged and elongate (subequal in length to petiolar node, vs. almost twice as long as petiolar node in *P. lagunculinoda*), with shorter scapes (mean SI 147 vs. 160), and generally smaller (mean HW 0.64 vs. 0.76). The major worker of *P. lagunculiminor* has shorter propodeal spines (mean PSLI 6 vs. 14) and somewhat more elongate postpetiole in dorsal view, but otherwise is very similar to the major worker of *P. lagunculinoda*.

This species is almost certainly an allopatric sister species of *P. lagunculinoda*, dividing north and south of the Motagua fault region of Guatemala. Within ranges there is relatively little variation in the separatory characters, and there is no indication that this is continuous geographic variation, rather than species differences.

Etymology: Similar to *P. lagunculinoda*, but smaller.

Pheidole lamancha **new species**

(Plate 30)

Pheidole JTL-268: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Veracruz: Est. Biol. La Mancha, 19.59741 -96.37818 ±60 m, 20 m, 16-Jul-2016, tropical dry forest, at bait (ADMAC, Ba-F-10-1-01-01) [UNAM, unique specimen identifier CASENT0641071]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC, USNM, UNAM]; same data except Ba-F-10-1-01-07 [DZUP, JTLC].

Geographic range. Mexico (Veracruz).

Diagnosis. ***Minor***: face foveolate, with variably developed narrow smooth region on medial frons; head rounded behind; promesonotal groove impressed; entire mesosoma uniformly foveolate; propodeal spines short, about one fifth length of posterior face of propodeum; first gastral tergite faintly foveolate on anterior one quarter, rest smooth and shining; abundant short erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color dark brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base subterete, wider at apex than at base; face with mixed foveolation, reticulate rugae throughout, becoming weaker posteriorly, and with irregular shiny patches on medial frons; propodeal spines about one fifth length of posterior face of propodeum; first gastral tergite faintly foveolae on anterior fourth, rest smooth and shiny; sides of head with abundant erect setae; mesosomal dorsum and tibiae with abundant erect setae; first gastral tergite mostly covered with abundant, fully appressed, short pubescence, with cluster of erect setae near postpetiolar insertion; head light red brown with medial brown spot on frons, contrasting with darker brown mesosoma and gaster.

Measurements, minor worker: HW 0.53, HL 0.59, SL 0.72, EL 0.14, WL 0.77, PSL 0.03, PTW 0.11, PPW 0.14, CI 90, SI 134, PSLI 6, PPI 133 (n=1).

Measurements, major worker: HW 1.00, HL 1.00, SL 0.74, EL 0.18, WL 1.00, PSL 0.04, PTW 0.19, PPW 0.29, CI 101, SI 73, PSLI 4, PPI 151 (n=1).

Biology. This species occurs in lowland tropical dry forest. So far it is only known from La Mancha Biological Station, where it is common at ground baits and occasional in Winkler samples of sifted litter and rotten wood.

Comments. This species has a distinctive pilosity pattern shared with *P. acamata*, *P. potosiana*, and *P. psilogaster*. On the major worker, the gaster is covered with a plush layer of short, subdecumbent pubescence and any longer erect setae are absent or restricted to a few near the postpetiolar insertion. This contrasts with the rest of the body, which has a more "normal" condition, with abundant long suberect setae on the tibiae and mesosomal dorsum. *Pheidole acamata* and *P. lamancha* have minor workers with foveolate face; the others have smooth shiny faces. The major worker of *P. acamata* has much weaker and more shining face sculpture compared to *P. lamancha*, and the color is yellow vs. dark brown.

Etymology: From the type locality.

***Pheidole laselvoides* new species**
(Plate 3)

Pheidole JTL-218: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Heredia: 22km N Volcan Barba, 10.333 -84.067 ± 2km, 500 m, 15-Mar-1985, wet forest, nest in rotten wood (J. Longino, JTL0209) [MUCR, unique specimen identifier INBIOCRI002279737]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC USNM, MUCR].

Geographic range. Nicaragua to Panama.

Diagnosis. ***Minor***: face smooth and shining; promesonotal groove absent; promesonotum and katepisternum smooth and shiny; dorsal face of propodeum foveolate; anterior and dorsal faces of pronotum separated by a single transverse carina; propodeal spines short triangular denticles, < one fifth length of posterior face of propodeum; gaster smooth and shining; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae lack erect setae; color red brown. ***Major***: inner hypostomal teeth small denticles, inconspicuous, about half way between midline and outer hypostomal teeth; scape base terete; face mostly smooth and shining, with fine, somewhat closely spaced longitudinal carinulae on anterior third; propodeal spines short triangular teeth, upturned, < one fifth length of posterior face of propodeum; gastral dorsum smooth and shining; side of head with short suberect setae; mesosomal and gastral dorsum with abundant flexuous erect setae; tibiae without erect setae.

Measurements, minor worker: HW 0.38, HL 0.42, SL 0.35, EL 0.09, WL 0.47, PSL 0.02, PTW 0.06, PPW 0.10, CI 90, SI 92, PSLI 5, PPI 158 (n=6).

Measurements, major worker: HW 0.69, HL 0.80, SL 0.41, EL 0.11, WL 0.63, PSL 0.03, PTW 0.11, PPW 0.19, CI 87, SI 60, PSLI 5, PPI 177 (n=6).

Measurements, queen: HW 0.65, HL 0.66, SL 0.42, EL 0.20, WL 0.98, PSL 0.04, PTW 0.19, PPW 0.30, CI 99, SI 65, PSLI 6, PPI 151 (n=2).

Biology. This species inhabits lowland rain forest. Workers recruit to ground baits and are collected in Winkler samples of sifted leaf litter and rotten wood from the forest floor. Nests have been observed mostly in soft rotten wood on the forest floor. Nest have also been found under epiphyte mats in old treefalls and under a stone.

Comments. *Pheidole laselva* and *P. laselvoides* are a cryptic species pair that were initially conflated. DNA barcoding revealed two broadly sympatric clades, and subsequent examination revealed morphological differences in the major worker. The major of *P. laselvoides* has more and finer carinulae on the face between the frontal carinae; and the pilosity on the side of the head is shorter and more appressed. The minor workers are currently inseparable by visual inspection. Wilson's *P. ebenina* was synonymized under *P. laselva* by Longino (2009), prior to understanding of the two cryptic species. It has the major face sculpture of true *P. laselva* and remains a synonym.

Etymology: Similar to *P. laselva*.

***Pheidole lineafrons* new species**
(Plate 54)

Pheidole JTL-273: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Puntarenas: Monteverde, 10.31125 -84.80465 ±20 m, 1480 m, 27-Mar-2018, cloud forest, nest in clay bank (J. Longino, JTL10137) [MUCR, unique specimen identifier CASENT0644875]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face shiny, with faint foveolation on anterior half, arcuate carinulae between eye and frontal carinae, subparallel transverse carinulae on posterior half; head tapering posteriorly to thin occipital carina; promesonotal groove very weakly impressed; pronotal dorsum transversely carinulate; lateral pronotum very weakly foveolate peripherally, smooth and shiny medially; katepisternum foveolate; propodeal spines in form of low angles, not spiniform; first gastral tergite smooth and shining; abundant flexuous erect setae on mesosomal and gastral dorsum; tibia lacking erect setae; color orange. ***Major***: inner hypostomal teeth pronounced, closely spaced; scape base terete; face with faint foveolation overlain with subparallel longitudinal rugulae medial to eye, arcuate rugulae in antennal fossa, faint longitudinal carinulae on frons between frontal carinae, weak short transverse carinulae on posteriormost vertex lobes, rest of face smooth and shiny; propodeal spines short, < one fifth length of posterior face of propodeum; first gastral tergite smooth and shiny; sides of head with abundant erect setae; mesosomal and gastral dorsum with abundant erect setae; tibia with erect setae.

Measurements, minor worker: HW 0.70, HL 0.87, SL 1.10, EL 0.15, WL 1.20, PSL 0.02, PTW 0.15, PPW 0.21, CI 80, SI 157, PSLI 2, PPI 139 (n=1).

Measurements, major worker: HW 1.57, HL 1.63, SL 1.29, EL 0.24, WL 1.54, PSL 0.05, PTW 0.25, PPW 0.40, CI 96, SI 82, PSLI 3, PPI 157 (n=1).

Biology. This species occurs in cloud forest. It is known from one collection. Nocturnal foragers recruited to a bait at the foot of a 4-month old landslide in mature forest. The landslide formed a steep bare soil face about 10 m across and 20 m tall. Minor workers recruited from a nest entrance about 2 m away in the bank. The entrance was an irregular hole, with no infrastructure. Major workers were gathered near and just inside the entrance.

Comments. This is a highly distinctive species. The face of the minor worker has fine arcuate carinulae similar to other cloud forest species *P. innupta* and *P. alfaroi*. Compared to *P. innupta* the minor worker is orange (dark brown in *P. innupta*), has longer scapes (mean SI 157 vs. 136), and the head is more tapering posteriorly. Comared to *P. alfaroi* the minor worker is larger (mean HW 0.70 vs. 0.60) and the head is more tapering.

Etymology: In reference to the transverse striations on the face of the minor worker.

Pheidole longiscapa

Pheidole longiscapa Forel, 1901: 358. Lectotype major and associated paralectotype minor worker: Venezuela, Carabobo: Puerto Cabello (Forel) [MHNG, unique specimen identifier CASENT0908185] (AntWeb image examined).

Pheidole longiscapa r. *martensis* Forel, 1914: 615. Syntype major, minor worker: Colombia (Gaige) [MHNG, unique specimen identifiers CASENT0908184 (minor), CASENT0908183 (major)] (AntWeb images examined). Synonymy by Wilson, 2003: 205.

Pheidole cocciphaga Borgmeier, 1934: 99, fig. 3. Lectotype major worker and associated paralectotype minor worker: Suriname, Paramaribo [MZSP] (not examined). See also: Wilson, 2003: 181. **New Synonym**.

Comments. *Pheidole longiscapa* is a somewhat variable, weedy species that occurs from Nicaragua to Colombia, and eastward to French Guiana. The synonymy of *P. cocciphaga* is based on measurements, Borgmeier's description and figure, and Wilson's figures.

Pheidole luteagossamer new species

(Plate 44)

Pheidole JTL-208: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Nicaragua, Jinotega: PN Cerro Saslaya, 13.77030 -85.02513 ±100 m, 1120 m, 14-May-2011, montane wet forest, at bait (LLAMA, Ba-D-03-1-04-09) [MCZC, unique specimen identifier CASENT0628292]. PARATYPES: major, minor workers: same data as holotype [MCZC]; same data except 13.76751 -85.02469 ±100 m, 1040 m (Ba-D-03-1-02-05) [USNM]; same data except (Ba-D-03-1-02-15) [DZUP];

same data except 13.76958 -85.02458 ±100 m, 1080 m (Ba-D-03-1-03-03) [JTLC]; same data except 13.76859 -85.0252 ±20 m, 1090 m, 12-May-2011, montane wet forest, nest in soil (J.Longino, JTL7522) [CAS].

Geographic range. Honduras, Nicaragua.

Diagnosis. ***Minor***: face uniformly foveolate; promesonotal groove distinct, impressed; entire mesosoma foveolate, pronotal dorsum overlain to variable extent with reticulate rugulae; propodeal spines about one third length of posterior face of propodeum; gaster smooth and shining; dorsal mesosoma, gaster, and tibiae with abundant, flexuous, erect setae; color yellow. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face with foveolation and carinulae between eyes and frontal carinae, completely smooth and shining elsewhere; propodeal spines about one fourth length of posterior face of propodeum; first gastral tergite smooth and shiny; head, mesosoma, gaster, and tibiae covered with long, somewhat silky, subdecumbent setae.

Measurements, minor worker: HW 0.62, HL 0.70, SL 0.91, EL 0.15, WL 0.93, PSL 0.07, PTW 0.12, PPW 0.16, CI 89, SI 146, PSLI 11, PPI 141 (n=5).

Measurements, major worker: HW 1.03, HL 1.04, SL 0.87, EL 0.17, WL 1.07, PSL 0.08, PTW 0.17, PPW 0.24, CI 100, SI 86, PSLI 8, PPI 141 (n=5).

Biology. This species occurs in montane wet forest. All collections have been from about 1000-1600 m. Foragers are epigaeic, diurnal or nocturnal, and can be locally abundant at baits. Workers also occur in Winkler samples. One nest was encountered in bare soil of a recent landslide. Workers at a bait led to a simple crack in the soil, with no obvious nest entrance. The main nest chamber with abundant workers and brood was about 15 cm deep.

Comments. *Pheidole luteagossamer* is an interesting combination of other species. The minor workers are indistinguishable from *P. acamata*, and the majors are very similar to *P. biolleyi* from Costa Rica. Majors of *P. biolleyi* have the dorsal mesosoma glassier, with less sculpture.

Etymology: In reference to the yellow color and the woolly pilosity of the major worker.

Pheidole machaquila **new species**

(Plate 14)

Pheidole JTL-193: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Petén: 13km NW Machaquilá, 16.44612 -89.54969 ±59 m, 400 m, 29-May-2009, tropical moist forest, at bait (LLAMA, Ba-B-06-4-04-17) [MCZC, unique specimen identifier CASENT0614273]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM, UVGC].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face uniformly foveolate; promesonotal groove absent, promesonotum evenly convex; entire mesosoma foveolate; propodeal spines about two thirds length of posterior face of propodeum; gaster shagreened, matte; face, mesosomal dorsum, and gastral dorsum with sparse, short, erect setae; tibiae without erect setae; color orange yellow. ***Major***: inner hypostomal teeth distinct, closely spaced, blunt medial tooth also prominent; scape base terete; antennal scrobes very shallow, not sharply delimited; entire face foveolate, overlain with irregular, mostly longitudinal rugulae, these strongest anteriorly, fading posteriorly; propodeal spines about two thirds length of posterior face of propodeum; first gastral tergite entirely matte; abundant erect setae on sides of head, dorsal mesosoma, and gaster; tibiae lacking erect setae.

Measurements, minor worker: HW 0.45, HL 0.54, SL 0.62, EL 0.10, WL 0.62, PSL 0.09, PTW 0.08, PPW 0.12, CI 84, SI 136, PSLI 20, PPI 144 (n=2).

Measurements, major worker: HW 0.93, HL 1.01, SL 0.67, EL 0.12, WL 0.82, PSL 0.12, PTW 0.13, PPW 0.22, CI 92, SI 72, PSLI 13, PPI 173 (n=2).

Biology. This species is known from one site in the Petén region of Guatemala. It was an area with small patches of second growth moist forest on a karst landscape. The one collection was from a ground bait, with a strong recruitment of minor and major workers.

Comments. This species is similar to *P. phanigaster*. The minor worker differs in matte gaster (shiny in *P. phanigaster*). The major worker differs in longer scapes (mean SI 72 vs. 61) and lighter orange color.

Etymology: From the type locality.

***Pheidole marmor* new species**
(Plate 18)

Pheidole JTL-149: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Zacapa: 8.5km NE Tucultán, 15.05872 -89.67638 ±50 m, 1100 m, 6-Jul-2007, pine oak forest, ex sifted leaf litter (J. Longino, JTL6016-s) [MCZC, unique specimen identifier JTLC000009834]. PARATYPES: major, minor worker, queen: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM, UVGC].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face and entire mesosoma uniformly foveolate; promesonotal groove present, distinctly impressed; propodeal spines short, one quarter to one third length of posterior face of propodeum; gaster shagreened on anterior half, smooth and shining posteriorly; mesosomal dorsum with sparse stiff setae, tibia lacking erect setae or with one or two erect setae, gastral dorsum lacking appressed pubescence, and with no to sparse erect setae; color dark red brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face uniformly foveolate, overlain with variably developed irregular rugulae laterally, rugulae strongest between eye and antennal fossa, fading posteriorly; promesonotal groove impressed; propodeal spines about one third length of posterior face of propodeum; gastral dorsum shagreened on anterior half, smooth and shining posteriorly; pilosity pattern similar to minor worker, except with additional sparse, short, fully appressed setae on gastral dorsum; color dark red brown.

Measurements, minor worker: HW 0.47, HL 0.58, SL 0.69, EL 0.12, WL 0.73, PSL 0.04, PTW 0.13, PPW 0.15, CI 81, SI 148, PSLI 9, PPI 118 (n=1).

Measurements, major worker: HW 0.78, HL 0.86, SL 0.69, EL 0.15, WL 0.86, PSL 0.07, PTW 0.16, PPW 0.22, CI 91, SI 89, PSLI 9, PPI 133 (n=1).

Measurements, queen: HW 0.95, HL 0.88, SL 0.82, EL 0.30, WL 1.52, PSL 0.10, PTW 0.33, PPW 0.46, CI 108, SI 86, PSLI 11, PPI 139 (n=1).

Biology. This species is known from one Winkler sample of sifted litter and rotten wood, in a mid-elevation mesic pine-oak forest. Numerous minor workers, major workers, and two dealate queens occurred in the sample.

Comments. This species is relatively distinctive with respect to measurements. In appearance it is like a small version of *P. pugnax*.

Etymology: In reference to the marble mines that were near the type locality.

***Pheidole moskitia* new species**
(Plate 21)

Pheidole JTL-206: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Gracias a Dios: Las Marias, 15.7092 -84.86232 ±120 m, 90 m, 9-Jun-2010, tropical rainforest, at bait (LLAMA, Ba-C-07-1-03-08) [MCZC, unique specimen identifier CASENT0612085]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC]; same data except 15.71200 -84.86305 ±25 m, 100 m, ex sifted leaf litter (LLAMA, Wm-C-07-1-02) [CAS]; same data except 15.71011 -84.86304 ±20 m (Wm-C-07-1-03) [USNM]; same data except 15.72235 -84.88480 ±20 m, 620 m, 10-Jun-2010, tropical rainforest, ex sifted leaf litter (LLAMA, Wm-C-07-1-07) [DZUP]; same data except 15.72153 -84.88173 ±20 m, 560 m (Wm-C-07-1-09) [JTLC].

Geographic range. Honduras.

Diagnosis. ***Minor***: face and mesosoma uniformly foveolate, face and dorsal pronotum overlain with distinct reticulate rugulae; promesonotum box-like, promesonotal groove absent; propodeal spines about one third length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum and gaster; tibiae 1-3 erect setae; color red brown. ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; entire face feebly foveolate, overlain with irregular longitudinal rugulae, sculpture strongest anteriorly, fading posteriorly; propodeal spines one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum and gaster; tibiae with 2-3 suberect setae.

Measurements, minor worker: HW 0.49, HL 0.54, SL 0.50, EL 0.09, WL 0.63, PSL 0.06, PTW 0.09, PPW 0.15, CI 90, SI 103, PSLI 12, PPI 176 (n=5).

Measurements, major worker: HW 0.99, HL 1.03, SL 0.55, EL 0.12, WL 0.81, PSL 0.07, PTW 0.16, PPW 0.35, CI 96, SI 56, PSLI 8, PPI 224 (n=5).

Biology. This species occurs in lowland wet forest. It is known from two sites in southeastern Honduras. It is moderately abundant in Winkler samples. One series recruited to a bait.

Comments. COI data on BOLD suggest this species is related to *P. beloceps*. It shares the general habitus of *P. beloceps*, *P. belonorte*, and *P. debilis* but is somewhat larger (mean HW of minor worker 0.49 vs. 0.47 or less) and the major worker has a broader head (mean CI of major worker 96 vs. 85 or less). The minor worker of both *P. moskitia* and *P. debilis* have the side of the pronotum uniformly foveolate, while *P. beloceps* and *P. belonorte* have a medial smooth patch.

Etymology: From the type locality (La Moskitia region of southeastern Honduras).

***Pheidole muralla* new species**
(Plate 17)

Pheidole JTL-204: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Olancho: PN La Muralla, 15.09707 -86.73684 ±50 m, 1500 m, 4-May-2010, cloud forest stream edge, at bait (J. Longino, JTL6990.1) [MCZC, unique specimen identifier CASENT0615595]. PARATYPES: major, minor workers: same data as holotype [CAS, JTLC, MCZC]; same data except 15.09609 -86.73297 ±30 m, 1610 m, cloud forest, at bait (LLAMA, Ba-C-01-1-03-09) [USNM]; 15.0959 -86.73233 ±60 m, 1600 m (LLAMA, Ba-C-01-1-05-04) [DZUP]; 15.09544 -86.73873 ±60 m, 1440 m (LLAMA, Ba-C-01-2-03-07) [JTLC].

Geographic range. Guatemala, Honduras.

Diagnosis. ***Minor***: face smooth and shining; promesonotum smooth and shining; katepisternum mostly smooth and shining, posterior margin with thin strip of sculpture; faint foveolation on lower portion of side of propodeum, upper portion and dorsal face smooth and shining; promesonotal groove absent; propodeal spines about one half length of posterior face of propodeum; gaster smooth and shining; mesosomal dorsum and gaster with abundant short setae; tibiae with abundant, short, subdecumbent setae; color dark brown, tibiae lighter yellow brown. ***Major***: inner hypostomal teeth prominent, closely spaced; scape base terete; head subrectangular; antennal scrobes weakly impressed, delimited by carinulae; posteromedian head and vertex lobes depressed (conspicuous in lateral view); face generally shiny, with smooth interspaces and prominent carinulae, these longitudinal anterolaterally, forming transverse arcs medially, and reticulate on vertex lobes; propodeal spines about one half length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; dorsal mesosoma and gaster with abundant flexuous erect setae; tibiae with abundant, scruffy, suberect setae; color similar to minor worker.

Measurements, minor worker: HW 0.47, HL 0.51, SL 0.45, EL 0.11, WL 0.62, PSL 0.04, PTW 0.09, PPW 0.13, CI 93, SI 96, PSLI 9, PPI 152 (n=5).

Measurements, major worker: HW 0.87, HL 0.99, SL 0.47, EL 0.14, WL 0.89, PSL 0.08, PTW 0.17, PPW 0.31, CI 88, SI 54, PSLI 10, PPI 179 (n=5).

Biology. This species occurs in cloud forest. It is most often collected at baits and in Winkler samples. A nest entrance was observed in a nearly vertical clay bank on a road edge in mature cloud forest. It was a tiny circular hole on the bank with a tongue-shaped apron of clay extending below the hole. The apron was covered with white dots that looked like fungal masses. The observation was at night, and a few minor workers were out on surface around hole. One of them was observed picking up one of the white particles. Excavation to about 10cm deep failed to locate chambers.

Comments. The minor worker of this species is similar to *P. albipes* but larger (mean HW 0.47 vs. 0.37), and the major worker is similar to *P. janzeni* but with longer propodeal spines (mean PSLI 10 vs. 1).

Etymology: From the type locality.

***Pheidole musacolor* new species**
(Plate 55)

Pheidole JTL-243: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Limón: Cerro Plátano, 9.86621 -83.24203 ±50m, 1110m, 19-Jun-2015, cloud forest, along steep ridge near peak, at bait (ADMAC, Ba-E-03-1-03-03) [MUCR, unique specimen identifier CASENT0636691]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head evenly rounded posteriorly; occipital carina thin; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum uniformly foveate; propodeal spines long, similar in length to posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color yellow. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base subterete, narrower than apical portion; face with irregular, rugulose foveolate sculpture anteriorly, to about level of eyes, remainder of face smooth and shiny; promesonotal groove impressed; propodeal spines about half length of posterior face of propodeum; gastral dorsum smooth and shining; abundant, erect, flexuous setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.73, HL 0.87, SL 1.20, EL 0.19, WL 1.12, PSL 0.18, PTW 0.14, PPW 0.20, CI 85, SI 164, PSLI 25, PPI 140 (n=1).

Measurements, major worker: HW 1.52, HL 1.56, SL 1.18, EL 0.25, WL 1.42, PSL 0.18, PTW 0.26, PPW 0.35, CI 97, SI 77, PSLI 12, PPI 132 (n=1).

Biology. This species occurs in montane wet forest. It is known from two ground baits.

Comments. This species appears to be part of a complex of large, yellow species that occur in the mountains of southern Costa Rica. It is similar to the species *P. familiaparra*, *P. savegre*, and *P. tinamu* from the Pacific slope. It is most similar to *P. savegre*, differing in finer, lighter-colored pilosity, and the major worker has a smoother, less sculptured face. The minor worker of *P. familiaparra* has a more tapered posterior head and a more pronounced occipital carina. The minor worker of *P. tinamu* is not readily distinguishable, but the major worker of *P. tinamu* is distinctive, with strongly heart-shaped head and strongly produced promesonotum. See additional notes under *P. tinamu*.

Etymology: The color of a banana.

***Pheidole musinermis* new species**
(Plate 42)

Pheidole JTL-123: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Cerro Plano, 9.48117 -83.96363 ±50 m, 1060 m, 6-Jul-2015, ridgetop cloud forest, at bait (ADMAC, Ba-E-06-2-04-07) [MUCR, unique specimen identifier CASENT0631280]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica, Panama.

Diagnosis. ***Minor***: face smooth and shining; head strongly tapering posteriorly; occipital carina strongly developed; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum faintly foveate; propodeal spines nearly absent; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color yellow. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base subterete, narrower than apical portion; face with irregular rugulae anteriorly, entire face with faint foveolate sculpture; promesonotal groove impressed; propodeal spines forming obtuse angles, not dentiform; gastral dorsum foveolate on anterior half; abundant, erect, flexuous setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.60, HL 0.87, SL 1.37, EL 0.17, WL 1.23, PSL 0.00, PTW 0.13, PPW 0.21, CI 69, SI 229, PSLI 0, PPI 154 (n=3).

Measurements, major worker: HW 1.59, HL 1.70, SL 1.32, EL 0.25, WL 1.78, PSL 0.02, PTW 0.31, PPW 0.45, CI 94, SI 83, PSLI 2, PPI 147 (n=2).

Biology. This species occurs in lower montane wet forest. Most collections are from ground baits, to which minors and majors recruit. Minor workers have been collected in a pan trap and a Winkler sample of sifted litter.

Comments. This species is part of a complex of large, yellow species that occur in Costa Rica. It is similar to *P. familiaparra*, *P. savegre*, *P. musacolor*, and *P. tinamu*, but is distinguishable by the lack of propodeal spines in the minor worker.

Etymology: The color of a banana, and lacking propodeal spines.

Pheidole natalie **new species**
(Plate 10)

Pheidole JTL-211: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Nicaragua, Jinotega: PN Cerro Saslaya, 13.76751 -85.02469 ±100 m, 1040 m, 14-May-2011, montane wet forest, at bait (LLAMA, Ba-D-03-1-02-07) [MCZC, unique specimen identifier CASENT0628205]. PARATYPES: major, minor workers: same data as holotype [MCZC]; same data except Ba-D-03-1-02-04 [CAS]; Ba-D-03-1-02-11 [DZUP]; Ba-D-03-1-02-15 [JTLC]; 13.76837 -85.02436 ±100 m (Ba-D-03-1-01-15) [USNM].

Geographic range. Mexico (Oaxaca) to Nicaragua.

Diagnosis. ***Minor***: face and mesosoma uniformly foveolate, with variably developed small smooth area on lower margin of lateral pronotum; promesonotum evenly convex, promesonotal groove absent or very weakly impressed; propodeal spines one fourth to one third length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum and gaster; tibiae with 2-3 erect setae; color orange (or rarely bicolored; see Comments). ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; face with distinct scrobes, delimited dorsally by frontal carinae and forming concave trough below them, ventral and posterior margins less delimited, surface of scrobe smooth and shiny; head depressed posteriorly, forming transverse depression between frontal carinae and vertex lobes, particularly visible in profile; face surface generally shiny, space between frontal carinae smooth, space between eye and antennal fossa and vertex lobes with widely separated, subparallel, longitudinal carinae; propodeal spines one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.44, HL 0.48, SL 0.44, EL 0.10, WL 0.59, PSL 0.04, PTW 0.08, PPW 0.13, CI 93, SI 99, PSLI 9, PPI 159 (n=13).

Measurements, major worker: HW 0.88, HL 1.05, SL 0.44, EL 0.14, WL 0.86, PSL 0.07, PTW 0.18, PPW 0.32, CI 85, SI 50, PSLI 8, PPI 184 (n=10).

Biology. This species occurs in cloud forest habitats. It is common at baits on the forest floor and in Winkler samples. Three nests have been observed. One was in a small patch of exposed clay soil. Workers came to a bait from a small round entrance hole. Excavation was attempted, following a very small tunnel in clay. It meandered and was very difficult to follow. At about 20 cm deep a few adult males and a larva were discovered loose in the jumbled clay, presumably from a disrupted chamber. Nearby were a few major workers in part of the tunnel system. Workers seemed to be thinly spread in tiny tunnels in the clay and a distinct chamber was never uncovered. Another nest was observed in a trail-side clay wall, following minor and major workers that came to bait. The entrance was a small clay turret. A third nest was observed under a stone.

Comments. This species is part of a complex of species discussed under *P. andersoni*. Three widely separated populations are here identified as *P. natalie* because they are morphologically very similar. The populations are a site in the Sierra Mazateca in Oaxaca, Mexico; Cusuco National Park in Honduras; and specimens from two sites in Nicaragua, Cerro Musún and Saslaya National Park. DNA barcodes closely cluster specimens from the two Nicaragua sites. However, there are no sequence data for specimens from Honduras and Mexico. Given the similarity of species across the complex, the three populations could easily be separate lineages that are not necessarily part of a single clade.

The population in Cusuco National Park in Honduras showed color polymorphism. At some baits the minor workers were all the usual uniform yellow orange. In others, minor workers showed the harlequin coloration of *P. balatro*, which is sympatric at the site, and *P. zannia*, which occurs in other parts of Honduras. *Pheidole natalie* and

P. zannia are similar and probably closely related. One possibility is that there is introgression or hybrization between *P. natalie* and *P. zannia*, with Cusuco being a contact zone. One bait with a strong recruitment had both color forms, and there was intergradation to some extent.

Etymology: In honor of Natalie Vandeven Longino, the newest member of the family.

Pheidole nephele **new species**

(Plate 23)

Pheidole JTL-205: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Olancho: 11km NNE Catacamas, 14.95031 -85.86229 ±106 m, 1470 m, 12-May-2009, cloud forest, at bait (J. Longino, JTL6513) [MCZC, unique specimen identifier CASENT0609968]. PARATYPES: major, minor workers: same data as holotype [MCZC]; same data except JTL6509.2 [CAS]; same data except ex sifted leaf litter (J. Longino, JTL6529-s) [DZUP, JTLC, USNM].

Geographic range. Honduras, Nicaragua.

Diagnosis. ***Minor***: face and mesosoma uniformly foveolate, face and dorsal pronotum overlain with faint reticulate rugulae to variable extent; promesonotal groove absent; propodeal spines about one half length of posterior face of propodeum; gaster smooth and shining; abundant flexuous erect setae on mesosomal dorsum and gaster; tibiae without erect setae; color light to dark brown. ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; face with very shallow scrobal impressions; face with subparallel, longitudinal carinae between eye and antennal fossa and between frontal carinae, foveolate in scrobal areas, posterior face and vertex lobes smooth and shiny; propodeal spines one third to one half length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum and gaster; tibiae with 0-3 suberect setae.

Measurements, minor worker: HW 0.50, HL 0.56, SL 0.48, EL 0.09, WL 0.65, PSL 0.06, PTW 0.09, PPW 0.15, CI 90, SI 94, PSLI 12, PPI 163 (n=14).

Measurements, major worker: HW 1.00, HL 1.11, SL 0.53, EL 0.14, WL 0.89, PSL 0.09, PTW 0.16, PPW 0.29, CI 90, SI 53, PSLI 9, PPI 187 (n=6).

Measurements, queen: HW 1.00, HL 0.99, SL 0.59, EL 0.28, WL 1.64, PTW 0.30, PPW 0.58, CI 101, SI 58, PPI 194 (n=5).

Biology. This species occurs in cloud forest habitats. It is common at baits on the forest floor and in Winkler samples. Nests have been found in chambers in rotten wood and under loose bark of rotten wood. At Cerro Saslaya in Nicaragua, this was a common species on the mossy peak at 1600 m. Populous nests could be found in rotten wood beneath epiphyte mats.

Comments. *Pheidole nephele* is very similar to another cloud forest species in the region, *P. rectisentis*. The major worker is relatively distinct. The vertex lobes are smooth and shiny, and the dorsal surface of the mandible is smooth and shiny with small puncta. In contrast, *P. rectisentis* majors have coarse reticulate rugose and foveolate sculpture over the entire face, including the vertex lobes, and the mandible has coarse striae on the sides of the basal half and coarse puncta on rest of the dorsal surface. Minor workers are extremely similar. Minors of *P. rectisentis* have more impressed striate sculpture on the basal half of the mandibles, paralleling the difference in the majors, but the difference is subtle. Also, foveolation on the side of the head behind the eye is somewhat stronger. *Pheidole rectisentis* may also have a few differentiated erect setae on the tibiae.

DNA barcoding data show a clade with three subclusters: La Muralla in Honduras, Sierra de Agalta in Honduras and the Ocotal area of Nicaragua, and Cerro Saslaya in Nicaragua. This suggests one lineage with multiple allopatric populations on mountain tops in Honduras and Nicaragua, with sufficient time and reproductive isolation to allow sequence divergence among the populations.

Etymology: Greek for cloud, in reference to the cloud forest habitat of this species.

Pheidole nitidicollis

Pheidole dimidiata var. *nitidicollis* Emery, 1896: 79. Lectotype major worker and associated paralectotype minor worker: Costa Rica, Heredia: Jiménez [a site near present day La Selva Biological Station] (Alfaro) [MCSN] (not examined).

Pheidole nitidicollis: Wilson, 2003: 474 (raised to species).

Pheidole sagana Wheeler, W.M. 1934: 169. Lectotype major worker and associated paralectotype minor worker: Mexico, Veracruz, Mirador (Skwarra) [MCZC] (examined). See also: Wilson, 2003: 501. Synonymy by Longino, 2009: 58.

Pheidole chalcoides Wilson, 2003: 397, figs. Holotype major worker and associated paratype minor worker: Mexico, Veracruz: 3 km west of Fortin De Las Flores, 1000 m (R. J. Hamton and A. B. Hamton) [MCZC] (examined). **New Synonym**.

Comments. The types of *P. chalcoides* are typical specimens of the widespread arboreal species *P. nitidicollis*.

Pheidole nubicola

Pheidole nubicola Wilson, 2003: 329, figs. Holotype major worker and associated paratype minor worker: Mexico, Tamaulipas: Rancho del Cielo, Sierra de Guatemala, 1070 m (Cornell University Expedition group, 1965) [MCZC] (examined).

Pheidole cielana Wilson, 2003: 275, figs. Holotype major worker and associated paratype minor worker: Mexico, Tamaulipas: Rancho Cielo, 17 km northwest of Gomez Farias, 1160 m (Philip S. Ward) [MCZC] (examined). **New Synonym**.

Pheidole petrensis Wilson, 2003: 337, figs. Holotype major worker and associated paratype minor worker: Mexico, Morelos: 24 km west of Cuernavaca, 2200 m (W. P. MacKay) [MCZC] (examined). **New Synonym**.

Comments. Additional material from Rancho Cielo reveals continuous character variation uniting Wilson's concepts of *P. cielana* and *P. nubicola* at this site. The types of *P. petrensis* from Morelos are also a close match, as is material from montane sites in Veracruz. I interpret this as a single widespread montane species in eastern Mexico.

Pheidole obturaculum new species

(Plate 33)

Pheidole JTL-266: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Veracruz: Las Cañadas, 19.1906 -96.99055 ±60 m, 1390 m, 1-Jul-2016, montane wet forest, at bait (ADMAC, Ba-F-07-1-04-09) [UNAM, unique specimen identifier CASENT0640871]. PARATYPES: major, minor workers: same data as holotype [UNAM]; Santuario, INECOL, Xalapa, 19.5123 -96.9357 ±60 m, 1330 m, 14-Jul-2016, cloud forest, at bait (ADMAC, Ba-F-09-1-03-03) [MCZC]; Ba-F-09-1-03-08 [CAS, USNM].

Geographic range. Mexico (Veracruz).

Diagnosis. ***Minor***: face uniformly foveolate; promesonotum evenly arched; promesonotal groove not impressed; most of mesosoma foveolate, except for medial shiny patch on lateral pronotum; propodeal spines about one fourth length of posterior face of propodeum; gaster smooth and shining; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster; color dark brown. ***Major***: inner hypostomal teeth stout, closely spaced; scape base flattened, curved at base, as wide at base as at apex; antennal scrobes pronounced, well-delimited dorsally and ventrally; face phragmotic, anterior frons, clypeus, and mandibles forming single, downturned, flattened surface; entire flat surface, including mandible surface, reticulate rugose; rest of face with faint foveolation, overlain with subparallel, longitudinal carinulae anteriorly, reticulate rugae posteriorly; propodeal spines about one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.56, HL 0.61, SL 0.54, EL 0.10, WL 0.76, PSL 0.04, PTW 0.12, PPW 0.16, CI 91, SI 98, PSLI 8, PPI 138 (n=2).

Measurements, major worker: HW 1.01, HL 1.36, SL 0.58, EL 0.16, WL 1.16, PSL 0.09, PTW 0.24, PPW 0.37, CI 74, SI 58, PSLI 9, PPI 159 (n=2).

Biology. This species occurs in cloud forest habitats. Minor and major workers recruit to ground baits.

Comments. This is clearly a member of the *P. lamia* complex, related to *P. lamia*, *P. pelor*, and *P. colobopsis*. *Pheidole lamia* and *P. pelor* are smaller, light-colored species from the southern United States. The minor workers of *P. colobopsis* and *P. obturaculum* are very similar. The major worker of *P. colobopsis* has more strongly developed phragmosis, with head expanding anteriorly in both face and lateral view. The head of the major worker

of *P. obturaculum* in face view is rectangular, not expanding anteriorly, and in lateral view the head is relatively less expanded anteriorly.

Etymology: Latin for stopper or plug, in reference to the phragmotic major worker.

***Pheidole passivaeferox* new species**
(Plate 25)

Pheidole JTL-231: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Heredia: La Selva Biological Station, 10.43333 -84.01667 ± 2 km, 50 m, 21-Jul-1986, lowland rainforest, nest in *Piper coenocladum* (J. Longino, JTL1429) [MUCR, unique specimen identifier INBIOCRI002279624]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Nicaragua, Costa Rica.

Diagnosis. ***Minor***: face smooth and shining, with variably developed faint patches of foveolation at margins; head rounded behind; promesonotal groove absent; pronotum mostly smooth and shining, with patches of weak foveolation on humeri and ventral margins; promesonotal dorsum grading to foveolate posteriorly; katepisternum foveolate; propodeal spines relatively thin and spiniform, about one third length of posterior face of propodeum; gaster smooth and shining; abundant, flexuous, almost woolly setae on mesosomal dorsum, tibiae, and gastral dorsum; color yellow brown. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; frontal carinae produced anteriorly as elevated, triangular teeth, most visible in profile; head elongate rectangular; scrobes shallowly impressed; face heavily sculptured, mostly reticulate rugose, rugae becoming more transversely oriented posteriorly; propodeal spines spiniform, about one fourth length of posterior face of propodeum; gastral dorsum smooth and shiny; abundant erect setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.51, HL 0.58, SL 0.40, EL 0.12, WL 0.73, PSL 0.04, PTW 0.12, PPW 0.16, CI 88, SI 79, PSLI 9, PPI 132 (n=7).

Measurements, major worker: HW 0.80, HL 1.08, SL 0.43, EL 0.14, WL 1.04, PSL 0.09, PTW 0.18, PPW 0.26, CI 74, SI 54, PSLI 11, PPI 141 (n=5).

Measurements, queen: HW 0.71, HL 0.90, SL 0.46, EL 0.24, WL 1.29, PSL 0.07, PTW 0.20, PPW 0.32, CI 80, SI 65, PSLI 10, PPI 164 (n=2).

Biology. This species occurs in lower rainforest. It is a specialized plant ant, nesting in domatia of several species of myrmecophytic *Piper* (Risch *et al.* 1977, Letourneau 1983, Tepe *et al.* 2004).

Comments. One of the myrmecophytic systems that has evolved in the Neotropics involves the plant genus *Piper* and specialized *Pheidole* inhabitants. A set of multiple *Piper* species have modified clasping petioles and stem pith that favors nesting by *Pheidole*. These *Piper* species occur in lowland rainforests from parts of Nicaragua, across all of Costa Rica, and into parts of adjacent Panama. The evolution of the plants involved has received attention (Tepe *et al.* 2004), as have the ecological relationships of ants and plants (Letourneau 1983), but the taxonomy of the ants has been neglected. The ant involved has been assumed to be a single species, *P. bicornis*. However, there are morphological discontinuities that suggest a clade of three related species.

The types of *P. bicornis*, which are from far southwestern Panama, and almost all the collections from the adjacent Pacific lowlands of Costa Rica have major workers with relatively broad heads (CI 80-83; n=2). All the collections from the Atlantic lowlands of Costa Rica and Nicaragua have noticeably more narrow heads (CI 72-76; n=5). Both of these species have the minor workers with a smooth, shiny face. Disjunctions of insect clades across the mountains of Costa Rica are repeatedly being shown to be relatively old, with varying degrees of morphological divergence and at a level of genetic and morphological separation that warrants species status.

An unexpected discovery was a third species, described here as *P. bicornisculpta*, from an ant *Piper* on the Pacific slope of Costa Rica, very near populations of true *P. bicornis*. This species has the major worker smaller overall (HW 0.92 vs. > 1.00), intermediate with respect to head shape (CI 78), and with a striking difference in the head shape and sculpture of the minor worker. The face of the minor is fully foveolate, overlain with faint rugulae. Additional differentiating characters are in the species description.

Etymology: In reference to the "passive aggressive" nature of host plant defense by this specialized plant ant (Letourneau 1983).

***Pheidole perissothrix* new species**
(Plate 9)

Pheidole JTL-175: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Izabal: 16km ESE Morales, 15.41764 -88.69683 ±70 m, 410 m, 19-May-2009, 2º lowland rainforest, ex sifted leaf litter (LLAMA, Wm-B-04-2-09) [MCZC, unique specimen identifier CASENT0611573]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC]; same data except 15.41274 -88.71023 ±27 m, 415 m (Wm-B-04-2-05) [DZUP, USNM]; 5km NW Morales, 15.51133 -88.86185 ±35 m, 195 m, 18-May-2009, 2º lowland rainforest, ex sifted leaf litter (LLAMA, Wm-B-04-1-04) [JTLC, UVGC].

Geographic range. Guatemala to Costa Rica.

Diagnosis. ***Minor***: face uniformly foveolate; promesonotal groove absent; entire mesosoma foveolate; propodeal spines about one third length of posterior face of propodeum; gaster smooth and shining; setae on face and dorsal mesosoma short, curved; setae on gastral dorsum short, decumbent, often minutely branched (typically trifid); tibiae without erect setae; color orange yellow. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; face with shallow antennal scrobes, dorsal margin delimited by extension of frontal carinae, ventral margin indistinct; face with subparallel, well-spaced, longitudinal carinae extending to vertex margin, interspaces smooth and shiny or with faint microsculpture; propodeal spines about one quarter length of posterior face of propodeum; gastral dorsum smooth and shining; pilosity on sides of head short, decumbent, other pilosity similar to minor worker.

Measurements, minor worker: HW 0.43, HL 0.47, SL 0.41, EL 0.08, WL 0.46, PSL 0.04, PTW 0.09, PPW 0.11, CI 91, SI 97, PSLI 9, PPI 128 (n=2).

Measurements, major worker: HW 0.72, HL 0.74, SL 0.43, EL 0.11, WL 0.60, PSL 0.05, PTW 0.13, PPW 0.21, CI 97, SI 60, PSLI 6, PPI 154 (n=2).

Biology. This species occurs in lowland wet to dry forest, typically in second growth areas. It is known mostly from Winkler samples of sifted litter and rotten wood. It occurs rarely at ground baits. Two collections from northwestern Costa Rica are a worker from a pitfall trip and a dealate queen from a Malaise trap.

Comments. *Pheidole perissothrix* in habitus is very similar to *P. glomericeps* and *P. flavens*, and it could easily be misidentified as these more common species. It differs in the distinctive short, curved, and often branched pilosity. Other "*flavens*" type species (*P. exigua*, *P. flavens*, *P. glomericeps*, *P. moerens*, *P. navigans*) have typical pilosity, which is longer, less curved, and suberect. COI barcoding on BOLD clusters two specimens from northwestern Costa Rica with a specimen from the Caribbean coast of Honduras. The image of a headless worker on BOLD matches the morphological features described above. The COI cluster is isolated in *Pheidole* and is not near *P. flavens* or *P. glomericeps*.

Etymology: In reference to the unusual setae.

***Pheidole platyscapa* new species**
(Plate 43)

Pheidole JTL-224: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Nicaragua, Madriz: 8km S Somoto, 13.40463 -86.58306 ±20 m, 1390 m, 22-Apr-2011, coffee farm, nest in stream bank (J.Longino, JTL7389) [MCZC, unique specimen identifier CASENT0619339]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM].

Geographic range. Nicaragua.

Diagnosis. ***Minor***: face smooth and shining; head rounded behind; occipital carina thin; promesonotal groove present; pronotum and dorsal mesonotum smooth and shining, rest of mesosoma foveolate; propodeal spines upturned, one quarter to one third length of posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color red brown. ***Major***: inner hypostomal teeth acicular, widely spaced; scape base thickened, somewhat flattened, curved, as wide at basal curve as at apex; face mostly smooth and shining, overlain with reticulate rugae anteriorly; propodeal spines about one fourth length

of posterior face of propodeum; gastral dorsum smooth and shiny; abundant erect setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.61, HL 0.73, SL 0.95, EL 0.16, WL 0.93, PSL 0.06, PTW 0.11, PPW 0.17, CI 84, SI 156, PSLI 9, PPI 151 (n=5).

Measurements, major worker: HW 1.17, HL 1.19, SL 0.98, EL 0.20, WL 1.18, PSL 0.08, PTW 0.20, PPW 0.29, CI 98, SI 84, PSLI 7, PPI 144 (n=4).

Biology. This species occurs in lower montane wet forest and in open, agricultural areas. Minor and major workers recruit to ground baits, and workers occur in Winkler samples of sifted litter and rotten wood. A nest was observed in soil of a stream bank, in a coffee plantation. While night collecting in a small dry stream channel in a coffee farm, a few minor workers were foraging on the bank. Baiting recruited more minor workers from a nest entrance that was an unadorned crack in a vertical bank. Excavation revealed nest chambers 5-10 cm deep, with abundant minors and majors and some brood. The nest continued deeper but was not excavated further.

Comments. This species is very similar to *P. guerrerana*, with which it is broadly sympatric. *Pheidole platyscapa* has the scape base of the major relatively broader and flatter, and the pilosity is shorter in both castes. DNA sequence data clearly separate the two species.

Etymology: In reference to the flattened scape.

Pheidole plebecula

Pheidole plebecula Forel, 1899: 68. Holotype major worker: Costa Rica, Alajuela (Alfaro) [MSNG, unique specimen identifier CASENT0904359] (AntWeb image examined).

Pheidole texticeps Wilson, 2003: 240, figs. Holotype major worker and associated paratype minor worker: Costa Rica, Heredia, La Selva Biological Station, 1988 (S. Cover) [MCZC] (examined). **New Synonym**.

Pheidole perdiligens Wilson, 2003: 213, figs. Holotype major worker and associated paratype minor worker: Costa Rica, Puntarenas, Corcovado National Park, Osa Peninsula, Sirena, 28 Feb 1979, secondary rainforest, <1/2mi from coast, rotten branch on forest floor (S. P. Cover CR312) [MCZC] (examined). **New synonym**. Synonymized under *P. texticeps* by Longino, 2009: 85.

Comments. Wilson (2003) was unable to locate the type of *P. plebecula* and left it *incertae sedis*. The types were located and imaged for AntWeb by the Fisher lab. The images easily match Wilson's concept of *P. texticeps*.

Local populations of *P. plebecula* vary greatly in color and sculpture. Color varies from yellow orange to dark brown, and to varying extent bicolored, with lighter head and mesosoma and darker gaster. The face of the major varies from being entirely foveolate/rugulose to completely smooth and shining. Pilosity can vary as well, with most populations having multiple pairs of stiff setae on the mesosomal dorsum, but some with no dorsal setae. One of the variants, from Volcán Atitlán, Guatemala, was initially separated as the morphospecies JTL199. In Economo *et al.* (2019) the two species *P. texticeps* and *P.* JTL199 appear together, with little genetic divergence. These can now both be identified as *P. plebecula*.

Pheidole probolonotum new species

(Plate 41)

Pheidole JTL-259: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Veracruz: Estación de Biología Los Tuxtlas, 18.58461 -95.07375 ±20 m, 150 m, 31-May-2016, mature wet forest, nest in clay bank (J. Longino, JTL9560) [UNAM, unique specimen identifier CASENT0631751]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, UNAM, USNM].

Geographic range. Mexico (Veracruz).

Diagnosis. ***Minor***: face partially smooth and shining, with discrete patches of faint foveolation scattered over surface; head weakly emarginate behind; promesonotal groove strongly impressed, mesonotum strongly produced, angulate; pronotum smooth and shiny; katepisternum foveolate; propodeal spines about two thirds length of posterior face of propodeum; gaster smooth and shining; pronotum with 0-2 pairs short stiff erect setae; tibiae lack

erect setae; gaster with very sparse, fully appressed short pubescence, 0-few longer erect setae; color dark brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face foveolate throughout, overlain with reticulate rugulae; mesonotum strongly produced; propodeal spines about two thirds length of posterior face of propodeum; gastral dorsum smooth and shiny; pilosity pattern similar to worker, with dorsal surfaces nearly devoid of erect setae.

Measurements, minor worker: HW 0.60, HL 0.67, SL 0.79, EL 0.16, WL 0.88, PSL 0.10, PTW 0.14, PPW 0.21, CI 91, SI 130, PSLI 16, PPI 148 (n=1).

Measurements, major worker: HW 0.93, HL 0.99, SL 0.73, EL 0.18, WL 0.95, PSL 0.12, PTW 0.21, PPW 0.33, CI 94, SI 78, PSLI 13, PPI 154 (n=1).

Biology. This species occurs in lowland rainforest. Workers recruit to ground baits and occur in Winkler samples of sifted litter and rotten wood. A nest was discovered in a vertical clay bank in forest. The entrance was an irregular opening, leading to shallow chambers. So far this species is known only from Los Tuxtlas Biological Station.

Comments. This species is a version of *P. plebecula*. *Pheidole plebecula* is highly geographically variable (see Comments under *P. plebecula*) and *P. probolonotum* is within the global range of variation of *P. plebecula.* However, it is sympatric with a regional form of *P. plebecula*. Compared to the regional form, the dorsal pilosity is reduced and the face of the minor worker has a mix of smooth and foveolate sculpture (smooth in the regional form of *P. plebecula*).

Etymology: In reference to the strongly projecting mesonotum.

Pheidole rima **new species**
(Plate 35)

Pheidole JTL-239: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Veracruz: 8km WSW Xalapa, 19.52181 -96.98883 ±50 m, 1500 m, 5-Mar-2015, wet riparian forest, under epiphytes (J. Longino, JTL9185) [UNAM, unique specimen identifier CASENT0633307]. PARATYPES: major, minor worker, dealate queen: same data as holotype [CAS, UNAM]; same data except 19.52279 -96.99104 ±20 m, 1500 m, 22-Jun-2016, 2nd growth cloud forest, nest in epiphytes (J. Longino, JTL9661) [MCZC, USNM].

Geographic range. Mexico (Veracruz, Oaxaca).

Diagnosis. ***Minor***: face foveolate, overlain with faint reticulate rugulae; head flattened to slightly excavate behind; occipital carina thin, not visible in face view; promesonotal groove absent; pronotal humeri with short triangular tubercles; mesosoma entirely foveolate; propodeal spines about as long as posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; bicolored, red head and mesosoma, contrasting black gaster. ***Major***: inner hypostomal teeth distinct, closely spaced, medial tooth also well developed; scape base terete; head somewhat cordate, posterior margin deeply excavate medially; scrobal spaces faintly impressed; face foveolate throughout, overlain with reticulate rugulae laterally and posteriorly, longitudinal rugulae medially between frontal carinae; propodeal spines about two thirds length of posterior face of propodeum; gastral dorsum smooth and shiny; abundant erect setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.57, HL 0.62, SL 0.66, EL 0.13, WL 0.77, PSL 0.10, PTW 0.12, PPW 0.16, CI 92, SI 117, PSLI 17, PPI 134 (n=2).

Measurements, major worker: HW 1.13, HL 1.12, SL 0.71, EL 0.17, WL 1.00, PSL 0.13, PTW 0.19, PPW 0.25, CI 101, SI 63, PSLI 11, PPI 131 (n=2).

Measurements, queen: HW 1.07, HL 0.99, SL 0.74, EL 0.27, WL 1.76, PSL 0.10, PTW 0.32, PPW 0.54, CI 108, SI 69, PSLI 10, PPI 166 (n=1).

Biology. This species occurs in montane wet forest, where it can be locally abundant. It appears to be mainly arboreal. Minor and major workers recruit to ground baits. Workers occur in Winkler samples of sifted litter and rotten wood, in beating samples, and in Malaise traps. Multiple nests have been observed under epiphytes in treefalls. A nest was observed in live stems of an understory scandent shrub. One foundress queen, tentatively identified as this species, was found in a chamber in a clay bank.

Comments. *Pheidole rima* (mountains of Veracruz and Oaxaca, Mexico, not including Sierra de Los Tuxtlas), *P. floricola* (Sierra de Los Tuxtlas to Costa Rica), *P. caltrop* (Panama), *P. pilispina* (Panama), and *P. gilva* (Peru) have a similar habitus. The minor worker is largely foveolate and the pronotal humeri are tuberculate. All the southern species are uniformly yellowish, while *P. rima* is bicolored, with red head and mesosoma, black gaster. The face of the minor worker of *P. rima* is uniformly foveolate, like *P. caltrop*, *P. pilispina*, and *P. gilva*. The face of *P. floricola* is a mix of foveolate and smooth sculpture. *Pheidole rima* and *P. floricola* are both arboreal species, and it is likely that *P. caltrop*, *P. pilispina*, and *P. gilva* are as well.

Etymology: In reference to Hudson's character Rima in Green Mansions, and the arboreal habit of this species.

Pheidole rogeripolita **new species**
(Plate 58)

Pheidole JTL-134: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Alajuela: Peñas Blancas River, 10.3 -84.73333 ±2 km, 850 m, 3-Mar-2005, wet forest, nest in clay bank (J. Longino, JTL5465) [MUCR, unique specimen identifier CASENT0636564]. PARATYPES: major, minor worker, queen: same data as holotype [JTLC, MUCR]; Costa Rica, Alajuela: 10km E Monteverde, 10.3107 -84.71356 ±50 m, 830 m, 15-May-2014, mature wet forest, nest in cavity in treetrunk (J. Longino, JTL8640) [CAS, DZUP, JTLC, MCZC, USNM].

Geographic range. Costa Rica, Panama.

Diagnosis. Similar in most respects to *P. rogeri*. The minor worker has a smooth, shiny face, rather than the lustrous, shagreened face of *P. rogeri*. The major worker is not readily distinguishable.

Measurements, minor worker: HW 0.84, HL 1.14, SL 1.56, EL 0.18, WL 1.63, PSL 0.42, PTW 0.14, PPW 0.23, CI 74, SI 185, PSLI 50, PPI 164 (n=2).

Measurements, major worker: HW 2.35, HL 2.59, SL 1.53, EL 0.28, WL 2.19, PSL 0.44, PTW 0.29, PPW 0.51, CI 91, SI 66, PSLI 19, PPI 173 (n=2).

Measurements, queen: HW 2.23, HL 2.14, SL 1.62, EL 0.48, WL 3.25, PSL 0.41, PTW 0.51, PPW 0.90, CI 104, SI 73, PSLI 19, PPI 175 (n=1).

Biology. This species occurs in lower montane, mature wet forest. It nests in clay soil on vertical banks. Several nests have been discovered and excavated. Nest 1: the entrance was a flared auricle-like structure of accreted soil; irregular galleries extended back into bank from the entrance; abundant workers, soldiers, brood were found about 5cm deep. Nest 2: on a concave clay bank, the entrance under a shelf, pointing downward; the nest entrance was a projecting, thin-walled, open-mouthed cylinder, made of accreted soil. Nest 3: in an abandoned wax tube of a *Trigona* bee nest, in a buttressed trunk, 1.5 m high; the wax tube covered a hemispherical chamber about 8 cm diameter; the entire colony with a single queen appeared to be in this chamber; a uniformly distributed layer of larvae were adhering to the vertical back wall of the chamber. Nest 4: incipient nest in a clay bank; inconspicuous circular entrance tunnel; nest a spherical chamber 3-4 cm deep; most of the colony collected; 16 minor workers, 1 colony queen, brood. Nest 5: stream edge in moist forest; nest in clay bank deep in alcove with overhanging roots.

Comments. *Pheidole rogeripolita* is a montane variant of the widespread lowland species *P. rogeri*. The two are sister taxa and diverged about 5 mya (*Pheidole* JTL134 in Economo *et al.* 2019).

Etymology: Similar to *P. rogeri*, but smooth and shiny, without a dull surface.

Pheidole savegre **new species**
(Plate 55)

Pheidole JTL-278: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Ranchos Tinamu, 9.4889 -83.95586 ±100m, 790m, 13-Jul-2015, montane wet forest, near streams, at bait (ADMAC, Ba-E-08-2-03-11) [MUCR, unique specimen identifier CASENT0646332]. PARATYPES: major, minor workers: same data as holotype [MUCR]; Costa Rica, San José: 2km ESE Ranchos Tinamu, 9.48543 -83.93936 ±100m, 490m, 10-Jul-2015, mature rainforest, edge of

forest near pasture and agricultural land, steep rocky terrain, at bait (ADMAC, Ba-E-07-3-04-14) [CAS, MCZC, USNM]; same data except Ba-E-07-3-04-01 [JTLC].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head somewhat tapering posteriorly; occipital carina weakly developed; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum uniformly foveate; propodeal spines long, similar in length to posterior face of propodeum; gaster smooth and shining; abundant, coarse, dark, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color yellow. ***Major***: inner hypostomal teeth widely spaced, in form of short points, in front of outer hypostomal teeth; scape base subterete, narrower than apical portion; face with irregular rugulae anteriorly, entire face with faint foveolate sculpture; promesonotal groove impressed; propodeal spines about half length of posterior face of propodeum; gastral dorsum faintly foveolate on anterior half; abundant, erect, flexuous setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.73, HL 0.95, SL 1.32, EL 0.19, WL 1.25, PSL 0.24, PTW 0.15, PPW 0.21, CI 77, SI 180, PSLI 33, PPI 142 (n=2).

Measurements, major worker: HW 1.61, HL 1.70, SL 1.38, EL 0.26, WL 1.69, PSL 0.23, PTW 0.28, PPW 0.40, CI 95, SI 86, PSLI 15, PPI 145 (n=2).

Biology. This species occurs in lowland to lower montane wet forest. Most collections are from ground baits. One worker is from a beating sample.

Comments. See comments under *P. tinamu*. The measurements and general habitus are very similar to *P. musacolor* from the Atlantic slope of Costa Rica. *Pheidole savegre* has coarser, darker setae, and the major has a more heavily sculptured face.

Etymology: From the type locality (Río Savegre area).

Pheidole sensipelada **new species**

(Plate 52)

Pheidole JTL-251: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Cerro Plano, 9.48446 -83.96228 ±200 m, 1030 m, 6-Jul-2015, cloud forest, at bait (ADMAC, Ba-E-06-2-03-14) [MUCR, unique specimen identifier CASENT0631275]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head rounded behind; promesonotal groove present, distinctly impressed; pronotum smooth and shiny; katepisternum foveolate; propodeal spines about one quarter length of posterior face of propodeum; gaster smooth and shining; dorsal mesosoma, petiole, and postpetiole with long flexuous erect setae; tibiae with very long erect setae, as long as or longer than twice width of tibia; gastral dorsum with extremely sparse, short, fully appressed pubescence, and either lacking erect setae or with a few long erect setae near postpetiolar insertion; color dark brown to black. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face almost entirely smooth and shining, with short longitudinal carinulae between eye and antennal fossa; promesonotal groove impressed; propodeal spines about one quarter length of posterior face of propodeum; gastral dorsum smooth and shiny; face with very sparse appressed pubescence similar to gaster; sides and posterior margin of head lacking erect setae; otherwise pilosity similar to minor worker.

Measurements, minor worker: HW 0.68, HL 0.74, SL 0.97, EL 0.18, WL 0.99, PSL 0.06, PTW 0.19, PPW 0.26, CI 91, SI 143, PSLI 9, PPI 134 (n=1).

Measurements, major worker: HW 1.07, HL 1.07, SL 0.85, EL 0.21, WL 1.09, PSL 0.08, PTW 0.32, PPW 0.41, CI 101, SI 80, PSLI 7, PPI 130 (n=1).

Biology. This species occurs in lowland to lower montane wet forest. The few collections are from ground baits and from a beating sample.

Comments. This species has the general habitus of *P. sensitiva*, with which it is sympatric. It differs from *P. sensitiva* in larger size (minor worker mean HW 0.68 vs. 0.59) and reduced pilosity.

Etymology: In reference to the very long flexuous setae on the mesosoma.

***Pheidole sepultura* new species**
(Plate 37)

Pheidole JTL-198: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Chiapas: Sierra Morena, 16.15238 -93.60100 ±50 m, 1340 m, 13-May-2008, mesophyll forest, at bait (LLAMA, Ba-A-01-2-01-02) [UNAM, unique specimen identifier JTLC000014191]. PARATYPES: major, minor workers: same data as holotype [CAS, MCZC, UNAM]; same data except Ba-A-01-2-01-13 [JTLC, USNM]; same data except 16.14346 -93.59271 ±65 m, 1380 m, 14-May-2008, pine-oak forest, at bait (LLAMA, Ba-A-01-4-01-01) [DZUP].

Geographic range. Mexico (Chiapas).

Diagnosis. ***Minor***: face foveolate, overlain with very faint irregular rugulae; mesosoma foveolate, pronotal dorsum overlain with reticulate rugulae; promesonotal groove present, distinctly impressed; propodeal spines about one third length of posterior face of propodeum; gaster shagreened/foveolate on anterior third, smooth and shining posteriorly; mesosomal dorsum and gaster with moderately abundant, somewhat stiffened erect setae; tibiae with 0-3 erect setae; color mottled orange and brown. ***Major***: inner hypostomal teeth widely spaced, acicular; scape base terete; face entirely foveolate, overlain with irregular rugulae, strongest between eye and antennal fossa, fading posteriorly, faint linear rugulae between frontal carinae; propodeal spines about one third length of posterior face of propodeum; gastral dorsum shagreened on anterior third, smooth and shining posteriorly; side of head lacking erect setae, vertex lobes with short, somewhat stiffened setae, rest of pilosity similar to minor worker; color mottled orange and brown.

Measurements, minor worker: HW 0.58, HL 0.68, SL 0.76, EL 0.14, WL 0.89, PSL 0.07, PTW 0.12, PPW 0.18, CI 85, SI 131, PSLI 12, PPI 149 (n=3).

Measurements, major worker: HW 0.97, HL 1.00, SL 0.77, EL 0.17, WL 1.04, PSL 0.11, PTW 0.21, PPW 0.30, CI 97, SI 80, PSLI 11, PPI 139 (n=3).

Biology. This species occurs in montane wet forest, both mesophyll cloud forest and pine-oak forest. Minor and major workers recruit to ground baits, and minor workers occasionally occur in Winkler samples of sifted litter and rotten wood.

Comments. The minor worker of this species is similar to *P. acamata* and *P. gulo*, but with more extensive foveolation on the anterior portion of the first gastral tergite. The major worker is similar to *P. acamata*, but has no erect setae on the sides of head, has abundant long setae on the gaster, and the scape is slightly flattened at the base. In Economo *et al.* (2019), this species is JTL198. It is in a clade that includes *P. spathipilosa* and *P. angusticeps* further south, and a large radiation in the North American temperate zone, both arid southwest and mesic southeast.

Etymology: From the type locality (La Sepultura Biosphere Reserve).

Pheidole sicaria

Pheidole sicaria Wilson, 2003: 232. Holotype major worker: Costa Rica, Puntarenas, Llorona, Corcovado National Park (P. S. Ward) [MCZC, not examined].

I use a broad definition of *Pheidole sicaria*, almost certainly comprising a set of somewhat separate genetic clusters distributed across Costa Rica and Panama. In addition to sharing a general morphometric profile, the minor workers have the face smooth and shiny, the head weakly tapered posteriorly in full face view, the promesonotal groove impressed, and the propodeal spines at least as long as the posterior face of the propodeum. The major workers have the inner hypostomal teeth widely spaced and acicular, and the face almost entirely smooth and shiny. They occur in lowland to mid-elevation mature wet forest, where they live exclusively in the low arboreal zone. Nests are found under epiphytes in old treefalls and in loose, irregular masses of debris lodged in low vegetation. Workers are collected in beating samples and Malaise traps, but rarely at ground baits or in Winkler samples of forest floor litter and rotten wood. One major worker was collected as prey in a *Simopelta* column.

However, there is inter-populational variation in details of propodeal spine shape and overall pilosity, and these separate forms can be in close proximity, suggesting a mosaic of genetically differentiated groups.

Type form: The type specimens of *P. sicaria* were collected by Phil Ward at Llorona in Corcovado National Park, on the Osa Peninsula of Costa Rica. This is a lowland rainforest site, at 100 m elevation. The minor workers

have relatively thin, somewhat upturned propodeal spines. The first gastral tergite has sparse appressed pubescence and scattered long erect setae (judging from the images provided in Wilson 2003). The major worker has the first gastral tergite densely pilose, scruffy, with suberect setae of variable lengths. The head is red brown.

Form 1: Small cloud forest patches occur in the center of the Osa Peninsula, around 700 m elevation. A collection by myself from this cloud forest area is similar in most respects, but the first gastral tergite of the major worker has pilosity like the minor worker: fully appressed sparse pubescence, and scattered long erect setae. Collections similar to this form are also known from around 500 m elevation on the Barva transect above La Selva Biological Station, and from 900-1000 m elevation on the eastern slopes of the Cordillera de Tilarán and Cordillera de Guanacaste.

Form 2: A distinct form, and almost certainly a separate species, occurs around 1100 m on the Barva transect and at similar elevation near Fila de Matama, on the Atlantic slope of the Talamanca range. The minor worker has longer, more robust, and less upturned propodeal spines. The pilosity on the gaster is a mix of suberect short setae and erect very long setae. The major worker has a yellow head, constrasting with the red brown body. The pilosity on the gaster is scruffy, like the type specimens.

Form 3: A series of minor workers were collected from low vegetation at a 400 m elevation site in Braulio Carrillo National Park, at the old Carillo station close to where the Guapiles highway is now. These workers have the robust spines of form 2, but the gastral pilosity is all of relatively short, erect setae. Also, the sculpture on the katepisternum is stronger, with the foveolation overlain with weak rugulae.

Form 4: This form is known from multiple collections from the Rio Savegre drainage on the Pacific slope of the Talamanca range, at a wet forest site around 800 m elevation (Ranchos Tinamu). The propodeal spines are thin and relatively upturned, like the types. The minor workers have the first gastral tergite with a relatively dense layer of fully appressed pubescence, and no or very few longer erect setae. The major worker has the head color somewhat mottled, intermediate between the types and form 2. The face is more strongly sculptured, with relatively more developed arcing carinulae on the anterior half of the face, and widely spaced, shallow puncta (not foveolation) on the vertex. The gastral pilosity is like the minor worker, with a dense layer of appressed pubescence, and sparse longer erect setae.

Form 5: Two collections from cloud forest sites in Panama are very similar to Form 1, differing only in somewhat longer, less upturned propodeal spines (but still thin, not enlarged at the base like forms 2 and 3).

Pheidole simonsi

Pheidole simonsi Wilson, 2003: 630, figs. Holotype major worker and associated paratype minor worker: Costa Rica, Heredia: La Selva Biological Station (Stefan Cover) [MCZC] (examined).

Pheidole arctos Wilson, 2003: 623, figs. Holotype major worker and associated paratype minor worker: Mexico, Tamaulipas: Gomez Fariás, 400–600 m (Cornell University Mexico Field Party, 1964) [MCZC] (examined). **New Synonym**.

Pheidole gangamon Wilson, 2003: 626, figs. Holotype major worker and associated paratype minor worker: Mexico, Veracruz: Pueblo Nuevo, near Tetzonapa (E. O. Wilson) [MCZC] (examined). **New Synonym**.

Pheidole thrasys Wilson, 2003: 631, figs. Holotype minor worker: Panama, Colón: Barro Colorado Island (William L. Brown and Elwood S. McCluskey) [MCZC] (examined). **New Synonym**.

Comments. Wilson (2003) named four species from Mexico and Central America that are all extremely similar and together form a very distinctive group with no similar species in the region. They are *P. arctos* from Tamaulipas, Mexico; *P. gangamon* from Veracruz, Mexico; *P. simonsi* from Costa Rica; and *P. thrasys* from Panama. The four taxa together clearly form a clade that is common in lowland wet forest throughout Central America and southern Mexico, exhibiting uniform habitat preference, behavior, and nesting habits. Minor workers are nearly uniform across the range. Major workers show some geographic variation, with southern versions having longer, thinner propodeal spines and longer dorsal pilosity. Specimens from Guatemala northward have shorter propodeal spines and are more bristly-looking, with shorter dorsal pilosity. DNA barcoding data are all from the southern populations and show two clusters. One has numerous Panama specimens and one specimen from Guanacaste, Costa Rica. Another cluster has numerous specimens from Guanacaste and many specimens from the Atlantic lowlands of Costa Rica, Nicaragua, and southern Honduras. Cryptic species may emerge with

further study, but at present there are no known morphological discontinuities at any one site or anywhere across the range of the clade.

Pheidole striaticeps

Pheidole striaticeps Mayr, 1870b: 987. Lectotype major worker: Mexico (Norton) [NHMW, unique specimen identifier CASENT0916072] (AntWeb image examined). See also: Wilson, 2003: 512.
Pheidole goeldii subsp. *chloe* Forel, 1908: 56. Syntype major, minor worker: Costa Rica, La Caja, vicinity of San Jose, 1100 m (Paul Biolley) [MHNG, unique specimen identifier JTLC000014074] (examined). **New Synonym**.
Pheidole chloe Forel: Wilson, 2003: 399 (raised to species).

Comments. *Pheidole striaticeps* is a widespread, moderately abundant species. AntWeb images of the type and associated paralectotypes of both *P. striaticeps* and *P. chloe* clearly reveal their conspecificity.

Pheidole tapanti new species
(Plate 26)

Pheidole JTL-240: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, Cartago: PN Tapantí, 9.75023 -83.78201 ±20 m, 1290 m, 8-Jun-2015, 2nd growth cloud forest, nest under epiphyte mat (J. Longino, JTL9224) [MUCR, unique specimen identifier CASENT0637804]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, MUCR, USNM].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face faintly but uniformly foveolate; promesonotal dorsum faintly foveolate; lateral pronotum smooth and shiny; katepisternum foveolate; promesonotal groove absent; propodeal spines one third length of posterior face of propodeum; gaster smooth and shining; abundant erect setae on mesosomal dorsum, tibiae, and gaster; color orange. ***Major***: inner hypostomal teeth small, about half way between midline and outer hypostomal teeth; scape base terete; face without scrobes; medial and anterior portions of face with very faint foveolation overlain with parallel, longitudinal carinulae; vertex lobes smooth and shining; propodeal spines one fourth length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.52, HL 0.56, SL 0.46, EL 0.13, WL 0.64, PSL 0.05, PTW 0.10, PPW 0.16, CI 93, SI 90, PSLI 9, PPI 151 (n=1).

Measurements, major worker: HW 1.01, HL 1.02, SL 0.51, EL 0.16, WL 0.86, PSL 0.06, PTW 0.17, PPW 0.25, CI 98, SI 51, PSLI 6, PPI 152 (n=1).

Biology. This species is known from one cloud forest site, where a nest was found beneath epiphytes in a recent treefall.

Comments. This species is similar to *P. boltoni*, another montane species in the northern cordilleras of Costa Rica. It differs from *P. boltoni* in orange color, somewhat smaller size (minor worker mean HW 52 vs 58), more convex promesonotum of minor worker in lateral view, and major worker with face sculpture more extensively smooth and shiny posteriorly.

Etymology: From the type locality.

Pheidole tikal new species
(Plate 4)

Pheidole JTL-229: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Petén: Cerro Cahuí, 16.99995 -89.71513 ±56 m, 195 m, 24-May-2009, tropical moist forest, at bait (LLAMA, Ba-B-05-4-01-12) [MCZC, unique specimen identifier CASENT0645181]. PARATYPES: major, minor workers: same data as holotype [MCZC, CAS]; same data except

17.00227 -89.71939 ±110 m, 305 m (Ba-B-05-4-06-02) [UVGC]; Parq. Nac. Tikal, 17.24115 -89.62226 ±111 m, 270 m, 23-May-2009, tropical moist forest, at bait (LLAMA, Ba-B-05-1-02-04) [USNM]; same data except Ba-B-05-1-02-18 [DZUP].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face and mesosoma foveolate, with foveolation absent on lower half of katepisternum; promesonotal groove absent; propodeal spines one fifth length of posterior face of propodeum; gaster smooth and shining; sparse short erect setae on mesosomal dorsum, tibiae, and gaster; color orange. ***Major***: inner hypostomal teeth distinct, closely spaced; scape base terete; face with distinct scrobes, delimited dorsally by frontal carinae and forming concave trough below them, ventral and posterior margins less delimited, surface of scrobe smooth and shiny; head weakly depressed posteriorly; face surface generally shiny, overlain with subparallel, longitudinal carinae; propodeal spines one third to one half length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum, tibiae, and gaster.

Measurements, minor worker: HW 0.39, HL 0.43, SL 0.37, EL 0.09, WL 0.47, PSL 0.02, PTW 0.07, PPW 0.10, CI 91, SI 95, PSLI 6, PPI 143 (n=6).

Measurements, major worker: HW 0.74, HL 0.92, SL 0.39, EL 0.12, WL 0.71, PSL 0.07, PTW 0.16, PPW 0.27, CI 81, SI 53, PSLI 9, PPI 173 (n=6).

Biology. This species occurs in lowland seasonal moist to dry habitats, scrubby vegetation, second growth forest, and mature forest. Most collections are minor workers and occasional major workers recruited to ground baits. Workers occur in Winkler samples of sifted litter and rotten wood.

Comments. See under *P. andersoni*.

Etymology: From the type locality.

Pheidole tinamu **new species**

(Plate 54)

Pheidole Biolleyi subsp. *Tristani* Forel, 1908: 50 (part): misidentified minor worker from Costa Rica, Santa Maria de Dota (J. F. Tristan) [MHNG, examined].

Pheidole JTL-122: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Costa Rica, San José: Cerro Plano, 9.48446 -83.96228 ±200m, 1030m, 6-Jul-2015, cloud forest, at bait (ADMAC, Ba-E-06-2-03-16) [MUCR, unique specimen identifier CASENT0646320]. PARATYPES: major, minor workers: same data as holotype except 9.48141 -83.96276 ±200m, 1070m, (Ba-E-06-1-04-09) [MCZC]; 9.48141 -83.96276 ±200m, 1070m (Ba-E-06-1-04-11) [CAS]; Ranchos Tinamu, 9.48568 -83.95673 ±100m, 850m, 13-Jul-2015, montane wet forest, in matrix of pasture and forest, probably old 2nd growth, at bait (Ba-E-08-1-01-05) [USNM]; (Ba-E-08-1-01-07) [DZUP]; 9.48895 -83.95624 ±100m, 760m, near streams, at bait (Ba-E-08-2-02-04) [JTLC].

Geographic range. Costa Rica.

Diagnosis. ***Minor***: face smooth and shining; head somewhat tapering posteriorly; occipital carina weakly developed; promesonotal groove present, distinctly impressed; lateral pronotum smooth and shiny; katepisternum uniformly foveate; propodeal spines long, similar in length to posterior face of propodeum; gaster smooth and shining; abundant, flexuous, erect setae on mesosomal dorsum, tibiae, and gastral dorsum; color yellow. ***Major***: inner hypostomal teeth widely spaced, in form of short points, in front of outer hypostomal teeth; scape base subterete, narrower than apical portion; head heart-shaped in face view; face with oblique, subparallel rugulae anteriorly, posterior two thirds of face smooth and shining; promesonotum strongly produced, with promesonotal groove shallow to absent; propodeal spines about half length of posterior face of propodeum; gastral dorsum faintly foveolate on anterior half; abundant, erect, somewhat bristly setae on face, sides of head, mesosomal dorsum, tibiae, and gastral dorsum.

Measurements, minor worker: HW 0.72, HL 0.93, SL 1.29, EL 0.18, WL 1.23, PSL 0.2, PTW 0.15, PPW 0.22, CI 77, SI 179, PSLI 27, PPI 148 (n=3).

Measurements, major worker: HW 1.88, HL 1.86, SL 1.3, EL 0.26, WL 1.77, PSL 0.18, PTW 0.32, PPW 0.49, CI 101, SI 70, PSLI 10, PPI 155 (n=2).

Biology. This species occurs in montane wet forest. Most collections are from ground baits. A few are in Winkler samples of sifted litter and rotten wood, and rare workers occur in Malaise and beating samples.

Comments. On the slopes above the Rio Savegre in Costa Rica there are three sympatric species, all of which have very similar minor workers that are large, yellow, and with long propodeal spines. During sampling in 2015, as part of the ADMAC project, *P. tinamu* was common at 1000 m elevation and less abundant at 800 m. *Pheidole familiaparra* occurred occasionally at 800 m. *Pheidole savegre* occurred occasionally at 800 m and 500 m. Relative to *P. tinamu*, the minor worker of *P. familiaparra* has a more strongly developed occipital carina, and the minor of *savegre* has coarser, darker setae. The major worker of *P. tinamu* has a heart-shaped head and the promesonotum is strongly produced, with shallow promesonotal groove. The other two species have the head with convex sides but not clearly heart-shaped, and the promesonotal groove is impressed.

A minor worker from the Wilson Botanical Garden is tentatively identified as this species. This is a similar montane wet forest site, less than 130 km south of the Rio Savegre collections.

A minor worker from Santa Maria de Dota was part of the syntype series of *P. biolleyi* subsp. *tristani*, a junior synonym of *P. biolleyi*. A major worker from Cartago was designated Lectotype (see under *P. biolleyi*), excluding this minor worker.

Etymology: Named for Ranchos Tinamu, the ecolodge that hosted us during sampling at the type locality.

Pheidole transversostriata

Pheidole transversostriata Mayr, 1887: 584. Lectotype major worker: Guyana [NHMW, unique specimen identifier CASENT0601287] (examined). See also: Wilson, 2003: 645.

Pheidole lacerta Wheeler, 1922: 6. Syntype major, minor worker: Trinidad, Port of Spain (not examined). Synonymy by Wilson, 2003: 645.

Pheidole transversostriata var. *nigridens* Forel 1901: 362. Syntype major, minor worker: Colombia, Magdalena: Sta. Marta (Forel) [MHNG, unique specimen identifiers CASENT0908300 (major), CASENT0908301 (minor)] (AntWeb images examined). Synonymy by Wilson, 2003: 645.

Pheidole scalaris Wilson, 2003: 643, figs. Holotype major worker and associated paratype minor worker: Costa Rica, Heredia: La Selva Biological Station (S. Cover) [MCZC] (examined). **New Synonym**.

Comments. Wilson (2003) surmised that *P. scalaris* could be a synonym of *P. transversostriata*. The two were separated by minor differences in sculpture on the minor worker and head shape of the major worker. So far there is no evidence of sympatry of separate forms. The distinctive major workers identify a widespread clade, and at this stage there is little value in using separate names for local variants.

Pheidole tsontekonwei new species

(Plate 56)

Pheidole JTL-203: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Mexico, Guerrero: Oapan, 17.97725 -99.46567 ±20 m, 742 m, 26-Jun-2011, nest in soil (J. Amith & J. Herrera) [UNAM, unique specimen identifier CASENT0624331]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, UNAM, USNM].

Geographic range. Mexico (Guerrero).

Diagnosis. ***Minor***: head subquadrate in full face view; face with patchy, faint foveolation, overlain with sparse longitudinal carinulae; promesonotal groove absent; mesosoma generally smooth and shining, with patches of very faint foveolation; propodeal spines thin, upturned, about one third length of posterior face of propodeum; gaster smooth and shining; mesosomal dorsum and gaster with abundant, short, erect setae; tibiae without erect setae; color light yellow brown. ***Major***: inner hypostomal teeth lacking; scape base terete; face with fine longitudinal carinulae on anterior third to half, transverse medial band smooth and shiny, vertex lobes with abundant transverse rugulae; propodeal spines short, upturned, about one third length of posterior face of propodeum; gastral dorsum smooth and shining; pilosity on sides of head very short, suberect, other pilosity similar to minor worker.

Measurements, minor worker: HW 0.77, HL 0.89, SL 0.85, EL 0.19, WL 1.19, PSL 0.09, PTW 0.14, PPW 0.26, CI 87, SI 110, PSLI 11, PPI 191 (n=5).

Measurements, major worker: HW 2.56, HL 2.58, SL 1.06, EL 0.30, WL 1.91, PSL 0.13, PTW 0.37, PPW 0.76, CI 99, SI 42, PSLI 5, PPI 208 (n=5).

Biology. This species was collected by Jonathan Amith during his ethnographic studies in coastal Guerrero, Mexico. It is a large seed harvesting ant that nests in the soil. Amith noted that the entrance of nest was a short, upright, hollow cylinder of white powdery material.

Comments. In Economo *et al.* (2019, as JTL203), this species is related to *P. pilifera* and other seed harvesting species of the arid southwest of North America. Although not strictly within the geographic scope of this work, this was an opportunity to name this highly distinctive species and to facilitate Amith's ethnographic work in the region.

Etymology: The name means "big head" in Nahuatl (J. Amith, pers. com.).

Pheidole tuculutan **new species**

(Plate 16)

Pheidole JTL-201: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Guatemala, Zacapa: 7.5km NE Teculután, 15.04367 -89.67501 ±30 m, 475 m, 28-Jun-2009, stream gully in dry scrub, at bait (J. Longino, JTL6785-s) [MCZC, unique specimen identifier CASENT0612794]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM, UVGC].

Geographic range. Guatemala.

Diagnosis. ***Minor***: face smooth and shiny; promesonotal groove absent; pronotal dorsum smooth and shiny, lateral pronotum smooth medially, foveolate peripherally, mesonotum weakly foveolate, dorsal face of propodeum foveolate, katepisternum foveolate; propodeal spines short, upturned, about one fifth length of posterior face of propodeum; gaster smooth and shining; mesosomal dorsum and gaster with abundant, short, stiff setae; tibiae without erect setae; color dark brown to black. ***Major***: inner hypostomal teeth present, closely spaced; scape base terete; antennal scrobes weakly impressed, not sharply delimited; head elongate, subrectangular; face mostly smooth and shiny, space between eye and antennal fossa foveolate, overlain with rugulae; medial frons between frontal carinae faintly foveolate, overlain with fine, widely spaced longitudinal carinulae; propodeal spines about one fifth length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with erect setae; dorsal mesosoma, gaster, and tibiae with abundant flexuous erect setae; color dark brown.

Measurements, minor worker: HW 0.47, HL 0.52, SL 0.41, EL 0.09, WL 0.62, PSL 0.04, PTW 0.10, PPW 0.14, CI 90, SI 88, PSLI 8, PPI 135 (n=4).

Measurements, major worker: HW 0.79, HL 1.22, SL 0.48, EL 0.13, WL 0.88, PSL 0.06, PTW 0.17, PPW 0.23, CI 65, SI 61, PSLI 8, PPI 136 (n=4).

Biology. This species is known from one site in Guatemala. It was an area of dry scrub habitat. Minor and major workers recruited to a ground bait placed in a stream gully.

Comments. This small, black species with very elongate head of the major is distinctive, not morphologically close to other species. In Economo *et al.* (2019) this species (as JTL201) is on a long branch, distantly related to other species. The closest relatives in that phylogeny bear little morphological resemblance.

Etymology: From the type locality.

Pheidole vafra

Pheidole vafra Santschi, 1923: 51. Lectotype major worker and associated paralectotype minor worker: Brazil, Sta. Catarina: Blumenau (Reichensperger) [NHMB, unique specimen identifiers CASENT0913469 (major), CASENT0913470 (minor)] (AntWeb images examined). See also: Wilson, 2003: 244.

Pheidole idiota Santschi, 1923: 53. Syntype major, minor worker, queen: Argentina, Cordoba: Alta Gracia (Bruch) [NHMB, unique specimen identifiers CASENT0913471 (major), CASENT0913472 (minor)] (AntWeb images examined). Synonymy by Wilson, 2003: 244.

Pheidole vafra subsp. *idiota*: Santschi, 1929: 284.

Pheidole laticornis Wilson, 2003: 203, figs. Holotype major worker and associated paratype minor worker: Costa Rica, Puntarenas: Palmar (E. O. Wilson). [MCZC] (examined). **New Synonym**.

Comments. This appears to be a widespread weedy species. The images of the types of *P. vafra* match the types of Wilson's *P. laticornis*.

Pheidole xiloa **new species**
(Plate 8)

Pheidole JTL-212: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Nicaragua, Managua: Laguna Xiloá, 12.22644 -86.31104 ±50 m, 90 m, 28-Apr-2011, 2nd growth dry forest, ex sifted litter (Davis sifter) (J.Longino, JTL7429-s) [MCZC, unique specimen identifier CASENT0619635]. PARATYPES: major, minor workers: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM]; same data except at bait (J.Longino, JTL7430-s) [JTLC].

Geographic range. Nicaragua.

Diagnosis. ***Minor***: face and mesosoma uniformly foveolate, face and dorsal pronotum overlain with faint reticulate rugulae to variable extent; promesonotal groove absent; propodeal spines about one half length of posterior face of propodeum; gaster smooth and shining; abundant flexuous erect setae on mesosomal dorsum and gaster; tibiae without erect setae; color light to dark brown. ***Major***: inner hypostomal teeth stout, closely spaced; scape base terete; face with shallow scrobal impressions; most of face smooth and shining, space between eye and antennal fossa foveolate overlain with longitudinal rugulae, with subparallel, longitudinal carinulae between frontal carinae; propodeal spines one third to one half length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant erect setae; abundant flexuous erect setae on mesosomal dorsum and gaster; tibiae with no erect setae.

Measurements, minor worker: HW 0.43, HL 0.47, SL 0.35, EL 0.09, WL 0.50, PSL 0.08, PTW 0.09, PPW 0.17, CI 91, SI 83, PSLI 18, PPI 187 (n=3).

Measurements, major worker: HW 0.74, HL 0.84, SL 0.38, EL 0.12, WL 0.63, PSL 0.08, PTW 0.14, PPW 0.31, CI 89, SI 51, PSLI 11, PPI 217 (n=3).

Biology. This species is known from one lowland, dry, scrubby site on the outskirts of Managua. Minor and major workers recruited to a ground bait, and minor and majors were collected in the vicinity of the bait using a Davis sifter.

Comments. The minor worker of this species has the habitus and sculpture of *P. harrisonfordi*. Unlike *P. harrisonfordi* and similar species, the major worker has most of the face smooth and shiny.

Etymology: From the type locality.

Pheidole zannia **new species**
(Plate 9)

Pheidole JTL-189: morphospecies code previously used on AntWeb.

HOLOTYPE: 1 major worker, Honduras, Olancho: 9km NNW La Union, 15.09397 -86.75244, ±50 m, 1470 m, 4 May 2010, road edge near cloud forest, nest in soil (J. Longino#6982) [CAS, unique specimen identifier CASENT0615634]. PARATYPES: major, minor worker, queen: same data as holotype [CAS, DZUP, JTLC, MCZC, USNM].

Geographic range. Guatemala, Honduras.

Diagnosis. ***Minor***: face smooth and shiny; posterior margin of head in face view rounded laterally, somewhat flattened posteriorly; promesonotal groove absent; dorsal promesonotum and propodeum foveolate; lateral pronotum foveolate with medial smooth, shiny patch; katepisternum mostly smooth and shiny, with or without strip of foveolation posteriorly; propodeal spines short, upturned, about one fourth length of posterior face of propodeum; gaster smooth and shining; erect setae on mesosomal dorsum and gaster; tibiae with a few short, erect setae; bicolored, with sharply contrasting black head and gaster, light orange mesosoma. ***Major***: head elongate, strongly incised between vertex lobes, posterior face transversely depressed between vertex lobes and anterior portion of head; inner hypostomal teeth present, closely spaced; scape base terete; antennal scrobes distinct, smooth and shiny, delimited dorsally by frontal carinae, ventrally by carinulae, not delimited posteriorly; face

longitudinally carinulate, interspaces smooth and shining; propodeal spines upturned, about one fourth to one third length of posterior face of propodeum; gastral dorsum smooth and shining; sides of head with abundant short erect setae; abundant short erect setae on mesosomal dorsum and gaster; tibiae with erect setae; color as in minor worker.

Measurements, minor worker: HW 0.43, HL 0.47, SL 0.42, EL 0.10, WL 0.57, PSL 0.04, PTW 0.08, PPW 0.13, CI 91, SI 98, PSLI 8, PPI 152 (n=11).

Measurements, major worker: HW 0.83, HL 1.00, SL 0.43, EL 0.13, WL 0.84, PSL 0.07, PTW 0.17, PPW 0.30, CI 83, SI 52, PSLI 9, PPI 178 (n=8).

Measurements, queen: HW 0.78, HL 0.81, SL 0.45, EL 0.25, WL 1.35, PSL 0.09, PTW 0.25, PPW 0.45, CI 96, SI 57 (n=1).

Biology. *Pheidole zannia* inhabits montane habitats from 1370 to 1740 m elevation, in areas with mesophyll cloud forest and mixed pine, oak, and *Liquidambar* forests. It prefers open and disturbed areas along roadsides, in coffee farms, and in second growth vegetation. For example, in La Muralla National Park near La Union, intensive Winkler sampling of mature cloud forest did not yield this species, but a nest was discovered (from which the type series was obtained) just outside the park and adjacent to the forest, along a road edge through pasture. This nest was in the soil of the road bank. There was a 2 mm tall turret marking the nest entrance, and the main nest chamber was about 10 cm deep, horizontally into the bank from the entrance. The main chamber contained a single colony queen, minor and major workers, and brood. Other collections have come from baiting or Winkler samples.

Comments. Other New World species with similar morphometric profile are *P. arboricola*, *P. crinita*, *P. gnomus*, *P. humeralis*, *P. metallescens*, *P. mosenopsis*, *P. neolongiceps*, *P. pygmaea*, *P. similigena*, *P. subarmata*, *P. triplex*, and *P. tysoni*. Most of these have major workers with the posterior half of the face smooth, lacking longitudinal carinulae, and there is no transverse impression on the face. *Pheidole gnomus*, from Ecuador, is similar to *P. zannia* but has transverse carinular on vertex lobes and more normal red brown coloration. *Pheidole mosenopsis*, from Bolivia and known only from the major, is similar but has less pronounced carinular on vertex lobes, no transverse impression on the face, more normal red brown coloration, and distinctive mandibles with flat dorsal surface and elevated basal margin. *Pheidole neolongiceps*, from Cuba, is similar but has more uniform longitudinal carinae on face, no transverse face impression, and dark coloration. *Pheidole triplex*, from Trinidad, has coloration approaching *P. zannia*. The major worker has a dark head, contrasting orange mesosoma, and red brown gaster. The minor worker is uniform yellow orange. Other than color, *P. triplex* is very similar to the widespread and common species *P. subarmata.*

Pheidole zannia is in a group of species related to *P. mera* (see Comments under *P andersoni*). The harlequin color pattern is unique and highly divergent in the group, placing it in a mimicry complex with the unrelated *P. balatro* (see Comments under *P. balatro*).

Etymology: The zanni were comic servant characters in sixteenth century Italian theater, from which harlequin characters were derived.

Acknowledgments

Hundreds of students and other collaborators contributed to field sampling from Mexico to Costa Rica. Particular thanks go to Michael Branstetter. Additional specimens were provided by Bob Anderson, Stefan Cover, and Phil Ward. This project was most recently supported by National Science Foundation grant DEB-1354739 (Project ADMAC), National Geographic Society Committee for Research and Exploration Grant 9568-14, and the University of Costa Rica (Vicerrectoría de Investigación, Project No.810-B4-531).

Literature cited

Borgmeier, T. (1934) Contribuição para o conhecimento da fauna mirmecológica dos cafezais de Paramaribo, Guiana Holandesa (Hym. Formicidae). *Archivos do Instituto de Biologia Vegetal (Rio de Janeiro),* 1, 93–111, estampa 111–112.

Economo, E.P., Huang, J.-P., Fischer, G., Sarnat, E. M., Narula, N., Janda, M., Guénard, B., Longino, J.T. & Knowles, L.L. (2019) Evolution of the latitudinal diversity gradient in the hyperdiverse ant genus *Pheidole*. *Global Ecology and Biogeography*, 28, 456–470.
https://doi.org/10.1111/geb.12867

Economo, E.P., Klimov, P., Sarnat, E.M., Guénard, B., Weiser, M.D., Lecroq, B. & Knowles, L.L. (2015) Global phylogenetic structure of the hyperdiverse ant genus *Pheidole* reveals the repeated evolution of macroecological patterns. *Proceedings of the Royal Society B: Biological Sciences,* 282, 20141416.
https://doi.org/10.1098/rspb.2014.1416

Economo, E.P., Sarnat, E.M., Janda, M., Clouse, R., Klimov, P.B., Fischer, G., Blanchard, B.D., Ramirez, L.N., Andersen, A.N., Berman, M., Guénard, B., Lucky, A., Rabeling, C., Wilson, E.O. & Knowles, L.L. (2015) Breaking out of biogeographical modules: range expansion and taxon cycles in the hyperdiverse ant genus *Pheidole*. *Journal of Biogeography,* 42, 2289–2301.
https://doi.org/10.1111/jbi.12592

Emery, C. (1896) Studi sulle formiche della fauna neotropica. XVII-XXV. *Bullettino della Società Entomologica Italiana, 28*, 33–107, Tav. I.

Forel, A. (1899) Formicidae. [part c]. *In: Insecta. Hymenoptera. Formicidae*. R.H. Porter, Dulau & Co., London, pp. 57–80.

Forel, A. (1901) Variétés myrmécologiques. *Annales de la Société Entomologique de Belgique,* 45, 334–382.

Forel, A. (1908) Fourmis de Costa-Rica récoltées par M. Paul Biolley. *Bulletin de la Société Vaudoise des Sciences Naturelles,* 44, 35–72.

Forel, A. (1914) Einige amerikanische Ameisen. *Deutsche Entomologische Zeitschrift,* 1914, 615–620.

Gauld, I.D. & Bolton, B. (1988) *The Hymenoptera*. Oxford, Oxford University Press. 332 pp.

Kempf, W.W. (1972) Catálogo abreviado das formigas da Região Neotropical. *Studia Entomologica,* 15, 3–344.

Letourneau, D.K. (1983) Passive aggression: an alternative hypothesis for the *Piper-Pheidole* association. *Oecologia,* 60, 122–126.
https://doi.org/10.1007/BF00379331

Lillico-Ouachour, A. & Abouheif, E. (2016) Regulation, development, and evolution of caste ratios in the hyperdiverse ant genus *Pheidole*. *Current Opinion in Insect Science,* 19, 43–51.
https://doi.org/10.1016/j.cois.2016.11.003

Longino, J.T. (2009) Additions to the taxonomy of New World *Pheidole* (Hymenoptera: Formicidae). *Zootaxa,* 2181, 1–90.

Longino, J.T. & Colwell, R.K. (2011) Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere,* 2, art29.
https://doi.org/10.1890/ES10-00200.1

Makhan, D. (2007) *Pheidole soesilae* sp. nov. from Suriname (Hymenoptera: Formicidae). *Calodema Supplementary Paper,* 59, 1–2.

Mann, W.M. (1916) The ants of Brazil. (The Stanford Expedition to Brazil, 1911, John C. Branner, Director). *Bulletin of the Museum of Comparative Zoology,* 60, 399–490, pls. 391–397.

Mayr, G. (1870a) Formicidae novogranadenses. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Klasse Abteilung I,* 61, 370–417, Tafel.

Mayr, G. (1870b) Neue Formiciden. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien,* 20, 939–996.

Mayr, G. (1887) Südamerikanische Formiciden. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wein,* 37, 511–632.

Mertl, A., Sorenson, M. & Traniello, J. (2010) Community-level interactions and functional ecology of major workers in the hyperdiverse ground-foraging *Pheidole* (Hymenoptera, Formicidae) of Amazonian Ecuador. *Insectes Sociaux,* 57, 441–452.
https://doi.org/10.1007/s00040-010-0102-5

Mertl, A.L. & Traniello, J.F.A. (2009) Behavioral evolution in the major worker subcaste of twig-nesting *Pheidole* (Hymenoptera: Formicidae): does morphological specialization influence task plasticity? *Behavioral Ecology and Sociobiology,* 63, 1411–1426.

Moreau, C.S. (2008) Unraveling the evolutionary history of the "hyperdiverse" ant genus *Pheidole* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution,* 48, 224–239.
https://doi.org/10.1016/j.ympev.2008.02.020

O'Hara, R.J. (1993) Systematic generalization, historical fate, and the species problem. *Systematic Biology,* 42, 231–246.
https://doi.org/10.1093/sysbio/42.3.231

Pie, M.R. & Traniello, J.F.A. (2007) Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole*. *Journal of Zoology,* 271, 99–109.
https://doi.org/10.1111/j.1469-7998.2006.00239.x

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364.
https://doi.org/10.1111/j.1471-8286.2007.01678.x

Risch, S., McClure, M., Vandermeer, J. & Waltz, S. (1977) Mutualism between three species of tropical *Piper* (Piperaceae) and their ant inhabitants. *American Midland Naturalist,* 98, 433–444.
https://doi.org/10.2307/2424991

Roger, J. (1863) Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses nebst Ergänzung einiger früher gegebenen Beschreibungen. *Berliner Entomologische Zeitschrift,* 7, 131–214.

https://doi.org/10.1002/mmnd.18630070116
Santschi, F. (1923) *Pheidole* et quelques autres fourmis néotropiques. *Annales de la Société Entomologique de Belgique,* 63, 45–69.
Santschi, F. (1929) Nouvelles fourmis de la République Argentine et du Brésil. *Anales de la Sociedad Cientifica Argentina,* 107, 273–316.
Sarnat, E.M., Fischer, G., Guénard, B. & Economo, E.P. (2015) Introduced *Pheidole* of the world: taxonomy, biology and distribution. *ZooKeys,* 543, 1–109.
https://doi.org/10.3897/zookeys.543.6050
Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr.net. (accessed 3 December 2018)
Tepe, E., Vincent, M. & Watson, L. (2004) Phylogenetic patterns, evolutionary trends, and the origin of ant-plant associations in *Piper* section *Macrostachys*: Burger's hypothesis revisited. *In:* L. A. Dyer & A. D. N. Palmer (Eds), *Piper: a model genus for studies of phytochemistry, ecology, and evolution.* Kluwer Academic Publishing, New York, pp. 156–178.
https://doi.org/10.1007/978-0-387-30599-8_9
Tschá, M.K. & Pie, M.R. (2018) Correlates of ecological dominance within *Pheidole* ants (Hymenoptera: Formicidae). *Ecological Entomology*, 44, 163–171.
https://doi.org/10.1111/een.12685.
Waxman, H.K., Muscedere, M.L. & Traniello, J.F. (2017) Behavioral performance and neural systems are robust to sensory injury in workers of the ant *Pheidole dentata*. *Brain, behavior and evolution,* 89, 195–208.
https://doi.org/10.1159/000470899
Wheeler, W.M. (1922) The ants of Trinidad. *American Museum Novitates,* 45, 1–16.
Wheeler, W.M. (1925) Neotropical ants in the collections of the Royal Museum of Stockholm. *Arkiv för Zoologi,* 17A (8), 1–55.
Wheeler, W.M. (1934) Neotropical ants collected by Dr. Elisabeth Skwarra and others. *Bulletin of the Museum of Comparative Zoology,* 77, 157–240.
Wilson, E.O. (2003) *Pheidole in the New World: A Dominant, Hyperdiverse Ant Genus*. Cambridge, Mass, Harvard University Press, 794 pp.

nigricula
HW 0.34, SI 89
Lowland wet forest

Common. At ground baits and in litter samples. Nest in rotten twigs in litter.




perpusilla
HW 0.35, SI 80
Lowland wet forest, open disturbed areas

Arboreal. Nest under epiphytes.

(10-seg. antenna)




nitella
HW 0.35, SI 83
Lowland-Montane wet forest

Common. At ground baits, in litter samples, in Malaise traps. Nests in dead wood, in live or dead plant cavities, under epiphytes.




mendicula
HW 0.36, SI 77
Lowland-Montane, wet to dry, old growth - disturbed

Occasional in litter samples. Nest in soil.

(11-seg. antenna)




PLATE 1.

otisi

HW 0.37, SI 81
Lowland wet forest

At ground baits and in litter samples. Forages on ground and in low arboreal zone. Nest in dead wood.

sagittaria

HW 0.37, SI 90
Lowland-Montane wet forest

In litter samples. Nest in dead wood.

albipes

HW 0.37, SI 99
Lowland wet forest

Common at baits and in litter samples. Nest in rotten wood, under loose bark.

ceibana

HW 0.37, SI 99
Lowland wet forest

Common at baits and in litter samples.

PLATE 2.

christopherseni
HW 0.38, SI 89
Lowland wet forest

Arboreal. Nest in live stems.

(large propodeal spiracle)

laselvoides
HW 0.38, SI 92
Lowland wet forest

Occurs at ground baits and in litter samples. Nest in rotten wood in litter and in soil.

laselva
HW 0.38, SI 96
Lowland wet forest

Occurs at ground baits and in litter samples. Nest in rotten wood in litter.

karolmorae
HW 0.38, SI 94
Lowland wet forest

Common in litter samples.

PLATE 3.

protensa

HW 0.39, SI 86

Lowland wet forest

Common. At ground baits and in litter samples. Nest in clay soil.

olsoni

HW 0.39, SI 88

Lowland-Montane wet forest

Locally abundant. At ground baits and in litter samples. Nest in dead wood, dead twigs in litter, under epiphytes.

janzeni

HW 0.39, SI 89

Lowland dry-moist forest, disturbed areas

At ground baits. Nest in dead stick in litter.

tikal

HW 0.39, SI 94

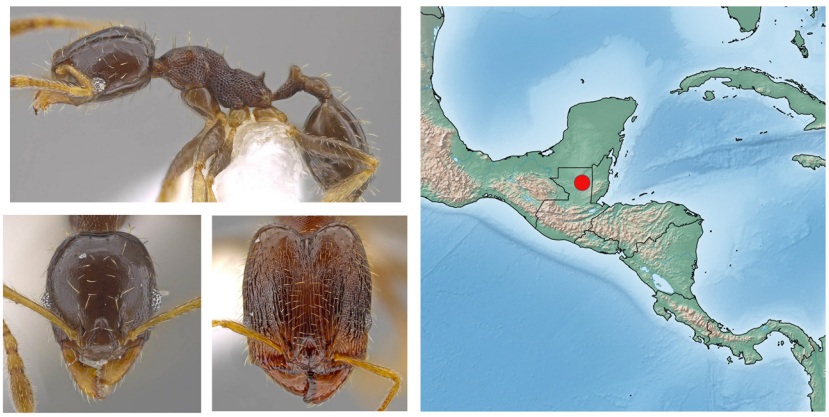
Lowland dry to moist, mature to scrubby vegetation

At ground baits and in litter samples.

PLATE 4.

depressinoda
HW 0.39, SI 110
Lowland moist forest

Occurs at ground baits and in litter samples. Nest in dead wood in litter.



multispina
HW 0.40, SI 81
Lowland wet forest

Common. At ground baits and in litter samples. Nest in dead wood on ground.

flavens
HW 0.40, SI 95
Lowland wet-dry, all habitats

Common. Generalized foraging and nesting habits.

kasparii
HW 0.41, SI 85
Mid to high montane wet forest

Occurs at ground baits and in litter samples. Nests in low arboreal zone, in dead wood, and in soil.

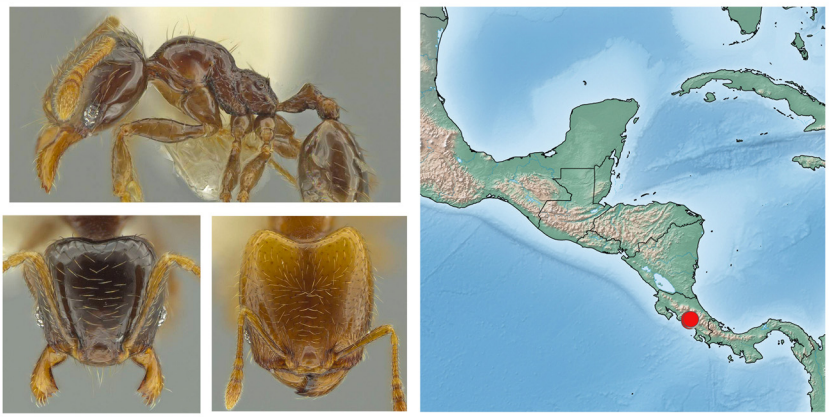


PLATE 5.

browni

HW 0.41, SI 85

Lowland-Montane wet forest

Common at baits and in litter samples. Nests in dead wood and in soil.

longinoi

HW 0.41, SI 85

Lowland wet forest

Rare. Arboreal. Nest in live stems in low arboreal zone.

transversostriata

HW 0.41, SI 86

Lowland wet forest

At ground baits and in litter samples. Nest in soil.

karolsetosa

HW 0.41, SI 86

Lowland wet forest

In litter samples.

PLATE 6.

beloceps
HW 0.41, SI 89
Lowland wet forest

Common in litter samples, occasional at baits. Nest in soil.



tuxtlasana
HW 0.41, SI 122
Lowland wet forest

Common. At ground baits and in litter samples. Nest unknown.



imbrilis
HW 0.42, SI 99
Montane wet forest

Occurs at ground baits and in litter samples.



glomericeps
HW 0.42, SI 101
Lowland wet-moist forest

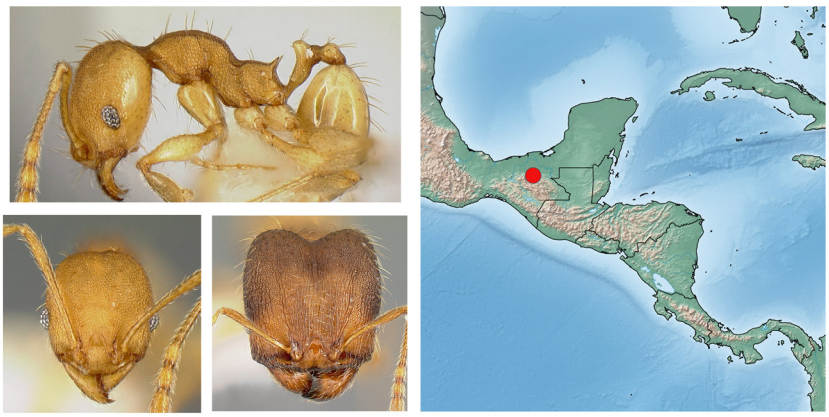
Common in litter samples, occasional at ground baits.



PLATE 7.

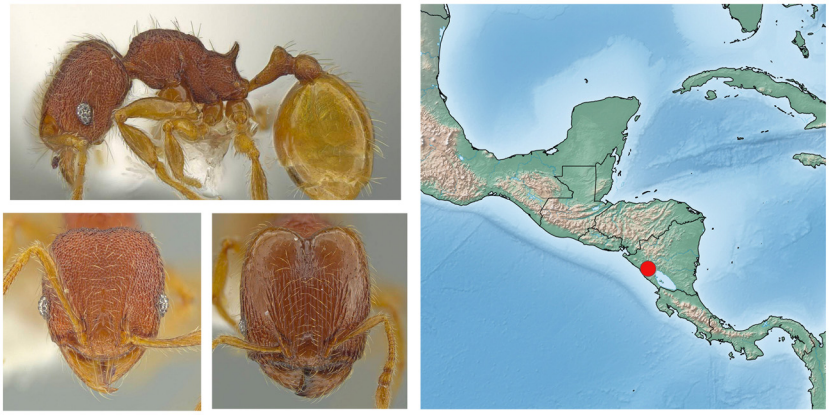
phanigaster
HW 0.42, SI 120
Lowland wet forest

At ground baits.



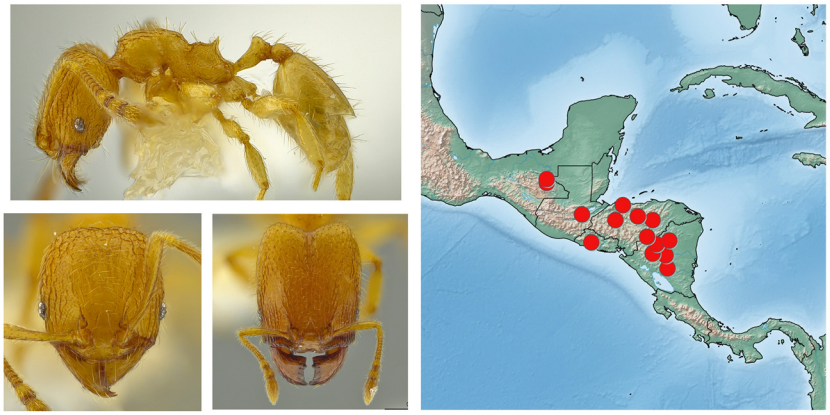
xiloa
HW 0.43, SI 83
Dry scrub habitat

At ground baits and in litter samples.



belonorte
HW 0.43, SI 85
Lowland-Montane wet forest

Occurs at ground baits and in litter samples.



caulicola
HW 0.43, SI 90
Lowland wet forest

Rare. Arboreal. Nest in dead stems in canopy.

PLATE 8.

arhuaca
HW 0.43, SI 95
Lowland wet forest

Rare. Nest in dead sticks.




perissothrix
HW 0.43, SI 97
Wet to dry habitat, second-growth vegetation

Occurs in litter samples, occasionally at baits.




zannia
HW 0.43, SI 98
Montane wet habitat, secondgrowth vegetation, open areas

At ground baits, occasional in litter samples. Nest in soil.




subarmata
HW 0.43, SI 100
Lowland wet-dry forest, 2nd growth vegetation, disturbed areas

Common in disturbed areas. Ground forager. Nest in soil.




PLATE 9.

rugiceps
HW 0.43, SI 143
Lowland wet forest

Very common. At ground baits and in litter samples. Nest in dead wood.

arboricola
HW 0.44, SI 93
Lowland wet forest

Common. Arboreal. Nest in live and dead plant cavities.

navigans
HW 0.44, SI 97
Lowland wet forest

Types from orchids from Veracruz. Invasive elsewhere.

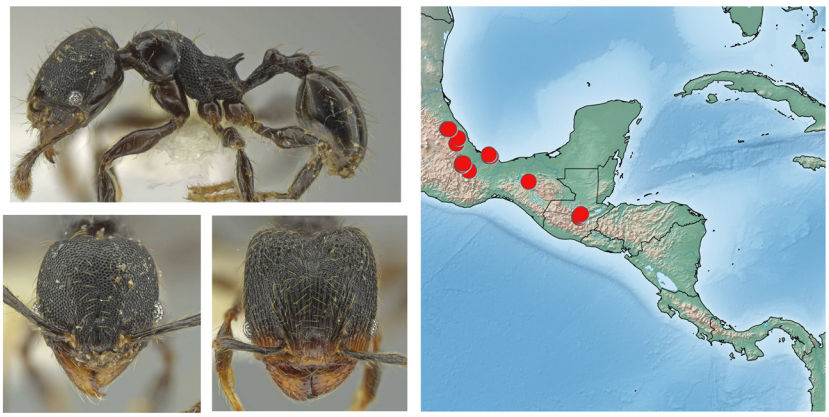
natalie
HW 0.44, SI 99
Montane wet forest

Occasional at ground baits and in litter samples. Nest in clay banks and under stones.

PLATE 10.

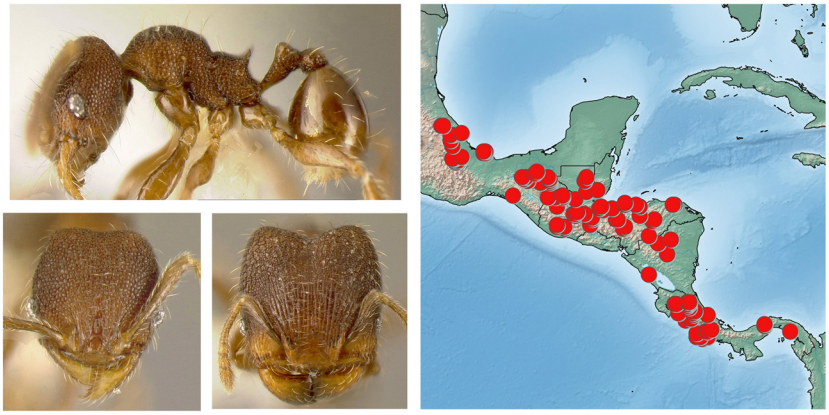
xyston
HW 0.44, SI 99
Montane wet forest

At ground baits and in litter samples. Nest in dead wood on ground.



harrisonfordi
HW 0.44, SI 103
Lowland-Montane wet forest

Very common in litter samples, occasional at ground baits. Nest in soil.



nebulosa
HW 0.44, SI 105
Lowland wet forest

Common. At ground baits, in litter samples, and in canopy. Nest in small cavities in dead wood.

hazenae
HW 0.44, SI 107
Montane wet forest

Rare. Occasional in litter samples. Nest under tree bark in low arboreal zone.

PLATE 11.

balatro
HW 0.44, SI 113
Montane wet forest

Common at baits and in litter samples.

carinote
HW 0.45, SI 86
Lowland wet forest

Common in litter samples.

andersoni
HW 0.45, SI 93
Montane wet forest

Occasional at ground baits and in litter samples. Nest in clay soil.

oaxacana
HW 0.45, SI 94
Montane wet forest

At ground baits, occasional in litter samples.

PLATE 12.

sparsisculpta
HW 0.45, SI 95
Lowland wet forest

Rare. In litter samples.

corniclypeus
HW 0.45, SI 99
Lowland wet forest

Occurs at ground baits and in litter samples.

cerina
HW 0.45, SI 108
Lowland wet forest

Forages in ground litter.
Nest in soil, under stones.

daphne
HW 0.45, SI 109
Lowland wet forest

Arboreal. In Malaise and fogging samples.

PLATE 13.

anastasii
HW 0.45, SI 113
Lowland wet forest

Common at baits. Forages in low arboreal zone. Nests in live and dead plant cavities.

machaquila
HW 0.45, SI 136
Moist forest, secondgrowth

Occurs at ground baits.

lucaris
HW 0.46, SI 88
Lowland wet forest

Rare. Arboreal. Nest under loose bark, low arboreal zone.

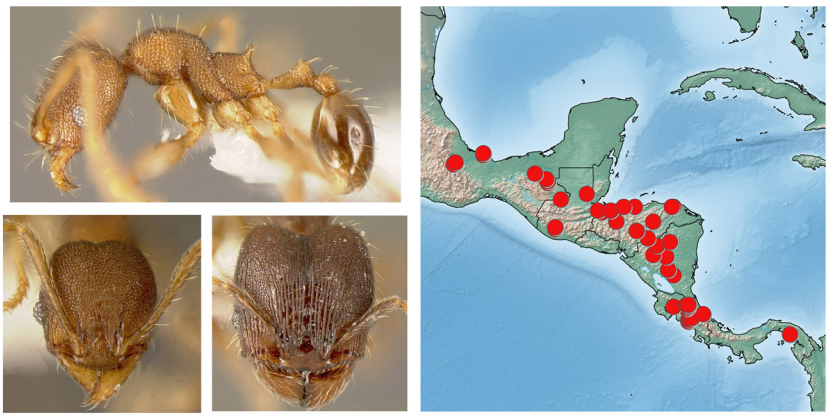
bilimeki
HW 0.46, SI 100
Lowland-Montane, disturbed areas

Common. Generalized foraging and nesting habits. Can be pest ant.

PLATE 14.

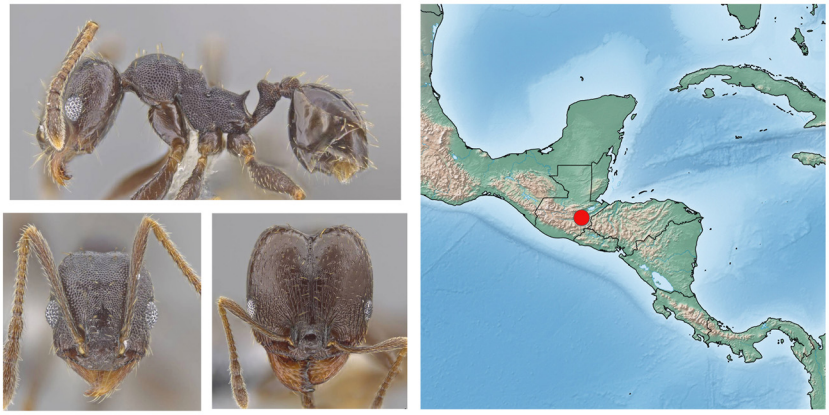
rectispina
HW 0.46, SI 113
Lowland-Montane wet forest

At ground baits and in litter samples. Nest in dead wood and in soil.



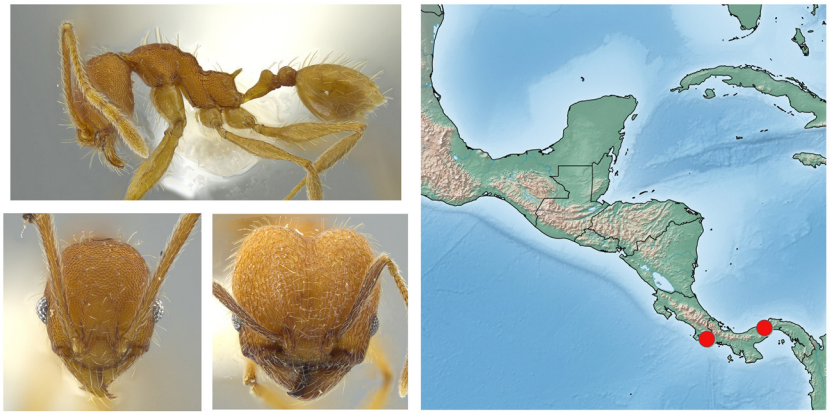
angustinigra
HW 0.46, SI 126
Dry scrub habitat

Occurs at ground baits



dasypyx
HW 0.46, SI 147
Lowland wet forest

Rare. In litter samples.



specularis
HW 0.47, SI 84
Lowland wet forest

Common. At ground baits and in litter samples. Nest in dead wood on ground, occasionally under epiphytes.

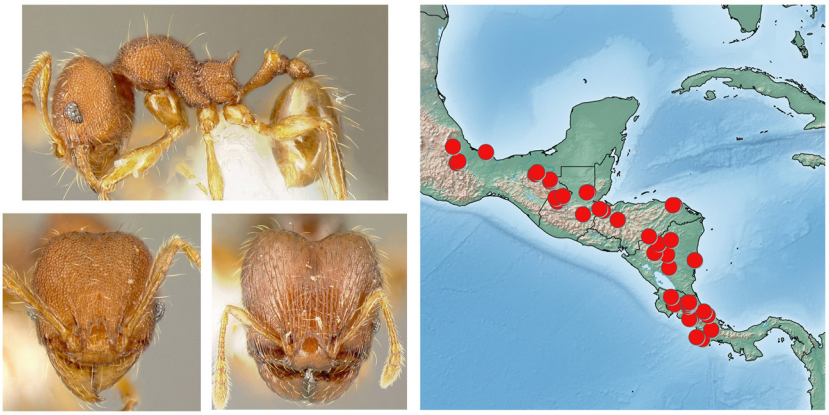


PLATE 15.

tuculutan
HW 0.47, SI 88
Dry scrub habitat

At ground baits.

debilis
HW 0.47, SI 89
Lowland wet forest

Common in litter samples, occasional at baits. Nest in soil and dead wood.

monteverdensis
HW 0.47, SI 93
Montane wet forest

Common in litter samples, Occasional at ground baits. Nest in rotten wood in litter.

brownampla
HW 0.47, SI 94
Montane wet forest

Common at ground baits and in Winkler samples.

PLATE 16.

muralla
HW 0.47, SI 96
Montane wet forest

Occurs at ground baits and in litter samples. Nest in clay bank.

tennantae
HW 0.47, SI 96
Lowland wet forest

In litter samples. Nest in dead wood.

floricola
HW 0.47, SI 99
Lowland wet forest

Arboreal. Nest in live or dead stems.

cataphracta
HW 0.47, SI 105
Lowland wet forest

Rare. Forages in low arboreal zone. Nest in live stems.

PLATE 17.

onyx
HW 0.47, SI 112
Lowland wet forest

Arboreal. Nest under epiphytes.

citrina
HW 0.47, SI 113
Lowland wet forest

Locally abundant. At baits and in litter samples.

punctatissima
HW 0.47, SI 120
Lowland-Montane, disturbed areas

Common. Generalized foraging and nesting habits.

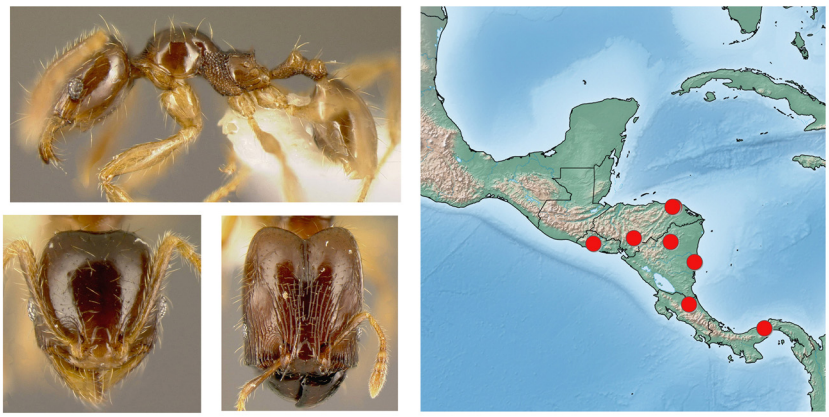
marmor
HW 0.47, SI 148
Montane pine-oak forest

Occurs in litter samples.

PLATE 18.

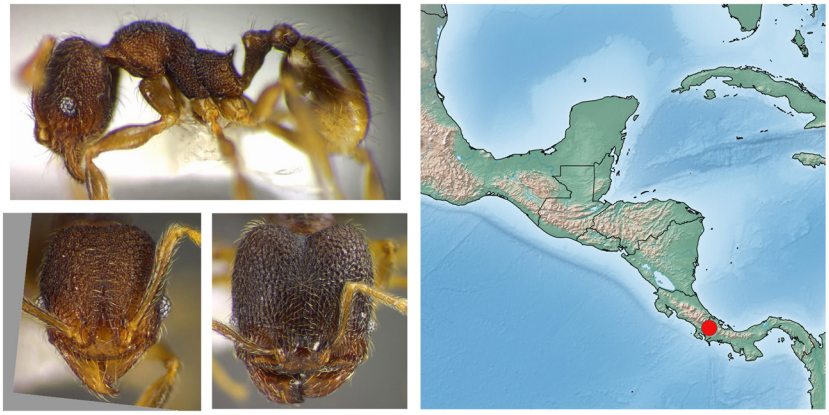
synarmata
HW 0.48, SI 89
Lowland wet forest

At ground baits and in litter samples. Nest in soil.



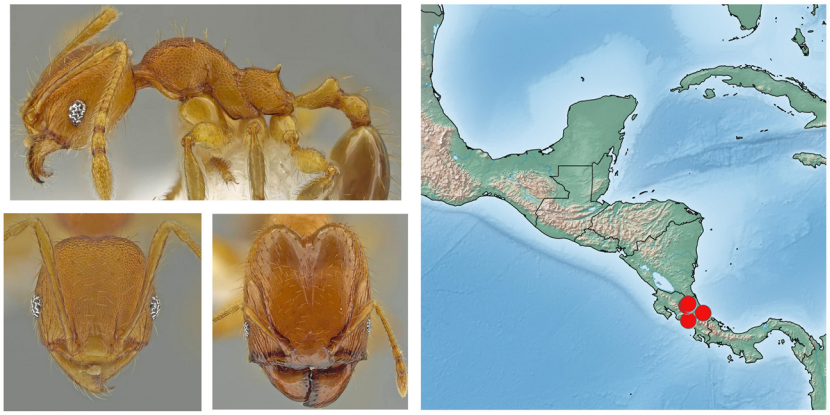
verricula
HW 0.48, SI 96
Montane wet forest

Rare. Nest in dead wood.



costaricensis
HW 0.48, SI 102
Lowland-Montane wet forest

Occurs at ground baits and in litter samples. Nest in soil.



nasutoides
HW 0.48, SI 110
Lowland wet forest

Rare. Arboreal. Nest in accumulated debris in low arboreal zone.

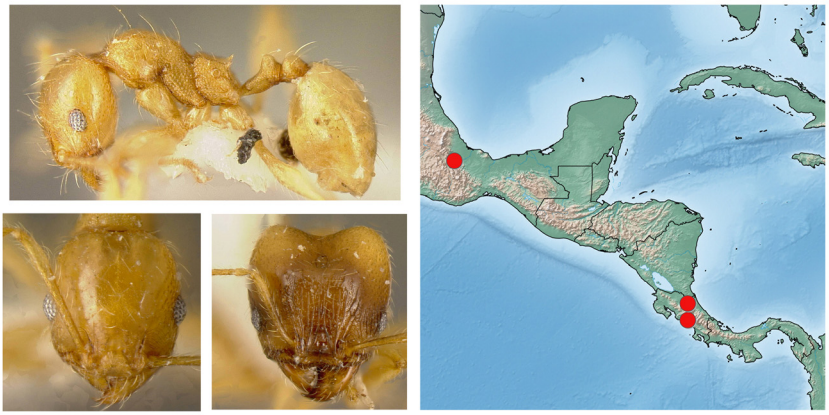
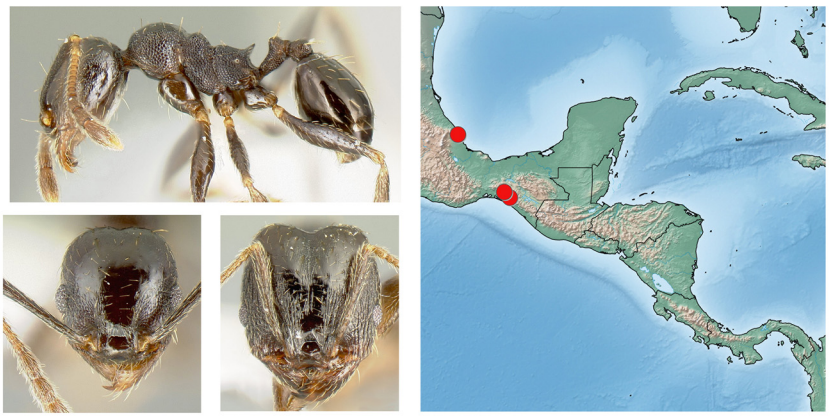


PLATE 19.

mackayi
HW 0.48, SI 126
Lowland-Montane, dry-moist, disturbed areas

At ground baits.

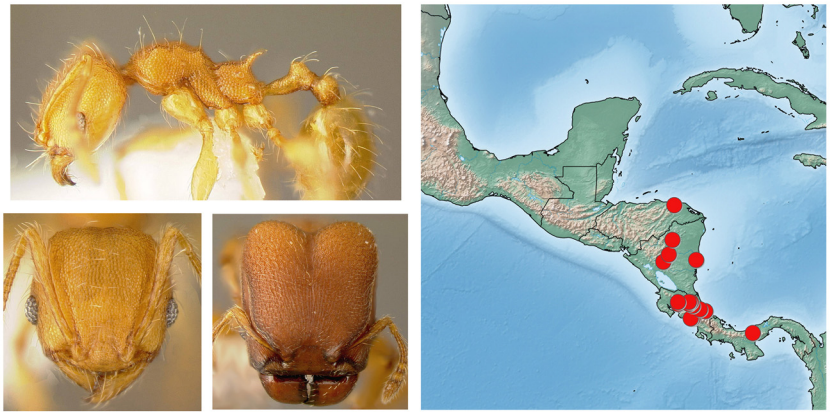


truncula
HW 0.49, SI 76
Montane wet forest

Arboreal. Nest in live or dead stems.

scrobifera
HW 0.49, SI 81
Lowland wet forest

Occasional at ground baits, litter samples. Nest in dead wood on ground.



nitidicollis
HW 0.49, SI 87
Lowland wet forest

Common. Arboreal. Nest in dead wood and under epiphytes.

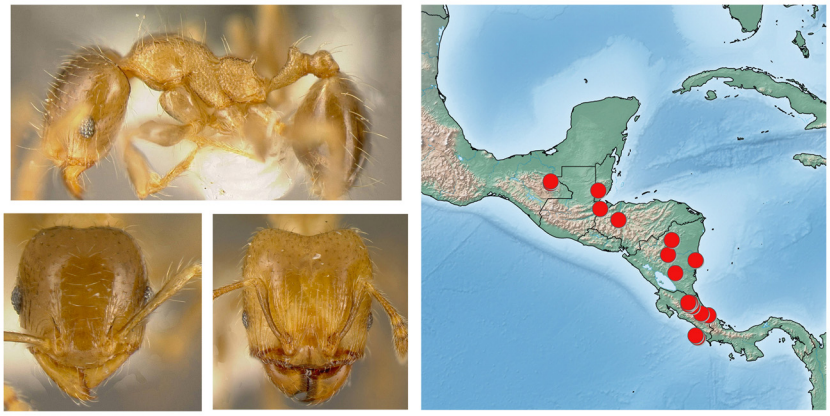


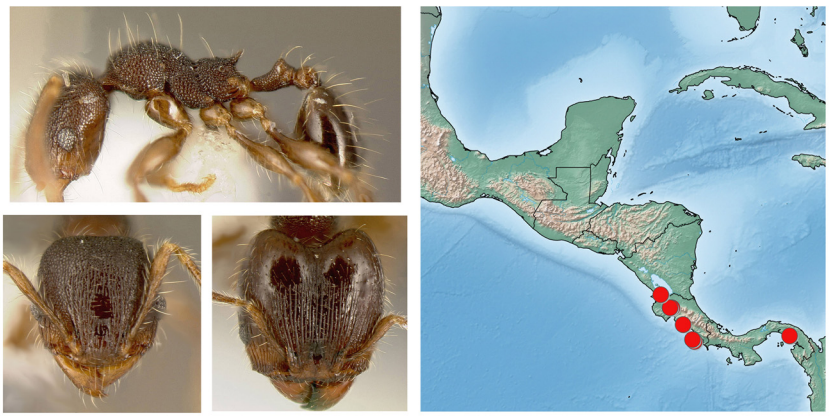
PLATE 20.

boliviana

HW 0.49, SI 89

Lowland, 2nd growth veg., disturbed areas

Nest in dead sticks and under loose bark, low arboreal zone.

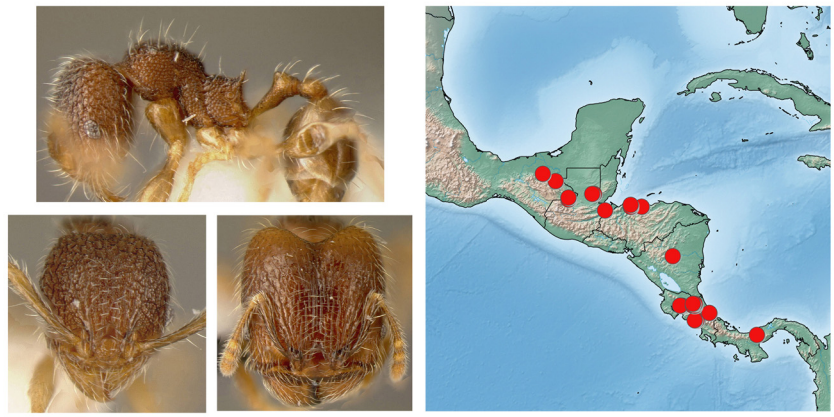


rectitrudis

HW 0.49, SI 89

Lowland wet forest

In litter samples. Nest in dead wood in litter, in soil under dead wood.

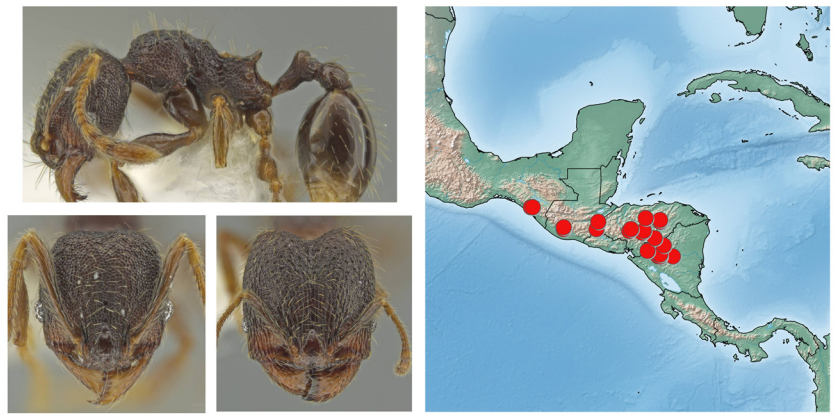


rectisentis

HW 0.49, SI 94

Montane wet forest

Abundant in litter samples. Nest in rotten wood and under epiphytes in low arboreal zone.



moskitia

HW 0.49, SI 103

Lowland wet forest

Occurs at ground baits and in litter samples.

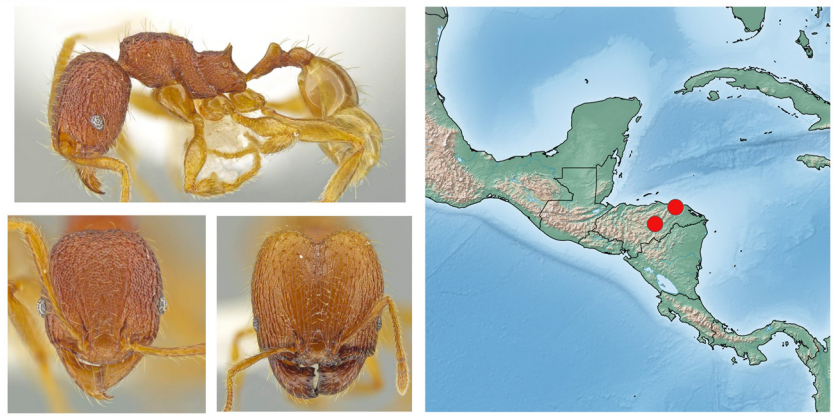


PLATE 21.

cramptoni
HW 0.49, SI 104
Lowland wet forest

Forages in low arboreal zone. Nest in live and dead plant cavities.




huarache
HW 0.49, SI 118
Lowland dry to moist habitat, often secondgrowth vegetation

Occurs at ground baits and in litter samples.




prostrata
HW 0.49, SI 169
Lowland wet forest

Forages and nests in low arboreal zone.




angulifera
HW 0.50, SI 83
Montane wet forest

Rare. Arboreal. Nest in dead branch in canopy.




PLATE 22.

hizemops
HW 0.50, SI 87
Montane wet forest

Occasional at ground baits and in litter samples. Nest in soil and under stones.

carinitida
HW 0.50, SI 92
Montane wet forest

Occurs at ground baits and in litter samples.

nephele
HW 0.50, SI 94
Montane wet forest

Occurs at ground baits and in litter samples. Nest in dead wood.

hasticeps
HW 0.50, SI 103
Montane, wet forest, pasture, disturbed areas

At ground baits and in litter samples. Nest in soil, under stones.

PLATE 23.

ulothrix
HW 0.50, SI 104
Lowland wet forest

Rare. Ground and low arboreal zone. Nest in dead wood.




agricola
HW 0.50, SI 113
Lowland dry forest

Occasional at ground baits.




angusticeps
HW 0.50, SI 136
Lowland dry forest, beach margin, disturbed areas

At baits.




vafra
HW 0.50, SI 150
Lowland wet-dry; open, disturbed areas

Ground foragers. Nest in soil.




PLATE 24.

passivaeferox
HW 0.51, SI 79
Lowland wet forest

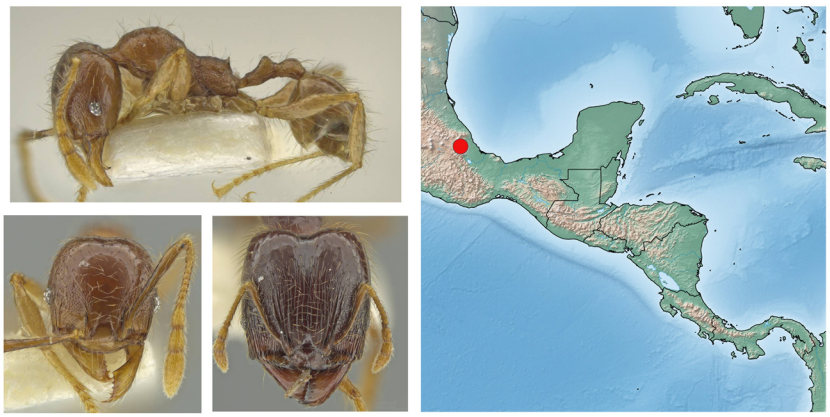
Ant-plant specialist in *Piper*.

bicornis
HW 0.51, SI 86
Lowland wet forest

Ant-plant specialist in *Piper*.

sabina
HW 0.51, SI 97
Montane

Known only from types.



brachyops
HW 0.51, SI 105
Dry-moist forest

Rare. At ground bait.

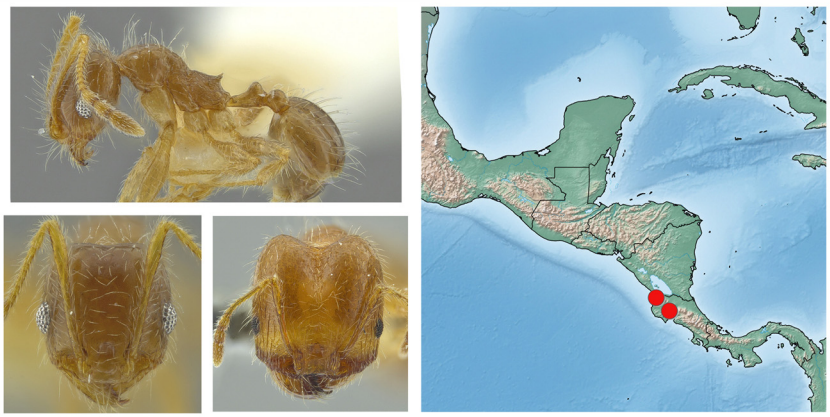


PLATE 25.

cahui
HW 0.51, SI 105
Lowland moist forest

Occurs at ground baits. Nest in soil.

chocoensis
HW 0.51, SI 195
Lowland wet forest

Rare. Forages on ground and low arboreal zone. In Malaise traps, at ground baits, occasional in litter samples.

tapanti
HW 0.52, SI 90
Montane wet forest

Nest under epiphytes in treefall.

lustrata
HW 0.52, SI 116
Lowland-Montane wet forest

Rare. Nest in soil at water-edge of streams.

PLATE 26.

veletis
HW 0.52, SI 136
Lowland wet forest

In litter samples. Nest in or under dead wood on ground.

potosiana
HW 0.52, SI 137
Lowland moist to wet forest, secondgrowth vegetation

Occurs at ground baits and in litter samples.

pararugiceps
HW 0.52, SI 159
Montane wet forest

Rare. At ground baits and in litter samples.

longiscapa
HW 0.52, SI 171
Lowland, open, disturbed areas

Weedy species. Forages on ground and in low arboreal zone. Nest in soil.

PLATE 27.

kukrana

HW 0.52, SI 189

Lowland dry to wet, forest to open habitats

Occurs at baits, ground and arboreal. Nests in soil and in small cavities in vegetation.

dryas

HW 0.53, SI 84

Lowland wet forest

Rare. Arboreal. Nest under epiphytes.

hansoni

HW 0.53, SI 90

Montane moist to wet forest

Occurs at ground baits. Nest under stone.

chalca

HW 0.53, SI 95

High montane, pasture, open areas

Nest under stones.

PLATE 28.

colobopsis
HW 0.53, SI 99
Lowland wet forest

Occasional at baits and in litter samples. Nest in clay soil.




mallota
HW 0.53, SI 120
Montane wet forest

Occurs at ground baits and in litter samples.




dossena
HW 0.53, SI 129
Lowland wet forest

Locally abundant. Forages and nests in low arboreal zone. Nest in cavities and under carton.




radoszkowskii
HW 0.53, SI 129
Lowland, dry forest, open disturbed habitats

Forages on ground and in low arboreal zone. Nest under dead wood.




PLATE 29.

lamancha
HW 0.53, SI 134
Lowland dry forest

Occurs at ground baits and in litter samples.




spathipilosa
HW 0.53, SI 174
Lowland wet forest

Rare. At ground baits. Nest in soil.




wardi
HW 0.54, SI 83
Lowland-Montane wet forest

At ground baits and in litter samples. Nest in dead wood on ground.




nigella
HW 0.54, SI 94
Lowland wet forest

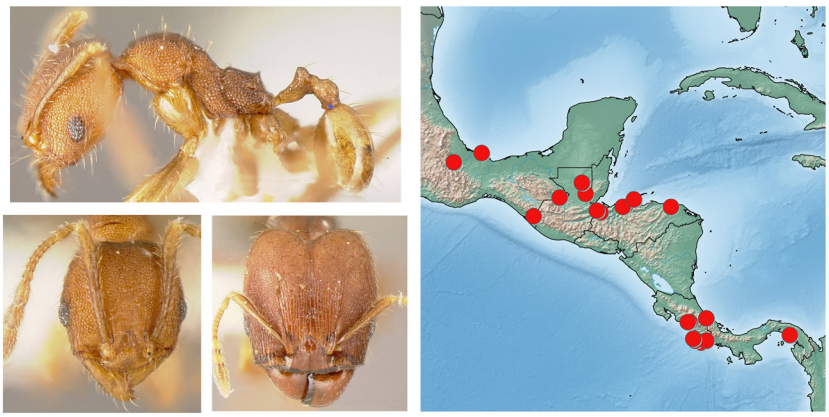
Occurs at ground baits. Nest in dead wood.




PLATE 30.

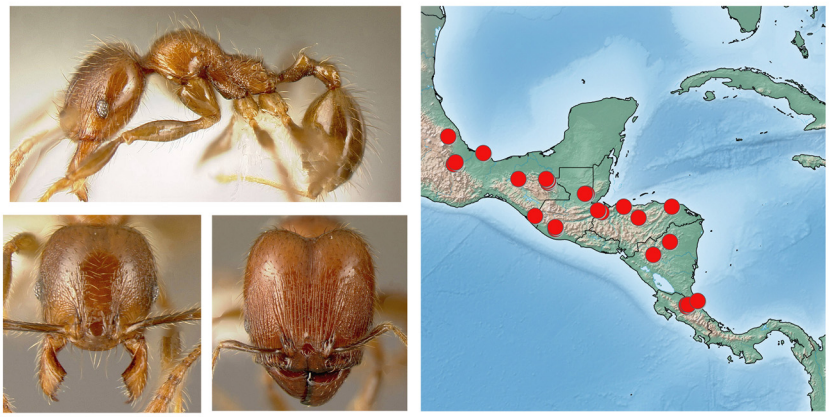
carapuna
HW 0.54, SI 97
Lowland wet forest

At ground baits and in litter samples. Nest in dead wood.



prattorum
HW 0.54, SI 97
Lowland-Montane wet forest

At ground baits and in litter samples. Nest in dead wood.



epiphyta
HW 0.54, SI 130
Lowland wet forest

Rare. Arboreal. Nest under epiphytes.

anima
HW 0.54, SI 139
Montane wet forest

Nest in dead wood.

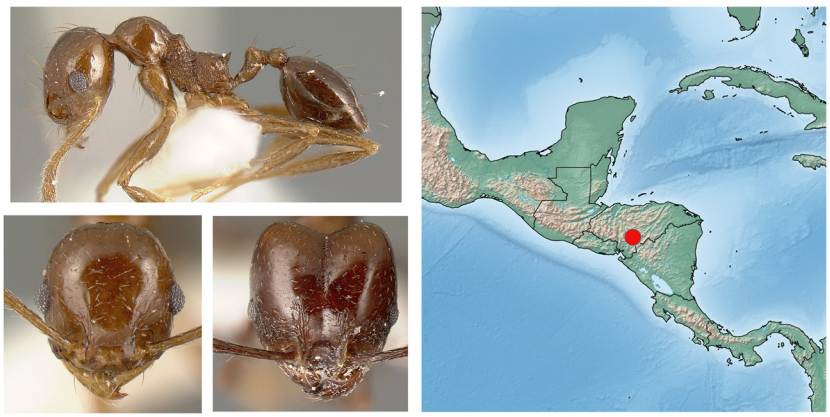
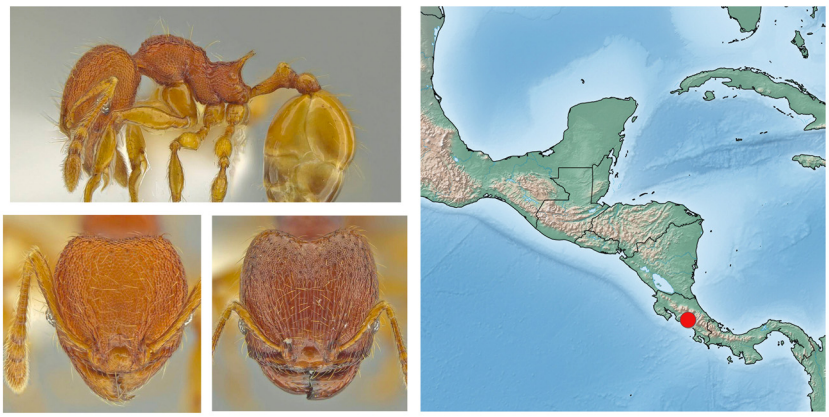


PLATE 31.

fincanaranjo
HW 0.55, SI 80
Montane wet forest

Occurs at ground baits and in litter samples.

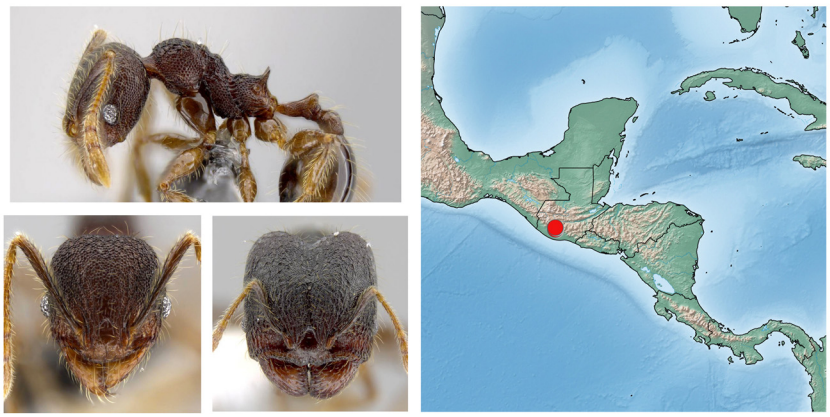


striaticeps
HW 0.55, SI 89
Lowland-Montane wet forest

Forages in low arboreal zone. Nest in dead wood and under loose bark in low arboreal zone.

atitlana
HW 0.55, SI 99
Montane wet forest

Occurs at ground baits and in litter samples.



amabilis
HW 0.55, SI 100
Lowland wet forest

Rare. Forages in low arboreal zone. Nest in cavities in live plants or in dead sticks on forest floor.

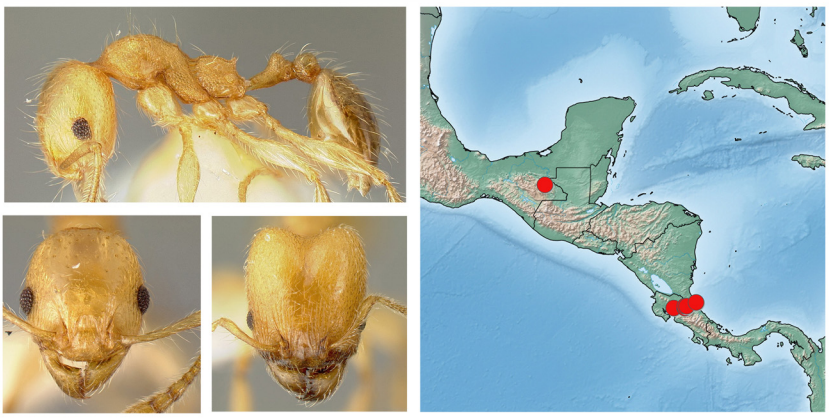


PLATE 32.

renae
HW 0.55, SI 106
Montane wet forest

Rare. In litter samples, occasional at ground bait.

diabolus
HW 0.55, SI 111
Lowland wet forest

Rare. Occasional in litter samples. Nest in dead wood on ground or in low arboreal zone.

umphreyi
HW 0.56, SI 96
Lowland-Montane wet forest

Rare. Low arboreal zone to arboreal. Nest in dead wood and under loose bark.

obturaculum
HW 0.56, SI 98
Montane wet forest

At ground baits.

PLATE 33.

megacephala
HW 0.56, SI 119
Urban areas

Invasive species. Locally abundant where introduced.

plebecula
HW 0.56, SI 132
Lowland wet forest

Common. Forages on ground and in low arboreal zone. At baits and in litter samples. Nest in soil.

acamata
HW 0.56, SI 137
Lowland wet forest

Common at baits and in litter samples. Nests in dead wood and in soil.

jelskii
HW 0.56, SI 179
Lowland dry forest, beach margins, disturbed areas

Widespread weedy species. Ground forager. Nest in soil.

PLATE 34.

rhinoceros
HW 0.57, SI 96
Lowland wet forest

At ground baits and in litter samples. Nest in dead wood.

rhinomontana
HW 0.57, SI 100
Montane wet forest

At ground baits and in litter samples. Nest in dead wood.

(note: color not different from *rhinoceros*)

rima
HW 0.57, SI 117
Montane wet forest

At ground baits, litter samples, beating samples, Malaise traps. Nest in low arboreal zone, under epiphytes, in live stems.

brandaoi
HW 0.57, SI 134
Lowland wet forest

Common at baits and in litter samples.

PLATE 35.

tschinkeli

HW 0.57, SI 142

Lowland-Montane wet forest

Common. At ground baits, in litter samples, in beating samples. Nest in dead wood.

psilogaster

HW 0.57, SI 150

Lowland-Montane wet forest

Common. Forages in low arboreal zone. Common at ground baits, occasional in litter samples. Nest in dead wood.

boruca

HW 0.57, SI 151

Lowland-Montane wet forest

Common at baits and in litter samples. Nest in and under rotten wood.

picobarva

HW 0.58, SI 99

Montane wet forest

Forages on ground and in low arboreal zone. Nest in dead wood and under stones.

PLATE 36.

boltoni

HW 0.58, SI 101

Montane wet forest

Nest in dead wood, under epiphytes.

erratilis

HW 0.58, SI 107

Lowland-Montane wet forest

Rare. Occasional in litter samples. Nest in dead wood in low arboreal zone.

sepultura

HW 0.58, SI 131

Montane wet forest

At ground baits, occasional in litter samples.

pugnax

HW 0.58, SI 133

Lowland-Montane, 2nd growth vegetation, disturbed areas

Common. Forages on ground and low arboreal zone. Nest in soil.

PLATE 37.

celaena
HW 0.58, SI 142
Lowland wet forest

At ground baits, occasional in litter samples. Nest in dead wood.




purpurea
HW 0.58, SI 149
Lowland-Montane wet forest

Common. At ground baits and in litter samples. Nest in soil.




hitoy
HW 0.58, SI 162
Lowland wet forest

Occurs at ground baits




besalon
HW 0.58, SI 172
Lowland wet forest

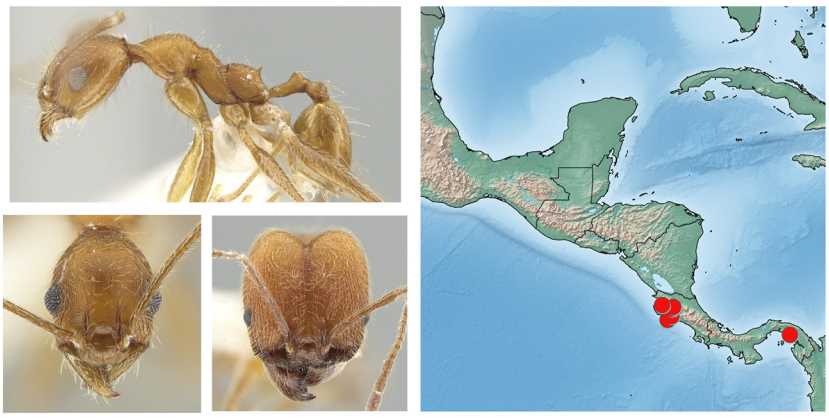
Nest in clay soil.




PLATE 38.

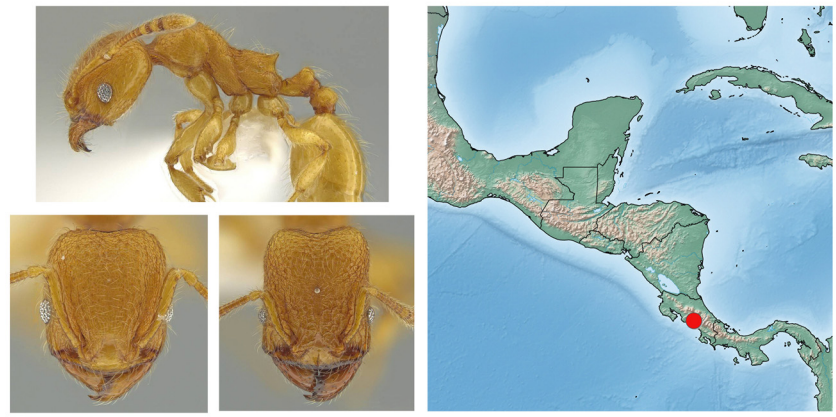
mantilla
HW 0.58, SI 180
Lowland dry forest, open areas

Forages on ground and in low vegetation.



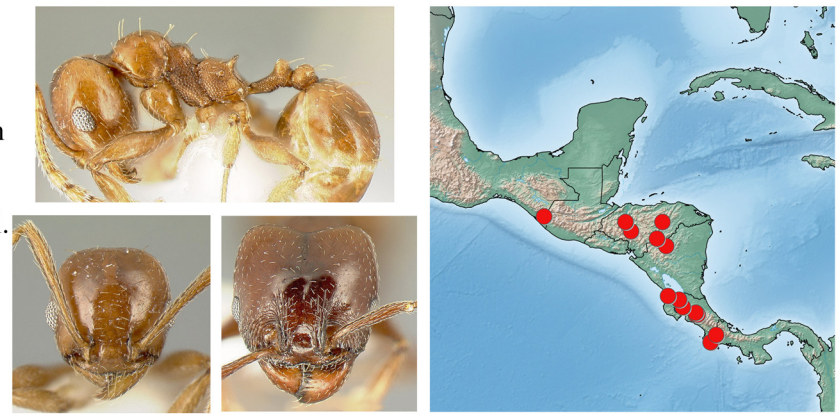
bicornisculpta
HW 0.59, SI 63
Montane wet forest

Ant-plant specialist in *Piper*.



synanthropica
HW 0.59, SI 109
Lowland-Montane dry forest, disturbed areas, open areas

Ground forager. Nest in soil.



branstetteri
HW 0.59, SI 120
Lowland-Montane wet to dry, 2nd growth vegetation.

Common at ground baits; occasional in litter samples.

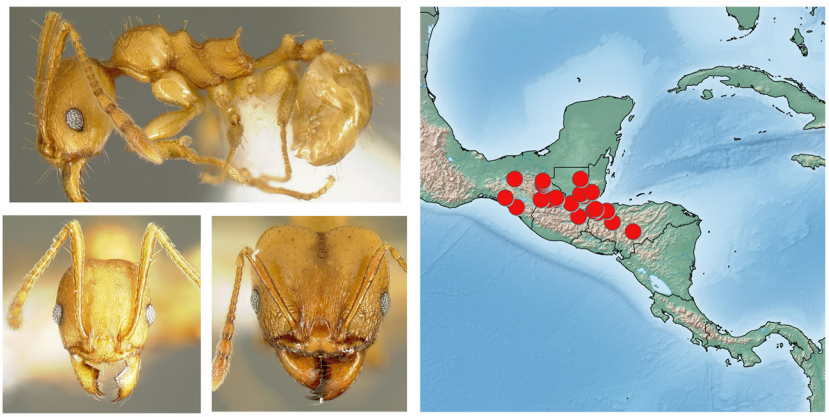


PLATE 39.

sensitiva

HW 0.59, SI 129

Lowland wet forest

At ground baits and in litter samples. Nest unknown.

tenuicephala

HW 0.59, SI 131

Montane wet forest

At ground baits and in litter samples. Nest in soil.

susannae

HW 0.59, SI 186

Lowland wet-dry forest, 2nd growth vegetation, disturbed areas

Common. Ground and canopy forager. Opportunistic nesting in cavities.

centeotl

HW 0.60, SI 97

Lowland dry-moist, open, disturbed areas.

PLATE 40.

vallifica

HW 0.60, SI 101

Lowland wet-dry; open, disturbed areas

Ground foragers. Nest in soil.

mesomontana

HW 0.60, SI 110

Montane wet forest

At ground baits and in litter samples.

probolonotum

HW 0.60, SI 130

Lowland wet forest

At ground baits and in litter samples. Nest in clay bank.

alfaroi

HW 0.60, SI 144

Montane wet forest

Common in litter samples, occasional at baits. Nest in and under dead wood.

PLATE 41.

guerrerana
HW 0.60, SI 157
High montane, wet forest

At ground baits and in litter samples. Nest in soil.

roushae
HW 0.60, SI 172
Lowland wet forest

Common at ground baits, occasional in litter samples. Nest unknown.

tanyscapa
HW 0.60, SI 181
Lowland wet forest

At ground baits, forages in low vegetation. Nest in soil.

musinermis
HW 0.60, SI 229
Montane wet forest

Occurs at ground baits and in litter samples.

PLATE 42.

bigote
HW 0.61, SI 97
Lowland wet forest

Rare. Nest in clay soil near streams.




piceonigra
HW 0.61, SI 129

(known only from types)



"Mexico"

pubiventris
HW 0.61, SI 153
Lowland-Montane, disturbed areas

At ground baits.




platyscapa
HW 0.61, SI 156
Montane wet habitat, forest and open areas

Occurs at ground baits and in litter samples. Nest in soil.




PLATE 43.

simonsi
HW 0.62, SI 98
Lowland wet forest

Common. At ground baits, occasional in litter samples. Nest in clay soil.




carinata
HW 0.62, SI 101
Montane wet forest

Rare. In litter samples, occasional at baits.




luteagossamer
HW 0.62, SI 146
Montane wet forest

Occurs at ground baits and in litter samples. Nest in clay bank.




nubicola
HW 0.62, SI 148
Montane wet forest

Occurs at ground baits, in litter samples, and in beating samples.




PLATE 44.

fallax

HW 0.62, SI 149

Lowland dry forest, disturbed areas

Common ground forager. Large nest in soil.

sicaria

HW 0.62, SI 164

Lowland-Montane wet forest

Arboreal. Forages in low arboreal zone. Nest under epiphytes and in accumulated debris.

indagarama

HW 0.62, SI 172

Lowland wet forest

Arboreal. In fogging samples and fresh treefalls.

indagatrix

HW 0.62, SI 173

Lowland-Montane wet forest

Common. Forages on ground and in low arboreal zone. Nests under dead wood and in cavities in low arboreal zone.

PLATE 45.

kelainos
HW 0.62, SI 177
Lowland wet forest

Occurs at ground baits. Nest in soil at stream edge.

gymnoceras
HW 0.62, SI 184
Montane wet forest

Common at ground baits and in Malaise traps. Rare in litter samples. Nest in soil and under dead wood.

walkeri
HW 0.63, SI 100
Lowland-Montane wet forest

Forages on ground and in low arboreal zone. Nest in dead wood on ground, live or dead stems in vegetation.

fossimandibula
HW 0.63, SI 102
Lowland wet forest

Rare. Occasional at baits. Nest in clay soil.

PLATE 46.

vestita
HW 0.63, SI 112
Lowland wet forest

Rare. Ground forager. Nest in clay soil.


diana
HW 0.63, SI 113
Montane wet forest

Arboreal. Nest under epiphytes.


deceptrix
HW 0.63, SI 117
High montane, wet forest

Common. At baits and in litter samples. Nest in soil and under stones.


arachnion
HW 0.63, SI 121
Lowland wet forest

Occasional at baits and in litter samples. Nest in dead wood on ground.


PLATE 47.

insipida
HW 0.63, SI 137
All habitats

Common. Forages on ground and in low arboreal zone. Nest in soil.




bucculenta
HW 0.63, SI 143
Montane wet forest

Rare. At ground bait.




gulo
HW 0.63, SI 164
Lowland-Montane wet forest

Common at ground baits, occasional in litter samples. Forages on ground and in low arboreal zone. Nest in soil and under dead wood.




hectornitida
HW 0.63, SI 184
Montane wet forest

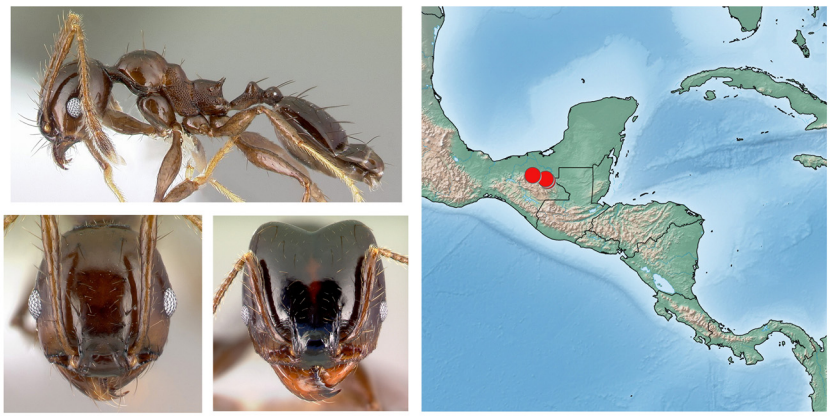
Occurs at ground baits and in litter samples. Nest in dead wood.




PLATE 48.

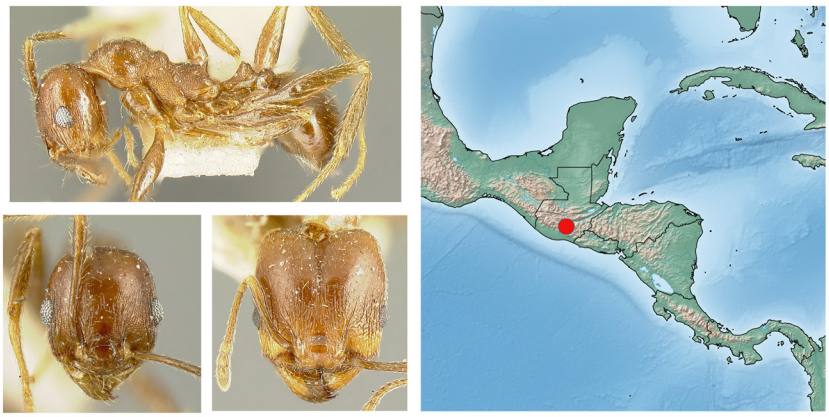
leoncortesi
HW 0.64, SI 124
Lowland wet forest

Common. At ground baits.



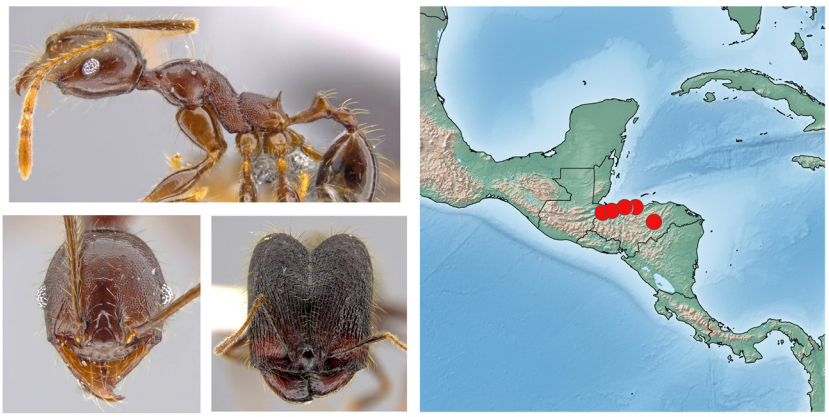
maja
HW 0.64, SI 126
Montane

(Known only from types.)



lagunculiminor
HW 0.64, SI 147
Lowland-Montane wet forest

Occurs at ground baits. Nest in clay banks.



hoelldobleri
HW 0.64, SI 158
Lowland wet forest

Arboreal. Nest in canopy and low arboreal zone, in live or dead plant cavities.

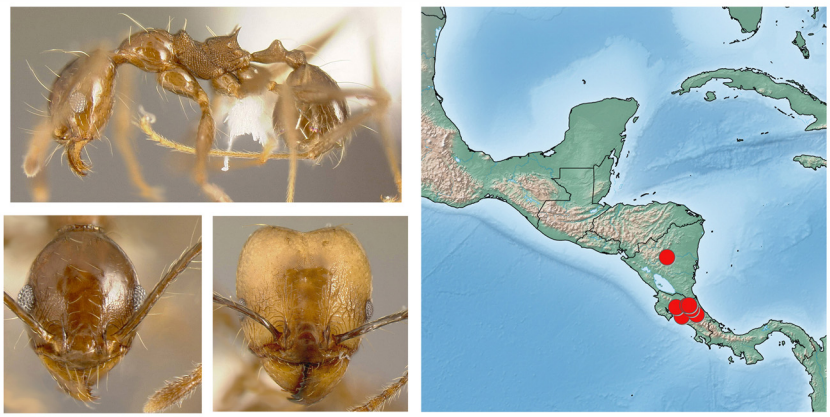


PLATE 49.

ajax
HW 0.64, SI 188
Lowland wet forest

Rare. Forages in low arboreal zone. Nest in cavities in live plants or in dead sticks on forest floor.




absurda
HW 0.65, SI 99
Lowland-Montane, wet forest to open areas

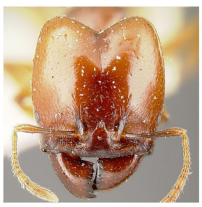
At ground baits and in litter samples. Nests in soil.




stulta
HW 0.65, SI 107
Montane

(Known only from types.)






hirsuta
HW 0.65, SI 163
Lowland wet forest

Occasional at ground baits and in litter samples. Nest in clay soil.




PLATE 50.

ajaxigibba
HW 0.65, SI 197
Lowland wet forest

Rare. Forages in low arboreal zone. Nest in dead wood.




cusuco
HW 0.66, SI 144
Montane wet forest

Common at ground baits; occasional in litter samples.




biolleyi
HW 0.66, SI 162
Montane wet forest

Occasional. Forages on ground and low vegetation. Nest in soil.




fiorii
HW 0.66, SI 213
Lowland wet forest

Locally abundant. Forages in low arboreal zone. Carton nest under leaves.




PLATE 51.

tisiphone
HW 0.67, SI 111
Montane wet, open areas

Ground foragers. Nest in soil.

sensipelada
HW 0.68, SI 143
Lowland-Montane wet forest

At ground baits, in beating sample.

violacea
HW 0.68, SI 154
Montane wet forest

Forages in low arboreal zone. Nest in carton nest, ant garden in low arboreal zone.

laelaps
HW 0.68, SI 173
Montane wet forest

Rare. At ground baits.

PLATE 52.

sebofila
HW 0.68, SI 176
Montane wet forest

Rare. At ground baits. Nest in soil.




innupta
HW 0.69, SI 136
Montane wet forest

Rare. Nest under epiphytes in canopy.




familiaparra
HW 0.69, SI 193
Montane wet forest

Occurs at ground baits.




excubitor
HW 0.70, SI 109
Lowland wet forest

Arboreal. Nest in live stems and under epiphytes.




PLATE 53.

lineafrons
HW 0.70, SI 157
Montane wet forest

Occurs at ground baits. Nest in clay bank.




rogeri
HW 0.71, SI 152
Lowland wet forest

At ground baits. Nest in clay soil.




eosimilis
HW 0.71, SI 153
Lowland-Montane wet forest

Occurs at ground baits and in litter samples. Nest in dead wood.




tinamu
HW 0.72, SI 179
Montane wet forest

At ground baits, occasional in litter, beating, Malaise samples.




PLATE 54.

traini
HW 0.73, SI 92
Montane wet forest

Rare. Ground forager.




musacolor
HW 0.73, SI 164
Montane wet forest

Occurs at ground baits.




savegre
HW 0.73, SI 180
Lowland-Montane wet forest

At ground baits, in beating sample.




caliginosa
HW 0.75, SI 147
Lowland-Montane wet forest

Occurs at ground baits and in litter samples.



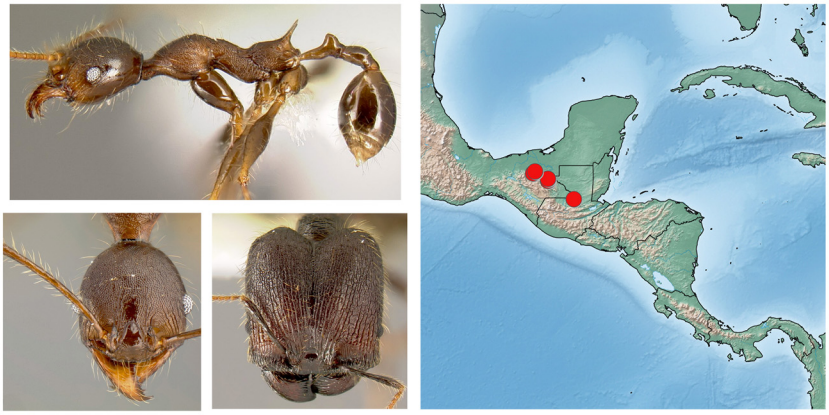

PLATE 55.

ectatommoides
HW 0.76, SI 114
Lowland wet forest

Rare. Nocturnal foragers in low arboreal zone. Nest in dead wood in low arboreal zone.

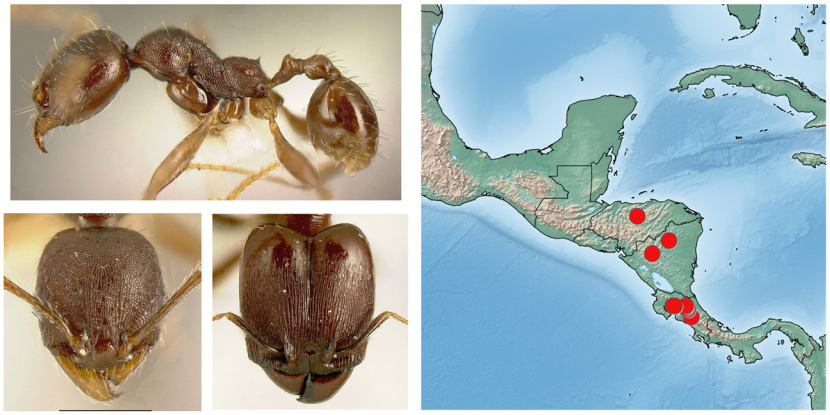
lagunculinoda
HW 0.76, SI 160
Lowland wet forest

At ground baits.



exarata
HW 0.77, SI 100
Montane wet forest

Arboreal. Nest in live stems and under epiphytes.



tsontekonwei
HW 0.77, SI 110

Nest in soil. Seed harvester.

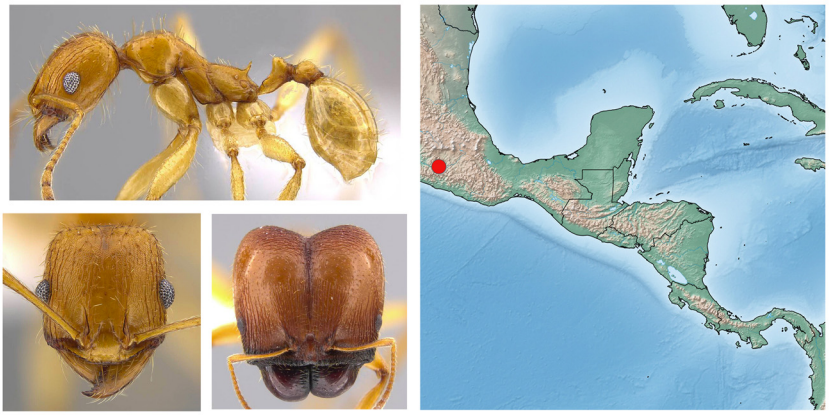
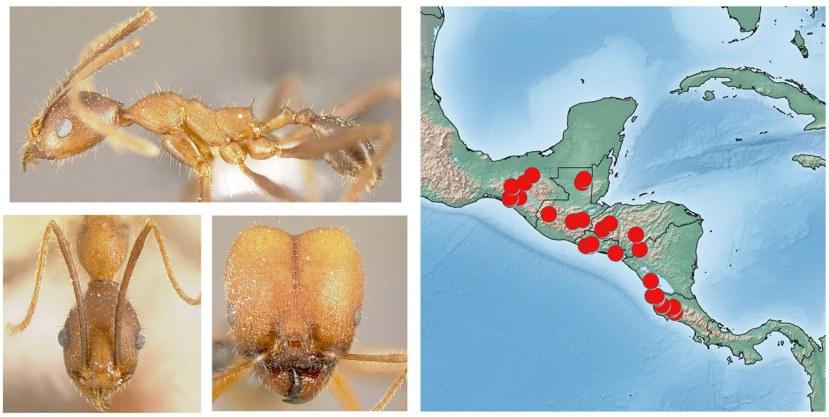


PLATE 56.

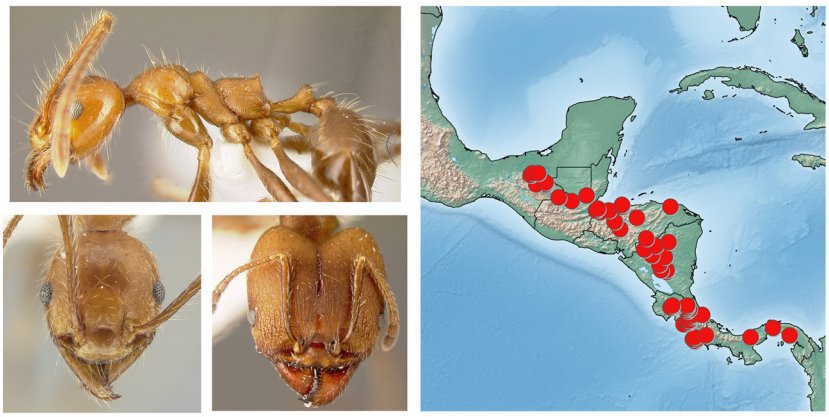
gouldi
HW 0.77, SI 190
Lowland dry-moist forest, open, disturbed areas.

Common ground forager. At baits. Nest in soil.



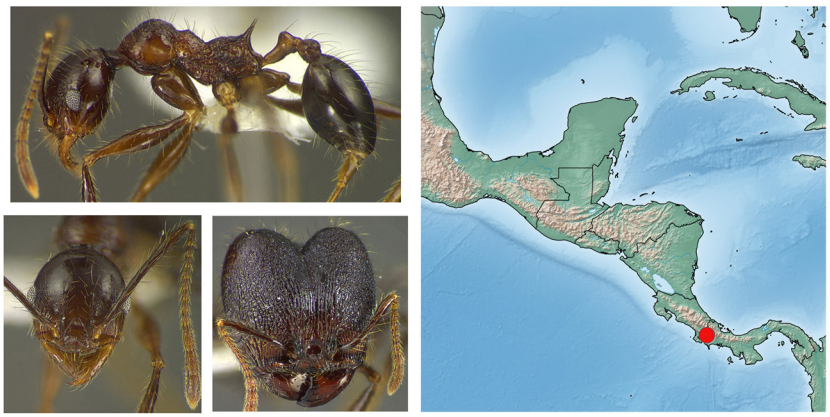
biconstricta
HW 0.78, SI 141
Lowland wet forest

Very common. Forages on ground and low arboreal zone. Nest in large dead wood.



lourothi
HW 0.78, SI 149
Montane wet forest

Rare. Nest in rotten log.



gauthieri
HW 0.80, SI 105
Lowland wet forest

Low density. Forages on ground and in low arboreal zone. Nest in dead wood in low arboreal zone.

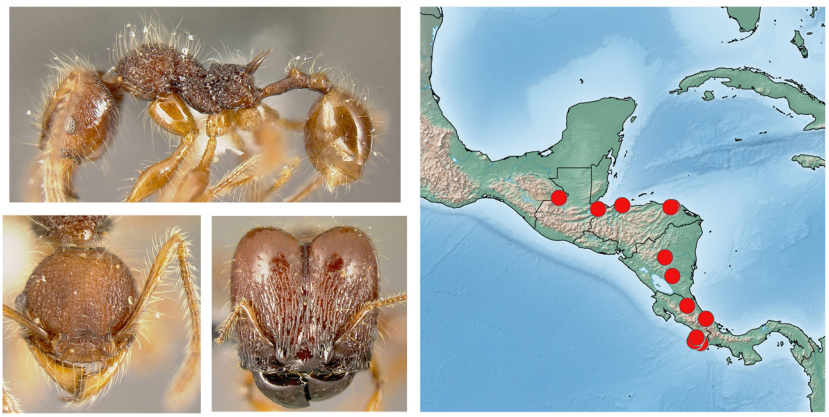


PLATE 57.

hector

HW 0.80, SI 181

Montane wet forest

Rare. Nest under dead wood.

rogeripolita

HW 0.84, SI 185

Montane wet forest

Nest in clay bank.

fimbriata

HW 0.86, SI 102

Lowland-Montane wet to dry

Nocturnal ground forager. Nest in soil.

eowilsoni

HW 0.91, SI 124

Lowland wet forest

Rare. Nest in clay bank.

PLATE 58.

ursus

HW 0.91, SI 124

Lowland-Montane wet forest

Forages on ground and in low arboreal zone. At baits, occasional in litter samples. Nest in dead stems in low arboreal zone.

vorax

HW 1.01, SI 113

Lowland wet forest

Forages on ground and in low arboreal zone. At baits, occasional in litter samples. Nest in dead wood on or near the ground.

PLATE 59.