



Pheidole bilimeki Reconsidered (Hymenoptera: Formicidae)

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Abstract

Pheidole bilimeki is a common ant species throughout northern South America, Central America, and southern Mexico. Character variation is reevaluated and *Pheidole bilimeki* is redefined. *Pheidole anastasii* **rev. stat.** and *P. jamaicensis* **rev. stat., n. stat.** are removed from synonymy and *P. jamaicensis* is elevated to species rank. *Pheidole anastasii* is a relatively uniform species that lives in plant cavities in the understory of closed canopy forest. *Pheidole jamaicensis* and *P. bilimeki* inhabit open areas and are often associated with human altered landscapes. *Pheidole anastasii* occurs in lowland Atlantic slope forests from Panama to Guatemala and southern Mexico (Chiapas); *P. jamaicensis* is restricted to the islands of Jamaica and Hispaniola; *P. bilimeki* occurs on Cuba, the Bahamas, and the American mainland. Differentiating characters are also provided for *Pheidole punctatissima*, a common species with habitus and habits similar to *P. bilimeki*.

Key words: Neotropical, ant, species, Myrmicinae

Introduction

The ant genus *Pheidole* contains over 600 New World species (Wilson 2003). Throughout the tropical and subtropical Americas, *Pheidole* are abundant and comprise a diverse component of local ant communities. Lowland rainforest habitats may contain over 70 species (Longino *et al.* 2002). Relative abundance distributions for *Pheidole* are typical of ecological communities in general, with a few species being very abundant and conspicuous, and the majority of species being less abundant and less obvious. In the northern Neotropics *Pheidole bilimeki* is often one of the abundant species. In highly disturbed areas another very common species is *P. punctatissima*, with minor workers that are nearly indistinguishable from those of *P. bilimeki*. Since these are among the most frequently encountered ants, it is particularly important to improve taxonomic understanding of the group.

Brown (1981) made initial progress on the group by recognizing the differences between *P. punctatissima* and several forms that had been attached to it as subspecies or varieties. He associated the various infraspecific forms with the species *P. annectens*. Wilson (2003) synonymized both *P. annectens* and *P. anastasii* under *P. bilimeki*. Thus the current concept of *P. bilimeki* is as a widespread and strongly polytypic species. However, molecular evidence suggested that *P. anastasii* was sister to two *Pheidole* species: *bilimeki* and *floridana* (Moreau 2008). We present here evidence that in Costa Rica there are two broadly sympatric species that both fall within the current concept of *P. bilimeki*. We attempt to better define species boundaries between these two species, and we discuss character variation throughout the range of *P. bilimeki*. We also discuss differentiating features of *P. punctatissima*, whose minor workers are very similar to *P. bilimeki*.

Methods

Observations were made at 50x or 63x magnification with a dissecting microscope. Most measurements were made with a micrometer stage with digital output in increments of 0.0001mm. However, variation in specimen orientation, alignment of crosshairs with edges of structures, and interpretation of structure boundaries resulted in measurement accuracy to the nearest 0.01 to 0.005mm, depending on sharpness of the defined boundary. All measurements are presented in mm.

Material from the following collections was examined for this study:

INBC: Instituto Nacional de Biodiversidad, Costa Rica.

JTLC: John T. Longino, personal collection, Olympia, WA, USA.

LACM: Los Angeles County Museum of Natural History, Los Angeles, CA, 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.

NMW: Naturhistorisches Museum, Vienna, Austria.

USNM: National Museum of Natural History, Washington, DC, USA.

Results

The group of species under discussion share the following morphological traits:

Minor worker: head width (not including eyes) 0.38 to 0.55mm; scape length 0.40 to 0.60mm; scape index ($100 * \text{scape length} / \text{head width}$) 95 to 125; face and mesosoma uniformly foveolate; promesonotal groove very weakly or not at all impressed; with short upturned propodeal spines; postpetiole broad and low, somewhat flattened, lower than petiolar node; first gastral tergite with anterior third to entire surface shagreened; pilosity on mesosomal dorsum sparse and stiff; pilosity on hind tibia fully appressed and short.

Major worker: head width 0.74 to 1.09mm; scape length 0.44 to 0.63mm; scape index 50 to 68; face largely foveolate rugose, with variable extent smooth and shiny posteriorly; hypostomal margin with two closely-spaced medial teeth; first gastral tergite with anterior third to entire surface shagreened.

We recognize in Costa Rica two distinct species, *P. anastasioi* and *P. bilimeki*, that can be separated on the basis of relative scape length in the minor worker, color, habitat preference, and nesting habits. Minor workers of *Pheidole anastasioi* have relatively longer scapes (Fig. 1) and the posterior margin of the head is more rounded, both majors and minors are uniformly yellow orange, nests are in plant cavities, and the species inhabits the shaded understory of mature or second growth wet forest. Minor workers of *P. bilimeki* have shorter scapes (Fig. 1) and the head is less rounded behind, both majors and minors are brown, nests are almost anywhere including in rotten wood and under stones, and the species inhabits mostly open and highly disturbed areas. The two species are sympatric throughout Costa Rica, but typically maintain a strict habitat separation. At La Selva Biological Station, in lowland rainforest on the Atlantic slope, *P. anastasioi* is one of the most abundant ants in the forest understory, and is never found in the laboratory clearing. In contrast, *P. bilimeki* is abundant in the laboratory clearing, where it can be a pest ant in buildings, yet is never found in the forest. At Sirena in Corcovado National Park in southeastern Costa Rica, *P. anastasioi* is a common understory ant in mature and second growth forest, much like it is at La Selva, while *P. bilimeki* is common in the vegetation of the upper beach margin and extending less than 20m into the forest.

Pheidole anastasioi has a relatively consistent morphology and behavior over most of its range. Most collections are from Costa Rica (over 350 separate collection events in JTL's specimen database) but a few collections have been examined from Panama, Nicaragua, Honduras, Guatemala, and Mexico (Chiapas). All collections are from wet forest habitats, most from below 500m elevation but with a few to a maximum of 1200m. The northernmost record is from rainforest near Tikal in the Peten of Guatemala, and these specimens

are indistinguishable from Costa Rican material. Within Costa Rica, occasional specimens have shorter scapes (Fig. 1). In at least one instance the variation is intranidal, and other workers have typical long scapes.

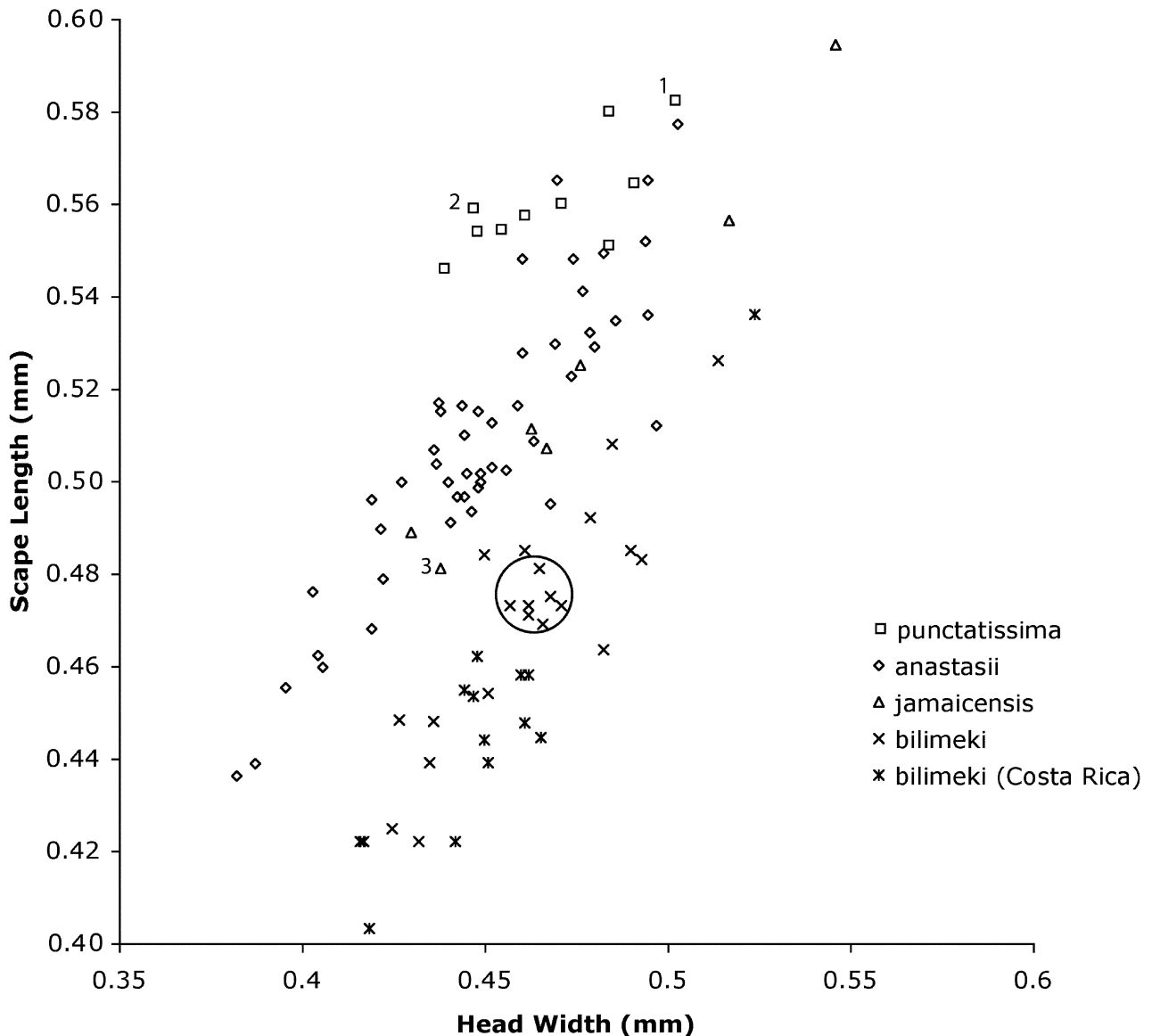


FIGURE 1. Relationship of minor worker head width and scape length for *Pheidole bilimeki* and related species. 1: from the type series of *P. punctatissima*. 2: syntype of *P. punctatissima napaea*. 3: syntype of *P. jamaicensis*. Circle: syntypes of *antoniensis*, *barbouri*, *cellarum*, *insulans*, *johnsoni*. A similar plot for major workers shows the same general trends but with less separation among the species.

Pheidole anastasii is a very abundant species in the low arboreal stratum of primary wet forest understory throughout Costa Rica. Nests may be found in almost any kind of cavity or sheltered space, and they may augment their nest space by building galleries and tunnels with carton or earthen construction. Nests have been observed in cavities in live stems of *Psychotria* (Rubiaceae), *Witheringia asterotricha* (Solanaceae), and *Pausandra trianae* (Euphorbiaceae), bracts of *Ischnosiphon* (Marantaceae), clasping petiole bases of Araceae, and the bulbous leaf bases of *Tillandsia bulbosa* (Bromeliaceae). It is a common opportunistic inhabitant of myrmecophytes such as saplings of *Cecropia*, portions of myrmecophytic *Ocotea* trees abandoned by *Myrmelachista*, and myrmecophytic *Piper* species. In every Costa Rican population of myrmecophytic melastomes (those with petiolar or laminar pouches; *Conostegia setosa*, *Clidemia* sp., *Tococa* sp.) that has

been observed (Corcovado, La Selva, Tortuguero), this species has been the most abundant inhabitant. It was the dominant ant in a study of *Conostegia setosa* at La Selva (Tennant 1994). The species also nests in dead sticks and branches on or above the forest floor, and under bark flaps on tree trunks. When nests are in myrmecophytic melastomes, carton galleries may occur on the outside, connecting pouches and extending down the stem to the ground. Colonies appear to be polydomous. Workers are generalist foragers, and may be taken at baits or in samples of sifted leaf litter. Colonies have occasionally been found as exotics in greenhouses in the United States (New York, Washington D.C.), which is no surprise given the frequency with which it is found in live plant cavities in Central America.

Specimens from the Caribbean coast of Panama, at the southernmost limit of the species, are the most aberrant. Minors and majors are identical to Costa Rican *P. anastasioi* with respect to shape and measurements, but differ in color. Instead of being clear yellow orange, minors are a dusky gray brown and majors similar but with the posterior third or more of the head yellow (approaching *P. punctatissima*). The specimens were collected in ant-plant domatia in forest understory, thus matching the behavior of *P. anastasioi*.

Specimens from Hispaniola and Jamaica exhibit a slightly different but consistent combination of characters that distinguish them from other *P. bilimeki*-like forms. The minor worker scapes are long, like *P. anastasioi* (Fig. 1). Minor and major workers are uniformly dark red brown. Collecting on Jamaica by JTL yielded collections from multiple habitats and nest sites. Collections were made in lowland second growth, wet forest on karst, and cloud forest. Nests were found beneath epiphytes, in rotten wood on the ground, and under stones. Multiple collections in the Dominican Republic by W. L. Brown in 1975 were from diverse habitats: evergreen forest, coffee plantation, limestone, ravine, and mixed hardwood-pine forest. The fact that the specimens from Hispaniola and Jamaica are somewhat differentiated from mainland and other *bilimeki*-like island (Cuba, Bahamas) forms suggests a period of isolation and shared ancestry, which justifies the recognition of *P. jamaicensis* as a distinct species.

This leaves the residue that is *P. bilimeki*. This is a heterogenous assemblage that may itself prove to be multiple species when more material is available. The main feature differentiating *P. bilimeki* from *P. anastasioi*, *P. jamaicensis*, and *P. punctatissima* is the shorter scapes. Typically specimens are uniformly red brown, but some collections from the northern part of the range, including the type of *P. bilimeki*, are yellow orange, like *P. anastasioi*. The sculpture on the first gastral tergite is highly variable. There is always some degree of shagreened, opaque sculpture anteriorly, around the postpetiolar insertion, but it varies from covering the entire tergite to covering only about the anterior third. Within nest series, shagreening is typically more extensive on minor workers than major workers; in many series where the first gastral tergite is completely shagreened in the minor worker, only the anterior third is sculptured in the major.

Pheidole bilimeki is a common species in open, recently or frequently disturbed habitats. It occurs in all tropical climate zones where ants occur: lowland dry forest, lowland wet forest, and montane habitats to about 1500m elevation. In Costa Rica it is a common ant of roadsides, nesting under stones or in dead fenceposts. It is a frequent pest ant in houses. It is a common ant at baits in second growth dry forest vegetation in seasonally dry Guanacaste Province. It can also be abundant in large disturbances deep within primary forest reserves. The Peñas Blancas Valley is a large forested reserve in the Cordillera de Tilarán in northern Costa Rica. In 2001 there was a large debris torrent that created a very large area currently undergoing primary succession. The area is about 5km from the edge of the reserve and human settlement. As of early 2008 the area was dominated by *P. bilimeki*.

Finally, there is the widespread weedy species, *P. punctatissima*. In terms of metric characters and sculpture, it is very like *P. anastasioi*. The minor workers are relatively large and the scapes relatively long (Fig. 1). The coloration is distinctive. The minor workers are always dark red brown to nearly black. The major workers have a color similar to that of associated minor workers over most of the body, but a posterior portion of the head is a sharply contrasting yellow. The coloration is uniform over much of the range, but populations in the mountains of Chiapas State in southern Mexico have the yellow spot greatly reduced. The shagreening on the gaster of minor workers is typically strong and covers the entire first gastral tergite.

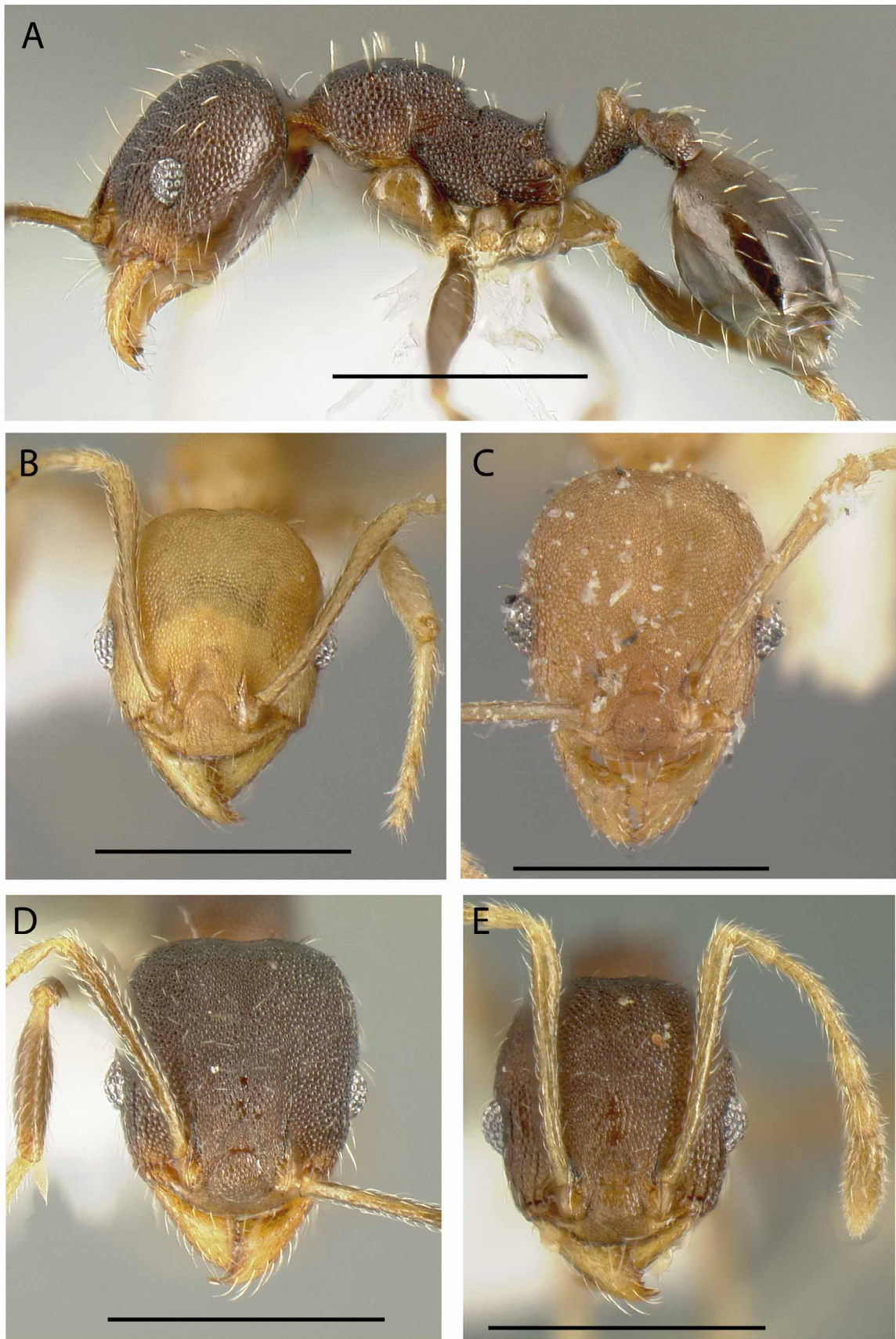


FIGURE 2. Lateral view of body (A) and dorsal (full-face) views of head (B–E) of minor workers. A. *Pheidole bilimeki*, Costa Rica (JTLC000015322). B. *Pheidole anastasioi*, Costa Rica (INBIOCRI001283143). C. *Pheidole punctatissima*, Costa Rica (INBIOCRI002279874). D. *Pheidole bilimeki*, Costa Rica (JTLC000015322). E. *Pheidole jamaicensis*, Jamaica (JTLC000015394). Scale bars = 0.5mm.

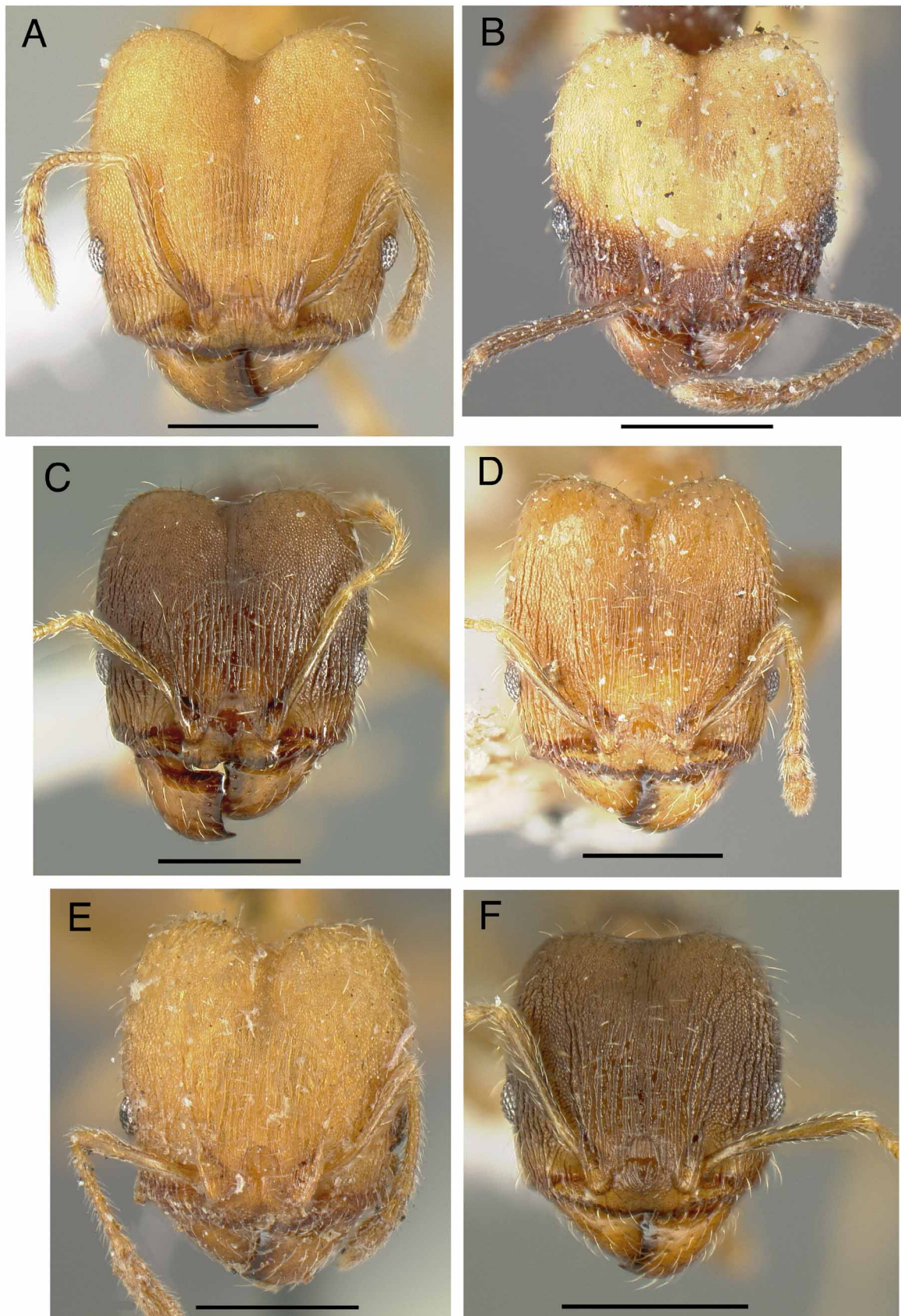


FIGURE 3. Dorsal (full-face) views of major worker head. A. *Pheidole anastasioi*, Costa Rica (INBIOCRI001283142). B. *Pheidole punctatissima*, Mexico (lectotype, CASENT0601256). C. *Pheidole jamaicensis*, Jamaica (JTLC000015837). D. *Pheidole bilimeki*, Costa Rica (*P. ares* syntype, JTLC000014091). E. *Pheidole bilimeki*, Mexico (holotype, CASENT0601281). F. *Pheidole bilimeki*, Costa Rica (JTLC000003345). Scale bars = 0.5mm.

Pheidole punctatissima is a slightly more arboreal version of *P. bilimeki*. It favors the same kind of open, disturbed habitats and has a similar geographic range, from Colombia to Tamaulipas, Mexico. In contrast to *P. bilimeki*, it is rarely if ever found nesting beneath stones. It is nearly always in dead wood on the ground or dead branches in the low arboreal zone. Like *P. bilimeki*, it can be a pest ant in houses. The fact that *P. punctatissima* has longer scapes and more arboreal habits than *P. bilimeki* reinforces a general pattern in ants, in which arboreal species tend to have longer scapes than ground-dwelling congeners.

These species have a history of being transported by human commerce, which is unsurprising given their abundance and, in the case of *P. bilimeki* and *P. punctatissima*, their association with disturbed areas. Both *P. anastasii* and *P. bilimeki* have been collected in greenhouses in temperate zone cities (e.g., *cellarum* Forel 1908 [= *bilimeki*]), and all three have the potential to be frequently encountered as exotics. The occurrence of *P. bilimeki* and *P. punctatissima* as building pests can also lead to spurious locality records. For example, an intensive survey of the ant fauna of the Volcan Barva transect in Costa Rica (Project ALAS), a forested elevational gradient from sea level to 2600m, yielded the rare occurrence of *P. bilimeki* from primary forest throughout the transect. However, the samples were all processed in the ALAS lab at La Selva Biological Station, where *P. bilimeki* was a pest ant in the building. The Barva Transect records were almost certainly laboratory contaminants.

The following key will separate minor workers of the four species considered in this paper.

- 1 Scape relatively short (SI 95–108, lower cloud of points in Fig. 1); posterior margin of vertex somewhat flattened (Fig. 2D); color usually brown, yellow in northern parts of range *bilimeki*
- Scape relatively long (SI typically 103–125, upper cloud of points in Fig. 1); posterior margin of vertex more rounded (Fig. 2 B, C, E); color brown or yellow 2
- 2 Color clear yellow orange (gray brown in one population on Caribbean coast of Panama); typically nesting in live plant cavities in wet forest understory *anastasii*
- Color red brown to nearly black; typically nesting in open, disturbed habitats 3
- 3 Scapes relatively shorter (SI 108–114, see Fig. 1) (major worker with face uniformly red brown) *jamaicensis*
- Scapes relatively longer (SI 114–125, see Fig. 1) (major worker with face bicolored, dark red brown anteriorly, yellow posteriorly) *punctatissima*

With the exception of *P. punctatissima*, the major workers of these species cannot always be identified. *Pheidole punctatissima* is readily distinguished from the other three by the distinctive coloration of the face (bicolored, dark brown anteriorly, yellow posteriorly). Major workers of the other species are the same color as their associated minor workers. Thus major workers of *P. anastasii* are usually yellow, and major workers of *P. bilimeki* and *P. jamaicensis* are usually red brown. However, color variation parallels that seen in minor workers.

Formal synonymy of the four species treated here is as follows:

***Pheidole anastasii* REVISED STATUS**

Figure 1, 2, 3

Pheidole anastasii Emery 1896:76. Syntype minor, major worker: Jimenez, Costa Rica [MCSN] (examined).

Pheidole bilimeki Mayr: Wilson 2003:378 (incorrect synonymy).

Pheidole bilimeki

Figure 1, 2, 3

Pheidole bilimeki Mayr 1870:985. Lectotype major worker: Mexico (Bilimek) [NMW] (examined).

Pheidole punctatissima subsp. *annectens* Wheeler, W.M. 1905:93. Lectotype major worker: Mangrove Key, Andros Island, Bahamas (Wheeler) [MCZC] (examined). Wilson 2003:378: junior synonym of *bilimeki*. *Pheidole floridana*

- var. *antoniensis* Forel 1901b:364. Syntype major and minor worker: San Antonio, Sierra Nevada de Santa Marta, Colombia (Forel) [MHNG] (examined). Wilson 2003:378: junior synonym of *bilimeki*.
- Pheidole floridana* subsp. *ares* Forel 1908:57. Syntype major and minor worker, male: Cote du Tablazo, 1500m, Costa Rica; San Juan de Tobozi, 1400m, Costa Rica (Biolley) [MHNG] (Cote du Tablazo specimens examined). Wilson 2003:378: junior synonym of *bilimeki*.
- Pheidole anastasioi* var. *cellarum* Forel 1908:55. Syntype major, minor workers: greenhouses in Zurich (Switzerland), Kew (Great Britain), Dresden (Germany) [MHNG] (examined). Forel 1901a:78: description of queen (as *P. anastasioi*, based on material from Guatemala intercepted at Hamburg; material labeled incorrectly as *cellarum* types in Forel collection). Forel 1915:34: description of queen in key. Wilson 2003:378: junior synonym of *bilimeki*.
- Pheidole floridana* var. *deplanata* Pergande 1896:883. Syntype major and minor worker: Tepic, Mexico (Eisen and Vaslit) [USNM]. Wilson 2003:378: junior synonym of *bilimeki*.
- Pheidole punctatissima* subsp. *insulana* Wheeler, W.M. 1905:93. Syntype major and minor worker: Southern Bight, Andros Islands, Bahamas; Blue Hills, New Providence Island, Bahamas (Wheeler) [MCZC] (examined). Wilson 2003:378: junior synonym of *bilimeki*.
- Pheidole anastasioi* var. *johnsoni* Wheeler, W.M. 1907:272. Syntype major and minor worker, male: Manatee, Honduras (Johnson) [MCZC] (examined). Wilson 2003:378: junior synonym of *bilimeki*.
- Pheidole anastasioi* var. *venezuelana* Forel 1905:159. Syntype major worker, male: Caracas, Venezuela (Meinert) [MHNG]. Wilson 2003:378: junior synonym of *bilimeki*.

***Pheidole jamaicensis* NEW STATUS, REVISED STATUS**

Figure 1, 2, 3

- Pheidole punctatissima* subsp. *jamaicensis* Wheeler, W.M. 1908:161. Syntype major and minor worker: 2.5mi W Port Antonio, Jamaica (Wight) [MCZC] (examined).
- Pheidole bilimeki* Mayr: Wilson 2003:378 (incorrect synonymy).

Pheidole punctatissima

Figure 1, 2, 3

- Pheidole punctatissima* Mayr 1870:400. Syntype major, minor worker: North America [assumed southern Mexico] (Norton) [NMW] (examined, major worker here designated Lectotype to insure nomenclatural stability). Forel, 1908:52: description of queen. See also: Wilson, 2003:618.
- Pheidole punctatissima* subsp. *napaea* Wheeler, W.M. 1934:165. Syntype major, minor worker: Mexico, Veracruz, Mirador (Skwarra 51a) (not examined). Junior synonym of *punctatissima*: Brown, 1981:525.

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