# Taxonomic revision of the *Pachycondyla apicalis* species complex (Hymenoptera: Formicidae)

ALEXANDER L. WILD

*Department of Entomology, University of California at Davis, One Shields Avenue, Davis, CA 95616, USA*
*alwild@ucdavis.edu*

## Abstract

The taxonomy of the Neotropical *Pachycondyla apicalis* species complex is revised. Contrary to the widely-held view that the *apicalis* complex contains only two species, *P. apicalis* (Latreille 1802) and *P. obscuricornis* (Emery 1890), morphological evidence indicates the existence of three broadly sympatric species. Examination of type specimens reveals that the name *obscuricornis* has been extensively misapplied in the literature, and that the valid name for the widespread species commonly misdiagnosed as *P. obscuricornis* is *P. verenae* (Forel 1922). True *P. obscuricornis* is shown to be an uncommonly collected South American species. The name *apicalis* is valid as currently employed for that species. A taxonomic key is provided, along with diagnoses, illustrations, and distributional data for all three species.

**Key words:** Pachycondyla, Neoponera, Ponerinae, Taxonomy

## Introduction

Ants in the *Pachycondyla apicalis* species complex are large, conspicuous insects found in Neotropical forests from southern Mexico to Paraguay. These ants comprise a small monophyletic assemblage of very similar species within a heterogeneous and much larger cosmopolitan genus, *Pachycondyla* F. Smith 1858 (c.a. 270 species, Bolton 1995), that is almost certainly paraphyletic (C. Schmidt, pers. comm.). Ants in the *apicalis* complex are epigaeic, predaceous, form small colonies, and are thought to display a relatively simple behavioral repertoire. Because these ants possess purportedly "primitive" traits (Peeters 1997), they have served as model organisms for studies of ant foraging (Fresneau 1985, Goss et al 1989), colony social structure (Fresneau 1984, Dietemann & Peeters 2000, Gobin et al 2003), and pheromone production and dissemination (Traniello & Hölldobler 1984, Soroker et al 1998).

Nearly all recent studies involving ants of the *apicalis* complex have employed Brown's (1957) scheme dividing the group into two widespread species: *P. apicalis* (Latreille 1802) with yellow antennal apices and a rounded petiolar node, and *P. obscuricornis* (Emery 1890) with dark antennal apices and a marginate petiolar node. However, the existence of specimens that do not sort easily under Brown's dichotomy (e.g., "sp. cf. *obscuricornis*" in Wild 2003), a recent suggestion from microsatellite DNA data that the traditional species-level characters are flawed (K. Kolmer, unpublished Ph.D. thesis), and the discovery of cryptic species in related lineages of *Pachycondyla* (Lucas et al 2002) prompt a reconsideration of the taxonomy of this group.

In the present study I show that morphological evidence indicates the existence of three, not two, species in the *P. apicalis* complex and that the name *P. obscuricornis* has been misattributed frequently in the literature. I provide a taxonomic key as well as diagnoses, distributional data, images, and synopses of the known biology for all three species.

**Materials and Methods**

*Species delineation*

I subscribe to the view that species are assemblages of interbreeding or potentially interbreeding populations (Mayr 1942). While I did not have resources in the present study to directly assess gene flow, biological species boundaries may be indirectly inferred through patterns of character state distribution in areas where populations come into sympatry. Since interbreeding can blur the distinctness of populations, consistent morphological separation between populations in sympatry may be taken as evidence for the lack of interbreeding and hence a proxy for species boundaries. In keeping with this perspective, I used consistent morphological differences in sympatry as the primary criterion for delineating species in the *P. apicalis* complex. Collections were considered to be sympatric if they fell within 50 km of each other.

*Specimens examined*

I examined a total of 311 worker, 20 gyne and 6 male specimens, including primary type specimens for all relevant names except Latreille's *Formica apicalis*. All specimens were dried and either point mounted or pinned. Males were examined for all three species but were too few in number and too variable within species to provide any robust estimates of species-specific characters. Entomological collections cited in this study are abbreviated as follows:

ALWC- Alexander L. Wild personal collection, Davis, California, USA.
INBP- Museo Nacional de la Historia Natural del Paraguay, San Lorenzo, Paraguay.
LACM- Natural History Museum of Los Angeles County, Los Angeles, California, USA.
MCSN- Museo Civico de Historia Natural 'Giacomo Doria', Genoa, Italy.

MCZC- Museum of Comparative Zoology, Cambridge, Massachusetts, USA.
MHNG- Muséum d'Histoire Naturelle, Geneva, Switzerland.
MZSP- Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
PSWC- Philip S. Ward personal collection, Davis, California, USA.
UCDC- R. M. Bohart Museum of Entomology, Davis, California, USA.

*Morphological characters*

All observations were made at 12–50x on a Wild stereo microscope. I conducted morphometric measurements on a subset of worker specimens (n = 51) using a dual-axis Nikon stage micrometer with a precision of 0.001 mm. I report measurements here to 0.01 mm.

I employed a number of standard morphometric characters. Head measurements are given with the head in full-face view, with the anterior clypeal margin and the posterior border of the head in the same focal plane. I consider ant heads to be prognathous, such that the clypeus is anterior and the frontal area is dorsal.

HL - Head length. In full-face view, the midline distance from the level of the maximum posterior projection of the posterior margin of the head to the level of the most anterior projection of the anterior clypeal margin

HW - Head width. In full-face view, the maximum width of the head posterior to the compound eyes.

SL - Antennal scape length. Measured from the apex of the first antennal segment to the base, exclusive of the radicle.

FL - Profemur length. In posterior view, measured along the longitudinal axis from the apex to the junction with the trochanter.

LHT - Metatibial length. In dorsal view, measured along the longitudinal axis from the apex to the level of the lateral condyles, excluding the medial proximal condyle.

PH - Petiole height. In lateral view, the distance from the ventrum of the petiolar sternite to the apex of the petiolar tergite, taken as a vertical measurement perpendicular to the longitudinal axis of the petiole.

PL - Petiole length. In lateral view, the maximum longitudinal distance between the anterior and posterior extentions of the petiolar node, excluding the anterior and posterior condyles.

WL - Weber's length. In lateral view, the distance between the anterior margin of the pronotum exclusive of the collar to the posterior margin of the metapleural bulla.

SI - Scape index. 100*SL/HW.

CI - Cephalic index. 100*HW/HL.

In addition to morphometric measurements, I examined a suite of morphological characters commonly used in ant systematics. These characters include pilosity, pubescence, body and appendage color, shape of the head, shape of the mesosoma, shape of the petiole, and mandibular dentition.

*Images and mapping*

All specimen photographs were taken using a hand-held Canon D60 digital SLR with a Canon MP-E 65mm 1–5x macro lens and a diffuse MT-24EX twin flash, 1/200 sec exposure at f/13. Images were recorded in Canon RAW format, with levels adjusted in Phase One's "Capture One" RAW conversion program (www.phaseone.com) and Adobe Photoshop 5.0.

Maps were drawn in the shareware program Versamap (www.versamap.com) on a Windows PC computer platform using coordinates provided on specimen labels or inferred from maps and gazetteers for specimens without coordinate data. A number of older specimens did not have sufficiently detailed labels to infer exact coordinates (e.g., "Brazil") and were excluded from the map.

**Taxonomy**

**Diagnosis of the *Pachycondyla apicalis* species complex**

Worker ants can be determined to belong to the *apicalis* complex by the following combination of character states. The most salient diagnostic features are italicized.

Head in full-face view longer than broad (CI 0.70–.86), lateral margins slightly convex, posterior margin slightly convex to slightly concave. *Eyes large and located near longitudinal mid-point of head, bulging out conspicuously past lateral margins in full-face view.* Integument anterior to eye with a distinct carina running from inner margin of eye to lateral clypeal margin. Clypeus with a broadly convex anterior margin. Mandibles elongate-triangular, nearly as long as head length; bearing 11–15 teeth along masticatory margin; lateral margins slightly concave in dorsal view; and the dorsal surface finely striate proximally, becoming smooth distally. Antennal scape variable in length (SI 1.10–1.59), but always clearly surpassing posterior margin of head in full-face view.

Pronotum with dorsal and lateral faces meeting at a blunt angle. Propodeum depressed slightly below level of mesonotum in lateral view; propodeal spiracle elongate, slit-like.

Petiole of varying shape, but always with a *broadly convex anterior surface reaching an apex near midpoint of node*. Petiole taller than declivitous face of propodeum (PH 1.12–1.78 mm), and usually about 3/4 as long as tall.

*Integument of body and appendages satiny and opaque; surface with a finely punctate sculpture and a dense, fine pubescence. Standing pilosity sparse, usually absent on mesosomal dorsum and on petiolar node* (rarely 1–2 erect setae in *apicalis*). Body color dark brown to black. Mandibles, tarsi, and antennal funiculus often lighter in color.

In addition to the morphological characters listed above, ants of the *P. apicalis*-complex in the field display a characteristic and immediately recognizable behavior, running erratically over the ground rapidly flicking their antennae in a manner similar to many wasps. This latter character appears to be a reliable field marker as most other *Pachycondyla* species display the more sedate antennal movements typical of most Formicidae.

**Key to workers of the *Pachycondyla apicalis* species complex**

1   Antennal scape relatively short (SL usually < 2.3 mm), shorter than head length; hypopygium densely pubescent in area adjacent to sting (Fig. 8); apical antennomeres light brown to dark brown, never bright yellow........................................ *obscuricornis*
-   Antennal scape relatively long (SL > 2.3 mm), longer than head length; hypopygium with moderate to sparse pubescence on area adjacent to sting (Fig. 7); apical antenno- mere color variable................................................................................................ 2
2   Posterolateral edges of petiole marginate (Fig. 9); petiolar node low (PH < 1.35 mm); head narrow in full-face view (HW < 1.9 mm); size relatively small (WL 3.4–4.1 mm); apical 3-6 antennomeres light to dark brown ............................................*verenae*
-   Posterolateral edges of petiole usually not marginate (Fig. 10); petiolar node higher (PH > 1.35 mm); head broad in full-face view (HW > 1.9 mm); size relatively large (WL 3.9–5.2 mm); apical 3-6 antennomeres usually bright yellow.................. *apicalis*


**Species synopses**

*Pachycondyla apicalis* **(Latreille)**
(Figs. 1, 2, 7, 10)


*Formica apicalis* Latreille 1802: 204.
*Formica flavicornis* Latreille 1802: 202. Synonymy by Brown (1957).
*Pachycondyla apicalis* (Latreille 1802); Mayr 1863: 439. First combination in *Pachycondyla*.
*Pachycondyla flavicornis* (Latreille 1802); Emery 1890: 58.
*Neoponera flavicornis* (Latreille 1802); Emery 1901: 47. First combination of *flavicornis* sensu Emery in *Neoponera*; also first combination of *apicalis* sensu Emery (a misidentification of *verenae* Forel 1922) in *Neoponera*.
*Neoponera latreillei* Forel 1905: 161. Replacement name for *Formica flavicornis* Latreille 1802, j. hom. of *Formica flavicornis* Fabr. 1798. Synonymy by Brown (1957).
*Neoponera obscuricornis* r. *latocciput* Forel 1921: 132. **NEW SYNONYMY**
*Neoponera obscuricornis latreillei* (Forel 1905); Wheeler and Wheeler 1952: 613-615. Description of larva.
*Neoponera apicalis* (Latreille 1802); Brown 1957: 230; Kempf 1972: 161 (part); Fresneau 1985: 109–166; Fresneau and Dupuy 1988: 1389–1399.
*Pachycondyla obscuricornis*; Reiskind 1977: 2–6. Not Emery (1890). Misidentification.
*Pachycondyla apicalis* (Latreille 1802); Goss et al 1989: 65–69. Revived combination in *Pachycondyla*, first use of implicit combination by Brown (1973).
*Pachycondyla apicalis* (Latreille 1802); Hölldobler and Wilson 1990: 385; Oliveira and Hölldobler 1990: 383–393; Soroker et al 1998: 1077–1090; Deitemann and Peeters 2000: 223–228; Longino 2004.
*Pachycondyla apicalis* (Latreille 1802); Brown, in Bolton 1995: 302. Stated as "revived combination."


**Type data:** *Formica apicalis* Latreille  **South America** [type not located]. *Formica flavi-*

*cornis* Latreille **French Guiana.** "Cayenne" [type not located]. *Neoponera obscuricornis* r. *latocciput* Forel: **Ecuador.** "Quito" (approx. loc.) [3w SYNTYPES, MHNG, examined].

**Other material examined:**

**Bolivia.** Santa Cruz: 10k NW Terevinto [PSWC]. **Brazil.** Amazonas: Ilha de Curarí [LACM]; Ypiranga, R. Iça-Putomayo [MCZC]; 300k E Humaita, Transamazonica Hwy [PSWC]; Ponta Negra, N of Manaus [MCZC]. Bahia: CEPEC/CEPLEC, Rodovia Ilhéus/ Itabuna [ALWC, MCZC]. Mato Grosso: Chapada dos Guimarães [PSWC]. Pará: San-tarem, Taperinha [MCZC]; Tucurui, Margem esq. [LACM]; Utinga tract, nr. Belem [MCZC]; "Pará" (s. loc.) [MCZC]. Rondônia: Porto Velho, Madeira [MCZC]; Rio Madeira, Madeira Mamore R. R. Camp #39 [MCZC]; Rio Madeira, Madeira Mamore R. R. Co. Camp #41 [LACM]. Rio de Janeiro: Ilha Grande [ALWC]. São Paulo: Res. Flor-estal Caraguatatuba [MCZC]. **Colombia.** Chocó 10 km SW S. Jose de Palmar, Rio Torito, Finca Los Guaduales [MCZC]. Guajira: R. Don Diego [MCZC]. Magdalena: Tay-rona Park, S park boundary above Calabasos [MCZC]. Valle: km 98, old road Cali to Buenaventura [MCZC]. **Costa Rica.** Cartago: "Natrolista Platanillo", 1mi S Tuís [UCDC]; Turrialba [MCZC]. Guanacaste: Guanacaste Cons. Area, Pitilla Research Sta-tion [UCDC]. Heredia: La Selva Biol. Sta. [LACM, MCZC, PSWC]; P. N. Braulio Car-rillo [LACM]. Limón: R. Toro Amarillo, vic. Guapiles [MCZC]; Sarapiquí R., Oro Verde Lodge [MCZC]; Zent [MCZC]. Puntarenas: Corcovado Nat. Park, nr. Rio Nino [MCZC]; Corcovado Nat. Park, Sirena [MCZC]; Palmar [MCZC]. **Ecuador.** Guayas: 10 mi. N. Manglar Alto [MCZC]; 3 km SW Bucay [MCZC]. Los Rios: Rio Palenque Biol. Sta. [LACM]. Morona-Santiago: Sucúa [LACM]. Napo: Misahualli [MCZC]. Pastaza: 2-8 mi. N. Puyo [MCZC]. Pichincha: ENDESA Forest Reserve [ALWC, UCDC]. Sucum-bios: Limon Cocha & vic. [MCZC]. **French Guiana.** Cayenne: Paracou Experimental Forest, 45k W of Karou [MCZC]. **Guatemala.** Petén: Nacum [MCZC]. Retalhuleu: El Asintal [UCDC]. Suchitepéquez: Finca Los Tarrales [ALWC]. **Guyana.** Cuyuni-Maz-aruni: Cuyani R. [MCZC]; Kamakusa [MCZC]; Kartabo [MCZC]. Upper Takutu-Upper Essequibo: N. Side Acari Mts. [PSWC]. **Honduras.** Atlántida: 14 km S La Ceiba [MCZC]; Lancetilla, nr. Tela [MCZC]. "Portillo Grande" (loc. indet.) [MCZC]. **Mexico.** Campeche: 10 Km E Campeche [MCZC]. Chiapas: Ocosingo, Laguna Ocotal Grande [MCZC]; Ruinas Palenque [LACM]. Oaxaca: Temescal [LACM]. Quintana Roo: 13 km S Señor, Cenote de Tos Viriol [LACM]; Cobá [LACM]; Felipe Carillo Puerto, Cenote de Juan Coh [LACM]. San Luis Potosí: 18 mi S. Tamazunchale [MCZC]; Huichihuayan [MCZC]. Veracruz: 2 mi W. Fortín, park cañon HWY 150 [MCZC]; Cueva de la Sala de Agua [MCZC]; El Palmar, 16 k W. Tezonapa [MCZC]; Laguna Encantada [MCZC]; Las Hamacas, 17k N Santiago, nr. Tuxtla [MCZC]; Los Tuxtlas [ALWC]; Presidio, Trail above Presidio [LACM]; Pueblo Nuevo nr. Tezonapa [MCZC]; Sa. Teoviscocla, nr. Cuichapa [MCZC]; Tlacotalpan (as "Tapalcapan") [MCZC]. Yucatan: Chichén Itzá [MCZC]; 1 km NE Tixcancal [LACM]; Actún Xpukil, 3k S Calcehtok [LACM]; Grutas de Balankanche 4 km E Chichén Itzá [LACM]. **Nicaragua.** Chinandega: (s. loc.) [MCZC]. Indio Mais

Res., San Juan and Sarapiquí Rivers [MCZC]. "Tuli Creek" (loc. indet.) [MCZC]. **Panama.** Darien: Cana [PSWC]. Panamá: Barro Colorado I. [LACM, MCZC, UCDC]. **Peru.** Huánuco: 12 km SW Tingo Maria [LACM]; Cueva de Castillo nr. Tingo María [LACM]; Monson Valley, Tingo Maria [MCZC]; Tingo Maria & vic. [MCZC]. Loreto: Previsto [LACM]; Quebrada Yanayaco, NE Iquitos [LACM]. Madre de Dios: Est. Biol. Cocha Cashu [LACM, MCZC]; 15 k NE Puerto Maldonado [MCZC]. San Martín: David-cillo, 30k NNE Tarapoto [PSWC]. **Surinam.** Raleigh Vallen-Voltzberg Res. Voltzberg camp [MCZC]; "Surinam" (s. loc.) [MHNG, 1w labeled *"latreille* Forel type"]. **Trinidad and Tobago.** St. George: Caura [MCZC]; Guanapo Valley Quarry Guanapo Rd. [MCZC]. **Venezuela.** Amazonas? ("Terr. Amazonas"): 3 km N. of San Carlos de Rio Negro [MCZC]. Araguá: Rancho Grande [MCZC]. Barinas: 17k SSW Ciudad Bolivia [PSWC]. Bolívar: 1k S confl. R. Nichare & Rio Caura [PSWC]; Nichare Field Stn., Río Tawadu [PSWC]. Delta Amacuro: 140k NE Barrancas, Cano Mariusa [LACM].

**Worker measurements:** (n = 19) HL 2.40–3.19, HW 1.96–2.72, SL 2.72–3.61, WL 3.96–5.17, FL 2.63–3.66, LHT 3.05–4.38, PL 1.04–1.36, PH 1.36–1.78, CI 0.77–.86, SI 1.28–1.47.

**Worker diagnosis:** A large species (WL > 3.9 mm) with the apical antennomeres colored bright yellow. Head somewhat longer than broad (CI 0.77–.86); mandibles elongate-triangular and bearing 12–15 teeth. Antennal scape longer than head length. Posterolateral margins of the propodeum rounded. Posterior and lateral faces of the petiole usually meeting at a rounded or an indistinct angle. Petiolar node relatively tall (PH > 1.35mm). Abdominal tergite 3 usually with erect setae, abdominal tergite 4 always with at least a posterior row of setae and often with additional setae. Hypopygium coarsely punctate posteriorly with shining interspaces in area adjacent to sting, bearing moderate to sparse sub-decumbent pubescence not completely obscuring integument (Fig. 7). Body and appendages dark brown to black, except for yellow apical antennomeres.

This species may be separated from *P. obscuricornis* by the longer antennal scape and from *P. verenae* by the lack of posterolateral margination of the petiole.

**Geographic variation:** The shape of the petiole changes noticeably between localities. In one specimen from Guyana the petiolar form approaches the marginate condition of *P. verenae*. Specimens vary considerably as well in the development of abdominal pilosity. Ants from Central America often lack erect setae on abdominal tergite 3, while specimens from elsewhere in the range commonly have anywhere between 2 and 25 erect setae on tergite 3, with Peruvian specimens being the most pilose; a few of the most pilose Peruvian specimens have erect setae on the mesosomal dorsum and petiolar node. Eye size appears to vary slightly between localities as well.

**Distribution:** Southern Mexico to southeastern Brazil.

**Biology:** *Pachycondyla apicalis* is a common and conspicuous insect in many Neo-tropical forests. Most observations and collection records are of single foragers on the ground or on low vegetation. According to the collection data associated with museum

specimens, *P. apicalis* occurs from sea level to 1600 meters (n = 40, median = 380 meters, mean = 642 meters). 14 collections were from primary or secondary rainforest or other kind of tall, moist forest. Two records were from rainforest edges and clearings, three from coffee plantations, one from cloud forest, and one from second growth thorn forest. This species has been observed nesting in rotting wood on or near the ground (Levings & Franks 1982, Dietemann & Peeters 2000, Longino 2004), in the ground (Levings & Franks 1982), and in the root mass of large *Ficus* trees within one meter of the ground (Fresneau 1985). One Colombian record in MCZC is from a *Guadua* sp.

Colonies are small, containing fewer than 200 workers (Fresneau 1985, Goss et al 1989, Dietemann & Peeters 2000), and monogynous (Dietemann & Peeters 2000). Dietemann and Peeters (2000) investigated the interactions between queens and workers, finding that workers can lay both trophic eggs and reproductive male eggs, some switching to reproductive male eggs in the absence of physical contact with the queen. Workers are apparently incapable of mating (Dietemann & Peeters 2000) and exhibit overt dominance interactions as well as egg-policing (Oliveira & Hölldobler 1990). Age polyethism in *P. apicalis* is described by Fresneau and Dupuy (1988). The formation of colony odor was studied by Soroker et al (1998), who tagged lipid precursors with radioactive tracers, injected them into ants, and conducted a series of experiments demonstrating that the molecules were spread through the colony by allogrooming of nestmates and not by trophallaxis.

Fresneau (1985) describes foraging behavior in a field population in Chiapas, Mexico. He found *apicalis* to be generalist predators and scavengers, collecting "20%…fruit debris and vertebrate carcasses and the remaining 80%…an assortment of 12 arthropod orders half of which were dead, and other half of which were living Lepidoptera and Coleoptera larvae."(Fresneau 1985, pg 110.) Longino (2004) observed that foragers readily take crushed tabanid flies and lepidopteran larvae. A collection by E. O. Wilson from Veracruz, Mexico, records *P. apicalis* preying on termites, and two *apicalis* workers in the MCZC collection were found at a tuna bait in Guanacaste, Costa Rica.

Foraging is done individually, without recruitment, and individual foragers over time show strong fidelity to a particular area (Fresneau 1985). Tandem-running has been observed during nest relocation (Fresneau 1985). Orientation is probably visual (Fresneau 1985). Goss et al (1989) test an optimal foraging model using *P. apicalis*, concluding that foraging in the observed colonies is sub-optimal. Interestingly, a group of computer scientists have used the foraging behavior of *P. apicalis* as a model for creating an internet search algorithm (Monmarché et al 2000).

*Pachycondyla apicalis*, as in other ponerine ants, subdues its prey by injecting venom through a sting. The venom may also have a defensive purpose and is described as tasting "bitter and burning" (Schmidt 1986). Cruz and Morgan (1997) investigate venom chemistry, Schmidt (1980) looks at venom toxicity, and Schmidt et al (1984) score *P. apicalis* sting-induced pain in humans as a "two" on a standardized ascending scale of one to four.

Pavan et al (1997) report on the auditory emissions of *P. apicalis*. As in most stridulating ants, the stridulatory organ is composed of a file on the fourth abdominal tergite and a scraper on the preceding tergite (Giovannotti 1996, Pavan et al 1997). Abdominal glands in the male are described by Hölldobler and Engel-Siegel (1982).

In Panama, *P. apicalis* serves as a model for the ant-mimic spider *Castianeira memnonia* (Koch) (Reiskind 1977). Reiskind (1977) reports the identity of the model as *P. obscuricornis*, but the voucher specimen at LACM is clearly *P. apicalis*. Additionally, his description of the yellow antennal apices and the photographs in the article unambiguously identify the ant as *P. apicalis*.

There is one record in MCZC of *Pachycondyla apicalis* in the gut contents of a leptodactylid frog, *Eleutherodactylus biporcatus* (Peters), in Nicaragua.


### *Pachycondyla obscuricornis* Emery
(Figs. 3, 4, 8)

*Pachycondyla flavicornis* var. *obscuricornis* Emery 1890: 58.
*Neoponera flavicornis* var. *obscuricornis* (Emery 1890); Emery 1901: 47. First combination in *Neoponera*.
*Neoponera obscuricornis* (Emery 1890); Kempf 1972: 162 (part).
*Pachycondyla obscuricornis* Emery 1890; Brown, in Bolton 1995: 308. Revived combination in *Pachycondyla*; this combination is implicit in Brown (1973) and explicit in Duelli and Duelli-Klein (1976) but as a misidentification of *verenae* (Forel 1922).
*Pachycondyla* sp. cf. *obscuricornis* Wild 2003: 12.


**Type data:** *Pachycondyla flavicornis* var. *obscuricornis* Emery. **Brazil.** Pará (s. loc.) [2w SYNTYPES, MHNG, examined; 1w SYNTYPE, MCSN, examined].

**Other material examined:**

**Bolivia.** Santa Cruz: Las Gamas, P. N. Noel Kempf Mercado [PSWC]. **Brazil.** Pará: Tucurui, Margem esq. [LACM]; Utinga tract, nr. Belem [MCZC]. **Ecuador.** Napo: Jatun Sacha 7k ESE Pto. Misahualli [PSWC]. **Paraguay.** Canindeyú: Res.Nat.Bosque Mbaracayú, Jejuimi [ALWC]. **Peru.** Huánuco: Monson Valley, Tingo Maria [LACM]. San Martín: Davidcillo, 30k NNE Tarapoto [PSWC].

**Worker measurements:** (n = 9) HL 2.23–2.47, HW 1.86–2.10, SL 2.09–2.32, WL 3.08–3.97, FL 2.25–2.49, LHT 2.44–2.77, PL 0.93–1.07, PH 1.42–1.55, CI 0.82–.86, SI 1.10–1.16.

**Worker diagnosis:** A smaller species (WL < 4.0mm) with a short antennal scape and a tall, rounded petiolar node. Head somewhat longer than broad (CI 0.82–.86); mandibles elongate-triangular and bearing 11–13 teeth. Antennal scape shorter than head length. Posterolateral margins of propodeum rounded. Posterior and lateral faces of petiole meeting at an indistinct angle. Petiolar node conical and relatively tall (PH > 1.4 mm). Abdominal tergite 3 and usually also abdominal tergite 4 lacking erect setae. Hypopygium

densely punctate-pubescent posteriorly, pubescence subdecumbent and covering integument (Fig. 8). Body and appendages dark brown to black; apical antennomeres and tarsomeres medium reddish-brown to dark brown.

This species may be readily separated from *apicalis* and *veranae* by the shorter antennal scapes.

**Geographic variation:** Specimens from the seven known localities appear remarkably uniform.

**Distribution:** Ecuador and northeastern Brazil to Paraguay.

**Biology:** Nearly all the information published under the name *P. obscuricornis* actually refers to *P. verenae* (see Discussion). Little is known about the biology of true *P. obscuricornis*. This rarely-encountered species appears to be a rainforest ant. The collection elevations run from around sea level to 700 meters. The records from San Martín Peru and Santa Cruz Bolivia are from rainforest, the Paraguayan specimens were collected as ground foragers in primary humid subtropical tall forest, and the Ecuadorian record is from the edge of a second growth rainforest. The single nest series, collected by Phil Ward in Davidcillo, 30 km NNE Tarapoto in San Martín, Peru, was in a rotting log.

*Pachycondyla verenae* **(Forel) NEW STATUS**
(Figs. 5, 6, 9)

*Neoponera apicalis* var. *verenae* Forel 1922: 90.
*Pachycondyla apicalis*; Emery 1890: 58-59. Not Latreille (1802). Misidentification.
*Neoponera apicalis*; Wheeler and Wheeler 1952. Not Latreille (1802). Misidentification, description of larva.
*Neoponera obscuricornis*; Brown 1957: 230; Kempf 1972: 162 (part). Not Emery (1890). Misidentification.
*Pachycondyla obscuricornis*; Duelli and Duelli-Klein 1976: 411. Not Emery (1890). Misidentification; first explicit combination of the name *obscuricornis* in *Pachycondyla*.
*Pachycondyla obscuricornis*; Hölldobler 1986: 89–99; Hölldobler and Wilson (1990): 266, 273, 280, 281, 292; Traniello and Hölldobler 1991: 783–794; Oliveira and Hölldobler 1991: 215; Lommelen et al 2002: 61–68; Wild 2003: 12; Longino 2004. Not Emery (1890). Misidentification.
*Pachycondyla verenae* (Forel 1922); Brown, in Bolton 1995: 311. (listed incorrectly as j. syn. of *P. apicalis*; synonymy by Brown [1957]). First explicit combination in *Pachycondyla*, the first implicit combination was by Brown (1973).

**Type data:** *Neoponera apicalis* var. *verenae* Forel. **Panama.** (s. loc.) [2w SYNTYPES, MHNG, examined].

**Other material examined:**

**Bolivia.** Santa Cruz: 10k NW Terevinto [PSWC]; 35k SSE Flor de Oro [PSWC]; Las Gamas, P. N. Noel Kempf Mercado [PSWC]. **Brazil.** Amazonas: Faz. Esteio, 80k NNE Manaus [PSWC]; Igarape Maua, S of Manaus [MCZC]; Km 34 Manaus to Itacoatiara Hwy [MCZC]. Bahia: CEPEC/CEPLEC, Rodovia Ilhéus/Itabuna [ALWC]. Goiás: Faz.

Acerio Jatai [MCZC]; Mun. Anápolis, Km. 46 on road to Goiana [MCZC]. Pará: Belém [LACM]; Mosqueiro [LACM]; Pirelli Plantation (Iraboca) nr. Belém [MCZC]. Rondônia: Rio Madeira, Madeira Mamore R. R. Co. Camp #39 [MCZC]; Rio Madeira, Madeira Mamore R. R. Co. Camp #41 [MCZC]. São Paulo: Agudos [MCZC]; Cachoeira das Emas (EEBP), Piraçununga [MCZC]; Faz. Campininha, Est. Ecol. Mogi Guaçu [PSWC]; Rio Claro [ALWC]. **Colombia.** Cauca: Isla Gorgona [MCZC]; nr. Yanaconas [MCZC]. Chocó: 10 km SW S. Jose de Palmar, Rio Torito, Finca Los Guaduales [MCZC]. Magdalena: 2-3 K above Minca [MCZC]; 2k ESE Minca [PSWC]; 4k N San Pedro [PSWC]. Meta: Transecto Sumapaz [PSWC]. Valle: km 98, old road Cali to Buenaventura [MCZC]. **Costa Rica.** Cartago: 8 km ESE Moravia [LACM]; Turrialba [LACM, MCZC]. Heredia: La Selva Biol. Sta. [LACM, PSWC]; Heredia (s. loc.) [LACM]. Limón: 10 km ESE Moravia [LACM]; R. Toro Amarillo, vic. Guapiles [MCZC]; Zent [LACM, MCZC]. Puntarenas: Corcovado Nat. Park, Llorona [LACM, MCZC, PSWC]; Ojo de Agua [LACM]; Res. Biol. Carara [LACM, PSWC]. **Ecuador.** Napo: Jatun Sacha 7k ESE Pto. Misahualli [PSWC]. Pichincha: 1 mi. W Santo Domingo de los Colorados [MCZC]; ENDESA Forest Reserve [ALWC]. "Durena" (loc. indet.) [LACM]. **French Guiana.** Cayenne: 35 km W Sinnamary [LACM]. **Guyana.** Cuyuni-Mazaruni: Bartica Dist. [MCZC]; Camaria [MCZC]; Cuyani R. [MCZC]; Kamakusa [MCZC]. Demerara-Mahaica: Dunoon [MCZC]. **Honduras.** Atlántida: 14 km S La Ceiba [MCZC]; Lancetilla, nr. Tela [MCZC]. Colón: Sangrelaya [LACM]. Olancho: El Boqueron [MCZC]. **Mexico.** Guerrero: (s.loc.) [MCZC]. Veracruz: Laguna Encantada [MCZC]; Las Hamacas, 17k N Santiago, nr. Tuxtla [MCZC]; Presidio, Trail above Presidio [LACM]; Pueblo Nuevo nr. Tezonapa [MCZC]. **Nicaragua.** Granada: Granada [LACM]. Rivas: Pica Pica [LACM]. Atlántico Sur: Masilena nr. Bluefields [MCZC]. **Paraguay.** Amambay: Parque Nacional Cerro Corá [ALWC, INBP]. Caaguazú: Pastoreo [MZSP]. Canindeyú: Col. 11 de Setiembre [ALWC]; Res. Nat. Bosque Mbaracayú, Lagunita [ALWC, MCZC]; Res. Nat. Bosque Mbaracayú, Aguara Ñu [ALWC]. Misiones: Ayolas [INBP]. Paraguarí: Parque Nacional Ybycuí [ALWC]. **Panama.** Chiriquí: Bugaba [MCZC]. Coclé: El Copé [LACM]. Colón: Gamboa, C. Z. [LACM]. Panamá: Barro Colorado I. [LACM, MCZC, UCDC]. **Peru.** Junin: (s. loc.) [MCZC]. Huánuco: 43 mi. E Tingo Maria [MCZC]; 5 mi. S. Las Palmas [LACM]. Madre de Dios: 15 k NE Puerto Maldonado [MCZC]; Est. Biol. Cocha Cashu [LACM]; Rio Tambopata, 10 km S Puerto Maldonado [LACM]. **Venezuela.** Bolívar: 49k ENE Tumeremo [PSWC]; Río Grande, Imataca For. Res. [PSWC]; Guárico P. N. Guatapo Hae. Elvira [MCZC].

**Worker measurements:** (n = 23) HL 2.16–2.51, HW 1.60–1.87, SL 2.36–2.77, WL 3.41–4.05, FL 2.26–2.66, LHT 2.63–3.17, PL 0.87–1.13, PH 1.12–1.33, CI 0.70–.79, SI 1.32–1.59.

**Worker diagnosis:** A smaller species (WL < 4.1 mm) with a long antennal scape and a short, posterolaterally emarginate petiole. Head narrow (CI < .79); mandibles elongate-triangular and bearing 12–14 teeth. Antennal scape longer than head length. Posterior and

lateral faces of propodeum distinct and meeting at a sharp angle which is sometimes produced into a small ridge. Posterior and lateral faces of petiole distinct, meeting at a relatively sharp margination. Petiolar node relatively short (PH < 1.35 mm). Abdominal tergite 3 lacking erect setae, tergite 4 occasionally with 1–2 erect setae along posterior margin. Hypopygium coarsely punctate posteriorly, with shining interspaces in area adjacent to sting, bearing moderate to sparse subdecumbent pubescence that does not completely obscure integument (as in Fig. 7). Body and appendages dark brown to black; apical antennomeres and tarsomeres medium reddish-brown to dark brown.

This species may be separated from *P. apicalis* and *P. obscuricornis* by the marginate form of the petiole.

**Geographic variation:** Specimens from the southern parts of the range have shorter antennal scapes (SL < 2.5mm) and broader heads (CI > .76), although they never approach the condition of *P. obscuricornis*. Additionally, specimens from Paraguay and southern Brazil show a less marked development of the posterolateral emargination of the petiolar node than specimens from elsewhere in the range.

**Distribution:** Southern Mexico to Paraguay.

**Biology:** Almost all the information published about *P. verenae* appears in the literature under the name *P. obscuricornis* (see Discussion).

This common species exhibits great flexibility in habitat. 14 specimen records are from rainforest or other types of wet forest, seven are from forest edge habitats, five from open natural habitats such as campo cerrado or savannah, one from pasture, one from tropical scrub forest, and one from a cacao plantation. Interestingly, southern populations seem to be more commonly collected in open habitats, while northern populations are more likely to be found in forest. This species displays similar nesting habits to *P. apicalis* and *P. obscuricornis*. Three nest records from specimen collection data were from rotting wood, and one from a grass clump in a pasture. Traniello and Hölldobler's (1984) study colony was collected nesting in a log in Panama, and Wild (2003) reports a nest in rotting wood in Paraguay.

*Pachycondyla verenae* is a predaceous and scavenging species. Foragers will also carry droplets of liquid held between their mandibles, a common trait in poneromorph ants (Hölldobler 1986). Longino (2004) has observed *P. verenae* attacking live lepidopteran larvae in Costa Rica, and captive colonies have taken crickets, cockroaches, termites, and other insect parts (Traniello & Hölldobler 1984, Oliveira & Hölldobler 1991, Gobin et al 2003). Foragers use visual cues (Duelli & Duelli-Klein 1976), and there is no recruitment to food sources (Traniello & Hölldobler 1984).

Colonies are small, reportedly with fewer than 100 workers. Gobin et al (2003) collected 27 colonies from La Selva in Costa Rica with a median number of 39 workers per colony. The study colony of Fresneau (1984) contained 57 workers, and that of Traniello and Hölldobler (1984) grew to about 80–90 workers. *P. verenae* appears to be polygynous. Traniello and Hölldobler's study colony had "several" fertile queens, and Fresneau (1984)

found developed ovaries in five of seven dealate queens. Oliveira & Hölldobler (1991) described the agonistic interactions between workers and unmated queens in a queenless laboratory colony. These dominance interactions have a measurable energetic cost to the colony (Gobin et al 2003).

*Pachycondyla verenae* has been the subject of considerable research on gland structure. Abdominal glands in the male were described by Hölldobler and Engel-Siegel (1982), the pygidial gland by Traniello and Hölldobler (1984), the metapleural gland was briefly investigated by Hölldobler and Engel-Siegel (1985), and the ultrastructure of the labial gland was reported by Lommelen et al (2002, 2003).

Tandem-running, a stereotyped behavior where an ant recruits a single nestmate at a time, was investigated in *P. verenae* by Traniello and Hölldobler (1984). *P. verenae* was found to employ tandem-running during nest relocation, mediated by a pheromone originating in the pygidial gland of the lead ant and spread to the hind-legs by a self-grooming behavior.

There is one record in MCZC of *P. verenae* in the gut contents of *Bufo coniferus* Cope in Nicaragua.


## Discussion

*Species boundaries*

The morphological evidence considered in conjunction with geography supports the separation of the *P. apicalis* complex into three species. All three are broadly sympatric from northern South America to southeastern Brazil, and the two more common species, *P. apicalis* and *P. verenae*, co-occur in Central America north to southern Mexico (Fig. 11). It is notable that every record of the rarer species *P. obscuricornis* involves sympatry with *P. apicalis* (2 sites), *P. verenae* (2 sites), or both (3 sites). Furthermore, 29 of 81 records of *P. apicalis* (35.8%) show sympatry with at least one of the other two species, and 29 of 60 records of *P. verenae* (48.3%) indicate sympatry as well. This pattern is likely to be an underestimate of local sympatry given that many records result from haphazard hand collecting and not from thorough myrmecological surveys. Sites that have been extensively surveyed (e.g., La Selva Biological Station in Costa Rica and the Mbaracayú Reserve in Paraguay) usually uncover at least 2 of the species.

Figures 12–17 illustrate some of the morphometric differences among these species. These differences are consistent across the entire range of the *apicalis* complex, including a number of sites where two or more species locally coexist. In particular, *P. obscuricornis* consistently has shorter antennal scapes than *P. apicalis* and *P. verenae* (Figs. 12, 13), a relatively broader head (Fig. 14), and a more pubescent hypopygium (Fig. 8). *Pachycondyla apicalis* can be separated from *P. verenae* by a taller petiolar node (Fig. 17), by a broader head (Fig. 16), by the lack of strong margination of the petiolar node, by the coloration of the antennal apices, and in South America (but not Central America) by the more

extensive pilosity. *Pachycondyla apicalis* is usually larger in most measurements than *P. verenae*, but there is enough overlap that size alone is not always diagnostic. Given the strength and consistency of the morphological differences across multiple instances of sympatry, significant gene flow between these species is unlikely.

The common species *P. verenae* and *P. apicalis* both show considerable variation across their ranges in a number of characters, including petiole shape, head shape, scape length, eye size, and pilosity. This variation is either localized or broadly allopatric over a north-south cline, and thus in spite of the overall amount of variation there appears to be no justification for further division of the complex. In contrast, *P. obscuricornis* shows almost no variation across its range, suggesting a recent origin or a population bottleneck.

Phylogenetic relationships among the three species are unknown. Some characters, such as antennal scape length and hypopygial pubescence, suggest a closer relationship between *P. apicalis* and *P. verenae*, while others, such as mesosomal and petiolar configuration, indicate a relationship between *P. obscuricornis* and *P. apicalis*. Molecular genetic data will likely provide the most satisfactory resolution to the problem. Given the variation in the life-histories of these ants (e.g., monogyny in *P. apicalis* and polygyny in *P. verenae*) and the amount of published biological information, a phylogeny could be of great utility.

*Nomenclature*

The amount of nomenclatural confusion in this complex is surprising considering the small number of species involved. Latreille (1802) described two similar species from South America, *Formica flavicornis* and *F. apicalis*. I have not seen type specimens of either, but the description of the shape of the node and the coloration of the antennal apices leaves little doubt about the identity of *apicalis*, a conclusion also reached by Brown (1957). The identity of *flavicornis* is not as clear. The name *flavicornis* is preoccupied by an older Fabricius (1798) species, and Forel (1905) provided *Neoponera latreillei* as a replacement name. Brown (1957) placed *flavicornis* and *latreillei* as a synonyms of *apicalis* on the basis of antennal coloration, a decision that I see no reason to challenge.

Emery was alone among previous workers in correctly recognizing three distinct entities, although he misapplied the name *apicalis*. In his 1890 paper "Voyage de M. E. Simon au Venezuela", he discussed a form with a strongly marginate petiolar node ("*apicalis*"), a form with a more rounded node and yellow antennal tips ("*flavicornis*"), and a new variety of *flavicornis* with dark antennal tips ("*obscuricornis*"). Material determined by Emery in MHNG confirms that these names correspond to *P. verenae*, *P. apicalis*, and *P. obscuricornis*, respectively. Emery was content to keep the two forms with the more rounded node as varieties of a single species rather than as separate species, so he placed *obscuricornis* as a variety of *flavicornis*, and later *latreillei* as a variety of *obscuricornis* in "Genera Insectorum" (Emery 1911) once Forel (1905) proposed *latreillei* as a replacement name for the preoccupied *flavicornis*.

Forel's handling of the group parallels Emery's but is less consistent. Examining the Forel collection at MHNG, I found that Forel largely followed Emery's treatment of the species with the marginate node as *apicalis* and that with the yellow antennal apices as *flavicornis/latreillei*. Forel also provided new names for relatively slight variants, *verenae* from Panama as a variety of *apicalis*, and *latocciput* from Ecuador as a race of *obscuricornis*. Why he assigned *latocciput* to *obscuricornis* instead of *latreillei* is not clear, all the more so since he acknowledges both taxa in the brief description. It is apparent, however, that he put more consideration into form than coloration.

Brown's (1957) primary contribution was the realization that Latreille's original description of *Formica apicalis* matched the species that Forel and Emery had been calling first *flavicornis* and then *latreillei*. He put these into synonymy under *apicalis*. Brown evidently did not examine relevant specimens in either Forel or Emery's collections, however, so he did not know that Emery and Forel used the name *apicalis* in a sense opposite to his own. This led him to infer erroneously that Forel's *Neoponera apicalis* var. *verenae* must be a variety of Latreille's *apicalis* instead of the oldest available name for the species with the marginate petiole.

Brown apparently did not see sufficient South American material prior to his 1957 publication to uncover the rarer species *P. obscuricornis*, as he lays out a case for the existence of "two and only two species" (Brown 1957, pg 231). Brown's two species, *"apicalis"* and *"obscuricornis"*, are unambiguously *apicalis* Latreille and *verenae* Forel. Under his two-species dichotomy, Brown argued in the absence of type material that Emery's *obscuricornis* could not be *apicalis* because of the antennal coloration. By default he treated it as the valid name for the other widespread species (*P. verenae* [Forel] in the present study). Apparently Brown did arrive much later at a three-species conclusion that was never published, although it is unlikely he recognized the third species as being Emery's *obscuricornis* (C. R. F. Brandão, *pers. comm*).

Brown's reorganization was perpetuated in an unpublished but widely circulated manuscript key to Neotropical *Pachycondyla*. Consequently, the common species *P. verenae* has been misdiagnosed consistently as *P. obscuricornis* in the literature and in museum collections. In those cases where voucher specimens of "*obscuricornis*" were available in this study (Kempf 1972, Duelli & Duelli-Klein 1976, Wild 2003, Longino 2004), as well as in Traniello and Hölldobler (1984) which contained sufficiently detailed photographs, all records actually pertain to *P. verenae*. Since there are no collection records of true *P. obscuricornis* from Central America, it is almost certain that other Meso-American studies of "*obscuricornis*" (e.g., Fresneau 1984, Oliveira & Hölldobler 1991, Lommelen et al 2002) also pertain to *P. verenae*. More ambiguous are South American references (e.g., Wheeler et al 1999, Düssman et al 1996). Given the relative rarity of true *P. obscuricornis*, most South American records may also refer to *P. verenae*, but the identity of these cannot be verified without the examination of specimens.

Unfortunately, taxonomic instability may continue to persist for some time in the

*Pachycondyla apicalis* complex. While the species-level nomenclature may stabilize with the recognition of three species, it is almost certain that the heterogeneous genus *Pachycondyla* is paraphyletic with respect to much of the rest of the tribe ponerini (C. Schmidt, unpublished molecular data). As generic taxonomy falls in line with new phylogenetic hypotheses, it is entirely possible that various generic names, including *Neoponera* for the species discussed here, will be resurrected to retain monophyly of the ponerine genera.

### Acknowledgements

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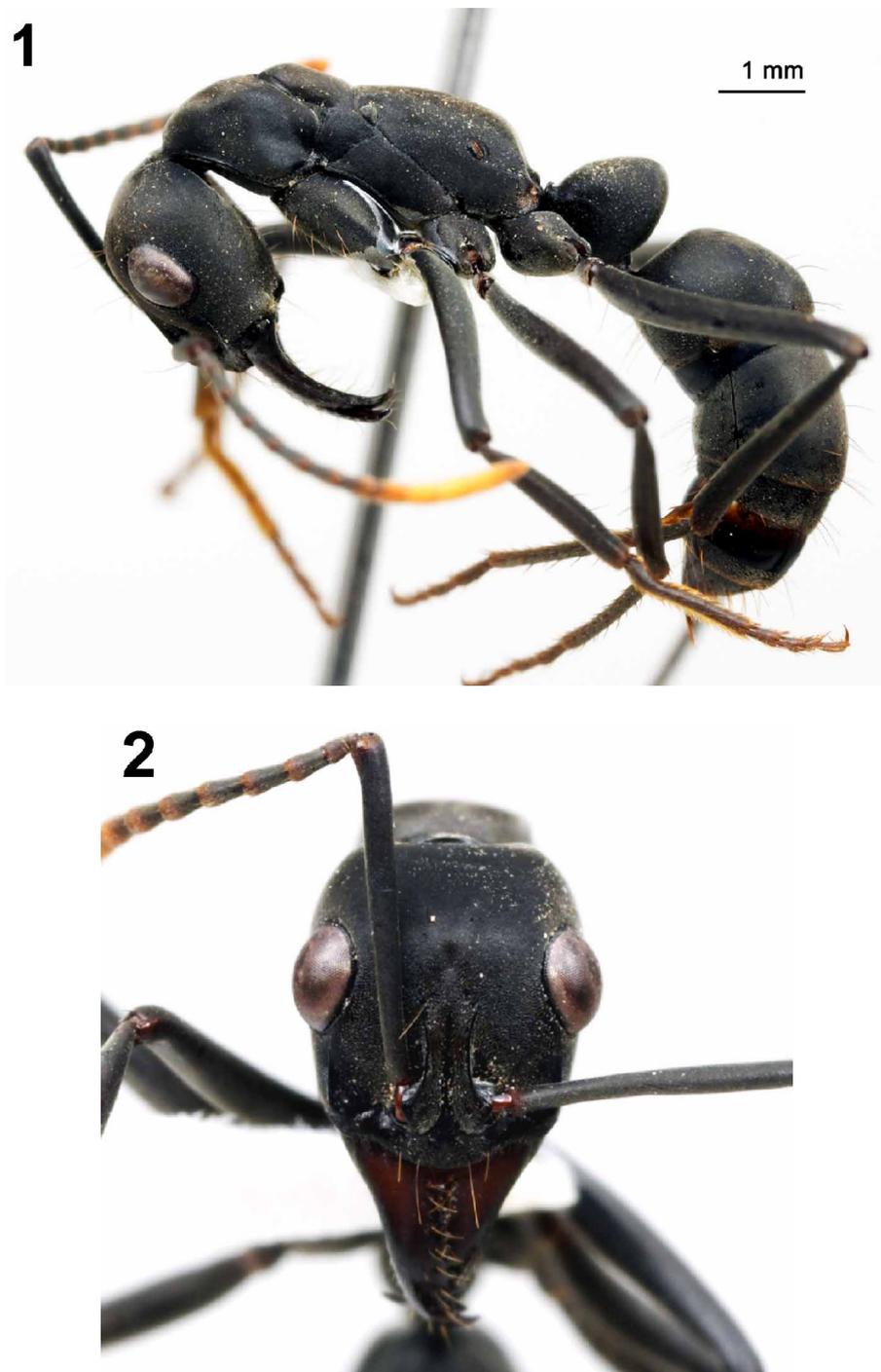
**FIGURES 1–2.** *Pachycondyla apicalis* worker specimen from Rio Nicharé confl. Rio Caura, Bolívar, Venezuela (6°30'N 64°50'W) [PSWC]. 1. Lateral view. 2. Full-face view.

**3**



1 mm

**4**



**FIGURES 3–4.** *Pachycondyla obscuricornis* worker specimen from the Mbaracayú Reserve, Canindeyú, Paraguay (24º08'S 55º30'W) [ALWC]. 3. Lateral view. 4. Full-face view.

FIGURES 5–6. *Pachycondyla verenae* worker specimen from 49 km ENE Tumeremo, Bolívar, Venezuela (7°28'N 61°06'W) [PSWC]. 5. Lateral view. 6. Full-face view.

**FIGURES 7–8.** Worker hypopygia, oblique ventral view. 7. *Pachycondyla apicalis*, same specimen as in Figs. 1–2. 8. *Pachycondyla obscuricornis*, same specimen as in Figs. 3–4.

**9**



**10**



**FIGURES 9–10.** Worker petiolar nodes, oblique lateral view. 9. *Pachycondyla verenae*, same specimen as in Figs. 5–6. 10. *Pachycondyla apicalis*, same specimen as in Figs. 1–2.

**11**
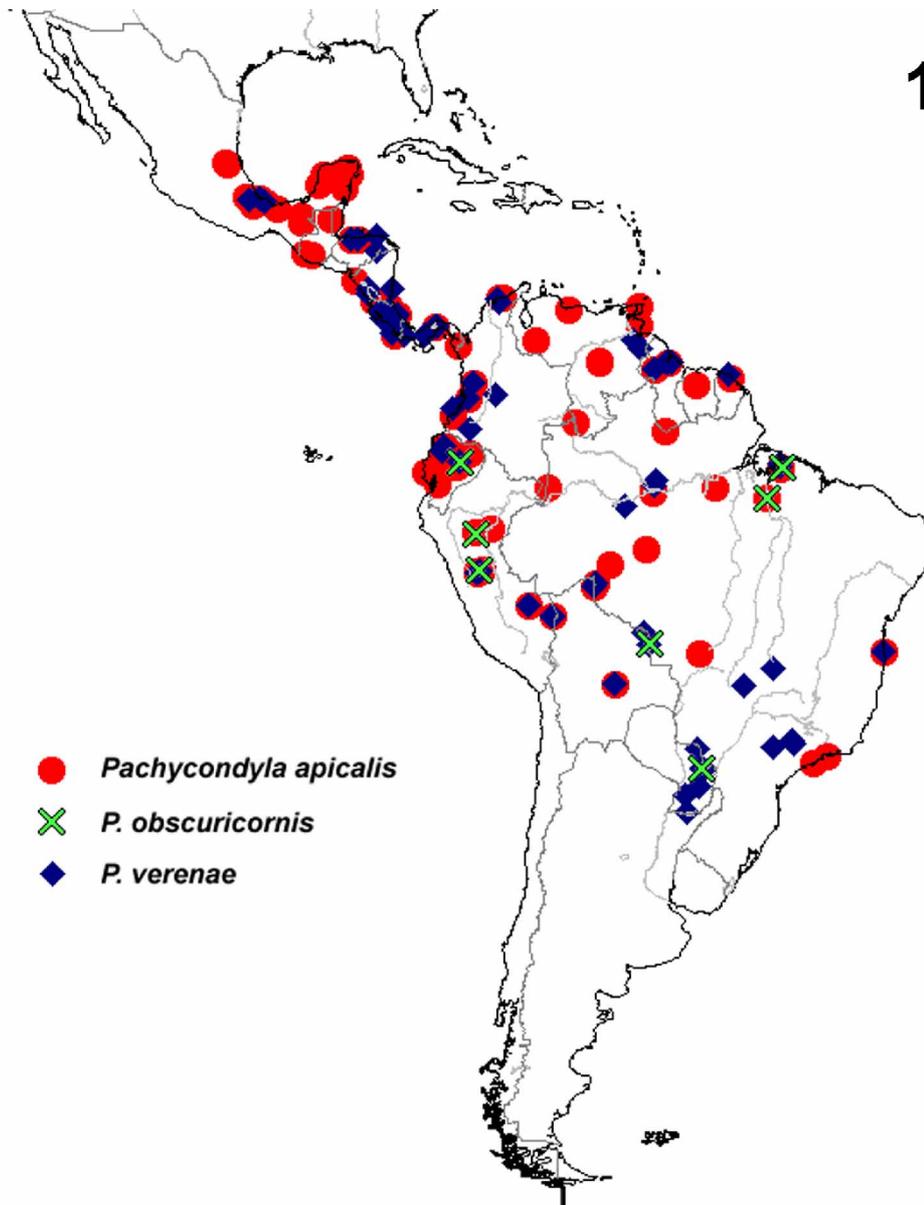


**FIGURE 11.** Distribution of ants in the *Pachycondyla apicalis* complex, based on specimens from ALWC, INBP, LACM, MCZC, MHNG, MZSP, PSWC, and UCDC.
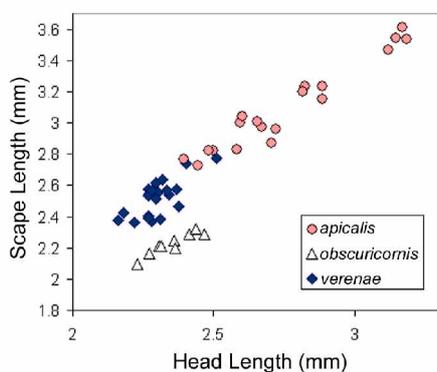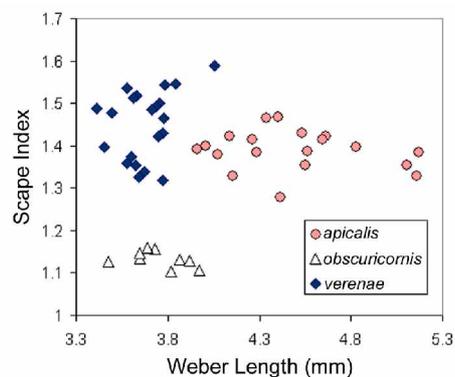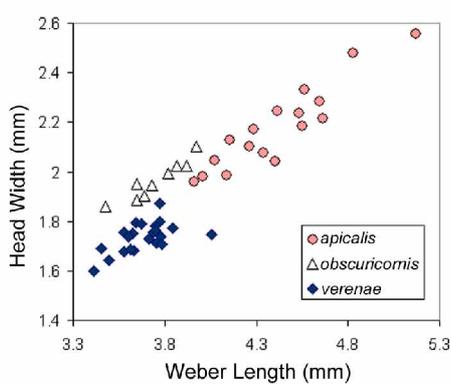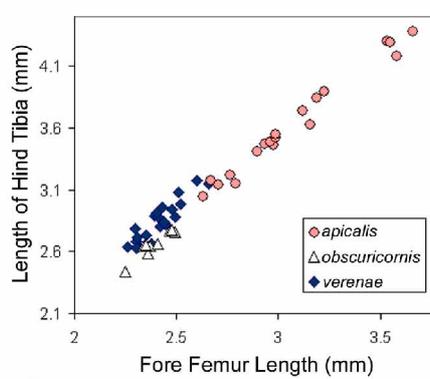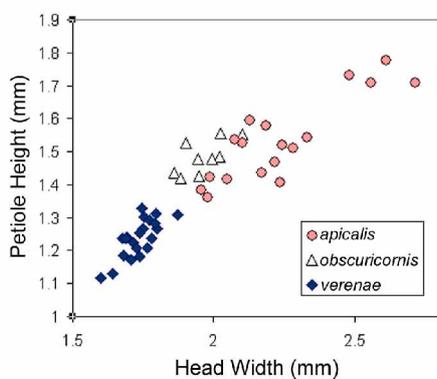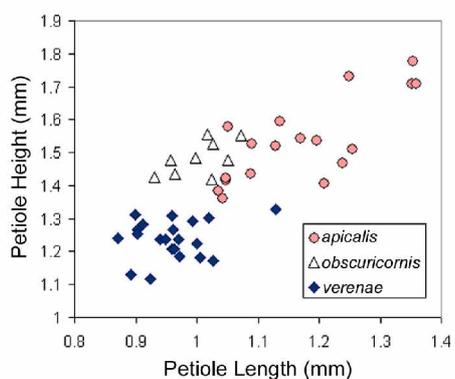
**FIGURES 12–17.** Morphometric plots of *Pachycondyla apicalis* (n = 19), *P. obscuricornis* (n = 9), and *P. verenae* (n = 23) worker specimens.  12. Scape Length versus Head Length.  13. Scape Index versus Weber Length.  14. Head Width versus Weber Length.  15. Hind Tibia Length versus Fore Femur Length.  16. Petiole Height versus Head Width.  17. Petiole Height versus Petiole Length.