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Global revision of the dulotic ant genus *Polyergus* (Hymenoptera: Formicidae, Formicinae, Formicini)

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Abstract

The genus *Polyergus* is characterized, and all valid species reinstated and re-described, and five new species described, based on morphometric, ecological, host-association, and biogeographic characteristics. *Polyergus* contains 14 species: 3 Palaearctic, 11 Nearctic. The *rufescens* group comprises western Eurasian *rufescens* Latreille 1804 including its former eastern subspecies *tianschanicus* Kuznetsov-Ugamsky 1927 **new synonymy**, and the following American species, informally called the *breviceps* complex: *breviceps* Emery 1893 **sensu stricto, revised status**, *bicolor* Wasmann 1901 **new status**, *mexicanus* Forel 1899 **new status**, *topoffi* **new species**, and *vinosus* **new species.** The *lucidus* group comprises *longicornis* M. R. Smith 1947 **new status**, *lucidus* Mayr 1870 **sensu stricto, revised status**, *montivagus* Wheeler 1915 **new status**, *oligergus* **new species**, *ruber* **new species**, and *sanwaldi* **new species**. The *samurai* group comprises two blackish forms: the western Asian *P. nigerrimus* Marikovsky 1963 and eastern Asian *P. samurai* Yano 1911. *Polyergus texana* Buckley 1866 is excluded from *Polyergus*.

Key words: dulosis, social parasitism, host specificity, taxonomy, key.

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Introduction to the genus *Polyergus*

Polyergus is a well-known ant genus, at least to Holarctic myrmecologists. These ants' summer-afternoon raids against colonies of *Formica* species have caught the attention of naturalists and entomologists for over two centuries. The literature on *Polyergus* dates at least to Latreille's (1798) description of *"Formica rufescens,"* followed a few years later (Latreille 1804) by his naming of the genus. The careful observations of Pierre Huber on this species in Switzerland (1810) constitute a classic ant natural history study. A century later, diversity and host specificity of North American populations of *Polyergus* were suggested by an array of forms described by Wheeler (summarized in Wheeler 1910, with additions in Wheeler 1915), but his nascent (sub)species concepts were lost to later synonymization. Even M. R. Smith's (1947) careful review of the species was soon overridden by the synonymies of Creighton (1950), though Gregg (1963) made a flawed effort to resuscitate part of Smith's system. Buschinger (2009) reviewed *Polyergus* biology in the context of a review of social parasitism in ants, noting (p. 4) that relatively few new parasitic ant species had been described since 1990, and that those described did not have accompanying biological information. This revision serves to break that pattern for *Polyergus*.

Huber published his observations on the mixed nests of *Polyergus rufescens* and hosts *F. fusca* and *F. cunicularia* in 1810. He was the first to surmise correctly that mixed colony populations of *Formica* and *Polyergus* were in nests rightly considered those of the parasite, even though comprising relatively few *Polyergus* and far more numerous *Formica* workers. He demonstrated that the *Formica* workers in *Polyergus* nests were raised from brood robbed from nearby *Formica* colonies. A single *Polyergus* queen enters and usurps the queen of a host *Formica*, and the *Polyergus-Formica* colony that ensues goes on to parasitize multiple neighboring host *Formica* colonies through brood robbing. After successful usurpation of the *Formica* queen and the eclosing of the first *Polyergus* workers, it is no longer correct to refer to the nest as a parasitized *Formica* colony. *Polyergus* colonies always contain an abundance of host workers, usually reported to outnumber *Polyergus* workers by 5–10 times, and their colonies are consistently reported as more populous and inhabiting a larger nest than is typical for the host species. Their nests are otherwise typical in habitat, structure, and materials for the particular host (Talbot 1967, Marlin 1971, King and Trager 2007, Tsuneoka 2008).

All *Polyergus* species are obligate parasites of one or more *Formica* species. Many parasitize only a limited set of species within a single species-group, at least locally. The hosts are usually members of either the *F. fusca* group (*sensu* Francoeur 1973) or the *F. pallidefulva* group (*sensu* Trager, *et al.* 2007). Here, study of field and museum samples indicates that published reports of *F. neogagates* group species as hosts of a variety of *Polyergus* species are often, but not always, erroneous. No member of the *lucidus*-group utilizes *F. neogagates*-group members as host, and in the *breviceps*-complex only *P. mexicanus* can be confirmed to do so. Talbot (1967) reported raids by *P. lucidus* on *F. neogagates* and *F. lasioides*, but she clearly stated that brood from these raids never matured in the *lucidus* nest. *Polyergus mexicanus* samples from California, Oregon, Nevada and one from Wisconsin were collected in association with various *F. neogagates* group hosts, but these populations also parasitize various members of the *F. fusca* group nearby.

Raiding for brood, mostly pupae of the host species, is essential for maintenance of the mixed species population of a *Polyergus* colony over the years of its life. The importance of scouts in initiation of raids has been confirmed for at least *P. rufescens* (Le Moli *et al.* 2001) and *P. lucidus* (Talbot 1967), and is probably a generic behavioral trait. Scouts head out late morning to early afternoon to find a target host nest, then return to their nest around the time of day when raids normally begin, typically mid- to late afternoon. Scouts actively recruit to the raid by running about jerkily, and probably secreting recruitment pheromone(s), among conspecific nestmates that often are already milling about the nest entrance. Talbot (1967) was able to induce short and somewhat atypical raiding behavior by painting a trail of a whole body extract of *Polyergus* workers from a nest entrance to a colony fragment of the host. In warmer climates, raids are typically late afternoon, after the daily maximum temperature, but they may coincide with the daily maximum in cooler climates of higher latitudes and altitudes. Wheeler (1910) reported raids of *bicolor* occurring in early afternoon, in a forest near Rockford, Illinois. Talbot (1967) saw one *lucidus* colony in Michigan raid during the morning four times, and I have seen this twice by *lucidus* in Missouri and once by *topoffi* **n. sp.** in Arizona (Trager, unpublished observations). Nonetheless, morning raiding still must be described as unusual.

Based on hundreds of raids of various *Polyergus* species seen over the years (Trager, unpublished observations), I will summarize the events of a typical raid. Instigated by a successful scout, a dense swarm of raiders heads off, slowly at first, then organizing into a column and hastening the pace. The columns are periodically interrupted as the raid progresses. When this occurs, there is the appearance of the group's not knowing where to go next. Then, a worker that apparently had run ahead of the main group (a scout/leader?) may be seen to return to the group and recruit the column in the right direction once again. Upon arriving at the host nest, *Polyergus* workers hesitate and amass outside the entrance, often clearing pebbles, twigs, and other impediments from the entrance of the host nest before they enter. Shortly after the first *Polyergus* enter, they begin emerging and head home bearing pupae, prepupae, or less commonly, last-instar larvae. Sometimes, especially early in the raiding season, raiders return one or more times the same afternoon to pillage additional pupae from a particularly productive host colony. Less often, a *Polyergus* colony raids more than one host colony in an afternoon, either simultaneously or sequentially. A commonly reported impression is local depletion or diminution of host species colonies in the neighborhood of the *Polyergus* colony (*e.g.*, Talbot 1967, Hasegawa and Yamaguchi 1997). Though the year's raiding begins roughly contemporaneously with the pupation of sexual brood of the host *Formica*, there are no reports of *Polyergus* transporting host sexual brood. Further study is needed to appreciate the impact on fitness of raided colonies.

Mating behavior is variable. In some species or populations, mating takes place on the ground near the natal nests or in raiding columns, before or during raids, and then the newly mated gynes enter into raided host nests shortly after mating (Talbot 1968, Topoff and Zimmerli 1993). In other species or populations of *Polyergus*, mating often takes place in early afternoon, away from the nest in unknown locations, apart from raiding activity. Which of these mating patterns happens may be a species or population-specific behavior. For example, *P. mexicanus* and *P. lucidus* gynes in eastern Missouri always emerge and mate mid-day to early afternoon, 2–4 hours before raiding occurs, while females of *P. mexicanus* in California (form "*umbratus*") at least sometimes accompany raids and mate along side them. Dealate females of *P. mexicanus* also may seek out host colonies to invade alone, as do at least some *P. lucidus* dealates, but a few *P. lucidus* dealates, after having mated earlier, accompany a raid, skirting along the sides as it progresses, then enter the just-raided host nest near the end of the raid.

What happens next has been elucidated in laboratory studies (Topoff and Zimmerli 1993). The recently mated *Polyergus* gyne creeps in or is dragged in by host workers. She seeks out the host queen, and if the colony has numerous workers (*i.e.,* the invaded colony is well established), the *Polyergus* gyne immediately attacks and kills the *Formica* queen, clamping onto her oozing corpse for several minutes, thus acquiring the host queen's scent (cuticular hydrocarbons), and probably gaining some nutrition by consuming her hemolymph. If the host queen is young and has few or no workers, Johnson *et al.* (2002) reported that the parasite gynes do not kill the *Formica* queens until the host colony reaches about 200 days of age. In Johnson's experiment, the *Polyergus* gynes were withdrawn after each of the trials over the experimental period of 29 weeks. This laboratory study extended into the winter, a highly unnatural circumstance, but the study nonetheless has interesting implications for the field. The flight season of *Polyergus* follows the peak flights of its host species, extending up to two months beyond it, and encounters of a *Polyergus* foundress and a young host gyne, with or without her nanitic first workers, may be common. If the parasite can manage to cohabit with the gyne and her young offspring into the next growing season, then kill the host queen and inherit her workers, this could result in a successful colony founding. In this study, I examined several colony samples containing nanitic workers (typical of young colonies) of both host *Formica* and *Polyergus* together. These might well have been the result of such a colony foundation scenario (See also Topoff and Mendez 1990).

The life span of colonies is not well documented, but it is not unusual for a student of these ants to return to a particular nest for several years of observations. Talbot (1967) reports a colony of *P. lucidus* at least 10 years old. There are no reports of the presence of more than a single queen in a *Polyergus* colony, though there are sometimes multiple ergatoids. Many or perhaps all species sometimes have these large, worker-like forms with swollen gasters containing apparently functional ovaries and occasionally, some hints of alary articulation. It is unclear whether ergatoids ever coexist in a colony with the dealate foundress. No one has documented oviposition or even the certain presence of a full spermatheca in such individuals, but if ergatoids are able to produce female offspring, they may well succeed the alate gyne after her death, and the colony may become essentially immortal.

There is a long tradition of referring to *Polyergus*, and other ants that build up a worker population through brood theft from a related species, as "slave-maker" ants, and to the host *Formica* species (or other genera) as their "slaves". The analogy of these ants' behavioral ecology to human slavery is imperfect, and potentially, not a little offensive (Herbers 2006). One can legitimately state that words derived from "slave" will cause some readers or students entering biology to cringe, especially as the study of dulotic ants continues to evolve from a field dominated by men of European and Japanese origin to one studied by people of many origins, including descendants of humans subjected to slavery. So it seems well advised to avoid these terms. The preferred terms for these behaviors are dulosis and dulotic, derived from the Greek word for slave. Herbers (2008) proposed alternative terminology that is to my mind equally inaccurate and possibly off-putting: piracy, pirate ants, and Hellenic "leistic". *Google Scholar* searches for these terms reveal that they have almost completely failed to catch on outside of Herbers' original suggestion, except for a publication or two by students from her lab. Of course, the behavior of these ants is not exactly analogous to any human institution or behavior, but the theft of young from their parents, against their will, to create a working caste for colony maintenance, feeding and brood rearing is not far from "enslavement." As has been shown by the fate of Herbers' terms (and other recent examples in biology), new terminology is often not accepted, when well-established terminology is in place and continues in frequent use. I suggest that these behaviors continue be referred to by the terms dulosis and dulotic, while doing our best to avoid the use of "slave" and its derivatives**.** Dulosis arguably describes the behavior of all *Polyergus*, as well as that of the species of the *Formica sanguinea* group, *Harpagoxenus, Protomognathus, Temnothorax* and *Strongylognathus* (and perhaps others with this behavioral syndrome yet to be discovered). The species of *Formica* and respective other genera that they parasitize may simply be called the host, or as already published in some European literature, auxiliaries or helper ants.

Sources of specimens for study

I have observed and collected specimens of *Polyergus*, whenever possible with accompanying host *Formica*, since childhood, but formally from the 1970s till the present, across the southern USA, and in the Midwest. Museum specimens borrowed for study or examined at various institutions augmented my material. Types or "syntypes" designated by Gustav Mayr, Carlo Emery, William Wheeler, and Auguste Forel became available on loan from and/or by visiting the following museums (and through the people who facilitated the loans): Museo Doria d'Historia Naturale Genova (MSNG—Roberto Poggi), Harvard University Museum of Comparative Zoology (MCZ—Stefan Cover), the California Academy of Sciences (CAS—Brian Fisher), the Los Angeles County Museum of Natural History (LACM—Roy Snelling, Weiping Xie), and the Muséum d'Histoire Naturelle de Genève (MHNG—Bernhard Merz). Other entomological collections consulted for smaller numbers of specimens included Mississippi State University (MEM—Joe MacGown), Louisiana State University (LSAM—Shawn Dash), the University of Texas—El Paso (WEMC-William and Emma Mackay), Archbold Biological Station (ABS—Mark Deyrup), the University of Wisconsin—Madison (WIRC—Jeff Gruber, Stephen Krauth), the Field Museum of Natural History (FMNH—Corrie Moreau), and the Senckenberg Museum für Naturkunde—Görlitz (SMNG—Bernhard Seifert, Roland Schulz). Alfred Buschinger most kindly sent a sample of *P. nigerrimus* from the type nest collection given to him by its collector, Pavel Marikovsky (these are now deposited with Dr. Buschinger's permission at CAS). Other fruitful sources of specimens have been Ray Howard Topoff, Portal, Arizona; Riitta Savolainen, Helsinki University; Candice Torres, a Ph. D. student at the University of California—Berkeley; Raymond Sanwald of Medford New York; and Lloyd Davis of Gainesville Florida, all of whom have generously shared and supplied specimens from their own collecting and research. Among these, the collections of Riitta Savolainen from across the United States and southern Canada, were especially numerous and valuable additions to the study material.

Specimen repositories and deposition of types.

Abbreviations of collections mentioned in this revision:

ABS	Archbold Biological Station, Lake Placid, Florida
AMNH	American Museum of Natural History, New York
CA	California Academy of Sciences, San Francisco
FMNH	Field Museum of Natural History, Chicago

FSCA	Florida State Collection of Arthropods, Gainesville
JCTC	James C. Trager personal collection
JTLC	John T. Longino personal collection
LACM	Los Angeles County Museum of Natural History
LSU	Louisiana State University, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MEM	Mississippi Entomological Museum, Starkeville
MNHN	Muséum National d'Histoire Naturelle, Paris
NCSU	North Carolina State University, Raleigh
RAJC	Robert A. Johnson personal collection, Tempe, Arizona
SMNG	Staatliches Museum für Naturkunde, Görlitz, Germany
USNM	National Museum of Natural History, Washington, D.C.
WEMC	William and Emma Mackay personal collection, El Paso Texas
WIRC	University of Wisconsin Insect Research Center, Madison
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg
ZMUC	University of Copenhagen Zoological Museum, Denmark

Holotypes and paratypes series will be divided among MCZ and CAS. The exception is that types of *P. vinosus* **n. sp.** will be returned to LACM, and some of the paratypes of *P. oligergus* **n. sp.** will be deposited at ABS and FSCA. Other identified material will be sent to the collections at AMNH and USNM, or returned to the various collections from which they originated.

Material and methods

Preliminary study of *Polyergus* specimens consisted of sorting specimens by a subjective impression of size, gracility, pattern and abundance of pilosity and pubescence, and by host and locality data. Point-mounted specimens of all apparent species were measured at 50X (100X for pilosity counts) under a Wild M5 stereo dissecting microscope with 20X oculars and ocular measuring ruler. Data were recorded and minimally processed in an Excel spreadsheet. The following measurements and indices were taken, though only those that proved useful in discriminating species are reported in the species accounts.

Full-face view—A view of the *de facto* dorsal (anatomical anterior) surface of the prognathous head of females of *Polyergus*, rendering the greatest measurable length, parallel to the long axis of the head, between the margins of the clypeus and vertex.

Vertex—In full-face view, this is the rear (anatomical dorsal) margin or region of the prognathous head capsule (often erroneously called the occiput or occipital margin in older literature).

HL—Head length: In full face view, the greatest length, parallel to long axis, between the distal margin of the clypeus and a line perpendicular to the most distal portion of the vertex margin.

HW—Head width: In full face view, perpendicular to the long axis, the greatest width of the head, including the outer margins of the compound eyes if they protrude beyond the lateral margins of the head.

SL—Scape length: The greatest measurable length (chord) of the scape, excluding the basal condyle and radicle.

EL—Eye length: The greatest measurable diameter across the outer margins of the exterior ring of facets of the compound eye.

½ VeM —Vertex macrosetae (stout, erect setae, hereafter simply called setae): The number of large setae, on one side of the vertex, whichever has more, arising from heavily sclerotized, brown or black, annular sockets, on the vertex region (in practice, this may require counting sockets from which the setae have fallen, viewing with bright lighting, 100X magnification, and by rotating the specimen from posterodorsal to posteroventral aspect).

½ PnM—Pronotum macrosetae, (stout, erect setae, hereafter simply called setae): The number of large setae, on one side of the pronotum, usually the left, arising from heavily sclerotized, brown or black, annular sockets, on the pronotum (in practice, this may require counting sockets from which the setae have fallen, viewing with bright lighting, 100X magnification, and by rotating the specimen from dorsal to lateral aspect).

PrW—Pronotum width: The greatest width of the pronotum in dorsal view.

WL—Weber's length: A standardized measure of the length of the thorax (mesosoma), from the anteroventral edge of the pronotum, exclusive of the "cervical" collar (anterior flange), to the posteroventral margin of the metapleuron (usually measured in lateral view, but can also be measured with accuracy in dorsal view, with the anteroventral pronotal edge and lateral posteroventral margin of the propodeum both in the same plane of focus).

PH—Petiole (node) height: The vertical distance between the lowest externally visible portion of the petiolar spiracular atrium and the dorsal outline of the petiolar node (measured in lateral view, with the side of the petiolar node in focus, and in practice, the dorsal apex slightly out of focus).

PW—Petiole (node) width: The greatest distance across the petiolar node, exclusive of the spiracular protuberances, perpendicular to the long axis, measured in any view that permitted the same level of both sides of the petiolar node to be seen in clear focus. In this study PW was measured just above the protuberances formed by the spiracular atria.

GL—Gaster length: The longitudinal distance from the anteriormost portion of the front face of the first gastral tergite (abdominal segment III) to the tip of the acidopore, exclusive of its ring of pilosity.

HFL—Hind femur length: The greatest measurable length of either of the two hind femora.

Calculated indices (most listed as fractions, multiplied by 100, for reporting as whole numbers in the species accounts and Table 1)

CI Cephalic index: HW/HL X 100
SI Scape index: SL/HW X 100
FSI Femur-scape index: HFL/SL X 100
HFI Hind femur index: HFL/HW X 100
LI Standardized length index: HL + WL (to 0.01mm)
TL Total length: HL + WL + GL (to 0.01mm)

EL, PH, and PW were acquired for most species, as were indices calculated from them, but in practice, these measurements and indices had little or no diagnostic value. They were not taken for several of the species measured later in this study, and are not reported in the species accounts below.

Locality information in the Distribution of Studied Specimens for each species is transcribed from labels, usually unmodified (punctuation errors, date formats, etc.), except occasionally for clarity.

Measurements listed at the head of each species account are formatted as "minimum-maximum (mean)". In a few cases in the descriptions, the format is "(absolute minimum found in only one or two specimens) minimum-maximum (absolute maximum found in only one or two specimens)".

Gynes and males of the species are not described in this revision. Males exhibit subtle morphological differences, if any, among the species, as well as apparently considerable variation within species (Wheeler 1968). Males of the *breviceps* and *lucidus* complexes do differ in density of gastral pubescence, like the females. Gynes, with further study, may prove to have useful morphometric characters, but available specimens were too few to investigate differences among species

A small number of series in the *breviceps* complex of western North America could not be placed with confidence in any of the species discriminated here. These may be the result of hybridization among *breviceps* and *mexicanus*, or perhaps these represent rare or cryptic species or unaccounted-for variation of the known ones. A thorough sampling of fresh material and a careful analysis of additional data not available for this study should help resolve these samples.

Diagnosis of the genus *Polyergus* Latreille 1804

Genus *Polyergus*: Holarctic distribution.

Outstretched specimens, clypeal margin to gastral tip length: alate gynes 8–10 mm, ergatoids 7–8.5 mm, monomorphic workers 4.5–7.5 mm, males 4–7 mm.

Workers with the characters of the tribe Formicini: a double row of stout setae (bristles) on the flexor (ventral) surface of the hind tibiae; anterior articulation of the petiole obscured by the metacoxae; upper surfaces of wings of both sexes with numerous suberect small setae, but lacking stout pilosity (Agosti 1994).

Head shape subquadrangular or subhexagonal or with angles rounded to yield subovate or suborbicular head capsule in full face view, anteriorly truncate due to straight or weakly concave clypeal margin, and with straight to either weakly convex or weakly concave vertex margin, and with weakly to notably rounded sides, at least behind the eyes, sometimes with contrastingly straight or even feebly concave genae; vertex "corners" always rounded, HW across the outer margins of the compound eyes roughly equaling (usually slightly less, far less often a bit greater than) the head length; in broad-headed species, eye margins often not protruding beyond head margins in full face view, slightly protruding in narrower-headed species. Mandibles falcate, the inner border denticulate, and with two rows of long, straight setae arising submarginally near inner margin, dorsal line of hairs sparse, longer and oblique anteriad, ventral hairs arising about 1 per every 3 denticles and perpendicular to inner margin. Palps short, segmentation reduced, 4,2 (reportedly, rarely 4,3). Clypeus foreshortened (compare to *Formica*), in full-face view it is a shallow trapezoidal, triangular, or lens-shaped sclerite positioned mostly between the mandibular bases, the posterior median portion weakly umbonate, with narrow, tapering, lateral lobes behind the mandibular bases, and a nearly straight or weakly concave inter-mandibular, apical margin (but somewhat convex in *samurai*). Frontal carinae reduced, extending about or slightly less than half their full length beyond the antennal fossae. Compound eyes ovoid, EL/HL 0.23–0.28, in full-face view about 0.3–0.35 of EL lies (on prognathous head) anterior to the midpoint of HL, and 0.65–0.70 of EL lies posterior to the midpoint of HL. Metapleural gland opening indistinct on the weakly bullose lower rear portion of the metapleuron, a transverse narrowly ovoid slit, rimmed by short, straight setae. Propodeal spiracles are narrow crescentic slits, placed on the propodeal lateral face just below the rounded transition of the dorsal to the posterior declivitous propodeal surfaces. Both pubescence and pilosity setae longitudinally costulate (Fig. 1, but some intersegmental proprioreceptors apparently are smooth), tapering; pubescence typically curved or hooked apically, and sometimes globular at the tip; base of pilosity in a shallow pit about 3–4X the width of the seta (and the pits reliably can be used in pilosity counts when the setae themselves have been lost), pilosity tapering to a rounded, truncate, or sharp tip.

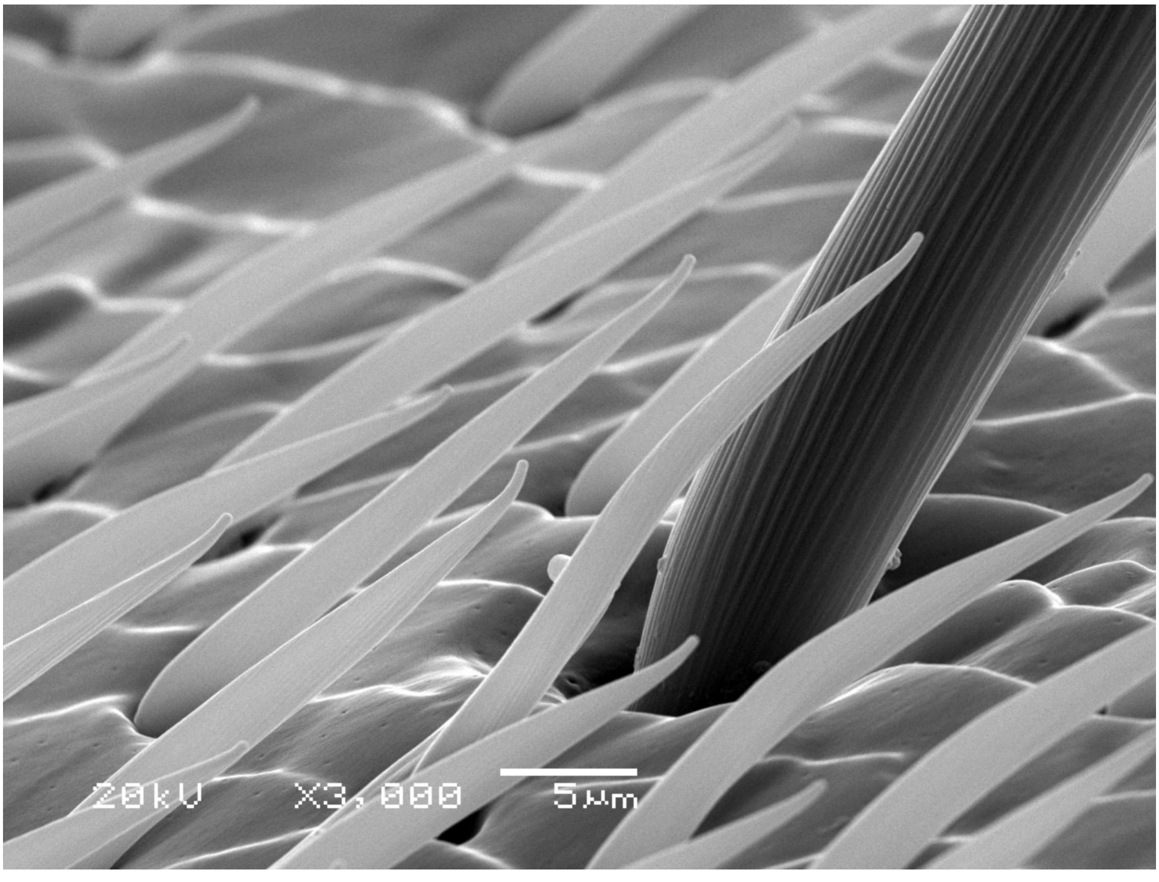


FIGURE 1. Pronotal pilosity and pubescence setae of *Polyergus mexicanus*, showing longitudinal costulae. SEM by Brendon Boudinot.

Gynes similar to conspecific workers but thorax bearing full sclerite representation, wings (before dealation) and alary articulations and musculature; larger than workers, with stouter heads, scapes and legs; petioles relatively and absolutely stouter on all axes; and the body, especially the head and legs, generally shinier than workers of the same species.

Ergatoid females resemble large conspecific workers, with enlarged petioles and gasters, sometimes with weakly developed vestiges of alary articulation.

Males currently recognizable only to species group within the genus, usually a bit smaller than workers (but the few known specimens significantly larger in *vinosus*), superficially similar to large *Lasius* males or those of *Myrmecocystus*, but with palp formula 4,2; with longitudinally costulate dorsal macrosetae (bristles), paired rows of suberect macrosetae on ventral surface of hind tibiae (though few and fine relative to those of females and other Formicini); and as in females of the tribe, with the anterior articulation of the petiole obscured by the metacoxae (visible between metacoxae in *Lasius* and *Myrmecocystus;* Agosti and Bolton 1990). Male petiolar profile tapering dorsad, cuneate or acutely rounded; petiolar dorsal margin concave or broadly and angularly notched, thus biumbonate.

Karyotype much like that of closely related *Formica*, N=27 (Imai 1966).

Polyergus workers have a pygidial gland, unique among formicines, consisting of a group of subcutaneous exocrine cells, the product of which exits through the porous anterior edge of the seventh tergite (Hölldobler 1984).

Etymology. The generic name *Polyergus* is derived from Greek poly- plus ergos, meaning much work or hard-working. This would seem an ironic name in regard to the amount of nest work performed by these obligate social-parasitic ants. However, the extent, vigor and organization of their work during brood raids is quite unmatched among other ants outside the doryloid section.

Synonymic list of *Polyergus* species
(in the order of the species accounts)

***Rufescens-breviceps* group**

—*rufescens* Latreille 1798
  =*rufescens tianschianicus* Kuznetsov-Ugamsky 1927 **syn. nov.**
—*breviceps* Emery 1893
—*bicolor* Wasmann 1901
  =*rufescens breviceps var. fusciventris* Wheeler 1917 (part), unavailable name
—*mexicanus* Forel 1899
  = *rufescens breviceps var. silvestrii* Santschi 1911, unavailable name
  =*laeviceps* Wheeler 1915
  =*umbratus* Wheeler 1915
  =*rufescens breviceps var. fusciventris* Wheeler 1917 (part), unavailable name
—*topoffi* **sp. nov**.
  = *rufescens breviceps var. montezuma* Wheeler 1914, unavailable name
—*vinosus* **sp. nov.**

***Samurai* group**

—*nigerrimus* Marikovsky 1963
—*samurai* Yano 1911
  =*samurai mandarin* Wheeler 1927 **syn. nov.**

***Lucidus* group**

—*lucidus* Mayr 1870
—*longicornis* M. R. Smith 1947
—*montivagus* Wheeler 1915
—oligergus **sp. nov.**
—ruber **sp. nov.**
—sanwaldi **sp. nov.**

Excluded species

—*texana* Buckley 1866. The length, color, and mandibular structure in Buckley's description are quite clearly not those of *Polyergus*.

Key to *Polyergus* workers

1 Entire body dark brown to blackish; pilosity of anterior first tergite gently curved to nearly straight; eastern temperate or desert central Asia . . . . . *samurai* group...2

- Body rich orange to brownish red, with varying amounts of dark brown or blackish coloring on the legs, lower mesosoma, and gaster; pilosity of anterior first tergite conspicuously bent or strongly flexuous in the one Eurasian species; European Atlantic Coast east to western Asia (about 88º E), otherwise North American 3

2 Browner, matte, larger species—LI of most workers > 375 (usually > 390); with longer scapes—SI of most workers 81–85; dry, open habitats, but of humid temperate Japan, Korea, China, eastern Russia; hosts *F. japonica, F. glabridorsis*, rarely others . . . . . *samurai*

- Blacker, somewhat shining, smaller species—LI < 375 (usually < 370); with shorter scapes—SI 74–81; steppe deserts of Mongolia, Tuva, adjacent south-central Russia; with *F. candida* or *F. kozlovi* as hosts. . . . . *nigerrimus*

3 Gastral tergites with pubescence very sparse or lacking, smooth and often strongly shining; North American, most abundant from Atlantic Coast states west to Mississippi Valley (one species extends west to southern Rocky Mountains) . . . . . *lucidus* group ...4

- Gastral tergites with dense pubescence yielding a silky sheen, obscuring the surface of the integument beneath; Eurasian and North American, in North America from western Great Lakes, prairie and Rocky Mountain states and provinces, to Pacific Coast and Mexican mountains . . . . . *rufescens* group ... 9

4 Vertex pilose, ½ VeM usually > 10; head and mesosomal dorsum matte and sides at most feebly shining; host *F. dolosa* 5

- Vertex less pilose, ½ VeM usually < 8; head and mesosomal dorsum matte or shiny; but if matte, then sparsely pilose; host is never *F. dolosa* 6

5 Scapes and legs shorter, SI < 105, usually < 100, FI < 140; northern species, New England west to the Dakotas . . . . *sanwaldi*

- Scapes and legs longer, SI > 100, but usually > 110, FI > 140; southern species, North Carolina to Florida, west to Mississippi and southern Missouri . . . . . *longicornis*

6 Rear portion of head less pilose, ½ VeM usually < 5; head and mesosoma matte or weakly shining on sides; host *F. pallidefulva* or *F. archboldi* 7

- Rear portion of head pilose, ½ VeM usually > 5; all tagmata at least partly shiny; host *F. incerta* or *F. biophilica* 8

7 Larger and less pilose species, LI of most specimens > 390; ½ VeM 0–1 (very rarely more); eastern Canada to northern Florida, west to Wisconsin, Colorado, New Mexico; host *F. pallidefulva* . . . . . *montivagus*

- Smaller and slightly more pilose, LI of most specimens < 390; ½ VeM 1–5; Florida; host *F. archboldi* . . . . . *oligergus*

8 Smaller, shorter-limbed, SL 1.19–1.36, HFL 1.72–2.04; northeastern, Midwestern, and higher altitude Appalachian distribution; host *F. incerta* . . . . . *lucidus*

- Larger, longer-limbed, SL 1.68–1.79, HFL 2.08–2.44; southern and south central USA and foothill Appalachian distribution; host *F. biophilica* . . . . . *ruber*

9 Pilosity of anterior first tergite usually gently curved to nearly straight; North American species 10

- Pilosity of anterior first tergite mostly strongly curved or conspicuously bent; continental Europe east to mountains of Kyrgyzstan, Kazakhstan, western China (about 88º E). . . . . *rufescens*

10 Vertex lacking pilosity or with ½ VeM < 8, usually < 4; pronotal erect pilosity usually all dorsal; hosts in the *F. fusca* group, or less often, in the *F. neogagates* group, but exclusive of the *F. cinerea* complex 11

- Vertex notably pilose, ½ VeM > 6, usually 10–30; pronotum always with some erect setae on sides near lower edges; hosts usually (at least predominantly) *F. montana, F. canadensis*, and/or *F. altipetens* . . . . . *breviceps*

11 Head and pronotum moderately pilose, ½ VeM < 6 (rarely more), ½ PnM usually > 4; sometimes with infuscated posterior tergites, if gaster appears entirely brown or blackish, ½ PnM > 4 12

- Head and pronotum non-pilose or sparsely pilose, ½ VeM 0, ½ PnM 0–2; distinctly bicolored, head and mesosoma red, gaster entirely dark brown to blackish; western Great Lakes states to Dakotas, Manitoba, usually in moist or bog forests; host *F. subaenescens* (less often *F. neorufibarbis*) . . . . . *bicolor*

12 Scapes fall short of vertex corners by a scape width or more, SI < 85; legs shorter, HFI < 120, usually < 110; hosts various, but apparently never *F. moki* 13

- Scapes nearly reaching to slightly surpassing vertex corners, SI > 85, usually > 90; legs longer, HFI > 120; coastal hills of southern CA and BC, MEX; host *F. moki* . . . . . *vinosus*

13 Head often and especially sides of mesosoma weakly to conspicuously shining; scapes not reaching vertex corners by about 1.5–2 scape widths, scapes distally clavate, SI 65–82, but usually < 77; legs shorter, HFI 99–120 (but usually < 113 and always < 110 in southern Arizona and Mexico); upper elevation conifer forests of Mexican mountains, north to British Columbia, Rocky Mountain and Plains states, east to Mississippi Valley; hosts are a wide variety of high elevation or northern *F. fusca* and *F. neogagates* group species. . . . . *mexicanus*

- Head and mesosoma typically entirely matte, or at most weakly shining; scapes longer, not reaching vertex corners by 1.5 scape widths or often less, scapes thickened distally, but at most weakly clavate, SI 75–86, usually > 79; legs longer, HFI 108–

121, usually > 115; HD, Mexico north to lower elevations of southern Arizona mountains in oak or mesquite woodlands; known hosts are various Mexican, hot climate *fusca* group species, including *F. gnava, F. foreliana, F. subcyanea* . . . . . *topoffi*

Species of *Polyergus*

Polyergus rufescens-breviceps group

Alate female, ergatoid and worker castes mostly red in color, with varying degrees of infuscation of the lower mesosoma, gaster and appendages, or less often, bicolored (red foreparts with dark gaster; nanitic workers from young colonies are typically bicolored); densely pubescent on all gastral tergites. Most parasitize certain members of the *F. fusca* group, but one also parasitizes several members of the *F. neogagates* group. Mainly western North American from British Columbia to Ontario, Canada, south through California to the highlands of Baja California and Hidalgo, Mexico, and east to the Mississippi Valley. One species occurs in much of Europe, and in Asia east to the mountains of western China, Kazakhstan and Kyrgyzstan.

Polyergus rufescens

Figures 3, 4, 5

Formica rufescens Latreille 1798: 44. Syntype worker, gyne: FRANCE [MNHN] (not examined).
Polyergus rufescens: Latreille 1804:179. Schenck, 1852:70 (male). Forel, 1874:137 (gynandromorph). André, 1882:163 (redescription of worker, gyne, male).
Polyergus testacea Fabricius 1804: 400. Holotype gyne: "CZECHOSLOVAKIA" (=CZECH REPUBLIC) [ZMUC] (not examined). Smith, 1858:57 (synonymy).
Polyergus rufescens tianschanicus Kuznetsov-Ugamsky 1927: 41. Syntype worker, gyne, male: KYRGYZSTAN, Issik-Kul, Tal des Dzhulek, Tian-Shan Mountains [ZIN] (not examined). **New Synonymy**.

Measurements (N=41) HL 1.23–1.72 (1.59), HW 1.20–1.66 (1.51), SL 0.99–1.31 (1.22), ½ VeM 0–11 (2.41), ½ PnM 3–13 (6.8), WL 1.96–2.60 (2.37), GL 1.44–2.18 (2.13), HFL 1.36–1.92 (1.78), CI 90–99 (95), SI 77–88 (81), HFI 110–130 (1.18), FSI 136–155 (146), LI 3.23–4.32 (3.96), TL 4.67–6.98 (6.14).

Worker description. Head subrectangular, its length greater than breadth; with conspicuous vertex pilosity (usually 6–12 setae) on most specimens from more western locations and no vertex pilosity (0–1 seta) on specimens from farther east; scape apex reaching about 1/4 the distance between eye and vertex corner, weakly clavate in the apical third, or gradually thickening apically; pronotum with (6)10–20 (25) erect setae; mesonotum with profile flat or very weakly convex for most of its length; propodeum evenly rounded; petiole high, its profile about equal in height to propodeum, petiole straight-sided, petiolar dorsum convex, not emarginate or weakly emarginate; first tergite densely pubescent, with numerous, bent or strongly flexuous, decumbent pilosity concentrated in anterior half of sclerite.

Head matte; mesonotum matte; gaster matte.

Color deep red (especially west) to orangey red (especially east) with weak to notable infuscation (deep, often purplish tinted, brown) of pleura, gaster and appendages in darker individuals.

This is the unique *Polyergus* species of Europe and western temperate Asia, and appears morphologically to be closely related to the *breviceps* group, particularly the essentially Mexican species *topoffi*. Future genetic study should deepen our understanding of the relationships of this apparent outlier of what is otherwise a western North American group, distinguished from all other red *Polyergus* by its Eurasian distribution. It is most similar to *topoffi* among the American species, differing by its slightly (average) narrower head and petiole, and denser, more regular array of bent or strongly flexuous, decumbent pilosity on the first tergite.

Specimens from western and especially southwestern Europe are darker in color than those from Asia. Populations of central western Europe have a more pilose vertex than those from the Iberian Peninsula, northern and eastern Europe, and central Asia (½ VeM usually 2–12, compared to ½ VeM 0–2). Lighter color and reduced pilosity were noted as characteristic of the subspecies *tianschianicus* in Kuznetsov-Ugamsky's (1927) description, but in fact, color variation seems to be a west to east clinal feature, and the reduced pilosity is a characteristic of peripheral populations, as it is also found in samples from the far west of the range. Thus, the two traits do not co-vary. In any case, the subspecies are indistinguishable by any other ecological, metric or obvious morphological characters; hence, my synonymy of this subspecies.

Etymology. Latreille coined this name from the Latin verbal form "rufescens", meaning reddish or fading to red.

Natural history. Found from Atlantic western Europe east to mountains of western China and "Central Asia". Extending to 57º N and 88º E, then south to the Caspian, Black, and Mediterranean Coasts.

The "classical" summaries of the behavior of this ant are from Huber (1810) and Wheeler (1910). In the last decade or so, a number of papers, especially those by le Moli's Laboratory in Italy, have refined our knowledge of this species, particularly regarding the role of secondary compounds in regulating their behavior (Castracani *et al*. 2003, 2005, 2008; Grasso *et al*. 2003, 2004, 2005; Le Moli *et al*. 2001; Romani *et al*. 2006; Visicchio *et al.* 2001, 2003, 2007). The following natural history is paraphrased from a summary kindly provided by Bernhard Seifert (pers. comm., 2009) "*P. rufescens* is characteristic of dry, semi-dry and sparse grasslands of any sort that supports sufficiently dense host populations. Hosts vary geographically and include a variety of species: *F. cunicularia* (16 observations), *F. fusca* (12), *F. rufibarbis* (10), *F. clara* (3), *F. gagates* (3) and *F. cinerea* (1). Local host species preferences are obvious, and considering the whole distributional range, host species selection appears to be a trade-off between host species abundance and mortality risk—strong and aggressive colonies of *F. clara* and *F. cinerea* are only attacked in the absence of less resistant alternatives. In many regions of Central Asia, *F. clara* is a main host, as it is a dominant species there and has smaller workers than in Central Europe." And from Roland Schultz (pers. comm., 2012) "The host of *P. rufescens* in cases from Kyrgyzstan, Kazakhstan and western China is *F. clara. Formica clara* is the most common "*Serviformica*" in the high steppes of the Tianshan Mountains of China and Kyrgyzstan, at the altitudes in which also *Polyergus* appears, below 2500 m. In one case, Seifert found 5 workers of *F. exsecta*, including one freshly eclosed from the pupa, among a lot of *F. clara* and *P. rufescens*." In a sample from the Tarbagatai Mountains Kazakhstan, Schulz confirmed a mix of *F. clara* and *F. rufibarbis* as hosts. In addition, I have series from the Pyrenees with *F. gerardi*, where this is the most abundant potential host. Seifert's abundance/trade-off hypothesis seems plausible and testable; there is much opportunity for careful study of host selection in this species (as also in the quite polylectic North American *P. mexicanus*).

Distribution of studied specimens. BULGARIA (Locality?) Her J. Morįk (JCTC); FRANCE (Dépt.?) Smith coll. Pres. By Mrs. Farren White 1899-303 (LACM); FRANCE BOUCHES du RHÔNE Marseilles. Lawn at Ctr. Nat. Rech. Sci. 2 Sept. 1986 L. Morel (JCTC); FRANCE SEINE-et-MARNE Fontain Bleau VI-59 (JCTC); GERMANY BAVARIA Würzburg VII-17-07 WM Wheeler (LACM); HOLLAND Roermond. VII-25-47 JKA van Boven (LACM); ITALY VENETO Verona. Settimo Coll. Priv. C. Baroni 17-9-56 (JCTC); REPUBLIC of SERBIA Yugoslavia, Serbia. Ratje, Zupa 13.VIII.1993. I Petrov (LACM); SLOVAKIA Czechslovakia, Slovakia May, 1984 P. Werner #358 (JCTC); SLOVAKIA Trebišov District. Somotor 5.7.72. K Denea (LACM); SPAIN CÁCERES V-85 (JCTC); SPAIN CATALUNYA El Corredor, Barcelona 10/Jul/1987 X. Espadaler #1 (JCTC); SPAIN CUENCA 30-V-81 (JCTC); SWITZERLAND TICINO Locarno VII-4-07 WM Wheeler (LACM); SWITZERLAND VAUD 1902-120. Col. Bingham (LACM); SWITZERLAND VAUD June-7, 1907 W.M.W. (LACM); SWITZERLAND VAUD Swisse. La Sarraz 6.6.49 (LACM); SWITZERLAND VAUD La Sarraz. 26.7.49. Bibikoff (LACM); SWITZERLAND: VAUD 8-VIII? Col. Bingham (LACM).

Polyergus breviceps

Figures 6, 7, 8

Polyergus rufescens breviceps Emery 1893: 666. Lectotype worker (here designated) USA, COLORADO Summit Co. Breckenridge. [MHNG, CASENT0179559] (examined).
Polyergus breviceps: Kannowski, 1956: 185; Wheeler, 1968: 163.

Material of the unavailable names *fusciventris, silvestrii, montezuma,* referred to *breviceps* by Creighton (1950), here referred to *P. bicolor, P. mexicanus,* and *P. topoffi*.

Former syntypes (N=3 on a single pin, including lectotype) HL 1.36–1.40 (1.37), HW 1.32–1.36 (1.35), SL 0.90–0.96 (0.92), ½ VeM 3–6 (5), ½ PnM 12–20 (16), WL 1.96–2.02 (1.99), GL 1.64–1.88 (1.77), HFL 1.32–1.36 (1.35), CI 97–100 (98), SI 66–71 (68), HFI 97–103 (101), FSI 138–53 (147), LI 3.32–3.40 (3.37), TL 4.96–5.28 (5.14).

Measurements (N=58) HL 1.24–1.60 (1.46), HW 1.28–1.64 (1.48), SL 0.84–1.08 (0.98), ½ VeM (3, one specimen) 5–17 (9.52), ½ PnM 8–22 (14.97), WL 1.88–2.40 (2.14), GL 1.64–2.60 (2.13), HFL 1.30–1.72 (1.52), CI 0.96–1.08 (1.01), SI 61–78 (67), HFI 94–115 (103), FSI 138–170 (155), LI 3.12–3.96 (3.60), TL 4.96–6.52 (5.73).

Worker description. *Polyergus breviceps* is more narrowly defined here than has been conventional in North American ant taxonomy. It is a broad-headed and short-limbed species, but most easily distinguished by its abundant pilosity. This is among the two smaller Nearctic species, though averaging somewhat larger than partially sympatric *bicolor*, and larger than some isolates of *mexicanus*.

Head suborbicular to (less often) subquadrate, its length and breadth about equal, or not uncommonly the breadth a bit greater, sides quite rounded, outer margins of eyes not or at most slightly extending beyond sides of head; vertex flat or broadly and shallowly concave, the flat portion or concavity about as wide as the space between mandibles; vertex pilosity conspicuous and abundant, usually 16–24 (6–30) macrosetae; scape not reaching vertex corners by about twice its maximum diameter, clavate in the apical third; pronotum usually with 22–36 (16–44) erect setae, including a few shorter ones near the lower margins; mesonotal profile flat or very weakly convex for most of its length; propodeum evenly rounded; petiolar dorsum rounded and shallowly emarginate; first tergite densely pubescent; first tergite pilosity flexuous, basally suberect and distally subdecumbent, about as dense in posterior half of tergite as in its anterior half, appearing to be in 5 or 6 transverse arrays.

Head matte; mesonotum matte; gaster matte; slightly shining lateral portions of all tagmata in some specimens. Color usually dull red with infuscation of dorso-posterior portions of tergites. Pilosity matching color of body to slightly darker, pubescence yellow gray.

Discussion. *Polyergus breviceps* is here restricted to a broad-headed and short-limbed species, one most easily distinguished by its abundant pilosity. In addition to its abundant pilosity and short scapes, it shows marked preference for *F. cinerea* group hosts and their typically open, moist grassland or sedge meadow habitat. More pilose examples of *mexicanus* found both at the northern and southwestern portions of its range are those most likely to be confused morphologically with *breviceps.* Where *mexicanus* and *breviceps* occur together (in close parapatry) in the West, *mexicanus* occurs in well drained soils, often in conifer forests on podzols, while *breviceps* occurs in wet meadows with organic-rich soils. Even when its pronotal and mesonotal dorsal pilosity is abundant, *P. mexicanus* lacks the pilosity on the sides of the pronotum, lacks or at least has little vertex pilosity, has a shinier head, and is deeper red in color, with gray rather than yellowish gray pubescence. In the Chicago region, *breviceps* is readily distinguished, even in the field, from the local version of *mexicanus* by its clearly smaller size, and its association with *F. montana*, contrasting with *mexicanus*'s larger size, and association with *F. subsericea*. In the Dakotas and Rockies, a closer examination may be required to discriminate *breviceps* from other *Polyergus*, though these other congeners are more often found in upland prairie, open woodland or forest, rather than the usually moist (including saline and alkaline) meadow habitats preferred by *breviceps*. True *breviceps* does not occur in Pacific Coast states or provinces.

The majority of the literature regarding *P. breviceps* regards either *mexicanus* or *topoffi* (Topoff 1982, 1985, Topoff *et al*. 1984, 1985a, 1985b, 1988a, 1988b, 1989, Topoff and Greenberg 1988, Topoff 1990, Topoff and Mendez 1990, Topoff and Zimmerli 1993, Zimmerli and Topoff 1994, and included references), and true *breviceps* is in fact little studied. As indicated in the synonymy above, the "type series" of *breviceps* included the original Breckenridge, CO material, plus two samples collected later at other localities that I identify as *bicolor* and *mexicanus*. I restrict the type to the Breckenridge material (CASENT0179559), and exclude the other samples, one being a sample of *bicolor* (CASENT0179561) and the other a sample of *mexicanus* (CASENT0179560). Once the characterization of *breviceps* is clear, it may be noted that there is remarkably little variation in this species, notwithstanding its broad but spotty distribution. Western samples have slightly, but insignificantly shorter average SL and HFL.

Etymology. Emery coined this name from the Latin "brevis" plus "-ceps" to mean short-headed (in contrast to the more elongate head shape of *rufescens*).

Natural history. This ant is common in wet to mesic prairies and mesic or wetter old fields of northwestern IN and the Chicago Region, and is distributed west to the Rocky Mountains and south to the White Mts. of northeastern AZ.

The raiding of *P. breviceps* follows familiar patterns described for other species. I have not directly observed mating and colony foundation, but have seen alates fly from the nest several hours before the late afternoon raids, and I also have seen a lone, dealate gyne wandering near a mound of *F. montana* in a prairie near Chicago. It would seem such lone gynes are capable of colony foundation, even with this rather aggressive host and its populous colonies. *Polyergus breviceps* is naturally a species of wet and mesic prairie and meadow habitats, though it persists in drier, but formerly wet, locations after habitat degradation and hydrological disruption, if the host remains abundant (I have observed this both in CO and IL). Wheeler (1910, p. 477) describes a situation near Florissant CO, of *Polyergus* (which I surmise to be *breviceps*) living with "*F. neocinerea*" (*F. canadensis*) in conspicuous mounds raised above the moist soil of a mountain meadow, and what he took to be the same species (but which I surmise to be *mexicanus*) living with *F. argentea* in less conspicuous nests on the wooded slopes above this meadow. In the Chicago region, tallgrass prairie restoration plantings are colonized by *F. montana* in just a few years, and *breviceps* seems to arrive almost or indeed concurrent with them, just a few years after conversion from plowed crop land. This may occur through *breviceps* gynes teaming up with young *F. montana* gynes or incipient host colonies, as has been reported for *P. topoffi.* (See account for this species, below.) *Polyergus breviceps* normally parasitizes members of the *F. cinerea* complex; *F. montana* in the humid prairies of the Great Lakes and northern Plains states, and *F. canadensis* in western mountain meadows. Some samples studied also included *F. altipetens* or less often, the less closely related *F. neoclara* or *F. occulta*. A few samples have been found from drier western grassland sites with these less pilose hosts, and these *breviceps* seem to average a bit less pilose than those with *cinerea* group hosts, but still have telltale pronotal lateral pilosity. These also differ in proportions (narrower head, slightly longer limbs) from typical *P. breviceps*, and may represent another species or a hybrid. Near Taos NM, I once observed raiding columns from two colonies of this species cross paths, resulting in a battle lasting two days, including over night, with high mortality. One of the colonies disappeared after this.

Distribution of studied specimens. ARIZONA Apache Co. Williams Valley 33°51.8'N 109°13.2'W 8690' Elev. 12-X-2004 #3490 RA Johnson (RAJC); COLORADO Alamosa Co. Alamosa, 2286m. Pasture 28-VI-1945 E. V. Gregg (FMNH); COLORADO Boulder Co. Niwot. Minims. Nest in garden. (colony P1) 16 Aug. 1982 JC Trager (incipient colony, JCTC); COLORADO Boulder Co. Niwot. (=incip. P1, Aug. 1982) 4 Jul. 1985 JC Trager (JCTC); COLORADO Boulder Co. Lagerman Reservoir, Niwot, 1548m. 26.x.1961. Mound in wet meadow. R. E. Gregg (FMNH); COLORADO Park Co. Hartsel VII-4-32 Creighton (FMNH); COLORADO Park Co. Taryall. R Savolainen #102/98 (JCTC); COLORADO (Gunnison Co?) Snodgrass Mtn. Gothic. 2920m. Masonry dome nest. J. Atticott (FMNH); COLORADO Gunnison Co. Crested Butte Savolainen 1998 43/98, 45/98; COLORADO Gunnison Co. Farnum Peak GG 1998 Savolainen 102/98, 108/98, 110/98 (JCTC); COLORADO Gunnison Co. Gothic 1998 Savolainen 39/98, 47/98, 49/98 (JCTC); COLORADO Routt Co. Steamboat Springs VII-1-1943 6800' Owen Bryant (FMNH); COLORADO Weld Co. St. Vrain Nuclear Site, Platteville 1478 m 10-VII-1976 Col. W. Brewer (FMNH); IDAHO Twin Falls Co. South rim, Snake River Canyon Twin Falls. 1067m, 11.vi.1967 sagebrush-rabbit brush. Mound near brush. R. E. Gregg w/ *F. neoclara* (FMNH); ILLINOIS Cook Co. Chicago VII-10-33 M Talbot (JCTC); ILLINOIS Cook Co. Chicago 4-30-33 M Talbot #33-45 (JCTC); ILLINOIS Cook Co. US45 Chicago Pond on top of mound M Talbot #33-221 (JCTC); ILLINOIS Cook Co. Chicago 8-102 140 St. off Halsted 10-30-38 AS Winds (JCTC); ILLINOIS Cook Co. Chicago 142 St. and Halsted, Harvey low prairie #11 13.VII.1939 R. E. Gregg (FMNH); ILLINOIS Kane Co. FermiLab prairie planting, on interp trail. 1800hr 23 Aug 2008 Abundant *F. montana* (lone gyne, JCTC); ILLINOIS Lake Co. Site 16 SBM 415 31 May 2011 Sean Menke (JCTC) ; ILLINOIS Will Co. Mokena 96th Ave. near W. L. S. Transmitter 4-IX-1942 prairie #24 R. E. Gregg (FMNH); INDIANA Lake Co. Hammond mound by ditch 4-27-1933 M Talbot #33-30 (JCTC); IOWA Dickinson Co. Iowa Lakeside Lab. August 1997 R Savolainen #s 63/97 & 67/97 (JCTC); NEBRASKA Morrill Co. North Platte River Wetlands. Salt Marsh. J. Jurzenski Coll'n #Morr01-07-25-01; NORTH DAKOTA Barnes Co. 2236 19.VII.1963 G.C. & J.N. Wheeler (LACM); NORTH DAKOTA Barnes Co. Conservation Area 19-VII-1963 #2236 G.C. & J.N. Wheeler (LACM); NORTH DAKOTA Cavalier Co. Waterloo Twp. 13/7/54 #77 Don Sather LACM); NORTH DAKOTA Grand Forks Co. 45 Mekinock 10-VII-1932 C.V. Johnson (LACM); NORTH DAKOTA Grand Forks Co. Powell VIII-1-1932 #701 C.V. Johnson (LACM); NORTH DAKOTA Grand Forks Co. T152NR52W Sec. 9 26-VII-1959 #2166 G.C. & J.N. Wheeler (LACM); NORTH DAKOTA Grand Forks Co. Oakville Township Oakville Prairie Sec. B 14-VII-1949 #408 G.C. & J.N. Wheeler (LACM); NORTH DAKOTA Grand Forks Co. 16-151-51 13-VII-1964 2552 G.C. & J.N. Wheeler (LACM); NORTH DAKOTA Ramsey Co. Twp. Fancher Sec. 22 VIII-17-1951 #157c and IX-11-1951 #188 P.B. Kannowski (LACM); NORTH DAKOTA Ramsey Co. Twp. DeGroat Sec. 18 IX-18-1951 #168 P.B. Kannowski (LACM); NORTH DAKOTA Ramsey Co. Twp. T53R64 Sec. 16 IX-30-1951 #221 P.B. Kannowski (LACM); NORTH DAKOTA Walsh Co. Twp. Ardoch s.4 2-VII-1950 #180 W.E. LaBerge (LACM); NORTH DAKOTA Ward Co. Kenmare VII-27-1954 G.C. & J.N. Wheeler (LACM).

Polyergus bicolor new status

Figures 9, 10, 11

Polyergus rufescens bicolor Wasmann 1901: 639. Syntype workers, gyne, male: USA,WISCONSIN Crawford Co., Prairie du Chien [MCZ, workers, red syntype label 22970] (examined); [LACM, workers, male, host, red “type series” label] (examined); [USNM, workers, 59719] (images examined).

Polyergus rufescens breviceps (part): Emery 1893: 666 (misidentification, mixed syntype series).

Polyergus rufescens subsp. *breviceps* var. *fusciventris* Wheeler 1917: 555 (part). Unavailable name; following material referred here: CANADA, MANITOBA, South Cypress RM. Treesbank. (Wheeler) [USNM #59925, USNM ENT 00529453] (image examined).

Syntype [LACM, red “type series” label, top specimen] HL 1.30, HW 1.28, SL 1.04, ½ VeM 0, ½ PnM 0, WL 1.96, GL 1.88, HFL 1.48, CI 98, SI 81, HFI 116, FSI 142, LI 3.26, TL 5.14.

Measurements (N=44) HL 1.24–1.66 (1.40), HW 1.24–1.74 (1.41), SL 0.92–1.16 (105), ½ VeM 0, ½ PnM 0–2 (0.58), WL 1.88–2.32 (2.08), GL 1.60–2.80 (2.07), HFL 1.40–1.68 (1.55), CI 97–105 (100), SI 64–81 (75), HFI 97–120 (110), FSI 137–158 (147), LI 3.12–3.98 (3.48), TL 4.83–6.58 (5.56).

Worker description. Head subquadrate to suborbicular, its length and breadth about equal, sides often quite rounded; vertex concave, the concavity about half the head width in breadth, completely lacking vertex pilosity; scapes short, not reaching vertex corners, notably clavate in the apical third; pronotum lacking pilosity, or rarely with 1–2 dorsal erect setae; mesonotum profile flat or very weakly convex for most of its length; propodeum profile a rounded weakly obtuse angle; petiole with rounded sides, petiolar dorsum rounded, not at all or only feebly emarginate; first tergite moderately pubescent, with pilosity much like that of *breviceps*, in 4–5 transverse arrays; first tergite pilosity flexuous, subdecumbent.

Head matte; mesonotum matte; gaster matte to weakly shining.

Color of head, mesonotum and often petiole dull red, gaster very dusky red (nearly black); forelegs often redder than middle and hind legs; pilosity reddish brown, pubescence fine and grayish.

Discussion. *P. bicolor* is usually easily distinguished from other Nearctic species by its distribution, distinctive two-tone coloring and sparse pilosity. Northern (ND to BC, CAN) populations of *P. mexicanus* may exhibit similar coloration, but *mexicanus* is always more pilose. Bicoloration and reduced pilosity occur commonly in the small workers from young colonies of *mexicanus*, causing possible confusion. Nanitics of *mexicanus* are usually recognizable by their slender heads with a rounded vertex and longish appendages, and at least a pair of erect pronotal setae. Large workers of other *breviceps*-complex species also may appear somewhat bicolored, but only rarely is the bicoloration so neatly defined by a nearly completely dark gaster as in *bicolor*, and these others have more pilosity on the head and mesosoma.

Etymology. Wasmann coined this name from the Latin nominal adjective “bicolor” meaning two-colored.

Natural history. This species is apparently endemic to the upper Mississippi Valley, from the western Great Lakes region west to the Dakotas and southern Manitoba. In the past it was found in southern Wisconsin and as far south as Rockford, Illinois, but it has not been seen in this area in recent decades.

P. bicolor normally parasitizes *F. subaenescens*, and normally nests with it in rotten stumps or fallen limbs in forests. Wheeler (1910) described raids occurring in early afternoon in a mature mesic forest in northern Illinois that originated from nests in stumps. Two samples examined in this study had *F. neorufibarbis* hosts, also a denizen of moist woods, especially tamarack bogs in the eastern part of its range. Through the course of this study I was not able to obtain or study any specimens of *bicolor* (nor of its host *F. subaenescens*) collected within about the last 50 years, from *bicolor*’s historic range, and I am led to wonder if they have contracted northward due to climatic warming or other causes. Just before submitting this manuscript, in July 2013, I collected a sample in northern Wisconsin. As in the published records, this sample occupied a rotting log with *F. subaenescens.* The log was about 35 cm in diameter, with bark beginning to loosen and wood in transition from white to red rot. At first glance, the mixed colony bore a striking resemblance to a young colony of the locally common *F. aserva.*

Distribution of studied specimens. ILLINOIS Winnebago Co. Rockford VII-12-01 WS Creighton (LACM);

IOWA Back Bone State Park June 19,1940 Wm. Buren (LACM); MICHIGAN Cheboygan Co. VII-21-47 #13 CH Kennedy (LACM); MICHIGAN Iron Co. Crystal Falls VII-2-37 & 7/21/37 & 7/21/38 (3 coll's) AC Cole (LACM); MINNESOTA Cook Co. Saganaga Lake, Chik Wauk Lodge 5-VII-1943 EV Gregg (FMNH); MINNESOTA Cook Co. Saganaga Lake Aug. 28, 1946 RE Gregg (FMNH); MINNESOTA Crow wing Co. Jenkins 7-10-40 WF Buren (LACM); MINNESOTA Hubbard Co. Akeley Aug. 12, 1941 Wm. Buren (LACM); MINNESOTA St, Louis Co. Duluth, 21.vi.1942, tamarack spruce bog. R. E. Gregg (FMNH); NORTH DAKOTA Bottineau 17-IX-38 #253 Joe Davis (LACM); NORTH DAKOTA Cass Co. Fargo 9-VI-1927 C. Schoberger (LACM); NORTH DAKOTA Cavalier Co. Storlie Twp. 13/7/54 (LACM); NORTH DAKOTA Cavalier Co. Fremont Twp. 7/9/54 #130 & #144 Don Sather (LACM); NORTH DAKOTA Cass Co. 10 Harwood Twp. X-10-36 C. Schonberger (FMNH); NORTH DAKOTA Pembina Co. Pembina VII-14-1949 EL Krause (LACM); NORTH DAKOTA Ramsey Co. Twp.153R 65S. 18 VIII-1-1951 #878 PB Kannowski (LACM); SOUTH DAKOTA Pennington Co. (Black Hills) Hill City Sept. 6, 1933 Creighton (LACM); SOUTH DAKOTA Todd Co. Okreak 21-VII-1941 HT Dalmat (LACM); WISCONSIN Bayfield Co. Chequamegon N.F. 46.6168N 91.2122 W Large, rotten jack pine log. 19 July 2013 J.C. Trager; CANADA ONTARIO Renfrew Co. Arnprior 1914 Wasmann (CAS).

Polyergus mexicanus **new status**

Figures 12, 13, 14

Polyergus rufescens subsp. *mexicanus* Forel 1899: 129. Syntype workers: MEXICO, locality not specified [MHNG] (examined). **New status**.

Polyergus rufescens subsp. *breviceps* var. *silvestrii* Santschi 1911: 7. Unavailable name; CALIFORNIA Yosemite (4 workers, 3 males, presumably in MHNG (not examined).

Polyergus rufescens laeviceps Wheeler 1915: 420. Syntype workers: USA, CALIFORNIA Marin Co. Mt. Tamalpais [MCZ, red syntype label 22972] (examined). **New Synonymy**.

Polyergus rufescens umbratus Creighton 1950: 560 (first available use of *Polyergus rufescens breviceps* var. *umbratus* Wheeler 1915: 419). Syntype workers: USA, CALIFORNIA, Santa Cruz Co., Brookdale [MCZ, red syntype label 22972; CAS, red MCZ syntype label 22972; USNM, 57659] (MCZ, CAS material examined). Incorrect synonymy under *P. breviceps* by Wheeler 1968:163. **New Synonymy**.

Polyergus rufescens subsp. *breviceps* var. *fusciventris* Wheeler 1917: 555 (part). Unavailable name; following material referred here: USA, COLORADO, El Paso Co. Pikes Peak [MCZ 21738] (examined).

Syntypes (N=6 on 3 pins) [MHNG] HL 1.52–1.62 (1.57), HW 1.45–1.60 (1.54), SL 1.08–1.13 (1.09), ½ VeM 0–1 (0.33), ½ PnM 5–6 (5.60), WL 2.20–2.40 (2.29), GL 2.04–2.40 (2.26), HFL 1.58–1.66 (1.62), CI 95–99 (98), SI 68–74 (71), HFI 104–112 (106), FSI 143–154 (148), LI 3.70–4.00 (3.86), TL 5.76–6.34 (6.12).

Measurements (N=122) HL 1.28–1.96 (1.57), HW 1.24–1.92 (1.53), SL 0.94–1.36 (1.11), ½ VeM 0–3 (rarely, 5+) (1.20), ½ PnM 3–9 (6.77), WL 1.92–2.80 (2.31), GL 1.34–2.68 (2.17), HFL 1.32–1.96 (1.64), CI 91–103 (99), SI 65–81 (73), HFI 95–121 (107), FSI 134–161 (146), LI 3.24–4.76 (3.85), TL 5.01–7.36 (6.02).

Worker description. This is the most widely distributed and most variable North American *Polyergus*, and accounts for most literature records of "*breviceps,*" other than the cited works of Howard Topoff and his students (regarding *topoffi*). Head variable in shape by region, but locally less so, subquadrate with nearly straight sides curving-convergent toward the vertex, to round-sided and convergent toward the mandibles (pomoid) or occasionally nearly suborbicular in outline, HL usually slightly greater than HW, to HW very slightly broader than HL, the latter corresponding with more rounded sides; vertex pilosity of 0–10 macrosetae (> 5 is uncommon); scapes not reaching vertex corners by about 2X their maximum width, curved, clavate in the apical third; HFL roughly equal to HL to slightly longer (rarely up to 1.2X, especially on West Coast); vertex weakly concave in full face view, corners often without erect setae, or each vertex corner may have 1–3 (up to 5) erect setae; pronotum with 4–10 (rarely up to 18) dorsal erect setae; mesonotum with profile flat or at most weakly convex for most of its length, but often convex and bulging in samples from along the West Coast and southwestern Canada ("*umbratus*" form), and occasionally inland samples; propodeum evenly rounded; petiole with sub-parallel, straight to slightly rounded sides; petiole about as broad as propodeum (above metapleura) in postero-dorsal view; petiolar dorsal margin nearly flat, or faintly convex and medially flattened, occasionally shallowly emarginate; first tergite densely pubescent; first tergite pilosity in 3 or 4 transverse arrays but concentrated in the anterior third; first tergite pilosity flexuous, suberect to subdecumbent.

Head glossy in many specimens from California, Arizona, and Mexico, decreasingly so eastward and northward, thus over most of the population weakly shining, even becoming matte in Canada and the Dakotas; mesonotum matte dorsally and somewhat to notably shining laterally, rarely entirely matte; gaster somewhat shining beneath pubescence and shinier laterally, where pubescence is dilute.

Color mostly red with infuscation of posterior portions of tergites (sometimes entire tergites, especially Canadian provinces and the Dakotas), and with slightly darker legs; pilosity browner than prevailing body color; pubescence gray (never yellowish as in *P. breviceps*).

Discussion. Forel erred when he characterized the types of this species as lacking pilosity. The five specimens of the type series, though their pronota and gastral tergites appear hairless, bear the darkly pigmented impressions of macrosetal bases typical in this genus. These impressions come in an array and in numbers within the range of macrosetal counts of other specimens belonging to this species that are in full possession of their macrosetae.

This species, described from an undetermined mountain locality in Mexico, now turns out to be the most widely distributed member of the species group, all called *breviceps* by Creighton (1950). During my early sorting of specimens (and for a long time thereafter), I tried to associate samples with the types of *fusciventris, laeviceps,* and *umbratus*, as well as a fluctuating number of "new species," but as the study progressed, there was an accumulating residue of samples that seemed transitional, or in which some members of a colony sample appeared to be one "species" and others a different "species," rendering them non-differentiable. The morphology of this widely distributed species does have some notable geographic trends:

- Samples from Mexico, Arizona (typical *mexicanus*) and the US and Canada west of the Rocky Mountains (*mexicanus sensu stricto*, "*laeviceps*" and "*umbratus*") most often have at least moderately shiny heads. Samples with *subpolita* and *neogagates* group hosts from southern and central coastal California, described as "*laeviceps*" by Wheeler, average the smallest and have on the average, proportionally the smallest, roundest, shiniest heads. It may be noted here that these and all other samples associated with *F. neogagates*-group hosts average smaller than the rest of the species' populations.
- Samples from the Santa Cruz Mts. and Sierra Nevada of Central California, to British Columbia, Idaho and western Alberta ("*umbratus*") often have convex ("bulging") mesonotal profiles. These samples match Wheeler's (1915) "*umbratus*", but curiously, just a year after describing this taxon, even Wheeler (1916) failed to recognize it when studying rather typical "*umbratus*" near Lake Tahoe (vouchers examined). An unpublished study (U. C. Berkeley Ph.D. dissertation, Candice W. Torres, personal communication) shows the California populations are distinct genetically from those east of the Sierra Nevada, but I have been unable to find consistent biological or morphological characters to distinguish them.
- Samples from north of southern Arizona and from eastern California and the Rocky Mountains eastward most often have less shiny heads. This is especially true of the populations of higher elevations in the Rockies, and those of the northern Great Plains and the Canadian prairie provinces.
- Samples from the Dakotas and Canadian prairie provinces are often a bit smaller than average, and bicolored, with orangey foreparts and partially dingy brown gasters, superficially resembling *P. bicolor*, but always more pilose. Even in this region, many specimens (often nest mates of bicolored individuals) are robust with heads a little narrower than long and nearly all red, like those from farther south and southwest. The bicolored samples from North Dakota led the Wheelers (1963), without the benefit of measurements and pilosity patterns observed in this study, to conclude that *bicolor* was yet another synonym of the catch-all taxon *breviceps, sensu lato*, but *bicolor* from the Dakotas can easily be recognized by pilosity and habitat characteristics (no to sparse pilosity, moist and forested habitat).
- Finally, samples from the New Mexico and Colorado Front Range and foothills ("*silvestrii*" Santschi[?], also called "*umbratus*" by Gregg 1963, but differing in their less convex mesonota from Wheeler's West Coast form) trend a bit larger than samples from elsewhere in the west, and this trend continues eastward, such that those from KS, IA, SD, IL, MO, AR, and western IN are conspicuously larger than western *mexicanus* or any other *breviceps*-complex species. These latter are associated with the large host species, *F. subsericea.*

In the upper Mississippi drainage south of MN, *P. mexicanus* is easily distinguished from *P. breviceps* by its larger size, silvery gray pubescence, and association with *F. subsericea*, contrasting with *P. breviceps*' smaller size, greater hairiness, yellowish pubescence and its association with *F. montana.* The greatest difficulties in recognizing *mexicanus* arise in the Dakotas, where it is sympatric with both *P. bicolor* and *P. breviceps*, and in southern Arizona and Mexico, where it is parapatric (possibly very narrowly sympatric) with *P. topoffi*. Where *P. mexicanus* occurs in parapatry with *P. topoffi*, the two are separated by elevation and host species. *Polyergus topoffi* has longer appendages and parasitizes *F. gnava* and other warm-climate *Formica* species, while *P. mexicanus* occurs at higher elevation, using montane conifer forest *Formica* hosts. Though distinct in Arizona and Mexico (character divergence), in the Midwest the proportions of *P. mexicanus* come very close to those of *P. topoffi* (character convergence), but *P. mexicanus* has on average shorter appendages throughout its range, pointing to the value of measuring several specimens from good samples. *Polyergus breviceps* averages smaller and consistently more pilose, usually most easily seen by examining the vertex pilosity. Where there is broad distributional overlap of the latter two species in the Rockies and the upper Mississippi Valley, careful study of morphology and metrics of 5 or more individuals per colony will give greater assurance of proper identification.

In more open habitats (fields, prairie reconstructions) in eastern Missouri, I have often found colonies of *P. mexicanus-F. subsericea* interspersed with, and within raiding distance of colonies of *P. lucidus-F. incerta*, and it is perhaps more often found among *F. rubicunda-F. subsericea* and/or *F. subintegra-subsericea* colonies in open woodland habitats. I have directly observed and seen indirect evidence of *F. subintegra* attacking and even bringing home pupae of *P. mexicanus*, as follows: One *F. subintegra-F. subsericea* colony observed in Missouri contained a contingent of a few dozen *P. mexicanus* workers that raided separately and later in the afternoon than the dulotic *Formica* whose nest they inhabited.

On two occasions in Missouri, I have observed *mexicanus* raid colonies of *F. pallidefulva*-group species. In contrast to their typically non-lethal interactions with their normal hosts, many workers and the queen of these non-host species were killed, and both killed adults and some live brood were carried home. The brood of these non-host *Formica* never developed to adulthood in the *mexicanus* nests. In effect, the usually strictly dulotic *Polyergus* became predators.

Natural history. Forel (1899) described this species from specimens collected in "Mexico". The specimens were collected by Brinkmann, who made other collections in the mountains of Durango that were passed on to Forel (P. S. Ward, pers. comm.), so it seems very likely the series was collected from a montane conifer forest there, similar to the podzolic soil conifer forests it inhabits in western USA. A sample collected by Creighton (at LACM) near el Salto, Durango, Mexico, has workers very similar to the MHNG types, and with *F. cf. occulta* host workers, as with southern Arizona samples. Southern samples are from relatively high altitude, with Chiricahua Mts. samples all from above 2200 m, a Vergel, Chihuahua, MEX sample came from about 2800 m (in an open conifer forest), and one from Nevada at a surprising 3200 m. To the north, this protean species is found at lower elevations and in various, mesic, open woodland or grassland-woodland mosaic habitats, but not in moist, closed-canopy forest (though it may occur in natural gaps and in clear-cuts within these), and only occasionally in open prairie. This is characteristically a species of woodlands with little or no shrub layer, usually of oak, oak-pine, or pine in the US Midwest, Ozark Hills and West Coast, and of airy conifer woodlands in the western mountains. It is also found in grassland-woodland ecotones, and prairie groves. Some IL and WI samples came from sandy prairie openings among sandy-soil black oak savannas. It occasionally nests in windbreak plantings of trees, and in less tended areas of parks, cemeteries, gardens and tree-studded lawns, where these are not heavily treated with pesticides.

Forel reported that the host was unknown, but the samples I have seen reveal that this species has a wide variety of hosts in the *F. fusca* and *neogagates* groups. In the southwestern USA and northern Mexico, the host is usually *F. cf. occulta*, a conifer woodland inhabitant that is larger and darker-colored than typical *F. occulta*. From elsewhere, I have studied samples with *F. argentea, F. podzolica, F. subsericea, F. fusca (marcida & subaenescens), F. accreta, F. microphthalma,* true *F. occulta, F. neoclara, F. pacifica, F. neorufibarbis, F. hewitti, F. neogagates, F. manni,* and *F. vinculans*. Moffett (2010) vividly describes and illustrates raids of this species (as *P. breviceps*) on *F. argentea* in eastern California.

Distribution of studied specimens. Types—MEXICO, presumably Durango (no further info); Chihuahua, El Vergel.

ARIZONA Apache Co. Hannagan Meadow 33°38.5'N 109°19.5'W 9080' #3216 21-VIII-2003 RA Johnson (LACM); ARIZONA Cochise Co. Barfoot Tr.1995 45/95 & 47/95 Savolainen (JCTC); ARIZONA Cochise Co. Chiricahua Mts. Rustlers Park 11.9km 260°W Portal. 2519m 31°54.63'N 109°16.23'W pine-fir-woodland 08.VIII.2007 #59 JCT (JCTC); ARIZONA Nevada Co. Indian Pine 2170 m. under rock VIII-28-64 P Rauch (LACM); ARIZONA Pima Co. Mt. Lemmon Aug. 07 J Bono (JCTC); ARIZONA Pima Co. Mt. Lemmon Aug. 07

J. Bono (JCTC); CALIFORNIA El Dorado Co. 16 km E Georgetown 38°55'N 120°39'W 1120 m #2166-S 19.Aug.1988 J. Longino (JTLC); CALIFORNIA El Dorado Co. El Dorado NF Desolation Wilderness 38°49'N 120°07'W 6500' 1800hr 10.VII.1999 #AWO641 A Wild (JCTC); CALIFORNIA Nevada Co. Sagehen Creek 1920m 39°26'N 120°14'W 13-15-VII-2000 #1168 AL Wild (JCTC); CALIFORNIA Nevada Co. Sagehen Crk. CWT #s99, 100,103, 104, 105 CW Torres (JCTC); CALIFORNIA (Placer or Butte Co?) Big Bend 159/97 Savolainen (JCTC); COLORADO Boulder Co. Boulder Flagstaff Mt. VII-7-28 W.S.Creighton (LACM); COLORADO Elbert Co. Cedar Point 1998 Savolainen 90/98 (JCTC); COLORADO Teller Co. Florissant 7-29-41 Wm. Buren (LACM); COLORADO Weld Co. Pawnee Nat'l Grassland Short grass prairie. 15 Aug. 1982 JC Trager (5); IDAHO Twin Falls Co. Twin Falls 4/29/1932 ACCole (LACM); IOWA Story Co. Ames Aug. 1, 1939, Aug. 5, 1939, Aug. 9, 1939, Aug. 13, 1939, Aug. 14, 1939, VIII-12-40 W Buren (LACM); INDIANA Tippecanoe Co. West Lafayette. July, 2008 pitfall trap C. Wang; IOWA Story Co. Ames Aug. 1-14, 1939 W. Buren (LACM); IOWA Story Co. Ames 8-12-40 W.Buren (LACM); KANSAS Jefferson Co. native prairie J Foster 27 July '94 (JCTC); MINNESOTA Crow Wing Co. Jenkins 7-10-40 W.F. Buren (LACM); MINNESOTA Traverse Co. Wheaton 7-12-40 W.F. Buren (LACM); MISSOURI Franklin Co. Meramec S.P. 416/95 1995 Savolainen (JCTC); MISSOURI Franklin Co. Shaw Nature Reserve Mound in pine plantation. (Numerous collections 1989-2011) JC Trager (JCTC); MONTANA: Ravalli Co. Darby Bitterroot N.F. Doug. Fir, ponderosa 20 Sept. 1995 Lubertazzi (JCTC); NEVADA Elko Co. Pole Canyon E. Humbolt Mts. July 38-31, 1934 WSCreighton (LACM); NEVADA Elko Co. 19-Aug.-77 G&J Wheeler (LACM); NEVADA Elko Co. Spruce Mt. Site Burn, Phase 1 40.51ȓN 114.79ȓW Ex. Pitfall trap 20 July 2006 (JCTC); NEVADA Elko Co. South Ruby Site Control, Kphase 1 40.07ȓN 115.65ȓW Ex. Pitfall trap #14111 19 July 2006 (JCTC); NEVADA Elko Co. South Ruby Site Control, Kphase 1 40.07ȓN 115.65ȓW Ex. Pitfall trap #14117 19 July 2006 (JCTC); NEVADA Eureka Co. Seven Mile Site Control Phase 1 39.20ȓN 116.53ȓW ex. Pitfall trap 19 July 2006 (JCTC); NEVADA Storey Co. 8 mi. NE Virginia City Frog Quarry 30-VI-1951 J. LaRivers (LACM); NEVADA Washoe Co. Hwy. 27 Mt. Rose 8000' 15-VI-70 #1086 G&J Wheeler (LACM); NEVADA Washoe Co. Little Valley 30-VII-72 #2499 G.&J. Wheeler (LACM); NEVADA Washoe Co. Mt. Rose 2682 m. elev. RRS77-41 30.VI-77 RR Snelling, CG&JN Wheeler (LACM); NEVADA: White Pine Co. T15NR622 7500' 14-vii-1970 #1315 G.&J. Wheeler (LACM); NEVADA: White Pine Co. 7000' 25-v-75 G.&J. Wheeler (LACM); NEW MEXICO Colfax Co. Cimarron, Cimarron Canyon Jul. 26,1952 #109 A.C. Cole (LACM); NEW MEXICO San Miguel Co. Beulah Sapello Canyon 8000' Jul. 22,1952 H-50 AC Cole (LACM); NORTH DAKOTA Bottineau Co. Pelican Lake. 1997 80/97 Savolainen (JCTC); NORTH DAKOTA Emmons Co. T136NR87W Sec. 28 VI-16-55 G. & N. Wheeler; NORTH DAKOTA Grand Forks Co. Inkster 1997 Savolainen 73/97 (JCTC); NORTH DAKOTA Pembina Co. Glasston VII-19-1949 #84 E.L.Krause (LACM); NORTH DAKOTA Pembina Co. Neche VII-2-1949 #12 & VII-4-1949 #18 E.L.Krause (LACM); NORTH DAKOTA Pembina Co. Walhalla vii-22-1949 #7 E.L.Krause (LACM); NORTH DAKOTA Rolette Co. Dunseith 87/1997 Savolainen (JCTC); SOUTH DAKOTA Pennington Co. Black Hills. Hill City Sep. 6,1935 Creighton (LACM); UTAH Cache Co. Logan. 16 Aug, 08. ESG Titus (LACM); UTAH Cache Co. Logan. 22.6.03. ESG Titus (LACM); UTAH Kane Co. 6 mi. N. Bryce Nat'l Park 2000 G Snelling (JCTC); UTAH Salt Lake Co. Midvale 9-9-52. G.F. Knowlton (LACM); UTAH Salt Lake Co. Salt Lake City 1932 GF Knowlton; UTAH Tooele Co.Uinta Mts. Bassets Spring Aug. 23-26, 1934 WS Creighton (LACM); UTAH Tooele Co. Uinta Mts. Deep Creek (now, =Ibapah) Aug. 27, 1934 WS Creighton (LACM); WASHINGTON Kittitas Co. Snoqualmie Pass E Slope 47°22'N 121°22'W 2511' Elev 20/Sep/2004 JL Smith & DB Moore (JTLC); WASHINGTON Skamania Co. Mt. St. Helens 1370m 11/Aug/1981 RSugg (JTLC); WASHINGTON Stevens Co. 21km N Colville 890m 48°44'N 117°53'W #5590 26/Jun/2005 JLongino (JTLC); WASHINGTON Whatcom Co. White Rock Spring VII-14-30 WM Mann (LACM); WASHINGTON Whitman Co. Pullman 22-Mar-1908 WM Mann (LACM); WASHINGTON Whitman Co. Pullman WM Mann May 19, 1909 (LACM); WASHINGTON Yakima Co. Mt. Rainier Yakima Pass VIII-23-34 A.J. Melander (LACM); WASHINGTON Yakima Co. Morse Creek & HWY 410 46°54'N 121°25'W 1200m #3916 16/Aug/1998 JLongino (JTLC); WASHINGTON Whitman Co. N end Rock Lake 47°14'N 117°35'W 600 m. #4106 10.Aug.1999 JLongino (JTLC); WASHINGTON Yakima Co. 15km NW Naches, Cleman Mt. 46°49'N 120°51'W 1500m #4566 25/Aug./2001 JLongino (JTLC); WASHINGTON Yakima Co. 15km NW Naches Cleman Mt. 46°49'N 120°51'W 1500m #4566 25. Aug.2001 JLongino (JTLC); WASHINGTON Yakima Co. 18.5km E Chinook Pass 46°53'N 121°17'W 1000m #6004 11.Jun.2007 JLongino (JTLC); WYOMING Teton Co. Teton Nat'l Park Aug. 9-17, 1955 A.C.Cole

CANADA ALBERTA Sturgeon Co. Red Water Natural Area. 53°56'27.66"N 112°57'17.19"W Jack pine, sand hills. 24 July-3 Aug. 2010 James Glasier; CANADA BRITISH COLUMBIA: Cortex Is. Channel Rock 50°06'N 125°02'W 30m #5641 19-21/Aug/2005 J Longino (JTLC); CANADA MANITOBA Morden 3 km E, 19 km S. 5 Sept. 1993 WBP-F205 WB Preston (JCTC); MEXICO CHIHUAHUA Mpio. Belleza 14 Abril, 1981 Wm. & E. Mackay 4772 (JCTC); MEXICO DURANGO 4 m. W of El Salto 20-Mar-53 WS Creighton (LACM).

Polyergus topoffi **new species**

Figures 15, 16, 17

Polyergus rufescens subsp. *breviceps* var. *montezuma* Wheeler 1914: 56. Unavailable name; following material referred here: MEXICO, HIDALGO Pachuca [MCZ; 1 gyne, 3 workers, and host *Formica*; red syntype label 9221] (examined, misspelled as "montezumia" on handwritten accompanying label); [USNM, 59726] (not examined; misspelled as "montezumia" in USNM type database).

Holotype worker: USA, ARIZONA, Cochise Co., Portal. Topoff property, N31°54.578 W109°08.909 CWT068 1472 m. Mesquite-Acacia thicket. JC Trager & CW Torres (MCZ)

Paratype workers: Same data as holotype [MCZ, CAS, LACM]

Holotype [ARIZONA, Cochise Co., as above] HL 1.62, HW 1.56, SL 1.22, ½ VeM 1, ½ PnM 9, WL 2.42, GL 2.40, HFL 1.80, CI 96, SI 78, HFI 115, FSI 148, LI 4.04, TL 6.44.

Paratypes (N=5) [ARIZONA, Cochise Co., as above] HL 1.56–1.64 (1.60), HW 1.52–1.60 (1.54), SL 1.20–1.24 (1.22), ½ VeM 0–1 (0.55),, ½ PnM 6–9 (7.20), WL 2.32–2.42 (2.39), GL 2.16–2.40 (2.24), HFL 1.72–1.80 (1.76), CI 95–98 (97), SI 75–82 (79), HFI 111–117 (1.14), FSI 139–148 (144), LI 3.88–4.04 (3.98), TL 6.12–6.44 (6.22).

montezuma material (N=3) [MCZ] HL 1.48–1.60 (1.53), HW 1.50–1.53 (1.50), SL 1.20 (all 3), ½ VeM 0 (all 3),, ½ PnM 12–15 (13.67), WL 2.36 (all 3), GL 2.16–2.24 (2.20), HFL 1.64–1.72 (1.68), CI 96–100 (98), SI 78–81 (80), HFI 111–112 (1.12), FSI 137–143 (140), LI 3.84–3.9 (3.89), TL 6.08–6.12 (6.09).

Measurements, exclusive of *montezuma* syntypes(N=31)) HL 1.48–1.68 (1.60), HW 1.40–1.64 (1.53), SL 1.16–1.28 (1.23), ½ VeM 0–1 (0.23), ½ PnM 4–9 (6.87), WL 2.16–2.52 (2.37), GL 1.84–2.56 (2.20), HFL 1.68–1.88 (1.77), CI 93–100 (96), SI 75–86 (80), HFI 108–121 (116), FSI 139–155 (145), LI 3.68–4.20 (3.97), TL 5.54–6.64 (6.16).

Worker description. Superficially rather similar to *mexicanus*, but slightly more gracile, and nearly restricted to a Mexican distribution. Head nearly rectangular or quadrate, straight-sided anterior to eyes, with vertex corners rounded, HL usually a bit greater than HW; with vertex pilosity lacking or up to 2 setae; scapes not reaching vertex corners by about 1.5 maximum scape widths, notably clavate in the apical third; pronotum with 8–22 dorsal erect setae (but see

Discussion. of *montezuma* "types", below); mesonotum with profile flat or only slightly convex for most of its length, with a short posterior declivity; propodeum evenly rounded with dorsal and declivitous faces, especially in smaller workers, usually at >90° angle; petiole straight-sided above spiracles, sides parallel or only slightly converging dorsad, flowing seamlessly into the semicircular petiolar dorsum; first tergite densely pubescent, pubescence very fine; first tergite pilosity evenly distributed or slightly denser anteriad, some setae flexuous near front of tergite, but most weakly flexuous or straight, suberect.

Head matte to weakly shining; mesonotum matte to weakly shining, with scant pubescence; gaster matte to weakly shining beneath pubescence, shinier on sides.

Color mostly tannish-red with infuscation of posterior portions of tergites and slightly darker legs. Mesosomal pilosity usually notably darker than body color, gaster pilosity more reddish; pubescence short and yellowish gray. Only minor individual variation was detected among the Arizona specimens studied, and the Mexican *montezuma* differed only in somewhat more abundant pilosity, but fit perfectly in the middle of the measurement cloud of other specimens measured.

Discussion. Of all the Nearctic species, *topoffi* is the one that most resembles Palearctic *rufescens* in sculpture, pilosity, head shape and appendage length. Where it overlaps with *mexicanus* in distribution, it is distinguished by a less shiny appearance and somewhat more tannish tinge to the base red color, longer scapes and legs, occurrence at lower elevations, and parasitism of different hosts. The scapes are longer than all other *breviceps* group species except *vinosus*. Wheeler's unavailable variety *montezuma*, collected near Pachuca, Hidalgo, Mexico by Mann, belongs in this species, as it fits neatly within middle the range of metrics for Arizona *topoffi* (except with somewhat more abundant pilosity), and also comes from a subxeric, semi-open habitat. The three worker specimens of *montezuma* are more pilose than most Arizona specimens, with 22–26 macrosetae on the pronotum, and the three specimens each possess a few erect macrosetae lower on the sides of the pronotum. The *montezuma* sample is associated with the host species *F. subcyanea*.

Etymology. I name this for Howard Topoff, who with his students has contributed so much to the modern literature on *Polyergus*, and in particular on this species. Howard also has a magnificent colony of this *Polyergus* near his house outside Portal AZ from which holotype specimen and paratypes were collected.

Natural history. *Polyergus topoffi* is relatively well-studied. Studies of a population in the vicinity of Portal, AZ, and at the Southwest Biological Research Station, just 5 miles to the west, make this among the best studied of North American species. Colony foundation, sexual behavior, scouting and raiding of this species are documented in numerous publications by Howard Topoff and his students, under the name *Polyergus breviceps* (Topoff 1982, 1985, Topoff *et al*. 1984, 1985a, 1985b, 1988a, 1988b, 1989, Topoff and Greenberg 1988, Topoff 1990, Topoff and Mendez 1990, Topoff and Zimmerli 1993, Zimmerli and Topoff 1994), and even in National Geographic Society videos made with these authors' cooperation, and at this writing, still occasionally aired on television nature programs. In the Chiricahua Mts. of AZ, the habitat of *topoffi* ranges from riparian desert scrub at 1450 m, to the ecotone of oak-juniper and conifer forest around 1900 m (and higher, in Mexico). It raids after the heat of the day, typically between 17:00 hr and dusk, robbing pupae from the host nests with little resistance and no mortality of the host workers, these known otherwise for their aggressive physical and chemical nest defense. Specimens of Wheeler's var. *montezuma* fit nicely, in metrics, color and surface texture, in the morphological concept of this species. Thus, subtropical, Madrean scrublands and oak woodlands of the Mexican highlands are another habitat of this ant.

Distribution of studied specimens. ARIZONA Cochise Co. Chiricahua Mtns. 2.5km 292° Portal 31°55.92'N 10910.67'W ocotillo-opuntia rocky slope 1600m 4-14-VIII-2005 JT Longino (JTLC); ARIZONA Cochise Co. Chiricahua Mts. Cave Cr. Canyon IX-10-1971 (LACM); ARIZONA Cochise Co. Chiricahua Mts. Cave Creek Canyon Idlewilde Cmpgr. Elev. 4950' #1466 8/4/1988; ARIZONA Cochise Co. S.W.R.S. 1995 Savolainen (1) 75/ 95; ARIZONA Cochise Co. Chiricahua Mts. Piney Canyon 5700' Elev. 31°58.1'N 109°19.2'W 3.VIII.1991 #11 RA Johnson (RAJC); ARIZONA Cochise Co. Chiricahua Mts. SW Research Sta. 31°53.0'N 109°12.3'W 5400' Elev. 9.VII.1993 #249 RA Johnson (RAJC); ARIZONA Cochise Co. Southwest Rsch. Section. 7-August-1986 H. Topoff P3, P5 (JCTC); SPCover (MCZ); ARIZONA Cochise Co. Chiricahua Mts. SWRS 5 m. W Portal Oak-Pine-Juniper Forest S of Station Elev. 5500' SPCover #1472 (MCZ); ARIZONA Cochise Co. Chiricahua Mts. 6 m. W Portal 21-29 July and (?) Aug. 1983 M. Pagani; ARIZONA Cochise Co. Portal July 3, 1956 #370 AC Cole (LACM); ARIZONA Cochise Co. Wilcox. Cochise Stronghold July 30,1954 #155,124,155 AC Cole (LACM); ARIZONA Gila Co. Jones Water Camp 14 July 1986 004 GC Snelling (JCTC); ARIZONA Cochise Co. Coronado NF Cave Creek Ranch 31.90300-109.13495±5m 1491m 31.VIII.2011 Zach Lieberman (JCTC); ARIZONA Cochise Co. Chiricahua Mtns. 9.3km W Portal 1900m 31.89956-109.23863±200m oak-pine-juniper woodland 10-VII-2011 Zach Lieberman (JCTC); ARIZONA Cochise Co. Chiricahua Mtns. 10.5km W Portal E Turkey Creek 31.90882-109.25211±200m 1960m pine-oak forest/Douglas fir 10.VIII.2011 Zach Lieberman (JCTC); ARIZONA Gila Co. Mazatzal Mtns. Pigeon Springs 33°42.5'N 111°20.1'W 5600' Elev. #112 22.v.1993 RA Johnson (RAJC); ARIZONA Santa Cruz Co. Patagonia Mts. 2000 Savolainen 12/00 (JCTC); ARIZONA Santa Cruz Co. Hershaw Creek 31°29.5'N 110°41.2'W 4550' Elev. #2207 26.VIII.1999 RA Johnson (RAJC); MEXICO. HIDALGO Pachuca. W. M. Mann.

Polyergus vinosus **new species**

Figures 18, 19, 20

Holotype worker USA, CALIFORNIA Millard Canyon, San Gabriel Mts. [LACM.]

Paratypes 2 gynes, 1 male, 4 workers (One of the latter possibly an ergatoid.) [LACM]

Holotype HL 1.39, HW 1.34, SL 1.34, ½ VeM 0, ½ PnM 3, WL 2.16, GL 1.93, HFL 1.72, CI 96, SI 100, HFI 128, FSI 128, LI 3.55, TL 5.48.

Paratype worker measurements (N=4) HL 1.39–1.64 (1.51), HW 1.34–1.60 (1.46), SL 1.32–1.40 (1.37), ½

VeM 0, ½ PnM 3–6 (3.80), WL 2.16–2.40 (2.27), GL 1.64–2.44 (2.02), HFL 1.72–1.95 (1.83), CI 95–98 (97), SI 88–100 (94), HFI 122–128 (125), FSI 128–139 (134), LI 3.55–4.04 (3.78), TL 5.48–6.48 (5.81).

Measurements (N=36) HL 1.23–1.67 (1.43), HW 1.20–1.60 (1.40), SL 1.14–1.41 (1.27), ½ VeM 0–2 (0.11), ½ PnM 0–7 (3.43), WL 1.93–2.48 (2.18), GL 1.64–2.82 (2.14), HFL 1.55–2.00 (1.73), CI 95–103 (98), SI 80–100 (91), HFI 113–133 (124), FSI 128–142 (136), LI 3.23–4.15 (3.60), TL 4.26–6.97 (5.69).

Worker description. Head truncate-ovate, its length usually slightly greater than breadth; scapes long for the *breviceps* species group (SI usually 85–95, never < 80), nearly reaching or even surpassing vertex corners, weakly clavate or gradually thickening in the apical third; pronotum with 0–6 (less often, up to 12, especially Santa Cruz Island population) dorsal macrosetae; mesonotum with profile weakly convex for most of its length, notably convex and "bulging" in the largest workers; propodeum subquadrate with a rounded angle; petiole sides rounded and converging dorsad, petiolar dorsum flat or even shallowly concave; first tergite densely pubescent; first tergite pilosity a relatively sparse 6–20 flexuous, mid-anterodorsal, suberect macrosetae and sometimes a few widely spaced ones in the posterior tergal half.

Head weakly shining; mesonotum weakly shining beneath fine gray pubescence; gaster weakly shining beneath fine gray pubescence.

Color mostly orange-red to wine red with scarcely any infuscation of gaster or appendages.

The most significant variation in this species is the greater pronotal pilosity of the Santa Cruz Island population, with ½ PnM 6–12, contrasting with 1–4 (rarely 5 or 6) on the mainland. Workers of Baja California are paler tan-orange in color (as in Fig. 6, possibly faded in preservation), and have a more rounded propodeal profile.

Etymology. "*Vinosus*" is Latin for red-wine-colored. Somewhat ironically, much of its habitat may be threatened by the conversion of its southern California oak woodland habitat to vineyards.

Natural history. This species is endemic to the Californian vegetation zone of southern CA and northern Baja California, Mexico, and is also found on Santa Cruz Island, CA. *Polyergus vinosus* is a species of mature chaparral, coast live oak woodland and savanna, rocky wooded canyons and oak-gray pine woodlands of the southern California coast hills. As far as known, its exclusive host species is *F. moki*, and the nests have the host species' usual cryptic placement among rocks, often near streams or along wet-weather drainages, and sometimes with a lightly thatched superstructure. Only a few raids have been observed, but from unpublished observations by Les Greenberg (U. C. Riverside, pers. comm.) and Geoff Trager (then a student at UC Santa Barbara, pers. comm.), we know that the raids take place in early to mid summer, in the latter half of the afternoon. The raiding season may begin and end earlier than that of species from colder, summer-rainy climates.

Distribution of studied specimens. CALIFORNIA Los Angeles Co. Tanbark Flats. San Gabriel Mts. VI-21-1956 GI Stage, coll. (LACM); CALIFORNIA Los Angeles Co. San Gabriel Mts. Millard Canyon. Aug. 1953 R.H. Crandall (also 7-16-1955 R.H. Crandall, LACM); CALIFORNIA San Bernardino Co. Lake Arrowhead. 30-VI-00 L. LaPierre (JCTC); CALIFORNIA Monterey Co. Limekiln Cr. T215R4E Sec. 34 SW 1070m 11/Feb/1984 J Longino (JTLC); CALIFORNIA San Diego Co. Mr. Laguna SOSU Observatory 9 June 72 JNH 78r J.H. Hunt (JCTC); CALIFORNIA San Diego Co. Laguna Mtn. 1342 m. under rock, pine meadow 26-v-2010 L. Davis (JCTC); CALIFORNIA Santa Barbara Co. Figueroa Mtn. under board, open pine woodland. April, 1979 JCT (JCTC); CALIFORNIA Santa Barbara Co. T4NR25W Sec. 16 1500' Chaparral #303 19/May/1985 J Longino (JTLC); CALIFORNIA Santa Barbara Co. Santa Cruz Island 0.5 km W Station 24 June 1984 S. Dinh & J. Nelson (LACM); CALIFORNIA Santa Barbara Co. Santa Cruz Isl. Forager Riparian woodland 23 June 2010 L Greenberg (JCTC); MEXICO, BAJA CALIFORNIA Sierra Juarez 15.8 m. S La Rumorosa 32°19.1'N115°59.5'W 4900' 25-III-2001 #2310 RA Johnson (RAJC).

Polyergus samurai group

This group consists of two species characterized by Asian distribution east of the 90th Meridian, blackish body color (may fade to dark brown in preserved specimens), rectangular to slightly acute propodeal angle, and dorsally tapering recurved petiolar node. Both have a less compressed, more *Formica*–like clypeus than other *Polyergus* species, perhaps a more basal character state.

Polyergus samurai

Figures 21, 22, 23

Polyergus rufescens samurai Yano 1911: 110. Syntype worker, gyne: JAPAN, Tokyo. [MCZ, red syntype label 21739] (examined, but not measured due to dermestid damage).

Polyergus samurai: Emery, 1925: 269; Wheeler, 1927: 3; Imai, 1966: 125 (karyotype); Terayama et al. 1993: 511 (ergatoid queen); Kupyanskaya, 1990: 209 (in eastern Siberia).

Polyergus samurai mandarin Wheeler 1927: 4. Syntype workers: CHINA, Tsinghua nr. Peking (= Pinyin: Qinghua nr. Beijing) [MCZ, red syntype label 21740] (examined). **New Synonymy**.

Measurements (N=24) HL 1.40–1.76 (1.56), HW 1.29–1.64 (1.47), SL 1.12–1.32 (1.22), ½ VeM 2–5 (2.92), ½ PnM 3–8 (5.67), WL 2.12–2.62 (2.41), GL 1.84–2.40 (2.15), HFL 1.68–2.04 (1.85), CI 92–97 (94), SI 76–93 (83), HFI 121–140 (126), FSI 143–159 (1.53), LI 3.52–4.38 (3.97), TL 5.40–6.72 (6.13).

Worker description. Head narrowly hexagonal (truncate-ovate), length greater than breadth; with moderate vertex pilosity; scapes about reaching vertex corners, gradually thickening apically in distal half; pronotum with 5–16 erect macrosetae; mesonotum with profile flat for most of its length, with short posterior declivity; propodeal profile subquadrate, with concave posterior declivity; petiole more or less straight-sided above spiracles or convergent dorsad, petiolar dorsum flat or convex, shallowly or not at all emarginate; first tergite densely pubescent; tergite pilosity relatively scant compared to other *Polyergus*, concentrated in anterior-lateral portions, weakly flexuous, relatively widely separated.

Head matte; mesonotum matte; gaster matte, sometimes weakly shining on the sides.

Color uniform dusky reddish brown or with a slightly darker gaster; with dusky yellow-brown appendages; pilosity yellowish brown.

Discussion. There was only minor variation among individuals detected among the specimens studied. Wheeler (1927) noted that the Chinese population he described as the subspecies *mandarin* was possibly blacker than the Japanese population. However, a small sample of workers from Beijing I obtained during this study had coloring indistinguishable from Japanese samples, and photographs sent to me of worker and male specimens from Hebei look typical, including the starkly white appendages of the male.

Polyergus samurai is probably not sympatric with any other species. It is easily distinguished from most other *Polyergus* species by its dark brown color, appearing nearly black in the field. It is closest to *nigerrimus,* a smaller, darker, shinier species that lives in arid regions to the west of the range of *samurai*. *Polyergus samurai* males are notable for their striking white wings (even the veins are very pale yellow), and whitish appendages, including the mouthparts. Gynes also have white wings, with pale brown veins, and partially light brown appendages. This is in contrast to the dark brown appendages, brownish veins and infuscation of the wings of both sexes of *nigerrimus*.

Etymology. This ant was named for the traditional Japanese warrior class, the "Samurai," presumably by analogy to calling these ants "Amazons" in European languages.

Natural history. This species occurs in humid temperate Asia: Japan, Korea, China and southeastern Russia (*teste* Kupyanskaya 1990). The hosts of *samurai* in Japan are *F. japonica* and rarely, *F. hayashi* and even *F. fukaii* (of the *F. exsecta* group), while the types of "subspecies *mandarin*" were collected with the *F. rufibarbis*-group species *F. glabridorsis*. *Polyergus samurai* is relatively well studied by several Japanese myrmecologists, but is only poorly known in its mainland Asian range. Terayama, et al. (1993) described four ergatoids found in two colonies of *samurai*, reporting they had "a well developed spermatheca", and surmised that they can produce female offspring (though they did not confirm insemination). Hasegawa and Yamaguchi (1994, 1995) reported for this species (and typically for the genus) that raids mostly occurred on warm, sunny days, and mating flights only occurred on sunny days. According to these authors, time of initiation of raids and walking speed of raiders are related to simple environmental variables, especially temperature. Tsuneoka (2008) reported that colonies had a single gyne, housed colony populations of the host *F. japonica* much larger than normal host colonies, and that the larger colony size in the parasite colony resulted in typical nest structure, but larger nest dimensions than those of unparasitized *F. japonica*.

Distribution of studied specimens. CHINA Beijing 3-VII-1987 Changlu Wang (JCTC); JAPAN: HYOGO Pref. Nakano, Yamaguchi-mura, Arima-gun, 14-VIII-1948. M. Azuma (JCTC); JAPAN KANAGAWA Pref. Odawara July 1977 M. Kubota #201 (JCTC); JAPAN KANAGAWA Pref. Odawara 8 Aug.1968 M. Kubota (JCTC) ; JAPAN KANAGAWA Pref. Kawasaki 17-VI-1978 S. Kubota (JCTC); JAPAN TOKYO Pref. Koganei

City 18-VIII-1977 S. Kubota; JAPAN SAITAMA Osato 26-VII-2006, 36°06’N, 139°13'E Toshiaki Nanbu leg. w/ Formica japonica (teste M. Yoshimura); JAPAN Okitsu (Hondo) 8-25-25 Silvestri. Reported from KOREA, but no specimens examined.

Polyergus nigerrimus

Figures 24, 25, 26

Polyergus nigerrimus Marikovsky 1963: 110. Syntype workers, gyne, male: RUSSIAN FEDERATION, TUVA, Kyzyl [ZIN] (not examined), [CAS; additional specimens from the original nest series, 7 workers, gyne, male] (examined). Kupyanskaya 1990: 208 (records from southern Russia, worker illustrated).

Syntypes (N=7) [CASENT, as above] HL 1.32–1.44 (1.40), HW 1.24–1.36 (1.32), SL 1.00–1.06 (1.03), ½ VeM 1–9 (4.71), ½ PnM 5–7 (6.29), WL 2.12–2.20 (2.17), GL 1.76–2.00 (1.93), HFL 1.60–1.68 (1.64), CI 94–96 (94.4), SI 74–81 (79), HFI 119–130 (125), FSI 157–160 (159), LI 3.48–3.60 (3.56), TL 5.24–5.60 (5.49).

Worker description. Smallish, TL averaging 5.5mm; blackish, weakly shining species of the Asian steppes. Head rounded hexagonal (truncate-ovate), its length detectably greater than breadth; with conspicuous vertex pilosity; scapes not reaching vertex, notably clavate in the apical third; pronotum with 10–14 dorsal erect setae; mesonotum with profile flat or very weakly convex for most of its length, with a short posterior declivity; propodeal profile subquadrate, taller than pronotum, with concave declivity profile; petiole with sides round, converging dorsad, petiolar dorsum emarginate; first tergite densely pubescent, with pilosity in 3 or 4 irregular transverse rows, first tergite pilosity gently curved, longer than the distance separating the individual setae.

Head weakly shining; mesonotum weakly shining dorsally, a bit smoother laterally; gaster weakly shining to matte dorsally, somewhat shiny laterally.

Color black to nearly black; legs and scapes dark brown; pilosity gray-brown.

Discussion. This species might be confused only with *samurai*, a more eastern, larger, more gracile, and more matte species. *Polyergus samurai* is more brown than black, and has more yellowish, rather than brown pilosity. Gynes and males of *nigerrimus* are black, somewhat shiny, smaller than gynes and males of *samurai,* with dark brown appendages; wings of both gynes and males have brown veins, and are medially infuscated (wings of *samurai* pale yellow to whitish throughout, with pale veins).

In this study, 7 W, 1 Q, 1 M from Marikovsky’s original collection, and images of workers from Mongolia (at www.antbase.net), were seen. The former were in the private collection of Alfred Buschinger, and are now housed at CAS. Little notable variation was observed in this small series. The characteristics of this species as described by Kupyanskaya (1990) from a wider geographic area confirm the impression of relative uniformity in metric and ecological characteristics. However, Kupyanksaya’s drawing of a *nigerrimus* worker shows abundant pilosity arising from the malar region, quite unlike the pilosity pattern of any *Polyergus* specimens I have studied, and the significance of this is not clear.

Etymology. This name is from the Latin superlative adjective “nigerrimus”, meaning very black or blackest. A hand written label accompanying the series reads “nigricans”, meaning blackish, but this name never reached publication.

Natural history. This ant is found in the shrub steppe lands of Mongolia and adjacent southern Russian Federation, and also might be sought in ecologically similar adjacent parts of northwestern China and perhaps Kazakhstan.

Marikovsky studied *P. nigerrimus* in the summer of 1960. In his description, Marikovsky (1963) noted that the specimens were taken with abundant host workers of *F. candida* in shrub steppe near the Yenisei River. Marikovsky reported a diffuse nest, with 7 entrances over a $10m^2$ area, but only the central one had a well-developed infrastructure and large population, including alates of both sexes, and an ergatoid. He described a raid involving about 400 *nigerrimus* workers, in the “evening when the sun was setting down” and ending during “falling darkness”. Despite attempts by the *F. candida* to bite the raiders and to wrest their pupal quarry from them, the *nigerrimus* simply pushed on home without attacking any of the defending *Formica* workers. Returning *nigerrimus* workers initially placed the stolen pupae in two of the peripheral nests, but later transferred the pupae to the main nest about 0.5m away.

I updated the identification of the host with Marikovsy's sample as *F. candida*, using Seifert's (2004) key. Marikovsky had identified them as *F. gagates*, and Kupyanska (1990) mentions *F. picea* as the host, also a species previously confused with *F. candida.* Kupyanskaya calls this an ant of the steppe, and Antonov (2008) also reports habitat of this ant as the steppe. Its host, by implication, in the Antonov study is *F. candida* (the only abundant potential host at the location). Antonov comments that *nigerrimus* "is extremely rare in natural habitats," but this may be an artifact of collecting intensity. The *F. kozlovi* host record is from a collection made by Martin Pfeiffer in Mongolia (also note Pfeiffer's images of *nigerrimus* at http://antbase.net/htdocs/formicinae/polyergus/polyergus_nigerrimus_marikovsky,_1963.html). Dubatalov (1998) also reports this ant from Mongolia.

Distribution from literature references for *Polyergus nigerrimus.* The type locality is RUSSIAN FEDERATION, TUVA, Kyzyl, (Marikovsky, 1963); also known from RUSSIAN FEDERATION, PRIMORSKIY KRAI, Primorye, 6km E Hasan & Haborovskiy Krai, Novokalachinsk; (Kupyanskaya, 1990); BURIYATIA, Kyakhta (Kupyanskaya, 1990), BURIYATIA, Gusinoozyorsk (Antonov 2008); MONGOLIA TOV Zorgol Mountain N47º10.203' E 106º04.446' (M. Pfeiffer, antbase.net [antbase.net no. 0031]); MONGOLIA AIMAK, 8 km S Ereentsay (Dubatalov, *teste* Kupyanskaya, 1990). None of these samples were examined in this study.

Polyergus lucidus group

This group comprises six, mostly eastern North American species, deep red to orange-red, often with conspicuously darker appendages, and very reduced pubescence and pilosity of the gastral dorsum. All parasitize members of the *F. pallidefulva* group. As a group these have relatively long appendages compared to the more pubescent, western North American species of the *Polyergus breviceps* complex.

Polyergus lucidus

Figures 27, 28, 29

Polyergus rufescens lucidus Mayr 1870: 952. Syntype worker, gyne, male: USA, CONNECTICUT (near Farmington?) [presumably at NMW] (not examined, but apparent syntypes at PMNH well described by Smith, 1947: 152). Forel, 1886: 200; Emery, 1893: 666; Wheeler, 1903: 659 (gynandromorph).

Polyergus lucidus: Dalla Torre, 1893: 214; Wheeler, 1917b: 465; Smith, 1947: 152; Creighton 1950: 557; Wheeler & Wheeler, 1968: 214 (larva).

Types not measured.

Measurements (N=38) HL 1.40–1.76 (1.59), HW 1.38–1.76 (1.53), SL 1.19–1.36 (1.27), ½ VeM 5–12 (7.25), ½ PnM 0–6 (2.67), WL 2.32–2.86 (2.49), GL 2.00–2.68 (2.32), HFL 1.72–2.04 (1.89), CI 93–100 (96), SI 75–91 (84), HFI 114–131 (123), FSI 140–158 (148), LI 3.72–4.62 (4.08), TL 5.72–7.12 (6.40).

Worker description. Head subrectangular to narrowly subtrapezoidal, HL greater than HW, and often widest about half way from eye to vertex (narrowing closer to eye in other *lucidus* group species); with conspicuous vertex pilosity of 10–16 macrosetae (rarely up to 24); scapes not reaching vertex corners by 1–2X maximum widths of scape, scape notably clavate in the apical third; pronotum with 1–8 (12) erect setae; mesonotal profile weakly convex; propodeal profile evenly rounded; petiole with convex sides; petiolar dorsum convex; first tergite lacking pubescence; first tergite pilosity sparse, straight, shorter than the distance separating the setae.

Head somewhat to very shiny; mesonotum shiny; gaster shiny.

Color red, often with infuscation of portions of legs and gastral tip.

Discussion. *Polyergus lucidus* is most likely to be confused with the broadly sympatric *montivagus*, from which it can be distinguished by shorter scapes, greater abundance of vertex and pronotal pilosity, and conspicuously greater shininess. Though I have not seen types, I follow Smith (1947) in the characterization of this species. Smith redescribed the species based on a worker at PMNH, with the same data and collector (Norton) as those described by Mayr.

Etymology. Latin "lucidus" means shining, an appropriate name for Mayr's species, the shiniest of all *Polyergus*.

Natural history. *Polyergus lucidus* is widely distributed from southern New England to Wisconsin, south to the mountain meadows and balds of the Carolinas and the tallgrass prairies of Missouri, matching most of the distribution of its unique host, *F. incerta* (but not seen from Nebraska and Kansas).

This species has been studied on Long Island, NY by Topoff and his students. Kwait and Topoff (1983, 1984) published on its raid organization and emigrations, reporting behavioral patterns familiar throughout the genus. At the same study site, Goodloe and Sanwald (1985) later studied host specificity in what I here report to be *lucidus* and *sanwaldi* with their distinct hosts, *F. incerta* and *F. dolosa* (reported as *nitidiventris* and *schaufussi*), respectively. These authors made the important finding that gynes arising from colonies with one of these hosts were not successfully adopted by the other host species, an early hint to me of their heterospecificity.

Distribution of studied specimens. INDIANA Tippecanoe Co. West Lafayette. 20-VIII-2008 nest in lawn C. Wang; MASSACHUSETTS Plymouth Co. Miles Standish S.F. Mass. Cover 65/2000 (MCZ); MICHIGAN Livingston Co. Edwin S. George Reserve. R. Savolainen 332/95 & 374 95 (JCTC); MISSOURI Franklin Co. Shaw Nature Reserve 18-Sept-2003 JCT (plus numerous other collections through 2011, JCTC); NEW YORK Putnam Co. Putnam Valley, 27-V-941, migrating from nest to body of dead phoebe (!). Col. R. O. Shuster; NEW YORK Suffolk Co. near Medford. mowed field. R. Sanwald 1997 (plus several other collections by R. Sanwald and JC Trager, JCTC); NEW YORK Warren Co. Lake George 22-VIII-1939 #77 Col. A. E. Emerson. (FMNH); NEW YORK Warren Co. Lake George. 28-VI-1945 Col. T. E. Snyder (FMNH); NORTH CAROLINA Watauga Co. Blue Ridge Parkway (no further info, NCSU); OHIO Jackson Co. Scratch Hollow. L. G. Wesson (JCTC); PENNSYLVANIA Chester Co. Malvern. nest in grass 7-Aug-2011 A. Nguyen (JCTC); WISCONSIN Sauk Co. Spring Green Pres. SNA 43º11'58"N / 90º03'32"W. 8-Aug-2005 Jeffrey P. Gruber (WIRC); WISCONSIN Shawano Co. Navarino Wildlife Area 44º39'11"N/88º34'49"W 19-Aug-2001 Jeffrey P. Gruber (WIRC)Sep-2003; WISCONSIN Washburn, Bass Lake T40N R13W s32 1050 ft. MB DuBois (JCTC); CANADA ONTARIO Pinery Prov. Park 1 Sept. 1994 #108 Umphrey 94-108. (JCTC).

Polyergus longicornis new status

Figures 30, 31, 32

Polyergus lucidus longicornis M. R. Smith 1947: 155. Syntype workers: USA, SOUTH CAROLINA, Florence [USNM, 57661] (images examined). **New status**.

Types not measured.

Measurements (N=18) HL 1.60–1.80 (1.71), HW 1.52–1.72 (1.62), SL 1.67–1.89 (1.77), ½ VeM 13–22 (17.78), ½ PnM 0–9 (3.78), WL 2.52–2.88 (2.73), GL 2.08–2.68 (2.34), HFL 2.22–2.56 (240), CI 91–99 (95), SI 101–117 (109), HFI 139–158 (149), FSI 130–144 (136), LI 4.16–4.68 (4.44), TL 6.44–7.32 (6.78).

Worker description. Head truncate-obovate to narrowly subhexagonal, generally more strongly tapering behind than in front of the eyes, HL > HW; with conspicuous and abundant vertex pilosity of 20–40 erect macrosetae; scapes at least equaling to notably longer than head, always surpassing vertex corners, gradually thickening apically, not notably clavate; pronotum with (3) 6–12 (18) erect macrosetae; mesonotal profile flat or very weakly convex for most of its length; propodeal profile evenly rounded, its dorsal and posterior faces indistinct; petiole a little narrower than propodeum, with convex sides, these convergent dorsad; petiolar dorsum convex, not emarginate; petiole in profile tapering and usually slightly recurved dorsad; first tergite very sparsely pubescent or completely lacking pubescence; first tergite pilosity sparse, usually a few on the anterior half, but these often deciduous; the macrosetae weakly flexuous.

Head matte; mesosoma matte; gaster weakly matte.

Color red with infuscation of appendages and posterior portions of tergites.

Discussion. *P. longicornis* is most likely to be confused with *ruber* and especially *sanwaldi*. *Polyergus longicornis* is distinguished from the largely sympatric *ruber* by its more abundant vertex pilosity, ½ VeM 13 + vs. 12 or less, nearly uniformly matte mesosoma and cephalic integument, and parasitism of *F. dolosa* rather than *F. biophilica*. *Polyergus longicornis* is distinguished from the allopatric, more northern *P. sanwaldi* by its proportionally longer scapes and legs, and its slightly narrower head (Fig. 2).

Etymology. Smith coined the name of this ant species as an adjective, from Latin "longus" + "cornus", referring to its long scapes.

Natural history. *Polyergus longicornis* is a southeastern species, known from the Carolinas and Georgia, west to Mississippi. It is found in the open pinelands and oak-pine woodlands on sandy soils with host populations of *F. dolosa*.

Distribution of studied specimens. FLORIDA Leon Co. Apalachicola Nat'l For. Rd. 307. Stand 246 June 2004 JR King Colony Series, Pine Flatwoods (JCTC); MISSISSIPPI Oktibbeha Co. Osborn 33º30'41"N 88º44'08"W 19 June 2003 J. G. Hill (MEM); MISSISSIPPI Pontetoc Co. Natchez Trace, mi. 247.5. 34º05'49"N 88º51'38"W 23 June 2003 JA MacGown (MEM); MISSISSIPPI Winston Co. Tombigbee Nat'l Forest 33º2'30"N 89º04'32"W. 10 July 2003 JA MacGown (MEM); NORTH CAROLINA Mecklenburg Co. Davidson 6-VI-39 CS Brimley (NCSU); NORTH CAROLINA Staley 15-VIII-1968 DL Wray (NCSU); NORTH CAROLINA Moore Co. Robbins in yard 7-VII-1985 Morris (NCSU); SOUTH CAROLINA McCormick Co. Baker Cr. St. Pk. Open pineland 28 June 1986 C Johnson (JCT).

Polyergus montivagus **new status**

Figures 33, 34, 35

Polyergus lucidus montivagus Wheeler 1915: 419. Syntype workers, gyne, male: USA, COLORADO Springs [CAS, MCZ red syntype label 22969, CASENT0172894 (worker), CASENT0172893 (male)] (examined).
Polyergus lucidus: Creighton, 1950 (incorrect synonymy).

Types not measured.

Measurements (N=32) HL 1.40–1.70 (1.55), HW 1.40–1.68 (1.51), SL 1.34–1.58 (1.44), ½ VeM 0–4 (0.53), ½ PnM 0–3 (0.29), WL 2.28–2.76 (2.46), GL 1.96–2.80 (2.29), HFL 1.92–2.24 (2.09), CI 93–104 (97), SI (83, one specimen) 88–104 (96), HFI 130–149 (135), FSI 138–156 (145), LI 3.68–4.44 (4.00), TL 5.68–7.16 (6.28).

Worker description. Head truncate-ovoid to subhexagonal, wider behind eyes, sides anterior to eyes straight or even weakly concave and convergent toward mandibular bases, head length usually slightly greater than breadth; vertex pilosity 0–2 erect setae present near each corner (4 on one side of a single specimen); scapes at least reaching, normally surpassing vertex corners, gradually thickening apically; pronotum with 0–2 (very rarely up to 5) dorsal erect setae; mesonotal profile weakly convex; propodeum profile a rounded right angle; petiole with weakly convex sides converging dorsad, petiolar dorsum flat or at most weakly concave emarginate; petiolar profile low, its apex when gaster is in horizontal position only a little higher than propodeal spiracle, petiolar front and rear surfaces convergent dorsad, front weakly convex, rear straight; first tergite lacking pubescence; first tergite pilosity 0–6 relatively short suberect macrosetae.

Head very faintly shining; mesonotum feebly shining, shinier on lateral pronotum; gaster shiny.

Color red, often with notably darker, even nearly blackish legs; scapes and mesometapleura infuscated; what little pilosity is present is dark brown.

Specimens from the southeastern portion of the range have a more gracile appearance, with proportionally longer appendages, and have somewhat smaller colony size than those elsewhere.

Discussion. *Polyergus montivagus* is most easily distinguished from other Nearctic species by its shining gaster, lack or near lack of pilosity, and association with *F. pallidefulva.* In the Northeast, its proportions approach those of *sanwaldi*, but in absolute metrics *montivagus* is smaller, and is nearly non-pilose. Where sympatric with *lucidus*, the latter is distinguished by the presence of 5 or more erect setae on the vertex corners, as opposed to never more than 4 (usually 0–2) in *montivagus*. Where sympatric with *oligergus*, *montivagus* is again distinguished by host preference, dark legs of mature specimens, and by its slightly larger size, average slightly shorter scapes and hind femora, and slightly less pilosity. Gynes of *montivagus* are notably larger than those of *oligergus* Indicative of this, WL almost 3.0 mm compared to about 2.5 mm, respectively, in three specimens of each that were available for measuring.

Etymology. Wheeler coined this adjectival name from Latin "mons, monti-" (hill) and "vagus" (wandering), apparently in reference to its discovery in the foothills of the Rocky Mountains.

Natural history. Although originally described from Colorado, and almost nowhere abundant, this species is now known to blanket nearly the entire distribution of its host, *F. pallidefulva*, though typically restricted to sites with sandy or at least well drained soil.

Talbot (1967, 1968) and Marlin (1968, 1969, 1971) studied this ant's behavior, reported as *lucidus* but determined by vouchers I have seen from their studies. *Polyergus montivagus* is an ant of meadows surrounded by woods, grassy areas that are shaded part of the day, sandy or loessic open woodlands, park-like habitats and lawns, where an abundance of the host species occurs. Its host is always *F. pallidefulva*. Talbot (1967) saw a colony in Michigan of *montivagus* with *F. pallidefulva* (reported as *F. p. nitidiventris*) that raided *F. neogagates & F. lasioides*, but brood of these species never survived to adulthood as workers in the *Polyergus* nest. There is a notable trend toward smaller colonies to the South and West. One colony dug by Talbot (1967) in Michigan contained 291 *montivagus* workers, 299 *montivagus* pupae, and over 4500 *F. pallidefulva* workers. I observed a raid by about 130 *montivagus* workers in southern IA, Marlin (1969) reported an average of 87 raiders in central IL, and I estimated a colony near Boulder CO to have 90–100 workers. A colony dug by King (King and Trager 2007) contained 70 *Polyergus* and over 500 *F. pallidefulva* workers. Raids that Talbot (1967) saw in Michigan occurred from mid June to early September. Marlin (1969) observed raids in Illinois from early June through mid September. These dates correspond to the periods when host worker pupae are most available. Raids take place late afternoon till dusk. Marlin and Talbot agreed in most details of the flight behavior of *montivagus.* Marlin (1971) described flight activity as follows: "Males left the nests only during the late morning and early afternoon (10 AM to 3 PM). They appeared in groups of five to 30 and milled about the nest area. On 9 days in 1966 males were active at one nest that produced no females that year. Alate gynes were active from noon until after 7 PM. On 10 days gynes left the nest without males." He also noted that females usually flew off, but saw two instances of females mating on the ground near the nest.

Distribution of studied specimens. COLORADO Boulder Co. Bluebell Canyon 1737m. 20-VI—16-VII-1979 Coll. U. Lanham (FMNH); COLORADO Boulder Co. Gregory Canyon 2035m. Meadow; under rock. 1-VIII-1955 #137 Col. J. Brown; COLORADO Boulder Co., Boulder Chautauqua Park Open Meadow 1 Aug. 2001 JCT (JCTC); COLORADO Montrose Co. South Rim, Black Canyon, 2438 m, 1-VIII-1955 Pinyon cedar oak woodland; under rock. G. Wheeler Det. R. E. Gregg (FMNH); FLORIDA Leon Co. Apalachicola Nat'l For. Rd. 367, Stand 232 Feb. 2006 J. R. King Colony series, Pine flatwoods (JCTC); ILLINOIS Tazewell Co. Washington in Lawn 11 Sep. 1988 JC Trager & M.B. Dubois (JCTC); IOWA Decatur Co. 5 mi. SE Leon, Timberhill Farm. White Oak Savanna 1 July 2006 Trager and Rericha. (JCTC); MICHIGAN Livingston Co. E.S. George Res. 7/12/70 70-40 M Talbot (JCTC); MICHIGAN Livingston Co. E.S. George Res. 9/20/75 75-119 M Talbot (JCTC); MICHIGAN Livingston Co. / ESGR R. Savolainen 248/98 (JCTC); MISSISSIPPI Lowndes Co. Hwy. 82 X 45 alt 33º29'17"N 88º39'38"W 19-26 June 2003 J. G. Hill (MEM); NEBRASKA Greeley Co. North Loup River. Mesic hilly grassland/wooded valley. J. Jurzenski Coll'n. #Gree01_06_30_01; NEW YORK Suffolk Co. Medford vicinity Nest in Mowed field. August 1985 R. Sanwald (males only, with *F. pallidefulva* workers, JCTC); WISCONSIN Adams Co. Quincy Bluff and Wetlands SNA 43°52'03"N 89°53'15"W 4/Jul/2009 Jeffrey P. Gruber (WIRC); WISCONSIN Monroe Co. FT. McCoy SNA 43°59'11"N 90°41'40"W 17 June 2007 Jeffrey P. Gruber (WIRC); WISCONSIN Richland Co. LWRSWA Lone Rock 43°11'38"N 90°14'20"W Nesting with Formica sp. Under weathered post on ground. Sandy prairie /oak savanna. 15 May, 2004 Jeffrey P. Gruber (WIRC); CANADA ONTARIO Pinery Prov. Park 25 Aug. 1983 SA Marshall (JCTC).

***Polyergus oligergus* new species**

Figures 36, 37, 38

Holotype worker: USA, FLORIDA Clay Co. 2 mi. N Keystone Hts. [CAS, CASENT0104430]. Paratypes: 15 workers, 2 gynes, 3 males: MCZ, CAS, FSCA, ABS].

Holotype measurements HL 1.41, HW 1.37, SL 1.48, ½ VeM 2, ½ PnM 0, WL 2.26, GL 2.18, HFL 1.98, CI 97, SI 108, HFI 145, FSI 134, LI 3.67, TL 5.85.

Paratype worker measurements (N=9) HL 1.36–1.56 (1.45), HW 1.31–1.52 (1.41), SL 1.40–1.58 (1.49), ½ VeM 0–3 (1.56), ½ PnM 0–1 (0.33), WL 2.16–2.48 (2.30), GL 2.08–2.28 (2.20), HFL 1.98–2.16 (2.06), CI 96–98 (97), SI 99–111, HFI 139–156, FSI 134–143 (139), LI 3.52–4.04 (3.75), TL 5.72–6.32 (5.96).

Measurements (N=44) HL 1.32–1.66 (1.48), HW 1.28–1.63 (1.45), SL 1.40–1.61 (1.51), ½ VeM 0–5 (2.55), ½ PnM 0–2 (0.93), WL 2.09–2.68 (2.36), GL 1.70–2.60 (2.09), HFL 1.98–2.32 (2.15), CI 94–102 (98), SI 93–113 (104), HFI 139–161 (148), FSI 134–154 (143), LI 3.48–4.34 (3.85), TL 5.23–6.94 (5.96).

Worker description. Head ovoid to subhexagonal, widest just behind eyes, sides anterior to eyes often slightly concave, the two sides appearing parallel from eyes to mandibular bases, head length usually only slightly greater than breadth; vertex pilosity (0) 2–5 macrosetae present near each corner; scapes at least surpassing vertex corners, gradually thickening apically, SI 93–113 (values below 100 for an ergatoid and a few other very large workers); pronotum with (0)1–4 dorsal erect setae; mesonotal profile weakly convex for most of its length; propodeal profile rounded with nearly flat portions of dorsal and posterior faces meeting at about a curved right angle; petiole with rounded sides converging dorsad, petiolar dorsum flat or at most weakly concave; petiolar profile low, normally not reaching height of propodeal spiracle, petiolar front and rear surfaces convergent dorsad, front convex, rear straight; first tergite lacking pubescence; first tergite pilosity 0–6 relatively short suberect macrosetae.

Head very faintly shining; mesonotum weakly shining, shinier on lateral pronotum; gaster shiny.

Color red with somewhat darker legs, scapes and mesometapleura; what little pilosity is present is a bit lighter than main body color.

Discussion. Smaller size, more vertex pilosity, proportionally and often absolutely longer hind femora, higher values for any proportion using HFL and most with SL, and association with *F. archboldi* distinguish this species from the similar *montivagus*.

Etymology. This species has the smallest worker populations of any *Polyergus* species. The name stems from Greek, *olig-* (few) plus *erg-* (work), roughly meaning few workers, and alliterating neatly with the genus name.

Natural history. *Polyergus oligergus* apparently lives only in Florida and only with *F. archboldi*. It is quite similar to *montivagus*, but averages visibly smaller than the average for that species, has a lower petiole, tends to be slightly more pilose, and has smaller colony populations. Further *P. montivagus* often has dark brown to blackish legs, while those of *P. oligergus* are usually only slightly darker, if at all, than body color. Gynes and males of *P. oligergus* are significantly smaller in every dimension than those of *P. montivagus*.

A colony dug by King (King and Trager, 2007) contained 40 mature *Polyergus* workers, with 340 *F. archboldi* workers. Near Gainesville FL, I observed numerous raids by 4 colonies, with from 25–38 raiders participating (Trager and Johnson, 1985). One remarkable raid observed after that paper was published, was carried out successfully by four *P. oligergus* workers against a small *F. archboldi* colony. Each of the 4 raiders emerged alive and bearing a pupa, while the estimated 100+ *F. archboldi* workers and their gyne rushed out of the nest and climbed up nearby plant stems or hid under leaf litter. Raids that Trager and Johnson (1985, reported as *lucidus*) saw in Florida occurred from mid-May through July (with one outlier in early September). I observed alates flying off from the nests between 11:00 and noon, about 6 hours before brood raids on the same day, on clear dry days in July. The colony from Putnam Co. FL contained a single, significantly larger, presumably ergatoid, individual.

Distribution of studied specimens. FLORIDA Alachua Co. San Felasco Hammock St. Pres. Sandhill woodland, raiding Formica. 14 May 1986 J. C. Trager (plus numerous specimens collected from 4 colonies at this location, 1986–1987, JCTC); FLORIDA Clay Co. 2 mi. N Keystone Hts. Nest under leaf litter. Sandhill. 15-VIII-10 J. Sivinski (JCTC); FLORIDA Columbia Co. 0.5 mile S Rt. 240 on Rt. 41 pitfall trap 15-18/April/2000 Lloyd R. Davis, Jr. (JCTC); FLORIDA Leon Co. Apalachicola Nat'l Forest Rd. 367, Stand 232 Feb. 2006 JR King Colony Series, Pine Flatwoods (JCTC); FLORIDA Osceola Co. Kissimmee St. 2 TNC-Des. Wild Pres. VII 17-23-2001 LL Pine/Palm/Grass Malaise trap TNC-staff el. 67 ft. 28.07N/81.26W (Z. Prusak Collection); FLORIDA Putnam Co. 3 mi. E Melrose Univ. Florida Ordway Preserve. Nest in sandhill woodland. 15 Aug. 1987 JC Trager (JCTC).

Polyergus ruber new species

Figures 39, 40, 41

Polyergus lucidus longicornis: Vargo and Gibbs 1987 (misidentification).

Holotype worker: USA, GEORGIA Clark Co. Athens. 165 Doe Run. [CAS, CASENT0281055]

Paratypes: 4 workers, 3 gynes, 3 males: Same data as holotype [MCZ, CAS].

Holotype measurements HL 1.90, HW 1.80, SL 1.79, ½ VeM 9, ½ PnM 3, WL 2.86, GL 2.60, HFL 2.44, CI 95, SI 99, HFI 136, FSI 136, LI 4.76, TL 7.36.

Paratype measurements (N=5) [MCZ, CAS, FSCA] HL 1.60–1.90 (1.75), HW 1.52–1.80 (1.64), SL 1.68–1.79 (1.71), ½ VeM 3–9 (6.8), ½ PnM 1–4 (2.2), WL 2.52–2.86 (2.66), GL 2.04–2.60 (2.34), HFL 2.09–2.44 (2.26), CI 93–95 (94), SI 99–113 (105), HFI 134–146 (138), FSI 124–136 (132), LI 4.12–4.76 (4.41), TL 6.16–7.36 (6.75).

Measurements (N=26) HL 1.52–1.90 (1.65), HW 1.42–1.80 (1.64), SL 1.68–1.79 (1.71), ½ VeM 3–9 (6.8), ½ PnM 1–4 (2.2), WL 2.52–2.86 (2.66), GL 2.04–2.60 (2.34), HFL 2.09–2.44 (2.26), CI 93–95 (94), SI 99–113 (105), HFI 124–136 (132), FSI 124–136 (132), LI 4.12–4.76 (4.41), TL 6.16–7.36 (6.75).

Worker description. This species is most similar to *longicornis*, but is shinier and has less pilosity. Head rectangular to weakly hexagonal, HL greater than HW; with conspicuous vertex pilosity consisting of (5) 8–20 erect macrosetae; scapes at least reaching, normally surpassing vertex corners, gradually thickening in distal half; pronotum with 0–6 dorsal erect setae; mesonotal profile weakly convex for most of its length; propodeal profile variable ranging from evenly rounded to a weakly obtuse, rounded angle; petiole narrow, sides convex and converging dorsad, petiolar dorsum rounded or with median portion flat, less often feebly concave; first tergite lacking pubescence; first tergite pilosity sparse, weakly flexuous or straight.

Head matte to very faintly shining; mesosoma matte dorsally but shining laterally; gaster weakly shining to shiny.

Discussion. This is among the three largest species of the *lucidus* group, almost in the same size range as *longicornis*, but characterized by a shinier head and mesosoma, especially the pronotum, and less abundant pilosity, especially on the vertex. Color is clear red with at most slight infuscation of the extremities.

P. ruber appears intermediate between *longicornis* and *lucidus* in its proportions, pilosity, and shininess. The sheen and lesser vertex pilosity distinguishes *ruber* from the more matte *longicornis* (*ruber* ½ VeM < 12 vs. *longicornis* > 13) while the longer appendages distinguish it from *lucidus* (*ruber* SI > 92+ vs. *lucidus* < 91).

Etymology. With the name *ruber*, Latin for red or ruddy, I refer to the brighter, all-red color of this ant species, in comparison to other southeastern species, especially the somewhat similar, but dark-legged *longicornis*.

Natural history. *Polyergus ruber* tracks its host, *F. biophilica*, in distribution, namely, a U-shaped range south from Maryland to Georgia, west to Louisiana, then north to eastern Missouri. It would be unsurprising if this ant showed up from collecting in at least southern Illinois.

Polyergus ruber was studied by Vargo and Gibbs (1987, reported as *lucidus longicornis*) in Athens, GA. Aside from its unique host association, *ruber* seems much like its relatives in the *lucidus* group in most respects. Raids were observed from early June to mid-August, and may have continued after these observations ended, as the activity was still vigorous, so perhaps starting just a few weeks earlier and persisting perhaps a bit longer than in other species of the group. I observed parts of a raid, and a mating flight that occurred several hours before the raid, in Georgia, and two raids of these ants in Missouri, all in July, and they are much like those of the other species. At both locations, pre-raiding milling was initiated around 1700 hr. The size of raiding parties in the Georgia colonies was estimated between 500 and 1000, quite large compared to other known *lucidus* group species. Colonies and raiding parties were somewhat smaller in Missouri. Vargo and Gibbs observed dealate gynes near the outskirts of nests before raids in late July, and saw one of these follow a raid and enter the raided nest. Habitats of this species included a variety of upland, grassy and open woodland types, with acid soils.

Distribution of studied specimens. GEORGIA Clarke Co. Athens. 165 Doe Run. Flight at noon. Raid at 1930hr. 10 July 1986 J. C. Trager (JCT) GEORGIA Clarke Co. Athens USA UGA Riverbend Lab. 3–11 July 1986 E. Vargo, JC Trager (JCTC); LOUISIANA St. Tammany Par. Lake Ramsey WMA SC3-3 Longleaf pine savanna. Pitfall trap. D Colby (multiple collections July–October 1997, LSU); MARYLAND Prince Georges Co. Berwyn [Heights] 6-25-1940 AB Gahas. W S Ross Coll. (FMNH); MISSISSIPPI Chickasaw Co. Tombigbee Nat'l Forest 33°55'39"N/88°50'57"W 20-27-June 2003 J. G. Hill (MEM); MISSOURI Lincoln Co. Cuivre River St. Pk. Sac Prairie 20 Apr. 1989 J.C. Trager (JCTC); NORTH CAROLINA Canover 1-VIII-32 Vanderford (NCSU); NORTH CAROLINA Burke Co. Morganton On ground 10-VI-1989 H. Barron (NCSU); NORTH CAROLINA Raleigh Raiding Nest 7-VII-1987 DL Stephan (NCSU); NORTH CAROLINA Granville Co. Oxford 1-VII-1977 F. Sutherland (NCSU); NORTH CAROLINA Durham Co. Durham K. Hedlund (no date) (NCSU); NORTH CAROLINA Wake Co. Cary June 10, 1984 DL Stephan (NCSU); NORTH CAROLINA Gaston Co. NE Cherryville Sept. 6, 1983 PJ Devine (NCSU).

***Polyergus sanwaldi* new species**
Figures 42, 43, 44

Holotype worker: USA, NEW YORK Suffolk Co. Medford vicinity. August 1988. R. Sanwald. [CASENT0281058]. Paratypes: 9 gynes, 8 males, 6 workers: same data as holotype [MCZ, CAS, AMNH].

Holotype measurements HL 1.80, HW 1.67, SL 1.60, ½ VeM 15, ½ PnM 4, WL 2.76, GL 2.68, HFL 2.24, CI 93, SI 96, HFI 134, FSI 134, LI 4.56, TL 7.24.

Paratype worker measurements (N=5) HL 1.72–1.80 (1.76), HW 1.63–1.74 (1.70), SL 1.62–1.64 (1.63), ½ VeM 11–15 (12.75), ½ PnM 2–4 (3), WL 2.68–2.83 (2.75), GL 2.12–2.24 (2.19), HFL 2.20–2.32, CI 95–99 (96), SI 93–101 (96), HFI 126–135 (132), FSI 134–143 (137), LI 4.44–4.60 (4.51), TL 6.67–6.76 (6.70).

Measurements (N=31) HL 1.52–1.90 (1.65), HW 1.42–1.80 (1.56), SL 1.50–1.79 (1.60), ½ VeM 3–12 (7.03), ½ PnM 0–4 (1.19), WL 2.36–2.86 (2.55), GL 1.69–2.60 (2.23), HFL 2.08–2.44 (2.20), CI 92–97 (95), SI 97–113 (103), HFI 134–150 (1.41), FSI 124–145 (138), LI 3.88–4.76 (4.20), TL 5.96–7.36 (6.43).

Worker description. Head rounded hexagonal, its length greater than breadth; with conspicuous vertex pilosity, about 20–30 setae; scapes falling slightly short of, to slightly surpassing vertex corners, faintly clavate in the apical third or gradually thickening apically; pronotum with 3–10 dorsal erect setae; mesonotal profile flat; propodeal profile subquadrate; petiole straight- to slightly convex-sided, petiolar dorsum evenly convex; first tergite lacking pubescence; first tergite pilosity sparse (usually < 10 macrosetae), straight, suberect, often deciduous (indicated only by macrosetal sockets in many specimens).

Head matte; mesonotum matte with only slightly smoother pronotal sides; gaster weakly shining.

Color mostly red with darker, brown appendages, and similarly dark lower lateral mesosoma, and posterior portions of tergites.

Discussion. *Polyergus sanwaldi* closely resembles *longicornis*, but has consistently shorter appendages (Fig. 2) and more northern (and apparently allopatric) distribution.

Etymology. This species is named for Raymond Sanwald, who led to its discovery through his interest in *Polyergus*, and his willingness to host years of studies by Howard Topoff and his students on the *Polyergus* species resident at Ray's Medford (Long Island) NY "Ant Ranch."

Natural history. I have studied samples of this ant originating from Massachusetts to northwestern Indiana and southern North Dakota. All samples originated from localities with deep, sandy soil. It seems likely it could be found in intervening sandy soil locations, such as the Oak Openings of Ohio or black oak savannas of northern Illinois, Wisconsin and southern Minnesota.

Goodloe and Sanwald (1985) and Goodloe, Sanwald and Topoff (1987) studied this ant in their work on host specificity of "*lucidus.*" The host of this species is exclusively *F. dolosa* (reported as *F. schaufussi*). These authors determined experimentally that mated gynes from colonies of *sanwaldi* were not accepted into groups of *F. incerta* workers, and likewise that gynes of *lucidus* were not accepted into groups of *F. dolosa*, while gynes introduced to groups of workers of the species of *Formica* in their home-nest most often were accepted. In the field, raids of the two species, again, were conducted only on the respective host species in the *Polyergus* home nest. Their papers were my first clue that *lucidus, sensu lato* might in fact be more than one species. The habitat of this species is sandy or sandy loam prairies and old fields, and sandy oak and pine savannas.

Distribution of studied specimens. INDIANA Porter Co. Westchester Township. Sec. 29. 8-VII-1957, Sidney Hatfield #97 (FMNH); INDIANA Porter Co. Westchester Township Sec.100. 11-VII-1957, Sidney Hatfield #100 (FMNH); MASSACHUSETTS, Norfolk Co. Blue Hills Reservation 5-IX-1919 GC&JN Wheeler (LACM, CASENT0172895); NEW JERSEY Ocean Co. Dwarf Pine Plains S.P. Cover. Unburned site E. of Tr. 539 5-12-86 #758 (MCZ); NEW JERSEY Ocean Co. East Dwarf Pine Plains. S.P.Cover. Burned (1983) Site W. of Rt. 539 5-13-86 #770.; NEW YORK Suffolk Co. Medford. Summer 1986 R. Sanwald (several collections, JCTC); NEW YORK Suffolk Co. Medford. Lab. Colony coll. Summer 1986 L. Goodloe (JCTC); NEW YORK Suffolk Co. Medford. 17 May, 1987, JC Trager, leg. (several collections, JCTC); NORTH DAKOTA #83 T144N R65W, sec. 7 Stutsman Co. 1-VIII-1959, Delton D. Halverson (LACM).

Acknowledgments

No revision can proceed without specimens, and reference to types is particularly important. For the loan of types and other museum materials of *Polyergus* I am thankful to all curators and collectors mentioned above in "**Sources of specimens for study**". Several other colleagues, not named here, sent one or a few samples each from interesting localities or as vouchers for their own studies, and I am grateful to all. I am further grateful to Dr. Kal Ivanov of Cleveland Sate University for an unusually well-executed translation from Russian of the description of *P. nigerrimus*, and for alerting me to the article of Antonov (2008). Cori Westcott cheerfully(!) transcribed thousands of labels that constitute the distribution information for the species, and was painstaking as a proofreader and sometimes corrections-typist in the final stages of editing the manuscript. Finally, I thank Brendon Boudinot of Evergreen College for Figure 1, and Brian Fisher and Michele Esposito of the California Academy of Sciences for the stacked digital images (CASENT images) that constitute the habitus figures (Figs. 3–44) of the species.

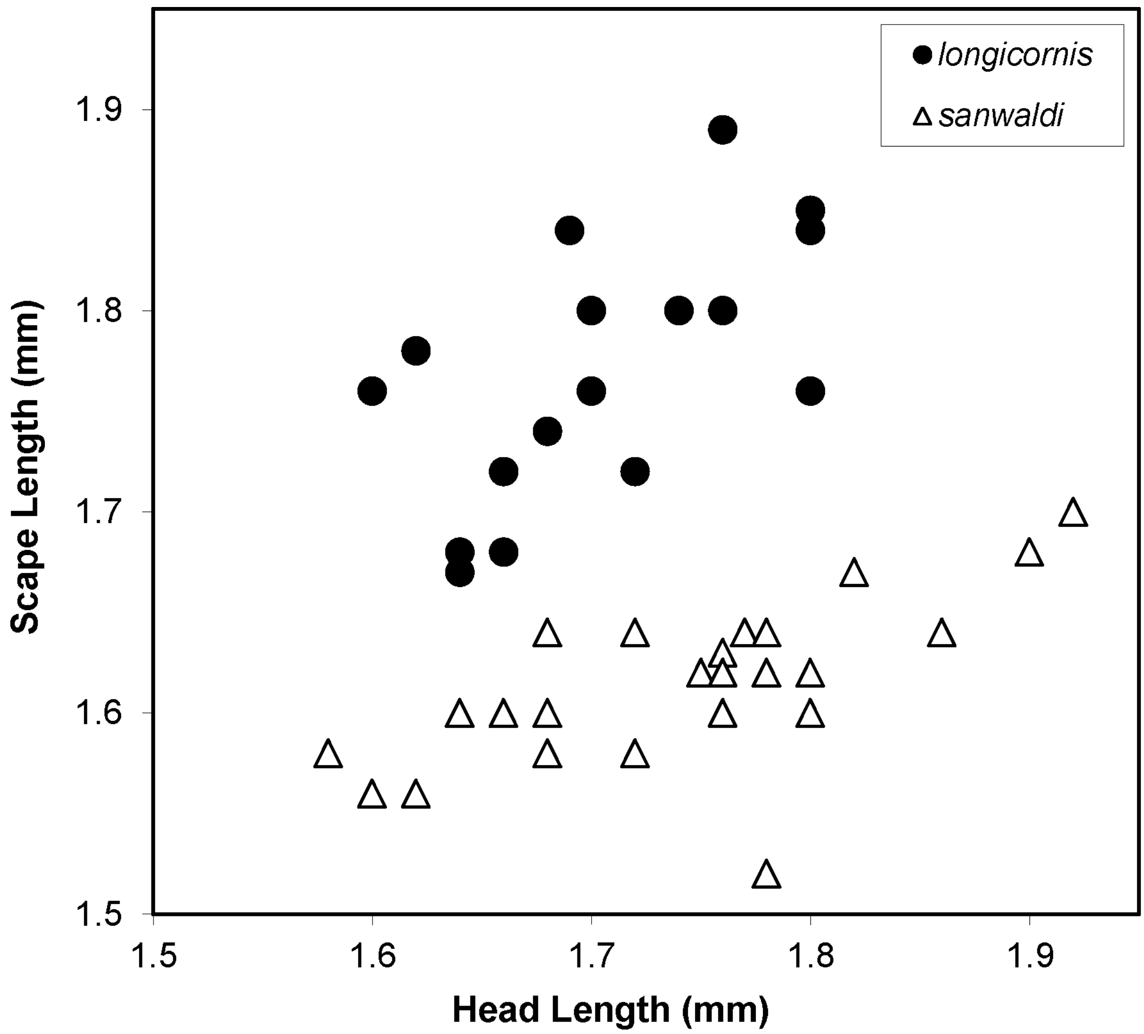
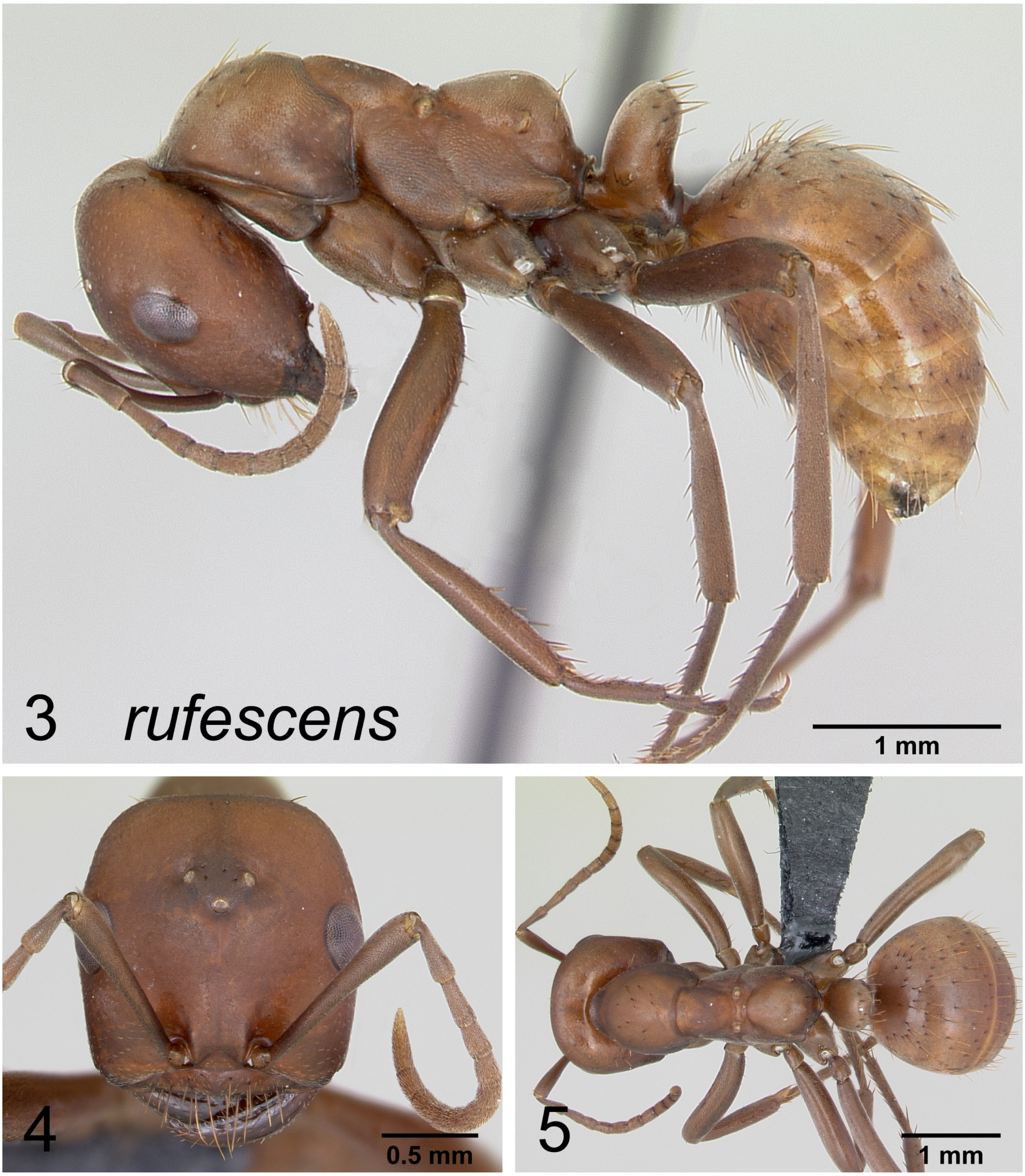
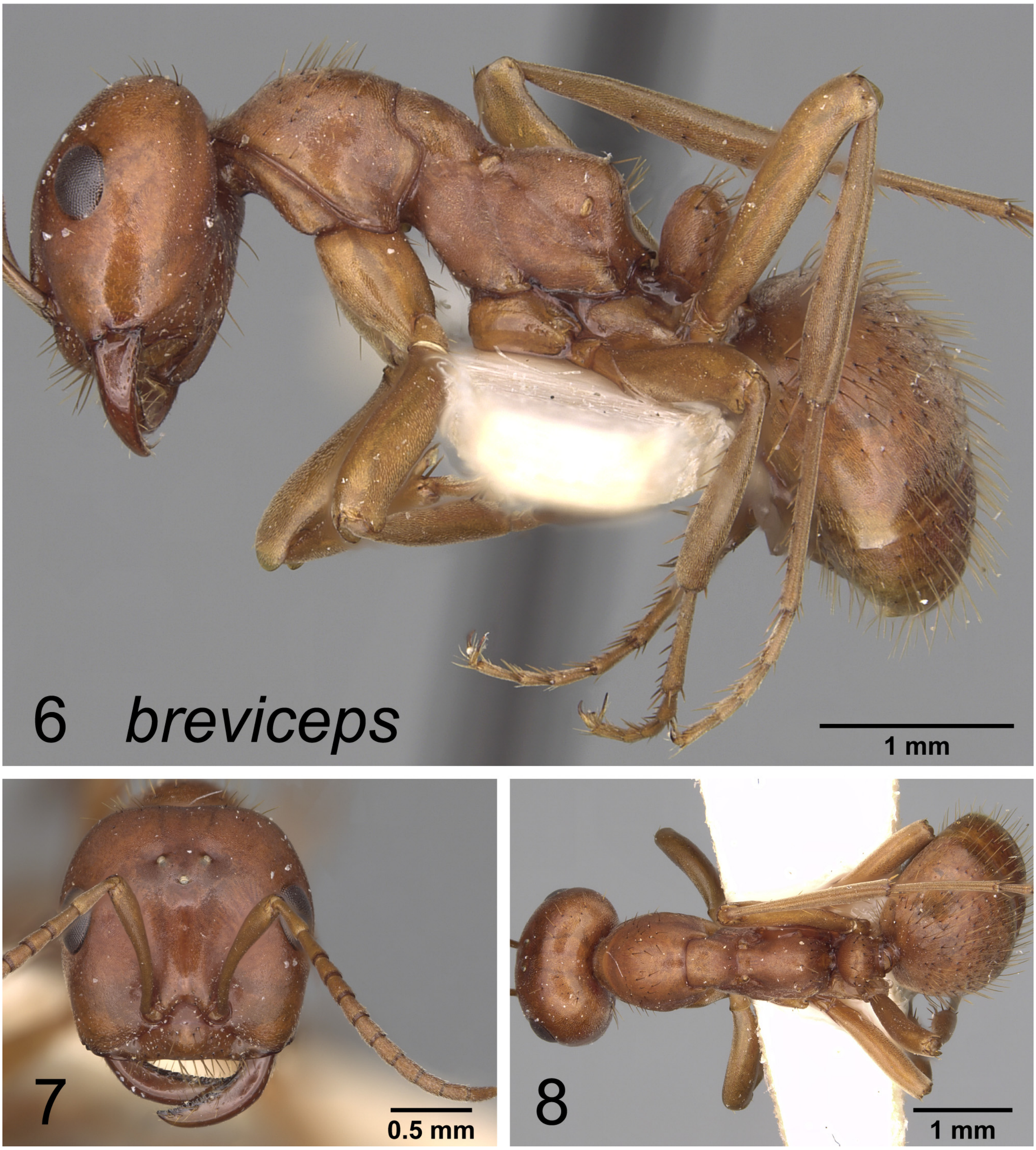


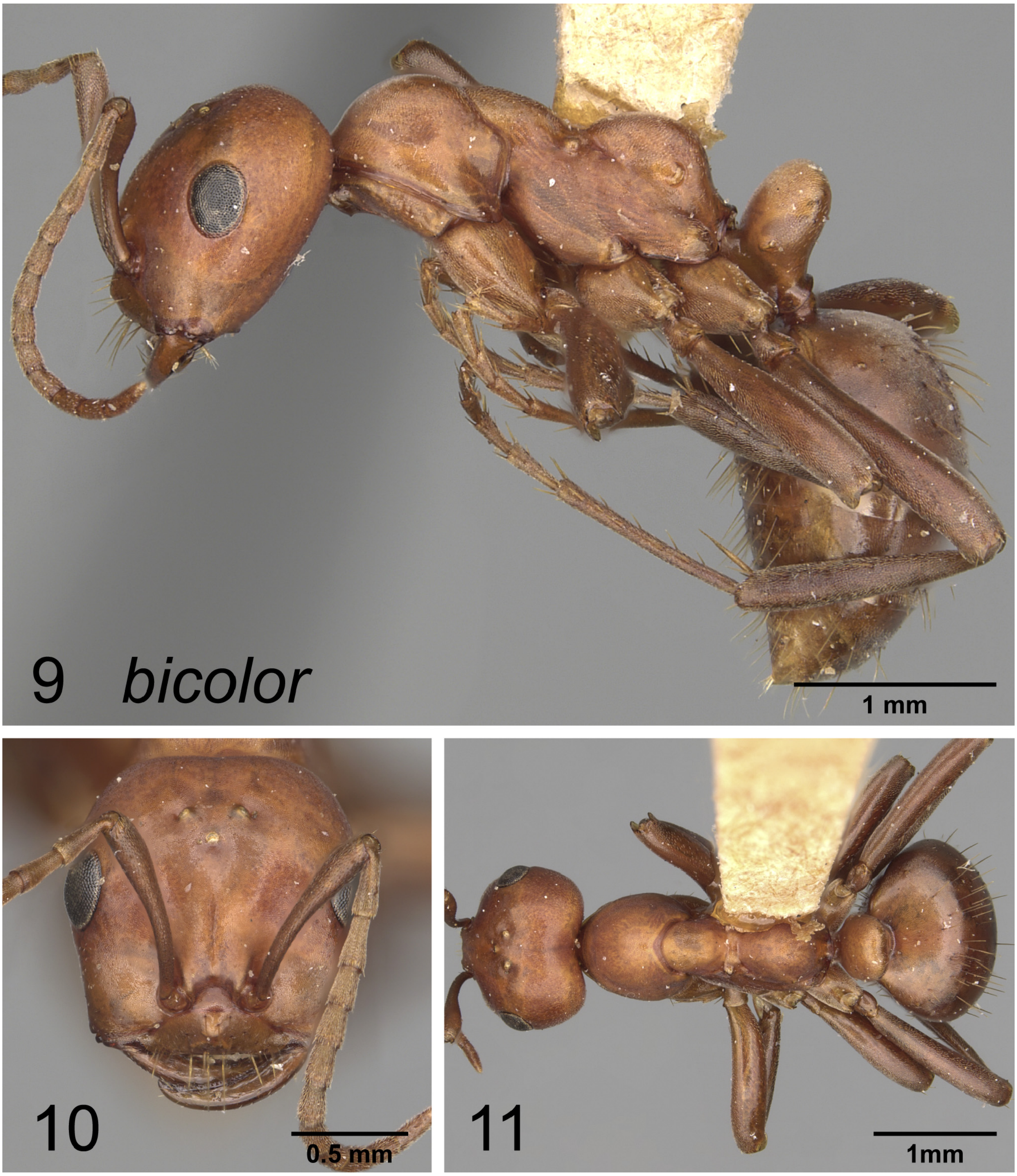
FIGURE 2. Scatter plot comparing head length/scape length ratios of *Polyergus longicornis* and *Polyergus sanwaldi.*



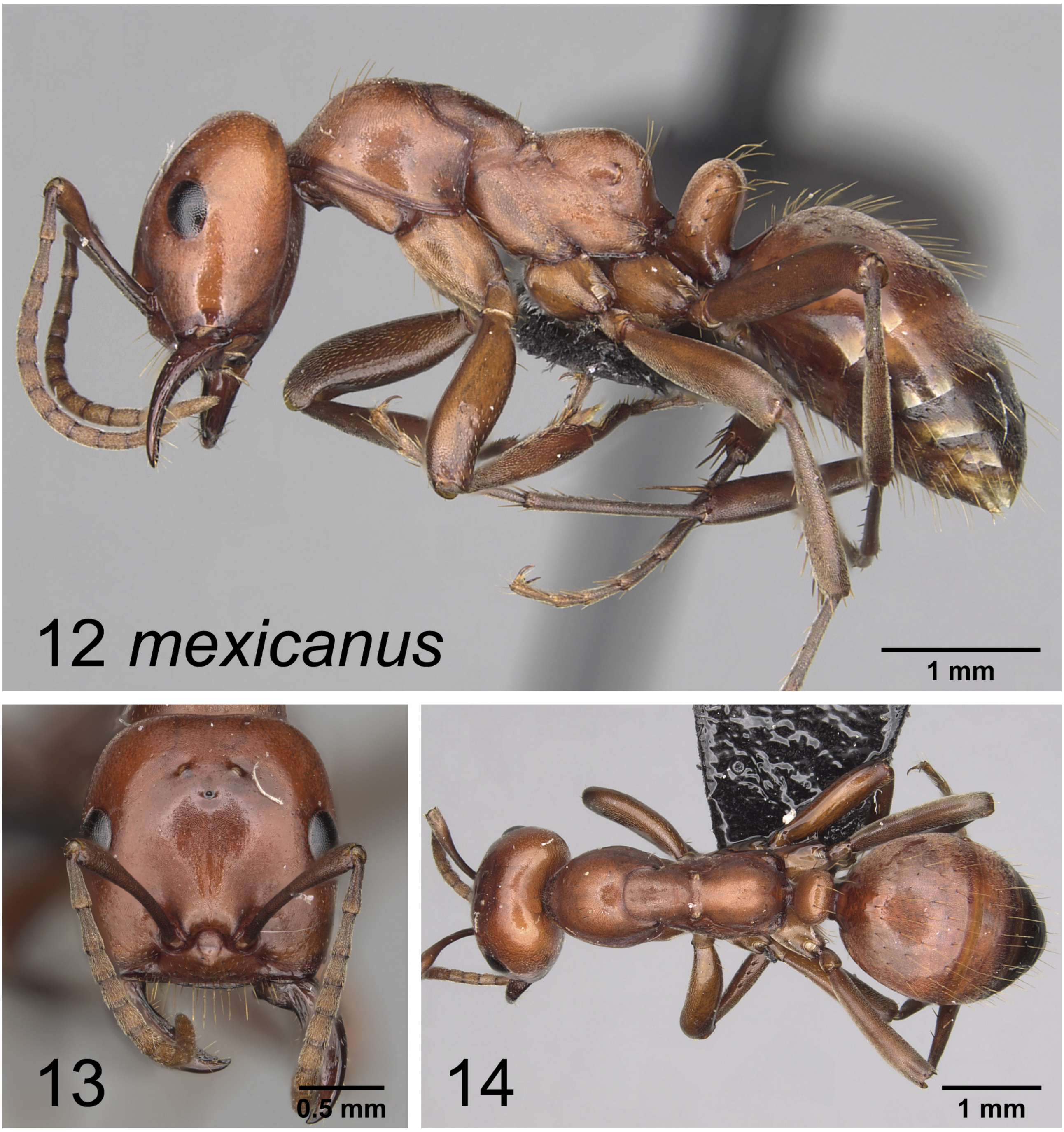
FIGURES 3–5. Lateral, full face, and dorsal views of *Polyergus rufescens* worker CASENT0173859. Photographs by April Nobile from www.AntWeb.org.



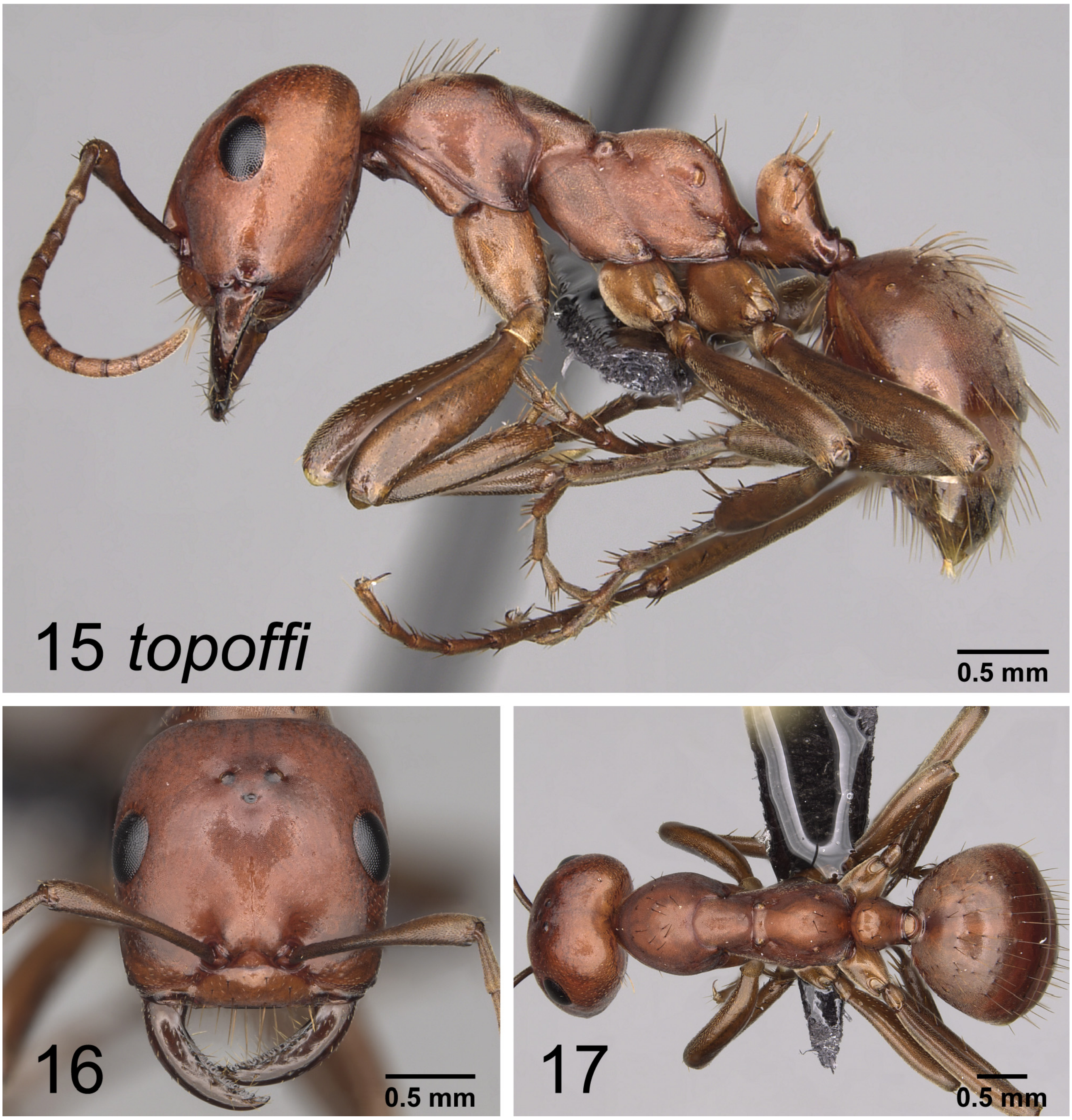
FIGURES 6–8. Lateral, full face, and dorsal views of *Polyergus breviceps* worker Polyergus breviceps CASENT0281065. Photographs by Shannon Hartman from www.AntWeb.org.



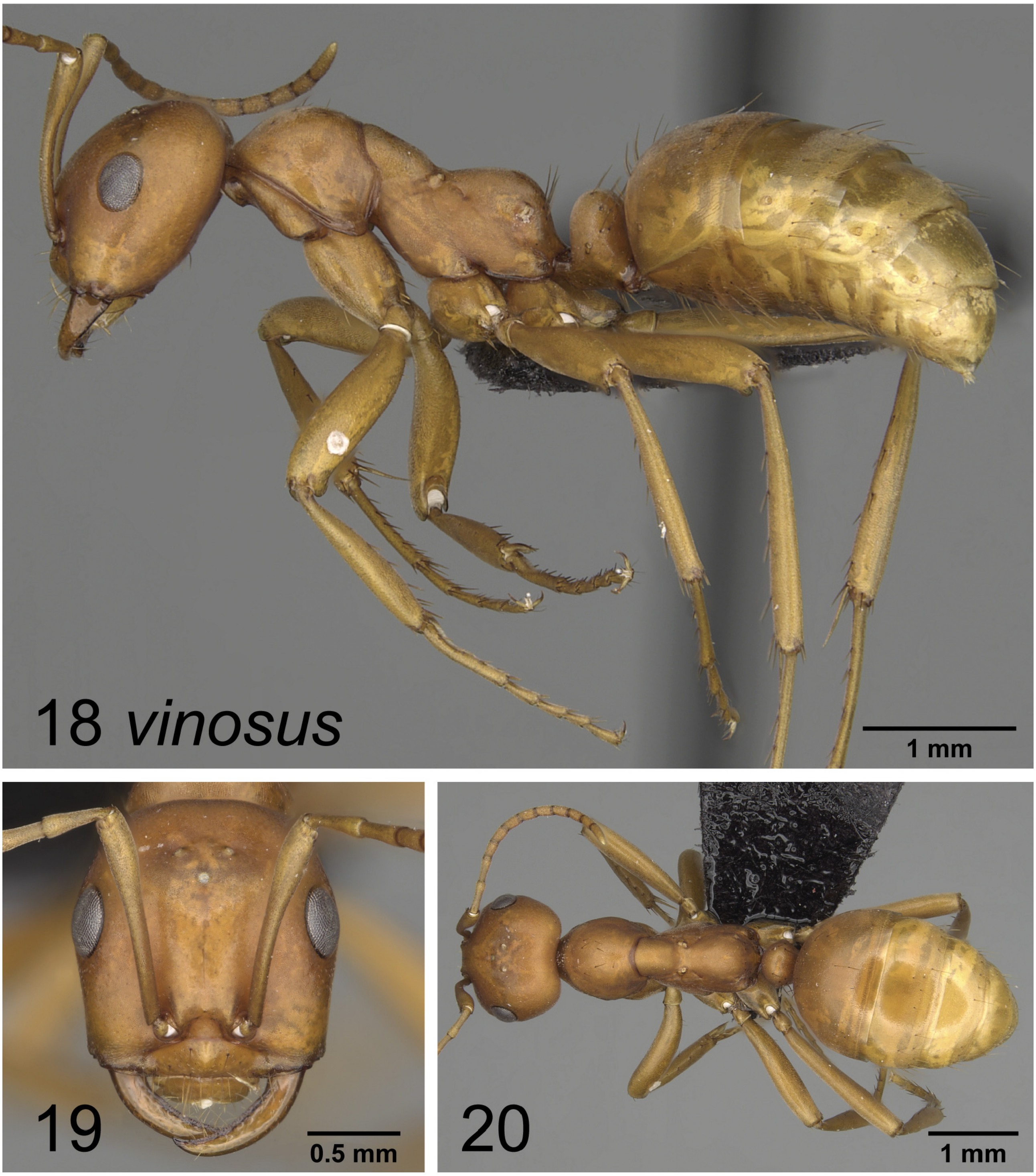
FIGURES 9–11. Lateral, full face, and dorsal views of *Polyergus bicolor* worker CASENT0281068. Photographs by Erin Prado from www.AntWeb.org.



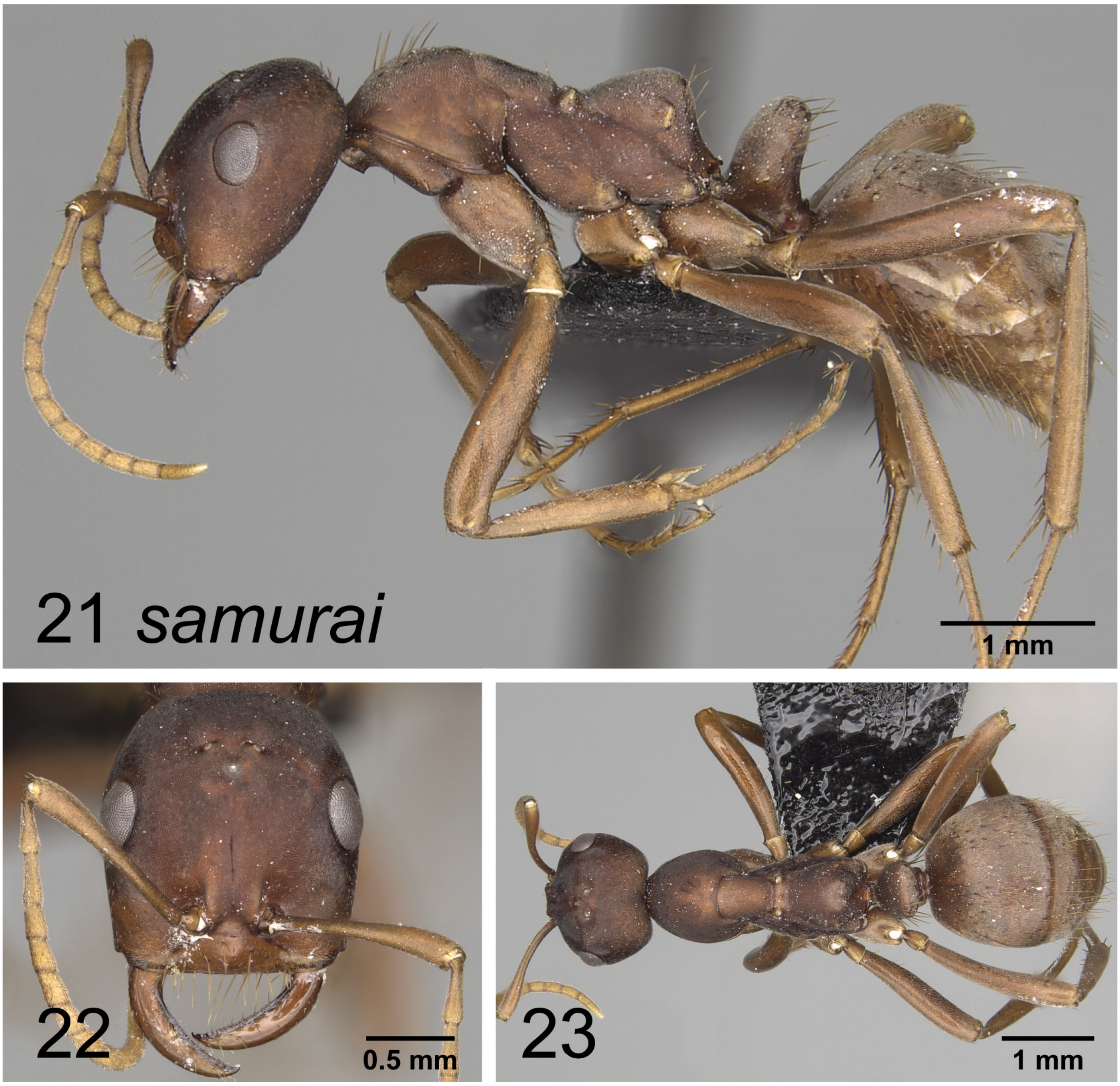
FIGURES 12–14. Lateral, full face, and dorsal views of *Polyergus mexicanus* worker CASENT0281071. Photographs by Shannon Hartman from www.AntWeb.org.



FIGURES 15–17. Lateral, full face, and dorsal views of *Polyergus topoffi* worker CASENT0281077. Photographs by Shannon Hartman from www.AntWeb.org.

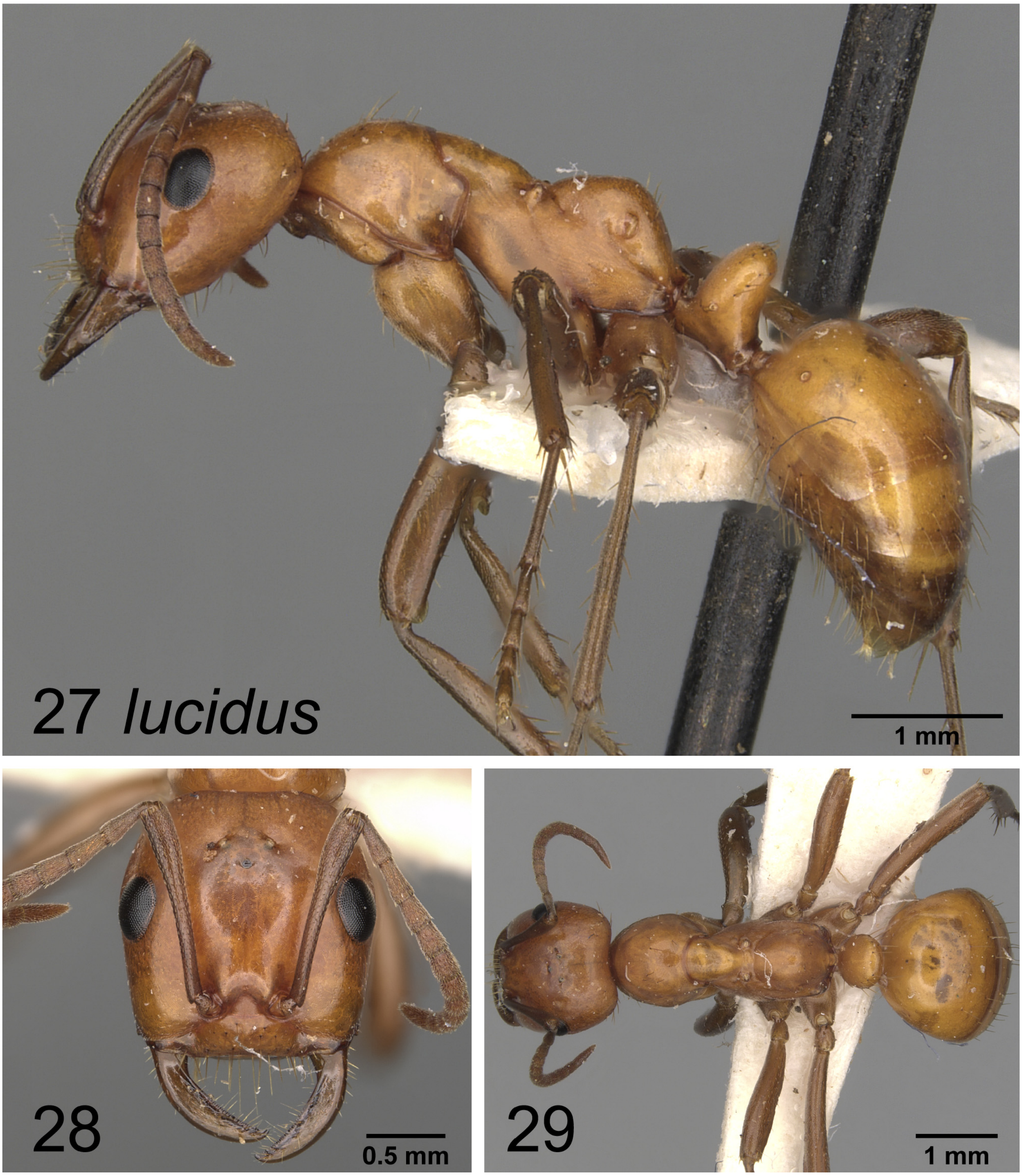


FIGURES 18–20. Lateral, full face, and dorsal views of *Polyergus vinosus* worker CASENT0281078. Photographs by Shannon Hartman from www.AntWeb.org.

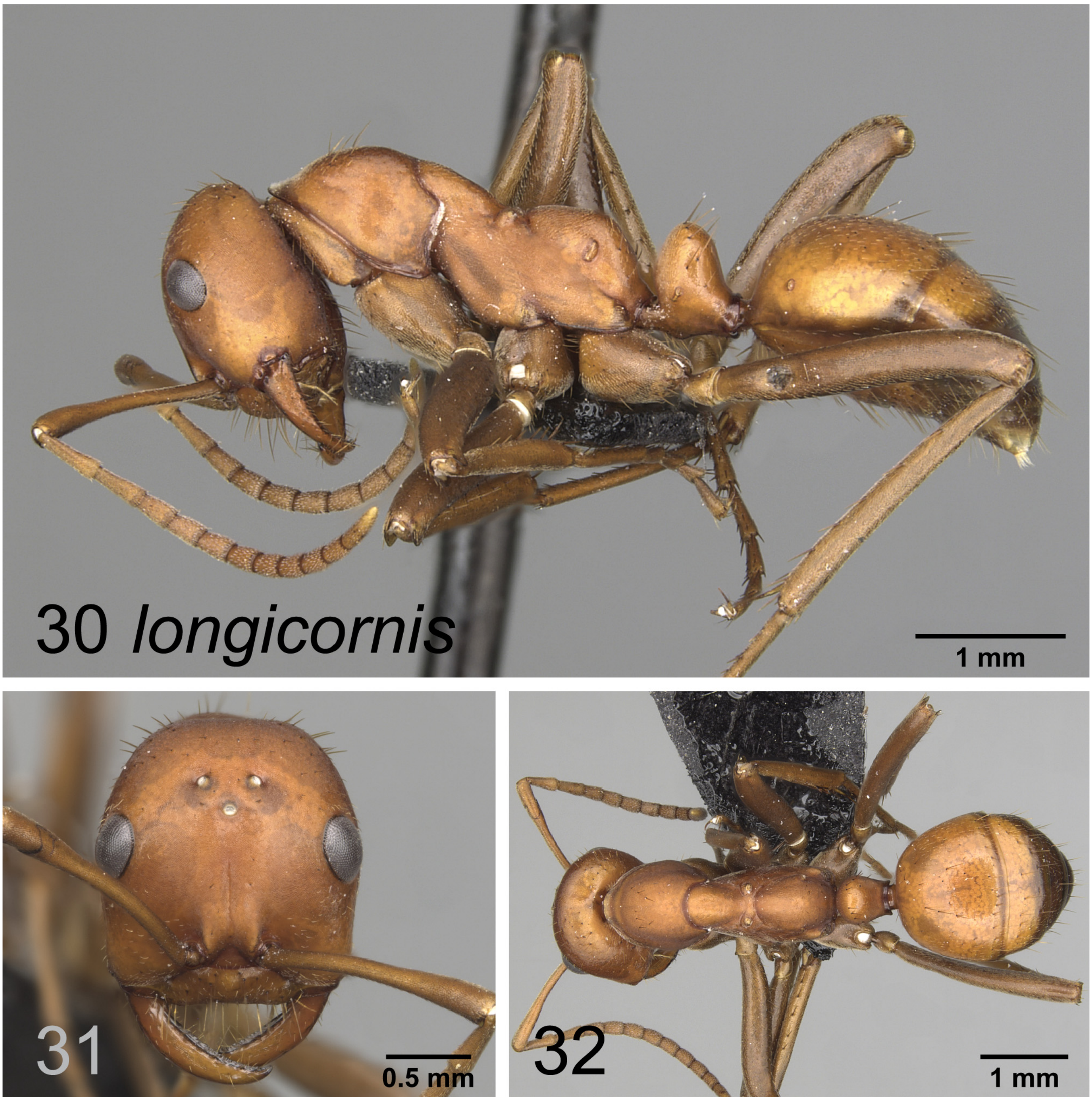


FIGURES 21–23. Lateral, full face, and dorsal views of *Polyergus samurai* worker CASENT0281083.Photographs by Shannon Hartman from www.AntWeb.org.

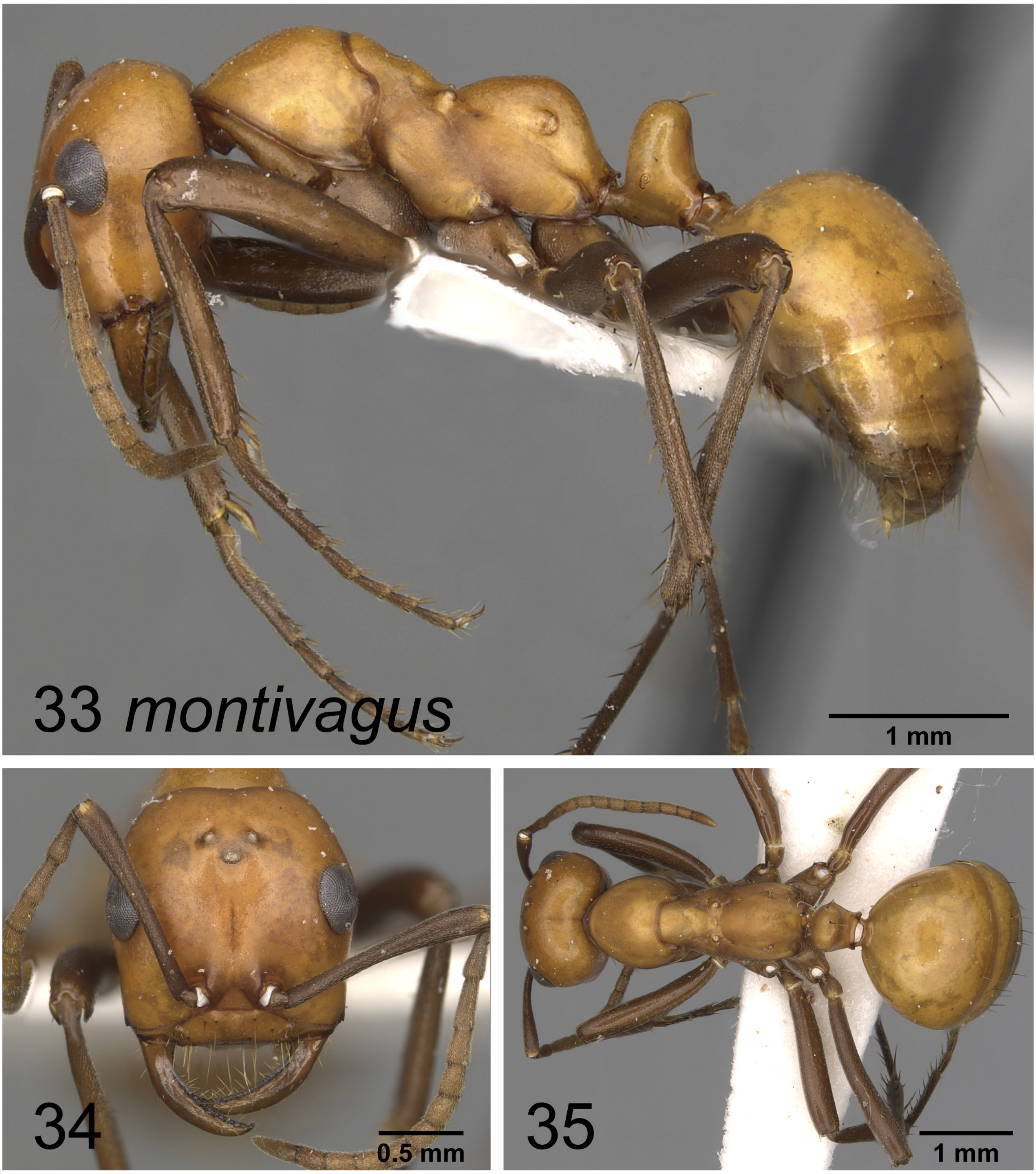
FIGURES 24–26. Lateral, full face, and dorsal views of *Polyergus nigerrimus* worker CASENT0173331. Photographs by April Nobile from www.AntWeb.org.



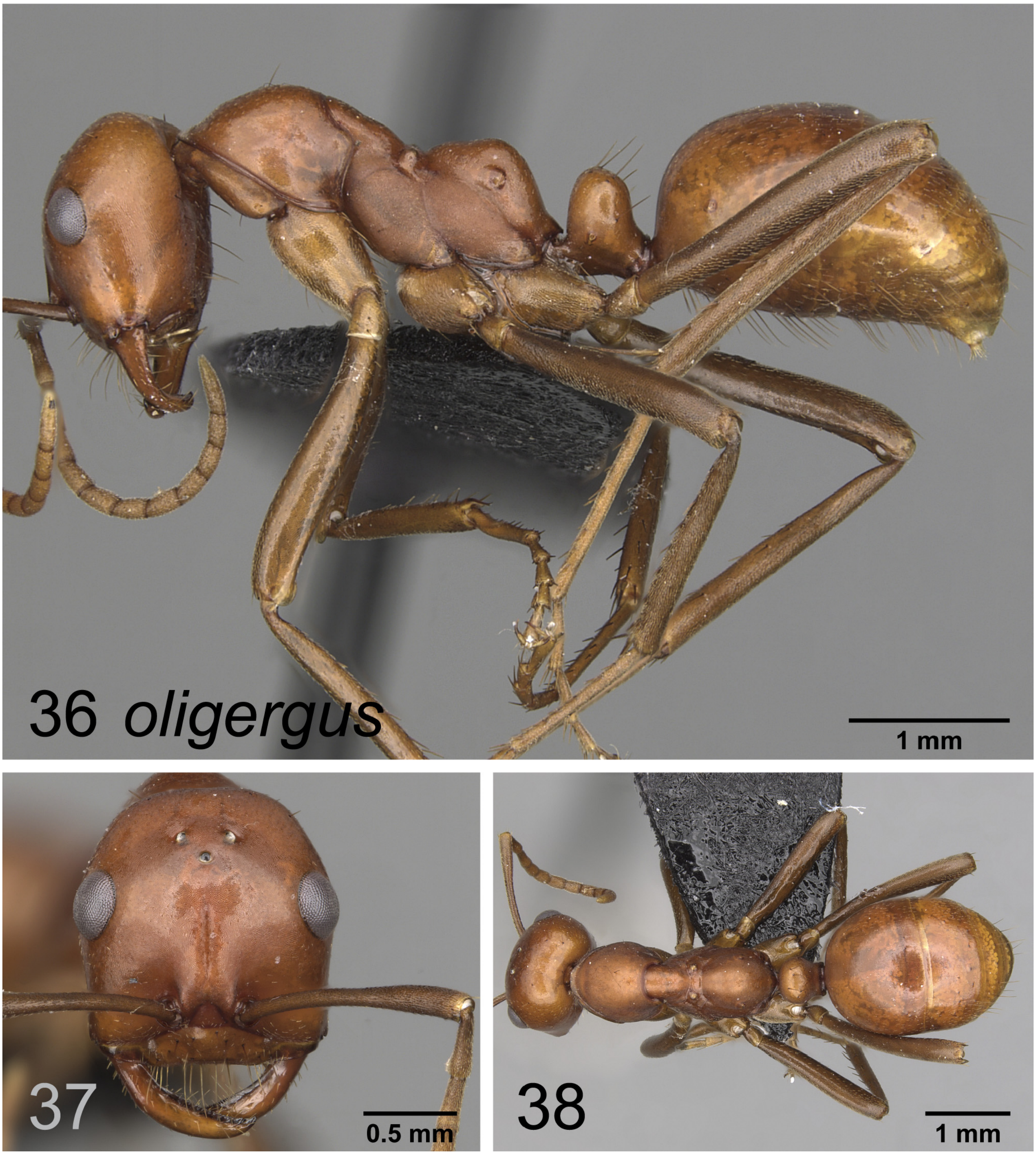
FIGURES 27–29. Lateral, full face, and dorsal views of *Polyergus lucidus* worker CASENT0281037. Photographs by Shannon Hartman from www.AntWeb.org.



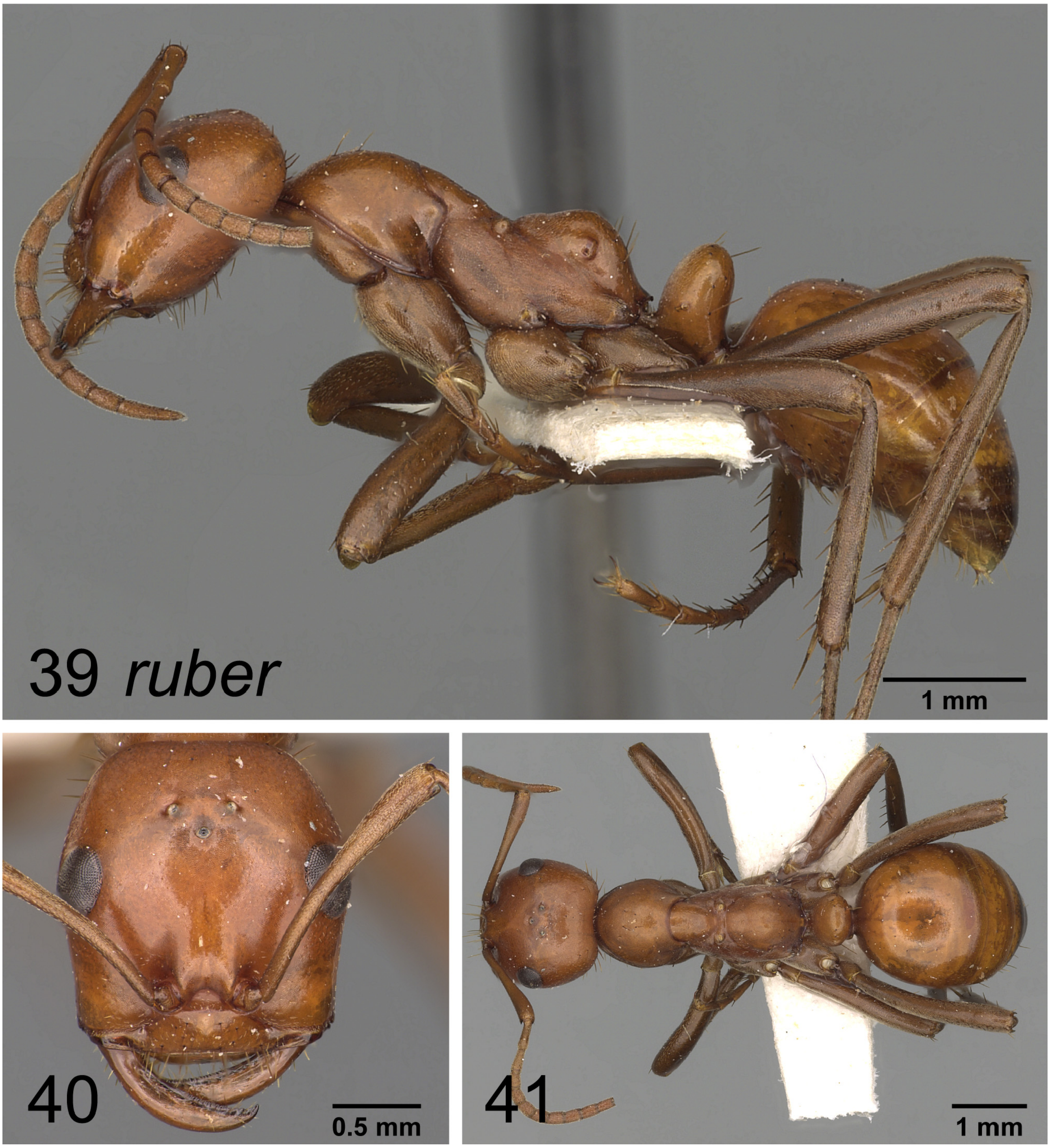
FIGURES 30–32. Lateral, full face, and dorsal views of *Polyergus longicornis* worker CASENT0281044. Photographs by Shannon Hartman from www.AntWeb.org.



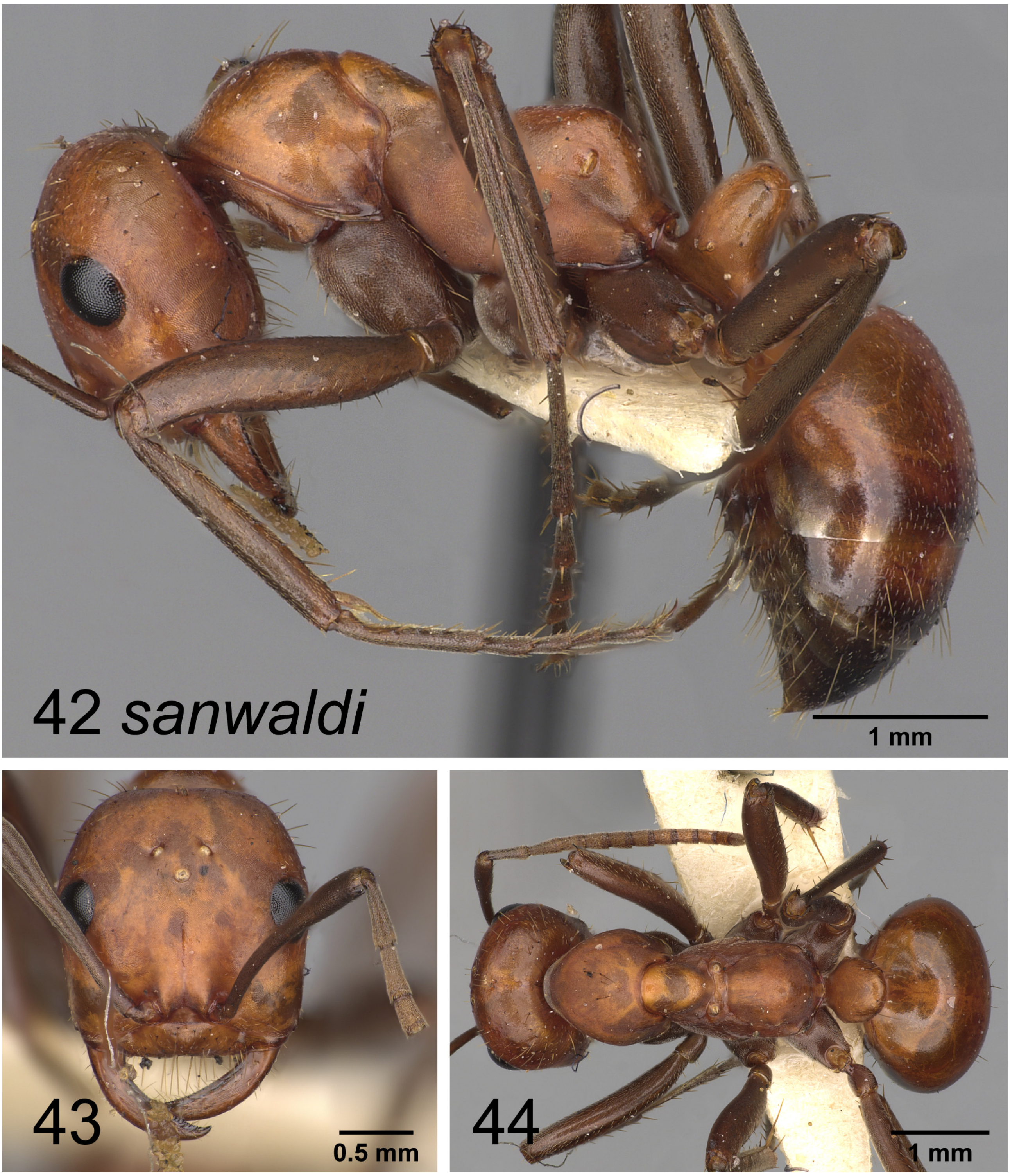
FIGURES 33–35. Lateral, full face, and dorsal views of *Polyergus montivagus* worker CASENT0281047. Photographs by Shannon Hartman from www.AntWeb.org.



FIGURES 36–38. Lateral, full face, and dorsal views of *Polyergus oligergus* worker CASENT0281053. Photographs by Shannon Hartman from www.AntWeb.org.



FIGURES 39–41. Lateral, full face, and dorsal views of *Polyergus ruber* worker CASENT0281055. Photographs by Shannon Hartman from www.AntWeb.org.



FIGURES 42–44. Lateral, full face, and dorsal views of *Polyergus sanwaldi* worker CASENT0281058. Photographs by Shannon Hartman from www.AntWeb.org.

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