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REVISION OF THE NEARCTIC ENDEMIC *FORMICA PALLIDEFULVA* GROUP

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ABSTRACT

We revise the Nearctic endemic *Formica pallidefulva* group based on study of types and other museum specimens and material in J. Trager's collection. The latter material originates from 30 years of accumulated samples, both from free-living colonies of *F. pallidefulva* group species, and from "slave" populations in colonies of *Polyergus lucidus s. l.*, which have single-species host populations. Among the currently available names for the group, the four valid taxa are *F. archboldi, F. dolosa, F. incerta* and *F. pallidefulva*. There is a fifth common, but previously unrecognized new species, described here as *Formica biophilica* Trager, **n. sp.** Earlier taxonomies of this group were constrained by typological thinking and inadequate treatment of metric characters. For this study, well preserved individuals, nest series and types of all but one taxon were studied (no types seen for *F. pallidefulva*). Analysis focused on form, length, abundance and distribution of macrochaetae (pilosity); length and density of microchaetae (pubescence); standard measurements and indices; distinct habitat preferences of the various species; and host selection by *Polyergus lucidus, s. l.* Our results leave little doubt that *F. incerta* **n. stat., rev. stat.** and *F. biophilica* **n. sp.** deserve recognition as species, that *F. nitidiventris* is a synonym of *F. pallidefulva* and that *F. schaufussi* is a synonym of *F. pallidefulva*. Thus, the current concept of *schaufussi* (incorrect in reference to the lectotype) must give way to the next available name for the same population, *dolosa* **n. stat**.

In this paper, we provide diagnoses, qualitative morphological characteristics, tabulated quantitative characters, natural history notes for all species and a key to the workers. As occurs in other groups of closely related ant species (*e.g*. Umphrey, 1996; Steiner *et al*., 2006), morphology is variable and partially overlapping, and species determinations will be more certain when based on nest series consisting of three or more workers in prime condition.

Key words: Hymenoptera, Formicidae, Formicinae, *Formica pallidefulva* group, taxonomy, morphometric characterization, natural history, habitat preferences, Nearctic, new species, lectotype designation.

INTRODUCTION

The *Formica pallidefulva* species group is endemic to the eastern and central United States, with two species extending west into the Great Plains and lower elevations in the Rocky Mountains and north into eastern Canada. The species of the *pallidefulva* group are distinguished from others in *Formica* by gracile body form and elongate appendages; integument moderately to strongly shining; propodeum in profile with the angle between dorsal and posterior faces completely obscured by rounding or at most indistinct (Fig. 6a-e); external mesometasternum of uniform simple structure throughout the group (Fig. 1), this structure unadorned or rarely with a few erect setae; male genitalia with elongate parameres; and behavior and habitat choice generally thermophilous. They mainly inhabit grassland and open woodland habitats; only *F. pallidefulva* Latreille is normally also associated with closed canopy forest. There are no social parasites in the group, and all have a clear size difference between the workers and queens. These species are hosts of dulotic *Polyergus lucidus* (*sensu lato*) and some *F. sanguinea* group species. They are also temporary hosts during colony-foundation for some species in the *F. rufa / microgyna* group (Wheeler, 1904; Creighton, 1950). Colonies typically contain 500 or fewer workers (Wheeler, 1904; Talbot, 1948). Nests are inconspicuous except when opening onto bare ground, but may bear a small mound nestled among herbaceous vegetation of grasslands or savannas, or occasionally a somewhat larger mound. Nests are quite often under stones or other cover objects in cooler parts of the range, but generally not so further south. Recruitment of individuals by social transport occurs during nest relocation, which may occur one or more times per year in some colonies. Robson & Traniello (1998) have given a thorough accounting of foraging and recruitment in *F. incerta* and *F. dolosa* (vouchers seen). Wheeler (1904) first described the "top-heavy" nests composed of broad chambers and narrow interconnecting passages of species in this group, and Talbot (1948) also described and illustrated them. Mikheyev & Tschinkel (2000) have provided a modern study of nest architecture and economics of nest building of one species. Milford (1999) reports the presence of a species in riparian forests along the Rio Grande. (Presumably, *F. pallidefulva* was the subject of these two recent studies, but vouchers were not available for identification). Bale *et al*.,(2004) reported on the role of "*F. schaufussi*" in dispersing seeds of trilliums, and how the ants hastened their retrieval and transport of these seeds when disturbed by yellowjackets (no vouchers seen).

Taxonomic history of the *Formica pallidefulva* group

The taxonomic history of this group begins with the description of the species *Formica "pallide-fulva"* by the French naturalist Latreille (1802). *F. schaufussi* was first described as a separate species by Mayr (1866). Emery (1893) relegated *F. schaufussi* to a subspecies of *F. pallidefulva*, and described several new varieties and subspecies of *F. pallidefulva*. The subgenus *Neoformica* was published twice in the same year by W. M. Wheeler to encompass these taxa, first while designating *F. pallidefulva* as its type species (1913a) and later in the formal description of the new subgenus in his revision of *Formica* (1913b). In the latter, Wheeler described the varieties *dolosa* (cursorily described as var. *meridionalis*, an unavailable name, by Wheeler in 1904, then renamed by him in 1912) and *succinea*. Buren (1944) first used the taxon *dolosa* at the subspecies rank. Two further subspecies, *F. p. delicata* (Cole 1938) and *F. p. archboldi* (M.R. Smith 1944), were added to the described forms in this group that Creighton attempted to organize in his classic *Ants of North America* (1950).

Creighton popularized the subgenus name *Neoformica* and attempted to organize the taxa in the group by reducing them (among those species treated in the present work) to three species; the Floridian *F. archboldi*, and two widely-distributed species, the relatively non-pilose *F. pallidefulva* (with northern and southern subspecies *nitidiventris* and *pallidefulva*) and the very

pilose *F. schaufussi* (with northern and southern subspecies *schaufussi* and *dolosa*). Leaving aside for later some nomenclatural problems with Creighton's scheme, it has become clear that his classification was an oversimplification, since it synonymized the ecologically and morphologically distinct *F. incerta*, and left unrecognized the new species described below. Both of these species have rather variable arrays of macrochaetae and if, as seems to be the case in many of the "identified" specimens we examined, abundance of pilosity is the primary or only trait used to identify them, rubbed specimens or individuals near the extremes of intraspecific variation within *F. incerta* or the new species may easily be misidentified as belonging to Creighton's concepts of either *pallidefulva* or *schaufussi*.

Finally, Wheeler's (and Creighton's) concept of *Neoformica* also encompassed *F. moki* Wheeler, its subspecies *grundmanni* (now a synonym of *xerophila*) and *xerophila* M. R. Smith (now a full species). These latter are all now considered members of the *F. fusca* group. Excluding these taxa, the monophyly of the *F. pallidefulva* group may be supposed on morphological (this study) and genetic grounds (Riitta Savolainen, personal communication). Nevertheless, Buren (1968) synonymized this and the other subgenera into *Formica*, and we will let this stand until a proper phylogeny of *Formica* is completed. *Neoformica* does continue to appear in print, even as a genus name, especially in the non-taxonomic ant literature (*e.g.* Abouheif & Wray, 2002)

Suggested and possible relatives of the *Formica pallidefulva* group

Several *Formica* species from outside of eastern North America have been suggested as members or relatives of the *F. pallidefulva* group.

Among these, *F. rufolucida* Collingwood is the most similar to members of the *pallidefulva* group in outward appearance, but we believe it is not a member of, or even a sister group to, the *pallidefulva* group. *Formica rufolucida* is a rather shiny species with long scapes and rounded propodeum from 7000 ft. elevation in the mountains of Burma (Myanmar). It was suggested as a geographically disjunct member of the *F. pallidefulva* group and placed in *Neoformica* by Collingwood (1962). Bolton (1995) questioned even the generic placement based on the extraordinary location, but a paratype specimen of this species sent by Mr. Collingwood confirms it as *Formica*. The thoracic sternal region of the specimen could not be examined, and males are unknown, but the examined specimen otherwise has the proportions and sculpture (although subtle) of the *fusca* group, not of the *pallidefulva* group.

The Iberian *F. subrufa* Roger has a superficial resemblance in the worker's proportions, sculpture and pilosity to *F. archboldi*, but the concave mesonotum of the workers and unusual proportions of the sexual forms of this Spanish species are quite different from those of any species in the *pallidefulva* group. Similarities between *F. subrufa* and the *pallidefulva* group could well be symplesiomorphies, as these groups are both near the base of the cladogram in a tentative, DNA-sequence based phylogeny of *Formica* being elucidated by Riitta Savolainen (personal communication).

F. moki and *F. xerophila* are western North American species that also have long scapes and a rounded propodeum. Despite their long limbs, these ants fall short of the gracile form of the *pallidefulva* group, especially the mesosoma, and are quite different in vestiture, and especially, sculpture. Furthermore, *F. moki* at least, is parasitized by *Polyergus breviceps* (*s. l.*), perhaps an indication of its closer relationship to other hosts of this species. The mesometasternum of *F. moki* differs in conformation and pilosity from that of *pallidefulva* group species described below. R. Snelling writes (personal communication) that the genitalia of *F. moki* are similar to *fusca* group males, lacking the elongated parameres of *pallidefulva* group males.

METHODS AND TERMINOLOGY

J. Trager collected specimens of these ants from the 1970's till the present, in locations from Long Island to Florida and Iowa to Colorado. Some colonies were reared for one or more years to obtain males of certain identity. The *Polyergus lucidus* complex was another focus of collection efforts over the same period, and colonies of these Amazon ants yielded host populations that seemed in the field to belong to a single *pallidefulva* group species per slavemaker colony, a suspicion confirmed in this study. Species of the *pallidefulva* group also turned up in sampled host populations of dulotic *Formica*, particularly *F. pergandei* Emery over much of its range and *F. creightoni* Buren in northern Missouri. In addition to Trager's extensive collections, MacGown also collected specimens of this species group in the southeastern United States from 1988 to the present, an area that sorely lacked distributional data. The result was a good sampling of all species from much of their natural range.

In SPECIMENS EXAMINED under each species, we list for each State only the counties from which specimens were collected, not the specific localities.

Museum specimens borrowed for study or examined *in situ* augmented the Trager material (JCT). Particularly important were types of Gustav Mayr, Carlo Emery, William M. Wheeler and Arthur Cole from the following museums (and the people who facilitated the loans): Museo Civico de Historia Natural "Giacomo Doria", Genova (MCSN-Roberto Poggi), Naturhistorisches Museum Wien (NMW-Stefan Schoedl), Harvard University Museum of Comparative Zoology (MCZ-Stefan Cover) and the Los Angeles County Museum of Natural History (LACM-Roy Snelling). Other important entomological collections consulted included those of Archbold Biological Station (AABS-Mark Deyrup), the Florida State Collection of Arthropods (FSCA-Jim Wiley), the entomology department collections of the University of Arkansas – Fayetteville (UAAM-Jim Whitfield), the University of Missouri – Columbia (UMRM-Robert Sites), Mississippi State University (MEM-Joe MacGown), and the University of Wisconsin – Madison (IRCW-Andrew Williams, Scott Sauer). The last is where the voluminous collections of Mr. Williams's Insect Associates of Prairie Plants study and the Prairie Insect Survey of the Wisconsin Department of Natural Resources are housed. Other colleagues too numerous to mention sent one or a few samples each from interesting localities or as vouchers for their own studies.

Drawings for Figures 1 and 4-6 were done on a Leica MZ 16 stereomicroscope, using a drawing tube. Figure 1 was drawn at 63×, Figures 4-6 were drawn at 50×, except for the pubescence maps (Figure 4, insets) that were drawn at 100×.

Metric characteristics included measurements of body parts (mm) and indices calculated from them, as well as tooth and hair counts, as listed below. Measurements and meristic characters were acquired at 50× or 100× magnification, and data were entered in spreadsheets and converted to hundredths of millimeters for analysis. Summarized morphometric data for all specimens examined are presented in Tables 1 and 2.

MdT - number of mandibular teeth including any conspicuous denticles added to the basic number of 7. Specimens with MdT=6 appeared in every case to be older individuals in which any denticles and one of the (usually) smaller teeth were worn away.

P5L, P6L - lengths of 5th and 6th labial palp segments.

PnML, PpML, TML - lengths of longest erect hair (M = macrochaeta) on dorsum of pronotum, propodeum and center dorsum of first gastral tergite.

TPL - length of a longest microchaeta (shorter, appressed hairs collectively called pubescence) among those visible on the disc of the first gastral tergite.

HL - head length from distal tip of clypeus to posterior margin of head in full face view.

HW - maximum head width (exclusive of eyes) in full face view.

EL - compound eye length, in oblique view of the head, showing full surface of eye.

SL - scape length, with viewing angle perpendicular to the scape.
WL - length of mesosoma (traditionally called Weber's Length of thorax), from anterior extremity of pronotum (exclusive of pronotal collar) to posterolateral extremity of mesopleuron.
PnW - width of pronotum.
PnM, MnM, PpM - number of erect or suberect macrochaetae on pronotum, mesonotum and propodeum.
TM - number of macrochaetae on first gastral tergite, exclusive of those along the posterior border.
CI - Cephalic index, HW / HL × 100
SI - Scape index, SL / HW × 100 (This is a good surrogate for relative length of the limbs, generally.)
OI - Ocular index, EL / HL × 100
CTI - Cephalothoracic index, HL / WL × 100
TWI - Thoracic width index PnW / WL × 100 (This is a good surrogate for overall gracility.)

We first analyzed the morphometric data with discriminant function analysis (DFA), a statistical procedure used to classify individuals and then predict group membership (species, in this case) based on a set of predictor variables (Tabachnick & Fidell, 1996). Because this method can consider a large number of variables, DFA can be applied to difficult taxonomic relationships when there are only small differences among taxa for any one characteristic (*e.g*. Bell, 1996; Burbrink, 2001; Floate & Whitham, 1995; Green *et al.*, 1996). In this analysis we performed stepwise DFA (using Wilks' Lambda as a measure of variable contribution with enter F at P = 0.05; removal F at P = 0.10) to test whether the specimens used to describe species in this revision actually belonged to statistically distinct groups that differed across a set of morphological measurements, thus verifying the morphologically-based taxonomy proposed in this paper. We also conducted univariate ANOVA on some of the morphometric data to distinguish between frequently confused pairs of species. All tests were performed with SPSS 11.5. The statistical analysis is meant to provide a quantitative complement to the morphological descriptions, natural history information and key to the species provided below. It follows the species accounts and precedes the key to species.

Species of the *Formica pallidefulva* group

Based on earlier observations, this study began with a working hypothesis of seven species in the group, namely the Floridian *archboldi* and three north/south species pairs: *schaufussi/dolosa* of well-drained, acid soils*; nitidiventris/pallidefulva* of mesic, neutral soils, *incerta*/new species of open grassland habitats. Measurements and other characteristics obtained during this study confirmed the separate species identities of *incerta* and the new species (described below as *F. biophilica* **n. sp.** Trager), while the first two pairs of taxa were found to represent extremes of regional variation within two single-species populations. Thus, there is a total of five distinct species, as below. The correct names for each population were determined through study of type specimens.

Formica archboldi M. R. Smith, 1944
Figures 4d, 5d, 6d

Formica pallidefulva subsp. *archboldi* Smith, M.R., 1944: 16. [*Examined.* Syntype workers] four workers on two pins, labeled, Florida: Archbold Biological Station, 10 miles south Lake Placid, Fla. X-7-43 T. C. Schneirla. Paratype No. 56765 U.S.N.M. (MCZ).

Formica (Neoformica) archboldi Creighton, 1950: 549. Raised to species.

DIAGNOSIS

Worker – The most evidently sculptured and the smallest member of the group, characteristic of Florida's upland pine and scrub habitats. *F. archboldi* has the largest eyes relative to head size of all species in this group (see OI, Table 1). Head and gaster very dark reddish brown, appearing blackish or dark gray-brown in the field; mesosoma often a little lighter than head, and sometimes both lighter than gaster. Gastral dorsum at most weakly shining, sheen dulled by numerous, shallow impressions (foveolae) and appressed pubescence composed of moderately dense grayish appressed microchaetae (Fig. 4d). Dorsal sclerites of mesosoma and gaster usually with moderately abundant, short, erect, brownish-gray erect macrochaetae, and pale grayish appressed microchaetae. Erect macrochaetae on mesosoma and usually on gaster are relatively short, straight and flattened with rounded, blunt or abruptly tapering tips; less often, at least some of those on gaster a bit longer and slightly curved, these less flattened and tapering.

Queen – Color, gastral pubescence and sculpture like the workers', with the usual differences in size. There is tessellation on the upper portion of head, pronotum, sides of mesothorax, propodeum and gastral dorsum; wings, when present, clear brownish to clear smoky gray. Pilosity longer and more flexuous than that of worker.

Male – Pubescence and pilosity abundant; mesosomal dorsum dull-punctate; entire body black, legs reddish brown or mesosoma lighter, dusky yellowish brown; wings clear brownish to clear smoky gray; pilosity like that of queen; gastral pubescence pale brownish yellow and very dense. Averages smaller than the otherwise difficult-to-distinguish males of *F. dolosa* and *F. biophilica*.

DISTINGUISHING FEATURES

Although a sample of this species in the Mayr collection is placed among his "s*chaufussi*" (anything in the group which was not typical *F. pallidefulva* is so placed in that collection), this dark brown to nearly black species has rarely been misidentified since its description in 1944 and is unlikely to be confused with any congener in the field. Mounted specimens that are shinier and less pilose than normal, or mislabeled ones (like those from "Virginia" in the Mayr collection), might be confused with darker color variants of *F. incerta* or *F. pallidefulva* without careful inspection. Occasionally other species, especially *F. biophilica*, may stain black when mounted on pins, which could lead to confusion with *F. archboldi.*

ETYMOLOGY

This species is named after Richard Archbold, founder of Archbold Biological Station, Lake Placid, Florida, the type locality.

RANGE AND HABITAT

Originally described from Archbold Biological Station in Highlands Co., Florida, this species in fact appears to be more abundant in northern Florida. It is a characteristic ant of the uplands of peninsular Florida and the eastern panhandle, and also recorded by D. R. Smith (1979) as occurring in Georgia and Alabama. One collection in the Mayr collection labeled "Virginia" is doubtless mislabeled. This ant is characteristic in relatively undisturbed, long-leaf pine sandhills and in scrub or sand pine woodland. Less often it may be found in the transition between these more open sandy habitats and drier portions of flatwoods, or southern live oak woodlands. In northern Florida, *F. archboldi* coexists with *F. dolosa* and *F. pallidefulva* in

sandhill vegetation, but to the south on the Lake Wales Ridge (including the type locality), this ant becomes more typical of moist soil among pond-edge vegetation in swales within the white sand scrub vegetation, and is largely replaced in sandhill woodland by *F. pallidefulva*. It is also reported from sandhill locations along the South Florida coasts, but probably is lacking from the Everglades.

SPECIMENS EXAMINED

FLORIDA: Alachua; Baker; Citrus; Collier; Duval; Hernando; Highlands; Hillsborough; Jackson; Leon; Levy; Liberty; Marion; Okochobee; Pasco; Putnam; Sumter; Suwannee; Volusia; Wakulla.

D.R. Smith (1979) reports *F. archboldi* from ALABAMA: no county listed. GEORGIA: no county listed.

NATURAL HISTORY

Within the *pallidefulva* group, this species is the most sensitive to human development and habitat alteration. During eight years of residence in Gainesville FL, J. Trager watched this species slowly disappear from sandhill woodland habitats near new housing developments, even when efforts were made to protect the native vegetation in green space around the houses. On the other hand, at Devil's Millhopper Geological State Park during the same years, ecological restoration efforts consisting of selective species removal (cutting down mesic-adapted trees) and introduction of prescribed fire to maintain the open vegetation structure, resulted in a resurgence of *F. archboldi* (and incidentally, *F. dolosa*) in the upland habitats of the site. A healthy population of *F. archboldi* could be considered an indicator of high natural area integrity, or at least a low level of habitat degradation, in Florida's pine and pine-oak woodlands.

Nests are usually located beneath wiregrass clumps (or beneath beard grass or sedges in scrub habitats), and occur less frequently in bare soil, at the base of a shrub or under oak-leaf litter. The entrance is often marked with a small accumulation of plant fragments and/or grasshopper dung. Returning foragers watched for ½-hour intervals in the afternoon foraging period typically brought in more of these plant fragments and dung pellets than they did prey items (J. Trager, unpublished). Worker pupae are typically enclosed in a light tan cocoon, sexual pupae in a darker, thicker cocoon. This species is the host of the small, dull variant of *Polyergus lucidus* that uses *F. archboldi* as its host in Florida (Trager & Johnson, 1985). *F. archboldi* lives outside the range of dulotic or other parasitic *Formica* species.

The cricket *Myrmecophila pergandei* Bruner commonly inhabits the nests of *F. archboldi*. Outside the nest, *F. archboldi* gathers honeydew from living plant surfaces and from leaf litter, and also actively tends and defends *Cinara* aphids and *Toumeyella* scales on "grass-stage" long-leaf pine saplings. The defense by *F. archboldi* as they tended scales was used to induce workers to "attack" a termite offered on the end of a pine needle, then following the light-bodied prey as a marker to follow as the worker returned to its nest. In two cases, this resulted in the discovery of a colony of the *Polyergus lucidus* variety mentioned above.

Foraging occurs mainly between 8 a.m. and noon and between 4 p.m. and dusk, from March through October. However, hemipteran colonies are tended around the clock. Peak foraging activity occurs from April through June. Returning foragers carry a variety of freshly killed insects into the nest. Most of these prey items are herbivorous insects, but also among them are occasional individuals of *Odontomachus brunneus* Patton. Just how it is that this smaller and less ferociously built *Formica* captures and kills this well-armed ponerine has not been observed. Trager & Johnson (1985) report on habits of *F. archboldi*.

Sexuals occur in the nests from late April through June. The alates are not attracted to lights. They apparently fly in early morning, around sunrise. Females must quickly dealate and

sequester themselves, as it appears no one has ever found either a newly mated female or incipient colony of this locally abundant ant.

Formica biophilica James C. Trager **new species**
Figures 4b, 5b, 6b

Formica pallidefulva: Creighton, 1950, in part [Misidentification]
Formica schaufussi subsp. *dolosa*: Creighton, 1950, in part [Misidentification]

TYPE DATA

HL 1.43; HW 1.15; EL 0.42; SL 1.70; WL 2.34; PnW 0.95; PnM 6 ; PpM 14 ; TM 30

Type specimen label: ALABAMA, Chilton Co., Interstate-65 rest area 3 mi. E of Thorsby. 1-X-1983. M.B., J.R., B.R. DuBois. (JCT). Holotype and three paratypes on two pins. The holotype and one paratype will be deposited at MCZ and the other two specimens will be added to the excellent material of this species collected in Alabama and elsewhere by W. S. Creighton, now housed at LACM.

DIAGNOSIS

Worker – Gracile, shiny, and the brightest yellow member of the group. Head, mesosoma and legs light reddish- to pale brownish yellow; head and mesosoma not at all or only a little lighter than gaster. Dorsal sclerites of mesosoma and especially the gaster with long, usually curved, erect macrochaetae. Number of macrochaetae on propodeum usually exceeds the number on the pronotum (20 of 32 specimens examined). Sheen of gaster readily visible through pubescence composed of pale, slender, grayish hairs of medium density (Fig. 4b). Erect macrochaetae on gaster long, commonly 0.25-0.30 mm, tapering to a point and curved (Fig. 6b).

Queen – Color, gastral pubescence and shininess like the workers', with the usual differences in size; with faint tessellation of upper portion of head, pronotum, sides of mesothorax, propodeum and gastral dorsum; wings, when present, clear to light brownish.

Male – Pubescence and pilosity abundant; mesosomal dorsum dull-punctate; head and gaster very dark brown, appearing black; mesosoma dusky yellowish brown, legs reddish brown; wings clear to light brownish. A little brighter in color, especially mesosoma, less pilose, pilosity also finer, and less pubescent than *dolosa*.

DISTINGUISHING FEATURES

F. biophilica and *F. incerta* are sympatric in the southern part of the latter's range. In the field, *F. biophilica* appears more brightly and uniformly reddish-yellow in color, and (if several workers of a colony are present) weakly polymorphic, whereas *F. incerta* is more brownish yellow, smaller overall, and usually (though not invariably) more monomorphic within colonies. Metrically, *F. biophilica* is more slender, has a proportionally longer mesosoma and narrower head than *F. incerta* (compare SI, TWI and CI values, Table 1). *F. biophilica* usually has more macrochaetae on the propodeum than on the pronotum (20 of 32 specimens), whereas *F. incerta* usually has more macrochaetae on the pronotum than on the propodeum (22 of 31 specimens).

F. biophilica is also somewhat more brightly and uniformly colored, shinier and overall less hairy, and has a sharper petiolar crest in profile than *F. dolosa*. The *F. biophilica* specimens examined in this study also had a significantly higher CTI and OI (were more slender and had relatively larger eyes) than *F. dolosa* (Table 1). In the South, the less pilose minor workers and nanitics of *F. biophilica* are difficult to differentiate from *F. pallidefulva*. Often a rather squarer

propodeal profile and more uniform bright reddish yellow color indicate *F. biophilica*. Additionally, on average the TWI of *F. pallidefulva* is larger than that of *F. biophilica* (Table 1). Ecologically, specimens from fens, bogs, swamps and fresh or salt marshes are most likely to be *F. biophilica*. In the northern part of the range of *F. biophilica*, its bright color will always distinguish it from the at least partially brown *F. incerta* and *F. pallidefulva*.

ETYMOLOGY

The name *biophilica* is given in allusion to E. O. Wilson's popularly inspirational coining "biophilia", meaning the love of other species as a part of human nature. Specimens from Alabama, Dr. Wilson's home state, were chosen as the type series to further honor his contributions to myrmecology, conservation and behavioral biology.

RANGE AND HABITAT

Found in mesic to hydric open habitats, including fields, prairies, lawns, fens, bogs, marshes and open woodlands, from the Carolinas to Missouri, south to northern Florida and central Texas. Northward, its occurrence is more sporadic, especially in formerly glaciated regions, where *F. biophilica* shifts to drier (thus warmer) loess and sandy grassland locations. It reaches central Illinois in the Illinois River outwash sand prairies and reaches southeastern New York in the sandy plains along the East Coast and on Long Island. The habitat overlaps that of *F. incerta* in unglaciated prairies and eastern meadows, and overlaps that of *F. dolosa* in southern pine woodland and savanna. *F. biophilica* is absent from the most xeric and infertile sites occupied by *F. dolosa*. In the Ozarks and other southern U.S. hills, *F. biophilica* occurs in groundwater fens, bogs, marshes and flatwoods. This is the only southern *Formica* that occurs in these wetland habitats, where it nests in the elevated hummocks of organic matter formed by grass or sedge tussocks. It is less common than *F. pallidefulva* in human habitats, but occasionally shows up in lawns, parks and campuses, especially in parts of the South where fire ants are less abundant.

SPECIMENS EXAMINED

ARKANSAS: Logan; ALABAMA: Butler; Chilton; DeKalb; Lawrence; Mobile; Morgan; St. Clair; Tuscaloosa; DELAWARE: Sussex; DISTRICT OF COLUMBIA: Washington; FLORIDA: Alachua; Columbia; Gadsden; Okaloosa; Polk; Walton; GEORGIA: Clarke; Habersham; Lumpkin; Rabun; ILLINOIS: Mason; LOUISIANA: Natchitoches; Tammany; Washington; MISSISSIPPI: Alcorn; Bolivar; Chickasaw; Lafayette; Lee; Monroe; Oktibbeha; Panola; Pontotoc; Tippah; MISSOURI: Franklin; Lincoln; Reynolds; Washington; NEW YORK: Rockland; SOUTH CAROLINA: Pickens; TENNESSEE: Davidson; Monroe; Sevier; TEXAS: Cass; Collin; Potter.

NATURAL HISTORY

Nests of *F. biophilica* have simple, cryptic openings in wetlands, grasslands or less often, in open woodlands. The entrance is usually hidden amongst grass or sedges. In springtime, colonies of *F. biophilica* may build a 10-25 cm diameter mound of soil and plant fragments nestled against a grass or sedge clump, this collapsing in disuse during the hot, dry weather of summer. In fens, bogs and wet meadows, when ground at the base is permanently or seasonally saturated, *F. biophilica* nests in the upper parts of graminoid tussocks. One colony under a strip of bark in unmowed grass in eastern Missouri contained four larvae of myrmecophilous staphylinid beetles, probably *Xenodusa cava* LeConte (but not collected for determination).

This species has been found as host to the slavemaker *Polyergus lucidus s. l.* in Washington, D.C., northern Georgia and east-central Missouri. The variety of this slavemaker parasitizing *F. biophilica* has longer scapes and is somewhat less shiny and slightly more pubescent than typical *P. lucidus lucidus* Mayr, which parasitizes *F. incerta*. *F. biophilica* occurs among the many hosts of *F. pergandei* in the prairies of Missouri, but has only been observed in combination with other host species. At one site, a *F. pergandei* nest contained a mélange of six slave species including (in order of decreasing relative abundance) *F. pallidefulva*, *F subsericea* Say, *F. biophilica*, *F. dolosa*, *F. incerta* and *F. obscuriventris* Mayr, certainly the most species-rich, naturally occurring ant colony on record!

Sexuals have been collected in nests in Missouri, Texas and Georgia in mid-June to early July, but no flight or colony-founding activity has been recorded. There is one example of a queen-male bilateral gynandromorph in a Missouri collection. The worker pupae are always enclosed in a pale tan cocoon, and the sexuals in a larger, darker cocoon.

Formica dolosa Buren, 1944 **stat. nov.**

Figures 1, 4e, 5e, 6e

Formica pallidefulva subsp. *schaufussi* var. *meridionalis* Wheeler, W. M. 1904: 370 [Unavailable name.]

Formica pallidefulva subsp. *schaufussi* var. *dolosa* Wheeler, W. M. 1912: 90 [Unnecessary replacement name for *meridionalis*; also unavailable.]

Formica pallidefulva subsp. *schaufussi*: Wheeler, W. M. 1913b: 552 (in part) [Misidentification.]

Formica pallidefulva subsp. *schaufussi* var. *dolosa*: Wheeler, W. M. 1913b: 554

Formica (*Neoformica*) *schaufussi* subsp. *dolosa* Buren, 1944: 309. [First available use of *dolosa*.] Syntype workers, Bull Creek, Travis Co., Texas (W. M. Wheeler) (MCZ) [*Examined*. Three workers on one pin, labeled "true types of *dolosa*" by S. Cover, and two gynes on one pin labeled syntypes by S. Cover]

Formica pallidefulva subsp. *schaufussi*: Emery, 1893: 654 [Misidentification.]

Formica schaufussi: Creighton, 1950: 551 [Misidentification.]

Formica schaufussi subsp. *dolosa*: Creighton, 1950: 551

Formica schaufussi: Robson & Traniello, 1998: (in part) [Vouchers examined.]

NOTE: We have selected a specimen in the Mayr collection (NMW) labeled "Nord Amerika / Schaufuss" as lectotype of *Formica schaufussi* Mayr, as this corresponds to the locality and collector information in Mayr's (1866) description. This sample clearly belongs to the much less pilose *Formica pallidefulva*. Thus, the name *Formica schaufussi* Mayr falls to the synonymy of *Formica pallidefulva*, below.

DIAGNOSIS

Worker – The largest, most pilose, most densely pubescent and least shiny of reddish-yellow members of the *pallidefulva* group (*F. archboldi* is duller, but always much darker and averages smaller). Weakly bicolored; head, mesosoma and legs light coppery red (south) to yellowish or reddish brown (north); gaster a little darker than head and mesosoma. Dorsal sclerites of mesosoma with abundant erect pilosity (Fig. 6e); erect macrochaetae on gaster abundant and long (longest macrochaetae 0.16-0.30 mm), straight to slightly curved. Mesosoma, especially propodeal dorsum, pubescent; gaster dulled by long, dense, pale grayish, appressed microchaetae (Fig. 4e). Gaster with small shallow foveolae in some samples, these nearly lacking in others. The propodeal crest is nearly always rounded in *F. dolosa*. The larger workers of this species are the largest eastern US *Formica*, matched within the genus only by the allopatric and otherwise quite different *F. ravida* Creighton.

Queen – Color, gastral pubescence, abundant pilosity and lack of shininess like the workers', with the usual differences in size. Sculpture a little more accented with notable fine tessellation of entire head, mesosoma and gastral dorsum; wings, when present, clear brownish to dark smoky gray. Three mesoscutal spots present as in *F. incerta*, but these pale and diffuse.

Male – Pubescence dense and pilosity abundant; surface sculpture punctate; head and gaster dark brown, mesosoma reddish brown to dark reddish brown with legs the same color; wings dark smoky gray. Larger than the nearly similar *F. incerta*, in which the mesosoma is normally about the same color as the head and gaster.

DISTINGUISHING FEATURES

The propodeal crest of *F. dolosa* is nearly always rounded in profile, and is typically sharp or even carinulate in the other species. This large, hairy, densely pubescent and faintly bicolored ant is most likely to be confused with *F. biophilica*. Compared to *F. biophilica*, *F. dolosa* has conspicuous appressed pubescence on the mesosoma, has more abundant, but slightly shorter gastral pilosity (longest macrochaetae up to 0.30 mm), has longer, denser pubescence on the gaster (compare Fig. 4b and 4e), and averages larger and heavier-bodied. The number of macrochaetae on the pronotum usually exceeds that on the propodeum of *F. dolosa*, (46 of 54 specimens) whereas the number on the propodeum more often exceeds that on the pronotum of *F. biophilica* (20 of 32 specimens). *F. dolosa* usually has relatively smaller eyes compared to *F. biophilica* (Table 1). In the field, *F. dolosa* occupies the drier end of the habitat spectrum, the two overlapping mainly in pine-oak woodlands of the Southeastern U.S., and in dry-mesic prairies further north. In the Northeastern U.S., larger, more pilose workers of *F. incerta* are often misidentified as *F. dolosa*, but *F. dolosa* averages larger and more pilose, has mesosomal pubescence and denser gastral pubescence, has longer scapes and legs; is generally lighter, more yellowish or reddish in color, and is more strictly associated with highly drained soils.

ETYMOLOGY

This name comes from the Latin adjective *dolosus*, meaning cunning or sly. Perhaps Wheeler was referring to the fleetness of its escape when alarmed, as this species is very shy and an excellent "escape artist".

RANGE AND HABITAT

Widely distributed from New England across the Great Lakes region, west to Wisconsin and Iowa and south to northern Florida, the Gulf Coast states and Texas. Records of this ant in Colorado by Gregg are all misidentified *F. incerta* (L. Rericha, personal communication). *F. dolosa* is decidedly most abundant on acid-soil sites. These include a variety of droughty or well-drained habitats such as barrens, glades, prairies or open oak or pine woodlands on silicaceous or loessic soils. Though reported (as *schaufussi*) from plowed fields and pastures in the Northeast, *F. dolosa* is not usually common in such communities. J. Trager found *F. dolosa* in calcareous glades in Alabama and Missouri, but it is not abundant in these sites. In stark contrast to *F. incerta* and *F. biophilica*, *F. dolosa* does not nest in mesic habitats or in moist, fertile soils.

SPECIMENS EXAMINED

ALABAMA: Lawrence; ARKANSAS: Logan; FLORIDA: Alachua; Bay; Columbia; Escambia; Gilchrist; Jackson; Jefferson; Lake; Leon; Liberty; Okaloosa; Santa Rosa; Suwannee; Walton; GEORGIA: Clarke; Lumpkin; ILLINOIS: Mason; MARYLAND: Allegany;

Dorchester; MASSACHUSETTS: Plymouth; Worchester MISSISSIPPI: Chickasaw; Choctaw; Lafayette; Lee; Lowndes; Noxubee; Oktibbeha; Pontotoc; Scott; Tishomingo; Winston; MISSOURI: Franklin; Johnson; Lincoln; Washington; NEW JERSEY: Ocean; NEW YORK: Nassau; Suffolk; NORTH CAROLINA: Nash OHIO: Adams; SOUTH CAROLINA: Aiken; Barnwell; McCormick; Oconee; TEXAS: Travis; WISCONSIN: Adams; Crawford; Dane; Grant; Iowa; Marshall; Sauk; Walworth; Waukesha.

NATURAL HISTORY

Nests may be hidden beneath a rock or piece of wood, but most nest entrances are at the base of a grass clump or other herbaceous plant. Some open onto bare ground, the entrance surrounded by a crater of excavated soil adorned with plant fragments, charcoal bits or fine gravel. J. MacGown collected *F. dolosa* in nests at the bases of large trees on relatively drier and more open ridges in mixed forests in northern Mississippi, and from an infrequently mowed area under loblolly pines near his house in Oktibbeha Co. Mississippi. The nest at the latter site was a low mound about 45 cm across and about 15 cm high at the midpoint. Part of the mound was inhabited by *Camponotus castaneus* Latreille.

In the East and Gulf Coast United States, *F. dolosa* is host to the slavemaker *Polyergus lucidus longicornis* M. R. Smith. J. Trager's collection contains samples of this slavemaker with *F. dolosa* slaves from Massachusetts, New York, New Jersey, South Carolina and Mississippi. In Missouri, *F. dolosa* is occasionally among the many hosts of *F. pergandei*, but we have only observed them in combination with other host species (see "Natural History" of *F. biophilica* for a case in point). In Florida, J. Trager observed *F. dolosa* and *F. archboldi* competing for domination of colonies of *Toumeyella* scales on long-leaf pine "grass-stage" seedlings. Occasionally, fights would arise in which the larger *F. dolosa* threw or chased *F. archboldi* workers to the ground.

Winged sexuals were collected in nests in mid-June in Florida and Georgia, and one male was found in a nest in western Missouri in August. Both worker and sexual pupae are always enclosed in a cocoon.

Formica incerta Buren **stat. rev., stat. nov.**

Figures. 4c, 5c, 6c

Formica pallidefulva subsp. *schaufussi* var. *incerta* Emery, 1893 [Unavailable name]
Formica (Neoformica) pallidefulva subsp. *schaufussi* var. *incerta*: Wheeler, 1913b
Formica (Neoformica) pallidefulva subsp. *incerta*: Buren, 1944 [First available use of *incerta*] Syntype workers, District of Columbia, iv-13-1886 (MCSN) [*Examined*. Five workers on three pins labeled paratypes by A. Francoeur]
Formica (Neoformica) pallidefulva: Creighton, 1950, in part
Formica (Neoformica) schaufussi: Creighton, 1950, in part
Formica schaufussi: Robson & Traniello, 1998, in part [Vouchers examined] (JCT)

DIAGNOSIS

Worker – A relatively shiny grassland *Formica* with a relatively broad head (mean CI = 86.77), sides of head more convex (Fig. 5c) and scapes relatively short (mean SI = 132.99). Head and gaster rich, dark brown (northeast) to brownish-yellow with darker tip (prairie region). Mesosoma and legs yellowish-brown to light yellowish-brown. Mesosoma often a little lighter than head, and both lighter than gaster. Specimens in the Great Plains portion of the range are nearly concolorous brownish yellow except for the darker gastral apex. Mesosomal macrochaetae of *F. incerta* typically conspicuously shortest on propodeum. Erect pilosity on gaster relatively short, straight or only slightly curved, if curved, usually below the mid-point of

the length of the macrochaetae. Gaster shiny, but its sheen dulled by faint tessellation and medium density pubescence (Fig. 4c) composed of pale grayish appressed microchaetae

Queen – Color, gastral pubescence and shininess like the workers', with the usual differences in size. Color pattern differing from workers' and from that of queens of all other species in that there are three distinct, dark spots on the mesoscutum, one anteromedian and two lateral over the parapsidal sulci. These may cover most of the mesoscutal area or may be reduced to longitudinal dark elliptical marks. Upper portion of head, pronotum, sides of mesothorax, propodeum and gastral dorsum with faint tessellation. Wings, when present, clear brownish to clear smoky gray.

Male – Pubescence and pilosity abundant; mesosomal dorsum dull-punctate; entire body uniform black or dull blackish brown, legs reddish brown; wings clear brownish to clear smoky gray. Averages smaller than the nearly similar *F. dolosa* and smaller and of more uniform blackish color than males of *F. biophilica*.

DISTINGUISHING FEATURES

Metrically, *F. incerta* is distinguished from the other species in the group by a relatively broad head and short scapes (CI and SI, Table 1). In the northeast part of its range, more pilose *F. incerta* individuals may be confused with *F. dolosa,* and *F. incerta* specimens with little pilosity may be confused with *F. pallidefulva*. The geographic range of *F. pallidefulva* completely overlaps that of *F. incerta,* and most places where they are found together in the field, *F. incerta* appears lighter in color and less shiny than *F. pallidefulva,* due to some faint tessellation on the mesosoma and somewhat longer, denser pubescence on the gastral dorsum of *F. incerta*. Mesosomal and gastral pilosity is usually much less abundant than in *F. dolosa* and averages slightly less abundant than in *F. biophilica.* Also, *F. incerta* is darker and shinier than sympatric *F. dolosa.* See *F. biophilica* account for the differences between *F. incerta* and that species.

ETYMOLOGY

This name was coined by Emery from the Latin adjective *incertus* meaning uncertain. This seems appropriate to describe Emery's own and subsequent authors' doubts regarding the validity of this species.

RANGE AND HABITAT

This species occurs from New England and the Great Lakes States west to Minnesota, Nebraska and low elevation grasslands of Colorado (and New Mexico?). It extends south in eastern US to the balds, meadows and old fields of the southern Appalachians. *F. incerta* is especially abundant in native mesic and dry-mesic grasslands, but also occurs in parks, campuses and lawns, fields and forest clear-cuts. In the Northeast, it occurs in heathland and sand barrens, and in the Midwest it is characteristic and abundant in prairie remnants, botanically diverse old fields and meadows, and native prairie reconstructions.

SPECIMENS EXAMINED

(CANADA) ONTARIO: Lambton. (UNITED STATES) CONNECTICUT: Litchfield; DELAWARE: Kent; DISTRICT OF COLUMBIA: Washington; ILLINOIS: DuPage; Madison; IOWA: Dubuque; Johnson; Winneshiek; KENTUCKY: Laurel; MAINE: Androscoggan; Cumberland; Kennebeck; MARYLAND: Allegany; Baltimore; MASSACHUSETTS: Essex; Worchester; MICHIGAN: Livingston; MINNESOTA: Crow Wing; MISSOURI: Audrain; Boone; Callaway; Franklin; Harrison; Jasper; Madison; St. Louis; NEBRASKA: Hall; NEW

JERSEY: Burlington; Essex; Gloucester; Salem; NEW YORK: Rockland; Suffolk; NORTH CAROLINA: Cocke; Haywood; OHIO: Adams; Butler; Champaign; Delaware; Hamilton; Hocking; Jackson; Montgomery; PENNSYLVANIA: Chester; Delaware; VIRGINIA: Farifax; Rapahannock; Washington; WISCONSIN: Crawford; Washburn; Waushara.

NATURAL HISTORY

Nests are in bare soil, or beneath a grass clump, in the latter case often with a small, irregular, conical (5-15 cm wide, 10-20 cm tall) mound of soil and plant fragments. This is often the first *Formica* species to become abundant on restored native grasslands, "Conservation Reserve Program" grassland plantings on former farmland and cut-over forests. A healthy population of *F. incerta* may facilitate colonization by its parasites *F. difficilis* and *F. pergandei*, if these occur nearby. It is less abundant than *F. pallidefulva* in lawns, campuses and parks.

This is often the most abundant *Formica* species in mesic tallgrass prairies from central Illinois, Nebraska and south to Oklahoma and northeast Arkansas, and also in balds, meadows and old fields at higher elevations of the southern Appalachian Mountains. Sweepnet samples from all these types of habitats rarely fail to include *F. incerta*, and thus insect collections housed at institutions near them may be rife with samples of individuals so captured. In the Great Lakes Region and New England, this species is more associated with sandy soils and pastureland and often nests under rocks. In the northern glaciated prairie region, *F. incerta* can be a dominant ant in sand prairies, but is largely displaced from sites with moister, finer-textured soils, which are dominated by aggressive, mound-building *Formica* species.

F. incerta appears to be the only host of *Polyergus lucidus lucidus* collections examined from New England states, New Jersey, southern Ontario, Wisconsin and Missouri. *F. incerta* is also frequent among the many hosts of *F. pergandei* and in western Missouri prairies commonly occurs as a slave of this species, either alone or in mixed populations with *F. subsericea*. *F. incerta* appears to be the primary host of alloparasitic (dispersing) queens of *F. difficilis* Emery, the queen of which bears a superficial resemblance to *F. incerta* workers. Indeed, Wheeler (1904) first used the term "temporary social parasitism" to describe the relationship he elucidated between *F. difficilis* (as var. *consocians*) and *F. incerta* in Connecticut.

This ant often visits extrafloral nectaries of sunflowers, partridge peas and other prairie plants. It also tends aphids and membracids on a variety of plants. *F. incerta* workers defend these sugar sources from non-nest mates of their own species, from other, smaller ant species and from some parasitoids. However, in areas where there are greater numbers of aggressive mound-building prairie *Formica* species (*e.g. F. montana* Wheeler, *F. obscuripes* Forel), *F. incerta* becomes more furtive and opportunistic in its honeydew gathering, as described below for *F. pallidefulva*. Foraging strategy and recruitment to food sources has been well studied in *F. incerta* (and incidentally, in *F. dolosa*) by Robson & Traniello (1998, and included references to their earlier work). These authors identified their study subject as *F. schaufussi* in the articles, but vouchers sent by Robson were examined for this revision. These were mostly *F. incerta*, but also included a sample of *F. dolosa*.

In grasslands, especially those recently burned, northern flickers (*Colaptes auratus*) prey heavily on *Formica* species, including *F. incerta*. This is especially so on sunny, late winter days when workers migrate intranidally toward the surface, seeking warmth.

Alates occur in the nests in July and August in New England and the northern prairies, and a few weeks earlier in the unglaciated prairie region and southern Appalachians. It is worth noting that the maturation of alates of *F. pallidefulva* may precede that of *F. incerta* in by two or three weeks, suggesting a possible temporal mechanism for reproductive isolation. Flights have not been observed, but several mated queens have been captured walking about in mid to late morning in Missouri. In the lab, these recently mated queens are "nervous" in captivity and often fail to rear their first workers, in contrast to the ready adaptability to captive conditions of *F.*

pallidefulva queens. Worker pupae are typically enclosed in a light tan cocoon and sexual pupae have darker tan cocoons. This is in contrast to the frequently naked worker pupae of *F. pallidefulva*, as was earlier noted by both Wheeler (1904) and Talbot (1948).

Formica pallidefulva Latreille
Figures 4a, 5a, 6a

Formica pallide-fulva Latreille, 1802 [Types not seen, supposedly type-compared material in MCZ examined]

Formica schaufussi Mayr, 1886 [Lectotype designated, labelled "N. Amer. / Schauf." (NHWC)] **Syn. nov.**

Formica pallidefulva subsp. *nitidiventris* Emery, 1893 [Type *examined*.] "310 B Wokland(?). D.C. with *Polyergus lucidus*. Paratype. *Formica nitidiventris* A. F.1968] **Syn. nov.**

Formica pallidefulva subsp. *fuscata* Emery, 1893. [Lectotype *examined*.] "Beatty PA. No. 314. LECTOTYPE *Formica pallidefulva* fuscata A. F. 1968. Synonymy, under *nitidiventris*, by Creighton, 1950: 551.

Formica pallidefulva var. *succinea* Wheeler, W. M. 1904 [Syntypes *examined*] Four workers on one pin, Bee Creek. Travis Co. TEX. XI.9.02 M.C.Z. Type 5-8 8844 var. *succinea* Wheeler. Synonymy by Creighton, 1950: 550.

Formica (Neoformica) pallidefulva: Wheeler, W. M., 1913 b [Vouchers examined] (MCZ)

Formica (Neoformica) pallidefulva subsp. *delicata* Cole, 1938 [Syntypes *examined*] 24 workers on 8 pins. Ten Sleep WY 9/31 A.C. Cole. Synonymy, under *nitidiventris*, by Creighton, 1950: 551.

Formica (Neoformica) pallidefulva: Creighton, 1950, in part [Vouchers examined] (MCZ, LACM)

Formica (Neoformica) pallidefulva subsp. *nitidiventris*: Creighton, 1950, in part [Vouchers examined] (MCZ, LACM)

DIAGNOSIS

Worker – Includes conventional reddish or brownish yellow *F. pallidefulva*, as well as darker populations known as *F. p. nitidiventris* and its synonyms *F. p. fuscata* and *F. p. delicata*. This is the shiniest *Formica* of this group (though smaller workers of *F. biophilica* and some series of *F. incerta* are also quite shiny). The mesosoma often lacks either appressed pubescence or erect pilosity, or has relatively few, short, erect macrochaetae (Fig. 6a). Pubescence, even on gaster, short and sparse (Fig. 4a). Sculpture faint to nearly smooth, best developed (to the point of slightly weakening the sheen) in the northeastern part of the range, where the form *fuscata* occurs. The gaster appears more voluminous than in other members of the group, and is quite shiny, as reflected in the name *nitidiventris*. Color is highly variable, generally uniform dark brown in Canada and New England, the Black Hills and western mountain areas, and concolorous coppery yellow or weakly bicolored (gaster a little browner) in the deep South. Various intermediate conditions occur in a broad band of territory from southern Missouri and northern Arkansas, across the upper South to the foothills of the southern Appalachians in Georgia and the Carolinas, and occasionally elsewhere. The transition area between typical *pallidefulva* and typical *nitidiventris* is a 300-mile wide band straddling the Mason-Dixon Line. In it, one may occasionally find single-queen colonies containing nearly the full range of color variation. The extreme color forms are weakly distinguished morphometrically, with far northern populations having slightly shorter scapes, but the variation is clinal through the zone of transition (mean SI = 143.08 in the South, 140.94 in transition zone, 139.68 in the North).

Queen – Color, gastral pubescence and shininess like the workers', with the usual differences in size. Sculpture very faint; pubescence short and sparse; pilosity sparse; wings, when present, clear to amber. Mesoscutum lacking the three dark spots characteristic of *incerta* queens, or these weakly distinct.

Male – Pubescence sparse; surface more shining than other species; rarely concolorous dark brown (in those colonies with the most uniformly dark workers), most commonly in north and

Rocky Mountains and clinal transition zone with head and gaster blackish and mesosoma a little lighter to clear yellowish brown; in south and Great Plains, concolorous honey-red or with only the head notably darker; wings clear to amber-colored.

DISTINGUISHING FEATURES

Most, if not all records of *pallidefulva* within the northern part of its range, where the color form "*nitidiventris*" occurs, are usually *F. biophilica* or occasionally are lighter color morphs of *F. incerta*. The short, sparse, gastral pubescence, lack or sparseness of pilosity on the mesosomal dorsum, and the short, straight and flattened gastral pilosity of *F. pallidefulva* is distinctive for this species in any of its color variants. The difference in SI strongly discriminates this species from *F. incerta* (Table 1). The setal characteristics, the shininess and "globulous" gaster of this species were expressly mentioned by Latreille (1802) in his original Latin description. Among the species in the group, *F. pallidefulva* is the only one to frequently lack detectable macrochaetae on the pronotum (34 of 57 specimens) and propodeum (33 of 57 specimens). When mesosomal dorsal pilosity is present in *F. pallidefulva*, the macrochaetae average shorter than in other species and are usually most numerous on the mesonotum rather than on the pronotum or on the propodeum (Table 1). Bright-colored southern *F. pallidefulva* may be distinguished from less pilose nanitic and small workers of *F. biophilica* by the nearly perfectly rounded propodeum and straight, flattened gastral macrochaetae of *F. pallidefulva* (versus often faintly right-angular propodeum and narrowly curviconical gastral macrochaetae in *F. biophilica*).

ETYMOLOGY

This name was coined by Latreille from the Latin adjectives "pallidus" plus "fulvus" meaning pale reddish yellow. This neatly describes the southern, lighter colored variants of this species. Northeastern, Midwestern and western mountain populations of this species are predominantly of darker, black-coffee-brown coloration, but even in these locations many individuals and colonies are bicolored and some may have coloring closer to that of southern populations.

RANGE AND HABITAT

Abundant and certainly the most widely distributed species of the group, *F. pallidefulva* occurs farther north, west and south than others in the group, except that *F. archboldi* perhaps extends farther south in Florida. *F. pallidefulva* occurs throughout the eastern United States and southeastern Canada, then west across the US Great Plains to the lower-elevation Rocky Mountains from Wyoming to New Mexico. *F. pallidefulva* also has considerable habitat latitude. This ant lives in a variety of native and anthropogenic plant communities and soil types, including dry-mesic to mesic grasslands, woodlands and forests, thickets, lawns, campuses and parks. It is most abundant in mesic, wooded or partially wooded areas, from city parks to closed-canopy forests. In the lower rainfall areas of the Great Plains, it is uncommon and probably restricted to riparian woodlands (Milford, 1999). In the Rocky Mountains, it occurs at lower elevations in meadows, mixed mesophytic forests and in parks and suburbs. *F. pallidefulva* does not occur in bogs, wet meadows or fens, where it is replaced, in the South by *F. biophilica* and in the North by other *Formica* species outside the *pallidefulva*-group such as *F. montana*, *F. glacialis* Wheeler, and others.

SPECIMENS EXAMINED

(CANADA) ONTARIO: Lambton; Lowick; QUEBEC: Chateauguay. (UNITED STATES) ALABAMA: Baldwin; Bibb; DeKalb; Lawrence; Morgan; Tuscaloosa; ARKANSAS: Logan; Washington; COLORADO: Boulder; DELAWARE: Kent; FLORIDA: Alachua; Brevard; Clay; Highlands; Liberty; GEORGIA: Clarke; Floyd; ILLINOIS: Tazewell; IOWA: Emmet; Johnson; Winneshiek; KANSAS: Douglas; Reno; Wallace; KENTUCKY: Nelson; MARYLAND: Allegany; Anne Arundel; Kent; Prince Georges; MASSACHUSETTS: Barnstable; MICHIGAN: Calhoun; Livingston; MISSISSIPPI: Alcorn; Chickasaw; Itawamba; Lafayette; Lee; Lowndes; Oktibbeha; Panola; Pontotoc; Tishomingo; Webster; Winston; MISSOURI: Audrain; Franklin; Johnson; Lincoln; Ste. Genevieve; St. Louis; NEBRASKA: Hall; Dawson; NEW MEXICO: Colfax; Otero; Rio Arriba; Union; NEW YORK: Orange; Suffolk; NORTH CAROLINA: Yancey; OHIO: Franklin; Sandusky; OKLAHOMA: Latimer; PENNSYLVANIA: Alegheny; Indiana; SOUTH CAROLINA: Anderson; Charleston; SOUTH DAKOTA: Jones; Pennington; TEXAS: Bastrop; Cass; Culberson; Hemphill; VIRGINIA: Montgomery; WYOMING: Crook; Washakie.

NATURAL HISTORY

Nests of *F. pallidefulva* may be located in bare soil of grassland and forest footpaths, beneath leaf litter, under small diameter (<10 cm) fallen tree limbs, or under bark of a decomposing stump. Less often the nest occupies a larger, punky, rotten log, especially during late spring when the sexual brood is being reared. *F. pallidefulva* is the only species in this group which normally inhabits closed-canopy mesic forests and which commonly nests in rotting wood. In non-wooded settings *F. pallidefulva* may build a small mound nestled in or beside a grass clump.

In the northern and Rocky Mountain parts of its range, at least, the dark brown form of *F. pallidefulva* is the host to the slavemaker *Polyergus lucidus montivagus* Wheeler. We have seen *F. pallidefulva* with this slavemaker in colonies from Long Island, southern Ontario, central Illinois, northern Missouri and Rocky Mountain foothill locales in Colorado and New Mexico. We have seen specimens that look like this *Polyergus* in the South (northern Mississippi) and we suspect it uses the reddish, southern form of *F. pallidefulva* there, but have not yet been able to confirm this with a nest collection. *Formica creightoni* raids this ant in northern Missouri oak woodlands, where its usual *F. neogagates* group hosts are lacking. *F. pallidefulva* is the most frequent of the many hosts of *F. pergandei* in Midwest woodlands and savannas.

In the lawns and gardens of the St. Louis, Missouri, area, *F. pallidefulva* is among the native ants most sensitive to subterranean invasion and extermination by the introduced and rapidly spreading invasive ant *Tetramorium tsushimae* (Steiner *et al.*, 2006). However, throughout much of the Southeast, *F. pallidefulva* often manages to coexist with low-density *Solenopsis invicta* Buren, *Solenopsis richteri* Forel, and *Solenopsis richteri* × *invicta* populations.

Occasionally, workers and sexuals become covered with a mite (*Oplitis* sp.?) that reduces their energy level and may cause the demise of the colony. In eastern Missouri, *F. pallidefulva* colonies are commonly raided by the slavemaker/ant-predator *F. rubicunda* Emery, which uses *F. pallidefulva* as prey only (*F. rubicunda* "enslaves" only *F. subsericea*). When nesting in rotting wood, *F. pallidefulva* colonies may sometimes be pillaged by pileated woodpeckers. *F. pallidefulva* often gathers honeydew beneath hemipteran-infested plants or from their leaf surfaces, but they have not often been observed to gather honeydew directly from the hemipterans. Furthermore, *F. pallidefulva* makes little effort to defend hemipterans, in contrast to *F. incerta* and *F. archboldi*, which often tend and defend them.

Sexuals are present in the nests as early as April in Florida, but not until July in New England and Canada. Males were observed to gather around the nest entrance around sunset in

Florida, and males are often lured to lights (but winged females are not) throughout the range. In Missouri, J. Trager observed males, followed by females, flying from the nest, one by one, shortly after sunrise. Despite rather frequent capture of males at lights after dusk, the actual mating flight period is in the morning. In eastern Missouri, J. Trager has over the years caught numerous recently mated females walking about in late morning or early afternoon. Dates of these captures occur from 26 June into early July.

Unlike other species of this group, worker pupae most often lack cocoons in *F. pallidefulva.* Wheeler (1904) first noted this contrast between *F. pallidefulva* and *F. incerta* in Connecticut, and it was also later noted by Talbot (1948) in Michigan. This difference holds true in numerous colonies of the two species sampled in Missouri by J. Trager. In some colonies of *F. pallidefulva*, male pupae may also lack cocoons, but queen pupae nearly always are enclosed in cocoons.

Morphometric analysis of species

Discriminant function analysis classified 97.3 percent of the specimens analyzed (177 of 182) consistently with their morphological species designations. The low rate of error demonstrates that the species do comprise distinctive groups of individuals that can be successfully identified using the morphological characteristics measured in this study. The five species in the *F. pallidefulva* group can be distinguished from one another by a number of morphological indices (Table 1) and body and hair measurements, summarized in Table 2.

Several body measurements distinguish among the species in this group, including species pairs that are visually quite similar. The species differ significantly in the shape of the head and size of the eye, as indicated by the significant pairwise differences among species for CI and OI (Table 1). In particular, on average *F. incerta* has a proportionally broader head and *F. archboldi* has proportionally larger eyes than the other species. As mentioned in the species description above, *F. biophilica* is morphologically quite similar to *F. incerta* but these two species are often differentiated from one another by the longer mesosoma and proportionally narrower head of the former often combined with subtle differences in the number and distribution of macrochaetae (Fig. 2). *F. biophilica* and *F. pallidefulva* also have a significantly higher scape index than *F. incerta* (Table 1), as indicated by the proportionally longer scapes of these two species compared with head width (Fig. 3).

Key to species (based mainly on worker)

1a Mesosomal dorsum without erect setae or with a small cluster on the mesonotum and/or a few erect hairs elsewhere; gaster shiny with sparse, short appressed pubescence and relative short, sparse, blunt pilosity (Figures 4a, 6a); color highly variable, ranging from bright tawny or coppery yellow (southern United States) to very dark brown (mountains in northern and western United States) and including many intermediate colorations; mesic habitats, from gardens, parks and prairies to closed-canopy forests, or more shaded parts of drier sites..... *pallidefulva*

b Mesosomal dorsum with several to many erect setae on pronotum, mesonotum and propodeum; gastral tergite I shiny to dull with appressed pubescence of medium to high density (Figures 4b-e, 4b-e); the average distance between the individual appressed setae approximately equaling the average length of setae to much less; various open grassland, heath, or barrens and open dry woodland habitats (mesic forests or forest edge in the extreme southern U.S.) 2

2a Mesosomal and gastral integument dulled by fine, but notable sculpture; mesosomal dorsum feebly or (at some viewing angles) not shining; gaster usually with dense pubescence (Figures 4d-e, 6d-e), appressed setae on gastral tergite I separated by about 0.5× (or less) the

average setal length (if gastral setae less abundant, then mesosomal and gastral integument dulled by fine sculpture); propodeum usually with visible pubescence..... 3

b Mesosomal and gastral integument somewhat shining, with fainter sculpture; gaster less densely pubescent (Figures 4b-c, 6b-c); gastral tergite I with appressed setae separated by about 0.5-1.0× their average length; propodeum with sparse pubescence or none..... 4

3a Reddish, often weakly bicolored; mesosoma with visible pubescence and gastral integument dulled or even velvety looking due to dense pubescence; larger workers' integument appearing matte in dorsal or oblique dorsal view; numerous erect macrochaetae on all dorsal surfaces, those on first tergite usually long, tapering and typically curved (Figure 6e); size generally larger, HL 1.31-2.06, HW 1.05-1.70, and WL 2.12-3.48; eyes proportionally smaller to head size (OI 28.58); widely distributed in eastern United States (rare west of 100th meridian); reddish-brown (northeastern United States) to light reddish (southeastern and midwestern United States) ..... *dolosa*

b Dark brown to blackish brown; with fine coriaceous sculpture on mesosoma and foveolae on gastral dorsal surface; erect setae shorter and fewer, at least on mesosoma, erect setae often blunt-tipped and without notable curvature, even on gastral tergite I (Figure 6d); size smaller, HL 1.31-1.58, HW 1.03-1.39, and WL 2.08-2.65; eyes proportionally larger (OI 31.26); found in long-leaf pine sandhills and scrub or sand pine woodlands in southeastern United States (Alabama, Florida, and Georgia) .....*archboldi*

4a Length of the longest macrochaetae of gastral tergite I, 0.15-0.22 mm (Figure 4c, 6c, Table 2); color dingy yellowish or reddish brown with gaster or head and gaster a little to significantly darker (midwestern United States, Great Plains) or more uniformly brown with only the mesosoma a bit more yellow (northeastern United States); overall size averages smaller (HL 1.15-1.64, HW 1.01-1.43, and WL 1.86-2.67); head wider and scapes shorter (See CI and OI, Table 1, also Figures 2 & 3); queen with three distinct dark spots on mesoscutum, one anteromedian and two lateral over parapsidal sulci (spots may be reduced to longitudinal dark elliptical marks)..... *incerta*

b Erect setae of first gastral tergite long and curved, longest macrochaetae 0.20 – 0.30 mm (Figure 4b, 6b, Table 2); color bright reddish-yellow or with gaster only slightly darker (Beware: Gaster of this species sometimes stains black in mounted specimens.); mesosomal dorsal integument a little more shining to quite smooth except in largest workers; overall size averages larger (HL 1.37-1.82, HW 1.05-1.56, and WL 2.22-2.93); head more narrow in smaller specimens and scapes longer (See CI and OI, Table 1, also Figures 2 and 3) in smaller specimens (larger workers tend to have wider heads and shorter scapes); queen lacking dark spots on mesoscutum ..... *biophilica*

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Table 1. Summary of morphological index values for species in the *F. pallidefulva* group. Means (and ranges) are presented for each measurement. We conducted univariate ANOVA with Tukey's HSD for post-hoc pairwise comparisons on each index for each species, and subscript letters denote significant differences among homogeneous subsets based on those analyses.

	Species				
Index	*F. archboldi*	*F. biophilica*	*F. dolosa*	*F. incerta*	*F. pallidefulva*
CI	**81.69** $_{a}$ (78.6-87.5)	**83.64** $_{b}$ (76.8-89.0)	**82.54** $_{ab}$ (71.9-88.5)	**86.77** $_{c}$ (81.8-91.5)	**82.07** $_{ab}$ (76.9-88.9)
SI	**147.43** $_{c}$ (139.4-154.6)	**142.53** $_{b}$ (126.6-162.3)	**145.30** $_{bc}$ (125.0-160.7)	**132.99** $_{a}$ (126.1-146.7)	**141.0** $_{b}$ (126.4-153.7)
OI	**31.26** $_{d}$ (29.5-35.0)	**29.38** $_{bc}$ (27.9-30.8)	**28.58** $_{a}$ (24.2-31.2)	**30.02** $_{c}$ (27.4-31.9)	**29.14** $_{ab}$ (27.4-31.9)
CTI	**61.72** $_{b}$ (59.7-64.3)	**61.41** $_{b}$ (58.2-64.7)	**60.42** $_{a}$ (56.8-64.2)	**62.04** $_{b}$ (58.8-64.7)	**61.70** $_{b}$ (58.8-64.7)
TWI	**40.12** $_{a}$ (38.2-42.9)	**40.55** $_{a}$ (37.7-43.8)	**40.59** $_{a}$ (36.9-44.1)	**41.90** $_{b}$ (38.2-44.8)	**41.89** $_{b}$ (37.9-45.3)

Table 2. Summary of morphometric data for the *F. pallidefulva* group. Means (and ranges) are provided for each measurement. The total number of individuals examined follows the specific epithet, although actual sample sizes for each metric varied because not every measure could be obtained from all specimens.

Morphometric	**Species**				
	F. archboldi n = 25	*F. biophilica* n = 32	*F. dolosa* n = 56	*F. incerta* n = 31	*F. pallidefulva* n = 57
MdT	**7.68** (7-9)	**7.75** (7-9)	**7.55** (6-10)	**7.35** (6-9)	**7.65** (6-10)
P5L	**0.18** (0.16-0.20)	**0.21** (0.18-0.24)	**0.21** (0.16-0.24)	**0.20** (0.16-0.22)	**0.21** (0.17-0.24)
P6L	**0.18** (0.17-0.22)	**0.22** (0.19-0.28)	**0.20** (0.17-0.24)	**0.20** (0.16-0.22)	**0.21** (0.16-0.24)
PnML	**0.09** (0.03-0.14)	**0.15** (0.08-0.24)	**0.18** (0.10-0.25)	**0.12** (0.06-0.16)	**0.08** (0.02-0.12)
PpML	**0.07** (0.05-0.11)	**0.11** (0.06-0.17)	**0.13** (0.07-0.19)	**0.09** (0-0.11)	**0.05** (0.03-0.08)
TML	**0.16** (0.14-0.21)	**0.23** (0.14-0.30)	**0.22** (0.16-0.30)	**0.18** (0.12-0.22)	**0.13** (0.10-0.20)
TPL	**0.05** (0.04-0.06)	**0.05** (0.04-0.06)	**0.06** (0.04-0.09)	**0.05** (0.04-0.06)	**0.02** (0-0.04)
HL	**1.45** (1.31-1.58)	**1.55** (1.37-1.82)	**1.69** (1.31-2.06)	**1.45** (1.15-1.64)	**1.48** (1.16-1.68)
HW	**1.19** (1.03-1.39)	**1.30** (1.05-1.56)	**1.40** (1.05-1.70)	**1.26** (1.01-1.43)	**1.21** (0.93-1.43)
EL	**0.45** (0.41-0.51)	**0.45** (0.40-0.53)	**0.48** (0.40-0.55)	**0.44** (0.37-0.48)	**0.43** (0.34-0.50)
SL	**1.75** (1.58-1.98)	**1.84** (1.68-2.06)	**2.02** (1.64-2.38)	**1.68** (1.35-1.92)	**1.71** (1.21-1.90)
WL	**2.35** (2.08-2.65)	**2.52** (2.22-2.93)	**2.80** (2.12-3.48)	**2.34** (1.86-2.67)	**2.40** (1.90-2.71)
PnW	**0.94** (0.83-1.09)	**1.02** (0.89-1.23)	**1.14** (0.87-1.37)	**0.98** (0.77-1.11)	**1.00** (0.80-1.15)
PnM	**11.36** (1-23)	**10.06** (2-20)	**37.00** (14-64)	**10.90** (4-17)	**0.86** (0-5)
MnM	**9.96** (3-19)	**7.13** (2-15)	**14.29** (5-32)	**6.03** (0-12)	**3.18** (0-10)
PpM	**13.92** (6-31)	**12.44** (6-35)	**26.42** (12-42)	**8.55** (0-16)	**0.86** (0-5)

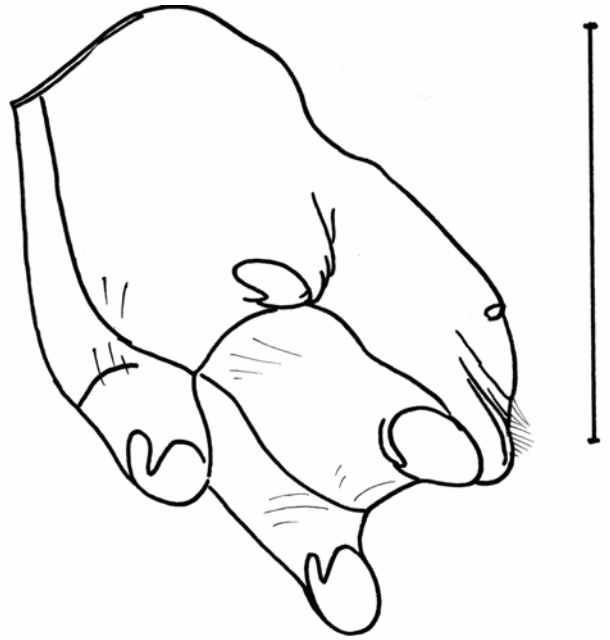

Figure 1. Mesometasternum of *Formica dolosa* drawn at approximately 45° angle with legs removed. The scale bar equals 1 mm.

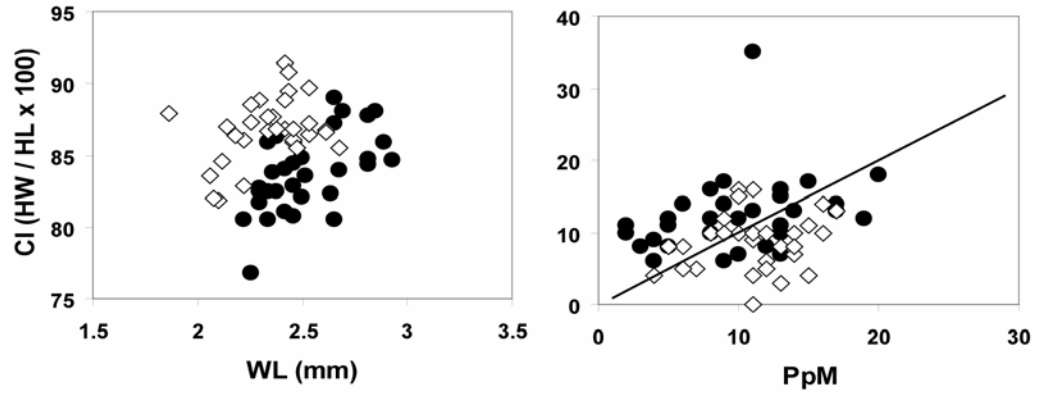

Figure 2. Morphological differences between *F. biophilica* and *F. incerta*: **a)** *F. biophilica* (closed circles) generally has a longer mesosoma (WL) relative to head proportions than *F. incerta* (open diamonds). **b)** Whereas *F. biophilica* rarely has more macrochaetae on the propodeum than the pronotum (12 of 32 specimens), this is more often the case for the *F. incerta* (22 of 31). The line indicates the relationship PnM = Ppm.

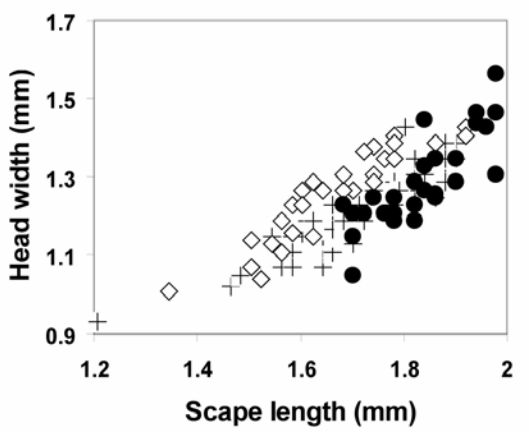

Figure 3. Scape length plotted against head width (= SI) for *F. biophilica* (closed circles), *F. incerta* (open diamonds) and *F. pallidefulva* (plus signs). Note that in addition to the separation of *F. incerta* from the other species, *F. biophilica*, on average, is somewhat larger than *F. pallidefulva*, with a minimum scape length of approximately 1.7 mm.

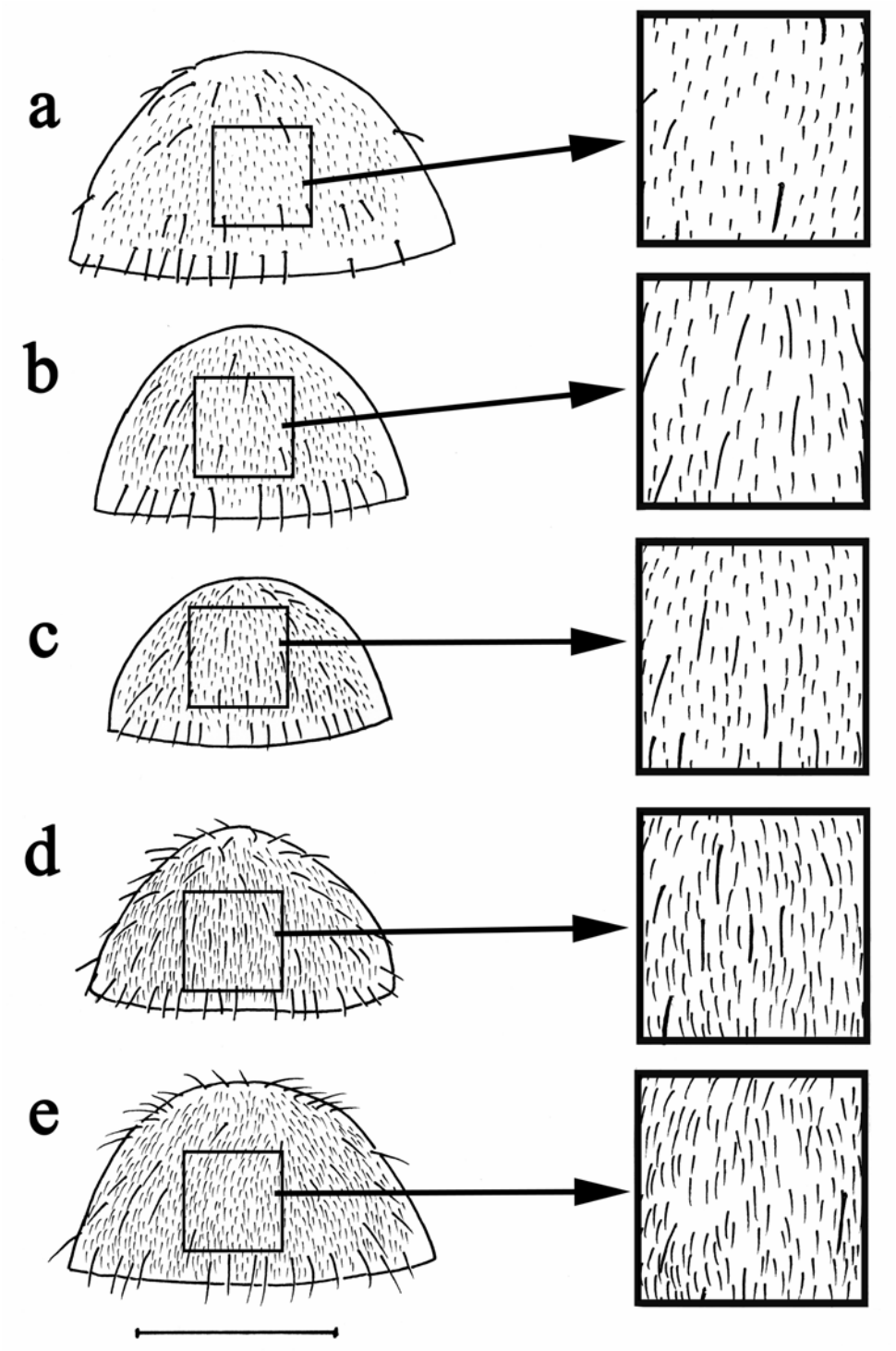

Figure 4. Dorsal views of first gastral tergites of *Formica pallidefulva* group workers: **A:** *F. pallidefulva;* **b:** *F. biophilica;* **c:** *F. incerta;* **d:** *F. archboldi;* **e:** *F. dolosa*. Scale bar = 1 mm.

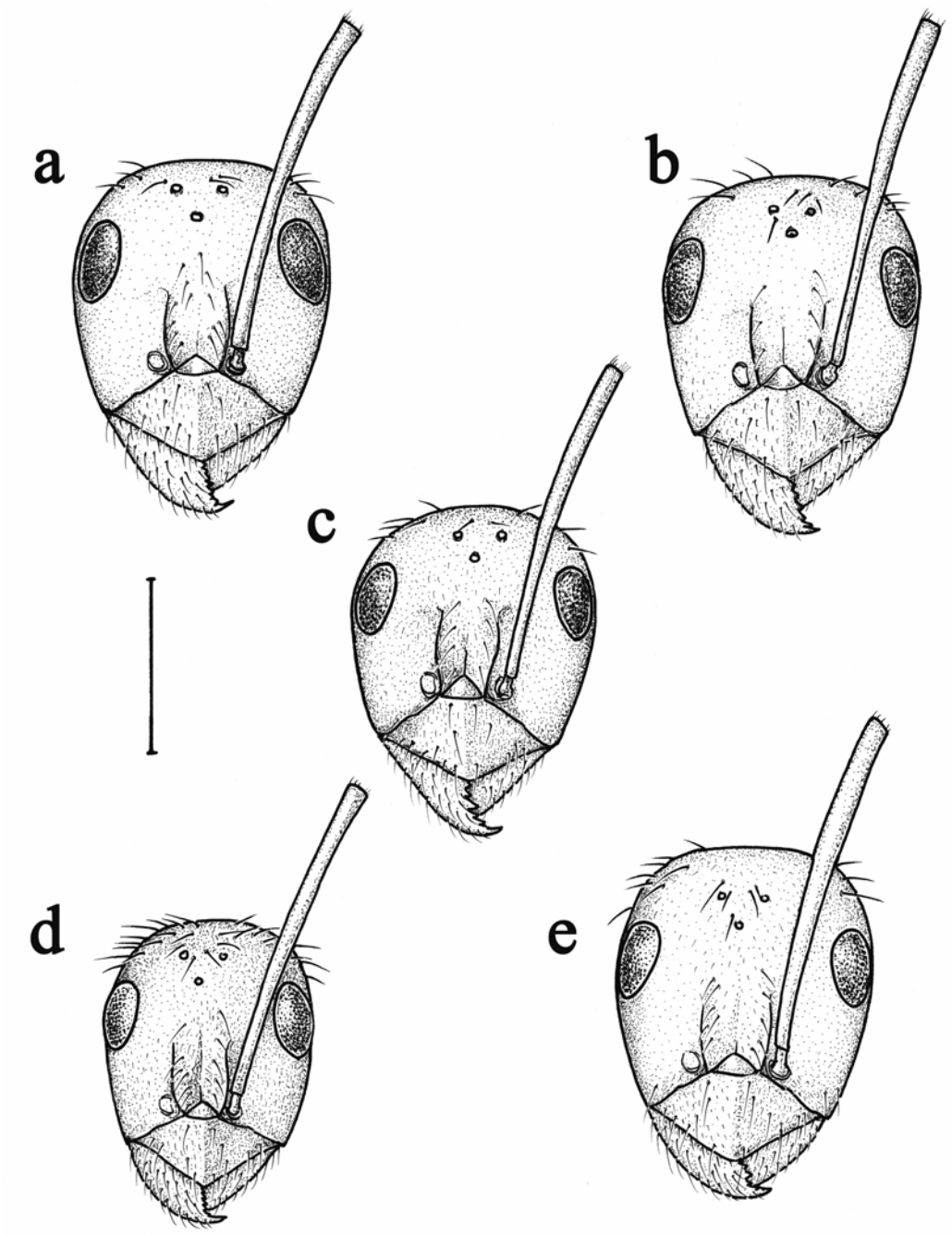

Figure 5. Full-face views of heads of *Formica pallidefulva* group workers: **a:** *F. pallidefulva;* **b:** *F. biophilica;* **c:** *F. incerta;* **d:** *F. archboldi;* **e:** *F. dolosa*. Scale bar = 1 mm.

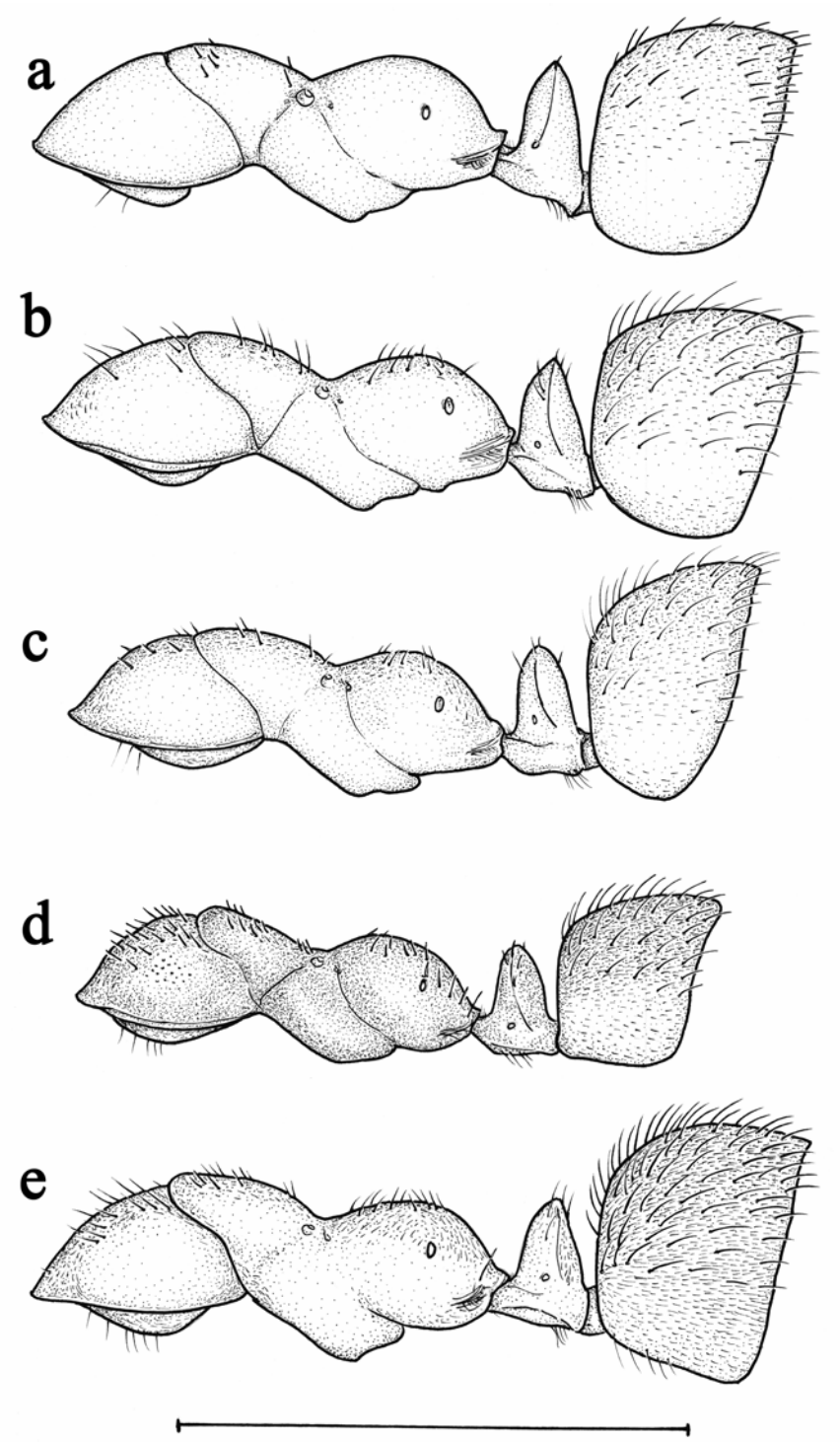

Figure 6. Lateral view of mesosoma, petiole, and first gastral tergite of *Formica pallidefulva* group workers: **a:** *F. pallidefulva;* **b:** *F. biophilica;* **c:** *F. incerta;* **d:** *F. archboldi;* **e:** *F. dolosa*. Scale bar = 3 mm.