

Deyrup, M., Cover, S. P. 2007. A new species of *Crematogaster* from the pinelands of the southeastern United States, pp. 100-112. In Snelling, R. R., B. L. Fisher, and P. S. Ward (eds). *Advances in ant systematics (Hymenoptera: Formicidae): homage to E. O. Wilson – 50 years of contributions*. Memoirs of the American Entomological Institute, 80.

**A NEW SPECIES OF *CREMATOGASTER* FROM THE PINELANDS OF THE
SOUTHEASTERN UNITED STATES**

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ABSTRACT

A new species of arboreal *Crematogaster*, *C. pinicola*, is described from the southeastern United States. It is a cryptic species closely related to the common *C. ashmeadi* Mayr, from which it can be distinguished primarily by its red and black coloration (uniform dark brown to black in *C. ashmeadi*), and by its narrow ecological specialization: it nests only in open-grown pines with thick twigs (*C. ashmeadi* occurs in many forest types and nests in a wide range of hardwoods and conifers). *Crematogaster pinicola* is believed to be a relic of the fire-maintained pine ecosystems that once dominated much of southeastern North America. A recent study shows that *C. pinicola* is a major part of the diet of the endangered red-cockaded woodpecker.

Key words: Hymenoptera, Formicidae, Myrmicinae, *Crematogaster*, new species, taxonomy, fire ecology.

INTRODUCTION

Like many other large ant genera, the genus *Crematogaster* presents ant taxonomists with an unending series of challenging taxonomic puzzles. These problems are not inconveniences: to the thoughtful myrmecologist they are further evidence that biodiversity is as subtle as it is spectacular. The solving of these problems is at the heart of what Wilson (1992) calls “the great Linnean enterprise,” the inventory of the biosphere.

The first useful account of the North American *Crematogaster* was Creighton’s (1950) treatment of the genus in the “Ants of North America.” From the past Creighton inherited a confusing list of ill-defined taxa, the customary legacy to modern taxonomists from the “Bronze Age” of Ant Taxonomy (1750 - 1950), an era characterized by much honest descriptive effort that was critically undermined by the lack of a biologically realistic conceptual framework. Creighton began the process of bringing order to the North American ant fauna, and to the *Crematogaster* in particular, by employing the newly popularized biological species concept to elicit meaning from what seemed to be an intractable morass of names and morphological variation (see Buhs, 2000 for a discussion of this development). Expanding on this pioneering work, Buren (1958, 1968) revised the North American *Crematogaster* again, incorporating much newly available information. Like Creighton, Buren made extensive use of distributional data and natural history observations in making taxonomic decisions and, as a result, his work still forms the basis for our modern understanding of the genus in North America. Not much has been added since Buren’s studies. Johnson (1988) reviews the eastern species and presents a key to them. In an excellent new revision of the *Crematogaster* of Costa Rica, Longino (2003) makes several taxonomic changes that affect the North American fauna.

The new species of *Crematogaster* described here was first recognized as an undescribed species separate from *C. ashmeadi* Mayr by William Buren himself. After retiring, Buren moved to Florida, where he retained his interest in *Crematogaster*. Hand-labeled specimens in Buren’s collection show he believed that the common southeastern *C. ashmeadi* included a second, previously unrecognized species distinguished by its red and black coloration. His student James Trager also knew of this species, as evidenced by specimens of *C. pinicola* collected in 1981 at the Archbold Biological Station and labeled by him “*Crematogaster* n. sp.” Buren probably would have described this species, but he became ill and died in 1983. The same ant is also the “undescribed species” of *Crematogaster* referred to by Deyrup and Trager (1986). In his review of eastern *Crematogaster*, Johnson (1988) was the first to address the problem of separate color forms in *C. ashmeadi* in print, but he did not arrive at a definite conclusion concerning their biological basis. We believe the accumulated evidence supports the hypothesis that the red and black form of *Crematogaster ashmeadi* is, in fact, a valid sibling species.

METHODS AND MATERIALS

Specimens were examined and measured using an ocular micrometer scale in a Leitz stereomicroscope at 40x. Measurement conventions and indices follow those used in Bolton (1994).

Crematogaster pinicola, new species

Figures 1-3

DIAGNOSIS: Workers morphologically indistinguishable from those of *C. ashmeadi*, except for a distinctive color difference in freshly collected material. In *C. pinicola* workers, the head,

mesosoma, petiole, postpetiole, and appendages are ferruginous red, and the gaster is black. In *C. ashmeadi*, mature specimens are always a uniform dark brown to black. A similar color distinction is seen in alate queens; those of *C. pinicola* are notably bicolored, those of *C. ashmeadi* are uniformly brown or black. Males of *C. pinicola* are generally somewhat lighter in color than those of *C. ashmeadi*, but are harder to distinguish reliably than the corresponding female castes. Note: detailed morphometric studies might possibly reveal the existence of minute, but consistent morphological differences between the two species, but a detailed examination of all three castes in both species has not provided hints that such differences exist.

Worker: Measurements (mm) (holotype in parenthesis): total length: 2.31-3.64 (3.22); head width at eyes: 0.67-0.90 (0.87); length of antennal scape: 0.44-0.60 (0.60); distance from mesothoracic spiracle to propodeal spiracle: 0.23-0.33 (0.31); distance from lower edge of propodeal spiracle to tip of propodeal spine: 0.12-0.17 (0.16). Head: in frontal view, posterior half smooth, shining, covered with sparse appressed silvery hairs separated at their bases by a distance slightly shorter than length of a hair; orientation of hairs convergent toward lower midline of frons; frons with a series of erect hairs in a line just mesad of imaginary vertical lines extending up from frontal carinae, 4 hairs on right side, 3 on left (in holotype); fine striae covering malar area, extending up about 1/3 of way along eye on inner side. Antennal scape with appressed hairs only. Mandible with 4 teeth. Mesosoma: pronotum with one standing curved humeral hair on each side; pronotum and mesonotum with sparse appressed silvery hairs, with bases separated by more than half length of a hair and less than twice length of a hair; pronotum and mesonotum shining, with very faint shagreening; mesopleuron finely, evenly reticulate up to level of mesothoracic spiracle; metapleuron with longitudinal carinae covering its upper 3/4, fine reticulations between more widely spaced carinae; propodeal spine in lateral view wedge-shaped, sharply pointed, with a fine dorsal carina; dorsal areas of propodeum with sparse, appressed silvery hairs divergent from the midline; all legs with sparse, appressed, silvery hairs. Gaster: First tergite sparsely covered with longitudinally oriented, appressed, silvery hairs whose bases are slightly closer together than the length of a hair; submarginal bands of similar, but longer hairs on tergites 1 - 3; a sparse submarginal band of erect hairs on tergites and sternites 1 - 4. Color: Body and appendages except for gaster ferruginous; gaster black.

Queen from nest of holotype (Fig. 3). Measurements (mm): total length: 7.48-7.90; head width at eyes: 1.44-1.54; length of mesosoma (lateral view): 2.20-2.45; length of forewing: 6.46-6.84. Head, legs, body reddish brown, except mesonotum, scutellum blackish brown, gaster black; wings hyaline, major veins pale testaceous. Mandible with 5 teeth, mandibular striae with sparse, coarse punctures; median ocellus separated from lateral ocelli by about 1.8 times diameter of lateral ocellus; anterior half of dorsum of head finely striate, including clypeus, except for lower median area of frons; posterior half of dorsum of head shining, finely punctate, with appressed hairs. Mesonotum strongly shining, no reticulate areas; fine striations on lateral margins of mesonotum and posterior quarter of mesopleuron; metapleuron coarsely but evenly striate, propodeum coarsely, unevenly striate; gaster shining, first gastral tergite with appressed hairs slightly longer than distance between their bases, and a few scattered, suberect longer hairs.

Male from nest of holotype (Fig. 2). Measurements (mm): total length: 3.02-3.24; head width at eyes: 0.62-0.66; length of mesosoma (lateral view): 1.06-1.30; length of forewing: 2.87-3.13. Head and body blackish brown; femora medium brown, lighter than head and body; tibiae, tarsi, mandibles testaceous; wings hyaline with no infuscation, heavier veins pale testaceous. Mandible with 3 subequal teeth; median ocellus separated from lateral ocelli by twice diameter of lateral ocellus; head with sparse sub-appressed hairs, those on occipital area procumbent, about as long as

distance between their bases; hairs on frons convergent toward midline; frons with a few conspicuous large punctures on each side; malar space weakly striate; area between eye and antennal sockets not striate; antennal scape shorter than last antennal segment. Mesosoma shining, without reticulate areas, smooth except for weak, fine striations on lateral areas of mesonotum and posterior fourth of mesopleuron, metapleuron more coarsely striate; mesonotum with sparse, short hairs embedded in elongate punctures, usually farther apart than length of a hair; wing venation as in figure 2; gaster smooth, shining, first gastral tergite with short, appressed, embedded hairs.

TYPE MATERIAL

USA: Florida: Highlands County, Archbold Biological Station, 24-VI-1996, M. Deyrup. Florida Scrub habitat. Nest in 6 cm diameter branch of *Pinus elliottii* in firelane. The entire type series is from a single colony. **Holotype** and 37 **paratypes** deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Deposition of additional **paratypes**: 24 workers, 2 alate queens, 2 males: Natural History Museum of Los Angeles County, Los Angeles, California; 17 workers, 2 alate queens, 1 male: Florida State Collection of Arthropods, Gainesville; 17 workers, 2 alate queens, 1 male: National Museum of Natural History, Smithsonian Institution, Washington, D.C.; 14 workers, 1 alate queen, 1 male: The Natural History Museum, London; 12 workers: collection of William Mackay, El Paso, Tex.; remaining type material: Archbold Biological Station, Lake Placid, Florida.

ETYMOLOGY

The specific epithet is derived from Latin: “pine dweller.”

DISCUSSION

Geographic Range and Variation in Florida.

The distribution map provided in Fig. 4 shows localities for collections documented by voucher specimens only. The real distribution of *C. pinicola* is undoubtedly much more extensive and continuous. Without mentioning specific collections, Johnson (1988) says that the species occurs in Georgia, South Carolina, and Alabama also. We have not seen Johnson’s specimens, but expect that *C. pinicola* will be found to occur widely on the southern coastal plain where suitable habitats are found. Material collected throughout Florida shows a remarkable consistency in color, size range, and morphology. *Crematogaster pinicola* is clearly less variable than its sister species, *C. ashmeadi*, which shows more obvious variation in size and color over its much wider geographic distribution.

In describing a species of ant that can be recognized visually only by its color we are aware that we are treading on the myrmecological equivalent of “thin ice.” Early ant systematists were notorious for naming new taxa (both specific and infraspecific) based on minute (and indeed, sometimes entirely imaginary) differences in color, sculpture, or pilosity. Creighton (1950) was withering in his criticism of these practices, and subsequent generations of ant taxonomists have been strongly conditioned to believe that color alone is unreliable as a separatory character on the species level. Much cumulative experience with the genus *Crematogaster* is an additional reason for caution. Color variation is not uncommon in *Crematogaster* species. For example, dark and bicolored variants have been observed in other *Crematogaster* of the eastern United States, notably *C. atkinsoni* and *C. pilosa*. In both species, northern specimens tend to be uniformly black

or brown in color, while bicolored specimens are sometimes found in Florida and elsewhere along the Gulf Coast. With precisely this in mind, Johnson (1988) treated *C. pinicola* as a color variant form of *C. ashmeadi*.

We believe that ecological evidence clearly indicates that *C. ashmeadi* and *C. pinicola* are reproductively isolated, and thus *C. pinicola* is a good species, not merely a color variant. While broadly sympatric with *C. ashmeadi* across most of Florida, *C. pinicola* is distinctively different in its ecology. It nests exclusively in pine trees, particularly slash pine (*Pinus elliottii*) and longleaf pine (*P. palustris*), which have relatively robust twigs. Pines occupied by *C. pinicola* are usually open-grown (i.e., well-separated from other trees) and surrounded by low brush or low perennial herbs and grasses. These pines may be in dry sandhill habitats or in wetter flatwoods habitats. Both habitat types are maintained by frequent fires that retard the invasion of other woody plant species. In sharp contrast, *C. ashmeadi* shows much wider ecological tolerances in nest site selection, and in habitat preferences. *C. ashmeadi* nests in pines, in many hardwoods including oaks (*Quercus* spp.), hickories (*Carya* spp.), ash (*Fraxinus caroliniana*), red maple (*Acer rubrum*), shrubs such as winged sumac (*Rhus copallina* L.), vines such as greenbriar (*Smilax* spp.) and grape (*Vitis* spp.) and in the hollow stems of large herbs such as dog fennel (*Eupatorium capillifolium*). Trees, shrubs, vines and herbs occupied by *C. ashmeadi* may be in open sites or under a dense canopy, and may be in dry or wet habitats. Pines growing in mixed hardwood stands, surrounded by high brush, or thickly covered with vines, are much more likely to be occupied by *C. ashmeadi* than *C. pinicola*. Our extensive collecting experience has shown that the two species show considerable segregation by habitat across much of Florida, but that zones of overlap, where pines mix with hardwoods, occur as well. Within these zones it is not uncommon to find *C. pinicola* in a large pine tree only a few meters from an oak inhabited by *C. ashmeadi*. What is especially noteworthy is that these forms maintain their integrity where they co-occur; we have not found color intergrades in these overlap areas, and we have not found dark queens with bicolored workers or bicolored queens with dark workers. Based on these observations, we conclude that the two forms are reproductively isolated and thus constitute separate, if closely related species.

Given the natural history described above, it is difficult to imagine a biologically convincing scenario for regarding these ants as two forms of a single, panmictic species. It would be necessary to hypothesize that something about the environment of open-grown pines usually (but not always) causes a developmental shift that makes all members of a colony bicolored. Furthermore, this shift must not occur in colonies in relatively shaded pines, in open-grown hardwoods or in open-grown shrubs, vines and weed stems. While not utterly inconceivable, this scenario is complex and inherently improbable, especially given that there are no known examples of anything comparable occurring in the Formicidae. Likewise, we find the observations reported by Johnson (1988) unconvincing as possible objections to regarding the two forms as good species. Johnson claims to have seen mixed foraging columns in overlap zones and says that colonies containing both color morphs have been found. In all our extensive collecting experience, we have never seen a single instance of either phenomenon. The rare occurrence of mixed colonies, however, is no serious impediment. Mixed colonies containing two non-parasitic ant species are not unknown, and they can be an accidental byproduct of territorial interactions in which nests are raided and brood stolen. Johnson (1988) also notes (correctly) that callow workers of *C. ashmeadi* are bicolored, with the gaster darker than the head and mesosoma, as in workers of *C. pinicola*. We observe that the head and mesosoma of *C. ashmeadi* callows are grayish in color because they lack the strong yellow to reddish undertones always present on the head and mesosoma of *C. pinicola* workers, regardless of age. As such, they do not offer convincing evidence of intergradation between the two forms. Note: it is sometimes difficult to assign names to museum

specimens of the *C. ashmeadi* - *C. pinicola* complex. Specimens of *C. ashmeadi*, which appear blackish in the field, often appear brownish in collections, especially if the specimens have been stored for several years in alcohol prior to mounting. The gaster may fade somewhat less than the head and mesosoma, so specimens may appear obscurely bicolored. Specimens of *C. pinicola* can fade from bright mahogany-red to a dull brown, converging in color with some specimens of *C. ashmeadi*. The authors cannot at present confidently identify all specimens in collections. Associations with alates are sometimes useful, as queens seem to show less color change than workers as they age. We have not found differences in male genitalic structures, so males are no help in resolving this problem.

Crematogaster pinicola provides evidence that speciation may occur in *Crematogaster* with negligible structural divergence. While morphometric studies could possibly reveal small morphological differences between *C. pinicola* and *C. ashmeadi*, the existence of such differentiation should not be presumed. Morphological differentiation is not necessarily an immediate or even an eventual consequence of speciation, and taxonomists must be careful not to make finding such differentiation a requirement for assigning species status. In this regard, Umphrey's (1996) work on the *Aphaenogaster rudis* complex is illuminating. He found that some cryptic species (defined as such by karyotypic differences) could be distinguished from congeners morphometrically, whereas other karyotypically distinct cryptic species were morphologically indistinguishable. No doubt, many cases similar to that of *C. pinicola* and *C. ashmeadi* will come to the attention of myrmecologists as our knowledge of the world ant fauna improves.

BIOLOGY

Prior to European settlement, much of the southeastern United States was covered with pine forests that were structured and maintained by frequent fires (Frost 1993). These forests might be on wet sites (flatwoods) or dry sites (sandhill) but they were similar in general structure, with a dense herbaceous ground layer and large, usually widely scattered pines, such as slash pine, *P. elliotii*, and longleaf pine, *Pinus palustris*. Shrubs and woody vines were suppressed by fire, but persisted in patches that were protected by natural fire breaks. The pines survived the fires by a series of adaptations, the most important of which (from an ant's point of view) were the thick, loose layers of insulating bark at the base of the tree, thick twigs (which are less flammable than fine twigs), and the tendency for the lower branches and twigs to die and drop off, even when they receive plenty of light (thus reducing the chance that fire will be carried into the crown of the tree). *Crematogaster pinicola* appears to be specialized to endure frequent fires by taking advantage of the fire adaptations of pines. When the lower twigs and branches begin to senesce, they are quickly attacked by scavenging insects. At the Archbold Biological Station in central Florida for example, these are scolytids, such as *Pityoborus comatus* and *Pityophthorus pulicarius* and cerambycids, such as *Eupogonius pauper*. The activities of the beetle larvae provide a succession of thick hollow twigs where *C. pinicola* can become established, even in young trees. Once established colonies gradually relocate up the trunk as branches die. As a tree matures, there are occasional dead twigs and branches up in the crown, and the buildup of thick layers of bark along the trunk provides another nesting area, especially where the outer bark is riddled with the abandoned galleries of moths. The creation of cavities in the bark by moths has been quantified by Tschinkel (2002). The thickest bark is at the base of the tree, and in large trees larvae and pupae of males and queens may be found near the root crown, sometimes below ground level. This brings part of the colony in contact with the diverse subterranean fauna of southeastern pinelands, including a large number of potential predators, such as army ants. On the other hand, the

sequestration of these larvae, especially the large queen larvae, at or below ground level may provide some protection from woodpeckers.

Walter Tschinkel and several associates have published detailed studies of the ecology of a pine-inhabiting *Crematogaster* (referred to as *C. ashmeadi*) in the Apalachicola National Forest in northern Florida. (Hahn and Tschinkel, 1997, Hess and James, 1998, Baldacci and Tschinkel, 1999, Tschinkel and Hess, 1999, and Tschinkel (2002). Tschinkel (pers. comm.) says the ants were, "were red and black, and considering their rather particular life cycle and nesting habits, quite distinct from the all-black species on hardwoods." Based on this comment, and our own collections on pines in the same area, we are confident that the ant studied by Tschinkel is *C. pinicola*, not *C. ashmeadi*.

In the Apalachicola National Forest, mating flights of *C. pinicola* occur in June and July (Tschinkel 2002). Nest-founding queens regularly occur in abandoned beetle galleries in small dead branches on pine saplings (Hahn and Tschinkel 1995, Baldacci and Tschinkel 1999). Small trees, under 7 m tall, are preferred, and trees with more than two dead branches are also preferred (Baldacci and Tschinkel, 1999). Such trees are far too small to support a mature colony of *C. pinicola*, which contains several tens of thousands of individuals (Tschinkel 2002). Workers from one colony are hostile to workers from other colonies (Tschinkel 2002), and it is possible that it is safest course of action for founding queens is to found a colony in a tree that is yet unsuitable for large colonies. Once established, these small founding colonies could then send scouts to find a large tree that is not already well defended by another colony. It appears that there is never more than one colony in a tree, and few colonies occupy more than one tree (Tschinkel 2002). Surveys, using baits and other methods, of trees in class sizes suitable for mature colonies revealed 55 to almost 90% of the trees were occupied by *C. pinicola* (Tschinkel and Hess 1999, Tschinkel 2002). The higher percentage was obtained by more diverse and intensive survey techniques, and is probably the more accurate figure (Tschinkel 2002). There are no co-dominant arboreal ants in these pine forests, although several other arboreal ant species may co-occur with *C. pinicola* (Tschinkel and Hess 1999).

Crematogaster pinicola may be an important part of the diet of southeastern pine woodpeckers, especially the endangered red-cockaded woodpecker, whose diet was studied by Hess and James (1998). In the Apalachicola National Forest they found that *C. pinicola* comprised about 43% of the woodpecker's arthropod diet, a degree of specialization on a single prey species that may be unique for insectivorous birds in the United States. Many birds show ephemeral specialization on single species of insects that are at a high point in a population cycle, but the red-cockaded woodpecker can afford persistent specialization because ant colonies themselves are abundant, long-lived, and available at all seasons. This ant revises the moral of Aesop's fable of the grasshopper and the ant: the improvident grasshopper may vanish in the winter, but the thrifty and industrious ant can be eaten all year long! The original distribution of *C. pinicola*, like that of the red-cockaded woodpecker, was probably centered in the distribution of the longleaf pine ecosystem. This ecosystem, which once covered approximately 92 million acres, from the southeastern tip of Virginia to eastern Texas, has been almost completely destroyed (97% of the old growth forest is gone), and much of what remains is highly fragmented and difficult to manage with fire (Frost 1993). *Crematogaster pinicola* may have undergone a major decline with the reduction of its habitat, but it is definitely not an endangered species. The gross inequalities imposed by size scale are all in favor of *C. pinicola*: while a single family group of the red-cockaded woodpecker requires about 40 hectares of foraging habitat (Hooper 1996), a single hectare of large pines could support many colonies and thousands of individuals of *C. pinicola*. The red-cockaded woodpecker is not threatened by loss of its food supply, but by the lack of

suitable nesting trees, and by its tendency to leave small, remnant patches of pine forest (Wilson 1992).

ACKNOWLEDGMENTS

This paper is dedicated to Edward O. Wilson, with special appreciation for his participatory enthusiasm for faunistics and basic taxonomy, an enthusiasm that adds considerable luster to these important endeavors. This research was supported by the Archbold Biological Station and by the Museum of Comparative Zoology, Harvard University. The collecting trip to the Apalachicola National Forest was supported by the Wilson Ant Collection Fund.

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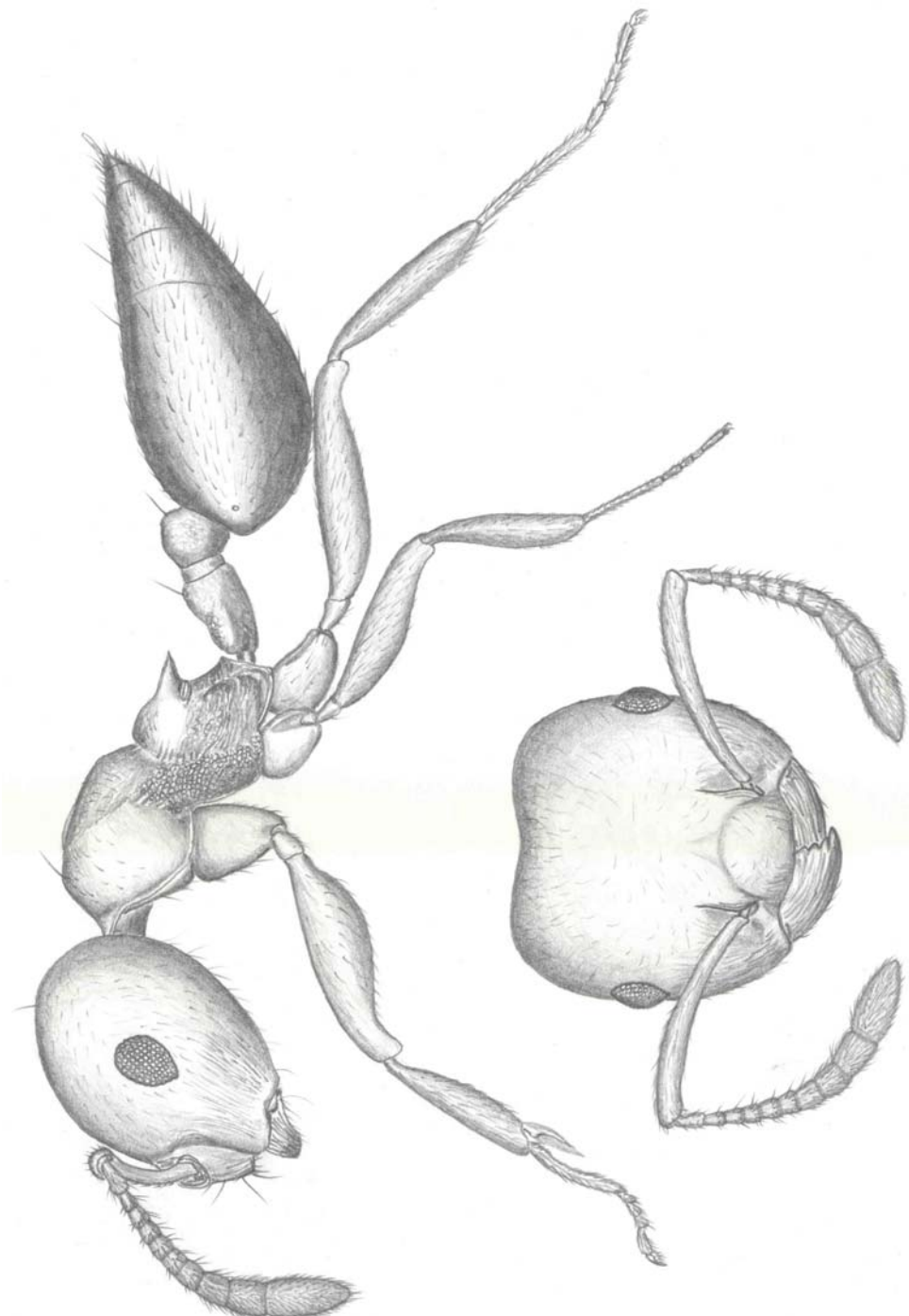


Figure 1. *Crematogaster pinicola*, worker; length of specimen 3.2 mm.



Figure 2. *Crematogaster pinicola*, male; length of specimen 3.2 mm.

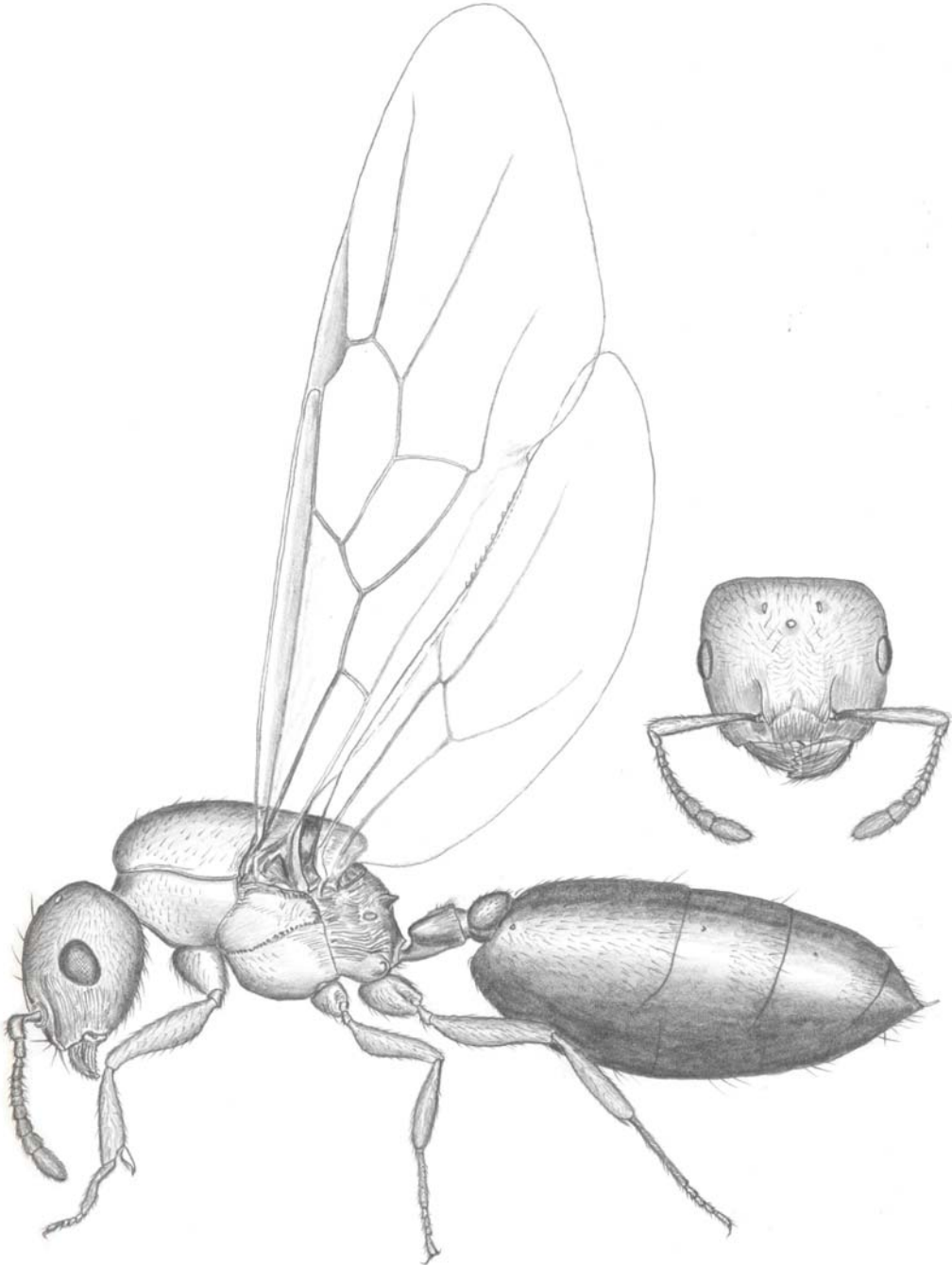


Figure 3. *Crematogaster pinicola*, alate queen; length of specimen 7.8 mm.

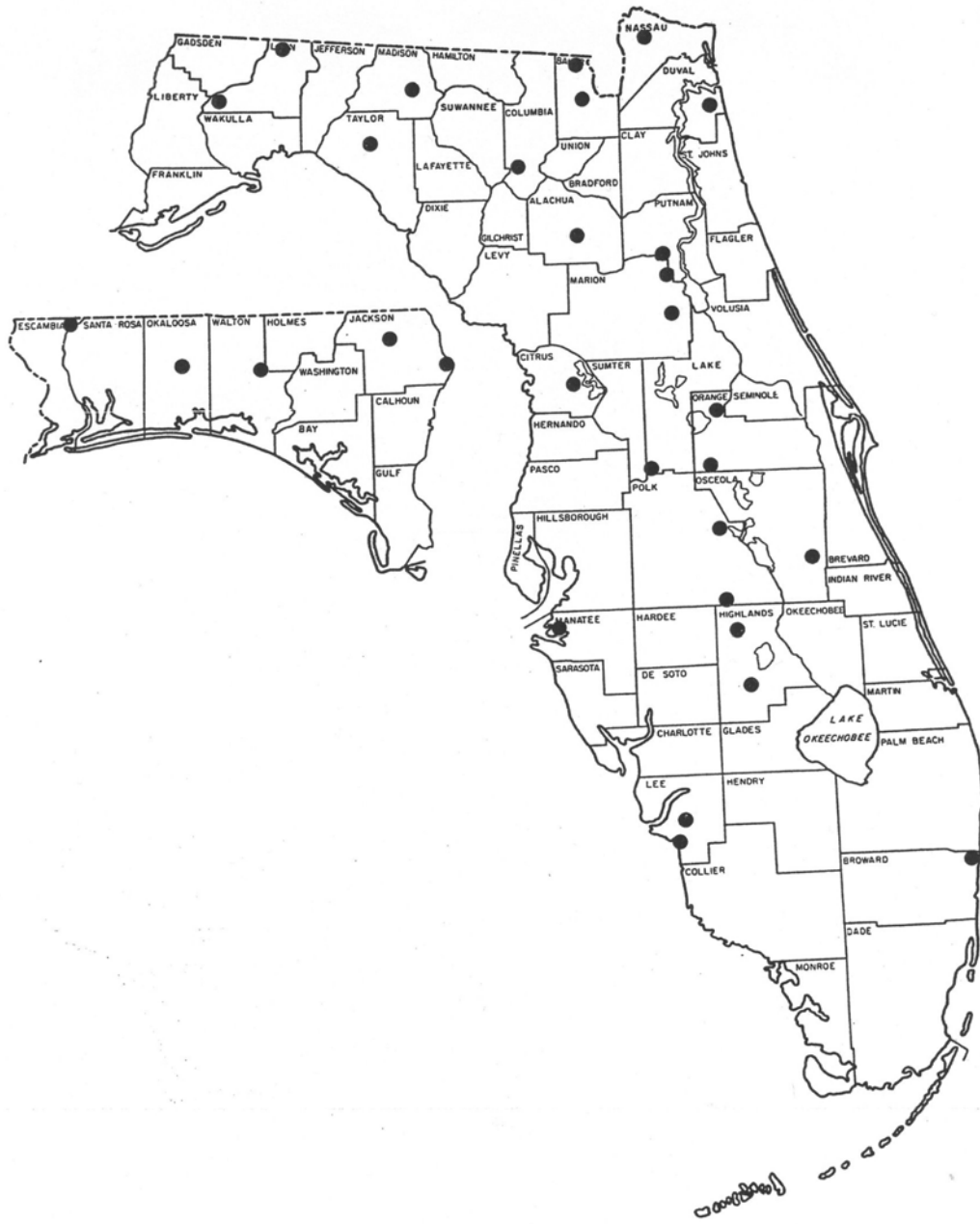


Figure 4. Collection localities for *C. pinicola*.