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COLONY STRUCTURE AND REDESCRIPTION OF MALES IN THE RARELY COLLECTED ARBOREAL ANT, *APHAENOGASTER MARIAE* FOREL (HYMENOPTERA: FORMICIDAE)

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Abstract.—Aphaenogaster mariae Forel is a rarely encountered North American arboreal ant that has eluded collectors for decades. Here, we provide the first formal documentation of a whole colony collection of the species found seventeen meters high in the canopy of the North Carolina Piedmont. We discovered a mature colony with more than 1000 individuals, including workers, alate reproductives, immatures, and intercastes. We present the first images of the males, larvae, pupae, and intercaste workers, redescribe the male, and provide natural history insights and colony demographics for this elusive species. Our collections suggest that *A. mariae* occurs at low densities consistent with its putative socially parasitic life history. Although much remains to be learned about this species, our results expand knowledge of its life history and facilitate future nest discovery and identification.

Key Words: temperate canopy ants, colony demography, temporary social parasitism

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In North America, the ant genus *Aphaenogaster* Mayr (Hymenoptera: Formicidae: Myrmicinae) comprises 23 valid species that vary widely in their ecology and distribution (DeMarco and Cognato 2016). *Aphaenogaster mariae* Forel, a rare species known only from the eastern United States (Janicki et al. 2016, Deyrup 2017, Guénard et al. 2017) (Fig. 1), was first described in 1886 after naturalist Mary Treat sent specimens she collected in Florida to Auguste Forel (Forel 1886). While most North American species of *Aphaenogaster* nest in soil, rotten logs, or under stones (Carroll 1975, DeMarco 2015), this species stands out due to its arboreal lifestyle. *Aphaenogaster mariae* nests in tree holes, dead branches, or under bark in the canopy of live trees, primarily oaks (*Quercus* spp.), or in standing, dead trees (Wesson and Wesson 1940, MacGown and Brown 2006). Since its description, *A. mariae* has eluded many myrmecologists, and there remains a dearth of natural history information, including basic knowledge about colony founding, demography, and lifecycle.

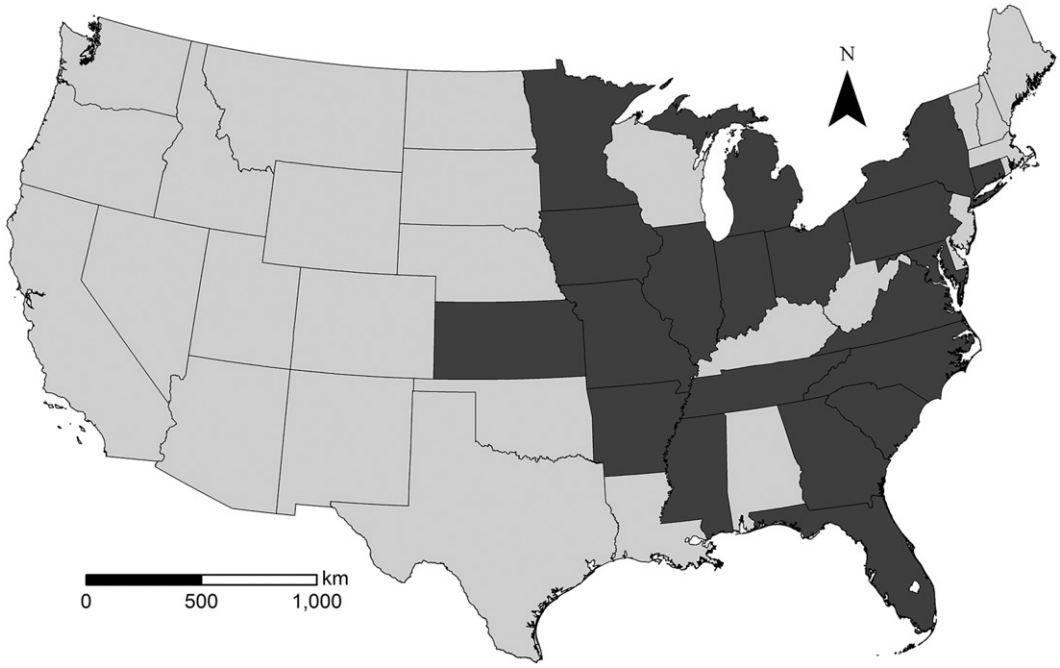


Fig. 1. Distribution map of *Aphaenogaster mariae*. US states (in dark gray) in which *A. mariae* has been recorded.

Workers of this species are usually collected as foragers without nest association (Carter 1962, Munsee 1967, DuBois 1985, MacGown and Brown 2006, Wilhelm and Rericha 2007, Ellison et al. 2012, MacGown et al. 2012, DeMarco 2015, Vogt et al. 2022). Stray alates have also been collected (Wheeler 1916, Carroll 1975, MacGown and Brown 2006), but nests have been only rarely encountered (Wesson and Wesson 1940, MacGown and Brown 2006), and the collection of an entire colony of this species has not been documented. Here, we report on a colony of *A. mariae* from a tree canopy in the North Carolina Piedmont. We provide an account of this colony's demography, redescribe the male (previously known only from two specimens), publish the first images of the males and immatures of the species, and discuss the results in light of scattered prior reports of its natural history.

Materials and Methods

Site and Collecting

We sampled ants from three healthy, mature white oak trees (*Quercus alba* L.) in a 1.5 sq. km fragment of secondary mixed hardwood forest in the North Carolina Wildlife Resource Commission's Butner–Falls of Neuse Game Lands (36.0058, -78.6812); each tree was at least 20 m from other sampled trees. We ascended each tree using single rope climbing techniques (SRT) and searched for arboreal ant nests by peeling bark, breaking dead branches, and following foragers (hand-collecting).

We located one nest of *Aphaenogaster mariae* in a dead branch of *Quercus alba* (diameter at breast height: 61.1 cm) 17 m from the ground on August 2, 2021. After following foragers to the branch, we observed a couple dozen workers entering and exiting the branch at multiple points along its length, including where

Fig. 2. Nest structure of *Aphaenogaster mariae*. Partly excavated nest of *A. mariae* illustrating nest structure and texture in a branch of about 15 cm diameter.

the dead branch met the live trunk. Nest entrances were not obviously distinguishable from other rotten openings or cavities. We broke off the entire branch (about 60 cm long x 15 cm wide x 10 cm deep) and froze it overnight. The following day, we excavated the branch (Fig. 2) and collected all larvae, workers, and alates (females and males) from the nest into 70% ethanol. We did not collect eggs because they were too small to reliably detect. Using current taxonomic keys, we identified the ants as *A. mariae* (Creighton 1950, DeMarco 2015). Voucher specimens are deposited in the NC State University Insect Museum (NCSU) (workers: NCSU_ENT00299518–NCSU_ENT00299520; females: NCSU_ENT00299521–NCSU_ENT00299523; males: NCSU_ENT00299524–NCSU_ENT00299526; intercastes: NCSU_ENT00299527–NCSU_ENT00299530).

Colony Demographics

We counted all ants and separated them into the following categories: worker, queen, male, pupa, larva, and intercaste. We preserved vouchers of each category and photographed specimens at various magnifications and focal depths (19–33) using a Canon EOS 60D DSLR equipped with a Canon MP-E 65 mm macro lens while lit with two diffused strobe/flash units. Using Zerene Stacker software (Zerene Systems LLC 2022), we then created focus-stacked images.

Morphology

We point-mounted and examined 20 additional male specimens for morphological characters. Using a digital micrometer measuring stage (Semprex KM33-R with 1in/25mm Mitutoyo 350-352 digital micrometer), we measured the following 11 characters on each specimen:

HL: head length; measured in full-face view in a straight line from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin.

HW: head width; measured in full-face view directly above the eyes.

EL: eye length; measured along the maximum diameter of the eye.

SL: scape length; maximum straight-line length of the scape excluding the condylar bulb.

MscL: mesoscutum length; measured from the pronotal-mesoscutal suture to the transscutal line.
MscW: mesoscutum width; maximum width of the mesoscutum in dorsal view.
ML: mesosoma length; measured in lateral view as diagonal length from the anterior point of pronotum to the posterior margin of the propodeal lobe.
PL: petiole length; maximum length of the petiole in lateral view.
PW: petiole width; maximum width of the petiole in dorsal view.
PPL: postpetiole length; maximum length of postpetiole in lateral view.
PPW: postpetiole width; maximum width of postpetiole in dorsal view.

From these measurements, we calculated three indices:

CI: cephalic index; HW/HL x 100.
SI: scape index; SL/HW x 100.
MI: mesosoma index; ML/MscW x 100.

Results and Discussion

Colony Demographics

The nest contained 1048 adult ants and 90 visible immatures. More than half of the adults were workers (57.6%), and most immatures were larvae (78.9%) (Table 1). We did not locate a dealate queen, but the nest contained 185 alate queens and 255 alate males. This colony's size and high proportion of alates indicates that it was likely well established in its lifecycle. For comparison, average worker numbers in the ground-nesting *Aphaenogaster rudis* species complex range from 266 to 613 per nest (Lubertazzi 2012) and mature colonies of *A. mariae*'s sister species, *Aphaenogaster tennesseensis* (Mayr) (DeMarco and Cognato 2016), are estimated to have several hundred to several thousand individuals (Carroll 1975, Deyrup 2017). The presence of alates in the nest in early August is consistent with *Aphaenogaster* colony phenology in North America, where nuptial flights commence from May to November (Lubertazzi 2012). Alates of *A. mariae* and *A. tennesseensis* may fly later in this time range, as alates of these species have been collected outside the nest in September (Wheeler 1916) and November (Carroll 1975) Our inability to find a dealate queen in this nest could stem from the true absence of the queen (common in *A. rudis*-group colonies (Lubertazzi 2012)) or incomplete collection of the colony. Despite our efforts to collect the entire nest, it may have continued deeper into the live tree trunk, or the queen may have escaped during collection.

Table 1. Demography of a single mature colony of *Aphaenogaster mariae*.

Adults		
Caste	**Count**	**Percent**
Worker	604	57.6
Queen (alate)	185	17.7
Queen (dealate)	0	0
Male	255	24.3
Intercaste	4	0.4
Total	1048	100
Immatures		
Caste	**Count**	**Percent**
Pupa	19	21.1
Larva	71	78.9
Total	90	100

We classified four adults as intercastes, because they had features characteristic of both queens and workers. These specimens had wing scars, wing buds, or deformed wings, but lacked ocelli and an expanded pronotum to accommodate flight musculature (Figs. 6–9). Because the queen-like traits exhibited by these individuals were largely malformed (Figs. 8, 9), we suspect these individuals represent intercaste workers

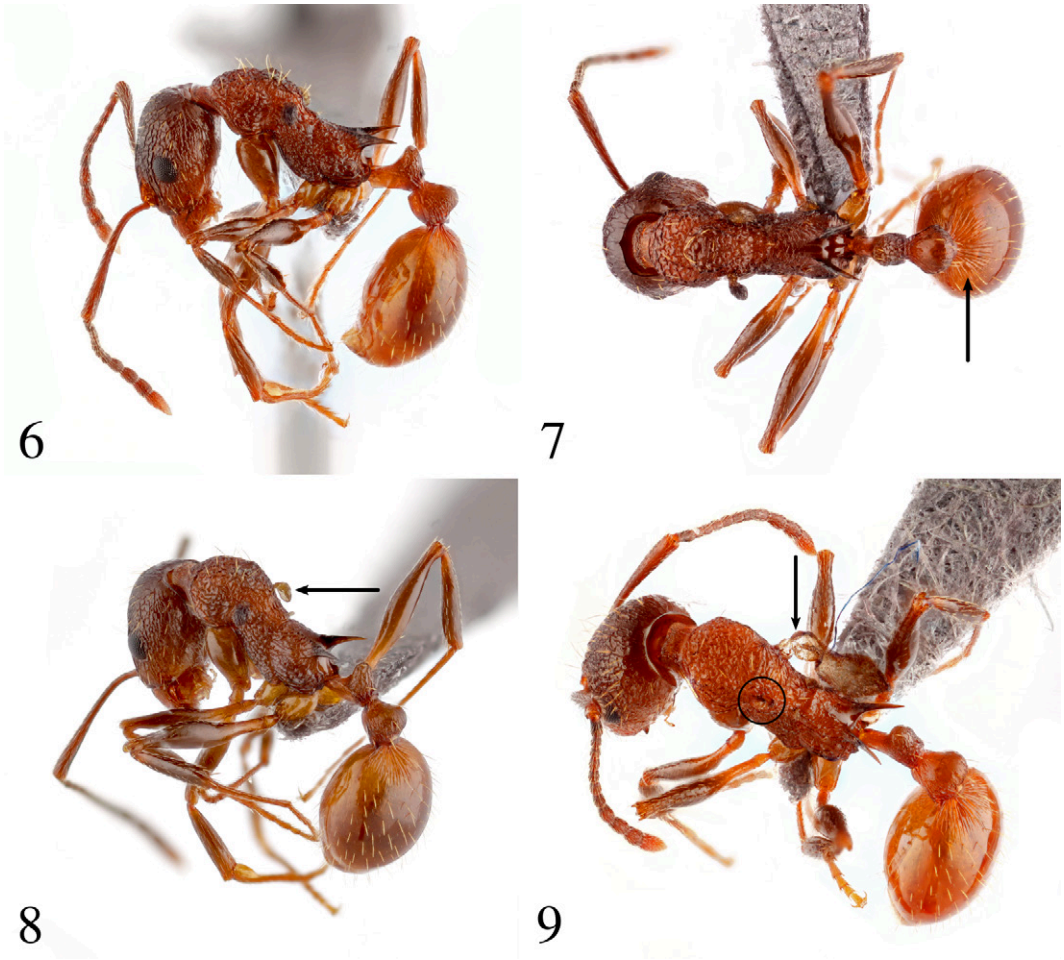
and are the product of abnormal larval development (Heinze 1998). Likely these ants were behaviorally akin to workers and do not represent reproductive, intermorphic queens.

Morphology

The defining characteristics of *Aphaenogaster mariae* are the delicate striae on the first gastral segment, which fan out from the attachment of the post-petiole in a starburst pattern (Figs. 4, 7, 13). These striae separate this species from all other North American species in the genus. The striae are well defined in the workers and queens, but only weakly developed in the males (Figs. 14–17).

While queens and workers of *A. mariae* are relatively well represented in museum collections and images are available on AntWeb (California Academy of Science 2022), the male of this species is known from only two specimens—one from a light trap in Georgia and one from Ohio that is purportedly deposited in the Los Angeles County Museum. We were unable to locate either specimen. While these males have been described (Carroll 1975, Mackay and Mackay 2017), the descriptions are not peer-reviewed, and the present collection provides an opportunity to redescribe the male with additional material. We provide images of all castes to support taxonomic descriptions and promote simpler identification of the species

Figs. 3–5. *Aphaenogaster mariae* worker. 3, Dorsal; arrow indicates characteristic striae radiating from the post-petiolar attachment. 4, Lateral. 5, Frontal.



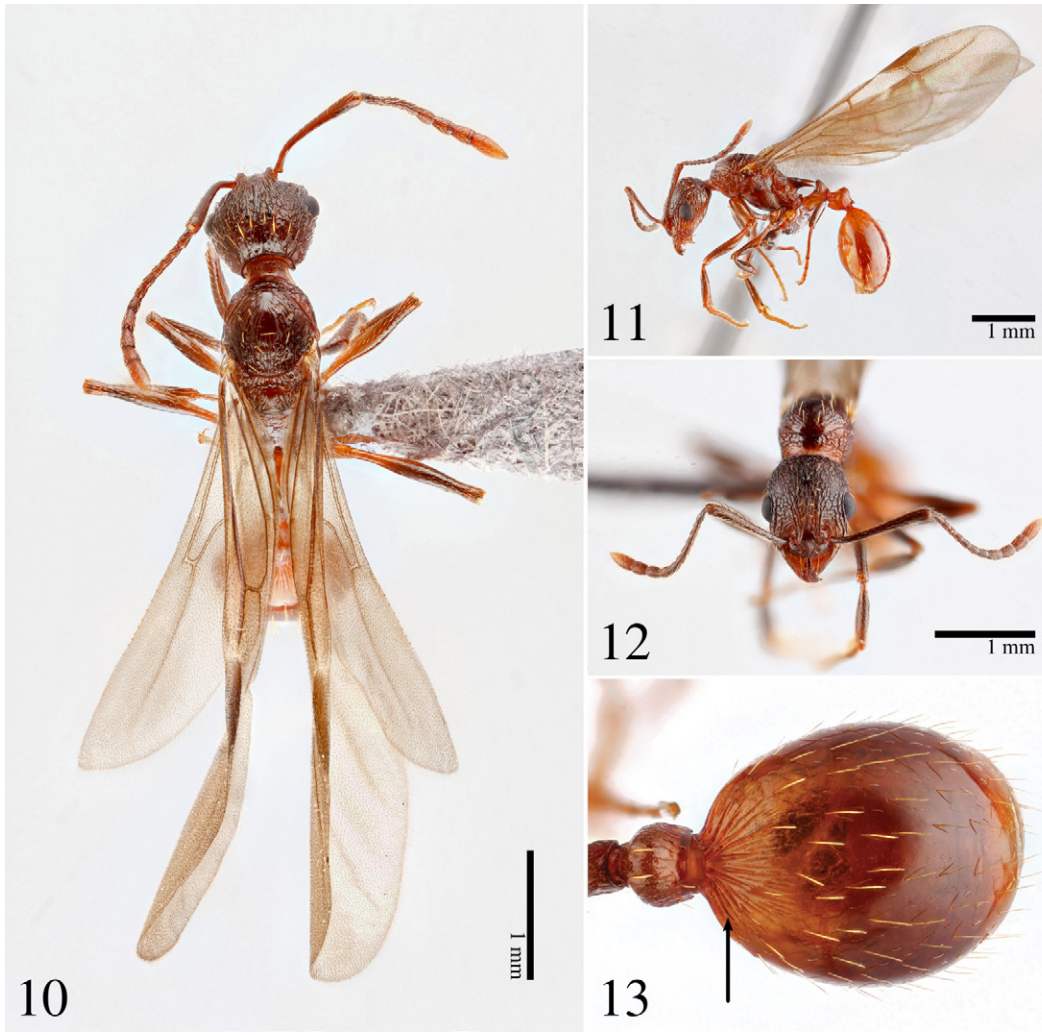
Figs. 6–9. *Aphaenogaster mariae* intercaste worker. 6, Lateral; note the worker-like appearance. 7, Dorsal; arrow indicates the characteristic striae radiating from the post-petiolar attachment. 8, Postero-lateral; arrow indicates wing bud. 9, Dorso-lateral; circle indicates wing scar and arrow indicates malformed wing.

(Figs. 14–17, 18–21). The images in this article will also be uploaded to AntWeb (California Academy of Science 2022).

Treatment of Male *Aphaenogaster mariae* Forel

Diagnosis (Figs. 14–17).—Among North American *Aphaenogaster*, male *A. mariae* are most similar in appearance to the sister species, *A. tennesseensis*. In both species, the males have a head that is wider posteriorly than anteriorly, a short postpetiole, and swollen metapleural processes, but *A. mariae* can be separated by the lack of distinct spines on the propodeum, the presence of erect dorsal setae, an anteriorly shining scutum, and metapleural processes that barely extend past the propodeum (Carroll 1975).

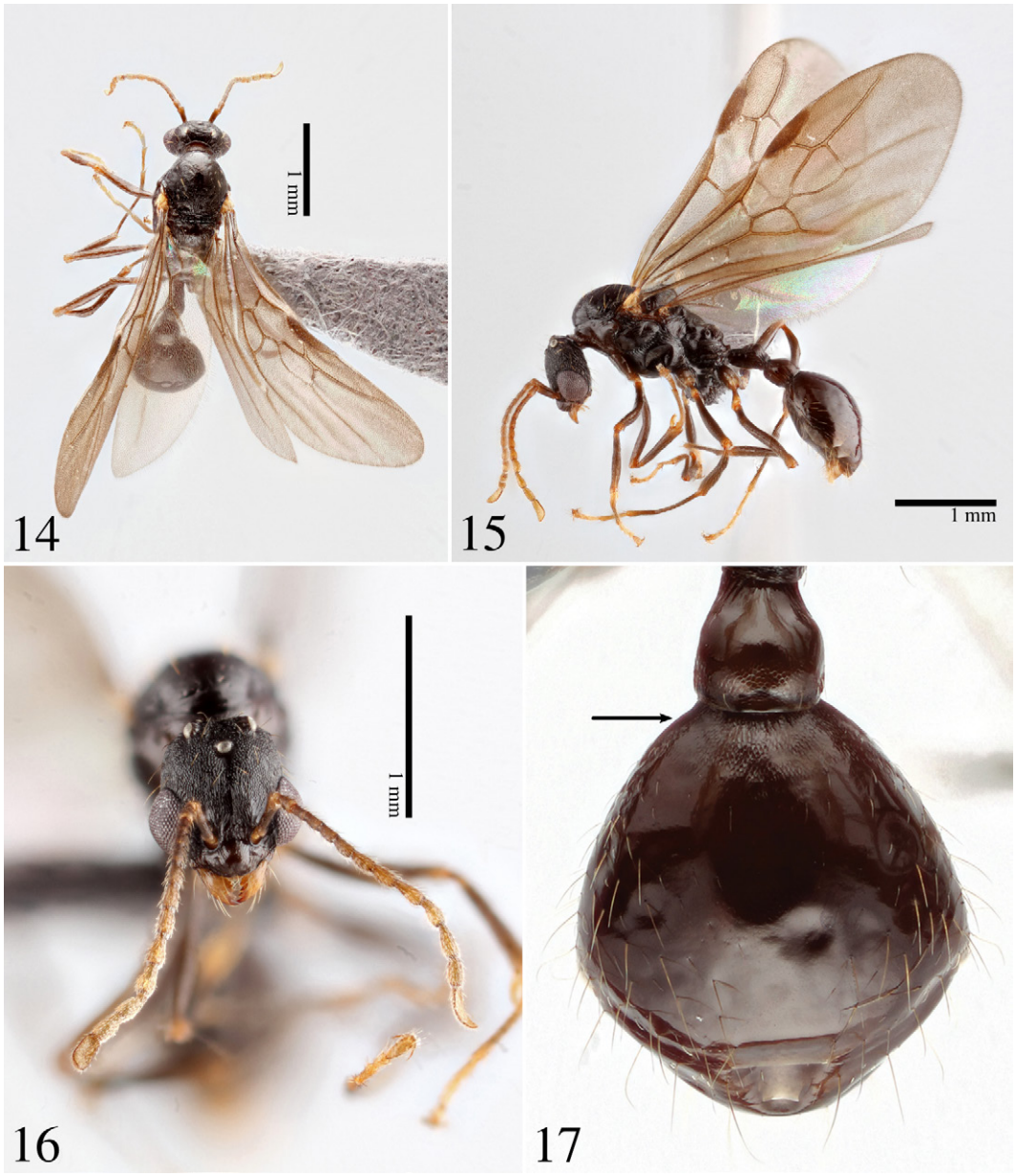
Measurements and indices.—Values are in mm and presented as mean ± SD (range). HL: 0.783 ± 0.02 (0.750–0.810); HW: 0.615 ± 0.02 (0.581–0.652); EL: 0.337 ± 0.01 (0.310–0.363); SL: 0.215 ± 0.02 (0.175–0.275); MscL: 0.782 ± 0.03



Figs. 10–13. *Aphaenogaster mariae* alate queen. 10, Dorsal. 11, Lateral. 12, Frontal. 13, Dorsal view of 1st gastral segment (A4); arrow indicates characteristic striae radiating from the post-petiolar attachment.

(0.744–0.829); MscW: 0.722 ± 0.02 (0.691–0.782); ML: 1.581 ± 0.07 (1.416–1.673); PL: 0.424 ± 0.03 (0.349–0.475); PW: 0.231 ± 0.01 (0.211–0.249); PPL: 0.359 ± 0.03 (0.271–0.393); PPW: 0.306 ± 0.01 (0.271–0.335); CI: 78.6 ± 2.25 (73.8–83.5); SI: 35.0 ± 3.39 (29.7–42.2); MI: 219.0 ± 12.0 (190.7–235.1).

Redescription.—*Coloration* (Figs. 14–17)*:* Head, mesosoma, and petiole dark brown. Postpetiole and gaster dark to medium brown. Pronotum, legs, antennae, and mandibles medium to light brown. *Head* (Fig 16): Head subrectangular and distinctly wider posteriorly than anteriorly, lateral surfaces below eyes straight or slightly converging, occipital margin straight, sometimes with slight emargination. Anterior margin of clypeus usually slightly convex, but sometimes straight or with a slight concavity. Eyes large and oval. Mandibles shiny and faintly punctate. Clypeus shiny with delicate longitudinal striations medially



Figs. 14–17. *Aphaenogaster mariae* male. 14, Dorsal. 15, Lateral. 16, Frontal. 17, Dorsal view of 1st gastral segment (A4); arrow indicates the barely impressed striae radiating from the post-petiolar attachment.

that become coarser laterally. Sparse rugose sculpturing on frontal triangle and between mandible insertion and anterior edge of eye. Frontal carinae short and convergent, ending about 2/3 up the eye. Frons densely punctate posteriorly becoming rugose anteriorly. Gena and temples densely punctate to foveolate. Vertex with transverse rugae posteriorly becoming more punctate anteriorly. Long erect setae line midline of head and ventral edge of gena. Three pairs of

Figs. 18–21. *Aphaenogaster mariae* juveniles. 18, Lateral view of larva early in development. 19, Lateral view of larva late in development; note the size and color difference from 18. 20, Lateral view of pupa early in development. 21, Lateral view of pupa late in development; note the color difference from 20. Scale bar applies to Figs. 18–21.

long erect setae on clypeus near mandible insertion. Erect to decumbent setae on mandible of varying lengths. Antennal scapes short with short, decumbent setae. *Mesosoma* (Figs. 14, 15): Mesosoma relatively slender. Mesoscutellum rounded, presenting an even convexity dorsally and gradually sloping laterally. Mesoscutellar disc projecting above maximum height of mesoscutellum. Propodeum subtrapezoidal, its dorsal surface usually flat and gently sloping, but occasionally slightly rounded. Propodeal spines absent, often replaced by a pair of thickened lobes. Lower metapleuron swollen posteriorly, ending in a flange that barely extends past the declivitous face of the propodeum. Pronotum finely reticulate. Anterior-most portion of mesoscutum smooth and shining. Finely lineate sculpture arising along longitudinal midline of mesoscutum, running along length of mesoscutum becoming rugose laterally. Mesoscutellar disc with longitudinal rugae. Medial dorsum of propodeum smooth and shining or delicately reticulate Lobes and declivitous face of propodeum rugose. Anepisternum finely lineolate anteriorly becoming carinulate posteriorly. Subalar area strongly costate. Katepisternum, metapleuron, and lateral propodeum lineolate to costate. Mesoscutum with sparse, long, erect setae and shorter, decumbent setae. Several erect setae on mesoscutellar disc. Propodeal lobes with fine, appressed pubescence. *Metasoma* (Figs. 14, 15, 17): In lateral view, petiole triangular with a rounded node and postpetiole oval and broadly convex. Dorsally, both petiole and postpetiole with shallow longitudinal suture centrally. Postpetiole barely longer than wide. Dorsum of petiole and postpetiole finely punctate or rugulose. Gaster feebly striolate with faint striae radiating from postpetiolar attachment. Few decumbent setae on postpetiole and sometimes petiole. Gaster with sparse setae of varying lengths.

Natural History

This article reports the first documented collection of a colony of the arboreal ant species *Aphaenogaster mariae*. The nest was in a dead branch 17 m in the canopy of a mature *Quercus alba* and presumably inaccessible to most collectors. While this ant's range spans much of the eastern United States, it is relatively rarely collected, likely due to its arboreal lifestyle. Wesson and Wesson (1940) are a notable exception, as they collected *A. mariae*

"frequently" from oaks while cataloguing ants of south-central Ohio, but their publication does not report any specific collecting methods. MacGown and Brown (2006) collected a series of *A. mariae* workers and four dealate queens and found a nest in a standing dead tree in the Tombigbee National Forest in Mississippi, but still listed the species as "uncommon" among their intensive terrestrial collections. In another study, MacGown et al. (2012) suggested that *A. mariae* can be "easily collected with peanut butter bait" on large oak and hickory trees and, indeed, most of the records of the species on AntWeb were collected with peanut butter (California Academy of Science 2022). *Aphaenogaster mariae* has also been collected by others at baits (Ellison et al. 2012, DeMarco 2015), in pitfall traps (Munsee 1967, MacGown and Brown 2006, Vogt et al. 2022), Lindgren funnel traps (AntWeb data), and in Berlese funnels (MacGown and Brown 2006, MacGown et al. 2012), but typically only as single individuals. It seems the most reliable method for collecting this species is by baiting trunks of mature hardwood trees with peanut butter, if the collector is primarily interested in workers, or active hand-collecting on oak trees as high in the canopy as possible, particularly if the collector is interested in locating nests (Wesson and Wesson 1940, Carter 1962, DuBois 1985, Frye and Frye 2012, MacGown et al. 2012).

It is possible that this ant is not actually rare, but only rarely collected with common ground-based collecting methods. If this were the case, canopy-focused collections might regularly detect this species. In the past three years, we have surveyed canopy ants at seven sites in central North Carolina by hand-collecting in 30 *Quercus alba* canopies and deploying baits (178 tuna and 178 jam) in 89 additional tree canopies. These efforts detected *A. mariae* at two sites and nests at only one. At the same site described here, we found two additional nests (not collected) in a dead branch at 15 m and 19 m high, each in a separate *Q. alba*. Both nests were similar in structure to the one described here. In addition, at this site and one other, we detected one worker per site at a canopy bait but observed no other individuals in those trees. This leads us to conclude that *A. mariae* is rarely collected not only because of its arboreal nesting strategy, but also because its populations occur in low, localized densities, at least in our study region.

An explanation for this species' relative rarity may exist in its reproductive strategy. Wheeler (1910) suggested that queens of *A. mariae* and the sister species, *A. tennesseensis*, may be temporary social parasites of other *Aphaenogaster* early in the colony lifecycle, relying on established nests of their congeners to provide for their incipient colony. Due to high host-specificity, social parasites are nearly always less abundant or more localized in distribution than their host species (Hölldobler and Wilson 1990, Thomas et al. 2005). While temporary social parasitism has yet to be proven for either species, dealate *A. mariae* queens have been collected from Berlese funnels that also contained nests of *A. fulva* (MacGown and Brown 2006). Both species exhibit relatively late nuptial flights (Wheeler 1916, Carroll 1975), which could allow socially parasitic queens to take advantage of nascent colonies of earlier-flying congeners. Additionally, queens of both species share morphology suggestive of social parasitism, including small body size (similar to the workers) and large propodeal spines—traits unique within the genus (Wheeler 1910, DeMarco 2015). If *A. mariae* is a temporary social parasite of *A. fulva* or other congeners, it would follow that populations of *A. mariae* would occur in relatively low and/or localized

densities. This could also explain the occurrence of dealate *A. mariae* queens in soil and leaf litter samples, despite their arboreal nesting habits (MacGown and Brown 2006). While she raises her first brood, a newly mated *A. mariae* queen may temporarily dwell in the soil nests of other *Aphaenogaster* species, ascending into the canopy once there is a well-established colony of her own workers.

Conclusions

Based on our observations and published literature, we suspect the apparent rarity of *A. mariae* is due not only to its arboreal lifestyle, but also to low, localized population densities, perhaps as a result of its reproductive strategy. Nevertheless, it appears that baiting tree trunks with peanut butter and hand-collecting in the canopies of mature trees, particularly oaks, are reliable methods for locating *A. mariae* and may ultimately help answer remaining questions. Historically, the ecology and biodiversity of temperate forest canopies has received far less attention than that of tropical forests. Yet many temperate species rely on canopy habitats, even if they are not canopy specialists (Ulyshen 2011). Our documentation of the first whole colony of an arboreal ant species 135 years after its description hints at exciting possibilities a little more than a dozen meters above the forest floor.

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