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The real deal: the ant species, *Pheidole sauberi* (Hymenoptera: Formicidae), first description of the queen and first record of a mermithergate in the Philippines

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Abstract

The occurrence of mermithism in ants is reported for the first time in the Philippines. The mermithergate worker and previously undescribed dealate queen of *Pheidole sauberi* are described. The mermithergate worker is intermediate in size between the major and minor workers and pale yellow in color, in contrast to the brown healthy workers, and has a much larger gaster than either uninfected subcaste. Colony demographics and nest ecology are also reported. This find offers an opportunity for interdisciplinary research on ant parasitism.

Keywords: transect survey, Mindanao, mermithism, entire nest series

Introduction

The infection of ants by nematodes has been known for more than two centuries (Gould 1747, Wheeler 1901, Wheeler 1928, Laciny 2021). Wheeler (1901) described the "macroërgates" of *Pheidole dentata* Mayr, 1886 that had the head and mesosoma of minor workers but possessed enormous gasters. The coiled nematode was visible through the stretched intersegmental membranes. Upon dissection, he also found that the nematode occupied the crop, with the head extended forward in the esophageal tract within the petiole of the ant. He speculated that since the nematode released eggs or larvae in the crop, these would be passed on to ant larvae through trophallaxis. Wheeler (1928) abandoned this speculation when contemporary researchers had actually observed that nematode larvae directly penetrated the intersegmental membranes of juvenile grasshoppers (Cobb et al. 1923).

Poinar (2012) reviewed the infection of ants by nematodes, including fossils in amber. Ten nematode families are represented by extant species while four nematode families are represented by extinct species from as long ago as 40 million years ago, suggesting a very long history of association between nematodes and ants (Poinar 2012). The instances of nematode infections of ants discussed by Poinar (2012) were recorded only from the Neotropical or Holarctic regions and none from the other faunal regions.

Nematode infection produces morphological changes in individual ants (Czechowski et al. 2007) that earlier researchers described as rare, but never again encountered, species (Czösz 2012). Using non-invasive x-ray microtomography, Czösz (2012) discovered coiled nematodes in the gasters of the unique holotype specimens of two species of the ant genus *Myrmica* Latreille, 1804. Whereupon he synonymized *M. symbiotica* (Menozzi, 1925) under *M. scabrinodis* Nylander, 1846 and confirmed the synonymy of *M. myrmecophila* Wassmann, 1910 under *M. sulcinodis* Nylander, 1846.

Another enigmatic ant species, *Pheidole symbiotica* Wassmann, 1909, was described from material collected in a nest of *Pheidole pallidula* (Nylander, 1849) from somewhere in Portugal by P.W. Deckelmeyer in 1849 (Borowiec & Salata 2015). Since its original description, *P. symbiotica* had never been found again until 2014. And because the original description was fairly brief, *P. symbiotica* had been alternatively considered a parasite or a subspecies of *P. pallidula* (Borowiec & Salata 2015, AntWiki 2021, Bolton 2021). Then, in 2014, L. Borowiec collected nine specimens corresponding to the description of *P. symbiotica* from two

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colonies in southern Italy (Borowiec & Salata 2015). Borowiec & Salata (2015) dissected two individuals and found large nematodes in the gasters, showing unequivocably that *P. symbiotica* is simply a teratological form of *P. pallidula.*

Using micro-CT imaging, Laciny et al. (2017) revealed the nematode infesting a strikingly morphologically different mermithogyne of the still undescribed *Colobopsis* sp. nrSA from Borneo, representing the first known record of mermithism in Southeast Asia. They, however, did not find workers infected by nematodes.

General et al. (2021) discussed how a rare and unrecognized ergatoid queen was initially confused with the ants that are morphologically modified by nematode infection (Wheeler 1901, 1928). After the publication of General et al. (2021), the senior author examined a vial containing an entire nest series of *Pheidole sauberi* Forel, 1905 and found workers of three size classes: major workers, minor workers, and pale workers of intermediate size but with rather large gasters. This contribution treats the discoveries from this entire nest series, particularly a real case of mermithism in Philippine ants, and not merely another morphological aberration.

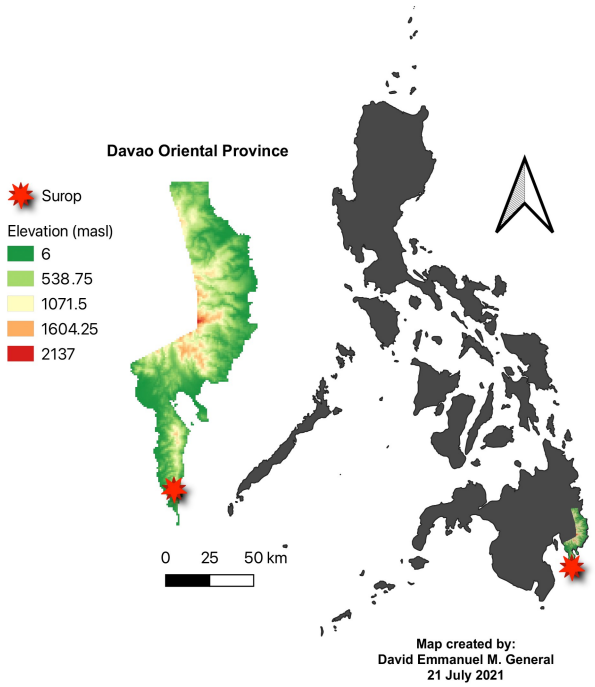

Figure 1. Approximate location of study site, Barangay [=Village] Surop, Municipality of Governor Generoso, Davao Oriental Province, Mindanao Island, Philippines.

Materials and Methods

A transect study of ant nests in rotten wood on the ground was conducted in Barangay [=Village] Surop, Municipality of Governor Generoso, Davao Oriental Province, Mindanao Island, Philippines (Fig. 1) on 24-28 January 2021. An entire nest series (collection code DMG534) of the ant species, *Pheidole sauberi*, is the focus of this contribution.

Measurements and abbreviations

All measurements are given in millimeters.

HL Head length, maximum length of head capsule, excluding mandibles, measured in full-face view in a straight line from the midpoint of posterior head margin to anterior clypeal margin.

HW Maximum head width, including eyes when they exceed the lateral margin of the head, measured in full face view.

SL Scape length, maximum length of scape, excluding basal neck and condyle, measured at the appropriate angle such that the scape is positioned perpendicularly to the viewer.

EL Maximum eye length, measured along the longest axis of eye.

PW Maximum width of pronotum, measured in dorsal view.

WL Weber's Length, mesosomal length measured from anterior edge of the pronotum (excluding the collar) to posterior edge of propodeal lobe.

GL Gaster length, measured in lateral view, from postpetiolar attachment to tip of gaster.

GH Maximum height of gaster, measured in lateral view, maximum transverse distance between dorsal surface and ventral surface of gaster.

GW Maximum width of gaster, measured in dorsal view.

Indices

CI Cephalic index: HW/HL x 100.

SI Scape index: SL/HW x 100.

EI Eye index: EL/HW x 100.

Specimens were examined with a Leica S6D stereomicroscope and measured using a Leica S8APO stereomicroscope with ocular micrometer. Images were created using a Leica MC120HD digital camera attached to the Leica S8APO stereomicroscope. These images were stacked using Combine ZM (Hadley 2014). The stacked images were edited with Adobe Photoshop CS5. The map was created in QGIS 3.14 (QGIS Development Team 2021).

Deposition

Voucher specimens will be deposited in the following institutions:

CMU - Central Mindanao University Museum, Maramag, Bukidnon, Philippines

MCZC - Museum of Comparative Zoology, Harvard University

PNM - Philippine National Museum, Manila, Philippines
UPLB - Entomological Collection of the Museum of Natural History, University of the Philippines Los Baños, Laguna, Philippines

Identification

Specimens of major and minor workers were dry-mounted on points and keyed out to species level using the keys of Eguchi (2001a) and then compared with images of *P. sauberi* in AntWiki (2021).

Material examined

Non-type major worker: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // PNM 14678] [Collection Code: DMG 534] (PNM) (Figs. 2, 17); Non-type minor worker: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // PNM 14679] [Collection Code: DMG 534] (PNM) (Figs. 3, 17); Non-type mermithergate worker: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // UPLBMNH HYM-01792] [Collection Code: DMG 534] (UPLB); Non-type mermithergate worker: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // UPLBMNH HYM-01793] [Collection Code: DMG 534] (UPLB); Non-type mermithergate worker: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // PNM 14680] [Collection Code: DMG 534] (PNM) (Figs. 4, 17); Non-type mermithergate worker: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // UPLBMNH HYM-01794] [Collection Code: DMG 534] (UPLB) (Fig. 5); Non-type queen: [PHILIPPINES: Davao Oriental, Gov. / Generoso, Bgy. Surop / 24-31.i.2021 / DMGeneral et al. // Ex. log nest / transect study // UPLBMNH HYM 01791] [Collection Code: DMG 534] (UPLB) (Figs. 6, 17).

Results

Demographics and ecology

The queenright colony was found in a piece of rotten wood on sloping ground in a disturbed second-growth lowland tropical rainforest. The nest population consisted of: (a) 94 major workers (Fig. 2); (b) 442 minor workers (Fig. 3); (c) 42 mermithergate workers (Figs. 4-5); (d) one dealate queen (Fig. 6); (e) nine mermithergate pupae; (f) uncounted normal worker pupae and larvae, many lost in the processing of the specimens. Figure 7 presents the relative sizes of the adult female subcastes. The mermithergate workers represent 7.27% of the adult ant population of the colony. There was also a myrmicine pupa, among the samples of the collected nest, with long appendages, possibly of *Pheidole plinii* Forel, 1911, which was also present

Table 1. Measurements and indices of the female subcastes of *Pheidole sauberi.*

	HL	HW	SL	EL	PW	WL	GL	GH	GW	CI	SI	EI
Major worker (PNM 14678)	0.90	0.91	0.50	0.10	0.42	0.74	0.66	0.38	0.53	102	54	11
Minor worker (PNM 14679)	0.48	0.45	0.50	0.08	0.28	0.56	0.50	0.25	0.38	95	111	17
Merrmithergate 1 (UPLBMNH HYM-01792)	0.56	0.53	0.48	0.08	0.30	0.58	0.78	0.45	0.50	94	91	15
Merrmithergate 2 (UPLBMNH HYM-01793)	0.51	0.50	0.48	0.10	0.29	0.58	0.77	0.46	0.46	97	97	19
Mermithergate 3 (PNM 14680)	0.53	0.50	0.48	0.08	0.29	0.59	0.70	0.45	0.43	94	97	16
Queen (UPLBMNH HYM-01791)	1.00	1.13	0.55	0.30	1.05	1.55	1.75	1.00	1.50	113	49	27

in the study site. This foreign pupa may be a food item, suggesting that *P. sauberi* raids other ant nests for food.

***Pheidole sauberi* Forel, 1905**

Pheidole sauberi Forel, 1905: 18 (major and minor worker described) INDONESIA (Java)

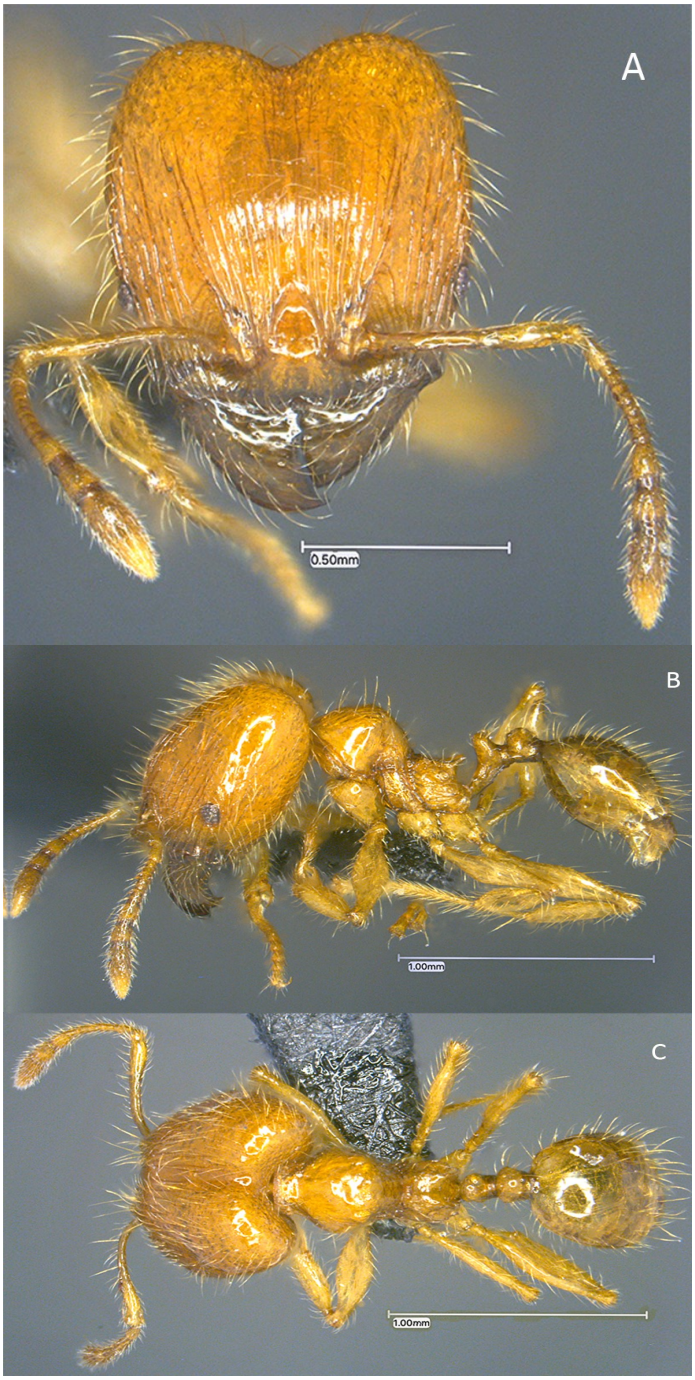

Figure 2. *Pheidole sauberi*, nontype major worker (PNM 14678), dorsal head view (A), lateral view (B), dorsal view (C).

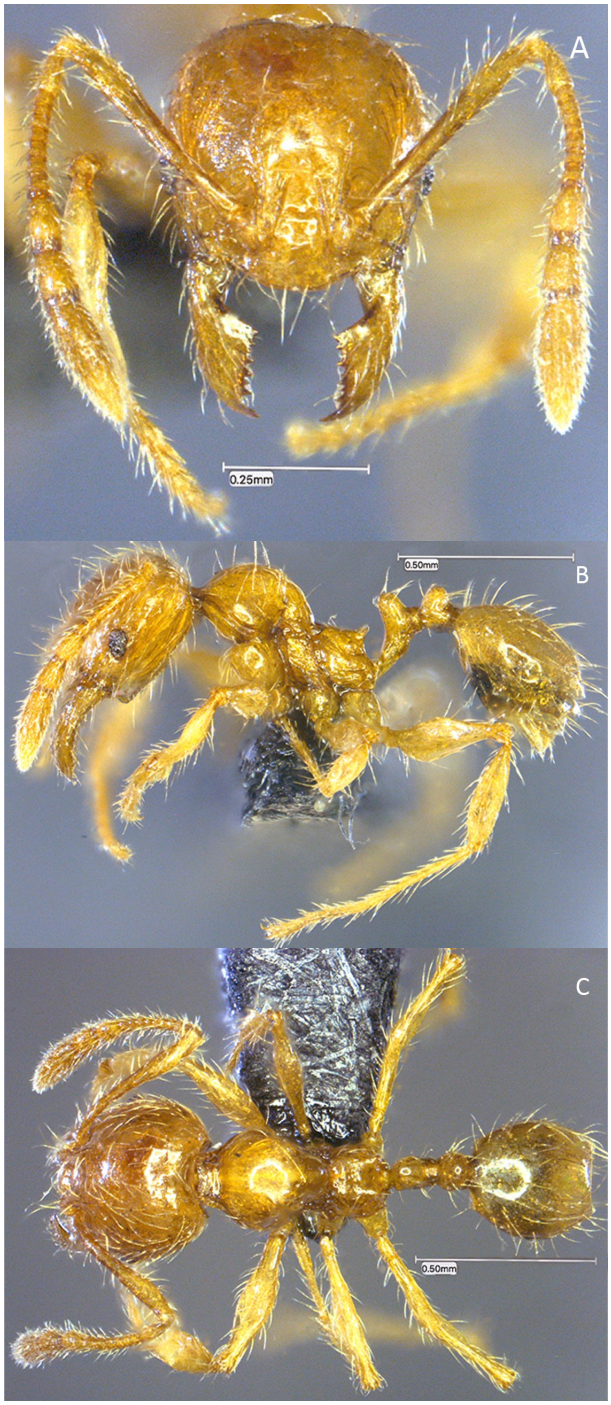

Figure 3. *Pheidole sauberi*, nontype minor worker (PNM 14679), dorsal head view (A), lateral view (B), dorsal view (C).

Pheidole sauberi Forel, 1905 Status as species: Eguchi (2001a, 2001b), Bolton (2021)

Description of the Mermithergate Worker

Mermithergate (Figs. 4, 5): posterior margin of head, in full-face view, narrowly and slightly emarginate medially;

occipital carina absent; clypeus without median longitudinal carina, with anterior margin entire; eye situated just in front of midlength of head; distance between mandibular insertion and anterior margin of eye at 1x maximum eye length; frontal carina and antennal scrobe extend almost to posterior margin of eye; antenna with 3-segmented club; scape extends beyond posterior margin of head by at least width of the widest part of scape; scape slightly incrassate at distal third; terminal segment about 1.1-1.2 times as long as two preceding segments together; promesonotal dome without prominence on posterior declivity; mesopleuron not divided by distinct transverse impression; propodeal spine about 1.5 times diameter of propodeal spiracle;

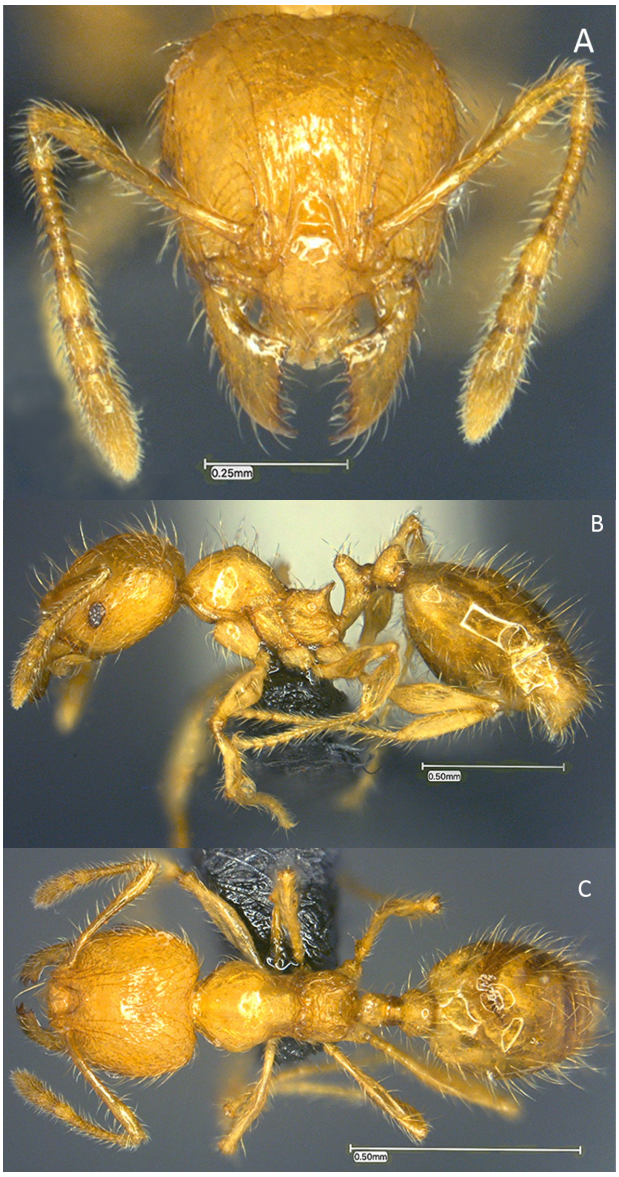

Figure 4. *Pheidole sauberi*, mermithergate worker (PNM 14680), dorsal head view (A), habitus in lateral view (B), habitus in dorsal view (C).

Figure 5. *Pheidole sauberi*, mermithergate worker (UPLBMNH HYM-01794), habitus in lateral view, intact but nematode protruding (A), habitus in lateral view, with gastral tergites removed (B), habitus in lateral view, with nematode extracted from gaster (C).

petiole about 2 x length of postpetiole, not including helcium; apex of petiolar node, in posterior view, entire; postpetiole, in dorsal view, at most 1.5 x width of petiole; dorsum and venter of head smooth and shining, except for concentric rugulae around antennal socket; promesonotum dorsally and laterally smooth; propodeum dorsally and laterally punctate; lateral face of petiolar peduncle punctate; dorsum of petiole, postpetiole and gaster smooth and shining; head and body concolorously pale yellow.

In summary, the mermithergate is intermediate in body size between the major and minor worker, however the gaster is is disproportionately larger. In addition, the mermithergate is distinctly paler in color than either worker.

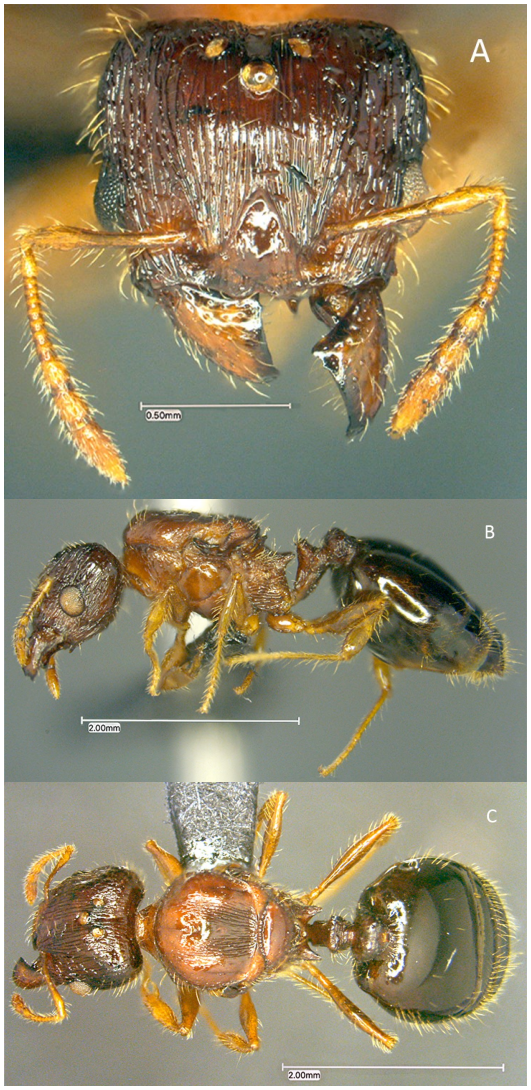

Figure 6. *Pheidole sauberi* dealate queen (UPLBMNH HYM-01791), dorsal head view (A), habitus in lateral view (B), habitus in dorsal view (C).

Description of the Dealate Queen

Dealate queen (previously undescribed) (Fig. 6): in full-face view, head widest at occipital corners; posterior margin of head broadly but shallowly emarginate; clypeus without median longitudinal carina, with anterior margin medially emarginate; ocelli present; eye situated at about 1/3 length of head; distance between mandibular insertion and anterior margin of eye about 0.5 x maximum eye length; frontal carina and shallow antennal scrobe extend to almost 4/5 length of head; hypostoma with 2 median processes; antenna with 3-segmented club; scape reaches about 4/5 length of head; scape slightly incrassate at distal third; terminal segment about subequal to two preceding segments together; mesoscutum and mesoscutellar disc dorsally flat; wing scar present; flight sclerites present; anepisternum separated from katepisternum by oblique mesopleural sulcus; propodeal spine horn-like, about 3 x diameter of propodeal spiracle; petiole about 1.5 x length of postpetiole, not including helcium; apex of petiolar node, in posterior view, entire; postpetiole, in dorsal view, at most 1.5 x width of petiole; dorsum of head longitudinally rugose, except for smooth median clypeus; subocular area of head ventrally longitudinally rugose; in lateral view, pronotum largely smooth but with single oblique ruga; anepisternum and katepisternum smooth and shining; propodeum transversely rugose; in dorsal view, mesoscutum longitudinally rugose; mesoscutellar disc smooth and shining; petiole and postpetiole punctate; gaster smooth; body dark brown, with lighter brown mesosoma and legs; pilosity composed of scattered, short erect hairs throughout the body surface.

Figure 7. *Pheidole sauberi*, composite of all female subcastes on one pin, habitus in lateral view (top to bottom: UPLBMNH HYM-01791; PNM 14678; PNM 14680; PNM 14679.)

Discussion

This is the first record of mermithism in ants in the Philippines. The nematode extracted from the specimen, UPLBMNH HYM-01794, (Fig. 5) provides unequivocal proof that the pale intermediate sized workers are nematode-infected workers or mermithergates. The coiled shape of the nematode

precludes identification (V. Paller, pers. comm. 2013, General et al. 2021), although it keys out in Poinar (2012) to Family Mermithidae.

The other mermithergates in the nest series have all been pickled in ethanol, also preserving the infecting nematodes in a coil. And, since only the dissected mermithergate exhibited a nematode bursting out of its gaster (Fig. 5), it is likely that the other mermithergates harbored even less mature nematodes. All the undissected mermithergate pupae and workers have been preserved for future study in the laboratory of Dr. Vachel Gay Paller of the University of the Philippines Los Baños, Institute of Biological Science.

Wheeler (1928) observed, from a laboratory colony of *P. dentata*, that the gaster of the infected ant quickly enlarged after eclosion. It is unclear, though, how Wheeler (1928) identified the infected pupae among the uninfected ones. In the current nest series of *P. sauberi*, the infected pupae are already clearly identifiable by their enlarged gasters.

The mature nematode of the family Mermithidae escapes the host by penetrating the intersegmental membranes of the abdomen (Cobb et al. 1923) or gaster (Poinar 2012, also see Fig. 5a). The nematode dissected from the mermithergate (Fig. 5) appears to be escaping from the gaster when the ant was pickled.

The extreme size difference between the dealate queen and the mermithergates (Table 1; Fig. 7) strongly suggests that the infected individuals are workers rather than reproductives. The reviews by Wheeler (1928) and Poinar (2012) illustrate a number of ant species where workers are infected. The mermithergate pupae, morphologically modified but being able to fully develop into adults while infected by a nematode, also illustrate the phenotypic plasticity and robustness of the polymorphic worker caste of *P. sauberi* (Laciny 2021).

We also describe and illustrate the previously undescribed dealate queen of *P. sauberi* (Eguchi 2001a, b, Bolton 2021). Another worker-associated dealate *Pheidole* queen can now be identified among the many female alates collected at lights or unassociated dealate queens captured in traps.

This is also the first distributional record of *P. sauberi* on Mindanao Island, with previous records from the islands of Luzon and Romblon (General & Alpert 2012, unpublished notes). Mindanao is poorly surveyed and is expected to yield many more discoveries of new distributional records of ants including those new to science.

This study also provides more proof that nest collection, whether in rotten wood, twigs, or under stones, provides a wealth of information aside from simple colony size and demographics. The prevalence of mermithism in Philippine ants is unknown and more nest collections in the Philippines may discover other ant species infected by nematodes, perhaps even belonging to different nematode families. Finally, the immature nematodes in the preserved mermithergates may be DNA-barcoded by a nematologist for future interdisciplinary studies of this ant-parasite system, as proposed by Laciny (2021).

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