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SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

The Male of the Ant Genus *Rhopalothrix* (Hymenoptera: Formicidae: Myrmicinae)

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Abstract
The male caste is firstly described for the ant genus *Rhopalothrix*. The male was collected as attached to the gyne during copula. Due to the rarity of the genus, the gyne and male are tentatively associated with *R. apertor* Longino and Boudinot 2013. The apomorphic features of *Rhopalothrix* male are discussed, and a preliminary identification key based on males to the genera in the *Basiceros*-genus group (formerly tribe Basicerotini) is provided.

Keywords Morphology · Systematics · Myrmicinae · Attini · Neotropics

Introduction

Male ants (Hymenoptera: Formicidae) are known for about 80% of all 339 genera described so far (AntWeb 2021). Regarding the subfamily Myrmicinae, considered "the grand challenge to understand with respect to males" (Boudinot 2015), out of 139 valid genera, males of at least 30 genera are unknown.

Rhopalothrix Mayr is an example of a genus from which males are not known. Being a rare genus of small cryptic ants, there are currently 16 valid species of *Rhopalothrix*. The genus has a disjunct distribution, with species recorded from two biogeographical regions: Australian (2 species) and Neotropical (14 species). In 1960, as part of a comprehensive revision of the "Basicerotini," Brown and Kempf revised the genus, recognizing seven species, and describing four new species, including the first description of a *Rhopalothrix* gyne. The next and last significant contribution to the systematics of *Rhopalothrix* was made in 2013, when Longino and Boudinot (2013) revised the Neotropical *isthmica* clade, describing eight new species and associating *Rhopalothrix* gynes with workers for the first time. Thus, currently, gynes are described for five *Rhopalothrix* species, from which winged gynes are known for three species; in four species gynes are associated with workers. Males remain unknown. Also, a nest has never been recovered and a live *Rhopalothrix* specimen has never been seen (Longino and Boudinot 2013).

In this paper, I present the first description of the male caste of the genus *Rhopalothrix*. A pin-mounted male and gyne have been located in the Canadian National Collection of Arachnid and Nematodes (CNC) and collected as attached to each other during copula (Fig. 1). This allowed the assignment of the male specimen to *Rhopalothrix* and subsequently to identify both specimens as *R. apertor* Longino and Boudinot 2013 following Longino and Boudinot's (2013) identification key.

Following the description, a preliminary diagnostic key to the Basiceros-genus group (sensu Ward et al. 2015) is presented.

Rhopalothrix and related genera were first included in the tribe Dacetini (Emery 1922). Interestingly, even *Blepharidatta* Wheeler ("extraneous element" as defined it Brown and Kempf (1960)) was a member of Dacetini at that time. After the establishment of Basicerotini (Brown 1949), some attempts were made to synonymize Basicerotini with Dacetini (Baroni Urbani and de Andrade 2007). Bolton in his most comprehensive morphological treatment of Formicidae (Bolton 2003) recognized separate tribes Basicerotini, Dacetini, and Blepharidattini. The molecular phylogeny of Myrmicinae (Ward et al. 2015) recovered that those tribes closely related to each other and to the fungus-growing ants

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Fig. 1 *Rhopalothrix apertor*, gyne and male. Scale bar is 1 mm

(Attini sensu Bolton (2003)), together with which they form the tribe Attini sensu novo. This Attini sensu Ward et al. (2015) also included former tribes Pheidolini, Cephalotini, and Phalacromyrmecini sensu Bolton (2003) plus several genera historically assigned to other groups (*Ochetomyrmex* Mayr, *Tranopelta* Mayr, *Allomerus* Mayr, *Lachnomyrmex* Wheeler, *Diaphoromyrma* Fernández, Delabie, do Nascimento, *Lenomyrmex* Fernández, Palacio).

Thus, all Myrmicinae are now divided into six tribes: Myrmicini, Pogonomyrmecini, Stenammini, Solenopsidini, Attini, and Crematogastrini; the Basicerotini is now regarded as a junior synonym of Attini (Ward et al. 2015). In the light of the new classification, it is important to recognize synapomorphic characters for the *Basiceros*-genus group and to reduce the current taxonomic uncertainty of the generic boundaries within the group (Probst et al. 2019).

Material and methods

Photographs were taken with a Nikon D1X digital camera attached to the microscope Leica Z6 APO. All measurements were made with an ocular micrometer and are presented in millimeters.

The following measurements were recorded:

HL: head length (measured in full-face view as a straight line from the median point of anterior clypeal margin to the midpoint of the vertexal margin);
HW: head width (maximum head width in full-face view, across the eyes);
SL: scape length (male: maximum length excluding articular condyle; gyne: straight line distance between the attachment point of the articular condyle and the attachment point of pedicel);
ML: mandible length (excluding apical fork);
ATL: apical tooth length;
WL: Weber's length (distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum);
TL: total body length;
Indices: Cephalic index CI (HW*100/HL) and scape index SI (SL*100/HW).

For the wing venation, Longino and Boudinot (2013) were followed. Photographs of Attini (sensu Ward et al. 2015) males available on AntWeb (AntWeb 2021) were used for comparison and illustration. Details of the specimens examined are given in Online Source 1.

Results

Species account

Rhopalothrix apertor Longino and Boudinot, 2013: Figs. 1–4

Rhopalothrix apertor Longino and Boudinot, 2013: 309, Figs. 1F, 2B, 3A, 6, 16. Holotype, worker: Costa Rica, Heredia, 4 March 2005 [California Academy of Sciences, San Francisco, CA, USA] (examined through AntWeb photographs).

Diagnosis (male). Entire body, including legs, foveate; foveae about the size of ommatidia, smaller on legs. Mandibles slender, at least twice as long as broad (excluding apical fork); at least apical and subapical teeth long and spiniform. Rugae on head absent. Notauli present. Antennae with 13 articles, filiform. Scape short, shorter than flagellomeres. Palp formula 1,1. Meso- and metatibiae lacking apical spurs. Forewing lacking discoidal cell,

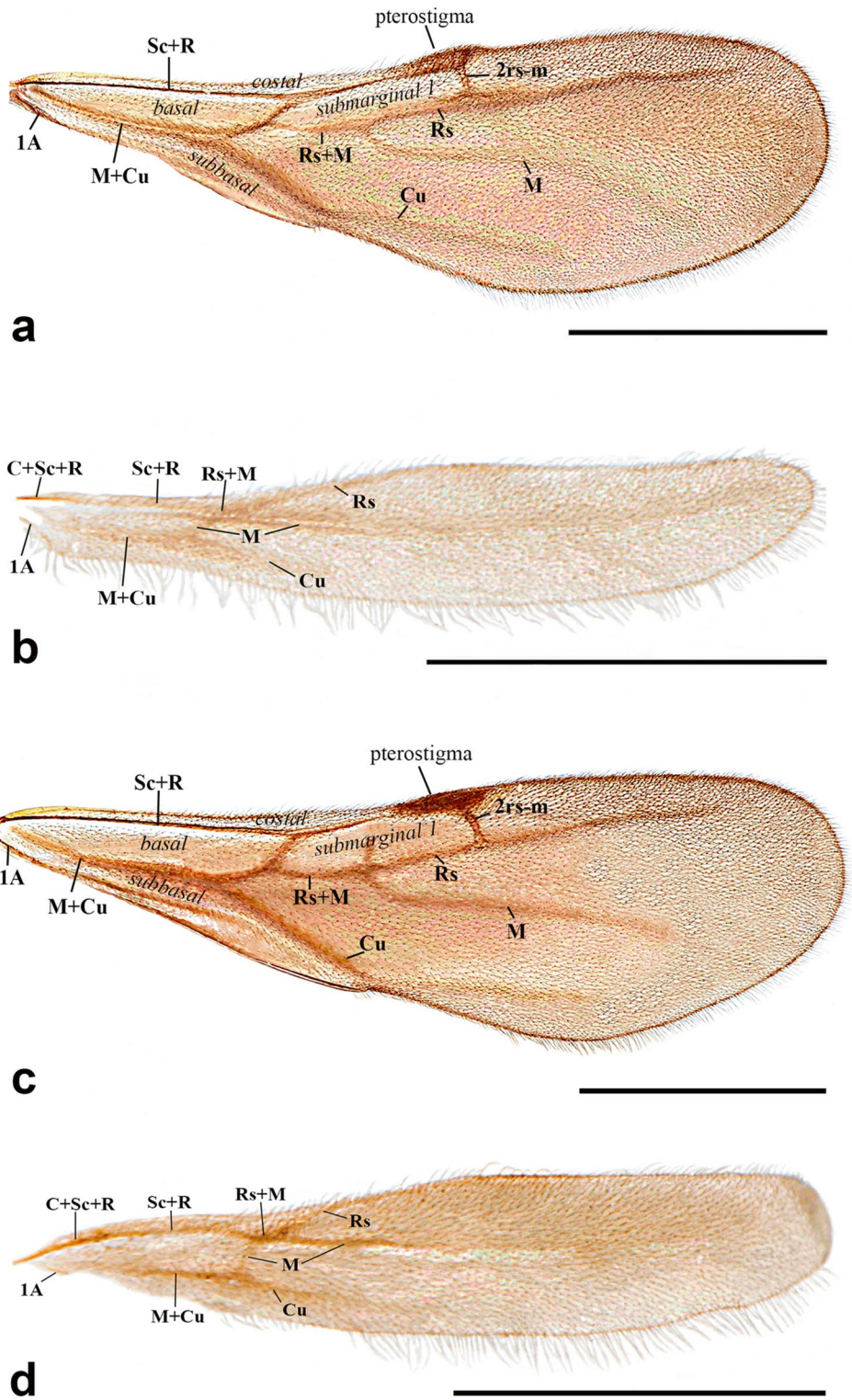


Fig. 2 Wings of *Rhopalothrix apertor*, gyne **a** forewing, and **b** hindwing; male **c** forewing, and **d** hindwing. Cell names are italicized; scale bars are 1 mm

marginal cell open; only basal and submarginal 1 cells fully closed; hindwing lacking closed cells.

Diagnosis (female castes; modified from Longino and Boudinot 2013**).** On the masticatory margin of mandible, at about mid-length, large, blunt, and peg-like tooth present. In workers, tooth at base of subapical tooth directed posteriorly; first gastral tergite largely devoid of setae, with one pair of squamiform setae at posterolateral margins; first gastral sternite with pronounced median keel. In gynes, forewing without discoidal cell, marginal cell open; only basal and

Fig. 3 *Rhopalothrix apertor*, male: **a** lateral, **b** dorsal, and **c** full-face views. Scale bars are 1 mm for **a** and **b**, 0.25 mm for **c**

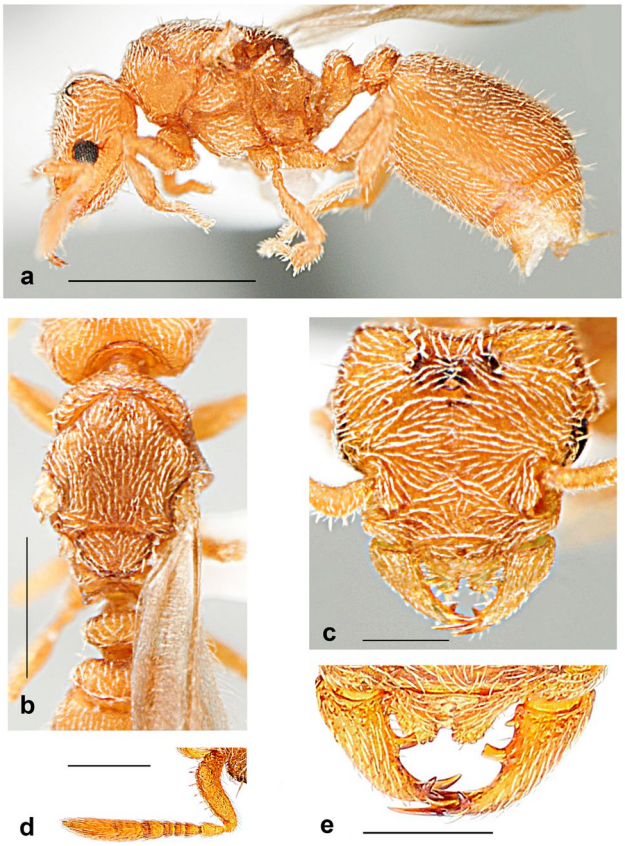


Fig. 4 *Rhopalothrix apertor*, gyne: **a** lateral, **b** dorsal, and **c** full-face views; **d** antenna, dorsal view; **e** mandibles and labrum, dorsal view. Scale bars are 1 mm for **a**, 0.5 mm for **b**, 0.25 mm for **c**, **d**, **e**

submarginal 1 are fully enclosed forewing cells; hindwing without closed cells.

Description (male, first description). HW 0.70, HL 0.58, ML 0.23, ATL 0.04, SL 0.15, WL 1.1, TL 3.4, CI 121, SI 21.

Body reddish brown, appendages lighter; cuticle adjacent to ocelli black. Head subglobular. Eyes large and bulging, placed anterior to cephalic mid-length. Shallow depression of cephalic dorsum extending from anterior ocellus to posterior clypeal margin. Elevated carina present on posterior head margin. Clypeus separated from frons by deep groove. Base of scape situated in well-defined cavity adjacent to minute frontal lobes. Mandibles elongated, bearing apical fork of two long and spiniform teeth, sub-equal in size; intercalary denticle present. Masticatory margin with two triangular teeth. Labrum subtriangular, broader than long; distal margin rounded, with median sinus forming short lobes; apicolateral margins short. Palp formula 1,1. Clypeus broad, evenly convex, antero-lateral areas elevated. Antennae filiform, long, 13-segmented. Scape not reaching median ocellus.

Mesosoma robust, higher than in conspecific gyne. Metakatepisternum partially separated from propodeum by shallow carina directed towards but not reaching propodeal spiracle. Notauli deep, with transversal costulae. Propodeal teeth obtuse. Ventral tooth of petiolar peduncle well-defined, directed anterad. Other mesosomal and waist characters similar to conspecific gyne.

Genitalia fully extended, probably due to the fact that male was collected while in copula. Parameres sub-triangular. Volsellae sock-shaped, with digitus bent mesad at nearly right angle. Aedeagus tube-like, flattened mesad. Subgenital plate subtriangular, almost twice longer than broad at base.

Morphology of legs and wings (exception of Media extending into submarginal cell 1 present on left forewing (Figs. 2c)) similar to conspecific gyne.

Integument densely foveate, opaque. Foveae larger than punctures in gyne, well-defined; largest foveae occur on pronotal sides; smallest and finest on gaster, resulting in a feebly shining gastral surface. Scutum and scutellum covered with longitudinal black rugae. Pilosity sparser than in gyne. Pilosity composed of tapered hairs, appressed and suberect, present on dorsal mesosoma, petiolar node, postpetiole, gaster, and legs. Propodeum glabrous. A few appressed hairs present on katepisternum and anepisternum. Mandibles with long hairs directed anteriad. Long

hairs present on clypeus, near ocelli, and on cephalic venter. Antennae covered with dense suberect hairs.

Description (gyne). HW 0.72, HL 0.62, ML 0.32, ATL 0.11, SL 0.35, WL 1.06, TL 3.0, CI 116, SI 48.

Body dark yellow; appendages light yellow; cuticle adjacent to ocelli black. Head subtriangular, occipital corners not rounded. Antennal scrobes running below compound eyes, lateroventrally, continuing posteriorly but not reaching posterior head margin. Frontal carinae, visible as gibbosities directed dorsad, present above antennal insertions. Cephalic dorsum flat, protruding near ocelli. Broad transverse depression runs across cephalic dorsum between eyes and posterior clypeal margin. Shallow depression present from area between lateral ocelli to posterior head margin. Elevated carina present on posterior head margin. Gibbosity present above eye, partially covering eye in full-face view. Rugae on head absent. Clypeus broadly inserted between modified frontal carinae; clypeus flat with lateral clypeal area elevated; anterior margin straight. Mandibles elongated, with 7 teeth. Apical fork with two long and spiniform teeth, sub-equal in size; intercalary denticle present. Masticatory margin with four teeth, three of which minute and triangular, one (situated at about mid-length of masticatory margin) large, blunt, and peg-like. Labrum subtriangular, with sinus up to 1\3 of its length; labral lobes bluntly rounded. Palps indistinguishable or torn off. Antennae 7-segmented with two-segmented club. Scape right-angled. Apical flagellomere as long as the sum of four preceding segments.

Mesoanepisternum, mesokatepisternum, and metanepisternum well developed and separated from each other by deep sutures. Metakatepisternum partly separated from propodeum by shallow carina. Scutum and scutellum flat. Parapsidal furrows narrow. Propodeal teeth well developed, sharp. Posterior face of propodeum slightly depressed medially. Propodeal lobes present. Propodeal spiracles round.

Petiole pedunculate; subpetiolar process ventrally present on peduncle. In dorsal view, petiolar and postpetiolar nodes oval-shaped; in dorsal view, anterior margin of postpetiolar node concave, posterior margin convex. In profile view, petiolar and postpetiolar nodes rounded.

Mid- and metatibiae lacking apical spurs. Tarsal claws simple.

Subcostal + Radial, Media + Cubital, 1Anal, second radiosectorial-media, Radial sectorial, Media, Cubital, and Radial sectorial + Media veins present on forewing. Subcostal + Radial, Medial + Cubital, 1Anal, second radiosectorial-media sclerotized veins. Costal, basal, subbasal, submarginal 1 cell present on forewing. Pterostigma well developed. The same veins present on hindwing except for second radiosectorial-media vein (and thus submarginal 1 cell absent on hindwing). Hindwing vein Costa + Subcostal + Radial and 1Anal vein sclerotized.

Integument finely punctuate; punctures shallow, undefined. Body covered with appressed setae. Stiff erect and suberect setae sparse, present on anterior edge of scape, posterior edge of head dorsum, mesosoma dorsum, coxae, petiolar and postpetiolar nodes, gaster, tarsi, outer tibial surface, and labral lobes. All setae tapered. Squamiform setae – commonly present in workers – absent.

Comments. The best diagnostic character of *Rhopalothrix* male is the apical fork of two long, spiniform teeth. The foveate integument on the male is shared by all genera of the *Basiceros*-genus group, as well as *Strumigenys* Smith F from the *Strumigenys*-genus group, *Cephalotes* Latreille, and at some extent, *Pheidole* Westwood from the *Pheidole*-genus group, but in those genera sculpture basically rugose-punctate with scattered irregular rugae; only in *Octostruma* Forel, some *Eurhopalothrix* Brown and Kempf and *Strumigenys* the sculpturation is virtually similar to *Rhopalothrix*. The systematic value of ant wing venation is not well understood due to a high degree of variability and dependence on wing size rather than phylogenetic history (Ogata 1991). Indeed, the lack of discoidal cell can only help differentiate *Rhopalothrix* males from the males from the *Pheidole*-genus group, some members of *Blepharidatta*-genus group, and from the *Daceton*-genus group.

Related genera

The tribe Attini (sensu Ward et al. 2015) can be conveniently divided into clades containing genera. Below I list potential male synapomorphies for Ward et al. clades, focusing mainly on mouthparts morphology and wing venation. It is worth mention that mandibular and palp morphologies might not be good characters to separate groups of genera due to the wide variation of mandibular shapes and instances of palpal reduction. However, it seems that the palp formula 5,3 (or intermediate 3,-, 4,2) and broad dentate mandibles (probably the ancestral state) are common. Scape morphology seems to be of systematic value only in the case of the *Atta*-genus group.

***Basiceros*-genus group (Figs. 5a–c)**. Includes six genera formerly constituting the tribe Basicerotini (Brown and Kempf 1960). Palp formula 1,1 or 1,2 (Bolton 2003); mandibles triangular (as broad as long), slender, or reduced (*Octostruma*, some *Eurhopalothrix*). Mandibular teeth triangular; only in *Rhopalothrix* apical fork present, with two long, spiniform teeth. Discoidal cell on forewing absent (present only in some *Basiceros*), marginal cell open (Cantone 2017).

***Strumigenys*-genus group (Figs. 5d,e)**. Includes the members of the former tribes Phalacromyrmecini (Bolton 2003), plus *Strumigenys* (sensu Baroni Urbani and de Andrade 2007). Palp formula 1,1 (known only in *Strumigenys*); mandibles reduced, with 0–3 denticles (*Strumigenys*) (Bolton 2003; Cantone 2017) or triangular with

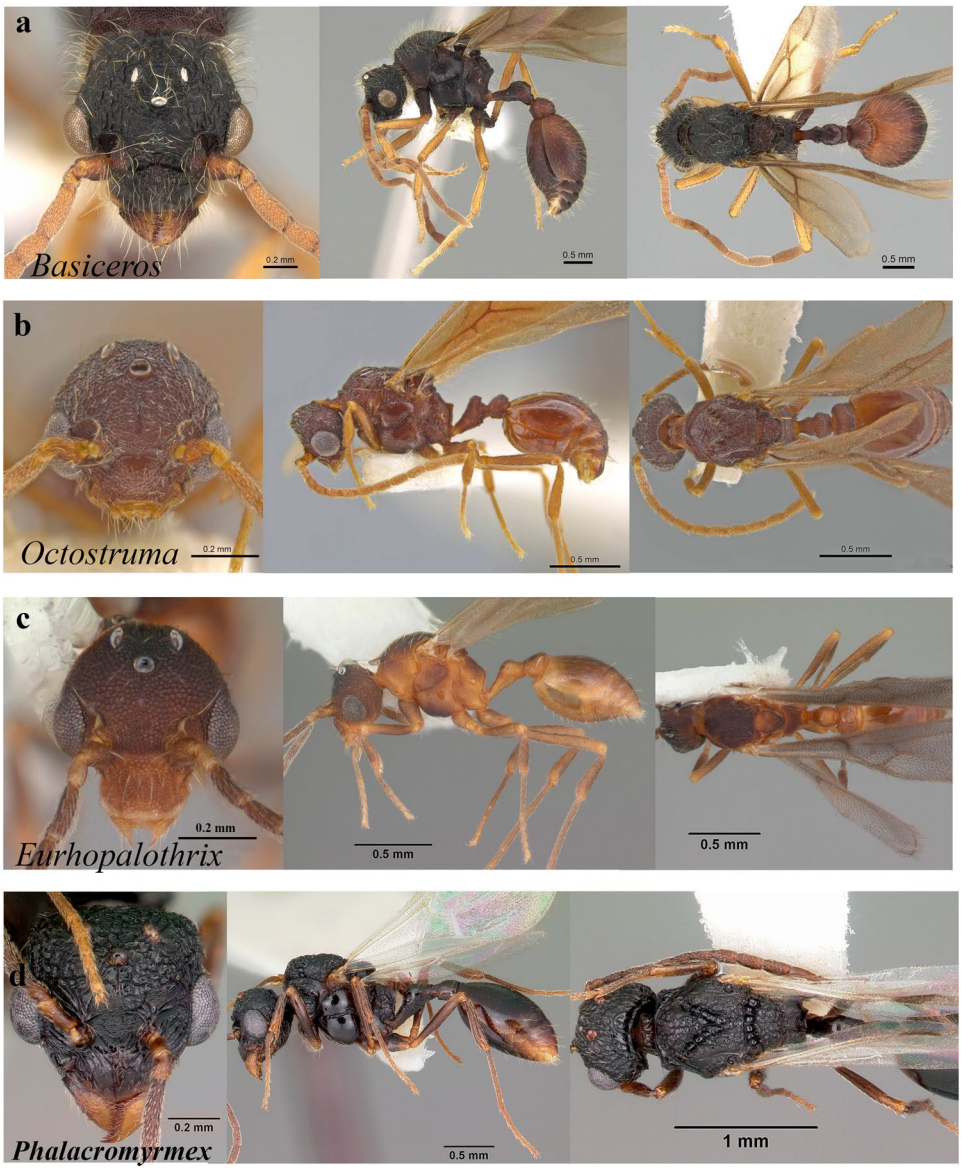


Fig. 5 Males of the tribe Attini (sensu Ward et al. 2015): **a** *Basiceros scambognathus* (Brown 1949); **b** *Octostruma amrishi* (Makhan 2007); **c** *Eurhopalothrix floridana* Brown and Kempf 1960; **d** *Phalacromyrmex* sp.; **e** *Strumigenys grandidieri* Forel 1892; **f** *Cephalotes alfaroi* (Emery 1890); **g** *Pheidole vigilans* (Smith 1858); **h** *Tranopelta gilva* Mayr 1866; **i** *Wasmannia auropunctata* (Roger 1863); **j** *Orectognathus mjobergi* Forel 1915; **k** *Mycetagroicus inflatus* Brandão and Mayhé-Nunes 2008; **l** *Sericomyrmex amabilis* Wheeler 1925. Photographs are from AntWeb (see Online Source 1 for details)

triangular teeth (*Pilotrochus* Brown, *Phalacromyrmex* Kempf). Discoidal cell on forewing absent, marginal cell open (Cantone 2017).

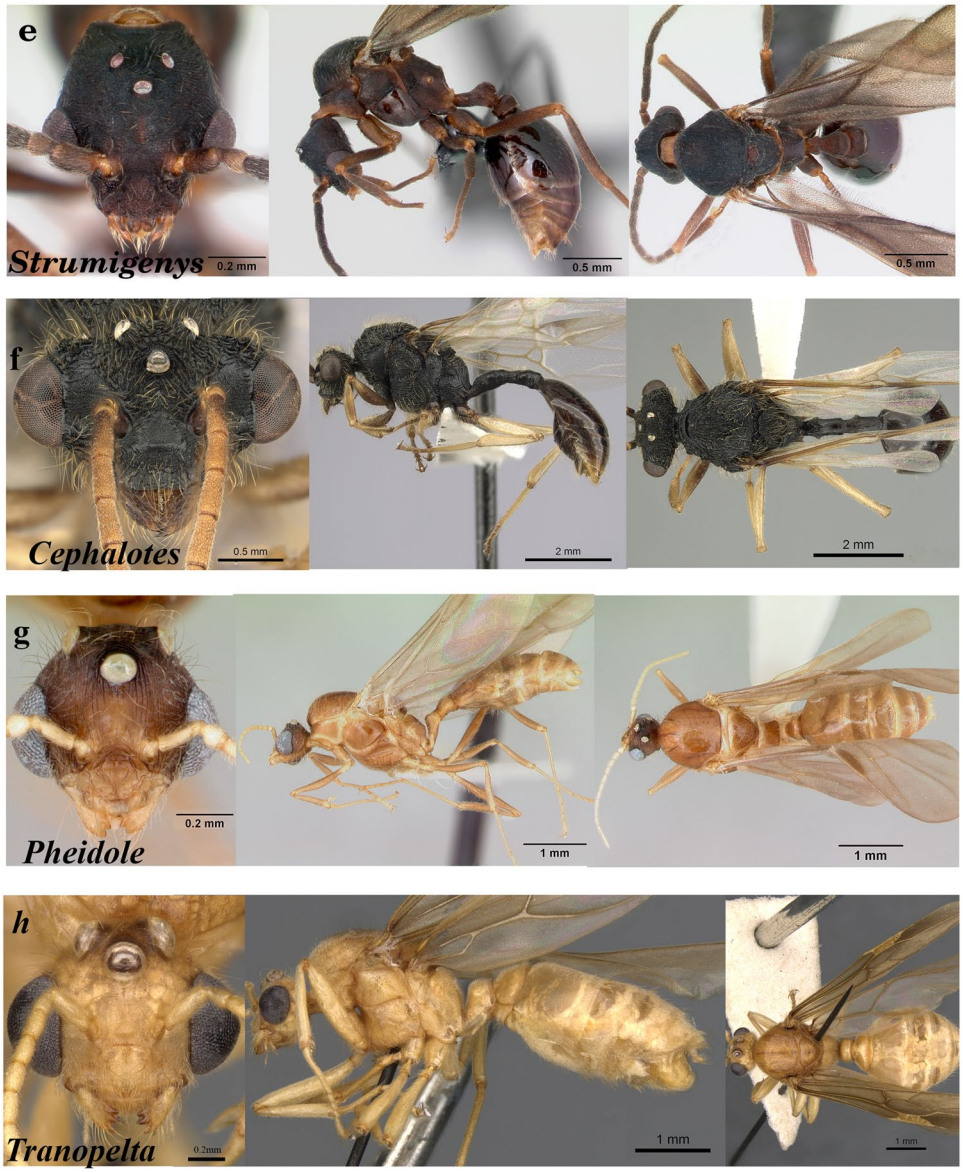
Pheidole-genus group (Figs. 5f,g). Includes the members of the former tribes Cephalotini and Pheidolini (Bolton 2003). Palp formula 1,0, 1,1 (inquilinous *Pheidole*), 2,2, 3,2 (other *Pheidole*), 5,3 (*Cephalotes, Procryptocerus* Emery). Mandibles triangular, with triangular teeth, or dentition reduced (one denticle present or edentate) (Bolton 2003). Discoidal cell on forewing present (Cantone 2017).

Tranopelta-genus group (Fig. 5h). Includes two genera– *Tranopelta* and *Ochetomyrmex*– previously thought to be unrelated (Bolton 2003). Palp formula 3,2; mandibles triangular with 3–4 teeth (Bolton 2003). Discoidal cell on forewing present, marginal cell open (Cantone 2017).

Blepharidatta-genus group (Fig. 5i). The members of the former tribe Blepharidattini (Bolton 2003) plus the genera *Allomerus*, *Lachnomyrmex*, *Diaphoromyrma*. Males are unknown for the last two genera. Palp formula 3,2 (undescribed for *Allomerus*). Mandibles triangular, with 5 teeth (*Allomerus, Wasmannia* Forel) (Bolton 2003) or sublinear, feeble, edentate in *Blepharidatta* (Kempf 1975) (described as having one tooth in Bolton 2003). Discoidal cell present on forewing in *Allomerus* and *Blepharidatta*, but absent in *Wasmannia*; marginal cell open (Cantone 2017). Parameres in *Wasmannia* strongly curved anteriorly (Cantone 2017).

Daceton-genus group (Fig. 5j). Includes the members of the former tribe Dacetini (Bolton 2003) (except *Strumigenys*), plus the genus *Lenomyrmex*. Males remain unknown for *Epopostruma* Forel, *Microdaceton* Santschi and *Lenomyrmex*. Palp formula 5,3 (reduced to 0,1 in *Acanthognathus*

Fig. 5 (continued)



Mayr) (Bolton 2003). Mandibles reduced, with 1 denticle or edentate (Bolton 2003). Discoidal cell present on forewing in *Mesostruma* Brown and *Orectognathus* Smith F; marginal cell open (Cantone 2017). Within the group, *Acanthognathus* male can be distinguished by having 12-segmented antennae (Bolton 2003).

***Atta*-genus group (Figs. 5k,l)**. Includes all genera of the former tribe Attini (Bolton 2003). Palp formula 3,2 or 4,2. Mandibles triangular, denticulate; rarely edentate (Bolton 2003; Cantone 2017). Antennal scape longer than the sum of the lengths of flagellomeres 1–3; scape shorter in *Apterostigma* Mayr, *Myrmicocrypta* Smith F, and *Mycocepurus* Forel, but in these genera longer or equal to 1st flagellomere; scape often reaching or surpassing vertexal margin. Some genera are characterized by 11–12 antennomeres and the lack of notauli. Discoidal cell on forewing absent, marginal cell closed (open in *Kalathomyrmex* Klingenberg and Brandão, *Mycetagroicus* Brandão and Mayhé-Nunes, and in some *Mycetophylax* Emery; but in the last two genera pterostigma reduced or absent). Some genera are characterized by absence of pterostigma or it is weakly developed (Cantone 2017).

Preliminary key for males of the Basiceros-genus group

I present below a preliminary key to the males of the *Basiceros*-genus group created from literature data and *Rhopalothrix* characters described in this study. Included in the key are only four genera, as males remain unknown for *Protalaridris* Brown and *Talaridris* Weber. The key is based on mandibular, palpal (Bolton 2003), antennal (Brown and Kempf 1960; Dietz 2004) and wing morphologies (Deyrup et al. 1997).

Fig. 5 (continued)

1. Mandibles elongated, at least twice as long as broad, with apical fork of two long, spiniform teeth……..…… .....*Rhopalothrix*
- Apical fork absent; mandibles with short triangular teeth, or teeth reduced…….....2
2. Antennal scape has a strong bristle on proximal corner of large bulge on inner side. Pterostigma absent or vestigial ……*Eurhopalothrix*
- Strong bristle on scape absent. Pterostigma well-developed ……..3
3. Antennal segments 8 and 9 twisted, virtually making antenna turns around its axis…….....*Basiceros*
- Antennal segments 8 and 9 not twisted……*Octostruma*

Discussion

The male here described is undoubtedly be assigned to the rarely collected and remarkable genus *Rhopalothrix*. There is a male from Viçosa, Brazil, depicted on AntWeb (ANTWEB1038182) and identified as *Rhopalothrix* sp. This male closely resembles the male described here, including very characteristic spiniform mandibular teeth and apical mandibular fork. It can be distinguished from the male described here by the presence of 7 mandibular teeth, black integument, and more deeply emarginate labrum. These are presumably species-level characters. The wing venation is almost identical in both males (more

reduced in the AntWeb specimen not having Media and Radial sector + Media veins on the forewing), and identical to the described *Rhopalothrix* gynes. Gynes are known for five *Rhopalothrix* species, and they all are very similar to workers; the gynes only differ from the conspecific workers in pilosity (numerous short setae in the gynes) and face integument (stronger grooves and gibbosities in the workers) (Longino and Boudinot 2013).

Regarding the species identity, the gyne described here shares the following characteristics with the *R. apertor* worker: shape of labrum; mandible with a tiny denticle near the base of masticatory margin; and a large blunt, peg-like tooth on the masticatory margin (Longino and Boudinot 2013). Two important features ("outer margin of mandible broadly flattened at base" and "base of subapical tooth with recurved acute tooth, directed posteriorly") are not as clear as in Longino and Boudinot's (2013) illustrations, but still present. The subapical tooth is not well developed, not as long as apical tooth. The pair of squamiform setae at posterolateral margins of the first gastral tergite is absent. These differences from the description of the *R. apertor* worker can be regarded as being caste dependent.

Nevertheless, the possibility exists that *R. apertor* is two cryptic species. Workers of *R. apertor* fall into two size classes: with HW 0.54–0.58 and HW 0.74. Head width in gynes and workers is similar for different species (*R. weberi* Brown and Kempf: gyne 0.40–0.54 mm, worker 0.38–0.39 mm; *R. triumphalis* Longino and Boudinot: gyne 0.69 mm, worker 0.57–0.65 mm; *R. subspatulata* Longino and Boudinot: gyne 0.51–0.53 mm, worker 0.42–0.49 mm). The gyne described here has HW of 0.72 mm, considerably longer when compared with the type series (based on workers). Although Longino and Boudinot (2013) have chosen the holotype and paratype of *R. apertor* from series of larger workers, it cannot be ruled out that the gyne and male described here belong to an undescribed species.

The label for the pin containing the gyne and male mentions "Costa Rica, Monteverde, 1500 m, 23–30/08/92 (D.M. Wood)." *Rhopalothrix* is so far unknown from the Monteverde cloud forest (1500 m a.s.l.) in spite of intensive collecting efforts (Longino and Bodinot 2013). Other *Rhopalothrix* species can live at these elevations, but *R. apertor* has been described as an inhabitant of lowland rainforests (150–500 m) (Longino and Boudinot 2013). However, data from AntWeb show that *R. apertor* was also collected at 1700 m (CASENT0632145), and this location – as well as the location for a paratype (INB0003667720)– is 150 km distant from Monteverde. Thus, there is a possibility that *R. apertor* inhabited Monteverde.

Although there is a possibility of interspecific hybridization between close ant species (e.g., Seifert 2021 and references therein), I considered it to be very unlikely that the gyne and male described here belong to different species.

Regarding the characters to differentiate *Rhopalothrix* from related genera, mandibular morphology appeared to be the most reliable. Unique dentition and the apical fork are clear autapomorphies of *Rhopalothrix* males. These characters are less pronounced than in the female castes, but other Attini in which the females bear the apical fork (e.g., *Strumigenys*, *Acanthognathus*) have males with strongly reduced mandibles lacking an apical fork. More distantly related genera can be also distinguished by the morphology of palps, scape, and venation. In the gyne and male described here, wing venations are similar for both castes, except for the male left forewing having a short transverse branch which penetrates submarginal cell 1. Aberrations in the ant wing venation are not rare: sometimes venation varies within the members of one species and even may differ between right and left wings (Smith 1957).

In conclusion, the first description of *Rhopalothrix* male presented here is a small, but hopefully valuable contribution towards the understanding of a much-needed taxonomic treatment of ant males.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13744-022-00947-w.

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Declarations

Conflict of interest The author declares no competing interests.

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