



A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to genera of the subfamily Proceratiinae

MASASHI YOSHIMURA¹ & BRIAN L. FISHER²

Department of Entomology, California Academy of Sciences, Golden Gate Park, 55 Music Concourse Drive, San Francisco, California 94118, U.S.A. E-mail: ¹myoshimura@ant-database.org, ²bfisher@calacademy.org

Abstract

Male-based keys to the ant genera of Proceratiinae in the Malagasy region (Madagascar, Mauritius, Reunion, Comoros, and Seychelles) are presented. All three extant genera known from the Malagasy region, *Discothyrea*, *Probolomyrmex*, and *Proceratium*, and an undescribed taxon, PRm01 from Seychelles, are included. Diagnoses and remarks on the subfamily Proceratiinae and its four genera, and a character table for these genera, are given. The males of all genera are illustrated.

Key words: Madagascar, Mauritius, Reunion, Comoros, Seychelles, wing, palp, labrum, diagnosis, key, *Discothyrea*, *Probolomyrmex*, *Proceratium*

Introduction

Male ants offer a wealth of information on the taxonomy, phylogeny, diversity and biology. For example, they often provide valuable characters for distinguishing genera and species in addition to those found in workers (Eguchi *et al.* 2006; Yoshimura *et al.* 2007), and understanding their phenology can provide additional insights into the life history and reproduction of many species (Kaspari *et al.* 2001).

A principal limitation to including male ants in behavioral and species-level taxonomic studies is the lack of genus-level identification tools. Bolton (2003) provided the first general summary of our current knowledge of male characters for extant genera, demonstrating that morphological information about male ants remains scarce and scattered among many sources. Further explorations and syntheses of male character systems are needed.

Previously we published male-based keys to subfamilies and ponerine genera in the Malagasy region (Yoshimura & Fisher 2007). Here we focus on the subfamily Proceratiinae. This grouping includes three extant genera, *Discothyrea*, *Proceratium* and *Probolomyrmex*, all of which are found in the Malagasy region. Previous studies have included partial male-based diagnoses of these genera. Brown (1958) provided diagnoses for males of *Discothyrea* and *Proceratium*, Ogata (1987) for *Discothyrea* and *Proceratium* in Japan, Emery (1911) for *Proceratium* (as *Sysphincta*), Baroni Urbani and De Andrade (2003) for *Proceratium*, Taylor (1965) for *Probolomyrmex*, and Brown (1975) for *Probolomyrmex* in comparison with *Platythyrea*. At least one of the proceratine genera (*Discothyrea*, *Proceratium*, or *Probolomyrmex*) was included in male-based keys for Africa (Wheeler 1922), for North America (Smith 1943), and for Japan (Yoshimura & Onoyama 2002). These three genera were assigned to the subfamily Proceratiinae when Bolton (2003) reorganized the subfamily Ponerinae. The monophyly of Proceratiinae as defined by Bolton (2003) was later confirmed by molecular phylogenetic studies (Ouellette *et al.* 2006; Brady *et al.* 2006; Moreau *et al.* 2006). Moreover, Bolton (2003) proposed several male apomorphic traits for the tribe Probolomyrmecini.

Here we provide a male-based key to all extant proceratine genera and diagnose the subfamily and genera.

Diagnoses are based primarily on material collected in the Malagasy region. When available, additional material outside this region was included. A character matrix table summarizes the characters and character states used in the analysis. Characters uniquely observed in the Malagasy region are discussed.

Materials and methods

This revision is primarily based on arthropod surveys in Madagascar that included over 6,000 leaf litter samples, 4,000 pitfall traps, 1,000 Malaise trap collections, and 9,000 additional hand collection events throughout Madagascar from 1992 through 2008 (see Fisher 2005 for additional details).

Observations were carried out under stereoscopic microscopes (LEICA MZ12 and M125). Digital color images were created using a JVC KY-F75 digital camera and Syncrosopy Auto-Montage (v 5.0) software. Each imaged specimen is uniquely identified with a specimen-level code (e.g. CASENT0003099) affixed to each pin.

Male specimens from the Malagasy Ant Collection at the California Academy of Sciences were primarily collected with Malaise traps. We sorted these into morphospecies with codes (e.g. *Proceratium* mgm01). Taxonomic information on the materials follows Bolton (1995), Baroni Urbani and De Andrade (2003), Bolton, *et al.* (2006), and the Japanese Ant Database Group (2008).

The male taxa listed below were studied to develop a key to genera of the subfamily. Each taxon name is followed by a letter code indicating the source of morphological information used to develop the key:

[g]: male specimens that were collected from a colony and associated with workers.

[m]: male specimens that were collected alone and not associated with workers, typically in Malaise traps.

[r]: information about male morphologies including wing venation obtained from published studies. In these cases, the references are shown in brackets.

[w]: information about wing morphologies obtained only from alate females in previously published studies. In these cases, the references are shown in brackets.

Discothyrea Roger.

D. kamiteta Kubota & Terayama [g]; *D. sauteri* Forel [g]; *D.* mgm01 [m]; *D.* mgm02 [m]; *D.* mgm03 [m].
Probolomyrmex Mayr.

P. dammermani Wheeler [g]; *P. longinodus* Terayama & Ogata [g]; *P. longiscapus* Xu & Zeng [g]; *P. vieti* Eguchi, Yoshimura & Yamane [g]; *P.* mgm01 [m]; *P.* mgm02 [m].

Proceratium Roger.

P. austronesicum De Andrade [w: Baroni Urbani and De Andrade 2003]; *P. avium* Brown [r: as *P. avioide* De Andrade, 2003 in Baroni Urbani and De Andrade 2003]; *P. brasiliense* Borgmeier [w: Baroni Urbani and De Andrade 2003]; *P. californicum* Cook [w: Baroni Urbani and De Andrade 2003]; *P. catio* De Andrade [w: Baroni Urbani and De Andrade (2003)]; *P. convexiceps* Borgmeier [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. crassicorne* Emery [r: Baroni Urbani and De Andrade 2003]; *P. creek* De Andrade [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. deelemani* Perrault [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. foveolatum* De Andrade [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. goliath* Kempf & Brown [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. itoi* (Forel) [g]; *P. japonicum* Santschi [g]; *P. longiscapus* De Andrade [w: Baroni Urbani and De Andrade 2003]; *P. mancum* Mann [w: Baroni Urbani and De Andrade (2003)]; *P. melinum* (Roger) [r: Baroni Urbani and De Andrade 2003]; *P. mexicanum* De Andrade [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. micrommatum* (Roger) [w: Baroni Urbani and De Andrade 2003]; *P. morisitai* Onoyama & Yoshimura [g]; *P. panamense* De Andrade [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. pergandei* (Emery) [r: Baroni Urbani and De Andrade 2003]; *P. silaceum* Roger [r: Baroni Urbani and De Andrade 2003]; *P. stictum*

Brown [r: as tentative attribution in Baroni Urbani and De Andrade 2003]; *P. watasei* (Wheeler) [g]; *P. mgm01* [m]; *P. mgm02* [g]; *P. mgm03* [m]; *P. mgm04* [m]; *P. mgm05* [m]; *P. mgm06* [m]; *P. mgm07* [m]; *P. mgm08* [m].

Genus PRm01 undescribed.

Undetermined single male from Seychelles CASENT0103485.

Terminology

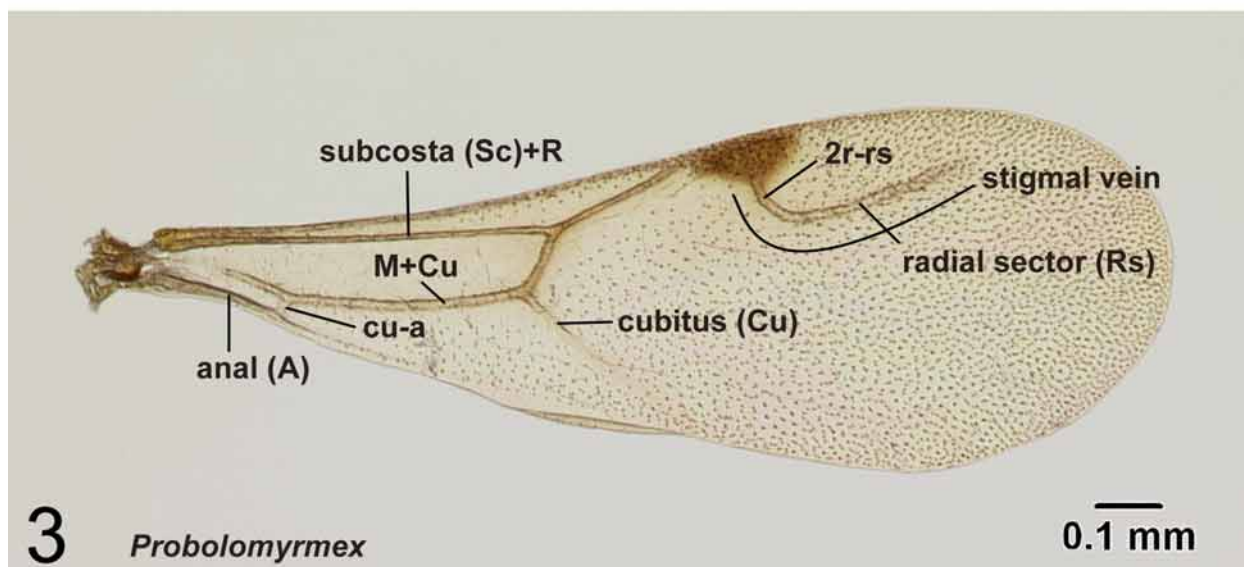
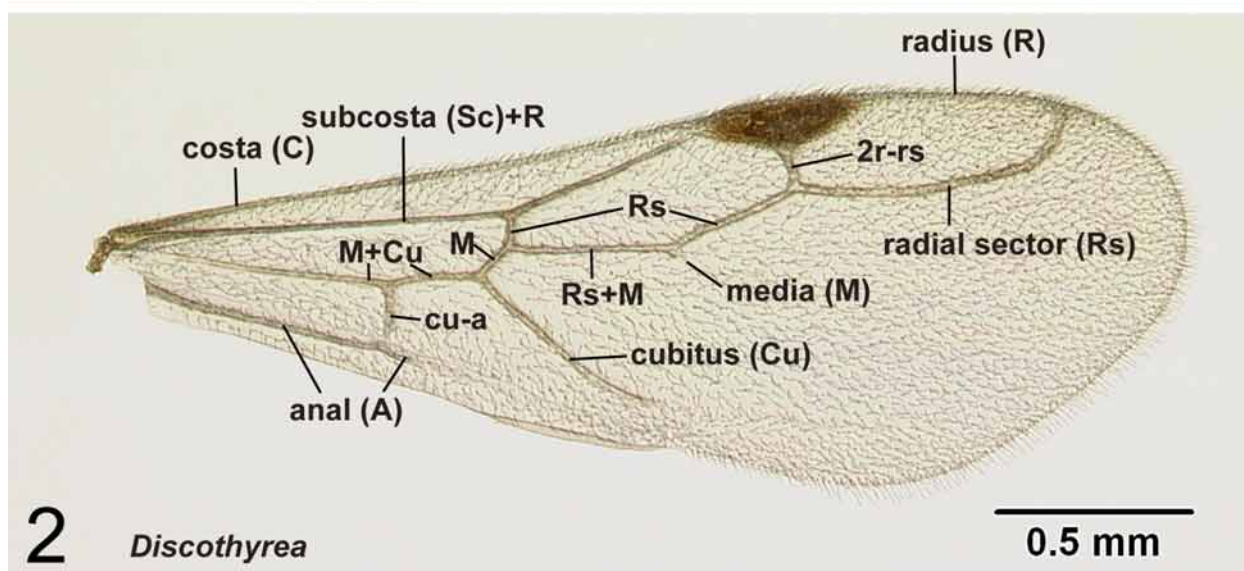
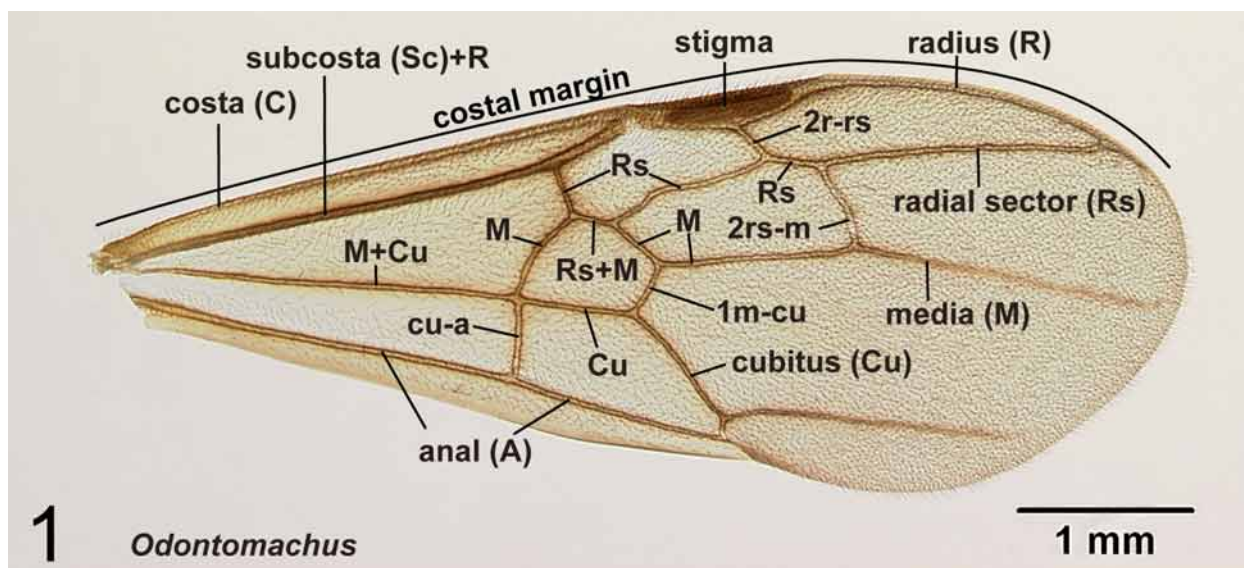
Morphological terminology follows our previous work (Yoshimura & Fisher 2007: figs 1, 2) and is based on Snodgrass (1935), Gauld and Bolton (1988), Bolton (1994), and Huber and Sharkey (1993). Use of the term pygostyle follows Snodgrass (1941); terminology of wing venation follows Wootton (1979) and Gauld and Bolton (1988). The applications of these terms in the Proceratiinae are illustrated in Figures 1–21 and 25–34).

Pygostyles. The presence of the pygostyle is an important diagnostic character of *Discothyrea* (Fig. 26). Pygostyle is used to refer to the pair of appendages on the tenth tergum of the abdomen of male Hymenoptera. Cerci, on the other hand, refer to appendages on abdominal tergum XI, not X (see also Yoshimura & Fisher 2007).

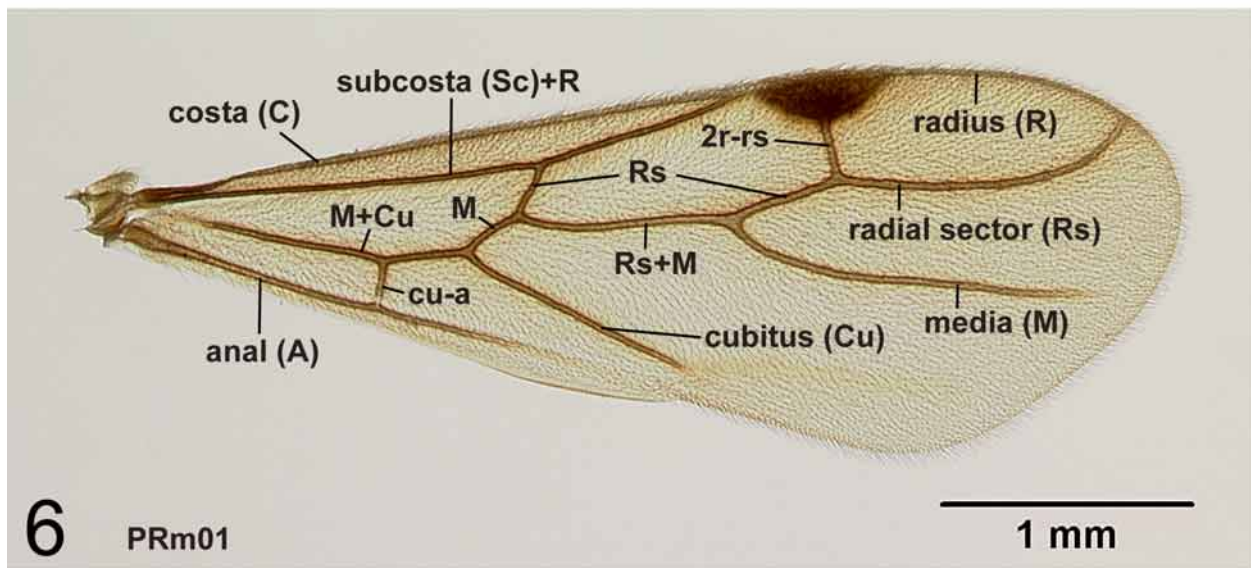
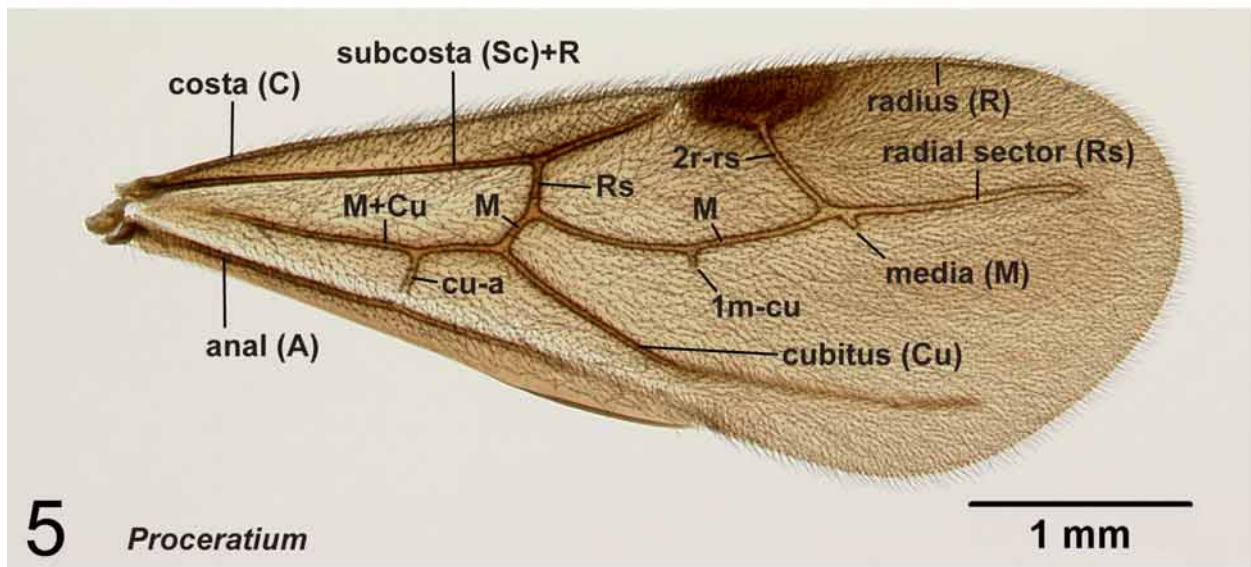
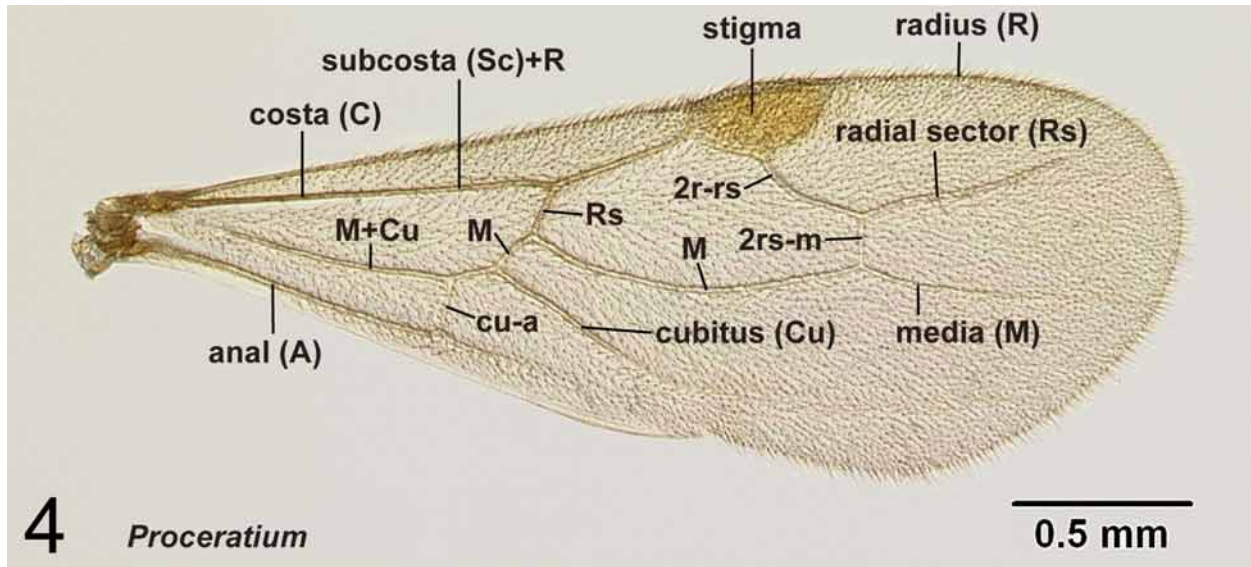
Venation and regions of wing. Wing venation and regions are useful characters to highlight differences between taxa. Forewing and hindwing designations are illustrated in Figures 1–12. Establishing homology of each vein was carried out based on comparisons to taxa with well-developed veins, as in the genus *Odontomachus* in Ponerinae (Figs 1, 7). Terms used to define veins follow the recommendation of Wootton (1979) and Gauld and Bolton (1988), which differ from terms used by other authors (Table 1).

TABLE 1. Terminology for fore- and hindwings. References are shown for terms used in the previous studies.

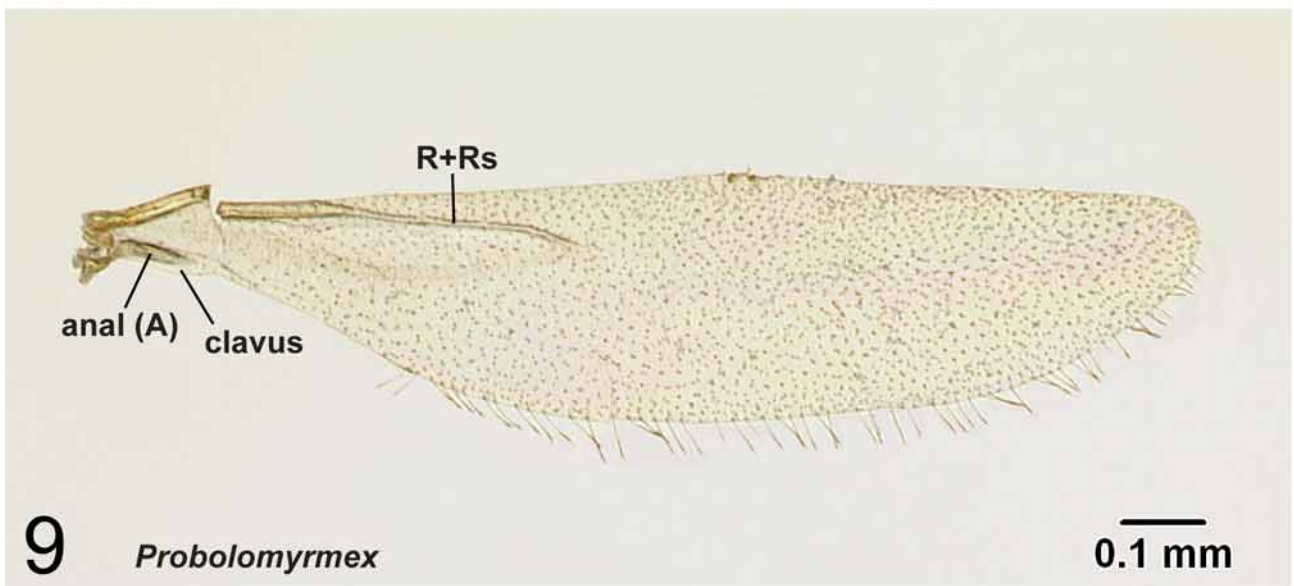
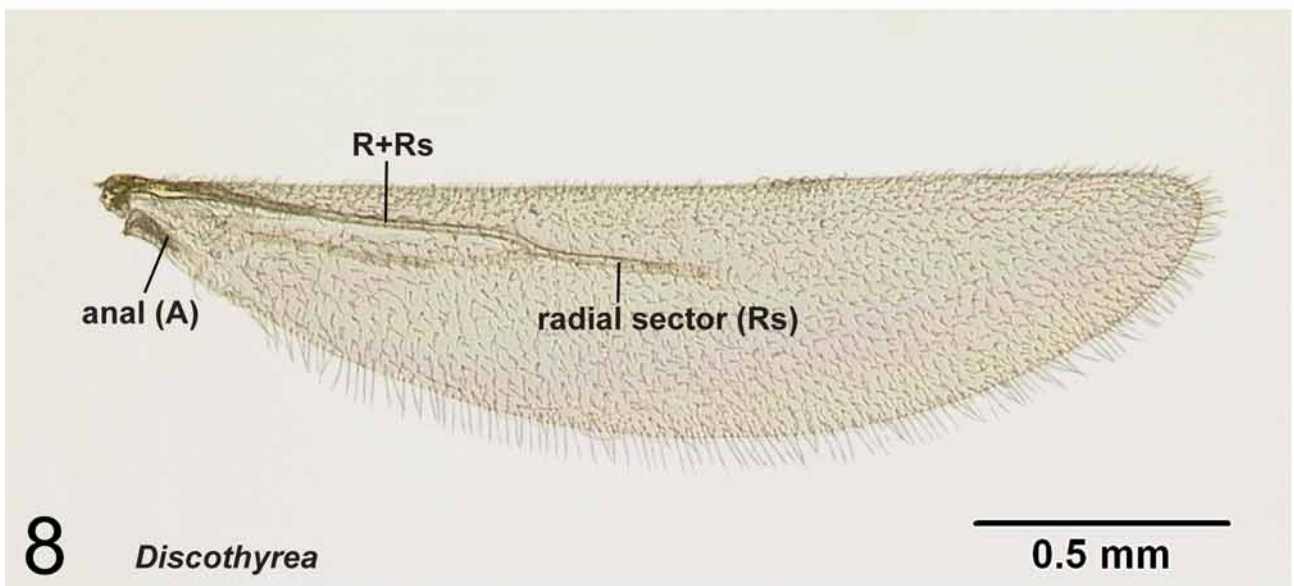
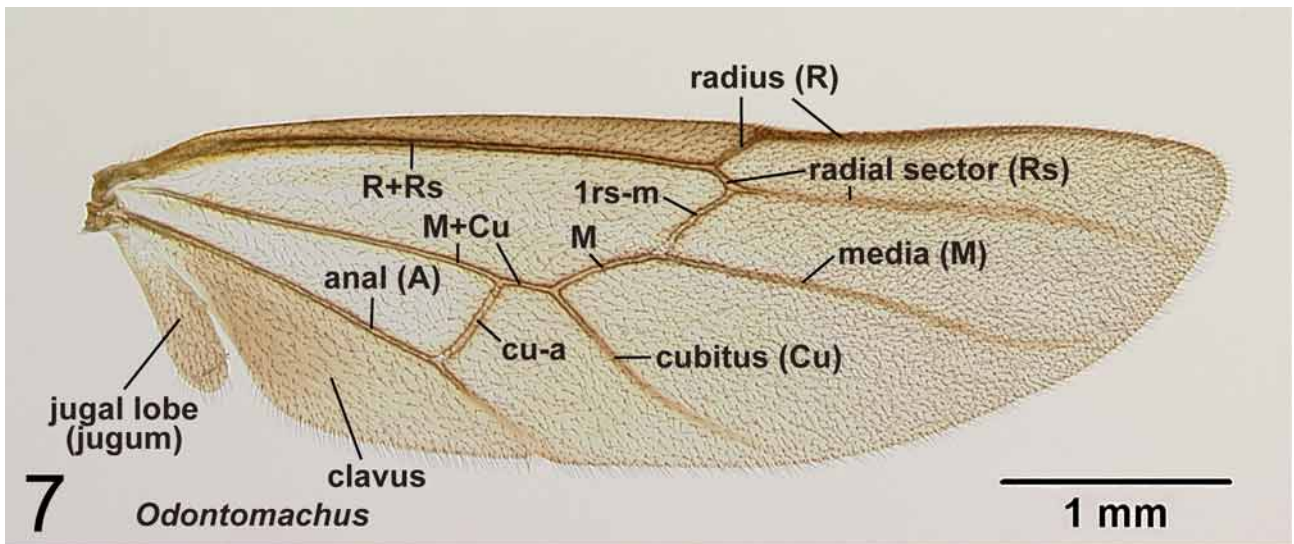
	This study (Figs 1–12)	Previous studies	
	Terms	Terms	References
Forewing	costal margin	anterior margin	Baroni Urbani and De Andrade (2003)
	radial sector (Rs)	Rsf1,2,3,4,5	Brown (1958; 1975), Baroni Urbani and De Andrade (2003)
	media (M)	Mf2, 3, 4	Brown (1958; 1975), Baroni Urbani and De Andrade (2003)
	cubitus (Cu)	CuA	Brown (1975), Baroni Urbani and De Andrade (2003)
	anal (A)	basal vein	Brown (1975)
	cu-a		
	2r-rs	2r	Brown (1975), Baroni Urbani and De Andrade (2003)
	2rs-m	r-m	Brown (1958), Baroni Urbani and De Andrade (2003)
	1m-cu	m-cu	Brown (1958)
jugal lobe	anal lobe	Brown (1975)	
Hindwing	R+Rs	R	Brown (1975)
	radial sector (Rs)	r-m	Baroni Urbani and De Andrade (2003)
	cubitus (Cu)	CuA + M	Baroni Urbani and De Andrade (2003)



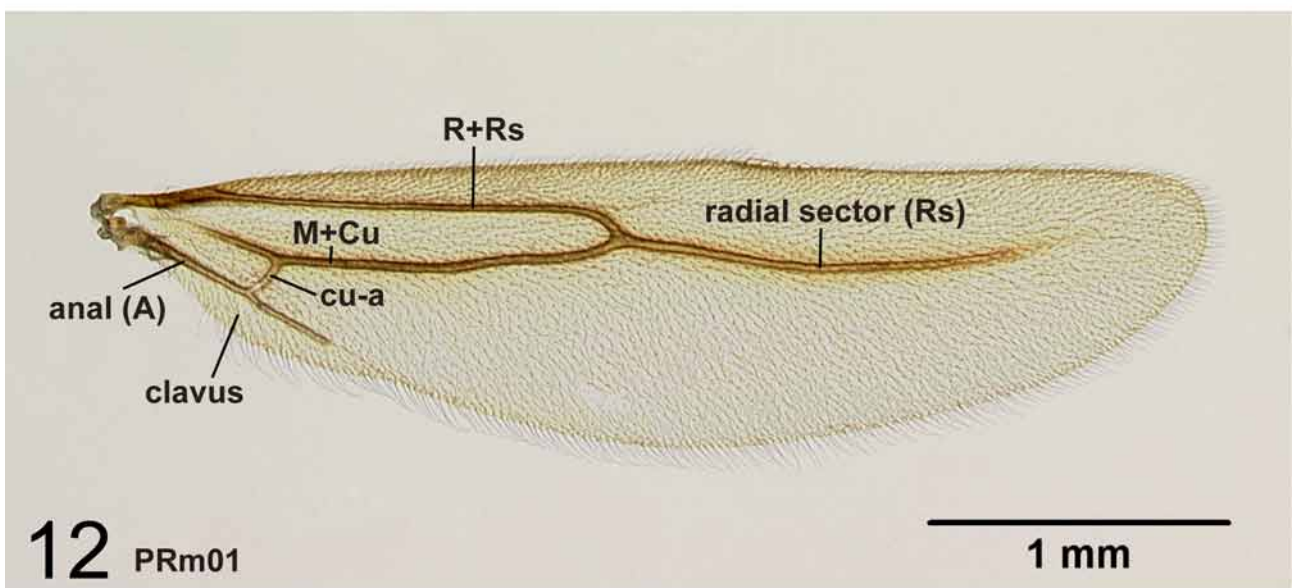
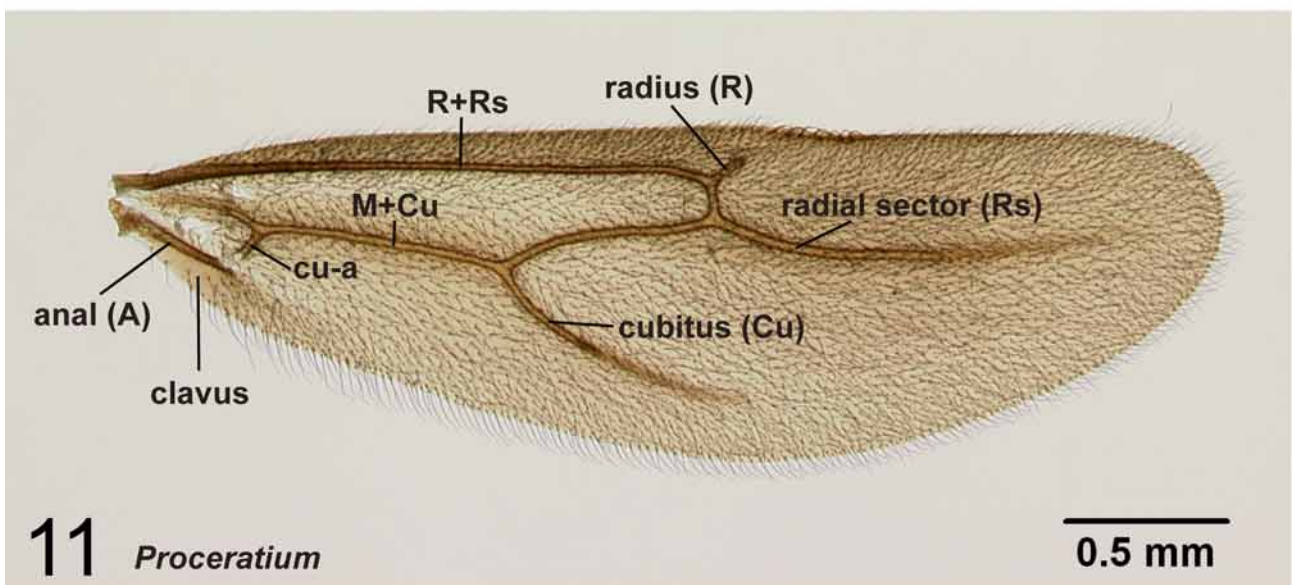
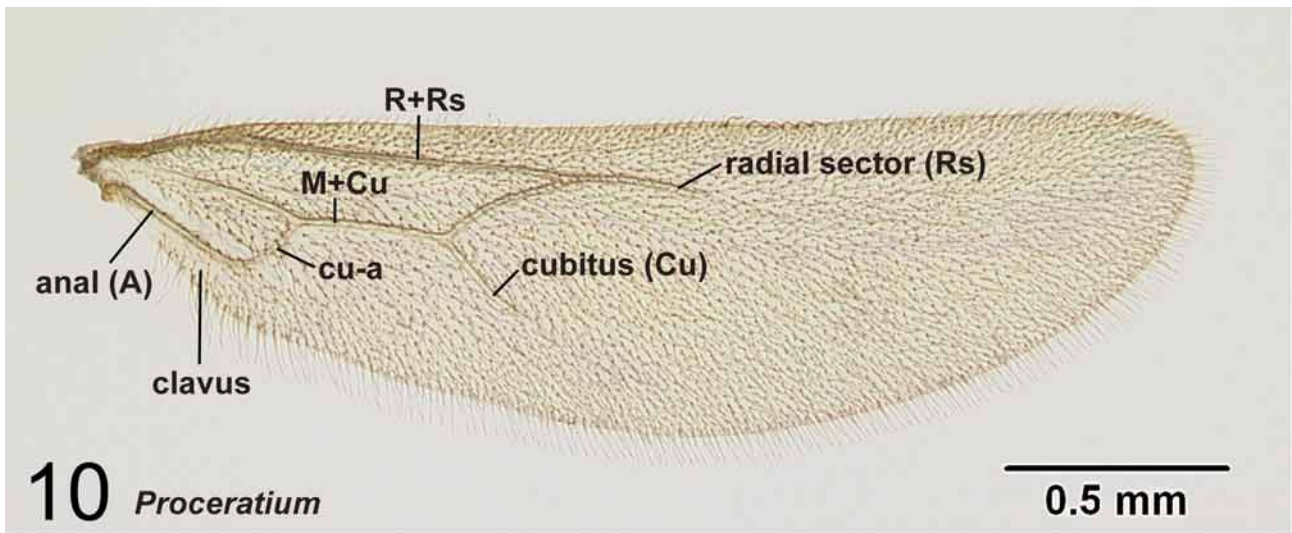
FIGURES 1–3. Forewings of male ants. 1, *Odontomachus coquereli* (CASENT0049797); 2, *Discothyrea mgm01* (CASENT0083649); 3, *Probolomyrmex mgm01* (CASENT0080551).



FIGURES 4–6. Forewings of male ants. 4, *Proceratium* mgm06 (CASENT0111236); 5, *Proceratium* mgm01 (CASENT0064081); 6, PRm01 sp. (CASENT0103485).



FIGURES 7–9. Hindwings of male ants. 7, *Odontomachus coquereli* (CASENT0049797); 8, *Discothyrea* mgm01 (CASENT0083649); 9, *Probolomyrmex* mgm01 (CASENT0080551).



FIGURES 10–12. Hindwings of proceratine males. 10, *Proceratium* mgm06 (CASENT0111236); 11, *Proceratium* mgm01 (CASENT0064081); 12, PRm01 sp. (CASENT0103485).

Results

Diagnosis of males of the subfamily Proceratiinae in the Malagasy region

Males alate. Antennal scape extending or not reaching posterior margin of head (Figs 13–15, 23). Notauli absent (Figs 16–18, 24). Oblique mesopleural furrow reaching pronotum at its posteroventral corner (Figs 19–21, 22). A single tibial spur present on front and hindleg, and mesotibia without or with a spur (Fig. 25). Petiole attached to abdominal segment III ventrally, so that dorsal constriction between the two segments is distinct and deep. Abdominal segment III slightly reduced compared with IV. A distinct constriction present between abdominal segments III and IV. Apical portion of abdominal sternum IX rounded or flat. Pygostyles absent or present (Fig. 26). Volsella never claw-shaped nor extended dorsally.

Venation on forewing is varied. Sc+R, cubitus (Cu) and anal (A) present in all genera. The cu-a is sometimes vestigial (Figs 2–6). On hindwing, media (M) apical to rs-m absent, the clavus reduced in size, and the jugum absent (Figs 8–12).

Remarks. The combination of characters above separates the subfamily Proceratiinae from all seven other subfamilies in the Malagasy region. In the Malagasy region, Proceratiinae differ from Amblyoponinae in having a lower attachment of the petiole to abdominal segment III; from Cerapachyinae in lacking a bispinose abdominal sternum IX and in having a moderate volsella; from Dolichoderinae and Formicinae in having a constriction between abdominal segments III and IV; from Myrmicinae and Pseudomyrmecinae in having a slightly reduced abdominal segment III compared with IV (abdominal segment III is much reduced compared with IV in Myrmicinae and Pseudomyrmecinae); and from Ponerinae in having a reduced clavus on the hindwing. We have included a key to Malagasy subfamilies in a previous study (Yoshimura & Fisher 2007).

Bolton (2003: 49) has proposed the lack of pygostyles (= cerci) as a diagnostic character of Proceratiinae; however, as discussed in the *Discothyrea* section below, pygostyles were observed in all males of *Discothyrea* examined in this study, both within and outside of the Malagasy region.

Key to genera of males of subfamily Proceratiinae in the Malagasy region

The key is based on the Table 2 character matrix. This key may not work outside the Malagasy region, as variations in genus level characters elsewhere have not been fully explored.

1. Frontal carinae merged into single median carina between antennal sockets (Figs 13, 14, 23). Cubitus (Cu) in hindwing absent (Figs 8, 9, 12)..... 2
- Frontal carinae diverging posteriorly or subparallel, but never merged into single carina (Fig. 15). Cubitus (Cu) in hindwing present (Figs 10, 11), rarely reduced but with short branch *Proceratium*
2. Antenna with 13 segments. Mesotibia with single spur (Fig. 25) 3
- Antenna with 12 segments. Mesotibia without spurs Genus PRm01.
3. Stigmal vein absent: radial sector (Rs) fully present in forewing, joining radius (R) at apical costal margin (Fig. 2). Pygostyles present (Fig. 26)..... *Discothyrea*
- Stigmal vein present: radial sector (Rs) absent in medial section of forewing and not reaching costal margin; radius (R) absent on the costal margin (Fig. 3). Pygostyles absent *Probolomyrmex*

Diagnoses of males of extant genera of Proceratiinae in the Malagasy region

Diagnoses of males of all Malagasy genera of Proceratiinae are given below. Diagnostic characters uniquely observed in each genus are given in italics.

TABLE 2. Character matrix for males of Malagasy Proceratiinae. For the 17 characters, character states are shown as 0, 1, exact number, or 0/1 (if both states were observed) for each genus. Number of species in which the character states was observed is given in parentheses following character state. Character states have been confirmed by direct observation or by descriptions in previous studies.

1. Frontoclypeal region projecting dorsally (1); not projecting dorsally (0)
2. Frontal carinae merged into a single median carina (1); not merged (0) between the antennal sockets
3. Antennal sockets opening posteriorly (1); dorsally (0)
4. The number of antennal segments
5. The labrum triangular with a single apical apex (1); bilobed (0)
6. The second segment of maxillary palp hammer-shaped (1); not hammer-shaped (0)
7. The number of the tibial spurs on front leg
8. The number of the tibial spurs on mid leg
9. The number of the tibial spurs on hind leg
10. Pygostyles absent (1); present (0)
11. The stigmal vein is observed on forewing (1); not observed (0)
12. Radius (R) in apical portion absent (1); present (0) in forewing
13. Radial sector (Rs) in forewing fails to reach costal margin (1); reaches costal margin (0)
14. M+Cu vestigial in hindwing (1); developed (0)
15. Radius (R) in hindwing fails to reach costal margin (1); reaches costal margin (0)
16. Cubitus (Cu) in hindwing absent (1); present (0)
17. cu-a in hindwing absent (1); present (0)

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Discothyrea</i>	1 (5)	1 (5)	1 (5)	13 (5)	0 (5)	0 (5)	1 (5)	1 (5)	1 (5)	0 (5)	0 (5)	0 (5)	0 (5)	1 (5)	1 (5)	1 (5)	1 (5)
<i>Probolomyrmex</i>	1 (6)	1 (6)	1 (6)	13 (6)	0 (3)	1 (6)	1 (6)	1 (6)	1 (6)	1 (6)	1 (6)	1 (6)	1 (6)	0(5)/ 1(1)	1 (6)	1 (6)	1 (6)
<i>Proceratium</i>	0 (23)	0 (26)	0 (23)	13 (26)	0 (12)	1 (25)	1 (12)	1 (12)	1 (12)	1 (12)	0 (33)	0(7)/ 1(25)	0(7)/ 1(25)	0 (32)	0(6)/ 1(26)	0 (32)	0(30)/ 1(2)
Genus PRm01	0 (1)	1 (1)	0 (1)	12 (1)	1 (1)	0 (1)	1 (1)	0 (1)	1 (1)	1 (1)	0 (1)	0 (1)	0 (1)	0 (1)	1 (1)	1 (1)	0 (1)

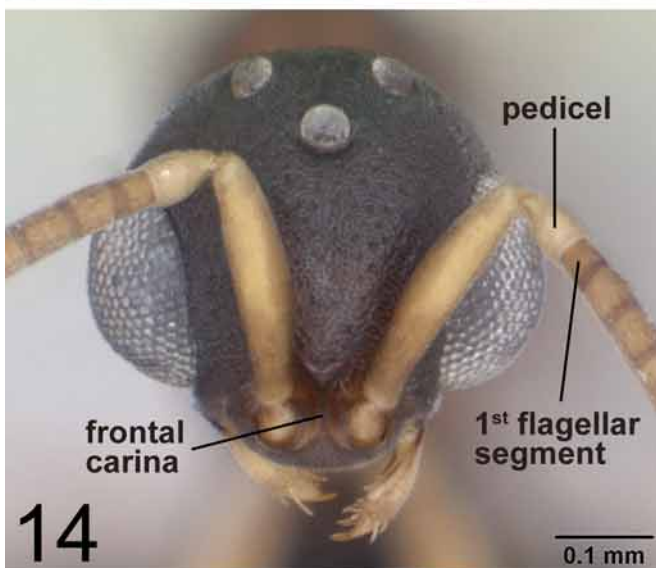
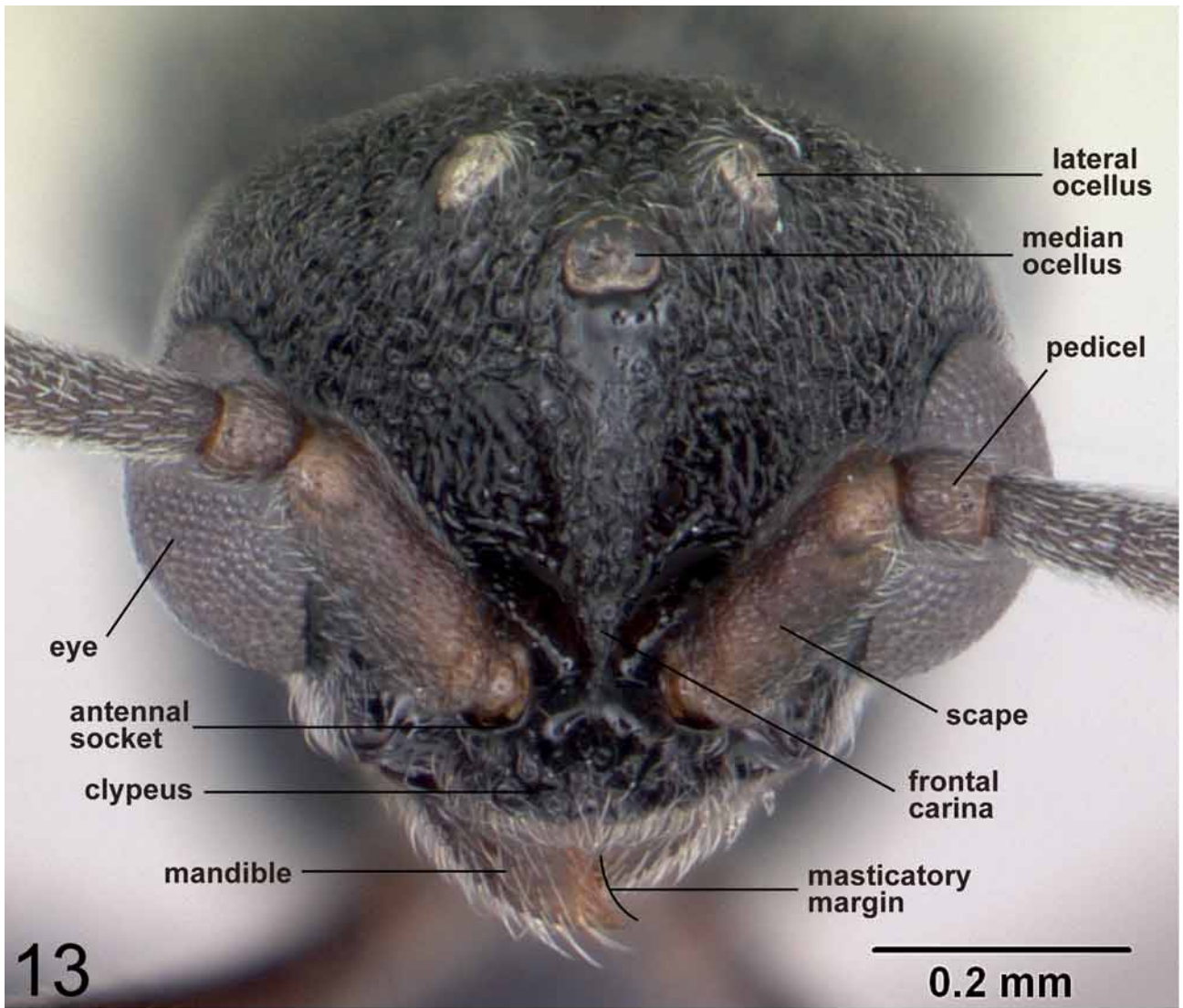
Discothyrea Roger, 1863

(Figs 2, 8, 13, 16, 19, 25–27, 31)

With characters of Proceratiinae. Mandible smaller than in conspecific worker, but also triangular to subtriangular. Frontoclypeal region projecting dorsally. Frontal carinae merged into a single median carina (Fig. 13). Antennal sockets opening posteriorly. Antenna consisting of 13 segments. Labrum bilobed apically (Fig. 27). Second segment of the maxillary palp not hammer-shaped (Fig. 31). Pro-, meso-, and metatibia with a single spur (Fig. 25). *Pygostyles present* (Fig. 26).

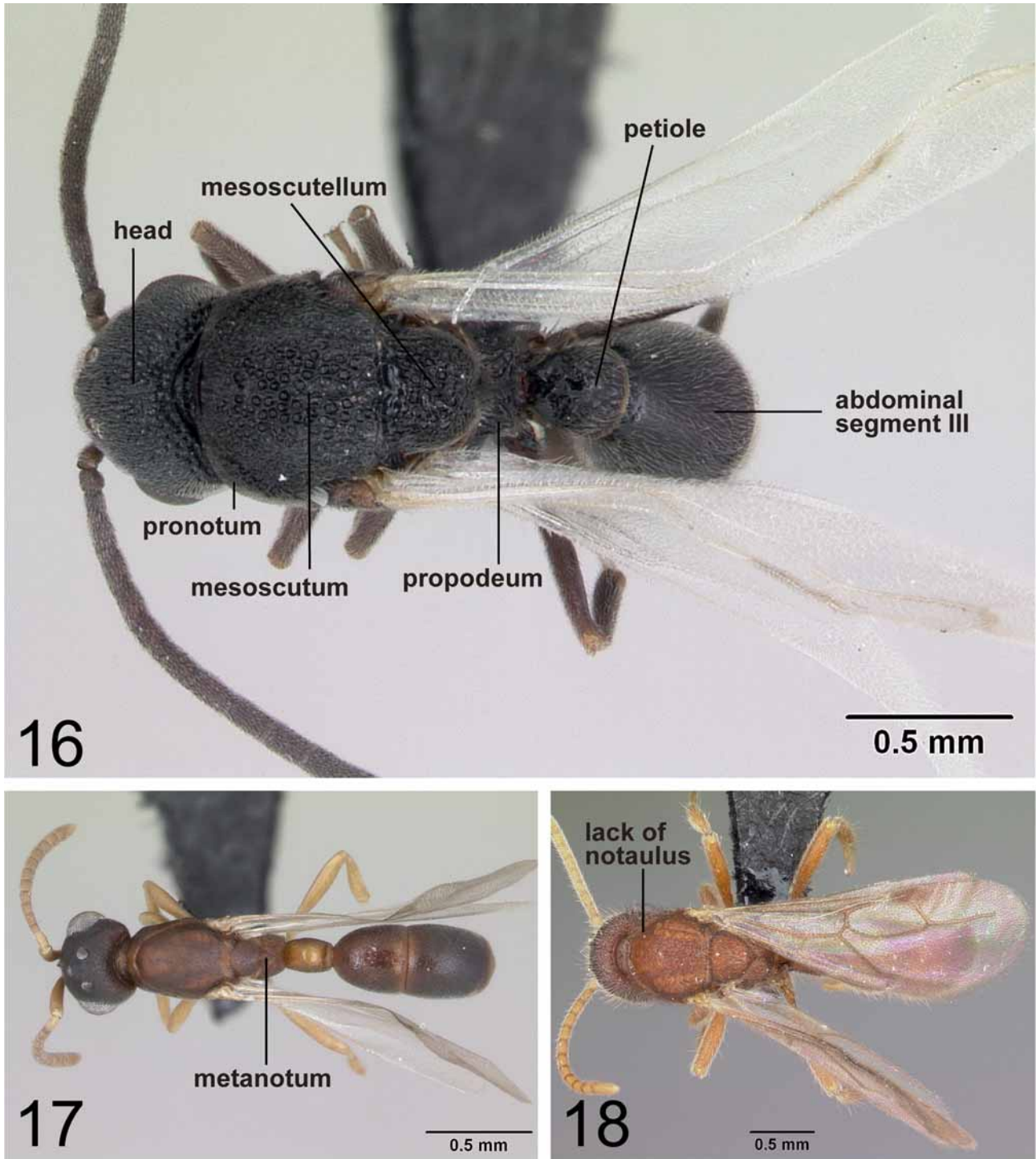
On forewing, the radius (R) completely developed, and radial sector (Rs) reaches to the costal margin (Fig. 2). On hindwing, M+Cu vestigial, free sections of the radius and cubitus, and cu-a absent (Fig. 8).

Remarks. Males of *Discothyrea* in the Malagasy region are distinguished easily from those of the three other proceratine genera by the presence of pygostyles. Bolton (2003: 48) proposed the absence of pygostyles as a diagnostic character of the subfamily Proceratiinae; however, we observed pygostyles in all male specimens examined in *Discothyrea* (Fig. 26). The presence of pygostyles in *Discothyrea sauteri* also has been illustrated in Ogata (1987: fig. 34). Baroni Urbani and De Andrade (2003) have indicated that the second maxillary palp is never hammer-shaped in *Discothyrea*. This character was reconfirmed in all specimens of *Discothyrea* examined in the present study (Fig. 31).

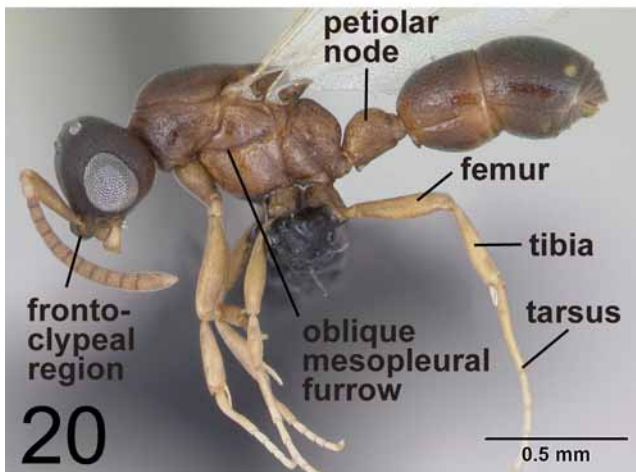
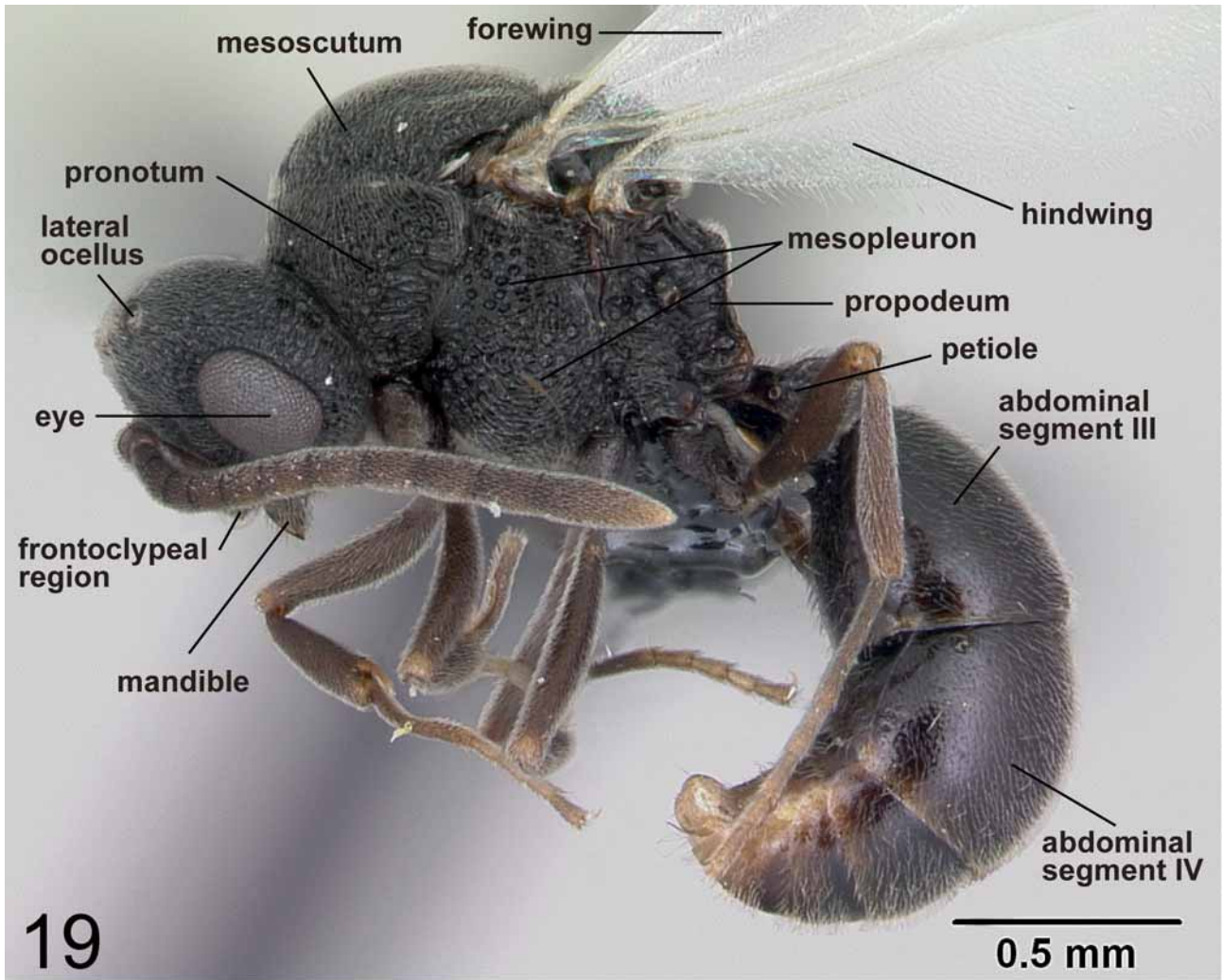


FIGURES 13–15. Head of Proceratiinae males in full-face view. 13, *Discothyrea* mgm01 (CASENT0083649); 14, *Probolomyrmex* mgm01 (CASENT0080551); 15, *Proceratium* mgm09 (CASENT0081854).

Forewing venation of *Discothyrea* (Fig. 2) is similar to PRm01 (Fig. 6), with the radial sector of forewing reaching its costal margin and the media branching from Rs+M distinctly basal to (before) the wing stigma. These characters are useful in separating *Discothyrea* and PRm01 from the other two genera in the Malagasy region. Also of note is that in one of the Malagasy species, *Discothyrea* mgm01, the media is reduced in length apical to Rs+M, but is still visible (Fig. 2). In other Malagasy species, and those examined from Japan, the media is longer and distinct apical to Rs+M.



FIGURES 16–18. Head to abdomen of Proceratiinae males in dorsal view. 16, *Discothyrea* mgm01 (CASENT0083649); 17, *Probolomyrmex* mgm01 (CASENT0080551); 18, *Proceratium* mgm09 (CASENT0081854).



FIGURES 19–21. Head to abdomen of Proceratiinae males in lateral view. 19, *Discothyrea* mgm01 (CASENT0083649); 20, *Probolomyrmex* mgm01 (CASENT0080551); 21, *Proceratium* mgm09 (CASENT0081854).

***Probolomyrmex* Mayr, 1901**

(Figs 3, 9, 14, 17, 20, 28, 32)

With characters of Proceratiinae. Mandible smaller than in conspecific worker, but also triangular to

subtriangular. Frontoclypeal region projecting dorsally. Frontal carinae merged into single median carina (Fig. 14). Antennal socket opening posteriorly. Antenna with 13 segments. Labrum bilobed apically (Fig. 28). Second segment of maxillary palp hammer-shaped (Fig. 32). Pro-, meso-, and metatibia with a single spur. Pygostyles absent.

On forewing, costa excluding basal portion, radius, radial sector between Rs+M and 2r-rs, and 2rs-m and m-cu crossveins absent, *the stigmal vein* (sensu Bolton 2003: 49) *formed by combination of 2r-rs and radial sector apical to the 2r-rs* (Fig. 3). On hindwing, M+Cu present or vestigial (unclear only in *P. mgm01*), free section of the radius and cubitus, and cu-a crossvein absent (Fig. 9). Radial sector apical to R+Rs present or absent.

Remarks. The genus *Probolomyrmex* in the Malagasy region is distinguished easily from the three other Malagasy proceratine genera by the forewing stigmal vein. See also discussions under *Discothyrea* and *Proceratium*.

Brown (1958) and Baroni Urbani and De Andrade (2003) have suggested that the hammer-shaped second segment of the maxillary palp is a synapomorphy of the genus *Proceratium* (Fig. 33). However, the hammer-shaped maxillary palp was also observed in all specimens of *Probolomyrmex* examined in the present study (Fig. 32).

All males of *Probolomyrmex* found in the Malagasy region belong to the *greavesi* group as defined by Eguchi *et al.* (2006: discussion). Of the diagnostic characters proposed by Eguchi *et al.* (2006), short frontoclypeal region, shorter first flagellar segment (third antennal segment) compared with the pedicel (second antennal segment) (Fig. 14), short petiolar node with steep anterior slope in lateral view (Fig. 20), and absence of Rs+M and media apical to Rs+M in forewing were observed (Fig. 3). These characters are useful in distinguishing the *greavesi* group from the *longinodus* group. However, cu-a in the forewing was present in all male specimens, and absence of media basal to Rs+M was unclear. Shape of the ninth abdominal sternum and the retractility of genitalia were unconfirmed.

***Proceratium* Roger, 1863**

(Figs 4, 5, 10, 11, 15, 18, 21, 29, 33)

With characters of Proceratiinae. Mandible smaller than in conspecific worker, but also triangular to subtriangular. Frontoclypeal region not projecting dorsally. *Frontal carinae separated, not merged into single median carina* (Fig. 15). Antennal sockets opening dorsally. Antenna with 13 segments. Labrum bilobed apically (Fig. 29). Second segment of the maxillary palp hammer-shaped (Fig. 33). Pro-, meso-, and metatibia with a single spur. Pygostyles absent.

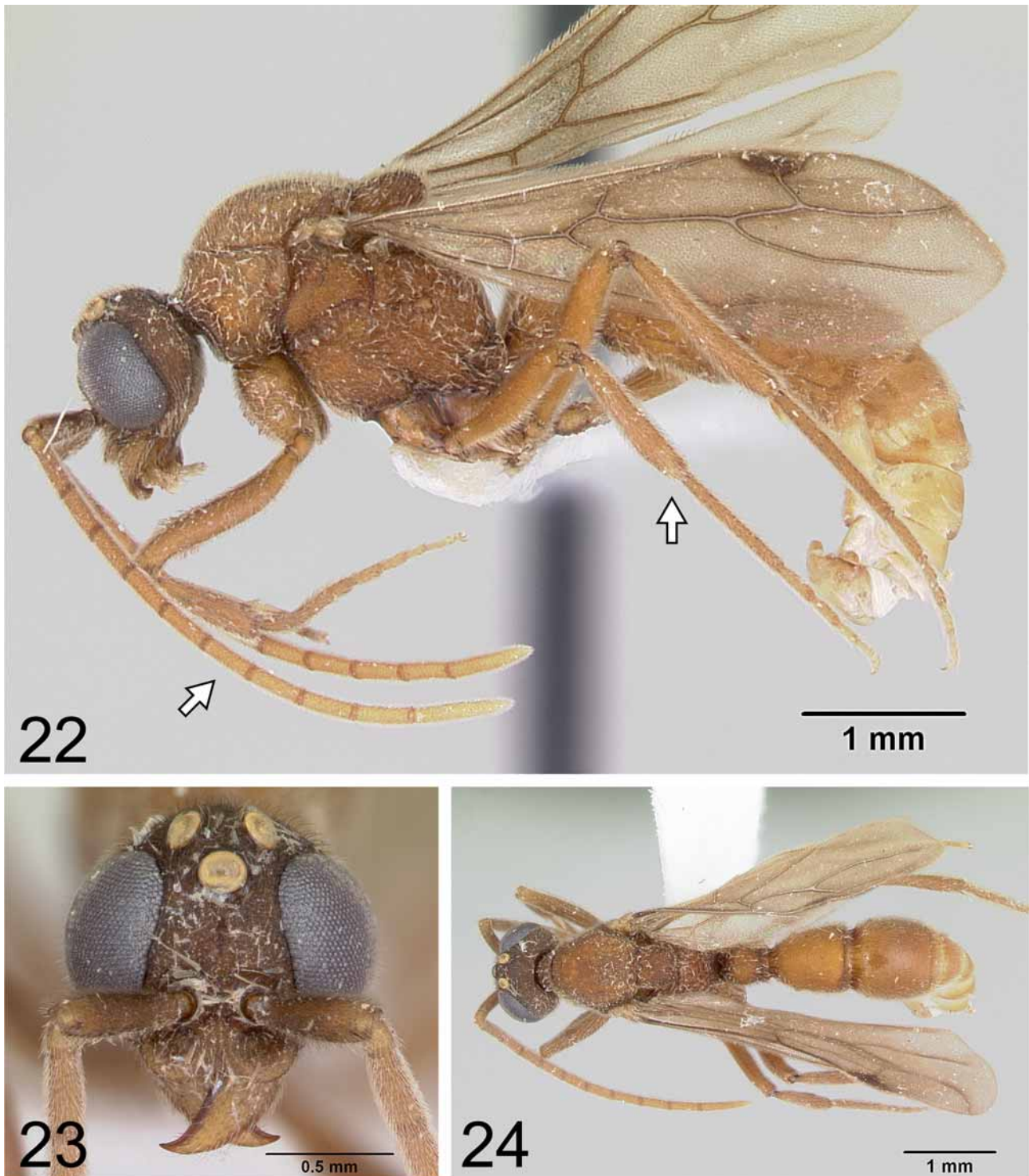
Forewing in Malagasy species with radial sector between Rs+M and 2r-rs absent, radius and radial sector apical to pterostigma reduced in length, so that the radial sector does not reach the costal margin (Figs 4, 5). *On hindwing, cubitus present*, free section of the radius present or absent. Radial sector and cu-a crossvein present (Figs 10, 11).

Remarks. *Proceratium* is the most common genus of Malagasy proceratine males collected by Malaise trap. *Proceratium* is distinguished easily from the other three Malagasy proceratine genera by the frontal carinae which do not merge into a single carina between antennal sockets (Fig. 15), and by the hindwing with cubitus (Figs 10, 11).

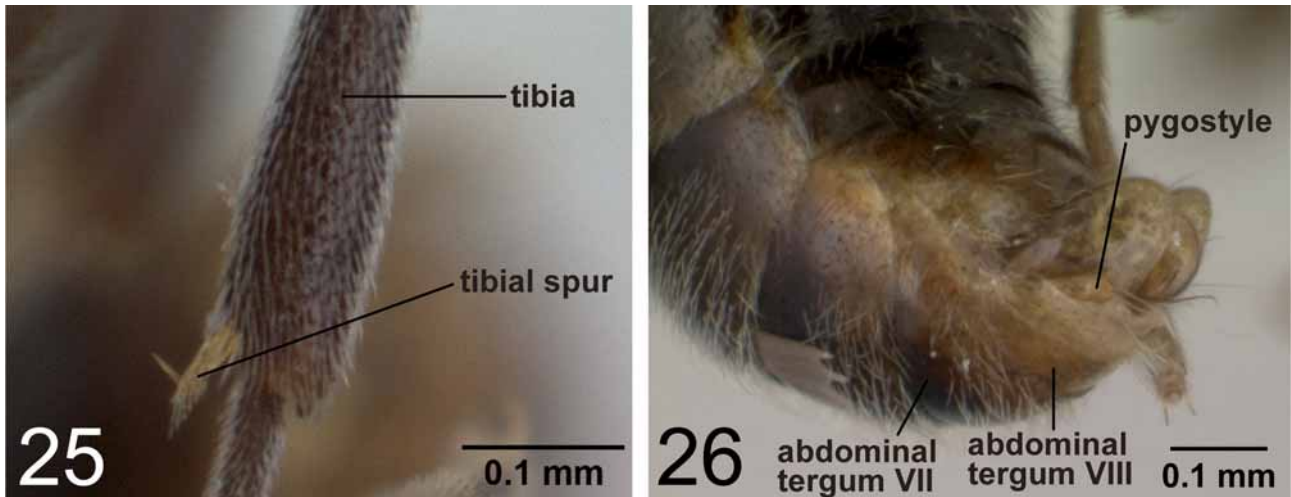
In Malagasy *Proceratium*, two patterns of forewing venation were observed (Figs 4, 5). Both patterns feature a radial sector that does not reach the costal margin, and a media that connects between Rs+M and 2rs-m. The former character separates Malagasy *Proceratium* from *Discothyrea* and the genus PRm01, and the latter separates it from *Probolomyrmex*.

In a study of world fauna that did not include taxa from Madagascar, Baroni Urbani and De Andrade (2003: 49) divided *Proceratium* forewing venations into five categories. Their categories 4 and 5 are closest to the two patterns shown in Figs 4 and 5 for the Malagasy taxa studied here. However, in contrast to their

categories 4 and 5, the Malagasy taxa have shorter 2r-rs. Also unlike their category 5, the media and 1m-cu are not always absent among the Malagasy specimens as in Figure 5. In a few specimens of one species (*Proceratium* mgm01), the media and 1m-cu are still recognizable.



FIGURES 22–24. Male of PRm01 sp. (CASENT0103485). 22, head to abdomen in lateral view; 23, head in full-face view; 24, head to abdomen in dorsal view.



FIGURES 25–26. Male of *Discothyrea* mgm01 (CASENT0083649). 25, mesotibia; 26, apical portion of abdomen.

Genus PRm01

(Figs 6, 12, 22–24, 30, 34)

Since only a single male specimen of this genus has been collected so far, we do not describe it as new here. However, we regard this male as belonging to an isolated genus, and its diagnostic characters and remarks are given below.

With characters of Proceratiinae. Mandible stout and shaped like a curved short blade such as a jambiya (Fig. 30). Frontoclypeal region not projecting dorsally. Frontal carinae merged into single carina between antennal sockets. Antennal sockets opening dorsally. *Antenna with 12 segments. Labrum triangular: narrowed apically, with a single apex* (Fig. 30). Second segment of the maxillary palp not hammer-shaped (Fig. 34). Pro- and metatibia with a single spur, *mesotibia without spurs*. Pygostyles absent.

On forewing, costa and radius completely developed, and radial sector reaches to the costal margin (Fig. 6). On hindwing, free section of radius and cubitus absent, radial sector, M+Cu, and cu-a crossvein present (Fig. 12).

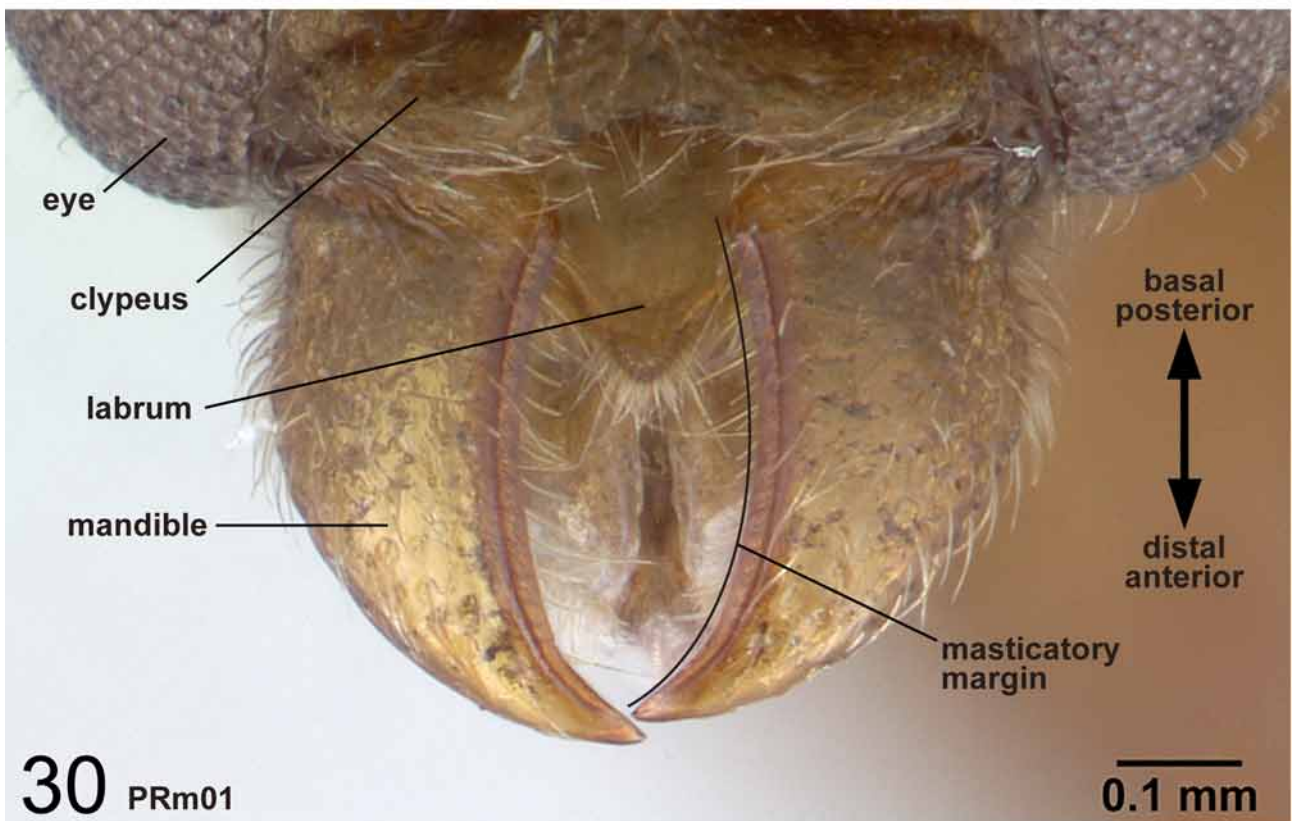
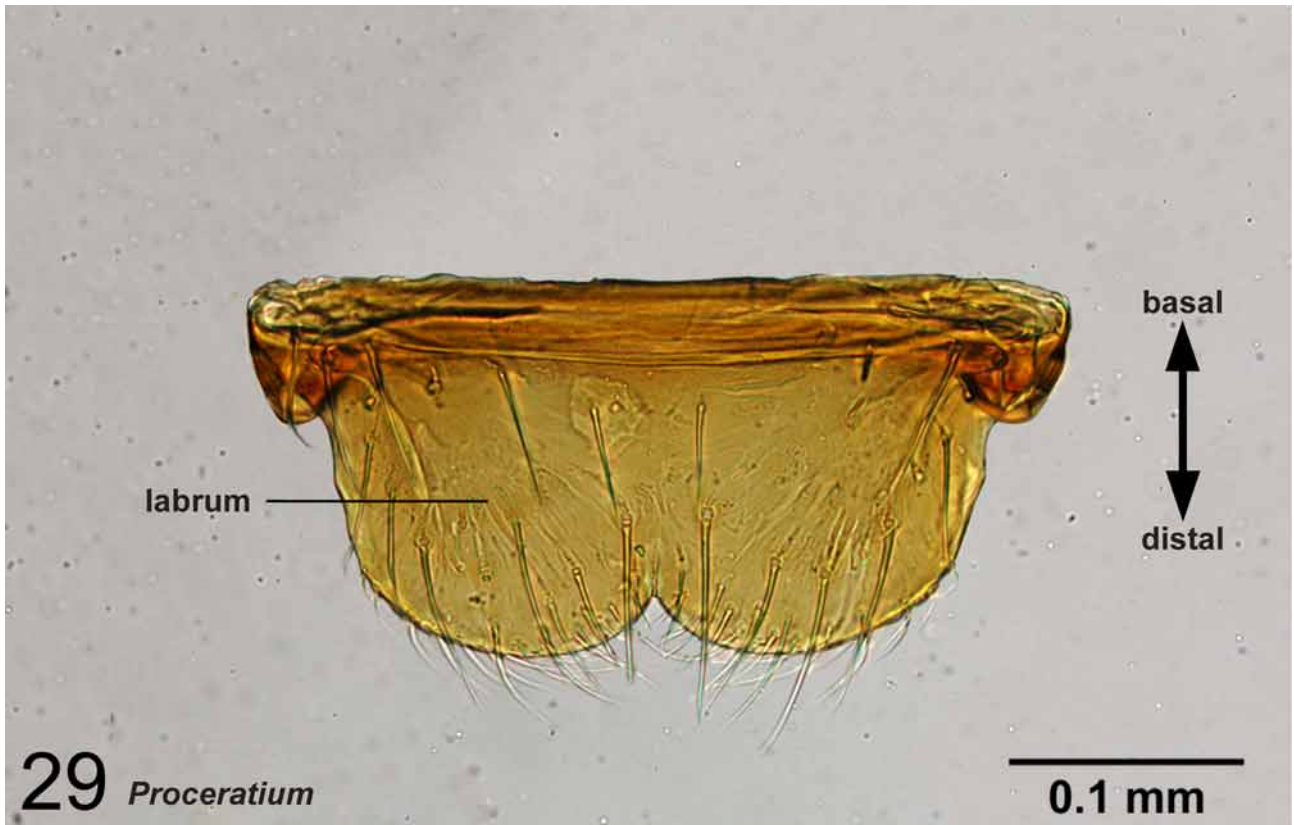
Remarks. The undescribed genus PRm01 can be distinguished easily from the other three Malagasy proceratine genera by the antennae consisting of 12 segments, a triangular labrum (Fig. 30), and the mesotibiae lacking a spur. PRm01 sp. is the first male known in Proceratiinae with a 12-segmented antenna. Bolton (2003: 49) has proposed 13-segmented antenna as a diagnostic character of both tribes in Proceratiinae; this now must be amended.

There is one erroneous report of a 12-segmented antenna in *Proceratium*. Kennedy and Talbot (1939) previously described a male of *Proceratium silaceum* Roger, 1863, and included a drawing and description of a male with a 12-segmented antenna (their figure 1). However, their figure 6 illustration shows an antenna with 13 segments for the same species. As Brown (1958) has pointed out, their figures and description disagree in palpal formula, and we conclude they also differ in antennal count. Baroni Urbani and De Andrade (2003: fig. 162) have included an SEM image of a male of *Proceratium silaceum*, on which the antenna clearly consists of 13 segments. Therefore, males of *Proceratium* have 13-segmented antennae and not 12 as erroneously reported by Kennedy and Talbot (1939).

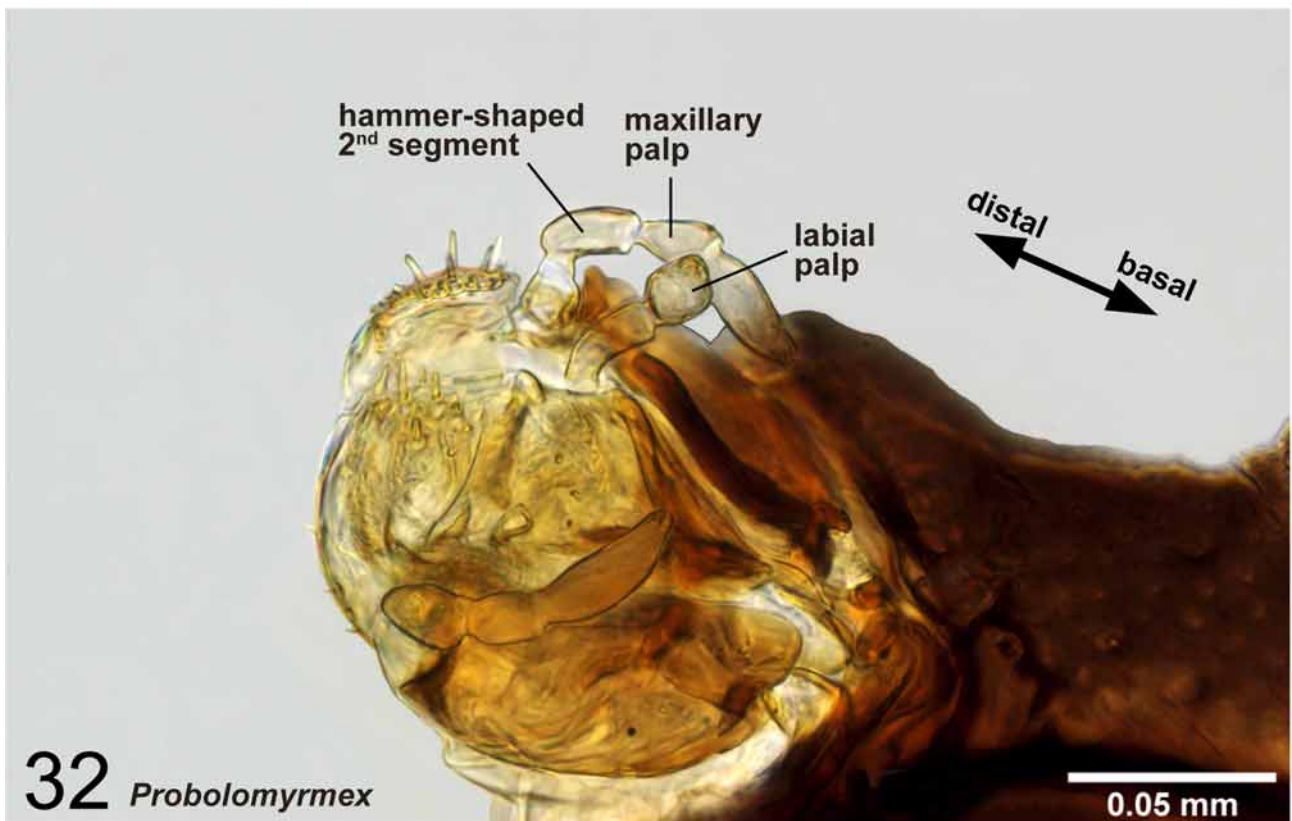
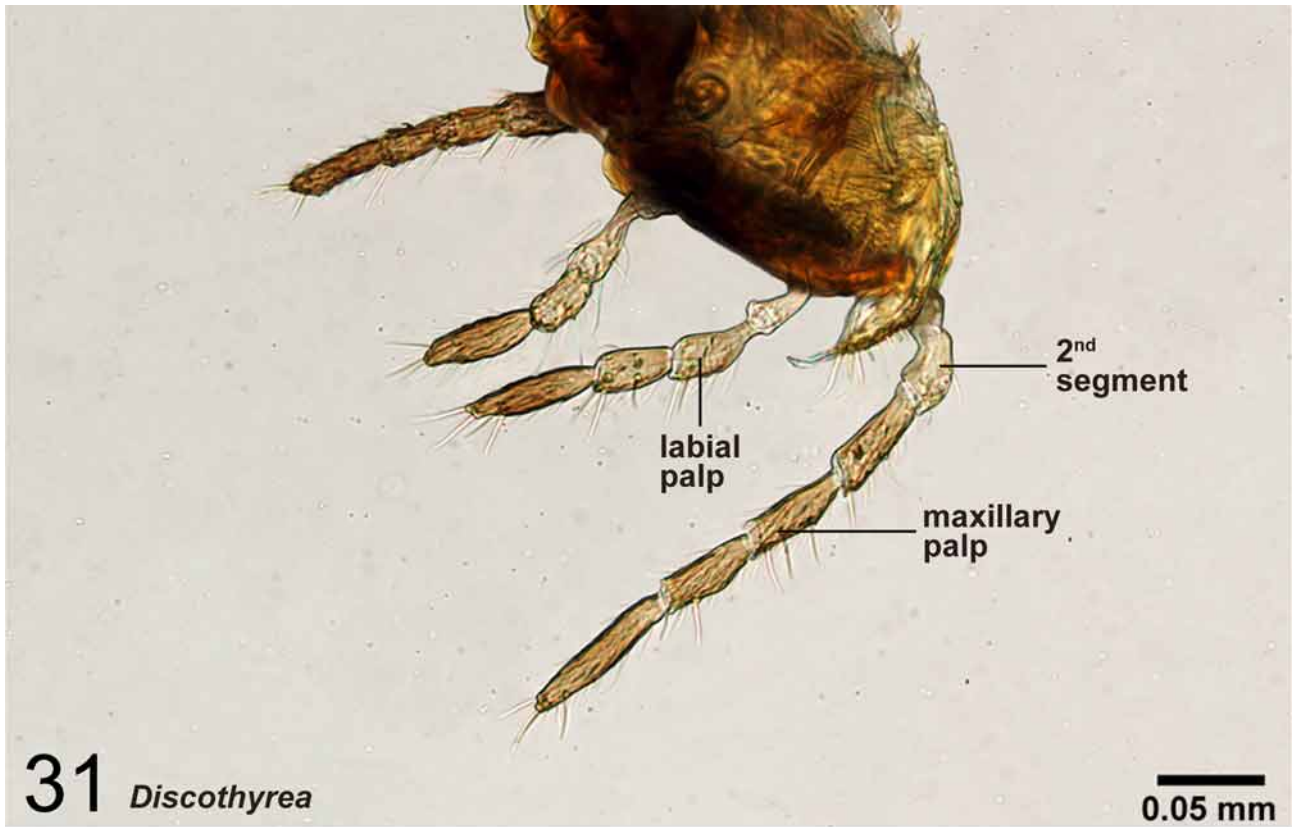
The triangular labrum is a unique character for PRm01 within the Proceratiinae (Fig. 30). An apically bilobed labrum is the usual pattern in the Formicidae (Gotwald 1969). The triangular labrum, a wide and bilobed clypeus, and stout mandibles with outward curved masticatory margins should be expected in conspecific workers. These characters may have a special function.



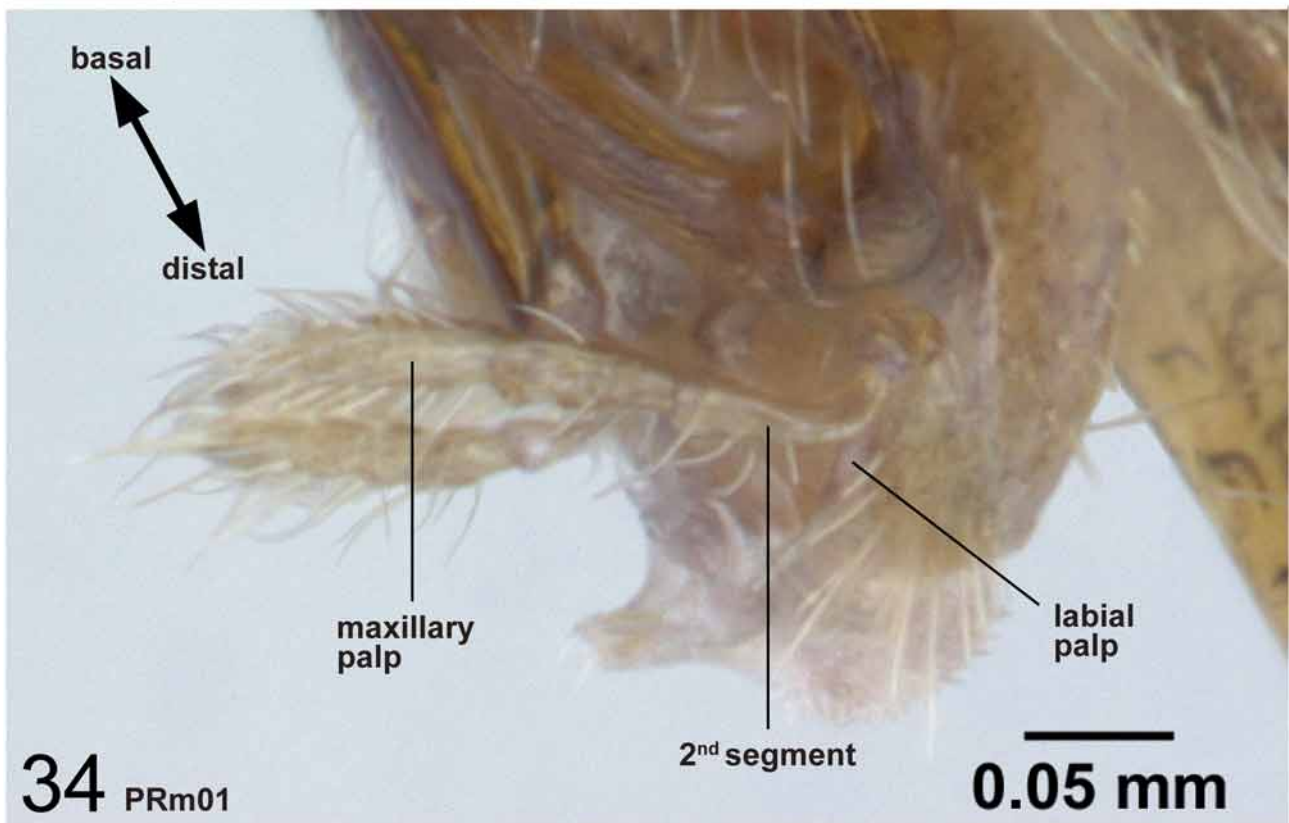
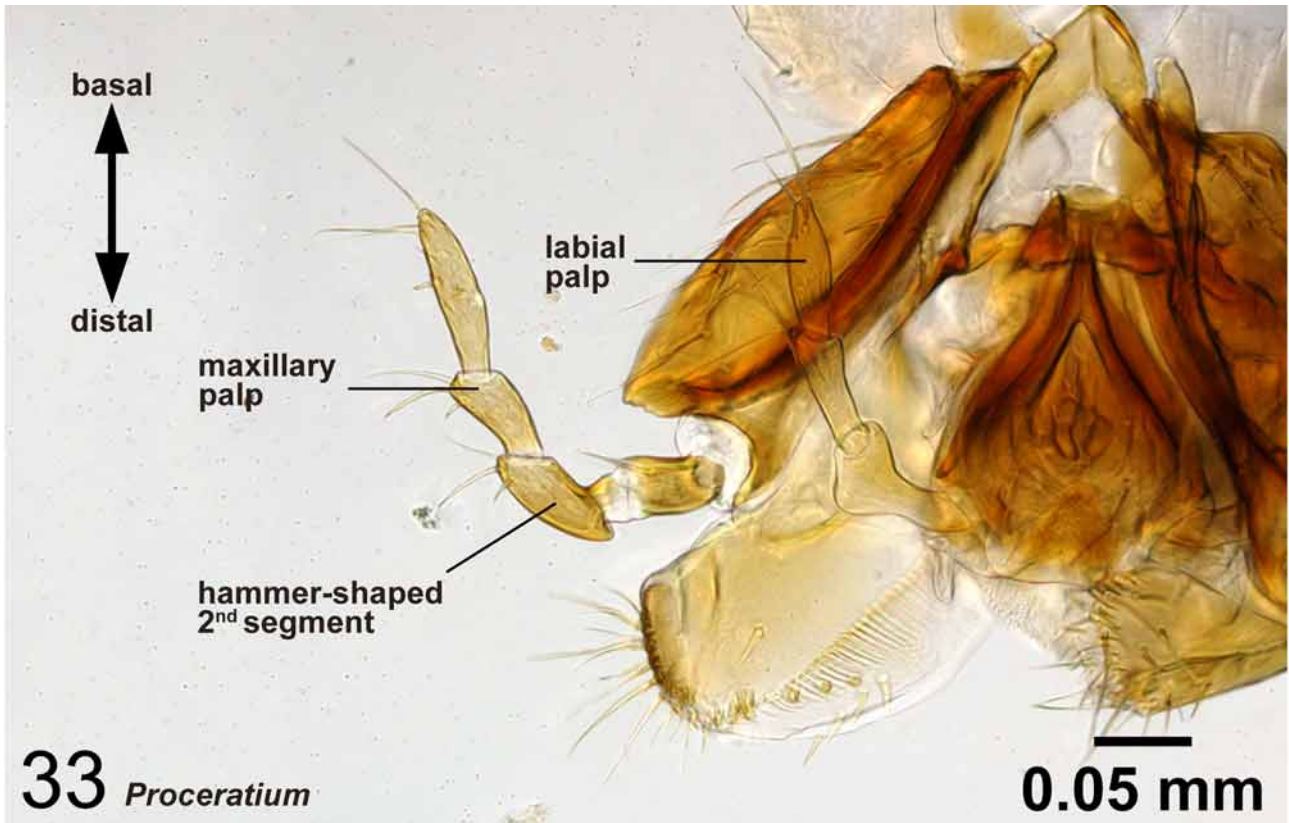
FIGURES 27–28. Labrum of proceratine males. Basal margin on top. 27, *Discothyrea* mgm01 (CASENT0083245) in internal view; 28, *Probolomyrmex* mgm01 (CASENT0525318) in external view.



FIGURES 29–30. Proceratine males. 29, Labrum of *Proceratium* mgm01 (CASENT0191991) in external view, basal margin on top; 30, Labrum and mandibles of PRm01 sp. (CASENT0103485) in oblique full-face view.



FIGURES 31–32. Mouthparts of proceratine males. 31, *Discothyrea* mgm01 (CASENT0083245), left palps on right side; 32, *Probolomyrmex* mgm01 (CASENT0525318), left palps on top.



FIGURES 33–34. Mouthparts of proceratine males. 33, *Proceratium* mgm01 (CASENT0191991), right palps on left side; 34, PRm01 sp. (CASENT0103485), right maxillary palp on front.

Only a single specimen was collected from the Seychelles (CASENT0103485). Similarity in forewing venations between PRm01 (Fig. 6) and *Discothyrea* (Fig. 2) suggests their close relationship (see *Discothyrea* section above); however, the male of PRm01 can be distinguished easily from those of *Discothyrea* by the following characters: frontoclypeal region not expanded dorsally, 12-segmented antennae, triangular labrum (Fig. 30), longer second maxillary palpal segment (Fig. 34), absence of pygostyles, lack of a mesotibial spur, presence of cu-a in hindwing (Fig. 6), larger size, and brighter color, as PRm01 is yellowish-brown (Fig. 22), while *Discothyrea* is black (Fig. 19). Formal description of this taxon awaits the future collection of additional males and the first workers.

Acknowledgments

This study was partially supported by the National Science Foundation under Grant No. DEB-0072713 and DEB-0344731. We would like to acknowledge Philip S. Ward and Wojciech Pulawski for their useful suggestions, April Nobile and Erin Prado for creating images, Michele Esposito for help with database management and for the arrangement of images, and Fernando Alvarez-Padilla for assistance with taking images. The fieldwork on which this study is based could not have been completed without the gracious support of the Malagasy people and the Arthropod Inventory Team (Balsama Rajemison, Jean Claude Rakotonirina, Jean-Jacques Rafanomezantsoa, Chrislain Ranaivo, Coco Randriambololona, Hanitriniana Rasoazanamavo, Nicole Rasoamanana, Clavier Randrianandrasana, Valerie Rakotomalala and Dimby Raharinjanahary).

References

- Baroni Urbani, C. & De Andrade, M.L. (2003) The ant genus *Proceratium* in the extant and fossil record (Hymenoptera: Formicidae). *Monografie del Museo Regionale di Scienze Naturali, Torino*, 36, 1–492.
- Bolton, B. (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge, Mass., 222 pp.
- Bolton, B. (1995) *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, Mass., 504 pp.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B., Alpert, G., Ward, P.S. & Naskrecki, P. (2006) *Bolton's catalogue of ants of the world: 1758–2005, CD-ROM*. Harvard University Press, Cambridge, MA.
- Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 18172–18177.
- Brown, W.L., Jr. (1958) Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). *Bulletin of the Museum of Comparative Zoology*, 118, 173–362.
- Brown, W.L., Jr. (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. *Search Agriculture (Ithaca, N. Y.)*, 5, 1–115.
- Eguchi, K., Yoshimura, M. & Yamane, S. (2006) The Oriental species of the ant genus *Probolomyrmex* (Insecta: Hymenoptera: Formicidae: Proceratiinae). *Zootaxa*, 1376, 1–35.
- Emery, C. (1911) Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. *Genera Insectorum*, 118, 1–125.
- Fisher, B.L. (2005) A model for a global inventory of ants: A case study in Madagascar. In: Jablonski, N.G. (Ed.) *Biodiversity: A Symposium Held on the Occasion of the 150th Anniversary of the California Academy of Sciences June 17–18, 2003*. Proceedings of the California Academy of Sciences, ser. 4, vol. 56, Suppl. I, San Francisco, California, pp. 78–89.
- Gauld, I. & Bolton, B. (1988) *The Hymenoptera*. Oxford University Press, Oxford, xii + 322 pp.
- Gotwald, W.H. (1969) Comparative morphological studies of the ants with particular reference to the mouthparts. *Cornell University Agricultural Experiment Station Memoir*, 408, 1–150.
- Huber, J.T. & Sharkey, M.J. (1993) Structure. In: Goulet, H. & Huber, T.J. (Eds.) *Hymenoptera of the World: An Identification Guide to Families*. Research Branch Agriculture Canada Publication 1894/E, Ottawa, pp. 13–59.

- Japanese Ant Database Group 2008 (2008) Japanese Ant Image Database 2008. Sendai, Japanese Ant Database Group, CD-ROM (in Japanese).
- Kaspari, M., Longino, J., Pickering, J. & Windsor, D. (2001) The phenology of a Neotropical ant assemblage – evidence for continuous and overlapping reproduction. *Behavioral Ecology and Sociobiology*, 50, 382–390.
- Kennedy, C.H. & Talbot, M. (1939) Notes on the hypogaecic ant, *Proceratium silaceum* Roger. *Proceedings of the Indiana Academy of Science*, 48, 202–210.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312, 101–104.
- Ogata, K. (1987) A generic synopsis of the poneroid complex of the family Formicidae in Japan (Hymenoptera). Part 1. Subfamilies Ponerinae and Cerapachyinae. *Esakia*, 25, 97–132.
- Ouellette, G.D., Fisher, B.L. & Girman, D. (2006) Molecular systematics of basal subfamilies of ants using 28S rDNA (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 40, 359–369.
- Smith, M.R. (1943) A generic and subgeneric synopsis of the male ants of the United States. *American Midland Naturalist*, 30, 273–321.
- Snodgrass, R.E. (1935) *Principles of insect morphology, with a new foreword by G. C. Eickwort (1993)*. Cornell University Press, New York, 1–86 pp +33 pls.
- Snodgrass, R.E. (1941) The male genitalia of Hymenoptera. *Smithsonian Miscellaneous Collections*, 99, 1–86.
- Taylor, R.W. (1965) A monographic revision of the rare tropicopolitan ant genus *Probolomyrmex* Mayr (Hymenoptera: Formicidae). *Transactions of the Royal Entomological Society of London*, 117, 345–365.
- Wheeler, W.M. (1922) Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. VII. Keys to the genera and subgenera of ants. *Bulletin of the American Museum of Natural History*, 45, 631–710.
- Wootton, R.J. (1979) Function, homology and terminology in insect wings. *Systematic Entomology*, 4, 81–93.
- Yoshimura, M. & Fisher, B.L. (2007) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to subfamilies and treatment of the genera of Ponerinae. *Zootaxa*, 1654, 21–40.
- Yoshimura, M. & Onoyama, K. (2002) Male-based keys to the subfamilies and genera of Japanese ants (Hymenoptera: Formicidae). *Entomological Science*, 5, 421–443.
- Yoshimura, M., Onoyama, K. & Ogata, K. (2007) The ants of the genus *Odontomachus* (Insecta: Hymenoptera: Formicidae) in Japan. *Species Diversity*, 12, 89–112.