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A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to subfamilies and treatment of the genera of Ponerinae

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ABSTRACT

Male-based keys to ant subfamilies and to the genera of Ponerinae in the Malagasy region (Madagascar, Mauritius, Reunion, Comores, and Seychelles) are presented. Seven subfamilies known from the Malagasy region in addition to an undetermined taxon are included in the subfamily key. All seven of the ponerine genera recorded in the region—*Anochetus*, *Hypoponera*, *Leptogenys*, *Odontomachus*, *Pachycondyla*, *Platythyrea*, and *Ponera*—are included. Diagnoses and remarks on the subfamily and genera within Ponerinae, and a character table for the ponerine genera, are given. The males of the seven ponerine genera are illustrated.

Key words: Madagascar, Mauritius, Reunion, Comoros, taxonomy, key

INTRODUCTION

Male ants offer a wealth of information on the diversity and biology of ants. They provide valuable characters for delimiting genera and species, and information on the phenology of ant reproduction. Ant taxonomists and ecologists, however, often overlook this source of information due to a lack of taxonomic tools. There are few regions in the world for which identification keys to genera of ant males are available, let alone keys to species. Japan is a notable exception (Yoshimura & Onoyama 2002).

The production of keys to genera based on males is impaired world-wide by the fact that this sex tends to be unknown or poorly represented in many genera. In Bolton (2003), the descriptions of 61 genera (22%) of the 281 extant genera state “Male: unknown.” Many of these unknown genera may be in collections but unassociated with their respective worker caste. The use of molecular techniques such as DNA barcoding, however, provides a new tool to associate males and worker castes (B.L. Fisher and M.A. Smith, unpublished).

As part of an initiative to document the diversity of ants in the Malagasy region (Fisher, 2005), we have set out to develop male-based keys to subfamilies and genera. Our aim is to use males to better understand the generic limits of ants in the Malagasy region. In addition, we hope to uncover a wealth of data on the reproductive biology of ants by providing tools to sort the vast number of males collected from Malaise traps. In this paper, we provide a male-based key to ant subfamilies and to the genera of the Ponerinae, for the Malagasy region.

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MATERIALS AND METHODS

This study is primarily based on arthropod surveys in the Malagasy region that included over 6,000 leaf litter samples, 4,000 pitfall traps, 1,000 Malaise trap collecting events and 8,000 additional hand-collecting events from over 200 localities throughout the region from 1992–2006 (Fisher 2005, B.L. Fisher unpublished).

Observations were carried out under LEICA stereoscopic microscopes (MZ12). Digital color images were created mostly by April Nobile using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage (v 5.0) software. Each imaged specimen discussed below is uniquely identified with a specimen-level code (eg. CASENT0003099) affixed to each pin. In addition, each specimen may also have a collection code, which is a field number that uniquely identifies collecting events (e.g. BLF01652).

Each taxon name is followed by a letter code indicating the source of morphological information used to establish 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 was obtained only from previously published studies. In these cases, the references are shown in brackets.

Most of the specimens in this study were sorted only to genus level; the high number of undescribed species in Madagascar makes species-level identification difficult. Taxonomic information on the materials follows Bolton (1995, 2003). No new taxa are formally described.

Males from the following genera were examined to construct the subfamily key.

Amblyoponinae Forel, 1893.

Adetomyrma Ward, 1994 [g]; *Amblyopone* Erichson, 1842 [m]; *Mystrium* Roger, 1862 [g]; *Prionopelta* Mayr, 1866 [g]; Undetermined genus [m].

Cerapachyinae Forel, 1893.

Cerapachys Smith, 1857 [g]; *Cylindromyrmex* Mayr, 1870 [g]; *Acanthostichus* Mayr, 1887 [m]; *Simopone* Forel, 1891 [g].

Dolichoderinae Forel, 1878.

Genus near *Tapinoma*; *Ochetellus* Shattuck, 1992 [r: Shattuck, 1992]; *Tapinoma* Foerster, 1850 [g]; *Technomyrmex* Mayr, 1872 [g]; Undetermined genus [m] (e.g. CASENT0080308 on www.antweb.org).

Formicinae Latreille, 1809.

Anoplolepis Santschi, 1914 [r: Yoshimura & Onoyama, 2002; Bolton, 2003]; *Brachymyrmex* Mayr, 1868 [g]; *Camponotus* Mayr, 1861 [g]; *Lepisiota* Santschi, 1926 [r: Bolton, 2003]; *Paratrechina* Motschoulsky, 1863 [g]; *Plagiolepis* Mayr, 1861 [m]; *Tapinolepis* Emery, 1925 [r: Bolton, 2003].

Myrmicinae Emery, 1877.

Aphaenogaster Mayr, 1853 [g]; *Cardiocondyla* Emery, 1869 [m]; *Carebara* Westwood, 1840 [g]; *Cataulacus* Smith, F., 1854 [g]; *Crematogaster* Lund, 1831 [g]; *Eutetramorium* Emery, 1899 [g]; *Monomorium* Mayr, 1855 [g]; *Melissotarsus* Emery, 1877 [g]; *Meranoplus* Smith, F., 1854 [r: Bolton, 2003]; *Metapone* Forel, 1911 [m]; *Nesomyrmex* Wheeler, W. M., 1910 [g]; *Pheidole* Westwood, 1839 [g]; *Pilotrochus* Brown, 1978 [m]; *Pristomyrmex* Mayr, 1866 [m]; *Pyramica* Roger, 1862 [m]; *Solenopsis* Westwood, 1840 [r: Bolton, 1994; 2003]; *Strumigenys* Smith, 1860 [g]; *Terataner* Emery, 1912 [g]; *Tetramorium* Mayr, 1855 [g]; *Vollenhovia* Mayr, 1865 [r: Bolton, 1994;

Yoshimura & Onoyama, 2002]; Undetermined genera [g & m].

Ponerinae Lepeletier de Saint-Fargeau, 1835.

Anochetus Mayr, 1861 [g]; *Hypoponera* Santschi, 1938 [g]; *Leptogenys* Roger, 1861 [g]; *Pachycondyla* Smith, 1858 [g]; *Platythyrea* Roger, 1863 [g]; *Ponera* Latreille, 1804 [r: Taylor, 1967]; *Odontomachus* Latreille, 1804 [g].

Proceratiinae Emery, 1895.

Discothyrea Roger, 1863 [m]; *Probolomyrmex* Mayr, 1901 [m]; *Proceratium* Roger, 1863 [m].

Pseudomyrmecinae Smith, 1952.

Tetraponera Smith, 1852 [g].

TERMINOLOGY

Terminology for general morphology follows Snodgrass (1935), Gauld & Bolton (1988), Bolton (1994) and Huber & Sharkey (1993). Use of the term pygostyle (see below) and descriptions of genitalia follow Snodgrass (1941); terminology of forewing venation follows Wootton (1979), Huber & Sharkey (1993), Brown & Nutting (1950), and Hölldobler & Wilson (1990). Morphological terms used are illustrated in Figs. 1, 2, and 7b. Abdominal segments are labeled with roman numerals starting with the propodeum.

Abdominal tergum VIII (Fig. 1a). Abdominal tergum VIII is commonly referred to as the pygidium. However, to avoid a problem of homology, we prefer the term abdominal tergum VIII. In insects, the pygidium is defined as the apical visible tergum of the abdomen (Nichols, 1989). In the Hymenoptera, the pygidium may refer to different abdominal segments. For example, in males of the Formicidae, the ninth tergum is commonly visible on the apical-most portion of the abdomen. We use the term abdominal tergum VIII to indicate the plate when an important characteristic such as the apical spine (= pygidial spine) is present.

Abdominal sternum IX (Fig. 1a). In Hymenoptera, this sclerite is referred to as the subgenital plate (Snodgrass, 1935; Yoshimura & Onoyama, 2002) or the hypopygium (Huber & Sharkey, 1993). The subgenital plate is defined as the sternum beneath the genital chamber (Snodgrass, 1935; Nichols, 1989), while the hypopygium is defined as the last visible sternum (Nichols, 1989). Both terms, however, are not homologous in males and females of the same taxon. The terms refer to the seventh sternum in females but the ninth sternum in males for most of the Hymenoptera. To avoid this problem of homology, we use the term abdominal sternum IX.

Pygostyles (Fig. 2b). A pair of appendages often occurs on the tenth tergum of the abdomen of male Hymenoptera. Snodgrass (1941) referred to these as pygostyles, but others often refer to them as cerci (Huber & Sharkey, 1993). For insects in general, however, the cerci refer to appendages on abdominal tergum XI, not X. Whether the pygostyles of Hymenoptera and the cerci of insects are homologous remains unclear (Snodgrass, 1941). For the sake of clarity, we use "pygostyles" to indicate these appendages.

Forewing venation (Fig. 1b). We include venation as an important character to highlight differences between taxa. Many previous male-based keys use the presence of cells on the forewing as a taxonomic character. But these cells are not formed by homologous veins, making their use as a taxonomic character possibly misleading. Brown & Nutting (1950) and Hölldobler & Wilson (1990) use the terms first and second radial cross veins to indicate cross veins connecting the radius and radial sector. We identify these two cross veins as 1r-rs and 2r-rs, respectively, following Huber & Sharkey (1993: 28). All names of longitudinal veins follow a recommendation by Wootton (1979).

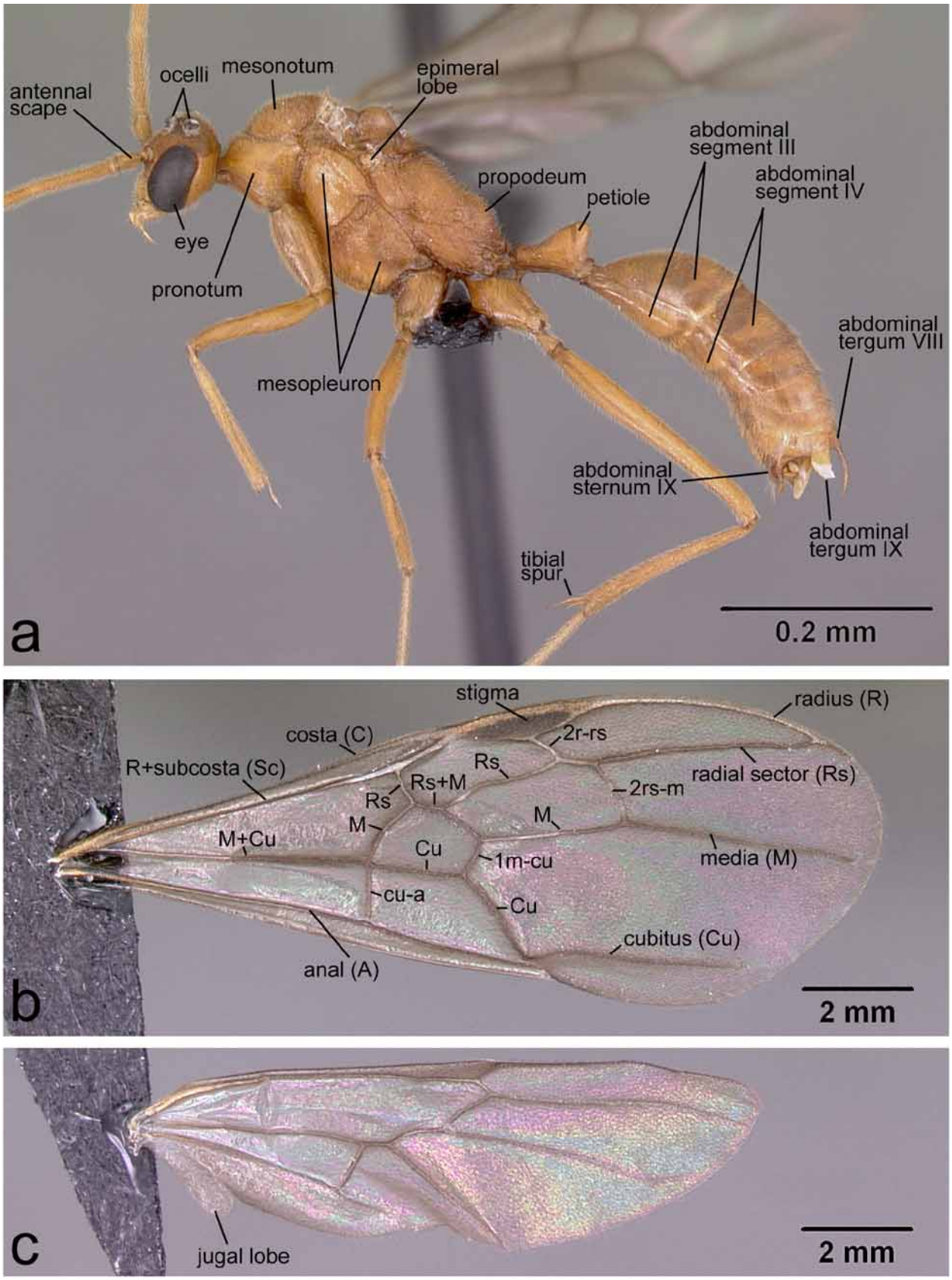

FIGURE 1. Male ant terminology. a–c, *Odontomachus coquereli* (CASENT 0049797). (a) head to abdomen in lateral view; (b) forewing; (c) hind wing.

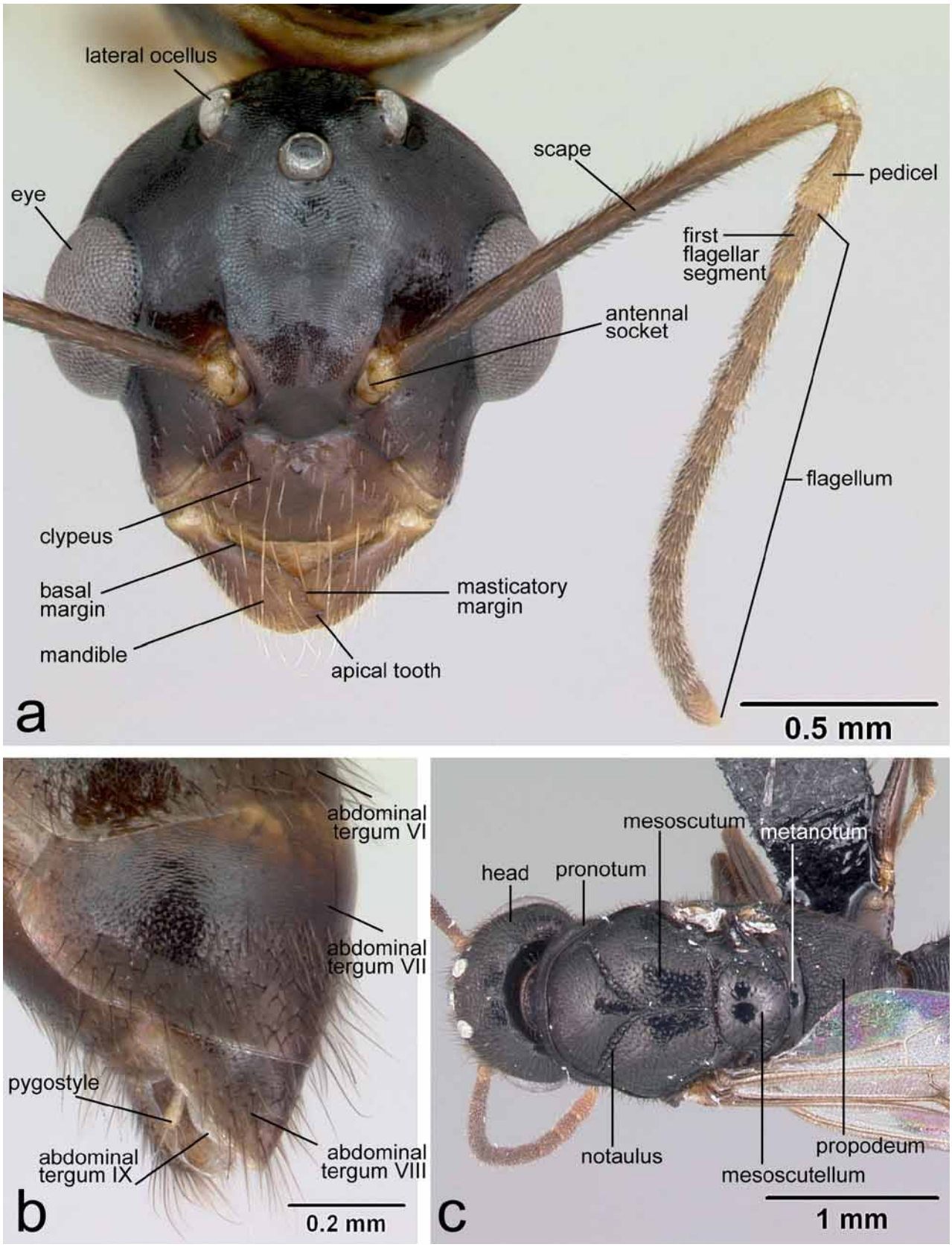

FIGURE 2. Male ant terminology. a, *Camponotus* Mad18 (CASENT 0497230); b–c, *Amblyopone* Mad01 (CASENT 0080397). (a) head in full-face view; (b) apical portion of abdomen in oblique lateral view; (c) head and mesosoma in dorsal view.

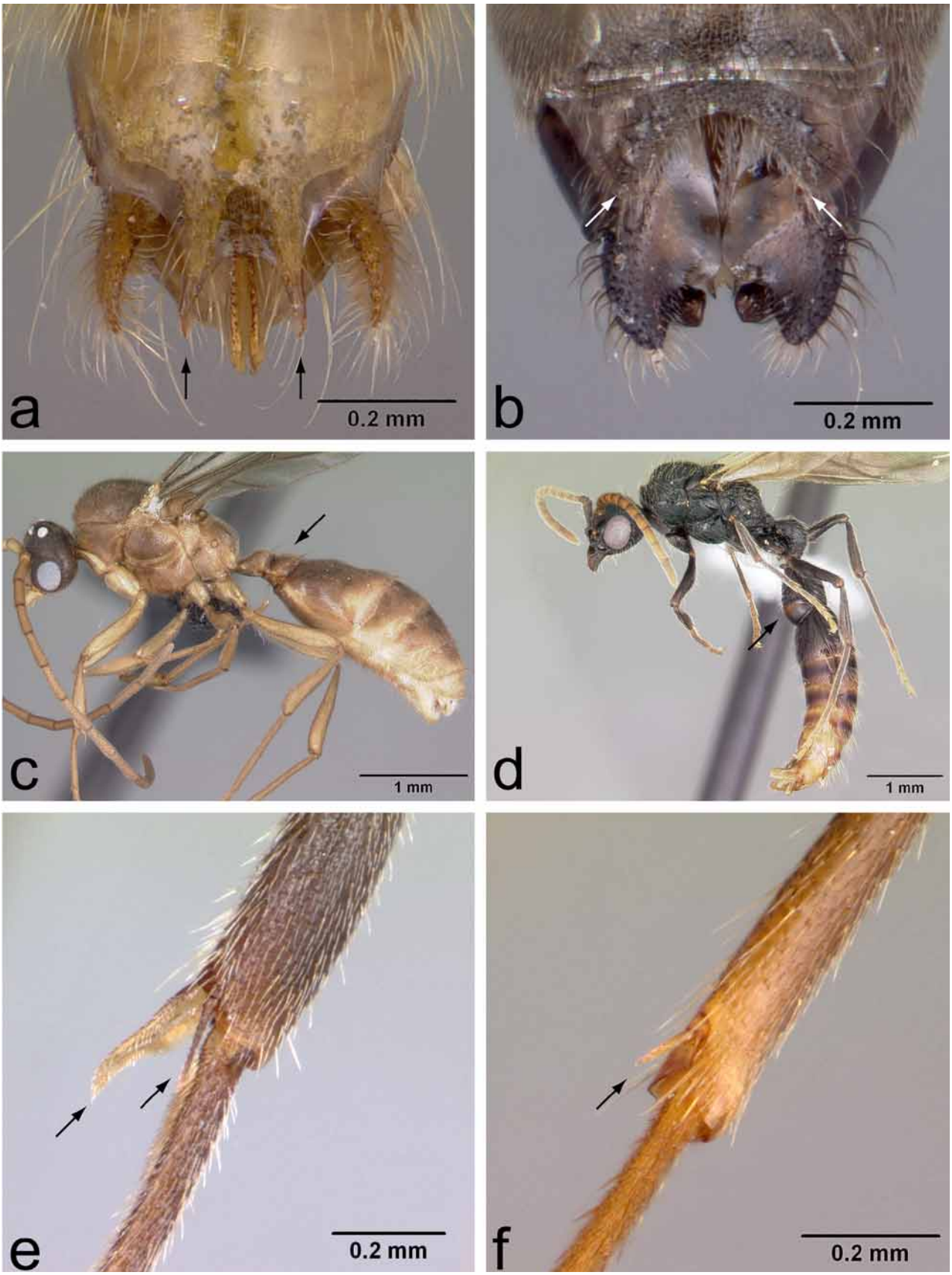

FIGURE 3. Males of Formicidae. a–d, *Cerapachys* Mad51 (CASENT 0001042); b, *Technomyrmex* Mad08 (CASENT 0049527); c, *Carebara* Mad02 (CASENT 0494540); e, *Tetraponera* Mad02 (CASENT 0053316); f, *Aphaenogaster swammerdami* (CASENT 0000990). (a–b) apical portion of the abdomen in ventral view; (c–d) head to abdomen in lateral view; (e–f) tibial spurs on hind leg.

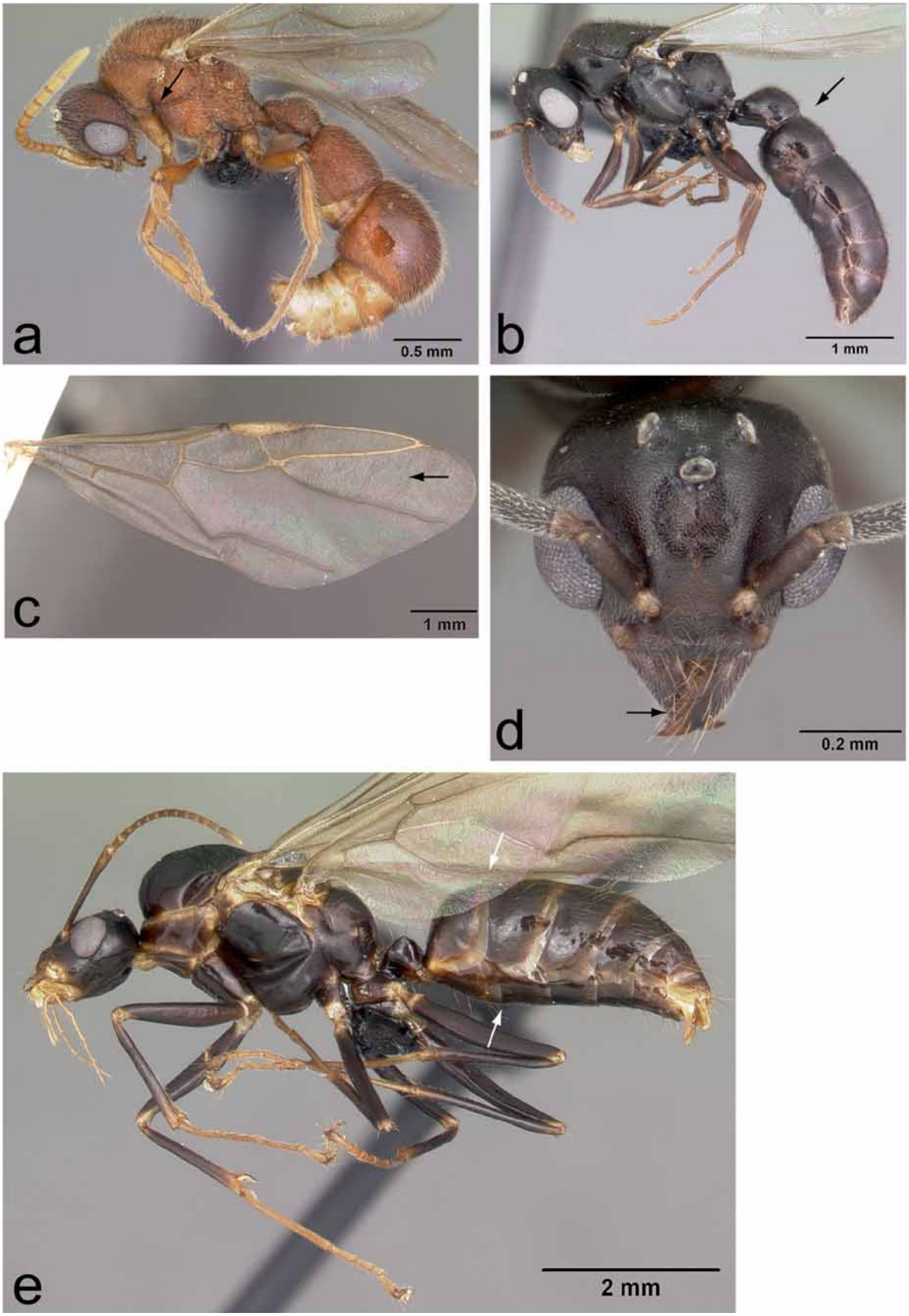

FIGURE 4. Males of Formicidae. a, *Proceratium* Mad09 (CASENT 0081854); b, *Amblyopone* Mad12 (CASENT 0080397); c, e, *Camponotus* Mad18 (CASENT 0497230); d, *Technomyrmex* Mad08 (CASENT 0049527). (a, b, e) head to abdomen in lateral view; (c), forewing; (d) head in full-face view.

Key to Subfamilies of Malagasy male ants (alate)
A few genera are divided into parts, reflecting distinct characters sets outlined in Table 1.

1. Two distinct, long, narrow spines or lobes present on apical portion of abdominal sternum IX (Fig. 3a) or, if absent, then mandibles extremely elongated, distinctly longer than head, and volsella massive, claw-shaped, directed dorsally. Pygostyles absent..... **Cerapachyinae**
- Spines or lobes absent on apical portion of abdominal sternum IX or the apical portion bilobed, with each lobe very wide (Fig. 3b). Mandibles not elongated, distinctly shorter than head. Volsella moderate, not claw-shaped, not directed dorsally. Pygostyles present or absent 2
2. Abdominal segment III much smaller than segment IV in lateral view (Fig. 3c) 3
- Abdominal segment III nearly as large as segment IV in lateral view (Fig. 3d) 4
3. Hind tibia with two spurs (Fig. 3e) ..... **Pseudomyrmecinae**
- Hind tibia with one spur or without spurs (Fig. 3f) ..... **Myrmicinae**
4. Anal region of hind wing vestigial. Oblique mesopleural furrow reaching pronotum close to its posteroventral corner (Fig. 4a)..... **Proceratiinae**
- Anal region of hind wing well developed. Oblique mesopleural furrow not reaching pronotum, its anterior termination well separated from the pronotum (Fig. 1a) 5
5. Petiole (abdominal segment II) broadly and dorsally attached to abdominal segment III; dorsal constriction between petiole and abdominal segment III very shallow or indistinct in lateral view (Fig. 4b..... ..... **Amblyoponinae**
- Petiole (abdominal segment II) narrowly and ventrally attached to abdominal segment III; dorsal constriction between petiole and abdominal segment III deep in lateral view (Fig. 6a)… 6
6. Scuto-scutellar suture usually longitudinally sculptured. Forewing clearly with cross vein 2rs-m (Fig. 1b); if vein weak then at least with vestigial branches on Radial sector and Media. Scape short, not reaching posterior margin of head in full-face view (Fig. 5c). Constriction between abdominal segments III and IV present in some cases. ..... **Ponerinae**
- Scuto-scutellar suture not longitudinally sculptured. Forewing usually without any trace of cross vein 2rs-m (Fig. 4c). Scape short (Fig. 4d) or long (Fig. 2a). Constriction between abdominal segments III and IV absent 7
7. Many minute, serrate teeth present on masticatory margin of mandible (Fig. 4d), or, if teeth absent, then scape not reaching posterior margin of head in full-face view ..... **Dolichoderinae**
- Several larger teeth present on masticatory margin of mandible (Fig. 2a). Scape long, distinctly exceeding posterior margin of head in full-face view (Fig. 2a)..... **Formicinae**

Key to Genera of Malagasy males of subfamily Ponerinae

1. Wings absent ..... ***Hypoponera*** (part 02; ergatoid males)
- Wings present..... 2
2. Mandibles stout and fully developed, masticatory margins overlap completely when mandibles fully closed. Antennal scrobe well defined (Figs. 10a, b) and extends as long as length of antennal scape. …. ..... ***Platythyrea***
- Mandibles very reduced in size and "lobate," the masticatory margins do not overlap completely when mandibles are fully closed. Antennal scrobe absent (Fig. 7e); if weakly defined, then length distinctly shorter than length of antennal scape 3
3. Pretarsal claw multidentate to pectinate (Fig. 7b) ..... ***Leptogenys***
- Pretarsal claw edentate or with at most two preapical teeth (Fig. 9e) 4
4. Hind wing with jugal lobe (Fig. 1c)..... 5

- Hind wing without jugal lobe (as in Fig. 7g) 8
5. Notauli present on mesoscutum (Fig. 9h) ..... ***Pachycondyla*** (part 02)
- Notauli absent (Fig. 9c)..... 6
6. Apical portion of abdominal tergum VIII not forming spine (Fig. 5e) ..... ***Anochetus***
- Apical portion of abdominal tergum VIII forming distinct spine (Fig. 8e) 7
7. Body usually yellow (Madagascar), rarely black (Seychelles); petiole more or less conical in frontal view, with single, narrowly rounded or sharp apex (Fig. 8b) ..... ***Odontomachus***
- Body black; petiole in frontal view with dorsal margin broadly or bluntly rounded (Fig. 9d)..... ..... ***Pachycondyla*** (part 01)
8. Apical portion of abdominal tergum VIII without down-curved spine (Fig. 6b) .. ***Hypoponera*** (part 01)
- Apical portion of abdominal tergum VIII with down-curved spine 9
9. Hind tibia with one spur (as in Fig. 6d) ..... ***Ponera***
- Hind tibia with two spurs (as in Fig. 7c)..... ***Pachycondyla*** (part 03 & 04)

TABLE 1. Character table of males of Malagasy Ponerinae. The status of each character (see list) is shown as 1, 0, or 1&0 (both states were observed) for each taxon or group. The status of the tibial spur is shown as the number of spurs. If a character could not be observed, the relevant cell is marked by "?". Asterisk (*) refers to comments that are given in the notes under the character list.

tribe	genus	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Ponerini	*Anochetus* (Fig. 5)	0	1	13	0	1	1	1?	0	0	0	1	1	2	2	0	0
	Hypoponera 01 (Fig. 6)	0	1	13	0	1	0	0	0	0	0	0	1	1	1	0	0
	Hypoponera 02 (ergatoid)	0	0	12	0	?	0	0	0	0	?	0	1	1	1	0	1
	Leptogenys 01 (Fig. 7)	0	1	13	1	1	1	0	0	0	0	0 (*3)	1	2	2	1	0
	Leptogenys 02 (Fig. 8f)	0	1	13	1	1	1	0	0	0 (*2)	0	1	1	2	2	1	0
	Leptogenys 03	0	1	13	0	1	1	0	0	0	0	0	1	2	2	1	0
	Odontomachus (Figs. 8a–e)	0	1	13	0	1	1	0	1	1	0	1	1	2	2	0	0
	Pachycondyla 01 (Figs. 9a–e)	0	1	13	0	1	1	0	0	1	0	1	1	2	2	0	0
	Pachycondyla 02 (Figs. 9f–i)	0	1	13	1	1	1	0	0	1 & 0	0	1	1	2	2	0	0
	Pachycondyla 03	0	1 (*1)	13	0	1	1	0	0	1	0	0	1	2	2	0	0
	Pachycondyla 04	0	1	13	1	1	1	0	0	1	0	0	1	2	2	0	0
	Ponera	0	1	13	?	1	?	0	0	1	0	0	?	?	1	0	0
Platy-thyreini	*Platythyrea* 01	1	0	13	1	1	1	0	0	1	0	1	1	2	2	0	0
	Platythyrea 02 (Fig. 10)	1	0	13	1	1	1	0	0	1	0	0	1	2	2	0	0

1 Antennal scrobe present (1); absent (0).
2 Mandible reduced in overall size (1); large and triangular (0).
3 Number of antennal segments.
4 Notauli are present on mesoscutum (1); absent (0).
5 Oblique mesopleural furrow reaching pronotum far away from pronotal posteroventral margin (1); close to pronotal posteroventral margin (0).
6 Epimeral lobe clearly present (1); indistinguishable (0).
7 Dorsolateral corner of petiole distinctly projecting (1): not projecting (0).
8 Dorsal margin of petiole, in frontal view, with single sharp apex (1); without single sharp apex, or rounded (0).
9 Apical margin of abdominal tergum IV strongly projecting into sharp spine (1); not strongly projecting or without spine (0).
10 Pygostyles present (0); absent (1).
11 Jugal lobe in hind wing present (1); absent (0).
12 Number of tibial spurs on front leg.
13 Number of tibial spurs on midleg.
14 Number of the tibial spurs on hind leg.
15 Claws multidentate to pectinate (1); unarmed or at most with two teeth (0).
16 Dealate (1); alate (0).

Notes

*1 In section 03 of the genus *Pachycondyla*, a species has mandibles that are somewhat triangular.
*2 In section 02 of the genus *Leptogenys*, apical margin of abdominal tergum VIII is not spinose but somewhat extended apically.
*3 In section 01 of the genus *Leptogenys*, a single species has a small jugal area, but the area is not lobed.

Diagnosis of male ants of the subfamily Ponerinae in The Malagasy region

Antenna filiform, consisting of 13 segments. Scape not reaching posterior margin of head. Oblique mesopleural furrow not reaching pronotum at its posteroventral corner. Scuto-scutellar suture usually longitudinally sculptured. Petiole attached to abdominal segment III ventrally, so that dorsal constriction between the two segments is distinct and deep. Abdominal segment III as large as segment IV. Apical portion of abdominal sternum IX not bi-spinose. Pygostyles well developed. Hind tibia with one or two spurs. Forewing with costa, subcosta, radius, radial sector, media, cubitus, and anal veins present, as are 2r-rs, 2rs-m, 1m-cu, and cu-a cross veins.

Remarks. Our key includes all seven ponerine genera recorded from the Malagasy region. Discussions of other groups in the key to subfamilies will appear in future publications. Ergatoid males are known from several genera (e.g. *Hypoponera* in Ponerinae, *Technomyrmex* in Dolichoderinae, and *Cardiocondyla* in Myrmicinae) but were excluded from this subfamily key. Ergatoid males of ponerine ants are easily distinguished by having: (1) abdominal segment III as large as segment IV; and (2) a distinct constriction between abdominal segments III and IV.

The characters used in the subfamily key are diagnostic for taxa in the Malagasy region only and might not apply to ants collected elsewhere. As in previous studies (Smith, 1943; Yoshimura & Onoyama, 2002), bi-spinose abdominal sternum IX is commonly used to separate the Cerapachyinae from other subfamilies. Bolton (2003) mentions a single species, the Neotropical *Pachycondyla crassinoda* (Latreille, 1802), having this character in the subfamily Ponerinae. We use the character of abdominal sternum IX because it is diagnostic within the Malagasy region. No known character is universally applicable to separate the males of Ponerinae, Formicinae, and Dolichoderinae. In this key, the longitudinally sculptured scuto-scutellar suture and the presence of the 2rs-m cross vein on the forewing is used to separate Ponerinae from the other two subfamilies, Formicinae and Dolichoderinae.

A few exceptions, however, exist for these character states in the region. For example, the scuto-scutellar suture in *Odontomachus coquereli* is smooth and shiny, not longitudinally sculptured. The 2rs-m cross vein on the forewing, however, is clearly present in *O. coquereli*. Outside the region, species of *Dolichoderus* have 2rs-m as illustrated in Brown & Nutting (1950: figs. 18 and 19, as the genera *Dolichoderus* and *Hypoclinea*). Some small species of *Ponera* have reduced venation (Brown & Nutting 1950). Bernard (1968) identified three dolichoderine genera—*Dolichoderus*, *Liometopum*, and *Iridomyrmex* - by the presence of 2rs-m ("two cubital cells"), and illustrated a forewing of the genus *Formica* with 2rs-m present (Bernard's figure 299).

Constriction between abdominal segments III and IV has often been used to separate Ponerinae from other subfamilies (Bernard, 1968; Collingwood, 1979; Wheeler & Wheeler, 1986; Czechowski et al., 2002). This state, represented by an exposed presclerite of the fourth segment, is also used to separate Ponerinae from Formicinae in male-based keys of Japanese ants (Yoshimura & Onoyama, 2002). Shattuck (1992) also suggests that dolichoderine males can be distinguished from ponerine males by an abdominal constriction. However, this character state is often unclear in several ponerine genera (e.g. *Hypoponera*, a part of *Pachycondyla*), including Malagasy species of these genera, and is not used in this key.

We use several regional characters to separate these three subfamilies (i.e. Ponerinae, Formicinae, and Dolichoderinae). All of the species in the subfamily Formicinae examined in this study have long antennal scapes, while those of the species in the subfamily Ponerinae are short. This difference between Ponerinae and Formicinae seems akin to that seen in European ants (Bernard, 1968). This is likely a useful character for distinguishing between the two subfamilies, but both types of scapes are found in dolichoderine genera.

Reduction in overall size of the mandible is used by Kutter (1977) to separate Ponerinae from Formicinae and Dolichoderinae. It is potentially useful in a region where only species of the tribe Ponerini are distributed. A very short clypeus, a ponerine character used by Bernard (1968), can be used for some of the genera in the tribe Ponerini.

Diagnosis of the genera of Ponerinae in the Malagasy region

All seven genera known from the Malagasy region are diagnosed in this key. Most genera are subdivided into several sections based on differences in the character states used to separate the Malagasy ponerine genera. The taxonomic significance of these sections cannot be evaluated until further species level work is done on groups that include both workers and associated males. CO1 barcode sequencing to link males to workers should be encouraged in future species level studies in Madagascar and elsewhere (B.L. Fisher and M.A. Smith, unpublished).

Characters that were used in constructing the key are listed in Table 1. The diagnostic characters used to establish the key are summarized below for each genus. However, as in the subfamilial diagnosis, several characters used in the key may not be applicable to other regions.

***Anochetus* Mayr, 1861**
(Fig. 5)

All males winged. Antennal scrobe absent. Mandible reduced. Basal cavity of the mandible extending to its front face, visible in full-face view. Notauli absent. Mesepimeron bearing distinct posterodorsal (epimeral) lobe that covers mesothoracic spiracle and forms a seemingly isolated plate. In most cases, each dorsolateral corner of petiole in anterior view with distinct projection. Dorsal margin of petiole, in anterior view, usually showing two apices. Apical margin of abdominal tergum VIII not projecting into sharp spine. Jugal lobe of hind wing present. Each middle and hind tibia with two spurs. Claws simple, not multidentate or pectinate.

Remarks. Five species are recognized in this region (B.L. Fisher and M.A. Smith, unpublished); four were examined in the present study. Species known from the Malagasy region have a distinct spine or tooth on each dorsolateral petiolar margin, and are easily separated from other genera by this character. However, males of a species (morphospecies *A.* blf-pat) from Aldabra do not have lateral teeth on the petiole. In addition, the male of a species (morphospecies *A.* blf-goo) from Madagascar is not yet known; given the morphology of workers, males might also lack lateral teeth on the petiole.

Males in the genus *Anochetus* are similar to those in *Odontomachus* and *Pachycondyla*, but can be separated from them by a combination of two characters: 1) absence of terminal spine of abdominal tergum VIII; and 2) absence of notauli on the mesoscutum.

***Hypoponera* Santschi, 1938**
(Fig. 6)

Morphological characters of wingless, ergatoid males similar to those of conspecific workers excluding genitalia. In winged males, antennal scrobe absent. Mandible reduced in size. Basal cavity of mandible extending to its front face and visible in full-face view. Notauli absent. Mesepimeron not bearing posterodorsal (epimeral) lobe. Petiole lacking dorsolateral projections. Dorsal margin of petiole, in anterior view, without a conical or pointed apex. Apical margin of abdominal tergum VIII without spine. Jugal lobe of hind wing absent. Middle and hind tibia with single spur. Claws simple, never multidentate or pectinate.

Remarks. Reduction or absence of the lobe on the mesepimeron (epimeral lobe) was found in males of only *Hypoponera* and *Ponera* in this region (Fig. 6a; Taylor, 1967). This character can be used to separate these two genera from other ponerines in the Malagasy region. To separate *Hypoponera* and *Ponera*, see remarks in the *Ponera* section. Taylor (1967) stated that the maxillary palpus had a single segment in *Hypoponera*, but males of *Hypoponera* having a two-segmented maxillary palpus were observed in the present study (Fig. 6c).

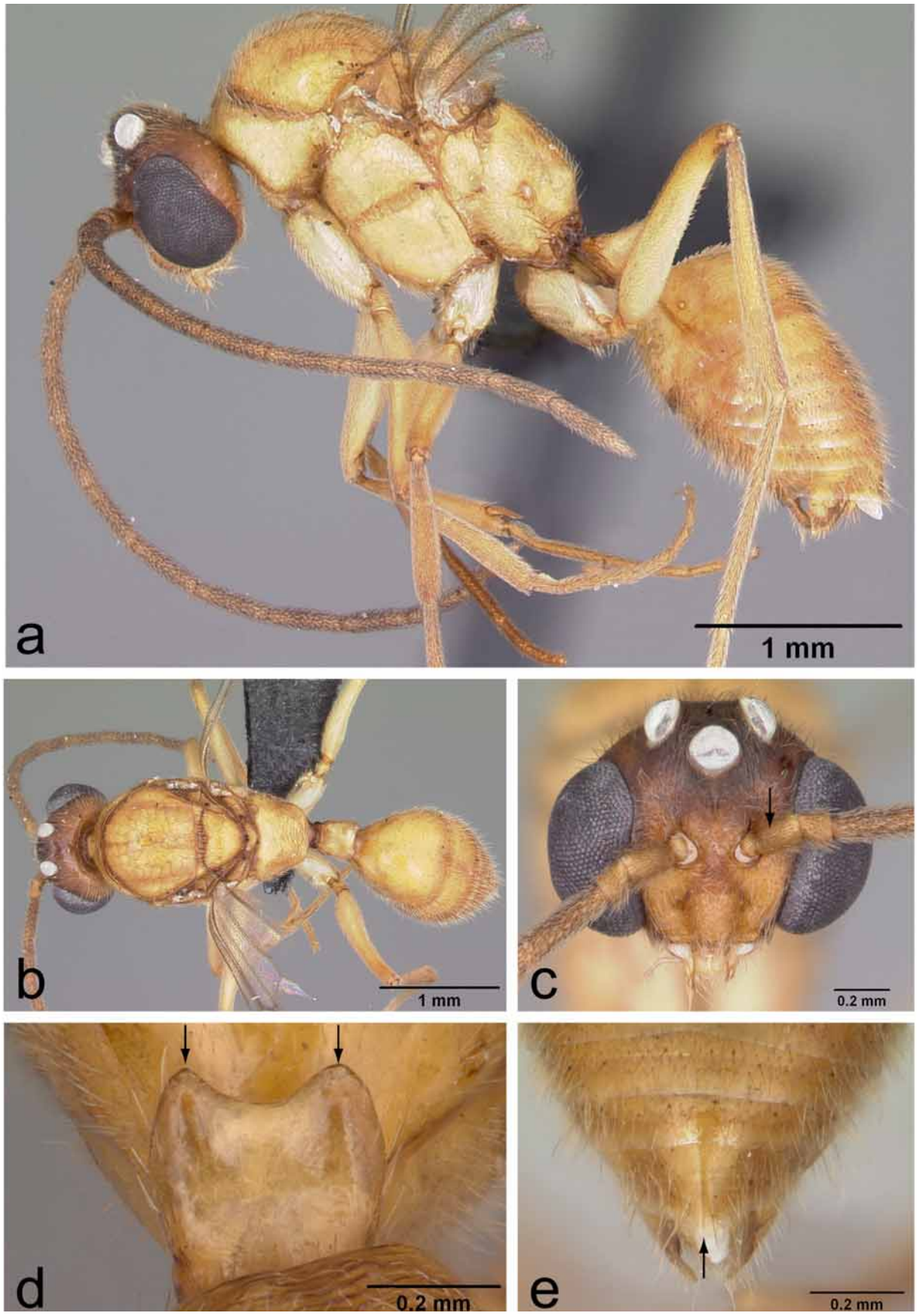

FIGURE 5. Male of *Anochetus madagascarensis* (CASENT 0442379). (a) head to abdomen in lateral view; (b) head to abdomen in dorsal view; (c) head in full-face view; (d) petiole in anterior view; (e) apical portion of the abdomen in dorsal view.

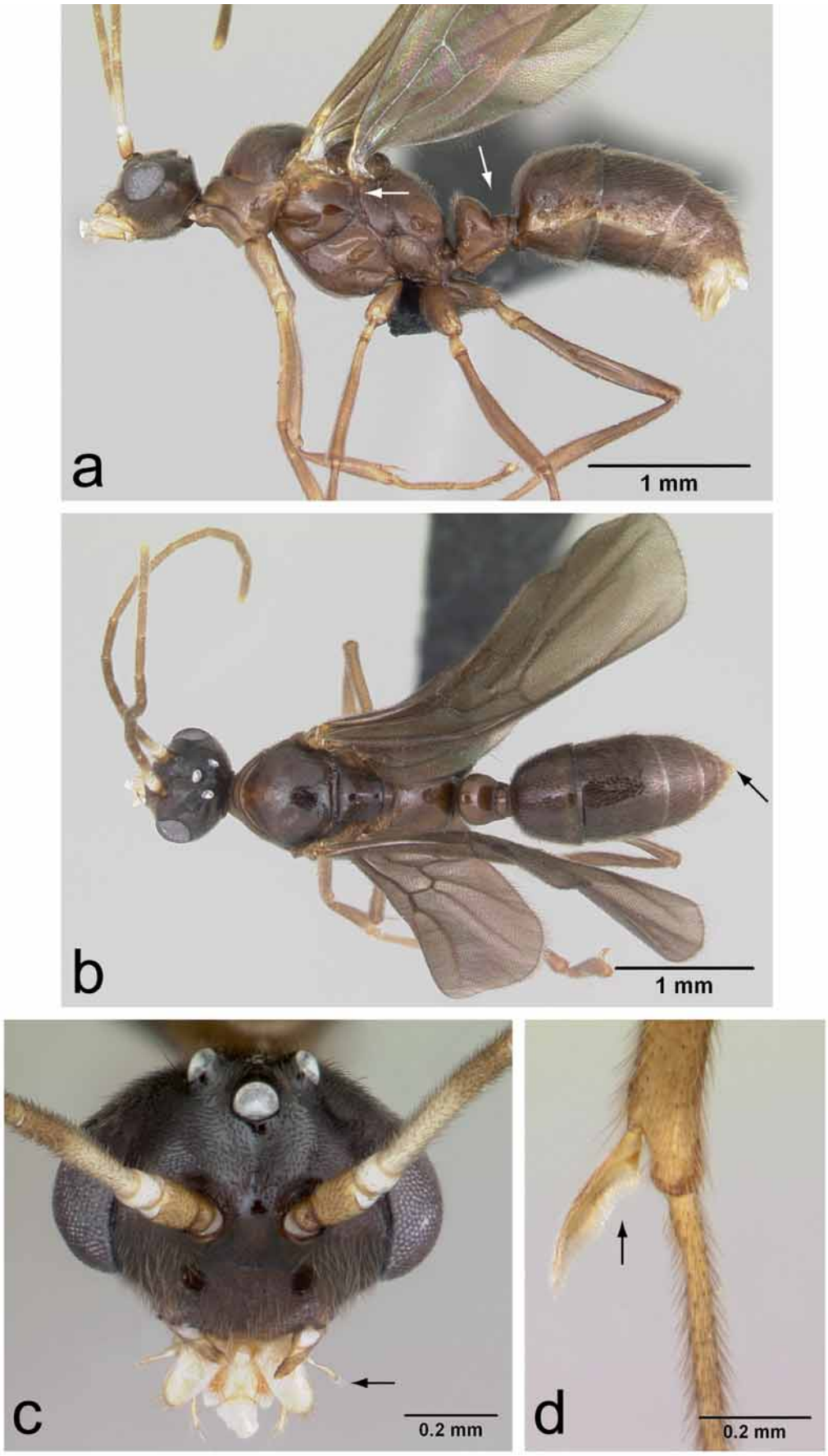

FIGURE 6. Male of *Hypoponera* Mad57 (CASENT 0430684). (a) head to abdomen in lateral view; (b) head to abdomen in dorsal view; (c) head in full-face view; (d) tibial spur on hind leg.

***Leptogenys* Roger, 1861**
(Figs. 7, 8f)

Males winged. Scrobe absent. Mandible reduced in size. Basal cavity of mandible extending to its front face and visible in full-face view. Notauli impressed on mesoscutum in most species. Mesepimeron bears distinct (epimeral) lobe posterodorsally, lobe covering mesothoracic spiracle and appearing to form isolated plate. Dorsolateral corner of petiole in anterior view without distinct projections. Dorsal margin of petiole in anterior view gently rounded, not forming a conical or pointed apex. Apical margin of abdominal tergum VIII occasionally featuring down-curved projection (Fig.8f). Jugal lobe of hind wing absent in most species. Each middle and hind tibia with two spurs. Pretarsal claw multidentate to pectinate.

Remarks. The multidentate or pectinate claws (Fig. 7b) easily separate this genus from other Malagasy ponerine males.

***Odontomachus* Latreille, 1804**
(Figs. 1, 8a–e)

Males winged. Antennal scrobe absent. Mandible reduced. Basal cavity of mandible extending to its front face and visible in full-face view. Notauli never impressed on mesoscutum. Mesepimeron bearing distinct (epimeral) lobe posterodorsally, lobe covering mesothoracic spiracle and seeming to form isolated plate. Dorsolateral corner of petiole in anterior view not projecting. Dorsal margin of petiole in anterior view more or less conical, with a narrowly rounded or pointed apex. Apical margin of abdominal tergum VIII projecting into sharp spine. Jugal lobe of hind wing present. Each middle and hind tibia with two spurs. Claws simple, never multidentate to pectinate.

Remarks. Two species are known in the Malagasy region. The males of both species are yellow to yellowish-brown. In the single species from the Seychelles (*O. simillimus*) the males are blackish. Males belonging to this genus are often similar to those in *Anochetus* and *Pachycondyla*. Characteristics separating this genus from *Anochetus* are noted in the *Anochetus* section. Characters separating it from *Pachycondyla* are: 1) petiolar apex more or less conical; 2) hind wing having a jugal lobe; 3) absence of notauli on the mesoscutum; and 4) a yellowish (rarely blackish) body color.

***Pachycondyla* Smith, F., 1858**
(Fig. 9)

Males winged. Antennal scrobe absent. Mandibles reduced in size. If triangular in form (one species) then the masticatory margins do not completely overlap each other even when fully closed. Basal cavity of mandible extends to its front face. Basal cavity visible in full-face view in species with reduced mandibles, but invisible in species with triangular mandible. Notauli not impressed on mesoscutum in large species but clearly impressed in several medium or small species. Mesepimeron bearing distinct (epimeral) lobe posterodorsally, lobe covering mesothoracic spiracle and forming a seemingly isolated plate. Dorsolateral corner of petiole in anterior view without distinct projection, usually evenly rounded. Apical margin of abdominal tergum VIII projecting strongly into sharp spine in most cases, though spine lacking in several small species. Jugal lobe of hind wing present in most but not all species. Each middle and hind tibia with two spurs. Claws simple or with one or two preapical teeth, but never multidentate or pectinate.

Remarks. This genus (sensu Bolton 1995) is now considered to be paraphyletic (P. S. Ward unpublished). In the region, the males are divided into four distinct groups (Table 1). We keep these groups separate to facilitate naming them once a new generic classification for *Pachycondyla* is developed based on molecular work.

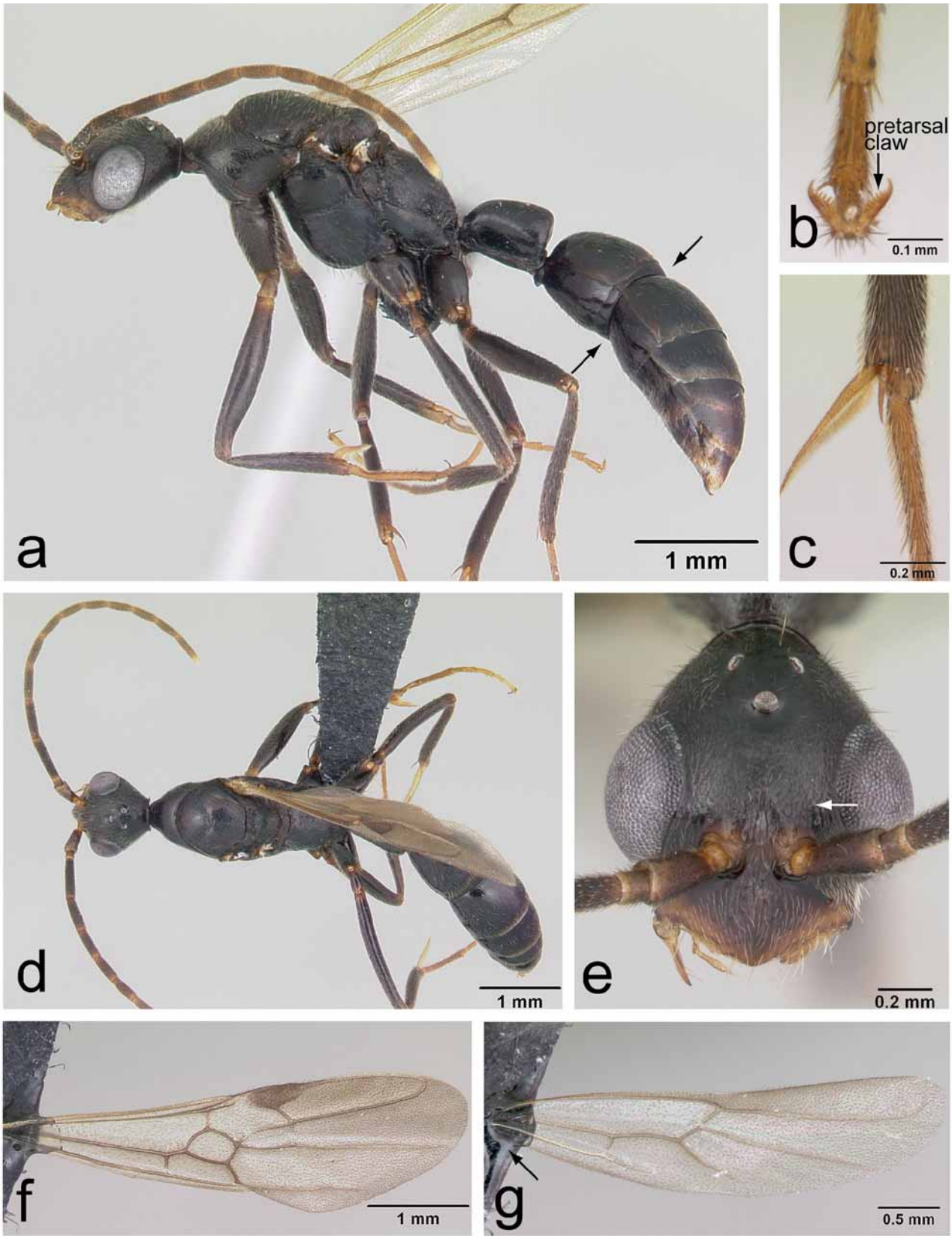

FIGURE 7. Male *Leptogenys* Mad02 (CASENT 0496777). (a) head to abdomen in profile; (b) pretarsal claw; (c) tibial spurs on hind leg; (d) head to abdomen in dorsal view; (e) head in full-face view; (f) forewing; (g) hind wing.

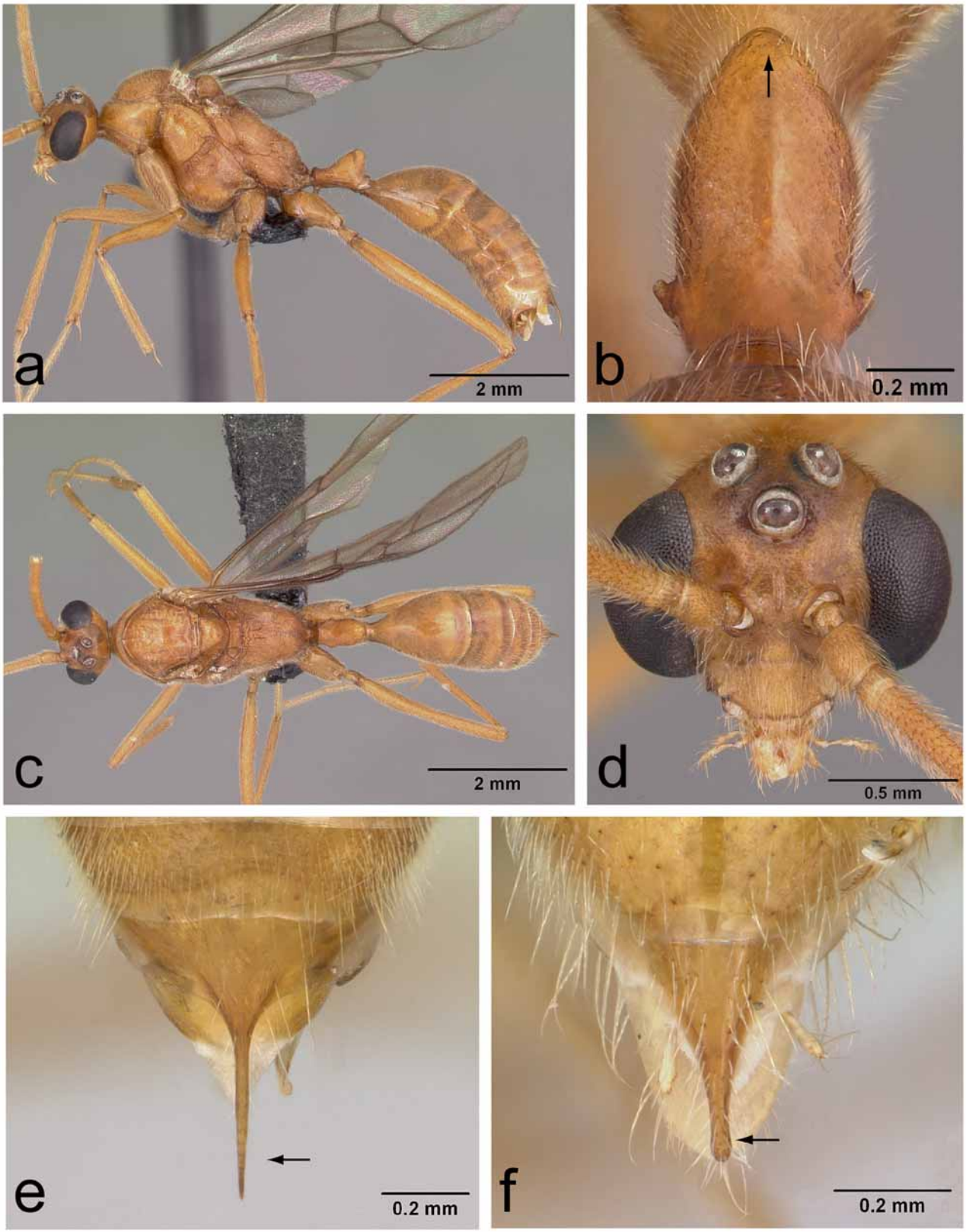

FIGURE 8. Males of Ponerinae. a–e, *Odontomachus coquereli* (CASENT 0049797). f, *Leptogenys* sp. (CASENT 0114506). (a) head to abdomen in lateral view; (b) petiole in anterior view; (c) head to abdomen in dorsal view; (d) head in full-face view; (e, f) apical portion of the abdomen in dorsal view.

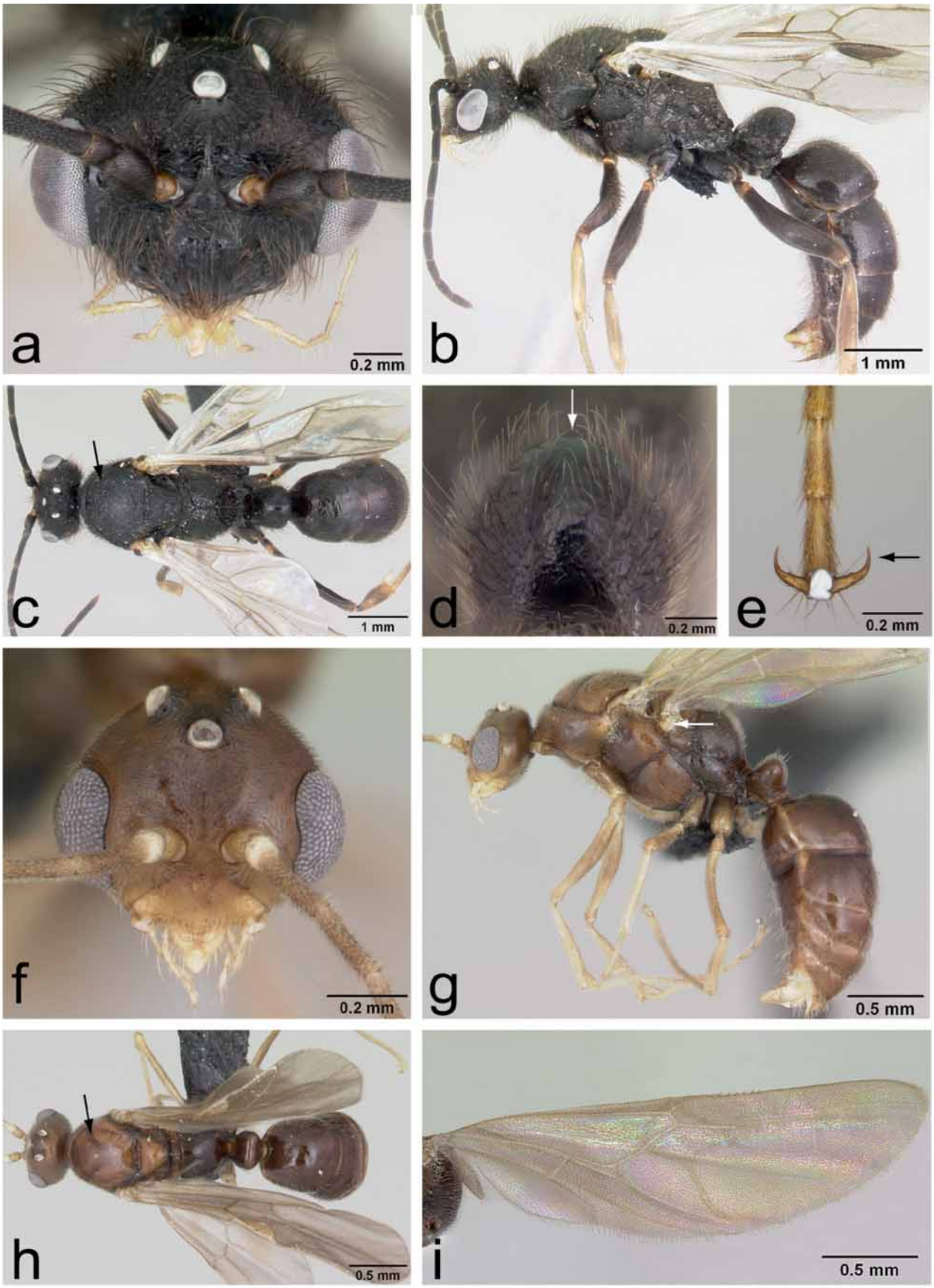

FIGURE 9. Males of *Pachycondyla*. a–e, *Pachycondyla* JCR09 (CASENT 0497079); f–i, *Pachycondyla* Mad08 (CASENT 0052325). (a, f) head in full face view; (b, g) head to abdomen in lateral view; (c, h) head to abdomen in dorsal view; (d) petiole in anterior view; (e) pretarsal claw; (i) forewing and hind wing.

Each is characterized by a combination of characters in the notauli, the terminal spine on abdominal tergum VIII, and the jugal lobe (Table 1). Section 01 consists of large, blackish-colored males (Figs. 9a–e), section 02 of small, yellowish-colored males (Figs. 9f–i), section 03 includes males having somewhat developed mandibles, and section 04 consists of reddish-colored males having a clypeus as long as males in *Leptogenys*. Several sections are similar to other genera; characters distinguishing *Pachycondyla* from those genera are given under the respective genera.

Platythyrea Roger, 1863

(Fig. 10)

Males winged. Antennal scrobe distinct. Mandible large, stout, triangular, with many teeth on its masticatory margin, and masticatory margins completely overlap when mandibles are fully closed. Basal cavity of mandible invisible in full-face view. Notauli impressed on mesoscutum. Mesepimeron bearing distinct (epimeral) lobe posterodorsally, lobe covering mesothoracic spiracle and seeming to form isolated plate. Dorsolateral corner of petiole in anterior view lacking distinct projection. Dorsal margin of petiole, in anterior view, broadly or narrowly rounded. Apical margin of abdominal tergum VIII does not project strongly into sharp spine. Jugal lobe of hind wing may or may not be present. Middle and hind tibiae with two spurs. Claws simple, never multidentate or pectinate. Body surface sparsely punctate.

Remarks. This genus is easily separated from other Malagasy ponerine males by the following combination of characters: 1) presence of the antennal scrobe; 2) large, stout, and triangular mandible; 3) two tibial spurs on each middle and hind leg; 4) large eyes; 5) sparse punctures on body surface; 6) standing pilosity sparse or absent; and 7) pruinose appearance.

Ponera Latreille, 1804

Males winged. Antennal scrobe absent. Mandible reduced in size. Basal cavity of mandible extending to its front face, visible in full-face view. Notauli absent. Mesepimeron without epimeral lobe. Each dorsolateral corner of petiole in anterior view lacking distinct projection. Dorsal margin petiole, in anterior view, without narrowly rounded or pointed apex. Apical margin of abdominal tergum VIII strongly projecting into sharp spine. Jugal lobe of hind wing absent. Middle and hind tibiae with single spur. Claws simple, never multidentate or pectinate.

Remarks. Only a single species is known from this region at present. Although the species is not rare, no males were found in material examined for this study. The above diagnosis is based on Taylor (1967). Males are similar to those in *Hypoponera*, but can be distinguished from the latter in having a distinct spine on the apical portion of abdominal tergum VIII. This character was given in Figure 10 of Taylor's revision (1967), although erroneously explained as AVII.

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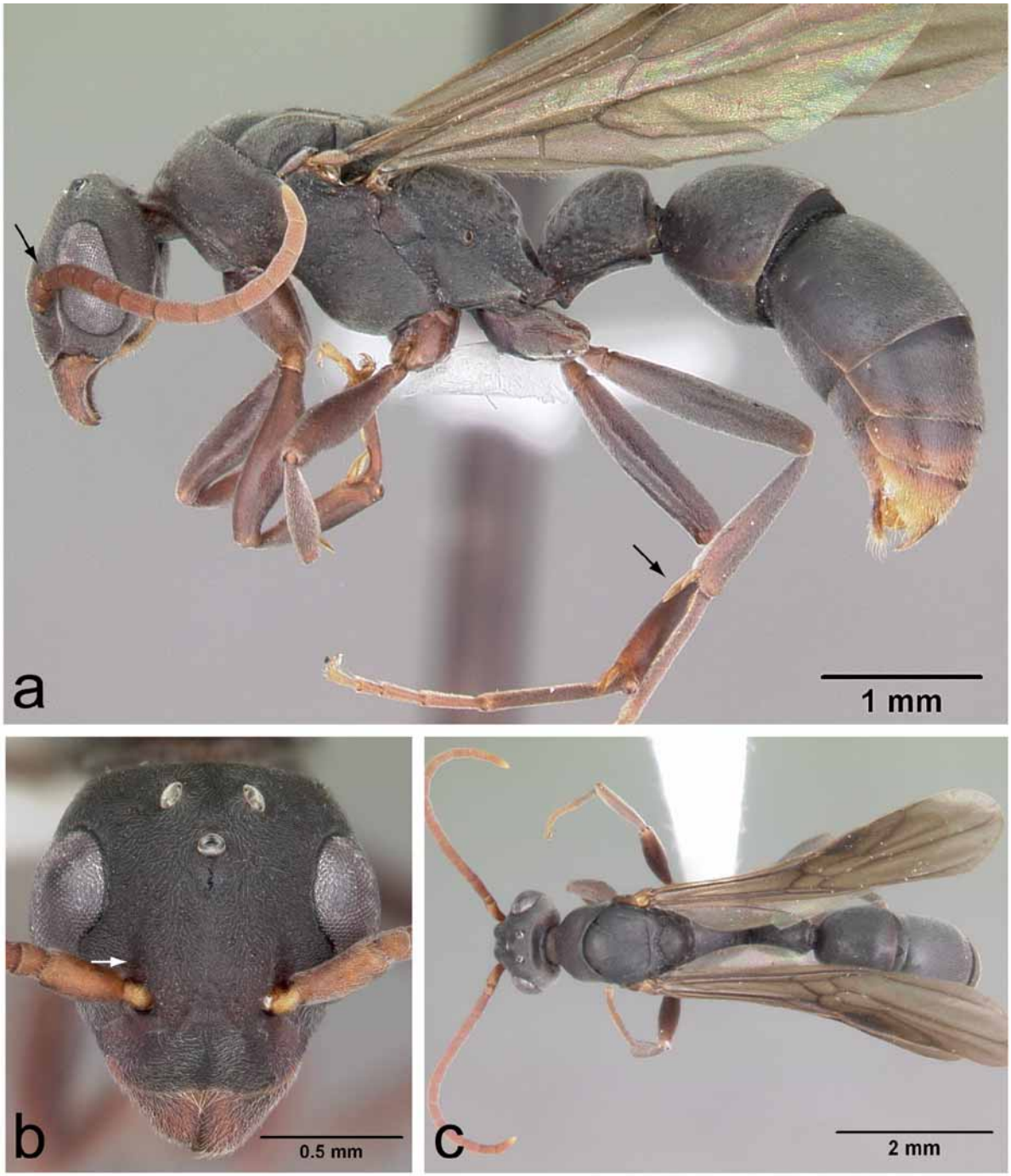

FIGURE 10. Male of *Platythyrea* Mad02 (CASENT 0442287). (a) head to abdomen in lateral view; (b) head in full-face view; (c) head to abdomen in dorsal view.

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