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

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Abstract

Keys to the males of the Dolichoderinae ant genera known from the Southwest Indian Ocean islands (Comoros, Madagascar, Mauritius, Mayotte, Reunion, and Seychelles) are provided. Diagnoses, discussion, illustrations, and a character matrix are provided for all five extant genera from the region: *Aptinoma, Ochetellus, Ravavy, Tapinoma,* and *Technomyrmex*. A male-based synopsis of the subfamily Dolichoderinae based on the five genera is also given. The previous diagnostic characters for the included genera are reconsidered. Terminologies for male genitalia and wing cells are reviewed.

Key words: Comoros, Madagascar, Mauritius, Mayotte, Reunion, Seychelles, matrix table, terminology, genitalia, wing, palp, labrum, diagnosis, key, *Aptinoma, Ochetellus, Ravavy, Tapinoma, Technomyrmex*

Introduction

Male ants can provide valuable morphological information to distinguish species, and for some groups are even more effective at distinguishing the genera or species than worker ants (Eguchi *et al.* 2006; Yoshimura *et al.* 2007, Fisher & Smith 2008, Yoshimura & Fisher 2009). The study of male characters can offer new information relevant to the phylogenetic analysis of ants. Before morphological information about males can be put to practical use, however, keys and proper diagnoses based on male characters must be developed. Such information can provide additional insights into the life history and reproduction of many species (Kaspari *et al.* 2001).

Despite the utility of such keys, few genus-level diagnoses and identification tools for male ants exist. This lack of information hinders the inclusion of males in behavioral and species-level taxonomic studies. 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 characters are therefore necessary.

This work builds on our previously published keys to male ants of the subfamilies as well as the ponerine and proceratine genera found in the Malagasy region (Yoshimura & Fisher 2007, 2009). Here we focus on the subfamily Dolichoderinae. At present, 28 extant dolichoderine genera are known worldwide, five of them in the Malagasy region.

Several studies have included descriptions of male characters found among the dolichoderine genera. Those by Shattuck (1995) and Brandão *et al.* (1999) are the most comprehensive, and provide valuable characters in the form of matrix tables. These studies build on the foundation established by Shattuck's earlier works (1992a, 1992b) which included a revised generic classification of the Dolichoderinae, generic diagnoses, and keys to genera. Before Shattuck's 1992a comprehensive synthesis, male characters of at least one of the dolichoderine genera were included in the following regional works: ants of Africa (Wheeler 1922), North America (Smith 1943), and Western and Northern Europe (Bernard 1968). Later, Yoshimura & Onoyama (2002) provided a male-based key to dolichoderine genera for Japan, and Czechowski *et al.* (2002) provided a key for Poland.

Genus-rank taxonomy in Dolichoderinae has undergone dynamic change in recent years. Since Brandão *et al.* (1999), five genera (*Aptinoma* Fisher, *Arnoldius* Dubovikoff, *Gracilidris* Wild & Cuezzo, *Nebothriomyrmex* Dubo-

vikoff, and *Ravavy* Fisher) have been described; *Chronoxenus* Santschi has been resurrected as a genus from synonymy by Dubovikoff (2005); and *Amyrmex* Kusnezov has been resurrected from synonymy and reassigned to Leptanilloidinae by Ward & Brady (2009). Male diagnoses for recently described genera in Madagascar (*Aptinoma* and *Ravavy*) were limited to the regional fauna (Fisher 2009). Further work is needed to develop global characters to diagnose these genera. In addition to the generic rank classification, Ward *et al*. (2010) proposed a new tribal system for Dolichoderinae based on molecular phylogenetic analyses. Of the five genera in the Malagasy region, *Aptinoma*, *Tapinoma*, and *Technomyrmex* were assigned to Tapinomini, *Ochetellus* was assigned to Leptomyrmecini, and *Ravavy* was assigned to Bothriomyrmecini.

Here we provide a key to males and diagnoses for all extant Malagasy dolichoderine genera. The diagnoses are based primarily on material collected in the Malagasy region. For *Ochetellus*, additional material from Japan and Hawaii was included because no male specimens from the Malagasy region were available. A matrix table summarizes the characters used in the analysis. Characters unique to each genus found in the Malagasy region are discussed. Characters used in previous studies are reconsidered.

Material and methods

This work is primarily based on material collected from arthropod surveys in Madagascar and nearby islands in the Southwest Indian Ocean. The surveys were conducted by B. Fisher and Malagasy ant researchers from the Madagascar Biodiversity Center in Antananarivo, Madagascar. These collections include more than 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 2009 (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 Syncroscopy Auto-Montage (v 5.0) software for magnifications less than 100x, and a compound microscope (Leica DM4000M), Nikon digital camera (DXm1200), and Helicon Focus version 4.10.2 software for magnifications greater than 100x. The images were edited in Adobe Photoshop and Illustrator. Each imaged specimen is uniquely identified with a specimen-level code (e.g. CASENT0003099) affixed to each pin.

The male specimens in the Malagasy Ant Collection at the California Academy of Sciences were primarily collected with Malaise traps. Some of the specimens within each dolichoderine genus were sorted to morphospecies. Morphospecies codes were applied to species not readily named. The morphospecies codes consist of a two-letter country code followed by a number; for example, *Tapinoma* mg07. Identification of a Japanese species, *Ochetellus glaber* (Mayr), was carried out based on the Japanese Ant Database Group (2008).

The male taxa listed below were studied to establish a key to genera of the subfamily. Each taxon name is followed by a letter code indicating the source of morphological information used to establish the key, and a CASENT specimen identifier indicating dissected specimens:

[p]: paratype(s)
[g]: male specimens that were collected from a colony and associated with workers. If the specimens were collected from another region, the location is shown in brackets.
[m]: male specimens that were collected alone and not associated with workers, typically in Malaise traps.

Dolichoderinae
Aptinoma Fisher
    A. mangabe Fisher [g: CASENT0175002].
Ochetellus Shattuck
    O. glaber (Mayr) [g: Japan, Hawaii: CASENT0179489].
Ravavy Fisher
    R. miafina Fisher [m: CASENT0179530].
Tapinoma Foerster
    T. melanocephalum Forel [g: CASENT0492372]; *T. subtile* Santschi [g: CASENT0179490]; *T.* mg02 [m: CASENT0179492]; *T.* mg04 [m: CASENT0081301]; *T.* mg07 [g: CASENT0179491]; *T.* mg10 [m: CASENT0179493]; *T.* mg11 [m: CASENT0179494].

Technomyrmex Mayr

> *T. albipes* (Smith, F.) [g: CASENT0189311]; *T. curiosus* Fisher & Bolton [p: CASENT0068743]; *T. difficilis* Forel [g: CASENT0179495]; *T. fisheri* Bolton [g: CASENT0179496]; *T. innocens* Fisher & Bolton [g: CASENT0179525]; *T. madecassus* Forel [m: CASENT0179526]; *T. mayri* Forel [m: CASENT0179527]; *T. pallipes* (Smith, F.) [g: CASENT0179528]; *T. vitiensis* Mann [g: CASENT0179529].

Terminology

Overall, our preference is for terms used generally in Hymenoptera over terms uniquely applied within Formicidae for homologous characters. Morphological terminology follows our previous work (Yoshimura & Fisher 2007: figs 1, 2; 2009: figs 1–21, 25–34) 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), and basimere and harpago follows Snodgrass (1957); terminology of wing venation follows Wootton (1979) and Gauld and Bolton (1988). Applications of these terms in the Dolichoderinae are illustrated in Figures 06, 11, 16–23, 29, 34, 46–62, 71, 76, 78, 80, and 8.

Ectal and mesal. We prefer the terms "ectal" (outer) and "mesal" (inner) to indicate the surface of a movable plate, especially when this plate has been dissected and removed from the body. Alternative naming systems such as ventral-dorsal and external-internal systems for indicating surfaces are less appropriate and confusing compared with the ectal-mesal system. The ventral-dorsal system is limited because it can only be applied when the plate is still attached to the body, the same term is applied to different surfaces, and mesal surfaces are not named. For example, the ectal surfaces of abdominal tergum VIII and sternum VIII are "dorsal" and "ventral," respectively. In addition, after dissection, "dorsal" is not an appropriate term for the "mesal" surface of abdominal sternum VIII. The external-internal system is not favored because "internal" is best reserved for indicating areas inside the body and not for naming surfaces of plates. Therefore, to avoid ambiguity in dissected plates, we use the terms "ectal" and "mesal."

Abdominal sternum IX (Figs 24–28). In previous studies, this sclerite is referred to as the subgenital plate (Snodgrass 1935; Ogata 1987; Shattuck 1992a, 1995; Brandão *et al*. 1999; Yoshimura & Onoyama 2002) or the hypopygium (Huber & Sharkey 1993; Serna & Mackay 2010). The subgenital plate is defined as the sternum (sternal sclerite) beneath the genital chamber (Snodgrass, 1935; Nichols, 1989), while the hypopygium is defined as the last visible sternum (Nichols, 1989). Neither of these terms, however, are homologous in males and females of the same taxon because they refer to different segments (usually VII in female ants and IX in male ants). Even within the same sex, the subgenital plate is not consistent between taxa (for example, VII in female Hymenoptera, and VIII in female Plecoptera). In general, across all insects, the subgenital plate can refer to the seventh, eighth, or ninth sternum, although usually sternum VII in females and IX in males. To avoid confusion in this matter, we prefer the term abdominal sternum IX (see also Table 1).

Pygostyles (Fig. 16). Pygostyle is used to refer to the pair of appendages on tergum X of the abdomen of male Hymenoptera. Cerci, on the other hand, should refer to appendages on abdominal tergum XI, not X (see also table 1; Yoshimura & Fisher 2007).

Genitalia (Figs 29–48). Several nomenclatural systems for genital characters in ants exist. In the present paper, we propose a set of terms that builds on comparative morphological studies of ontogeny by Snodgrass (1957). A summary of our preferred terms applied to the genitalia, including abdominal sternum IX and the pygostyle, and how they relate to terms used by previous studies, is presented in Table 1.

It is important to note that we follow the revised terminology of Snodgrass, 1957, for the definition of "paramere" and its two constituent parts, "basimere" and "harpago." Note that we also use "harpago" (pl. harpagones) rather than "telomere" to indicate the distal region of the paramere. Snodgrass revised his 1941 definition of paramere, where the term only referred to what we now call the harpago, in 1957 to include both basimere and harpago. As noted by Schulmeister (2001), this revision of the definition and conflicting hypotheses about the homology between these organs in pupal and adult stages created confusion about the use of the term. To avoid such ambiguity, it is important for studies to provide a specific reference for the terms used.

TABLE 1. Overview of terminology used to describe genitalia. References are shown for terms used in previous studies.

Author	Taxon	genital capsule	basal ring	basimere	harpago	aedeagus	basivolsella	cuspis	digitus	abdominal sternum IX	pygostyle
This study (Figs 22–48)	Formicidae			**paramere**				**volsella**			
Michener (1944)	Insecta		gonobase	gonocoxite / gonoforceps	gonostyli	penis valve		volsella			
Snodgrass (1957)	Insecta	phallus	basal ring	basimere / paramere	telomere / harpago	aedeagus		cuspis / volsella	digitus	abdominal sternum IX	
Snodgrass (1941)	Hymenoptera		basal ring / lamina annularis	basiparamere / lamina parameralis	paramere	aedeagus	basal lamina volsellaris	cuspis volsellaris	digitus volsellaris	abdominal sternum IX	pygostyle
Smith (1970)	Hymenoptera		gonobase		gonostyle			cuspis	digitus		
Gauld & Bolton (1988)	Hymenoptera		basal ring	paramere		aedeagus		cuspis	digitus	hypopygium	cerci
			gonocardo	gonosquemae		penis		distivolsella	gonolacinia	subgenital plate	pygostyle
Schulmeister (2001)	Hymenoptera	genital capsule	cupula / basal ring	gonostipes / latimere	harpe	aedeagus + valvura	basivolsella	distivolsella / cuspis	digitus	9th sternite	
Peck (1937)	Ichneumonidae		gonocardo	gonostypes / paramere	gonosquama	aedeagus	basivolsella	distivolsella	gonolacinia		
Kratochvíl (1959)	Formicidae	genitalia	basal ring	paramere	apodeme of the paramere	aedeagus	volsellar lobe	cuspis	digitus	9th sternum	
Ogata (1987)	Poneroid complex		basal ring	paramere	paramere	aedeagal plate		cuspis	digitus	subgenital plate	
Watkins (1976)	Dorylinae			stipites		sagitta	volsellae				
Birket-Smith (1981)	Dorylinae	genitalia	cupula	stipes	harpide / kleisiandes	aedeagus		cuspis / volsella	digitus		
Shattuck (1992a)	Dolichoderinae			paramere		aedeagus		cuspis / volsella	digitus	subgenital plate	pygostyle
Kempf (1956)	*Cephalotes* (as *Paracryptocerus*)		basal ring	parameral plate	paramere	penial valve	volsellar plate	cuspis	digitus	subgenital plate	
Sarna & Mackay (2010)	*Procryptocerus*		basal ring / epipygium	paramere		aedeagus		cuspis volsellaris	digitus volsellaris	hypopygium	pygostylus

We have made every effort to choose terms that are homologous among Hymenoptera. However, we agree with Berkit-Smith (1981) and Schulmeister (2001) that basimere and harpago may not be homologous even among Formicidae. Restricting the use of these terms to only homologous cases, as suggested by Schulmeister (2001), is impractical. To avoid implications of homology, we define harpago as the distal, secondarily divided region of the paramere, and the basimere as the parameral region excluding the harpago.

In addition to the terms used by Snodgrass (1957), we favor "genital capsule" from Schulmeister (2001) instead of "phallus" in Snodgrass (1957), and "basivolsella" from Peck (1937).

In Table 1, we also include terms used in a detailed morphological study of the myrmicine genus *Procryptocerus* (Serna & Mackay, 2010). However, we disagree with a number of terms used by Serna & Mackay to describe the genitalia. For example, "basal ring" is misidentified in their figures 41, 42, and 43, and "epipygium" is misidentified in figure 38. In their figures 41 and 43 the true basal ring consists of a short, ring-shaped sclerite basal to the basimere, but not the paired sclerite they indicate. The structure labeled as the epipygium in their figure 38 is actually the basimere. In addition, their table 1 does not include abdominal segments IX, X, and genitalia in the proposed naming system of the ant metasoma. For example, they define the posterior metasoma as including only abdominal segment III to pygidium (abdominal segment VIII in males). This should be revised to include the last abdominal parts, which would include segments IX, X and genitalia in males.

Venation and cells on the wings (Figs 49–61). We use veins, not cells, to describe wing characters and discuss the homology of wing characters between dolichoderines and genera in other subfamilies (see Table 2 for comparison of cell terminology). Closed cells on the wings are not necessarily formed by homologous veins. For example, the submarginal cells in *Discothyrea* and *Proceratium* are not homologous (Yoshimura & Fisher 2009: figs 2 and 5): in *Discothyrea*, the cell is formed by the subcosta, Radial sector, Rs+M, and 2r-rs (i.e. submarginal 1: see Fig. 49), while in *Proceratium*, the submarginal cell is formed by the subcosta, Radial sector, Media, 2r-rs, and 2rs-m (i.e. submarginal 1+2: see Fig. 49).

TABLE 2. Wing cell terminology. References are shown for terms used in previous studies. The current study does not consider wing cells and argues for the adoption of the use of veins in morphological studies.

Gauld & Bolton (1988)	costal+ sub-costal	submarginal 1	submarginal 2	submarginal 3	submarginal 4	marginal 1	marginal 2
		parastigmal 1+2					
Bingham (1903)	costal	radial				radial	
Hölldobler & Wilson (1990)	costal	1st submarginal	2nd submarginal			marginal	
Shattuck (1992a, 1995); Brandão *et al.* (1999)		cubital	cubital			radial	
Huber & Sharkey (1993)	costal+subcostal	1st radial 1+2nd radial 1	radial sector	1st radial sector 2	2nd radial sector 2	3d radial 1	radial sector 1
Sarna & Mackay (2010)	costal	submarginal 1				submarginal 2	

continued.

Gauld & Bolton (1988)	basal	discal 1	discal 2	discal 3	subbasal	subdiscal	
Bingham (1903)	medial				submedial	submedial	
Hölldobler & Wilson (1990)	median	1st discoidal			submedian	2nd discoidal	
Shattuck (1992a, 1995); Brandão *et al.* (1999)		1st discoidal					
Huber & Sharkey (1993)	radial	1st discoidal	2nd medial	3d medial	1st cubital	2nd cubital	3d cubital
Sarna & Mackay (2010)	basal radial	discal 1			subbasal cubital	discal 2	

The names of cells and veins have also been misleadingly interpreted due to homonymy or misidentification. For example, the cubital cells in Shattuck (1992, 1995) and Huber & Sharkey (1993) are considered homonyms (see Table 2); and in Serna & Mackay (2010: fig. 46), marginal cell 1, subdiscal cell, 2r-rs, and radial sector (Rs) are misidentified as submarginal cell 2 (SMC2), discal cell 2 (DC2), radiosectorial 1 (Rs1), and radiosectorial 2 (Rs2), respectively.

In previous studies of Dolichoderinae, the number of closed cells on the fore- and hindwings were commonly used to highlight differences between taxa (as in Shattuck 1992a, 1995; Brandão *et al*. 1999; and Lucky & Ward 2010). The focus on cells, however, diverted attention away from careful comparative studies of venation patterns. As Brown & Nutting (1950) write, "The lack of attention to the veins themselves has warped and hindered the entire approach to the subject." Furthermore, the names applied to wing cells are inconsistent even within Hymenoptera (see the cubital cell in Table 2).

In the present study, the homology of each vein across taxa was determined based on comparative studies of taxa with well-developed veins, such as species in the ponerine genus *Odontomachus* (Figs 49, 55). Terms used to define veins follow the recommendation of Wootton (1979) and Gauld and Bolton (1988). Names of veins and cells are summarized in Figures 49–61, and terms used in previous studies are shown in Table 2.

Results

Diagnosis of males of the subfamily Dolichoderinae in the Malagasy region

Males alate or ergatoid. Scape extending beyond posterior margin of head less than half of the scape length or not reaching this margin (Figs 1–5: see each genus for more detail). Mesopleural oblique furrow reaching anterior margin of mesopleuron at posteroventral corner of pronotum or far ventrally from corner (Figs 6–10). Notauli absent (Figs 11–15). Scuto-scutellar suture simple. Single, well-developed spur present on pro-, meso-, and metatibia. Petiole attached to abdominal segment III ventrally, so that dorsal apex of petiolar node much lower than dorsal margin of abdominal segments III in lateral view. Abdominal segment III larger than or same size as segment IV (Figs 6–10). No constriction present between abdominal segments III and IV. Posterior portion of abdominal sternum IX bilobed or broadly spatulate, but never bispinose. Pygostyles present in the Malagasy region (Fig. 16) but present or absent elsewhere. Basimere extremely well-developed across basal half of paramere and distinctly differentiated from harpago, which is restricted to distal portion of paramere (Figs 34–38). Volsella directed ventrally, sometimes spinose, but never stout and claw-shaped nor extended dorsally.

Venation on forewing varies. Radius (R), Sc+R, radial sector (Rs), cubitus (Cu), anal (A), 2r-rs, and cu-a present in all genera. Media (M) often vestigial between Rs+M and 2rs-m (Figs 50–54). 2rs-m often vestigial or continuous with media. On hindwing, R+Rs and anal present. Radius and media apical to rs-m absent. M+Cu, cubitus, 1rs-m, and cu-a variable. Clavus moderate in size, and jugum absent (Figs 56–61).

Remarks. The above combination of characters separates the subfamily Dolichoderinae from the six other subfamilies known from the Malagasy region. In the Malagasy region, Dolichoderinae differ from Amblyoponinae in having a lower attachment of the petiole to abdominal segment III; from Cerapachyinae in lacking a bispinose abdominal sternum IX (Figs 24–28) and in having a moderate volsella; from Formicinae in having the basimere entirely developed across the basal half of the paramere (Figs 34–40; as discussed below), and in having either a short antennal scape not reaching the posterior margin of the head (Figs 1–5) or many serrate denticles on the masticatory margin of the mandible (Figs 72, 75, 76); from Myrmicinae and Pseudomyrmecinae in having a slightly reduced or same-sized abdominal segment III compared with IV (abdominal segment III is much reduced compared with IV in Myrmicinae and Pseudomyrmecinae); from Ponerinae in lacking the media apical to rs-m on the hindwing, in having a simple scuto-scutellar suture lacking longitudinal sculpture, and in having a basimere much expanded relative to the harpago; and from Proceratiinae in lacking a constriction between abdominal segments III and IV (Figs 6–10). These subfamily differences are summarized in the male-based key to Malagasy subfamilies (Yoshimura & Fisher 2007).

Here we provide a key and diagnoses for alate males only. Ergatoid males, however, have been reported in *Technomyrmex* in Dolichoderinae, *Hypoponera* in Ponerinae, and *Cardiocondyla* in Myrmicinae. The ergatoid males of *Technomyrmex* are easily separated from the males of the latter two taxa by the absence of a constriction between abdominal segments III and IV.

No single character has been proposed to universally distinguish dolichoderine males from formicine males. Here we propose a new character, the shape of the basimere, to distinguish the two subfamilies. The basimere in dolichoderine males is extremely well-developed across the entire basal half of the paramere, and notably differentiated from the harpago in shape. In some cases (e.g. *Tapinoma*) the suture dividing them is unclear. In these cases their shapes clearly define their boundaries, with the harpago visibly restricted to the distal portion of the paramere (Figs 34–38). In formicine males, by contrast, the harpago visibly extends to the base of the paramere on the ventral side (Fig. 39). Thus the basimere does not fully occupy the entire base of the paramere. This difference between the subfamilies has been tested with material from Madagascar, but further studies are needed with material from other biogeographic regions to evaluate whether this difference applies worldwide.

In addition to the new character above, dolichoderine males can be separated from formicine males in the Malagasy region by a combination of two characters. First, all males in Formicinae have a long antennal scape which exceeds the posterior margin of the head, while dolichoderine males, other than in *Tapinoma*, have a short antennal scape which does not reach the margin (Figs 1–3, 5). Second, the masticatory margin of the mandible in *Tapinoma* is covered with many serrate denticles (Fig. 75), while no formicine male has such a series of serrate denticles.

Ponerinae can easily be separated from Dolichoderinae in most cases by the presence of the media on the hindwing (Fig. 55). Although the media is vestigial in a small number of *Hypoponera* males, in these species the scuto-scutellar suture is sculptured longitudinally as in Yoshimura & Onoyama (2002: fig. 23). Dolichoderine males in the Malagasy region have neither the media on the hindwing nor longitudinal sculpture on the scuto-scutellar suture. In addition, the form of the basimere is a useful character to distinguish males of the two subfamilies. The basimere in dolichoderine males is extremely well-developed and differentiated in shape from the harpago (Figs 34–38), while that in ponerine males is moderate and poorly differentiated from the harpago so that the separation between them is not recognizable (Fig. 40). This difference in the parameral character was used for a key to genera in Krafchick (1959) to distinguish between Dolichoderinae and Ponerinae. Krafchick discussed the terminology of the male genitalia and his terms were included in Table 1. Unfortunately, this study is only available as a Ph.D. thesis; none of the data have been published. In addition to the differences listed above, ponerine males other than *Ponera* and *Hypoponera* have two metatibial spurs, while all dolichoderine males have a single metatibial spur.

In addition to the Dolichoderinae, other taxa described or illustrated with a clear division between the basimere and harpago occur in Ecitoninae (Snodgrass 1941; Krafchick 1959), Formicinae (Snodgrass 1941), Myrmeciinae (Ward & Brady 2003), and Myrmicinae (Snodgrass 1941; Krafchick 1959; Serna & Mackay 2010). However, the homology of their "harpago" remains questionable.

The presence or absence of pygostyles appears consistent within genera of the Dolichoderinae. Pygostyles were observed in all dolichoderine genera occurring in the Malagasy region. However, according to Shattuck (1992a, 1995) and Brandão *et al*. (1999), pygostyles are not present in all dolichoderine genera. Therefore, the usability of this character as a diagnostic character at the subfamily level depends on the region of study.

Some dolichoderine species have an acute tip on the digitus of the volsella. However, in all dolichoderine males that have an acute tip it is moderate in size and directed ventrally, never stout and claw-shaped nor directed dorsally as in some males of Cerapachyinae.

Key to genera of males of Dolichoderinae in the Malagasy region

This key, based on the character matrix in Table 3, may not apply outside of the Malagasy region, as variations in genus-level characters elsewhere have not been fully explored. Distinctions between two globally distributed genera, *Tapinoma* and *Technomyrmex*, are mentioned separately in the remarks for *Tapinoma*.

1.   In ventral view, harpago greatly expanded mesally, forming a distinct and more or less flat ventral face (Fig. 22) . . . .
. . . . *Technomyrmex*
-     In ventral view, harpago narrow, without a distinct ventral face (Figs 23) 2
2.   Distal portion of abdominal sternum IX broadly spatulate (Fig. 24) . . . . *Aptinoma*
-     Distal portion of abdominal sternum IX bilobed with central margin deeply or shallowly concave (Figs 25–27) 3
3.   Masticatory margin of mandible wholly covered with many serrate denticles (Fig. 75) . . . . *Tapinoma*
-     Masticatory margin of mandible with one to several large teeth, not wholly covered with many serrate denticles (Figs 73, 74) .
. . . . 4
4.   Mandible broadly spatulate, with a single long, acute tooth present on distal apex of mandible (Fig. 74). Petiole narrowly attached to abdominal segment III (Fig. 19). Basal portion of aedeagus with narrow ventral lobe (Figs 36, 41) . . . . *Ravavy*

-	Mandible triangular, with several stout teeth present on masticatory margin (Fig. 73). Petiole broadly attached to abdominal segment III (Fig. 18). Basal portion of aedeagus without ventral lobe (Figs 34, 43) . . . . *Ochetellus*

TABLE 3. Character matrix for males of Malagasy Dolichoderinae. For the 28 characters which seem useful for distinguishing among dolichoderine genera, character states are shown as 0, 1, 2; as ?, for status difficult to judge; or 0/1, if both states 0 and 1 were observed for each genus. Number of species in which the character states were observed is given in parentheses following the character state. Character states have been confirmed by direct observation or by dissection.

1.	Medial hypostoma absent (1); present (0)
2.	Mandible broadly spatulate with long, acute tooth on its distal-most potion (1); mandible triangular (0)
3.	Basal angle of the mandible indistinct (1); distinct (0)
4.	Basal margin of the mandible wholly covered with serrate denticles (2); partially covered with a smooth basal part (1); does not have any denticles and smooth (0)
5.	Serrate teeth present on masticatory margin of mandible (1); no such teeth on margin (0)
6.	Palpal formula 6,3 (1); 6,4 (0)
7.	Concavity on apical portion of the labrum reduced so that the longest setae are located far out from the apices of the lobes (1); concavity not reduced so that the longest setae are located near the apices of the lobes (0)
8.	Scape longer than flagellar segments 1+2 and exceeds posterior margin of the head in full-face view (2); longer than flagellar segments 1+2 but not exceeding posterior margin of the head (1); shorter than flagellar segments 1+2 (0)
9.	Pedicel barrel-shaped (1); conical (0)
10.	First flagellar segment bent laterally (1); straight (0)
11.	Axillae medially compressed (1); not compressed medially, anterior and posterior margins roughly parallel (0)
12.	Petiole expanded laterally and widened dorsally (1); not unusually expanded (0)
13.	Petiolar scale strongly inclined anteriorly (1); vertical (0)
14.	Petiole broadly attached to abdominal segment III (1); narrowly attached (0)
15.	Abdominal segment III projected anteriorly (2); vertical (1); elongate posteriorly (0)
16.	Abdominal segment III with a groove or indentation on its anterior face (1); without a groove or indentation (0)
17.	Pygostyles absent (1); present (0)
18.	Distal portion of abdominal sternum IX broadly spatulate (1); bilobed (0)
19.	Apicoventral portion of basimere with a process (1); without process (0)
20.	Ventral portion of the harpago expanded mesally forming a flat ventral face (1); narrows and without an expanded ventral face (0)
21.	Harpago separated from the basimere by a membranous region (1); entire and without membranous region (0)
22.	Basoventral portion of the aedeagus with a narrow, large lobe (1); without lobe (0)
23.	On the forewing, media between Rs+M and 2rs-m completely absent (1); at least partially present (0)
24.	On the forewing, 1m-cu absent (1); present (0)
25.	On the hindwing, M+Cu absent (1); present (0)
26.	On the hindwing, 1rs-m+M absent (1); present (0)
27.	On the hindwing, free section of the cubitus absent (1); present (0)
28.	On the hindwing, cu-a absent (1); present (0)

Genus/Character	1	2	3	4	5	6	7	8	9	10
Aptinoma	0(1)	0(1)	1(1)	2(1)	1(1)	1(1)	1(1)	0(1)	0(1)	0(1)
Ochetellus	0(1)	0(1)	1(1)	0(1)	0(1)	0(1)	0(1)	0(1)	1(1)	0(1)
Ravavy	1(1)	1(1)	0?(1)	0(1)	0(1)	1(1)	0(1)	0(1)	0(1)	1(1)
Tapinoma	0(7)	0(7)	1(7)	1(7)	1(7)	0(6)/1(1)	0(7)	2(4)/1(3)	0(7)	0(7)
Technomyrmex	0(9)	0(9)	1(9)	2(9)	1(9)	0(9)	1(8)/?(1)	0(9)	0(9)	0(9)

continued.

Genus/Character	11	12	13	14	15	16	17	18	19
Aptinoma	1(1)	0(1)	0(1)	0(1)	1(1)	1(1)	0(1)	1(1)	1(1)
Ochetellus	0(1)	1(1)	0(1)	1(1)	1(1)	0(1)	0(1)	0(1)	0(1)
Ravavy	0(1)	0(1)	0(1)	0(1)	1(1)	1(1)	0(1)	0(1)	0(1)
Tapinoma	1(6)/?(1)	0(6)/1(1)	1(7)	0(7)	2(6)/1(1)	1(7)	0(7)	0(7)	1(7)
Technomyrmex	1(9)	0(9)	1(9)	0(9)	2(9)	1(9)	0(9)	0(9)	0(8)

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continued.

Genus/Character	20	21	22	23	24	25	26	27	28
Aptinoma	0(1)	1(1)	0(1)	0(1)	0(1)	0(1)	1(1)	1(1)	0(1)
Ochetellus	0(1)	1(1)	0(1)	1(1)	0(1)	0(1)	0(1)	0(1)	0(1)
Ravavy	0(1)	0(1)	1(1)	1(1)	0(1)	0(1)	0(1)	1(1)	0(1)
Tapinoma	0(7)	0(2)/1(5)	0(7)	1(7)	0(1)/1(6)	0(7)	0(5)/1(2)	0(5)/1(2)	0(6)/1(1)
Technomyrmex	1(9)	0(9)	0(9)	0(9)	0(6)/1(3)	1(9)	1(9)	1(9)	1(9)

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

Diagnostic characters uniquely observed in each genus are given in italics.

Aptinoma Fisher, 2009
(Figs 2, 7, 11, 16, 17, 24, 30, 35, 42, 50, 56, 62, 67, 72, 77)

With characters of Dolichoderinae. All known males alate. Median hypostoma present (Fig. 62). Mandible triangular, but its basal angle indistinct. Basal and masticatory margins of mandible wholly covered with many serrate denticles (Fig. 72). Apical tooth on masticatory margin longer than subapical one. Palpal formula 6,3 (one specimen of *A. mangabe* dissected: Fig. 77). Third maxillary palpal segment nearly as long as fourth. Labrum not bilobed, with single distal apex and concavity on its distal margin absent (Fig. 67). Antennal scape excluding its basal condyle shorter than length of flagellar segments 1+2 (Fig. 2). Pedicel conical. First and second flagellar segments straight. Axillae on mesonotum medially compressed, anterior and posterior margins not parallel. Petiolar node raised vertically, its anterior margin nearly as long as the posterior margin in lateral view (Fig. 7). Node not much expanded laterally. Petiole narrowly attached to abdominal segment III. Anterior surface of abdominal segment III with indentation that fits posterior surface of petiolar node. Pygostyles present.

Distal portion of abdominal sternum IX broadly spatulate (Fig. 24). Apicoventral portion of basimere with spine-like projection (Fig. 30). Harpago moderate in size, and widely separated from basimere by membranous region (Figs 30, 35). Harpago narrow in ventral view, without a distinct ventral face (as in Fig. 23). Basal portion of aedeagus without any distinct ventral lobe (Fig. 42). Ventral margin of aedeagus with denticles.

Forewing not extremely elongate apical to wing stigma, its radial sector reaches costal margin, media and 2rs-m recognizable apical to Rs+M, and 1m-cu present (Fig. 50). On hindwing, M+Cu, free sections of radial sector and cubitus almost vestigial, and cu-a weak but still present (Fig. 56).

Remarks. Genus *Aptinoma* is endemic to Madagascar and only males of *Aptinoma mangabe* are presently known. Fisher (2009) proposed the combination of a shorter scape compared with flagellomeres 1+2, a palpal formula of 6,3, and a raised petiolar node as a diagnostic set of characters for *Aptinoma* in the Malagasy region. Here we propose a character unique to *Aptinoma* that consistently separates this genus from the other genera and provide additional characters to separate *Aptinoma* from the other Malagasy dolichoderine genera.

Males of *Aptinoma* are distinguished easily from other Malagasy dolichoderine genera by an abdominal sternum IX which is distally broadly spatulate (Fig. 24). This character is so far globally unique to *Aptinoma*. In the Malagasy region, *Technomyrmex* and *Tapinoma* are superficially the most similar to *Aptinoma*. *Aptinoma* and *Technomyrmex* share the following unique characters: basal margin of the mandible wholly covered with serrate denticles and the concavity on the distal margin of the labrum reduced (Figs 72, 76). *Aptinoma* and *Tapinoma* share a unique projection on the apicoventral portion of the basimere (Figs 29, 30). The petiolar node in *Aptinoma* rises almost vertically, although the sternum is thickened posteriorly and the whole shape of the petiole seems to decline anteriorly (Figs 7, 17). Therefore, the petiolar node in *Aptinoma* is best described as vertical, not as declining anteriorly as described in Fisher (2009).

The phylogenetic analysis of Ward *et al*. (2010) gives the intra-tribal relationship of Tapinomini as (((*Aptinoma* + *Tapinoma*) + *Liometopum* Mayr) + (*Axinidris* Weber + *Technomyrmex*)). They propose two hypotheses for the evolution of the "highly reduced petiole" seen in *Aptinoma*, *Tapinoma*, and *Technomyrmex*. The question is

whether the petiole evolved once at the root of Tapinomini or at least twice at the roots of (*Aptinoma + Tapinoma*) and *Technomyrmex* independently. If we limit the discussion to males, the present result, a vertical petiolar node in *Aptinoma*, supports the theory that an anteriorly-declined and reduced petiolar node evolved independently in *Tapinoma* and *Technomyrmex*, and that there has been no reversal in *Aptinoma*, *Axinidris*, and *Liometopum*.

Additional discussion of characters is included in the remarks for *Ochetellus*.

Ochetellus Shattuck, 1992
(Figs 1, 8, 12, 18, 20, 25, 31, 34, 43, 46, 51, 57, 63, 68, 73, 78)

With characters of Dolichoderinae. All known males alate. Median hypostoma present (Fig. 63). Mandible triangular, but its basal angle indistinct. Basal margin of mandible without denticles and smooth, and masticatory margin with several stout teeth and minute denticles (Fig. 73). Apical tooth on masticatory margin longer than subapical one. Palpal formula 6,4 (one specimen of *O. glaber* from Japan was dissected: Fig. 78). Third maxillary palpal segment longer than fourth, but shorter than combined length of fourth and fifth. Distal margin of labrum widely concave and bilobed, with longest setae located near apices of lobes (Fig. 68). Scape excluding its basal condyle shorter than length of flagellar segments 1+2 (Fig. 1). *Pedicel barrel-shaped*. Lateral margins of first flagellar segment slightly convex, and those of second segment straight. Axillae not medially compressed, anterior and posterior margins roughly parallel. Petiolar node raised vertically, its anterior margin as long as posterior margin in lateral view. Node strongly expanded laterally so that its posterior attachment conceals anterior portion of abdominal segment III in dorsal view. *Petiole broadly attached to abdominal segment III* (Fig. 18). *Anterior surface of abdominal segment III without indentation* (Fig. 20). Pygostyles present.

Distal portion of abdominal sternum IX bilobed, its distal margin widely concave (Fig. 25). Apicoventral portion of basimere without projection (Fig. 31). Harpago moderate in size, widely separated from basimere by membranous region, narrow in lateral view, without distinct ventral face (as in Fig. 23). Basal portion of aedeagus does not bear distinct ventral lobe (Fig. 43). Ventral margin of aedeagus with denticles.

Forewing not extremely elongate apical to wing stigma, its radial sector reaches costal margin (Fig. 51), media absent apical to 1m-cu, short branch of 2rs-m recognizable, and 1m-cu present. On hindwing, M+Cu and 1rs-m+M present, free sections of radial sector and cubitus vestigial, cu-a present (Fig. 57), clavus larger.

Remarks. Only males of *Ochetellus glaber* collected in Japan and Hawaii were available. Males of *Ochetellus* are distinguished easily from those of the four other Malagasy dolichoderine genera by a barrel-shaped pedicel (not narrowed basally), a laterally expanded petiole broadly attached to abdominal segment III (Fig. 18), and lack of an indentation on the anterior surface of abdominal segment III (Fig. 20). A laterally expanded petiole is found in one species of *Tapinoma* (*Tapinoma* mg11); however, its attachment with the third abdominal segment is narrow. The basal margin of the mandible is completely smooth; the only Malagasy dolichoderine genera that lack dentition on the basal margin are *Ochetellus* (Fig. 73) and *Ravavy* (Fig. 74). The posterior margin of mesoscutum is notched, but this character is also found in a species of *Tapinoma* (*Tapinoma* mg10).

Several of the present results for *Ochetellus glaber* disagree with those in previous studies. In this study, a median notch was observed on the posterior margin of the medial hypostoma (Fig. 63), while *Ochetellus* has been assigned by Shattuck (1992a) to a group having the hypostomal margin entire. The third maxillary palpal segment is longer than the fourth but shorter than the fourth plus fifth, while in Shattuck (1992a), *Ochetellus* has been assigned to a group with the third segment equal in length to the fourth. Abdominal segment III rises vertically in *Ochetellus glaber*, although this character has been regarded as elongate posteriorly in Shattuck (1995) and Brandão *et al.* (1999). The distal margin of the ninth abdominal sternum is concave (Fig. 25), while the margin in Shattuck (1992a, 1995) and Brandão *et al.* (1999) is regarded as entire and flat. The cuspis on the volsella is present (Fig. 46), but is recorded as absent in Shattuck (1992a, 1995) and Brandão *et al.* (1999).

Shattuck (1992a, 1995) and Brandão *et al.* (1999) proposed many male diagnostic characters to distinguish and analyze the relationships among dolichoderine genera. A number of the characters they provide are useful and have been included in the present study. However, some are more useful for recognizing species than genera. The anteromedial margin of the clypeus, inner margin of the compound eye, relative length of the third maxillary palpal segment compared with the fourth, relative length of the first flagellar segment compared with its width, the degree to which the petiole is concealed by abdominal segment III in dorsal view, and the presence of the cuspis varied considerably even within a single genus. The variation seen for the above characters is shown in Table 4.

TABLE 4. Character matrix for males of Malagasy Dolichoderinae. Intra-generic variations were observed in these characters, making them useful for distinguishing among species rather than genera. For the six characters, character states are shown as 0, 1, 2; as ?, for states difficult to judge; or 0/1, if both states 0 and 1 were observed for each genus. Number of species in which the character states were observed is given in parentheses following character state. Character states have been confirmed by direct observation or by dissection.

1. Anteromedial margin of the clypeus is never notched or concave (0); broadly and shallowly concave (1); distinctly notched medially (2)
2.   Inner margin of the eye in full-face view convex (2); concave (1); flat (0)
3. The third maxillary palpal segment is shorter than the fourth (0); equal with the fourth (1); longer than the fourth (2)
4. The first flagellar segment is three or more times as long as broad (2); less than three times but more than twice as long as broad (1); twice or less long as broad (0)
5. Indentation of abdominal segment III completely conceals the petiole in dorsal view (1); conceals only base of the petiole (0)
6. Cuspis of the volsella is absent (1); present (0)

Genus/Character	1	2	3	4	5	6
Aptinoma	1(1)	0(1)	1(1)	0(1)	0(1)	0(1)
Ochetellus	0(1)	0(1)	2(1)	0(1)	0(1)	0(1)
Ravavy	1(1)	0(1)	2(1)	2(1)	0(1)	1(1)
Tapinoma	0(1)/1(6)	0(4)/1(2)/?(1)	0(1)/1(4)/2(2)	0(1)/1(2)/2(4)	1(5)/?(2)	0(4)/1(3)
Technomyrmex	0(3)/1(6)	0(1)/1(7)/2(1)	0(1)/1(8)	0(4)/1(4)/2(1)	0(1)/1(3)/?(5)	0(8)/1(1)

Some character states proposed in Shattuck (1992a, 1995) and Brandão *et al*. (1999) were identical among all Malagasy genera examined in the present study and as a result are omitted from the character matrix (Tables 3, 4). In all of the material examined, the following character states were shared across genera: (1) the posterior margin of the clypeus is located anterior to the line drawn through posterior-most points of the antennal condyles; (2) the anterior clypeal setae are short and do not reach the anterior margin of the mandible; (3) the axillae fuse into a single horizontal plate in most cases without any longitudinal suture dividing them; (4) the pygostyle is present; (5) the digitus of the volsella has a down-curved tip; (6) the ventral margin of the aedeagal plate is dentate; (7) the pterostigma is developed without a "pterostigmal appendage" (Wheeler 1934: fig. 2); and (8) the radial sector in the forewing reaches the costal margin. In addition, we omitted a character for the location of posterior clypeal margin relative to the antennal condyle because no dolichoderine genus in the Malagasy region was distinguished by this character. The value of these characters to separate Malagasy genera from those in other regions was not assessed.

Some diagnostic characters proposed by Shattuck (1992a, 1995) were omitted from the character matrix because they proved difficult to score. The omitted characters include: concavity of the declivity of the propodeum, presence of a petiolar scale, angle of petiolar dorsum, development of the subpetiolar process, and size of the harpago. For example, the dorsal and declivitous margins of the propodeum are often completely continuous and without any divisions and landmarks between them, although only *Ravavy miafina* has a much longer dorsal margin. In addition, the "ventral lobe of the volsella" (sensu Shattuck 1992a) was not included because it could not be recognized.

In most males examined, we observed a process in the buccal cavity near the base of the mandible that projected inward. However, it was difficult to judge whether this process is the "anterior hypostomal flange" proposed by Shattuck (1992a, 1995). One species that clearly lacks this process is *Ravavy miafina*, while others seemed to have at least a weak process. Ward *et al*. (2010) included the lack of the process as part of their diagnosis of the tribe Leptomyrmecini. However, *Ravavy* also lacks this process and is a member of the tribe Bothriomyrmecini. In contrast, *Ochetellus*, which has this process, is a member of the Leptomyrmecini. Therefore, the hypostomal process is not always a useful character to diagnose the Leptomyrmecini.

Ravavy **Fisher, 2009**
(Figs 3, 6, 13, 19, 21, 26, 32, 36, 41, 52, 58, 64, 69, 74, 79)

With characters of Dolichoderinae. All known males alate. *Median hypostoma absent* (Fig. 64). *Mandible broadly spatulate* (Fig. 74). Basal angle of mandible distinct, basal margin lacking teeth and denticles. *Distal apex of mandible with single, long, acute tooth*. Palpal formula 6,3 (one specimen of *R. miafina* dissected: Fig. 79). Third maxillary palpal segment longer than fourth, but shorter than the combined length of fourth and fifth. Distal margin of labrum deeply concave and bilobed, longest setae located near apices of lobes (Fig. 69). Scape excluding its basal condyle shorter than length of flagellar segments 1+2 (Fig. 3). Pedicel conical. *First and second flagellar segments slightly bent*. Axillae weakly compressed medially, anterior and posterior margins not parallel. Petiolar node raised vertically, its anterior margin nearly as long as posterior margin in lateral view, not much expanded laterally. Petiole narrowly attached to abdominal segment III (Fig. 19). Anterior surface of abdominal segment III with indentation that fits posterior surface of petiolar node (Fig. 21). Pygostyles present.

Distal portion of abdominal sternum IX bilobed, its distal margin widely concave (Fig. 26). Apicoventral portion of basimere without projection (Fig. 32). Harpago moderate in size, visibly distinct but not separated from basimere by a membranous region. Harpago narrow in lateral view, without distinct ventral face (as in Fig. 23). *Basoventral portion of aedeagus with long and narrow lobe ventrally* (Figs 36, 41). Ventral margin of aedeagus with denticles.

Forewing elongated apical to wing stigma, its radial sector (Rs) reaches costal margin (Fig. 52), media between Rs+M and 2rs-m unrecognizable, 2rs-m reduced in length, and 1m-cu present. On hindwing, M+Cu, 1rs-m+M, and free section of radial sector present, free section of cubitus vestigial, cu-a present (Fig. 58).

Remarks. Genus *Ravavy* is endemic to Madagascar and males of *Ravavy* are known only for *R. miafina*. These males are distinguished easily from those of the four other Malagasy dolichoderine genera by the absence of the median hypostoma (Fig. 64), a broadly spatulate mandible with a long and acute tooth on its distal apex (Fig. 74), lack of serrate and minute denticles on the masticatory margin of the mandible, the first flagellomere slightly bent, dorsal margin of the propodeum in lateral view much longer than its declivitous margin (Fig. 6) (see also remarks of *Ochetellus*), the presence of a long and narrow basoventral lobe on the aedeagus (Figs 36, 41), and the forewing elongate apical to the stigma (Fig. 52). Ward *et al*. (2010) listed a lacking or reduced median hypostoma as a tribal diagnosis of Bothriomyrmecini, to which *Ravavy* belongs.

The genus *Ravavy* was described by Fisher (2009). Although the mandible character proposed by Fisher (2009) distinguishes this genus from all other dolichoderines, our current study allows a more comprehensive comparison of additional characters with genera that do not occur in Madagascar. We offer the following revised and expanded analysis of diagnostic characters. Fisher (2009) proposed the elongate basal margin and reduced masticatory margin of the mandible as unique to *Ravavy*; however, outside of Madagascar, those two characters can also be seen in a figure of a male *Forelius* in Shattuck (1992a: fig. 78). The shape of the mandible in *Ravavy* is better described as broadly spatulate, with a single acute tooth on its apex. The acute tooth is not necessarily the apical tooth, because several vestigial denticles can be seen distal to it (Fig. 74). The attachment between the petiole and abdominal segment III is best described as narrow, since the width is relatively small compared with that in *Ochetellus* (Fig. 18); the broad attachment between the petiole and abdominal segment III is a unique character of *Ochetellus*. Though described as absent in the original description (Fisher, 2009), a reexamination of fresh material revealed that an indentation on the anterior face of abdominal segment III is present in *Ravavy* (Fig. 21). The lack of this indentation in the males examined is limited to *Ochetellus* (see also *Ochetellus*) (Fig. 20).

A male of *Leptomyrmex* Mayr in Shattuck (1992a: figs 100, 101) may appear superficially similar to a *Ravavy* male due to its long head, long mesosoma, and non-triangular mandible. Based on descriptions of males of *Leptomyrmex* provided in previous studies (Wheeler 1934; Shattuck 1992a, 1995; Brandão *et al*. 1999; and Lucky & Ward 2010), these two genera differ in the following characters: the medial hypostoma is lacking in *Ravavy* (Fig. 64), while present in *Leptomyrmex*; palpal formula is 6,3 in *Ravavy* (Fig. 79), while 6,4 in *Leptomyrmex*; the mandible has only one or two vestigial denticles in addition to a long tooth in *Ravavy* (Fig. 74), while it has many serrate denticles in *Leptomyrmex*; axillae are present in *Ravavy*, while absent in *Leptomyrmex*; an indentation is present on the third abdominal segment in *Ravavy* (Fig. 21), while no indentation or groove is found on the segment in *Leptomyrmex*; posterior margin of abdominal sternum IX is concave in *Ravavy* (Fig. 26), while convex to entire in *Leptomyrmex*; the pterostigma is developed as usual without a "pterostigmal appendage" (Wheeler 1934:

fig. 2) in *Ravavy*, while the pterostigma is reduced in size and the "pterostigmal appendage" is developed in most macro-*Leptomyrmex*.

Additional discussion of characters is included in the remarks for *Ochetellus*.

Tapinoma Foerster 1805
(Figs 4, 9, 14, 23, 27, 29, 37, 44, 47, 53, 59, 60, 65, 70, 75, 80)

With characters of Dolichoderinae. All known males alate. Medial hypostoma present (Fig. 65). Mandible triangular, but its basal angle indistinct. Basal margin of mandible partially covered with serrate denticles and with smooth margin on its basal portion (Fig. 75). Masticatory margin of mandible wholly covered with serrate denticles. Apical tooth on masticatory margin longer than subapical one. Palpal formula 6,4 or 6,3 (one specimen each of seven species and morphospecies dissected: Fig. 80: Table 3). Length of third maxillary palpal segment varies from shorter to longer than fourth. Distal margin of labrum deeply concave and bilobed, longest setae located near apices of lobes (Fig. 70). Scape excluding basal condyle longer than flagellar segments 1+2 (Fig. 4). Pedicel conical. First and second flagellar segments straight. Axillae medially compressed, anterior and posterior margins not parallel. Petiolar node strongly inclined anteriorly, its anterior margin much shorter than posterior margin in lateral view. Node not much expanded laterally in most cases. Petiole narrowly attached to abdominal segment III. Anterior surface of abdominal segment III with indentation that fits posterior surface of petiolar node. Pygostyles present.

Distal portion of abdominal sternum IX bilobed, its distal margin widely or narrowly concave (Fig. 27). Apicoventral portion of basimere with projection (Fig. 29). Harpago moderate in size, separated from basimere by membranous region or a suture, and narrow in ventral view without ventral face (Fig. 23). Basal portion of aedeagus without distinct ventral lobe (Fig. 44). Ventral margin of aedeagus with denticles.

Forewing not extremely elongated apical to wing stigma, radial sector reaches costal margin (Fig. 53), media absent between Rs+M and 2rs-m, and 1m-cu absent in most cases. On hindwing, M+Cu present, 1rs-m+M, free sections of radial sector and cubitus, and cu-a present or absent (Figs 59, 60).

Remarks. Males of seven species (some of them morphospecies) were examined. Males of *Tapinoma* are distinguished easily from those of the four other Malagasy genera by an antennal scape which is longer than flagellomeres 1+2, and basal margin of the mandible partially covered with serrate denticles with a smooth basal portion (Fig. 75). In addition to these unique characters, an anteriorly inclined petiolar node is found only in *Tapinoma* and *Technomyrmex* and an apicoventral process of the basimere is found only in *Tapinoma* (Fig. 29) and *Aptinoma* (Fig. 30).

The following is a summary of the characters in Table 3 that distinguish between *Tapinoma* and *Technomyrmex*: basal margin of the mandible (character 4), apical portion of the labrum (character 7), relative length of the antennal scape (character 8), a process on the basimere (character 19), shape of the harpago (character 20), media on the forewing (character 23), and M+Cu on the hindwing (character 23). These differences hold up even though *Technomyrmex* is listed as having multiple states for the labrum (characters 7), and *Tapinoma* with a polymorphism for the scape (character 8). The ambiguity in *Technomyrmex* is due to an inability to dissect a paratype of *Technomyrmex curiosus*. Though *Tapinoma* is polymorphic in scape length, it never overlaps with the status observed in *Technomyrmex*.

A reduction of wing venation is observed in two species: *T. subtile* (Fig. 60) and *T.* mg07. The hindwings of both species are much narrower than the other males of *Tapinoma* in the Malagasy region, and 1rs-m+M, free sections of radial sector and cubitus, and also cu-a are weak or absent. In all other species in the Malagasy region, these veins are distinct (as in Fig. 59).

Several of the present results for *Tapinoma* disagree with those in previous studies. A median notch on the anterior margin of the median hypostoma is found in all male *Tapinoma* (Fig. 65) save *T. subtile*, while the margin in Shattuck (1992a) is regarded as entire. The inner margin of the eye in full-face view is concave in several species, while in Shattuck (1992a) the margin is regarded as flat. Palpal formula is 6,3 in a small species, *Tapinoma subtile* (Fig. 80), while the formula of *Tapinoma* in Shattuck (1992a, 1995) and Brandão *et al.* (1999) is regarded as 6,4. Relative length of the third maxillary palpal segment compared with the fourth varies from shorter than to longer than the third (See Table 4). Basal margin of the mandible is partially covered with serrate denticles with a smooth portion on its base (Fig. 75), while the margin in Shattuck (1992a, 1995) and Brandão *et al.* (1999) is

recorded as wholly smooth. The length of the antennal scape is longer than that of flagellomeres 1+2 in all males of *Tapinoma* examined, but in some the scapes do not reach the posterior margin of the head in full-face view (as in Fig. 4); by contrast, both Shattuck (1992a, 1995) and Brandão *et al.* (1999) regarded the scape in *Tapinoma* as exceeding the posterior margin of the head. The relative length of the first flagellomere compared with its width varies from less than 1.5 times to more than three times (See Table 4), while the length in Shattuck (1992a) is regarded as less than two times. Posterior margin of the mesoscutum is notched medially in one species (*T.* mg10), while the character of the margin in Shattuck (1992a, 1995) and Brandão *et al.* (1999) is regarded as entire. A laterally expanded petiole can be seen in a male *Tapinoma* (*T.* mg11), although its dorsum is blunter than that in *Ochetellus*. Abdominal segment III does not always cover the petiole completely by overhanging anteriorly and seems to be nearly vertical in one male (*T.* mg11), although the segment of *Tapinoma* in Shattuck (1995) and Brandão *et al.* (1999) is regarded as overhanging the petiole, so that the petiole is invisible in dorsal view. The harpago is not separated from the basimere by a membranous region in two species of *Tapinoma* (*T.* mg02 and *T.* mg11) in the Malagasy region (Fig. 29), while this character of *Tapinoma* in Shattuck (1992a, 1995) and Brandão *et al.* (1999) is regarded as divided into two parts separated by a membranous region. The cuspis on the volsella can be found in four (*T. melanocephalum*, *T.* mg04, *T.* mg10, and *T.* mg11 as in Fig. 47) out of seven Malagasy species, while this character is regarded as absent in *Tapinoma* by Shattuck (1992a, 1995).

Additional discussion of characters is included in the remarks for *Ochetellus*.

Technomyrmex Mayr, 1872
(Figs 5, 10, 15, 22, 28, 33, 38, 45, 48, 54, 61, 66, 71, 76, 81)

With characters of Dolichoderinae. Ergatoid males known, but all males in Malagasy region alate. Medial hypostoma present (Fig. 66). Mandible triangular, but its basal angle indistinct. Basal margin and masticatory margin of mandible wholly covered with serrate denticles (Fig. 76). Apical tooth on masticatory margin longer than subapical one. Palpal formula 6,4 (one specimen of each of eight species dissected: Fig. 81). Third maxillary palpal segment shorter than or as long as fourth. Concavity on distal margin of labrum absent in most cases; when visible, it is much reduced in size and longest setae located distant from apices of lobes (Fig. 71). Scape excluding its basal condyle shorter than length of flagellar segments 1+2. Pedicel conical (Fig. 5). First and second flagellar segments straight. Axillae medially compressed, anterior and posterior margins not parallel. Petiolar node strongly inclined anteriorly, its anterior margin much shorter than posterior margin in lateral view, not much expanded laterally. Petiole narrowly attached to abdominal segment III. Anterior surface of abdominal segment III with indentation that fits posterior surface of petiolar node. Pygostyles present.

Distal portion of abdominal sternum IX bilobed, its distal margin widely concave (Fig. 28). Apicoventral portion of basimere without projection. Harpago moderate in size, separated from basimere only by suture, without membranous region between them (Figs 33, 38)*, expanded mesally in ventral view, forming distinct and more or less flat ventral face* (Fig. 22). Basal portion of aedeagus does not bear distinct ventral lobe (Fig. 45).

Forewing not extremely elongated apical to wing stigma, its radial sector reaches to costal margin (Fig. 54), media partially absent between Rs+M and 2rs-m, and 1m-cu absent in many cases. On hindwing, *M+Cu absent*, M+1m-cu, free sections of radial sector and cubitus, and cu-a absent (Fig. 61).

Remarks. Males of nine species were examined. They are distinguished easily from those of the four other Malagasy dolichoderine genera by the ventral portion of the harpago, which is expanded mesally to form a ventral face (Fig. 22), and the absence of M+Cu on the hindwing (Fig. 61). *Technomyrmex* and *Aptinoma* uniquely share the following characters: the basal margin of the mandible is wholly covered with serrate denticles (Fig. 76) and the concavity on the distal margin of the labrum is reduced (Fig. 71). In *Technomyrmex* and *Tapinoma* the petiolar node is inclined. The central notch of the labrum is reduced in size or absent, although it is still visible in several males of *Technomyrmex*. When the notch is visible in *Technomyrmex*, the longest setae on the labrum are located distant from the apices of the lobes formed by the central notch, while in the other dolichoderine genera with bilobed labrum, the setae are mostly located on the apex of each lobe (Figs 68–70).

Several of the present results for *Technomyrmex* disagree with previous studies. A median notch or groove on the anterior margin of the median hypostoma is found in all males of *Technomyrmex* (Fig. 66), while the margin in Shattuck (1992a) is regarded as entire. The inner margin of the eye in full-face view is slightly concave in most

species, while in Shattuck (1992a) the margin is regarded as flat. The anteromedial margin of the clypeus is not concave in several species (*T. difficilis*, *T. fisheri*, and *T. innocens*); the margin of *Technomyrmex* in Shattuck (1992a, 1995) and Brandão *et al.* (1999) is treated as broadly concave. The relative length of the first flagellomere compared with its width varies from less than two times to three times (see Table 4), while the length in Shattuck (1992a) is regarded as less than two times. Abdominal segment III does not always cover the petiole completely by overhanging it anteriorly in *Technomyrmex* (e.g. *T. mayri*), although this segment in *Technomyrmex* in Shattuck (1992a, 1995) is regarded as overhanging the petiole so that the latter is invisible in dorsal view. The cuspis on the volsella is absent in one species (*T. madecassus*: Fig. 48), while regarded as present in *Technomyrmex* by Shattuck (1992a, 1995).

Additional discussion of characters is included in the remarks for *Ochetellus*.

Acknowledgments

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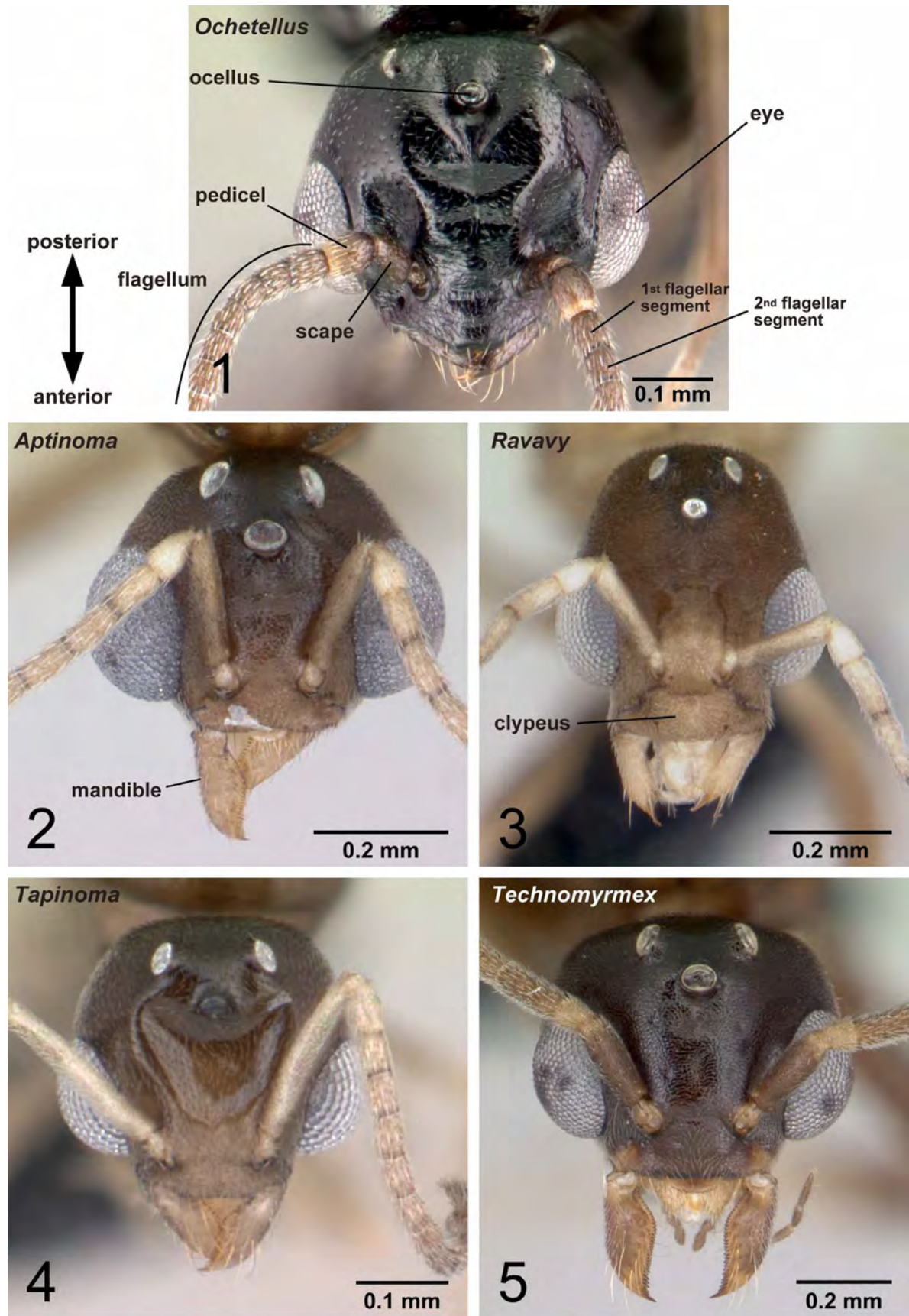
FIGURES 1–5. Head of dolichoderine males in full-face view. 1, *Ochetellus glaber* (CASENT0191065); 2, *Aptinoma mangabe* (CASENT0173594); 3, *Ravavy miafina* (CASENT0474633); 4, *Tapinoma subtile* (CASENT0136850); 5, *Technomyrmex difficilis* (CASENT0049968).
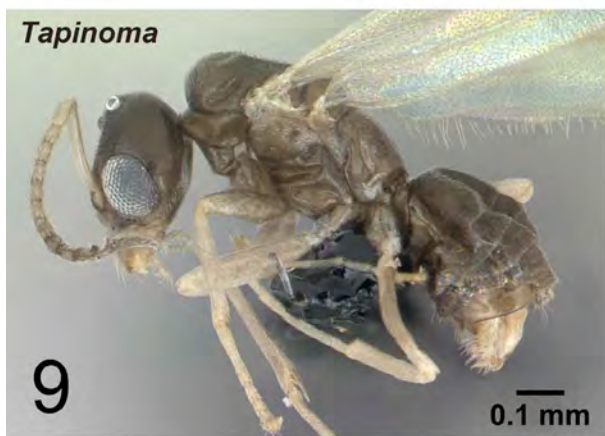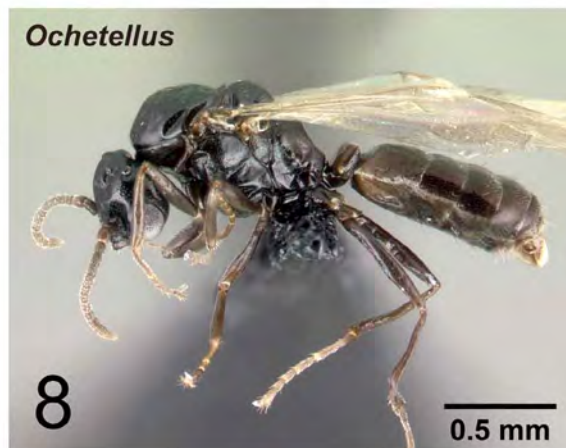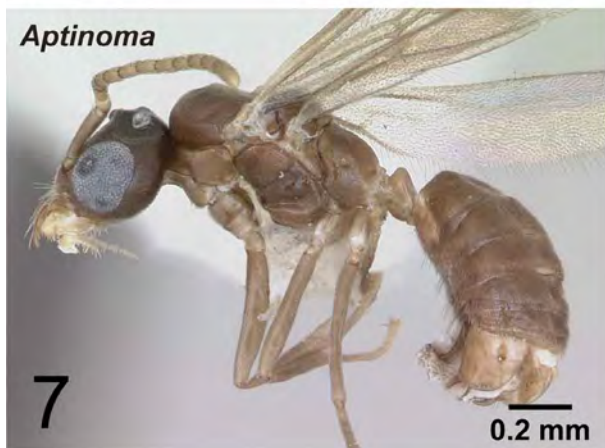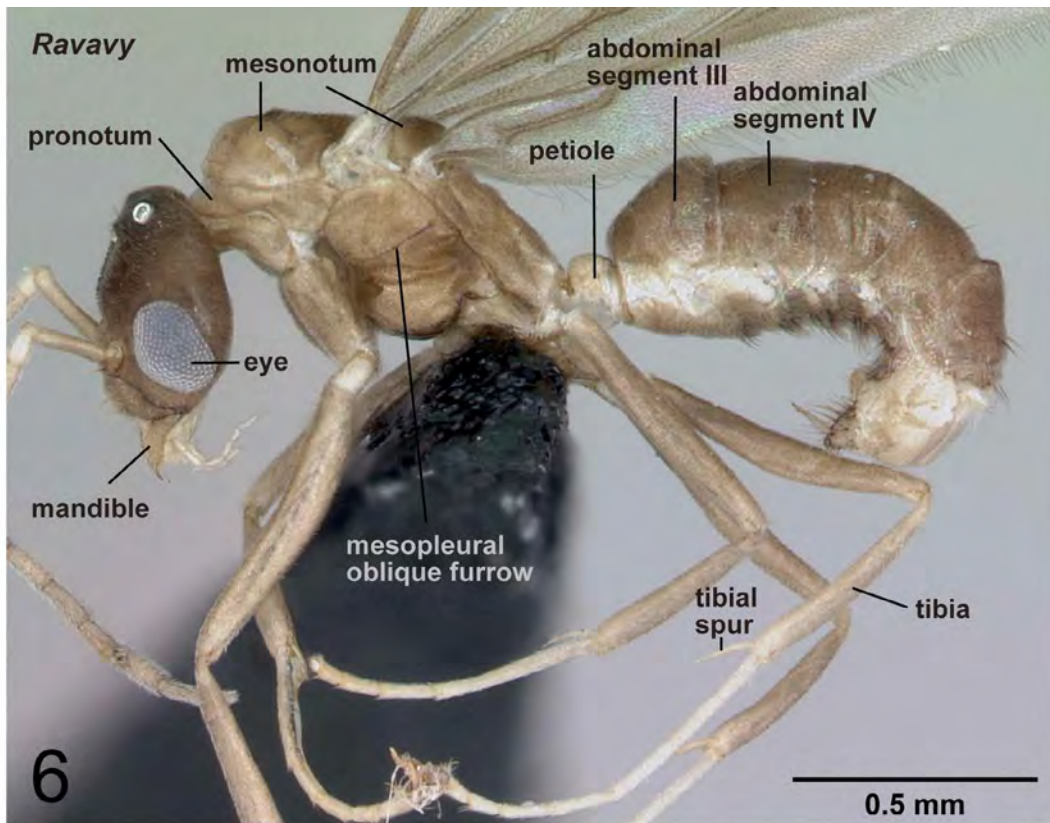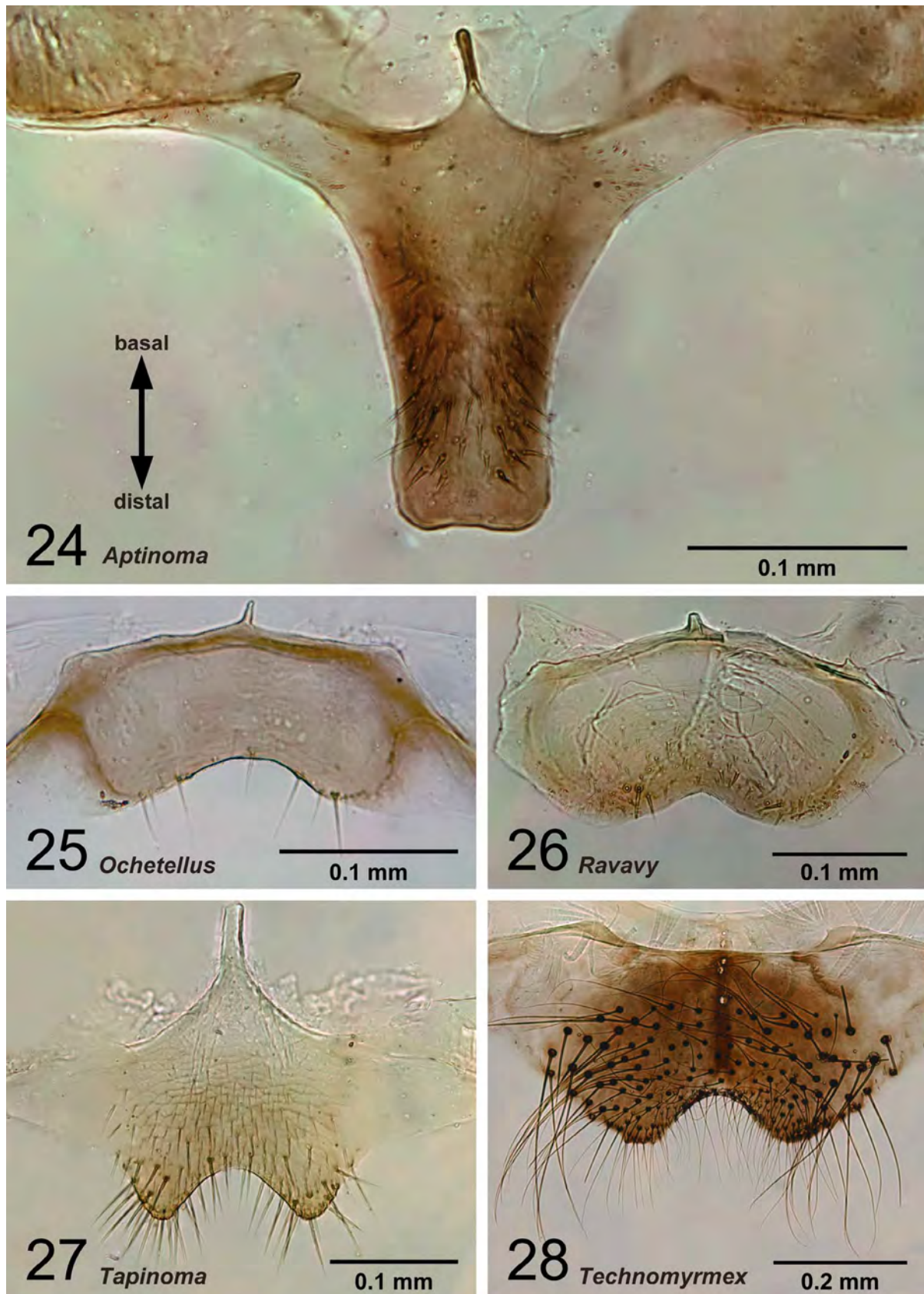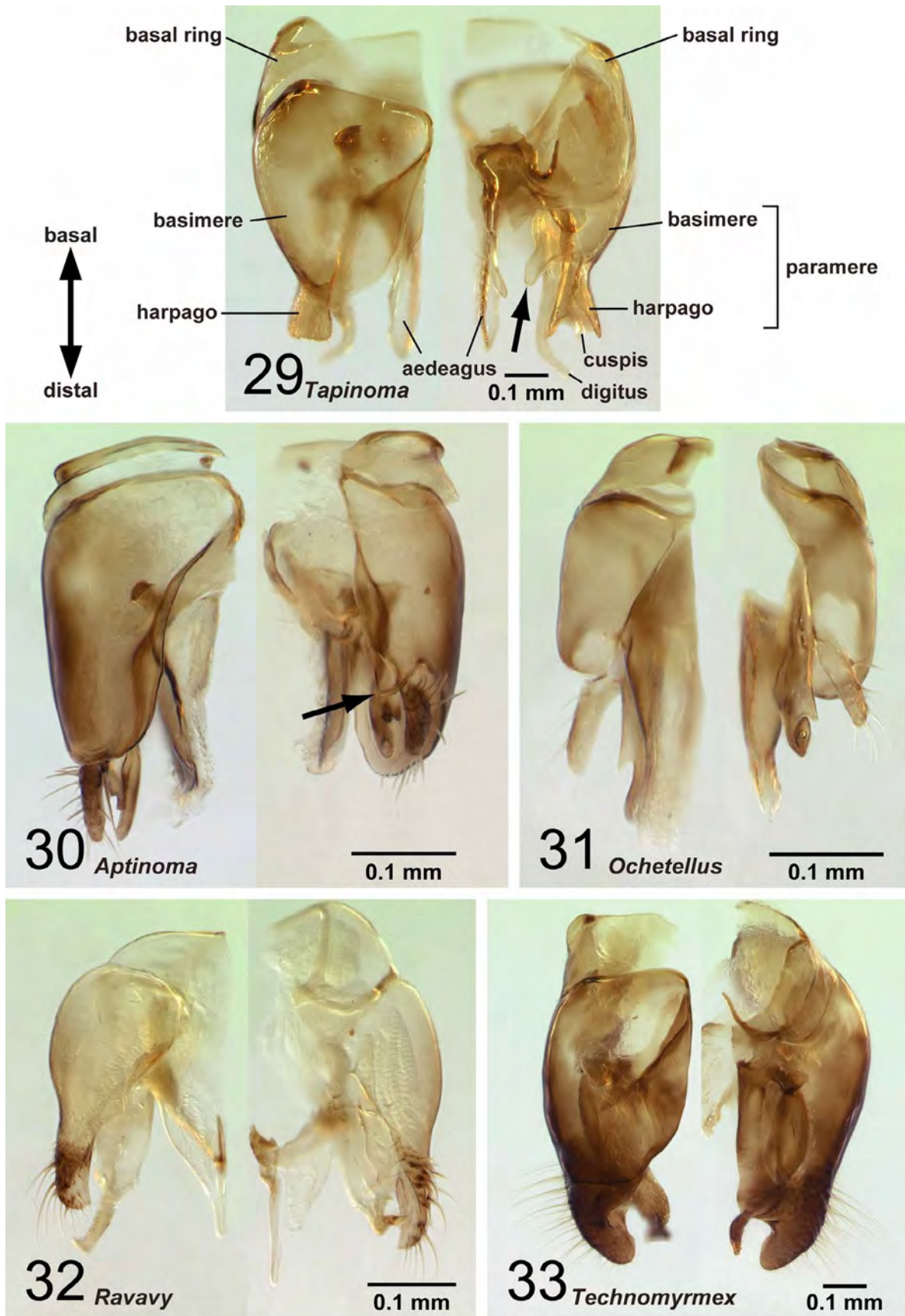
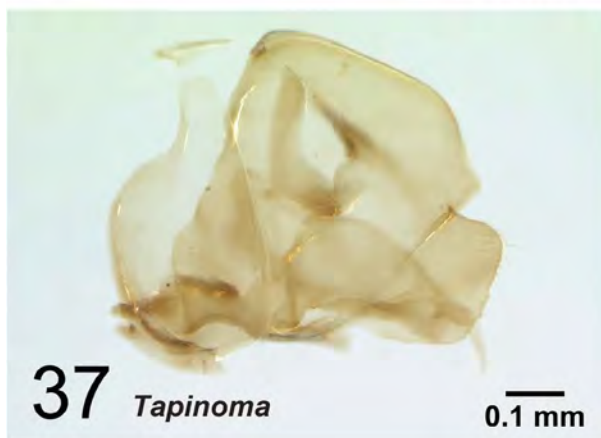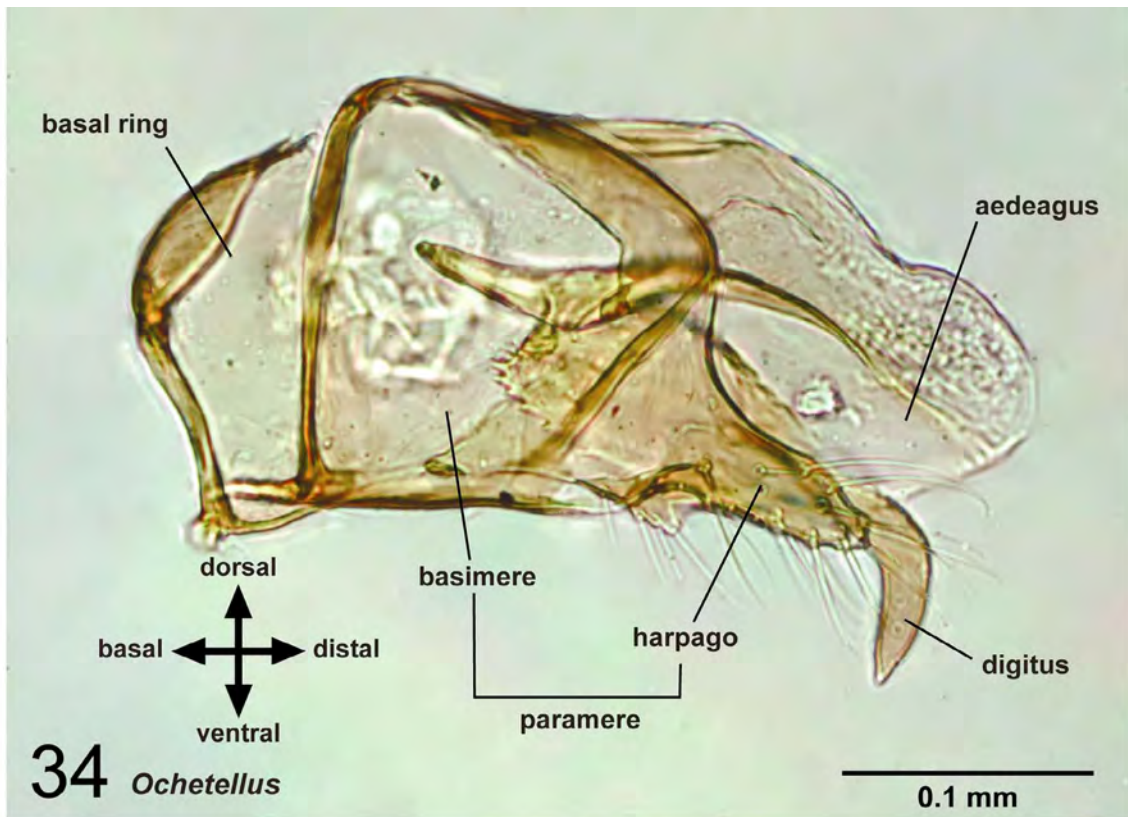**FIGURES 6–10.** Head to abdomen of dolichoderine males in lateral view. 6, *Ravavy miafina* (CASENT0474633); 7, *Aptinoma mangabe* (CASENT0173594); 8, *Ochetellus glaber* (CASENT0191065); 9, *Tapinoma subtile* (CASENT0136850); 10, *Technomyrmex difficilis* (CASENT0049968).
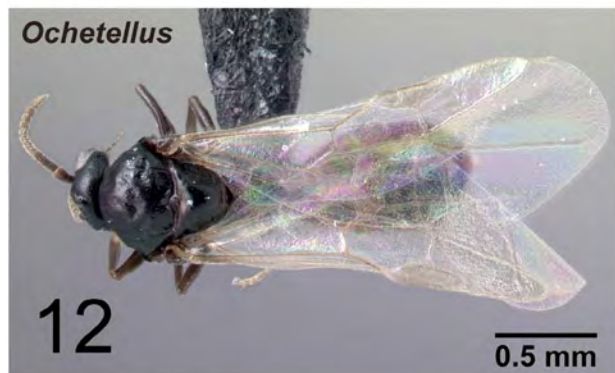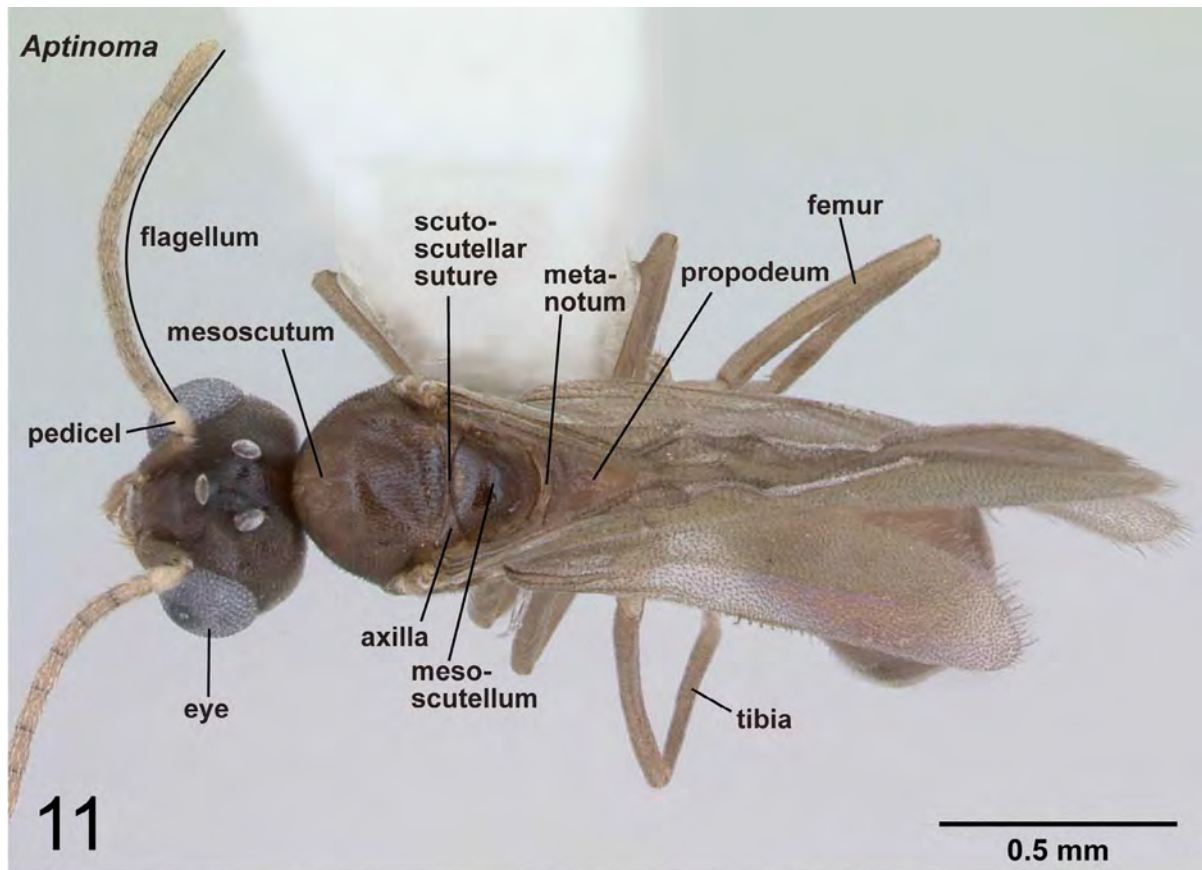
FIGURES 11–15. Head to abdomen of dolichoderine males in dorsal view. 11, *Aptinoma mangabe* (CASENT0173594); 12, *Ochetellus glaber* (CASENT0191065); 13, *Ravavy miafina* (CASENT0474633); 14, *Tapinoma subtile* (CASENT0136850); 15, *Technomyrmex difficilis* (CASENT0049968).
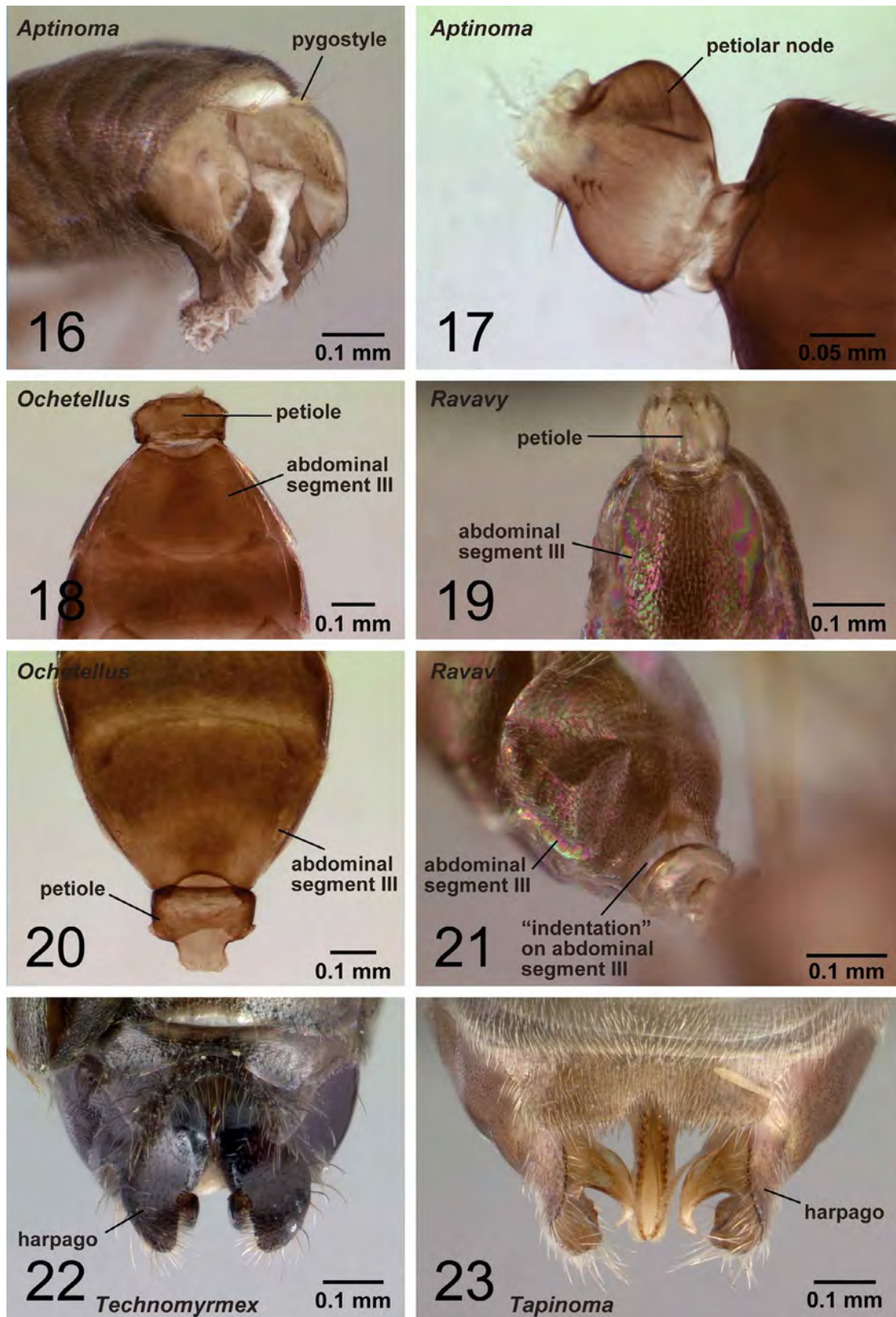
FIGURES 16–23. Males of Dolichoderinae. 16, *Aptinoma mangabe* (CASENT0173594); 17, *Aptinoma mangabe* (CASENT0175002); 18, 20, *Ochetellus glaber* (CASENT0179489); 19, 21, *Ravavy miafina* (CASENT0080308); 22, *Technomyrmex curiosus* (paratype: CASENT0070364); 23, *Tapinoma* mg10 (CASENT0115650). 16, distal portion of abdomen in oblique posterior view; 17, petiole in lateral view; 18, 19, petiole and abdominal segments in ventral view; 20, petiole and abdominal segments in dorsal view; 21, petiole and abdominal segments in oblique frontal view; 22, 23, genitalia in ventral view.

FIGURES 24–28. Abdominal sternum IX of dolichoderine males in ectal view. 24, *Aptinoma mangabe* (CASENT0175002); 25, *Ochetellus glaber* (CASENT0179489); 26, *Ravavy miafina* (CASENT0179530); 27, *Tapinoma melanocephalum* (CASENT0492372); 28, *Technomyrmex madecassus* (CASENT0179526).

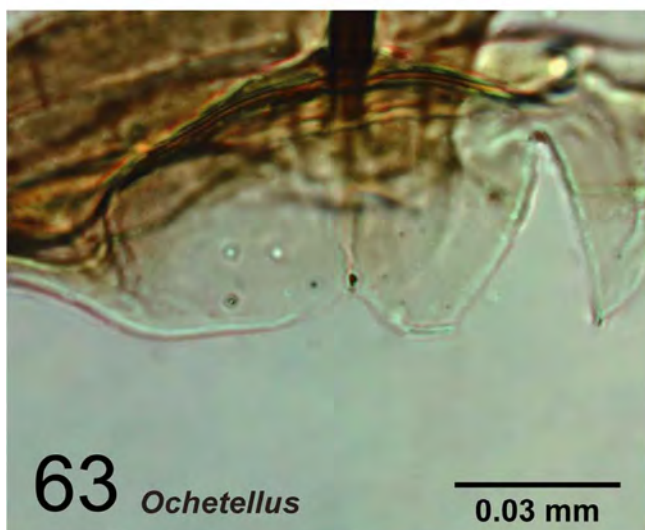**FIGURES 29–33.** Genital capsules of dolichoderine males. 29, *Tapinoma* mg11 (CASENT0179494); 30, *Aptinoma mangabe* (CASENT0175002); 31, *Ochetellus glaber* (CASENT0179489); 32, *Ravavy miafina* (CASENT0179533); 33, *Technomyrmex madecassus* (CASENT0179526). Right side, ventral view; left side, dorsal view.

FIGURES 34–38. Genital capsules of dolichoderine males in lateral view. 34, *Ochetellus glaber* (CASENT0179489); 35, *Aptinoma mangabe* (CASENT0175002); 36, *Ravavy miafina* (CASENT0179533); 37, *Tapinoma* mg11 (CASENT0179494); 38, *Technomyrmex madecassus* (CASENT0179526).
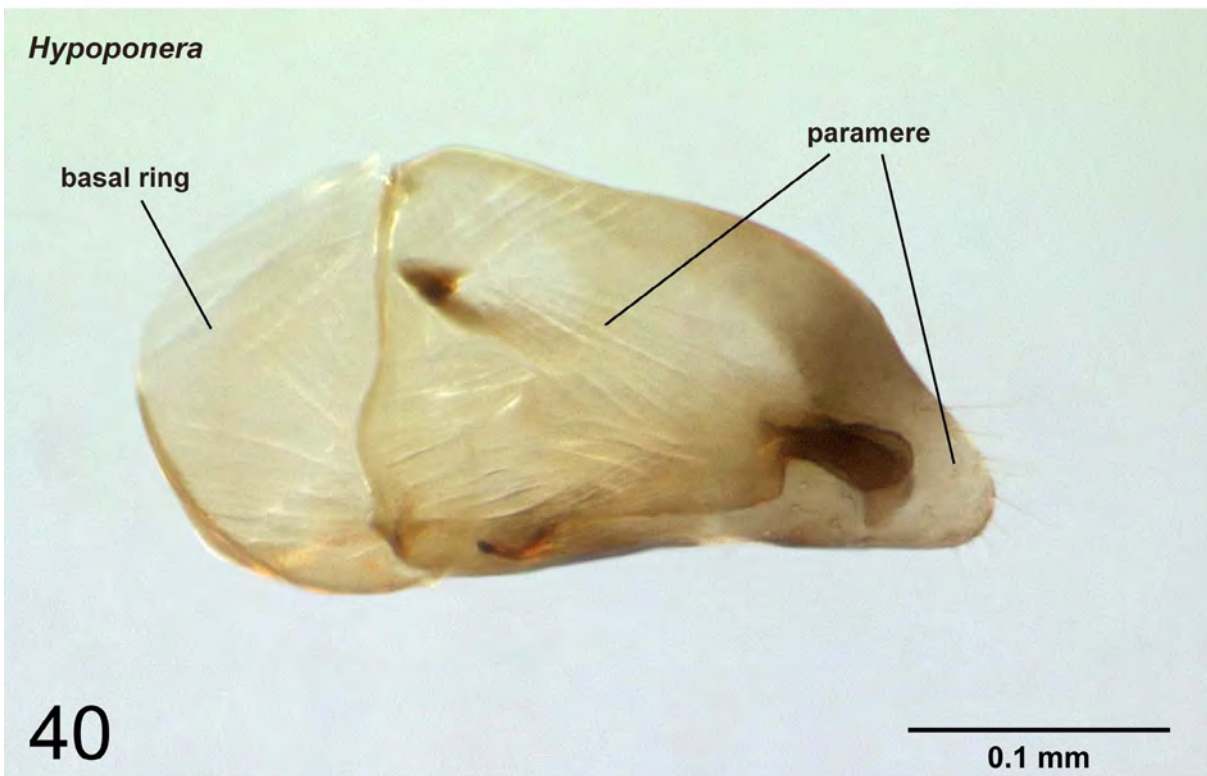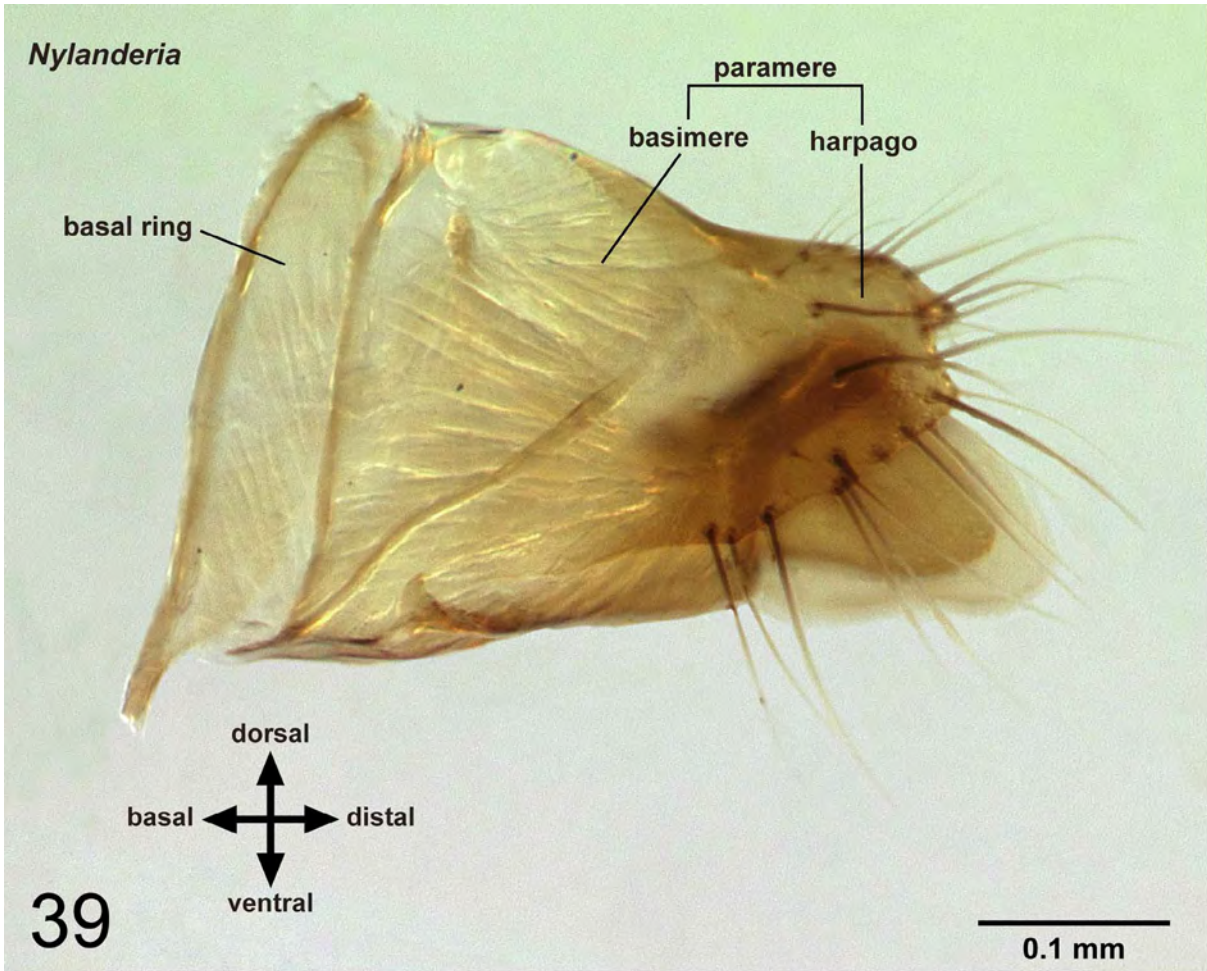
FIGURES 39–40. Genital capsules of males in lateral view. 39, *Nylanderia* sp. (CASENT0196761); 40, *Hypoponera* sp. (CASENT0196760.
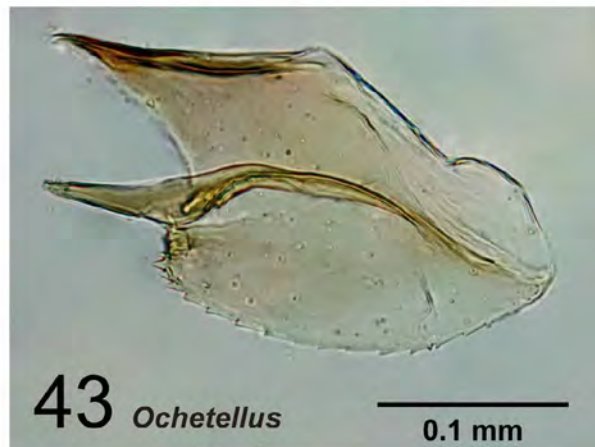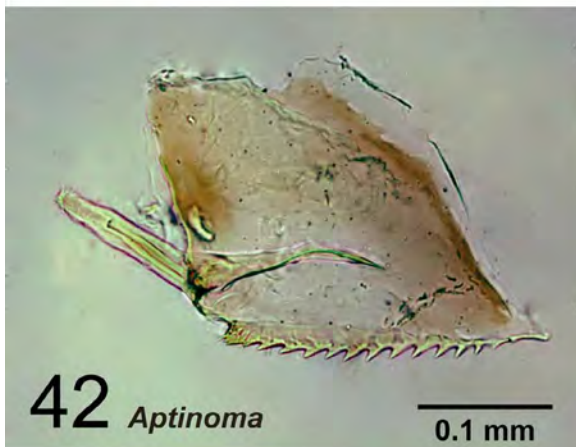
FIGURES 41–45. Aedeagal plates of dolichoderine males in lateral view. 41, *Ravavy miafina* (CASENT0179530); 42, *Aptinoma mangabe* (CASENT0175002); 43, *Ochetellus glaber* (CASENT0179489); 44, *Tapinoma* mg11 (CASENT0179494); 45, *Technomyrmex madecassus* (CASENT0179526).
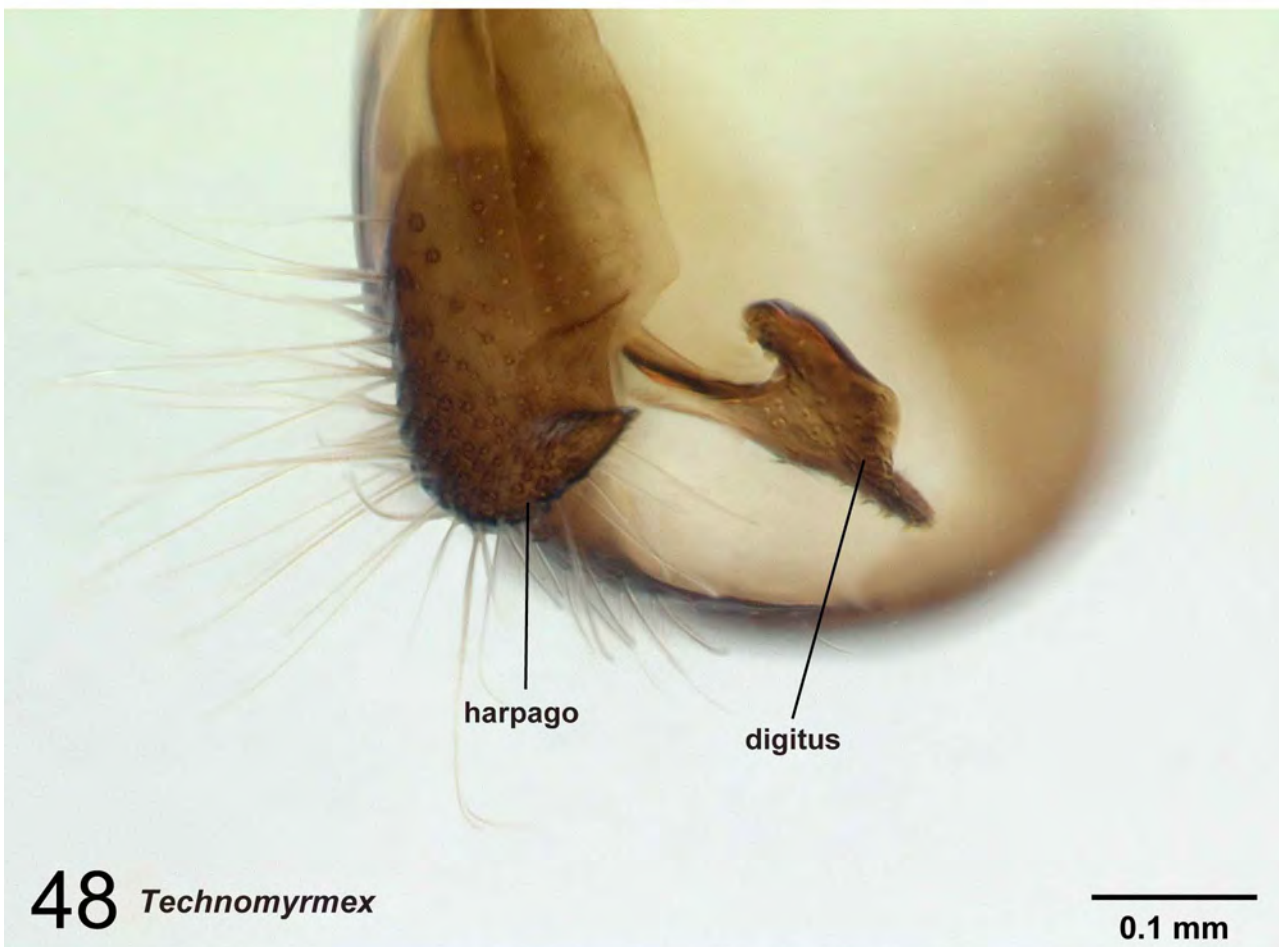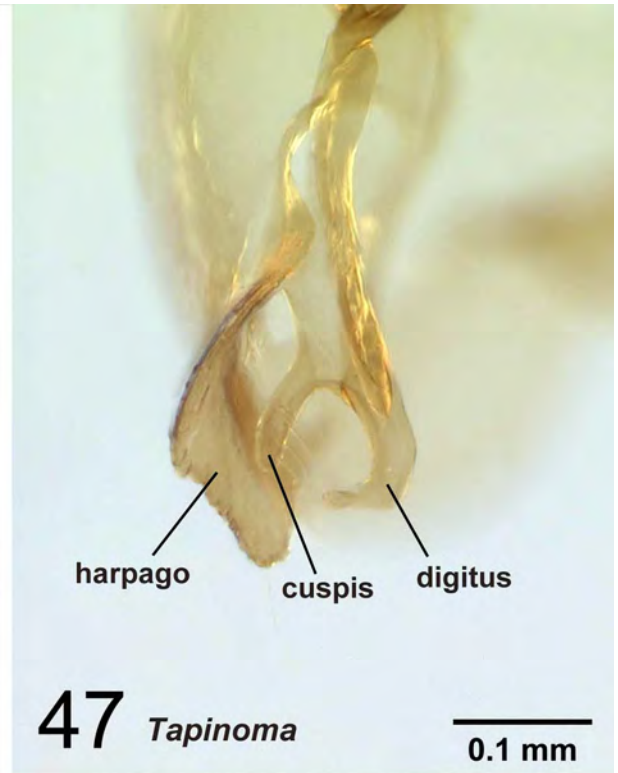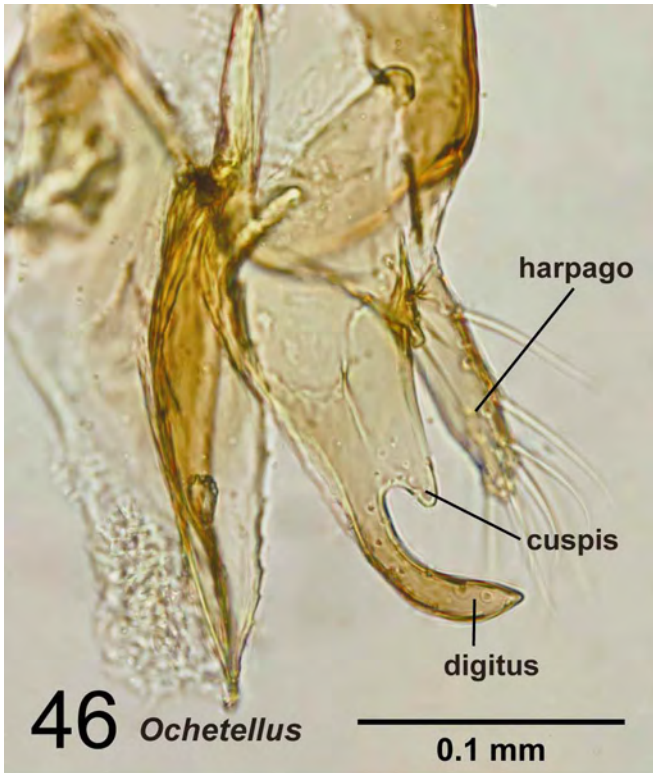
FIGURES 46–48. Volsella of dolichoderine males in oblique posterior view. 46, *Ochetellus glaber* (CASENT0179489); 47, *Tapinoma* mg11 (CASENT0179494); 48, *Technomyrmex madecassus* (CASENT0179526).
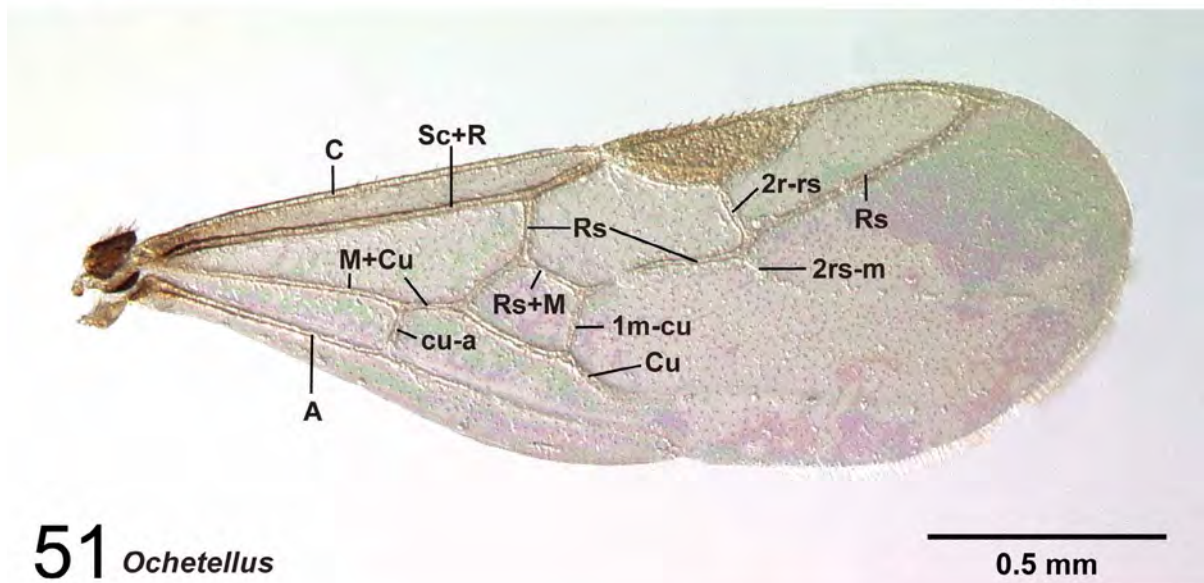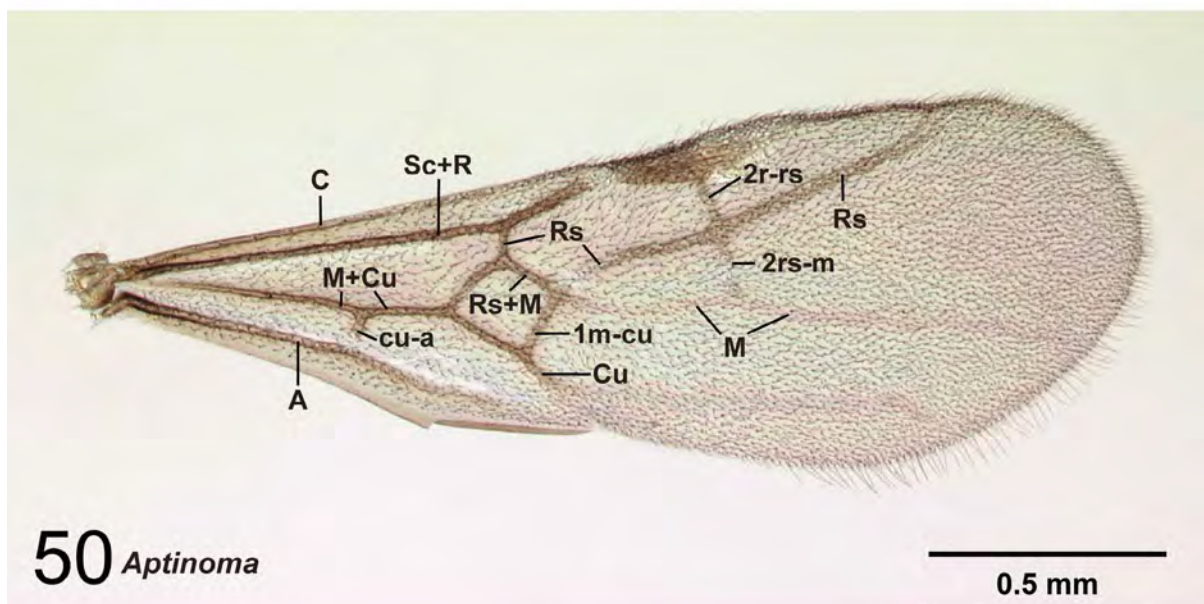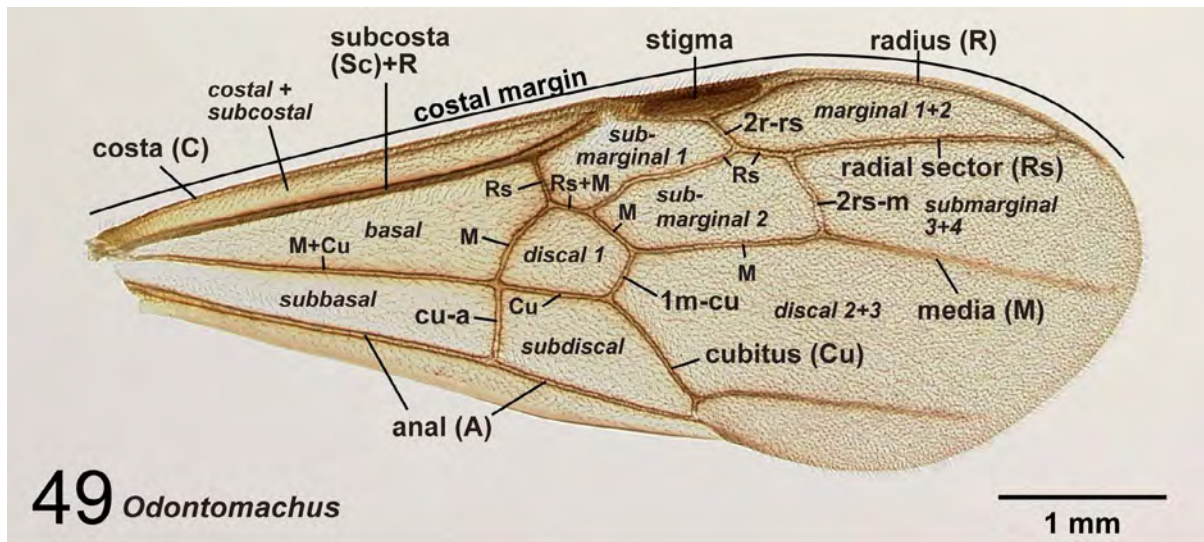
FIGURES 49–51. Forewings of male ants. 49, *Odontomachus coquereli* (CASENT0049797); 50, *Aptinoma mangabe* (CASENT0175002); 51, *Ochetellus glaber* (CASENT0179489).
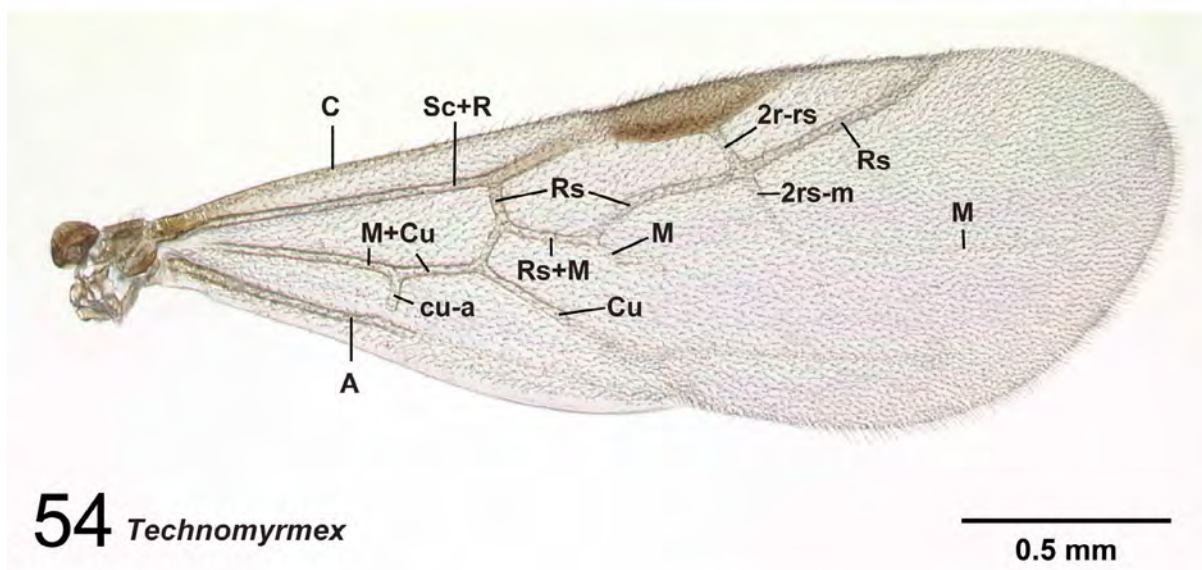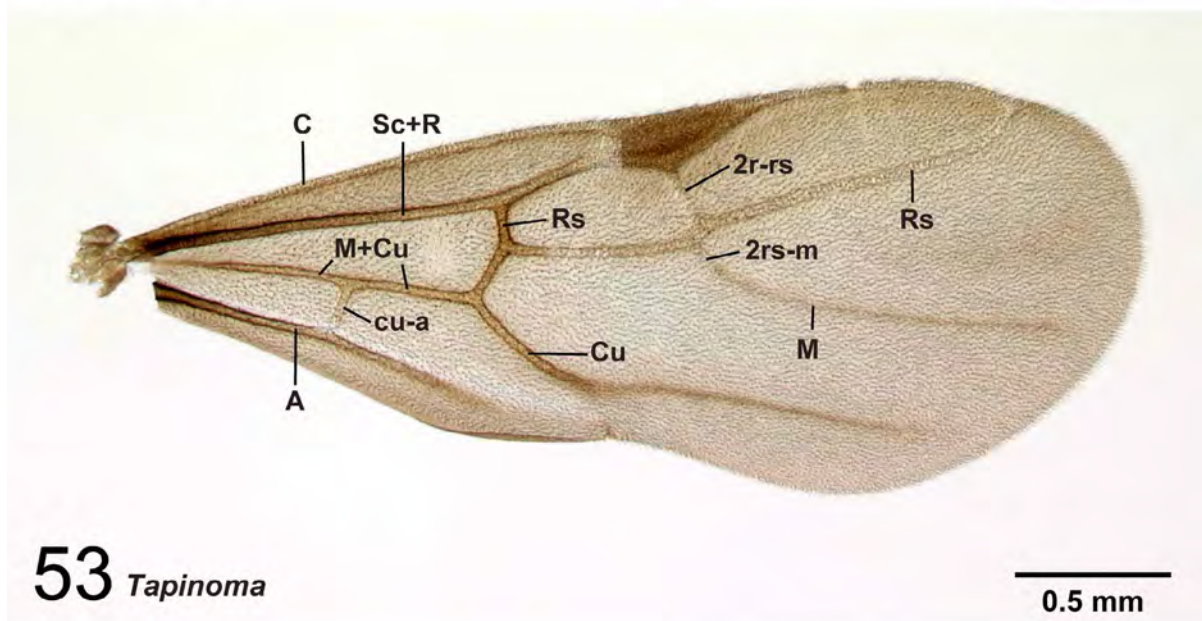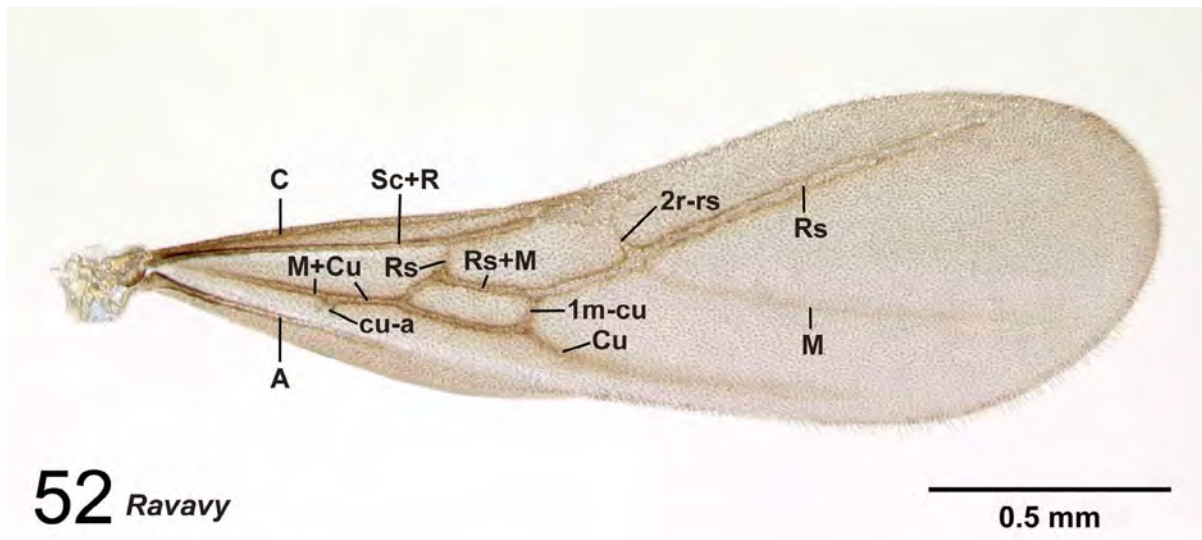
FIGURES 52–54. Forewings of male ants. 52, *Ravavy miafina* (CASENT0179530); 53, *Tapinoma* mg10 (CASENT0179493); 54, *Technomyrmex madecassus* (CASENT0179526).
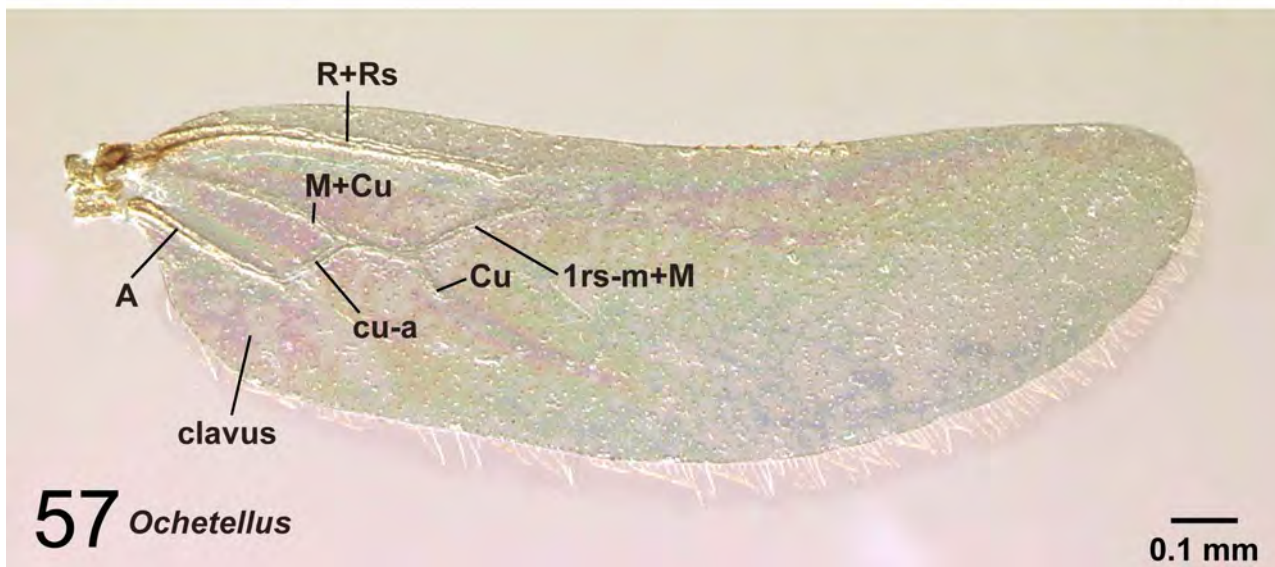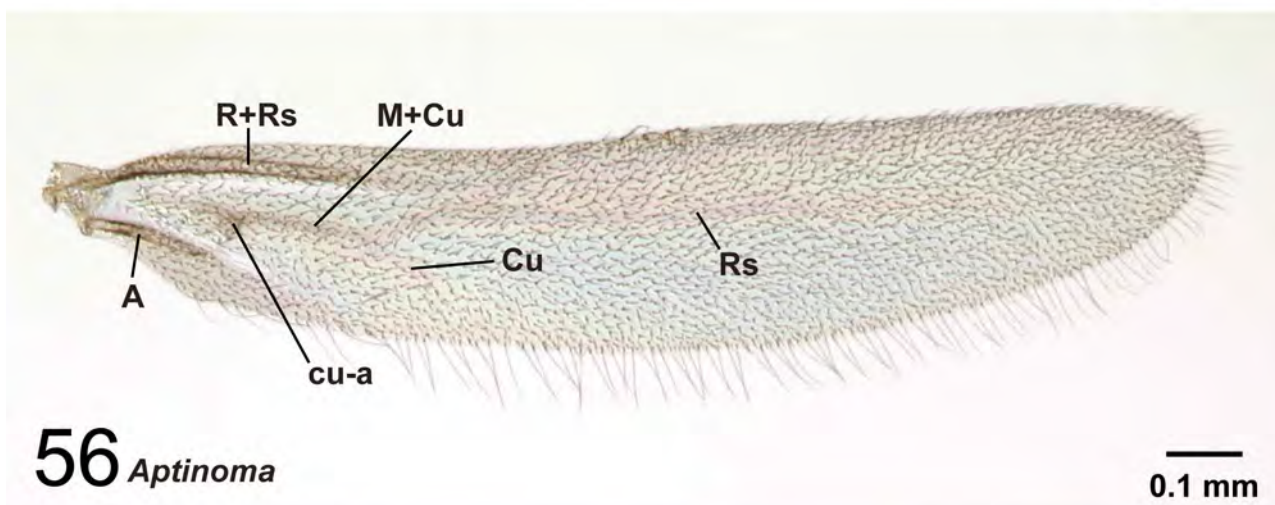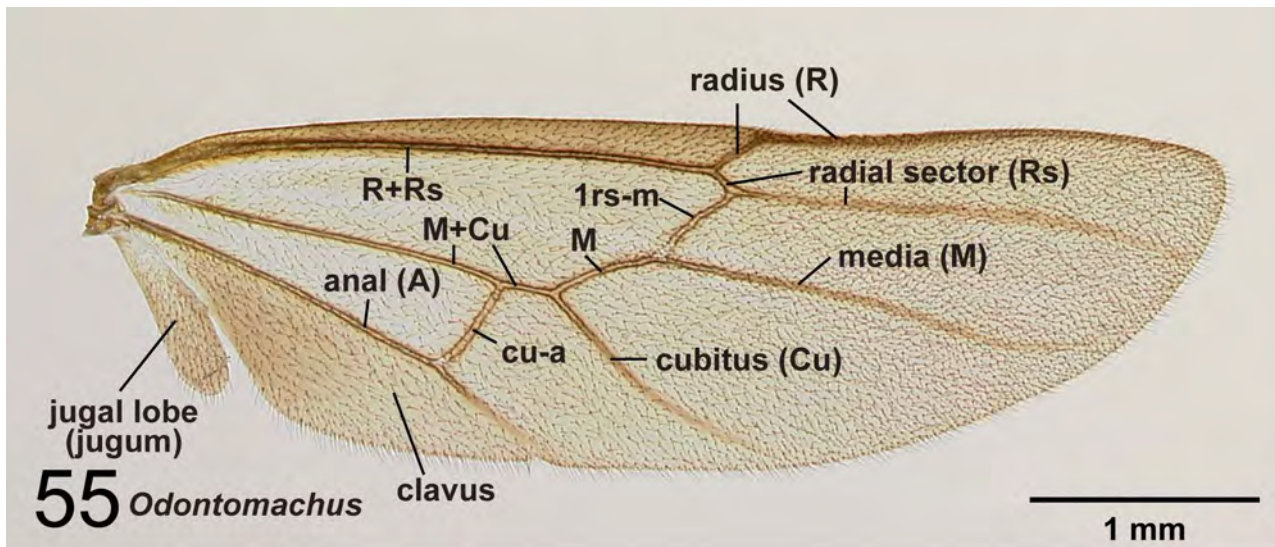
FIGURES 55–57. Hindwings of male ants. 55, *Odontomachus coquereli* (CASENT0049797); 56, *Aptinoma mangabe* (CASENT0175002); 57, *Ochetellus glaber* (CASENT0179489).
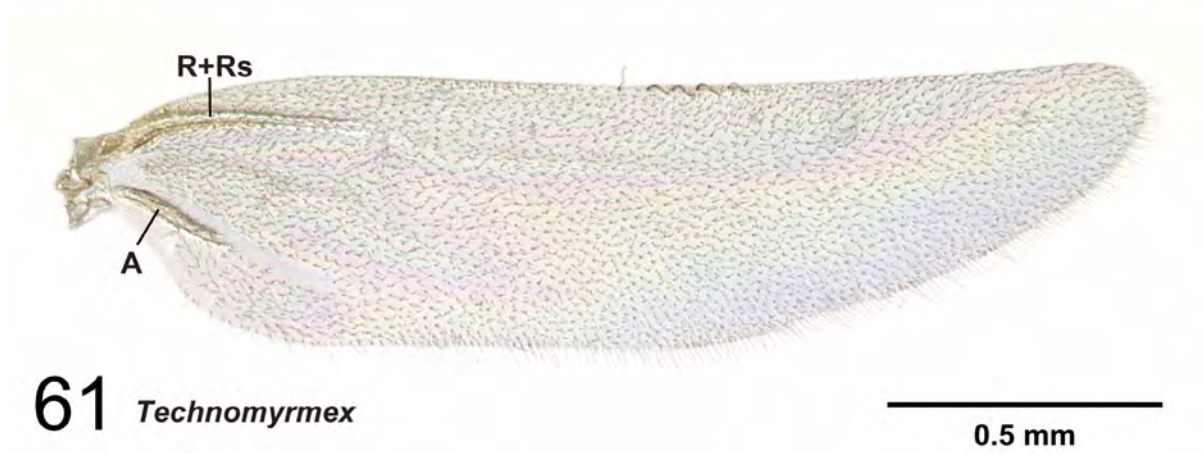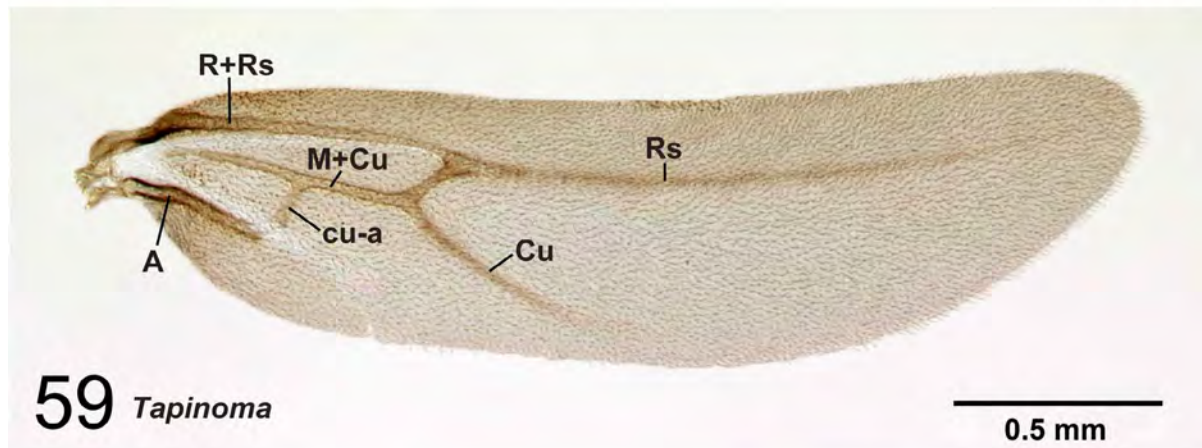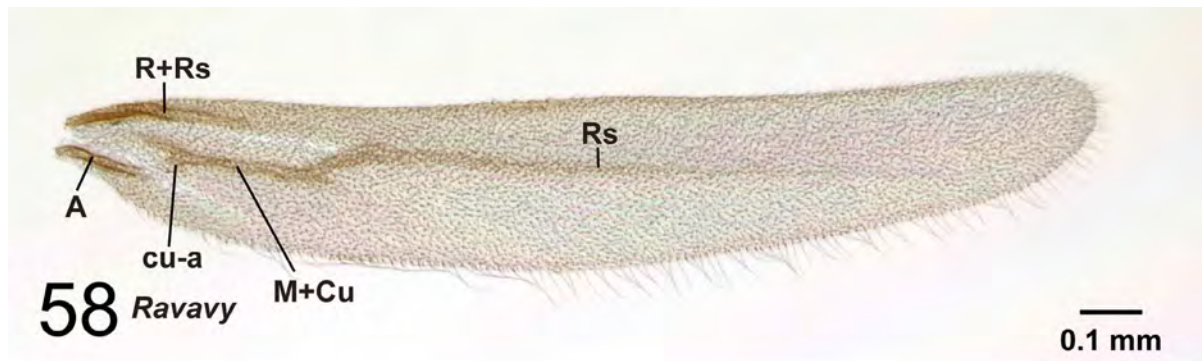
FIGURES 58–61. Hindwings of dolichoderine males. 58, *Ravavy miafina* (CASENT0179530); 59, *Tapinoma* mg10 (CASENT0179493); 60, *Tapinoma subtile* (CASENT0179490); 61, *Technomyrmex madecassus* (CASENT0179526).
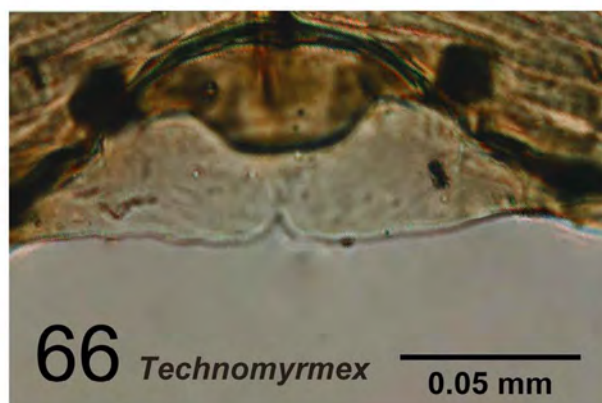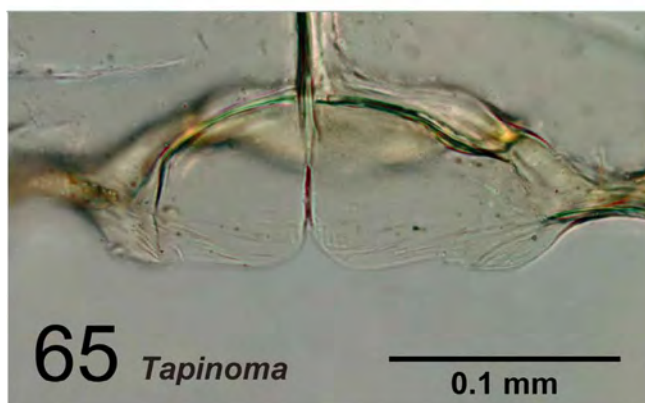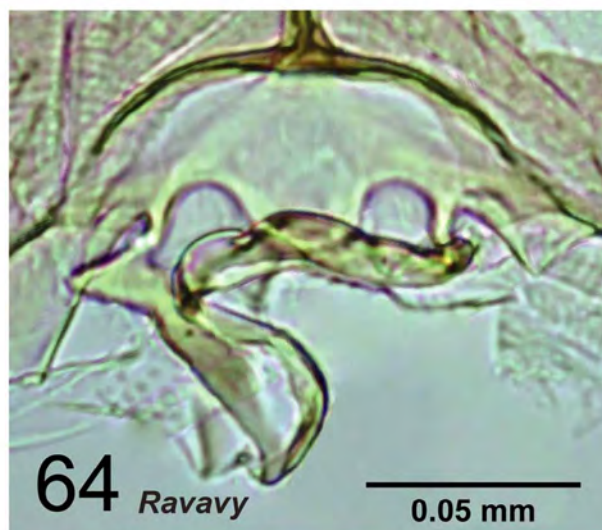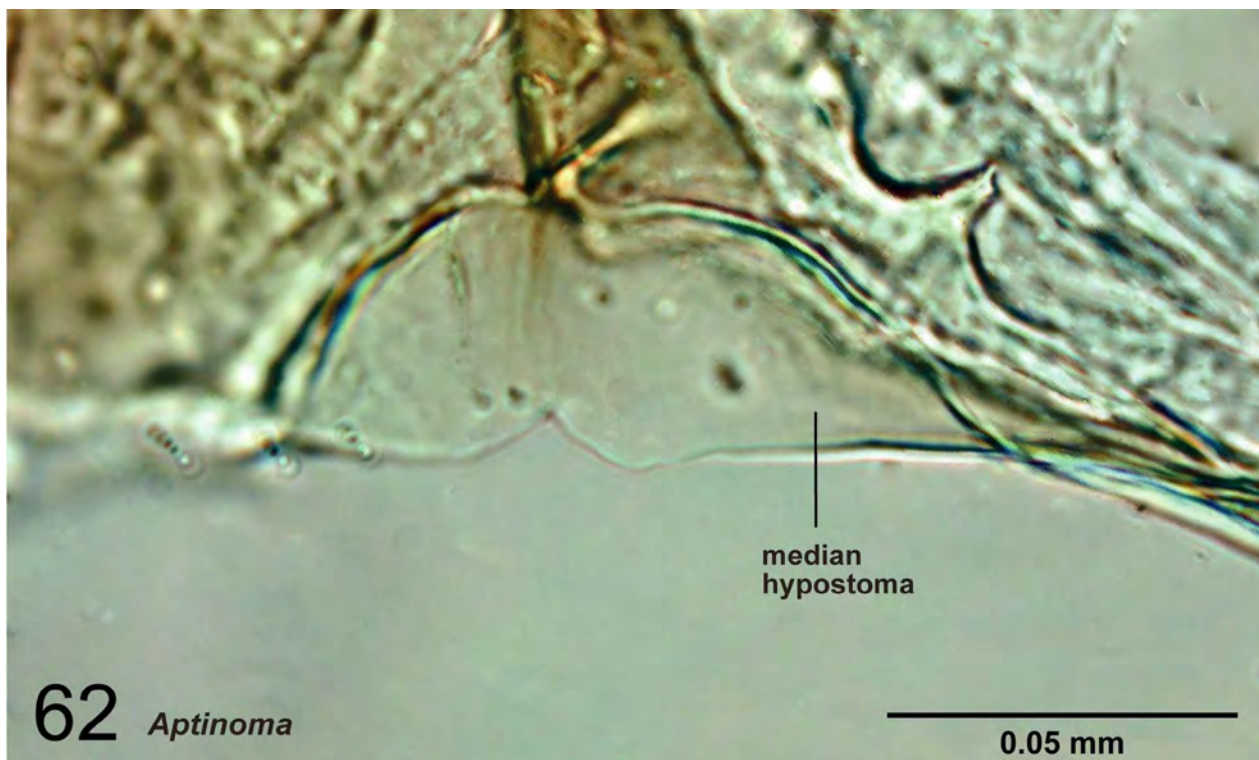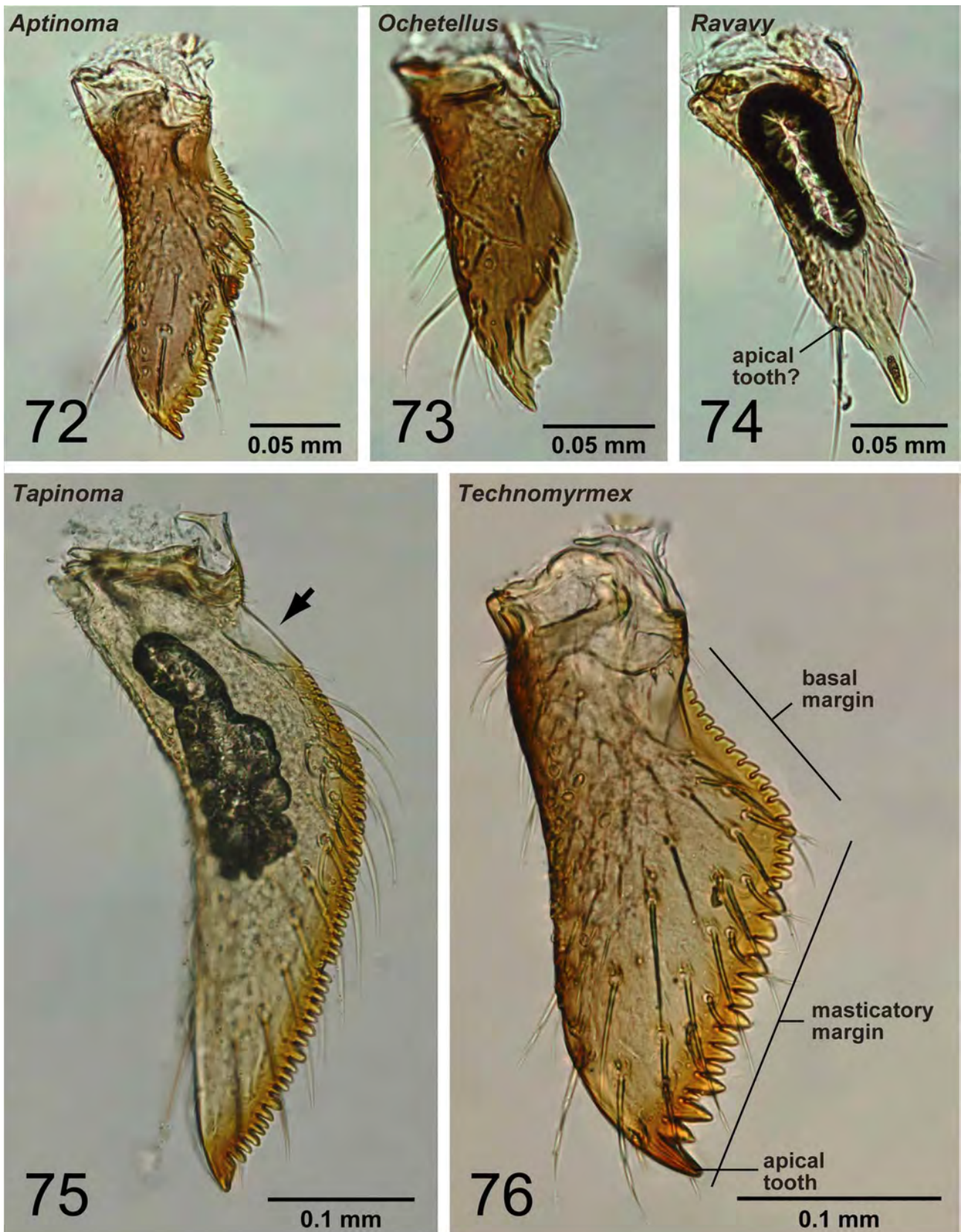
FIGURES 62–66. Median hypostoma of dolichoderine males in ectal view. 62, *Aptinoma mangabe* (CASENT0175002); 63, *Ochetellus glaber* (CASENT0179489); 64, *Ravavy miafina* (CASENT0179533); 65, *Tapinoma* mg11 (CASENT0179494); 66, *Technomyrmex pallipes* (CASENT0179528).
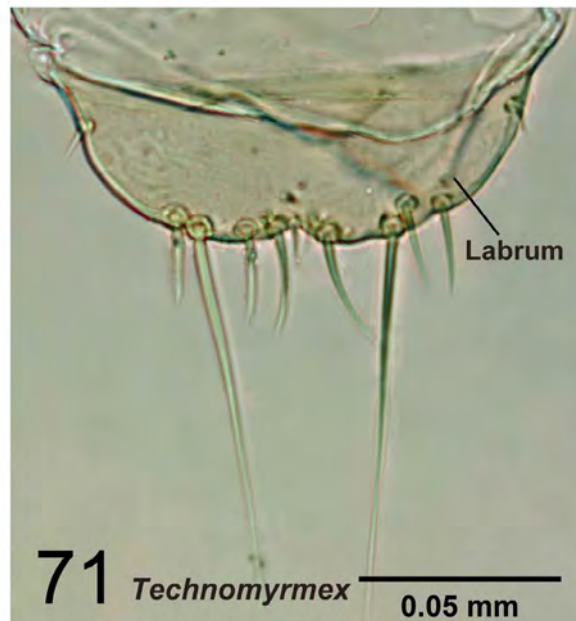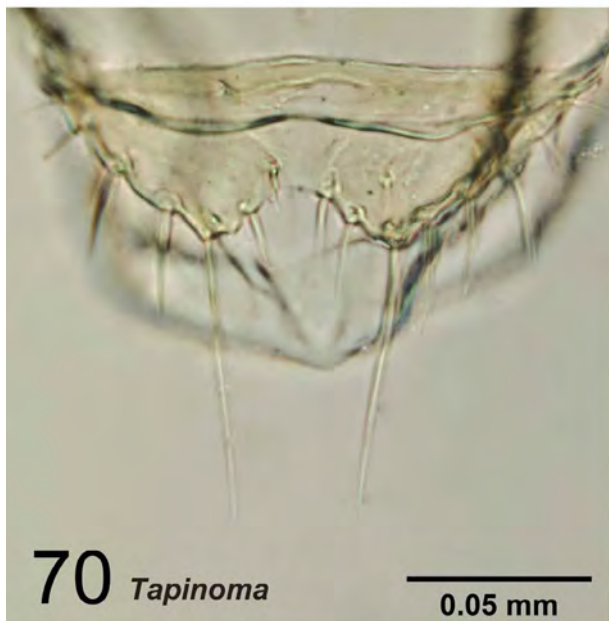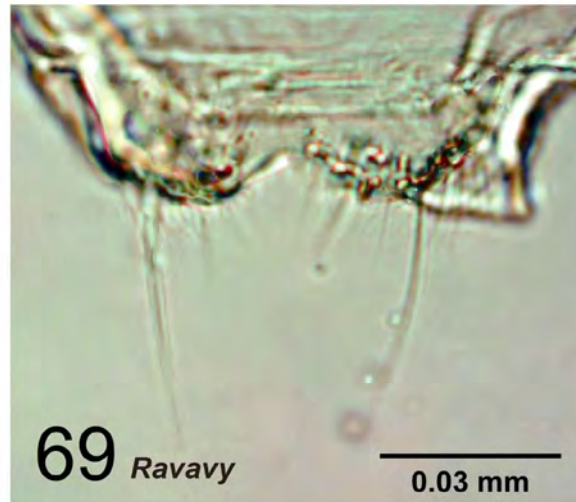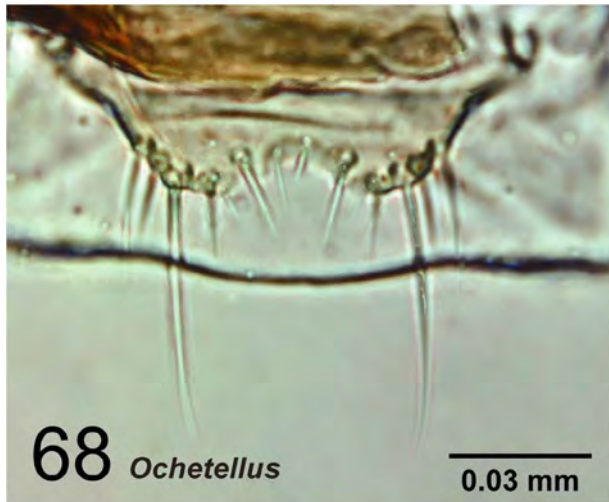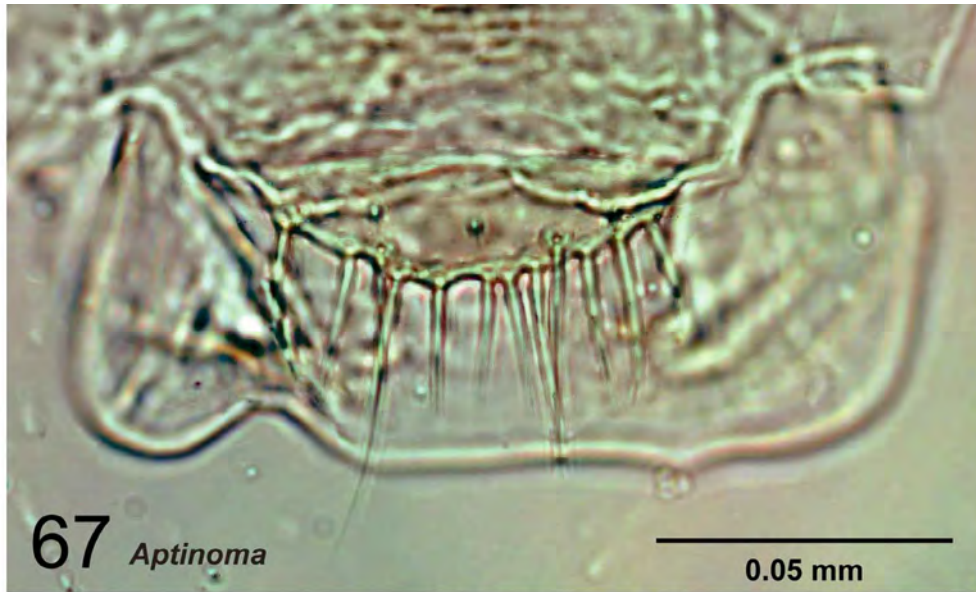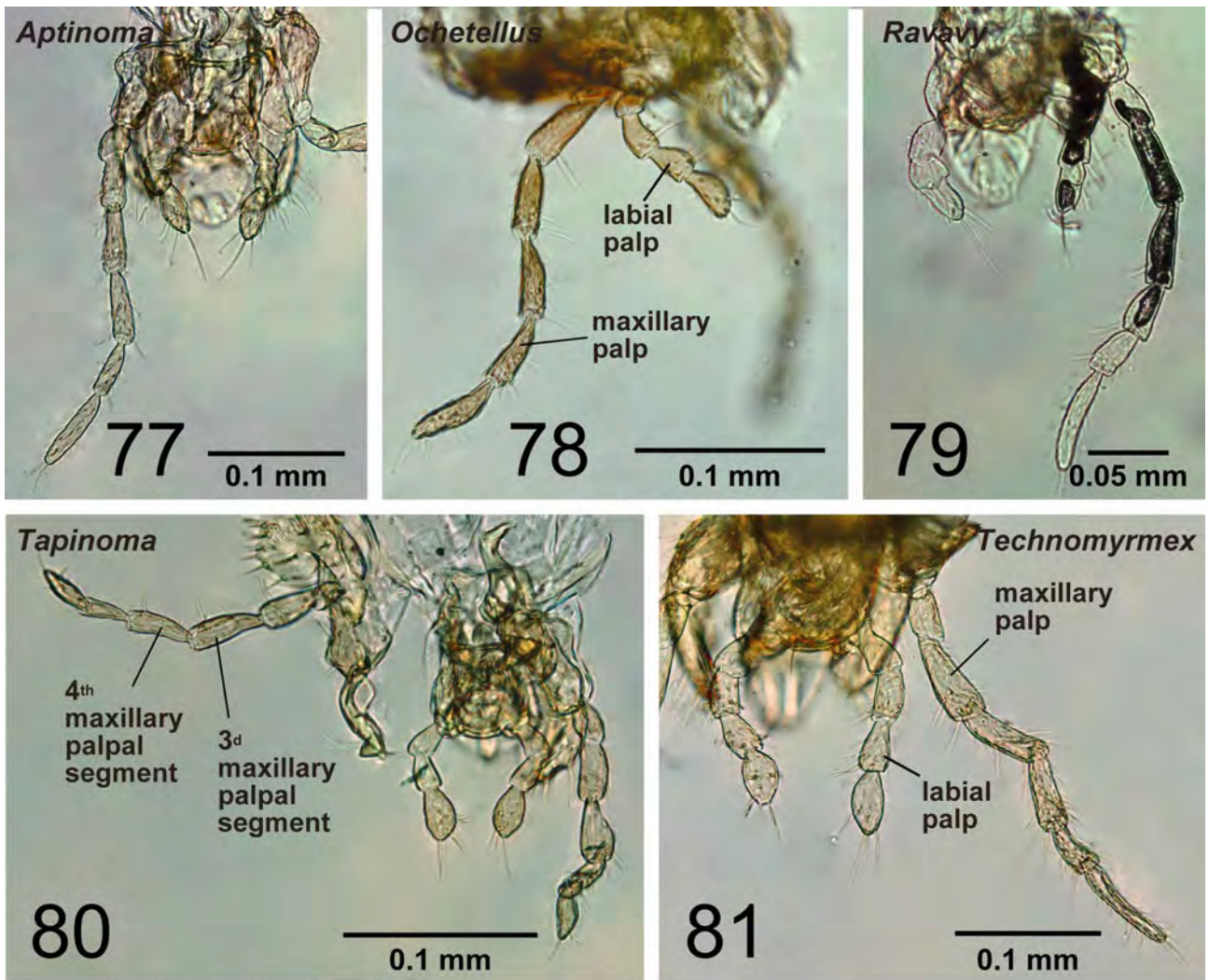
FIGURES 67–71. Labrums of dolichoderine males. 67, *Aptinoma mangabe* (CASENT0175002); 68, *Ochetellus glaber* (CASENT0179489); 69, *Ravavy miafina* (CASENT0179530); 70, *Tapinoma* mg11 (CASENT0179494); 71, *Technomyrmex pallipes* (CASENT0179528). 67, 68, 70, in ectal view; 69, 71, in mesal view.

FIGURES 72–76. Mandibles of dolichoderine males. 72, *Aptinoma mangabe* (CASENT0175002); 73, *Ochetellus glaber* (CASENT0179489); 74, *Ravavy miafina* (CASENT0179530); 75, *Tapinoma* mg11 (CASENT0179494); 76, *Technomyrmex pallipes* (CASENT0179528).

FIGURES 77–81. Mouthparts of dolichoderine males. 77, *Aptinoma mangabe* (CASENT0175002); 78, *Ochetellus glaber* (CASENT0179489); 79, *Ravavy miafina* (CASENT0179530); 80, *Tapinoma subtile* (CASENT0179490); 81, *Technomyrmex pallipes* (CASENT0179528). 77, 79–81, in mesal view; 78, in lateral view.