

# **Article**



# A revision of the Malagasy endemic genus *Adetomyrma* (Hymenoptera: Formicidae: Amblyoponinae)

# MASASHI YOSHIMURA<sup>1</sup> & BRIAN L. FISHER<sup>2</sup>

Department of Entomology, California Academy of Sciences, Golden Gate Park, 55 Music Concourse Drive, San Francisco, California 94118, U.S.A.

E-mail: 1myoshimura@ant-database.org; 2bfisher@calacademy.org

#### **Abstract**

The species-rank taxonomy of the genus *Adetomyrma* Ward, 1994 is revised. Nine species are distinguished with eight described as new: *A. aureocuprea* **sp. nov.**, *A. bressleri* **sp. nov.**, *A. caputleae* **sp. nov.**, *A. cassis* **sp. nov.**, *A. caudapinniger* **sp. nov.**, *A. cilium* **sp. nov.**, *A. clarivida* **sp. nov.**, *A. goblin* **sp. nov.** Worker-male associations are identified for all worker-based species: *A. bressleri*, *A. caputleae*, *A. goblin* along with *A. venatrix* Ward, 1994 from which the male is described for the first time. Five new species are described only from males. An ergatoid queen of *Adetomyrma* is described for the first time. Keys to species for workers and males are given.

Key words: Male, worker, queen, ergatoid, Malagasy region, Madagascar, Malaise trap, key to species, morphological characters, genitalia, Amblyoponini, aureocuprea, bressleri, caputleae, cassis, caudapinniger, cilium, clarivida, goblin, venatrix

#### Introduction

The genus *Adetomyrma* Ward, 1994 was described as a Malagasy endemic monotypic genus. Ward (1994) assigned this genus to Amblyoponini within the subfamily Ponerinae on the basis of the worker morphology of the type species *Adetomyrma venatrix* Ward, 1994. Later, Bolton (2003) raised this tribe to subfamily status as Amblyoponinae.

Subsequent molecular studies have confirmed the placement of *Adetomyrma* within the Amblyoponinae (Saux *et al.* 2004; Ouellette *et al.* 2006; Moreau *et al.* 2006; Brady *et al.* 2006). Yoshimura & Fisher (2012) recently proposed a new genus diagnosis and description for *Adetomyrma* based on the morphological characters of the males.

In this study, we propose a species-level taxonomic system for the genus *Adetomyrma*. Comprehensive morphological and distributional examinations using the accumulated material distinguish nine species in this genus; eight of them are described as new. The male of *Adetomyrma venatrix* is described for the first time. Out of the eight newly-named species, three are described only from workers, all of which are associated with males, and five are described only from males. Queens are known only in two species and one of these is ergatoid. Also, keys to species for the workers and males are given.

#### Materials and methods

# Abbreviations of depositories

BMNH: The Natural History Museum (British Museum, Natural History), London, U.K.

CASC: California Academy of Sciences, San Francisco, California, U.S.A.

MCZC: Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.

MHNG: Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland.

NHMB: Naturhistorisches Museum, Basel, Switzerland.

PBTZ: Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar.

**Materials.** The material on which this work is based was collected during arthropod surveys in Madagascar and nearby islands in the Southwest Indian Ocean conducted by B. Fisher and Malagasy ant researchers from the Madagascar Biodiversity Center in Antananarivo, Madagascar. Their work in the region includes 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 2011 (see Fisher 2005 for additional details). All non-type material examined is deposited in CASC and PBTZ.

**Methods.** Observations and dissections were carried out under stereoscopic microscopes (LEICA M125). Digital color images were created using a LEICA DFC425 digital camera. LEICA Application Suite software (ver. 3.8) was used for images taken at magnifications less than 100×, and a compound microscope (Leica DM4000M) and Nikon digital camera (DXm1200) Helicon Focus version 4.10.2 software were used for images taken at magnifications greater than 100×. The images were edited in Adobe Photoshop and Illustrator. Each imaged or dissected specimen is uniquely identified with a specimen-level unique identifier (*e.g.* CASENT0003099) affixed to each pin.

**Measurements and indices.** The following measurements and indices (illustrated in Figs 1–6) are cited in the text. The values are presented in mm.

Head length (HL), maximum length of head in full-face view between lines drawn across anterior margin of clypeus and posterior margin of head (worker, queen, male; including ocelli in male and queen).

Head width (HW), maximum width of head in full-face view, including eyes (worker, queen, and male).

Head depth (HD), maximum depth of head in lateral view measured perpendicular to full-face view plane (worker).

Scape length (SL), length of scape excluding radicle (worker, queen, and male).

Eye length (EL), maximum length of eye measured in lateral view (queen and male).

Weber's length of mesosoma (WL), maximum diagonal distance in lateral view, from base of anterior slope of pronotum to metapleural lobe (worker, queen, and male).

Pronotal width (PnW), maximum width of pronotum in dorsal view (worker).

Mesonotal width (MnW), maximum width of mesonotum in dorsal view (worker, queen, and male).

Propodeal width (PpW), maximum width of propodeum in dorsal view (worker and queen).

Petiolar width (PtW), maximum width of petiole in dorsal view (worker and queen).

Cephalic index (CI), HW/HL  $\times 100$  (worker, queen, and male).

Scape index (SI), SL/HW ×100 (worker, queen, and male).

Eye index (EI), EL/HL ×100 (queen and male).

Mesonotal index (MnI), MnW/HW ×100 (worker and male).

Propodeal index (PpI), PpW/MnW ×100 (worker and queen).

Petiolar index (PtI), PtW/PpW ×100 (worker and queen).

**Terminology.** Morphological terminology follows our previous work (Yoshimura & Fisher 2007: figs 1, 2; 2009: figs 1–21, 25–34; 2011: figs 1–3, 6, 11, 16–23, 34, 39, 40, 46–61, 76–81; 2012: figs 1–6, 8–13, 16), and is based on Snodgrass (1935), Gauld and Bolton (1988), Bolton (1994), and Huber & Sharkey (1993). Use of the term pygostyle follows Snodgrass (1941) while basimere and harpago follows Snodgrass (1957); terminology of wing venation follows Wootton (1979) and Gauld & Bolton (1988); specialized conical setae for anterior clypeal projections follows Ward (1994).

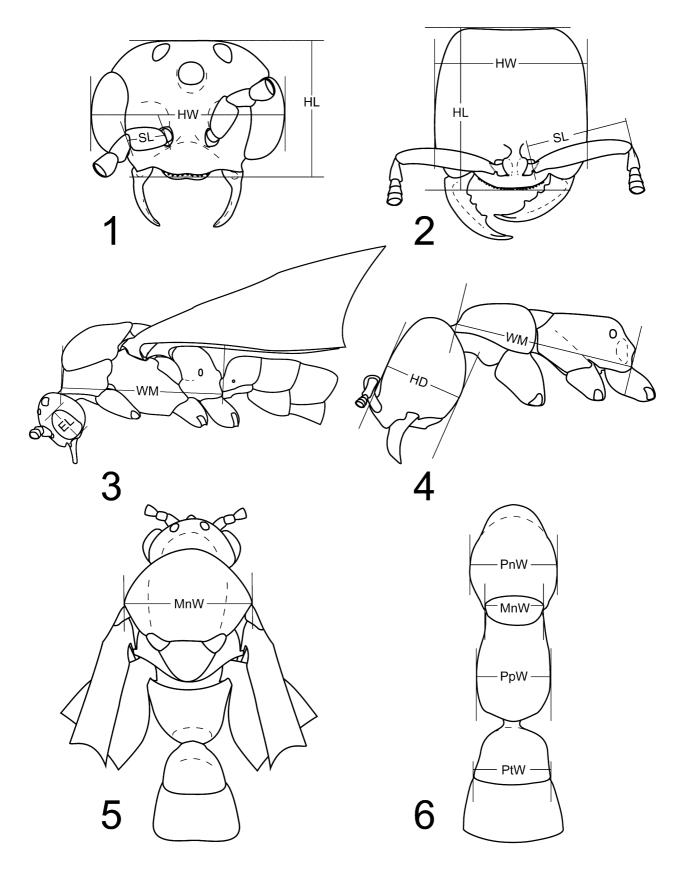
# Results

# Genus Adetomyrma

Adetomyrma Ward, 1994: 160. Type-species: Adetomyrma venatrix, by original designation.

Adetomyrma in Ponerinae, Amblyoponini: Ward, 1994: 159.

Adetomyrma in Amblyoponinae, Amblyoponini: Bolton, 2003: 42, 153.



**FIGURES 1–6.** Measurements for *Adetomyrma* species. 1, 3, 5, male; 2, 4, 6, worker. 1, 2, head in full-face view; 3, 4, body in lateral view; 5, 6, Body in dorsal view. Abbreviations are explained in Measurements and indices section.

# Diagnosis of worker

The diagnostic characters uniquely observed in *Adetomyrma* within the subfamily Amblyoponinae are given in italics.

- 1. Compound eye lacking.
- 2. Anterior margin of clypeus with specialized conical setae.
- 3. Mandible falcate without a distinct basal angle.
- 4. Teeth on inner margin of the mandible completely replaced by the basal denticles excluding apical two teeth.
- 5. Apical and subapical teeth developed.
- 6. No basal large projection present on basal portion of mandibular inner margin.
- 7. Constriction between petiole and abdominal segment III absent.
- 8. Constriction between pre- and post-sclerites on abdominal segment IV absent.

# Diagnosis of male

The diagnostic characters uniquely observed in *Adetomyrma* within the subfamily Amblyoponinae are given in italics.

- 1. Frontal carinae absent.
- 2. Anterior margin of clypeus with specialized conical setae.
- 3. Antenna consisting of 13 segments.
- 4. Mandible with single, blunt apical tooth.
- 5. Palpal formula 3,3 / 2,3 / 2,2.
- 6. Notaulus distinct or absent.
- 7. Mesepimeron with or without distinct posterodorsal lobe (epimeral lobe).
- 8. Mesotibia with two spurs in most cases, rarely with single spur.
- 9. Metatibia with two spurs.
- 10. No constriction present between petiole and abdominal segment III in dorsal view.
- 11. Abdominal segment IV with or without tergosternal fusion.
- 12. Pretergite of abdominal segment IV not distinctly differentiated from posttergite, without transverse furrow between them.
- 13. Pygostyles present.
- 14. Distal margin of abdominal sternum IX concave.
- 15. Separation between basimere and harpago usually indistinct but distinct in some species.
- 16. Basal projection on cuspis well developed.
- 17. Basicoventral portion of the aedeagus in lateral view extended basally in most cases, shape of extension somewhat triangular to subtriangular, with relatively sharper distal apex.
- 18. Serrate denticles absent on basal portion of ventral margin of aedeagus in lateral view.
- 19. Pterostigma well-developed on forewing.
- 20. Radial sector on forewing wholly or partially absent between M+Rs and 2r-rs.
- 21. Radial sector on forewing fails to reach costal margin.
- 22. 2r-rs on forewing connected with radial sector posterior to pterostigma.
- 23. 2rs-m absent on forewing.
- 24. cu-a on forewing located far from junction between media and cubitus.
- 25. Radius absent on hindwing in most cases but rarely weakly developed.
- 26. 1rs-m absent on hindwing.
- 27. Media on hindwing usually present apical to 1rs-m.

#### Generic diagnosis remarks

Generic diagnostic characters for the worker caste listed above build on those proposed in Ward (1994). Here we update some of those characters based on new material and new morphological data. The listed characters are consistently observed in all *Adetomyrma* workers, and distinguish *Adetomyrma* from the other Amblyoponine genera.

Male diagnostic characters follow those in Yoshimura & Fisher (2012).

For queens, all worker diagnostic characters are applicable except the developed compound eye and the presence of the constriction between petiole and AIII.

# List of Adetomyrma species

A list of *Adetomyrma* species is given below. Sexes and castes known in each species are given in brackets as: w, worker; aq, alate queen; eq, ergatoid queen; m, male. Associations from species codes used in previous studies are given in the remarks for each species.

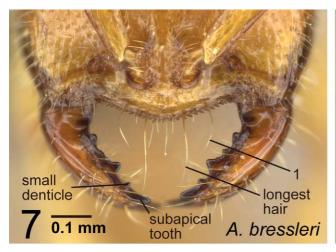
aureocuprea sp. nov. [m]
bressleri sp. nov. [w, m]
caputleae sp. nov. [w, eq, m]
cassis sp. nov. [m]
caudapinniger sp. nov. [m]
cilium sp. nov. [m]
clarivida sp. nov. [m]
goblin sp. nov. [w, aq, m]
venatrix Ward, 1994: 161 [w, m]

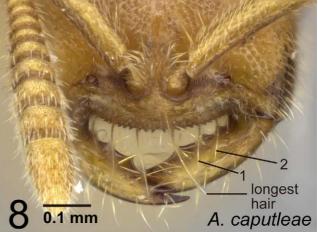
#### Key to species of Adetomyrma

#### Workers

Workers of aureocuprea, caudapinniger, cilium, and clarivida are unknown.

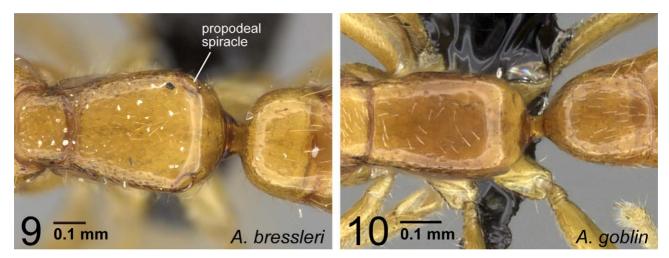
- -. Two or more hairs present lateral to the longest hair on the anterior margin of the clypeus in full-face view (Fig 8). Denticle absent on base of subapical (second form apex) tooth (Fig 8) with a gap present between basal dentition and apical teeth. . . 3



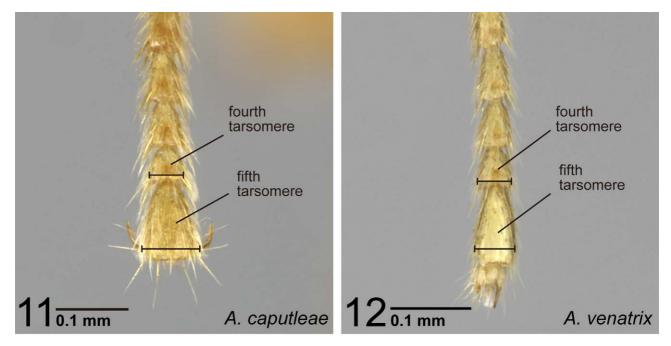


**FIGURES 7–8.** Clypeus and mandible of *Adetomyrma* workers in oblique full-face view. 7, *A. bressleri* (CASENT0205995: holotype); 8, *A. caputleae* (CASENT0227994: paratype). 7, only a single hair is present lateral of the longest anterior clypeal hair; 8, two or more hairs are present lateral of the longest anterior clypeal hair. 7, a denticle is present on the base of the subapical tooth; 8, no denticle is present on the base of the subapical tooth.

- 2. Propodeal spiracle large, visible in dorsal view at posterior lateral corner of propodeum (Fig 9). In lateral view, petiolar spiracle large, its horizontal diameter as long as the distance between the spiracle and anterior margin of petiolar node . . . bressleri

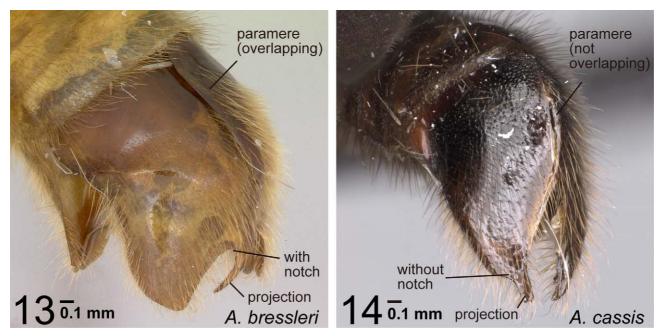


**FIGURES 9–10.** Propodeum of *Adetomyrma* workers in dorsal view. 9, *A. bressleri* (CASENT0205995: holotype); 10, *A. goblin* (CASENT0227981: holotype). 9, the propodeal spiracles are visible in dorsal view; 10, the propodeal spiracles are not visible in dorsal view.



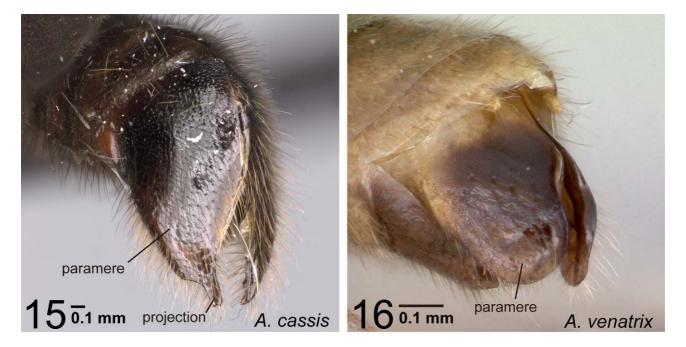
**FIGURES 11–12.** Metatarsus of *Adetomyrma* workers in posterior view. 11, *A. caputleae* (CASENT0227994: paratype); 12, *A. venatrix* (CASENT0489808). 11, the fifth tarsomere distinctly wider compared to fourth; 12, the fifth tarsomere almost the same width as fourth.

#### Males



**FIGURES 13–14.** Terminal abdominal segments of *Adetomyrma* males in oblique dorsal view. 13, *A. bressleri* (CASENT0008693); 14, *A. cassis* (CASENT0163620: holotype). 13, paramere is broadly overlapping dorsally, and with a deep notch separating between a needle-like projection and paramere; 14, paramere is not or narrowly overlapping dorsally, and without a deep notch between a needle-like projection and the paramere.

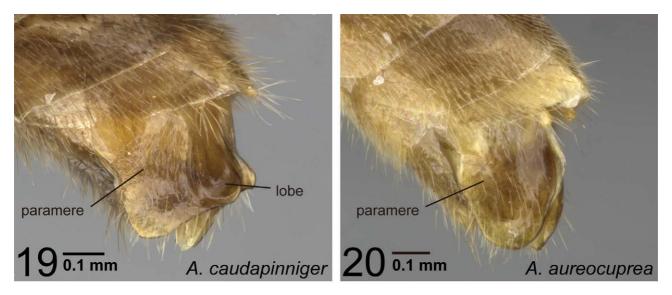
- 2. Posterior portion of paramere narrow, forming a blunt, needle-like projection (Fig 15). Large species (WL>2.1mm). . . . cassis
- -. Posterior portion of paramere wide, not forming a needle-like projection (Fig 16). Small to medium species (WL<2.1mm) . . 3



**FIGURES 15–16.** Terminal abdominal segments of *Adetomyrma* males in oblique dorsal view. 15, *A. cassis* (CASENT0163620: holotype); 16, *A. venatrix* (CASENT0079480). 15, paramere with a needle-like projection on its posterodorsal portion; 16, paramere without needle-like projection on its posterodorsal portion.

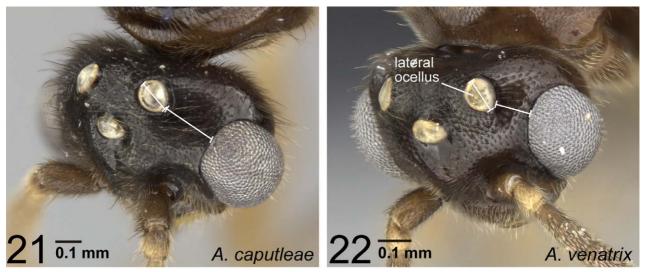


**FIGURES 17–18.** Mesosoma of *Adetomyrma* males in dorsal view. 17, *A. goblin* (CASENT0084070); 18, *A. venatrix* (CASENT0151606). 17, notaulus and parapsidal line are clearly impressed on the mesoscutum; 18, notaulus is not impressed but parapsidal line is impressed.



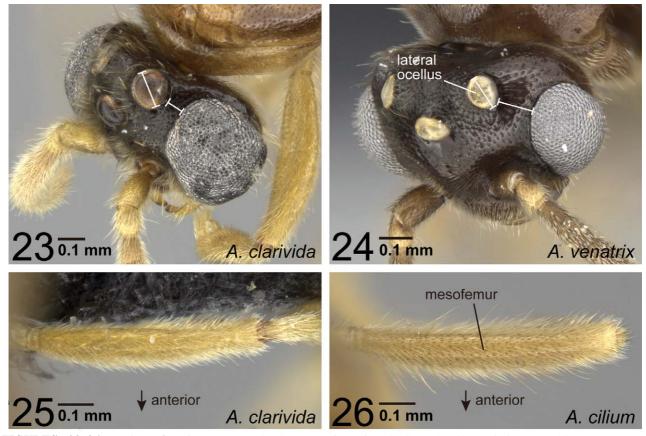
**FIGURES 19–20.** Paramere of *Adetomyrma* males in lateral view. 19, *A. caudapinniger* (CASENT0244415: holotype); 20, *A. aureocuprea* (CASENT0227991: holotype). 19, a broad and distinct lobe is present on posterodorsal portion of the paramere; 20, a broad and distinct lobe is absent on posterodorsal portion of the paramere.

- -. Lateral ocellus relatively large and close to eye; distance between them less than 1.5× maximum diameter of lateral ocellus (Fig 22). Subpetiolar process variable, but usually poorly developed and often without hairs. Body color brown to yellow. 6



**FIGURES 21–22.** Head of *Adetomyrma* males in oblique dorsal view. 21, *A. caputleae* (CASENT0227999: paratype); 22, *A. venatrix* (CASENT0151606). 21, lateral ocellus is distant from the eye; 22, lateral ocellus is close to the eye.

- 6. Distance between lateral ocelli about same length or less than maximum diameter of mid ocellus. Distance between lateral ocellus and eye 0.5× or less than maximum diameter of lateral ocellus (Fig 23). Hairs on compound eye more than 0.33× of horizontal diameter of mid ocellus. Anterior face of mesofemur with only subdecumbent short hairs (Fig 25)..... clarivida



**FIGURES 23–26.** Males of *Adetomyrma*. 23, 25, *A. clarivida* (CASENT0064259: holotype); 24, *A. venatrix* (CASENT0151606); 26, *A. cilium* (CASENT0007808: holotype). 23, 24, head in oblique dorsal view; 24, 26, mesofemur in dorsal view. 23, lateral ocellus is large, and close to the eye; 24, lateral ocellus is small, and distant from the eye; 25, only short hairs are present on the anterior face of the mesofemur; 26, short and long hairs are present on the anterior face of the mesofemur.



**FIGURES 27–28.** Eye of *Adetomyrma* males in full-face view. 27, *A. cilium* (CASENT0007808: holotype); 28, *A. aureocu-prea* (CASENT0227991: holotype). 27, hairs on the eye longer than 0.5× length of horizontal diameter of the mid ocellus; 28, hairs on the eye are shorter than 0.25× length of horizontal diameter of the mid ocellus.

- 8. Body color uniform dark brown (Fig 37). Parapsidal line clearly impressed, usually highlighted with darker pigment. *venatrix*

#### **Oueens**

Queens are known only in *Adetomyrma caputleae* (ergatoid) and *A. goblin* (alate), and these two queens are easily distinguished by the absence (*A. caputleae*) or presence (*A. goblin*) of wings and lateral ocelli. A comparison of the morphology of the males of these two species suggests that larger males with a larger mesosoma are associated with ergatoid queens. If this pattern holds true for the other remaining species, then all *Adetomyrma* queens other than *A. goblin* might be ergatoid.

# **Review of species**

Adetomyrma aureocuprea sp. nov.

(Figs 20, 28, 29, 38, 47, 56, 64)

**Holotype.** Male: CASENT0227991, BLF07304: MADAGASCAR, Fianarantsoa, Parc National d'Isalo, 9.1 km 354° N Ranohira, 22° 28.9′ S, 45° 27.7′ E, 725 m alt., gallery forest, at light, 27–31.i.2003, Fisher, Griswold *et al.* leg. [CASC]

**Paratypes.** 4 males: CASENT0247003 [CASC], CASENT0247004 [BMNH], CASENT0490920 [MHNG], CASENT0490924 [MCZC], with same data as holotype.

Worker and queen unknown.

**Male. Description.** Measurements: holotype. HL 0.57, HW 0.87, SL 0.16, EL 0.43, WL 1.42, MnW 0.9, CI 152.4, SI 18, EI 74.8, MnI 103.9.

HL 0.44–0.63, HW 0.59–0.91, SL 0.11–0.17, EL 0.3–0.45, WL 1.03–1.54, MnW 0.63–0.88, CI 135.6–145.7, SI 17.9–19.6, EI 67.4–75, MnI 97.1–106.3 (5 specimens measured).

Eye large and prominent, varied in size, but posterior margin not exceeding posterior margin of mid ocellus in full-face view (Fig 47). Distance between lateral ocellus and eye about same as diameter of lateral ocellus. Palpal formula 3,3 (three maxillary and three labial). Notaulus absent on mesoscutum. Parapsidal line usually unclear,

sometimes weakly impressed but never pigmented with darker color (Fig 38). Anterior margin of petiole longer than dorsal margin in lateral view (Fig 29). Subpetiolar process not developed, without hairs (Fig 29).

Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere (Fig 20). No distinct projection or lobe present on posterodorsal portion of paramere. Basal ring not reduced, covering whole anterior margin of paramere in lateral view. Basal projection on cuspis clear but not extraordinarily well developed. Aedeagus in lateral view as in Figure 56: distal portion narrowed distal to ventral projection, apical margin relatively sharp, but without small projection on its posteroventral portion, posteroventral margin of ventral projection convex.

Hair on compound eyes short, about  $0.25 \times$  diameter of mid ocellus (Fig 28). With mesofemur in dorsal view, anterior face with dense appressed hairs, and sometimes several longer subdecumbent hairs on basal portion. Ventral margin of eye not edged with darker pigment or punctures. Body bicolored, head brown and remainder yellow (Fig 29).

**Etymology.** This species name is derived from the Latin words aureus (golden) and cupreus (coppery), referring to the body coloration. The species epithet is treated as a noun in apposition, and thus invariant.

**Distribution.** MADAGASCAR: as in Figure 64.

**Additional material examined:** in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Parc National Montagne d'Ambre [1st campsite], 12° 30.87′ S, 49° 10.88' E, 960 m alt., rainforest; Ampasindava, Forêt d'Ambilanivy, 3.9 km 181° S Ambaliha, 13° 47.92' S, 48° 9.7' E, 600 m alt., rainforest; Sofia Region, district of Port-Berger, Ambovomamy 20 km N of Port-Berger, 15° 27.07′ S, 47° 36.8′ E, 86 m alt., secondary forest on white sandy area; Boeny Region, district of Marovoay, Ampijoroa National Park, 160 km North of Maevatanana on RN 04, 16° 19.16′ S, 46° 48.8′ E, 42 m alt., deciduous forest; Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 16° 24.4′ S, 45° 18.6′ E, 100 m alt., tropical dry forest; Boeny Region, district of Soalala Analamanitra forest, 14 km SW of Mitsinjo, 16° 42′ S, 45° 42′ E, 19 m alt., dense dry forest; Betsiboka Bassin, Riv: Mamokomita, Manjokavaradrano, 17° 38′ S, 46° 54.33′ E; Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 18° 42.57′ S, 44° 43.09′ E, 150 m alt., tropical dry forest on Tsingy; Menabe Region, district of Morondava, Beroboka village NE of Morondava, Antsarongaza dry forest 7.5 km E of Beroboka, 19° 58.65′ S, 44° 39.98′ E, 50 m alt., dry forest; Menabe Region, district of Morondava, Beroboka village NE of Morondava, Antsarongaza gallery forest 7 km E of Beroboka, 19° 58.65′ S, 44° 39.92′ E, 128 m alt., gallery forest; Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20° 35.6′ S, 46° 33.8′ E, 1550 m alt., montane rainforest; Base Makay, 21° 13.37′ S, 45° 19.49′ E, 490 m alt., gallery forest on sandy soil; Atsimo Andrefana Region, district of Betioky, 30 km E Betioky, Beza Mahafaly Special Reserve (around Research Station), 23° 41.19' S, 44° 35.46' E, 165 m alt., gallery dry deciduous forest; Parc National d'Isalo, 9.1 km 354° N Ranohira, 22° 28.9' S, 45° 27.7' E, 725 m alt., gallery forest; 1 km E of Isalo National Park Interpretive Center, Fianarantsoa Prov., 22° 37.6′S, 45° 21.49′ E, 885 m alt., dry wash; Horombe Region, district of Ihosy, Betapia (Border of Fianarantsoa and Tulear): 9 km SW of Ilakaka Saphir town, 22° 37.73′ S, 45° 21.67′ E, 1036 m alt., Uapaca forest; Horombe Region, district of Ihosy, Isalo National Park, 900 m E of ANGAP Interpretation Center, 22° 37.6′ S, 45° 21.49° E, 701 m alt., open area near stream; Manombo Special Reserve, 32 km SE of Farafangana, 23° 1.31° S, 47° 43.2´E, 36 m alt., lowland rainforest; Atsimo Andrefana Region, district of Tulear II, Mikea deciduous dry forest 3 km N Andranomavo village, 22° 54.22′ S, 43° 28.53′ E, 30 m alt., deciduous dry forest; Fiherenana, 23° 10.62′ S, 43° 57.65′ E, 100 m alt., gallery forest; Fiherenana, 23° 14.12′ S, 43° 52.25′ E, 50 m alt., degraded gallery forest; Sept Lacs, 23° 31.25′ S, 44° 9.58′ E, 130 m alt., gallery forest mixed with spiny thicket trees; Forêt de Mite, 20.7 km 29° WNW Tongobory, 23° 31.45′ S, 44° 7.28′ E, 75 m alt., gallery forest; Sept Lacs, 23° 31.65′ S, 44° 9.27′ E, 70 m alt., gallery forest; Parcel I, Beza Mahafaly Reserve, near research station, Tulear Province, 23° 41.19′ S, 44° 35.46' E, 165 m alt., dry deciduous forest; Parcel II, Beza Mahafaly Reserve, near Bellevue, Tulear Province, 23° 41.39' S, 44° 34.53' E, 180 m alt., spiny forest; Parc National d'Andohahela, Forêt de Manantalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, 24° 49.02′ S, 46° 36.6′ E, 150 m alt., spiny forest/thicket; Androy Region, district of Tsihombe, 74 km S of Tsihombe, Cap Ste Marie Reserve, 25° 35.26′ S, 45° 9.78′ E, 37 m alt., spiny bush.

**Remarks.** Adetomyrma aureocuprea is only known from males. A. aureocuprea is easily separable from the other Adetomyrma males by the yellowish body color, no mesoscutal notaulus, poorly developed subpetiolar process, lack of posterodorsal projection or lobe on the paramere, short hairs on the compound eye, and vestigial parapsidal line.

The males of *Adetomyrma aureocuprea* display remarkable morphological variation in, for example, the size of the eye and ocelli, head shape, mesonotal shape, petiolar shape, and hairs on body surface. *A. aureocuprea* (Fig 64) is completely sympatric with *A. bressleri* (Fig 65), *A. caputleae* (Fig 66), *A. goblin* (Fig 71), and *A. venatrix* (Fig 72), and was collected within a 20 km radius of *A. cilium* (Fig 69) and within a 70 km radius of *A. caudapinniger* (Fig 68). The morphological differences between all species are clear and consistent in each case of sympatric and geographically close localities, even though apparent similarity may be shown to a character of another *Adetomyrma* species collected from distant localities. In addition to the above species, the distribution of *A. aureocuprea* is parapatric with *A. clarivida* (Fig 70). Separation between *A. aureocuprea* and *A. clarivida* is strongly supported by the morphological differences observed in the aedeagus (Figs 56 and 61).

This new species corresponds to the following species code used in previous studies: mgm05 (in part): Yoshimura & Fisher 2012.

# Adetomyrma bressleri sp. nov.

(Figs 7, 9, 13, 30, 39, 48, 57, 65, 73, 74, 81)

**Holotype.** Worker: CASENT0205995, BLF26111: MADAGASCAR, Antsiranana, Parc National Montagne d'Ambre, 12° 30.83′ S, 49° 10.67′ E, 984 m alt., montane rainforest, ground nest, 2.iii.2011, B.L.Fisher *et al.* leg. [CASC]

**Paratypes.** 4 workers: CASENT0205996 [BMNH], CASENT0205997 [MHNG], CASENT0205998 [MCZC], CASENT0205999 [NHMB], with same data as holotype; 1 male, CASENT0205990, BLF26044: MADAGAS-CAR, Antsiranana, Parc National Montagne d'Ambre, 12° 30.83′ S, 49° 10.67′ E, 984 m alt., montane rainforest, Malaise trap, 23–24.ii.2011, B.L. Fisher *et al.* leg. [CASC]

**Worker. Description.** Measurements: holotype. HL 0.85, HW 0.8, SL 0.45, HD 0.5, WL 1.03, PnW 0.46, MnW 0.25, PpW 0.41, PtW 0.38, CI 93.6, SI 56.9, MnI 31.8, PpI 159.8, PtI 94.1.

HL 0.84–0.9, HW 0.73–0.8, SL 0.46–0.48, HD 0.48–0.55, WL 0.98–1.08, PnW 0.45–0.48, MnW 0.24–0.27, PpW 0.38–0.43, PtW 0.37–0.41, CI 86.7–89.5, SI 59.7–63.2, MnI 30.7–34, PpI 152.8–168.8, PtI 93.1–97.7 (4 paratypes measured).

Head subquadrate in full-face view: longer than wide, sides slightly convex, wider around midlength of head capsule, weakly converging anteriorly and posteriorly, posterior margin concave (Fig 81). Clypeal principal surface deflected ventrally. Anterior margin of clypeus broadly convex, furnished with row of about 26 small, specialized, conical setae. Frontal carinae in full-face view short and low, expanded laterally as small frontal lobes about 1.5× wider than length of antennal insertions. Mandible subfalcate, without distinct basal and masticatory margins, inner margin with two apical teeth and five basal denticles (Fig 7): one small denticle on base of subapical tooth (second tooth from apex) (Fig 7); out of five denticles, second and fifth denticles from apical-most one larger than others; second denticle largest (longest); third denticle small and adjacent with second one, and division between them unclear on its base; basal-most denticle sometimes divided into two adjacent small, low denticles (observed in CASENT0205999). Palpal formula 3,3 (three maxillary and three labial). Antennal scape shorter than head length. Pedicel (second antennal segment) shorter than combined length of next three (third to fifth) antennal segments. Antenna gradually broadened from third segment and not forming distinct club. Dorsal outline of mesosoma in lateral view somewhat arched, mesonotum raised from pronotal and propodeal dorsum, metanotal groove often clearly impressed. Pronotum in dorsal view longer than broad, with convex sides. Mesonotum in dorsal view short, slightly wider than long. Metapleuron fully fused with propodeum, but divided by shallow furrow. Dorsal face of propodeum almost as wide as pronotum, less than 1.5× longer than wide, sides strongly converging toward mesonotum (Fig 74). Propodeal dorsal margin in lateral view less than 2× the length of the declivitous margin, rounding gently into the latter. Propodeal spiracle large, located close to propodeal dorsal margin in lateral view, fully visible in dorsal view. Subpetiolar process distinctly developed, shaped like an irregular axe blade. Shallow and sparse punctures covering head, mesosoma, and abdomen. Clypeus with two groups of hairs; mid clypeal hairs directed dorsally, and anterior clypeal hairs deflected anteriorly. Mid clypeal hairs consisting of one long hair and one or two shorter hairs around the long one. With clypeus in full-face view, anterior clypeal hairs consisting of one pair of long hairs and a single shorter hair laterally (Fig 7).

Queen unknown.

**Male. Description.** Measurements: HL 0.82–0.86, HW 1.18–1.26, SL 0.27–0.3, EL 0.44–0.51, WL 2.22–2.35, MnW 1.55–1.69, CI 140.4–147.2, SI 22.9–24.4, EI 54.1–59.3, MnI 129.3–140.6 (5 individuals measured).

Eye well-developed and prominent, posterior margin not exceeding posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye long,  $3 \times$  longer than diameter of lateral ocellus. Palpal formula 3,3 (three maxillary and three labial). Notaulus absent on mesoscutum (Fig 39). Parapsidal line clearly impressed. Anterior margin of petiole longer than dorsal margin in lateral view. Subpetiolar process well-developed, with dense hairs ventrally.



FIGURES 29–37. Males of *Adetomyrma* in lateral view. 29, *A. aureocuprea* sp. nov. (CASENT0227991: holotype); 30, *A. bressleri* sp. nov. (CASENT0008693); 31, *A. caputleae* sp. nov. (CASENT0079552); 32, *A. cassis* sp. nov. (CASENT0163620: holotype); 33, *A. caudapinniger* sp. nov. (CASENT0244415: holotype); 34, *A. cilium* sp. nov. (CASENT0007808: holotype); 35, *A. clarivida* sp. nov. (CASENT0064259: holotype); 36, *A. goblin* sp. nov. (CASENT0084070); 37, *A. venatrix* (CASENT0151606).

Left and right parameres broadly overlapping along almost entire length of basimere (Fig 13). Distinct, flattened, and needle-like projection present on each posterodorsal portion of paramere (Fig 13). Basal ring reduced to about  $0.33\times$  of parameral maximum height in lateral view. Basal projection on cuspis extraordinarily well developed, as large as digitus, and replacing the usual position of cuspis; cuspis also well developed and elongate, and surrounding digitus. Aedeagus in lateral view as in Figure 57; mid portion distinctly widened and distal portion extremely narrowed; ventral projection vestigial and inconspicuous; its apical portion narrowed but hard, and curved as a hook.

Hair on compound eyes long, almost as long as diameter of mid ocellus (Fig 48). Mesofemur in dorsal view with anterior face covered in dense subdecumbent hairs. Ventral margin of eye edged with darker pigment but without minute punctures on the area. Body yellow with bicolored head, brown on its dorsal face and yellow on its ventral face (Fig 30).

**Etymology.** The specific epithet is a patronymic referring to Dr. Barry Lee Bressler, retired physicist, former adjunct professor of physics at Virginia Polytechnic Institute and State University, and amateur naturalist, in recognition of his interest in myrmecology and his support for research on ants. The species epithet is treated as a noun in apposition, and thus invariant.

**Distribution.** MADAGASCAR: as in Figure 65.

**Additional material examined**: in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Sakalava Beach, vegetated beach dunes, 12° 15.77′ S, 49° 23.85′ E, 10 m alt., across sandy trail in dwarf littoral forest; 7 km N Joffreville, camp 2 of Fisher, 12° 20′ S, 49° 15′ E, 360 m alt., in dry forest; Parc National Montagne d'Ambre, 12° 30.83′ S, 49° 10.67′ E, 984 m alt., montane rainforest; Parc National Montagne d'Ambre, first campsite, 12° 30.87′ S, 49° 10.88′ E, 960 m alt., rainforest; Parc National Montagne d'Ambre, lemur trail, 12° 31′ S, 49° 11′ E, 975 m alt., rainforest; Parc National Montagne d'Ambre, Petit Lac road, 12° 31.22′ S, 49° 10.75′ E, 1125 m alt., rainforest; Parc National Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12° 35.78′ S, 49° 9.57′ E, 1300 m alt., montane rainforest; Andasibe National Park, botanic garden near entrance, west of ANGAP office, 18° 55.58′ S, 48° 24.47′ E, 1025 m alt., tropical forest.



FIGURES 38–46. Males of *Adetomyrma* in dorsal view. 38, *A. aureocuprea* sp. nov. (CASENT0227991: holotype); 39, *A. bressleri* sp. nov. (CASENT0008693); 40, *A. caputleae* sp. nov. (CASENT0079552); 41, *A. cassis* sp. nov. (CASENT0163620: holotype); 42, *A. caudapinniger* sp. nov. (CASENT0244415: holotype); 43, *A. cilium* sp. nov. (CASENT0007808: holotype); 44, *A. clarivida* sp. nov. (CASENT0064259: holotype); 45, *A. goblin* sp. nov. (CASENT0084070); 46, *A. venatrix* (CASENT0151606).

**Remarks.** Workers of *Adetomyrma bressleri* are clearly distinguished from other genus members by a combination of a single shorter hair lateral to the longest one on the anterior clypeal margin in full-face view, the presence of a small denticle on the basal portion of the mandibular subapical tooth, and a large propodeal spiracle that is located posterodorsally and fully visible in dorsal view. *A. bressleri* is easily distinguished from other *Adetomyrma* males by its giant yellow body, parameres overlapping broadly on almost the whole length of the basimere, and a flattened, needle-like projection on the posterodorsal portion of the paramere (Fig 13).

The males of *A. bressleri* (= mg03: Yoshimura & Fisher 2012) have been collected numerous times by Malaise traps at the higher elevations of Montagne d'Ambre (900–1300m). The first collection date from Malaise traps was in 2001. Since then, three expeditions to Montagne d'Ambre have been organized to find the female castes, but not until 2011 was the worker caste finally found. To find the worker caste, Malaise traps were set up and monitored for the collection of males. Once males were collected, logs and branches on the ground around the trap were inspected. On the last day of the trip in 2011, workers were found in a log near a trap that had collected males. As

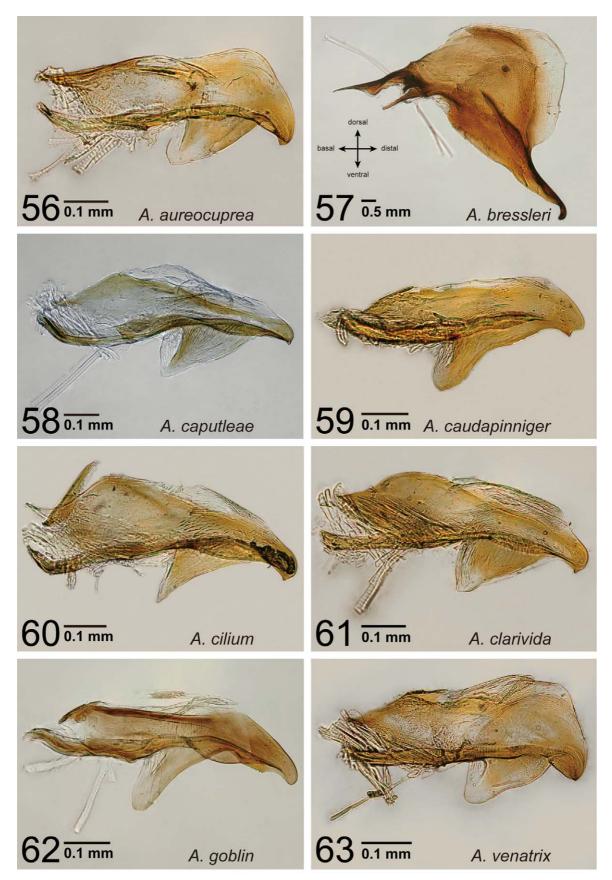
the log was pulled apart for worker ants (BLF26111), the nearby Malaise trap (BLF26044), which was moved directly above the log, captured males leaving the log. These collections did not yield a visible queen but included 291 workers and 814 larvae.

Although the males of *A. goblin* (Fig 71) and *A. aureocuprea* (Fig 64) were collected from either the same location or localities close to where *A. bressleri* was found (Fig 65), we differentiate the workers of the former two species from the latter with confidence. The association between males and workers in *A. goblin* has been clarified by colony series material. The morphological similarities of the males of *A. aureocuprea* and *A. venatrix* strongly suggest that the workers of *A. aureocuprea* share several important characters with that of *A. venatrix*, including the lack of a basal denticle on the base of the subapical mandible tooth (as in Fig 8), and two shorter hairs lateral to the longest hair on the anterior margin of the clypeus in full-face view (Fig 8). In contrast, the worker of *A. bressleri* has a basal denticle (Fig 7), and only a single hair lateral to the longest anterior clypeal hair in full-face view (Fig 7).

This new species corresponds to the following species code below used in previous studies: mg03: Yoshimura & Fisher 2012.



FIGURES 47–55. Head of *Adetomyrma* males in full-face view. 47, *A. aureocuprea* sp. nov. (CASENT0227991: holotype); 48, *A. bressleri* sp. nov. (CASENT0008693); 49, *A. caputleae* sp. nov. (CASENT0079552); 50, *A. cassis* sp. nov. (CASENT0163620: holotype); 51, *A. caudapinniger* sp. nov. (CASENT0244415: holotype); 52, *A. cilium* sp. nov. (CASENT0007808: holotype); 53, *A. clarivida* sp. nov. (CASENT0064259: holotype); 54, *A. goblin* sp. nov. (CASENT0084070); 55, *A. venatrix* (CASENT0151606).



**FIGURES 56–63.** Aedeagal plate of *Adetomyrma* males in lateral view. 56, *A. aureocuprea* **sp. nov.** (CASENT0008678); 57, *A. bressleri* **sp. nov.** (CASENT0218012); 58, *A. caputleae* **sp. nov.** (CASENT0218011); 59, *A. caudapinniger* **sp. nov.** (CASENT0111791); 60, *A. cilium* **sp. nov.** (CASENT0218014); 61, *A. clarivida* **sp. nov.** (CASENT0111802); 62, *A. goblin* **sp. nov.** (CASENT0218010); 63, *A. venatrix* (CASENT0063101).

(Figs 8, 11, 21, 31, 40, 49, 58, 66, 75, 76, 82, 85, 87, 89, 91, 92)

**Holotype.** Worker: CASENT0227992, BLF02537, MADAGASCAR, Antananarivo, 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 18° 28.4′ S, 47° 57.6′ E, 1300malt., montane rainforest, ex rotten log, 5–13.xii.2000, Fisher, Griswold *et al.* leg. [CASC]

Paratypes. 7 workers: CASENT0004352 [BMNH], CASENT0227993 [CASC], CASENT0227994 [CASC], CASENT0227995 [CASC], CASENT0227996 [MCZC], CASENT0227997 [MHNG], CASENT0227998 [NHMB], 7 males: CASENT0004353 [BMNH], CASENT0011473 [CASC], CASENT0227978 [CASC], CASENT0227979 [CASC], CASENT0227980 [MCZC], CASENT0227999 [MHNG], CASENT0247048 [NHMB], with same data as holotype.

**Worker. Description.** Measurements: holotype. HL 0.72, HW 0.7, SL 0.44, HD 0.5, WL 1.01, PnW 0.47, MnW 0.26, PpW 0.36, PtW 0.39, CI 97.4, SI 63.1, MnI 36.5, PpI 142.7, PtI 106.3.

HL 0.57–0.72, HW 0.53–0.7, SL 0.35–0.45, HD 0.36–0.5, WL 0.81–1.05, PnW 0.36–0.45, MnW 0.2–0.26, PpW 0.3–0.37, PtW 0.27–0.4, CI 91.9–97.9, SI 60.4–68.9, MnI 37.2–38.8, PpI 140.7–149.5, PtI 91.3–107 (10 individuals measured).

Head quadrate in full-face view, almost as long as wide; sides slightly convex, widening near the mandibular insertions, converging posteriorly; posterior margin almost flat (Fig 82). Clypeal principal surface deflected ventrally. Anterior margin of clypeus broadly convex with small, shallow central concavity, and furnished with a row of about 26 small, specialized conical setae. Frontal carinae in full-face view short and low, expanded laterally as small frontal lobes covering more than about 2× the length of antennal insertions. Mandible subfalcate, without distinct basal and masticatory margins (Fig 8): inner margin with two apical teeth and three basal denticles; no denticle on base of subapical tooth (second tooth from apex); apical-most denticle slightly larger than other two; sometimes basal-most (third from apical-most one) denticle divided into two adjacent small, low denticles (CASENT004363). Palpal formula 3,3 (three maxillary and three labial). Antennal scape shorter than head length. Pedicel (the second antennal segment) shorter than combined length of next three (third to fifth) antennal segments. Antenna gradually broadened from third segment and not forming a distinct club. Dorsal outline of mesosoma in lateral view flattened, mesonotum not raised from pronotal and propodeal dorsum. Pronotum in dorsal view longer than broad, with convex sides. Mesonotum in dorsal view short, 2× as wide as long. Metapleuron fully fused with propodeum, division of the two plates not distinguishable in lateral view. Dorsal face of propodeum narrower than pronotum, about 1.5× longer than wide, with subparallel sides converging slightly toward mesonotum (Fig 76). Propodeum in lateral view, its dorsal margin 2× or less the length of its declivity, and rounding gently into the latter. Propodeal spiracle medium sized, distant from propodeal dorsal margin in lateral view, usually not visible in dorsal view. Subpetiolar process distinctly developed, shaped like an irregular axe blade. Shallow and dense punctures covering dorsal head, mesosoma, abdomen, and ventral head. Clypeus with two groups of hairs; mid clypeal hairs directed dorsally, and anterior clypeal hairs deflected anteriorly. Mid clypeal hairs consisting of one long hair and one to several shorter hairs around the long one. With head in full-face view, anterior clypeal hairs consisting of one pair of long hairs and two (sometimes three) shorter hairs laterally (Fig 8).

**Queen. Description.** Measurements: HL 0.92–1.07, HW 1.05–1.18, SL 0.53–0.56, EL 0.07–0.07, WL 1.4–1.48, MnW 0.55–0.68, PpW 0.74–0.78, PtW 0.81–0.93, CI 108.1–114.6, SI 47.1–51, EI 6.9–7.2, MnI 51.1–57.7, PpI 114.2–134.4, PtI 110–126.1 (3 individuals measured).

Wingless. Head quadrate in full-face view (Fig 89), almost as long as wide; sides slightly convex; posterior margin slightly concave. Eye small, consisting of about seven ommatidia. Mid ocellus vestigial in a small concavity. Lateral ocelli absent. Clypeal principal surface not strongly deflected. Anterior margin of clypeus with central concavity, and furnished with a row of about 17 small, specialized, conical setae. Frontal lobes separated by midposterior portion of clypeus. Mandible subfalcate, without distinct basal and masticatory margins, inner margin with two apical teeth and two low and dull basal denticles, no denticle on base of subapical tooth (second tooth from apex). Antennal scape  $0.5\times$  as long as combined length of pedicel and flagellum. First flagellomere as long as wide. Distal antennal segments not forming distinct club. In lateral view, mesosomal dorsum somewhat flattened (Fig 85); pronotum occupying entire anterior and about  $0.33\times$  of dorsal margins; mesonotum reduced in size and only occupying about  $0.33\times$  of mesosomal dorsal margin; metanotum not visible; propodeum occupying about  $0.33\times$  of remaining dorsal and posterior margins. With mesosoma in dorsal view, division between mesoscutum

and mesoscutellum often unclear (Fig 87); axillae not distinct; metanotum reduced into narrow tip; and propodeum distinctly widened posteriorly. Propodeal spiracle in lateral view located close to propodeal declivity in lateral view, distance from declivity margin as long as diameter of spiracle. Petiole stouter than that in conspecific worker (Fig 87), distinctly wider than long, width approximately same as that of propodeum in dorsal view, anterodorsal portion more protruding anteriorly in lateral view. When metasoma seen in dorsal view, little difference in width present between posterior portion of petiole and anterior portion of abdominal segment III.

Clypeus with long hairs; division of mid clypeal hairs and anterior clypeal hairs unclear. With head in full-face view, anterior portion of clypeus with one pair of long hairs and two (sometimes three) shorter hairs laterally (Fig 89). Body surface with denser appressed hairs than in conspecific workers.

**Male. Description.** Measurements: HL 0.64–0.73, HW 0.91–1.1, SL 0.2–0.26, EL 0.39–0.44, WL 1.84–2.03, MnW 1.13–1.27, CI 143–151.2, SI 21–24.3, EI 60.4–67, MnI 114.8–124.1 (5 individuals measured).

Eye well developed and prominent, posterior margin not exceeding posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye longer than 1.5× diameter of lateral ocellus (Fig 21). Palpal formula 3,3 (three maxillary and three labial). Notaulus absent on mesoscutum. Parapsidal line clearly impressed (Fig 40). Anterior margin of petiole as long as or shorter than dorsal margin in lateral view. Subpetiolar process well developed, usually with more than five hairs ventrally.

Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere. No distinct projection or lobe present on posterodorsal portion of paramere. Basal ring not reduced, covering whole anterior margin of paramere in lateral view. Basal projection on cuspis clear but not extraordinarily well developed. Aedeagus in lateral view as in Figure 58; narrowing from base of ventral projection; apical margin relatively sharp with a small, broadly triangular projection on posteroventral portion; posteroventral margin of ventral projection convex.

Hair on compound eyes short,  $0.33 \times$  to  $0.5 \times$  diameter of mid ocellus. Mesofemur in dorsal view, its anterior face with dense decumbent hairs, and sometimes one or two longer suberect hairs. Ventral margin of eye not edged with darker pigment or punctures. Body color uniform dark brown (Fig 31).

**Etymology.** This species name is derived from the Latin words caput (head) and lea (lioness), referring to the stout, thick head of the new species. The species epithet is treated as a noun in apposition, and thus invariant.

**Distribution.** MADAGASCAR: as in Figure 66.

Additional material examined: in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Analamanga Region, district of Ankazobe, Ambohitantely, 46 km NE of Ankazobe, 18° 11.88′ S, 47° 16.89′ E, 701 m alt., sclerophyll forest; 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 18° 28.4′ S, 47° 57.6′ E, 1300 m alt., montane rainforest; Ankokoy Forest, 3 km E Ibity, malaise in Uapaca forest, 20° 4.05′ S, 46° 59.97′ E, 1700 m alt., Uapaca forest; Amoron'i Mania Region, district of Ambositra, Italaviana Uapaca forest, 135km SE of Antsirabe, 20° 10.4′ S, 47° 5.16′ E, 1359 m alt., Uapaca forest; Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20° 35.6′ S, 46° 33.8′ E, 1550 m alt., montane rainforest; 27.4 km SSW Ambositra, 20° 46.2′ S, 47° 11.2′ E, 1600 m alt., disturbed montane rainforest; Parc naturel communautaire, 26.8 km SW Ambositra, 20° 46.5′ S, 47° 11.02′ E, 1755 m alt., disturbed montane rainforest; Miandritsara Forest, 40 km S of Ambositra, 20° 47.56′ S, 47° 10.54′ E, 822 m alt., rainforest; Vohiparara broken bridge, Fianarantsoa Prov., 21° 13.57′ S, 47° 22.19′ E, 1110 m alt., high altitude rainforest; radio tower, Ranomafana National Park, Fianarantsoa Prov., 21° 15.05′ S, 47° 24.43′ E, 1130 m alt., forest edge, mixed tropical forest, open area; Fitovavy Fitovinany Region, district of Ifanadiana, 12 km W of Ranomafana, 21° 15.05′ S, 47° 24.43′ E, 1127 m alt., forest edge, open area; JIRAMA water works near river, Ranomafana National Park, Fianarantsoa Prov., 21° 14.91′ S, 47° 27.13′ E, 690 m alt., open area near stream; Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., 21° 15.99′ S, 47° 25.21′ E, 1020 m alt., mixed tropical forest; Foret d'Ambalagoavy Nord, Ikongo, Ambatombe, 21° 49.65′ S, 47° 20.33′ E, 625 m alt.; Parc National d'Andringitra, Plateau d'Andohariana, 35.9 km 205° Ambalavao, 22° 9.14′ S, 46° 53.95′ E, 2000 m alt., ericoid thicket.

**Remarks.** The worker of *Adetomyrma caputleae* is easily distinguished from that of *A. bressleri* and *A. goblin* by the lack of a small denticle on the basal portion of the subapical tooth and by having more than one hair lateral to the longest anterior clypeal hairs (Fig 8), and from *A. venatrix* (Fig 84) by the flattened posterior margin of the head in full-face view (Fig 82) and the swollen ventral margin of the head in lateral view. In the male, this species is distinguished from other *Adetomyrma* species by the combination of a smaller lateral ocellus distant from the eye, the relatively longer dorsal margin than anterior margin of the petiole, the paramere without projection or lobe, and the brown body color.

Geographical variation in male characters can be observed in body size, wing color, head shape, and the development of the subpetiolar process and its hairs. The smallest specimens are often similar to males of *A. venatrix*; however, the diagnostic characters above still separate *A. caputleae* from *A. venatrix*. Specimens from Forêt d'Atsirakambiaty (20° 35.6′ S, 46° 33.8′ E, 1550 m alt.) show larger morphological differences from the others in wing color and head shape. The Forêt d'Atsirakambiaty specimens were separately listed as *A.* mg05 in Yoshimura & Fisher (2012). However, our detailed examination revealed that the apparent differences appear in only one parapatric population. Moreover, the morphological differences are not very consistent, which are observed even within members of a single colony. Therefore these morphological differences should be regarded as intraspecific variations.

This new species corresponds to the following species codes used in previous studies:

sp.2a: Saux *et al.*sp.2b: Saux *et al.* 2004; Moreau *et al.*MAD02: Brady *et al.*sp.Ma-02: Ouellette *et al.*sp.Ma-04: Ouellette *et al.*mg02: Yoshimura & Fisher, 2012

mg05: Yoshimura & Fisher, 2012

#### Adetomyrma cassis sp. nov.

(Figs 14, 15, 32, 41, 50, 67)

**Holotype.** Male: CASENT0163620, BLF24309: MADAGASCAR, Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16° 46.36′ S, 49° 15.93′ E, 450 m alt., rainforest, 4 Malaise traps, 20–24.ii.2010, B.L.Fisher *et al.* [CASC]

Worker and queen unknown.

**Male. Description.** Measurements: holotype. HL 0.74, HW 1.08, SL 0.3, EL 0.43, WL 2.22, MnW 1.33, CI 144.8, SI 27.9, EI 58.1, MnI 123.8.

Eye well-developed and prominent, posterior margin not exceeding posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye long, about 3× longer than diameter of lateral ocellus. Palpal formula 3,2? (three maxillary and two? labial: observed without dissection). Notaulus absent on mesoscutum (Fig 41). Parapsidal line clearly impressed. Anterior margin of petiole as long as dorsal margin in lateral view. Subpetiolar process well-developed, with dense hairs ventrally.

Left and right parameres narrowly overlapping on dorsal small part of basimere (Figs 14, 15). Distinct, flattened projection present on each posterior portion of paramere with small denticles on distal and mesal portions of projection (Figs 14, 15).

Hair on compound eyes long, longer than diameter of mid ocellus (Fig 50). Mesofemur in dorsal view with anterior face covered in dense, subdecumbent hairs. Ventral margin of eye edged with darker pigment but without minute punctures on the area. Body color almost uniform dark brown but head darker (Fig 32).

**Etymology.** This species name is derived from the Latin word cassis (helm), and refers to the shape of its genital capsule, which looks like a Corinthian helm. The species epithet is treated as a noun in apposition, and thus invariant.

**Distribution.** MADAGASCAR: as in Figure 67.

**Remarks.** Adetomyrma cassis is only known from a single male collected in Réserve Spéciale Ambatovaky. The male of A. cassis is distinguished easily from other Adetomyrma males by a distinct and flatted projection on the posterior portion of the paramere (Fig 15). This projection is not separated from the paramere by a deep notch (Fig 14) as in A. bressleri (Fig 13).

This genital character observed in *Adetomyrma cassis* is completely unique and sufficient to regard this male as a distinct species, although we have found neither another specimen nor sympatric distribution with other *Adetomyrma* species.

#### Adetomyrma caudapinniger sp. nov.

(Figs 19, 33, 42, 51, 59, 68)

**Holotype.** Male: CASENT0244415, MG-29-75: MADAGASCAR, Fianarantsoa, Miandritsara Forest, 40 km S of Ambositra, 20° 47.56′ S, 47° 10.54′ E, 822 m alt., low altitude rainforest, Malaise trap, 15–24.i.2007, Rin'ha, Mike leg. [CASC]

**Paratypes.** 1 male: CASENT0244416, with same data as holotype [CASC]; 1 male: CASENT0244402, MG-29–76: same locality and method as holotype, 24–31.i.2007, Rin'ha, Mike leg. [CASC]

Worker and queen unknown.

**Male. Description.** Measurements: holotype. HL 0.57, HW 0.86, SL 0.2, EL 0.39, WL 1.48, MnW 0.93, CI 151.3, SI 23.4, EI 68.1, MnI 107.8.

HL 0.51–0.6, HW 0.71–0.88, SL 0.15–0.2, EL 0.36–0.43, WL 1.26–1.6, MnW 0.75–0.98, CI 138.6–147.5, SI 21.2–23.4, EI 66.5–71.8, MnI 103.2–111.1 (2 paratypes and 2 individuals measured).

Eye well-developed and prominent (Fig 51), posterior margin not exceeding the posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye as long as or slightly longer than diameter of lateral ocellus. Palpal formula 2,2 (two maxillary and two labial). Notaulus absent on mesoscutum (Fig 42). Parapsidal line clearly impressed. Anterior margin of petiole shorter than dorsal margin in lateral view (Fig 33). Subpetiolar process developed as spinose with one to two hairs ventrally.

Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere. Distinct lobe present on posterodorsal portion of paramere, making posterior portion appearing bilobed (Fig 19). Basal ring not reduced, covering whole anterior margin of paramere in lateral view. Basal projection on cuspis clear but not extraordinarily well developed. Aedeagus in lateral view as in Figure 59; slightly narrowed after ventral projection; apical margin with two distinct apices, one relatively blunt and one with a small ventral projection; posteroventral margin of ventral projection somewhat concave.

Hair on compound eyes short, less than  $0.25 \times$  diameter of mid ocellus. Mesofemur in dorsal view, anterior face with dense subdecumbent hairs, and often with several longer subdecumbent hairs. Ventral margin of eye not edged with darker pigment or punctures. Body weakly bicolored, head darker than the rest of the body (Fig 33).

**Etymology.** This species name is derived from the Latin words caudapinna (tail fin) and gero (have), referring to the distinctive paramere. Pinniger can be both a noun and adjective, but is treated as a noun here, and thus invariant.

Distribution. MADAGASCAR: as in Figure 68.

**Additional material examined**: in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Miandritsara Forest, 40 km S of Ambositra, 20° 47.56′ S, 47° 10.54′ E, 822 m alt., low altitude rainforest; Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., 21° 15.99′ S, 47° 25.21′ E, 1020 m alt., mixed tropical forest.

**Remarks.** This species is only known from males. The male of *Adetomyrma caudapinniger* is distinguished easily from other *Adetomyrma* males by its bilobed paramere (Fig 19) and 2,2 palpal formula.

These characters, as well as those observed in the aedeagus, are unique to *Adetomyrma caudapinniger*, and a separation of this species from the remaining *Adetomyrma* species is clear and consistent. For example, *A. aureocuprea*, which is superficially similar to *A. caudapinniger*, has a simple paramere (Fig 20) and a 3,3 palpal formula.

This new species corresponds to the following species code used in previous studies:

mgm05 (in part): Yoshimura & Fisher 2012.

# Adetomyrma cilium sp. nov.

(Figs 26, 27, 34, 43, 52, 60, 69)

**Holotype.** Male: CASENT0007808, BLF05009: MADAGASCAR, Toliara, Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 24° 45.83′ S, 46° 45.1′ E, 900 m alt., montane rainforest, Malaise trap, 21–25.i.2002, Fisher-Griswold Arthropod Team leg. [CASC]

**Paratypes.** 2 males: CASENT0007089 [BMNH], CASENT0227987 [MHNG], with same data as holotype; 1 male: CASENT0007096, BLF05013: same locality as holotype, pitfall trap, 21–25.i.2002, Fisher-Griswold Arthropod Team leg. [CASC]

Worker and queen unknown.

**Male. Description.** Measurements: holotype. HL 0.65, HW 0.88, SL 0.2, EL 0.46, WL 1.62, MnW 0.98, CI 134, SI 22.9, EI 71.1, MnI 112.2.

HL 0.61–0.65, HW 0.86–0.96, SL 0.19–0.21, EL 0.44–0.5, WL 1.48–1.71, MnW 0.88–1.08, CI 136.7–147.6, SI 21.3–22.5, EI 72.5–76.7, MnI 102.2–117.8 (3 paratypes and 1 individual measured).

Eye well developed and prominent (Fig 52), its posterior margin not exceeding posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye varies from equal to or shorter than diameter of lateral ocellus, but always longer than  $0.5 \times$  diameter of lateral ocellus. Palpal formula 2,3 (two maxillary and three labial). Notaulus absent on mesoscutum (Fig 43). Parapsidal line clearly impressed. Anterior margin of petiole longer than dorsal margin in lateral view (Fig 34). Subpetiolar process developed, but presence of hairs on process variable.

Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere. No distinct projection or lobe present on posterodorsal portion of paramere. Basal ring not reduced, covering whole anterior margin of paramere in lateral view. Basal projection on cuspis clear but not extraordinarily well developed. Aedeagus in lateral view as in Figure 60: slightly and gradually narrowed from ventral projection; apical margin relatively sharp, with a small, broadly triangular projection on posteroventral portion; posteroventral margin of ventral projection concave.

Hairs on compound eyes long, as long as or longer than diameter of mid ocellus. Mesofemur in dorsal view, anterior face with dense subdecumbent and many long suberect hairs (Fig 26). Ventral margin of eye not edged with darker pigment or punctures. Body bicolored, head brown and remainder yellow (Fig 34).

**Etymology.** This species name is derived from the Latin word cilium (eyelash), and refers to the long hairs on its compound eye. The species epithet is treated as a noun in apposition, and thus invariant.

**Distribution.** MADAGASCAR: as in Figure 69.

**Additional material examined**: in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 24° 45.51′ S, 46° 51.22′ E, 275 m alt., rainforest.

**Remarks.** *Adetomyrma cilium* is only known from males. The male of *A. cilium* is distinguished easily from the other *Adetomyrma* males by a combination of long hairs on the eye (Fig 27), long suberect hairs on the anterior surface of the mesofemur (Fig 26), and a well-developed subpetiolar process.

Adetomyrma cilium is relatively similar to A. clarivida. In this study, we regard these two as different species because of consistent differences in the mesofemur hairs (Fig 26 vs. Fig 25) and development of the subpetiolar process. Additionally, these species differ in the shape of the aedeagus and the palpal formula.

This new species corresponds to the following species code used in previous studies: mgm04: Yoshimura & Fisher 2012.

#### Adetomyrma clarivida sp. nov.

(Figs 23, 25, 35, 44, 53, 61, 70)

**Holotype.** Male: CASENT0064259, MG-31-22: MADAGASCAR, Antsiranana, SAVA Region, district of Sambava, Marojejy National Park, 5 km W of Manantenina village, 1st camp site (Mantella), 14° 26.29′ S, 49° 46.44′ E, 487 m alt., low altitude rainforest, Malaise trap, 18–30.v.2005, Rin'Ha, Mike leg. [CASC]

**Paratypes.** 1 male: CASENT0063789, MG-31–15: same locality and method as holotype, 11–18.iii.2005, Rin'Ha, Mike leg. [CASC]; 1 male: CASENT0064384, MG-31-19: same locality and method as holotype, 16–28.iv.2005, Rin'Ha, Mike leg. [BMNH]; 1 male: CASENT0109019, MG-31–17: same locality and method as holotype, 25.iii – 4.iv.2005, Rin'Ha, Mike leg. [CASC]

Worker and queen unknown.

**Male. Description.** Measurements: holotype. HL 0.64, HW 0.7, SL 0.2, EL 0.52, WL 1.58, MnW 0.98, CI 109.8, SI 28.3, EI 82, MnI 140.3.

HL 0.6–0.68, HW 0.91–0.97, SL 0.18–0.2, EL 0.49–0.54, WL 1.45–1.63, MnW 0.87–0.99, CI 142.1–150.2, SI 18.6–21, EI 77.8–81.5, MnI 95.5–107.7 (3 paratypes and 2 individuals measured).

Eye extremely large and prominent (Fig 53): posterior margin exceeding posterior margin of mid ocellus in full-face view in most cases. Distance between lateral ocellus and eye shorter than  $0.5 \times$  of diameter of lateral ocellus (Fig 23). Palpal formula 3,3 (three maxillary and three labial). Notaulus absent on mesoscutum (Fig 44).

Parapsidal line usually clearly impressed, sometimes weak and unclear. Anterior margin of petiole longer than its dorsal margin in lateral view (Fig 35). Subpetiolar process developed as triangular process without ventral hairs.

Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere. No distinct projection or lobe present on posterodorsal portion of paramere. Basal ring not reduced, covering whole anterior margin of paramere in lateral view. Basal projection on cuspis clear but not extraordinarily well developed. Aedeagus in lateral view as in Figure 61: narrowed after ventral projection; apical margin relatively blunt, with a small, broadly triangular projection on its posteroventral portion; posteroventral margin of ventral projection convex.

Hair on compound eyes short,  $0.33 \times$  to  $0.5 \times$  diameter of mid ocellus. Mesofemur in dorsal view, anterior face covered with dense subdecumbent hairs, but without longer hairs (Fig 25). Ventral margin of eye edged with darker pigment and minute punctures. Body bicolored, head brown and remainder yellow (Fig 35).

**Etymology.** This species name is derived from the Latin word clarividus (clairvoyant), referring to the large eye size of the new species. The species epithet is treated as a noun in apposition, and thus invariant.

**Distribution.** MADAGASCAR: as in Figure 70.

**Additional material examined**: in addition to the type material, specimens from the following locality was examined in this study: MADAGASCAR. Parc National Marojejy, 14° 26.29′ S, 49° 46.44′ E, 488 m alt., rainforest.

**Remarks.** Adetomyrma clarivida is only known from males. The male of A. clarivida is distinguished easily from the other Adetomyrma males by a combination of large eye size (Fig 53), the large ocellus, which is located close to the posterior eye margin (Fig 23), the mesofemur lacking long hairs on its anterior surface (Fig 25), less developed subpetiolar process, and the hairs on the compound eye, which are more than  $0.33\times$  of the horizontal diameter of the mid ocellus.

Adetomyrma clarivida is morphologically similar to A. cilium and A. aureocuprea. However, A. clarivida lacks long hairs on the mesofemur (Fig 25), while A. cilium has short and long hairs (Fig 26); A. clarivida has a 3,3 palpal formula, while A. cilium has a 2,3 formula; A. clarivida has longer hairs on the eye which are more than 0.33× of mid ocellus diameter, while A. aureocuprea has shorter hairs which are about 0.25× of mid ocellus diameter (Fig 28). The distance between the lateral ocellus and eye in A. clarivida (0.5× of lateral ocellus diameter) is shorter (Fig 23) than the distance in A. aureocuprea (the same as lateral ocellus diameter). Although A. aureocuprea shows great variation in the size of the eye and some specimens of A. aureocuprea are apparently similar to A. clarivida, a combination of the characters in the eye hairs and ocellus-eye distance consistently separates A. clarivida from A. aureocuprea.

This new species corresponds to the following species code used in previous studies: mgm03: Yoshimura & Fisher 2012.

#### Adetomyrma goblin sp. nov.

(Figs 10, 17, 36, 45, 54, 62, 71, 77, 78, 83, 86, 88, 90, 93, 94)

**Holotype.** Worker: CASENT0227981, BLF14240, MADAGASCAR, Fianarantsoa, Forêt de Vevembe, 66.6 km 293° Farafangana, 22° 47.46′ S, 47° 10.91′ E, 600 m alt., rainforest, transition to montane forest, ex rotten log, soil, 24.iv.2006, B.L. Fisher *et al.* leg. [CASC]

**Paratypes.** 5 workers: CASENT0071148 [BMNH], CASENT0227982 [CASC], CASENT0227983 [MCZC], CASENT0227984 [MHNG], CASENT0227989 [NHMB], 4 males: CASENT0191378 [BMNH], CASENT0227985 [CASC], CASENT0227986 [MCZC], CASENT0227988 [MHNG], with same data as holotype.

**Worker. Description.** Measurements: holotype. HL 0.58, HW 0.47, SL 0.39, HD 0.36, WL 0.77, PnW 0.33, MnW 0.19, PpW 0.27, PtW 0.27, CI 81.3, SI 83.2, MnI 40.9, PpI 141.1, PtI 100.7.

HL 0.46–0.6, HW 0.39–0.5, SL 0.28–0.39, HD 0.26–0.36, WL 0.39–0.83, PnW 0.26–0.35, MnW 0.16–0.21, PpW 0.22–0.3, PtW 0.21–0.3, CI 79.2–84.1, SI 68.2–81.9, MnI 42–46.8, PpI 124.4–142.3, PtI 91.4–107.8 (1 paratype and 9 individuals measured).

Head subquadrate in full-face view (Fig 83), longer than wide, sides almost parallel, posterior margin slightly concave. Clypeus short, principal surface deflected ventrally. Anterior margin of clypeus somewhat flattened on mid portion, furnished with a row of about 18 small, specialized, conical setae. Frontal carinae in full-face view short and low, expanded laterally as small frontal lobes covering no more than about 2× the length of the antennal

insertions. Mandible subfalcate, without distinct basal and masticatory margins (Fig 83); inner margin with two apical teeth and four basal denticles; one small denticle on base of subapical tooth (second tooth from apex); out of four denticles, middle two denticles larger (longer) than the other two; third denticle from apical-most one largest; largest denticle sometimes divided into two adjacent denticles (observed in CASENT0127558, CASENT0438260). Palpal formula 3,3 (three maxillary and three labial). Antennal scape shorter than head length. Pedicel (second antennal segment) approximately equal to combined length of next three (third to fifth) antennal segments. Antenna gradually broadened from third segment and not forming a distinct club. Dorsal outline of mesosoma in lateral view somewhat rounded and continuous. Pronotum in dorsal view longer than broad, with convex sides. Mesonotum in dorsal view short, 2× as wide as long. Metapleuron fully fused with propodeum, division of two plates not distinguishable in lateral view. Dorsal face of propodeum slightly narrower than or as wide as pronotum, about 1.5× longer than wide, with subparallel sides converging slightly toward mesonotum (Fig 78). Propodeum in lateral view, dorsal margin about 2× to 2.5× length of declivitous margin, and rounding gently into the latter. Propodeal spiracle small, located distantly from propodeal dorsal margin in lateral view (Fig 77), not visible in dorsal view (Fig 10). Subpetiolar process distinctly developed, shaped like an irregular axe blade. Shallow and sparse punctures covering head, mesosoma, and abdomen; those on head dorsum denser than on the other parts.

Clypeus with two groups of hairs: mid clypeal hairs directed dorsally, and anterior clypeal hairs deflected anteriorly. Mid clypeal hairs consisting of one long hair and one or two shorter hairs around the long one. With head in full-face view, anterior clypeal hairs consisting of one pair of long hairs and single shorter hair laterally.

**Queen. Description.** Measurements: HL 0.57–0.61, HW 0.48–0.53, SL 0.37–0.41, EL 0.14–0.16, WL 0.9–0.99, MnW 0.39–0.49, PpW 0.35–0.41, PtW 0.28–0.34, CI 81.8–88.1, SI 71.2–79.6, EI 23.5–26.2, MnI 80–93.3, PpI 81.9–90.6, PtI 77.9–84.1 (6 individuals measured).

Winged. Head distinctly longer than wide in full-face view, sides slightly convex, posterior margin concave. Eye large and well-developed (Fig 90). Mid and lateral ocelli developed (Fig 90). Clypeal principal surface not strongly deflected. Anterior margin of clypeus shallowly concave, and furnished with a row of about 17 small, specialized, conical setae. Frontal lobes closely approximated. Mandible subfalcate, without distinct basal and masticatory margins: inner margin with two apical teeth and four long and distinct basal denticles; one small denticle on base of subapical tooth (second tooth from apex); out of four, middle two denticles larger (longer) than the other two; and third denticle from apical-most one largest. Antennal scape longer than 0.5× of the combined length of pedicel and flagellum. First flagellomere wider than long. Distal antennal segments not forming distinct club. With mesosoma in lateral view (Fig 86), its dorsum somewhat flattened; pronotum occupying whole anterior and about 0.25× of dorsal margin; mesonotum developed and occupying about 0.5× of mesosomal dorsal margin; metanotum developed and occupying small part of mesosomal dorsal margin; propodeum occupying remaining dorsal margin (less than 0.25×), and whole mesosomal posterior margin. With mesosoma in dorsal view, division between mesoscutum and mesoscutellum clear; axillae distinct; metanotum developed; and propodeum narrowed posteriorly (Fig 88). Propodeal spiracle in lateral view located far from propodeal declivity: distance from declivity margin longer than diameter of spiracle. Petiole similar to that in conspecific worker. With metasoma in dorsal view, with no width difference between posterior portion of petiole and anterior part of abdominal segment III.

Clypeus with two groups of hairs: mid clypeal hairs directed dorsally, and anterior clypeal hairs deflected anteriorly. Mid clypeal hairs consisting of one long hair and one to several shorter hairs around the long one. With head in full-face view, anterior clypeal hairs consisting of one pair of long hairs and a single shorter hair laterally. Hairs on body surface similar to those in conspecific workers.

**Male. Description.** Measurements: HL 0.41–0.75, HW 0.49–0.75, SL 0.09–0.96, EL 0.23–0.32, WL 0.79–1.28, MnW 0.42–0.75, CI 118.6–145.9, SI 17.3–18.7, EI 32.7–61.1, MnI 85.1–100.7 (5 individuals measured).

Eye well developed and prominent (Fig 54), posterior margin not exceeding posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye long, 2× as long as diameter of lateral ocellus. Palpal formula 3,3 (three maxillary and three labial). Notaulus distinctly impressed on mesoscutum (Fig 17). Parapsidal line clearly impressed. Anterior margin of petiole longer than dorsal margin in lateral view (Fig 36). Subpetiolar process not developed or weakly developed, usually without hairs ventrally.

Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere. No distinct projection or lobe present on posterodorsal portion of paramere. Basal ring not reduced: whole anterior margin of paramere in lateral view covered with this ring. Basal projection on cuspis clear but not extraordinarily well

developed. Aedeagus in lateral view as in Figure 62: basal to mid portion relatively narrow; ventral projection relatively narrow; distal portion slightly narrowed after ventral projection; serrate denticles present on posteroventral margin; apical margin relatively dull, and without a small, broadly triangular projection on its ventral portion; posteroventral margin of ventral projection concave.

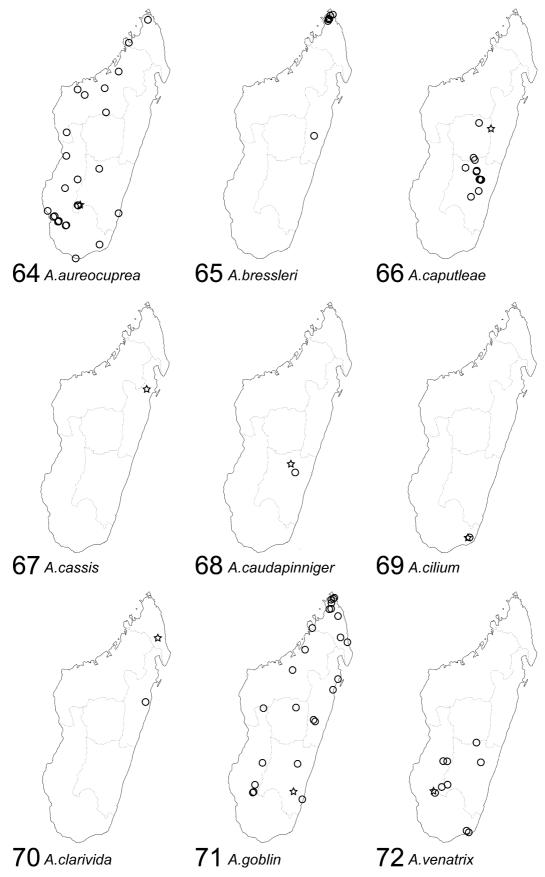
Hair on compound eyes short, less than  $0.25 \times$  diameter of mid ocellus. Mesofemur in dorsal view, its anterior face covered with short appressed or subdecumbent hairs. Ventral margin of eye not edged with darker pigment or punctures. Body color a uniform black to blackish brown (Fig 36).

**Etymology.** This species name refers to the goblin-like features of the new species: the males are small and black, and the workers possess long dentition on their masticatory margin. The species epithet is treated as a noun in apposition, and thus invariant.

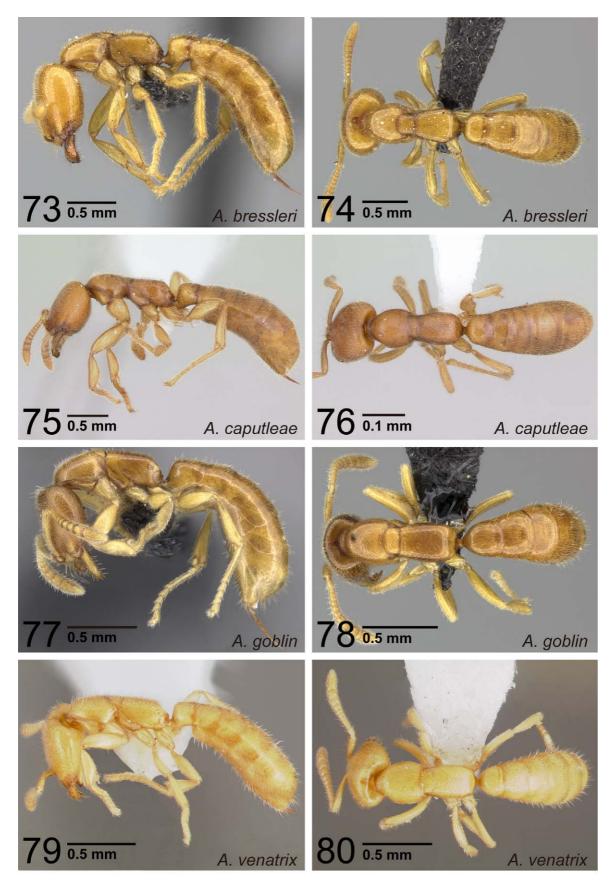
**Distribution.** MADAGASCAR: as in Figure 71.

**Additional material examined:** in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Sakalava Beach, vegetated beach dunes, 12° 15.77′ S, 49° 23.85′ E, 10 m alt., across sandy trail in dwarf littoral forest; Montaigne Francais, 12° 19.5′ S, 49° 20′ E, 150 m alt., along forested limestone ridge; 7 km N Joffreville, camp 2 of Fisher, 12° 20′ S, 49° 15′ E, 360 m alt., in dry forest; Parc National Montagne d'Ambre, first campsite, 12° 30.87′ S, 49° 10.88′ E, 960 m alt., rainforest; Parc National Montagne d'Ambre, lemur trail, 12° 31´ S, 49° 11´ E, 975 m alt., rainforest; Parc National Montagne d'Ambre, Petit Lac road, 12° 31.22′ S, 49° 10.75′ E, 1125 m alt., rainforest; Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 12° 32.07′ S, 49° 10.77′ E, 925 m alt., montane rainforest; Réserve Spéciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, 12° 51.82′ S, 49° 13.55′ E, 210 m alt., tropical dry forest; Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 12° 54.53′ S, 49° 6.59′ E, 80 m alt., tropical dry forest; Forêt de Binara, 7.5 km 230° SW Daraina, 13° 15.3′ S, 49° 37′ E, 375 m alt., tropical dry forest; Ampamakiambato, 45 km SW Ambanja, 13° 58.23′ S, 48° 9.5′ E, 145 m alt., roadside; Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14° 26.2′ S, 49° 46.5′ E, 450 m alt., rainforest; Parc National Marojejy, 14° 26.29′ S, 49° 46.44′ E, 488 m alt., rainforest; Forêt Ambanitaza, 26.1 km 347° Antalaha, 14° 40.76′ S, 50° 11.02´E, 240 m alt., rainforest; Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, 16° 16.03´S, 47° 2.92´ E, 210 m alt., tropical dry forest; Res. Ambodiriana, 4.8 km 306° Manompana, along Manompana river, 16° 40.34′ S, 49° 42.07′ E, 125 m alt., rainforest; Parcelle E3 Tampolo, 17° 16.86′ S, 49° 25.81′ E, 10 m alt., littoral forest; S.F. Tampolo, 10 km NNE Fenoarivo Atn., 17° 16.95′ S, 49° 25.8′ E, 10 m alt., littoral rainforest; Réserve Spéciale d'Ambohitantely, Forêt d Ambohitantely, 20.9 km 72° NE d Ankazobe, 18° 13.52′ S, 47° 17.21′ E, 1410 m alt., montane rainforest; Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18° 16′ S, 45° 24.4′ E, 1050 m alt., montane rainforest; Forêt Ambatovy, 14.3 km 57° Moramanga, 18° 51.05° S, 48° 19.2° E, 1075 m alt., montane rainforest; Andasibe National Park, botanic garden near entrance, west of ANGAP office, 18° 55.58′ S, 48° 24.47′ E, 1025 m alt., tropical forest; Fitovavy Fitovinany Region, district of Ifanadiana, 12 km W of Ranomafana, 21° 15.05′ S, 47° 24.43′ E, 1127 m alt., forest edge, open area; Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., 21° 15.99′ S, 47° 25.21′ E, 1020 m alt., mixed tropical forest; Base Makay 03, 21° 13.19′ S, 45° 19.44′ E, 500 m alt., gallery forest on sandy soil southern Isoky-Vohimena Forest, 59 km NE Sakaraha, 22° 28′ S, 44° 51′ E, 730 m alt., tropical dry forest; Zombitse National Park, Tulear Prov., near road, 22° 50.43′ S, 44° 43.87′ E, 825 m alt., spiny deciduous forest. Parc National de Zombitse, 19.8 km 84° E Sakaraha, 22° 50.6′ S, 44° 42.6′ E, 770 m alt., tropical dry forest; near ANGAP office, Zombitse National Park, Tulear Prov., 22° 53.19′ S, 44° 41.53′ E, 840 m alt., deciduous spiny forest; Forêt de Vevembe, 66.6 km 293° Farafangana, 22° 47.46′ S, 47° 10.91′ E, 600 m alt., rainforest, transition to montane forest; Réserve Forestière d'Agnalazaha, Mahabo, 42.9 km 215° Farafangana, 23° 11.63′ S, 47° 43.38′ E, 20 m alt., littoral rainforest.

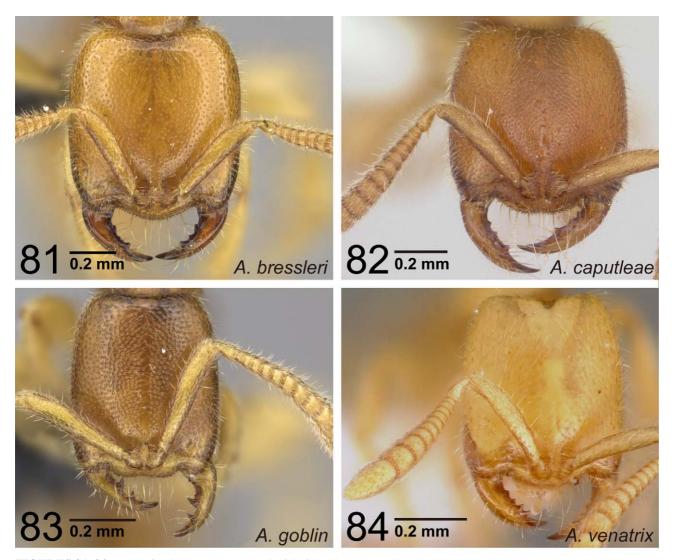
**Remarks.** The worker of *Adetomyrma goblin* is distinguished easily from other *Adetomyrma* species by the combination of a single shorter hair lateral to each longest hair on the anterior margin of the clypeus; the presence of a small denticle on the basal portion of the mandibular subapical tooth; and the small, lateral propodeal spiracle, which is not visible in dorsal view (Fig 10). The male of *A. goblin* is easily distinguished from those of other *Adetomyrma* species by its small black appearance and the clearly impressed notaulus on the mesoscutum (Fig 17). Our observations suggest that only *A. goblin* produces alate queens within the genus *Adetomyrma*.



**FIGURES 64–72.** Distribution maps for *Adetomyrma* species. 64, *A. aureocuprea* **sp. nov.**; 65, *A. bressleri* **sp. nov.**; 66, *A. caputleae* **sp. nov.**; 67, *A. cassis* **sp. nov.**; 68, *A. caudapinniger* **sp. nov.**; 69, *A. cilium* **sp. nov.**; 70, *A. clarivida* **sp. nov.**; 71, *A. goblin* **sp. nov.**; 72, *A. venatrix*. Star symbols represent the type locality.



**FIGURES 73–80.** Workers of *Adetomyrma* in lateral view and dorsal view. 73, 74, *A. bressleri* **sp. nov.** (CASENT0205995: holotype); 75, 76, *A. caputleae* **sp. nov.** (CASENT0004358); 77, 78, *A. goblin* **sp. nov.** (CASENT0227981: holotype); 79, 80, *A. venatrix* (MCZTYPE34786). 73, 75, 77, 79, lateral view; 74, 76, 78, 80, dorsal view.



**FIGURES 81–84.** Head of *Adetomyrma* workers in full-face view. 81, *A. bressleri* **sp. nov.** (CASENT0205995: holotype); 82, *A. caputleae* **sp. nov.** (CASENT0004358); 83, *A. goblin* **sp. nov.** (CASENT0227981: holotype); 84, *A. venatrix* (MCZTYPE34786).

Considerable variation was observed in the male characters of *Adetomyrma goblin*, including body size, wing color, width of flagellum, and hairs on abdominal surface. Some individuals were separately listed as the different morphospecies *A.* mgm02 in Yoshimura & Fisher (2012) based on the darker, smoked color of their wings. However, no other character is consistent or synchronous with this division, and moreover, *A.* mgm02 is not sympatrically distributed with the other *A. goblin* males. Therefore, here we regard all of those morphological differences as intraspecific variations in a single species, *A. goblin*.

This new species corresponds to the following species codes used in previous studies:

sp.: Saux et al. 2004,

mg01: Yoshimura & Fisher 2012, mgm02: Yoshimura & Fisher 2012.

#### Adetomyrma venatrix Ward, 1994

(Figs 12, 16, 18, 22, 24, 37, 46, 55, 63, 72, 79, 80, 84)

*Adetomyrma venatrix* Ward, 1994. Holotype: worker, MCZ34786, PSW#11932, MADAGASCAR, Zombitse Forest, along Route Nationale 7, 15 km E Sakaraha, 22°54'S, 44°41'E, 15, 760 m alt., tropical dry forest, ex rotten log, ii.1993, P. S. Ward leg. [MCZC]; two paratype workers [CASENT0172771: CASC, CASENT0249634: MCZC] with same data as the holotype were examined.

**Worker. Description.** Measurements: holotype. HL 0.54, HW 0.46, SL 0.32, HD 0.32, WL 0.73, PnW 0.32, MnW 0.2, PpW 0.25, PtW 0.24, CI 84.8, SI 70.2, MnI 43.9, PpI 127, PtI 94.5.

HL 0.47–0.55, HW 0.42–0.48, SL 0.28–0.33, HD 0.29–0.34, WL 0.63–0.73, PnW 0.28–0.31, MnW 0.18–0.21, PpW 0.23–0.26, PtW 0.22–0.27, CI 83.5–92.9, SI 63.7–69.7, MnI 39.4–45.1, PpI 123.2–134.9, PtI 91–103.5 (2 paratypes and 9 individuals measured).

The following updated worker description is based largely on that in Ward (1994). Head subquadrate in fullface view, longer than wide; sides slightly convex, widening near the mandibular insertions, converging posteriorly, posterior margin concave (Fig 84). Clypeus short, principal surface deflected ventrally. Anterior margin of clypeus broadly convex, and furnished with a row of about 20 small, specialized, conical setae. Frontal carinae in full-face view short and low, expanded laterally as small frontal lobes covering more than about 0.33× of length of antennal insertions. Mandible subfalcate, without distinct basal and masticatory margins (Fig 84); inner margin with two apical teeth and four basal denticles; no denticle on base of subapical tooth (second tooth from apex); out of four denticles, apical two denticles larger (longer) than other two; apical two sometimes fused into one blunt, low denticle (observed in CASENT0129948). Palpal formula 3,3 (three maxillary and three labial). Antennal scape shorter than head length. Pedicel (second antennal segment) approximately equal to combined length of next three (third to fifth) antennal segments. Antenna gradually broadened from its third segment and not forming a distinct club. Dorsal outline of mesosoma in lateral view somewhat rounded, continuous; mesonotum not strongly raised from pronotal and propodeal dorsum. Pronotum in dorsal view longer than broad, with convex sides. Mesonotum in dorsal view short, 2× as wide as long. Metapleuron fully fused with propodeum, division of two plates not distinguishable in lateral view. Dorsal face of propodeum narrower than pronotum, about 1.5× longer than wide, with subparallel sides converging slightly toward mesonotum (Fig 80). Propodeum in lateral view, dorsal margin 2.5× length of declivitous margin, rounding gently into latter. Propodeal spiracle large, located distantly from propodeal dorsal margin in lateral view, partially visible in dorsal view. Subpetiolar process distinctly developed, variably shaped like an irregular axe blade. Shallow, sparse punctures covering dorsal head, mesosoma, abdomen, and ventral head; those on head dorsum denser than on other parts. Clypeus with two groups of hairs: mid clypeal hairs directed dorsally, and anterior clypeal hairs deflected anteriorly. Mid clypeal hairs consisting of one long hair and one or two shorter hairs around long one. With head in full-face view, anterior clypeal hairs consisting of one pair of long hairs and two shorter hairs laterally (Fig 84).

**Male. Description.** Measurements: HL 0.56–0.63, HW 0.77–0.87, SL 0.15–0.17, EL 0.37–0.4, WL 1.32–1.58, MnW 0.89–1.02, CI 132.3–140.9, SI 19.1–20.1, EI 63.3–65.8, MnI 113.4–125 (5 individuals measured).

Eye well developed and prominent (Fig 55), posterior margin not exceeding posterior margin of mid ocellus in full-face view. Distance between lateral ocellus and eye slightly longer than diameter of lateral ocellus (Fig 22). Palpal formula 3,3 (three maxillary and three labial). Notaulus absent on mesoscutum. Parapsidal line clearly impressed with darker pigment. Anterior margin of petiole longer than dorsal margin in lateral view. Subpetiolar process poorly developed, without hairs ventrally.

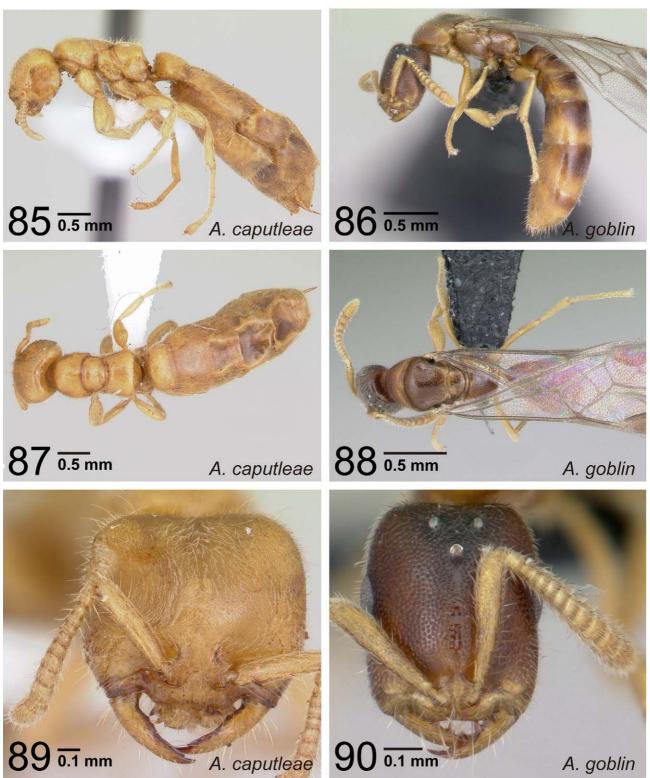
Left and right parameres not overlapping or narrowly overlapping on dorsal small part of basimere (Fig 14). No distinct projection or lobe present on posterodorsal portion of paramere. Basal ring not reduced, covering whole anterior margin of paramere in lateral view. Basal projection on cuspis clear but not extraordinarily well developed. Aedeagus in lateral view as in Figure 63: distal portion narrowed after ventral projection; apical margin relatively wide and dull; dorsal and ventral margins after basal projection almost symmetric; posteroventral portion without a broadly triangular projection; posteroventral margin of ventral projection convex in basal half and concave in distal half.

Hair on compound eyes short, about  $0.25 \times$  diameter of mid ocellus (Fig 55). Mesofemur in dorsal view, anterior face covered with dense and short subdecumbent hairs, lacking hairs. Ventral margin of eye not edged with darker pigment or punctures. Body color uniform dark brown to brown (Fig 37).

**Distribution.** MADAGASCAR: as in Figure 72.

**Additional material examined**: in addition to the type material, specimens from the following localities were examined in this study: MADAGASCAR. Amoron'i Mania Region, district of Ambositra, Italaviana Uapaca forest, 135 km SE of Antsirabe, 20° 10.4′ S, 47° 5.16′ E, 1359 m alt., Uapaca forest; Makay Mts., 21° 12.59′ S, 45° 20.51′ E, 525 m alt.; 21° 13.37′ S, 45° 19.49′ E, 490 m alt., gallery forest on sandy soil; radio tower, Ranomafana National Park, Fianarantsoa Prov., 21° 15.05′ S, 47° 24.43′ E, 1130 m alt., forest edge, mixed tropical forest, open area; Parc National d'Isalo, 9.1 km 354° N Ranohira, 22° 28.9′ S, 45° 27.7′ E, 725 m alt., gallery forest; Forêt

d'Analalava, 29.6 km 280° W Ranohira, 22° 35.5′ S, 45° 7.7′ E, 700 m alt., tropical dry forest near road, Zombitse National Park, Tulear Prov., 22° 50.43′ S, 44° 43.87′ E, 825 m alt., spiny deciduous forest; near ANGAP office, Zombitse National Park, Tulear Prov., 22° 53.19′ S, 44° 41.53′ E, 840 m alt., deciduous spiny forest; Anosy Region, district of Fort-Dauphin, Andohaela National Park Parcelle II, Tsimela, 42 km W of Fort-Dauphin, 24° 56.21′ S, 46° 37.6′ E, 177 m alt., transition forest; Grand Lavasoa, 25.9 km W of Tolagnaro, 25° 5.26′ S, 46° 44.94′ E, 450 m alt., rainforest.



**FIGURES 85–90.** Queens of *Adetomyrma* species. 85, 87, 89, *A. caputleae* **sp. nov.** (CASENT0004350); 86, 88, 90, *A. goblin* **sp. nov.** (CASENT0007401); 85, 86, lateral view; 87, 88, dorsal view; 89, 90, head in full-face view.

**Remarks.** The worker of *Adetomyrma venatrix* is easily distinguished from the other *Adetomyrma* species by the combination of two shorter hairs lateral to the longest hair on anterior margin of the clypeus, the lack of a small denticle on the basal portion of the mandibular subapical tooth, and the concave posterior margin of the head in full-face view. Males of *A. venatrix* are distinguished easily from other *Adetomyrma* males by their brown body color (Fig 37), the mesoscutum without notaulus (Fig 18), the relative closeness of the lateral occillus to the eye (Fig 22), a clear parapsidal line, and a petiole with an anterior margin longer than its dorsal margin (Fig 37).

The male of *Adetomyrma venatrix* is relatively similar to that of *A. aureocuprea*, although the former species can be separated from the latter by its brown body color and the clearly impressed parapsidal line. Morphological differences between these two species are relatively small, and *A. aureocuprea* shows large morphological variation. However, these two species have a sympatric distribution (Figs 64 and 72) and the morphological differences in each sympatric site are consistent.

Although male specimens have not been collected with conspecific workers, males were determined to be conspecific by a comparison to the other *Adetomyrma* species known from the type locality of *venatrix* and through CO1 sequencing (Fisher unpublished data). *A. goblin*, which has a known worker-male association, is the only other species known from the type locality of *venatrix* and their males are quite distinct.

*Adetomyrma venatrix* corresponds to the following species code used in previous studies: mgm01: Yoshimura & Fisher 2012.



**FIGURES 91–94.** Colonies of *Adetomyrma*. 91, 92, *A. caputleae* (collection BLF02531, ex rotten log); 93, 94, *A. goblin* (collection BLF14240, ex rotten log, soil). 91, larvae, naked pupae, and workers; 92, pupae, workers, and a large ergatoid queen; 93, elongate larvae feeding between sclerites of a Tenebrionidae larva; 94 two workers grooming a larva. 91, 92, photos by Brian Fisher; 93, 94, photos by Alex Wild.

# Acknowledgements

This study was partially supported by the National Science Foundation under Grant No. DEB-0072713, DEB-0344731, and DEB-0842395. We would like to acknowledge Philip S. Ward and Stefan P. Cover for the loan of type materials, Georg Fischer, Francisco Hita Garcia, Wojciech J. Pulawski, and Robert Zuparko for editorial suggestions. We are grateful to Alex L. Wild for providing images; Ryan K. Perry, Erin Prado, and April Nobile for creating montage images; Michele Esposito for help with database management and for the arrangement of images; and Charles Griswold for the use of the compound microscopic imaging system. The fieldwork on which this study is based could not have been completed without the gracious support of the Malagasy people, Michael Bollinger, and the Arthropod Inventory Team (Balsama Rajemison, Jean Claude Rakotonirina, Jean-Jacques Rafanomezantsoa, Chrislain Ranaivo, Coco Randriambololona, Hanitriniana Rasoazanamavo, Nicole Rasoamanana, Clavier Randrianandrasana, Valerie Rakotomalala, and Dimby Raharinjanahary).

#### References

- Bolton, B. (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge, Mass., 222 pp.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Brady, S.G., Schultz, T.R. & Fisher, B.L. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 18172–18177.
- Fisher, B.L. (2005) A model for a global inventory of ants: A case study in Madagascar. *In:* Jablonski, N.G. (Ed.) *Biodiversity:* A Symposium Held on the Occasion of the 150th Anniversary of the California Academy of Sciences June 17–18, 2003. Proceedings of the California Academy of Sciences., ser. 4, vol. 56, Suppl. I, San Francisco, California. 295 p, pp. 78–89. Gauld, I. & Bolton, B. (1988) *The Hymenoptera*. Oxford University Press, Oxford, xii + 322 pp.
- Huber, J.T. & Sharkey, M.J. (1993) Structure. *In:* Goulet, H. & Huber, T.J. (Eds.) *Hymenoptera of the World: An Identification Guide to Families*. Research Branch Agriculture Canada Publication 1894/E, Ottawa, pp. 13–59.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: Diversification in the age of angiosperms. *Science*, 312, 101–104.
- Ouellette, G.D., Fisher, B.L. & Girman, D.J. (2006) Molecular systematics of basal subfamilies of ants using 28S rRNA (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 40, 359–369.
- Saux, C., Fisher, B.L. & Spicer, G.S. (2004) Dracula ant phylogeny as inferred by nuclear 28S rDNA sequences and implications for ant systematics (Hymenoptera: Formicidae: Amblyoponinae). *Molecular Phylogenetics and Evolution*, 33, 457–468.
- Snodgrass, R.E. (1935) *Principles of insect morphology, with a new foreword by G. C Eickwort.* (1993). Cornell University Press, New York, 1–86 pp +33 pls.
- Snodgrass, R.E. (1941) The male genitalia of Hymenoptera. Smithsonian Miscellaneous Collections, 99, 1-86.
- Snodgrass, R.E. (1957) A revised interpretation of the external reproductive organs of male insects. *Smithsonian Miscellaneous Collections*, 135, 1–60.
- Ward, P.S. (1994) *Adetomyrma*, an enigmatic new ant genus from Madagascar (Hymenoptera: Formicidae) and its implications for ant phylogeny. *Systematic Entomology*, 19, 159–175.
- Wootton, R.J. (1979) Function, homology and terminology in insect wings. Systematic Entomology, 4, 81–93.
- Yoshimura, M. & Fisher, B.L. (2007) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to subfamilies and treatment of the genera of Ponerinae. *Zootaxa*, 1654, 21–40.
- Yoshimura, M. & Fisher, B.L. (2009) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to genera of the subfamily Proceratiinae. *Zootaxa*, 2216, 1–21.
- Yoshimura, M. & Fisher, B.L. (2011) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to genera of the subfamily Dolichoderinae. *Zootaxa*, 2794, 1–34.
- Yoshimura, M. & Fisher, B.L. (2012) A revision of male ants of the Malagasy Amblyoponinae (Hymenoptera: Formicidae) with resurrections of the genera *Stigmatomma* and *Xymmer*. *PLoS ONE*, 7, e33325.