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ZOOTAXA



Revision of the Malagasy ponerine ants of the genus *Leptogenys* Roger (Hymenoptera: Formicidae)

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Abstract

Leptogenvs is the most diverse ponerine ant genus in the world; it is widespread throughout tropical and subtropical regions and there are over 200 extant species described. Most species have ergatoid queens, and many have falcate, bowed mandibles and are specialists on isopod prey. Here, the Malagasy Leptogenys are revised with 60 species recognized, of which 40 are newly described, 18 redescribed, and two subspecies raised to species rank and redescribed. Included in the revision are a key to species based on the worker caste, geographic distributions, descriptions of intraspecific variation, and notes on natural history. The following species are redescribed: L. acutirostris Santschi, L. alluaudi Emery, L. angusta (Forel), L. antongilensis Emery, L. arcirostris Santschi, L. coerulescens Emery, L. falcigera Roger, L. gracilis Emery, L. grandidieri Forel, L. incisa Forel, L. maxillosa (F. Smith), L. oswaldi Forel, L. pavesii Emery, L. ridens Forel, L. saussurei (Forel), L. stuhlmanni Mayr, L. truncatirostris Forel, and L. voeltzkowi Forel. The following are raised to species and redescribed: L. imerinensis Forel stat. rev., stat. n.; and L. suarensis Emery stat. rev., stat. n. The following are described as new: L. alamando sp. n., L. alatapia sp. n., L. ambo sp. n., L. andritantely sp. n., L. anjara sp. n., L. avaratra sp. n., L. avo sp. n., L. barimaso sp. n., L. bezanozano sp. n., L. borivava sp. n., L. chrislaini sp. n., L. comajojo sp. n., L. diana sp. n., L. edsoni sp. n., L. fasika sp. n., L. fiandry sp. n., L. fotsivava sp. n., L. johary sp. n., L. lavavava sp. n., L. lohahela sp. n., L. lucida sp. n., L. malama sp. n., L. mangabe sp. n., L. manja sp. n., L. manongarivo sp. n., L. mayotte sp. n., L. namana sp. n., L. namoroka sp. n., L. pilaka sp. n., L. rabebe sp. n., L. rabesoni sp. n., L. ralipra sp. n., L. sahamalaza sp. n., L. tatsimo sp. n., L. toeraniva sp. n., L. tsingy sp. n., L. variabilis sp. n., L.vatovavy sp. n., L. vitsy sp. n., and L. zohy sp. n. Most of these species are endemic to the region. Of the endemic species, two are restricted to the Comoros (L. comajojo, L. mayotte), 52 occur only in Madagascar, and two are shared by both islands (L. fiandry, L. gracilis). Three species in the *maxillosa* group, considered introduced to the region, are recorded from Madagascar, Comoros, Mauritius, Reunion, and Seychelles. Leptogenys stuhlmanni, the only species in the stuhlmanni group, which was collected and first described from Moheli by Forel in 1907, has not been rediscovered and may have gone locally extinct.

Key words: taxonomy, *Leptogenys*, Malagasy region, Madagascar, micro-endemics, key to species, *attenuata* group, *fiandry* group, *incisa* group, *maxillosa* group, *saussurei* group, *stuhlmanni* group, *toeraniva* group, *truncatirostris* group

1. Introduction

The ant genus *Leptogenys* Roger is one of the most diverse and abundant ponerines throughout the tropical and subtropical regions (Wheeler 1922a, 1922b; Bolton 1975; Peeters & Ito 2001). The genus has attracted attention due to its wide variety of social organizations and colony structures (Peeters & Crew 1985; Villet 1989; Davies et al. 1994; Ito 1996) as well as its remarkably diverse range of behaviors (e.g. Maschwitz & Schrnegge 1983; Maschwitz et al. 1989; Steghaus-Kovac & Maschwitz 1993; Dejean & Evraerts 1997; Hlaváè & Janda 2009). *Leptogenys* range from large-eyed epigaeic species to small-eyed cryptobiotic species that inhabit the soil layers or forage through the leaf litter. Such variation occurs across the geographical distribution of the genus. The *maxillosa* species-group includes widespread species that have expanded well beyond their native ranges (Bolton 1975; McGlynn 1999). The worker caste of the genus can be distinguished largely by the distinct pectinate ventral margin of the tarsal claws. In 1995, Bolton listed 206 valid species of *Leptogenys*, and further taxonomic revisions have added more species in Asia (Xu 2000) and the New World (Lattke 2011). The present contribution provides the first comprehensive taxonomic revision of *Leptogenys* from the Malagasy region and the results will also encourage studies on the behavior, reproductive biology, and feeding strategies of this group in Madagascar.

The taxonomic history of the genus *Leptogenys* includes several junior synonyms as a result of the remarkable morphological diversity in the group. Several genera and subgenera were described by earlier ant taxonomists based on variation in the shape of the mandible, the number of mandibular teeth, the form of the clypeus, the presence of teeth on the anterior clypeal margin, and the number of peg-like teeth on the ventral margin of the tarsal claws. *Leptogenys* Roger 1861 now includes the following junior synonyms: *Prionogenys* Emery 1895b, *Lobopelta* Mayr 1862, *Odontopelta* Emery 1911, *Machaerogenys* Emery 1911, *Dorylozelus* Forel 1915, and *Microbolbos* Donisthorpe 1948. These genera originally were in their own tribe, Leptogenyini, but the morphological features used to separate this group were eventually considered insufficient, and Brown (1963) synonymized the tribe with Ponerini. A molecular phylogenetic study of the Ponerinae by Schmidt (2013) corroborates the placement of *Leptogenys* in the Ponerini.

Prior to this revision, 18 species and subspecies of *Leptogenys* were described from the Malagasy region and grouped into the three subgenera *Leptogenys*, *Lobopelta*, and *Machaerogenys* (Forel 1891; Emery 1911; Santschi 1912). Often these species were not associated with clear diagnostic characters and did not take into account similar and closely related species. In his revisionary work on the species from the Ethiopian region, Bolton (1975) reviewed the 14 known species from the Malagasy region, and not only confirmed the synonymy of *Dorylozelus* and *Microbolbos* under *Leptogenys*, but added *Lobopelta* and *Machaerogenys* as new synonyms. Bolton's review provided an identification key to the worker caste, but made no attempt to describe each species. Although Bolton's work was one of the first comparative studies to integrate similar and closely allied species into species-groups, insufficient geographic sampling was available at that time to justify a more detailed comparative study.

Recent surveys of arthropods in the Malagasy region uncovered a wealth of new species and showed that *Leptogenys* is one of the dominant ponerine ants widely distributed across all types of forest habitats. Workers are usually found foraging on the forest floor or in the leaf litter and only rarely on vegetation. They nest terrestrially under the soil, rocks, logs, or rootmat ground layers and in rotten logs, branches, in rotting bamboo, and rotten tree stumps. Most of the Malagasy species are endemic to Madagascar. In all Malagasy species, winged queens are absent, which limits their ability to disperse across the complex topography and various ecological barriers in the region. In the absence of alate queens, reproduction of *Leptogenys* in the region may be by fission, which enhances population viscosity and may result in important morphological variation across a species' geographic range. Though queens do not fly, males of *Leptogenys* are alate and are one of the most frequently collected ant genera in Malaise traps throughout Madagascar. Given this reproductive strategy, *Leptogenys* is an ideal taxon for comparative studies of species recognition and biogeography.

Despite the lack of molecular phylogenetic work to define species-groups within the Malagasy fauna of *Leptogenys*, species groups based on morphology were used as a tool to facilitate the analysis of the genus. In the present revision, 60 species of *Leptogenys* have been recognized and classified into eight species-groups on the basis of the worker caste morphology.

Based on our analysis, *Leptogenys* exhibits a wide range of phenotypic diversity segregated both among spatially isolated habitats and along continuous environmental gradients. This rich diversity along ecological

gradients and from disjunct localities demonstrates the importance of identifying the ecological causes and biogeographic processes that have generated this evolutionary diversification. The results of this analysis will contribute to conservation priority setting and ecological monitoring in the Malagasy region.

2. Material and methods

Collections. All specimens and type materials were examined and/or deposited in the following Museum collections:

| BMNH | Natural History Museum, London, U.K. |
|------|--|
| CASC | California Academy of Sciences, San Francisco, CA, USA. |
| LACM | Los Angeles County Museum, Los Angeles, CA, USA. |
| MCZC | Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. |
| MHNG | Museum d'Histoire Naturelle, Geneva, Switzerland. |
| MNHN | Museum National d'Histoire Naturelle, Paris, France. |
| MSNG | Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy. |
| NHMB | Naturhistorisches Museum, Basel, Switzerland. |
| PBZT | Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar. |
| PSWC | P. S. Ward Collection, University of California at Davis, CA, USA. |
| SAMC | South African Museum, Cape Town, South Africa. |
| ZMHB | Museum für Naturkunde der Humboldt Universität, Berlin, Germany. |

Species boundaries. The species limits for *Leptogenys* are conceived on the basis of the biological species concept, which defines a species as an assemblage of natural populations that is reproductively isolated from other assemblages (Mayr 1963). Morphological character differences are among the tools used to indicate reproductive boundaries between sexually reproducing populations. In the present study, it is used to indirectly infer the species limits for Malagasy *Leptogenys* species.

The likely high population viscosity caused by flightless female reproductives has two consequences with regard to species delimitation. First, low dispersal may promote diversity through allopatric speciation, resulting in a high number of local endemics. Second, species with large distributions may show large geographic variation in morphology because of the limited gene flow. The challenge therefore is evaluating morphological variation across samples from distinct populations and determining when samples represent a variable widespread species or multiple local endemics. In this study, single morphologically variable species were delimited when specimens showed both a continuum of character gradation between populations and a lack of clear phenotypic discontinuities. Challenges arose when a small number of specimens collected from a broad geographic range formed a phenotypic cluster yet were still quite variable within the cluster. In most cases such clusters were treated as single variable species.

The species hypotheses proposed in this study should be viewed as a starting point for molecular studies that can evaluate the species boundaries and evolutionary mechanisms that influence morphological diversity (as reviewed by Vences *et al.* 2009). With this study, phylogeographic analyses can now be undertaken to explore the cause of differentiation among populations of some morphologically variable species and to evaluate their historical distribution and relationships with closely related species. The high number of micro-endemics, combined with a high rate of deforestation in Madagascar, suggests that this group is especially vulnerable to species loss.

Analysis of morphological characters. Character examinations. Morphological observations were made using a Leica MZ12.5 binocular microscope. Two major types of hairs (setae) are discernible on the dorsum of the ant body (Rakotonirina & Fisher 2013a, 2013b). The first type is erect or suberect and stands vertically or at an angle equal to or more than 45°. The second type is termed pubescence, described as thin and shorter hairs that generally lay on the body surface of the ant or at an angle less than 45° for most of their length.

An identification key to species is presented using characters of the worker caste. Winged queens are not known for any of the *Leptogenys* species from the Malagasy region, suggesting that they all reproduce by ergatoid

queens or mated workers. We found that the general diagnosis of workers can also be used to identify ergatoid queens.

Measurements and Indices. To evaluate interspecific distinctions in size and shape, standard morphometric measurements were made on a representative sample of workers for each *Leptogenys* species. Some species have ergatoid queen specimens for which similar measurements were also taken. Using an orthogonal pair of micrometers, all measurements were recorded to the nearest 0.001 mm and rounded to the second decimal place. Indices are expressed as a percentage and rounded to the nearest whole number. Ranges are presented as minimum and maximum when more than one specimen was measured.

Head length (HL): the midline length of the head capsule in full-face view excluding the mandible, measured from the posterior margin (or, if the posterior margin is concave, from the midpoint of a line drawn across the posterior most extension of the vertex lobes) to the anterior extremity of the clypeal margin.

Head width (HW): the width of the head in full-face view, measured at the widest portion of the head, excluding the eyes.

Cephalic index (CI): HW/HL, \times 100.

Scape length (SL): straight line length of the first antennal segment excluding the basal constriction.

Scape index (SI): SL/HW, \times 100.

Pronotum width (PW): the maximum width of the pronotum with mesosoma in dorsal view.

Weber's length (WL): with mesosoma in profile, the distance between the point at which the pronotum meets the cervical shield and the most posterior extension of the metapleuron.

Petiolar node width (PNW): the maximum width of the node in dorsal view.

Petiolar node height (PNH): the height of the node in profile, measured vertically from the ventral margin at the junction between the ventral margin of the node and subpetiolar process to the dorsal border of the node.

Petiolar node length (PNL): the maximum length of the node in dorsal view.

Lateral petiolar node index (LNI): PNH/PNL, $\times 100$.

Dorsal petiolar node index (DNI): PNW/PNL, \times 100.

Images. All species recognized in the present revision are imaged and made available on AntWeb (www.antweb.org). For each species, high-resolution, color photographs of full-face views of the head, profile and dorsal views of the entire specimen were taken using a JVC KY-75 or Leica DFC450 digital camera attached to a Leica MZ16 APO microscope and Leica Application Suite (v5.0) software.

Maps. Specimen data were managed using Biota (Colwell 1996). Maps of species distribution were created using the Diva GIS program (Hijmans *et al.* 2011). Most historical specimens lacked detailed locality information and were excluded from the distribution maps.

ICZN Code. Designation of a lectotype from syntype specimens, based on article 74 in the ICZN code, is essential in order to ensure a stable nomenclature. Thus the words "present designation" are utilized when a lectotype that closely matches the original description is designated. The expression "stat. rev." is to revalidate a name formerly judged invalid. The expression "stat. n." indicates the rise of a subspecific name to species rank for the first time. In most cases new specific names are invariant, attributive, genitive nouns or nominative singular nouns in apposition.

Other abbreviations. The following abbreviations related to locality information are also made to indicate the status of protected areas and forest habitats in the Malagasy region:

PN: Parc National; **RS:** Réserve Spéciale; **F:** Forêt; **RF:** Réserve Forestière, **RP:** Réserve Privée; **FC:** Forêt classée; **SF:** Station forestière; **RNI:** Réserve Nationale Intégrale.

3. Results

Taxonomic synopsis of the genus Leptogenys

Leptogenys Roger, 1861: 41. Type species: Leptogenys falcigera Roger, 1861: 42; by subsequent designation of Bingham, 1903: 52.

Lobopelta Mayr, 1862: 733 [as subgenus of *Leptogenys* by Emery, 1911: 101. Synonym of *Leptogenys* by Bolton 1975: 240]. Type species *Ponera diminuta* F. Smith, 1857: 69; by subsequent designation of Bingham, 1903: 54.

- *Prionogenys* Emery, 1895b: 348. Type species: *Prionogenys podenzanai* Emery, 1895b by monotypy. [Synonym of *Leptogenys* by Taylor, 1988: 33].
- Odontopelta Emery, 1911: 101 [as subgenus of Leptogenys]. Type species: Leptogenys turneri Forel, 1900: 67, by monotypy. [Synonym of Leptogenys by Brown, 1973: 183; confirmed by Taylor & Brown, 1985: 32].
- Machaerogenys Emery, 1911: 100 [as subgenus of Leptogenys]. Type species: Leptogenys (Machaerogenys) truncatirostris Forel, 1897: 195, by original designation. [Synonym of Leptogenys by Bolton 1975: 240].
- Dorylozelus Forel, 1915: 25. Type species: Dorylozelus mjobergi Forel, 1915, by monotypy (= Leptogenys tricosa Taylor, 1969: 132, substitute name for *D. mjobergi* due to secondary homonymy in Leptogenys). [Synonym of Leptogenys by Taylor, 1969: 132].
- *Microbolbos* Donisthorpe, 1948: 170. Type species: *Microbolbos testaceus* Donisthorpe, 1948: 170; by original designation. [Synonym of *Leptogenys* by Wilson, 1955: 136].

Morphological diagnosis of the worker caste of Malagasy Leptogenys.

Workers of *Leptogenys* from the Malagasy region can be identified by the following features, most of which are also characteristic of all known ergatoid queens. Winged queens are not known for the Malagasy *Leptogenys*.

- 1 Antennal segments 12.
- 2 Frontal lobe small and only partially covers the antennal socket, the major portions of which are exposed in full-face view.
- 3 Mandible with one to three teeth; usually with two, apical and preapical teeth.
- 4 Mandible subtriangular, short-linear, or elongate and curvilinear; in the last condition incapable of closing against the clypeus. Basal groove variably developed: it may be a broad channel, a narrow groove, faint and vestigial, or absent.
- 5 Palp formula 4,4 for the *attenuata* group (*L. angusta, L. coerulescens,* and *L. variabilis*), *fiandry* group (*L. fiandry*), *incisa* group (*L. barimaso, L. gracilis, L. voeltzkowi*), and *stuhlmanni* group (*L. stuhlmanni*).
- 6 Clypeus usually triangularly convex, rarely rounded or broadly transverse.
- 7 Median clypeal carina typically present (except for *L. truncatirostris* and *L. diana*); reduced in *maxillosa* group.
- 8 Compound eyes always present but variable in size, mostly larger than the maximum diameter of antennal scape; located roughly at the midline of the head when viewed in profile.
- 9 Compound eyes may or may not project beyond lateral margins of head in full face view.
- 10 Tibial spurs double on mesotibia and metatibia; on each tibia the anterior spur small, simple to barbulate, theposterior spur larger and pectinate.
- 11 Ventral margin of tarsal claws pectinate or armed with peg-like teeth.
- 12 Metanotal groove usually impressed, but very rarely indistinct.
- 13 Propodeal spines absent, but some species have lobes or blunt tubercles.
- 14 Propodeal spiracle elliptic or slit-like.
- 15 Metapleural gland opening roughly at the posteroventral angle of mesosoma, its orifice directed posteriorly.
- 16 Petiolar node variable in shape, ranging from short and node-like to elongate in dorsal view and compressed laterally in the anterior half.
- 17 Helcium most often at anteroventral angle of the third abdominal segment and rarely at near mid-height of its anterior face.
- 18 Prora usually small and directed ventrally; in all species of the *toeraniva* group except one (*L. avaratra*) the prora voluminous and globular, directed anteroventrally and separated from the rounded anteroventral angle by a large indentation.
- 19 Constriction between the third and fourth abdominal segments either conspicuously distinct or absent.
- 20 Stridulitrum present on pretergite of abdominal segment IV, frequently extensive and conspicuous.
- 21 Sculpture varying from smooth and shiny to shagreened and opaque to reticulate-rugulose.
- 22 Color ranging from light brown to black with opalescent reflection and lighter appendages.
- 23 Ergatoid queen similar to worker, but characterized by the following distinctive features: head laterally rounded and much broader, one or no ocellus present, eye diameter greater than that of worker; propodeum bulky and much more rounded posteriorly, reduced mesosomal flight sclerites present; petiole relatively shorter and broader in dorsal view; gaster more voluminous and with considerably denser, more elongate and very slender hairs and pubescence, particularly on dorsum of the body.

Malagasy species groups

Classifying species-rich ant genera into species groups based on the similarity of their morphological characters has proven extremely useful (e.g. Bolton 1975, 2000, 2007; Heterick 2006). Building on Bolton's *Leptogenys* species group classification (Bolton 1975), we divide *Leptogenys* from the Malagasy region into eight species groups, of which two are new.

The *maxillosa* group is composed of widespread tramp species that colonize natural, disturbed and urban garden habitats in many tropical and subtropical localities. Three species from this group are known from the Malagasy region. The *stuhlmanni* group, which is highly diverse in Africa, possesses a single species (*L. stuhlmanni*) in the Malagasy region. The *attenuata* group, with 13 species, occupies the western dry forests of Madagascar and the humid forest habitats of the Malagasy region. These 13 species are restricted to the Malagasy region. Morphologically similar species are present in other tropical and subtropical regions, including the *attenuata* group of Africa (Bolton 1975), the *chinensis* group of Southeast Asia (e.g. of China Xu 2000), and the *conigera* group of Australia (Taylor 1988). One of the most diverse groups, composed of 17 species and including several rare species, is the *incisa* group. Its members show striking morphological variability and are difficult to diagnose based on morphology. In Madagascar, this group is generally known from the dry forests of the north and the rainforests of the east. The *saussurei* group, containing seven species, has only been collected from the wet forests of northern and eastern Madagascar. The *truncatirostris* group, with nine species, is another remarkable species group known to occur along the western dry forests of Madagascar and is especially dominant in the spiny bushes and thickets of the south. The distributions of many of its species are especially localized.

Two new species groups, both endemic to the Malagasy region, have been identified in this revision: the *fiandry* group and the *toeraniva* group. Both of these groups have short antennal scapes and very small eyes which suggest they live underground and therefore are very difficult to find. Both species groups are restricted to Madagascar, except for one species belonging to the *fiandry* group, *L. fiandry*, that also occurs in the Comoros Islands.

Identification key to species groups of the workers of Malagasy Leptogenys

| 1. | In full-face view, mandible either subtriangular or elongate but canable of closing tightly against the anterior margin of clypeus |
|----|---|
| | without a gap between them |
| - | In full-face view, mandible elongate and narrow, not capable of closing tightly against the clypeus; the apices slightly crossing each other and leaving a large gap between themselves and the clypeus when closed |
| 2. | With gaster in profile, prora generally globular and usually voluminous, directed anteroventrally; anteroventral angle of third abdominal sternite rounded; helcium usually situated almost to mid-height of anterior margin of third abdominal sternite separated by large indentation |
| - | With gaster in profile, prora flattened and small and directed ventrally along a vertical line; anteroventral angle of third abdom- inal sternite angulate; helcium situated at lower level near the anteroventral angle of third abdominal segment; prora and anteroventral angle of third abdominal sternite not separated by large indentation |
| 3. | In full-face view, greatest width of eye roughly equal to or less than the greatest width of antennal scape; small species (HW: |
| | 0.60–0.83, PW: 0.59–0.70) <i>fiandry</i> group |
| - | In full-face view, greatest width of eye markedly greater than the maximum width of antennal scape; generally larger species |
| | (HW: 0.75–1.92, PW: 0.60–1.62) |
| 4. | Distance between anterior level of torulus and anteromedian margin of clypeus distinctly less than the distance between outer margin of torulus and outer margin of base of the mandible; mandible elongate and narrow; anterior clypeal margin widely |
| | transverse, broadly rounded or convex, usually bordered with white yellowish lamellae truncatirostris group |
| - | Distance between anterior level of torulus and anteromedian margin of clypeus equal to or greater than the distance between outer margin of torulus and outer margin of base of the mandible; mandible short and robust, subtriangular or with convex |
| | inner margin; anterior clypeal margin medially projecting into a triangular lobe, edge sharp or bordered with subopaque lamella |
| 5. | Dorsum of head and mesosoma smooth apart from piligerous pitsattenuata group |
| - | Sculpture on dorsum of head and pronotum variable, ranging from densely reticulate-rugulose, densely reticulate punctulate or densely punctulate to scattered punctures or punctulate |
| 6. | Inner margin of mandible, at about mid-length, with angulate convexity; in profile, posterolateral margin of petiolar node with- out denticle or blunt angle, dorsum of pronotum either finely reticulate-rugulose or transversely finely striate-rugulose |
| - | Inner margin of mandible without convexity at mid-length; in profile, posterolateral margin of petiolar node with small tooth, denticle or blunt angle; sculpture of the dorsum of head and mesosoma not the same as above |

| 7. | In full-face view, eye diameter usually less than the greatest width of antennal scape; mandible short and more or less straight |
|----|--|
| | |
| - | In full-face view, eye diameter markedly greater than the maximum width of antennal scape |
| 8. | Dorsum of head, mesosoma, petiolar node, and abdominal segments III and IV without standing hairs, but strongly shagreened |
| | and covered with dense pruinose pubescence maxillosa group |
| - | Dorsum of at least some parts of the body covered with standing hairs, not strongly shagreened and not densely covered with |
| | pubescence |
| 9. | Third antennal segment approximately twice as long as the second; dorsum of head smooth apart from scattered punctures; |
| | pronotum dorsally weakly sculptured; constriction between third and fourth abdominal segments indistinct |
| | |
| - | Third antennal segment less than twice as long as the second; dorsum of head and mesosoma very strongly sculptured; gaster |
| | noticeably constricted between third and fourth abdominal segmentsincisa group (part) |

Checklist of Leptogenys species from the Malagasy region

attenuata group

angusta (Forel, 1892). Madagascar. coerulescens Emery, 1895a. Madagascar. comajojo Rakotonirina and Fisher, sp. n. Anjouan, Mohéli and Mayotte Islands. edsoni Rakotonirina and Fisher, sp. n. Madagascar. fasika Rakotonirina and Fisher, sp. n. Madagascar. grandidieri Forel, 1910. Madagascar. johary Rakotonirina and Fisher, sp. n. Madagascar. lucida Rakotonirina and Fisher, sp. n. Madagascar. malama Rakotonirina and Fisher, sp. n. Madagascar. mangabe Rakotonirina and Fisher, sp. n. Madagascar. manongarivo Rakotonirina and Fisher, sp. n. Madagascar. variabilis Rakotonirina and Fisher, sp. n. Madagascar. zohy Rakotonirina and Fisher, sp. n. Madagascar. fiandry group alamando Rakotonirina and Fisher, sp. n. Madagascar. anjara Rakotonirina and Fisher, sp. n. Madagascar. fiandry Rakotonirina and Fisher, sp. n. Madagascar, Mohéli Island. rabesoni Rakotonirina and Fisher, sp. n. Madagascar. incisa group alluaudi complex alluaudi Emery, 1895a. Madagascar. incisa Forel, 1891. Madagascar. pilaka Rakotonirina and Fisher, sp. n. Madagascar. *imerinensis* complex antongilensis Emery, 1899. Madagascar. barimaso Rakotonirina and Fisher, sp. n. Madagascar. chrislaini Rakotonirina and Fisher, sp. n. Madagascar. gracilis Emery, 1899. Madagascar, Mohéli Island. imerinensis Forel, 1891, stat. rev., stat. n. Madagascar. lavavava Rakotonirina and Fisher, sp. n. Madagascar. manja Rakotonirina and Fisher, sp. n. Madagascar. namana Rakotonirina and Fisher, sp. n. Madagascar. oswaldi Forel, 1891. Madagascar. suarensis Emery, 1895a, stat. rev., stat. n. Madagascar. tatsimo Rakotonirina and Fisher, sp. n. Madagascar. voeltzkowi complex sahamalaza Rakotonirina and Fisher, sp. n. Madagascar.

vitsy Rakotonirina and Fisher, sp. n. Madagascar. voeltzkowi Forel, 1897. Madagascar. maxillosa group falcigera Roger, 1861. Madagascar; Mohéli, Mayotte and Mauritius; widespread in Asia, Australia, Hawaiian and Pacific Islands. = insularis Smith, F. 1879. maxillosa (F. Smith, 1858). Madagascar; Mohéli, Mauritius, Reunion and Seychelles; South Africa, Cuba, Brazil, Philippines. = *falcata* Roger, 1861. = vinsonella (Dufour, 1864). = cribrata Emery, 1895c. pavesii Emery, 1892. Madagascar; Mohéli and Mayotte; Cameroun, Kenya, Somalia, Tanzania. = maxillosa sericea Weber, 1942. saussurei group acutirostris Santschi, 1912. Madagascar. ambo Rakotonirina and Fisher, sp. n. Madagascar. andritantely Rakotonirina and Fisher, sp. n. Madagascar. Iohahela Rakotonirina and Fisher, sp. n. Madagascar. ralipra Rakotonirina and Fisher, sp. n. Madagascar. saussurei (Forel, 1891). Madagascar. vatovavy Rakotonirina and Fisher, sp. n. Madagascar. stuhlmanni group stuhlmanni Mayr, 1893. Mohéli; Kenya, Mozambique, Tanzania. = comorensis Forel, 1907. toeraniva group avaratra Rakotonirina and Fisher, sp. n. Madagascar. avo Rakotonirina and Fisher, sp. n. Madagascar. bezanozano Rakotonirina and Fisher, sp. n. Madagascar. toeraniva Rakotonirina and Fisher, sp. n. Madagascar. truncatirostris group arcirostris complex arcirostris Santschi, 1926. Madagascar. alatapia Rakotonirina and Fisher, sp. n. Madagascar. borivava Rakotonirina and Fisher, sp. n. Madagascar. ridens complex fotsivava Rakotonirina and Fisher, sp. n. Madagascar. namoroka Rakotonirina and Fisher, sp. n. Madagascar. ridens Forel, 1910. Madagascar. tsingy Rakotonirina and Fisher, sp. n. Madagascar. truncatirostris complex diana Rakotonirina and Fisher, sp. n. Madagascar. truncatirostris Forel, 1897. Madagascar. Species group uncertain mayotte Rakotonirina and Fisher, sp. n. Mayotte Island. rabebe Rakotonirina and Fisher, sp. n. Madagascar.

Identification key to species of the worker caste of Malagasy Leptogenys

The following key based on the worker caste will also work for known ergatoid queens.



FIGURE 1. Head in full-face view showing shapes of mandibles and their tightness against clypeus when fully closed. A: *L. edsoni* (CASENT0247255). B: *L. lohahela* (CASENT0001203). C: *L. alatapia* (CASENT0489586). D: *L. voeltzkowi* (CASENT0077685).

- With abdominal segment 3 (first gastral segment) in profile, prora generally globular and voluminous, directed anteroventrally; prora and the rounded anteroventral angle of third abdominal sternite usually separated by large indentation (Fig. 2A, 3D) . . 3
 With abdominal segment 3 (first gastral segment) in profile, prora flattened, small and directed ventrally in a vertical line;



FIGURE 2. Anterior margin of third abdominal segment in profile. A: *L. bezanozano* (CASENT0175420). B: *L. ralipra* (CASENT0051142). C: *L. coerulescens* (CASENT0076558).



FIGURE 3. Form of head in full-face view, shape of petiolar node and location of prora in profile. A & B: *L. avaratra* (CASENT0041949). C & D: *L. toeraniva* (CASENT0072075).

- 4. Antennal scape with erect hairs whose length is equal to the maximum width of the scape (Fig. 4A); propodeal declivity mostly smooth; in profile, dorsal face of petiolar node sloping posteriorly (Fig. 4B) *bezanozano*



FIGURE 4. Head in full-face view indicating length of hairs on antennal scape and shape of petiole in profile. A & B: *L. bezanozano* (CASENT0041949). C & D: *L. toeraniva* (CASENT0072075).



FIGURE 5. Head in full-face view presenting size of eye and sculpture of head capsule. A: *L. avo* (CASENT0034742). B: *L. toeraniva* (CASENT0072075).

| 6. | In full-face view, greatest width of eye roughly equal to or less than the greatest width of antennal scape (Fig. 6A); smaller spe- |
|----|---|
| | cies (HW: 0.60–0.83, PW: 0.59–0.70) |
| - | In full-face view, greatest width of eye markedly greater than the maximum width of antennal scape (Fig. 6B); generally larger |
| | species (HW: 0.75–1.92, PW: 0.60–1.62) |



FIGURE 6. Head in full-face view indicating the size of eye. A: L. anjara (CASENT0175331). B: L. grandidieri (CASENT0478869).

- Masticatory margin of mandible with three teeth, a median tooth between the sharp apical tooth and the blunt basal angle; in profile, subpetiolar process simple with only an anteroventral triangular lobe or blunt tooth, posterior lobe absent (Fig. 7A) ...
 Masticatory margin of mandible with two teeth, a sharp apical tooth or lamella and a small, very short, preapical one or a blunt
- angle; in profile, subpetiolar process double, consisting of an anteroventral lobe or tubercle followed posteriorly by a thin cuticular extension or a lobe in the middle of the ventral margin (Fig. 7B, 7C).



FIGURE 7. Petiolar node in profile, showing variation in subpetiolar process. A: *L. alamando* (CASENT0034626). B: *L. fiandry* (CASENT0463434). C: *L. anjara* (CASENT0175331).



FIGURE 8. Head in full-face view showing sculpture of the dorsum and mandibles. A: *L. rabesoni* (CASENT0195430). B: *L. anjara* (CASENT0175331).

- In profile, petiolar node distinctly longer than high (LNI: 88); in lateral view, propodeal lobe indistinct (Fig. 9B)..... anjara



FIGURE 9. Mesosoma and petiole in profile. A: L. fiandry (CASENT0463434). B: L. anjara (CASENT0175331).

- Distance between anterior margin of torulus and anteromedian margin of clypeus equal to or greater than the distance between outer margin of torulus and outer margins of base of mandibles; mandibles short and robust, subtriangular or with convex inner margin, not strongly crossing each other, the apices meeting or slightly overlapping when fully closed against anterior margin of clypeus; anterior clypeal margin medially projecting into a triangular lobe, dorsoventrally thin, with sharp edge or subopaque lamella (Fig. 10B).



FIGURE 10. Head in full-face view showing shape of mandibles and comparing distance between anterior level of torulus and anteromedian margin of clypeus with distance between outer margin of torulus and outer margins of base of mandibles. A: *L. ridens* (CASENT002200). B: *L. mangabe* (CASENT0074674).



FIGURE 11. Full-face view of head showing the presence of median carina on clypeus and the shape of mandibles. A: *L. truncatirostris* (CASENT0163581). B: *L. arcirostris* (CASENT0491659).

- In full-face view, anterior margin of clypeus transverse and wide, the junction of lateral portion to the anterior margin angulate;



FIGURE 12. Anterior margin of clypeus in full-face view. A: L. diana (CASENT0261104). B: L. truncatirostris (CASENT0163581).



FIGURE 13. Head in full-face view showing shape of clypeus and its length relative to width of antennal scape. A: *L. borivava* (CASENT0430091). B: *L. fotsivava* (CASENT0001423).



FIGURE 14. Shape of head in full-face view. A: L. alatapia (CASENT0489586). B: L. arcirostris (CASENT0491659).

- 15. Dorsum of head, mesosoma, petiole, and gaster covered with conspicuous pubescence but with few suberect short hairs (Fig. 15A); antennal scape relatively short (SI: 103–112); larger species (HW: 1.18–1.38, HL: 1.27–1.43, WL: 2.08–2.32). *arcirostris*



FIGURE 15. Mesosoma and petiole in lateral view. A: L. arcirostris (CASENT0491659). B: L. borivava (CASENT0430091).

| 16. | Antennal scape longer (SL: 1.67-1.99, SI: 122-129); eye maximum diameter twice as large as maximum width of antennal |
|-----|--|
| | scape (Fig. 16A) ridens |
| - | Antennal scape shorter (SL: 1.15–1.66, SI: 111–120); eye maximum diameter less than twice maximum scape width (Fig. 16B) |
| | |



FIGURE 16. Head in full-face view showing length of antennal scape and size of eye. A: *L. ridens* (CASENT0002200). B: *L. namoroka* (CASENT0034713).



FIGURE 17. Size and location of eye relative to lateral border of head in full-face view. A: *L. fotsivava* (CASENT0001423). B: *L. tsingy* (CASENT0000793).

18. In dorsal view, petiolar node broader than long (DNI: 134–146); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced amount of pubescence; sculpture of these sclerites much coarser (Fig. 18A); head subquadrate; smaller species (HW: 1.20–1.34, HL: 1.42–1.56, WL: 2.17–2.39).
- In dorsal view, petiolar node approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant short suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma, petiolar node and gaster with abundant suberect hairs and reduced approximately as broad as long (DNI: 115); dorsum of mesosoma approximately as broad as long (DNI: 115); dorsum of mesosoma approximately approxi



FIGURE 18. Petiolar node and third abdominal tergite in dorsal view. A: L. tsingy (CASENT0000793). B: L. namoroka (CASENT0034713).



FIGURE 19. Sculpture of head and mesosoma in dorsal view. A: *L. variabilis* (CASENT0022060). B: *L. ralipra* (CASENT0051142). C: *L. oswaldi* (CASENT0496083).



FIGURE 20. Length of third antennal segment and anterior portion of petiolar node in dorsal view. A: *L. johary* (CASENT0175314). B: *L. angusta* (CASENT0134131). C: *L. edsoni* (CASENT0147522). D: *L. mangabe* (CASENT0074674).



FIGURE 21. Mesosoma in dorsal view. A: L. johary (CASENT0175314). B: L. angusta (CASENT0134131).

- 163-203); body color dark brown to reddish brown.....argusta

FIGURE 22. Head in full-face view showing size of eye relative to width of antennal scape. A: *L. zohy* (CASENT0102922). B: *L. angusta* (CASENT0134131).

1 mm

| 23. | In full-face view, eye not breaking the outline of the side of the head (Fig. 23A) | 24 |
|-----|--|----|
| - | In full-face view, eye breaking the outline of the side of the head (Fig. 23B) | 26 |



FIGURE 23. Location of eye when head in full-face view. A: L. malama (CASENT0067685). B: L. variabilis (CASENT0486515).

- Mandible smooth and shining between sparse punctures (Fig. 24B); standing hairs either absent on propodeal dorsum, or present but very short and reduced in number; with petiole in profile, often with an impression immediately posterior to the anterodorsal angle; smaller species (HW: 0.96–0.98, PW: 0.80–0.83); color black without bluish reflection or opalescence25



FIGURE 24. Sculpture of mandible. A: L. coerulescens (CASENT0076558). B: L. malama (CASENT0076558).



FIGURE 25. Mesosoma in profile. A: L. malama (CASENT0067685). B: L. lucida (CASENT0294372).



FIGURE 26. Petiole in lateral view. A: L. grandidieri (CASENT0478869). B: L. variabilis (CASENT0022060).

| 27. | In profile, metapleuron finely rugulose (Fig. 27A); sometimes dorsal and posterior portions of mesopleuron finely rugulose or |
|-----|---|
| | with superficial rugulae |
| - | In profile, metapleuron generally smooth and shiny, mesopleuron smooth or with scattered punctures (Fig. 27B) |
| | manongarivo |



FIGURE 27. Mesosoma in profile showing sculpture of metapleuron. A: L. grandidieri (CASENT0478869). B: L. manongarivo (CASENT0247267).



FIGURE 28. Mesosoma in profile showing sculpture of mesopleuron and metapleuron. A: *L. edsoni* (CASENT0247255). B: *L. fasika* (CASENT0141839).



FIGURE 29. Head in full-face view showing sculpture of mandible and median lobe of clypeus. A: *L. comajojo* (CASENT0132279). B: *L. edsoni* (CASENT0147522).



FIGURE 30. Length of petiolar node in dorsal view. A: *L. mangabe* (CASENT0074674). B: *L. variabilis* (CASENT0022060). C: *L. fasika* (CASENT0416215).

- In dorsal view, petiolar node more elongate (DNI: 67–86), anterior portion markedly narrower and distinctly compressed laterally (Fig. 30B); in lateral view, the node longer than high (LNI: 91–105), anterior rim attached directly to anterior face of node (Fig. 31B); dorsum of body with yellowish brown hairs; generally smaller in size (HW: 0.75–1.08, PW: 0.60–0.91)..*variabilis*



FIGURE 31. Lateral view of petiolar node. A: L. fasika (CASENT0416215). B: L. variabilis (CASENT0022060).



FIGURE 32. Cephalic full-face view comparing shapes of mandible. A: L. mayotte (CASENT0134302). B: L. saussurei (CASENT0175418).



FIGURE 33. Eye location and sculpture of head in full-face view. A: L. oswaldi (CASENT0496083). B: L. mayotte (CASENT0134302).

| 34. | With mesosoma in dorsal view, metanotal groove distinctly visible (Fig. 34A) | . 35 |
|-----|--|------|
| - | With mesosoma in dorsal view, metanotal groove indistinct (Fig. 34B) | .37 |



FIGURE 34. Mesosoma in dorsal view. A: L. lohahela (CASENT0001203). B: L. vatovavy (CASENT0059729).

| 35. | In dorsal view, posterior margin of petiolar node medially emarginated (Fig. 35A) | saussurei |
|-----|---|-----------|
| - | In dorsal view, posterior margin of petiolar node straight, not medially emarginated (Fig. 35B) | 36 |



FIGURE 35. Shape of posterior margin of petiolar node in dorsal view. A: *L. saussurei* (CASENT0175418). B: *L. acutirostris* (CASENT0047656).

| 36. | Smaller species (HW 1.49-1.73, HL 2.02-2.29); in profile posterolateral margin of petiolar node with a small sharp tooth (Fig. |
|-----|--|
| | 36A)lohahela |
| - | Larger species (HW 1.79-1.92, HL 2.61-2.85); in profile posterolateral margin of petiolar node with a blunt lobe or angle, not |
| | a small sharp tooth (Fig. 36B) |



FIGURE 36. Petiolar node in lateral view showing the shape of posterolateral margin. A: *L. lohahela* (CASENT0001203). B: *L. acutirostris* (CASENT0047656).

| 37. | In dorsal view, posterior margin of petiolar node straight, not medially excised (Fig. 37A) | ambo |
|-----|---|------|
| - | In dorsal view, posterior margin of petiolar node noticeably medially excised (Fig. 37B) | 38 |



FIGURE 37. Shape of posterior margin of petiolar node in dorsal view. A: *L. ambo* (CASENT0175328). B: *L. andritantely* (CASENT0175412).

Apical margin of mandible clearly with three teeth, the apical and two preapical teeth (Fig. 38A) vatovavy



FIGURE 38. Number of teeth on apical portion of mandible. A: *L. vatovavy* (CASENT0059729). B:*L. ralipra* (CASENT0051142).

38.



FIGURE 39. Mandibular and cephalic sculptures in full-face view, and shape of anteromedial clypeal margin. A: *L. andritantely* (CASENT0175412). B: *L. ralipra* (CASENT0051142).



FIGURE 40. Shape of mandible and eye size relative to width of antennal scape. A: *L. rabebe* (CASENT0163120). B: *L. manja* (CASENT0068233).



FIGURE 41. Lateral view of ant body. A: L. falcigera (CASENT0002223). B: L. gracilis (CASENT0129782).



FIGURE 42. Full-face view of head showing shape of translucent lamella surrounding anterior clypeal margin. A: *L. pavesii* (CASENT0132269). B: *L. maxillosa* (CASENT0137950).



FIGURE 43. Form of petiolar node in dorsal view. A: L. maxillosa (CASENT0137950). B: L. falcigera (CASENT0002223).

- 44. Third antennal segment approximately twice as long as the second; dorsum of head smooth apart from scattered punctures (Fig. 44A); pronotum weakly sculptured dorsally; constriction between third and fourth abdominal segments indistinct......



FIGURE 44. Length of third antennal segment relative to the second and sculpture of head dorsum. A: *L. stuhlmanni* (CASENT0104565). B: *L. imerinensis* (CASENT0274176).

| 45. | Anteromedian lobe of clypeus without anteriorly projecting peg-like setae near its margin above the lamella (Fig. 45A); lar | ger |
|-----|---|------|
| | species (HW: 1.87–2.49, PW: 1.37–1.47) | 46 |
| - | Anteromedian lobe of clypeus with two, three or more anteriorly projecting peg-like setae near its margin above the lame | ella |
| | (Fig. 45B); smaller species (HW: 1.08–1.73, PW: 0.82–1.22) | 48 |



FIGURE 45. Head in full-face view showing peg-like setae projecting from near margin of anteromedian lobe of clypeus. A: *L. alluaudi* (CASENT0054724). B: *L. voeltzkowi* (CASENT0077685).



FIGURE 46. Full-face view of head indicating location of eyes and the extent of lamella covering anterior clypeal margin. A: *L. alluaudi* (CASENT0054724). B: *L. pilaka* (CASENT0134025).

- 47. Head more elongate (CI: 85), mandible broader, strongly curved near the base, entire surface of the blade with dense and fine longitudinal striations (Fig. 47A) *incisa*



FIGURE 47. Shape of head and sculpture of mandible in full-face view. A: L. incisa (CASENT0463438). B: L. pilaka (CASENT0428200).



FIGURE 48. Head in full-face view showing shape of anterior clypeal margin and area covered by translucent lamella. A: *L. manja* (CASENT0068233). B: *L. vitsy* (CASENT0470280). C: *L. chrislaini* (CASENT0107500).

- 49. Antennal scape relatively long (SI ≥130), more than its apical third extending beyond posterior margin of the head (Fig. 49A)
 Antennal scape relatively short (SI ≤ 123), less than its apical third extending beyond posterior margin of the head (Fig. 49B).
- $\frac{1}{2}$



FIGURE 49. Length of antennal scape in full-face view. A: L. tatsimo (CASENT0122874). B: L. namana (CASENT0134243).

- 50. Mandibles finely longitudinally striate, with piligerous pits; with head in full-face view, the convex inner margin of mandible with distinct broad convexity approximately at apical third portion of the blade (Fig. 50A)..... *antongilensis*



FIGURE 50. Shape of inner margin of mandible in full-face view. A: L. antongilensis (CASENT0107408). B: L. manja (CASENT0068233).



FIGURE 51. Width of lamella fringing anterior clypeal margin and shape of mandible in full-face view. A: *L. tatsimo* (CASENT0122874). B: *L. manja* (CASENT0068233).

| 52. | In dorsal view, mesosoma seemingly with four visible segments, an additional protruding small sclerite (a partially differenti- |
|-----|---|
| | ated metanotum) distinctly visible within the metanotal groove (Fig. 52A) |
| - | In dorsal view, mesosoma consists of three visible segments, with no additional discernible segment in the metanotal groove |
| | (Fig. 52B) |



FIGURE 52. Mesosoma in dorsal view showing the number of segments.A: *L. suarensis* (CASENT0110562). B: *L. namana* (CASENT0488652).



FIGURE 53. Head in full-face view showing number of anteriorly projecting peg-like setae and shape of fringing lamella on anteromedian margin of clypeus A: *L. suarensis* (CASENT0110562). B: *L. gracilis* (CASENT0129782).

| 54. | Median clypeal carina sharp; with head in full-face view, hypostomal teeth visible (Fig. 54A); smaller species (HW: 1.10-1.25, |
|-----|--|
| | WL: 2.25–2.64) |
| - | Median clypeal carina blunt; with head in full-face view, hypostomal teeth not visible (Fig. 54B); larger species (HW: |
| | 1.51–1.55, WL: 2.92–3.10) imerinensis |


FIGURE 54. Full-face view of head showing median clypeal carina and hypostomal teeth. A: *L. namana* (CASENT0488652). B: *L. imerinensis* (CASENT0274176).



FIGURE 55. Shape of anteromedian lobe of clypeus in full-face view and hairs on antennal scape. A: *L. voeltzkowi* (CASENT0077685). B: *L. barimaso* (CASENT0496058).

| 56. | In full-face view, eye not breaking the outline of side of the head; larger species (HW: 1.30–1.59, WL: 2.26–2.72) (Fig. 56A). |
|-----|--|
| | voeltzkowi |
| - | In full-face view, eye breaking the outline of side of the head; smaller species (HW: 1.08–1.32, WL: 2.26–2.47) (Fig. 56B). 57 |



FIGURE 56. Location of eyes in full-face view. A: L. voeltzkowi (CASENT0101989). B: L. vitsy (CASENT0470280).



FIGURE 57. Shape of mandible in full-face view and hair types on antennal scape. A: *L. vitsy* (CASENT0470280). B: *L. sahamalaza* (CASENT0416181).



FIGURE 58. Shape of anteromedian portion of clypeus and form of basal portion of mandible. A: *L. lavavava* (CASENT0067405). B: *L. chrislaini* (CASENT0107500). C: *L. barimaso* (CASENT0496058).

- 59. Dorsum of head and body with standing hairs longer than the maximum diameter of eyes; in full-face view, head more or less elongate (CI: 80–84), mandible not strongly arched near the base and inner margin evenly slightly concave from the base to the apex (Fig. 59A); antennal scape relatively long (SI> 133), apical third surpassing the posterior margin of head.....barimaso
- Dorsum of head and body with standing hairs whose length is less than the maximum diameter of eyes; in full-face view, head shorter (CI: 83–88), mandible distinctly arched near the base and becomes feebly concave to almost straight towards the apex (Fig. 59B); antennal scape usually short (SI< 133); only the apical fourth surpassing the posterior margin of head.... *chrislaini*



FIGURE 59. Shape of head in full-face view and length of hairs relative to eye diameter and form of mandible. A: *L. barimaso* (CASENT0496058). B: *L. chrislaini* (CASENT0107500).

Malagasy species of *Leptogenys*

The attenuata group

In full-face view, mandible subtriangular, inner margin distinctly convex or with a blunt basal angle and closing tightly against anterior margin of clypeus; apical portions just superimposed when at rest; basal groove broadly impressed. Head shape variable but generally elongate and slightly broadened anteriorly. Eye most often large, maximum diameter greater than widest portion of antennal scape. Clypeus with median carina; anteriorly projecting medially into triangular lobe, lobe anterior margin with or fringed by semi-translucent lamella at least on apex; median clypeal carina elongate and sharp. Antennal scape long, at least 1/4 of its apical portion surpassing

posterior margin of head. Propodeal declivity either transversely striate or smooth and shining. Petiole variable in width and length, but node generally longer than broad in dorsal view; in profile, posterior margin of petiolar node without small tooth or denticle. Helcium located roughly at anteroventral angle of third abdominal segment. Constriction between third and fourth abdominal segments slightly visible. Dorsum of head, mesosoma, petiolar node, and gaster entirely smooth and shining apart from small piligerous punctures.

The *attenuata* group includes at least two complexes of closely related species. One complex, which includes *L. angusta*, *L. johary* and *L. zohy*, can be separated by the very long petiolar node (LNI: 49–77), which is strongly constricted anteriorly in dorsal view, and the presence of a long third antennal segment, which is at least twice as long as the second segment. The second species complex, which contains the remaining10 species, is characterized by a much shorter petiolar node (LNI: 77–121) with a slightly constricted anterior portion, and the average length of the third antennal segment is less than twice the length of the second.

Leptogenys angusta (Forel)

(Figures 20B, 21B, 22B, 60, 73)

Lobopelta angusta Forel, 1892: 519. Lectotype worker, present designation, Madagascar, Antananarivo Province, Andrangoloaka forest (Sikora), AntWeb CASENT0101834 (MHNG). Paralectotypes: 2 workers, Toamasina, Moramanga, two workers on the same pin with specimen codes CASENT0101798, CASENT0101972 (MHNG) [examined]. [Combination in Leptogenys (Lobopelta): Emery, 1911: 101; Wheeler, 1922b: 1012; in Leptogenys: Bolton, 1975: 296].

WORKER. Diagnosis. Third antennal segment noticeably long, more than twice the length of second segment; eye large, breaking line of side of head, maximum diameter about one third the length of lateral cephalic margin; in dorsal view mesonotum as long as broad and petiolar node remarkably elongate and strongly narrowed anteriorly; antenna and leg elongate (SI: 163–203).

Measurements (28 specimens). HW: 1.13–1.57, HL: 1.78–2.47, CI: 62–68, SL: 1.88–3.20, SI: 163–203, PW: 0.96–1.35, WL: 2.88–4.21, PNH: 0.70–1.00, PNL: 1.06–1.58, PNW: 0.49–0.78, DNI: 43–53, LNI: 59–72.

Description. Head distinctly elongate, diverging anteriorly; posterior margin weakly concave medially. Basal angle of mandible obtus or with small tooth. In full-face view, eye large, maximum diameter twice as large as or greater than twice the maximum width of scape; usually breaking line of lateral border of head. Antennal scape long, apical half roughly surpassing posterior margin of head; third antennal segment markedly elongate, more than twice the length of the second. In dorsal view, mesonotum as long as broad. Propodeum with toothlike lobe or blunt angle on posterolateral margin; propodeal spiracle elliptical. Petiolar node elongate, in dorsal view more than twice as long as broad; anterior half strongly pinched laterally. Overall body relatively long.

Mandible smooth with scattered piligerous punctures; most of body smooth and shining, except the lower half of lateral face of propodeum at level of propodeal spiracle, with occasional effaced transverse striation in profile. Dorsum of body with erect and suberect hairs: brown, longer and more robust on head and near base of scape, but yellow, shorter and more slender on mesosoma and gaster; pubescence present. Dorsum of head with paired hairs along midline. Coloration black to dark brown, with lighter appendages, and tip of gaster.

QUEEN. Measurements (2 specimens): HW: 1.29–1.65, HL: 1.83–2.38, CI: 69–70, SL: 1.01–1.28, SI: 150–154, PW: 1.93–2.54, WL: 2.86–3.71, PNH: 0.76–1.02, PNL: 0.73–0.98, PNW: 0.68–0.84, DNI: 86–94, LNI: 103–105. Overall body of ergatoid queen shorter than that of worker; petiolar node as long as high in profile; gaster remarkably voluminous. Ocelli absent. Hairs numerous, erect hairs slender and pubescence longer.

Discussion. Leptogenys angusta is one of the largest species in the attenuata group in Madagascar. Compared to the maximum diameter of the eye of *L. zohy*, which is less than the maximum diameter of the scape, that of *L. angusta* is twice as wide as the widest part of the scape. Leptogenys johary has a much shorter third antennal segment that is twice as long as the second while *L. angusta* has a much longer third antennal segment that is more than twice as long as the second.

Leptogenys angusta is comprised of two morphological variants. The larger form is characterized by a much more elongate head that slightly increases in width anteriorly and by a much larger eye (maximum diameter one third the length of side of head). The second is recognized by its smaller size, shorter head, very weakly diverging sides anterior to eye level, and smaller eye with a diameter between one third and one fourth the length of the lateral cephalic border. It is important to note that intermediates between these two forms have been encountered.



FIGURE 60. Leptogenys angusta worker CASENT0134131. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. This species is widely distributed in the humid forests of eastern Madagascar. However, the species is also found on the grassland in Ambatovy and in tropical dry forest in Antsahabe Daraina, adjacent to montane forests and lowland rainforests. The two morphs within the species segregate across environmental gradients, suggesting that different selection pressures are at work among these different habitats. The larger form occurs generally in the lower altitude of the northeastern forests of Madagascar while the smaller form is known from the montane forest in the central-east to south-east of the island.

Collections for L. angusta have been made from litter sifting, malaise, pitfall, and yellow pan traps. Whereas

some individual worker specimens search for prey on the ground, others have been observed foraging on lower vegetation. Colony nests of this species have been found in rotten logs and in rotten branches on the ground. One colony was found with a staphyliniid beetle belonging to the subfamily Pselaphinae.

Additional material examined. Province Antananarivo: [Andrangoloaka] (MHNG); Province Antsiranana: RS Anjanaharibe-Sud, 6.5 km SSW Befingotra, 875 m, rainforest (B.L. Fisher) (CASC); Betaolana Forest, along Bekona River, 880 m, rainforest (B.L. Fisher et al.) (CASC); F Ambanitaza, 26.1 km 347° Antalaha, 240 m, rainforest (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, 550 m, tropical dry forest (B.L. Fisher) (CASC); F de Binara, 9.1 km 233° SW Daraina, 650-800 m, rainforest (B.L. Fisher) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, rainforest (B.L. Fisher et al.) (CASC); PN Montagne d'Ambre, 3.6 km 235° SW Joffreville, 925 m, montane rainforest (Fisher, Griswold et al.) (CASC); PN Montagne d'Ambre, Antomboka, 970 m, montane rainforest (B.L. Fisher et al.) (CASC); Galoko Chain, Mont Galoko, 520 m rainforest (B.L. Fisher et al.) (CASC); Galoko Chain, Mont Galoko, 980 m, montane forest (B.L. Fisher et al.) (CASC); 30 km N of Antalaha, 3 km W to hill near Amboahangy, 50 m, lowland rainforest (G.D. Alpert) (MCZC); 30 km N of Antalaha, 5 km W to hill near Amboahangy, 50 m, secondary rainforest (Alpert et al.) (MCZC); Province Fianarantsoa: F d'Ambalagoavy Nord, Ikongo, Ambatombe, 625 m (R. Harin'Hala, M.E. Irwin) (CASC); F de Vevembe, 66.6 km 293° Farafangana, 600 m, rainforest, transition to montane forest (B.L. Fisher et al.) (CASC); PN Ranomafana: Talatakely, guava forest (C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raherilalao, J.S. Ranorianarisoa, J. Schwei) (CASC); Talatamaty forest, 900 m, montane rainforest (E. Rajeriarison) (MCZC); near the cabin, 925 m, montane rainforest (E. Rajeriarison) (MCZC); Ambatolahy Forest, 700–800 m, montane rainforest (E. Rajeriarison) (MCZC); 7 km W, 900–1000 m, montane rainforest (W.E. Steiner) (MCZC); RS Ivohibe, 7.5 km ENE Ivohibe, 900 m, rainforest (B.L. Fisher, Sylvain) (CASC); Ranomafana (A. Pauly) (CASC); Province Mahajanga: RS Marotandrano, Marotandrano 48.3 km S Mandritsara, 865 m, rainforest (J.C. Rakotonirina) (CASC); Province Toamasina: [Moramanga] (Sikora) (MHNG); PN Masoala, Ambanizana, 930–1110 m, montane rainforest (D. Andriamalala, D. Silva, et al.) (CASC); Ambatovy, 12.4 km NE Moramanga, 1000 m, grassland (B.L. Fisher et al.) (CASC); F Ambatovy, 14.3 km 57° Moramanga, 1075 m, montane rainforest (Malagasy ant team) (CASC); Analamay, 1068 m, montane rainforest (Malagasy ant team) (CASC); Bevolota, 17.1 km N Andasibe, 995 m, montane rainforest (B.L. Fisher et al.) (CASC); FC Andriantantely, 530 m, rainforest (H.J. Ratsirarson) (CASC); FC Didy, 960 m, rainforest (H.J. Ratsirarson) (CASC); FC Sandranantitra, 450 m, rainforest (H.J. Ratsirarson) (CASC); Manakambahiny Forest, near Vavatenina (A. Pauly) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m, rainforest (Fisher, Griswold et al.) (CASC); P.N. Mantadia, 895 m, rainforest (H.J. Ratsirarson) (CASC); PN Zahamena, Onibe River, 780 m, rainforest (B.L. Fisher et al.) (CASC); Réserve Ambodiriana, Manompana River, 4.8 km 306° Manompana, 125 m, rainforest (B.L. Fisher et al.) (CASC); RNI Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 390 m, rainforest (B.L. Fisher et al.) (CASC); RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 520 m, rainforest (B.L. Fisher et al.) (CASC); RNI Betampona, Betampona, 35.1 km NW Toamasina, 500 m, rainforest (B.L. Fisher et al.) (CASC); RS Ambatovaky, Sandrangato River, 360-500 m, rainforest (B.L. Fisher et al.) (CASC); SF Analamazaotra, Analamazaotra, 1.3 km S Andasibe, 980 m, montane rainforest (B.L. Fisher et al.) (CASC); Torotorofotsy, 1070 m, montane rainforest, marsh edge (Malagasy ant team) (CASC); 1 km W Andampibe, Cap Masoala, 125 m, lowland rainforest (G.D. Alpert) (MCZC).

Leptogenys coerulescens Emery

(Figures 2C, 24A, 61, 74)

Leptogenys coerulescens Emery, 1895a: 339. Lectotype worker, present designation, Madagascar, Diego-Suarez (Alluaud, 1893), AntWeb CASENT0102027 top worker specimen of two workers on a pin (MSNG). Paralectotype workers, with same data but specimen coded as CASENT0102026 and CASENT0102025 (MSNG) [examined]. [Combination in Leptogenys (Lobopelta): Emery, 1911: 102; Wheeler, 1922b: 1012; in Leptogenys: Bolton, 1975: 296, 1995: 230].

WORKER. Diagnosis. One of the largest species; third antennal segment less than twice the length of second segment; in full-face view, eye not breaking outline of side of head; mandible punctulate, interspersed with short, fine longitudinal striation or dense and fine elongate punctures.



FIGURE 61. Leptogenys coerulescens worker CASENT0076558. A: lateral view. B: head in full-face view. C: dorsal view.

Measurements (25 specimens). HW: 1.52–1.74, HL: 1.92–2.15, CI: 76–84, SL: 2.33–2.71, SI: 145–163, PW: 1.23–1.46, WL: 3.22–3.73, PNH: 1.09–1.25, PNL: 0.92–1.13, PNW: 0.86–1.06, DNI: 84–105, LNI: 100–121.

Description. Head more or less elongate, width greatest at about mid-length immediately posterior to eye; sides distinctly convex; posterior margin straight. In full-face view, eye not breaking outline of side of head; size larger, maximum diameter roughly one-fourth the length of side of head. Antennal scape long, distal half surpassing posterior margin of head. Third antennal segment less than twice the length of second. With mesosoma in profile propodeal dorsum slightly convex; propodeal lobe absent or with blunt angle; opening of propodeal spiracle circular. In dorsal view, petiolar node more or less elongate but slightly broader posteriorly than anteriorly. With petiole in profile, node about as high as long.

Mandible finely punctate, with fine and short longitudinal striation or dense elongate punctures. Declivitous

surface most often smooth, rarely transversely rugulose or with striation. Remainder of body dorsum smooth and shining. Dorsum of head, mesosoma, petiolar node and gaster covered with whitish-yellow, standing short hairs and pubescence. Color black with bluish reflection or opalescence, apical portion of appendages reddish brown or ferruginous red.

QUEEN. Measurements (3 specimens): HW: 1.52–1.64, HL: 1.90–1.97, CI: 80–84, SL: 2.14–2.41, SI: 141–147, PW: 1.21–1.31, WL: 3.08–3.18, PNH: 1.05–1.17, PNL: 0.75–0.82, PNW: 1.01–1.06, DNI: 124–146, LNI: 134–153. As in worker but with broader head and shorter antennal scape. No trace of ocelli. Mesosoma slightly rounded and much shorter, without wing sclerites. Hairs and pubescence more slender and abundant.

Discussion. One of the largest species (HW: 1.52–1.74, PW: 1.23–1.46) in the *attenuata* group, *L*. *coerulescens* can be recognized by its size, the location of the eye and the presence of punctures with fine striation on the mandible.

Two extremes characterize the variation within this species. One extreme is represented by specimens sampled from the dry forest habitats. The dorsal outline of the propodeum in profile is slightly convex and the petiole in dorsal view is shorter and anteriorly more slender. This variant is most similar to the type specimens. The second extreme, collected from rainforest areas, is characterized by a straight propodeal dorsum, and a more elongate and anteriorly robust petiolar node. Across the range of this species, both the shape of the propodeum and the form of the petiolar node show continuous variation and transitional states. Phenotypic variants within this species occur along ecological gradients across the forest habitats of Daraina in the northeast of Madagascar and in the disjunct forests of Ambilanivy, Anabohazo, Manongarivo and Ankarana in the northwest of the island. These results illustrate the importance of recognizing habitats that harbor distinct allopatric populations and maximizing the protection of contiguous environmental gradients to maintain the viability of morphologically diverse populations.

Distribution and biology. Although the distribution of *L. coerulescens* is limited to northern Madagascar, this species occupies a wide range of habitats including lowland and montane rainforests as well as littoral and dry forest habitats adjacent to these mesic forests. Collection data indicate that this species forages on the forest floor and on low vegetation as well as through the leaf litter. *Leptogenys coerulescens* nests mainly under the ground and in rotten logs, but occasionally in rotten tree stumps, under rootmat ground layers or under rocks.

Additional material examined. Province Antsiranana: F de Binara, 7.5 km 230° SW Daraina, 375 m, tropical dry forest (B.L. Fisher) (CASC); F de Binara, 9.1 km 233° SW Daraina, 800 m, rainforest (B.L. Fisher) (CASC); F de Binara, 9.4 km 235° SW Daraina, 1100 m, montane rainforest (B.L. Fisher) (CASC); F de Bekaraoka, 6.8 km 60° ENE Daraina, 150 m, tropical dry forest (B.L. Fisher) (CASC); F d'Ampondrabe, 26.3 km 10° NNE Daraina, 175 m, tropical dry forest (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, 550 m, tropical dry forest (B.L. Fisher) (J.C. Rakotonirina) (CASC); F d' Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, 425 m, rainforest (B.L. Fisher) (CASC); PN Montagne d'Ambre, Crête, 1110 m, montane rainforest (B.L. Fisher et al.) (CASC); P.N. Montagne d'Ambre, Roussettes, 1025 m, montane rainforest (B.L. Fisher et al.) (CASC); P.N. Montagne d'Ambre, Antomboka, 885 m, montane rainforest (B.L. Fisher et al.) (CASC); P.N. Montagne d'Ambre, Pic Bades, 900 m, montane rainforest (B.L. Fisher et al.) (CASC); P.N. Montagne d'Ambre, [1st campsite], 960 m, rainforest (Irwin, Schlinger, Harin'Hala) (CASC); P.N. Montagne d'Ambre, [lemur trail], 975 m, rainforest (Irwin, Schlinger, Harin'Hala) (CASC); P.N. Montagne d'Ambre, [Petit Lac road], 1125 m, rainforest (R. Harin'Hala) (CASC); Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, 600 m, tropical dry forest (J.C. Rakotonirina) (CASC); RS Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m, tropical dry forest (Alpert et al.) (CASC); RS Ankarana, 7 km SE Matsaborimanga, 150 m, rainforest (P.S. Ward) (PSWC) (MCZC); RS Ankarana, 150 m (Alpert et al.) (MCZC); RS Ankarana, English camp, 150 m (G.D. Alpert) (MCZC); PN Montagne d'Ambre, Vic Fitsahana-Antomboka River, 670 m (I. Constable) (MCZC); Sakalava Beach [vegetated beach dunes], 10 m, across sandy trail in dwarf littoral forest (R. Harin'Hala) (CASC); 7 km N Joffreville [camp 2 of Fisher], 360 m, tropical dry forest (R. Harin'Hala) (CASC); Galoko Chain, Mont Galoko, 520 m, rainforest (B.L. Fisher et al.) (CASC).

Leptogenys comajojo Rakotonirina and Fisher, sp. n.

(Figures 29A, 62, 75)

Holotype worker: The Comoros, Mayotte Island, Mont Combani, -12.8063, 45.1531, 370 m, rainforest, ex rotten log, 25 Nov 2007 (B.L. Fisher *et al.*), BLF18671, CASENT0132279 (CASC).

Paratypes: 3 workers with same data as holotype but with specimen codes: CASENT0247285, CASENT0247286, CASENT0247287 (CASC, BMNH).

WORKER. Diagnosis. Third antennal segment less than twice the length of second; eye breaking outline of side of head; mandible finely microreticulate apart from scattered piligerous punctures; median lobe of clypeus longitudinally striate; in profile, lower half of lateral surface of propodeum and each side of meso-metapleural suture finely rugose; with petiole in profile, posterodorsal angle of node not projecting posteriorly nor overhanging posterior node margin.

Measurements (11 specimens). HW: 0.89–0.98, HL: 1.25–1.37, CI: 70–72, SL: 1.24–1.38, SI: 138–149, PW: 0.76–0.83, WL: 2.02–2.20, PNH: 0.58–0.65, PNL: 0.53–0.57, PNW: 0.41–0.47, DNI: 76–85, LNI: 106–114.



FIGURE 62. Leptogenys comajojo holotype worker CASENT0132279. A: lateral view. B: head in full-face view. C: dorsal view.

Description. Head subrectangular and longer than broad, not strongly broadened anteriorly; sides subparallel; posterior border almost straight. Eye with maximum diameter approximately one fifth of the length of side of head; in cephalic full-face view, breaking outline of lateral margin of head. Antennal scape surpassing posterior margin of head by one fourth its length. Third antennal segment shorter than double the length of the second. Inner margin of mandible convex at apical third and with a short, blunt, preapical tooth. With mesosoma in profile, median portion of propodeal posterior border with toothlike lobe. In lateral view, petiolar node higher than long; posterior and dorsal faces meet at a right-angle.

Anteromedian lobe of clypeus striate. Mandible sparsely punctulate with fine microreticulation. Dorsum of head, mesosoma and petiolar node smooth and shining apart from piligerous pits. Generally, mesopleuron and metapleuron transversely striate or finely reticulate-rugose, except for upper half of lateral propodeal surface, but at least surface immediately adjacent to meso-metapleural suture and lower half of posterior portion of mesosoma between propodeum and metapleuron covered with this sculpture. Standing hairs and pubescence present on dorsum of head and rest of body dorsum. Color black with bluish reflection or opalescence; tip of gaster and apical portion of appendages dark brown to brown.

Discussion. Distinguishing *L. comajojo* from similar species such as *L. edsoni* can be challenging, but the species is differentiated by its finely microreticulate mandible and the presence of striation on the anteromedial clypeal lobe while *L. edsoni* has smooth mandibles and anteromedian clypeal lobe. The roughly right posterodorsal angle of the petiolar node renders it separable from *L. grandidieri* and *L. manongarivo*, both of which have a posterodorsal angle of the petiolar nodethat projects posteriorly and overhangs the posterior face.

Distribution and biology. *Leptogenys comajojo* has a distribution restricted to the mesic forests of two islands in the Comoros, Mohéli and Mayotte. This species occupies not only natural lowland and montane rainforests, but also disturbed high montane areas. Colony nests have been collected from rotten logs and under the soil, and workers are known to forage through leaf litter and on lower vegetation.

Additional material examined. COMORES: Comoros Islands: Mohéli Island: Ouallah, 500 m, rainforest (B.L. Fisher *et al.*) (CASC); Mohéli, Ouallah, 750 m, montane rainforest (B.L. Fisher *et al.*) (CASC); Anjouan Island: Lac Dzialandée, 900 m, disturbed montane rainforest (B.L. Fisher *et al.*) (CASC); Mayotte Island: Mont Combani, 370 m, rainforest (B.L. Fisher *et al.*) (CASC); Mont Chongui, 380 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys edsoni Rakotonirina and Fisher, sp. n.

(Figures 1A, 20C, 28A, 63, 76)

Holotype worker: Madagascar, Toliara, RS Kalambatritra, Betanana, -23.4144, 46.459, 1360 m, montane rainforest, ex rotten log, 8 Feb 2009 (B.L. Fisher *et al.*) collection code: BLF21432, specimen code: CASENT0247255 (CASC).

Paratypes: 5 workers same data as holotype but with the following specimen codes: CASENT0247209, CASENT0247252, CASENT0247253, CASENT0247254, CASENT0247256 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Third antennal segment less than twice the length of second; eye breaking outline of side of head; mandible smooth and shining apart from scattered piligerous punctures; median lobe of clypeus mostly smooth and not markedly striate; metapleuron and each side of meso-metapleural suture finely rugose; with petiole in profile, posterodorsal angle of node not projecting posteriorly nor overhanging posterior margin.

Measurements (15 specimens). HW: 0.78–1.05, HL: 1.18–1.49, CI: 67–71, SL: 1.01–1.40, SI: 124–135, PW: 0.68–0.84, WL: 1.77–2.21, PNH: 0.53–0.68, PNL: 0.47–0.68, PNW: 0.44–0.57, DNI: 81–97, LNI: 85–116.

Description. Head rectangular, sides almost straight and parallel to one another and meeting in rounded angle with very slightly concave posterior margin. In full-face view, eye diameter roughly one fifth the length of side of head, breaking line of side of head. Antennal scape extending beyond posterior cephalic margin by about one third of its length. Third antennal segment less than twice the length of the second. Posterior margin of propodeum at about level of propodeal spiracle with toothlike lobe. In profile, petiolar node higher than long; anterior face shorter than the posterior and rounding to dorsum, which meets the posterior face at a distinct angle, posterodorsal angle not projecting posteriorly and not overhanging posterior margin of node.



FIGURE 63. Leptogenys edsoni holotype worker CASENT0247255. A: lateral view. B: head in full-face view. C: dorsal view.

Mandible smooth and shining between scattered punctures. Dorsum of head, median clypeal lobe, mesosoma, and petiolar node generally smooth and shining apart from small piligerous pits. Transverse striation or fine reticulate-rugae cover the propodeal declivity and along meso-metapleural suture; occasionally similar sculpture covers mesopleuron and lower half of propodeal lateral surface. Dorsum of body with short, yellowish-brown erect hairs and pubescence. Body color dark brown to black; tip of gaster and apical portion of appendages light brown.

QUEEN. Measurements (2 specimens): HW: 0.94–1.01, HL: 1.35–1.38, CI: 69–73, SL: 1.15–1.22, SI: 121–123, PW: 0.73–0.79, WL: 1.91–1.99, PNH: 0.65–0.71, PNL: 0.45–0.47, PNW: 0.59–0.64, DNI: 133–136, LNI: 146–150. Worker characters are also found in ergatoid queens, but the latter has a much shorter head, shorter but wider petiolar node, enlarged gaster and many more slender and numerous erect hairs. The mesosoma also lacks complete thoracic sclerites.

Discussion. *Leptogenys edsoni* can be separated from similar species in the *attenuata* group by its smooth anteromedian clypeal lobe and mandibles, the fine reticulate-rugae on the sides of posterior portion of mesosoma, and the straight posterolateral margin of the petiolar node.

Distribution and biology. Endemic to Madagascar, *L. edsoni* is generally distributed in the mountainous regions of the southeast of the island and rarely in lowland rainforests. This species occurs from Vohiparara near the PN Ranomafana in the northernmost range to the RS Kalambatritra in the south. *Leptogenys edsoni* is known to nest most frequently in rotten logs and occasionally under the ground. Foraging occurs on the forest floor and in leaf litter.

Additional material examined. Province Fianarantsoa: Vohiparara broken bridge, 1110 m, montane rainforest (R. Harin'Hala) (CASC); PN Andringitra, F Ravaro 12.5 km SW Antanifotsy, 1500–1800 m, montane rainforest (S. Razafimandimby) (CASC); PN Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC);

PN Ranomafana, 7 km W, 700–1000 m, montane rainforest (W.E. Steiner) (MCZC); PN Ranomafana, 950 m, montane rainforest (E. Rajeriarison) (MCZC); PN Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, 1250 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, 940 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ivohibe, 8.0 km E Ivohibe, 1200 m, montane rainforest (S. Razafimandimby) (CASC); RS Ivohibe, 7.5 km ENE Ivohibe, 900 m, rainforest (S. Razafimandimby) (CASC); RS Ivohibe, 7.5 km ENE Ivohibe, 900 m, rainforest (S. Razafimandimby) (CASC); 9.0 km NE Ivohibe 900 m, rainforest (S. Razafimandimby) (CASC); 2 km W Andrambovato, along Tatamaly River, 1075 m, montane rainforest (B.L. Fisher *et al.*) (CASC); 45km S. Ambalavao, 785 m, rainforest (B.L. Fisher) (CASC); FC Vatovavy, 7.6 km 122° Kianjavato, 175 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Befarara, 1390 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ambinanitelo, 1325 m, montane rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys fasika Rakotonirina and Fisher, sp. n.

(Figures 28B, 30C, 31A, 64, 77)

Holotype worker: Madagascar, Antsiranana, Forêt d'Orangea, 3.6 km 128° SE Remena, -12.25889, 49.37467, 90 m, littoral rainforest, ground nest, 22–28 Feb. 2001 (Fisher, Griswold *et al.*) collection code: BLF03224, specimen code: CASENT0416215 (CASC).

Paratypes: 6 workers, with same data as holotype but specimen coded: CASENT0247203, CASENT0247242, CASENT0416216, CASENT0416217, CASENT0416218, CASENT0416220 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Third antennal segment of normal length, less than twice the length of the second; eye breaking outline of side of head; mandible smooth and shining apart from scattered piligerous punctures; metapleuron generally smooth. With petiole in profile, posterodorsal angle of node not projecting posteriorly nor overhanging the posterior margin; node as long as high (LNI: 100–106), anterior face of node visibly separated from sharp anteriorpetiolar ridge. In dorsal view, petiole robust (DNI: 83–89), width decreasing gradually from anterad, anterior portion of node not clearly compressed laterally; hairs whitish yellow.

Measurements (9 specimens). HW: 1.20–1.31, HL: 1.64–1.76, CI: 73–75, SL: 1.63–1.81, SI: 135–145, PW: 0.98–1.11, WL: 2.62–2.86, PNH: 0.80–0.95, PNL: 0.78–0.89, PNW: 0.70–0.77, DNI: 83–89, LNI: 100–106.

Description. Head elongate, weakly broadened anteriorly, sides slightly diverging to front, meeting generally the straight posterior margin in convex line. In cephalic full-face view, eye with maximum diameter one-fourth the length of lateral margin of head, breaking outline of side of head. Antennal scape long, surpassing posterior cephalic margin by one third its length. Third antennal segment less than twice the length of second. Propodeal lobe lacking. In dorsal view, petiolar node massive, width decreasing gradually from back to front, anterior portion without clear lateral compression. In profile, node approximately as long as high; distance between anterior face of node and anterior sharp ridge for junction to propodeum distinct.

Mandible smooth apart from scattered piligerous punctures; clypeus finely rugose or with scattered piligerous punctures. Dorsum of head and body generally smooth and shining; side of mesosoma and propodeal declivitous surface smooth and shiny. Body covered with dense whitish yellow standing hairs and pubescence. Integument black, with bluish reflection or opalescence; tip of gaster and distal part of appendages light brown to yellow.

Queen unknown.



FIGURE 64. Leptogenys fasika holotype worker CASENT0416215. A: lateral view. B: head in full-face view. C: dorsal view.

Discussion. Workers of *L. fasika* might be confounded with those of *L. variabilis*, but the former is larger (HW: 1.20–1.31, PW: 0.98–1.11), the antennal scape relatively longer and the petiolar node as long as high in profile; the node in dorsal view is more robust, without distinct lateral compression on the anterior portion; and the color of hairs on dorsum of body is whitish yellow. By contrast, *L. variabilis* workers are smaller (HW: 0.75–1.08, PW: 0.60–0.91) and have a shorter antennal scape; a much longer petiolar node in lateral view (LNI: 91–105) that is narrower with clearly laterally pinched anterior portion in dorsal view; hairs on body dorsum yellowish-brown.

Distribution and biology. Leptogenys fasika is restricted to the northern tip of Madagascar along the sandy habitats of Ampombofofo, Analabe, Orangea, and Sakalava beach, where worker specimens have been found

foraging on the ground and on the lower portions of shrub vegetation. In these sandy localities, the species generally nests under the ground and very rarely in rotten logs or under stones.

The most recent collecting event for this species was in Orangea in May 2010. In this sandy soil forest, this species nested in the ground and was observed foraging on the surface during the day for beetles, flies, and crickets. As solitary foragers returned with large prey, at half a meter from the nest entrance recruitment would begin to help the foragers carry their prey into the nest.

Additional material examined. Province Antsiranana: F d'Orangea, 3.6 km 128° SE Remena, 90 m, littoral rainforest (Fisher, Griswold *et al.*) (Alpert *et al.*) (CASC); F d'Orangea, 3.6 km 128°SE Ramena, 35 m, littoral forest (J.C. Rakotonirina) (CASC); F d'Analabe, 30.0 km 72° ENE Daraina, 30 m, littoral rainforest (B.L. Fisher) (CASC); Baie de Sakalava, 10 m, coastal scrub (B.L. Fisher *et al.*) (CASC); F d'Ampombofofo, 25 m, littoral forest (B.L. Fisher *et al.*) (CASC); Sakalava Beach [vegetated beach dunes], 10 m, across sandy trail in dwarf littoral forest (R. Harin'Hala) (CASC).

Leptogenys grandidieri Forel

(Figures 6B, 26A, 27A, 65, 78)

Leptogenys (Lobopelta) grandidieri Forel, 1910: 17. Holotype worker, Madagascar, Fort-Dauphin (Sikora), AntWeb CASENT0101589 (MHNG) [examined]. [Combination in Leptogenys (Lobopelta): Emery, 1911: 102; Wheeler, 1922b: 1012; in Leptogenys: Bolton, 1975: 296, 1995: 231].

WORKER. Diagnosis. Third antennal segment of normal length, less than twice of the length of the second; eye breaking outline of sides of head; basal half of mandible finely longitudinally striate, apical portion faintly striate or smooth between sparse punctures; metapleuron finely rugulose; posterior portion and anterodorsal level of mesopleuron finely rugulose or with superficial rugulae; posterodorsal angle of node projecting posteriorly and overhanging its posterior margin.

Measurements (9 specimens). HW: 0.83–0.89, HL: 1.24–1.34, CI: 65–68, SL: 1.16–1.25, SI: 138–144, PW: 0.70–0.75, WL: 1.92–2.07, PNH: 0.56–0.60, PNL: 0.53–0.57, PNW: 0.43–0.49, DNI: 79–89, LNI: 101–111.

Description. Head subrectangular, lateral margin meets in rounded angle the slightly medially concave posterior border. In cephalic full-face view, eye breaking outline of side of head; maximum diameter between one-fourth and one-fifth the length of lateral cephalic border. One-fourth the length of antennal scape extending beyond posterior margin of head. Third antennal segment normal, less than twice the length of the second. Basal margin of mandible broadly rounded, rarely with blunt angle or very small preapical tooth. Propodeal lobe toothlike. With petiolar node in profile, posterodorsal angle projecting posteriorly and overhanging posterior margin; anterior margin shorter than posterior margin, node higher than long and inclined anterad.

Mandible finely longitudinally striate from base to midlength; distally, sculpture becomes faintly striate or smooth between sparse punctures. Median lobe of clypeus smooth, besides sparse, small punctures. Dorsum of head, mesosoma and petiolar node generally smooth and shining. Sides of mesosoma, at least on suture between mesopleuron and metapleuron, transversely striate or finely reticulate-rugose; most often this sculpture can be found on mesopleuron and metapleuron. Propodeal declivity transversely striate or rugulose. Standing hairs present on dorsum of head, mesosoma, petiolar node and gaster. Body color dark brown to reddish brown with lighter appendages.

QUEEN. Measurements (2 specimens): HW: 0.92–0.94, HL: 1.33–1.34, CI: 69–70, SL: 1.17–1.18, SI: 126–127, PW: 0.77, WL: 1.95–1.96, PNH: 0.71–0.72, PNL: 0.47–0.48, PNW: 0.64–0.65, DNI: 135–137, LNI: 147–153. Characters as in worker but head broader, without ocelli and with shorter scape. Mesosoma with incomplete thoracic sclerites. In dorsal view, petiolar node much broader than long. Gastral segments enlarged.

Discussion. Leptogenys grandidieri is easily recognized by the combination of the following characters: the striation on mandible, the presence of sculpture on the sides of the mesosoma, and the backward projection of the posterodorsal angle of petiolar node over its posterior margin. This species is very similar to *L. edsoni* but in the later the dorsal and posterior faces of petiole meet at a right-angle. Leptogenys manongarivo is similar with respect to the posterior projection of the posterodorsal corner of petiolar node, but *L. manongarivo* lacks sculpture on the sides of the mesosoma.

Distribution and biology. The high and mid-elevational montane rainforest in the PN Andohahela in the

south-east of Madagascar is the only site where *L. grandidieri* is known. The species is absent from the dry forest habitats adjacent to these mesic forests in the park. Individual workers of this species have been found foraging on the forest floor and through leaf litter. Nests were discovered under the ground and in rotten logs.



FIGURE 65. Leptogenys grandidieri worker CASENT0478869. A: lateral view. B: head in full-face view. C: dorsal view.

Additional material examined. Province Toliara: PN Andohahela: 11 km NW Enakara, 800 m, rainforest (B.L. Fisher) (CASC); 10 km NW Enakara, 430 m, rainforest (B.L. Fisher) (CASC); 13 km NW Enakara, 1250 m, montane rainforest (B.L. Fisher) (CASC); 6 km SSW Eminiminy, 330 m, rainforest (P.S. Ward) (PSWC) (MCZC); 29.5 km WNW Tolanaro, Vasiha Montane, 500 m, rainforest (K.C. Emberton) (CASC); Col de Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, montane rainforest (Fisher, Griswold Arthropod Team) (CASC); Manampanihy River, 5.4 km 113° ESE Mahamavo, 36.7 km 343° NNW Tolagnaro, 650 m, rainforest

(Fisher, Griswold Arthropod Team) (CASC); 1 km E Mahamavo, 600 m, rainforest (P. Rabeson) (MCZC); 5 km WNW Mandiso, 400 m, rainforest (E. Rajeriarison) (MCZC); 6 km ESE Imonty, 1000 m, montane rainforest (G.D. Alpert) (MCZC); [Fort Dauphin S.G. Madagascar] (MHNG).

Leptogenys johary Rakotonirina and Fisher, sp. n. (Figures 20A, 21A, 66, 79)

Holotype worker: Madagascar, Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest, under stone, 17–21 Mar 2003 (Fisher, Griswold *et al.*) collection code: BLF08310, specimen code: CASENT0496266 (CASC).



FIGURE 66. Leptogenys johary worker CASENT0175314. A: lateral view. B: head in full-face view. C: dorsal view.

Paratypes: series of 8 workers, with same data as holotype but specimen coded: CASENT0496267, CASENT0496268, CASENT0196535, CASENT0247199, CASENT0247200, CASENT0247201, CASENT02472 02, CASENT0247273 (CASC, PBZT).

WORKER. Diagnosis. Third antennal segment twice as long as second segment; eye large, maximum diameter about one-fourth the length of lateral cephalic margin; breaking line of side of head; in dorsal view, mesonotum broader than long and petiolar node remarkably elongate and strongly narrowed anteriorly.

Measurements (8 specimens). HW: 0.95–0.98, HL: 1.38–1.47, CI: 66–69, SL: 1.37–1.48, SI: 143–153, PW: 0.74–0.83, WL: 2.21–2.33, PNH: 0.57–0.60, PNL: 0.73–0.80, PNW: 0.41–0.43, DNI: 51–57, LNI: 73–77.

Description. Head elongate, very slightly diverging anteriorly, sides subparallel; posterior margin weakly concave. Mandible basal margin with blunt angle or preapical tooth. In full-face view, eye maximum diameter roughly one fourth the length of side of head; location breaking outline of side of head. Antennal scape long, about one third of its length surpassing posterior cephalic border; third antennal segment distinctly long, twice as long as the second. In dorsal view, mesonotum broader than long. Posterolateral margin of propodeum approximately at level of propodeal spiracle with toothlike lobe; propodeal spiracle rounded. With petiole in dorsal view, node elongate, twice as long as broad and greatly narrowed anteriorly.

Mandible and clypeus smooth interspersed with scattered piligerous punctures; rest of body dorsum and propodeal declivity generally smooth and shining. Standing hairs arise from very small punctures, with longer, erect hairs on head and pronotum and much shorter hairs on rest of body dorsum. Body color brown to dark brown, with lighter appendages.

Queen unknown.

Distribution and biology. The northernmost range of *L. johary* in Madagascar is limited to the montane rainforest of the PN Masoala between 800–897 m, Amparihibe at 846 m, and the rainforest of Makira between 470–600 m. The southernmost distribution of this species is restricted to the RNI Betampona at an elevational range of 525–550 m and the FC Didy at 960 m. Individual workers of this species have been discovered foraging on the forest floor and in leaf litter. One nest was found under a rock.

Additional material examined. Province Antsiranana: Amparihibe (SB), 846 m, rainforest (K.A. Jackson, D. Carpenter) (BMNH); Province Toamasina: PN Masoala, Be Dinta, 6.2 km SSE Ambanizana, 600 m, rainforest (V. Razafimahatratra) (CASC); PN Masoala, Ambohitsitondroina, 6.9 km NE Ambanizana, 825 m, rainforest (B.L. Fisher) (CASC); PN Masoala, Ambanizana, 800–897 m, montane rainforest (D. Andriamalala, D. Silva, *et al.*) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m, rainforest (Fisher, Griswold *et al.*) (CASC); Montagne d'Akirindro, 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); RNI Betampona, 34.1 km 332° Toamasina, 525–550 m, rainforest (B.L. Fisher) (CASC); FC Didy, 960 m, rainforest (H.J. Ratsirarson) (CASC).

Leptogenys lucida Rakotonirina and Fisher, sp. n.

(Figures 25B, 67, 80)

Holotype worker: Madagascar, Toamasina, Corridor Forestier Analamay-Mantadia, Tsaravoniana, -18.75737, 48.42302 ± 100 m, 1018 m, rainforest, ex rotten log, 08–09 Nov 2012 (B.L. Fisher *et al.*) collection code: BLF30246 specimen code: CASENT0294372 (CASC).

WORKER. Diagnosis. Length of third antennal segment less than twice of length of second segment; in fullface view, eye not breaking outline of side of head; mesopleural sulcus broad and shallow, transversely sculptured, oriented to level of posteroventral corner of pronotum; legs brown and light brown towards apical portion.

Measurements (8 specimens). HW: 0.96–1.07, HL: 1.32–1.43, CI: 72–77, SL: 1.20–1.39, SI: 122–135, PW: 0.75–0.84, WL: 2.09–2.25, PNH: 0.57–0.66, PNL: 0.57–0.66, PNW: 0.43–0.53, DNI: 73–86, LNI: 94–108.

Description. Head longer than broad; lateral margin slightly convex and rounding to nearly straight posterior margin. In full-face view, eye medium-sized, maximum diameter about one-fourth to one-fifth of length of lateral cephalic border; not extending beyond line of lateral border of head. Antennal scape relatively long, surpassing posterior cephalic margin by one third its length. Third antennal segment normal, less than twice the length of the second. Widest portion of inner margin of mandible rounded, without blunt angle or preapical tooth. In profile, mesopleural sulcus a broad, shallow and parallel dashed line running toward level of posteroventral corner of

pronotum. Propodeal lobe toothlike, blunt. In dorsal view, petiolar node longer than broad, width decreasing anteriorly; in lateral view, node about as long as high; anterior margin straight, shallow transversal impression rarely distinct at junction between anterior and dorsal margin; dorsal margin forming a distinct angle with straight posterior margin.

Mandible smooth and shining between sparse, small punctures. Head, clypeus, mesosoma, declivitous surface, petiolar node and gaster generally smooth and shining; scattered small punctures present on head dorsum. Posterior portion of pronotal dorsum, petiolar node and first two gastral tergites usually lacking standing hairs and pubescence; dorsum of propodeum may have short suberect hairs. Body color and dark brown to brown, appendages brown and slightly lighter toward the apices.

QUEEN. Measurements (1 specimen): HW: 1.07, HL: 1.50, CI: 72, SL: 1.37, SI: 127, PW: 0.83, WL: 2.10, PNH: 0.65, PNL: 0.46, PNW: 0.59, DNI: 128, LNI: 142. From PN Zahamena. Closely resembles worker in overall body shape except that the ergatoid queen possesses a much broader head, shorter but wider petiolar node, enlarged gastral segments and incompletely developed thoracic sclerites.



FIGURE 67. Leptogenys lucida holotype worker CASENT0294372. A: lateral view. B: head in full-face view. C: dorsal view.

Discussion. *Leptogenys lucida* appears very similar to *L. malama*, but the smaller-sized body, the orientation of the mesopleural suture to the level of posteroventral angle of the pronotum in lateral view and the generally lighter color of the entire portion of the legs relative to the overall color of the body can separate it from the latter, which possesses larger body size and a mesopleural suture oriented to the level of posterodorsal angle of the pronotum.

Distribution and biology. The distribution of *L. lucida* includes the montane rainforest of the PN Mantadia-Andasibe and the rainforest of the PN Zahamena in central-eastern Madagascar. It also occurs in lowland rainforests of the PN Mananara-Nord, RS Ambatovaky and RNI Betampona. Workers have been found foraging on the ground and low vegetation, while their nests are most often located in rotten logs and soil layers.

Additional material examined. Province Toamasina: RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 520 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Mananara-Nord, 7.1 km 261° Antanambe, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Bevolota 17.1 km N Andasibe, 995 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, 360–520 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Zahamena, Besaky River, 760 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Zahamena, Onibe River, 780 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Zahamena, Tetezambatana Forest, near junction of Nosivola and Manakambahiny Rivers, 860 m, rainforest (B.L. Fisher *et al.*) (CASC); Ankerana, 725 m, rainforest (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 939–1036 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys malama Rakotonirina and Fisher, sp. n.

(Figures 23A, 24B, 25A, 68, 81)

Holotype worker: Madagascar, Toamasina, RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, -17.8867, 49.2025, 520 m, rainforest, ex rotten log, 2 Dec 2005 (B.L. Fisher *et al.*) collection code: BLF13310, specimen code: CASENT0067685 (CASC).

Paratypes: 4 workers, same data as holotype but with specimen codes: CASENT0247251, CASENT0247250, CASENT0247249, CASENT0247248 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Third antennal segment of normal length, less than twice the length of second segment; in full-face view, eye not breaking outline of side of head; mesopleural sulcus narrow and smooth, oriented to level of posterodorsal corner of pronotum; legs black to dark brown and tarsi light brown.

Measurements (12 specimens). HW: 1.08–1.41, HL: 1.48–1.84, CI: 73–78, SL: 1.40–1.80, SI: 123–133, PW: 0.85–1.11, WL: 2.29–2.90, PNH: 0.67–0.86, PNL: 0.64–0.86, PNW: 0.52–0.66, DNI: 71–85, LNI: 97–112.

Description. Head elongate and broadest at level of eye; posterior portion of lateral margin rounding to slightly concave posterior margin; side nearly straight in front of eyes. Eye medium, greatest diameter between one-fourth and one-fifth of length of side of head; in cephalic full-face view, eye not breaking border of side of head. Antennal scape long, reaching posterior cephalic margin by one third its length. Length of third antennal segment normal, less than twice the length of the second. Mandible inner margin broadly rounded at widest portion, without blunt angle or preapical tooth. With mesosoma in profile, mesopleural sulcus narrow and not cross-ribbed, running toward level of posterodorsal corner of pronotum. Posterior margin of propodeum at level of spiracle with protruding toothlike lobe. In dorsal view, petiolar node elongate and narrowed anteriorly; in profile, node roughly as long as high; anterior margin forming a convex line with the dorsum; shallow impression usually present at junction between both faces; petiolar dorsum meets in distinct angle with straight posterior margin.

Mandible smooth and shining between sparse, small punctures. Head, clypeus, mesosoma, declivitous surface, petiolar node and gaster generally smooth and shining; scattered small punctures present on head dorsum. Posterior portion of pronotal dorsum, petiolar node and first two gastral tergites usually lacking standing hairs and pubescence; dorsum of propodeum may have short, suberect hairs. Body color and basala portion of appendages black to dark brown, tarsae and apex of gaster lighter in color.

Discussion. Leptogenys malama is morphologically similar to other species within the *attenuata* species group but can be recognized by the position of eye in the front of the head, which does not break the line of the lateral cephalic border; by the smooth and shiny mandible; and by the absence of standing hairs on the propodeal dorsum. This species can be differentiated from *L. lucida*, its most similar species, by its larger size and in lateral view the mesopleural sulcus running towards the posterodorsal corner of the pronotum.



FIGURE 68. Leptogenys malama holotype worker CASENT0067685. A: lateral view. B: head in full-face view. C: dorsal view.

Within this species, three forms are observed. The first has a shallow impression on the anterior portion of petiole dorsum when viewed in profile and usually there are no standing erect hairs on the dorsum of the mesosoma and petiolar node. It has been collected from RNI Betampona, Mananara Nord, Ambatovy, and PN Mantadia. The second form has a strongly visible suture between the metapleuron and the side of the propodeum, and it has a pair of protuberances on the posterodorsal angle of the propodeum. It occurs in PN Marojejy, montane forest of Anjanaharibe and Akirindro of the Makira Reserve, and PN Masoala. The third form is recognized by its microreticulate procoxa, finely rugulose sides of mesopleuron and lower half of propodeum, sculptured suture between metapleuron and propodeum, and transversely striate propodeal declivity. It is known only from the west of Andampibe, Cap Masoala, at 125 m. Ants of this form may constitute a good species but until more information is gathered we consider them part of *L. malama*.

The disjunct distribution of populations within this species seems to have resulted in the diversification of forms in each separate area.

Distribution and biology. *Leptogenys malama* occupies the humid forests between 225 m and 1080 m in eastern Madagascar. The three morphotypes observed within this species occur from the PN Marojejy in the north through the PN Mantadia in the south. This species usually forages terrestrially and workers are often found on the forest floor and in leaf litter. Workers occasionally explore lower vegetation even though their nests are consistently located in rotten logs or in soil.

Additional material examined. Province Antsiranana: PN Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, rainforest (B.L. Fisher et al.) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, rainforest (B.L. Fisher et al.) (CASC); RS Anjanaharibe-Sud, 6.5 km SSW Befingotra, 875 m, rainforest (B.L. Fisher) (CASC); Amparihibe (SB), 846 m, rainforest (K.A. Jackson, D. Carpenter) (BMNH); Province Toamasina: RNI Betampona, Betampona 35.1 km NW Toamasina, 500 m, rainforest (B.L. Fisher et al.) (CASC); RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 520 m, rainforest (B.L. Fisher et al.) (CASC); PN Mananara-Nord, 7.1 km 261° Antanambe, 225 m, rainforest (B.L. Fisher et al.) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m, rainforest (Fisher, Griswold et al.) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold et al.) (CASC); FC Didy, 960 m, rainforest (H.J. Ratsirarson) (CASC); 6 km ESE Andasibe (=Perinet), 900 m, rainforest (P.S. Ward) (PSWC) (MCZC); F Ambatovy, 12.4 km NE Moramanga, 1080 m, montane rainforest (B.L. Fisher et al.) (CASC); F Ambatovy, 14.3 km 57° Moramanga, 1075 m, montane rainforest (B.L. Fisher) (CASC); F Ambohitsitondroina, 6.9 km NE Ambanizana, 825 m, rainforest (B.L. Fisher) (CASC); PN Mantadia, 895 m, rainforest (H.J. Ratsirarson) (CASC); Manakambahiny, near Vavatenina Forest (A. Pauly) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 950-1064 m, rainforest (B.L. Fisher et al.) (CASC); Ankerana, 725 m, rainforest (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 918-983 m, rainforest (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 1018–1039 m, rainforest (B.L. Fisher et al.) (CASC); 1 km W Andampibe, Cap Masoala, 125 m, lowland rainforest (G.D. Alpert) (MCZC).

Leptogenys mangabe Rakotonirina and Fisher, sp. n.

(Figures 10B, 20D, 30A, 69, 82)

Holotype worker: Madagascar, Toliara, RS Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, -18.26667, 45.40667, 1050 m, montane rainforest, ex rotten log, 13–17 Jan 2003 (Fisher, Griswold *et al.*) collection code: BLF07090, specimen code: CASENT0196537 (CASC).

Paratype worker: with same data as holotype but specimen coded as: CASENT0496843 (CASC).

WORKER. Diagnosis. Third antennal segment of normal length, less than twice the length of the second; eye breaking outline of side of head; mandible smooth and shining apart from scattered piligerous punctures; in profile, lower half of propodeum from level of metathoracic spiracle and level of propodeal spiracle generally smooth; with petiole in profile, posterodorsal angle of node not projecting posteriorly nor overhanging posterior margin of node; in dorsal view, node much longer, roughly twice as long as wide.

Measurements (7 specimens). HW: 1.07–1.17, HL: 1.55–1.66, CI: 69–71, SL: 1.50–1.69, SI: 140–146, PW: 0.85–0.97, WL: 2.41–2.59, PNH: 0.65–0.73, PNL: 0.81–0.87, PNW: 0.51–0.57, DNI: 61–67, LNI: 77–90.

Description. Head longer than broad; maximum width of head at about level of eyes; side very weakly convex posteriorly rounding to medially slightly concave posterior margin. Eye medium, maximum diameter about one-fourth the length of lateral cephalic border; in cephalic full-face view, small portion of eye extending beyond side line of head. Antennal scape long, more than one-third of its apical section surpassing posterior margin of head. Length of third antennal segment regular, less than twice the length of the second. Propodeal lobe vestigial or absent. In dorsal view, petiolar node relatively long, about twice as long as broad; anterior portion slightly compressed laterally. With petiole in profile, node inclined anteriorly, anterior margin shorter and posteriorly sloped compared to the relatively vertical posterior margin; dorsal outline broadly convex and rounding to both margins.

Mandible with surface smooth and shiny, interspersed by few punctures. Body dorsum generally smooth and

glossy apart from scattered piligerous small punctures. Lateral portion of mesosoma smooth and shining; declivitous surface smooth, without transverse striation. Dorsum of head and body covered with whitish-yellow erect hairs and pubescence. Body black with bluish reflection; appendages dark brown, with light brown apices; tip of gaster of much lighter color.

Queen unknown.

Discussion. *Leptogenys mangabe* can be separated from *L. johary* by its shorter third antennal segment, which is less than twice the length of the second segment; and from *L. variabilis* and *L. fasika* by its much longer petiolar node, which is twice as long as broad in dorsal view.



FIGURE 69. Leptogenys mangabe worker CASENT0074674. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. Ant surveys conducted on Madagascar indicate that *L. mangabe* has a discontinuous spatial distribution across forest habitats on the island. It has been collected from the lowland rainforests of Ambanitaza in northeastern Madagascar, the montane rainforest of the RS Ambohijanahary in the mid-west and the dry transitional forest of the PN Zombitse in the southwest of the island. Foraging activity by individual workers is usually on the ground surface and rarely in leaf litter. Colonies have been recorded from rotten logs.

Additional material examined. Province Antsiranana: F Ambanitaza, 26.1 km 347° Antalaha, 240 m, rainforest (B.L. Fisher) (CASC); Province Toliara: RS Ambohijanahary, F d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 1050 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Zombitse, 19.8 km 84° E Sakaraha, 770 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC).



FIGURE 70. Leptogenys manongarivo holotype worker CASENT0247267. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys manongarivo Rakotonirina and Fisher, sp. n.

(Figures 27A, 70, 83)

Holotype worker: Madagascar, Antsiranana, RS Manongarivo, 12.8 km 228° SW Antanambao, -13.9767, 48.4233, 780 m, rainforest, ground forarger, 11–17 Oct. 1998 (B.L. Fisher) collection code BLF01859, specimen code: CASENT0247267 (CASC).

Paratypes: 6 workers with the same data as holotype but with the following specimen codes: CASENT015360, CASENT0196539, CASENT0196540, CASENT0247269, CASENT0247268, CASENT0247270 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Length of third antennal segment less than twice the length of the second; eye breaking outline of sides of head; basal half of mandible finely longitudinally striate; finely microreticulate, interspersed with punctulae; side of propodeum smooth; posterodorsal angle of node projecting posteriorly and overhanging its posterior margin.

Measurements (7 specimens). HW: 0.96–0.98, HL: 1.41–1.42, CI: 68–69, SL: 1.57–1.61, SI: 163–164, PW: 0.80–0.83, WL: 2.27–2.28, PNH: 0.59–0.60, PNL: 0.57–0.58, PNW: 0.42–0.42, DNI: 73–74, LNI: 103–105.

Description. Head subrectangular and longer than broad; width greatest at about mid-length immediately behind the eye; side slightly convex, posterior margin more or less straight. In full-face view, eye medium-sized, maximum diameter roughly one-fourth the length of lateral cephalic border; breaking outline of sides of head. Antennal scape long, more than one-third of of its length surpassing posterior cephalic border. Length of third antennal segment less than twice the length of the second. Inner margin of mandible with short, angulate preapical tooth at its broadest width. In side view, propodeal posterior margin with toothlike lobe at level of spiracle. With petiole in lateral view, posterodorsal angle slightly overhanging posterolateral margin of node; node inclined, anterior face short, forming a convex line with dorsal margin, posterior face high; node relatively higher than long.

Mandible finely microreticulate, with sparse punctulae; median lobe of clypeus coarsely striate. Lateral surface of mesosoma generally smooth and shining; propodeal declivity distinctly transversely striate. Dorsum of head and body covered with standing hairs and pubescence. Color dark brown to brown; appendages and gaster brown with much lighter apices.

Discussion. *Leptogenys manongarivo* is similar to *L. grandidieri* with respect to the shape of the petiolar node, whose posterodorsal margin feebly overhangs the posterolateral margin, but *L. manongarivo* is easily distinguished by the smooth surface of the sides of its mesosoma, while *L. grandidieri* is characterized by the presence of sculpture on the sides of the mesosoma.

Distribution and biology. This species is restricted to the rainforest of the RS Manongarivo in northwestern Madagascar. The only specimens are a few workers that were found foraging on the ground in a single collecting event, suggesting that the species is locally endemic.

Leptogenys variabilis Rakotonirina and Fisher, sp. n.

(Figures 19A, 23B, 26B, 30B, 71, 84)

Holotype worker: Madagascar, Mahajanga, PN Namoroka, 16.9 km 317° NW Vilanandro, -16.40667, 45.31, 100 m, tropical dry forest, ex rotten log, 12–16 Nov 2002 (Fisher, Griswold *et al.*) collection code: BLF06654, specimen code: CASENT0486515 (CASC)

Paratypes: series of 8 workers, with same data as holotype but specimen coded: CASENT0486516. CASENT 0247272, CASENT0486514, CASENT0247208, CASENT0247207, CASENT0247206, CASENT0247205, CASENT0247204 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Third antennal segment of normal length, less than twice the length of the second; eye breaking outline of side of head; mandible smooth and shining apart from scattered piligerous punctures; in profile, lower half of propodeum from level of metathoracic spiracle and level of propodeal spiracle generally smooth. With petiole in profile, posterodorsal angle of node not projecting posteriorly nor overhanging posterolaterally; node longer than high (LNI: 91–105), anterior narrow ridge of junction to mesosoma attached directly to anterior face of node. In dorsal view, petiolar node longer and slim (DNI: 67–86), anterior portion distinctly but not strongly compressed laterally; yellowish-brown hairs on body dorsum.



FIGURE 71. Leptogenys variabilis worker CASENT0022060. A: lateral view. B: head in full-face view. C: dorsal view.

Measurements (33 specimens). HW: 0.75–1.08, HL: 1.03–1.50, CI: 68–75, SL: 0.92–1.60, SI: 122–155, PW: 0.60–0.91, WL: 1.59–2.45, PNH: 0.49–0.79, PNL: 0.49–0.76, PNW: 0.37–0.63, DNI: 67–86, LNI: 91–105.

Description. Head longer than broad, sides slightly diverging anteriorly and posteriorly rounding to more or less straight posterior margin. In full-face view, eye medium-sized, maximum diameter about one-fourth the length of lateral cephalic margin; breaking outline of lateral cephalic border. Antennal scape long, roughly one fourth its length extending over posterior margin of head. Third antennal segment normal, length less than twice the length of the second. In lateral view, propodeal lobe lacking. In profile, petiolar node clearly longer than high, anterior narrow ridge at junction to propodeum attached directly to anterior face of node, with no visible distance between them. In dorsal view, petiolar node elongate and slim, length less than twice its greatest width; anterior portion distinctly compressed laterally, width not gradually decreasing from rear to front.

Mandible smooth apart from scattered hair pits; clypeus rugulose or with sparse punctures but never entirely

smooth. Dorsum of head and body, lateral surface of mesosoma and declivitous surface generally smooth and shining. Yellowish-brown standing hairs and pubescence cover the head and body; lateral portion of body almost without erect hairs. Integument dark brown to black; appendages brown basally and yellow-orange on apical portion; tip of gaster lighter in color. Some specimens represent bluish or opalescent reflection.

QUEEN. Measurements (4 specimens). HW: 0.95–1.00, HL: 1.32–1.38, CI: 72–73, SL: 1.29–1.32, SI: 132–135, PW: 0.73–0.79, WL: 1.93–2.07, PNH: 0.60–0.63, PNL: 0.44–0.51, PNW: 0.53–0.58, DNI: 110–131, LNI: 118–139. Ergatoid queens and workers of *L. variabilis* are very similar to each other, but as usual head broader, antennal scape much shorter, erect hairs more slender and numerous, and gastral segments greatly enlarged for the queen; thoracic sclerites present but incomplete and finally petiolar node relatively broader in dorsal view and shorter than high in profile.

Discussion. See discussion of L. variabilis under L. fasika where the comparison of both species is provided.

Variation. *Leptogenys variabilis* is one of the most highly variable taxa in the *attenuata* group. Its populations involve extensive variation of morphological characters and may encompass more than one species. In fact, we found two distinctive forms for this species, one of which has medium-sized worker specimens (HW: 0.90–1.06) and a distinctly elongate petiolar node (LNI: 91–96). The second form is smaller (HW: 0.75–0.89), with much shorter and robust petiolar node (LNI: 93–100). Erect hairs and pubescence on dorsum of the body of these two forms are light brown or brown.

The two forms occur sympatrically in some localities such as RS Ambre, Montagne des Français, Ampombofofo, and Forêt d'Analabe, suggesting that these forms constitute separate species. However, these differences are not supported when morphological diversity across the species' whole range is considered. Some worker specimens show intermediate forms of characters such as body size, and the shape of petiolar node, which has a tendancy to be much shorter and robust.

Distribution and biology. The majority of samples for *L. variabilis* have been recorded from dry forest habitats in western Madagascar, though a few specimens were collected in montane rainforests around which transitional habitats to either littoral rainforest or dry forests occurred. *Leptogenys variabilis* forages most often on the ground and in leaf litter but rarely on lower vegetation. Nest series have been collected frequently from rotten logs, under the soil, and beneath rocks. A few specimens have been found in rotten branches on the ground, under rootmat litter on rock, under rotten logs, and in rotting bamboo.

Additional material examined. Province Antananarivo: RS Ambohitantely, F d Ambohitantely, 20.9 km 72° NE Ankazobe, 1410 m, montane rainforest (Fisher, Griswold et al.) (CASC); Province Antsiranana: Ambondrobe, 41.1 km 175° Vohemar, 10 m, littoral rainforest (B.L. Fisher) (CASC); Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, 600 m, tropical dry forest (Fisher, Griswold et al.) (J.C. Rakotonirina) (CASC); F d'Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6km 356° N Betsiaka, 425 m, rainforest (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, 550 m, tropical dry forest (B.L. Fisher) (J.C. Rakotonirina) (CASC); F d'Ampombofofo, 25 m, littoral forest (B.L. Fisher et al.) (CASC); F d'Ampondrabe, 26.3 km 10° NNE Daraina, 175 m, tropical dry forest (B.L. Fisher) (CASC); F d'Analabe, 30.0 km 72° ENE Daraina, 30 m, littoral rainforest (B.L. Fisher) (CASC); F de Bekaraoka, 6.8 km 60° ENE Daraina, 150 m, tropical dry forest (B.L. Fisher) (CASC); F de Binara, 7.5 km 230° SW Daraina, 375 m, tropical dry forest (B.L. Fisher) (CASC); F de Binara, 9.4 km 235° SW Daraina, 1100 m, montane rainforest (B.L. Fisher) (CASC); F d'Anabohazo, 21.6 km 247° WSW Maromandia, 120 m, tropical dry forest (Fisher, Griswold et al.) (J.C. Rakotonirina) (CASC); Montagne des Français, 7.2 km 142° SE Antsiranana (=Diego Suarez), 180 m, tropical dry forest (Fisher, Griswold et al.) (J.C. Rakotonirina) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, rainforest (B.L. Fisher et al.) (CASC); PN Montagne d'Ambre [1st campsite], 960 m, montane rainforest (R. Harin'Hala) (CASC); PN Montagne d'Ambre, Fozalanana, 475 m, tropical dry forest (B.L. Fisher et al.) (CASC); RS Ambre, 3.5 km 235° SW Sakaramy, 325 m, tropical dry forest (Fisher, Griswold et al.) (CASC); RS Ankarana, 7 km SE Matsaborimanga, 150 m, rainforest (P.S. Ward) (PSWC) (MCZC); RS Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m, tropical dry forest (Fisher, Griswold et al.) (CASC); RS Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Galoko Chain, Mont Galoko, 520 m, rainforest (B.L. Fisher et al.) (CASC); Galoko Chain, Mont Galoko, 980 m, montane forest (B.L. Fisher et al.) (CASC); Lokobe forest, Nosy Be, 100 m, tropical dry forest (G.D. Alpert) (MCZC); Province Fianarantsoa: F d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 1550 m, montane rainforest (Fisher, Griswold et al.) (CASC); Province Mahajanga: Mahavavy River, 10.6 km 148° SSE Mitsinjo, 50 m, tropical dry forest

(Fisher, Griswold *et al.*) (CASC); PN Ankarafantsika, SF Ampijoroa, 5.4 km 331° NW Andranofasika, 70 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN d'Ankarafantsika, SF Ampijoroa, 40 km 306° NW Andranofasika, 130 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 16.9 km 317° NW Vilanandro, 100 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 17.8 km 329° WNW Vilanandro, 100 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 150 m, tropical dry forest on Tsingy (Fisher-Griswold Arthropod Team) (CASC); PN Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, 50 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, 30 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC).

Leptogenys zohy Rakotonirina and Fisher, sp. n.

(Figures 22A, 72, 89)

Holotype worker: Antsiranana: Grotte d'Andrafiabe, RS Ankarana, -12.9423, 49.0644, 53 m, 20 Sept 1981 (J.M. Wilson), collection code: ANTC5284, specimen code: CASENT0102922 (BMNH).

WORKER. Diagnosis. Third antennal segment noticeably long, more than twice the length of the second segment; eye small, maximum diameter less than greatest width of scape, not breaking outline of lateral margin of head; in dorsal view, mesonotum as long as broad and petiolar node remarkably elongate and strongly narrowed anteriorly; antennae and legs very long (SI: 263).

Measurements (1 specimen). HW: 1.60, HL: 2.63, CI: 61, SL: 4.21, SI: 263, PW: 1.33, WL: 4.42, PNH: 0.85, PNL: 1.73, PNW: 0.63, DNI: 37, LNI: 49.

Description. Head particularly elongate and weakly broadened toward base of mandible. In full-face view, eye small, maximum diameter less than twice of the maximum width of scape; not breaking outline of side of head. Antennal scape very long and thin, more than apical third portion extending beyond posterior border of head. Third antennal segment three times as long as the second. With mesosoma in dorsal view, mesonotum as long as broad, propodeal spiracle elliptical. In dorsal view, petiolar node extremely long and slender, more than twice as long as broad, its anterior half portion strongly compressed laterally. Legs markedly long compared to overall body length.

Mandible and clypeus smooth, with sparse punctures. Lower half of propodeal declivity transversely striate or rugulose. Dorsum of head and rest of body generally smooth and shining. Standing hairs present on dorsum of body, longer and robust on midline of head and base of scape, and shorter and slender on mesosoma and gaster. Reddish brown in color; appendages basally light brown and with yellow apices; tip of gaster light brown.

Queen unknown for this species.

Discussion. *Leptogenys zohy* is very similar to *L. angusta* but can be distinguished by its small eyes, which do not extend beyond lateral margin of head, and by its elongate appendages and light body color.

Though we lack information on the nesting site of this species, the small eyes, elongate appendages, and light body color of this species suggests this species may have adapted to a cavernicolous life. In Madagascar, even though some species have reduced eyes and light body color, their appendages are much shorter relative to those of *L. zohy. Leptogenys khammouanensis* is the only reported cave species of *Leptogenys* and was found in Laos (Roncin & Deharveng, 2003). This species was found deep in the caves and has reduced eyes, light pigmentation, and elongate body appendages. Lattke (2011) cautioned in using these morphological characters (eye size, color, and body shape) as indicators of underground habits because there are epigaeic foraging species with equally small eyes, elongate body and reddish legs. Thus, further studies will be needed in Ankarana to investigate the biology, nesting and foraging habits of *L. zohy*.

Distribution and biology. This species is represented by one worker specimen found in the Grotte of Andrafiabe in the Tsingy of Ankarana. It is not known if the single worker collected was nesting in the cave or simply a stray forager.



FIGURE 72. Leptogenys zohy holotype worker CASENT0102922. A: lateral view. B: head in full-face view. C: dorsal view.



FIGURES 73–78. Distribution maps of the Leptogenys angusta group in the Malagasy region.



FIGURES 79-84. Distribution maps of the Leptogenys angusta group in the Malagasy region.

The *fiandry* group

Head rectangular, only slightly broadened in front of eyes. Eye either small or large, if small then maximum width less than greatest width of antennal scape. Anterior clypeal margin projecting medially into triangular lobe borderedby semi-translucent lamella. Mandible short and falcate, capable of closing tightly against clypeus; basal groove deeply impressed; blades slightly increasing in width from base to apical third and becoming narrow toward apical sharp tooth; preapical tooth inserted at apical third portion; inner margin with narrow and thin translucent lamella. Antennal scape relatively short, only one-fifth of its length extending beyond posterior cephalic margin; third segment apparently as long as the fourth. Metanotal groove strongly impressed, without transverse striation. Propodeal lobe indistinct. With petiolar node in lateral view, anterior margin much shorter than posterior; anterior margin rounding into the dorsum, which joins posterior margin at an apparently distinct angle. Helcium at anteroventral angle of third abdominal segment. Constriction between third and fourth abdominal segments visible.

Dorsum of head and mesosoma mostly smooth and shining apart from scattered hair-bearing punctures or covered with fairly dense and fine punctures. Mandible smooth or longitudinally striate. Mesopleuron and lower half of sides of propodeum most often finely microrugulose. Propodeal declivity transversely striate. Light brown hairs and pubescence present on body. Integument with glossy reflection, blackish-brown to light brown in color, with lighter apical portion of gaster and appendages.

This group consists of four species, recognized generally by their smaller body size, smaller eye and the presence of dense and fine reticulate-rugae or reticulate punctures on mesopleuron and lower half of lateral propodeal surface.

Leptogenys alamando Rakotonirina and Fisher, sp. n.

(Figures 6A, 7A, 85, 90)

Holotype worker: Madagascar, Toamasina, Montagne Akirindro, 7.6 km 341° NNW Ambinanitelo, -15.2883, 49.5483, 600 m, rainforest, sifted litter, 17–21 Mar 2003 (Fisher, Griswold *et al.*) collection code: BLF08250, specimen code: CASENT0034626 (CASC).

Paratypes: 3 workers and 1 ergatoid queen, of same data as holotype but specimen coded as: CASENT0034621, CASENT0034622 (ergatoid queen), CASENT0034624, CASENT0034625 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Eye small, maximum width less than maximum diameter of antennal scape; body smooth and shining; mandibular blades smooth and shining; masticatory margin with three teeth, one apical and two preapical; mesopleuron and lower half of lateral propodeal surface with dense and fine reticulate rugulae.

Measurements (7 specimens). HW: 0.61–70, HL: 0.91–1.02, CI: 66–72, SL: 0.76–0.89, SI: 117–133, PW: 0.52–0.59, WL: 1.38–1.54, PNH: 0.44–0.48, PNL: 0.38–0.50, PNW: 0.35–0.39, DNI: 72–90, LNI: 89–110.

Description. Head weakly broader in front than behind; lateral border almost straight. Eye reduced, with maximum width distinctly less than broadest width of scape. Anterior clypeal margin medially terminating at triangular lobe, bordered by narrow semi-translucent lamella. Mandible short and capable of placing firmly against clypeus; masticatory margin armed with three teeth, one apical plus two preapical (median tooth smallest). Antennal scape relatively short, barely surpassing posterior cephalic margin. In profile, posterior border of propodeum with small toothlike lobe. With petiole in lateral view, node about as high as long, anterior face rounding to the dorsum, joining posterior face at distinct angle. Subpetiolar process simple, consisting only of anterior tooth or lobe followed by smooth ventral margin. In profile, prora extending as sharp, ventrally directed lobe anterior to anteroventral angle of third abdominal segment.

Mandible smooth and shiny between scattered punctures. Dorsum of head, mesosoma and petiolar node smooth and shining with sparse, small piligerous punctures. With mesosoma in profile, mostly anterior half of mesopleuron and lower half of propodeum finely reticulate. Fine reticulation also present around mesometapleural suture. Long erect hairs present on scape and dorsum of body and shorter suberect hairs abundant.

QUEEN. Measurements (3 specimens). HW: 0.67–0.74, HL: 0.94–1.00, CI: 70–74, SL: 0.80–0.87, SI: 117–120, PW: 0.56–0.58, WL: 1.39–1.44, PNH: 0.47–0.49, PNL: 0.38–0.40, PNW: 0.43–0.45, DNI: 111–114, LNI: 118–128. Worker traits are observed in ergatoid queen, but ergatoids have the following specific characters: shorter head, mesosoma with incomplete thoracic sclerites, shorter petiolar node, and enlarged gaster. Hairs on dorsum of body numerous and slender.

Distribution and biology. The collections of *L. alamando* were made in lowland rainforests between 20 m and 775 m. Its geographic range extends from northeastern Madagascar in Marojejy, through the central-eastern region in Mananara-Nord and Betampona, to the southeast in the forests of Ambalagoavy Nord. This species is terrestrial; workers have been mostly recorded foraging through the leaf litter and on the forest floor. The colonies are found in rotten logs.

Additional material examined. Province Antsiranana: PN Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, rainforest (B.L. Fisher *et al.*) (CASC); Province Fianarantsoa: F d'Ambalagoavy Nord, Ikongo, Ambatombe, 625 m, rainforest (R. Harin'Hala & M.E. Irwin) (CASC); Province Toamasina: Nosy Mangabe, 20 m, rainforest (P.S. Ward) (PSWC) (MCZC); FC Andriantantely, 530 m, rainforest (H.J. Ratsirarson) (CASC); Montagne Akirindro, 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); PN Mananara-Nord, 7.1 km 261° Antanambe, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Réserve Ambodiriana, Manompana River, 4.8 km 306° Manompana, 125 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, 34.1 km 332° Toamasina, 550 m, rainforest (B.L. Fisher) (CASC).



FIGURE 85. Leptogenys alamando holotype worker CASENT0034626. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys anjara Rakotonirina and Fisher, sp. n.

(Figures 7C, 8B, 9B, 86, 91)

Holotype worker: Madagascar, Antsiranana, Réserve Anjanaharibe-Sud, 11.0 km WSW Befingotra, -12.75, 49.45, 1565 m, montane rainforest, 16–20 Nov 1994 (B.L. Fisher) collection code BLF01234, specimen code CASENT0175331 (CASC).

WORKER. Diagnosis. Eye small, maximum width less than maximum diameter of antennal scape; body smooth and glossy; mandibular blades smooth and shining; masticatory margin with two teeth, one apical and second preapical; mesopleuron and lower half of sides of propodeum with dense and fine microrugulation; petiolar node longer than high in profile; propodeum unarmed; dorsum of body with slender erect hairs.

Measurements (1 specimen). HW: 0.83, HL: 1.24, CI: 67, SL: 1.13, SI: 137, PW: 0.70, WL: 1.91, PNH: 0.58, PNL: 0.66, PNW: 0.46, DNI: 70, LNI: 88.



FIGURE 86. Leptogenys anjara holotype worker CASENT0175331. A: lateral view. B: head in full-face view. C: dorsal view.

0.5 mm

1 mm

Description. Head long, slightly diverging anteriorly. Eye small, maximum width less than maximum diameter of antennal scape. Anterior clypeal margin projecting into prominent median lobe. Mandible short and capable of closing tightly against clypeus; apical and preapical teeth present on apical portion. Antennal scape feebly extending beyond posterior margin of head. Metanotal groove visible but not transversely striate. Propodeal lobe indistinct. In lateral view, petiolar node distinctly longer than high; anterior face shorter than the posterior, causing node to incline anteriorly. Subpetiolar process composed of an anterior tooth followed by a posterior lobe with an indentation between them. Prora shaped as sharp, ventrally directed lobe at anteroventral angle of third abdominal segment.

Mandible smooth and shiny, with sparse piliferous pits. Dorsum of head, mesosoma and petiolar node smooth and shining apart from very small punctures from which hairs arise. Mesopleuron and lower half of lateral surface of propodeum covered with fine reticulo-rugulation. Erect long and suberect short hairs present on antennal scape and dorsum of body. Body dark-brown in color, with glossy reflection, appendages and tip of gaster lighter coloration.

Queen unknown for this species.

Discussion. Leptogenys anjara can be distinguished from *L. alamando* by the presence of two teeth on mandibular masticatory margin and the complex subpetiolar process. The latter species has three mandibular teeth and simple subpetiolar process. Leptogenys anjara is separable from *L. fiandry* by its larger size and the remarkable length of its petiolar node (DNI: 70).

Distribution and biology. Its known distribution is limited to a single collection from a locality in the montane rainforest of the RS Anjanaharibe-Sud. Pitfall traps were used to capture the lone specimen. Its exceptionally close resemblance to other two species (*L. fiandry* and *L. alamando*) suggests that it may be a cryptic species whose workers forage underground and rarely hunt on the forest floor.

Leptogenys fiandry Rakotonirina and Fisher, sp. n.

(Figures 7B, 9A, 87, 92)

Holotype worker: Madagascar, Antsiranana, Forêt d' Antsahabe, 11.4 km 275° W Daraina, -13.2117, 49.5567, 550 m, tropical dry forest, ex rotten log, 14 Dec 2003 (B.L. Fisher *et al.*) collection code: BLF10234, specimen code: CASENT0247245 (CASC).

Paratypes: series of 7 worker specimens, same data as holotype but with the following specimen codes: CASENT0076745, CASENT0076746, CASENT0076747, CASENT0247243, CASENT0247244, CASENT0247246, CASENT0196531 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Eye small, maximum width less than maximum diameter of antennal scape; body smooth and shining; mandible smooth and shining; masticatory margin with two teeth, one apical and the second preapical; mesopleuron and lower half of sides of propodeum densely and finely reticulate-rugulose; node approximately as high as long in profile; posterior margin of propodeum with distinct toothlike lobe; dorsum of body with slender erect hairs.

Measurements (16 specimens). HW: 0.60–0.69, HL: 0.74–0.99, CI: 66–85, SL: 0.65–0.86, SI: 109–131, PW: 0.47–0.59, WL: 1.23–1.48, PNH: 0.38–0.50, PNL: 0.42–0.50, PNW: 0.36–0.44, DNI: 81–91, LNI: 90–106.

Description. Head elongate and very slightly diverging anteriorly, lateral borders nearly parallel to each other. Eye small, maximum width less than greatest width of antennal scape. Anteromedian clypeal margin projecting into triangular lobe. Mandible short and armed with two teeth, apical and preapical; blades widest at insertion of preapical tooth. Antennal scape short, feebly extending beyond posterior cephalic margin. In lateral view, posterior margin of propodeum with small toothlike lobe. In profile, petiolar node roughly as high as long; subpetiolar process consisting of anteroventral tooth followed by an indentation and then a posterior lobe. At anteroventral angle of third abdominal segment, prora projecting into sharp, ventrally directed lobe.

Mandible smooth and shiny with scattered punctures. Dorsum of head, mesosoma and petiolar node smooth and shining besides very small piligerous pits. Anterior half of mesopleuron and propodeum generally finely reticulate in profile, sometimes mesopleural suture surrounded by fine reticulation. Sparse long hairs and short erect hairs present on scape and dorsum of body. Body color blackish dark-brown to brown with lighter appendages and apex of gaster.



FIGURE 87. Leptogenys fiandry worker CASENT0463434. A: lateral view. B: head in full-face view. C: dorsal view.

QUEEN. Measurements (3 specimens). HW: 0.68–0.74, HL: 0.94–0.99, CI: 72–74, SL: 0.72–0.79, SI: 106–114, PW: 0.57–0.62, WL: 1.33–1.39, PNH: 0.47–0.49, PNL: 0.33–0.38, PNW: 0.46–0.47, DNI: 123–139, LNI: 124–148. Ergatoid queens look very similar to workers, but differ in the following characters: ergatoids have a broader and more ovoid head, shorter and robust mesosoma with decreased development of thoracic sclerites, shorter petiolar node, and enlarged gaster. With gaster in profile, helcium slightly higher on anterior margin of third abdominal segment. Hairs on dorsum of body more abundant and somewhat long and more slender.

Discussion. Workers of *L. fiandry* are similar to those of *L. alamando* but are easily separable by the presence of two teeth on the apical portion of its mandible and its complex subpetiolar process, which consists of one anterior tooth and a second posterior lobe. *Leptogenys alamando*'s mandibular masticatory margin is armed with three teeth, and its subpetiolar process lacks the second posterior lobe.

Distribution and biology. Leptogenys fiandry is widely distributed across different habitats in the northern

half of Madagascar. These range from dry forest, particularly in Tsingy, to transitional humid and littoral forests, as well as montane rainforest. Comoros Island is also known to harbor the species. Specimens of *L. fiandry* have been sampled using the sifted litter method and pitfall traps. They are quite common in their habitats and have been found foraging on the ground, nesting under rocks and rootmat layers, and in rotten logs and sticks on the forest floor.

Additional material examined. MADAGASCAR: Province: Antsiranana: RS Ankarana, 7 km SE Matsaborimanga, 150 m (P.S. Ward) (PSWC); RS Manongarivo, 14.5 km 220° SW Antanambao, 1175 m (B.L. Fisher) (CASC); RS Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m (Fisher, Griswold et al.) (CASC); RS Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m (Fisher, Griswold et al.) (CASC); F d'Ambilanivy, 3.9 km 181° S Ambaliha, Ampasindava, 600 m (Fisher, Griswold et al.) (CASC); F d'Anabohazo, 21.6 km 247° WSW Maromandia, 120 m (Fisher, Griswold et al.) (CASC); RNI Lokobe, 6.3 km 112° ESE Hellville, Nosy Be, 30 m (Fisher, Griswold et al.) (CASC); F de Bekaraoka, 6.8km 60° ENE Daraina, 150 m (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, 550 m (B.L. Fisher) (J.C. Rakotonirina) (CASC); Ambondrobe, 41.1 km 175° Vohemar, 10 m (B.L. Fisher) (CASC); F Ambato, 26.6 km 33° Ambanja, 150 m (B.L. Fisher) (CASC); Galoko Chain, Mont Galoko, 1100 m, montane forest (B.L. Fisher et al.) (CASC); Galoko Chain, Mont Galoko, 980 m, montane forest (B.L. Fisher et al.) (CASC); Coco Beach Hotel Ambatoloaka, Nosy Be (G.D. Alpert) (MCZC); Province Mahajanga: PN Namoroka, 9.8 km 300° WNW Vilanandro, 140 m (Fisher, Griswold et al.) (CASC); PN Namoroka, 16.9 km 317° NW Vilanandro, 100 m (Fisher, Griswold et al.) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, 30 m (Fisher, Griswold et al.) (CASC); PN Baie de Baly, 12.4 km 337° NNW Soalala, 10 m (Fisher, Griswold et al.) (CASC); RS Marotandrano, Marotandrano 48.3 km S Mandritsara, 865 m (B.L. Fisher et al.) (CASC); COMOROS: Mohéli Ouallah, 750 m (B.L. Fisher et al.) (CASC).

Leptogenys rabesoni Rakotonirina and Fisher, sp. n.

(Figures 8A, 88, 93)

Holotype worker: Madagascar, Mahajanga, Mitsinjo, Tsiombikibo Forest m., -16.0833, 45.8667, dry forest, on ground, 18 Apr 1993 (P. Rabeson) MCZ code: MCZ0.1117W, AntWeb specimen code: CASENT0195430 (MCZC).

Paratypes: 3 workers with same data as holotype but with MCZ codes: MCZ0.1117W, MCZ0.1118W and following AntWeb specimen codes: CASENT0195431, CASENT0195432, CASENT0195429 (MCZC, CASC).

WORKER. Diagnosis. Eye maximum width roughly equal to widest portion of antennal scape; dorsum of body mostly punctate; mandibular blades striate; masticatory margin with two teeth, one apical and a second preapical; mesopleuron and lower half of lateral surface of propodeum densely and finely reticulate-rugulose; node approximately as high as long in profile; posterior margin of propodeum with distinct toothlike lobe; dorsum of body with short subdecumbent or apressed hairs.

Measurements (4 specimens). HW: 0.77–0.81, HL: 1.07–1.10, CI: 70–73, SL: 0.83–0.90, SI: 108–115, PW: 0.54–0.67, WL: 1.60–1.70, PNH: 0.50–0.53, PNL: 0.45–0.49, PNW: 0.45–0.47, DNI: 96–100, LNI: 106–112.

Description. Head weakly broader in front and slightly narrower in the back; sides almost straight. Maximum width of eye roughly equal to largest width of scape. Anterior clypeal margin projecting into triangular lobe covered with narrowly rounded semi-translucent lamella. Mandible with three teeth, one apical plus two preapical, middle tooth very small and resembles denticle or blunt angle. Antennal scape barely surpassing posterior cephalic margin. Propodeum without distinct lobe. In lateral view, petiolar node approximately as high as long; anterior and posterior faces meeting dorsum in a distinct angle. Subpetiolar process consisting of anterior tooth or lobe and small posterior triangular tooth. In profile, anteroventral angle of third abdominal segment protruding anteriorly as sharp ventrally directed lobe.

Mandible longitudinally striate, interspersed with sparse punctures. Dorsum of head covered with dense and fine small punctures. Pronotum and petiolar node with punctures but not as dense and as strong as those on head; propodeum and third and fourth abdominal segments generally smooth dorsally. With mesosoma in profile, mostly lower half of mesopleuron and propodeum finely reticulate rugulose or finely striate. Erect hairs absent from antennal scape except for the basal portion; long erect hairs may be present on anterior border of pronotum. Hairs on dorsum of the remainder of pronotum and mesonotum to gaster short and subdecumbent or appressed.
Discussion. This species is easily distinguishable from other species within the same species group by its longitudinally striate mandible. The mandible of other species is smooth and shiny.

Distribution and biology. This species is only recorded once from the dry forest habitats of Tsiombikibo near Mitsinjo in western Madagascar where the worker specimens were found foraging on the ground.





FIGURE 88. Leptogenys rabesoni holotype worker CASENT0195430. A: lateral view. B: head in full-face view. C: dorsal view.



FIGURES 89–94. Distribution maps of the Leptogenys zohy (angusta group), Leptogenys fiandry group and Leptogenys alluaudi (L. incisa group) in the Malagasy region.

The incisa group

Mandible elongate and narrow, with sharp apical tooth; usually not capable of closing tightly against clypeus, only their apical portions crossing each other when fully closed; very seldom are their inner margins convex and very seldom do they close tightly without a gap against the clypeus when at rest. Mandibular inner margin with narrow subopaque lamella; preapical tooth may be present near sharp apical one; basal groove narrow, vestigial or almost effaced. Head variably shaped, either subrectangular, ovoid or trapezoidal; head can be short and broad or narrow and elongate; posterior margin generally straight. Eye large, diameter greater than maximum width of antennal scape; either breaking or in front of outline of lateral border of head. Antennal scape with at least apical third surpassing posterior cephalic margin. Clypeus diversely shaped, projecting anteriorly into broad triangular lobe or apically terminated into toothlike spine, with a narrowly circular or obtusely triangular extension; translucent or semi-translucent lamella bordering clypeal margin, sometimes very narrow and barely visible in a few specimens; median clypeal carina long and usually sharp except for *L. imerinensis*. With mesosoma in dorsal view, metanotal groove with a straight or curved suture; posterior of metanotal groove, an additional suture present, dividing mesosoma into a fourth section. Propodeal lobe toothlike if present. In profile, petiole nodiform, either roughly as long as high, or longer than high. Constriction between third and fourth abdominal segments weakly to strongly visible.

Dorsum of head, mesosoma and petiolar node lacking smooth areas, most often densely and finely reticulaterugose, superimposed with small punctures. Erect or suberect hairs present on dorsum of head and rest of body, generally with sparse pubescence. Integument black to dark brown, with lighter coloration on apex of appendages.

One of the largest species groups of *Leptogenys* from the Malagasy region, the *incisa* group contains 17 species that can be divided into three species complexes: the *alluaudi*, *imerinensis*, and *voeltzkowi*. The *alluaudi* complex includes *L. alluaudi*, *L. incisa* and *L. pilaka*, characterized by the absence of peg-like setae projecting anteriorly on the anteromedial clypeal margin and by its larger size. The *voeltzkowi* complex, with *L. voeltzkowi*, *L. vitsy* and *L. sahamalaza*, is distinguished by the presence of peg-like setae on the anterior margin of the clypeus and the restriction of a membranous spot to the small and rounded median lobe of the clypeus. The *imerinensis* complex contains the rest of the species and can be recognized by the broadly triangular or spine-like shape of the anteromedial clypeal lobe, which is equipped with at least one pair of peg-like setae.

The *incisa* group is among the species-rich groups that show remarkable morphological variations within species. Populations within species sometimes show more variation than groups among species. In the present study, complexes of phenotypic divergences have been found based on mandible shape, the form of the anterior clypeal margin and the shape of the petiolar node.

All of these species occur only in Madagascar except *L. gracilis*, one of the smaller species within the species group, which is also found on the Comoros Islands.

Leptogenys alluaudi Emery

(Figures 45A, 46A, 94, 95)

Leptogenys alluaudi Emery, 1895a: 338. Holotype worker, Madagascar, Diego Suarez, Avril-August, 1893 (Alluaud) (NHMB) [examined]. [Combination in Leptogenys (Leptogenys): Emery, 1911: 99; Wheeler, 1922b: 1010; in Leptogenys: Bolton, 1975: 297, 1995: 229].

WORKER. Diagnosis. Peg-like setae absent near the anterior margin of median lobe of clypeus; head nearly subquadrate, eye not breaking lateral cephalic margin, basal portion of mandible slightly curved, not extending beyond outline of the sides of head.

Measurements (12 specimens). HW: 2.20–2.50, HL: 2.25–2.55, CI: 97–103, SL: 2.30–2.61, SI: 97–107, PW: 1.46–1.62, WL: 3.62–4.01, PNH: 1.21–1.31, PNL: 1.06–1.16, PNW: 1.01–1.16, DNI: 94–103, LNI: 107–119.

Description. Head generally as broad as long or broader than long; lateral border weakly convex and feebly diverging anteriorly throughout their length. Eye large, not breaking sidelines of head. Antennal scape relatively short (SI: 97–107), less than one third of apical portion surpassing posterior cephalic margin. Clypeus concave laterally and strongly converging anteriorly, ending in narrow angular lobe with fringing lamella. Mandible elongate and narrow, feebly curved near base; with concave inner margin; blades not strongly crossing each other

and not closing tightly against clypeus; basal groove narrowly impressed. Mesosoma in profile high and short; propodeal lobe absent. With petiole in side view, node about as high as broad; straight and vertical anterior face and anteriorly sloping posterior meeting convex dorsal margin at rounded angle. Third and fourth abdominal segments with feeble constriction between them.



FIGURE 95. Leptogenys alluaudi worker CASENT0054724. A: lateral view. B: head in full-face view. C: dorsal view.

Mandible mostly smooth, with scattered punctures and faintly effaced striation. Head reticulate-rugose dorsally; sides and posterior third finely microreticulate with sparse, large punctures. Mesosoma and petiolar node densely and finely reticulate-rugose to microreticulate, superimposed with scattered large and elongate punctures; declivitous surface with transverse rugulae. Third and fourth abdominal tergites smooth apart from widely spaced punctures. Standing yellowish hairs present on entire dorsum of body with less pubescence. Color black; tip of gaster and appendages brown to reddish brown.

Discussion. *Leptogenys alluaudi* is sympatric with *L. pilaka* in the PN Montagne d'Ambre and both species appear to be closely related to each other. Together with *L. incisa,* they constitute the *alluaudi* species complex. They look very similar in body size, shape of the clypeus, and absence of peg-like setae on the anterior clypeal margin. *Leptogenys alluaudi* is one of the largest species within the group (HW: 2.20–2.50). It can be distinguished from *L. pilaka* and *L. incisa* by its subquadrate head (CI: 97–103) and the position of its eyes, which do not break the lateral border of the head. In *L. pilaka* and *L. incisa,* the head is elongate (CI: 85–97) and the eyes project beyond lateral margins of head in full face view.

Distribution and biology. *Leptogenys alluaudi* is confined to northern Madagascar. It has been recorded in dry forest, littoral forest, and montane rainforest. This species generally forages on the forest floor as well as in leaf litter, and nests mostly in rotten logs and rarely in rotting tree stumps.

Additional material examined. Province Antsiranana: [Vohemar; 11] (A. Cabrera) (NHMB); Ambondrobe, 41.1 km 175° Vohemar, 10 m, littoral rainforest (B.L. Fisher) (CASC); F Ambanitaza, 26.1 km 347° Antalaha, 240 m, rainforest (B.L. Fisher) (CASC); F Ampombofofo, 25 m, littoral forest (B.L. Fisher *et al.*) (CASC); F d'Analabe, 30.0 km 72° ENE Daraina, 30 m, littoral rainforest (B.L. Fisher) (CASC); F de Bekaraoka, 6.8 km 60° ENE Daraina, 150 m, tropical dry forest (B.L. Fisher) (CASC); F d'Orangea, 3.6 km 128°SE Ramena, 35 m, littoral forest (J.C. Rakotonirina) (CASC); Montagne des Français, 7.2 km 142° SE Antsiranana, 180 m, tropical dry forest (Fisher, Griswold *et al.*) (J.C. Rakotonirina) (CASC); PN Montagne d'Ambre, Fozalanana, 475 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); RS Ambre, 3.5 km 235° SW Sakaramy, 325 m, tropical dry forest (B.L. Fisher) (CASC); PN Montagne d'Ambre, Secondary forest (I. Constable) (MCZC).

Leptogenys antongilensis Emery

(Figures 50A, 96, 112)

Leptogenys incisa var. antongilensis Emery, 1899: 272. Lectotype worker, present designation, Madagascar, Toamasina, Bia di Antongil, 1897–1898 (A. Mocquerys), AntWeb CASENT0102015 (MSNG). Paralectotype worker with same data as lectotype but with CASENT0102016 (MSNG) [examined]. [Raised to species and combination in Leptogenys (Machaerogenys): Emery, 1911: 100; Wheeler, 1922b: 1011; in Leptogenys: Bolton, 1975: 298, 1995: 230].

WORKER. Diagnosis. Anteromedian border of clypeus above semi-translucent lamella with anteriorly projecting peg-like setae; antennal scape relatively long (SI: 132–138), more than a third of apical portion extending beyond posterior cephalic margin; inner margin of mandible blades generally convex and distinctly broadest at mid-length; mesosoma with three visible segments, no other impression as a sclerite in appearance on dorsum of propodeum.. **Measurements (8 specimens).** HW: 1.49–1.58, HL: 1.86–1.97, CI: 80–82, SL: 2.03–2.13, SI: 132–138, PW: 1.22–1.30, WL: 3.13–3.40, PNH: 0.88–0.94, PNL: 0.96–1.05, PNW: 0.87–0.95, DNI: 88–94, LNI: 88–94.

Description. Head subrectangular, slightly broader in front than at the posterior; sides slightly convex and diverging. Posterior margin of head very weakly concave. Eye protruding and projecting beyond lateral margins of head. Antennal scape very long, almost reaching posterior cephalic margin at midpoint. Clypeus with broad, triangular anteromedian lobe; anterior clypeal margin bordered with more or less wide, semi-transparent lamella. Mandible elongate, inner margin convex and blades broadest at midlength, but not capable of closing tightly against clypeus when their apices intersect. Hypostomal teeth short and notvisible with head in full-face view. Mesosoma elongate and relatively low in lateral view; in dorsal view three sections visible, no additional suture present posterior of metanotal groove. With petiole in dorsal view, node longer than broad, and fairly broader than high in profile; posterior margin inclined anteriorly and anterior face vertical, both forming convex lines to rounded dorsal margin.



FIGURE 96. Leptogenys antongilensis worker CASENT0107408. A: lateral view. B: head in full-face view. C: dorsal view.

Mandible longitudinally striate, striation occasionally interrupted by smooth spaces and scattered piligerous punctures. Dorsum of head, mesosoma, and petiolar node densely and finely reticulate-punctate to densely and finely reticulate-rugose, with sparse small punctures between sculptures. Third and fourth abdominal tergites smooth and shiny, with small punctures. Body covered with thin erect hairs and pubescence. Black in color; appendages and gaster with brown apical section.

Discussion. This species is generally similar to *L. manja*, but can be easily identified by the fine longitudinal striation on its mandible and the convex inner margin of the blades. In *L. manja*, the mandibles are smooth and the inner margin of the blades is evenly concave. It can be separated from *L. tatsimo* by its three-segmented mesosoma and the narrow lamella bordering the anterior clypeal margin.

Distribution and biology. *Leptogenys antongilensis* is limited to the lowland rainforest of northeastern Madagascar. It mainly forages on the forest floor and nests in rotten logs and rotten tree stumps, though foraging behavior may also occur on lower vegetation.

Additional material examined. Province Antsiranana: F Ambanitaza, 26.1 km 347° Antalaha, 240 m, rainforest (B.L. Fisher) (CASC); F de Binara, 9.1 km 233° SW Daraina, 650–800 m, rainforest (B.L. Fisher) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); 30 km N of Antalaha, 5 km W to hill near Amboahangy, 50 m, secondary rainforest (Alpert *et al.*) (MCZC); Province Toamasina: [Antongil] (Mocquerys) (MSNG); PN Mananara-Nord, 7.1 km 261° Antanambe, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambodiriana, 4.8 km 306°Manompana, along Manompana River, 125 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, 475–520 m, rainforest (B.L. Fisher *et al.*) (CASC). Cap Masoala, 1 km W Andampibe, lowland rainforest, 125 m (G.D. Alpert) (MCZC); Fotodriana, Cap Masoala, lowland rainforest, 25 m (G.D. Alpert) (MCZC).

Leptogenys barimaso Rakotonirina and Fisher, sp. n.

(Figures 55B, 58C, 59A, 97, 113)

Holotype worker: Madagascar, Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.2883, 49.5483, 600 m, rainforest, ex rotten branch on ground, 17–21 Mar 2003 (Fisher, Griswold *et al.*), collection code: BLF08268, specimen code: CASENT0496058 (CASC).

Paratypes: 5 workers with same data as holotype but specimen coded as: CASENT0496059, CASENT0496057, CASENT0247235, CASENT0247236, CASENT0247237 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Small peg-like setae present from near anterior border of narrowly semi-circular anteromedial clypeal lobe; mandible with inner margin evenly and slightly concave; antennal scape long (SI> 130), more than apical third surpassing posterior cephalic margin; eye breaking outline of sides of head; dorsum of head and body with standing hairs longer than maximum diameter of eye; posterior margin of petiolar node without constriction immediately above posteroventral angle.

Measurements (7 specimens). HW: 1.16–1.36, HL: 1.45–1.65, CI: 80–84, SL: 1.66–2.00, SI: 133–147, PW: 0.93–1.07, WL: 2.41–2.87, PNH: 0.80–0.94, PNL: 0.82–1.00, PNW: 0.75–0.93, DNI: 88–96, LNI: 91–102.

Description. In full-face view, head elongate and broader in front than behind; side noticeably convex and diverging anteriorly throughout length. Eye large and distinctly convex, breaking line of lateral cephalic border. Antennal scape markedly long, with more than one third its length extending beyond posterior cephalic margin. Anterior clypeal margin extending suddenly into a narrowly rounded median lobe which is bordered by a yellow-orange lamella. Mandible long and narrow, inner margin broadly concave and leaving a gap between clypeus and blades when closed; basal groove narrow. Preapical tooth or denticle may be present on each blade. In full-face view, hypostomal teeth not visible. Mesosoma in dorsal view, with impressed and transversely rugulose metanotal groove; in profile, overall shape short and high; posterolateral border of propodeum without toothlike lobe. In lateral view, petiolar node more or less elongate, dorsal outline of node convex and posterior margin inclined anteriorly; in dorsal view, node longer than broad. Constriction between abdominal segments III and IV distinct.

Mandibular blade covered with interrupted short and fine striation and scattered punctures. Dorsum of head, mesosoma and petiolar node coarsely reticulate-rugose, with large punctures or foveae in between; some punctures widely spaced; declivitous surface transversely rugulose. Dorsum of head and body with long standing hairs longer than greatest diameter of eye; pubescence reduced. Color black to reddish-brown, with dark brown to lighter appendages.

Discussion. Leptogenys barimaso is similar to L. chrislaini and L. lavavava, but in L. barimaso the inner margin of the mandible is evenly concave, the anteromedian portion of the clypeus is narrow with a rounded lobe, and abdominal tergites III and IV have long standing hairs whose length is greater than the maximum diameter of the eye. The abrupt projection of the anterior margin of the clypeus into a narrowly angulate lobe, the subquadrate head, the strongly curved basal portion of the mandible, and the shorter hairs on abdominal tergites III and IV render L. chrislaini separable from L. barimaso. In L. lavavava, the median portion of clypeus is projecting anteriorly into a toothlike spine and the basal portion of mandible is remarkably curved, extending laterally beyond the widest level of the sides of the head.



FIGURE 97. Leptogenys barimaso holotype worker CASENT0496058. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. A few localities in the northeast of Madagascar harbor *L. barimaso*. The species is known to occupy not only the natural littoral and humid forests, but also the disturbed and fragmented forest habitats in the region. *Leptogenys barimaso* forages on the ground and in leaf litter, but it also hunts on lower vegetation. Its nests are mainly in rotten logs and rarely in rotten branches on the forest floor.

Additional material examined. Province Antsiranana: RS Anjanaharibe-Sud, 6.5 km SSW Befingotra, 875 m, rainforest (B.L. Fisher) (CASC); F de Binara, 9.1 km 233° SW Daraina, 650–800 m, rainforest (B.L. Fisher) (CASC); Betaolana Forest, Ambodihazovolabe village along Ambolokopatrika River, 740 m, disturbed forest patch next to tavy (B.L. Fisher *et al.*) (CASC); 5 km SW Antalaha, 50 m (G.D. Alpert) (MCZC); Res. Anjanaharibe-Sud, 17 km W Andapa, 875 m, primary rainforest (G.D. Alpert) (MCZC); Province Toamasina: Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Nosy Mangabe, 7.43 km S Maroantsetra, 3 m, littoral rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys chrislaini Rakotonirina and Fisher, sp. n.

(Figures 48C, 58B, 59B, 98, 114)

Holotype worker: Madagascar, Antsiranana: Ambondrobe, 41.1 km 175° Vohemar, -13.7153, 50.1017, 10 m, littoral rainforest, ex rotten log, 30 Nov 2004 (B.L. Fisher), collection code: BLF11141, specimen code: CASENT0107500 (CASC).

Paratypes: 5 workers with same data as holotype but specimen coded as: CASENT0247262, CASENT0247263, CASENT0247264, CASENT0247265, CASENT0247266 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Median portion of clypeus abruptly projecting anteriorly into short, narrowly angulate lobe; small peg-like setae projecting anteriorly from near anterior margin of lobe; basal portion of mandible distinctly arched in full face view, but not extending laterally beyond cephalic outline; antennal scape relatively short; in full-face view, eye breaking lateral cephalic margin; head subquadrate; in lateral view, posterior border of petiolar node without constriction near its posteroventral angle.

Measurements (9 specimens). HW: 1.51–1.73, HL: 1.80–2.01, CI: 83–88, SL: 1.64–2.11, SI: 104–133, PW: 1.07–1.23, WL: 2.76–3.14, PNH: 0.88–0.99, PNL: 0.84–1.00, PNW: 0.84–0.93, DNI: 88–108, LNI: 92–111.

Description. Head subquadrate, sides almost straight and weakly rounding to a slightly concave posterior margin. Eye large and slightly protruding, maximum diameter greater than widest part of scape. Antennal scape relatively short, usually less than a fourth of its apical portion attaining posterior cephalic margin. Clypeus anteriorly projecting into narrowly triangular median lobe, borderedby bluntly triangular subopaque lamella. Mandible elongate, strongly curved near base, but not extending laterally beyond lateral cephalic border; feebly concave to almost straight towards the apex; basal groove narrow; preapical tooth or denticle may be present near sharp apical tooth. In full-face view, hypostomal teeth short and bluntly triangular. With mesosoma in dorsal view, metanotal groove impressed and transversely striate; in lateral view, propodeum relatively high and short; posterior margin of propodeum with blunt angles at level of propodeal spiracle. Petiolar node roughly as high as broad in profile, with anteriorly sloped posterior margin; constriction absent near posteroventral angle of node; in dorsal view, petiolar node as long as broad or slightly longer than broad. Constriction between third and fourth abdominal segments feebly visible.

Mandible basally striate; median portion smooth with faint striation and scattered piligerous pits; about apical third portion densely and finely striate. Head dorsum reticulate-rugose to densely and finely reticulate-rugose, interspersed with punctures which become larger and more widely spaced near posterior margin. Mesosoma and petiolar node densely and finely reticulate-rugose, with scattered punctures; pronotal punctures much smaller than those on rest of mesosoma; propodeal declivity with transverse rugulae. Gastral tergites one and two finely microreticulate and with shallow, elongate large punctures. Entire body covered with slender erect hairs and very abundant pubescence. Antennal scape with suberect hairs shorter than maximum diameter of scape. Black species, with reddish-brown appendages having lighter apices.

Discussion. Leptogenys chrislaini closely resembles L. barimaso but L. chrislaini can be separated by the abrupt projection of the anterior margin of the clypeus into a narrowly angulate lobe, the subquadrate head, and the strongly curved basal portion of the mandible. It can be confused with L. lavavava but the latter has an elongate head, spiniform anteromedial clypeal lobe, and broadly curved mandibular blades which extend laterally beyond the lateral cephalic margin.

Populations of *L. chrislaini* from the two known localities show differences in some morphological characters. Worker specimens from Makirovana Forest are slightly larger and have longer antennal scapes than those from Ambondrobe.



FIGURE 98. Leptogenys chrislaini holotype worker CASENT0107500. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. This species is known only from the littoral forest of Ambondrobe near Vohemar and the humid forest of Makirovana near Sambava in northeastern Madagascar. It forages in leaf litter and nests in rotten logs.

Additional material examined. Province Antsiranana: Ambondrobe, 41.1 km 175° Vohemar, 10 m, littoral rainforest (B.L. Fisher) (CASC); Makirovana Forest, 390 m, rainforest (B.L. Fisher *et al.*) (CASC).

(Figures 41B, 53B, 99, 115)

Leptogenys gracilis Emery, 1899: 271. Lectotype worker, present designation, Madagascar, Bia di Antongil, 1897–1898 (A. Mocquerys), AntWeb specimen code: CASENT0102017 (MSNG). Paralectotype worker with same data as lectotype but with the following specimen code: CASENT0102018 (MSNG) [examined]. [Combination in Leptogenys (Leptogenys): Emery, 1911: 99; Wheeler, 1922b: 1010; in Leptogenys: Bolton, 1975: 298, 1995: 231].

WORKER. Diagnosis. Two peg-like setae projecting anteriorly from near anterior margin of median lobe of clypeus; translucent lamella of clypeus forming three distinct angles anteriorly; median longitudinal clypeal carina sharp; antennal scape relatively short (SI: 107–121), less than one fourth its length extending beyond posterior margin of head; additional suture present between metanotal groove and propodeum, thus in dorsal view, four divisions present on mesosoma, mandible striate, interspersed with punctures.

Measurements (7 specimens). HW: 0.96–1.13, HL: 1.17–1.32, CI: 82–87, SL: 1.09–1.32, SI: 107–121, PW: 0.81–0.91, WL: 1.99–2.31, PNH: 0.65–0.72, PNL: 0.61–0.79, PNW: 0.63–0.74, DNI: 86–108, LNI: 87–109.

Description. Head roughly longer than broad, slightly broader in front of eye than at the back; lateral margin broadly convex and feebly diverging; posterior margin slightly concave medially. Eye large and protruding; exceeding line of lateral cephalic border when head in full-face view. Antennal scape short, approximately only one-fourth of its length reaching posterior margin of head. Clypeus broadly triangular; lateral margin slightly convex with obtusely angulate anteromedian border fringed by continuous translucent lamella; near border of anteromedian lobe with pair of anteriorly projecting peg-like setae; median clypeal carina sharp. Mandible elongate and slender, inner margin with slightly blunt angle near base and weakly concave towards apex; basal groove vestigial to almost effaced; preapical denticle present close to apical tooth. Hypostomal teeth short and not visible in full-face view of head. Metanotal groove impressed; in dorsal view, mesosoma with four visible segments, an additional suture present between metanotal groove and propodeum; propodeum unarmed. With petiole in dorsal view, node either as long as or longer than broad; in lateral view, dorsal border convex and forming blunt angle with vertical anterior face and forward sloping posterior face. Constriction visible between abdominal segments III and IV.

Mandible most often longitudinally striate and sparsely punctulate. Dorsum of head densely and finely reticulate-rugose, interspersed with punctures or foveae near posterior cephalic margin. Promesonotum and dorsum of petiolar node densely and finely microreticulate and coarsely punctate or reticulate-rugose; punctures elongate on promesonotum and round on petiolar node; propodeal declivity transversely rugulose. Third and anterior half of fourth abdominal tergites smooth and shiny between fairly sparse punctures, rest of segments smooth and shining. Body covered with yellowish, erect, slender hairs and pubescence. Integument black, appendages dark brown with lighter tarsae, antennal funiculi, and tip of gaster.

Discussion. *Leptogenys gracilis* can be confounded with *L. sucrensis* but has generally striate mandibles and two peg-like setae projecting above the triangular translucent lamella of the anteromedian margin of the clypeus, whereas the latter possesses generally smooth and shining mandible and three to four peg-like setae anteriorly projecting above the broadly rounded fringing lamella of the anteromedian margin of the clypeus.

In the Malagasy region, *L. gracilis* is distributed in distantly isolated areas, and the disjunct populations vary in morphology. Populations differ in the length of petiolar node, the width of the fringing lamella on the anterior clypeal margin, and the abundance of erect hairs and pubescence. This diversity is currently considered intraspecific geographical variation.

Distribution and biology. *Leptogenys gracilis* is distributed generally in northeastern Madagascar where it occupies littoral and lowland rainforests at altitudes between 3 m and 50 m. Worker specimens have also been collected from the transitional humid forest of Ambilanivy in the Ampasindava peninsula and from montane forest on Mohéli Island, The Comoros. It primarily forages on the ground and nests in rotten logs.

Additional material examined. MADAGASCAR: Province Antsiranana: Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Ampasindava, Andranomatavy Forest, 543 m, tropical dry forest (B.L. Fisher *et al.*); 30 km N of Antalaha, 5 km W to hill near Amboahangy, secondary rainforest (Alpert *et al.*) (MCZC); Province Toamasina: Nosy Mangabe, 7.43 km S Maroantsetra, 5 m, littoral rainforest edge (B.L. Fisher *et al.*) (CASC); Nosy Mangabe (G.D. Alpert) (MCZC); Fotodriana, Cap Masoala, 25 m, lowland rainforest (G.D. Alpert) (MCZC); Ile Sainte Marie, F Ambohidena, 22.8 km 44°

Ambodifotatra, 20 m, littoral rainforest (B.L. Fisher *et al.*) (CASC); COMOROS: **Mohéli Island:** Ouallah, 750 m, montane rainforest (B.L. Fisher *et al.*) (CASC).



FIGURE 99. Leptogenys gracilis worker CASENT0129782. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys imerinensis Forel, stat. rev., stat. n.

(Figures 44B, 54B, 100, 116)

Leptogenys incisa var. imerinensis Forel, 1891: 242. Lectotype worker, present designation, Madagascar, Foret d'Andrangoloaka [-19.0, 47.95, 1389 m] (Sikora), AntWeb CASENT0101795 (lower specimen of two workers on a pin) (MHNG). Paralectotype worker, same data as lectotype but with specimen code: CASENT0101825 [examined]. Stat. n. [As subspecies of Leptogenys incisa and combination in Leptogenys (Leptogenys): Emery, 1911: 100; Wheeler, 1922b: 1011; in Leptogenys and junior synonym of Leptogenys incisa: Bolton, 1975: 298].

WORKER. Diagnosis. Anterior margin of medial clypeal lobe with one pair of small, peg-like setae projecting anteriorly; medial clypeal carina bluntly rounded along its length; antennal scape relatively short (SI: 115–118), less than its apical third extending beyond posterior margin of head; in dorsal view, mesosoma consists of three visible segments, without discernible segment between metanotal groove and propodeum; larger species.

Measurements (5 specimens). HW: 1.51–1.55, HL: 1.72–1.78, CI: 87–89, SL: 1.74–1.81, SI: 115–118, PW: 1.15–1.20, WL: 2.92–3.10, PNH: 0.88–0.90, PNL: 0.88–0.94, PNW: 0.81–0.88, DNI: 90–95, LNI: 94–100.

Description. Head subquadrate, with sides weakly convex and anteriorly diverging; posterior cephalic margin feebly concave. Eye large and slightly convex. With antennal scape laid straight back on head, in full-face view, its apex surpasses the posterior margin by roughly one-third its length. Clypeus broadly triangular, covered with narrow translucent lamella; median lobe with bluntly rounded longitudinal carina; pair of peg-like setae present on anteromedian margin. Mandible long and slender, with slightly stronger curve near base; inner margin concave, with small preapical tooth or denticle near sharp apical tooth; basal groove narrowly impressed. In cephalic full-face view, hypostomal teeth not visible. In profile, mesosoma short and high; posterior margin of propodeum without toothlike lobe. In dorsal view, metanotal groove impressed, transverse rugulae present; small and narrow sclerite present between metanotal groove and propodeum; in oblique profile, surface of propodeal declivity well delimited, junction between posterior and lateral faces of propodeum angulate. With petiole in dorsal view, node longer than broad; in profile, node relatively long, anterior face rounding to the dorsum, forming a distinct angle with a posterior face that slopes slightly forward. Constriction between third and fourth abdominal segments clearly visible.

Mandible mostly smooth and shining, interspersed with piliferous punctures, apical halves with almost effaced, fine striation. Head dorsum finely rugulose in front of level of eyes, sculpture becoming densely and finely reticulate-rugulose towards posterior portion, with larger punctures near posterior cephalic border. In dorsal view, mesosoma generally densely and finely microreticulate, superimposed by shallow, elongate punctures on promesonotum, and dense and fine reticulate-rugulae on propodeal dorsum; declivitous surface with transverse rugae. Sculpture of dorsum of petiolar node as on promesonotum but with rounded punctures. Abdominal tergites III and IV densely microreticulate, superimposed with shallow elongate punctures, punctures much more superficial than those on promesonotum. Erect hairs slender; pubescence less on dorsum of mesosoma, petiolar node and the following abdominal tergites. Body color black, with brown apical portion of appendages and tip of gaster.

Discussion. Leptogenys imerinensis can be separated from *L. namana* by its blunt median clypeal carina and larger size, while the latter has a sharp median clypeal carina and smaller body size. It can be confounded with *L. manja*, but the latter possesses longer antennal scape (SI: 136–140). The species may be confounded with *L. suarensis* and *L. gracilis* but the latter two species have four mesosomal divisions (an additional suture is present between the metanotal groove and the propodeum) in dorsal view and a smaller body size, while *L. imerinensis* has only three mesosomal segments and is larger.

This species has been considered a subspecies of *L. incisa* since its first description. Bolton (1975), in his review of the species from the Malagasy region, was not able to discern the species boundaries of some forms because his study was based on only a few type specimens and insufficient collections. Based on the analysis of the new collections sampled from ant surveys in 2012, it is now clear that *L. imerinensis* merits species designation.

Over the past 15 years of ant inventories in Madagascar, *Leptogenys imerinensis* was only found during the 2012 ant surveys in the Corridor Forestier Analamay-Mantadia and the Ankerana Forest.

Lectotype and paralectotype specimens of *L. imerinensis* chosen during this study are those that were collected from the type locality "Forêt d'Andrangoloaka" mentioned by Forel in his original description of the subspecies.

Distribution and biology. *Leptogenys imerinensis* only occurs on the central-eastern plateau of Madagascar. Its first description was based on worker and male specimens found in Andrangoloaka and Perinet. Recent ant surveys in 2012 have found this species in the Ankerana Forest and the PN Mantadia-Andasibe.

Recently-recorded worker specimens were found foraging on lower vegetation and one colony was found in a rotten log. JCR was able to observe the hunting behavior of the workers during field work in the forest corridor of Analamay-Mantadia. They ran closely one after another, in a single line and along the forest floor and on lower vegetation, to locate the prey site, about 10 meters from the nest. Then they returned to the nest individually with the prey, which consisted of isopods. Subsequently, workers emerged from the nest one after the other and ran singly before arriving at the site of the prey. Each worker returned to the nest individually or in pairs with one

isopod clutched between the clypeus and their curved, elongate, and narrow mandibles. Some workers were not carrying any prey when they returned to the nest.

Additional material examined. Province Toamasina: Centre de Madagascar (Sikora) (MHNG, MSNG); Perinet Mangé (W.L. Brown) (MCZC); Torotorofotsy, 1005 m, montane rainforest (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 918–1044 m, rainforest (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 939 m, rainforest (B.L. Fisher *et al.*) (CASC); Ankerana, 1035 m, montane forest (B.L. Fisher *et al.*) (CASC).



FIGURE 100. Leptogenys imerinensis worker CASENT0274176. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys incisa Forel

(Figures 47A, 101, 117)

Leptogenys incisa Forel, 1891: 113. Syntype workers, Madagascar, Montagne de Lokobe, Nosy-be (O'Swald) (location of types unknown). [Combination in *Leptogenys (Leptogenys)*: Emery, 1911: 100; Wheeler, 1922b:1010; in *Leptogenys*: Bolton, 1975: 298, 1995: 231].



FIGURE 101. Leptogenys incisa worker CASENT0463438. A: lateral view. B: head in full-face view. C: dorsal view.

WORKER. Diagnosis. Anteromedian border of clypeus, posterad of semi-translucent lamella without anteriorly projecting, small, peg-like setae. In full-face view, head distinctly elongate (CI: 85); eye breaking lateral cephalic

margin; mandible strongly curved near the base, blades more or less broad, with slightly convex inner margin at about distal third, outer surfaces with dense and fine longitudinal striations; large species.

Worker measurements (1 specimen). HW: 1.87, HL: 2.19, CI: 85, SL: 2.67, SI: 143, PW: 1.42, WL: 3.83, PNH: 1.26, PNL: 1.18, PNW: 1.13, DNI: 96, LNI: 107.

Description. Head elongate and distinctly increasing in width from rear to front; lateral margin weakly convex along their length. Eye large, protruding from surface of head and breaking lateral cephalic border. Antennal scape relatively long (SI: 143). Clypeus with a narrowly triangular anteromedial margin; lateral margin slightly convex and strongly converging anteriorly, bordered with narrow lamella which becomes obtusely angulate on the anterior clypeal margin. Mandible long and strongly curved near the base; inner margin broadly convex at about distal third; basal groove impressed. Hypostomal teeth not visible when head in full-face view. In lateral view, mesosoma short and high; propodeal dorsum forming distinct angle with declivity; posterolateral margin of propodeum at about the level of propodeal spiracle with toothlike lobe. With mesosoma in dorsal view, metanotal groove impressed; metanotal sclerite indistinct. Visible constriction present between third and fourth abdominal segments.

Mandible densely and finely striate, with sparse, small punctures. Head dorsum with longitudinal rugulae in front at the level of anterior margin of eyes and with dense, transverse reticulate-rugulae behind the level of eyes; large, shallow punctures present on the effaced rough sculpture near the occiput. Pronotum finely microreticulate, superimposed with coarse punctures. Rest of mesosoma, dorsum and petiolar node coarsely and transversely rugose. Propodeal declivity with transverse rugae. Third abdominal tergite covered with small and quite sparse punctures. Standing hairs long and slender, with reduced pubescence on mesosoma, petiolar node and gaster. Integument black, with dark brown appendages and light brown tarsal segments and apex of gaster.

Discussion. In addition to the strongly curved basal portion of its mandible, *L. incisa* has generally broader blades whose outer surfaces are finely, longitudinally striate. Its head is much more elongate than that of *L. alluaudi* and *L. pilaka*. In *L. alluaudi* and *L. pilaka*, the mandibles are not strongly curved near the bases, narrower and generally smooth besides piligerous punctures.

Although we were not able to find and examine the type specimens of *L. incisa*, the original description of the species (Forel 1891) closely matches the appearance of the worker specimens collected from Ambilanivy forest and the Galoko Chain.

Distribution and biology. Only known from Madagascar, *L. incisa* is represented by one worker specimen collected from the transitional forest of Ambilanivy in the north-west peninsular area of Ampasindava and a few specimens from the Chains of Galoko Mountain. A few specimens were found foraging through leaf litter and others were found nesting in a rotten log.

Additional material examined. Province Antsiranana: Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Galoko Chain, Mont Galoko, 520 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys lavavava Rakotonirina and Fisher, sp. n.

(Figures 58A, 102, 118)

Holotype worker: Madagascar, Toamasina, RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, -17.8867, 49.2025, 520 m, rainforest, ex rotten log, 3 Dec 2005 (B.L. Fisher *et al.*), collection code: BLF13354, specimen code: CASENT0067405 (CASC).

Paratypes: 5 workers with same data as holotype but with the following specimen codes: CASENT0247261, CASENT0247260, CASENT0247259, CASENT0247258, CASENT0247257 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Median portion of clypeus abruptly projecting anteriorly into a toothlike spine; a pair of peg-like setae projecting anteriorly from the side, near the apex of the spine; basal portion of mandible distinctly, broadly curved, extending laterally beyond the widest level of the sides of head; antennal scape relatively short; in full-face view, eye breaking lateral cephalic margin; erect hairs of antennal scape longer than maximum width of scape; posterior face of petiolar node without impression or groove near its posteroventral portion.

Measurements (7 specimens). HW: 1.60–1.73, HL: 2.06–2.18, CI: 77–81, SL: 1.88–2.06, SI: 117–123, PW: 1.12–1.18, WL: 3.04–3.28, PNH: 0.80–0.87, PNL: 0.89–0.97, PNW: 0.77–0.85, DNI: 85–91, LNI: 86–93.



FIGURE 102. Leptogenys lavavava holotype worker CASENT0067405. A: lateral view. B: head in full-face view. C: dorsal view.

Description. In full-face view, head widest in front of eye; lateral margin somewhat convex but width increasing anteriorly toward the base of mandible. Eye medium, maximum diameter larger than greatest width of scape. Scape relatively long, less than one third of the length reaching posterior margin of head. Anteromedian margin of clypeus abruptly projecting into sharp, toothlike spine; pair of peg-like setae present near its apex. Mandible long and narrow, outer margin strongly convex near base, extending laterally beyond the outline of side of head and becoming relatively straight toward the apices, terminating into slightly curved, sharp apical tooth; large gap present between clypeus and blades when latter at rest; preapical tooth completely absent, or present on one or both blades near apical tooth; basal groove visible. In full-face view, hypostomal teeth not visible. With mesosoma in side view, propodeum fairly long and low; posterolateral margin without lobe. In dorsal view,

metanotal groove distinct, with transverse rugulae; small transverse sclerite present between groove and propodeum. Node of petiole longer than broad in dorsal view, width reduced toward the anterior margin. With petiole in profile, node longer than high; the shorter anterior margin forming a convex outline with the dorsal margin, which meets the slightly anteriorly inclined posterior margin at distinct angle; posterior margin of node without constriction at posteroventral angle. Abdominal segments III and IV with visible constriction.

Sculpture of mandibular blades finely striate and interspersed with small piligerous pits. Dorsum of head, mesosoma and petiolar node densely and finely reticulate-rugose; coarse rugae present on propodeal dorsum. Third abdominal tergite reticulate-punctulate to densely punctulate. Slender, yellowish, erect hairs present; pubescence quite abundant. Body color black, appendages dark brown, with lighter apices; apical portion of antennal segments brown but becoming yellow toward the apex.

Discussion. This species is easily recognized by the spiniform shape of the anteromedian lobe of clypeus, the broad convexity of the base of mandible extending laterally beyond the level of the lateral cephalic margin, and the elongate antennal scape. The other similar species such as *L. chrislaini* and *L. barimaso* have shorter anteromedial clypeal lobe and the base of the mandible does not project beyond the lateral cephalic margin in full face view.

Distribution and biology. The distribution of this species is confined to two localities in the central-east of Madagascar, the RNI Betampona and the RS Ambatovaky, between 390 m and 520 m. It forages most frequently on the forest floor and rarely on lower vegetation. Colony nests were found only in rotten logs.

Additional material examined. Province Toamasina: RNI Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 390 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 520 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, Betampona 35.1 km NW Toamasina, 500 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, 450 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys manja Rakotonirina and Fisher, sp. n.

(Figures 40B, 48A, 50B, 51B, 103, 119)

Holotype worker: Madagascar, Toamasina: Réserve Ambodiriana, 4.8 km 306° Manompana, along Manompana River, -16.6723, 49.7012, 125 m, rainforest, ground forager, 19 Nov 2005 (B.L. Fisher *et al.*), collection code: BLF12837, specimen code: CASENT0068233 (CASC).

WORKER. Diagnosis. Peg-like setae present on the anteromedial clypeal lobe, projecting anteriorly from above the much narrower semi-translucent lamella; width of lamella less than the minimum diameter of antennal scape; scape relatively long (SI 136–140), more than apical third portion extending beyond posterior cephalic margin. Mandible generally smooth apart from short striation and sparse punctures; blade narrow and not strongly curved at the base, inner margin concave. Dorsum of mesosoma composed of three segments.

Measurements (2 specimens). HW: 1.57–1.59, HL: 1.85–1.86, CI: 85, SL: 2.16–2.20, SI: 136–140, PW: 1.23–1.29, WL: 3.32–3.47, PNH: 0.92–0.96, PNL: 1.04–1.06, PNW: 0.87–0.90, DNI: 82–86, LNI: 87–92.

Description. Head fairly long, much wider at front than behind. Eye strongly protruding from head surface. Antennal scape distinctly long, more than one-third of its length extending beyond posterior cephalic margin. Anterior margin of clypeus medially broadly angulate with a blunt apex; semi-translucent membrane on lateral and anteromedian margin of clypeus narrower than minimum diameter of scape. Mandible long and slender, not strongly curved at base; inner margin concave, apical tooth obtuse and not reaching anterior margin of clypeus when mandibles close. Hypostomal teeth short and not visible when head in full-face view. In dorsal view, mesosoma characterized by three visible segments; metanotal groove impressed; in lateral view, dorsum of propodeum slightly convex and relatively long and low, rounding to short declivitous surface. With petiole in profile, node roughly elongate, anterior face vertical and posterior margin inclined anteriorly and rounding with convex dorsal margin. Strong constriction present between third and fourth abdominal segments.

Mandible smooth, with effaced longitudinal striation and sparse punctures. Head and mesosoma densely reticulate-rugose dorsally; propodeal declivity transversely rugose. Node of petiole laterally reticulate-rugose; the dorsum mostly finely microreticulate, interspersed with widely spaced, large punctures. Standing hairs and pubescence present on dorsum of body. Body black, with ferruginous-brown apex of appendages and tip of gaster.



FIGURE 103. Leptogenys manja holotype worker CASENT0068233. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. *Leptogenys manja* occurs in lowland rainforests of Ambodiriana Reserve at 125 m and the RS Manombo at 30 m. In lowland rainforests, workers of *L. manja* forage through the leaf litter and on lower vegetation. Based on its geographic distribution, the presence of morphological differences within *L. manja* may have been caused by geographical isolation of populations between the two disjunct localities.

Additional material examined. Province Fianarantsoa: RS Manombo, 24.5 km 228° Farafangana, 30 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys namana Rakotonirina and Fisher, sp. n.

(Figures 49B, 52B, 54A, 104, 120)

Holotype worker: Madagascar, Fianarantsoa, PN Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, -21.29, 47.4333, 1100 m, montane rainforest, beating low vegetation, 27–31 Mar 2003 (Fisher, Griswold *et al.*), collection code: BLF08401, specimen code: CASENT0488652 (CASC).



FIGURE 104. Leptogenys namana holotype worker CASENT0488652. A: lateral view. B: head in full-face view. C: dorsal view.

WORKER. Diagnosis. Anterior margin of median lobe of clypeus with two small, peg-like setae; medial clypeal carina sharp; antennal scape relatively short (SI: 115–118), less than apical third extending beyond posterior cephalic margin; in dorsal view, mesosoma consists of three visible segments, with no distinct segment between metanotal groove and propodeum; propodeal posterior margin with toothlike lobe; head dorsum densely and finely reticulate-rugose; propodeal dorsum coarsely rugose; declivity surface not distinctly delimited, side of propodeum roughly rounding to the declivity. Smaller species.

Measurements (9 specimens). HW: 1.10–1.25, HL: 1.31–1.51, CI: 78–83, SL: 1.31–1.50, SI: 118–128, PW: 0.92–1.06, WL: 2.25–2.64, PNH: 0.75–0.84, PNL: 0.71–0.83, PNW: 0.71–0.78, DNI: 91–105, LNI: 95–107.

Description. Head in full-face view subrectangular, lateral border slightly convex and weakly diverging anteriorly. Eye large, weakly convex; in full-face view, location feebly breaking outline of lateral border of head. Antennal scape moderately short, apical fourth section approximately surpassing posterior margin of head. Clypeus with convex lateral lobes, whose margin converge anteriorly into a triangular median lobe; anteromedian lobe

bordered with two peg-like setae; narrow translucent lamella broadly convex along lateral border of clypeus and angulate at anteromedian margin; median longitudinal carina of clypeus sharp. Mandible elongate and slender, fairly curved at base and inner margin slightly concave; preapical denticle present near sharp apical tooth; basal groove vestigial to faintly effaced. Hypostomal teeth visible in full-face view of head. Metanotal groove impressed; mesosoma in dorsal view consists of three segments, with no additional suture visible between metanotal groove and propodeum. In profile, mesosoma generally long and low; posterolateral margin of propodeum with toothlike lobe; declivitous surface not clearly defined, lateral surface and dorsum of propodeum joining declivity in a rounded angle. Petiolar node in profile generally as high as broad, dorsal margin convex and anterior and posterior faces weakly inclined anteriorly. In dorsal view, petiolar node longer than broad and slightly narrower in front than behind. Constriction distinctly visible between third and fourth abdominal segments.

Mandible generally sparsely punctate, with a smooth and shining surface on basal portion and fine striation near apex. Sculptures of head dorsum, mesosoma and petiolar node densely and finely reticulate-punctate to densely and finely reticulate-rugose. Third abdominal tergite finely microreticulate, with scattered shallow punctures; the fourth almost smooth and shining. Erect, slender, yellowish hairs present on dorsum of body, pubescence abundant on head and appendages and reduced or lacking on rest of body dorsum. Integument black, tarsa, apex of antenna, mandible and gaster brown or light brown.

Discussion. *Leptogenys namana* is morphologically quite variable, especially in the width of the translucent lamella, the extent of sculpture on the head, mesosoma and petiolar node, the presence of toothlike propodeal lobe, and the shape of the petiolar node. A worker specimen from the RS Marotandrano has a finely reticulate-punctate head dorsum, microreticulate propodeal dorsum superimposed with sparse punctures, and the absence of a toothlike lobe on propodeal posterior margin. Some specimens from southern Madagascar have a propodeal declivity not well delimited by posterolateral margin, with the sides of the propodeum rounding to the almost slightly convex declivitous surface.

Distribution and biology. *Leptogenys namana* is widespread in the humid forest habitats of eastern Madagascar, but are rarely found, particularly in the north of the island. Worker specimens were found foraging on lower vegetation, even though the colony nests were collected from rotten logs.

Additional material examined. Province Fianarantsoa: PN Ranomafana, 8 km SW Valohoaka camp, montane rainforest, 1040 m (W.E. Steiner) (MCZC); RS Ivohibe 8.0 km E Ivohibe, 1200 m, montane rainforest (Sylvain) (CASC); PN Isalo, Ranohira Canyon de Sinze Forest (E. Rajeriarison) (MCZC); Province **Mahajanga**: RS Marotandrano, Marotandrano 48.3 km S Mandritsara, 865 m, transitional humid forest (B.L. Fisher *et al.*) (CASC); Province **Toamasina**: Amparihibe (SB), [-15.0353, 49.5839, 846 m] (K.A. Jackson & D.E. Carpenter) (BMNH); PN Mananara-Nord, 7.1 km 261° Antanambe, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Province **Toliara**: PN Andohahela, 6 km SSW Eminiminy, 250 m (E. Rajeriarison) (MCZC).

Leptogenys oswaldi (Forel)

(Figures 33A, 105, 121)

Lobopelta oswaldi Forel, 1891: 119. Holotype worker, Madagascar, Toamasina, 30 miles au Nord-Ouest de Tamatave (O'swald) AntWeb CASENT0101837 (MHNG) [examined]. [Accepted by Dalla Torre 1893: 45. Combination in Leptogenys (Lobopelta): Emery, 1911: 102; Wheeler, 1922b: 1012; in Leptogenys: Bolton, 1975: 297, 1995: 233].

WORKER. Diagnosis. Mandible subtriangularly elongate and not strongly crossing when fully closed against clypeus; anteromedian lobe of clypeus broadly triangular; eye interrupting lateral cephalic border in full-face view of head; dorsum of head densely and finely reticulate-rugose.

Measurements (10 specimens). HW: 1.49–1.67, HL: 1.86–2.06, CI: 79–83, SL: 1.84–2.11, SI: 119–129, PW: 1.19–1.36, WL: 2.92–3.26, PNH: 0.84–0.96, PNL: 0.85–0.95, PNW: 0.75–0.97, DNI: 83–102, LNI: 93–103.

Description. Head longer than wide and widest at mid-length immediately behind the level of eyes; lateral margin weakly convex throughout the length. Eye slightly protruding and breaking outline of side of head. Antennal scape relatively long (SI: 119–129). Median portion of clypeus projecting anteriorly into broad triangular lobe, bordered by a subopaque lamella, and having a pair of small, peg-like setae. Mandible long and narrow near base; blade distinctly widest at about apical third, where the inner margin forms a rounded or blunt basal angle; with preapical tooth approximately at apical fourth of length; capable of closing tightly against clypeus; basal

groove broadly impressed. Hypostomal teeth not seen in cephalic full-face view. With mesosoma in dorsal view, metanotal groove impressed and with few cross-ribs; in profile, mesosoma relatively high and short; propodeal lobe absent or consisting of blunt angle; propodeal dorsum joining declivity with blunt angle. With petiole in profile, anterior face of node forming convex line with dorsal margin, terminating into distinct angle with anteriorly sloped posterior face. Constriction between third and fourth abdominal segments noticeably strong.



FIGURE 105. Leptogenys oswaldi worker CASENT0496083. A: lateral view. B: head in full-face view. C: dorsal view.

Mandible finely longitudinally striate, interspersed with few punctures. Dorsum of head in front of eye level longitudinally rugulose, and densely and finely reticulate-rugulose through posterior section; microreticulate sculpture with scattered punctures present near posterior border. Prontoum finely microreticulate, interspersed with sparse punctures; rest of mesosoma densely and finely reticulate-rugulose. Propodeal declivity either shagreened or

transversely rugose. Dorsum of petiolar node and third abdominal tergite finely microreticulate superimposed with small punctures. Erect hairs short and robust, pubescence abundant on dorsum of body. Integument black, appendages black to dark brown near base and light brown to yellow at apical portion.

Discussion. Leptogenys oswaldi is the only species within the *incisa* group that has mandibles capable of closing tightly against the anteromedian lobe of the clypeus. This species can be confused with *L. mayotte* of Mayotte Island because its mandible is also capable of closing against the clypeus, but the eyes of *L. oswaldi* extend beyond the lateral cephalic border, whereas those of *L. mayotte* do not break the outline of the sides of the head.

Previously, *L. oswaldi* has been placed in the *saussurei* group by Bolton (1975) in his review of the species in the Malagasy region, but he suspected that the species may not belong to this species group. In the present study, most of morphological characters of *L. oswaldi* show that it largely differs from the species within the *saussurei* group, but that it is very similar to *L. antongilensis* and the other species within the *incisa* group. Thus, *L. oswaldi* is now transferred to the *incisa* group.

In Madagascar, *L. oswaldi* is the only species of the ant genus *Leptogenys* that has an ecogeographic east-west distribution (cf. Vences and Glaw 2002; Yoder and Heckman, 2006), along which fairly pronounced morphological variation exists. Populations in the eastern humid forests are characterized by much longer standing hairs and abundant pubescence on the body, while populations inhabiting the dry forests of western Madagascar are covered with shorter erect hairs on the dorsum of the body and are almost without pubescence. Intermediates are found across the geographic range.

Distribution and biology. *Leptogenys oswaldi* occurs in the northern half of Madagascar and its ranges from rainforest habitats in the east to the dry forests in the west of the island. This geographic distribution pattern demonstrates its ability to colonize a wide range of habitats including tsingy, dry, littoral, and humid forests. The species forages both on lower vegetation and on the surface of the ground. Individual workers have been collected from litter sifting, in malaise traps, and with lights. Nest series have been found in rotten branches and dead branches above the ground, in rotten logs and beneath tree bark.

Additional material examined. Province Antsiranana: PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, rainforest (B.L. Fisher et al.) (CASC); PN Marojejy P#12, 375 m, rainforest (Alpert et al.) (MCZC); Galoko Chain, Mont Galoko, 520 m, rainforest (B.L. Fisher et al.) (CASC). Province Mahajanga: PN Ankarafantsika, SF Ampijoroa, 5.4 km 331° NW Andranofasika, 70 m, tropical dry forest (Fisher, Griswold et al.) (CASC); PN Namoroka, 9.8 km 300° WNW Vilanandro, 140 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, 210 m, tropical dry forest (Fisher, Griswold et al.) (CASC); RF Beanka, 50.2 km E Maintirano, 250 m, tropical dry forest on tsingy (B.L. Fisher et al.) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, 30 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Province Toamasina: Andranobe, 6.3 km S Ambanizana, 150 m, rainforest (B.L. Fisher) (CASC); Analalava, 7.0 km 255° Mahavelona, 50 m, littoral rainforest (B.L. Fisher et al.) (CASC); F Ambohidena, Ile Sainte Marie, 22.8 km 44° Ambodifotatra, 20 m, littoral rainforest (B.L. Fisher et al.) (CASC); F Kalalao, Ile Sainte Marie, 9.9 km 34° Ambodifotatra, 100 m, rainforest (B.L. Fisher et al.) (CASC); Mahavelona (Foulpointe), sandy forest (A. Pauly) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold et al.) (CASC); Réserve d'Ambodiriana, 4.8 km 306° Manompana, along Manompana River, 125 m, rainforest (B.L. Fisher et al.) (CASC); RNI Betampona, Betampona 35.1 km NW Toamasina, 500 m, rainforest (B.L. Fisher et al.) (CASC); RS Ambatovaky, Sandrangato River, 450 m, rainforest (B.L. Fisher et al.) (CASC); SF Tampolo, 10 km NNE Fenoarivo Atsinanana, 10 m, littoral rainforest (B.L. Fisher) (CASC); Ambato, 14 km W Cap Est, 100 m, secondary rainforest (Alpert et al.) (MCZC); Fotodriana, Cap Masoala, 25 m, secondary rainforest (G.D. Alpert) (MCZC.).

Leptogenys pilaka Rakotonirina and Fisher, sp. n.

(Figures 46B, 47B, 106, 122)

Holotype worker: Madagascar, Antsiranana, RS Ankarana, 22.9 km 224° SW Anivorano Nord, -12.9089, 49.1098, 80 m, tropical dry forest, ex rotten log, 10–16 Feb 2001 (Fisher, Griswold *et al.*) collection code: BLF02867, specimen code: CASENT0428200 (CASC).

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FIGURE 106. Leptogenys pilaka holotype worker CASENT0428200. A: lateral view. B: head in full-face view. C: dorsal view.

Paratypes: 4 workers with same data as holotype but with the following specimen codes: CASENT0428201, CASENT0428202, CASENT0428116, CASENT0247223 (CASC, BMNH, PBZT).

WORKER. Diagnosis. Small, peg-like setae absent from near anteromedian margin of clypeus, above anteriorly fringing semi-translucent lamella; in full-face view, eye extending beyond lateral cephalic margin; head short (CI: 94–97); antennal scape relatively short; mandible narrow, inner margin not convex and slightly curved near bases; blades mostly smooth with faint longitudinal striation.

Measurements (5 specimens). HW: 1.98–2.17, HL: 2.09–2.23, CI: 94–97, SL: 2.38–2.52, SI: 116–123, PW: 1.37–1.47, WL: 3.45–3.66, PNH: 1.14–1.22, PNL: 1.04–1.11, PNW: 0.97–1.09, DNI: 90–99, LNI: 106–112.

Description. Head more or less elongate and broader anteriorly than posteriorly; lateral border weakly convex and diverging from back to front. Eye large, jutting from head surface and splitting lateral cephalic margin. Antennal scape relatively short. Lateral margin of clypeus convex and rounding to short, narrowly triangular anteromedian lobe; edge of clypeus fringed with narrow and obtusely angulate semi-translucent lamella. Mandible long and slender, weakly curved near base; inner margin concave; apical portions not strongly intersecting and not closing tightly against clypeus. Hypostomal teeth not visible when head in full-face view. In lateral view, mesosoma relatively high and short; with bluntly angulate junction between propodeal dorsum and declivity; propodeal lobe with blunt angle. In dorsal view, mesosoma with three visible segments, metanotal groove impressed. Constriction between third and fourth abdominal segments fairly visible.

Mandibles are mostly smooth and shining, though sparse and short striation may be present. Dorsum of head finely longitudinally rugulose from front to level of anterior margin of eye, becoming densely and finely reticulaterugose toward mid-length of head, rest of head dorsum with fine microreticulate rugulae superimposed with large and shallow elongate punctures. Anterior portion of pronotum finely microreticulate, superimposed with coarse punctures; rest of mesosomal dorsum and petiolar node microreticulate, overlaid by a mixture of fine and coarse transverse rugae and shallow, large elongate punctures. Declivitous surface transversely rugose. Third abdominal tergite with elongate small punctures. Standing hairs present, pubescence abundant on head dorsum but very sparse on rest of body dorsum. Coloration black, basal portion of appendages brown, apical portion and tip of gaster light brown.

Discussion. *Leptogenys pilaka* is very similar to *L. incisa* and *L. alluaudi*, but is separable from *L. alluaudi* by the location of its eyes, which split the lateral outline of the head. In *L. alluaudi*, the eyes do not break the lateral cephalic margin. The species can be separated from *L. incisa* by its broader head and by the narrower mandibular blades which are not strongly curved at the base and have a largely smooth and shiny surface.

Queens of L. pilaka are unknown.

Distribution and biology. *Leptogenys pilaka* occurs in northern Madagascar, in the transitional forest of the RS Ankarana at 80 m and in the lower montane rainforest of PN Montagne d'Ambre at 885 m. Worker specimens were found foraging on the forest floor, and the colony nests were located in the rotten logs.

Additional material examined. Province Antsiranana: RS Ankarana, 22.9 km 224° SW Anivorano Nord, 12°54'32.0"S 49°06'35.4"E, 80 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Montagne d'Ambre, Antomboka, 12°30'1.3"S 49°10'30.0"E, 885 m, montane rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys sahamalaza Rakotonirina and Fisher, sp. n.

(Figures 57B, 107, 123)

Holotype worker: Madagascar, Antsiranana, Forêt d'Anabohazo, 21.6 km 247° WSW Maromandia, -14.3089, 47.9143, 120 m, tropical dry forest, pitfall trap, 11–16 Mar 2001 (Fisher, Griswold *et al.*), collection code: BLF03335, specimen code: CASENT0416181 (CASC).

WORKER. Diagnosis. Anterior clypeal margin projecting medially into a narrow, rounded lobe; small peglike setae present near apical portion of the lobe; antennal scape short; less than apical fourth reaching posterior margin of head; eye extending beyond the lateral cephalic margin when head viewed in full face; mandible with curved angle near the base; posterior face of petiolar node with a large groove at its posteroventral section, near the junction to gaster; antennal scape and tibia with subdecumbent short hairs; third abdominal tergite finely reticulaterugulose.

Measurements (1 specimen). HW: 1.32, HL: 1.46, CI: 90, SL: 1.54, SI: 117, PW: 0.96, WL: 2.44, PNH: 0.85, PNL: 0.72, PNW: 0.81, DNI: 112, LNI: 118.

Description. Head more or less subquadrate, sides slightly convex and diverging anteriorly. Eye medium and weakly convex, maximum diameter just exceeding widest part of antennal scape, and splitting line of lateral cephalic border when head in full-face view. Antennal scape relatively short, with less than one third its length reaching posterior cephalic margin. In full-face view, anterior clypeal margin projecting into narrowly rounded lobe, which is bordered by subopaque, yellowish membrane. Mandible elongate and narrow, noticeably curved near base; rest relatively straight and slightly curving when close to apical tooth, leaving a gap with clypeus when closed; basal groove impressed and preapical tooth lacking. With mesosoma in dorsal view, metanotal groove distinct and transversely striate; in profile, propodeum short and high. Petiolar node generally as broad as high in

profile; anterior margin rounding to the dorsum, which meets the posterior margin at a distinct angle; distinct constriction present on posterior border of node at posteroventral angle. Abdominal segments III and IV with visible constriction between them.

Mandible striate and interspersed with widely spaced punctures. Dorsum of head and pronotum densely and finely reticulate-rugulose; remainder of mesosoma and petiolar node with dense and fine reticulate-rugulae, superimposed by sparse, larger punctures. Third abdominal tergite densely and finely reticulate-rugulose with widely spaced, long punctures; the fourth covered with shallow, elongate punctures. Dorsum of body covered by standing hairs and pubescence; hairs on antennal scape and tibiae short and subdecumbent. Color of integument black, with apical portion of appendages and tip of gaster brown.





FIGURE 107. Leptogenys sahamalaza holotype worker CASENT0416181. A: lateral view. B: head in full-face view. C: dorsal view.

Discussion. Leptogenys sahamalaza is versy similar to L. vitsy and L. voeltzkowi in that they have peg-like setae on the anterior margin of the clypeus, the lamella is restricted to the small and rounded median lobe of the clypeus, the antennal scape lacks erect hairs, and that the posterior margin of the node is constricted at the posteroventral angle near the junction to gaster. However, L. voeltzkowi is larger in size, their eyes do not break the outline of side of the head. In L. vitsy, the mandibles are almost straight near the base, the antennal scape and the tibia are covered with erect to suberect short hairs and the third abdominal tergite is densely punctate.

Distribution and biology. *Leptogenys sahamalaza* is a very rare species of *Leptogenys* known only from one worker specimen found foraging on the ground of the dry forest habitat in the PN Sahamalaza in northwestern Madagascar.

Leptogenys suarensis Emery, stat. rev., stat. n.

(Figures 52A, 53A, 108, 124)

Leptogenys incisa var. suarensis Emery, 1895a: 336, 338, Lectotype worker, present designation, Madagascar, Diego Suarez, 1893 (Alluaud) (MSNG), AntWeb CASENT0102014. Paralectotype worker, with same data as lectotype but specimen coded as CASENT0280591 (MSNG) [examined]. Stat. n. [As subspecies of Leptogenys incisa and combination in Leptogenys (Leptogenys): Emery, 1911: 100, Wheeler, 1922b: 1011; in Leptogenys and junior synonym of Leptogenys incisa: Bolton, 1975: 298, 1995: 233].

WORKER. Diagnosis. Three to four peg-like setae present near anterior margin of median lobe of clypeus; median longitudinal clypeal carina sharp; translucent lamella of clypeus usually broadly rounded; antennal scape relatively short (SI: 101–108), less than apical fourth portion extending beyond posterior margin of head; in dorsal view, mesosoma apparently of four visible segments, with an additional suture present between metanotal groove and propodeum; mandible generally smooth and shiny between sparse piligerous punctures.

Measurements (9 specimens). HW: 1.09–1.47, HL: 1.27–1.62, CI: 86–95, SL: 1.16–1.57, SI: 101–108, PW: 0.86–1.14, WL: 2.20–2.77, PNH: 0.68–0.81, PNL: 0.73–0.89, PNW: 0.65–0.82, DNI: 86–97, LNI: 90–99.

Description. Head subrectangular, slightly longer than broad; sides feebly convex and gradually diverging towards base of mandible; posterior cephalic margin more or less straight. Eye large and protruding from head surface, maximum diameter twice as great as maximum width of scape; in full-face view, portion of eye extending beyond outline of lateral cephalic border. Antennal scape relatively short, less than one fourth its length surpassing posterior margin of head. Clypeus broadly angular, usually with short, rounded, anteromedian lobe fringed by broadly rounded translucent lamella; three to four peg-like setae projecting anteriorly from above lamella near median margin of lobe; median longitudinal carina sharp. Mandible long and slender; blades broadly concave; basal groove vestigial and preapical tooth or denticle mostly absent. Hypostomal teeth not visible with cephalic full-face view. With mesosoma in dorsal view, metanotal groove curved with an additional suture present between groove and propodeum; groove with transverse striation; in side view, propodeum generally short and high. With petiole in profile, node either as broad as high or broader than high, and inclined anteriorly; with shorter anterior face and anteriorly sloping posterior face rounding to generally convex dorsal margin. Constriction between third and fourth abdominal segments weak.

Mandible mostly smooth and shining between sparse punctures. Body sculpture densely and finely reticulatepunctate to densely and finely reticulate-rugose; propodeal declivity with transverse rugulae. Third and anterior half of fourth abdominal tergites with dense, shallow punctures which become shallower at posterior half of fourth abdominal tergite. Standing, yellowish, long and slender hairs present and pubescence quite abundant. Black species with bluish reflection or opalescence in some specimens.

Discussion. *Leptogenys suarensis* and *L. gracilis* are morphologically similar to each other, but see discussion under *L. gracilis* account.

Leptogenys suarensis is one of the smallest species within the *incisa* group and presents a variety of morphological traits. The synonymy of *L. incisa* var. *suarensis* with *L. incisa* by Bolton (1975) was based on a limited number of specimens (only the type of *L. incisa* var. *suarensis*) and the original description of the type of *L. incisa*. Observation of more specimens obtained from the recent ant surveys in Madagascar show that the two taxaare different species and that *L. suarensis* merits species-rank status.



FIGURE 108. Leptogenys suarensis worker CASENT0110562. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. *Leptogenys sucrensis* occurs generally in the dry forests and littoral habitats in the north of Madagascar. It is also known from the humid forest of Binara near Daraina.

Additional material examined. MADAGASCAR: Province Antsiranana: PN Montagne d'Ambre, Fozalanana, 475 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); F d'Ampombofofo, 25 m, littoral forest (B.L. Fisher *et al.*) (CASC); F de Binara, 9.1 km 233° SW Daraina, 650–800 m, rainforest (B.L. Fisher) (CASC); F d'Ampondrabe, 26.3 km 10° NNE Daraina, 175 m, tropical dry forest (B.L. Fisher) (CASC); RS Analamerana, 16.7 km 123° Anivorano-Nord, 225 m, tropical dry forest (B.L. Fisher) (CASC); RS Analamerana, 28.4 km 99°

Anivorano-Nord, 60 m, tropical dry forest (B.L. Fisher) (CASC); PN Montagne d'Ambre, Crête, 1110 m, montane rainforest (B.L. Fisher *et al.*) (CASC); Montagne des Français, 7.2 km 142° SE Antsiranana, 180 m, tropical dry forest (Fisher, Griswold *et al.*) (J.C. Rakotonirina) (CASC); RS Ambre, 3.5 km 235° SW Sakaramy, 325 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC).

Leptogenys tatsimo Rakotonirina and Fisher, sp. n.

(Figures 49A, 51A, 109, 125)



FIGURE 109. Leptogenys tatsimo holotype worker CASENT0122874. A: lateral view. B: head in full-face view. C: dorsal view.

Holotype worker: Madagascar, Toliara, Grand Lavasoa, 25.9 km W Tolagnaro, -25.0877, 46.749, 450 m, rainforest, ex rotten log, 30 Nov 2006 (B.L. Fisher *et al.*) collection code: BLF15384, specimen code: CASENT0122874 (CASC).

Paratypes: 4 workers, same data as holotype but specimen coded: CASENT0247279, CASENT0247280, CASENT0247281, CASENT0247282 (CASC, BMNH, MHNG).

WORKER. Diagnosis. Anterior border of medial clypeal lobe with anteriorly projecting, small peg-like setae from above much broader semi-translucent lamella; lamella width as great as minimum diameter of antennal scape; scape relatively long (SI 144–147), more than apical third portion extending beyond posterior cephalic margin. Mandible roughly broad and smooth apart from short striation and sparse punctures; blades strongly curved near base, increasing in width toward apical section. In dorsal view, dorsum of mesosoma consisting of four segments, with an additional suture between metanotal groove and propodeum.

Measurements (3 specimens). HW: 1.53–1.68, HL: 1.90–2.06, CI: 81–82, SL: 2.25–2.44, SI: 144–147, PW: 1.23–1.31, WL: 3.46–3.54, PNH: 0.92–1.02, PNL: 1.01–1.07, PNW: 0.85–0.95, DNI: 84–88, LNI: 91–95.

Description. In full-face view, head elongate and slightly increasing in width toward the front of eye; sides broadly convex. Eye somewhat protruding, position dividing lateral margin of head. Antennal scape particularly long, with more than one third of its length surpassing posterior cephalic margin. Anteromedian lobe of clypeus broadly angulate with a blunt apex, connected with generally convex lateral margin and bordered with wide, fringing, semi-translucent membrane. Mandible long and broad, strongly curved near base; gradually increasing in width, apical tooth obtuse; not capable of closing tightly against median lobe of clypeus if apices superimposed. In full-face view, hypostomal teeth not visible. With mesosoma in dorsal view, metanotal groove impressed, additional shallow and fine transverse sulcus present between metanotal groove and propodeum; in lateral view, propodeal dorsum roughly straight and elongate, joining distinctly short declivity in blunt angle. Petiolar node in profile more or less elongate, with anterior and posterior margin rounding to convex dorsal margin. Constriction between third and fourth abdominal segments strong.

Mandible generally smooth apart from faint short striation and sparse punctures. Dorsum of head and mesosoma densely reticulate-rugose; propodeal declivity rugulose. Lateral portion of petiolar node reticulate-rugose, and dorsally finely microreticulate, with sparse large punctures. Body dorsum covered with standing hairs and pubescence. Color black; apex of appendages and extremity of gaster ferruginous-brown.

Discussion. Leptogenys tatsimo and L. manja look very similar, but L. tatsimo has a broader mandible, a conspicuous fringing lamella on the clypeus, and an additional suture between the metanotal groove and the propodeum in dorsal view (four apparent segments on the dorsum of the mesosoma). Leptogenys manja is characterized by the slender mandibular blades, a narrow, semi-translucent lamella on the clypeus, and three mesosomal segments in dorsal view.

Distribution and biology. *Leptogenys tatsimo*i s a humid forest dweller of southeastern Madagascar. The species nests in rotten logs and forages on the forest floor.

Additional material examined. Province Toliara: Grand Lavasoa, 25.9 km W Tolagnaro, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Andohahela, 6 km SSW Eminiminy, rainforest, 250 m (P. Rabeson) (MCZC).

Leptogenys vitsy Rakotonirina and Fisher, sp. n.

(Figures 48B, 56B, 57A, 110, 126)

Holotype worker: Madagascar, Mahajanga, PN Ankarafantsika, Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, -16.2672, 47.0486, 210 m, tropical dry forest, sifted litter, 9–14 Apr 2001 (Fisher, Griswold *et al.*), collection code: BLF03664, specimen code: CASENT0470280 (CASC).

Paratype worker: same data as holotype but with specimen code: CASENT0470279 (CASC).

WORKER. Diagnosis. Anteromedian clypeal margin characterized by narrowly rounded lobe; peg-like setae present near apical portion, above semi-translucent lamella; antennal scape short (SI< 130); less than one-fourth of its length surpassing posterior margin of head; in full-face view, eye feebly extending beyond outline of lateral cephalic margin; posterior margin of petiolar node with constriction at its posteroventral angle, near junction to gaster; antennal scape and tibia with erect to suberect short hairs; third abdominal tergite densely punctate.

Measurements (4 specimens). HW: 1.08–1.25, HL: 1.26–1.46, CI: 84–86, SL: 1.22–1.54, SI: 113–126, PW: 0.83–0.94, WL: 2.09–2.47, PNH: 0.76–0.89, PNL: 0.66–0.69, PNW: 0.74–0.81, DNI: 112–118, LNI: 115–132.



FIGURE 110. Leptogenys vitsy holotype worker CASENT0470280. A: lateral view. B: head in full-face view. C: dorsal view.

Description. Head roughly elongate, slightly wider anteriorly; lateral border weakly convex and rounding into more or less straight posterior margin. Eye medium, very slightly protruding from head surface, and breaking outline of cephalic lateral margin. Antennal scape relatively short. Clypeus with bluntly angulate lateral margin, which taper strongly into narrowly rounded anteromedian lobe; narrow, yellow spot fringing lobe and pair of peglike setae projecting anteriorly near anteromedial clypeal margin, above lamella. Mandible elongate and slender, nearly straight and without curve near base; blades not capable of closing tightly against clypeus; basal groove a faintly effaced sulcus; preapical teeth either present near apex or absent. With mesosoma in dorsal view, metanotal groove impressed, with cross-ribs; in profile, mesosoma high and short; propodeal lobe indistinct. With petiole in lateral view, node excised or with impression immediatly above posteroventral angle; node about as high as broad, anterior face meeting in convex line with dorsal margin, which in turn makes distinct angle with posterior face. Constriction between third and fourth abdominal segments feeble.

Mandible longitudinally striate, interspersed with piliferous punctures; head dorsum densely and finely rugulose-punctate, with sparse larger punctures or foveae. Pronotum finely microreticulate or densely and finely rugose, superimposed with quite dense, large punctures. Rest of mesosoma dorsum and petiolar node densely and finely reticulate-rugose, with scattered shallow punctures. Propodeal declivity transversely rugulose. Third abdominal tergite densely punctate; shallow elongate punctures covering the fourth. Standing hairs and pubescence present on body dorsum; antennal scape and tibiae with short erect or suberect hairs. Black in color, with brown to light brown apices of appendages and tip of gaster.

Discussion. This species is represented by four worker specimens collected from two sites that are geographically distant and isolated from one another. Morphological variation observed among populations is limited to the larger size of the specimens found in the Makay Mountains. Additional collections, specifically of nest series with different castes, from these localities and intermediate localities, are needed to accurately evaluate the species boundaries and the possible effects of geographic isolation.

Distribution and biology. *Leptogenys vitsy* is known from two separate and distant dry forests: Ankoririka of the PN Ankarafantsika in the west and the Makay Mountains in the southwest of the island. Very few records were obtained for *L. vitsy* and its biology is unknown, but a small number of workers have been found foraging through the leaf litter.

Additional material examined. Province Toliara: Makay Mountains, -21.2098, 45.3418, 525 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC).

Leptogenys voeltzkowi Forel

(Figures 1D, 55A, 56A, 111, 127)

Leptogenys voeltzkowi Forel, 1897: 194. Lectotype worker, present designation, Madagascar, Antsiranana, Nosy-be (Voeltzkow), AntWeb specimen code CASENT0101888 (MHNG). Paralectotypes: two workers with same data but with the following specimen codes: CASENT0101947, CASENT0101989 (MHNG) [examined]. [Combination in Leptogenys (Leptogenys): Emery, 1911: 100; Wheeler, 1922b: 1011; in Leptogenys: Bolton, 1975: 298, 1995: 234].

WORKER. Diagnosis. Median portion of clypeus projecting anteriorly into short, narrowly rounded lobe; anteriorly projecting peg-like setae present from near anterior margin of median lobe of clypeus, above semi-translucent lamella; antennal scape relatively short (SI: 101–114), less than one fourth its length surpassing posterior margin of head; in full-face view, eye not breaking line of cephalic lateral border; in profile, posterior margin of petiolar node with constriction at posteroventral angle, near junction to gaster; dorsum of body without erect hairs longer than maximum diameter of eye.

Measurements (9 specimens). HW: 1.30–1.59, HL: 1.39–1.72, CI: 90–95, SL: 1.31–1.60, SI: 101–114, PW: 0.90–1.15, WL: 2.26–2.72, PNH: 0.77–0.92, PNL: 0.62–0.71, PNW: 0.71–0.84, DNI: 113–125, LNI: 123–134.

Description. Head weakly broader at front than behind; sides feebly convex and diverging anteriorly; posterior margin very weakly concave. Eye large, slightly protruding from surface of head, and not breaking outline of side of head. Antennal scape relatively short (SI: 101–114). Clypeus with convex lateral margin, which strongly tapers into narrowly rounded anteromedian lobe; thin, rounded subopaque lamella surrounding anteromedial clypeal lobe. Mandible elongate and slender, feebly angulate near base and not fully closed against clypeus, leaving gap when at rest; basal groove narrowly impressed. In dorsal view, mesosoma with impressed metanotal groove; in profile, mesosoma somewhat high and short, with broadly convex dorsal margin; propodeal lobe absent. Posterior face of petiolar node impressed or with groove at about posteroventral portion, near junction to gaster; in profile, node about as high as broad, anterior face meeting in convex line with dorsal margin, forming distinct angle with posterior face. Constriction between third and fourth abdominal segments weakly noticeable.

Mandible generally smooth between sparse punctures, with piligerous pits; head dorsum densely reticulaterugulose, interspersed with small punctures. Dorsum of mesosoma, node of petiole and abdominal tergites III and IV generally punctate, with fine microreticulation. Sides of mesosoma rugulose at the suture between mesopleuron and metapleuron. Standing hairs and pubescence present on dorsum of head, but very short or absent on other parts of body dorsum. Black species, appendages dark brown with lighter apical portion; tip of gaster brown.

Discussion. This species can be separated from the remainder of the group by the following combination of characters: the very short standing hairs, which may be absent, on dorsum of the body, and the eyes usually not breaking the line of the cephalic lateral margin.

Specimens from the forest of Binara near Daraina have a head that is narrower posteriorly, eyes that break the outline of the sides of the head, and mandibles that increase in width from the basal third to near the apical teeth. Workers from RS Manongarivo and RS Marotandrano have a weak convexity at the mid-length of their mandible, and the width of the blades decreases towards the apical portion. Mandibular blades of specimens from both localities are longitudinally striate.



FIGURE 111. Leptogenys voeltzkowi worker CASENT0077685. A: lateral view. B: head in full-face view. C: dorsal view.



FIGURES 112–117. Distribution maps of the Leptogenys incisa group in the Malagasy region.



FIGURES 118–123. Distribution maps of the Leptogenys incisa group in the Malagasy region.



FIGURES 124-129. Distribution maps of the Leptogenys incisa group, L. mayotte and L. rabebe in the Malagasy region.
Distribution and biology. The pattern of distribution for *L. voeltzkowi* shows that it occupies the dry, transitional humid, lowland, and littoral forests in the north and northeast of Madagascar. It forages in leaf litter and nests mainly in rotten wood and under rocks.

Additional material examined. Province Antsiranana: [Nosibé; Nossi-bé; Museum Paris Collection, Ernest André 1914] (Völzkow) (MNHN); [Nossibe] (Voeltzkow) (MCZC) (ZMHB); [Nossi-bé, C. Emery 1925] (Völzkow) (MSNG); RS Manongarivo, 12.8 km 228° SW Antanambao, 780 m, rainforest (B.L. Fisher) (CASC); RS Ankarana, 22.9 km 224° SW Anivorano-Nord, 80 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); F de Binara, 9.1 km 233° SW Daraina, 650-800 m, rainforest (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, 550 m, tropical dry forest (B.L. Fisher) (CASC); Ambondrobe, 41.1 km 175° Vohemar, 10 m, littoral rainforest (B.L. Fisher) (CASC); PN Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, rainforest (B.L. Fisher *et al.*) (CASC); Galoko Chain, Mont Galoko, 1100 m, montane forest (B.L. Fisher *et al.*) (CASC); Province **Mahajanga:** RS Marotandrano, Marotandrano, 48.3 km S Mandritsara, 865 m, transition humid forest (B.L. Fisher *et al.*) (CASC).

The maxillosa group

Mandible narrow, long and curved with relatively broadly concave inner margin; not able to close tightly against clypeus; preapical tooth or denticles either absent or present and situated near sharp apical tooth. Head broadened anteriorly; sides slightly convex. Anteromedian clypeal margin projecting into obtusely angulate lobe and covered with a translucent fringing lamella median clypeal carina short. Eye large, maximum diameter noticeably greater than maximum width of scape. Antennal scape exceeding posterior cephalic margin by one fourth of its length. With mesosoma in dorsal view, metanotal groove weakly noticeable and not impressed. Constriction between abdominal segments III and IV distinctly visible.

Entire body densely and finely reticulate-rugulose to densely and finely reticulate-punctate, interspersed with larger punctures. Standing hairs absent from dorsum of body and first three abdominal segments, but long hairs only present on anterior border of clypeus and on mandibular blades. Whitish-yellow pubescence very dense all over the body. Integument black, with tip of gaster and apices of appendages brown.

Leptogenys falcigera Roger

(Figures 41A, 43B, 130, 133)

- Leptogenys falcigera Roger, 1861: 42. Holotype worker, Sri Lanka (H. Nietner) [location of type not known]. [Combination in *Ponera (Leptogenys)*: F. Smith, 1871: 322; in *Leptogenys (Leptogenys)*: Forel, 1900: 304, 309; Emery, 1911: 99; Wheeler, 1922b: 1010].
- *Leptogenys insularis* F. Smith, 1879: 675. Lectotype worker, present designation, Hawaii, Oahu Island (T. Blackburn), AntWeb specimen code: CASENT0102272 (BMNH) [examined]. [Junior synonym of *Leptogenys falcigera:* Wilson & Taylor, 1967: 30; confirmed by Bolton, 1975: 252].

WORKER. Diagnosis. Mandible not closing tightly against broadly convex anterior clypeal margin; dorsum of body without standing hairs, but covered with very dense pubescence; sculpture shagreenate; anterior margin of clypeus covered with narrowly angulate translucent lamella; three peg-like setae usually projecting anteriorly from median border of clypeus; in dorsal view petiolar node longer than broad or as long as broad.

Measurements (16 specimens). HW: 1.41–1.66, HL: 1.42–1.69, CI: 96–105, SL: 1.34–1.58, SI: 90–100, PW: 0.94–1.10, WL: 2.29–2.73, PNH: 0.76–0.90, PNL: 0.65–0.80, PNW: 0.66–0.80, DNI: 93–109, LNI: 109–122.

Description. Head broader than long, increasing in width to front, sides slightly convex and diverging anteriorly along length. Eye large, maximum diameter greater than widest portion of scape; extending beyond lateral edge of head in full-face view. Anteromedian lobe of clypeus borderedby narrow and obtusely angulate translucent lamella; usually three and rarely two or four peg-like setae projecting anteriorly at anterior margin of median lobe at base of lamella. Mandible slightly curved near base and become roughly straight apically; preapical tooth or denticle of mandible either absent or present near apical tooth. In dorsal view, petiolar node most often longer than broad and infrequently as long as broad.



FIGURE 130. Leptogenys falcigera worker CASENT0002223. A: lateral view. B: head in full-face view. C: dorsal view.

Dorsum of head, mesosoma, petiolar node, and third and fourth abdominal segments without standing hairs; whitish yellow pubescence very abundant. Head and body with dense shagreenate sculptures, interspersed with larger punctures. Black species with lighter tip of gaster; appendages dark brown to reddish brown basally and brown to light brown toward apex.

Discussion. This species is very similar to *L. maxillosa* but can be easily separated by its elongate and narrower petiolar node (*L. falcigera*: DNI: 93–109; *L. maxillosa*: DNI: 113–133). *Leptogenys falcigera* can be distinguished from *L. pavesii* by the narrow and medially obtuse translucent lamella fringing its median clypeal lobe and the presence of three peg-like setae projecting anteriorly from the anterior margin of the median lobe. In *L. pavesii*, this fringing lamella is wide and broadly rounded and two peg-like setae project anteriorly from the anterior margin of the median lobe of the clypeus.

F. Smith's worker type specimen is located at BMNH and was examined during the course of this study; it bears a blue syntype label in concordance with Smith's description that the type-series includes several workers: "Not rare,..., workers only taken". Conversely, the BMNH Accessions register only indicates a single specimen was deposited: "1879 no. 40. 1 *Leptogenys insularis* Sm. Sandwich Is (Oahu), presented by Rev. T. Blackburn, Honolulu". Though this may imply that additional syntypes may not exist, and that the single specimen at BMNH is a holotype, we nonetheless designate this specimen as the lectotype.

Distribution and biology. *Leptogenys falcigera* is widespread but not common in the Malagasy region. This species generally occupies coastal areas and disturbed habitats in each island of the region and is thought to be introduced. In Madagascar, it is the dominant ponerine ant in the spiny forest/thicket habitat of the southern tip of the island. The dominance of this species in the south suggests that the species may be native or arrived on this island long ago, or recently introduced and rapidely spread in this type of habitat. The species was able to survive and dominate this southern region because environmental factors here resemble its place of origin. Workers of *L. falcigera* forage on the forest floor, in leaf litter, and on lower vegetation, and nest in live tree stems, in dead twigs or branches above the ground, and in rotten logs.

Additional material examined. COMORES: Comoros Island: Mohéli, Lac Boundouni, 25 m, tropical dry forest (B.L. Fisher et al.) (CASC); Mayotte Island: RF Sohoa, 10 m, coastal dry forest (B.L. Fisher et al.) (CASC); MADAGASCAR: Madagascar (MSNG); Province Antsiranana: Antalaha, 23 m, urban/garden (B.L. Fisher et al.) (CASC); Antalaha (G.D. Alpert) (MCZC); Nosy Be Airport (G.D. Alpert) (MCZC); Province Fianarantsoa: Farafangana, 10 m, urban gardens (B.L. Fisher et al.) (CASC); Manakara, 10 m, urban gardens, coastal Casuar inaequisetifolia (B.L. Fisher et al.) (CASC); Province Mahajanga: PN Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, 50 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); F de Tsimembo, 8.7 km 336° NNW Soatana, 20 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, 30 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Province Toamasina: Tamatave (MSNG); Mahanoro, 15 m, urban/garden (B.L. Fisher et al.) (CASC); Baie d'Antongil (Moquerys) (MSNG); Province Toliara: Fort-Dauphin (Sikora) (MSNG); Mandena, 8.4 km NNE 30° Tolagnaro, 20 m, littoral rainforest (B.L. Fisher) (CASC); RS Cap Sainte Marie, 14.9 km 261° W Marovato, 160 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); F de Mite, 20.7 km 29° WNW Tongobory, 75 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); F de Tsinjoriaky, 6.2 km 84° E Tsifota, 70 m, spiny forest/ thicket (Fisher-Griswold Arthropod Team) (CASC); F de Beroboka, 5.9 km 131° SE Ankidranoka, 80 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); Dauphin Hotel, Fort-Dauphin (P. Rabeson) (MCZC); Ifaty, desert scrub forest (W.E. Steiner) (MCZC); MAURITIUS: Rodrigues: Baie Pistache (Michael Madl) (CASC).

Leptogenys maxillosa (F. Smith)

(Figures 42B, 43A, 131, 134)

- Ponera maxillosa F. Smith, 1858: 93. Lectotype worker, present designation, Mauritius (Dr. Beke), AntWeb specimen code: CASENT0102266 (BMNH). Paralectotype male, with same data as lectotype but with specimen code: CASENT0102267 (BMNH) [examined]. [Combination in *Leptogenys*: Roger, 1861: 43; in *Leptogenys*): Emery, 1911: 99; Wheeler, 1922a: 787, 1922b: 1011].
- Leptogenys falcata Roger, 1861: 42. Syntype workers, Cuba and Brazil [location of type unknown]. [Combination in Leptogenys (Leptogenys): Forel, 1895: 117; Emery, 1911: 99; Wheeler, 1922a: 787, 1922b: 1011. Junior synonym of Leptogenys maxillosa: Forel, 1901: 46].
- Formica vinsonnella Dufour, 1864: 210. Holotype worker, Reunion [location of type not known]. [Combination in Leptogenys and subspecies of Leptogenys maxillosa: Emery, 1894: 68; Forel, 1912: 159; in Leptogenys (Leptogenys): Emery, 1911: 99; Wheeler, 1922b:1011; in Leptogenys and junior synonym of Leptogenys maxillosa: Bolton, 1975: 254].
- Leptogenys cribrata Emery, 1895c: 20. Syntype workers, South Africa, Vrijburg (E. Simon) (MSNG) [not examined]. [Combination in Leptogenys (Leptogenys): Emery, 1911: 99; provisionally junior synonym of Leptogenys maxillosa: Bolton, 1975: 254].

WORKER. Diagnosis. Mandible not closing tightly against clypeus; dorsum of body without standing hairs, but covered with dense pubescence; sculptures shagreenate; anteromedian lobe of clypeus covered with narrowly angulate translucent lamella; two peg-like setae projecting anteriorly from anterior margin of median lobe; in dorsal view, petiolar node broader than long.

LEPTOGENYS IN THE MALAGASY REGION



FIGURE 131. Leptogenys maxillosa worker CASENT0137950. A: lateral view. B: head in full-face view. C: dorsal view.

Measurements (10 specimens). HW: 1.16–1.39, HL: 1.25–1.36, CI: 93–102, SL: 1.24–1.36, SI: 96–106, PW: 0.83–0.97, WL: 1.90–2.22, PNH: 0.71–0.78, PNL: 0.51–0.58, PNW: 0.63–0.72, DNI: 113–133, LNI: 127–146.

Description. Head diverging from back to front; sides remarkably convex and head widest at eye level. Eye large, with maximum diameter larger than maximum width of antennal scape; situated at outline of lateral cephalic margin. Translucent lamella narrow on anterior margin of clypeus and medially bluntly angulate at median lobe; pair of peg-like setae projecting anteriorly from near anterior border of median lobe of clypeus. Mandibles with weak angle near their insertion; shape becomes more or less straight towards apices; preapical tooth or denticle absent. With petiole in dorsal view, node distinctly broader than long.

Standing hairs lacking on dorsum of head and body except on clypeus and near tip of gaster. Entire body strongly shagreened and covered with abundant pruinose pubescence. Body color black; appendages brown to reddish brown; apices of appendages and tip of gaster light brown.

Discussion. Leptogenys maxillosa can be separated from *L. falcigera* by the shape of its petiolar node, which is wider than long. In *L. maxillosa,* the anteromedian lobe of the clypeus is fringed by a narrow and obtusely angulate translucent lamella, while in *L. pavesii*, this fringing lamella is wide and broadly rounded.

Distribution and biology. *Leptogenys maxillosa* is widely distributed at lower elevations between 7 m and 90 m in the dry forest habitats of Comoros Island and Reunion, in mixed forest sites in Seychelles, and in littoral forest areas in the north of Madagascar. Specimens of this species also inhabit environments modified by human activities such as houses and urban gardens. These findings imply that *L. maxillosa* may have been introduced to the Malagasy region, although its first description was based on worker specimens from Mauritius. This species forages on the forest floor and on low vegetation, and its colonies can be found in rotten logs, rotting tree stumps, rotten pockets, and under the bark of live trees.

Additional material examined. COMOROS: Mohéli Island: Lac Boundouni, Mohéli, 25 m, dry forest (B.L. Fisher *et al.*) (CASC); MADAGASCAR: Province Antsiranana: Ambanja, 30 m, urban/garden (B.L. Fisher *et al.*) (CASC); Ambanja, 28 m, in house (B.L. Fisher *et al.*) (CASC); Antsiranana, 43 m, urban/garden (B.L. Fisher *et al.*) (CASC); Nosy Faly, Tafiambotry, 35.3 km N Ambanja, 7 m, littoral rainforest (B.L. Fisher *et al.*) (CASC); Nosy Be airport, 25 m, urban garden (B.L. Fisher *et al.*) (CASC); MAURITIUS: [Mauritius; 87] (J. Vinsón) (MNHN) (BMNH); [Mauritius] (BMNH); REUNION: Etang Sale, 90 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); SEYCHELLES: [Mahé] (Ch. Alluaud, 1892) (MSNG); Big Sister I.; IV BS (U. Müller) (BMNH); Aldabra Picard (V. Spaull) (BMNH); Aldabra atoll, Isle Picard (P. Mundel) (MCZC); North Island (J. Gerlach) (CASC); Aride Island, 75 m, mixed forest (B.L. Fisher *et al.*) (CASC).

Leptogenys pavesii Emery

(Figures 42A, 132, 135)

Leptogenys pavesii Emery, 1892: 111. Syntype workers, Somalia (Robecchi) (MSNG) [not examined]. [Combination in Leptogenys (Leptogenys): Emery, 1911: 99; Wheeler, 1922a: 787].

Leptogenys maxillosa sericea Weber, 1942: 46. Syntype workers, Sudan, Imatong Mountains (N.A. Weber) (MCZC) [examined]. [Junior synonym of Leptogenys pavesii: Bolton, 1975: 255; here synonymy confirmed].

WORKER. Diagnosis. Mandible not closing tightly against clypeus; dorsum of body without standing hairs, but covered with abundant pruinose yellowish pubescence; sculptures shagreenate with sparse punctures; anteromedian lobe of clypeus covered with broadly rounded translucent lamella, pair of peg-like setae projecting anteriorly from near anterior margin of median lobe.

Measurements (7 specimens). HW: 1.17–1.33, HL: 1.26–1.39, CI: 93–96, SL: 1.23–1.41, SI: 102–106, PW: 0.85–0.96, WL: 1.98–2.21, PNH: 0.66–0.76, PNL: 0.56–0.69, PNW: 0.56–0.64, DNI: 94–106, LNI: 111–125.

Description. Head broader than long, noticeably increasing in width to front of eyes; lateral border slightly convex. Eye large, breaking outline of sides of head. Antennal scape long, about one fourth of distal portion extending beyond posterior cephalic margin. Anteromedian lobe of clypeus with wide and broadly rounded translucent lamella; a pair of anteriorly projecting peg-like setae present near anterior margin of clypeal median lobe. Node of petiole longer than broad when viewed dorsally.

Standing hairs on dorsum of body absent apart from those on clypeus and near apex of gaster, though much longer pruinose yellowish pubescence is abundant. Body heavily shagreenate, superimposed with sparse, shallow punctures. Color black, with dark brown to brown apical portion of appendages and tip of gaster.

Discussion. Leptogenys pavesii is very similar to *L. falcigera* and *L. maxillosa* but can be easily distinguished by the wide and broadly rounded translucent lamella bordering the anteromedian lobe of the clypeus. In *L. falcigera* and *L. maxillosa*, this translucent lamella is narrow and angulate.

Distribution and biology. *Leptogenys pavesii* is rarely collected but found on three different islands in the Malagasy region. In the Comoros, this species is found on Mayotte and Mohéli. On Madagascar it lives in the extreme north. On all three islands, *L. pavesii* occupies dry forest habitats, mangrove areas and urban gardens. Workers of the species forage both on the forest floor and on lower vegetation and inhabit rotten logs and tree bark. Collection data indicate that this species is able to colonize coastal regions and human-modified habitats in these islands and it could be introduced to the Malagasy region.

Additional material examined. COMOROS: Mohéli Island: Lac Boundouni, 25 m, dry forest (B.L. Fisher *et al.*) (CASC); Mayotte Island: Dapani, 1 m, mangrove, coastal scrub (B.L. Fisher *et al.*) (CASC); Mont Combani, 370 m, rainforest (B.L. Fisher *et al.*) (CASC); Sazile (R. Jocque & G. DeSmet) (CASC); Sazile, 35 m, dry forest (B.L. Fisher *et al.*) (CASC); MADAGASCAR: Province Antsiranana: Antsiranana, 43 m, urban/garden (B.L. Fisher *et al.*) (CASC).



FIGURE 132. Leptogenys pavesii worker CASENT0132269. A: lateral view. B: head in full-face view. C: dorsal view.





The saussurei group

Mandible short and robust, subfalcate, capable of closing tightly against median lobe of the clypeus; inner margin convex and covered with semi-translucent lamella, which becomes more transparent and broader from broadest width of blades towards apex; basal groove narrowly impressed. Head shape variable among species, but lateral borders not strongly diverging anteriorly and posterior margin straight. Clypeus broadly triangular anteriorly, with anteromedian lobe rounded or bidentate; median clypeal carina long and sharp. Eye large, maximum diameter greater than widest portion of antennal scape. Antennal scape relatively long. With mesosoma in profile, posterolateral margin of propodeum equipped with toothlike lobe at level of propodeal spiracle, whose opening may be elliptical or slit-like. In lateral view, petiolar node longer than high; vertical anterior margin slightly shorter than sloping posterior, which may have a sharp tooth, denticle or blunt tubercle at mid-height. Subpetiolar process simple, consisting of anterior hook-like teeth or a tubercle; a convex surface may be present posteriorly. Helcium at lower level in profile, located at anteroventral angle of third abdominal sternite angulate; prora and anteroventral angle of third abdominal sternite not separated by large indentation. Gaster not constricted between first and second segments.

Clypeus longitudinally rugulose, with sparse punctures. Dorsum of head, mesosoma and petiolar node variably sculptured, mostly with large, sparse punctures grading to smaller, dense ones; head in front of the level of eye longitudinally rugulose or striate; mesosoma and node of petiole seldom with rugulation. Standing hairs present; pubescence sparse or absent. Body color black to reddish-black, with bases of appendages dark brown which becomes orange-brown at the apices and gastral apex.

In this species group, ergatoid queens are not known and the data indicate that the species may reproduce by mated workers.

Leptogenys acutirostris Santschi

(Figures 35B, 36B, 136, 143)

Leptogenys saussurei st. acutirostris Santschi, 1912: 150. Holotype worker, Madagascar (Le Moult) (NHMB) AntWeb specimen code: CASENT0101130 [examined]. [Combination in Leptogenys (Lobopelta): Wheeler, 1922b: 1012; in Leptogenys: Bolton, 1975: 297, 1995: 229. Raised to species by Bolton, 1975: 297].

Worker Diagnosis. Mandible elongate and robust, capable of closing tightly against clypeus; anterior clypeal margin medially projecting into triangular lobe; clypeus with sharp edge laterally and bordered with lamella anteriorly. Eye large, diameter markedly greater than maximum width of antennal scape. Dorsum of head and mesosoma distinctly sculptured; with mesosoma in dorsal view, metanotal groove distinctly visible. In dorsal view, posterior margin of petiolar node straight not medially emarginate; in profile posterolateral margin without small tooth, but blunt angle.

Measurements (9 specimens). HW: 1.75–1.92, HL: 2.31–2.85, CI: 67–78, SL: 2.24–2.42, SI: 122–130, PW: 1.50–1.62, WL: 3.68–3.98, PNH: 1.29–1.44, PNL: 1.21–1.34, PNW: 1.07–1.23, DNI: 85–93, LNI: 104–111.

Description. Head rectangular, lateral border slightly convex at level of eyes. Clypeus with large triangular median lobe, bordered with semi-translucent lamella, not bidentate anteriorly; lateral edge continuous and sharp. Translucent lamella on mandibular inner margin forming two close preapical teeth or blunt angles before reaching more distant, sharp apical tooth. In profile, mesopleural sulcus indistinct. With mesosoma in dorsal view, metanotal groove distinctly visible. In dorsal view, petiolar node elongate, posterior margin straight, not medially excised; in profile posterior margin without small teeth at mid-height, but with blunt angle.

Head dorsum in front of level of anterior margin of eye longitudinally rugose, but densely punctate between level of anterior and posterior of ocular margin; posteriorly punctures become larger and scattered, spaces between them smooth. Mandible with fine longitudinal striation near base and sparsely punctuate towards apex. Mesosoma and petiolar node with interspersed punctures, the space between them are smooth and shining; sides may be faintly striate or reticulate-rugose. Upper level of propodeal declivity generally smooth and with transeverse striation or rugulation at level of propodeal lobe. Gaster generally smooth. Color with bluish reflection.



FIGURE 136. Leptogenys acutirostris worker CASENT0047656. A: lateral view. B: head in full-face view. C: dorsal view.

Discussion. Leptogenys acutirostris is very similar to *L. saussurei* and *L. lohahela* due to the presence of a metanotal groove, but the excised posterior margin of the petiolar node of *L. saussurei* renders it distinguishable from *L. acutirostris. Leptogeenys acutirostris* can be separated from *L. lohahela* by its larger size and the presence of a blunt angle on the posterolateral margin of the node. In *L. lohahela*, body size is smaller and a sharp denticle is present on the posterolateral margin of the petiolar node.

Distribution and biology. An endemic to Madagascar, *L. acutirostris* is found in the lowland rainforest in the northeast of the island. Its range is between the PN Marojejy in the north and RS Ambatovaky in the South. It has been found foraging on the forest floor and in leaf litter. *Leptogenys acutirostris* generally nests in rotten logs.

Additional material examined. Province Antsiranana: PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); 6.5 km SSW Befingotra, RS Anjanaharibe-Sud, 875 m, rainforest (B.L. Fisher) (CASC); PN Marojejy P#12, 375 m, rainforest (G.D. Alpert) (MCZC); Province Toamasina: Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, Griswold *et al.*) (CASC); RS Ambatovaky, Sandrangato river, 520 m, rainforest (B.L. Fisher et al.) (CASC); RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina; 520 m, rainforest (B.L. Fisher *et al.*) (CASC); Montagne d'Akirindro, 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); F d'Ambohitsitondroina, 6.9 km NE Ambanizana, 825 m, rainforest (B.L. Fisher) (CASC); [Madagascar; MARS] (NHMB).

Leptogenys ambo Rakotonirina and Fisher, sp. n.

(Figures 37A, 137, 144)

Holotype worker: Province Antsiranana, RS Manongarivo, 14.5 km 220° SW Antanambao, -13.9983, 48.4167, 1175 m, montane rainforest, ex rotten log, 19–25 Oct 1998 (B.L. Fisher) collection code: BLF01951, specimen code: CASENT0175361 (CASC).

WORKER. Diagnosis. Mandible short and robust, capable of closing tightly against clypeus; anterior clypeal margin medially projecting into triangular lobe; clypeus with sharp edge or lamella. Eye large, maximum diameter larger than maximum width of antennal scape. Dorsum of head and mesosoma distinctly sculptured; with mesosoma in dorsal view, metanotal groove indistinct; petiolar node in dorsal view, with straight posterior margin.

Measurements (3 specimens). HW: 1.01–1.21, HL: 1.55–1.75, CI: 65–70, SL: 1.38–1.64, SI: 129–140, PW: 0.92–1.08, WL: 2.30–2.65, PNH: 0.83–1.04, PNL: 0.82–0.98, PNW: 0.70–0.86, DNI: 86–98, LNI: 101–116.

Description. Head distinctly elongate, sides almost straight and diverging slightly anteriorly along length; posterior margin roughly straight. Eye placed anteriorly, the center closer to base of mandible than to midlength of lateral outline of head. Clypeus with median lobe terminating into double small teeth anteriorly; lateral border fringed with semi-translucent lamella. Lamellate membrane of mandibular inner margin rounding into basal preapical tooth, followed by median blunt angle, then sharp apical tooth. In dorsal view, metanotal groove absent; with mesosoma in profile, mesopleural sulcus indistinct, suture between metapleural and propodeum lacking. In dorsal view posterior margin of petiole straight, not medially excised.

In profile, anterolateral portion of head from level of eye finely rugose, usually superimposed with large punctures. With head in dorsal view, dorsum densely punctate or reticulate-rugose, with large punctures between them; punctures sparser towards posterior cephalic margin. Mandible with longitudinal striolae and scattered punctures. In dorsal view, pronotum punctate; rest of dorsum of mesosoma sparsely punctulate. In profile, mesopleuron and lower half of lateral surface of propodeum generally smooth, with scattered punctures; upper half of lateral surface of propodeum finely rugulose apart from punctures. Petiolar node dorsally with scattered punctures; in profile, lower half of lateral surface generally smooth, and upper surface finely rugulose with superimposed punctures. Gaster smooth between scattered, small punctures.

Discussion. This species can be distinguished from the rest of the *saussurei* group by the indiscernible metanotal groove and the absence of a median excision on the posterior margin of the petiolar node as seen dorsally.

Only three specimens of *Leptogenys ambo* exist. They all look very similar but an individual specimen collected from PN Marojejy is smaller, which makes the shapes of the mesosoma and petiolar node slightly different. At first glance, this specimen would form a distinct species, but after the examination of all three specimens, we consider it to be conspecific with *L. ambo*. The worker specimen from RS Anjanaharibe-Sud is very similar to that of PN Marojejy in that both have an elongate head (CI: 65–67) and petiolar node (DNI: 86, LNI: 101–105), the median blunt tooth of the mandible is situated closer to the basal preapical tooth than to the apex, and the lamella on the lateral border of the clypeus is continuous and not undulate. In contrast, the specimen from RS Manongarivo is slightly different from the others due to its shorter head (CI: 70) and petiolar node (DNI: 98, LNI: 116), the median blunt angle of mandible is situated a great distance from the basal preapical tooth, and the lamella covering the lateral border of clypeus is not continuous but distinctly forms a few small lobes.



FIGURE 137. Leptogenys ambo holotype worker CASENT0175361. A: lateral view. B: head in full-face view. C: dorsal view.

More samples from these localities and other sites in-between, such as the montane forest of Tsaratanana, are needed to further characterize morphological variation, and to determine whether these specimens actually represent two or three different species.

Distribution and biology. *Leptogenys ambo* is known only from the montane rainforests in the north of Madagascar. It has been collected from a pitfall trap in Anjanaharibe-Sud, and foraging on the forest floor in Marojejy. One single worker was found nesting in a rotten log in the RS Manongarivo.

Additional material examined. Province **Antsiranana:** RS Anjanaharibe-Sud, 9.2 km WSW Befingotra,1280 m, montane rainforest, pitfall trap (B.L. Fisher) (CASC); PN Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 1325 m, montane rainforest (B.L. Fisher) (CASC),

Leptogenys andritantely Rakotonirina and Fisher, sp. n. (Figures 37A, 39A, 138, 145)



FIGURE 138. Leptogenys andritantely holotype worker CASENT0175412. A: lateral view. B: head in full-face view. C: dorsal view.

Holotype worker: Province Toamasina, FC Andriantantely, -18.695, 48.8333, 530 m, rainforest, ex rotten log, 4–10 Dec. 1998 (H.J. Ratsirarson) collection code: HJR065, specimen code: CASENT0175412 (CASC).

WORKER. Diagnosis. Anterior clypeal margin medially projecting into broad triangular lobe; clypeus bordered with semi-translucent lamella. Mandible short and robust, capable of closing tightly against clypeus; longitudinally striate; apical margin of mandible with one apical tooth and one preapical tooth. Eye large, maximum diameter larger than maximum width of antennal scape. Dorsum of head costulate and dorsum of pronotum and mesonotum transversely rugulose. In dorsal view, metanotal groove absent, posterior margin of petiolar node medially excised; larger species (HW: 1.77, HL: 2.29, PW: 1.45).

Measurements (1 specimen). HW: 1.77, HL: 2.29, CI: 77, SL: 2.26, SI: 128, PW: 1.45, WL: 3.57, PNH: 1.42, PNL: 1.09, PNW: 1.19, DNI: 109, LNI: 130.

Description. Head widest immediately behind level of eyes; sides generally parallel to each other in front of eye and broadly convex posteriorly, rounding to posterior margin. Medial clypeal lobe triangularly broad, without a pair of denticles or tubercles on its apex, lateral margin bordered with undulating, semi-translucent lamella. Inner margin of mandible convex, bordered with lamellate membrane that forms one preapical tooth before reaching the sharp apical one. With mesosoma in profile, mesopleural sulcus distinct. In dorsal view, metanotal groove indistinct. With petiole in dorsal view, posterior margin of node medially excised; in lateral view, posterolateral margin strongly inclined posteriorly, blunt angle present at middle height.

Clypeus finely rugulose; mandible longitudinally striate. Head laterally costulate, dorsum coarsely rugose, with shallow punctures. With mesosoma in dorsal view, pronotum and mesonotum transversely rugulose, superimposed with superficial punctures. Propodeal and petiolar dorsum generally smooth apart from widely spaced punctulae; lower half of their sides smooth, upper half faintly rugose and shallowly punctate. Propodeal declivity transversely rugulose or striate near dorsal margin and at level of propodeal lobe and smooth in-between. Gaster normally smooth and shining.

Discussion. This species can be confused with *L. vatovavy*, but the apical margin of the mandibles of the latter is armed with three teeth. *Leptogenys ralipra* looks similar to *L. andritantely* with respect to the number of teeth on the mandibles, but the former is smaller in size (HW: 0.98–1.04, PW: 0.86–0.94), has a densely punctulate to punctate head, a bidentate anteromedian clypeal margin; its mandible is smooth and shiny between scattered punctures, the dorsum of pronotum and mesonotum is punctate. *Leptogenys andritantely* is easily distinguished from the rest of members of the *saussurei* group by the costulate sculpture on the sides of the head and the transverse rugulae on the pronotal and mesonotal dorsum.

Distribution and biology. *Leptogenys andritantely* is restricted to forest habitat in Andriantantely at 530 m. It has been collected only once, a single worker from a rotten log.

Leptogenys lohahela Rakotonirina and Fisher, sp. n.

(Figures 1B, 34A, 36A, 139, 146)

Holotype worker: Madagascar, Toliara, PN Andohahela, Col de Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, -24.7639, 46.7517, 900 m, montane rainforest, ground forager, 21–25 Jan 2002 (Fisher, Griswold Arthropod Team) collection code: BLF05234, specimen code: CASENT0001203 (CASC).

Paratypes: 2 workers with same data as holotype but with specimen codes: CASENT0001198, CASENT0247210 (CASC, BMNH).

Worker Diagnosis. Mandible short and robust, capable of closing tightly against clypeus; anterior clypeal margin medially projecting into triangular lobe; clypeus with sharp edge or lamella. Eye large, diameter markedly greater than maximum width of antennal scape. Dorsum of head and mesosoma noticeably sculptured; with mesosoma in dorsal view, metanotal groove distinctly visible. In dorsal view, posterior margin of petiolar node straight, not medially excised; in profile posterolateral margin of petiolar node with small, sharp tooth.

Measurements (7 specimens). HW: 1.49–1.73, HL: 2.02–2.29, CI: 72–75, SL: 1.98–2.26, SI: 128–137, PW: 1.30–1.42, WL: 3.07–3.38, PNH: 1.13–1.34, PNL: 0.93–1.19, PNW: 0.92–1.06, DNI: 88–108, LNI: 112–122.

Description. Head more or less rectangular, width not increasing from level of eyes to the front, but slightly decreasing behind level of eye toward posterior border of head. Median lobe of clypeus triangular and prominent, without anterior teeth on each side of median carina; lateral margin not interrupted and sharp. Metanotal groove

visible with mesosoma viewed dorsally; in profile, mesopleural sulcus indistinct, but upper portion at level of metathoracic spiracle with wide, shallow impression. In dorsal view, petiolar node longer than broad, posterior margin straight and not medially excised.



FIGURE 139. Leptogenys lohahela holotype worker CASENT0001203. A: lateral view. B: head in full-face view. C: dorsal view.

With head in profile, anterolateral portion from level of eye reticulate-rugose; in full-face view, the dorsum with dense punctures which become shallower and more scattered near posterior cephalic margin. Mandible finely striate, interspersed with piligerous punctures. Dorsum of pronotum distinctly with larger and denser punctures compared to the rest of dorsum of mesosoma. In dorsal view, petiolar node covered with smaller and sparser punctures; in profile, upper half of sides of node densely punctate, superimposed with faint rugulae.

Discussion. Leptogenys lohahela can be confused with L. sausurei and L. acutirostris with respect to the presence of metanotal groove, but the latter species are larger in size, the posterior margin of the petiolar node, in dorsal view, is medially emarginated for L. sausurei, and the posterolateral margin of petiolar node, in profile, is with a blunt angle, not a small sharp tooth for L. acutirostris.

Distribution and biology. *Leptogenys lohahela* is limited to the rainforest of the PN Andohahela in southern Madagascar. It has been collected from leaf litter sampling and pitfall traps. The species forages on the forest floor and nests in rotting tree stumps.

Additional material examined. Province Toliara: PN Andohahela, Col de Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, montane rainforest (Fisher, Griswold Arthropod Team) (CASC); Ilapiry Montane, 9.2 km N Tolanaro, 500 m, rainforest (K.C. Emberton) (CASC); PN Andohahela, Mahamavo, 600 m (P. Rabeson) (MCZC).

Leptogenys ralipra Rakotonirina and Fisher, sp. n.

(Figures 2B, 38B, 39B, 140, 147)

Holotype worker: Madagascar, Toamasina, Torotorofotsy, -18.8707, 48.3474, 1070 m, montane rainforest, marsh edge, ex rotten log, 29 Mar 2004 (Malagasy ant team) collection code: BLF10717, specimen code: CASENT0051142 (CASC).

Paratypes: 2 workers, same data as holotype but specimen coded as: CASENT0196893, CASENT0247274 (CASC, BMNH).

WORKER. Diagnosis. Mandible short and robust, capable of closing tightly against clypeus; anterior clypeal margin medially projecting into triangular lobe; clypeus with sharp edge or lamella. Eye large, maximum diameter larger than maximum width of antennal scape. Dorsum of head and mesosoma distinctly sculptured; with mesosoma in dorsal view, metanotal groove indistinct. In dorsal view, posterior margin of petiolar node noticeably excised medially. Apical margin of mandible with one apical tooth and only one preapical tooth. Mandible smooth and shiny between scattered punctures; head densely punctulate to punctate; smaller species.

Measurements (7 specimens). HW: 0.98–1.04, HL: 1.34–1.44, CI: 71–73, SL: 1.16–1.25, SI: 118–120, PW: 0.85–0.94, WL: 1.99–2.22, PNH: 0.84–0.90, PNL: 0.72–0.80, PNW: 0.75–0.81, DNI: 101–108, LNI: 112–119.

Description. Head not broadened anteriorly, lateral border broadly convex with greatest width at level of eyes. Anteromedian lobe of clypeus ending apically with two denticles or tubercles; lateral margin bordered with rippled subopaque lamella. Mandible with one apical and one preapical tooth. With mesosoma in dorsal view, metanotal groove indistinct; in profile, mesopleural sulcus not visible, but upper portion with wide, shallow impression at level of metathoracic spiracle. Petiolar node elongate in dorsal view, posterior margin medially excised.

Mandible generally smooth between coarse punctures. In full-face view, dorsum of head in front of level of anterior margin of eye finely and densely reticulate-rugose with scattered, large punctures. Sculptures between anterior and posterior margin of eyes rugose, superimposed with punctures; behind level of posterior margin of eye, punctures become larger and widely scattered toward posterior border of head. Dorsum of mesosoma and petiolar node sparsely punctate. With mesosoma in profile, mesopleuron and lower half of propodeum mostly smooth; upper half of propodeum and sides of node with reticulate-rugulose sculpture, intermingled with sparse punctures. Gaster generally smooth apart from scattered, small piligerous punctures.

Discussion. *Leptogenys ralipra* can be recognized by the absence of a metanotal groove, the excised posterior border of the petiolar node, and particularly by its smaller size and smooth and shiny mandible. In *L. ambo*, the posterior margin of the petiolar node is not medially excised. The apical margin of the mandibles is armed with three teeth in *L. vatovavy*. The longitudinally striate mandibles, longitudinally rugulose head, densely punctate superimposed with transverse rugulae of dorsum of pronotum and mesonotum and the larger species (HW: 1.77, HL: 2.29, PW: 1.45) of *L. andritantely* distinguishes it from *L. ralipra*.



FIGURE 140. Leptogenys ralipra holotype worker CASENT0051142. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. *Leptogenys ralipra* is restricted to the montane rainforest of east-central Madagascar. It has been collected only from the Moramanga region. Worker specimens of *L. ralipra* have been found foraging in leaf litter and nesting in rotten logs and rotten sticks on the ground.

Additional material examined. Province Toamasina: Analamay, 1068 m (Malagasy ant team) (CASC); Torotorofotsy, 1070 m, montane rainforest (Malagasy ant team) (CASC); F d'Ambatovy, 14.3 km 57° Moramanga, 1075 m, montane rainforest (B.L. Fisher) (CASC); Ankerana, 865 m, montane forest (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, rainforest (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 918–1044 m, rainforest (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 1036 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys saussurei (Forel)

(Figures 32B, 35A, 141, 148)

Lobopelta saussurei Forel, 1891: 121. Holotype worker, Madagascar, Mahanoro, côte Est de Madagascar (de Saussure) (MHNG) AntWeb specimen code: CASENT0101805 [examined]. [Recognised by Dalla Torre, 1893: 45. Combination in Leptogenys (Lobopelta): Emery, 1911: 102; Wheeler, 1922b: 1012; in Leptogenys: Bolton, 1975: 297, 1995: 233].



FIGURE 141. Leptogenys saussurei worker CASENT0175418. A: lateral view. B: head in full-face view. C: dorsal view.

WORKER. Diagnosis. Mandible elongate and robust, capable of closing tightly against clypeus; anterior clypeal margin medially projecting into triangular lobe; anterior clypeal margin medially projecting into triangular lobe; clypeus with sharp edge or lamella. Eye large, diameter markedly greater than maximum width of antennal scape. Dorsum of head and mesosoma distinctly sculptured; with mesosoma in dorsal view, metanotal groove distinctly visible. In dorsal view, posterior margin of petiolar node medially emarginate.

Measurements (8 specimens). HW: 1.42–1.75, HL: 1.92–2.44, CI: 71–78, SL: 1.80–2.59, SI: 126–148, PW: 1.27–1.57, WL: 3.04–3.80, PNH: 1.21–1.47, PNL: 1.02–1.22, PNW: 0.96–1.21, DNI: 92–105, LNI: 118–132.

Description. Head elongate, sides broadly convex but slightly converging posteriorly from level of eye. Clypeus projecting anteriorly into non-bidentate triangular median lobe. Lamellate extension of inner mandibular margin widest at distal third, from which first preapical tooth is followed by another, closer blunt angle before rising into sharp apical tooth. With mesosoma in profile, mesopleural sulcus incomplete or absent; in dorsal view metanotal groove distinctly visible. With petiole in dorsal view, node longer than broad, with markedly excised posterior margin; in side view, posterolateral margin armed with one sharp tooth.

Anterior portion of head from base of mandible to level of eye reticulate-rugose, interspersed with punctures. In full-face view, dorsum of head behind level of anterior margin of eye with dense punctures, which become larger and widely spaced towards its posterior margin. Mandible finely striate between sparse punctures. In dorsal view, pronotum punctate, remainder of mesosoma with scattered punctures. Petiolar node sparsely punctate, faint striation or rugoreticulum may be present on upper half of lateral section. Gastral segments mostly smooth and shining. Body with bluish reflection.

Discussion. Leptogenys saussurei is one of the largest species in the group. As in *L. acutirostris* and *L. lohahela*, it has a visible metanotal groove, but the posterior margin of the petiolar node is not medially excised in *L. saussurei* as it is in these two species.

Distribution and biology. One of the most widely distributed species in the *saussurei* group, *L. saussurei* ranges from RS Ambatovaky in the north to the PN Andohahela in the south. Between these two sites, the species has been recorded from the rainforest of the PN Mantadia and RS Manombo to the montane rainforest of the RS Ivohibe. *Leptogenys saussurei* forages terrestrially, and can be found on the forest floor and in leaf litter. It nests in rotten logs and dead branches on the ground.

Additional material examined. Province Antananarivo: [Andrangoloaka] (Sikora) (MHNG); Province Fianarantsoa: RS Ivohibe, 8.0 km E Ivohibe, 1200 m, montane rainforest (Sylvain) (CASC); RNI Andringitra, 43 km S Ambalavao, 825 m, rainforest (B.L. Fisher) (CASC); 9.0 km NE Ivohibe, 900 m, montane rainforest (Sylvain) (CASC); Manombo, 36 m, rainforest (Rin'Ha, Irwin) (CASC); RS Manombo, 24.5 km 228° Farafangana, 30 m, rainforest (B.L. Fisher *et al.*) (CASC); 7 km W PN Ranomafana, 1000 m, montane rainforest (W.E. Steiner) (MCZC); Province Toamasina: Corridor Forestier Analamay-Mantadia, Ambatoharanana, 995 m, rainforest (B.L. Fisher *et al.*) (CASC); [Mahanoro 1 km 168] (MHNG); Province Toliara: PN Andohahela, 13 km NW Enakara, 1280 m, montane rainforest (B.L. Fisher) (CASC); PN Andohahela, Col de Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, montane rainforest (B.L. Fisher, Griswold and Arthropod Team) (CASC); PN Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 275 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys vatovavy Rakotonirina and Fisher, sp. n.

(Figures 34B, 38A, 142, 154)

Holotype worker: Province Fianarantsoa, FC Vatovavy, 7.6 km 122° Kianjavato, -21.4, 47.94, 175 m, rainforest, ex rotten log, 6–8 June 2005 (B.L. Fisher *et al.*), collection code: BLF12344, specimen code: CASENT0059729 (CASC)

WORKER. Diagnosis. Mandible short and robust, capable of closing tightly against clypeus; anterior clypeal margin medially projecting into triangular lobe; clypeus with sharp edge or lamella. Eye large, maximum diameter larger than maximum width of antennal scape. Dorsum of head and mesosoma distinctly sculptured. In dorsal view, metanotal groove absent, posterior margin of petiolar node medially excised; apical portion of mandible blades armed with three teeth.

Measurements (1 specimen). HW: 1.18, HL: 1.62, CI: 73, SL: 1.55, SI: 131, PW: 1.09, WL: 2.61, PNH: 1.04, PNL: 0.85, PNW: 0.91, DNI: 107, LNI: 122.

Description. Head more or less elongate and increasing in width from back to front; sides slightly convex and diverging anteriorly throughout their length. Center of eye closer to midlength of lateral border of head than to base of mandible. Anteromedian lobe of clypeus projecting into a pair of small triangular teeth or denticles; lateral

portion bordered with undulate, semi-translucent lamella. Apical margin of mandible armed with three teeth: apical tooth followed by two preapical teeth or denticles. With mesosoma in dorsal view, metanotal groove not visible; in profile, groove between metapleuron and propodeum present. Petiolar node noticeably excised medially in dorsal view.



FIGURE 142. Leptogenys vatovavy holotype worker CASENT0059729. A: lateral view. B: head in full-face view. C: dorsal view.

FIGURES 143–148. Distribution maps of the Leptogenys saussurei group in the Madagascar.

Sculpture of clypeus rugulose interspersed with widely spaced punctures. With head in profile, lateral margin anterior to the eye, densely reticulate-rugulose, superimposed with dense punctures. Dorsum of head from level of eyes coarsely and densely reticulate-rugose, with large punctures which become sparser toward the posterior margin of head. Mandible smooth with faint or effaced longitudinal striolae. Pronotal dorsum finely reticulate-rugose and superimposed with fairly large punctures; rest of dorsum of mesosoma sparsely shallowly punctate. With mesosoma in profile, mesopleuron smooth between scattered punctures; anterodorsal portion of propodeum and petiolar node rugoreticulate, superimposed with widely spaced punctures.

Discussion. This species closely resembles *L. ralipra* and *L. andritantely* in that all three have an indistinct metanotal groove and excised posterior margin of the petiolar node. It can be separated from *L. ralipra* by the presence of three teeth on the apical margin of the mandible, and from *L. andritantely* by the smaller size, the presence of a pair of denticles on the apex of the anterior clypeal margin, and the rugo-reticulate sculpture of its head and mesosoma.

Distribution and biology. Leptogenys vatovavy has only been collected once, a single worker in a rotten log.

The stuhlmanni group

With only one species recorded from the Malagasy region, the species group description coincides with the species description.

Leptogenys stuhlmanni Mayr

(Figure 149)

- Leptogenys (Lobopelta) stuhlmanni Mayr, 1893: 198. Syntype workers, Mozambique, Quilimane (Stuhlmann) [location of type not known]. [Combination in Leptogenys (Leptogenys): Emery, 1911: 100; Wheeler, 1922a: 787; in Leptogenys: Bolton, 1975: 261].
- *Leptogenys comorensis* Forel, 1907: 76. Lectotype worker, present designation, Comoros Islands, Mohéli (Voeltzkow) AntWeb CASENT0104565 (ZMHB). Paralectotypes: 6 workers with same data as lectotype but specimens coded as: CASENT0101826, CASENT0101871, CASENT0101876, CASENT0101904, CASENT0101967, CASENT0101968 (MHNG) [examined]. [Combination in *Leptogenys (Leptogenys)*: Emery, 1911: 99; Wheeler, 1922b: 1010; in *Leptogenys* and junior synonym of *Leptogenys stuhlmanni*: Bolton, 1975: 262; here synonymy confirmed].

WORKER. Diagnosis. Mandible elongate and narrow, not capable of closing tightly against the clypeus; dorsum of body covered with erect hairs; eye large, with maximum diameter greater than widest portion of antennal scape; third antennal segment approximately twice as long as the second; dorsum of head smooth apart from scattered punctures; pronotum dorsally weakly sculptured; constriction between third and fourth abdominal segments indistinct.

Measurements (1 specimen). HW: 1.58, HL: 1.76, CI: 90, SL: 2.30, SI: 145, PW: 1.14, WL: 3.26, PNH: 0.80, PNL: 0.77, PNW: 0.59, DNI: 77, LNI: 134.

Description. Head longer than broad, distinctly diverging from back to front; posterior margin roughly straight. Mandible long and feebly curved near bases, with parallel outer and inner margin; blades generally same width from bases to apices and not able to close tightly against anterior margin of clypeus; basal groove a broad sulcus. In full-face view, eye large, maximum diameter twice as large as maximum width of scape; location not breaking outline of lateral cephalic margin. Antennal scape very long, more than one third its length extending beyond posterior border of head; third antennal segment strikingly elongate, length more than twice the length of the second. Clypeus projecting anteriorly and strongly converging into narrowly triangular lobe; median clypeal carina long and sharp. In dorsal view, mesonotum distinctly longer than broad and metanotal groove present. In profile, propodeal posterior margin rounded, without toothlike lobe or blunt angle; propodeal spiracle elongate. Petiolar node as long as high in lateral view; in dorsal view node longer than broad, with lateral margin feebly converging. Helcium situated near lateroventral angle of anterior margin of third abdominal segment. Constriction between third and fourth abdominal segments indistinct.

Dorsum of head, promesonotum, petiolar node and gastral tergites generally smooth and shining apart from punctures. Punctures on body vary in size and space, ranging from much larger and closely spaced from head

dorsum to very small, scattered punctures on third and fourth abdominal segments. Rugulae may be present in front of eyes. Propodeal dorsum with faintly effaced, fine rugulae between small punctures; propodeal declivity transversely striate or with rugulae. Erect hairs present from antennae and head dorsum to gaster. Body color dark brown, with light brown tip of gaster; appendages brown and become light brown towards apices.

Discussion. *Leptogenys stuhlmanni* is large and may be confused with the few large species of the *incisa* group due to its elongate mandible and the gap between the clypeus and the mandibles when the latter are closed. But *L. stuhlmanni*'s body surface is generally smooth and shining between punctures and its particularly long third antennal segment provides a clear distinction from these other species.

FIGURE 149. Leptogenys stuhlmanni worker CASENT0104565. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys stuhlmanni is the only species of the *stuhlmanni* group that has been found in the Malagasy region, on Mohéli Island of the Comoros. Interestingly, this species was collected only once on this island, sometime between 1903 and 1905; it has not been seen in the region since. Even the use of modern collecting methods during

the 2008 arthropod inventory project across the Comoros Islands did not catch any workers of *L. stuhlmanni*. These results suggest that this species requires very restricted environmental conditions, and the destruction of natural forest habitats in Mohéli might have caused it to go locally extinct.

Leptogenys comorensis, a junior synonym of L. stuhlmanni (by Bolton 1975 and confirmed by this study), was first described by Forel (1907) when he received specimens from Voeltzkow after a trip to the Comoros Islands and Madagascar between 1903 and 1905. These specimens were collected from Mohéli in the Comoros and Lake Alaotra in central eastern Madagascar. In his original description, Forel doubted the pattern of distribution of this species and doubted its presence at Lake Alaotra. During the course of this study, we were not able to examine the worker specimen stated to be found in Lake Alaotra, as its location is unknown. Also, the extensive ant inventories during the past 15 years in Madagascar have caught no worker of *L. stuhlmanni*, suggesting that Forel was right to doubt the presence of this species in Madagascar.

Distribution and biology. Besides its occurrence in Mohéli, *L. stuhlmanni* is also known from the east coast and southern portions of Africa, where itis restricted to open areas and dry forest habitats.

Additional material examined. COMOROS ISLANDS: Mohéli (Voeltzkow) (MCZC); AFRICA: Kenya, Nakuru National Park, 1760 m, grassland/Acacia woodland (D. M. Olson & L. Farley) (PSWC); Tanzania, Mkomazi Game Reserve, Umba River camp site, open woodland (H.G.Robertson) (SAMC).

The toeraniva group

Mandible short, with convex inner margin; blades widest at about distal half or apical third and capable of closing tightly against clypeus; basal groove distinctly impressed; preapical tooth or denticle present near the broadly lamellate apical tooth. Clypeus bordered laterally with large lobe, anterior margin projects anteriorly into triangular median lobe, which is bordered with a semi-translucent lamella; two to three peg-like setae are present near anterior margin of median lobe of the clypeus; median clypeal carina long and sharp. Head apparently subrectangular; sides almost straight throughout their length and rounding into posterior cephalic margin. Eye usually small, with their greatest diameter less than the maximum width of antennal scape. With mesosoma in dorsal view, mesonotum broader than long; metanotal groove strongly impressed with cross-ribs or only consisting of a line; in profile, opening of propodeal spiracle rounded. Petiolar node variously shaped, either about as long as high or longer than high in profile; dorsal margin convex or straight; anterior and posterior faces at the same height or posterior face at lower level so that the node is inclined posteriorly; subpetiolar process consisting of anteriorly broad tooth followed by posterior rounded lobe with an indentation between them. Prora voluminous and lobe-like; anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anterovent

Body variously sculptured, but generally in dorsal view promesonotum and node of petiole with sparse punctures and propodeum rugulose interspersed with coarser punctures. In profile, mesopleuron, lateral section of propodeum and petiolar node, and anterior half of third abdominal segment either rugulose with sparse punctures or densely to typically punctate. Standing, erect, yellowish hairs and little pubescence present.

Most species in this species group are cryptic and rarely collected. They exhibit a high degree of local endemism.

Leptogenys avaratra Rakotonirina and Fisher, sp. n.

(Figures 3A, 3B, 150, 155)

Holotype worker: Madagascar, Antsiranana, Montagne des Français, 7.2 km 142° SE Antsiranana (= Diego Suarez), -12.3228, 49.3382, 180 m, tropical dry forest, ex rotten log, 22–28 Feb 2001 (Fisher, Griswold *et al.*) collection code: BLF03177, specimen code: CASENT0416208 (CASC).

Paratypes: 1 ergatoid queen and 4 workers, with same data as holotype but with the following specimen codes: CASENT0416209 (ergatoid queen), CASENT0416210, CASENT0247238, CASENT0247239, CASENT0247240 (CASC, BMNH, MHNG, PBZT).

FIGURE 150. Leptogenys avaratra holotype worker CASENT0416208. A: lateral view. B: head in full-face view. C: dorsal view.

WORKER. Diagnosis. Mandible capable of closing tightly against clypeus; maximum diameter of eye less than greatest width of scape. In full-face view head subquadrate (CI: 78–82); in profile, helcium located very low near the anteroventral angle of third abdominal segment; prora voluminous and anteroventral section of third abdominal sternite rounded; indentation weakly visible between prora and anteroventral angle.

Measurements (4 specimens). HW: 0.91–0.99, HL: 1.17–1.21, CI: 78–82, SL: 1.22–1.29, SI: 130–133, PW: 0.77–0.82, WL: 1.76–1.90, PNH: 0.65–0.70, PNL: 0.63–0.68, PNW: 0.58–0.66, DNI: 90–99, LNI: 102–107.

Description. Head subquadrate, lateral margins nearly straight and joining posterior margin in convex line. Maximum eye diameter about half the greatest width of scape. Clypeus with convex lateral lobes which converge abruptly into narrow anteromedian lobe; lobe covered with semi-translucent lamella. Mandible short and narrow,

inner margin convex at about apical third of length; blades capable of closing tightly against clypeus. Scape long, roughly one-third of its length extending beyond posterior cephalic margin. In dorsal view, metanotal groove visible but not cross-ribbed. With petiole in dorsal view, node roughly as long as broad; in profile node as broad as high, with vertically straight anterior and posterior faces, both of which round into broadly convex dorsal face. Helcium located at lower level near anteroventral angle of third abdominal segment. Prora relatively voluminous and anteroventral portion of third abdominal sternite rounded; prora and anteroventral section not separated by strong indentation. Constriction between third and fourth abdominal segments indistinct.

Dorsum of head with sparse, shallow punctures. Dorsal surface of mesosoma, petiolar node, and abdominal tergites III and IV sparsely punctulate to punctate; elongate punctures sometimes present, with fairly effaced, fine rugulae. In profile, mesopleuron and lower lateral surface of propodeum and petiolar node reticulate-rugose; propodeal declivity transversely rugulose. Integument reddish brown, appendages and tip of gaster ferruginous-red.

QUEEN. Measurments: HW: 0.90, HL: 1.12, CI: 80, SL: 1.10, SI: 121, PW: 0.72, WL: 1.64, PNH: 0.55, PNL: 0.55, PNW: 0.60, DNI: 109, LNI: 100. Ergatoid queen looks very similar to worker due to its lack of ocelli, but differs by the short and broadly convex dorsal outline of the mesosoma, the anteroposteriorly flattened petiolar node and a much larger gaster.

Discussion. Worker specimens of *L. avaratra* are very similar to other species within the *toeraniva* species group, but can be separated by the square form of the petiolar node in dorsal view, and the location of the prora near the anteroventral angle of the third abdominal segment. In the other species in this group, the petiolar node is approximately as high as long in profile, and the prora is separated from the rounded anteroventral angle of third abdominal sternite by an indentation.

This species has been found from two different sites. Specimens from the two sites differ in the extent and depth of the sculpture.

Distribution and biology. This species is only known from the dry forest habitats of Montagne des Francais in the north and the transitional humid forests of Antshabe near Daraina in the northeast of Madagascar. This rare species nests in rotten logs and forages through leaf litter.

Additional material examined. Province Antsiranana: F d' Antsahabe, 11.4 km 275° W Daraina, 550 m, transitional humid forest (B.L. Fisher) (CASC).

Leptogenys avo Rakotonirina and Fisher, sp. n.

(Figures 5A, 151, 156)

Holotype worker: Province Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, -15.1783, 49.635, 1100 m, montane rainforest, sifted litter, 12–16 Mar 2003 (Fisher, Griswold *et al.*), collection code: BLF08150, specimen code: CASENT0034742 (CASC).

WORKER. Diagnosis. Mandible capable of closing tightly against clypeus; eye not flattened, slightly protruding from head capsule; antennal scape with erect hairs shorter than maximum width of scape; eye larger, maximum diameter greater than the maximum width of scape. Propodeal declivity transversely striate; in profile, anterodorsal and posterodorsal margin of petiolar node at the same height and helcium located approximately near mid-height of anterior margin of third abdominal segment. Prora voluminous and anteroventral section of third abdominal sternite rounded; prora and anteroventral angle separated by strong indentation.

Measurements (2 specimens). HW: 1.01, HL: 1.42–1.45, CI: 69–71, SL: 1.44–1.49, SI: 143–147, PW: 0.84–0.87, WL: 2.21–2.24, PNH: 0.79–0.83, PNL: 0.76–0.83, PNW: 0.69–0.71, DNI: 83–93, LNI: 100–104.

Description. Width of head slightly increasing from back to front; lateral border almost straight and meets the posterior margin in a rounded angle. Maximum eye diameter distinctly greater than widest part of scape. Mandible elongate with convex inner margin, closing tightly against clypeus. Antennal scape surpassing posterior margin of head by one third of its length. Metanotal groove impressed, with transverse striation. In dorsal view, petiolar node distinctly longer than broad. With petiole in profile, node roughly as high as broad, junction of anterior and posterior faces to dorsal margin in convex line; subpetiolar process consisting of ventrally directed lobe anteriorly followed by an indentation and small tooth posteriorly. Constriction between third and fourth abdominal segments lacking. Helcium roughly situated near mid-height of third abdominal segment; prora voluminous and anteroventral angle of third abdominal sternite rounded.

FIGURE 151. Leptogenys avo holotype worker CASENT0034742. A: lateral view. B: head in full-face view. C: dorsal view.

Dorsum of head coarsely rugose and interspersed with large punctures from anterior portion of head to posterior third, behind which the sculptures become scattered punctures. Pronotum transversely rugulose, with sparse punctures. Dorsum of mesonotum, propodeum and petiolar node reticulate-rugulose. Sides of mesosoma coarsely rugose, with fine reticulation superimposed with large punctures. In lateral view, anterior half of third abdominal tergite finely rugulose, the interspaces of which are punctate.

Discussion. This species is known from two specimens, one from each of two sites. The specimen from PN Masoala has eye diameter roughly as large as the greatest width of the scape; petiolar node in profile approximately

as high as long; propodeum shorter, the dorsum of which meets the declivity in a distinct angle; and no sculpture apart from piligerous punctures on the third abdominal tergite. By contrast, the holotype specimen from Anjanaharibe Makira is characterized by a larger eye whose diameter is distinctly greater than the maximum width of the scape; petiolar node in profile elongate, with convex dorsal margin; propodeal dorsum elongate, meeting the declivity in an almost rounded angle; and strong sculpture on the body with punctures present between fine rugulation on the third abdominal tergite.

Distribution and biology. The two worker specimens of *L. avo* were from high altitude localities in eastern Madagascar. They were found foraging in the leaf litter of montane rainforest.

Additional material examined. Province Toamasina: PN Masoala, Ambohitsitondroina, 6.9 km NE Ambanizana, 825 m, rainforest (B.L. Fisher) (CASC).

Leptogenys bezanozano Rakotonirina and Fisher, sp. n.

(Figures 2A, 4A, 4B, 152, 157)

Holotype worker: Province Toamasina, P.N. Mantadia, -18.7917, 48.4267, 1070 m, rainforest, ex rotten log, 25 Nov–1 Dec 1998 (H.J. Ratsirarson), collection code: HJR010, specimen code: CASENT0175420 (CASC).

Paratype worker: with same data as holotype but specimen coded as: CASENT0196894 (CASC).

WORKER. Diagnosis. Mandible capable of closing tightly against clypeus; eye small, maximum diameter less than greatest width of scape; in full face view, head rectangular; antennal scape with erect hairs longer than maximum width of scape; in profile, anterior face of petiolar node higher than posterior face and helcium located roughly near mid-height of anterior margin of third abdominal segment. Prora lobe-like and anteroventral section of third abdominal sternite rounded; strong indentation exists between prora and anteroventral angle.

Measurements (3 specimens). HW: 0.81–0.86, HL: 1.09–1.15, CI: 74–75, SL: 1.06–1.16, SI: 130–134, PW: 0.69–0.74, WL: 1.72–1.84, PNH: 0.53–0.60, PNL: 0.66–0.78, PNW: 0.60–0.67, DNI: 86–91, LNI: 77–84.

Description. Head rectangular, sides approximately parallel to each other posteriorly and slightly diverging from level of eye to clypeus. Eye small, maximum diameter less than widest portion of scape. Lateral margin of clypeus convex and anteromedian lobe generally triangular, both separated by impression or notch. Mandible short, blades increasing in width towards their apices and capable of closing tightly against median lobe of clypeus. Scape relatively long, about one third of its length surpassing posterior margin of head; with long, erect hairs roughly equal in length to maximum width of scape. In dorsal view, metanotal groove impressed, with transverse striation. With petiole in dorsal view, node markedly longer than broad. In profile, node broader than high with straight dorsal margin and lower posterior face so that node inclined posteriorly. When viewed from side, helcium located roughly close to mid-height of anterior face of third abdominal segment; anteroventral section distinctly rounded and separated from prora by strong emargination. Without constriction between third and fourth abdominal segments.

In full-face view, anterior portion of head in front of level of eye rugulose and mostly smooth and shiny apart from piligerous punctures behind the level of eyes to posterior cephalic margin. In dorsal view, pronotum sparsely, shallowly punctate; rest of mesosomal dorsum, petiolar node and third abdominal tergite punctate. Mesopleuron, lateral portion of propodeum and anterior half of third abdominal segment rugulose; sides of petiolar node densely punctate. Color reddish brown, with yellowish-orange appendages.

Discussion. The species in the *toeraniva* group look similar to each other, but *L. bezanozano* differs from *L. avaratra* by its elongate head and the large indentation between the prora and the anteroventral angle of the third abdominal sternite. *Leptogenys avo* and *L. toeraniva* have much shorter hairs on the antennal scape, transversely striate propodeal declivity, and a not sloping dorsal margin of the petiolar node.

Distribution and biology. *Leptogenys bezanozano* occurs in the high mountains of central-eastern Madagascar. It was found nesting in a rotten log in the rainforest of Mantadia and foraging in leaf litter in the montane rainforest of Torotorofotsy.

Additional material examined. Province Toamasina: Torotorofotsy, 1070 m, montane rainforest marsh edge (Malagasy ant team) (CASC).

FIGURE 152. *Leptogenys bezanozano* holotype worker CASENT0175420. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys toeraniva Rakotonirina and Fisher, sp. n.

(Figures 3C, 3D, 4C, 4D, 5B, 153, 158)

Holotype worker: Province Toamasina, RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, -17.924, 49.1997, 390 m, rainforest, sifted litter, 28 Nov 2005 (B.L. Fisher *et al.*), collection code: BLF13125, specimen code: CASENT0072075 (CASC).

Paratype worker: from same locality as holotype, but -17.8867, 49.2025, 520 m, rainforest, ground forager, 2 Dec 2005 (B.L. Fisher *et al.*), collection code: BLF13322, specimen code: CASENT0067668 (CASC).

WORKER. Diagnosis. Mandible capable of closing tightly against clypeus; eye small, maximum diameter less than greatest width of scape; in full-face view, head rectangular; antennal scape with erect hairs shorter than maximum width of scape; eye smaller, maximum diameter much less than the maximum width of scape. With petiole in lateral view, anterior face of node the same height as posterior face. In profile, helcium located generally near mid-height of anterior margin of third abdominal segment; prora voluminous and anteroventral section of third abdominal sternite rounded; prora and anteroventral angle separated by large indentation.

Measurements (**4** specimens). HW: 0.85–1.01, HL: 1.21–1.45, CI: 69–73, SL: 1.16–1.49, SI: 132–147, PW: 0.74–0.87, WL: 1.90–2.24, PNH: 0.70–0.83, PNL: 0.70–0.83, PNW: 0.64–0.71, DNI: 83–93, LNI: 94–104.

FIGURE 153. Leptogenys toeraniva holotype worker CASENT0072075. A: lateral view. B: head in full-face view. C: dorsal view.

FIGURES 154–158. Distribution maps of *Leptogenys vatovavy* (saussurei group) and the *Leptogenys toeraniva* group in Madagascar.

Description. Head oblong, lateral margin approximately straight from anterior portion of head to posterior third and rounding gradually to posterior border. Eye small, greatest diameter less than maximum width of scape. Clypeus projecting anteriorly into prominent triangular lobe; semi-translucent lamella on lateral and anteromedian lobes separated by impression or notch. Mandible with convex inner margin; blades widest at apical third and closing tightly against clypeus when at rest. In full-face view, antennal scape long, surpassing posterior cephalic border by one-third of apical portion. In dorsal view, metanotal groove distinct and cross-ribbed. Petiolar node noticeably longer than broad in dorsal view. In profile, node longer than high, with anterior and posterior faces at the same height and meeting the dorsal face in rounded angle; subpetiolar process double, consisting of anterior triangular tooth and posterior rounded lobe separated by indentation. In side view, helcium located approximately near mid-height of anterior margin of third abdominal segment; prora voluminous and anteroventral angle of third abdominal sternite rounded; prora and anteroventral section separated by strong indentation.

Dorsum of head, promesonotum, petiolar node and gastral tergites generally smooth and shining, with scattered small punctures from which hairs arise. Sculptures of head in front of eye rugulose, which become punctate at level of eyes and sparsely punctate in posterior cephalic portion. Propodeal dorsum with faintly fine rugulae between punctures; propodeal declivity transversely striate. Scape with erect hairs shorter than greatest width of scape. Color dark brown, with lighter appendages and tip of gaster.

Discussion. Leptogenys toeraniva is similar to L. bezanozano but easily identified by the presence of short, erect hairs on the antennal scape, transversely rugulose propodeal declivity, and the anterior and posterior margins of the petiolar node are the same height. Leptogenys bezanozano has erect hairs that are as long as or longer than the maximum width of its scape, a smooth, shiny propodeal declivity, and a shorter posterior face of the petiolar node.

Workers collected from the two known localities differ in some morphological characters. Specimens from Betampona have smaller eyes whose maximum diameter is less than greatest width of scape; the mandible is smooth and shining; and the anteromedian lobe of the cypeus has a pair of anteriorly projecting peg-like setae. In contrast, worker specimens from Makirovana forest have larger eyes, the maximum diameter slightly greater than maximum diameter of scape; mandible smooth and shining on basal half and finely striate on distal half; and the anteromedian lobe of the cypeus with three anteriorly projecting peg-like setae.

Distribution and biology. *Leptogenys toeraniva* occurs in the lowland forest of RNI Betampona and Makirovana near Sambava. This species was mostly found foraging under leaf litter and rarely on the forest floor, even though many different collecting methods have been used to collect ants across Madagascar. In addition to its smaller eyes and its rarity, this result supports the idea that *L. toeraniva* is a hypogaeic species, living generally under the soil layers.

Additional material examined. Province Antsiranana: Makirovana Forest, 550 m, rainforest (B.L. Fisher *et al.*) (CASC).

The truncatirostris group

Mandible elongate and variably curved, but capable of closing tightly against clypeus; preapical tooth may be present; basal groove narrow. Head either strongly broader anterad than posterad or width changing very slightly along sides. In full-face view, eye may be small, greatest width slightly greater than widest part of scape, medium, with width about one and a half times the maximum width of scape, or large, with width at least twice as great as maximum diameter of scape; slightly convex and may or may not break the outline of lateral margin of head. Clypeus without a prominent projecting median lobe, anterior margin broadly evenly rounded or truncated and widely transverse; median longitudinal carina either present or absent. Distance between anterior level of antennal insertion and anteromedian margin of clypeus distinctly less than the distance between outer margin of torulus and outer margin of base of mandible. With mesosoma in dorsal view, metanotal groove impressed, with transverse striation; propodeal declivity transversely striate. With petiole in lateral view, node approximately as high as broad; dorsum convex and anterior face shorter than sloping posterior border. Gaster constricted between first and second segments. Sculpture of body mostly reticulate-rugulose, superimposed with small punctures, rarely with faintly effaced sculptures or scattered punctures.

Three complexes of closely related species can be distinguished within the *truncatirostris* group on the basis of the shape of the mandible and the characteristics of the clypeus. First is the *arcirostris* complex, consisting of *L*.

alatapia, L. arcirostris, and *L. borivava,* which can be separated from other complexes by the presence of the median longitudinal carina on the clypeus, a particularly short clypeus whose anterior margin is wide and broadly convex, and the superimposition of the mandibular blades when tightly closed against the anterior clypeal margin. The second is the *ridens* complex, represented by *L. fotsivava, L. namoroka, L. ridens* and *L. tsingy*,that can be identified by the presence of the median longitudinal carina on the clypeus, the rounded clypeus, and the fact that the mandibles cross each other when tightly closed against the anterior clypeal margin. Finally there is the *truncatirostris* complex, including *L. diana* and *L. truncatirostris*, for which the clypeus is anteriorly truncate or broadly rounded and lacks a median longitudinal carina, in profile mandibular blades bend forward so that their bases are inserted in a distinct angle relative to the head dorsum, then strongly curved down nearly at basal third, the blades widest at distal half and gradually narrower toward the sharp apical tooth, the interior margin of blades broadly arch from the distal half to the apex, and the surface from distal half to apex has dense and fine striae.

Based on the collection records from the ant surveys in Madagascar, members of the *truncatirostris* species group may not have ergatoid queens, perhaps relying on mated workers instead.

Leptogenys alatapia Rakotonirina and Fisher, sp. n.

(Figures 1C, 14A, 159, 168)

Holotype worker: Madagascar, Fianarantsoa, Forêt d'Analalava, 29.6 km 280° W Ranohira, -22.5917, 45.1283, 700 m, *Uapaca* woodland, under stone, 1–5 Feb 2003 (Fisher, Griswold *et al.*) collection code: BLF07470, specimen code: CASENT0489586 (CASC).

Paratypes: series of 8 workers, with same data as holotype but specimen coded as: CASENT0489585, CASENT0489587, CASENT0489588, CASENT0196382, CASENT0247219, CASENT0247220, CASENT0247221, CASENT0247222 (CASC, BMNH, MHNG, MCZC, PBZT).

WORKER. Diagnosis. Clypeus with median carina; distance between anterior level of torulus and anteromedial clypeal margin roughly less than maximum width of scape, head short; clearly broader than long in full-face view and broadened anteriorly.

Measurements (4 specimens). HW: 1.54–1.63, HL: 1.44–1.50, CI: 105–109, SL: 1.53–1.60, SI: 98–100, PW: 0.93–1.00, WL: 2.32–2.48, PNH: 0.74–0.78, PNL: 0.60–0.67, PNW: 0.63–0.71, DNI: 103–110, LNI: 113–129.

Description. In full-face view, head broader than long and remarkably broadened anteriorly; sides distinctly diverging from back to base of mandible; posterior margin weakly concave medially. Eye medium, located in frontal portion of head and not breaking outline of lateral cephalic border. Antennal scape relatively short. Clypeus broad and evenly rounded anteriorly, anterior margin bordered by whitish lamella; median portion with longitudinal carina; median lobe narrow, width as great as widest part of scape. With head in full-face view and mandible fully closed, blades superimposed each other, whole internal face of first blade tightly closed against clypeus along its length and most of distal portion of the second against external surface of the distal portion of the first. In dorsal view, metanotal groove impressed and transversely striate; with mesosoma in profile, propodeal lobe lacking. With petiole in lateral view, outline of the node a convex line from anterior margin to posterodorsal angle, which ends in slight, anteriorly sloping posterior margin.

Mandible basally longitudinally striate, with scattered punctures, and smooth in the distal third of blades. Dorsum of head, mesosoma and petiolar node covered with dense and fine reticulate-punctures to dense and fine reticulate-rugae. Third abdominal tergite densely punctate. Erect hairs few and short; pubescence abundant. Integument black to dark brown, with brown appendages whose apices are lighter in color.

Discussion. The broader head (CI: 105–109) and relatively shorter scape (SI: 98–100) of *L. alatapia* make it easy to distinguish from *L. arcirostris* and *L. borivava*. In *L. arcirostris*, the scape is much longer (SI: 103–112). In *L. borivava*, in addition to its longer scape (SI: 111–129), the dorsum of its head, mesosoma, petiole, and gaster are covered with long erect and suberect hairs.

Distribution and biology. *Leptogenys alatapia* is restricted to the plateau in the south of Madagascar and particularly in *Uapaca* woodland habitats in the PN Isalo. Specimens of this species have been found foraging on the ground and they nest under rocks.

Additional material examined. Province Fianarantsoa: F d'Analalava, 29.6 km 280° W Ranohira, 700 m, *Uapaca* woodland (Fisher, Griswold *et al.*) (CASC); PN Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, 990 m, *Uapaca* woodland (Fisher, Griswold *et al.*) (CASC).

FIGURE 159. Body of *Leptogenys alatapia* worker CASENT0072075. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys arcirostris Santschi

(Figures 11B, 14B, 15A, 160, 169)

Leptogenys (Machaerogenys) arcirostris, Santschi; 1926: 25. Holotype worker, Madagascar, Moramanga (Descarpentries) AntWeb specimen code: CASENT0101132 (NHMB) [examined]. [Combination in Leptogenys: Bolton, 1975: 295, 1995: 230].

FIGURE 160. Leptogenys arcirostris worker CASENT0491659. A: lateral view. B: head in full-face view. C: dorsal view.

WORKER. Diagnosis. Clypeus with median carina, width when measured from anterior level of torulus to anteromedian margin of clypeus less than or equal to maximum diameter of scape; in full-face view head longer than broad, antennal scape relatively short; few short suberect hairs and abundant pubescence present on dorsum of head, mesosoma and gaster.

Measurements (10 specimens). HW: 1.18–1.38, HL: 1.27–1.43, CI: 93–97, SL: 1.32–1.46, SI: 103–112, PW: 0.72–0.95, WL: 2.08–2.32, PNH: 0.68–0.74, PNL: 0.53–0.62, PNW: 0.60–0.68, DNI: 107–115, LNI: 119–133.

Description. Head broader in front than behind, the sides more or less straight, diverging anteriorly and rounding in a convex line with a straight posterior margin. Eye large, not breaking the lateral cephalic border.

Antennal scape relatively short (SI: 103–112). In full-face view, clypeus with broad and evenly rounded anterior margin, fringed by wide, white-yellowish membrane; median lobe short, width when measured from anterior level of torulus to anteromedian margin of clypeus less than or equal to maximum diameter of scape; medial longitudinal carina present. With head in full-face view and mandible fully closed, blades superimposed on one another, with internal surface of first blade tightly closed against clypeus along their length and that of the second blade against external face of the first. In dorsal view, metanotal groove transversely striate; in lateral view, propodeal lobe bluntly angular. With petiole in profile, anterior face of node vertically straight, posterior face convex, both forming rounded angles with dorsal margin.

Mandible longitudinally striate, interspersed with piligerous punctures. Dorsum of head, pronotum and petiolar node densely and finely reticulate-punctate, punctures becoming smaller near posterior margin of head. Rest of dorsum of mesosoma finely reticulate-rugose. Mesopleuron and lower part of propodeum reticulate-rugulose, with scattered large punctures. Propodeal declivity transversely rugulose. Third abdominal tergite densely and finely reticulate-punctate. Standing short hairs few; pubescence quite abundant on dorsum of head and rest of body. Color black to dark brown; base of appendages brown, their apices and tip of gaster lighter in color.

Discussion. *Leptogenys arcirostris* is closely related to *L. borivava* and *L. alatapia* but in *L. borivava*, the body size is smaller (HW: 0.97–1.01, WL: 1.77–1.87), and the dorsum of the head, mesosoma, petiole, and gaster is with reduced pubescence and covered with long standing erect and suberect hairs. The head is much broader (CI: 105–109) in *L. alatapia*.

Distribution and biology. Recent surveys of ants across Madagascar have found this species only in the southern part of the island. It ranges from the montane rainforests of Atsirakambiaty near Itremo and Anja Reserve to the gallery forests of the PN Isalo and Mitea Forest, through the spiny forests/thickets of the PN Tsimanampetsotsa and the dry forest habitats of Vohidava near Amboasary. However, the type locality of *L. arcirostris* is Moramanga, in central-eastern Madagascar. *Leptogenys arcirostris* can survive in a wide range of habitats and may have had a larger geographic range, extending to Moramanga, in the recent past. Anthropogenic disturbance and deforestation may have caused local extinction in the northern part of its range.

Worker specimens of *L. arcirostris* look for prey on the surface of the forest floor and in leaf litter, and their colonies are mostly found in rotten logs and under rocks.

Additional material examined. Province Fianarantsoa: F d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 1550 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Isalo, 9.1 km 354° N Ranohira, 725 m, gallery forest (Fisher, Griswold *et al.*) (CASC); Anja Reserve, 990 m, degraded forest below granite out crop (B.L. Fisher *et al.*) (CASC); Province Toliara: RP Berenty, F de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, 35 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); F de Mite, 20.7 km 29° WNW Tongobory, 75 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); PN Tsimanampetsotsa, F de Bemanateza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, 90 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); F Vohidava 89.2 km N Amboasary, 850 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); Ifaty, desert scrub forest (W.E. Steiner) (MCZC); Ifaty, 26 km N Tulear m., spiaggia (L. Bartolozzi, S. Tiati, C. Raharimina) (MCZC).

Leptogenys borivava Rakotonirina and Fisher, sp. n.

(Figures 13A, 15B, 161, 170)

Holotype worker: Madagascar, Toliara, PN Tsimanampetsotsa, Mitoho Cave, 6.4 km 77° ENE Efoetse, 17.4 km 170° S Beheloka, -24.0472, 43.7532, 40 m, spiny forest/thicket, 18–22 Mar 2002 (Fisher-Griswold Arthropod Team) collection code: BLF06227, specimen code: CASENT0430091 (CASC).

Paratypes: 5 workers, with same data as holotype but with the following specimen codes: CASENT0430092, CASENT0196377, CASENT0247216, CASENT0247217, CASENT0247218 (CASC, BMNH, MHNG, PBZT).

WORKER. Diagnosis. Clypeus with median carina; distance between anterior level of torulus and anteromedial clypeal margin less than maximum width of scape, head approximately longer than broad in full-face view; antennal scape relatively short; long, erect and suberect hairs with few pubescence present on dorsum of head, mesosoma and gaster.

Measurements (6 specimens). HW: 0.97–1.01, HL: 1.05–1.10, CI: 92–94, SL: 1.12–1.18, SI: 115–119, PW: 0.68–0.73, WL: 1.77–1.87, PNH: 0.63–0.65, PNL: 0.53–0.60, PNW: 0.58–0.64, DNI: 104–110, LNI: 109–117.

FIGURE 161. Leptogenys borivava holotype worker CASENT0430091. A: lateral view. B: head in full-face view. C: dorsal view.

Description. Head elongate with greatest width at bases of mandible; sides slightly convex and diverging anteriorly along their length; posterior margin fairly straight. Eye large and breaking outline of sides of head. Antennal scape relatively long (SI: 115–119). In full-face view, anterior clypeal margin broadly rounded, bordered with wide and white membrane; medial clypeal lobe narrow, its width measured from anterior level of torulus to anteromedian margin of clypeus roughly the same as the greatest width of scape; medial longitudinal carina present on clypeus. With head in full-face view and mandible in full closure, blades laid over each other, with internal surface of first blade placed against clypeus along its length and most of distal portion of the second against external surface of distal portion of the first. With mesosoma in dorsal view, metanotal groove cross-ribbed, very small segment may be present between groove and propodeum. In lateral view, propodeal lobe absent. Petiolar node slightly inclined anteriorly, with shorter anterior face and much longer posterior face, both faces sloped forward; dorsal surface broadly convex.
Mandible sculptures longitudinally striate for basal half and smooth and shining for distal half. Dorsum of head densely and finely punctate, punctures becoming sparser on posterior third of head; rugulation present in front of level of eyes. Dorsum of mesosoma and petiolar node densely and finely reticulate-rugose. Third abdominal tergite finely punctate, fourth with shallow, large punctures anteriorly and smooth posteriorly. Body dorsum covered with long standing hairs and little pubescence. Black to dark brown in color, with brown basal portion of appendages and light brown apices and tip of gaster.

Discussion. *Leptogenys borivava* can be separated from *L. alatapia* by its elongate head (CI: 92–94). It can be distinguished from *L. arcirostris* by the relatively long scape (SI: 115–119), the presence of numerous standing long hairs, and sparse pubescence on the dorsum of the body.

Distribution and biology. All specimens of *L. borivava* were collected from the spiny forest/thicket habitats on the Mahafaly Plateau and PN Tsimanampetsotsa in southwest Madagascar. They were found foraging on the ground and nest colonies were recorded from rotten logs.

Additional material examined. Province Toliara: Mahafaly Plateau, 6.2 km 74° ENE Itampolo, 80 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); PN Tsimanampetsotsa, Mitoho Cave, 6.4 km 77° ENE Efoetse, 17.4 km 170° S Beheloka, 40 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC) (MCZC); PN Tsimanampetsotsa, Sotto pietre calcarae alla base della falesia (L. Bartolozzi, S. Tiati, C. Raharimina) (MCZC).

Leptogenys diana Rakotonirina and Fisher, sp. n.

(Figures 12A, 162, 171)

Holotype worker: Madagascar, Antsiranana, RS Ambre, Sakaramy, -12.4423, 49.2288, 402 m, tropical dry forest, ex rotten log, 15 May 2011 (B.L. Fisher *et al.*) collection code: BLF27337, CASENT0261104 (CASC).

Paratype worker: with same data as holotype but specimen coded: CASENT0261074 (CASC).

WORKER. Diagnosis. Clypeus broadly rounded, without projecting anteromedian lobe; median clypeal carina lacking; lateral portion joins anterior margin of clypeus in a convex line. In profile, mandible strongly bent downward; in full-face view, blades clearly broadened and flattened at about mid-length, with longitudinal and fine striation; inner margin evenly curved from distal half to apical sharp tooth; in profile, third abdominal segment microreticulate (coriaceous) with scattered punctures; dorsum of mesosoma, petiolar node, and gaster without pubescence.

Measurements (5 specimens). HW: 1.66–1.77, HL: 1.81–1.89, CI: 91–43, SL: 1.79–1.85, SI: 105–109, PW: 1.13–1.20, WL: 2.89–3.15, PNH: 0.96–1.05, PNL: 0.87–0.95, PNW: 0.87–0.91, DNI: 95–100, LNI: 108–117.

Description. Head subquadrate, not diverging anteriorly; sides nearly straight; posterior margin slightly concave. Eye large, occupying one-third to one-fourth the length of lateral cephalic margin and extending beyond line of sides of head. Antennal scape relatively short, roughly one-fifth of its length surpassing posterior cephalic margin. In profile, mandible strongly bent downward; in full-face view blade increasing in width at distal half, then gradually, narrowly arched toward apex; small preapical tooth may be present. Anterior clypeal margin meets lateral portions in rounded angle, anterior lamella limited to anteromedian portion, not broadly covering the clypeus; medial longitudinal carina absent. Antennal scape relatively short, roughly one-fifth of apical portion surpassing posterior cephalic margin. With mesosoma in dorsal view, metanotal groove cross-ribbed; in lateral view, posterolateral border of propodeum smooth, without toothlike lobe.

Outer surface of mandible from distal half to apex densely and finely striate, softcuticleand golden in color. Dorsum of head, mesosoma and petiolar node densely reticulate-punctulate. Third abdominal tergite generally microreticulate or coriaceous, with scattered punctures. Dorsum of mesosoma, petiolar node, and gaster covered with erect hairs; pubescence absent. Color black, with brown to light brown apical portion of appendages and tip of gaster.

Discussion. This species can be confused with *L. truncatirostris*, but the latter is characterized by a broad anterior margin of the clypeus with angulate lateral margins; the abundant pubescence on the dorsum of the mesosoma, petiolar node and gaster; and dense reticulate punctures on the third abdominal segment.



FIGURE 162. Leptogenys diana holotype worker CASENT0261104. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. *Leptogenys diana* is restricted to the dry forest of the Montagne des Français and RS Ambre near the northern tip of the island, in two disjunct populations. It has been found foraging on the ground and nesting under rocks and in rotten logs. Though its hunting habits are not known, the shape of the mandible with the strange, soft striate outer surface, and the limited anterior clypeal lamella, no doubt have interesting behavioral implications.

Additional material examined. Province Antsiranana: RS Ambre, Sakaramy, 402 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); Montagne des Français, 7.2 km 142° SE Antsiranana (=Diego-Suarez), 180 m, tropical dry forest (J.C. Rakotonirina) (CASC).

Leptogenys fotsivava Rakotonirina and Fisher, sp. n.

(Figures 13B, 17A, 163, 172)

Holotype worker: Madagascar, Toliara, Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, -20.045, 44.6622, 100 m, tropical dry forest, ground nest, 28 Nov–3 Dec 2001 (Fisher-Griswold Arthropod Team) collection code: BLF04671, specimen code: CASENT0001423 (CASC).



FIGURE 163. Leptogenys fotsivava holotype worker CASENT0001423. A: lateral view. B: head in full-face view. C: dorsal view.

Paratypes: series of 6 workers with the same data as holotype but with the following specimen codes: CASENT0001421, CASENT00011422, CASENT0247211, CASENT0247212, CASENT0247213, CASENT0247214 (CASC, BMNH, MHNG, MCZC, PBZT).

WORKER. Diagnosis. Clypeus with median carina, distance between anterior level of torulus and anteromedial clypeal margin greater than maximum width of scape; antennal scape relatively short; eye medium, maximum diameter between one-third and one-fourth the length of side of head; breaking outline of side of head; dorsum of mesosoma, petiolar node and gaster with few short suberect hairs and dense pubescence.

Measurements (8 specimens). HW: 0.98–1.17, HL: 1.18–1.33, CI: 82–90, SL: 1.15–1.39, SI: 112–119, PW: 0.72–0.84, WL: 1.91–2.15, PNH: 0.66–0.73, PNL: 0.53–0.57, PNW: 0.56–0.65, DNI: 106–115, LNI: 124–137.

Description. Head longer than broad in full-face view, width weakly increasing from behind to front, sides generally straight anteriorly from posterior level of eyes and rounding into a more or less straight posterior margin. Eye medium, maximum diameter between one-third and one-fourth the length of side of head; small girth slightly breaking outline of sides of head. Antennal scape relatively short, about one-fourth of the length extending beyond posterior cephalic border. Median clypeal carina present; anteromedial clypeal margin rounded and covered with semi-translucent membranous spot. In full-face view, median lobe of clypeus relatively long, distance measured from anterior level of torulus to anteromedian clypeal margin greater than maximum diameter of scape. In full-face view, if mandible tightly closed against clypeus, basal two-thirds of blades touching anterior margin of clypeus while their apical third portions overlapping each other and extending downward in front of clypeus. With mesosoma in dorsal view, metanotal groove impressed, with faint cross-ribs. In lateral view, propodeal lobe absent. With petiole in dorsal view, node roughly as broad as long.

Mandible longitudinally striate nearly to midlength; remaining portion smooth and shining apart from sparse punctures. Dorsum of head, mesosoma and petiolar node densely and finely reticulate-rugose to densely and finely reticulate-punctate. Third abdominal tergite densely and finely reticulate-punctate dorsally and mostly finely punctate laterally; fourth generally finely punctate. Pubescence numerous on entire dorsum of body, with sparse, suberect, short hairs. Color black to dark brown, with reddish-brown basal portion of appendages and light brown apices.

Distribution and biology. *Leptogenys fotsivava* is distributed in natural dry forest habitats, gallery forests, and *Uapaca* woodlands in southern Madagascar, but also occurs in anthropogenic habitats. It has been found foraging on the surface of the ground and through leaf litter. Colony nests are known to be in soil layers and under rocks. Raiding behavior has been observed in the PN Isalo along a portion of the Sahanafa River.

Additional material examined. Province Fianarantsoa: F d'Analalava, 29.6 km 280° W Ranohira, 700 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Isalo, Sahanafa River, 29.2 km 351° N Ranohira, 500 m, gallery forest (Fisher, Griswold *et al.*) (CASC); PN Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, 990 m, *Uapaca* woodland (Fisher, Griswold *et al.*) (CASC); PN Isalo, 28 km NNW Ranohira, 490 m, gallery forest (G.D. Alpert) (MCZC); Province Toliara: F de Kirindy, 15.5 km 64° ENE Marofandilia, 100 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); Malaimbandy, 180 m, urban/garden (B.L. Fisher *et al.*) (CASC); Kirindy forest, 48 km ENE Morondava, 100 m, tropical dry forest (Alpert *et al.*) (MCZC).

Leptogenys namoroka Rakotonirina and Fisher, sp. n.

(Figures 16B, 18A, 164, 173)

Holotype worker: Madagascar: Mahajanga, PN Namoroka, 16.9 km 317° NW Vilanandro, -16.4067, 45.31, 100 m, tropical dry forest, sifted litter, 12–16 Nov 2002 (Fisher-Griswold, Arthropod Team) collection code BLF06582, specimen code: CASENT0034713 (CASC).

WORKER. Diagnosis. Clypeus with median carina; distance between anterior level of torulus and anteromedial clypeal margin greater than maximum width of scape, antennal scape relatively short; eye small, maximum diameter roughly one-fifth the length of side of head; not extending beyond lateral cephalic border when head in full-face view; petiolar node approximately as broad as long (DNI: 115) in dorsal view; dorsum of mesosoma, petiolar node and gaster with few, short, suberect hairs and dense pubescence; dense and fine sculptures; larger species (HW: 1.38, HL: 1.58, WL: 2.47).

Measurements (1 specimen). HW: 1.38, HL: 1.56, CI: 88, SL: 1.66, SI: 120, PW: 0.95, WL: 2.47, PNH: 0.86, PNL: 0.70, PNW: 0.81, DNI: 115, LNI: 122.

Description. Head elongate and larger in front than behind; sides deviating outward anteriorly and rounding to medially slightly concave posterior border. Eye small; in full-face view, eye not extending beyond line of lateral

cephalic border. Antennal scape relatively short, surpassing posterior margin of head by one third of its length. Clypeus broadly rounded anteriorly, bordered with white-yellowish lamella; in full-face view, median lobe of clypeus elongate, width taken from anterior level of torulus to anteromedial clypeal margin greater than maximum diameter of scape. Mandible when fully closed, basal two-thirds of blades placed tightly against anterior margin of clypeus, rest of apical portion overlapping each other and projecting further in front of clypeus. With mesosoma in dorsal view, metanotal groove impressed and transversely striate; in lateral view, propodeal lobe lacking. In dorsal view, petiolar node roughly as broad as long.







FIGURE 164. Leptogenys namoroka holotype worker CASENT0072075. A: lateral view. B: head in full-face view. C: dorsal view.

Mandible longitudinally striate, with sparse punctures. Dorsum of head, mesosoma and petiolar node densely and finely reticulate-rugose to densely and finely reticulate punctate. Propodeal declivity transversely rugose. Third abdominal tergite densely and finely reticulate-punctate; fourth densely and finely punctate. Pubescence abundant on entire dorsum of body, with sparse, suberect, short hairs. Color blackish dark brown, appendages dark brown at base and brown at tarsal segments and apex of gaster.

Discussion. *Leptogenys namoroka* is very similar to *L. tsingy* in that they have small eyes, which do not break the lateral border of the head in full-face view, but *L. tsingy* is smaller in size (WL: 2.17–2.39), has broader petiolar node (DNI: 134–146) and is covered with abundant short suberect hairs and sparse pubescence on the dorsum of the mesosoma, petiolar node and the gaster.

Distribution and biology. This species is known only from one specimen collected from the dry forest habitat of the PN Tsingy de Bemaraha in western Madagascar. It was found foraging in leaf litter.

Leptogenys ridens Forel

(Figures 10A, 16A, 165, 174)

Leptogenys ridens Forel, 1910: 16. Holotype worker, Madagascar, Fort Dauphin SG (Sikora) (MHNG) AntWeb specimen code: CASENT0101884 [examined]. [Combination in *Leptogenys (Machaerogenys)*: Emery, 1911: 100; Wheeler, 1922b:1011; in *Leptogenys*: Bolton, 1975: 295, 1995: 233].

WORKER. Diagnosis. Clypeus with median carina, long median lobe, distance between anterior level of torulus and anteromedial clypeal margin greater than maximum width of scape; antennal scape relatively long, more than one third of its length surpassing posterior cephalic margin; eye larger, maximum diameter twice as large as maximum width of antennal scape.

Measurements (8 specimens). HW: 1.29–1.59, HL: 1.50–1.76, CI: 86–92, SL: 1.67–1.99, SI: 122–129, PW: 0.92–1.11, WL: 2.49–2.92, PNH: 0.84–1.01, PNL: 0.67–0.81, PNW: 0.75–0.91, DNI: 106–117, LNI: 115–128.

Description. Head elongate and distinctly broadened anteriorly; sides noticeably diverging in front of eyes and curving into roughly straight posterior border. Eye large, maximum diameter twice as large as widest portion of antennal scape, or about one-third of length of lateral cephalic margin; eye girth not cutting lateral outline of head in full-face view. Scape relatively long (SI: 122–129), more than one third of the length surpassing posterior cephalic margin. Clypeus with medial longitudinal carina; broadly rounded anterior margin trimmed by white-yellowish membrane; median lobe relatively elongate, length between anterior level of antennal insertion and anteromedial clypeal margin greater than maximum diameter of scape when head in full-face view. In full-face view, apical third of mandible not following shape of anterior clypeal margin. With mesosoma in dorsal view, metanotal groove impressed and cross-ribbed; in profile propodeal lobe indistinct. Petiole nodiform in lateral view, convex dorsal border broadly rounding to vertical anterior margin and joining the slightly medially convex posterior margin in a convex line.

Mandible longitudianally striate, interspersed with piligerous punctures. Dorsum of head densely and finely reticulate-punctate. Mesosoma finely reticulate-rugose to densely and finely punctate. Dorsum of petiolar node and third abdominal tergite finely punctate; sparse punctures present on their sides. Suberect hairs short, pubescence abundant. Black in color, with reddish-brown apices of appendages and apex of gaster.

Discussion. *Leptogenys ridens* is larger in size and has a relatively longer antennal scape (SI: 122–129) and larger eyes when compared to very similar species such as *L. fotsivava, L. namoroka* and *L. tsingy*. In the latter three species, the maximum diameter of the eye is less than twice the maximum scape width, and the scape is relatively shorter (SI: 111–120).

Distribution and biology. *Leptogenys ridens* is restricted to the south of Madagascar. It occurs from the tropical dry forests in the southwest, through the spiny forest/thicket of Mahafaly Plateau and the extreme south, and to the gallery forest of RP Berenty in the southeast. Workers forage on the forest floor and colony nests are mainly in rotten logs.

Additional material examined. Province Toliara: [Fort Dauphin S.G. Madagascar] (MHNG); RS Beza Mahafaly, Parcel 1, 130 m, tropical dry forest (P.S. Ward) (PSWC) (MCZC); RS Beza Mahafaly, P.#1, 160 m, tropical dry forest (E. Rajeriarison) (MCZC); RP Berenty, F de Bealoka, Mandraré River, 14.6 km 329° NNW

Amboasary, 35 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); RP Berenty, F d'Anjapolo, 21.4 km 325° NW Amboasary, 65 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); 12.7 km 287° W Marovato, 130 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); Mahafaly Plateau, 6.2 km 74° ENE Itampolo, 80 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); F de Tsinjoriaky, 6.2 km 84° E Tsifota, 70 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); F de Beroboka, 5.9 km 131° SE Ankidranoka, 80 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); PN Tsimanampetsotsa, F de Bernanteza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, 90 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); PN Tsimanampetsotsa, F de Bernanteza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, 90 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); PN Tsimanampetsotsa, F de Bernanteza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, 90 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); PN Tsimanampetsotsa, F de Bernanteza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, 90 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC).



FIGURE 165. Leptogenys ridens worker CASENT0002200. A: lateral view. B: head in full-face view. C: dorsal view.

Leptogenys truncatirostris Forel

(Figures 11A, 12B, 166, 175)

Leptogenys truncatirostris Forel; 1897: 195. Lectotype worker, Madagascar, Nosy-be (Voeltzkow) present designation, AntWeb specimen code: CASENT0101940 (MHNG) [examined]. Paralectotypes: series of 6 workers same data but specimen coded as: CASENT0101914, CASENT0101714, CASENT0101975, CASENT0101727, CASENT0101626 (MHNG) [examined]. [Description of males from Anjouan and Grand Comores of The Comoros Islands: Forel, 1907: 76. Combination in *Leptogenys (Machaerogenys)*: Emery, 1911: 101; Wheeler, 1922b: 1011; in *Leptogenys*: Bolton, 1975: 295].



FIGURE 166. Leptogenys truncatirostris worker CASENT0163581. A: lateral view. B: head in full-face view. C: dorsal view.

WORKER. Diagnosis. Clypeus wide and transverse, without projecting anteromedian lobe; median clypeal carina lacking; lateral portion meets the anterior margin of clypeus in a blunt angle. In profile, mandible curved dorsally with midpoint markedly dorsal of mandible insertion; distal half of blade slightly broader and flattened, the surface

with effaced fine striation; in profile, third abdominal segment densely and finely punctate, dorsum of mesosoma, petiolar node, and gaster with numerous pubescences.

Measurements (15 specimens). HW: 1.55–1.79, HL: 1.67–1.89, CI: 93–101, SL: 1.65–1.94, SI: 103–110, PW: 1.00–1.16, WL: 2.67–3.10, PNH: 0.88–1.03, PNL: 0.75–0.94, PNW: 0.72–0.89, DNI: 84–106, LNI: 106–119.

Description. Head broadest anterior to eyes; sides slightly diverging anteriorly throughout its length; posterior margin weakly concave. Eye large, size between one-third and one-fourth the length of side of head; not breaking outline of lateral cephalic margin in full-face view. Mandible elongate; in profile, mandible strongly bent downward; in full-face view, blade widest near distal half, then progressively decreasing in breadth through apical tooth; preapical tooth may be present. Clypeus widely transverse anteriorly, junction of lateral section with anterior margin visibly angulate; anterior margin bordered by wide and thick yellowish membrane; median carina absent. Antennal scape fairly short, extending beyond posterior border of head by roughly one-fourth its length. With mesosoma in dorsal view, metanotal groove with transverse stration; in profile, propodeal lobe a blunt angle or absent.

Dorsum of head reticulate-punctulate to reticulate rugulose. Apical half of mandible densely and finely striate and with reddish-orange surface. In dorsal view, mesosoma and petiolar node densely and finely reticulaterugulose, interspersed with small punctures; propodeal declivity transversely striate. In profile, third abdominal tergite variably sculptured, either densely punctulate or microreticulate with scattered punctulae. Standing hairs and abundant pubescence present on mesosoma, petiolar node, and gaster. Body color black to dark brown; appendages brown at the base and becoming lighter toward the apex.

Variation. *Leptogenys truncatirostris* shows considerable geographic variation. Two different forms have been recorded together in the RS Bemarivo. The form that most closely matches the holotype has the mandible with a slender median portion. The other form possesses mandibles that are much more robust and have a broadened median portion. Specimens collected from another site, RP Berenty, have a more rounded anterior clypeal margin.

Discussion. *Leptogenys truncatirostris* is very similar to *L. diana* but the latter can be distinguished by the broadly rounded anterior clypeal margin, the absence of pubescence on the dorsum of the body, and the presence of microreticulation with sparse punctures on the third abdominal tergite. Also, the basal third of the mandible is more robust and the distal half is broader and finely striate.

Distribution and biology. As one of the most common species within the *truncatirostris* group, *L. truncatirostris* is widespread in western Madagascar, occurring from dry forest on Tsingy, gallery forest, littoral forests in the north to south-west as well as spiny bush and thicket habitats in the extreme south of the island. This species also can be discovered in anthropogenic habitats such as disturbed forests and roadsides. Foraging behavior for this species is carried out mostly on the forest floor and rarely above ground on low vegetation. In the RP Berenty, workers of *L. truncatirostris* were found carrying larvae and cocoons and exhibiting tandem running during a nest relocation. This species generally nests in rotten logs, rotting bamboo, in soil layers, under rocks and under dead wood.

Additional material examined. MADAGASCAR: Province Antsiranana: [Nosi bé] (Voeltzkow) (MSNG), [Nosi bé] (F. Santschi) (NHMB); RNI Lokobe, 6.3 km ESE Nosy be Hellville, 191 m, tropical dry forest (J.C. Rakotonirina) (CASC); Nosy be, 5 m, roadside (B.L. Fisher et al.) (CASC); Nosy be, 5 m, roadside (B.L. Fisher et al.) (CASC); Nosy Faly, Tafiambotry, 35.3 km N Ambanja, 7 m, littoral rainforest (B.L. Fisher et al.) (CASC); F d'Anabohazo, 21.6 km 247° WSW Maromandia, 120 m, tropical dry forest (J.C. Rakotonirina) (CASC); Nosy Faly, 40m, open secondary vegetation (B.L. Fisher et al.) (CASC); Nosy Faly, 15 m & 40 m, open secondary vegetation (B.L. Fisher et al.) (CASC); Coco Beach Hotel Ambatoloaka, Nosy Be (G.D. Alpert) (MCZC); Province Mahajanga: PN Namoroka, 16.9 km 317° NW Vilanandro, 100 m, tropical dry forest (Fisher, Griswold et al.) (CASC); PN Baie de Baly, 12.4 km 337° NNW Soalala, 10 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Mahavavy River, 6.2 km 145° SE Mitsinjo, 20 m, gallery forest (Fisher, Griswold et al.) (CASC); Mahavavy River, 10.6 km 148° SSE Mitsinjo, 50 m, tropical dry forest (Fisher, Griswold et al.) (CASC); F Ambohimanga, 26.1 km 314° Mampikony, 250 m, tropical dry forest (B.L. Fisher) (CASC); PN Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 150 m, tropical dry forest on Tsingy (Fisher-Griswold Arthropod Team) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, 30 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Manerinerina, 76.6 km N Antsohihy, 247 m, disturbed forest (B.L. Fisher et al.) (CASC); PN Ankarafantsika, Ampijoroa SF, 5.4 km 331° NW Andranofasika, 70 m, tropical dry forest (Fisher, Griswold et al.) (CASC); Ankarafantsika, 5 km SSW Ampijoroa, 160 m, tropical dry forest (Goodman leg.) (CASC); PN Ankarafantsika, Ampijoroa SF, 40 km 306° NW Andranofasika, 130 m, tropical dry forest (Fisher, Griswold et al.) (CASC); PN Ankarafantsika, Forêt de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, 135 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); F de Tsimembo, 8.7 km 336° NNW Soatana, 20 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); Province **Toliara:** Fort-Dauphin (Sikora) (Gift by C. Emery, 1925) (MSNG); Beza-Mahafaly, 27 km E Betioky, 135 m, tropical dry forest (B.L.Fisher) (CASC); RP Berenty, F de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, 35 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); RP Berenty, F de Malaza, Mandraré River, 8.6 km 314° NW Amboasary, 40 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); RP Berenty, 25 m, tropical dry forest (P.S. Ward) (MCZC); Berenty, 12 km N.W. Amboasary, B.M. 1983–201 (J.S. Noyes, M.C. Day) (BMNH); F de Mite, 20.7 km 29° WNW Tongobory, 75 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); F de Kirindy, 15.5 km 64° ENE Marofandilia, 100 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); F de Mahavelo, Isantoria River, 5.5 km 37° NE Ifotaka, 115 m, spiny forest/thicket (Fisher-Griswold Arthropod Team) (CASC); Makay Montane, 525–510 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Montane, 500 m, gallery forest with bamboo (B.L. Fisher *et al.*) (CASC).

Leptogenys tsingy Rakotonirina and Fisher, sp. n.

(Figures 17B, 18A, 167, 175)

Holotype worker: Madagascar, Mahajanga, PN Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, -18.7094, 447182, 150 m, tropical dry forest on Tsingy, ex rotten log, 16–20 Nov 2001 (Fisher-Griswold Arthropod Team) collection code: BLF06538, specimen code: CASENT0493181 (CASC).

Paratypes: 3 workers with the same data as holotype but specimen coded as CASENT0196369, CASENT0493182, CASENT0247215 (CASC, BMNH).

WORKER. Diagnosis. Clypeus with median carina, distance between anterior level of torulus and anteromedial clypeal margin greater than maximum width of scape; antennal scape relatively short; eye small, maximum diameter roughly one-fifth the length of sides of head, not extending beyond lateral cephalic border when head in full-face view; node broader than long (DNI: 134–146); dorsum of mesosoma, petiolar node and gaster with few short suberect hairs and dense pubescence; dense and fine sculpture; smaller species (HW: 1.20–1.34, HL: 1.42–1.56, WL: 2.17–2.39).

Measurements (6 specimens). HW: 1.20–1.34, HL: 1.42–1.50, CI: 85–89, SL: 1.33–1.53, SI: 111–115, PW: 0.88–0.96, WL: 2.17–2.39, PNH: 0.82–0.90, PNL: 0.55–0.64, PNW: 0.78–0.86, DNI: 134–146, LNI: 134–150.

Description. In full-face view, head roughly subquadrate, but slightly wider in front of level of eyes; sides meeting more or less concave posterior margin in a convex line. In full-face view, maximum eye diameter about one-fifth the length of lateral cephalic margin; eye location not interrupting lateral border of head in full-face view. Antennal scape relatively short, only one-fourth of distal portion reaching posterior cephalic border. In full-face view, anteromedial clypeal margin bordered by whitish lamella; length of median lobe of clypeus measured from anterior level of antennal insertion to anteromedial clypeal margin roughly greater than maximum width of scape. With head in full-face view and mandible fully closed, basal two-thirds of blades tightly closed against anterior margin of clypeus while distal thirds cross each other and apparently project downward in front of anteromedial clypeal margin. With mesosoma in dorsal view, metanotal groove distinct, marked by few transverse striae. In lateral view, posterolateral margin of propodeum without visible lobe. Petiolar node wider than long in dorsal view, with posterior margin straight and lateral margin broadly rounding to convex anterior margin.

Mandible longitudinally striate, superimposed with scattered small punctures. Propodeal declivity with transverse rugulae. Body generally covered by coarse rugae with higher ridge, dorsum of head, mesosoma and petiolar node reticulate-rugulose interspersed by scattered foveoles or large punctures. Third and fourth abdominal tergites reticulate-rugulose but with denser and more elongate punctures. Dorsum of body covered by short and numerous standing hairs and sparse pubescence. Integument black to dark brown and appendages generally brown, tip of gaster and apical portion of appendages lighter in color.

Discussion. *Leptogenys tsingy* is very similar to *L. namoroka*, but the former has the petiolar node broader than long in dorsal view (DNI: 134–146), body sculpture much coarser, and more suberect hairs and sparse pubescence, whereas the latter has a much longer petiolar node (DNI: 115), finer body sculpture, fewer short, suberect hairs and abundant pubescence. Both species belong to the *ridens* species complex, together with *L. ridens* and *L. fotsivava*. As a consequence, *L. tsingy* can be confused with *L. ridens* and *L. fotsivava*, but *L. ridens* is characterized by a

longer antennal scape and larger eyes and *L. fotsivava* has much larger eyes that break the outline of the sides of the head.

Distribution and biology. The distribution of *L. tsingy* is limited to the dry forest habitats on Tsingy in the PN Tsingy de Bemaraha and PN Namoroka between 100 m and 150 m. The species nests in rotten logs and dead branches above the ground, and forages in leaf litter.

Additional material examined. Province Mahajanga: PN Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 150 m, tropical dry forest on Tsingy (Fisher-Griswold Arthropod Team) (CASC); PN Namoroka, 17.8 km 329° WNW Vilanandro, 100 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC).



FIGURE 167. Leptogenys tsingy holotype worker CASENT0493181. A: lateral view. B: head in full-face view. C: dorsal view.



FIGURES 168–173. Distribution maps of the Leptogenys truncatirostris group in Madagascar.



FIGURES 174-176. Distribution maps of the Leptogenys truncatirostris group in Madagascar.

Uncertain species group

Leptogenys mayotte Rakotonirina and Fisher, sp. n.

(Figures 32A, 33B, 128, 177)

Holotype worker: Mayotte, Mont Chongui, -12.959, 45.1341, 380 m, rainforest, ex rotten log, 28 Nov 2007 (B.L. Fisher *et al.*) collection code: BLF18914, specimen code: CASENT0134302 (CASC).

Paratypes: 3 workers with same data as holotype but specimen coded as: CASENT0134301, CASENT0134303, CASENT0132571 (CASC, BMNH).

WORKER. Diagnosis. Mandible subtriangular and tightly closing against margin of broadly triangular clypeus; eye located slightly toward frontal portion of head and not breaking outline of lateral cephalic border; dorsum of head reticulate-punctulate, promesonotal dorsum transversely striate, superimposed with sparse, small punctures.

Measurements (6 specimens). HW: 1.80–1.96, HL: 2.23–2.32, CI: 80–84, SL: 1.98–2.08, SI: 104–113, PW: 1.15–1.24, WL: 3.05–3.17, PNH: 0.88–0.95, PNL: 0.80–0.88, PNW: 0.76–0.80, DNI: 91–97, LNI: 108–111.

Description. Head narrowing from posterior of eyes to base of mandible; sides evenly rounding to posterior cephalic margin. Eye not breaking outline of side of head. Antennal scape relatively short (SI: 104–113). Clypeus with large, triangular anteromedian lobe bordered by semi-translucent yellow-orange membrane; median clypeal carina long and sharp. Mandible elongate, inner margin with blunt basal angle at midlength and outer margin slightly concave; blades tightly closing against clypeal margin; basal groove broadly impressed; preapical tooth present near sharp apical tooth. Hypostomal teeth not visible when head in full-face view. Metanotal groove impressed; with mesosoma in lateral view, propodeum high and short, posterolateral border without toothlike lobe; dorsal margin rounding to declivitous face. In profile, petiolar node approximately as high as broad; anterior face forming convex line with dorsal margin which in turn ends at a distinct angle to anteriorly inclined posterior face. Constriction between third and fourth abdominal segments feebly distinct.



FIGURE 177. Leptogenys mayotte holotype worker CASENT0134302. A: lateral view. B: head in full-face view. C: dorsal view.

Mandible finely longitudinally striate, with small piligerous punctures. Dorsum of head finely rugulose anterior to level of eyes and toward center of head capsule, sculpture becoming densely and finely reticulatepunctulate posteriorly. Promesonotum finely transversely striate or rugulose, interspersed with scattered small punctures; propodeal dorsum with dense and fine transverse striae or rugae; declivitous surface transversely striate. Third and fourth abdominal tergites mostly smooth and shining apart from piligerous small pits. Erect hairs long on promesonotum, petiolar node and gaster, but suberect and short on propodeum; pubescence sparse or absent on dorsum of body. Black to dark brown species, apices of appendages and tip of gaster lighter in color.

Discussion. Leptogenys mayotte is one of the largest species in the ponerine ant genus Leptogenys and can be separated from L. oswaldi of the *incisa* group by the combination of the following two characters: the eyes not breaking the outline of the sides of the head, and the presence of dense and fine transverse striation or rugulae on

the pronotal dorsum. *Leptogenys mayotte* and *L. oswaldi* are easily distinguished from the remainder of the *incisa* group by the form of the mandibles, which are elongate, with convex inner margins, and capable of closing tightly against the triangular clypeus.

Distribution and biology. *Leptogenys mayotte* occurs only in the rainforest habitats of Mayotte Island. Nest series have been found only in rotten logs.

Additional material examined. THE COMOROS: Mayotte Island: Coconi, DAF Campus, 12°49'60.0"S 45°07'60.0"E (R. Jocqué) (CASC); Mont Chongui, 12°57'32.5"S 45°08'2.8"E, 380 m, rainforest (B.L. Fisher *et al.*) (CASC).

Leptogenys rabebe Rakotonirina and Fisher, sp. n.

(Figures 40A, 129, 178)

Holotype worker: Madagascar, Toamasina, RS Ambatovaky, Sandrangato river, -16.8175, 49.295, 360 m, rainforest, ex rotten log, 25 Feb 2010 (B.L. Fisher *et al.*) collection code: BLF24761, specimen code: CASENT0163120 (CASC).

WORKER. Diagnosis. Mandible not closing tightly against clypeus at rest; eye small with maximum diameter less than greatest width of antennal scape; antennal scape short, extending beyond posterior cephalic margin by one-fifth of its apical portion.

Measurements (3 specimens). HW: 0.95–1.00, HL: 1.22–1.24, CI: 77–82, SL: 1.03–1.10, SI: 102–115, PW: 0.79–0.80, WL: 1.79–1.82, PNH: 0.72–0.73, PNL: 0.48–0.54, PNW: 0.64–0.69, DNI: 119–143, LNI: 134–152.

Description. Head longer than broad, widest at level of eyes, with slightly convex lateral border. Eye small, maximum diameter about half of greatest width of scape. Antennal scape relatively short, only about one-fifth of its length surpassing posterior cephalic margin. Anterior clypeal margin with narrow triangular median lobe, bordered with thin, semi-translucent lamella; lateral portion narrow and bordered by broad lamellate membrane; three peg-like setae projecting anteriorly from anterior margin of median lobe. Mandibles elongate and linear, not closing tightly against margin of clypeus when their apices cross one another; basal groove distinctly impressed. With mesosoma in dorsal view, metanotal groove impressed and transversely striate. In lateral view, petiolar node slightly higher than broad, with straight anterior and posterior faces and fairly convex dorsal margin. Subpetiolar process consisting of toothlike extension anteriorly followed by rounded lobe posteriorly, with indentation between them. In lateral view, helcium located approximately at mid-height of anterior margin of third abdominal segment; prora large and lobe-like; anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded. Prora and anteroventral angle of third abdominal sternite usually rounded.

Sculpture of head dorsum rugulose-punctate or reticulate punctate anteriorly, becoming punctate posteriorly. In dorsal view, pronotum and petiolar node mostly smooth and shining, with scattered superficial punctures; mesonotum, propodeum, and third and fourth abdominal tergites shallowly punctate. Mesopleuron and metapleuron densely and finely rugose. Color dark brown to reddish-orange with brown or lighter appendages.

Discussion. Leptogenys rabebe can be confused with species in the toeraniva group but is easily differentiated by the discontinuous lamellate membrane on the lateral and anteromedian lobes of the clypeus, leaving a gap between the sides of the anteromedian lobe of the clypeus and mandibles when the latter are fully closed. Its prora is located near the anteroventral angle of third abdominal sternite. In the toeraniva group, the mandibles are capable of closing tightly against the clypeus and there is usually a large indentation between the prora and the rounded anteroventral angle of third abdominal sternite. Leptogenys rabebe closely resembles the species in the incisa group but these latter species have larger eyeswhose maximum diameter is markedly greater than the maximum width of antennal scape and the mandible is more arched from the base to the apex.

Distribution and biology. This species is restricted to the northeast of Madagascar and has been collected from the transitional humid forest of Marotandrano near Mandritsara, the lowland rainforest of Ambatovaky, and the Montagne d'Akirindro of Makira. It nests in rotten logs and forages mainly in leaf litter.

Additional material examined. Province Mahajanga: RS Marotandrano, Marotandrano 48.3 km S Mandritsara, 865 m, transitional humid forest (B.L. Fisher *et al.*) (CASC); Province Toamasina: Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC).



FIGURE 178. Leptogenys rabebe holotype worker CASENT0163120. A: lateral view. B: head in full-face view. C: dorsal view.

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References

- Bingham, C. (1903) The Fauna of British India, including Ceylon and Burma. Hymenoptera 2. Ants and Cuckoo wasps. Taylor and Francis, London, 506 pp.
- Bolton, B. (1975) A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian region with a review of the Malagasy species. *Bulletin of British Museum of Natural History, Entomology*, 31, 235–305.
- Bolton, B. (1995) *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, Massachusetts, 512 pp.
- Bolton, B. (2000) The ant tribe Dacetini. Memoirs of the American Entomological Institute, 65, 1–1028.
- Bolton, B. (2007) Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute*, 35, 1–150.
- Brown, W.L. Jr. (1963) Characters and synonymies among the genera of ants, part 3. Some members of the tribe Ponerini. *Breviora*, 190, 1–10.
- Brown, W.L. Jr. (1973) A comparison of Hylean and Congo-West African rainforest ant faunas. *In*: Meggers, B.J., Ayensu, E.S.
 & Duckworth, W.D. (Eds.), *Tropical Forest Ecosystems in Africa and South America: a Comparative Review*. Smithsonian Institution Press, Washington, D.C., pp. 161–185.
- Colwell, R.K. (1996) *Biota. The biodiversity database manager.* Sinauer Associates, Sunderland, Massachusetts, 860 pp + application software.
- Dalla Torre, K.W. (1893) Catalogus Hymenopterorum Hucusque Descriptorum Systematicus et Synonymicus. Vol. 7. Formicidae (Heterogyna). W. Engelmann, Leipzig, 289 pp.
- Davies, S.J., Villet, M.H., Blomefield, T.M. & Crewe, R.M. (1994) Reproduction and division of labour in *Leptogenys schwabi* Forel (Hymenoptera Formicidae), a polygynous, queenless ponerine ant. *Ethology Ecology and Evolution*, 6, 507–517. http://dx.doi.org/10.1080/08927014.1994.9522975
- Dejean, M. & Evraerts, C. (1997) Predatory behavior in the genus *Leptogenys*: A comparative study. *Journal of Insect Behavior*, 2, 177–191.
- Donisthorpe, H.S.J.K. (1948) Microbolbus testaceus, a new genus and species of ponerine ant. The Entomologist, 81, 170-171.
- Dufour, L. (1864) Note sur une nouvelle espèce de fourmi. (Formica Vinsonnella). Annales de la Société Entomologique de France, 4, 210.
- Eberhard, W.G. (1986) Sexual selection and animal genitalia. Harvard University Press: Cambridge, Massachusetts, 244 pp.
- Emery, C. (1892) Sopra alcune formiche raccolte all'Ingegnere L. Bricchetti Robecchi nel paese dei Somali. Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova), 12, 110–122.
- Emery, C. (1894) Mission scientifique de M. Ch. Alluaud aux îles Séchelles (mars, avril, mai 1892). 2ème mémoire. Formicidés. *Annales de la Société Entomologique de France*, 63, 67–72.
- Emery, C. (1895a) Mission scientifique de M. Ch. Alluaud dans le territoire de Diego-Suarez (Madagascar-Nord). (Avril-août 1893). Annales de la Société Entomologique de Belgique, 39, 336–345.
- Emery, C. (1895b) Descriptions de quelques fourmis nouvelles d'Australie. *Annales de la Société Entomologique de Belgique*, 39, 345–358.
- Emery, C. (1895c) Voyage de M. E. Simon dans l'Afrique australe (janvier-avril 1893). 3ème mémoire. Formicidés. *Annales de la Société Entomologique de France*, 64, 15–56.
- Emery, C. (1899) Formiche di Madagascar raccolte dal Sig. A. Mocquerys nei pressi della Baia di Antongil (1897-1898). Bollettino della Societa Entomologica Italiana, 31, 263–290.
- Emery, C. (1911) Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. Genera Insectorum, 118, 1-125.
- Forel, A. (1891) Les Formicidés. [part]. *In*: Grandidier, A. (Ed.), *Histoire physique, naturelle, et politique de Madagascar. Vol. XX. Histoire naturelle des Hyménoptères. Deuxième partie (28e fascicule)*. Hachette et Cie, Paris, v + 237 pp.
- Forel, A. (1892) Nouvelles espèces de formicidés de Madagascar. (Récoltées par M. Sikora) Annales de la Société Entomologique de Belgique, 36, 516-535.
- Forel, A. (1895) A fauna das formigas do Brazil. Boletim do Museu Paraense de Historia Natural e Ethnographia, 1, 89–143.
- Forel, A. (1897) Ameisen aus Nossi-Bé, Majunga, Juan de Nova (Madagaskar), den Aldabra-Inseln und Sansibar. Gesammelt von Herrn Dr. A. Voeltzkow aus Berlin. Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft, 21, 185–208.
- Forel, A. (1901) Formiciden des Naturhistorischen Museums zu Hamburg. Neue Calyptomyrmex-, Dacryon-, Podomyrma-, und Echinopla-Arten. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, 18, 45–82.
- Forel, A. (1907) Ameisen von Madagaskar, den Comoren und Ostafrika. In Voeltzkow, A. (Ed.), Reise in Ostafrika in den

Jahren 1903–1905. Stuttgart, pp. 75–92.

Forel, A. (1910) Glanures myrmécologiques. Annales de la Société Entomologique de Belgique, 54, 6–32.

- Forel, A. (1912) The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A. Volume 4, No. 11. Fourmis des Seychelles et des Aldabras, reçues de M. Hugh Scott. Transactions of the Linnean Society of London, Zoology, 15, 159–167.
- Forel, A. (1915) Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia, 1910-1913. 2. Ameisen. Arkiv för Zoologi, 9 (16), 1–119.
- Heterick, B. (2006) A revision of the Malagasy ants belonging to genus *Monomorium* Mayr, 1855 (Hymenoptera: Formicidae). Proceedings of the California Academy of Sciences, 57, 69–202.
- Hijmans, R.J., Guarino, L. & Mathur, P. (2011) *DIVA-GIS, version 7.5*. A geographic information system for the analysis of species distribution data. Available from: http://www.diva-gis.org (accessed 24 April 2013)
- Hlaváč, P. & Janda, M. (2009) *Leptogenopapus mirabilis*, a new genus and species of Lomechusini (Coleoptera: Staphylinidae, Aleocharinae) from Papua New Guinea associated with ants of the genus *Leptogenys* Roger. *Zootaxa*, 2062, 57–64.
- Ito, F. (1996) Colony composition and morphological caste differentiation between ergatoid queens and workers in the ponerine ant genus *Leptogenys* in the Oriental tropics. *Ethology Ecology and Evolution*, 9, 335–343. http://dx.doi.org/10.1080/08927014.1997.9522876
- LaPolla, J.S., Hawkes, P.G. & Fisher, B.L. (2011) Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World, Part I: *Nylanderia* in the Afrotropics. *Zootaxa*, 3110, 10–36.
- Lattke, J.E. (2011) Revision of the New World species of the genus *Leptogenys* Roger (Insecta: Hymenoptera: Formicidae: Ponerinae). *Arthropod Systematics and Phylogeny*, 69, 127–264.
- Maschwitz, U. & Schrnegge, P. (1983) Forage communication, nest moving recruitment, and prey specialization in the oriental ponerine *Leptogenys chinensis*. *Oecologia*, 57, 175–182. http://dx.doi.org/10.1007/bf00379578
- Maschwitz, U., Steghaus-Kovac, S., Gaube, R. & Hãnel, H. (1989) A South-east Asian ponerine ant of the genus *Leptogenys* (Hymenoptera: Formicidae) with army ant life habits. *Behavioral Ecology and Sociobiology*, 24, 305–316. http://dx.doi.org/10.1007/bf00290907
- Mayr, G. (1862) Myrmecologische Studien. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien, 12, 649-776.
- Mayr, G. (1893) Formiciden von Herrn Dr. Fr. Stuhlmann in Ost-Afrika gesammelt. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, 10, 193–201.
- Mayr, E. (1963) Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts, 797 pp.
- McGlynn, T.P. (1999) The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography*, 26, 535-48.
 - http://dx.doi.org/10.1046/j.1365-2699.1999.00310.x
- Peeters, C.P. & Crewe, R.M. (1985) Insemination controls the reproductive division of labour in a ponerine ant. *Naturwissenschaften*, 71, 50-51.
 - http://dx.doi.org/10.1007/bf00365989
- Peeters, C. & Ito, F. (2001) Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annual Review of Entomology*, 46, 601–630.
- Rakotonirina, J.C. & Fisher, B.L. (2013a) Revision of the *Pachycondyla wasmannii*-group (Hymenoptera: Formicidae) from the Malagasy region. *Zootaxa*, 3609, 101–141.

http://dx.doi.org/10.11646/zootaxa.3609.3.12

- Rakotonirina, J.C. & Fisher, B.L. (2013b) Revision of the *Pachycondyla sikorae* species-group (Hymenoptera: Formicidae) in Madagascar. *Zootaxa*, 3683, 447–485.
 - http://dx.doi.org/10.11646/zootaxa.3683.4.8
- Raxworthy, C.J. & Nussbaum, R.A. (1995) Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. *Journal of Zoology*, 235, 525–558. [Lond.] http://dx.doi.org/10.1111/j.1469-7998.1995.tb01767.x
- Roger, J. (1861) Die Ponera-artigen Ameisen (Schluss). Berliner Entmologische Zeitschrift, 5, 1–54.
- Roncin, E. & Deharveng, L. (2003). Leptogenys khammouanensis sp. nov. (Hymenoptera: Formicidae). A possible troglobitic species of Laos, with a discussion on cave ants. Zoological science, 20, 919–24. http://dx.doi.org/10.2108/zsj.20.919
- Santschi, F. (1912) Fourmis d'Afrique et de Madagascar. Annales de la Société Entomologique de Belgique, 56, 150-167.
- Santschi, F. (1926) Trois notes myrmécologiques. Annales de la Société Entomologique de France, 95, 13-28.
- Schmidt, C. (2013) Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). Zootaxa, 3647, 201–250. http://dx.doi.org/10.11646/zootaxa.3647.2.1
- Smith, F. (1857) Catalogue of the hymenopterous insects collected at Sarawak, Borneo; mount Ophir, Malacca; and at Singapore by A. R. Wallace. *Journal of the Proceedings of the Linnean Society, Zoology*, 2, 42–130. http://dx.doi.org/10.1111/j.1096-3642.1857.tb01759.x
- Smith, F. (1858) Catalogue of the hymenopterous insects in the collection of the British Museum. Part VI. Formicidae, London, UK, 216 pp.
- Smith, F. (1871) A catalogue of the aculeate Hymenoptera and Ichneumonidae of India and the Eastern Archipelago.

Zoological Journal of the Linnean Society, 11, 285–415.

- Smith, F. (1879) Descriptions of new species of aculeate Hymenoptera collected by the Rev. Thos. Blackburn in the Sandwich Islands. Zoological Journal of the Linnean Society, 14, 674–685. http://dx.doi.org/10.1111/j.1096-3642.1879.tb02459.x
- Steghaus-Kovac, S. & Maschwitz, U. (1993) Predation on earwigs: a novel diet specialization within the genus *Leptogenys* (Formicidae: Ponerinae). *Insectes Sociaux*, 40, 337–340. http://dx.doi.org/10.1007/bf01242370
- Taylor, R. (1969) The identity of *Dorylozelus mjobergi* Forel (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society*, 8, 131–133.
- Taylor, R.W. & Brown, D.R. (1985) Hymenoptera: Formicoidea. *In: Zoological Catalogue of Australia. Vol. 2.* Australian Government publishing Service, Canberra, Australia, pp. 1–149.
- Taylor, R.W. (1988) The nomenclature and distribution of some Australian and New Caledonian ants of the genus Leptogenys Roger (=Prionogenys Emery, n. syn.) (Hymenoptera: Formicidae: Ponerinae). General and Applied Entomology, 20, 33–37.
- Vences, M. & Glaw, F. (2002) Molecular phylogeography of *Boophis tephraeomystax*: a test case for east-west vicariance in Malagasy anurans (Amphibia, Anura, Mantellidae). *Spixiana*, 25, 79–84.
- Vences, M., Wollenberg, K.C., Vieites, D.R. & Lees, D.C. (2009) Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, 24, 456–465.

http://dx.doi.org/10.1016/j.tree.2009.03.011

Villet, M.H. (1989) A syndrome leading to ergatoid queens in ponerine ants (Hymenoptera: Formicidae). *Journal of Natural History*, 23, 825–832.

http://dx.doi.org/10.1080/00222938900770431

- Ward, P.S. (2001) Taxonomy, phylogeny and biogeography of the ant genus *Tetraponera* (Hymenoptera: Formicidae) in the Oriental and Australian regions. *Invertebrate Taxonomy*, 2001, 15, 589–665.
- Weber, N.A. (1942) New doryline, cerapachyine and ponerine ants from the Imatong Mountains, Anglo-Egyptian Sudan. *Proceedings of the Entomological Society of Washington*, 44, 40–49.
- Wheeler, W.M. (1922a) A synonymic list of the ants of the Ethiopian region. *Bulletin of the American Museum of Natural History*, 45, 711–1004.
- Wheeler, W.M. (1922b) Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. IX. A synonymic list of the ants of the Malagasy region. *Bulletin of the American Museum of Natural History*, 45, 1005–1055.

Wilson, E.O. (1955) The status of the ant genus *Microbolbos* Donisthorpe. *Psyche*, 62, 136. http://dx.doi.org/10.1155/1955/82646

- Wilson, E.O. & Taylor, R.W. (1967) The ants of Polynesia. Pacific Insects Monographs, 14, 1-109.
- Xu, Z. (2000) Five new species and one new record species of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) from Yunnan Province, China. *Entomologia Sinica*, 7, 117–126.

http://dx.doi.org/10.1111/j.1744-7917.2000.tb00348.x

Yoder, A.D. & Heckman, K. (2006) Mouse lemur phylogeography revises a model of ecogeographic constraint in Madagascar. *In*: Fleagle, J. & Lehman, S.M. (Eds.), *Primate Biogeography: Progress and Prospects*. Kluwer, pp. 255–268.